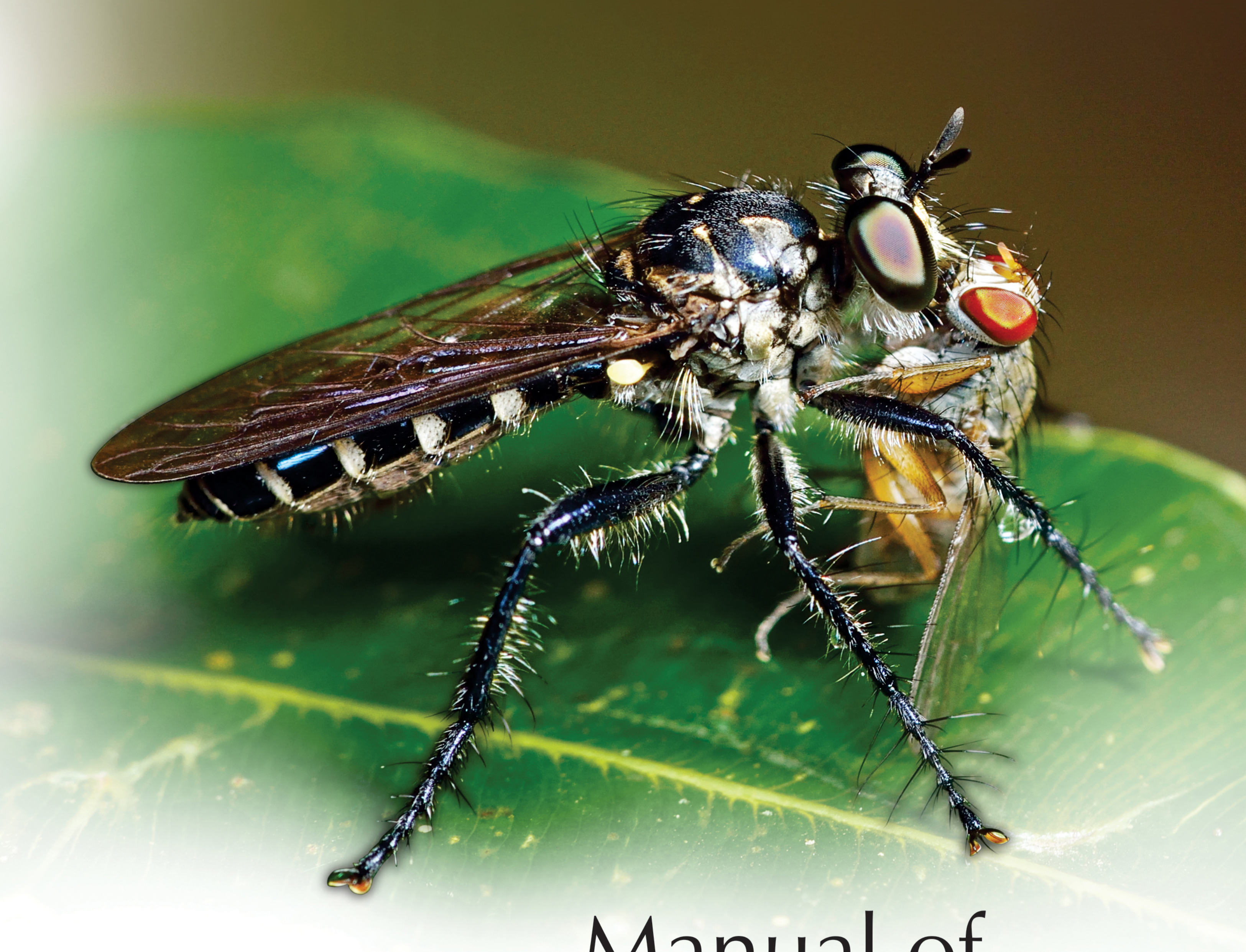

Manual of AFROTROPICAL DIPTERA

Volume 1

Edited by Ashley H. Kirk-Spriggs & Bradley J. Sinclair
With photographs by Stephen A. Marshall and a foreword by George McGavin

SURICATA 4

Photograph © K. Pannecoucke.

SURICATA 4

Manual of
Afrotropical Diptera

Volume 1

Introductory chapters and keys to Diptera families

Edited by
Ashley H. Kirk-Spriggs & Bradley J. Sinclair

Editorial Assistance
Burgert S. Muller

SANBI
Biodiversity for Life
South African National Biodiversity Institute

Pretoria, South Africa
2017

SURICATA

Suricata is the generic name of the suricate (*meerkat*), which is near-endemic to the arid western parts of southern Africa (occurring in Namibia, South Africa and Botswana; and just entering into a very small area in the extreme south of Angola). Behaviourally, suricates are socially inclusive and innately inquisitive, symbolising the commitment of South African National Biodiversity Institute (SANBI) to include all biodiversity and serve all of Africa and the scientific curiosity that precedes and drives research and publication of research results. Sister journal to SANBI's *Strelitzia*, *Suricata* is a peer-reviewed journal and publishes original and applied research, such as monographs, revisions, checklists, red lists, atlases and faunas of any taxa belonging to Regnum Animalia (the Animal Kingdom).

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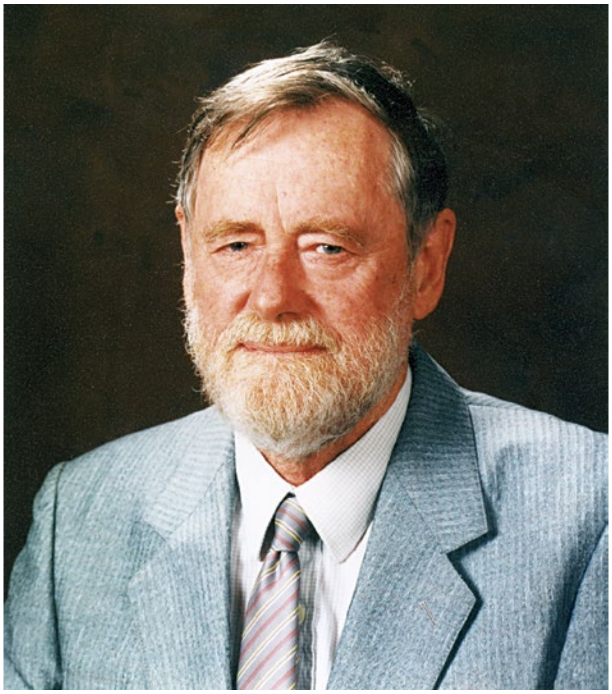
DEDICATION TO BRIAN ROY STUCKENBERG (1930–2009)



The *Manual of Afrotropical Diptera* is dedicated to the memory of the late Brian Roy Stuckenberg, regarded by many as "the father of modern African dipterology". Brian was a formidable scholar with an encyclopaedic knowledge of the dipterological literature. He was in many ways unusual among South African entomologists, in that he took a strong interest in more theoretical and philosophical aspects of biological enquiry, especially phylogenetic systematics and biogeography. Always progressive in his thinking, in 1958 Brian published his revision of Malagasy Blephariceridae, which was the first publication in English to apply Hennig's theory of cladistics. In a distinguished career that spanned 56 years, Brian published over 100 publications, including studies of at least 23 families of Diptera. As a mark of the respect in which he was held by his peers, over 100 species and five genera of Diptera were named in his honour, together with taxa in at least 11 other insect orders.

The reader is referred to the following publication, for additional information on Brian's life and career: Kirk-Spriggs, A.H. 2012. Dedication – the life, career and major achievements of Brian Roy Stuckenberg (1930–2009). *In*: Gedenkschrift in honour of Brian Roy Stuckenberg (1930–2009). *African Invertebrates* **53**: 1–34.

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FOREWORD

George McGavin

George McGavin was born in Glasgow and educated at Daniel Stewart's College in Edinburgh. He studied Zoology at Edinburgh University, followed by a PhD in entomology at Imperial College and the Natural History Museum in London. After 25 years as an academic at Oxford University, looking after the world famous Hope Entomological Collections, he became a television presenter, working mainly for productions from the BBC Natural History Unit in Bristol. George is an Honorary Research Associate of the Oxford University Museum of Natural History and a Research Associate of the Department of Zoology at Oxford University, as well as a Fellow of the Linnean Society and the Royal Geographical Society, an Honorary Fellow of the Royal Society of Biology and an Honorary Life Fellow of the Royal Entomological Society. As well as his many TV appearances George has written numerous books on insects and other animals.

What is it about the natural world that is so endlessly absorbing? Perhaps it is because, to paraphrase the British scientist John Burdon Sanderson Haldane (1892–1964), it is not only stranger than we can imagine, it is stranger than we could possibly imagine. My first serious study of insects concerned plant bugs (Hemiptera) and although they are interesting animals – what insects are not – I now feel rather short changed. If only I had found the wonderful world of flies at that formative stage in my career. The Diptera are without doubt the most ubiquitous and extraordinary of all insects. The impact they have had on human beings has been and continues to be truly immense. In popular consciousness, the word "fly" usually conjures up images of dirt, disease and death, more so perhaps in Africa than elsewhere, but it is the activities of relatively few species that have had a negative impact. It is an inescapable fact that flies cause tremendous losses of crops and other important plants and enormous numbers of wild and domestic animals and perhaps as many as one person in six are affected by fly-borne diseases. But the feeding habits and abilities of the vector species have been hijacked by pathogens and it would be totally illogical to tar all flies with the same brush. Flies are one of the dominant and most ecologically diverse insect orders and most fly species are crucial to the functioning of global ecosystems. The sheer variety of fly lifestyles is astounding. As pollinators, herbivores, parasites, parasitoids and predators and as vital part of the processes of decomposition and nutrient recycling they are a completely indispensable group of animals.

Halteres, or balancing organs as they are sometimes known, are unique to flies and even most wingless species such as louse flies and bat flies have a pair. The genetic tweaking that converted the hind wings of their antecedents into these gyroscopic stabilisers opened up a whole world of possibilities and for the past 245 million years or so flies have taken full advantage of their unparalleled aerial supremacy. No one can watch a hover fly darting and hovering and not be mesmerised by the utter beauty and brilliance of their flight and it is not surprising that their flight mechanics and control systems are being studied.

I spent twenty-five years looking after the insect collections in the Oxford University Museum of Natural History and some of the specimens I would take great pleasure in showing visitors included the holotype of *Glossina morsitans* – collected in Africa by Dr. David Livingstone (1813–1873) and sent back to John Obadiah Westwood (1805–1893) in Oxford for description. The life cycle of *tsetse* shows just how flexible and versatile dipterans can be. There is no need for a risky, free-living, larval stage when the female *tsetse* can nurture her single larva *in utero*. I have since had close encounters with *tsetse* in Africa. Another favourite show-and-tell was a box of strange, mud cylinders with perforated margins like three-dimensional postage stamps. These intriguing artefacts are made by the larvae of certain species of horse fly that live in ephemeral pools. As the larvae mature the pools often dry up, so to avoid being ripped apart and desiccated, the larvae burrow up and down in the stiffening mud. Their path isolates a neat cylinder inside which they pupate. As the ground dries as hard as concrete the cracks that form bypass the cylinders and the flies survive.

I was lucky enough to have had the opportunity to study the insect fauna of savanna tree canopies in Tanzania for a few years and the masses of specimens I collected by pesticide mist blowing was both staggering and overwhelming in equal measure. In the end it was necessary, as with many mass collection studies, to simply assign individuals to RTU's (recognisable taxonomic units) – a technical-sounding phrase that actually means – "I don't really know what this species is, but it's not like the other species in the sample". I knew in my heart it was not good enough, but I had to make some headway with the mounds of material under my microscope. I shudder to think what amazing species are still languishing in tubes of alcohol. If only I had had this book to hand I could have done and learned so much more. The *Manual of Afrotropical Diptera* will be an indispensable guide and reference, both for those just starting on the path to entomological enlightenment and those who have made it their life's work to study the most successful and enduring multi-cellular organisms to have ever lived on Earth. Just as important, the *Manual* will be an inspiration to anyone wanting to contribute something to science, but not yet sure how to do it. A multitude of fly species awaits collection and description and the biology of many named species is unknown and the larvae of many others have not yet been found or described.

I am delighted that this major work will bring the diverse and astonishing Afrotropical fly fauna to a much wider audience. The four volumes of the *Manual* are the result of a collaboration of over ninety international experts, truly "Lords of the Flies" and is the first ever synopsis of the 108 families of flies that occur in the Afrotropical Region. It is quite simply a superb achievement and will be an essential research tool and teaching aid for as long as people pick up a collecting net or empty a Malaise trap.

The natural world and its innumerable six-legged inhabitants, is the only thing that has ever really interested me and it will continue to enthral me until I die. If I have a choice in the matter, when I die I would like to be laid out in a tropical forest where I would be rapidly consumed and then recycled. A large number of the atoms that I have had on loan would surely end up in the bodies of flies. I can think of no better end.

Dr. George McGavin

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Ashley H. Kirk-Spriggs

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The following sponsors are acknowledged for supporting publication:

The **National Museum, Bloemfontein** (South Africa) now has the largest collection of Diptera on the African continent, with over 209,374 accessioned specimens. The collection is a unique research tool, as it comprises recent, high quality material from numerous poorly sampled Afrotropical countries, including Benin, Burundi, Cameroon, Democratic Republic of Congo, Kenya, Réunion Is., Madagascar, Malawi, Mauritius, Namibia, South Africa (Eastern and Western Cape, Free State, Mpumalanga, KwaZulu-Natal Provinces), Togo and Zambia. The collection is widely used by local and international researchers, with over 25,000 dry-pinned specimens currently on loan to specialists. The National Museum is, therefore, a centre of excellence for the study of dipterology on the continent and the collection represents an extremely important national asset and research tool. Two full-time dipterists are employed by the Museum, which actively encourages the study of the Diptera collection by specialist researchers and offers collection access and bench space at no cost to *bona fide* researchers. R. Nuttall (Director) and the Council of the National Museum is thanked for supporting the project.

NATIONAL MUSEUM
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The **KwaZulu-Natal Museum** (South Africa) is a leading centre for dipterological research in the Afrotropical Region. The Museum has a proud history of over 50 years of research on Diptera and has accrued a collection of Diptera from over 98 countries, comprising approximately 205,000 specimens, representing over 7,000 species. It further holds an extensive type collection of over 2,000 species of Diptera. It houses the collections of B.R. Stuckenberg and J.G.H. Londt (both previous Directors of the institution), as well as part of the Diptera collection of the former South African Institute for Medical Research (including the collection of F. Zumpt and associated types). Currently it also houses one of the most comprehensive collections of Asilidae in the world. It offers *bona fide* researchers access to the extensive collection of Diptera and bench space at no cost. The Director and the Council of the KwaZulu-Natal Museum are thanked for supporting the project.

KwaZulu-Natal
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South African National Biodiversity Institute (South Africa). SANBI is responsible for exploring, revealing, celebrating and championing biodiversity for the benefit and enjoyment of all of South Africa's people. As well as being the custodian of the National Botanical Gardens' system, SANBI is a respected authority in research and has an unmatched research record in the indigenous, naturalised and alien flora of South and southern Africa and beyond. SANBI's research management covers systematics and collections expansion, conservation and applied biodiversity science and climate change. The Institute's knowledge management and planning branch, strives to make biodiversity science more available and accessible through various "mainstreaming" projects and initiatives. M. Hamer is thanked for supporting the project.

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E Oppenheimer & Son and the Diamond Route (South Africa). The Diamond Route is a massive South African national project which focuses on linking the conservation properties of the Oppenheimer family and De Beers. These properties conserve vast areas and provide a safe haven for a wide variety of unique, rare and ecologically important plants and animals. E. Oppenheimer & Son sponsored a wine reception and banner for the official launch of the project in 2010 and also provided funding for illustrations to be prepared for the *Manual*. D. MacFadyen is thanked for securing funding in support of the project.

E OPPENHEIMER & SON
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SOUTH AFRICA

The Samuel Wendell Williston Diptera Research Fund (USA). A Smithsonian administered endowment fund, established for the increase and diffusion of knowledge about Diptera. Williston was a great biologist, who made significant contributions to palaeontology, entomology, medicine and education. He was the first native dipterist, the first to produce generic monographs of Nearctic Diptera, the first to curate and study the Diptera of the US National Museum and the first to make a contribution to that collection. This man and his achievements, thus epitomise what this fund was established to support. The Samuel Wendell Williston Diptera Research Fund is a major sponsor for the project and has provided funding to cover production costs. F.C. Thompson and T. Dikow are thanked for securing funding in support of the project.

S.W. Williston Diptera Research Fund

Natural History Museum, London (UK). The international collection holds important type material of Diptera, some dating back to the 18th century, most notably of taxa described by F. Walker, J.M.F. Bigot, E.A. Brunetti, F.W. Edwards and E.E. Austen. The collection holds extensive material from the Afrotropical Region, much of which was generated during Africa's colonial period. The *Manual* project was in receipt of funding from the Dr. E.C. Zimmerman Bursary (administered through the Museum), specifically to cover the cost of illustrations to be prepared for the *Manual*. A. Polaszek is thanked for securing funding in support of the project.

NATURAL HISTORY MUSEUM

The Schlinger Foundation, a not-for-profit organisation, promotes and supports research and education in systematics, natural resources and environmental sciences, and within those, particularly projects that involve flies (order Diptera) and spiders (order Araneae). The Schlinger Foundation does not accept unsolicited applications for project support. The Schlinger Foundation is a major sponsor for the project and has provided funding to cover production costs. M.E. Irwin is thanked for securing funding in support of the project.

General acknowledgements

This *Manual* represents the first regional initiative for any insect order on the African continent. Production of any regional manual of this kind is a monumental task that involves a multitude of people throughout the international dipterological community. Without the dedication of time, energy and commitment of this community as a whole, such projects would be impossible and it is an accolade to the spirit of cooperation that abounds in this community that this *Manual* is now published (the fourth regional Diptera manual of its kind!). As Editor-in-chief I express my very sincere thanks to the over 90 chapter authors who have submitted such professional and comprehensive chapters and made this *Manual* possible. The Afrotropical Diptera faunas of numerous families has never been properly reviewed in the past and no identification keys were available, so for many authors this has entailed the examination of extensive material from the region, dealing with complex issues of defining the limits of genera (and nomenclature) and the construction of entirely new identification keys and synopses of the fauna.

As with many great ideas, the seed concept of a *Manual of Afrotropical Diptera* was sown in the pub! The idea was first raised over drinks when Thomas Pape visited Namibia way back in 1999. Thomas' idea grew from this initial suggestion and over the intervening years various informal discussions were held with dipterists based in South Africa and elsewhere, including D.A. Barraclough, J.G.H. Londt, M.B. Mostovski and the late B.R. Stuckenberg, to assess the feasibility and practicalities of embarking on such a project. One concern that was expressed by many, was our ability (or otherwise), of securing willing authors, prepared to contribute chapters on each and every family that occurs in the region. The project became more formalised in 2009 and the first list of potential chapter contributors was compiled, with the assistance of various dipterists from around the world. The Editorial Panel was established at the same time and invitations to contribute chapters were distributed to potential authors. With the assistance of M.B. Mostovski, the official website was launched in 2009, which provided extensive information for contributing authors. The project was officially launched at the 7th International Congress of Dipterology, San José, Costa Rica, in 2010 (ICD7), with a wine reception sponsored by E. Oppenheimer & Son. M.B. Mostovski was initially Assistant Editor, but dropped out of the project shortly before leaving South Africa in January 2014, after which the task was very ably taken on by B.J. Sinclair. The original plan was to publish the *Manual* in two volumes in 2015, but it soon became apparent after the closing date for chapter submissions (November 2014), that this would not be possible, as numerous chapter authors had not then submitted and the processing of chapters was taking far longer than anticipated. It was also decided around this time that due to the length of the very large Tachinidae chapter (with over 400 key couplets), we would need to publish the *Manual* in three rather than two volumes. It was, therefore, announced at the 8th International Congress of Dipterology, Potsdam, Germany (ICD8), that Volume 1 would be published in 2016 (later extended to 2017), with the aim to publish Volumes 2 and 3 in 2018, to coincide with ICD9, which will be held in Africa for the first time. Near to the completion of Volume 1 it became apparent, however, that this had become unmanageably large and could not be published as a single volume. It was therefore decided to split this into two volumes with the final *Manual* eventually appearing as four separate volumes.

I take this opportunity to thank B.J. Sinclair for his insights into issues of terminology and for his meticulous final checking of completed and typeset chapters. Our Editorial Panel (D.A. Barraclough, M. Coetzee, J.M. Cumming, M. De Meyer, T. Dikow, N. Dorchin, T. Ekrem, A. Freidberg, M. Hauser, S.A. Marshall, T. Pape, J.H. Skevington and N.E. Woodley) has rendered an invaluable service in preparation of the *Manual*, especially J.M. Cumming, who has checked numerous issues of terminology and the intricacies of establishing a standard list of abbreviations that are applied consistently throughout the four volumes. Some Editorial Panel members also handled the review process for a few chapters during the initial phases before I took over this function in person. Although not a member of our Editorial Panel, N.L. Evenhuis has willingly provided advice and information that has proved invaluable throughout the project. B.S. Muller (Graphics Editor) has done a truly outstanding job of dealing with the hundreds of plates and individual figures, re-drawing many digitally and has very ably maintained the *Manual* website, almost since the project's inception. I made up and labelled the majority of plates for chapters in Volumes 1 and 2, but since his appointment to the staff of the National Museum (Bloemfontein) in April 2016, he has largely taken over all matters related to plates and figures. Our contractual artists, T. Smit, L. Coetzee and L. Strachan prepared hundreds of digitally re-drawn images which have been highly acclaimed by numerous authors and their input has done much to improve the overall look and quality of production. G. McGavin very willingly supplied the foreword and has taken an enthusiastic interest in the project. I thank him for endorsing the project by association. These acknowledgments would be incomplete without mentioning R. Idema, whose wonderful illustrations (previously published in the *Manual of Nearctic Diptera*), have been used extensively by various authors throughout this *Manual*.

My aim with this *Manual* was to have a fresh approach to the use of illustrations and take advantage of the digital techniques that are now available to us. This is the first regional manual to use colour extensively and it is largely due to the contribution of S.A. Marshall's amazing photographs of living flies that this could be achieved. He has shown unrivalled dedication in capturing images specifically for this *Manual* and has undertaken fieldtrips to Madagascar, Mauritius, Namibia, South Africa (twice) and Tanzania. I accompanied him on five of these trips and I thank him sincerely for his good humour and company in the field and for his insights into fly behaviour. The vast majority of chapter authors acknowledged him for inclusion of frontispiece images (which are not repeated below).

Permission to reproduce images from previously published sources is the responsibility of respective chapter authors. Sources of original figures are indicated at the ends of the figure legends, so will not be listed separately in this *Manual*. The project as a whole had written permission to reproduce images (as required) from the *Manual of Nearctic Diptera* and the *Manual of Central American Diptera* by Robert M. Forrest (NRC Research Press, National Research Council of Canada). Permission to reproduce images from *Contributions to a Manual of Palaearctic Diptera* was provided by L. Papp and for *African Invertebrates* (formerly *Annals of the Natal Museum*) by B.S. Muller. The Trustees of the Natural History Museum (London, UK) are thanked for permission for images from previous British Museum (Natural History) and Natural History Museum publications to be reproduced, which was kindly arranged by N. Chillingworth, E. McAlister, A. Polaszek and D.B. Whitmore.

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INTRODUCTION AND BRIEF HISTORY OF AFROTROPICAL DIPTEROLOGY

1

Ashley H. Kirk-Spriggs

General introduction

The Diptera ("true flies" or "two-winged flies" as they are known) constitute one of the largest orders of insects in the biosphere. They are as diverse morphologically and biologically as they are numerous and many groups have evolved spectacular structural adaptations commensurate with their environment and biology. During their long evolutionary history, virtually every terrestrial niche has been occupied by the Diptera, making them one of the most successful groups of organisms on Earth. Many have co-evolved in association with other organisms and become highly specialised parasites or parasitoids of a range of disparate groups of plants and animals. Whether focusing on their systematics, biology, biogeography, conservation, or the more applied aspects, the Diptera remain a fascinating and intriguing group.

The applied significance of the Diptera cannot be overestimated. On the negative side, they are especially significant in Africa, as numerous species are vectors of deadly insect-borne diseases and other pathogens to humans and their livestock (*e.g.*, Culicidae, Glossinidae and Ceratopogonidae), including malaria, trypanosomiasis (and the animal equivalent *nagana*), leishmaniasis and African horse sickness, to name but a few. Others are serious agricultural pests and can significantly affect crop yields or damage produce (*e.g.*, Tephritidae, Cecidomyiidae, Chloropidae and some Muscidae), thereby negatively impacting a country's ability to export produce and, consequently, its Gross Domestic Product.

On the positive side, the role of Diptera in pollination has received increasing attention in recent years, with studies indicating that the Diptera may be far more significant in pollination biology than previously considered. Many parasitoid

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species (especially the Tachinidae) are potential agents in biological control, while others are now used routinely in forensic investigations (Calliphoridae, Piophilidae, *etc*.). The Diptera are also probably the most significant group in terms of the degeneration and decomposition of animal and other organic matter, being instrumental in the breakdown and release of nutrients back into the soil.

Figures for 2013, available from *Systema Dipterorum* (Pape & Thompson 2013), indicate that 160,042 species of Diptera are known worldwide, of which 20,350 are known from the Afrotropical Region (excluding Oman and United Arab Emirates), representing 13% of the world fauna (T. Pape, pers. comm. 2017). The Afrotropics are still in what Irwin *et al*. (2003: 701) termed the "discovery phase", being the part of a timeline during which most species in a given environment are discovered and described. According to the most recent predictions (Kirk-Spriggs & Stuckenberg 2009: 170), there are upwards of 30,000 species remaining to be described from the Afrotropics, indicating that only two-fifths of the Diptera fauna of that region are currently known. If the total number of species added to the regional list from 1981–2006 is considered (3,371), this gives an average of 129 new species annually. Hypothetically, at that average rate of taxonomic growth it would take almost three centuries (231–289 years) to reach the end of the discovery phase for the Afrotropical Region (Kirk-Spriggs & Stuckenberg 2009: 171). Africa has fewer Diptera taxonomists and systematists than any other continent and it is essential we encourage a new generation of Africa-based dipterists to take on the critical task of describing these new taxa before they disappear entirely, due to habitat destruction.

The main purpose of this *Manual of Afrotropical Diptera* is to provide an up-to-date, well-illustrated, easily interpretable means for identifying families and genera of two-winged flies of the continental Afrotropical Region, its associated oceanic islands and the southernmost Arabian Peninsula (as defined in detail below). It is also designed to be a basic reference work to a wide spectrum of biosystematic information on Diptera for professional biologists, teachers, university students and informed amateurs. The main aim of the *Manual* is to foster a better understanding of the science of dipterology, especially in Africa, and encourage the study of Diptera by new generations of dipterists based in Africa and elsewhere.

Although this *Manual* is designed for a wide array of workers from amateurs to specialists, some fundamental knowledge is necessary for its use. A working familiarity with entomological terminology and methodology, as well as some training in basic taxonomic principles is essential. Chapters 3 deals with the morphology and terminology of adults and Chapter 13 with larvae and both include detailed glossaries of terms that are used consistently throughout the *Manual*, as well as other alternative terms used formerly in the dipterological literature.

Afrotropical regional fauna and endemicity

A total of 108 families of Diptera occur in the Afrotropical Region (the same number as North America), representing 83% of the 130 extant families known globally. The best represented families in the region (with over 500 described species each) are: Asilidae (1,685); Bombyliidae (1,384); Chironomidae (604); Culicidae (780); Dolichopodidae (770); Limoniidae and Tipulidae (*ca* 1,045); Muscidae (1,035); Syrphidae (*ca* 600); Tabanidae (*ca* 800); Tachinidae (1,126); and Tephritidae (*ca* 1,000) (figures from chapters included in this *Manual*). This may, at least in part, reflect the degree of taxonomic study rather than the true number of species. The least known families in the region, with more than a 1,000 predicted undescribed species are: Asilidae (1,900); Cecidomyiidae (5,000–10,000); Ceratopogonidae (2,000); Dolichopodidae (1,000–1,500); Limoniidae (1,500); Mycetophilidae (2,000); Phoridae (2,000–3,000); Sciaridae (2,000); Sphaeroceridae (1,000–2,000); and Tachinidae (1,000) (Kirk-Spriggs & Stuckenberg 2009: 184–187).

Four families are endemic to the region (in the extant fauna): Glossinidae, Marginidae, Mormotomyiidae and Natalimyzidae, although Glossinidae and Natalimyzidae are known in the fossil record from North America and Europe respectively (Grimaldi & Engel 2005: 545; Tschirnhaus & Hoffeins 2009). Mormotomyiidae and Natalimyzidae are currently monotypic, but numerous undescribed species of Natalimyzidae are known from the Afrotropics. The occurrence of the family Trichoceridae in the Afrotropics is questionable, but the family is included in both the Key to Diptera families—adults (Chapter 12) and Key to Diptera families—larvae (Chapter 13).

Content of the work

Volume 1 includes 11 general introductory chapters, plus the identification keys to families for adults and larvae (Chapters 12 & 13). Volume 2 includes 43 chapters (Chapters 14–56) that deal with individual families of nematocerous Diptera and lower Brachycera. Volume 3 covers Brachycera: Cyclorrhapha (excluding Calyptratae) and includes 51 individual family chapters (Chapters 57–107); and Volume 4 covers Brachycera: Cyclorrhapha: Calyptratae, with 12 individual family chapters (Chapters 108–119), including the very large chapter dealing with the Tachinidae (Chapter 118). The families Limoniidae and Tipulidae (Volume 2, Chapter 14) are dealt with in a single chapter and the Campichoetidae (the family status of which remains uncertain) is dealt with as part of the Diastatidae (Volume 3, Chapter 104). A taxonomic index is provided in each of the four volumes. Volumes 2, 3 and 4 also include a table of contents, a list of authors and author acknowledgements for chapters in these respective volumes.

There were no pre-set limits to lengths of chapters, thus lengths vary greatly. The longer chapters do, for the most part, reflect the larger families, or those families of greater economic importance, that are generally better studied and for which more information is available. As with all multi-authored projects of this kind, some authors submit the bare minimum, while others prefer to be more expansive. The editors have not attempted to expand shorter chapters or substantially reduce larger ones. Spelling of words follows British rather than American orthography.

Geographical scope of the Manual

The Afrotropical Region as defined for this *Manual* includes all the numbered countries, islands or island groups indicated by the numbers 1–73 on Fig. 1. Madagascar and its adjacent islands, treated as a separate zoogeographical region by some zoologists (*e.g*., Ficetola *et al*. 2017), is treated here as an integral part of the Afrotropical Region. This largely follows Crosskey's (1980: 32) concepts of the region with, for practical reasons, the regional boundaries between the continental Afrotropical and Palaearctic Regions — being the northern state boundaries of Mauritania, Mali, Niger, Chad and Sudan (Nos 1–5 on Fig. 1). The Hogger Mountains of the central Sahara, that span Algeria, Chad and Mali exhibit a primarily Palaearctic fauna and flora, but include some Afrotropical floral and faunal elements (Kirk-Spriggs & McGregor 2009; see Chapter 9).

Crosskey's (1980) concept of the boundary of the Afrotropical part of the Arabian Peninsula as the northern borders of Yemen and South Yemen alone is here regarded as too conservative, given compelling evidence from other groups, such as the Rhopalocera (Larsen 1984) and the Neuroptera (Hölzel 1998), which support a wider concept of the region and mirrors that of amphibians as illustrated by Holt *et al*. (2013, fig. 3A). Ficetola *et al*. (2017) go further and include Saudi Arabia and even Iran (essentially including the Eremian Realm into the Afrotropical Region, where others have it is a nebulous Palaearctic/Oriental/Afrotropical Region). This issue has been discussed at some length by Kirk-Spriggs & Stuckenberg (2009: 157–158) and Kirk-Spriggs & McGregor (2009). The region as defined here, therefore, extends the concept of the Afrotropical Region farther eastwards, to include the modern coastal Arabian states of Yemen, Oman and United Arab Emirates (Nos 11–14 on Fig. 1).

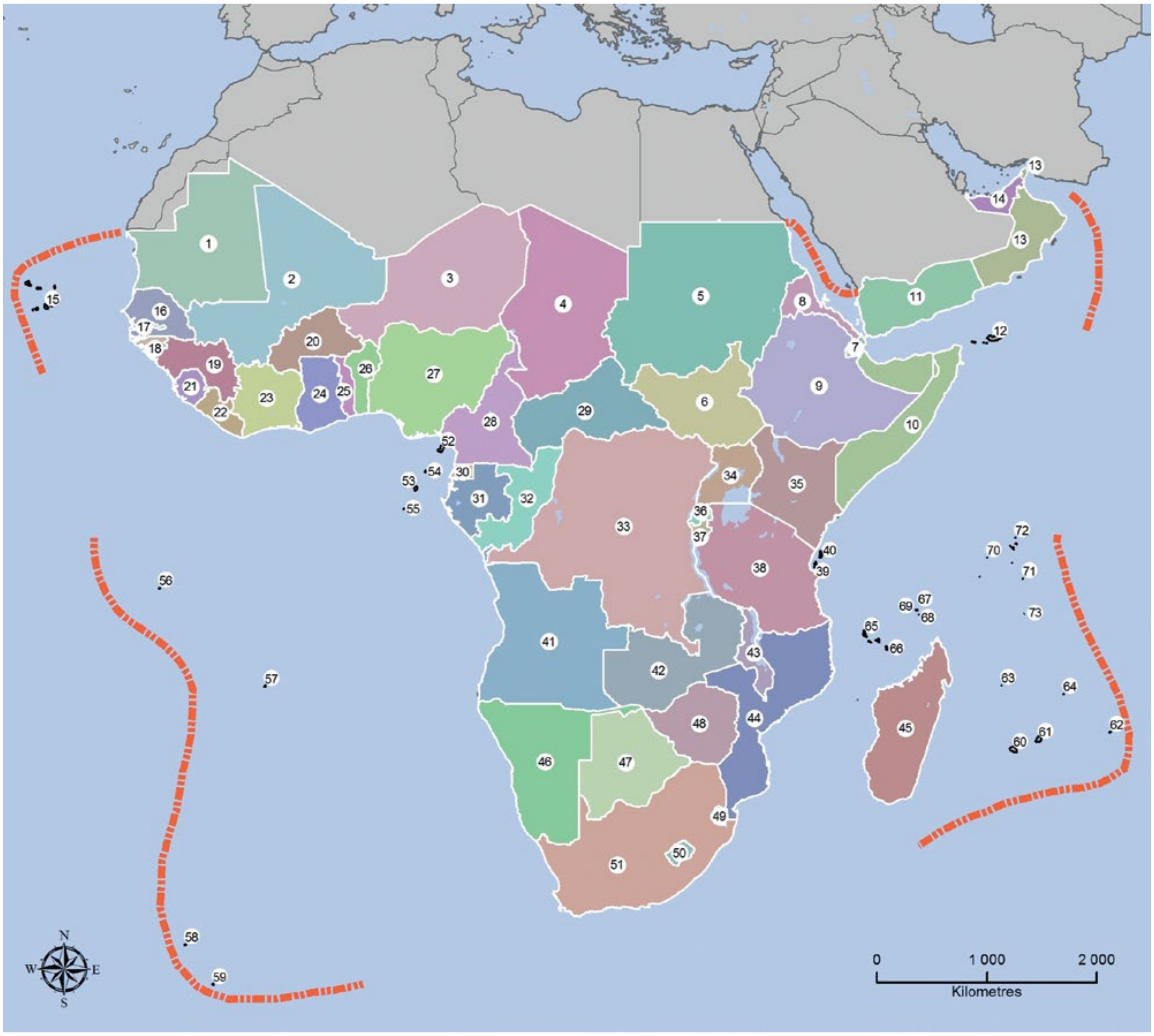


Fig. 1.1. Map indicating extent of Afrotropical Region as applied in this *Manual*, with states (countries), islands and island groups numbered (1–73) as in the accompanying Table 1 (G.K. McGregor; based on Crosskey 1980: 32, with additions and amendments).

Table 1.1. List of contemporary Afrotropical states (countries), islands and island group names, number references on Fig. 1; and earlier, alternative and Arabic name(s) used in the literature.

State or island names used in the *Manual*	**Reference number on Fig. 1**	**Earlier, alternative and Arabic name(s)**
Agaléga Is. (Mauritius)	73	
Aldabra Is. (Seychelles)	67	
Amirante Is. (Seychelles)	70	
Angola	41	Portuguese West Africa
Annobón Is. (Equatorial Guinea)	55	Also referred to as Annabon, Anabon, Pagalu or Pigalu
Ascension Is. (British)	56	
Astove Is. (Seychelles)	68	
Benin	26	Dahomey; French West Africa (in part)
Bioko Is. (Equatorial Guinea)	52	Fernando Póo; Fernando Po; Masie Ngueme Biyogo Island
Botswana	47	Bechuanaland
Burkina Faso	20	French West Africa (in part); Upper Volta
Burundi	37	Ruanda-Urundi (Urundi in part)
Cabo Verde (Cape Verde Is.)	15	
Cameroon	28	French Cameroons (with southern British Cameroons additionally); French Equatorial Africa (in part); also spelt Cameroun
Central African Republic	29	Ubangi-Shari; French Equatorial Africa (in part); Central African Empire
Chad	4	French Equatorial Africa (in part)
Coëtivy Is. (Seychelles)	71	
Comoros	65	Officially l'Union des Comores, comprising main islands of Grande Comore (Ngazidja), Mohéli (Mwali) and Anjouan (Ndzuani)
Cosmoledo Is. (Seychelles)	69	
Côte d'Ivoire	23	French West Africa (in part); Assinie territory; also referred to as Ivory Coast
Democratic Republic of Congo	33	Congo Free State; Belgian Congo; Republic of the Congo (Léopoldville); State of Katanga; Zaïre (officially Republic of Zaïre)
Djibouti	7	Afars and Issas Territory; French Somaliland
Equatorial Guinea	30	Spanish Guinea (excluding Bioko Is. and Annobón Is.); Rio Muni
Eritrea	8	Abyssinia with Ethiopia; Italian Eritrea; Italian East Africa
Ethiopia	9	Abyssinia with Eritrea
Gabon	31	French Equatorial Africa (in part)
Gambia	17	Senegambia (in part)
Ghana	24	Gold Coast with British Togoland (*i.e.*, part of earlier German Togoland)
Gough Is. (British)	59	"Gonçalo Álvares"
Guinea	19	French Guinea
Guinea-Bissau	18	Portuguese Guinea
Kenya	35	British East Africa
Lesotho	50	Basutoland; officially Kingdom of Lesotho
Liberia	22	Grain Coast
Madagascar	45	French Madagascar
Malawi	43	Nyasaland; more correctly Malaŵi
Mali	2	French Sudan; French West Africa (in part)

Table 1.1. List of contemporary Afrotropical states (countries), islands and island group names, number references on Fig. 1; and earlier, alternative and Arabic name(s) used in the literature (cont.).

State or island names used in the *Manual*	Reference number on Fig. 1	Earlier, alternative and Arabic name(s)
Mauritania	1	French West Africa (in part)
Mauritius	61	"Dina Arobi", "Cirne", "Île de France"
Mayotte Is. (French)	66	Maore
Mozambique	44	Portuguese East Africa; also spelt Moçambique
Namibia	46	"Cimbebas"; German South West Africa; South-West Africa (as province of South Africa)
Niger	3	French West Africa (in part)
Nigeria	27	Present Nigeria with southern part of British Cameroons (now in Cameroon); Biafra (in part)
Oman	13	Majan; Muscat and Oman; officially Sultanate of Oman; سلطنة عُمان *Salṭanat Umān*
Pemba Is. (Tanzania)	40	الجزيرةالخضراء
Republic of Congo	32	French Congo; Middle Congo; Congo – Brazzaville; French Equatorial Africa (in part); Congo
Réunion Is. (French)	60	"Bourbon"
Rodriquez Is. (Mauritius)	62	
Rwanda	36	Ruanda-Urundi (Ruanda in part)
Saint Brandon Is. (Mauritius)	64	Also known as Cargados Carajos Sholes
Saint Helena Is. (British)	57	
São Tomé and Príncipe	53/54	
Senegal	16	French West Africa (in part); Senegambia (in part)
Seychelles	72	
Sierra Leone	21	
Socotra Is. (Yemen)	12	Also spelt Soqotra; سُقُطْرَى *Suquṭra*
Somalia	10	Benadir; Italian Somaliland with British Somaliland
South Africa	51	"Caffraria"; Cape Colony; Bophuthatswana (in part); Kaffraria (in part); Union of South Africa
South Sudan	6	"Nubia"; Anglo-Egyptian Sudan; Sudan
Sudan	5	"Nubia"; Anglo-Egyptian Sudan
Swaziland	49	Officially Kingdom of Swaziland
Tanzania	38	German East Africa with Zanzibar and Pemba islands; Tanganyika Territory with same islands
Togo	25	French Togoland; German Togoland (excluding part later British-administered and now part of Ghana)
Tristan da Cunha Is. (British)	58	
Tromelin Is. (French)	63	"Île des Sables"
Uganda	34	Uganda Protectorate
United Arab Emirates	14	Trucial States; Emirates of Oman; دولة دولة الإمارات العربية المتحدة *Dawlat al-Imārāt al-'Arabīyah al-Muttaḥidah*
Yemen	11	"Sheba"; "Arabia félix"; Aden with Aden Protectorate; اليَمَن *al-Yaman*
Zambia	42	Northern Rhodesia
Zanzibar Is. (Tanzania)	39	Also referred to as Unguja
Zimbabwe	48	Southern Rhodesia

The geographical concept adopted here for the region also follows Crosskey (1980), in including the South Atlantic islands of Ascension (56), Saint Helena (57), Tristan da Cunha (58) and Gough (59) in the *Manual* coverage, in addition to the Cape Verde Islands (15) (hereafter referred to by the modern state name Cabo Verde), the Gulf of Guinea islands of Bioko (52), São Tomé and Príncipe (53/54) and Annobón (55) and the islands of the western Indian Ocean (islands and island groups numbered 60–73 on Fig. 1) that are conventionally ascribed to the Afrotropical Region in its wider sense. The islands of Zanzibar (39) and Pemba (40), situated off the coast of Tanzania were not listed by Crosskey (1980: 29–31), but are indicated on Fig. 1 and in the above Table 1. The sub-Antarctic islands of the southern Indian Ocean (including Marion Island) are excluded.

Defined "subregions" in the Afrotropical Region, as applied in the text are as follows: **Atlantic Ocean Islands** (Ascension Is., Cabo Verde, Gough Is., Saint Helena Is. and Tristan da Cunha Is.); **Central Africa** (Angola, Atlantic Ocean islands (Annobón Is., Bioko Is. [formerly Fernando Póo], São Tomé and Príncipe), Cameroon, Central African Republic, Chad, Democratic Republic of Congo, Equatorial Guinea, Gabon, Malawi, Republic of Congo and Zambia); **East Africa** (Burundi, Djibouti, Eritrea, Ethiopia, Kenya, Rwanda, Somalia, South Sudan, Sudan, Tanzania [incl. Pemba Is. and Zanzibar Is.] and Uganda); **Indian Ocean Islands** (Aldabra Is., Amirante Is., Comoros, Cosmoledo Is., Europa Is., Madagascar, Mauritius, Réunion Is., Seychelles and Tromelin Is.); **Southern Africa** (Botswana, Lesotho, Mozambique, Namibia, South Africa, Swaziland and Zimbabwe); **Southern Arabian Peninsula** (Yemen [incl. Socotra Is. and Abd al Kuri Is.], Oman and United Arab Emirates); and **West Africa** (Benin, Burkina Faso, Côte d'Ivoire, Gambia, Ghana, Guinea, Guinea-Bissau, Liberia, Mali, Mauritania, Niger, Nigeria, Senegal, Sierra Leone and Togo). Although Mozambique spans both Southern and East Africa it is listed only under Southern Africa.

State and island names applied in the Manual

Modern names are used for Afrotropical states (countries) throughout the *Manual*. An alphabetical list of names applied (Table 1), together with the reference numbers used on Fig. 1, are provided above to enable the countries and island/island groups concerned to be located. The list also indicates former names (if any) by which states and islands/island groups have been known in the past and recorded in the literature, alternative names and Arabic names (where applicable). This information is largely based on the list provided by Crosskey (1980: 29–31), with additions and amendments. All continental African states are republics, so with the exception of Republic of Congo and Democratic Republic of Congo (which require distinction) this is not included in state names to obviate repetitive use of the words "Republic of".

The state name Côte d'Ivoire is preferred over the anglicised name Ivory Coast and is used throughout the text. If islands or island groups comprise independent states (*i.e.*, Cabo Verde, Comoros, Madagascar, Mauritius, São Tomé and Príncipe and Seychelles), then these are cited according to accepted state names. The abbreviation "Is." for "Island" is only applied for islands that form part of Afrotropical states (*i.e.*, Aldabra, Amirante, Annobón, Astove, Bioko, Coëtivy, Cosmoledo, Pemba, Rodriquez, Saint Brandon, Socotra and Zanzibar), or islands that are protectorates of other countries (*i.e.*, Ascension, Gough, Mayotte, Réunion, Saint Helena, Tristan da Cunha and Tromelin). The term "Region" is only applied to true zoogeographical regions, while the Holarctic is referred to as "Realm", to avoid confusion.

Principle changes in state and island names since publication of Crosskey (1980) comprise the following: Cargados Carajos Is. (= Saint Brandon Is.); Congo (= Republic of Congo); Ethiopia (= Ethiopia and Eritrea); Fernando Póo Is. (= Bioko Is.); Southern Rhodesia (= Zimbabwe); Sudan (= Sudan and South Sudan); Upper Volta (= Burkina Faso); and Zaïre (= Democratic Republic of Congo). Crosskey (1980: 31) noted some impending name changes that were not adopted in his *Catalogue*, *i.e.*, Central African Republic to Central African Empire, Fernando Póo to Macias Nguema and Annobón to Pagalu, for which currently accepted names are now Central African Republic, Bioko Is. and Annobón Is., respectively. The state name Namibia was applied in Crosskey's (1980) *Catalogue*, in accordance with United Nations practice, but Namibia did not attain official independence until 1990.

A colonial map (*ca* 1914) is provided as Fig. 2, to aid in interpreting colonial African names referred to below. It has only been practicable to include superseded names in their English language forms, *e.g.*, British East Africa or German East Africa, but not Afrique orientale anglaise or Deutsch Ost-Afrika.

Introductory chapters

Thirteen introductory chapters are included in this volume. The first chapters summarise the state of regional knowledge in the fields of agricultural and veterinary, medical, phytosanitary and forensic dipterology. Other chapters deal with collection and preservation, adult morphology and terminology, natural history, biogeography, conservation and phylogeny of Diptera, and present identification keys to families: one to adults (Chapter 12) and one to larvae (Chapter 13). The key to Diptera families — adults is the first colour photographic key to appear in any regional Diptera manual and the key to Diptera families — larvae is the first complete key to all families that occur in the Afrotropical Region (for which the immature stages are known). These introductory chapters are included as brief summaries only and further details in most of these subject fields are included in the individual family chapters. Due to the diverse subject matter of the introductory chapters no standard headings were adopted and these are included at the authors' discretion.

Family chapters

Each family chapter includes a chapter number and vernacular name(s). The vernacular names used are based on those applied in previous regional manuals, those used by Marshall (2012), or in some cases, the preferences of individual authors. These names are not formalised and have no bearing on any standardisation of terminology and if no generally acceptable vernacular name was available for families these were given names using a derivation of the family group name, *e.g.*, psilid flies (for Psilidae), heleomyzid flies (Heleomyzidae) and cryptochetid flies (Cryptochetidae).

Each family chapter includes a frontispiece photograph of a "typical" example of the family (usually supplied by Stephen A. Marshall). For some of the larger families with diverse appearance, additional photographic plates have been provided to illustrate the diversity of the group (if suitable images were available).

Chapters include a short description and diagnosis (in telegraphic style), a summary of the known biology and immature stages, a section on economic significance (if any) and sections dealing with the classification and identification of the family. The term "diagnosis" as applied here is used in the broadest sense and may comprise either a short list of characters that define the family precisely, or a more detailed description of characters defining constituent genera (at the discretion of the author(s) concerned). If a telegraphic diagnosis was provided by the author(s) for immature stages, then this is included under the "Diagnosis" heading, if not, a general description of immature stages is provided in narrative style under the heading "Biology and immature stages".

Fig. 1.2. Map of European colonies and protectorates in continental Africa, the Arabian Peninsula and Madagascar *ca* 1914 (G.K. McGregor; after M. Siegel, Rudgers Cartography 2010, with amendments available at: http://exhibitions.nypl.org/africanaage/maps.html).

If two or more genera occur in the Afrotropical Region, a dichotomous identification key to adults is provided (written in telegraphic style) in all cases, usually to genera only, but in a few cases to subgenera (*e.g.*, Simuliidae) and/or informal species-group names. For consistency, all identification keys are indicated in titles as keys to Afrotropical genera only, even if these keys include higher taxonomic ranks (subfamilies and tribes) or lower taxonomic ranks (subgenera) and/or informal species-group names. For some families, especially groups with aquatic larvae that are highly diagnostic and are used routinely (*e.g.*, Ceratopogonidae, Culicidae and Simuliidae), identification keys to larvae and, in a few cases, to pupae, are also provided at the discretion of the author(s).

The identification keys are also intended for students and novice dipterists, so every effort has been made to specify main body parts referred to and to wing veins, cells and crossveins, rather than to the abbreviations alone (*i.e.*, "Wing vein M_4" rather than "M_4", "cell m_2" rather than "m_2" and "crossvein *r–m*" rather than "*r–m*" alone). Likewise, all structures on figures referred to in the diagnoses and identification keys are indicated on the respective figures using standard abbreviations to assist student dipterists in interpreting structures. Characters of the male and female terminalia are specified separately in the keys to indicate that dissected specimens should be examined in these cases.

Following the content developed by the editors of the *Manual of Central American Diptera*, each family chapter also includes a synopsis of the fauna section, which includes (a usually brief) account of the known status of each genus (listed alphabetically) that occurs in the region. These accounts usually comprise the following: generic name and author; higher taxonomic ranking (subfamilial and tribal placement – if applicable); geographical range of the genus (including an indication of endemicity if applicable); number of species globally and number of Afrotropical species; distribution of Afrotropical species (listed by name if three or less or summarised if more than three); indication of the number of undescribed species; any taxonomic issues; confirmatory characters (if additional to those provided in the identification key); biology and immature stages known; and reference to identification keys that are available.

References, text citations and abbreviations

References are provided in each individual chapter, rather than these being listed (collectively) at the end of each volume. The general format of references follows that provided in the Instructions for Authors for the peer-reviewed journal *African Invertebrates*. Journal titles are provided in full and wherever possible follow those listed in the "*World list of scientific periodicals*". In some questionable cases we retain the format provided by authors. Titles of books in English are given in lower case in all instances (except for proper nouns). Pagination is provided for chapters in books, but not the full pagination of the entire book; page numbers are provided in the text for all information originating from published books. Reference lists are ordered alphabetically by single author and dual author names and dates and references with three or more authors (cited as "*et al*." in the text) by first author name and date only, to assist with easy location of multi-author references in the lists. Multiple text reference citations are listed alphabetically by author and date, rather than in date sequence, unless there is a sequential reason for doing so. DOI numbers are provided for publications that only appear electronically.

A comprehensive list of standard abbreviations for adult and larval structural terminology was developed during the course of the *Manual's* preparation, which was based on the abbreviations applied in the Adult morphology and terminology chapter and expanded upon, based on the abbreviations listed in J.F. McAlpine's unpublished annotated list, which was developed during preparation of the *Manual of Nearctic Diptera*. Every attempt has been made to apply these abbreviations consistently throughout the *Manual*. All abbreviations that appear on the plates are included as an alphabetical list directly after each chapter plate legend and will not be repeated here as a separate list.

All author names of taxa, other than J.C. Fabricius (abbreviated to "F.") and C. Linnaeus (abbreviated to "L."), are provided in full. All wing veins, cells and crossveins are indicated by standard abbreviations in italic script. Following standard protocols, all veins use upper case (*e.g.*, C, M, R_1, Rs, M_{2+3}) and wing cells lower case (*e.g.*, c, r_1, m_3, r_{2+3}) and all crossveins lower case (*e.g.*, *r–m*, *m–m*). Following British convention, a full stop is not used after an abbreviation if the last letter of the word forms the last letter of that abbreviation, e.g., "Fig. 1", as opposed to "Figs 3, 4" and "ed.", as opposed to "eds". All Latin terms and abbreviations are placed in italic script, *e.g.*, *et al.*, *i.e.*, *in litt*, *sensu lato*, *sensu stricto*, *via*, *vice versa*, *etc*. and nouns derived from African languages are also placed in italic script, e.g., *tsetse* (derived from the Tswana language) and *vlei* (Afrikaans).

General abbreviations and Latin terms used commonly in the text are as follows: AD – *anno Domini*; BP – before present; *ca* – *circa* (approximately); *cf.* – *confer* (compare); cont. – continued; *e.g.* – *exempli gratia* (for example); ed. – editor; eds – editors; *et al.* – *et alia* (and others); *etc.* – *et cetera* (and other things); F. – Fabricius; *i.e.* – *id es* (that is); *in litt.* – *in litteris* (in correspondence); in prep. – in preparation; *incertae sedis* – of uncertain placement; incl. – including; Is. – island(s); L. – Linnaeus; m – meters or meters above sea level; Mt – Mount; My – million years; Mya – million years ago; No. – number; Nos – numbers; pers. comm. – personal communication; pers. obs. – personal observation; preocc. – preoccupied; *sensu* – in the sense of; *sensu lato* – in the broad sense; and *sensu stricto* – in the strict sense.

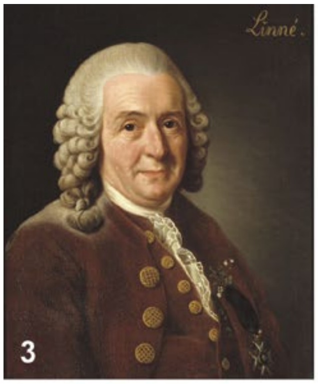
New taxon names and undescribed genera

This *Manual* is not a revisionary work, so only published taxon names are included and no changes in status, synonymy or other nomenclatural changes have been allowed. Some authors have indicated in some cases where changes in the generic status of some taxa "should" be formally made in the future.

Some authors have included undescribed genera in the identification keys and synopsis sections of family chapters. These are referred to as "Undescribed genus" (if only one), or "Undescribed genus A" and "Undescribed genus B", *etc.*, if more than one. In such cases, new genera included in these chapters should be cited in future publications as, e.g., "Undescribed genus A *sensu* Sinclair & Cumming (2017)". Some authors also include extralimital genera in keys that are not formally recorded from the Afrotropical Region, but are likely to occur there and in these cases generic names and authors are placed in square brackets.

Illustrations

All illustrations are of Afrotropical species, unless otherwise stated, in which case these are indicated as "(non-Afrotropical)" in figure legends. Most illustrations that appear in this *Manual* were supplied by the authors themselves. This is the first regional manual to use colour extensively and authors were actively encouraged to submit colour digital images to illustrate their chapters. Some authors did so, while others submitted more traditional pen and ink type or digitally generated images. In numerous cases original illustrations were re-drawn digitally, either by our artists (T. Smit or L. Coetzee) or by our Graphics



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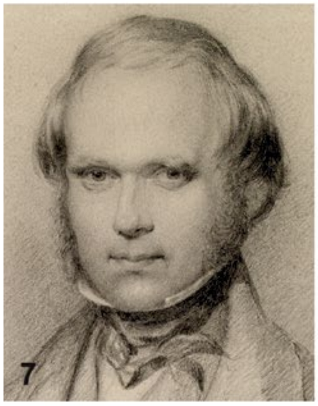

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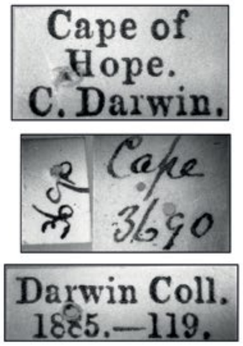

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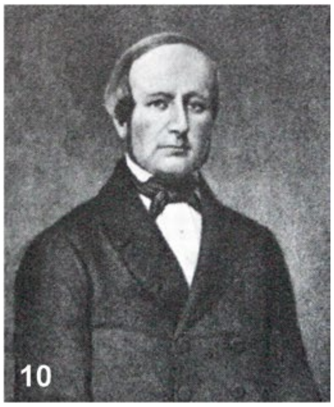

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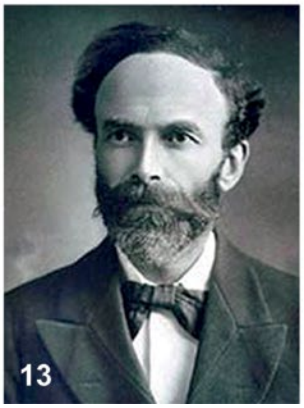

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Figs 1.3–14. Historical figures in the history of Afrotropical dipterology: (3) Carl Linnaeus (after 1761 Carolus a Linné) (1707–1778); (4) Anders Sparrman (1748–1820); (5) Carl Pehr Thunberg (1743–1828); (6) C. Rijk [Ryk] Tulbagh (1699–1771); (7) Charles Robert Darwin (1809–1882); (8) Darwin holotype labels on *Acarterus darwini* Sinclair (Hybotidae), from Cape of Good Hope; (9) Johan Christian Fabricius (1745–1808); (10) Johan August Wahlberg (1810–1856); (11) Charles John Andersson (1827–1867); (12) Axel Wilhelm Eriksson (1846–1901); (13) Robert Newstead (1859–1947); (14) Bror Yngve Sjöstedt (1866–1948). Figs 3, 9, 14, 10 (https://en.wikipedia.org), Figs 4, 11, 12 (https://sok.riksarkivet.se), Fig. 5 (http://www.slon-tea.ru), Fig. 6 (http://www.bidorbuy.co.za), Fig. 7 (https://www.darwinproject.ac.uk), Fig. 8 (courtesy B.J. Sinclair), Fig. 13 (https://www.chesterwalls.info).

Editor (B.S. Muller), in order to either improve line quality or the consistency of images that appear on the same plate. Some authors submitted images from previously published sources, especially the *Manual of Nearctic Diptera*. The responsibility to acquire permission to use images from copyright holders (other than those for which we have blanket permission – see acknowledgements), was and remains the responsibility of individual chapter authors (as clearly stated on the *Manual* website and as re-iterated to all authors by the editors). The editors and publisher therefore, accept no responsibility for any copyright infringements on the part of chapter author(s). The original sources of all images reproduced from published sources (as indicated to the editors) are, however, acknowledged at the end of each plate legend in respective chapters. Illustrations that were re-drawn as part of the editorial process or were indicated as having been modified in some way by the authors themselves, are specified as such by the use of "after" (e.g., "after Crosskey 1969, fig. 43") and in such cases these images are deemed as "modified from the originals".

Figure numbers are cited sequentially in each separate chapter. Chapter numbers are only indicated in the legends for figures (*e.g.*, Figs 3.4–7) to allow ease of citation in subsequent works, but are not included in regular text figure citations. All illustrations provided by authors must be cited in the text at least once to warrant their inclusion in the chapter. If figures are not referred to in the diagnoses or identification keys, then authors were instructed that these be referred to in the synopses sections, e.g., See Fig. 8 for an example of the antenna of the genus, Figs 19, 20 for the head and Fig. 28 for wing venation.

Editorial and peer-review process

All chapters included in this *Manual* were subject to rigorous peer-review. All submitted chapters first underwent an initial edit prior to review, during which any major omissions and editorial comments were dealt with between the editors and the authors. All chapters were then reviewed by at least two external reviewers (usually three) and by the Editor-in-chief, Assistant Editor and Graphics Editor. Authors were asked to supply names and contact details of proposed reviewers, but the final decision as to which reviewers were approached was made by the Editor-in-chief and the process was confidential. Reviewers were given the option on the referee's comments form of "I wish to be identified" [to authors], "I am prepared to be identified" or "I do not wish to be identified". Disclosure was made to authors based on this and in the case of those who opted for "I am prepared to be identified", the name of the referee was only disclosed, if authors required clarification on specific points raised during the review process.

Brief history of Afrotropical dipterology

To chronicle the history of Afrotropical dipterology in detail is beyond the scope of this chapter and would easily warrant a book of its own. Published information related specifically to the history of dipterological research in the region has not been published and there is considerably more information available on entomological research conducted in Southern and West Africa in general than for Central and East Africa. This brief account is by no means comprehensive and complete, but focuses on research that has led to published results (usually substantial) specifically on the Diptera, and has relied heavily on the accounts of Brinck (1955) and Medler (1980).

It can be speculated that prior to Linnaeus's time some insects were collected in the environs of Southern and West African ports, during the period when ships from Europe were establishing trading routes or were engaged in trade with the African interior. Large and showy specimens may have been obtained by sailors to sell to European dealers as "cabinet specimens" (Medler 1980: 7) and all manner of biological specimens brought to Sweden from South Africa during this period were regarded as "curiosities" and were delivered by officers of Swedish ships, who had procured them in Cape Town. Following the establishment of the Swedish East Africa Company in 1731, its directors had a standing demand for such "curiosities" (Brinck 1955: 12).

The Cape Settlement was established in 1652 by Commander Jan van Riebeeck (1619–1662) and shortly after (in 1656) the Swedish naturalist Nils Matson Kiöping (*ca* 1621–1680) visited Table Bay and the Cape Peninsula, returning with a collection of mammals and birds, part of which went to the Academy of Uppsala, Sweden, where a few were still present when Carl Linnaeus (1707–1778) (Fig. 3) began his work (Brinck 1955: 12; Hanström 1955: 1).

The true beginnings of entomological discovery and scientific description in Africa began during Linnaeus's time, who had established a scientific approach to the description of species and an ordered binomial system for naming biological organisms. The sheer variety of plant material sent to Linnaeus by C. Rijk [Ryk] Tulbagh (1699–1771) (Fig. 6), governor of the Dutch Colony (under the Dutch East India Company) from 1751–1771, excited Linnaeus (Talbot 1977: 5). As a result, Linnaeus sent eight of his pupils to the Cape: Carl Frederic Gröndahl (1760–1816), Michael Grubb (1728–1808), G. Lange, Frans Pehr Oldenburg (1740–1774), Carl Gustaf Osbeck (1766–1841), Daniel Carlsson Solander (1733–1782), and most notably, Anders Sparrman (1748–1820) (Fig. 4) and Carl Pehr Thunberg (1743–1828) (Fig. 5), who collected insect material, including Diptera, in the Cape Colony (for Thunberg types see Wallin & Wallin 2001).

Sparrman and Thunberg had both trained as physicians at Uppsala and arrived in the Cape independently in 1772. Sparrman had been sent on a collecting trip by the Swedish explorer Captain Carl Gustaf Ekeberg (1716–1784) (with whom he had travelled in China 1756–1765), and by Linnaeus himself, under whom he had studied. However, Sparmann did not initially remain long in the Cape: in November of the same year he arrived (1772) he was offered a position to sail with Captain James Cook (1728–1779) as assistant to the two naturalists on board the ship *Resolution*. Thunberg had been commissioned by the Dutch botanists Johannes Burman (1707–1780) and Nicolaas Laurens Burman (1734–1793) (father and son) and other sponsors in Amsterdam to collect botanical specimens in South Africa and Japan (Talbot 1977: 7). Thunberg was the first of Linnaeus's pupils to travel extensively in the Cape interior, details of which are provided by Talbot (1977: 5–7) and in his own journal accounts (see Forbes 1986).

In March 1775, less than three weeks after Thunberg's departure for Java in the East Indies, Sparrman returned from the 28-month voyage with Cook, in which he had participated in the first eastwards circumnavigation of the globe. In July he set off for a nine-month trek through the southern and eastern districts of the Cape, penetrating much farther into the interior than Thunberg had done (Talbot 1977: 7). Both Thunberg and Sparrman were guided by the young frontiersman Daniel Ferdinand Immelman (1756–1800) on their trips into the interior. The fascinating and informative travel journals of Sparrman have been published by the Van Riebeeck Society (Forbes 1975, 1976). These accounts give important insights into the routes taken and collecting conducted by this early pioneer.

The first fly described from the Afrotropical Region was *Bombylius capensis* (now in the genus *Australoechus* Greathead) (Fig. 15), described by Carolus Linnaeus (Fig. 3) in 1767, p. 1009, from "*Cap b. spei*" [= Cape of Good Hope, South Africa], collected by C. Rijk Tulbagh. Like many people of his day, Tulbagh showed a great interest in natural history, particularly botany and established an animal and plant collection in the gardens of the Company, a remnant of which exists to this day. As noted above, Tulbagh is probably best known for sending numerous botanical specimens to Linnaeus, but he also sent insects (including Diptera) and in an undated letter from Linnaeus to Tulbagh he wrote "I have acknowledged the curious insects with which you have, long ago, so generously and kindly furnished me" (Smith 1821: 568). Additional correspondence between Linnaeus and Tulbagh was published by Jackson (1918).

During the same period in West Africa the French naturalist Ambroise Marie François Joseph Palisot, Baron de Beauvois (1752–1820) collected insects on his 1781–1797 voyage, which included stopovers in Benin and Warri (Medler 1980: 7) and in 1786 he set out to found a colony at Oware at the mouth of the Niger River, in what is today Nigeria. Palisot merged specimens from there with collections from neighbouring Benin. He periodically sent natural history specimens to France, but the greater part of his collection was destroyed when the British invaded the colony and razed the trading post where his material was kept.

Fig. 1.15. The first fly species described from the Afrotropical Region – type specimen (from various angles) of *Bombylius capensis* Linnaeus, 1767 (now in the genus *Australoechus* Greathead), described from "*Cap b. spei*" [= Cape of Good Hope, South Africa] and collected by C. Rijk [Ryk] Tulbagh (reproduced by permission of the Linnean Society of London).

During the late 18th and early 19th centuries, Johan Christian Fabricius (1745–1808) (Fig. 9) was in receipt of specimens originating from the Danish Guinea colony in Ghana (mostly labeled as "Guinea"), either collected by, or from the collections of Johann Wilhelm Hesse (1764–?), Niels Tønder Lund (1749–1809), Paul Erdmann Isert (1756–1789), Peter Thonning (1775–1848) and Ove Ramel Sehested (1757–1838) (Hopkins 2013). Sixteen species of Diptera based on this material were described by Fabricius between 1794 and 1805 (Table 2).

The itinerary of the *Beagle* voyage (1831–1836) indicates that Charles Robert Darwin (1809–1882) (Fig. 7) docked in the Cape of Good Hope from Mauritius on 29 April 1836, sailing on 9 May 1836 for Saint Helena Is. (Smith 1987). During this brief visit, Darwin spent most of his time geologising, as he did on much of the *Beagle* voyage elsewhere. Andrew Smith (1797–1872), the Scottish surgeon, naturalist and zoologist and the first Superintendent of the South African Museum in Cape Town (now Iziko South African Museum), accompanied him to the important Cape Peninsula sites and Darwin collected a variety of rock specimens. He kept a geological notebook in which are recorded visits made from Simon's Town to Cape Town, Table Mountain, Lion's Head and Rump, the Sea Point Contact, the road to Paarl, Paarl Rock, the Drakenstein Mountains, Franschhoek and the pass to Houw Hoek, Sir Lowry's Pass and the Cape Flats. Darwin also collected insects, frogs, plant and other specimens of interest, most of which are now housed in British institutions (James 2009). Darwin's insects were reviewed by Smith (1987, 1996), which indicate that Darwin collected Curculionidae, Dryopidae and Tenebrionidae (Coleoptera), Cicadellidae (see Theron 1983), Dictyopharidae, Lygaeidae and Tropiduchidae (Hemiptera), with Simon's Bay being a consistent locality cited for insect captures. Dipterologically, Smith (1987) recorded the tachinid *Leskia darwini*, described by Emden (1960: 391) and Sinclair (1996) described *Acarterus darwini* (Hybotidae), based on two specimens labelled "Cape of Hope. C. Darwin" (Fig. 8), discovered in accessions material of the Natural History Museum, London, U.K. This latter material was cited as "? *Syneches* sp. (Empididae)" by Smith (1996), the two papers appearing in the same year.

Collecting activity probably increased sharply after 1800, as naturalists began accompanying explorers and traders in the African interior (Medler 1980: 7) and in West Africa a notable amount of insect collecting was undertaken by European missionaries. In the 1850s, for example, the United Presbyterian Church of Scotland opened a mission station at Old Calabar near Duke Town in southern Nigeria. The Reverend Hope Masterton Waddell (1804–1895), Reverend Hugh Goldie (1866–1895), W.C. Thomson and John R. Wylie sent collections of insects to the Scottish lawyer, botanist, zoologist and entomologist Andrew Dickson Murray (1812–1878) in Edinburgh. Most of these were Coleoptera, but also other insect orders, some of which were distributed to various specialists (Medler 1980: 7). After Murray's death, his important collection was auctioned on 9–11 April 1878. According to Chalmers-Hunt (1976: 8, 112), much of the insect material (mainly comprising Coleoptera), was purchased by W. Janson for the British Museum (Natural History) (Chalmers-Hunt 1976: 8, 112). No Diptera are mentioned.

Table 1.2. Diptera species described by Johan Christian Fabricius originating from the Danish Guinea colony in Ghana (originally labeled as "Guinea"), indicating collector/collection names (after Zimsen 1964).

Described taxon name	Current placement	Family	Year	Collectors/Collections
Anthrax nemesis	*Exoprosopa* Macquart	Bombyliidae	1805	Peter Thonning
Anthrax sisyphus	*Ligyra* Newman	Bombyliidae	1805	Peter Thonning
Asilus morio	Unplaced Asilidae	Asilidae	1805	Paul Erdmann Isert
Dacus armatus	*Dacus* (*Dacus*)	Tephritidae	1805	Peter Thonning
Dacus inflexus	*Elassogaster* Bigot	Platystomatidae	1805	Paul Erdmann Isert
Dasypogon tridentatus	*Storthyngomerus* Hermann	Asilidae	1805	Niels Tønder Lund
Dictya stictica	*Peltacanthina* (*Peltacanthina*)	Platystomatidae	1805	Peter Thonning
Laphria rufibarbis	*Proagonistes* Loew	Asilidae	1805	Peter Thonning
Laphria serripes	*Hoplistomerus* Macquart	Asilidae	1805	Ove Ramel Sehested
Milesia obliqua	*Eumerus* Meigen	Syrphidae	1805	Niels Tønder Lund
Musca fasciata	*Bogosiella pomeroyi* Villeneuve	Tachinidae	1805	Peter Thonning
Musca megacephala	*Chrysomya* Robineau-Desvoidy	Calliphoridae	1794	Paul Erdmann Isert
Musca moerens	*Engistoneura* Loew	Platystomatidae	1794	Paul Erdmann Isert
Musca vittata	*Carpophthoromyia* Austen	Tephritidae	1794	Paul Erdmann Isert
Stratiomys hastata	*Platyna* Wiedemann	Stratiomyidae	1805	Peter Thonning
Tipula filipes	*Maekistocera* Wiedemann	Tipulidae	1805	Johann Wilhelm Hesse

Johan August Wahlberg (1810–1856) (Fig. 10), was a Swedish naturalist, who travelled through large parts of southern Africa, especially the Natal Province, South Africa and Namibia. He was sent by the Swedish Academy for Science to collect plants and animals in southern Africa for the Royal Academy of Sciences in Stockholm. Walhberg's extensive collections of insects, including many Diptera, are housed in the Swedish Museum of Natural History and his journals and letters have been published by the Van Riebeeck Society (Hummel & Craig 1992), which provides interesting insights into his travels and collecting.

Early traders and explorers who generated biological specimens from this era were Charles John Andersson (1827–1867) (Fig. 11), a Swedish adventurer, trader, explorer and collector of natural history specimens, who published a series of articles and popular books on his travels (Andersson 1855, 1856, 1873, 1875) and the Swedish ornithologist Axel Wilhelm Eriksson (1846–1901) (Fig. 12), both of whom concentrated their trading and collecting efforts in what is today Namibia. Part of Andersson's insect collections were sold off to European collectors, but his insect collection resulting from his Okavango River Expedition was donated to the South African Museum in 1860. Eriksson left Sweden for the Cape late in 1865 to join Andersson, who was at that time already a famous explorer, to help him with his trading and bird collecting. He made substantial collections of birds, insects and mammals. A number of his specimens were sent to the South African Museum in Cape Town, including insects from the Transvaal and Matabeleland in 1885 and from the former Damaraland and Ovamboland (Namibia) in 1888 and 1891, respectively and a collection of insects from northern Damaraland (Namibia) in 1899, including some 20 species new to the Museum. A collection of insects was also sent to the Entomological Museum in Lund and a minor collection to the Zoological Institute of Uppsala University. By subsequent donations part of his material went to the British Museum (Natural History) (now the Natural History Museum, London, U.K.) and the Riksmuseum, Stockholm, Sweden (Brinck 1955).

During the latter part of the 19th and early 20th centuries there was considerable insect collecting activity in Africa. Lepesme (1950) listed some of the localities visited by early collectors. Henry C. Deyrolle, for example, undertook a voyage to Gabon in 1856–1857, under the auspices of Le Comte de Mniszech, together with the American coleopterist James Thomson (1828–1897). This voyage resulted in the discovery of numerous new species, with the Diptera treated by Bigot (1858). The French botanist, taxonomist and explorer of tropical Africa, Auguste Jean Baptiste Chevalier (1873–1956) undertook expeditions to the French colonial empire, including Côte d'Ivoire in 1908 and Lake Chad in 1902–1904 (Medler 1980: 8). Another Swedish naturalist, Bror Yngve Sjöstedt (1866–1948) (Fig. 14), who was Professor and curator at the Swedish Museum of Natural History undertook several expeditions to West and East Africa, notably to Mt Kilimanjaro and Mt Meru in Tanzania, for which the Diptera were dealt with by Speiser (1907, 1909*a*, *b*, 1910*a*, *b*) and Sjöstedt himself (1908) (Fig. 16).

Following the scramble for Africa by European colonial powers, known as the period of New Imperialism or the Partition of Africa (1881–1914), numerous expeditions were undertaken in Africa, especially as the interior opened up through exploration. Collecting expeditions or "missions" to West and Central Africa were conducted with increasing frequency, as the British (see below), Belgian (see below), French and German colonies became established and consolidated. Specimens generated through these expeditions were sent back to Europe and were incorporated into private collections or European museums. Near the turn of the 20th century, specialists associated with the then Deutsches Entomologisches Institut and the then Museum für Naturkunde der Königlichen Friedrich-Wilhelm-Universität published on insect material sent to Berlin by German collectors in the colonies, including Reinhold Wilhelm Buchholz (1837–1876), Leopold Konradt (1853–?1910), Eugen Hintz (1868–1932), Lorenz Oldenberg (1863–1931), Paul Preuss (1862–1926), Herbert Oskar Hermann Kurt von Rothkirch und Panthen (1884–1916), August Schultze (1837–1907) and Fritz G. Theorin (Medler 1980: 8) and material resulting from collecting by German botanist and ethnologist Günther Tessmann (1884–1969) in Cameroon, Gabon and Guinea (1904–1914), was dealt with in a series of publications, including Grünberg (1915) for Diptera.

In later years of the 20th Century, French collectors and others published on expeditions, such as reports on the 1939 mission of P. Lepesme, Renaud Paulian (1913–2003) and André Villiers (1915–1983) in western Cameroon; on the 1947 Mission of the Swiss Museum; on the collections of Jean Risbec (1895–1964), C. de Reamy, Philippe Bruneau de Mire (1921–?); and on the results of the Jørgen Dahl (*ca* 1925–1998) and Sven Jorgen R. Birket-Smith (1920–1983) Danish Expedition to the French Cameroons (1949–1950). Since WWII, capacity was built in West Africa by, for example, Institut Français d'Afrique Noir (IFAN) (now Institut Fondamental d'Afrique Noire; see below) in Dakar, Senegal, which served as an important centre for French-orientated research and faunistic surveys. A. Villiers was first chief of the Entomology Section and, during his residence in Senegal (1945–1956), collected widely in Benin, Bioko Is. (Equatorial Guinea), Côte d'Ivoire, Guinea, Mauritania, Republic of Congo, Senegal and Togo (Medler 1980: 11). A notable collection was made by Belgian forest entomologist Jean Decelle (1907–1996), while residing in Bingerville, Côte d'Ivoire from 1961 to 1964, and was deposited in the Royal Museum of Central Africa, Tervuren, Belgium. Results on the Diptera were published for the Asilidae (Oldroyd 1968*a*), Tabanidae (Oldroyd 1968*b*) and Tephritidae (Munro 1969).

Early research on African Diptera during the colonial period (1881–1914) largely focused on vectors of diseases to humans and their livestock, such as *tsetse*, mosquitoes and horse flies and colonial powers in possession of much of Africa during the 19th and first half of the 20th centuries invested considerable manpower and resources to the understanding and ultimate eradication of such vectors. Workers that contributed substantially to early knowledge of taxonomy and behaviour of African Diptera vectors from this period include Ernest Edward Austen (1867–1938) (see biography below) and Robert Newstead (1859–1947) (Fig. 13), who published extensively on *tsetse* and other blood-sucking flies. Numerous institutes and research stations investigating agricultural pests and disease vectors were established throughout colonial Africa, many of which employed dipterists from overseas who made substantial contributions and collected extensively in the region.

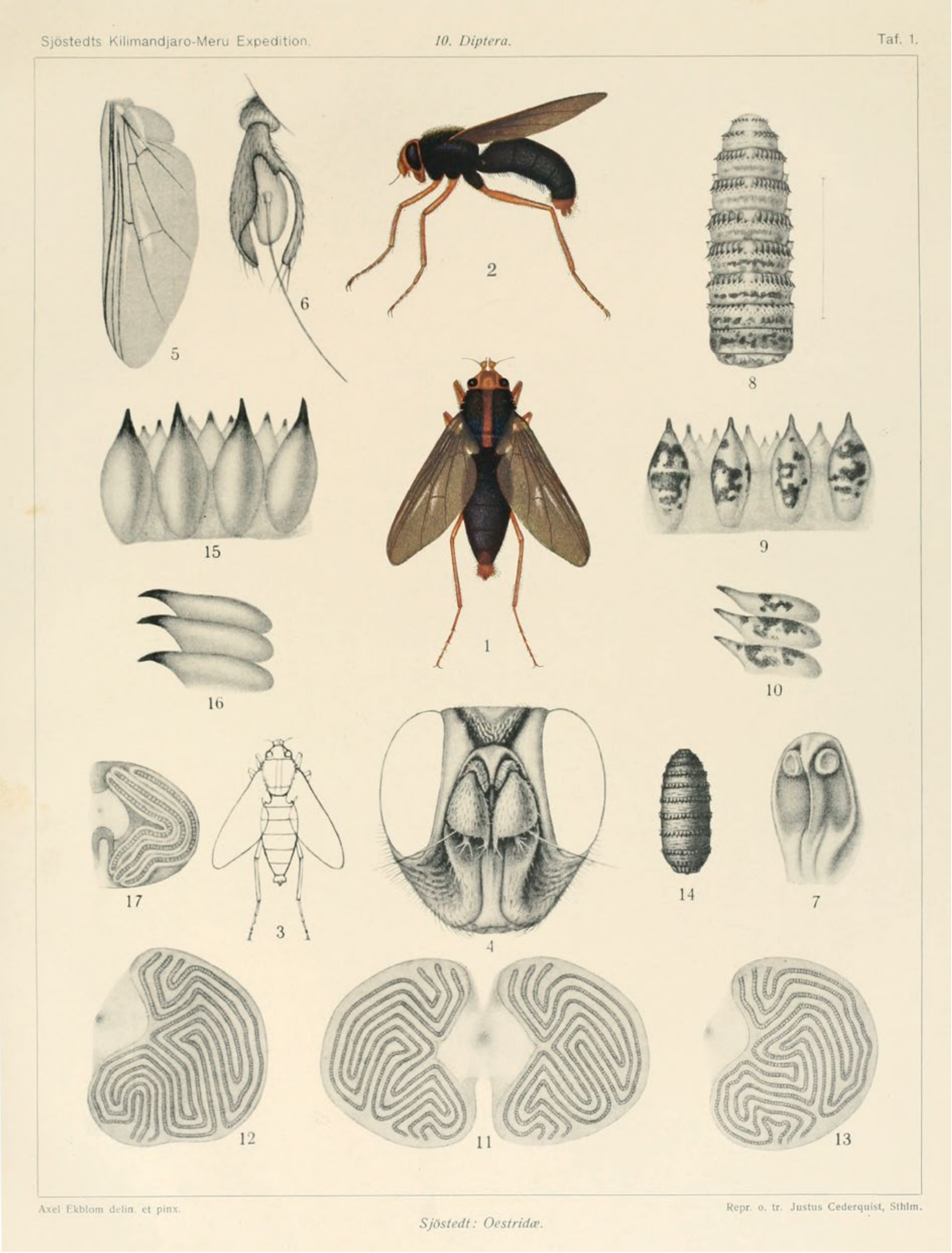

Fig. 1.16. Original scanned plate from Sjöstedt (1908), illustrating the adult and immature stages of the Rhinoceros bot fly, "*Spathicera* (*Gyrostigma*) *meruensis*" (= *Gyrostigma rhinocerontis* Owen) (Oestridae), from Mt Meru, Tanzania.

Much of the pioneering work on biological control of insect pests in the Afrotropical Region was undertaken by the dipterist David John Greathead (1931–2006) (see biography below), who reviewed opportunities for biological control in the region (Greathead 1971, 1986, 1989). There have been many useful compilations of knowledge on insects associated with agriculture and forestry, including the following Afrotropical references (adapted from Miller & Rogo 2001): Burundi (Buyckx 1962), Cameroon (Nonveiller 1984), East Africa (Kenya, Tanzania and Uganda) (Gardner 1957; Le Pelly 1959), Eritrea (Nastasi & Wolden-Haimanot 1967), Ethiopia (Abate 1991; Hill 1966; Walker & Boxall 1974), Ghana (Forsyth 1966; Wagner *et al*. 1991), Madagascar (Reckhaus 1997), Mauritius (Mamet 1992; Mamet & Williams 1993), Niger (CIDA 1983), Nigeria (Medler 1980; Roberts 1969; Toye 1986), Republic of Congo (Buyckx 1962), Réunion Is. (Vayssières *et al*. 2001), Rwanda (Buyckx 1962), Seychelles (Kingsland & Shepard 1983), South Africa (Annecke & Moran 1982; Swain & Prinsloo 1986), Tanzania (Bohlen 1978) and Uganda (Brown 1967).

The establishment of the first museums in South Africa: the South African Museum in Cape Town in 1825 and the Albany Museum in Grahamstown in 1855, heralded a new era for South African entomology. Others followed in Madagascar, Rhodesia, Kenya, *etc*. The first dipterist employed in a South African museum was Albert John Hesse (1895–1987) (see biography below), who took up the post of entomologist at the South African Museum in 1924, where he served for 51 years, leaving the Museum in 1974. He was extremely prolific and published two major monographs: on the Bombyliidae (Hesse 1938, 1956*a*, 1956*b*) and the Mydidae (Hesse 1969). A complete list of his published works is listed in Robertson & Whitehead (1989). Details of other prominent dipterists employed at institutions in the Afrotropical Region are provided below in the biographies and collections sections.

Brian Roy Stuckenberg (1930–2009) (Fig. 77) (see biography below) of the Natal Museum (now KwaZulu-Natal Museum) was one of the first to collect Diptera extensively in Madagascar, undertaking two expeditions in December 1955 and January 1956. On the second of these expeditions he travelled over 5,000 km on the island, visiting 28 different collecting localities and generated thousands of flies, all of which were field-pinned. The Swiss dipterist Fred Keiser-Jenny (1895–1969) and his wife also collected Diptera in Madagascar in 1950s (now deposited in the Naturhistorisches Museum, Basel, Switzerland). Many of both Keiser-Jenny's and Stuckenberg's collecting localities have subsequently been destroyed and their Diptera material is, therefore, unique (Kirk-Spriggs 2012). Additional information on dipterological research in the Afrotropics is included in the biotic surveys, biographies and collections sections below.

Biotic surveys of Afrotropical Diptera – past and present

This section highlights some of the more significant biotic studies of Diptera (expeditions, missions), conducted in the past, as well as more contemporary surveys that have led to significant publications on the Diptera.

Surveys of Afrotropical Diptera began following the onset of European colonialism in Africa. Initial sampling targeted Diptera of medical and agricultural significance on the continent. Later, European powers with colonial territories in Africa engaged in surveys that generated specimens used today for baseline biodiversity information. As a result, 70% of these historical specimens are now deposited in European and North American collections (Miller & Rogo 2001).

The main museums holding Diptera collections in Africa are: the National Museum, Bloemfontein, KwaZulu-Natal Museum, Pietermaritzburg, National Museum of Namibia, Iziko South African Museum and National Museums of Kenya. Other smaller collections are housed in other South African museums and other institutions on the African continent. Details of all extralimital collections with substantial holdings of Afrotropical Diptera are currently listed on the *Manual of Afrotropical Diptera* web pages http://afrotropicalmanual.org/.

British Museum (Natural History) expeditions

The Natural History Museum, London, U.K. holds one of the most important collections of historical Diptera from the Afrotropical Region, due to Britain's colonial interests in Africa. Collections were amassed through early studies of medical and veterinary Diptera, through the Imperial Bureau of Entomology and its successor, the Commonwealth Institute of Entomology.

In the first half of the 20th century, the British Museum (Natural History) (now the Natural History Museum, London) played a significant role in generating material and organised expeditions to various British and other territories during the African colonial period, including East Africa (1924–1931), Abyssinia (1927–1939) and South-West Arabia (1937–1938), the last two arranged by Hugh Scott (1885–1960). One notable example, that generated substantial Diptera material, was the Ruwenzori Expedition in Kenya and Uganda (1934–1935), with Frederick Wallace Edwards (1888–1940) and David Roden Buxton (1910–2003) sampling Diptera. Sampling was mainly conducted in the Aberdare Mountains, Mount Elgon, the Birunga (or Virunga) Mountains and in various localities in the Ruwenzori Mountains. Results of the Expedition were published in three volumes: volume 1 (parts 1–7) dealt with the Diptera "Nematocera"; volume 2 (parts 1–9) with Diptera Brachycera and Cyclorrhapha; and volume 3 (parts 1–13) other Insecta. The Museum undertook a second expedition to Ruwenzori in 1952, which was also published in three volumes, but these contributions did not deal with the Diptera.

In 1972, entomologists from the Museum, undertook the "British Museum (Natural History) Southern Africa Expedition 1972" – a five-month long collecting expedition to southern Africa. The Expedition comprised Brian Henry Cogan (1940–living) (sampling Diptera), Michael Charles Day (1943?–living) (Hymenoptera), Peter Michael Hammond (1941–living) (Coleoptera), David Hollis (1938–living) (Hemiptera and orthopteroids) and Richard Irwin Vane-Wright (1942–living) (Lepidoptera) (Fig. 20). They travelled in a second-hand three-tonne army lorry (Figs 17–19), which they themselves had specially converted into a mobile laboratory, and shipped out from the United Kingdom to Cape Town, arriving at the end of December 1971. The 12,800 km journey (Fig. 21) began in December in Cape Town, South Africa, travelling northwards through Namibia, into Angola, then southwards as far as Windhoek, across the Kalahari *sandveld*, through Botswana and back into South Africa, south *via* the Karoo, arriving back in Cape Town in May 1972. The habitats studied varied from sand deserts to tropical rainforests and from dry riverbeds to swampland. Most of the Diptera obtained were collected by B.H. Cogan, but all members contributed. The Expedition as a whole generated well over 1 million insect specimens. The mobile laboratory was later modified for fossil hunting and crossed the Sahara twice, until it eventually had to be abandoned in North


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Figs 1.17–21. The British Museum (Natural History) Southern Africa Expedition 1972: (17) three-tonne army lorry converted into mobile laboratory (Bull's Party Rocks, Ameib Ranch, Erongo Mts, Namibia); (18) same, crossing ephemeral river during flash flood, Namibia (P.M. Hammond walking); (19) same, breaking camp, Namibia; (20) working space in mobile laboratory (left to right): B.H. Cogan, M.C. Day, P.M. Hammond and D. Hollis; (21) map of Expedition route (indicated in red). Figs 17–20 (photographs courtesy R.I. Vane-Wright); Fig. 21 (B.S. Muller; after Cogan *et al*. 1975, fig. 1; made with Natural Earth).

Africa (Cogan *et al*. 1975; R.I. Vane-Wright, pers. comm. 2014). Results of the Expedition were not published as a dedicated volume of results, but the Diptera collection resulting from this Expedition represents an outstanding contribution to the Museum's Diptera holdings, much of it from very poorly sampled countries, especially Angola and Botswana.

Other notable donations of material from the Afrotropics include those of Walter Mayne Graham (1864–1935) (from Ghana 1908), Sheffield Airey Neave (1879–1961) (Central and East Africa; series of donations between 1907–1913), Rowland Edwards Turner (1863–1945) (South Africa; series of donations during the 1920s and 1930s), Harold Oldroyd (1913–1978) (Cameroon 1950), Eric Burtt (1908–1976) (Glossinidae from Tanganyika 1959), Alan Stubbs (1940–living) (Kenya 1972), Robert Stephen Copeland (1945–living) (Kenyan Tephritidae 2004) and D.J. Greathead (series of donations by him and his estate up to 2008, especially Asilidae and Bombyliidae). Although most of these collectors were dipterists, some such as Turner and Neave also donated material of other insect orders.

Also of note is the London School of Hygiene and Tropical Medicine collection, which was donated in 1996 and includes numerous Afrotropical Diptera of medical and veterinary importance and the collection of the Natural Resources Institute, which was donated to the Museum in 1997. There are also a few collections of Malagasy material and from Seychelles, the Percy Sladen Trust Expedition material from the early 20th century and more recently the collection of Willie Horace Thomas ("Timothy", "Tiger") Tams (1891–1980) and Ian William Beresford Nye (1924–?) from 1966. Brian Henry Cogan and Anthony Michael Hutson (1944–living), who were both employed at the Museum, made a large collection on Aldabra Is. in 1968, and three years later Hutson made another large collection (including *ca* 5,000 Diptera) from Mauritius and the Chagos Archipelago (N. Wyatt, pers. comm. 2017).

Muséum national d'histoire naturelle, Paris, France

The Diptera collection of Muséum national d'histoire naturelle, Paris is one of the most significant historical Diptera collections housed in Europe. The collection is divided into a general collection, classified into families and separate nominal collections entities. The heart of the collection is composed of two historical collections, that of the German dipterist Johann Wilhelm Meigen (1764–1845) and the French dipterist Pierre Justin Marie Macquart (1776–1855), both dating from the 19th century; they contain about 5,000 holotypes. In total the collection contains 2.5 million specimens, 8,000 holotypes and about 30,000 species or 20% of the described Diptera.

The Diptera section of the Museum was formally established, with the employment of Eugène Séguy (1890–1985) in 1919. Based on his own collection, various acquisitions and an impressive quantity of indeterminate specimens, he gradually built up a general collection which was added to the Meigen and Macquart collections. Later, he was also responsible for the addition of the Louis Pandellé (1824–1905), Jean Pierre Omar Anne Edouard Perris (1808–1878) and Léon Jean Marie Dufour (1780–1865) collections to the Muséum. By the early 1950s, the Muséum's Diptera collection had become one of the largest in the world.

From 1883–1938 the French entomologist Charles A. Alluaud (1861–1949) made 24 voyages to Africa and to the Atlantic and western Indian Ocean islands. Almost all his explorations appear to have been driven by his interest in biogeography. He undertook three major expeditions to East Africa, concentrating on the sampling of East African mountains: Mt Kilimanjaro and the Lake Victoria region (or Nyanza) (1903–1904); Mt Kilimanjaro and Ruwenzori (1908–1909); and Mt Kenya and Mt Kilimanjaro (1911–1912). The last was in company with René Jeannel (1879–1965) and resulted in 80 publications.

He also undertook expeditions to Assinie (Côte d'Ivoire) and the west coast of Africa (1886); Tunisia and Tripolitania (1898–1899); Egyptian Sudan (1905–1906); Morocco (Permanent Mission) (1919–1924); Sahara, Niger and Côte d'Ivoire (1930–1931); the Spanish Rif (1932); and Tunisia (1935–1936). He assembled an important collection of insects during these expeditions, later donating these to the Muséum. He was the author of 165 entomological publications. Publications on the Diptera resulting from these expeditions include: Becker (1914, 1915), Bezzi (1923), Bigot (1891), Edwards (1914), Giglio-Tos (1895), Kieffer (1913), Riedel (1914) and Stein (1914).

American Museum Congo Expedition (1909–1915)

North American museums also played a significant role in developing base-line biodiversity information on Diptera in Africa, but less so than their European counterparts. Perhaps the most significant early contributions was the American Museum Congo Expedition (1909–1915), which was arranged by Herbert Lang (1879–1957) (Fig. 22) and James Paul Chapin (1889–1964) (Fig. 23). Lang was a German taxidermist and photographer who had already assisted on an expedition to Kenya in 1906. They departed from New York harbour for the west coast of Africa in May 1909, planning to be in the Congo for two years to collect as many animals and ethnographic objects as possible. After numerous amendments they eventually spent six years in the Congo under gruelling conditions deep in the interior. During this period they sampled 100,000 invertebrates, including numerous Diptera. At the onset of WWI they hurriedly packed and transported their extensive collection along the Congo River across country, where it was eventually transported to the United States.

All the Diptera resulting from this Expedition were worked up, almost exclusively by Charles Howard Curran (1894–1972), in a series of three reports published in the *Bulletin of the American Museum of Natural History* (Curran 1927*a*, 1928*a*, *b*) and separate papers in the *American Museum Novitates*, *etc*. Twenty-eight families were treated as follows: Asilidae (Curran 1927e; 1928*a*), Bibionidae (Curran 1927*a*), Bombyliidae (Curran 1927*a*), Calliphoridae (Curran 1927*b*, *c*; 1928*a*), Chloropidae (Curran 1928*a*), Conopidae (Curran 1928*a*), Diopsidae (Curran 1928*b*, *c*), Dolichopodidae (Curran 1927*a*), Drosophilidae (Curran 1928*a*), Lauxaniidae (Curran 1928*a*), Lonchaeidae (Curran 1927*b*; 1928*a*), Micropezidae (Curran 1928*a*, *b*), Muscidae (Curran 1928*a*), Piophilidae (Curran 1928*b*), Pyrgotidae (Curran 1928*a*), Rhagionidae (Curran 1928*b*), Rhiniidae (Curran 1927*b*), Sarcophagidae (Curran 1934), Scenopinidae (Curran 1928*b*), Sepsidae (Curran 1928*b*), Stratiomyidae (Curran 1928*b*, *c*), Syrphidae (Curran 1927*a*), Tabanidae (Bequaert 1932, Hine 1927), Tachinidae

(Curran 1927*b*, *c*, *d*; 1928*a*), Tephritidae (Curran 1927*a*), Therevidae (Curran 1928*b*), Tipulidae (Alexander 1920) and Ulidiidae (Curran 1928*b*).

Belgian Congo national parks and missions

Three National Parks were established in what is today Democratic Republic of Congo during the Belgian colonial era: Albert National Park (the first African National Park), Upemba National Park and Garamba National Park. Three scientific missions generated Diptera material from these parks, which is now housed in the Royal Belgian Institute of Natural Sciences, Brussels and the Royal Museum of Central Africa, Tervuren, Belgium. The herpetologist Gaston-François de Witte (1897–1980) directed the scientific missions in Albert National Park (1933–1935) (see de Witte 1937; Figs 26–28) and to Upemba National Park (1946–1949) (see de Witte 1966; Figs 24, 25); and the entomologist Henri Jules de Saeger (1901–1994) directed the scientific mission in Garamba National Park (1949–1952) (see de Saeger 1954).

These scientific exploration missions used local collectors and technicians to sample and prepare long series of Diptera specimens in the field (Figs 24, 25). De Witte was evidently happy with the preparators he employed during the Albert National Park mission (1933–1935), as the notes associated with one photograph (No. 2528, dated 26/11/1948) reads "*Devant le hangar servant de laboratoire se tient Mr Kanzeguhera, préparateur originaire de Rutshuru, qui a travaillé au PNA et participé aux missions dans le PNU* [In front of the laboratory hangar stands Mr. Kanzeguhera, a native technician from Rutshuru, who worked at the NAP [Albert National Park] and participated in missions in the PNU [Upemba National Park]]". This indicates that 12 years later, G.F. de Witte re-employed at least some collectors and technicians during the Upemba National Park mission (1946–1949) (H. De Koeijer, pers. comm. 2017). The relatively poor condition of some Diptera material resulting from these missions may have been due to transport problems; some of the material taking more than five years to reach Belgium due to the onset of WWII. Material was studied by numerous specialists and an important series of publications resulted. Many authors used these publications as a means to publish regional revisions of specific groups. Publications (available as PDF files) and historical archives of the missions are available at the "Archives of the former National Parks of the Belgian Congo" website http://www.apncb.be/.

The Albert National Park (1933–1935) mission publications included treatments of 25 families of Diptera: Anisopodidae (Tollet 1956), Asilidae (Bromley 1951), Bibionidae (Hardy 1950*a*), Calliphoridae (Zumpt 1956), Celyphidae (Vanschuytbroeck 1953*b*), Ceratopogonidae (Goetghebuer 1948), Chaoboridae (Verbeke 1958), Chironomidae (Freeman 1955*a*), Conopidae (Vanschuytbroeck 1950*a*), Culicidae (Wolfs 1958), Dolichopodidae (Vanschuytbroeck 1951), Heleomyzidae (Collart 1946), Hippoboscidae (Bequaert 1953), Micropezidae (Verbeke 1951), Phoridae (Meyer 1958), Pipunculidae (Hardy 1950*b*, 1959*b*), Psilidae (Verbeke 1952), Rhiniidae (Zumpt 1958*a*), Sarcophagidae (Zumpt 1958*b*, 1972), Sciomyzidae (Verbeke 1950), Simuliidae (Freeman 1951), Sphaeroceridae (Vanschuytbroeck 1948), Tabanidae (Oldroyd 1950), Tachinidae (Mesnil 1954) and Therevidae (Vanschuytbroeck 1950*b*).

The Upemba National Park (1946–1949) mission publications included treatments of 16 families of Diptera: Asilidae (Janssens 1954), Bibionidae (Hardy 1952), Bombyliidae (Hesse 1958), Celyphidae (Vanschuytbroeck 1953*a*), Chironomidae (Freeman 1955*b*), Culicidae (Mattingly 1955), Dolichopodidae


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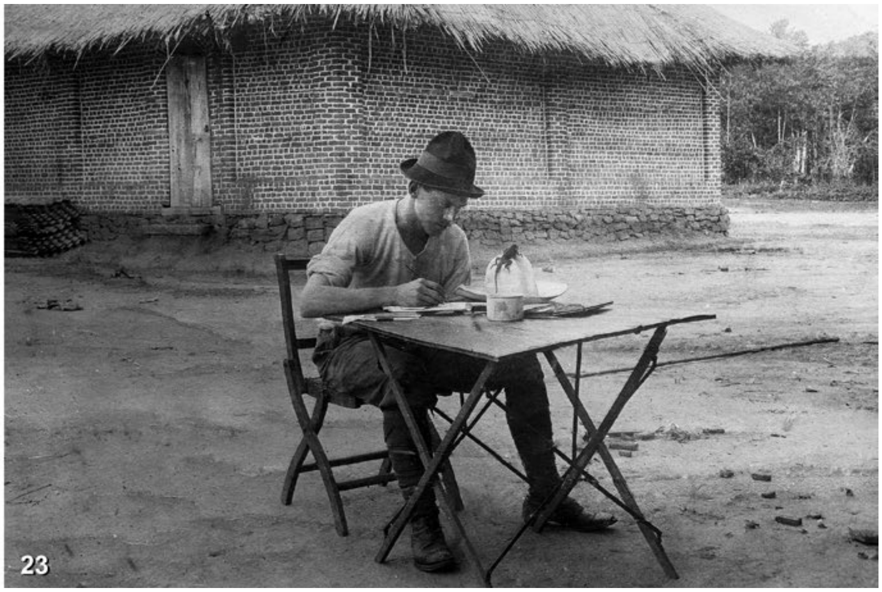
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Figs 1.22–23. American Museum Congo Expedition (1909–1915): (22) portrait of Herbert Lang (1879–1957); (23) James Paul Chapin (1889–1964) drawing a lizard placed atop his hat at the expedition's base camp in Avakubi. Figs 22, 23 (image # 32297 and 36617, respectively: courtesy American Museum of Natural History Library).

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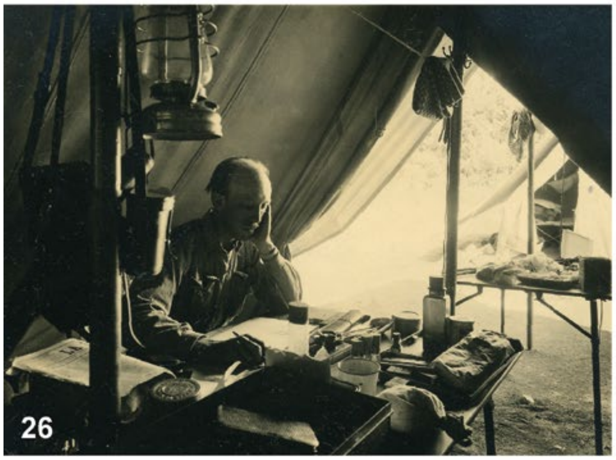

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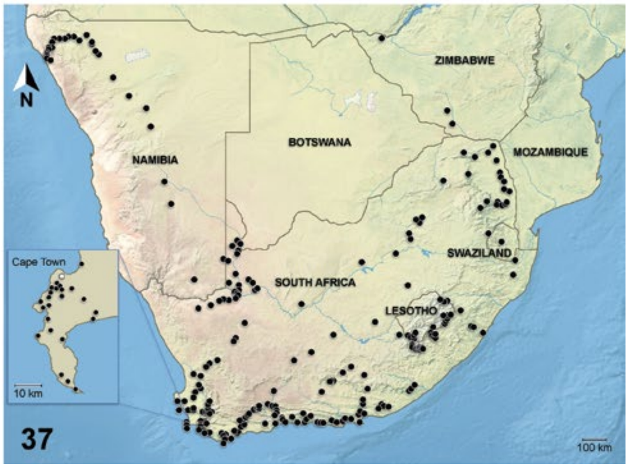
Figs 1.24–28. Belgian Congo missions of exploration (National Park Upemba: Mission G.F. de Witte (1946–1949) and National Park Albert: Mission G.F. de Witte (1933–1935)): (24) G.F. de Witte (1897–1980) (centre) with entomological collectors and technicians in front of the laboratory (Parc National de l'Upemba, 1948) (de Witte/RBINS); (25) René Verheyen (1907–1961) (far left), G.F. de Witte (mid right) and André Janssens (1906–1954) (far right), with local collectors in Kalumengongo (Parc National de l'Upemba, 1947) (de Witte/RBINS); (26) G.F. de Witte seated inside tent at Kamatembe (Parc National Albert, 1934) (de Witte/RBINS); (27) G.F. de Witte inside laboratory in Rutshuru (Parc National Albert, 1934) (de Witte/RBINS); (28) G.F. de Witte posing in vegetation constituting *Lobelia* and *Alchemilla* on the volcano Muhabura (Parc National Albert, 1934) (de Witte/RBINS). Figs 24–28 (photographs courtesy the Royal Belgian Institute of Natural Sciences, Brussels, Belgium).

(Vanschuytbroeck 1952), Glossinidae (Henrard 1951), Neriidae (Aczél 1955), Pipunculidae (Hardy 1952), Pyrgotidae (Aczél 1958), Sciomyzidae (Verbeke 1961), Simuliidae (de Meillon 1959*b*), Sphaeroceridae (Vanschuytbroeck 1959*d*), Stratiomyidae (Lindner 1958) and Tabanidae (Leclercq 1955).

The Garamba National Park (1949–1952) mission publications included treatments of 15 families of Diptera: Bibionidae (Hardy 1961), Bombyliidae (Bowden 1962), Celyphidae (Vanschuytbroeck 1959*a*), Chironomidae (Freeman 1962), Dolichopodidae (Vanschuytbroeck 1959*b*), Pipunculidae (Hardy



Figs 1.29–37. Lund University Southern Africa Expedition 1950–51: (29) Greys Pass, 5 miles S.W. of Citrusdal, South Africa, 1950 (Loc. No. 31) (left to right: G. Rudebeck, G. Brinck-Lindroth, I. Rudebeck and Piet ?); (30) G. Rudebeck at Kirstenbosch, South Africa, 1950; (31) P.S.V. Brinck with *Welwitschia mirabilis* plant, Namibia, 1950; (32) G. Rudebeck, sampling at Steenbras, South Africa, 1951; (33) P.S.V. Brinck (left) and G. Brinck-Lindroth (right) at Steenbras, South Africa, 1951; (34) P.S.V. Brinck (left) and G. Brinck-Lindroth (right) sampling at Wilde Vogel Vlei, Cape Peninsula, South Africa, 1950 (Loc. No. 14); (35) P.S.V. Brinck sampling at Langebaan Lagoon, Saldanha Bay, South Africa, 1950 (Loc. No. 20); (36) P.S.V. Brinck sampling insects with a net, [locality unknown], Namaqualand, South Africa; (37) map of 356 localities sampled during the expedition (data from Brinck & Rudebeck 1955, maps I–V). Fig. 29 (photograph P.S.V. Brinck), Figs 30–33 (photographs I. Roth), Figs 34–36 (photographs G. Rudebeck), Fig. 37 (B.S. Muller; made with Natural Earth). All photographs courtesy Carita Brinck.

1961), Psilidae (Verbeke 1968), Pyrgotidae (Vanschuytbroeck 1963), Scatopsidae (Cook 1964), Sciomyzidae (Verbeke 1963), Sepsidae (Vanschuytbroeck 1961), Sphaeroceridae (Vanschuytbroeck 1959*c*), Stratiomyidae (Lindner 1964), Tabanidae (Leclercq 1961) and Tachinidae (Verbeke 1962).

The Lund University Swedish South Africa Expedition (1950–1951)

Lund University, Sweden, undertook a major collecting expedition to southern Africa in the early 1950s. The zoologist Bertil Hanström (1891–1969) organised the Expedition and acquired the necessary funding, but did not take part in the Expedition himself, although acting in the capacity of first editor for the results that followed. Instead he sent Per Simon Valdemar Brinck (1919–2013) (Figs 31, 33–36) and Gustaf Rudebeck (1913–2005) (Figs 29, 30, 32) to undertake the sampling. Brinck and Rudebeck had recently completed their PhDs at the University of Lund and this was their first appointment. Both were accompanied by their wives, Gunvor Brinck-Lindroth (Figs 29, 33, 34) and Inga Rudebeck (Fig. 29). The Expedition commenced in October 1950 and ended in August 1951. Extensive sampling was conducted in Botswana, Namibia, South Africa, Swaziland and Zimbabwe at a total of 356 sampling localities (see Brink & Rudebeck 1955; original maps I–V summarised in Fig. 37). Diptera were sampled using Malaise traps, sweep netting (Fig. 36) and other methods (Figs 32–35). The Expedition brought to Lund the largest collections of species and specimens ever received by the Zoological Institute, Lund.

Published chapters resulting from the Expedition represent one of the most significant collective bodies of taxonomic work on southern African Diptera. Results were published in 15 major volumes, as *South African animal life* (1955–1974), which included reviews of 56 families of Diptera: Acroceridae (Schlinger 1963), Agromyzidae (Spencer 1960), Asilidae (Hull 1967), Athericidae (Stuckenberg 1960), Bibionidae (Hardy 1960), Blephariceridae (Stuckenberg 1956), Bombyliidae (Hesse 1955, 1965), Calliphoridae (Zumpt 1959), Camillidae (Hackman 1960), Canacidae (Wirth 1960), Ceratopogonidae (de Meillon 1959*a*), Chironomidae (Freeman 1955*c*), Chloropidae (Sabrosky 1959), Coelopidae (Ardö 1964), Conopidae (Smith 1967*b*), Culicidae (Muspratt 1959), Curtonotidae (Hackman 1960), Diopsidae (van Bruggen 1961), Dolichopodidae (Vanschuytbroeck 1960), Drosophilidae (Hackman 1960), Empididae (Smith 1967*a*), Ephydridae (Wirth 1960; Cogan 1970), Fanniidae (Chillcott & Pont 1970), Heleomyzidae (Cogan 1970), Hippoboscidae (Bequaert 1959*b*; Jobling 1959), Keroplatidae (Matile 1974), Lonchaeidae (McAlpine 1960), Milichiidae (Cogan 1970), Muscidae (Paterson 1960), Mydidae (Bequaert 1959*a*), Nemestrinidae (Hull 1961), Oestridae (Cogan 1970), Phoridae (Beyer 1959), Pipunculidae (Hardy 1959*a*), Psychodidae (de Meillon 1955*b*; Satchell 1956), Ptychopteridae (Alexander 1964), Pyrgotidae (Vanschuytbroeck 1967), Rhagionidae (Stuckenberg 1960), Rhinophoridae (Zumpt 1959), Sarcophagidae (Zumpt 1959), Scathophagidae (Vockeroth 1958), Scatopsidae (Cook 1965), Scenopinidae (Cogan 1970), Sepsidae (Hennig 1960), Simuliidae (de Meillon 1955*a*), Sphaeroceridae (Hackman 1965), Stratiomyidae (Lindner 1959), Syrphidae (Hull 1964), Tabanidae (Oldroyd 1956), Tachinidae (Verbeke 1970), Tanyderidae (Alexander 1964), Tephritidae (Munro 1960), Thaumaleidae (Stuckenberg 1961), Tipulidae (Alexander 1964), Ulidiidae (Steyskal 1960) and Vermileonidae (Stuckenberg 1960).

Namibian bioinventory surveys (1997–2003)

Between 1997 and 2003 the National Museum of Namibia, Windhoek conducted an extensive bioinventory survey of the Diptera fauna of Namibia, mainly using Malaise traps and other passive sampling techniques. Sampling was conducted throughout the country and the Diptera collection was developed through staff training and the collection of high quality field-pinned specimens (Kirk-Spriggs 1998). Coverage of Diptera records for the country (based on then existing collection records and records generated through the survey), can be assessed by examining the combined records of Calliphoridae (incl. Rhiniidae) that were mapped by Kurahashi & Kirk-Spriggs (2006) (Fig. 39) for Namibia and for the genus *Curtonotum* Macquart (Curtonotidae) in the Afrotropical Region as a whole by Kirk-Spriggs & Wiegmann (2013) (Fig. 38). In this latter case, the outline of Namibia is clearly visible, due to the high density of symbols indicating records. These maps combined indicate that Namibia is now one of the better sampled countries for Diptera in the Afrotropics.

Material resulting from the survey was distributed to specialists and resulted in numerous published faunal reviews of the Namibian Diptera fauna, including: Acroceridae (Barraclough 2000), Bombyliidae (Greathead 2000*b*, 2006), Calliphoridae (incl. Rhiniidae) (Kurahashi & Kirk-Spriggs 2006), Dolichopodidae (Grichanov *et al*. 2006), Muscidae (Couri *et al*. 2012), Sepsidae (Ozerov 2000) and Tephritidae (Hancock *et al*. 2001, 2003). A series of publications also appeared dealing with specific Diptera genera in the families: Asilidae (*Habropogon* Loew; Londt 1999), Camillidae (*Katacamilla* Papp; Kirk-Spriggs *et al*. 2002), Chloropidae (*Apotropina* Hendel; Kirk-Spriggs *et al*. 2001*b*), Heleomyzidae (*Tephrochlamys* Loew; Woźnica 2001), Mythicomyiidae (*Doliopteryx* Hesse; Evenhuis 2000), Rhiniidae (*Thoracites* Brauer *et* Bergenstamm; Kurahashi 2001), Sarcophagidae (*Hoplacephala* Macquart; Pape 2006), Scenopinidae (*Cyrtosathe* Winterton & Metz; Winterton & Metz 2005), Sphaeroceridae (*Archicollinella* Duda; Kirk-Spriggs 2007*a*), Tachinidae (*Eomedina* Mesnil; Cerretti & Wyatt 2006) and Tephritidae (*Dacus* F.; Hancock & Drew 2001), *etc*. Material resulting from the survey continues to be examined by specialists and cited in taxonomic revisions and other faunal reviews, e.g., Kameneva & Korneyev (2016), Kirk-Spriggs & Wiegmann (2013), Korneyev (2015) and MacGowan (2005).

Biodiversity of the Brandberg massif, Namibia (1999–2000)

In 1999 the National Museum of Namibia initiated the Brandberg massif pilot inventory study, Namibia's highest mountain, situated on the edge of the Namib Desert. This was the first major study of its kind dealing with an African inselberg. Sampling was conducted using Malaise traps, pan traps, light traps and pitfall traps (see Marais & Kirk-Spriggs 2000 for details). Material was amassed from a number of separate sampling events.

Results of the Brandberg survey were published in a dedicated volume (Kirk-Spriggs & Marais 2000), which included accounts of 16 families of Diptera: Agromyzidae (Tschirnhaus *et al*. 2000), Bombyliidae (Greathead 2000*a*), Chloropidae (Ismay 2000), Chyromyidae (Ebejer 2000), Dolichopodidae (Grichanov 2000), Empidoidea (Sinclair 2000), Heleomyzidae (Woźnica 2000), Milichiidae (Swann 2000), Muscidae (Deeming 2000), Mythicomyiidae (Tschirnhaus *et al*. 2000), Pipunculidae (De Meyer 2000), Sciaridae (Vilkamaa 2000), Stratiomyidae (Tschirnhaus *et al*. 2000), Syrphidae (Whittington 2000), Tephritidae (Hancock 2000) and Therevidae (Tschirnhaus *et al*. 2000). Additional results were later published on the Vermileonidae (Stuckenberg 2000), Mythicomyiidae (Evenhuis 2001; Kirk-Spriggs & Evenhuis 2008) and Atelestidae (Sinclair & Kirk-Spriggs 2010).

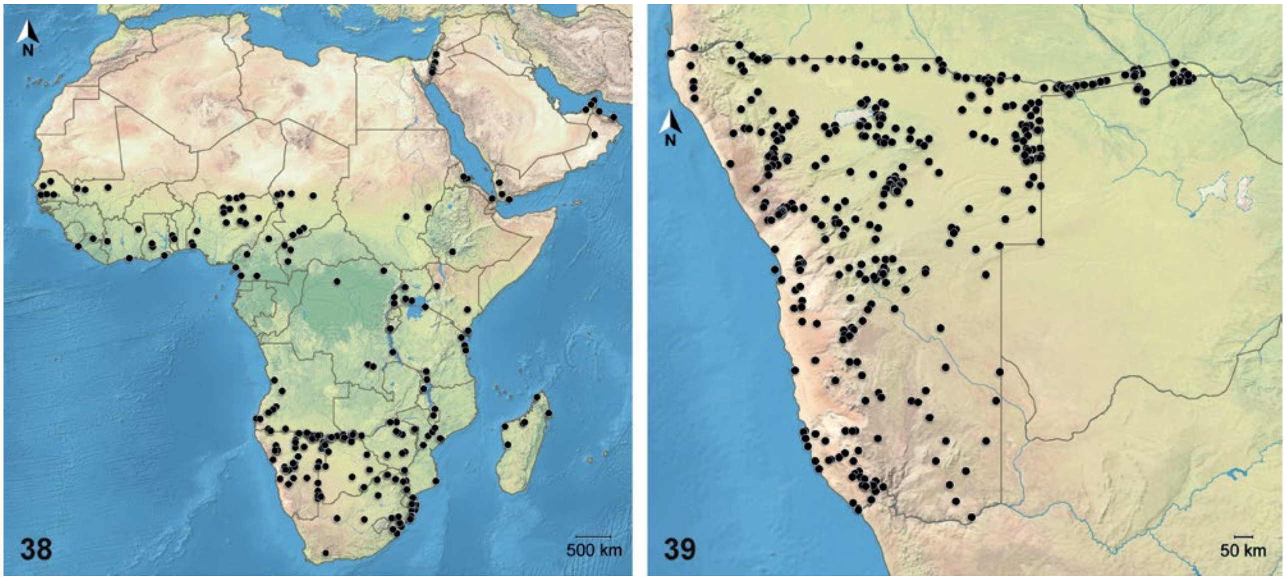
National Museum of Namibia's Marine-littoral Survey 1998

In 1998 the National Museum of Namibia, Windhoek (in collaboration with staff of Museum für Naturkunde der Humboldt-Universität zu Berlin, Germany), conducted an extensive survey of intertidal insects, focusing primarily on the sampling of the orders Diptera and Coleoptera (Figs 40, 41). Scientists that actively participated in the expedition were Eugène Marais (1959–living) (Expedition leader), Ashley Howard Kirk-Spriggs (1962–living) (both National Museum of Namibia, Windhoek) and Manfred Uhlig (1949–living) (Museum für Naturkunde, Berlin). Other participants were Barbara Uhlig, Jan Meeser, Wilferd Versfeld, Hannes Steyn and Nico Olivier. Diptera were sampled at 69 sampling stations (62 in Namibia and 17 in South Africa) (Fig. 47), from the Kunene River mouth on the Namibian/Angolan border to Tsitsikamma in the Eastern Cape Province, South Africa (see Kirk-Spriggs *et al*. 2001*a*, for full list of sampling stations). Samples were taken every 35 km on the northern half of the Namibian seaboard and at *ca* 150 km intervals on the South African seaboard. Due to problems with access to the Namibian Diamond Area samples could only be taken at limited sampling stations in the south of the country after the main survey was completed. Sampling concentrated on flies associated with kelp (Figs 42, 44–46) and Cape fur seal colonies (Fig. 43) and was mainly conducted using netting and searching. Adult flies were also reared from larvae and puparia sampled from kelp and beneath decomposing Cape fur seals.

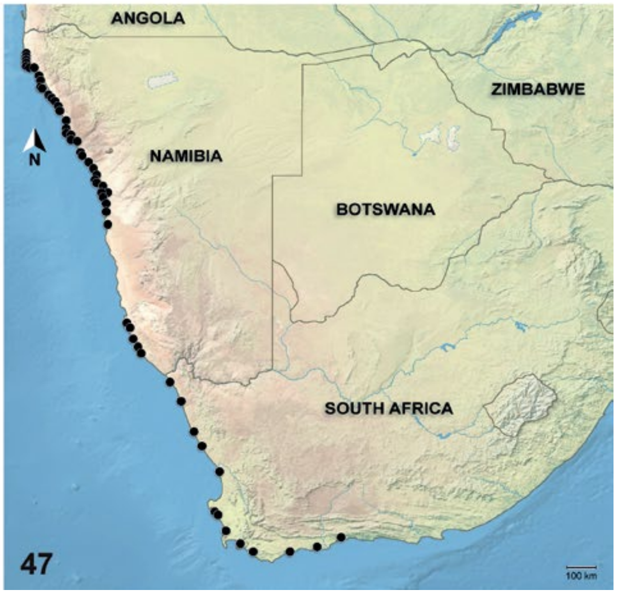
Results of the Diptera component resulted in four publications (Kirk-Spriggs 2003*a*, *b*, 2007*b*; Kirk-Spriggs *et al*. 2001*a*); Kirk-Spriggs *et al*. (2001*a*) dealing with ten families of flies and providing identification keys.

Arthropod Survey of Madagascar's Protected Areas

The *Arthropod Survey of Madagascar's Protected Areas* was initiated by Michael Edward Irwin (1940–living) (Figs 48, 78), of the University of Illinois, U.S.A. and Evert Irving Schlinger (1928–2014) in 1998 and was funded through the Schlinger Foundation. The main focus of the sampling effort is to generate extant material of the Diptera families Acroceridae and Therevidae, but the timescale and geographical range of the sampling conducted have resulted in the largest and most comprehensive collection of Diptera ever amassed from Madagascar. The project is coordinated within Madagascar by Rasolondalao Harin'Hala Hasinjaka (Rin'ha) (1972–living) (Figs 50, 51. 53) and operates under the auspices of MICET (Madagascar Institut pour la Conservation des environments Tropicaux). The project has been ongoing for 18 years (1998–2017) and is scheduled to end its collecting activities in another one or two years. Harin'Hala has liaised with local communities and overseen the deployment and maintenance of Malaise traps by local villagers (Fig. 50) and the sorting of samples, many to the family level (summarised in Fig. 52), by students from the University of Antananarivo (Fig. 51). The project involves the



Figs 1.38–39. Diptera distributions in Africa and Namibia: (38) plotted distribution records for the genus *Curtonotum* Macquart (Curtonotidae) in Africa; (39) plotted distribution records of Calliphoridae and Rhiniidae in Namibia. Fig. 38 (B.S. Muller; after Kirk-Spriggs & Wiegmann 2013, fig. 322; made with Natural Earth), Fig. 39 (B.S. Muller; after Kurahashi & Kirk-Spriggs 2006, fig. 45; made with Natural Earth).



Figs 1.40–47. National Museum of Namibia's Marine-littoral Survey 1998 (all Namibia, except Fig. 46): (40) campsite at Rocky Point (left to right: Barbara Uhlig, Nico Olivier, Eugène Marais, Wilferd Versfeld and Ashley Kirk-Spriggs); (41) on dunes at Bosluisbaai; (42) sampling sandy beach, Ugab River mouth; (43) sampling Diptera from seal carcass Kunene River mouth; (44) sampling Diptera (left) and Coleoptera (right), Kunene River mouth; (45) sampling from kelp on pebble beach, Möwe Bay; (46) sampling on rocky coast, West Coast National Park, South Africa; (47) map indicating 69 Diptera sampling stations. Figs 40–46 (courtesy B. & M. Uhlig; Museum für Naturkunde Berlin, Germany), Fig. 47 (B.S. Muller; after Kirk-Spriggs *et al*. 2001*a*, fig. 81; made with Natural Earth).

long-term monitoring of Diptera and other arthropods using Malaise traps, mostly in protected areas encompassing all of Madagascar's major biomes and vegetation types. Traps are serviced weekly and often maintained at a given site for a year or more. To date, 107 localities have been sampled (Fig. 55). All material has been collected directly into 96% ethanol making it, in many cases, suitable for DNA extraction. Sorted material has routinely been carried by scientists visiting Madagascar to the United States of America and to the California Academy of Sciences in San Francisco, where it is now managed and loaned to interested researchers throughout the world.

Additional sampling as part of the project was undertaken by M.E. Irwin (Fig. 78), E.I. Schlinger and Frank Downs Parker (1936–living) (over several years) and by Stephen Archer Marshall (1954–living) (in 2014), Martin Hauser (1967–living) (2004 and 2014), Stephen David Gaimari (1968–living) (2014) and A.H. Kirk-Spriggs (2007 and 2014).

From 1997–2000 Brian Lee Fisher (1964–living) and Charles Edward Griswold (1945–living) of the California Academy of Sciences, U.S.A., initiated the *Terrestrial Arthropod Inventory of Madagascar*, which aimed to document a broad range of

Figs 1.48–55. Arthropod Survey of Madagascar's Protected Areas: (48) M.E. Irwin (Project leader) clearing ox-cart trail, Analangidro dry forest, Melaky Region, 2007; (49) Townes-style Malaise trap, deployed at Ambakaka palm forest, Atsimo Andrefana Region, 2010; (50) R. Harin'Hala (far right) training local villagers in servicing Malaise traps, Ambovomamy secondary forest, Sofia Region, 2008; (51) sorting facility at Bibikely Biodiversity Center, with sorters from the University of Antananarivo (far right: R. Harin'Hala); (52) vials of Diptera sorted to family level; (53) R. Harin'Hala (local coordinator) at ValBio Research Station; (54) large baobab trees, Mitoho Forest (transitional), Atsimo Andrefana Region, 2008; (55) map of Madagascar, indicating 107 localities sampled during the survey. Figs 48–54 (photographs courtesy of M.E. Irwin), Fig. 55 (B.S. Muller; made with Natural Earth).

taxa, but with emphasis on ants (Hymenoptera: Formicidae) and spiders (Araneae). One of the project's seven primary goals was, however, to sort, curate and identify at least to morphospecies all species of the Diptera families Acroceridae and Therevidae, together with eight other diverse groups of invertebrates. This project has also generated a considerable amount of Diptera material, which, like that of the Irwin project, is housed in the California Academy of Sciences. Although organised and funded separately, these two projects are essentially linked by the fact that they share sorting facilities at the Bibikely Biodiversity Centre facility, located within the Tsimbazaza National Zoological Day-Night Park in Antananarivo.

Irwin *et al*. (2003) published an important assessment of the biodiversity of Diptera in Madagascar, based largely on results from these projects, and a total of 24 other publications that deal with Diptera generated through the *Arthropod Survey of Madagascar's Protected Areas* and the *Terrestrial Arthropod Inventory of Madagascar* have appeared to date, covering 13 families of Diptera: Asilidae (Dikow & Bayless 2009; Londt 2012, 2015), Bombyliidae (Maass *et al*. 2016), Conopidae (Couri & Barros 2010; Couri & Pont 2006; Stuke 2012, 2015), Curtonotidae (Kirk-Spriggs 2010*c*, 2011), Dolichopodidae (Capellari & Grichanov 2012), Muscidae (Couri 2008; Couri *et al*. 2006), Mycetophilidae (Hippa 2008), Mydidae (Kondratieff 2009; Kondratieff *et al*. 2005), Mythicomyiidae (Evenhuis 2007), Syrphidae (Lyneborg & Barkemeyer 2005; Reemer & Bot 2015; Ssymank 2010; Thompson & Hauser 2015), Tabanidae (Zeegers 2014), Therevidae (Hauser & Irwin 2005) and Vermileonidae (Stuckenberg 2002).

Eastern Arc Biodiversity Programme

This programme aims at exploring the invertebrate biota of Tanzania's Eastern Arc mountain range, and in particular, that of the Udzungwa Mountains, combining sampling and species inventories with the testing of specific ecological questions. The ancient forests of the Eastern Arc Mountains contain a unique biota, with a high degree of endemicity (*e.g*., Enghoff 2014) and as these mountains are sprinkled in a "sea" of savanna, the mountain range has been compared with the Galápagos Is., although the Eastern Arc biota is far more complex than that of the Galápagos (Scharff *et al*. 2015). The knowledge of the fauna of arthropods in Udzungwa is exceedingly sparse (Pape & Scharff 2015) and the Diptera fauna has so far received only very fragmentary treatment (*e.g*., Doczkal & Pape 2009; Kaae *et al*. 2015; Kirk-Spriggs 2010*d*).

Operations are based at the Udzungwa Ecological Monitoring Centre, with most activities taking place in the nearby Udzungwa Mountains National Park (1,990 km^2). Since 2013, local staff has continuously been trained for the collecting of both specimens and field data and various collecting protocols for arthropods in tropical forests have been tested and optimised for estimating local species richness (Malumbres-Olarte *et al*. 2016). Extensive Malaise trap samples have been deposited in the Natural History Museum of Denmark, but limited resources for sorting and mounting are impairing progress. A memorandum of understanding (MoU) has been established between Tanzania National Parks (TANAPA), the Natural History Museum of Trento, Italy and the Natural History Museum of Denmark, on the collaborative management and financing of the Udzungwa Ecological Monitoring Centre from 2017–2022. More specifically, this MoU will facilitate accommodation and logistic ground support (field assistants) for planned fieldwork as well as teaching (T. Pape, pers. comm. 2017).

United Arab Emirates Insect Project

The United Arab Emirates (UAE) Insect Project was initiated and sponsored by H.H. Sheikh Tahnoon Bin Zayed Al Nahyan and has been coordinated since its inception by the Dutch entomologist Antonius van Harten (1946–living) (Fig. 58), with the assistance of Khalid Mahmood (1977–living), who deployed traps and maintained the passive trapping programme (Fig. 57). Sampling methods adopted during the project include Malaise traps, light traps, pan traps, pitfall traps, sweep netting and the use of Berlese funnels. Passive sampling was undertaken at 36 localities (Fig. 62), representative of the diverse habitat types evident in the country (*e.g*., Figs 60, 61) (van Harten 2008). The survey material (aside from the pinned Lepidoptera) is preserved in ethanol and figures for August 2011 indicate a total of 13,520 samples. The project has involved the sorting and distribution of thousands of specimens to researchers throughout the world. Part of the insect material resulting from the project, termed the "UAE Invertebrate Collection", is housed in the Abu Dhabi Department of Environment, other specimens have been deposited in the institutions indicated in the various chapters.

An important aspect of the project has been inviting specialist entomologists to visit UAE and sample their respective groups of interest and the project received 33 visiting specialists from 14 countries between 2005 and 2011. Diptera specialists that visited UAE are: Thomas Pape (1960–living) (visited in 2005) (Fig. 59), Krzysztof Szpila (1974–living) (in 2005), John Christopher Deeming (1939–living) (in 2006), Frank Menzel (1960–living) (in 2007), Andreas Stark (1958–living) (in 2007 and 2010), M. Hauser (in 2008), Jens-Hermann Stuke (1967–living) (in 2008), Jaroslav Bosák (1965–living) (in 2008 and 2009), Milan Hradský (1930–living) (in 2008), Matthias Jaschhof (1963–living) (in 2009), Catrin Jaschhof (1966–living) (in 2009), Wayne Neilsen Mathis (1945–living) (in 2010), Tadeusz Zatwarnicki (1958–living) (in 2010) and Ruud van der Weele (1965–living) (in 2011) (A. van Harten, pers. comm. 2017).

Results of the Diptera component of the survey have been published in six volumes of *"Arthropod Fauna of the UAE"* (2008–2017), which included accounts of 50 families of Diptera: Anthomyiidae (Deeming & van Harten 2014), Anthomyzidae (Deeming 2008*b*), Asilidae (Bosák & Hradský 2011; Bosák *et al*. 2014), Asteiidae (Deeming 2010*b*), Bibionidae (Deeming 2009*a*), Calliphoridae (incl. Rhiniidae) (Deeming 2008*d*), Canacidae (Munari 2008, 2010), Carnidae (Deeming 2017), Cecidomyiidae (Harris & van Harten 2010; Jaschhof & Jaschhof 2011), Ceratopogonidae (Szadziewski *et al*. 2011), Chamaemyiidae (Raspi 2008), Chironomidae (Andersen & Mendes 2010; Giłka 2009), Chloropidae (Deeming 2011), Chyromyidae (Ebejer 2008), Conopidae (Stuke 2008*a*; 2017), Corethrellidae (Giłka & Szadziewski 2009), Curtonotidae (Kirk-Spriggs 2008), Diopsidae (Hauser *et al*. 2011), Dolichopodidae (Gatt 2014; Naglis 2014; Naglis & Bickel 2017), Drosophilidae (Sidorenko & Nakonechnaya 2010), Empididae (Chvála & Stark 2011; Plant 2009), Ephydridae (Mathis *et al*. 2017), Heleomyzidae [Trixoscelidinae treated as separate family below] (Woźnica 2008), Hippoboscidae (Deeming 2009*c*), Limoniidae (Hancock 2011), Lonchaeidae (MacGowan 2008), Milichiidae (Deeming 2017), Muscidae (Deeming 2008*c*), Muscomorpha (Schuster & Deeming 2011),

Figs 1.56–62. United Arab Emirates Insect Project: (56) Townes-style Malaise trap, deployed at Wadi Wurayah; (57) project assistant Khalid Mahmood (1977–living), deploying yellow pan traps at Wadi Wurayah; (58) project coordinator Antonius van Harten (1946–living); (59) Thomas Pape (1960–living) in mangroves north of Ajman (one of 14 visiting dipterist specialists who participated in the project); (60) trapping locality Ar-Rafah; (61) trapping locality Wadi Wurayah; (62) map indicating localities where traps were deployed (original data from van Harten 2008). Figs 56–61 (photographs courtesy A. van Harten), Fig. 62 (B.S. Muller; made with Natural Earth).

Mydidae (Deeming 2008*a*; Dikow 2010), Mythicomyiidae (Evenhuis 2009), Nemestrinidae (Deeming 2009*b*), Odiniidae (Gaimari 2011), Oestridae (Deeming 2009*e*), Phoridae (Disney 2008), Psychodidae (Ježek & van Harten 2009), Rhagionidae (Deeming 2010*a*), Rhinophoridae (Zeegers 2008), Scathophagidae (Deeming 2009*d*), Scenopinidae (Ebejer 2009), Sepsidae (Stuke 2008*b*), Sphaeroceridae (Gatt 2008), Stratiomyidae (Hauser 2008, 2014), Syrphidae (Smit *et al*. 2017), Tabanidae (Ježek *et al*. 2017), Tachinidae (Zeegers 2010), Tephritidae (Merz 2008, 2011), Therevidae (Hauser 2017), Trixoscelididae [now treated as subfamily of Heleomyzidae] (Woźnica 2009) and Ulidiidae (Kameneva & Korneyev 2010).

Boyekoli Ebale Congo Expedition 2010

In 2010, three Belgian consortium institutions: the Royal Museum for Central Africa, the Royal Belgian Institute of Natural Sciences and the National Botanical Garden of Belgium, in collaboration with the University of Kisangani (UNIKIS), Democratic Republic of Congo, organised the multidisciplinary *Boyekoli Ebale Congo Expedition* (meaning study of the Congo River), on the Congo River in Democratic Republic of Congo. This Expedition represented one of Europe's major initiatives to celebrate the *International Year of Biodiversity* in 2010. Thirty-six non-Congolese scientists, mainly Belgians, took part in the Expedition over a period of two months (May–June 2010). Other Expedition scientists originated from France, Germany, Hungary, Italy, the Netherlands, South Africa and the United States. Subjects studied included aquatic insects, archaeology, biogeochemistry, botany, entomology, fishes and their parasites, geology, cartography, herpetology, limnology, linguistics, mammals and their parasites and organic pollutants. Congolese scientists and students worked closely with foreign researchers to facilitate collaboration and allow for skills transfer (Kirk-Spriggs 2010*a*, *b*).

Four dipterists took part in the Expedition: Rudolf Meier (1963–living) (Fig. 66), who was studying the behaviour of Sepsidae; A.H. Kirk-Spriggs who was sampling Diptera in general (especially Curtonotidae); Patrick [Joseph Maurice] Grootaert (1952–living), who was studying Empidoidea; and Massimiliano Virgilio (1970–living), who was engaged in studies of economically important Tephritidae (Fig. 67). The Expedition was split into two phases, with Grootaert and Virgilio participating in May and Meier and Kirk-Spriggs in June. The Expedition traversed the Congo River in two baleinières (the Congolese name for locally built wooden boats) (Figs 63, 64) from the town of Bumba to Kisangani (Fig. 68), stopping en route for up to 10 days to allow for sampling. Sampling was conducted using Malaise traps, baited hanging traps, sweep netting (Fig. 65) and hand collecting.

Results of the Expedition have not been published collectively, but some publications resulting directly from the dipterological sampling have already appeared, *e.g*., Dolichopodidae (Grichanov *et al*. 2011), Hybotidae (Grootaert & Shamshev 2013*a*, *b*, 2014*a*, *b*), Sepsidae (Zhao *et al*. 2013), Tephritidae (Virgilio *et al*. 2011, 2013) and material sampled during the Expedition continues to feed into larger regional revisions, *e.g*., Couri & Pont (2014), Couri *et al*. (2013), Kameneva & Korneyev (2016), O'Hara & Cerretti (2016), *etc*.

International Survey of Afrotropical Diptera (National Museum, Bloemfontein)

Vast tracts of the Afrotropics remain under-sampled for Diptera (*e.g*., Fig. 38). The National Museum, Bloemfontein (now the largest non-specialised collection of Diptera in the region), has been undertaking extensive sampling of Diptera in various African countries in the past eight years, which was formalised as the "*International Survey of Afrotropical Diptera*" in 2017. This survey is being conducted in order to generate high quality pinned specimens for systematic study and to build a comprehensive collection of Afrotropical Diptera based in Africa.

Sampling is organised by staff of the National Museum and involves scientific engagement with other international institutions around the world, with two or three fieldtrips organised each year. Sampling is mainly conducted using Malaise traps (*e.g*., Figs 69, 72, 73), but sweep netting, baited hanging traps, pan traps and light traps are also deployed. To date fieldtrips have been conducted in Benin, Burundi, Cameroon, Democratic Republic of Congo, Kenya, Réunion Is., Madagascar, Malawi, Mauritius, Namibia, South Africa (Eastern and Western Cape, Free State, Mpumalanga, KwaZulu-Natal Provinces), Togo and Zambia. Material is distributed to specialists around the world for identification and description.

Diptera of the Mascarene Islands

In 2015 the National Museum organised a month-long expedition to Réunion Is. in the Indian Ocean (Figs 71–73, 75), with the original intention of publishing a series of papers in a dedicated volume dealing with the Diptera of the island. This project was expanded in 2016 to become "*The Diptera (Insecta) of the Mascarene Islands*". Sampling was conducted in pristine forest habitats in Mauritius in 2016 (Figs 69, 70, 76); and a more extensive month-long survey of the lowlands of Mauritius (including Round Is.) and Rodrigues Is. is planned in 2018. So far the project has involved A.H. Kirk-Spriggs (Project coordinator), Gunnar Mikalsen Kvifte (1987–living) (Réunion Is. and Mauritius), Martin John Ebejer (1953–living), Kurt August Maria Jordaens (1970–living) (Réunion Is. only), Burgert Smith Muller (1983–living) and S.A. Marshall (Mauritius only). Sampling is mainly conducted using Malaise traps (Figs 69, 72, 73), baited hanging traps, pan traps, fruit fly traps (Fig. 70) and by sweep netting. Specialist collecting of the families Syrphidae (*e.g*., Fig. 74), Psychodidae and Micropezidae has also been carried out. Specimens are mainly field-pinned, with spirit material preserved in 96% ethanol and suitable for DNA extraction. Sorted material is distributed to specialists and a dedicated volume in a new "*Memoirs of Afrotropical Dipterology*" series to be published by the National Museum is planned in the future.

Suggested future priority surveys and ways forward

Given ever-increasing habitat destruction in the Afrotropics, due to subsistence farming and urban development, it is important to determine priority areas where Diptera sampling needs to be urgently conducted. The last remaining West African rainforests (identified as one of Africa's biodiversity hotspots; Myers *et al*. 2000) are rich in endemic species, are under serious threat and require dedicated sampling. The more tropical Angolan section of the Great Escarpment remains poorly sampled and Angola's tropical inselbergs remain entirely unknown. Afromontane forests associated with the Great Rift Valley in East Africa are seriously under threat and require urgent sampling efforts. Intertidal Diptera of the West and East Africa seaboards (including Madagascar) remain virtually unknown and require surveying, and the highly fragmented coastal forests of East Africa (identified of as one of Africa's biodiversity hotspots; Myers *et al*. 2000) also require urgent sampling.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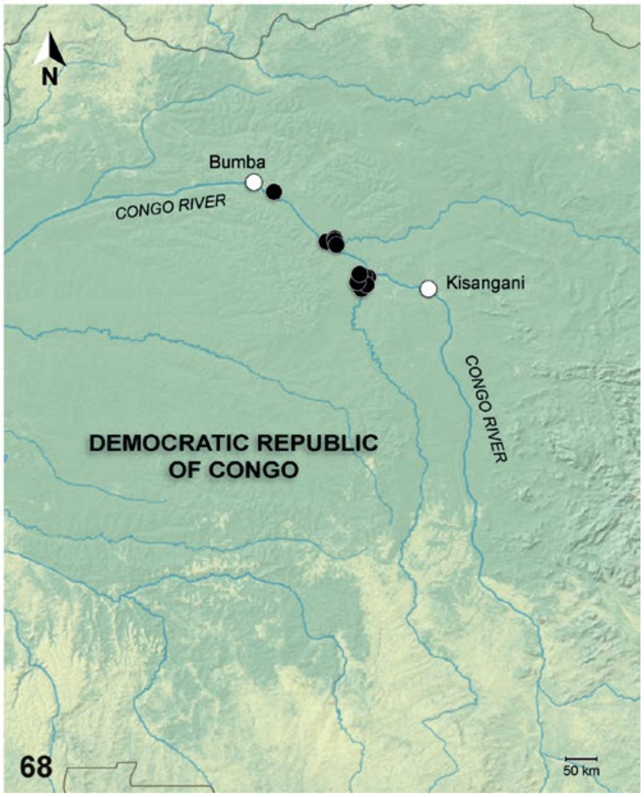
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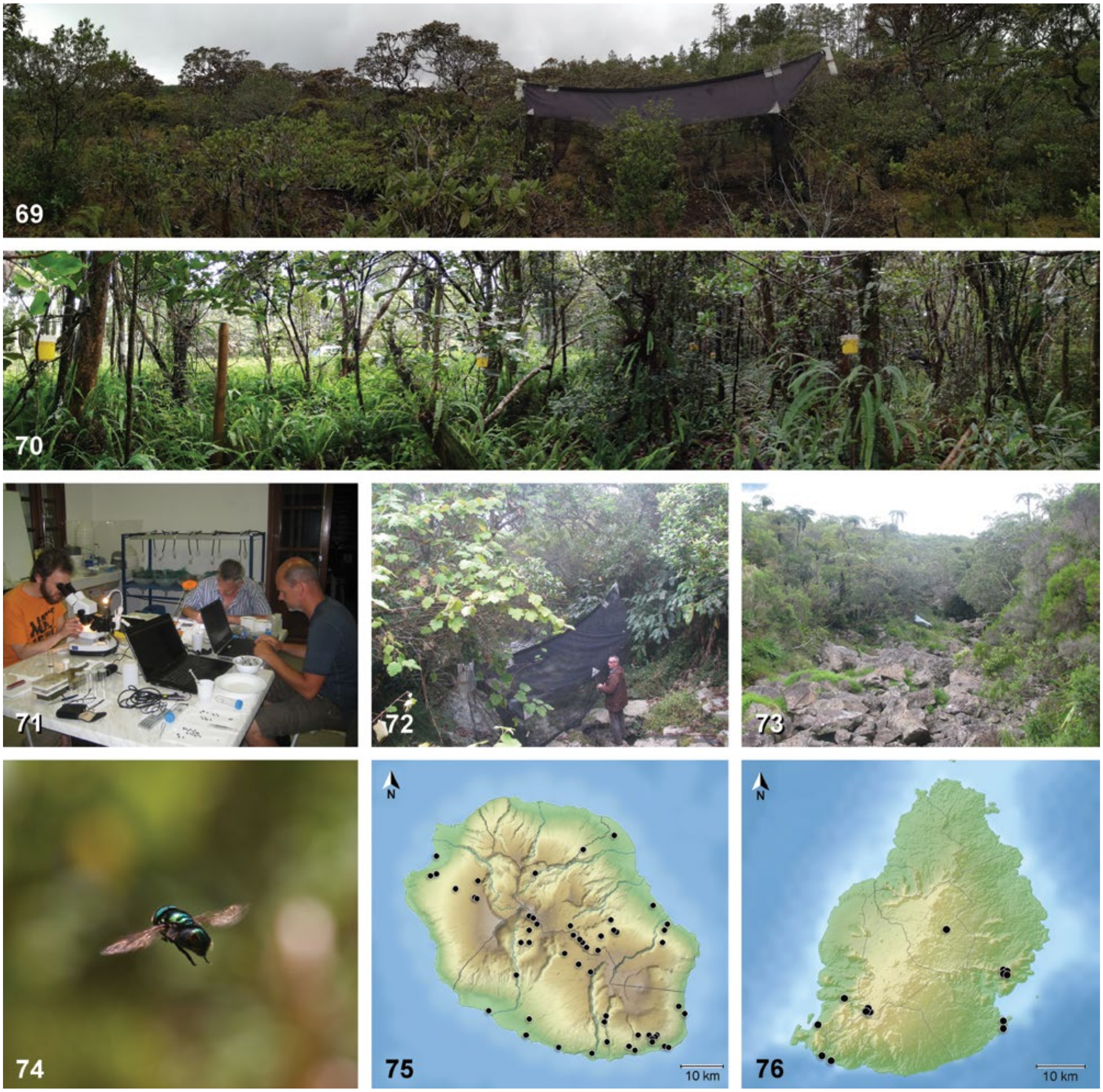
Figs 1.63–68. Boyekoli Ebale Congo Expedition 2010: (63) one of two wooden baleinières used to transport scientists on the Congo River; (64) working conditions on board the baleinières while moored; (65) sweep netting at Lieki village; (66) Rudolf Meier (1963–living); (67) (left to right) Ashley Howard Kirk-Spriggs (1962–living), Patrick Joseph Maurice Grootaert (1952–living) and Massimiliano Virgilio (1970–living); (68) map of Democratic Republic of Congo, indicating route followed and Diptera sampling stations. Figs 63, 64, 66 (photographs A.H. Kirk-Spriggs), Fig. 65 (photograph courtesy K. Pannecoucke), Fig. 67 (photograph R. Meier); Fig. 68 (B.S. Muller; made with Natural Earth).

There is a need for dedicated Diptera expeditions to targeted habitats and selected African mountains. A more coordinated effort is required to arrange large sampling efforts in the Afrotropics and such efforts should lead to dedicated publications. Passive sampling protocols need to be standardised to allow for comparisons of surveys (e.g., the Brandberg massif model) and, finally, there is a need for establishment of an *African Diptera Sorting Facility* that can process samples generated through surveys in Africa and distribute these to specialists.



Figs 1.69–76. Diptera Survey of Mascarene Islands: (69) Gressitt & Gressitt-style Malaise trap, upland heath forest, Pétrin, Mauritius; (70) fruit fly lure traps, Macchabée Forest, Mauritius; (71) laboratory at Mare Loungue Research Station, La Réunion (left to right: G.M. Kvifte, A.H. Kirk-Spriggs and K.A.M. Jordaens); (72) Malaise trap in gully, Bois de Sans Souci, La Réunion; (73) riverbed, Bras Chansons, La Réunion; (74) *Ornidia obesa* (F.) (Syrphidae) common on both islands; (75) map of La Réunion indicating sampling stations; (76) map of Mauritius indicating sampling stations. Figs 69, 70 (photographs courtesy B.S. Muller), Fig. 71 (photograph courtesy M.J. Ebejer), Figs 72, 74 (photographs courtesy G.M. Kvifte), Fig. 73 (photograph A.H. Kirk-Spriggs), Figs 75, 76 (B.S. Muller; http://www.mapsland.com).

Biographies of twelve leading Afrocentric dipterists

There are several dozen dipterists (living and deceased), who have made very substantial and lasting contributions to our knowledge of Afrotropical Diptera. The following 12 have been selected based on contributions to specific areas of dipterology, *i.e.*, agricultural and veterinary pests and vectors, human disease vectors, biological control, biology and behaviour, taxonomy and biogeography.

Ernest Edward Austen (1867–1938) (inset) was born in the United Kingdom and was educated at Rugby School, where his enthusiasm for natural history was already so marked as to isolate him somewhat from his school fellows. He attended the University at Heidelberg, Germany and in 1889 joined the staff of the British Museum (Natural History) (now the Natural History Museum, London, U.K.), where he was put in charge of the Diptera collection, serving as Keeper of Entomology from 1927 until his retirement in 1932. He travelled to Brazil as naturalist on the cable ship *Faraday* (1895–1896) and collected insects in Brazil and in 1899 travelled with Sir Ronald (then Major) Ross (1857–1932) (of the Liverpool School of Tropical Medicine) to study mosquitoes in Sierra Leone, West Africa. From there he travelled to South Africa and served as City Imperial Volunteer (C.I.V.) in the Anglo Boer War. At the onset of WWI he was called up and served as company commander in the Artist's Rifles, but following a short spell in France, was transferred to the Egyptian Expeditionary Force. Aside from his official duties on malarial and fly control work in Palestine, which gained him the Distinguished Service Order (D.S.O.), he made an extensive collection of Diptera in the country. This material was not worked up until after his retirement, when he published "*The Bombyliidae of Palestine*" in 1937. On his return from the Anglo Boer War he concentrated his attention on blood-sucking flies, publishing his "*Monograph of the* tsetse *flies*" in 1908, "*Handbook of the* tsetse *flies*" in 1911 and "*The British bloodsucking flies*" in 1906. He served on the Council of the Zoological Society of London, U.K. and was at one time Vice-President of the Royal Society of Tropical Medicine and Hygiene. An obituary was published by Blair (1938), on which these notes are based. Photograph courtesy N.L. Evenhuis.

David Andrew Barraclough (1958–living) (inset; Fig. 81) was born in Johannesburg, South Africa and graduated from Maritzburg College. He enrolled at the University of Natal, Pietermaritzburg, South Africa in 1978, being awarded a BSc (Honours) degree in 1982 and an MSc degree in 1984. He took up the position of Curator of Entomology at the Natal Museum (now KwaZulu-Natal Museum) in 1982; a position he held until 1985, when he left South Africa to pursue a PhD at the University of New South Wales, Sydney, Australia. He was awarded a PhD in 1990, for a thesis entitled "Systematics of the Australasian Dexiini (Diptera: Tachinidae), exclusive of *Prosena* Le Peletier & Serville". He returned to South Africa and the Natal Museum in 1990 as Head of Department of Entomology and in 1996 became Head of Department of Arthropoda (an amalgamation of the Entomology and Arachnology Departments), a post he held until his resignation in 2002. From 2002 to 2014 he worked part-time as an Honorary Research Fellow in the School of Biological Sciences (now Life Sciences) at the University of KwaZulu-Natal, Durban. Whilst at the Natal Museum he was Assistant Editor (1990–1994) and later Editor (1994–2002) of the *Annals of the Natal Museum* (now *African Invertebrates*) and the *Natal Museum Journal of Humanities* (now *Southern African Humanities*). Barraclough has made outstanding contributions to the taxonomy, systematics and biogeography of Diptera, particularly pertaining to Southern Africa and the Afrotropical Region, although he has also published on the faunas of North America, the Arabian Peninsula and Australasia. He is a world authority on the systematics of more than 10 families of Diptera and has published on the following families (numbers of publications in parentheses): Acroceridae (7); Anthomyzidae (1); Aulacigastridae (1); Bombyliidae (1); Camillidae (12); Carnidae (1); Clusiidae (2); Ctenostylidae (3); Diastatidae (3); Micropezidae (5); Muscidae (1); Natalimyzidae (2); Nemestrinidae (5); Neminidae (1); Neriidae (2); Odiniidae (1); Oestridae (formerly Gasterophilidae) (1); Opomyzidae (1); Sciomyzidae (3); Tachinidae (18); and Ulidiidae (2). At the end of 2006, with David Kendray McAlpine (1934–living), he described a new family of acalyptrate Diptera, the Natalimyzidae and the systematics, biogeography and biology of Southern Africa's long-proboscid genera of Nemestrinidae have remained one of his major research interests for the past 10 years. At the time of writing (February 2017), he is engaged in revisions/reviews of the nemestrinid genera *Moegistorhynchus* Macquart and *Prosoeca* Schiner (D.A. Barraclough, pers. comm. 2017). Photograph courtesy KwaZulu-Natal Museum.

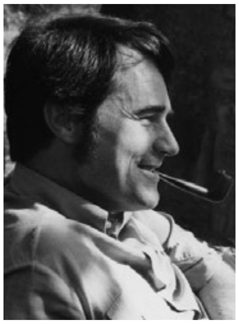
Alexander Cuthbertson (1901–1942) (inset) was born in Glasgow, Scotland, U.K. He was educated at the West of Scotland Agricultural College, where he obtained a Diploma in Agriculture. In June 1926 he joined the Department of Agriculture, Salisbury in Southern Rhodesia (now Harare, Zimbabwe). He was a keen naturalist, interested in insects and birds and he took up the study of the Tipulidae (crane flies) of western Scotland while still at college. After joining the Rhodesian Department of Agriculture he broadened his taxonomic and biological interests, taking up studies of higher groups of Diptera, making considerable progress, particularly in a series of papers during the 1930s, dealing with the biology, habits and immature stages of the Diptera of Zimbabwe, many of which still represent the only Afrotropical studies of their kind. He was also involved in early studies of Mt Chirinda and donated 130 specimens from there to the British Museum (Natural History) (now the Natural

History Museum, London, U.K.) in 1930. As an avid insect collector he was eventually made curator of the entomological collections. His publication record is not extensive, probably due to his short life, and mainly covers Muscidae, Tachinidae and agents of myiasis. He was more interested in behaviour and immature stages and showed little inclination towards describing species. He kept up a voluminous correspondence with researchers around the world, however, and distributed material freely to museums elsewhere in Africa and around the world, including the Iziko South African Museum, Cape Town, South Africa, the Commonwealth Agricultural Bureau (now housed in the Natural History Museum), the Hunterian Museum, University of Glasgow, U.K. and the National Museum of Natural History, Washington D.C., U.S.A. Cuthbertson died suddenly in July 1942 in his laboratory following a period of work-related stress and army manoeuvre exertions. The esteem in which he was held by his peers is reflected in 45 African Diptera taxa being named in his honour. Most of these eponymic taxa (representing 15 families), were named prior to his death, but a significant number have appeared afterwards, the most recent being an asilid in 2004. The insect collection of the former Department of Agriculture, Salisbury, which includes the bulk of Cuthbertson's Diptera material, now forms part of the collections of the Plant Protection Research Institute, Harare, Zimbabwe (see below). A short obituary was published by Munro (1942) and a forthcoming paper providing a biographical account of his life is in preparation (Hancock & Moore in prep.), on which these notes are based. Photograph Smithsonian Institution Archives (image SIA2017-020132).

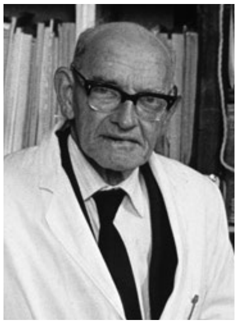
John Christopher Deeming (1939–living) (inset) was born in 1939 at Potters Bar, Hertfordshire, U.K. Following schooling at Potters Bar and obtaining his General Certificate of Education, he was appointed as Scientific Assistant in the Entomology Department of the British Museum (Natural History) (now the Natural History Museum, London, U.K.), in October 1955. His first two years at the Museum (1955–1956) were spent as an Assistant in Entomology and the remaining eight (1957–1964) in the Diptera Section. During this latter period he assisted H. Oldroyd and his visitors to the section, documented, identified and incorporated material, undertook fieldwork in Britain and Europe and published some research, mainly on Sphaeroceridae, under the tutelage of Owain Westmacott Richards (1901–1984). This period (1965–1966) also included two years National Service as a gunner in the British Army on the Rhine in Germany (1959–1961). In January 1966, he moved to Nigeria to take up the position of Entomologist in the Department of Crop Protection, Institute for Agricultural Research of the Ahmadu Bello University, Samaru, Nigeria. His main duties were the building of a comprehensive insect collection for use in research and teaching, undertaking extensive fieldwork throughout (the former) Northern Region and providing identification services and advice to the Ministry of Agriculture. He also engaged in training of field and laboratory staff, undertook research on shoot flies and cotton pests, held field trials, undertook locust scouting and visited areas of pest outbreaks; and during the yellow fever outbreak of the Nigerian Civil War (also known as the Biafra War 1967–1970), he carried out a mosquito survey. He also undertook editorial work for the Entomological Society of Nigeria and in the late 1970s, taught an insect taxonomy course to MSc students. He returned to the United Kingdom in December 1979, initially spending six months writing up research on Afrotropical Chloropidae, funded through a grant from the Inter-University Council for Higher Education Overseas. He was appointed as Research Assistant in the Department of Zoology, National Museum of Wales, Cardiff, U.K. in 1980, where he was employed until his retirement in 2006. His main duties entailed collection curation, identification and research, principally on the Diptera and Hemiptera. He has undertaken extensive fieldwork in Cyprus, France, Gambia, Greece, Hungary, Ibiza Is., Italy, Kenya, Lebanon, Malta, Nigeria, Oman, Saudi Arabia, Tunisia and the United Kingdom. He was awarded a PhD by the University of Wales College, Cardiff in 1998, for a thesis entitled "Taxonomy of cyclorrhaphous Diptera associated with cereals and grasses in Africa and Arabia". Since retirement he has co-edited the six published volumes of "*Arthropods of the UAE*" and in the same series was author on papers dealing with the families: Anthomyzidae, Calliphoridae, Muscidae and Mydidae (in Volume 1); Bibionidae, Hippoboscidae, Nemestrinidae, Oestridae and Scathophagidae (Volume 2); Asteiidae (Volume 3); Chloropidae, Diopsidae and cyclorrhaphous Diptera associated with vertebrates (Volume 4); Anthomyiidae (Volume 5); and Carnidae and Milichiidae (Volume 6). He is well known for his encyclopaedic knowledge of Diptera and his main research focus has been taxonomic studies of *Atherigona* Rondani and Chloropidae shootflies, Milichiidae and Sphaeroceridae. He has published over 100 scientific contributions, dealing with 27 Diptera families and has described 146 species of Diptera (J.C. Deeming, pers. comm. 2017). Photograph courtesy A. Deeming.

Michael Chidozie Dike (1954–2015) (inset) was born in 1954 to the family of Chief Michael Chukwukere Dike at Ubaha-Orodo, Owerri in Imo State, Nigeria. He schooled at Trinity High School, Oguta, where he obtained his WASC (grade one) certification and a General Certificate of Education (as an external candidate of the University of London, U.K.) in 1971. He then enrolled at the University of Nigeria, Nsukka, where he obtained a BSc degree in Zoology in 1978, going on to obtain an MSc degree in Plant Protection from Ahmadu Bello University, Samaru, Nigeria in 1983. It was around this time that he developed an active interest in the taxonomy of *Atherigona* Rondani (Muscidae) shootflies of economic importance. He travelled overseas and studied for a PhD at the University of Wales College, Cardiff, U.K., under the tutelage of J.C. Deeming (see biography above), being awarded the degree in 1987, for a thesis entitled "Taxonomic studies on Afrotropical shootflies of the genus *Atherigona* Rondani (Diptera: Muscidae)". He also obtained a certificate in Insect Taxonomy from the Commonwealth Institute of Entomology, London, U.K. in 1981. Upon his return to Nigeria he held two brief positions as Tutor, School of Health Technology, Kaduna (1978–1979) and Senior Biology Master, Abbot Boys Secondary School, Ihiala (July–September 1979), before being appointed as Graduate Assistant at Ahmadu Bello University in 1979. He then rose through the ranks to become Professor of Entomology and Insect Taxonomy in 1997, a position he held until his death in 2015. He taught several courses at undergraduate and graduate levels in the Department of Crop Protection and supervised numerous postgraduate students. He further served as Head of Department of Crop Protection (2000–2004), Deputy Dean (2005–2007) and later Dean of the Faculty of Agriculture (2009–2011). He was also responsible for the Diptera collection of the Institute for Agricultural Research Samaru, which is administered through Ahmadu Bello University (see below). He published over 100 publications on diverse topics in applied entomology, but his most significant contribution to dipterology was his published research on *Atherigona*. In 1989 he published two papers, one a key to the males of Afrotropical species of the subgenus *Atherigona sensu stricto* and included the descriptions of new species and the other describing new species. He published a key to males of Nigerian species in 1990 and an identification key to males of the subgenus *Acritochaeta* Grimshaw in the same year. He also published on ultrastructure of the male trifoliate process in 1992, intraspecific variability in *A. lineata* Adams in 1994 and morphometric discrimination between two populations of *A. tomentigera* Emden in 1996. He died tragically in a car accident in northern Nigeria in 2015. Dike was one of very few practicing Diptera taxonomists in Africa based outside of South Africa. An order of funeral service was compiled by Akpa (2015), on which these notes are largely based. Photograph courtesy O. Banwo.

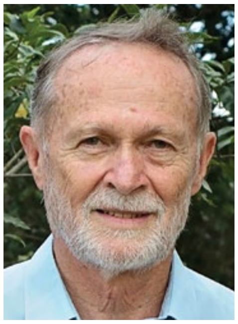
Botha de Meillon (1902–2000) (inset) was born in Prieska in the Northern Cape Province of South Africa. He attended the University of Witwatersrand, Johannesburg, South Africa and was one of the first to graduate with a BSc (Honours) degree in 1925. He joined the South African Institute for Medical Research, Johannesburg (SAIMR) in 1926 and obtained an MSc degree in 1926 and a DSc in 1934, the last for his outstanding work on the taxonomy of anopheline mosquitoes of South Africa. He became head of the Department of Medical Entomology (SAIMR) in 1930, a position he held until his retirement in 1962. Following his retirement, he worked for the World Health Organization in Brazzaville, Congo (now Republic of Congo), on malaria and in Rangoon, Burma (now Yangon, Myanmar), on filariasis. His last formal appointment (1965–1973) was to lead the United States Army Mosquito Project, administered by the Smithsonian Institution, Washington D.C., U.S.A. (later to become the South-East Asia Mosquito Project and then the Walter Reed Biosystematics Unit). He also undertook several consultancies in South Africa and for the United States Department of Agriculture, after which he worked mainly from home. His career spanned 70 years from 1926 to 1996, during which time he published 213 journal articles, books and book chapters. During his long career he received numerous awards and honours and his impact on the scientific discipline of medical entomology was immense. He is widely regarded as one of South Africa's most influential dipterists, producing the standard taxonomic works on African Anophelinae (Culicidae), Simuliidae, Siphonaptera and Ceratopogonidae. Other groups that received his attention were Culicinae mosquitoes, sandflies, myiasis-producing flies, ticks, bedbugs, snails and schistosomiasis. His extensive Diptera collection formed part of the now defunct SAIMR collection, which was transferred to the National Institute for Communicable Diseases, Johannesburg, South Africa (see below). An obituary was published by Coetzee (2001), on which these notes are based. Photograph courtesy M. Coetzee.



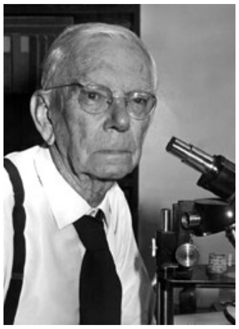
David John Greathead (1931–2006) (inset) was born in Kensington, London, United Kingdom. His childhood was divided between the United Kingdom and South Africa, where he attended St. Andrew's Preparatory School from 1940–1945. After his return to the United Kingdom he completed his schooling at Merchant Taylors' School. He followed his passion for entomology and graduated from the University of London's Imperial College of Science and Technology (now Imperial College London, U.K.), with a BSc in Zoology in June 1953 and was later awarded a PhD and a DSc. In 1953 he was recruited by Dr (later Sir) Boris Uvarov (1886–1970) to work at the Desert Locust Survey (DLS). During this time he was involved in fieldwork and research in Ethiopia, Somalia, Kenya and the then Aden Protectorate (now part of Yemen), rearing numerous Diptera of different families from damaged locust egg pods and publishing results. He joined the Commonwealth Agricultural Bureaux (CAB, now Centre for Agriculture and Biosciences International) in 1962 to set up their first African base with the founding of the Commonwealth Institute of Biological Control (CIBC) East African Station at Kawanda Research Station in Uganda. From East Africa he moved back to the United Kingdom in 1973, later becoming Assistant Director and then Director of the International Institute of Biological Control (IIBC) (formerly CIBC), retiring from IIBC in 1991, but continuing in association with the Centre for Population Biology, Imperial College, to be actively engaged in bombyliid taxonomic research up to the time of his death. He was an expert on biological control of insect pests and weeds and notably a world authority on the taxonomy of Bombyliidae (bee flies) and Nemestrinidae (tangled-veined flies), of which he had an incredible knowledge, publishing extensively on the Afrotropical fauna. Some of his early insect material was originally deposited in the Natural Resources Institute, London, U.K., which was donated to the Natural History Museum, London, U.K. in 1997 (see above). Other portions were donated up until 2008. A detailed obituary was published by Murphy & Cock (2007), on which these notes are based. Photograph courtesy S.K. Gess.



Albert John Hesse (1895–1987) (inset) was born in Potchefstroom, South Africa where he received part of his schooling (1904–1909). He studied further at Wellington (1909–1913) and attended the South African College School in Cape Town and graduated from Boy's High School, Stellenbosch in 1915. He enrolled at the South African College (now the University of Cape Town) in 1916, continuing his studies in 1917 at Transvaal University College, Pretoria, majoring in chemistry, zoology and geology and qualifying with a BSc (Honours) degree in 1918. He then continued his studies at Edinburgh University, Scotland, U.K. and in 1922 received a PhD in Zoology and Parasitology. His field of subsequent study at the School of Tropical Medicine, London, U.K., was helminthology. He took up the post of field assistant to the Director of the Calcutta Museum, India in 1921 and for a short period in the same year was Honorary Assistant Parasitologist at the Zoological Gardens, Regents Park, London, U.K. On his return to South Africa, he was unsuccessful in securing a position as parasitologist at Onderstepoort Institute of Veterinary Science (now Onderstepoort Veterinary Institute), and instead joined the South African Museum (now Iziko South African Museum) as an entomologist in 1924. His entomological interests were very broad, ranging from forensic entomology to detailed studies of Hemiptera, Coleoptera, Hymenoptera and notably Diptera. He undertook field expeditions in the Karoo and Cape Province of South Africa and in South West Africa (now Namibia). Of his 50 publications, the most significant are his revisions of southern African Bombyliidae (bee flies) and Mydidae (Mydas flies), on both of which he was recognised as an international authority. He retired from the South African Museum in 1974, after 51 years of unbroken service and was awarded a DSc *honoris causa* by the University of Stellenbosch. An obituary and list of publications was published by Robertson & Whitehead (1989), on which these notes are largely based. Photograph © Iziko Museums of Cape Town.

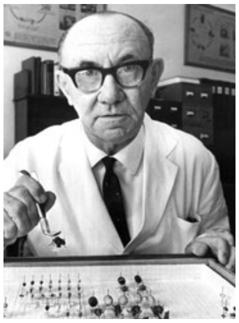


Jason Gilbert Hayden Londt (1943–living) (inset; Fig. 80) was born in Johannesburg, South Africa and schooled at Parktown Boys' High School, Johannesburg, where he graduated in 1961. He undertook his tertiary education at Rhodes University, Grahamstown, South Africa, obtaining a BSc (Honours) degree in 1969, a MSc degree on the ecology of larval ticks in 1971 and a PhD entitled "Aspects of the biology of *Boophilus decoloratus* (Koch, 1844) (Acarina: Ixodidae)" in 1974. He took up the post of Senior Professional Officer at the Onderstepoort Veterinary Research Institute, South Africa, in 1975, where he continued work on the biology and ecology of southern African cattle ticks (Ixodidae). A year later in 1976, he accepted the position of Assistant Director at the Natal Museum, Pietermaritzburg, South Africa (now KwaZulu-Natal Museum), where he developed a research interest in the taxonomy of Afrotropical robber flies (Asilidae) and Mecoptera. He was appointed as Director (1994–2003), and was obliged to consider his research activities as secondary. Despite this, he continued to conduct research on the taxonomy of Afrotropical Asilidae and Mecoptera, much of this in his own time. Following his formal retirement in 2003 he has continued to research and publish on Afrotropical Asilidae. He has undertaken extensive fieldwork in South Africa, as well as Côte d'Ivoire, Kenya, Malawi and Namibia and during the course of his career has developed the largest collection of Afrotropical Asilidae in world. Among his more major achievements are revisions of some of the more dominant genera of Afrotropical Asilidae, including *Pegesimallus* Loew (1980), *Dasophrys* Loew (1981), *Neolophonotus* Engel (1985–1988) (reputed to be the most speciose genus of Asilidae in the world), *Damalis* F. (1989), *Scylaticus* Loew (1992), *Gonioscelis* Schiner (2004), *Rhabdogaster* Loew (2006), *Ancylorhynchus* Berthold (2011) and *Oligopogon* Loew (2014). He has published over 150 journal articles and book chapters and is widely regarded as the world-authority on Afrotropical Asilidae. He is currently Director *Emeritus* of the KwaZulu-Natal Museum and an Honorary Research Fellow of the University of KwaZulu-Natal. Photograph courtesy J.G.H. Londt.



Hugh Kenneth Munro (1894–1986) (inset) was born in Pretoria, South Africa, a direct decedent of the 1820 settler James Hayden, and graduated from Pretoria Boys' High School in 1910. Although he began work with the Transvaal provincial administration, an early interest in entomology, focused by contact with the lepidopterist Antonie Johannes Theodorus Janse (1877–1970), led his transfer in 1912 to the newly created entomological section, headed by Charles Pugsley Lounsbury (1872–1955), in the Union Department of Agriculture. Determined to become a professional entomologist, shortly after joining the section he matriculated at the University of South Africa. These studies were interrupted by two years National Service during WWI, but he completed the requirements and obtained his BSc degree in 1919. In 1921 he was appointed as entomologist to East London, where he dealt primarily with general advisory and phytosanitary work, also undertaking research on the sheep blowfly problem on which he later published. In 1925 he was posted back to Pretoria to take charge of the insect collection (then five cabinets), which he developed into what is today the National Collection of Insects (see below). At the same time he became increasingly active in the collection and rearing of fruit flies (Tephritidae) and made significant contributions to the systematics of the group and in 1946 was awarded a DSc degree by the University of Witwatersrand. Munro was an active field collector and undertook expeditions to various parts of South Africa and participated in a number of expeditions in company with the well-known South African businessman and museum sponsor Bernard Carp (1901–1966). Munro was a leading authority on the systematics of Tephritidae, who by 1974 had published over 85 publications, of which 65 dealt with Tephritidae, describing over 300 species and 37 genera. He retired in 1954 at the age of 60, but continued with his lifelong work, being re-appointed on a temporary basis in his former department. A biography and list of publications was published by Brown (1974), on which these notes are largely based. Photograph courtesy National Collection of Insects (ARC-PPRI).

Brian Roy Stuckenberg (1930–2009) (inset; Fig. 77) was born in Walmer in the Eastern Cape, South Africa and attended Grey High School in Port Elizabeth, where he graduated in 1947. It was during this early period that he developed a keen interest in natural history, which was actively encouraged by John Adams Pringle (1909–2001), then Director of the Port Elizabeth Museum and Snake Park (1937–1953) (now Bayworld) and later the Natal Museum. He matriculated at Rhodes University in Grahamstown, South Africa, where he completed his BSc degree in 1950, his Honours degree in 1951 and his MSc Degree in 1953. His MSc thesis was entitled "Studies of *Paragus* (Diptera, Syrphidae)", for which he was awarded a distinction. He was appointed as Scientific Officer in Entomology at the Natal Museum (now KwaZulu-Natal Museum) in 1953, where he was to remain his entire professional career. At the end of his three-year tenure he was appointed to the full-time staff in December 1956. From the very beginning of his entomological career he decided to specialise in Diptera, which he regarded as the most important group of insects. Early in his career he conducted two expeditions to Madagascar, then virtually unknown dipterologically: the first from December 1955 to January 1956 and the second from November 1957 to April 1958. In 1972, he was awarded a PhD by the University of Natal for his excellent research on Old World Lauxaniidae. He went on to become Assistant Director and later Director of the Museum, which impacted on his dipterological research. After his official retirement in 1994, however, he continued as Director *Emeritus* and Honorary Research Associate of the Museum. During this period he eagerly returned to specialist research on the Diptera and began again to collaborate with entomologists from around the world. From 1994 to the time of his death he published a series of superlative papers which dealt principally with the phylogenetically enigmatic and biologically fascinating "wormlions" (family Vermileonidae). In a distinguished career that spanned 56 years, he published over 100 publications, including studies of at least 23 families of Diptera. He collected extensively in South Africa, as well as Angola, Kenya, Lesotho, Madagascar, Malawi, Mozambique, Namibia, Swaziland, Zimbabwe, Chile and Argentina. During the 20 years he was Head of Entomology at the Natal Museum, he emerged as Africa's leading dipterist, building one of the largest collections of Afrotropical flies in the world. He actively encouraged the study of this collection by specialist researchers and the number of scientific publications that resulted laid the foundations of modern African dipterology as we know it today. As a mark of the respect in which he was held by his peers, over 100 species and five genera of Diptera were named in his honour, together with taxa in at least 11 other insect orders (Coleoptera, Dermaptera, Heteroptera, Hymenoptera, fossil Grylloblattida, Lepidoptera, Neuroptera, Odonata, Plecoptera, Psocoptera and Strepsiptera) and four other classes of invertebrates (Malacostraca, Oligochaeta, fossil Ophiuroidea and Tardigrada). A detailed biography and list of publications was published by Kirk-Spriggs (2012), on which these notes are based. Photograph courtesy of the late P. Stuckenberg.



Fritz Konrad Ernst Zumpt (1908–1985) (inset) was born in Germany and completed his schooling in 1927. He attended the Humboldt University, Berlin, Germany, where he received a PhD degree *Magna cum laude* in 1931. He joined the staff of the Tropical Institute, Hamburg, Germany in 1934, first as assistant and later as Head of the Department of Applied Biology. At this time he decided to concentrate on medical entomology and he undertook several trips to both East and West Africa and became an expert on *tsetse*, in 1936 publishing a book on their characteristics, life histories and control. He also worked on ticks, mites, bedbugs and various groups of medically significant Diptera. During WWII he was called up to the German Army, serving as a non-combatant, attached to the public health division, being responsible for control of insect-borne diseases. In 1948 he joined the staff of the South African Institute of Medical Research, Johannesburg, South Africa. He immediately set to work with the energy that characterised his 32 years in the department. He researched ticks, *tsetse* and trypanosomiasis in the former Zululand (now KwaZulu-Natal) and Mozambique and carried out experimental work on flies thought to be involved in the epidemiology of poliomyelitis. He undertook extensive fieldwork throughout South Africa and neighbouring countries. He sampled vast quantities of arthropod parasites and studies of these resulted in the publication of three volumes of *"Arthropod parasites and vertebrates in Africa south of the Sahara"*, which he edited. Zumpt became the Head of Department of Medical Entomology in 1962 and was awarded a DSc by the University of Witwatersrand, mainly for his enduring book *"Myiasis in man and animals in the Old World"*, but also for his other publications. Up until his retirement in 1980 he published 15 books and 321 scientific papers, making him one of the most prolific natural scientists in Africa. He was a highly respected scientist with an international reputation in the field of higher Diptera and was sought after by scientists throughout the world. His extensive collection of Diptera, initially housed in the South African Institute of Medical Research in Johannesburg, was formally transferred to the KwaZulu-Natal Museum in the 1980s. A detailed obituary and list of his books was published by Anonymous (1986), on which these notes are largely based. Photograph courtesy M. Coetzee.

Diptera collection resources in the Afrotropical Region

Insect collections and insect identification services are intrinsically linked and the ability of a country, especially a developing African country, to provide a critical identification service is highly dependent on the availability and proximity of a well-identified, staffed and maintained insect collection (see Miller & Rogo 2001 for overview). This is especially true for the Diptera, as the order is highly significant in terms of disease vectors, agricultural pests, forensics, *etc*. This fact has led to the publication of a number of important papers that have reviewed the current status of collection resources in various regions of Africa.

Published reviews for South African entomological research and collections are numerous and include Janse (1940, 1945, 1947), Lounsbury (1940), Smit (1960), Koch (1962), Stuckenberg (1964), Jacot-Guillarmod (1969), Coaton (1974), Holm (1975), Scholtz (1999), Coetzee (1999), Materu (1981) and Giliomee (2013). South Africa has developed a "Strategy for zoological taxonomy (2013–2020)" (Hamer 2013), which is attempting to address some of the problem noted. Reviews on the same themes for other African countries and for Africa as a whole have been published by Akingbohungbe *et al*. (1981), Dudley (1981), Kumar (1981), Miller & Rogo (2001), Ritchie (1987) and Sands (1981).

The following section provides an overview of the major collections of Diptera housed in the Afrotropics as defined in this *Manual*, based on information requested from collection curators. Collections in North Africa are not included. In some cases, especially for collections housed in Angola, Malawi and Uganda, no responses were received from curators and information on these collection resources is summarised below. The status of some developing country collections remains uncertain and some at least have suffered from neglect or may have been destroyed altogether.

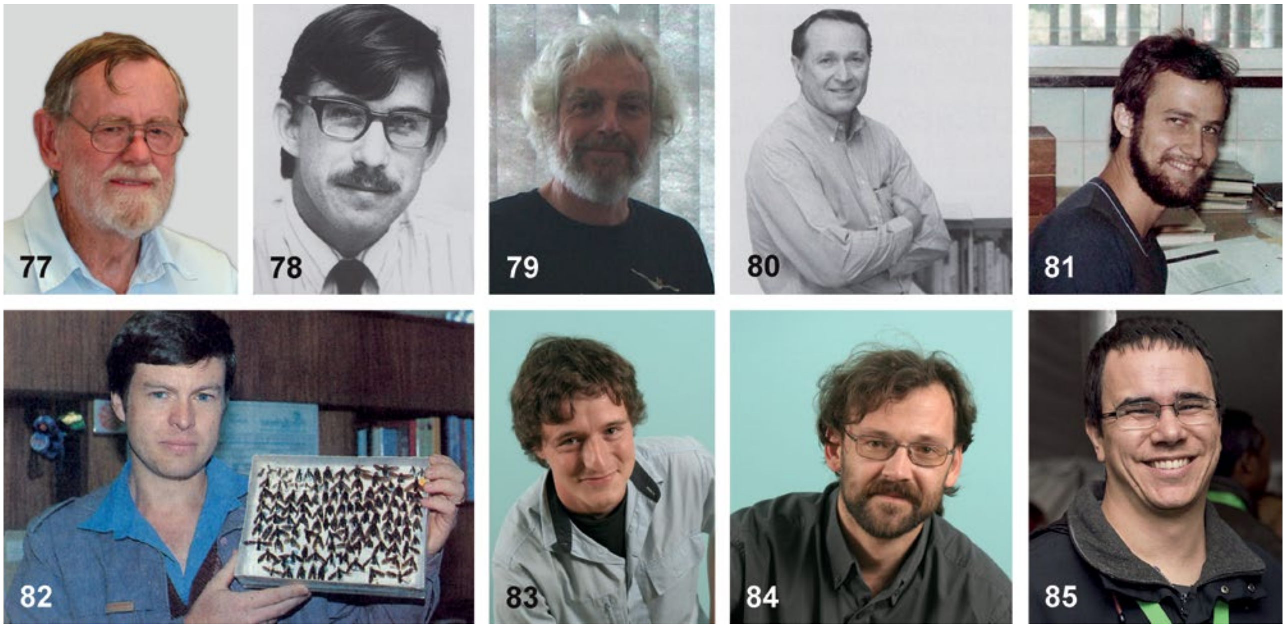
West Africa

Benin

International Institute of Tropical Agriculture, Cotonou

The Diptera collection of the International Institute of Tropical Agriculture, Benin (IITA) forms part of the largest collection of insects in West Africa, with more than 350,000 specimens. The collection includes *ca* 10,000 Diptera, mainly Tephritidae (*ca* 3,000 specimens), Syrphidae (*ca* 1,500) and Asilidae (1,000), with other families making up the remainder. About 400 Diptera are currently identified to species level and 106 to genus level. An estimated 70% of the Diptera collection requires curation beyond family level. Material in the collection originates mainly from Benin, Nigeria and Togo. All specimens are pinned and are preserved in 1,400 drawers in Cornell steel cabinets in a permanently air conditioned facility (Figs 94, 95) (G. Goergen, pers. comm. 2015).

The collection was established in the mid-1990s, with initial collection efforts resulting from research carried out as part of an Africa-wide biological control project against the Cassava mealybug, *Phenacoccus manihoti* Matile-Ferrero (Pseudococcidae), for which insects associated with this pest were thoroughly studied. This resulted in the determination of *ca* 300 species and 1,000 specimens, including some Diptera, of which a cecidomyiid predacious on mealybugs was identified as new to science (Harris 1981). Identification work was almost exclusively reliant on the assistance of various specialists



Figs 1.77–85. Dipterists employed at the KwaZulu-Natal Museum, South Africa (1953–2016): (77) Brian Roy Stuckenberg (1930–2009) (employed 1953–1994); (78) Michael Edward Irwin (1940–living) (1971–1974); (79) Raymond Martin Miller (1941–living) (1976–1978); (80) Jason Gilbert Hayden Londt (1943–living) (1978–2003); (81) David Andrew Barraclough (1958–living) (1982–1985; 1990–2002); (82) Andrew Eric Whittington (1963–living) (1990–1993); (83) Gregory Bernard Peter Davies (1979–living) (2003–2009); (84) Mikhail Borissovich Mostovski (1969–living) (2003–2014); (85) Burgert Smith Muller (1983–living) (2008–2016). Figs 77–85 (photographs courtesy KwaZulu-Natal Museum).

from established centres of excellence in overseas institutions. To preserve this scientific asset, this material was eventually merged with insect collections resulting from pest management activities on other crops at IITA's headquarters in Nigeria, to establish a reference collection at Cotonou Station, Benin. Intensive inventory activities began in the mid-1990s within the framework of a biodiversity research project funded by the Austrian Ministry of Foreign Affairs in successive phases until 2008, with some support from the Swiss Agency for Development and Cooperation over a 12-month period. Since that time, the collection has benefited from IITA's core funding to cover the salary of a collection technician and associated costs for the physical preservation and storage of the collection. The collection has been built with acquisitions of 10,000–15,000 specimens per year over the past two decades, and aside from 1,200 core specimens, has been entirely built by Georg Goergen (1959–living) who supplied the information included here). Today it constitutes the basis for the regional identification service provided by IITA.

Numerous Diptera specimens were determined by J.C. Deeming (see biography above), mainly while in charge of the insect collections of the Institute for Agricultural Research Samaru (see below). Frugivorous Tephritidae were identified by Marc De Meyer (1960–living) (Fig. 91) (data available at: http://projects.bebif.be/fruitfly/index.html) and non-frugivorous Tephritidae by Amnon Freidberg (1945–living). More recently, K.A.M. Jordaens has applied molecular techniques to investigate the syrphid holdings previously sorted by M. De Meyer (Jordaens *et al*. 2015).

Côte d'Ivoire

Centre National de Recherche Agronomique (CNRA), Adiopodoumé

The Insect collection of Centre National de Recherche Agronomique (CNRA) was inherited from the former Office de la Recherche Scientifique et Technique d'Outre-mer (ORSTOM) (now L'Institut de recherche pour le développement, France (IRD), after being abandoned since 1990. The collection was in a state of neglect when donated and staff of the institution have taken steps to improve storage and conservation of the collection. The collection is significant for insect systematics locally and internationally and includes material sampled by students of the École Normal Supérieure, Paris, who conducted field research near Toumodi, under the direction of Professor Lamotte and other specimens in the collection originate from Lamto, Abengourou and the Banco Forest Reserve in Abidjan, *etc*.

The collection is especially rich in Hemiptera (23,508 specimens), Coleoptera (17,305), Lepidoptera (6,645) and Orthoptera (3,825). The Diptera component comprises 1,826 specimens of 11 families with 20 identified genera and 26 identified species. This was probably largely built through investigations of agricultural problems, but no further information is currently available on collectors who contributed to development of the collection. The entire collection is pinned and stored in 18 store boxes. Most of the labels are handwritten either in ballpoint pen or pencil. Steps are currently underway to conserve and digitise the collection (Koffi & Kouassi 2003).

Nigeria

Institute for Agricultural Research Samaru (Ahmadu Bello University, Zaria)

The insect collection began with a very small reference collection at the Regional Research Station, Samaru, which was established by Mac A. Choyce (1920–1995) and Michael Gordon Emsley (1930–living), who were both cotton entomologists, and up until the early 1960s was housed in a very small room and was curated by Ross Wilson. The collection was developed during this period by William R. Reed, Peter H. Giles, Roy Booker and Keith Murray Harris (1932–living). Harry Caswell (1911–*ca* 1990), who set up the insect collection at Ibadan University (see below), did the same when he took up the post at Samaru, gathering material together and ordering J.J. Hill cabinets with cork strips and naphthalene slots. Upon the establishment of the Ahmadu Bello University the collection was incorporated into the institution, although contact with the Ministry of Agriculture remained strong. Material in the collection is Nigerian in origin, although some material resulting from identifications given to other African countries have been incorporated. Major dipterists who subsequently curated and added to the collection are K.M. Harris (employed 1955–1962), J.C. Deeming (employed 1966–1979) (see biography above) and M.C. Dike (employed 1979–2014) (see biography above). The collection was curated by Matthew Chori between 1979 and 2005.

The precise size of the Diptera collection is unknown, but certainly amounts to many thousands of specimens and benefited immensely from J.C. Deeming's collection development and curatorial input. The main collection is dry-pinned and is stored in glass-topped drawers in Hill cabinets, with a smaller spirit and slide collection. About 80% of the Diptera collection is identified at least to genus level, with *ca* 4,000 species in the collection, that were considered when drafting the *Insects of Nigeria: checklist and bibliography* by Medler (1980). The collection has not been digitised and is currently without a Curator.

Part of the small collection at the substation of Mokwa (on the River Niger), housed in identical cabinets, was transferred to Samaru by the termite entomologist R.A. Johnson. Some duplicate specimens from the Samaru collection are now housed in the National Museum of Wales, Cardiff, U.K., including some unidentified Chloropidae which have now been worked up.

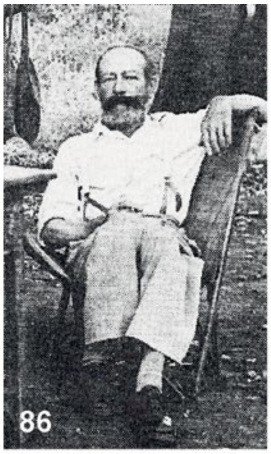
Department of Plant Science, Obafemi Awolowo University, Ile Ife

The small Diptera collection housed at Obafemi Awolowo University comprises *ca* 1,400 specimens, of which 114 (*ca* 8.3%) have been identified to genus level and 74 (*ca* 5.3%) to species. Forty-six families of Diptera are represented in the collection (A. Akingbohungbe, pers. comm. 2015). The collection is mostly dry-pinned and stored in wooden cabinets with glass-topped drawers.

The collection forms part of a larger insect collection housed in the Department of Crop Production and Protection (formerly Department of Plant Science) at the University. This was originally a foundation collection of insect pests of crops that was instigated by John L. Libby (1919–1979) of the University of Wisconsin-Madison between 1966 and 1968, while on a USAID contract based at the University. This collection formed the basis of his publication *Insect pests of Nigerian crops* (Libby 1968). Subsequently, he was succeeded on another USAID contract by John Thomas Medler (1914–2006), of the same university, who widened the scope of the collection substantially to include all insects. Medler undertook numerous field trips to various parts of Nigeria in order to build the collection. The collection was also developed by other university staff and through students, as part of the requirement for the introductory entomology course. Professor Medler made spirited efforts to get insects in the collection identified, by sending specimens out to various recognised authorities on various groups for assistance with identifications. This formed part of his larger USAID-sponsored project, which he eventually published in 1980, entitled *Insects of Nigeria: checklist and bibliography* (Medler 1980). This remains one of very few checklists available for African insects (Miller & Rogo 2001).

Department of Crop Protection and Environmental Biology, University of Ibadan

The insect collection of the Department of Crop Protection and Environmental Biology, University of Ibadan, was established by H. Caswell in *ca* 1948. The collection was developed through fieldwork by previous and current staff, notably John Bowden (1924–2012), H. Caswell, Albert Ukuaghegbele Obotie (1927–2015), J.A.S. Ojo and Obi Okoto (between the years 1957–1974) and originates exclusively from Nigeria. The collection is especially rich in Lepidoptera, Hymenoptera and Coleoptera, but includes 328 specimens of Diptera. The best represented families of Diptera in the collection are: Tachinidae (61 specimens), Muscidae (21), Syrphidae (20), Asilidae (20), Culicidae (19), Tabanidae (18), Stratiomyidae (16), Tephritidae (16), Ephydridae (14), Calliphoridae (13), Platystomatidae (12) and Glossinidae (10), but material of 23 other Diptera families are represented in the collection. Through collaboration between departmental staff and the British Museum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Figs 1.86–93. Portraits of dipterists: (86) Victor Gurner Logan van Someren (1896–1976), curator of the Coryndon Museum (1930–1940) on safari in 1970; (87) René Michel du Toit (1904–1988), pioneer in *Culicoides* research; (88) Fritz Gaerdes (1892–1975), amateur collector who was based at Okahandja, Namibia; (89) Per Forchhammer (1921–2001), amateur collector who was based at Serowe, Botswana; (90) Robert Stephen Copeland (1945–living), Tephritidae expert based in Kenya; (91) Marc De Meyer (1960–living), Pipunculidae and Tephritidae expert based in Belgium; (92) Serge Quilici (1955–2015), Tephritidae expert who was based in La Réunion; (93) Nzigidahera Benoit (1964–living), based in Burundi. Fig. 86 (Someren 1988, fig. 3), Figs 87 (http://www.s2a3.org.za), Fig. 88 (http://www.namibiana.de), Fig. 89 (courtesy A.B.C. Niemann), Fig. 90 (https://www.flickr.com), Fig. 91 (http://planthealth.sggw.pl), Fig. 92 (http://umr-pvbmt.cirad.fr), Fig. 93 (http://enb.iisd.org).

(Natural History) (now the Natural History Museum, London, U.K.), the level of identification is very high, with *ca* 99% of the collection identified to genus level and *ca* 85% to species. The collection was used by John Thomas Medler (1914–2006) in preparation of his *Insects of Nigeria: checklist and bibliography* (Medler 1980).

Specimens are pinned and stored in glass-topped drawers in wooden cabinets (Figs 113, 114). Previous Diptera curators were H. Caswell (employed 1951–1954) and A.U. Oboite (employed 1954–1987). The collection has not been digitised, but according to Medler (1980), an internal report on the collection was compiled by H.J. Sutton in 1964 and a list of genera and species of Diptera in the collection is available (A.A. Omoloye, pers. comm. 2017).

Senegal

Institut Fondamental d'Afrique Noire (IFAN), Dakar

The insect collection of Institut Fondamental d'Afrique Noire, Dakar is one of the two most significant collections of Diptera housed in and representing West Africa and was established in 1936, at the inception of IFAN. The collection was developed through fieldwork by successive staff and their collaborators, throughout West Africa, with a small part of the collection originating from exchanges and donations. Specimens in the collection mainly originate from West African countries, including Benin, Burkina Faso, Côte d'Ivoire, Guinea, Mali, Mauritania, Niger and Senegal. Former dipteran curators were A. Villiers (employed 1945–1956), Michel Condamin (employed 1950–1973; 1978–1988), Roger Roy (1929–living) (employed 1958–1992), Bernadette Soltani (employed 1988), Aïssatou Dramé (1958–living) (employed 1988–1991) and Sun Heat Han (employed 1992–1996).

The Diptera collection amounts to *ca* 4,000 specimens, representing 3% of the collection as a whole, with the best represented families in terms of the number of specimens, being the Diopsidae, Muscidae, Tabanidae, Glossinidae and Calliphoridae and in terms of the number of species the Tabanidae, Muscidae, Calliphoridae, Bombyliidae, Syrphidae, Diopsidae, Culicidae, Chironomidae, Tephritidae, Asilidae, Stratiomyidae, Glossinidae and Tachinidae. Specimens in the collection are all identified to genus level, with only 8% not identified to species level. The specimens are dry-pinned and housed in store boxes (Fig. 96). Digitisation of the entire collection of the laboratory was initiated in the 1990s and is now complete.

Central Africa

Angola

The 27 years of the Angolan Civil War (1975–2002) and associated military interference, coupled with financial constraints, staff shortages and lack of in-country expertise, have impacted negatively on entomological collections developed during the Portuguese colonial period (usually regarded as 1484–1975) and housed in the country. There was formerly a small insect collection housed in Museu Nacional de História Natural de Angola, but the collection no longer exists and the Musée Régional de Dundo collection has been closed to the public and to the scientific community since 2005. No further information on the Diptera holdings of these two institutions is currently available. It is to be hoped that these can be properly assessed and digitised in the future as part of an initiative, funded through the Global Biodiversity Information Facility (see below).

Instituto de Investigação Agronómica, Huambo (IIA)

The Agronomic Research Institute in Huambo, Angola, houses two important collections, dating from the Portuguese colonial period (pre-1975), that remain largely unknown: (1) the herbarium, comprising *ca* 60,000 specimens, and probably includes isotypes of holotypes destroyed during German bombing in Belgium during WWII; and (2) the insect collection, with *ca* 65,000 specimens, which was initially developed for agricultural purposes, with representation of pests and pollinators, but developed into a general entomology collection. The order Diptera is represented by *ca* 3,000 specimens, most of which are identified to family level and the following families are represented: Agromyzidae, Asilidae, Chloropidae, Dolichopodidae, Drosophilidae, Empididae, Ephydridae, Micropezidae, Milichiidae, Sepsidae, Stratiomyidae, Syrphidae, Tabanidae and Tephritidae (S. Fernandes, pers. comm. 2017). The collections survived the Angolan Civil War, during which time the herbarium was moved to Luanda and the insects were kept safe from the constant military intrusion and bombing, thanks to the former Curatorial Assistant, Francisco Elias (1951–living), now retired. Since July 2016, both collections are being organised, identified (whenever possible), digitised and prepared for publishing in order to restore their role and relevance to the scientific community. This has been possible through a Biodiversity for Development (BID) National Grant awarded to SASSCAL (Southern African Science Service Centre for Climate Change and Adaptive Land Management), Angola by the Global Biodiversity Information Facility (GBIF), who are coordinating a project named "Strengthening the institutional network in Angola to mobilise biodiversity data". The main goals of the project are the capacity building of institutional personnel on digitising, publishing and managing biodiversity data and the publication of this and other national collections through GBIF (D. Elizalde, pers. comm. 2017).

Burundi

Office Burundais pour la Protection de l'Environnement (OBPE) (ex Institut National pour l'Environnement et la Conservation de la Nature), Bujumbura

This small collection was established in 2009, originally through projects financed by the Royal Belgian Institute of Natural Sciences, under a memorandum of understanding with the OBPE. The collection has subsequently developed through on-going pollination projects and fruit fly monitoring programmes.

The Diptera collection comprises *ca* 46,000 specimens, originating exclusively from Burundi. The best represented families are the Syrphidae, Tephritidae and Chironomidae, with *ca* 30% identified to genus level (Syrphidae: 60%; Chironomidae: 60%; Tephritidae: 100%). The main collectors who have contributed to the collection are M. De Meyer (Fig. 91), R.S. Copeland (Fig. 90) and Nzigidahera Benoit (1964–living) (Fig. 93). Part of the collection is pinned and stored in locally made storage boxes and part is preserved in ethanol. There has not been a dedicated curator of Diptera and the collection has not been digitised.

Malawi

Malawi houses several historical collections of Diptera, but obtaining recent information on their status has proved difficult, with most contacted institutions not responding. Dudley (1981) published a report on the status of insect collections in the country at that time and identified four institutions in Malawi that potentially have insect collections of note.

Bvumbwe Experimental Station, Limbe

The Diptera collection of the Bvumbwe Experimental Station comprises 1,880 specimens, representing 476 species; the majority of which were identified by staff of the British Museum (Natural History) (now the Natural History Museum, London, U.K.) and the Commonwealth Institute of Entomology, London, U.K. Forty-five families of Diptera are represented in the collection, with the Asilidae, Bombyliidae, Culicidae, Tabanidae and Tachinidae, being best represented.

About 90% of the collection has full label information and from the specimen labels the majority were generated by five collectors: W. Lamborn (collected 1922–1933), C. Mason (1914–1915), C. Smee (1921–1946), R.C.H. Sweeney (1957–1965) and J. Whelland (1967–1973). Lamborn was a specialist on vector insects and was probably not employed specifically at Bvumbwe and since J. Whelland's departure in 1973 only 40 specimens have been added to the collection.

The collection is pinned and stored in eight glass-topped insect drawers, with additional material in six store boxes. Parts of the collection have suffered from serious insect infestations in the past and many of the specimens have been damaged as a result (*ca* 15–20%). The collection is poorly maintained, has not been digitised and there is currently no curator responsible for the collection (C. Dudley, pers. com. 2017).

Chichiri Museum, Blantyre (Museum of Malawi, Nyasaland Museum)

Dudley (1981) noted that the collection comprises *ca* 3,000 specimens in total, mostly Lepidoptera and Odonata, but includes a small collection of biting flies donated by R. Wood. No further information is available of the collection and the status remains unknown.

Department of Biological Sciences, Chancellor College, University of Malawi, Zomba

Dudley (1981) stated that the Chancellor College insect collection was begun in 1968 by G. Shulten. The collection was subsequently developed through donations from the geneticist Hans Reiner Feijen (1946–living), resulting from research on rice pests. Unfortunately, almost all this material was removed by two former members of staff when they returned to the Netherlands. The insect collection was since developed by Cornel O. Dudley during the first 12 years he was employed in the Biology Department (1972–1984). He continued to develop the collection after re-joining the Department in 1997 until 2004, during which time he attempted to return the collection to some sort of professional stature. The collection comprises *ca* 18,000 specimens, representing some 4,000 species. Collection strengths are Coleoptera, Hemiptera, Lepidoptera and Orthoptera. The holdings of Diptera are not currently known. The greater part of the collection (95%) comprises dry-pinned specimens stored in glass-topped insect drawers in wooden cabinets. The remaining 5% is stored in ethanol. Only some 700 species are identified in the collection.

Forestry Research Institute of Malawi (FRIM), Zomba

This small collection was established during the colonial era and largely represents insects related to forestry research in Malawi. Dudley (1981) noted that the collection comprises *ca* 9,000 specimens, representing 2,000 insects identified to species or at least to genus level, with the orders Coleoptera and Lepidoptera making up 75% of the named material. The Diptera component is small, representing 270 specimens of nine families (Bombyliidae, Calliphoridae, Cecidomyiidae, Diopsidae, Muscidae, Phoridae, Platystomatidae, Sarcophagidae and Tachinidae). The Tachinidae is the best represented family in the collection; many of which have been reared and have associated puparia. The specimens are fully labelled and material in the collection was largely collected by N.P. Dumbo, R.F. Lee and R.C.H. Sweeney and *ca* 95% of the collection is identified to species or genus level, some by specialists. The collection is housed in store boxes (Fig. 99) and is regularly maintained to prevent pest infestations. The collection has not been digitised.

East Africa

Kenya

National Museums of Kenya, Nairobi (Coryndon Museum)

The National Museum of Kenya houses the largest collection of Diptera in East Africa, comprising *ca* 250,000 specimens, with the earliest specimens in the insect collection dating back to 1888. The Diptera families Tephritidae (*ca* 13,000 specimens), Agromyzidae, Culicidae, Syrphidae, Bombyliidae and Tabanidae are best represented. The Museum also has the largest collection of the endemic family Mormotomyiidae. Most specimens in the collection originate from Kenya and Uganda and the collection also incorporates material of the former Amani Hill Research Station, Tanzania (now Amani Research Centre). The majority of specimens are pinned, with some slide-mounted and spirit preserved specimens. The pinned specimens are preserved in glass-topped insect drawers in a series of J.J. Hill cabinets (Figs 107, 108) (L. Njoroge, pers. comm. 2015).

The Museum was established in 1910 by the East Africa and Uganda Natural History Society; the Society's main goal being to conduct an ongoing critical scientific examination of the natural attributes of the East African habitat. The first paid curator, the herpetologist Arthur Loveridge (1891–1980) was employed in 1914 and served until *ca* 1918. He was then replaced by the first part-time entomological curator Alfred Francis John Gedye (1899–1963). The museum later became the official Coryndon Museum in 1930 (named after Sir Robert

Thorne Coryndon (1870–1925), former Governor of British East Africa and patron of the Society) with Victor Gurner Logan van Someren (1896–1976) (Fig. 86) serving as its first official Curator from 1930–1940. After his resignation in 1940 he was replaced by Louis Seymour Bazett Leakey (1903–1972). Following Kenyan independence in 1963 the Coryndon Museum officially became the National Museums of Kenya.

The Annual Report of the East Africa and Uganda Natural History Society for the year 1937 (Someren 1938), indicates that the entomological collections were being actively built at that time and it was noted (p. 194) that "Outstanding contributions were made by Messrs. MacArthur, R.E. Toker, Blom-Bjorner, Allen Turner, A.L.H. Townsend, A.F.J. Gedye, G. van Someren, the Department of Agriculture, Kampala, and the Curator". During that period material was also being identified by overseas specialists and it is noted in the same report (p. 194) "Sir Guy Marshall of the Imperial Institute of Entomology, and members of the Division of Entomology, British Museum, rendered, as hitherto, invaluable service in the determination of many thousands of insects submitted to them". During the 1930s van Someren built an extensive collection of Tephritidae by sampling indigenous fruits at different localities in Kenya and the rearing of associated flies. That material is still housed in the Museum and several new species were described by the eminent South African dipterists H.K. Munro (see biography above) (Munro 1938). Populations of the endemic Kenyan family Mormotomyiidae were rediscovered at the type locality (modern spelling Ukasi Hill) in December 1948 by V.G.L. van Someren and his son Gurner Robert Cunningham-van Someren (1914–1997) and the collection houses this extensive material (some of which was also distributed to North American and European museums as examples) (Copeland *et al*. 2011; Emden 1950). During the 1960s and 1970s, Robert Herbert Carcasson (1918–1982) and Michael Peter Clifton (1941–living) sent large numbers of Diptera to the Natural History Museum, London, U.K. (then the British Museum (Natural History)) for identification by Kenneth George Valentine Smith (1929–living). This means that *ca* 99% of the Diptera in the collection is identified at least to genus level (L. Njoroge, pers. comm. 2015).

Subsequently, the Diptera collection has been built through similar initiatives on the rearing of Tephritidae by R.S. Copeland (Fig. 90) in the 1990s (in collaboration with the International Centre for Insect Physiology and Ecology, Nairobi), by Ellinor Catherine Cunningham-van Someren (1916–?), who worked chiefly on mosquitoes, by M. De Meyer (Fig. 91) during the period 1992–1997, who focused on development of the Syrphidae


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Figs 1.94–96. Examples of Diptera collection facilities in West Africa: (94) collection room of International Institute of Tropical Agriculture, Cotonou, Benin; (95) same, curation of Asilidae collection; (96) collection room of Institut Fondamental d'Afrique Noire, Dakar, Senegal. Figs 94, 95 (photographs courtesy G. Goergen), Fig. 96 (photograph courtesy A.A. Niang).

collection (M. De Meyer, pers. comm. 2015). More recent contributions to the collection have been made by the current head of the Invertebrate Zoology Section, Laban Njoroge (1974–living) (who is working on Culicidae) (Fig. 108) and the German BIOTA and Taita Hills Biodiversity Projects, which have contributed a substantial amount of spirit material, some of which is being distributed to interested researchers for identification and descriptive purposes (B. Bytebier, pers. comm. 2015).

International Centre for Insect Physiology and Ecology, Nairobi

The Diptera collection of the International Centre for Insect Physiology and Ecology, Nairobi comprises *ca* 15,000–20,000 specimens. The Tephritidae is the best represented family by far (*ca* 9,000 specimens), with reasonable holdings of the families Asilidae (2,200), Diopsidae (750) and Micropezidae (500). Virtually all specimens in the collection originate from Kenya and *ca* 70% of the collection is identified at least to genus level. Most specimens are pinned and are stored in wooden cabinets with glass-topped drawers or in store boxes (R.S. Copeland, pers. comm. 2015).

The Diptera collection was established in the 1980s and was built mostly through staff fieldwork. The major donor is R.S. Copeland (Fig. 90), who has built the Tephritidae collection through rearing programmes from indigenous fruits. The collection has never had a dedicated Diptera curator and has not been digitised (R.S. Copeland, pers. comm. 2015).

Division of Vector borne Diseases, Nairobi (Kenya Medical Department)

Ellinor Catherine Cunningham-van Someren's collection of mosquitoes was housed in the Department for many years, but part of the collection has now been transferred for safe custody to the National Museums of Kenya (L. Njoroge, pers. comm. 2015).

Kenya Agricultural and Livestock Research Organization, Nairobi (Kenya Agriculture Research Institute)

The Kenya Agricultural and Livestock Research Organization collection was established in the early 1900s, with the earliest record dating from 1913. The collection mainly comprises species of agricultural significance and was established through field sampling and through farmers' requests (enquiries). The collection originates exclusively from Kenya. The Diptera collection is small, comprising *ca* 240 species, with the best represented families being the Tachinidae (39 specimens), Tephritidae (26), Muscidae (31), Anthomyiidae (14), Asilidae (15), Simuliidae (19) and Syrphidae (19). The collection is pinned in store boxes, with some slide-mounted and spirit preserved material. About 90% of the collection is identified to species level. There have not been any formal Diptera curators and the collection has not been digitised.

Uganda

Uganda houses some important historical collections of Diptera, but obtaining recent information on their status has proved difficult, with most contacted institutions not responding. Scott E. Miller (National Museum of Natural History, Washington D.C, U.S.A.), produced a brief unpublished report for the EAFRINET survey of collections, based on his visits to collections in the Kampala area in the late 1990s. Miller identified six institutions in Uganda that potentially have insect collections of note. The Uganda National Museum, Kampala, purportedly only has a small collection in poor condition, which is not associated with research activities and this institution is not listed below (S.E. Miller, pers. comm. 2016).

Vector Control Division, Department of Entomology, Ministry of Agriculture, Animal Industry and Fisheries, Entebbe (formerly Tsetse Control Department)

The collection of Vector Control Division was established in the 1970s and continues to be built through survey work by district entomologists. The collection comprises over 100,000 specimens of biting flies, specifically Glossinidae, *Chrysops* Meigen and *Haematopota* Meigen (Tabanidae) and *Stomoxys* Geoffroy (Muscidae), some dating from the early 1900s (J. Muguwa, pers. comm. 2017). Specimens in the collection originate exclusively from Uganda and over 90% are identified at least to genus level. All specimens are pinned and are kept in wooden store boxes (Fig. 116). The building which formally served as a museum was taken over for other purposes and the collection is now stored in different offices within the department. The collection has not been digitised and there is currently no curator (A. Masabagidudu, pers. comm. 2017).

Uganda Virus Research Institute (UVRI), Entebbe

The institute may have a collection of Culicidae and other biting arthropods from intensive surveys undertaken at Zika Forest, as well as country-wide surveys (S. Miller, pers. comm. 2016), but no response was received to enquiries and the status of the collection (if it does exist) remains unknown.

Department of Zoology, Entomology & Fisheries Science, Makerere University

The insect collection mainly comprises Orthoptera and Lepidoptera, but there are *ca* 20 drawers of miscellaneous insects (S.E. Miller, pers. comm. 2016). It is not clear whether Diptera are represented in the collection, no response was received to enquiries and the status of the collection remains unknown.

College of Agricultural and Environmental Sciences, Makerere University, Department of Crop Science

The collection apparently comprises three main components: a collection of crop pests (some organised by crop), evidently curated by D.S. Hill (*ca* 1968), but including older specimens, which is stored in 40 small drawers; a general collection of insects, housed in *ca* 50 Schmidt-type boxes and assorted alcohol vials and slide-mounted specimens (the slides mostly used for teaching) (S.E. Miller, pers. comm. 2016). It is not clear whether Diptera are represented in the collection, no response was received to enquiries and the status of the collection remains unknown.

