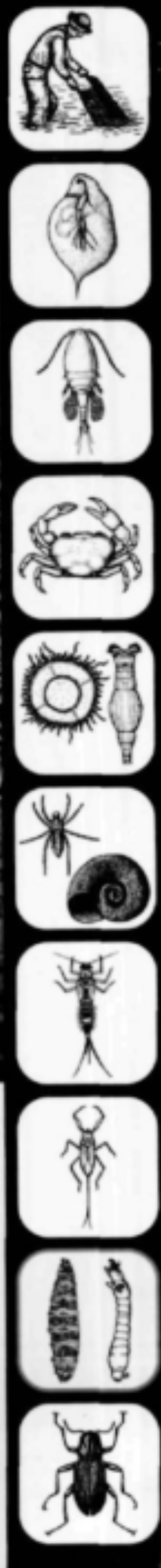
Guides to the

Freshwater Invertebrates of Southern Africa



Volume 9: Diptera

Editors: JA Day, AD Harrison & IJ de Moor

TT 201/02

Water Research Commission

Guides to the

Freshwater Invertebrates of Southern Africa

Volume 9: Diptera

Editors: JA Day, AD Harrison & IJ de Moor

Prepared for the Water Research Commission

September 2002

WRC Report No. TT 201/02

February 2003

Obtainable from:

Water Research Commission
Private Bag X03
GEZINA
0031

The publication of this guide emanates from a project entitled: *The Invertebrates of South Africa – Identification keys*
(WRC Project No. 916)

DISCLAIMER

This book has been reviewed by the Water Research Commission (WRC) and approved for publication. Approval does not signify that the contents necessarily reflect the views and policies of the WRC, nor does mention of trade names or commercial products constitute endorsement or recommendation for use.

ISBN 1 86845 900 4

Printed in the Republic of South Africa

Cover photograph: Soetendalsvlei by JA Day

Since there is a possibility that revised editions of this series of guides may be printed in the future, we welcome constructive suggestions, particularly in relation to keys used to identify various taxa. These suggestions should be submitted in writing to the Executive Director, Water Research Commission (address given above). All such correspondence must be marked 'For the attention of Project K5/916/0/1'.

CONTENTS

PREFACE

This identification guide is one of a series of ten books that include keys to most of the fresh- and brackish-water invertebrates of southern Africa. The paucity of identification guides suitable for non-specialists has become a yawning gap in the tools available to scientists, managers and scholars concerned with the assessment and management of water resources. It is hoped that the present guides will be of value to these and other users, and that the environment will benefit as a result. The principle aim of this series is to synthesize much of the existing knowledge on the identification of freshwater invertebrates into a standard format that is accessible to users who wish to identify taxa beyond their field of expertise.

It is a truism that identification guides are perpetually out of date, particularly in terms of nomenclature, due to advances in systematics. To keep abreast with some of the changes in nomenclature, readers are referred to the *Checklist of Aquatic Insects and Mites* (http://www.ru.ac.za/aquatalogue). There is also a possibility that the present series will be revised periodically, but this is contingent on future funding.

Identification of taxa to species level is the ideal to which we would like to strive, but for a number of reasons this is not always possible: the present knowledge of taxa does not often permit such detailed identification, and in instances where taxa are well-known, identification to such a fine resolution is usually constrained by space considerations and cost effectiveness. In some instances, particularly for small, relatively well-researched groups such as the freshwater molluscs, taxa have been identified to species level. Since new species are constantly being discovered, users of these guides are cautioned against attempting to 'make' unusual specimens 'fit' existing keys to species level. Users are encouraged to inform experts of such specimens, to take note of new distribution records, and to lodge all collections with well-known museums, particularly those that are depositories for collections of freshwater invertebrates (e.g. the Albany Museum, the South African Museum and the Transvaal Museum).

This series includes an initial introductory volume containing general information and a key to the families of invertebrates. Subsequent volumes contain keys to different invertebrate groups, most often logically clustered together but in some instances the need for cost-effectiveness has resulted in the creation of some rather uncomfortable 'bedfellows', such as the arachnids and molluscs that are combined in Volume 6.

It should be noted that references have been limited to key publications that will assist the reader in finding valuable sources of information. They are, therefore, referred to as 'Useful References' and may include some publications not cited in the text.

The books in the series are the culmination of years of effort by a large number of people and organizations: Shirley Bethune, Jenny Day, Barbara Stewart, Nancy Rayner and Maitland Seaman started the project in 1986; Jenny Day, Bryan Davies and Jackie King initiated contact with authors and began the editing process, and Barbara Stewart and Elizabeth Louw later became involved in editing the Crustacea chapters. A decade later, Chris Dickens successfully obtained funding from the Water Research Commission (WRC) for the completion of the project, and later took on the job of Project Leader; Steve Mitchell managed the project from the WRC; Jenny Day took on the role of senior scientific editor, and Irene de Moor was contracted as managing editor from 1998. All of those above (with the exception of Nancy Rayner and Elizabeth Louw) as well as Mark Chutter, Ferdy de Moor, Lil Haigh, Arthur Harrison, Rob Hart, and Martin Villet, are part of the Editorial Board that was initially formed in