Kawanda Agricultural Research Station, Kampala

In 1962, D.J. Greathead founded the Commonwealth Institute of Biological Control (CIBC) East African Station at Kawanda

Research Station in Uganda. It apparently includes an impressive collection of some 900 small drawers (*ca* 45 cabinets, averaging 20 drawers each), plus additional material stored in Schmidt-type boxes. The collection includes specimens from the following historical entomologists: G.C. Gowdy (1910s), G.D.H. Carpenter (1920s), G.L.R. Hancock (1920s), H. Hargreaves (1930s), T.H.C. Taylor (1930s) and D.J. Greathead (1960s). The insect collection shares a tightly packed room (open ventilation) with a small herbarium (S. Miller, pers. comm. 2016). No response was received to enquiries and the status of the collection remains unknown.

Indian Ocean Islands

Madagascar

Botany and Zoologique Parc of Tsimbazaza, Antananarivo

The insect collection, housed in the Parc Botanique et Zooligique de Tsimbazaza (attached to the Fauna Department of the Entomology Division), is the largest collection of insects in Madagascar. It was established in 1952, during the French colonial period, being the former collection of l'Institut Scientifique de Madagascar. The collection was largely developed and curated by the French dipterist R. Paulian and the majority of specimens in the collection were collected by Paulian himself (dating from 1951 to 1957), with some specimens donated by B.R. Stuckenberg (dated 1957), R.R. Miller (1954), John F. Lamberton (1946) and others.

The Diptera collection is small, comprising *ca* 1,227 specimens, but is highly significant historically and is usually overlooked by researchers. Much of Paulian's Diptera material is deposited in the Paris Museum, but this collection represents an important additional source of specimens. Material originates exclusively from Madagascar and *ca* 80% of the collection is identified at least to genus level. Thirty fly families are represented and the collection appears to have been widely used by researchers, including material identified (in the 1950s) by various leading dipterists, namely: Charles Paul Alexander (1889–1981), Pieter Hendrick van Doesburg (1892–1971), Fritz Isidore van Emden (1898–1958), Paul Freeman (1916–2010), Dilbert Elmo Hardy (1914–2002), [Emil Hans] Willi Hennig (1913–1976), Salvador Vicente Peris [Torres] (1922–2007), H.K. Munro, H. Oldroyd and Paul [J.M.] Vanshuytbroeck (1912–?), and at least in the case of the Limoniidae includes numerous types. The collection is pinned and is stored in a 25 glass-topped drawers in a wooden cabinet (Figs 105, 106). The collection is well maintained and is currently being digitised (V. Andriamananony & R. Harin'Hala, pers comms 2017).

La Réunion

Unité Mixte de Recherche: Peuplements Végétaux et Bioagresseurs en Milieu Tropical (UMR PVBMT), St. Pierre

UMR PVMT is a joint research unit, associating CIRAD (Centre de Coopération Internationale en Recherche Agronomique pour le Développement), Université de La Réunion and INRA (Institut National de la Recherche Agronomique).

The insect collection (based at CIRAD), was formally established in 1962, mainly through field collections for agricultural research projects. The small Diptera collection comprises *ca* 1,200 specimens, with the best represented families being the Tephritidae and Syrphidae, with *ca* 60% of the collection identified at least to genus level. The main dipterists who contributed to the Diptera collection are Jean-Georges Pointel (1928–living), Serge Quilici (1955–2015) (Fig. 92) and Jean-François Vayssière (1951–living).

The collection originates chiefly from La Réunion and other Indian Ocean islands and includes important historical specimens of Diptera and more recent Diptera material resulting from fruit fly monitoring and long-term sampling programmes using Malaise traps. The main collection is pinned and stored in commercial store boxes and more recent survey material is preserved in ethanol and stored in a freezer and the DNA barcoding of spirit preserved material is currently underway. There have not been any formal Diptera curators and the collection has not been digitised.

Southern Africa

Botswana

Botswana National Museum, Gaborone

The Botswana National Museum was established in 1967 and was officially opened to the public in 1968. The entomological collection is housed in the Colonial Building, as part of the Natural History Division in the Village suburb of Gaborone. The collection was established through fieldwork in Botswana (using sweep nets, Malaise traps, butterfly traps, pitfall traps, yellow pan traps and Chempac® fruit fly traps) and through research and donations. Fieldwork was mainly undertaken by Jimmy Mashonja (former Museum entomologist, who retired in 2003), Elisah Namati (1972–living), Ofentse Pat Sithole (1977–living) and Moreetsi Bogosi. Donations originate from the *Tsetse* Project, Per Forchhammer (1921–2001) (Fig. 89), Bruce James Hargreaves (1942–living) and the Diptera collection originates entirely from Botswana. Per Forchhammer was the main donor of Diptera. His collection is well curated with specimens fully labelled, although some specimens are not georeferenced. Per Forchhammer was a publishing Danish entomologist who worked as a school teacher at Swaneng Hill Senior Secondary School, Serowe. He developed a major insect and snake collection in an old classroom at Farmer's Brigade, next to Swaneng Hill School, while based in Serowe, with records indicating that he was collecting non-dipteran insects as early as the 1980s. He mostly collected in the vicinity of his home at Farmer's Brigade, using a Malaise trap and other methods and distributed material of various insect groups widely to specialists around the world. Material he collected is, therefore, widely cited and is housed in various museums around the world, through donation or exchange. He published several articles on insects (mostly on Cerambycidae and other Coleoptera) and on reptiles, *e.g.* in the *Botswana Notes and Records* and in the Danish journal *Natura Jutlandica*. He was also instrumental in establishing the Serowe Museum (now the Khama III Memorial Museum) (C. Stockmann, pers. comm. 2017). Later he donated his collection to the Botswana National Museum.

The precise size of the Diptera collection is unknown, but the best represented families are the Asilidae, Calliphoridae, Drosophilidae, Glossinidae, Muscidae, Sarcophagidae and Tabanidae. Other Diptera families represented in the collection include: Culicidae, Curtonotidae, Drosophilidae, Ephydridae, Hippoboscidae, Milichiidae, Syrphidae, Tephritidae and Tipulidae, plus numerous unidentified specimens. It is not known what percentage of the collection is identified to genus and species. The dry-pinned specimens are preserved in store boxes and the spirit material in 70% or 96% ethanol. The dry collection is well maintained and the curation rooms are air-conditioned. At least part of the collection has been digitised in a secured entomology database (O.P. Sithole, pers. comm. 2017).

Mozambique

Museu de História Natural, Maputo (Museu Dr Álvaro de Castro)

Museu de História Natural, Maputo, Mozambique (MHN), was established in 1913 as the Provincial Museum and was located at various sites until its establishment in the current Manueline building in 1932, as Museu Dr Álvaro de Castro. Museu de História Natural is one of the major research institutions disseminating information on the faunal biodiversity of Mozambique. The collections comprise significant information on the richness and diversity of Mozambique's fauna for display and scientific purposes.

The entomological collection of MHN is the largest entomological collection in Mozambique, amounting to *ca* 170,000 insect specimens, representing almost all orders of insects that occur in the country. The Diptera collection is small, comprising *ca* 1,990 specimens, about 98% (*ca* 1,950 specimens) of which are identified to species level, with most (57%, *ca* 1,110 specimens) representing the single common species *Tabanus taeniola* Palisot de Beauvois (Tabanidae). Only 2% (about 40 specimens) of Diptera are identified to family level. The majority of Diptera specimens in the scientific collection of insects are derived from the entomological studies by Maria Corinta Ferreira (née Melo) (1922–?2003) and Gunderico Wladimiro Santos Ferreira (1921–1999), established during the colonial period (prior to 1975), mainly from the South Zone (Maputo and southern Gaza Provinces) in 1949 and in the Central Zone of Mozambique (Songo) in 1973.

The collection is preserved in glass-topped drawers in wooden cabinets (Fig. 104) and the majority of specimens have full locality data. These data are being incorporated into the new database as part of the process of re-organisation and digitisation of biological data in the collection.

Namibia

National Museum of Namibia, Windhoek (Landesmuseum; South West Africa Museum; State Museum)

A detailed account of the history of the Museum was published by Otto-Reiner (2007), on which these notes are largely based. The origin of the National Museum, Namibia began with the foundation of the "Deutsch-Südwest-Afrika Landesmuseum Windhuk", during the German colonial period. The Landesmuseum was begun shortly after the arrival of Governor Bruno von Schuckmann (1857–1919), who initiated the development of a local museum. The first meeting took place at "Hotel Kronprinz" on 5 October 1907, with the first museum committee elected the same year. As the collections grew, the Museum occupied several buildings during various times in central Windhoek until the outbreak of WWI, when the then Museum Council was called up for active service. As no efforts were made to have the Museum collections designated as neutral property, the bulk of the collection was stolen by occupying forces. The few remaining collections were taken over by the South African Administration for South West Africa, who handed them to the Municipality. Entomological holdings during this period are not known, but there are insect specimens currently in various major European museums, especially in Germany, that are labelled "Landesmuseum" that originate from this early period in the Museum's history.

Following formation of the South West African Scientific Society in 1926, the Administration of South West Africa entrusted the Society with the organisation and management of museum collections. The Society and Museum were allocated the mess and two adjoining rooms of the Officer's Casino, formerly known as "Kommissariat", where the Museum collection had been housed from 1903 to 1908, and thus the South West African Museum was born. From 1937 onwards, after a period as honorary and part-time curatorship, Erich Zelle (1884–1969) was eventually appointed as full-time curator in 1950. The Museum moved again to Schmerenbeck House, where it was housed from 1950 to 1962. In 1957 the Administration of South West Africa took over the Museum from the Scientific Society, after which it was officially named the State Museum (from 1957–1995), with the first Director Albert Johan Dirk Meiring (1899–?).

The entomological collection was without a curator until 1962, when the German school teacher and collector Fritz Gaerdes (1892–1975) (Fig. 88) was made honorary curator. The Entomology Department was only formally established in 1970, with appointment of Mary-Louise Penrith (1942–living) as chief professional officer (employed 1970–1983), the collection being established in the Alte Feste towers. Her research at that time focused on Tenebrionidae (Coleoptera), but it is noted that she increased the entomological collection by 18,327 specimens in 1972 alone. In 1973, F. Gaerdes donated his extensive insect collection to the Department, which he amassed over a fifty-year period. Part of F. Gaerdes's Diptera collection was studied by Erwin Lindner (1888–1988) who published a significant series of papers dealing with Namibian Diptera (Lindner 1972, 1973, 1974, 1975, 1976, 1977). This collection represents the most significant donation to the entomological collection and in 1990 the Museum staged an exhibition highlighting its significance. Due to space constraints, in 1974 the entomological collections were temporarily moved to the 3rd floor of the former Enke-House (later known as "Bastion"). In 1980 all staff and collections were moved to Carl List Haus, where the museum occupied the top 4 floors until 1993, when it was moved to its present location. A second entomological post was created in 1976 that was filled by Schalk van der Merwe Louw (1952–living), who served until 1980, after which he was replaced by John A. Irish (1958–living), who served from 1981–1990. Following Penrith's resignation in 1985, Irish took over the post of Chief Professional Officer, after which Eugène Marais (1959–living) was appointed as second entomologist in

1986. Two other curators were appointed, Martina Luise Wolff (née Pusch) (1967–living) (employed 1990–1993) and Carole Susan Roberts (1961–living) (employed 1989–1992). The entomology collections were moved to their current premises, known as Museum ACRE in 1993. Following Namibian Independence in March 1990 the Museum was officially renamed the National Museum of Namibia in 1995.

By 1995 the Entomology Centre had a core collection of Diptera, incorporating material collected by F. Gaerdes, the former curators noted above, plus Shirley Bethune (1959–living) (employed 1982–1983) and Barbara Anne Curtis (1954–living) (employed 1986–1992), both of whom had worked on aquatic invertebrates. In 1995, A.H. Kirk-Spriggs spent six months as a volunteer in the Department, returning in 1997 under the auspices of Voluntary Services Overseas. He was based at the Museum until 2003, during which time he actively worked on development of the Diptera collection through fieldwork throughout the country, mostly with E. Marais. This material was distributed widely to international specialists and resulted in numerous publications dealing specifically with the Diptera of Namibia (see above), mostly published in the Museum's in-house journal *Cimbebasia*. In 1998 the Department undertook a major survey of intertidal Arthropoda from the Kunene River mouth on the Angolan/Namibian border to the Eastern Cape of South Africa (Kirk-Spriggs *et al*. 2001*a*) as well as an extensive survey of the Brandberg massif (Namibia's highest mountain), that was published in a dedicated volume and included 12 chapters dealing with Diptera (Kirk-Spriggs & Marais 2000) (see above).

The Diptera collection has not been digitised and the precise number of specimens is unknown, but can be predicted to be *ca* 150,000 specimens, making this one of the largest regional collections. Most are pinned and fully labelled and are stored in unit trays or plastic boxes with lids. There is also extensive sorted material from Malaise traps and other sampling methods that cover the entire country. The collection was entirely re-sorted and identified to family by A.H. Kirk-Spriggs. About 30% of the collection has been identified to generic level or beyond and there are numerous primary types that are stored separately. The entomological collection has fallen into decline since 2003 and is currently without a curator, although steps have been taken to resolve this.

South Africa

National Museum, Bloemfontein

The National Museum was founded on 20 July 1877 during a public meeting in Bloemfontein's City Hall. Although there were entomology collections, especially butterflies, that predate the inception of the Department, the Entomology Department was formally established on 1 May 1975, when G.W.S. Ferreira, who had studied at the University of Coimbra, Portugal and was formerly employed at the University of Lourenço Marcques, Moçambique, took up the position of entomologist. Three months later, during April, he was joined by his wife, M.C. Ferreira, who had held the position of Director of the Institute for Scientific Research of Moçambique (employed 1959–1974) and Professional officer at Museu Dr Álvaro de Castro, Lourenço Marques (employed 1948–1959), prior to her appointment at the National Museum (see Antune 2016, for recent biography). Both received leave of absence from Bloemfontein to attend pension-related court cases in Mozambique in 1979 and never returned to the Museum (Van der Bank 2001), both returning to Portugal in 1980. G.W.S. & M.C. Ferreira were coleopterists and prior to 2008 the Museum has employed coleopterists consistently who concentrated on development of the Coleoptera collection. A core collection of *ca* 1,500 Diptera was developed by subsequent curators, including J.A. Irish and Leon Nico Lotz (1957–living), mainly as a result of surveys of Navel Hill and other hills in the central Bloemfontein area, but chiefly comprised a more extensive collection of spirit-preserved Hippoboscidae developed by Elize [Elsabé] Jacoba Visagie (1967–living) (who has published several papers on South African Hippoboscidae).

Ashley H. Kirk-Spriggs took up the position of curator in November 2008, with an emphasis on developing the Afrotropical Diptera collection. As a result, the Diptera collection is now the largest non-specialised collection of Diptera on the African continent, with over 209,374 accessioned specimens. All families that occur in the Afrotropics are now represented in the collection. It is a unique research tool, as it comprises recent, high quality material from numerous poorly sampled Afrotropical countries, including: Benin, Burundi, Cameroon, Democratic Republic of Congo, Kenya, Réunion Is., Madagascar, Malawi, Mauritius, Namibia, South Africa (Eastern and Western Cape, KwaZulu-Natal and Free State), Togo and Zambia. The collection also incorporates former collections of the Alexander McGregor Museum (Kimberley) and University of Pretoria collections of Diptera (both of which were formally donated in 2009).

The majority of the collection is pinned and is stored in glass-topped drawers using a unit tray system (Figs 100, 101). There is also an extensive spirit collection with the majority of samples preserved in 96% ethanol and suitable for DNA extraction.

The Department currently has two full-time Diptera taxonomists on the staff, A.H. Kirk-Spriggs and B.S. Muller. The collection is widely used by local and international researchers and parts of the collection have been identified by leading experts. Currently over 25,000 pinned specimens are on loan to specialists. The National Museum, Bloemfontein is, therefore, a centre of excellence for the study of dipterology on the continent and the collection represents an extremely important national asset and research tool, which raises the international profile of research in the field in South Africa.

All pinned specimens and sorted spirit-preserved specimens have been fully digitised and the database is fully maintained. There are several hundred residue samples, mostly of Malaise and pan trap catches that still require sorting, identification and digitisation.

KwaZulu-Natal Museum, Pietermaritzburg (Natal Museum)

The Diptera collections of the KwaZulu-Natal Museum are the second largest on the African continent and the Museum has been the leading institution for dipterological research in the region for the past six decades. An excellent account of the history of the Department was published by Barraclough & Whittington (1994), with additional information provided by Guest (2006) and Davies (2009), on which these notes are largely based.


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Figs 1.97–101. Examples of Diptera collection facilities in Southern and Central Africa: (97) cabinet containing the pinned Diptera collection of Onderstepoort Veterinary Institute, South Africa; (98) same, part of the slide collection, comprising 150 slide boxes; (99) insect collection room of the Forestry Research Institute of Malawi, Zomba; (100) drawer of identified Anthomyiidae from the National Museum, Bloemfontein; (101) same, one of six 40-drawer cabinets housing the Diptera collection. Figs 97, 98 (photographs courtesy K. Labuschagne), Fig. 99 (photograph courtesy B.S. Muller), Figs 100, 101 (photographs courtesy C. Venter).

Prior to 1953 the then Natal Museum had not appointed a professional entomologist to the staff. This changed in 1953 with the appointment of B.R. Stuckenberg (Fig. 77) (see above for biography). Stuckenberg had worked on Diptera for his master's degree at Rhodes University and concentrated on developing the Diptera collection. Stuckenberg actively encouraged the study of the collection by leading Diptera authorities of the day and this is reflected in the level of identification in the collection and the number of primary types (see below). In 1970, Stuckenberg was appointed Assistant Director and in 1971 M.E. Irwin (Fig. 78) (a PhD graduate of the University of California, U.S.A.), was appointed on a three-year contract to run the Entomology Department. Following Irwin's departure in 1974, Raymond Martin Miller (1941–living) (a PhD graduate from Iowa State University, U.S.A.) (Fig. 79) was appointed in 1976. Stuckenberg became Director in 1976 and J.G.H. Londt (Fig. 80) (see biography above) from Onderstepoort Veterinary Institute was appointed as Assistant Director. Following Miller's resignation, Londt became Acting Head of Entomology in 1978, a post he held until 1990. In 1982 D.A. Barraclough (Fig. 81) (see biography above) was appointed as Senior Professional Officer, but resigned in 1985. After completing his PhD in Australia, Barraclough returned as Head of the Arthropoda Department in 1990. In the same year Andrew Eric Whittington (1963–living) (Fig. 82) was appointed to the Entomology Department; the first time Entomology had been fully staffed. Whittington resigned in 1993 and Barraclough in 2002, to be replaced by Mikhail Borissovich Mostovski (1969–living) (Fig. 84), who took up the position of Head of the Arthropoda Department in 2003 and who in turn resigned in 2014. Gregory Bernard Peter Davies (1979–living) (Fig. 83) was appointed in 2003 and resigned in 2009. B.S. Muller (Fig. 85) joined the Museum in 2008 as Research Technician and was promoted to Curator in 2009, but resigned in 2016. At the time of this writing the Department is currently without a curator.

Notable associations with the Department have been Pamela Jean Stuckenberg (née Usher) (1933–2013), who for *ca* 20 years (1955–1975) undertook a great deal of curatorial work, accompanying her husband Brian on fieldtrips and worked on the taxonomy of Tabanidae, R.M. Miller who has continued to add material, sort and curate the collection and Torsten Dikow (1975–living), who was an international student based at the then University of Natal (1999–2000) and spent every free afternoon at the Museum working on the collections, familiarising himself with the Asilidae and working with J.G.H. Londt on two small revisions in 2000. He also undertook field expeditions with Museum staff.

According to figures from an internal report by Davies (2009), the pinned Diptera collection amounted to an estimated 205,000 specimens, amounting to 87% of the KwaZulu-Natal Museum pinned insect total. The collection was then housed in 832 glass-topped insect drawers (Fig. 103) in four metal rack units in two rooms (Fig. 102). In 1976 the Museum acquired the former Transvaal Museum collection of Diptera in exchange for the Kenneth Misson Pennington (1897–1974) collection of butterflies and in 1983 the important F.K.E. Zumpt (see biography above) collection of medically important Calliphoridae, Muscidae, Oestridae, Rhiniidae and Sarcophagidae from the former South African Institute of Medical Research. The collection as a whole includes more than 1,275 primary types (almost entirely holotypes) and 5,474 secondary types. This includes primary types of two-thirds of the families recorded from the region and primary/secondary types of 1,948 species. The collection also includes reference material of extralimital families of flies for reference purposes.

Albany Museum, Grahamstown

The Albany Museum is the second oldest museum in South Africa. In 1855, a group of five doctors, George Allan Hutton (1830–1889), William Edmunds (1829–1872), R.M. Armstrong, William Guybon Atherstone (1814–1898) and D.D.M. McDonald, met for the purpose of forming a medical society. The "Graham's Town Medico-Chirurgical Society" was thus formed, with Alexander Melvin (1792–1868) as the first President. The first Curator of the Albany Museum was Burt J. Glanville (employed: 1858–1882) and the first reference located to entomology in the Albany Museum is Glanville's *Report on the Albany Museum for the year 1858*. Entomology at the museum took off after the zoologist John Hewitt (1880–1961) took over as Director of the Museum in 1910. He made collections of insects and there are some specimens in the contemporary collections with labels bearing his name.

The Diptera collections of the Albany Museum are stored in two separate departments, the Department of Entomology and Arachnology (terrestrial Diptera) (DEA) and the Department of Freshwater Invertebrates (aquatic Diptera) (DFWI). The DEA was formally established in 1958 with the appointment of Charles Fréderic Jacot Guillarmod (1912–1979), although specimens incorporated in the collection originate from much earlier dates. The collection of DFWI was founded much later in 1972, from the amalgamation of several institutional collections, primarily material from the National Institute of Water Research (NIWR) of the CSIR. Both the DFWI and DEA collection were largely built through the efforts of previous and current curatorial staff. The main Diptera donors of DFWI were Ferdinand Cornelis de Moor (1947–living) (Simuliidae), Arthur Desmond Harrison (1921–2007) and Katharine Marjorie Frances Scott (1913–1998) (Chironomidae). Diptera material in DEA originates from various donors, including (Mrs George) Bliss White (née Atherstone) (1823–1907), John Hewitt, (Reverend Father) Joseph A. O'Neil (1867–1952), Friedrich Wolfgang Gess (1936–2013), Sarah Kathleen Gess (née Greathead) (1938–living) and A.H. Kirk-Spriggs (who was the only former Diptera Curator: 2006–2008). Diptera material in DFWI mostly originates from South Africa and DEA material from South Africa (especially Eastern Cape), Lesotho, Namibia and Madagascar. The collection includes a number of Diptera reared from the nests of Hymenoptera, prey of *Bembix* F. (Crabronidae), flower visiting records and Asilidae with prey.

The DFWI Diptera collection comprises *ca* 50,000 separate catalogue entries (most with several specimens) and 22 families of aquatic Diptera are represented in the collection, with the Chironomidae (> 20,000 specimens and 6 types), Ceratopogonidae (> 2,000), Simuliidae (10,000) and Culicidae (1,000), being the best represented. Other less common families in the collection include Blephariceridae, Dixidae and Thaumaleidae. Approximately three-quarters to one-half of the collection is identified at least to genus level. The majority of specimens are preserved in ethanol and most of the collection has been digitised.

The DEA Diptera collection comprises *ca* 25,000 Diptera specimens, *ca* 20,000 pinned specimens, stored in 90 glass-topped insect drawers and *ca* 5,000 specimens in ethanol. The best represented families in the collection are the Asilidae (12 drawers), Bombyliidae (10), Tabanidae (6), Muscidae (6), Syrphidae (4), Tephritidae (3), Calliphoridae (3) and Tachinidae (3). The collection was re-curated and ordered by A.H. Kirk-Spriggs, who identified all material to family level. The percentage of the collection identified to species and/or genus has not been calculated. Only 2,940 Diptera have been digitised to date.

National Collection of Insects (ARC-PPRI), Pretoria

The South African National Collection of Insects (SANC), Plant Protection Research Institute, Agricultural Research Council, is one of the four components comprising the National Collections cluster, the others being arachnids, fungi and nematodes. A number of outstanding entomologists and other scientists have contributed knowledge and taxonomic expertise and have left an indelible legacy in the form of scholarly works and physical collections in the 104-year history of SANC. These have contributed significantly to the fundamental knowledge-base of biodiversity and agricultural sciences in South Africa and beyond. Among them is the acclaimed dipterist H.K. Munro (see biography above), the founder and main contributor to the extensive holdings of Diptera in SANC, but who is best remembered as one of the world's preeminent fruit fly (Tephritidae) taxonomists. He is consequently the central figure in the narrative of the Diptera collections of SANC.

The South African National Collection of Insects grew from the Parasite Laboratory located in a house in Wessels Street, Sunnyside, Pretoria, which was established to deal with issues related to biological control of agricultural pests. In 1912, this became the Division of Entomology in the Department of Agriculture of the Union of South Africa. Munro was transferred from East London to Pretoria in 1925 and inherited five insect cabinets, which became the core of SANC. Munro concentrated on Diptera, becoming internationally renowned for his taxonomic work on fruit flies. He was also in great demand to identify many other families of flies. In 1962, the Division of Entomology became the Plant Protection Research Institute (PPRI), situated in the Agriculture Buildings in Beatrix Street, Pretoria. This building, known as the "V-Building" was initially constructed as a military hospital during World War II, but was fortunately never used for its intended purpose. Munro remained in the V-Building long after his official retirement, to continue his research that culminated in his revision of the subfamily Dacinae. The Diptera collection was finally moved in 1979 to join the rest of the National Collection of Insects at Vredehuis near the Union Buildings in Pretoria. On the formation of the Agricultural Research Council in 1992, PPRI was transferred from the Department of Agriculture and SANC was incorporated into the Biosystematics Division, which comprised all collections mentioned above. In 2010 all the collections were moved from two localities within Pretoria to a custom-built building for the Biosystematics Division at Roodeplaat, east of Pretoria.

The Diptera collection was built through the active fieldwork of H.K. Munro, including his participation in the Vernay-Lang Kalahari Expedition of 1930. He also identified many flies submitted by state entomologists posted at the many field stations run by the Department of Agriculture throughout the country. Munro developed extensive international contacts and exchanged material with specialists throughout the world, but especially concentrated on African species. Many specimens were sent to the then Commonwealth Institute of Entomology in London, U.K. for identification if there was no reference material in South Africa. Several entomologists have donated Diptera collected during field trips, including Mervyn William Mansell (1944–living) and other staff members, and the collection is especially rich in species of agricultural and environmental importance, including many reared specimens with associated host data. Specimens continue to be submitted for identification after being intercepted in shipments; where they are found to be causing damage; or as part of university or other institute field surveys. Diptera associated with alien invasive plants in their countries of origin are also deposited in case these prove to be useful as biological control agents. Large orphan collections have been incorporated from other sources, including ARC-PPRI Rosebank (Cape Town), the Entomology collections of the ARC-Vegetable and Ornamental Plant Institute the University of Pretoria and the Council for Scientific and Industrial Research, Australia (CSIRO) collection of the University of Cape Town.

Mansell was the next custodian of the Diptera collection (employed 1979–2004), initially working with Munro and continuing today to provide his expertise in the identification of Diptera long after his retirement. More recent work on the Tephritidae has been undertaken by M. De Meyer (Fig. 91), Ian Murray White (1954–living), Amnon Freidberg (1945–living) and David Lawrence Hancock (1950–living). J.G.H. Londt (Fig. 80) (see biography above) has also kept the Asilidae up to date. The Bombyliidae were studied by A.J. Hesse (see biography above) and J. Bowden and the Tachinidae were identified by Roger Ward Crosskey (1930–living), C.H. Curran and D.A. Barraclough (Fig. 81) (see biography above). A valuable collection of termitophilous Phoridae was contributed by William Geoffrey Harrower Coaton (1911–1983), which was studied by Ronald Henry Lambert Disney (1938–living).

The collection comprises *ca* 48,000 predominantly pinned Diptera specimens, representing *ca* 4% of SANC overall collection holdings. The collection includes 490 primary types of Diptera. A total of 82 families of Diptera is represented, with the dominant families being Tephritidae (133 genera), Tachinidae (93), Asilidae (68), Syrphidae (44), Muscidae (39), Chloropidae (23) and Bombyliidae (21). About 70% of the main reference collection has been identified at least to genus level. Pinned material is stored in glass-topped drawers in wooden cabinets using a unit tray system (Figs 109, 110). Slide mounts of wings prepared by H.K. Munro are stored in wooden slide cabinets. Associated literature, card indices and correspondence are stored in the same collection room. There are a few specimens preserved in 70% ethanol, including Cecidomyiidae and termitophilous Phoridae stored in vials in larger bottles in a wet collection storage room maintained at low temperature.

Digitisation of the Diptera collections commenced in 2000, with only specimens from South Africa identified to species level being recorded. Each digitised specimen has a blue database label attached. Only the Asilidae collection has been updated since then to reflect changes in nomenclature. There are currently 4,100 digitised series. The database was designed by Mansell and Brian Kenyon.

No Diptera taxonomist or curator is currently employed by the Institute, but the former Collections Manager, Rosalind Patricia Urban (1950–living) (employed 1992–2015), curated the Diptera from 2004 until retirement. Recent curation efforts have concentrated on reorganising the Diptera into a more current classification system and incorporating about two cabinets full of previously unsorted material which was identified to family level by A.H. Kirk-Spriggs.

Iziko South African Museum, Cape Town (South African Museum)

The South African Museum was founded in 1825 and its collections are the oldest of their kind in South Africa with the earliest specimens dating from the 1840s. Although there were insects at the Museum from its earliest days, it was really only when Roland Trimen (1840–1916) first became involved with the Museum in 1866 that the Museum's insect collection had its inception (van Noort & Robertson 2012).

Albert J. Hesse (see biography above) was the first full-time dipterist employed at the Museum and indeed in South Africa and his contribution was substantial. He began work at the Museum in 1924, overlapping with the coleopterist Louis Albert Péringuey (1855–1924) for about a year. When he began the job, he was well qualified as a parasitologist, but had no entomological training. Hesse holds the record as the longest serving member of staff in the Museum, having worked there for 51 years. He reached retirement age in 1955, but was employed for 19 years after this, only leaving the Museum in 1974. Hesse's main research interest was Diptera and he published some large revisions of the Bombyliidae and Mydidae (Hesse 1938, 1956*a*, 1956*b*, 1960, 1969) (Cochrane 2006; van Noort & Robertson 2012). During the Hesse period, Harold Gordon Wood (1907–?) worked as an honorary entomologist and produced papers on Dixidae (Wood 1933, 1934) and a monograph on the crane flies (Tipulidae) of the south-western Cape (Wood 1952).

The majority of Diptera material in the collection was collected by A.J. Hesse and other Museum staff. Hesse undertook extensive expeditions to the former South West Africa (Namibia) (the Kaokoland Expeditions) in 1923, 1925, 1926 and 1933, with Reginald Frederick Lawrence (1897–1987) (Arachnologist, 1922–1935) and Charles W. Thorne (1906–1962) and Humphrey Zinn (general technicians at the Museum). He also took part in South African Museum Expeditions in the 1920s to the Western and Eastern Cape Provinces of South Africa and his favourite area for collecting, the Karoo in South Africa. There are numerous specimens in the Diptera accessions resulting from these expeditions, especially from S.W. Africa, representing important early Diptera material from Namibia and elsewhere. The collection also includes important material collected by Hans Heinrich Justus Carl Ernst Brauns (1857–1929) in the Willowmore area of the Eastern Cape, South Africa (although the bulk of his material is now housed in the KwaZulu-Natal Museum).

According to figures supplied for October 2015, there are 14,682 digitised catalogue records of Diptera in the collection, representing 41,275 specimens (van Noort *et al*. 2015). This only comprises digitised curated specimens and there are *ca* 30 drawers of pinned unidentified Diptera material that still require digitisation. A.H. Kirk-Spriggs has sorted material in the accessions to family on several occasions in order to make material more accessible to specialists. Pinned specimens are preserved in glass-topped insect drawers in wooden cabinets, using a unit tray system. The majority of the pinned specimens are digitised.

The entomology collection includes thousands of bulk insect samples (*ca* 9,500 unique collecting events), collected over the past 25 years by Simon van Noort (1964–living), Hamish Gibson Robertson (1959–living) and colleagues. These samples are preserved in 96% ethanol and emanate from inventory surveys conducted in Central African Republic, Gabon, Namibia, South Africa, Tanzania and Uganda, using a wide variety of collecting methods, including Malaise traps, sweeping, yellow pan traps, pitfall traps, Winkler bag extraction of leaf litter, and UV-light trapping, as well as general hand collecting. The samples remain unsorted, but contain many thousands of Diptera.

National Institute for Communicable Diseases, Johannesburg (South African Institute of Medical Research)

The Diptera collection now housed in the National Institute for Communicable Diseases (NICD) is the collection formally housed in the South African Institute for Medical Research, Johannesburg (SAIMR). The SAIMR was incorporated into the National Health Laboratory Service (NHLS) in 2002 and the NICD is an in-house institute of the NHLS. At the time of writing (August 2016), there are plans for NICD to become part of the "National Public Health Institute of South Africa" embedded in the National Department of Health.

The Diptera collection comprises *ca* 43,000 specimens. The Diptera families Culicidae (*ca* 30,000 specimens), Ceratopogonidae (8,000), Psychodidae (3,000) and Simuliidae (2,000) are best represented. All specimens are identified at least to genus level and probably 95% to species. Material originates mainly from the SADC region, but with a good number of specimens from Côte d'Ivoire, Democratic Republic of Congo, Ethiopia, Kenya, Nigeria, Uganda and the Indian Ocean islands. The material is either pinned (stored in 125 wooden cabinets) (Figs 111, 112), or slide-mounted (stored in 170 slide boxes) in a permanently air-conditioned facility (M. Coetzee, pers. comm. 2015).

The Diptera collection was begun in *ca* 1930 by B. de Meillon (see biography above), who undertook extensive Culicidae surveys in South Africa and neighbouring countries until the end of WWII and the advent of DDT for house spraying, at which time the malaria problem was thought to have been solved. He then changed his focus to other medically important Diptera and developed the Ceratopogonidae and Simuliidae collections. Fritz K.E. Zumpt (see biography above) was employed as Curator from 1948 to 1981, during which time he actively developed an extensive collection of Calliphoridae (incl. Rhiniidae), Muscidae, Oestridae and Sarcophagidae. Hugh Edward Haldane Paterson (1926-living) was also employed during the early 1950s under Zumpt, collecting and identifying Muscidae and also describing new species. This important collection was transferred as a donation to the KwaZulu-Natal Museum in 1983 (see above). The Psychodidae collection was established by Ian Hugh Davidson (1953–living) in the 1980s. The Culicidae collections (Figs 111, 112) have been added to over the years by James Muspratt (1910–1985), Peter Graham Jupp (1936–living), Bruce Merton McIntosh (1919–2005) (employed 1958–1980), Maureen Coetzee (1951–living) and Anthony

John Cornel (1962–living), the last two named providing collections where the slide-mounted immature stages are linked to the corresponding pinned adults. Many of the Anophelinae (Culicidae) species have also been characterised genetically, either chromosomally, enzymatically or by molecular methods (M. Coetzee, pers. comm. 2015). The collection is partially digitised and lists of Culicidae and Ceratopogonidae type specimens have been published (Segerman 1990, 1995).

Onderstepoort Veterinary Institute, Onderstepoort, Pretoria

The Onderstepoort Veterinary Institute (OVI) is administered through the Agricultural Research Council of South Africa (ARC-OVI). The Institute deals with the diagnostics, biosystematics and control of insects of veterinary importance, as well as technology transfer to commercial and subsistence farmers, students and the general public. The maintenance and expansion of the reference collections, databases and identification keys as well as the development of new research areas form an integral part of projects (G. Venter, pers. comm. 2015).

The collection was established in the 1970s and comprises pinned, alcohol and slide-mounted specimens (Fig. 98). The collection consists mainly of Diptera (95%), although some other orders are also represented, including Coleoptera, Lepidoptera, Neuroptera, Phthiraptera and Siphonaptera. The Diptera collection includes the genera *Musca* L. and *Stomoxys* Geoffroy (Muscidae), mostly collected by Errol Matson Nevill (1938–living), *Glossina* Wiedemann (Glossinidae), *Aedes* Meigen, *Anopheles* Meigen and *Culex* L. (Culicidae) and *Culicoides* Latreille (Ceratopogonidae). Establishment of the *Culicoides* collection can be linked back directly to René Michel du Toit's (1904–1988) (Fig. 87) seminal discovery that *Culicoides* (not mosquitoes) are vectors of the viruses that cause bluetongue and African horse sickness. This occurred in 1943 in the midst of WWII. At the time B. de Meillon (who was employed at the South African Institute for Medical Research) (see biography above) was South Africa's premier (and only) vector taxonomist and, by the early 1930s, had already commenced his studies on South African *Culicoides*. Shortly after WWII, Onderstepoort initiated its own *Culicoides* programme and towards this end

Figs 1.102–106. Examples of Diptera collection facilities in Southern Africa and the Indian Ocean islands: (102) Diptera collection room of KwaZulu-Natal Museum, South Africa; (103) same curated drawer of Tabanidae; (104) Diptera collection cabinet of Museu de História Natural, Maputo, Mozambique; (105) same, Parc Botanique et Zooligique de Tsimbazaza, Antananarivo, Madagascar; (106) same. Figs 102, 103 (photographs courtesy B.S. Muller), Fig. 104 (photograph courtesy K.F.L. Muambalo); Fig. 105 (photograph courtesy G. Goergen); Fig. 106 (photograph courtesy M. Hauser).

employed Otto Georg Hans Fiedler (1912–1998), who went on to produce (in 1951) a small monograph on the 22 species that occur in the region. Foreign visiting scientists continued these studies, *e.g.*, Victor [Vitor] Manuel Pais Caeiro (1929–2007) from Portugal, who in 1961 completed a monograph of the *Culicoides* of Angola. Thereafter, as a protégé of R.M. du Toit, E.M. Nevill joined the Onderstepoort team. He continued to build on the biting midge collections and in collaboration with

Figs 1.107–112. Examples of Diptera collection facilities in East and Southern Africa: (107) insect collection room of National Museums of Kenya, Nairobi; (108) same, photographic imaging of Culicidae collection; (109) insect collection room of the National Collection of Insects (ARC-PPRI), Pretoria, South Africa; (110) same, re-organisation of the Diptera collection; (111) part of the *Aedes* Meigen (Culicidae) collection of the National Institute for Communicable Diseases, South Africa; (112) same, drawer of identified *Anopheles* Meigen (Culicidae) mosquitoes. Figs 107, 108 (photographs courtesy L. Njoroge), Figs 109, 110 (photographs courtesy V. Uys), Figs 111, 112 (photographs courtesy M. Coetzee).

Michel Cornet (1930–living) and Jean Clastrier (1910–1997) developed knowledge of the taxonomy of *Culicoides* and *Leptoconops* Skuse. Rudolf Meiswinkel (1952–living) was appointed in 1983 and focused narrowly on the subgenus *Avaritia* Fox, in particular the *Culicoides imicola* species complex. The collection was mainly built through fieldwork and surveys conducted since 1990 by R. Meiswinkel and Karien Labuschagne (1972–living). The research focus since 1990 has been almost exclusively on *Culicoides* species and their distribution throughout South Africa. This focus includes the lengthy and detailed studies conducted by Gert Johannes Venter (1960–living) on the few species, in particular *C. imicola* Kieffer and *C. bolitinos* Meiswinkel, known to act as vectors for those viruses that in livestock, across the continent, cause diseases, such as bluetongue, African horse sickness and equine encephalosis.

The pinned collection is housed in one large cabinet, consisting of 42 drawers (Fig. 97) and two smaller cabinets with 10 drawers each. Specimens with collecting information are stored in small separate boxes arranged by genus. The spirit-preserved collection consists mainly of *ca* 15,000 black light trap samples of *Culicoides* (*ca* > 40 million specimens), sampled since 1990. Data on collection site/area, total number of *Culicoides* in each sample, together with species breakdown (female: nulliparous, parous, gravid, blood-fed and males) are recorded on both a database and a file system. This collection is fully digitised and is updated constantly. The slide collection consists of *ca* 12,000 microscope slides of 720 species from 190 localities. The collection includes more than 200 *Culicoides* and 500 other nematocerous species, such as the genera *Atrichopogon* Kieffer, *Bezzia* Kieffer, *Dasyhelea* Kieffer, *Forcipomyia* Meigen (Ceratopogonidae) and *ca* 60 other genera. The slide-mounted collection is stored on *ca* 100 slide boxes.

In addition, colonies of *Glossina* (*Austenina*) *brevipalpis* Newstead and *G.* (*G.*) *austeni* Newstead (Glossinidae) were established at the Institute from material obtained from *Tsetse* and Trypanosomiasis Research Institute (TTRI), Tanga, Tanzania and Seibersdorf, Austria in 2002. In South Africa these two *tsetse* species occur mainly in the game reserves and rural communities close to reserves in northern KwaZulu-Natal Province and cause *nagana* in animals. This represents the only *G. brevipalpis* laboratory colony in the world (G. Venter, pers. comm. 2015).

Research at ARC-OVI is focused on the role of insects in disease transmission, with Diptera research restricted to the control of *tsetse* and *Culicoides* species as vectors of animal trypanosomiasis and orbiviruses respectively. The *Culicoides* reference collection is indispensable in species identification and the creation of risk maps. Behavioural and competitive studies conducted with flies obtained from *tsetse* colonies will form the baseline for field control of *nagana*. The Diptera collection is almost fully digitised.

Durban Natural Science Museum, Durban (Durban Natural History Museum)

The entomological collections of the Durban Natural Science Museum comprise *ca* 141,000 specimens, *ca* 7,226 of which are Diptera. The best represented families are Asilidae (743 specimens), Syrphidae (608), Bombyliidae (479), Tephritidae (376), Culicidae (364) and Tabanidae (301). About 70% of specimens are identified at least to genus level. Most specimens are pinned and are stored in wooden cabinets with glass-topped drawers (K. Williams, pers. comm. 2015).

The collection was established in the early 1900s, but did not have a dedicated curator until 1976, when Clive Desmond Quickelberge (1930–living) was appointed as the first curator of entomology. His main interest was butterflies. Some Diptera specimens pre-date the establishment of the main collection, having collecting dates from the 1840s. The collection was mainly built through donations and staff fieldwork. Significant donors in the Diptera collection include: Cecil Newton Barker (1856–1936), Harold Walter Bell-Marley (1873–1946), Alfred Lionel Bevis (1897–1984), Rupert Augustus Lacy Brandon[1] (1872–?), Richard Kendall Brooke (1930–1996), Bevis & William Mark Davidson (1887–1961), Walter James Lawson (1937–living) and C.D. Quickelberge. Specimens originate from Lesotho, Malawi, Mozambique, South Africa, Swaziland, Zimbabwe, with several others smaller contributions (K.A. Williams, pers. comm. 2015).

The collection was moved from the main Museum at City Hall to the Research Centre of the Museum in 2008. This new facility has more space available, allowing collection growth and has a gas fire-release system, so in the event of a fire specimens would not suffer water damage, and the collection room has climate control. The Diptera collection has been fully digitised and collection development currently focuses on Diptera of forensic significance.

Stellenbosch University, Stellenbosch

The Diptera reference collection of Stellenbosch University is a small, but important collection of historical importance. It was established in *ca* 1919, probably encouraged by the then Head of Department Charles Kimberlin Brain (1881–1954). Students were trained in the use of identification keys; they were also expected to hand in a collection which was later added to the departmental collection (J. Giliomee, pers. comm. 2016).

The collection comprises 4,275 pinned Diptera specimens, representing 57 families, with the best represented and identified being the Tephritidae (855 specimens), Tabanidae (770) and Culicidae (622). About 10% of the collection is identified at least to genus level. Specimens in the collection mainly originate from South Africa, with some material from other African countries, including Kenya, Liberia, Malawi, Mozambique, Namibia, Sierra Leone, Tanzania (incl. Zanzibar) and Uganda. There is also extralimital material, especially of Culicidae from China (Hong Kong), Israel, Italy, Japan and Macedonia. The Diptera collection appears to have been largely developed by Johan Georg Theron (1924–1988), former professor in the Department, whose specimens form the core of the collection, but there are numerous collectors named on the labels including the following better known collectors: William Mansfield Aders (1881–1934), A.L. Bevis, J.H.J.C.E. Brauns, Patrick Alfred Buxton (1892–1955), William Alfred Stedwell Lamborn (1877–1960), J.G.H. Londt (Fig. 80) (see biography above), H. Macfarlane, E.M. Malan, H.K. Munro (see biography above) and S.A. Neave. Material in the collections has been identified by numerous leading dipterists, including Enrico Adelemo Brunetti (1862–1927), Gilbert Ernest Bryant (1878–1965), R.W. Crosskey, B. de Meillon (see biography above), F.W. Edwards, J.W. Edwards, P. Freeman, H.K. Munro (see biography above), J.G. Theron and F.I. van Emden.

As this is a university collection, there has never been a full-time curator. The collection forms part of the Insect Museum of the Department of Conservation Ecology and Entomology. The collection is stored is glass-topped insect drawer in J.J. Hill cabinets. There is evidence of pest infestations in some parts of the collection, but the Diptera are largely unaffected. The collection has not been digitised.

Rhodes University, Grahamstown

The small insect collection of the Department of Zoology and Entomology of Rhodes University was developed in the late 1960s and was mostly accumulated through specimens from students' coursework collections. The majority of the more interesting specimens were transferred to the Department of Entomology and Arachnology of the Albany Museum, including the significant Diptera collection of Patrick Elliot Hulley (1937–living). The majority of specimens in the collection originate from South Africa, with some material from other southern African countries.

The Diptera collection comprises *ca* 3,000 specimens, only about 1% of which are identified to genus level. The best represented families are the Asilidae, Bombyliidae, Tabanidae and Calliphoridae, but generally larger-bodied specimens are represented. Specimens are stored in glass-topped insect drawers in wooden cabinets. As this is a university collection, there has never been a full-time curator. A.H. Kirk-Spriggs identified parts of the collection to family level and re-curated it. The collection has not been digitised.

University of Pretoria, Pretoria

The Diptera Collection of the Department of Zoology and Entomology of Pretoria University was officially donated to the National Museum, Bloemfontein in 2009 and is now being incorporated into the main collection and being digitised.

Zimbabwe

Natural History Museum of Zimbabwe, Bulawayo (Rhodesia Museum, National Museum of Rhodesia)

The collection of the Natural History Museum of Zimbabwe, Bulawayo, is the largest collection in the Southern African subregion outside South Africa (Ritchie 1987), with collections estimated at *ca* five million specimens (including 3,200 primary types). The collections are especially rich in the orders Odonata, Lepidoptera and Diptera (Hancock *et al*. 1995; Ritchie 1987). The collection includes *ca* 12,403 Diptera, mainly Tephritidae (*ca* 626 specimens; 322 of which are types), but Hancock *et al*. (1995) listed type material of Diptera in the families Asilidae, Bibionidae, Bombyliidae, Calliphoridae (incl. Rhiniidae), Ceratopogonidae, Mydidae (as Mydaidae), Nemestrinidae, Platystomatidae, Sarcophagidae, Sciomyzidae, Stratiomyidae, Syrphidae, Tachinidae, Tephritidae (incl. Tachiniscidae), Therevidae, Tipulidae and Vermileonidae (as Rhagionidae). The Diptera material mainly originates from Botswana, Cameroon, Democratic Republic of Congo, Malawi, South Africa, Uganda, Zambia, Zimbabwe and Seychelles, with 83% of Diptera currently identified to species level and 17% to genus level. All specimens are pinned and are preserved in 89 glass-topped drawers in J.J. Hill cabinets.

The Rhodesia Museum was established in 1902, initially with rooms in the Bulawayo Public Library. The Museum moved several times between 1910 and 1960, when construction of the current building began, which opened to the public in 1964. In 1936 the Government acquired the museum and it was renamed the National Museum of Rhodesia. In 1981, following centralisation, the National Museum was renamed the Natural History Museum of Zimbabwe and all natural science collections from elsewhere in the country were incorporated. The Entomology Department was formally established in 1911, with the first curator being the renowned hymenopterist George Arnold (1881–1963), who served as Curator from 1917 to 1947, when he formally retired. He was replaced by Elliot Charles Gordon Pinhey (1910–2000), who served as Keeper of Invertebrate Zoology from 1955 until his retirement in 1980. The only dipterist to be employed as Curator in the Museum was D.L Hancock (appointed as lepidopterist with an understanding that he would also work on Diptera), who served from 1981–1986. During this period he concentrated on surveying the Tephritidae fauna of Zimbabwe (also sampling Platystomatidae and Diopsidae), later publishing an annotated checklist of species (Hancock 2003), and on development of the Tephritidae collection. Most other flies in the collection were collected during general staff collecting trips or by interested members of the public. The catalogue of Hancock *et al*. (1995) indicates that Diptera material was examined and identified by numerous leading dipterists, including C.P. Alexander, Michel Bequaert (1890–1974), C.H. Curran, D.E. Hardy, A.J. Hesse (see biography above), Bertram Maurice Hobby (1905–1983), John Russell Malloch (1875–1963), H.K. Munro (see biography above) and B.R. Stuckenberg (see biography above) (Fig. 77). The collection of Tephritidae, which was largely built by D.L. Hancock, is currently the subject of a digitisation project by M. Mansell.

Plant Protection Research Institute, Harare (Department of Agriculture, Salisbury)

The Diptera collection of the former Department of Agriculture, Salisbury (then Southern Rhodesia), represents one of the most significant historical collections of Diptera from Zimbabwe. It was established by the Scottish dipterist A. Cuthbertson (see biography above), who joined the Department in 1926, with the earliest Diptera specimens dating from 1927.

The collection comprises 7,541 specimens of 1,328 species. Sixty families of Diptera are included in the collection, with the best represented being the: Tachinidae (1,054 specimens; 156 species), Muscidae (907; 164), Calliphoridae (incl. Rhiniidae) (686; 97), Asilidae (600; 124), Tabanidae (454; 73), Syrphidae (357; 55), Bombyliidae (354; 99), Tephritidae (317; 73), Culicidae (311; 48), Tipulidae (incl. Limoniidae) (274; 57), Sarcophagidae (274; 52) and Diopsidae (229; 27). The collection consists of specimens originating from Malawi (as Nyasaland) and Zimbabwe (as Southern Rhodesia), but also includes specimens from other countries, resulting from exchanges and donations. The collection is especially rich in reared material, resulting from Cuthertson's research on biology and behaviour and includes some type material.

There are 40 donors of material in the Diptera collection (based on specimen data labels), with significant local donors being Bertram Durrell Barnes (1888–1969), A. Cuthbertson, J.E. Drysdale, C.V. Messer and M.C. Mossop. Better known international dipterists and collectors who contributed to the collection include A.L. Bevis, J.H.J.C.E. Brauns, C.H. Curran, B. de Meillon, D.L. Hancock, H.K. Munro, H. Oldroyd, James Jenkins Simpson (1881–1936) and H.G. Wood. All specimens are pinned and are preserved in 52 glass-topped drawers in J.J. Hill cabinets. The collection is well arranged (Fig. 115), but has not been formally digitised. A detailed list of drawer contents is available (S. Nyamutukwa, pers. comm. 2017).

Endnote

[1] Brandon was a magistrate in the former Zululand (later in Lüderitz, Namibia). He collected a *tsetse* in his courthouse and donated it to the Durban Museum. This subsequently turned out to be a new species and was published in 1915 (N.L. Evenhuis, pers. comm. 2015).

Figs 1.113–116. Examples of Diptera collections in West, Southern and East Africa: (113) part of insect collection, University of Ibadan, Nigeria; (114) same, drawer of Sarcophagidae (inset detail); (115) drawer of Tephritidae, PPRI collection, Harare, Zimbabwe; (116) Diptera collection store boxes, Vector Control Division, Entebbe, Uganda. Figs 113, 114 (photographs courtesy A.A. Omoloye), Fig. 115 (photograph courtesy S. Nyamutukwa), Fig. 116 (photograph courtesy A.G. Masaba).

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COLLECTION AND PRESERVATION OF DIPTERA

2

Ashley H. Kirk-Spriggs

Introduction

This chapter is chiefly intended for students of dipterology, to assist in applying the most effective techniques for sampling and preparing Diptera. The chapter does not comprehensively deal with all methods, as space does not allow it, nor does it deal with collection curation and management.

Collecting and sampling techniques for insects, in general, have been covered in a number of publications, *e.g.*, Ford (1973), Oldroyd (1970), although many techniques outlined in these publications have subsequently been improved upon. The British Museum (Natural History) (1900) published a guide to collecting Diptera and various collecting techniques and methods are outlined in Chandler (2010). A comprehensive account of techniques for collecting and preserving insects, spiders and mites is provided by Martin (1977). Some techniques for Diptera specifically were covered in Brown (2009: 1–7) and Marshall (2012: 549–555), but no comprehensive chapters dealing specifically with collecting and sampling techniques have been published in the previous regional Diptera manuals. This chapter is based largely on personal experiences of sampling and preserving Diptera in the Afrotropical Region and elsewhere in the tropics and includes those methods the writer has found to be most effective in sampling and preserving a wide range of fly families. Superscript numbers used in the below text apply to the examples of equipment suppliers as listed in the Appendix.

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Collecting

Flies are fragile and great care is required in their collection and preparation if good quality specimens are to result.

Sweep netting

Sweep netting is a highly effective method for sampling Diptera and can be used in most habitat types. The sweep net (Fig. 1) is the basic piece of sampling equipment employed by the majority of dipterists for general sampling and various designs of nets are available[1, 2, 5, 7]. Dipterists have their own preferences as to which net design suits their needs best, but the basic net comprises a sturdy wire or alloy frame, a wooden or metal handle and a fine-meshed net bag. Dipterists who use the net principally for netting individual flies generally prefer a finer meshed net bag, while those who use the net primarily for sweeping prefer a coarser net bag that is less likely to get entangled in vegetation, or be torn by thorns, *etc*.

Sweep nets can be used to net individual, or swarming, flies in flight or, more normally, to sweep through low vegetation and the lower branches of trees, bushes and shrubs (Fig. 1). The net can also be swept over leaf litter and other substrates, or be used to sample directly from dung and other decomposing animal or vegetable matter. Extraction of flies from the net can be achieved, either by collecting the larger flies directly into individual vials (*e.g.*, Fig. 39), or by extracting smaller flies with an aspirator (pooter)[1, 2, 3, 5, 7] (*e.g.*, Fig. 38). This latter normally requires placing the head into the net bag and holding the apex of the net up towards the light while flies are aspirated from the net (Fig. 2). Some dipterists prefer to concentrate flies in a net with a tube-shaped apex the same size as the killing bottle, thus facilitating transfer of the entire catch into a killing tube.

Another method of extracting flies from sweep net samples (used for many years by hymenopterists), known as a "photoeclector", is employed by some dipterists (Černý & von Tschirnhaus 2014, figs 1–3). This comprises a wooden box painted black inside, with a funnel and emergence container. A sweep net sample is placed into the black box and the lid (with the funnel and emergence chamber attached) is replaced. Over time flies then moved from the sample towards the light and eventually end up in the emergence chamber. This method appears to extract more specimens and species from each sweep net sample than use of an aspirator alone (Černý & von Tschirnhaus 2014).

Malaise trapping

The Malaise trap (Figs 9–14) can perhaps be regarded as the single greatest advancement in the general sampling of Diptera, and other flying insects, to have been developed in the past eight decades. Since the Swedish entomologist René Malaise (1892–1978) developed the first trap (Malaise 1937), there have been numerous other designs, modifications and improvements, but the principle of the Malaise trap remains largely the same.

A Malaise trap is essentially a flight interception trap that relies on the fact that many flying insects are positively heliotropic (meaning they move towards the light). Marshall (1982) noted, however, that many small flies rarely move to the apex of the Malaise trap and thus are not captured. He noted that pan traps placed under the barrier panel of the Malaise trap collect larger numbers of some families of Diptera than either the trap-head collecting device of the Malaise trap alone, or pans deployed away from the trap. Malaise trapping catches can, therefore, be optimised by using these two methods in combination.

Whatever the design, a Malaise trap superficially resembles a tent with open sides for insects to fly into and a tall barrier panel that directs them upwards into a cylinder containing a killing agent.

As an example of the effectiveness of Malaise traps in the collection of a wide range of families, it is perhaps worthwhile noting, that in the past decade or so the writer has sampled 96 of the 108 recorded Afrotropical families using this method, including the rarely collected families Atelestidae, Marginidae and Neminidae. The families not collected include those that are exceedingly rare, or have limited habitat-specific distributions, or only occur in the inter-tidal zone, where such traps are not normally deployed.

Selection of Malaise trap sites is important in maximising the number of flying insects that pass through the opening of the trap, and this must be largely determined by assessing the natural features of the site, such as topography, vegetation, wind and presence of water.

As these traps mainly collect insects that fly close to the ground, or around obstacles, natural corridors, or "flight paths", should be identified through which traps can be deployed. Flight paths include, bush paths, forest trails, natural clearings and edges, disused secondary roads, natural breaks in the vegetation, streams and *wadies*, ephemeral river beds and drainage channels (in arid areas). Of course, in open savanna country and tropical forests where trees may be quite evenly spaced, the positioning of traps is somewhat hit and miss, but traps that are unproductive can always be moved elsewhere.

For ground sampling, two main Malaise trap designs are now widely used by dipterists: the Townes-style trap (Townes 1962, 1972) and the Gressitt and Gressitt-style trap (Gressitt & Gressitt 1962) and these shall be dealt with separately below. As many insects are of course associated primarily with the forest canopy, specially modified "aerial Malaise traps" have also been developed that can be hoisted into the canopy[7].

The Townes-style trap[1, 2, 3, 4, 5, 7] (Figs 9–11, 13) is approximately 2 meters in length, with a sloping roof and killing bottle at one end. These traps are ideal for deploying across narrow flight paths, such as breaks in vegetation between shrubs, bush paths and across narrow stream beds. Several slightly different designs are available commercially[1, 2, 3, 4, 5]. An alternative is to have the netting component of the trap made by a seamstress locally and then look for suitable components to construct your own collecting heads.

The Gressitt and Gressitt-style trap[2, 3, 4] (Figs 12–14) is considerably larger (6 meters in length and at least twice the height) and the opening of the trap has a surface area approximately

Figs 2.1–8. General and passive sampling methods for Diptera: (1) use of a sweep net; (2) extraction of specimens from a sweep net using an aspirator (pooter); (3) hanging "butterfly trap", baited with fermenting fruit bait; (4) fogging forest trees with a backpack mist sprayer; (5) fogging sheets to collect specimens below forest trees; (6) light trap ("sheeting"); (7, 8) emergence traps deployed on stream margins. Figs 1, 2 (photographs K. Pannecoucke), Figs 4, 5 (photographs courtesy C. Haddad), Fig. 6 (photograph S. Otto), Figs 7, 8 (photographs courtesy M. Ivkovic).

Figs 2.9–14. Examples of Malaise traps deployed in various habitat types: (9) Townes-style trap, deployed in Central Zambezian Miombo Woodlands (Kafue National Park, Zambia); (10) same, deployed in disturbed Guineo-Congolian Rainforest (Likombo Forest, Democratic Republic of Congo); (11) same, deployed in *Acacia* savanna (Florisbad, Free State, South Africa); (12) Gressitt and Gressitt-style trap, deployed in *Brachystegia* woodland (Réserve Naturelle de Rumonge, Burundi); (13) Townes-style trap (left) and Gressitt and Gressitt-style trap (right), deployed in Mountain Fynbos gully (Jamaka farm, Western Cape, South Africa); (14) Gressitt and Gressitt-style trap, deployed in Rift Valley Afromontane forest (Parc National de la Kibira, Burundi). Fig. 13 (photograph © S.A. Marshall).

10 times greater than that of the Townes-style trap (both sides considered). The killing bottles are much larger and are positioned at both ends. These factors combined result in captures that are exponentially greater. Traps are expensive, but well worth the investment. They are available from a number of equipment suppliers, but those supplied by John W. Hock are consistently good[3]. When purchasing a trap it is best to stipulate that the trap should be fine-meshed and preferably a dark colour. It is also best to purchase traps with alcohol heads rather than dry heads, as these are suitable for both wet and dry sampling.

The trap is specifically designed to be strung between two trees and it is important, when selecting a site, to ensure that the trees are not too far apart, or too close together. The trees selected should also have a suitable fork or branch at the correct height and thickness to support the trap. Another factor is to ensure that both bottles are in direct sunlight if possible. One end of the trap invariably collects better than the other and it is usually the one in better light. Once a suitable flight path and trees have been selected the main supporting ropes can be tied to a suitable flat stone or heavy piece of wood and be lobed over the fork or branch and hoisted up. Some shifting from end to end is usually required to get the trap at the correct height, but once this is done the other ropes used to hold the trap open can be unfurled and tied to suitable branches, vegetation, or large stones (dependant on what is available). It is advisable to add plastic covers over the collecting heads of Malaise traps (Figs 13, 14), as these may leak during heavy downpours and thunderstorms.

There are two general approaches to sampling with Malaise traps: dry and wet sampling. Wet sampling is very straightforward and 70% or 96% ethanol is added to the collecting bottle/s of the trap. This method is widely used for most general Malaise trap sampling, especially if traps are deployed in remote areas, or if long-term sampling is undertaken.

For dry sampling a killing agent (preferably hydrogen cyanide, although *Vapona* strips are also effective) is added to the collecting bottle/s and the trapped flies are collected dry in layers of tissue paper. A convenient dispenser for hydrogen cyanide is a film canister-sized plastic pot in which hydrogen cyanide is first placed and is then covered in plaster of Paris. The lids of the pots should have a circular hole cut through and have fine-meshed netting glued across. Pots must be kept moist and a few drops of acetic acid can improve the release of the cyanide gas. Dry traps need to be regularly serviced, usually in the early morning and late afternoon, but also at noon under very hot or dry conditions. The trap contents are emptied into a relaxing container and the flies are sorted and pinned dry (see sections below). The disadvantages of this method are that traps need to be accessible and must be serviced regularly.

Pan trapping

The use of pan traps of various colours to sample insects is now quite widespread practice among entomologists in various disciplines (*e.g.*, Cambell & Hanula 2007). Pan traps are effective for the sampling of a range of Diptera families, especially saprophagous flies in moist areas. If traps are placed on posts, or otherwise raised, they may also be effective for anthophilous groups. Yellow pans are most widely used, but blue and white pans are also productive and often collect different species. Any container of any size can be used, but plastic bowls are widely used and can be purchased cheaply direct from the manufactures[17].

Propylene glycol, a slow evaporating alcohol, can be used as a preservative for long-term pan trapping, but is expensive and less effective for smaller acalyptrates, probably due to its high surface tension. The use of water (plus sodium benzoate, salt, or other preservatives), with a few drops of detergent to break the surface tension is highly effective, but traps should be serviced regularly to prevent captured specimens from bloating and splitting. One drawback of this method is that specimens collected in this manner are generally not suitable for later DNA extraction (whereas with propylene glycol they are).

The main drawbacks associated with pan trapping are: flooding, following excessive rainfall, wind, theft and disturbance by domestic and wild animals. Holes can be punched in the rims of pan traps, so they drain without the loss of material and pans may be covered by screening to prevent flooding, but in the latter case this may result in a drop in trap efficiency. Traps can also be prevented from being blow away by securing them with pegs or a few rocks placed more or less evenly around the rim.

It is best not to place pans in areas where domestic livestock and wild animals are active. Pans tend to be deployed along paths that are also frequently used by livestock and, as a consequence, pans may be tipped over. Primates (especially Vervet monkeys and baboons), can be a menace, and once they have discovered a line of pans, will move systematically from one to the next turning each over and spilling the contents.

Light trapping

For the general entomologist, light trapping is an essential method for capturing a range of insects in many orders, but is not generally used as a major sampling technique by most dipterists. Light trapping is, however, often highly productive for Diptera, especially during the few hours following dusk, when many crepuscular species are active. Some species, or even families, of flies are strictly nocturnal (e.g., Ctenostylidae and Pyrgotidae) and light trapping is, therefore, the most productive technique for their capture. No two night's light trapping are the same in terms of species and trap catches also vary widely from site to site and from season to season. In general, tropical areas are most productive, but trapping in any habitat is a worthwhile exercise.

Perhaps the best method of light trapping for general Diptera sampling is known as "sheeting", in which a white bed sheet is strung between two poles, or is tied to other suitable natural supports (trees or shrubs). A mercury vapour bulb (MV), or black light, is hung in front of the sheet supported by a pole, powered either direct from the mains supply, if close to buildings, or by a portable generator in remote areas (in the case of MV lights), or by a 12 volt or motorcycle battery (for black lights). The sheet should not end at ground level, but be extended out onto the ground and can be held in place by a few large rocks to prevent the sheet blowing around. Care should be taken in the position of the light source. It should be positioned in the centre of the sheet, but should not be touching. MV bulbs get hot and the sheet can scorch, or even burn. Larger flies coming to light can be captured in individual glass vials and smaller flies can be collected direct off the sheet using an aspirator (Fig. 40).

Sheeting is advantageous in several ways: the sheet acts as a reflector, thus increasing the illuminated area; it is easier to capture flies against a white background; and the collector has the option to precisely select those flies to be captured as soon as they appear. The disadvantages are: the sheet needs to be regularly serviced; locating flies among a mass of other insects, especially moths, is often problematic; and MV bulbs have a habit a cracking, or shattering, even with a very light downfall of rain.

Emergence trapping

Emergence traps[3, 5, 7] are another often productive means of sampling flies (Figs 7, 8). Various designs are employed, but the basic trap is a conical frame, with fine-meshed netting on the slides and a collection bottle at the top. Marshall (2012: 553, foreground) illustrates a superior design of emergence trap that covers a greater surface area and has been used to effectively sample a wide variety of flies. Emergence traps can be placed over virtually any kind of substrate or potential breeding medium, but these traps are used more extensively to sample aquatic flies as they emerge. Following eclosion emergent flies enter the trap and move towards the collection bottle.

Baits, bait traps, sprays and lures

A range of flies are attracted to various natural or synthetic baits. These can be divided into three major groups: products of fermentation; products of vegetable decomposition (including dung); and products of animal decay. Flies visit such baits either to lay their eggs (or living larvae) for breeding purposes, or in the case of gravid female flies, for a protein meal required for maturation of developing ova.

Of particular attractiveness are fermenting liquids, due to the alcohols, esters and similar organic compounds that are released. An amazing array of flies (*e.g.*, Anisopodidae, Aulacigastridae, Anthomyiidae, Curtonotidae, Calliphoridae, Drosophilidae, Heleomyzidae, Micropezidae, Muscidae, Neriidae, Platystomatidae, Stratiomyidae, Sarcophagidae, *etc*.), can be captured using a simple fruit bait mixture of mangoes, bananas and/or guavas, mixed with a little sugar and brewer's (or baker's) yeast, which is then left in a warm place to ferment. Various other decomposing baits, including carrion (decomposing fish appears to work best), dung or faeces and decomposing fungi, can also be used to attract flies. Such baits can be left in natural situations (*e.g.*, smeared on leaves and fallen tree trunks), to be checked on a regular basis for flies, or can be used in passive traps.

A simple passive trap to deploy such baits is the hanging "butterfly trap" (Fig. 3). These traps were originally developed for the trapping of butterflies and are available commercially[5, 7]. A cheaper alternative is to make your own using flower pot holders, fine netting and wire. Only a small gap is left at the bottom of the trap into which flies enter and are then unable to escape. Trapped flies can be extracted either by removing the base of the trap and removing the flies with vials or an aspirator, or the entire trap can be placed in a bag with hydrogen cyanide.

Flies are also frequently attracted to other sweet liquids and a common method of sampling flies, especially in tropical forests, is to make a mixture of honey, water and cola (carbonated drink) and spray the solution onto leaves or fallen tree trunks with a mist-sprayer. These sites are then checked regularly for alighting flies. This method appears to generally be less productive in the Afrotropics than in other zoogeographical regions of the world, although effectiveness of these "artificial honeydew" sprays may be humidity-related and the method is probably more effective during the rainy season in more tropical regions (S.A. Marshall, pers. comm. 2015).

Various synthetic lures are now commercially available to monitor fruit flies (Tephritidae) of phytosanitary significance. Most of these are male-only parapheromone (*i.e*., chemicals not naturally used in intraspecific communication, but elicit responses similar to true pheromones) attractants (Cunningham 1989). These include: Cuelure[15], Methyl eugenol[15], PheroLure (EGOlure[16]), Terpinyl acetate[15], Trimedlure[15], *etc*. All of these will sample only a limited range of species, often within a particular genus (Anonymous 2013). These lures are deployed in the field using various trapping devices (Anonymous 2013) and flies can either be killed using Dichlorvos strips and be sampled dry for later pinning, or traps can be charged with propylene glycol to preserve specimens in spirit. In addition, there are also female-biased synthetic food lures that attract a wider range of fruit fly species.

Fogging

Fogging (often termed canopy fogging) is a method by which a pyrethrum-based insecticide (usually mixed with oil or water) is released into the canopy of trees, using a mist-blower and the drop down catch is collected using plastic or cloth sheets arranged below (Figs 4, 5). Fogging is not widely used by general collectors, but is a very effective means for the sampling of canopy-inhabiting flies, with the Diptera ranking fourth among other orders sampled (see review in Kirk-Spriggs & Stuckenberg 2009: 164–165). Sampled insects are normally removed from sampling sheets by use of a hand-held car vacuum cleaner and the catch is preserved in ethanol for later sorting.

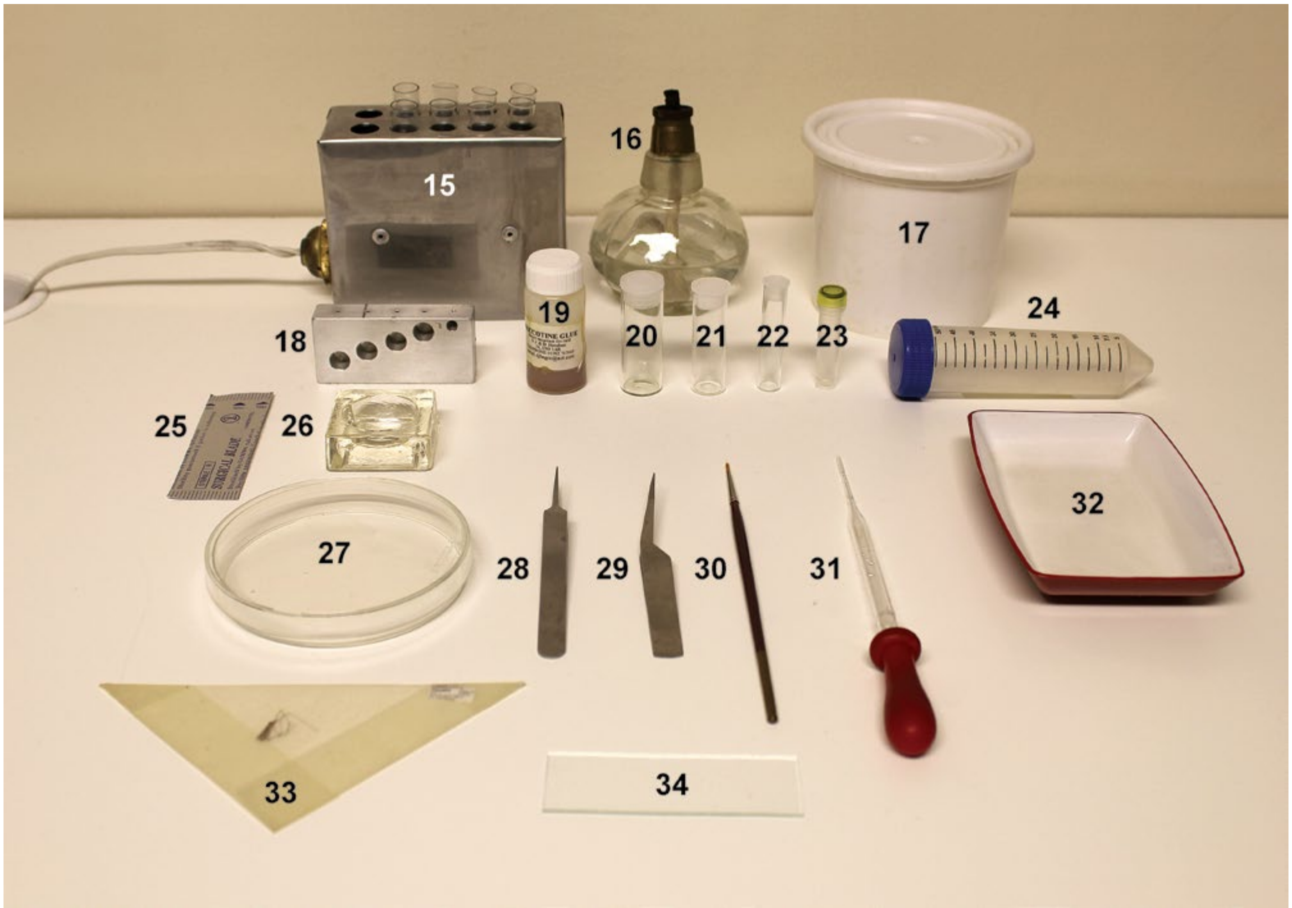
Hilltopping

Hilltopping is a phenomenon, apparently restricted to insects, in which males and virgin, or multiple-mating females, instinctively seek a topographical summit in order to mate. Flies often congregate at such sites and visiting isolated hilltops, usually in the early morning, can prove highly productive for the collection of flies. Skevington (2008: 1800), for example, lists 34 families of Diptera (not all of which are Afrotropical), that have hilltopping species. There are less data on hilltopping flies in Africa than for other regions, but hilltopping has been recorded for African butterflies (*e.g*., Lawrence & Samways 2002) and there is nothing to suggest that this phenomenon does not occur regularly for flies in the Afrotropical Region, at least under favourable conditions.

Preservation and preparation of specimens

Equipment for preparation of Diptera

The following basic tools are those preferred by the writer (other dipterists may prefer other equipment): **dry bath incubator**[12] (used for hot maceration of fly terminalia; terminalia can also be macerated cold) (Fig. 15); **spirit lamp**[1] (used to prepare genitalia vials, if preferred) (Fig. 16); **plastic relaxing pots**, with tight-fitting lids (used to relax specimens) (Fig. 17); **pinning stage**[1] (used to stage specimens and append labels at the correct heights) (Fig. 18); ***Seccotine* glue**[6] (used to glue specimens to point-mounts, pins, repairs, *etc*.; many alternative adhesives are available) (Fig. 19); **glass vials** with polythene stoppers (3 sizes: 10 ml[8], 7.5 ml[8], 2.5 ml[9]; used for permanent storage of spirit-preserved flies) (Figs 20–22); **50 ml centrifuge tubes** with screw caps[10] (used for field preservation of Malaise trap residues, coloured pan trap samples, *etc*.) (Fig. 24); **surgical (scalpel) blades**[10] (used to trim Nu-poly strips when double-mounting specimens) (Fig. 25); **excavated glass blocks**[1] (used for genital dissections and for slide preparations) (Fig. 26); **Petri dishes** (used to sort small spirit samples) (Fig. 27); **watchmaker's forceps**[1, 2] (size 4 used to micro-pin specimens, *etc*.; size 5 for genital dissections) (Fig. 28); **stork-billed (featherweight) forceps**[1, 2, 5, 7] (used for sorting spirit samples and handling delicate specimens) (Fig. 29); **camel hair brush** (used to clean or transfer delicate specimens) (Fig. 30); **glass pipettes** (used for decanting chemicals and for filling genitalia vials) (Fig. 31); **plastic sorting trays** (of various sizes, used to sort larger spirit samples) (Fig. 32); **glassine envelopes** (used for dry preservation) (Fig. 33); **glass slides and cover slips** (used to slide-mount specimens) (Fig. 34); **aspirator**[1, 2, 3, 7] (used to collect smaller Diptera) (Fig. 38); **modified tropical vials**[8] (used for field collection of Diptera) (Fig. 39); **Nu-poly strips**[1] (used to double-mount micro-pinned specimens) (Figs 54, 55); continental length stainless steel and black tempered **insect pins**[1, 2, 6, 18] (Nos. 1, 2 and 3; used for direct-pinning, staging, point-mounting, *etc*.); **micro-pins** (minutens)[1, 2, 6, 18] (Nos. 10, 15 and 20; used to micro-pin specimens in the field).



Figs 2.15–34. General equipment for specimen preparation: (15) dry bath incubator; (16) spirit lamp; (17) plastic relaxing container, with tight-fitting lid; (18) pinning stage; (19) *Seccotine* glue; (20–22) glass vials with polythene stoppers (3 sizes: 10 ml, 7.5 ml, 2.5 ml); (23) Eppendorf vial; (24) 50 ml centrifuge tube with screw cap; (25) surgical (scalpel) blades; (26) excavated glass block; (27) petri dish; (28) watchmaker's forceps; (29) stork-billed (featherweight) forceps; (30) camel hair brush; (31) glass pipette with rubber teat; (32) plastic sorting tray; (33) glassine envelope; (34) glass slide (and cover slips; not illustrated).

Chemicals for preparation of Diptera

The following chemicals are those preferred by the writer to preserve and prepare specimens: **2-ethoxyethanol** (for preparation of dry-pinned specimens from ethanol); **acetone** (for degreasing specimens); **Canada balsam** or **Euparal** ® (mounting media for slide-mounting; Canada balsam is less widely used today, but is still a recommended mounting agent for some fly groups); **clove oil** or **cedarwood oil** (to clear specimens during slide preparation); **ethanol** (for permanent preservation of specimens and genital dissections, *etc*.); **ethyl acetate** (to kill specimens in the field and for specimen preparation); **glacial acetic acid** (for genital dissections); **glycerine jelly** (to embed specimens for examination and illustration; some dipterists now use hand sanitiser gel, which serves the same purpose); **glycerol** (for temporary slides and genitalia vials); ***p*-chlorocresol** (to prevent mould growth in pinning boxes and trays); **potassium cyanide** (to kill insects in dry Malaise trapping); **potassium hydroxide** (caustic potash) (to macerate specimens for genital dissections; lactic acid is widely used by many dipterists and serves the same purpose); **propylene glycol** (preservative in pan traps and other trap types); **silica gel** (to dry specimens in the field).

Dry preservation

Only certain groups of flies should be preserved dry for general taxonomic purposes. These include the majority of the Cyclorrhapha and certain families of lower flies (*e.g*., Tipulidae, Simuliidae, Mycetophilidae and Keroplatidae), but this is dependent on the preferences of individual specialists. The majority of lower flies should, however, be preserved in ethanol for later slide-mounting (see below).

Diptera that are preserved in a dry state become dry and brittle after only moderate exposure to the air and can only be safely pinned when suitably relaxed. The best results are, therefore, obtained by pinning flies as soon as they are dead or shortly after. Flies to be pinned must, therefore, be retained in a relaxed state if these are to be later pinned without damage.

Keeping dry specimens relaxed

Specimens collected dry in Malaise traps, hanging traps, or by sweeping, *etc*., can be kept moist and pliable for pinning purposes by storing in relaxing containers, both before and after the initial sorting and selection of specimens to be pinned has taken place (see below). The use of various chemicals to keep specimens relaxed, such as ethyl acetate, may affect specimens later selected for DNA extraction, so should be avoided.

Plastic pots with tight-fitting lids are ideal (Fig. 17). A wad of folded toilet tissue can be pressed into the base of the pot and then dampened (not saturated), with a few drops of tap water. Ten or 15 sheets of tissue are then wrapped around the hand to form a wad that is loosely inserted above. The pot is then left in a warm place for an hour or so. Before the relaxing container is used (each time), it is important to check that the enclosed tissue paper has not become saturated. If so, an additional wad of tissue can be added directly on top. The inside walls of the pot and lid should also be dried with clean tissue each time the container is used otherwise small specimens will stick and become damaged.

Dry specimens from traps can then be emptied directly into the relaxing container and will stay relaxed until initially sorted and pinned. Specimens should not be left for protracted periods, or moulds will develop.

Initial sorting of dry specimens

Once a Malaise trap has been serviced and the dry specimens emptied into the relaxing container, the specimens must then be initially field-sorted, in order to separate those specimens

Figs 2.35–37. Field-pinning and examples of field-pinned specimens: (35) micro-pinning specimens in the field (Democratic Republic of Congo); (36) four plastic trays of micro-pinned Diptera (and other insects) from Madagascar; (37) box of direct-pinned Diptera (and other insects) from Democratic Republic of Congo. Fig. 35 (photograph R. Meier).

to be immediately dry-pinned from those to be preserved in ethanol. Such field sorting must be undertaken out of direct sunlight and in an absolutely wind-still environment, as very tiny flies (e.g., Cecidomyiidae and Sciaridae), are prone to rapid desiccation and to be blown away, even by the slightest breeze.

Procedures followed for field-sorting dry samples:

1. All or part of the sample (dependent on its size) is tapped out of the relaxing container (Fig. 17) onto a cleaned and thoroughly dried sorting tray (check through tissue layers for any specimens missed).
2. All butterflies and moths should then be removed before they drop additional scales.
3. By use of stork-billed forceps (Fig. 29) the sample is then gently sorted through in a systematic manner.
4. Specimens to be pinned are gently lifted by the wings and placed in clean and dried relaxing containers (one for specimens to be direct-pinned and one for micro-pinning).
5. Once all the obvious flies have been removed check through the tray again for any smaller flies that may have been missed.
6. Once all the flies to be dry-pinned have been removed, the remainder are then carefully tapped onto glossy paper and transferred direct into a centrifuge vial (Fig. 24) of ethanol.
7. A field data label is added to the vial written in pencil.
8. Once sorted, it is advisable to leave relaxing containers for half an hour, or so, to allow further relaxing before pinning is begun.

Direct-pinning

Direct-pinning is the process whereby larger Diptera specimens are pinned directly though the thorax from above, using rigid and sharp stainless steel continental length pins (see below). The process of direct-pinning is straightforward enough, but requires a steady hand.

Direct-pinning with a continental pin thinner than a No. 1 is not advised. No. 0 pins are far too thin and bend easily and are not sufficiently thick to hold the labels in place and prevent these from swinging around, or becoming loose.

Only freshly killed, or suitably relaxed, specimens should be prepared in this way. Pinning specimens previously preserved in alcohol does not work effectively, as these specimens no longer retain the necessary body fluids, fats and oils within the thoracic cavity to adhere the specimen to the pin and subsequently swivel around uncontrollably. An alternative means of pinning larger "ex alcohol" specimen is to glue these to a pin (see below).

Choice of pins

There are no hard and fast rules as far as pinning specimens is concerned, but the selection of the correct pins in the preparation of specimens is important. For direct-pinning, continental length, nylon-headed, stainless steel pins are preferred (sizes No. 1, 2 and 3 cover most dipterological needs). Although a cheaper alternative, black tempered-steel pins should not be used to pin directly through a specimen, as these pins (even if of good quality), are subject to corrosion, especially in humid climates. Likewise, brass pins are unsuitable, as these form verdigris, which may eventually damage and split the specimen. Black nylon-headed, tempered-steel continental pins are used as a cheaper alternative to pin through point-mounts and specimen stages only.

Procedures followed for direct-pinning:

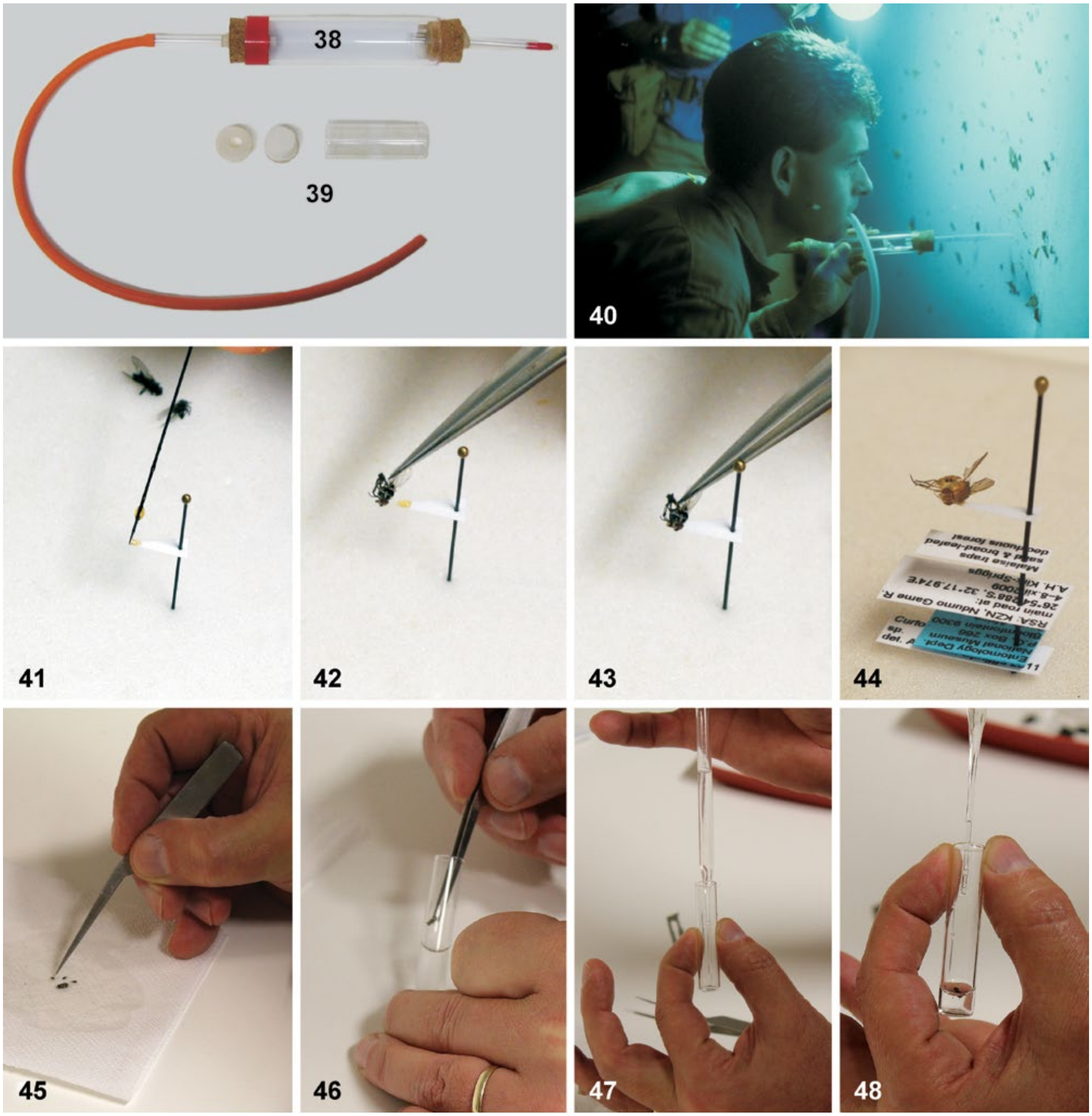
1. Tap out a small selection of flies to be pinned from the relaxing container onto the pinning box or tray.
2. The specimen selected is carefully lifted by a wing using watchmaker's forceps (Fig. 28).
3. The specimen is lightly gripped between the index finger and thumb, dorsal side uppermost (Fig. 49).
4. A continental, stainless steel pin is carefully inserted slightly off centre of the thorax, care being taken to pin the specimen straight on the pin (it is unavoidable in some cases that the pin will detach a leg, as this may exist through a coxal cavity and in such cases the detached leg should be retained, either glued to the pin immediately below, or preferably, to a mounting card pinned beneath) (Fig. 50).
5. Holding the head of the pin, the specimen is gently raised to the appropriate height on the pin from beneath, using watchmaker's forceps (Fig. 51), care being taken not to damage the legs and setation (enough space needs to be left above the specimen to grip the pin with the fingers without touching the specimen, but with sufficient room below to hold all the labels). No attempt should be made to arrange legs, or other body parts, as this can lead to damage.
6. Following direct-pinning the specimens can be pinned into a store box with a tight-fitting lid and a field label added at the end of the series (Fig. 37).

Micro-pinning

In the case of fresh specimens that require dry-mounting, but are too small to be direct-pinned with a pin smaller than a No. 1 continental pin, these can be micro-pinned using headless, stainless steel micro-pins (also known as "minutens"). Three sizes of micro-pins are now widely available, Nos. 20, 15 and 10 (the finest). Black-tempered steel micro-pinned should again be avoided as these may corrode.

Micro-pins come in a jumbled mass when supplied and it is advisable to pin an ample supply ahead of each fieldtrip into flat trays (see Fig. 35, foreground). This makes for easier handling and pinning and prevents spillage of expensive pins in the field that cannot be easily retrieved (a magnet is useful however).

An excellent storage method for Diptera specimens micro-pinned in the field is to pin these direct into flat Perspex trays (dimensions 125 x 80 x 20 mm), that have been previously lined with plastazote (closed cell, cross-linked polyethylene foam) (Fig. 36). These are available from a number of equipment suppliers[1, 6] and can be purchased with, or without, plastazote inserts. Specimens can be quite closely packed in these trays and hundreds of pinned flies can be stored in a very small



Figs 2.38–48. Equipment and techniques for preparing Diptera: (38) aspirator (pooter), used to collect smaller Diptera; (39) modified tropical dry collecting tube (note bored hole in polythene lid and muslin insert); (40) use of the aspirator to sample from light sheet; (41–44) procedures followed for point-mounting Diptera: (41) *Seccotine* glue adhered to point-mount using pin; (42) fly specimen placed on point-mount using watchmaker's forceps; (43) specimen orientated into correct position; (44) completed point-mounted specimen with associated labels added (Curtonotidae); (45–48) procedures followed for chemical preparation of Diptera from ethanol: (45) fly specimens placed on tissue paper to absorb excess ethanol; (46) specimen placed in vial containing 2-ethoxyethanol using stork-billed forceps; (47) 2-ethoxyethanol decanted from vial using glass pipette; (48) ethyl acetate decanted into vial using glass pipette. Fig. 40 (photograph D. Dudgeon), Figs 41–48 (photographs M. van Rensburg).

space (Fig. 36). The trays stack well and can be held together with an elastic band during transportation.

It is a good idea to select one such tray, with a relatively thick plastazote insert, as the "pinning tray" and to undertake all initial pinning on this tray alone. When a short series of flies has been amassed in the pinning tray these can then being transferred to a separate tray for storage.

Filled pinning trays should be kept as cool as possible while in the field and should never be left in direct sunlight with the lids on, as this causes condensation to form and for the specimens to "steam" and become greasy. The tray lids must be regularly opened to allow specimens to dry out. Open trays can be exposed to direct sunlight to air-dry, but then these should be covered with netting to prevent living flies (Muscidae and Sarcophagidae are particularly troublesome), from alighting on and damaging specimens and must also be placed in an "ant-free" environment. Freshly exposed specimens may also be subject to infestation by the phorid *Megaselia scalaris* (Loew) (Kirk-Spriggs & Marais 1999), whether covered in netting or not.

A far safer way to dry specimens in the field is to carefully place each open tray or store box in an appropriately sized sealable plastic bag in which indicator silica gel has been placed. Care should be taken that the seals of the bags are fully closed, if not, disastrous ant infestations may result. Indicator silica gel should be replaced daily, especially during the first few days of the drying process. Indicator silica gel generally comes in the colours purple or yellow. Purple silica gel turns pink when saturated and is preferred, as saturation is easier to discern than for yellow silica gel, which turns white.

To prevent moulds from developing in humid climates, a few crystals of *p*-chlorocresol can be placed between short lengths of folded sticky tape and be pinned into the corner of each tray or box. This method is highly effective in mould prevention.

Procedures followed for micro-pinning:

1. Tap out a small selection of flies to be pinned from the relaxing container onto the pinning tray.
2. Select a specimen to be pinned, and using watchmaker's forceps (Fig. 28), gently position the fly onto its right side.
3. Select a suitably sized micro-pin from the sizes available (Fig. 35).
4. Lightly secure the fly in place with the index finger, and with the forceps, insert the micro-pin cleanly, diagonally (obliquely) through the fly's thorax (thus not damaging the same thoracic pleura on the two sides).
5. When a series of flies have been pinned these should be gently blown from several angles to dislodge any Lepidoptera scales and can then be transferred to a storage tray (for later staging).
6. Add a field label to the tray, or series, providing details of the locality, date of capture and collecting method (*e.g.*, Figs 36, 53).

Double-mounting (staging)

Double-mounting, or staging, refers to micro-pinned specimens that are secondarily double-mounted onto a support, or "stage". This method has several advantages: it allows the specimen to be easily viewed from most angles, the white background of the mounting strip reflects light when viewing the specimen and the staging material helps cushion specimens against damage, through sudden jolts, or excessive and prolonged motion (*e.g.*, during protracted periods in the postal system). One disadvantage of double mounts is that specimens are more prone to breakage when removing the abdomen for dissection (relative to point-mounts) and unless specimens were micro-pinned obliquely through the thorax important ventral characters cannot be easily viewed.

In the past, *Polyporus*, the white pith of the bracket fungus found on oak trees, was used as a staging medium, but this is subject to deterioration over time and permanent synthetic alternatives are now available. By far the best currently on the market is Nu-poly[1], as the strips are uniformly cut and the material is sufficiently dense to hold No. 10 sized micro-pins firmly in place. These are also packed in Perspex boxes with tight-fitting lids that are later useful for the storage of labels, pins, specimens, *etc*.

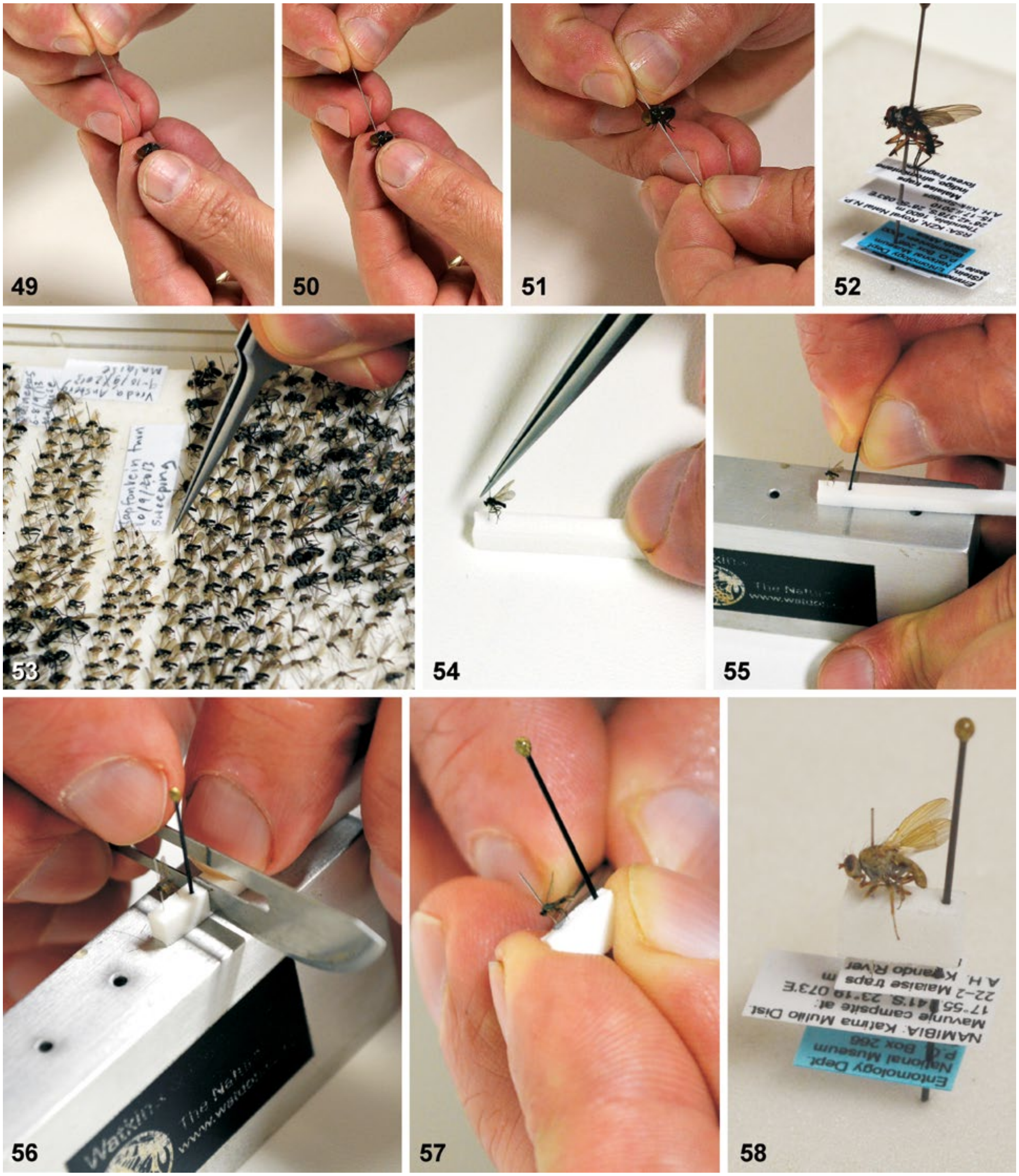
Procedures followed for double-mounting (staging):

1. The uncut mounting strip is placed on the flat surface of a bench (narrow side uppermost).
2. A micro-pinned specimen is carefully removed from the pinning tray with watchmaker's forceps (Fig. 53) and is partially inserted into the mounting strip (the head or antennae should not overlap in front) (Fig. 54).
3. A nylon-headed, black-tempered steel continental pin (Nos. 2 or 3) is partially inserted into the strip posterior to the specimen (close, but not touching).
4. The strip is lifted by the continental pin and pushed through to the second highest level of the pinning stage (Fig. 55).
5. While the pin is still in the stage, the strip is neatly cut transversely across, using a sharp scalpel blade or razor blade (Fig. 56).
6. Holding the trimmed mounting strip between the index finger and thumb, the micro-pin is gripped beneath the specimen using watchmaker's forceps and is carefully inserted deeper into the stage (the specimen should be inserted close to the stage, but no part of the specimen should touch) (Fig. 57).

Point-mounting

Point-mounting entails the gluing of smaller dry specimens onto the tip of a triangular card cut for the purpose. Preparation of specimens this way is generally faster than double-mounting and has the advantage that the ventral side of the specimen is clearly visible. It is also often easier to snap off the abdomen of point-mounted specimens, while double-mounted specimens are prone to spinning or breakage when the abdomen is levered off. There are two main disadvantages with point-mounting: firstly, as one side of the thorax is glued to the point the characters on that side are obscured, and secondly, a point-mount does not offer much protection for the specimen (although the attached labels help).

Special card punches, similar to those used to punch railway tickets, are available commercially[3] to cut point-mounts of a



Figs 2.49–58. Procedures followed for direct-pinning and double-mounting (staging) of Diptera: (49–52) direct-pinning of Diptera: (49) specimen gently held between index finger and thumb; (50) continental length stainless steel pin pushed through thorax from above; (51) specimen raised to correct height on pin; (52) pinned and fully labelled direct-pinned specimen (Anthomyiidae); (53–58) double-mounting (staging) of Diptera: (53) specimen to be double-mounted carefully removed from pinning tray; (54) carefully pinned in Nu-poly mounting strip; (55) continental length black tempered pin with nylon head pushed through strip to appropriate height using pinning stage; (56) strip neatly cut transversally using sharp scalpel blade; (57) micro-pin inserted deeper into stage; (58) pinned and fully labelled double-mounted specimen (Ephydridae). Figs 49–58 (photographs M. van Rensburg and C. Venter).

uniform size and several sizes are available. These enable a large number of point-mounts to be cut quickly and neatly. Pre-cut point-mounts are also available from some equipment suppliers, but are only supplied in one size and have the apex of the point rounded-off, making the gluing of smaller specimens problematic.

According to personal preference, point-mounts may be cut "acutely" (usually for minute specimens), "truncate", "downcurved" at the tip, or "stepped" at the tip.

The correct glue used to attach specimens to the point-mount is also important. *Seccotine*, or other hoof and bone-based adhesives that are water soluble, are probably best. Clear nail varnish is not recommended, as formerly advised in many South African universities, as this is subject to cracking, distortion and discolouration over time (museum specimens prepared using nail varnish must, in most cases, be immersed in acetone to be re-mounted).

Procedures followed for point-mounting:

1. Punch a selection of sizes of pre-cut point-mounts using a point punch and pre-pin.
2. Line up a series of specimens to be point-mounted.
3. With a continental length pin, add a blob of *Seccotine* to the tip of the point (Fig. 41).
4. With watchmaker's forceps, carefully lift the specimen by the wing and gently place the thorax onto the glue (Fig. 42) (alternatively, for speed mounting the glued point-mount can simply be touched against the specimen).
5. Carefully press the specimen into the glue, taking care not to pierce the cuticle or damage setation.
6. While the glue is still wet, straighten and orientate the specimen onto the point-mount using a pin or forceps (Fig. 43).

Gluing specimens to pins

While smaller specimens prepared using critical-point-drying and chemical methods (see below) can be glued to point-mounts (see above; Figs 41–44), larger specimens are normally glued directly to stainless steel, continental length pins. Some dipterists prefer to glue all specimens to pins (even when field mounting), which saves money and field box space, but point-mounting is generally preferred for smaller specimens, as the ventral side is easier to view on point-mounted specimens.

Papering

Flies of the superfamily Tipuloidea are notorious for losing their legs. Various means of preventing this are employed by specialists in this group (mostly the folding away of legs while specimens are still relaxed). An alternative for the non-specialist is to place specimens in individual glassine envelopes[1, 2] in the field (Fig. 33). Again appropriate field labels need to be added to each packet. These can be transferred to transparent envelopes in the collection, allowing easy examination.

Degreasing specimens

Some dry-pinned specimens invariably become greasy as oils and fats from within the body leach through the cuticle and obscure vestiture, *etc*., and some genera of flies appear to be more prone to this than others (*e.g*., *Bengalia* Robineau-Desvoidy in the Calliphoridae). Specimens can be degreased by immersing the entire specimen in acetone overnight. For larger flies the acetone may need to be changed several times over subsequent days in order to fully degrease the specimen. It is important that all labels be removed beforehand and that the nylon head of the pin be not immersed in the acetone, as this may dissolve.

Slide-mounting

Specialists in various families have developed different techniques for the slide-mounting of their respective groups of study, but the basic procedures for maceration, clearing and slide-mounting are relatively standard. What differ are the parts of a specimen that are dismembered and the orientations in which they are mounted on a slide (Figs 66–68). The example provided below refers specifically to the slide-mounting of the Chironomidae, following Andersen *et al*. (2013), but should serve as a general guide for slide-mounting other whole flies.

For many Diptera families, especially the traditional Nematocera, specimens need to be mounted with care on microscope slides to enable proper examination at high magnifications. Slide mounts may be either "temporary" or "permanent" mounts, dependent on the purpose. Temporary mounts are sufficient for identification alone and in some groups are obligatory, as multiple viewing angles are required and preparations are easily stored in genital capsules or vials. Permanent mounts are customary for some groups and are often better for high magnification microscopy.

Procedures followed for preparation of permanent slide mounts of ethanol preserved specimens:

1. Label the microscope slide using no more than ⅓ of the slide area.
2. Parts that do not need maceration are dissected off the body and placed in Euparal ® or Canada balsam under appropriately sized cover slips. This can be done directly from 96% ethanol for Euparal ®. For Canada balsam the parts must first pass through ethanol layered with cedarwood or clove oil. For Chironomidae the parts that are mounted at this stage are wings, antennae and one set of legs. Antennae are often placed under the same cover slip as legs.
3. The remainder of the specimen is macerated in warm 10% potassium hydroxide (KOH) solution in a dry bath incubator (Fig. 15) or glass Petri-dish (Fig. 27) on a hot plate for five or 10 minutes, until cleared.
4. The specimen is removed and placed into glacial acetic acid for five minutes, then transferred to distilled water for 5 minutes.
5. The specimen is transferred to 75% ethanol for 10 minutes and 96% or absolute ethanol for 15 minutes.
6. The specimen is transferred to ethanol layered over either by cedarwood or clove oil for 15 minutes (if Euparal ® is used the cedarwood or clove oil stage can be omitted).
7. The specimen is dismembered so that the remaining constituent parts (according to group) can be mounted separately

under different cover slips. For the Chironomidae three additional cover slips usually suffice, with the head beneath one, abdomen with terminalia beneath one and thorax with one set of legs beneath the last cover slip. Associated reared larval and pupal stages should also be mounted on the same slide under separate cover slips.

8. The relevant parts are mounted in a small droplet of Canada balsam or Euparal ®, on a clean microscope slide. The constituent parts are orientated to the correct position using a pin and a cover slip is gently lowered at an angle using a pair of fine forceps to avoid air bubble formation.
9. Once all constituent parts have been mounted the slide can be allowed to dry, preferably in a drying oven.

Alternatively, if DNA is extracted from whole specimens using enzyme digestion in lysis buffer, the cleared exoskeleton can be added to the ethanol in point 5 (above).

Micro-slides

In some instances it may be necessary to prepare slides of the terminalia or other structures of dry-pinned flies (phallus, spermathecae, the female postabdomen, *etc*.). As it is advisable to keep these structures associated directly with the specimen concerned, rather than a separately stored microscope slide, the micro-slide serves this purpose (see Oldroyd 1970, fig. 92). These can be made by hand by punching holes from a pre-cut strip of 600 gram white, acid-free card with a hole-punch. A 13 mm diameter cover slip is then attached to the card, so the punched hole is positioned directly in the centre and is attached using Euparal ®, Canada balsam or PVA wood glue. Once dry the mounts are trimmed with a pair of scissors and can use used like a regular slide, with the 13 mm cover slip acting as the "slide". A smaller cover slip of 5 mm diameter can then be used when mounting structures and the micro-mount can be pinned to the specimen concerned. When examination is required the micro-mount can be placed on a clean microscope slide and be viewed normally.

Data labels

The appending of labels with appropriate and accurate data is essential for all specimens and samples (*e.g.*, Figs 52, 58). A specimen without data labels is useless for scientific purposes and the specimen, plus its associated labels, form an integral unit in scientific study; the associated labels reflecting both its origins and history. For this reason existing labels should never be removed, irrespective of how trivial they may appear.

Essential data that should be appended to a specimen are: country, district, province, or name of national park/reserve, specific locality name, GPS coordinates (usually in degrees, minutes and seconds), date/s of capture, name/s of collector/s, collecting methodology and habitat type (optional but advisable), or other biological observations of capture, *e.g.*, "swarming at dusk", or "alighting on bracket fungus".

Labels should be kept as small as possible, while allowing text to be easily read. In order to keep these of a manageable size, it is often advisable to split the collecting methodology/biological observation and habitat type data onto a separate label, the smaller of the two being appended to the specimen first.

In the past the majority of labels were either hand-written with Indian ink, or were commercially printed, but today with computer technology and printers readily available to most, large numbers of labels can be easily generated and amended, although a few basic principles need to be applied in their production.

For dry preservation, labels can be printed on 600 gram white, acid-free card using a laser printer (150 gram or 180 gram is also adequate for labels). A simple, clear font that is easily legible at small point size needs to be used. Arial font, printed at 3.5 point size produce good, clearly legible labels of a suitable size to append to pinned specimens (see Figs 52, 58).

Care should be taken that appended labels sit neatly and evenly beneath the specimen, thus offering protection from mechanical damage. Labels should not project too far beyond the specimen.

Labels are added to specimens using a pinning stage[1] (Fig. 18). Alternatively sheets of high density foam can be cut to the appropriate thicknesses and serve the same purpose. This ensures that labels are added at uniform heights and that these are sufficiently widely spaced to allow details to be easily read, without having to remove the labels. The pinning stage is also used when preparing point-mounts.

For permanent labels for spirit-preserved specimens these can be laser printed onto Teslin A4 plastic paper[13], now widely used in many national collections. An electronic file of labels should be maintained in the event that duplicate labels are required in the future and to extract label information directly for specimen digitisation.

Genital dissection

For many families of flies species can only be reliably identified by examination of the male or female genitalia (terminalia). This requires the removal of all, or part of, the abdomen and maceration to dissolve the membranous parts and connective musculature to leave the sclerotised structures visible for examination.

Procedures followed for genitalia dissections:

1. Dependant on the group, the abdomen is detached from the specimens, using a pin, micro-scissors or watchmaker's forceps (Fig. 28). It is a good idea to clear the bench area before removing an abdomen and to do so over a Petri-dish on the microscope stage, so this is easier to find if it "pings" off during removal.
2. The abdomen is placed in a vial containing 5 or 10% potassium hydroxide (KOH), lactic acid or sodium hydroxide in a dry bath incubator (Fig. 15) and is heated until the specimen is suitably macerated (dependant on the size of the specimen concerned). The abdomen can also be macerated overnight in cold KOH at ambient temperature. Care must be taken not to over macerate specimens, as this may obscure important characters. KOH is corrosive and should be handled with care.
3. Once macerated, the specimen is removed and transferred to an excavated glass block (Fig. 26), containing

70% ethanol, with few drops of glacial acetic acid (to neutralise the effect of the KOH).

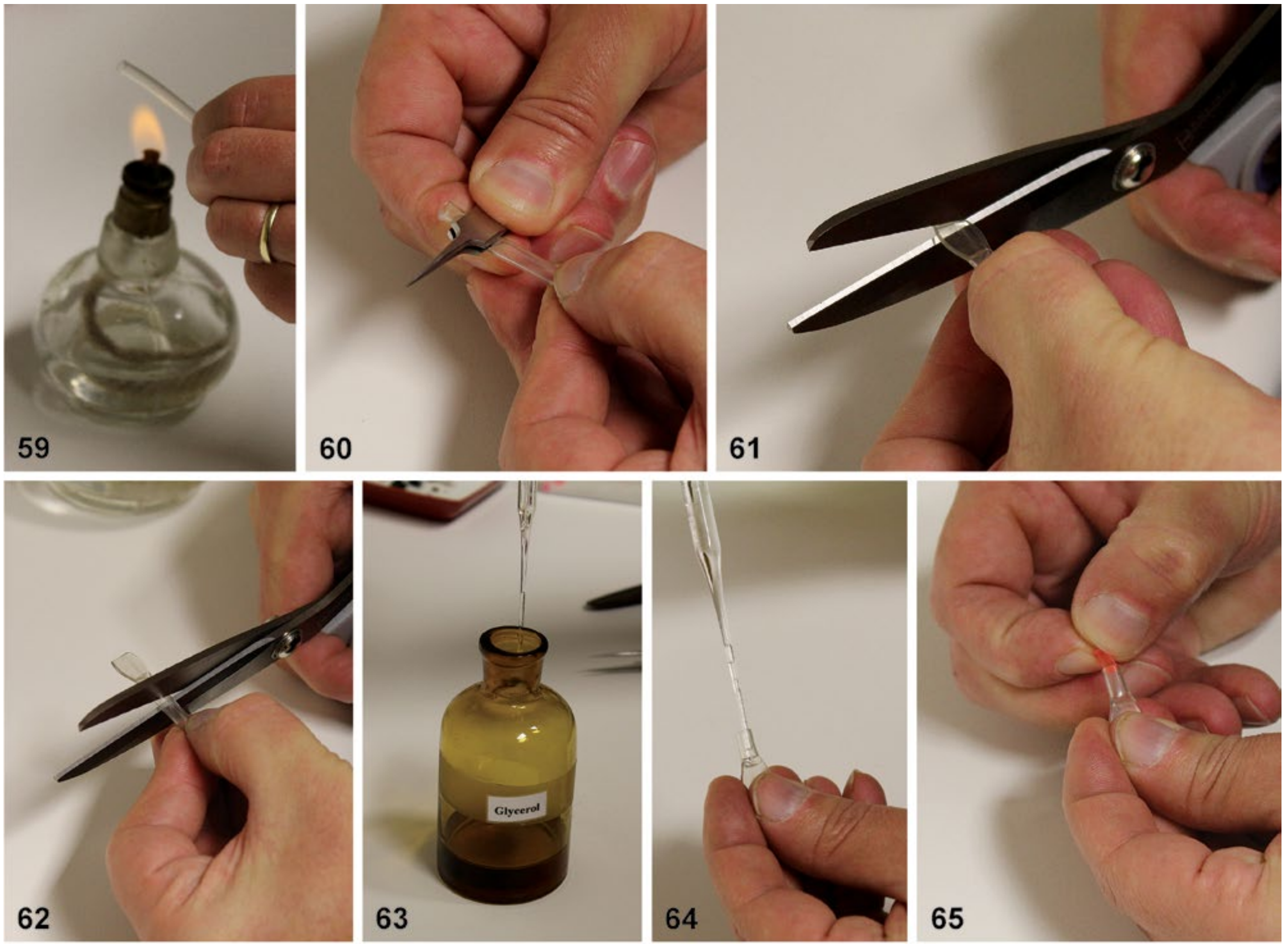
4. The abdomen is then dissected under a binocular microscope, either using continental length pins (for larger specimens), or micro-pins inserted into the ends of match sticks (for smaller specimens).
5. Following dissection and examination all dissected parts should be retained and be placed in a genitalia vial in glycerol to be pinned beneath the specimen concerned (see below section).

Genitalia vials

Various types of genitalia vials are available commercially[2], but these are expensive, some are not made of transparent plastic (making it difficult to see structures through the vial wall) and the stoppers have a habit of popping out if the air bubble is not removed when this is inserted. It is generally better, therefore, to make your own. These can be made from clear PVC 3 mm internal diameter tubing with a flexible polyurethane (or PVC) stopper[6]. PVC tubing is also available very cheaply from some hardware stores and pet shops. The flexible polyurethane stopper comes in a single length and stoppers need to be cut to size (*ca* 5 mm in length) using a scalpel blade.

Procedures followed for preparation of genitalia vials:

1. Heat the end of the PVC tubing over a spirit lamp (Fig. 16) until suitably softened (do not allow to burn) (Fig. 59).
2. While still softened use the flat blades of watchmaker's forceps (Fig. 28) to seal the tubing together by holding the blades together for several seconds (Fig. 60).
3. The jagged end of the flattened tubing is trimmed with a pair of scissors (Fig. 61).
4. Using scissors the PVC tubing is then cut to the appropriate length (*ca* 1 cm) (Fig. 62).



Figs 2.59–65. Procedures followed for preparation of genitalia vials: (59) PVC tubing softened over spirit lamp; (60) using flat blades of watchmaker's forceps to press softened tube together and seal; (61) jagged flattened end of tubing trimmed with scissors; (62) tubing trimmed to correct length using scissors; (63) glycerol decanted into glass pipette; (64) glycerol inserted into genitalia vial using glass pipette; (65) insertion of pre-cut polyurethane stopper to close vial. Figs 59–65 (photographs M. van Rensburg).

5. Using a glass pipette (Fig. 31), or suitably narrow eye dropper, glycerol is decanted into the prepared vial (Figs 63, 64). Care should be taken not to overfill the vials or the stopper may eventually pop out.
6. The pre-cut polyurethane stopper is inserted into the open end of the tubing (Fig. 65). Alternatively, both ends of the tubing can be heat-sealed, but this prevents easy re-examination of structures.

Wet preservation

There are several steps that can be taken to ensure good quality Diptera specimens generated through passive collecting methods that sample directly into fluid (alcohol, or propylene glycol). In the case of Malaise trap samples the greatest problem is the frequently large numbers of moths and butterflies sampled simultaneously. As with dry collecting, these are the bane of the dipterist's life, as they readily drop their scales, which later become entwined between folded legs and setation, especially of the smaller Diptera. The long-term effect of Lepidoptera scales can be greatly reduced by pouring the sample into a sorting tray and physically removing as many moths and butterflies as possible as soon as the Malaise trap is emptied (preferably in the field before they are subject to agitation). The soiled alcohol can then be gently strained-off (not sieved, as this also damages fragile flies), and can be replaced with fresh. An additional problem leading to mechanical damage of fragile Diptera in such samples are large spiny insects (*e.g.*, Coleoptera and Orthoptera), that also frequently find their way into such traps. These can be removed at the same time as the Lepidoptera and be placed in separate vials.

There are similar issues with pan trap samples. Pans, especially those deployed in forested habitats, frequently contain twigs, leaves, stones and other debris. Larger debris is best removed with forceps before each pan sample is strained as this can help prevent mechanical damage to the more delicate Diptera.

Long-term storage of unsorted, mixed samples leads to a reduction in the concentration of alcohol, due to fluid exchange between the preserved specimens and also dissolved nectar from bees. To ensure good quality specimens over time, it is desirable to regularly and frequently change alcohol, especially within the first six months of preservation. Samples should be stored away from direct sunlight, preferably in a freezer.

Preparation of dry specimens from ethanol

Preparing good quality, dry-mounted specimens that were originally preserved in alcohol has long been a problem for dipterists. The bleaching of colour from specimens preserved in alcohol for extended periods appears to be unavoidable. Good preparations can now be achieved using various complex or simpler chemical techniques.

Critical-point-drying (CPD) is an excellent technique for drying specimens that is now widely used by many dipterists in the developed world. The technique is advantageous as structures such as compound eyes do not collapse (as they often do in air-dried specimens), the wings usually dry absolutely flat and specimens prepared in this manner remain pliable. Critical-point-drying units are available commercially[19] and for modern units the procedure is fully automated. Batches of samples can be dried simultaneously and large numbers of small specimens can be processed efficiently, but the technique is less practical for larger-bodied flies. (S.A. Marshall, pers. comm. 2015). CPD drying units are not available in Africa and need to be obtained from overseas suppliers. Commercial units are very expensive and affordability may, therefore, be a major factor for African institutions. If technical support is available, a simple, manual dryer can be constructed at a fraction of the cost and a design for such a unit is provided by Marshall (1990).

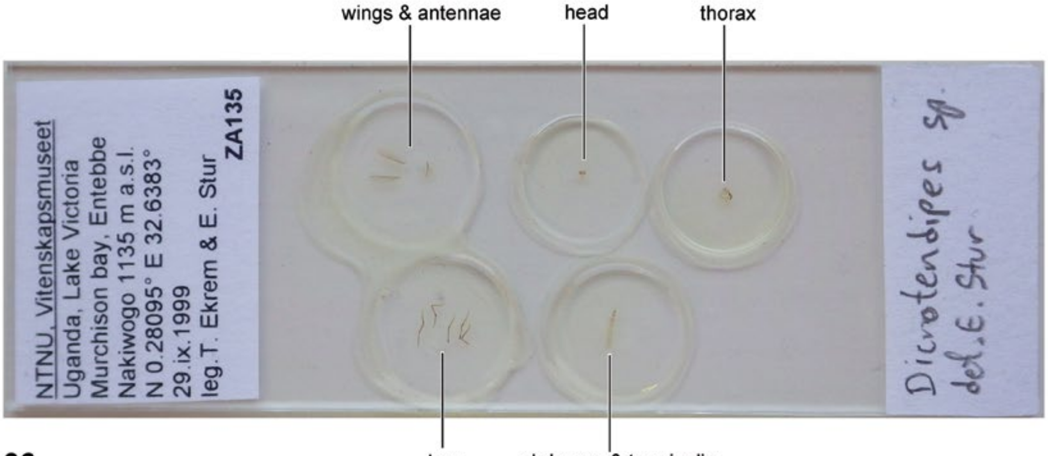
One simple chemical method for dry preparations, involving the use of 2-ethoxyethanol and ethyl acetate, is outlined below. In this technique both chemicals can be re-used on multiple occasions. These preparations should ideally be performed in a fume cupboard, or at least in a well-ventilated room. Care is also required in the handling of these chemicals and country-specific health and safety regulations may apply to their use. An alternative is to use acetone alone, should a fume cupboard not be available.

Procedures followed for preparing dry-mounted specimens from ethanol:

1. Carefully pour alcohol preserved specimens into an appropriately sized sorting tray, dish, or excavated glass block (some dipterists pin specimens individually prior to drying).
2. By use of stork-billed forceps lift each specimen by the wing and place on dry tissue paper to absorb excess alcohol (Fig. 45).
3. With stork-billed forceps place specimens into a glass vial containing 2-ethoxyethanol (the specimen/s must be covered by the chemical) (Fig. 46).
4. Leave to stand for 24 hours.
5. By use of a pipette draw-off the 2-ethoxyethanol until the inside the vial is virtually dry (chemical can be re-used) (Fig. 47).
6. With a pipette, decant ethyl acetate into the vial until the specimen/s is fully covered (Fig. 48).
7. Leave again to stand for 24 hours.
8. Using stork-billed forceps gently removed the specimen from the vial and place on dry tissue paper until the specimen has sufficiently dried (chemical can be re-used) (Fig. 45).
9. Once dry, larger specimens can be glued directly onto a pin and/or smaller specimens onto point-mounts (see sections above).
10. Once mounted, the specimen can be gently blown to release the arista and setation.

Preservation for molecular studies

Molecular data from nucleic acids (DNA, RNA) and proteins are a major source of important information for phylogenetics, population genetics, comparative and functional genomics and species discrimination. Field preservation does not require highly specialised equipment or conditions, but does entail careful planning for collection of live flies directly into appropriate storage media, as these molecules degrade rapidly after the organism dies, especially in conditions of high heat, humidity, or moisture that are suitable for enzymatic digestion after cell death. In all cases, collection of flies for molecular studies



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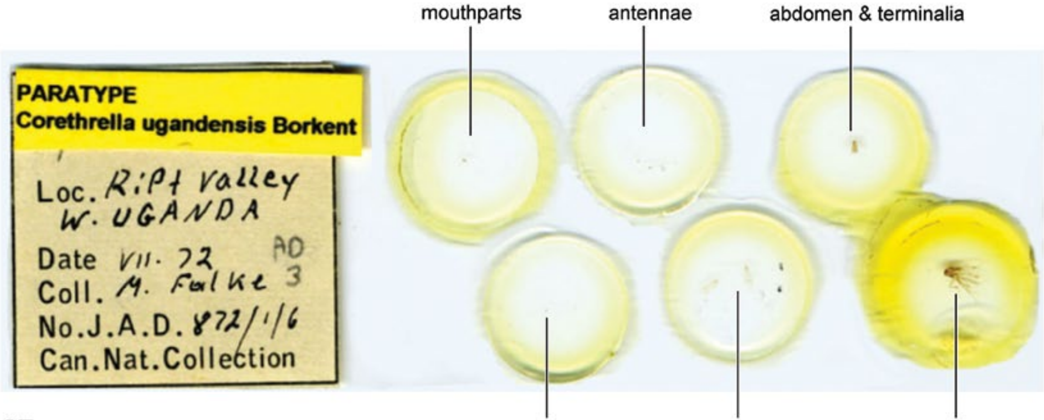

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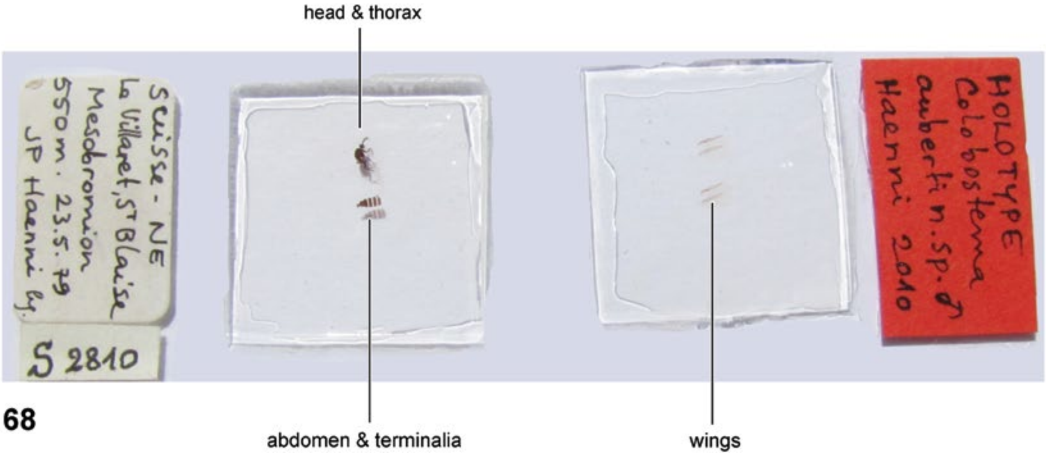

68

Figs 2.66–68. Examples of permanent slide mounts of Diptera (indicating dismembered parts and slide labels): (66) *Dicrotendipes* sp. (Chironomidae); (67) paratype of *Corethrella ugandensis* Borkent (Corethrellidae); (68) holotype of *Colobostema auberti* Haenni (Scatopsidae). Fig. 66 (courtesy T. Ekrem), Fig. 67 (courtesy B.J. Sinclair), Fig. 68 (courtesy J.-P. Haenni).

should be accompanied by well-preserved voucher specimens with complete collecting metadata to enable cross-validation of species identification and scientific re-use of samples for multiple purposes. The increasing loss of natural habitats and threat of anthropogenic extinctions makes it especially valuable to collect and store flies for current and future studies of biodiversity, ecology and genetics. Long-term cryostorage facilities that preserve specimens and their genome are now a major component of natural history collections (Droege *et al*. 2013).

Nucleic acids are preserved by precipitation in alcohol. Material specifically intended for nucleic acid extraction should be killed directly in and stored in ethanol or isopropanol of higher concentrations (96–100%). Higher alcohol concentrations are valuable in limiting dilution by the addition of water contained in the specimens themselves. Formalin should never be used, not even for the shortest period, as DNA is degraded making it unavailable for molecular study. It is best if specimens are thoroughly dehydrated by changing the 96% ethanol several times before being stored for long periods. It is also best to store specimens in cold temperatures (preferably deep frozen (-80°C); or in a standard freezer (-20°C). Malaise trap samples can also be collected directly into 96% ethanol to enable DNA extraction, but in these cases unsorted samples need to be changed regularly, until properly sorted (see above). Specimens collected directly into propylene glycol are also suitable for DNA extraction.

Many current studies make use of next generation sequencing technologies (NGS) that allow the rapid harvest of all expressed genes (mRNA; transcriptomes), capture specific gene targets (DNA), or perform shot-gun or partial genome sequencing (nuclear or mitochondrial genomes) (Ekblom & Galindo 2011). These methods provide a large amount of information about genes and the genome, about gene expression and about levels of genetic variation, but in general, they require a large amount of well-preserved tissue for high laboratory yields. DNA and RNA are rapidly degraded by ubiquitous nucleases and RNases are particularly common and destructive. For this reason, specimens intended for transcriptome or expression studies are best collected live into specialised RNA stabilisation solutions that are specifically optimised to preserve RNA. The most common of these is RNA*later*® (Ambion) a viscous salt solution that preserves RNA at room temperature, is non-toxic, and does not require storage in cold temperatures. RNA*later*® does not rapidly penetrate tissues from larger flies and so it is often best to break or grind the fly with a sterile pestle after placing it in the solution. If solutions such as RNA*later*® are not available, high yield of RNA is obtainable from live specimens killed directly in 100% ethanol and stored continuously at low temperatures (-20°C).

It is often possible to extract DNA from specimens that have been rapidly dried using silica gel (see above), or killed in cyanide tubes and pinned, but results are highly variable and dependent on the conditions of death, moisture content, and temperature in storage. Best results for nucleic acid recovery from dried specimens are from specimens not older than 5–10 years, but recovery of small fragments of highly abundant genes, such as those found in the mitochondrial genome, can extend to as much as 55 years or more of pinned storage (Mitchell 2015). Methods used to rapidly preserve colour and external morphology, such as critical-point-drying, or soaking in ethyl acetate, are destructive of nucleic acids and should not be used if specimens are to be used for molecular projects. DNA samples are normally stored in Eppendorf vials[20] (Fig. 23) or in nalgene cryovials[11].

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Appendix. International and local equipment suppliers.

There are no companies based in southern Africa that exclusively supply entomological equipment, although some general laboratory suppliers stock selected items. For this reason, it is necessary to look overseas for suppliers of many specialised items. A list of the major ones referred to in the text (with superscript numbers), is provided below.

[1]**Watkins & Doncaster the Naturalist**, P.O. Box 5, Cranbrook, Kent, TN18 5EZ, UK.
Website: http://www.watdon.co.uk/the-naturalists/

[2]**BioQuip Products**, 2321 Gladwick Street, Rancho Dominguez, CA 90220, USA.
Website: http://www.bioquip.com/html/catalog.htm

[3]**John W. Hock Company**, 7409 NW 23rd Avenue, Gainesville, Florida 32606, USA.
Website: http://www.johnwhock.com/

[4]**Sante traps**, 1118 Slashes Road, Lexington, Kentucky 40502-1826, USA.
Website: http://www.santetraps.com/

[5]**B & S Entomological Services**, 37 Derrycarne Road, Portadown, County Armagh, BT62 1PT, Northern Ireland, UK.
Website: http://www.entomology.org.uk/contact.htm

[6]**D.J. & D. Henshaw**, 34, Rounton Road, Waltham Abbey, Essex EN9 3AR, UK.
E-mail: djhagro@aol.com

[7]**Bugdorm Cages and Traps**, MegaView Science Co., Ltd., No. 656–2, Fuya Road, Taichung 40762, Taiwan.
Website: http://www.BugDorm.com

[8]**Bonpak**, Longmeadow Business Park East, Edendale, Gauteng, South Africa.
Website: http://www.bonpak.co.za/Contact-Us.php

[9]**Dr. Hans-Jürgen Thorns**, Biologie-Bedarfs-Handel, Eestl. Stadtgraben 50, 94469 Deggendorf, Germany.
Website: http://www.biologie-bedarf.de

[10]**Lasec/SA**, 52 Old Mill Road, Ndabeni, Cape Town, 7405, South Africa.
Website: http://www.lasecsa.co.za/index.php?id=8

[11]**Canadawide Scientific Ltd.**, 2300 Walkley Road, Ottawa, ON K1G 6B1, Canada.
Website: http://canadawide.ca/products/337-800.0.html?item_id=337-800-04

[12]**McKinley Scientific**, 33C Wilson Drive Sparta, NJ 07871, USA.
Website: http://www.mckscientific.com/productDetails.htm?Fisher-Scientific-Isotemp-Analog-2-Plate-Dry-Bath-Incubators-46

[13]**Busy Bee Binding and Lamination Solutions CC**, 32 Jenkins Street, Elandspark, Gauteng, South Africa.
Website: http://busybeebinding.wozaonline.co.za/

[14]**Sorygar Ltd.**, C/Quinta del Sol 37, Las Rozas, 28231 Madrid, Spain.

[15]**IPS (International Pheromone Systems) Ltd.**, Units 10–15, Meadow Lane Industrial Estate, Ellesmere Port, Cheshire, CH65 4TY, UK.
Website: http://www.internationalpheromone.co.uk/

[16]**Insect Science**, Ento Park, 9 Industrial Street, New Industrial Area, Tzaneen, Limpopo Province 0850, South Africa.
Website: http://www.insectscience.co.za/

[17]**Volume Injection Products**, 759 Smoky Ridge Farm, Quinera, East London, Eastern Cape, South Africa.
Website: http://vipplastics.co.za/

[18]**Entomoravia**, CSL.C.Krize 967, Slavkov u Brna, 684 01, Czech Republic.
Website: http://entomoravia.eu/index.php/insect-pins

[19]**Tousimis**, 2211 Lewis Ave, Rockville, MD 20851, USA.
Website: http://www.tousimis.com/critical_point_dryers/MEMS_drying_system.html

[20]**Eppendorf North America**, 102 Motor Parkway, Hauppauge, NY 11788, USA.
Website: http://www.eppendorf.com/int/index.php?action=products&contentid=191

ADULT MORPHOLOGY AND TERMINOLOGY 3

Jeffrey M. Cumming and D. Monty Wood

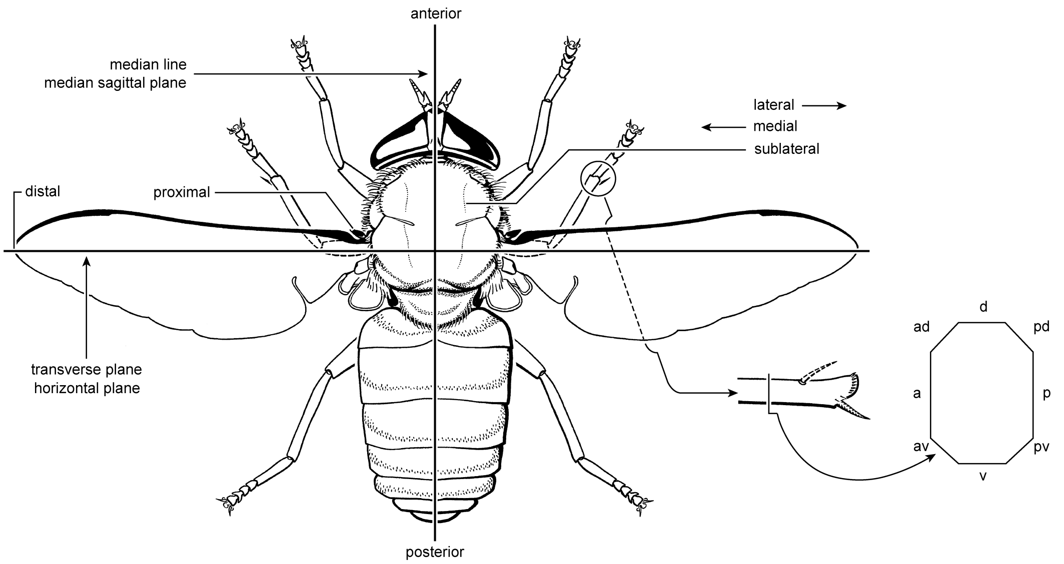
Introduction

This chapter introduces and describes the terms used for the identification of adult flies in this *Manual*, although the discussion of terms is not exclusively restricted to Diptera occurring in the Afrotropical Region. The information provided herein is based mainly on the terminology presented by Cumming & Wood (2009), which largely followed McAlpine (1981), with certain modifications subsequently adopted by Kotrba (2000), Merz & Haenni (2000) and Sinclair (2000). The most significant changes made to the previous treatment presented by Cumming & Wood (2009) include definitions of a few additional terms now in common usage (*e.g.*, postpedicel, pseudacanthophorites) and a more complete listing of synonyms. Three additional wing figures are also included, which depict some modified terms for venation (Wootton & Ennos 1989; Saigusa 2006), that are used as an alternative to the system presented in McAlpine (1981). This alternative system, which is based on a better homologised Diptera and Mecoptera fore wing base, is now used throughout this *Manual* and should be considered the standard.

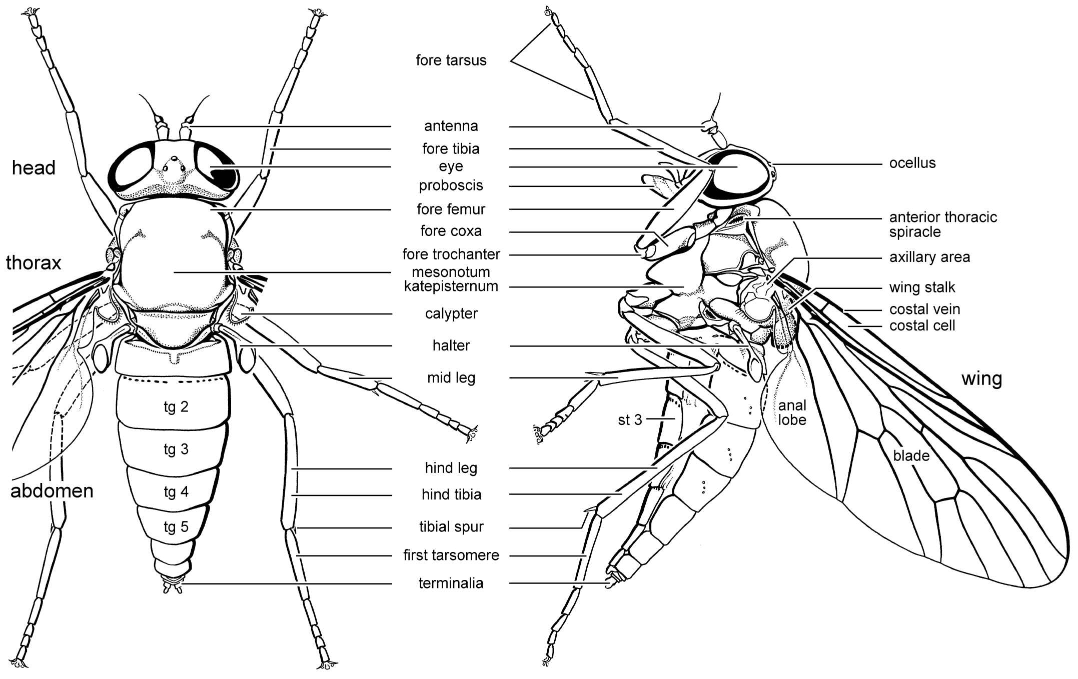
Terms are arranged alphabetically by major body region for the **head**, **thorax** and **abdomen** (Figs 1–3). Within the three major regions general discussions of components of the **compound eye**, **antenna**, **mouthparts**, **wing**, **legs**, **female terminalia** and **male terminalia** are followed by glossaries of terms used, grouped together under each of these headings. Preferred terms appear in *boldface* font followed by synonyms within brackets in *regular* font. Sometimes the corresponding singular (sing.) or plural (pl.) form is also given in brackets.

Each thoracic and abdominal segment is organised into a dorsal **tergum** (with a sclerotised **tergite**) and a ventral **sternum** (with a sclerotised **sternite**), connected together by a lateral **pleuron**, or **pleural membrane** (Figs 2, 3). The **tracheae** of the respiratory system open externally as **spiracles** on the sides of some of these segments. Parts of the integument, including the cuticle of the head, are variously covered in vestiture of different types. **Macrotrichia**, which are innervated and project from sockets called **alveoli** (sing. **alveolus**), include **bristles**, **setae**, **setulae** and **hairs**, depending on their relative size, as well as some enlarged spines on certain structures (*e.g.*, **acanthophorite spines** in female terminalia). Larger macrotrichia are generally referred to as setae and smaller macrotrichia are referred to as setulae; the terms bristle and hair are less frequently used. The arrangement of macrotrichia on the integument is referred to as **chaetotaxy**. Macrotrichia often function as sense organs or **sensilla** (sing. **sensillum**) with over 15 different types of sensilla having been defined in insects, including Diptera, based on their morphology and function (Nichols 1989: 670). **Microtrichia** include various minute projections of the cuticle that lack alveoli, such as the dust-like **pruinescence** (pollinosity) and the pubescent-like **tomentum** that dulls the surface of many sclerites, providing pattern and colour. Microtrichia that form spots are referred to as **maculae** (sing. **macula**), whereas microtrichia that form lines are referred to as **fasciae** (sing. **fascia**). Transverse lines of microtrichia are called **bands**, whereas longitudinal lines are termed **stripes,** or **vittae**.

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 1. Introductory chapters and keys to Diptera families. *Suricata* 4. South African National Biodiversity Institute, Pretoria; pp. 89–133.



1 *Tabanus* ♀



2 *Symphoromyia* ♀ 3 *Symphoromyia* ♀

Figs 3.1–3. Main anatomical divisions and parts of adult flies: (1) dorsal view of *Tabanus americanus* Forster (Tabanidae) ♀, to show orientation and anatomical planes (inset of vertical section through distal portion of right mid tibia showing external surfaces); (2) *Symphoromyia montana* Aldrich (Rhagionidae) ♀, dorsal view; (3) same, lateral view (both non-Afrotropical). Figs 1–3 (after McAlpine 1981, figs 1–3).

Abbreviations: a – anterior; ad – anterodorsal; av – anteroventral; d – dorsal; p – posterior; pd – posterodorsal; pv – postero-ventral; st – sternite; tg – tergite; v – ventral.

Head

The segments that make up the head are fused into a somewhat spherical, or oval head capsule bearing hypognathous **mouthparts** formed into a **proboscis** (a synapomorphy of all Diptera, in which the **labrum**, **mandibles**, **hypopharynx** and **maxillae**, when present, are enclosed in a trough-like **labium**). Except for the mouthparts, these head segments are no longer clearly recognisable. For descriptive purposes, however, the head capsule has been arbitrarily divided into regions: the **frons** above the **antennae** and between the **compound eyes** anterodorsally, the **vertex** at the top of the head bearing the **ocellar triangle** when present, the **genae** below the eyes, the **face** and **clypeus** between the eyes and below the antennae and the **occiput** behind the eyes forming the usually flattened posterior surface of the capsule (Figs 4–7). The inner skeleton of the head capsule is formed by the arms of the **tentorium**.

The chaetotaxy of the head is diagnostically important in many groups of Diptera. The orientation of setae is described as **proclinate** (= directed forward), **reclinate** (= directed backward), **inclinate** (medioclinate) (= directed inward), or **lateroclinate** (eclinate, exclinate) (= directed outward).

In Tipulidae and in a few members of other families, the face, clypeus and genae are elongated anteriorly to form a **rostrum**, carrying the mouthparts further forward, similar to a weevil (Fig. 40). A condition referred to as **colocephaly**, in which the head is disproportionately small with reduced widely separated eyes and vestigial non-functional mouthparts, occurs in both sexes of some species of Blephariceridae (Stuckenberg 2004).

Glossary

anteclypeus, see **clypeus**.

anterior tentorial pit, see **tentorium**.

callus (pl. **calli**): bare, sometimes swollen areas on the frons of many female Tabanidae, including the **basal callus** (frontal callus), at the ventral limit of the frons above the subcallus and level with the lower margins of the compound eyes and the **median callus**, a narrow oval area between the ocellar triangle and basal callus (see **subcallus**). Calli also occur on the frons and face of some Therevidae.

cerebral sclerite, see **vertex**.

cibarium, see below under Mouthparts.

clypeal ridge, see below under Mouthparts.

clypeus (frontoclypeus) (Figs 4, 30, 33, 34, 36, 37, 39): that part of the head capsule between the labrum ventrally and the face dorsally, often extending almost to the antennal bases. In blood-feeding nematocerous families and Tabanomorpha, the clypeus is particularly prominent as a roundish convex sclerite (Fig. 30). By contrast, the clypeus of Cyclorrhapha and of Schizophora especially, has become reduced to a U- or Y-shaped sclerite hinged to and distinctly delineated dorsally from, the lower facial margin and often somewhat separated from it by the frontoclypeal membrane (Figs 4, 6, 37). In a few groups (e.g., Blephariceridae) the clypeus is divided into a proximal **postclypeus** and a distal **anteclypeus** (see also under Mouthparts).

cornicula (sing. **corniculum**) (patagia): permanently everted sac-shaped structures on the posterior surface of the head of males of some Psychodidae (*i.e.*, certain Psychodinae) that are presumed to be scent organs.

coronal suture, see under **frontal vitta**.

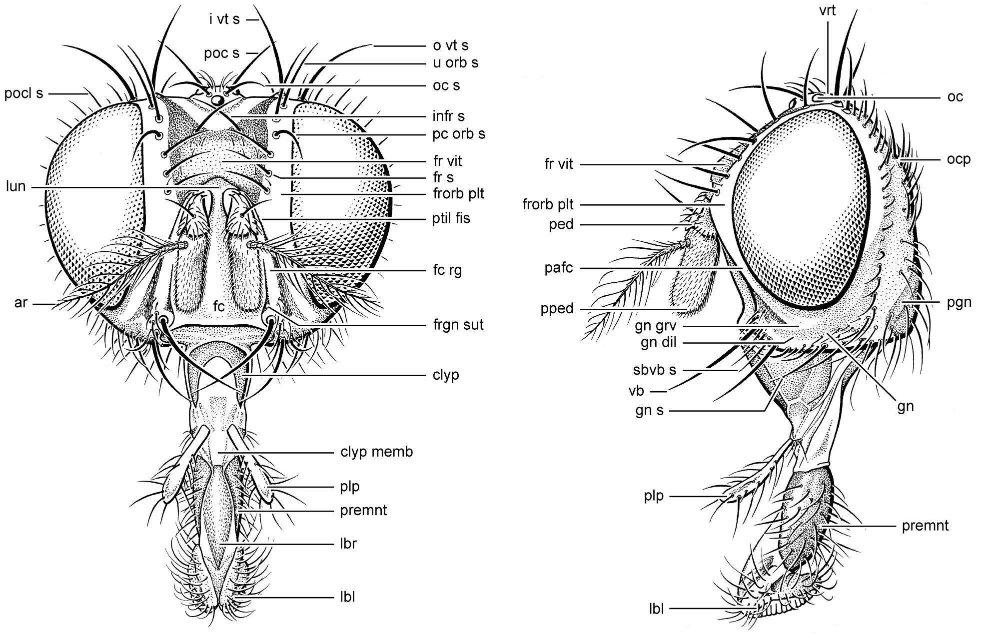
face (Figs 4, 32): in Diptera the region on the anteroventral surface of the head capsule between the antennal sockets dorsally, the compound eyes laterally (or ptilinal fissures in Schizophora, which separate the face from the parafacial) and the clypeus ventrally, often partially surrounding the clypeus dorsolaterally. Among nematocerous families and orthorrhaphous Brachycera, especially among blood-feeding forms, the face has become greatly reduced and the convex sclerite between antennal bases and mouthparts is the clypeus, which internally supports the insertion of muscles that dilate the cibarium. In Muscomorpha *sensu* Woodley (1989) generally and in Cyclorrhapha in particular, the clypeus is reduced and the face has become the major sclerite between the antennae and mouthparts. The face may be concave (and thus invisible in profile), or convex, with a midlongitudinal ridge, or bulge. It is usually bare, although it is variously adorned with stout, curved setae (the mystax) in most Asilidae.

facial carina: a midlongitudinal (vertical) ridge on the face, extending forward between the first flagellomeres in many Schizophora and in some species extending up between the antennal bases to unite with the lunule.

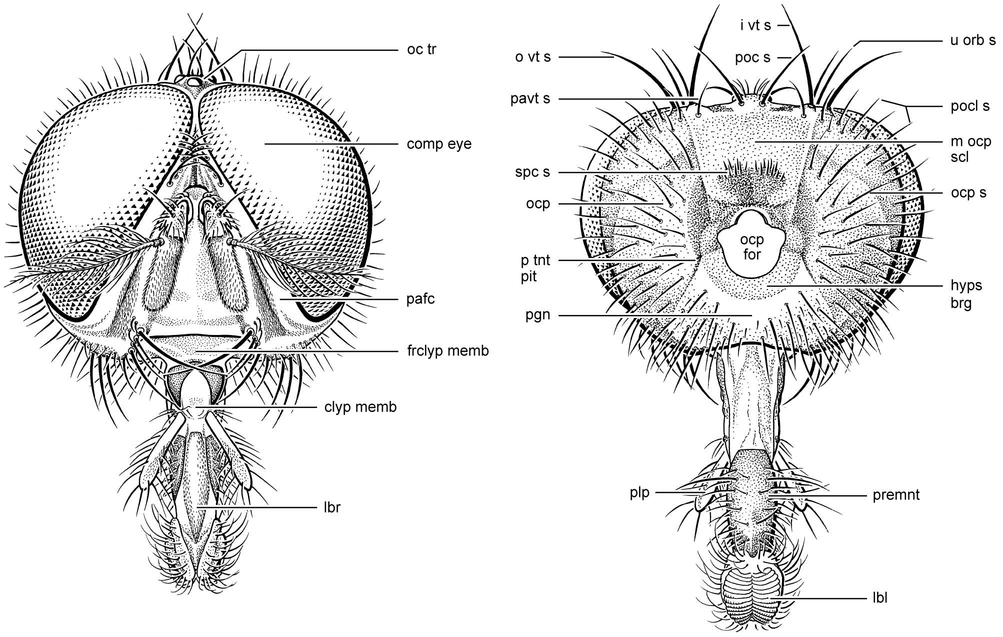
facial ridge (Fig. 4): the lateral margin of the face of Schizophora, delineated laterally by the ptilinal fissure and especially obvious in those forms in which the face is concave. The facial ridge often supports a vertical row of setae, or setulae, some of which can be stout, or elongate (see **supravibrissal seta** and **vibrissa**).

facial tubercle: a medial swelling on the face, especially among some Syrphidae.

frons (front) (Fig. 32): in Diptera the frons refers to the area between the compound eyes above the antennae. Morphologically, this is the postfrons, which is only part of the true frons of a generalised insect (McAlpine 1981) that extends to the clypeus as the prefrons. This latter region is, in Diptera, called the face. The frons is almost always complete in females, but may be partially or entirely reduced by medial enlargement of the compound eyes that meet in the midline in many flies, especially in males (see **holoptic** under Compound eye). Among nematocerous families and orthorrhaphous Brachycera, the frons is a simple sclerite, continuous from eye-to-eye and usually without setae, although hairs or scales are often present. In most Tabanidae bare shiny patches, termed calli (see **callus** above), are present on the frons, including the subcallus, basal callus and median callus. In Schizophora the frons becomes subdivided into a midlongitudinal frontal vitta and paired lateral fronto-orbital plates. The frontal vitta is expandable, allowing enlargement of the head and protrusion of the ptilinum during eclosion, while the lateral area, the fronto-orbital plate, is



4 *Hylemya* ♀ 5 *Hylemya* ♀



6 *Hylemya* ♂ 7 *Hylemya* ♀

Figs 3.4–7. Anatomical features of adult fly head: (4) *Hylemya alcathoe* (Walker) (Anthomyiidae), anterior view ♀; (5) same, lateral view ♀; (6) same, anterior view ♂; (7) same, posterior view ♀ (non-Afrotropical). Figs 4–7 (after McAlpine 1981, figs 8–11).

Abbreviations: ar – arista; clyp – clypeus; clyp memb – clypeolabral membrane; comp eye – compound eye; fc – face; fc rg – facial ridge; fr s – frontal seta; fr vit – frontal vitta; frclyp memb – frontoclypeal membrane; frgn sut – frontogenal suture; frorb plt – fronto-orbital plate; gn – gena; gn dil – genal dilation; gn grv – genal groove; gn s – genal seta; hyps brg – hypostomal bridge; i vt s – inner vertical seta; infr s – interfrontal seta; lbl – labellum; lbr – labrum; lun – lunule; m ocp scl – median occipital sclerite; o vt s – outer vertical seta; oc – ocellus; oc s – ocellar seta; oc tr – ocellar triangle; ocp – occiput; ocp for – occipital foramen; ocp s – occipital seta; p tnt pit – posterior tentorial pit; pafc – parafacial; pavt s – paravertical seta; pc orb s – proclinate orbital seta; ped – pedicel; pgn – postgena; plp – palpus; poc s – postocellar seta; pocl s – postocular seta; pped – postpedicel; premnt – prementum; ptil fis – ptilinal fissure; sbvb s – subvibrissal seta; spc s – supracervical seta; u orb s – upper orbital seta; vb – vibrissa; vrt – vertex.

sclerotised, usually bears setae and is usually different from the vitta in colour and texture, especially among Calyptratae. Secondary sclerotised plates, the interfrontal plates, which may bear rows of interfrontal setae, have developed in a few acalyptrate families (*e.g.*, Sphaeroceridae, Milichiidae).

frontal plate (Fig. 41): the anteroventral portion of the fronto-orbital plate, between the frontal vitta and the compound eye in Cyclorrhapha. It usually bears a longitudinal row of setae; the frontal setae (see **fronto-orbital plate**).

frontal setae (Fig. 4): a longitudinal row of setae arising on the frontal plate in most Cyclorrhapha; bordering the frontal vitta in Calyptratae and many acalyptrates. Frontal setae may be proclinate, or reclinate and are inclined medially to interdigitate with each other over the vitta. In most Phoridae these setae are quite large relative to the size of the head and they may be oriented in transverse rows as well as longitudinal rows.

frontal vitta (interfrons, interfrontal area, mesofrons) (Figs 4, 5): among Schizophora, during eclosion, the midlongitudinal area of the frons is expandable, thereby facilitating protrusion of the ptilinum and swelling of the head capsule. After eclosion and escape from the soil, or host cocoon, the ptilinum is retracted inside the head (leaving only the ptilinal fissure as external evidence of its former presence) and the cuticle of the frontal vitta shrinks, hardens and darkens. The vitta is bounded laterally by the sclerotised and usually setose and tomentose frontal plates. Although generally bare, the vitta may bear scattered setae and in some acalyptrate families (*e.g.*, Clusiidae, Milichiidae), a pair of larger setae, the **interfrontal setae** (Fig. 4). In some families (*e.g.*, Sphaeroceridae), paired longitudinal strap-like plates, the **interfrontal plates**, are present on the frontal vitta; each usually bears a row of interfrontal setae. In others (*e.g.*, Clusiidae, Chloropidae), the entire frontal vitta becomes more fully sclerotised and virtually indistinguishable from the frontal plates and may bear setae over its entire surface (*e.g.*, many Ulidiidae), thus resembling the frons of lower Cyclorrhapha. In many Phoridae a midlongitudinal line on the frons, which has been termed the coronal suture, may be the precursor of the frontal vitta.

frontoclypeal membrane, see **clypeus** below under Mouthparts.

frontoclypeal pit, see **anterior tentorial pit** under **tentorium**.

frontoclypeal suture, see **clypeus** below under Mouthparts.

frontogenal suture (Fig. 4): a paired line, in Cyclorrhapha, on the face, seldom used taxonomically. Usually faintly impressed, this suture extends from the vibrissal angle to the base of the antenna and delineates the facial ridge laterally, from the rest of the face, or facial plate, medially.

fronto-orbital plate (parafrontal plate) (Figs 4, 5, 42): the paired seta-bearing sclerite between the frontal vitta and the compound eye in Cyclorrhapha. Among nematocerous families and orthorrhaphous Brachycera, the entire frons is a simple sclerite, usually without setae (although hairs or scale-like setae may be present). Among Cyclorrhapha, however, the median area (frontal vitta) of the frons is expandable, allowing protrusion of the ptilinum during eclosion, while the lateral area, the fronto-orbital plate, is sclerotised and usually different from the vitta in colour and texture. In its simplest form, found in most acalyptrates and all calyptrates, the fronto-orbital plate is undivided and extends from the vertex to the level of the antennal bases. In a few acalyptrate taxa, however, this plate is subdivided into an anteroventral plate, the **frontal plate**, and a posterodorsal plate, the **orbital plate**, best exhibited by some Tephritidae.

fronto-orbital seta (Figs 4, 41, 42): any seta on the fronto-orbital plate sometimes differentiated into frontal and orbital setae. When differentiated into two longitudinal rows, the frontal setae are usually medial and anterior to the orbital setae. In Calyptratae, frontal and orbital setae form a continuous row and may not be readily differentiated, except by a change in size; the uppermost frontal setae are the smallest, while the adjacent orbital setae above and behind them are larger, becoming shorter towards the vertex.

gena (pl. **genae**) (cheek) (Fig. 5): that part of the head capsule between the compound eye and the subcranial margin. The gena is seldom of taxonomic importance in nematocerous families, or orthorrhaphous Brachycera, but in Cyclorrhapha, concurrent with the development of bristle-like setae, it has taken on greater importance. In Cyclorrhapha the setae on the occiput are continuous with those of the gena and may extend ventrally to the lower cranial margin, obliquely toward the vibrissa, or may curve up toward the eye margin to form a genal dilation. This setose part of the gena may be narrow, or broad, depending on the size of the eye in relation to the height of the head capsule. Along the ventral cranial margin there is usually a row of setae in Calyptratae that extends anteriorly almost to the vibrissae, separated from the subvibrissal setae by a narrow gap. McAlpine (1981: 15) separated the gena into two areas, the gena dorsally and a narrow bare ventral strip adjacent to the subcranial margin, the **subgena**, separated from the gena by the subgenal suture; however, from a taxonomic viewpoint this separation may not be of vital importance.

genal dilation (Figs 5, 42): of importance only in Schizophora, the widened part of the setose portion of the gena, just behind the vibrissa.

genal groove (Figs 5, 42): at the ventral terminus of the ptilinal fissure, lateral to the vibrissa, at the point of intersection of the facial ridge, parafacial and gena, is a triangular area of cuticle that was expanded during ptilinal eversion. In a well-hardened adult (it often collapses in a teneral specimen), the genal groove shows evidence of having been once expanded, similar to the cuticle of the frontal vitta. The cuticle of the genal groove is often coloured differently from adjacent cuticle of the parafacial, or gena and in some Tachinidae it may be quite extensive and rugose. Setae are seldom present.

genal seta (Fig. 5): in addition to the row of setae along the ventral margin of the gena, some setae and setulae may also be present on the surface of the gena itself.

inner vertical seta (**medial vertical seta**): (Figs 4, 7, 41, 42): a paired seta, usually the largest seta arising from the top of the head, lateral to the ocellar triangle. It is the uppermost in the row of postocular setae that extends from the vertex, behind the eye, to the gena. McAlpine (1981: 14) and Cumming &

Wood (2009: 13) applied the term inner vertical seta, while Merz & Haenni (2000: 34) preferred medial vertical seta. The inner and outer, or medial and lateral, vertical setae are adjacent to each other and the terms are equivalent, with usage depending on whether one prefers English, or latinised adjectives. McAlpine is here followed on the grounds that more dipterists are likely to be familiar with inner and outer, rather than medial and lateral. The inner vertical setae are often reclinate, or inclinate and may be parallel, or cruciate medially (see **outer vertical seta**).

interfrontal plate, see **frontal vitta**.

interfrontal seta (Fig. 4): any paired setae, other than scattered hairs, on the frontal vitta, between the frontal setae; found in Phoridae, Lonchopteridae and certain acalyptrate taxa (*e.g.*, some Clusiidae). In a few families of acalyptrates (*e.g.*, Sphaeroceridae and Milichiidae), a pair of strap-like sclerites has developed in the frontal vitta and the row of setae on these plates is referred to as the interfrontal setae (see **frontal vitta**).

lateral vertical seta, see **outer vertical seta**.

lunule (Figs 4, 41): present only in Schizophora, the narrow crescent-shaped part of the frons between the ptilinal fissure at its dorsal extremity and the antennal bases. Usually bare and shiny, it bears small setae in some Lonchaeidae (*e.g.*, *Dasiops* Rondani, Lonchaeini), many Ulidiidae and some Tachinidae (*e.g.*, *Oestrophasia* Brauer & Bergenstamm).

medial vertical seta, see **inner vertical seta**.

median occipital sclerite (Fig. 7): the somewhat rectangular mid-dorsal region of the back of the head in most Brachycera, between the ocellar triangle dorsally and the occipital foramen ventrally and delineated laterally by a suture extending from a point between the inner and outer vertical setae to the occipital foramen. Paired groups of small setae, the **supracervical setae**, may be present above the occipital foramen.

mystax (Fig. 34): a patch of stout, curved setae on the face of most Asilidae extending anteriorly like a moustache, probably to protect the head from struggling, or stinging prey.

nasus, see **rostrum**.

occipital foramen (Fig. 7): the opening in the middle of the back of the head where it is connected to the cervix.

occipital setae (Fig. 7): the setae scattered over the surface of the back of the head, not including postocular setae, which form a fringe behind the eyes.

occiput (Figs 5, 7): the upper portion of the postcranium, or back of the head; it may be convex, as in most nematocerous families; relatively flat as in most Schizophora; or concave, as in some other Brachycera (*e.g.*, Pipunculidae, some Bombyliidae and Syrphidae) (see **median occipital sclerite** and **postcranium**).

ocellar triangle (Figs 6, 41): on the midline, at the vertex, or uppermost part of the head, a triangular setose sclerite bears the three ocelli in most Diptera. It and the ocelli are absent in all members of Culicomorpha, Psychodidae and Tipulidae, as well as in several other nematocerous families (*e.g.*, many Cecidomyiidae), but they are almost always present in Cyclorrhapha (absent in Ctenostylidae and most Pyrgotidae). Although usually approximately equilateral, the triangle, which points forward, may be elongate as in some Chloropidae and Cryptochetidae, extending anteriorly to partially split the frontal vitta in half. In the phorid genus *Stichillus* Enderlein, the triangle is extremely broad, such that the ocelli form a nearly straight transverse line. If the ocellar triangle is raised, as in some Tabanidae, Bombyliidae and Asilidae, it is referred to as an **ocellar tubercle**. In some Mycetophilidae the ocellar triangle is absent, although two, or three ocelli may be present.

ocellar tubercle, see **ocellar triangle**.

ocellar seta (Figs 4, 41): in Cyclorrhapha and some other Brachycera, a single pair of small to large setae, larger and distinctly differentiated from the surrounding hairs, arising on the ocellar tubercle between the anterior and posterior ocelli (rarely on either side of the anterior ocellus, as in the heleomyzid subfamily Trixoscelidinae and the tachinid genus *Actinodoria* Townsend). Ocellar setae may be proclinate, reclinate, or inclined laterally; they may be sexually dimorphic in direction (proclinate and almost parallel in males of the tachinid genus *Trafoia* Brauer & Bergenstamm, but inclined laterally in females); doubled, especially in bristly taxa; or absent and thus not differentiated from the hairs that are normally present on the tubercle.

ocellus (pl. **ocelli**) (Figs 3, 5): in most Diptera three ocelli, or simple eyes, are present on the ocellar triangle, arranged as one might expect, in a triangle. In some Mycetophilidae, however, the median ocellus is absent and the lateral ones are widely separated. Ocelli are absent in several nematocerous groups (all Culicomorpha, Psychodidae, Tipulidae and various taxa scattered among several other families, *e.g.*, many Cecidomyiidae), as well as some Brachycera (*e.g.*, often brachypterous and apterous species).

orbital plate (Fig. 41): in Schizophora, the upper part of the fronto-orbital plate, bearing the orbital setae (see **fronto-orbital plate**).

orbital seta (prevertical seta) (Figs 4, 41, 42): any seta arising from the orbital plate. They are usually reclinate in both sexes. In almost all females of Calyptratae and in some males as well, an additional pair, or two pairs, of proclinate orbital setae are present, lateral to the row of reclinate orbital setae.

outer vertical seta (**lateral vertical seta**) (Figs 4, 7, 41, 42): a paired, usually lateroclinate seta that is in line with, but usually distinctly larger than, the rest of the postocular setae; duplicated in some Psilidae; each seta is medially inclined in most Phoridae (see **inner vertical seta**).

paraclypeal sclerite (clypeal sclerite): sclerite, or pair of sclerites that arises in the frontoclypeal membrane between clypeus and lower facial, or genal margin in some Tachinidae, *e.g.*, *Clausicella* Rondani and *Ginglymia* Townsend.

parafacial (pl. **parafacials** or **parafacialia**) (Figs 5, 6, 42): that part of the face between the facial ridge and the eye in Schizophora. Dorsally, the parafacial is only arbitrarily separable from the frons, usually at the level of the insertion of the antenna, or at the position of the anteriormost frontal seta in Tachinidae. Ventrally, the parafacial is separated from the gena by the genal groove.

paravertical setae (Figs 7, 41, 42): a small pair, or two pairs of setae behind the postocellar setae and between the inner vertical setae.

peristomal seta, see **subvibrissal seta**.

postclypeus, see **clypeus**.

postcranium (Figs 5, 7): the entire back of the head according to McAlpine (1981: 16), who divided the postcranium into a dorsal portion, the occiput and a ventral part, the postgena. Merz & Haenni (2000: 29) regarded the terms postcranium and occiput to be synonymous and used occiput and postgena to describe the dorsal and ventral portions of the back of the head.

posterior tentorial pit, see **tentorium**.

postgena (Figs 5, 7): the ventral part of the back of the head, continuous with the gena laterally. In some primitive nematocerous families (*e.g.*, Tanyderidae), the postgenae are separated medially by a membrane; in most Diptera, however, they meet one another medially, or else the membrane between them has become sclerotised, to form the bottom portion of the postcranium (see **postcranium**).

postocellar setae (postvertical seta) (Figs 4, 7, 41, 42): a pair of small setae arising directly posterior to the ocellar triangle. In a few taxa these setae are doubled and are then distinguished as the medial and lateral postocellar setae (Merz & Haenni 2000: 34).

postocular setae (Figs 4, 7, 41): a single erect row of hairs on either side of the head forming a fringe behind each eye, beginning dorsally just below the outer vertical seta and extending ventrally to the gena. The postocular setae also delineate the postcranium.

postvertical seta, see **postocellar seta**.

proboscis (Fig. 3): the specialised mouthparts of Diptera that are partially enclosed in a tubular labium. They are rigidly attached to the head capsule in nematocerous families, especially biting forms, slightly articulated, but essentially non-retractible in non-Cyclorrhapha and fully retractible in most Eremoneura (Empidoidea and Cyclorrhapha), unless exceptionally elongate, in which case the apex projects anteriorly (see also under Mouthparts).

ptilinal fissure (frontal suture, ptilinal suture) (Fig. 4): all that is visible of the **ptilinum** after it has been retracted, extending as an inverted U-shaped line from the genal groove, just behind the vibrissa, dorsally around the lunule to join the frontal vitta. The fissure delineates the face from the parafacial and the lunule from the frons. Often, an individual fails to retract the ptilinum fully, leaving a gap in the fissure, or a portion of the ptilinum protruding. Some tachinid parasites of hairy caterpillars occasionally get the barbed hairs of their host caught up in the ptilinum as they force their way out of the host cocoon, leaving these hairs protruding from the fissure (see Brooks 1945).

ptilinum (Fig. 4): one of the most characteristic synapomorphies of the Schizophora and the basis of the name (fly with fissure), the ptilinum is an inflatable sac-like part of the front of the head that can be protruded between the face and the frons to exert pressure on the anterior cap of the puparium to force it open. In the tachinid genus *Gonia* Meigen, the cuticle of the ptilinum is covered with small thorn-like spines for rasping the soil ahead of the escaping fly (Strickland 1953). As the adult fly hardens, the ptilinum is retracted inside the head, leaving only a faint line, the **ptilinal fissure**, as evidence of its existence.

rostrum (Fig. 40): in Tipulidae and a few genera in other families, the face, clypeus and genae are elongated, forming a tube-like extension of the front of the head, called the rostrum, which is sometimes prolonged apically into a projection referred to as the **nasus**.

stemmatic bulla (Fig. 8): a small rounded shiny tubercle behind the margin of the eye in some Simuliidae (often with reduced compound eyes) and a few Chironomidae (*e.g.*, *Oreadomyia albertae* Kevan & Cutten-Ali-Khan), that is believed to be a remnant of the larval eye. The bulla lacks the transparent cornea and internal organisation of an ocellus and is unlikely to be homologous to one.

subcallus: in Tabanidae, that part of the front of the head between frons, antennae and genae, sometimes swollen, or shiny, or both (see **callus**).

subcranial cavity (oral cavity): in Cyclorrhapha, especially among Schizophora, the proboscis can be retracted into the ventral area of the head capsule by muscles inserted along the lower margin of the face (epistoma). Among schizophorans living at high latitudes and altitudes, the lower facial margin is usually projected anteriorly, perhaps to give these muscles greater range of motion in cold conditions and/or to exploit nectar and pollen from the generally small-sized flowers found in these environments. Although the subcranial cavity is often referred to as the “mouth”, or oral cavity, the true mouth is inside the proboscis (see above) and the mouthparts are outside the mouth, not within.

subgena, see under **gena**.

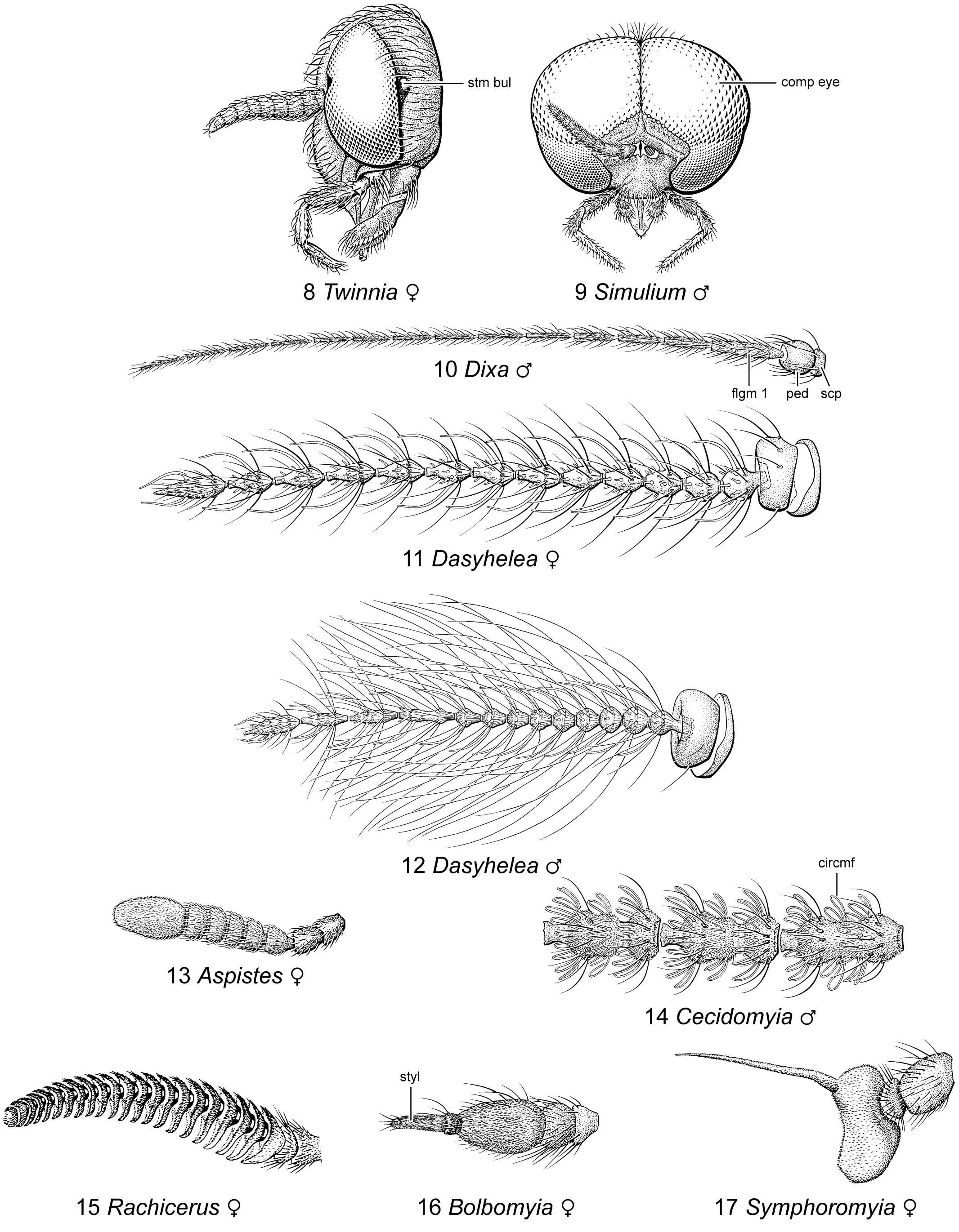
subvibrissal ridge: the lower cranial margin between the vibrissa and ventral margin of the gena in Schizophora.

subvibrissal seta (peristomal seta) (Figs 5, 42): large seta(e) on the subvibrissal ridge below the vibrissa. Usually only one or two setae are present, but in some Tachinidae there are more than four on each side, making the vibrissa appear raised above the ventral cranial margin.

supracervical setae, see under **median occipital sclerite**.

supravibrissal seta (Fig. 42): setae on the facial ridge above the vibrissa; taxonomically important in Calyptratae.

tentorium (Fig. 36): inner skeleton of the head capsule formed by paired sets of anterior, dorsal and posterior arms; the anterior and posterior arms arise, respectively, from externally visible **anterior tentorial pits** (frontoclypeal pits) (Fig. 36) and **posterior tentorial pits** (Fig. 7).



8 *Twinnia* ♀

9 *Simulium* ♂

10 *Dixa* ♂

11 *Dasyhelea* ♀

12 *Dasyhelea* ♂

13 *Aspistes* ♀

14 *Cecidomyia* ♂

15 *Rachicerus* ♀

16 *Bolbomyia* ♀

17 *Symphoromyia* ♀

Figs 3.8–17. Heads and antennae of adult flies: (8) head of *Twinnia* sp. (Simuliidae), lateral view ♀; (9) same, *Simulium decorum* Walker (Simuliidae), anterior view (left antenna omitted) ♂; (10) antenna of *Dixa brevis* Garrett (Dixidae) ♂; (11) same, *Dasyhelea pseudoincisurata* Waugh & Wirth (Ceratopogonidae) ♀; (12) same ♂; (13) same, *Aspistes harti* Malloch (Scatopsidae) ♀; (14) same, *Cecidomyia resinicola* (Osten Sacken) (Cecidomyiidae) ♂; (15) same, *Rachicerus obscuripennis* Loew (Xylophagidae) ♀; (16) same, *Bolbomyia macgillisi* Chillcott (Rhagionidae) ♀; (17) same, *Symphoromyia inurbana* Aldrich (Rhagionidae) ♀ (all non-Afrotropical). Figs 8, 9 (after Peterson 1981, figs 2, 3), Figs 10–17 (after McAlpine 1981, figs 12, 13, 14, 21, 20, 22, 28, 29, respectively).

Abbreviations: circmf – circumfilum; comp eye – compound eye; flgm – flagellomere; ped – pedicel; scp – scape; stm bu – stemmatic bulla; styl – stylus.

vertex (Fig. 5): the uppermost portion of the head capsule, with no definite boundaries. In the keroplatid subfamily Macrocerinae, a separate defined plate that occupies all or most of the vertex and bears the ocelli, is referred to as the **cerebral sclerite** (Matile 1990).

vibrissa (Figs 5, 42): in Schizophora an exceptionally large anteromedially directed seta that occupies a prominent position on the vibrissal angle at the base of the facial ridge; it is especially well-developed in Calyptratae, but also robust in some acalyptrate families (Barraclough 1995). An important landmark, it may be above, below, or at the level of the lower facial margin and is continuous with the setae of the facial ridge (supravibrissal setae) and those of the subvibrissal ridge. The vibrissa is also usually flanked laterally by a few much smaller setae.

vibrissal angle: in Schizophora, the angle, when viewed in profile, on which the vibrissa arises, formed between the facial ridge above and the subvibrissal ridge below.

Compound eye

The compound eyes (Figs 6, 40, 42) usually occupy most of the side of the head, but may be so extensive, particularly in males, that they make up nearly all of the head (Fig. 9). The eyes of some members of the Diopsidae, Periscelididae, Platystomatidae, Richardiidae (non-Afrotropical), Tephritidae and Ulidiidae are located at the end of narrow stalks. In some groups, such as cavernicolous, termitophilous, or ectoparasitic forms, the eyes are considerably reduced, or absent. Eye colour is usually uniform reddish-brown to dark brown or black, but can appear bright metallic in certain taxa. In some families, such as Tabanidae, Syrphidae, Richardiidae and Tephritidae, a pattern of bands and patches is frequently evident in living specimens.

Glossary

dichoptic (Fig. 4): the condition in which the compound eyes do not meet between antennae and vertex (see **holoptic** below).

eye bridge: in Sciaridae and some Cecidomyiidae, the compound eyes are narrowly connected medially above the antennae to form an eye bridge; this narrow connection is just a specialised example of holopticism.

facet: the transparent cuticular covering, or cornea, of an individual **ommatidium**.

holoptic (Figs 6, 9): the condition in which the compound eyes meet in the midline between the antennae and vertex. Males of many families are holoptic and the ommatidia in the upper part of the eye of these males are often larger than those of the lower part (Fig. 9), sometimes strikingly so (*e.g.*, most Simuliidae and Bibionidae, some Tabanidae and Empididae, most Syrphidae). This phenomenon is associated with males that hover, or swarm while awaiting the arrival of females. Although not actually touching medially, the eyes of many male calyptrates and some acalyptrates (*e.g.*, Lonchaeidae, Milichiidae and Ctenostylidae), are closer together than those of their conspecific females (*cf*. Figs 4, 6) and again, it is assumed that this condition allows the male greater visual accuity to chase and capture females in the air. Both males and females of some Blephariceridae, Acroceridae and Hybotidae (*e.g.*, Hybotinae) are holoptic, again probably associated with greater visual powers while hunting for hosts or prey. In the tachinid genera *Phasia* Latreille and *Trichopoda* Berthold the eyes of the female, although not strictly holoptic, are more closely approximated medially than those of the male (see **dichoptic** above).

ommatidium (pl. **ommatidia**): a unit of the compound eye consisting of a corneal lens (seen externally as a single **facet** on the compound eye), crystalline cone, pigment cells, rhabdome and retinula cells, which together connect to nerve fibres. As mentioned above in the definition of **holoptic**, some ommatidia are larger than others, presumably to admit more light. Most enlarged ommatidia are found in the dorsal portion of male eyes (Fig. 9); however enlarged ommatidia may be found ventrally, as in males of the simuliid *Parasimulium* Malloch, the cecidomyiid *Trisopsis* Kieffer and the phorid *Auxanommatidia* Borgmeier. Some asilids have enlarged ommatidia in the central part of the compound eye, *e.g.*, *Holcocephala* Jaennicke.

ommatrichia (eye hairs): between some ommatidia fine straight hairs may arise that give the eye a pilose appearance; these hairs, referred to as ommatrichia, or eye hairs, may be long and easily visible, or so short as to require strong magnification to be seen. They may be dense, arising between every ommatidium, or sparse, arising only between every third or fourth ommatidium.

Antenna

Antennae vary extensively within Diptera and often exhibit marked sexual dimorphism. Each antenna is made up of three basic parts (or **antennomeres**), the basal segment, or **scape**, the second segment, or **pedicel** and the third segment referred to as the **flagellum**, which contains varying numbers of **flagellomeres** (the more terminal antennomeres) (Figs 10, 40).

Glossary

ascoids: translucent thin-walled sensoria found on the flagellomeres of many Psychodidae; they may be branched or unbranched and are variously shaped.

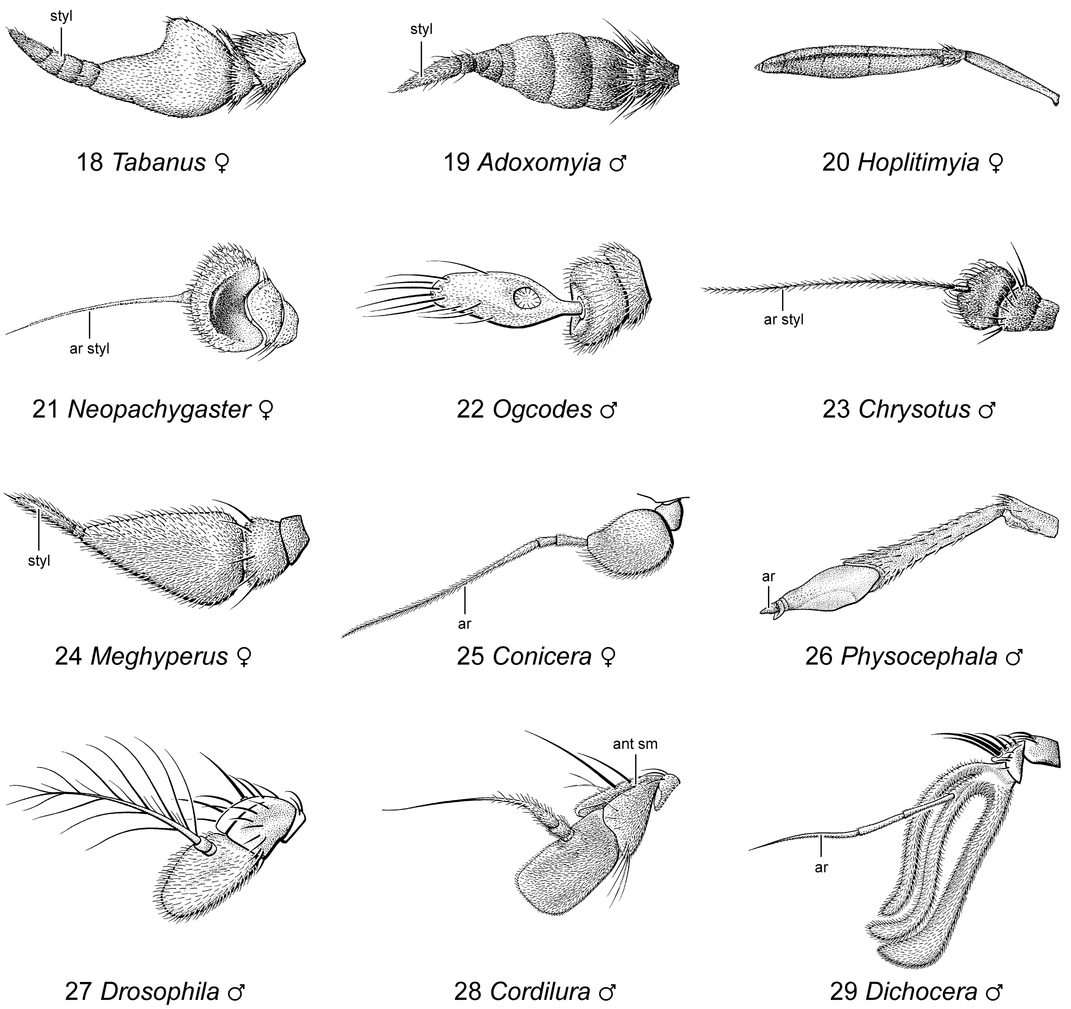
annular ridge, see **pedicel**.

antennal seam (pedicellar cleft, pedicellar seam) (Fig. 28): in Calyptratae and some acalyptrate families a longitudinal groove on the dorsolateral surface of the pedicel and corresponding apical notch. The seam is a useful character for recognising larger Calyptratae, but because of its occurrence in Tephritidae, Aulacigastridae, Periscelididae, Mormotomyiidae, some Platystomatidae and its slight manifestation in a few other acalyptrate families (*e.g.*, some Drosophilidae), this character is not very helpful for separating small calyptrates from acalyptrates. McAlpine (2011) gives a more complete account of the distribution of the antennal seam (as pedicellar cleft) in Schizophora.

antennal socket (Fig. 36): an opening in the frontal plate where the scape arises.

arista (Figs 4, 25, 26, 29, 41, 42): a term used for the last three articles of the flagellum (antennomeres 8–10, with 10 being the longest) in all Cyclorrhapha (Stuckenberg 1999), except the basal family Opetiidae (non-Afrotropical). These articles are generally slender and may arise either dorsally, or terminally on the postpedicel, but occasionally they are short (Fig. 26), or they may be absent altogether, as in males of the phorid genus *Abaristophora* Schmitz. Similar appearing apical whip-like flagellomeres occur in Athericidae and some Vermileonidae, Rhagionidae, Stratiomyidae and Empidoidea (Figs 21, 23). These apical flagellomeres are sometimes referred to as an arista, but because different antennomeres are involved (either 9–10, or 8–10 with 9 being the longest), they are best referred to as an arista-like stylus (Stuckenberg 1999) (see **stylus**). The arista of Cyclorrhapha is sometimes bare, or covered in a vestiture of microtrichia. The arista is referred to as **bare**, **micropubescent**, **pubescent**, **pectinate**, or **plumose** depending on the presence, or increasing length of the microtrichia. In pectinate, or plumose forms the individual microtrichia are usually referred to as **branches** (or rays).

aristomere (Fig. 25): one of three articles, or flagellomeres, that make up the arista in Cyclorrhapha. Usually, the basal aristomeres are very small and most of the arista is formed by the terminal article.



18 *Tabanus* ♀ 19 *Adoxomyia* ♂ 20 *Hoplitimyia* ♀

21 *Neopachygaster* ♀ 22 *Ogcodes* ♂ 23 *Chrysotus* ♂

24 *Meghyperus* ♀ 25 *Conicera* ♀ 26 *Physocephala* ♂

27 *Drosophila* ♂ 28 *Cordilura* ♂ 29 *Dichocera* ♂

Figs 3.18–29. Antennae of adult flies (lateral views): (18) *Tabanus sulcifrons* Macquart (Tabanidae) ♀; (19) *Adoxomyia rustica* (Osten Sacken) (Stratiomyidae) ♂; (20) *Hoplitimyia constans* (Loew) (Stratiomyidae) ♀; (21) *Neopachygaster maculicornis* (Hine) (Stratiomyidae) ♀; (22) *Ogcodes albiventris* Johnson (Acroceridae) ♂; (23) *Chrysotus pallipes* Loew (Dolichopodidae) ♂; (24) *Meghyperus* sp. (Atelestidae) ♀; (25) *Conicera dauci* (Meigen) (Phoridae) ♀; (26) *Physocephala furcillata* (Williston) (Conopidae) ♂; (27) *Drosophila colourata* Walker (Drosophilidae) ♂; (28) *Cordilura ustulata* Zetterstedt (Scathophagidae) ♂; (29) *Dichocera orientalis* Coquillett (Tachinidae) ♂ (all non-Afrotropical). Figs 18–29 (after McAlpine 1981, figs 30, 23, 25–27, 36, 33, 37, 38, 41, 43, 45 (as *D. tridens*), respectively).

Abbreviations: ant sm – antennal seam; ar – arista; ar styl – arista-like stylus; styl – stylus.

caestus (pl. **caesti**), see **pedicel**.

circumfila (sing. **circumfilum**) (Fig. 14): slender thread-like sensoria that encircle the flagellomeres of the antennae of some Cecidomyiidae and in certain species, particularly in males, form loops, or sinuous patterns.

conus: a narrow, thumb-like condyle, or conus of the pedicel that is inserted into the base of the first flagellomere. A conus is present in ceratomerine Empidoidea and several dolichopodid genera (*e.g.*, *Dolichopus* Latreille, *Tachytrechus* Haliday and *Syntormon* Loew) and a similar feature is present and appears to be a synapomorphy of almost all Cyclorrhapha, except the basal families Opetiidae (non-Afrotropical) and Platypezidae (Cumming *et al*. 1995: 143) (see **pedicel**).

first flagellomere (flagellomere 1, basal flagellomere, **postpedicel**, third antennal segment) (Figs 5, 10, 40, 42): the first article of the flagellum that is articulated to the apex of the pedicel. In nematocerous Diptera the first flagellomere is not strikingly differentiated from the following adjacent flagellomeres, but in Brachycera it is usually larger than the second and usually the largest portion of the antenna. Many exceptions occur, for example, in some Stratiomyidae, where the first three flagellomeres are similar to one another in size (Fig. 19) and, therefore, contrast with the remaining ones. In other Brachycera the flagellar base usually undergoes some degree of fusion, so that what is referred to as the first flagellomere is generally a compound structure. This enlargement and specialisation led Stuckenberg (1999) to propose that the flagellar base be termed the **postpedicel** (Figs 5, 42), irrespective of how many articles were fused together. In Cyclorrhapha, the first flagellomere, in contrast to the pedicel, is not setose, although it is usually finely pilose. The deep trichoid sensilla-containing invaginations, that each exit through a pore on the lateral surface of the first flagellomere of Ironomyiidae (non-Afrotropical), Syrphoidea and Schizophora, are termed **sacculi** (McAlpine 2011). These invaginations are not considered homologous with the **postpedicellar pouches** observed in the empidoid genus *Hormopeza* Zetterstedt and platypezid genus *Microsania* Zetterstedt (McAlpine 2011), which appear to be used to detect smoke that attracts these flies (Sinclair & Cumming 2006).

flagellomere (Figs 5, 10, 40, 42): any one of several articles constituting the flagellum. Flagellomeres are not true segments in that they are not individually musculated. According to Hennig (1973), the basal number of flagellomeres is 14 in nematocerous Diptera (although over 100 have been counted in an African psychodid), eight in the Lower Brachycera, three in the Asilomorpha and Empidoidea and four in Cyclorrhapha. Unfortunately, this number may not always be safely used to recognise all members of these taxa, for the number of flagellomeres varies widely in some nematocerous groups, depending on the species and is at times difficult to count (although most nematocerous Diptera with a reduced number of flagellomeres still have more than two palpal segments). For example, Simuliidae have 7–9 flagellomeres, Ceratopogonidae 6–13, Chironomidae 1–15, Scatopsidae 5–10, the cecidomyiid *Baeonotus* Byers has only six, while *Bibio* Geoffroy has seven. On the other hand, the xylophagid *Rachicerus* Walker has 20–36 flagellomeres (Fig. 15), no doubt secondarily subdivided (but it can be recognised as a brachyceran by its two-segmented palpus).

flagellum (Figs 5, 10, 40, 42): that part of the antenna beyond the pedicel and articulated to it; it is the third true segment of the antenna, divided into varying numbers of flagellomeres. The individual flagellomeres may bear long setae (**verticils**), especially among males of Culicomorpha (Fig. 12); in some taxa these long setae may be erected by hemolymph pressure during mating flights to make the antennae more receptive to wing beats of the female (see **pedicel**).

pedicel (Figs 5, 10, 40, 42): the second segment of the antenna. In male Culicomorpha (except Thaumaleidae, Simuliidae and some Ceratopogonidae), the pedicel is enlarged and globular (Fig. 30) and contains a sense organ (Johnston's organ), that is used for detecting wing-beat vibrations of the female. In some Conopidae, Pyrgotidae, Sciomyzidae and Ulidiidae the pedicel is extremely long, making up more than half the length of the antenna (Fig. 26) and in these families the antenna is porrect (*i.e.*, held extending forward). McAlpine (2011) described a number of useful taxonomic characters on the pedicel of higher Diptera, such as the **annular ridge** and paired **caesti**, which are modified raised surfaces that articulate with the first flagellomere (also see **conus**), and a recessed dome-like cuticular component of a chordotonal organ termed the **pedicellar button**.

pedicellar button, see **pedicel**.

postpedicel, see **first flagellomere**.

postpedicellar pouch, see **first flagellomere**.

sacculus (pl. **sacculi**), see **first flagellomere**.

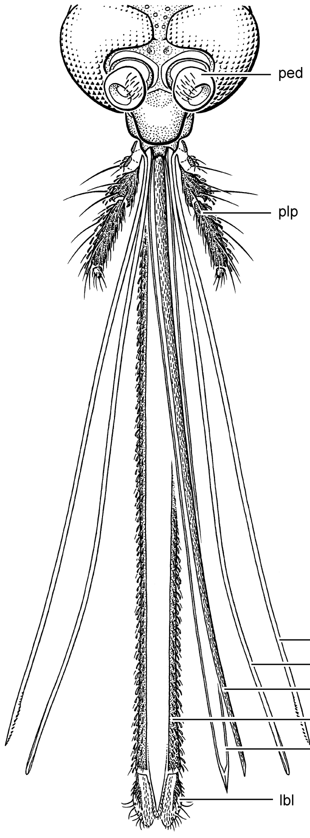
scape (Figs 10, 40): the first segment of the antenna, usually rather insignificant, except in the lower Brachycera, where it can be the longest segment of the antenna, as in the bombyliid genus *Lepidophora* Westwood. The scape is usually setose. In the tachinid genus *Microphthalma* Macquart, the apex of the scape extends as a flange over the pedicel.

stylus (style) (Figs 16, 18, 19, 21, 23, 24): the terminal flagellomeres, ending in antennomere 10 (flagellomere 8) in the orthorrhaphous Brachycera and Opetiidae (non-Afrotropical), that usually arise at the apex of the first flagellomere. The stylus is sometimes composed of as many as six terminal flagellomeres, but usually contains as few as one or two articles (Stuckenberg 1999). The bare hyaline process at the apex of the antenna in many asiloids and empidoids (actually antennomere 10 according to Stuckenberg (1999)), has also been referred to as the antennal style (Yeates 1994) (see **arista**).

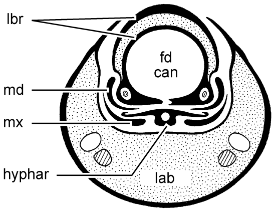
verticil, see **flagellum**.

Mouthparts

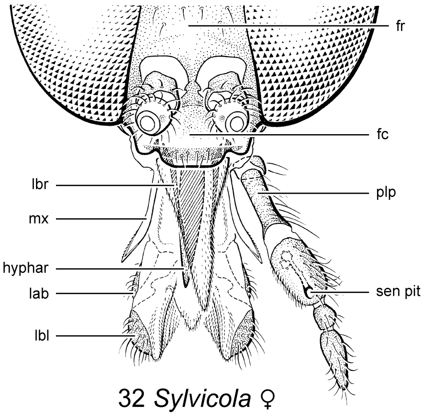
Unless their mouthparts are non-functional (*e.g.*, some Oestridae), all Diptera have, at a minimum, a **labrum**, a **hypopharynx** and a **labium** (Fig. 32). The **mandibles** and/or **maxillae** are reduced in most flies, apart from females of blood-sucking (with few exceptions) nematocerous families (Figs 30, 33) and lower Brachycera, and are absent in many taxa.



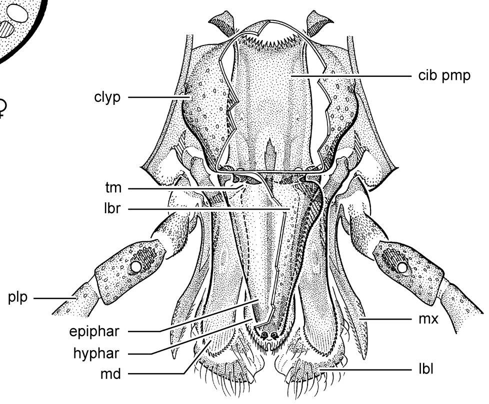
30 *Aedes* ♀



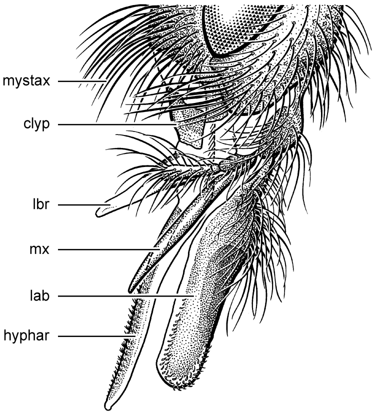
31 *Culex* ♀



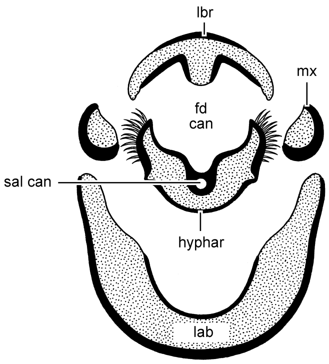
32 *Sylvicola* ♀



33 *Simulium* ♀



34 *Laphria* ♀



35 *Laphria* ♀

Figs 3.30–35. Heads and mouthparts of adult flies: (30) anterior view of lower part of head (antennae omitted) and mouthparts (individual stylets separated to show form and relationships) of *Aedes canadensis* (Theobald) (Culicidae) ♀; (31) cross-section through proboscis of *Culex pipiens* L. (Culicidae) ♀; (32) anterior view of lower part of head and mouthparts, with components separated, of *Sylvicola fenestralis* (Scopoli) (Anisopodidae) ♀; (33) anterior view of mouthparts and clypeus, cut away to show cibarium, of *Simulium vittatum* Zetterstedt (Simuliidae) ♀; (34) lateral view of lower part of head and mouthparts of *Laphria thoracica* F. (Asilidae) ♀; (35) same, cross-section through proboscis ♀ (all non-Afrotropical). Figs 30–32, 34, 35 (after McAlpine 1981, figs 46–48, 54, 53, respectively), Fig. 33 (after Peterson 1981, fig. 8).

Abbreviations: cib pmp – cibarial pump; clyp – clypeus; epiphar – epipharynx; fc – face; fd can – food canal; fr – frons; hyphar – hypopharynx; lab – labium; lbl – labellum; lbr – labrum; md – mandible; mx – maxilla; ped – pedicel; plp – palpus; sal can – salivary canal; sen pit – sensory pit; tm – torma.

Glossary

basiproboscis: a term used in Asilidae for the basal part of the proboscis that is enclosed by the base of the prementum. It is generally distinct from the more distal portion of the proboscis, which in asilids, is enclosed by the solidly fused apex of the prementum and the labella (see **distiproboscis**).

capitate proboscis, see **proboscis** below.

cardo (pl. **cardines**): the basal segment of the maxilla. It is scarcely detectable in most adult Diptera and is not used taxonomically, except in the larva.

cibarium (Figs 33, 36): the pump for drawing up liquid food; the internal sclerotised tube connected to and continuous with the food canal within the rolled labrum, derived from the posterior portion of the preoral cavity at the beginning of the pharynx. The cibarium is useful taxonomically in the Simuliidae. A small **hyoid sclerite** also occurs ventrally along the proximal margin of the cibarium in Calyptratae.

clypeal ridge (Fig. 36): a primarily internal ridge in Brachycera, that arises obliquely from the clypeus and articulates with the labrum and cibarium at the labrofulcral articulation point. It is derived from the clypeus, but is sometimes confused with the tormae that are derived from laterobasal processes of the labrum (see **torma** below).

clypeus (frontoclypeus) (Figs 4, 30, 33, 34, 36, 37, 39): really a part of the head capsule, rather than one of the mouthparts, but incorporated into the proboscis in Brachycera. In nematocerous families, the clypeus is a rounded convex sclerite between the labrum and the face and in blood-sucking flies it occupies most of the space between the antennae and mouthparts. Internally it supports the origins of the cibarial dilator muscles. In the Brachycera, exclusive of Tabanomorpha, the proboscis is more mobile and the clypeus has become reduced and is hinged at the **frontoclypeal suture**, the lower margin of the face. In Schizophora, the clypeus is even more widely separated from the face by the **frontoclypeal membrane** (Fig. 6) and the entire proboscis is capable of considerable extension and retraction (see also under Head).

distiproboscis: in Asilidae the labella are solidly fused to the apex of the prementum as part of the sheath through which the hypopharynx is driven into the prey (Fig. 34); this fused distal portion of the proboscis is generally distinct from the more basal part, which is enclosed by the base of the prementum (see **basiproboscis**).

epipharyngeal blades, see **labrum**.

epipharynx, see **labrum**.

geniculate proboscis, see **proboscis** below.

hyoid sclerite, see **cibarium**.

hypopharynx (lingua) (Figs 30–37, 39): the tongue, an unpaired median stylet-like extension of the posterior margin of the mouth, conveying the salivary canal. All flies that feed have a hypopharynx, if only for wetting dried honeydew so it can more easily be sucked up. The hypopharynx is of critical importance in blood-sucking flies for conducting anticlotting substances to the wound during feeding. In Asilidae, the hypopharynx is long and sharp (Fig. 34) and is the only mouth-part to enter the prey. Asilid saliva must be highly toxic as well as proteolytic, for asilids can subdue, in seconds, stinging prey larger than themselves, then later suck out the liquefied contents of the prey. When handled they can also inflict a painful bite.

labellum (pl. **labella**) (Figs 4, 5, 7, 30, 32, 33, 36–38, 40): homologous to the labial palpus, primitively two-segmented (as in Blephariceridae and Tanyderidae), but in most Diptera each palpus is reduced to a single, highly modified structure for sponging up fluids (see **pseudotracheae**). Although a paired structure, the two labella (**labellar lobes**), are fused medially into a single cupped structure at the end of the prementum, which is pressed onto the substrate during feeding. Channels on the ventral side, the pseudotracheae, all lead to the midline, from which point saliva can be pumped into them *via* the hypopharynx to wet the substrate and dissolve sugars or salts present there, or liquid food can be sucked up from them *via* the food canal in the labrum, aided by suction from the cibarial pump. The labella may be greatly reduced in some species, especially those with a long proboscis for taking nectar from tubular flowers (many Bombyliidae), or the labella themselves may also be greatly elongate for accomplishing the same task (*e.g.*, *Siphona* Meigen, in the Tachinidae). In the Asilidae (Fig. 34), the labella are fused to the apex of the prementum to form a solid sheath, through which the sharp hypopharynx is projected into the prey (see **distiproboscis**).

labium (Figs 30–35, 39): as in all mandibulate arthropods, the labium is homologous to the second maxillae, or most posterior pair of segmental head appendages. In Diptera these paired appendages are completely fused medially, to form a trough-like sheath surrounding the remaining mouthparts from behind and thus the labium is usually the most conspicuous part of the proboscis. The sheath itself is made up of the basal **postmentum** (mentum) and the apical **prementum**, terminating distally in the medially fused **labella** (**labellar lobes**). In most Diptera, the postmentum is insignificant, forming the ventral external closure of the head capsule, while the prementum and the labella are the predominant parts of the proboscis. The labium is hinged at its base and can be extended while feeding, or folded forward when at rest. In nematocerous Diptera and non-Schizophora this hinge is not very extensible and in blood-feeding forms it is even more closely associated with the head capsule, to provide stability to the mouthparts when they are inserted into the host. In Schizophora, however, the labium is particularly mobile, connected to the lower cranial margin by a substantial membranous cuticle that allows considerable extension so that the fly does not need to bend down to feed, but merely has to extend the proboscis. In blood-feeding Calyptratae, such as the stable flies, *Stomoxys* Geoffroy (Muscidae) (Figs 38, 39), *tsetse* (Glossinidae) and louse flies (Hippoboscidae), the entire proboscis is jabbed into the host with the help of recurved spines on the labella (see **prestomal teeth**).

labrum (Figs 4, 6, 30–37, 39): the upper lip, a triangular or elongate flap extending anteroventrally from the clypeus and hinged to it along the clypeolabral suture. Its ventral surface is grooved to form, along with the dorsal surface of the hypopharynx, the food canal. In most flies, the labrum is visible externally as a triangular, or elongate stylet between the encircling edges of the prementum, but it and the hypopharynx, can extend beyond the labella if the labium is withdrawn, which is apparently how predaceous Empidoidea stab their prey. In most Empidoidea the ventral wall of the labrum (**epipharynx**) is developed into apical tooth-like projections, referred to as **epipharyngeal blades** (or armature), that flank the median pointed labral tip (Bletchly 1954). These sharp blades are used for piercing and cutting tissue and are most heavily sclerotised in the empidoid family Dolichopodidae (Fig. 36).

lacinia (pl. **laciniae**) (galea) (Figs 30–36): the stylet of the maxilla in Diptera, misinterpreted by some authors as the galea, as indicated by McAlpine (1981: 20) and Wood & Borkent (1989: 1337). It is best developed in blood-feeding nematocerous and lower brachyceran families, as well as in some predaceous taxa; reduced, or vestigial in most other Diptera; absent in Cyclorrhapha. Set with retrorse teeth apically in blood-feeding groups and used to anchor the mouthparts in the skin of the host while the mandibles are cutting a hole, or in the case of mosquitoes, to gain purchase while the mandibles are inserted further (see **maxilla**).

mandible (Figs 30, 31, 33): a paired appendage of the head on either side of the mouth opening; a triangular or elongate stylet, which in blood-sucking forms is often set with saw-like teeth apically, for cutting the skin. In female members of Simuliidae (Fig. 33) and most Ceratopogonidae that blood-feed, the mandibles partially overlap one another and function as a pair of scissors, using as a fulcrum a tubercle on one mandible that fits into a depression on the other. Functional mandibles are also found in females of some Tanyderidae, most Blephariceridae, some Psychodidae (in several subfamilies), Culicidae, Corethrellidae, two genera of Chironomidae and many Tabanomorpha, all of which are apparently either predaceous, or blood-feeding.

maxilla (pl. **maxillae**) (Figs 30–36): a paired appendage of the head that arises behind the mandible and bears the palpus as its only external manifestation; it is hidden within the proboscis as a stylet, the lacinia. Well-developed in the blood-feeding forms mentioned under mandible, the lacinia is reduced, or vestigial in most Diptera and absent in Cyclorrhapha (see **cardo**, **lacinia**, **palpus** and **stipes**).

mentum, see **postmentum**.

palpifer: differentiated sclerotised region of the stipes that supports the palpus in certain taxa (*e.g.*, Hybotidae in the Empidoidea, as well as some Phoridae) (see **stipes**).

palpomere, see under **palpus**.

palpus (maxillary palpus, palp) (Figs 4, 5, 7, 30, 32, 33, 36, 37, 39, 40, 42): although part of the maxilla, this relationship is not readily apparent because the rest of the maxilla is enclosed in the labium and the palpus arises at, or near the base of the prementum. In nematocerous families the palpus is primitively divided into five segments (incorrectly referred to as palpomeres); although in many taxa there appear to be only four (probably because of great reduction of the basal segment). Further reductions in segment number occur in various nematocerous groups. The third segment of both sexes of most nematocerous families bears a sensory pit or vesicle (Lutz's organ), which is essentially an invagination that opens to the exterior *via* a pore. This pit is cavernous in females of many blood-sucking species and contains a cluster of club-shaped sensilla that are sensitive to carbon dioxide. The palpus in Brachycera is reduced to two segments in the lower Brachycera, even in blood-sucking forms belonging to the Tabanidae, Rhagionidae and Athericidae. Only one segment is present in the Eremoneura (Empidoidea and Cyclorrhapha); the apparent basal segment of the two-segmented palpus seen in some Phoridae (Brown 1992) is probably a palpifer (see above). Among several genera of Tachinidae, the single segment is reduced in size, or is lacking altogether.

postmentum (mentum): the basal sclerite of the labium retained in only a few nematocerous families, such as Blephariceridae, Tanyderidae, Anisopodidae, Psychodidae and Ceratopogonidae (Stuckenberg 2004).

prementum (haustellum, theca) (Figs 4, 5, 7, 36–38): the distal tubular portion of the labium forming the supporting sheath of the proboscis, terminating in the labella.

prestomal teeth (Fig. 38): bicuspid blades situated between the pseudotracheae at the base of the labella in Calyptratae; they are enlarged in predaceous groups (*e.g.*, coenosiine Muscidae, Scathophagidae) and are especially prominent in blood-feeding calyptrates (*e.g.*, stomoxyine Muscidae, Hippoboscoidea).

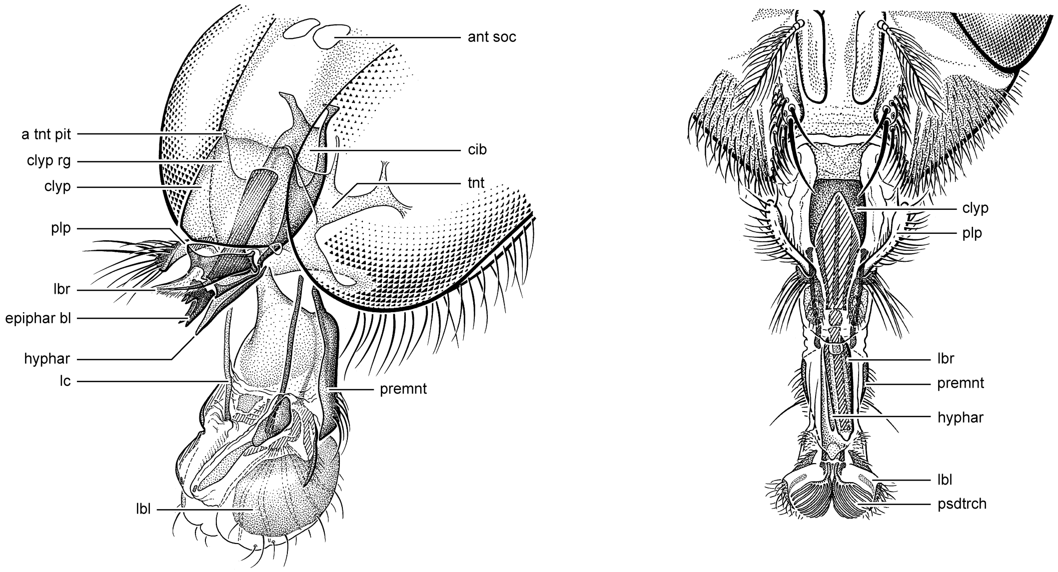
proboscis (Fig. 3): all of the mouthparts ensheathed in the labium extending from the subcranial cavity of the head capsule (often referred to as the "mouth"). In Schizophora the proboscis is capable of considerable extension and retraction, often being entirely withdrawn into the head capsule and the membrane joining it to the subcranial margin is correspondingly more extensive. When a proboscis is thin and bent with long labella, it is termed **geniculate**, whereas when it is thicker (*i.e.*, square to slightly rectangular), with short labella, it is termed **capitate** (see also under Head).

pseudotracheae (sing. **pseudotrachea**) (Fig. 37): interconnected channels on the ventral surface of the labella of many Brachycera that radiate out from the midline where the tips of the labrum and hypopharynx meet; they are reinforced with rings of chitin (hence the reference to tracheae) that are open ventrally.

salivary canal (Fig. 35): the common salivary duct that in most Diptera extends the length of the hypopharynx to open at its apex. Saliva is used to wet the food so it can be dissolved and taken up by the pseudotracheae when present and to convey hemolytic enzymes to the host while blood-feeding to prevent clotting of the blood meal, or proteolytic enzymes in predaceous taxa to paralyse the prey and liquefy its tissues for consumption. Diptera cannot take solid food unless it is sufficiently finely divided (such as pollen grains), to be sucked up the food canal along with other liquids. Various pathogens (*e.g.*, viruses, bacteria and protozoa, such as *Plasmodium* spp. that cause malaria), take advantage of the salivary canal to enter new hosts while an infected fly is blood-feeding.

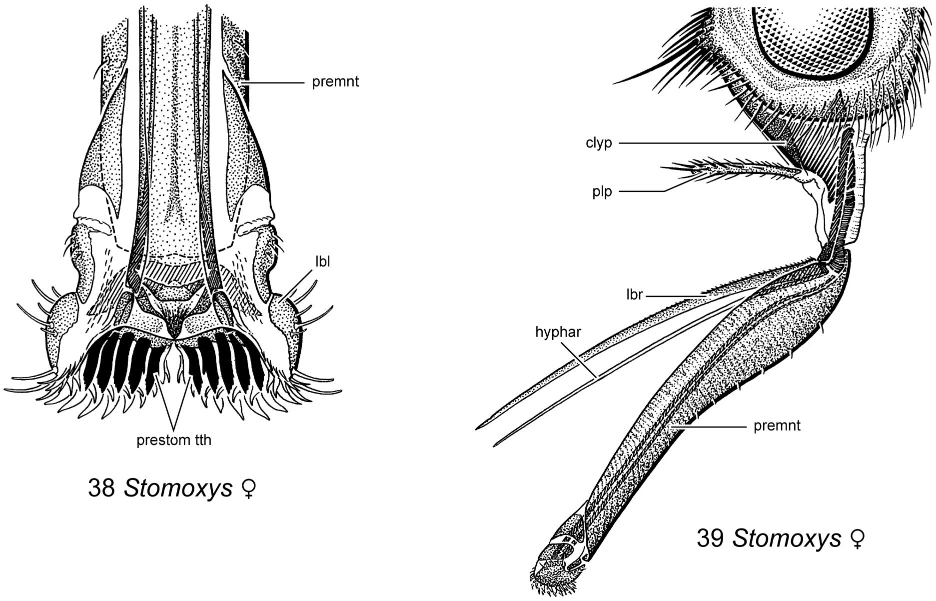
stipes: the distal segment of the maxilla, bearing the lacinia and the palpus (see **palpifer**).

syntrophium (fascicle) (Figs 31, 35): term proposed by Jobling (1976) for the complex of mouthparts that functionally enclose the food and salivary canals, namely the labrum and



36 *Condylostylus* ♀

37 *Calliphora* ♀



38 *Stomoxys* ♀

39 *Stomoxys* ♀

Figs 3.36–39. Mouthparts (displayed to show form and relationships): (36) anterolateral view of proboscis with cibarium and tentorium of *Condylostylus sipho* (Say) (Dolichopodidae) ♀ (non-Afrotropical); (37) anterior view of proboscis and lower part of head of *Calliphora vomitoria* (L.) (Calliphoridae) ♀ (non-Afrotropical); (38) anterior view of enlarged apex of proboscis showing prestomal teeth of *Stomoxys calcitrans* (L.) (Muscidae) ♀; (39) same, lateral view of proboscis and lower part of head. Figs 36–39 (after McAlpine 1981, figs 51, 58, 57, 55, respectively).

Abbreviations: a tnt pit – anterior tentorial pit; ant soc – antennal socket; cib – cibarium; clyp – clypeus; clyp rg – clypeal ridge; epiphar bl – epipharyngeal blade; hyphar – hypopharynx; lbl – labellum; lbr – labrum; lc – lacinia; plp – palpus; premnt – prementum; prestom tth – prestomal teeth; psdtrch – pseudotrachea; tnt – tentorium.

hypopharynx, as well as the mandibles and maxillary laciniae when present, but not the labium.

torma (pl. **tormae**) (Fig. 33): a small laterobasal sclerite of the labrum situated on each side of the base of the epipharynx near the clypeolabral suture; tormae are best developed in those nematocerous families and orthorrhaphous Brachycera that possess piercing mouthparts (see also **clypeal ridge** above).

Thorax

In Diptera, the three thoracic segments, the **prothorax**, **mesothorax** and **metathorax**, are intimately fused together into a single spheroidal, or rectangular capsule, consisting almost entirely of the mesothorax, with its associated wing and leg muscles, while the prothorax and metathorax are reduced to a minimum, enough to support the leg musculature of the first and third pairs of legs and in the metathorax, the halter (Figs 40–42). Each segment is divided into a dorsal tergal region, the **notum** (pl. **nota**), a small ventral plate, the **sternum** (pl. **sterna**), which in the mesothorax and metathorax may be largely, or entirely internal and thus invisible externally and on each side of the thorax a lateral plate, the **pleuron** (pl. **pleura**).

The notum of the prothorax, the **pronotum**, is divided transversely into an anterior **antepronotum** and a posterior **postpronotum**, which appears to bear the **anterior thoracic spiracle** (mesothoracic spiracle). In nematocerous families the antepronotum is well-developed, while the postpronotum is reduced to a narrow band. The reverse is true in the Brachycera, in which the antepronotum is insignificant, while the postpronotum is expanded laterally to form the anterolateral corners of the thorax, sometimes bearing several setae of taxonomic importance. The notum of the mesothorax, the **mesonotum** (Fig. 2), occupying most of the dorsal surface of the thorax, is divided transversely into four areas, the **prescutum**, **scutum**, **scutellum** and **postnotum**. The prescutum is a rather vaguely defined anterior portion of the mesonotum, best seen in some nematocerous Diptera and is delineated laterally by the **prescutal pit**, whose position on each anterolateral corner of the scutum marks the former position of the pupal respiratory organ.

The most extensive area of the mesonotum, the scutum, is itself divided by the **transverse suture** into a **presutural area** and a **postsutural area** in most taxa. The presutural area in nematocerous families is bordered laterally by a narrow sclerite referred to as the **paratergite**. In nematocerous Diptera and most orthorrhaphous Brachycera the scutum is generally clothed in fine hairs or, in some Bombyliidae, scale-like hairs, while in Asilidae, Therevidae and Empidoidea, as well as in most Cyclorrhapha, some of the setae are stout and bristle-like. In the Eremoneura (Empidoidea and Cyclorrhapha) and particularly the Calyptratae, these setae tend to be arranged in four paired groups of longitudinal rows interspersed with much smaller erect, or recumbent setae; the **acrostichal setae** constitute the median row(s), flanked by **dorsocentral setae**, then by **intra-alar setae** and, just above the wing base, the **supra-alar setae**. The relative size and arrangement of these setae is of great taxonomic importance. The number of presutural *versus* postsutural setae in each row (Fig. 41) is sometimes denoted as a formula, with the presutural and postsutural setae separated by a "+" symbol (*e.g.*, **dc 3 + 4** denotes three presutural *versus* four postsutural dorsocentrals and **acr 4 + 2–3** denotes four presutural *versus* two to three postsutural acrostichals). Lateral to the transverse suture in Cyclorrhapha and some Empidoidea (*e.g.*, Dolichopodidae), is a small diamond-shaped, or triangular sclerite, the **notopleuron**, typically bearing one or two setae, while in the posterolateral corner of the scutum is the **postalar callus**, also bearing two or three setae. Laterally, above the calypter, the edge of the scutum turns down to form the **postalar wall**. A triangular part of this wall, just behind the wing base, the **tympanal fossa** or **tympanic pit**, bears setae in some Calliphoridae and Tachinidae (Fig. 46).

The scutellum is sharply delineated from the scutum by the **scutoscutellar suture**; typically the scutellum bears one or two pairs of marginal setae, a basal pair and an apical pair. Additional marginal setae, including one or more pairs of lateral setae as well as subapical setae and additional pairs, the discal scutellar setae, may be present on its surface.

The postnotum (formerly sometimes considered to be the notum of the metathorax), may be subdivided by a pair of grooves into a medial portion, the **mediotergite** and a lateral portion, the **laterotergite**; the laterotergite may be further divided by a horizontal groove into a dorsal **anatergite** and a ventral **katatergite**. In some Cyclorrhapha, particularly in Tachinidae, the mediotergite may be bordered dorsally by a transverse convex bulge, the **subscutellum**. The notum of the metathorax, the **metanotum**, connects the postnotum to the first abdominal tergite and usually is barely visible externally.

The side of the thorax, the pleuron, is separated from the scutum by the **lateral parapsidal suture**. It is considered derived from basal elements of the subcoxal region of the leg of the same segment that have come to occupy the lateral parts of the thorax, between the notum and sternum. In the dipteran thorax almost all of the side of the thorax is made up of the various components of the mesopleuron and the names of these components, for simplicity, are not preceded by the prefix meso-, while those corresponding parts of the prothorax and metathorax are prefixed by pro- and meta- accordingly.

The wing-bearing segment, the mesothorax, is reinforced by an invaginated strut extending from wing base to leg base, the **pleural suture**, a synapomorphy found in all winged insects, even those that have secondarily become wingless, including wingless adult Diptera. This suture separates the mesopleuron into an anterior episternum and a posterior epimeron. Each of these plates is further divided horizontally by the **anapleural suture** into a dorsal **anepisternum** (mesopleuron, of older terminology) and a ventral **katepisternum** (sternopleuron), in front of the pleural suture and a dorsal **anepimeron** (pteropleuron) and a ventral **katepimeron** (barette) behind the suture. The anepisternum, in Calyptratae and some other Schizophora, typically bears a vertical row of strong setae, as well as associated finer setulae, in front of the base of the wing, the anepisternal setae, while the anepimeron has a small tuft of hair, sometimes with a very large associated seta in some genera, the anepimeral (or pteropleural) seta, just below the wing base. Beneath the katepimeron and between the mid coxa and the posterior thoracic spiracle is the **meron** (hypopleuron), a sclerite derived from the mid coxa.

The **propleuron** and **metapleuron** are each, like their corresponding nota, greatly reduced relative to the mesopleuron.

The propleuron is indistinctly subdivided into an anterior **proepisternum** and a posterior **proepimeron**, although the pleural suture is indistinct (as there is no associated wing). The metapleuron is also subdivided into an anterior **metepisternum** and a posterior **metepimeron** by the rather indistinct **metapleural suture**. The metepisternum is indistinctly subdivided horizontally into a dorsal **metanepisternum** and a ventral **metakatepisternum**, directly behind the meron; these pleurites may be greatly reduced in some taxa and thus difficult to identify.

The sternal region of the thorax is much less extensive than the notal and pleural regions. The most extensive sternal sclerite is the **prosternum**, which is sometimes divided into an anterior **presternum** and a posterior **basisternum**. In some groups the prosternum fuses laterally with the proepisternum to form a sclerotised **precoxal bridge**. The **mesosternum** is mostly invaginated in Diptera, as a narrow internal phragma and is usually reduced externally. Similarly the **metasternum** is almost entirely invaginated.

Glossary

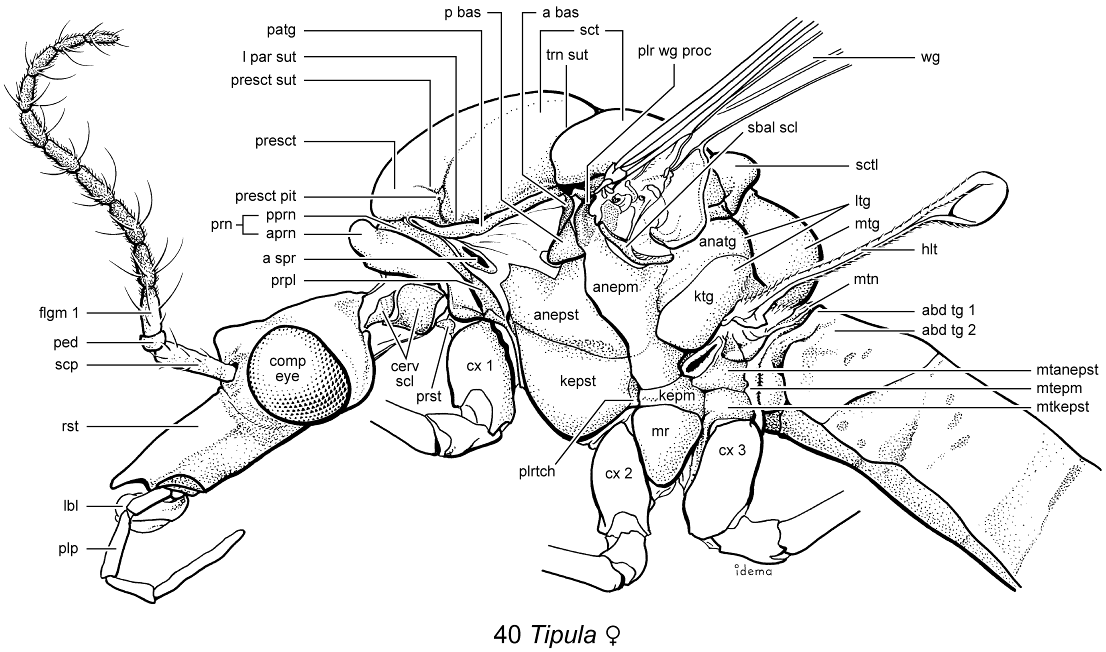
acrostichal setae (Fig. 41): the most medially placed longitudinal rows of setae on the scutum, generally referred to only in Eremoneura (Empidoidea and Cyclorrhapha), but occasionally used in other groups (*e.g.*, Chironomidae). Acrostichals vary from a single median row (uniserial, *e.g.*, most Platypezidae), to a pair of rows (biserial), or occasionally to two pairs of rows (*e.g.*, certain Empidoidea). In acalyptrates, they are usually reduced to a single pair of rows anterior to the scutoscutellar suture, but are more extensive in Calyptratae.

anapleural suture, see under **episternum**.

anatergite (Figs 40, 42): the dorsal portion of the laterotergite, dorsal to the katatergite; in Brachycera it has come to occupy a position behind rather than above the katatergite and thus is the intermediate portion of the postnotum, usually appearing as a flat, or concave area between the calypter and the halter. It may bear tiny setae (**infrasquamal setulae**) under the lower calypter in some Calyptratae (see **laterotergite**).

anepimeral setae (pteropleural setae) (Fig. 42): a tuft of setae, sometimes including also a large seta, arising from a small area below the wing base.

anepimeron (pteropleuron) (Figs 40, 42): the sclerite, or area of the mesopleuron below the wing base, between the



40 *Tipula* ♀

Fig. 3.40. Lateral view of head, thorax and base of abdomen of *Tipula trivittata* Say (Tipulidae) ♀ (non-Afrotropical). Fig. 40 (after McAlpine 1981, fig. 64).

Abbreviations: a bas – anterior basalare; a spr – anterior spiracle; abd tg – abdominal tergite; anatg – anatergite; anepm – anepimeron; anepst – anepisternum; aprn – antepronotum; cerv scl – cervical sclerite; comp eye – compound eye; cx – coxa; flgm – flagellomere; hlt – halter; kepm – katepimeron; kepst – katepisternum; ktg – katatergite; l par sut – lateral parapsidal suture; lbl – labellum; ltg – laterotergite; mr – meron; mtanepst – metanepisternum; mtepm – metepimeron; mtg – mediotergite; mtkepst – metakatepisternum; mtn – metanotum; p bas – posterior basalare; patg – paratergite; ped – pedicel; plp – palpus; plr wg proc – pleural wing process; plrtrch – pleurotrochantin; pprn – postpronotum; presct – prescutum; presct pit – prescutal pit; presct sut – prescutal suture; prn – pronotum; prpl – propleuron; prst – prosternum; rst – rostrum; sbal scl – subalar sclerite; scp – scape; sct – scutum; sctl – scutellum; trn sut – transverse suture; wg – wing.

pleural suture in front and the laterotergite behind, usually bearing setae only in the anterodorsal corner, below the base of the wing (see **epimeron**).

anepisternal cleft (pleural membrane) (Fig. 40): a U- or V-shaped membranous area on the dorsal part of the anepisternum.

anepisternal setae (mesopleural setae) (Fig. 42): setae on the anepisternum, which in Calyptratae and some other Schizophora form a vertical row, or band of setae, including a row of stout appressed setae, arising in front of the pleural suture and curving back over the base of the wing. Anterodorsally placed anepisternal setae directly above and behind the anterior thoracic spiracle are referred to as **poststigmatal setae** (*e.g.*, in the lonchaeid genus *Dasiops*). Anepisternal setae that occur behind the anterior thoracic spiracle in certain Culicidae are referred to as **postspiracular setae**.

anepisternum (mesopleuron) (Figs 40, 42): the part of the mesopleuron in front of the wing base, between the anterior thoracic spiracle and the pleural suture, and bounded ventrally by the katepisternum; secondarily divided in some Diptera (*e.g.*, metopinine Phoridae) (see **episternum**).

antepronotum (Fig. 40): the anteriormost subdivision of the pronotum, distinct in nematocerous families and virtually obsolete in Cyclorrhapha.

anterior lappet, see under **posterior spiracle**.

anterior spiracles (Fig. 40): a pair of spiracles on the thorax (mesothoracic spiracles), that appear associated with the prothorax (true prothoracic spiracles are absent). They are usually located behind the postpronotum and between it and the mesothorax; in some Phoridae and Hippoboscidae they open dorsally on top of the postpronotum.

basalare (Fig. 40): a vertical strut, or small sclerotised area at the base of the wing above the anepisternum, usually divided into an **anterior basalare** (dorsal basalare) and a **posterior basalare** (ventral basalare).

basisternum, see under **prosternum**.

cervix (Fig. 40): the neck; the primarily membranous area joining the head and thorax.

cervical sclerite (Fig. 40): one to three pairs of small sclerites in the membrane of the neck connecting the head and thorax (Michelsen 1996).

coxopleural streak (Fig. 42): the fissure separating the katepimeron from the meron in some calyptrates.

dorsocentral setae (Fig. 41): the paired rows of setae on the scutum lateral to the acrostichal setae and flanked by the intra-alar and/or supra-alar setae; they are generally referred to only in Eremoneura (Empidoidea and Cyclorrhapha), but are occasionally used in other groups (*e.g.*, Chironomidae). In Empidoidea and many acalyptrates, dorsocentrals are the most prominent scutal setae. In Calyptratae they are usually present on both the presutural and postsutural areas of the scutum, but their occurrence on these areas is more varied in the remainder of the Schizophora.

epimeron (Figs 40, 42): that part of the pleuron behind the pleural suture, divided by the **transepimeral suture** into an upper part, the anepimeron and a lower part, the katepimeron.

episternum (Figs 40, 42): that part of the pleuron in front of the pleural suture, divided by the **anapleural suture** into an upper part, the anepisternum and a lower part, the katepisternum.

greater ampulla (infra-alar bulla, subalar knob) (Fig. 42): a globular protuberance of the anepimeron below the base of the wing and in front of the anepimeral setae (arising from the basal portion of the pleural wing process), in many Syrphidae, certain acalyptrates (*e.g.*, Periscelididae, Ropalomeridae (non-Afrotropical), some Psilidae, some Sciomyzidae and most Tephritidae) and Calyptratae (see **pleural wing process**).

halter (pl. **halteres**) (Figs 2, 3, 40–42, 47): the highly modified wing of the metathorax in Diptera; it is a club-like structure consisting of a knob, or capitulum on a stalk, or stem, arising from its base in front of the posterior thoracic spiracle (see **prehalter**). Halteres function as balancing organs during flight.

humeral pit, see **prescutal pit**.

humeral setae, see **postpronotal setae**.

humerus, humeral callus, see **postpronotal lobe**.

hypopleural setae, see **meral setae**.

hypopleuron, see **meron**.

infrasquamal setulae: hairs on the anatergite just below the base of the lower calypter.

intra-alar setae (Fig. 41): on the scutum, the longitudinal row of setae lateral to the dorsocentral setae. In some Cyclorrhapha, particularly in Calyptratae, the first or anterior pair of presutural intra-alar setae, together with the first supra-alar seta, have been referred to as **posthumeral setae**.

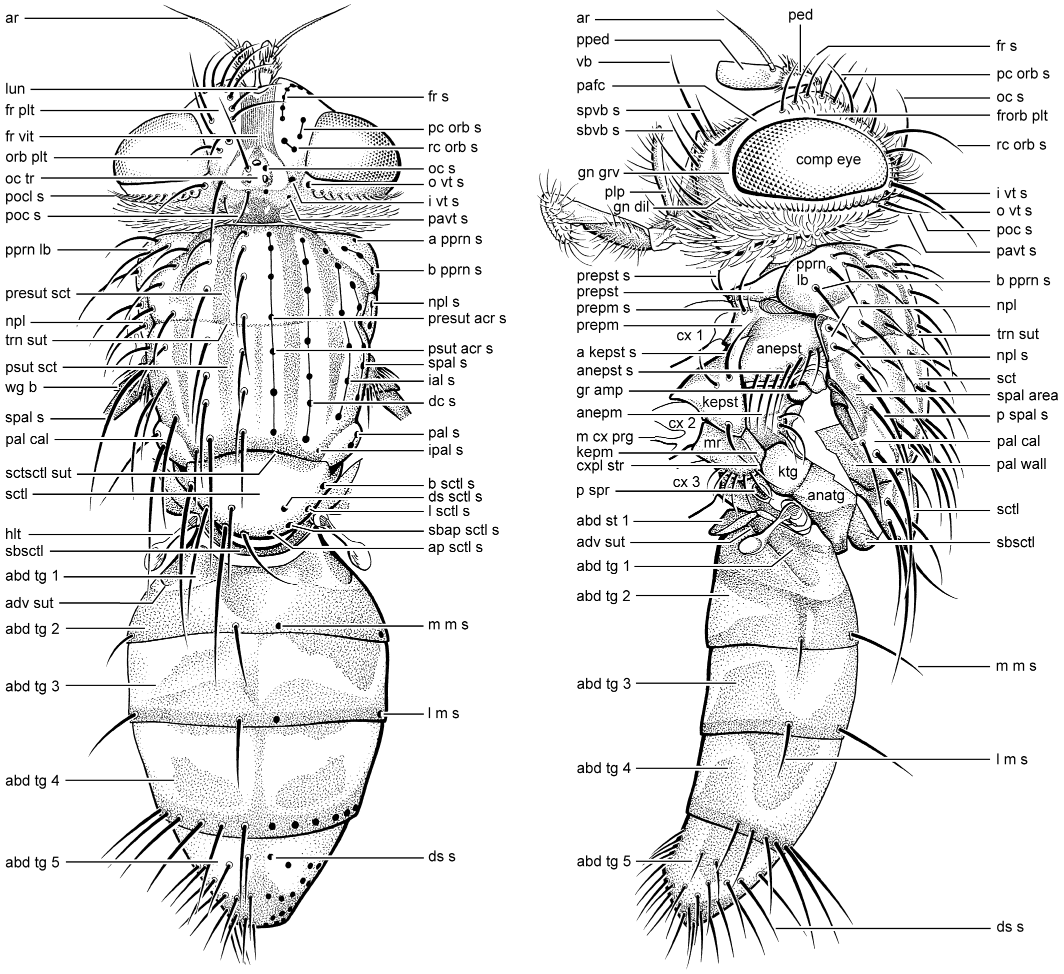
intrapostalar seta (Fig. 41): seta on the scutum near the postalar callus, considered by Merz & Haenni (2000, fig. 44) to be the posteriormost intra-alar seta.

katatergite (Figs 40, 42): the ventral (in nematocerous Diptera), or anterior (in Brachycera) portion of the laterotergite, appearing as a bulging sclerite just above the posterior spiracle, usually without setae, but in Asilidae bearing a vertical row, or patch of large setae (see **laterotergite**).

katepimeral setae: fine hairs on the katepimeron, or barette.

katepimeron (barette) (Figs 40, 42): the small sclerite between the anepimeron and the meron, below the anepimeron; in Schizophora reduced to a small rectangular band of cuticle that may bear one or more hairs. It may be scarcely recognisable in some acalyptrates (see **epimeron**).

katepisternal setae (sternopleural setae) (Fig. 42): in Schizophora one to four or more setae arising near the dorsal margin of the katepisternum; when three are present, they are usually arranged in a triangle, with the smallest seta being the most



41 *Exorista* ♀

42 *Exorista* ♀

Figs 3.41–42. Head, thorax and abdomen of adult fly: (41) *Exorista larvarum* (L.) (Tachinidae), dorsal view ♀; (42) same, lateral view (non- Afrotropical). Figs 41, 42 (after McAlpine 1981, figs 65, 66).

Abbreviations: a kepst s – anterior katepisternal seta; a pprn s – anterior postpronotal seta; abd st – abdominal sternite; abd tg – abdominal tergite; acr s – acrostichal seta (indicated as presut and psut acr s); adv sut – adventitious suture; anatg – anatergite; anepm – anepimeron; anepst – anepisternum; anepst s – anepisternal seta; ap sctl s – apical scutellar seta; ar – arista; b pprn s – basal postpronotal seta; b sctl s – basal scutellar seta; comp eye – compound eye; cx – coxa; cxpl str – coxopleural streak; dc s – dorsocentral seta; ds s – discal seta; ds sctl s – discal scutellar seta; fr plt – frontal plate; fr s – frontal seta; fr vit – frontal vitta; frorb plt – fronto-orbital plate; gn dil – genal dilation; gn grv – genal groove; gr amp – greater ampulla; hlt – halter; i vt s – inner vertical seta; ial s – intra-alar seta; ipal s – intrapostalar seta; kepm – katepimeron; kepst – katepisternum; ktg – katatergite; l m s – lateral marginal seta; l sctl s – lateral scutellar seta; lun – lunule; m cx prg – mid coxal prong; m m s – median marginal seta; mr – meron; npl – notopleuron; npl s – notopleural seta; o vt s – outer vertical seta; oc s – ocellar seta; oc tr – ocellar triangle; orb plt – orbital plate; p spal s – posterior supra-alar seta; p spr – posterior spiracle; pafc – parafacial; pal cal – postalar callus; pal s – postalar seta; pal wall – postalar wall; pavt s – paravertical seta; pc orb s – proclinate orbital seta; ped – pedicel; plp – palpus; poc s – postocellar seta; pocl s – postocular seta; pped – postpedicel; pprn lb – postpronotal lobe; prepm – proepimeron; prepm s – proepimeral seta; prepst – proepisternum; prepst s – proepisternal seta; presut acr s – presutural acrostichal seta; presut sct – presutural scutum; psut acr s – postsutural acrostichal seta; psut sct – postsutural scutum; rc orb s – reclinate orbital seta; sbap sctl s – subapical scutellar seta; sbsctl – subscutellum; sbvb s – subvibrissal seta; sct – scutum; sctl – scutellum; sctsctl sut – scutoscutellar suture; spal area – supra-alar area; spal s – supra-alar seta; spvb s – supravibrissal seta; trn sut – transverse suture; vb – vibrissa; wg b – wing base.

ventrally located. In other Diptera numerous setae or setulae are sometimes present on the katepisternum.

katepisternum (sternopleuron) (Figs 40, 42): the large bulging sclerite in front of the mid coxa, usually the largest sclerite on the ventral surface of the thorax (but greatly reduced in Asilidae because of forward movement of the mid coxa). The prothorax lacks a katepisternum, while that of the metathorax, the metakatepisternum, is a small sclerite just above the hind coxa. The katepisterna of the mesothorax meet each other mid-ventrally, enclosing the mesosternum, which is invaginated as a narrow internal phragma (see **episternum**).

lappets, see under **posterior spiracle**.

laterotergite (metapleuron, pleurotergite) (Figs 40, 42): the lateral extension of the **postnotum**, located between the wing base and the base of the halter, usually subdivided into **anatergite** and **katatergite** by an indistinct vertical groove. In orthorrhaphous Brachycera it usually bears pile or hairs and in asilids and some empidoids, a group of setae. It is usually bare in calyptrates and is arched over by the lower calypter, although the anatergite may support a small group of hairs near its dorsal edge (see **infrasquamal setulae**).

lesser ampulla, see **subalar sclerite**.

mediotergite (metatergite) (Fig. 40): often mistakenly called the postnotum, even though it is only the convex median portion of this sclerite, lying directly behind and beneath the scutellum. It is usually bare and in most Chironomidae is creased by a median longitudinal furrow (see **postnotum**).

meral setae (hypopleural setae) (Fig. 42): erect setae, usually forming a row of stout setae on the posterior edge of the meron in front of the posterior spiracle.

meron (hypopleuron) (Figs 40, 42): believed to be derived from the pleural part of the mid coxa, this sclerite lies behind the katepisternum, between the mid coxa and the posterior spiracle. It is usually bare, except in a number of families of calyptrates and is important taxonomically in separating the Muscoidea (Scathophagidae, Fanniidae, Anthomyiidae and Muscidae), in which it is bare, from the Oestroidea (Calliphoridae, Sarcophagidae, Rhinophoridae, Tachinidae and Oestridae), in which there is a vertical row, or patch of setae (see **meral setae**).

mesonotum (Figs 2, 41): the major part of the dorsum of the thorax, except for the narrow anterior band, the pronotum and the even narrower posterior band, the metanotum. It is divided into prescutum, scutum, scutellum and postnotum, with the scutum being by far the largest portion. In the past, the term mesonotum has often been applied to the scutum alone.

mesopleural setae, see **anepisternal setae**.

mesopleuron (see also **anepisternum**) (Figs 40, 42): the entire side of the mesothorax, which includes everything between the edge of the scutum above and the coxae below and between the anterior spiracle and the halter and posterior spiracle. Earlier authors used the term to apply only to the anepisternum of the mesothorax, the sclerite anterior to the pleural suture.

metakatepisternum (Fig. 40): the anteroventral portion of the metapleuron, between the metanepisternum above and the hind coxa below (see **metepisternum**).

metanepisternum (Fig. 40): the anterodorsal portion of the metapleuron, between the posterior spiracle and halter above and the metakatepisternum below (see **metepisternum**).

metanotum (Fig. 40): the sclerite forming the dorsum of the metathorax, between postnotum (mesothorax) and first abdominal segment; in most Diptera it is so narrow as to be scarcely recognisable, unless the abdomen is bent down out of the way.

metapleural suture (Fig. 40): an indistinct groove on the metathorax extending from the base of the halter to the hind coxa that divides the metepisternum from the metepimeron. The metapleural suture is equivalent to the mesopleural suture (see **pleural suture**) that extends between the wing base and the mid coxa.

metapleuron (Figs 40, 42): the side of the metathorax, always greatly reduced relative to the mesopleuron, extending from the halter to the hind coxa and between the meron and the abdomen; bearing the posterior spiracle.

metepimeron (Fig. 40): that part of the metapleuron behind the metapleural suture, fairly large in orthorrhaphous Brachycera and pilose on its upper part, but in Cyclorrhapha usually reduced to a sliver of bare cuticle.

metepisternum (Fig. 40): the sclerite in front of the metapleural suture, between the posterior spiracle and the hind coxa. It is usually indistinctly divided by a furrow into an upper part, the metanepisternum and a lower part, the metakatepisternum and seems to be without setae in all flies.

notopleural cleft: a depression on the anterior surface of the notopleuron of some Phoridae, often covered by a ridge of cuticle. It is associated with the opening of a **notopleural gland** (Disney 2004).

notopleural setae (Figs 41, 42): a pair of stout setae on the notopleuron in most Cyclorrhapha, as well as in some orthorrhaphous Brachycera (*e.g.*, Asilidae, Therevidae and Empidoidea), where the number of setae is variable. Sarcophaginae are unusual in having four notopleural setae, the usual large pair, interspersed by two smaller ones.

notopleuron (Figs 41, 42): a small triangular subdivision of the scutum just behind the postpronotum and in front of the transverse suture of the scutum, best delineated in Cyclorrhapha.

operculum, see under **posterior spiracle**.

paratergite (Fig. 40): a narrow triangular wedge of cuticle along the lateral edge of the scutum extending between the postpronotum and the wing base in many nematocerous families and orthorrhaphous Brachycera. Usually bare, it may be setose in some taxa (*e.g.*, certain Ceratopogonidae), or have scales in some Culicidae.

phragma: an invaginated internal fold of cuticle to strengthen the sclerite and serve as a point of muscle attachment.

pleural suture (Fig. 40): a furrow on the side of the thorax between the wing base and mid coxa, marking an inward folding of cuticle to provide rigidity to the mesopleuron.

pleural wing process (subalifer) (Fig. 40): a vertical extension of the anepimeron that articulates with the base of the wing (see **greater ampulla**).

pleurotergite, see **laterotergite**.

pleurotrochantin (Fig. 40): a small sclerite between the katepisternum and katepimeron that is present in a few nematocerous groups (*e.g.*, *Tipula* L., *Plecia* Wiedemann and Culicomorpha).

plumule (plumula), see under **subalar sclerite**.

postalar callus (Figs 41, 42): an oval portion of the posterolateral corner of the scutum, lateral to the scutellum. The postalar callus is weakly developed, or indistinct in acalyptrates; in the Cyclorrhapha it usually bears a pair of setae.

postalar seta (Fig. 41): one or two setae (more in some Tachinidae) on the postalar callus.

postalar wall (Fig. 42): the vertical surface of the thorax below the postalar callus.

posterior lappet, see under **posterior spiracle**.

posterior spiracle (Fig. 42): the spiracle of the metathorax, just below and slightly anterior to the base of the halter. The anterior, ventral and posterior edges of the posterior spiracle are usually fringed with fine hairs, leaving a small opening near the dorsal margin of the spiracle. These fringes of hairs are usually organised to form the **anterior** and **posterior lappets** and vary greatly in size, extent and colour; those hairs of the posterior lappet may be consolidated to form an **operculum** that covers most of the spiracular opening.

posthumeral setae, see presutural setae under **intra-alar setae** and/or **supra-alar setae**.

postmetacoxal bridge (postcoxal bridge): in some wasp-waisted Tachinidae (particularly some Phasiinae) and some Asilidae, the area enclosed by the metepimera, the hind coxae and the first abdominal sternite is sclerotised to form the postmetacoxal bridge. A postmetacoxal bridge is also present in some acalyptrate families, such as Syringogastridae, Somatiidae and Tanypezidae (all three non-Afrotropical), as well as in some genera of Richardiidae (non-Afrotropical), Platystomatidae and Tephritidae. In all these acalyptrate groups, however, the postmetacoxal bridge does not include the first abdominal sternite. The bridge may be darkly pigmented, thus easily recognised, or pale and similar to membrane, but then it is reinforced by parallel transverse ridges.

postnotum (mediotergite, mesophragma) (Fig. 40): the convex sclerite forming the posterior surface of the dorsal part of the thorax, behind and below the scutellum (as the **mediotergite**), extending laterally and anteriorly (as the **laterotergite**) between the calypter and the posterior spiracle.

postpronotal lobe (humeral callus, humerus) (Figs 41, 42): rather insignificant in nematocerous Diptera, the postpronotal lobe forms the anterolateral corner of the dorsum of the thorax in Brachycera.

postpronotal setae (humeral setae) (Figs 41, 42): setae on the postpronotal lobe that are universally present in calyptrates and also in some orthorrhaphous Brachycera and nematocerous families (*e.g.*, Culicidae). Their arrangement in certain groups, such as Tachinidae, is of considerable taxonomic value.

postpronotum (Figs 40–42): the posterior part of the dorsum of the pronotum, separated from the antepronotum by a transverse suture and better developed in Brachycera than in the nematocerous Diptera. In Brachycera the postpronotum and its enlarged lateral lobes are intimately associated with the scutum (see **postpronotal lobe**).

postscutellum, see **subscutellum**.

postspiracular scale: a small raised scale-like lobe found just behind the posterior spiracle in Athericidae and Tabanidae.

postspiracular setae, see **anepisternal setae**.

poststigmatal setae, see **anepisternal setae**.

postsutural: pertaining to the posterior part of the scutum behind the transverse suture.

prealar seta, see first postsutural supra-alar seta, under **supra-alar setae**.

precoxal bridge: a sclerotised connection between the prosternum and the proepisternum, in front of and above the fore coxae.

prehalter: a distinct lobe arising from the base of the halter in Ptychopteridae.

prescutal pit (humeral pit) (Fig. 40): a small depression on the anterolateral corner of the scutum, behind the postpronotal lobe, that marks the position of the base of the pupal respiratory organ.

prescutal suture (Fig. 40): an indistinct furrow extending medially from the prescutal pit, present in some nematocerous families; not to be confused with the transverse suture.

prescutellum (proscutellum): a small, transverse lens-shaped bulge found immediately in front of the scutellum (*e.g.*, in certain groups of Tabanomorpha and basal Phoridae).

prescutum (Fig. 40): the anteriormost portion of the mesonotum in front of the prescutal suture, evident in some nematocerous families.

presternum, see under **prosternum**.

presutural (Fig. 41): pertaining to the anterior part of the scutum in front of the transverse suture.

presutural seta, see presutural supra-alar setae under **supra-alar setae**.

proepimeral setae (prostigmatal setae, stigmatal setae) (Fig. 42): in Cyclorrhapha, setulae and setae that arise on the proepimeron, below the anterior spiracle and above the fore coxa and in front of the anepisternum and katepisternum of the mesothorax.

proepimeron (Fig. 42): that part of the prothoracic pleuron behind the propleural suture that extends from the anterior spiracle to the fore coxa. The posterior margin of the proepimeron usually blends in with the mesepisternum and is not readily distinguishable from it.

proepisternal setae (propleural setae) (Fig. 42): one or more setae at the ventral margin of the proepisternum and/or a patch of hairs on the midregion, the "disc of the propleuron".

proepisternum (Fig. 42): that part of the propleuron anterior to the propleural suture, above the prosternum and behind the cervical sclerites of the neck (also see **precoxal bridge**). In Cyclorrhapha it usually bears one or more setae, the proepisternal setae, at its ventral angle. In Tabanidae, the proepisternum is distinctly divided into an upper proanepisternum and a lower prokatepisternum; its upper portion is strongly inflated and covered with pile, while in Cyclorrhapha this region is usually concave and bare (pilose in most Calliphoridae and some Tachinidae).

pronotum (Figs 40–42): the dorsal part of the prothorax, divided transversely by an indistinct fissure into an antepronotum and a postpronotum that bears the postpronotal lobes. In nematocerous families the antepronotum is larger than the postpronotum, while the reverse tends to occur in Brachycera.

propleural setae, see **proepisternal setae**.

propleuron (Fig. 40): the side of the prothorax, between the pronotum dorsally and the fore coxa (see **proepimeron** and **proepisternum**).

proscutellum, see **prescutellum**.

prosternum (Fig. 40): a parallel-sided, or trapezoidal, concave sclerite between the fore coxae, sometimes with setae along its edges, or over its surface (also see **precoxal bridge**). The prosternum is often divided into an anterior more dorsal **presternum** and a posterior more ventral **basisternum** (*e.g.*, many nematocerous Diptera).

prostigmatal setae, see **proepimeral setae**.

pteropleural setae, see **anepimeral setae**.

pteropleuron, see **anepimeron**.

scutellar setae (Fig. 41): paired setae along the margin of the scutellum, the marginal setae, which in Schizophora are usually termed **basal**, **lateral**, **subapical** (preapical) and **apical scutellar setae**, depending on their position and **discal setae**, which arise from the midregion.

scutellum (Figs 40–42): the rounded, or triangular projection behind the scutum over the base of the abdomen, separated from the scutum by the scutoscutellar suture.

scutum (mesonotum) (Figs 40–42): essentially the dorsal surface of the mesothorax between the pronotum and the scutellum, separated into a small prescutum (in some nematocerous families) and the true scutum, which is in turn divided by the transverse suture into a presutural and a postsutural area.

sternopleural setae, see **katepisternal setae**.

sternopleuron, see **katepisternum**.

stigmatal setae, see **proepisternal setae**.

subalar knob, see **greater ampulla**.

subalar sclerite (subalar ridge, vallar ridge) (Fig. 40): a thin sclerite behind the pleural wing process, which is situated in the subalar membrane between the insertion of the wing and the dorsal margin of the anepimeron. In Syrphidae the posteroventral margin is usually extended and fringed with long hairs to form the **plumule**. In Schizophora the subalar sclerite is frequently dilated into one or more protuberances, with the anteriormost swollen portion often referred to as the **lesser ampulla** (see **greater ampulla**).

subscutellum (infrascutellum, postscutellum) (Figs 41, 42): a transverse bulge between the scutellum and the postnotum, particularly well-developed in some Tephritidae, Curtonotidae, some Calliphoridae, a few Oestridae and all Tachinidae.

supra-alar setae (Figs 41, 42): on the scutum, the longitudinal row of setae lateral to the intra-alar setae and above the base of the wing. In some Cyclorrhapha, particularly in Calyptratae, the first (anterior) presutural supra-alar seta and the first or anterior pair of presutural intra-alar setae have jointly been referred to as **posthumeral setae**, while the posterior presutural supra-alar seta has been referred to as the **presutural seta**. The first (anterior) postsutural supra-alar seta has also sometimes been termed the **prealar seta** in Calyptratae.

suprasquamal ridge (Fig. 46): a narrow oval sclerite, usually bare, or with a tuft or tufts of erect hairs, running anteroventrally along the medial edge of the lower calypter between the upper calypter and the anterolateral corner of the scutellum and hidden by the wing membrane unless the wing is bent downwards.

transepimeral suture, see under **epimeron**.

transverse suture (Figs 40, 42): a furrow across the scutum that divides it into a presutural and postsutural area; of particular importance in Calyptratae with reference to position of setae.

tympanal fossa (Fig. 46): membrane between the suprasquamal ridge and postalar wall strengthened by a rib-like sclerite, the **tympanal ridge**; the lowermost membranous portion that opens towards the wing base in Calyptratae is referred to as the **tympanic pit**.

tympanic pit, see **tympanal fossa**.

Wing

Only the front or mesothoracic pair of wings is developed for flight in Diptera (Figs 2, 3, 43a, 43b, 45a, 45b). Each wing is attached to the mesothoracic segment through the **axillary area**, which consists of a series of articulated **axillary sclerites** linked along the posterior margin by several membranous lobes (*i.e.*, **anal lobe**, **alula**, **upper calypter** and **lower calypter**), that may, or may not, be present depending on the group (Figs 44a, 44b).

The venation of the wing varies greatly throughout the order and is of tremendous taxonomic value. The stalk contains the bases of the six main longitudinal veins, the **costal** (***C***), **subcostal** (***Sc***), **radial** (***R***), **medial** (***M***), **cubital** (***Cu***) and **anal** (***A***) veins. In the most generalised condition each of the longitudinal veins consists of two main branches, a convex anterior branch and a concave posterior branch (Figs 44a, 44b), except for the costa and subcosta, which are unbranched. The longitudinal veins are sometimes connected by **crossveins**, which together delimit portions of wing membrane called **cells**, named after the vein anterior to them. Following the convention consistently adopted by McAlpine (1981), but contrary to Merz & Haenni (2000), longitudinal veins are designated by uppercase abbreviations and crossveins and cells are designated by lowercase abbreviations. Cells and crossvein abbreviations are not easily confused, because crossvein abbreviations can be recognised by the inclusion of a hyphen (*e.g.*, *r–m*) in their formation; the only exception being the humeral crossvein (*h*) for which no associated cell is named.

There are two wing venation systems currently in use in Diptera; the widely used traditional system outlined by McAlpine (1981) and Merz & Haenni (2000) (Figs 43b, 44b, 45b) and the alternative system proposed by Wootton & Ennos (1989) and Saigusa (2006). Both systems were discussed by Cumming & Wood (2009), but only the traditional system was figured. The alternative system is based on a better homologised Diptera and Mecoptera fore wing base and has been adopted as the standard, for use throughout this *Manual*. It has also been corroborated in a comparative study of wing structure of primitive Mesozoic fossil Diptera by Shcherbakov *et al*. (1995). Under this system, the Diptera wing vein A_1 (as used in McAlpine 1981) is homologised with the Mecoptera vein *CuP*, CuA_1 (*sensu* McAlpine 1981) is considered M_4, whereas CuA_2 is *CuA* and the posterior cubital cell (*cup*) is cell *cua* (Figs 43a, 44a, 45a). The faint vein paralleling *CuA* (*CuP sensu* McAlpine 1981; Fig. 43b) is interpreted as a pseudovein in the new alternative system.

The veins may be bare, or covered with various types of macrotrichia, whereas the membrane is either bare and shiny, or more or less dull owing to a covering of microtrichia. In Blephariceridae and the north temperate Deuterophlebiidae (non-Afrotropical), a secondary net-like pattern of fine folds is also present on the membrane. The wing is often tinted with colour and sometimes patterned. Clear wings are referred to as **hyaline**, whereas darkened wings are referred to as **fumose** or **infuscated**.

Functional (**macropterous**) wings are more or less elongate-oval in shape, with rounded, or somewhat pointed apices. Partial or total reduction (**stenoptery** – narrowed, but complete wings, **brachyptery** – wings reduced in length, or **aptery** – wings absent) may occur, often only in one sex, in connection with peculiar habits or niches (*e.g.*, ectoparasitism, cave- and litter-dwellers, high mountain species).

Glossary

alula (axillary lobe) (Figs 44a, 44b, 45a, 45b): a lobe of the wing membrane at the base of vein *A* between the calypter and anal lobe, not to be confused with a calypter.

alular incision (axillary incision) (Figs 44a, 44b, 45a, 45b): a cleft in the posterior wing margin near the base, separating the alula from the anal lobe.

anal cells (Figs 43a, 43b): each of the cells behind the anal vein or veins, vein A_1 and vein A_2. Using the traditional system of McAlpine (1981: 31) and Merz & Haenni (2000: 45) there are two anal cells, **cell a_1** and **cell a_2** in Tipulidae and Trichoceridae (non-Afrotropical) (Fig. 43b), whereas other Diptera have at most only one anal cell, **cell a_1**; in Eremoneura (Empidoidea and Cyclorrhapha) at least, the first anal vein is fused with the apex of vein CuA_2 and the cell behind this vein (cell *cup* or *cua*) has also been referred to as the anal cell (see **cubital cells**). The alternative system of Wootton & Ennos (1989) and Saigusa (2006) recognises only one anal cell (**cell a_1**; Fig. 43a) in the groundplan of the Diptera (see **anal vein**).

anal lobe (Figs 43a–45b): that part of the wing membrane along the hind margin near the base, usually rounded, distal to the alula.

anal vein (Figs 43a–45b): the last veins of the series behind the cubital vein, generally present in the traditional system of McAlpine (1981: 31) and Merz & Haenni (2000: 45) as two veins, **A_1** and **A_2** (Fig. 43b). In Tipulidae and Trichoceridae (non-Afrotropical), both these veins reach the margin independently, while in most other Diptera A_2 appears to be extremely shortened or absent (Starý 2008). Wootton & Ennos (1989) and Saigusa (2006) interpret A_1 in the traditional system as vein *CuP*, while they consider the *CuP* to be a pseudovein (Figs 43a–45a). Therefore in their alternative system, Wootton & Ennos (1989) and Saigusa (2006) essentially recognise only one anal vein (A_1) in the groundplan of Diptera, which is equivalent to vein A_2 in the traditional system. Veins in the anal area of the wing fuse together in Brachycera, so that the traditional first anal vein is actually CuA_2+A_1 (Fig. 45b), or *CuA+CuP* (Fig. 45a) in the alternative system (see **cubital vein**).

anterior cubital cell, see **cubital cells**, ***cua***.

arculus, see **medial vein**, anterior branch (***MA***).

axillary incision, see **alular incision**.

axillary lobe, see **alula**.

axillary sclerites (axillary plates) (Figs 44a, 44b): three or four irregularly shaped plates behind the base of vein *R* and between the bases of veins *M*, *Cu* and *A* and the thorax.

basal costal cell, ***bc*** (Figs 43a–45b): a small cell between vein C and the subcosta (*Sc*) at the base of the wing, closed distally by the humeral crossvein.

basal medial cell, ***bm*** (second basal cell) (Figs 43a–45b): a small cell near the base of the wing that is closed distally by the *bm–cu* crossvein in the traditional system of McAlpine (1981: 31) and Merz & Haenni (2000: 45), or by the *bm–m* crossvein in the alternative system of Wootton & Ennos (1989) and Saigusa (2006).

basal medial crossvein, ***bm–m*** (Fig. 45a), see **basal medial–cubital crossvein**.

basal medial–cubital crossvein, ***bm–cu*** (*tb*) (Fig. 45b): the crossvein between the base of vein *M* (M_1 or M_{1+2}) and CuA_1, closing the basal medial cell apically in the traditional system of McAlpine (1981: 31) and Merz & Haenni (2000: 45). Crossvein *bm–cu* is actually the same as crossvein *m–cu* including the base of M_3, but the designation "*b*" is used to distinguish crossvein *bm–cu* from crossvein *dm–cu* when both occur (see **discal medial–cubital crossvein**, ***dm–cu* and medial–cubital crossvein**, ***m–cu***). Crossvein *bm–cu* is equivalent to ***bm–m***, or the base of M_4 (Fig. 45b), in the alternative system proposed by Wootton & Ennos (1989) and Saigusa (2006).

basal radial cell, ***br*** (cell *r*, first basal cell) (Figs 43a–45b): a small cell near the base of the wing between the radial vein and vein *M*, closed distally by the *r–m* crossvein.

basicosta (**basicostale**, humeral plate) (Figs 44a, 44b, 45a, 45b): a scale-like sclerite between the tegula and the base of the costa. Saigusa (2006) considers the basicosta of Calyptratae (Figs 44a, 44b) as interpreted by McAlpine (1981: 28), to be homologous with the basisubcostale (basisubcosta) of Mecoptera.

calypter (pl. **calypteres**) (squama) (Figs 44a, 45a, 44b, 45b, 46): one of two rounded lobes at the base of the wing, between the alula and thoracic wall in many Diptera (*e.g.*, Acroceridae, Tabanidae, Calyptratae); when the wing is at rest the smaller **upper calypter**, the more anterior of the two, folds over the larger **lower calypter**, which forms a cup-like hood over the halter in Cyclorrhapha.

cell: any part of the wing membrane delineated by veins, crossveins and/or the wing margin.

costa, see **costal vein**.

costagial break (Figs 45a, 45b): a point of weakness in the costa near the base, proximal to the humeral crossvein, occurring infrequently in some families of Schizophora.

costal breaks (Figs 45a, 45b): a series of three points of weakness, or flexure in the costa of taxonomic importance in Schizophora (see **costagial break**, **humeral break** and **subcostal break**).

costal cell (Figs 43a–45b): the wing membrane between the costal (C) and subcostal (*Sc*) veins distal to the humeral crossvein (*h*), often closed apically by the subcosta terminating in the costa.

costal margin: the anterior margin of the wing, usually delimited by the costa.

costal section (costal sector): pertaining to the relative lengths of four sections of the costa that are delimited by points of termination of crossvein *h* and of veins R_1, R_{2+3}, R_{4+5} and M_1; section 1 is between *h* and R_1, section 2 is between R_1 and R_{2+3}, section 3 is between R_{2+3} and R_{4+5} and section 4 is between R_{4+5} and M_1. The relative lengths of the costal sections are important taxonomically in certain families of Eremoneura (Empidoidea and Cyclorrhapha).

costal spine: one or two short stout setae arising from the front of vein *C* in some families of Schizophora, usually at the level of the subcostal break.

costal vein, or **costa**, ***C*** (Figs 43a–45b): the sclerotised thickened anterior edge of the wing, extending around the wing tip in some families, but ending at the apex of vein R_{4+5}, or *M* in most Diptera.

crossband: a transverse band of colour on the wing, especially important taxonomically in Tephritoidea; White *et al*. (1999: fig. 33.3) defined nine types of crossbands in Tephritidae based on their position on the wing membrane, namely the **humeral band** (over the humeral crossvein), **subbasal band** (over the humeral crossvein and cells *br*, *bm* and *cua*), **subcostal band** (over cells *sc*, *br*, *bm* and *cua*), **discal band** (over the pterostigma, cell *dm* and *r–m* crossvein), **accessory costal band** (between the discal and subapical bands), **radial-medial band** (over at least the *r–m* crossvein, but not the pterostigma), **subapical band** (over at least the *dm–m* crossvein), **anterior apical band** (from cell r_1 along the apex of wing), **posterior apical band** (between the subapical and anterior apical bands).

crossvein (transverse vein): any short vein, usually at a strong angle to the major longitudinal veins, connecting two of them and therefore enclosing a cell.

cubital cells, ***cua***$_1$ (**cell *M*$_4$**, fifth posterior cell), ***cua*** and ***cup*** (anal cell, basal cubital cell) (Figs 43a–45b): in the traditional system of McAlpine (1981: 31) and Merz & Haenni (2000: 45) the **anterior cubital cell**, **cell *cua*$_1$**, is enclosed by the cubital fork, formed by veins CuA_1 and CuA_2; the posterior cubital cell, **cell *cup***, is behind it, between veins *CuP* and A_1 (in older terminology it is also called the anal cell) (Figs 43b–45b). In the alternative system proposed by Wootton & Ennos (1989) and Saigusa (2006), where vein *CuP* is regarded as a pseudovein, the latter cell is formed by veins *CuA* and *CuP* and is referred to as the **anterior cubital cell**, or **cell *cua*** (Figs 43a–45a); it has also been referred by Steyskal (1984) and White *et al*. (1999: 884), as the basal cubital cell, or cell *bcu*). In the alternative system, **cell *cup***, when present, occupies the anterior portion of the anal area of the wing and is open at the costal margin.

cubital fork (Figs 43b, 45b): the branching of veins CuA_1 and CuA_2 in the traditional system of McAlpine (1981: 31) and Merz & Haenni (2000: 45), enclosing **cell *cua*$_1$** (referred to as the fifth posterior cell in older terminology), or **cell *m*$_4$** in the alternative system of Wootton & Ennos (1989) and Saigusa (2006) (Figs 43a, 45a).

cubital vein or **cubitus**, ***Cu*** (Figs 43a–45b): the fifth vein of the wing, behind the media, vein *M*. It branches into an anterior branch, **vein *CuA*** and a posterior branch, **vein *CuP***. In the traditional system of McAlpine (1981: 31) and Merz & Haenni (2000: 45) vein *CuA* (*Cu*) further branches into ***CuA*$_1$** (Cu_1) and ***CuA*$_2$** (Cu_2) (Figs 43b, 45b); CuA_1, along with the crossvein at its base, has also been interpreted as **vein *M*$_4$** (Byers 1989; Wootton & Ennos 1989; Saigusa 2006) (Figs 43a, 45a) (see **medial vein**).

cubitus, see **cubital vein**.

discal cell, ***d*** (Figs 43a, 43b): the wing membrane between veins M_1 and M_3, closed apically by the base of vein M_2 and the *m–m* crossvein.

discal medial cell, ***dm*** (*d–m*) (Figs 45a, 45b): in Cyclorrhapha vein *M* is unbranched and in the traditional system of McAlpine (1981: 31) and Merz & Haenni (2000: 45) the *dm* cell lies between *M* and vein CuA_1. It is closed apically by the discal medial-cubital crossvein, *dm–cu*. Cell *dm* also occurs in some groups of orthorrhaphous Brachycera (*e.g.*, Bombyliidae, Scenopinidae, Empidoidea). In the alternative system proposed by Wootton & Ennos (1989) and Saigusa (2006), the *dm* cell lies between veins M_1 and M_4, and is closed apically by crossvein *dm–m*.

discal medial crossvein, ***dm–m*** (Fig. 45b), see **discal medial–cubital crossvein**.

discal medial–cubital crossvein, ***dm–cu*** (posterior crossvein, *tp*) (Fig. 45b): the crossvein between vein *M* (M_1 or M_{1+2}) and CuA_1 closing the discal medial cell apically in the traditional system of McAlpine (1981: 31) and Merz & Haenni (2000: 45) (see **basal medial–cubital crossvein**, ***bm–cu***); it is equivalent to ***dm–m*** (Fig. 45a) in the alternative system proposed by Wootton & Ennos (1989) and Saigusa (2006).

false vein: vein-like thickenings in the membrane of certain groups of nematocerous Diptera that resemble veins, perhaps as a result of folding in the pupal stage (see **pseudovein** and **spurious vein**).

humeral break (Figs 45a, 45b): a weakness, or point of flexure in the costa just beyond the level of the humeral crossvein.

humeral crossvein, ***h*** (Figs 43a–45b): a short crossvein between the costa and subcosta, separating the basal costal cell from the costal cell proper.

humeral plate, see **basicosta**.

jugum (neala): a triangular prolongation at the base of the wing in some Psychodidae (*e.g.*, Psychodinae); not homologous with the jugum or neala of the fore wing of higher insects.

longitudinal vein, see above under Wing and also below under **radial vein**.

lower calypter (lower squama, squamula thoracica) (Figs 44a–46): in most Diptera a fringed flap of membrane at the base of the wing attached to the thoracic wall; in Cyclorrhapha it is usually quite conspicuous, evenly convex dorsally and sometimes even somewhat transparent, forming a hood over the halter.

lower squama, see **lower calypter**.

marginal cell, see **cell r_1** under **radial cells**.

media, see **medial vein**.

medial cells (Figs 43a, 43b): **cell m_1** (second posterior cell in older terminology) is behind vein M_1, **cell m_2** (third posterior cell) is behind vein M_2 and **cell m_3** (fourth posterior cell) is behind vein M_3. Wootton & Ennos (1989) and Saigusa (2006) consider vein CuA_1 to be vein M_4 (Figs 43a, 45a) and the cell behind this as **cell m_4** (fifth posterior cell), but in the traditional terminology adopted by McAlpine (1981: 31) and Merz & Haenni (2000: fig. 47) this cell is termed **cell cua_1**, the anterior cubital cell.

medial crossvein, ***m–m*** (*mm*) (Figs 43a, 43b): a crossvein in some nematocerous Diptera that connects veins M_2 and M_3 to close the discal cell; the apparent crossvein between veins M_1 and M_2 that partially closes the discal, or discal medial cell in some orthorrhaphous Brachycera, is interpreted as the base of M_2.

medial–cubital crossvein, ***m–cu*** (*mcu*) (Fig. 43b): the crossvein between vein M_3 and CuA_1 in the traditional system of McAlpine (1981: 31) and Merz & Haenni (2000: 45) that closes the basal medial cell apically in some nematocerous and orthorrhaphous Brachycera families; Wootton & Ennos (1989) and Saigusa (2006) interpret this vein as the base of M_4 and not as a crossvein; the actual *m–cu* crossvein in their system is positioned more posteriorly between M_4 and *CuA* (Fig. 43a) (see **basal medial–cubital crossvein**, ***bm–cu***).

medial vein, or **media**, ***M*** (Figs 43a–45b): literally the middle vein, between the radius, vein *R* and cubitus, vein *Cu*. Made up primarily of the posterior branch(es) of the media. Although it is unbranched in Schizophora and various other taxa, many non-schizophorans have two branches, $\boldsymbol{M_1}$ and $\boldsymbol{M_2}$ and some (certain nematocerous groups and lower Brachycera) have $\boldsymbol{M_3}$, associated with a discal cell. When M_2 and M_3 are absent, the single branch is referred to as M_1 or M_{1+2}. Byers (1989), Wootton & Ennos (1989), Shcherbakov *et al.* (1995) and Saigusa (2006) have convincingly argued for the interpretation of CuA_1 as $\boldsymbol{M_4}$ (see **cubital vein**) (Figs 43a–45a) on the basis of homology with the fore wing base of Mecoptera. The anterior branch of the media (***MA***) (**arculus**) is reduced to a short transverse vein near the base of the wing (Figs 43b, 44b); Saigusa (2006) considers the true *MA* to be absent in Diptera.

node: the junction of the radial sector with R_1, sometimes enlarged, often pigmented in species with patterned wings and usually bearing setae, at least in Cyclorrhapha.

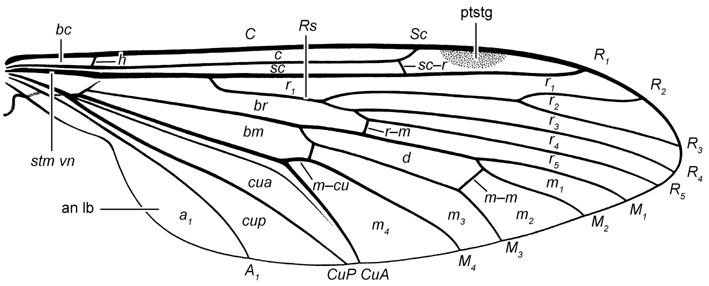
petiole: an ambiguous term, either a stem vein, at or near the base of the wing, or the fusion of the apices of two adjacent veins at, or near the wing margin, *e.g.*, R_{4+5} and M_1 in many calyptrates do not end separately in the margin, but fuse to produce a "closed" cell r_{4+5}. In many orthorrhaphous Brachycera, medial and cubital cells as well as radial cells may be "closed and petiolate" at the margin by anastomosis of the apices of veins.

posterior cell, see either **cell r_{4+5}** or **cell r_5** (first posterior cell) under **radial cells**, or **cells m_1, m_2, m_3, m_4 (cua_1)** (second, third, fourth and fifth posterior cells) under **medial cells**.

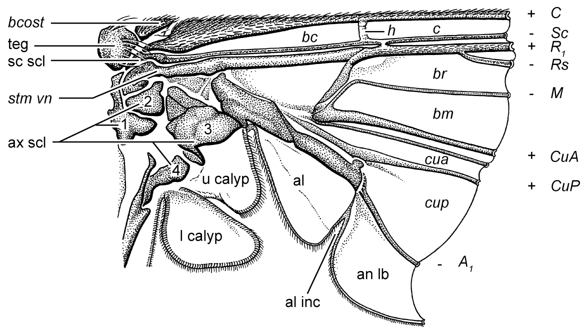
posterior crossvein, see **discal medial–cubital crossvein**, ***dm–cu***.

posterior cubital cell, see **cubital cells**, ***cup***.

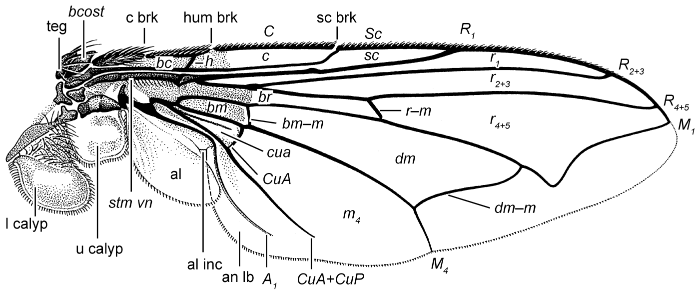
pseudovein: a thickening in the membrane resembling a true vein, but without enclosed tracheal trunk. See **false vein** and **spurious vein**.



43a Ground-plan of Diptera wing



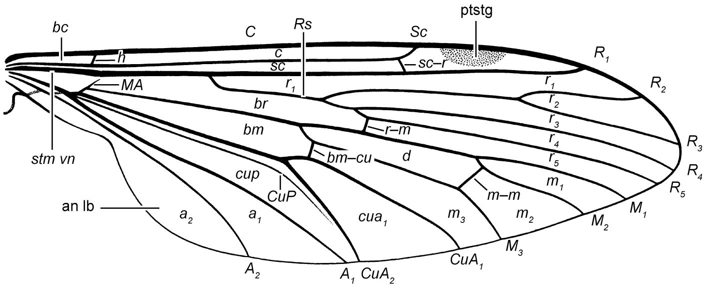
44a *Tabanus* ♀



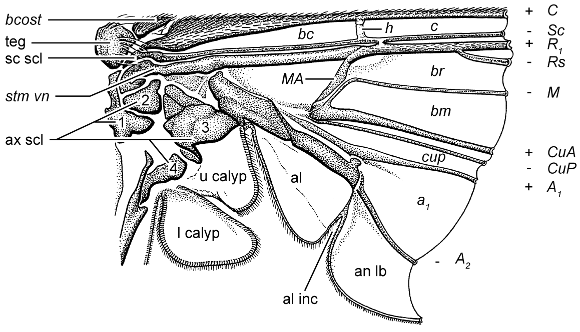
45a *Compsomyiops* ♀

Figs 3.43a–45a. Wings (dorsal views) outlining alternative venation system of Wootton & Ennos (1989) and Saigusa (2006): (43a) hypothetical groundplan of a basal dipteran; (44a) wing base, showing axillary sclerites of *Tabanus americanus* Forster (Tabanidae) ♀; (45a) complete wing, with calypteres of *Compsomyiops callipes* (Bigot) (Calliphoridae) ♀ (both non-Afrotropical). Figs 43a–45a (after McAlpine 1981, figs 67, 68, 69 (as *Paralucilia wheeleri*)).

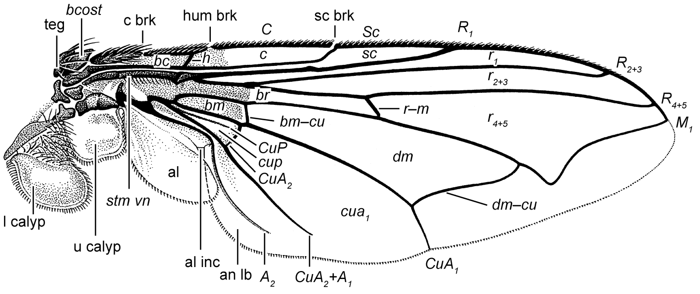
Abbreviations: A_1 – first branch of anal vein; a_1 – first anal cell; al – alula; al inc – alular incision; an lb – anal lobe; ax scl – axillary sclerites; *bc* – basal costal cell; *bcost* – basicosta; *bm* – basal medial cell; *bm–m* – basal medial crossvein; *br* – basal radial cell; *C* – costal vein; *c* – costal cell; c brk – costagial break; *CuA* – anterior branch of cubital vein; *cua* – anterior cubital cell; *CuA+CuP* – anterior branch of cubital vein + posterior branch of cubital vein; *CuP* – posterior branch of cubital vein; *cup* – posterior cubital cell; *d* – discal cell; *dm* – discal medial cell; *dm–m* – discal medial crossvein; *h* – humeral crossvein; hum brk – humeral break; l calyp – lower calypter; *M* – medial vein, or media; M_1 – first branch of media; m_1 – first medial cell; M_2 – second branch of media; m_2 – second medial cell; M_3 – third branch of media; m_3 – third medial cell; M_4 – fourth branch of media; m_4 – fourth medial cell; *m–cu* – medial–cubital crossvein; *m–m* – medial crossvein; ptstg – pterostigma; R_1 – anterior branch of radius; r_1 – first radial cell; R_2 – upper branch of second branch of radius; r_2 – second radial cell; R_{2+3} – second branch of radius; r_{2+3} – second + third radial cell; R_3 – lower branch of second branch of radius; r_3 – third radial cell; R_4 – upper branch of third branch of radius; r_4 – fourth radial cell; R_{4+5} – third branch of radius; r_{4+5} – fourth + fifth radial cell; R_5 – lower branch of third branch of radius; r_5 – fifth radial cell; *r–m* – radial–medial crossvein; *Rs* – radial sector; *sc* – subcostal cell; *Sc* – subcostal vein; sc brk – subcostal break; *sc–r* – subcostal–radial crossvein; sc scl – subcostal sclerite; *stm vn* – stem vein; teg – tegula; u calyp – upper calypter.



43b Ground-plan of Diptera wing



44b *Tabanus* ♀



45b *Compsomyiops* ♀

Figs 3.43b–45b. Wings (dorsal views) outlining traditional venation system: (43b) hypothetical groundplan of a basal dipteran; (44b) wing base, showing axillary sclerites of *Tabanus americanus* Forster (Tabanidae) ♀; (45b) complete wing, with calypteres of *Compsomyiops callipes* (Bigot) (Calliphoridae) ♀ (both non-Afrotropical). Figs 43b–45b (after McAlpine 1981, figs 67, 68, 69 (as *Paralucilia wheeleri*)).

Abbreviations: A_1 – first branch of anal vein; a_1 – first anal cell; A_2 – second branch of anal vein; a_2 – second anal cell; al – alula; al inc – alular incision; an lb – anal lobe; ax scl – axillary sclerites; *bc* – basal costal cell; *bcost* – basicosta; *bm* – basal medial cell; *bm–cu* – basal medial–cubital crossvein; *br* – basal radial cell; *C* – costal vein; *c* – costal cell; c brk – costagial break; *CuA* – basal part of anterior branch of cubital vein; CuA_1 – first branch of anterior branch of cubital vein; cua_1 – anterior cubital cell; CuA_2 – second branch of anterior branch of cubital vein; *CuP* – posterior branch of cubital vein; *cup* – posterior cubital cell; *d* – discal cell; *dm* – discal medial cell; *dm–cu* – discal medial–cubital crossvein; *h* – humeral crossvein; hum brk – humeral break; l calyp – lower calypter; *M* – medial vein, or media; M_1 – first branch of media; m_1 – first medial cell; M_2 – second branch of media; m_2 – second medial cell; M_3 – third branch of media; m_3 – third medial cell; *MA* – anterior branch of media; *m–m* – medial crossvein; ptstg – pterostigma; R_1 – anterior branch of radius; r_1 – first radial cell; R_2 – upper branch of second branch of radius; r_2 – second radial cell; R_{2+3} – second branch of radius; r_{2+3} – second + third radial cell; R_3 – lower branch of second branch of radius; r_3 – third radial cell; R_4 – upper branch of third branch of radius; r_4 – fourth radial cell; R_{4+5} – third branch of radius; r_{4+5} – fourth + fifth radial cell; R_5 – lower branch of third branch of radius; r_5 – fifth radial cell; *r–m* – radial–medial crossvein; *Rs* – radial sector; *sc* – subcostal cell; *Sc* – subcostal vein; sc brk – subcostal break; *sc–r* – subcostal–radial crossvein; sc scl – subcostal sclerite; *stm vn* – stem vein; teg – tegula; u calyp – upper calypter.

pterostigma (stigma) (Fig. 43a, 43b): a darkened part of the membrane at the apex of cell *sc*, often ending before the apex of vein R_1, but sometimes extending into cell r_1.

radial cells (Figs 43a, 43b, 45a, 45b): each of the cells behind one of the branches of the radial vein; as such, **cell** $\boldsymbol{r_1}$ (marginal cell in older terminology) lies behind vein R_1, **cell** $\boldsymbol{r_{2+3}}$ (first submarginal cell) lies behind vein R_{2+3}, **cell** $\boldsymbol{r_2}$ lies behind vein R_2, **cell** $\boldsymbol{r_3}$ lies behind vein R_3 and **cell** $\boldsymbol{r_4}$ (second submarginal cell) and **cell** $\boldsymbol{r_{4+5}}$ or **cell** $\boldsymbol{r_5}$ (first posterior cell in older terminology) lie behind veins R_4 and R_{4+5} or R_5.

radial–medial crossvein, ***r–m*** (anterior crossvein, *rm*, *ta*) (Figs 43a, 43b, 45a, 45b): an important landmark in all Diptera, except those with reduced wing venation, the crossvein connecting the most posterior branch of the radius and the media, closing the basal radial cell. Many species with patterned wings have a dark macula (spot) around crossvein *r–m*. In Acroceridae a second radial-medial crossvein (***r–m2***) (plus rarely a third) is sometimes present towards the apex of the wing.

radial sector, ***Rs*** (Figs 43a–44b): the posterior branch of the radius, vein *R*, arising from R_1 at the node; the node and the first part of *Rs* usually bear setae in Cyclorrhapha.

radial vein or **radius**, ***R*** (first, second and third longitudinal veins) (Figs 43a–45b): the main and largest, vein of the wing, usually subdivided into two main branches, the anterior branch $\boldsymbol{R_1}$ (first longitudinal vein) and the posterior branch, or radial sector ***Rs***, comprising $\boldsymbol{R_{2+3}}$ (second longitudinal vein), which is again often subdivided into $\boldsymbol{R_2}$ and $\boldsymbol{R_3}$, especially in nematocerous Diptera and $\boldsymbol{R_{4+5}}$ (third longitudinal vein), also usually subdivided in nematocerous and orthorrhaphous brachyceran families into $\boldsymbol{R_4}$ (upper branch of third longitudinal vein) and $\boldsymbol{R_5}$ (lower branch of third longitudinal vein). Auxiliary crossveins occur between some radial veins in a few groups, such as certain genera of Bombyliidae and Empididae.

radius, see **radial vein**.

remigium, see **stem vein** and **subcostal sclerite** *sensu* Hall (1948).

spurious vein: in Syrphidae, a longitudinal vein-like thickening in the membrane between veins *R* and *M*, bisecting crossvein *r–m* and ending in cell r_{4+5}.

squama, see **calypter**.

squamula alaris, see **upper calypter**.

squamula thoracica, see **lower calypter**.

stem vein (remigium) (Figs 43a–44b): the thickened base of vein *R* between the wing base and base of vein *M*. It may be setose or bare. In some calliphorids it bears an even row of fine setae along its posterior edge, dorsally (in Chrysomyinae) and also ventrally (in Toxotarsinae).

stigma, see **pterostigma**.

subcosta, see **subcostal vein**.

subcostal break (Figs 45a, 45b): a weakness, or point of flexure in the costa just before or at the level of the apex of the subcosta.

subcostal cell, ***sc*** (Figs 43a, 43b, 45a, 45b): the membrane between the subcosta and radius, closed distally either by vein R_1, or by the *sc–r* crossvein.

subcostal–radial crossvein, ***sc–r*** (Figs 43a, 43b): a crossvein between the subcosta and radius; it is located near the apex of the subcosta in some primitive nematocerous families, but is placed much more basally in various groups of orthorrhaphous Brachycera (Stuckenberg 2001). The *sc–r* crossvein is absent in Cyclorrhapha, except in most Syrphidae and some Conopidae.

subcostal sclerite (remigium *sensu* Hall (1948)) (Figs 44a, 44b): a narrow triangular sclerite on the underside of the wing at the base of vein *R*, bearing a few setae in some calyptrates, *e.g.*, *Lucilia* subgenus *Lucilia* Robineau-Desvoidy.

subcostal vein or **subcosta**, ***Sc*** (Figs 43a–45b): a slender vein between costa and radius that may end blindly in the membrane, or terminate in the costa. In a few groups the subcosta terminates in R_1 (*e.g.*, most Dolichopodidae), or appears to fuse with it.

submarginal cells, see **cells** $\boldsymbol{r_{2+3}}$ and $\boldsymbol{r_4}$ under **radial cells**.

supernumerary crossvein: any additional crossvein between longitudinal veins present in certain genera of some families (*e.g.*, Nemestrinidae, some Asilidae and Curtonotidae).

tegula (Figs 44a–45b): scale-like sclerite at the base of the wing, adjacent to the basicosta, usually bearing setae along its distal margin.

transverse vein, see **crossvein**.

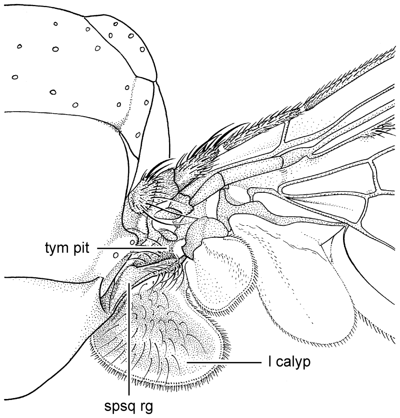
upper calypter (squamula alaris, upper squama) (Figs 44a–45b): a lobe at the base of the wing along its posterior edge, between lower calypter and alula. When the wing is at rest, it is usually folded over the lower calypter.

upper squama, see **upper calypter**.

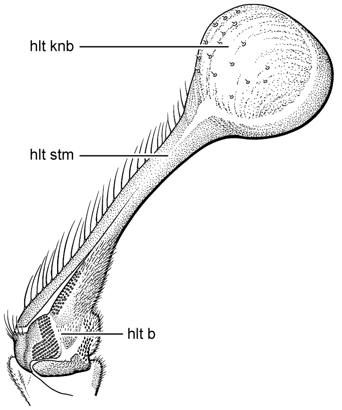
vein: thickened, sclerotised reinforcements of the wing, arising as outgrowths of the tracheal system.

Legs

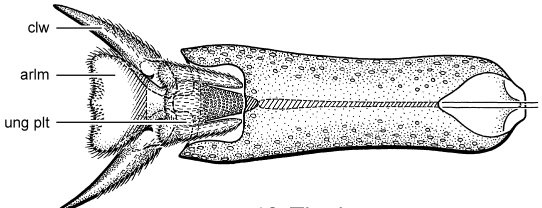
The three pairs of walking legs, namely the **fore leg**, **mid leg** and **hind leg** are each made up of a **coxa** (pl. **coxae**), **trochanter**, **femur** (pl. **femora**), **tibia** (pl. **tibiae**) and **tarsus** (pl. **tarsi**) (Figs 2, 3). Each of the legs may show conspicuous modifications related to prey-catching, predator avoidance, digging and cleaning behaviour. Secondary sexual features associated with courtship and copulation may also be apparent on the legs. The position of these modifications on the different leg surfaces is determined by assuming that each leg is fully extended laterally at a right angle from the main axis of the body (Fig. 1), so that it has an anterior (a), dorsal (d), posterior (p) and ventral (v) surface. Intermediate surfaces are described as



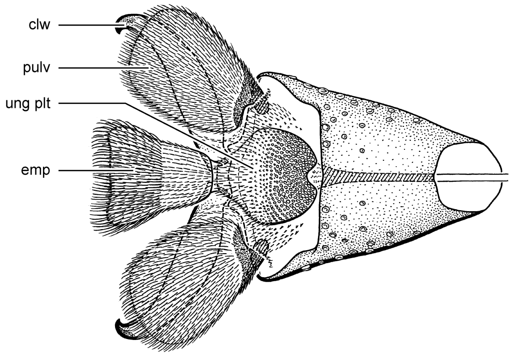
46 *Calliphora* ♀



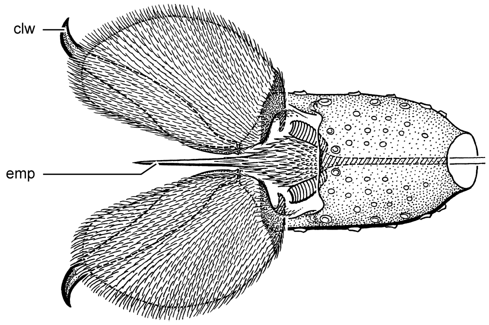
47 *Bibio* ♂



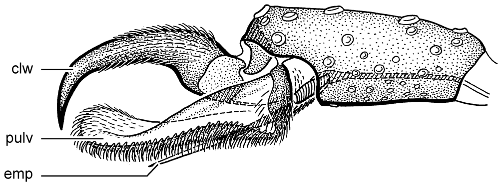
48 *Tipula* ♂



49 *Stratiomys* ♂



50 *Musca* ♂



51 *Musca* ♂

Figs 3.46–51. Wing base, halter and fifth tarsomeres: (46) base of wing of *Calliphora* sp. (Calliphoridae) ♀ (non-Afrotropical); (47) halter of *Bibio* sp. (Bibionidae) ♂ (non-Afrotropical); (48) ventral view of acropod and fifth tarsomere of *Tipula dorsimacula* Walker (Tipulidae) ♂ (non-Afrotropical); (49) same, *Stratiomys badia* Walker (Stratiomyidae) ♂ (non-Afrotropical); (50) acropod and fifth tarsomere of *Musca autumnalis* De Geer (Muscidae), ventral view ♂; (51) same, lateral view. Fig. 46 (after Shewell 1987, fig. 12), Figs 47–51 (after McAlpine 1981, figs 70, 73, 75, 78, 77, respectively).

Abbreviations: arlm – arolium; clw – claw; emp – empodium; hlt b – halter base; hlt knb – halter knob; hlt stm – halter stem; l calyp – lower calypter; pulv – pulvillus; spsq rg – suprasquamal ridge; tym pit – tympanic pit; ung plt – unguitractor plate.

anterodorsal (ad), posterodorsal (pd), posteroventral (pv) and anteroventral (av).

Glossary

acropod (posttarsus) (Figs 48–51): small terminal sclerite closely associated with the fifth tarsomere bearing the unguitractor plate ventrally and the claws, pulvilli and arolium distally.

apical comb: a row of fine setulae at the apex of the tibiae in some families of Diptera, apparently used for grooming various body parts.

arolium (Fig. 48): median protrusion at the distal end of the acropod that is associated with the fifth tarsomere, usually bearing a median process (*i.e.*, empodium or mediolobus).

basitarsus, see **first tarsomere** under **tarsomere**.

calcar: a large distinctive posterodorsal bristle-like seta on the hind tibia of some Calyptratae.

calcipala: a flange-like lobe that extends distally from the inner surface of the first tarsomere of the hind leg of some Simuliidae; its edge is serrated suggesting a grooming function (Adler *et al*. 2004: 41).

claw (tarsal claw, unguis) (Figs 48–51): one of a pair of hook-like structures that arise from the dorsolateral surface of the acropod.

coxa (Fig. 3): the basal segment of each leg that articulates with the thorax.

ctenidium (pecten): comb-like row (or rows) of stout setae, on the anteroventral surface of the apical portion of the fore femur in several families of Diptera, but on the dorsal surface of the tibiae in some Phoridae; frequently one bristle-like seta on the fore femur, referred to as a **ctenidial spine**, is distinctively larger than the other setae.

empodium (Figs 49–51): median process of the acropod found in most Diptera that arises from the ventral surface of the arolium; when present it is generally referred to as either **pulvilliform** (*i.e.*, flap-like and similar in shape to pulvilli) (Fig. 49), or **setiform** (Figs 50, 51). However, Röder (1984, 1986) considers both forms as non-homologous structures. He interprets the setiform median process as an outgrowth of the unguitractor plate, which he refers to as the empodium, whereas the pulvilliform median lobe (termed the **mediolobus**) is derived from the membranous area distal to the unguitractor plate.

femur (pl. **femora**) (Figs 2, 3): the most substantial subbasal segment of the leg between the trochanter and tibia.

mediolobus, see pulvilliform under **empodium**.

metatarsus, see **first tarsomere** under **tarsomere**.

pecten, see **ctenidium**.

pedisulcus: an acute or blunt notch-like indentation on the dorsal surface of the second tarsomere of the hind leg in both sexes of some Simuliidae.

posttarsus, see **acropod**.

preapical seta: a dorsal, or anterodorsal seta near the apex of the femora or tibiae; presence or absence of preapical setae is taxonomically important in the Dolichopodidae and at the family level in acalyptrates.

pulvilli (sing. **pulvillus**) (Figs 49, 51): paired flap-like processes of the acropod found in most Diptera; the pulvilli, in combination with the empodium (or mediolobus) act to grip the substrate.

setal palisade: longitudinal rows of enlarged setae on the dorsal surface of the tibiae in some Phoridae.

spur: an enlarged spine often present at the apex of the tibia; true spurs are articulated and may be single, or paired, whereas unarticulated spurs are actually processes of the distal tibial margin and are not homologous to true spurs.

tarsomere (Figs 2, 3): each tarsus is subdivided into five tarsomeres in almost all Diptera, namely the **first** (basitarsus, metatarsus), **second**, **third**, **fourth** and **fifth** (distitarsus) **tarsomeres**; the fifth tarsomere is associated distally with the claw-bearing acropod. The number of tarsomeres is reduced in only a few Cecidomyiidae and Phoridae.

tarsus (pl. **tarsi**) (Fig. 3): the distal segment of the leg, subdivided with few exceptions into five tarsomeres. A few authors (*e.g.*, Adler *et al*. 2004: 41) consider the first tarsomere (basitarsus) to be a true segment distinct from the remaining tarsomeres, but this interpretation is not followed here.

tibia (Figs 2, 3): the middle segment of the leg between the femur and the tarsus, generally not as stout as the femur.

trochanter (Fig. 3): a small immovable segment between the coxa and the femur that is usually fused with the femur.

unguis (pl. ungues), see **claw**.

unguitractor plate (Figs 48, 49): ventral sclerite of the acropod.

Abdomen

In the dipteran groundplan the abdomen is composed of 10 segments, plus the **proctiger** that bears a pair of **cerci** and the **anus**. The basal segments that are anterior to the modified genital segments are collectively referred to as the **preabdomen**. The remaining complex of modified genital and anal segments, including any adjacent segments that are modified for copulation and oviposition, are referred to as the **terminalia** (postabdomen) (Figs 2, 3, 52, 66).

Glossary

abdominal plaques (Fig. 59): circular patches along the anterior margin of the preabdominal tergites and sternites of nematocerous Diptera and orthorrhaphous Brachycera. These patches represent external remnants of attachment sites of muscles in the pupa (Stoffolano *et al*. 1988) and are absent in Cyclorrhapha, because the pupa is immobile and contained inside a puparium.

abdominal spiracles (stigmata) (Fig. 56): the external openings of the tracheae on the abdominal segments; in what is assumed to be the primitive condition, each abdominal segment has one pair of spiracles, with each spiracle located laterally in the pleural membrane of the segment. In Diptera there are no more than eight pairs in the female, seven in males, but this number is frequently reduced in various taxa across the order, especially in Cyclorrhapha, where the spiracles can also become incorporated into the lateral margins of the tergites.

adventitious suture, see under **syntergite**.

anus (Figs 70, 87): posterior opening of the digestive tract, positioned at the apex of the abdomen between the cerci (see **proctiger**).

cercus (pl. **cerci**) (Figs 52, 56, 59, 71, 72, 88): one of a pair of terminal appendages on either side of the anus that are derived from the proctiger; in the female groundplan they are composed of two segments, but are reduced to a single segment in most higher Diptera; in males the cerci consist of only one segment. In some taxa the cerci are fused together, or are reduced and indistinguishable from other components of the proctiger.

cingulum: structure of unknown function that protrudes between abdominal segments 4 and 5 in certain male hydrophorine Dolichopodidae (*e.g.*, *Hydatostega* Philippi and *Scellus* Loew); the cingulum usually terminates in a pair of flag-like appendages that are often haired and/or are brightly coloured.

discal setae: setae found on the disk of the preadominal tergites in many Calyptratae, referred to as median, or lateral depending on their position (see **marginal setae**).

marginal setae: setae found along the posterior margin of the preadominal tergites in many Calyptratae; referred to as median, or lateral depending on their position (see **discal setae**).

preabdomen: basal segments anterior to the modified genital segments or terminalia. The preabdomen generally consists of segments 1–7 in the nematocerous Diptera and orthorrhaphous Brachycera, segments 1–6 in female Cyclorrhapha and segments 1–5 in male Cyclorrhapha.

proctiger (anal segment) (Figs 70, 87): in a strict sense the anus-bearing region posterior to (or arising from) segment 10, but generally used for all associated structures behind segment 9 (**cerci**, **epiproct**, **hypoproct**, **paraprocts**) in male Diptera (Wood 1991) and in females of at least Cyclorrhapha.

rectal papillae (Fig. 60): prominent ovoid structures on the wall of the rectum that appear to reabsorb water passing through the gut. Most Diptera have four rectal papillae, but some Asilidae have five and Apioceridae and Mydidae, which are among the most dry-adapted flies, have many more (14–80 papillae) (Woodley 1989: 1387).

stigmata (sing. stigma), see **abdominal spiracles**.

syntergite: in Cyclorrhapha and some orthorrhaphous Brachycera, the fused tergites of the first two abdominal segments are referred to as syntergite 1 + 2. A line of fusion, the **adventitious suture**, is usually recognisable, but is seldom distinct. Only tergites 1 and 2 are affected; the sternites usually remain separate and distinct, although in Tabanidae, Pyrgotidae and Ctenostylidae they may be fused into a **synsternite** (or one may be absent).

terminalia (postabdomen) (Figs 2, 3): complex of genital and anal segments, including any adjacent segments that are modified for copulation and oviposition. The terminalia generally consist of segments 8–10 (including the proctiger) in the nematocerous Diptera and orthorrhaphous Brachycera, segments 7–10 (including the proctiger) in female Cyclorrhapha, and segments 6–10 (including the proctiger) in male Cyclorrhapha.

Female terminalia

The terminalia of the female include the genital and anal segments of the abdomen posterior to the preabdomen that are modified for oviposition and copulation (Figs 52–65). The segments involved vary depending on the group, but generally consist of segments 8–10 (including the proctiger) in the nematocerous Diptera and orthorrhaphous Brachycera, as well as segment 7 in the Cyclorrhapha. The definitions presented here for the female postabdomen incorporate terminology adopted by Kotrba (2000) and focus primarily on external structures, but also include certain internal structures of ectodermal origin, which are more or less sclerotised, or pigmented and are useful for diagnosing certain groups.

Glossary

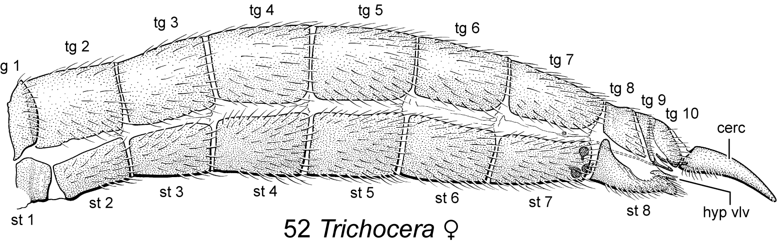
acanthophorites (Figs 57, 58, 60, 61): spine-bearing hemitergites found in many orthorrhaphous Brachycera that are derived from tergite 10 (see **pseudacanthophorites**); **acanthophorite spines** are innervated and project from alveoli; they are therefore a type of macrotrichia. In some groups of Empidoidea (*e.g.*, *Microphor* Macquart) acanthophorite spines are reduced to **acanthophorite setae**.

accessory glands (appendicular glands, colleterial glands, parovaria) (Fig. 63): paired glandular organs of ectodermal origin that are derived from segment 9; they are unpaired in a few groups. In the viviparous Pupipara (Glossinidae and Hippoboscidae), the accessory glands produce nutrient for the developing larvae and are referred to as **milk glands**; the “milk glands” of the viviparous Mesembrinellinae (Calliphoridae), however, are derived from the spermathecae (Kotrba 2000: 80).

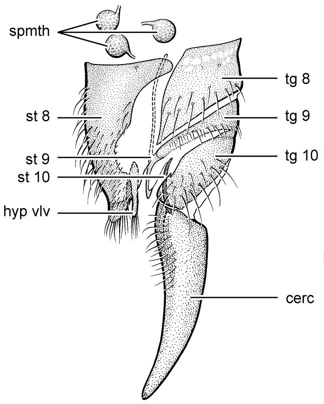
aculeus (ovipositor blade) (Fig. 63): the piercing part of the ovipositor in Tephritoidea that is generally retracted with the eversible ovipositor membrane inside the oviscape; the aculeus consists of an elongate tergite and sternite 8, in addition to the proctiger, which in Tephritidae is usually fused with tergite 8 beyond the cloacal opening and sternite 8 to form a piercing **aculeus tip** (see **cloaca**).

adanal plates: small paired sclerites ventrolateral of, or fused to, the cerci in nycteribiine Hippoboscidae.

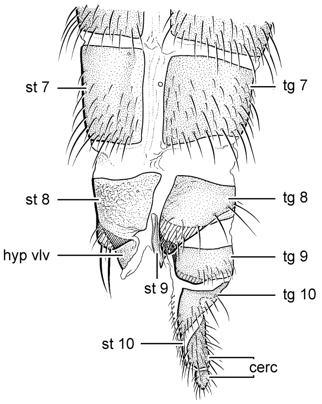
anal lobe: a ventrally directed extension of segment 10 found in many Simuliidae, not to be confused with the anal lobe of the wing.



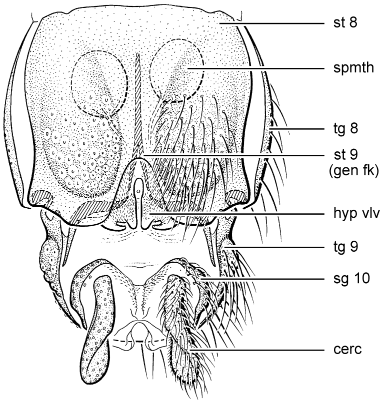
52 *Trichocera* ♀



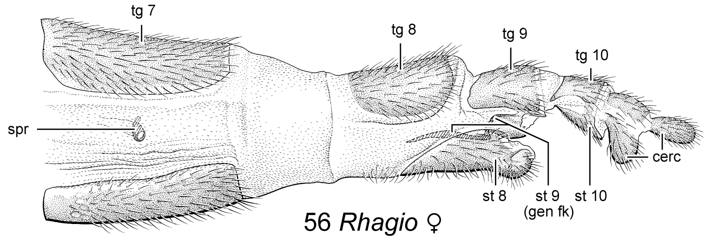
53 *Trichocera* ♀



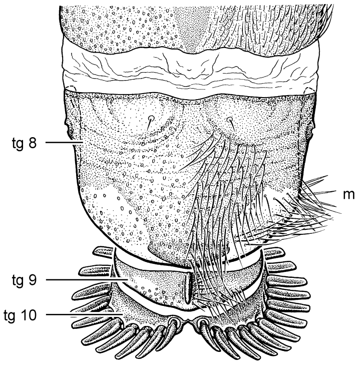
54 *Boletina* ♀



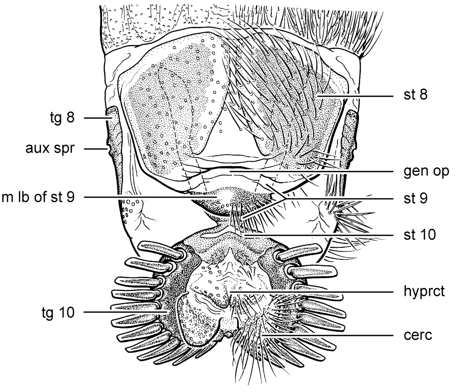
55 *Chironomus* ♀



56 *Rhagio* ♀



57 *Rhaphiomidas* ♀



58 *Rhaphiomidas* ♀

Figs 3.52–58. Female abdomens and terminalia: (52) lateral view of entire abdomen of *Trichocera columbiana* Alexander (Trichoceridae – non-Afrotropical); (53) same, enlarged view of terminalia; (54) lateral view of terminalia of *Boletina* sp. (Mycetophilidae); (55) ventral view of terminalia of *Chironomus plumosus* (L.) (Chironomidae); (56) lateral view of terminal segments of abdomen of *Rhagio mystaceus* (Macquart) (Rhagionidae); (57) terminal segments of abdomen of *Rhaphiomidas acton* Coquillett (Mydidae), dorsal view; (58) same, ventral view (all non-Afrotropical). Figs 52–58 (after McAlpine 1981, figs 79, 80, 83, 86, 94, 99, 100).

Abbreviations: aux spr – spiracle; cerc – cercus; gen fk – genital fork; gen op – genital opening; hyp vlv – hypogynial valve; hyprct – hypoproct; m lb – median lobe; sg – segment; spmth – spermatheca; spr – spiracle; st – sternite; tg – tergite.

basicercus (Figs 54, 56): basal segment of the two-segmented cercus found in some female nematocerous Diptera and orthorrhaphous Brachycera.

bursa (bursa copulatrix): general term for a pouch of various homologies in the genital chamber, which during mating receives a spermatophore, or male genitalia and/or sperm (see **ventral receptacle**). The **bursa inseminalis** is a posterodorsal pouch of the genital chamber found in certain nematocerous groups; it receives sperm during copulation.

cercus (pl. **cerci**) (Figs 53–56, 58–65): one of a pair of terminal appendages on either side of the anus derived from the proctiger. The cerci are composed of two segments in the female groundplan, but are reduced to a single segment in many nematocerous Diptera and orthorrhaphous Brachycera, as well as in all Eremoneura (Empidoidea and Cyclorrhapha) (see **basicercus**).

cloaca (Fig. 63): in Tephritidae, the terminal portion of the vagina and rectum fuse to form a cloaca, which has a single external opening, the **cloacal opening**, between the divided sclerites of sternite 8.

epigynium: tergite 8 of the female terminalia.

epiproct (supra-anal plate, tergite 10) (Fig. 64): the dorsal sclerite of the proctiger.

eversible ovipositor membrane (eversible membrane, eversible ovipositor sheath, inversion membrane, ovipositubus, oviprovector) (Figs 62, 63): the elongate membranous area of the ovipositor in various acalyptrate Diptera (*e.g.*, Agromyzidae and Tephritoidea), between syntergosternite 7 (oviscape) and segment 8 (aculeus), which is inverted for retraction of the tip of the ovipositor inside the oviscape. The eversible ovipositor membrane usually bears minute cuticular denticles (previously referred to, collectively, as the rasper), as well as paired dorsal and ventral sclerites basally, termed taeniae (see **taeniae**).

fertilisation chamber: in Schizophora an unpaired evagination arising from the anteroventral portion of the vagina where eggs are fertilised during oviposition; it is further developed as the ventral receptacle (Fig. 63) in most acalyptrate Schizophora (see **ventral receptacle**).

furca, see **genital fork**.

genital chamber: ectodermal invagination leading anteriorly toward the common oviduct from the genital opening behind sternite 8; in Cyclorrhapha the genital chamber forms a tubular organ termed the vagina. The **primary gonopore** is generally positioned at the anterior end of the genital chamber, where the spermathecal ducts and accessory glands open on the chamber's dorsal wall (see **vagina**).

genital fork (furca, sternite 9, vaginal apodeme) (Figs 55, 56, 61): an internalised sclerite of the dorsal wall of the genital chamber derived from sternite 9, absent or unrecognisable in most Cyclorrhapha (see **sternite 9**).

genital opening (secondary gonopore, vulva) (Fig. 58): external opening of the genital chamber, or vagina, located medially behind sternite 8 (see **cloaca**).

hypogynial valve (gonapophysis, hypovalve, ovipositor lobe, ovipositor valve, sternal valve) (Figs 52–55): one of a pair of lateral processes arising from sternite 8.

hypogynium (subgenital plate): sternite 8 of the female terminalia.

hypoproct (anal sclerite in nycteribiine Hippoboscidae, intra-anal plates in Tipulidae, sternite 10, subanal plate) (Fig. 65): the ventral sclerite of the proctiger.

insula: median sclerite derived from sternite 8 or 9 in Culicidae and clothed with microtrichia or macrotrichia.

milk glands, see **accessory glands**.

morula gland, see **ventral receptacle**.

ovipositor (intersegment 6/7 and 7/8, ovicauda, oviscapt): the parts of the terminalia that are modified for oviposition, involving different segments and structures in different groups.

ovisac, see **uterus**.

oviscape (ovipositor sheath, oviscapt) (Figs 62, 63): the basal conical or tubular segment of the ovipositor that is usually formed by fusion of tergite and sternite 7 into **syntergosternite 7.** The oviscape forms a tubular sheath that generally receives the retracted apical components of the ovipositor (*e.g.*, as in Tephritoidea).

paraproct (Fig. 55, sg 10): one of a pair of lateral sclerites arising from the proctiger.

primary gonopore, see under **genital chamber**.

proctiger, see above under Abdomen.

pseudacanthophorites: spine-bearing cerci found in some species of tethinine Canacidae (Freidberg & Beschoski 1996), which like acanthophorites are used for digging during oviposition. Similar spine-bearing cerci are also present in some Tephritidae and Curtonotidae.

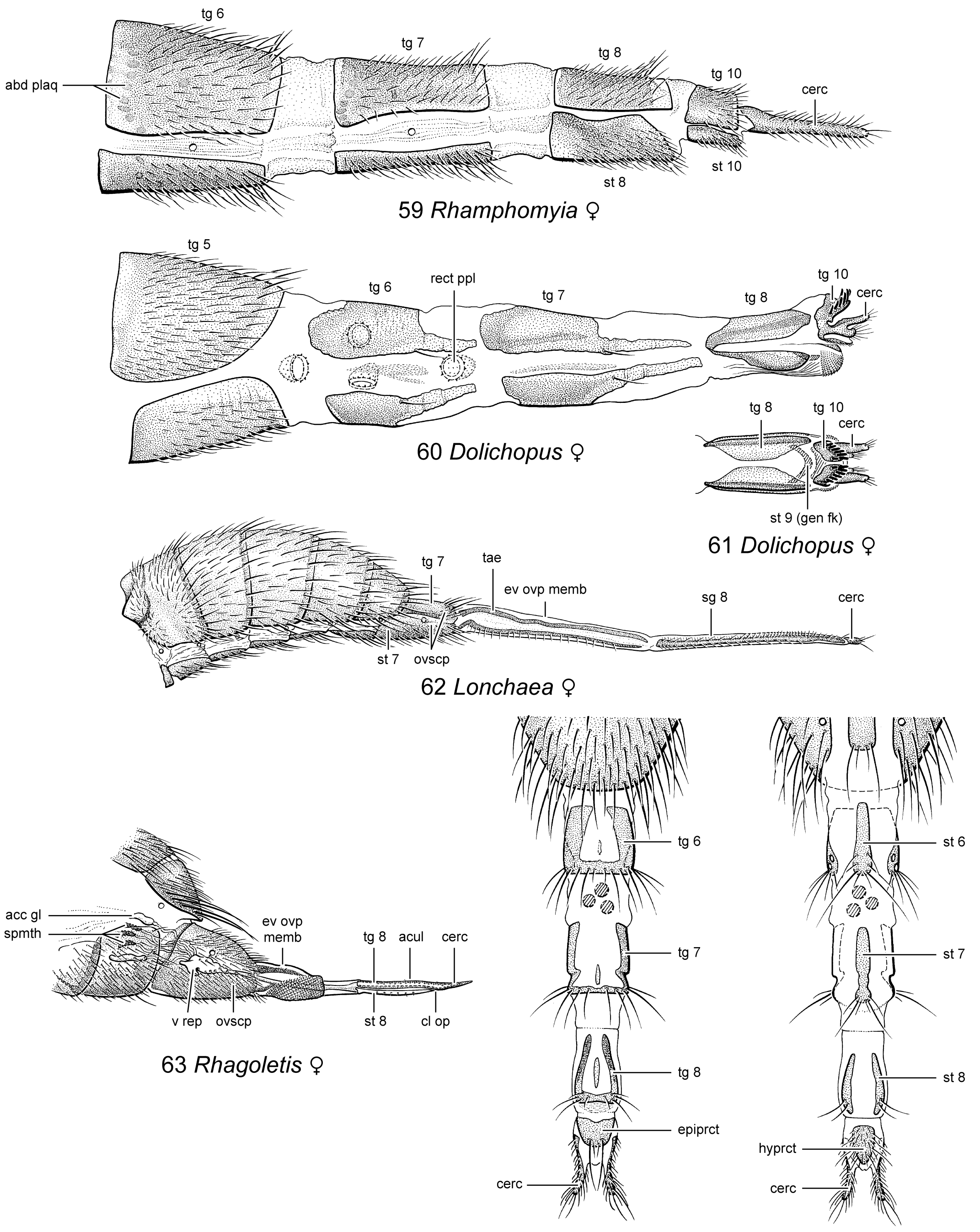
sand chamber: haired invagination of segment 8 found in most Bombyliidae that is used as a receptacle where the eggs are coated with sand. A similar structure is found in a few Asilidae.

secondary gonopore, see **genital opening**.

sperm pump: musculated section of a spermathecal duct found in many orthorrhaphous Brachycera and a few Cyclorrhapha (*e.g.*, *Stylogaster* Macquart in Conopidae), not to be confused with the sperm pump of males.

spermatheca (pl. **spermathecae**) (sperm receptacle, receptaculum seminis) (Figs 53, 55, 63): sperm-storage organ derived from segment 8, generally more or less heavily sclerotised and usually spherical, or cylindrical; most Diptera possess three spermathecae, but the number may vary from zero to four depending on the group (some Diptera considered to lack spermathecae possess membranous spermathecal capsules that are difficult to discern).

spermathecal duct (spermiduct): a sclerotised duct that leads from each spermatheca to the dorsal wall of the genital chamber (or genital fork), where it opens near the primary



59 *Rhamphomyia* ♀

60 *Dolichopus* ♀

61 *Dolichopus* ♀

62 *Lonchaea* ♀

63 *Rhagoletis* ♀

64 *Anthomyia* ♀

65 *Anthomyia* ♀

Figs 3.59–65. Female abdomens and terminalia (concluded): (59) lateral view of terminal segments of abdomen of *Rhamphomyia filicauda* Henriksen & Lundbeck (Empididae); (60) lateral view of terminal segments of abdomen of *Dolichopus brevipennis* Meigen (Dolichopodidae); (61) same, ventral view of last four segments; (62) lateral view of entire abdomen of *Lonchaea polita* Say (Lonchaeidae); (63) lateral view of terminal segments of abdomen of *Rhagoletis pomonella* (Walsh) (Tephritidae); (64) extended terminal segments of abdomen of *Anthomyia pluvialis* (L.) (Anthomyiidae), dorsal view; (65) same, ventral view (all non-Afrotropical). Figs 59–62, 64, 65 (after McAlpine 1981, figs 101–103, 110, 105, 106, respectively), Fig. 63 (after Foote & Steyskal 1987, fig. 43).

Abbreviations: abd plaq – abdominal plaque; acc gl – accessory gland; acul – aculeus; cerc – cercus; cl op – cloacal opening; epiprct – epiproct; ev ovp memb – eversible ovipositor membrane; gen fk – genital fork; hyprct – hypoproct; ovscp – oviscape; rect ppl – rectal papilla; sg – segment; spmth – spermatheca; st – sternite; tae – taenia; tg – tergite; v rep – ventral receptacle.

gonopore; in many Diptera with three spermathecae, two of the three ducts unite before connecting to the genital chamber.

spermathecal sac: sac-like structure associated with the spermathecae in Therevidae, Scenopinidae, Apsilocephalidae and Evocoidae (the last two named non-Afrotropical); in Therevidae the sacs vary greatly in size and shape, depending on the species involved and range in number from zero to three (but not two). Their function is unknown, but they may act as intermediate storage organs for sperm and nutrients prior to transfer of sperm to the spermathecae (Winterton *et al*. 1999).

sternite 9 (preatrial and postatrial sclerites in Culicidae) (Figs 53–56, 58, 61): present, but generally reduced in female Diptera, often internalised as a sclerite of the dorsal wall of the genital chamber and indistinguishable, or absent in most Cyclorrhapha (see **genital fork**).

syntergosternite 7, see **oviscape**.

taeniae (sing. **taenia**) (Fig. 62): in many Tephritoidea paired strip-like dorsal and ventral sclerites on the basal portion of the eversible ovipositor membrane (see **eversible ovipositor membrane**).

theca (ventral genital plate): the ventral prolongation of the sternal portion of segment 5 found in certain Conopidae (most Conopinae and Myopinae), presumably as an aid in clasping the aculeate hymenopteran host during oviposition.

uterus (incubation pouch, ovisac): the anterior portion of the vagina, which tends to be enlarged and possesses an increased tracheal supply in various viviparous and ovolarviparous Cyclorrhapha for the retention of developing eggs.

vagina: the tubular extension of the genital chamber in Cyclorrhapha that stretches from the common oviduct to the genital opening located behind sternite 8 (see **genital chamber**).

ventral receptacle (morula, morula gland) (Fig. 63): in most acalyptrate Diptera an unpaired organ that arises from the anteroventral part of the vagina, which is derived from the fertilisation chamber found in Schizophora (see **fertilisation chamber**). It functions as a chamber for fertilisation and/or as a sperm reservoir and when enlarged is often correlated with reduced spermathecae (Kotrba 2000: 82). The ventral receptacle is extremely diverse in shape and sclerotisation; when it is multi-chambered (*e.g.*, most Tephritoidea and Diopsidae), it has been referred to as a morula, or morula gland.

vulva, see **genital opening**.

Male terminalia

The main components of the male terminalia consist of the copulatory structures of the primary genital segment (segment 9), as well as the proctiger, which together form the **hypopygium**. The basic components of the hypopygium are the **epandrium** (tergite 9), the **hypandrium** (sternite 9), paired two-segmented **gonopods** derived from appendages of segment 9, a median tubular **aedeagus**, **parameres** and the **proctiger**. The **terminalia** (male postabdomen, protandrium) are also considered to include modified adjoining anterior sclerites, such as segment 8 in many nematocerous families and orthorrhaphous Brachycera and segments 6–8 in many Cyclorrhapha (Figs 66–88). Structures of the male terminalia follow the uniform set of terms for the entire Diptera that were presented in a series papers by Wood (1991), Sinclair *et al*. (1994) and Cumming *et al*. (1995), as modified by Sinclair (2000) and subsequently reviewed by Sinclair *et al*. (2013). Alternate views on the homology of structures of the male terminalia, particularly those concerning the Eremoneura (Empidoidea and Cyclorrhapha), are summarised by Sinclair (2000, table 1).

In Diptera the apical portion of the male abdomen and terminalia may be bent or flexed forward ventrally and may also be rotated facultatively, or obligatorily through 45° to 360° (*e.g.*, 180° rotation shown in Figs 68, 70). Modifications involving **flexion** and **rotation**, including the 360° **circumversion** that characterises Cyclorrhapha, are adaptations for protecting the genitalia when at rest and for allowing an upright mating position (see Sinclair *et al*. 2013). McAlpine (1981: 56) summarised the occurrence of flexion and rotation throughout the Diptera, while Cumming *et al*. (1995) reviewed the condition in Eremoneura.

Glossary

accessory glands, see **ejaculatory duct**.

acrophallus (Fig. 88): the distinctive region of the distiphallus that surrounds the phallotrema or external genital opening in Calyptratae, often bearing small denticles (see **distiphallus**).

adminiculum, see **ventral plate**.

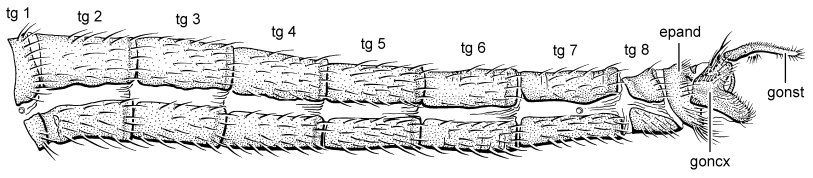
aedeagal apodeme, see **ejaculatory apodeme** and **phallapodeme**.

aedeagal guide, see **phallic guide**.

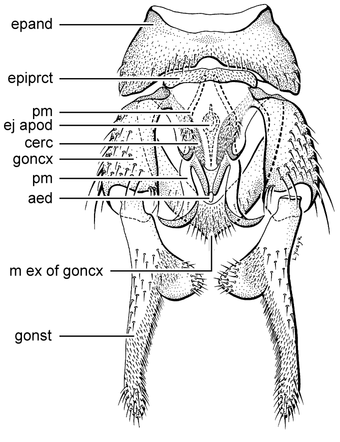
aedeagal tines (endophallic tines) (Fig. 72): elongate, slender sickle-shaped filaments within the sperm sac of Athericidae, Tabanidae and the tabanomorph genus *Bolbomyia* Loew, which arise from the base of the endoaedeagal process; possible precursors of aedeagal tines have also been noted in *Rhagio* F. (Rhagionidae) by Sinclair *et al*. (1994). The tines are pushed posteriorly along with the endoaedeagal process beyond the parameral sheath and functional gonopore, by contraction of the muscles of the ejaculatory apodeme (Bonhag 1951).

aedeagus (penis, phallosome) (Figs 67–70): tubular intromittent organ generally possessing a single external opening (phallotrema), although a tripartite aedeagus is present in several families. In the groundplan of the Brachycera the aedeagus is mostly membranous and largely enclosed in a parameral sheath; in Stratiomyomorpha and Muscomorpha *sensu* Woodley (1989: 1373) the aedeagus is indistinguishably fused to the parameral sheath to form the phallus (see **phallus**). The aedeagus is also reduced to a membranous sac in Culicomorpha (Sinclair 2000: 65 ; Sinclair et al. 2007), presumably correlated with the transfer of preformed spermatophores in many of the included families (*e.g.*, in Ceratopogonidae, see **ventral plate**).

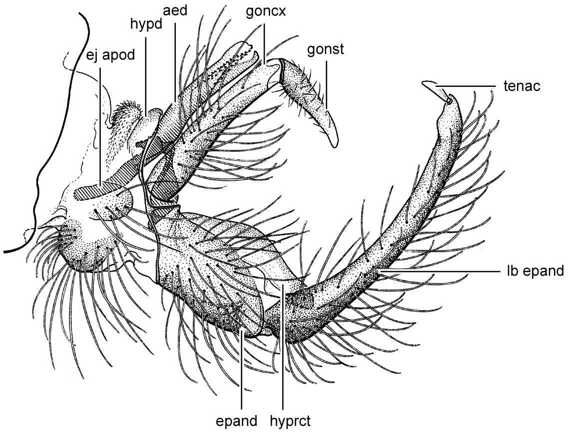
annulus, see **syntergosternum**.



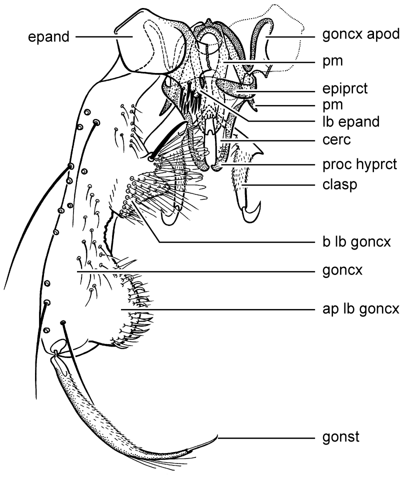
66 *Trichocera* ♂



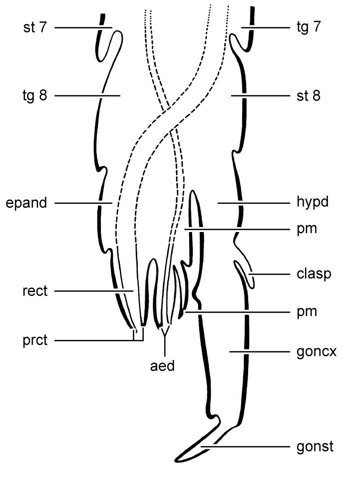
67 *Trichocera* ♂



68 *Psychoda* ♂



69 *Aedes* ♂



70 *Aedes* ♂

Figs 3.66–70. Male abdomen and terminalia: (66) lateral view of entire abdomen of *Trichocera garretti* (Alexander) (Trichoceridae – non-Afrotropical); (67) same, dorsal view of terminalia; (68) lateral view of terminalia in post-emergence position, subsequent to 180° rotation, of *Psychoda phalaenoides* (L.) (Psychodidae); (69) dorsal view of terminalia of *Aedes hexodontus* Dyar (Culicidae); (70) longitudinal section through terminal segments of abdomen, subsequent to 180° rotation of terminalia shortly after emergence, of *Aedes* sp. (Culicidae) (all non-Afrotropical). Figs 66, 67, 69, 70 (after McAlpine 1981, figs 111, 115, 116, 120), Fig. 68 (after Quate & Vockeroth 1981, fig. 18).

Abbreviations: aed – aedeagus; ap lb goncx – apical lobe of gonocoxite; b lb goncx – basal lobe of gonocoxite; cerc – cercus; clasp – claspette; ej apod – ejaculatory apodeme; epand – epandrium; epiprct – epiproct; goncx – gonocoxite; goncx apod – gonocoxal apodeme; gonst – gonostylus; hypd – hypandrium; hyprct – hypoproct; lb epand – lobe of epandrium; m ex – median extension; pm – paramere; prct – proctiger; proc hyprct – process of hypoproct; rect – rectum; st – sternite; tenac – tenaculum; tg – tergite.

bacilliform sclerite (processus longus) (Figs 81–84, 88): one of a pair of rod-like thickenings of the subepandrial sclerite that extend from the anterodorsal surface of the phallus to the posterolateral corner of the epandrium, or to the base of the surstylus, in Eremoneura (Empidoidea and Cyclorrhapha) and the non-Afrotropical families Apystomyiidae and Apsilocephalidae. In most Schizophora the bacilliform sclerites are the main component of the subepandrial sclerite and articulate with the hypandrial arms near the base of the phallus, although in some acalyptrates the bacilliform sclerites are secondarily reduced and do not extend to the surstyli (see **subepandrial sclerite**).

basiphallus (phallobase): the main proximal portion of the phallus in Cyclorrhapha that is continuous with the apical **distiphallus**. In many Cyclorrhapha the basiphallus bears a distinct dorsal lobe termed the **epiphallus** (Fig. 88).

cercus (pl. **cerci**) (forceps, mesolobus, superior forceps, syncercus, valvula medialis) (Figs 66–69, 71, 72, 74–85, 87, 88): one of a pair of single-segmented terminal appendages on either side of the anus derived from the proctiger. In many taxa the cerci are reduced and indistinguishable from other components of the proctiger, but in some groups the cerci are enlarged and clasper-like, or are fused together (syncercus or mesolobus).

claspette, see **ventral plate**.

distiphallus (hypophallus, mesophallus, ventrolateral process) (Figs 85, 88): the main apical portion of the phallus in Cyclorrhapha that arises from the proximal **basiphallus**; in Calyptratae the distinctive region of the distiphallus that surrounds the phallotrema (genital opening) is referred to as the **acrophallus**. The distiphallus is subdivided into various structures (some listed as synonyms in brackets above) in different groups of Schizophora, such as the taxonomically important basolateral paired **paraphallus** in many Agromyzidae and Clusiidae (Lonsdale & Marshall 2012; Nowakowski 1973), the swollen apical **glans** in Tephritoidea, the basal membranous **saccus** and more slender terminal sclerotised **filum** in Anthomyzidae (Roháček & Barber 2005), and the diverse terminal processes (*e.g.*, **vesica**, **harpes**, **juxta** and **stylus)** of certain Sarcophagidae (Giroux *et al*. 2010; Roback 1954).

ejaculatory apodeme (aedeagal apodeme *sensu* McAlpine (1981: 53) concerning lower Diptera, ejacapodeme, endophallus apodeme) (Figs 67, 68, 71–73, 82, 84, 85, 87, 88): unpaired apodeme of the sperm pump inserted at the base of the sperm sac; the ejaculatory apodeme supports muscles that assist in compressing the pump (see **sperm pump**). The ejaculatory apodeme is absent in all Culicomorpha (Sinclair 2000: 69; Wood 1991).

ejaculatory duct (Fig. 87): duct or ducts of ectodermal origin that run from the mostly endodermal **vasa deferentia** (at the point where the **accessory glands** connect), to the base of the endophallus (usually at the sperm pump) (see **sperm pump**).

endoaedeagal process (endoaedeagus, endophallus, posterior part of aedeagus) (Fig. 72): in Brachycera a slender sclerotised posterior extension, that arises from the apex of the ejaculatory apodeme in most Xylophagomorpha, Tabanomorpha, some Nemestrinidae, Asilidae and possibly Bombyliidae (Sinclair *et al*. 1994); the endoaedeagal process is absent in Stratiomyomorpha and Eremoneura (Empidoidea and Cyclorrhapha).

endoaedeagal tube (Ductusrohr, endoaedeagus): slender, inconspicuous membranous tube within the sperm sac of many Asiloidea and some Bombyliidae; the endoaedeagal tube appears to be a posterior extension of the ejaculatory duct; it is perforated with pores and often covered in spinules, granules, or platelets (Sinclair 2000: 69).

endophallus: inner seminal duct of the aedeagus, or phallus extending from the sperm sac.

epandrium (dorsal sclerite, periandrium, tergite 9) (Figs 67–80, 82–85, 87, 88): tergite 9 of the male genital segment, fused to the hypandrium (sternite 9) to form a ring in the dipteran groundplan (Wood 1991), but secondarily separated in some nematocerous groups and almost all Brachycera (see **hypandrium**). The epandrium is a subrectangular sclerite in most nematocerous Diptera and basal orthorrhaphous Brachycera, but is deeply cleft posteriorly, or completely divided in many asiloids and Eremoneura (Empidoidea and Cyclorrhapha), associated with its involvement in clasping (see **surstylus**). Many Psychodidae also have clasper-like epandrial lobes (see Sinclair *et al*. 2013) that have been referred to as cerci (= cercopodia) or surstyli.

epiphallus (Fig. 88): a distinct lobe in many Cyclorrhapha that arises from the dorsomedial surface of the basiphallus. The enlarged dorsal portion of the parameral sheath of the phallus that is found in many Bombyliidae has also been referred to as the epiphallus (Yeates 1994).

epiproct (tergite 10) (Figs 67, 69): the middorsal sclerite of the proctiger, positioned between the lateral cerci; it is lost in males of Acroceridae and all Heterodactyla (Bombyliidae, Asiloidea, Eremoneura) (Sinclair 2000: 72).

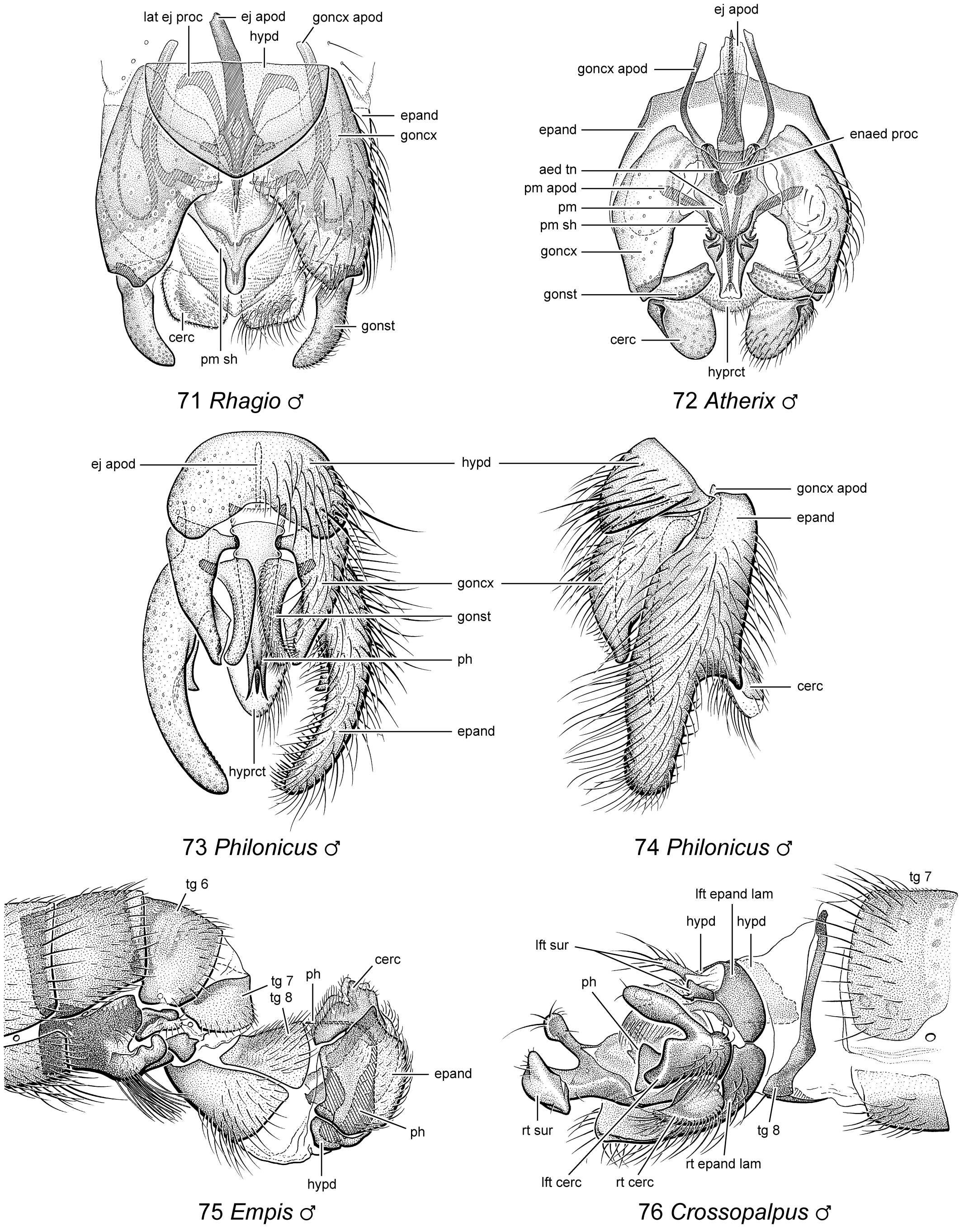
filum, see **distiphallus**.

glans (pl. **glandes**) (aedeagal glans) (Fig. 85): swollen expandable apical portion of the distiphallus in many Tephritoidea.

gonocoxal apodeme (basal piece in Culicidae, basimeral apodeme, dorso-inner anterior process, sternapodeme) (Figs 69, 71, 72, 74): a process that projects anteriorly from each gonocoxite, or the gonocoxal region of the composite hypandrial sclerite (see **hypandrium**). The gonocoxal apodemes (as a pair) indicate the position of the medially attached parameres in the nematocerous Diptera, or the parameral sheath in Brachycera (see **phallus**). Gonocoxal apodemes are inconspicuous in many nematocerous families. They are greatly reduced and do not project beyond the hypandrium in those Empidoidea with permanent male genitalic rotation, as well as in all Cyclorrhapha (Cumming *et al*. 1995).

gonocoxal plate, see **ventral plate**.

gonocoxite (basimere, basistyle, coxite, gonocoxa) (Figs 66–74): basal component of the two-segmented clasping gonopod. The gonocoxites are assumed by Wood (1991) and Sinclair *et al*. (1994) to be separate from each other in the dipteran groundplan, although Griffiths (1996) has questioned



Figs 3.71–76. Male terminalia (continued): (71) ventral view of *Rhagio vertebratus* (Say) (Rhagionidae); (72) same, *Atherix lantha* Webb (Athericidae); (73) ventral view of *Philonicus* sp. (Asilidae); (74) same, left lateral view; (75) lateral view of terminal abdominal segments and terminalia of *Empis browni* Curran (Empididae); (76) right lateral view of *Crossopalpus armata* (Melander) (Hybotidae) (all non-Afrotropical). Fig. 71 (after James & Turner 1981, fig. 14), Fig. 72 (after Webb 1981, fig. 6), Figs 73, 74 (after Wood 1981, figs 74, 75), Figs 75, 76 (after Steyskal & Knutson 1981, figs 52, 51 (as *Drapetis*), respectively).

Abbreviations: aed tn – aedeagal tine; cerc – cercus; ej apod – ejaculatory apodeme; enaed proc – endoaedeagal process; epand – epandrium; goncx – gonocoxite; goncx apod – gonocoxal apodeme; gonst – gonostylus; hypd – hypandrium; hyprct – hypoproct; lat ej proc – lateral ejaculatory process; lft cerc – left cercus; lft epand lam – left epandrial lamella; lft sur – left surstylus; ph – phallus; pm – paramere; pm apod – parameral apodeme; pm sh – parameral sheath; rt cerc – right cercus; rt epand lam – right epandrial lamella; rt sur – right surstylus; tg – tergite.

this polarity. Gonocoxites are fused together midventrally, generally with the hypandrium, in some nematocerous and lower brachyceran groups, as well as in all Eremoneura (Empidoidea and Cyclorrhapha) (see **gonopod**).

gonopod: one of a pair of two-segmented claspers that are composed of a proximal gonocoxite and a distal gonostylus; in the dipteran groundplan the gonopods remain separate from each other and from the hypandrium, but fusion of the gonocoxal portions with each other and often with the hypandrium, appears to have occurred independently numerous times within the order (Wood 1991) (see **gonocoxite** and **gonostylus**).

gonostylus (clasper, distimere, dististyle, telomere, stylus) (Figs 66–73): the distal articulated clasping lobe of the two-segmented gonopod, usually positioned on the apical margin of the goncoxite, but retracted to a subapical position in Asiloidea *sensu* Sinclair *et al*. (1994). It is subdivided into two branches in most Tipulidae (Ribeiro 2006) and sometimes bears thickened setae (rostral spines) basally. Gonostyli are hypothesised by Sinclair (2000: 54) and Sinclair & Cumming (2006) to be absent in Eremoneura (Empidoidea and Cyclorrhapha) (see **postgonite** concerning use of gonostylus in Cyclorrhapha).

harpes, see **distiphallus**.

hypandrial arms (gonocoxal arms) (Figs 83, 84): dorsal extensions of the hypandrium (composite gonocoxal-hypandrial sclerite) in Schizophora, which articulate with the base of the bacilliform sclerites.

hypandrium (sternite 9, ventral sclerite) (Figs 68, 70, 71, 73–85, 88): sternite 9 of the male genital segment; fused laterally with the epandrium (tergite 9) and separate from the gonopods (gonocoxites) in the groundplan of Diptera (Wood 1991). In some orthorrhaphous Brachycera and all Eremoneura (Empidoidea and Cyclorrhapha), the hypandrium and gonocoxites are indistinguishably fused together; in these groups this entire ventral composite structure is referred to as the hypandrium following Sinclair *et al*. (1994) and Cumming *et al*. (1995).

hypophallus, see **distiphallus**.

hypoproct (decasternum, opisthophallus, paraproct, sternite 10) (Figs 68, 69, 72, 73, 79, 80, 83, 84): the midventral sclerite of the proctiger, positioned between the lateral cerci and continuous with the subepandrial membrane anteriorly (see **subepandrial membrane** and **subepandrial sclerite**).

hypopygium: the male genital capsule, made up of the copulatory structures of the primary genital segment (segment 9) and the proctiger; not to be confused with the terminalia that may also include modified adjoining anterior sclerites.

interbase, see **paramere**.

juxta, see **distiphallus**.

lateral ejaculatory process (aedeagal dorso-anterior sclerite, external ejaculatory sclerite, lateral aedeagal apodeme) (Fig. 71): one of a pair of sclerites of the brachyceran sperm pump, inserted laterally on the anterodorsal wall of the sperm sac; each lateral ejaculatory process supports a muscle that assists in compressing the pump (see **sperm pump**). Lateral ejaculatory processes are absent in most Stratiomyomorpha, Hilarimorphidae (non-Afrotropical), Apystomyiidae (non-Afrotropical) and Eremoneura (Empidoidea and Cyclorrhapha) (Sinclair *et al*. 2013).

median sclerite (aedeagus in Simuliidae): strap-like dorsal extension of the ventral plate that supports the floor of the membranous aedeagal sac in Simuliidae (see **ventral plate**).

mesophallus, see **distiphallus**.

parameral sheath, see **paramere** and **phallus**.

paramere (aedeagus in Culicidae, dorsal plate, paraphysis, phallus *sensu* Belkin (1968) in Dixidae, penis valve in Chaoboridae, tegmen in Blephariceridae) (Figs 67, 69, 71, 72): one of a pair of posteriorly directed processes each attached to a gonocoxal apodeme; in many groups parameres are fused to each other medially over the aedeagus to form a single plate. In Tipuloidea the dorsolateral portion of the paramere that connects to the gonocoxal apodeme is referred to as the **interbase**. The parameres in Brachycera form a covering termed the **parameral sheath** that partially surrounds the apex of the aedeagus (Figs 71, 72); in the Muscomorpha *sensu* Woodley (1989) and most Stratiomyomorpha this sheath is fused to the aedeagus to form a modified composite intromittent organ referred to as the phallus (see **phallus**).

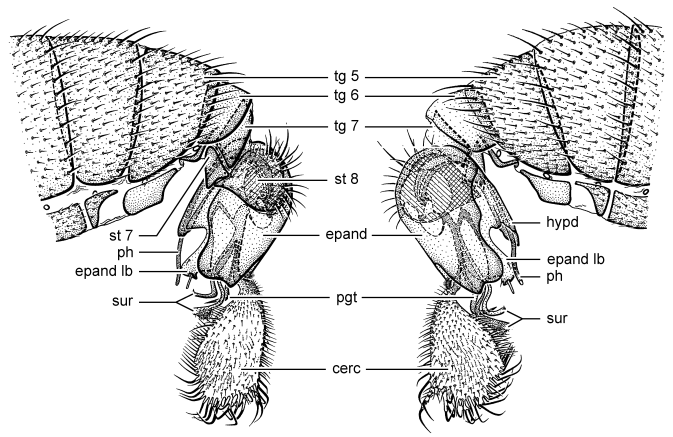
paraphallus, see **distiphallus**.

phallapodeme (aedeagal apodeme *sensu* authors concerning Cyclorrhapha) (Figs 80–83, 85, 88): novel structure in the Cyclorrhapha found in every major lineage, except Opetiidae (non-Afrotropical), which is derived from a median longitudinal invagination of the hypandrium (composite gonocoxal-hypandrial sclerite). In the basal cyclorrhaphan lineages the phallapodeme tends to surround and support the base of the phallus while remaining broadly connected to the hypandrium (*e.g.*, as in the platypezid *Microsania*); in Syrphoidea and Schizophora the phallapodeme is no longer extensively connected to the hypandrium and is typically a rod-like lever that assists in moving the base of the phallus and the postgonites; occasionally in some schizophoran families (*e.g.*, Diopsidae, most Tephritoidea), the anterior portion of the phallapodeme becomes secondarily fused to the hypandrium (see **phallic guide**).

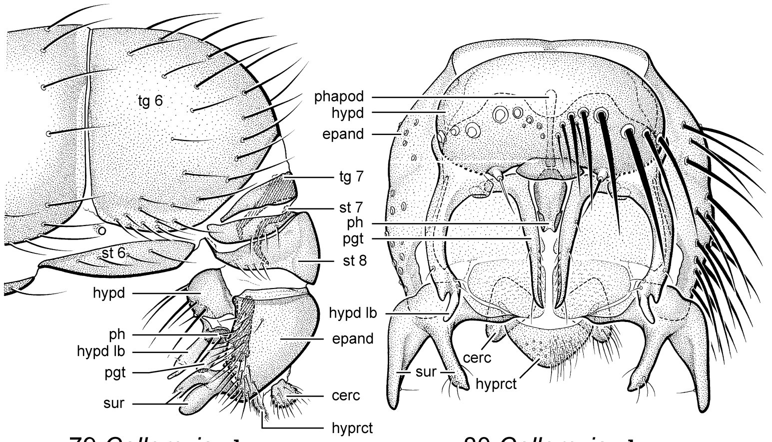
phallic guide (aedeagal guide, fulcrum *sensu* Roháček & Barber (2005) in Anthomyzidae, intermedium) (Figs 82, 85): general term for any ventromedial posteriorly directed lobe that is derived from the gonocoxites; in Cyclorrhapha it arises from the gonocoxal portion of the hypandrium and connects to the phallapodeme, or appears simply as a ventral extension of the phallapodeme.

phallic plate (aedeagal dorsal sclerite, ventral proctiger sclerite, "y" sclerite): in Eremoneura (Empidoidea and Cyclorrhapha), a short to long sclerotised extension of the base of the phallus towards the base of the subepandrial sclerite (or bacilliform sclerites) and the hypandrial arms; the phallic plate is extremely long in Neriidae and Micropezidae.

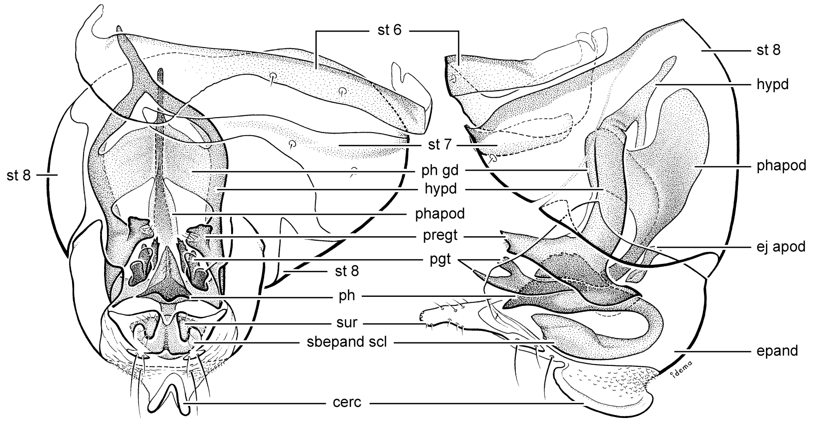
phallotrema (pl. **phallotremata**) (genital opening, secondary gonopore): external genital opening at the apex of the



77 *Dolichopus* ♂ 78 *Dolichopus* ♂



79 *Callomyia* ♂ 80 *Callomyia* ♂



81 *Neopiophila* ♂ 82 *Neopiophila* ♂

Figs 3.77–82. Male terminalia (continued): (77) left lateral view of *Dolichopus brevipennis* Meigen (Dolichopodidae); (78) same, right lateral view; (79) left lateral view of terminal segments of abdomen of *Callomyia* sp. (Platypezidae); (80) same, ventral view of terminalia; (81) ventral view of *Neopiophila setaluna* McAlpine (Piophilidae); (82) same, lateral view (all non-Afrotropical). Figs 77–82 (after McAlpine 1981, figs 128, 129, 132, 133, 135, 136).

Abbreviations: cerc – cercus; ej apod – ejaculatory apodeme; epand – epandrium; epand lb – epandrial lobe; hypd – hypandrium; hypd lb – hypandrial lobe; hyprct – hypoproct; pgt – postgonite; ph – phallus; ph gd – phallic guide; phapod – phallapodeme; pregt – pregonite; sbepand scl – subepandrial sclerite; st – sternite; sur – surstylus; tg – tergite.

aedeagus or phallus, as opposed to the **primary gonopore**, which opens into the sperm pump.

phallus (aedeagus *sensu* authors concerning Stratiomyomorpha and Muscomorpha *sensu* Woodley (1989)) (Figs 73, 75–85, 87, 88): the modified intromittent organ in the brachyceran lineages Stratiomyomorpha and Muscomorpha *sensu* Woodley (1989); the phallus is formed by the fusion of the parameral sheath and the aedeagus it encircles to produce a composite structure. In Cyclorrhapha the phallus is often subdivided into specialised regions referred to as the **basiphallus**, **epiphallus**, **distiphallus** and **acrophallus**.

postgonal apodeme (basal piece, Gelenkfortsatz, gonostylar apodeme): small subdivided sclerite at the base of the postgonite in most oestroid Calyptratae.

postgonite (gonostylus *sensu* Cumming *et al*. (1995) concerning Cyclorrhapha, opisthoparamer, paramere *sensu* McAlpine (1981: 53) concerning Eremoneura, paraphysis) (Figs 77–84, 87, 88): one of a pair of processes located near the base of the phallus in Eremoneura (Empidoidea and Cyclorrhapha), that are derived from the gonocoxal portion of the hypandrium (Sinclair 2000: 61; Sinclair & Cumming 2006); they are movably articulated at their base in Cyclorrhapha (except Opetiidae – non-Afrotropical), but partially fused to the hypandrium in most Empidoidea (for review of homology interpretations, see Sinclair 2000, table 1).

pregonite (proparamer, suspensory sclerite) (Figs 81, 82, 87, 88): one of a pair of lobes derived from the hypandrium (composite gonocoxal-hypandrial sclerite), in many Schizophora, positioned anteroventrally to the postgonites.

prensisetae (Fig. 85): short, stout teeth-like setae on the distal margin of the surstyli in certain acalyptrate groups, such as Drosophilidae and Tephritoidea.

primary gonopore, see under **phallotrema**.

proctiger, see above under Abdomen.

prosophallus, see **ventral plate**.

pseudocercus (pl. **pseudocerci**) (ventral epandrial lobe): apical subdivision of the epandrium found in some acalyptrate taxa (*e.g.*, some Sphaeroceridae) (see also **surstylus**).

rostral spine, see **gonostylus**.

saccus, see **distiphallus**.

sperm duct, see **sperm pump**.

sperm pump (genital vesica) (Figs 67, 68, 71–73, 82, 84, 85, 87, 88): in the groundplan of Diptera composed primarily of the **ejaculatory apodeme** (with its associated muscles) and the **sperm sac**; it is located between the ejaculatory duct(s) and the endophallus. In Cyclorrhapha (including Opetiidae – non-Afrotropical) and a few other non-cyclorrhaphan groups, the sperm pump is separated from the base of the phallus by a long **sperm duct** (Figs 85, 87, 88). The sperm pump is lost in Culicomorpha (Sinclair 2000: 71), correlated presumably with the transfer of preformed spermatophores in many of the included families.

sperm sac (endophallus *sensu* Bonhag (1951)) (Figs 85, 87): the membranous reservoir of the sperm pump.

stylus, see **distiphallus**.

subepandrial membrane: the membranous roof of the deeply invaginated pouch that separates the epandrium and proctiger from the gonopods and hypandrium; this intersegmental membrane extends from the hypoproct anteriorly to the anterodorsal margin of the paramere or parameral sheath (the Dorsal-Brücke *sensu* Hennig (1976)). An extensive sclerite, or pair of sclerites, develops in the subepandrial membrane in numerous families of lower Brachycera and all Eremoneura (Empidoidea and Cyclorrhapha) (see **subepandrial sclerite**).

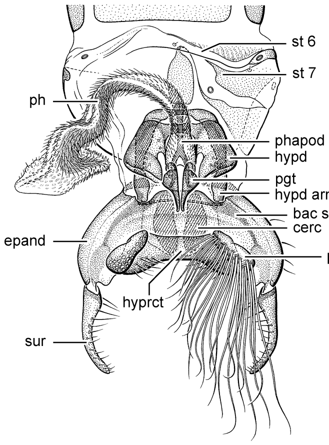
subepandrial sclerite (decasternum, mediandrium, sternite 10, ventral epandrial sclerite) (Figs 81–84, 88): the extensive sclerite, or pair of sclerites, that develop in the subepandrial membrane of many Brachycera. In the Eremoneura (Empidoidea and Cyclorrhapha) and the non-Afrotropical families Apsilocephalidae and Apystomyiidae, the subepandrial membrane is sclerotised along its entire length, so that the subepandrial sclerite articulates with the anterodorsal surface of the phallus; in these groups this sclerite contains a pair of rod-like extensions, termed bacilliform sclerites, that extend to the posterolateral corners of the epandrium, or to the base of the surstyli (see **bacilliform sclerite**).

surstylus (pl. **surstyli**) (außerer Forceps, gonostylus *sensu* Zatwarnicki (1996) concerning Eremoneura, inferior forceps, paralobe, paralobus, telomere *sensu* Griffiths (1972: 31) concerning Cyclorrhapha, valvula lateralis) (Figs 76–85, 87, 88): apical clasping lobe derived from a posterolateral outgrowth of the epandrium; the external surface of each surstylus is formed by the epandrium, whereas the inner surface is formed basally by the bacilliform sclerite. In some taxa each surstylus is divided into more than one lobe described by their position on the epandrium (*e.g.*, **lateral** *versus* **medial**, **outer** *versus* **inner**, **dorsal** *versus* **ventral**). Unlike other apical lobes of the epandrium (*e.g.*, pseudocercus, ventral epandrial lobe), each surstylus is abducted by the lever-like action of the bacilliform sclerite and adducted by a single muscle (Cumming *et al*. 1995). Although somewhat similar looking epandrial processes occur in a few nematocerous families (*e.g.*, Ptychopteridae, Psychodidae and Canthyloscelidae (non-Afrotropical)), true surstyli occur only in Eremoneura (Empidoidea and Cyclorrhapha) and in the non-Afrotropical families Apsilocephalidae and Apystomyiidae. They are usually clearly articulated lobes as in almost all Cyclorrhapha, but are only weakly articulated in some basal groups of Empidoidea and Apystomyiidae.

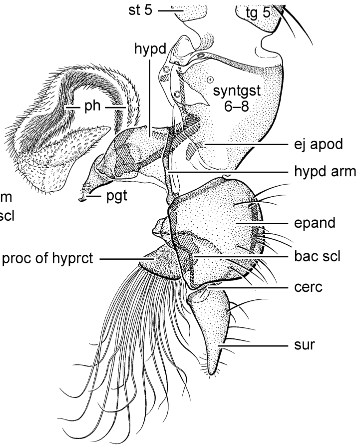
syncercus, see **cercus**.

syntergosternum (Fig. 86): a more or less symmetrical ring located between segments 5 and 9, or 6 and 9 in most Cyclorrhapha as a result of circumversion (*i.e.*, 360° genitalic rotation), composed of the distorted remnants of segments 6–8, or 7–8. The asymmetrical ring formed by the fusion of sternites 6–8 in many Schizophora, is referred to as the **annulus** (Lonsdale *et al*. 2010).

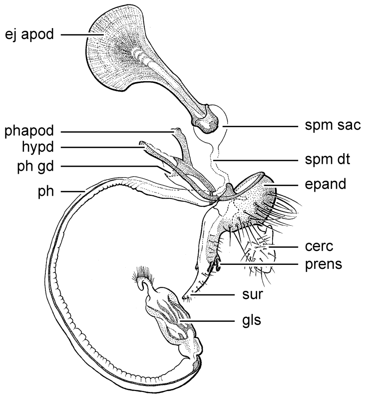
tegmen, see **paramere** and **ventral plate**.



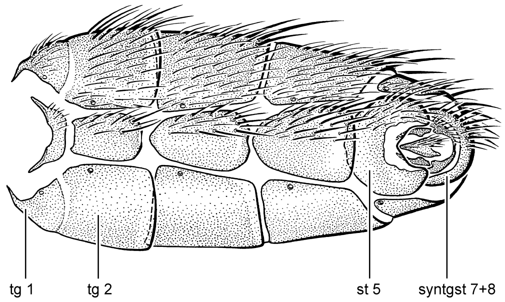
83 *Meoneura* ♂



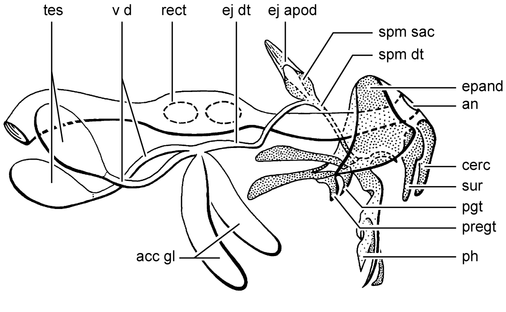
84 *Meoneura* ♂



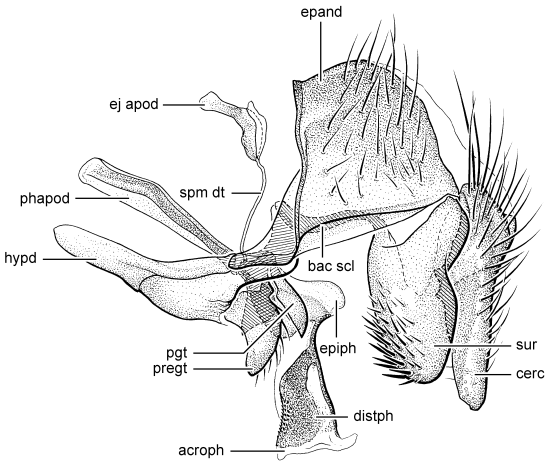
85 *Rhagoletis* ♂



86 *Melanophora* ♂



87 *Phormia* ♂



88 *Masistylum* ♂

Figs 3.83–88. Male abdomen and terminalia (concluded): (83) terminalia of *Meoneura obscurella* (Fallén) (Carnidae), ventral view; (84) same, lateral view; (85) terminalia of *Rhagoletis pomonella* (Walsh) (Tephritidae), lateral view; (86) abdomen of *Melanophora roralis* (L.) (Rhinophoridae), ventral view; (87) diagrammatic longitudinal section through genitalia and terminalia of *Phormia regina* (Meigen) (Calliphoridae); (88) terminalia of *Masistylum arcuatum* (Mik) (Tachinidae), lateral view (all non-Afrotropical). Figs 83, 84, (after Sabrosky 1987, figs 7, 8), Fig. 85 (after Foote & Steyskal 1987, fig. 41), Figs 86–88 (after McAlpine 1981, figs 137, 138, 141).

Abbreviations: acc gl – accessory gland; acroph – acrophallus; an – anus; bac scl – bacilliform sclerite; cerc – cercus; distph – distiphallus; ej apod – ejaculatory apodeme; ej dt – ejaculatory duct; epand – epandrium; epiph – epiphallus; gls – glans; hypd – hypandrium; hypd arm – hypandrial arm; hyprct – hypoproct; pgt – postgonite; ph – phallus; ph gd – phallic guide; phapod – phallapodeme; pregt – pregonite; prens – prensiseta; proc – process; rect – rectum; spm dt – sperm duct; spm sac – sperm sac; st – sternite; sur – surstylus; syntgst – syntergosternite; tes – testis; tg – tergite; v d – vas deferens.

tenacula (sing. **tenaculum**) (retinacula) (Fig. 68): stiff flattened setae on the inner apical surface of the clasper-like epandrium (see Sinclair *et al*. 2013) of many Psychodidae.

vas deferens (pl. **vasa deferentia**), see **ejaculatory duct**.

ventral appendage, see **ventral plate**.

ventral epandrial lobe, see **pseudocercus**.

ventral plate (aedeagus in Ceratopogonidae, **adminiculum** in Tipulidae, **claspettes** in Culicidae, prosophallus in Dixidae, tegmen, ventral appendage or **gonocoxal plate** in Thaumaleidae, volsellae in Chironomidae) (Fig. 69): medial ventral structure in Culicomorpha that is derived from the gonocoxites; often a single medial plate, but clearly divided and furnished with hooks in some taxa (Culicidae and most Chironomidae); absent in Corethrellidae and Chaoboridae. The ventral plate is articulated in the Chironomoidea (exclusive of Thaumaleidae), when present, where it assists to enlarge the female genital chamber, prior to the transfer of a preformed spermatophore (Wood & Borkent 1989). A similar structure sometimes referred to as the tegmen occurs in Sciaridae.

vesica, see **distiphallus**.

volsella, see **ventral plate**.

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NATURAL HISTORY OF DIPTERA 4

Stephen A. Marshall and Ashley H. Kirk-Spriggs

Introduction

Adults

Adult flies are usually relatively short-lived, highly mobile insects, often with very different habitat requirements from the larvae. Some are non-feeding, many are predators, and several are blood-feeders. Numerous anthophilous taxa consume nectar and pollen, and various groups imbibe honeydew to meet their energy requirements. Swarming, usually of males, but sometimes of females, is found across the order, but is especially common in the lower Diptera. Most flies reproduce sexually and the order exhibits an immense range of inter- and intra-sexual behaviours, including male–male territorial battles and displays, visual and chemical signals, nuptial gifts and mate guarding.

Mating strategies and behaviour

Mating strategies in the Diptera are highly varied and often complex. The Sepsidae (see Chapter 79) (Fig. 19), for example, use elaborately modified fore femora and complex behaviour to facilitate successful copulations (Tan *et al*. 2011). Mate guarding occurs in several families, mostly of higher Brachycera, although it is also observed in some Limoniidae (see Chapter 14). Males of *Antocha* (*Orimargula*), for example, embed their claspers in the female's abdomen (Young 1994) (Fig. 20), presumably to prevent other males from copulating and some, including *Hovamyia apicistyla* Alexander (Fig. 21), apparently reach the same end by remaining *in copula* for long periods. Males of mate-guarding Limoniidae often use their long legs to straddle the guarded females (Adler & Adler 1991) and similar behaviour is well documented in long-legged Brachycera, such as Neriidae (see Chapter 63) (Mangan 1979) and Mormotomyiidae (see Chapter 101) (Copeland *et al*. 2014).

Many flies form mating swarms, usually made up all or mostly of males, exhibiting characteristic sexually dimorphic characters associated with the swarming habit. Swarming males often have expanded or plumed antennae and almost all have enlarged eyes that meet over the top of the head, presumably to efficiently spot females that fly into the swarms. Swarming is characteristic of several families of lower Diptera and a few families of Brachycera, but is best known in the Chironomidae (see Chapter 35) and Chaoboridae (see Chapter 30), in which males frequently form enormous and conspicuous aggregations. Vast swarms of Afrotropical *Chaoborus* Lichtenstein, known as "lake flies", can be dense enough to be harvested as food ("*kungu* cakes") and even pose a health hazard to

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 1. Introductory chapters and keys to Diptera families. *Suricata* 4. South African National Biodiversity Institute, Pretoria; pp. 135–152.

fishermen engulfed in suffocating swarms. Males of several mosquito species (Culicidae; see Chapter 31) form large swarms, often over a stationary marker, such as a dark rock or tree branch tip and sometimes high in the forest canopy. For sympatric species, these swarm markers differ between different species, providing spatial separation of the species. Corbet & Haddow (1962) report observing swarms of male mosquitoes and male Tabanidae from a 120 m tower projecting above

Figs 4.1–6. Examples of anthophily in Diptera (all South Africa): (1) long-tongued *Bombylella* sp. (Bombyliidae) feeding on nectar in flight; (2) copulating pair of long-tongued *Psilodera hessei* Schlinger (Acroceridae) nectar-feeding at rest; (3) pollen-feeding *Neomyia* sp. (Muscidae); (4) same, *Eupeodes* sp. (Syrphidae); (5) copulating pair of *Rhigioglossa* (*Rhigioglossa*) *nitens* Chainey in inflorescence (Tabanidae); (6) nectar-feeding *Simulium* sp. (Simuliidae) on *Euphorbia* flower. Photographs © S.A. Marshall.

the forest canopy at Zika, Uganda; the tabanids swarmed only at dawn, the mosquitoes only at dusk.

Swarming behaviour is by no means restricted to lower flies. Some Syrphidae (see Chapter 60), especially the subfamily Eristalinae, swarm around the margins of tree canopies in southern Africa and swarming also occurs in some Afrotropical Rhiniidae (see Chapter 115). Both sexes of the rhiniid *Stomorhina cribrata* (Bigot) commonly form small swarms of about 10 individuals, in direct sunlight usually just above head height and *Stegosoma vinculatum* Loew have been observed swarming before dawn, one metre from the ground beneath savanna trees in Namibia (Kurahashi & Kirk-Spriggs 2006). Some flies have strikingly silver abdomens that reflect sunlight during swarming and presumably act as mate attractants. These include the milichiid genera *Milichia* Meigen (*sensu lato*), *Milichiella* Giglio-Tos and *Pholeomyia* Bilimek that form swarms visible from long distances and the stratiomyid genus *Platyna* Wiedemann that forms small swarms in forest sun spots.

Mating behaviour in some groups of flies involves the exchange of oral exudates (trophallaxis). Freidberg (1981, 1982) discussed trophallaxis in the tephritid species *Schistopterum moebiusi* Becker and *Spathulina sicula* Rondani (as *S. tristis*). Males of *S. moebiusi* secrete material from the labella onto a leaf of the host-plant prior to copulation; the female then feeds on the material and allows the male to mount and copulate with her. Mating pairs of *S. sicula* practice post-mating trophallaxis; after the male dismounts, the mates join their probosces and a milky fluid is transferred directly from male to female. This last behaviour is assumed to offer these flies selective advantages, such as an increase in egg production (Freidberg 1982). Similar behaviour occurs in other acalyptrate families, including the Asteiidae (see Chapter 92), Ephydridae (see Chapter 100), Micropezidae (see Chapter 62), Platystomatidae (see Chapter 70) and Ulidiidae (see Chapter 69).

Some acalyptrates establish leks where males defend mating territories, typically arenas distinct from oviposition or feeding sites. This behaviour is common in the Clusiidae (see Chapter 81) and in some Piophilidae (see Chapter 68) (Fig. 22). Courtship displays involving strikingly patterned wings occur in several acalyptrate families, such as the Chloropidae (Siphonellopsinae) (see Chapter 96), Platystomatidae, Sepsidae, Tephritidae (see Chapter 71) and Ulidiidae. These species often display on or in the vicinity of the larval breeding medium. Some calyptrate groups, such as the genus *Sarcophaga* Meigen (Sarcophagidae; see Chapter 116), also locate mates in the vicinity of the larval breeding medium and can be found *in copula* on surrounding vegetation or on the ground (Fig. 24). Others, especially Tachinidae (see Chapter 118) (Fig. 23), but also many Sarcophagidae and other Calyptratae, as well as Conopidae, Pipunculidae, Tabanidae and scattered genera in several other families frequent hilltops in search of mates. Rare species and species with mobile larval food sources (for example parasitoids) are most likely to exhibit hilltopping behaviour.

Eggs, oviposition and larvipary

Diptera normally lay eggs in or near larval habitats. Many chironomids, for example, lay strings of eggs over or near larval habitat and several tipulids have sharp ovipositors for injecting eggs into wood or soil. The most common oviposition strategy in the higher flies is to insert a soft, telescoping abdominal tip into a substrate to embed eggs (e.g., Figs 25–27), but exceptions abound. Aquatic Diptera often deposit strings or masses of eggs and many groups of lower Brachycera oviposit on materials overhanging larval substrates. Athericidae (see Chapter 38), for example, lay exposed communal egg clusters, where adult females (and in some Afrotropical species males) remain to guard these following oviposition (Fig. 28). Although adult flies lack the appendicular ovipositor that occurs in females of many other insect orders, the terminal abdominal segments of many groups are modified for penetrating hosts or other substrates. Fruit flies (Tephritidae) (Fig. 27) and leaf-mining flies (Agromyzidae; see Chapter 86), for example, are among several families with a stiff oviscape used to penetrate plant material or to house structures (piercer, aculeus) that serve to insert eggs into host-plants. Many parasitic flies have stout piercers for injecting eggs into their hosts (*e.g.*, Pyrgotidae; see Chapter 72) (Fig. 39), while others, including Apioceridae (see Chapter 46), Scenopinidae (see Chapter 50) and Mydidae (see Chapter 47) in the lower Brachycera, possess acanthophorite spines to assist in oviposition in soil and sand. A similar function is served by the pseudacanthophorites (spine-bearing cerci) found in some acalyptrate families, including Curtonotidae (see Chapter 103) (Fig. 53) and tethinine Canacidae (see Chapter 94) (Fig. 50, inset). Many Bombyliidae (see Chapter 45) (*e.g.*, Fig. 1) use movements of the acanthophorite spines at the tip of the abdomen to collect fine sand grains into a sand chamber on the abdomen, where the eggs are given a protective coating of sand prior to deposition.

Parasitic flies in the family Tachinidae (Figs 23, 36) exhibit a diversity of oviposition strategies, with some species laying large eggs externally on the host, some inserting eggs into the host, some producing enormous numbers of microtype eggs to be ingested by potential hosts and others producing larvae adapted to locating hosts. Some fly eggs undergo long dormancy periods prior to hatching, *e.g.*, *Katacamilla* Papp (Camillidae; see Chapter 102) (Kirk-Spriggs *et al*. 2002), others hatch immediately upon release.

Ovovivipary, in which eggs hatch in the oviduct (uterus) prior to deposition and viviparity, in which the external egg stage is abbreviated to the point that it is essentially bypassed, are common in the Diptera (see Meier *et al*. 1999, for thorough review of the subject). Some important Afrotropical lineages (Glossinidae; see Chapter 108 and Hippoboscidae; see Chapter 109) (Figs 29, 30) carry this to the extreme, hatching a single egg at a time internally and ultimately depositing a prepupa that puppariates immediately (pseudo-placental viviparity). Larvipary no doubt developed independently several times in the Diptera and is common in a number of families of Calyptratae. Most Sarcophagidae (*e.g.*, Figs 16, 24) are multilarviparous, with several first-instar larvae being deposited simultaneously. Macrolarviparous species, in which larval development partly takes place in the oviduct and a single larva is deposited, are found in several families, including Anthomyiidae (see Chapter 111) (*e.g.*, Fig. 26) and Calliphoridae (see Chapter 114) (*e.g.*, Figs 32, 51, 52) in the Afrotropics.

Larvae

Virtually all lower Diptera have four larval instars (exceptions being some Simuliidae and Thaumaleidae) and all higher Diptera have three. In general, most of a fly's life is spent in the larval stage, with short egg, pupal and adult stages prevailing. Larvae are legless and usually pale and soft-bodied although a few, such as some Cecidomyiidae (see Chapter 22), Chamaemyiidae (see Chapter 76) and Syrphidae (Fig. 4), are relatively colourful exposed predators. Most fly larvae develop immersed in moist to wet organic matter ranging from decomposing plant material through to the bodies of living and dead animals. Relatively few, such as the predaceous Mydidae and Therevidae (see Chapter 49) that hunt in desert soils, occur in drier environments. Larvae of many fly species are parasitoids or predators and many others develop in the tissues of living plants and fungi. Most Diptera larvae, however, are saprophagous on an astonishing diversity of decomposing organic material and associated microbes.

Natural history – specific habits and habitats

Specific examples of specialised dipteran natural histories can be found in every family chapter included in this *Manual*, so only a brief general overview is provided here, with an emphasis on those habits that have particular relevance to the Afrotropical Diptera fauna. Species of agricultural, veterinary and medical significance, including blood-feeding disease vectors and species that cause myiasis (the infestation of live humans and/or other animals) are discussed in Chapters 5–7. Other published general reviews of the natural history of flies include those of Brown *et al*. (2009), Courtney *et al*. (2009), Marshall (2012), Oldroyd (1966) and Skevington & Dang (2002).

Figs 4.7–10. Examples of aquatic Diptera larvae: (7a) larva of *Afrothaumalea stuckenbergi* Sinclair (Thaumaleidae) in cliff-side seepage (South Africa); (7b) same adult; (8) undetermined Blephariceridae larva (centre left) and *Simulium* sp. (Simuliidae) larvae on rock in fast-flowing stream (non-Afrotropical); (9) predatory larva of undetermined Athericidae species (South Africa); (10) *Culex territans* Walker (Culicidae) pupa (above) and larva (below) in stagnant waters (non-Afrotropical). Fig. 7 (Sinclair 2015, figs 1, 4). Photographs © S.A. Marshall.

Flies and flowers

The most conspicuous and charismatic of flies are probably those that frequent flowers, where many taxa ingest sugar-rich nectar to enable their metabolically costly flight (*e.g.*, Figs 1, 2). Some flies also consume pollen and some visit flowers in search of hosts or mates (*e.g.*, Fig. 5). Several Afrotropical flies have developed intricate associations with their hosts and the resultant co-evolution of plants and pollinators has resulted in a high degree of specialisation, such as that exhibited by long-tongued flies and sympatric flowers with long corollas (*e.g.*, Fig. 1). The most spectacular of these are long-tongued pollinators in the families Acroceridae (see Chapter 42) (Fig. 2), Nemestrinidae (see Chapter 43) and Tabanidae (see Chapter 39), in which the rostrum is often considerably longer than the body. *Moegistorhynchus longirostris* Wiedemann (Chapter 10, fig. 2), a South African nemestrinid with the longest proboscis relative to body size of all known insects, is a keystone species as an obligate pollinator for a guild of long-tubed flowers in the families Geraniaceae, Iridaceae and Orchidaceae (Barraclough & Slotow 2010) (see Chapters 10, 43). Similar associations occur between *Prosoeca* Schiner (Nemestrinidae) and *Philoliche* Wiedemann (Tabanidae) and long-tubed South African flowers. Kirk-Spriggs & Stuckenberg (2009: 159) note rostrum development in at least four other families of Fynbos-inhabiting flies, including *Arthroteles* Bezzi (Rhagionidae; see Chapter 37), *Peringueyomyina barnardi* Alexander (Tanyderidae; see Chapter 15), *Rhynchoheterotricha stuckenbergae* Freeman (Sciaroidea, unassigned to family; see Chapter 23) and *Forcipomyia* (*Rhinohelea* de Meillon & Wirth) (Ceratopogonidae). Rostrum development for nectivory is also apparent in the Lygistorrhinidae (see Chapter 19) and some Vermileonidae (see Chapter 36), among others.

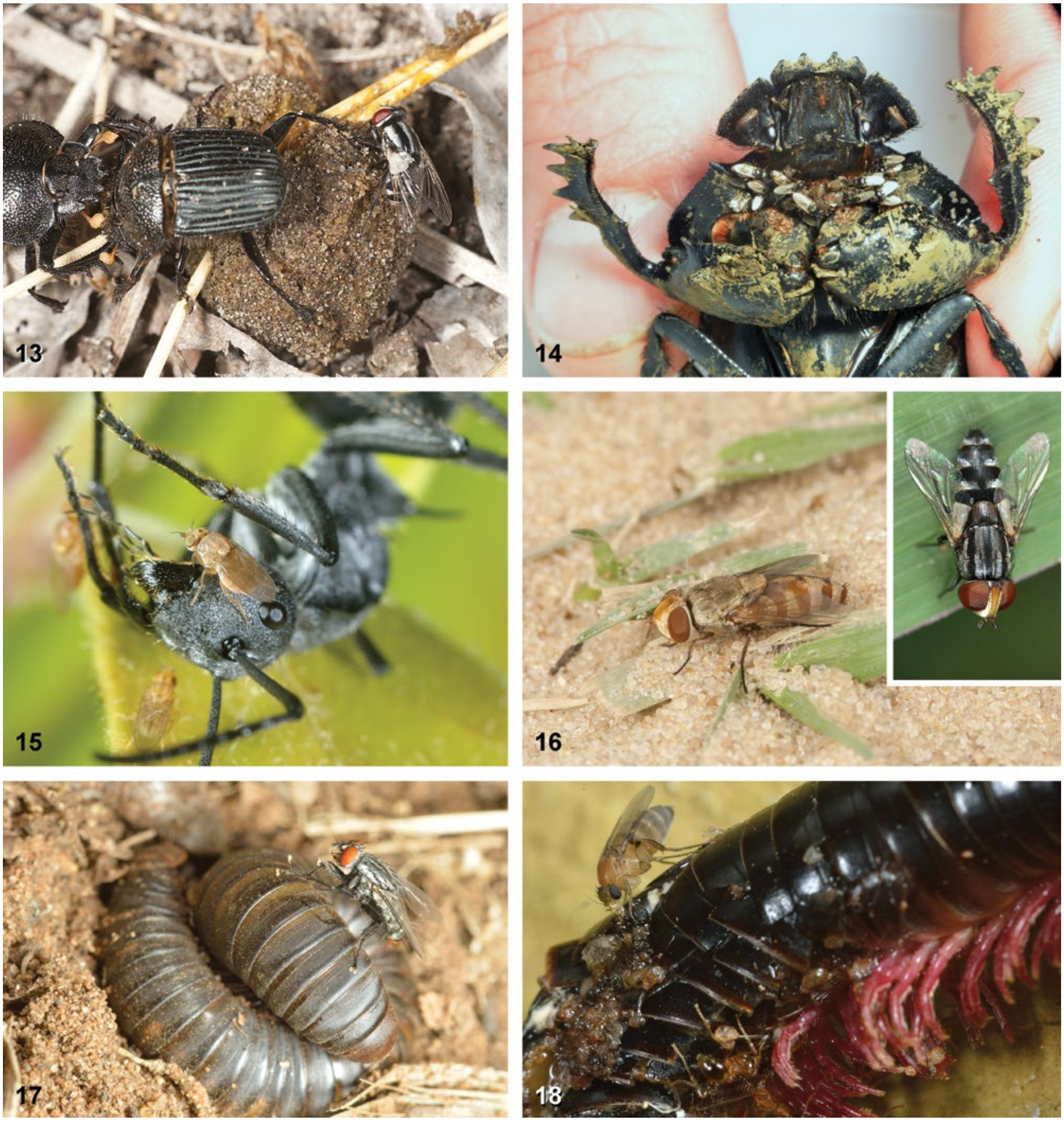
Flowers of stapeliads (Apocynaceae), emit olfactory stimuli, imitating dung or decaying organic matter. Calyptrate flies constitute the most important group pollinating these plants, with females sometimes ovipositing directly into flowers (see Meve & Liede 1994 for review). Several aroids (Araceae) have a similar relationship with flies, such as drosophilids and sphaerocerids, attracted by odours that emulate dung or decomposing fruit (see Gibernau 2003, for review).

Less conspicuous, but perhaps more important, are the critical pollination services provided to a wide range of economically important plants. Cacao, for example, is pollinated in Africa exclusively by minute species of the biting midge genus *Forcipomyia* Meigen (Ceratopogonidae; see Chapter 34) (*e.g.*, Posnette 1950; Winder & Silva 1972), and flower flies (Syrphidae) (*e.g.*, Fig. 4) are major pollinators of a wide variety of crops (Rader *et al*. 2016). Other flies (*e.g.*, Calliphoridae and Rhiniidae) are also important pollinators of crops in Africa, especially subtropical fruits, including mango (*e.g.*, Nurul Huda *et al*. 2015).

Mimicry

Many higher flies, especially those that visit flowers, resemble better-defended stinging Hymenoptera that frequent the same habitats. Syrphidae are among the most abundant and best-known Batesian mimics of aculeate Hymenoptera (*e.g.*, Gilbert 2005; Golding *et al*. 2001) and the Afrotropical fauna includes syrphid mimics of honey bees (*Apis* L.), carpenter bees (*Xylocopa* Latreille) and a diversity of wasps. The flower flies *Eristalis tenax* (L.) and superficially similar species of *Eristalinus* Rondani (Fig. 41), for example, look and sound like honey bees and some *Ceriana* Rafinesque species bear a striking similarity to eumenine wasps. Other flower-visiting bee and wasp mimics occur in the families Bombyliidae, Conopidae (see Chapter 66), Nemestrinidae, Stratiomyidae and Tabanidae. Several non-anthophilous Diptera, especially the Asilidae (see Chapter 48) genera *Hyperechia* Schiner (Fig. 43), *Laxenecera* Macquart and *Proagonistes* Loew and the Oestridae (see Chapter 119) genera *Gasterophilus* Leach and *Gyrostigma* Hope (Fig. 42), also include strikingly bee-like, or wasp-like species. Apparent ant mimicry occurs in several acalyptrates, including most Sepsidae (see Chapter 79) (Fig. 19), some Ephydridae

Figs 4.11–12. Examples of decomposition by Diptera: (11a) writhing mass of undetermined Calliphoridae larvae on corpse (non-Afrotropical); (11b) adult *Chrysomya* sp. (Calliphoridae) gathering near carcass (Namibia); (2) pooting Piophilidae from a putrefying pachyderm during later stages of decomposition (Namibia). Photographs © S.A. Marshall.



Figs 4.13–18. Examples of kleptoparasitism and predation in Diptera: (13) *Musca albina* Wiedemann (Muscidae) ovipositing in dung ball being buried by the dung beetle *Scarabaeus damarensis* Janssens (Scarabaeidae) (Namibia); (14) *Ceroptera* sp. (Sphaeroceridae) kleptoparasitic on the elephant dung beetle *Pachylomera femoralis* Kirby (Scarabaeidae) (Namibia); (15) *Conioscinella* sp. (Chloropidae), attracted to an ant being consumed by a jumping spider; (16) *Craticulina* sp. (Namibia) and *Miltogramma* sp. (South Africa) (inset); Miltogramminae (Sarcophagidae), kleptoparasitic on the prey of aculeate wasps; (17) *Sarcophaga* sp. (Sarcophagidae) predaceous on a dying myriapod (South Africa); (18) same, *Megaselia* sp. (Phoridae) (South Africa). Fig. 13 (Marshall & Pont 2012, fig. 4). Photographs © S.A. Marshall.

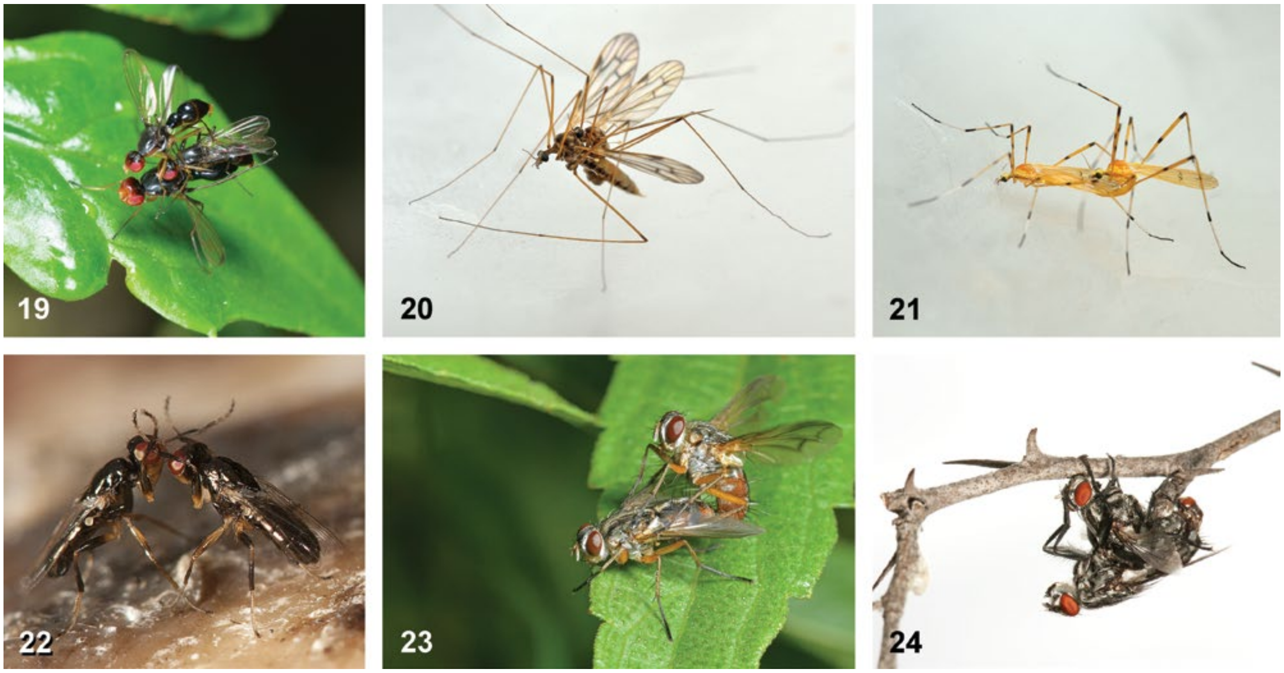
(*Rhynchopsilopa* Hendel), some Anthomyzidae (*Apterosepsis* Richards; see Chapter 87) and some Chloropidae (*Alombus* Becker, *Anatrichus* Loew, *Mimosepsis* Sabrosky and *Myrmecosepsis* Kertész). Some, such as the long-legged Afrotropical Micropezidae, apparently mimic ichneumonoid wasps in colour, shape and behaviour. While less obviously adaptive than mimicry of stinging Hymenoptera, apparent mimicry of beetles is found in a number of acalyptrate families, especially the Celyphidae (beetle flies; see Chapter 75), but also in some other acalyptrates. Chloropidae in the genus *Nomba* Walker, for example, have the scutellum greatly enlarged and superficially similar to beetle elytra. A few species of Lauxaniidae (see Chapter 74), Tephritidae, Platystomatidae and Chloropidae fold their wings tightly against their bodies to create a strikingly beetle-like appearance.

Phytophagous Diptera

Although most adult flies observed on flowering plants are beneficial pollinators rather than plant pests, larvae of numerous fly families across the entire order cause plant tissue damage by leaf-mining, stem-boring, root-feeding, or gall-forming. Fly species that induce galls (specialised plant structures that house the galling insect) mostly occur in the families Agromyzidae (see Chapter 5, fig. 9), Anthomyiidae (*e.g.*, Fig. 26), Cecidomyiidae (see Chapter 22, figs 43–50) and Tephritidae (*e.g.*, Fig. 27). The two last-named families also include a wide range of non-galling species that feed on living and dead plant tissue (see Chapters 5, 8 and 71).

Aquatic Diptera

The vast majority of individual aquatic insects and well over half of all aquatic species belong to the order Diptera. Aquatic or semi-aquatic larvae exhibit a high degree of resource partitioning, with many restricted to specific habitats and microhabitats, such as submerged wood or the leaves of aquatic plants. Most specialised aquatic species are in the large families Ceratopogonidae and Chironomidae, but several Diptera families are entirely or mostly aquatic and many more include some aquatic species. Entirely aquatic families, most of which are early lineages of lower Diptera, occur not only in familiar habitats, such as rivers and ponds, but also in the full spectrum of extreme aquatic and semi-aquatic habitats. Madicolous habitats (seepages), for example, support several fly taxa including an abundance and diversity of Chironomidae as well as the highly specialised family Thaumaleidae (see Chapter 33) (Fig. 7b). Thaumaleid larvae (Fig. 7a) have open dorsal spiracles and thrive in thin films of water, where they can graze on diatoms while keeping the spiracles open to the surface. Co-occurring Chironomidae, by contrast, have an apneustic respiratory system and lack open spiracles.



Figs 4.19–24. Examples of mating behaviour in Diptera: (19) two males of *Adriapontia* sp. (Sepsidae) using elaborately modified fore femora and a complex behaviour to facilitate successful copulation (South Africa); (20) male of *Antocha* (*Orimargula*) sp. (Limoniidae) claspers imbedded deeply in the sides of the female's abdomen for mate guarding (Madagascar); (21) mating pair of *Hovamyia apicistyla* Alexander (Limoniidae) exhibiting prolonged copulation, probably a manifestation of mate guarding (Madagascar); (22) males of *Piophila casei* (L.) (Piophilidae) engaging in agonistic behaviour defending territories on a dead elephant (Namibia); (23) *Nemoraea* sp. (Tachinidae) *in copula* (Tachinidae frequently seek mates at hill top sites, where mating pairs are most likely to be seen); (24) *Sarcophaga* sp. mating (Sarcophagidae often seek mates near oviposition sites and are frequently seen *in copula* near larval habitats). Photographs © S.A. Marshall.

Aquatic habitats range from swift to stagnant waters, with specialised Diptera dominating from extreme to extreme. The most torrential of flowing waters, for example, support the specialised torrenticolous family Blephariceridae (see Chapter 16) (Fig. 8) and some species of the strictly lotic family Simuliidae (see Chapter 32) (Fig. 8), while stagnant waters of various sorts support a broader range of Diptera families, including Chironomidae, Culicidae (Fig. 10), Ceratopogonidae, Chaoboridae and others. The Culicidae, a group entirely associated with stagnant waters, is the most medically important of all insect families. The Simuliidae (Figs 6, 8), a family found only in flowing waters, is the second most important. Most other biting flies, including the Tabanidae, are also aquatic or semi-aquatic in the larval stages and many, such as the Athericidae (Fig. 9) are common predators in streams. The enormous importance of understanding the biology of disease vectors, most of which are aquatic Diptera, renders the study of aquatic flies a particularly important aspect of dipterology. This is especially true in the Afrotropical Region, where mosquito-borne, black fly-borne, biting midge-borne, sand fly-borne and *tseste*-borne diseases are among the most important socio-economic problems.

Diptera and decomposing material

Many (probably most) fly species develop within non-living organic matter, such as dead woody or herbaceous plant material, decaying fungi, dead animals or dung. Such material is often very rich in bacteria and other micro-organisms and many Diptera larvae feed, at least in part, by filtering out and ingesting micro-organisms. Bibionomorpha are generally associated with fungi. Early lineages of Cecidomyiidae, for example, are fungal-feeders and even the gall-forming lineages of this family often inoculate host-plants with fungal spores that the larvae feed upon inside the gall. Dung and carrion, among the most ubiquitous of resources, are dominated by the larvae of higher Diptera (maggots), many of which have pharyngeal filters to facilitate microbial grazing and many of which are at least facultatively

Figs 4.25–28. Examples of oviposition and egg masses in Diptera: (25) *Pegesimallus* sp. (Asilidae) inserting eggs into soil (South Africa); (26) *Anthomyia* sp. (Anthomyiidae) ovipositing into faeces (South Africa); (27) *Ceratitis* (*Ceratalaspis*) *cosyra* (Walker) (Tephritidae) inserting eggs into mango fruit (Namibia); (28) Athericidae adults (undescribed species) with communal egg masses deposited in clusters over larval habitat (South Africa). Photographs © S.A. Marshall.

Figs 4.29–34. Examples of parasitism in Diptera: (29) *Glossina austeni* Newstead (Glossinidae) feeding on human (South Africa); (30) *Hippobosca rufipes* von Olfers (Hippoboscidae) on domestic ox (Namibia); (31) *Meloehelea* sp. (Ceratopogonidae) imbibing cantharidin-laced hemolymph from a blister beetle (*Meloe hottentotus* Péringuey) (South Africa); (32) *Cordylobia anthropophaga* (Blanchard & Bérenger-Féraud) (Calliphoridae), known as the *Tumbu* fly or Putzi fly, which includes humans among its hosts (Namibia); (33) *Cobboldia loxodontis* Brauer (Oestridae) lays eggs near the mouth or base of elephant's trunks, larvae are internal parasites (Namibia); (34) *Hydrotaea* sp. (Muscidae) lapping up secretions around a monitor lizard's eye (South Africa). Photographs © S.A. Marshall.

predaceous during part of their development. Adults of many fly families are attracted to decomposing organic matter and several families occur on animal dung. Some of the adult flies attracted to decomposition routinely pick up pathogenic micro-organisms and move them from filth to food. Calliphoridae and Muscidae (see Chapter 113), especially *Musca* L. species, with such habits are serious pests responsible for the transmission of many enteric diseases (see Chapters 5, 113 & 114). Calliphoridae associated with decomposing vertebrate carrion can also be a disease hazard (see Chapter 5), but provide a critical clean-up service by breaking down carrion (*e.g*., Figs 11, 12). The same species are routinely used by forensic entomologists to infer time and place of death and thus can be useful in criminal and other investigations (see Chapter 7).

Diptera as predators and parasitoids

Predaceous adults occur across the order, although they are relatively uncommon in the lower Diptera (found in some Blephariceridae, Ceratopogonidae, Chironomidae and possibly Tanyderidae). Most predaceous adult Diptera are in the lower Brachycera (Asilidae) and Empidoidea, with adult predation universal in the former group and the rule in the latter group. Predaceous adults are less common in the Cyclorrhapha, although they appear in a few Phoridae and some acalyptrate families (Ephydridae, Micropezidae) and characterise major lineages of Muscidae, Scathophagidae and Calliphoridae. Species of *Bengalia* Robineau-Desvoidy (Calliphoridae: Bengaliinae), for example, appear to be specialised predators of social insects (ants and termites) (Sivinski *et al*. 1999). Another interesting example of ant predation in the Diptera is exhibited by the peculiar Old World genus *Rhynchopsilopa* Hendel (Ephydridae), which has been observed mounting the abdomens of ants (*Crematogaster* Lund) and using a long proboscis to penetrate and feed within the ant's abdomen (Freidberg & Mathis 1984; similar behaviour is found in some Neotropical Phoridae). These flies probably use their modified porrect antennae to locate ants' nests and trails by sensing pheromones produced by their hosts and they may be abundant when high densities of ants occur.

Predaceous larvae occur throughout the order, with predation apparently the groundplan state for the Brachycera and remaining the rule throughout the lower Brachycera and Empidoidea. Larvae in these groups are mostly subterranean, aquatic or semi-aquatic predators that hunt prey within the substrate. Relatively few groups of Diptera have exposed predaceous larvae, but conspicuous aphid-feeding larvae occur in some lower Diptera (Cecidomyiidae), lower Cyclorrhapha (Syrphidae: Syrphinae) and Cyclorrhapha (Chamaemyiidae). Larvae of many species, especially in the Calyptratae, are facultatively predaceous. Muscidae, for example, often shift from saprophagy to predation in later instars.

In some families predation is internal, *i.e*., the newly hatched larva penetrates its host and consumes it from the inside. The line between predation, in which multiple prey are consumed and parasitoidism, in which only a single host is consumed, can be a blurry one, but it is unequivocally crossed in several lineages of both the lower Brachycera and in Cyclorrhapha.

Parasitoid larvae that develop in or on a single host, killing the host in the process, appear in several distantly related fly lineages. Larvae of the lower brachyceran family Acroceridae (Fig. 2), for example, are all internal parasitoids of spiders (Araneae) and mites (Acari) and known larvae of the lower cyclorrhaphan ("Aschiza") family Pipunculidae (see Chapter 61) are almost all parasitoids of auchenorrhynchous Hemiptera (the only known exception, the Holarctic genus *Nephrocerus* Zetterstedt is a parasitoid of Tipulidae). One of the largest fly families, the Tachinidae (Fig. 36), is made up entirely of endoparasitoids, mostly of insects, but also of other, closely related arthropods. Other fly families made up entirely of parasitoids include Nemestrinidae (nymphs and adults of Orthoptera, scarabaeid beetle larvae and Mantodea), Rhinophoridae (see Chapter 117, terrestrial Isopoda), Conopidae (aculeate Hymenoptera and Orthoptera), Cryptochetidae (see Chapter 107; monophlebine scale insects in the family Margarodidae) and Pyrgotidae (*e.g*., Fig. 39; adult scarabaeid beetles). A few other acalyptrate families, such as the Sciomyzidae (see Chapter 78), include some parasitoids and some small acalyptrate families and subfamilies with little-known biologies (such as the Ctenostylidae (see Chapter 73), non-Afrotropical Phaeomyiidae and the tephritid subfamily Tachiniscinae) may yet turn out to be made up entirely of parasitoids. Parasitoidism has also evolved independently in subgroups of further families in the lower Cyclorrhapha and Calyptratae. The vast family Phoridae (see Chapter 59) (*e.g*., Fig. 18), for example, exhibits a wide range of parasitoid strategies and includes parasitoids of a great diversity of hosts (see Disney 1994; Feener & Brown 1997). Parasitoidism is also common in the calyptrate families Calliphoridae (several genera) and Sarcophagidae (the genus *Blaesoxipha* Loew).

Parasitism and kleptoparasitism

Parasitism, in which hosts are partially consumed, but not killed, is common amongst adult Diptera across the order. In addition to the well-known families of lower Diptera with adults that feed on the blood of a range of vertebrates including humans, specialised lineages of lower Diptera have adults that feed only on amphibian (frog) blood (Corethrellidae; see Chapter 29), or on hemolymph of particular groups of invertebrate hosts (some Ceratopogonidae) (Fig. 31). Blood-feeding in lower Brachycera is best known in the Tabanidae, but also occurs in some Athericidae (Fig. 28) and Rhagionidae. Parasitic Cyclorrhapha are best known for blood-feeding Muscidae, such as *Haematobia* Le Peletier & Serville, *Haematobosca* Bezzi and *Stomoxys* Geoffroy, but parasitic adult higher flies are also found in the related calyptrate families Hippoboscidae (louse flies and bat flies) (Fig. 30) and Glossinidae (*tsetse*) (Fig. 29), both of which lack free-living larvae and feed only as parasitic adults.

Some Diptera also feed on lachrymal secretions and other body fluids of various animals, including humans, and are of medical or veterinary significance. These include *Hydrotaea* Robineau-Desvoidy (Muscidae) that feed at the eyes of various wild and domesticated animals, including lizards (Fig. 34) (*e.g*., Dusbábek *et al*. 1982). The "eye flies" *Siphunculina* Rondani (Chloropidae) (Kanmiya 1989; Nartshuk 2001), *Amiota* Loew and *Phortica* Schiner (Drosophilidae) (Máca & Otranto 2014) and *Cryptochetum* Rondani (Cryptochetidae) (Nartshuk 2000: 349) exhibit similar habits.

Figs 4.35–40. Examples of predation and parasitoidism in Diptera: (35) *Bengalia* spp. (Calliphoridae) hovering over ant brood exposed beneath bark (inset above: adult consuming ants' brood; inset below: alighting on driver ant adult) (South Africa); (36) most species of *Catapariprosopa* Villeneuve (Tachinidae: Phasiinae) are parasitoids of true bugs (Hemiptera) (South Africa); (37) *Pegesimallus* sp. (Asilidae) with impaled tiphiid wasp for consumption (South Africa); (38) *Promachus* sp. (Asilidae) feeding upon another asilid (South Africa); (39) *Tephritopyrgota* sp. (Pyrgotidae) attracted to a light at night (Madagascar) (Pyrgotidae are parasitoids on adult scarabaeid beetles); (40) *Xenomyia* sp. (Muscidae) have predaceous adults, seen here preying on aquatic insects in a thin water film (Tanzania). Photographs © S.A. Marshall.

The Afrotropical muscid *Passeromyia heterochaeta* (Villeneuve) is parasitic on birds, with larval habits ranging from scavenging in birds' nests to subcutaneous blood-feeding on nestlings (Pont 1974). Parasitic calliphorids in the Afrotropical Region include *Auchmeromyia* Brauer & Bergenstamm (*e.g.*, Fig. 51) and *Pachychoeromyia* Peris (Fig. 52), larvae of which are obligatory blood-sucking parasites of mammals. The Congo floor maggot, *Auchmeromyia senegalensis* (Macquart), for example, commonly occurs in traditional dwellings in Africa, where its larvae feed on sleeping humans. First-instar larvae of the *Tumbu* fly, *Cordylobia anthropophaga* (Blanchard & Bérenger-Féraud) (Fig. 32)), induce boils (or *tumbu*) beneath the skin of small and large mammalian hosts, including humans (see Kurahashi & Kirk-Spriggs 2006 for review). Larvae of the related highly diverse calyptrate family Oestridae (Figs 33, 42), an important group centred in the Afrotropics, are all obligate internal parasites, developing beneath the skin, in the gut, or in the nasal cavities of mammalian hosts. The African Oestridae include several large endemic species of which the most impressive is *Gyrostigma rhinocerontis* Owen (Fig. 42), a huge fly (body length *ca* 3 cm, excluding appendages), with larvae that occur in the gut of rhinoceroses (see Zumpt 1965 for a review of Oestridae and other myiasis-producing flies).

A kleptoparasite is an animal that takes prey or other food that has been caught, collected, or otherwise prepared by another animal. Kleptoparasitism is not uncommon in the Diptera (see Sivinski *et al*. 1999 and references therein) and is probably best known in the subfamily Miltogramminae (Fig. 16) of the Sarcophagidae (*e.g.*, Greathead 1963; Nesbitt 1976; Pape 1996: 10–12; Spofford & Kurczewski 1990, 1992). These flies, which exhibit various kleptoparasite strategies, are especially common in sandy areas where there is an abundance of hosts. The common name "satellite fly" reflects their common habit of closely following solitary aculeate wasps as they transport paralyzed insect prey (caterpillars, spiders, *etc*.) to nests as provisions for their own developing larvae. The fly may larviposit directly onto the insect prey as it is being carried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Figs 4.41–44. Examples of mimicry in Diptera (all South Africa): (41) *Eristalinus* sp. (Syphidae) and several other Afrotropical Syrphidae genera look and sound like *Apis* L. bees (Apidae); (42) adult rhinoceros bot flies, *Gyrostigma rhinocerontis* Owen (Oestridae), closely resemble and move like pompilid wasps (Hymenoptera); (43) the robust black and yellow-banded *Hyperechia marshalli* Austen (Asilidae) is a mimic of carpenter bees of the genus *Xylocopa* Latreille (Apidae) (Fig. 44). Figs 41, 43, 44 (photographs © S.A. Marshall), Fig. 42 (photograph © S. van Noort (Iziko Museums of South Africa)).

Figs 4.45–50. Examples of specialised habits in Diptera: (45) tarry mass on ceiling of rock shelter, formed by thousands of aggregating adult *Apotropina gregalis* (Lamb) (Chloropidae) (South Africa) (inset); (46) Cecidomyiidae routinely rest on spiders' webs, perhaps as a refuge from attack by other predators (Tanzania); (47) phlebotomine Psychodidae (inset) are associated with leaf bases and several of these were exposed by peeling leaf bases from this Traveller's palm (Madagascar); (48) larvae of Vermileonidae, known as wormlions (inset), construct conical prey capture pits in open dust or fine sand sheltered by rock overhangs (Madagascar); (49) *Wandolleckia achatinae* Cook (Phoridae), which has apterous females (inset), is phoretic on giant African land snails of the genus *Achatina* Lamarck (Tanzania); (50) some families of flies, such as the Canacidae (inset), occur almost exclusively in association with marine algae in intertidal or supra-littoral zones (South Africa). Photographs © S.A. Marshall.

by the wasp, or wait until the wasp has completed and provisioned a nest (usually a burrow) before darting in to larviposit in the nest before it is sealed. The developing fly larvae then kill the hymenopterous larvae and feed on the food resource themselves. Other notable examples of kleptoparasitism include some Phoridae and Milichiidae, *e.g.*, *Milichia patrizii* Hennig, which follow columns of ants and termites to steal or feed on prey (see Disney 1994 for review; Wild & Brake 2009). Some kleptoparasitic flies, especially Chloropidae (Fig. 15) and Milichiidae, are associated with particular prey (often chemically defended prey, such as aculeates, Pentatomidae or Staphylinidae) of larger invertebrate predators, such as spiders and Asilidae. The kleptoparasitic flies feed at puncture wounds on the prey.

Several flies are kleptoparasitic on the food sequestered by dung-rolling scarab beetles. *Musca albina* Wiedemann (Muscidae), for example, has been recorded ovipositing in dung balls being buried by the dung beetle *Scarabaeus damarensis* Janssens (Scarabaeidae) (Fig. 13), thus utilising this food resource for larval development (Marshall & Pont 2012). Some Sphaeroceridae, including all species of the genus *Ceroptera* Macquart, are kleptoparasites of dung-rolling scarabaeine beetles, such as the elephant dung beetle *Pachylomera femoralis* Kirby (Fig. 14), in the Afrotropics and elsewhere.

Unusual biologies and specialisations

Flies occur almost everywhere and a complete list of microhabitats occupied by the Diptera is beyond the scope of this chapter. A few selected examples of unusual biologies and habitat specialisations amongst Afrotropical flies are outlined below.

Thick, black films of a tar-like substance covered in thousands of small flies are a fairly common feature in rock shelters in southern Africa (Fig. 45). These mass aggregations are formed by the chloropid fly *Apotropina gregalis* (Lamb) (Fig. 45, inset), and aggregations (which may be seasonal) have also been recorded from human dwellings, usually on the ceilings of out-buildings and verandas. The tar-like exudate of the flies was analysed using GC-MS by Kirk-Spriggs *et al*. (2001*b*), who noted a number of constituent chemicals identified with attractant or pheromone qualities in other Diptera families.

Numerous flies, especially in the small, specialised acalyptrate families Marginidae (see Chapter 82), Neminidae (see Chapter 89) and Periscelididae (Stenomicrinae) (see Chapter 91), are closely associated with partially furled leaves of various plants and some of these presumably breed in the moist material at the base of the furl. Leaf bases of palms are also important micro-habitats for flies (Fig. 47), such as phlebotomine Psychodidae (Fig. 47, inset), which may be common in this narrow micro-habitat, but not found anywhere else in the same locality.

Larvae of the family Vermileonidae, known as wormlions (Fig. 48, inset), are highly habitat restricted and construct conical pits in fine, friable, dusty soils, in caves, rock overhangs and riverbeds (Fig. 48). Larvae flick dust particles to cause their insect prey to fall into the centre of the pit, where they are then enveloped by the larva for consumption.

Several highly specialised Phoridae occur in the Afrotropics. *Wandolleckia achatinae* Cook, for example, has apterous females (Fig. 49, inset) phoretic on the giant African land snails of the genus *Achatina* Lamarck (Fig. 49) and larvae that develop in the host snail's excrement (Baer 1953). Some Phoridae are specifically associated with dead and dying myriapods (Fig. 18), with *Megaselia equitans* Schmitz found on the backs of the large millipede *Archispirostreptus transmarinus* (Schmitz) and *M. audreyae* Disney on large *Pachybolus* O.F. Cook (Disney 1978). *Ritchiephora diplopodae* Disney & Ritchie is also recorded as parasitising millipedes in the Afrotropics (Disney & Ritchie 1997).

Millipede-fly associations can involve other families, including the Sarcophagidae and Sphaeroceridae. Many *Sarcophaga* (Sarcophaginae) develop in dead or dying invertebrates and some are specifically attracted to myriapods (Fig. 17). The Afrotropical sphaerocerid *Acuminiseta pallidicornis* Villeneuve is phoretic on adult millipedes as adults. The flies leave their millipede hosts to oviposit in millipede excrement as it is produced (Disney 1974).

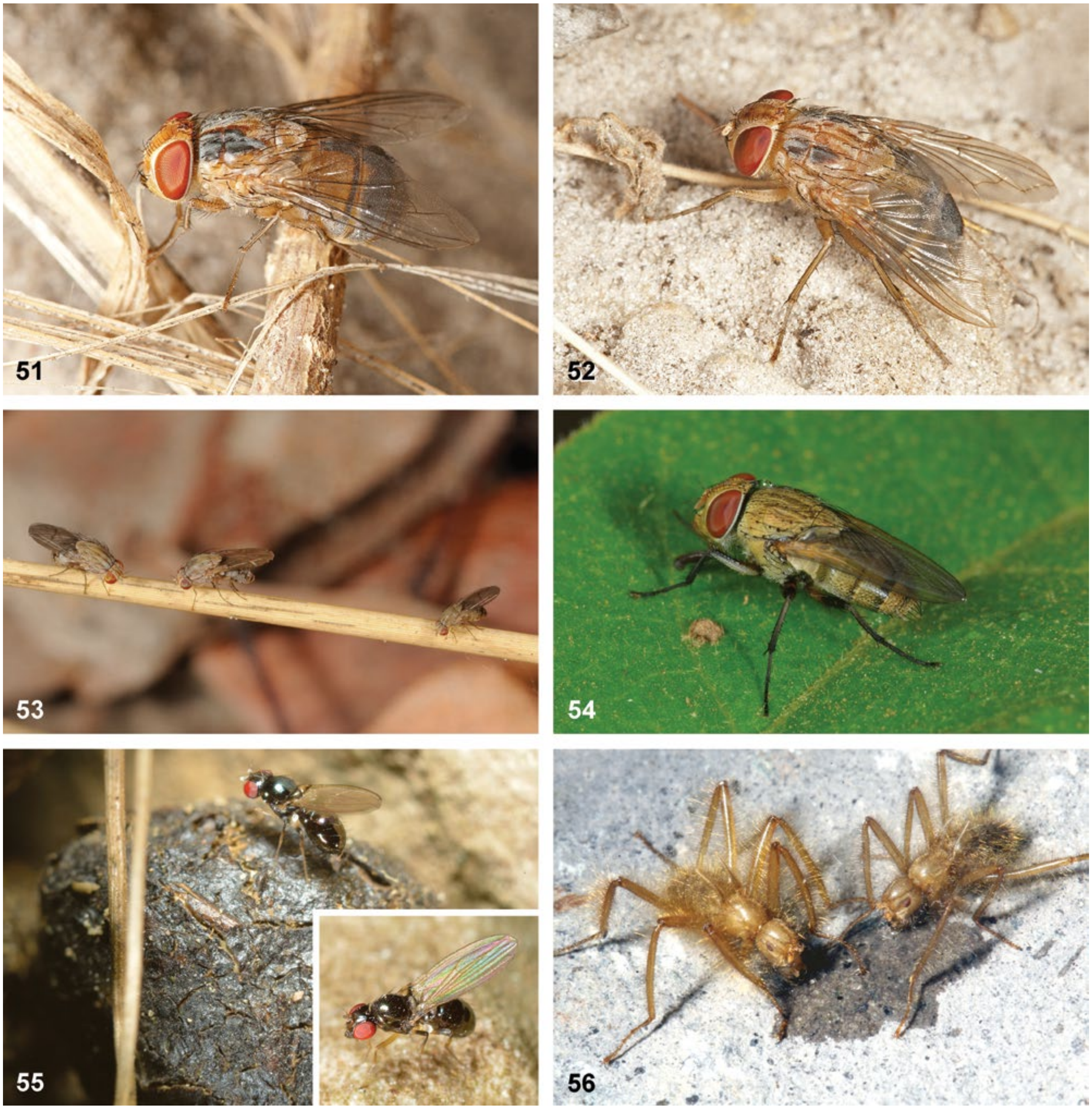
Some families, especially the Canacidae (Fig. 46, inset), Coelopidae (see Chapter 77) and selected genera or species in the families Anthomyiidae, Chironomidae, Dolichopodidae (see Chapter 56), Hybotidae (see Chapter 52), Sarcophagidae, Sphaeroceridae (see Chapter 99), Tabanidae, Therevidae, *etc*., are specifically associated with marine shorelines (Fig. 50) and can be abundant in both supra-littoral and intertidal zones (see Kirk-Spriggs *et al*. 2001*a*, for review).

Adults and larvae of a number of Calliphoridae occur in the burrows of Warthog, *Phacochoerus aethiopicus* (Pallas) (Suidae), Aardvark, *Orycteropus afer* (Pallas) (Orycteropidae) and Aardwolf, *Proteles cristatus* Sparrman (Hyaenidae), in the Afrotropics. These include the genus *Auchmeromyia* (Fig. 51) and the large and conspicuous species *Pachychoeromyia praegrandis* (Austen) (Fig. 52), both of which have larvae that suck the blood of their mammalian hosts by scraping the skin with their mouthhooks. Adults of both sexes may be abundant in and around the burrows of their hosts and larvae of all stages are often numerous in the loose sand of burrows. Adults are nocturnal or crepuscular and are often attracted to fermenting liquids (Kurahashi & Kirk-Spriggs 2006). Such burrows are also frequently used as daytime roosts by other nocturnal or crepuscular flies, including Culicidae, Dolichopodidae and Curtonotidae. At least eight species of the genus *Curtonotum* Macquart (Fig. 53) have been recorded as roosting in burrows in the region, often with more than one species roosting in the same burrow (Kirk-Spriggs & Wiegmann 2013).

Hyraxes, *Procavia* Storr (also known as dassies) inhabit rocky outcrops and overhangs, often in inaccessible areas. These small mammals use communal latrines and the resulting large accumulations of droppings are used as a breeding medium by a number of Diptera families including Camillidae (*e.g*., Fig. 55) and Carnidae (see Chapter 93), although Scatopsidae (see Chapter 26) have also been reared from hyrax droppings (AHK-S, pers. obs.). The camillid *Katacamilla procavia* Barraclough has been reared from hyrax droppings in Namibia and other endemic Afrotropical camillid genera, including *Afrocamilla* Barraclough (Fig. 55), are associated with Rock hyrax droppings (Barraclough 1998). Rock hyrax abodes in xeric

Namibia are also the only known habitat for two Afrotropical species of the psychodid genus *Nemopalpus* Macquart (Stuckenberg 1978), a genus otherwise occurring in afforested areas of the Old and New World tropics (Stuckenberg 1962).

Droppings of other small mammals and birds and their nests are also used as a medium for larval development in some families, such as Chyromyidae (see Chapter 97) and Carnidae, with the carnid *Meoneura prima* (Becker) having



Figs 4.51–56. Examples of specialised habits in Diptera: (51) *Auchmeromyia bequaerti* (Roubaud) (Calliphoridae) larvae inhabit Aardvark burrows and feed on host blood (Namibia); (52) same, *Pachychoeromyia praegrandis* (Austen) (Calliphoridae) (Namibia); (53) *Curtonotum* spp. (Curtonotidae) commonly roost in burrows of small mammals, often sympatrically and in large numbers (Namibia); (54) at least some *Rhyncomya* sp. (Rhiniidae) larvae are associated with termitaria (South Africa); (55) *Afrocamilla* sp. (Camillidae) are associated with rock hyrax abodes (South Africa); (56) *Mormotomyia hirsuta* Austen (Mormotomyiidae) inhabit horizontal rock fissures inhabited by bats (Kenya). Figs 51–55 (photographs © S.A. Marshall), Fig. 56 (photograph © R.S. Copeland (International Centre of Insect Physiology and Ecology)).

been found in association with concentrations of droppings along the permanent runs of the communal Namaqua rock mouse (*Aethomys namaquensis* (A. Smith)) in Namibia (Kirk-Spriggs 2001).

Some genera of termites (Isoptera) construct elaborately aerated termitaria that house millions of termites and often form prominent features of the savanna landscape in the Afrotropics. The associated fungus gardens are occupied by various specialised fly groups and the termites themselves are consumed by some fly species. Larvae of the Calliphoridae genera *Hemigymnochaeta* Corti and *Tricyclea* Wulp, for example, are associated with termites of dry forests and savannas and *H. unicolor* (Bigot) has been reared in numbers from the fruiting bodies of the fungus *Termitomyces schimperi* (Pat.), which grows from termite hills in the rainy season in Namibia (Kurahashi & Kirk-Spriggs 2006). Cuthbertson (1935) reared larvae of *H. varia* (Hough) (as *H. pallens*) from the broken down fungus beds of termites, and adults from Aardvark burrows in termite nests in Zimbabwe. Species of *Tricyclea* are also associated with ants as larvae and have been collected in the food stores of termite mounds and in heaps of rubbish piled up by ants and termites (Ferrar 1987: 87).

Larvae of some (possibly most) Afrotropical genera of Rhiniidae also appear to be associated with termites (*e.g.*, Fig. 54), although not always exclusively so and evidence of such associations is in most cases largely circumstantial, with the habits of some genera entirely unknown. Larvae of at least four Afrotropical genera have some known associations with termites (Kurahashi & Kirk-Spriggs 2006) and some Miltogramminae are also associated with termite nests (see Pape 1996: 11).

Some highly specialised Phoridae, especially the tribe Termitoxeniini, are associated with termites and ants in the Afrotropics. Many species with adult females that inhabit colonies of ants and termites are flightless (*e.g.*, *Aenigmatistes* Shelford, *Thaumatoxena* Breddin & Börner – see Coaton & Sheasby 1972, figs 67A, B), being transported by the winged males to the host colonies during nuptial flights. *Dohrniphora isoptorum* Disney larvae are recorded as parasitising alate termites (*Odototermes*) of both sexes (Disney & Darlington 2000).

Adult biting midges of the family Ceratopogonidae feed on a remarkable range of vertebrate (see Chapter 34, fig. 8) and invertebrate hosts (see Chapter 34, figs 20–25; Fig. 31), sometimes causing irritation or disease in humans and domestic animals. *Culicoides* Latreille, for example, includes vectors of African horse sickness and other pathogens in Africa (see Chapter 5). One of the more interesting Africa-specific biting midge host associations is found in five *Culicoides* (*Avaritia*) species that apparently feed exclusively behind the ears of elephants, where the skin is at its thinnest (Meiswinkel & Braack 1994). The immature stages develop in the dung of elephants.

Some Afrotropical fly taxa are specifically associated with seepages and pools on granitic outcrops, often in xeric areas, in which the larvae develop. The larvae of *Polypedilum* (*Polypedilum*) *vanderplanki* Hinton (Chironomidae) inhabit temporary granite pools and can resist dehydration and drought for 17 years or more (Adams 1983; Hinton 1951, 1960) and immature stages and adults of the monotypic chironomid genus *Afrochlus* Freeman occur in and around granitic outcrop seepages in Zimbabwe. Another genus of Chironomidae, *Archaeochlus* Brundin, is associated with similar seepages, temporary streams and ephemeral riverbed pools in Lesotho, Namibia and the Eastern Cape of South Africa (Cranston & Edward 1998). In the Simuliidae, *Paracnephia* Rubtsov species also usually occur in ephemeral streams on outcrops of ancient geological formations, such as granite outcrops near Harare, Zimbabwe and on granitic inselbergs such as the Brandberg massif in the Namib Desert of Namibia. In the south-western Cape of South Africa, sedimentary deposits of Table Mountain Sandstone and some granitic outcrops where streams only flow intermittently also support several species. Likewise, larvae of *Odontomyia* Meigen (Stratiomyidae) occur in small pools on granite outcrops, with larval development taking a year or more and larvae aestivating in organic detritus in puddle depressions during the dry season (Lachaise & Lindner 1973).

Caves represent an important specialised habitat for Diptera in various families (see Matile 1994; Vandel 1965, for review), but true troglobionts are rare in the Diptera. Guanobious Diptera, with larvae that develop in bat guano, occur in several families, including the Camillidae, Milichiidae, Phoridae, Psychodidae (see Chapter 24) and Sphaeroceridae, but show few phenotypic modifications compared to their non-cavernicolous relatives. *Katacamilla cavernicola* Papp (Camillidae), for example, occurs in both the parietal and troglophilic zones and has been reared from bat and pigeon guano. Eggs remain dormant within guano for extended periods until larval development is apparently triggered by periodic moistening by bat urine or other liquids (Kirk-Spriggs *et al*. 2002). Horizontal rock fissures inhabited by bats are home to the Afrotropical species *Mormotomyia hirsuta* Austen (Mormotomyiidae) (Fig. 56), which is confined to rocky outcrops in Kenya (Copeland *et. al*. 2011, 2014). These remarkable flightless flies have larvae that develop in bat guano.

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AGRICULTURAL AND VETERINARY SIGNIFICANCE OF DIPTERA 5

Keith M. Harris

Introduction

Some of the adverse effects of Diptera on human activities in tropical and southern Africa are attributable to the many species of medical significance (see Chapter 6), but there are also substantial direct impacts on cultivated plants and domesticated animals. These are mostly relevant to agriculture and horticulture, with forestry little affected, but with some important effects on the stored products of agriculture and of inland and coastal fisheries. Relevant families and species are briefly reviewed below, as well as those that are of beneficial importance as pollinators and/or as natural enemies of pest species. This chapter provides an overview and readers are referred to the systematic chapters for each relevant family that contain much additional information.

Research on the most important and widespread groups of dipterous and other pests in sub-Saharan Africa began in the late 19th and early 20th centuries, driven by the priorities of the European colonial powers, especially Britain, France, Portugal, Germany, Belgium and Italy. The British Government provided the basis for studies of pest species with the establishment of the Entomological Research Committee (Tropical Africa) in 1909. This initiative quickly resulted in extensive surveys and research. In 1910 the *Bulletin of Entomological Research* was launched, initially to publish the results of this work, and in 1913 the Imperial Institute of Entomology (later the Commonwealth Institute of Entomology), was founded to provide identifications, information, liaison and other support. Most of the research undertaken over the following three decades was concentrated on biting flies of medical and veterinary importance, especially Glossinidae, Tabanidae, Culicidae and Ceratopogonidae, and involved close collaboration between field workers in Africa and taxonomic specialists based in the British Museum (Natural History) in London (now The Natural History Museum). Prominent among these were Ernest Edward Austen (1867–1938) and Fredrick Wallace Edwards (1888–1940), to whom the *Catalogue of the Diptera of the Afrotropical Region* (Crosskey 1980: [iii]) was dedicated. Similar initiatives were undertaken by other European countries with colonial territories in Africa and, although there was some degree of collaboration,

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 1. Introductory chapters and keys to Diptera families. *Suricata* 4. South African National Biodiversity Institute, Pretoria; pp. 153–161.

research was generally piecemeal and was often driven by national, local and personal interests.

During the second half of the 20th century, scientific studies of dipterous pests in Africa and elsewhere gathered considerable momentum and many international and regional organisations, notably the Food and Agricultural Organization of the United Nations (FAO), the World Health Organization (WHO); the Consultative Group on International Agricultural Research (CGIAR) Institutes – especially the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), the International Institute of Tropical Agriculture (IITA), the International Laboratory for Research on Animal Diseases (ILRAD) and the International Livestock Centre for Africa (ILCA) – now amalgamated into the International Livestock Research Institute (ILRI); the West Africa Rice Development Association (WARDA, now the Africa Rice Center), and the International Centre of Insect Physiology and Ecology (ICIPE), increasingly interacted with national programmes and institutions. Interest in major and minor pest species developed and much important research was undertaken. There is still scope for further studies, however, especially on the objective assessment of harmful and beneficial effects and the development of effective pest management programmes. There is little doubt that overall losses to dipterous pests in agriculture in Africa are considerable and that local losses may be catastrophic, but it is often difficult to quantify these – and it is equally problematic to quantify benefits that may be accountable to beneficial species.

Information on symptoms, identification, prognosis and management of the most important species is becoming much more widely and easily available through on-line sources, such as www.infonet-biovision.org, the CAB International Compendia on Crop Protection and on Animal Health and Production, the World Animal Health Information Database (WAHID) and other databases.

Diptera as pests of cultivated plants

There are many dipterous pests that debilitate cultivated plants at various stages of their growth. The most important are generally those that cause direct damage to the harvested produce, especially grain, fruits, vegetables and flowers. The damage usually results from direct feeding by larvae of phytophagous species, sometimes enhanced by secondary bacterial and/or fungal pathogens. As far as is known, the transmission of viruses or virus-like organisms is not involved. The following brief reviews are arranged alphabetically by family.

Agromyzidae (Chapter 86). Various species are leaf, seed or stem miners of many different cultivated and wild plants (Fig. 9). A number of invasive species are of importance in international trade, and other species damage food crops. Ornamental plants produced in Africa for European markets may be affected by species of *Liriomyza* Mik and *Phytomyza* Fallén and food crops, especially legumes (*Phaseolus* beans, soybean and gram), are prone to attack by species of *Ophiomyia* Brazhnikov and *Melanagromyza* Hendel. Spencer (1973) provided an account of the Agromyzidae of economic importance, on a worldwide basis, and that work has been revised and updated by Dempewolf (2004), based at the Zoological Museum, University of Amsterdam.

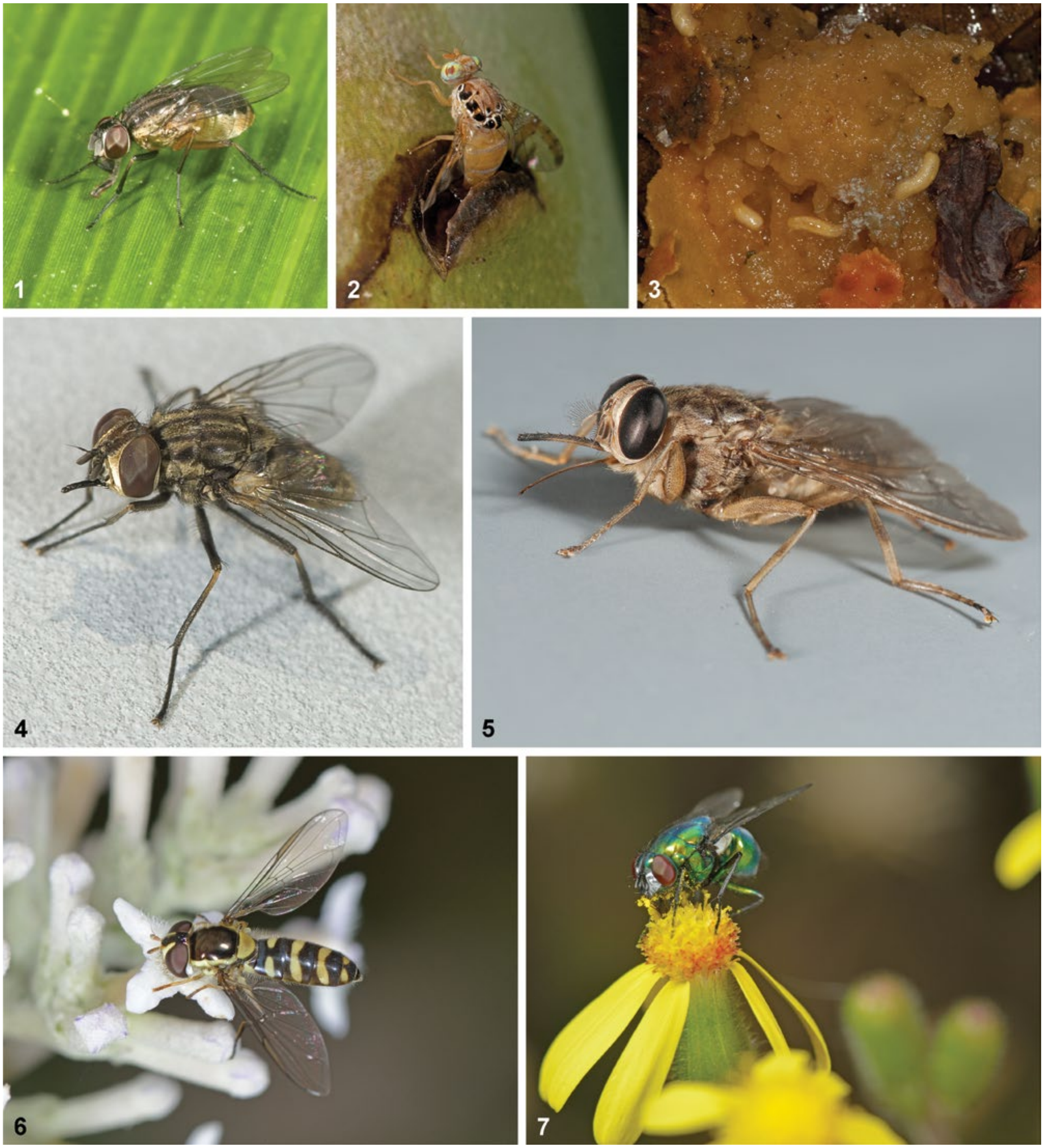
Cecidomyiidae (Chapter 22). Two species have particularly important impacts on African cereal crops by reducing grain yields: the Sorghum midge, *Stenodiplosis sorghicola* (Coquillett) [= *Contarinia sorghicola*] (Fig. 11) and the African rice gall midge, *Orseolia oryzivora* Harris & Gagné (Fig. 10). *Stenodiplosis sorghicola* is an African species that has long been established as an alien species in Asia, Australia, North and South America and elsewhere throughout the tropics and sub-tropics. It is one of the most widespread and damaging pests of grain sorghum (Harris 1985). Recent research in Africa has been coordinated by ICRISAT. Resistant varieties have been developed, mainly as a result of plant breeding programmes in India and the United States, but this pest continues to cause substantial yield losses in the semi-arid areas of Chad, Niger and Nigeria (Ajayi *et al.* 2001) and is still a potentially serious pest throughout Africa. *Orseolia oryzivora* is also an indigenous African species, currently known only from Africa. It is a major biotic constraint to the production of rain-fed and irrigated lowland rice and is becoming an increasing problem with the expansion and intensification of rice production in sub-Saharan Africa. Yield losses of 25–80% have been recorded in farmers' crops and severe outbreaks have occurred in Burkina Faso and south-east Nigeria (Nwilene *et al.* 2006: 3). Other cecidomyiid species affecting yields of cultivated plants in Africa include the Millet grain midge, *Geromyia penniseti* (Felt), and the Sesame pod midge, *Asphondylia sesami* Felt.

Chloropidae (Chapter 96). A few species are minor pests, especially on cereal crops and grasses. In West Africa *Pachylophus beckeri* Curran is a pest of rice (Heinrichs & Barrion 2004: 34) and *Dicraeus pennisetivora* Deeming is a pest of pearl millet (Deeming 1979). Various species of *Oscinella* Becker are also of some importance (Deeming 2003).

Diopsidae (Chapter 64). Some species are recorded as pests of rice, especially *Diopsis macrophthalma* Dalman [= *longicornis* Macquart], which is a common stem-boring species of rain-fed and lowland irrigated rice in West Africa and also occurs in other parts of tropical Africa (Heinrichs & Barrion 2004: 27). Other species, notably *D. apicalis* Dalman and *D. collaris* Westwood may also be involved.

Muscidae (Chapter 113). A few species are pests of cultivated plants, including the genus *Atherigona* Rondani (Fig. 1), chief of which is the Sorghum shootfly, *Atherigona soccata* Rondani. This is an important pest of sorghum at the seedling stage and may also affect other cereal crops. Pearl millet may be attacked mainly by *A. naqvii* Steyskal. Larvae feeding within young plants kill the growing points, with resultant production of "dead hearts", a symptom also produced by some other pests. Shootfly infestations inhibit crop growth and reduce yields.

Tephritidae (Chapter 71). This family includes some of the economically most important pests of agriculture and horticulture in tropical and southern Africa. They cause substantial and persistent direct damage to fruits (citrus, guava, melon, papaya, pomegranate, star fruit, *etc*.) (*e.g.*, Fig. 3) and to vegetables (avocado, cucumber, egg plant, squash, tomato, *etc*.), but are additionally of great importance in international trade (see Chapter 8). This results from the invasive nature of some species, exemplified by the Medfly, *Ceratitis capitata* (Wiedemann) (*e.g.* Fig. 2), a species that was originally native to Africa, but has spread outside the continent and poses a major and sustained threat



Figs 5.1–7. Examples of Diptera of agricultural and veterinary significance: (1) *Atherigona* sp. (Muscidae); (2) *Ceratitis* (*Ceratalaspis*) *cosyra* (Walker) (Tephritidae); (3) fruit infested by larvae of a *Ceratitis* sp.; (4) *Stomoxys* sp. (Muscidae); (5) *Glossina* sp. (Glossinidae); (6) *Allograpta* sp. (Syrphidae); (7) *Neomyia* sp. (Muscidae). Photographs © S.A. Marshall.

to horticulture in Australia, the United States and elsewhere. This has important impacts on fruit exports from Africa as expensive monitoring and detection programmes are required to meet plant health and quarantine requirements. Conversely, the African fruit industry is under threat from exotic species, such as *Bactrocera cucurbitae* (Coquillett), *B. dorsalis* (Hendel) (= *B. invadens* Drew, Tsuruta & White), *B. latifrons* (Hendel) and *B. zonata* (Saunders), that have been accidentally introduced from other continents (De Meyer *et al*. 2010). In addition, much damage is done by various indigenous species, including the coffee fruit flies (*Trirhithrum* Bezzi spp.) (White *et al*. 2003), the Olive fruit fly (*Bactrocera oleae* (Rossi)) and various species of *Dacus* F. (Fig. 8). Collaborative international research has increased in recent years, with important inputs from ICIPE, Nairobi, Kenya, through the African Fruit Fly Initiatives; from the United States Agency for International Development (USAID) and the United States Department of Agriculture (USDA), through various funded projects, and from project ENBI WP13 based at the Royal Museum for Central Africa, Tervuren, Belgium (De Meyer & White 2004). ICIPE has published a field guide to the management of economically important tephritid fruit flies in Africa (Ekesi & Billah 2006).

Diptera as veterinary pests

Mullen & Durden (2009) have provided a detailed review of medical and veterinary entomology on a worldwide basis that contains much information that relates to the veterinary importance of Diptera in Africa. Additional information relevant to Africa is included in the World Animal Health Information Database (WAHID) (Anonymous 2010). In most cases there is little or no information on the assessment of the economic losses involved. The following summary is based mainly on these two sources of information.

Psychodidae (Chapter 24). Livestock, domestic animals and wildlife are affected directly by blood loss and irritation caused by the bites of adult Phlebotominae, especially by species of *Phlebotomus* Rondani & Berté. In addition, they may also suffer from leishmaniasis and vesicular stomatitis diseases which are transmitted by phlebotomines. The veterinary importance of these interactions has yet to be fully assessed in Africa.

Ceratopogonidae (Chapter 34). Various species of ceratopogonids, especially species of *Culicoides* Latreille, are vectors of viruses, protozoans and filarial nematodes in Africa and elsewhere in the world. The veterinary importance of these vectors in Africa results from transmission of bluetongue (Figs 13, 14) and epizootic haemorrhagic diseases in ruminants, African horsesickness (AHS) in equines (Fig. 12), and onchocerciasis in various domestic and wild animals.

Bluetongue disease, transmitted by *Culicoides imicola* Kieffer and other species of *Culicoides*, was first recognised in South Africa in the early 1930s, but is now present on all continents, except Antarctica. In addition to its widespread occurrence in Africa, it is also present in North and South America, the Middle East, Asia, Australia and parts of Oceania. Since 1998 it has extended northwards in Europe. Infected animals, mainly sheep, but also goats, cattle and deer, develop a range of symptoms. Mortality rates are 30–70% in sheep and may exceed 90% in wild deer and antelopes. In addition, reproduction may be affected, resulting in low birth rates, congenital deformities, stillbirths and abortions. Epizootic haemorrhagic disease is very similar to bluetongue in many respects, but occurs mainly in wild ruminants, especially deer. African horsesickness virus, related to bluetongue virus and also transmitted by *Culicoides* midges, mainly affects horses, mules and donkeys. Mortality is 70–95% in horses, about 50% in mules and about 10% in donkeys. Major outbreaks in southern Africa are strongly related to the warm phases of the El Niño cycle.

Simuliidae (Chapter 32). Large, persistent swarms of adult simuliids feeding on livestock and poultry cause weight loss, reduced egg and milk production, malnutrition in young animals, dermatitis and epidermal necrosis, impotence in bulls, and delayed pregnancies. In some cases the animals that they attack are killed and many of these deaths result from acute toxaemia and anaphylactic shock. Death may occur within a few hours of attack and there have been cases in the past when hundreds or thousands of animals have died when exposed to high populations of biting simuliids. Species of the *Simulium* (*Metomphallus*) *bovis* de Meillon complex are recorded as spreading diseases, such as bovine onchocerciasis affecting cattle and wildlife and species in the *S.* (*Nevermannia*) *nigritarse* Coquillett complex are recorded as spreading *Leucocytozoon* sp. parasites in poultry (Palmer & de Moor 1998). Wildlife may also be affected by transmission of filarial nematodes, protozoans and various pathogens.

Culicidae (Chapter 31). Adult mosquitoes cause irritation, blood loss and allergic reactions that sometimes result in the death of livestock from anaemia and stress. In addition, blood-feeding females transmit equine encephalitis, Japanese encephalitis, West Nile virus, Rift Valley fever and other viral diseases of livestock and poultry, plus various sporozoans and filarial nematodes. Rift Valley fever, mainly transmitted by species of *Aedes* Meigen, has caused epizootics in cattle, goats and sheep in sub-Saharan Africa, with outbreaks generally involving many thousands of animals, causing substantial, but unspecified, economic losses. Other mosquito-transmitted viruses include Wesselsbron virus, affecting sheep, goats and cattle, and fowlpox, affecting chickens. Mosquitoes are also vectors of avian and primate malaria and of dog heartworm.

Tabanidae (Chapter 39). Painful and persistent biting by adult tabanids, mainly species of *Chrysops* Meigen, *Haematopota* Meigen, and *Tabanus* L., affects livestock, especially cattle and horses, and sustained attacks limit weight gains of beef cattle, reduce milk yields of cows and damage hides. Tabanids are also vectors of various viruses, bacteria and protozoons, including *surra* and related trypanosomiases and rickettsial anaplasmosis. The incidence of *surra* disease, which occurs mainly in northern Africa, increases significantly during the rainy season, when biting fly populations are high. It mainly affects horses and camels, but buffaloes, donkeys, mules and various other animals may be attacked. Mortality in untreated horses and camels may be 100% and is often sudden, but in cattle and other species, infections tend to be chronic rather than acute. Tabanids are the most important vectors, but other haematophagous flies may also be involved.

Fanniidae and **Muscidae** (Chapters 112 and 113). The combined overall adverse effects of biting and non-biting muscid flies on livestock production in Africa must be considerable, but have not been adequately assessed. In the United States, estimates of annual losses attributed to stable flies (*Stomoxys*

Figs 5.8–11. Examples of damage caused by agriculturally significant Diptera: (8) cultivated butternut squash, exhibiting damage by *Dacus bivittatus* (Bigot) (Tephritidae) in South Africa; (9) cultivated potato leaves exhibiting leafminer damage by *Liriomyza huidobrensis* (Blanchard) (Agromyzidae) in South Africa; (10) galls of the African rice gall midge, *Orseolia oryzivora* Harris & Gagné, on irrigated rice in Nigeria; (11) grain sorghum head severely damaged by Sorghum midge, *Stenodiplosis sorghicola* (Coquillett) (both Cecidomyiidae) in Nigeria (infested spikelets fail to produce grain). Figs 8, 9 (photographs © D. Visser, ARC-Roodeplaat), Figs 10, 11 (photographs © K.M. Harris).

Geoffroy) and horn flies (*Haematobia* Le Peletier & Serville) exceed US$1 billion and additional annual losses to the face fly, *Musca autumnalis* De Geer, are estimated at more than US$120 million. In Africa, cattle, goats, sheep, camels, horses, pigs, poultry and wild animals are all affected. Biting species, especially *Stomoxys calcitrans* (L.) (Fig. 4) and *Haematobia irritans* (L.), are of major importance as bites are painful and cause persistent wounds. Attacked cattle, horses and small ruminants bunch, stamp, kick and switch their tails in futile attempts to deter these and other flies. This may result in long-term stress, loss of condition and reduction of the production of meat and dairy products. In addition to these biting muscids, species of *Musca* L., *Fannia* Robineau-Desvoidy (Fanniidae) and other genera often maintain high populations around livestock and human habitations and incessant adult activity causes irritation and stress. Some muscids are also known or potential vectors of bacteria and other pathogens (Fig. 17), including species of the protozoan genus *Besnoitia* (Fig. 15).

Glossinidae (Chapter 108). *Tsetse* (*Glossina* Wiedemann spp.) (Fig. 5) are among the most important dipterous pests in Africa as they are the main vectors of trypanosomiasis, including *nagana* disease in cattle (Fig. 16). This is the most economically important disease of livestock in Africa, occurring in most countries and over a total area of about ten million square kilometres between 14°N and 29°S. The greatest impact is on cattle, but horses, pigs, goats, sheep and camels may also be affected. Chronic disease, involving anaemia and general weakness, is common and early death may result from secondary infections. Presence of this disease restricts the development of animal production over about one third of Africa and the scarcity of domesticated animals results in a severe lack of animal protein for human nutrition and a lack of draught animals for use in crop production. Wildlife sustains a reservoir of trypanosomes, with at least thirty species of animal and a number of *Glossina* species involved.

Calliphoridae *sensu stricto* (Chapter 114). Species of calliphorids that attack livestock are responsible for wound or traumatic myiasis, which causes substantial mortality, debilitation and economic losses. The most important of these are the screw-worms, which are obligate parasites of mammals, with larvae invading all types of wounds on a wide range of hosts. They kill infested animals by eating into healthy tissues and vital organs and inducing septicaemia, almost always killing untreated hosts. The main species in tropical and sub-tropical Africa is the Old World screw-worm fly, *Chrysomya bezziana* Villeneuve, which is present throughout most of Africa and across South-east Asia to Papua New Guinea and the Philippines. It is a major cause of primary myiasis (especially in cattle), infesting body orifices and wounds, ranging from sites of insect and tick bites to thorn scratches and other lacerations. Infestations of the umbilicus of newborn calves are especially prevalent and wounds resulting from castration, branding, shearing, docking and ear-tagging may also be invaded.

Another species, the New World screw-worm fly, *Cochliomyia hominivorax* (Coquerel), was accidentally introduced into Libya in the late 1980s, posing a major threat to Africa, but prompt recognition by veterinary staff in Libya and dipterists based in the Natural History Museum in London, was quickly followed by an international FAO/IAEA (International Atomic Energy Agency) sterile male release programme in collaboration with the Libyan government. By 1991 the pest had been eradicated, at a total cost of less than US$35 million, which was provided from multi-donor funding (Vargas-Terán *et al*. 2005: 629). This was a most effective and economically valuable livestock pest control programme as it prevented estimated recurrent losses in the Mediterranean province and Africa of more than US$1 billion a year (Van der Vloedt & Butt 1990). This case emphasises the need for continuous vigilance to prevent the establishment of alien pests in Africa, and the importance of international cooperation.

Untreated cases of primary myiasis may develop into secondary myiasis in necrotic tissues involving other calliphorids, notably *Lucilia cuprina* (Wiedemann) causing “blowfly strike”, of sheep (Fig. 18), and species of *Calliphora* Robineau-Desvoidy. Other Diptera, especially Sarcophagidae, Muscidae and Oestridae may also be involved.

Sarcophagidae (Chapter 116). Various species of flesh fly have been associated with cutaneous and gastrointestinal myiasis of livestock and some species of *Wohlfahrtia* Brauer & Bergenstamm are primary invaders of wounds and body orifices. They are generally of lesser importance than calliphorids and oestrids.

Oestridae (Chapter 119). Species of Old World skin bot flies (Hypodermatinae), especially *Hypoderma* Latreille spp., are mainly pests of cattle, but may also attack sheep, goats, deer and other animals. Harassment of livestock by egg-laying females induces the panic behaviour known as “gadding” and, in addition, “warble” wounds caused by larvae feeding in the skin reduce the value of hides. Nasal bot flies (Oestrinae), especially species of *Oestrus* L. and *Rhinoestrus* Brauer, also have serious harmful effects, as do the stomach bot flies (Gasterophilinae), especially species of *Gasterophilus* Leach that attack horses. In most cases infestation of livestock by oestrids causes chronic ill-health and loss of condition, but individuals may die from falls and physical injury during “gadding”, which may induce abortion in pregnant cattle.

Diptera as parasitoids and predators

Larvae of many dipterous families develop as parasitoids, or are predators on pests of cultivated plants and of livestock. Their impacts in Africa have seldom been assessed.

Among the parasitic families, the most notable is the Tachinidae, with species that attack lepidopterous stem borers of cereal crops, army-worms, cotton boll-worms, timber beetles, cotton stainer bugs and many others (Crosskey 1984). At least six exotic species have been introduced into tropical or southern Africa as potential agents of classical biological control, but without success (Harris 1998: 265). Larvae of many species of Bombyliidae also develop on a wide range of hosts, mainly on Hymenoptera, but also on Lepidoptera, Coleoptera and Diptera. Species of *Exhyalanthrax* Becker parasitise puparia of *tsetse* and of other cyclorrhaphous Diptera, and other genera are parasites of lepidopterous stem borers, army-worms and sawfly larvae. Other generally less important families include: Nemestrinidae, some of which are parasitoids of locusts and grasshoppers; some Phoridae that are parasitoids of coccinellids; Pipunculidae that are endoparasites of leafhoppers and planthoppers; Sciomyzidae that are internal parasitoids of snails, and Acroceridae which are internal parasites of spiders. Species of Cryptochetidae are parasitic in monophlebine coccids and have been used in biological control in North America and Africa.

Among the predaceous groups, larvae of some Cecidomyiidae are known to be specialised predators on mealybugs and scale insects in Africa (Harris 1968); larvae of some Scenopinidae are known to feed on dermestid beetles attacking stored products; adult Asilidae are general predators on other insects; some larval Bombyliidae are predators on egg pods of locusts and grasshoppers (as are some Calliphoridae and Curtonotidae); many species of Syrphidae, especially Syrphinae, are predators on aphids; Chamaemyiidae are predators on Homoptera; some Drosophilidae, especially species of *Cacoxenus* Loew and *Gitona* Meigen, prey on mealybugs and some Muscidae in the subfamily Limnophorinae are predators on Simuliidae and Culicidae.

Diptera as pests of processed dry fish and farm produce

In many African countries fish caught in inland and coastal fisheries are preserved by various methods of curing, including air-drying, salting and smoking. At high temperature and humidity

Figs 5.12–18. Livestock exhibiting symptoms of fly-borne diseases: (12) typical lesions in horse suffering from African horsesickness, a deadly disease caused by the African horsesickness orbivirus, transmitted by *Culicoides imicola* Kieffer (Ceratopogonidae) (note swollen supra-orbital fossae and hyperaemia of eyelids); (13) superficial lesions in sheep suffering from bluetongue, a serious disease of sheep caused by the bluetongue orbivirus, also transmitted by *Culicoides* (note the oedema and hyperaemia of the face); (14) same, advanced stage (note cyanotic tongue); (15) besnoitiosis, or elephant skin disease in cattle; a widely occurring disease in Africa caused by a protozoal parasite *Besnoitia besnoiti*, transmitted mechanically by blood-sucking insects including Muscidae and Tabanidae; (16) young cow affected by *nagana* in northern Uganda, a serious disease of cattle transmitted by *tsetse*; (17) cow exhibiting symptoms of lumpy skin disease indicated by clear skin lesions, a disease transmitted by *Stomoxys* spp. and *Musca* (*Byomya*) *confiscata* Speiser (Muscidae) (although transmission attempts failed); (18) "sheep strike" infestation caused by larvae of *Lucilia cuprina* Wiedemann (Calliphoridae). Figs 12–14 (Verwoerd 2012, figs 1, 2; photographs courtesy D.W. Verwoerd), Fig. 15 (photograph courtesy R. Bigalke), Fig. 16 (photograph © J. Esterhuizen), Fig. 17 (courtesy D.W. Verwoerd), Fig. 18 (source: Google images).

these processes attract considerable numbers of adult flies which oviposit on the fish during processing, resulting in infestations by maggots which cause substantial direct losses in quantity and quality and may also affect public health. The most important and widespread families involved are Calliphoridae, especially species of *Calliphora*, *Chrysomya* Robineau-Desvoidy and *Lucilia* Robineau-Desvoidy, various genera of Muscidae and Sarcophagidae, and to a lesser extent, species of Ephydridae, Milichiidae, Phoridae and Piophilidae (Haines & Rees 1989). Representatives of these families may also infest farm produce, especially meat and dairy products. Sun-drying of "mopane worms" (caterpillars of the moth *Gonimbrasia belina* Westwood and other species of African Saturniidae), may also be similarly affected, although there appear to be no published records.

Diptera as pollinators

Adults of many different families of Diptera visit flowers, but with a few exceptions, consequent pollination is probably erratic and is not well documented. Bombyliidae, Syrphidae (Fig. 6), Calliphoridae and Muscidae (Fig. 7) are most likely to be general pollinators and members of about thirty families, mostly Brachycera, may also be involved. Ceratopogonidae, and to a lesser extent Cecidomyiidae, are the main pollinators of cocoa in West Africa (Frimpong *et al*. 2009) and in other areas where the crop is grown. Flies may also be of some importance as pollinators of mango trees, but there is no critical assessment available for Africa.

Although there may not be any direct relevance to agriculture, horticulture or forestry, recent studies noted by Kirk-Spriggs & Stuckenberg (2009: 158) indicate that some flies (notably Nemestrinidae, Bombyliidae and Tabanidae, but also occasional members of other families) may be important pollinators of the Cape Fynbos flora. These show some remarkable convergent adaptations of the mouthparts (especially elongation) for feeding from nectaries in flowers with long corolla tubes. These authors also mention the significance of fly species as pollinators of some savanna trees.

Diptera as biocontrol agents

The potential for use of indigenous predaceous and parasitic Diptera in integrated management of crop pests exists, but has yet to be fully developed, although there have been some attempts to use Tachinidae in the biological control of lepidopterous stem borers of cereal crops (Harris 1998: 265). Similarly, the use in Africa of Diptera in classical biological control is minimal, but there are some instances where biological control of invasive weed species of *Acacia* (Fabaceae) and *Leptospermum* (Myrtaceae) has been attempted by introduction of phytophagous Cecidomyiidae to South Africa from Australia (Dorchin & Adair 2011).

Conclusions

As the population of Africa continues to increase, the need for enhanced and efficient agricultural production becomes more urgent. In this context, the importance of dipterous pests to crop and livestock production will also increase. Existing, long-standing restraints, such as those imposed on livestock by *tsetse* infestations, and on crop production by major pests, shall have to be overcome through determined efforts at national and international levels. Retrospective assessments of past losses will help to order priorities, but forward planning must look to the future and guard against the introduction of new pests and the creation of new problems.

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MEDICAL SIGNIFICANCE OF DIPTERA 6

Maureen Coetzee

Introduction

Of all arthropod orders, the Diptera contain the most species that transmit pathogens or are harmful to humans. Yet, of the 108 families represented in the Afrotropical Region, only 10 are of medical importance. Furthermore, within these families, relatively few species are implicated in disease transmission. For example, the Culicidae (see Chapter 31), widely regarded as the most important dipterans due to the mosquito species involved in filarial worm and malaria parasite transmission, is represented by more than 780 species in the region. At most, only 20 of these species are in any way important as vectors of disease, representing around 2.5% of this diverse family.

Diptera and diseases

For thousands of years, arthropods have been known to be harmful to humans and references to this effect can be found in the *Talmud*, *Koran* and *Bible*. Service (1978) provides a succinct account of this history, going back thousands of years to the time of Aristophanes, Aristotle and Pliny. Many of these early biologists refer to ectoparasites of humans, including lice, bedbugs, ticks, mosquitoes and other flies. Marshes, even in those days, were associated with fevers.

Flies are the most frequently quoted pestilence in very early works, with the best known example being the biblical passage describing the swarm of flies sent to Egypt (Exodus 8: 24). The fact that the plague of flies is said to have been preceded by a plague of frogs that died in vast numbers and were left to rot, is a scenario that would account for an infestation of the higher flies involved in carrion degeneration (Service 1978). The development of fly larvae (maggots) in wounds was mentioned by Homer in the 19th book of the *Iliad* and many works refer to the danger of maggots breeding in lesions and eyes. During the Middle Ages and Renaissance periods in Europe, distinct correlations between insects and disease were made. For example, in 1898, Professor Lustig of Florence stated that Italian peasants had long suspected that mosquitoes carried malaria (Nuttall 1899: 181).

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 1. Introductory chapters and keys to Diptera families. *Suricata* 4. South African National Biodiversity Institute, Pretoria; pp. 163–174.

Prior to that, King (1883: 646) wrote that in 1848, Dr Josiah Nott published an essay on the insect origin of yellow fever in the *New Orleans Medical and Surgical Journal*, also suggesting "… the 'mosquitoes of the lowlands' as a probable cause of malarial fever, in place of the marsh-vapors". King then presented the evidence of the day to support this theory (King 1883).

It was, however, in the late nineteenth century that definitive proof was provided that some pathogens can undergo obligatory development in insects and that insects actually transmit them back to humans. A large body of research was conducted in the late 1800s by numerous scientists in Europe and North America to determine the role of insects in the transmission of diseases to humans. The majority, however, thought that insects, having acquired the pathogens from humans, subsequently died at drinking water sources (streams, springs, *etc.*) and that pathogens were then ingested (Nuttall 1899: 221).

The most influential discovery was that of Patrick Manson from the London School of Hygiene and Tropical Medicine, who showed that *Culex quinquefasciatus* Say transmits Bancroftian filariasis (*Wuchereria bancrofti*) (Manson 1878). Subsequently, it was demonstrated that mosquitoes transmit malaria parasites; and a variety of ticks, mites and insects were incriminated in quick succession as vectors of disease-causing organisms.

Malaria (vectors: Culicidae)

The causative agent of malaria was determined in the 1890s, as a result of the individual research efforts of Laveran, Grassi and Ross, amongst others, as a parasite belonging to the genus *Plasmodium* (Plasmodiidae) and transmitted to humans by the bite of anopheline mosquitoes (Service 1978). Prior to this, fevers had been associated with "bad air" (in Italian, "mal aria"), swamps, and other unsavoury localities.

Today, malaria is confined mainly to the tropics and subtropics, having been eradicated from most of Europe and North America (Service 1980: 46). In its 2013 report, the World Health Organization states that globally, approximately 3.4 billion people are at risk of contracting malaria and it is estimated that there were in excess of 200 million cases in 2012 (WHO 2013*a*). More than 620,000 (upper estimate around 790,000) malaria deaths occurred worldwide in 2012, 90% of them in the Afrotropical Region and 77% amongst children under five years of age. This represents a 49% decrease in deaths in Africa between 2000 and 2012. The economic burden of malaria in Africa remains extremely high, however, with loss of growth in Gross Domestic Product ranging from below 0.5% (*e.g.*, Ghana) to almost 9% (*e.g.*, Chad). An estimated USD1.5–2.2 billion is required annually to combat the disease in malaria-endemic countries (Okorosobo *et al*. 2011).

The malaria parasite's life cycle (Fig. 1) takes place in two very different hosts – vertebrates (non-sexual phase) and invertebrates (both sexual and asexual phases). In general, sporozoites of *Plasmodium* spp. that have humans as hosts are injected into the skin of a person by an infected mosquito, where the sporozoites move easily by gliding in the dermal tissue (Ménard *et al*. 2013). An unknown proportion of these sporozoites make their way to the liver, presumably by travelling in the bloodstream. They undergo replication in hepatocytes and the merozoites thus formed are then released into the bloodstream within "packages" called merosomes (recently discovered and not illustrated in Fig. 1). Merozoites from ruptured merosomes invade red blood cells (Fig. 10). Here, multiplication occurs yet again, until merozoites burst out of the erythrocytes to infect new red blood cells. It is this last mentioned blood cycle phase that causes the symptoms of malaria (characteristically, they include chills and fevers). A small number of the parasites become sexual gametocytes (Fig. 11), which are sucked up by mosquitoes that feed on the infected person. The cycle in the mosquito takes about 10–14 days under optimum conditions. Immediately after the mosquito has ingested a blood meal, the male and female parasite gametocytes mate to form a zygote known as an ookinete. It penetrates the gut wall to become an oocyst that is situated virtually on the outside of the midgut wall. Sporozoites develop in the oocyst by asexual reproduction, and when it ruptures, the sporozoites travel to the salivary glands of the mosquito, from where they are then transferred to the next person(s) that the mosquito bites (Fig. 12) (Service 2012: 37). The mosquito remains infective for the rest of its life.

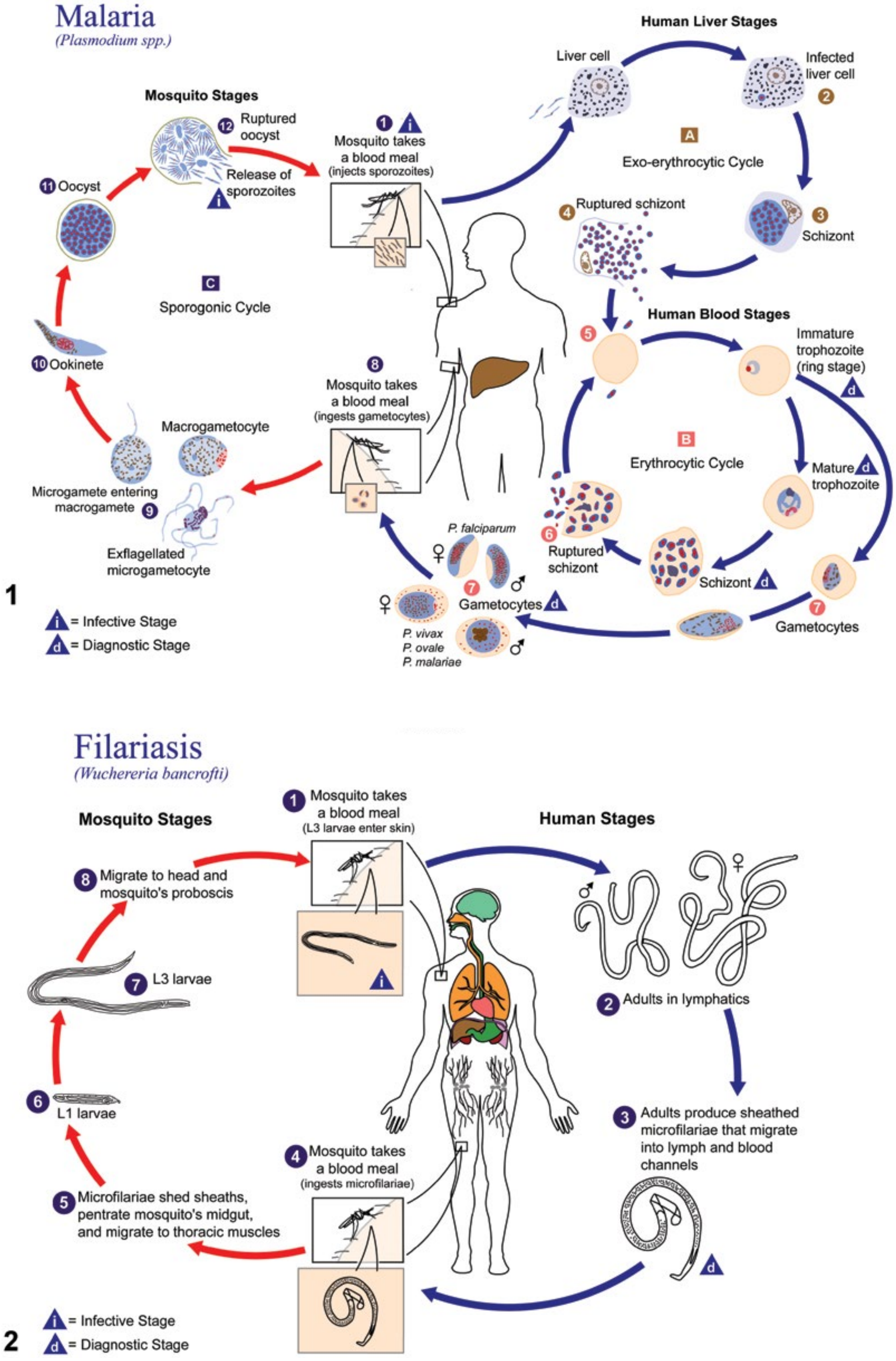
The malarial parasite species that affect humans are the following:

Plasmodium falciparum – causes cerebral and other severe forms of malaria and is responsible for most of the malaria deaths worldwide. The pathogenesis includes adherence of parasitised erythrocytes to the wall of small blood capillaries in the brain and internal organs. This is not relapsing malaria and once treated with appropriate, effective drugs, a person will only contract clinical *P. falciparum* malaria again after being bitten by an infective mosquito. Recrudescences do occur if treatment is for some reason inadequate, or the parasite is resistant to the drug(s) used for treatment.

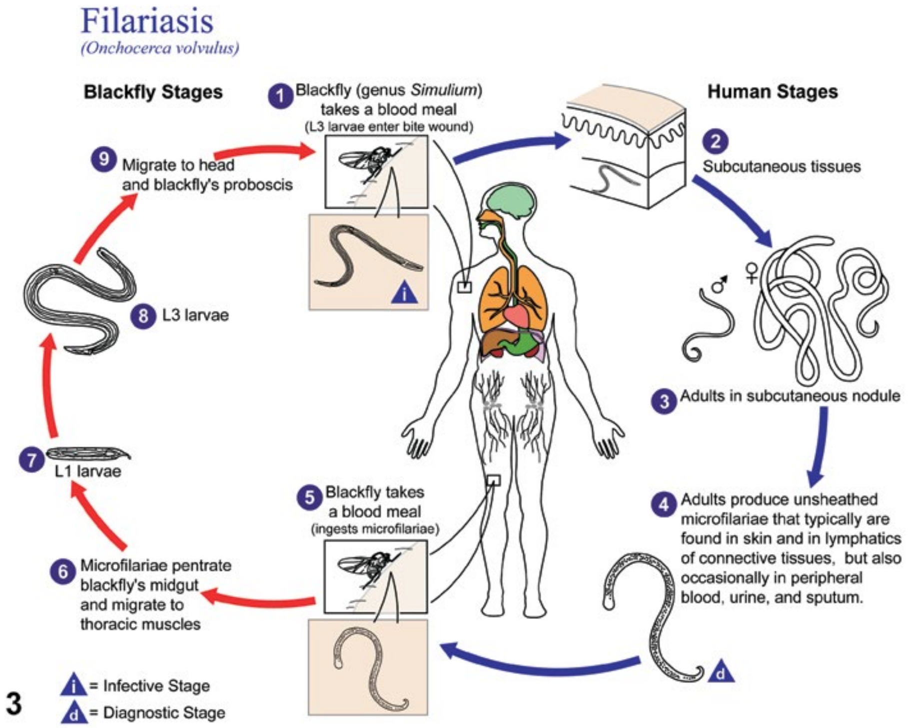
Plasmodium vivax – causes illness that is generally less severe than that resulting from *P. falciparum* infection. *Plasmodium vivax* has a dormant hypnozoite stage (Markus 2011) in the liver and relapses can occur periodically for up to a few years, unless these liver stages are killed. The idea that hypnozoites are the source of such *P. vivax* recurrences is, however, an assumption, albeit a long-standing one. It might well be correct, although *P. vivax* recurrences could possibly have a dual origin (Markus 2012). *Plasmodium vivax* has a lower temperature threshold than *P. falciparum* and is often the only species of malaria parasite found in some temperate regions of the world.

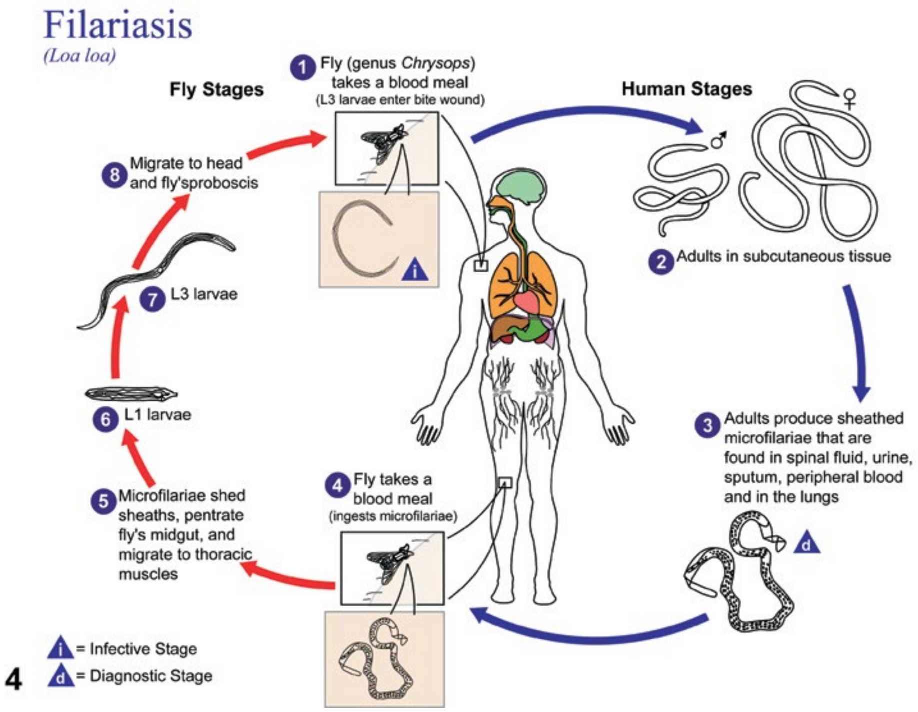
Plasmodium ovale – restricted to Africa and Asia, this is the rarest of the human malaria parasites. It too is thought to have a hypnozoite stage and that these hypnozoites may cause the periodic recurrences that can take place for up to a few years. Evidence has been presented for the existence of two separate biological species (despite being given designated names that indicate sub-specific status): *P. ovale curtisi* and *P. ovale wallikeri* (see Sutherland *et al*. 2010). The two species occur in sympatry in five West African countries.

Plasmodium malariae – less common than either *P. falciparum* or *P. vivax* and considered to give rise to benign disease compared with that caused by these other two species.



Figs 6.1–2. Life cycles of fly-borne pathogens: (1) *Plasmodium falciparum* (malaria); (2) *Wuchereria bancrofti* (filariasis – elephantiasis). Fig. 1 (image ID# 3405 – created 2002; CDC – DPDx/ Alexander J. da Silva, PhD, Melanie Moser), Fig. 2 (image ID# 3425 – created 2003; CDC/Alexander J. da Silva, PhD/Melanie Moser).





Figs 6.3–4. Life cycles of fly-borne pathogens: (3) *Onchocerca volvulus* (filariasis – river blindness); (4) *Loa loa* (filariasis). Fig. 3 (image ID# 3413 – created 2002; CDC/Alexander J. da Silva, PhD/Melanie Moser), Fig. 4 (image ID# 3399 – created 2002; CDC/Alexander J. da Silva, PhD/Melanie Moser).

Nevertheless, this parasite is sometimes responsible for a form of kidney failure that may prove fatal. Although it apparently does not have a hypnozoite stage in its life cycle, it has a remarkable capacity to persist for more than 50 years in an unknown site(s) in the body, but probably including the bloodstream (Markus 2012).

Plasmodium knowlesi – a primate malaria parasite similar to *P. malariae*. It is now commonly found to infect humans in Malaysia and other South-east Asian countries, with alarmingly high mortality rates.

If diagnosed early and treated with appropriate drugs, malaria is a curable disease. Furthermore, prevention of mosquito bites is an effective means of avoiding infection by the parasites. The two major vector control methods are use of long-lasting insecticide-impregnated bed nets (LLINs) and indoor house spraying with residual insecticides (IRS). Supplementary control measures are larviciding with chemicals; use of biological control agents; environmental management to limit breeding habitats; and personal protection methods such as the use of topical repellents, mosquito coils and household aerosols.

Challenges facing malaria control programmes worldwide include resistance by parasites to the drugs used for treatment, and resistance by mosquitoes to the insecticides approved by the World Health Organization for use in vector control. The current recommended treatment of uncomplicated malaria in most African countries is with artemisinin combination therapy (ACT) (WHO 2013*a*). The World Health Organization has issued guidelines for the management of insecticide resistance in mosquitoes, using rotational, or mosaic spraying, or mixtures of different classes of insecticides (WHO 2012).

Filariases (vectors: Ceratopogonidae, Culicidae, Simuliidae and Tabanidae)

Bancroftian filariasis

The World Health Organization estimates that more than 120 million people in 73 countries globally, have lymphatic filariasis, with around 40 million disfigured (Figs 19, 20) or incapacitated by the disease. Thirty percent of these cases occur in the Afrotropical Region (WHO 2013*b*).

Infection is caused by nematodes of the superfamily Filariodidea, with *Wuchereria bancrofti* (Onchocercidae), being the most common. Adult worms lodge in the lymphatic vessels and nodes, causing local inflammation and disruption of the normal functioning of the immune system. They can live for up to approximately 8 years, and during this time release millions of microfilariae into the bloodstream. These are picked up by the mosquito vectors and go through three developmental stages over 10–14 days, under optimal conditions, before being transmitted by the mosquito to the next human bitten (Fig. 2).

The African form of *W. bancrofti* is known as nocturnally periodic, which describes the time of greatest abundance of microfilariae in the circulating blood (Fig. 13). This periodicity is highly adapted to the feeding behaviour of the vector mosquitoes, whose peak biting times are from 23h00–03h00. Transmission of the parasite is curtailed through mass administration of two different drugs that clear microfilariae from the bloodstream.

The main vectors of African *W. bancrofti* are *Culex quinquefasciatus* and the malaria vectors *Anopheles gambiae* Giles and *An. funestus* Giles (Culicidae; see Chapter 31). *Culex quinquefasciatus* is controlled by the same interventions that target malaria vectors, but this mosquito generally tends to exhibit higher levels of resistance to insecticides. It breeds in polluted water and pit latrines and is more difficult to control at the larval stage. Pit latrine designs (Morgan 2009) and the use of expanded polystyrene balls have aided greatly in controlling this vector.

Onchocerciasis

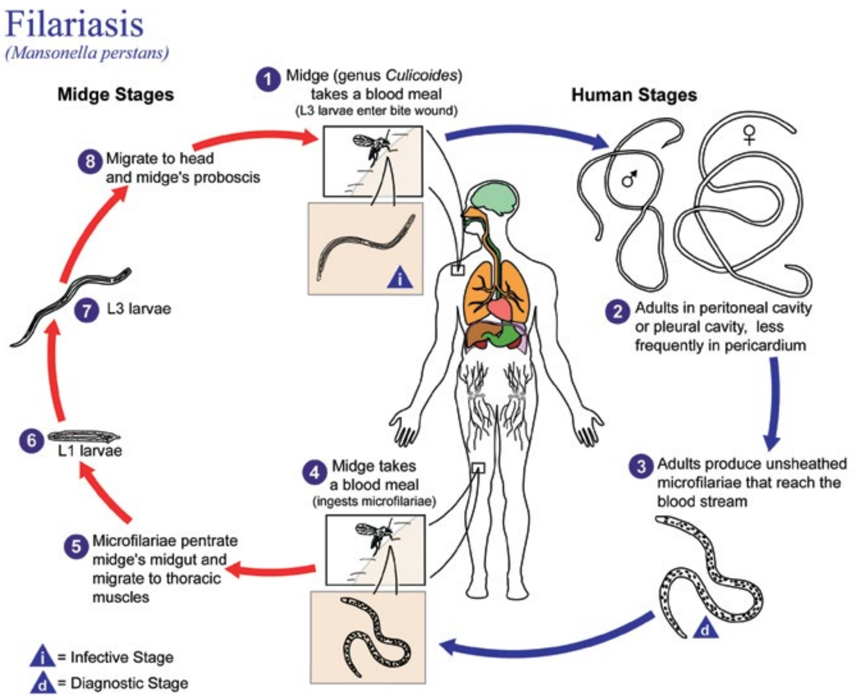
Onchocerca volvulus (Onchocercidae) (Figs 3, 14) causes a disease commonly known as river blindness, with 90% of cases occurring in Africa. Infection with the parasite manifests in three ways: irritating dermatitis, subcutaneous nodules, and eye lesions that can result in blindness. Loss of vision, in particular, is the result of dead microfilariae releasing symbiotic bacteria, resulting in severe inflammatory responses. Treatment is with ivermectin for the microfilariae and the antibiotic doxycycline for the *Wolbachia* (Rickettsiaceae) symbiotic bacteria (Russell *et al*. 2013: 80).

Onchocerciasis is transmitted by "black flies" of the genus *Simulium* Latreille (Simuliidae; see Chapter 32). They breed in fast-flowing rivers and streams, hence the common name river blindness. *Simulium* flies are very small, with mouthparts that "saw" into the skin, creating a pool of blood from which the fly feeds. This facilitates penetration of the filarial worms into the human body. Control of the adult flies is difficult, because of their exophagic behaviour. Consequently, most control efforts have been aimed at the larval stages. Both organophosphates and DDT have been used to kill larvae, but at doses that are non-toxic to fishes and crabs. The most successful control programme was that launched in West Africa in 1974 and which continued until 2002, covering 11 countries and over 30 million people (Russell *et al*. 2013: 80). This was followed by the "African Programme for Onchocerciasis Control", based on mass ivermectin administration, to combat the disease in 19 participating countries. The programme is ongoing, under the auspices of the World Health Organization.

Loa loa

Carried by flies of the family Tabanidae (see Chapter 39) and belonging to the genus *Chrysops* Meigen, this human filarial parasite is transmitted in the rainforests of tropical Africa from Nigeria to western South Sudan, and south through Democratic Republic of Congo to northern Angola. The adult worms move through loose connective tissue and are particularly noticeable when crossing the conjunctiva of the eye (Fig. 21). The microfilariae (Figs 4, 15) have a diurnal periodicity corresponding to the daytime feeding habits of the *Chrysops* flies (Service 2012: 123).

Loiasis is a relatively benign disease that is treated with long (3-week) courses of relatively slow-acting anthelmintics, such



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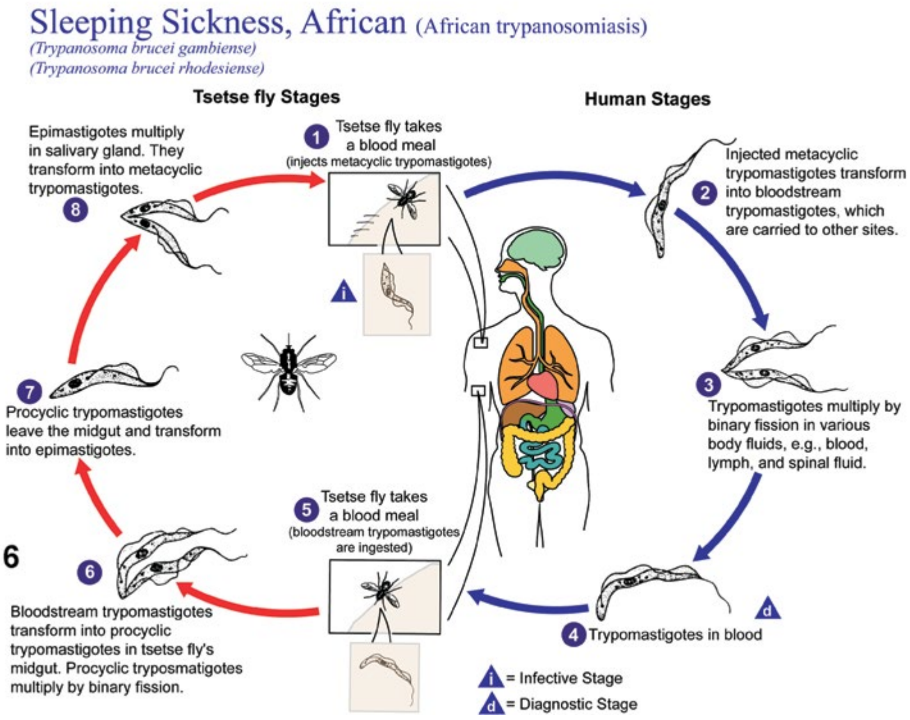

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Figs 6.5–6. Life cycles of fly-borne pathogens: (5) *Mansonella perstans* (filariasis); (6) *Trypanosoma brucei* (sleeping sickness). Fig. 5 (image ID# 3403 – created 2002; CDC/Alexander J. da Silva, PhD/Melanie Moser), Fig. 6 (image ID# 3418 – created 2003; DPDx/ Alexander J. da Silva, PhD, Melanie Moser).

as albendazole or diethylcarbamazine, which target adult worms. Ivermectin very rapidly kills the microfilariae, but this can result in fatal encephalitis if they are present in the blood in very large numbers. Ivermectin, therefore, needs to be used with caution for mass drug administration for onchocerciasis in loiasis-endemic areas. Preventive measures against fly bites, such as the wearing of protective clothing and use of repellents, are advisable.

Mansonella

Two species occur in the Afrotropical Region: *Mansonella perstans* (Figs 5, 16), widespread in the tropical rainforests of West and Central Africa and extending as far south as Zimbabwe, and *M. streptocerca* (Onchocercidae), confined mainly to West and Central Africa. Both are transmitted by biting midges of the genus *Culicoides* Latreille (Ceratopogonidae; see Chapter 34) (Russell *et al*. 2013: 60). *Mansonella* is considered to be less important than the other filarial worms, with infections by the former often being asymptomatic. *Mansonella* can, however, be responsible for skin rashes, subcutaneous lesions, fever, arthralgia, headaches and neurological disorders. Cerebral filariasis caused by *M. perstans* has been reported from Zimbabwe (Dukes *et al*. 1968), where the epidemiology of the disease indicates that it is confined mainly to the Zambezi River basin (Clarke *et al*. 1971).

The biting midges are notoriously difficult to control, breeding in dung, leaf rot and compost heaps. Where they are considered as a biting nuisance, personal protection and use of repellents are recommended.

Sleeping sickness (trypanosomiasis) (vectors: Glossinidae)

Human African trypanosomiasis (HAT), better known as "sleeping sickness", is widespread in much of the tropics and subtropics of Africa. Currently, an estimated 30,000 people in 36 African countries are infected. The population at risk is around 70 million people (WHO 2013*c*).

Trypanosomes are protozoan parasites that are transmitted to vertebrates by *tsetse*, all of which are in the genus *Glossina* Wiedemann (Glossinidae; see Chapter 108) (Fig. 6). There are two forms of HAT, *Trypanosoma brucei gambiense* and *T. b. rhodesiense* infections (Gambian and Rhodesian sleeping sickness, respectively). They are geographically and ecologically distinct and produce different clinical symptoms in humans. In both forms of the disease, the trypanosomes (Fig. 17) firstly multiply in subcutaneous tissue at the bite site, then in blood and lymph nodes, causing bouts of fever, headaches and joint pains. In the more acute, Rhodesian form, illness may rapidly progress to fatal myocarditis and multi-organ failure. In an established infection, the trypanosomes invade the central nervous system, and it takes days or weeks after transmission (Rhodesian) to years (Gambian) for this to result in symptoms manifesting as either acute meningoencephalitis (Rhodesian form), or confusion, lassitude and daytime somnolence and eventually coma and death (Gambian form). Untreated, death from Rhodesian sleeping sickness occurs within days to weeks and up to four years after infection with the Gambian form (Russell *et al*. 2013: 386). Treatment is difficult and no vaccines are available.

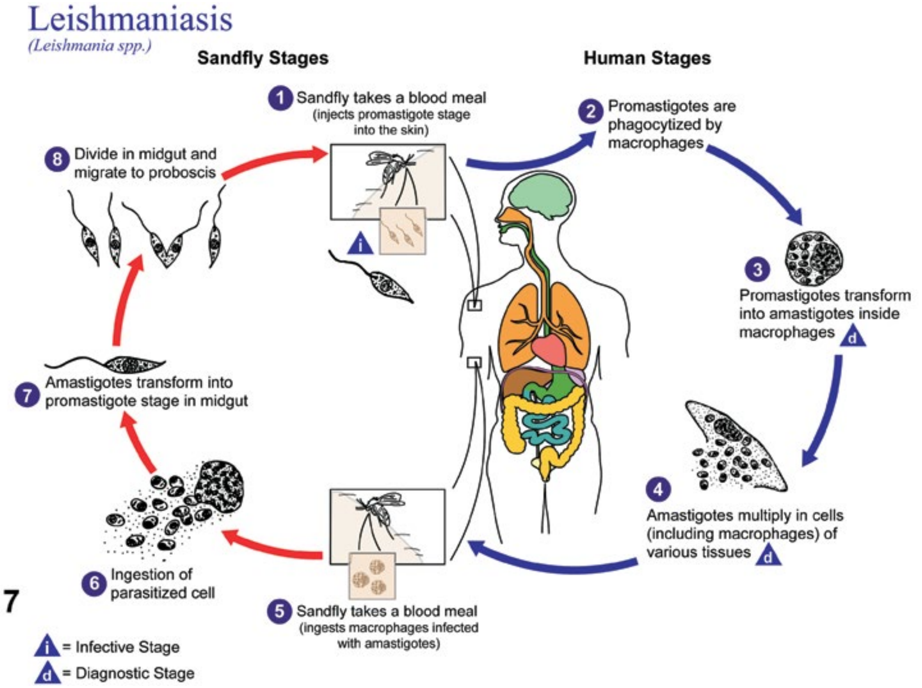

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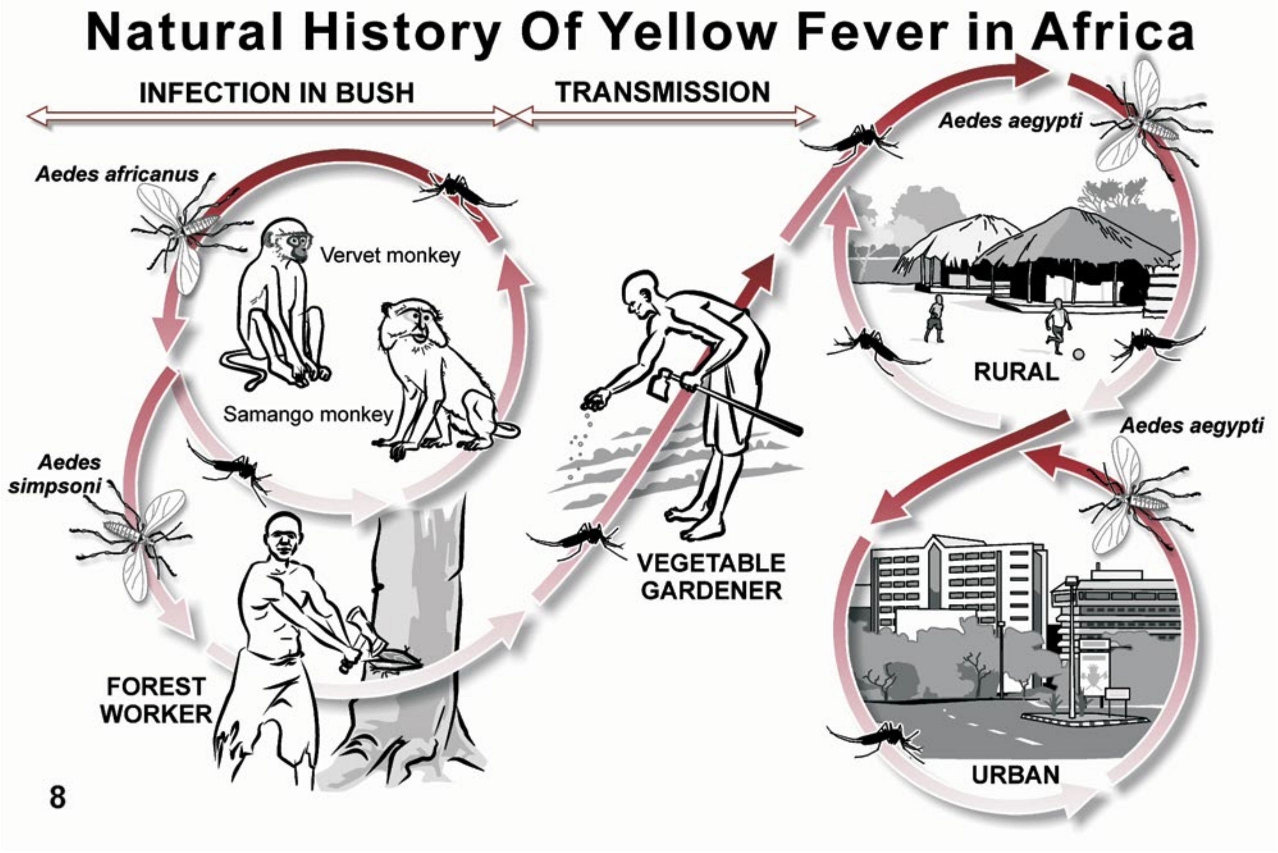
Fig. 6.7. Life cycle of fly-borne *Leishmania* spp. (leishmaniasis). Fig. 7 (image ID# 3400 – created 2002; CDC- DPDx/ Alexander J. da Silva, PhD, Blaine Mathison).



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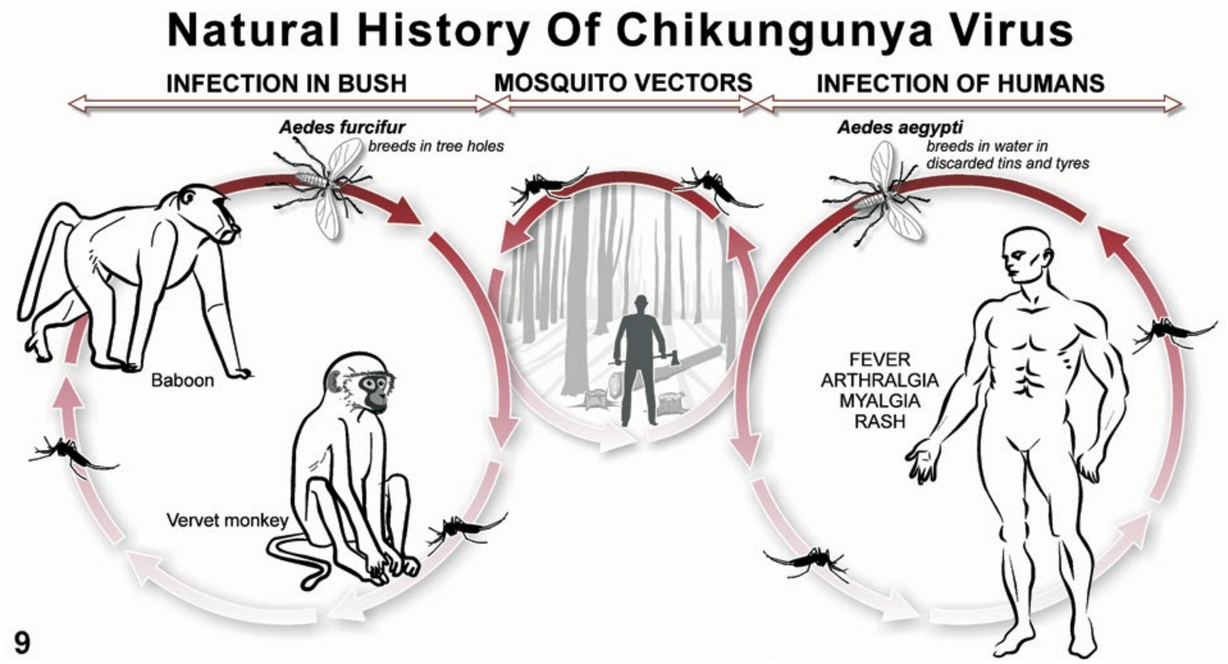

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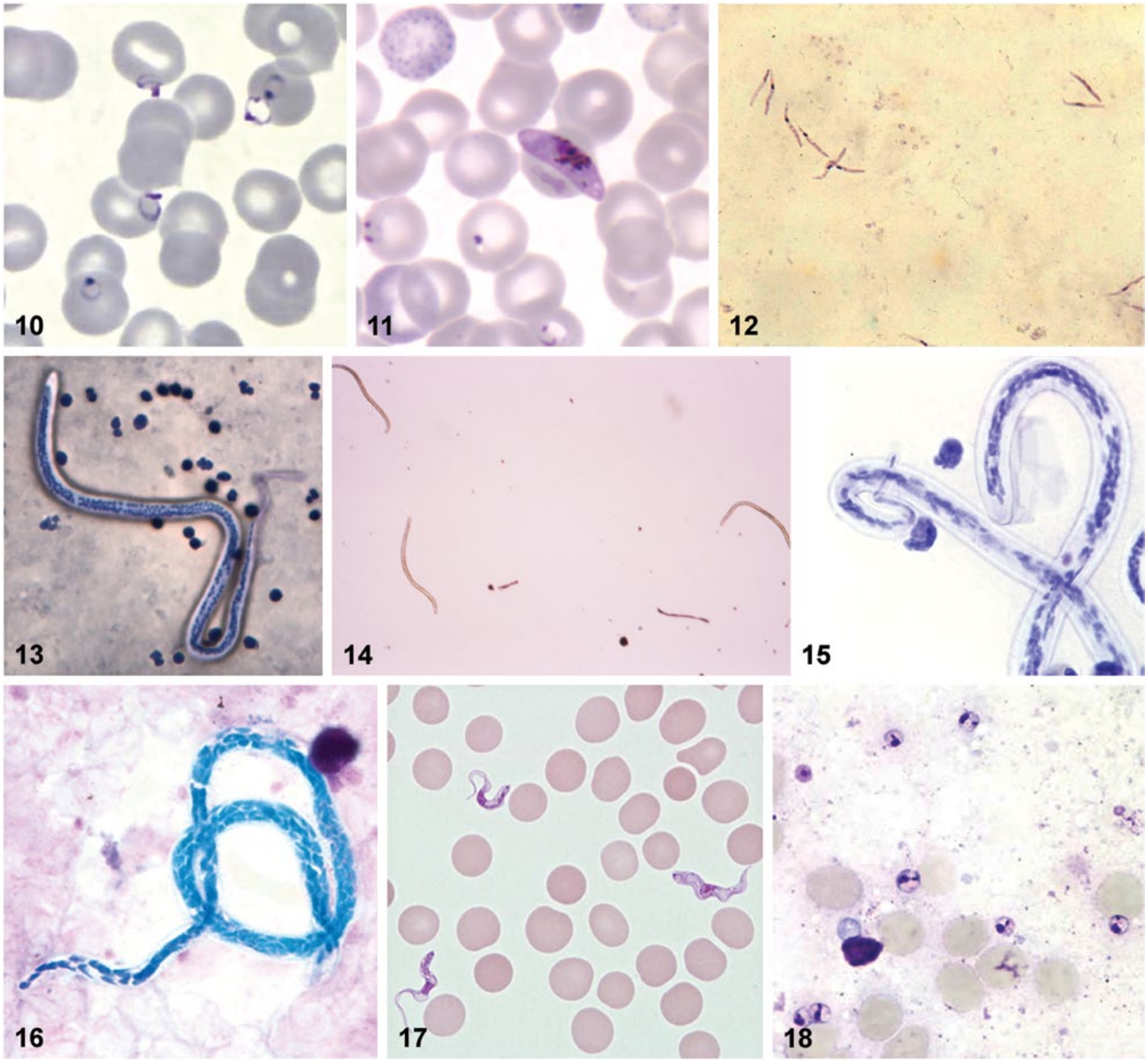
Figs 6.8–9. Transmission cycles of fly-borne pathogens: (8) yellow fever virus; (9) chikungunya virus.

Both male and female *tsetse* feed on blood and are capable of transmitting the trypanosomes (Service 1980: 100). The parasites take approximately 18–35 days to undergo sexual development in flies before flies become infective and pass on the parasites to the next human that they bite.

The female *tsetse* does not lay eggs as most Diptera typically do. Instead, a single mature egg passes into a uterus, where the larva develops internally through three instars. Regular blood meals are required by the female to ensure that sufficient nutrients are available to feed the larva. After about ten days, the mature larva is then deposited onto loose, sandy soil, where it burrows into the substrate and immediately pupariates. The pupal stage can last for 3–7 weeks, depending on temperatures (Service 2012: 132). Females mate only once during their lifetime.

The control of *tsetse* is aimed at the adults and ranges from insecticidal spraying of vegetation known to harbour resting flies, to targets and traps of various sorts. The fly's natural attraction



Figs 6.10–18. Fly-borne pathogens: (10) *Plasmodium falciparum* ring forms in the blood; (11) same, gametocyte and ring forms; (12) same, sporozoites obtained from the salivary glands of an infected mosquito; (13) *Wuchereria bancrofti* microfilaria in the blood; (14) *Onchocerca volvulus* microfilariae; (15) *Loa loa* microfilaria; (16) *Mansonella perstans* microfilaria; (17) trypomastigotes of *Trypanosoma* in the blood; (18) *Leishmania* amastigotes in the blood.

to large, dark objects (potential food sources), led to the development of traps baited with odour and/or colour attractants and associated use of insecticides to kill flies (Torr *et al*. 2005).

Leishmaniasis (vectors: Psychodidae)

Leishmaniasis is endemic in 88 countries around the globe, with approximately 1.5–2 million new cases reported annually. It is estimated that 12 million people are currently infected with the parasite (WHO 2014). There are three main clinical forms of leishmaniasis: cutaneous, mucocutaneous and visceral. The epidemiology of the disease is complex, with the degree of involvement of humans varying greatly across regions, depending on the parasite species, strain and reservoir host.

In Africa, cutaneous leishmaniasis (Fig. 22) is the most common form, caused by parasites in the genus *Leishmania* (Trypanosomatidae) and transmitted (Figs 7, 18) by "sand flies" of the genus *Phlebotomus* Rondani & Berté (Psychodidae; see Chapter 24). Infection causes lesions on the skin (Fig. 22), which require relatively long treatment periods (WHO 2014). The common reservoir hosts are dogs, rodents (gerbils) and Rock hyraxes. The disease is mainly distributed across North Africa and localised transmission occurs in West, East and southern Africa (Service 2012: 104). The visceral form of leishmaniasis (kala-azar) is endemic in Sudan, Ethiopia and East Africa, and is fatal if left untreated. An increase in the frequency of co-infection with HIV has resulted in visceral leishmaniasis becoming an important opportunistic disease in AIDS (CDC 2014; WHO 2014).

Sand flies are minute insects that are very difficult to control. Where they are associated with humans and domestic animals, indoor house spraying and the use of insecticide-impregnated bed nets for malaria control, have also resulted in a decrease in the number of leishmaniasis cases. The same interventions have been used for managing severe epidemics, or in highly endemic areas. Many species of sand flies rest outdoors, however, *e.g.*, in rodent burrows or termite hills. Moreover, the larval breeding sites are mostly unknown, usually making sand fly control very difficult (Service 2012: 106).

Arboviruses (vectors: Culicidae)

Amongst the Diptera, only mosquitoes are of any importance in the transmission of arboviruses. Within the Culicidae (see Chapter 31), the genera *Aedes* Meigen, *Culex* L. and *Mansonia* Blanchard contain the most important vector species, although the malaria parasite hosts *An. gambiae* and *An. funestus* can play a minor role. In the Afrotropical Region, these viruses include yellow fever, chikungunya, Sindbis, West Nile, Wesselsbron, o'nyong-nyong, Zika and Rift Valley fever. Dengue virus, previously uncommon in Africa (Jupp 1996: 5), is becoming an increasing problem in East and West Africa. Most of the arboviruses are zoonoses, the non-human vertebrate hosts commonly being birds, monkeys, rodents or domestic animals.

Yellow fever virus, the most important arboviral disease on the African continent, has two types of transmission cycle, namely sylvatic and urban cycles (Fig. 8). The former involves a monkey reservoir host, whereas the latter is human-to-human transmission. The mosquito vectors belong to *Aedes* (*Stegomyia*), with two species responsible for the sylvatic cycle; and *Aedes aegypti* (L.), which transmits the virus amongst humans (Fig. 8).

There is no specific treatment for (and vaccines are not available for) other important arboviral diseases of which there have been major outbreaks in the recent past, such as that resulting from West Nile virus importation into the United States, and chikungunya (Fig. 9) on the Indian Ocean islands and in south Asia, and Zika virus in Brazil. These outbreaks resulted in mortality rates that were of concern to affected communities. The vectors of West Nile and chikungunya/Zika are *Culex* and *Aedes* spp., respectively.

Arboviral infections in general are difficult to treat, with therapy mostly aimed at alleviation of symptoms, such as joint pains and fever. Symptoms can sometimes last for many months and can be very debilitating. If illness is complicated by encephalitis, or hepatitis, infection can even cause high mortality in severe outbreaks. The only arbovirus for which there is a vaccine is yellow fever and immunisation is mandatory for travellers in the Afrotropical Region.

The common vectors of arboviruses in Africa are also vectors of some parasitic diseases that affect humans. The control interventions used for malaria target all human-biting mosquitoes, including the culicines and aedines and can, therefore, be effective in controlling arboviruses along with particular parasitic diseases.

Myiasis (vectors: Calliphoridae and Sarcophagidae)

The invasion of human and other vertebrate organs and tissues by fly larvae is known as myiasis (see Kuria *et al*. 2015, for a recent review of South African cases). Some fly larvae feed on living tissue, whereas others feed on necrotic tissue. In general, myiasis is a more serious disease in domestic animals than humans, but infestations in humans can be alarming and in rare cases cause considerable pain and even irreversible damage when the mucous membranes, eyes or frontal sinuses have been penetrated (Service 2012: 158). In some instances, larvae of certain fly species are used for wound debridement, while those larvae that feed on corpses are useful in forensic entomology.

Cordylobia anthropophaga Blanchard & Bérenger-Féraud (Calliphoridae; see Chapter 114), also known as *Tumbu* fly, Mango fly or Putsi fly, lays its eggs in damp places, especially on soiled clothing. Upon hatching, the larvae penetrate the skin, causing boil-like lesions that are both itchy and painful as the larva develops (Fig. 23). The larva (Fig. 24) can be expelled from the lesion by first smothering with medicinal liquid paraffin and then gently pressing around the swelling. Lancing of the lesion is definitely not recommended, as puncturing the larva may cause serious infection of the surrounding area, resulting in quite severe scarring.

Additional examples of the involvement of Calliphoridae in naturally acquired human myiasis are provided in Chapter 114.

Larvae of *Lucilia sericata* Meigen (Calliphoridae) feed on decomposing tissue and have been used for wound debridement, also known as maggot therapy, whereby sterile early instar larvae are used to clean skin ulcers, pressure sores and surgical wounds (Service 2012: 168). Identification of the flies is critical, however, as similar-looking species produce larvae that feed on living tissue and can cause facultative myiasis.

Other diseases

All of the pathogens discussed in this chapter so far undergo obligatory development cycles within the vectors. There are, however, numerous bacteria, viruses, parasites and helminths that can be transmitted mechanically by non-biting flies in the families Muscidae (Chapter 113), Sarcophagidae (see Chapter 116) and Calliphoridae (see Chapter 114). These flies are collectively known as "filth flies" because of their propensity to breed in and feed on human and animal excrement and as "synanthropic" flies because of their close association with humans (Graczyk *et al.* 2001). The transmission of pathogens is either through the adherence of pathogens to the setae on the tarsi of the flies, or the flies ingest the pathogens and then either regurgitate or defaecate on human food. Many pathogens have been isolated from flies, for example the bacteria *Shigella, Vibrio, Staphylococcus* and *E. coli*; the protozoan parasites *Sarcocystis, Toxoplasma, Giardia* and *Entamoeba*; and viruses such as *Polio* and *Coxsackievirus* (Graczyk *et al.* 2001, 2005). Most of these pathogens, however, do not survive on, or in, the fly for more than a few hours and the role of the flies in the spread of disease is largely circumstantial (Service 2012: 145). One exception to the above is the eye disease known as trachoma (caused by *Chlamydia trachomatis*), in the aetiology of which the "bazaar" fly, *Musca sorbens* Wiedemann, is known to play an important role.

Flies associated with faeces, or other unhygienic matter, are always a cause for concern and their unsavoury habits when visiting our food is more than enough reason to discourage their breeding. Basic hygiene, burying faeces, turning compost heaps regularly and not allowing litter to accumulate, go a long way in controlling flies that pester humans. The Muscidae and Fanniidae that are often associated with poultry (*Fannia* spp.) and domestic mammals (blood-sucking *Stomoxys* spp.), may require professional pest control with residual insecticides.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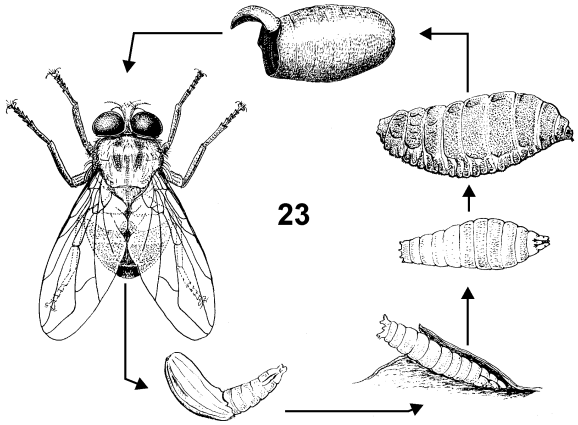
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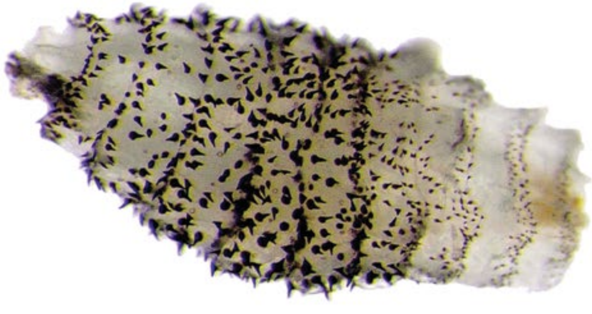
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Figs 6.19–24. Symptoms of fly-borne diseases, life cycle and larva of *Cordylobia* (Calliphoridae): (19) lymphatic filariasis caused by *Wuchereria bancrofti*; (20) same; (21) *Loa loa* in the conjunctiva of the eye; (22) typical lesion caused by *Leishmania* parasites; (23) life cycle of the myiasis fly *Cordylobia anthropophaga* Blanchard & Bérenger-Féraud; (24) third-instar larva of *C. anthropophaga*. Fig. 19 (http://www.neglecteddiseases.gov), Fig. 20 (http://www.news-medical.net), Fig. 21 (http://www.cdc.gov), Fig. 22 (http://www.ucsf.edu).

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FORENSIC SIGNIFICANCE OF DIPTERA 7

Martin H. Villet

Introduction

Forensic entomology involves the use of insects to provide evidence in legal matters, from murder and smuggling, to insurance, fraud and pollution and is, therefore, a very broad topic. Several Afrotropical Diptera are forensically significant in many cases (Smith 1986: 77–132) and many other species may be relevant in a small proportion of legal cases. As with many other synanthropic insects, certain forensically significant Afrotropical Diptera are acquiring increasing international significance, as humans have facilitated their exchange between Africa and other continents (*e.g.*, Guimarães *et al*. 1979; Prins 1979; Verves 2004; Williams & Villet 2006*a*). As might be expected from their association with corpses, the Calliphoridae and Sarcophagidae are pre-eminent in forensic entomology in the Afrotropical Region, but at least 18 other families (Table 1) have been recorded in situations where they could provide forensic evidence.

Non-taxonomic research on African flies that is relevant to forensic entomology has been published since 1923 (Villet 2015; Williams & Villet 2006*b*). This research was initially veterinary, followed by a phase of medical research, then theoretical ecology and evolutionary studies and, finally, explicitly forensic research (Villet 2015; Williams & Villet 2006*b*). Similar research on other continents has a slightly longer and more

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 1. Introductory chapters and keys to Diptera families. *Suricata* 4. South African National Biodiversity Institute, Pretoria; pp. 175–193.

varied history (Anderson 2001; Dadour *et al*. 2001*a*; Hough 1897; Introna *et al*. 1988; Klotzbach *et al*. 2004; Smith 1986: 11; Tomberlin & Benbow 2015). In cases where no research on a topic has been undertaken on Afrotropical species, the reader will be referred to overseas studies from which more detail can be obtained.

The legal context of forensic entomology usually necessitates fairly detailed insight into the natural history and biology of the insects involved. Because of this need for detail in a wide spectrum of legal situations, many expert witnesses specialise in particular, ecologically distinctive subject areas and forensic entomology is now generally subdivided into four foci serving different bodies of law and their related client groups: medico-criminal, stored product, urban and environmental forensic entomology. Flies are most crucial to the first mentioned area and appear more adventitiously in the other three.

Medico-criminal forensic entomology

This specialisation addresses criminal cases involving insect evidence and therefore involves the state and criminal law. It tends to involve deaths, whether by murder, suicide or accident, but has also addressed neglect, assault, fraud, theft and drug running. In these cases, evidence is generally drawn from the ecology and developmental physiology of the relevant flies. A set of South African case reports that illustrate the application of such evidence has been published (Louw & van der Linde 1993).

Species from at least 20 families of flies have been recorded on corpses and carcasses in Africa (Table 1; see Figs 10–16). Although they are phylogenetically diverse, many are members of the Calyptratae, indicating a phylogenetic component to community membership. Most of the families have also been

Figs 7.1–9. Examples of forensically significant Diptera: (1) male *Calliphora vicina* Robineau-Desvoidy (Calliphoridae); (2) male *Chrysomya putoria* (Wiedemann) (Calliphoridae); (3) female *Ch. marginalis* (Wiedemann) (= *Ch. regalis* Robineau-Desvoidy) (Calliphoridae); (4) (left) male *Ch. marginalis* and (right) male *Ch. albiceps* (Wiedemann) (Calliphoridae); (5) *Musca domestica* L. (Muscidae); (6) *Bactrocera dorsalis* (Hendel) (= *B. invadens* Drew, Tsura & White) (Tephritidae); (7) *Hermetia illucens* (L.) (Stratiomyidae); (8) *Megaselia scalaris* (Loew) (Phoridae); (9) *Piophila casei* (L.) (Piophilidae). Photographs © S.A. Marshall.

Figs 7.10–16. Examples of forensically significant Diptera infestations: (10) mass eclosion of *Chrysomya marginalis* (Wiedemann) (= *Ch. regalis* Robineau-Desvoidy) and *Ch. albiceps* (Wiedemann) on elephant carcass; (11) females of *Ch. albiceps* feeding near calliphorid larvae on bird carcass; (12) egg masses of *Ch. rufifacies* (Macquart) on pig carcass (non-Afrotropical); (13) larvae of *Ch. rufifacies* and adult male of *Ch. megacephala* (F.) on pig carcass; (14) puparia of *Chrysomya* sp. on pig carcass; (15) larvae of *Ch. chloropyga* (Wiedemann), *Ch. marginalis* and *Ch. inclinata* Walker (Calliphoridae) on elephant carcass; (16) mature larvae of *Ch. rufifacies* on Angus cow carcass. Figs 10, 11, 15 (photographs © C.S. Richards), Figs 12–14, 16 (photographs © J. Farrell).

Table 7.1. Diptera collected from carrion in Africa. Guild definitions follow Braack (1986, 1987) and Villet (2011): Adventive = visiting unpredictably; Coprophagous = feeding on intestinal contents; Facultatively predatory = larvae feed on heterospecific larvae; Haematophagous = blood-sucking; Necrophagous = larvae feeding on dead body tissue or adults feeding on corpse fluids.

Family	**Genus/species**	**Guild**		**Reference/s**
		Larvae	**Adults**	
Asilidae	*Bactria* sp.	Absent	Adventive	Braack 1986
	Euscelidia rapax Westwood	Absent	Adventive	Braack 1986
	Hoplistomerus nobilis Loew	Absent	Adventive	Braack 1986
	Neolophonotus sp.[1]	Absent	Adventive	Braack 1986
	Ommatius sp.	Absent	Adventive	Braack 1986
	Stichopogon caffer Hermann	Absent	Adventive	Braack 1986
	S. punctus Loew[2]	Absent	Adventive	Braack 1986
Calliphoridae	*Auchmeromyia bequaerti* (Roubaud)			Braack 1986
	A. senegalensis (Macquart)	Absent		Ellison 1990
	Bengalia sp.	Absent		Braack 1986
	Calliphora croceipalpis Jaennicke	Necrophagous	Necrophagous	Meskin 1986; Prins 1982
	C. vicina Robineau-Desvoidy	Necrophagous	Necrophagous	Hegazi *et al*. 1991
	C. vomitoria (L.)	Necrophagous	Necrophagous	K. Szpila, pers. comm. 2012; T. Tantawi, pers. comm, 2013
	Chrysomya albiceps (Wiedemann)	Necrophagous / Facultatively predatory	Necrophagous	Braack 1986; Ellison 1990; Louw & van der Linde 1993; Meskin 1986; Prins 1982; Tantawi *et al*. 1998; Ullyett 1950
	Ch. chloropyga (Wiedemann)	Necrophagous	Necrophagous	Braack 1986; Ellison 1990; Meskin 1986; Prins 1982; Rognes & Paterson 2005; Ullyett 1950
	Ch. inclinata Walker	Necrophagous	Necrophagous	Braack 1986
	Ch. marginalis (Wiedemann)	Necrophagous	Necrophagous	Braack 1986; Ellison 1990; Louw & van der Linde 1993; Meskin 1986; Prins 1982[3]; Ullyett 1950
	Ch. megacephala (F.)	Necrophagous	Necrophagous	Prins 1982
	Ch. putoria (Wiedemann)	Necrophagous	Necrophagous	Braack 1986; Ellison 1990; Rognes & Paterson 2005
	Hemigymnochaeta incerta Zumpt	Absent		Braack 1986
	H. unicolor (Bigot)	Absent		Braack 1986
	Hemigymnochaeta spp.	Absent		Braack 1986
	Hemipyrellia fernandica (Macquart)	Necrophagous	Necrophagous	Meskin 1986

Family	Genus/species	Guild		Reference/s
		Larvae	Adults	
Calliphoridae (cont.)	*Lucilia cuprina* (Wiedemann)	Necrophagous	Necrophagous	Braack 1986; Louw & van der Linde 1993; Meskin 1986; Ullyett 1950
	L. illustris (Meigen)	Necrophagous	Necrophagous	Hegazi *et al.* 1991
	L. sericata (Meigen)	Necrophagous	Necrophagous	Braack 1986; Hegazi *et al.* 1991; Louw & van der Linde 1993; Meskin 1986; Prins 1982; Tantawi *et al.* 1998; Ullyett 1950
	Lucilia spp.	Necrophagous	Necrophagous	Ellison 1990
	Pollenia sp.			Hegazi *et al.* 1991
	Tricyclea semicinerea Bezzi			Braack 1986
	Tricyclea sp.	Necrophagous	Necrophagous	Braack 1986; Ellison 1990
Carnidae[4]	*Meoneura* n. sp.		Necrophagous	Braack 1986
Chloropidae	*Apotropina* n. sp.			Braack 1986
	Chloropsina sp.			Braack 1986
	Conioscinella sp. 1			Braack 1986
	Conioscinella sp. 2			Braack 1986
	Conioscinella sp. 3			Braack 1986
	Oscinella sp.			Braack 1986
	Siphunculina ornatifrons (Loew)		Necrophagous	Braack 1986
	S. punctifrons Sabrosky			Braack 1986
	Siphunculina sp.			Braack 1986
Curtonotidae	*Curtonotum bicuspis* Kirk-Spriggs[5]	Absent	Adventive	Braack 1986
Ephydridae	*Chlorichaeta albipennis* (Loew)	Absent	Necrophagous	Braack 1986
	Discomyza eritrea Cresson	Absent	Necrophagous	Braack 1986
	Mosillus beckeri (Cresson)	Absent	Necrophagous	Braack 1986
Fanniidae[6]	*Fannia leucosticta* (Meigen)		Necrophagous	Braack 1986; Tantawi *et al.* 1998
Hybotidae[7]	*Crossopalpus* n. sp. near *aenescens* Wiedemann	Absent	Adventive	Braack 1986
Lauxaniidae	*Cestrotus* n. sp.	Absent	Adventive	Braack 1986
	Homoneura (*Keisomyia*) n. sp.	Absent	Adventive	Braack 1986
Milichiidae	*Desmometopa m-nigrum* (Zetterstedt)		Necrophagous	Braack 1986
	Leptometopa latipes (Meigen)		Necrophagous	Braack 1986

Table 7.1. (cont.) Diptera collected from carrion in Africa. Guild definitions follow Braack (1986, 1987) and Villet (2011): Adventive = visiting unpredictably; Coprophagous = feeding on intestinal contents; Facultatively predatory = larvae feed on heterospecific larvae; Haematophagous = blood-sucking; Necrophagous = larvae feeding on dead body tissue or adults feeding on corpse fluids.

Family	Genus/species	Guild		Reference/s
		Larvae	Adults	
Milichiidae (cont.)	*Leptometopa* n. sp.		Necrophagous	Braack 1986
	Milichiella lacteipennis (Loew)		Necrophagous	Braack 1986
Muscidae[8]	*Atherigona* (*Acritochaeta*) *aberrans* Malloch	Absent	Necrophagous	Braack 1986
	A. (*Atherigona*) *naqvii* Steyskal	Absent	Necrophagous	Braack 1986; Skidmore 1985: 302
	A. (*A.*) *steeleae* van Emden	Absent	Necrophagous	Braack 1986; Skidmore 1985: 299
	Atherigona spp. indet.	Absent	Necrophagous	Braack 1986; Ellison 1990; Skidmore 1985: 289
	Graphomya maculata ssp. *leucomelas* Wiedemann[9]	Coprophagous / Facultatively predatory	Coprophagous	Braack 1986; Skidmore 1985: 377
	Gymnodia mervinia (Walker)	Coprophagous / Facultatively predatory	Coprophagous	Braack 1986
	G. tonitrui (Wiedemann)	Coprophagous / Facultatively predatory	Coprophagous	Braack 1986; Skidmore 1985: 430
	Haematobia spinigera Malloch[10]	Absent	Haematophagous	Braack 1986; Skidmore 1985: 282
	H. thirouxi spp. *potans* (Bezzi)[10]		Haematophagous	Braack 1986; Skidmore 1985: 282
	Haematobosca latifrons (Malloch)			Braack 1986; Skidmore 1985: 282
	Hydrotaea ignava (Harris)	Necrophagous / Facultatively predatory	Necrophagous	Skidmore 1985: 111; Tantawi *et al.* 1998
	Morellia nilotica (Loew)		Coprophagous	Braack 1986; Skidmore 1985: 200
	Musca (*Byomya*) *conducens* Walker		Haematophagous / Coprophagous	Braack 1986; Skidmore 1985: 241
	M. (*B.*) *sorbens* Wiedemann		Haematophagous / Coprophagous	Braack 1986; Skidmore 1985: 244
	M. (*Eumusca*) *lusoria* Wiedemann		Coprophagous	Braack 1986; Skidmore 1985: 258
	M. (*E.*) *xanthomelas* Wiedemann		Coprophagous	Braack 1986; Skidmore 1985: 256
	M. (*Musca*) *domestica* ssp. *calleva* Walker	Coprophagous / Necrophagous / Facultatively predatory	Coprophagous / Necrophagous	Braack 1986; Louw & van der Linde 1993; Skidmore 1985: 232
	M. (*M.*) *domestica* ssp. *curviforceps* Saccà & Rivosecchi	Coprophagous / Necrophagous / Facultatively predatory	Coprophagous / Necrophagous	Braack 1986; Skidmore 1985: 232
	Musca spp.		Coprophagous	Ellison 1990; Skidmore 1985: 228
	Muscina stabulans (Fallén)	Coprophagous / Facultatively predatory		Hegazi *et al.* 1991; Skidmore 1985: 60

Family	Genus/species	Guild		Reference/s
		Larvae	**Adults**	
Muscidae[8] (cont.)	*Hydrotaea capensis* (Wiedemann)	Necrophagous / Facultatively predatory	Coprophagous / Necrophagous	Braack 1986; Ellison 1990; Skidmore 1985: 114
	Stomoxys sp.		Haematophagous	Braack 1986; Skidmore 1985: 271
	Stygeromyia maculosa Austen		Coprophagous	Braack 1986; Skidmore 1985: 288
	Synthesiomyia nudiseta (van der Wulp)		Necrophagous	Skidmore 1985: 63; Tantawi *et al.* 1998
Phoridae	*Hypocerides spinulicosta* Beyer		Necrophagous	Braack 1986
	Megaselia curtineura (Brues)		Necrophagous	Braack 1986; Thevan *et al.* 2010
	M. sp. near *pauculitincta* Beyer		Necrophagous	Braack 1986
	Plethysmochaeta sp.		Necrophagous	Braack 1986
Piophilidae[11]	*Piophila casei* (L.)	Necrophagous	Necrophagous	Braack 1986; Louw & van der Linde 1993
	P. megastigmata McAlpine	Necrophagous	Necrophagous	Braack 1986; McAlpine 1978
	Piophila sp.	Necrophagous	Necrophagous	Ellison 1990
Platystomatidae	*Palpomya asphaltina* (Wiedemann)			M.H. Villet, pers. obs.[12]
Rhiniidae	*Rhyncomya forcipata* Villeneuve[13]			Braack 1986
	Stegosoma vinculatum Loew[13]			Braack 1986
Sarcophagidae	*Blaesoxipha* (*Blaesoxipha*) *setosa* (Salem)	Absent	Adventive[14]	Hegazi *et al.* 1991
	Sarcophaga (*Bercaea*) *africa* (Wiedemann)[15, 16]	Necrophagous	Necrophagous	Braack 1986; Louw & van der Linde 1993
	S. (*Boettcherisca*) *peregrina* (Robineau-Desvoidy)	Necrophagous	Necrophagous	K. Szpila, pers. comm. 2012
	S. (*Liopygia*) *argyrostoma* (Robineau-Desvoidy)	Necrophagous	Necrophagous	Tantawi *et al.* 1998
	S. (*Liopygia*) *nodosa* Engel[16]	Necrophagous	Necrophagous	Braack 1986
	S. (*Liopygia*) *ruficornis* (F.)	Necrophagous	Necrophagous	Verves 2003
	S. (*Liosarcophaga*) *aegyptica* Salem	Necrophagous	Necrophagous	Tantawi *et al.* 1998
	S. (*Liosarcophaga*) *tibialis* Macquart	Necrophagous	Necrophagous	New record for Afrotropical Region
	S. (*Parasarcophaga*) *hirtipes* Wiedemann[16]	Necrophagous	Necrophagous	Braack 1986
	S. (*Prionophalla*) *langi* Curran	Necrophagous	Necrophagous	New record for Afrotropical Region
	Wohlfahrtia indigens Villeneuve	Necrophagous	Necrophagous	Hegazi *et al.* 1991
	W. nuba (Wiedemann)	Necrophagous	Necrophagous	Amoudi 1993; Hegazi *et al.* 1991

Table 7.1. (cont.) Diptera collected from carrion in Africa. Guild definitions follow Braack (1986, 1987) and Villet (2011): Adventive = visiting unpredictably; Coprophagous = feeding on intestinal contents; Facultatively predatory = larvae feed on heterospecific larvae; Haematophagous = blood-sucking; Necrophagous = larvae feeding on dead body tissue or adults feeding on corpse fluids.

Family	Genus/species	Guild		Reference/s
		Larvae	Adults	
Sepsidae	*Australosepsis niveipennis* (Becker)		Coprophagous	Braack 1986
	Paratoxopoda depilis (Walker)		Coprophagous	Braack 1986
	Xenosepsis sp.		Coprophagous	Braack 1986
Sphaeroceridae	*Coproica demeteri* L. Papp		Coprophagous	Braack 1986
	Coproica ferruginata (Stenhammar)		Coprophagous	Braack 1986
	Coproica sp.		Coprophagous	Braack 1986
	Gymnometopina sp.		Coprophagous	Braack 1986
	Elachisoma braacki L. Papp		Coprophagous	Braack 1986
	Limosina sp. 1		Coprophagous	Braack 1986
	Limosina sp. 2		Coprophagous	Braack 1986
	Lotobia sp.		Coprophagous	Braack 1986
	Norrbomia marginata (Adams)[17]		Coprophagous	Braack 1986
	N. sarcophaga L. Papp[18]		Coprophagous	Braack 1986
	Poecilosomella angulata (Thomson)		Coprophagous	Braack 1986
	Bifronsina bifrons (Stenhammar)[19]		Coprophagous	Braack 1986
Stratiomyidae	*Hermetia illucens* (L.)	Necrophagous	Necrophagous	Lord *et al.* 1994
Tabanidae	*Tabanus biguttatus* Weidemann	Absent	Haematophagous	A. Brassine, pers. comm. 2013[20]

[1] Originally recorded as *Neolophonotus* (*Lophopeltis*) sp.; [2] Originally recorded as *S. punctum*; [3] Recorded as *Chrysomya regalis* Robineau-Desvoidy, 1830 by Prins (1982), a junior synonym of *Ch. marginalis*, which is itself a junior primary homonym of *M. marginalis* Fourcroy, 1785 and *Musca marginalis* Fallén, 1824 that was subsequently conserved by Opinion 1507 of the ICZN (International Commission on Zoological Nomenclature 1988); [4] Originally recorded as Milichiidae; [5] Originally recorded as *Curtonotum cuthbertsoni* Duda, a complex of eight species subsequently revised by Kirk-Spriggs & Wiegmann (2013); [6] Originally recorded as Muscidae, family now spilt; [7] Originally recorded as Empididae, family now spilt; [8] Although over 900 species of Muscidae occur in the Afrotropical Region, very few visit carrion regularly and it is not clear that any routinely breed in carrion unless faeces are present, although larvae of some species prey facultatively on other maggots (Skidmore 1985: 1; Smith 1986: 122); [9] Originally recorded as *Graphomya leucomelas* Wiedemann; [10] Originally recorded as *Haematobosca*; [11] Seven species of Piophilidae were recorded from the Afrotropical Region by Cogan (1980: 633–634) and apparently all breed in carrion; [12] Adults were observed on large mammal carcasses; [13] Originally recorded as Calliphoridae, family now spilt; [14] T. Pape, pers. comm. 2013; [15] Originally recorded as *Sarcophaga haemorrhoidalis* (Fallén) by Braack (1986) and Louw & van der Linde (1993); [16] Originally recorded as Calliphoridae, family now spilt; [17] Originally recorded as *Copromyza* (*Borborillus*) *marginatus* (Adams); [18] Originally recorded as *Copromyza* (*Borborillus*) *sarcophaga* Papp; [19] Originally recorded as *Limosina* (*Bifronsina*) *bifrons* Stenhammar; [20] Adult horse flies were observed feeding on mammals that were culled several hours earlier.

recorded from carrion in the Holarctic Realm (Smith 1986: 77) and Neotropical Region (Carvalho & de Mello-Patiu 2008). Several families that have not been recorded from decomposing carrion in Africa have representative species associated with this niche overseas, *e.g.*, Dolichopodidae, Micropezidae, Neriidae and Ulidiidae (Cornaby 1974), implying that the list in Table 1 is far from complete. Many species recovered from carrion are, however, opportunistic, adventive, or incidental taxa that are feeding rather than breeding (Villet 2011). Females of *Atherigona* spp. (Muscidae), for example, visit carrion to obtain protein for oogenesis, but their larvae mine shoots of grasses (Skidmore 1985: 289).

Morphological identification of the various life stages of most of these taxa has not been systematically reviewed, but there is an extensive and scattered taxonomic literature. The eggs of eight relevant calliphorids (Mendonça *et al*. 2008; Meskin 1991; Sanit *et al*. 2013) one sarcophagid (Sukontason *et al*. 2005), one muscid (Sanit *et al*. 2013) and one phorid (Greenberg & Wells 1998) have been illustrated. Some of the larvae or pupae are described (Aspoas 1991; Kirk-Spriggs 1999, 2003; Prins 1982; Smith 1986: 68; Sukontason *et al*. 2001, 2002, 2006; Szpila & Villet 2011; Zumpt 1965: 1) and keys to the principal species are available for larvae (Szpila & Villet 2011; Tantawi & El-Kady 1997) and adults (Barraclough 1995; Couri 2007; Couri *et al*. 2006; Kurahashi & Kirk-Spriggs 2006; McAlpine 1977; Smith 1986: 68; Zumpt 1956, 1965: 1, 1972).

Molecular identification data have been provided for identifying African blow flies (Harvey *et al*. 2003, 2008; Marinho *et al*. 2012; Tourle *et al*. 2008; Wells *et al*. 2001; Williams & Villet 2013), flesh flies (Bajpai & Tewari 2010; Meiklejohn *et al*. 2011, 2013; Zehner *et al*. 2004) and phorids (Boehme *et al*. 2010). All taxa can be tested against the GenBank database using the BLAST tools (http://blast.ncbi.nlm.nih.gov/Blast.cgi) and the Barcode of Life Database using the BOLD Identification System (Ratnasingham & Hebert 2007).

Because the focus of medico-criminal forensic entomology is predominantly on deaths, one of its primary goals is to estimate when death occurred, commonly by using evidence from developmental physiology, autecology and community ecology. There is also a growing literature regarding toxicological evidence drawn from insects (Table 3).

Developmental physiology

The development of immature necrophagous flies provides a biological clock that can be used to estimate a minimum post-mortem interval ($\mathrm{PMI}_{\mathrm{min}}$) within the first two to four weeks of death, a limit set by the length of flies' life cycles (Villet & Amendt 2011). Essentially, an estimate of the age of the oldest immature necrophagous flies found on an organism provides an estimate of the least amount of time that the organism has been dead. Although the approach is conceptually simple, its application can be considerably complicated by the contingencies of a particular case (Villet *et al*. 2010: 109) and is, therefore, left to expert witnesses. Relevant issues include the quality of empirical data regarding development (Richards & Villet 2009), analytical, physiological, toxicological and ecological factors affecting the accuracy and precision of estimates of the $\mathrm{PMI}_{\mathrm{min}}$ (Richards & Villet 2008; Villet *et al*. 2010: 109) and the need to create independent developmental models for each species (Richards *et al*. 2009*a*), perhaps even correcting for geographical latitude (Richards *et al*. 2008), because species, and even populations, may exhibit variation (Richards *et al*. 2008; Tarone *et al*. 2011) that may be attributed to physiological adaptation to climatic conditions (Richards *et al*. 2009*b*, *c*).

Forensic-quality models of development have been provided for African populations of *Chrysomya albiceps* (Wiedemann) (Figs 10, 11), *Ch. chloropyga* (Wiedemann), *Ch. putoria* (Wiedemann) (Fig. 2), *Ch. megacephala* (F.) (Fig. 13) (Calliphoridae) and *Sarcophaga tibialis* Macquart (Sarcophagidae) (Table 2). Detailed studies of species introduced into, or accidentally exported from, Africa have been undertaken overseas (Table 2) and data for 19 species of flesh flies have been reviewed (Villet *et al*. 2006). Although there are data for extralimital populations of other relevant species, such as *Hermetia illucens* (L.) (Stratiomyidae) (Fig. 7), *Megaselia scalaris* (Loew) (Phoridae) (Fig. 8), *Piophila casei* (L.) (Piophilidae) (Fig. 9) and various Muscidae, explicitly forensic models have not been developed for indigenous African populations.

Autecology

Medico-criminal evidence may also be drawn from the general ecology of flies. Although few Afrotropical species have been studied explicitly from this perspective, aspects of the ecology of some African carrion-breeding blowflies are documented, including their seasonality, geographical distributions, thermophysiological characteristics of larvae and adults, climatic niches, vagility, courtship, oviposition sites, fecundity, ability of larvae and adults to burrow through loose soil, parasitoids, predators, and aspects of their feeding preferences (Braack 1981; Braack & de Vos 1987, 1990; Braack & Retief 1986; Meskin 1986; Omar 1995; Prins 1982; Richards *et al*. 2009*b*, *c*; Ullyett 1950; Williams & Villet 2006*a*; Zumpt 1961, 1965: 1; Zumpt & Ledger 1967; Zumpt & Patterson 1952) and studies have been conducted overseas on species that have been introduced to the Afrotropical Region.

Autecology may give particular specimens taphonomic significance. Despite their association with man, some Afrotropical species of blowflies are not ubiquitous (Richards *et al*. 2009*b*, *c*) and their occurrence on corpses in localities where they do not naturally occur, may indicate that the body has been transported long distances (Richards *et al*. 2009*c*). The presence of particular blowfly puparia in archaeological contexts has been used to infer the details of funereal rituals (Abdel-Maksoud *et al*. 2011). On other continents, benthic fly larvae, such as midge larvae (Chironomidae), have been used to estimate how long a body has been immersed in fresh water based on their seasonality and vagility (Keiper & Casamatta 2001).

Community ecology

The ensemble of species, or ecological community, associated with a dead body changes in a relatively predictable pattern as it ages (Braack 1981, 1987; Villet 2011) and the structure of the community can, therefore, be used to infer minimum post-mortem intervals, although with sufficient caveats (Braack 1987; Villet 2011) that it is, again, best left to expert witnesses. Hegazi *et al*. (1991) reported a community of eight species of flies from fish and snail carrion in Egypt, all predominantly active in summer (Table 1), and Tantawi *et al*. (1998)

Table 7.2. Diptera for which developmental data suitable for estimating thermal accumulation models are available.

Family	Genus/species	Country	Reference/s
Calliphoridae	*Calliphora vicina* Robineau-Desvoidy	United Kingdom	Kaneshrajah & Turner 2004
	Chrysomya albiceps (Wiedemann)	Egypt; South Africa	Al-Misned *et al*. 2002; Richards *et al*. 2008
	Ch. *chloropyga* (Wiedemann)	South Africa	Richards & Villet 2008; Richards *et al*. 2009*a*
	Ch. *megacephala* (F.)	Japan; South Africa	Nishida 1984; Richards & Villet 2009
	Ch. *putoria* (Wiedemann)	Brazil; South Africa	Oliveira *et al*. 2007; Richards *et al*. 2009*a*
	Lucilia cuprina (Wiedemann)	Australia	Dallwitz 1984
	L. *sericata* (Meigen)	Austria	Grassberger & Reiter 2001
Fanniidae	*Fannia canicularis* (L.)	USA	Meyer & Mullens 1988
Muscidae	*Hydrotaea rostrata* (Robineau-Desvoidy)	Australia	Dadour *et al*. 2001*b*
Phoridae	*Megaselia abdita* Schmitz	USA	Greenberg & Wells 1998
	M. *scalaris* (Loew)	USA	Disney 2008; Greenberg & Wells 1998
Piophilidae	*Piophila* (*Piophila*) *casei* (L.)	Italy	Russo *et al*. 2006
Sarcophagidae	*Sarcophaga* (*Bercaea*) *africa* (Wiedemann)	South Africa; Nigeria	Aspoas 1991; Madubunyi 1986
	S. (*Boettcherisca*) *peregrina* (Robineau-Desvoidy)	Japan	Nishida 1984; Nishida *et al*. 1986
	S. (*Liopygia*) *argyrostoma* (Robineau-Desvoidy)	Egypt; Austria	Hafez 1940; Grassberger & Reiter 2002; Zohdy & Morsy 1982
	S. (*Liopygia*) *nodosa* Engel	South Africa	Aspoas 1991
	S. (*Liopygia*) *ruficornis* (F.)	Egypt	Amoudi *et al*. 1994
	S. (*Liosarcophaga*) *redux* Walker[1]	South Africa	Al-Misned 2003*b*; Aspoas 1991
	S. (*Liosarcophaga*) *tibialis* Macquart	South Africa	Aspoas 1991; Villet *et al*. 2006
	Wohlfahrtia nuba (Wiedemann)	Egypt	Amoudi 1993
Stratiomyidae	*Hermetia illucens* (L.)	USA	Tomberlin *et al*. 2002

[1] Originally reported as *Sarcophaga* (*Liosarcophaga*) *dux* Thomson.

described the pattern of ecological succession of larvae in rabbit carrion in Egypt. Ellison (1990) commented on the interaction between vertebrate scavengers and populations of fly larvae and Meskin (1986) showed how the autecology of individual species contributes to community assembly in South Africa, through niche partitioning. The literature on African carrion community succession was reviewed by Villet (2011).

Toxicology

Deaths may occur through poisoning and insects can provide two means of detecting drugs and poisons in corpses and carcasses (Campobasso *et al*. 2004; Tracqui *et al*. 2004). First, such chemicals may affect the growth of necrophagous insects, so that anomalies in their development can alert forensic entomologists to their presence. Lord (1990: 9) discussed some American cases. Work on the effects of drugs on Afrotropical flies has revealed a variety of responses, but no underlying pattern (Table 3).

The second means of detecting drugs and poisons is by testing for their presence in necrophagous insects that have been feeding on the corpse or carcass. Modern analytical methods are generally sufficiently precise that this approach is not necessary (Tracqui *et al*. 2004), but there are a few contexts in which it remains relevant. These are situations where no corpse tissue is available for direct testing, but there are remains of insects, exuviae, or puparia. Certain chemicals are sequestered in the cuticle of insects (including puparia), where they can provide indirect evidence of toxification, even months or years later (Definis-Gojanović *et al*. 2007; Miller *et al*. 1994). Research in this direction has been undertaken in Africa on *Chrysomya albiceps* (Calliphoridae) (Al-Misned 2001, 2003a) and work overseas has used the introduced species *Lucilia sericata* (Meigen) (Calliphoridae) (e.g., Bourel *et al*. 1999, 2001; Campobasso *et al*. 2004; Hecht *et al*. 2007; Kharbouche *et al*. 2008), *Calliphora vicina* Robineau-Desvoidy (Calliphoridae) (Fig. 1) (*e.g.*, Sadler *et al*. 1997*a*, *b*; Hédouin *et al*. 2001; O'Brien & Turner 2004; Pien *et al*. 2004), *Sarcophaga ruficornis* (F.) (Sarcophagidae) (Goff *et*

Table 7.3. Toxicological studies of Diptera occurring in Africa.

Family	Genus/species	Population	Drug	Effect	Reference
Calliphoridae	*Chrysomya albiceps* (Wiedemann)	Brazil	diazepam	larvae developed faster; pupariation delayed; eclosion delayed	Carvalho *et al*. 2001
	Ch. chloropyga (Wiedemann)	South Africa	medroxyprogesterone acetate	no effect	Silva & Villet 2006
	Ch. chloropyga (Wiedemann)	South Africa	norethisterone enanthate	no effect	Silva & Villet 2006
	Ch. megacephala (F.)	Brazil	nandrolone decanoate		Souza *et al*. 2011
	Ch. putoria (Wiedemann)	Brazil	diazepam	larvae developed faster; pupariation delayed; eclosion delayed	Carvalho *et al*. 2001
	Ch. putoria (Wiedemann)	Brazil	cocaine	larvae developed faster	Carvalho *et al*. 2012
	Ch. putoria (Wiedemann)	Brazil	nandrolone decanoate		Souza *et al*. 2011
	Lucilia sericata (Meigen)	Belgium	morphine	larvae developed slower	Bourel *et al*. 1999
	L. sericata (Meigen)	Switzerland	codein	larvae developed faster	Kharbouche *et al*. 2008
	L. sericata (Meigen)	China	ketamine	larvae developed faster; larger trophocytes	Zou *et al*. 2013
	L. sericata (Meigen)	Brazil	cocaine	larvae developed faster	Carvalho *et al*. 2012
	L. sericata (Meigen)	Egypt	cadmium	larvae developed slower	Al-Misned 2001, 2003
	L. sericata (Meigen)	Brazil	nandrolone decanoate		Souza *et al*. 2011
Sarcophagidae	*Sarcophaga* (*Liosarcophaga*) *tibialis* Macquart	South Africa	hydrocortisone	larvae developed slower	Musvasva *et al*. 2001
	S. (*Li.*) *tibialis* Macquart	South Africa	sodium methohexital	larvae developed slower; eclosion sooner	Musvasva *et al*. 2001
	S. (*Liopygia*) *ruficornis* (F.)	Hawaii	methamphetamine		Goff *et al*. 1992
	S. (*L.*) *ruficornis* (F.)	Hawaii	amitriptyline		Goff *et al*. 1993
	S. (*L.*) *ruficornis* (F.)	Hawaii	phencyclidine		Goff *et al*. 1994
	S. (*L.*) *ruficornis* (F.)	Hawaii	3,4-methylenedioxymethamphetamine		Goff *et al*. 1997; Sadler *et al*. 1997*c*
	S. (*Prionophalla*) *peregrina* (Robineau-Desvoidy)	Hawaii	cocaine		Goff *et al*. 1989
	S. (*P.*) *peregrina* (Robineau-Desvoidy)	Hawaii	heroin		Goff *et al*. 1991

Table 7.4. Families and genera of Diptera regularly found in stored foodstuffs (after Hill 2002).

Family	Genus/genera	Family	Genus/genera
Agromyzidae	various	Phoridae	*Megaselia* Rondani
Anthomyiidae	*Delia* Robineau-Desvoidy	Piophilidae	*Piophila* Fallén
Calliphoridae	*Calliphora* Robineau-Desvoidy; *Lucilia* Robineau-Desvoidy	Psilidae	*Psila* Meigen
Cecidomyiidae	*Contarinia* Rondani	Sarcophagidae	*Sarcophaga* Meigen
Drosophilidae	*Drosophila* Fallén	Scenopinidae	*Scenopinus* Latreille
Lonchaeidae	*Lonchaea* Fallén	Sciaridae	*Pnyxia* Johannsen; *Sciara* Meigen
Muscidae	*Musca* L.	Syrphidae	*Eumerus* Meigen; *Merodon* Meigen
Mycetophilidae	*Mycetophila* Meigen	Tephritidae	various

al. 1997; Sadler *et al*. 1997*c*) and *Megaselia scalaris* (Phoridae) (Fig 8) (Miller *et al*. 1994), as models.

A variety of necrophagous flies have proved suitable as entomotoxicological specimens, as have carrion beetles (Bourel *et al*. 2001), so it is likely that practically any necrophage can serve this forensic purpose, providing enough relevant tissue is available. Sadler *et al*. (1997*a*, *b*) pointed out some crucial caveats to this line of evidence.

Criminal neglect of people and animals

Domestic animals, children and the elderly may be neglected by their caregivers, leading to various forms of myiasis (Benecke 2010: 627; Cooper & Cooper 2008; Zumpt 1965: 1). Where the sufferer is still alive, the estimated age of the immature flies provides an indication of the minimum duration of neglect. If the sufferer has died, the premortem presence of muscid larvae in sores or soiled nappies may complicate the estimation of post-mortem intervals (Benecke 2010: 627), but may still be evidence of criminal neglect.

Lucilia sericata (Calliphoridae), *Muscina stabulans* (Fallén), *Musca domestica* L. (Muscidae) (Fig. 5) and *Fannia canicularis* (L.) (Fanniidae) (Anderson & Huitson 2004; Benecke 2010: 627; Chapman 1944), are commonly present in cases of neglect. Zumpt (1965: 1) provided an excellent compilation of case material for the myiasis-causing flies of the Old World.

Stored product forensic entomology and biosecurity

Cases involving stored products tend to address issues governed by common and civil law, such as claims from commercial insurances. Biosecurity refers to the prevention of movement of pest species across national and international boundaries and borders, particularly in association with travellers and imported goods, plants and animals.

Stored products

Stored products that become infested with insects are usually dried, which means that the relevant insects are predominantly beetles and moths and that flies rarely have significance here. However, flies of fifteen families have been recorded as predictable contaminants of stored foodstuffs (Table 4) and *Ch. putoria*, *Ch*. *megacephala* and *Ch*. *albiceps* will attack drying fish (Esser 1991; Meynell 1978).

Scenopinus fenestralis (L.) (Scenopinidae) is a dipteran predator in the larval stage of the immature stages of moths (Lepidoptera) and carpet beetles (Dermestidae: *Anthrenus* Müller) associated with stored grain (Harney 1993: 108), so its presence may indicate infestations by its prey.

Biosecurity and phytosanitation

Exported and imported products can carry insects to countries where they are not present, but can become serious economic pests, through both the loss of resources and domestic productivity and the loss of export markets, or threats to local flora and fauna (Pimentel *et al*. 2005; Youm *et al*. 2011). For example, *Bactrocera dorsalis* (Hendel) (= *B. invadens* Drew, Tsura & White) (Tephritidae) (Fig. 6), a species that originated in Asia and appeared in the Afrotropics in 2003, has apparently depressed indigenous populations of *Ceratitis cosyra* Walker (Tephritidae) (Rwomushana *et al*. 2009) and caused a loss to Kenya's fruit industry of about KSh477.6 million annually in revenues from South Africa in 2006–2007, due to a ban on importing Kenyan fruit that risked introducing the pest to South Africa (Muchemi *et al*. 2010: 1418); similar import bans have been emplaced by Mauritius, Seychelles, the European Union and the United States. Besides their involvement in insurance cases associated with rejected exports, forensic entomologists may assist various national inspection services to enforce a spectrum of trade agreements and import legislation.

The list of flies that are relevant under this heading includes every agricultural, medical and veterinary pest that is not already present in the receiving port.

Urban forensic entomology

This facet of forensic entomology can be conveniently divided into two spheres of litigation: domestic situations within homes, which primarily concern commercial domestic pest control issues, and community health issues, which characteristically involve industrial pest control. In either case, pestilent flies in urban areas can lead to litigation, usually between private parties and under common and civil law and a forensic entomologist may provide evidence of the source of the pests.

Community health

These situations commonly involve synanthropic flies that pose public health risks. For instance, *Lucilia cuprina* (Wiedemann), which can carry shigella dysentery, became a problem in Cape Town, South Africa, after a change in the municipal refuse management system (Tourle *et al*. 2008). Muscoid flies, especially *M. domestica* and *Muscina stabulans*, can be a nuisance for neighbours of refuse dumps, stables, pig farms, abattoirs and similar breeding sites of flies. *Chrysomya chloropyga*, *Ch. putoria* and *Ch. megacephala* breed in chicken farms (Hulley 1983) and fish markets (Esser 1991; Meynell 1978). Similarly, mosquitoes (Culicidae) may breed in rain barrels and clogged gutters in urban areas and in rainwater accumulated in discarded tyre casings, leading to local nuisances. *Eristalis tenax* (L.) (Syrphidae) larvae intermittently appear in tap water, which can lead to litigation.

Domestic settings

Domestic disputes over recalcitrant fly infestations may arise between homeowners and fumigation companies. In Namibia, Nigeria and South Africa, *Apotropina gregalis* (Lamb) (Chloropidae) spontaneously forms dense aggregations in sheltered places, including houses and soils them conspicuously (Kirk-Spriggs *et al*. 2001). Pest exterminators may face unsatisfied customers if infestations recur, which they usually do.

Flies associated with contaminated foodstuffs in industrial settings (Table 4) may also infest food within the home. Similarly, myiasis of animals and people may occur in non-criminal settings (Zumpt 1965: 1), but involves the same species as were discussed under "Criminal neglect of people and animals" above. An unusual exception is the psychological condition of delusory parasitosis, or Ekbom Syndrome, where a person holds an unshakable belief that an infestation is present, even though the insect cannot be found (Freudenmann & Lepping 2009; Hinckle 2010). There are several possible explanations for this situation and a forensic entomologist may help to produce evidence that can discriminate amongst them by seeking confirmatory specimens and assessing whether the biology of the perceived infestation matches that of any known fly, or other parasite.

Environmental forensic entomology

Environmental forensic entomology is concerned with common and civil law relating to the health of natural and human environments and may, therefore, be litigated in relation to public and environmental good, e.g., the South African Water Law. It uses insects as environmental "canaries" and "sentinels" to provide evidence of environmental conditions (McGeoch 1998), such as pollution by petrochemical products, fertilisers, poisons (including herbicides, insecticides and heavy metals) and oestrogen-mimicking compounds. The evidence may include acute effects, such as extinction of populations and changes in community structure; subacute effects such as altered reproductive patterns; and chronic effects such as developmental anomalies and bioaccumulation of chemicals (Gerhard 2002).

Environmental monitoring

Flies can serve as biological (including environmental, ecological and biodiversity) indicators (McGeoch 1998). Environmental indicators respond predictably and measurably to environmental change, while ecological indicators provide information about the condition of the environment (Pollet 2009). Other forms of biological monitoring (*e.g.*, biodiversity indicators), are less likely to be relevant to legal cases, but could provide evidence in environmental impact assessments.

Environmental change may be indicated by many species of flies (Pollet 2009), but some have been investigated particularly thoroughly because they are pests, e.g., some African Blackflies (Simuliidae) (Myburgh & Nevill 2003). Although not deployed in a forensic setting, this application has also been illustrated using African midges (Chironomidae) (Eggermont *et al*. 2008; Walker 2001: 43).

Community-based indices of ecological health of rivers have been developed in South Africa (South African Scoring System v. 5 [SASS5]; Dickens & Graham 2002) and Kenya (Benthic Index of Biotic Integrity [B-IBI]; Masese *et al*. 2009). The SASS5 method is ISO-accredited (Dickens & Graham 2002) and, therefore, particularly attractive as forensic evidence. Both indices take aquatic flies into account. Community patterns have also been investigated in relation to organic pollution in Nigeria, but again without an explicitly forensic context (Arimoro *et al*. 2007).

Ecotoxicology

The forensic principles of ecotoxicology are similar to those mentioned under "Medico-criminal forensic entomology" above. The presence of polluting chemicals may be indicated by flies that show either acute effects, such as increased mortality, or chronic effects, such as abnormal morphology, or disrupted developmental schedules. Chironomid midges have received particular attention in this context (Gerhardt *et al*. 2004; Janssens de Bisthoven *et al*. 2004, 2005). Additionally, as in medico-criminal cases, flies can provide forensic samples because they may accumulate chemicals, such as mercury, cadmium, chromium and selenium in their bodies during development (Al-Misned 2001, 2003*a*; Jensen *et al*. 2005; Nuorteva & Nuorteva 1982; Trumble & Jensen 2004), providing both a direct means for detecting pollutants and a way to trace their origin by considering the biology of the flies.

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PHYTOSANITARY SIGNIFICANCE OF DIPTERA 8

Mervyn W. Mansell

Introduction

Diptera are one of the most significant orders of insects, if not the most important of all, with regard to influence upon human activities, insect diversity, adaptability, ecological ranges and beneficial environmental services. This is highlighted by accompanying introductory chapters in this *Manual* that deal with the agricultural and veterinary, medical and forensic significance of the order (see Chapters 5–7). Although the vast majority of flies are beneficial within the environment and to humankind, a few species compete directly with man, animals and other insects for food resources which, in turn, influences food sustainability, trade, wealth generation and environmental threats by competitive invasive species. A few species are also of major medical and veterinary significance, either as vectors of human and animal diseases, or as direct causative agents (see Chapters 5 & 6).

The impact of Diptera on trade, wealth generation from agriculture and consequent sustainable livelihoods is among the most deleterious effects of flies. Paradoxically, their phytosanitary importance is limited to very few families and almost exclusively to the true fruit flies of the family Tephritidae. Even within this family, there are a limited number of species of phytosanitary significance, but the economic and social impact of these notorious pests is incalculable. The term "phytosanitary" is essentially the control of plant diseases, especially in agricultural crops, but also in ornamentals and threats to the natural environment, and flies play a highly significant role in this.

Although the most obvious phytosanitary impact of flies lies in the economic losses incurred through trade restraints, there are far wider ramifications, ranging from pests that do not appear on international quarantine lists, preventative measures, that include quarantine restrictions, detection and surveillance and management, to pre- and post-harvest treatments, all of which are guided by international protocols and bilateral agreements between countries. There are further aspects that include research and information programmes and the losses incurred by both commercial and small-scale enterprises that are difficult to assess in absolute financial or socio-economic terms.

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 1. Introductory chapters and keys to Diptera families. *Suricata* 4. South African National Biodiversity Institute, Pretoria; pp. 195–202.

This chapter highlights the most significant species that impact upon trade and market access, both within countries and between external trading partners and also the devastating consequences of flies on sustainable rural livelihoods, where damage caused by flies has far-reaching financial and social implications. The main focus is on the family Tephritidae, which are used as examples for the phytosanitary activities that ensure crop protection, trade and food security.

Diptera of phytosanitary significance

International quarantine pests

Each country that trades internally, or externally, formulates pest lists across a wide spectrum of organisms of which insects comprise a significant proportion. These lists are designed as a first line of defence against deleterious species that could impact negatively upon agricultural production and trade and hence upon the economy and social stability of the importing country or region within a country.

The pest lists of the United States of America Department of Agriculture (USDA), the European Plant Protection Organization (EPPO), the South African Department of Agriculture, Forestry and Fisheries (DAFF) and others, reveal a limited number of Diptera families of which Tephritidae provide the overwhelming majority. Other families include Agromyzidae and Drosophilidae. Essentially, only three families of Diptera are currently regarded as international threats to agriculture and trade and these comprise species that do not occur naturally in an importing country. Several other families, *i.e.*, Cecidomyiidae, Chloropidae and Muscidae, can be serious local phytosanitary pests that do not pose an imminent threat to importing countries, or do not infest commodities that are being traded. When any of the local pests are perceived as a potential invasive risk they are included in pest lists of an importing country.

The number of species that appear on the pest lists is relatively limited, compared to the actual extent of the order and most pest lists only incriminate one family, the Tephritidae, and in particular, five genera, *Anastrepha* Schiner, *Bactrocera* Macquart, *Ceratitis* MacLeay, *Dacus* Fabricius and *Rhagoletis* Loew (*Anastrepha* and *Rhagoletis* are not recorded from the Afrotropical Region).

The genus *Ceratitis* contains a number of pest species that include the world's worst tephritid pest, *C. capitata* (Wiedemann): the Mediterranean fruit fly or Medfly (White & Elson-Harris 1992) (Fig. 1), the provenance of which is the Afrotropical Region (De Meyer *et al*. 2004), but has now spread across five continents. Other Afrotropical *Ceratitis* species that appear on quarantine pest lists include the Natal fruit fly, *C. rosa* Karsch (Fig. 2), which has been introduced outside its native region, including the Mascarene Is. and Seychelles (White *et al*. 2001). Others include the Marula, or Mango fruit fly, *C. cosyra* (Walker) (Fig. 3), the Madagascan fruit fly, *C. malgassa* Munro and *C. punctata* (Wiedemann), all of which are endemic to the Afrotropics and have a wide variety of wild and cultivated hosts, including several staple crops.

Only one species of African *Dacus*, *D. ciliatus* (Loew) (Fig. 4), the Lesser pumpkin fly, or Ethiopian fruit fly, appears on quarantine pest lists and is now widespread beyond the Afrotropics.

One endemic species of *Bactrocera*, the Olive fruit fly, *B. oleae* (Rossi) (Fig. 5), two further invasive *Bactrocera* species and a *Zeugodacus* Hendel have also established in the Afrotropical Region. Of these, the Melon fly, *Z. cucurbitae* (Coquillett) (Fig. 6) (see Virgilio *et al*. 2015 for details of updated name), is widespread, while the Peach fruit fly, *B. zonata* (Saunders), is now known from Egypt, Libya, Mauritius, Réunion Is. and Sudan, and the Malaysian fruit fly, *B. latifrons* (Hendel), only from Kenya and Tanzania. The recent invasion of Africa by the Asian fruit fly, *B. invadens* Drew, Tsurutu & White (recently synonymised with the Oriental fruit fly, *B. dorsalis* (Hendel) by Schutze *et al*. (2014)) (Fig. 7), has resulted in a pest that is proving far more destructive and invasive than *Ceratitis capitata* and is now cause for major concern from both quarantine and food security perspectives. These invasive species are comprehensively documented by De Meyer *et al*. (2007), in an active website hosted by the Royal Museum for Central Africa, Tervuren, Belgium.

Only two other families, Agromyzidae (Leaf-mining flies) and Drosophilidae (Vinegar flies), currently appear on the major pest lists. The leaf-miners are represented by three species of *Liriomyza*: *L. huidobrensis* (Blanchard), *L. sativae* Blanchard and *L. trifolii* (Burgess), all of which are now known from the Afrotropical Region. One species of vinegar fly, *Drosophila suzukii* Matsumura, the Spotted-wing *Drosophila*, has not yet been recorded in Africa, but is a growing concern, at least in Europe and has the potential to spread into the Afrotropical Region in the near future.

African pests of phytosanitary significance

The major local pests of phytosanitary significance and pest status also reflect a limited number of Diptera representing only six families: Agromyzidae, Cecidomyiidae, Chloropidae, Diopsidae, Muscidae and Tephritidae (as discussed in Chapter 5). Once again, fruit flies predominate and further species can be added to the discussion in Chapter 5 and above. *Ceratitis* spp. include: *C. fasciventris* Bezzi; *C. anonae* Graham; *C. quinaria* (Bezzi) the Five-spotted fruit fly and *C. rubivora* (Coquillett) the Blackberry fly. The genus *Dacus* includes several important local pests of mainly the Cucurbitaceae in *D. bivittatus* (Bigot) (Fig. 8), the Pumpkin fly that is common and widespread, *D. frontalis* Becker (Fig. 9), *D. punctatifrons* Karsch and *D. vertebratus* Bezzi, the Jointed pumpkin fly. In the genus *Trirhithrum*, *T. nigerrimum* (Bezzi) and *T. coffeae* Bezzi are well known pests of coffee (White & Elson-Harris 1992). All of the economically important Tephritidae that occur in Africa have been summarised and keyed in a field guide edited by Ekesi & Billah (2007), which is now also available in French and Portuguese.

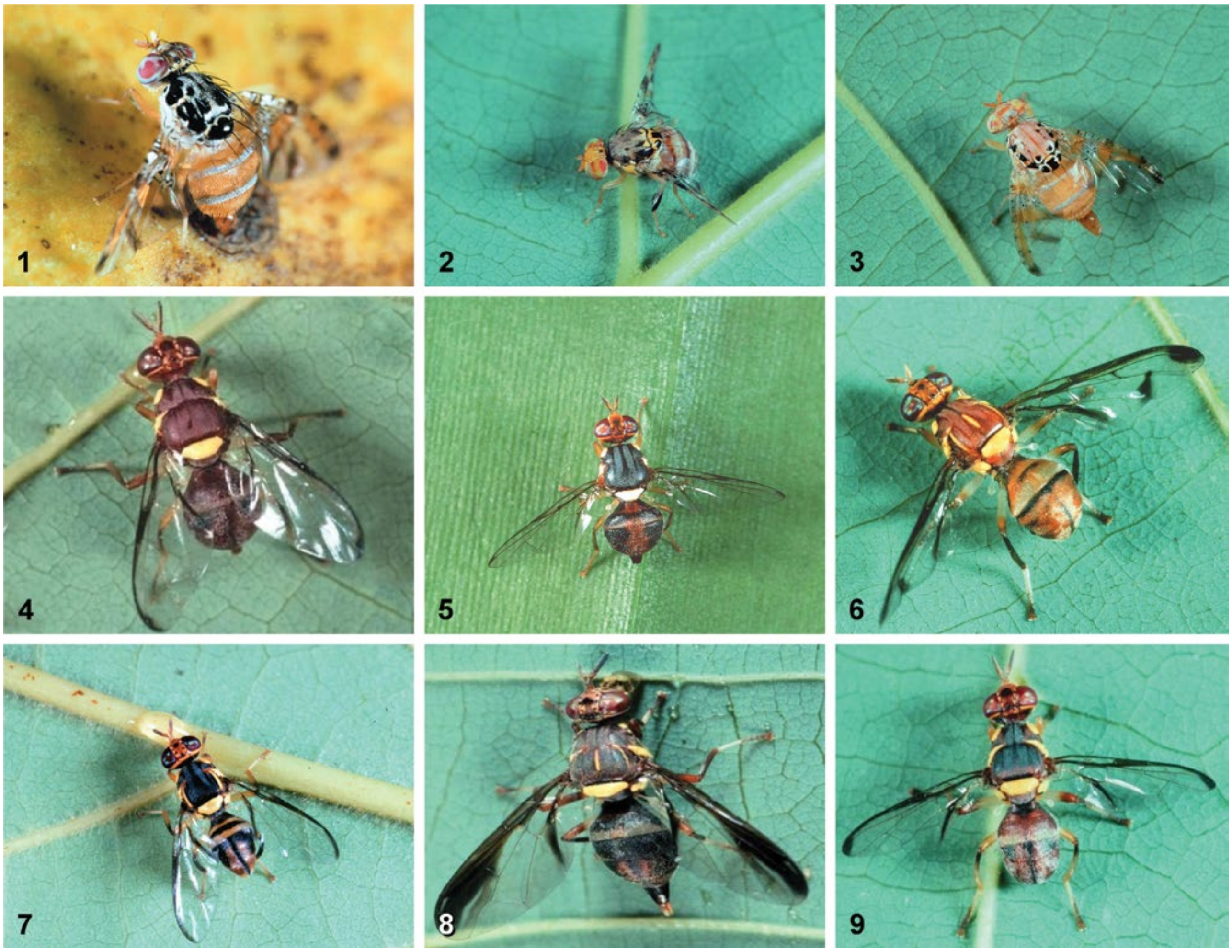
Phytosanitary conventions

Each country has the sovereign right to impose phytosanitary measures on the importation of plant material, plant products, associated potting substrates, packaging, wooden pallets and containers. These measures are designed to prevent the accidental or deliberate importation of alien pests that could impact on the biodiversity or biosecurity of the importing country. Technically justified phytosanitary measures are formulated within a set of international standards developed by the International Plant Protection Convention (IPPC) of the United Nations Food and Agriculture Organization (FAO).

A background to the IPPC, its origins and objectives are provided by Wikipedia and are paraphrased here to place it within context. The IPPC was established in 1951 as a multilateral treaty overseen by the FAO that aims to secure coordinated and effective action to prevent and control the introduction and spread of pests of plants and plant products. The Convention extends beyond the protection of cultivated plants to the protection of natural flora and plant products.

While the IPPC's primary focus is on plants and plant products moving in international trade, the Convention also covers research materials, biological control organisms, germplasm banks, containment facilities, food aid, emergency aid and anything else that can act as a vector for the spread of plant pests, including containers, packaging materials, soil, vehicles, vessels and machinery. The IPPC that was created by member countries of the FAO, emphasises three core areas: international standard setting; information exchange and capacity development for the implementation of the IPPC, and associated international standards, known as the International Standards for Phytosanitary Measures (ISPMs), that can be accessed at: https://www.ippc.int/core-activities/standards-setting/ispms. There are currently 62 ISPMs including their annexes that have been adopted, of which 15 deal specifically with Tephritidae, highlighting the significance of fruit flies in international phytosanitary issues.

The Commission of Phytosanitary Measures of the IPPC has developed a strategic framework with the following objectives: protecting sustainable agriculture and enhancing global food security through the prevention of pest spread; protecting the environment, forests and biodiversity from plant pests; facilitating economic and trade development through the promotion



Figs 8.1–9. Habitus of phytosanitary significant fruit flies (Tephritidae): (1) *Ceratitis capitata* (Wiedemann); (2) *C. rosa* Karsch; (3) *C. cosyra* (Walker); (4) *Dacus ciliatus* (Loew); (5) *Bactrocera oleae* (Rossi); (6) *Zeugodacus cucurbitae* (Coquillett); (7) *B. dorsalis* (Hendel) (= *B. invadens* Drew, Tsurutu & White); (8) *D. bivittatus* (Bigot); (9) *D. frontalis* Becker. Photographs © R.S. Copeland.

of harmonised scientifically based phytosanitary measures; and developing phytosanitary capacity for members to accomplish the preceding three objectives. By focusing the Convention's efforts on these objectives, the Commission on Phytosanitary Measures of the IPPC intends to: protect farmers from economically devastating pest and disease outbreaks, protect the environment from the loss of species diversity, protect ecosystems from the loss of viability and function as a result of pest invasions, protect industries and consumers from the costs of pest control or eradication, facilitate trade through ISPMs that regulate the safe movements of plants and plant products and protect livelihoods and food security by preventing the entry and spread of new pests of plants into a country.

Besides the international conventions, trading partners also hold regular bilateral meetings to determine and agree upon trade agreements and protocols on specific products.

Phytosanitary protocols and procedures

The procedures and protocols that are required for the management and control of phytosanitary pests have been formulated to reduce infestation or, rarely, to eliminate the threat permanently. These are aimed at meeting the requirements of trading partners and safeguarding food security in production areas. The latter is particularly significant in any phytosanitary context, as over 80% of rural populations in Africa are engaged in the agricultural sector, either as small-scale producers, subsistence farmers, or informal traders, mainly women (Fig. 11), who are almost entirely dependent on these activities for food security and income generation. Infestations of pests, especially Tephritidae, have a severe adverse effect upon this sector and its sustainability. The threat has recently been exacerbated by the introduction of several invasive species of *Bactrocera*, in particular *B. invadens* (now *B. dorsalis*) and *B. cucurbitae* (now *Z. cucurbitae*) which directly affect staple crops, including mango, citrus, guava and Cucurbitaceae.

Phytosanitary measures can be broadly divided into three categories: surveillance and pre-harvest and post-harvest treatments.

Surveillance. This is invariably the first and then subsequent ongoing activity that underpins other phytosanitary measures. Guidelines for surveillance have been formulated in ISPM 06 (1997), ISPM 26 (2014) and ISPM 30 (2011) of the IPPC. Surveillance begins with Detection surveys to determine the presence of a pest species, then Delimitation surveys to establish the exact geographical extent of infestation, followed by continual Monitoring surveys to follow the pest spread and efficacy of control measures. Surveillance is crucial to the determination and maintenance of Pest Free Areas (PFAs), or Areas of Low Pest Prevalence (ALPPs), whose requirements are specified in ISPM 04 (1995), ISPM 26 (2014), ISPM 22 (2005) and ISPM 30 (2011), respectively and are essential phytosanitary requirements in trade negotiations between countries.

Surveillance usually comprises the use of parapheromone-baited traps (Jang *et al.* 2014), with specific lures designed to mimic natural attractants for specific species (not only fruit flies), as well as natural products, such as hydrolysed yeast, vinegar and fruit extracts (see IAEA 2013, for extensive guidelines for surveillance and bait formulae). Traps are deployed in applicable formats, depending on the area covered. Further techniques involve rearing specimens from fruits and vegetables, or indigenous hosts and fruit sampling and cutting.

In recent years, extensive surveillance programmes have been in progress in South Africa and other African countries. In South Africa, a permanent trapping programme is maintained by the National Plant Protection Organisation of South Africa (NPPOZA), within the Department of Agriculture Forestry and Fisheries (DAFF), in collaboration with private producers, research organisations, provincial departments of agriculture, and fruit industry associations (Barnes & Venter 2008). This led to the first detection of *B. invadens* (now *B. dorsalis*) on the northern borders of South Africa and subsequent attempts at eradication (Manrakhan *et al*. 2011).

The International Centre for Insect Physiology and Ecology (ICIPE), Nairobi, Kenya, initiated the African Fruit Fly Initiative (AFFI) to conduct research and surveillance on fruit flies, primarily Medfly, in Kenya, Tanzania and Uganda (Lux 1999). It was this programme that led to the first detection of an alien species in a methyl eugenol-baited trap and rearing from an indigenous *Strychnos* (Loganiaceae) host in Kenya (Lux *et al*. 2003). Initially identified as *B. dorsalis*, the species was later formally described as *B. invadens* by Drew *et al*. (2005), but has now been returned to synonymy with *B. dorsalis*, by Schutze *et al*. (2014).

In 2004, the United States Department of Agriculture (USDA), through its Animal and Plant Health Inspection Services (USDA-APHIS) division in Pretoria, South Africa initiated an African Fruit Fly Programme that provided basic trapping equipment and technical support, including an identification service and training courses to the following African countries: Angola, Botswana, Ethiopia, Madagascar, Malawi, Mozambique, Namibia, Rwanda, Senegal, Swaziland and Zambia, which included on-site visits (Figs 10–15). The surveys, which were initially detection and delimiting surveys for the production of pest lists, led to the initial detection of two invasive species, *Z. cucurbitae* (then *B. cucurbitae*) and *B. dorsalis* (then *B. invadens*), in several of these countries, and contributed significantly to tracking the rapid spread of *B. dorsalis* throughout sub-Saharan Africa. The APHIS initiative was later augmented by USDA Foreign Agriculture Service (USDA-FAS), through the advisory and coordination role of the SPS advisors, working in concert with APHIS since 2008. Additionally, a programme supported by the British Department for International Development (DFID) and its implementing agency Trademark Southern Africa (TMSA), who provided vital funding for subsequent surveys, training and fruit fly management, thereby enabling the local agriculture departments in Malawi, Swaziland, Zambia and Zimbabwe to manage their own surveillance and management programmes. Funding has also been provided by the United States Agency for International Development (USAID) through various projects, and from project ENBI WP13, based at the Royal Museum of Central Africa, Tervuren, Belgium (De Meyer & White 2004: http://projects.bebif.be/enbi/fruitfly).

USAID funding supported three specialised training courses in the surveillance and management of fruit flies at ICPE in 2009, 2012 and 2013. The Insect Pest Control Sub-programme of the International Atomic Energy Agency, in Vienna, Austria, initiates and manages several regional projects in Africa, among others in West Africa and in countries situated in, or bordering on, the Indian Ocean (Mozambique, Tanzania), with the aim of preventing the introduction of exotic fruit fly species, or control of fruit flies of economic significance, along with coordinated research projects focusing on research aspects related to insect pests.

Pre-harvest treatments. This involves a number of techniques aimed at the control and management of pest populations and include: orchard sanitation; integrated pest management programmes (IPM), that are increasingly being extended into area-wide programmes (AW-IPM), due to the high vagility of insects; sterile insect techniques (SIT), which are being applied in the Western Cape Province of South Africa (Barnes *et al*. 2004); insecticide application; male annihilation techniques (MAT); fungal pathogens, biological control; and restrictions on movement of produce from infected areas.

Post-harvest treatments. Once produce has been harvested, there are a number of options available to ameliorate against infestations posing a threat to trading in that commodity. Pack house and export quarantine inspections can detect infested products by visual examination and cutting of random samples to determine the presence of infestation. Port authorities are specifically trained for this purpose and are often employed by an importing country on a permanent basis in the country of origin. For example, such an agreement is in place at Cape Town harbour, where a permanent local expert is employed by USDA-APHIS to inspect all fruit bound for the United States of America. The employee is frequently assisted by temporary duty inspectors from the USDA-APHIS during peak export periods of particular commodities (*e.g.*, citrus). The sampling procedures are informed by ISPM 31 (2009), as well as the preceding ISPM 20 (2004) and ISPM 23 (2005).

Importing countries may also insist upon further measures, including irradiation, fumigation, heat treatment through water-baths or forced hot air, or prolonged cold treatment, depending on the type of crop. For example, citrus is treated by cold storage during shipment as it is not suitable for any form of heat treatment, while mangos are best subjected to heat treatments. A number of irradiation protocols are in place for fruit flies, including *C. capitata* (ISPM 28, Pt14 (2011)) and other pests under its annexes from ISPM 28: 1–14. A heat treatment protocol is available under ISPM 28: Annex 15 (2014) for *B. cucurbitae* (now *Z. cucurbitae*) on a species of *Cucumis* (Cucurbitaceae). Commodities are then further subjected to close scrutiny at ports of entry, where infestations that exceed a set threshold may result in the entire shipment being rejected at considerable financial loss to the exporting country and producers.

Commercial impact of Diptera

The global commercial impact of Diptera is impossible to determine, although it certainly runs into hundreds of millions of dollars annually, when actual losses and costs of prevention and management are considered. The socio-economic aspects are even more difficult to ascertain, as one cannot attach a monetary value to the deprivation caused by insect pests through loss of food sustainability and potential income generation.

Figs 8.10–15. Monitoring and training courses on phytosanitary Diptera in Africa: (10) first surveys in Mozambique; (11) survey at informal market run by women traders, Mbabane, Swaziland; (12) field training in Zambia; (13) participants in field training in Zambia; (14) fruit fly training course in Zambia; (15) fruit fly training course in Zimbabwe. Fig. 11 (photograph S. Gebeyehu), Figs 12–14 (photographs M. Matimelo), Fig. 15 (photograph L. Makumbe).

The most compelling example of actual costs is revealed by the MOSCAMED programme, an acronym for Programa de Erradicación de la Moscadel Mediterraneo, which essentially focuses on a single species of fruit fly, the Afrotropical *C. capitata*. This programme was specifically established to control the spread of Medfly into Mexico and the United States. The MOSCAMED programme commenced in Guatemala in 1975, with Medfly pupae imported from Vienna for the establishment of a SIT programme (Tween 2004). According to the IICA (Inter-American Institute for Cooperation in Agriculture), the programme's objective is to prevent, control and eradicate outbreaks of the Mediterranean fruit fly in Mexico and cooperate with neighbouring countries to create barriers that will contain any outbreaks (IICA 2014). A study by IICA analysed the programme's cost structure and estimated that for the past 31 years it had cost USD352 million for Moscamed-Mexico and USD767 million for the regional MOSCAMED programme, a total of USD1,119 million. During the years it has been in operation, however, the programme has generated direct benefits worth USD66,421 million (IICA 2014), providing convincing figures regarding the potential impact that could be caused by a single dipteran species.

In Africa, the spread of *B. dorsalis* (as *B. invadens*) has led to significant commercial losses over a short term, as exemplified by two local examples. In 2008, *B. dorsalis* (as *B. invadens*) was detected at Cuamba in Niassa Province, Mozambique (Correia *et al*. 2008). This led to an embargo on fruit exports from Mozambique into South Africa, particularly from the Maputo area, an important production region for fruit exports to South Africa, especially bananas. This was despite the production areas in the south of the country being far removed from Cuamba in the north. USDA-APHIS, Pretoria was requested to conduct surveys in banana plantations near Maputo (Fig. 10) that showed that *B. dorsalis* (as *B. invadens*) was not present in the area, which could be considered pest free. Normal exports were resumed after bilateral discussions, but it was estimated that the two-week closure resulted in at least a USD1 million loss to producers (A. Gomez, pers. comm. 2009). Subsequent studies were furthermore carried out to establish that green bananas were not susceptible to attacks by *B. dorsalis* (as *B. invadens*) (Cugala *et al.* 2014).

In Australia, a similar invasion to that of *Bactrocera dorsalis* (then *B. invadens*) in Africa involved the Papaya fruit fly, *B. papayae* Drew & Hancock, now also synonymised with *B. dorsalis* (Schultze *et al*. 2014). The Papaya fruit fly was detected in Cairns, northern Queensland, Australia, in 1995 (Cantrell *et al*. 2002). It took three years and a budget of AUD33.5 million to eradicate the pest in Australia (http://www.agriculture.gov.au/biosecurity/quarantine/naqs/naqs-target-lists/fruitflies). The total cost, including loss to the fruit industry, due to trade restrictions and harvest losses, is estimated to amount to AUD100 million.

The presence of *B. dorsalis* (as *B. invadens*) in Kenya caused a financial loss to Kenya's fruit industry, mainly avocados, of about KSh477.6 million annually in exports to South Africa between 2006–2007, due to a ban on importing Kenyan fruit that risked introducing the pest to South Africa (Muchemi *et al*. 2010).

Discussion

Phytosanitary issues have many ramifications, ranging from the targeted pests and their accurate identification, to management and control of the pest, pre- and post-harvest treatments, international conventions and protocols, trade issues, bilateral agreements between trading partners, the restriction of product movement within countries, or regions, environmental concerns and even to political manoeuvring and protectionism. Potentially invasive species, which can be spread by formal and informal trade, or inadvertently through lack of awareness during passenger transit, will have an influence on almost every facet of these related issues and the Diptera provide two excellent examples. *Ceratitis capitata* (Medfly) was previously regarded as the world's worst fruit pest (White & Elson-Harris 1992) and its impact has been documented over many years in different parts of the world. Medfly is now being superseded by the recently invasive *B. dorsalis* (*B. invadens* – the "Invader fly"). The major causes for concern was its unexpected detection in Africa in 2003 (Lux *et al*. 2003) and the alarming rate in which it has spread throughout Africa south of the Sahara, that has left every country in the region infested. This fly is causing extensive damage in all agricultural sectors and in trade issues farther afield and must rate as one of the most successful examples of invasion biology on record. The success of *B. dorsalis* can be attributed to a number of factors: its rapid adaptation to a very wide spectrum of host species, both native and commercial (De Meyer *et al*. 2007), ensuring that a food resource is always available; its remarkable vagility, leading to rapid natural dispersal; the aggressive nature in fending off competitor species and, indeed, even the displacement of indigenous fruit flies, *e.g.*, *C. cosyra* (Ekesi *et al*. 2009); and its apparent ability to adapt climatically. It is also capable of multiple ovipositions, leading to high population numbers, *e.g.*, 112 individuals attracted within 10 minutes to a methyl eugenol-baited trap in a mango orchard in Arbaminch, Ethiopia (pers. obs.). Invasive *B. dorsalis* also appears to be a rapidly evolving species, as manifest by its adaptability to hosts and climate, exacerbated by the current lack of local natural enemies.

The recent synonymy of *B. invadens* with *B. dorsalis* does not detract from the fact that it remains an extremely serious pest, especially now in Africa. This seemingly standard taxonomic procedure, however, has far-reaching implications for phytosanitary issues and trade. Countries formerly free of the fly with the epithet of *Bactrocera invadens*, but which were infested with *B. dorsalis* will no longer be able to use this quarantine restriction as a legitimate barrier to trade and new negotiations will have to be initiated to address the taxonomic change.

Recent examples show that it will be impossible to eradicate the pest from a country through human intervention. The most extensive and thorough eradication programme in Africa was recently implemented by South Africa upon detection of *B. dorsalis* on the northern borders of the country (Manrakhan *et al*. 2011). The pest was not eradicated from South Africa, despite considerable resources and has since spread to other parts of the country including the Gauteng Province. The only viable and inexpensive long-term solution, or outcome, shall depend on how long indigenous parasites, parasitoids and other natural enemies will take to exploit the flourishing resource to bring it within economic threshold levels by natural biological control.

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BIOGEOGRAPHY OF DIPTERA 9

Ashley H. Kirk-Spriggs and Burgert S. Muller

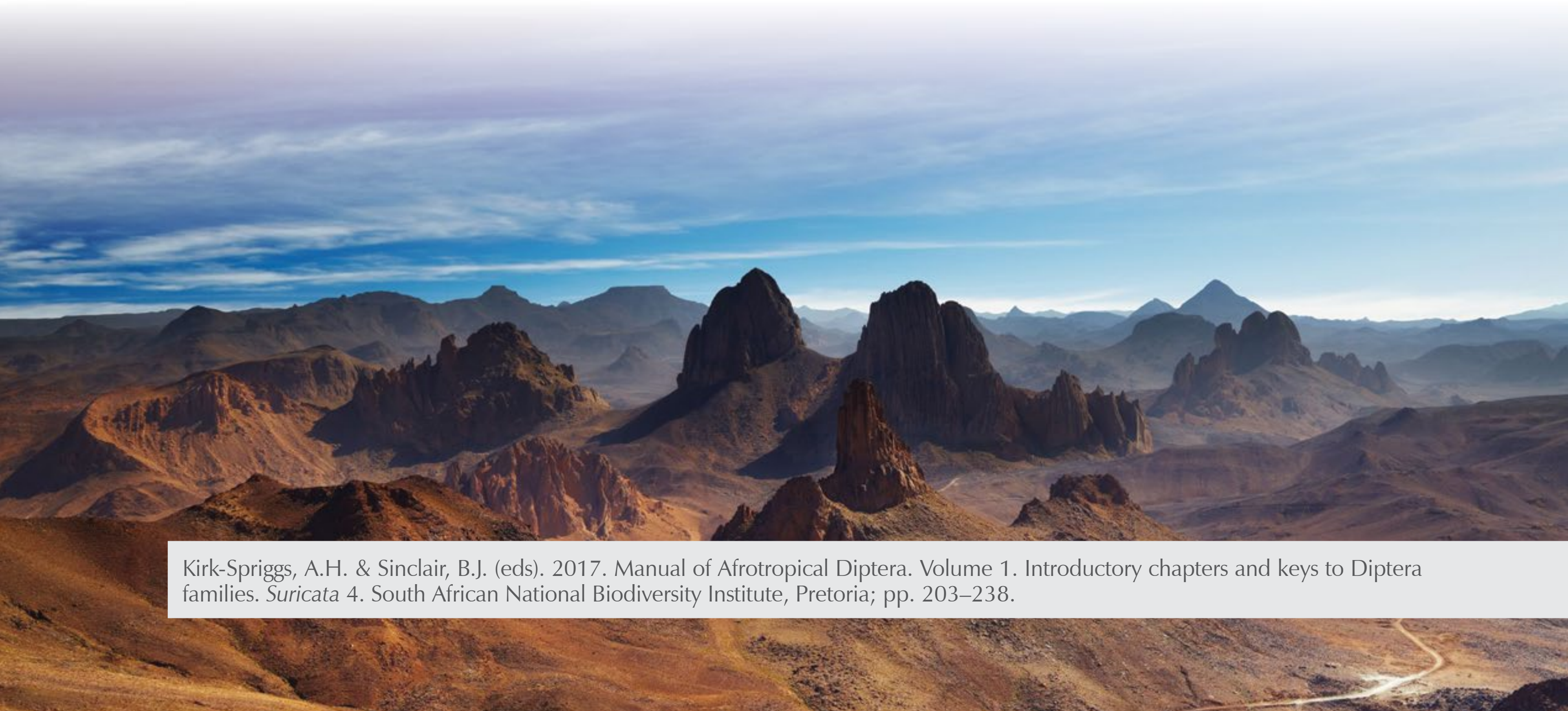
Introduction

Biogeography entails the study of the geographic distribution of taxa and their attributes in space and time. This requires the interpretation of a suite of abiotic and biotic information sets, if the distribution of organisms is to be understood. Many factors are obvious, such as geology, topography, elevation, precipitation, soil types and vegetation, but the relations to palaeoclimatology, evaporation rates and proximity to the sea, mountains and arid zones are more problematic to explain. In recent years, data on palynology, palaeobotany, palaeontology, geomorphology, plate tectonics, volcanism, desertification and other climatic trends, has increased greatly.

Diptera species occur in ranges governed by such biotic and abiotic environmental factors and distribution ranges are determined by physical and climatic factors and topography, while environmental parameters also constrain distributions. Historical factors determine more basic patterns of distribution, however, including those that may relate more directly to the formation of species (Cranston 2005: 283). As stated by Croizat (1958), present-day biotic distributions represent ancient patterns that have been disrupted (vicariated) by such factors as altered geology and climate, sea level changes, *etc*. In historical biogeography, widespread ancestral species are viewed as being divided into vicariant populations (incipient species) by sea-level changes, oceanic formation, orogeny, aridity or glaciation. The disjunct distribution of related organisms are interpreted in dispersal biogeography as having arisen when groups originate in one place, diffuse (range expand) until some kind of barrier is reached, disperse ("jump") across these pre-existing barriers, then differentiate subsequently in isolation. This theory is central to the concept of speciation by natural selection as promulgated by Charles Darwin and Alfred Russell Wallace.

Studies of the distribution patterns of Diptera have been influential in biogeographical thought, *e.g.*, Brundin (1966), de Jong (1998), Hennig (1960), Matile (1990) and Munroe (1974) (Cranston 2005: 274), but probably less so than for more sedentary groups of invertebrates. More recent published dipterological studies have focused primarily on disjunctions between continental faunas, especially ancient groups exhibiting an austral vicariance pattern attributable to common Gondwanan continental ancestry (*e.g.*, Cranston & Edwards 1992; Krosch *et al*. 2011; Martin *et al.* 2003; Miranda-Esquivel & Coscarón 2003; Sæther & Ekrem 2003; Sinclair 2003) (see below).

Stuckenberg (1962) published an account of palaeogenic (meaning of, or relating to the Paleogene period) elements in the South African insect fauna, which included some ancient groups of Diptera, but it was Bowden (1978), who was the first to discuss the biogeography of the order Diptera in Africa, especially the concept of faunal disjunctions between southern Africa, the Mediterranean Province and elsewhere. Bowden (1973, 1978: 777) was dismissive of the concept of sub-Saharan Africa as being a valid floral and faunal division between the Holarctic and African realms and termed this "the sub-Saharan syndrome"; the essentially Eurocentric viewpoint that genera and species occurring in the southern Palaearctic and North Africa must be different from those occurring south of the Sahara. He provided examples of genera in the family Bombyliidae which had formerly been regarded as separate taxa in the two regions, but were merely faunal disjunctions (see Kirk-Spriggs & McGregor 2009).



Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 1. Introductory chapters and keys to Diptera families. *Suricata* 4. South African National Biodiversity Institute, Pretoria; pp. 203–238.

Since Bowden's review, relatively few publications have appeared that deal exclusively with the biogeography of Afrotropical Diptera, most accounts being included in taxonomic papers, *e.g.*, Barraclough & Slotow (2010), Chen & Máca (2012), Coffman *et al*. (1992), De Meyer (2001), Garros *et al*. (2005), Grace-Lema *et al*. (2015), Harvey *et al*. (2003), Kirk-Spriggs (2010*a*, *b*, 2011), Kirk-Spriggs & Wiegmann (2013), Lachaise *et al*. (1998), Lamas & Nihei (2007), Löwenberg-Neto *et al*. (2012), Morita (2008), Shamshev & Grootaert (2010), Stuckenberg (1997, 1998, 2003), Stuckenberg & Fisher (1999), Swart *et al*. (2015) and Williams *et al*. (2016).

Some literature was discussed by Kirk-Spriggs (2003) in an introductory study of African biogeographical patterns and two major reviews that deal specifically with Afrotropical Diptera have been published (Kirk-Spriggs & McGregor 2009; Kirk-Spriggs & Stuckenberg 2009), on which this chapter is very largely based, with some supplementary sections and updated information.

Gondwanan plate tectonics and the formation of Africa

Prior to its separation, Africa formed an integral part of the great southern supercontinent of Gondwanaland, which first formed during the Neoproterozoic Pan-African-Brazilian orogeny (720–580 Mya). The most extensive geomorphic features of Africa, however, relate to the period that postdates the breakup of Gondwana (Figs 1–3), which took place *ca* 145 Mya on the east coast of southern Africa and *ca* 125 Mya on its west coast (Fig. 4). As a result of this breakup, the isolated African continent, as it is known today, came into being (Maud 2012).

The opening of the South Atlantic Ocean closely followed the emplacement of the plume-related Parana-Etendeka continental flood basalts (137–127 Mya) in Brazil and Namibia (Turner *et al.* 1994). In the South Atlantic, sea-floor spreading began at *ca* 135–130 Mya (Jones 1987), although the physical separation of the continents was probably not synchronous along the line of rifting (McLoughlin 2001).

Translational movement of Brazil and equatorial Africa along the Guinea Fracture Zone (Fig. 4) may have maintained low latitude connections between the continents until 119–105 Mya (Fairhead & Binks 1991; Jones 1987). Similarly, transform faulting between southernmost Africa and the easterly extension of the Falklands Plateau may have maintained continental connections or close proximity of southern Africa and South America until *ca* 105 Mya (Barron 1987; Barron & Harrison 1980; McLoughlin 2001) (Figs 2, 4).

At *ca* 95–84 Mya a new phase of rifting was initiated in the proto-Indian Ocean separating Madagascar from the Seychelles–India block (Plummer & Belle 1995). India, including its northern extension under thrust Tibet, separated from Australia and east Antarctica by the Hauterivian (*ca* 132 Mya) (Barron 1987; Veevers & Li 1991) (Fig. 4). Relatively rapid seafloor spreading in the southern Indian Ocean resulted in the Seychelles–India block movement northwards into mid latitudes by the Late Cretaceous (Barron 1987). Eruption of the Deccan traps flood basalts *ca* 65 Mya, accompanied a repositioning of the western Indian Ocean (Carlsberg Ridge) spreading ridge and resulted in separation of India and the Seychelles block. The Seychelles block subsequently became fixed with respect to Africa, while India continued its rapid northward movement, reaching equatorial latitudes by the Eocene and colliding with southern Asia *ca* 43 Mya (Gerlach 2013; McLoughlin 2001).

Diptera in the fossil record

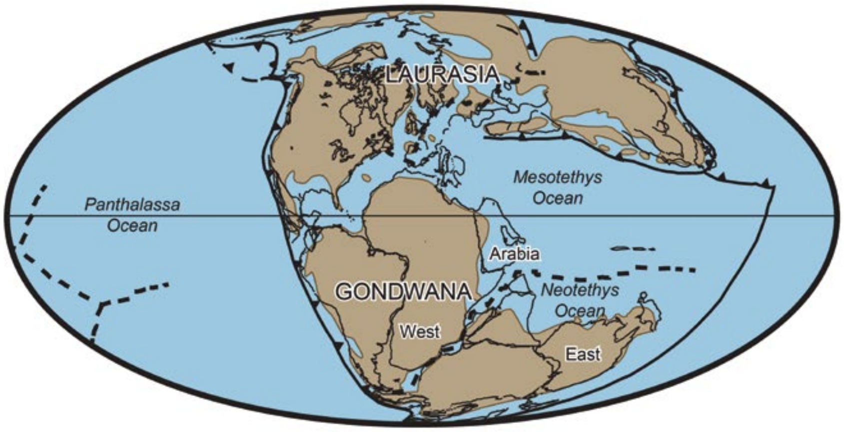
Studies of the Diptera are hampered by the lack of fossils, although excellent fossils are known from resins ranging in age from Early to Middle Cretaceous from Lebanon (Schlüter 2003) (*e.g.*, Azar *et al*. 2003, 2009; Choufani *et al*. 2015; Grimaldi 1996; Grimaldi & Cumming 1999; Hennig 1970, 1971; Schlee 1972; Veltz *et al*. 2007) (Figs 5–7). Lebanon was then part of the African tectonic plate, separated from Eurasia by the Tethys Sea and these flies have obvious relatives in the extant Afrotropical fauna (Kirk-Spriggs 2003). Epiclastic sediments overlying a diamondiferous kimberlite in central Botswana have also yielded an assemblage of fossils, including flowering plants and whole-bodied insects. Their deposition has been dated as (Early) Late Cretaceous (Cenomanian-Coniacian). The Cretaceous Crater Lake waters apparently were inhospitable, with insects dying soon after landing on the surface of the lake (Schlüter 2003). The site has yielded numerous Diptera compression fossils (*e.g.*, McKay & Rayner 1986; Rayner 1987, 1993; Waters 1989*a*, *b*), but these are invariably poorly preserved (Kirk-Spriggs 2003).

Gondwanan elements in the Afrotropics

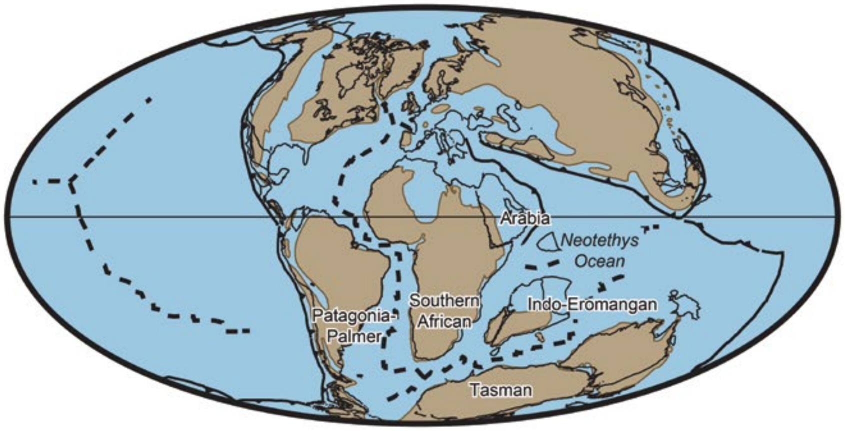
South Africa has the most distinctive invertebrate fauna in the Afrotropics. The fauna includes various taxa, the phylogenetic relationships of which indicate them to be of ancient occurrence in the region (Kirk-Spriggs 2003; Stuckenberg 1962). The explanation for their presence has been that they are remnants of a fauna that diversified and dispersed across the Gondwanan landmass before fragmentation (Figs 1–3, 4). These so-called "palaeogenic elements" thus have been termed "Gondwanan" and their presence in South Africa is of great interest, especially as their distribution pattern concurs with a biogeographical situation also involving South America and Australia. Each of these three continents has essentially two insect faunas, a southern one, mostly associated with relatively temperate environments, the other mainly in more northerly, warmer or even tropical latitudes. These austral insect faunas have taxa in common and appear to share an evolutionary history that reflects continental drift. Two areas of such putative Gondwanan insects occur in the Afrotropics namely, in South Africa and in Madagascar (Kirk-Spriggs & Stuckenberg 2009: 177). These are considered separately below.

South African elements

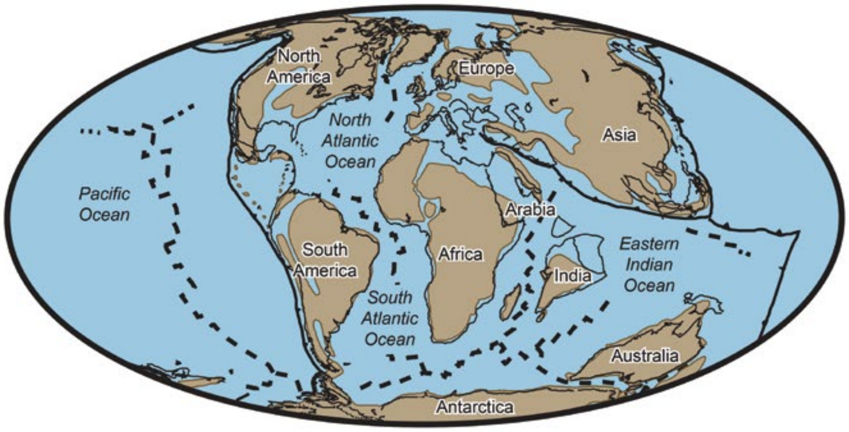
South Africa has some of Africa's oldest mountains. They are of two kinds, with entirely different origins. In the south of the country, extending more or less east-west, with a smaller interlocking north-south section in the west, is a series of elongate ranges, constituted by similar sedimentary rocks, known as the



1 Late Jurassic (152 Mya)



2 Middle Cretaceous (94 Mya)



3 Latest Cretaceous (69.4 Mya)

Figs 9.1–3. Continental reconstructions of the breakup of Gondwanaland, from the Middle and Late Mesozoic: (1) Late Jurassic (152 Mya) reconstruction indicating initial rifting between east and west Gondwana, separation of Lhasa, West Myanmar and Woyla terranes from northern Gondwana; (2) Early Middle Cretaceous (94 Mya) reconstruction shortly after isolation of Africa from other Gondwanan landmasses, opening of eastern Indian Ocean and emplacement of Kerguelen Plateau basalts; (3) Latest Cretaceous (69.4 Mya) reconstruction shortly before eruption of the Deccan Traps indicating progressive isolation of Gondwanan landmasses and rapid northward migration of India. Figs 1–3 (after McLoughlin 2001, fig. 3).

Cape Fold Mountains (*e.g.*, Fig. 8). They are part of an ancient orogeny that predated the break-up of Gondwana. At that time they were continuous with old mountains in south-eastern Australia, with the trans-Antarctic ranges and even with a small range in the Buenos Aires Province of Argentina known as the Sierra de la Ventana (Rapela *et al*. 2003).

In eastern South Africa the Great Escarpment is called the Drakensberg over much of its length (*e.g.*, Fig. 9). Orogeny was initiated with the separation of Antarctica from south-eastern Africa in the Jurassic (Figs 1, 4), when a new drainage system formed in the hinterland of the new South African coastline, flowing eastwards towards an expanding Indian Ocean. Extremely prolonged water erosion established by this drainage, operating throughout the Mesozoic and twice rejuvenated by Cenozoic episodes of continental uplift, created this escarpment in eastern South Africa. It was progressively eroded westward, until the presence of a massive, almost horizontal sequence of hard basaltic rocks retarded the rate of erosion and resulted in steep exposure of an underlying, very thick sequence of sediments. With permanent benefit of summer rains derived from an expanding and warm Indian Ocean, this escarpment could acquire and retain freshwater and terrestrial invertebrate faunas during much of the Mesozoic and Cenozoic (Kirk-Spriggs & Stuckenberg 2009: 177; Partridge & Maud 1987).

These mountains preserve ancient landforms supporting a characteristic biota including taxa of putative Gondwanan derivation, namely Blephariceridae, Thaumaleidae, Psychodidae, Empididae, Africa's only tanyderid and early branching Chironomidae amongst other flies with possible austral relationships. Documented cases of Gondwanan relicts are reviewed below:

Apioceridae (see Chapter 46). Yeates & Irwin (1996) proposed that the subgenus *Apiocera* (*Pyrocera* Yeates & Irwin) (Fig. 15) represents the sister-group to the Southern Hemisphere species and that the Afrotropical subgenus *A.* (*Ripidosyrma* Hermann) are in turn the sister-group to the clade of Chilean and Australian species, which presents evidence for a true Gondwanan origin.

Blephariceridae (see Chapter 16). The subfamily Edwardsininae has a largely Gondwanan distribution, being restricted to south-eastern Australia, southern South America and Madagascar, whereas Blepharicerinae is widespread in both hemispheres.

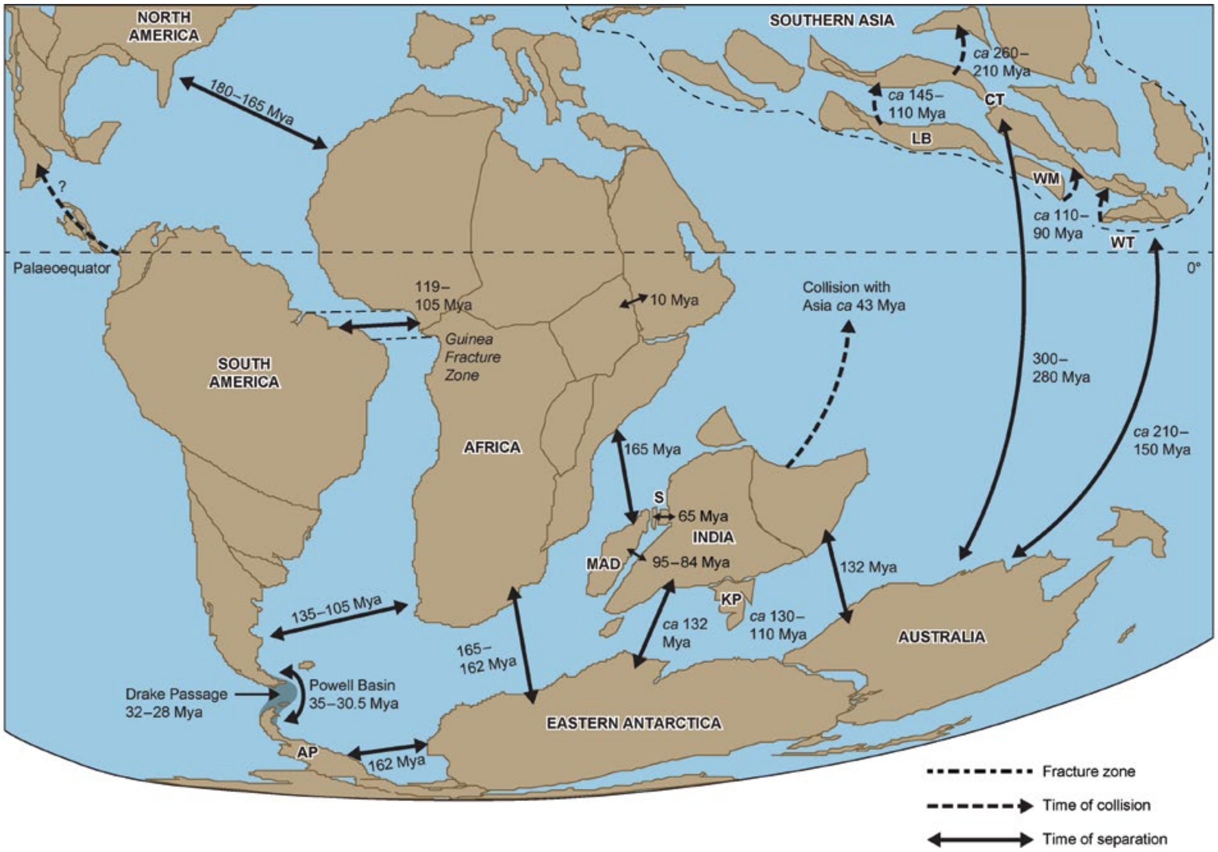


Fig. 9.4. Reconstruction of the South Atlantic–Indian Ocean–Neotethys Ocean regions during the Early Cretaceous (110 Mya), indicating the timing of separation and amalgamation of Gondwanan and Asian terranes (after McLoughlin 2001, fig. 4A).

Abbreviations: AP – Antarctic Peninsula; CT – Cimmerian Terranes; KP – Kergulen Plateau; LB – Lhasa; MAD – Madagascar; S – Seychelles Block; WM – West Myanmar; WT – Woyla Terrane.

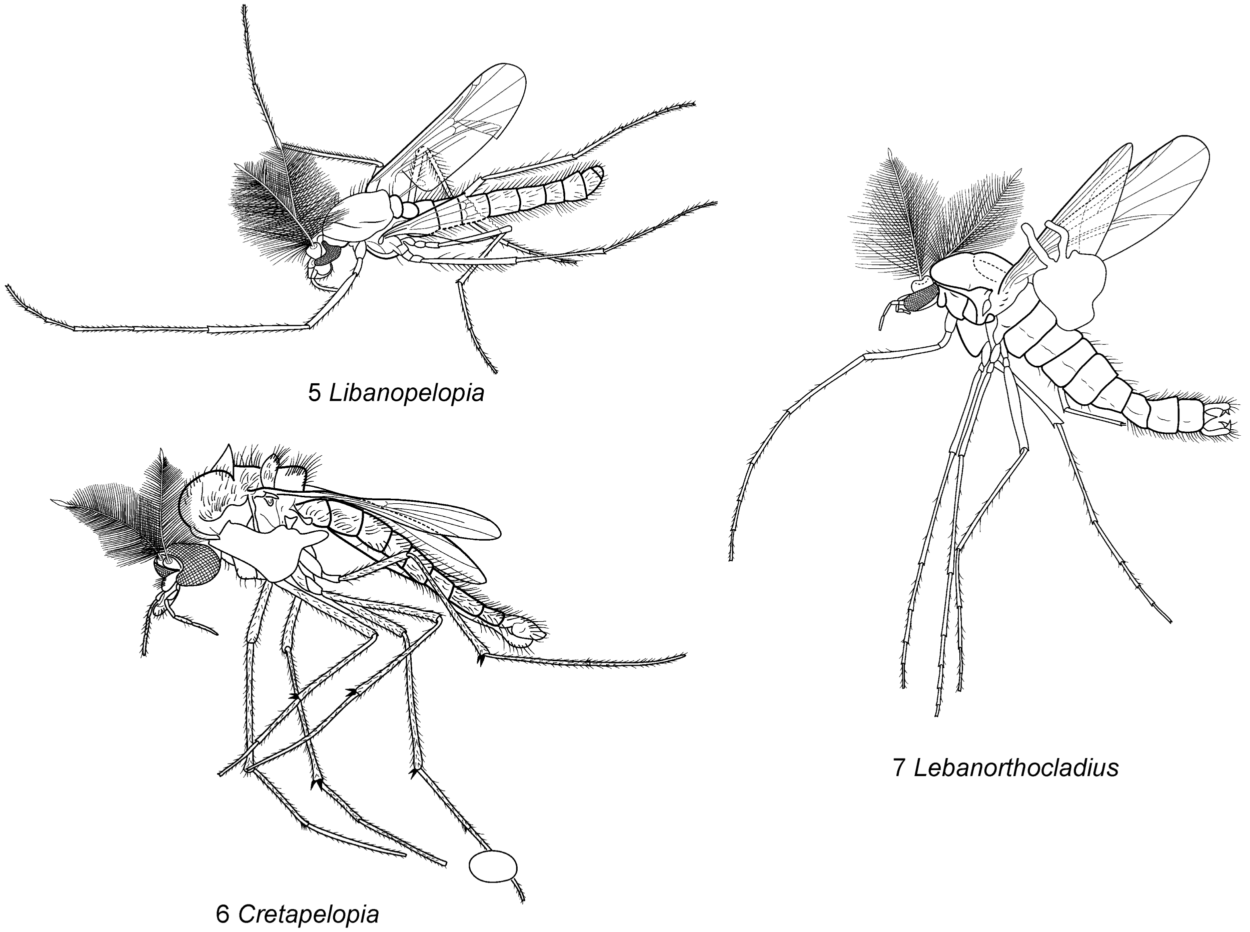
All South African species belong to the blephariceríne genus *Elporia* Edwards. It and the Malagasy genus *Aphromyia* Courtney belong to a lineage historically placed in the tribe Paltostomatini, a possibly paraphyletic assemblage that also includes several Neotropical genera. Elucidating the relationships between *Aphromyia*, *Elporia* and the various Neotropical blepharicerine genera remain problematic, due to the lack of congruence across character data. Despite uncertainties regarding relationships of "paltostomatine" genera, a good case can be made for a Gondwanan origin of at least the Edwardsininae (G.W. Courtney, pers. comm. 2017).

Chironomidae (see Chapter 35). The subfamily Podonominae has a high diversity in the Southern Hemisphere, consistent with a Gondwanan origin. Southern African genera, namely *Archaeochlus* Brundin and *Afrochlus* Freeman, have connections with Australian *Austrochlus* Cranston (Cranston *et al*. 2010; Martin *et al*. 2003; Sæther & Ekrem 2003). Another Gondwanan midge is the orthoclad genus *Elpiscladius*, described by Harrison & Cranston in 2007, and substantiated using molecular data by Cranston *et al*. (2010). Later Cranston *et al*. (2012) explored molecular derived dating for Gondwanan nodes of significance to southern Africa and noted other possible Gondwanan elements occurring in the fauna.

Empididae (see Chapter 51). The apparent highly localised occurrence of the genus *Edenophorus* Smith, being active during the winter months and its phylogenetic position, suggest that the genus should be classified as a Gondwanan element (Sinclair 2002, 2003).

Homalocnemidae (see Chapter 55). The deep branching genus *Homalocnemis* Philippi (Fig. 13) was recorded from the margins of the Namib Desert of Namibia by Chvála (1991); the genus is recorded also from Chile and New Zealand (see below).

Mydidae (see Chapter 47). The endemic South African genus *Tongamya* Stuckenberg (Fig. 14) is phylogenetically related to *Megascelus* Philippi from Chile and *Neorhaphiomidas* Norris from Australia, which represents a true Gondwanan radiation of the subfamily Megascelinae (T. Dikow, pers. comm. 2017).



5 *Libanopelopia*

6 *Cretapelopia*

7 *Lebanorthocladius*

Figs 9.5–7. Examples of fossil Chironomidae described from Cretaceous Lebanese amber inclusions: (5) *Libanopelopia cretacica* Veltz, Azar & Nel; (6) *Cretapelopia salomea* Veltz, Azar & Nel; (7) *Lebanorthocladius furcatus* Veltz, Azar & Nel. Figs 5–7 (after Veltz *et al*. 2007, figs 1, 4, 9).

Psychodidae (see Chapter 24). At least two instances of Gondwanan distributions are known within Afrotropical Psychodidae. In the subfamily Trichomyiinae, the distinctive subgenus *Trichomyia* (*Gondwanotrichomyia* Duckhouse) was erected for two species limited to montane evergreen forests of eastern South Africa (Duckhouse 1980), but also occurs in Australia, New Zealand and Chile (G.M. Kvifte, pers. comm. 2017). In the subfamily Bruchomyiinae, the phylogenetic analyses of Wagner & Stuckenberg (2016) indicates Afrotropical species of *Nemopalpus* Macquart (Fig. 12) and *Eutonnoiria* Alexander form an early branching clade, with the Oriental and Australasian species as successive sister-groups to the Neotropical radiation. There is, therefore, a clear Gondwana origin indicated in the general patterns for these groups.

Rhagionidae (see Chapter 37). A genus with species of "archaic" habitus, *Atherimorpha* White, has been recorded as well-represented in South Africa (Nagatomi & Nagatomi 1990), inhabiting mesic montane grasslands and the Fynbos flora of the Cape Fold Mountains. *Atherimorpha* is a Gondwanan element, distributed also in south-east Australia, Tasmania and temperate South America (Stuckenberg 1962).

Simuliidae (see Chapter 32). The genus *Paracnephia* Rubtsov (including *Procnephia* Crosskey), as recognised by Adler & Crosskey (2016), exhibits a Gondwanan austral distribution, with the 10 described Australasian species considered to be phylogenetically closely related to Afrotropical species. *Paracnephia* is not monophyletic, however, represents a "dumping ground" in the family and there is not a single character to support it (K. Moulton, pers. comm. 2017). Molecular evidence presented by Moulton (2003), although not robust, did not recover support for a close relationship between Afrotropical *Paracnephia* and any other Gondwanan deep branching simuliine segregate.

Tabanidae (see Chapter 39). *Stuckenbergina* Oldroyd is the only Afrotropical representative of the tribe Pangoniini. This tribe otherwise has a notable austral distribution, involving elements shared between South America and Australia. The two described South African species are associated with the Cape Fold Mountains (Kirk-Spriggs & Stuckenberg 2009: 179).

Thaumaleidae (see Chapter 33). Only three species of this small family associated with seepages have been described from the Afrotropics (Sinclair 2015; Sinclair & Stuckenberg 1995). One occurs in the Natal Drakensberg and two in the Cape Fold Mountains of South Africa. They constitute the endemic South African genus *Afrothaumalea* Stuckenberg (Fig. 16), which is part of a monophylum of genera also occurring in Australasia and temperate South America. The closest relative of *Afrothaumalea* appears to be the Australian and southern Chilean genus *Niphta* Theischinger (Sinclair & Stuckenberg 1995).

Malagasy elements

Schlinger (1961), suggested that the Malagasy endemic genus *Parahelle* Schlinger in the Acroceridae may be closely related to the genera *Helle* Osten Sacken from New Zealand and *Megalybus* Philippi from Chile, thus representing a Gondwanan origin. Winterton *et al*. (2007), pointed out, however, that *Parahelle* is actually more closely related to the genus *Thyllis* Erichson which occurs in Madagascar, thus refuting such an association.

Among the Diptera of Madagascar, the blephariceridgenus *Paulianina* Alexander is, therefore, the only taxon for which a Gondwanan origin can be plausibly postulated. *Paulianina* is the sister-group of the austral Neotropical-Australian genus *Edwardsina* Alexander and the two genera together constitute the early branching subfamily Edwardsininae (Kirk-Spriggs & Stuckenberg 2009: 180). The biogeography of *Edwardsina* had long attracted attention; the genus having been considered a likely Gondwanan relict by earlier dipterists. *Paulianina* is classified in a different subfamily to that of the South African genus *Elporia* (Blephariceriнae) and the recently described Malagasy genus *Aphromyia*, the sister-group of which may be the Brazilian *Kelloggina* (see above), so a separate explanation for the presence of Edwardsininae in Madagascar could be expected.

The undescribed Malagasy genus referred to by Paulian (1954) and Kirk-Spriggs & Stuckenberg (2009: 180) was recently described as the genus *Aphromyia*, based on the single species *A. stuckenbergi* Courtney (Courtney 2015). The species is known only from river systems draining off the Central highlands (Andringitra massif). Its inclusion in the subfamily Blepharicerinae, along with the South African genus *Elporia* implies that the species may be derived from tropical sub-Saharan Africa, outside the range of *Elporia*.

Immature stages of an unnamed species of Blephariceridae are known from the Kumbo massif (Banso Mountains) in north-west Cameroon (Germain *et al*. 1967) and nearby parts of southern Nigeria. Although perhaps related to the genus *Elporia*, the larval stages differ in having one additional pair of prolegs, so affinities of this species remain uncertain until adults can be studied.

Climate and changing vegetation

Pleistocene glaciation

During the Pleistocene Ice age, Africa was not glaciated. The Ice age produced very arid conditions, but no (or little) glacial landforms (Kirk-Spriggs & Stuckenberg 2009: 155). There were centres of Pleistocene glaciation, however, in the High Atlas and Djurjura Mountains of North Africa, Mt Atakor in the Hoggar Mountains of the central Sahara (Fig. 11), the Semien Mountains and Mt Bada in Ethiopia and Mt Elgon, Mt Kenya, Mt Kilimanjaro and the Ruwenzori Mountains of East Africa (Fig. 17). There is further evidence of Pleistocene periglacial activity on the Tibesti Mountains of the central Sahara and the Drakensberg Mountains of South Africa. Today, glaciers are restricted to Mt Kenya, Mt Kilimanjaro and the Ruwenzori Mountains (Mark & Osmaston 2008; Osmaston & Harrison 2005) (Fig. 17). In a study of Diamesinae (Chironomidae), Willassen & Cranston (1986) concluded that these mountains have endemics related phylogenetically to Europe rather than Gondwana, while in a study of the genus *Wiedemannia* Zetterstedt (Empididae), Sinclair (1999) concluded that species occurring in the Ruwenzori Range are most closely related to Southern African species and as a whole phylogenetically close to a European subgenus.

Aridification of the Sahara

The Afrotropics are biogeographically limited northwards by the young Sahara Desert. It is generally accepted (Kroepelin

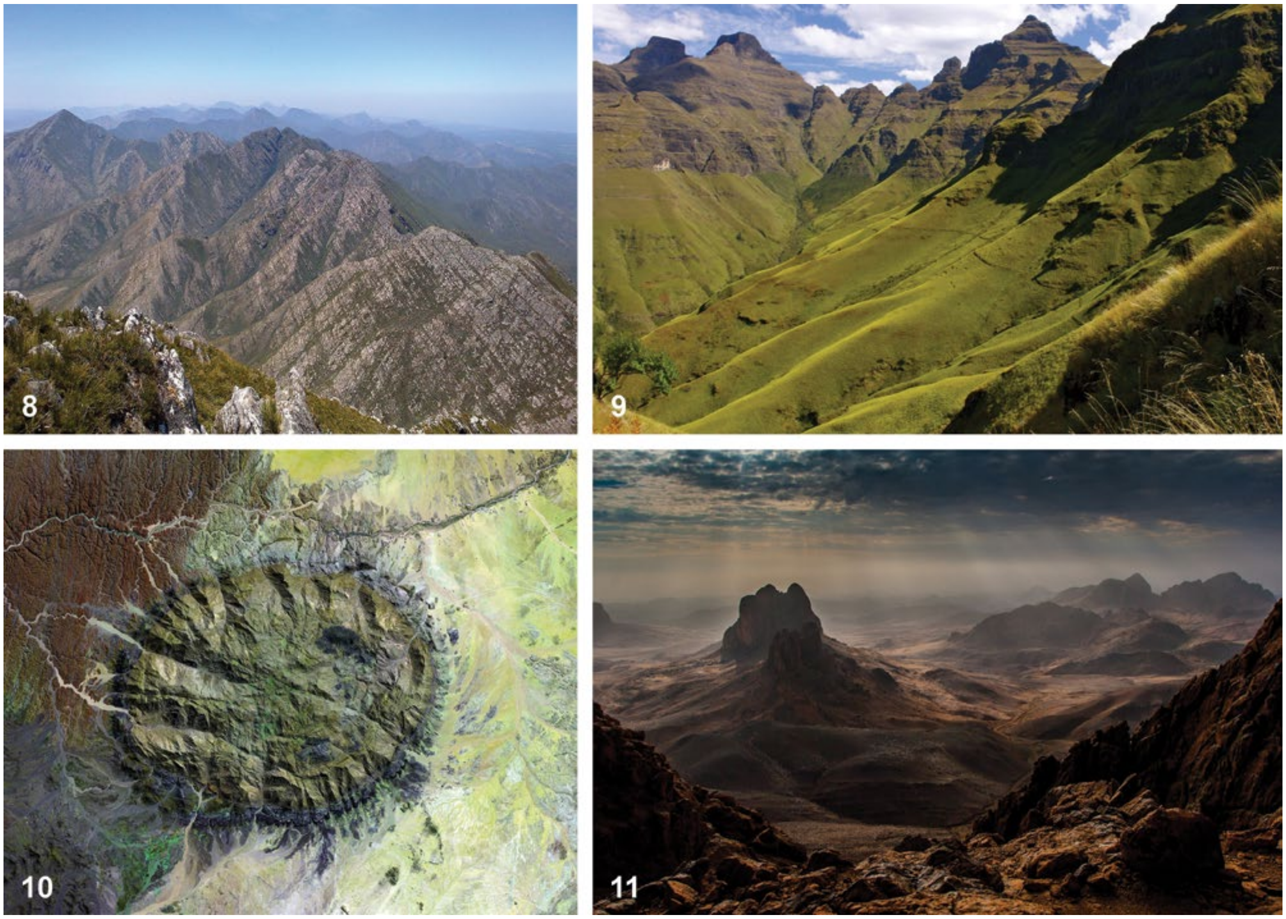
2006), that aridification of the Sahara is recent (2–3 Mya), originating in the Pliocene and becoming hyper-arid in the Pleistocene, with remarkable aridification in North Africa at the onset of the Quaternary ice ages (Maley 1996). Zhang *et al*. (2014), however, noted that more recent discovery of Aeolian dune deposits (*ca* 7 Mya), suggested a considerably older age, although this interpretation is hotly contested; there is no clear mechanism to explain aridification around this time and archaeological evidence of hominid settlements indicated otherwise (Fig. 23). The Sahara was previously an enormous savanna and grassland (Fig. 25), which may have extended ranges of some Afrotropical Diptera much closer to the Mediterranean (*e.g.*, Adams & Faure 1998).

Kirk-Spriggs & McGregor (2009) provided an extensive review of Diptera disjunctions between southern Africa and the Mediterranean Province and provided examples of Vermileonidae in the Atlas Mountains and the Canary Is. and species of *Habropogon* Loew (Asilidae) and *Nemopalpus* Macquart (Psychodidae) in countries bordering the Mediterranean as examples of isolated relicts of the fauna that predated aridification (Figs 18–20).

Hoggar and Tibesti Mountains of central Sahara

The Sahara, which occupies approximately 7,000,000 km^2, is a huge sandy area, which over vast areas is truly almost abiotic, due to extremely high daytime temperatures, lack of rain and of associated vegetation. The insects occurring along the northern fringe are subject to a winter rainfall regime and many may have been there since Miocene times (Kirk-Spriggs & McGregor 2009).

The Sahara today is, however, not the uniform desert it appears to be. In the driest central areas there are isolated mountain ranges, such as Hoggar (or Ahaggar) in Algeria (*e.g.*, Fig. 11), with its two southern spurs, the Adrar des Iforas in southern Algeria and northern Mali and the Aïr massif in north-central Niger and the Tibesti Mountains in northern Chad. Precipitation is markedly higher on these mountains than the surrounding hyper-arid peneplain and semi-permanent or episodic pools are evident at higher elevations. In the Hoggar, for example, Tamanrasset (22°50′N, 5°28′E), receives a mean annual precipitation of 51 mm and Assekrem (23°18′N, 5°41′E),



Figs 9.8–11. Significant topographical features of the African landscape: (8) the Cape Fold Mountains (Tsitsikamma Mountains, Eastern Cape); (9) the Drakensberg Mountains (Mpumalanga Province); (10) the Brandberg massif, Namibia from space; (11) the Hoggar Mountains of the Central Sahara. Fig. 8 (https://commons.wikimedia.org), Fig. 9 (http://mustseeplaces.eu), Fig. 10 (image NASA), Fig. 11 (Lunar Landscape © B. Djajasasmita; CC BY-NC-ND 2.0).

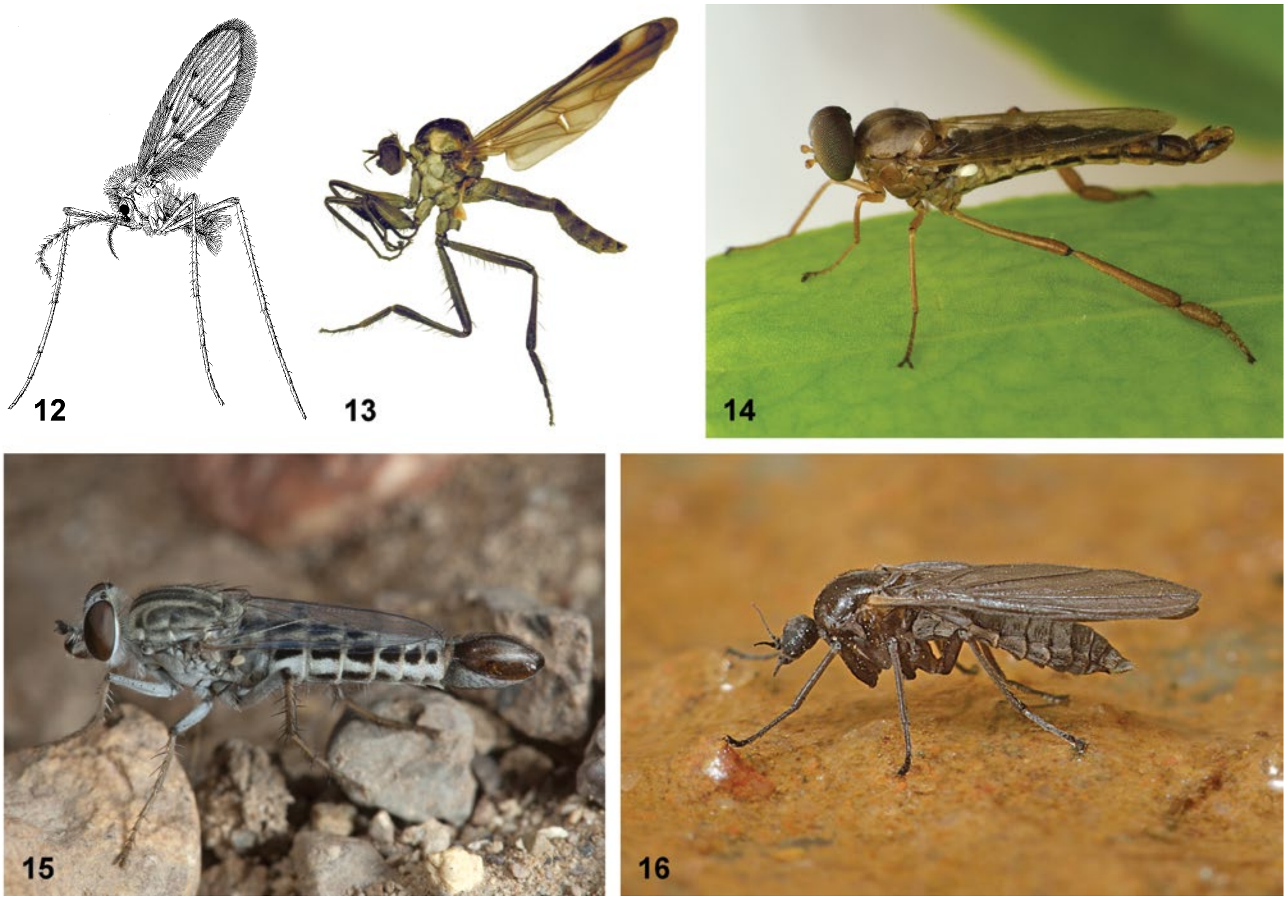
164 mm, as compared to In Salah (27°12′N, 2°29′E), Algeria, for example, which receives only 16 mm (Gardi 1967: 62; Kirk-Spriggs & McGregor 2009).

These mountains are intersected with deep, often densely vegetated valleys and the foothills are vegetated with endemic plants of Sahelian origin (Quézel 1978), thus enabling Holarctic species to spread farther south and Afrotropical species farther northwards (Müller 1974: 49). The central Saharan mountains should perhaps be regarded as what Cranston (2005: 282) terms a "filter bridge", *i.e.*, allowing limited transgressions compared with true "corridors", but more so than "sweepstake" routes of dispersal (Kirk-Spriggs & McGregor 2009).

The fauna comprises a mixture of Palaearctic and Afrotropical faunal elements, with some endemic species. Interestingly, even in 1876 A.R. Wallace was clearly aware of the significance of Holarctic faunal elements in these mountains. He regarded the Ethiopian Region as beginning south of the Tropic of Cancer, but excluded the central Saharan mountains (Fig. 21). Séguy (1950) listed 47 species of Diptera in 18 families from the Aïr massif and elsewhere in the Sahara. These families were usually represented by single species, although the families Asilidae (9 species) and Muscidae (11 species) were better represented. Séguy concluded that the majority of the species examined were indeed of Mediterranean provincial origin, with twenty species originating from the hotter parts of eastern Africa (Sudan and Egypt as far as the Arabian Peninsula), with five cosmopolitan species and nine new species. Kirk-Spriggs & McGregor (2009) tabulated published and unpublished data for the Ephydridae and Muscidae recorded from the Aïr massif.

Megalakes of the Sahara and their catchments

During the postglacial period the now arid central parts of the Sahara were considerably wetter. The stages of development of Lake Chad during the Holocene have been used as an indication of such climatic conditions (Grove & Pullen 1963) and have been the subject of numerous studies (*e.g.*, Ghienne *at al.* 2002; Maley 1977; Schuster *et al.* 2003, 2005). In one of the more recent studies, Drake & Bristow (2006) indicated that the palaeolake Megachad was one of four giant lakes with



Figs 9.12–16. Examples of purported Gondwanan elements in the Southern African Diptera fauna: (12) *Nemopalpus transvaalensis* Stuckenberg (Psychodidae); (13) *Homalocnemis perspicuus* (Hutton) (non-Afrotropical) (Homalocnemidae); (14) *Tongamya miranda* Stuckenberg (South Africa) (Mydidae); (15) *Apiocera* (*Ripidosyrma*) *painteri* Cazier (non-Afrotropical) (Apioceridae); (16) *Afrothaumalea stuckenbergi* Sinclair (South Africa) (Thaumaleidae). Fig. 12 (Wagner & Stuckenberg 2016, fig. 1), Fig. 13 (Kirk-Spriggs & Stuckenberg 2009, fig. 6.2), Figs 14–16 (photographs © S.A. Marshall).

adjacent catchments that linked to straddle the desert (Fig. 22, A–D). These lakes were situated in major lowland basin areas between the high central Saharan Mountains and their effect on the associated flora and fauna of these must have been considerable. Between them these lakes covered an area equivalent to 10% of the Sahara and together these water bodies and associated wetlands would have provided a corridor for animal dispersal, including hominids, to migrate north across what is now the Sahara (Drake & Bristow 2006) (Fig. 35, B). Lake Megachad was the largest of these lakes and at its maximum extent (*ca* 7,500–6,950 BP) was larger than any lake in existence today (371,000 ± 13,000 km^2). Radiocarbon dates (Schuster *et al.* 2003) from regressive shorelines suggest that the lake only began to contract around 4,410 and 5,280 BP. By 4,000 BP it had split into three separate lakes, namely: Lake Chad, Lake Fitri and Lake Bodele. Other regressive shorelines have been dated from archaeological evidence on the plains that became exposed by the final demise of the lake and these appear to be much younger (Drake & Bristow 2006) (Fig. 23) (Kirk-Spriggs & McGregor 2009).

These lakes and their associated catchments, situated in basins between the central Saharan mountains, could clearly have acted as a humid route of dispersal as recently as 4,000 BP,

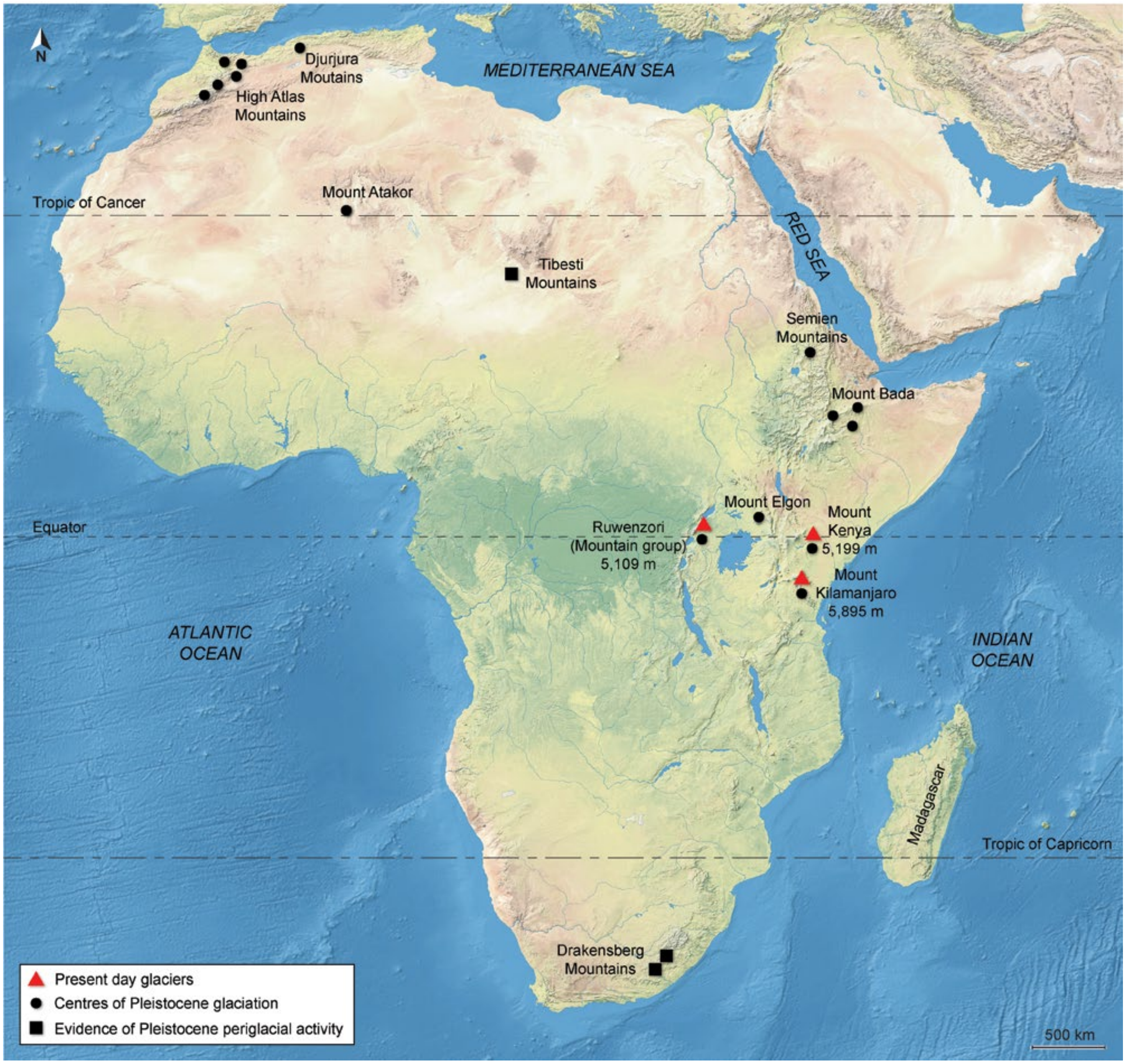


Fig. 9.17. Centres of Pleistocene glaciation, evidence of Pleistocene periglacial activity and present-day glaciers (after Young & Hastenrath 1991, fig. 1; made with Natural Earth).

when these lakes began to recede, and this route is regarded as a "central high Africa corridor" (Fig. 35, B); a filter-bridge between the Mediterranean Province and southern Africa. Kirk-Spriggs & McGregor (2009) cited examples of Mediterranean provincial species of Ephydridae and the muscid genus *Lispe* Latreille, occurring as far south as the Aïr massif in northern Niger as examples of relict montane Diptera of Mediterranean provincial origin in the southern Hoggar Mountains; these groups being associated with the margins of standing water.

Changing vegetation (Miocene–Quaternary)

The origins and history of the vegetation in Africa has had a profound impact on the modern distribution of the flora and fauna of the region, including the Diptera. The Neogene and Quaternary were marked by a succession of changes which affected the climate and played an important role in modifying African flora and faunas. As a result of global and local events, the forested environments began to dry and the faunal composition changed with altitude (Kirk-Spriggs 2010*b*).

Miocene East African plant communities are all of tropical affinities and this implies that much of Africa would have been positioned at the Equator from the Middle Cretaceous to the Oligo-Miocene, when tropical forests formed a continuous belt that stretched across the African continent from coast to coast (*e.g.*, Clarke & Burgess 2000; Kirk-Spriggs & Stuckenberg 2009: 163) (Fig. 24). During lower and basal Middle Miocene times, northern Africa was also clothed in tropical forest and woodland, while during the Late Miocene its vegetation affinities shifted toward savanna and semi-arid types (Kirk-Spriggs 2010*b*; Pickford 1999).

The establishment of contact between Africa and Eurasia at the end of the Lower Miocene coincides with a major increase in the degree of seasonality in world climates, while closure of the choke point of the Isthmus of Panama (see below) during the Pliocene likely sparked the onset of high-latitude Quaternary glaciations through the reorganisation of oceanic currents (Pickford 1999).

Expansion of grasslands began in the Upper Miocene (*ca* 8–7 Mya), but grasses remained a low component of the environment until the Late Pliocene (Senut *et al*. 2009) (Fig. 25). As the grasslands and savannas expanded, at the expense of moist lowland forests, these forests were retained only at high elevations on mountains and plateaus, especially along the Rift Valley escarpments and in the Eastern Arc Mountains. In a study of birds, Fjeldså & Bowie (2008), noted that these upland forest remnants retain local populations that gradually became genetically divergent, but remained morphologically very much alike.

The Pliocene is regarded as the epoch during which the modern world began to emerge (Burckle 1996). It covers the transition between the warm temperate climate of the Miocene and the cold Pleistocene. The Pliocene is, therefore, considered a period of transition. The final linkage of North and South America (*e.g.*, the formation of the Isthmus of Panama) and the closure of other choke points (being strategic narrow routes providing passage through or to another region), the accelerated uplift of mountains and plateaus, the growth of ice sheets in Greenland and West Antarctica, and in the Pleistocene, the periodic growth of continental ice sheets extending into mid latitudes of the Northern Hemisphere all impacted on the climate of the Pliocene epoch, which in turn must have influenced various evolutionary pathways leading to modern flora and fauna. The Pliocene also apparently underwent unusually warm periods; it was, therefore, warm and wet during the first half (5–3 Mya) and cooler and dryer during the second (Burckle 1996; Kennett 1996; Kirk-Spriggs & McGregor 2009).

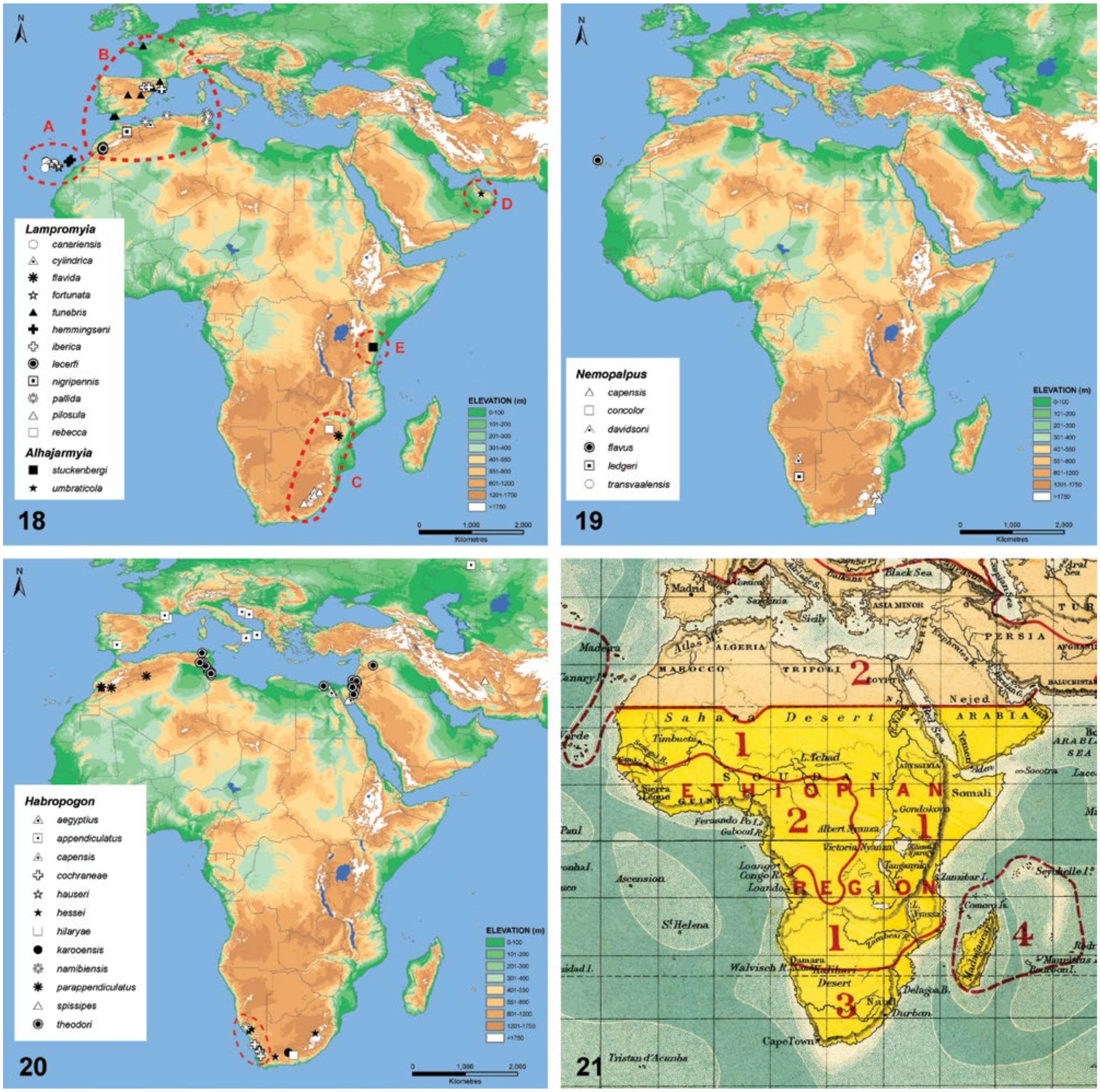
The global climate of the past 50 My has generally shown a long-term cooling trend and only during limited intervals has this trend accelerated in step-like fashion (Burckle 1996; Kennett 1996). During the Pleistocene temperatures fell synchronously everywhere and cooled the atmosphere sufficiently to reduce evaporation from the oceans, resulting in glacial periods. The effects of these were felt worldwide and mountain glaciers increased on all high mountains in the tropics, including the African mountains along the rift valley, allowing the migration of cold stenotherms from the Holarctic to the African Realms (Fig. 35, route C). Besides the lowering of temperatures, there was apparently an increase in rainfall over much of the world during inter-glacials and a shift of temperature rain zones towards the tropics into the subtropical desert zones. Lakes increased in size in southwestern North America, southwest Asia, East Africa, South America and Australia; and what are now arid regions on southwestern North America, North Africa (Sahara), Australia, *etc*. were evidently better watered and better vegetated than now and less of a barrier to non-desert animals. During the rainy inter-glacial ages, forests tended to expand and during the dryer glacial periods steppe and desert (Kirk-Spriggs & McGregor 2009).

During the last glacial maxima (18,000 BP), the temperature of the Atlantic Ocean dropped 4–5°C, whereas that of the Indian Ocean was similar to that of present (Lovett *et al*. 1988). This implies that during the last glacial maxima the climate of East Africa was similar to that of today, resulting in the overall climatic stability of forests in eastern Africa (Lovett *et al*. 1988).

It has been suggested that the pan-African forest either broke up only once, at the onset of East African aridification during the Oligocene–Early Miocene (*ca* 33–20 Mya), or expanded and contracted on multiple occasions following this initial breakup (Couvreur *et al*. 2008). Using molecular phylogenies and Bayesian divergence dates Couvreur *et al*. (2008) tested the origin of African forest linkages of the plant family Annonaceae and provided strong evidence that East African endemic lineages have multiple origins, dated to significantly different times spanning the Oligocene and Miocene epochs. These successive origins (*ca* 33, 16 and 8 Mya) coincide with known periods of aridification and geological activity in Africa that would have recurrently isolated Guineo-Congolian rainforest.

Afrotropical biomes

Most interpretations of contemporary distributions are based on White's (1983) vegetation map of Africa (Fig. 26), although an alternative biome map of Africa was published by Mendelsohn *et al*. (2002) (Fig. 27). In tropical sub-Saharan Africa generally there are two vast biomes, equatorial rainforest (usually termed the Guineo-Congolian rainforest), mostly in the western lowlands and savanna that occupies the greater part of the continent. The dipteran fauna of the region bears the imprint of vast savanna evolution in the tropics and a complex vegetational biome history in the subtropical south (Mucina & Rutherford 2006). Madagascar has its own complex biome history and several interpretations have been adopted by different workers to explain the distribution of organisms (Figs 28–30). Kirk-Spriggs (2011) provided a brief account of Madagascar's biomes and interpreted the distribution of species of *Curtonotum*

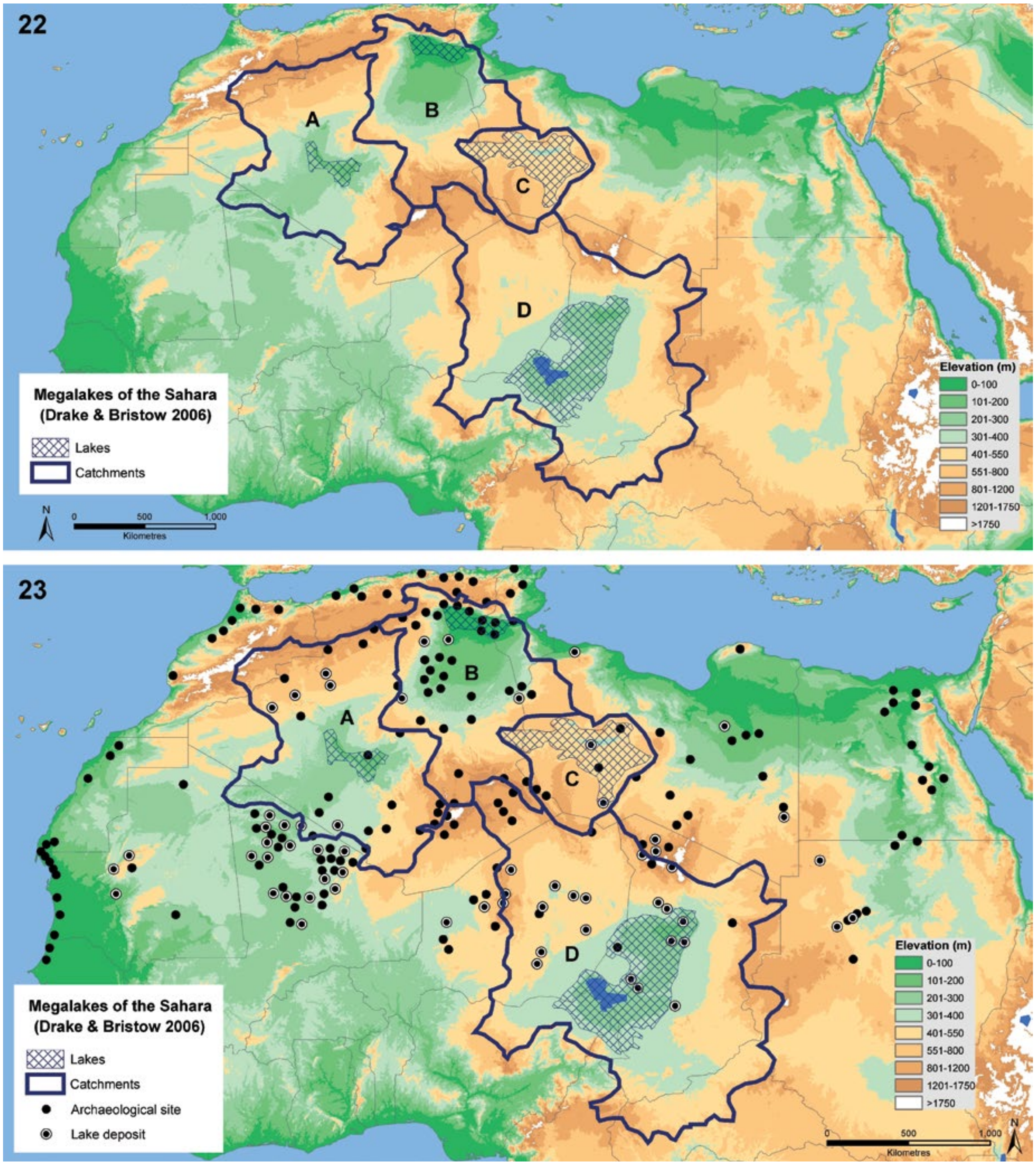


Figs 9.18–21. Disjunctions in the Diptera of Southern, East and North Africa and Wallace's (1876) map of African zoogeographical regions: (18) *Lampromyia* Macquart and *Alhajarmyia* Stuckenberg (Vermileonidae); (19) *Nemopalpus* Macquart (Psychodidae); (20) *Habropogon appendiculatus* species-group in the Palaearctic and *Habropogon* (Asilidae) species in the Afrotropics; (21) Wallace's (1876) map of Africa, indicating zoogeographical regions. Figs 18–20 (after Kirk-Spriggs & McGregor 2009, figs 1, 2, 7; South Sudan not indicated), Fig. 21 (Wallace 1876: iii).

Abbreviations: A – *Lampromyia canariensis* species-group; B – *L. cylindrica* species-group; C – *L. pilosula* species-group; D – *Alhajarmyia umbraticola* (Stuckenberg & Fisher); E – *A. stuckenbergi* Swart, Kirk-Spriggs & Copeland.

Macquart (Curtonotidae; see Chapter 103) according to these defined biomes and other zones.

South Africa has the most diverse and distinctive Diptera fauna in the Afrotropics. The country is ecologically complex, with 24 bioclimatic regions in the scheme of Phillips (1959). The Cape Floral Kingdom, *Capensis*, occurs in two famously diverse biomes with *ca* 13,000 endemic plant species: these are the Fynbos shrubland of the Cape Fold Mountains and the Succulent Karoo (Taylor 1978: 173). So much topographic,



Figs 9.22–23. Saharan megalakes and archaeological evidence of hominid occupation: (22) Quaternary megalakes and their catchments (*ca* 7500–6950 BP); (23) distribution of lake deposits and archaeological sites in northern Africa at *ca* 8000–9000 BP (after Goudie 1996), in relation to Quaternary Saharan megalakes. Figs 22, 23 (Kirk-Spriggs & McGregor 2009, figs 19, 20).

Abbreviations: A – Basin of Chotts; B – Ahnet-Moyer Megalake; C – Lake Magafezzan; D – Megachad.

climatic and floristic diversity promoted radiation among the Diptera and there are species-rich, systematically complex faunas of the families Asilidae (see Chapter 48), Bombyliidae (see Chapter 45), Empididae, Limoniidae (see Chapter 14), Mydidae, Nemestrinidae (see Chapter 43), Tabanidae, Therevidae (see Chapter 49) and Vermileonidae (see Chapter 36). Recent studies prove flies to be important as pollinators in the Cape flora and there are numerous and often remarkable examples of convergent adaptations of the mouthparts for feeding in co-adapted flowers (*e.g.*, Barraclough 2006*a*; Karolyi *et al*. 2014; Kirk-Spriggs & Stuckenberg 2009: 158; Manning & Goldblatt 1995; Morita (2008); Struck 1992, 1994).

The Fynbos flora is notable for its great taxonomic diversity and profuse flowering of nectar-bearing plants, many of which have nectaries recessed in tubular corollas. This resource has evidently produced a co-adaptive response among Diptera in that elongation of the proboscis has evolved. Such an adaptation is frequent in species within the Acroceridae, Bombyliidae, Nemestrinidae and Tabanidae and in some other families among the Fynbos flies. Such proboscis development is, in some of these cases, unique in the families concerned (Stuckenberg 1998). Kirk-Spriggs & Stuckenberg (2009: 159) reviewed examples noting the following: *Arthroteles* Bezzi (Rhagionidae), *Peringueyomyina barnardi* Alexander (Tanyderidae; see Chapter 15), *Rhynchoheterotricha stuckenbergae* Freeman (Sciaroidea, unassigned to family; see Chapter 23) and *Forcipomyia* subgenus *Rhinohelea* de Meillon & Wirth (Ceratopogonidae). In addition the genera *Braunsophila* Kröber and *Xestomyza* Wiedemann in the Fynbos-associated fauna have some of the longest proboscis lengths in the usually short-snouted Therevidae (M. Hauser, pers. comm. 2017).

In the montane environment of the Drakensberg escarpment in the east of the country, another rich flora is present, where many nectar-feeding flies occur. Among these is a species of *Arthroteles* obviously derived from the main occurrence of the genus in the Cape Fold Mountains. Proboscis elongation is also conspicuous among the Drakensberg dexiine Tachinidae (Kirk-Spriggs & Stuckenberg 2009: 159).

The Succulent Karoo biome occurs in southern Namibia and north-west South Africa with a botanical diversity that is unparalleled by any other arid region on Earth. The biome is home to more than 5,000 higher plant species, almost 40% of which are endemic and 18% of which are threatened. It has the richest succulent flora in the world, harbouring about one-third of the world's *ca* 10,000 succulent species. Other unique features include the diversity of miniature succulents (435 species) and geophytes (630 species). Examples of species apparently restricted to the Succulent Karoo of southern Namibia include Vermileonidae (Stuckenberg 2000), Mythicomyiidae (Evenhuis 2000; see Chapter 44), Dolichopodidae (Grichanov *et al*. 2006; see Chapter 56), Rhiniidae (Kurahashi & Kirk-Spriggs 2006; see Chapter 115) and Tephritidae (Hancock *et al*. 2001; see Chapter 71) (Kirk-Spriggs & Stuckenberg 2009: 163).

Rainforests

Africa is unusual in that the equatorial rainforests (Fig. 26, A) have had a history of radical disturbance due to Neogene climate change. Present-day Guineo-Congolian forests of Gabon, Congo, western Uganda and Angola were part of a vast desert during the Miocene (Fig. 31) and that the supposed permanence of the position of Africa's rainforests since the Oligocene is a myth. The modern rainforest occurs on very thin soil (1–2 m depth), overlaying up to 250 m of aeolian sands (Fig. 31 (inset)), indicating that the extant tropical rainforest of the Congo only set root in the area in relatively recent geological time (Maley 1996; Pickford 1999; Senut *et al.* 2009).

It is noteworthy that the Guineo-Congolian forests of Central Africa were not identified as a biodiversity hotspot by Myers *et al*. (2000) and Kirk-Spriggs & Stuckenberg (2009: 164) hypothesised that the equatorial rainforest fauna is remarkably

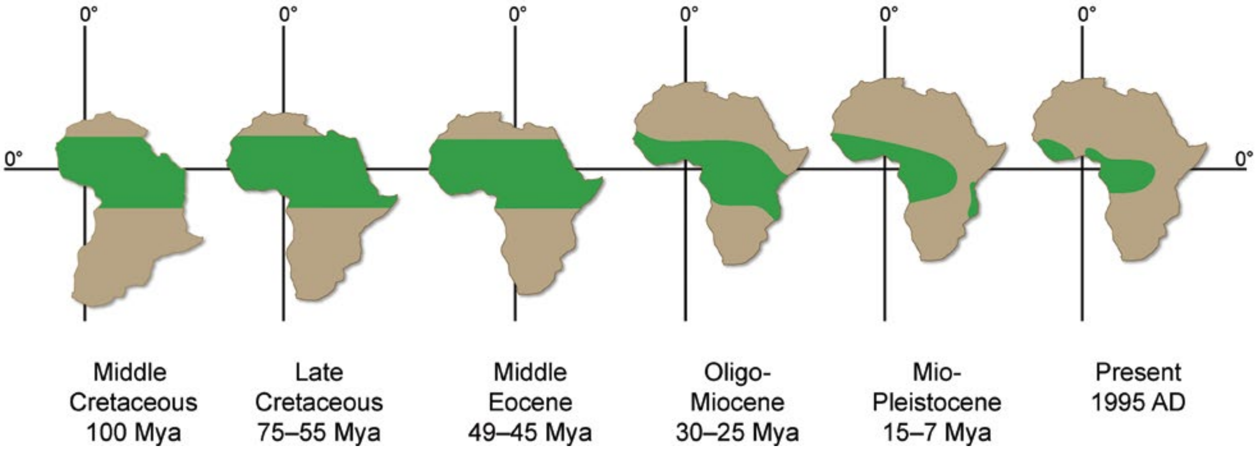
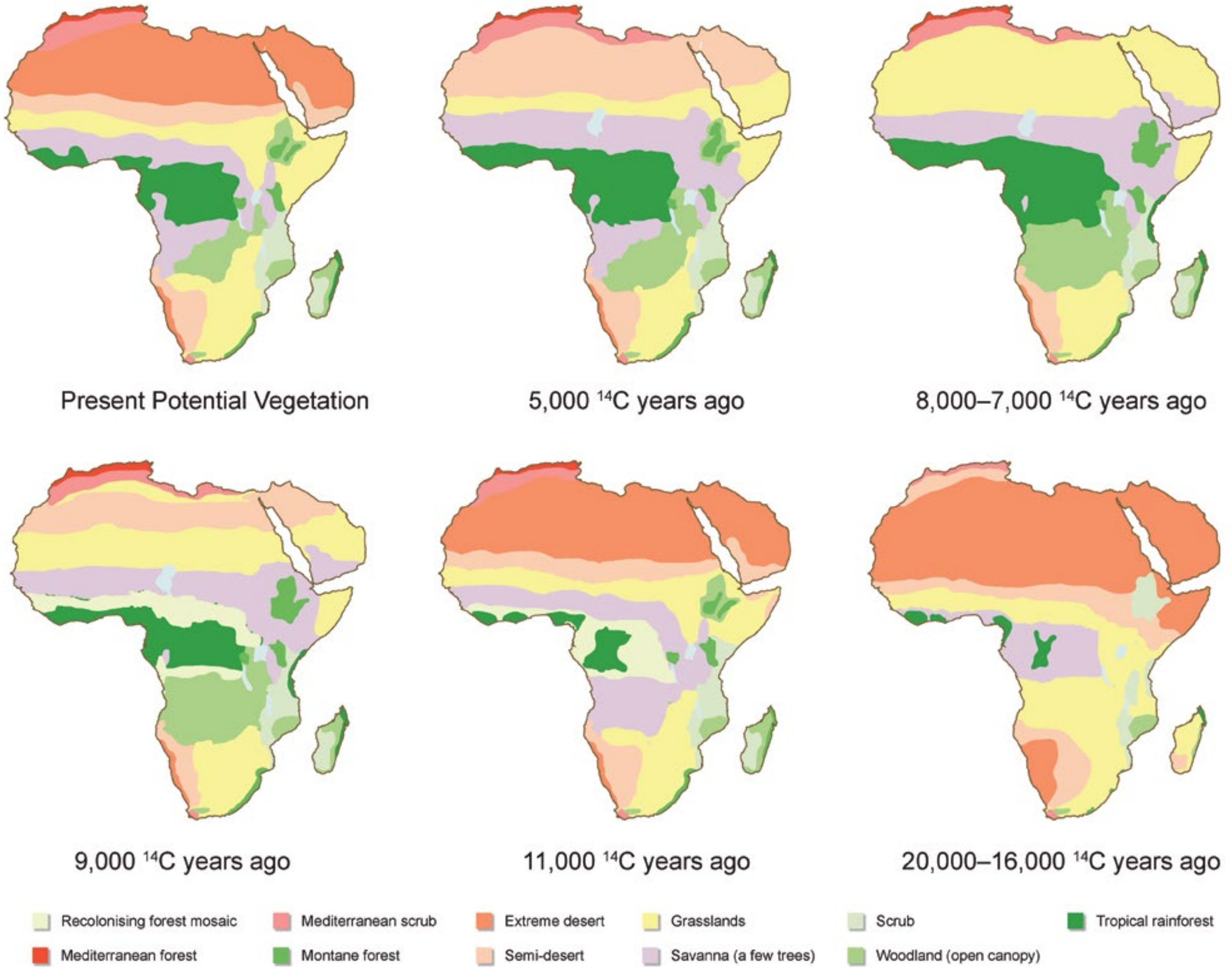


Fig. 9.24. Inferred changes to the extent and distribution of forest cover in Africa since the Middle Cretaceous (shoreline changes are not represented; changes in the position and orientation of the African continent are due to continental drift) (after Clarke 2000).

low in diversity and there is no evidence of a highly adapted canopy fauna (Meadows 1996). Grootaert & Shamshev (2013) recorded 32 species of Hybotidae, resulting from the Boyekoli Ebale Congo Expedition 2010 (see Chapter 1), 25 of which were described as new to science. They noted that their results challenge this hypothesis, but it is here argued that Hybotidae are ground-dwelling and numerous new species are common in virtually all habitat types, so these results do not detract from the overall conclusion.

Coastal forests of eastern Africa

The highly fragmented moist forests that today form the Eastern Arc Mountains of Tanzania and Kenya, are well known for their biological diversity and high degree of floral and faunal endemism (*e.g.*, Burgess *et al*. 1998*a*, 2007; Enghoff 2014; Lovett, 1988, 1989; Lovett *et al*. 1988) and the Eastern Arc/Coastal Forests have collectively been ranked as the second-most important "endemism hotspot" on continental Africa (Burgess *et al*. 1998*a*; Myers *et al*. 2000). This "hotspot" is believed to contain at least 1,500 endemic plants, 16 mammals, 22 birds, 50 reptiles and 33 amphibians (Burgess & Clarke 2000; Burgess *et al*. 1998*b*; Lovett & Wasser 1993; Myers *et al*. 2000). The invertebrates have received disproportionately less attention. Burgess *et al*. (1998*a*: 43, table 3) noted that 265 invertebrate species are regarded as endemic to single mountain blocks and that the most endemic-rich mountains are the East and West Usambaras, the Udzungwas and (especially) the Ulugurus. The Diptera was not treated as part of their analysis and knowledge of the arthropods in general is extremely poor (Pape & Scharff 2015). The Diptera have received even less attention than other invertebrates (Doczkal & Pape 2009; Kaae *et al*. 2015; Kirk-Spriggs 2010*b*). Kirk-Spriggs (2010*b*) plotted the distribution of the East African endemic genus *Tigrisomyia* Kirk-Spriggs (Curtonotidae), which occurs throughout the Eastern Arc, but also extends southwards into the Malawi section of the Great Rift Valley forests, a pattern also noted by Blackburn & Measey (2009) in some Eastern Arc frogs.



Present Potential Vegetation

5,000 ^{14}C years ago

8,000–7,000 ^{14}C years ago

9,000 ^{14}C years ago

11,000 ^{14}C years ago

20,000–16,000 ^{14}C years ago

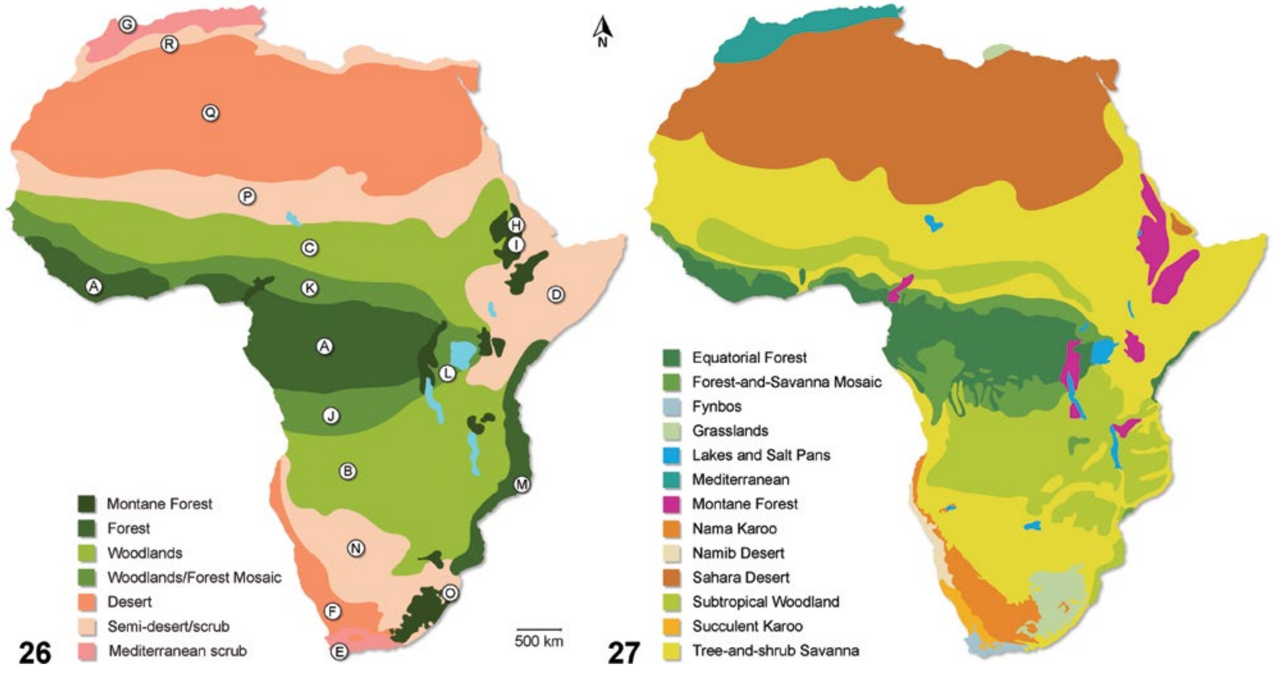
Fig. 9.25. Reconstruction of vegetation history of continental Africa (20,000 BP to present), indicating expansion of grasslands and retraction of forests (after Adams & Faure 1998).

The ancient crystalline mountains that form the Eastern Arc and those associated with the Malawi Rift system were probably in existence from the Cretaceous (*e.g.,* Beek *et al.* 1998; Daszinnies *et al.* 2008; Lovett *et al.* 1988; Sowerbutts 1972) and the strong floristic affinities of Afromontane forests in the Eastern Arc and the Malawi Rift mountains with species occurring in the extant forests of the Guineo-Congolian rainforest have been noted by numerous authors. Dowsett-Lemaire (1989), for example, noted that Afromontane near-endemic trees have satellite populations in mid-altitude forest in south-central Africa (on the Zaïre-Zambezi watershed) and in some upland areas of Congo, Gabon and Cameroon, suggesting a former connection *via* an Eocene pan-African rainforest. Lovett *et al.* (1988) note similar affinities in the angiosperm flora of the Eastern Arc. Evidence of such linkages is also apparent in some genera of African Odonata (Clausnitzer 2003).

Afromontane forests

Afromontane forest occurs in South Africa, on the eastern escarpment and other sites with orographic rain (Partridge & Maud 1987). Similar forests are scattered along the rift valley escarpments in successive countries to the north and on uplands and isolated mountains. To the north, the Ethiopian Highlands, which began to rise in the Tertiary (*ca.* 75 Mya), form a rugged mass of mountains in Ethiopia, Eritrea and northern Somalia in north-eastern Africa, reaching elevations of 1,500–4,600 m. The opening of the series of rift valleys at the end of the Pliocene divided these highlands, thus creating Africa's great salt lakes. This rifting gave rise to large, alkali basalt shield volcanoes in the Ethiopian and Virunga regions beginning about 25–29 Mya. The associated forests of these mountains share a characteristic dipteran fauna whose patterns of endemism and cladogenesis suggest that the apparent ecological gaps between these forests may not in fact invariably be barriers to dispersal and faunal exchange. Species of the chamaemyiid genus *Leucopis* subgenus *Leucopella* Malloch (see Chapter 76) have been shown to occur in the Great Rift Valley forests and the Ethiopian Highlands, but one species is restricted to the Arabian Peninsula (Gaimari & Raspi 2002). A similar distribution is exhibited by true examples of the curtonotid genus *Cyrtona* Séguy, species of which appear to have radiated along the Great Rift Valley forests and dispersed into coastal areas of South Africa (Kirk-Spriggs & Stuckenberg 2009: 165).

There may be a localised montane hot spot in the Cameroon area, where a still undescribed blepharicerid occurs (see



Figs 9.26–27. Phytochoria and biomes of continental Africa: (26) phytochoria of Africa as defined by White (1983); (27) the biomes of continental Africa. Fig. 26 (after Kirk-Spriggs & Stuckenberg 2009, fig. 6.1), Fig. 27 (after Mendelsohn *et al.* 2002: 97).

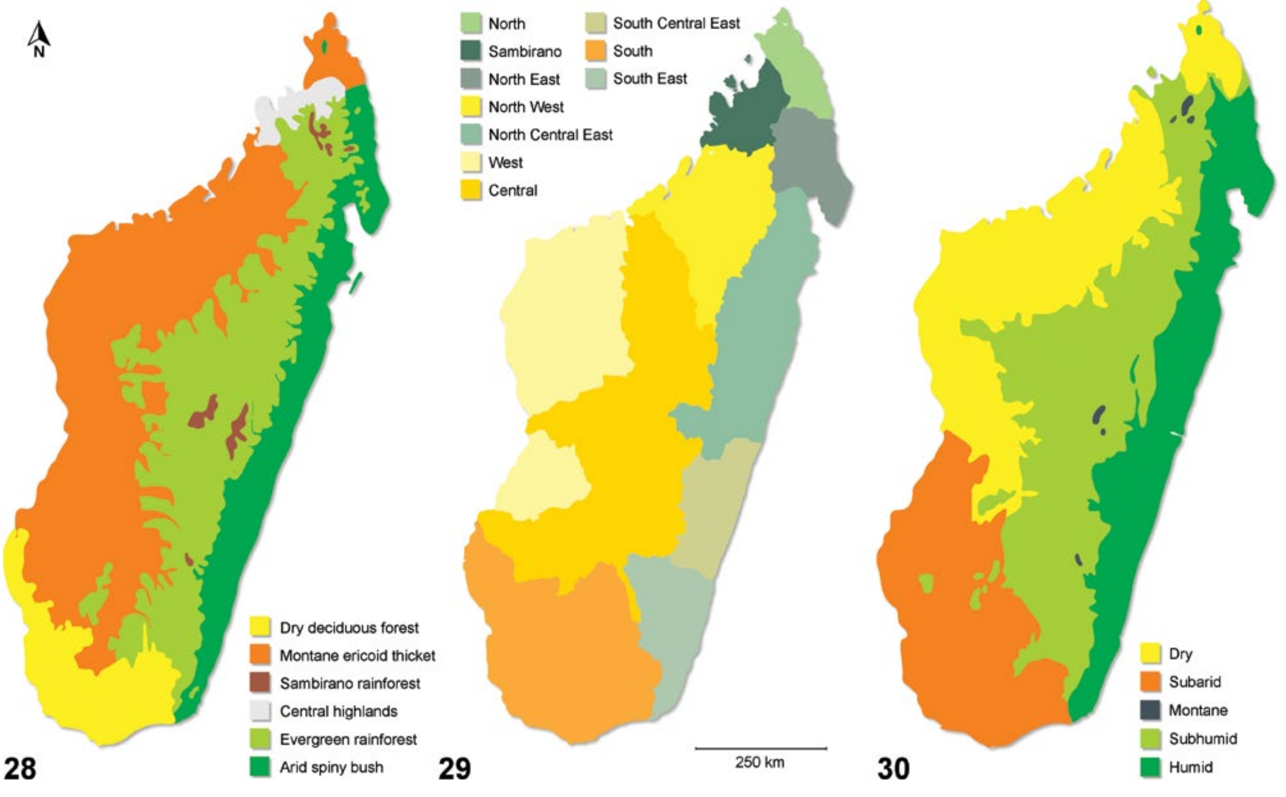
Abbreviations: A – Guineo-Congolian centre of endemism; B – Zambezian centre of endemism; C – Sudanian centre of endemism; D – Somalia-Masai centre of endemism; E – Cape centre of endemism; F – Karoo-Namib centre of endemism; G – Mediterranean centre of endemism; H – Afromontane archipelago-like regional centre of endemism; I – Afro-alpine archipelago-like region of extreme floristic impoverishment; J – Guineo-Congolian/Zambezia transition zone; K – Guineo-Congolian/Sudania transition zone; L – Lake Victoria regional Mosaic; M – Zanzibar-Inhambane regional Mosaic; N – Kalahari-Highveld transition zone; O – Tongoland-Pondoland regional Mosaic; P – Sahel transition zone; Q – Sahara transition zone; R – Mediterranean/Sahara transition zone.

above). This is supported by the Cameroon forests supporting endemicity for birds (Stuart *et al*. 1993) and butterflies (de Jong & Congdon 1993). The Ruwenzori massif in Uganda also has some remarkable Diptera, such as the endemic, monotypic psychodid genus *Eutonnoiria* Alexander, one of only three endemic genera of Psychodidae in Africa (Duckhouse & Lewis 1980).

Savanna

Savanna (termed the Sudano-Zambezian Region, Fig. 26, B, C) is characteristic of much of the vast expanse of the flat landscape of tropical Africa surrounding the Guineo-Congolian Region (Werger & Coetzee 1978: 303). It varies from grassland to woodland with grasses and it is an old biome with a highly adapted invertebrate fauna, which forms complex mosaics as exhibited, for example, in the chrysomelid beetle genus *Monolepta* Chevrolat (Kirk-Spriggs 2003; Wagner 2001). With the limited rainfall confined to the warmest months, the Diptera of the savanna are highly seasonal and also fire-adapted (Phillips 1965). The vast extent of this relatively homogeneous grassland is reflected in the wide distribution of many of the flies (*e.g.*, Asilidae and Bombyliidae), with even small graminivorous acalyptrates, *e.g.*, Chloropidae, ranging from Ethiopia to South Africa. Although great expanses of the African savanna remain poorly sampled and our knowledge is largely based on scattered records and type localities, centres of endemicity in the grasslands are apparent. Poor sampling of African grasslands in general may be largely due to the misconception that such habitats are largely monotonous (Kirk-Spriggs & Stuckenberg 2009: 166).

The environment has produced convergent adaptations of body form, colouring and behaviour among the smaller flies. Ismay (2000: 273) has noted, for example, the number of small species of Chloropidae (see Chapter 96) in the Afrotropics that are bright yellow in colour with a distinct black, shiny pleural macula. He notes that this similarity occurs in the chloropid genera *Arctuator* Sabrosky, *Conioscinella* Duda, *Oscinimorpha* Lioy and *Pselaphia* Becker as occurring in Namibia and in some Milichiidae (see Chapter 95), Phoridae (see Chapter 59) and Hybotidae (see Chapter 52). Water-retaining cavities and rot holes in savanna trees are important breeding sites for taxa, and synchronous, wet-season flowering of trees provides a critical resource of nectar and pollen for many Diptera. The role of Diptera as pollinators of flowering trees is surely underestimated in Africa. Radiation of the larger savanna mammals prompted diversification of the Oestridae (see Chapter 119), the greatest development having been in the Afrotropics and the Palaearctic Region: the two African rhinoceros species are hosts to the larvae of the two magnificent species of *Gyrostigma* Brauer, the future of which is looking increasingly precarious with the dwindling numbers of their hosts (Barraclough 2006*b*) (see Chapters 10 & 119) (Kirk-Spriggs & Stuckenberg 2009: 167).



Figs 9.28–30. Biomes, biogeographic and bioclimatic zonation of Madagascar: (28) biomes of Madagascar; (29) biogeographic zonation of Madagascar; (30) bioclimatic zonation of Madagascar. Figs 28–30 (after Kirk-Spriggs 2011, figs 105–107).

Arabian Peninsula

Conventional biogeographical reconstructions on a globe of constant dimensions during Jurassic/Cretaceous times (*e.g.*, Figs 1, 2) indicate that non-African Arabia formed the western end of the Neotethys Ocean that separated a northern Laurasia from a southern Gondwana (Fig. 1). This ocean has been conceived as narrow, probably epicontinental in the west, broadening out to a vast, deep oceanic expanse at the eastern end, where it separated the Australian plate from Asia and the developing terranes of South-East Asia. Cranston & Judd (1989) noted that geological evidence of sea-level changes (*e.g.,* Adams *et al.* 1983) suggests that the Arabian Peninsula lay predominantly beneath the Neotethys, with the exception of high ground bordering the Rift Valley along the north-west trending Red Sea (Figs 1–3). The retreat of the Neotethys Ocean in the Late

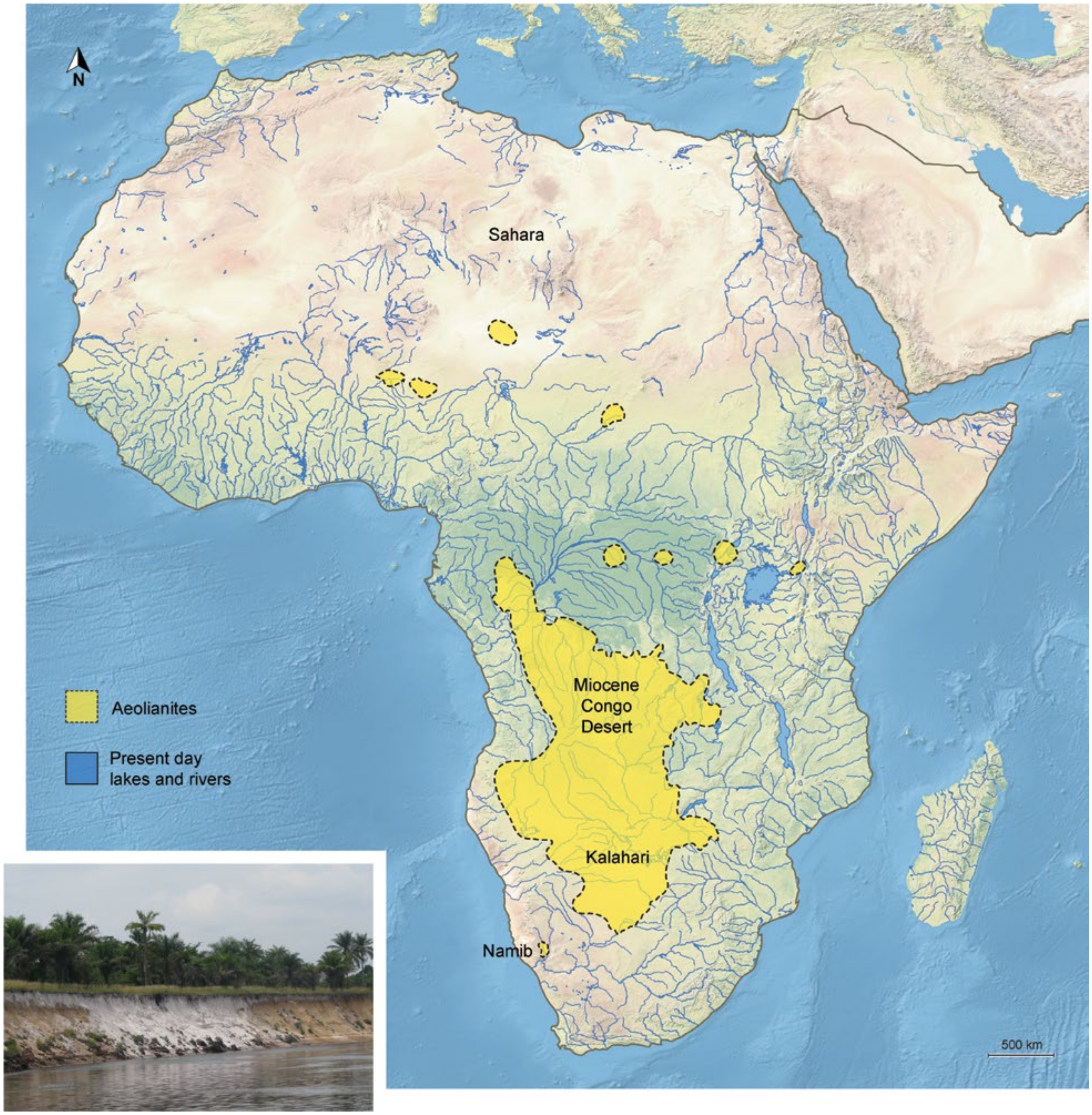


Fig. 9.31. Miocene deserts of the Congo Basin, indicating that areas that today are among the continent's most humid regions (represented by the current permanent rivers), were arid to hyper-arid during this period (inset: photograph of Miocene dune-bedding in bank of Congo River). Fig. 31 (after Senut *et al*. 2009, fig. 1; made with Natural Earth).

Palaeogene (Oligocene, *ca* 34–24 Mya) exposed the present-day Arabian Peninsula. This was followed by aridification of the Arabian Peninsula at the beginning of the Miocene, with intensification during the Pliocene and Quaternary (Pickford 1999, 2000; Pickford *et al.* 2006).

Afrotropical species of Chironomidae in Arabia are restricted to long-term non-inundated montane areas along the Red Sea (Cranston & Judd 1989). Endemism is low with only one postulated vicariant speciation across the Red Sea opening proposed. All other Afrotropical species in the Arabian Peninsula are morphologically undifferentiated from populations on the opposite (Ethiopian) side of the Red Sea. In a study of the more recent genus *Curtonotum*, Kirk-Spriggs & Wiegmann (2013) noted that *C. simile* Tsacas (the only species that occurs on the Arabian Peninsula) also occurs across the Red Sea in Eritrea (Fig. 34), but is otherwise widely distributed in the Arabian Peninsula, occurring as far north as Israel and as far east as Oman. Its closely related sister species, *C. saheliense* Tsacas occurs in continental Africa, in the semi-arid zones to the west of the Ethiopian Highlands, which likely acted as a barrier inducing vicariant speciation. Kirk-Spriggs (2010*a*) also recorded *Axinota ahdabi* Kirk-Spriggs (Curtonotidae) at elevations of 1,400 and 2,200 m in the Asir highlands of Yemen. This species belongs to a predominantly Oriental species-group and the founder species may have arrived from the Orient *via* Polar Continental air masses that affect the Arabian Peninsula in winter and originate from central Asia (Fisher & Membery 1998: 8, fig. 2.1). As the climate became more arid the species may have retreated into the uplands of the Asir range.

Namib Desert and Brandberg massif

Along the Atlantic coast of Namibia and southern Angola is the spectacular Namib Desert, the oldest in Africa, the aridification of which began in the early Middle Miocene (*ca* 16 Mya) (Barnard 1998). Aridification of the Namib Desert also impacted on the adjacent mountains (Namibian Escarpment and desert inselbergs). The Diptera fauna includes some peculiar, desert-adapted mydids that survive through autogeny; the flies have vestigial mouthparts and their larvae store nutrients for oogenesis (Wharton 1982). Adaptations to extreme xeric conditions are also demonstrated in the camillid genus *Katacamilla* Papp, recorded as breeding in dung in rock hyrax abodes and in arid bat caves in Namibia; eggs have been shown to survive extended periods of desiccation in a viable state, larval development being triggered by seasonal precipitation or the urine of bats and other cave-dwelling mammals (Barraclough 1998; Kirk-Spriggs *et al*. 2002).

An extraordinary discovery of an old lineage of Diptera was unexpected in the Namib Desert: a species of *Homalocnemis* Philippi (Fig. 13) (see above) was collected on a flowering succulent between the desert dunes and the beach. Other species of the genus occur in humid forests in Chile and New Zealand (Chvála 1991). Other notable examples of flies restricted to the hyper-arid region of Namibia include *Orthactia deserticola* Lyneborg (Therevidae) and *Zumba antennalis* (Villeneuve) (Rhiniidae) (Kirk-Spriggs & Stuckenberg 2009: 160) and the genera *Eremohaplomydas* Bequaert and *Namibimydas* Hesse (Mydidae).

On the edge of the Namib Desert is the impressive Brandberg massif (Fig. 10); Namibia's highest mountain (highest peak Konigstein 2,575 m), which comprises a massive inselberg 650 km^2 in size, rising 1.8 km above the Namib peneplain. The Brandberg is a granitic ring complex, which pre-dates the break-up of Gondwana and thus also the change in continental climatic and environmental conditions that prevailed during the Plio-Pleistocene (Marais & Kirk-Spriggs 2000: 91). Geologically, it consists of a series of alkaline granites that intruded into the throat of an active volcano in the Early Cretaceous (*ca* 300 Mya) (Miller 2000: 17). The extensive undulating upland plateau (*ca* 2000 m) exhibits a winter rainfall climate and associated flora and shares floral elements with the Succulent Karoo biome of southern Namibia (Kirk-Spriggs 2003). The orographic rainfall and vegetation of the Brandberg, coupled with its long isolation, has created refugia for Gondwanan faunal elements and it has a relatively high proportion of endemic species as a result. Most strikingly was discovery of the genus *Alavesia* Waters & Arillo (Atelestidae; see Chapter 54), previously known only from Cretaceous amber from Burma and Spain (Sinclair & Kirk-Spriggs 2010) and the monotypic *Sciarotricha biloba* Hippa & Vilkamaa (Sciaridae; see Chapter 21) confined to the upland plateau, which is the only representative worldwide of the subfamily Sciarotrichinae (Hippa & Vilkamaa 2005). Other notable endemic species include the dolichopodid *Schistostoma brandbergensis* Shamshev & Sinclair, the vermileonid *Leptynoma* (*Perianthomyia*) *monticola* Stuckenberg, the mythicomyiid genus *Hesychastes* Evenhuis and species *Psiloderoides dauresensis* Kirk-Spriggs & Evenhuis (Kirk-Spriggs & Stuckenberg 2009: 162).

Coastal habitats

While most of Africa has undergone ceaseless climate fluctuations, generating the expansion and contractions of forests and savannas over millennia, the continent's arid coasts have remained relatively stable (Barnard 1998). A study of the marine-littoral biogeography of the Diptera of the south-western and southern African seaboard (Kirk-Spriggs *et al*. 2001) showed the influence of the cold Benguela and warm Agulhas currents (Fig. 32) and the associated primary production of kelp (Kirk-Spriggs & Stuckenberg 2009: 166). The Benguela Upwelling System is also significant, as it results in fog, which is the main source of moisture in the hyper-arid Namib Desert of Namibia. Kirk-Spriggs *et al*. (2001) mapped the distribution of the three species of *Afrotethina* Munari (Canacidae; see Chapter 93) on the south-western seaboard, which clearly inhabit defined marine zones (Fig. 33). Some families of flies are almost exclusively coastal, *i.e.*, Canacidae and Coelopidae (see Chapter 77), while some large families of flies include intertidal genera in the region, *e.g.*, Anthomyiidae (*Fucellia* Robineau-Desvoidy; see Chapter 111); Asilidae (*Clinopogon* Bezzi and *Haroldia* Londt); Chironomidae (*Telmatogeton* Schiner and *Thalassomya* Schiner); Chloropidae (*Eutropha* Loew); Dolichopodidae (*Amphithalassius* Ulrich, *Aphrosylus* Haliday, *Argyrochlamys* Lamb, *Cemocarus* Meuffels & Grootaert and *Plesiothalassius* Ulrich); Sphaeroceridae (*Archicollinella* Duda and *Thoracochaeta* Duda; see Chapter 99); Tabanidae (*Adersia* Austen, *Braunsiomyia* Bequaert and *Neavella* Oldroyd); and Therevidae (*Acathrito* Lyneborg).

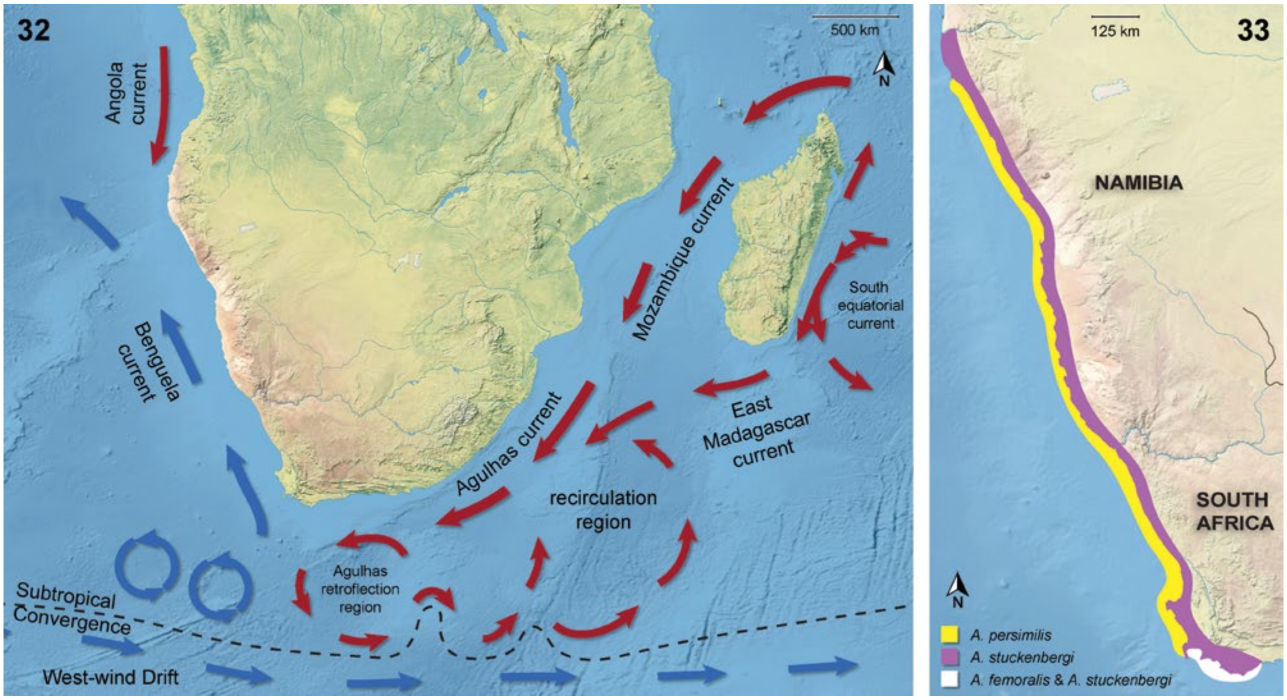
Oceanic islands

Oceanic islands have long attracted the interest for biogeographers in terms of dispersal and historical biogeography. Those oceanic islands in the Atlantic and Indian Oceans that form part of the Afrotropical Region (as defined in Chapter 1, fig. 1), are of three distinct origins that have had a profound effect on the composition of the flora and fauna: 1) islands formed of fragments of the supercontinent of Gondwana; 2) volcanic islands resulting from oceanic hot spots; and 3) islands associated with the African continental shelf. The greater number of oceanic islands that form part of the Afrotropical Region have resulted from oceanic hotspots; portions of the Earth's crust where lava pushes up from beneath the mantle and creates a volcano. This may be caused by a rising mantle plume or some other cause. Hotspots may occur far from tectonic plate boundaries.

Islands of Gondwanan origin

Both Madagascar and Seychelles are ancient fragments of Gondwana which separated from Pangea from the Middle Jurassic to the Early Cretaceous (Figs 1–3, 4). The Madagascan Diptera encompass a remarkable mix of relationships, but only one apparent endemic Gondwanan relict; the blephariceriid genus *Paulianina* (see above). Oriental and African relationships occur in numerous families, though few with South Africa. Some large families are poorly represented — there are few Bombyliidae (18 species in eight genera, 16 of which are endemic) and Nemestrinidae are represented by only one species. Much of the fauna could still be unknown — the first vermileonid was discovered quite recently by M.E. Irwin (Stuckenberg 2002), two species of Rhinophoridae await description, at least 100 undescribed species of Lauxaniidae have been collected and additional families are likely to be recorded. With fewer than 2,500 recorded species, considerably more collection and study of Malagasy Diptera is being coordinated (see Chapter 1) (Kirk-Spriggs & Stuckenberg 2009: 167, 168) and additional study of sampled material is required.

There has been little consensus among biologists in respect to the origins of Madagascar's unique biota (Wilmé *et al.* 2006), although most appear to agree that this resulted either from vicariance (in the case of "ancient" groups), or from some form of long-distance dispersal event followed by founder effect speciation and various means of *ad hoc* "sweepstake" and "stepping stone" scenarios (*e.g.*, Cox 1998; Heads 2009; Trewick 2000; Yoder & Nowak 2006), have been promulgated to explain this (De Wit 2003; Krause *et al.* 1997). This latter represents transoceanic distribution of African founder individuals from 65.5 Mya to the present, with rafting and flight being the main explanation for such events. Yoder & Nowak (2006) noted overwhelming evidence of Cenozoic dispersal, with many endemic clades of Malagasy taxa having closest sister-group relationships with African taxa. In respect to Apoidea (Hymenoptera), Eardley *et al.* (2009) have, for example, suggested dispersal *via* vegetation rafts arising from tsunamis, or from extreme floods in East Africa (the larger rivers depositing



Figs 9.32–33. Oceanic currents and distribution of Canacidae in Southern Africa: (32) ocean currents around the Southern Africa coast; (33) geographical distribution of the three species of *Afrotethina* Munro (Canacidae) on the south-western seaboard of Africa. Fig. 32 (after Linacre 2002, fig. 1 and Brown & Jarman 1978, fig. 1, combined), Fig. 33 (after Kirk-Spriggs *et al.* 2001, fig. 80; made with Natural Earth).

suitable material into the Mozambique Channel), to explain faunal connections between continental Africa and Madagascar (Kirk-Spriggs 2010a).

In a review of the Diptera of Madagascar, Irwin *et al.* (2003) discussed the origins and composition of the fauna. They noted that endemism in the Brachycera is rather high with 17% of genera and 79% of species found only there. Some conclusions published in that chapter are, however, in need of critical review on a family by family basis. In the case of the Asilidae, for example, a more recent unpublished assessment (M. Hauser, pers. comm. 2017), indicates there to be a very strong continental Afrotropical affinity with the Malagasy fauna and also a strong element of continental Afrotropical/Oriental genera, but this connection is rather Oriental to Africa to Madagascar and not necessarily Oriental to Madagascar. It is also apparent that the asilid taxa shared with the Neotropics and Madagascar are largely those with a global distribution. Interpretation of fly distribution on Madagascar has been limited by the poor number of specimens available. Tsacas (1974), for example, based his preliminary studies of Malagasy *Curtonotum* on only 38 specimens. Substantial additional material is now available through "An Arthropod Survey of Madagascar's Protected Areas" (see Chapter 1) and examination of this material is enabling a more complete interpretation of distribution on the island. Kirk-Spriggs (2011), for example, recorded 13 species of *Curtonotum* from Madagascar, 12 of which are endemic to the island. The Malagasy fauna represents 35% of the Afrotropical fauna as a whole and all species-groups of Malagasy fauna were probably derived from African founder individuals. A similar pattern is exhibited in the Stratiomyidae, with all native Malagasy taxa appearing to result from dispersal from the continental Afrotropics, with Madagascar having a rather high percentage of species compared with the mainland (M. Hauser, pers. comm. 2017).

Being granitic in composition, the Mahé-Praslin group of mid-oceanic Seychelles are continental in origin (see above). In this they are unique, as all other truly mid-oceanic islands (other than Madagascar) are of volcanic origin. The granitic Seychelles islands are in fact exposures of a submerged, elongate microcontinent that lies amid the western Indian Ocean. Before 160 Mya, however, the Indian Ocean did not exist and the Seychelles microcontinent was sandwiched between north-eastern Madagascar and western India, within the supercontinent of Gondwana (Fig. 4) (McLoughlin 2001). At *ca* 160 Mya Gondwana split into two and Madagascar-Seychelles-Indian lay along the margin of Gondwana. East Gondwana then gradually disintegrated, with Antarctica-Australia carving off at 120 Mya and Seychelles-Indian leaving Madagascar at *ca* 85 Mya. By 65 Mya the Seychelles microcontinent had reached its current position in respect to Madagascar, although still attached to India (Fig. 2) (Gerlach 2013; Plummer & Belle 1995).

The Diptera fauna of Seychelles is diverse, as compared to other Indian Ocean islands of volcanic origin. Sæther (2004) reviewed the Chironomidae and noted that 28 species are known from the islands, most of which were endemic. Some

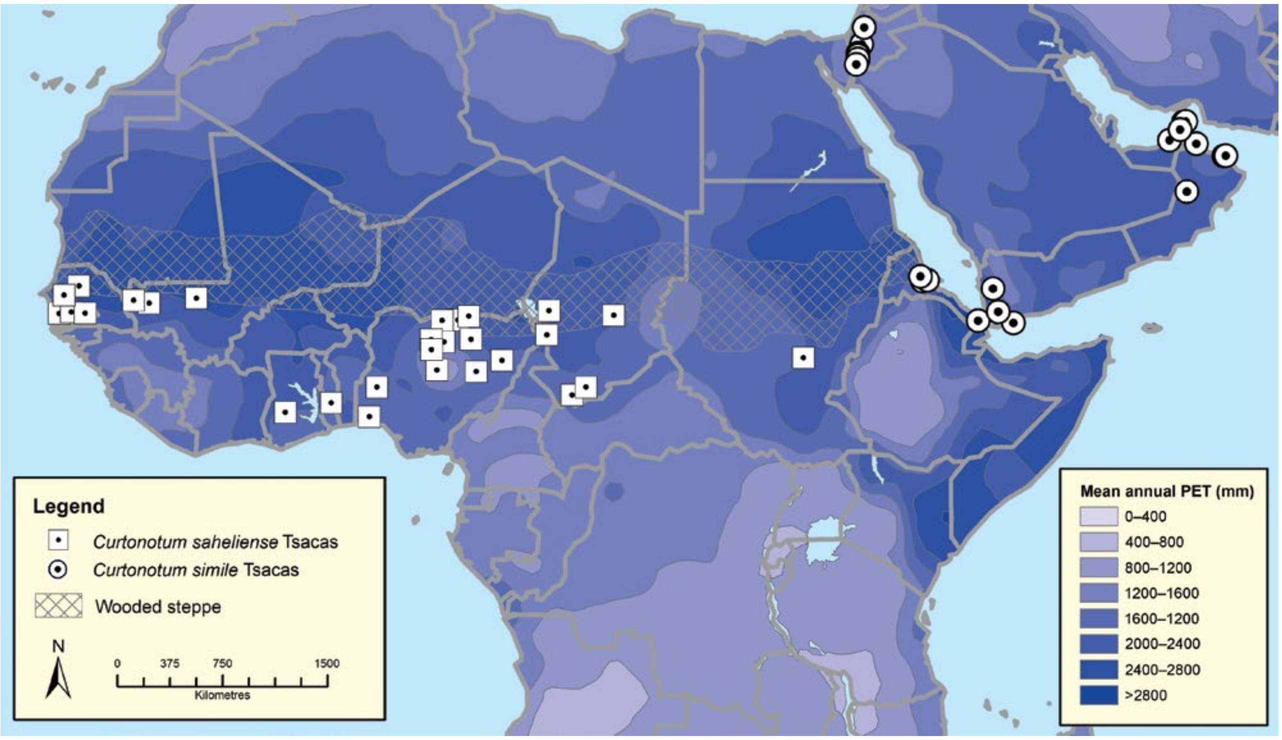


Fig. 9.34. Distribution of the two sister species, *Curtonotum saheliense* Tsacas and *C. simile* Tsacas (Curtonotidae) in continental Africa and the Arabian Peninsula, mapped over mean annual precipitation (Kirk-Spriggs & Wiegmann 2013, fig. 327; South Sudan not indicated).

species among the (probable) marine intertidal chironomids are known from Micronesia, or have close relatives in the Oceanic, Oriental or eastern Palaearctic Regions, whereas other species were widespread in the continental Afrotropics. The diverse fauna of Ceratopogonidae, with species in 14 genera, was described by Clastrier (1983) and Cariou *et al*. (2009: 380) noted that the fauna of Drosophilidae includes eight virtually cosmopolitan species, seven in common with continental Africa and two in common with both the Afrotropical and Oriental Regions. They noted that seventeen species are probably

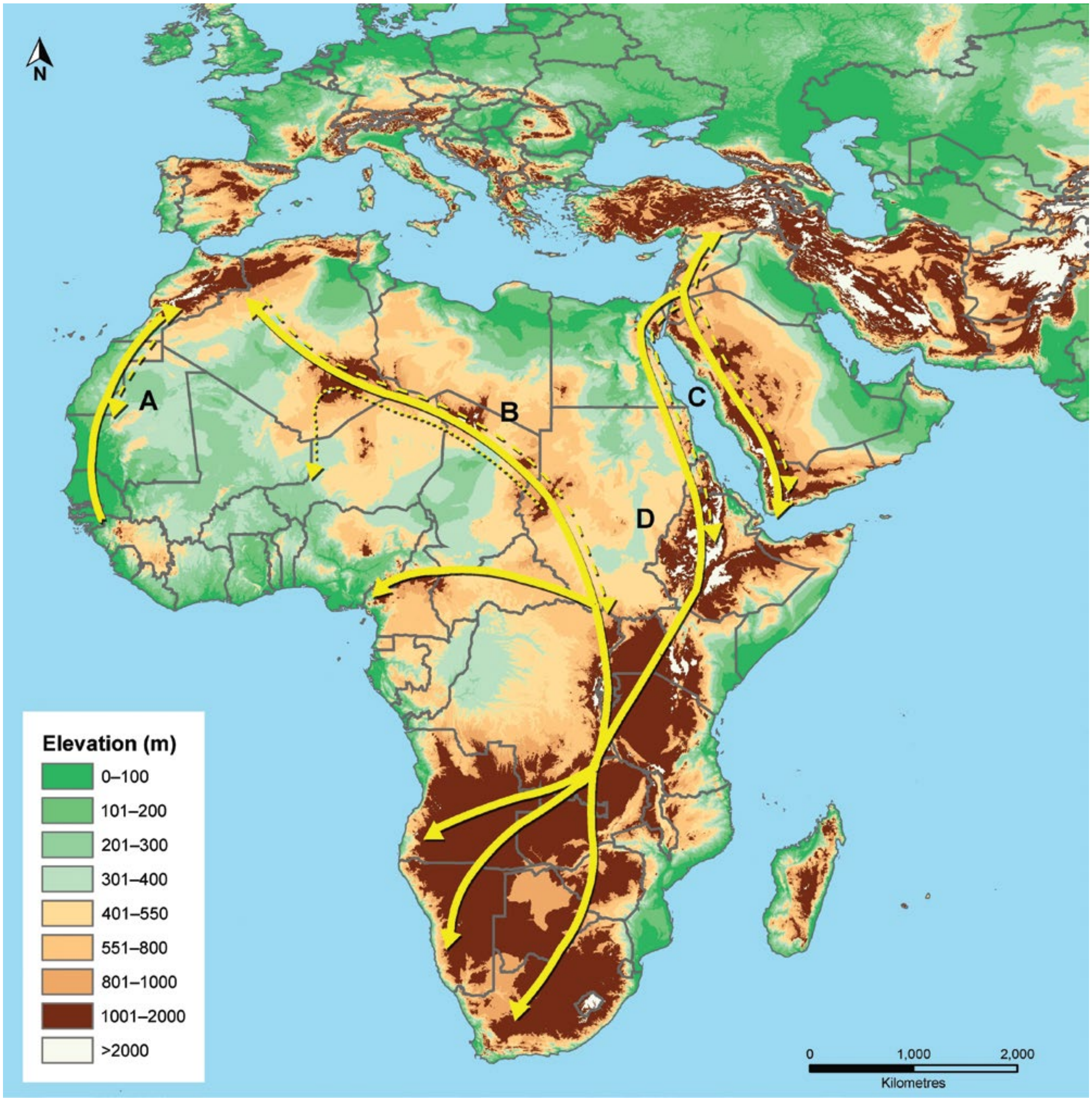


Fig. 9.35. Proposed faunal migration routes in the Afrotropical Region during the Pliocene and Pleistocene: yellow dark arrows indicate tropical elements; dotted arrows indicate southern Saharan orophilic elements; dashed arrow indicate Mediterranean provincial elements (after Quézel 1978; South Sudan not indicated).

Abbreviations: A – Atlantic coastal corridor; B – central high Africa corridor; C – Rift Valley corridor; D – Eastern high Africa corridor.

endemic and the remaining species probably also occur on Madagascar. A significant contribution to the knowledge of the Diptera of the Seychelles was published recently by Gerlach (2009).

Dispersal biogeography

Dispersal biogeography (reviewed by Cranston 2005: 282), views organisms as having identifiable centres of origin from which they spread. For the Afrotropical Region, Kirk-Spriggs & McGregor (2009) proposed four possible migration (or dispersal) routes (or corridors) between the Holarctic and Africa and within continental Africa and the Arabian Peninsula during the Pliocene and Pleistocene (Fig. 35): an Atlantic coastal corridor (Fig. 35, A); a central high Africa corridor (Fig. 35, B); a Rift Valley corridor (Fig. 35, C); and an Eastern high Africa corridor (Fig. 35, D). Topographical features of the African continent are significant for fly distribution. The Great Rift Valley of East Africa, High Africa and mountain chains of the Arabian Peninsula have likely acted as pathways for floral and faunal radiation. The evidence of Lake Megachad and other Saharan palaeolakes (see above) indicate that faunal transfer may have occurred along a humid central high Africa corridor (or other probable routes illustrated in Fig. 35), between the Mediterranean Province and southern African regions or *vice versa*, as evidenced by Mediterranean provincial and tropical African floral elements retained in and around the central Saharan

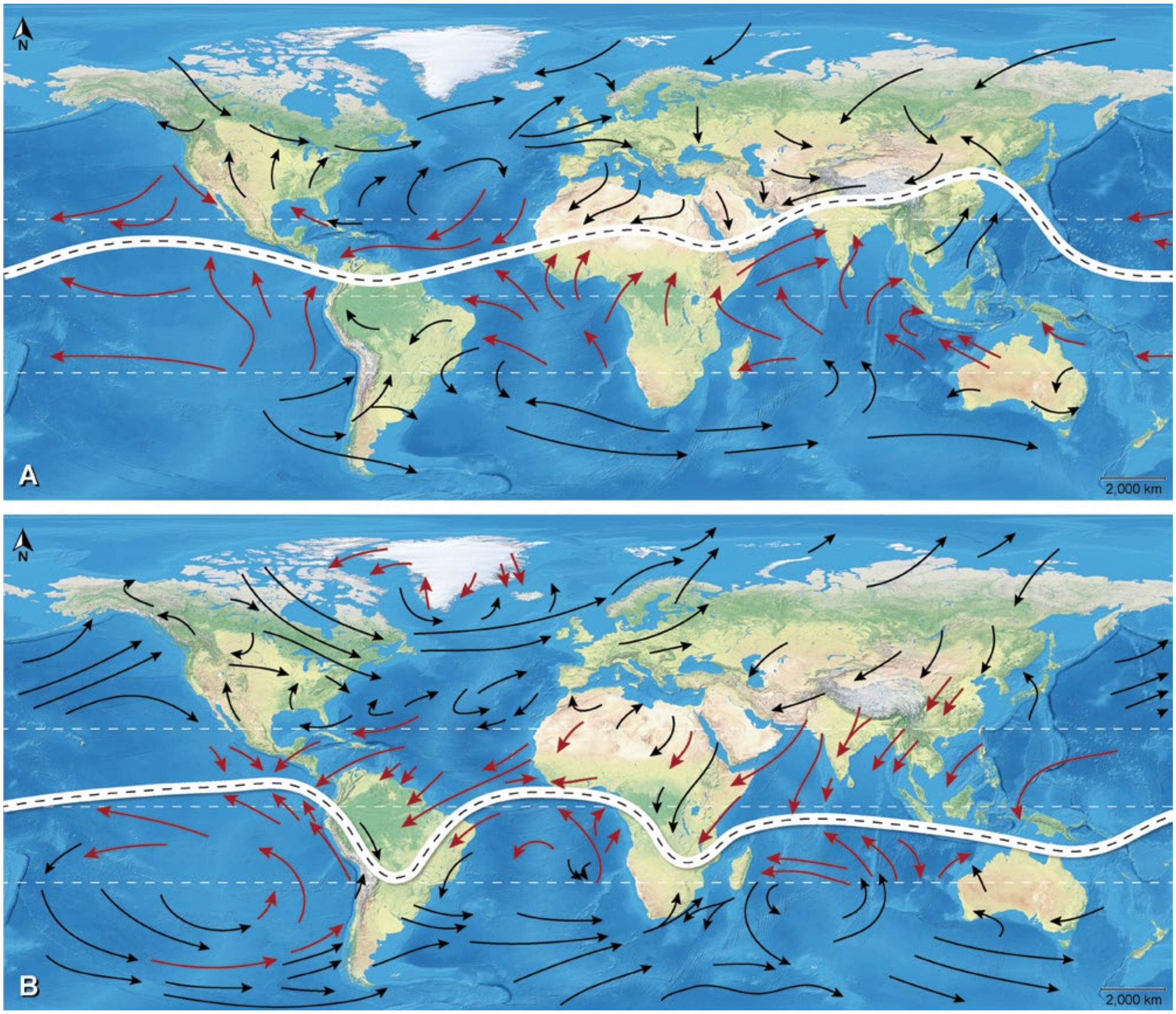


Fig. 9.36. Prevailing surface winds in July (A) and January (B) indicating seasonal distribution of the Inter-Tropical Convergence Zone (ITCZ) (sinuous bands containing dashed line), prevailing winds (maroon arrows) and most frequent winds (black arrows). The ITCZ exhibits distinct salient in summer over north-eastern Asia (A) and over South America and Southern Africa (B) (after Johnson 1969; made with Natural Earth).

mountains. Diptera studies in the Aïr massif have revealed a significant number of Mediterranean provincial species which occur on the southern Hoggar, evidence supporting a recent connection of the two regions during pluvial periods.

Anemochory or atmospheric dispersal has and continues to play a role in dispersal, at least of small weak-flying Diptera. Diptera are highly mobile and a recent review (Kirk-Spriggs & McGregor 2009) has highlighted the significance of aerial dispersal in the colonisation of oceanic islands and as a means of mixing faunas within and between zoogeographical realms and regions (Kirk-Spriggs 2010*a*).

Many plants and animals increase their ranges by passive mechanisms of dispersal; those which do so by means of wind or water are termed anemochore (Udvardy 1969: 34) or anemohydrochorous (Müller 1974: 35). As Cranston (2005: 281) states: "The occurrence of particular insects in the aerial planktonic drift supports dispersal powers, as does the regular arrival (not necessarily establishment) of non-native taxa on the opposite shores of bodies of water, such as the English Channel or the Tasman Sea." Numerous studies have examined the aerial distribution of insects in the upper atmosphere (*e.g.*, Chapman *et al*. 2004; Freeman 1945; Glick 1939; Hardy & Milne 1938; White 1974) and it has been demonstrated that the atmosphere of temperate regions contain a variable density (0.1–110 × 106 per km^2 to 4,300 m) of flying and drifting airborne arthropods termed "aerial plankton" by some authors (Bowden & Johnson 1976; Pugh 2003; White 1974).

Most authors have ranked the small weak-flying Diptera (especially smaller "Nematocera" and Cyclorrhapha), as the most significant components of this "aerial plankton", along with the Hemiptera; Diptera being one of the few orders of insects with species reaching elevations exceeding 4,000 metres. The families Chironomidae, Ceratopogonidae and Psychodidae in the "Nematocera" and Chloropidae, Phoridae, Syrphidae (see Chapter 60), Ephydridae (see Chapter 100), Drosophilidae and Agromyzidae (see Chapter 86) in the Cyclorrhapha are particularly common in such samples (Bowden 1978: 779). Recent examination of Diptera resulting from sticky panels affixed to tethered helium-filled balloons at 100–200 m above ground level in Mali, sampled 17 families of Diptera, with the Chironomidae, Chloropidae, Drosophilidae, Lauxaniidae and Muscidae being dominant in samples (A.H. Kirk-Spriggs, pers. obs.).

Small insects, spiders and mites in the upper atmosphere can be transported considerable distances and have been sampled on ships far out to sea (*e.g.*, Bowden & Johnson 1976; Harrell & Holzapfel 1966; Harrell & Yoshimoto 1964; Pryor 1964), as a result of which this means of dispersal has been partly attributed to the colonisation of oceanic islands (*e.g.*, Gressitt & Yoshimoto 1963). Although the distance they can travel at low altitudes is dependent on flight capacity (Pugh 2003), at altitudes of 4,000 m or more these small insects are said to drift passively for prolonged distances of 200–800 km (Bowden & Johnson 1976; Pugh 2003). If such insects are to colonise successfully, then this is obviously dependent on survival and the viability of the habitat in which they eventually find themselves.

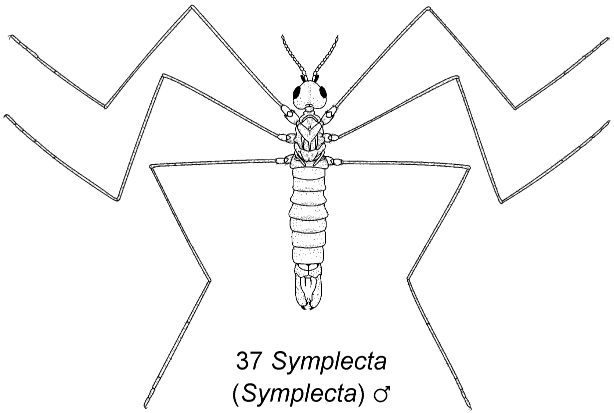
A prime factor in north–south dispersal between zoogeographical realms and zones are winds associated with the Inter-Tropical Convergence Zone (ITCZ) (Fig. 36), which experiences a major seasonal shift from equatorial Africa in July (the hottest month in the Sahara) and southern Africa in July (the coldest). In July prevailing winds move northeast, east or south towards the Equator, whereas in January these move south-westwards across the Sahara and sweep through southern Africa. Corbet (2003) has demonstrated that such winds are instrumental in the migration of certain Odonata to and from wetter areas and the effect therefore on small weak-flying Diptera can be assumed to be at least a magnitude greater.

There is also little evidence to suggest that prevailing winds evident today were the same in the distant or recent past and strong winds (jet streams) that frequently blow in entirely different directions from that of surface winds may also lead to dispersal (Udvardy 1969: 35). Bowden (1978) considered these factors in his examination of the zoogeography of southern African Diptera. He restricted his interpretation of zoogeography to the Brachycera, particularly the Asilidae, Bombyliidae, Mydidae and Nemestrinidae, drawing few examples from the "Nematocera" and Cyclorrhapha. This was in part due to the fact that most of the families selected were rare in, or absent from, aerial catches and many are host-associated or specific, with definable ages of evolution.

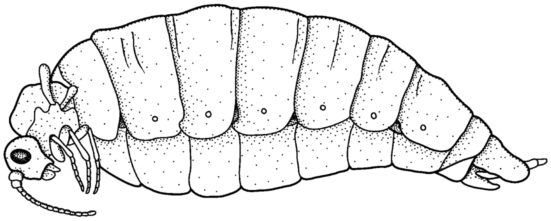
Wing reduction in Afrotropical Diptera

Wing reduction in insects is common (Brues 1903; Byers 1969; Hackman 1964; Hemmingsen 1956; Papp 1979; Richards 1957, 1960, 1965, 1968). Reduction of wings with accompanying flightlessness is known from more than 20 families of Diptera (Hackman 1964) and Bezzi (1918) listed 384 species exhibiting wing reduction globally. Some of the best documented cases relate to the Pacific Hawaiian Is. (*e.g.*, Evenhuis 1997; Hardy & Delfinado 1974). Such wing reductions can be broadly categorised as responses to three general types of selective pressure: 1) climatic, especially to cold or overcast habitats, in alpine areas, high latitudes and islands; 2) adaptation to parasitism, either as inquilines in the nests of social insects or on vertebrate hosts; and 3) life in cryptic habitats, where wings would have little function or be easily damaged (Bickel 2006). Hackman (1964) divided Diptera with reduced wings into nine groups: (1) high elevation Diptera; (2) Diptera in arctic, subarctic and sub-Antarctic mainland habitats; (3) nival Diptera; (4) Diptera of oceanic islands; (5) Diptera on seashores; (6) marine Diptera; (7) Diptera in various terricolous and hypogeous habitats; (8) Diptera in nests of Hymenoptera and termites; and (9) parasites of warm-blooded animals. Not all of these groups apply to Afrotropical Diptera, notably groups 2 and 3.

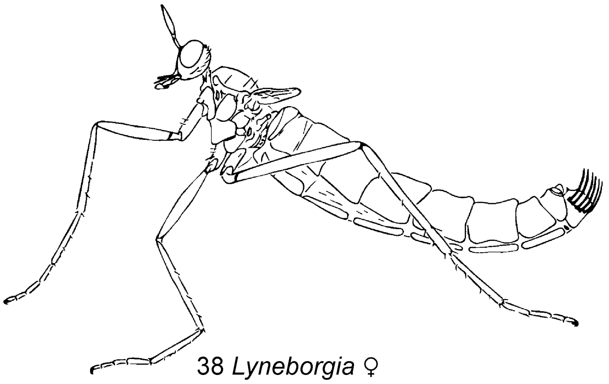
Hackman further defined four categories of wing reduction in Diptera as follows: 1) distinctly reduced, not permitting flight, broad and more or less blunt, shorter than abdomen, if wing small, at least radial veins still distinct (brachyptery); (2) very narrow, not permitting flight, at least radial veins distinct (stenoptery); (3) reduced to a tiny appendage of varying shape, broad or narrow, at most with only traces of radial vein (microptery), or (4) reduced to minute scale, at most carrying some setae, or entirely absent (aptery). Flightlessness affects other structures, such as the reduction or loss of halters, loss of flight muscle and associated thoracic shrinkage and modification of the legs for cursorial life (Bickel 2006). In addition,



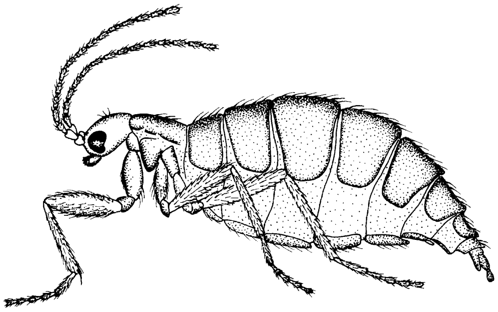
37 *Symplecta*
(*Symplecta*) ♂
(Limoniidae)



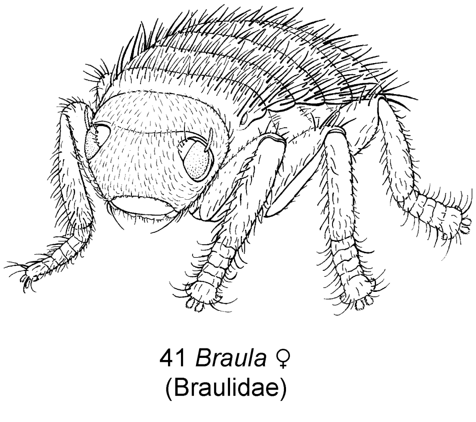
39 *Epidapus* (*Pseudoaptanogyna*) ♀
(Sciaridae)



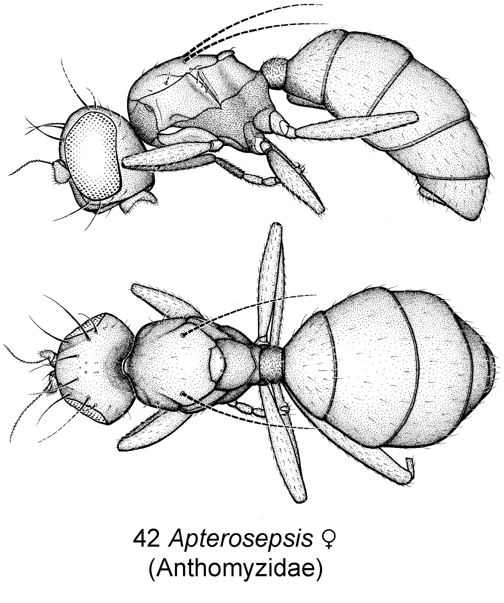
38 *Lyneborgia* ♀
(Therevidae)



40 *Pnyxia* ♀
(Sciaridae)



41 *Braula* ♀
(Braulidae)



42 *Apterosepsis* ♀
(Anthomyzidae)

Figs 9.37–42. Examples of Diptera with reduced wings: (37) *Symplecta* (*Symplecta*) *holdgatei* (Freeman) (Limoniidae), dorsal view, micropterous ♂ endemic to Gough Is. (Tristan du Cunha group); (38) *Lyneborgia stenoptera* Irwin (Therevidae), lateral view, brachypterous ♀ endemic to coastal South Africa; (39) *Epidapus* (*Pseudoaptanogyna*) *pallidus* (Séguy) (Sciaridae), lateral view, micropterous ♀; (40) *Pnyxia scabiei* (Hopkins) (Sciaridae), lateral view, apterous ♀; (41) *Braula* sp. (Braulidae), frontolateral view, apterous ♀ ectoparasitic on honey bees; (42) *Apterosepsis basilewskyi* Richards (Anthomyzidae), lateral view (above), dorsal view (below), micropterous ♀ endemic to Mt Meru, Tanzania. Fig. 37 (after Jones *et al*. 2003, fig. 27), Fig. 38 (Irwin 1973, fig. 3), Fig. 39 (after Séguy 1961, fig. 1), Fig. 40 (Menzel & Mohrig 2000, fig. 428), Fig. 41 (Barraclough 1995, fig. 18).

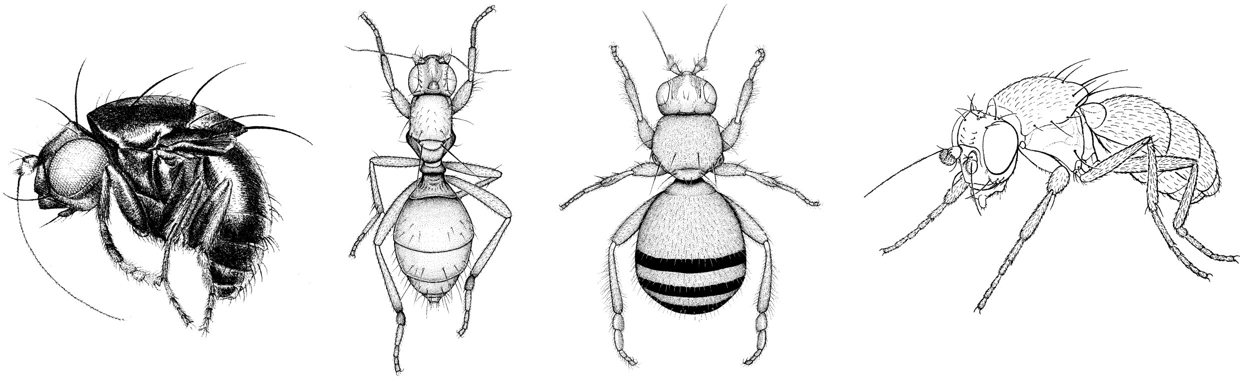
43 *Carnus* ♀ (Carnidae)

44 *Aenigmatistes* ♀ (Phoridae)

45 *Wandolleckia* ♀ (Phoridae)

46 *Dolichocephala* ♂ (Empididae)

47 *Stilpon* ♀ (Hybotidae)



48 *Reunionia* ♂ (Sphaeroceridae)

49 *Pismira* ♀ (Sphaeroceridae)

50 *Ocellipsis* ♀ (Sphaeroceridae)

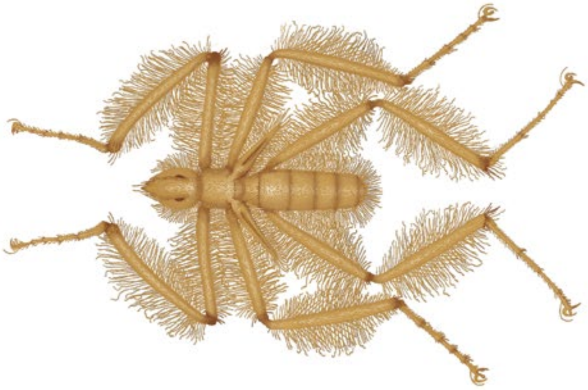
51 *Scutellista* ♀ (Sphaeroceridae)

Figs 9.43–51. Examples of Diptera with reduced wings (cont.): (43) *Carnus hemapterus* Nitzsch (Carnidae), lateral view, micropterous ♀ associated with nestling birds (non-Afrotropical); (44) *Aenigmatistes* sp. (Phoridae), lateral view, apterous ♀, associated with termitaria; (45) *Wandolleckia achatinae* Cook (Phoridae) apterous females, associated with giant African land snails of the genus *Achatina* Lamarck; (46) *Dolichocephala fugitivus* (Garrett Jones) (Empididae), lateral view ♂, endemic to the Ruwenzori Mountains, Uganda; (47) *Stilpon leleupi* Smith (Hybotidae), frontal view, ♀ from indigenous forests of South Africa; (48) *Reunionia unica* Papp (Sphaeroceridae), lateral view, ♂ endemic to Réunion Is.; (49) *Pismira uvira* Richards (Sphaeroceridae), lateral view, ♀ from Democratic Republic of Congo; (50) *Ocellipsis cyclogaster* Richards (Sphaeroceridae), lateral view, ♀ endemic to Mt Elgon, Kenya; (51) *Scutelliseta mischogaster* Norrbom (Sphaeroceridae), frontolateral view, associated with indigenous forests in South Africa. Figs 43–45 (photographs © S.A. Marshall), Fig. 48 (after Papp 1979, fig. 7), Figs 49, 50 (after Roháček *et al*. 2001, figs 21, 18, respectively), Fig. 51 (Barraclough 1995, fig. 19).

newly emerged imagines may be fully winged, but lose at least the greater part of the wing when they reach the feeding locality. Such caduceus wings are known in relatively few dipterous families and include parasitic flies, such as the blood-sucking *Carnus hemapterus* Nitzsch (Carnidae; see Chapter 93) (Fig. 43) on nestling birds, the genera *Ascodipteron* Adensamer and *Lipoptena* Nitzsch (Hippoboscidae; see Chapter 109) and all females of the subfamily Termitoxeniinae (Phoridae), that are associated with termites (R.H.L. Disney, pers. comm. 2016).

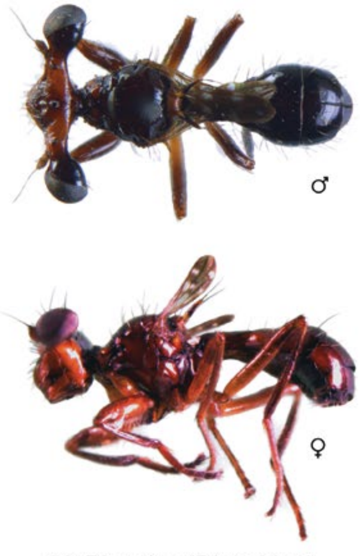
Examples of wing reduction are found in 17 families of Diptera that occur in the Afrotropics. Some are associated with birds, mammals and bees (Braulidae (see Chapter 105), Carnidae, Hippoboscidae and Mormotomyiidae (see Chapter 101)), but most are either restricted to remote oceanic islands (both Atlantic and Indian Oceans) or to remote mountain peaks at high elevations and so have great biogeographical significance, although all families with flightless representatives are reviewed below for the sake of completeness. Due to the lack of diagnostic wing characters and strange body forms exhibited by many flightless species, ascribing these to the correct family has proven problematic in some cases, *e.g.*, *Apterosepsis basilewskyi* Richards (Fig. 42) (see Chapter 87), which has been placed in the families Sepsidae (see Chapter 79), Chloropidae


52 *Melophagus* ♀ (Hippoboscidae)


53 *Mormotomyia* ♂ (Mormotomyiidae)


54 *Alombus* (Chloropidae)


55 *Scaptomyza* (Drosophilidae)



56 *Diopsina* (Diopsidae)

Figs 9.52–56. Examples of Diptera with reduced wings (cont.): (52) *Melophagus ovinus* (L.) (Hippoboscidae), dorsolateral view, ♀ ectoparasitic on sheep; (53) *Mormotomyia hirsuta* Austen (Mormotomyiidae) dorsal view, ♂ associated with bats in rock fissures in Kenya; (54) *Alombus* sp. (Chloropidae), lateral view (above), dorsal view (below); (55) *Scaptomyza* (*Parascaptomyza*) *frustulifera* (Frey) (Drosophilidae), dorsal view (above), lateral view (below), ♂ confined to Tristan da Cunha Is. group; (56) *Diopsina draconigena* Feijen (Diopsidae), dorsal view, ♂ (above), lateral view ♀ (below), from the Drakensberg Mountains, South Africa. Fig. 52 (photograph © S.A. Marshall), Fig. 54 (H. Taylor, Natural History Museum London, U.K.), Fig. 55 (courtesy S.F. McEvey), Fig. 56 (Feijen & Feijen 2013, figs 10, 11).

and now Anthomyzidae and the phylogenetic position of the monotypic *Mormotomyia hirsuta* Austen (Mormotomyiidae), has been contentious; the family having been placed both in the Acalyptratae and Calyptratae by various authors. Molecular studies have or are assisting in the interpretation of some of these relationships. A concise account of flies exhibiting wing reduction in the Afrotropics is outlined below:

Anthomyzidae (see Chapter 87). The apterous, ant-mimicking species *Apterosepsis basilewskyi* (Fig. 42) is only known from two female specimens restricted to high elevations on Mt Meru in Tanzania, East Africa (Roháček & Barber 2008). The species has been ascribed to several families in the past (see above) and was only relatively recently confirmed as a representative of Anthomyzidae (Roháček 1998).

Braulidae (see Chapter 105). Three apterous species of the genus *Braula* Nitzsch (*e.g.*, Fig. 41) occur in the Afrotropics: the virtually cosmopolitan *B. coeca* Nitszch, with two subspecies (*B. coeca angulata* Örösi Pál and *B. coeca sensu stricto*), *B. kohli* Schmitz and *B. pretoriensis* Örösi Pál. Both sexes are apterous and adults occur in the hives of honey bees, often as ectoparasites on the bees themselves (Cogan 1980: 627). The phylogenetic position of the family has been contentious and it is currently placed in the superfamily Ephydroidea (Wiegmann *et al*. 2011).

Carnidae (see Chapter 93). One widespread species of the genus *Carnus* Nitzsch, *C. hemapterus* (Fig. 43), has caduceus wings and is associated with nestling birds (see above). Although Papp (1984: 119) listed the species from the Afrotropics, Barraclough (1994) was unable to confirm this. The only *Carnus* confirmed from the region is an undescribed species recorded by De Coninck (1986) from Democratic Republic of Congo, which is parasitic on nestlings of Brown-hooded kingfisher, *Halcyon albiventris* Scopoli (Alcedinidae); a species widespread throughout southern Africa (Barraclough 1994).

Chironomidae (see Chapter 35). Three coastal species of *Clunio* Haliday with apterous females occur in the Afrotropics: *C. africanus* Hesse from South Africa, *C. gerlachi* Sæther from Seychelles and *C. jonesi* Sæther & Andersen from Gough Is. Adults occur on marine shorelines and larvae develop in the intertidal zone, particularly on rocky shores (Andersen *et al.* 2013: 210).

Chloropidae (see Chapter 96). The genus *Alombus* Becker (Fig. 54) comprises 11 species, apterous in both sexes that are endemic to mountains in Democratic Republic of Congo and Tanzania (Richards 1965). One species. *A. seminitidus* Villeneuve is more widely distributed and occurs on mountains in Burundi, Democratic Republic of Congo, Rwanda and Uganda. There is also an undescribed apterous species of *Myrmecosepsis* Kertész recorded from Nigeria by Sabrosky (1980: 701) and one species of the genus *Conioscinella* Duda (*C. aptera* Sabrosky from Kenya), is also apterous (J.W. Ismay, pers. comm. 2016).

Diopsidae (see Chapter 64). The brachypterous species *Diopsina draconigena* Feijen (Fig. 56) has both sexes with reduced wings and is restricted to high elevations on mountains in Lesotho and South Africa (Drakensberg Mountains) (Feijen 1981; Feijen & Feijen 2013).

Drosophilidae (see Chapter 106). Three stenopterous species of *Scaptomyza* (*Parascaptomyza* Duda) occur in the remote South Atlantic Tristan da Cunha Is. group (incl. Inaccessible Is.), namely *S. angustipennis* (Frey), *S. freyi* Hackman and *S. frustulifera* (Frey) (Fig. 55) (S.F. McEvey, pers. comm. 2016).

Empididae (see Chapter 51). Three stenopterous empidid species are known from high elevations in the Ruwenzori Mountains of Uganda (Garrett Jones 1940): *Wiedemannia reducta* Garrett Jones and two species of *Dolichocephala* Macquart (*D. fugitivus* (Garrett Jones) (Fig. 46) and *D. tali* (Garrett Jones)). The last two mentioned species were originally assigned to monotypic genera, but were later synonymised by Sinclair (1995). All three species have the wing reduced in both sexes.

Hippoboscidae (see Chapter 109). All Hippoboscidae are ectoparasitic on birds and mammals in the adult state, with the single exception of the genus *Ascodipteron*, where females embed themselves in the skin of their bat host and become endoparasitic (Maa 1965). The family includes fully winged, brachypterous, stenopterous and apterous forms. Species of the subfamily Nycteribiinae (here including the strebline grade) are all associated with bats (Chiroptera) and exhibit a range of fully winged to apterous forms. In the Afrotropics the subfamily Hippoboscinae includes apterous *Melophagus ovinus* (L.) (Fig. 52), two stenopterous species of the genus *Crataerina* Olfers and caduceus *Lipoptena cervi* (L.) (see above) (Hackman 1964).

Hybotidae (see Chapter 52). The brachypterous species *Stilpon leleupi* Smith (Fig. 47) is recorded from two indigenous forests (Dukuduku Forest and Ngomi Forest) in the KwaZulu-Natal Province of South Africa (Smith 1969).

Limoniidae & Tipulidae (see Chapter 14). Three species of Limoniidae with both sexes apterous occur in the Afrotropics: *Austrolimnophila* (*Austrolimnophila*) *buxtoni* Alexander, endemic to the Ruwenzori Mountains, Uganda; *Quathlambia stuckenbergi* Alexander from South Africa; and *Symplecta* (*Symplecta*) *holdgatei* (Freeman) (Fig. 37) endemic to Gough Is. (Tristan de Cunha group). In addition, five species of the genus *Platylimnobia* Alexander, with both sexes apterous occur in South Africa and one species, *P. brinckiana* Alexander is brachypterous. Within the Tipulidae, twelve species of *Leptotarsus* (*Longurio* Loew) with normally winged males and apterous females occur in South Africa and an additional 17 southern African species of the same subgenus, for which females remain unknown, may have brachypterous or apterous females. Two high elevation species of *Tipula* (*Tipula* L.) have both sexes apterous: *T.* (*T.*) *hollanderi* Theowald (males with more developed wings at lower elevations) from the Bale Mountains of Ethiopia and *T.* (*T.*) *subaptera* Freeman from Mt Kilimanjaro, Tanzania. Four additional species of the same subgenus have normally winged males and apterous females and three species with winged males with unknown females probably have apterous females (H. de Jong, pers. comm. 2016).

Mormotomyiidae (see Chapter 101). This monotypic family comprises the single stenopterous species *Mormotomyia hirsuta* (Fig. 53) associated with bats in horizontal rock fissures in Kenya (Austen 1936; Copeland *et al*. 2011, 2014). Kirk-Spriggs *et al*. (2011) studied the structure of the wing and reduced halter of the species. It is likely that wing reduction is related to close confinement within narrow rock fissures. Morphological studies of the female reproductive tract (Kirk-Spriggs *et al*. 2011), and antennal structure (McAlpine 2011), coupled with an unpublished molecular study (B.M. Wiegmann, pers. comm. 2017), indicate the family belongs to the superfamily Ephydroidea.

Phoridae (see Chapter 59). In terms of the loss of wings in the female sex the Phoridae dominate entirely, including all genera of the subfamily Termitoxeniinae (Hackman 1964). Many species with adult females that inhabit colonies of ants and termites are flightless, being transported by the winged males to the host colonies during nuptial flights. Females of *Aenigmatistes* Shelford, for example, that inhabit termitaria in the Afrotropics, exhibit striking modifications and are almost cockroach-like in form (Fig. 44). The mountain-dwelling genera *Aptinandria* Schmitz and *Arrenaptenus* Schmitz have apterous males and apterous females of *Wandolleckia achatinae* Cook (Fig. 45) are associated with *Achatina* Lamarck, the giant African land snails, with their larvae feeding on the faeces (Baer 1953). Numerous other genera and species are associated with ants and termites or with leaf litter and other terricolous habitats (see Disney 1994, for review).

Sciaridae (see Chapter 21). All known females of *Epidapus* (Fig. 39) are apterous or brachypterous, with four species known from Guinea, Seychelles and South Africa (Menzel 2017). The virtually cosmopolitan *Pnyxia scabiei* (Hopkins) (Fig. 40) (Menzel 2017) has both fully winged and brachypterous male forms occurring together, while the female is invariably apterous (Hackman 1964).

Sphaeroceridae (see Chapter 99). Fourteen genera of Sphaeroceridae in the Afrotropics include flightless species. Diversification of flightless Sphaeroceridae has taken place on the mountains of Central and East Africa (Hackman 1964), with the following entire genera of endemic apterous species in both sexes: *Aluligera* Richards (20 species, endemic to the Ruwenzori Mountains, Uganda, the Uluguru Mountains, Tanzania, Mt Elgon, Kenya and mountains in Democratic Republic of Congo, Ethiopia and Rwanda); *Mesaptilotus* Richards (14 species, endemic to the Ruwenzori Mountains of Uganda and mountains in Democratic Republic of Congo and Rwanda); *Ocellipsis* Richards (Fig. 50) (13 species, endemic to Mt Elgon, the Aberdare range and the Elgeyo escarpment of Kenya); *Oribatomyia* Richards (2 species, endemic to mountains in Democratic Republic of Congo); *Paraptilotus* Richards (9 species, endemic to Mt Elgon, the Aberdare range, Kenya and Mt Tola, Ethiopia); and *Pismira* Richards (Fig. 49) (4 species, endemic to mountains of Democratic Republic of Congo). Some other monotypic apterous species occur in these mountains: *Gobersa leleupi* De Coninck (Uluguru Mountains, Tanzania); *Kabaria spinisterna* Richards (Kahuzi in Democratic Republic of Congo); *Lobeliomyia scotti* Richards (Mt Chillalo, Ethiopia); and *Trisetomyia triseta* (Richards) (Simien, above Lori, Ethiopia). Some occur among litter in hollow stems of plants, in forest litter and in grassy soils at high elevations (Hackman 1964). At least in *Mesaptilotus*, *Ocellipsis* and *Paraptilotus* some species may be altitudinally restricted (Richards 1957). Another notable genus *Scutelliseta* Richards, with 18 described species (Fig. 51), is restricted to indigenous forests in South Africa (Norrbom & Kim 1985; Richards 1968). The monotypic *Safaria brachyptera* Richards, 1950, from Rwanda are associated with doryline ants. Flightless Sphaeroceridae may be confined to oceanic islands. The sole apterous representative of the genus *Phthitia* Enderlein, *P*. (*P.*) *sanctaehelenae* (Richards), is endemic to Saint Helena (Atlantic Ocean). In the Indian Ocean the monotypic *Reunionia unica* Papp (Fig. 48) is endemic to Réunion Is. and two species of the endemic Malagasy genus *Ocellusia* Séguy are restricted to high elevations, *O. achroma* Séguy (Montagneux de Andohahelo) and *O. jugorum* Séguy (Montagneux de l'Ankaratra) (Richards 1957, 1960, 1965, 1968).

Therevidae (see Chapter 49). Two species of the endemic genus *Lyneborgia* Irwin, *L. ammodyta* Irwin and *L. stenoptera* Irwin (Fig. 38), occur in coastal habitats in South Africa. The female of one species is apterous and of the other brachypterous. The genus is rare and the reduced wing condition is unique amongst Therevidae (Irwin 1973).

Conclusion

This chapter summarises much of the published information on the biogeography of Afrotropical Diptera, but our knowledge is far from complete. Publications centre on southern African Diptera fauna and far less is known regarding West, Central and East Africa, especially the Horn of Africa and the West African rainforests. This lack of knowledge is reflected in the content of this chapter and would certainly warrant further study.

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CONSERVATION OF DIPTERA 10

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Background to fly conservation

While there have been losses of biodiversity over geological time, the current threats to biodiversity continue at an alarming rate (*e.g.*, Butchart *et al*. 2010). Insects are no exception to this, especially in view of the current rate of tropical forest loss. It is estimated that 11,200 species of insects have gone extinct since the year 1600, with a possible 100,000–500,000 going extinct over the next 300 years (Mawdsley & Stork 1995: 357). These are of course only rough estimates, although McKinney (1999) suggests that the estimated number of extinctions may be far too conservative, even by three orders of magnitude, with possibly one quarter of all species of insects under some threat of extinction. This estimate is probably accurate, bearing in mind that the overall level of threat when viewed against the fact that of the 3,623 species of terrestrial invertebrates assessed on the IUCN Red List, 42% are threatened with extinction. This may be an overestimate however, as there is likely to be here a bias towards threatened species over a broad assessment of all species irrespective of threat level (Gerlach *et al*. 2012: 54). Certainly, these losses will continue for some time, if McKee *et al*.'s (2003) model for bird and mammal species is to be believed, where the average nation is likely to see an increase in number of threatened species of 7% by 2020 and 14% by 2050. While extinction rates continue to be high, there has nevertheless been some conservation success, although generally insufficient to offset the main drivers of biodiversity loss, which include agricultural and urban expansion, deforestation and invasive alien species (Hoffman *et al*. 2010).

Pressures on African insects continue to be great, with South African butterflies under threat from various human activities, particularly loss of habitat, spread of alien plants and animal species, and changes in fire regimes (Edge *et al*. 2013: 30; Henning *et al*. 2009), while for South African dragonflies the greatest overall threat is from invasive alien trees (Samways 2006). Using the Sampled Red List Index approach, Clausnitzer *et al*. (2009) estimated that approximately 11% of Afrotropical dragonflies are threatened or near threatened, although no extinctions have been recorded to date on continental Africa. Despite the various impoverishing impacts, there have been

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Table 10.1. Current threatened or presumed extinct Red Listed Diptera species. Abbreviations: CR – Critically Endangered; EN – Endangered; EX – Extinct; VU – Vulnerable.

Species	Family	Biogeography	Ecosystem	Red List Category
Brennania belkini Philip	Tabanidae	Mexico, USA	Terrestrial	VU
Stonemyia volutina Bigot	Tabanidae	USA	Terrestrial	EX
Campsicnemus mirabilis (Grimshaw)	Dolichopodidae	Hawaii	Terrestrial	EX
Drosophila lanaiensis Grimshaw	Drosophilidae	Hawaii	Terrestrial	EX
Edwardsina gigantean Zwick	Blephariceridae	Australia	Freshwater	EN
Edwardsina tasmaniensis Tonnoir	Blephariceridae	Tasmania	Freshwater	CR

some successful conservation activities through landscape initiatives, such as instigation of large-scale ecological networks (Samways *et al*. 2010), removal of invasive alien trees (Samways & Sharratt 2010; Samways *et al*. 2011), and in the case of butterflies, through proclamation of reserves for particular species (Henning *et al*. 2009).

Against this general background and progress with other insect groups in Africa, a first assessment of the conservation status of Afrotropical flies is here presented and some tentative recommendations for their conservation are made.

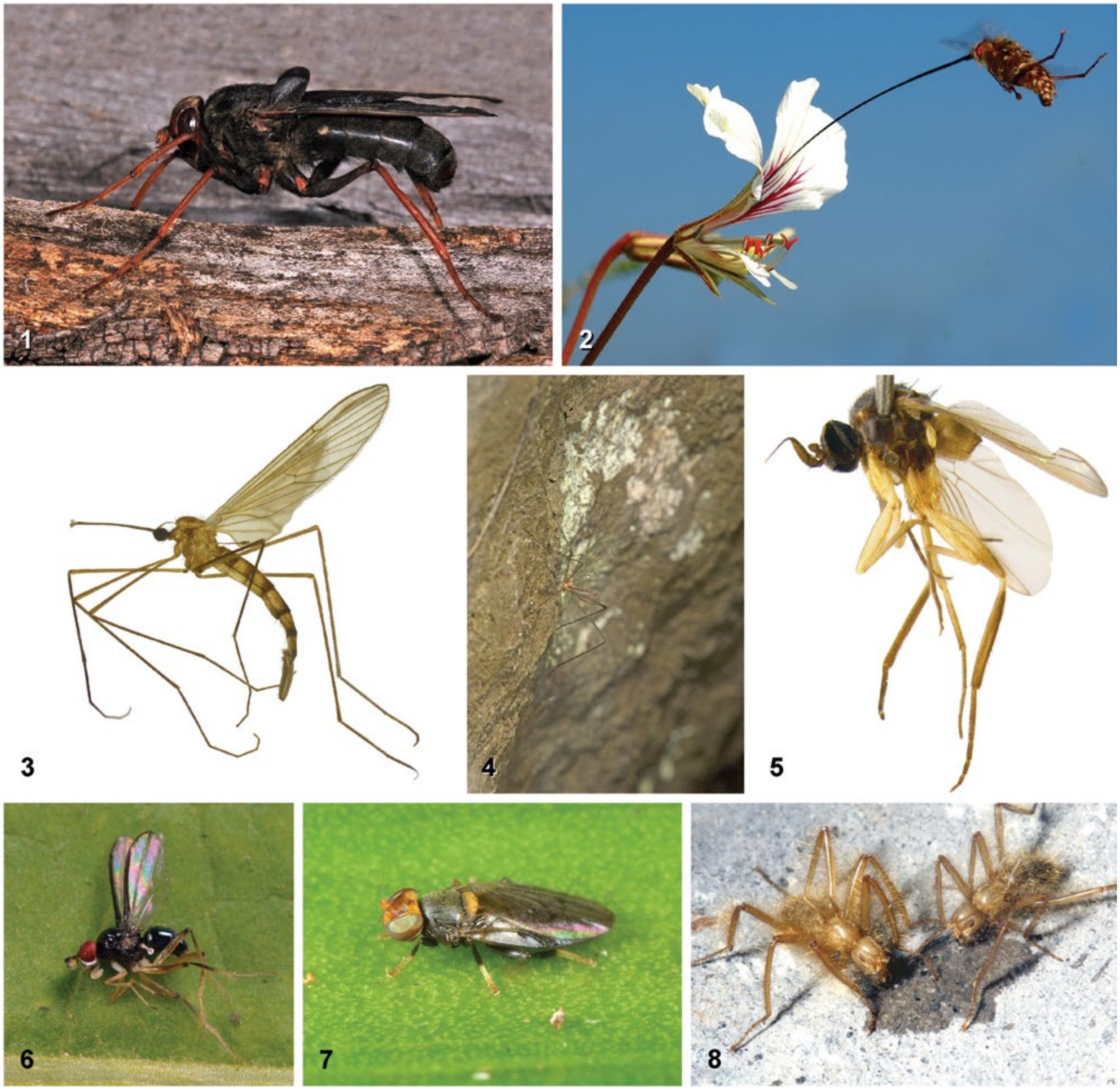
Threats to flies in general

Only seven species of flies are currently Red Listed, none of which are Afrotropical (IUCN 2010) (Table 1). Three species are considered extinct, and one possibly extinct, but currently Red Listed as Critically Endangered. The point is that despite flies being a relatively poorly studied taxon in terms of conservation assessment, some species at least, and probably many more, are under threat, with extinction already taking place, mostly through habitat loss, but also due to the impact of alien invasive species on islands (Courtney *et al*. 2009; Englund 2008). Bearing in mind how few fly species have been assessed in terms of the threats to them, this small number of Red Listed fly species is sufficient to indicate that this is the "tip of the iceberg" of many more species already threatened or about to go extinct, with some of these very likely to be Centinelan extinctions (extinction of a species before being scientifically described). Certainly, more species of threatened flies are being put on regional Red Lists (*e.g.*, Simuliidae of Finland (Ilmonen 2006), Dolichopodidae in Belgium (Pollet 2000) and Diptera in general in Britain (Falk 1991; Shirt 1987)), with some receiving special conservation action, such as the British Aspen hoverfly *Brachyopa* (*Hammerschmidtia*) *ferruginea* (Fallén) (Syrphidae) (Rotheray *et al*. 2009).

Courtney *et al*. (2009) list some other species of concern that are not on the Red List. The endemic flesh fly of Bermuda, *Microcerella bermuda* Pape (Sarcophagidae), has not been recorded for over a century, while the sole representative of the family Mormotomyiidae, *Mormotomyia hirsuta* Austen (Fig. 8), was only re-discovered at the type locality in eastern Kenya in 2010, over 60 years since it was last collected (Copeland *et al*. 2011; see Chapter 101). Two of the three species of rhinoceros bot flies, *Gyrostigma* Brauer spp. (Oestridae), have declined as their hosts have declined (see Chapter 119). The Oriental *Gyrostigma sumatrensis* Brauer is only known from larvae expelled by the Sumatran rhinoceros, *Dicerorhinus sumatrensis* (Fischer) (Rhinocerotidae), confined to certain European zoological gardens prior to 1950; no information is available from wild populations. The Afrotropical *G. conjungens* Enderlein infests the Black rhinoceros, *Diceros bicornis* L., but has not been recorded since 1961, although the second Afrotropical species, *G. rhinocerontis* Owen (Fig. 1), has increased as its White rhinoceros, *Ceratotherium simum* Burchell, host population has increased (Barraclough 2006). Courtney *et al*. (2009) also note that the European bone skipper, *Thyreophora cynophila* (Panzer) (Piophilidae), was common in west central Europe in the late 18th century, where it could be observed walking on the carcasses of dogs, horses and mules in the early spring. Fifty years after it was described in 1798, it disappeared and was only rediscovered in Spain 160 years after it was thought to be extinct (Martín-Vega *et al*. 2010). This last mentioned example highlights the dangers of assuming extinction in some cases.

In a study conducted in South Africa, Armstrong (2002) used insects to determine priority areas for conservation biology in KwaZulu-Natal Province. He included insects of five orders and eight families and of the 37 insect species considered in the overall assessment, 14 (37.8%) were Diptera: Asilidae. This is important, as it indicates that at least some of the larger and better studied Afrotropical Diptera families can serve as indicators of habitat change and be of practical use in conservation assessments.

There are several major challenges, taxonomic, biological and perception-based, facing fly conservation, which are those also facing many other taxa which are poorly known, numerous and not easily endeared to the public. The taxonomic challenge relates to the fact that specifically targeted conservation can only really take place once the taxonomy has been clarified. Following closely on the heels of the taxonomic challenge is the biological challenge, which refers to not having sufficient information on the ecology, inter-relationships and general ecology of the various focal species to be able to make informed and sound conservation management decisions. The perception challenge relates to the fact that certain types of species do not muster public sympathy and sometimes even that of conservation biologists, and flies are surely among them. It takes a great deal of persuasion to convince many influential sectors, especially the public one, that flies are worth conserving, simply because they are seen as "dirty" and/or a "pest". This is why it is essential not only to give vernacular as well as scientific names to species of conservation concern, but also to photograph them to show the public at large, and even policy makers, that certain species are not only beautiful and wonderful products of evolution, but are also highly threatened and deserve protection. One means to increase public awareness is for specialists to publish popular articles on the blight of endangered fly species, examples being Barraclough's (2007, 2014) articles in popular magazines on Rhinoceros bot flies and Sessions & Johnson's (2005) article on pollination by long-proboscid Nemestrinidae. Similarly, re-discovery of the charismatic "Terrible hairy fly", *Mormotomyia hirsuta*



Figs 10.1–8. Examples of rare or threatened Diptera species: (1) *Gyrostigma rhinocerontis* Owen (Oestridae); (2) *Moegistorhynchus longirostris* (Wiedemann) (Nemestrinidae); (3) *Peringueyomyina barnardi* Alexander (Tanyderidae); (4) *Edwardsina* sp. (Blephariceridae) (non-Afrotropical genus); (5) *Alavesia daura* Sinclair & Kirk-Spriggs (Atelestidae); (6) *Margo* sp. (Marginidae); (7) *Nemula* sp. (Neminidae); (8) *Mormotomyia hirsuta* Austen (Mormotomyiidae). Fig. 1 (photograph © S. van Noort (Iziko Museums of South Africa)), Fig. 2 (photograph © S.D. Johnson), Fig. 3 (photograph © I. Madriz), Fig. 4, 6, 7 (photographs © S.A. Marshall), Fig. 5 (photograph © B.J. Sinclair), Fig. 8 (photograph © R.S. Copeland).

(Mormotomyiidae) in 2010 received extensive media coverage, with numerous articles published in the popular press and on Internet sites.

The Xerces Society for Invertebrate Conservation, based in the USA, is making a huge contribution towards raising awareness of the plight of invertebrates and is actively putting in place conservation management of many threatened invertebrates and their habitats, including flies. Among the focal species is the Delhi Sands flower-loving fly, *Rhaphiomidas terminatus abdominalis* Cazier (Mydidae), which is listed under the United States Endangered Species Act, and which is threatened by urban development in southern California. The Xerces Society also draws attention to the fact that many flies are beneficial, from aquatic midges that serve as an abundant food source for migratory birds, to the fly pollinators of apples, peppers, mangoes and cashews. For conservation to be effective, it is essential that assessments are made to highlight those species in need of protection, while at the same time emphasising that not all flies are harmful, with many being important for maintenance of ecosystem processes. Even so-called "harmful" flies play important roles in natural ecosystems, in terms of, for example, pollination, disease and parasite transmission, and as food for other organisms, all of which result in healthy ecosystems (*e.g.*, Hudson *et al*. 2006). Certain species are parasitised by disease-causing organisms which they may then transmit to humans or domestic livestock. Eradication of these vectors, especially locally but even globally, is mooted. This is short-sighted and results in harm to biodiversity as a whole, including to beneficial non-target flies. For example, *Exhyalanthrax lugens* (Loew) (Bombyliidae), which parasitises *tsetse* (*Glossina* Wiedemann spp.) (Glossinidae) pupae, was eradicated from areas of northern KwaZulu-Natal, South Africa, that were aerially sprayed with DDT, even prior to eradication of *G. pallidipes* Austen (Fiedler & Kluge 1954; Fiedler *et al*. 1954). This bee fly did not return to the sprayed areas after aerial spraying ceased, nor did *E. abruptus* (Loew), another parasite of *tsetse* pupae, recorded from the Mkhuze Game Reserve in KwaZulu-Natal Province, in a subsequent survey by Greathead *et al*. (2006). This suggests that aerial spraying can have long-term impacts on non-target species and that the natural biological control of other *tsetse* species in the region was impaired. The elimination of parasitoids and potential competitors (*e.g.*, *G. pallidipes*) from the sprayed region may have had the effect of allowing populations of other *tsetse* species to increase and even expand into habitats where they were not known to occur historically (Esterhuizen *et al*. 2005).

Rare and endangered families of Afrotropical Diptera

Published conservation assessments of Diptera (specifically) in the Afrotropical Region are few. Some authors make reference to conservation status of flies in taxonomic papers, but these are difficult to locate and are usually not based on detailed habitat-specific assessments. As noted above, Barraclough (2006) assessed the status of the rhinoceros bot flies, *Gyrostigma* spp. (Oestridae) and Barraclough & Slotow (2010) studied the South African endemic keystone pollinator *Moegistorhynchus longirostris* (Wiedemann) (Nemestrinidae) (Fig. 2). This large, conspicuous species, with the longest proboscis relative to body size of all known insects, feeds on nectar and is considered to be co-evolved with the long-tubed flowers it pollinates in the Cape Floristic Region. Barraclough & Slotow (2010) mapped the distribution of the species and undertook a conservation assessment based on the vegetation types of Mucina & Rutherford (2007). They tabulated 12 localities, five of which are in vegetation types regarded as "Endangered", two as "Critically Endangered", one "Vulnerable" and two "Least Threatened".

The only published synthesis is that of Duxbury & Barraclough (1994), who assessed 11 rarely encountered Diptera families (only 10 of which are now regarded as families), occurring in southern Africa and discussed their conservation status. In the section below these and other families are discussed, in light of new information amassed in the past 20 years, since this work was published and incorporating new information from chapters included in this *Manual*. Duxbury & Barraclough (1994) include reference to the "family" Tachiniscidae, which was subsequently transferred to the family Tephritidae (subfamily Tachiniscinae) and this group will not be further discussed here.

Tanyderidae (see Chapter 15) (Fig. 3). Duxbury & Barraclough (1994) reviewed the conservation status of the family. The monotypic genus *Peringueyomyina* Alexander is represented by the single species, *P. barnardi* Alexander (Fig. 3), which is restricted to a relatively small region of the south-western Cape of South Africa (in Fynbos in the ancient Cape Fold Mountains). Although the species has been recorded from at least six different localities in the region it remains extremely rare and poorly collected. *Peringueyomyina* larvae have been found beneath large boulders in white gravel and sand pits along the edges of a forest streamlet.

Blephariceridae (see Chapter 16) (Fig. 4). The Blephariceridae are an ancient group and Stuckenberg (1962) regarded these as a palaeogenic element in the southern African fauna. Three endemic genera occur in the Afrotropics. *Aphromyia* Courtney is a monotypic genus with the single species, *A. stuckenbergi* Courtney, recorded from a single mountain range, the Andringitra massif in the Central highlands of Madagascar. Courtney (Chapter 16) notes that due to habitat degradation, this species may now be extinct and recent attempts to recollect the species at the type locality have proved unsuccessful. The genus *Paulianina* Alexander, with eight described species, is also endemic to Madagascar and numerous undescribed species are known. All species occur in the Central highlands and Evergreen rainforest biomes on the east side of the island. Courtney (Chapter 16) also notes that it is likely that some of these species may have gone extinct. The genus *Elporia* Edwards, with 19 described species is restricted to the Cape Fold Mountains and Great Escarpment of South Africa, but there is a possibility that further species may be discovered. The immature stages of Blephariceridae are torrent-dwellers, occurring in clear, well-oxygenated mountain streams and are, therefore, highly susceptible to pollution.

Corethrellidae (see Chapter 29). Duxbury & Barraclough (1994) reviewed the conservation status of the family and noted that they appear to be associated with Afromontane forests. This is now known not to be the case with West African species occurring in coastal areas (see Borkent 2008, fig. 114). At that time the biology of the family was unknown and only three species of the genus *Corethrella* Coquillett were known from the Afrotropical Region, *C. harrisoni* Freeman, from Magoebaskloof in the Limpopo Province, South Africa, *C. pallitarsis* Edwards from Benin and Nigeria and *C. picticollis* Edwards from Nigeria and Uganda. The genus was recently revised by Borkent (2008) and five species are now recorded from the Afrotropics. A recent survey using light traps in Madagascar also revealed the presence of seven species, six of which are new. Larvae are aquatic and adults are known to feed on the blood of frogs, with adult females being attracted (often in large numbers) to the calls of male frogs. The combination of aquatic habitats and the likely dependency on male frog blood (some species are able to lay viable eggs without blood, at least for the first generation), makes these species vulnerable, considering the pressures on water resources and the decline of frog populations. Frog-call traps have not been deployed in the Afrotropical Region and the use of such traps will certainly lead to additional records and perhaps species.

Thaumaleidae (see Chapter 33). Duxbury & Barraclough (1994) reviewed the conservation status of the family and suggested that it may represent a palaeogenic, austral element associated with montane areas. At that time, only one species of the Afrotropical endemic genus *Afrothaumalea* Stuckenberg had been described (thus far restricted to South Africa), *A. pamelae* Stuckenberg from the Cathedral Peak area, KwaZulu-Natal Province. One undescribed species was also noted from Maanschynkop in the Western Cape Province, and additional material (see Addendum in Duxbury & Barraclough (1994)) was cited from Kynsna, Diepwalle, in the Eastern Cape Province (which may also represent a new species). Two species have subsequently been described, *A. capensis* Sinclair & Stuckenberg (based on the Maanschynkop material noted above) and the recently described *A. stuckenbergi* Sinclair, from the Cederberg Mountains of the Western Cape Province (Sinclair 2015). All life stages of Thaumaleidae are associated with thin films of water flowing over surfaces, including streams cascading over large rocks, spray zones on boulders in streams, seepages near waterfalls and roadcuts. Specimens are undoubtedly rare in collections due to the lack of specialist collecting in these habitats and additional material and species should be expected from other isolated mountain systems in South Africa and perhaps elsewhere in southern Africa.

Atelestidae (see Chapter 54). The family Atelestidae was first recorded from the Afrotropical Region by Sinclair & Kirk-Spriggs (2010), based on two newly described extant species of the genus *Alavesia* Waters & Arillo (Fig. 5) from Namibia. Both species are confined to the upland plateau (1750 m) of the Brandberg massif (an isolated inselberg on the edge of the Namib Desert), and represent palaeogenic relict species. The genus was originally based solely on fossil species from Early to Late Cretaceous ambers of Spain and Burma and these two species represent living fossils. The two species were collected in Malaise traps set across riverbeds following heavy precipitation. The Brandberg is well known for its endemic fauna and flora and is designated as a protected area.

Homalocnemidae (see Chapter 55). The family Homalocnemidae (as Empididae) was first recorded from the Afrotropical Region by Chvála (1991), based on the single species, *Homalocnemis namibiensis* Chvála, recorded from the coastal region of Namibia. A single female specimen is known, collected from a flowering succulent growing between Namib Desert dunes and the beach. Elsewhere the genus *Homalocnemis* Philippi is known from South America and New Zealand and was regarded by Chvála (1991) as a Gondwanan element. This genus is thought to be a survivor of a Namibian mid-Tertiary woodland fauna (Kirk-Spriggs & Stuckenberg 2009: 161). *Homalocnemis namibiensis* was not collected in a protected area and its conservation status remains uncertain.

Ctenostylidae (see Chapter 73). Duxbury & Barraclough (1994) reviewed the conservation status of the family and noted that they appear to be associated with Afromontane forests. At that time, only two species of the genus *Ramuliseta* Keiser were known from the Afrotropics, *R. palpifera* Keiser (as *R. lindneri* Keiser), from southern and East Africa and *R. madagascarensis* Hennig from Madagascar. A third new species is known from Madagascar. *Ramuliseta palpifera* was formerly known from only three localities in South Africa, but appears to be widespread in southern Africa; both *R. madagascarensis* and the undescribed Malagasy species (noted above) are only known from the unique female holotypes collected in tropical rainforest habitats. Virtually nothing is known about the biology of the family. They are nocturnal and adult flies are normally collected at mercury vapour light traps, although adult flies are only rarely collected.

Natalimyzidae (see Chapter 80). The family Natalimyzidae was described by Barraclough & McAlpine (2006), based on the single species, *Natalimyza milleri* Barraclough & McAlpine, 2006, from South Africa. Although the family is currently monotypic, a total fauna of more than 30 species could be expected, with *ca* 20 species present in South Africa alone (Barraclough & McAlpine 2006). The family is best known from southern and eastern South Africa and Zimbabwe, but is also known from Nigeria and Kenya. Although extant species of the family appear to be endemic to the Afrotropics, fossil inclusions in Baltic amber (Eocene of Europe) are known (Tschirnhaus & Hoffeins 2009). Extant species appear to be associated primarily with grasslands in the larval and adult stages (Barraclough 2007), but have also been sampled in Afromontane forest.

Marginidae (see Chapter 82). Duxbury & Barraclough (1994) reviewed the conservation status of the family, which is endemic to the Afrotropics. At that time, only two species of the genus *Margo* McAlpine were known from the Afrotropics, *M. aperta* McAlpine, from Chirinda Forest Reserve in Zimbabwe and *M. clausa* McAlpine from the mid-eastern coastal mountain belt of Madagascar. Additional material of a probably undescribed species (Fig. 6) has recently been collected from four localities in Madagascar. Marginidae is one of the most poorly studied and understood Diptera families in the Afrotropical Region and McAlpine (1991) noted it to be one of the families of Afrotropical Diptera most at risk of extinction, due to habitat degradation. Specimens have been sampled in Malaise traps in Madagascar (A.H. Kirk-Spriggs, pers. obs.) and additional sampling in Afromontane forest in other southern African countries may still reveal additional material or species.

Odiniidae (see Chapter 83). Duxbury & Barraclough (1994) reviewed the conservation status of the family, noting that they appear to be widespread in southern Africa, mostly in arid and semi-arid areas. As currently known, the Afrotropical fauna comprises only eight described species in five genera, namely:

Afrodinia Cogan (2 species), *Odinia* Robineau-Desvoidy (2), *Coganodinia* Gaimari & Mathis (1), *Paratraginops* Hendel (1) and *Traginops* Coquillett (2) (Gaimari & Mathis 2011). Duxbury & Barraclough (1994) noted that Odiniidae are probably only apparent rarities and focused collecting may reveal them to be not uncommon in selected habitats. Adults are not uncommon in Malaise trap samples and may be numerous, especially in samples examined from Madagascar (A.H. Kirk-Spriggs & S.D. Gaimari, pers. obs.). Odiniidae are closely associated with trees, especially those infested with other insects, or actively exuding sap. Other breeding media include rotting wood and fungi and adults are also attracted to fruit fly and yeast-baited traps. Larvae are chiefly found associated with the galleries of wood-boring Coleoptera, and to a lesser extent, Lepidoptera. The biology of the group was thoroughly reviewed by Kirk-Spriggs & Barraclough (2009) and Gaimari & Mathis (2011).

Aulacigastridae (see Chapter 88). Duxbury & Barraclough (1994) reviewed the conservation status of the family, noting that species appear to be restricted to refugia, in or adjacent to Afromontane forest. At that time, only three species of the genus *Aulacigaster* Macquart were known from the Afrotropical Region, two from the central KwaZulu-Natal Drakensberg, South Africa and one from Cameroon. The genus was recently revised by Rung & Mathis (2011) and now comprises five described Afrotropical species: *A. africana* Barraclough, described from the Drakensberg of South Africa, but now with additional material in the National Museum, Bloemfontein from Tsitsikamma National Park and Hogsback in the Eastern Cape Province; *A. perata* Barraclough, from 50 km east of Bamenda in Cameroon; *A. borbonica* Hilger & Kassebeer from Réunion Is.; *A. malawana* Rung & Mathis from Nyika National Park in Malawi; and *A. freidbergi* Rung & Mathis, from Nyika National Park in Zambia. This likely represents only a fraction of the actual diversity of the genus in the region. Adults of *A. africana* have been collected in hanging traps baited with fermenting fruit and from fresh baboon dung (S.A. Marshall, pers. comm. 2015). Immature stages of one Afrotropical species, *A. africana*, where described by Papp (2008). Larvae appear to be peculiar to weeping wounds and sap fluxes of deciduous trees.

Neminidae (see Chapter 89). Duxbury & Barraclough (1994) reviewed the conservation status of the family and noted that they appear to be associated with Afromontane forest over most of their range. At that time, only two species of the genus *Ningulus* McAlpine were known from the Afrotropics, *N. simatus* McAlpine from the Eastern Cape Province, South Africa and an undescribed species from Chimanimani National Park in eastern Zimbabwe. The Afrotropical fauna is now known to comprise seven species in three genera: *Nemo* McAlpine (2 species); *Ningulus* (2); and *Nemula* Freidberg (3), the last named being confined to Madagascar (Fig. 7). Nothing is known regarding the biology of Neminidae, except that some have been collected on monocotyledons, in particular *Strelitzia* and *Ravenala madagascariensis* Sonn. (both Strelitziaceae) and *Alocasia* (Araceae). *Nemula* species are associated with tropical rainforest in Madagascar and appear to be common where they occur (A.H. Kirk-Spriggs, pers. obs.). Adults are rarely collected using passive sampling methods and active searching on these plants is required to obtain them. This may partly explain their rarity in collections.

Neurochaetidae (see Chapter 90). Duxbury & Barraclough (1994) reviewed the conservation status of the family. Two genera occur in the Afrotropical Region, the monotypic genus *Neurocytta* McAlpine, with the single species *N. prisca* McAlpine, known from a limited area in Zimbabwe (Chimanimani, as "Melsetter") and probably associated with plants of the genus *Strelitzia* (Strelitziaceae), and *Neurotexis* McAlpine, an endemic genus with 11 species confined to Madagascar. Species occur in wet habitats, especially rainforests and appear to be closely associated with particular monocotyledonous host-plants, within which the larvae feed and on which adults occur. Humid environments near leaf bases and sometimes other crevices in plants, often containing pools of water, appear to be most favourable.

Mormotomyiidae (see Chapter 101). The Mormotomyiidae is the only truly monotypic family of flies endemic to the Afrotropical Region (the family Natalimyzidae is currently monotypic (see above), but is know from numerous undescribed extant species and from Eocene Baltic amber inclusions from Europe). The single species *Mormotomyia hirsuta* Austen was formerly regarded as the "rarest fly in the world" (F.C. Thompson, pers. comm. 2010). The species was previously only know from the type locality, Ukasi Hill, in eastern Kenya and populations were re-discovered in 2010. An extensive survey of suitable habitats in eastern Kenya (Copeland *et al*. 2014), recently revealed additional populations in the two hills adjoining Ukasi (Ngauluka and Makilu Hills) and a population at Mbuinzau Hill, at a distance of 187 km from the type locality. *Mormotomyia hirsuta* inhabit horizontal rock fissures inhabited by bats and the larvae develop in bat guano.

Campichoetidae (treated with Diastatidae in Chapter 104). Duxbury & Barraclough (1994) reviewed the conservation status of the family noting that all species have been collected at Afromontane areas at or below 1500 m. Only two species of the genus *Campichoeta* Macquart occur in the Afrotropical Region: *C. edwardsi* Barraclough, from Ethiopia and Kenya and *C. natalensis* Barraclough, from South Africa, both of which were previously known only from unique holotypes. There is recent material of *C. natalensis* (including the unknown male), in the National Museum, Bloemfontein, sampled in the eastern Free State Province, South Africa, in *Leucosedea*-dominated scrub, at an elevation of 1,660 m (42.5 km from the edge of the true Drakensberg escarpment and 31.3 km from the type locality) and one female specimen sampled in the Western Cape Province, South Africa, from *Acacia* valley woodland, at an elevation of only 336 m (870 km from the type locality). All the aforementioned material was sampled in Malaise traps deployed over slow-flowing, vegetated streams. These records indicate that the genus is more widely distributed than previously thought and is not confined to medium to high elevation Afromontane forest. Rarity in collections may, therefore, represent poor collecting effort in suitable habitats.

Conservation biogeography in the Afrotropical Region

Maps are an essential first stage in conservation planning, with the world having been divided into 867 ecoregions (Olson *et al*. 2001), with the Afrotropics being divided largely according to White's (1983) phytogeographic regions. In addition, several hotspots (HSs) of major diversity (and also at threat) have also been identified, which in the Afrotropics include the Guinean forests of West Africa HS, Eastern Afromontane HS, Horn of Africa HS, Coastal forests of Eastern Africa HS, Madagascar and the Indian Ocean islands HS, Maputaland-Pondoland-Albany HS, Cape Floristic Region HS and the Succulent Karoo HS (Mittermeier *et al*. 2004) (Fig. 9).

These areas are rich in endemic species and are also under threat from various human impacts. The Madagascar and the Indian Ocean islands HS, for example, is of special interest in terms of Diptera conservation, with Irwin *et al*. (2003) noting that endemism among the Diptera is extremely high, with 80% of species being endemic to Madagascar alone (see Chapter 9). Within the family Curtonotidae (see Chapter 103), 13 species of the genus *Curtonotum* Macquart occur on Madagascar, representing 35% of the regional fauna as a whole, only one species of which occurs both on Madagascar and the continental Afrotropical Region (Kirk-Spriggs 2011). There are also at least 15 undescribed species of the curtonotid genus *Cyrtona* Séguy *sensu lato* endemic to the Cape Floristic Region HS (Kirk-Spriggs, in prep.) and Sæther & Ekrem (2003) have highlighted endemism in Chironomidae in the Coastal forests of Eastern Africa HS.

Hotspots are not the only areas for consideration of endemics, with an African assessment of dragonflies (Dijkstra *et al*. 2011) illustrating, for example, that the Angolan Highlands are another geographical area of note for endemic species. It is in these areas of high endemism in particular that searches and assessments should be made as a priority, as these areas are likely to be home to some of the most threatened species with long lineages (Ware *et al*. 2009). In the case of dragonflies, it is the Cape Floristic Region which has one of the highest

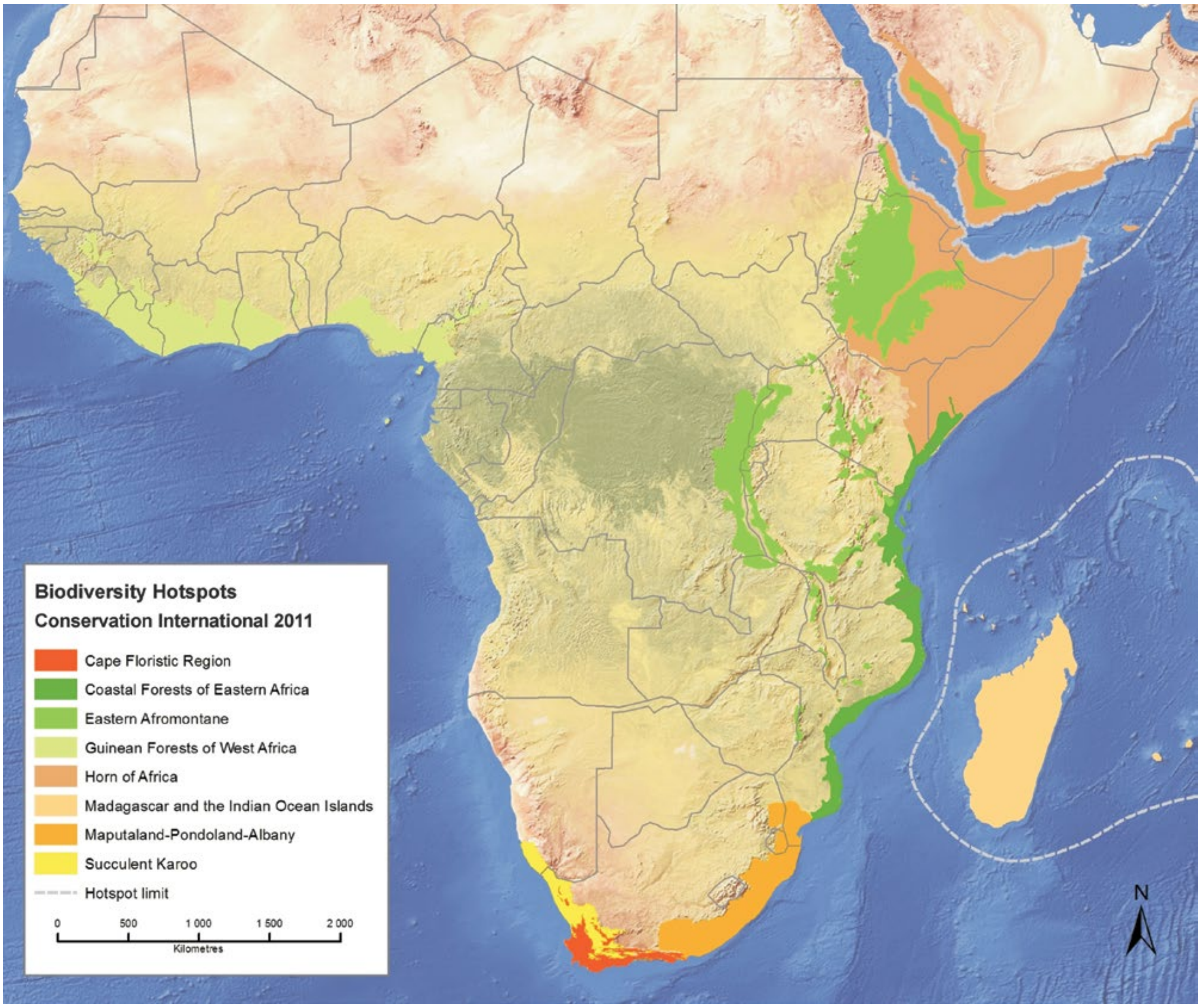


Fig. 10.9. Topographical map of the Afrotropical Region, indicating Biodiversity Hotspots (source: "Biodiversity Hotspots", Conservation International 2011).

number of threatened species in Africa (Dijkstra *et al*. 2011: 156). Threatened species also occur outside these HSs, however, as in the case of several highly threatened butterflies (Edge *et al*. 2013: 20). For flies, therefore, it makes sense to consider firstly those areas where rare and threatened butterflies (Edge *et al*. 2013: 20) and dragonflies (Samways 2008) have already been found, and initially concentrate efforts in those regions (this of course assumes some level of congruency; see Stuckenberg (1962)). This does not exclude global assessments nor regional assessments elsewhere. Maintenance of biodiversity involves incorporating ecological processes into conservation planning (Pressey *et al*. 2007), while recognising those ecological factors, as well as evolutionary ones, that are essential for mitigation planning in the future (Klein *et al*. 2009). Furthermore, it is also important to appreciate the long pedigree of history of an area as a means for focusing conservation planning for the present (Jackson & Hobbs 2009). This is so for insects, which have undergone many dynamic spatial shifts as their hostplants have shifted their geographical ranges over time (Ponel *et al*. 2003), with this being an important consideration for buffering climate change in the future (Samways *et al*. 2006). These large-scale processes are important in Africa, where past events dictate current distributions (Suhling *et al*. 2010: 67), with, nevertheless, some relict species having survived for many millions of years, especially in the Cape Provinces of South Africa (Ware *et al*. 2009).

Another consideration is that of El Niño Southern Oscillation events, which play a major role in determining the spatial dynamics at a large scale, with dragonflies, for example, retreating to wet refugia in dry years and expanding outwards again in wet years (Samways 2010). The message here is that large-scale conservation is about ensuring that the landscape is sufficiently intact to prevent any major regime shifts (Scheffer & Carpenter 2003), through maintenance of ecosystem connectance, function and resilience. This involves recognition that various adverse effects can be synergistic with, for example, climate change being highly synergistic with landscape fragmentation (Stork 2010; Travis 2003). As insects ramify virtually all ecosystem processes they may well be on the brink of a range of major discontinuities (Samways 1996), emphasising again the importance of maintaining as much of the landscape intact as possible.

As South Africa has three of the world's 34 biodiversity HSs, and these are currently highly impacted (Driver *et al*. 2012), and likely to be more so in the future, a dynamic conservation approach is required. One such approach has five key components (Hannah *et al*. 2002); (1) regional modelling of biodiversity response to change (with the reservation here that little is known of most flies' responses to climate change); (2) systematic selection of protected areas with climate change as an integral selection factor; (3) management of biodiversity across regional landscapes, including core protected areas and their surrounding matrix, with climate change as an explicit management factor; (4) mechanisms to support regional co-ordination of management, both across international borders and across the interface between park and non-park conservation areas; and (5) provision of resources, from countries with the greatest resources and greatest role in generating climate change to countries in which climate-change effects and biodiversity are highest. This of course is to a large extent a theoretical ideal, with much local conservation being able to be achieved by focusing on local needs of the biota and humans in a specific area, at the species, multi-species and landscape levels. For example, in southern Africa protected areas can be expanded by building on large-scale ecological networks, which are corridors and nodes of set-aside land in and among production areas (Pryke & Samways 2012). This landscape approach is an enabling mechanism for many species that require good quality habitat more typical of protected areas than of production areas.

Conservation of landscapes, habitats and mesofilters

At the sub-regional/within-hotspot/within-ecoregion spatial scale there are certain landscapes, habitats and mesofilters that require special focus (Crous *et al*. 2013), particularly when coupled with threat. The landscape scale approach is over several hundreds of meters to several kilometers and is the spatial scale at which most practical conservation management takes place. Yet any one species occurs in a particular habitat which is the area necessary for a species to carry out all its life functions and this includes all the resources (biotic, such as vegetation types, and abiotic, such as soil types and rockiness). The "mesofilter" refers to features on the landscape that provide heterogeneity and are essential for certain organisms to carry out their particular life functions, such as a log, a rot hole, or a hilltop. This has, for example, been done for the Karkloof blue butterfly, *Orachrysops ariadne* (Butler) (Lycaenidae) (Samways & Lu 2007), and an Afromontane butterfly assemblage (Crous *et al*. 2014). The reason that the mesofilter needs to be considered for flies is that certain features of the landscape may be important and even critical to them.

Ancient high elevation Afromontane forests and grasslands in Africa appear to be especially significant in terms of fly endemism, including the Great Rift Valley of East Africa, the southern African Great Escarpment and other topographical features. Examples among Afrotropical Diptera are Blephariceridae, Psychodidae, Empididae, Africa's only tanyderid and early branching Chironomidae, confined to the ancient Cape Fold Mountains of South Africa (Stuckenberg 1962; Kirk-Spriggs & Stuckenberg 2009: 158). Isolated inselbergs also appear to be significant for Diptera in Africa and a biodiversity study of the Brandberg massif (Namibia's highest mountain), which concentrated primarily on Diptera (Kirk-Spriggs & Marais 2000), revealed some significant endemic and relict groups, including the first extant species of *Alavesia* Waters & Arillo, a Cretaceous-era genus, and the first records of the family Atelestidae (see above; Chapter 54) from the Afrotropical Region (Sinclair & Kirk-Spriggs 2010) (see Chapter 9). In terms of overall fly diversity it has been noted that the mesic savannas (termed the Sudano-Zambezian Region) of Africa are probably the most species-rich (Kirk-Spriggs & Stuckenberg 2009: 166)

Translating threats into opportunities

As there are such great challenges for insect conservation to address, it is prudent to instigate the Precautionary Principle (Fauna and Flora International 2006: 1), which invokes our being sensitive to the complexity of biodiversity, while not letting that complexity and lack of scientific certainty hold up conservation action. This means engaging systematic conservation planning for biodiversity in general, while recognising that various types of transformed land outside formal reserves also have conservation value, especially for flower visitors, including flies (Vrdoljak & Samways 2014). It is important then not just to undertake assessments of proclaimed conservation areas, but also to undertake assessments in surrounding areas. The issue then becomes one of time and resources and results in strategic decisions having to be made. Such decisions may be, for example, to concentrate on one taxon within the Diptera, *e.g.*, Syrphidae, which has been identified by the IUCN/Species Survival Commission/Invertebrate Conservation Sub-Committee as a priority taxon within invertebrates in general, as they are functionally significant, relatively well known scientifically, easily recognised and conspicuous in the eyes of citizen scientists. Some are also threatened (Rotheray & MacGowan 2000), while expansion of forest cover in the Netherlands in recent years has led to their overall increase (Reemer 2005).

Another approach to prioritisation is to take a functional group (*e.g.*, pollinators) and focus on these. An example of this would be the pollinators of flowers of the Cape Floristic Region HS, as both the fly pollinator and the flower mutualist are both significant conservation subjects (Brand 2009; Johnson & Steiner 1997; Kehinde & Samways 2012). Such pollinator groups are possibly an important conservation priority in view of the services that they provide.

Another approach would be that of "triage" and treat areas that are well protected as already conserving a multitude of fly species and, therefore, do not require immediate conservation action. It remains desirable, however, to ascertain which assemblages of fly species occur in such protected areas. At the other extreme are those landscapes that are so heavily degraded that they can also be temporarily given low priority, as the species that occur there are likely to be widespread generalists. Urban and peri-urban gardens could be considered as a case in point. Caution is required, however, as gardens can have significant value for certain invertebrates, especially as sources of nectar, compost heaps, ponds and other mesofilters, that can have conservation value for various organisms, including many insects (Owen 1991: 358), especially when these are stepping stone habitats for individuals of various species, and even more so when they are habitats *per se* (Armstrong *et al.* 2013: 50). Between these two extremes of minimally and maximally disturbed landscapes, is the agricultural landscape, which may be important for many pollinating insects, for example, including flies of the agricultural matrix of the Cape Floristic Region (Vrdoljak & Samways 2014). These agricultural areas can be the subjects of a synthetic management approach (Samways 2007), in which several principles are put in place that provide a best-option framework on which to maintain biodiversity, including flies, in an area. In this framework, it is important to maintain adjacent natural habitat to production areas for local conservation and the supply of ecosystem services (Gaigher & Samways 2014). Maintaining framework options for landscape management for conservation are important, not only for making the overall landscape more acceptable to many species, but also for accommodating the vagaries of El Niño Southern Oscillation cycles, and in the longer term, that of global climate change. This may be viewed in another way, and where taxonomic expertise exists (which is relatively good for Afrotropical Diptera), flies should be mainstreamed into general biodiversity conservation, which could be done given sufficient funding resources (McGeoch *et al*. 2011).

Assessment of species with regards to the level of threat that they face may come about through a regional or sub-regional assessment. This has not yet been undertaken for Afrotropical flies in any part of the continent, at least not as a cohesive strategy with the specific goal of Red Listing species. This could at least be partially considered, especially in southern Africa, again because there is a good baseline of taxonomic expertise globally.

Flies have also been considered as bioindicators of environmental quality (Courtney *et al*. 2009), especially the larvae of Chironomidae, but also moth flies, *Psychoda* Latreille (Psychodidae) and "rat-tailed maggots", *Eristalis* Latreille spp. (Syrphidae), which are generally tolerant of low oxygen levels in freshwater. Other fly species are sensitive to perturbations of environmental conditions, especially Blephariceridae (Bredenhand & Samways 2009) and the non-Afrotropical Deuterophlebiidae. Rotheray *et al*. (2001) used saproxylic flies for habitat quality assessment and conservation planning, while Holston (2005) used stiletto flies (Therevidae) as an indicator of habitat heterogeneity and succession stages in a dune system, and Sommagio (1999) suggested syrphids as bioindicators of environmental quality. Various authors have used saproxylic flies in both North America and Europe to indicate the quality of forest habitats and their management (Fast & Wheeler 2004; Good & Speight 1996; Økland 1994, 1996, 2000; Økland *et al*. 2004, 2008; Speight 1986) and dolichopodid flies for moist habitat and freshwater quality and management (Englund *et al*. 2007; Pollet 1992, 2001; Pollet & Grootaert 1996).

Synthesis and conclusions

Based on experiences with other taxa in Africa and on some of the initiatives with fly conservation elsewhere, it is possible to develop a strategy for the conservation of Afrotropical Diptera, based on several spatial scales (Table 2). Dragonflies have recently been assessed across Africa (Dijkstra *et al*. 2011), but this took considerable resources and could be undertaken as the taxonomy of the group is relatively tractable and there are sufficient experts across the continent for this to be achievable. Even so, several dozen new species have been discovered. The process involved undertaking a Red List assessment of all species, not all of which are threatened, most being "Least Concern", with some "Data Deficient". At the regional scale, Red List assessments can be undertaken by local personnel with an intimate knowledge of the group. As with the continental scale of assessment, this also means mapping of the known localities of the species. The results of such assessments can be used to identify hotspots of both endemism and threat, with both often going hand-in-hand. Once such assessments are completed, the possibility exists to compare such results with other taxa through complementarity studies. At this regional level, recommendations can be made as to where conservation action should be focused, as is the case with dragonflies in the Cape Floristic Region, where invasive alien trees are a key threat (see above).

Table 10.2. Suggested conservation actions for Afrotropical Diptera at various spatial scales.

Spatial scale	Conservation action
Continental	Biogeographical assessment of species, including Red Listing; comparison with other taxa (complementarity studies); identifying further Diptera hotspots.
Regional	Biogeographical assessment of species, including Red Listing; comparison with other taxa (complementarity studies); identifying further Diptera hotspots; making recommendations for Diptera conservation along with other taxa.
Sub-regional	Identification of local hotspots; identifying threats; systematic conservation planning.
Landscape (100s m–several km)	Deployment of a synthetic management approach where Diptera are mainstreamed with other focal taxa, which may involve selection of certain taxa, functional groups or size classes; identification of water quality bioindicators, and of bioindicators of landscape quality.
Mesoscale (10s m–100s m)	Identification of the importance of various landscape features that may be significant for certain species (*e.g.*, hilltops for mate meeting, wetlands as sites for certain larvae, logs for saproxylic species).
Habitat (single species)	Species-specific conservation action, involving an understanding of the biology and habitat requirements of the species; ongoing monitoring of the species (*i.e.*, updating of the Red List assessment) and of populations of the species.

Undertaking a broad-scale Red List Assessment of Afrotropical Diptera is, however, fraught with difficulties. Africa lacks specialist Diptera researchers and most published distribution information in taxonomic papers is generated from label data of historical museum specimens, many of which date from the European colonial era. What may be more feasible is to make taxon-based assessments for some of the better researched and taxonomically stable groups, *e.g.*, Asilidae, Bombyliidae or Syrphidae, or on certain functional groups, such as pollinators (Brand 2009; Vrdoljak & Samways 2014), or flies associated with vertebrates, many of which are also threatened. Another approach is to hone in on large-sized individuals, which are easily recognised. When this is done, it is often possible to engage citizen scientists. This would take some years to develop in Africa, although citizen scientist initiatives, such as *iSpot* (http://www.ispot.org.za/), may be relevant at the regional level.

At the sub-regional scale, it is possible to survey flies and identify local hotspots or areas for conservation action, which has been done for example for dragonflies of the Tsitsikamma forest (Simaika & Samways 2011). Results from such studies can also be fed into systematic conservation planning where flies inside and outside reserves can be identified and used alongside other taxa to identify new areas requiring conservation. Again, this has been done for dragonflies (Simaika & Samways 2010) and for butterflies (Mecenero *et al*. 2013), with a regional assessment having been done for the KwaZulu-Natal Province of South Africa (Goodman 2000).

At the landscape level, flies have been used in Europe to assist with landscape planning, especially in connection with forest health, but the group has yet to be used for such activities in Africa, although a start is being made using the flower-visiting guild (Brand 2009; Vrdoljak & Samways 2014). Flies can also feature in freshwater assessment, with proportionately high chironomid levels being indicative of poor water quality (Dickens & Graham 2002; Samways *et al*. 2011) and combined with decreases in other, sensitive fly taxa, the effect of river impoundment can be determined (Bredenhand & Samways 2009), as can recovery when invasive alien trees are removed (Magoba & Samways 2010).

At the yet smaller, mesoscale, flies can assist for example in the local planning of large-scale ecological networks (Samways *et al*. 2010), which are a major mitigation measure for addressing the commercial afforestation of the landscape. For example, a study has been made on the importance of hilltopping behaviour in butterflies (Lawrence & Samways 2002), which has also been documented for numerous families of flies (*e.g.*, Skevington (2008)).

Flies have been used, together with other taxa, in assessing how well flower-visiting assemblages survive in ecological networks (Bullock & Samways 2005) and to assess recovery of ecological integrity through removal of alien plants under the South African Working for Water Programme (Magoba & Samways 2010). Lastly, at the habitat scale of conditions suitable for optimal survival of single species, assessments need to be continued, especially as there are so many localised endemics, some of which have specific relationships with certain endemic flowers (Johnson & Steiner 1997). Rostrum development associated with nectaries recessed in tubular corollas is a well known phenomenon in some Fynbos-associated flies in the Cape Floristic Region; best known examples being within the families Bombyliidae, Nemestrinidae and Tabanidae. Other examples occur in diverse families, including the Rhagionidae, Tanyderidae, Sciaridae and Ceratopogonidae (Kirk-Spriggs & Stuckenberg 2009: 159).

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PHYLOGENY OF DIPTERA 11

Brian M. Wiegmann and David K. Yeates

Introduction

The current status of Diptera phylogenetics is here reviewed, with emphasis on newer contributions and progress since the thorough reviews of the subject by Woodley *et al*. (2009) and Yeates *et al*. (2007).

Diptera (true flies) are among the most diverse lineages of holometabolous insects and this makes systematics research to reconstruct their phylogeny a complex and dynamic area of evolutionary biology. Reconstructing the Diptera Tree of Life involves integration of all available evidence from comparisons of extant and extinct flies and incorporates a range of analytical methods, drawn from multiple disciplines (Trautwein *et al*. 2012). As detailed throughout this *Manual*, Diptera have diverse habits and ecological roles, that span trophic and ecological niches (phytophages, parasitoids, decomposers, predators, *etc*.) and the order includes major pests of crops and livestock (see Chapter 5), vectors of human and animal pathogens (see Chapters 5 & 6) and pollinators (see Chapter 4). The numerous benefits from understanding the processes leading to this diversity make gaining a robust estimate of the phylogenetic tree especially valuable. This tree will serve as an organising framework for fly classification and nomenclature and as the context for understanding the timing and pattern of evolutionary change, to trace the origin of morphological and ecological adaptations, to understand biogeographical distributions and to document diversification itself. This chapter provides a current consensus on the phylogeny of Diptera, but it is stressed that new phylogenetic hypotheses are regularly proposed and new evidence is rapidly accruing.

The pioneering German dipterist and theoretician [Emil Hans] Willi Hennig (1913–1976), established a methodological framework for seeking and assessing character state evidence (synapomorphy) in support of monophyletic groups and he established the explicit goal of using phylogenetic relationships as the basis of taxonomic classification (Hennig 1950). Hennig

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 1. Introductory chapters and keys to Diptera families. *Suricata* 4. South African National Biodiversity Institute, Pretoria; pp. 253–265.

published prolifically on fly phylogeny, morphology, and taxonomy throughout his career (Meier 2005: 55; Schmitt 2013: 113). Many of the groups he defined remain among the best-supported clades in the order. The system of names and higher-level groupings used in this *Manual* follows the Hennigian dictum of phylogeny-based classification, but also reflects authoritative usage of accepted clade names in the scientific literature, and wherever possible, is based on the weight of current evidence from all possible sources. The higher-level classification used throughout this chapter is based on clade names applied by Pape *et al*. (2011) and Wiegmann *et al*. (2011).

Recent advances in DNA sequencing technology, computational power, quantitative phylogenetic methods and data integration have all contributed to an increase in our understanding of fly phylogeny. Consequently, the most up-to-date estimates include both careful consideration of the morphological evidence, along with assessment of molecular data from available gene sequences. The history of phylogenetic research on flies and the substantial debate over morphological interpretations have been reviewed extensively in recent years (Lambkin *et al*. 2013; Sinclair *et al*. 2013; Woodley *et al*. 2009). Here, the focus is only on the emerging pattern of well-supported clades from multiple recent studies, to place Afrotropical fly diversity within a phylogenetic context, and where possible, to point the reader to studies that challenge or refute current consensus. It is fully expected that detailed analyses of morphology and major new genomic comparisons will continue to improve our view of the fascinating and rich history of fly evolution.

The origin and closest relatives of flies

Diptera are a monophyletic lineage with a number of morphological synapomorphies uniting them (Grimaldi & Engel 2005: 494; Yeates & Wiegmann 1999). Flies are easily recognised by their drastically reduced metathoracic wings, which (if present) are modified as knob-like halteres that function as balancing organs during flight. Most adult flies have mouthparts that are unique among insects, being either specialised for sponging-up liquid food or piercing mouthparts that allow access to liquids from sap and nectar to vertebrate blood or insect hemolymph. Approximately 158,000 species of Diptera (*ca* 19,000 of which occur in the Afrotropics) have been described in *ca* 180 families, although total species diversity is undoubtedly considerably higher. Large faunal surveys have revealed the vastly underappreciated diversity of fly species in the tropics (Brown 2005; Condon *et al*. 2008) and large numbers of undescribed species are undoubtedly also found in the many other habitats and biomes globally where flies occur. Nearly all estimates of fly species diversity are based on taxa that have been added to the scientific literature based on morphological or cytological diagnosis. In recent years, molecular studies have revealed many “cryptic” species (Bickford *et al.* 2007) – species that can only be detected by DNA sequencing or other molecular methods – and “species complexes” – closely related species that may have formerly been only recognised as a single taxon, or that require multiple sources of evidence to confirm the identity of representative taxa (Krüger *et al.* 2000; Schutze *et al.* 2015). These findings make it clear that our current count of fly species diversity is a vast underestimate.

Morphological and molecular evidence supports a group termed Antliophora comprising a sister-group relationship between flies and a clade containing fleas (order Siphonaptera) and Scorpionflies (order Mecoptera). This group is supported by shared characteristics of the mouthparts, head musculature and internal structures of the larval head capsule (Beutel *et al*. 2011). Antliophoran monophyly and the position of the Diptera has also been supported by recent molecular systematic analyses, that examined combined evidence from only a handful of nuclear protein coding genes (Wiegmann *et al*. 2009), as well as more definitive studies, that used large gene harvests from genomes (Niehuis *et al*. 2012) and transcriptomes (Misof *et al*. 2014).

Phylogenetic inferences and divergence times place the origin of flies in the Permian, *ca* 260 MYA (Misof *et al*. 2014; Wiegmann *et al*. 2011). The earliest known fossil flies are from the Triassic, *ca* 240 MYA, with fossil representatives of major infraorders known as early as 220–200 MYA (Blagoderov *et al*. 2007; Grimaldi & Engel 2005: 497). An impressive diversity of fossil specimens of both extinct and extant Diptera families continues to be revealed, both as compression fossils (*e.g.*, Mostovski 2009) and as amber inclusions (*e.g.*, Tschirnhaus & Hoffeins 2009). These fossils reveal the rich history of diversification, the origins and/or loss of morphological and behavioural attributes, and adaptations, character state distributions and prehistoric biogeographic ranges that can be mapped across the history of the order. Because flies are ecologically diverse, exhibiting a wide range of larval feeding habits, it is possible to infer the age and phylogenetic origin of distinctive ecological traits, such as blood-feeding, gall induction, leaf-mining and endoparasitism, using both the morphology of fossil flies and the traces left in the palaeontological record (Labandeira 2005: 242). Virtually all molecular studies of Diptera reveal a genome-wide evolutionary rate increase in flies, relative to other extant holometabolan insects (Friedrich & Tautz 1997; Savard *et al*. 2006). This “long branch” places the “crown group”, containing all extant lineages of flies, in a more recent position within the Early- to Mid-Jurassic, quite removed from the putative split of flies from their common ancestor with fleas and Scorpionflies in the Permian. For this reason, it is difficult to correlate the expected age of origin of flies with clearly assignable dipteran synapomorphies found in Mesozoic and Paleozoic specimens. New fossil discoveries continue to expand on the rich history of flies, with details that can be incorporated into phylogenetic studies, taking advantage of new methods that combine evidence from fossils, morphology, phylogenetic trees and gene sequences (Ronquist *et al*. 2012; Silvestro *et al*. 2015).

The earliest fly lineages and major groupings

The phylogenetic tree illustrated in Fig. 1 depicts a recent hypothesis of higher-level relationships from a combined quantitative analysis of gene sequence data (Wiegmann *et al*. 2011). The figure also indicates nodes that are well-supported in most modern studies using morphological and/or molecular characters. This tree is one of several hypotheses resulting from the FLYTREE Consortium; an international team of fly systematists who published a large novel phylogenetic tree, based on a combined analysis of five nuclear genes. A major confounding factor in resolving relationships among fly groups is the rapid radiation of new fly lineages that occurred at three distinct episodes in fly history. This pattern of episodic radiation is also observed in other mega-diverse holometabolan insect orders (McKenna *et al*. 2015; Regier *et al*. 2013). It is characterised by the nearly contemporaneous origins of many distinctive groups, but with limited evidence of relationships and a pattern of short branch lengths on reconstructed trees (corresponding to the amount of shared

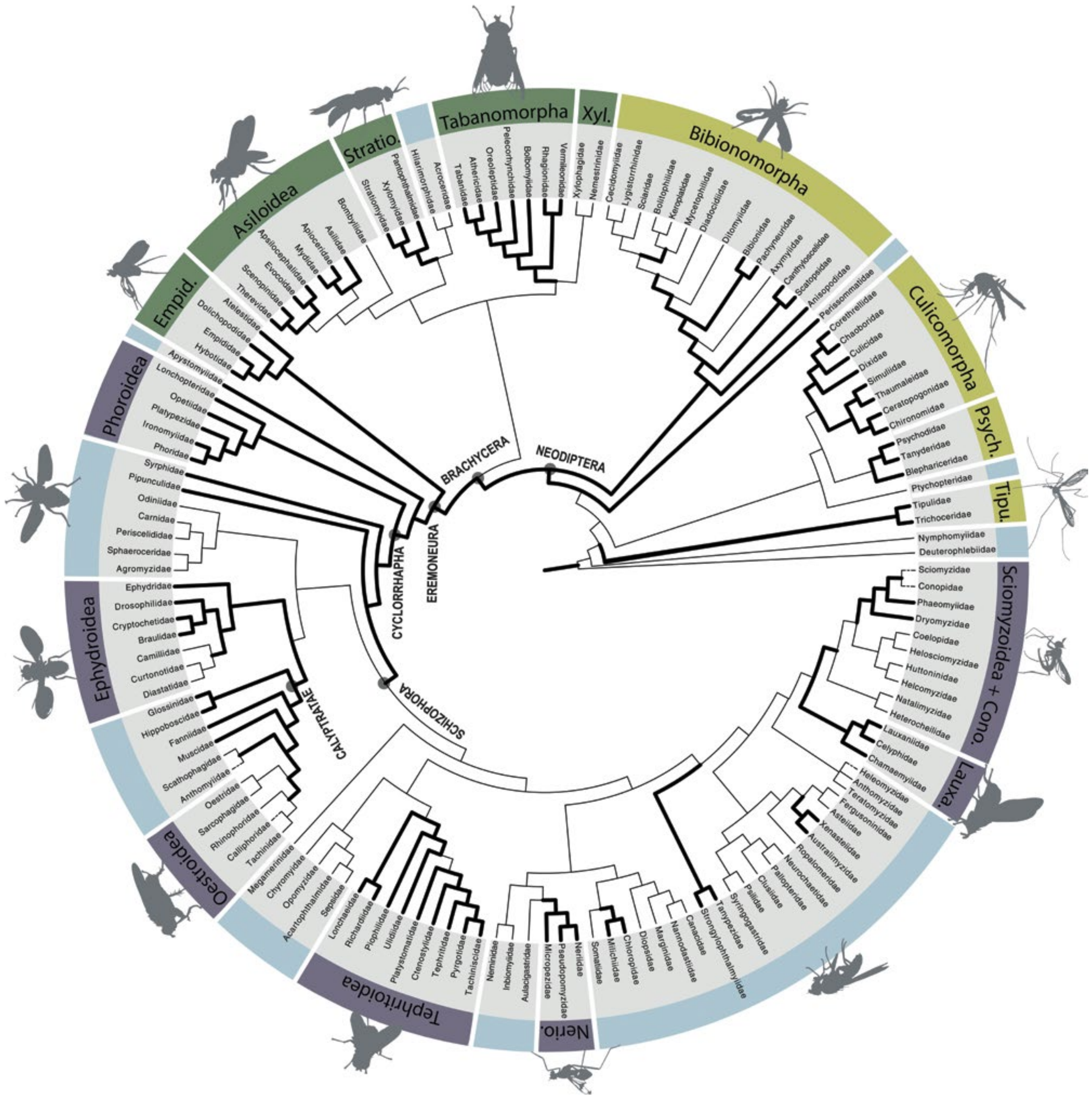

Fig. 11.1. Phylogenetic tree of Diptera based on analysis of multiple nuclear genes from Wiegmann *et al*. (2011). Clades depicted by bold lines are those for which molecular and/or morphological data show strong support in multiple recent studies. Families depicted by dashed lines are paraphyletic in recent studies. Only those families with species sampled in Wiegmann *et al*. (2011) are included in the tree.

Abbreviations: Cono. – Conopoidea; Empid. – Empidoidea; Lauxa. – Lauxanioidea; Nerio. – Nerioidea; Psych. – Psychodomorpha; Stratio. – Stratiomyomorpha; Tipu. – Tipulomorpha; Xyl. – Xylophagomorpha.

genetic signal among taxa). Using an evolutionary model that combines phylogeny, extant species numbers and clade age to identify nodes on the phylogeny where lineage diversification is higher or lower than expected, the FLYTREE analysis found three major episodes of diversification (Wiegmann *et al*. 2011). The first was early in fly history, occurring in the Triassic, *ca* 220 MYA and involved the origins of the earliest extant lineages and major fly morphotypes. The second rapid radiation also occurred in the Triassic, *ca* 180 MYA among the lineages of early Brachycera and a third radiation at the end of the Cretaceous *ca* 65 MYA involved the large number of families in schizophoran Cyclorrhapha (Wiegmann *et al*. 2011). The remarkable diversity of Cyclorrhapha could be ascribed to the rapid origin of new lineages in that era, but may also be due a lower than average extinction rate, when projected to the present. This pattern reflects the great ecological success of higher flies, their ability to rapidly colonise and exploit new environments and take on new feeding roles, as well as their sheer abundance, broad distribution and prodigious reproductive efficiency. Divergence times analyses, using molecular data, fossil-based calibrations and phylogeny, have become an important method to assess temporal context and establish evidence-based estimates of ages for Diptera clades. Divergence times, based on molecular data for splits between major clades of Diptera, have been published by Bertone & Wiegmann (2009); Bertone *et al*. (2008), Wiegmann *et al*. (2003, 2011), Winkler *et al*. (2015), Winterton & Ware (2015), Zhao *et al*. (2013) and numerous others.

The first of the extant fly lineages are two highly specialised non-Afrotropical families, Deuterophlebiidae (15 species) and Nymphomyiidae (6), the larvae of which are adapted to occur in flowing, freshwater aquatic environments. These families have been difficult to place phylogenetically, due to their unique adult morphology and specialised larval morphology (Courtney 1994; Schneeberg *et al*. 2012). There is considerable ongoing debate regarding the placement of these families and their possible close relationship. Nucleotide data from 28S rDNA and up to five nuclear genes support the placement of these groups at the base of the phylogeny, separate from all other Diptera, but it is uncertain whether they are sister-groups, or sequentially placed separate lineages, diverging before the origin of the common ancestor of all other extant Diptera. It appears likely that these relatively species-poor clades represent vestiges of the earliest fly diversity that remains today in relatively undisturbed montane or riverine habitats (Schneeberg *et al*. 2012) and that they branched off separately from the lineage leading to all other flies. It is interesting to note that there are other similarly unique extant fly families that, like these, have only a few species and are ambiguously placed within larger, well-characterised higher-level groups, their position depending on the data set used and analytical protocol. These "relict" taxa are often found to be sister lineages of major fly groups and are difficult to interpret phylogenetically, due to their unique morphology and poorly known biologies.

Traditional fly classifications separated the order into two suborders, separated largely on the basis of antenna type and body shape: "Nematocera" (Thread-horned flies) and Brachycera (Short-horned flies). Most modern classifications now attempt to incorporate an explicitly phylogenetic system that recognises five major groups, sometimes called infraorders or suborders: Bibionomorpha, Brachycera, Culicomorpha, Psychodomorpha and Tipulomorpha. Within these groups, classifications differ, according to conflicting evidence and scale of analysis. Virtually all quantitative phylogenetic research has, however, supported the monophyly and composition of these five clades. Separate morphological (Hennig 1973: 19; Lambkin *et al*. 2013; Michelsen 1996; Oosterbroek & Courtney 1995; Wood & Borkent 1989) and molecular-based (Bertone *et al*. 2008; Wiegmann *et al*. 2011) studies disagree in various respects concerning the composition and inter-relationships of the nematoceran infraorders. Conflicting interpretations of adult *versus* immature characters gives conflicting evidence of the higher-level relationships among the earliest lineages of flies (Yeates & Wiegmann 1999; Yeates *et al*. 2007). The aforementioned rapid radiation of major clades in the Triassic has also meant there is no clear signal of relationships within these groups found in the analysis of molecular data. Thorough reviews of the relationships within the nematocerous Diptera are presented in Bertone *et al*. (2008), Oosterbroek & Courtney (1995), Wood & Borkent (1989) and Woodley *et al*. (2009).

Tipulomorpha includes the families Tipulidae, Limoniidae and the non-Afrotropical Cylindrotomidae, Pediciidae and Trichoceridae. The first four mentioned families include families that were originally included in Tipulidae (Crane flies), but are now raised to family-rank within the Tipuloidea (Petersen *et al*. 2010). Tipuloidea and Trichoceridae are supported by multiple morphological characters (Oosterbroek & Courtney 1995; Starý 2008), but support was not found in a recent study of adult head morphology (Neugart *et al*. 2009). Nonetheless, molecular datasets confirm the sister-group relationship between Tipuloidea and Trichoceridae (Petersen *et al*. 2010; Wiegmann *et al*. 2011).

Culicomorpha is a large clade, including mosquitoes, midges, black flies and biting midges (*i.e*., Ceratopogonidae, Chaoboridae, Chironomidae, Corethrellidae, Culicidae, Dixidae, Simuliidae and Thaumaleidae), supported by nucleotide and morphological data (Borkent 2012; Lambkin *et al*. 2013; Wiegmann *et al*. 2011). Morphological cladistic analyses (Borkent 2012; Sæther 2000) and molecular studies (Wiegmann *et al*. 2011) support a monophyletic Culicoidea (*i.e*., Chaoboridae, Corethrellidae, Culicidae and Dixidae) and a sister-group relationship for Simuliidae and Thaumaleidae (Bertone *et al*. 2008; Borkent 2012; Moulton 2000), but differing character systems conflict in regard to the position of Chironomidae and Ceratopogonidae.

Psychodomorpha (or Psychomorpha) (Amorim & Yeates 2006) now includes three families, Blephariceridae, Psychodidae and Tanyderidae, all of which include larvae that occur in freshwater, but otherwise differ radically from one another in many features traditionally used for phylogenetic analysis. For this reason, multiple concepts of "Psychodomorpha" have been proposed in previous studies, that recovered disparate affinities for all three of these families and some also included various current bibionomorph taxa, such as Scatopsidae, in the concept of this group (Amorim 2000; Oosterbroek & Courtney 1995; Wood & Borkent 1989: 1353). Morphological data from Lambkin *et al*. (2013) placed Psychodidae at the base of the Bibionomorpha, but character support is limited and uncertain, chiefly due to the fact that Lambkin *et al*.'s study focuses on features that could be scored across all Diptera.

Bertone *et al*. (2008) and Wiegmann *et al*. (2011), using nucleotide data from 28S rDNA and multiple nuclear genes, confirmed the relationship between just these three families, with Blephariceridae the sister to the other two families, which is here considered to be the currently best-supported hypothesis for the placement of these groups.

Bibionomorpha is a large clade of 17 families that includes March flies (Bibionidae), Fungus gnats (Mycetophilidae), Gall midges (Cecidomyiidae), Black fungus gnats (Sciaridae), Minute black scavenger flies (Scatopsidae) and Wood gnats (Anisopodidae), along with several smaller families. Bibionomorphan relationships remain somewhat uncertain. A recent phylogenetic analysis, based on nuclear and mitochondrial ribosomal gene fragments (Ševčík *et al*. 2014), conflicts with the phylogenetic arrangement illustrated in Fig. 1 from Wiegmann *et al*. (2011), but in both analyses support is limited for relationships among the major bibionomorph clades. Nevertheless, virtually all phylogenetic studies of Bibionomorpha support monophyly of the Sciaroidea, a clade including Cecidomyiidae, Keroplatidae, Lygistorrhinidae, Mycetophilidae, Sciaridae and the non-Afrotropical Bolitophilidae, Ditomyiidae and Rangomaramidae (Amorim & Rindal 2007; Ševčík *et al*. 2013, 2014; Wiegmann *et al*. 2011).

Defining the sister-group of the extremely diverse clade Brachycera has been especially difficult. Hennig (1968) provided evidence from adult characters for a relationship between the Brachycera and Bibionomorpha. Michelsen (1996) revealed morphological features that show a sister-group relationship between the Brachycera and a redefined Bibionomorpha, based on adult thoracic sclerites and musculature. This grouping, the Neodiptera, has also been supported by recent analyses of molecular (Bertone *et al*. 2008; Caravas & Friedrich 2013; Wiegmann *et al*. 2011) and morphological datasets (Lambkin *et al*. 2013; Sinclair *et al*. 2013). The small Australian family Perissommatidae (5 species) is another relict nematoceran lineage of uncertain phylogenetic position. Molecular data place the perissommatids as sister to Neodiptera (Bertone *et al*. 2008; Wiegmann *et al*. 2011).

Lower Brachycera – a challenging phylogenetic puzzle

Phylogenetic relationships among the families and higher-level groups that comprise the earliest lineages of the Brachycera remain one of the most challenging areas of fly phylogeny to resolve by any data or analysis type. The lower Brachycera (= "Orthorrhapha") are generally large flies, many of which are predators or parasitoids as larvae and these are divided into three large infraorders Xylophagomorpha (Xylophagidae), Stratiomyomorpha (Pantophthalmidae (non-Afrotropical), Stratiomyidae and Xylomyidae), Tabanomorpha (Athericidae, Rhagionidae, Tabanidae, Vermileonidae and the non-Afrotropical families Austroleptidae, Oreoleptidae, Pelecorhynchidae and Bolbomyiidae), and a number of superfamilies (Nemestrinoidea, Asiloidea, Empidoidea) (Yeates 2002). The Tabanomorpha includes three families that include some species that feed on vertebrate blood (Athericidae, Rhagionidae and Tabanidae) (Wiegmann *et al*. 2000). The Horse flies (Tabanidae) and Snipe flies (Rhagionidae) are diverse lineages that are distributed globally, with many Afrotropical species; both have been the subject of recent quantitative phylogenetic studies of molecular and morphological features (Kerr 2010; Lessard *et al*. 2013; Morita *et al*. 2016).

Lower Brachycera also includes several additional clades, including Nemestrinoidea (Acroceridae and Nemestrinidae), Bombyliidae and Asiloidea (Apioceridae, Asilidae, Mydidae, Scenopinidae and Therevidae and the non-Afrotropical families Apsilocephalidae and Evocoidae). Relationships among and within these groups has been the subject of much detailed comparative morphological and molecular study over the past 20 years, and no single analysis has yet provided well-supported resolution for the relationships at the higher-level. Major studies of Therevidae and their relatives (Winterton & Ware 2015; Winterton *et al*. 2016), Bombyliidae (Trautwein *et al*. 2011; Yeates 1994), Asilidae (Dikow 2009*b*) and Asiloidea (Trautwein *et al*. 2010) have provided important new hypotheses for the relationships around most of the larger families, but with some lingering uncertainty. Analysis of only the nuclear 28S ribosomal DNA recovered paraphyly for the lower Brachycera (Wiegmann *et al*. 2003), a result that is also found in all morphological analyses of these taxa over the past 40–50 years (Hennig 1973: 8; Woodley 1989: 1373; Yeates 2002). By contrast, the more extensively sampled multigenic study of Wiegmann *et al*. (2011) unexpectedly recovered high bootstrap support for the monophyly of Orthorrhapha (as depicted in Fig. 1), but it remains to be seen whether this unique finding will find further support in analyses of even larger datasets.

While quantitative phylogenetic analyses have shed new light on some areas of the lower brachyceran tree, there is still very little convincing evidence to resolve several major questions—notably there is too little information from any data type to place the Acroceridae, Bombyliidae, Hilarimorphidae (non-Afrotropical) and Nemestrinidae. These are morphologically disparate groups with specialised morphologies and larvae that are mostly endoparasites of insects or arachnids. The Hilarimorphidae is a small family of unknown habits, with morphological features that suggest conflicting affinities to multiple lineages in the lower brachyceran tree, including Bombyliidae and Empidoidea. Large genomic datasets may be the best source of new evidence on this challenging area of fly phylogeny and such studies are currently underway in the laboratories of the authors of this chapter.

The Empidoidea, Dance flies and their relatives (Atelestidae, Brachystomatidae, Dolichopodidae, Homalocnemidae, Empididae, Hybotidae and Oreogetonidae (non-Afrotropical)), are a well-supported monophyletic group and have been the focus of important comparative morphological and molecular studies (Moulton & Wiegmann 2004, 2007; Sinclair & Cumming 2006). Empidoidea and Cyclorrhapha ("higher flies") together form a monophyletic group termed Eremoneura. Once again, a relict lineage, the non-Afrotropical family Apystomyiidae comprising the single North American species, *Apystomyia elinguis* Melander, is well-supported in multiple molecular data analyses as the sister-group to all higher flies (Trautwein *et al*. 2010; Wiegmann *et al*. 2011). *Apystomyia* has an enigmatic mix of asiloid-, empidoid- and cyclorrhaphan-like morphological features, making it particularly difficult to place based on only one or a few characters. The strong support for *Apystomyia* + Cyclorrhapha is found in quantitative studies that have ruled out legitimate alternatives, such as a placement at the base of the Asiloidea or Empidoidea (*i.e.*, Sinclair *et al*. 2013). This appears to be another example of a species-poor lineage that has with extant representatives of an early diversification among the stem lineages of a major radiation.

Higher fly phylogeny – Cyclorrhapha and the radiation of schizophoran families

The brachyceran clade Cyclorrhapha includes over half of all true flies in over 70 families. Loss of the larval head capsule and pupation in the hardened third-instar larval skin (puparium) are the major autapomorphies of this group (McAlpine 1989: 1398; Yeates & Wiegmann 1999). Cyclorrhapha include some of the best known flies, especially the House fly (*Musca domestica* L., Muscidae), *tsetse* (*e.g.*, *Glossina morsitans* Westwood, Glossinidae), the Mediterranean fruit fly (*Ceratitis capitata* (Wiedmann), Tephritidae) and the Laboratory fruit fly or Vinegar fly (*Drosophila melanogaster* Meigen, Drosophilidae), among a vast array of lesser known, but extraordinarily diverse, fly families.

The first-branching lineages of the Cyclorrhapha (= "Aschiza") are included in two superfamilies, Phoroidea (Phoridae, Platypezidae and the non-Afrotropical families Ironomyiidae, Opetiidae and Sciadoceridae) and Syrphoidea (Syrphidae). The small parasitic family Pipunculidae (Big-headed flies) have traditionally been considered sister-group to Syrphidae and placed within the Syrphoidea (Rotheray & Gilbert 2008). However, molecular datasets invariably place the pipunculids as sister to Schizophora, the next large monophyletic radiation in the order (Wiegmann *et al*. 2011; Young *et al*. 2016). A detailed morphological study of the metapleuron in these flies found synapomorphies in support of the latter arrangement (Tachi 2014).

The division Schizophora is a vast group of over 50,000 species and includes diverse taxa that have adapted to exploit virtually every food resource available to terrestrial and freshwater aquatic organisms (Yeates & Wiegmann 1999). All flies in this group possess a membranous head sac (ptilinum) which, when inflated, allows the pharate adult to eclose by breaking off a cleanly excised cap from the anterior end of the puparium. Schizophora are further divided into the well-supported, monophyletic Calyptratae (McAlpine 1989: 1492; Yeates & Wiegmann 1999), with the remaining taxa forming the most likely paraphyletic acalyptrate grade (Hennig 1971; Wiegmann *et al*. 2011; Yeates & Wiegmann 1999). Most modern studies confirm this arrangement, with the Calyptratae placed as sister to some subgroups of the acalyptrates (Vicoso & Bachtrog 2013; Wiegmann *et al*. 2011; Zhao *et al*. 2013).

The acalyptrates include 20% of fly species diversity in over 60 families. Six large, widely distributed families (Agromyzidae, Chloropidae, Drosophilidae, Ephydridae, Lauxaniidae and Tephritidae) make up > 50% of the species in the entire assemblage (Yeates & Wiegmann 2005: 27). Most researchers recognise up to 10 broadly defined superfamilies of putatively closely related families (McAlpine 1989: 1429): Carnoidea, Conopoidea, Diopsoidea, Ephydroidea, Lauxanioidea, Nerioidea, Opomyzoidea, Sciomyzoidea, Sphaeroceroidea and Tephritoidea, but of these only Ephydroidea (other than the recent inclusion of the small families Braulidae, Cryptochetidae and Mormotomyiidae), Lauxanioidea, Nerioidea and Tephritoidea are consistently defined in terms of their constituent families. Relationships, definition and inclusion for nearly all other superfamilies are not well-supported by convincing morphological synapomorphies and there is very weak support in molecular phylogenetic data (Wiegmann *et al*. 2011). Tephritoidea and Ephydroidea emerge as monophyletic groups in several molecular studies (*e.g.*, Han & Ro 2005), but fully resolving the relationships within and among the rapid radiation of acalyptrate families and higher-level lineages remains one of the most difficult questions in systematic entomology.

Calyptrate flies are divided into 13 families that are important agriculturally (*e.g.*, Anthomyiidae), medically (*e.g.*, Glossinidae, Muscidae and Oestridae) and forensically (*e.g.*, Calliphoridae and Sarcophagidae), or as potential biological control agents (*e.g.*, Tachinidae). Calyptratae also include several groups of specialised vertebrate ectoparasites (Hippoboscidae) or producers of myiasis (Calliphoridae, Oestridae and Sarcophagidae). Calyptrate phylogeny has been a challenge to resolve with morphology or small genetic data sets (Kutty *et al*. 2010; Pape 1992, 2001). Most studies support an early branching Glossinidae and Hippoboscidae, a paraphyletic muscoid grade (Anthomyiidae, Fanniidae, Muscidae and Scathophagidae) (Junqueira *et al*. 2016; Kutty *et al*. 2008, 2010; Wiegmann *et al*. 2011; Zhang *et al*. 2016; Zhao *et al*. 2013) and a monophyletic Oestroidea (Calliphoridae, Mesembrinellidae (non-Afrotropical), Mystacinobiidae (non-Afrotropical), Oestridae, Rhiniidae Rhinophoridae, Sarcophagidae and Tachinidae). The muscoid grade appears to approach a stable resolution with a basal Fanniidae, a next-branching Muscidae and a combined Scathophagidae and Anthomyiidae sister to the Oestroidea. Relationships within the Oestroidea are still confounded by high diversity, short branch lengths, conflicting morphological data and low branch support. Increasing evidence indicates that the traditional Calliphoridae are not monophyletic (Marinho *et al*. 2012; Rognes 1997), and two former subfamilies are increasingly recognised at full familial level as Rhiniidae (*e.g.*, Pape *et al*. 2011) and Mesembrinellidae (Marinho *et al*. 2012, 2016).

Patterns of diversification, ecological specialisation and macro-evolution

Fly phylogeny provides a framework for mapping the history of adaptations and diversification through time. A major feature of the story of fly evolution is that flies exhibit an extraordinary diversity of biological traits, such as feeding habits, behaviours and life histories. Mapping these features on new phylogenetic hypotheses for flies (Wiegmann *et al*. 2011), for all insects (Wiens *et al*. 2015), or for particular families or subgroups (Kutty *et al*. 2014; Morita *et al*. 2016), demonstrates that flies have repeatedly switched between habits and habitats. Although many fly groups are well known as decomposers of decaying organic matter (saprophagy) and dung-feeding (coprophagy), the phylogeny reveals multiple independent origins of phytophagy (plant-feeding), mycophagy (fungus-feeding), haematophagy (vertebrate blood-feeding), predation, endoparasitism (feeding within living animals as parasitoids) and myiasis (internal feeding in vertebrates). Wiegmann *et al*. (2011), attempted to calculate the multiple independent origins of some of these traits and found at least ten independent origins of blood-feeding, 24 origins of phytophagy and 17 origins of endoparasitism, dispersed widely across lineages, with multiple origins within clades and variously contained within early, middle and late expansions of the diversity of Diptera. As phylogenetic research continues to reach into fly lineages (to the specific level) and maps the evolutionary pattern of newly recorded habits and feeding roles, additional independent origins of these traits will certainly be revealed. These patterns are illuminated in many recent studies that apply new phylogenetic evidence to pinpoint the origin and evolution of feeding strategies and host shifts in flies, or that document the coevolution of flies with their host organisms or their natural enemies (Condon *et al*. 2008, 2014; Winkler *et al*. 2015). A phylogenetic perspective on questions surrounding the influence of sexual selection on the evolution of mating strategies, mating success and elaborated sexually selected morphological features and behaviours are allowing a more detailed understanding how fly biology shaped their spectacular evolutionary success (Bonduriansky 2011; Bowsher *et al*. 2013; Husak *et al*. 2011; Puniamoorthy 2008).

Phylogenetic studies of Afrotropical Diptera

Modern phylogenetic studies on Afrotropical Diptera began with the work of South African dipterist Brian Roy Stuckenberg (1930–2009) (Kirk-Spriggs 2012). Stuckenberg pioneered the use of Hennigian phylogenetic reasoning to investigate relationships and develop classification; first in a work on Malagasy Blephariceridae (Stuckenberg 1959) and then throughout his career in works on morphology, classification and biogeography of various dipteran families, especially in the lower Brachycera. Many phylogenetic studies include Afrotropical clades within a broader worldwide sampling to resolve global connections (*e.g.*, Amorim & Rindal 2007; Dikow 2009*a*; Morita *et al*. 2016; Yassin *et al*. 2008). A few key studies have specifically addressed distribution patterns and the biogeography of the continent and/or some of its regions (Cranston *et al*. 2012; Krosch *et al*. 2009, 2012). Studies are now emerging that use integrative taxonomic approaches to investigate phylogeny within comprehensive revisionary analyses of the Afrotropical fauna. For example, a detailed phylogenetic revision of family Curtonotidae, or Quasimodo flies (Kirk-Spriggs & Wiegmann 2013), established monophyly and species-level relationships for the family and connected new information from its African diversity to components in other regions worldwide. Phylogenetic work, including Afrotropical Diptera of economic and/or medical importance, has been undertaken using modern methods that integrate morphological and molecular data to investigate relationships and assess the origins, distribution and identification of significant pests. Comparative genomics and molecular phylogenetics have spurred major contributions to understanding relationships among *Anopheles* Meigen species (Culicidae) that vector malaria (Fontaine *et al*. 2015; Neafsey *et al*. 2015), of Afrotropical True fruit flies (Krosch *et al*. 2012; Virgilio *et al*. 2009, 2015), as well as *tsetse* (Dyer *et al*. 2008; International *Glossina* Genome Initiative 2014), sand flies (Grace-Lema *et al*. 2015) and black flies (Krueger & Hennings 2006).

Problem taxa in the Afrotropical fauna

Biodiversity research in the Afrotropical Region over the past century has brought to light a great many unique species and lineages of flies that are difficult to place in the phylogeny. Most notably, rare and little known groups of acalyptrate flies have been elevated to familial level and are considered to be lineages, the phylogenetic placement of which is complicated by their specialised morphology, or distinctive combination of multiple morphological characters that would place them in recognised higher-level groups. Perhaps the most astounding example is the "Terrible hairy fly", *Mormotomyia hirsuta* Austen (Mormotomyiidae). This fly was re-discovered in Kenya in 2010 after only a few specimens were known from collections made in the 1930s and 40s. This peculiar fly is associated with bat roosts and has greatly reduced wings and eyes and long limbs and setae – morphological interpretations of the species made in the 20th century by multiple authors provided conflicting, somewhat speculative attempts to place the group. New observations allowed thorough morphological and molecular studies to be conducted and these place Mormotomyiidae consistently in the Ephydroidea (Copeland *et al*. 2011, 2014; Kirk-Spriggs *et al*. 2011; Wiegmann, unpubl.). This is another example of a "relict" lineage, in which a single known representative is placed sister to a more species-rich extant radiation and also exemplifies the extraordinary diversity of dipteran lineages and biologies that are yet to be fully explored in the Afrotropics. Similarly, the family Marginidae (for *Margo aperta* McAlpine and *M. clausa* McAlpine) was placed tentatively in the Opomyzoidea (McAlpine 1991) and the Natalimyzidae (for *Natalimyza milleri* Barraclough & McAlpine, but with many additional species yet to be described) in the Sciomyzoidea (Barraclough & McAlpine 2006). The latter lineage is a relict of a much broader ancient distribution, as specimens have been identified in Eurasian Eocene amber inclusions (Tschirnhaus & Hoffeins 2009). A better understanding of schizophoran acalyptrate higher-level groups and a more complete taxon sampling across all groups of potentially close affinity will likely be required to place these and other unique lineages

Recent advances and future prospects

Comparative morphology and Diptera phylogenetics

Morphological study to identify new characters and character systems remains an important source of new evidence on fly phylogeny. A number of recent studies have extended the search for synapomorphies deeper inside the fly anatomy and across little-studied taxa to reveal and interpret new skeletal-structural and muscular variation. Among these are major new works that use new imaging and computational technology, such as microCT tomography, to image and reconstruct anatomical features in three dimensions, to illuminate both functional and structural aspects of whole character systems (*e.g.*, Wipfler *et al*. 2012) and fossilised amber inclusions (*e.g.*, Kehlmaier *et al*. 2014). These comparative studies are critically important for increasing the precision of inferences of homology and phylogenetic utility for characters that have been difficult to score, or that conflict with other features. Recent detailed studies that have been carried out in a phylogenetic context include major new and revisionary studies on male genitalic variation and homology (*e.g.*, Sinclair *et al.* 2007, 2013; Spangenberg *et al.* 2012) and adult head structures (*e.g.*, Schneeburg & Beutel 2011). Studies that examine comparative morphology and functional variation bring exciting new tests of homology and facilitate assessment of adaptive convergence (*e.g.*, Friedemann *et al.* 2014; Rotheray & Lyszkowski 2015). Morphological studies are an indispensable part of phylogenetic study and are critical in Diptera due to their wide anatomical diversity, in both extinct and extant forms, and thus provide both primary and validating evidence of relationships.

Molecular data – gene and taxon sampling

The era of methodological and theoretical advancements in the use of genetic variation in DNA and protein sequences revitalised fly phylogenetics (Yeates & Wiegmann 2012) and made it easier to gather evidence for many species at every level of investigation throughout the order. The refinement of these tools has allowed a steady increase in the inclusiveness, scope and analytical rigour of investigations of fly relationships. A critical aspect of the use of genetic data is choosing genes to sequence that will provide sufficient variation that accrues at predictable or unbiased rates, that can be modelled and that can be easily amplified and sequenced by standard laboratory methods for most of the study taxa. In recent years, it has been demonstrated that small datasets comprised of only a few genes, often have insufficient variation, or contain conflicting evidence when applied to difficult radiations of taxa (Winkler *et al.* 2015). It is now widely held that combinations of genes from differing genomic sources (nuclear *versus* mitochondrial; protein coding *versus* ribosomal), are likely the best evidence of relationships when sampling is limited and variation is relatively unpredictable (Winkler *et al.* 2015). Multi-gene datasets have now been applied to phylogenetic questions in virtually all of the large and commonly encountered fly families. These studies provide new evidence for relationships among families analysed in the context of divergences within and between major fly clades, *e.g.*, Gibson *et al.* (2010) for Conopoidea; Trautwein *et al.* (2010) and Winterton & Ware (2015) for Asiloidea; Tóthová *et al.* (2013) for Sciomyzoidea; Ševčík *et al.* (2013, 2014) for Sciaroidea and Bibionomorpha and Marinho *et al.* (2016) for Oestroidea, among numerous others. All these studies provide a growing evidence-base for completing the Fly Tree of Life, promoting the use of the same genes and applying similar or interoperable strategies across taxonomic boundaries to continue to resolve and re-frame some of the most difficult questions in fly evolutionary history.

Phylogenomics

The ease with which whole or partial genomes and transcriptomes can now be sequenced using high throughput sequencing technology (Yeates *et al.* 2016) has allowed for new analyses of fly phylogeny from datasets of unprecedented size and scale. The use of phylogenomics began in Diptera with studies that obtained sequences for all of the genes contained in the mitochondrial genome (*i.e.*, 13 nuclear genes, 22 tRNA genes and two ribosomal RNAs) (Cameron *et al.* 2007). Phylogenetic analyses from mitogenomics have provided additional and corroborating support for the general pattern of relationships corresponding to established clades across the higher-level phylogeny of flies (Beckenbach 2012; Beckenbach & Joy 2009; Cameron *et al.* 2007; Caravas & Friedrich 2013; Junquiera *et al.* 2016; Li *et al.* 2015; Zhang *et al.* 2016; Zhao *et al.* 2013). These studies are useful in providing a phylogenetic comparison of evolutionary rate dynamics and information content for mitochondrial genes. Because mitochondrial genes evolve at a faster rate than do many genes of the nuclear genome, and mitochondrial genomes are maternally inherited, the phylogenetic signal in these sequences tend to be most informative for the divergences in the order of *ca* 15 MY and younger (Simon *et al.* 2006), but have also been shown to be informative at many levels (Cameron 2014). Most mitochondrial phylogenomic studies in Diptera have been poorly sampled and focused primarily on model study organisms, or on comparisons between published sequences and a few newly added species. Several of the most recent examples, however, have included more extensive taxon samples from published mitogenomes along with newly sequenced taxa, e.g., Zhao *et al.* (2013), or have conducted large mitochondrial gene harvests, using new sequencing technology (Junquiera *et al.* 2016; Zhang *et al.* 2016).

Major phylogenomic analyses of Diptera using hundreds to thousands of orthologous genes sampled from the nuclear genome are the most recent and exciting development in fly phylogenetics. A promising new technique called hybrid enrichment or anchored hybrid enrichment (Lemmon *et al.* 2012) allows hundreds of genes to be sequenced, assayed by specially targeted probes that are designed by reference to full genomes or transcriptomes. The first use of this technique in Diptera (Young *et al.* 2016) demonstrates the potential of this technique, producing a resolved, very well supported phylogeny of Syrphidae that is consistent with previous studies using other, smaller molecular datasets and morphology. In transcriptomics, gene sequences are obtained from simultaneously sequencing all of the expressed mRNA, the transcriptome, in a single high throughput sequencing run, or by direct sequencing of large chromosomal regions directly from genomic DNA. Bioinformatic analyses are used to assemble and retain only genes that are single copy orthologs and, therefore, good indicators of species phylogeny and these processes lead to molecular datasets that may contain more than 3,000 genes for analysis. The 1K Insect Transcriptome Evolution Project (1Kite.org), is an international research consortium that has now sequenced and is analysing over 1,400 insect species for insect phylogeny reconstruction (Misof *et al.* 2014). The project includes flies from over 70 families (over 90 species) and these data should have a revolutionary impact on our understanding of fly relationships and will provide a great resource of fly genetic data to evaluate phylogenetic information content, rates of evolution, analysis strategies and sampling effects. A first study of insect order level relationships and divergence times of insect clades showed unprecedented strong support for multiple areas of insect phylogeny, including the placement, monophyly and taxonomically accurate arrangement of 13 sampled Diptera in the study (Misof *et al.* 2014). With the promise of exciting new hypotheses and corroboration to evaluate, analyses are now underway using these data to resolve phylogenetic understanding within each of the major radiation zones in flies (lower Diptera; orthorrhaphous Brachycera and Schizophora). As genomic data are sampled more extensively for all lineages of Diptera, new resolution and continuing challenges will be illuminated by a more fully resolved Fly Tree of Life.

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KEY TO DIPTERA FAMILIES — ADULTS

12

Stephen A. Marshall, Ashley H. Kirk-Spriggs, Burgert S. Muller, Steven M. Paiero, Tiffany Yau and Morgan D. Jackson

Introduction

Family-level identifications are critical to understanding, researching, or communicating about flies. Armed with a family name it is possible to make useful generalisations about their importance and biology, it is easy to search for further information using the family name as a search term and it is straightforward to use the name as a doorway to more specific or generic-level treatments, such as the chapters included in this *Manual*.

Many flies, such as mosquitoes (Culicidae; see Chapter 31), horse flies (Tabanidae; see Chapter 39) and most robber flies (Asilidae; see Chapter 48), flower flies (Syrphidae; see Chapter 60) and bee flies (Bombyliidae; see Chapter 45), are instantly recognisable to the family level, based on their general appearance and will be familiar to most students and naturalists. Most flies, however, require attention to diagnostic features for family identification, and the diversity of Diptera and their diagnostic features often demand the use of taxonomic identification keys to sift through combinations of diagnostic features in search of a family name. Identification keys guide users through a series of decisions that gradually narrow the field down until a taxon (in this case, at the rank of family) is reached. Most identification keys, like those in this *Manual*, are linear and dichotomous, rather like a road with a series of forks with informative signs, but some keys (such as Hamilton *et al*. 2006) are based on a matrix of characters from which you can choose in any order, rather than following a fixed path.

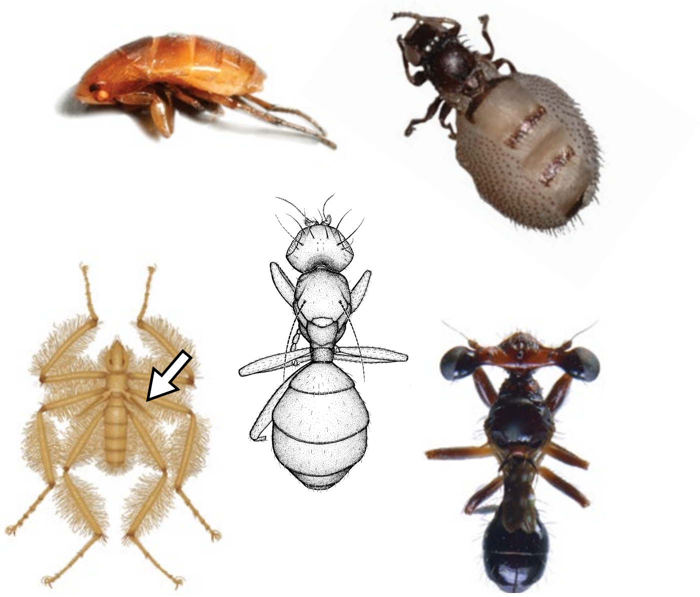
There is an old adage that identification keys are "Written for people who cannot use them, by people who do not need them". This tongue-in-cheek witticism contains a grain of truth, as specialists usually define their taxa on the basis of combinations of subtle characters inappropriate for general identification keys and diagnose them more on the basis of experience and general appearance than on precise combinations of easily visible characters. The resulting difficulties are exacerbated when traditionally recognised and easily diagnosed families are broken up into multiple families on the basis of phylogenetic analyses, without an emphasis on practical diagnosis of the newly recognised families. These problems, combined with the historical difficulty of adequately illustrating published identification keys, have led to a widespread misconception that flies are difficult to identify to the familial level. The current key is intended to be as easy to use as possible and thus includes extensive illustrations and emphasises relatively simple external characters. Specialised terminology is kept to a minimum and characters are generally illustrated and defined in the couplets.

An earlier draft of the below identification key was distributed to all family chapter authors for the *Manual of Afrotropical Diptera* for input and correction, and as a result, represents a collaborative product of the entire *Manual* team. It also draws on the many previously published Diptera family identification keys, including the only previously published key to all families of Afrotropical Diptera (Barraclough & Londt 1985) and the more recent key to families of Afrotropical acalyptrate flies (Barraclough 1995). More influential, however, were the recent identification keys to other regional fly faunas, such as Central America (Buck *et al*. 2009) and Europe (Oosterbroek 2006). The simplified identification key to world fly families published in Marshall (2012) was used as a starting point to develop the current key.

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 1. Introductory chapters and keys to Diptera families. *Suricata* 4. South African National Biodiversity Institute, Pretoria; pp. 267–355.

1. Wings present, normally developed, longer than thorax.

2

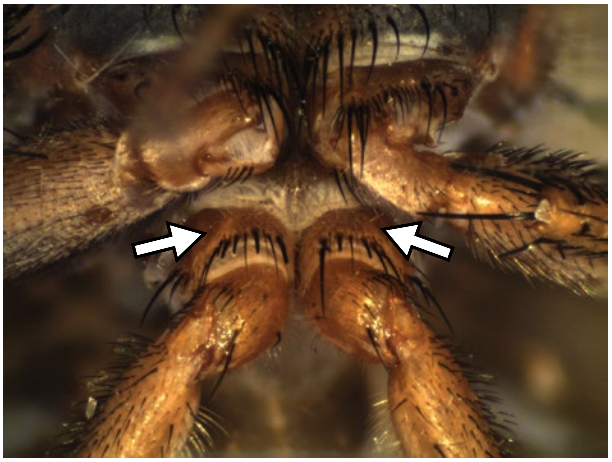


1′. Wings absent (apterous taxa) or vestigial (brachypterous, stenopterous or micropterous taxa) (arrowed), shorter than thorax or elongate with all venation close to costal vein.

143

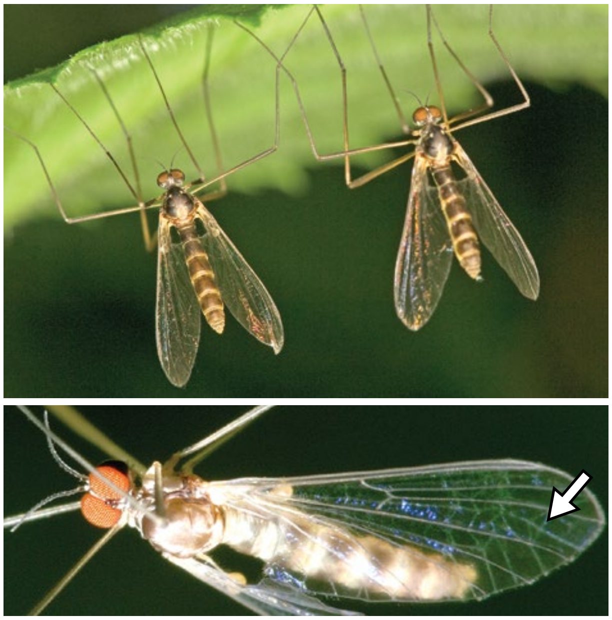
2 (1). Strikingly modified parasites of birds or mammals, usually strongly flattened. Hind coxae (arrowed) widely separated; tarsal claws large, curved. Antenna short, inconspicuous.

Hippoboscidae [in part, incl. Nycteribiinae & strebline grade] (Chapter 109)



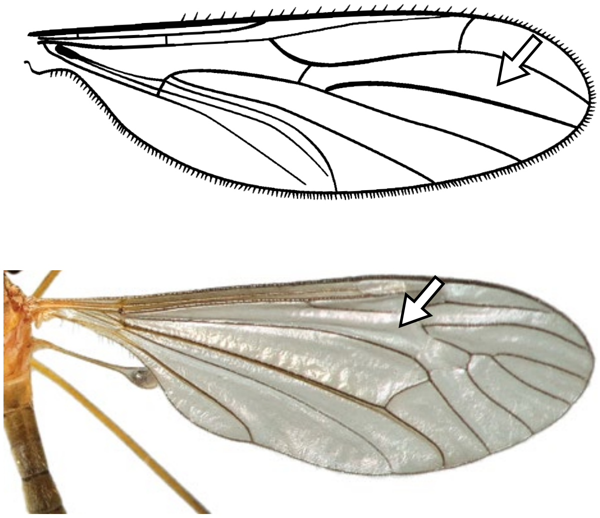
2′ (1). Not strikingly modified parasites of birds or mammals, if flattened then not found on vertebrate hosts (but sometimes in their nests). Hind coxae (arrowed) contiguous or virtually so; tarsal claws variable. Antenna long, usually distinct.

3



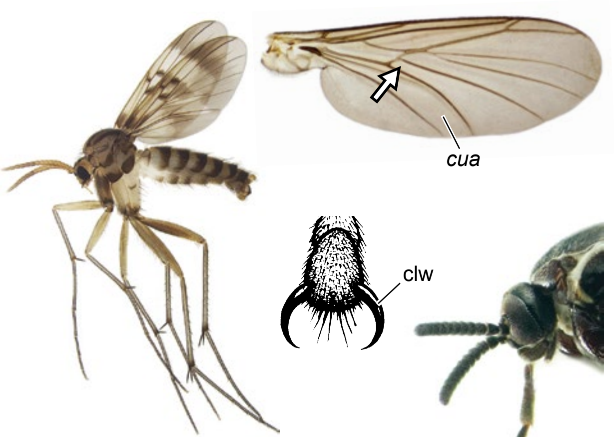
3 (2′). Wing membrane (arrowed) with net-like pattern of folds between true veins. Occurring near fast-flowing water.

Blephariceridae (Chapter 16)



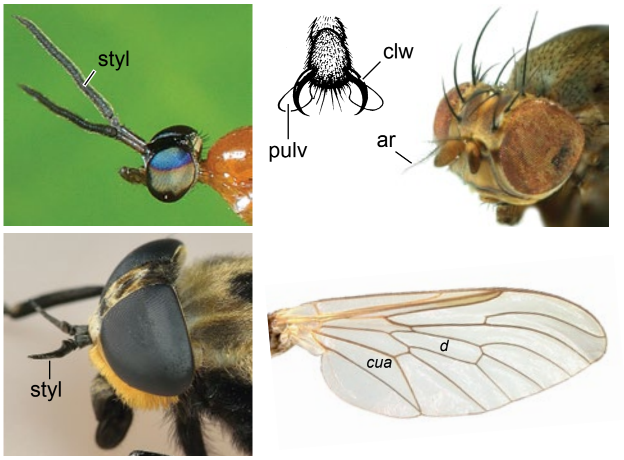
3′ (2′). Wing membrane (arrowed) without net-like pattern of folds between true veins, but sometimes with corrugations. Occurring in various habitats.

4



4 (3′). Antenna with 6 or more (usually many more) distinct "segments" (at least 4 flagellomeres, plus basal scape and pedicel); flagellomeres similar, but clearly separate from one another. Wing usually without closed discal cell (arrowed), but if discal cell present, then legs without distinct pair of pulvilli beneath tarsal claws (clw). Cell *cua* invariably open. Often delicate, long-legged flies (most lower Diptera; nematocerous flies, the traditional suborder NEMATOCERA; in part, most).

5



4′ (3′). Antenna with 8 flagellomeres at most; postpedicel often with hair-like arista (ar) or tapered stylus (styl), sometimes thin and annulated. Wing usually with closed discal cell (*d*), if this cell absent, then legs with distinct pulvilli (pulv) beneath tarsal claws (clw) OR arista (ar) with long dorsal branches. Cell *cua* almost always closed, often reduced, at base of wing. Relatively robust flies (most higher Diptera (suborder BRACHYCERA)).

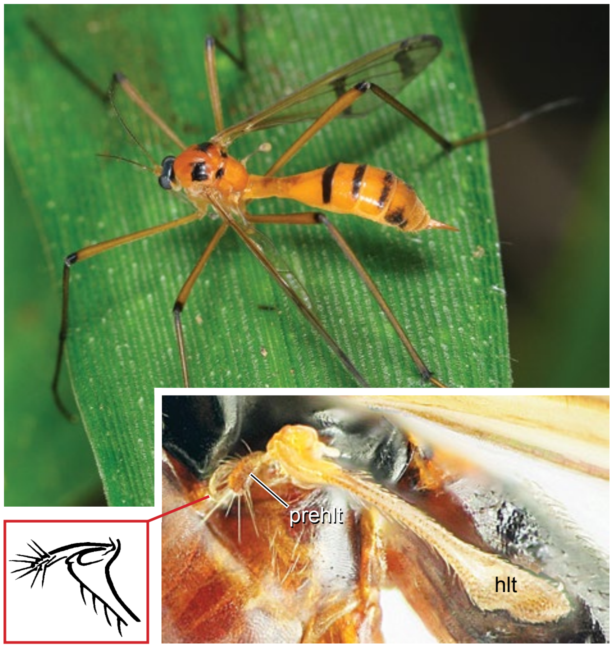
29

5 (4). Ocelli absent.

6

5′ (4). Ocelli present (arrowed).

18

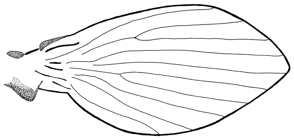


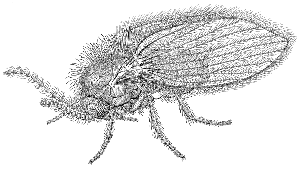
6 (5). Thorax with distinct lobe (prehalter; prehlt) at base of true halter (hlt).

Ptychopteridae (Chapter 27)

6′ (5). Thorax without distinct lobe (prehalter) at base of true halter (arrowed).

7

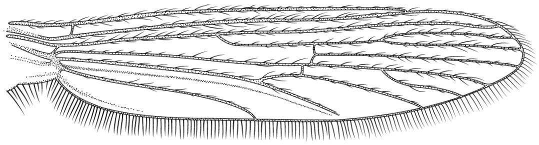


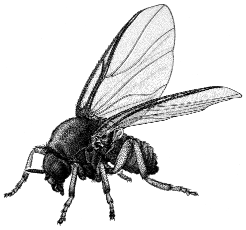


7 (6′). Small, setulose (hairy), moth-like flies. Wing often broad and pointed, with numerous parallel veins unconnected by crossveins, except in basal part of wing. Antennal pedicel (second antennal segment) not conspicuously larger than scape (first antennal segment).

Psychodidae (Chapter 24)

SYCORACINAE are uncommon, relatively bare moth flies with atypical wing shape and venation, as illustrated below. PHLEBOTOMINAE may also be challenging to key because of their minute size, often under 2 mm.





7′ (6′). Size variable, not densely hairy and moth-like. Wing rarely broad and pointed, often with crossveins in distal ½, veins not parallel; if partly clothed in scales or long setulae, then antennal pedicel conspicuously enlarged and often cup-like.

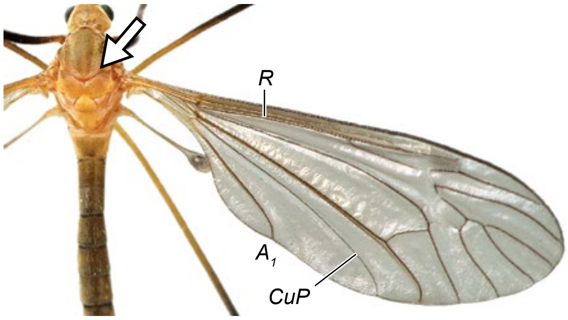
8

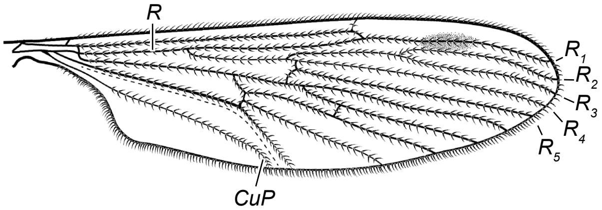
Wing length: 2 mm

PSYCHODIDAE
subfamily Sycoracinae

Wing length: 1.5 mm

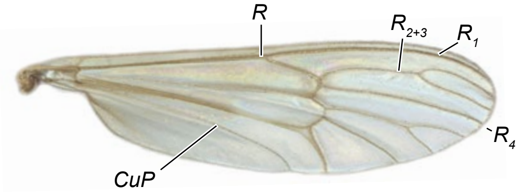
PSYCHODIDAE
subfamily Phlebotominae





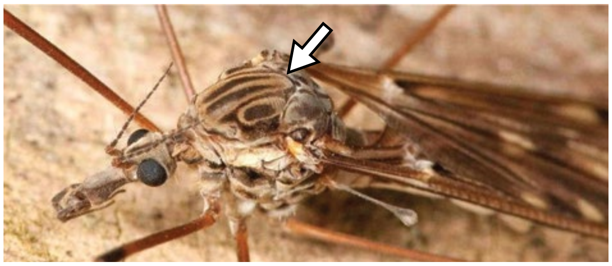
8 (7′). Long-legged flies. Wing veins *CuP* and A_1 reaching wing margin (two complete veins in anal region of wing) (Limoniidae and Tipulidae, common) or A_1 absent and radial vein (*R*) with 5 branches reaching wing margin (Tanyderidae, very rare). Scutum almost always with dorsal V-shaped transverse suture (arrowed).

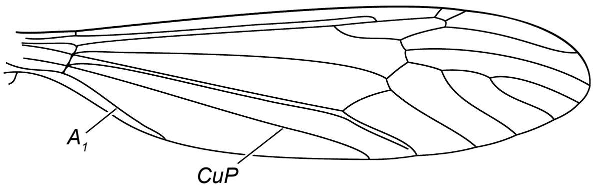
9



8′ (7′). Appearance variable, but usually not conspicuously long-legged. Wing vein *CuP* usually reaching wing margin, vein A_1 usually absent or not reaching wing margin (one complete vein in anal region of wing); radial vein (*R*) with fewer than 5 branches. Scutum never with distinct V-shaped transverse suture.

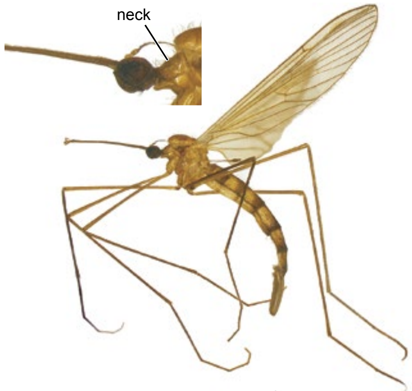
10

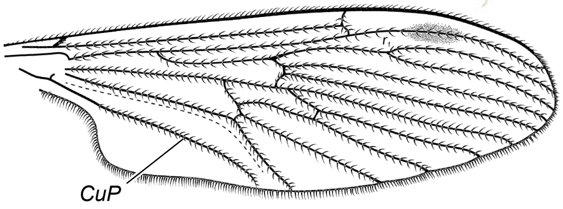




9 (8). Scutum with distinct V-shaped transverse suture (arrowed); neck not elongate. Wing veins *CuP* and A_1 reaching wing margin. Common, widespread and diverse.

Limoniidae and Tipulidae [in part; most] (Chapter 14)

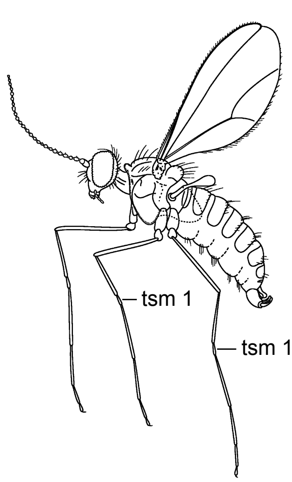


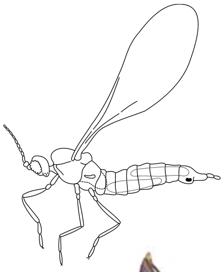


9′ (8). Scutum with incomplete V-shaped transverse suture; neck elongate. Wing vein *CuP* reaching wing margin and vein A_1 absent. Rare.

Tanyderidae (Chapter 15)

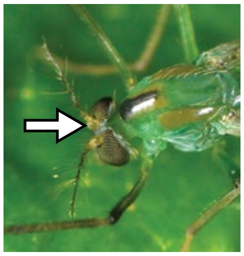
Peringueyomyina barnardi Alexander: only Afrotropical species of Tanyderidae.





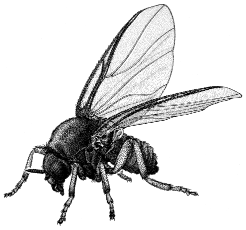
10 (8′). Tarsus with 5 tarsomeres, tarsomere 1 (tsm 1) shorter than tarsomere 2, or tarsus with 4 tarsomeres at most. Fore and hind tibiae without apical spurs. Wing usually with 3 or 4 (at most 5) veins reaching wing margin. Size usually only 1–3 mm and delicate-bodied. Antenna usually very long; pedicel not enlarged. Mostly with terrestrial immature stages.

Cecidomyiidae [in part] (Chapter 22)



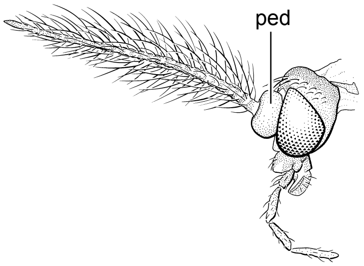
10′ (8′). Tarsomere 1 (tsm 1) at least as long as tarsomere 2 or, if shorter (some *Forcipomyia* Meigen in Ceratopogonidae), then fore and hind tibiae each with apical spur. Wing with at least 6 veins reaching wing margin. Size variable; if delicate-bodied, then antennal pedicel (arrowed) conspicuously enlarged, often cup-like, especially in males. Mostly with aquatic or semi-aquatic immature stages (CULICOMORPHA).

11



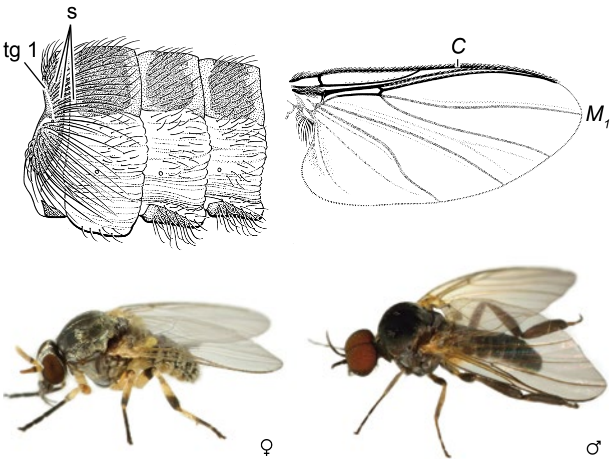
11 (10′). Stout-bodied flies. Antenna short, not or only marginally longer than head (some Chironomidae with antennae the same length as head have fewer flagellomeres (4–7 rather than 9 or 10)), usually conspicuously thickened; pedicel not enlarged and cup-shaped. Abdominal tergite 1 with or without fringe of elongate setae laterally. Wing usually conspicuously broad.

12



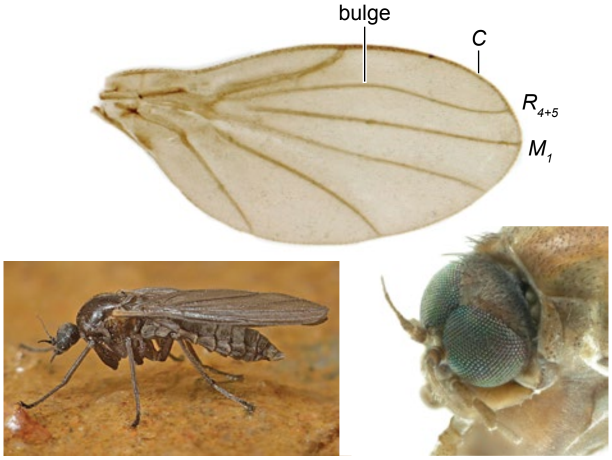
11′ (10′). Relatively slender-bodied flies. Antenna short to longer than head; antennal pedicel (ped) cup-shaped or not enlarged. Abdominal tergite 1 without lateral fringe, at most with short lateral setae or virtually bare. Wing variable, usually elongate.

13



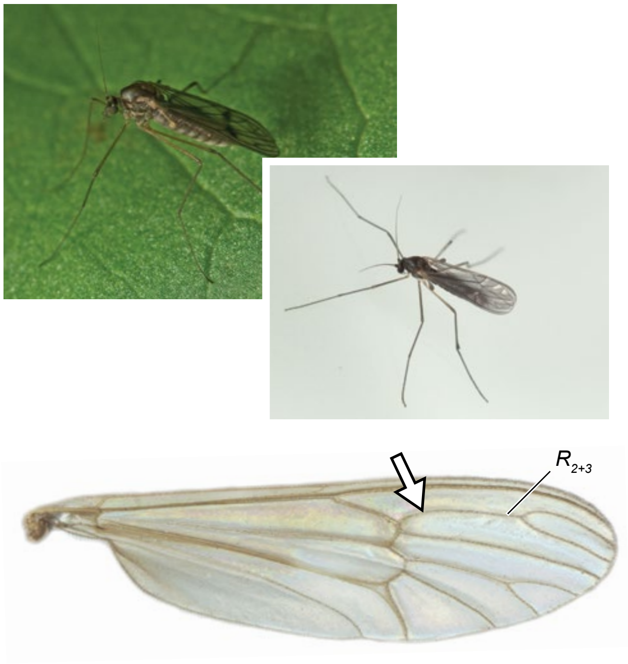
12 (11). Abdominal tergite 1 (tg 1) with fringe of elongate setae (s) laterally. Wing conspicuously broad basally. Vein R_{4+5} absent, costal vein (C) restricted to anterior margin. Antenna evenly thick from base to distal articles or almost uniform in width from base to apex. Compound eyes of female separate; contiguous in males. Commonly collected biting flies, usually associated with running water.

Simuliidae (Chapter 32)



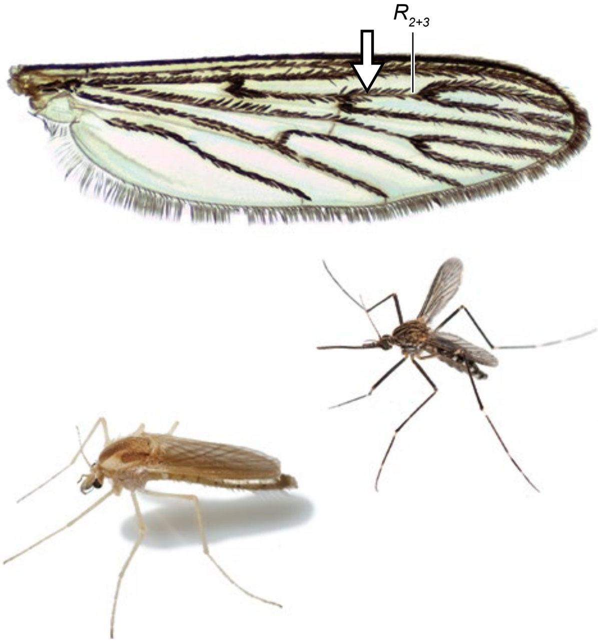
12′ (11). Abdominal tergite 1 without fringe of elongate setae laterally. Wing not conspicuously broad basally. Vein R_{4+5} present, with distinct anterior bulge, costal vein (C) continuing around wing, although weaker along posterior margin. Antenna thick at base, but tapered and slender distally. Compound eyes contiguous in both sexes. Rarely collected non-biting flies, associated specifically with seepages and splash zones.

Thaumaleidae (Chapter 33)



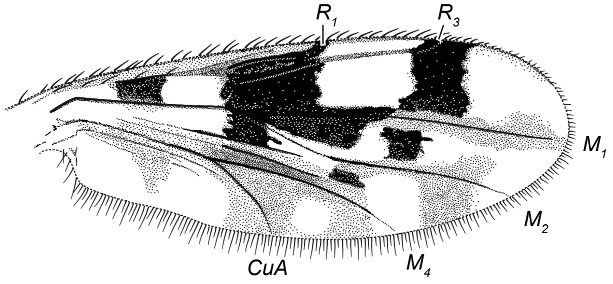
13 (11′). Wing vein R_{2+3} arched towards anterior margin (arrowed), forked.

Dixidae (Chapter 28)



13′ (11′). Wing vein R_{2+3} straight or virtually so (arrowed), not arched; simple or forked.

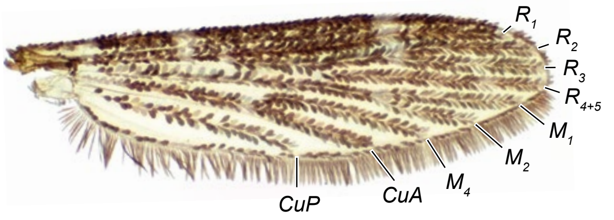
14

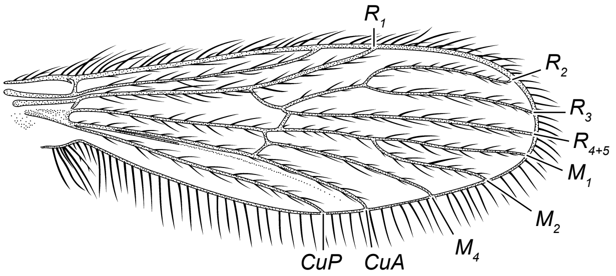


14 (13′). Wing with 8 or fewer longitudinal veins reaching margin. Hind margin of wing with simple setulae.

15

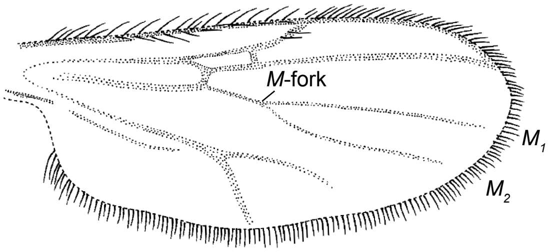
Some uncommon Mycetophilidae that lack ocelli (*e.g.*, *Syndocosia* Speiser) key at this point, but have long coxae and tibial spurs, typical of fungus gnats (see couplet 28).

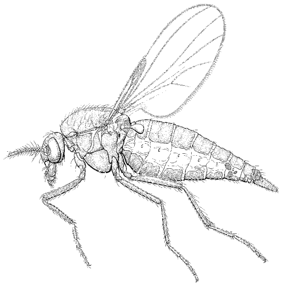




14′ (13′). Wing with 9 or more longitudinal veins reaching wing margin. Hind margin of wing with scales or flattened hairs.

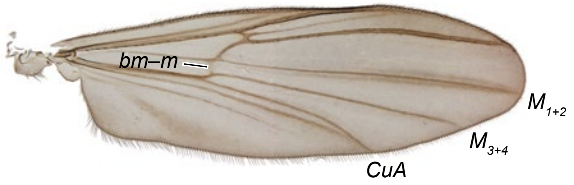
16





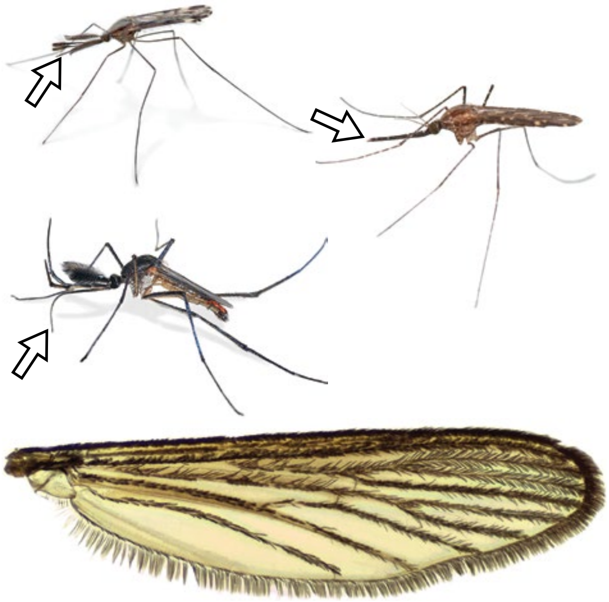
15 (14). Wing vein M_{1+2} usually forked (= *M*-fork), but *M*-fork often indistinct; basal medial crossvein absent. Subscutellum without longitudinal groove.

Ceratopogonidae (Chapter 34)



15′ (14). Wing vein M_{1+2} simple. Subscutellum (sbsctl) usually with distinct groove; if absent (in small subfamily PODONOMINAE), then wing with basal medial crossvein (*bm–m*).

Chironomidae [in part; most] (Chapter 35)

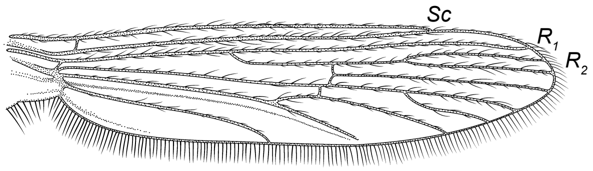


16 (14′). Proboscis (arrowed) elongate; palpus with scales. Body, legs, wing margin and wing veins often with scales.

Culicidae (Chapter 31)

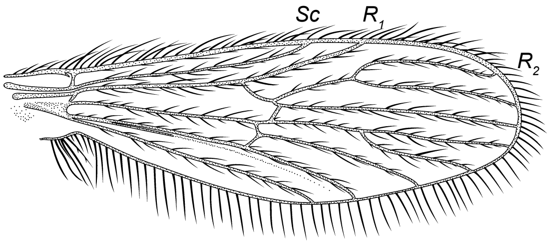
16′ (14′). Proboscis short, proboscis and palpus without scales. Distinct scales restricted to hind margin of wing, although body and wing densely setulose and setae on wing veins often somewhat flattened.

17



17 (16′). Wing vein R_1 elongate, ending closer to vein R_2 than to subcostal vein (*Sc*). Femora all of equal diameter. Usually larger flies (wing length: 2–5 mm).

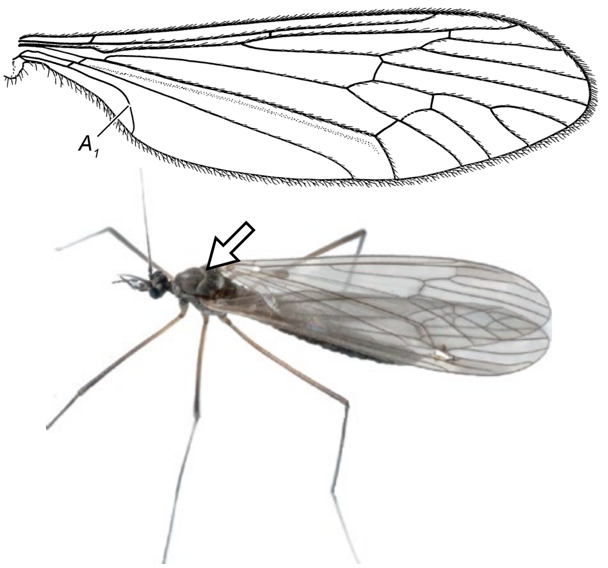
Chaoboridae (Chapter 30)



17′ (16′). Wing vein R_1 short, ending closer to subcostal vein (*Sc*) than to vein R_2. Mid femur notably thicker than fore- or hind femur. Small to minute flies (wing length: 1–2 mm).

Corethrellidae (Chapter 29)

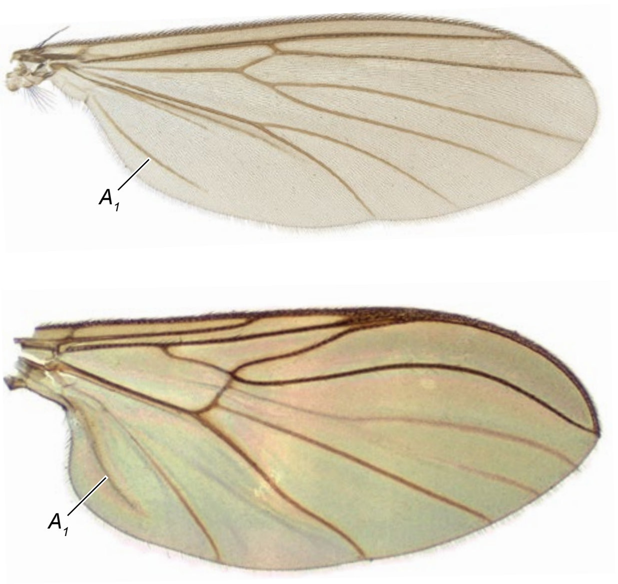
Frog flies; rarely collected.



18 (5′). Scutum with complete V-shaped transverse suture (arrowed). Wing with anal vein (A_1) complete (reaching wing margin).

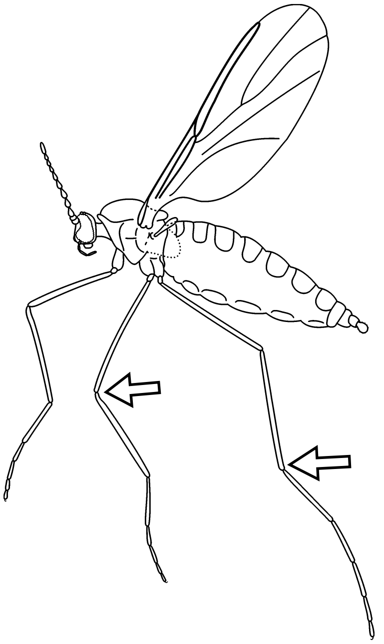
[Trichoceridae]

Questionably recorded from Ethiopia and Nigeria.



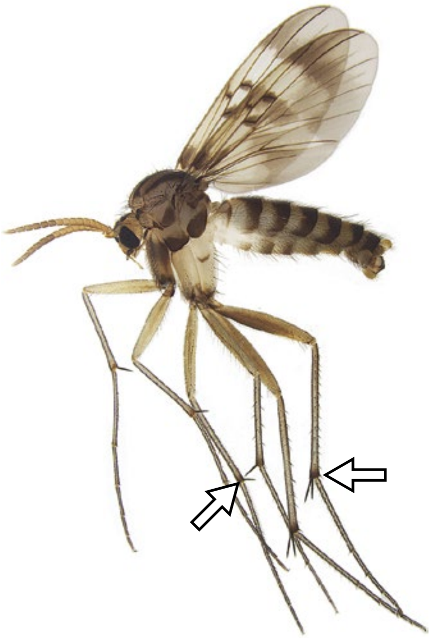
18′ (5′). Scutum without complete V-shaped transverse suture. Wing vein A_1 incomplete (not reaching wing margin) or absent.

19



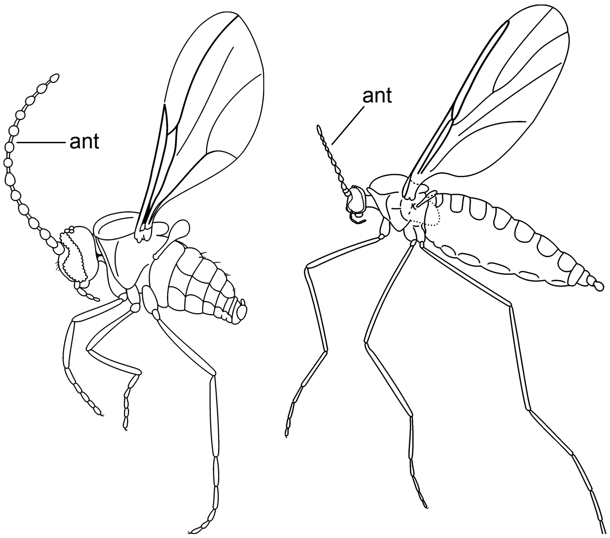
19 (18′). Mid and hind tibiae without conspicuous apical setae or spurs (arrowed).

20



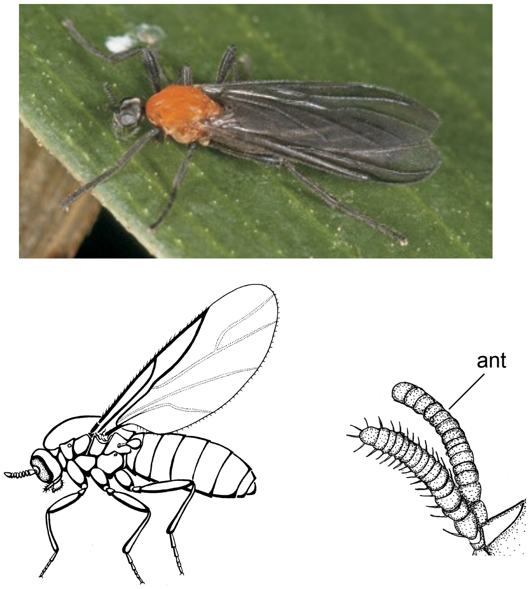
19′ (18′). Mid and hind tibiae with conspicuous apical setae or spurs (arrowed).

22



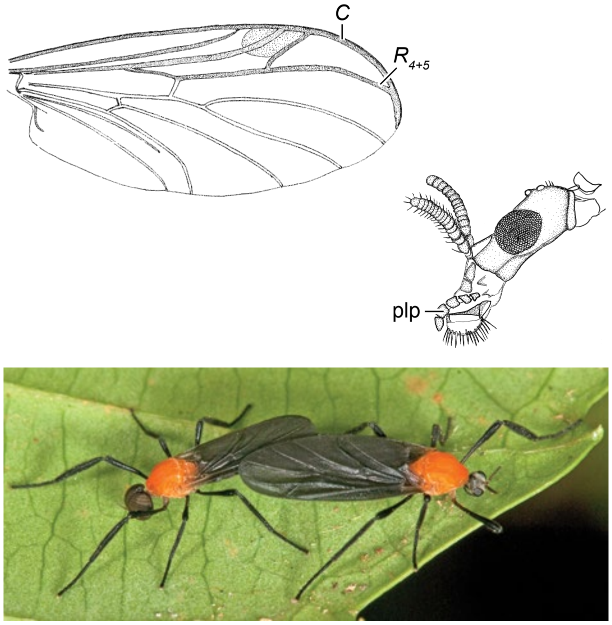
20 (19). Antennal flagellomeres (ant) spherical to elongate, usually resembling beads on a string. Wing venation reduced (at most 6 veins reaching wing margin). Tiny fragile flies, usually with conspicuously long antennae.

Cecidomyiidae [in part] (Chapter 22)



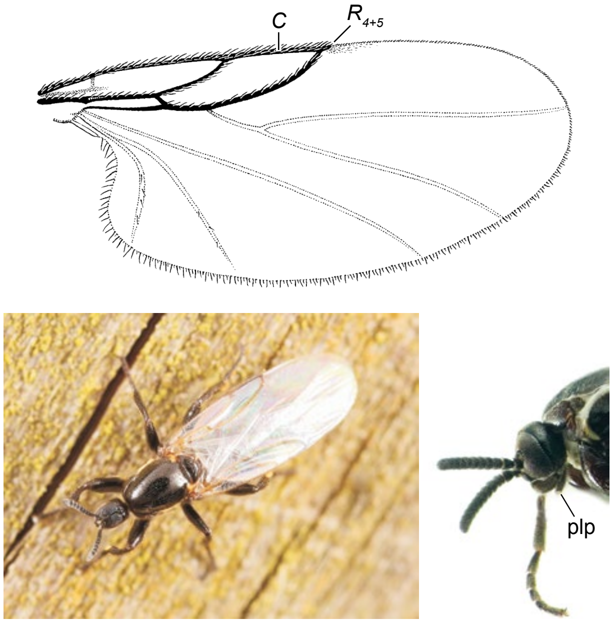
20′ (19). Antennal flagellomeres (ant) compact, not spherical. Wing with 6 or more veins reaching margin. Relatively robust flies with relatively short antenna.

21



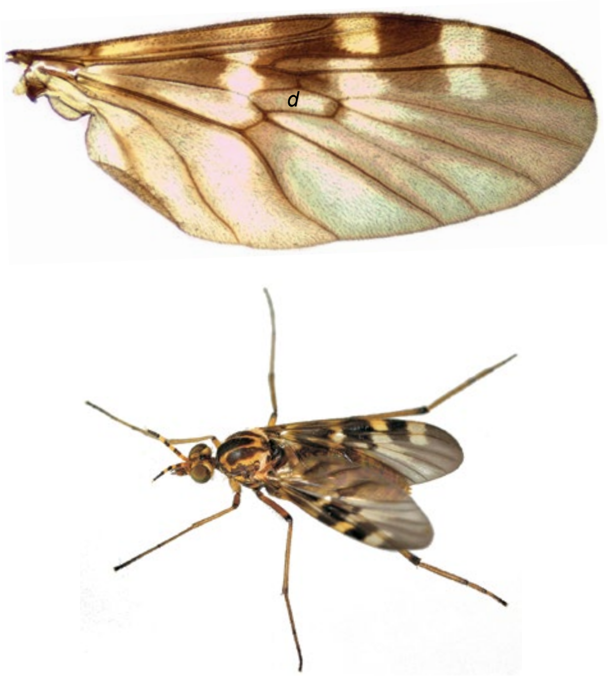
21′ (20′). Palpus (plp) with more than one segment. Costal vein (C) and vein R_{4+5} ending close to wing tip, C often extending beyond apex of vein R_{4+5}.

Bibionidae [in part] (Chapter 17)



21 (20′). Palpus (plp) with one segment. Costal vein (C) ending well before wing tip, terminating near end of vein R_{4+5}.

Scatopsidae (Chapter 26)

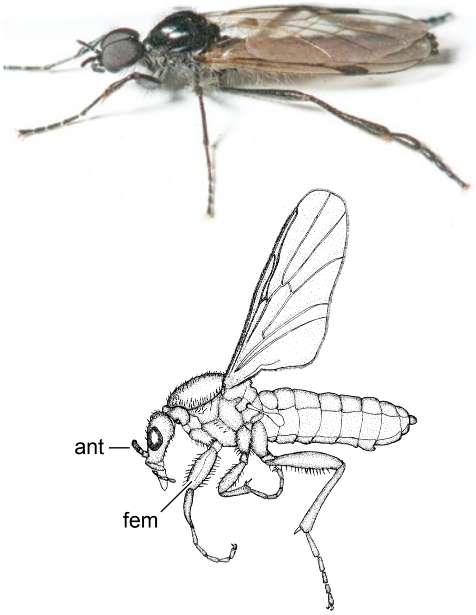


22 (19′). Wing with closed discal cell (*d*) in central part.

Anisopodidae [in part] (Chapter 25)

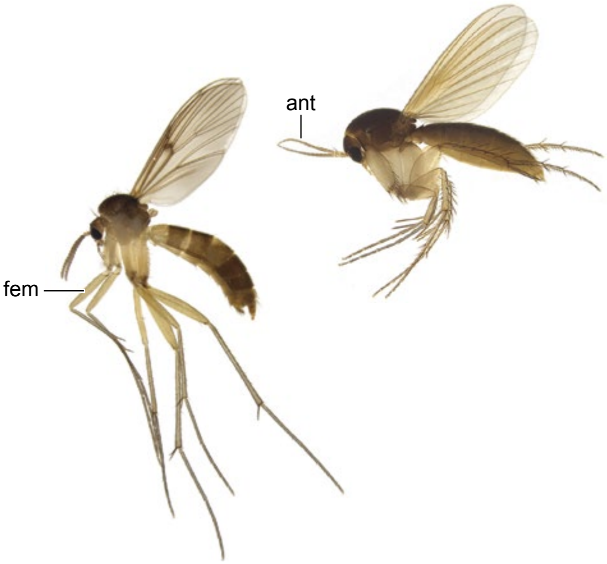
22′ (19′). Wing without closed discal cell in central part (although a small closed radial cell may be present).

23



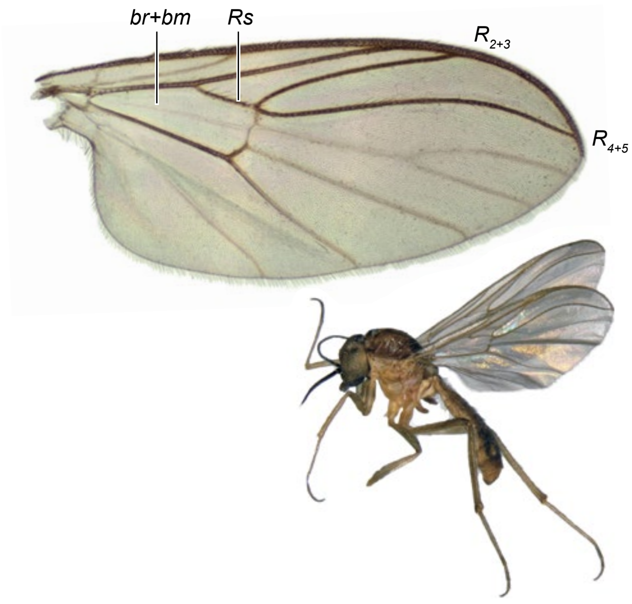
23 (22′). Antenna (ant) short, comprising 4–12 short, compact flagellomeres inserted low on head. Fore femur (fem) markedly broad and robust.

Bibionidae [in part] (Chapter 17)



23′ (22′). Antenna (ant) usually long, with 14 flagellomeres (fewer in *Metanepsia* Edwards and some *Exechia* Winnertz (Mycetophilidae)), inserted at or above middle of head (except in some Sciaridae). Fore femur (fem) usually slender and less robust.

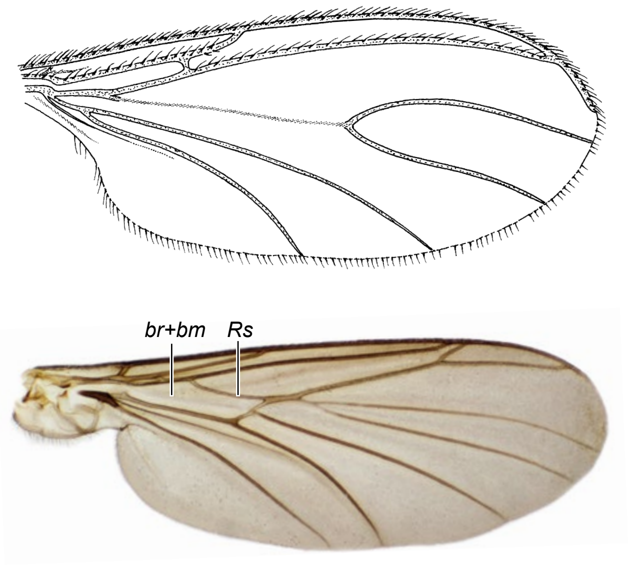
24



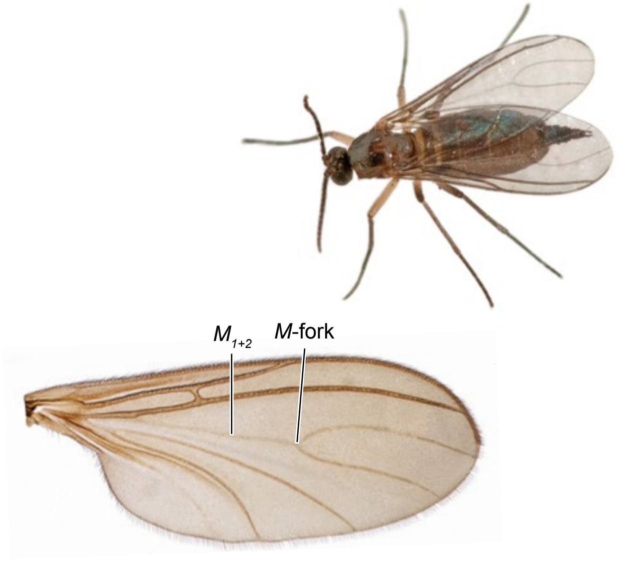
24 (23′). Wing with large basal cell (*br+bm*) from which 6 veins arise; radial sector (*Rs*) forked into veins R_{2+3} and R_{4+5} at corner of basal cell.

Anisopodidae [in part] (Chapter 25)

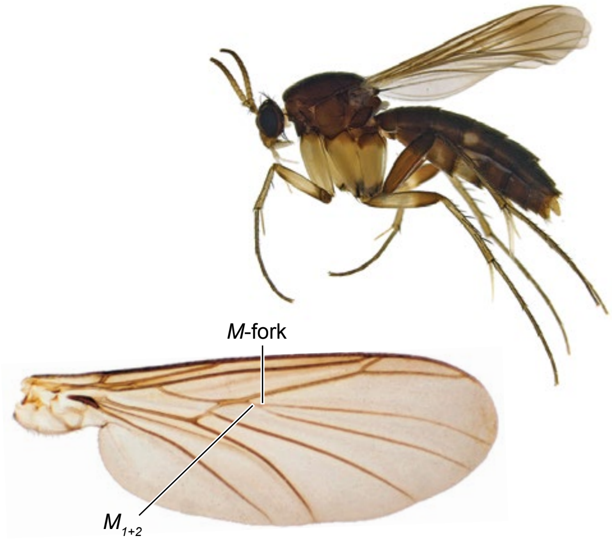
MYCETOBIINAE, sometimes treated as family Mycetobiidae.



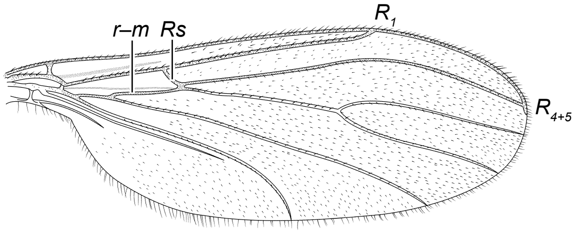
24′ (23′). Wing with or without basal cell (*br+bm*), if present, then radial sector (*Rs*) EITHER unforked OR forked far beyond corner of basal cell, thus with at most 5 veins arising from basal cell (superfamily SCIAROIDEA, other than Cecidomyiidae). 25



25 (24′). Median wing vein (M_{1+2}) forked, stem of fork long (usually at least as long as *M*-fork). Thorax and abdomen broadly joined. Usually small, dark-bodied and uniformly pigmented (Sciaridae [in part] and superfamily Sciaroidea unassigned to family). 26

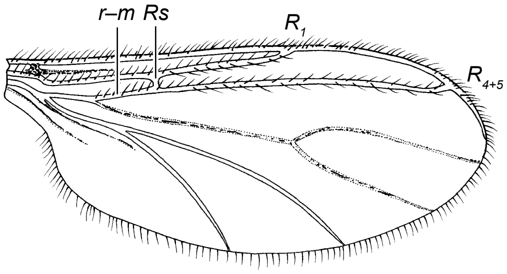


25′ (24′). Median wing vein (M_{1+2}) usually forked, stem of *M*-fork short (usually much shorter than fork). Thorax and abdomen narrowly joined. Size and colour variable, habitus characteristic (Mycetophilidae *sensu lato*). 27



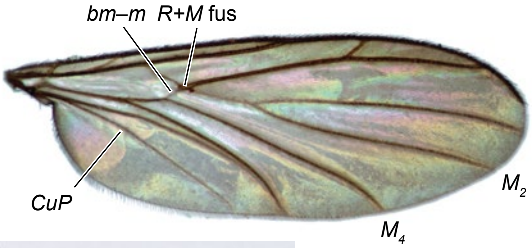
26 (25). Head without dorsal eye bridge (eyes separated dorsally). Wing with radial sector (*Rs*) EITHER long and oblique to *r–m*+ R_{4+5} OR as short as in Sciaridae, but then *r–m* not in line with R_{4+5}.

***Heterotricha*-group** (Sciaroidea unassigned to family) (Chapter 23)



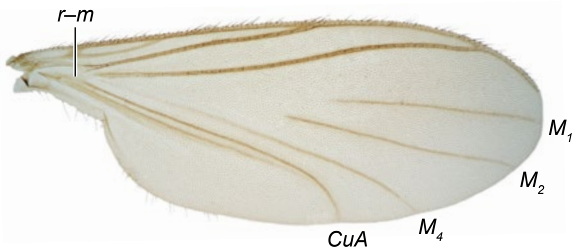
26′ (25). Head almost invariably with complete dorsal eye bridge (eyes contiguous above head; arrowed). Wing with radial sector (*Rs*) conspicuously short and perpendicular to *r–m*+R_{4+5}, that are in line with each other (*Pnyxia* Johannsen the exception, in lacking dorsal eye bridge and in possession of long, oblique *Rs*).

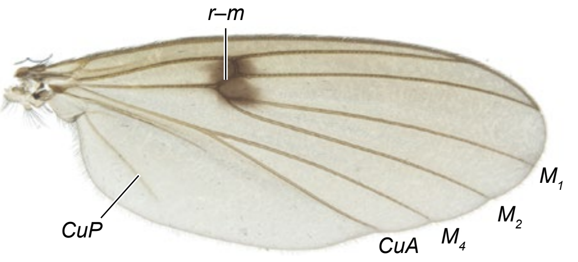
Sciaridae [in part; most] (Chapter 21)



27 (25′). Wing veins M_2 and M_4 connected by subvertical *bm–m* crossvein; crossvein *r–m* almost invariably replaced by a *R+M* fusion (*R+M* fus) (except in *Asynaphleba* Matile); vein *CuP* sometimes traceable to wing margin. Antenna usually EITHER relatively short (most KEROPLATINAE) and sometimes flattened (tribe KEROPLATINI) OR strikingly long and thin (most MACROCERINAE).

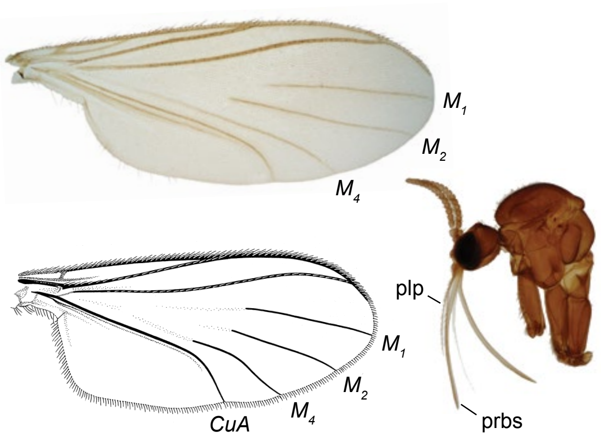
Keroplatidae (Chapter 18)





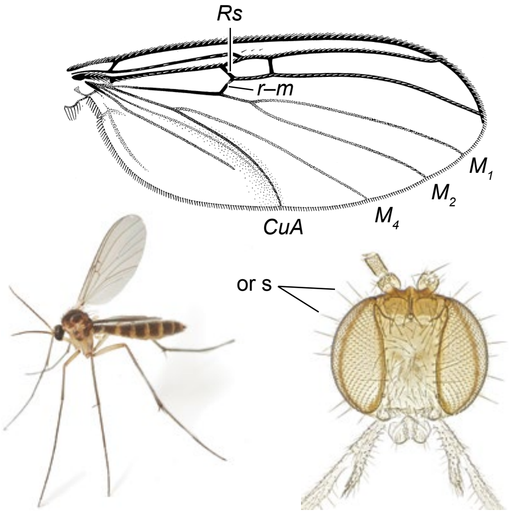
27′ (25′). Wing veins M_2 and M_4 not directly connected by crossvein; crossvein *r–m* present and never replaced by fusion; vein *CuP* not reaching wing margin. Antennae various, rarely short and flattened or strikingly long.

28



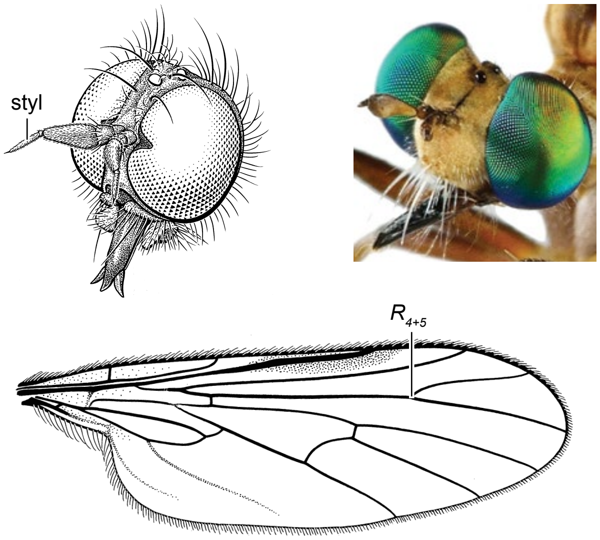
28 (27′). Bases of wing veins M_1 and M_2 erased, their distal parts reaching wing margin as unconnected veinlets. Radial sector (*Rs*) and crossveins (*r–m* and *bm–m*) entirely reduced or barely traceable at very base of wing. Vein M_4 EITHER erased basally, OR adjoining vein *CuA*. Occiput without row of projecting orbital setae. Proboscis (prbs) and palpus (plp) usually conspicuously long.

Lygistorrhinidae (Chapter 19)



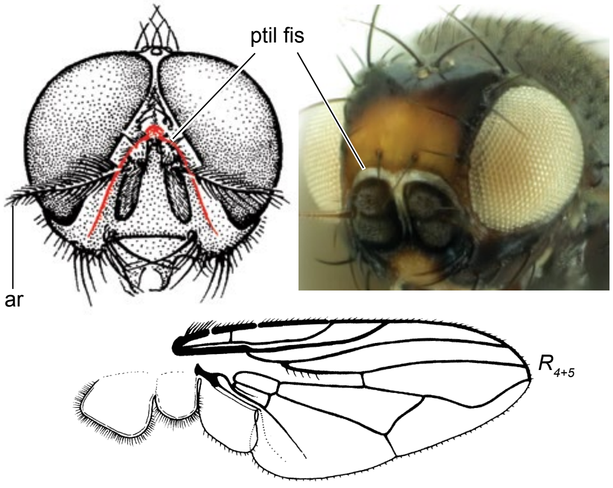
28′ (27′). Bases of wing veins M_1 and M_2 fully developed, or only vein M_1 present (in addition to *CuA*). If bases of veins M_1 and M_2 erased, then occiput with row of projecting orbital setae (or s). Radial sector (*Rs*) and crossvein *r–m* usually present and well developed. Proboscis and palpus reduced, of normal length or sometimes long.

Mycetophilidae *sensu stricto* **(**Chapter 20)



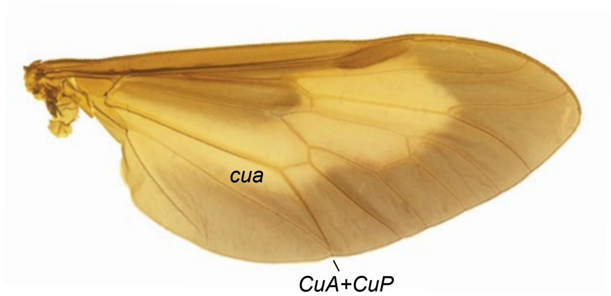
29 (4′). Ptilinal fissure absent (exceptionally with oblique fissure in *Ptilobactrum* Bezzi (Syrphidae), but then antennal flagellomere 1 almost as long, or longer than height of head). Wing vein R_{4+5} often (but not always) forked. Antennal postpedicel usually with tapered stylus (styl).

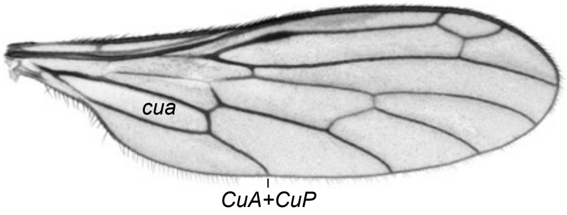
30

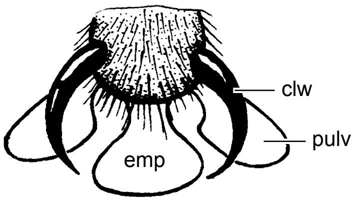


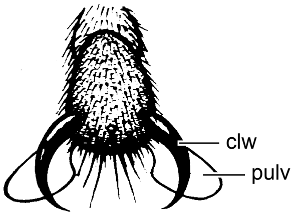
29′ (4′). Ptilinal fissure (ptil fis) present (sometimes weak in Conopidae and vestigial in *Sepedon* Latreille – a distinctive genus of Sciomyzidae – and may be obscured beneath anterior margin in species with large ocellar triangle). Wing vein R_{4+5} unforked. Antenna usually with hair-like or feather-like arista (ar) (lost in a few uncommon acalyptrates, stylus-like in some Conopidae) (SCHIZOPHORA).

58









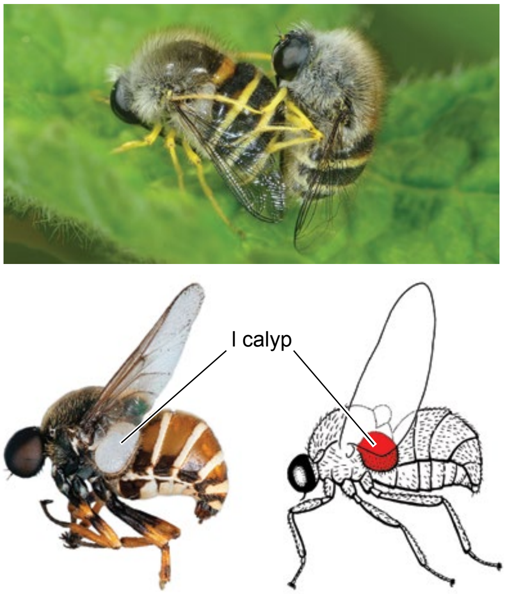
30 (29). Terminal tarsomere with 3 pads, comprising 2 pulvilli (pulv) beneath claws (clw) and pillow-like empodium (emp) medially. Wing with anterior cubital cell (*cua*) open or closed, if closed then cell invariably distinctly longer than vein *CuA+CuP* (TABANOMORPHA, plus Acroceridae and Nemestrinidae).

31

30′ (29). Terminal tarsomere with 2 pulvilli (pulv) beneath claws (clw) and usually bristle-like empodium. Wing with anterior cubital cell (*cua*) variable, but for taxa with empodium slightly broadened, cell *cua* very short, distinctly shorter than vein *CuA+CuP* (ASILOMORPHA, EMPIDOIDEA and ASCHIZA).

41

Empodium slightly broadened in a few water-skating Empidoidea, but these have the anterior cubital cell (*cua*) short, not pointed.

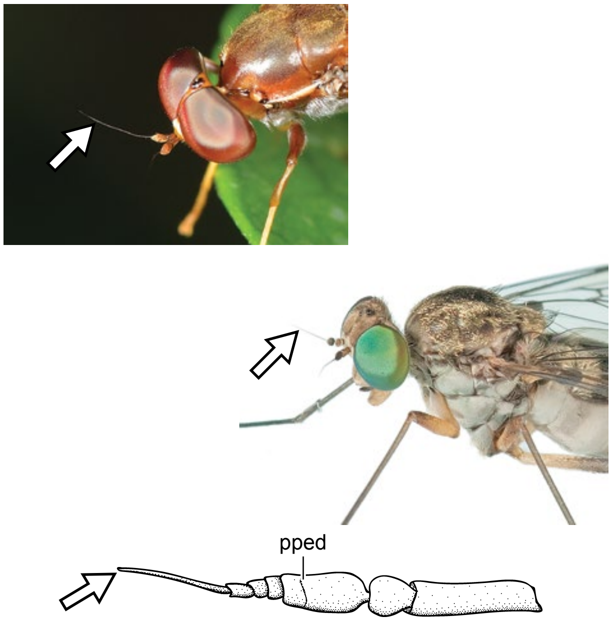


31 (30). Lower calypter (l calyp) very large. Both sexes with compound eyes meeting on top of head. Thorax often strikingly humpbacked and head often small to very small in proportion to thorax.

Acroceridae (Chapter 42)

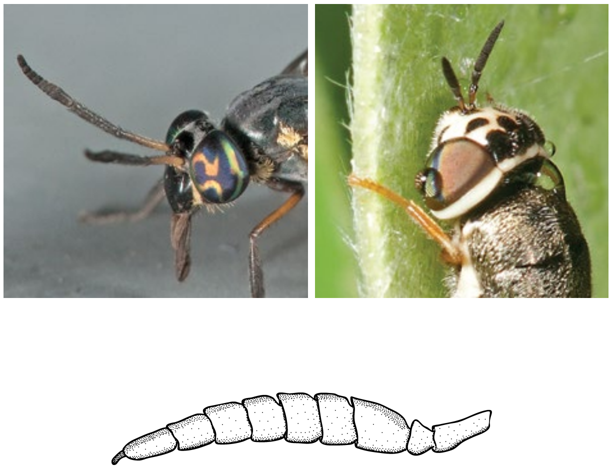
31′ (30). Lower calypter not enlarged. Compound eyes of female distinctly separate on top of head. Thorax usually not strikingly humpbacked and head usually at least $\frac{1}{2}$ as wide as thorax.

32



32 (31′). Antenna ending in long, thin arista-like stylus (arrowed), much thinner than postpedicel (pped) (= first flagellomere or third antennal segment).

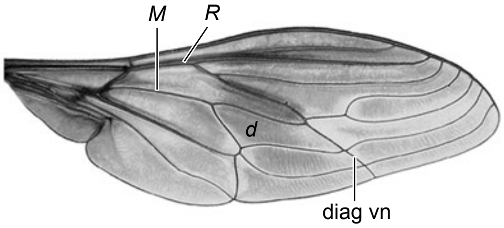
33



32′ (31′). Antenna not ending in long, thin arista-like stylus; distal flagellomeres of various forms, but never strikingly slender, hair-like or arista-like.

37

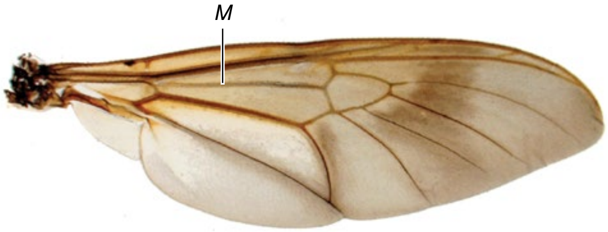
Ambiguous cases key both ways.

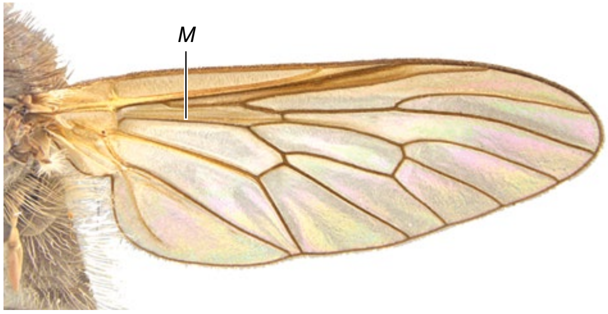


33 (32). Wing veins appearing "tangled", branches of medial vein (*M*) curved forward and convergent with radial vein branches (*R*) before apex (apical section of M_2 diverges away from M_1 to end beyond apex of wing in *Atriadops* Wandolleck); with composite diagonal vein (diag vn) straight from discal cell (*d*) to outer wing margin.

Nemestrinidae (Chapter 43)

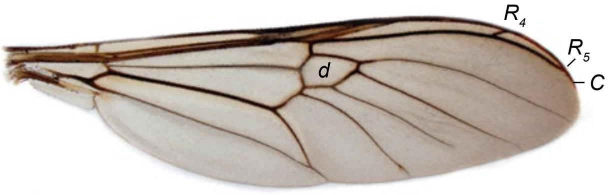
Often superficially similar to Bombyliidae, which have seta-like empodium.





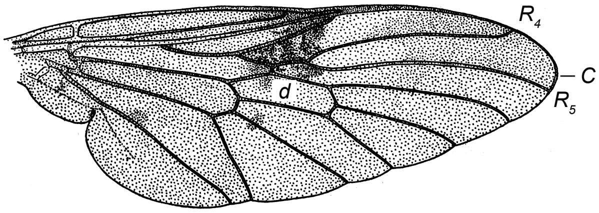
33′ (32). Wing veins not appearing "tangled", branches of medial vein (*M*) not curved forward, ending in wing margin beyond wing apex; without diagonal vein.

34



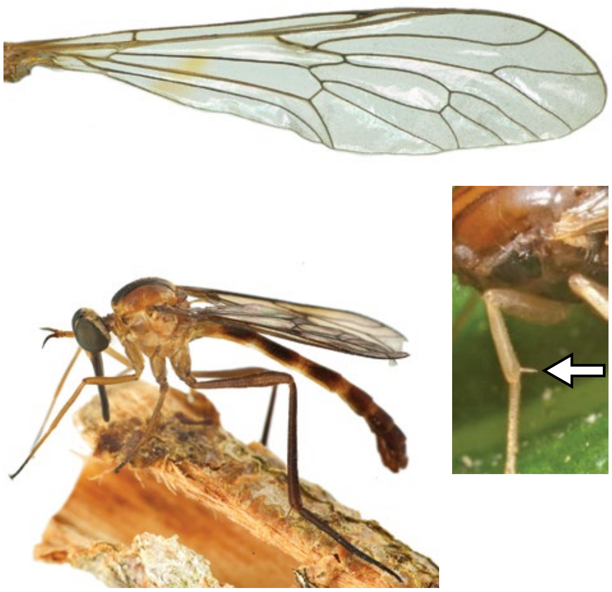
34 (33′). Radial wing veins grouped together, ending before wing tip; costal vein (*C*) also usually ending well before wing apex; discal cell (*d*) short, usually forming distinct short, often squarish cell in middle of wing.

Stratiomyidae [in part] (Chapter 41)



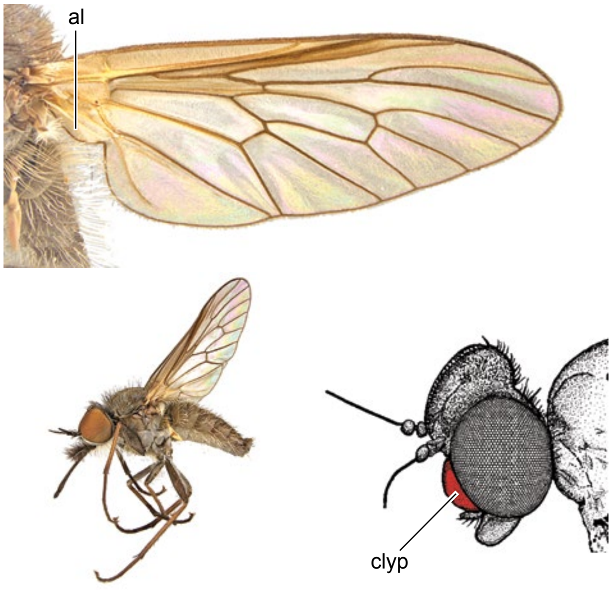
34′ (33′). Radial wing veins not grouped together before wing tip; costal vein (*C*) ending at or beyond wing tip; discal cell (*d*) much longer than wide.

35



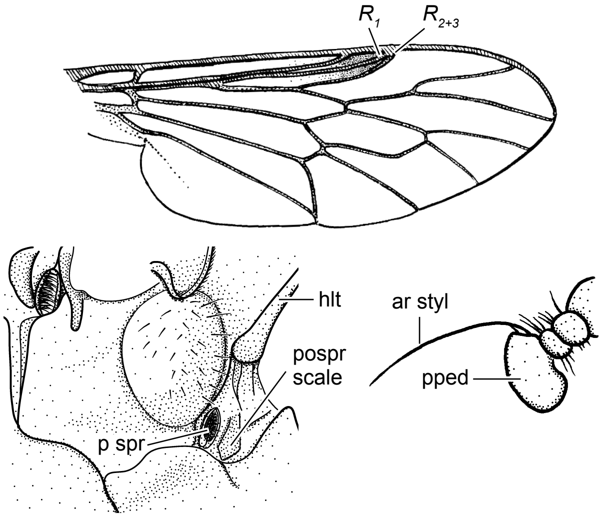
35 (34′). Wing base narrow; alula extremely reduced and narrow to absent. Fore tibia usually with apical spur (arrowed) (spur may be small and inconspicuous, rarely absent). Head with clypeus flat.

Vermileonidae [in part] (Chapter 36)



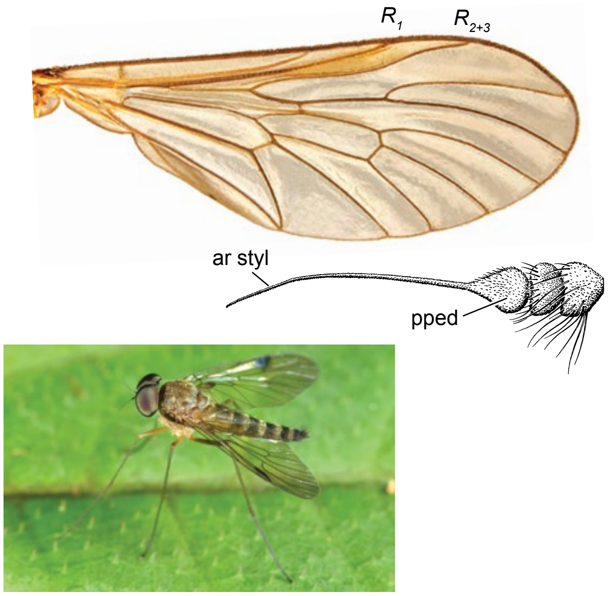
35′ (34′). Wing base not conspicuously narrowed; alula (al) present. Fore tibia usually without apical spur (spur present in some Athericidae). Head with clypeus (clyp) convex, bulbous.

36



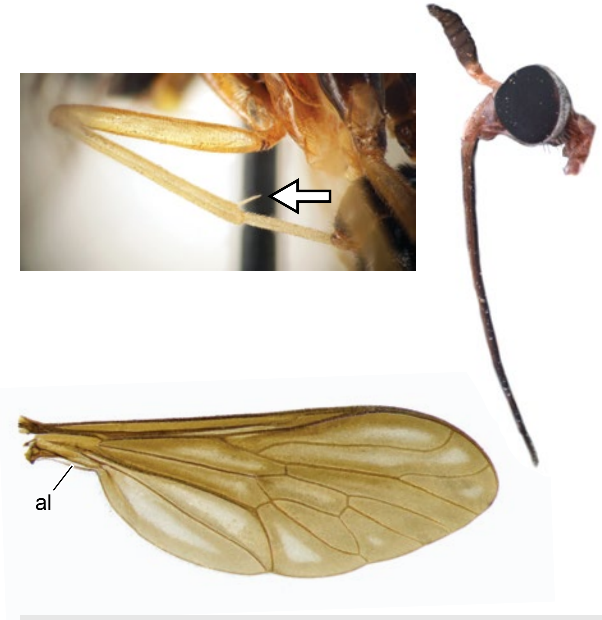
36 (35′). Thorax with postspiracular scale (pospr scale; lobe behind posterior spiracle (p spr), just below halter (hlt)); also found in Tabanidae). Antennal postpedicel (pped) ovoid to (usually) reniform (kidney-shaped), or virtually so; arista-like stylus (ar styl) inserted dorsally. Wing veins R_1 and R_{2+3} closely approximated or touching at apex.

Athericidae (Chapter 38)



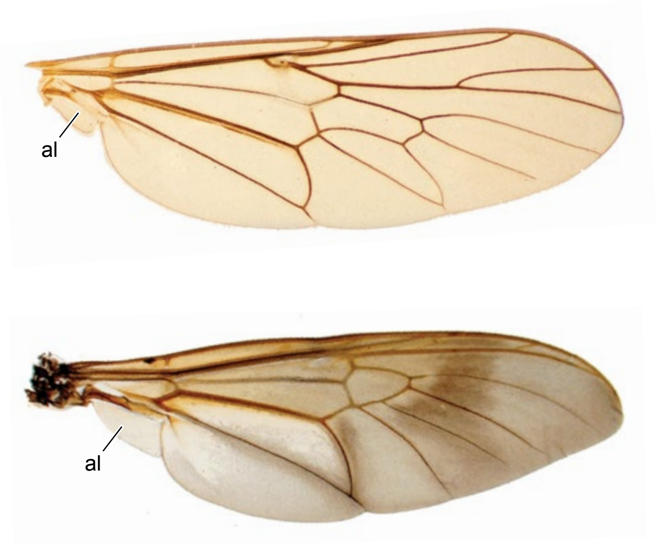
36′ (35′). Thorax without postspiracular scale. Antennal postpedicel (pped) oval or conical, arista-like stylus (ar styl) inserted apically. Wing veins R_1 and R_{2+3} distinctly separated at apex.

Rhagionidae [in part] (Chapter 37)



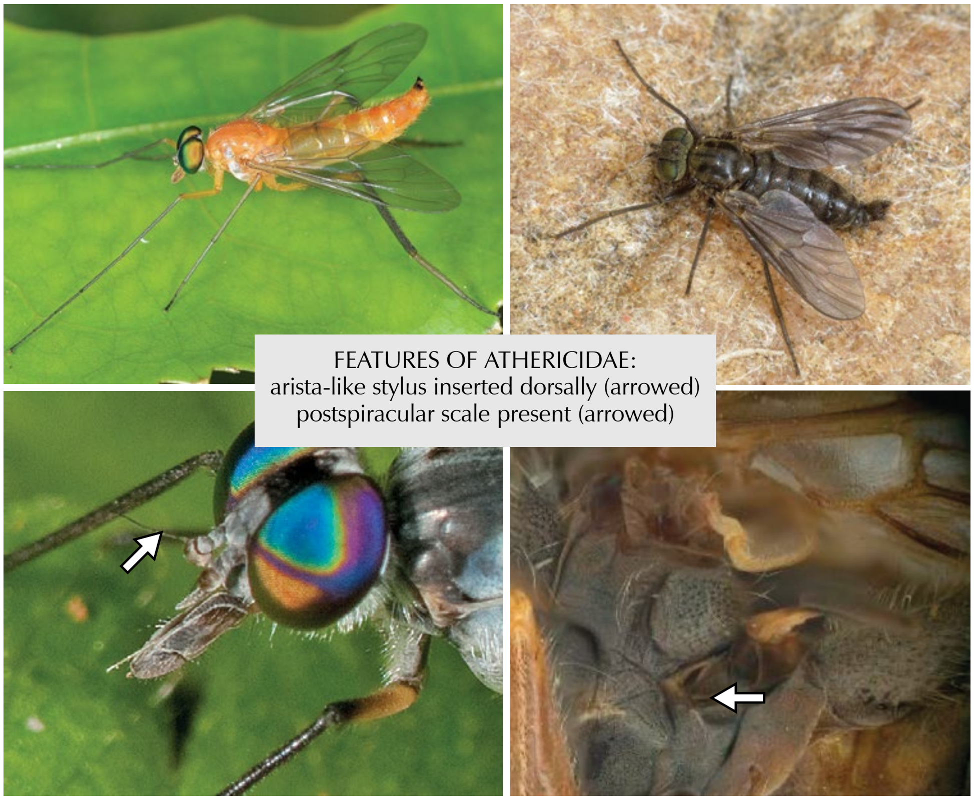
37 (32′). Wing base narrow; alula (al) extremely reduced and narrow to absent. Fore tibia usually with apical spur (arrowed) (spur may be small and inconspicuous, rarely absent).

Vermileonidae [in part] (Chapter 36)

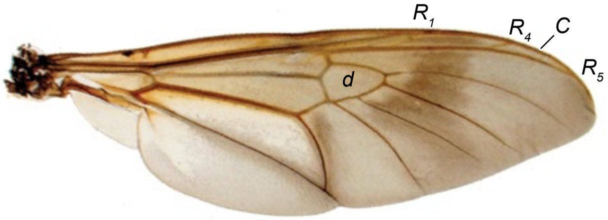


37′ (32′). Wing base not conspicuously narrowed; alula (al) present and well-developed. Fore tibia without apical spur.

38

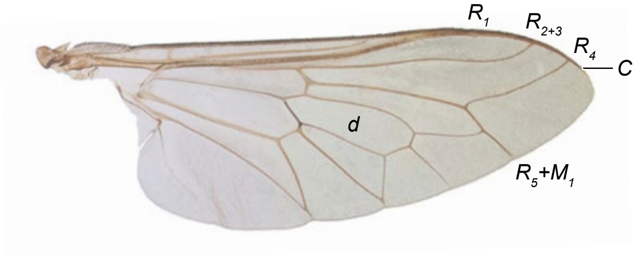


FEATURES OF ATHERICIDAE:
arista-like stylus inserted dorsally (arrowed)
postspiracular scale present (arrowed)



38 (37′). Radial wing veins (*R*) grouped together, ending before wing tip; costal vein (*C*) also usually ending well before wing apex; discal cell (*d*) forming distinct squarish cell in middle of wing (rarely absent).

Stratiomyidae [in part; most] (Chapter 41)



38′ (37′). Radial wing veins (*R*) not grouped together before wing tip; costal vein (*C*) ending at or beyond wing apex; discal cell (*d*) much longer than wide.

39

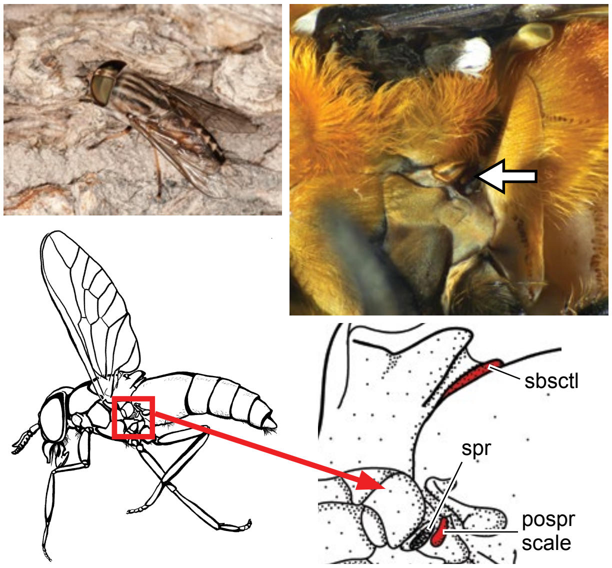
EXAMPLES OF STRATIOMYIDAE

Ptecticus Loew

Ampsalis Walker

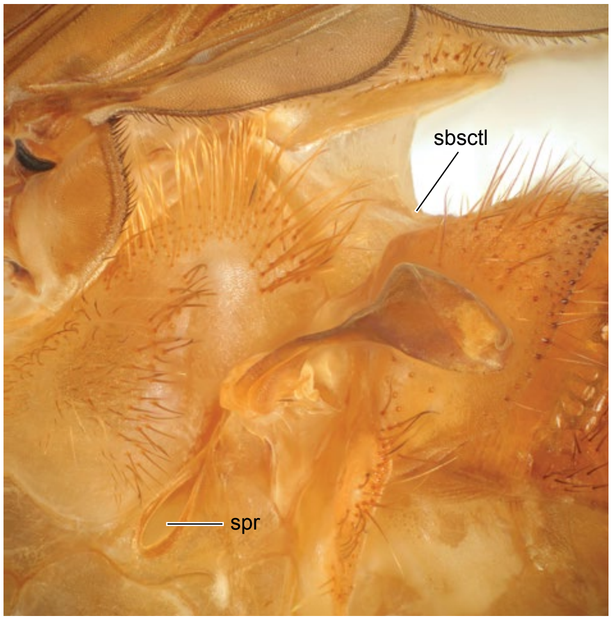
Zulumyia Lindner

Psapharomys Grünberg



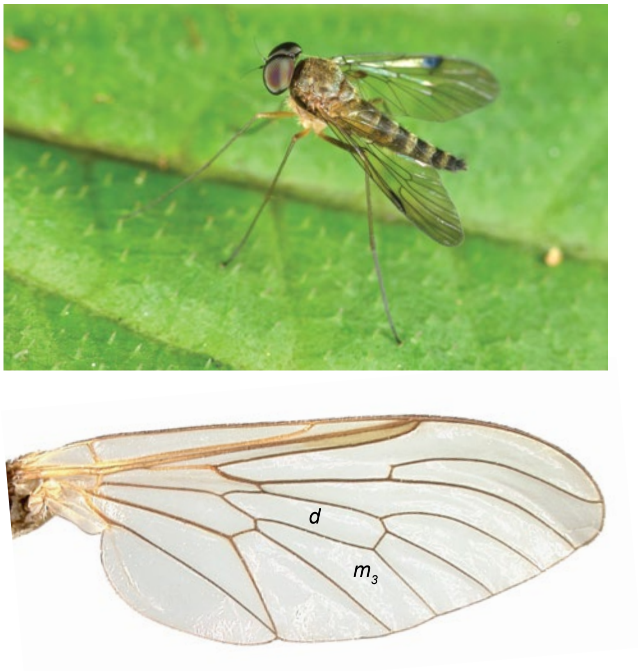
39 (38′). Thorax with postspiracular scale (pospr scale) or scale-like fold (narrow scale-like elevation behind posterior spiracle (spr), just below halter; arrowed); subscutellum (sbsctl) strongly developed, bulging. Female usually with biting mouthparts.

Tabanidae (Chapter 39)



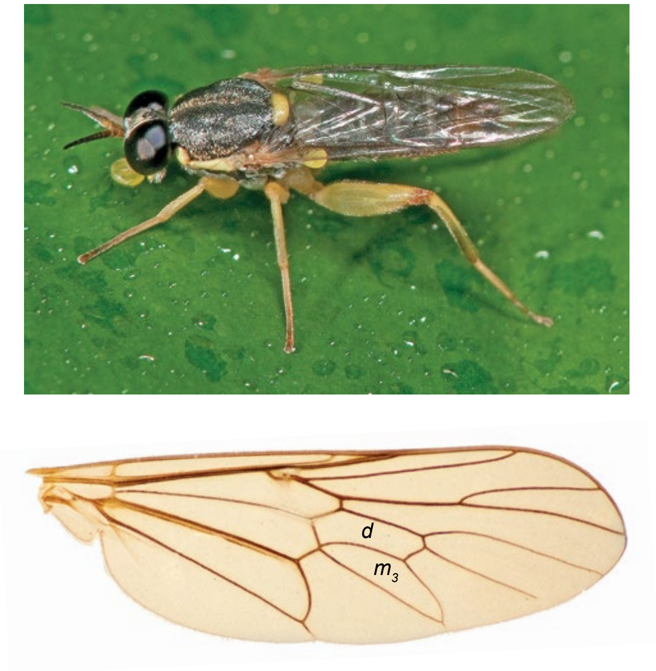
39′ (38′). Thorax without postspiracular scale or scale-like fold; subscutellum (sbsctl) undeveloped. Both sexes non-biting in Afrotropical species.

40



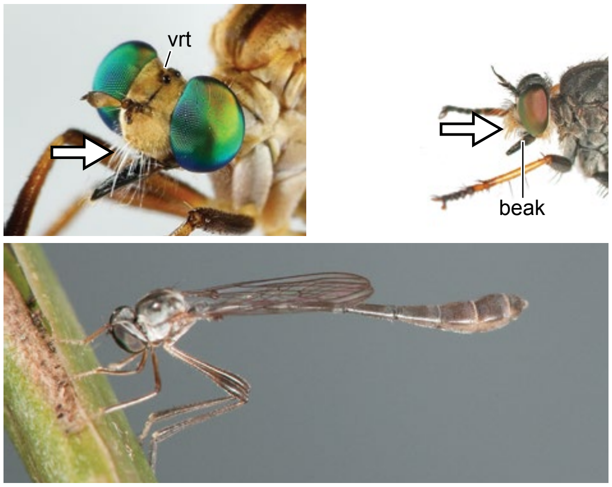
40 (39′). Wing with open cell m_3 immediately below discal cell (*d*).

Rhagionidae [in part] (Chapter 37)



40′ (39′). Wing with closed cell m_3 immediately below discal cell (*d*).

Xylomyidae (Chapter 40)

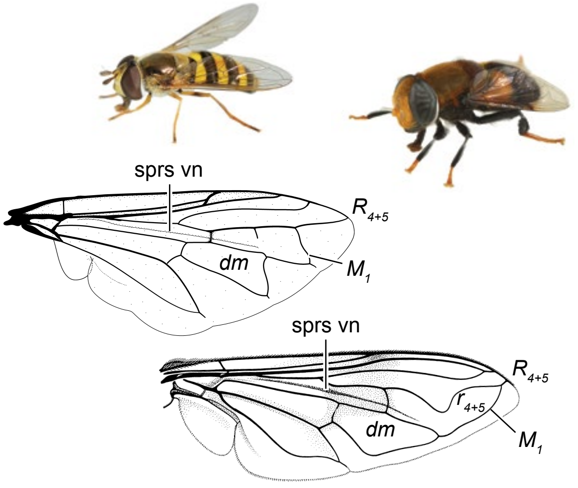


41 (30′). Face with mystax (arrowed) (usually formed of strong setae, but sometimes only setulae), either occupying entire face or restricted to lower margin. Visible mouthparts forming stout or blade-like, bare, shiny beak (distiproboscis; usually anteriorly directed), used for piercing prey. Legs with numerous macrosetae. Head usually with large bulging eyes, widely separated by depressed vertex (vrt).

Asilidae (Chapter 48)

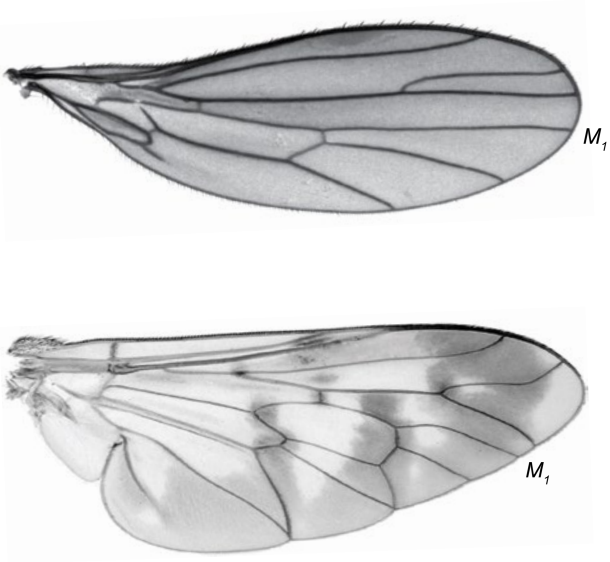
41′ (30′). Face without mystax (sometimes dispersed setulae, not setae, present). Visible mouthparts rarely forming stout and shiny beak used for piercing prey, but if so, then anteriorly or ventrally directed. Legs not conspicuously macrosetose, and fore leg never so. Eyes rarely separated by distinctly depressed vertex (but slightly so in some Apioceridae and Mydidae).

42



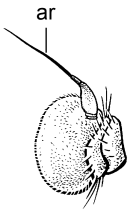
42 (41′). Wing with "spurious vein (sprs vn)" (longitudinal vein-like thickening in membrane between veins *R* and *M*) and/or first branch of vein *M* joining unbranched vein R_{4+5}, forming closed cell r_{4+5}; branches of vein *M* often turned up to run parallel or virtually parallel to wing margin (sometimes M_1 turned abruptly up to meet R_{4+5} well before margin, in combination with discal medial cell (*dm*) closed).

Syrphidae (Chapter 60)



42′ (41′). Wing without "spurious vein"; branches of vein *M* not turned up to run parallel to wing margin; vein M_1 usually running more or less straight to wing margin.

43

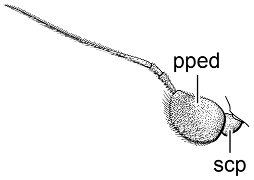


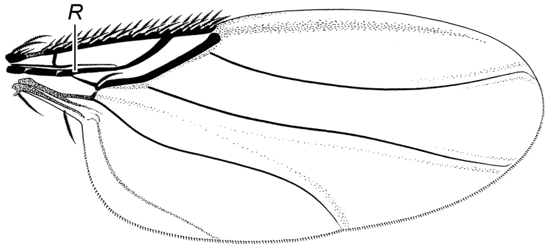
43 (42′). Head hemispherical, usually very large in proportion to thorax, invariably made up almost entirely of compound eyes. Antenna with dorsal arista (ar).

Pipunculidae (Chapter 61)

43′ (42′). Head not conspicuously large compared to thorax, rarely hemispherical (some Bombyliidae have the head hemispherical, but have an apical antennal stylus (styl) or arista-like stylus).

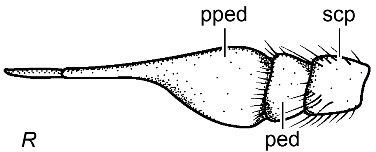
44

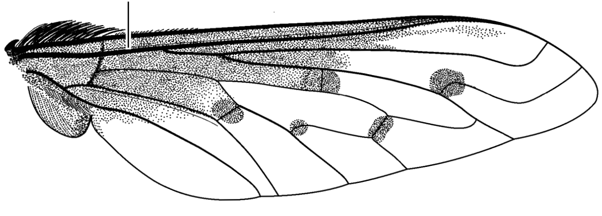


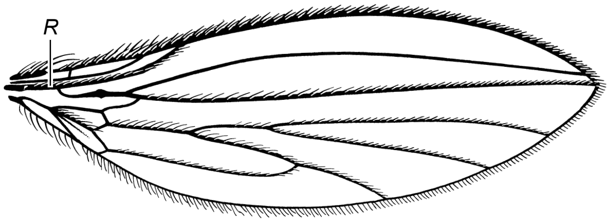


44 (43′). Wing with first few veins (radial veins) usually short, thick and crowded towards wing base; other veins weaker, unconnected by crossveins. Antennal pedicel usually hidden within postpedicel (pped). Generally humpbacked, bristly flies with distinctive habitus.

Phoridae [in part; most] (Chapter 59)

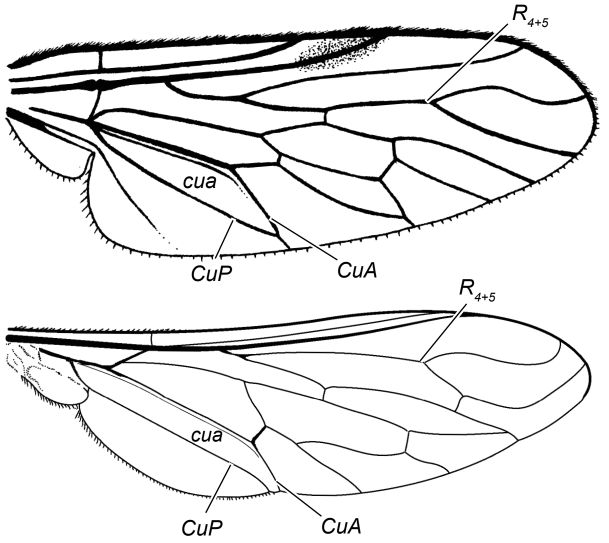






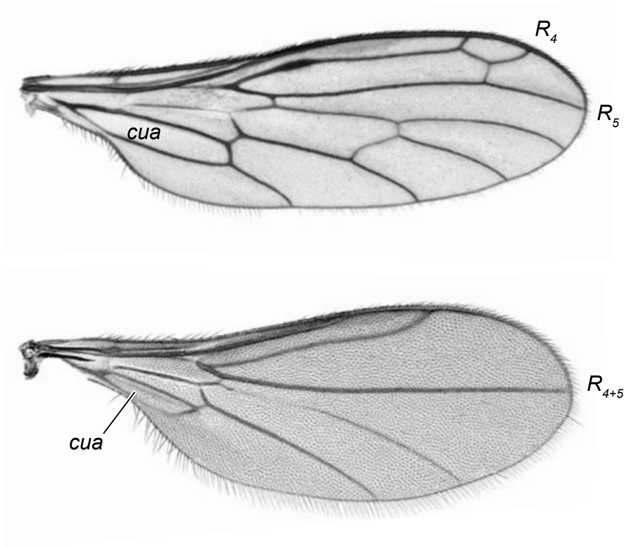
44′ (43′). Wing with radial veins not thickened and crowded towards wing base, crossveins usually present or absent (as in Lonchopteridae). Antennal pedicel (ped) not hidden within postpedicel (pped).

45



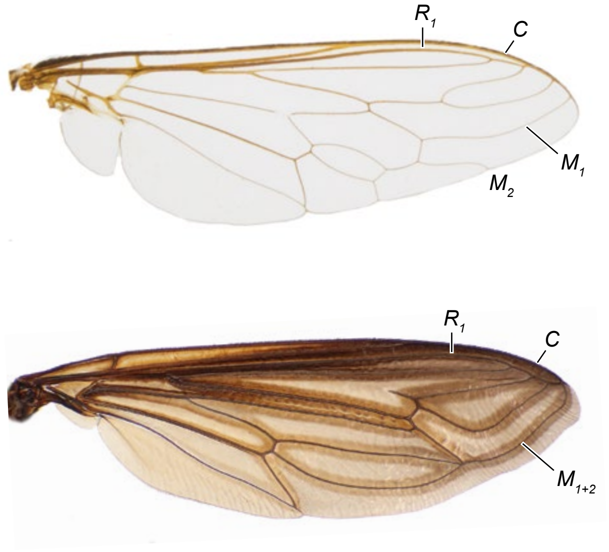
45 (44′). Wing with long, usually pointed anterior cubital cell (*cua*), EITHER closed very close to wing margin, OR open to wing margin (vein *CuA* joining vein *CuP* near wing margin or ending in margin separate from end of vein *CuP*) and with vein R_{4+5} forked. Non-predaceous flies.

46



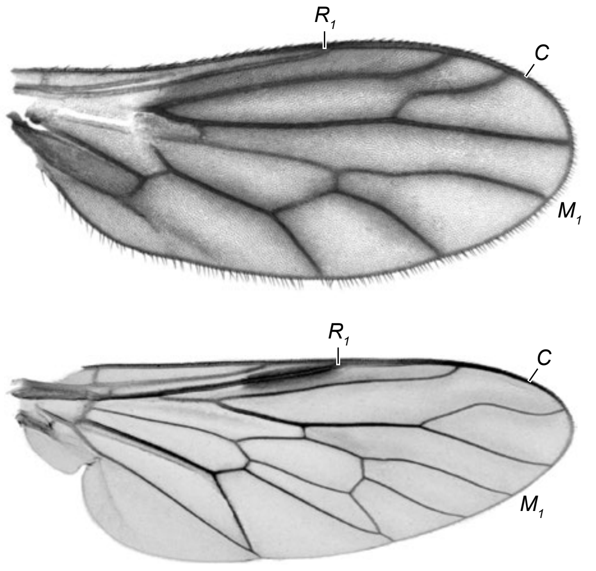
45′ (44′). Wing with anterior cubital cell (*cua*), if present, usually shorter and separated from wing margin by more than its width (rare exceptions usually have vein R_{4+5} unforked, extending to the wing margin as single vein, or are predaceous empidoids with unusual wing venation).

50



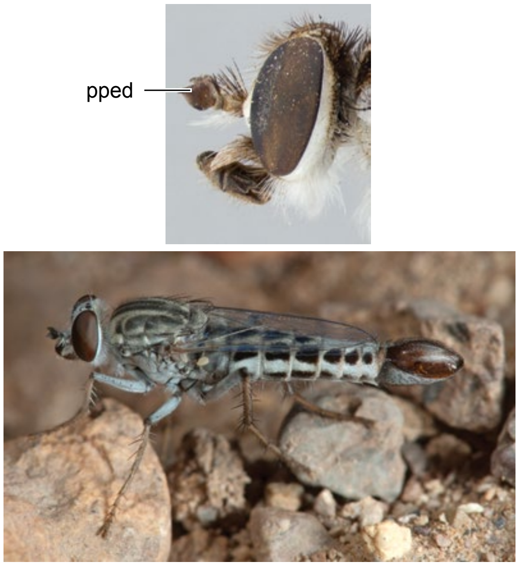
46 (45). Wing veins distally curved anteriorly; vein M_1 (in Apioceridae) or M_{1+2} (in Mydidae) reaching costal vein (*C*) or R_1 before wing apex. Usually large, robust flies (body length: 8–35 mm).

47



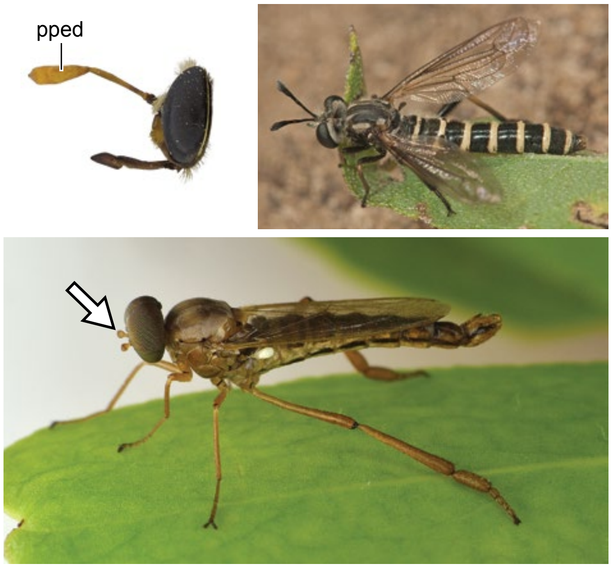
46′ (45). Wing veins not conspicuously curved anteriorly before wing apex; vein M_1 ending in costal vein (*C*) beyond wing apex. Size variable.

48



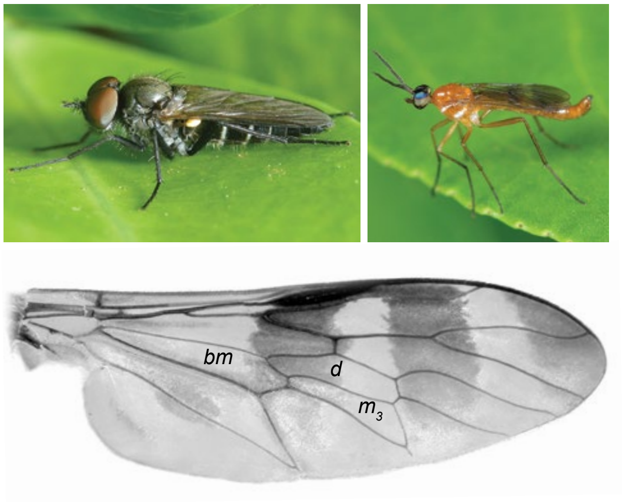
47 (46). Antenna invariably short, postpedicel (pped) shorter than head and similar in length to combined scape and pedicel. Vertex of head with 3 circular, easily visible ocelli. Brown and grey flies uniform in appearance.

Apioceridae (Chapter 46)



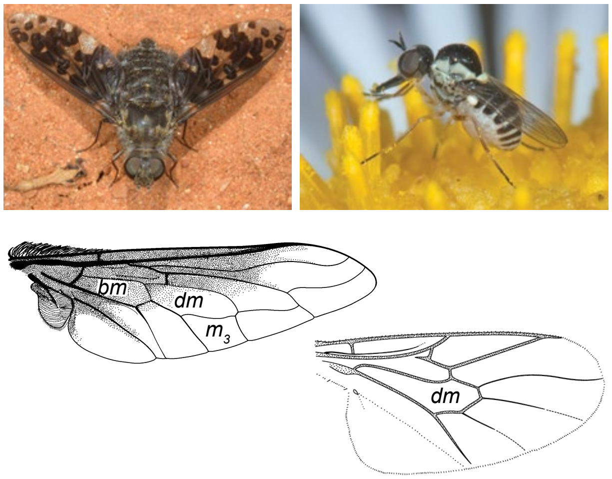
47′ (46). Antenna usually long, with postpedicel (pped) comprised of stalk and clubbed apex; rarely short (arrowed). Vertex of head with 3 elongated ocelli positioned on ridge, only anterior ocellus easily visible. Form and colour variable.

Mydidae (Chapter 47)



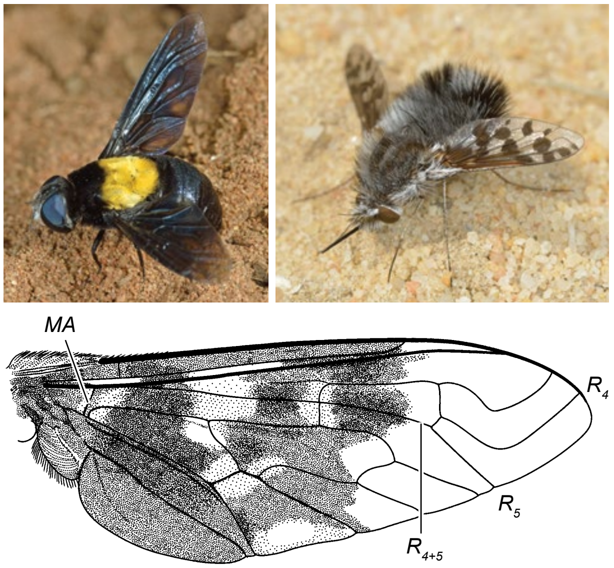
48 (46′). Wing with basal median cell (*bm*) truncate (squared) distally, with separate veins arising from 4 separate corners; discal cell (*d*) present and elongate, cell m_3 tapered (open or closed). Slender flies, often superficially similar to Asilidae.

Therevidae [in part; most] (Chapter 49)



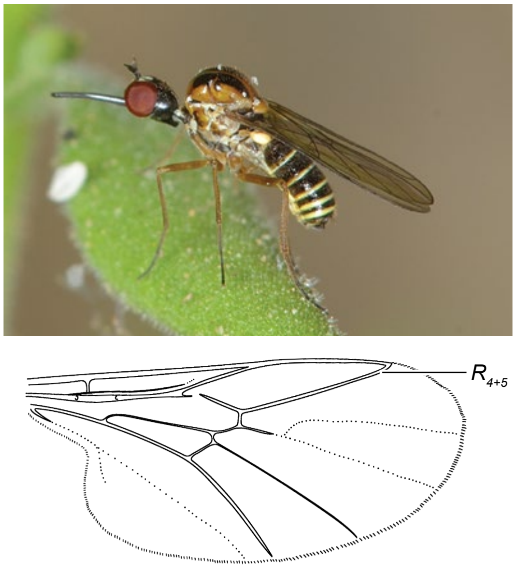
48′ (46′). Wing with basal median cell (*bm*) with veins arising from 3 corners (or sometimes absent, see above); discal cell, or discal medial cell (*dm*), present or absent, never followed by tapered cell m_3 (cell m_3 absent or broadened towards wing tip). Usually stout, short-bodied, often fuzzy flies, with long wings, but sometimes elongate and slender and sometimes tiny and empid-like.

49



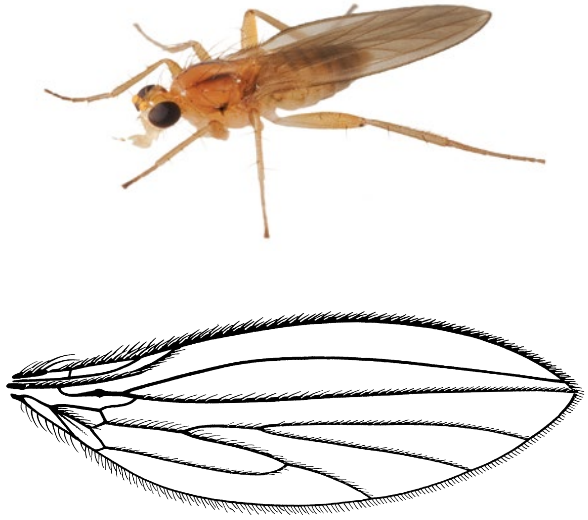
49 (48′). Wing vein R_{4+5} forked, with arculus (vein *MA*) (except in *Heterotropus* Loew). Wings held away from body at rest. Usually larger (length: 2–20 mm; usually 5–15 mm), usually fuzzy, robust flies, but shape variable.

Bombyliidae (Chapter 45)



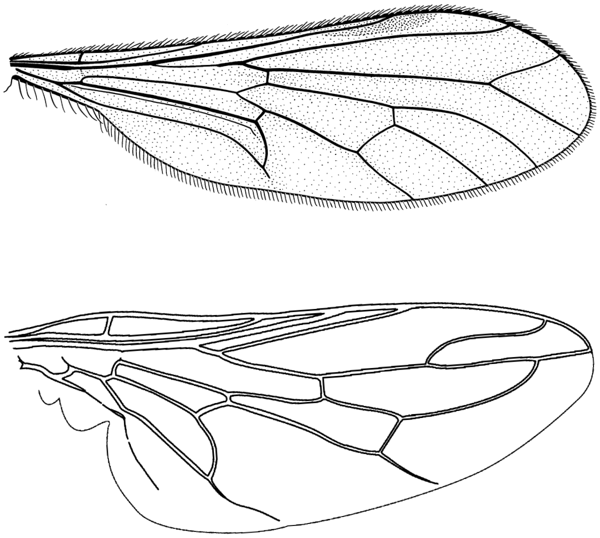
49′ (48′). Wing vein R_{4+5} unforked, without arculus (vein *MA*). Wings invariably held together over abdomen at rest. Afrotropical species very small (length: 1–3 mm), usually humpbacked, but sometimes with fuzzy appearance (*e.g.*, *Psiloderoides* Hesse).

Mythicomyiidae (Chapter 44)



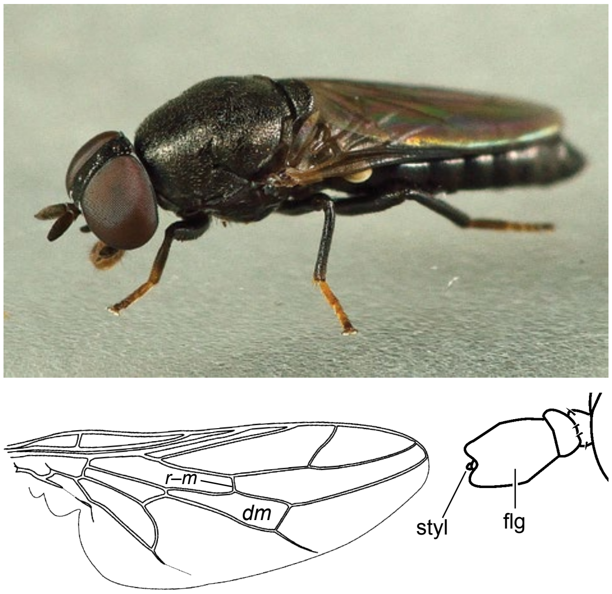
50 (45′). Wing pointed at apex, with parallel longitudinal veins, without crossveins beyond base; most veins with short black setae on dorsal surface.

Lonchopteridae (Chapter 58)



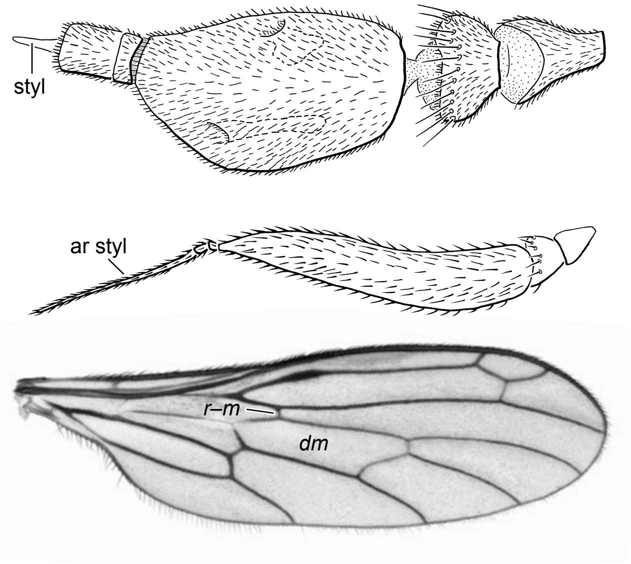
50′ (45′). Wing rounded at apex, with veins divergent, usually with crossveins; veins bare on dorsal surface.

51



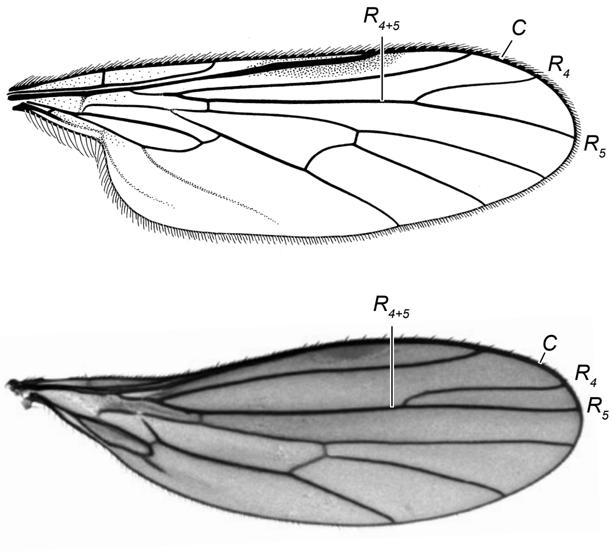
51 (50′). Antenna apparently 3-segmented, flagellum (flg) with minute stylus (styl) inserted in apical pit. Head without setae. Wing crossvein *r–m* positioned at or beyond middle of discal medial cell (*dm*).

Scenopinidae (Chapter 50)



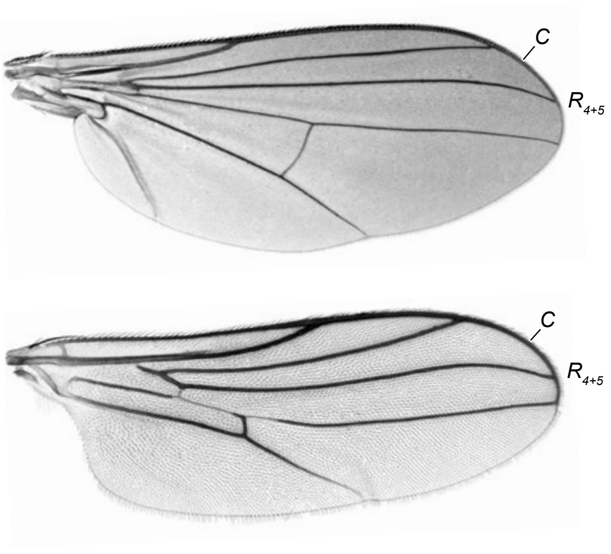
51′ (50′). Antenna apparently 4–5 segmented, with an exposed stylus (styl) or arista-like stylus (ar styl) terminally. Head usually with setae. Wing crossvein *r–m* (if present) usually positioned before middle of discal medial cell (*dm*).

52



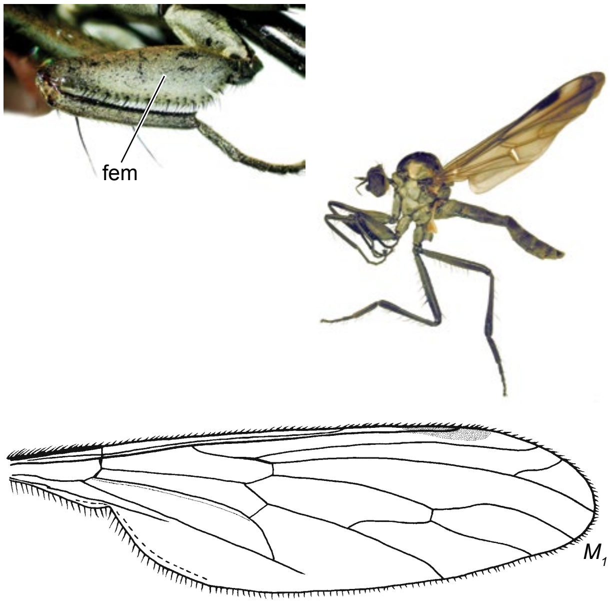
52 (51′). Wing vein R_{4+5} usually forked. Thorax with laterotergite setulose OR costal vein (C) extending around wing tip. If R_{4+5} unforked, and laterotergite bare or costal vein not extending around wing tip, then first antennal segment with setae above.

53



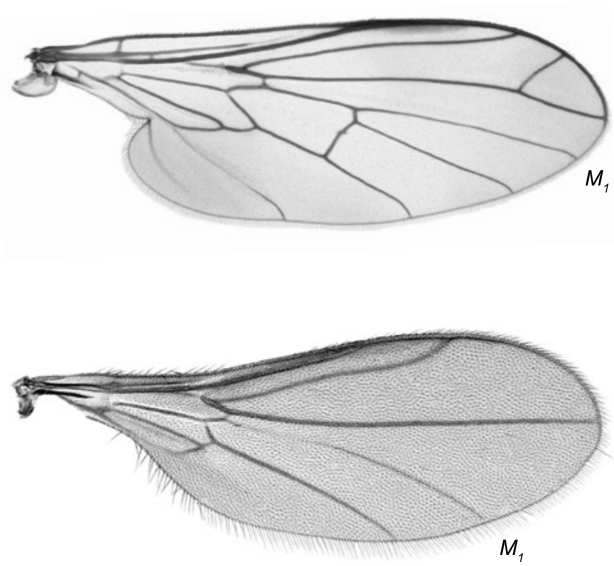
52′ (51′). Wing vein R_{4+5} unforked. Thorax with laterotergite bare and costal vein (C) ending at wing tip (except in the Dolichopodidae subfamilies MICROPHORINAE and PARATHALASSIINAE). First antennal segment usually bare.

55



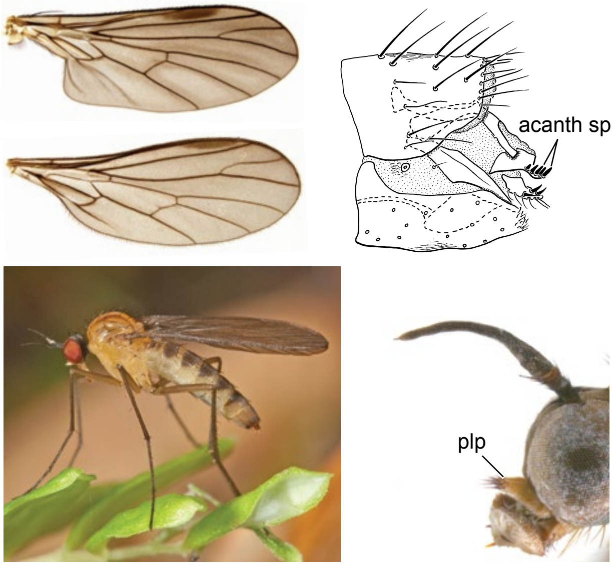
53 (52). Mid leg raptorial, with femur (fem) strongly swollen. Wing vein M_1 distinctly curved anteriorly in proximal ⅓. Abdomen of female pointed apically.

Homalocnemidae (Chapter 55)



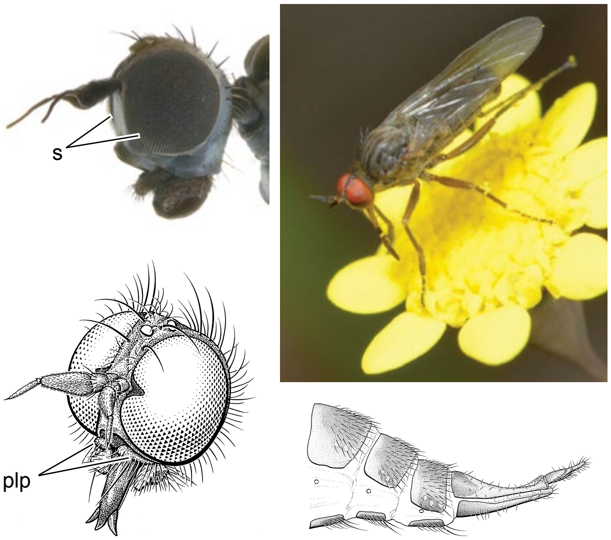
53′ (52). Mid leg not raptorial, rarely with femur swollen, but if so, then wing vein M_1 straight or gently and evenly arched towards wing margin. Abdomen of female pointed or truncate.

54



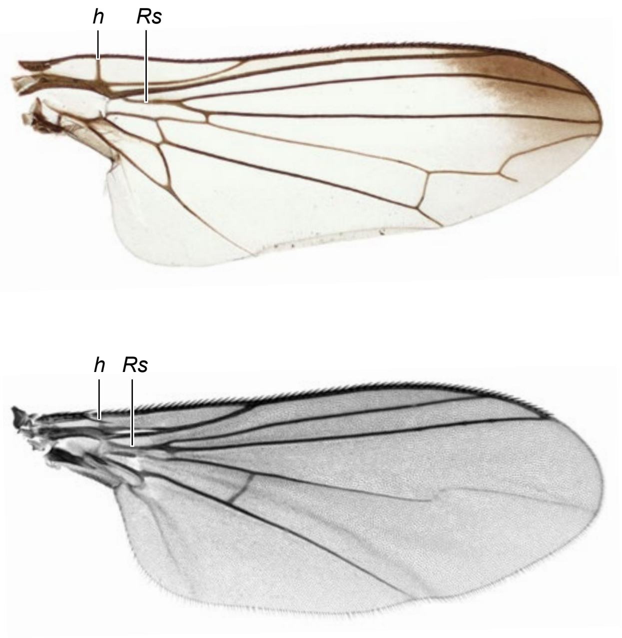
54 (53′). Fore leg simple, never raptorial. Wing broad or slender, if slender then eye bare; if wing broad, then palpus (plp) straight, projecting obliquely from head. Abdomen of female truncate, bearing acanthophorite spines (acanth sp).

Brachystomatidae (Chapter 53)



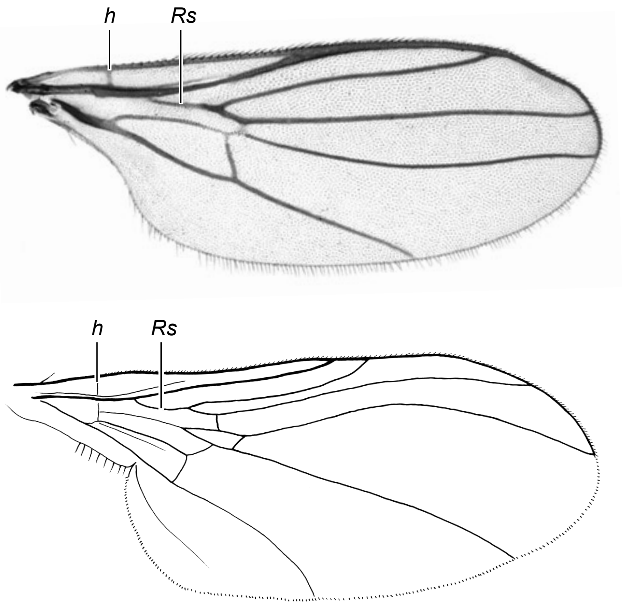
54′ (53′). Fore leg raptorial or simple. Wing broad or slender, if slender and fore leg simple, then eye with ommatrichia (fine setulae; s); if wing broad, then palpus (plp) usually strongly upcurved along ventral margin of head. Abdomen of female pointed apically, lacking acanthophorite spines.

Empididae [in part; most] (Chapter 51)



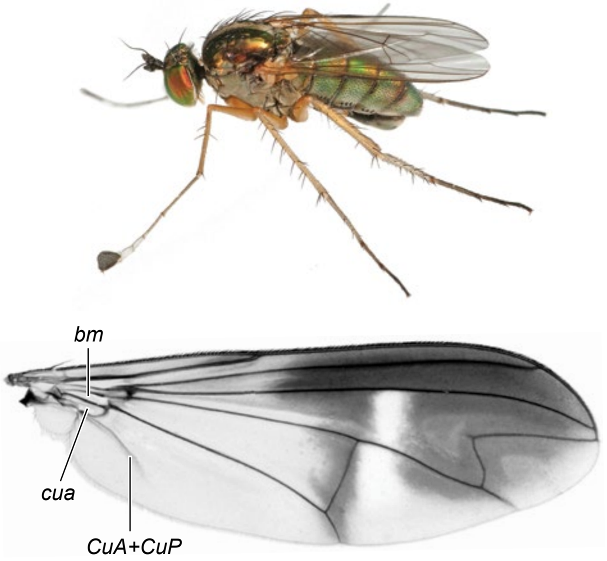
55 (52′). Wing with radial sector (*Rs*) originating at or near level of humeral crossvein (*h*).

56



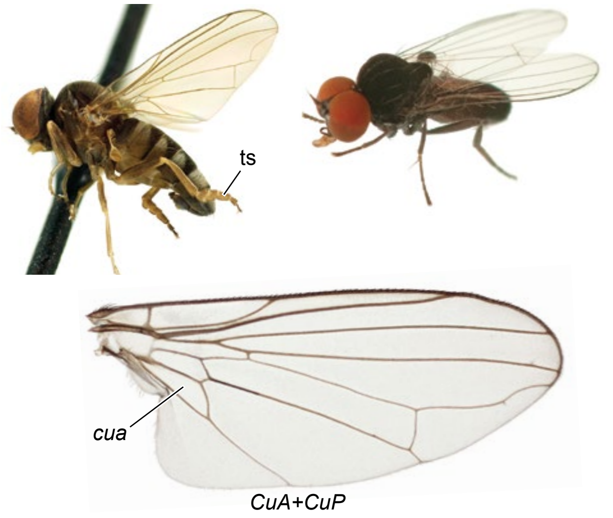
55′ (52′). Wing with radial sector (*Rs*) originating well distal to level of humeral crossvein (*h*).

57



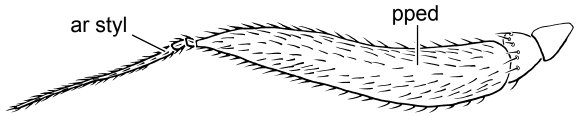
56 (55). Wing vein *CuA+CuP* weak, not reaching wing margin; anterior cubital cell (*cua*) absent or short, subequal to cell *bm*, apex rounded. Eye, tarsus and vestiture variable. Commonly metallic green flies.

Dolichopodidae (Chapter 56)



56′ (55). Wing vein *CuA+CuP* reaching wing margin; anterior cubital cell (*cua*) elongate, often ending in acute angle. Thorax with acrostichal setae reduced to single row or absent. Hind leg with tarsus (ts) often greatly enlarged and flattened. Often velvety black flies, males holoptic (head with eyes meeting at vertex).

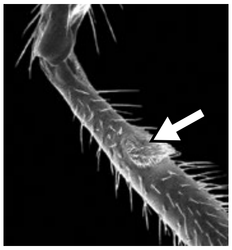
Platypezidae (Chapter 57)

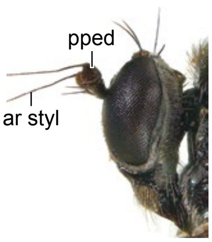


57 (55′). Antennal postpedicel (pped) elongate and tapered, always longer than 3-articled arista-like stylus (ar styl). Fore tibia without posteroventral gland at base. Base of palpus without plate or palpifer. Male terminalia unrotated.

Atelestidae (Chapter 54)

Apparently extremely rare, only known from Brandberg massif, Namibia.

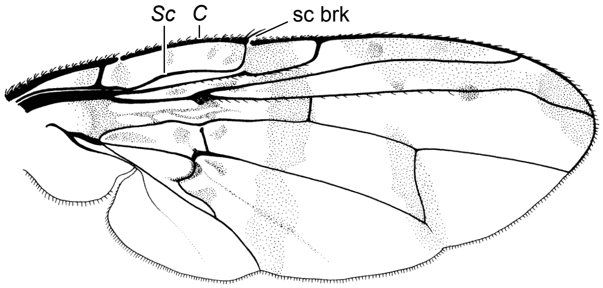


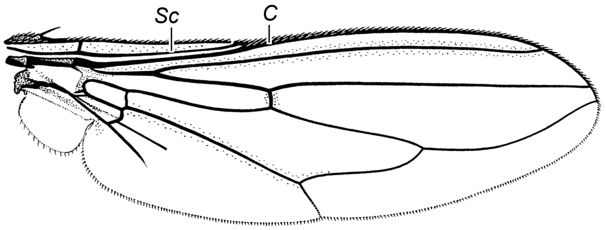


57′ (55′). Postpedicel (pped) shorter than arista-like stylus; if postpedicel longer, arista-like stylus (ar styl) 1 or 2-articled. Fore tibia with posteroventral gland at base (arrowed). Base of palpus with sclerotised plate or palpifer. Male terminalia usually rotated to right side of abdomen.

Hybotidae [in part; most] (Chapter 52)

Very common throughout Afrotropics.

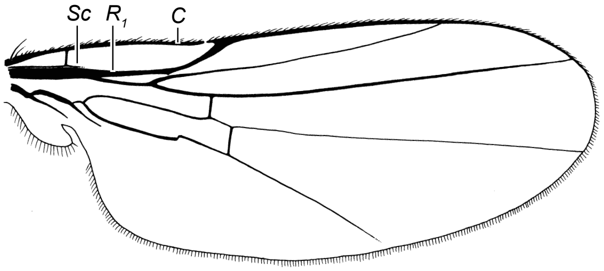


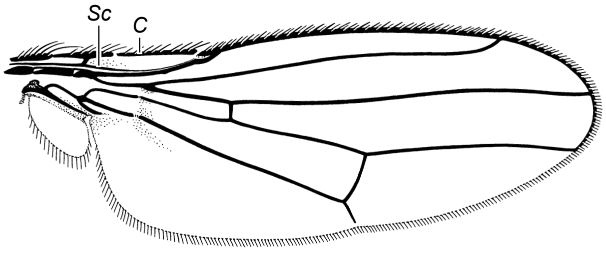


58 (29′). Subcostal wing vein (*Sc*) complete, ending in costal vein (*C*), or *Sc* virtually complete and sharply bent forward to subcostal break (sc brk). Size 2–30 mm.

59

Doubtful cases key both ways.



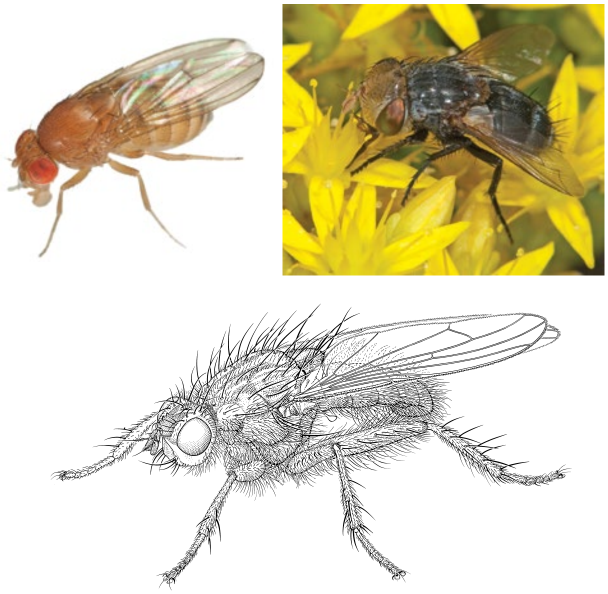


58′ (29′). Subcostal wing vein (*Sc*) incomplete, not reaching costal vein (*C*), EITHER ending in vein R_1 OR fading out in membrane. Size 0.5–10.0 mm, but usually < 5 mm (the traditional ACALYPTRATAE [in part]).

109

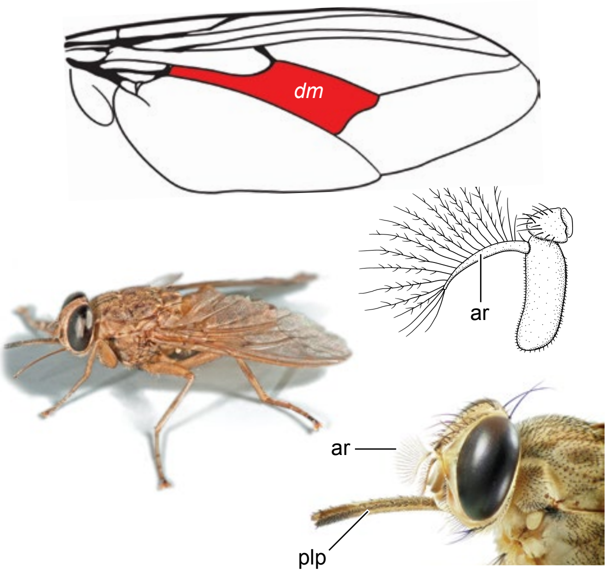
59 (58). Robust, flies with dense, soft setulae (long or short, but without stout setae), from bee- or wasp-like to speckled; mouthparts reduced (at most tiny remnants). Head without vibrissa.

Oestridae (Chapter 119)



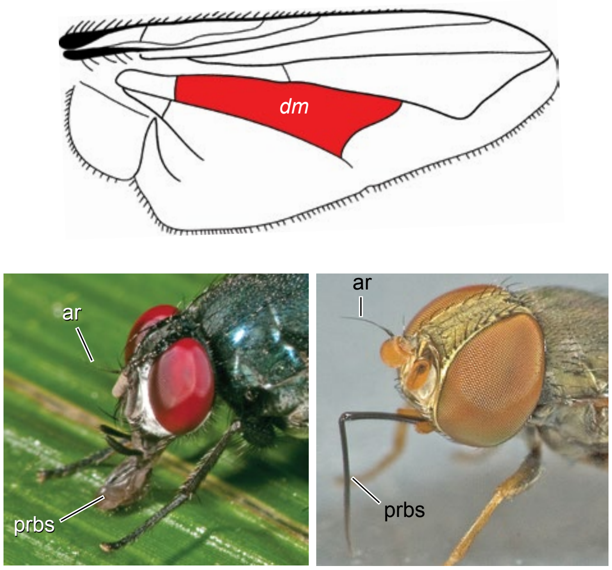
59′ (58). Size and shape variable, but if mouthparts reduced, then body with stout setae (sometimes conspicuously shortened). If robust and bee-like then head with vibrissa.

60



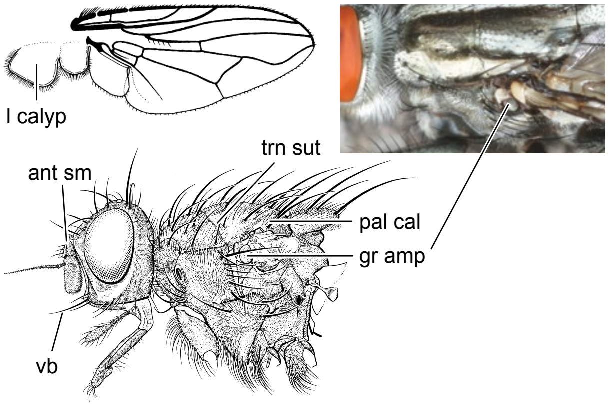
60 (59′). Antennal arista (ar) with long dorsal feathered branches (long dorsal "hairs" or "rays" each multi-branched). Wing with discal medial cell (*dm*) distinctly hatchet-shaped. Proboscis and palpus (plp) 2 x as long as head.

Glossinidae (Chapter 108)



60′ (59′). Antennal arista (ar) variable; if with long dorsal branches, then branches not feathered and multi-branched. Wing with discal medial cell (*dm*) not hatchet-shaped. Proboscis (prbs) and palpus variable.

61

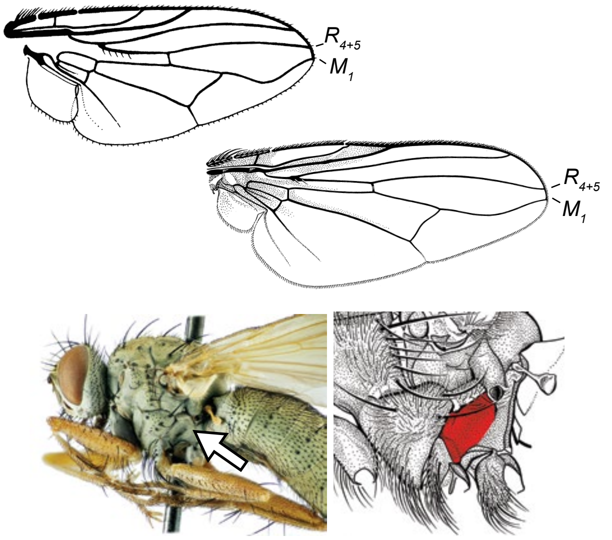


61 (60′). Thorax with greater ampulla (gr amp) well developed; scutum with transverse suture (trn sut) complete or usually only absent between achrostichal setal rows. Postalar callus (pal cal) well demarcated from adjacent scutum by oblique depression. Lower calypter (l calyp) usually large (except in Scathophagidae). Head normally with strong vibrissa (vb); antennal pedicel with longitudinal seam dorsolaterally (ant sm). Usually relatively large, distinctively robust and "bristly" flies (CALYPTRATAE [in part; most]).

62

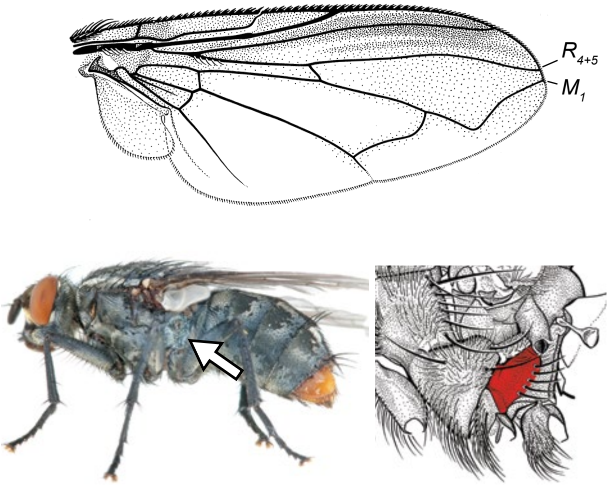
61′ (60′). Thorax usually with diminutive greater ampulla, or entirely absent (exceptions lack vibrissa); scutum without transverse suture between dorsocentral rows. Postalar seta(e) usually not inserted on distinct callus. Lower calypter not strongly developed. Head with or without vibrissa; antennal pedicel with or without dorsolateral seam. Size variable, but often small (the traditional ACALYPTRATAE [in part]).

73



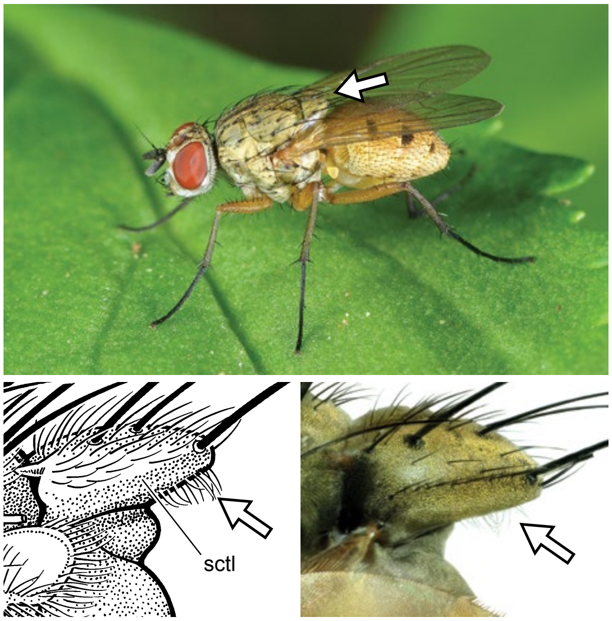
62 (61). Thorax with meron (arrowed; in red) bare, or with only indistinct fine setulae, more rarely with a few scattered setae, those along posterior margin no longer than those along dorsal margin. Wing vein M_1 usually straight or gently bent (distinctly bent in some Muscidae) (MUSCOIDEA).

63



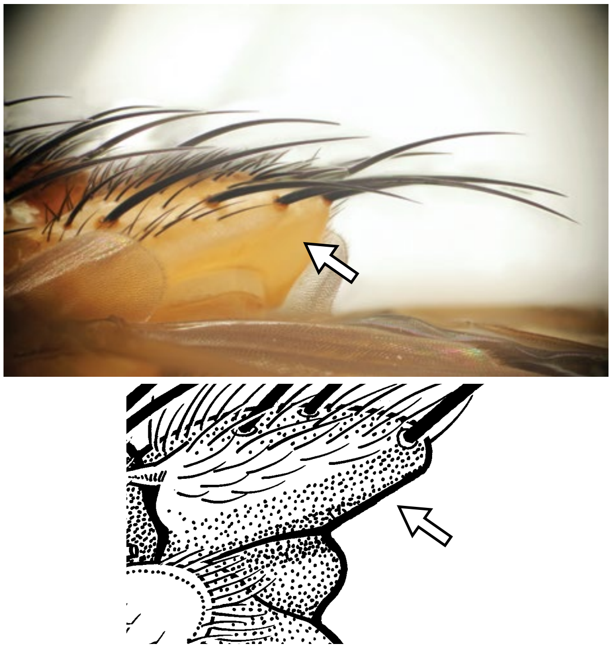
62′ (61). Thorax with meron (arrowed; in red) almost invariably with vertical row of strong, erect setae near posterior margin (between base of hind leg and posterior spiracle). Wing vein M_1 variable, but usually with distinctive bend where it turns forward towards apex of vein R_{4+5} (OESTROIDEA [in part; most]).

67



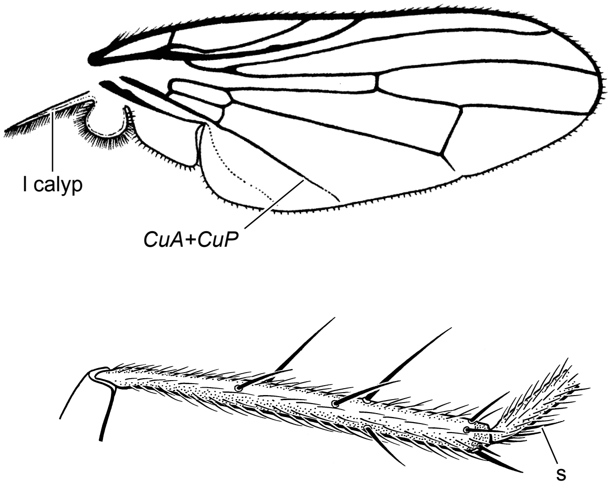
63 (62). Scutellum (sctl) with microscopic, fine, erect setulae (arrowed) on underside (especially just below tip).

Anthomyiidae [in part; most] (Chapter 111)



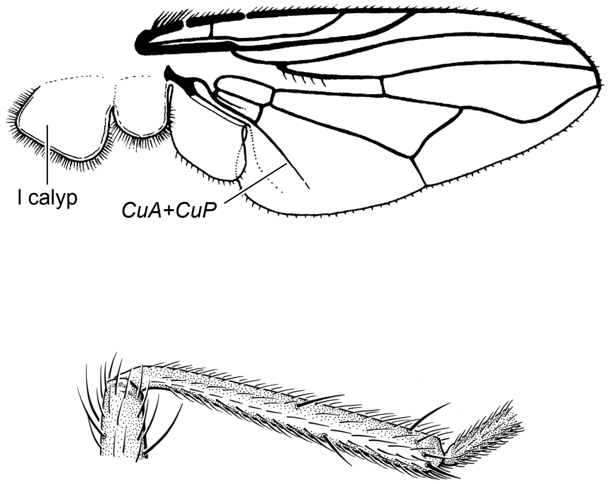
63′ (62). Scutellum with underside bare (arrowed), sometimes with a few setulae along margin.

64



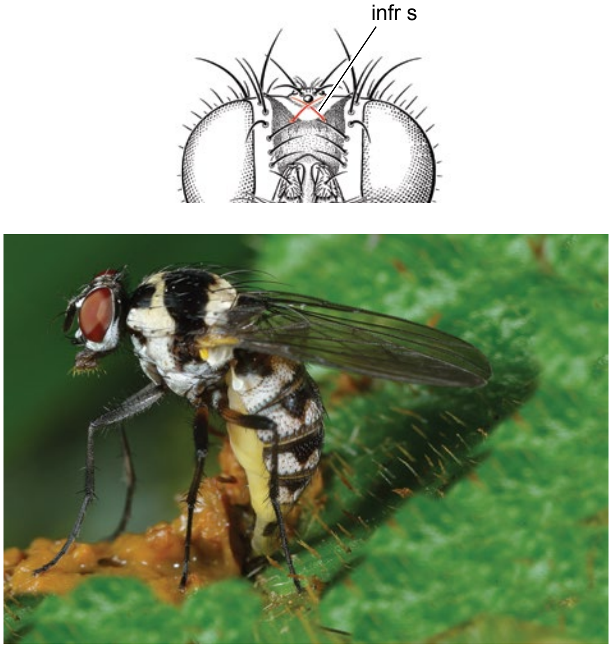
64 (63′). Wing vein *CuA+CuP* long, usually reaching wing margin at least as a fold; lower calypter (l calyp) narrow, parallel-sided; hind leg with short ventral seta (s) near base of first tarsal segment.

65



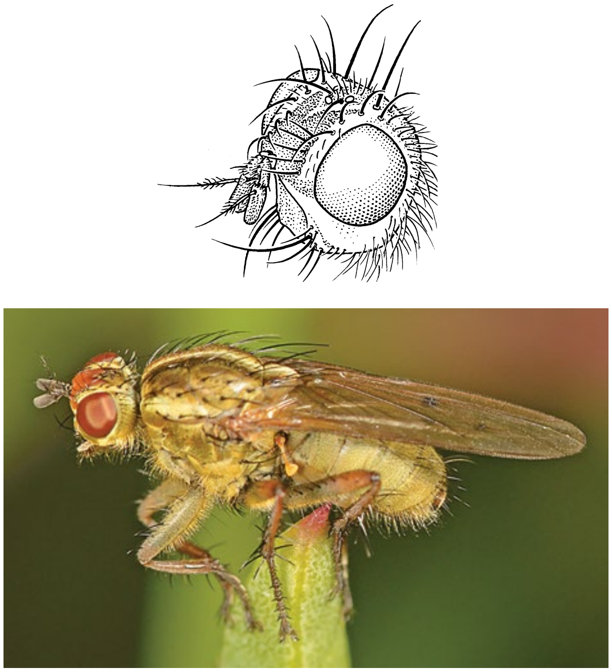
64′ (63′). Wing vein *CuA+CuP* short, fading out before wing margin; lower calypter (l calyp) broad, shape variable, if exceptionally narrow, then hind leg without ventral seta near base of first tarsal segment.

66



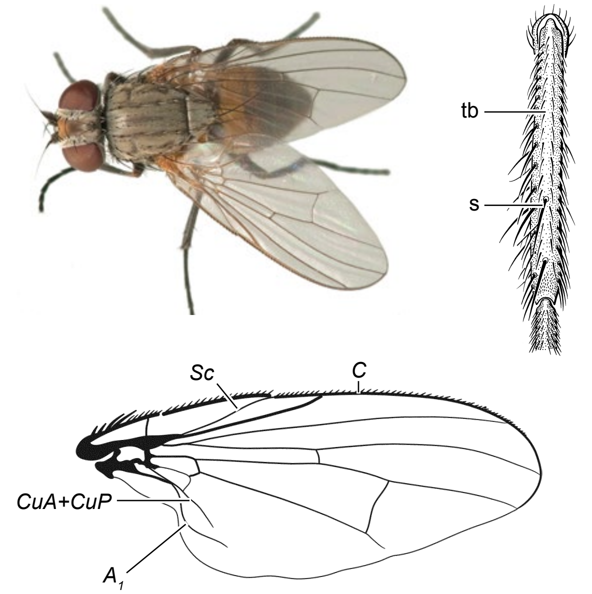
65 (64). Frons with cruciate interfrontal setae (infr s; in red).

Anthomyiidae [in part] (Chapter 111)



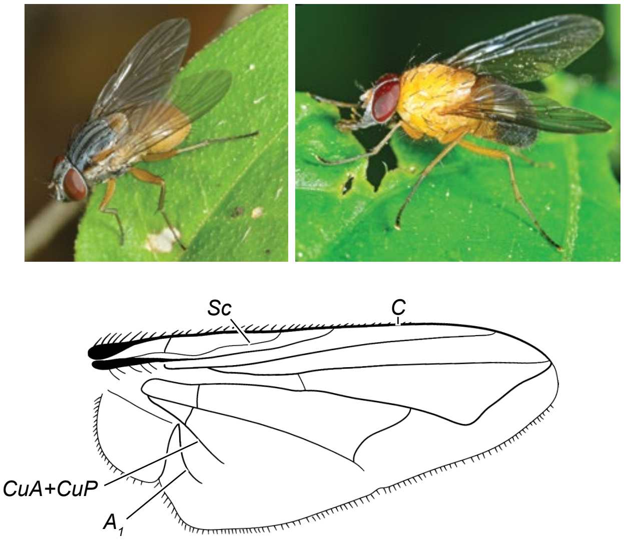
65′ (64). Frons without interfrontal setae.

Scathophagidae (Chapter 110)



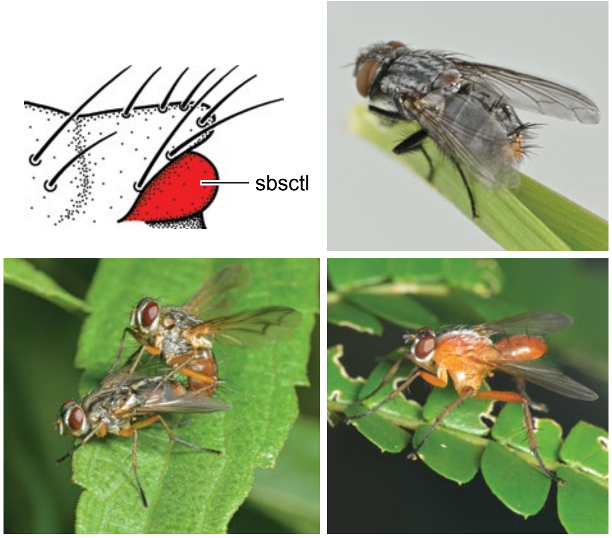
66 (64′). Anal wing vein (A_1) usually curved forward on trajectory that would intersect vein *CuA+CuP* if extended; subcostal vein (*Sc*) straight in distal ½. Hind tibia (tb) with dorsal seta (s) near middle.

Fanniidae (Chapter 112)



66′ (64′). Anal wing vein (A_1) not curved forward on trajectory that would intersect vein *CuA+CuP* if extended; subcostal vein (*Sc*) usually curved towards costal vein (C) in distal ½. Hind tibia often with anterodorsal seta near middle, but without true dorsal seta.

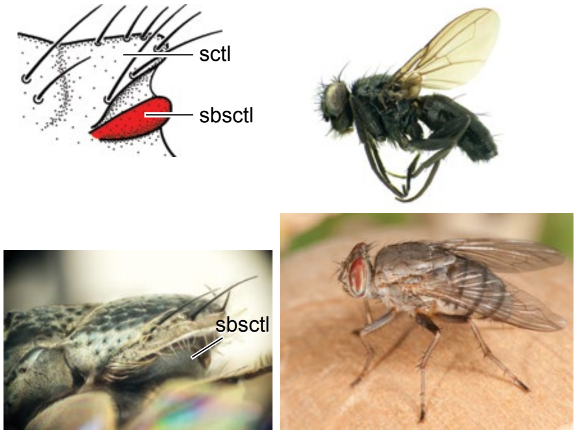
Muscidae (Chapter 113)



67 (62′). Subscutellum (sbsctl) forming prominent convex lobe immediately beneath scutellum. Abdominal sternite 2 partly obscured by overlapping margins of tergite 1+2; sternite 2 not fully exposed. Wings in life usually held apart at *ca* 45° angle.

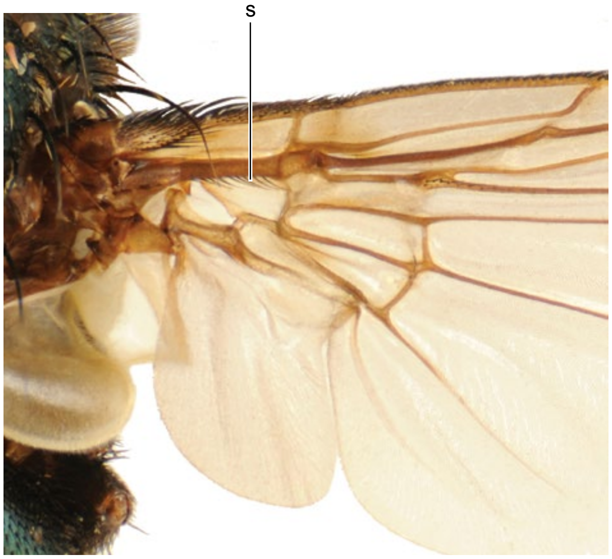
Tachinidae (Chapter 118)

Extremely diverse, abdomen often conspicuously bristly.



67′ (62′). Subscutellum (sbsctl) absent or relatively weakly developed, if convex (some Rhinophoridae and bengaliine Calliphoridae; in red), then membranous part (between scutellum (sctl) and subscutellum) as broad as, or broader than convex sclerotised part of subscutellum. Abdominal sternite 2 not partly obscured; sternite 2 fully exposed (except in Rhinophoridae, with margins of tergite 1+2 abutting margin of sternite 2). Wings in life variable, but often overlapping abdomen to greater degree.

68

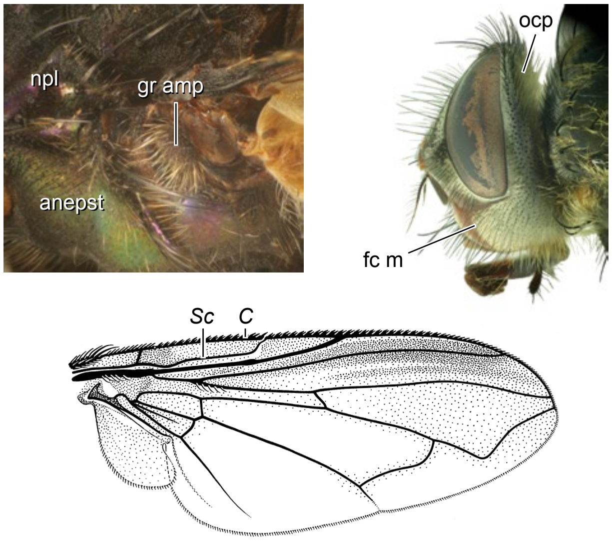


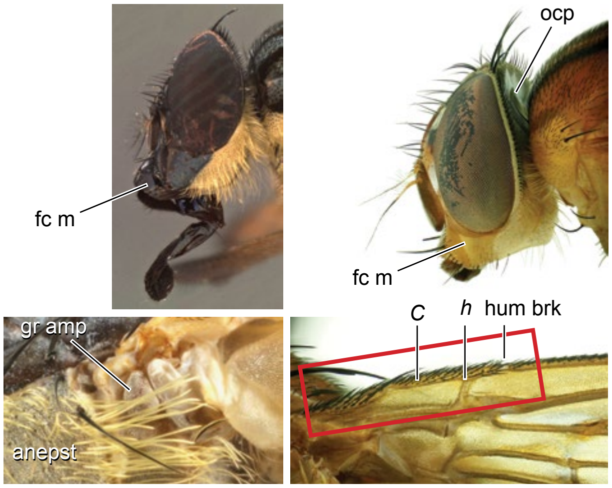
68 (67′). Upper surface of wing with setae (s) (sometimes very small) on posterodorsal surface of stem vein.

69

68′ (67′). Upper surface of wing without setae on posterodorsal surface of stem vein.

70





69 (68). Wing with underside of costal vein (*C*) setulose as far as end of subcostal vein (*Sc*). Head with occiput (ocp) setulose in dorsal $^{1}/_{2}$; ventral facial margin (fc m) usually not protruding. Thorax with greater ampulla (gr amp) setose. Without shiny black maculae around sockets at base of setulae (CHRYSOMYINAE).

Calliphoridae [in part] (Chapter 114)

69′ (68). Wing with underside of costal vein (*C*) setulose only as far as humeral break (hum brk) (just beyond humeral crossvein (*h*)), bare beyond this point. Head with occiput (ocp) usually with neither setulae nor microtomentum in dorsal $^{1}/_{2}$; ventral facial margin (fc m) usually distinctively protruding. Thorax with greater ampulla (gr amp) bare. Often with shiny black maculae around sockets at base of setulae.

Rhiniidae (Chapter 115)

RHINIIDAE
Stomorhina Rondani

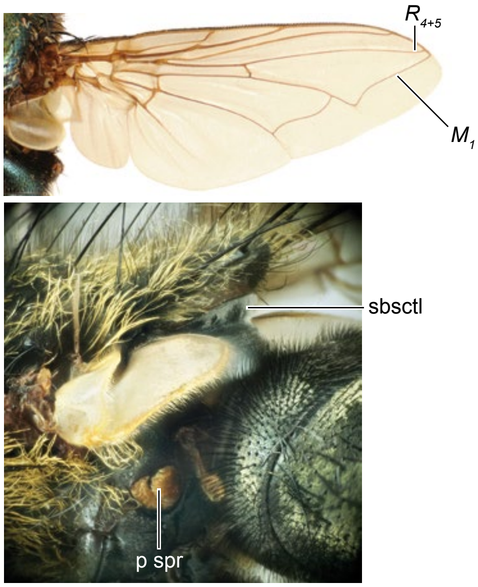
CALLIPHORIDAE: CHRYSOMYINAE
Chrysomya Robineau-Desvoidy

70 (68′). Lower calypter (l calyp) oval or tongue-shaped, directed away from scutellum. Body usually uniformly dull, sometimes partly or entirely yellow, but rarely shiny metallic or distinctly fasciate, chequered or maculate.

71

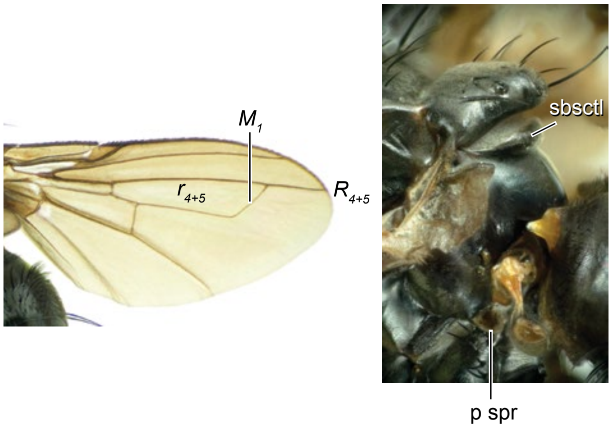
70′ (68′). Lower calypter (l calyp) broader, not directed away from scutellum, running along scutellum for part of its length. Body usually EITHER shiny metallic, OR conspicuously fasciate, chequered or maculate; sometimes mostly yellow with dark parts.

72



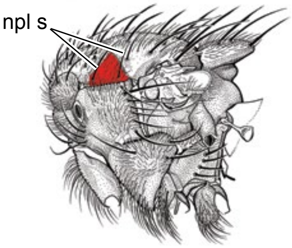
71 (70). Subscutellum (sbsctl) flat; posterior thoracic spiracle (p spr) with unequal anterior and posterior lappets (like flaps). Wing vein M_1 curved towards wing tip, but not meeting vein R_{4+5} before margin.

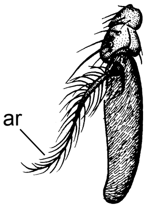
Calliphoridae [in part] (Chapter 114)



71′ (70). Subscutellum (sbsctl) at least slightly convex, but widely separated from scutellum; posterior thoracic spiracle (p spr) small, usually rounded or triangular, usually surrounded by uniform and continuous fringe of short setulae or flanked by similar anterior and posterior tufts (fringe undifferentiated in some species). Wing vein M_1 sometimes turned abruptly up to meet vein R_{4+5} well before margin, creating a closed cell r_{4+5} (but vein M_1 sometimes gently bent to almost straight or evanescent).

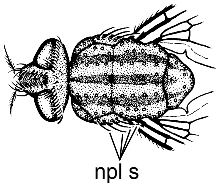
Rhinophoridae (Chapter 117)

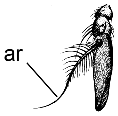




72 (70′). Body often metallic green, blue or black, at least abdomen usually with metallic lustre, many species yellow to brown. Lower calypter with or without setulae on dorsal surface. If abdomen grey and black chequered, then thorax with yellow crinkly hair-like setae (*Pollenia* Robineau-Desvoidy, recently introduced). Thorax with 2 notopleural setae (npl s; in red). Antennal arista (ar) usually plumose to tip.

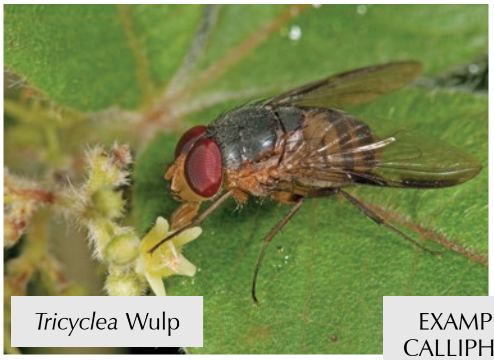
Calliphoridae [in part; most] (Chapter 114)

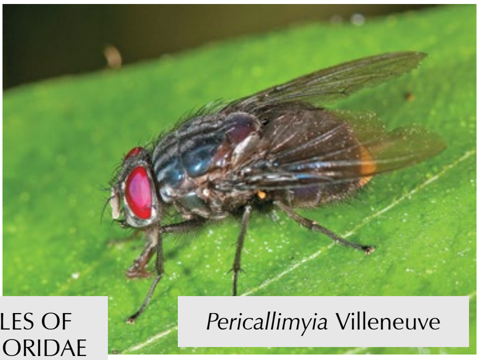




72′ (70′). Body not metallic and shiny (except an undescribed *Blaesoxipha* Loew from Madagascar), but if so, then lower calypter without setulae on dorsal surface and thorax with 4 notopleural setae (npl s; circled in red). Most species EITHER black and grey with dorsum of thorax often striped (and abdomen chequered, maculate or fasciate), antennal arista (ar) bare or plumose in basal $^{2}/_{3}$ and with 2–4 notopleural setae (MILTOGRAMMINAE [in part], PARAMACRONYCHIINAE [in part] and SARCOPHAGINAE), OR more uniformly pigmented, tachinid-like flies, with arista virtually bare and 2 notopleural setae (MILTOGRAMMINAE [in part] and PARAMACRONYCHIINAE [in part]).

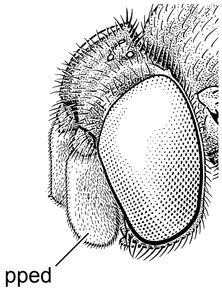
Sarcophagidae (Chapter 116)

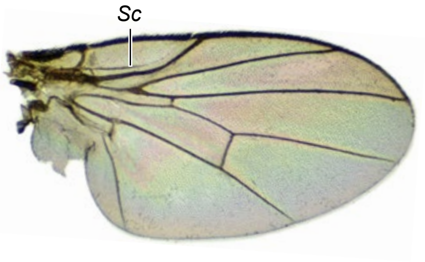

Tricyclea Wulp

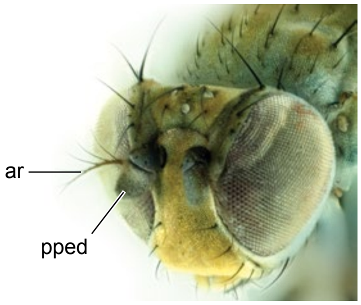

Pericallimyia Villeneuve

EXAMPLES OF CALLIPHORIDAE


Bengalia Robineau-Desvoidy







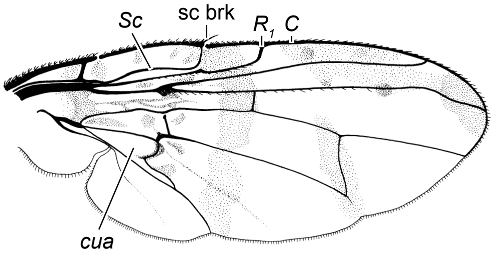
73 (61′). Antennal postpedicel (pped) wide, without arista. Minute and stout flies; black with blue metallic sheen. Subcostal wing vein (*Sc*) complete, but difficult to discern.

Cryptochetidae [in part] (Chapter 107)

Specimens interpreted as having subcostal vein complete.

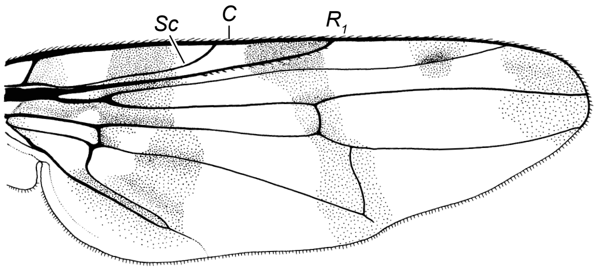
73′ (61′). Antennal postpedicel (pped) with arista; rarely absent or reduced, but if so, then body neither stout nor black with blue metallic sheen; postpedicel variable. Subcostal wing vein (*Sc*) complete or abruptly bent forward distally.

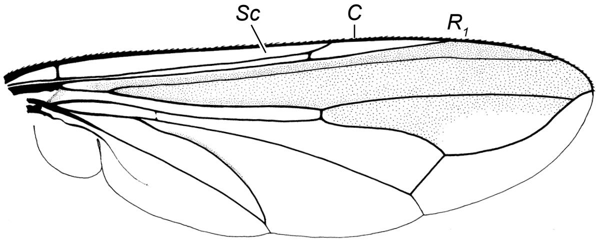
74



74 (73′). Subcostal wing vein (*Sc*) almost always abruptly bent forward to costal vein (*C*) distally (usually weak or transparent beyond bend) and vein R_1 setulose dorsally; subcostal break (sc brk) present; anterior cubital cell (*cua*) usually lobate, lobe usually pointed; wings usually patterned. Head almost always with inclinate frontal setae and reclinate orbital setae; ocelli present; vibrissa absent.

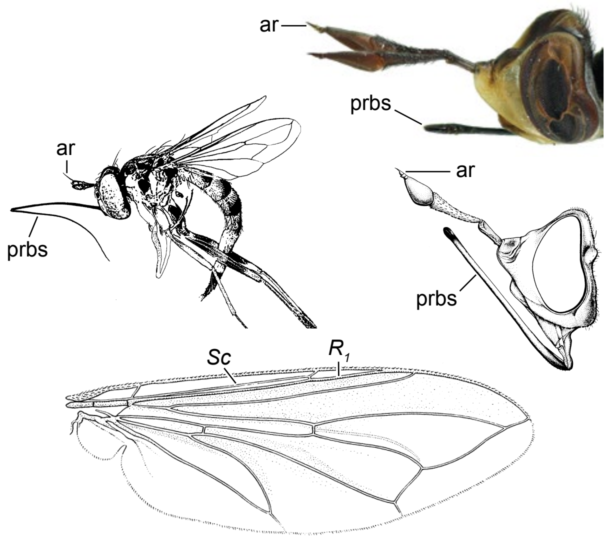
Tephritidae (Chapter 71)





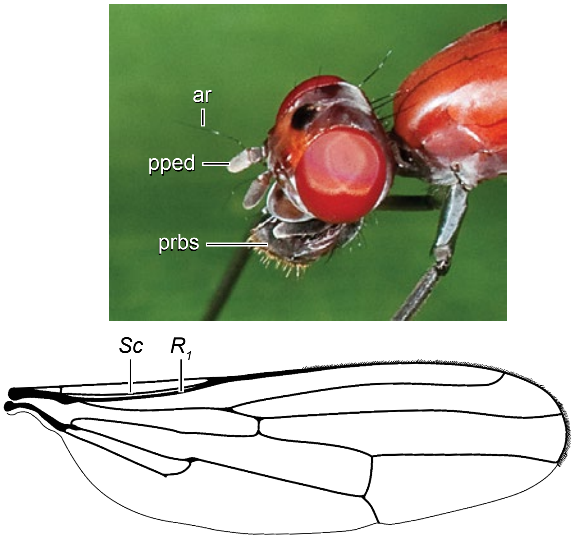
74′ (73′). Subcostal wing vein (*Sc*) not abruptly bent forward to costal vein (*C*) distally (rare exceptions EITHER have vein R_1 bare, subcostal break absent, frons without inclinate frontal setae, ocelli absent, OR vibrissa present). Other characters variable.

75



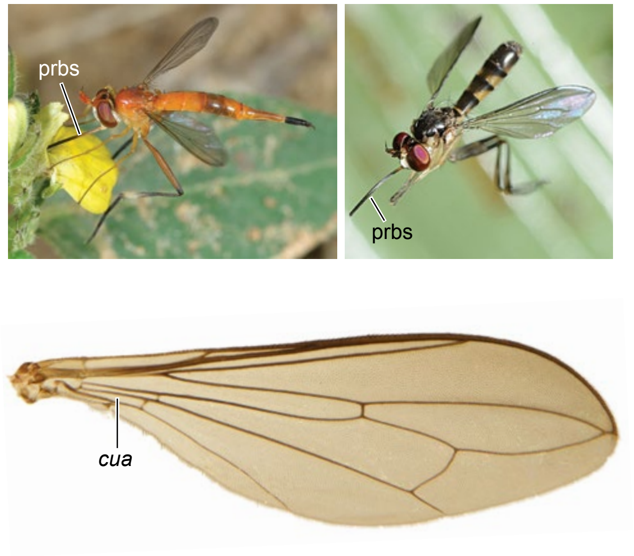
75 (74′). Subcostal wing vein (*Sc*) usually touching vein *R_1* or connected to it by crossvein. Antennal arista (ar) short or stylus-like (longer in some MYOPINAE). Proboscis (prbs) usually long and sharply bent forward (relatively short in MYOPINAE). Body often without distinct setae.

Conopidae (Chapter 66) 76



75′ (74′). Subcostal wing vein (*Sc*) usually not touching vein *R_1* or connected to it by crossvein. Antennal arista (ar) longer than antennal postpedicel (pped). Proboscis (prbs) short (except in some small black Milichiidae). Body usually with distinct setae (although many Diopsidae lack distinct setae).

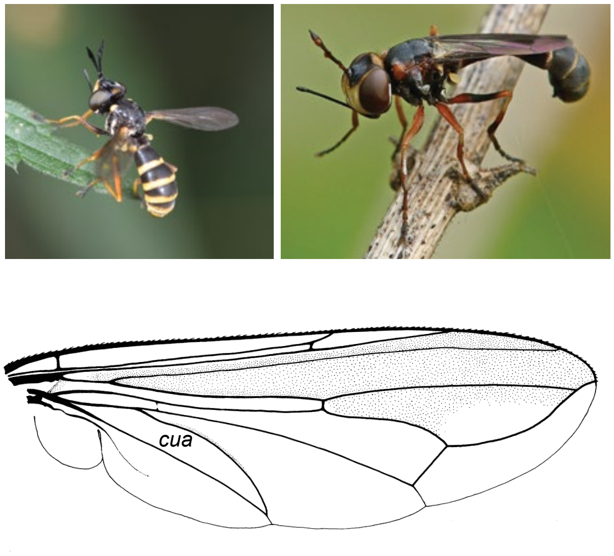
77



76 (75). Anterior cubital wing cell (*cua*) short, usually not pointed. Slender, long-legged flies, with distinct setae and strikingly elongate and geniculate (bent medially) proboscis (prbs).

Conopidae [in part] (Chapter 66)

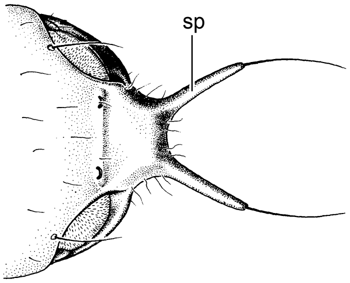
STYLOGATERINAE, sometimes treated as the separate family Stylogastridae.



76′ (75). Anterior cubital wing cell (*cua*) long, usually pointed. Body relatively robust, often without distinct setae, often bee-like or wasp-like. Proboscis variable.

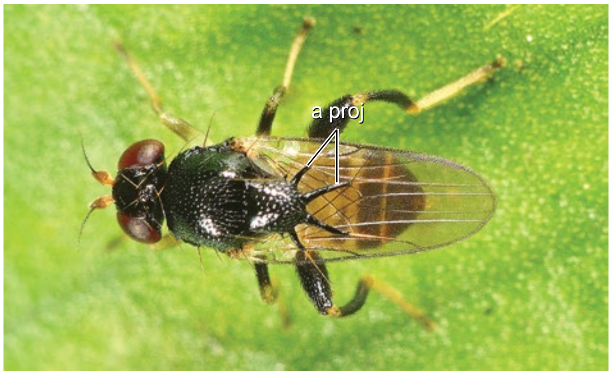
Conopidae [in part] (Chapter 66)

Subfamilies other than STYLOGASTRINAE.



77 (75′). Scutellum with 2 distinct, spine-like (sp) or tubular apical projections, often ending in setae. Head usually conspicuously broad, with eyes on distinct stalks (except in subfamily CENTRIONCINAE). Fore femur often thickened, armed with two rows of stout ventral tubercles and often 2 rows of stout ventral spines.

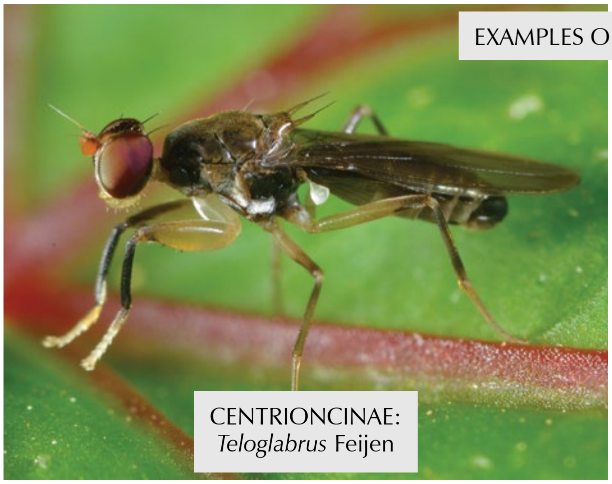
Diopsidae [in part; most] (Chapter 64)



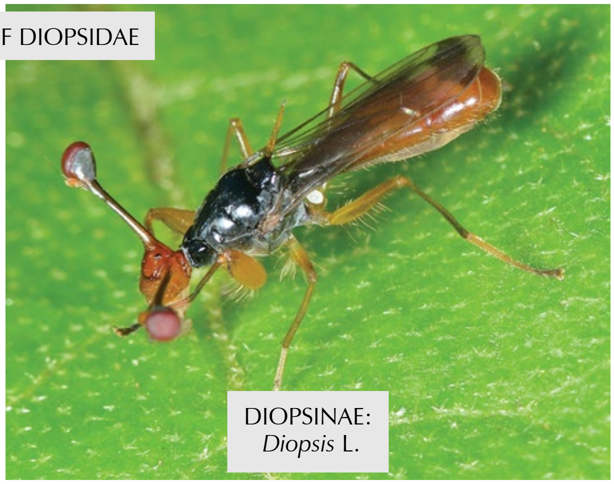
77′ (75′). If scutellum with long apical projections (a proj) (rarely), then head not conspicuously broad, eyes not stalked and fore femur not thickened and armed with tubercles and/or spines.

78

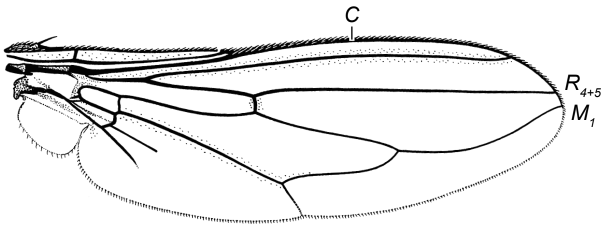
EXAMPLES OF DIOPSIDAE



CENTRIONCINAE: *Teloglabrus* Feijen

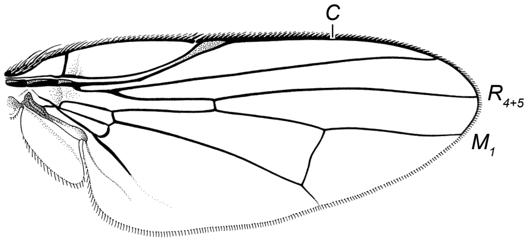


DIOPSINAE: *Diopsis* L.



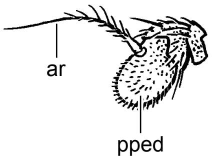
78 (77′). Wing veins R_{4+5} and M_1 converging towards wing tip; costal vein (C) never spinose. Head without ocellar setae. Size usually > 7 mm, usually slender and long-legged.

79



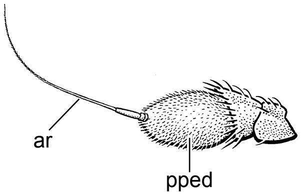
78′ (77′). Wing veins R_{4+5} and M_1 almost invariably parallel or divergent; exceptions have costal vein (C) spinose. Head almost always with ocellar setae (sometimes minute and difficult to discern). Size variable, usually not slender and long-legged.

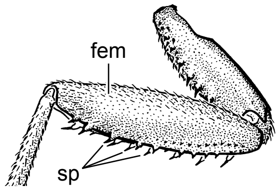
80



79 (78). Arista (ar) dorsobasal (inserted near base of antennal postpedicel (pped)). Fore femur without ventral spines. Head with vibrissa absent or slender and inconspicuous.

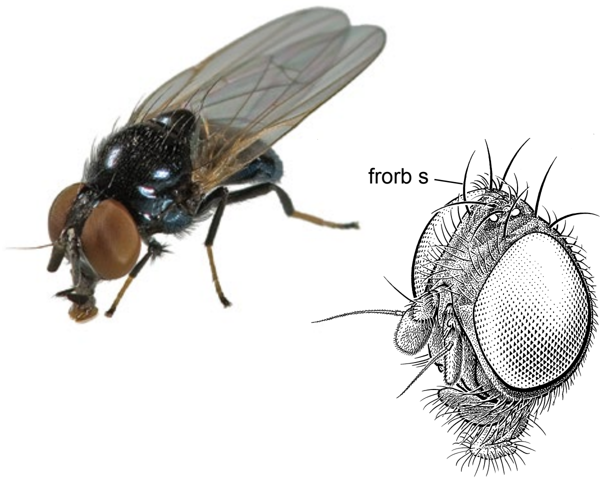
Micropezidae (Chapter 62)

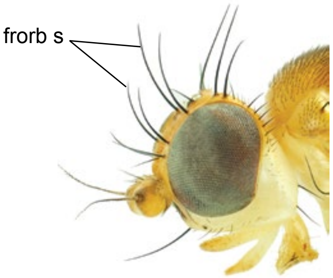


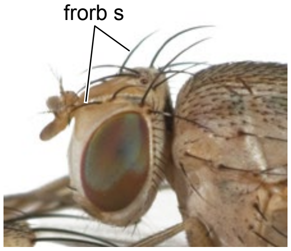


79′ (78). Arista (ar) apical or virtually so (inserted near apex of antennal postpedicel (pped)). Fore femur (fem) with ventral spines (sp). Head with vibrissa absent or short and stout.

Neriidae (Chapter 63)







80 (78′). Halter (hlt; see below) colour black or dark brown; wing membrane without distinct markings. Thorax with anepisternum (anepst; see below) with row of setae (s; see below) along posterior margin. Vibrissa absent. Head with 1 pair of fronto-orbital setae (frorb s). Female with lance-like ovipositor (ovp; see below) with fused apical cerci. Usually small, shiny blue-black or metallic green flies.

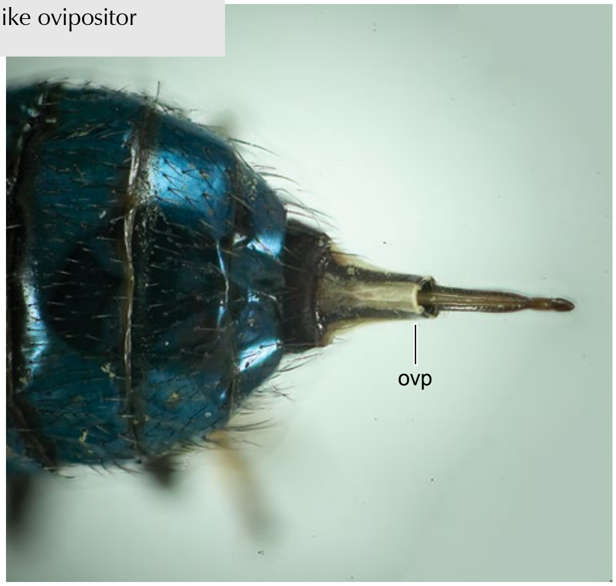
Lonchaeidae (Chapter 67)

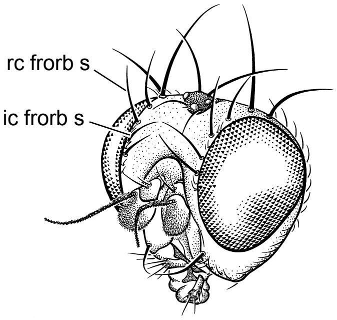
80′ (78′). Halter colour and wing membrane variable. Thorax with anepisternum with or without row of setae on posterior margin. Vibrissa present or absent. Head usually with 2 or more pairs of fronto-orbital setae (frorb s). Female ovipositor variable. Size and colour variable, rarely shiny blue-black or metallic.

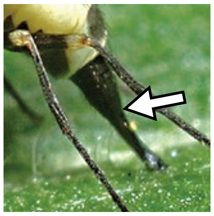
81

FEATURES OF LONCHAEIDAE:

anepisternum with setae along posterior margin
halter black
females with lance-like ovipositor

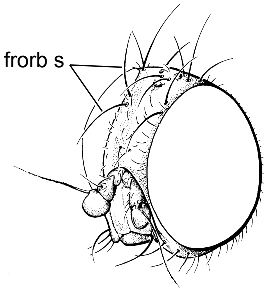


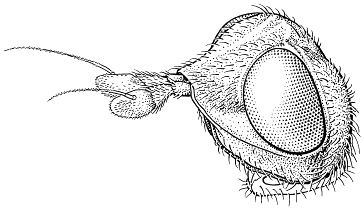




81 (80′). Wing never conspicuously patterned; if wing with slight marking, then never with dorsal setulae on vein R_1. Thorax with anepisternum (in red) with an irregular row of 1 long and some shorter setae along posterior margin. Head with inclinate ventral fronto-orbital setae (ic frorb s), together with 1 or more reclinate fronto-orbital setae (rc frorb s) (rarely absent). Female abdomen with conspicuously dark and hard conical oviscape (arrowed) (exceptionally yellowish).

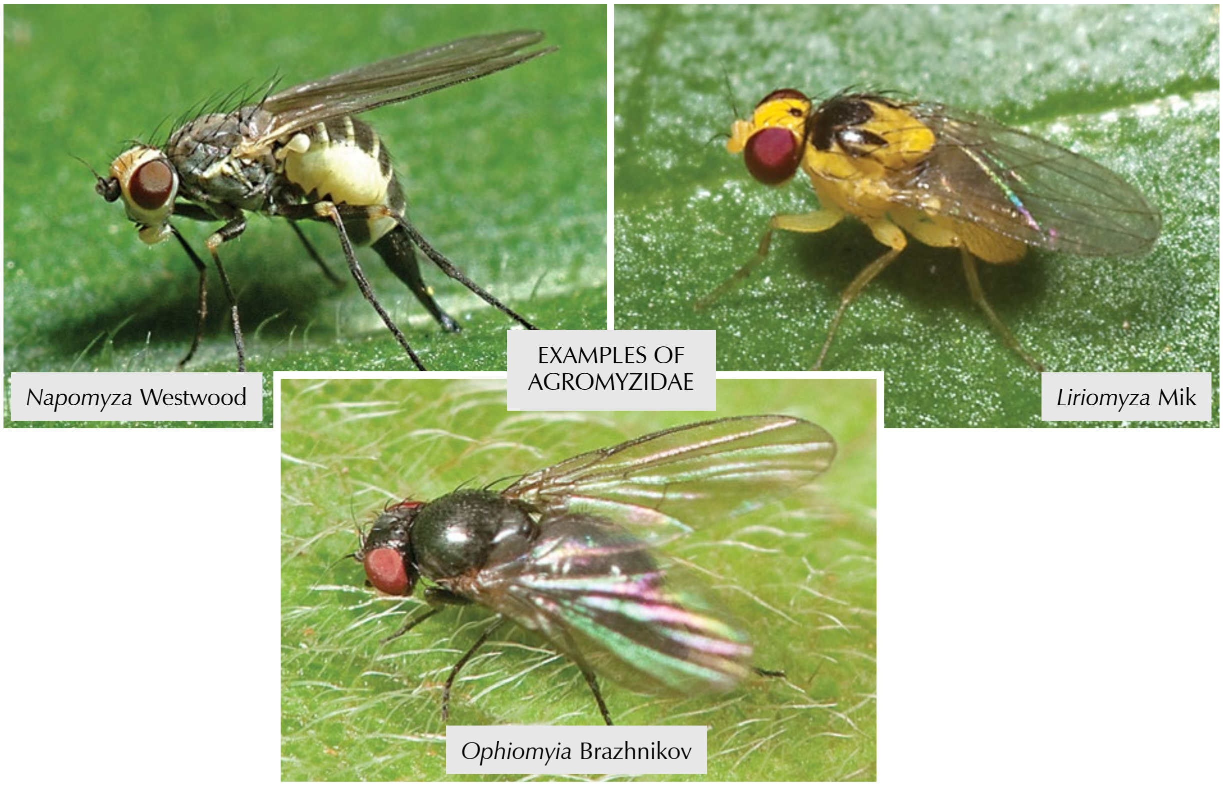
Agromyzidae [in part] (Chapter 86)





81′ (80′). EITHER wing membrane strongly patterned and fronto-orbital setae present, OR fronto-orbital setae absent, OR thorax with anepisternum (in red) without row of setae on posterior margin. Head usually with 2 or more pairs of fronto-orbital setae (frorb s). Female abdomen variable.

82



EXAMPLES OF AGROMYZIDAE

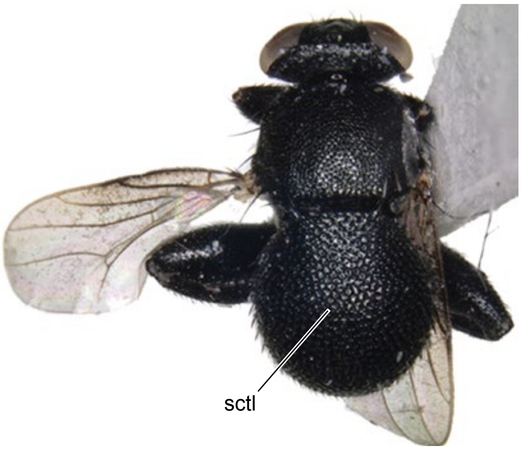
Napomyza Westwood

Liriomyza Mik

Ophiomyia Brazhnikov

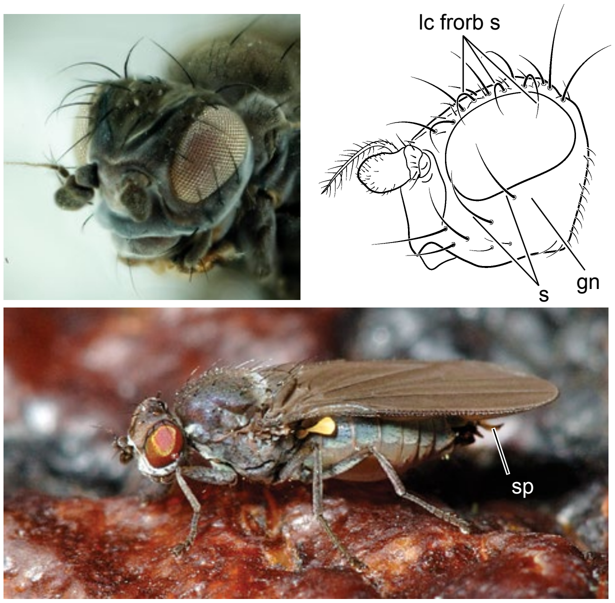
82 (81′). Scutellum (sctl) distinctively inflated, usually larger than scutum (sct) and often largely covering wings (creating beetle-like appearance); margin of scutellum smooth, not spinose.

Celyphidae (Chapter 75)



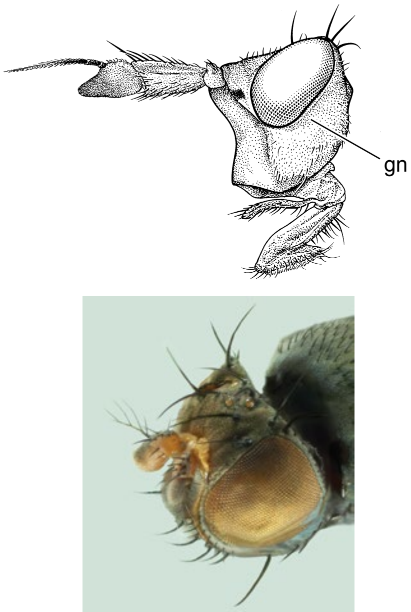
82′ (81′). Scutellum (sctl) rarely greatly enlarged, but if so (Chloropidae genus *Nomba* Walker), then margin spinose rather than smooth.

83



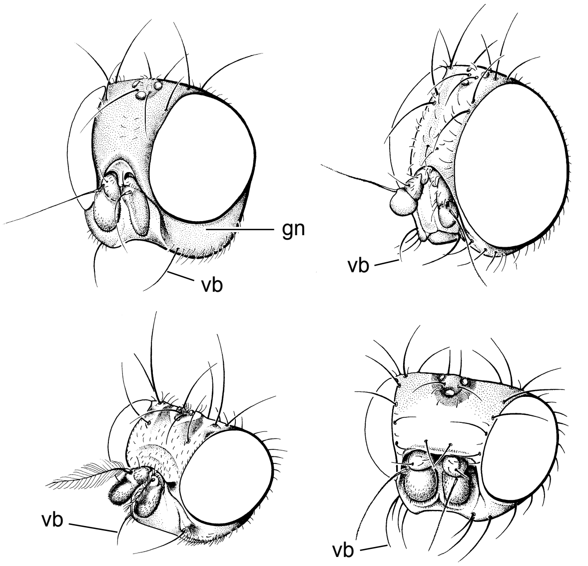
83 (82′). Head with gena (gn) with 1 to several strong upcurved setae (s) below compound eye; frons with 2 or more lateroclinate fronto-orbital setae (lc frorb s). Female abdomen ending in upcurved spines (sp).

Canacidae [in part] (Chapter 94)



83′ (82′). Head with gena (gn) without prominent upcurved setae; frons rarely with series of lateroclinate fronto-orbital setae. Female abdomen variable.

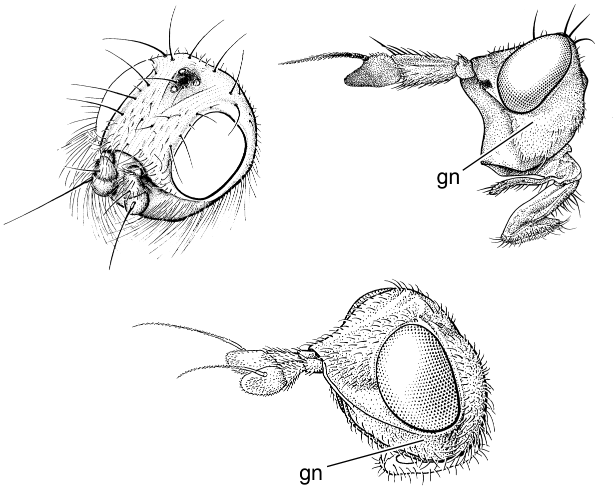
84



84 (83′). Head with vibrissa (vb) (vibrissal angle or anterior angle of gena (gn) with 1, or occasionally 2, setae clearly larger and usually differently oriented than nearby setae).

85

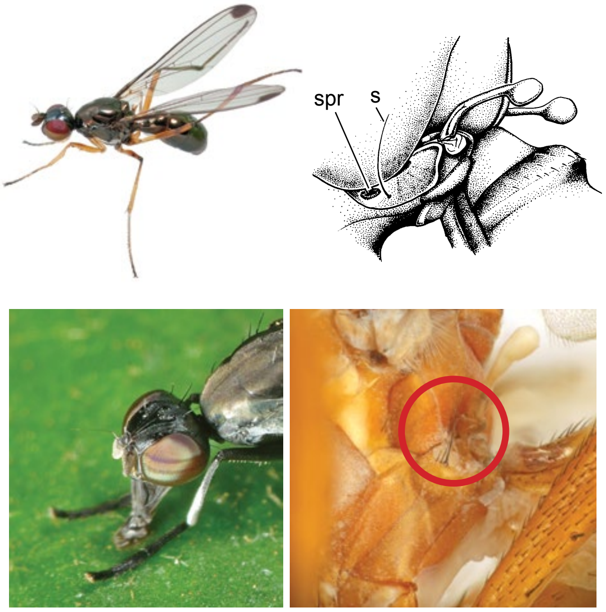
Families without true vibrissae, but sometimes with vibrissa-like setae, key both ways.



84′ (83′). Head without vibrissa (but gena (gn) sometimes densely setulose or with enlarged vibrissa-like setae).

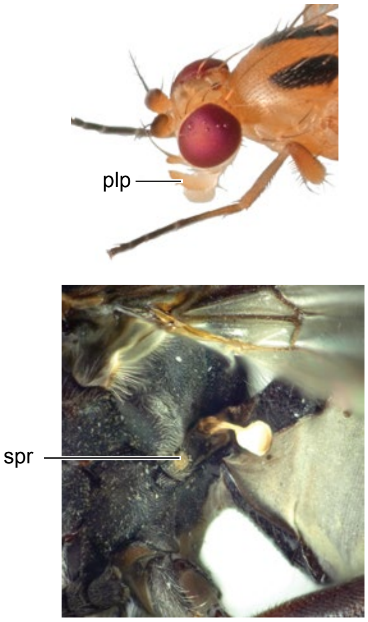
98

Families without true vibrissae, but sometimes with vibrissa-like setae, key both ways.



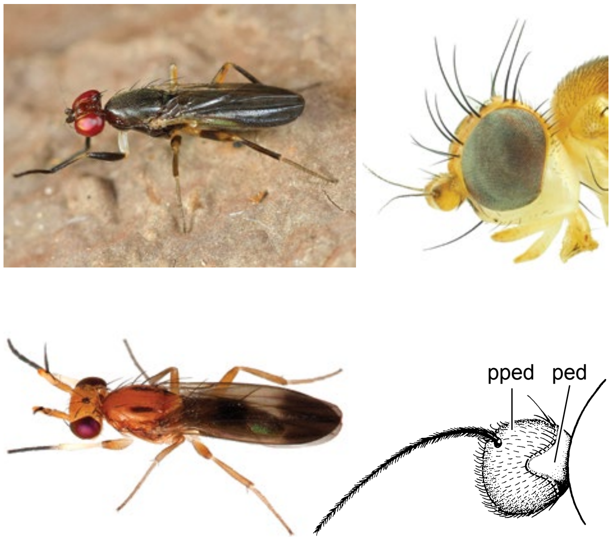
85 (84). Posterior thoracic spiracle (spr) with at least 1 seta (s) near ventral margin (red circled). Palpus usually minute or absent. Form usually ant-like.

Sepsidae [in part] (Chapter 79)



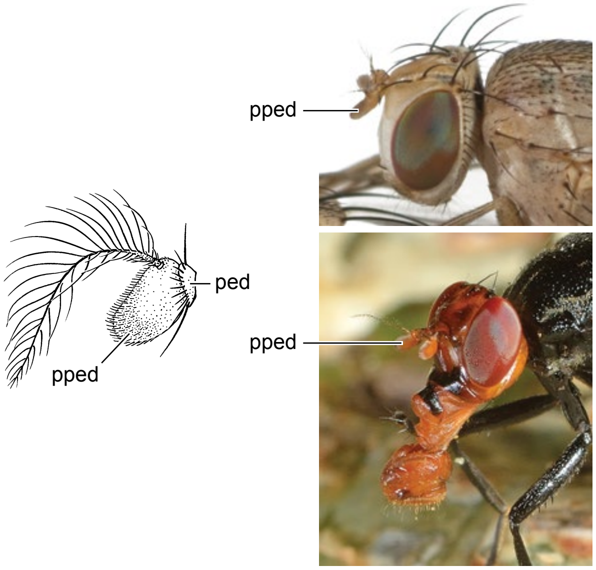
85′ (84). Posterior thoracic spiracle (spr) without seta near ventral margin. Palpus (plp) present. Form rarely ant-like.

86



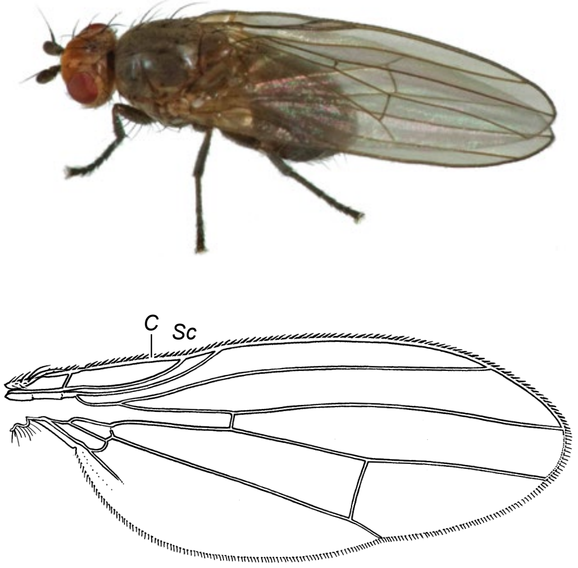
86 (85′). Antennal pedicel (ped) with small lobe on outer distal margin, projecting into postpedicel (pped). Small (length usually 2–6 mm), slender flies, often brightly coloured and all or partly yellow or orange (sometimes brown or black). Wing membrane usually at least partly infuscate.

Clusiidae (Chapter 81)



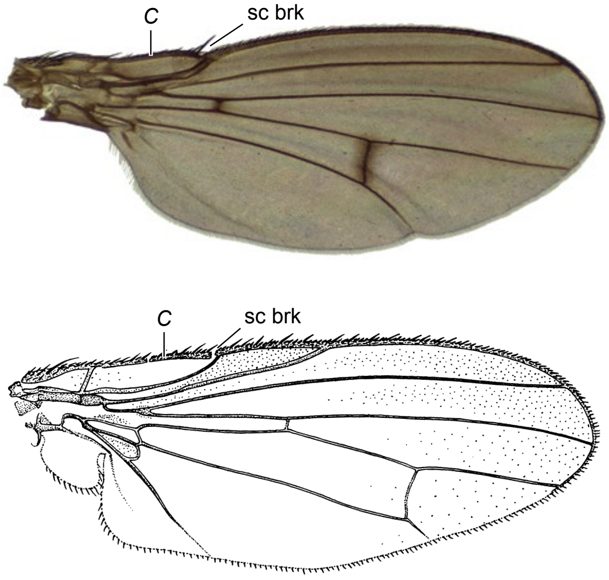
86′ (85′). Antennal pedicel (ped) without small lobe on outer distal margin. Size and colouration variable. Wing membrane usually hyaline, but sometimes maculate or partly infuscate.

87



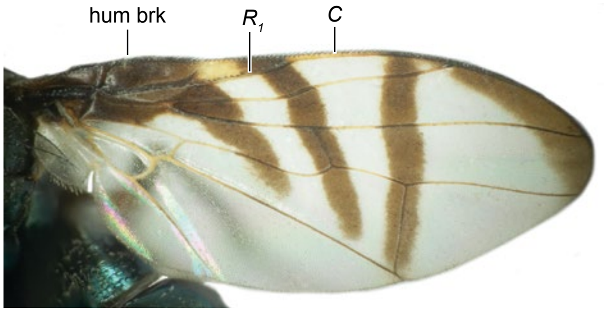
87 (86′). Costal wing vein (C) not broken at end of subcostal vein (Sc) (*i.e.*, without subcostal break); never spinose.

88



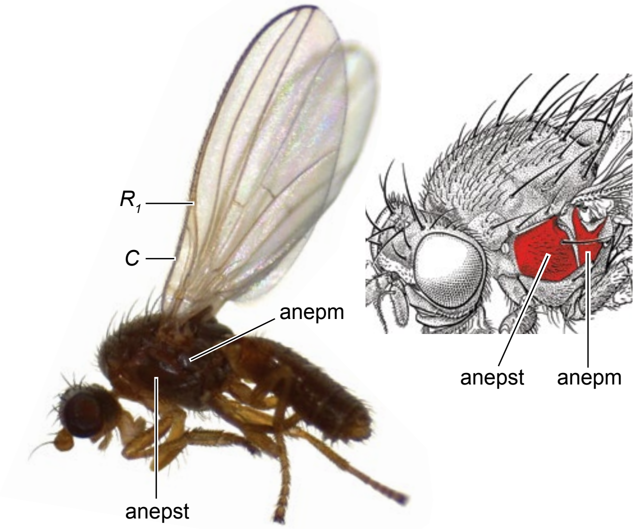
87′ (86′). Costal wing vein (C) broken at end of subcostal vein (Sc) (*i.e.*, with subcostal break; sc brk); sometimes spinose.

90



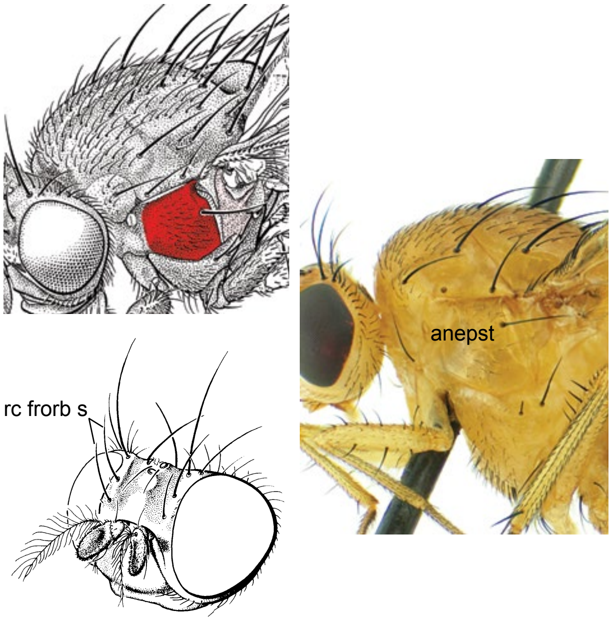
88 (87). Wing vein R_1 and sometimes other veins, with small dorsal setae throughout length; costal vein (C) with humeral break (hum brk). Thorax with anepimeron and anepisternum setose.

Platystomatidae [in part] (Chapter 70)



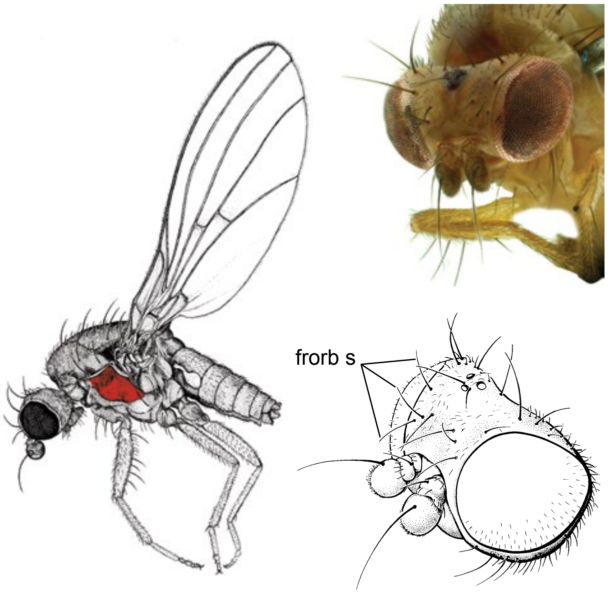
88′ (87). Wing vein R_1 usually entirely bare dorsally, sometimes setose in basal ½ only; costal vein (C) without humeral break. Anepisternum (anepst) variable, anepimeron (anepm) bare.

89



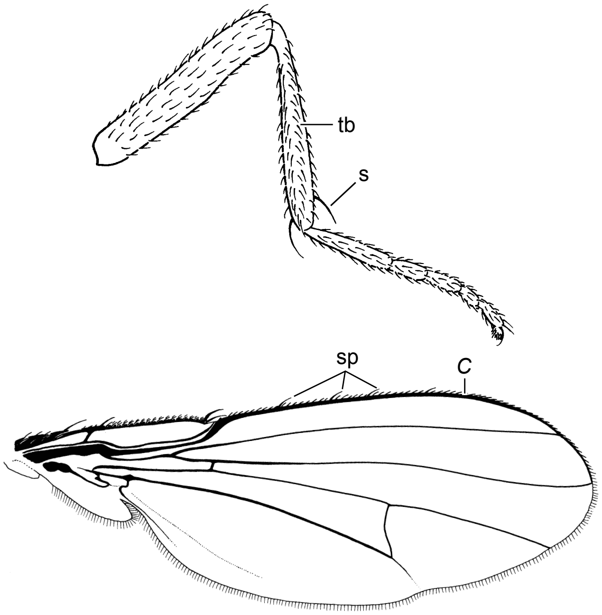
89 (88′). Thorax with anepisternum (in red) setose. Head with 1–2 pairs of reclinate fronto-orbital setae (rc frorb s). Size, shape and colour variable.

Lauxaniidae [in part] (Chapter 74)



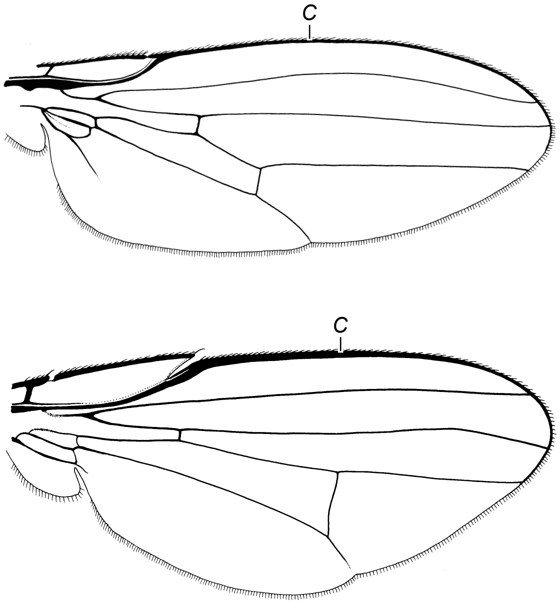
89′ (88′). Anepisternum (in red) bare. Head with fronto-orbital setae (frorb s) arranged in 3 or more differently oriented pairs. Elongate yellow to brown flies, *ca* 3–5 mm in length.

Natalimyzidae [in part] (Chapter 80)



90 (87′). At least one leg with strong preapical dorsal seta (s) on tibia (tb). Costal wing vein (C) often spinose (sp).

91



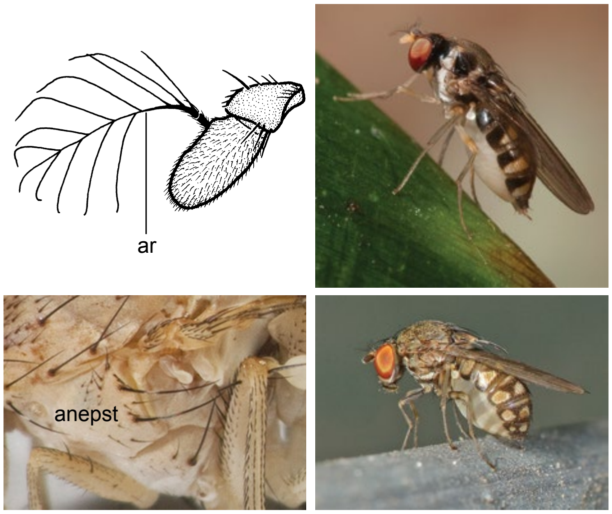
90′ (87′). Tibiae without preapical dorsal setae. Costal vein (C) rarely spinose.

92

EXAMPLES OF PLATYSTOMATIDAE

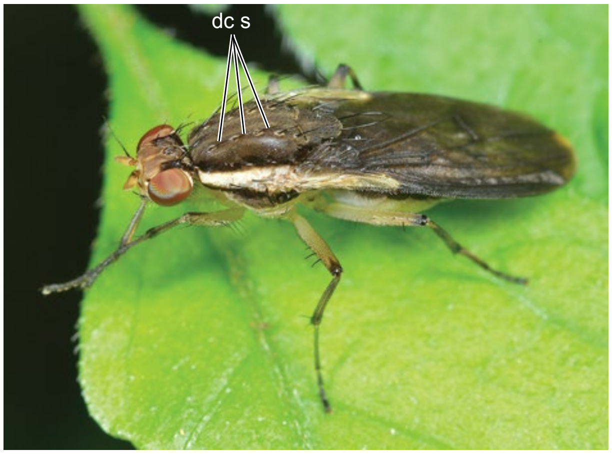

Oeciotypa Hendel


Engistoneura Loew



91 (90). Thorax with dorsum strongly arched; anterior ½ with uniformly small setae (without presutural dorsocentral setae). Anepisternum (anepst) setose. Arista (ar) almost invariably with long branches at least dorsally (dorsal and ventral branches rarely short). If 2 fronto-obital setae present, then the anterior pair distinctly proclinate.

Curtonotidae (Chapter 103)



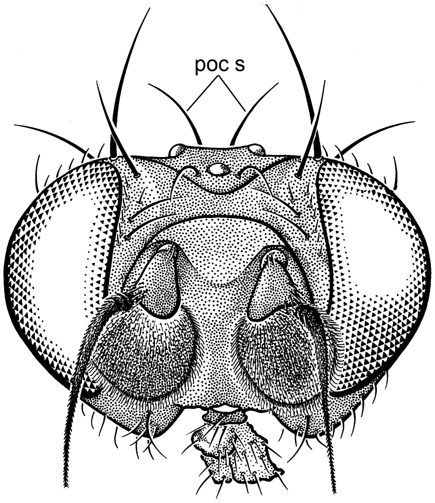
91′ (90). Thorax with dorsum not strongly arched. Anepisternum variable. Arista variable, but if plumose, then anterior ½ of thorax with dorsocentral setae (dc s) and with single reclinate fronto-orbital seta (*Suillia* Robineau-Desvoidy).

Heleomyzidae [in part; most] (Chapter 98)

EXAMPLES OF HELEOMYZIDAE

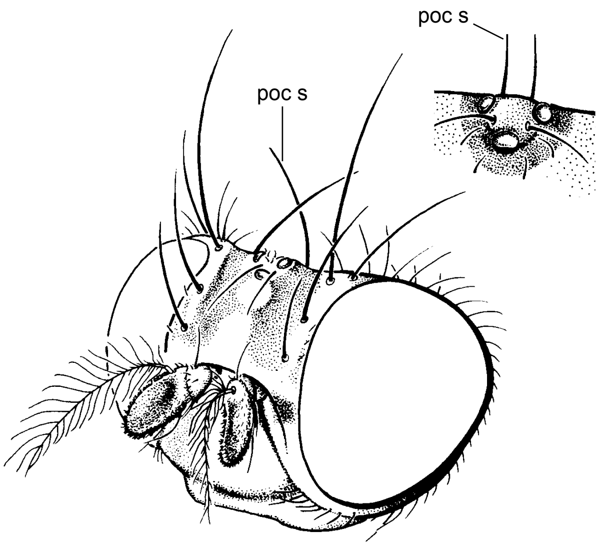

Suillia Robineau-Desvoidy


Trixoscelis Robineau-Desvoidy



92 (90′). Head with postocellar setae (poc s) divergent (very rarely parallel; absent in *Ophiomyia arabica* (Deeming) (Agromyzidae)).

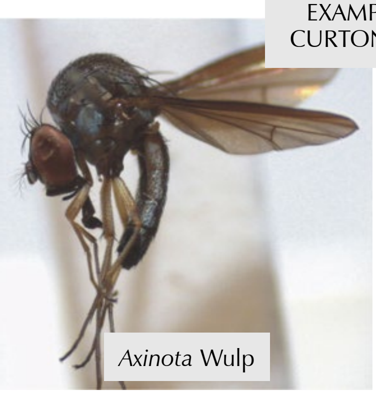
93



92′ (90′). Head with postocellar setae (poc s) convergent, parallel or absent.

94

EXAMPLES OF CURTONOTIDAE

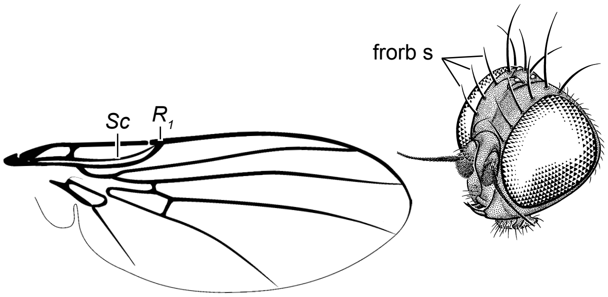


Axinota Wulp

Curtonotum Macquart

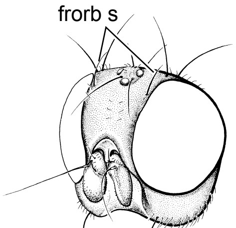
Tigrisomyia Kirk-Spriggs

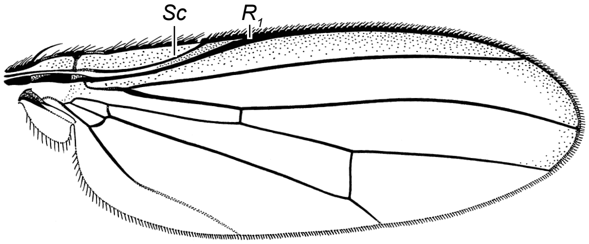
Cyrtona Séguy



93 (92). Subcostal wing vein (*Sc*) indistinct apically or ending close to end of vein R_1. Head with 2–8 pairs of fronto-orbital setae (frorb s), ventral pairs inclinate. Female abdomen with conspicuously dark and hard conical oviscape (exceptionally yellowish). Female cerci at tip of ovipositor, obtuse and separated. Body usually 2–4 mm in length.

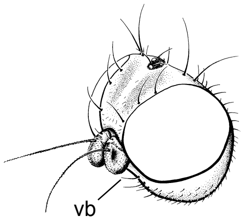
Agromyzidae [in part] (Chapter 86)

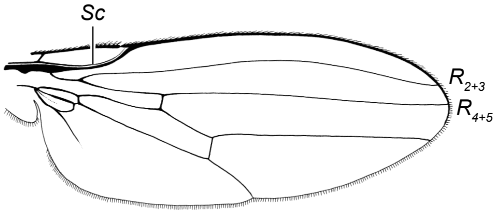




93′ (92). Subcostal wing vein (*Sc*) distinct, apex separate from vein R_1. Head with 0–4 pairs of fronto-orbital setae (frorb s), ventral pairs rarely inclinate. Female abdomen with telescoping apex, without hard tubular oviscape. Female cerci forming the tip of eversible piercing-type ovipositor, fused. Body usually 3–6 mm in length.

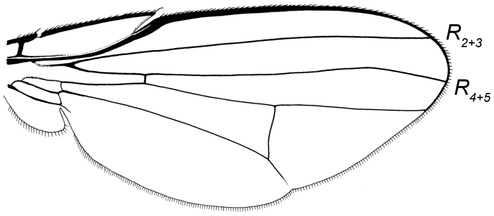
Piophilidae (Chapter 68)





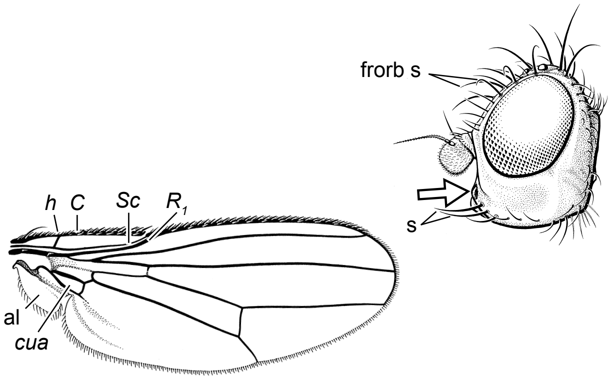
94 (92′). Wing veins R_{2+3} and R_{4+5} converging slightly towards wing tip. Small (usually 0.5–3.0 mm in length), usually all or partly pale yellowish, with pale setae and metallic green or red eyes (may be faded in dry specimens). Wing membrane hyaline and subcostal vein (*Sc*) distally weak. Head with vibrissa (vb) small and inconspicuous.

Chyromyidae [in part] (Chapter 97)



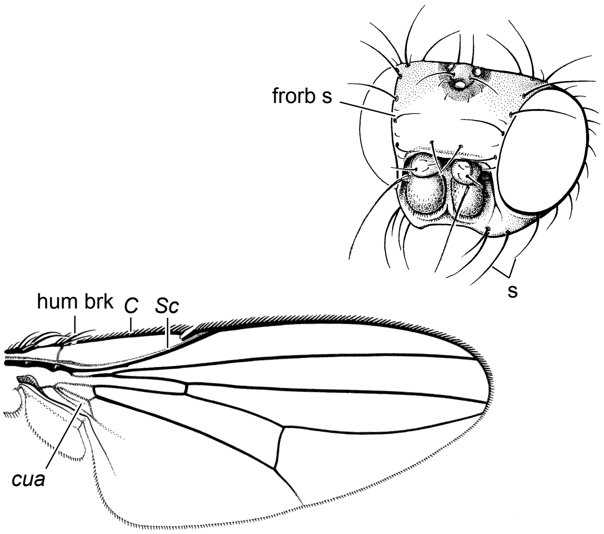
94′ (92′). Wing veins R_{2+3} and R_{4+5} not converging towards wing tip. Eye not metallic (sometimes reddish), rarely yellow. Size and wing variable. Head usually with distinct setae on vibrissal angle.

95



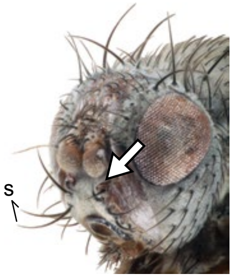
95 (94′). Costal wing vein (*C*) without humeral break (with a weakening beyond humeral crossvein (*h*), that could be interpreted as a break in *Suffomyia* Freidberg); subcostal vein (*Sc*) joining vein R_1 just before *C*. Ventral fronto-orbital setae (frorb s) reclinate to lateroclinate (not inclinate). Area just above vibrissa-like seta (s) (true vibrissa in *Dasyrhicnoessa* Hendel) usually with small shiny knob (arrowed) (if absent then disc of scutellum bare, or anterior cubital cell (*cua*) of wing open distally and/or alula (al) strongly reduced). Body often silvery pruinose. Associated with saline environments.

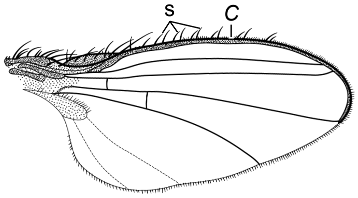
Canacidae [in part] (Chapter 94)

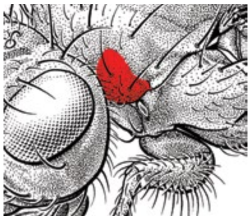


95′ (94′). Costal wing vein (*C*) with distinct humeral break (hum brk); subcostal vein (*Sc*) variable. Head with ventral fronto-orbital setae (frorb s) inclinate (incurved). Area just above vibrissa-like seta (s) usually without small shiny knob. Body rarely silvery pruinose. Associated with various habitats.

96

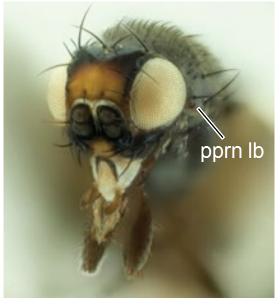


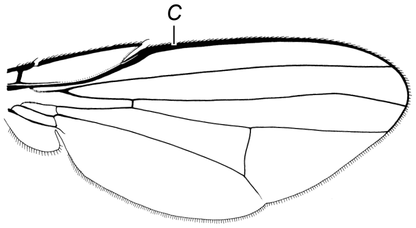




96 (95′). Head with area immediately above vibrissa-like seta (s) with small shiny knob (arrowed). Thorax with postpronotal lobe (in red) with 3 differently oriented setae. Costal vein (*C*) with robust, long spine-like setae (s). Associated with coastal habitats.

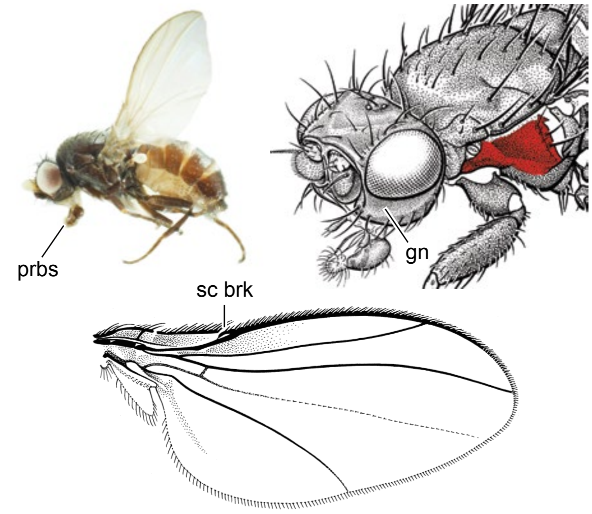
Canacidae [in part] (Chapter 94)





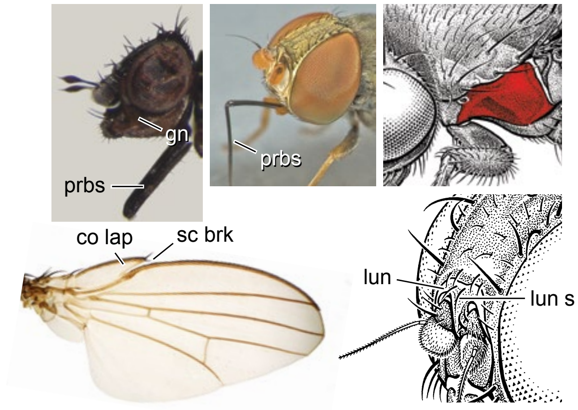
96′ (95′). Head with area immediately above vibrissa-like seta unmodified, lacking small shiny knob. Thorax with postpronotal lobe (pprn lb) variable, but not with 3 distinct, differently oriented setae. Costal vein (C) without spine-like setae. Associated with various habitats, but not coastal.

97



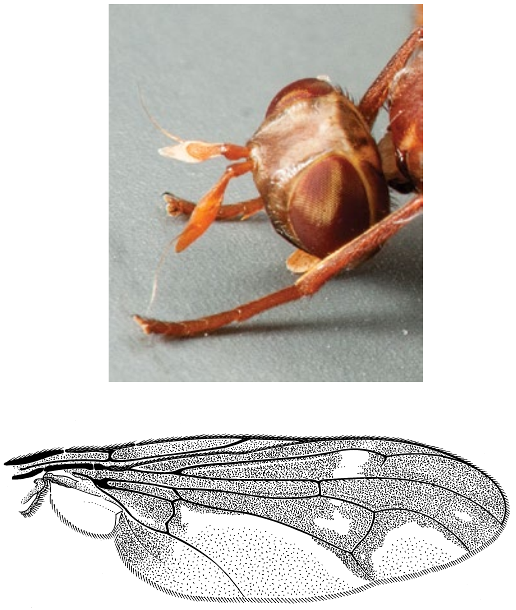
97 (96′). Proboscis (prbs) short, not geniculate (not bent medially). Anepisternum (in red) with setulae or setae. Vibrissa inserted below ventral margin of compound eye. Subcostal break (sc brk) without costal lappet. Antennae inserted in deep, distinct depressions; vibrissal angle of gena (gn) never prolonged into elongated triangle. Body length: 1–3 mm.

Carnidae [in part] (Chapter 93)



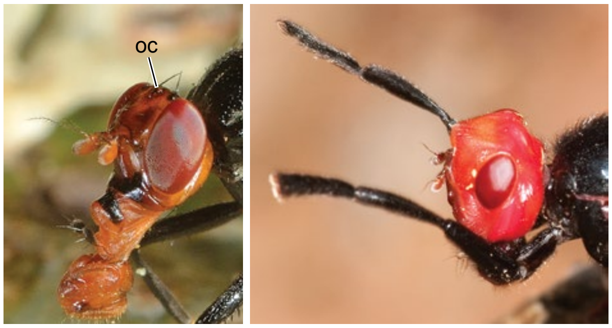
97′ (96′). Proboscis (prbs) geniculate (bent medially). Anepisternum (in red) bare, or head with vibrissa inserted well above ventral margin of compound eye; if anepisternum setose and vibrissa below margin of eye, then lunule (lun) and lunular setae (lun s) obvious. Wing with subcostal break (sc brk) sometimes very large and flanked by costal lappet (co lap). Antennae not usually inserted in deep depressions, if in deep depressions, then vibrissal angle of gena (gn) prolonged into elongated triangle. Body length: 1–7 mm.

Milichiidae [in part] (Chapter 95)



98 (84′). Head without ocelli. Wing membrane usually patterned, never uniformly black. Uncommon crepuscular or nocturnal flies.

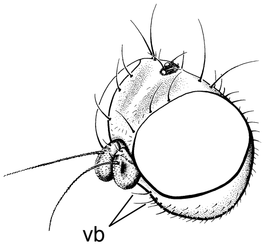
Pyrgotidae [in part] (Chapter 72)

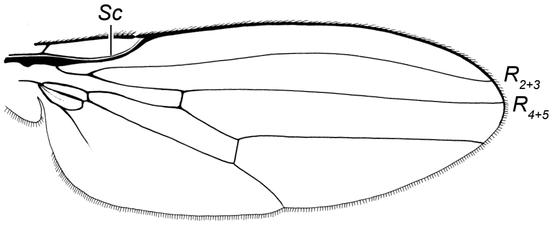


98′ (84′) Head normally with ocelli (oc) (often absent in *Bromophila* Loew (Platystomatidae), with wing membrane entirely black). Common, normally diurnal flies.

99

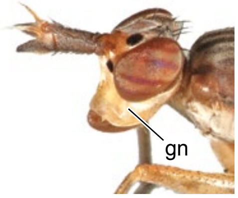
PLATYSTOMATIDAE
Bromophila caffra (Macquart)
Atypical Afrotropical species with loss or reduction of ocelli.

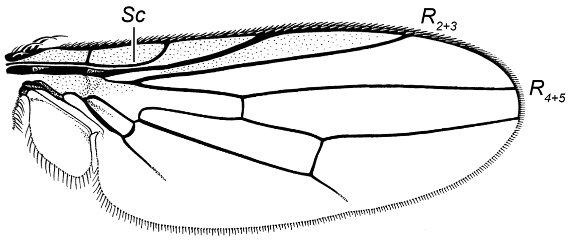




99 (98′). Wing veins R_{2+3} and R_{4+5} converging slightly towards wing tip. Small (usually body length: 0.5–3.0 mm), usually all or partly pale yellowish, with pale setae and metallic green or red eyes (may be faded on dry specimens). Wing membrane hyaline and subcostal vein (*Sc*) weak distally. Head with small and inconspicuous vibrissa (vb).

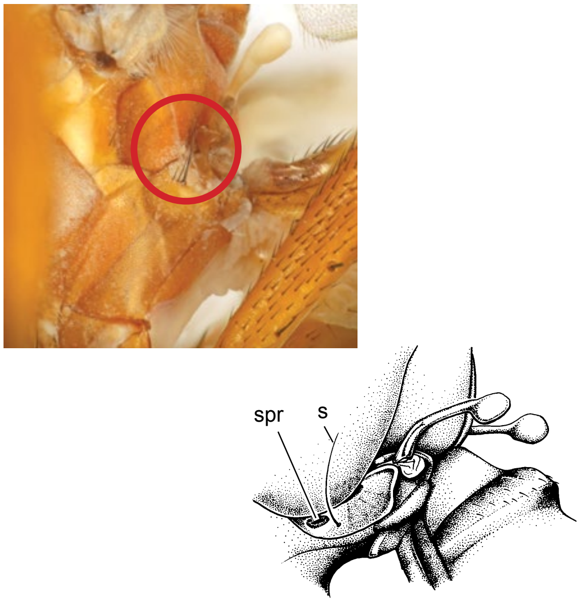
Chyromyidae [in part] (Chapter 97)





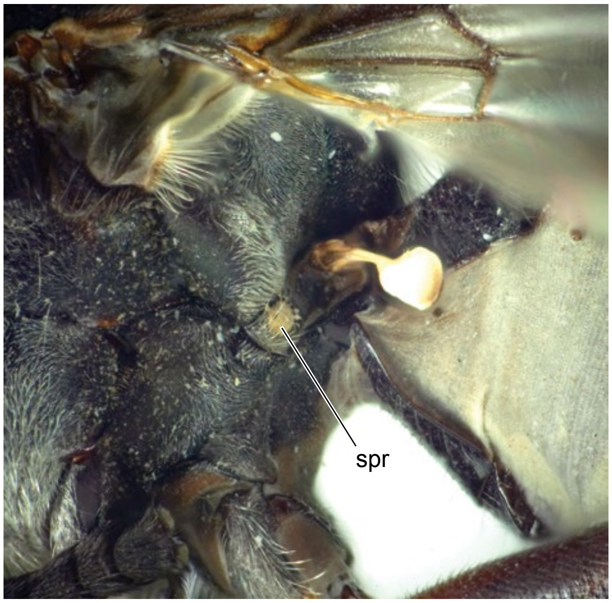
99′ (98′). Wing veins R_{2+3} and R_{4+5} not converging towards wing tip. Size and appearance variable, but never pale yellow with metallic eyes. Wing membrane variable, subcostal vein (*Sc*) usually distinct distally. Head without vibrissa, but gena (gn) sometimes with multiple long setulae.

100



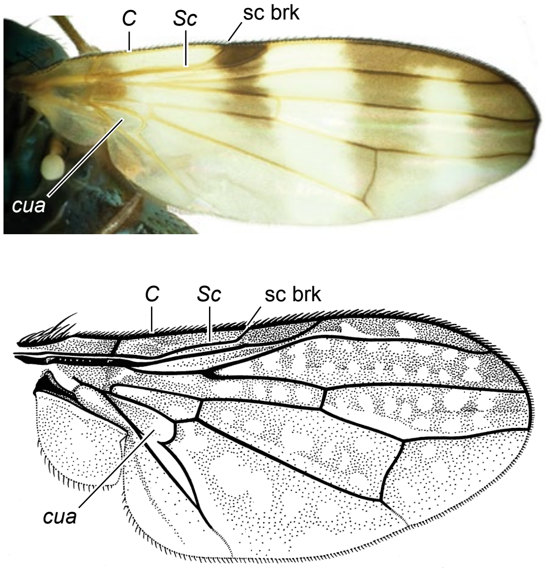
100 (99′). Posterior thoracic spiracle (spr) with at least 1 seta (s) along ventral margin (red circled). Ant-like flies, with spherical head and reduced palpus.

Sepsidae [in part] (Chapter 79)



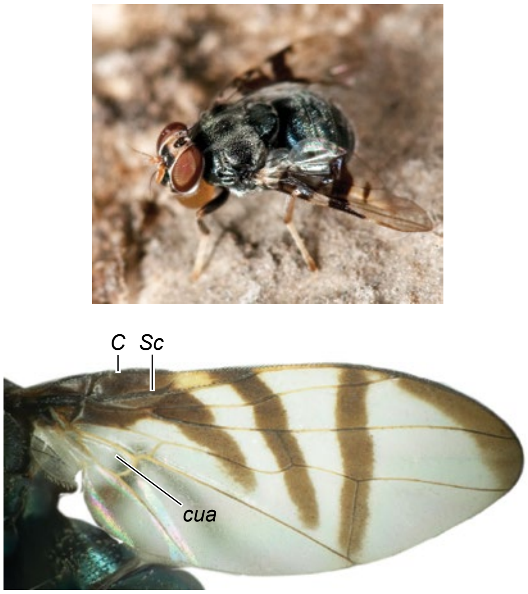
100′ (99′). Posterior thoracic spiracle (spr) without setae along ventral margin. Rarely ant-like flies, head not spherical, palpus usually well-developed.

101



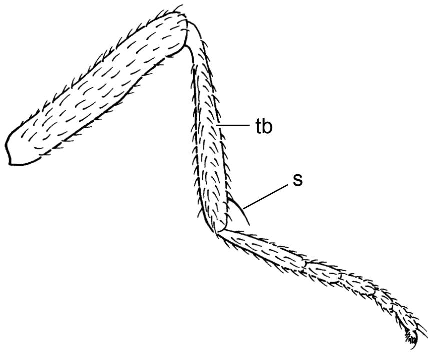
101 (100′). Costal wing vein (C) broken, or discontinuous near apex of subcostal vein (*Sc*) (subcostal break (sc brk) often indistinct, best viewed with transmitted light); anterior cubital cell (*cua*) usually with pointed posterior angle.

Ulidiidae [in part] (Chapter 69)



101′ (100′). Costal wing vein (C) unbroken (without distinct subcostal break or fracture near end of subcostal vein (*Sc*)); anterior cubital cell (*cua*) variable.

102

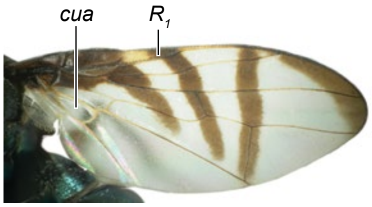


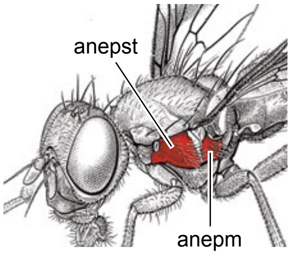
102 (101′). All tibiae without preapical dorsal seta.

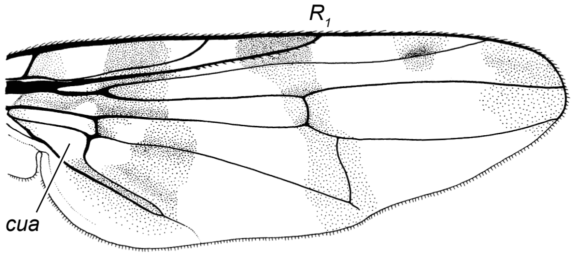
103

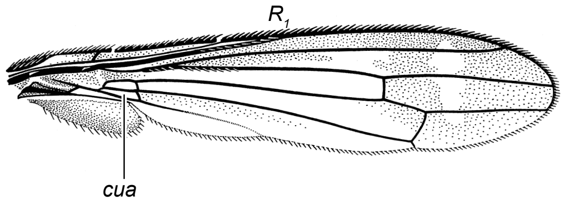
102′ (101′). Some or all tibiae (tb) with preapical dorsal seta (s).

106







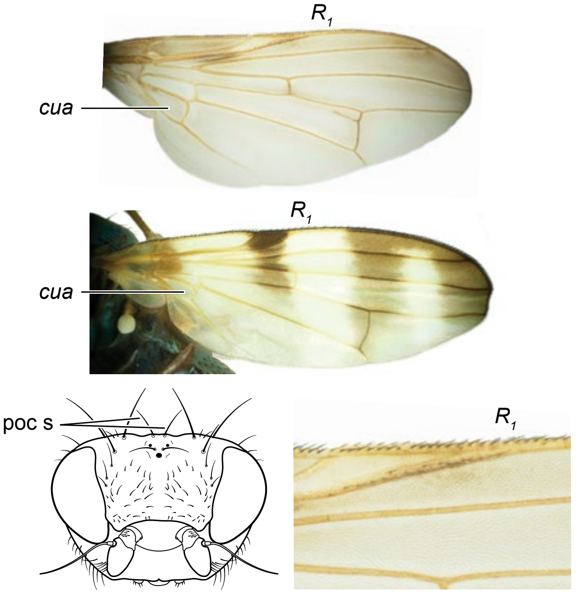


103 (102). Wing vein R_1, and sometimes other veins, with dorsal setae throughout length. Thorax with anepimeron (anepm) and anepisternum (anepst) with setae. Anterior cubital wing cell (*cua*) never posterodistally extended.

Platystomatidae [in part] (Chapter 70)

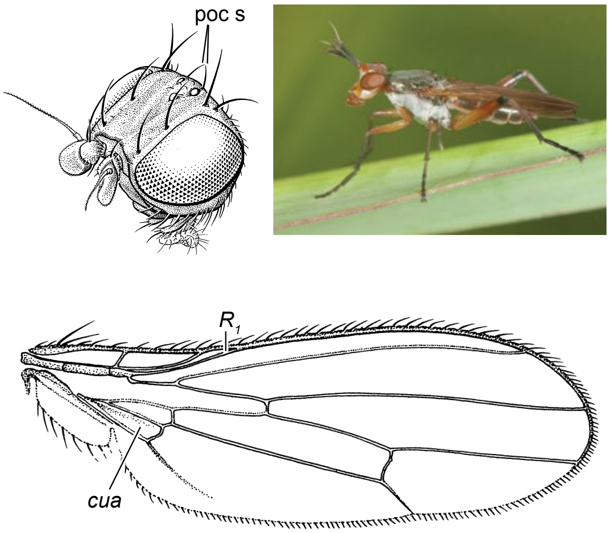
103′ (102). Wing vein R_1 usually bare dorsally, if partially setulose, then anepimeron without setae. Anepisternum variable. Anterior cubital cell (*cua*) sometimes posterodistally extended.

104



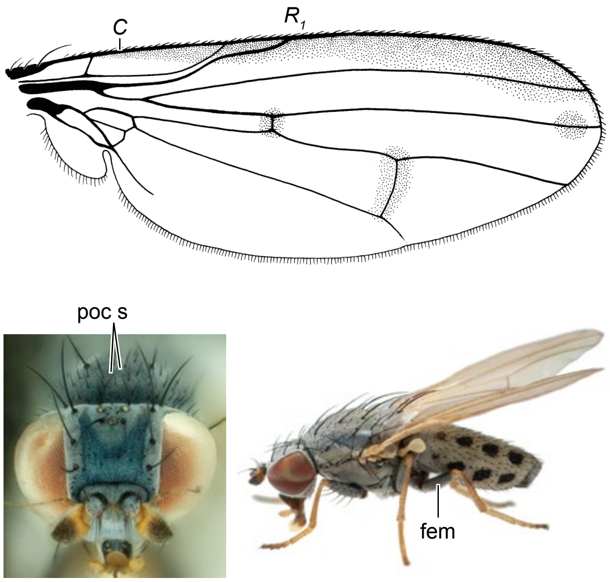
104 (103′). Postocellar setae (poc s) divergent. EITHER wing with distal part of vein R_1 spinulose dorsally, OR anterior cubital cell (*cua*) with distal point; membrane usually strongly patterned.

Ulidiidae [in part] (Chapter 69)



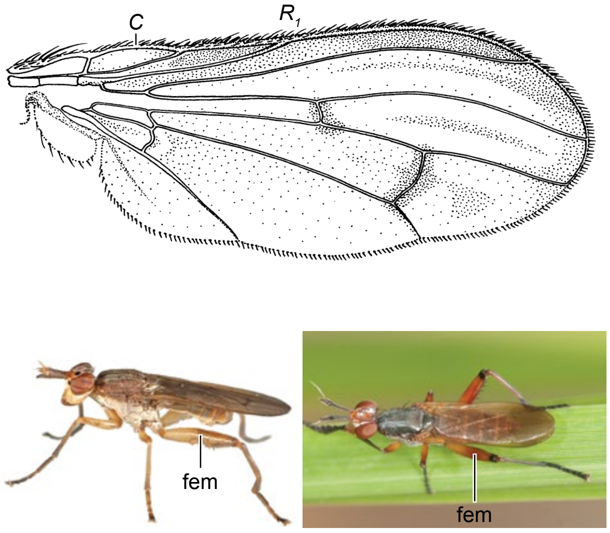
104′ (103′). Postocellar setae (poc s) usually convergent or absent, sometimes parallel or slightly divergent. Wing vein R_1 bare; anterior cubital cell (*cua*) without point; membrane usually hyaline, without conspicuous markings or pattern.

105



105 (104′). Hind femur (fem) not swollen, lacking ventral rows of spines. Wing vein R_1 with slight bend before meeting costal vein (C). Postocellar setae (poc s) absent or convergent.

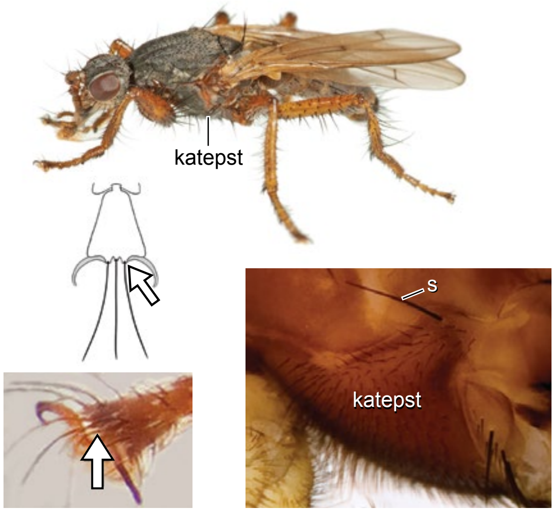
Chamaemyiidae (Chapter 76)



105′ (104). Hind femur (fem) thicker than mid femur, usually with ventral rows of spines. Wing vein R_1 evenly curved to costal vein (C). Head with postocellar setae parallel or slightly divergent.

Sciomyzidae [in part] (Chapter 78)

Species in which preapical tibial seta inconspicuous.

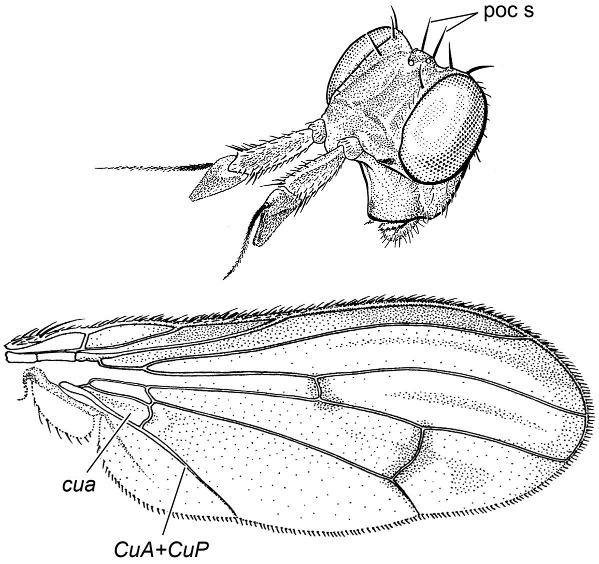


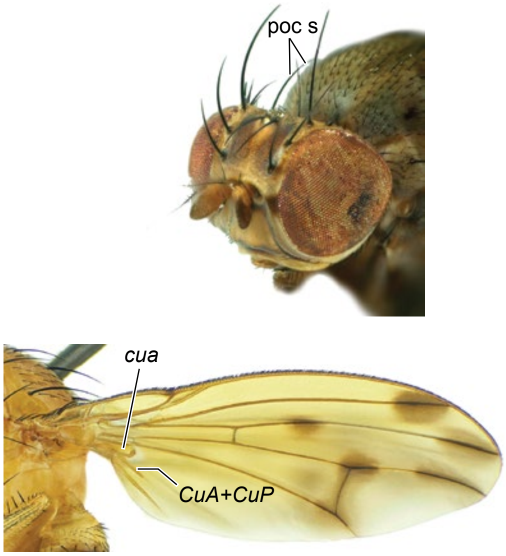
106 (102′). Katepisternum (katepst) with large anteriorly directed seta (s) in posterodorsal corner. All legs with last tarsal segment (terminal tarsomere) triangular, flattened, wider than other segments, with 2–3 setiferous tubercles on distal margin above claws (arrowed). Marine coastal flies, usually dorsoventrally flattened, with densely setose gena and legs.

Coelopidae (Chapter 77)

106′ (102′). Katepisternal seta, if present, directed dorsally or posteriorly. Fore leg with terminal tarsomere similar to penultimate tarsomere, without enlarged apical setae. Habitat and appearance variable. None-marine coastal flies (although Sciomyzidae may occur in coastal habitats); body shape normal, gena and legs not densely setose.

107



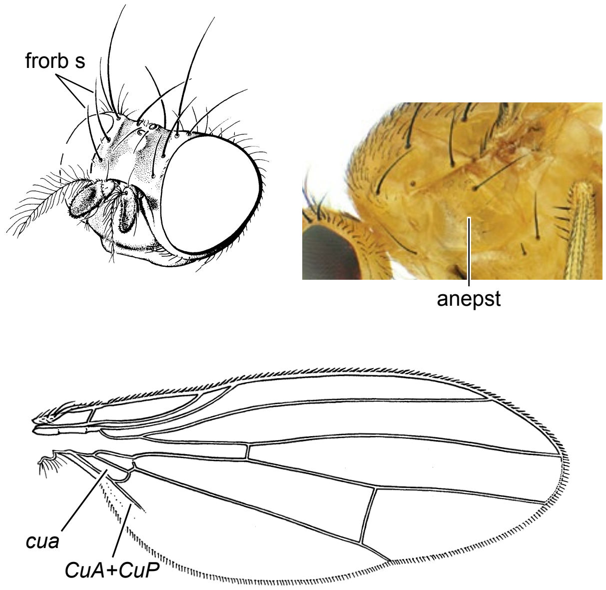


107 (106′). Wing vein *CuA+CuP* (from posterior angle of anterior cubital cell (*cua*)) usually extending to or almost to wing margin. Postocellar setae (poc s) divergent or parallel, rarely absent, but if so, then scutellum with 1 pair of setae.

Sciomyzidae [in part] (Chapter 78)

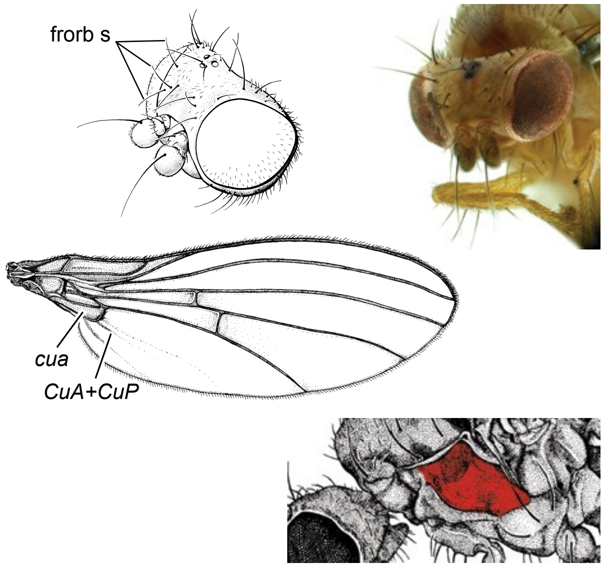
107′ (106′). Wing vein *CuA+CuP* (from posterior angle of anterior cubital cell (*cua*)) short, ending well before wing margin. Postocellar setae (poc s) convergent, rarely absent or parallel, but if so, then scutellum with 2 pairs of setae.

108



108 (107′). Wing vein *CuA+CuP* sclerotised beyond apex of anterior cubital cell (*cua*). Head usually with 1–2 fronto-orbital setae (frorb s). Thorax with prosternum broad; anepisternum (anepst) with setae.

Lauxaniidae [in part; most] (Chapter 74)

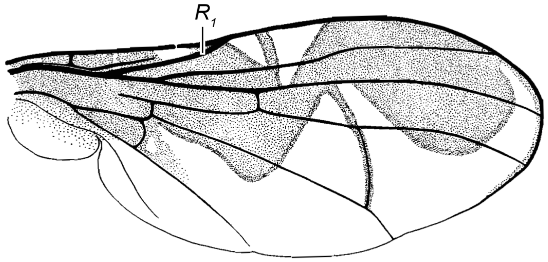


108′ (107′). Wing vein *CuA+CuP* not sclerotised beyond apex of anterior cubital cell (*cua*). Head usually with more than 3 fronto-orbital setae (frorb s), angled in different directions. Thorax with prosternum narrow-oval; anepisternum (in red) without setae.

Natalimyzidae [in part] (Chapter 80)

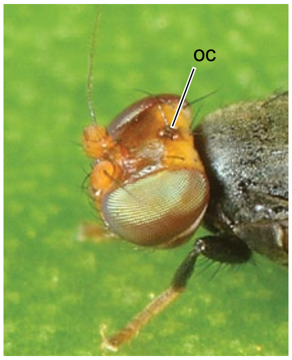
LAUXANIIDAE

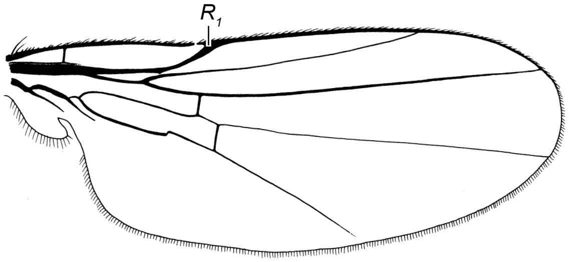
NATALIMYZIDAE



109 (58′). Ocelli absent. Wing vein R_1 usually setulose dorsally (not visible in wing above).

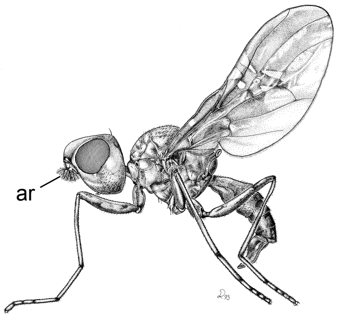
110

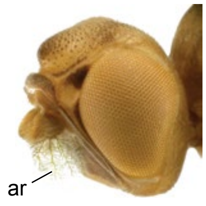




109′ (58′). Ocelli (oc) present. Wing vein R_1 usually bare dorsally.

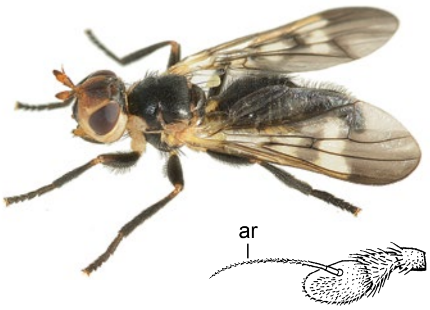
111





110 (109). Head strikingly large (almost as large as thorax); proboscis small to absent. Female antenna with arista (ar) multi-branched, highly distinctive. Rarely collected, usually at lights.

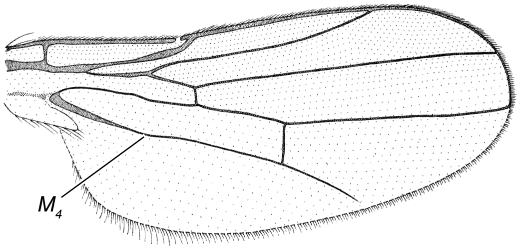
Ctenostylidae (Chapter 73)

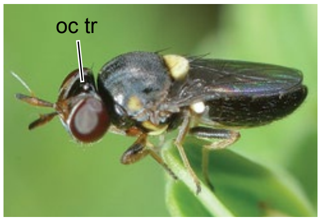


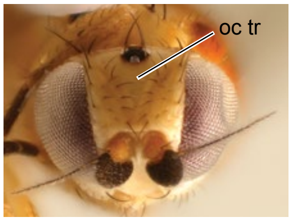
110′ (109). Head not unusually large; proboscis (prbs) well-developed. Female antenna with arista (ar) not multi-branched. Common, usually collected at lights.

Pyrgotidae [in part] (Chapter 72)

Species for which wing vein *Sc* may be interpreted as incomplete.

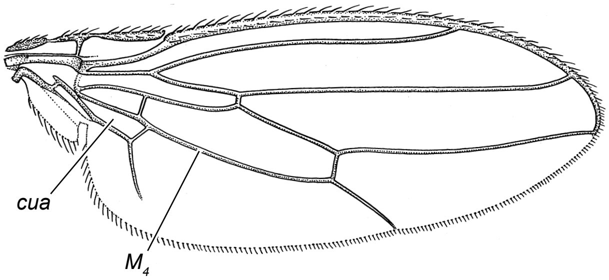


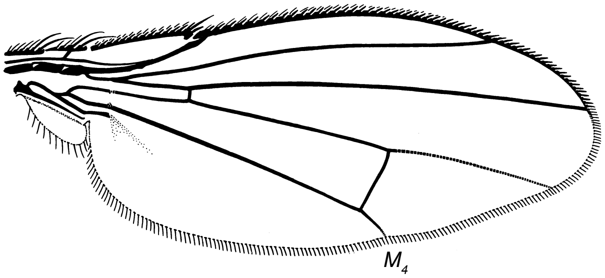




111 (109′). Thorax with propleuron with a raised vertical ridge (propleural carina; prpl car); in some cases obscured by head, usually sharp but sometimes indistinct; see below). Head with ocellar triangle (oc tr) often large, prominent and shiny (in *ca* 50% of species; may be obscured if frons pruinescent). Wing with anterior cubital cell (*cua*) absent; vein M_4 usually with characteristic kink.

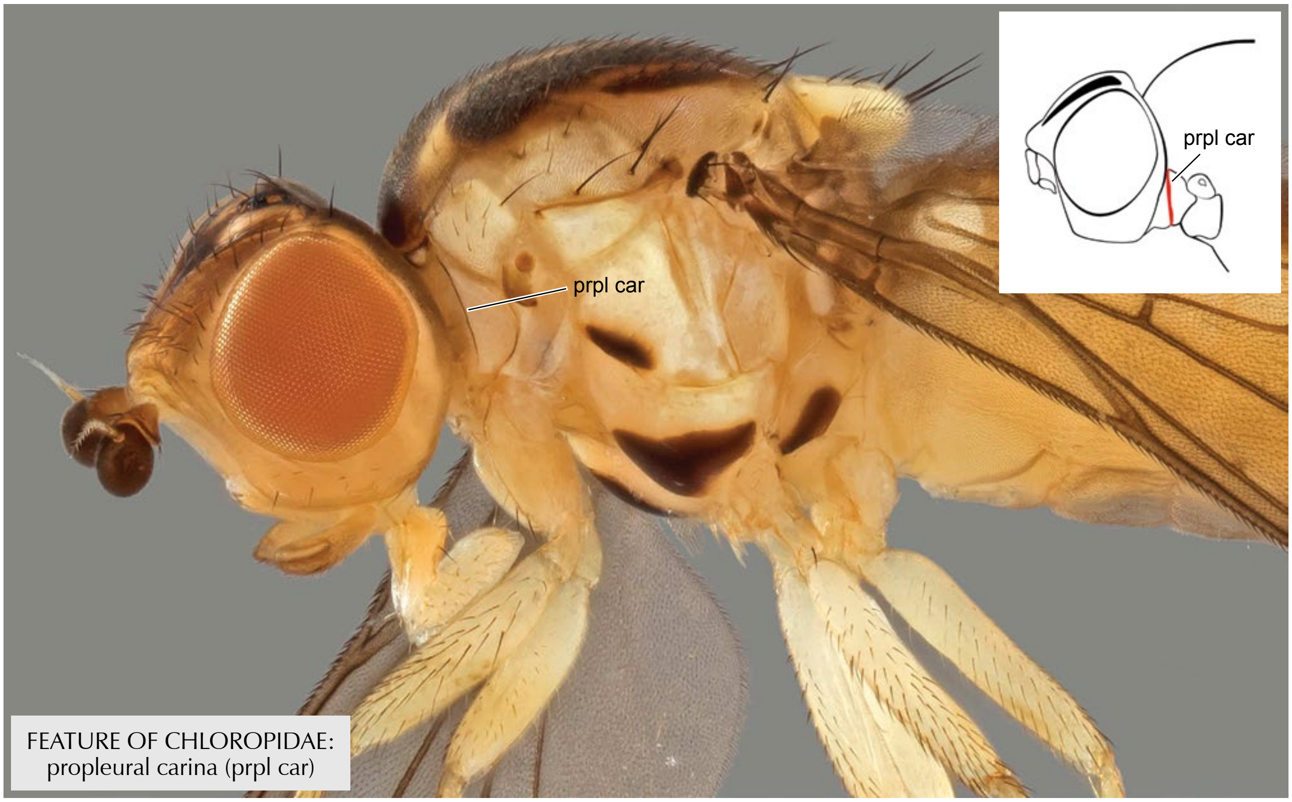
Chloropidae [in part; most] (Chapter 96)



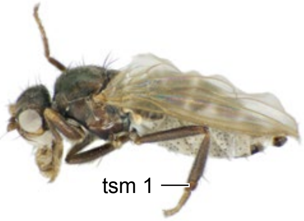


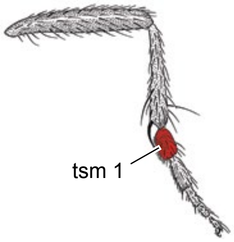
111′ (109′). Thorax without propleural carina (if apparently present, then anterior cubital cell (*cua*) complete). Head with ocellar triangle usually smaller; wing cell (*cua*) open or closed, but vein M_4 without kink.

112



FEATURE OF CHLOROPIDAE:
propleural carina (prpl car)



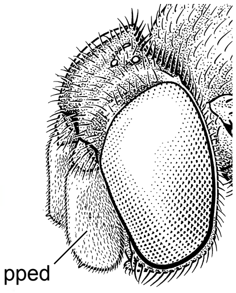


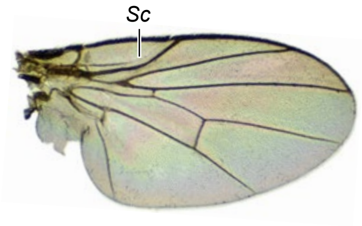
112 (111′). Hind tarsomere 1 (tsm 1) conspicuously short, swollen (in red), broader than distal tarsomeres (sometimes with multiple tarsomeres swollen and short).

Sphaeroceridae [in part; most] (Chapter 99)

112′ (111′). Hind tarsomere 1 (tsm 1) not swollen, usually slender and longer than tarsomere 2.

113

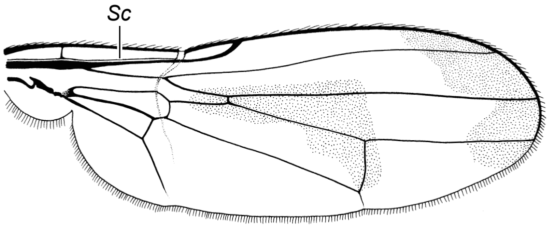




113 (112′). Antennal arista absent or virtually so, and postpedicel (pped) wide. Minute and stout flies; black with blue metallic sheen. Subcostal wing vein (*Sc*) complete, but may be difficult to discern.

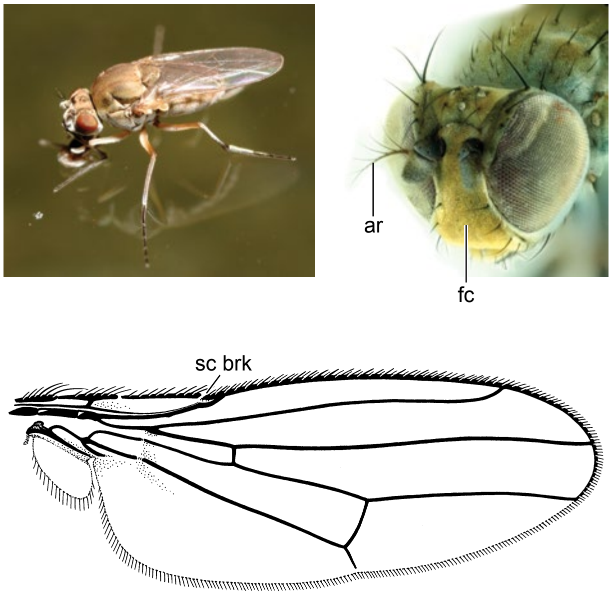
Cryptochetidae [in part] (Chapter 107)

Specimens misinterpreted as having subcostal vein incomplete.



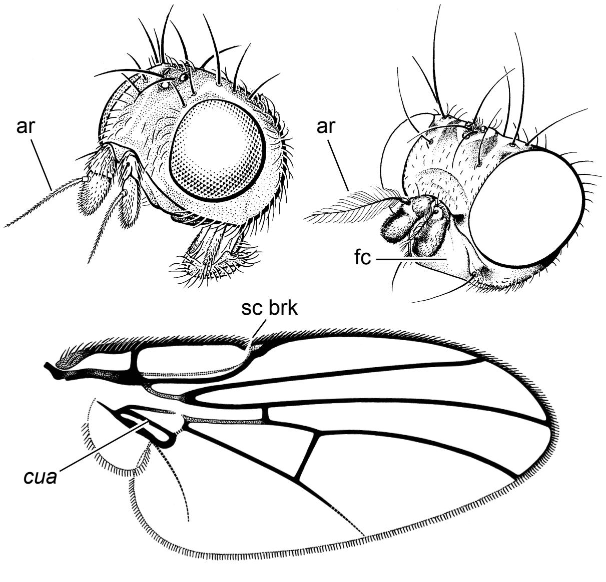
113′ (112′). Antennal arista (ar) rarely absent or reduced, but if so, then body neither stout nor black with blue metallic sheen. Antennal postpedicel variable. Subcostal wing vein (*Sc*) complete or incomplete, usually distinct.

114



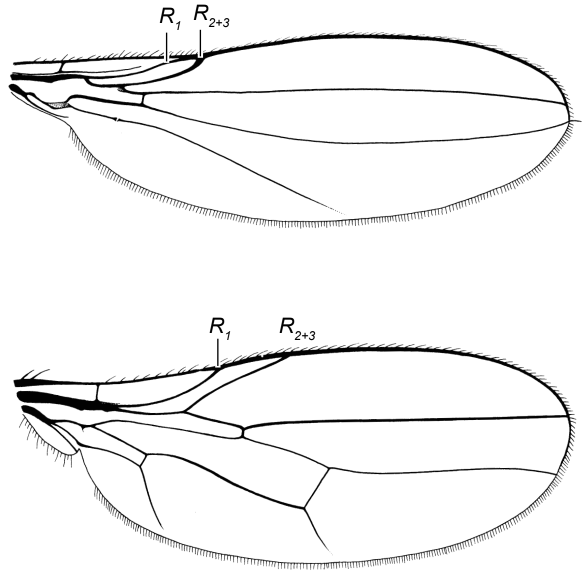
114 (113′). Antennal arista (ar) with long dorsal branches only, anterior cubital wing cell (*cua*) absent and subcostal break (sc brk) present. Face (fc) often prominent.

Ephydridae [in part] (Chapter 100)



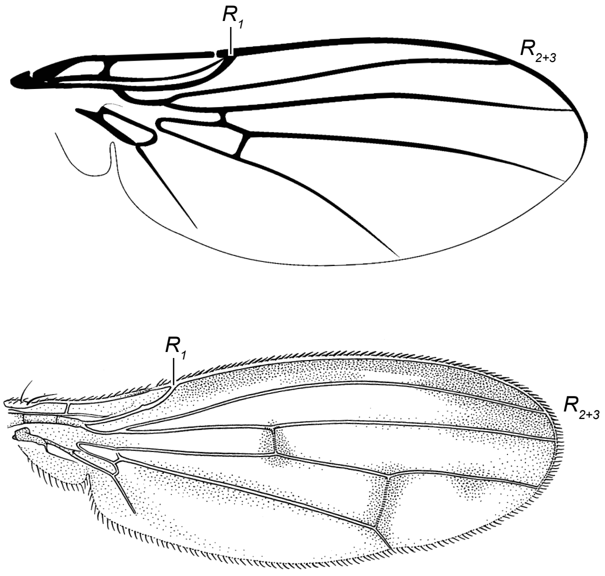
114′ (113′). Antennal arista (ar) bare, pubescent or with branches both above and below; rarely with long dorsal branches only, but if so, then EITHER anterior cubital wing cell (*cua*) complete, OR subcostal break (sc brk) absent. Face (fc) variable.

115



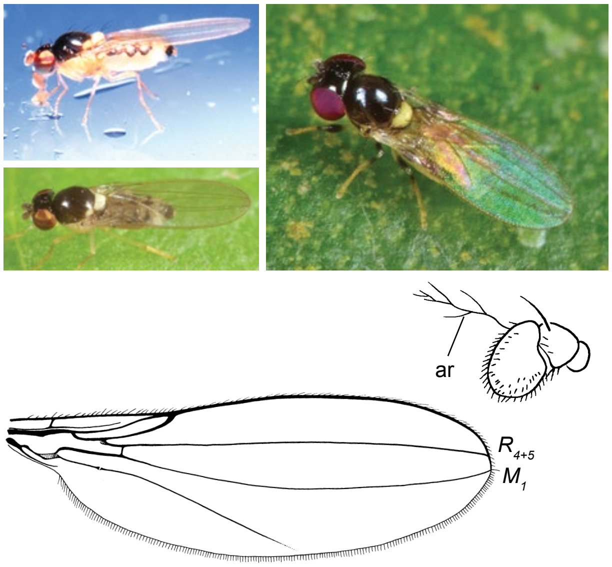
115 (114′). Wing vein R_{2+3} very short, ending much closer to apex of vein R_1 than to wing tip.

116



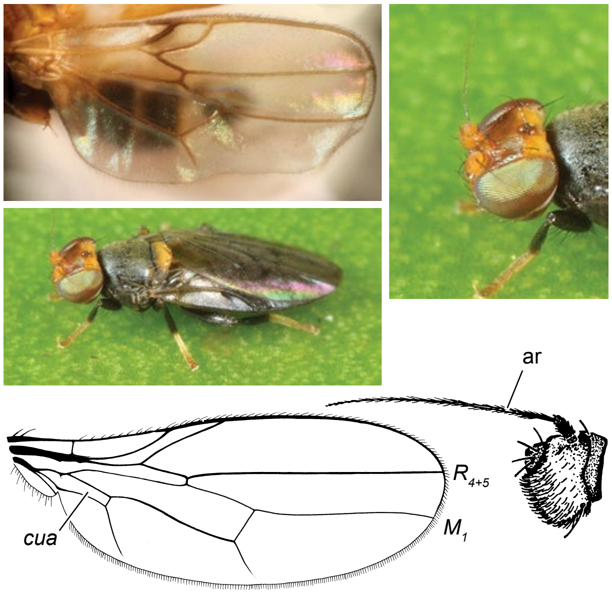
115′ (114′). Wing vein R_{2+3} long, ending much closer to wing tip than to apex of vein R_1.

117



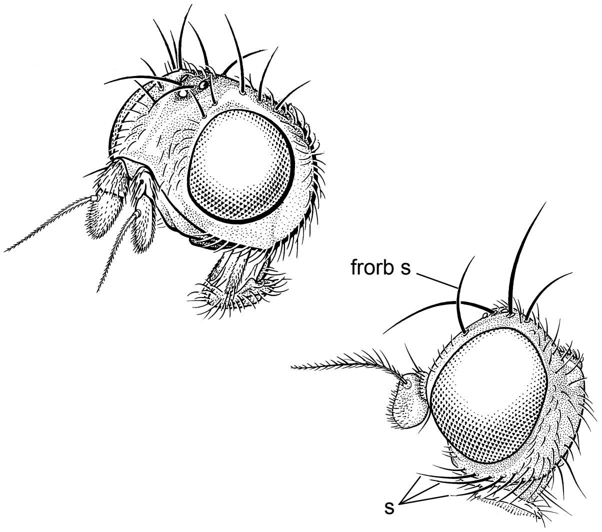
116 (115). Anterior cubital wing cell (*cua*) absent or indistinct; veins R_{4+5} and M_1 distally convergent, often with setula near apex of vein M_1. Antennal arista (ar) sometimes with zigzagging branches (alternating dorsal and ventral branches) in apical ⅔.

Asteiidae (Chapter 92)



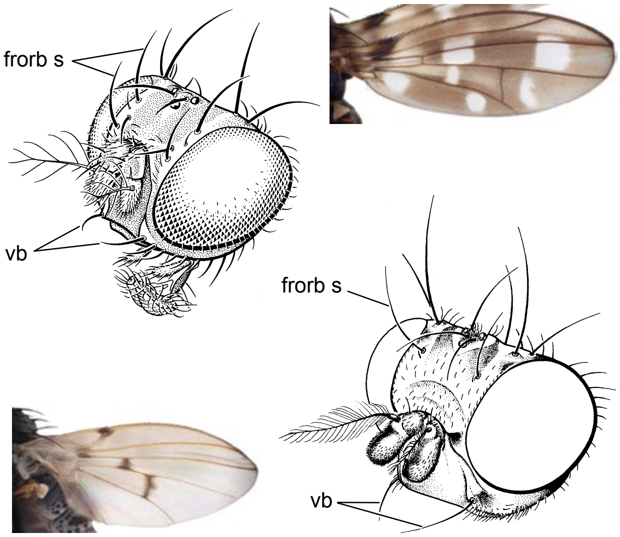
116′ (115). Anterior cubital wing cell (*cua*) complete; veins R_{4+5} and M_1 not converging, without setula near apex of vein M_1. Antennal arista (ar) evenly pubescent.

Neminidae (Chapter 89)



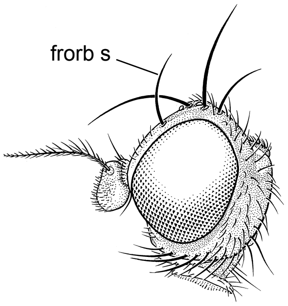
117 (115′). Head without vibrissa and facial setae at anteroventral angle of head, although sometimes with vibrissa-like setae (s) (*Geomyza* Fallén (Opomyzidae)), but then with 1 fronto-orbital seta (frorb s) and usually apical wing macula.

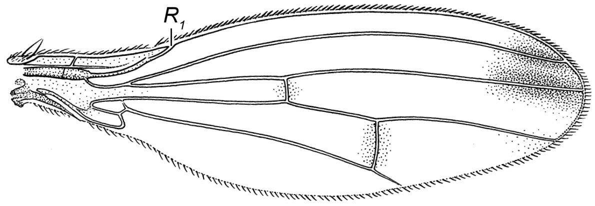
118



117′ (115′). Head with vibrissa (vb) or other enlarged setae at anteroventral angle, or lower face bulging, with vibrissa-like setae. If wing with apical macula, then head with more than 1 fronto-orbital seta (frorb s).

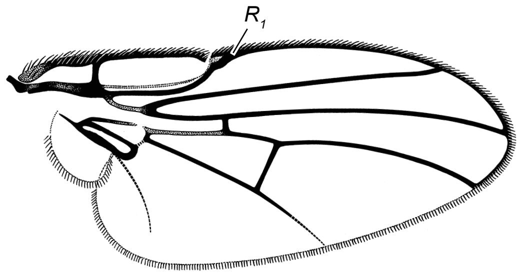
123

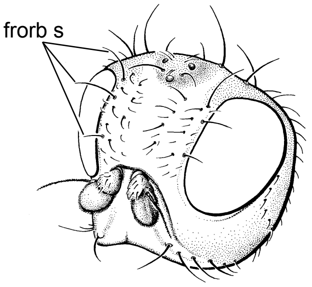




118 (117). Wing membrane markings usually including apical macula; vein R_1 with apical kink. Katepisternum with 1 seta. Head with 1 pair of fronto-orbital setae (frorb s).

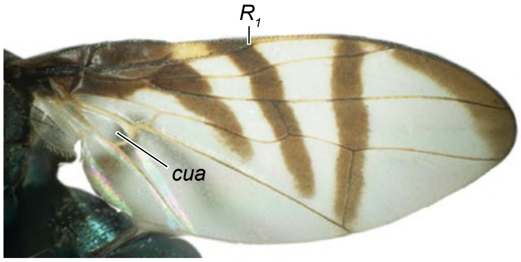
Opomyzidae (Chapter 84)





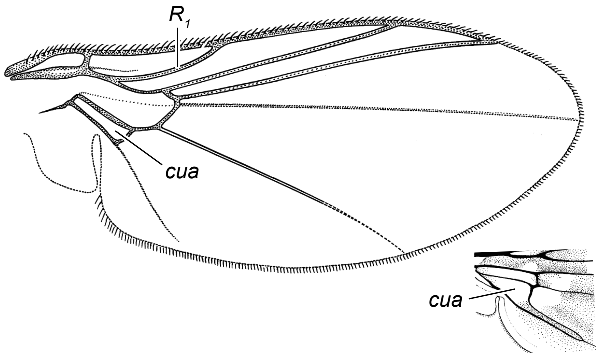
118′ (117). Wing membrane hyaline or patterned, but if with apical macula, then without katepisternal seta (arrowed); vein R_1 not kinked. Head usually with more than 1 pair of fronto-orbital setae (frorb s).

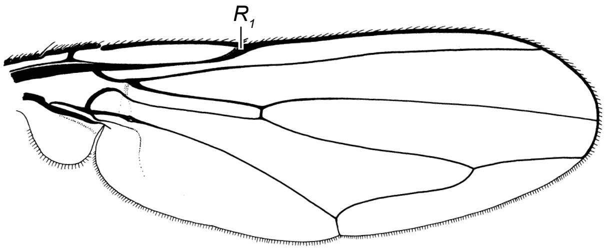
119



119 (118′). Wing vein R_1 (and sometimes other veins) with dorsal setae throughout its length (not clearly visible on wing above). Anterior cubital cell (*cua*) never posterodistally extended (PLASTOTEPHRITINAE).

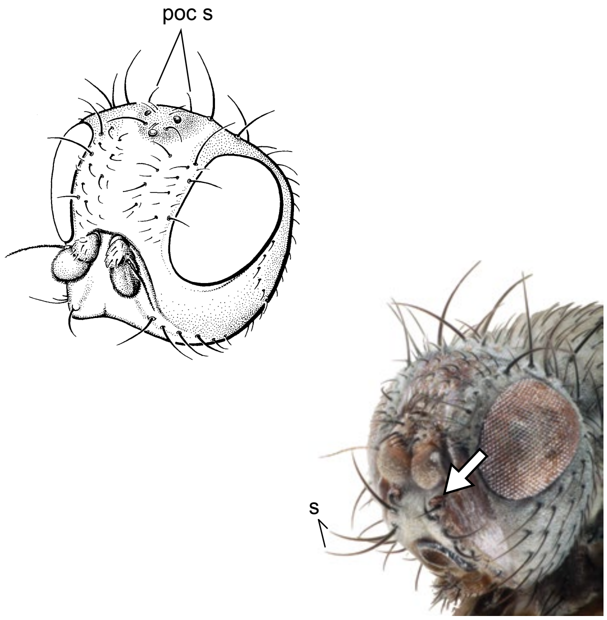
Platystomatidae [in part] (Chapter 70)





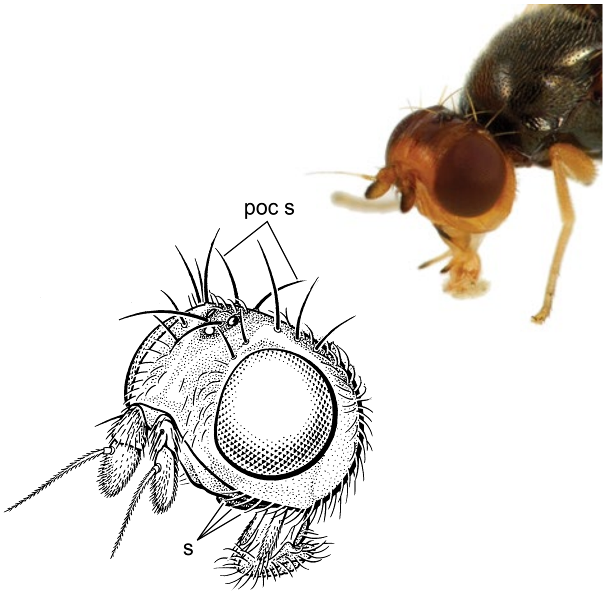
119′ (118′). Wing vein R_1 bare throughout its length. Anterior cubital cell (*cua*) variable, sometimes posterodistally extended (inset), or absent.

120



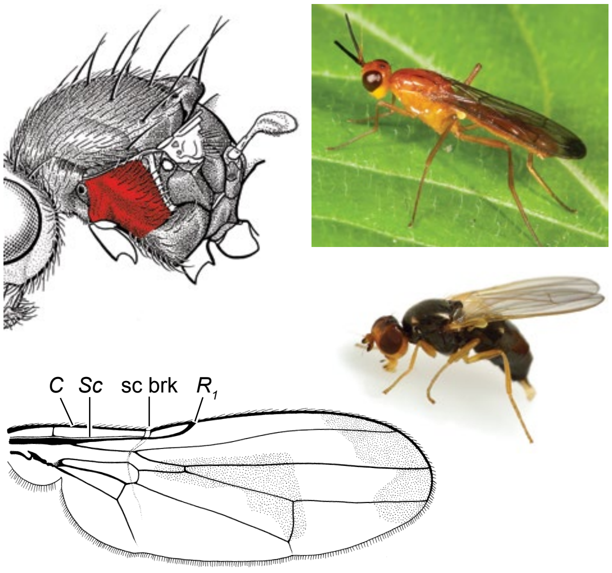
120 (119′). Head with postocellar setae (poc s) convergent; area immediately above apparent vibrissa (vibrissa-like setae (s)) with small shiny tubercle (arrowed).

Canacidae [in part] (Chapter 94)



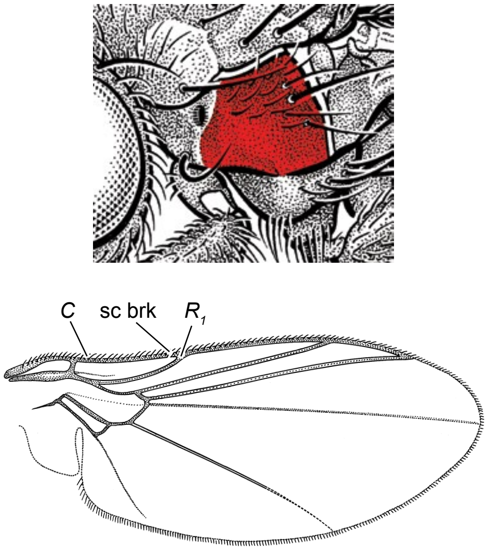
120′ (119′). Head with postocellar setae (poc s) divergent or absent; area immediately above apparent vibrissae (vibrissa-like setae (s)) without small shiny tubercle.

121



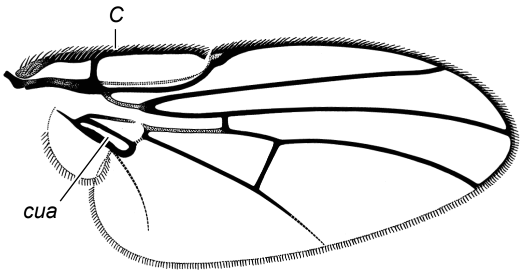
121 (120′). Thorax with anepisternum (in red) with fine setulae only. Costal wing vein (*C*) with subcostal break (sc brk) positioned well before end of vein R_1 (dorsal to end of subcostal vein (*Sc*)).

Psilidae (Chapter 65)



121′ (120′). Thorax with anepisternum (in red) with 1 or more setae. Costal wing vein (*C*) with subcostal break (sc brk) positioned near end of vein R_1.

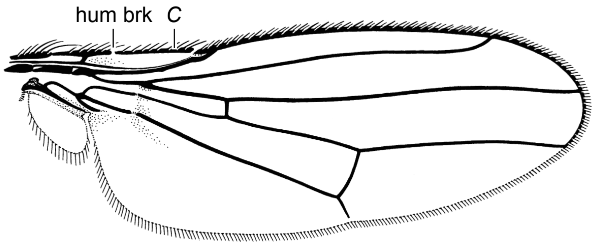
122



122 (121′). Wing with anterior cubital cell (*cua*) complete; costal vein (C) without humeral break. Head with face not conspicuously bulging.

Agromyzidae [in part] (Chapter 86)

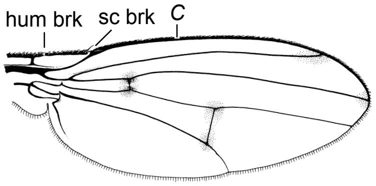
Atypical species without distinct vibrissa.

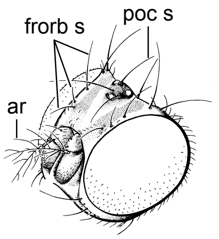


122′ (121′). Wing with anterior cubital cell (*cua*) incomplete (or absent); costal vein (C) with humeral break (hum brk). Head with face (fc) usually bulging (although an elongate knob between and below antennal scapes may be present in *Ophiomyia* Braschnikov (Agromyzidae)).

Ephydridae [in part] (Chapter 100)

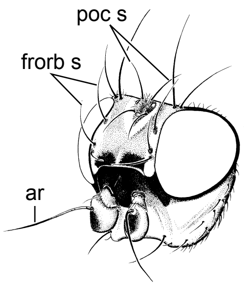
Atypical species without distinct vibrissa.

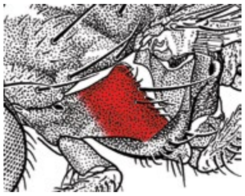




123 (117′). Antennal arista (ar) with long dorsal and (usually) ventral branches AND costal vein (C) with conspicuous breaks (humeral (hum brk) and subcostal (sc brk) breaks). Head with proclinate and reclinate fronto-orbital setae (frorb s); postocellar setae (poc s) convergent. Rarely metallic. Fore femur usually without ventral spine, anepisternum bare, costal vein (C) without spines.

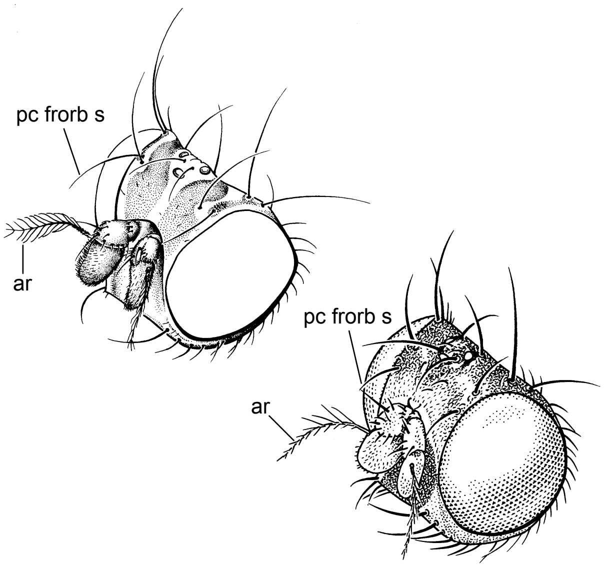
Drosophilidae [in part; most] (Chapter 106)





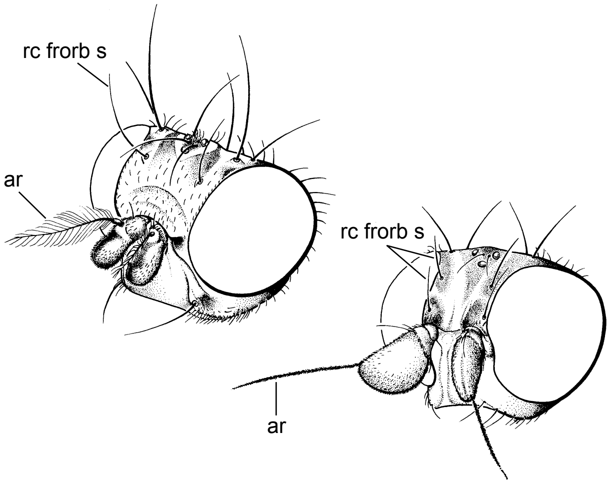
123′ (117′). If antennal arista (ar) with long branches, then EITHER postocellar setae (poc s) divergent or absent, head without proclinate and reclinate fronto-orbital setae (frorb s), body metallic and fore femur with ventral spine and costal vein (C) without conspicuous breaks, OR costal vein (C) with spines. Anepisternum (in red) with or without setae.

124



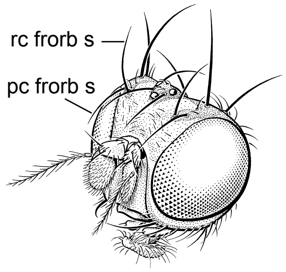
124 (123′). Head with 1 pair of proclinate fronto-orbital setae (pc frorb s) (may be reduced or scale-like; absent in females of 1 species with long plumose antennal arista (ar)) and 1 or 2 pairs of reclinate fronto-orbital setae.

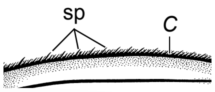
125

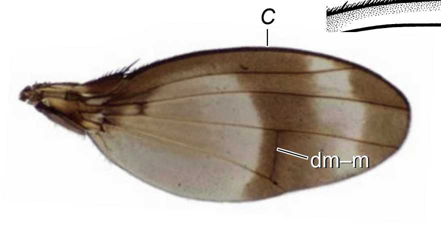


124′ (123′). Head with fronto-orbital setae all similarly oriented, reclinate (rc frorb s) or lateroclinate, OR with anterior seta inclinate and posterior seta medial to and almost horizontally alighted with anterior seta (except in Xenasteiidae, but then tiny flies (1.3–1.7 mm) confined to Indian Ocean islands with reduced wing venation; vein *M* largely evanescent). Antennal arista (ar) bare to plumose.

127

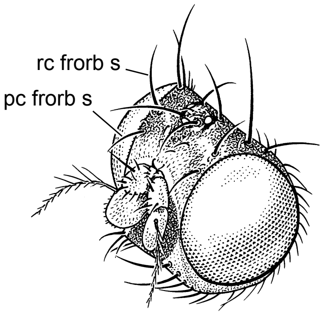


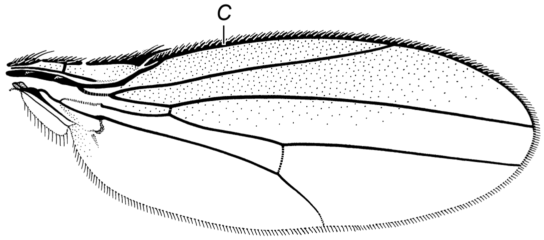




125 (124). Costal wing vein (C) relatively stout, with erect spinules (sp) amongst the usual small setae. Head with strong proclinate fronto-orbital seta (pc frobs s) inserted dorsolaterally to strong reclinate fronto-orbital seta (rc frorb s). Wing membrane often infuscate basally and over *dm–m* crossvein, sometimes more extensively patterned or banded (as above); unpatterned in *Campichoeta* Macquart.

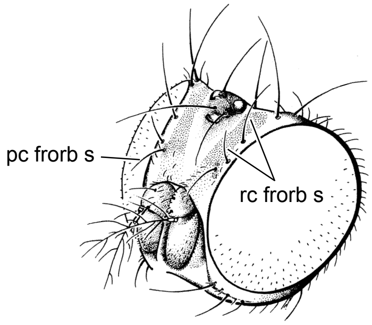
Diastatidae (incl. Campichoetidae) (Chapter 104)

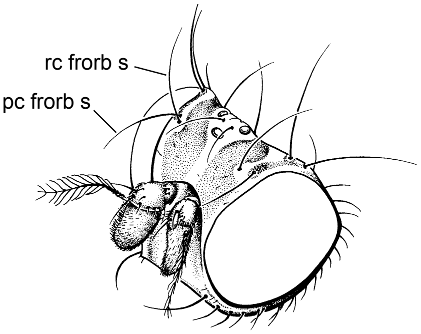




125′ (124). Costal wing vein (C) with setae uniformly small, reclinate. Head without proclinate fronto-orbital seta (pc frorb s), or arising anteriorly to reclinate fronto-orbital seta (rc frorb s). Wing membrane variable, usually hyaline.

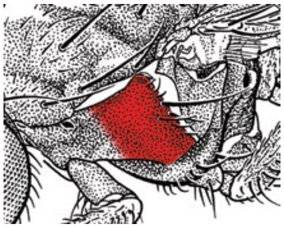
126





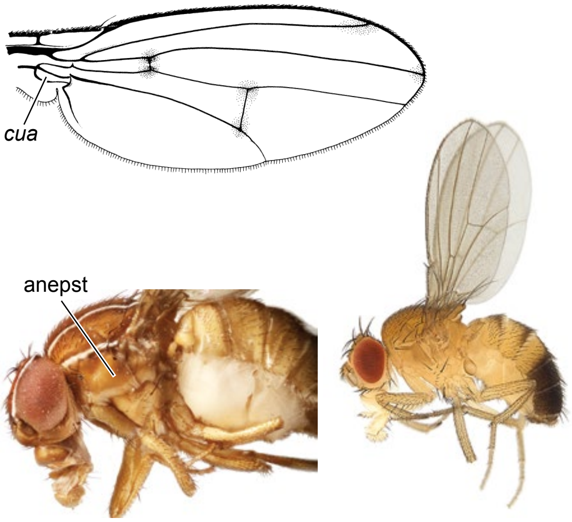
FEATURES OF DROSOPHILIDAE AND DIASTATIDAE

Drosophilidae almost invariably have 2 reclinate (rc frorb s) and 1 proclinate (pc frorb s) fronto-orbital setae (the latter scaleform in several *Apenthecia* Tsacas species), with the anterior reclinate seta **no farther from the eye than the proclinate seta** (pc frorb s) and often reduced in size or minute. Similar setae are found in only a few other families, including Camillidae and Diastatidae, that also have a plumose antennal arista. Camillidae have an open anterior cubital cell (*cua*) (closed in Drosophilidae), a setulose anepisternum (bare in Drosophilidae) and a ventral spine on the fore femur. Diastatidae have a spinose costal vein (C) and the anterior **reclinate fronto-orbital seta (rc frorb s) farther from the eye than the proclinate fronto-orbital seta (pc frorb s)**; the anepisternum is setulose (*Diastata* Meigen) or bare (*Campichoeta* Macquart).



126 (125′). Thorax with anepisternum (in red) setulose. Antennal arista with long branches above, short branches below. Wing with anterior cubital cell (*cua*) open. Fore femur with anteroventral spine near apex. Mostly dark flies with metallic lustre (*Katacamilla* Papp entirely pale).

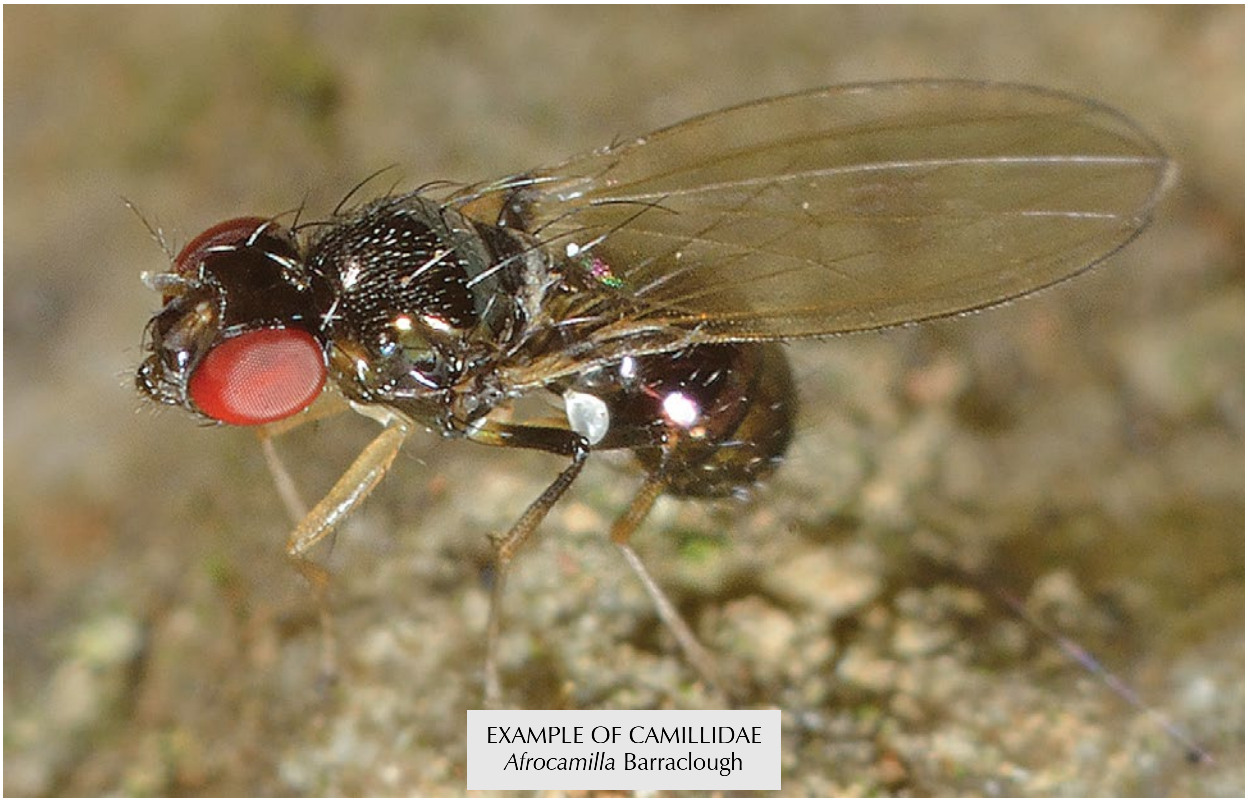
Camillidae (Chapter 102)



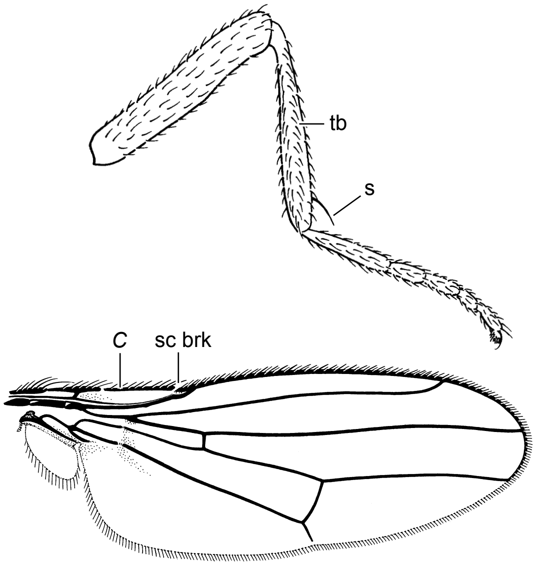
126′ (125′). Thorax with anepisternum (anepst) bare. Antennal arista variable. Wing with anterior cubital cell (*cua*) usually closed. Fore femur rarely with ventral spine. Colour variable, rarely metallic.

Drosophilidae [in part] (Chapter 106)

Atypical species key here.

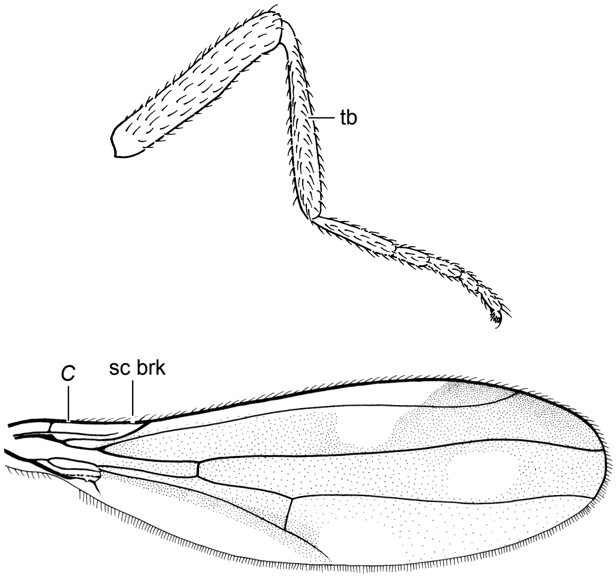


EXAMPLE OF CAMILLIDAE
Afrocamilla Barraclough



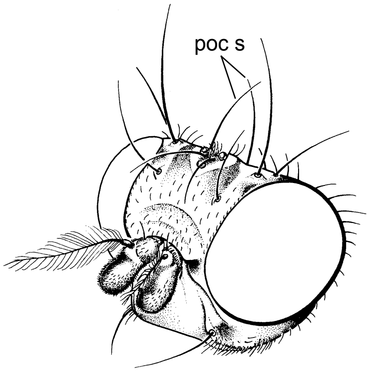
127 (124′). At least 1 tibia (tb) with dorsal preapical seta (s). Costal vein (C) with subcostal break (sc brk) (except in Marginidae, but then small flies (1.7–3.0 mm) with wing membrane often darkly pigmented marginally).

128



127′ (124′). Tibiae (tb) without dorsal preapical seta (although sometimes with scattered anterodorsal or posterodorsal setae). Costal vein (C) with or without subcostal break (sc brk).

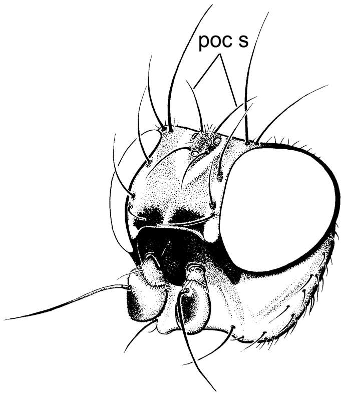
131



128 (127). Postocellar setae (poc s) convergent.

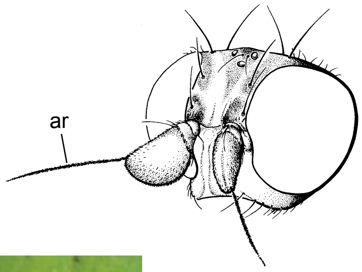
Heleomyzidae [in part] (Chapter 98)

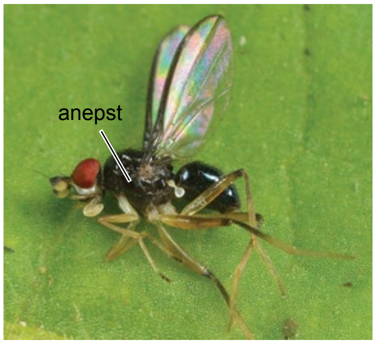
Atypical forms with indistinct subcostal vein.

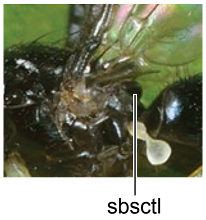


128′ (127). Postocellar setae (poc s) divergent, parallel or absent.

129

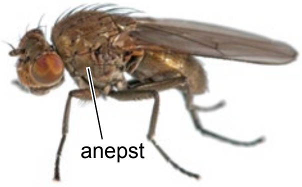


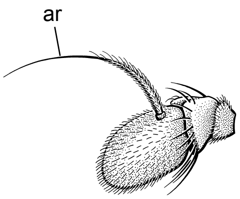




129 (128′). Subscutellum (sbsctl) bulging below scutellum; anepisternum (anepst) bare or with 1 minute seta. Wing membrane often with marginal pigmentation. Antennal arista (ar) inserted apically or pre-apically.

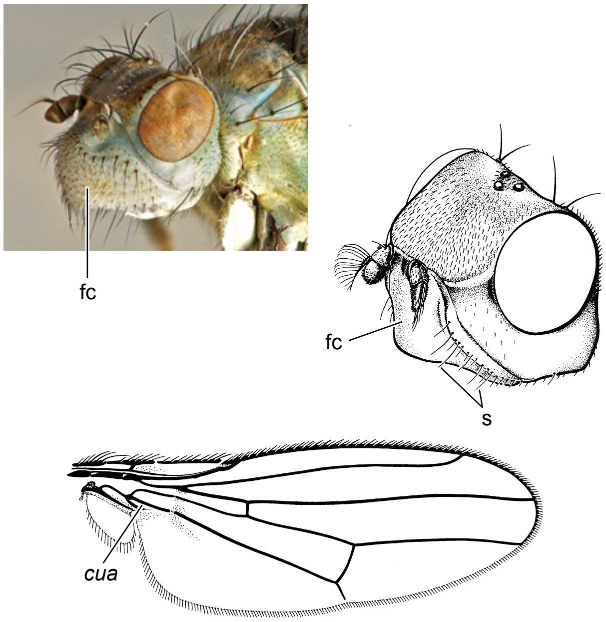
Marginidae (Chapter 82)





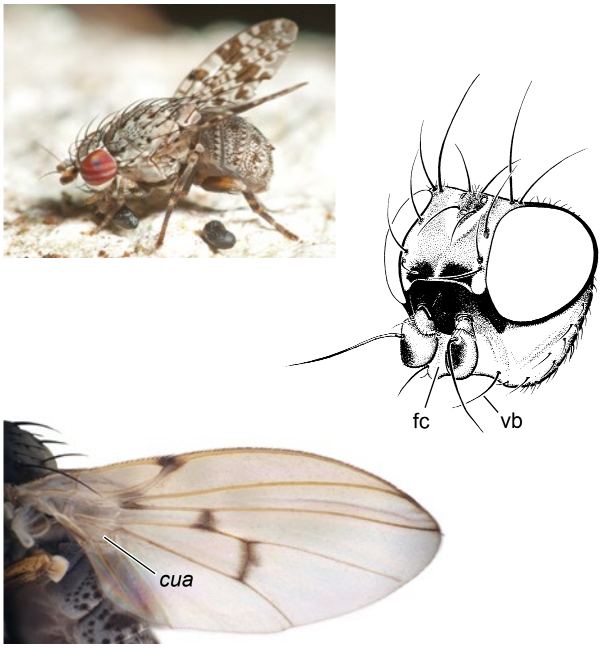
129′ (128′). Subscutellum inconspicuous, not bulging below scutellum; anepisternum (anepst) usually with setae (except in some Odiniidae). Wing membrane hyaline or with pigmentation other than marginal band. Antennal arista (ar) inserted dorsobasally.

130



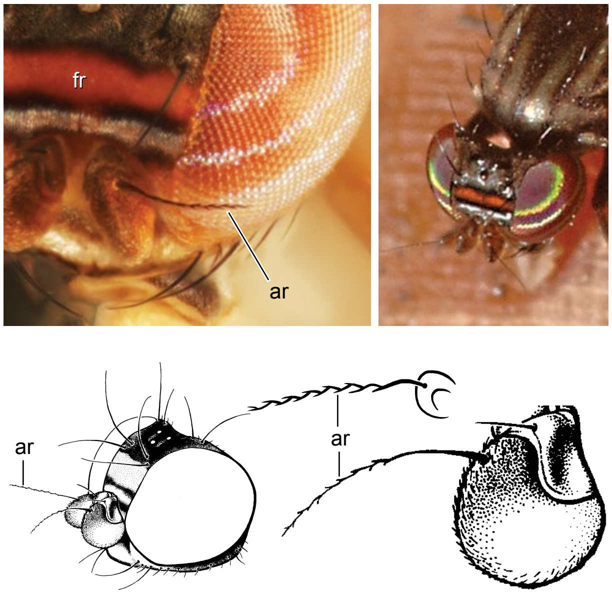
130 (129′). Anterior cubital wing cell (*cua*) open or absent. Face (fc) usually bulging; often with vibrissa-like setae (s), but without distinct vibrissa.

Ephydridae [in part] (Chapter 100)



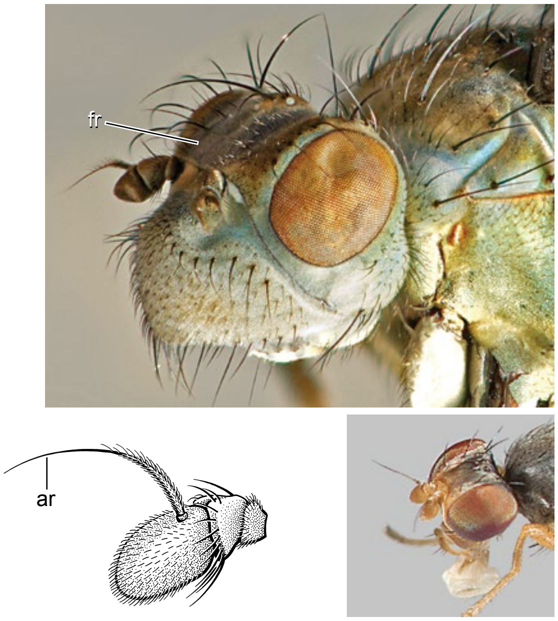
130′ (129′). Anterior cubital wing cell (*cua*) closed. Face (fc) flat. Strongly setose flies with distinct vibrissa (vb).

Odiniidae (Chapter 83)



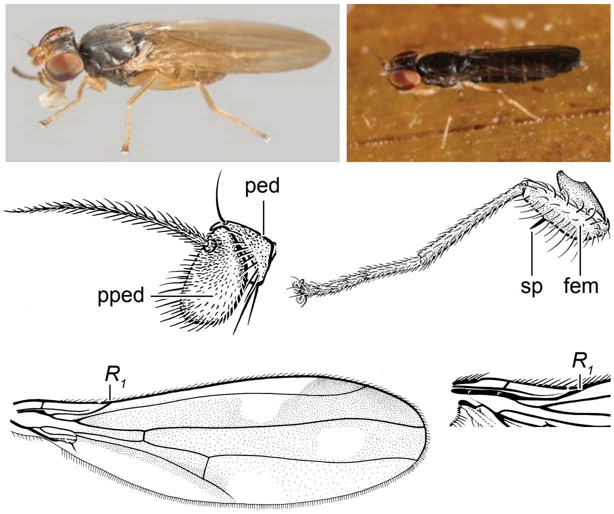
131 (127′). Antennal arista (ar) distally zigzaging with alternating dorsal and ventral branches; frons (fr) distinctly bicoloured, with lower part forming a bright transverse band.

Aulacigastridae (Chapter 88)



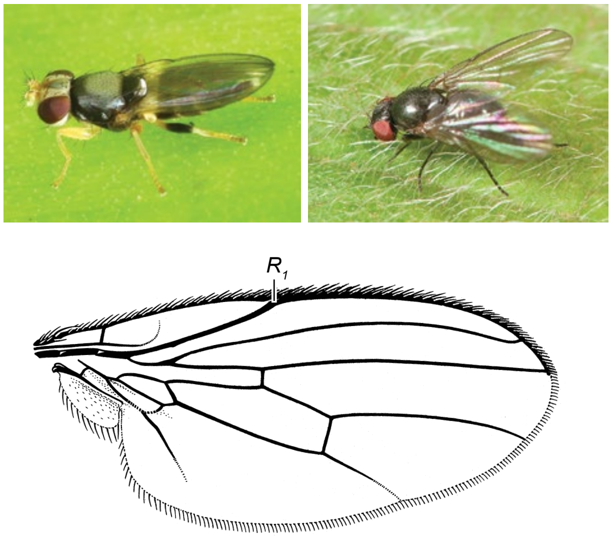
131′ (127′). Antennal arista (ar) straight; ventral and dorsal branches present or absent; frons (fr) without bright transverse band.

132



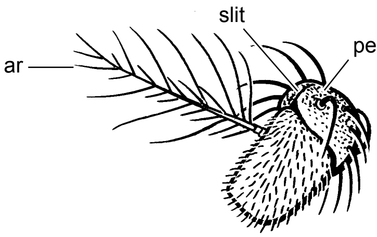
132 (131′). Fore femur (fem) with stout ventral spine (sp) in distal ½ (*Scelomyza* Séguy) and/or wing vein R_1 with distinct preapical kink. Antenna decumbent (postpedicel (pped) below pedicel (ped)), but porrect in *Amnonthomyza* Roháček and *Barbarista* Roháček. Usually elongate, slender flies with narrow wings.

Anthomyzidae [in part; most] (Chapter 87)



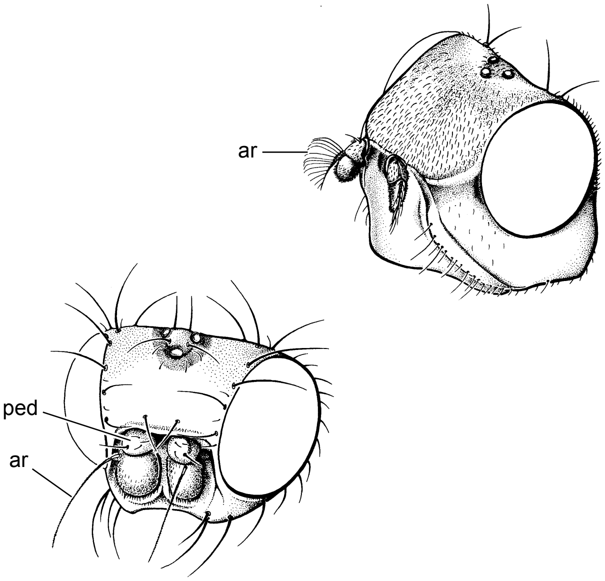
132′ (131′). Fore femur without stout ventral spine. Wing vein R_1 with preapical kink present (Agromyzidae), indistinct or absent. Body shape, antenna and wings variable.

133



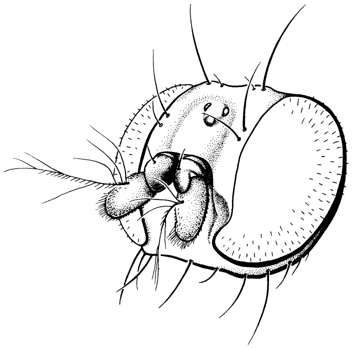
133 (132′). Antennal arista (ar) usually with long branches above and below, sometimes short plumose; antennal pedicel (ped) with dorsal slit or notch.

134



133′ (132′). Antennal arista (ar) bare or pubescent; antennal pedicel (ped) usually without dorsal slit or notch.

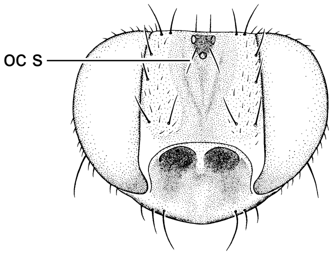
136

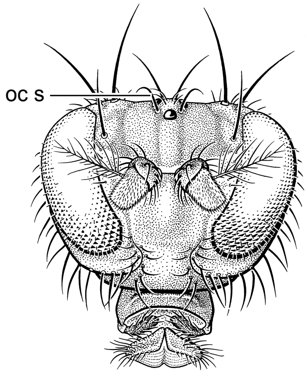


134 (133). Head without ocellar setae.

Periscelididae [in part] (Chapter 91)

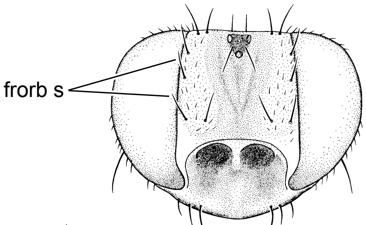
Most Afrotropical Periscelididae in subfamily STENOMICRINAE; sometimes treated as family Stenomicridae.

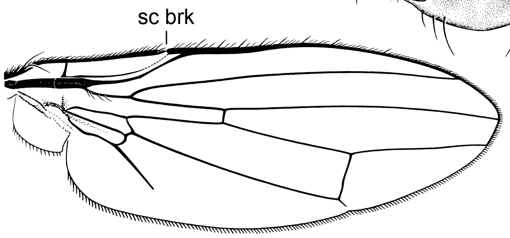




134′ (133). Head with ocellar setae (oc s).

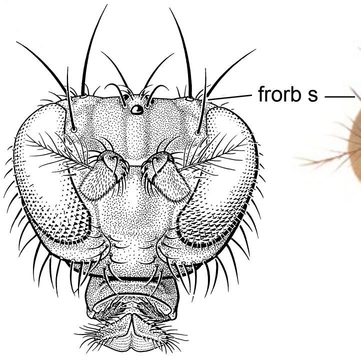
135

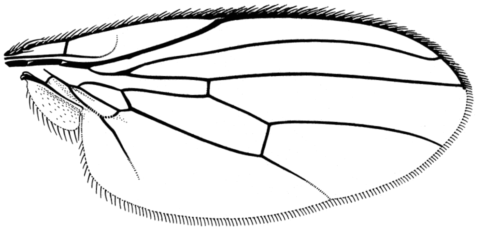




135 (134′). Head with at least 2 fronto-orbital setae (frorb s). Subcostal break (sc brk) present.

Neurochaetidae (Chapter 90)

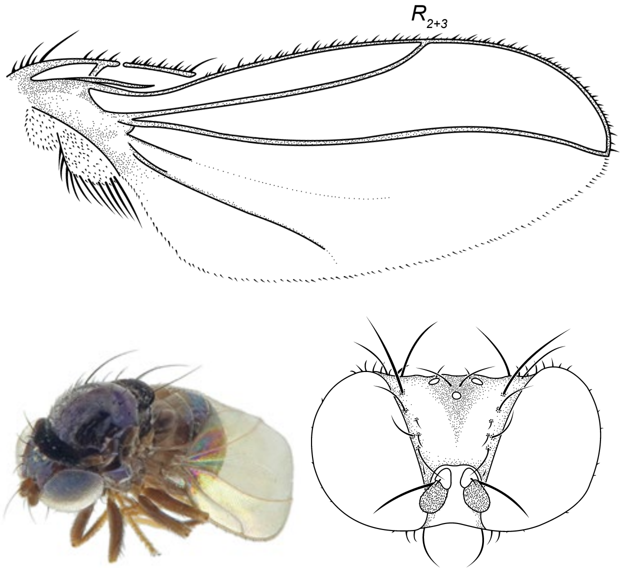




135′ (134′). Head with 1 pair of fronto-orbital setae (frorb s). Subcostal break absent.

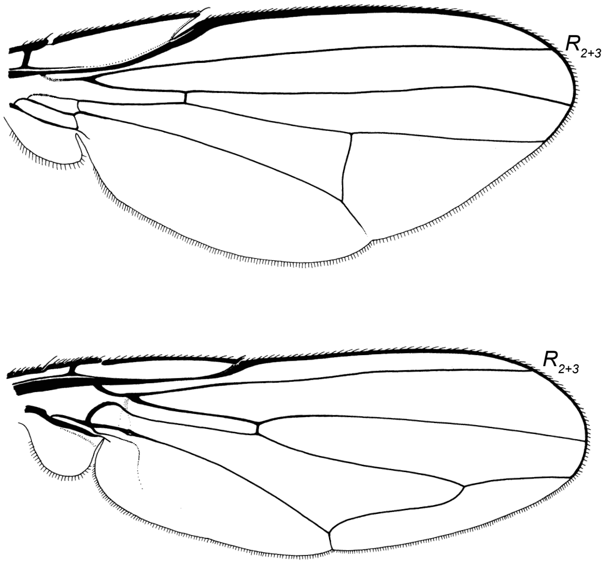
Periscelididae [in part] (Chapter 91)

Periscelis Loew (uncommon in Afrotropics).



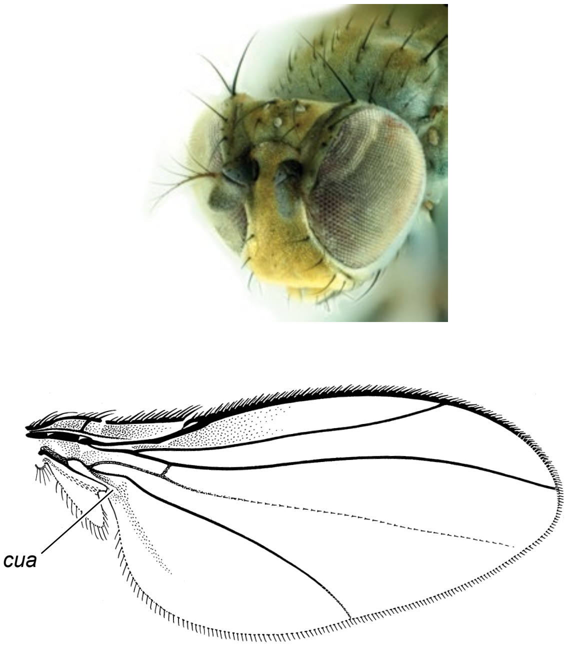
136 (133′). Wing vein R_{2+3} reaching at most to ⅔ wing length. Minute flies (< 1.8 mm in length), usually associated with seashores or other saline habitats.

Xenasteiidae (Chapter 85)



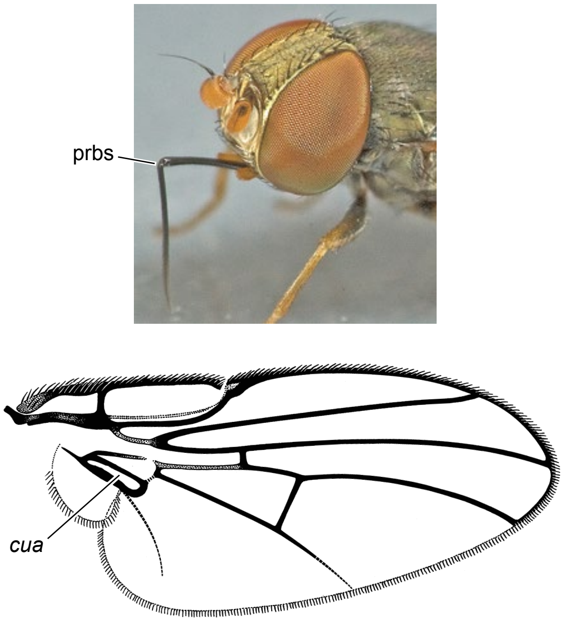
136′ (133′). Wing vein R_{2+3} ending well beyond ⅔ wing length. Size and habitat variable.

137



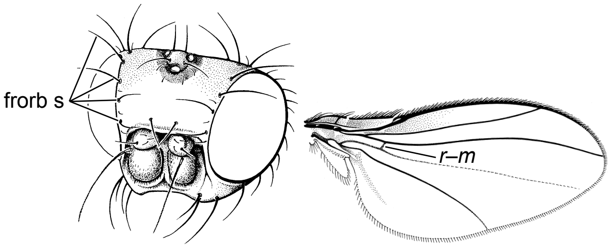
137 (136′). Anterior cubital wing cell (*cua*) open or absent. Proboscis short.

138



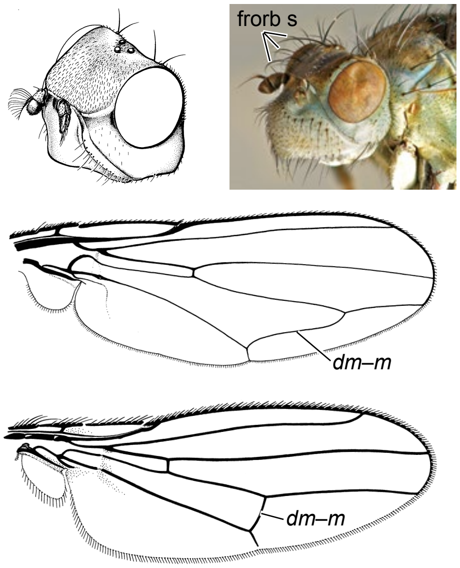
137′ (136′). Anterior cubital wing cell (*cua*) closed. Proboscis (prbs) sometimes long and geniculate (bent medially).

139



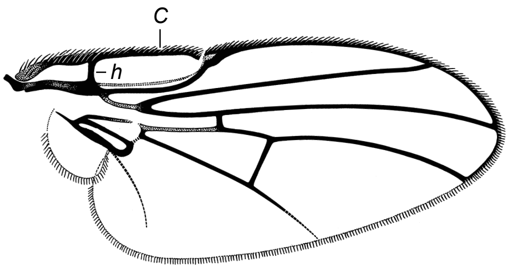
138 (137). Head with 4 fronto-orbital setae (frorb s), the lower 2 inclinate. Crossveins positioned near wing base; halter usually pale. Body usually 1–2 mm in length.

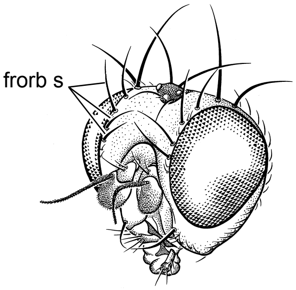
Carnidae [in part] (Chapter 93)



138′ (137). Head with 0–4 fronto-orbital setae (frorb s), the lower 2 if present not inclinate. Wing with crossveins positioned at or beyond middle of wing; halter usually dark. Body variable, but often larger than 2 mm in length.

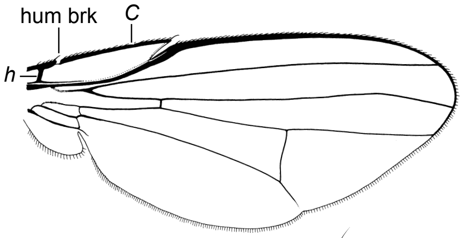
Ephydridae [in part] (Chapter 100)

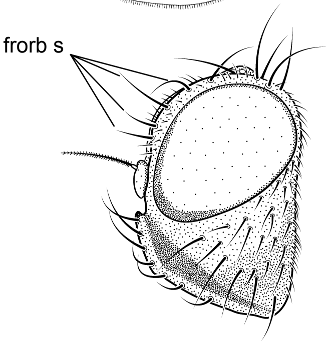




139 (137′). Costal wing vein (C) without humeral break (near humeral crossvein (*h*)). Head with fronto-orbital setae (frorb s) variable, but if numerous and inclinate, then female terminalia with conical, non-retractile oviscape (ovscp).

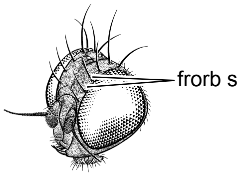
140





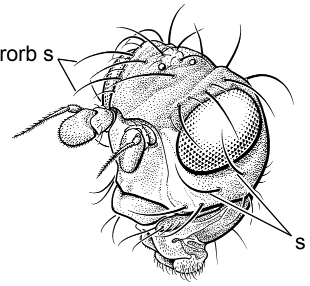
139′ (137′). Costal wing vein (C) with humeral break (hum brk) near humeral crossvein (*h*). Head with at least 3 (usually 4 or more) fronto-orbital setae (frorb s), some usually inclinate. Female terminalia without conical, non-retractile oviscape.

141



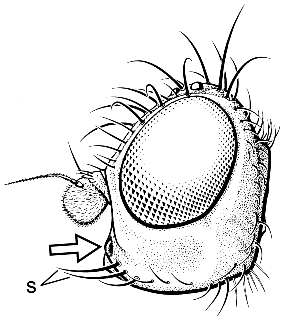
140 (139). Head without upturned setae below compound eye; fronto-orbital setae (frorb s) never lateroclinate. Female terminalia with stout, tubular non-retractile oviscape (ovscp). Usually not associated with seashores.

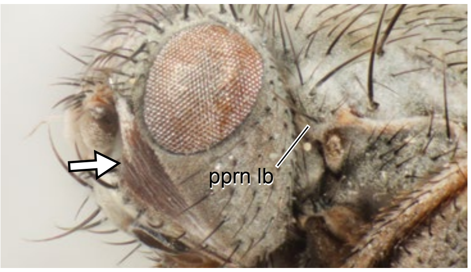
Agromyzidae [in part] (Chapter 86)



140′ (139). Head with 1 to several upturned setae (s) below compound eye; fronto-orbital setae (frorb s) usually lateroclinate. Female terminalia without tubular oviscape, often with upcurved, spinose cercus. Associated with seashores.

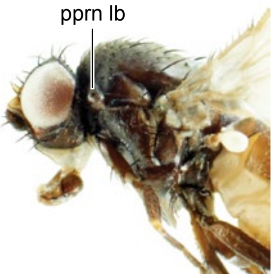
Canacidae [in part] (Chapter 94)





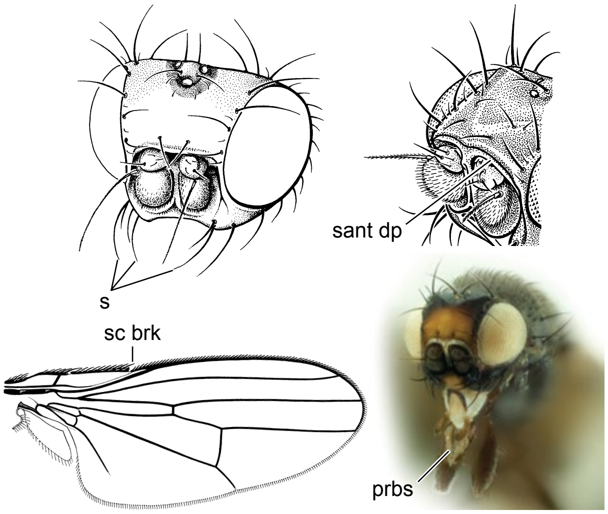
141 (139′). Head with area immediately above apparent vibrissa (vibrissa-like seta (s)), with small shiny process (arrowed). Postpronotal lobe (pprn lb) of thorax with 3 differently oriented setae.

Canacidae [in part] (Chapter 94)



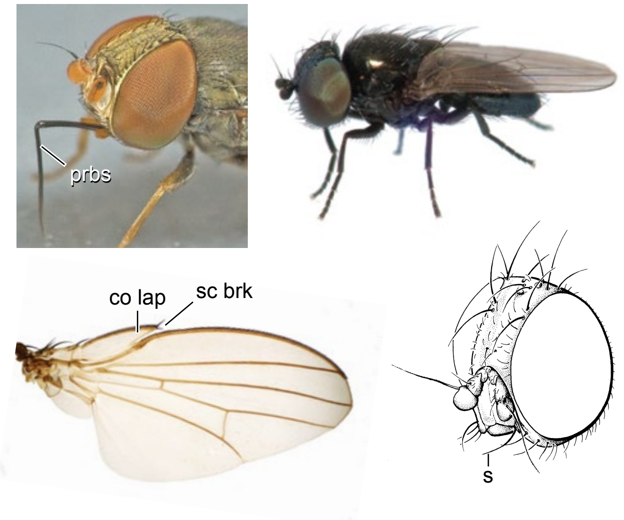
141′ (139′). Head with area immediately above apparent vibrissa (vibrissa-like seta), unmodified, without small shiny process. Postpronotal lobe (pprn lb) of thorax variable, but not with 3 distinct, differently oriented setae.

142



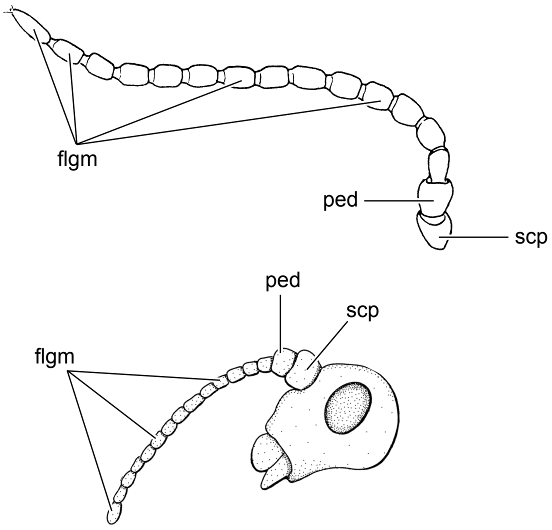
142 (141′). Proboscis (prbs) short and straight; vibrissa-like setae (s) inserted below ventral margin of compound eye; antenna often in subantennal depression (sant dp) separated by sharp ridge. Wing with subcostal break (sc brk) small, without costal lappet. Thorax with anepisternum with setulae or setae. Body length: 1–3 mm.

Carnidae [in part] (Chapter 93)



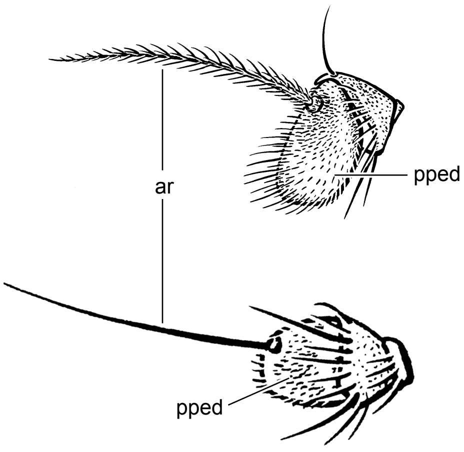
142′ (141′). Proboscis (prbs) geniculate (bent medially), EITHER thorax with anepisternum bare, OR head with vibrissa-like setae (s) inserted well above ventral margin of compound eye. Head usually without subantennal depression, if present, then shallow. Wing with subcostal break (sc brk) sometimes very large and flanked by costal lappet (co lap). Body length: 1–6 mm.

Milichiidae [in part] (Chapter 95)



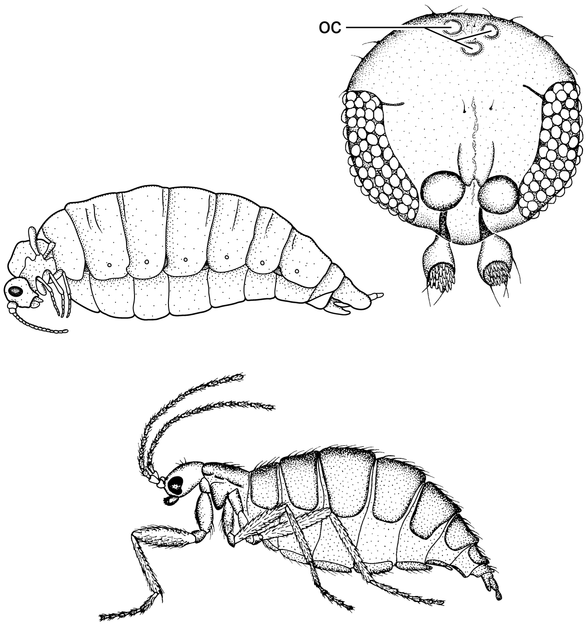
143 (1′). Antenna with 6 or more (usually many more) distinct flagellomeres (at least 4 distal flagellomeres (flgm), plus basal scape (scp) and pedicel (ped)), flagellomeres similar, but clearly separated from one another.

144



143′ (1′). Antenna with fewer than 6 distinctly separated flagellomeres; postpedicel (pped) often with hair-like antennal arista (ar), or tapered stylus, sometimes thin and annulated.

146



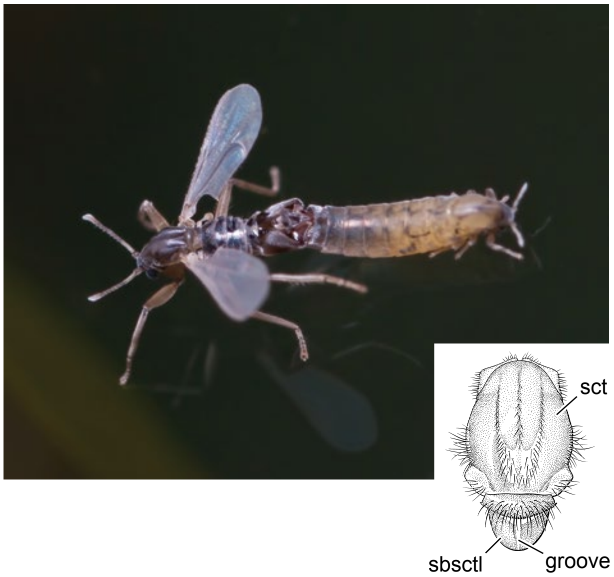
144 (143). Ocelli (oc) present.

Sciaridae [in part] (Chapter 21)

Epidapus Haliday (4 spp., Seychelles & South Africa; females of some species unknown, but likely micropterous or brachypterous) & *Pnyxia* Johannsen (1 sp., Madagascar).

144′ (143). Ocelli absent.

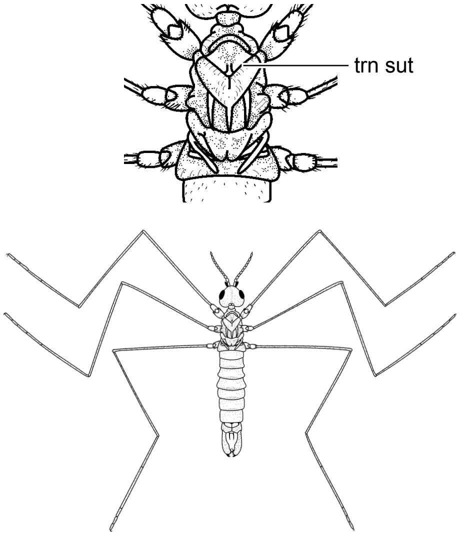
145



145 (144′). Thorax without complete V-shaped transverse suture across scutum (sct); subscutellum (sbsctl) with distinctive longitudinal groove.

Chironomidae [in part] (Chapter 35)

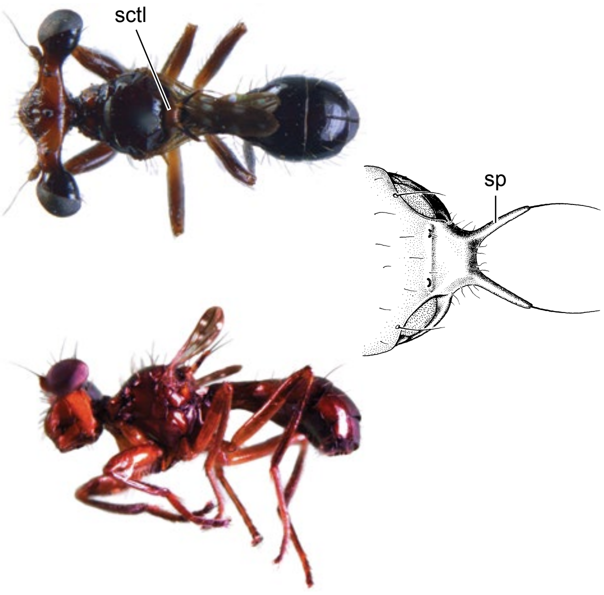
Clunio Haliday [in part] (3 coastal spp., *C. africanus* Hesse, 1937 (South Africa), *C. gerlachi* Sæther, 2004 (Seychelles) & *C. jonesi* Sæther & Andersen, 2011 (Gough Is.)).



145′ (144′). Thorax with complete V-shaped transverse suture (trn sut) across scutum; subscutellum without distinctive longitudinal groove.

Limoniidae & Tipulidae [in part] (Chapter 14)

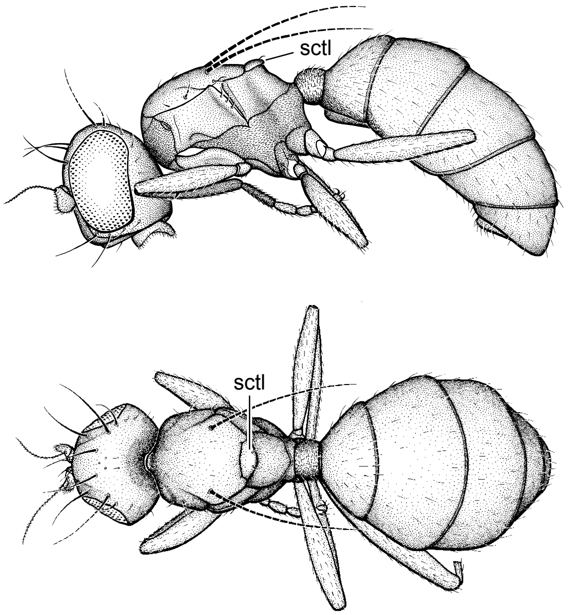
Austrolimnophila (*Austrolimnophila*) *buxtoni* Alexander (Ruwenzori Mountains), *Quathlambia stuckenbergi* Alexander (South Africa), *Symplecta* (*Symplecta*) *holdgatei* (Freeman) (Gough Is.), *Platylimnobia* Alexander (South Africa), *Leptotarsus* (*Longurio* Loew) (South Africa), *Tipula* (*Tipula* L.) (Bale Mountains & Mt Kilimanjaro).



146 (143′). Scutellum (sctl) with 2 distinct, spine-like or tubular apical projections (sp), ending in setae. Head distinctly "stalk-eyed".

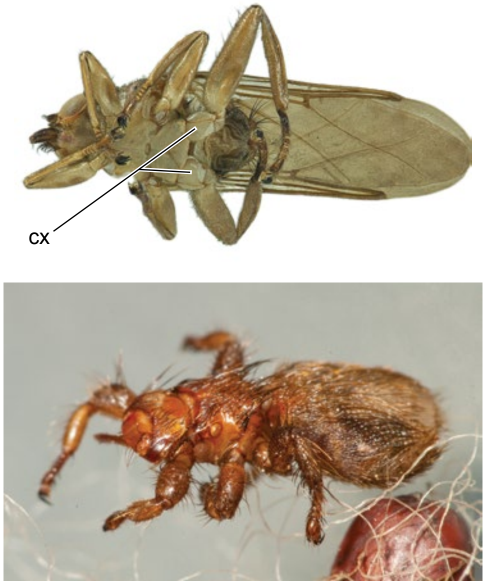
Diopsidae [in part] (Chapter 64)

One species, *Diopsina draconigena* Feijen (Lesotho & South Africa).



146′ (143′). Scutellum (sctl) without distinct, spine-like or tubular apical projections. Head normal, not "stalk-eyed".

147



147 (146′). Hind coxae (cx) widely separated; tarsal claws stout, strongly recurved, sometimes bifid. Ectoparasites of birds, bats and other mammals.

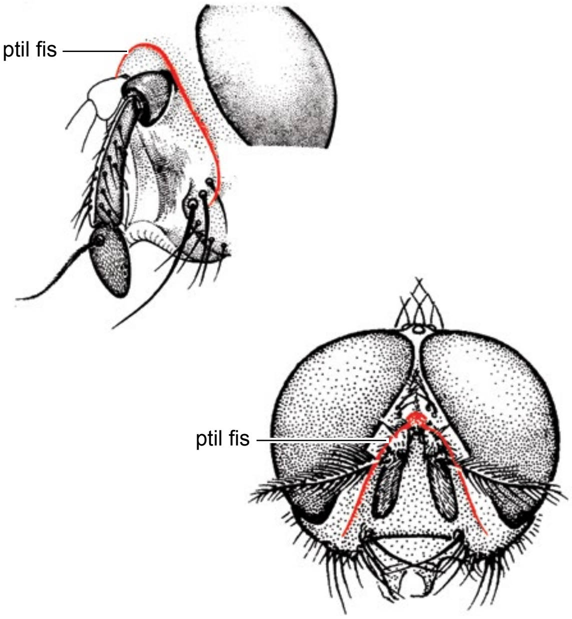
Hippoboscidae [in part, incl. Nycteribiinae & strebline grade] (Chapter 109)

147′ (146′). Hind coxae (cx) closely approximated; tarsal claws variable, but rarely conspicuously enlarged. Usually free-living, sometimes associated with nestling birds (Carnidae), honey bees (Braulidae) or bat roosts (Mormotomyiidae).

148

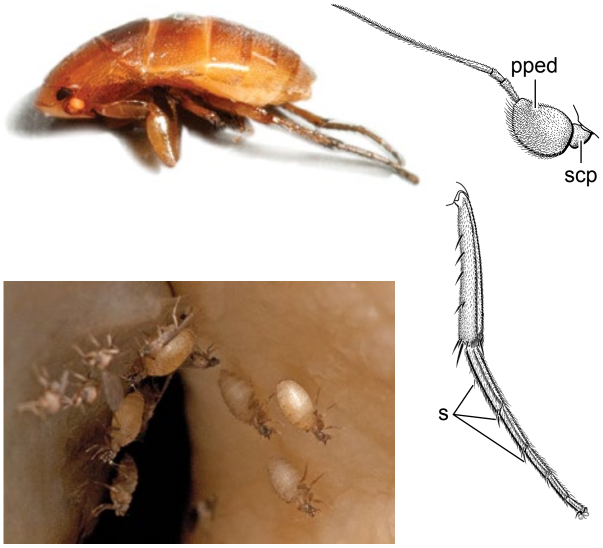
148 (147′). Ptilinal fissure absent.

149



148′ (147′). Ptilinal fissure (ptil fis) present (in red).

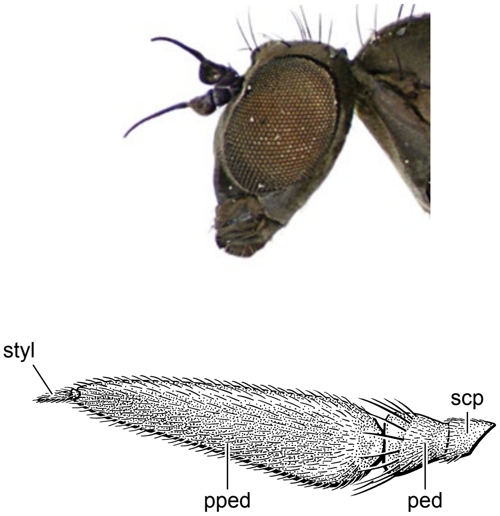
152



149 (148). Antenna apparently 2-segmented plus arista; antennal pedicel concealed within postpedicel (pped). Hind tarsus with 1–4 longitudinal rows of stout setae (s).

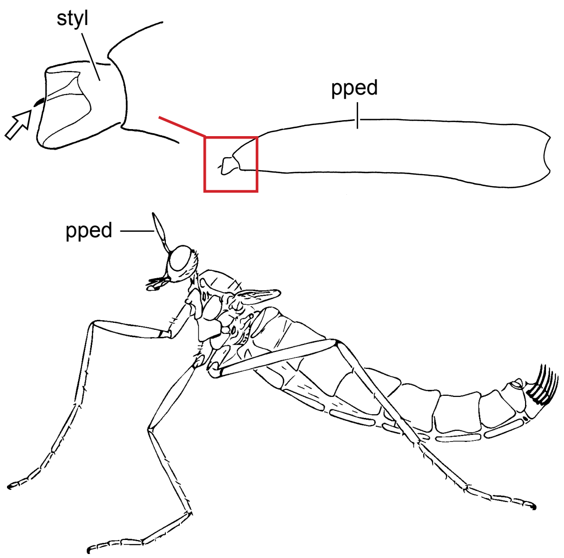
Phoridae [in part] (Chapter 59)

16 widespread genera, incl. all TERMITOXENIINAE females that shed outer part of wings.



149′ (148). Antenna with more than 3 "segments"; antennal pedicel (ped) distinct, not concealed within postpedicel (pped). Hind tarsus without longitudinal rows of stout setae.

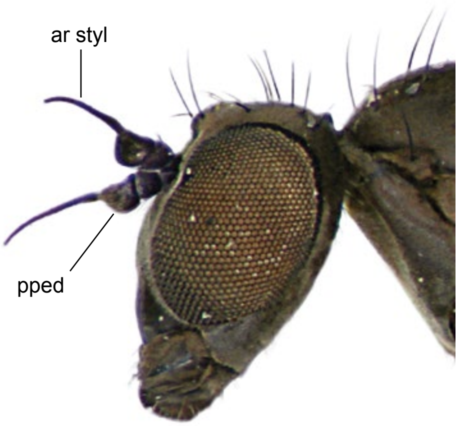
150



150 (149′). Antenna with short stylus (styl) bearing recessed apical bristle-like receptor (arrowed); postpedicel (pped) as long or longer than head.

Therevidae [in part] (Chapter 49)

Lyneborgia Irwin (South Africa).



150′ (149′). Antenna with stylus or arista-like stylus (ar styl) arising from apex of postpedicel (pped), without recessed apical bristle-like receptor; postpedicel shorter than head.

151

151 (150′). Wing strap-like.

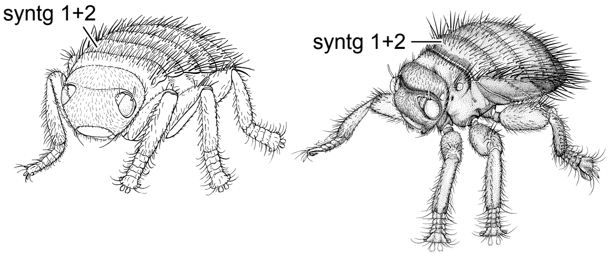
Empididae [in part] (Chapter 51)

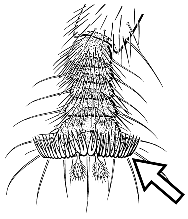
Dolichocephala Macquart [in part] & *Wiedemannia* Zetterstedt (Ruwenzori mountains, Uganda).

151′ (150′). Wing relatively broad.

Hybotidae [in part] (Chapter 52)

Stilpon Loew [in part] (South Africa).

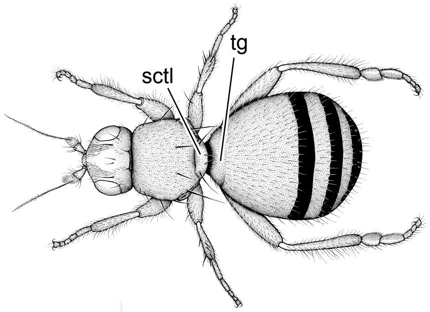


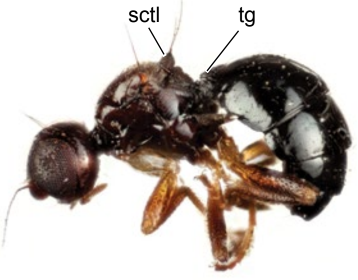


152 (148′). Scutellum absent or greatly reduced. Thorax foreshortened, less than ½ length of head (viewed from above), closely adjoined by abdominal syntergite 1+2 (syntg 1+2). Tarsi without claws, but with broad inflexed comb (arrowed) of numerous microscopic teeth. Specifically associated with honey bees.

Braulidae (Chapter 105)

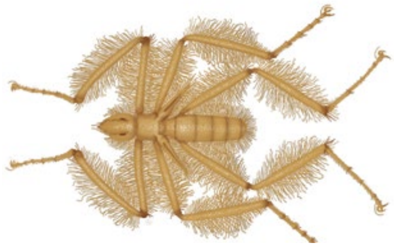
Braula Nitzsch (widespread).





152′ (148′). Scutellum (sctl) conspicuous. Thorax at least as long as head and clearly separated from abdominal tergites (tg). Tarsi with claws, comb absent. Not associated with honey bees.

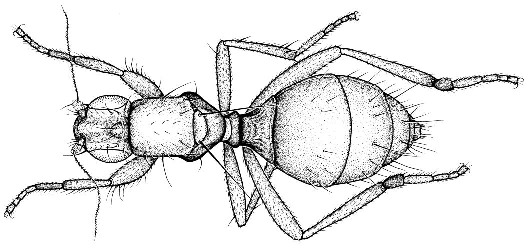
153



153 (152′). Head, body, legs and strap-like wings clothed in long brown setulae. Eyes greatly reduced, lozenge-shaped. Halter greatly reduced. Associated with bats in horizontal rock fissures.

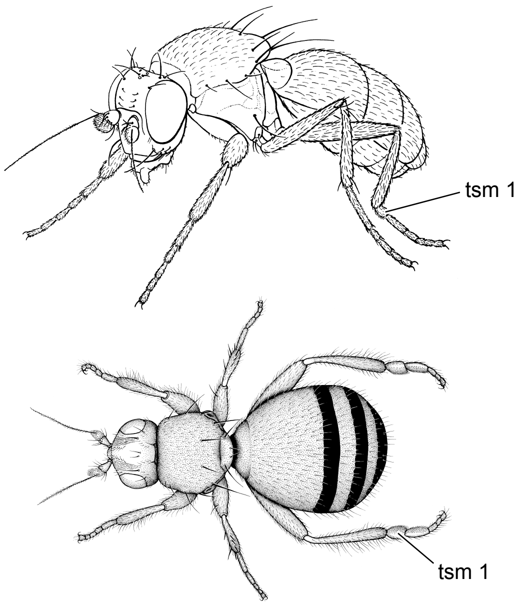
Mormotomyiidae (Chapter 101)

Mormotomyia hirsuta Austen (Kenya).



153′ (152′). Head, body and legs not excessively setulose. Wings absent or reduced. Halteres present or absent. Eyes not greatly reduced. Not associated with bats in horizontal rock fissures.

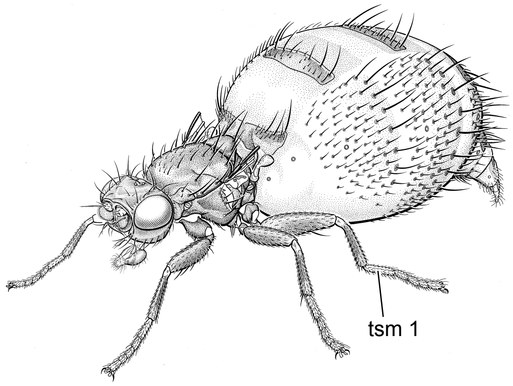
154



154 (153′). Hind tarsomere 1 (tsm 1) swollen, at most as long as tarsomere 2.

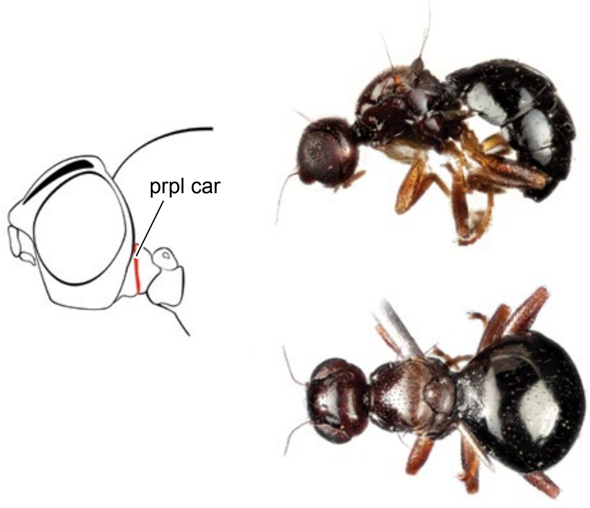
Sphaeroceridae [in part] (Chapter 99)

14 genera (Central, East and Southern Africa, St. Helena Is. & Réunion Is.).



154′ (153′). Hind tarsomere 1 (tsm 1) not swollen, longer than tarsomere 2.

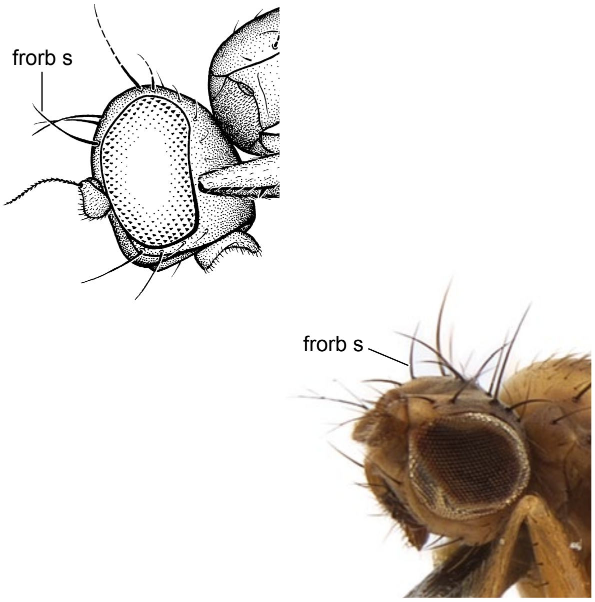
155



155 (154′). Thorax with sometimes sharp propleural vertical ridge (propleural carina; prpl car). Head without fronto-orbital setae (small setulae may be present).

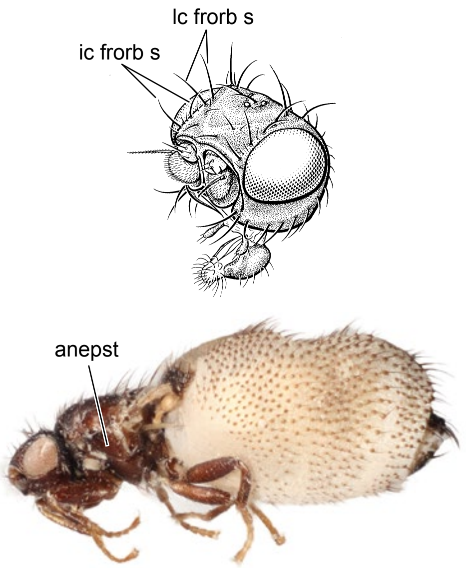
Chloropidae [in part] (Chapter 96)

Alombus Becker (Central and East Africa), *Conioscinella* Duda [in part] (Ruwenzori Mts, Kenya), *Elachiptera* Macquart [in part] (Mt. Kilimanjaro, Tanzania); *Myrmecosepsis* Becker (Nigeria).



155′ (154′). Thorax without propleural carina. Head with at least 1 well-developed pair of fronto-orbital setae (frorb s).

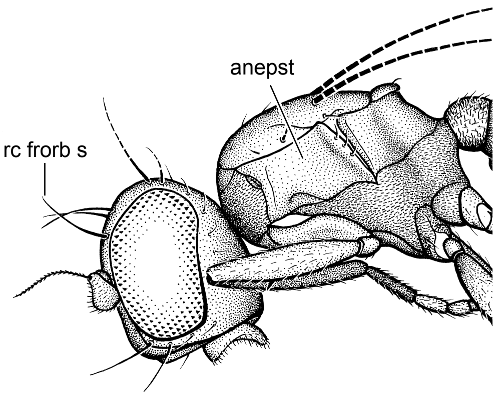
156



156 (155′). Thorax with anepisternum (anepst) setose. Head with 2 inclinate (ic frorb s) and 2 lateroclinate (lc frorb s) fronto-orbital setae. Associated with nestling birds and birds′ nests.

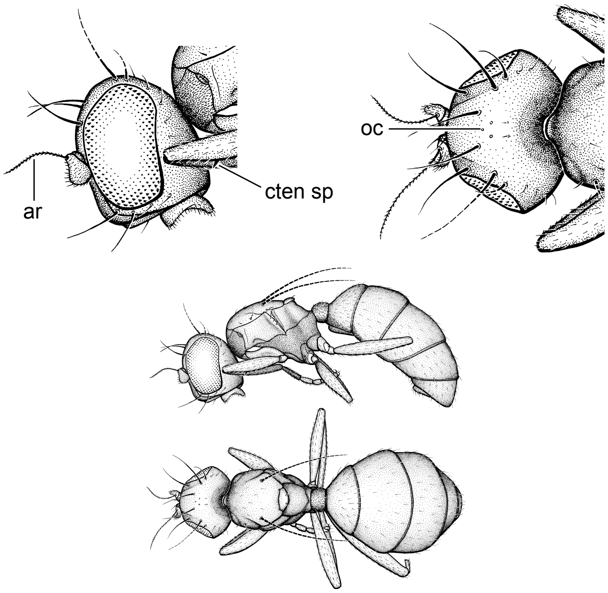
Carnidae [in part] (Chapter 93)

Carnus Nitzsch [in part] (potentially widespread).



156′ (155′). Thorax with anepisternum (anepst) bare. Head with reclinate fronto-orbital setae (rc frorb s). Not associated with nestling birds and birds′ nests.

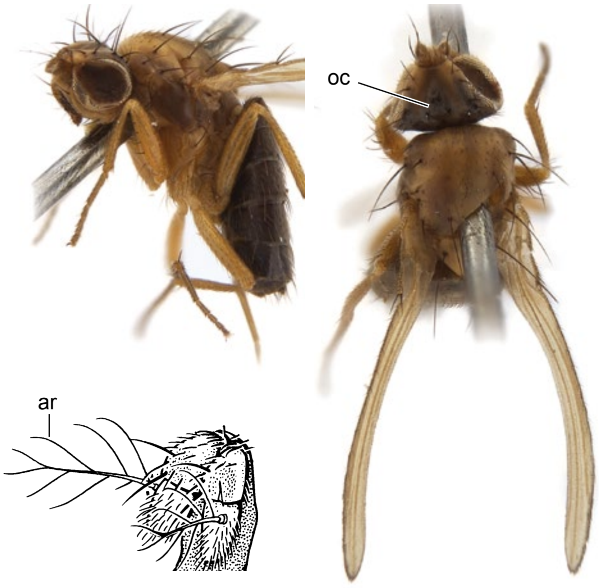
157



157 (156′). Antennal arista (ar) pubescent. Fore femur with stout ventral spine (ctenidial spine; cten sp). Ocelli (oc) greatly reduced.

Anthomyzidae [in part] (Chapter 87)

Apterosepsis basilewskyi Richards (Tanzania).



157′ (156′). Antennal arista (ar) with long dorsal branches. Fore femur without stout ventral spine (ctenidial spine). Ocelli (oc) distinct, well-developed.

Drosophilidae [in part] (Chapter 106)

Scaptomyza (*Parascaptomyza* Duda) [in part] (3 spp., Tristan da Cunha Is. group).

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KEY TO DIPTERA FAMILIES — LARVAE

13

Art Borkent and Bradley J. Sinclair

Introduction

The Diptera are one of the most morphologically and ecologically diverse groups of organisms on Earth. Their larvae occur in virtually all habitats, other than most marine environments (some do occur in the intertidal zone and some chironomids are pelagic). They can be found from marine coastlines to the highest mountain peaks, from the tropics to within kilometres of polar ice and the only indigenous free-living holometabolous insect known from Antarctica is a chironomid midge. Larvae of various species occur in nearly every conceivable terrestrial and aquatic microhabitat and include browsers, fungivores, gall-formers, herbivores, leaf-miners, wood-miners and parasites, parasitoids and predators (of other insects, other arthropods, molluscs and of vertebrates), and as saprovores, present in a remarkable array of decaying organic matter, of both plant and animal origin. Many species are vital to healthy terrestrial and aquatic ecosystems. The role, for example, of various maggots in the decomposition of dead animals and dung is immeasurable.

The larvae of many aquatic Diptera are vital to freshwater ecosystems and the Chaoboridae (see Chapter 30) and Chironomidae (see Chapter 35) are widely used as indicators of water quality in both lotic and lentic habitats (Jones 2008; Raunio & Anttila-Huhtinen 2008; Raunio & Muotka 2005; Rosenberg 1992). Their presence affects all other living organisms in these aquatic ecosystems and their subfossils are used to interpret Holocene and Quaternary lake and bog histories, thereby providing important information regarding past climatic conditions (Eggermont & Verschuren 2007; Eggermont *et al*. 2006; Elias 2010; Sweetman & Smol 2006; Walker 2007; Walker & Cwynar 2006).

Larvae also affect human health and wealth. Some larvae are agricultural pests; others lead to disease and even death, both in livestock and humans. As pests, they may occur in cultivated mushrooms, fruits and a host of other crops and foodstuffs, both fresh and preserved. They may also occur in water treatment plants (and may appear in tap water). Myiasis is a term indicating the presence of fly larvae in a vertebrate host and

Kirk-Spriggs, A.H. & Sinclair, B.J. (eds). 2017. Manual of Afrotropical Diptera. Volume 1. Introductory chapters and keys to Diptera families. *Suricata* 4. South African National Biodiversity Institute, Pretoria; pp. 357–411.

these range from beneficial (when maggots remove only necrotic tissue), to lethal in living tissues.

Despite their ubiquitous importance, larvae of most Diptera remain poorly known. In general, only the aquatic Chaoboridae and Chironomidae and a few medically and agriculturally significant families, *e.g.*, Culicidae (see Chapter 31) and Simuliidae (see Chapter 32), are reasonably well described. Although at least some larvae have been described for virtually all families of Diptera, the larvae of most species within these families remain undescribed in the Afrotropical Region. Of the total number of species that are named as adults from the Afrotropics, it is likely that less than 5% of these are known as larvae and consequently nothing is known of the primary habitat of these species – a fly collected on the wing usually provides little or no evidence as to where the immature stages may develop. Of course, phylogenetic relationships often provide a clue as to where an unknown larva may occur – for example, the described larvae of all Culicidae and Simuliidae occur in aquatic habitats.

In many instances locating, rearing and studying larvae is not difficult and reveals a great deal of knowledge about the species. Such knowledge is critical if we are ever to truly understand and explain the diversification and biodiversity of Afrotropical Diptera and assess their significance in economic and environmental terms. Furthermore, in some families in which a concerted effort has been made to study larvae (*e.g.*, Culicidae, Syrphidae and Tabanidae), characters have been discovered that allow many, if not all, to be identified to species. DNA barcoding of both adults and immatures can also facilitate confident identification and association of larvae and pupae and this technique will likely play an important role in the future identification of immatures in the Afrotropical Region (and elsewhere) (*e.g.*, Schwenkenbecher *et al*. 2009; Stur & Ekrem 2011; Yanse *et al*. 2013).

As such, because a small percentage of species of most families are known as larvae, the identification key below must generally be regarded as provisional. Characters are sometimes based on material known from outside the region and some unusual and derived taxa will almost certainly not key out satisfactorily. Specimens of the nematocerous and lower brachyceran families are more likely to key out correctly than those of the Cyclorrhapha, where knowledge is more rudimentary and incomplete. Some families of acalyptrates are especially similar to one another.

A list of morphological terms applied to larval structures in this text and in general use throughout this *Manual* is provided at the end of this chapter as an Appendix. The terms listed largely follow those applied by Courtney *et al*. (2000).

Diagnosis of Diptera larvae

Diptera larvae can be difficult to recognise as representatives of the order, particularly within the morphologically diverse nematocerous families. Lower brachyceran and cyclorrhaphan larvae are probably less difficult, due to their more uniform appearance and distinctive mouthparts. The following list of characters, based on the keys to hexapods provided by Borror *et al*. (1989) and Hill *et al*. (1987), provides a complex diagnosis that indicates some larvae to be distinctive, while others are more difficult to distinguish from those of other Holometabola.

- Without pairs of true segmented legs (fleshy prolegs may be present) and aquatic OR:
- Without pairs of segmented legs; mouthparts with functional mandibles or mouthhooks; abdominal segmentation distinct; head capsule distinct (usually pigmented and exserted); mouthparts prognathous; terminal abdominal segment forming single undivided unit (not with pair of short pointed processes); labium without spinneret; without spiracles on thorax OR:
- Without segmented legs; mouthparts with functional mandibles or mouthhooks; with distinct abdominal segmentation, these without longitudinal folds; head capsule distinct (usually pigmented and everted); without thoracic spiracles; labium without spinneret; if with abdominal spiracles, then terminal spiracle much larger than others OR:
- Without segmented legs; functional mouthparts with mandibles; maxillae not opposable; abdominal segmentation distinct; body posterior to small head capsule with 13 segments; usually with ventral spatula posterior to head capsule OR:
- Without segmented legs; head capsule indistinct or absent; mouthparts reduced to mouthhooks; spiracles on prothorax at or near caudal end; abdominal segmentation distinct.

Identification

This contribution is the first family identification key specifically written to the larvae of Afrotropical Diptera. In the past, keys from other regions were used for identification. The current key is based in part on Teskey's (1981*b*) larval identification key from the *Manual of Nearctic Diptera*, the key of Borkent & Rotheray (2009), from the *Manual of Central American Diptera* and the Cyclorrhapha key from Ferrar (1987). An earlier, but still useful work is Hennig's (1948, 1950, 1952) *"Die larvenformen der Dipteren"*.

The following identification key is directed primarily at keying last-instar larvae, but should work for many earlier-instar larvae for nematocerous Diptera and lower Brachycera, whereas some earlier instars of the Cyclorrhapha will not successfully key to family. Histoblasts and pupal structures develop strongly during the last larval instar and when either or both of these are well-developed and evident, can be used to identify this stage.

Larvae of the following families are unknown and are not included in the identification key below: Ctenostylidae (Chapter 73), *Heterotricha*-group (Sciaroidea, unassigned to family) (Chapter 23), Lygistorrhinidae (Chapter 19), Marginidae (Chapter 82), Natalimyzidae (Chapter 80), Neminidae (Chapter 89) and Xenasteiidae (Chapter 85). Celyphidae (Chapter 75) are not included, due to lack of detailed studies. The

Empidoidea families, exclusive of Dolichopodidae, *i.e*, Atelestidae, Brachystomatidae, Empididae, Homalocnemidae and Hybotidae (Chapters 51–55), are not keyed out separately and are treated collectively as Empidoidea (exclusive of Dolichopodidae) in the key below. Trichoceridae are included in the below identification key, as a published record of *Trichocera annulata* Meigen, 1818 from Ethiopia is included in the catalogue of Dahl & Alexander (1976) and an unidentified *Trichocera* Meigen sp. from Nigeria is recorded by Njila *et al*. (2014). Both these records are in need of corroboration.

Key to Diptera families (larvae) of the Afrotropical Region

1. Larva small, usually < 5 mm in length, white, yellow-orange or red; head capsule small (Fig. 2); mouthparts inconspicuous (Figs 1–3); paired cephalic bars projecting posteriorly from lateral margins (Fig. 3); prothorax of third- (last) instar with or without sternal spatula ventrally (Fig. 2) (also in some second-instars); respiratory system amphipneustic (spiracles on prothorax and abdominal segment 8) in first-instar, peripneustic (spiracles on prothorax and abdominal segments 1–8) in second- and third- (last) instars (Fig. 1); inhabiting plant galls or free-living in various terrestrial habitats . . . . Cecidomyiidae (Chapter 22)

– Larva size and colour variable; head capsule or internal cephaloskeleton with well-differentiated mouthparts; paired cephalic bars present or absent; prothorax without sternal spatula; respiratory system and habitats various 2

2. Mandibles normally moving against one another obliquely or in horizontal plane, usually with 2 or more apical teeth, rarely hook-like or sickle-shaped (*e.g.*, Fig. 4); head capsule usually complete and permanently exserted (eucephalic) (*e.g.*, Figs 5–20), but if partially retracted within thorax and incomplete as result of posterior excisions in capsule (Tipulidae *sensu lato*, couplet 3) (*e.g.*, Figs 23–25), then lacking tentorial arms (NEMATOCEROUS FAMILIES [in part]). 3

– Mandibles moving in vertical plane parallel to one another, usually hook-like or sickle-shaped and with or without secondary apical teeth (*e.g.*, Figs 67, 69); head capsule variably reduced posteriorly and partially or almost entirely retracted within thorax (hemicephalic) or replaced by internal cephaloskeleton (*e.g.*, Figs 48, 57, 76, 79, 84, 89, 99), but if appearing complete and permanently exserted, then with slender metacephalic rod extending into prothorax (*e.g.*, Figs 50, 51) (BRACHYCERA) 24

3. Head capsule longitudinally excised dorsally to varying degrees (Figs 23–25), in extreme cases reduced to several slender rods; capsule can be partially or entirely retracted into thorax; respiratory system usually metapneustic (spiracles on or near apex of abdominal segment 8), only rarely apneustic (without spiracles); occurring mostly in wet soil or decaying wood . . . .Tipulidae (incl. Limoniidae) (Chapter 14)

– Head capsule complete and non-retractable into thorax; respiratory system variable; habitats various 4

4. Head, thorax and first abdominal segment fused into compound cephalic division; suctorial disc present ventromedially on compound segment and on each of 5 following segments (Fig. 9); body firmly attached length-wise to objects in stream beds (generally rocks) . . . . .Blephariceridae (Chapter 16)

– Head, thorax, and first abdominal segment distinct, not fused into compound cephalic division (*e.g.*, Figs 5–8, 10–20); suctorial discs absent; not firmly attached to objects in stream bed or if attached (Simuliidae) (*e.g.*, Fig. 16), then with body projecting into water column. 5

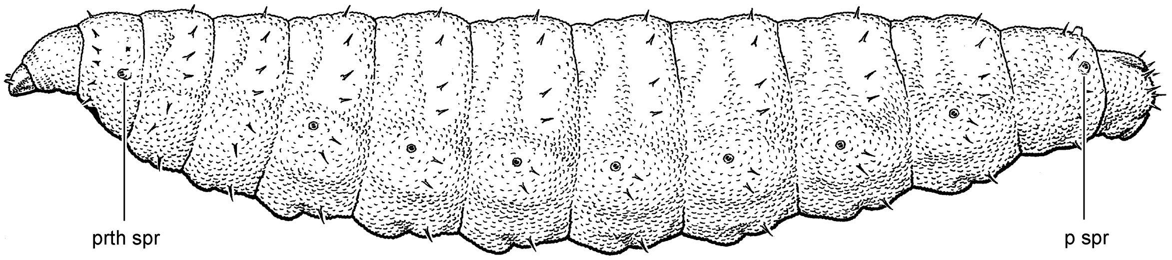
5. Respiratory system holopneustic (spiracles on prothorax, metathorax and abdominal segments 1–8) or peripneustic (spiracles on prothorax and abdominal segments 1–8); posterior spiracles usually conspicuously larger than other 7 pairs of abdominal spiracles (*e.g.*, Fig. 8); in decaying organic matter or feed on roots 6

– Respiratory system not as above; habitats various 7

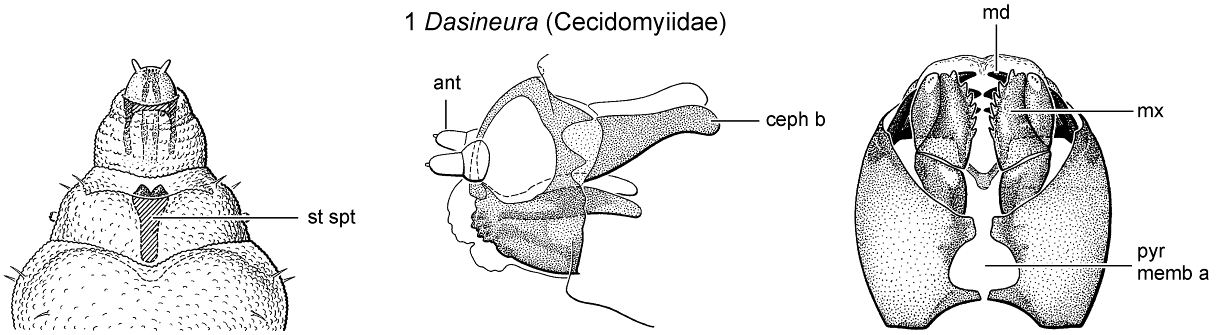
6. Respiratory system holopneustic (spiracles on prothorax, metathorax and abdominal segments 1–8) (Fig. 8); all segments usually with tuberculous or spinous processes (Fig. 8); among plant roots, in decaying organic matter and soils rich in humus. . . . . Bibionidae (Chapter 17)

– Respiratory system peripneustic (spiracles on prothorax and abdominal segments 1–8); only terminal abdominal segment sometimes having tuberculous or spinous processes, although other segments sometimes with broad tumid swellings associated with creeping welts (Fig. 7); in decaying organic matter, rotting wood, fungi, dung and dropping of vertebrates and in soil. . . . . . Scatopsidae (Chapter 26)

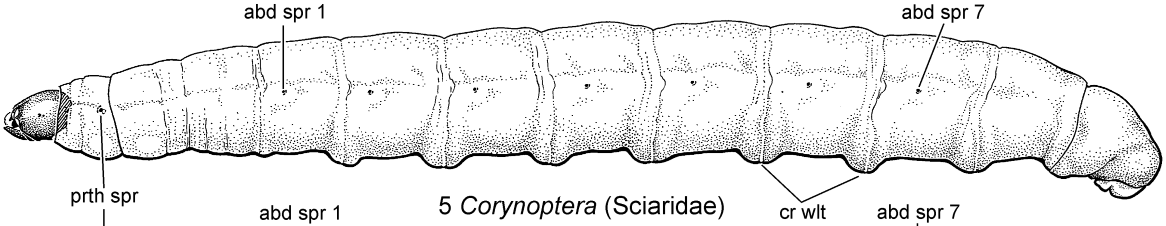
7. Respiratory system hemipneustic (spiracles on prothorax and abdominal segments 1–7) (*e.g.*, Figs 5, 6), rarely propneustic (spiracles on prothorax) or apneustic (without spiracles); mandible or maxilla or both flattened or lamellate, at least maxilla and some with mandible with serrate margin composed of large, similarly sized teeth (*e.g.*, Figs 4, 26–29); associated with fungi or decaying vegetable matter, especially dead wood and rich soils; some forming net- or sheet-like webs and feed on spores or are predaceous. 8



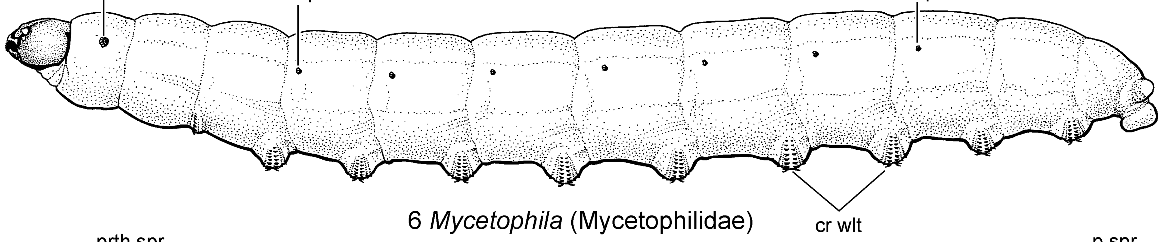
1 *Dasineura* (Cecidomyiidae)



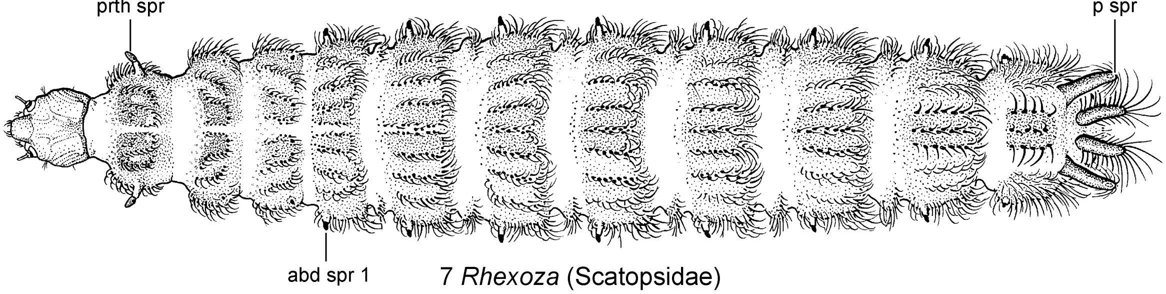
2 *Dasineura* (Cecidomyiidae) 3 *Cecidomyia* (Cecidomyiidae) 4 *Corynoptera* (Sciaridae)



5 *Corynoptera* (Sciaridae)



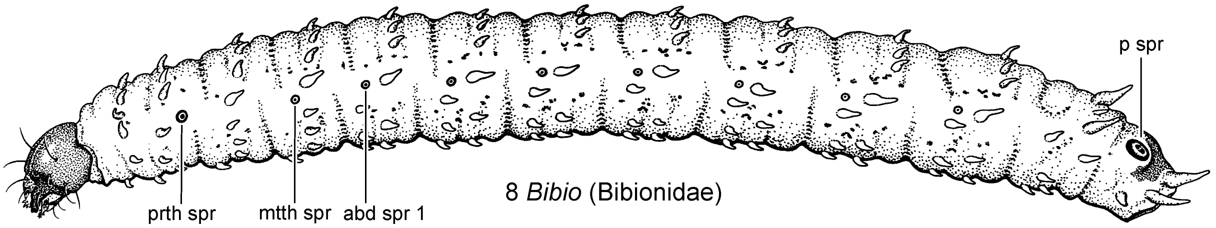
6 *Mycetophila* (Mycetophilidae)



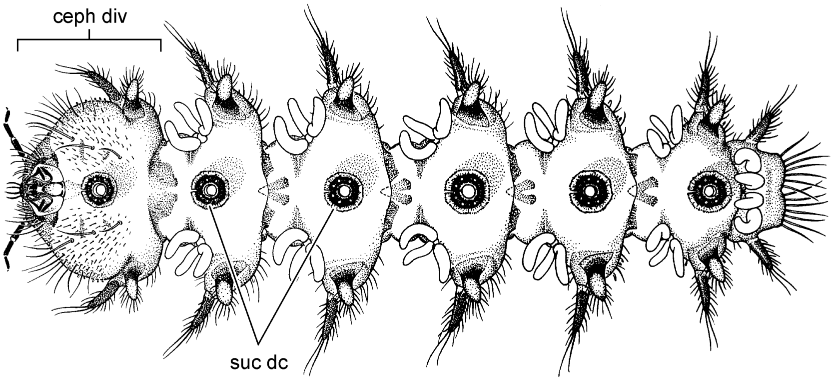
7 *Rhexoza* (Scatopsidae)

Figs 13.1–7. Larval habitus and head capsules (all non-Afrotropical): (1) habitus of *Dasineura* sp., lateral view (Cecidomyiidae); (2) same, head, prothorax and mesothorax, ventral view; (3) head of *Cecidomyia* sp., lateral view (Cecidomyiidae); (4) head of *Corynoptera* sp., ventral view (Sciaridae); (5) same, habitus, lateral view; (6) same, *Mycetophila* sp., lateral view (Mycetophilidae); (7) same, *Rhexoza* sp., dorsal view (Scatopsidae). Figs 1–3 (Gagné 1981, figs 5, 7, 8), Figs 4, 5 (Steffan 1981, figs 33, 35), Fig. 6 (Vockeroth 1981, fig. 97), Fig. 7 (Cook 1981*a*, fig. 24).

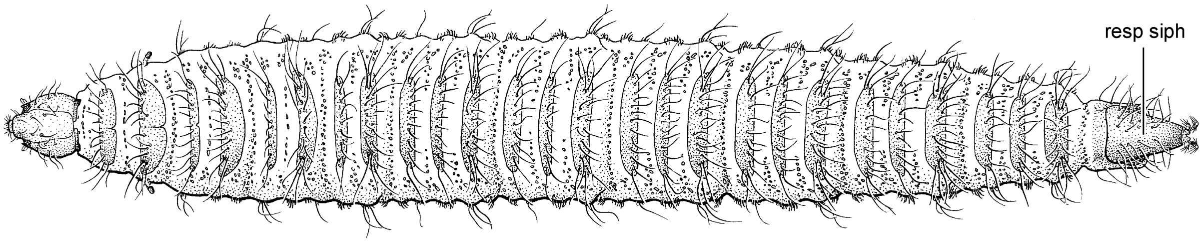
Abbreviations: abd spr – abdominal spiracle; ant – antenna; ceph b – cephalic bar; cr wlt – creeping welt; md – mandible; mx – maxilla; p spr – posterior spiracle; prth spr – prothoracic spiracle; pyr memb a – pyriform membranous area; st spt – sternal spatula.



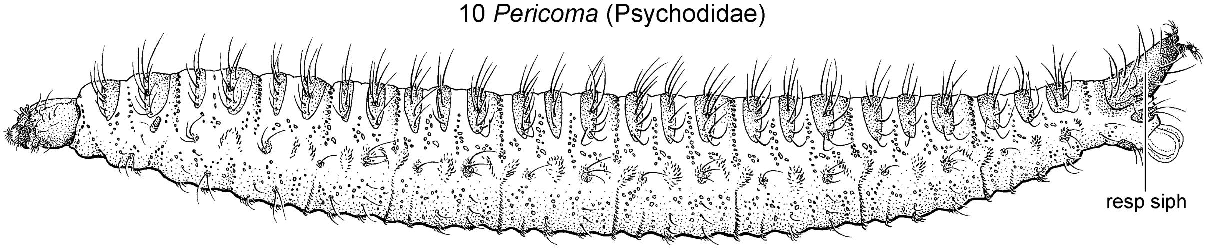
8 *Bibio* (Bibionidae)



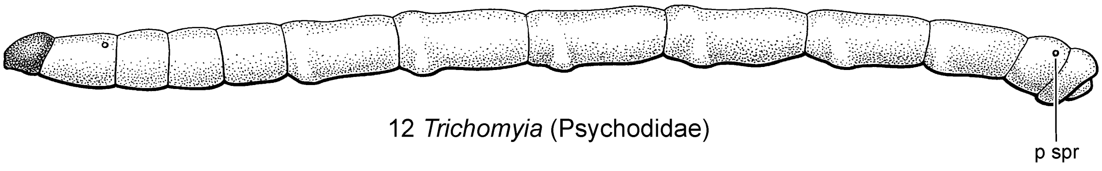
9 *Philorus* (Blephariceridae)



10 *Pericoma* (Psychodidae)



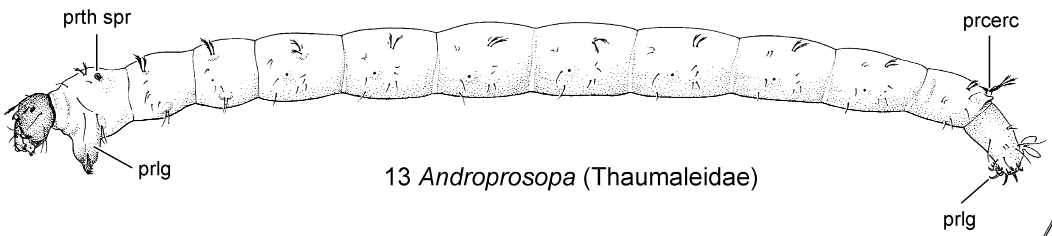
11 *Pericoma* (Psychodidae)



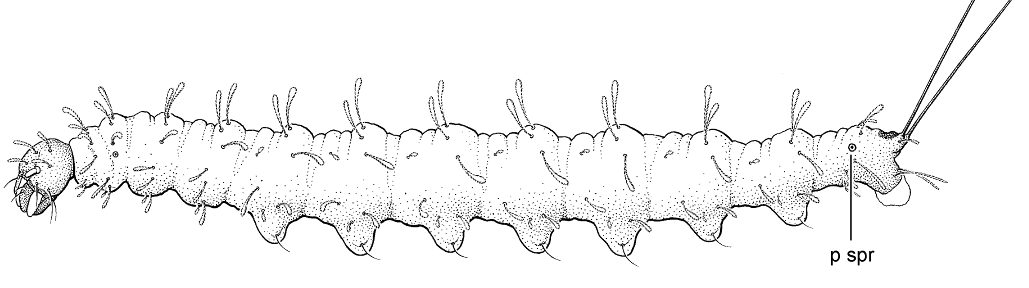
12 *Trichomyia* (Psychodidae)

Figs 13.8–12. Larval habitus (all non-Afrotropical): (8) *Bibio* sp., lateral view (Bibionidae); (9) *Philorus californicus* Hogue, ventral view (Blephariceridae); (10) *Pericoma* sp., dorsal view (Psychodidae); (11) same, lateral view; (12) *Trichomyia urbica* Haliday (Psychodidae). Fig. 8 (Hardy 1981, fig. 14), Fig. 9 (Hogue 1981, fig. 8), Figs 10–12 (Quate & Vockeroth 1981, figs 14, 15, 17).

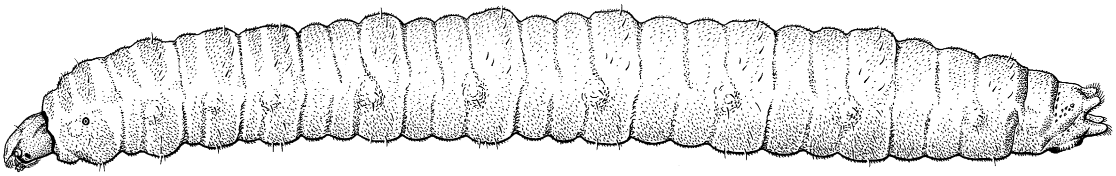
Abbreviations: abd spr – abdominal spiracle; ceph div – cephalic division; mtth spr – metathoracic spiracle; p spr – posterior spiracle; prth spr – prothoracic spiracle; resp siph – respiratory siphon; suc dc – suctorial disc.



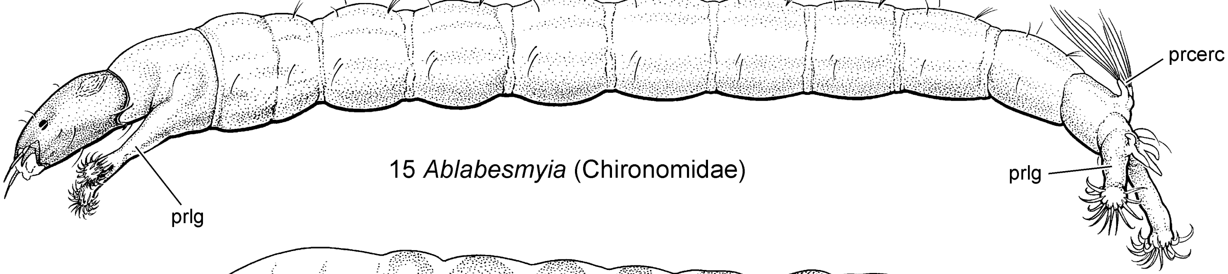
13 *Androprosopa* (Thaumaleidae)



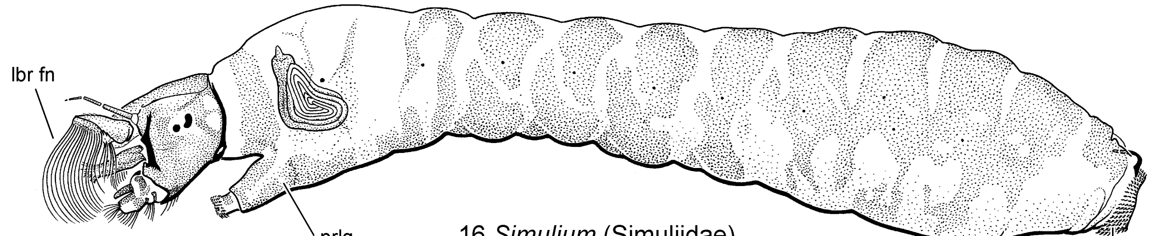
14a *Lutzomyia* (Psychodidae)



14b *Trichocera* (Trichoceridae)



15 *Ablabesmyia* (Chironomidae)



16 *Simulium* (Simuliidae)

Figs 13.13–16. Larval habitus, lateral views (all non-Afrotropical): (13) *Androprosopa* sp. (Thaumaleidae); (14a) *Lutzomyia vexator* (Coquillett) (Psychodidae); (14b) *Trichocera* sp. (Trichoceridae); (15) *Ablabesmyia* sp. (Chironomidae); (16) *Simulium venustum* (Say) (Simuliidae). Fig. 13 (Stone & Peterson 1981, fig. 4, as *Thaumalea*), Fig. 14a (Quate & Vockeroth 1981, fig. 16), Fig. 14b (Alexander 1981*a*, fig. 7), Fig. 15 (Oliver 1981, fig. 114), Fig. 16 (Peterson 1981*b*, fig. 76).

Abbreviations: lbr fn – labral fan; p crct – posterior circlet; p spr – posterior spiracle; prcerc – procercus; prlg – proleg; prth spr – prothoracic spiracle.

– Respiratory system amphipneustic (spiracles on prothorax and abdominal segment 8), metapneustic (spiracles on abdominal segment 8) (*e.g.*, Fig. 20) or apneustic (without spiracles) (*e.g.*, Figs 16–19); mandible and maxilla not flattened, mandible without serrate margin, although some with additional rows of small teeth; habitats various, mostly aquatic or in wet mud 10

8. Mid ventral corners of head capsule (or genae) closely approximated medially, enclosing pyriform membraneous area (Fig. 4); abdominal creeping welts without sclerotised spicules (Fig. 5); in decaying vegetative matter, especially dead wood and rich soils, rarely phytophagous . . . . Sciaridae (Chapter 21)

– Mid ventral portion of head capsule fused or closely approximated, but not enclosing pyriform membraneous area (*e.g.*, Figs 28, 29); abdominal creeping welts with (*e.g.*, Fig. 6) or without sclerotised spicules; in various terrestrial habitats. 9

9. Respiratory system hemipneustic (spiracles on prothorax and abdominal segments 1–7) (Fig. 6); feed on or in fungal fruiting bodies, but also on fungal hyphae and spores, in wide array of terrestrial habitats, some web-forming. . . . . .Mycetophilidae (Chapter 20)

– Respiratory system apneustic (without spiracles) or propneustic (spiracles on prothorax); form exposed webs and feed on fungal spores or are predaceous. Keroplatidae (Chapter 18)

10. Posterior spiracles inserted at apex of posteriorly directed respiratory siphon at apex of abdomen (Fig. 30); in saturated mud in shallow aquatic habitats . . . . Ptychopteridae (Chapter 27)

– Posterior spiracles present or absent, if present then situated subapically on abdomen, either dorsolaterally at surface or on dorsally or posterodorsally directed respiratory siphon (*e.g.*, Figs 31, 33, 34), if at apex of abdomen (some Anisopodidae), then not on siphon (*e.g.*, Fig. 40); various, aquatic or terrestrial habitats (wet moss, under bark, dung, *etc*.) 11

11. Thoracic segments fused and indistinctly differentiated, forming round or somewhat flattened compound segment wider than abdominal segments (*e.g.*, Figs 31–34); preanal group of long ventral setae or ventral brush present on terminal abdominal segment (*e.g.*, Figs 35, 36); lateral tufts of long setae often present on thorax and abdominal segments 1–8 (*e.g.*, Figs 31, 33, 34); in lentic aquatic habitats. 12

– Thoracic segments usually individually distinguishable and about equal in diameter to or narrower than, widest abdominal segments (some larvae may have expanded thoraces immediately prior to pupation) (*e.g.*, Figs 15–20); ventral group of long setae on terminal abdominal segment absent; setae on thorax and abdominal segments 1–8 relatively short and simple or at most, inconspicuously tufted (*e.g.*, Figs 10, 11, 14a); in lotic and lentic aquatic habitats 14

12. Head capsule with prominent brush of setae present on either side of labrum (Fig. 37), somewhat reduced in *Toxorhynchites* Theobald (Fig. 38); antenna usually with short apical setae, arising from anterolateral margin of head capsule (Fig. 37); in ground pools and phytotelmata, many in temporary aquatic habitats . . . . Culicidae (Chapter 31)

– Head capsule with setae absent or few in number and not divided into 2 groups on either side of labrum to form brush; antenna each with long apical setae, bases closely approximated, arising from anteromedial region of head capsule (*e.g.*, Figs 31, 32); in ground pools and phytotelmata, temporary or permanent aquatic habitats 13

13. Head capsule laterally compressed, without lateral row of stout spines (Fig. 32); pair of prominent air sacs present on both thorax and abdominal segment 7 (Fig. 32); in permanent small pools and lakes . . . . .Chaoboridae (Chapter 30)

– Head capsule not laterally compressed, with lateral row of stout spines (Fig. 31); without air sacs (Fig. 31); in ground pools and phytotelmata . . . . .Corethrellidae (Chapter 29)

14. Paired crochet-bearing prolegs present ventrally on abdominal segment 1 and usually on abdominal segment 2 (Fig. 20); abdomen with 2 flattened posterolateral processes posterior to posterior spiracles, with setose margins, that project above conical dorsally sclerotised process, bearing anus and anal papillae ventrally (Fig. 20); in small lotic and lentic aquatic habitats, when feeding with typical U-shaped body position in meniscus . . . . .Dixidae (Chapter 28)

– Prolegs absent on abdominal segments 1 and 2 (*e.g.*, Figs 15–19); abdomen without posterior, flattened, fringed postspiracular processes and without conical dorsally sclerotised anal process; in wide array of aquatic, semi-terrestrial (saturated soils) or terrestrial habitats (under bark, in moss, dung, *etc*., when feeding body straight or only somewhat curved). 15

15. Prothorax with 1 proleg or pair of prolegs ventrally (retracted into body cavity in some specimens) (*e.g.*, Figs 13, 15–18) 16

– Prothorax without prolegs (*e.g.*, Figs 10–12, 14a) 19

16. Head capsule with pair of conspicuous, folding labral fans dorsolaterally (sometimes closed in preserved specimens) (Fig. 16); abdomen swollen posteriorly, terminal abdominal segment ending in ring or circlet, of numerous radiating rows of minute hooked spines (Fig. 16); in flowing water . . . . Simuliidae (Chapter 32)

– Head capsule without labral fans; abdomen not conspicuously swollen posteriorly; terminal abdominal segment without radiating rows of hooked spines posteriorly, but sometimes with 1 or 2 anal prolegs bearing crochets (*e.g.*, Figs 13, 15, 17, 18); in wide array of aquatic habitats, semi-terrestrial, wet habitats (saturated soils) or terrestrial (under bark, in moss, dung, *etc.*) 17

17. Respiratory system amphipneustic (spiracles on prothorax and abdominal segment 8) (Fig. 13); prothoracic spiracle on short stalk; posterior spiracles opening into transverse cleft between finger-like processes (procerci) on abdominal segment 8; prothoracic and terminal prolegs unpaired; in shallow trickles over rock faces and associated vegetation . . . . Thaumaleidae (Chapter 33)

– Respiratory system apneustic (without spiracles) (*e.g.*, Figs 15, 17, 18) or rarely, metapneustic (spiracles on abdominal segment 8); prothoracic or terminal prolegs usually paired, even if distinction is only slight separation of apical spines or crochets, terminal prolegs absent in some; in wide array of aquatic, semi-terrestrial (saturated soils) or terrestrial habitats (under bark, in moss, dung, *etc.*) 18

18. All body segments with prominent tubercles or setae or both (Figs 17, 18); head capsule with large epipharyngeal complex in center of head capsule; in small aquatic, semi-terrestrial and terrestrial habitats (under bark, in moss, dung, *etc.*) (*Atrichopogon* Kieffer, some *Forcipomyia* Meigen) . . . . Ceratopogonidae [in part] (Chapter 34)

– At most, terminal 1 or 2 abdominal segments with prominent tubercles (procerci) and setae (Fig. 15); head capsule without conspicuously developed epipharyngeal complex; in wide array of aquatic habitats, semi-terrestrial, and less commonly, terrestrial habitats . . . . Chironomidae (Chapter 35)

19. Abdominal segment 8 with moderately elongate fleshy process, arising posteromedially to spiracle; abdominal segment 9 with paired processes arising dorsolaterally (Fig. 39); known only from monotypic genus from Western Cape Province, South Africa; under overhanging boulders, in white gravelly sand spits along stream margins . . . . Tanyderidae (Chapter 15)

– Abdominal segment 8 without elongate fleshy process arising from near posterior spiracles; abdominal segment 9 without paired processes; habitats variable 20

20. Respiratory system apneustic (without spiracles); larva slender, smooth, with uniform thoracic and abdominal segments (Figs 41, 42); if abdominal segments secondarily divided, then head capsule with elongate apodemes extending from head capsule into thorax (*Leptoconops* Skuse) (Fig. 43); long setae absent or if present only on terminal abdominal segment (Figs 41, 42); in wide array of aquatic habitats, saturated terrestrial habitats (soils, decaying vegetative matter, manure, *etc.*) . . . . Ceratopogonidae [in part] (Chapter 34)

– Respiratory system amphipneustic (spiracles on prothorax and abdominal segment 8) or metapneustic (spiracles on abdominal segment 8); cuticle usually somewhat wrinkled, with (*e.g.*, Fig. 40) or without, secondarily divided segments; head capsule lacking long internal apodemes; with (*e.g.*, Figs 10, 11) or without (*e.g.*, Figs 12, 14a, 14b), distinctive setation or sclerotised plaques present on most segments; habitats variable 21

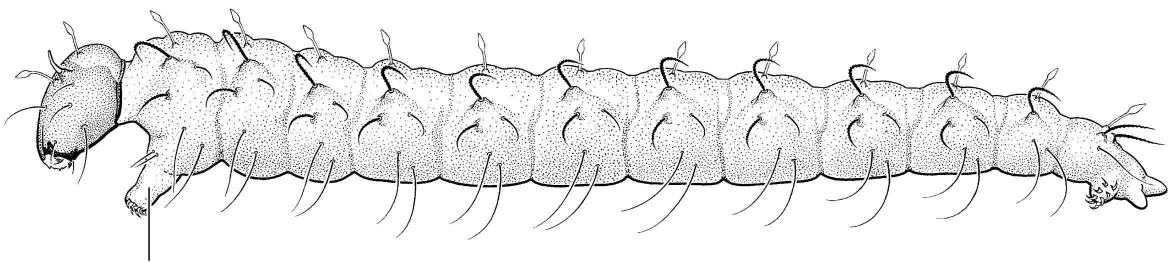
21. Secondary segmentation of prothorax and abdominal segments evident, with segments having distinct narrow annulus anteriorly (Fig. 40); posterior spiracles sessile, on surface of terminal abdominal segment and placed either laterally or apically, with apically positioned spiracles surrounded by 5 small lobes (Figs 44–46); in decaying organic matter . . . . Anisopodidae (Chapter 25)

– Secondary segmentation either not evident or usually with thoracic and first abdominal segments subdivided into two sections and remaining abdominal segments subdivided into three elementary sections (*e.g.*, Figs 10–12, 14b); posterior spiracles either mounted on respiratory siphon (*e.g.*, Figs 10–11) or as above, but if sessile and apical in position then surrounded by only four lobes (*e.g.*, Fig. 14b) 22

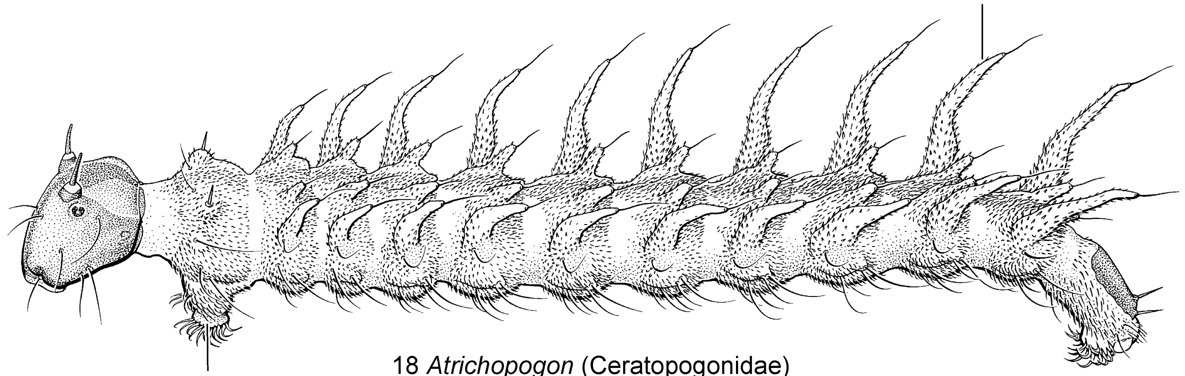
22. Posterior spiracles and pair of fan-like setal brushes borne dorsally at caudal margin of sclerotised plate on terminal abdominal segment, or at apex of short respiratory siphon, projecting posterodorsally from terminal abdominal segment (Figs 10, 11); sclerotised plaque or plaques evident dorsally on one or more secondary segmental divisions; in aquatic or semiaquatic habitats or in decaying organic material (PSYCHODINAE) . . . . Psychodidae [in part] (Chapter 24)

– Posterior spiracles not borne on respiratory siphon; sclerotised plaques absent; habitats various 23

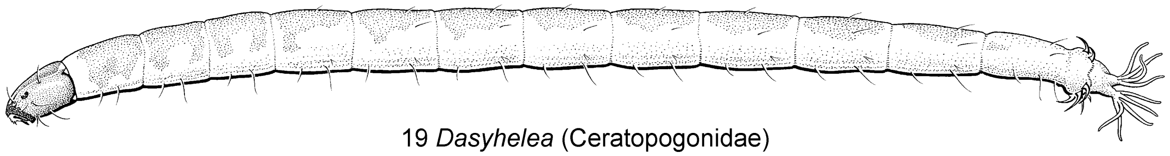
23. Posterior spiracles situated laterally on terminal or penultimate abdominal segment (Figs 12, 14a); either setae (some of which are clavate) on integument prominent and systematically arranged, with some long setae on dorsum of terminal segment (Phlebotominae) (Fig. 14a), or setae short, unmodified or absent (Trichomyiinae) (Fig. 12); habitats various . . . . Psychodidae [in part] (Chapter 24)



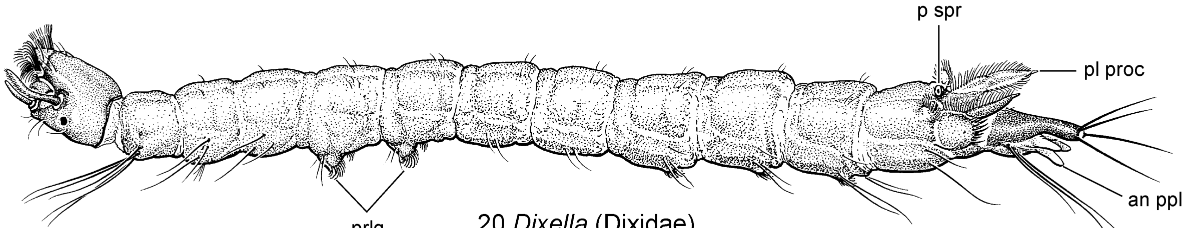
17 *Forcipomyia* (Ceratopogonidae)



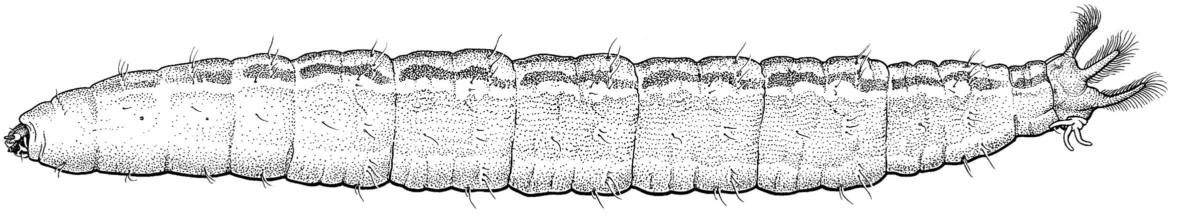
18 *Atrichopogon* (Ceratopogonidae)



19 *Dasyhelea* (Ceratopogonidae)



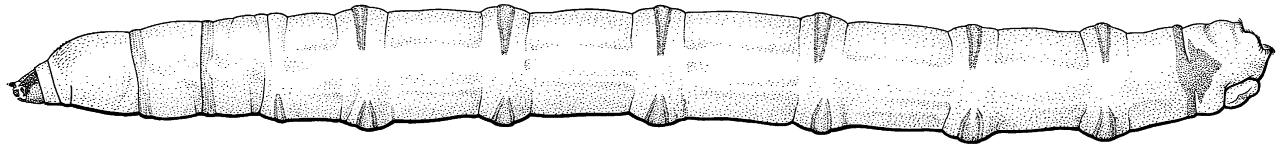
20 *Dixella* (Dixidae)



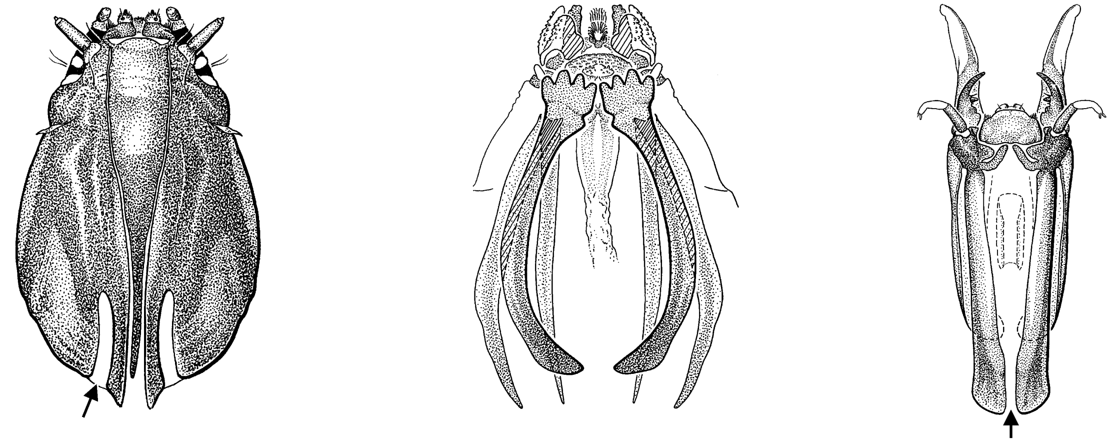
21 *Prionocera* (Tipulidae)

Figs 13.17–21. Larval habitus, lateral views (all non-Afrotropical): (17) *Forcipomyia* sp. (Ceratopogonidae); (18) *Atrichopogon* sp. (Ceratopogonidae); (19) *Dasyhelea* sp. (Ceratopogonidae); (20) *Dixella* sp. (Dixidae); (21) *Prionocera* sp. (Tipulidae). Figs 17–19 (Downes & Wirth 1981, figs 130–132), Fig. 20 (Peters 1981, fig. 10, as *Dixa*), Figs 21 (Alexander & Byers 1981, fig. 66).

Abbreviations: abd tub – abdominal tubercle; an ppl – anal papilla; p spr – posterior spiracle; pl proc – posterolateral process; prlg – proleg(s).



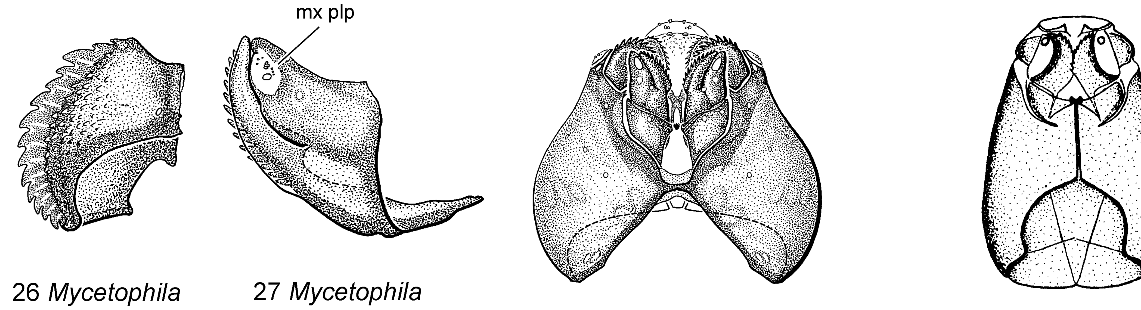
22 *Limonia* (Limoniidae)



23 *Prionocera* (Tipulidae)

24 *Molophilus* (Limoniidae)

25 *Limnophila* (Limoniidae)

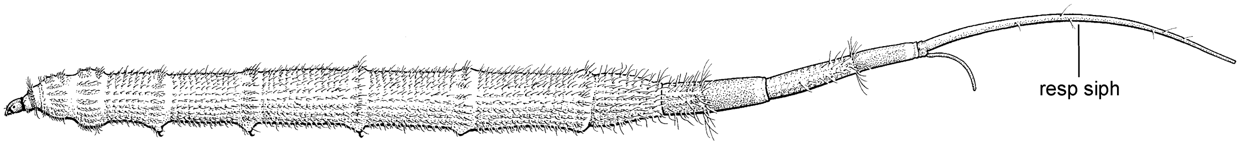


26 *Mycetophila* (Mycetophilidae)

27 *Mycetophila* (Mycetophilidae)

28 *Mycetophila* (Mycetophilidae)

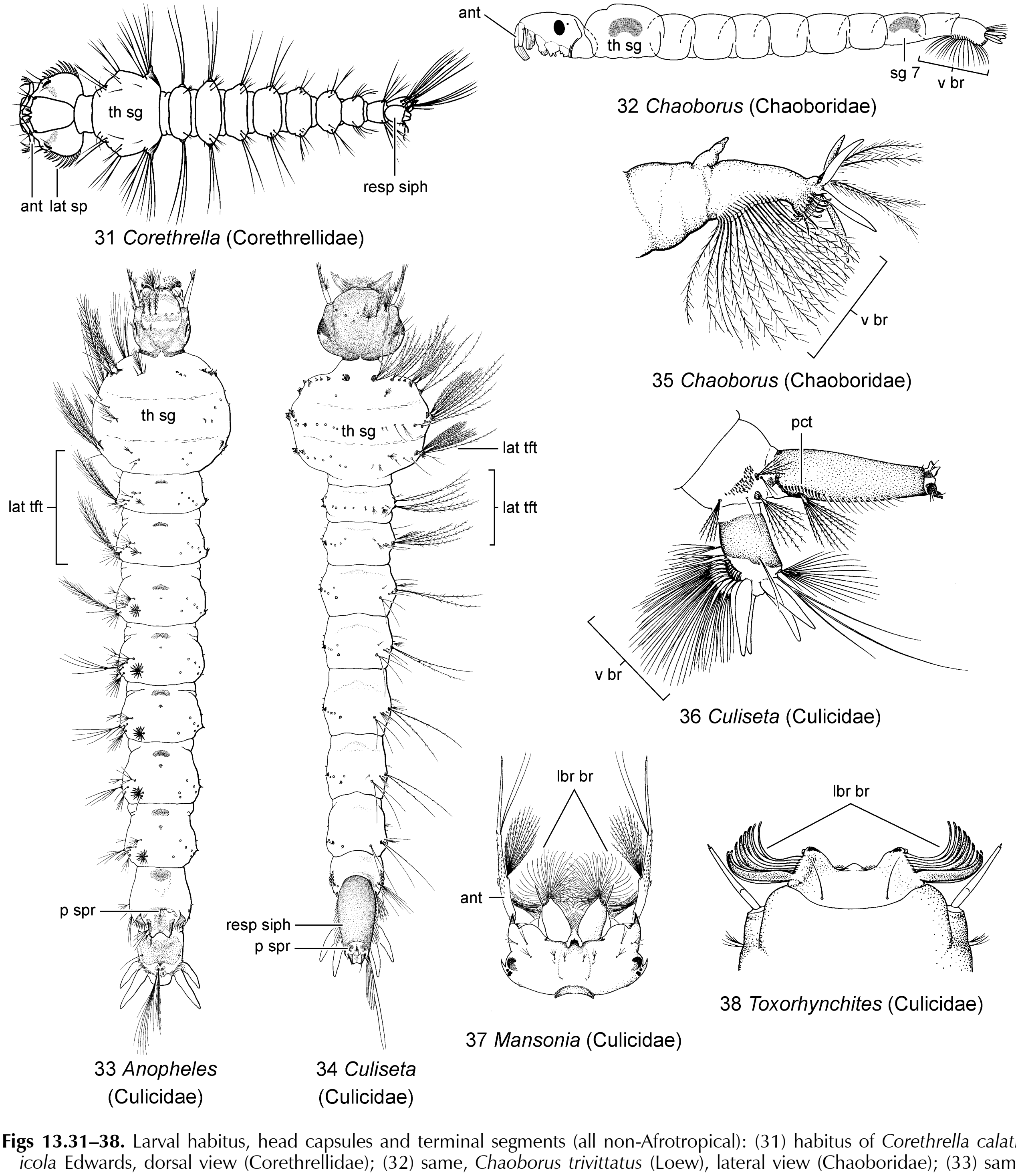
29 *Mycomya* (Mycetophilidae)



30 *Ptychoptera* (Ptychopteridae)

Figs 13.22–30. Larval habitus and head capsules (all non-Afrotropical): (22) habitus of *Limonia* sp., lateral view (Limoniidae); (23) head of *Prionocera* sp., dorsal view (Tipulidae) (arrow indicates posterior excision); (24) same, *Molophilus* sp., ventral view (Limoniidae); (25) same, *Limnophila* sp., dorsal view (Limoniidae) (arrow indicates posterior excision); (26) mandible of *Mycetophila fisherae* (Laffoon), ventral view (Mycetophilidae); (27) same, maxilla, ventral view; (28) same, head, ventral view; (29) same, *Mycomya marginata* (Meigen) (Mycetophilidae); (30) habitus of *Ptychoptera* sp., lateral view (Ptychopteridae). Figs 22–25 (Alexander & Byers 1981, figs 67, 76, 82, 83), Figs 26–28 (Vockeroth 1981, figs 98–100), Fig. 29 (after Brauns 1954, fig. 20.I), Fig. 30 (Alexander 1981*b*, fig. 5).

Abbreviations: mx plp – maxillary palpus; resp siph – respiratory siphon.



31 *Corethrella* (Corethrellidae)

32 *Chaoborus* (Chaoboridae)

35 *Chaoborus* (Chaoboridae)

36 *Culiseta* (Culicidae)

37 *Mansonia* (Culicidae)

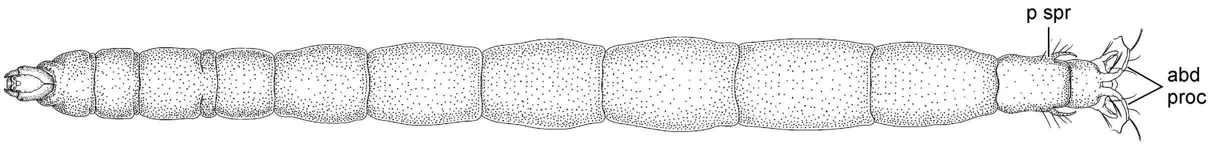
38 *Toxorhynchites* (Culicidae)

33 *Anopheles* (Culicidae)

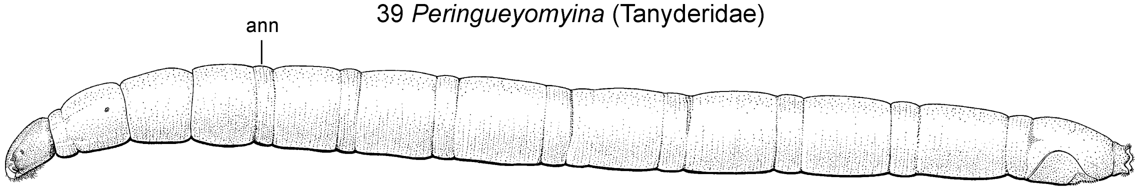
34 *Culiseta* (Culicidae)

Figs 13.31–38. Larval habitus, head capsules and terminal segments (all non-Afrotropical): (31) habitus of *Corethrella calathicola* Edwards, dorsal view (Corethrellidae); (32) same, *Chaoborus trivittatus* (Loew), lateral view (Chaoboridae); (33) same, *Anopheles earlei* Vargas, dorsal view (Culicidae); (34) same, *Culiseta incidens* (Thomson) (Culicidae); (35) terminal segments of *Chaoborus* sp., lateral view (Chaoboridae); (36) same, *Cul. inornata* (Williston), lateral view (Culicidae); (37) head capsule of *Mansonia titillans* (Walker), ventral view (Culicidae); (38) same, *Toxorhynchites rutilus* (Coquillett), dorsal view (Culicidae). Fig. 31 (after Edwards 1930, fig. 1a), Fig. 32 (after Borkent 2009, fig. 3), Figs 33, 34, 36, 37, 38 (Stone 1981, figs 33, 34, 31, 23, 26, respectively), Fig. 35 (Cook 1981*b*, fig. 14).

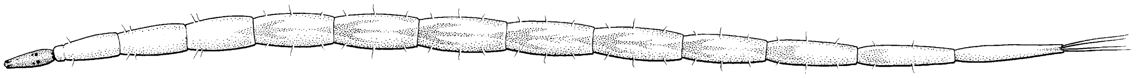
Abbreviations: ant – antenna; lat sp – lateral spines; lat tft – lateral tuft; lbr br – labral brush; p spr – posterior spiracle; pct – pectin; resp siph – respiratory siphon; sg – segment; th sg – thoracic segment; v br – ventral brush.



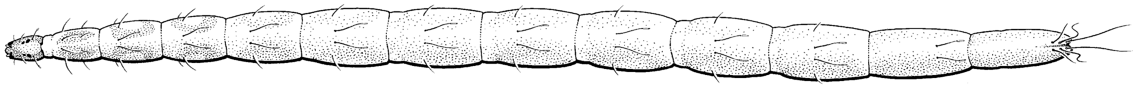
39 *Peringueyomyina* (Tanyderidae)



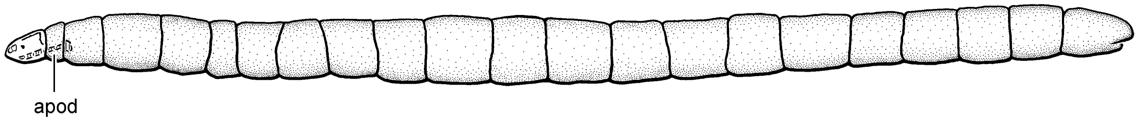
40 *Sylvicola* (Anisopodidae)



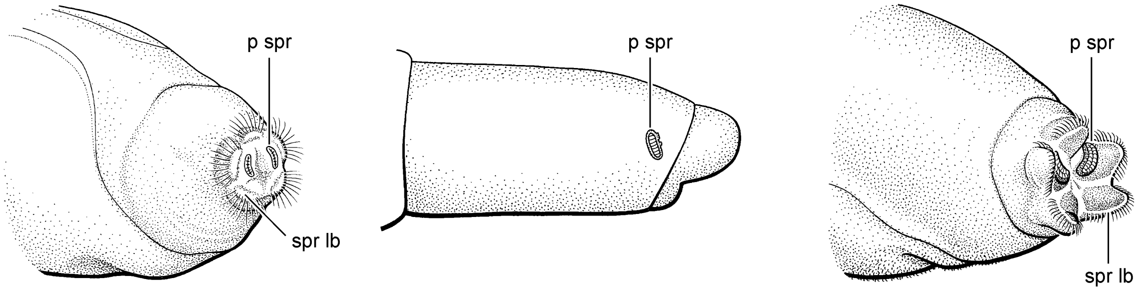
41 *Bezzia* (Ceratopogonidae)



42 *Culicoides* (Ceratopogonidae)



43 *Leptoconops* (Ceratopogonidae)



44 *Mycetobia* (Anisopodidae) 45 *Olbiogaster* (Anisopodidae) 46 *Sylvicola* (Anisopodidae)

Figs 13.39–46. Larval habitus and terminal segments: (39) habitus of *Peringueyomyina barnardi* Alexander, dorsal view (Tanyderidae); (40) same, *Sylvicola punctatus* (F.), lateral view (Anisopodidae) (non-Afrotropical); (41) same, *Bezzia* sp., dorsal view (Ceratopogonidae); (42) same, *Culicoides* sp. (Ceratopogonidae); (43) same, *Leptoconops spinosifrons* (Carter), lateral view (Ceratopogonidae); (44) terminal segments of *Mycetobia divergens* Walker, posterolateral view (Anisopodidae) (non-Afrotropical); (45) same, *Olbiogaster africanus* Edwards, lateral view (Anisopodidae); (46) same, *S. punctatus*, posterolateral view (Anisopodidae) (non-Afrotropical). Fig. 39 (source: Madriz (Chapter 15), fig. 16), Fig. 40 (Peterson 1981a, fig. 19), Figs 41, 42 (Downes & Wirth 1981, figs 133, 134), Fig. 43 (after Laurence & Mathias 1972, fig. 1), Figs 44–46 (Peterson 1981a, figs 20–22).

Abbreviations: abd proc – abdominal process; ann – annulus; apod – apodeme; p spr – posterior spiracle; spr lb – spiracular lobe.

– Posterior spiracles situated at apex of terminal abdominal segment, surrounded by four fleshy lobes (Fig. 14b); setae various; in decaying vegetable matter. . . . . [Trichoceridae (questionably recorded from Ethiopia and Nigeria)]

24. Sclerotised portions of cranium always present and usually partially exposed externally (*e.g.*, Figs 48, 57, 66, 76, 83); labrum, mandibles or maxillae, readily recognisable (LOWER BRACHYCERA) 25

– External sclerotised portions of cranium entirely absent; only membranous pseudocephalon anterior to prothorax remaining, normally bearing 2 pairs of papilla-like projections (considered vestiges of antenna and maxillary palpus) (*e.g.*, Fig. 89); characteristically shaped cephaloskeleton retracted entirely within prothorax or almost entirely absent in some, usually parasitic or parasitoid, species (*e.g.*, Figs 99, 155); homologs of labrum, mandibles, and maxillae not clearly evident (CYCLORRHAPHA) 42

25. Body dorsoventrally compressed; integument hardened by calcareous deposits accumulated in small rounded or hexagonal facets that impart shagreened appearance; head capsule permanently partially exposed and capable of only slight independent movement in life (*e.g.*, Figs 47, 48) 26

– Body of varied form; integument not hardened and not faceted with calcium deposits, sometimes tough and leathery; head capsule capable of considerable independent movement in life 27

26. Prothoracic and mesothoracic segments with smooth dorsal field (Fig. 47); anus bordered anteriorly by transverse row of strong posteriorly directed, teeth-like projections (Fig. 47); saprophagous, under bark of decaying trees and logs . . . . Xylomyidae (Chapter 40)

– Prothoracic and mesothoracic segments with shagreened pattern on dorsum (Fig. 48); anus not bordered anteriorly by teeth-like projections; saprophagous, in compost heaps, decaying vegetation, under bark or aquatic in rivers, ponds, tree holes, seepages, *etc*. . . . . Stratiomyidae (Chapter 41)

27. Body long and slender, eel-like, with 20 apparent segments; posterior spiracles situated laterally on fourth segment from end (*e.g.*, Figs 49, 52); head capsule appearing complete and permanently extended, flexibly articulated posteriorly, with slender or spatulate metacephalic rod lying within thorax (*e.g.*, Figs 50, 51) 28

– Body not eel-like, with no more than 12 apparent segments; posterior spiracles on terminal or penultimate abdominal segment; head capsule more or less reduced, especially posteroventrally and partially retracted within thorax, with or without single broad or nonspatulate metacephalic rod lying within thorax or with 2 apparent rods present 29

28. Head capsule with metacephalic rod expanded posteriorly (Fig. 50); tentorial arms extending posteriorly beyond head capsule; Keilin's organ on each side of thoracic segments, shorter than diameter of segments and situated ventrolaterally (Fig. 49); predaceous in soil and decaying wood. . . . . Therevidae (Chapter 49)

– Head capsule with metacephalic rod slender throughout (Fig. 51); tentorial arms not extending beyond head capsule; Keilin's organ on each side of thoracic segments as long as diameter of segments, situated dorsolaterally on mesothorax and ventrolaterally on prothorax and metathorax (Fig. 52); predaceous on insects in houses, in stored foodstuffs, grass clumps and in wood . . . . Scenopinidae (Chapter 50)

29. Body plump and grub-like (*e.g.*, Figs 53, 55, 56); head usually small, almost entirely retracted within thorax, with only mandibles or maxillae, and at least vestige of labrum, visible externally; parasitoids of or predaceous upon other Arthropoda 30

– Body usually elongate, slender, in some greatly enlarged (*e.g.*, Figs 58–62, 77, 78, 80, 83); portions of dorsal plate of head capsule and mouthparts visible externally; free-living 32

30. Body robust, tough, leathery; terminal abdominal segment with posterodorsal margin scalloped by blunt projections (Fig. 53); mandible large and shovel-shaped (Fig. 54); parasitoids of grasshoppers, katydids and beetle larvae . . . . Nemestrinidae (Chapter 43)

– Body whitish, with thin transparent integument; terminal abdominal segment, otherwise; mandible slender and pointed, often smaller than maxilla; parasitoids of spiders and insects 31

31. Body pear-shaped, with enlarged abdomen (Fig. 55); internal parasitoids of spiders. . . . . Acroceridae (Chapter 42)

– Body moderately crescent-shaped, tapered anteriorly and posteriorly (Fig. 56); parasitoids or predators of other insects . . . . Bombyliidae [in part] (Chapter 45)

32. Body with terminal abdominal segments distinctly enlarged; integument wrinkled and densely clothed in dense microtrichia; abdominal segment 1 ventrally with single median proleg; abdominal segment 7 with transverse dorsal row or comb of spine-like tubercles along posterior margin (Fig. 58); posterior spiracles situated dorsally on abdominal segment 8; construct conical pits in fine, dusty soil, usually beneath rock overhangs, for capturing prey . . . . Vermileonidae (Chapter 36)

– Body usually cylindrical or greatly enlarged posteriorly (*e.g.*, Figs 59–62, 77, 80), lacking dense microtrichia; prolegs, if present, situated on several segments; abdominal segment 7 lacking dorsal row of spine-like tubercles; posterior spiracles, if present, situated caudally on terminal abdominal segment or dorsolaterally on penultimate or terminal abdominal segment; habitats various 33

33. Mandibular brush of retrorse (backwardly bent) spines, situated above base of each mandible and attached to mandible, such that when it strikes downward, brush of spines pulled forward from beneath semi-transparent membranous covering and spines erected (*e.g.*, Figs 65, 66); head capsule with portion of cranium lying within thorax continuous with anterior exposed portion, without apparent break, although desclerotisation may suggest bilateral division; tentorial arms solidly connected to tentorial phragmata (except in *Rhagio* F., Fig. 67); darkly pigmented stemmata occasionally visible through head capsule (Rhagionidae, Fig. 68) 34

– Mandibular brush absent; head capsule with posterior portion of cranium (metacephalic rod) lying within thorax separated from anterior exposed portion by clear seam allowing independent flexibility between 2 portions (*e.g.*, Figs 75, 79); if continuous, base of labrum and maxillae with several stout spine-like setae (*e.g.*, Fig. 73); tentorial arms also flexibly attached to tentorial phragmata; stemmata unpigmented 36

34. Abdominal segments 1–7 with slender tubercles of progressively increasing size, situated laterally and dorsolaterally (Fig. 59); all abdominal segments with pair of elongate prolegs ventrally, each proleg with semi-circle of subapical and apical claws (Fig. 59); respiratory system functionally apneustic (single non-functional spiracle present); in stream beds. . . . . Athericidae (Chapter 38)

– Abdominal segments 1–7 at most with short prolegs, bearing 1 or more concentric rows of spines (*e.g.*, Figs 60–62); respiratory system metapneustic (spiracles on abdominal segment 8) or amphipneustic (spiracles on prothorax and abdominal segment 8); habitats various 35

35. Posterior spiracles lying within fissures on either side of pair of abutting vertically linear bars (Fig. 70) or retractable, laterally compressed spine (Figs 71, 72), situated at apex of short respiratory siphon or comparable slightly domed area delimited caudally on terminal abdominal segment; tracheal trunks closely approximated within terminal abdominal segment and siphon; terminal abdominal segment lacking tubercles; several or all anterior 7 abdominal segments with encircling row of projections, sometimes bearing apical spicules and functioning as prolegs (Figs 60, 61); in wetland soils, especially marshes, bogs and margins of streams and ponds . . . . Tabanidae (Chapter 39)

– Posterior spiracular openings exposed, each circular or oval; tracheal trunks distinctly separated caudally; terminal abdominal segment either deeply cleft caudally to form 2 or 4 lip-like lobes or bearing pair of sclerotised horn-like processes dorsally and pair of rounded lobes ventrally (Fig. 64); posterior spiracles on caudal face of dorsal lobes (Fig. 63); first 7 abdominal segments with ventral creeping welts (Fig. 62); in moist, humus-rich soils; occasionally amongst stream vegetation . . . . Rhagionidae (Chapter 37)

36. Portion of cranium lying within thorax continuous with anterior exposed portion without apparent break; base of labrum and maxillae with several stout, spine-like setae (Figs 73, 74); free-living in sand (*Heterotropus* Loew) . . . . Bombyliidae [in part] (Chapter 45)

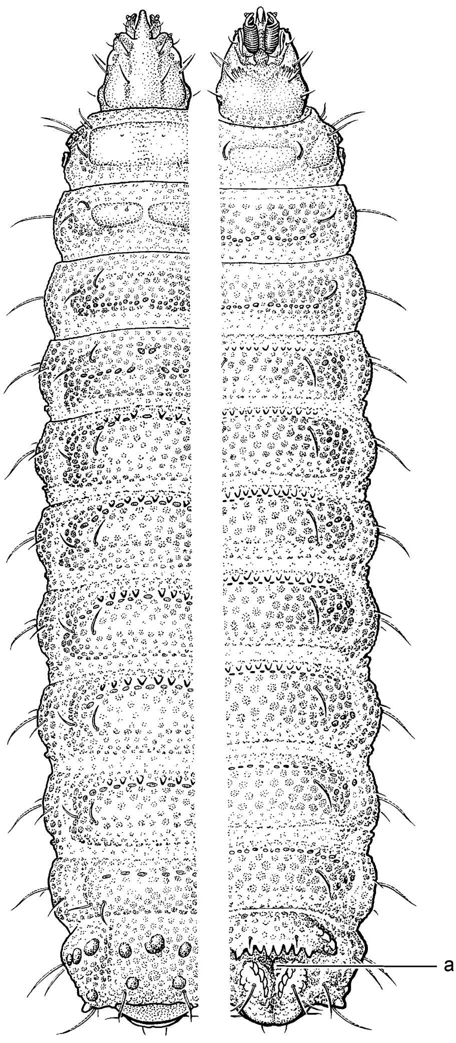
– Posterior portion of cranium (metacephalic rod), lying within thorax and clearly separated and articulated to anterior exposed portion; labrum and maxillae lacking stout, spine-like setae; habitats various 37

37. Several abdominal segments bearing pair of slender, finger-like prolegs (Fig. 81); predators of insect egg pods and inquilines in ants' nests . . . . Mythicomyiidae (Chapter 44)

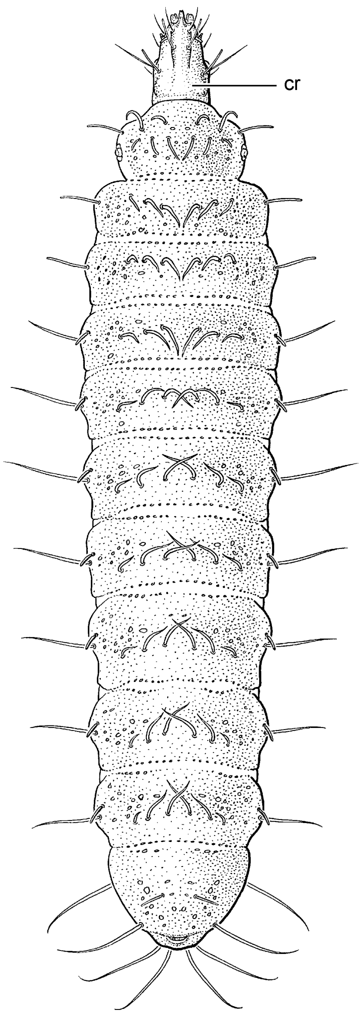
– Abdominal segments without slender, finger-like prolegs; habitats various 38

38. Head with single relatively narrow or broader metacephalic rod (*e.g.*, Fig. 75); rod sometimes split almost to base; sclerotised ventral plate (or submentum) present ventrally on head capsule; maxilla large and heavily sclerotised, more prominent than slender mandible (*e.g.*, Figs 75, 76); 9 abdominal segments present; respiratory system functionally amphipneustic (spiracles on prothorax and abdominal segment 8), although remnants of spiracles forming complete holopneustic system (spiracles also on metathorax and abdominal segments 1–7), usually visible; posterior spiracles situated laterally on abdominal segment 8 (*e.g.*, Figs 77, 78); larva usually large at maturity (> 2 cm); predators occurring in terrestrial habitats (soil, wood, *etc.*) 39

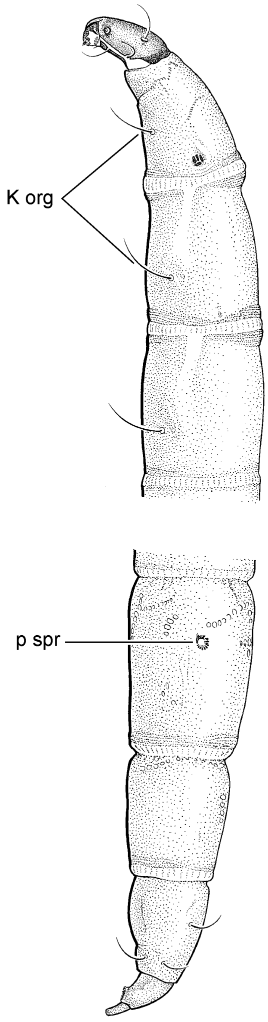
– Head with slender metacephalic rod thickened and darkly pigmented laterally, giving paired appearance (*e.g.*, Fig. 85), clearly divided into pair of rods posteriorly; metacephalic rod and 2 tentorial arms most prominent features of head (*e.g.*, Figs 82, 84); ventral plate (or submentum) absent; maxilla mostly membranous and not heavily sclerotised or more prominent than mandible (*e.g.* Fig. 82); 8 abdominal



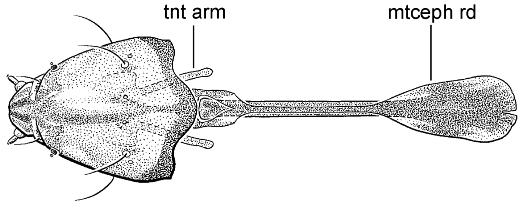
47 *Solva* (Xylomyidae)



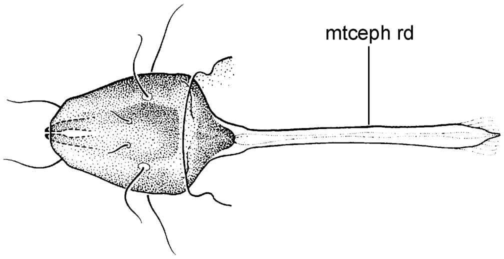
48 *Zabrachia* (Stratiomyidae)



49 *Thereva* (Therevidae)



50 *Thereva* (Therevidae)



51 *Scenopinus* (Scenopinidae)

Figs 13.47–51. Larval habitus, head capsules and thoracic and terminal segments (all non-Afrotropical): (47) habitus of *Solva pallipes* (Loew), dorsal view (left) ventral view (right) (Xylomyidae); (48) same, *Zabrachia polita* Coquillett, dorsal view (Stratiomyidae); (49) head, thoracic and terminal segments of *Thereva fucata* Loew, lateral view (Therevidae); (50) same, head capsule, dorsal view; (51) same, *Scenopinus* sp. (Scenopinidae). Fig. 47 (James 1981*a*, figs 7, 8), Fig. 48 (James 1981*b*, fig. 73), Figs 49, 50 (Irwin & Lyneborg 1981, figs 23, 24), Fig. 51 (Kelsey 1981, fig. 12).

Abbreviations: an – anus; cr – cranium; K org – Keilin's organ; mtceph rd – metacephalic rod; p spr – posterior spiracle; tnt arm – tentorial arm.

segments present (*e.g.*, Figs 83, 87); posterior spiracles, when present, located caudally on terminal abdominal segment; respiratory system amphipneustic (spiracles on prothorax and abdominal segment 8), metapneustic (spiracles on abdominal segment 8) or apneustic (without spiracles); usually small (< 1 cm); aquatic (*e.g.*, streams, seepages, wet marine sand, *etc.*) or terrestrial (*e.g.*, wood, under bark, *etc.*) . . . 41

39. Head capsule with maxillae laterally compressed, tending to cup mandibles and similar in length to mandibles; maxillary palpus situated apically (Fig. 76); in loose soil or sand, and possibly decaying wood . . . . Mydidae (Chapter 47)

– Head capsule with maxillae more or less dorsoventrally compressed, often toothed apically and concave ventrally, to form gouge-like digging structures, usually much longer than mandibles; maxillary palpus situated laterally (*e.g.*, Figs 75, 79); habitats various 40

40. Posterior spiracles lying laterally near anterior margin of abdominal segment 8 (Fig. 80); in loose soil or sand . . . . Apioceridae (Chapter 46)

– Posterior spiracles situated dorsolaterally, well posterior to anterior margin of abdominal segment 8 (Fig. 77); in loose soil or sand and decaying wood . . . . Asilidae (Chapter 48)

41. Head capsule with metacephalic rods moderately expanded to spatulate posteriorly (Fig. 82); terminal abdominal segment, either with either 4 or rarely 2 ventral primary lobes surrounding posterior spiracles (Fig. 83) or evenly rounded (in plant-mining forms); 7 abdominal creeping welts present (rarely anterior pair modified as prolegs); mostly predators, in damp soil; rarely phytophagous . . . . Dolichopodidae (Chapter 56)

– Head capsule with metacephalic rods slender throughout (*e.g.*, Fig. 84); terminal abdominal segment, either bearing single median protuberance beneath posterior spiracles (*e.g.*, Fig. 86) or if more than 1 terminal lobe present, then respiratory system often apneustic (without spiracles) and 7 or 8 pairs of abdominal creeping welts or prolegs with apical hook-like crochets present (*e.g.*, Figs 87, 88); predators, in aquatic or semi-aquatic habitats, damp soil, rotten wood, dung, *etc.* . . . . Empidoidea (exclusive of Dolichopodidae) (Chapters 51–55)

42. Body markedly flattened dorsoventrally; with or without, feathery body processes (*e.g.*, Figs 90, 93, 97). 43

– Body approximately cylindrical (at most only slightly flattened dorsoventrally) or squat and dome-shaped; without feathery body processes (although occasionally with simple processes) 51

43. Body with thin striated lateral margins on tergal plates of all segments; long filamentous processes present on terminal abdominal segment and first 2 thoracic segments (Fig. 90); in moist decaying vegetation, leaf litter, *etc.* . . . . Lonchopteridae (Chapter 58)

– Body without thin striated lateral margins on tergal plates of all segments; long filamentous processes, if present, not restricted to terminal abdominal segment and first 2 thoracic segments; habitats various 44

44. Body with conspicuous, usually fringed, lateral processes (*e.g.*, Figs 92, 93, 97) 45

– Body without conspicuous lateral processes (Note: Calliphoridae found in termites' nests have filamentous processes, but body is cylindrical not dorsoventrally flattened) 49

45. Left and right posterior spiracular plates at least partially joined medially (Figs 116, 117); mainly predators of Aphididae (Hemiptera) . . . . Syrphidae [in part] (Chapter 60)

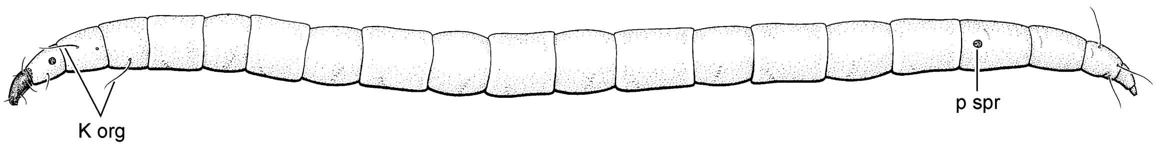
– Left and right posterior spiracular plates clearly separate (Figs 92, 94); habitats various 46

46. Prothoracic spiracle simple, each with 1 to several sessile spiracular openings arrayed peripherally at apex of short tubular or conical projection (*e.g.*, Fig. 91); cephaloskeleton with basal and intermediate sclerites slender, thinly sclerotised and fused together; intermediate sclerite usually prolonged anteriorly into single or multi-toothed sclerite, with dorsolateral mouthhooks (*e.g.*, Figs 95, 96) 47

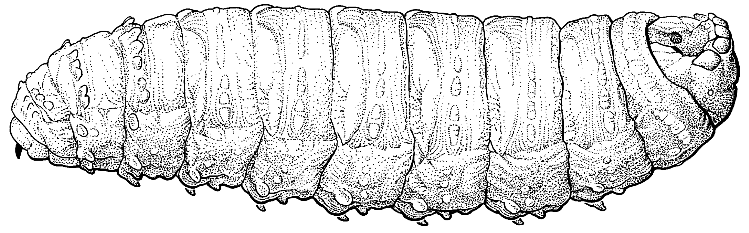
– Prothoracic spiracle either absent or bearing 2 or more, short papillae (e.g., Fig. 98) or long filaments branching from apex of spiracular stalk; cephaloskeleton with basal and intermediate sclerites often more strongly sclerotised than above and usually separated (as in Fig. 89); intermediate sclerite fused to hook-like labial sclerite, only in first-instar larva of some species; mouthhooks positioned on apex of cephaloskeleton. 48

47. Posterior spiracles each on short, conical, apically sclerotised spiracular support, with 4 spiracular openings on each spiracle arranged radially around ecdysial scar (Fig. 91); occurring in fungal fruiting bodies . . . . Platypezidae [in part] (Chapter 57)

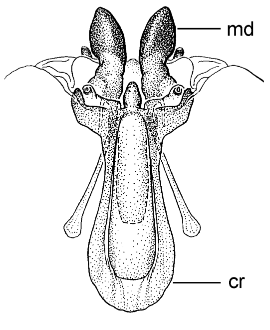
– Posterior spiracles variously supported, each with spiracular openings arranged in 2 pairs, placed one behind the other (Fig. 94); saprophagous, in various kinds of decaying organic matter, ants' and termites' nests, *etc.*; predaceous or parasitoids . . . . Phoridae [in part] (Chapter 59)



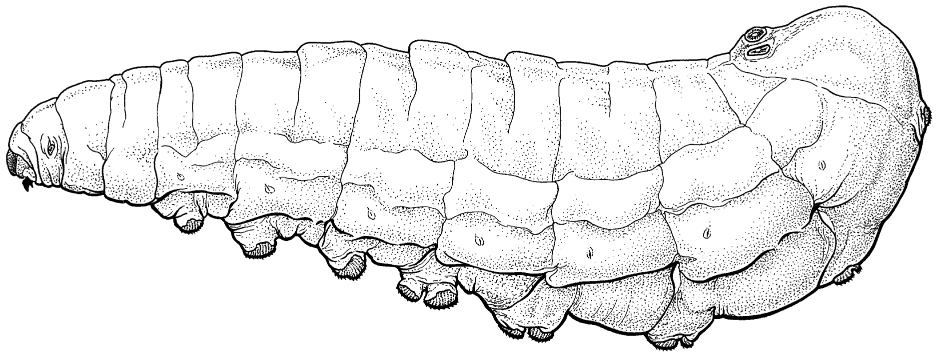
52 *Scenopinus* (Scenopinidae)



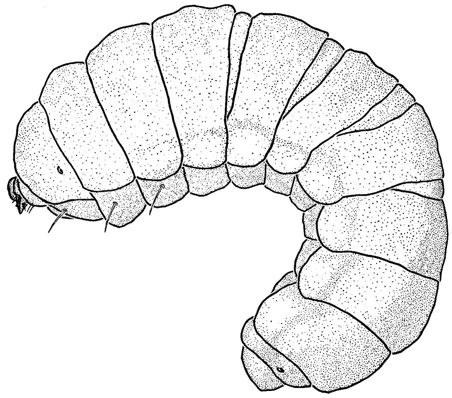
53 *Trichopsidea* (Nemestrinidae)



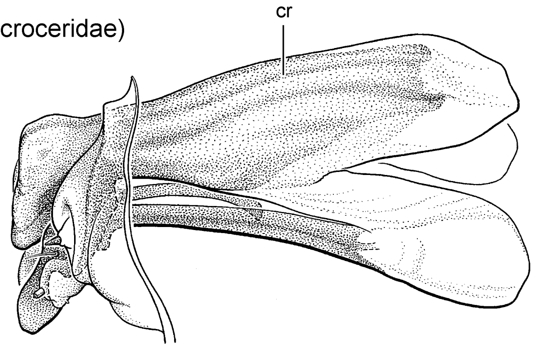
54 *Trichopsidea* (Nemestrinidae)



55 *Exetasis* (Acroceridae)



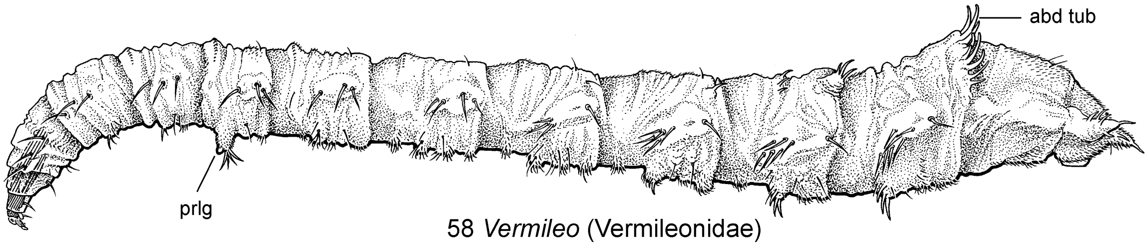
56 *Systoechus* (Bombyliidae)



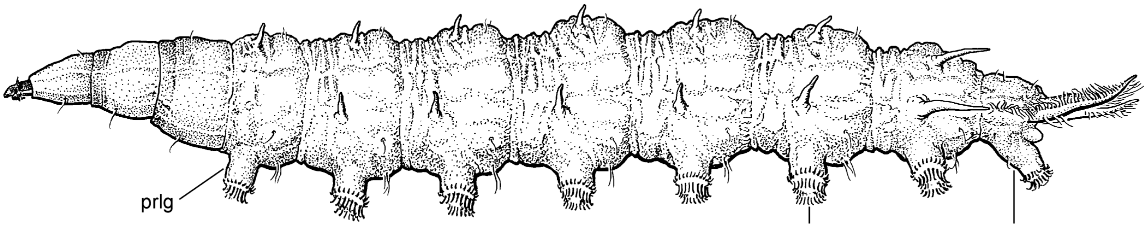
57 *Sparnopolius* (Bombyliidae)

Figs 13.52–57. Larval habitus and head capsules (all non-Afrotropical): (52) habitus of *Scenopinus* sp., lateral view (Scenopinidae); (53) same, *Trichopsidea clausa* Cockerell (Nemestrinidae); (54) same, head capsule, dorsal view; (55) habitus of *Exetasis eickstedtae* Schlinger, lateral view (Acroceridae); (56) same, *Systoechus vulgaris* Loew (Bombyliidae); (57) head capsule of *Sparnopolius* sp., lateral view (Bombyliidae). Fig. 52 (Kelsey 1981, fig. 11), Figs 53, 54 (Teskey 1981*d*, figs 4, 5), Fig. 55 (Schlinger 1981, fig. 28), Fig. 56 (after Berg 1940, fig. 3), Fig. 57 (Hall 1981, fig. 59).

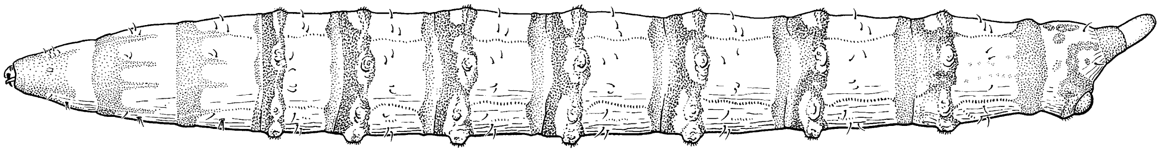
Abbreviations: cr – cranium; K org – Keilin's organ; md – mandible; p spr – posterior spiracle.



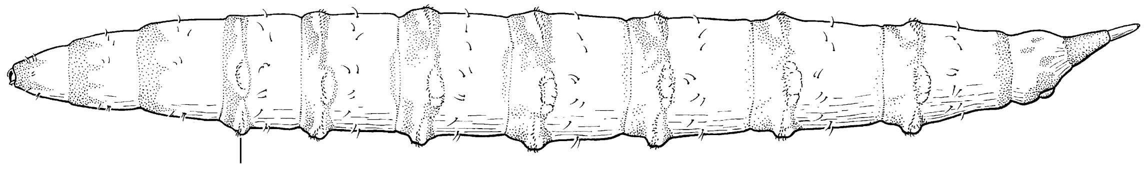
58 *Vermileo* (Vermileonidae)



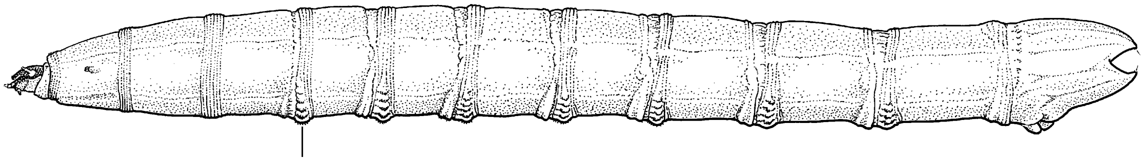
59 *Atherix* (Athericidae)



60 *Tabanus* (Tabanidae)



61 *Chrysops* (Tabanidae)

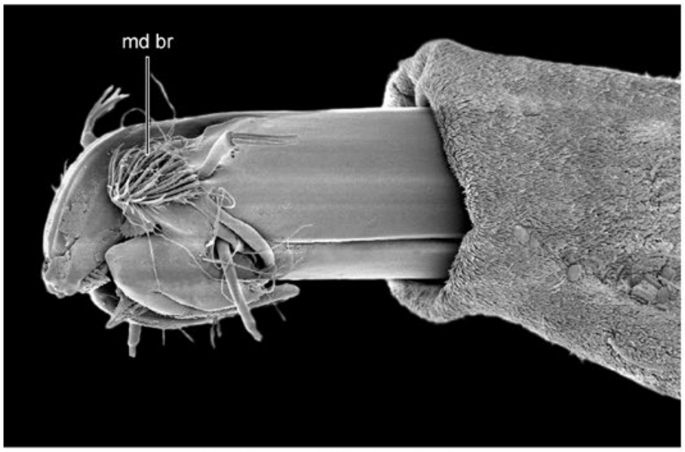


62 *Rhagio* (Rhagionidae)

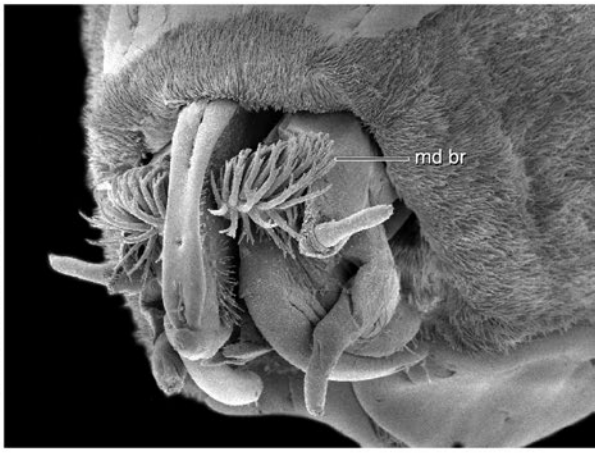
63 *Rhagio* (Rhagionidae) 64 *Chrysopilus* (Rhagionidae)

Figs 13.58–64. Larval habitus and larval terminal segments, lateral views (all non-Afrotropical): (58) habitus of *Vermileo comstocki* Wheeler (Vermileonidae); (59) same, *Atherix* sp. (Athericidae); (60) same, *Tabanus reinwardtii* Wiedemann (Tabanidae); (61) same, *Chrysops furcatus* Walker (Tabanidae); (62) same, *Rhagio* sp. (Rhagionidae); (63) same, terminal segments; (64) same, *Chrysopilus flavibarbis* Adams (Rhagionidae). Fig. 58 (Teskey 1981*c*, fig. 5), Fig. 59 (Webb 1981, fig. 7), Figs 60, 61 (Pechuman & Teskey 1981, figs 51, 52), Figs 62–64 (James & Turner 1981, figs 18, 19, 21).

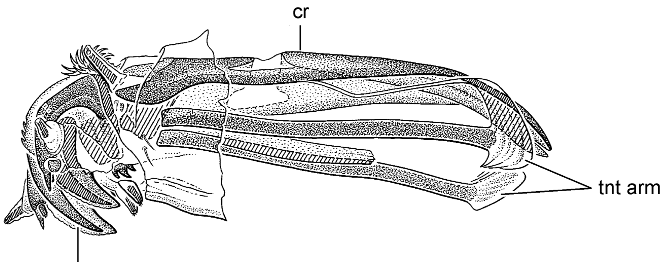
Abbreviations: abd tub – abdominal tubercle; cr wlt – creeping welt; crt – crotchets; p spr – posterior spiracle; prlg – proleg; spr lb – spiracular lobe.



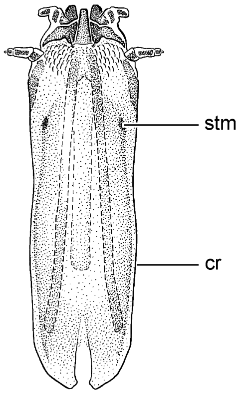
65 *Atherix* (Athericidae)



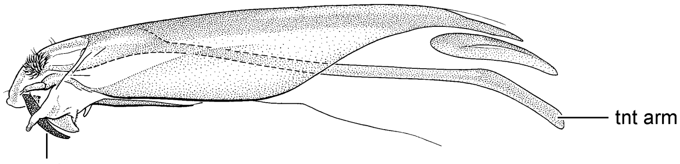
66 *Tabanus* (Tabanidae)



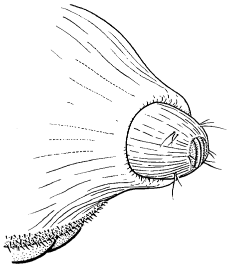
67 *Rhagio* (Rhagionidae)



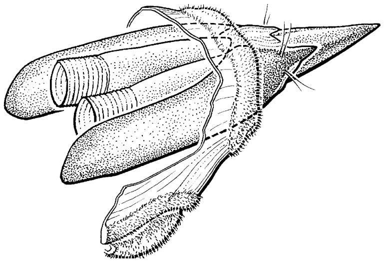
68 *Chrysopilus* (Rhagionidae)



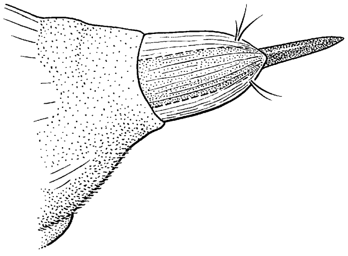
69 *Tabanus* (Tabanidae)



70 *Tabanus* (Tabanidae)



71 *Merycomyia* (Tabanidae)



72 *Chrysops* (Tabanidae)

Figs 13.65–72. Larval head capsules and terminal segments (all non-Afrotropical): (65) head capsule of *Atherix* sp., lateral view (Athericidae); (66) same, *Tabanus* sp. (Tabanidae), oblique anterolateral view; (67) same, *Rhagio* sp. (Rhagionidae), lateral view; (68) same, *Chrysopilus proximus* (Walker), dorsal view (Rhagionidae); (69) same, *Tabanus reinwardtii* Wiedemann, lateral view (Tabanidae); (70) terminal segments of *T. marginalis* F., posterolateral view (Tabanidae); (71) same, *Merycomyia whitneyi* (Johnson), dorsolateral view (Tabanidae); (72) same, *Chrysops cincticornis* Walker, lateral view (Tabanidae). Figs 65, 66 (Courtney *et al*. 2000, figs 82, 97), Fig. 67 (James & Turner 1981, fig. 22), Fig. 68 (after James & Turner 1981, fig. 15), Figs 69–72 (Pechuman & Teskey 1981, figs 56, 55, 58, 59, respectively).

Abbreviations: cr – cranium; md – mandible; md br – mandibular brush; stm – stemmata; tnt arm – tentorial arm.

48. Posterior spiracles each on short nonsetiferous tuberculate process, situated dorsally near anterior margin of last abdominal segment; process terminating in 3 lobes, each bearing spiracular opening; body with pinnately setiferous-like tubercles (Fig. 97); saprophagous, in a range of decaying organic matter. . . . . Fanniidae (Chapter 112)

– Posterior spiracles each on long slender spiculate tuberculate process, arising caudally on terminal abdominal segment; process not divided apically, bearing ring of peristigmatic tufts; other spiculate tubercles on body differing from spiracular tubercle, only in its shorter length (Fig. 98); develop in sap runs; water-filled leaf bases, *etc*. . . . . Periscelididae (Chapter 91)

49. Left and right posterior spiracular plates at least partially joined medially (Figs 115, 116); mainly predators of Aphididae (Hemiptera) . . . . Syrphidae [in part] (Chapter 60)

– Left and right posterior spiracular plates clearly separate; habitats various. .50

50. Posterior spiracular plates lying flat; each plate with 3 straight to curved openings set in a radiating pattern; aquatic, semi-aquatic or terrestrial, usually associated with Gastropoda, rarely with Oligochaeta (as parasitoids or predators) . . . . Sciomyzidae [in part] (Chapter 78)

– Posterior spiracular plate protuberant; spiracular openings usually set on the ends of finger-like lobes or papillae (Fig. 156); predators of Adelgidae, Aphididae and Coccidoidea (Hemiptera). . . . . .Chamaemyiidae [in part] (Chapter 76)

51. Prothoracic spiracles positioned near one another on dorsal surface of prothorax (Fig. 100); mouthhooks with longitudinal axis at oblique or right angles to remainder of cephaloskeleton, usually bearing 2 or more pairs of equal-sized, anteriorly directed teeth (Fig. 99); phytophagous, mostly leaf-miners . . . . Agromyzidae (Chapter 86)

– Prothoracic spiracles situated laterally or absent; mouthhooks usually on same plane as remainder of cephaloskeleton, either bearing fewer than 2 pairs of teeth or bearing 2 or more pairs of teeth of equal or unequal size; habitats various 52

52. Prothoracic spiracle simple, each with 1 to several sessile spiracular openings arrayed peripherally at apex of short tubular or conical projection (*e.g.*, Fig. 91); cephaloskeleton with basal and intermediate sclerites slender, thinly sclerotised and fused together; all instar larvae with intermediate sclerite usually prolonged anteriorly into single or multi-toothed sclerite, with dorsolateral mouthhooks (*e.g.*, Figs 95, 96). 53

– Prothoracic spiracle either absent or bearing 2 or more, short papillae (*e.g.*, Figs 160, 186, 196) or long filaments branching from apex of spiracular stalk; cephaloskeleton with basal and intermediate sclerites fused or separated, often more strongly sclerotised than above; only first-instar larva of some species with intermediate sclerite fused to hook-like labial sclerite; mouthhooks positioned on apex of cephaloskeleton 54

53. Posterior spiracles each on short conical, apically sclerotised, spiracular support, with 4 spiracular openings on each spiracle, arranged radially around ecdysial scar (Fig. 91); occurring in fungal fruiting bodies . . . . Platypezidae [in part] (Chapter 57)

– Posterior spiracles variously supported, each with spiracular openings arranged in 2 pairs placed one behind the other (Fig. 94); saprophagous, in various types of decaying organic matter, ants' and termites' nests, *etc.;* predaceous or parasitoids . . . . Phoridae [in part] (Chapter 59)

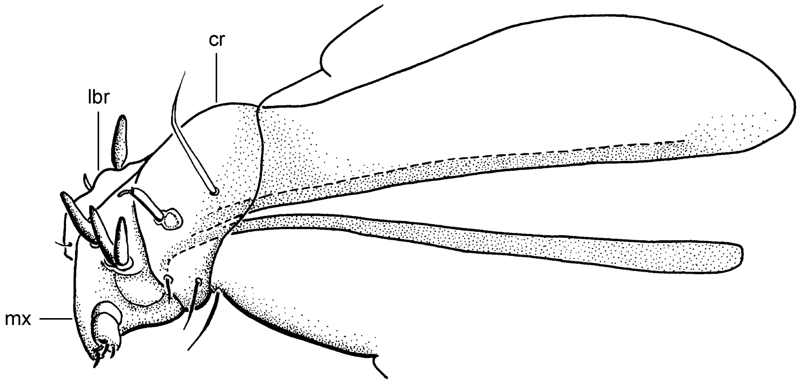
54. Larva up to 2 mm in length, oval to globular in shape; either 2 separate pairs of posterior spiracles present or posteriormost pair united into single plate; posterior spiracles on each side usually visibly joined by slender convoluted branches of felt chamber (Figs 101, 102); cephaloskeleton lacking; develop within female uterus, mature larval form deposited on bat roost walls . . . . Hippoboscidae [in part] (Chapter 109)

– Larva of varied length and shape; not more than 1 pair of posterior spiracles present; without modified felt chamber; cephaloskeleton usually present; habitats various 55

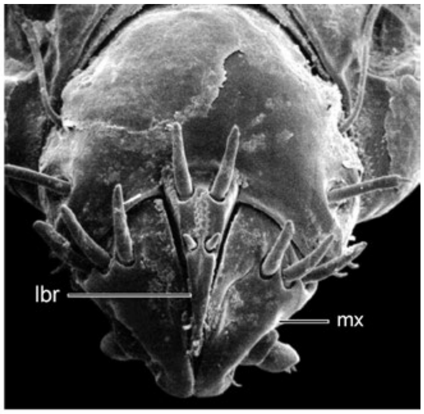
55. Posterior spiracles in form of 1 or 2 posteriorly directed spines, bearing spiracular openings (*e.g.*, Fig. 103). 56

– Posterior spiracles not in form of spines, sometimes with hooked or spine-like projection from edge of spiracular plate, but without spiracular openings 61

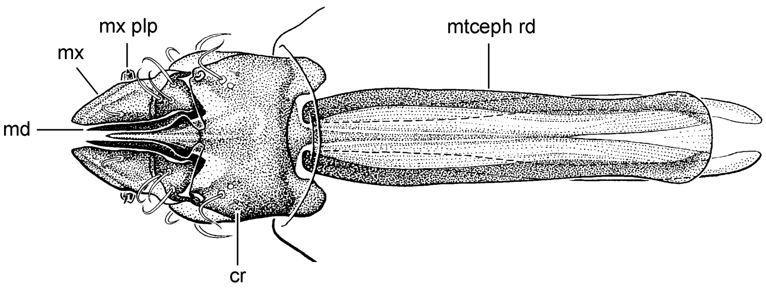
56. Body usually relatively broad; posterior spiracles thorn-like, situated dorsally; terminal abdominal segment with pair of slender filaments, at least as long as body, usually considerably longer in second- and third-instars (Fig. 103); parasitoids of Monophelebinae (Hemiptera: Coccidae: Margarodidae). . . . . .Cryptochetidae (Chapter 107)



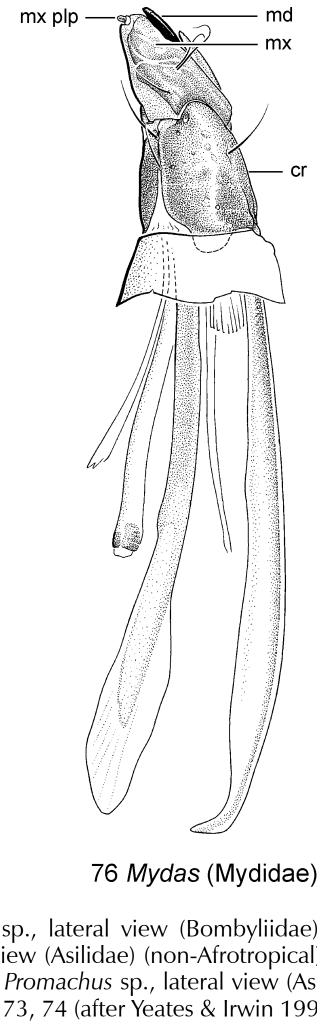
73 *Heterotropus* (Bombyliidae)



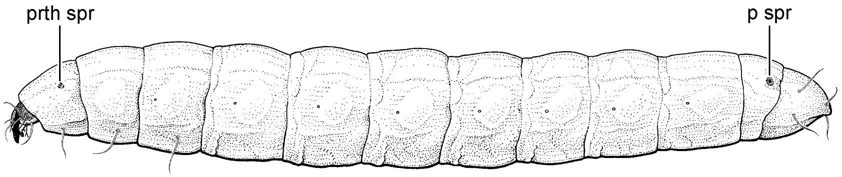
74 *Heterotropus* (Bombyliidae)



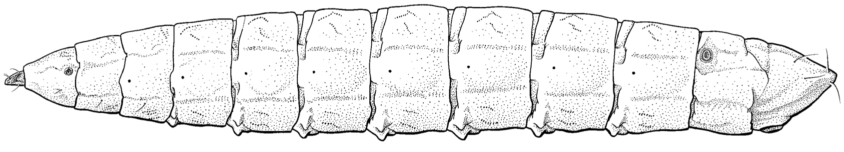
75 *Promachus* (Asilidae)



76 *Mydas* (Mydidae)



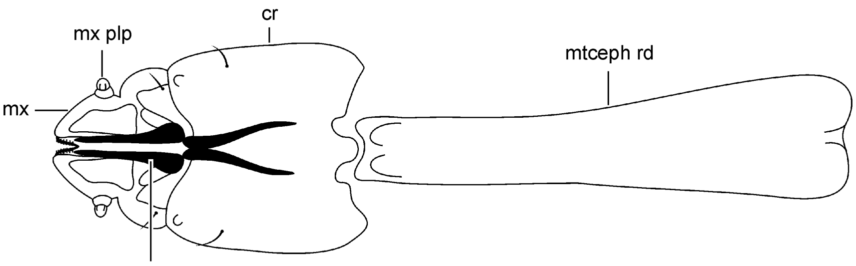
77 *Promachus* (Asilidae)



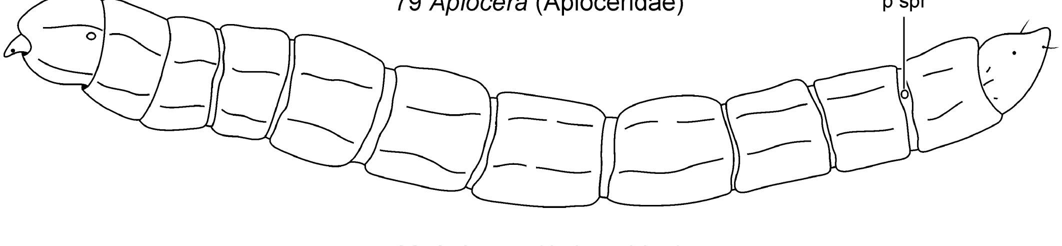
78 *Mydas* (Mydidae)

Figs 13.73–78. Larval habitus and head capsules: (73) head capsule of *Heterotropus* sp., lateral view (Bombyliidae); (74) same, scanning electron micrograph, anterior view; (75) same, *Promachus* sp., dorsal view (Asilidae) (non-Afrotropical); (76) same, *Mydas clavatus* (Drury), lateral view (Mydidae) (non-Afrotropical); (77) habitus of *Promachus* sp., lateral view (Asilidae) (non-Afrotropical); (78) same, *M. clavatus*, lateral view (Mydidae) (non-Afrotropical). Figs 73, 74 (after Yeates & Irwin 1992, figs 40, 43), Figs 75, 77 (Wood 1981, figs 78, 76, respectively), Figs 76, 78 (Wilcox 1981, figs 29, 28, respectively).

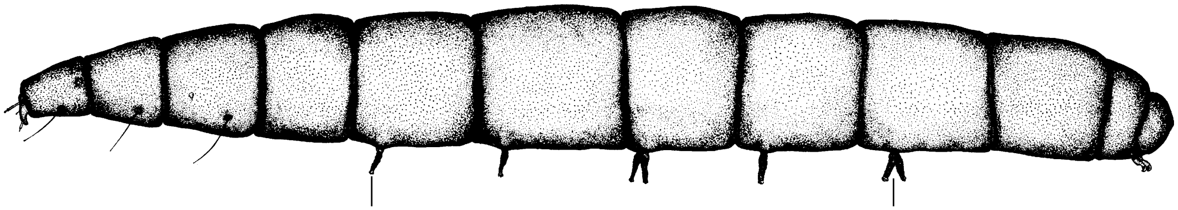
Abbreviations: cr – cranium; lbr – labrum; md – mandible; mtceph rd – metacephalic rod; mx – maxilla; mx plp – maxillary palpus; p spr – posterior spiracle; prth spr – prothoracic spiracle.



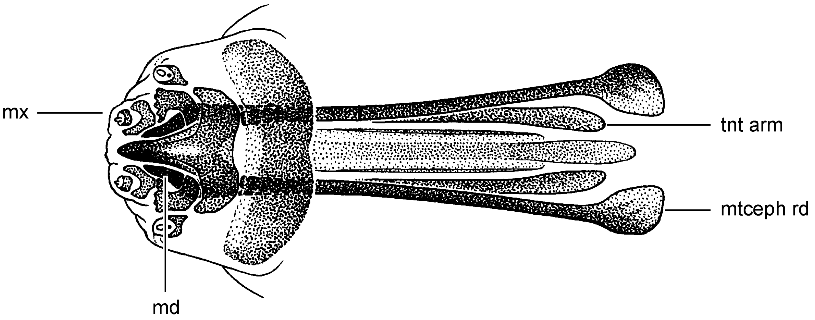
79 *Apiocera* (Apioceridae)



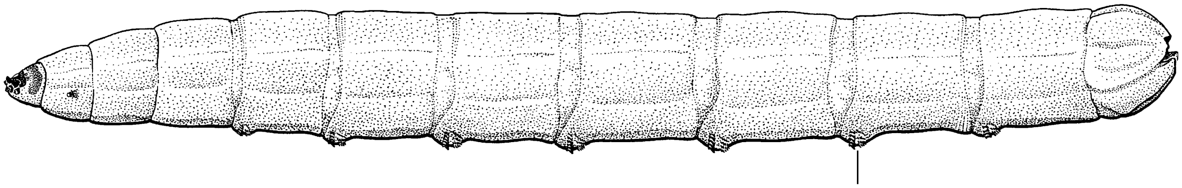
80 *Apiocera* (Apioceridae)



81 *Glabellula* (Mythicomyiidae)



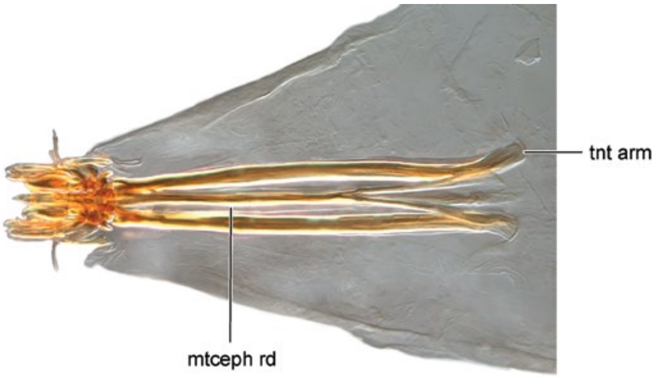
82 *Medetera* (Dolichopodidae)



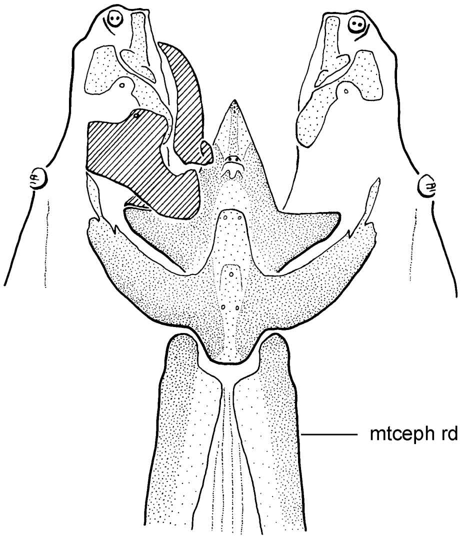
83 *Medetera* (Dolichopodidae)

Figs 13.79–83. Larval habitus and head capsules (all non-Afrotropical): (79) head capsule of *Apiocera hispida* Cazier, dorsal view (Apioceridae); (80) same, habitus, lateral view; (81) habitus of *Glabellula arctica* (Zetterstedt), lateral view (Mythicomyiidae); (82) head capsule of *Medetera* sp., dorsal view (Dolichopodidae); (84) same, habitus, lateral view. Figs 79, 80 (after Toft & Kimsey 1982, figs 2, 6), Fig. 81 (Andersson 1974, fig. 1), Figs 82, 83 (Robinson & Vockeroth 1981, figs 43, 44).

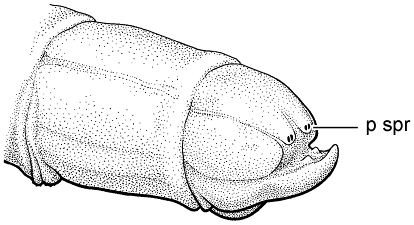
Abbreviations: cr – cranium; cr wlt – creeping welt; md – mandible; mtceph rd – metacephalic rod; mx – maxilla; mx plp – maxillary palpus; p spr – posterior spiracle; prlg – proleg; tnt arm – tentorial arm.



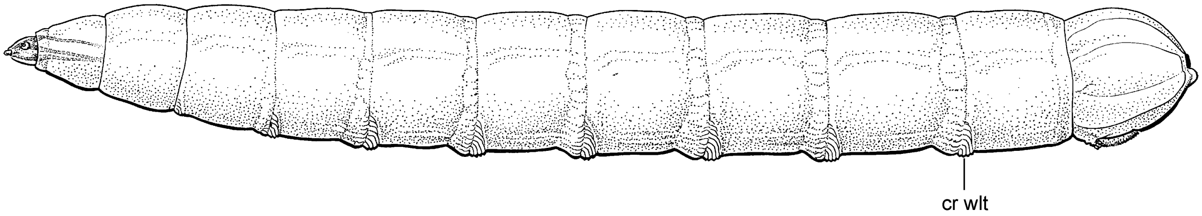
84 *Hemerodromia* (Empididae)



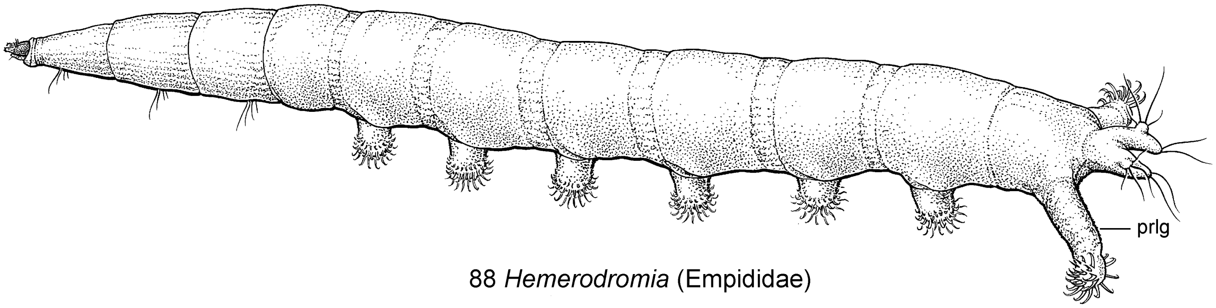
85 *Liancalus* (Dolichopodidae)



86 *Phyllodromia* (Empididae)



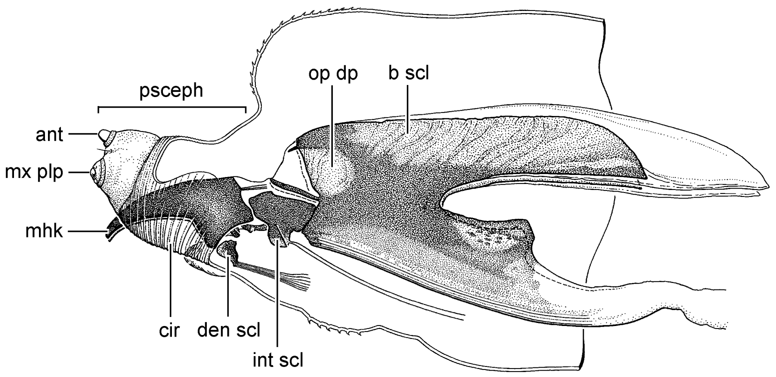
87 Empidini (Empididae)



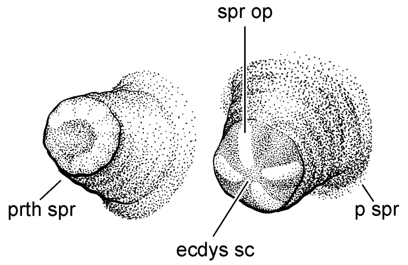
88 *Hemerodromia* (Empididae)

Figs 13.84–88. Larval habitus, head capsules and terminal segments (all non-Afrotropical): (84) head capsule of *Hemerodromia* sp., dorsal view (Empididae); (85) same, *Liancalus* sp., dorsal view (Dolichopodidae); (86) terminal segments of (?) *Phyllodromia* sp., oblique posterolateral view (Empididae); (87) habitus of Empidini, lateral view (Empididae); (88) same, *Hemerodromia* sp., oblique posterolateral view (Empididae). Fig. 84 (source: Sinclair & Daugeron (Chapter 51), fig. 40); Fig. 85 (after Sinclair 1992, fig. 19), Figs 86–88 (Steyskal & Knutson 1981, figs 63, 57 (as *Rhamphomyia*), 56, respectively).

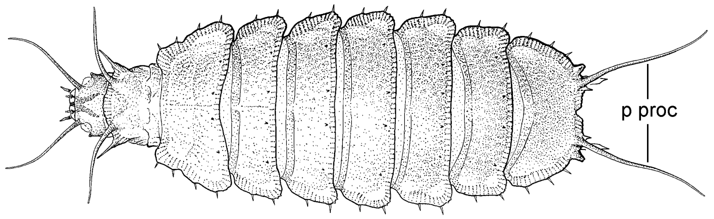
Abbreviations: cr wlt – creeping welt; mtceph rd – metacephalic rod; p spr – posterior spiracle; prlg – proleg; tnt arm – tentorial arm.



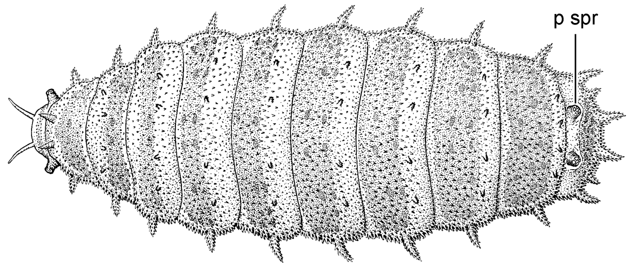
89 *Phormia* (Calliphoridae)



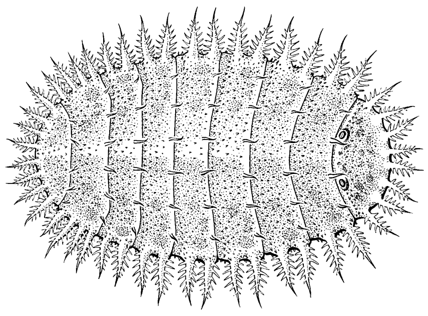
91 *Platypeza* (Platypezidae)



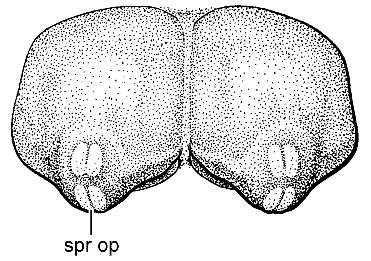
90 *Lonchoptera* (Lonchopteridae)



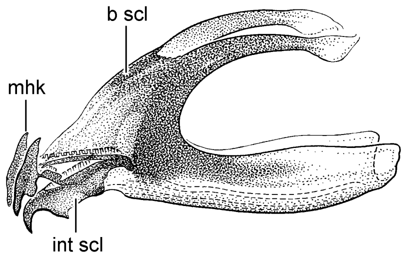
92 *Platypeza* (Platypezidae)



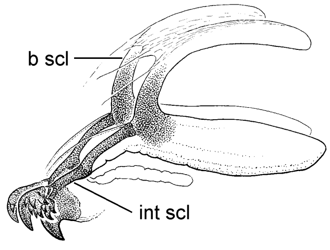
93 *Callomyia* (Platypezidae)



94 *Dohrniphora* (Phoridae)



95 *Spiniphora* (Phoridae)



96 *Megaselia* (Phoridae)

Figs 13.89–96. Larval habitus, cephaloskeletons, prothoracic and posterior spiracles (all non-Afrotropical): (89) cephalothorax of *Phormia regina* Meigen, lateral view (Calliphoridae); (90) habitus of *Lonchoptera* sp., dorsal view (Lonchopteridae); (91) prothoracic spiracle (left, dorsolateral view) and posterior spiracular plate (right, dorsal view) of *Platypeza* sp. (Platypezidae); (92) same, habitus, dorsal view; (93) same, *Callomyia gilloglyorum* Kessel (Platypezidae); (94) posterior spiracular plate of *Dohrniphora cornuta* (Bigot), dorsal view (Phoridae); (95) cephaloskeleton of *Spiniphora* sp., lateral view (Phoridae); (96) same, *Megaselia* sp. (Phoridae). Fig. 89 (after Teskey 1981*a*, fig. 12), Figs 90–96 (Teskey 1981*b*, figs 40, 42, 43, 41, 47, 49, 50, 51, respectively).

Abbreviations: ant – antenna; b scl – basal sclerite; cir – cirri; den scl – dental sclerite; ecdys sc – ecdysial scar; int scl – intermediate sclerite; mhk – mouthhook; mx plp – maxillary palpus; op dp – optic depression; p proc – posterior process; p spr – posterior spiracle; prth spr – prothoracic spiracle; psceph – pseudocephalon; spr op – spiracular opening.

– Body elongate; posterior spiracles not situated dorsally; terminal abdominal segment lacking long filaments; free-living 57

57. Posterior spiracular plate joined to form single posterior spine (Fig. 104); spiracular openings small and subapical (Fig. 105); aquatic (*Chrysogaster* Meigen) . . . . Syrphidae [in part] (Chapter 60)

– Posterior spiracles paired, with 2 separate spines; spiracular openings terminal; habitats various. . . . 58

58. Terminal abdominal segment attenuated posteriorly into more or less elongate respiratory tube (siphon); posterior spiracles closely approximated on separate protrusions, each with a spine-like tip (Figs 106, 107); aquatic or semi-aquatic; some on marine coastlines . . . . Ephydridae [in part] (Chapter 100)

– Terminal abdominal segment not prolonged into siphon; posterior spiracles widely separated (*e.g.*, Fig. 108); habitats various. 59

59. Cephaloskeleton narrow and elongate, laterally compressed; with single median mouthhook (Fig. 109); leaf-miners. . . . . Ephydridae [in part] (Chapter 100)

– Cephaloskeleton not elongate and compressed, mouthhooks paired; habitats various 60

60. Terminal abdominal segment bearing 1 or more pairs of tubercles; spines of posterior spiracles lacking fringe of seta-like projections (Fig. 110); cephaloskeleton mouthhooks with 4 or more blunt teeth ventrally and large sub-basal tooth (Fig. 111); leaf-miners (*Scaptomyza graminum* (Fallén, 1823)). . . . . Drosophilidae [in part] (Chapter 106)

– Terminal abdominal segment lacking tubercles; spines of posterior spiracles with subapical fringe of seta-like projections (Fig. 113); cephaloskeleton mouthhooks with 1–2 small teeth ventrally and no large sub-basal tooth (Fig. 112); stem-borers of rice (*Diopsis longicornis* Macquart, 1835). . . . . Diopsidae [in part] (Chapter 64)

61. Left and right posterior spiracular plates joined along inner margin to form single plate (*e.g.*, Figs 114, 115). 62

– Posterior spiracular plates clearly separated 65

62. Posterior spiracles widely separated, but situated on single prominent, sclerotised plate (Fig. 114); broad soft-bodied larvae; parasitoids of Auchenorrhyncha (Hemiptera) and Tipulidae (Diptera) . . . . .Pipunculidae (Chapter 61)

– Posterior spiracular plates closely approximated, not on prominent sclerotised plate (*e.g.*, Figs 115, 123, 124); body well sclerotised and thickened; habitats various 63

63. Body with dense pubescence or systematically arranged spicules or tubercles; posterior spiracles elevated on structures ranging from single short prominence to long and retractile respiratory tube or siphon (Figs 118–121); prothoracic spiracles usually on short, knob-like stalk; predators of Aphididae (Hemiptera), mycophagous/phytophagous or saprophagous. . . . . Syrphidae [in part] (Chapter 60)

– Body lacking dense pubescence, prominent spicules and tubercles; posterior spiracles either sessile, or if elevated on respiratory tube, then prothoracic spiracles elongate; free-living in subtidal habitats or parasitic in other arthropods 64

64. Posterior spiracles sometimes set on short respiratory tube; posterior spiracles closely approximated, separated by slight depression (Fig. 123); prothoracic spiracles with elongate central axis (Fig. 122); free-living in aquatic habitats (marine), feeding on algae. . . . . Canacidae (Chapter 94)

– Posterior spiracles sessile, not separated by depression (Figs 133, 134); prothoracic spiracles absent or if present, then not elongate; parasitoids of insects and occasionally other Arthropoda . . . . .Tachinidae [in part] (Chapter 118)

65. Posterior spiracular plate each with numerous rounded, oval or short slit-like spiracular openings, these openings randomly arranged or situated along margin of spiracular plate (*e.g.*, Fig. 137) or associated with intricately convoluted coral-like or serpentine bands, resembling a maze (*e.g.*, Figs 127, 132, 134); body usually with numerous swollen wrinkles or otherwise swollen and rounded to pear-shaped (*e.g.*, Fig. 129) 66

– Posterior spiracular plate with 3 isolated oval or slit-like, relatively large and sometimes sinuous spiracular openings (*e.g.*, Figs 143–146, 191), rarely with 4–6 such openings (*e.g.*, Figs 168, 169); body usually slender and subcylindrical or flattened 72

66. Posterior spiracular plates each with bulbous or dome-shaped protuberance (*e.g.*, Figs 126–128, 130) 67

– Posterior spiracular plate each more or less flat (*e.g.*, Figs 132, 134, 137) 69

67. Larva strongly attenuated anteriorly with expanded abdomen (Fig. 129); posterior spiracular plates dome-shaped, clearly separated, with spiracular openings often grouped into small clusters (Figs 126–128) or with linear clusters of pores radiating from ecdysial scar; parasitoids of adult insects, such as bees and wasps (Hymenoptera) . . . . Conopidae (Chapter 66)

– Larva not strongly attenuated anteriorly; posterior spiracular plates bulbous, set on common, heavily sclerotised base, covering most of the posterior end of larvae; female adult deposits single mature larva 68

68. Larva oval in shape; posterior spiracular openings grouped into linear patterns (Fig. 130); single mature larva ejected to pupate in sheltered places, nests or on host . . . . Hippoboscidae [in part] (Chapter 109)

– Larva elongate, longer than wide (Fig. 131); posterior spiracular openings more uniformly distributed; single mature larva deposited and burrows into soil, hollow stumps or tree rot-holes . . . . Glossinidae (Chapter 108)

69. Posterior spiracular plates kidney-shaped, each comprising series of curvilinear bands with 8–14 yellowish to orange clusters of round or oval to short bar-like spiracular openings in each band, and with uppermost cluster extended into short spine (Fig. 132); parasitoids of adult Scarabaeidae (Coleoptera) . . . . Pyrgotidae (Chapter 72)

– Posterior spiracular plates not as above; habitats various 70

70. Cuticle without strong spines; posterior spiracular plates each with numerous spiracular openings, elevated on coral-like sculpturing of spiracular plate, not set in pit or cleft; spiracular plate usually more or less clearly tripartite (Figs 133, 134); parasitoids in insects and occasionally other Arthropoda . . . . Tachinidae [in part] (Chapter 118)

– Cuticle with strong spines (*e.g.*, Fig. 135); posterior spiracular plates often in transverse cleft of terminal abdominal segment and capable of being occluded within cavity, when opposing surfaces are brought together (*e.g.*, Fig. 136); endoparasitic in mammals 71

71. Cephaloskeleton with mouthhooks well-developed (Fig. 138); endoparasites (in nasal cavities of large mammals) (OESTRINAE) . . . . Oestridae [in part] (Chapter 119)

– Cephaloskeleton with mouthhooks usually rudimentary (Fig. 139); endoparasites (in skin of large mammals) (HYPODERMATINAE) . . . . Oestridae [in part] (Chapter 119)

72. Body with 1 or 2 rows of stout spines partially or entirely encircling most segments (*e.g.*, Fig. 140) or mostly clothed in spinous scales (*e.g.*, Figs 141, 142); body often stout, blunt posteriorly, strongly tapered anteriorly; endoparasitic in mammals 73

– Characteristics not as above; habitats various 75

73. With 1 or 2 rows of stout spines partially or entirely, encircling anterior margin of most segments (Fig. 140); endoparasitic in gut of horses, zebras, rhinoceroses and elephants (GASTEROPHILINAE [in part]) . . . . Oestridae [in part] (Chapter 119)

– Without rows of stout spines; segments mostly clothed in spinous scales (*e.g.*, Figs 141, 142); endoparasitic in skin of mammals 74

74. Posterior spiracular plate with 3 parallel, virtually horizontal spiracular openings (Figs 143, 144); endoparasitic in skin of elephants (GASTEROPHILINAE [in part]) . . . . Oestridae [in part] (Chapter 119)

– Posterior spiracular plate with 3 curved, to highly sinuous spiracular openings, radiating from ecdysial scar (Figs 145, 146); parasitic subcutaneously in mammals (*Cordylobia* Grünberg) . . . . Calliphoridae [in part] (Chapter 114)

75. Posterior spiracular plate with 1 or more subtriangular or hook-like lobes (*e.g.*, Figs 147, 150–152). . . 76

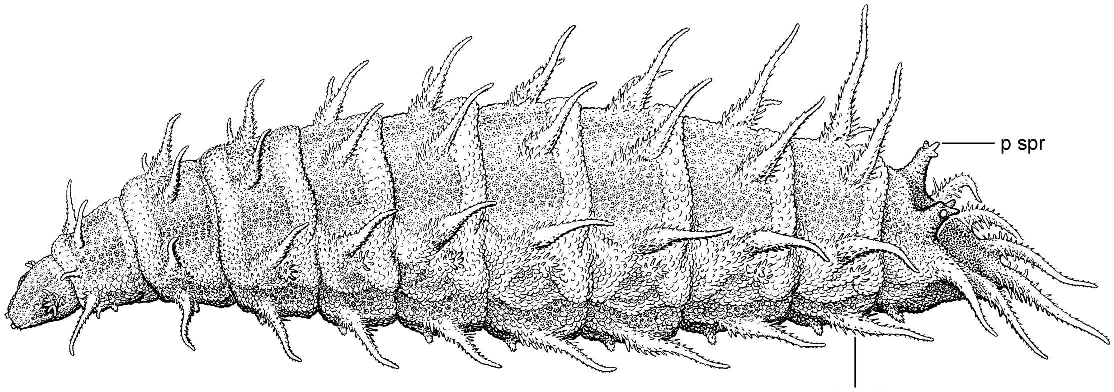
– Posterior spiracular plate without subtriangular or hook-like lobes, although plate sometimes with irregular margin or each spiracular opening on separate finger-like projection 80

76. Posterior spiracular plate with spine arising from median portion (Fig. 147); endoparasitic on insects and occasionally other Arthropoda . . . . Tachinidae [in part] (Chapter 118)

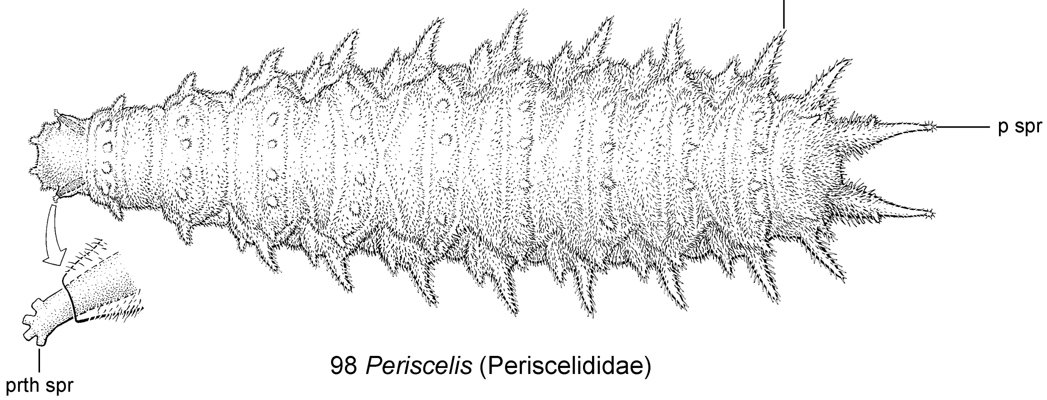
– Posterior spiracular plate with spines, subtriangular and hook-like projections, arising from margin; habitats various 77

77. Posterior spiracular openings not set in symmetrical radiating pattern; openings often curved and elongate (Figs 148, 149); phytophagous or saprophagous . . . . Micropezidae (Chapter 62)

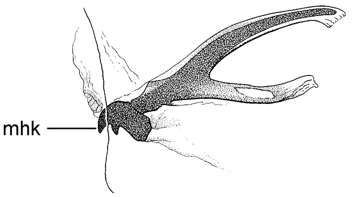
– Posterior spiracular openings set in symmetrical radiating pattern (*e.g.*, Fig. 150); openings simple and oval or slit-like; habitats various 78



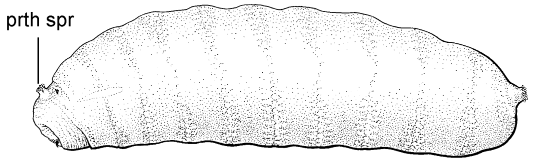
97 *Fannia* (Fanniidae)



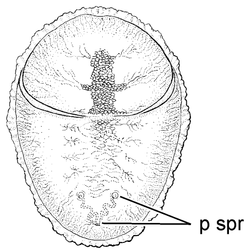
98 *Periscelis* (Periscelididae)



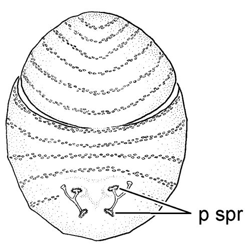
99 *Phytomyza* (Agromyzidae)



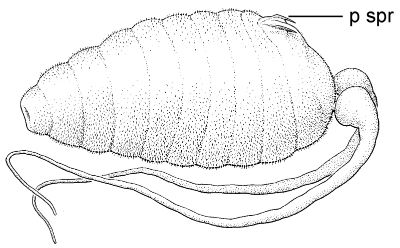
100 *Phytomyza* (Agromyzidae)



101 *Basilia* (Hippoboscidae)



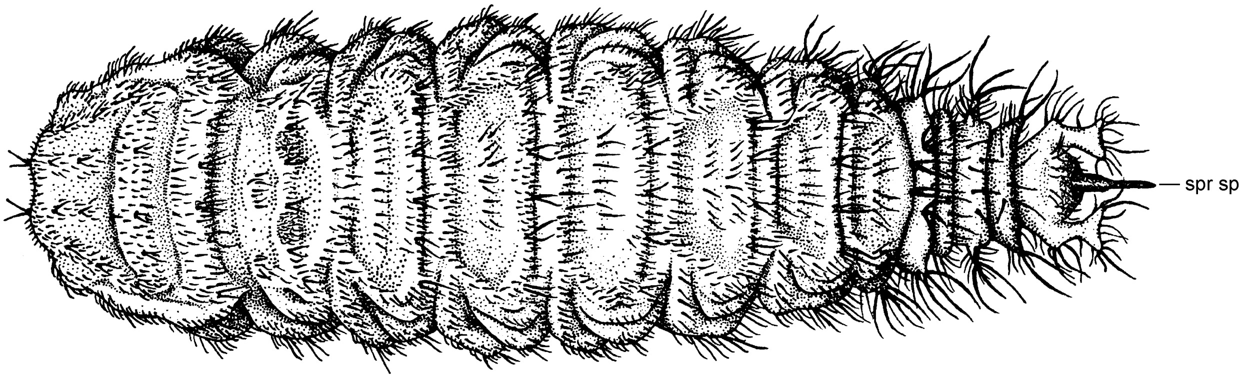
102 *Trichobius* (Hippoboscidae)



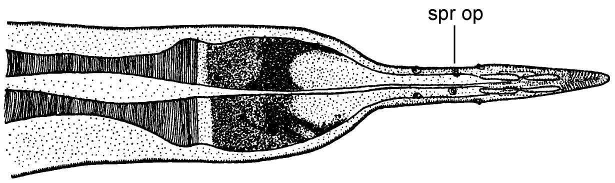
103 *Cryptochetum* (Cryptochetidae)

Figs 13.97–103. Larval habitus, cephaloskeleton, prothoracic spiracle and puparia (all non-Afrotropical): (97) habitus of *Fannia canicularis* (L.), dorsolateral view (Fanniidae); (98) habitus and left prothoracic spiracle (arrowed) of *Periscelis annulata* (Fallén), dorsal view (Periscelididae); (99) cephaloskeleton of *Phytomyza chelonei* Spencer, lateral view (Agromyzidae); (100) same, habitus, lateral view; (101) puparium of *Basilia corynorhini* (Ferris), dorsal view (Hippoboscidae); (102) same, *Trichobius caecus* Edwards (Hippoboscidae); (103) larval habitus of *Cryptochetum yokohama* (Kuwana), lateral view (Cryptochetidae). Figs 97–103 (Teskey 1981*b*, figs 53–55, 3, 4, 6, 7, 38, respectively).

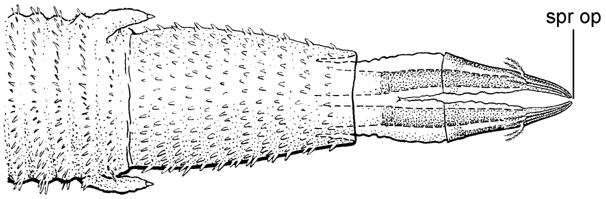
Abbreviations: abd tub – abdominal tubercle; mhk – mouthhook; p spr – posterior spiracle; prth spr – prothoracic spiracle.



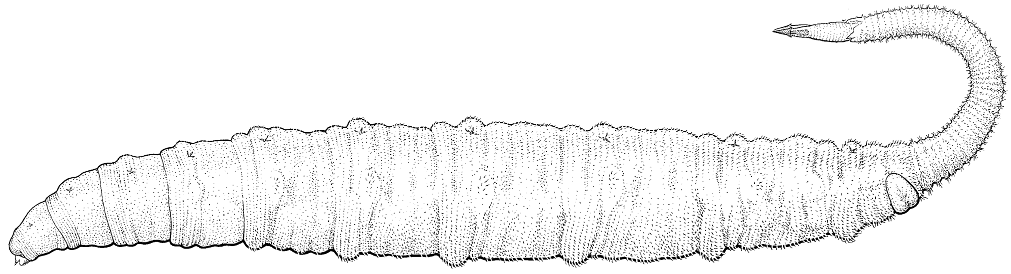
104 *Chrysogaster* (Syrphidae)



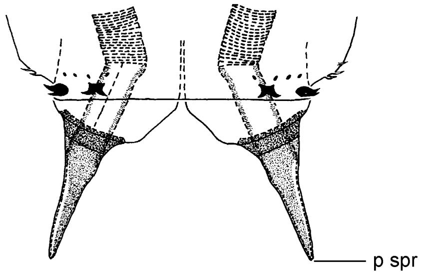
105 *Chrysogaster* (Syrphidae)



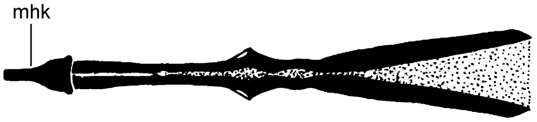
106 *Notiphila* (Ephydridae)



107 *Notiphila* (Ephydridae)



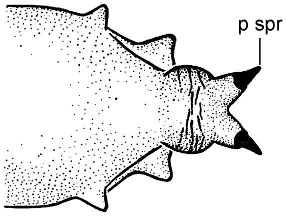
108 *Hydrellia* (Ephydridae)



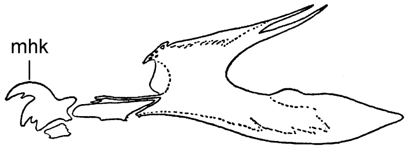
109 *Hydrellia* (Ephydridae)

Figs 13.104–109. Larval habitus, cephaloskeleton and terminal segments (all non-Afrotropical): (104) habitus of *Chrysogaster hirtella* Loew, dorsal view (Syrphidae); (105) same, posterior spiracles; (106) posterior segments of *Notiphila* sp., dorsal view (Ephydridae); (107) same, habitus, lateral view; (108) terminal segments of *Hydrellia spinicornis* Cresson, dorsal view (Ephydridae); (109) cephaloskeleton of *H. notiphiloides* Cresson, dorsal view (Ephydridae). Fig. 104 (after Hartley 1961, fig. 62), Fig. 105 (after Varley 1937, fig. 1C), Figs 106, 107 (Teskey 1981*b*, figs 61, 62), Figs 108, 109 (after Deonier 1971, figs 79, 84).

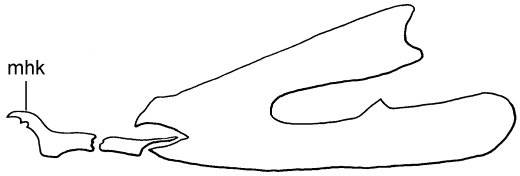
Abbreviations: mhk – mouthhook; p spr – posterior spiracle; spr op – spiracular opening; spr sp – spiracular spine.



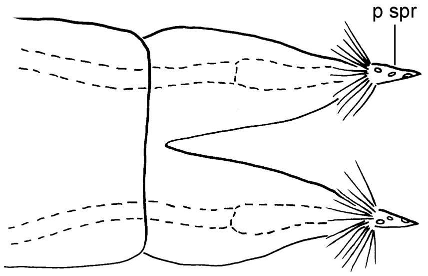
110 *Scaptomyza* (Drosophilidae)



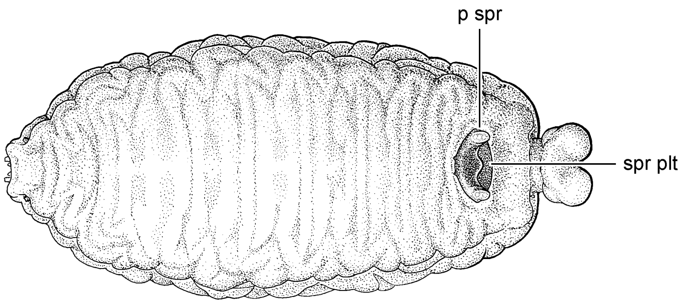
111 *Scaptomyza* (Drosophilidae)



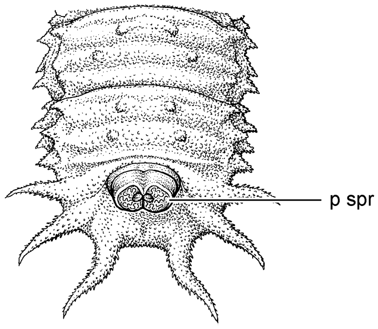
112 *Diopsis* (Diopsidae)



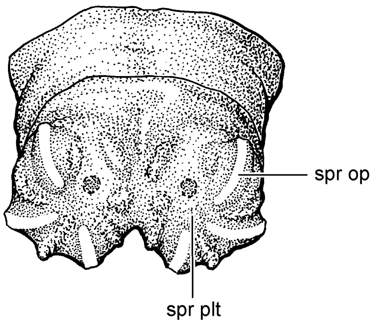
113 *Diopsis* (Diopsidae)



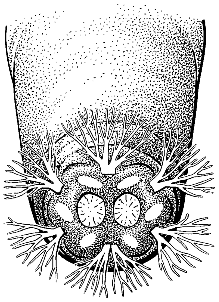
114 *Pipunculus* (Pipunculidae)



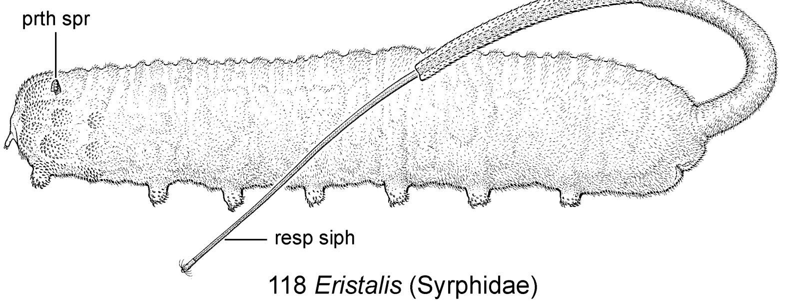
115 *Volucella* (Syrphidae)



116 *Syrphus* (Syrphidae)



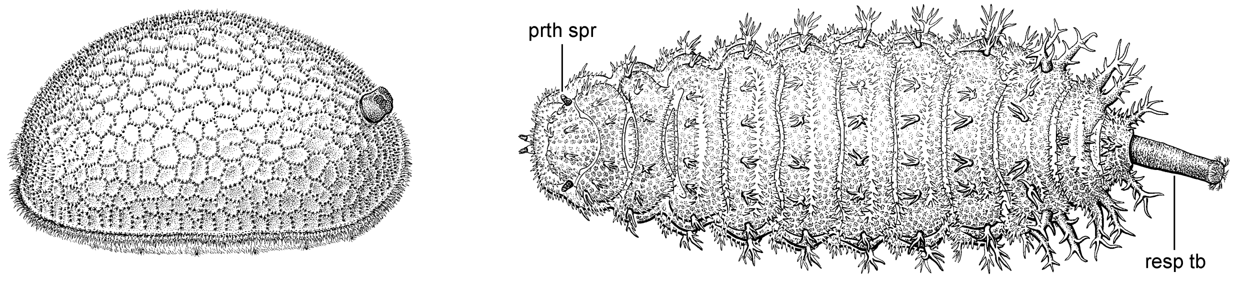
117 *Brachyopa* (Syrphidae)



118 *Eristalis* (Syrphidae)

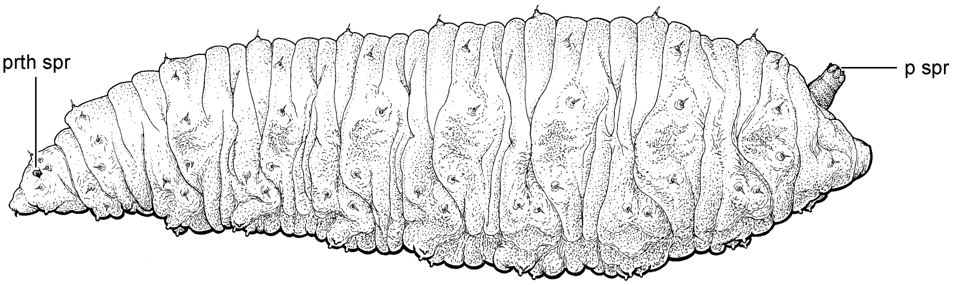
Figs 13.110–118. Larval habitus, cephaloskeletons and terminal segments (all non-Afrotropical, except Figs 110–113): (110) terminal segments of *Scaptomyza graminum* (Fallén), dorsal view (Drosophilidae); (111) same, cephaloskeleton, lateral view; (112) same, *Diopsis longicornis* Macquart (Diopsidae); (113) same, terminal segments, dorsal view; (114) habitus of *Pipunculus* sp., dorsal view (Pipunculidae); (115) terminal segments of *Volucella bombylans* (L.), posterodorsal view (Syrphidae); (116) posterior spiracles of *Syrphus knabi* Shannon, dorsoventral view (Syrphidae); (117) posterior spiracles of *Brachyopa* sp., dorsoventral view (Syrphidae); (118) habitus of *Eristalis tenax* (L.), lateral view (Syrphidae). Fig. 110 (after Hennig 1952, fig. 253), Fig. 111 (after Okada 1968, fig. 14F), Figs 112, 113 (after Descamps 1957, figs 10i, 10f, as *thoracica*), Figs 114–118 (Teskey 1981*b*, figs 1, 14, 18, 20, 15, respectively).

Abbreviations: mhk – mouthhook; p spr – posterior spiracle; prth spr – prothoracic spiracle; resp siph – respiratory siphon; spr op – spiracular opening; spr plt – spiracular plate.

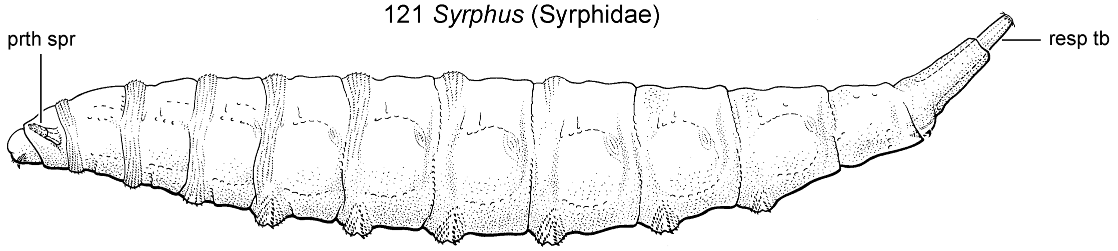


119 *Microdon* (Syrphidae)

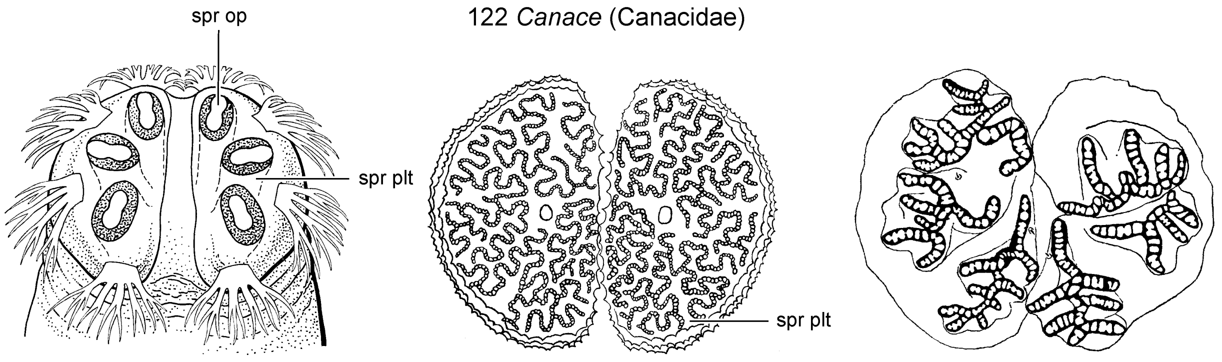
120 *Brachyopa* (Syrphidae)



121 *Syrphus* (Syrphidae)



122 *Canace* (Canacidae)



123 *Canace* (Canacidae)

124 *Therobia* (Tachinidae)

125 *Acemya* (Tachinidae)

Figs 13.119–125. Larval habitus and posterior spiracles (all non-Afrotropical): (119) habitus of *Microdon* sp., dorsolateral view (Syrphidae); (120) same, *Brachyopa* sp., dorsal view (Syrphidae); (121) same, *Syrphus knabi* Shannon, lateral view (Syrphidae); (122) habitus of *Canace macateei* Malloch, lateral view (Canacidae); (123) same, posterior spiracles, posterior view; (124) same, *Therobia leonidei* (Mesnil) (Tachinidae); (125) same, *Acemya acuticornis* Robineau-Desvoidy (Tachinidae). Figs 119–123 (Teskey 1981*b*, figs 12, 19, 17, 37, 39, respectively); Figs 124, 125 (after Léonide 1969, figs 37, 23, respectively).

Abbreviations: p spr – posterior spiracle; prth spr – prothoracic spiracle; resp tb – respiratory tube; spr op – spiracular opening; spr plt – spiracular plate.

78. Cephaloskeleton with all constituent parts unpigmented, except mouthhooks; in decaying wood. . . . . .Clusiidae (Chapter 81)

– Cephaloskeleton with all constituent parts darkly pigmented; habitats various 79

79. Cephaloskeleton with basal sclerite elongate, posterior extensions of dorsal and ventral cornua longer than anterior portion of basal sclerite; ventral cornu without dorsal expansion (*e.g.*, Figs 153, 154); phytophagous in stems and roots . . . . Psilidae and Platystomatidae [in part] (Chapters 65 & 70)

– Cephaloskeleton with basal sclerite broad, posterior extensions of dorsal and ventral cornua subequal in length to anterior portion of basal sclerite; ventral cornu with dorsal expansion (Fig. 155); scavengers mainly in damaged plant tissues or decaying vegetation . . . . Lonchaeidae [in part] (Chapter 67)

80. Posterior spiracles each on separate finger-like projection or papilla extending from spiracular plate (*e.g.*, Figs 158, 159) 81

– Posterior spiracles not set on finger-like projections, although margins of spiracular plate sometimes with slight protrusions 83

81. Cephaloskeleton narrow and elongate, with intermediate sclerite fused to basal sclerite (Fig. 157); integument clothed in fine pubescence or spicules (Fig. 156); predators and parasitoids of Adelgidae, Aphididae and Coccidoidea (Hemiptera) . . . . .Chamaemyiidae [in part] (Chapter 76)

– Cephaloskeleton broad and short, with intermediate and basal sclerites separated (*e.g.*, Figs 161, 163); integument not clothed in pubescence or spicules; habitats various 82

82. Small larvae, < 5 mm in length; prothoracic spiracles with 3 papillae (Fig. 160); mouthhooks slender, without subapical teeth (Fig. 161); saprophagous in decaying organic matter or coprophagous in nests of birds and mammals . . . . .Carnidae (Chapter 93)

– Large larvae, 5–9 mm in length; prothoracic spiracles with 5 or more papillae (Fig. 162); mouthhooks robust, with subapical teeth (Fig. 163); phytophagous, usually leaf-mining, some fungus breeding . . . . Anthomyiidae [in part] (Chapter 111)

83. Posterior spiracular plate with margins irregular, extensions coinciding with spiracular opening (*e.g.*, Figs 164, 165). 84

– Posterior spiracular plate with margins more or less evenly rounded. 86

84. Cephaloskeleton with dental sclerite fused to mouthhook, enlarging ventral margin of base of mouthhook; basal sclerite with cornua very elongate, much longer than anterior portion of sclerite (Fig. 166); phytophagous in flower heads . . . . .Tephritidae [in part] (Chapter 71)

– Cephaloskeleton with dental sclerite usually separate from mouthhook; if dental sclerite fused to mouthhook, then cornua of basal sclerite subequal in length to anterior portion of sclerite; habitats various. 85

85. Abdominal segment 8 with conspicuous triangular lobes, encircling posterior face of segment; cephaloskeleton robust, with pronounced base to mouthhooks and intermediate sclerite, either fused to or closely associated with basal sclerite (Fig. 163); in fungi or phytophagous. . . . . Anthomyiidae [in part] (Chapter 111)

– Abdominal segment 8 with inconspicuous lobes or lobes absent; cephaloskeleton less pronounced, with base of mouthhook generally not enlarged and intermediate sclerite clearly separate from basal sclerite (Fig. 167); in fungi or saprophagous . . . . Heleomyzidae [in part] (Chapter 98)

86. Posterior spiracular plates each with 2 spiracular openings; in flower heads (*Myopites* Blot) (Note: most first- and second-instar larvae with only 2 pairs of spiracular openings will key out here) . . . . .Tephritidae [in part] (Chapter 71)

– Posterior spiracular plates each with 3 or more spiracular openings; habitats various 87

87. Posterior spiracular plates each with 4 or more equal-sized spiracular openings 88

– Posterior spiracular plates each with 3 equal-sized spiracular openings. 91

88. Posterior spiracular plates each with spiracular openings arranged in 2 pairs, placed one behind the other (Fig. 94); saprophagous, in various kinds of decaying organic matter, ants' and termites' nests, *etc*.; predaceous or parasitoids . . . . Phoridae [in part] (Chapter 59)

– Posterior spiracular plates each with 4 or more spiracular openings not arranged in above pattern . . . 89

89. Posterior spiracular plates with 4 slit-like spiracular openings, forming C-shaped pattern (Fig. 168); in decaying vegetable matter . . . . Neriidae (Chapter 63)

– Posterior spiracular plates with 4 or more openings (*e.g.*, Figs 169, 170); if 4 spiracular openings, then not forming C-shaped pattern; habitats various 90

90. Posterior spiracular plates with distinct peristigmatic tufts (Fig. 169); in damp or aquatic habitats . . . . Ephydridae [in part] (Chapter 100)

– Posterior spiracular plates without distinct peristigmatic tufts (Fig. 170); parasitoids of other insects and occasionally other Arthropoda . . . . Tachinidae [in part] (Chapter 118)

91. Posterior spiracular openings distinctly curved or sinuous 92

– Posterior spiracular openings straight or virtually so 99

92. Posterior spiracular openings moderately to very sinuous (*e.g.*, Figs 171, 173, 175) 93

– Posterior spiracular openings simple, C-shaped 95

93. Mouthhooks with robust base, usually without dental sclerite (Fig. 172); basal sclerite without cibarial ridges in cibarium; parasitoids of other insects, occasionally other Arthropoda . . . . Tachinidae [in part] (Chapter 118)

– Mouthhooks with more slender base, usually with dental sclerite (*e.g.*, Fig. 174); basal sclerite with cibarial ridges present in cibarium; habitats various, not parasitoids 94

94. Posterior spiracular openings often highly sinuous, each consisting of 2 or more loops (Fig. 173); terminal abdominal segment with tubercles inconspicuous around posterior spiracular plates; parasites of birds; saprophagous, predaceous or phytophagous . . . . Muscidae [in part] (Chapter 113)

– Posterior spiracular openings less sinuous, each consisting of single loop (Figs 175, 178); terminal abdominal segment with short tubercles around posterior spiracular plates (Fig. 176); usually breeding in dung and other decaying plant matter; some associated with carrion . . Sepsidae [in part] (Chapter 79)

95. Posterior spiracular plates with even fringe of branched peristigmatic tufts at margins (Fig. 177); breeding in wracks of marine algae on marine beaches . . . . Coelopidae (Chapter 77)

– Posterior spiracular plates without peristigmatic tufts at margins or restricted to 3–4 separated tufts; habitats various 96

96. Posterior spiracular openings tightly clustered, arranged in circle (*e.g.*, Fig. 180) 97

– Posterior spiracular openings aligned along vertical axis of spiracular plate (*e.g.*, Figs 182). 98

97. Prothoracic spiracle usually with papillae projecting to either side of more or less elongate central axis (Fig. 179); usually breeding in dung and other decaying plant matter; some associated with carrion. . . . . Sepsidae [in part] (Chapter 79)

– Prothoracic spiracle with papillae aligned in row (Fig. 181); parasites of birds; saprophagous, predaceous or phytophagous . . . . Muscidae [in part] (Chapter 113)

98. Posterior spiracular plate with groups of peristigmatic tufts around margin (Fig. 182); often breeding in decaying matter, ranging from fish to plant material . . . . Milichiidae [in part] (Chapter 95)

– Posterior spiracular plate without distinct peristigmatic tufts (Fig. 183); in bacteria-rich habitats . . . . Sphaeroceridae [in part] (Chapter 99)

99. Terminal abdominal segment attenuated posteriorly into more or less elongate respiratory tube, usually capable of some invagination (*e.g.*, Figs 184, 185) 100

– Terminal abdominal segment not extending posteriorly 102

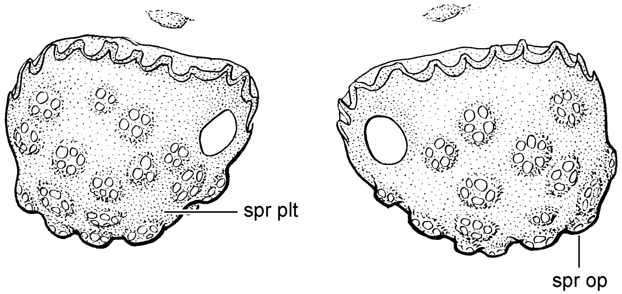
100. Terminal abdominal segment without tubercles; caudal respiratory tube capable of some invagination (Fig. 184); in tree sap runs . . . . Aulacigastridae (Chapter 88)

– Terminal abdominal segment with tubercles; caudal respiratory tube not capable of invagination; habitats various. 101

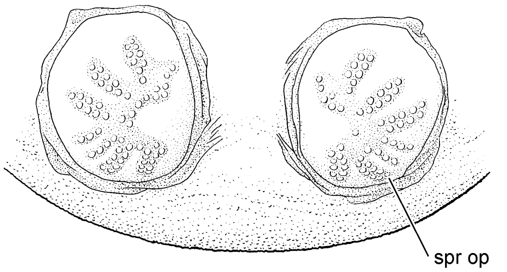
101. Terminal abdominal segment usually distinctly bulbous, compared to remainder of abdomen, often clothed in spine-like projections (Fig. 185); prothoracic spiracle with papillae projecting along an elongate central axis (Fig. 186); usually breeding in dung and other decaying plant matter; some associated with carrion . . . . Sepsidae [in part] (Chapter 79)

– Terminal abdominal segment not distinctly bulbous, lacking spine-like projections (Fig. 187); prothoracic spiracle in form of cluster of numerous long, thread-like filaments or papillae (Fig. 188); in rotting fruit, fungi or vegetable matter . . . . Drosophilidae [in part] (Chapter 106)

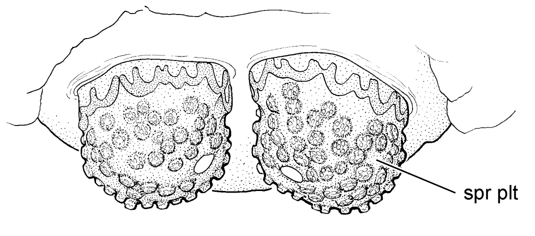
102. First 4 body segments and terminal abdominal segment with encircling rows of small tubercles (Fig. 189); respiratory system metapneustic (spiracles on abdominal segment 8); posterior spiracular plates sessile; cephaloskeleton with basal and intermediate sclerites fused; mining wax walls of honey bee combs . . . . Braulidae (Chapter 105)



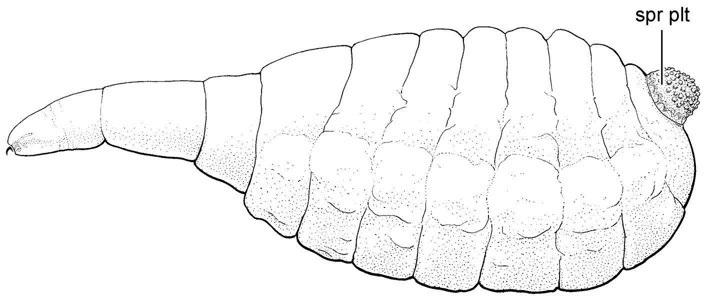
126 *Zodion* (Conopidae)



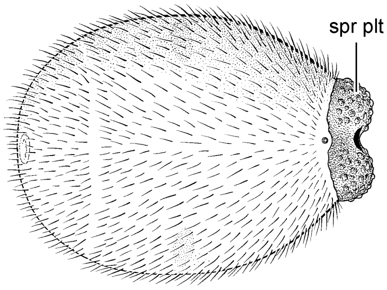
127 *Thecophora* (Conopidae)



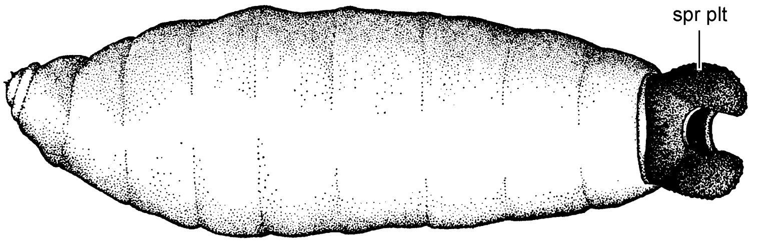
128 *Physocephala* (Conopidae)



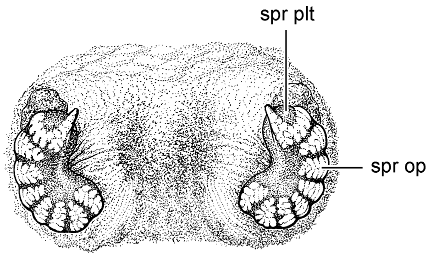
129 *Physocephala* (Conopidae)



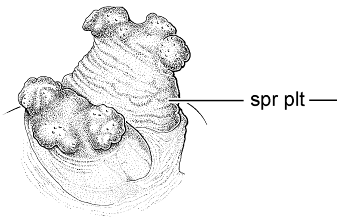
130 *Olfersia* (Hippoboscidae)



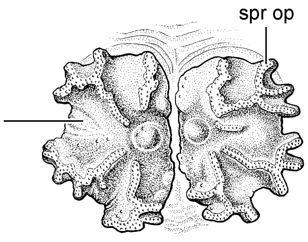
131 *Glossina* (Glossinidae)



132 *Sphecomyiella* (Pyrgotidae)



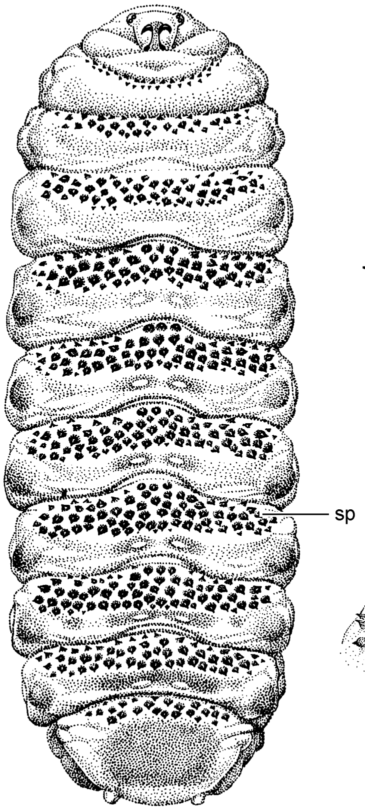
133 *Ceracia* (Tachinidae)



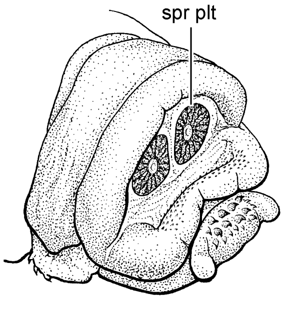
134 *Blepharomyia* (Tachinidae)

Figs 13.126–134. Larval habitus and posterior spiracles (all non-Afrotropical, except Fig. 131): (126) posterior spiracles of *Zodion* sp., posterior view (Conopidae); (127) same, *Thecophora* sp. (Conopidae); (128) same, *Physocephala bimarginipennis* Karsch (Conopidae); (129) same, habitus, lateral view; (130) habitus of *Olfersia spinifera* (Leach), dorsal view (Hippoboscidae); (131) same, *Glossina swynnertoni* Austen (Glossinidae); (132) posterior spiracles of *Sphecomyiella valida* (Harris), posterior view (Pyrgotidae); (133) same, *Ceracia dentata* (Coquillett), lateroventral view (Tachinidae); (134) same, *Blepharomyia* sp. (Tachinidae), posterior view. Figs 126–130, 132–134 (Teskey 1981*b*, figs 8–11, 2, 5, 21, 24, respectively), Fig. 131 (after Burtt & Jackson 1951, fig. 6).

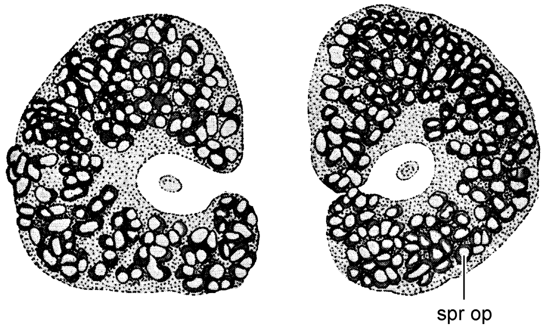
Abbreviations: spr op – spiracular opening; spr plt – spiracular plate.



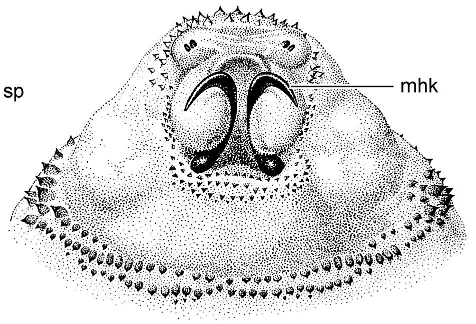
135 *Oestrus* (Oestridae)



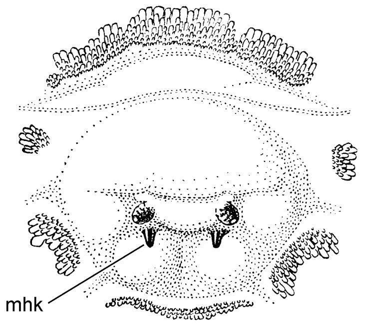
136 *Oestrus* (Oestridae)



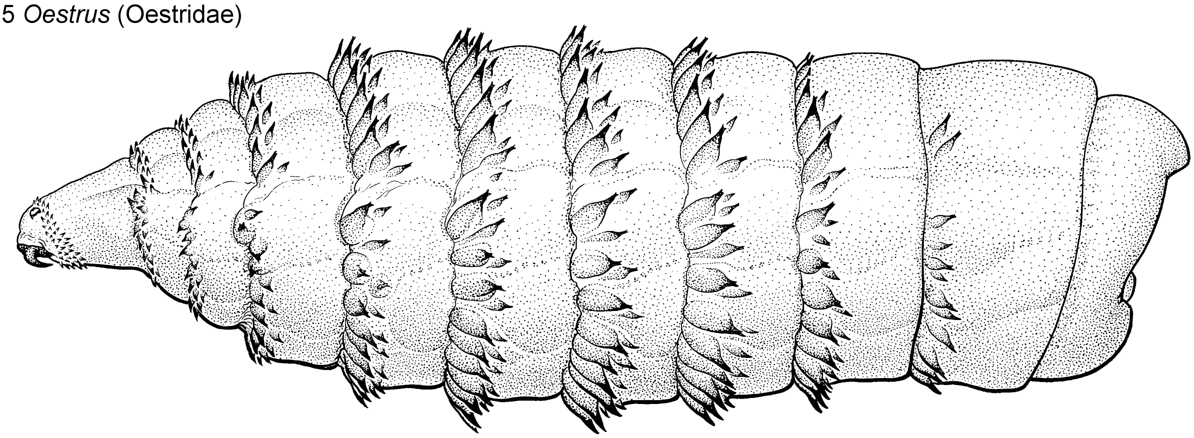
137 *Oestrus* (Oestridae)



138 *Rhinoestrus* (Oestridae)



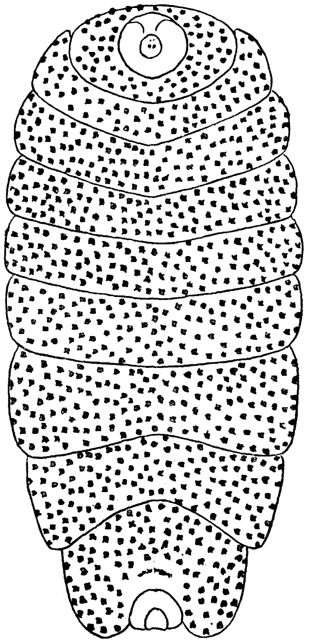
139 *Strobiloestrus* (Oestridae)



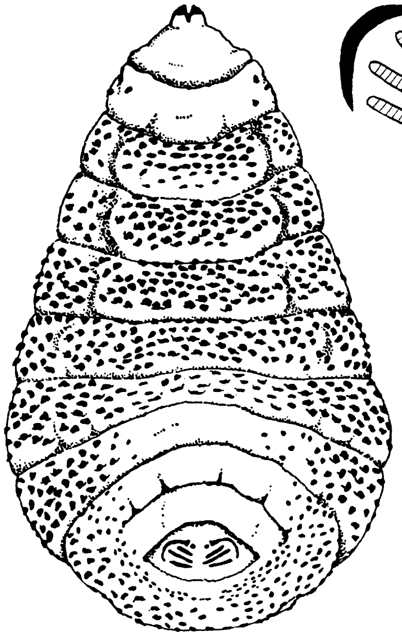
140 *Gasterophilus* (Oestridae)

Figs 13.135–140. Larval habitus, anterior segments, posterior spiracles and terminal segments of Oestridae: (135) habitus of *Oestrus ovis* L., ventral view; (136) same, terminal segments, posterolateral view; (137) same, posterior spiracles, posterior view; (138) anterior segments of *Rhinoestrus purpureus* (Brauer), ventral view; (139) anterior segments of *Strobiloestrus vanzyli* Zumpt, anterior view; (140) habitus of *Gasterophilus intestinalis* (De Geer), lateral view. Figs 135, 138 (Grunin 1966, figs 188, 206), Figs 136, 140 (Teskey 1981*b*, figs 36, 33, respectively), Fig. 137 (after Zumpt 1965, fig. 250), Fig. 139 (Grunin 1964, fig. 24, as *Dermatoestrus*).

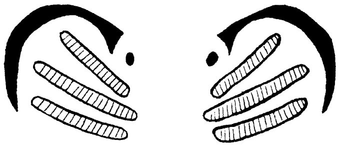
Abbreviations: mhk – mouthhook; sp – spicule; spr op – spiracular opening; spr plt – spiracular plate.



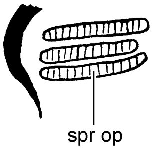
141 *Neocuterebra* (Oestridae)



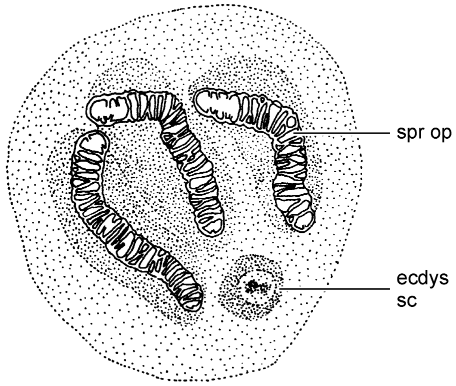
142 *Ruttenia* (Oestridae)



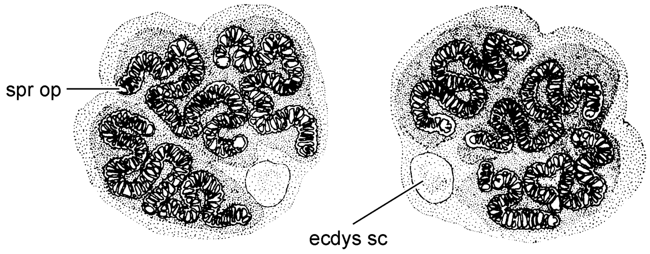
143 *Ruttenia* (Oestridae)



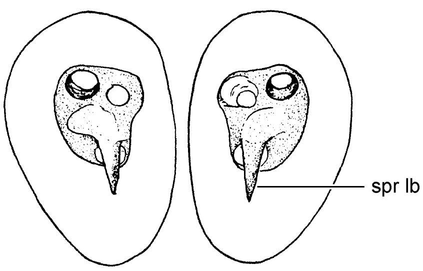
144 *Neocuterebra* (Oestridae)



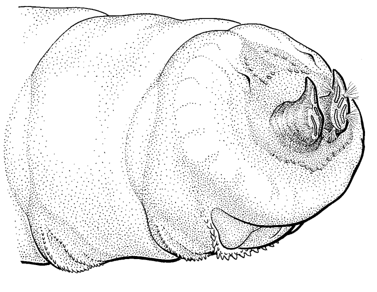
145 *Cordylobia* (Calliphoridae)



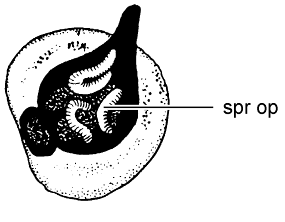
146 *Cordylobia* (Calliphoridae)



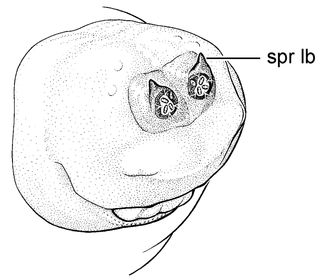
147 *Hyalomyodes* (Tachinidae)



148 *Compsobata* (Micropezidae)



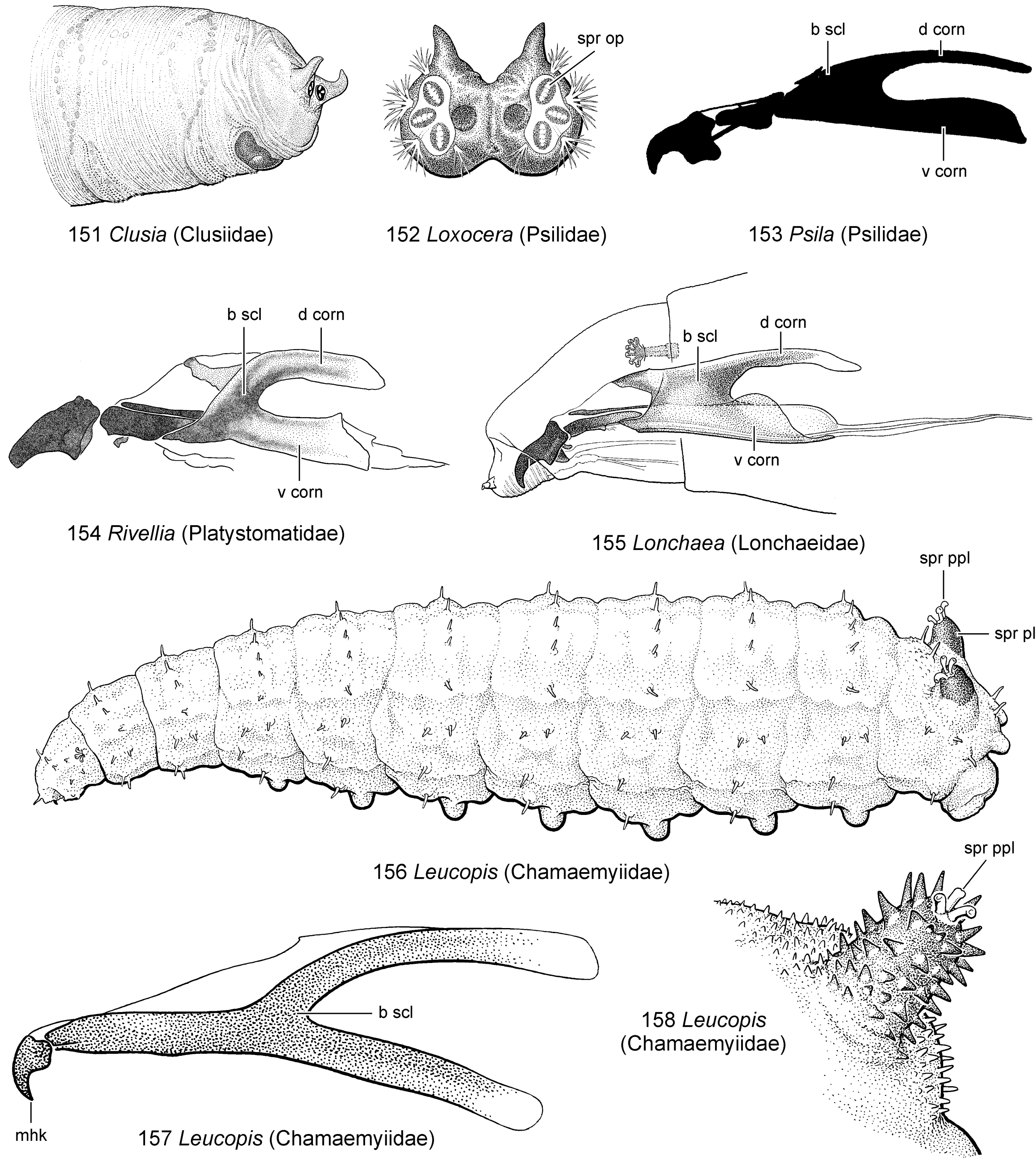
149 *Calobatella* (Micropezidae)



150 *Lonchaea* (Lonchaeidae)

Figs 13.141–150. Larval habitus and posterior spiracles: (141) habitus of *Neocuterebra squamosa* Grünberg, ventral view (Oestridae); (142) same, *Ruttenia loxodontis* Rodhain, dorsal view (Oestridae); (143) same, posterior spiracles, posterior view; (144) left posterior spiracle of *N. squamosa*, posterior view (Oestridae); (145) same, *Cordylobia ruandae* Gedoelst, posterior view (Calliphoridae); (146) posterior spiracles of *C. rodhaini* Gedoelst, posterior view (Calliphoridae); (147) posterior spiracles of *Hyalomyodes brasiliensis* Townsend, posterior view (Tachinidae) (non-Afrotropical); (148) terminal segments of *Compsobata univitta* (Walker), posterolateral view (Micropezidae) (non-Afrotropical); (149) right posterior spiracle of *Calobatella petronella* (L.), posterior view (Micropezidae) (non-Afrotropical); (150) terminal segments of *Lonchaea corticis* Taylor, posterolateral view (Lonchaeidae) (non-Afrotropical). Figs 141, 143, 144 (after Zumpt 1958, figs 1a, 1c, 3), Figs 142, 145, 146 (after Zumpt 1965, figs 178, 83, 88, respectively), Fig. 147 (Guimarães 1978, fig. 5), Figs 148, 150 (Teskey 1981*b*, figs 91, 87, respectively), Fig. 149 (Lobanov 1960, fig. c).

Abbreviations: ecdys sc – ecdysial scar; spr lb – spiracular lobe; spr op – spiracular opening.


151 *Clusia* (Clusiidae)

152 *Loxocera* (Psilidae)

153 *Psila* (Psilidae)

154 *Rivellia* (Platystomatidae)

155 *Lonchaea* (Lonchaeidae)

156 *Leucopis* (Chamaemyiidae)

157 *Leucopis* (Chamaemyiidae)

158 *Leucopis* (Chamaemyiidae)

Figs 13.151–158. Larval habitus, cephaloskeletons, cephalothorax, posterior spiracles and terminal segments (all non-Afrotropical): (151) terminal segments of *Clusia* sp., ventrolateral view (Clusiidae); (152) posterior spiracles of *Loxocera cylindrica* Say, posterior view (Psilidae); (153) cephaloskeleton of *Psila hennigi* (Thompson & Pont), lateral view (Psilidae); (154) same, *Rivellia viridulans* Robineau-Desvoidy (Platystomatidae); (155) cephalothorax of *Lonchaea corticis* Taylor, lateral view (Lonchaeidae); (156) habitus of *Leucopis simplex* Loew, lateral view (Chamaemyiidae); (157) same, cephaloskeleton, lateral view; (158) right posterior spiracular plate of *Leucopis* sp., lateral view (Chamaemyiidae). Figs 151, 152, 156–158 (Teskey 1981*b*, figs 89, 86, 73–75, respectively), Fig. 153 (after Ashby & Wright 1946, fig. 4c, as *rosae*), Fig. 155 (McAlpine 1987, fig. 25).

Abbreviations: b scl – basal sclerite; d corn – dorsal cornu; mhk – mouthhook; spr op – spiracular opening; spr plt – spiracular plate; spr ppl – spiracular papilla; v corn – ventral cornu.

– If tuberculate processes present on thoracic segments, then also present on most abdominal segments or nearly as long as body width; respiratory system usually amphipneustic (spiracles on prothorax and abdominal segment 8), with posterior spiracular plates elevated or in deep cavity; cephaloskeleton with basal and intermediate sclerites usually separate; habitats various. 103

103. Posterior spiracular plates set in deep spiracular cavity, the margins of which are capable of closure, like a pair of lips (Fig. 190); spiracular openings usually set nearly vertically; necrophagous, coprophagous and parasitoids/predators on insects, snails, reptiles and amphibians (PARAMACRONYCHIINAE and SARCOPHAGINAE) . . . . Sarcophagidae [in part] (Chapter 116)

– Posterior spiracular plates not set in deep and closable cavity, at most in a shallow depression; orientation of spiracular openings various; habitats various 104

104. Prothoracic spiracle comprising numerous long, thread-like filaments, often withdrawn into pocket in body cuticle (Fig. 188); in rotting fruit, fungi or vegetable matter . . . . Drosophilidae [in part] (Chapter 106)

– Prothoracic spiracle not as above; habitats various 105

105. Posterior spiracular plates each with 3 slit-like spiracular openings lying virtually parallel to each other (*e.g.*, Figs 191–194) 106

– Posterior spiracular plates with openings set at an angle to each other 110

106. Cephaloskeleton with slender to broad accessory oral sclerites beneath mouthhooks (Fig. 216); parasites of birds; saprophagous, predaceous or phytophagous . . . . Muscidae [in part] (Chapter 113)

– Cephaloskeleton without accessory oral sclerites; habitats various 107

107. Posterior spiracular openings set virtually horizontal; without sclerotised spiracular peritreme (Fig. 192); in fruits and flower heads. . . . . Tephritidae [in part] (Chapter 71)

– Posterior spiracular openings set vertically or angle between horizontal and vertical (*e.g.*, Figs 191, 193, 194), if spiracular openings horizontal, then with peritreme; habitats various 108

108. Posterior spiracular openings set roughly vertically or nearly horizontal, with spiracular peritreme incomplete surrounding ecdysial scar (as in Fig. 191); kleptoparasites of solitary bees and wasps (MILTOGRAMMINAE) . . . . Sarcophagidae [in part] (Chapter 116)

– Posterior spiracular openings set at an angle between vertical and horizontal; spiracular peritreme complete (*e.g.*, Figs 193, 194); habitats various 109

109. Posterior spiracular plate with ecdysial scar in upper inner margin (at 2 and 10 o'clock position) (Fig. 193); body typically with few or no distinct bands of spicules; commonly in decaying vegetable matter . . . . Platystomatidae [in part] (Chapter 70)

– Posterior spiracular plate with ecdysial scar in lower inner margin (at 4 and 8 o'clock positions) (Fig. 194); body typically with conspicuous band of spicules around most segments; breeding in carrion and other media. . . . . Calliphoridae [in part] (Chapter 114)

110. Prothoracic spiracle bicornate, divided into 2 halves (*e.g.*, Fig. 195), sometimes indistinctly (*e.g.*, Fig. 162). 111

– Prothoracic spiracle not divided into 2 halves. 116

111. Prothoracic spiracle divided into 2 separate branches, with 2 groups of papillae widely separated (Fig. 195); in aquatic or wet habitats, feeding on algae . . . . Ephydridae [in part] (Chapter 100)

– Prothoracic spiracle with papillae more evenly distributed, without large gap between branches; habitats various. 112

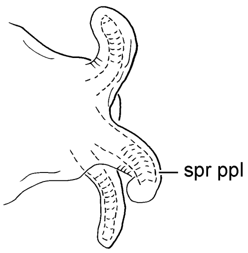
112. Terminal abdominal segment with small, but distinct tubercles surrounding posterior margin (*e.g.*, Figs 197, 198). 113

– Terminal abdominal segment without tubercles on posterior margin. 115

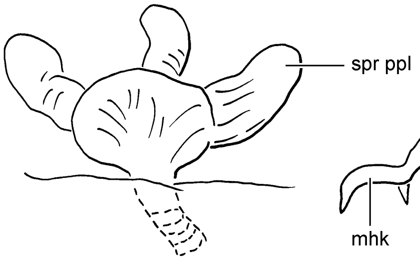
113. Prothoracic spiracle not distinctly separated into 2 halves (Fig. 162); spiracular peritreme weakly defined, posterior spiracular openings cutting into edge of plate (Fig. 164); mostly phytophagous . . . . Anthomyiidae [in part] (Chapter 111)

– Prothoracic spiracle distinctly separated into 2 halves (*e.g.*, Fig. 196); spiracular peritreme complete and darkly sclerotised, posterior spiracular openings distant from edge of plate (*e.g.*, Fig. 197) 114

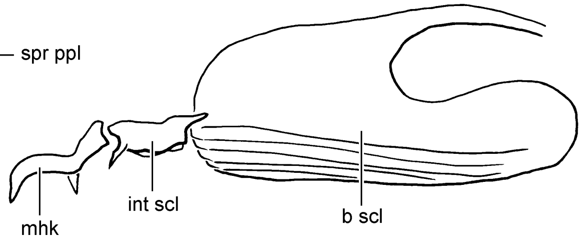
114. Posterior spiracular openings either sessile or set on slightly raised supporting structures (Fig. 196); Afrotropical species develops in cattle dung, being predaceous on other Arthropoda . . . . Scathophagidae (Chapter 110)



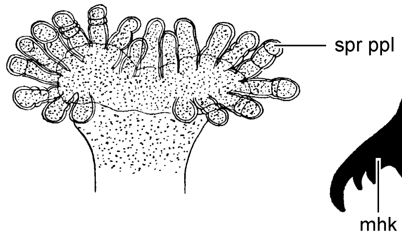
159 *Meoneura* (Carnidae)



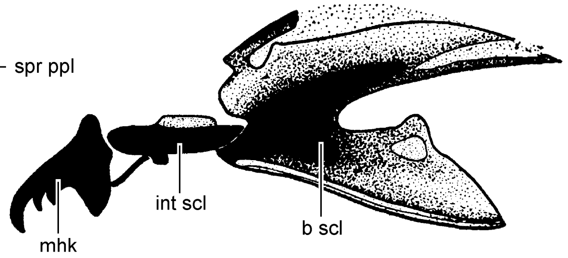
160 *Meoneura* (Carnidae)



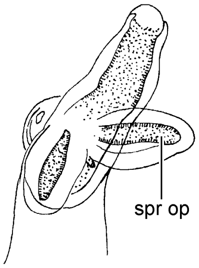
161 *Meoneura* (Carnidae)



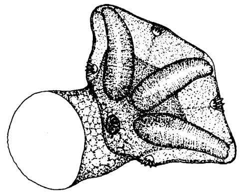
162 *Pegomya* (Anthomyiidae)



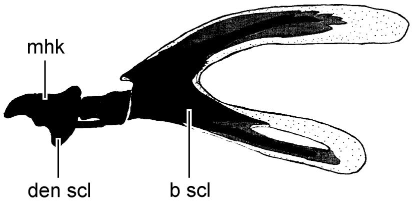
163 *Pegomya* (Anthomyiidae)



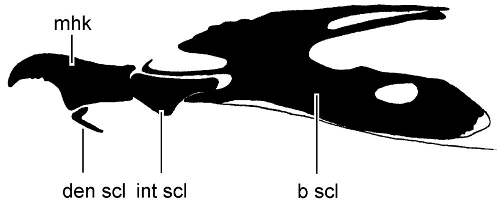
164 *Pegomya* (Anthomyiidae)



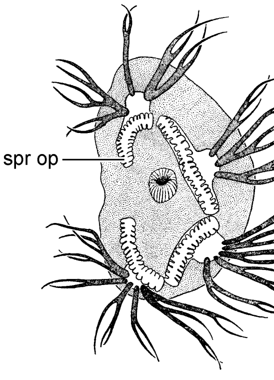
165 *Procecidocharoides* (Tephritidae)



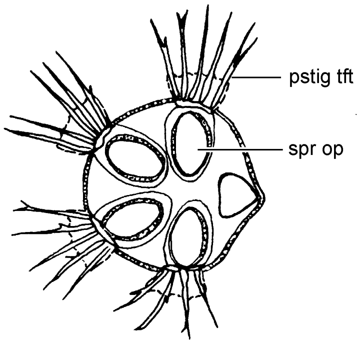
166 *Terellia* (Tephritidae)



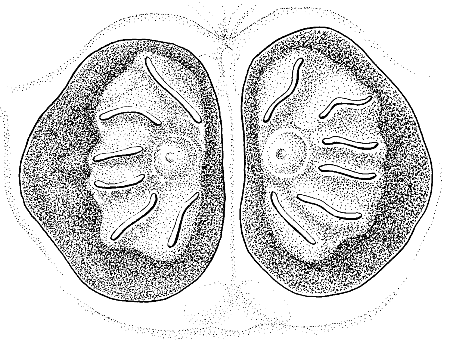
167 *Suillia* (Heleomyzidae)



168 *Telostylinus* (Neriidae)



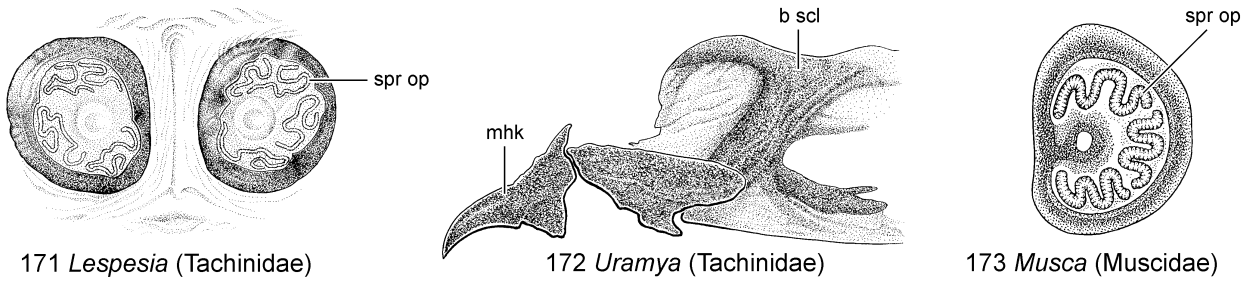
169 *Parydra* (Ephydridae)



170 *Zaira* (Tachinidae)

Figs 13.159–170. Cephaloskeletons, prothoracic and posterior spiracles (all non-Afrotropical): (159) posterior spiracle of *Meoneura obscurella* (Fallén), lateral view (Carnidae); (160) same, prothoracic spiracle; (161) same, cephaloskeleton; (162) prothoracic spiracle of *Pegomya solennis* (Meigen), lateral view (Anthomyiidae); (163) cephaloskeleton of *P. hyoscyami* (Panzer), lateral view (Anthomyiidae); (164) right posterior spiracle of *P. solennis*, posterior view (Anthomyiidae); (165) left posterior spiracle, *Procecidocharoides penelope* (Osten Sacken), posterior view (Tephritidae); (166) cephaloskeleton of *Terellia ceratocera* (Hendel), lateral view (Tephritidae); (167) same, *Suillia lurida* (Meigen) (Heleomyzidae); (168) right posterior spiracle of *Telostylinus lineolatus* (Wiedemann), posterior view (Neriidae); (169) left posterior spiracle of *Parydra quadrituberculata* Loew, posterior view (Ephydridae); (170) posterior spiracles of *Zaira* sp., posterior view (Tachinidae). Figs 159–161 (after Engel 1931, figs 3–5), Figs 162, 164 (after Vos-de Wilde 1935, figs 41, 43, as *nigritarsis*), Fig. 163 (Roback 1951, fig. 6), Fig. 165 (after Stoltzfus 1974, fig. 6), Fig. 166 (after Persson 1963, fig. 63, as *Cerajocera*), Fig. 167 (after Hennig 1952, fig. 179); Fig. 168 (after Berg 1947, fig. 5), Fig. 169 (after Deonier & Regensburg 1978, fig. 16), Fig. 170 (Teskey 1981*b*, fig. 28).

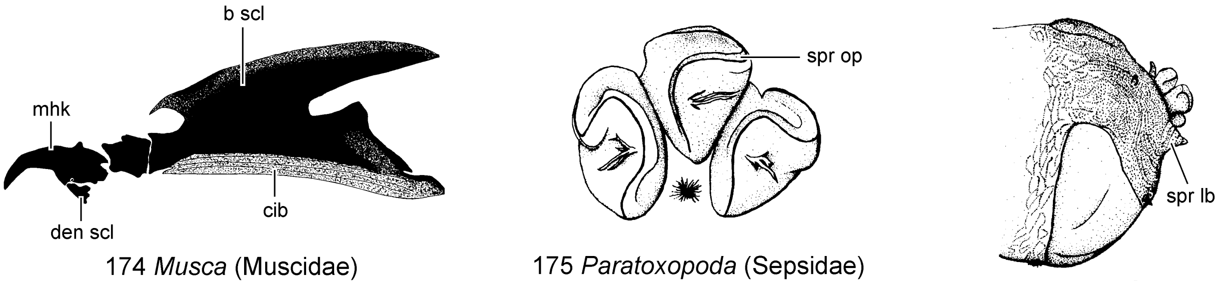
Abbreviations: b scl – basal sclerite; den scl – dental sclerite; int scl – intermediate sclerite; mhk – mouthhook; pstig tft – peristigmatic tuft; spr op – spiracular opening; spr ppl – spiracular papilla.



171 *Lespesia* (Tachinidae)

172 *Uramya* (Tachinidae)

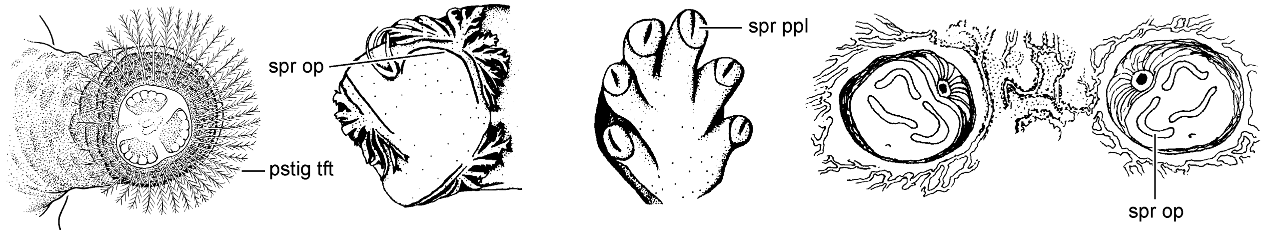
173 *Musca* (Muscidae)



174 *Musca* (Muscidae)

175 *Paratoxopoda* (Sepsidae)

176 *Paratoxopoda* (Sepsidae)

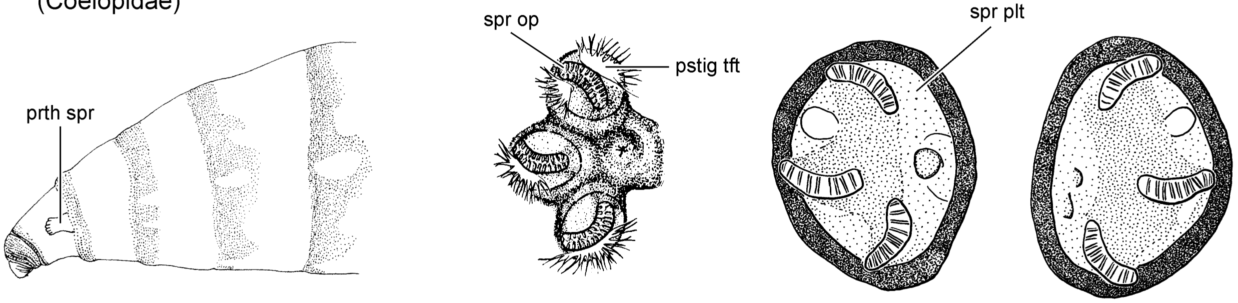


177 *Coelopa* (Coelopidae)

178 *Sepsis* (Sepsidae)

179 *Sepsis* (Sepsidae)

180 *Passeromyia* (Muscidae)



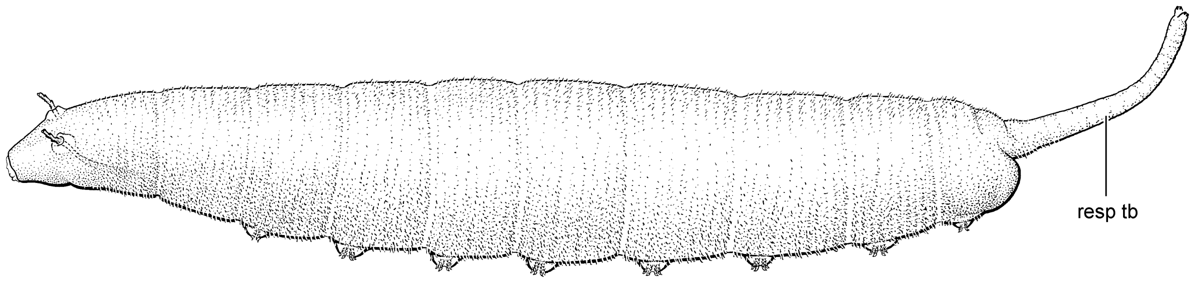
181 *Passeromyia* (Muscidae)

182 *Pholeomyia* (Milichiidae)

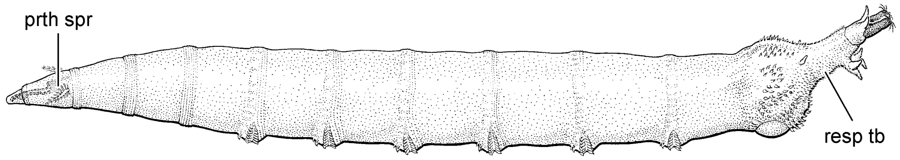
183 *Lotophila* (Sphaeroceridae)

Figs 13.171–183. Larval cephaloskeletons, prothoracic and posterior spiracles and anterior and terminal segments: (171) posterior spiracles of *Lespesia callosamiae* Beneway, posterior view (Tachinidae) (non-Afrotropical); (172) cephaloskeleton of *Uramya halisidotae* (Townsend), lateral view (Tachinidae) (non-Afrotropical); (173) right posterior spiracle of *Musca domestica* L., posterior view (Muscidae); (174) same, cephaloskeleton, lateral view; (175) left posterior spiracle of *Paratoxopoda amonane* Vanschuytbroeck, posterior view (Sepsidae); (176) same, terminal segments, lateral view; (177) right posterior spiracle of *Coelopa frigida* (F.), posterior view (Coelopidae) (non-Afrotropical); (178) left posterior spiracle of *Sepsis lateralis* Wiedemann, posterior view (Sepsidae); (179) same, prothoracic spiracle, lateral view; (180) posterior spiracles of *Passeromyia heterochaeta* (Villeneuve), posterior view (Muscidae); (181) same, anterior segments, lateral view; (182) left (?) posterior spiracle of *Pholeomyia comans* Sabrosky, posterior view (Milichiidae) (non-Afrotropical); (183) posterior spiracles of *Lotophila atra* (Meigen), posterior view (Sphaeroceridae) (non-Afrotropical). Figs 171–173, 177 (Teskey 1981*b*, figs 27, 31, 99, 85, respectively), Fig. 174 (after Smith 1986, fig. 247), Figs 175, 176, 178, 179 (after Meier 1996, figs 152, 155, 268, 270), Figs 180, 181 (Skidmore 1985, figs 18f, 17b, respectively), Fig. 182 (after Moser & Neff 1971, fig. 10), Fig. 183 (after Schumann 1962, fig. 7).

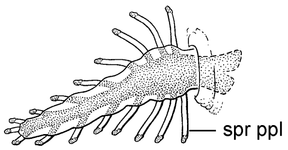
Abbreviations: b scl – basal sclerite; cib – cibarium; den scl – dental sclerite; mhk – mouthhook; prth spr – prothoracic spiracle; pstig tft – peristigmatic tuft; spr lb – spiracular lobe; spr op – spiracular opening; spr plt – spiracular plate; spr ppl – spiracular papilla.



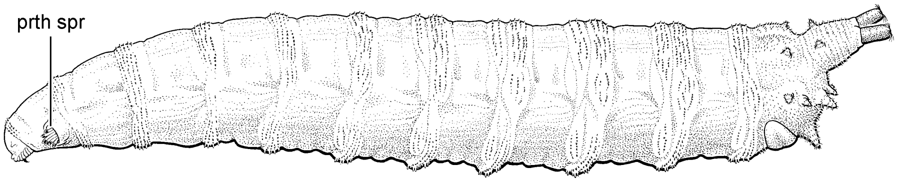
184 *Aulacigaster* (Aulacigastridae)



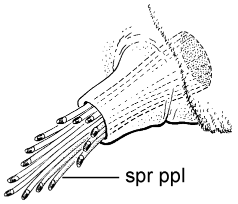
185 *Sepsis* (Sepsidae)



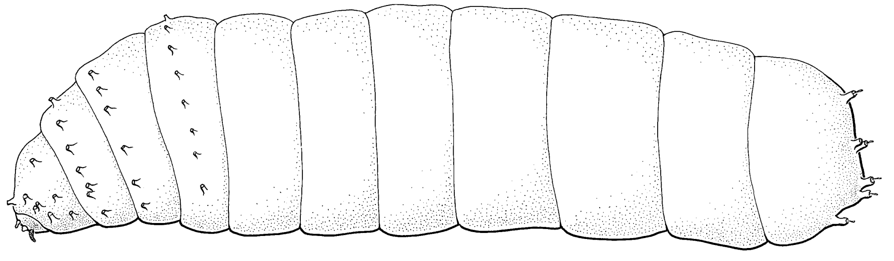
186 *Sepsis* (Sepsidae)



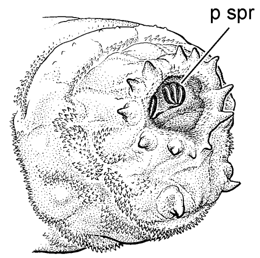
187 *Drosophila* (Drosophilidae)



188 *Drosophila* (Drosophilidae)



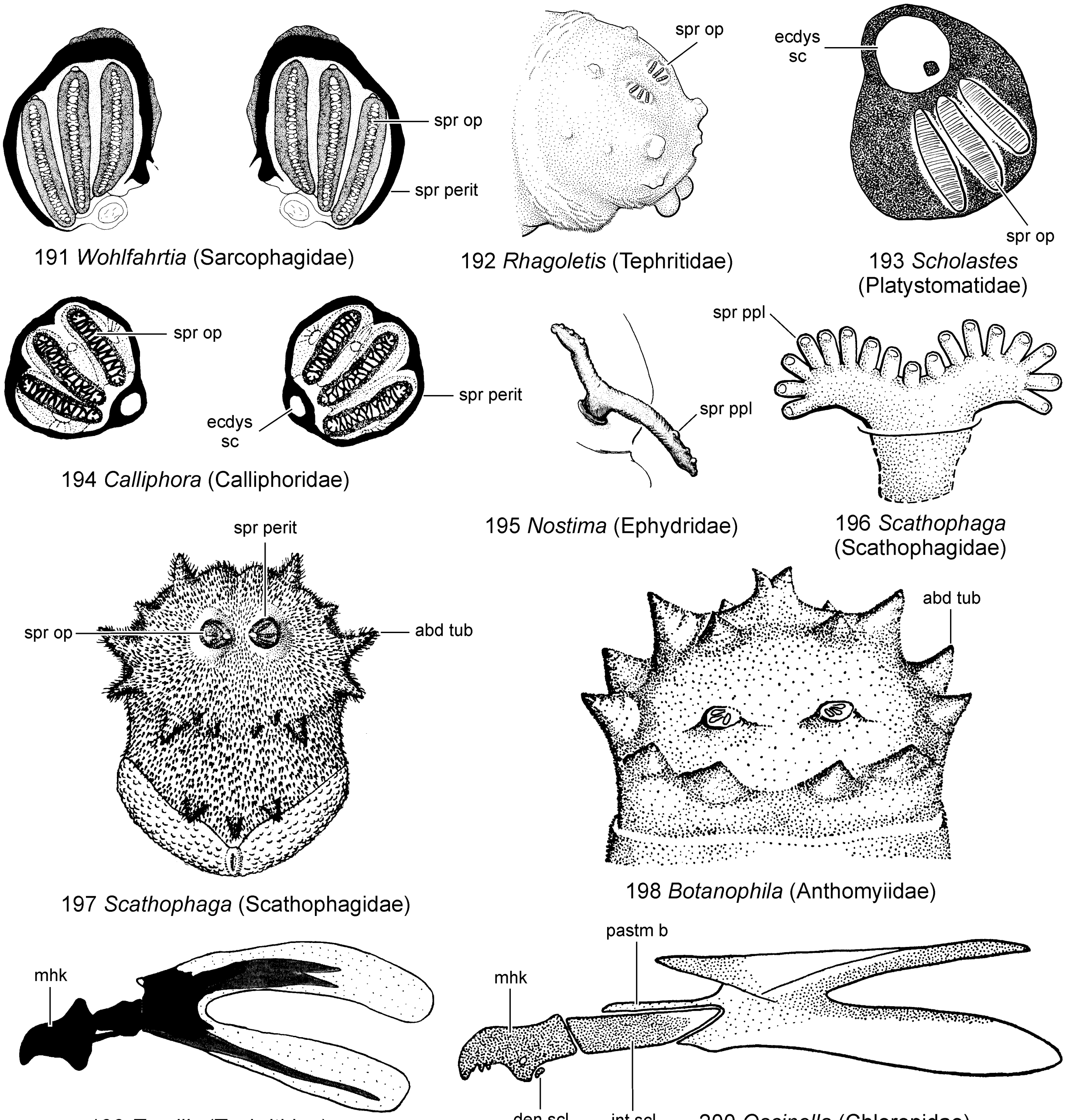
189 *Braula* (Braulidae)



190 *Ravinia* (Sarcophagidae)

Figs 13.184–190. Larval habitus, prothoracic spiracles and terminal segments (all non-Afrotropical, except Figs 187, 188): (184) habitus of *Aulacigaster leucopeza* (Meigen), dorsolateral view (Aulacigastridae); (185) same, *Sepsis neocynipsea* Melander & Spuler (Sepsidae); (186) same, prothoracic spiracle, lateral view; (187) habitus of *Drosophila melanogaster* Meigen, dorsolateral view (Drosophilidae); (188) same, prothoracic spiracle, lateral view; (189) habitus of *Braula coeca* Nitzsch, lateral view (Braulidae); (190) terminal segments of *Ravinia querula* (Walker), posterolateral view (Sarcophagidae). Figs 184–190 (Teskey 1981*b*, figs 64–66, 59, 60, 52, 84, respectively).

Abbreviations: p spr – posterior spiracle; prth spr – prothoracic spiracle; resp tb – respiratory tube; spr ppl – spiracular papilla.



191 *Wohlfahrtia* (Sarcophagidae)

192 *Rhagoletis* (Tephritidae)

193 *Scholastes* (Platystomatidae)

194 *Calliphora* (Calliphoridae)

195 *Nostima* (Ephydridae)

196 *Scathophaga* (Scathophagidae)

197 *Scathophaga* (Scathophagidae)

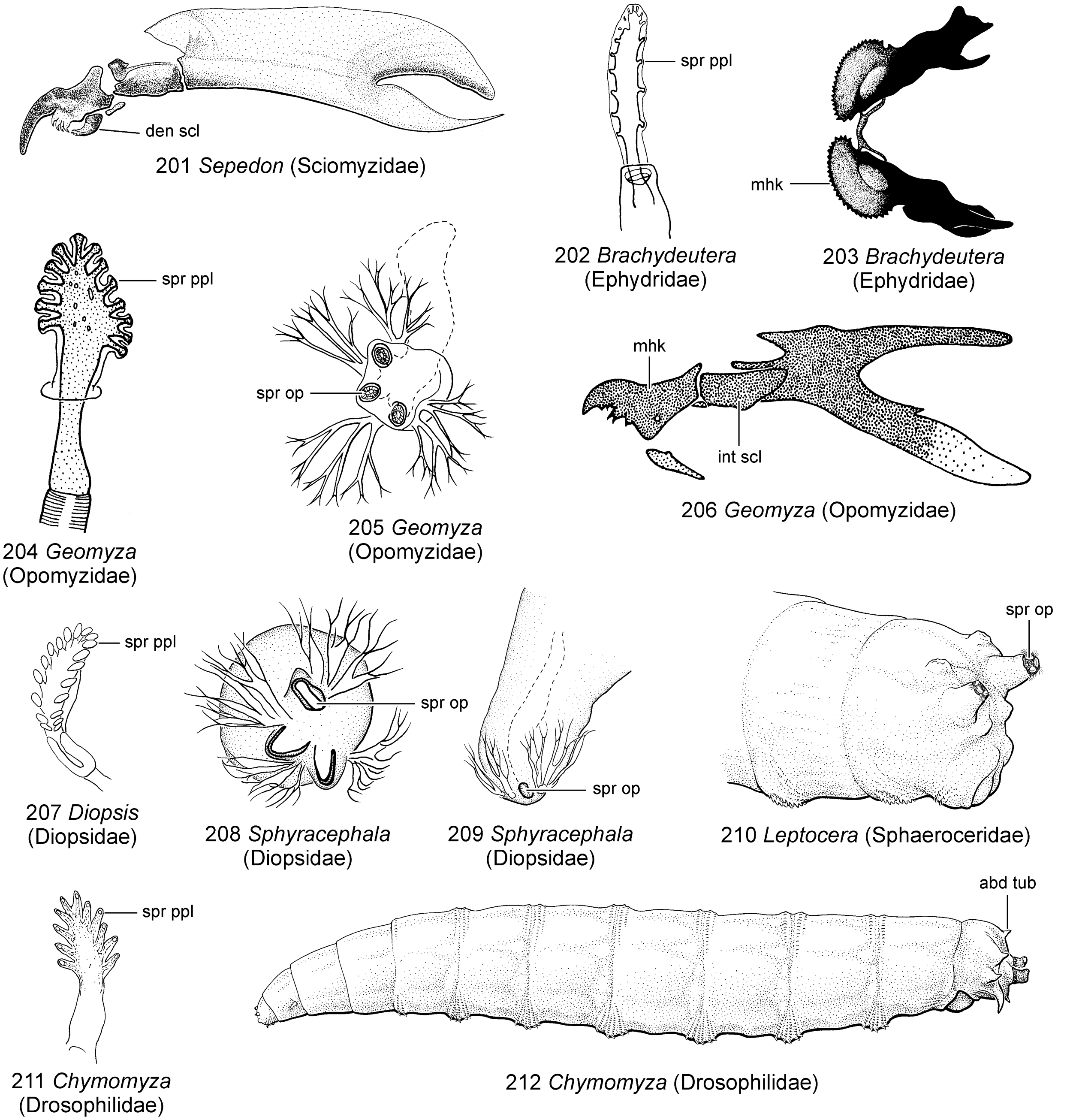
198 *Botanophila* (Anthomyiidae)

199 *Terellia* (Tephritidae)

200 *Oscinella* (Chloropidae)

Figs 13.191–200. Cephaloskeletons, prothoracic and posterior spiracles and terminal segments (all non-Afrotropical, except Figs 196, 197): (191) posterior spiracles of *Wohlfahrtia magnifica* (Schiner), posterior view (Sarcophagidae); (192) terminal segments of *Rhagoletis pomonella* (Walsh), dorsolateral view (Tephritidae); (193) right posterior spiracle of *Scholastes aitapensis* Malloch, posterior view (Platystomatidae); (194) same, *Calliphora augur* (F.) (Calliphoridae); (195) prothoracic spiracle of *Nostima approximata* Sturtevant & Wheeler, lateral view (Ephydridae); (196) same, *Scathophaga stercoraria* (L.), lateral view (Scathophagidae); (197) same, terminal segments, posteroventral view; (198) same, *Botanophila fugax* (Meigen), posterodorsal view (Anthomyiidae); (199) cephaloskeleton of *Terellia plagiata* (Dahlbom), lateral view (Tephritidae); (200) same, *Oscinella frit* (L.) (Chloropidae). Fig. 191 (after Lehrer & Fromunda 1986, fig. 5E), Figs 192, 196 (Teskey 1981*b*, figs 105, 81, respectively), Fig. 193 (after Bohart & Gressitt 1951, Plate 4 [unnumbered]), Fig. 194 (Zumpt 1965, fig. 70), Fig. 195 (Foote 1983, fig. 4), Fig. 197 (Zimin 1948, fig. 19D), Fig. 198 (after Miles 1950, fig. 1), Fig. 199 (after Persson 1963, fig. 71, as *Cerajocera*), Fig. 200 (after Nye 1958, fig. 56).

Abbreviations: abd tub – abdominal tubercle; den scl – dental sclerite; ecdys sc – ecdysial scar; int scl – intermediate sclerite; mhk – mouthhook; pastm b – parastomal bar; spr op – spiracular opening; spr perit – spiracular peritreme; spr ppl – spiracular papilla.


201 *Sepedon* (Sciomyzidae)

202 *Brachydeutera* (Ephydridae)

203 *Brachydeutera* (Ephydridae)

204 *Geomyza* (Opomyzidae)

205 *Geomyza* (Opomyzidae)

206 *Geomyza* (Opomyzidae)

207 *Diopsis* (Diopsidae)

208 *Sphyracephala* (Diopsidae)

209 *Sphyracephala* (Diopsidae)

210 *Leptocera* (Sphaeroceridae)

211 *Chymomyza* (Drosophilidae)

212 *Chymomyza* (Drosophilidae)

Figs 13.201–212. Larval habitus, cephaloskeletons, prothoracic and posterior spiracles and terminal segments (all non-Afrotropical, except Fig. 207): (201) cephaloskeleton of *Sepedon* sp., lateral view (Sciomyzidae); (202) prothoracic spiracle of *Brachydeutera neotropica* Wirth, lateral view (Ephydridae); (203) mouthhooks of *B. hebes* Cresson, dorsal view (Ephydridae); (204) prothoracic spiracle of *Geomyza tripunctata* Fallén, lateral view (Opomyzidae); (205) same, left (?) posterior spiracle, posterior view; (206) same, cephaloskeleton, lateral view; (207) prothoracic spiracle of *Diopsis apicalis* Dalman, lateral view (Diopsidae); (208) left posterior spiracle of *Sphyracephala brevicornis* (Say), posterior view (Diopsidae); (209) same, dorsal view; (210) terminal segments of *Leptocera* sp., dorsolateral view (Sphaeroceridae); (211) prothoracic spiracle of *Chymomyza costata* (Zetterstedt), lateral view (Drosophilidae); (212) same, habitus, lateral view. Figs 201, 210, 212 (Teskey 1981*b*, figs 58, 94, 72, respectively), Fig. 202 (after Lizarralde de Grosso 1972, fig. 9), Fig. 203 (Hardy & Delfinado 1980, fig. 129f), Figs 204, 206 (after Nye 1958, figs 39, 37), Fig. 205 (after Thomas 1938, fig. 4A), Fig. 207 (after Descamps 1957, fig. 23a), Fig. 211 (after Hackman *et al.* 1970, fig. 16).

Abbreviations: abd tub – abdominal tubercle; den scl – dental sclerite; int scl; intermediate sclerite; mhk – mouthhook; spr op – spiracular opening; spr ppl – spiracular papilla.

– Posterior spiracular openings set on short supporting structures, at least 1.5 times longer than terminal abdominal tubercles (*e.g.*, Fig. 210); possibly in decaying vegetable matter. . . . Diastatidae (Chapter 104)

115. Cephaloskeleton without parastomal bar; dental sclerite fused to mouthhooks (Fig. 199); in flowerheads. . . . . .Tephritidae [in part] (Chapter 71)

– Cephaloskeleton with parastomal bar; dental sclerite separate from mouthhooks (Fig. 200); usually in stems and shoots of grasses and cereals . . . . .Chloropidae [in part] (Chapter 96)

116. Prothoracic spiracle with papillae distributed along elongate central axis (*e.g.*, Figs 202, 207, 211). . . 117

– Prothoracic spiracle fan- or rosette-shaped or otherwise, not with elongate central axis 123

117. Terminal abdominal segment without tubercles 118

– Terminal abdominal segment with small tubercles on posterior margin 121

118. Prothoracic spiracle slender, not expanded apically, with papillae sessile, not projecting from shaft (Fig. 202); cephaloskeleton with mouthhooks flattened laterally, with saw-tooth edges (Fig. 203); in wet habitats (*Brachydeutera* Loew) . . . . Ephydridae [in part] (Chapter 100)

– Prothoracic spiracle expanded apically, with papillae projecting beyond expanded shaft (*e.g.*, Figs 204, 207, 211); cephaloskeleton with mouthhooks not laterally flattened; habitats various. 119

119. Posterior spiracular openings circular (Fig. 205); cephaloskeleton with mouthhooks bearing numerous distinct ventral teeth (Fig. 206); stem-borers in grasses (*Geomyza* Fallén) . . . . Opomyzidae [in part] (Chapter 84)

– Posterior spiracular openings elongate or oval; cephaloskeleton with mouthhooks bearing at most 1 or 2 indistinct ventral teeth; habitats various. 120

120. Posterior spiracular openings curved over apex of dome-shaped fleshy protuberance (Figs 208, 209); in vegetable matter . . . . Diopsidae [in part] (Chapter 64)

– Posterior spiracular openings confined to apex of narrow, tubular projections (Fig. 210); in dung and other decaying matter . . . . Sphaeroceridae [in part] (Chapter 99)

121. Cephaloskeleton with right and left dental sclerites fused medially, forming toothed median ventral arch beneath mouthhooks (Figs 201, 217); aquatic, semi-aquatic or terrestrial, usually associated with Gastropoda, rarely with Oligochaeta (as parasitoids or predators) . . . . . . Sciomyzidae [in part] (Chapter 78)

– Cephaloskeleton with dental sclerites not fused (not to be confused with accessory oral sclerites, see above); habitats otherwise 122

122. Terminal abdominal segment conspicuously spiny (Fig. 185); usually breeding in dung and other decaying plant matter; some associated with carrion . . . . Sepsidae [in part] (Chapter 79)

– Terminal abdominal segment not conspicuously spiny (Fig. 212); beneath bark, in insect galleries, tunnels and sap runs . . . . Drosophilidae [in part] (Chapter 106)

123. Abdominal segments 2–7 with rows of crockets on raised ventral pads or prolegs (Fig. 213); cephaloskeleton without accessory oral sclerites beneath mouthhooks; terminal abdominal segment with pair of ventral processes on each side of anus; prothoracic spiracles with 3 papillae (Fig. 214); in spathe chambers of flowers, saprophagous . . . . Neurochaetidae (Chapter 90)

– Abdominal segments 2–7 without rows of crockets on raised ventral pads or prolegs, if prolegs present, then cephaloskeleton with slender to broad accessory oral sclerites beneath mouthhooks; terminal abdominal segment without pair of ventral processes on each side of anus; prothoracic spiracles with more than 3 papillae; habitats various 124

124. Posterior spiracles situated on median sloping faces of spiracular prominences, appearing capable of being closed together to seal off spiracles (Fig. 215); in dried-up carrion and fungi and infesting proteinaceous foodstuffs . . . . Piophilidae (Chapter 68)

– Posterior spiracles not on sloping faces; not closable; habitats various. 125

125. Cephaloskeleton with slender to broad accessory oral sclerites beneath mouthhooks (Fig. 216); parasites of birds; saprophagous, predaceous or phytophagous . . . . .Muscidae [in part] (Chapter 113)

– Cephaloskeleton without accessory oral sclerites; habitats various 126

126. Cephaloskeleton with right and left dental sclerites fused medially, forming toothed median ventral arch beneath mouthhooks (Figs 201, 217); aquatic, semi-aquatic or terrestrial, usually associated with Gastropoda, rarely with Oligochaeta (as parasitoids or predators) . . . . . . Sciomyzidae [in part] (Chapter 78)

– Cephaloskeleton with dental sclerites not fused (not to be confused with accessory oral sclerites, see above); habitats otherwise 127

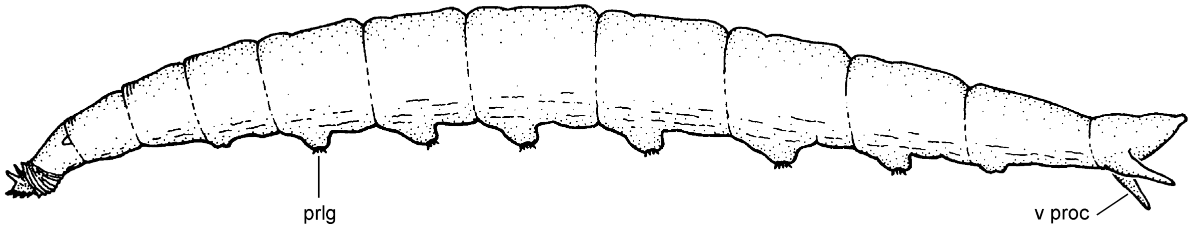
127. Cephaloskeleton strong, stout, heavily sclerotised, lacking parastomal bars (*e.g.*, Fig. 172); parasitoids of various Arthropoda 128

– Cephaloskeleton usually more slender and not thickly sclerotised, parastomal bars usually present; habitats various; not parasitoids 129

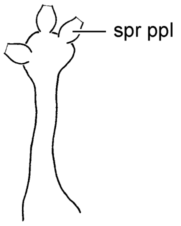
128. Parasitoids in woodlice (Oniscoidea) . . . . Rhinophoridae (Chapter 117)

– Parasitoids in Insecta, Araneae, Myriopoda and Scorpiones (but not Oniscoidea) . . . . Tachinidae [in part] (Chapter 118)

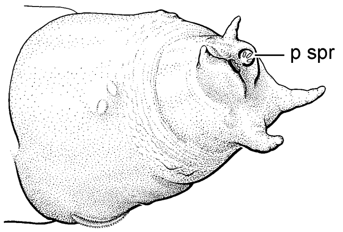
129. Posterior spiracular openings radiating from ecdysial scar at right angles to each other, with ecdysial scar set medially (*e.g.*, Fig. 218) 130



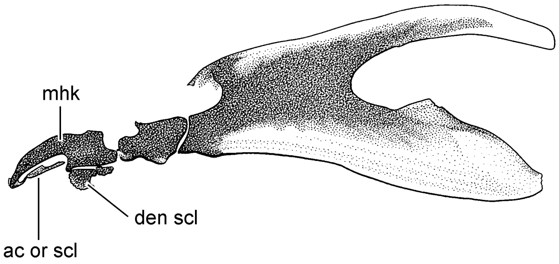
213 *Neurochaeta* (Neurochaetidae)



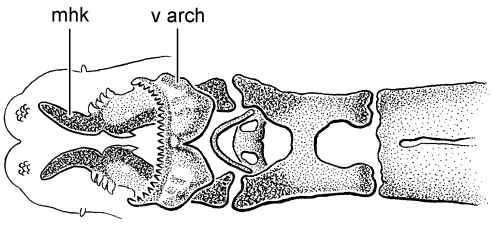
214 *Neurochaeta* (Neurochaetidae)



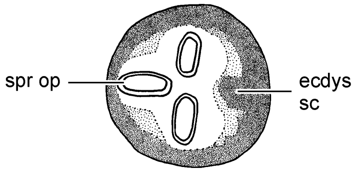
215 *Lasiopiophila* (Piophilidae)



216 *Potamia* (Muscidae)



217 *Sepedon* (Sciomyzidae)



218 *Lonchaea* (Lonchaeidae)

Figs 13.213–218. Larval habitus, prothoracic and posterior spiracles, cephaloskeletons and terminal segments (all non-Afrotropical): (213) habitus of *Neurochaeta inversa* McAlpine, lateral view (Neurochaetidae); (214) same, prothoracic spiracle, lateral view; (215) terminal segments of *Lasiopiophila pilosa* (Staeger), posterolateral view (Piophilidae); (216) cephaloskeleton of *Potamia* sp., lateral view (Muscidae); (217) same, *Sepedon* sp., ventral view (Sciomyzidae); (218) left posterior spiracle of *Lonchaea sylvatica* Beling, posterior view (Lonchaeidae). Figs 213, 214 (after McAlpine 1978, figs 4, 23), Figs 215–217 (Teskey 1981*b*, figs 69, 101 (as *Dendrophaonia*), 57, respectively), Fig. 218 (Krivosheina & Mamaev 1967, fig. 152.11).

Abbreviations: ac or scl – accessory oral sclerite; den scl – dental sclerite; ecdys sc – ecdysial scar; mhk – mouthhook; p spr – posterior spiracle; prlg – proleg; spr op – spiracular opening; spr ppl – spiracular papilla; v arch – ventral arch; v proc – ventral process.

– Posterior spiracular openings radiating from ecdysial scar at distinctly less than right angles (*e.g.*, Fig. 219). 131

130. Terminal abdominal segment with distinct tubercles (Fig. 220); Keilin's organs on prothoracic segment closely approximated (Fig. 221), those on meso- and metathoracic segments more widely separated; associated with dung, droppings and guano of birds and small mammals, often frequenting burrows, caves and rock overhangs . . . . Camillidae [in part] (Chapter 102)

– Terminal abdominal segment without tubercles (Fig. 222); Keilin's organs equally separated on each thoracic segment; associated with wood, fruits and various rotting media. . . . . Lonchaeidae [in part] (Chapter 67)

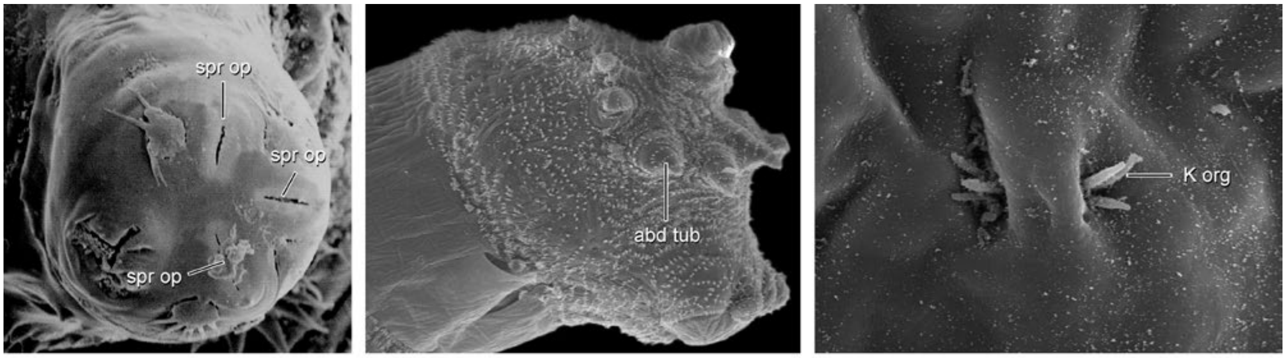
131. Terminal abdominal segment without distinct tubercles 132

– Terminal abdominal segment with tubercles (*e.g.*, Fig. 220) 139

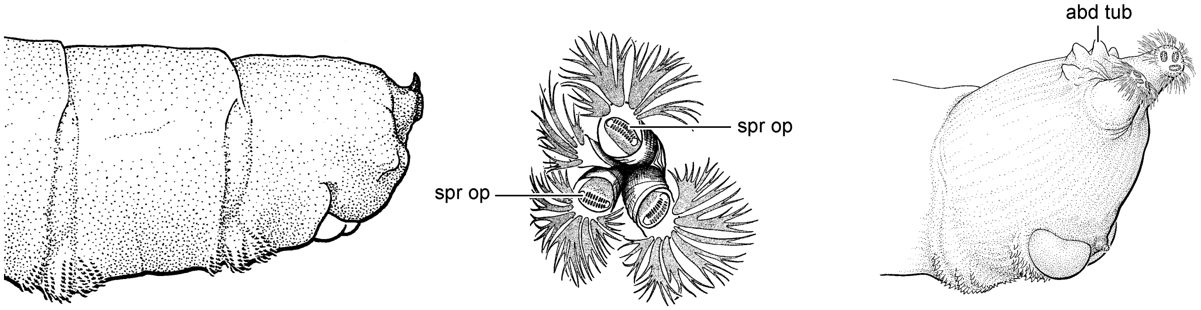
132. Cephaloskeleton heavily built of phytophagous type (*e.g.*, Figs 200, 206), with robust mouthhooks (often with multiple teeth) and intermediate sclerite; stem-borers . . . . Opomyzidae [in part] and Chloropidae [in part] (Chapters 84 & 96)

– Cephaloskeleton more narrowly built of saprophagous type (*e.g.*, Fig. 226), with slender mouthhooks (lacking teeth) and intermediate sclerite; habitats various 133

133. Central posterior spiracular opening positioned closer to ventral than to dorsal spiracular opening (*e.g.*, Fig. 223) 134



219 *Katacamilla* (Camillidae) 220 *Katacamilla* (Camillidae) 221 *Katacamilla* (Camillidae)



222 *Lonchaea* (Lonchaeidae) 223 *Leptometopa* (Milichiidae) 224 *Desmometopa* (Milichiidae)

Figs 13.219–224. Prothoracic and posterior spiracles, Keilin's organ and terminal segments (all non-Afrotropical, except figs 219–221): (219) scanning electron micrograph of left posterior spiracle of *Katacamilla cavernicola* Papp (Camillidae); (220) same, terminal segments, lateral view; (221) same, Keilin's organ on prothoracic segment, ventral view; (222) terminal segments of *Lonchaea corticis* Taylor, lateral view (Lonchaeidae); (223) left posterior spiracle of *Leptometopa coquilletti* (Hendel), posterior view (Milichiidae); (224) terminal segments of *Desmometopa m-nigrum* (Zetterstedt), posterolateral view (Milichiidae). Figs 219–221 (after Kirk-Spriggs *et al*. 2002, figs 19, 17, 13, respectively), Fig. 222 (McAlpine 1987, fig. 24), Fig. 223 (Hennig 1956, fig. 10A), Fig. 224 (Teskey 1981*b*, fig. 70).

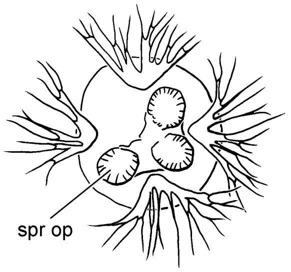
Abbreviations: abd tub – abdominal tubercle; K org – Keilin's organ; spr op – spiracular opening.

– Spiracular openings not as above 135

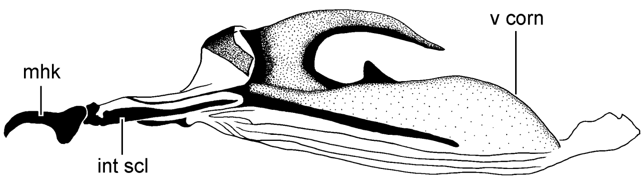
134. Terminal abdominal segment often with ridge of dorsal tubercles at base of spiracular prominences (Fig. 224); cephaloskeleton with ventral cornu lacking dorsal expansion; in various decaying media and birds' nests. . . . . .Milichiidae [in part] (Chapter 95)

– Terminal abdominal segment without ridge of tubercles at base of spiracular prominences; cephaloskeleton with ventral cornu bearing distinct dorsal expansion (as in Fig. 226); reared from birds' nests, bird and bat guano, mammal nests and burrows and decaying wood . . . . Chyromyidae (Chapter 97)

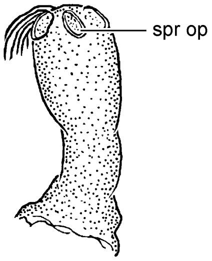
135. Posterior spiracular openings circular (Fig. 225); cephaloskeleton weakly sclerotised and pale pigmented (Fig. 226); saprophagous, reared from fungi, rotting bark and plant stems . . . . . . Asteiidae (Chapter 92)



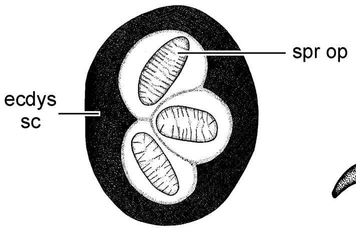
225 *Asteia* (Asteiidae)



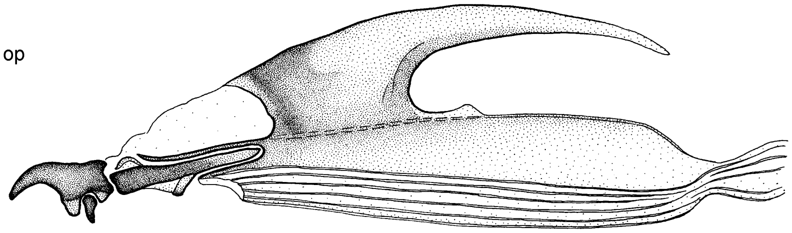
226 *Asteia* (Asteiidae)



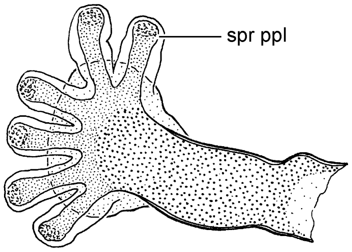
227 *Neoalticomerus* (Odiniidae)



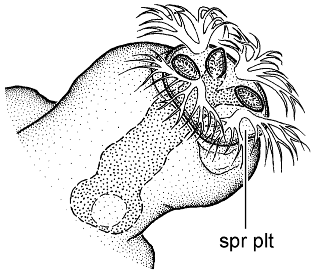
228 *Platystoma* (Platystomatidae)



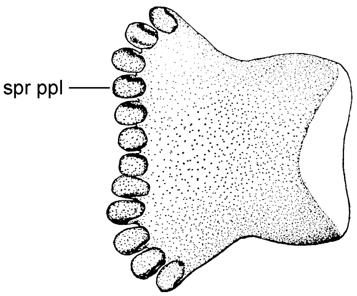
229 *Quametopia* (Anthomyzidae)



230 *Quametopia* (Anthomyzidae)



231 *Quametopia* (Anthomyzidae)



232 *Physiphora* (Ulidiidae)

Figs 13.225–232. Larval cephaloskeletons, prothoracic and posterior spiracles and terminal segments (all non-Afrotropical): (225) right posterior spiracle of *Asteia* sp., posterior view (Asteiidae); (226) same, cephaloskeleton, lateral view; (227) left posterior spiracle of *Neoalticomerus seamansi* Shewell, lateral view (Odiniidae); (228) right posterior spiracle (from puparium) of *Platystoma euphorbiinum* Enderlein, posterior view (Platystomatidae); (229) cephaloskeleton of *Quametopia terminalis* (Loew), lateral view (Anthomyzidae); (230) same, prothoracic spiracle, lateral view; (231) same, left posterior spiracle, lateral view; (232) prothoracic spiracle of *Physiphora alceae* (Preyssler), lateral view (Ulidiidae). Figs 225, 226 (after Papp 1998, figs 15, 16), Fig. 227 (after Shewell 1960, fig. 9), Fig. 228 (after Hennig 1945, fig. 3), Figs 229–231 (after Roháček & Barber 2011, figs 60, 62, 63), Fig. 232 (after Allen & Foote 1967, fig. 21, as *demandata*).

Abbreviations: ecdys sc – ecdysial scar; int scl – intermediate sclerite; mhk – mouthhook; spr op – spiracular opening; spr plt – spiracular plate; spr ppl – spiracular papilla; v corn – ventral cornu.

– Posterior spiracular opening elongate; cephaloskeleton well-sclerotised, usually darkly pigmented; habitats various 136

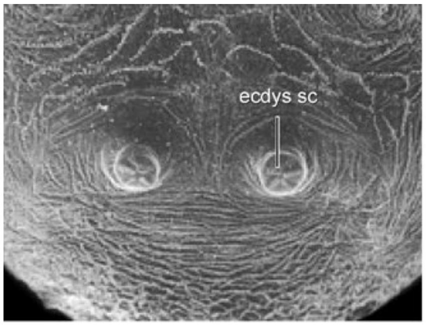
136\. Posterior spiracular openings curving over rounded spiracular prominences (Fig. 227); in tunnels of wood-boring insects. . . . . Odiniidae (Chapter 83)

– Posterior spiracular openings not obviously curving over edges of rounded spiracular prominences; habitats various 137

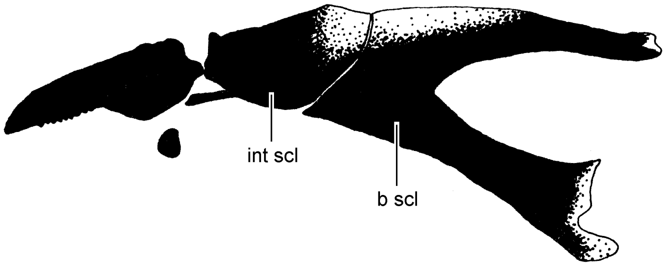
137\. Posterior spiracular plate with ecdysial scars positioned at *ca* 3 and 9 o'clock positions (Fig. 228); generally saprophagous . . . . Platystomatidae [in part] (Chapter 70)

– Posterior spiracular plate with ecdysial scars positioned at 2 and 10 o'clock postion or 1 and 11 o'clock position; habitats various 138

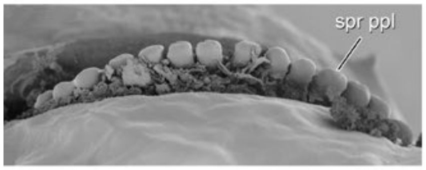
138\. Prothoracic spiracles each with 3–6 papillae (Fig. 230); posterior spiracles mounted on tubular prominence (Fig. 231); generally associated with various wetland plants . . . . . . Anthomyzidae (Chapter 87)



233 *Curtonotum* (Curtonotidae)

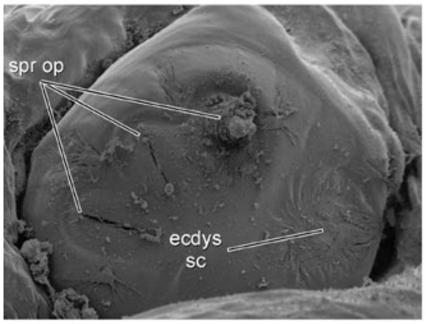


234 *Curtonotum* (Curtonotidae)

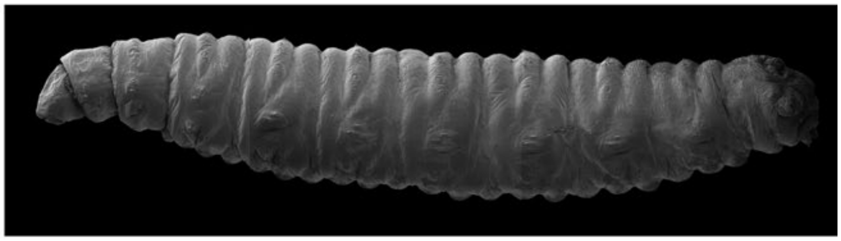


235 *Mormotomyia* (Mormotomyiidae)

237 *Mormotomyia* (Mormotomyiidae)



236 *Mormotomyia* (Mormotomyiidae)



238 *Mormotomyia* (Mormotomyiidae)

Figs 13.233–238. Prothoracic and posterior spiracles, cephaloskeleton and larval habitus: (233) posterior spiracles (puparium) of *Curtonotum helvum* (Loew), posterodorsal view (Curtonotidae) (non-Afrotropical); (234) cephaloskeleton of *C. simile* Tsacas, lateral view (Curtonotidae); (235) prothoracic spiracle of *Mormotomyia hirsuta* Austen, lateral view (Mormotomyiidae); (236) same, left posterior spiracle, posterior view; (237) same, habitus, dorsal view; (238) same, lateral view. Fig. 233 (Kirk-Spriggs 2008, fig. 28), Fig. 234 (Greathead 1958, fig. 1, as *cuthbertsoni*), Figs 235–238 (Kirk-Spriggs *et al*. 2011, figs 26, 24, 1, 2, respectively).

Abbreviations: b scl – basal sclerite; ecdys sc – ecdysial scar; int scl – intermediate sclerite; sp op – spiracular opening; spr ppl – spiracular papilla.

– Prothoracic spiracles each with more than 6 papillae (*e.g.*, Fig. 232); posterior spiracles sessile or on prominence; saprophagous, phytophagous or associated with carrion, spider egg sacs, *etc*. . . . . Chloropidae [in part] and Ulidiidae (Chapters 96 & 69)

139. Keilin's organs on prothoracic segment closely approximated (Fig. 221), those on meso- and metathoracic segments more widely separated; associated with dung, droppings and guano of birds and small mammals, often frequenting burrows, caves and rock overhangs. . . . Camillidae [in part] (Chapter 102)

– Keilin's organ equally spaced on each thoracic segment; habitats various 140

140. Cephaloskeleton of phytophagous form (cibarium without cibarial ridges), with stout, broad mouthhooks (Fig. 199), usually with long ventral teeth; phytophagous . . . . .Tephritidae [in part] (Chapter 71)

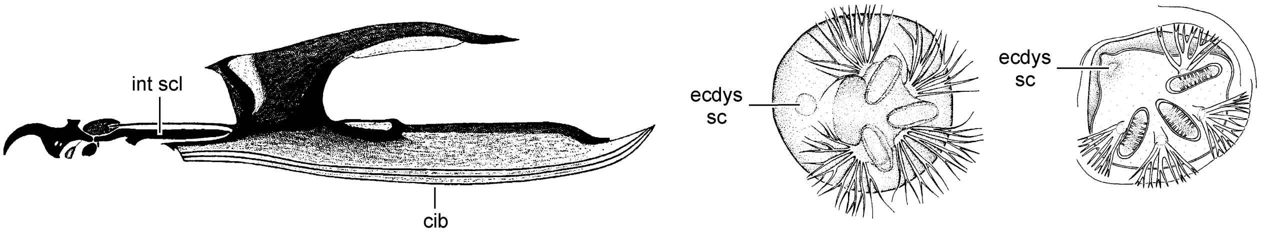
– Cephaloskeleton of saprophagous form (cibarium with cibarial ridges), with more slender mouthhooks (*e.g.*, Fig. 239); if mouthhooks stout and broad, then ventral teeth indistinct (*e.g.*, Fig. 234); habitats otherwise. 141

141. Posterior spiracular openings radiating from ecdysial scars positioned at 2 and 10 o'clock position (Fig. 233); cephaloskeleton robust, with intermediate sclerite broad and tightly fitted to basal sclerite (Fig. 234); *Curtonotum* Macquart scavengers, reared from decomposing Orthoptera egg pods. . . . . Curtonotidae (Chapter 103)

– Posterior spiracular openings arranged differently; cephaloskeleton slender, elongate; if robust, intermediate sclerite distinctly separated from basal sclerite; habitats various 142

142. Abdominal segments 1–7 subdivided into 3 dorsal and ventral secondary annulations or folds (Figs 237, 238); prothoracic spiracles broad with 18 papillae (Fig. 235); posterior spiracular plate with ecdysial scar off-set, such that spiracular openings not radiating from scar (Fig. 236); breed in accumulated bat guano . . . . Mormotomyiidae (Chapter 101)

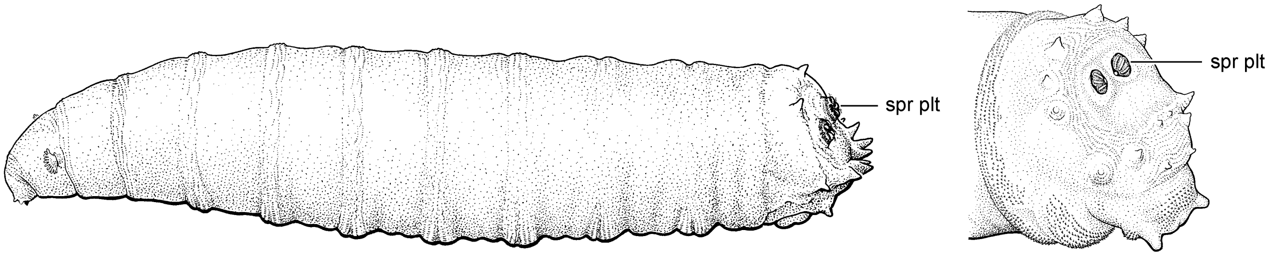
– Not with above combination of characters; if abdomen appearing annulated, then spiracular openings radiating from medially positioned ecdysial scar; habitats various 143



239 *Minettia* (Lauxaniidae)

240 *Minettia* (Lauxaniidae)

241 *Tapeigaster* (Heleomyzidae)



242 *Delia* (Anthomyiidae)

243 *Cynomya* (Calliphoridae)

Figs 13.239–243. Cephaloskeleton, posterior spiracles, larval habitus and terminal segment: (239) cephaloskeleton of *Minettia lyraformis* Shewell, lateral view (Lauxaniidae) (non-Afrotropical); (240) same, right, posterior spiracle, posterior view; (241) same, *Tapeigaster annulipes* Macquart (Heleomyzidae) (non-Afrotropical); (242) habitus of *Delia radicum* (L.), lateral view (Anthomyiidae) (non-Afrotropical); (243) terminal segments of *Cynomya cadaverina* Robineau-Desvoidy, posterolateral view (Calliphoridae) (non-Afrotropical). Figs 239, 240 (after Miller & Foote 1976, figs 56, 87), Fig. 241 (after McAlpine & Kent 1982, fig. 31), Figs 242, 243 (Teskey 1981*b*, figs 76, as *Hylemya brassicae*, 82, as *Cynomyopsis*).

Abbreviations: cib – cibarium; ecdys sc – ecdysial scar; int scl – intermediate sclerite; spr plt – spiracular plate.

143. Cephaloskeleton with intermediate sclerite narrow and elongate, longer than mouthhooks (Fig. 239); posterior spiracles situated on short prominences; posterior spiracular plate with ecdysial scar positioned medially (Fig. 240); saprophagous, occurring in leaf litter, rotting wood, bark, birds' nests, *etc*. . . . . Lauxaniidae (Chapter 74)

– Not with above combination of characters; habitats various 144

144. Posterior spiracular openings arranged with longitudinal axes aligned, such that 2 spiracular openings are virtually parallel to each other and the third nearly at right angle (Fig. 223); each posterior spiracle set on distinct prominence; terminal abdominal segment often with transverse ridge of 3–4 small tubercles on dorsum, near base of spiracular prominences (Fig. 224); in various rotting media and birds' nests . . . . .Milichiidae [in part] (Chapter 95)

– Not with above combination of characters; habitats various 145

145. Posterior spiracular openings positioned at widely divergent angles to each other, with ecdysial scars at 2 and 10 o'clock position; or ecdysial scars at 3 and 9 o'clock position and dorsal spiracular opening positioned at right angle to scar (Fig. 241); spiracles set on tubular lobes; body surface relatively smooth; in various rotting media and animal nests. . . . . Heleomyzidae [in part] (Chapter 98)

– Posterior spiracles not as above; if similar, then body with uneven tubercles or swellings; habitats various 146

146. Posterior spiracular plates usually set on at least slightly raised supporting structures (Fig. 242) (however, spiracular plate sessile in some species); phytophagous . . . . Anthomyiidae [in part] (Chapter 111)

– Posterior spiracular plates sessile (*e.g.*, Fig. 243); saprophagous, predators and scavengers . . . . .Calliphoridae [in part] and Rhiniidae (Chapters 114 & 115)

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Appendix. Glossary of morphological terms used in the text and on the figures.

abdominal spiracle (abd spr) (Figs 5–8): spiracle found on one of abdominal segments 1–8.

accessory oral sclerite (ac or scl) (Fig. 216): part of the mouthparts of larvae of Cyclorrhapha, comprising separate and variously shaped brown or black sclerites, located between and beneath the mouthhooks.

adanal plate: see **anal plates**.

amphipneustic (Fig. 77): respiratory system comprised of paired spiracles on prothorax and on abdominal segment 8.

anal pad (a pd) (perianal pads): located on either side of anus on terminal abdominal segment.

anal papillae (an ppl) (rectal papillae, rectal gills) (Fig. 20): fleshy projections from anus; some larvae with capability to withdraw these into hindgut.

anal plates: series of plates surrounding anus in some Psychodidae, including the **adanal plate** (ada plt), **lateroanal plate** (lat an plt) and **preanal plate** (prea plt).

anal sclerite (an scl): X- or Y-shaped sclerite, generally present anterodorsally to posterior proleg in Simuliidae.

annulus (ann) (Fig. 40): segment-like ring, pseudosegmentation or subdivision of thorax and/or abdomen.

antenna (ant) (Figs 3, 31, 32, 37, 89): generally tubular extension, with 0–6 divisions, in some reduced to pimple-like projection, with various sensilla.

anus (an) (Fig. 47): posterior opening of hindgut situated on terminal abdominal segment.

apneustic: respiratory system lacking external spiracles.

apodeme (apod) (Fig. 43): internal chitinous extension of exoskeleton, to which muscles are attached.

basal mandibular sclerite (b md scl): inverted U-shaped sclerite, bearing paired condyles and mandibular apodemes in lower Brachycera.

basal sclerite (b scl) (tentoropharyngeal sclerite, pharyngeal sclerite) (Figs 89, 95, 153–155, 157, 161, 163, 166, 167, 172, 174, 234): largest and most posterior component of cephaloskeleton in larvae of Cyclorrhapha.

cephalic bar (ceph b) (Fig. 3): posteriorly directed, rod-like projection from lateral margin of head (Cecidomyiidae).

cephaloskeleton (cephsk) (Figs 89, 95, 96, 99, 109, 111, 112, 153–155, 157, 161, 163, 166, 167, 172, 174, 199–201, 206, 216, 217, 226, 229, 234, 239): internal head skeleton typical of larvae of Cyclorrhapha, comprising mandibles at apex and U-shaped, basal sclerite at posterior end.

cervical sclerite (cerv scl): small dorsal sclerites on posterior margin of head capsule in larval Simuliidae.

cibarial pump: see **cibarium**.

cibarium (cib) (cibarial pump) (Fig. 174): filter pump enclosed by ventral cornu, operated by cibarial dilator muscles.

cirri (cir) (oral ridges; facial combs) (Fig. 89): roughened cuticular surfaces surrounding mouth opening in larvae of Cyclorrhapha.

cornu (d corn, v corn) (Figs 153–155): either one of dorsal or ventral posterior arm-like projections of basal sclerite in cephaloskeleton of larvae of Cyclorrhapha.

cranium (cr) (Figs 48, 54, 57, 67, 68, 73, 75, 76, 79): the sclerotised external cuticle of eucephalic head capsule.

creeping welts (cr wlt) (Figs 5, 6, 62, 83, 87): raised locomotory pads on borders of ventral surface of metathorax and most abdominal segments. Distinguished from rest of ventral surface by their surface sculpture, which often consists of transverse bands of papillae, setae or spicules.

crochets (crt) (Fig. 59): hook-like cuticular extensions at end of prolegs and creeping welts.

dental sclerite (den scl) (Figs 89, 166, 167, 174, 200, 201, 216): small, separate sclerite beneath base of mouthhooks in many Schizophora, where part of mandibular abductor apodeme is carried; fused into single dentate transverse bar (termed **ventral arch** (v arch) (Fig. 217)) in Sciomyzidae.

ecdysial scar (ecdys sc) (Figs 145, 146, 193, 194, 228, 233, 236, 240, 241): part of spiracular plate, often at centre, but also may be on rim, circular in outline shape, with numerous radiating lines (like spokes of wheel).

epipharyngeal bar (epiphar b): sclerite positioned between premandibles and posterior to median ends of tormae.

epipharyngeal complex (epiphar cplx): strongly chitinised structure ventral to anteroventral surface of labrum, often bearing food-gathering brushes or fans of setae and spicules.

eucephalic (Figs 12–16): larva with well-developed, fully exposed head capsule, typical of most nematocerous families.

felt chamber (f chbr): part of some spiracles, situated between spiracular plate and trachea.

frontoclypeal apotome (frclyp apot) (cephalic apotome): generally prominent mid dorsal sclerite of head capsule.

hemicephalic (Figs 47–51): larva with reduced, partially desclerotised and retracted head capsule, typical of larvae of most lower Brachycera (*e.g.*, Stratiomyidae and Tabanidae).

hemipneustic (Figs 5, 6): respiratory system comprised of paired spiracles on prothorax and abdominal segments 1–7 (absent on abdominal segment 8).

histoblast (imaginal bud, imaginal disc): group of cells formed as precursors of pupal/adult appendages during larval development.

holopneustic (Fig. 8): respiratory system comprised of paired spiracles on prothorax, metathorax and each of the eight abdominal segments.

hypostoma (hyps): anteriorly toothed, ventromedial area of head capsule, bordered laterally by genae; of controversial developmental origin (either maxillary or labial).

intermediate sclerite (int scl) (hypopharyngeal sclerite) (Figs 89, 95, 96, 161, 163, 167, 200, 206, 226, 234, 239): H-shaped (in dorsoventral view) sclerite of larvae of Cyclorrhapha that connects mandibles with basal sclerite. May be fused posteriorly with basal sclerite.

Keilin's organ (K org) (Figs 49, 52, 221): pair of ventrolateral (rarely dorsolateral) setae/sensilla on each thoracic segment.

labium (lab): part of mouthparts, lower lip.

labral brush (lbr br) (Figs 37, 38): group of spicules and elongate bristles (non-innervated) on ventral surface of labrum, used to direct food into oral cavity of some nematocerous Diptera.

labral fan (lbr fn) (Fig. 16): elongate rows of bristles on ventral surface of labrum of Simuliidae; homologous to labral brush in some other nematocerous Diptera.

labrum (lbr) (Figs 73, 74): part of mouthparts, the upper lip.

lateroanal plate: see **anal plates**.

mandible (md) (Figs 4, 54, 69, 75, 79): part of mouthparts (in nematocerous Diptera and lower Brachycera), a paired, food-gathering structure, consisting of 1–4 connected sclerites, often appearing at apex of head; of great structural diversity.

mandibular brush (md br) (Figs 65, 66): posteriorly directed sclerotised spines at base of abductor apodeme in larvae of Tabanomorpha.

mandibular prostheca (md prsth): separate lobe on mandible, bearing tuft of bristles.

maxilla (mx) (Figs 4, 73–76, 79): part of mouthparts, membranous or sclerotised arm-like structure, posterior to mandible, that may be partially fused with mandible in larvae of some Brachycera and is reduced in larvae of Cyclorrhapha.

maxillary palpus (mx plp) (Figs 27, 75, 76, 79, 89): 1-segmented, cylindrical protuberance on maxilla, bearing various sensilla.

mesothorax (msth): second thoracic segment.

metacephalic rod (mtceph rd) (Figs 50, 51, 75, 79, 82, 84, 85): slender, rod-like projection articulated to head and extending into prothorax of larvae of some lower Brachycera.

metapneustic (Fig. 20): respiratory system comprised of paired spiracles on abdominal segment 8.

metathorax (mtth): third thoracic segment.

mouthhook (mhk) (Figs 89, 95, 99, 109, 111, 112, 138, 139, 157, 161, 163, 166, 167, 172, 174, 199, 200, 203, 206, 216, 217, 226): the anteriormost part of the cephaloskeleton of larvae of Cyclorrhapha (as defined in Lambkin *et al*. (2013); their chararacter 37: cyclorrhaphan "monocondylous" mandible); presumably a composite structure derived from both mandibular and maxillary origins.

optic depression (op dp) (Fig. 89): dark background depression on basal sclerite of cephaloskeleton.

papillae (ppl): fleshy projections varying from small, domed structures, comprising surface sculpture of larval integument, to long tube-like structures, such as anal papillae.

parastomal bars (pastm b) (Fig. 200): part of cephaloskeleton of larvae of Cyclorrhapha; paired rod-like structures extending over intermediate sclerite and attached to basal sclerite.

pectin (pct) (Fig. 36): row of comb-like spicules on posterolateral area of respiratory siphon of Culicidae.

peripneustic (Fig. 7): respiratory system comprised of paired spiracles on prothorax and abdominal segments 1–8 (not present on metathorax).

peristigmatic tuft (pstig tft) (Figs 169, 177, 182): multibranched projections on spiracular plate.

pharyngeal filter (phryn flt): complex filtering modification of pharynx of larvae of some nematocerous Diptera.

posterior spiracles (p spr) (Figs 1, 7, 8, 12, 14, 20, 33, 34, 39, 44–46, 49, 52, 63, 77, 80, 86, 91, 92, 97, 98, 101–103, 108, 113–115, 121, 190, 215): paired respiratory organs on segment 8, usually larger than respiratory organs elsewhere on body, in some on extension (see **respiratory siphon** and **respiratory tube**).

postgenal cleft (pgn clft): weakly sclerotised cuticle at posteromedial margin of head capsule in Simuliidae.

preanal plate: see **anal plates**.

premandible (premd): sclerite articulating posteriorly with torma, present in some families.

prementum: component of labium beneath hypostoma and hypopharynx.

prepupa: somewhat pupa-shaped mature larva immediately prior to pupation.

procercus (prcerc) (Figs 13, 15): elongate lobe or tubercle on abdominal segment 8 or 9, bearing 1–20 short or elongate apical and 2 lateral setae in Thaumaleidae and most Chironomidae.

prognathous: head capsule position with mouthparts anteriorly directed.

proleg (prlg) (pseudopod) (Figs 13, 15–18, 20, 58, 59, 81, 88, 213): fleshy protuberance, single or paired, often retractile, cylindrical, locomotory structure, on ventral surface of some thoracic and/or abdominal segments; apex often with rows of black or brown spine-like crochets. Distinguished from creeping welt by indentation at apex to which muscles are attached.

propneustic: respiratory system comprised of paired spiracles on prothorax.

prothoracic spiracles (prth spr) (Figs 1, 5–8, 13, 77, 91, 98, 100, 118, 120–122, 181, 185, 187): paired respiratory openings, each bearing at apex varied number and arrangements of spiracular openings.

prothorax (prth): first thoracic segment.

pseudocephalon (psceph) (Fig. 89): outer membranous part of cyclorrhaphan larval head.

pubescence: vestiture of spicules.

respiratory siphon (resp siph) (Figs 10, 11, 30, 31, 34, 118): extension of tube-bearing spiracles of abdominal segment 8 in larvae of some nematocerous Diptera; encircled by sclerotised plate in some Psychodidae.

respiratory tube (resp tb) (Figs 120, 122, 184, 185): posterior extension of caudal segment in larvae of Cyclorrhapha with spiracles at apex.

spiracle (spr): external opening of tracheal system (see anterior/posterior spiracles).

spiracular opening (spr op) (stigmatal opening) (Figs 91, 94, 105, 106, 116, 123, 126, 127, 132–134, 137, 144–146, 149, 132, 164, 168, 169, 171, 173, 175, 178, 180, 182, 191–194, 197, 205, 208–210, 218, 219, 223, 225, 227, 228): individual opening(s) of prothoracic and posterior spiracles.

spiracular papilla (spr ppl) (Figs 158, 162, 186, 188, 195): cuticular projection of the anterior spiracle (rarely posterior) of Cyclorrhapha larvae, with apical spiracular opening; typical third-instar larvae with 5–20 papillae.

spiracular peritreme (spr perit) (Figs 191, 194, 197): margin of spiracular plate, generally pigmented.

spiracular plate/disc (spr plt, spr disc) (Figs 114, 116, 123, 124, 126, 128–134, 136, 156, 183, 231, 242, 243): sclerotised area surrounding apex each of anterior (prothoracic) and posterior (segment 8) spiracular opening(s), interspiracular setae, ecdysial scars and associated structures.

stemmata (stm) (eye spot) (Fig. 68): eye of nematocerous Diptera and orthorrhaphous Brachycera, consisting of lens or crystalline sphere, on surface of head capsule.

sternal spatula (st spt) (Fig. 2): spoon-shaped, sclerotised structure on ventromedial surface of prothorax of third-instar larvae (and occasionally of second-instars) of some Cecidomyiidae, usually consisting of internal shaft (often reduced) and anterior external blades and/or teeth of varied structure.

submentum (smt): part of mouthparts; plate-like organ at apex of labium.

suctorial disc (suc dc) (Fig. 9): modified cuticular extension on ventral surface of larvae of Blephariceridae and some Psychodidae, used to tightly appress larvae to aquatic substrates.

tentorial arm (tnt arm) (Figs 50, 82, 84): internal extensions of endoskeleton of head capsule.

torma (tm): sclerite situated between lateral angle formed at junction of labrum and clypeus; in some situated between lateral corners of labrum.

tubercle (tub) (Figs 97, 98): fleshy or sclerotised dome-shaped, to elongate tube-like structure, numbers often present on dorsal and lateral parts of thorax and abdomen.

ventral brush (v br) (Figs 32, 35, 36): series of long setae along midventral line of the anal segment in larvae of some Culicoidea.

TAXONOMIC INDEX TO VOLUME 1

Ashley H. Kirk-Spriggs

This index is restricted to the taxonomic names associated with Diptera that appear in Volume 1 of this *Manual*. Similar names of plants and animals other than Diptera are excluded. Bibliographical references are not indexed. Non-Afrotropical taxon names are also listed.

Taxonomic names are provided for all taxonomic ranks below order level (*i.e.*, series, subfamilies, superfamilies, tribes, genera, subgenera, species and subspecies). Other major divisions, such as lower Brachycera and orthorrhaphous Brachycera, are also indexed. Taxonomic names of ranks above genus level are provided in upper case *regular* font and genus, species and subspecies names in *italic* font. If a text citation, illustration and/or family key citation appear on the same page, the page number is repeated in the order in which they appear. Names in tables are treated as *regular* font. Authors' names are provided for genus, species and subspecies names and in such cases these names are followed by the names of the genera to which they are assigned. Subgeneric names are indexed in the same way as generic names and subspecific names in the same way as specific names. *Boldface* page numbers indicate where family names appear in the identification keys to families; italicised numbers indicate the location of illustrations of these taxa.

A complete index of taxonomic names of Diptera is included in Volume 4.

Ashley H. Kirk-Spriggs (Coordinator and Editor-in Chief) was born in Cambridgeshire in the United Kingdom and was educated at St. Ivo Comprehensive School, where he developed an interest in entomology under the tuition of Henry Berman (who established St. Ivo Entomology and Natural History Society). He obtained a Post-graduate Diploma in Applied Insect Taxonomy (with distinction, 1984) and Master of Philosophy degrees (1994) from University of Wales College of Cardiff and a PhD from Rhodes University, South Africa (2012). He participated in the Royal Entomological Society's Project Wallace Expedition to Sulawesi in 1985 and has travelled and collected widely in South-east Asia, Europe and throughout Africa. He was previously employed at the National Museum of Wales (Cardiff), the National Museum of Namibia (Windhoek) (with VSO) and the Albany Museum (South Africa) and is currently employed as Head of Entomology at the National Museum, Bloemfontein (South Africa). He was Editor of *Cimbebasia* (scientific in-house journal of the National Museum of Namibia) (1997–2003) and was Guest Editor for Gedenkschrift in honour of Brian Roy Struckenberg (*African Invertebrates* **53**). He has published over 100 scientific and popular articles and is a National Science Foundation (South Africa) B2 rated scientist.

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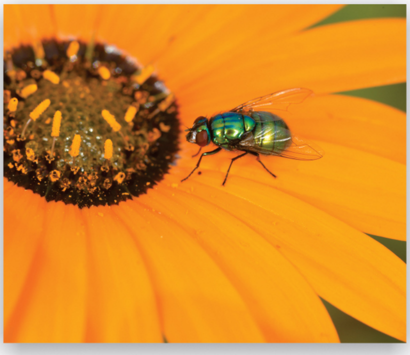

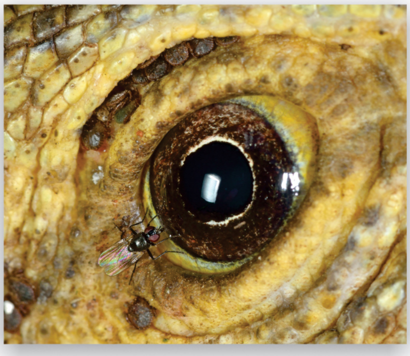

True flies, or **Diptera**, constitute one of the largest orders of insects in the biosphere, with over 160,000 described species worldwide, more than 20,000 of which occur in the Afrotropical Region. They are as diverse morphologically and biologically as they are numerous and many groups have evolved spectacular structural adaptations that are commensurate with their environment and biology. During their long evolutionary history, virtually every terrestrial niche has been occupied by the Diptera, making them one of the most successful groups of organisms on Earth. Many have co-evolved in association with other organisms and become highly specialised parasites or parasitoids of a range of disparate groups of plants and animals. Whether focusing on their systematics, biology, biogeography, conservation, or the more applied aspects, the Diptera remain a fascinating and intriguing group. This four volume book, a collaboration of **over 90 international experts** on Diptera, is the first-ever synopsis of the **108 families** of flies known from the Afrotropical Region and includes discussions on biology and immature stages, economic importance, classification, identification to the genus level, as well as a synopsis of each genus. This work provides the basics for understanding the diversity of a major order of insects in a large tropical and sub-tropical region and is the first such synopsis of its kind for any major insect order occurring in the Afrotropics.

Volume 1 includes 11 general **introductory chapters** dealing with the history of Afrotropical dipterology, collection and preservation, morphology and terminology, natural history, agricultural and veterinary, medical, forensic and phytosanitary significance, biogeography, conservation and the phylogeny of flies. The volume also includes **identification keys** to all Afrotropical fly families for both adult and larval stages. The text is richly illustrated with over **1,600 illustrations**, including **40 colour maps**, **800 colour** and **60 black and white images** and **690 line drawings** of flies.

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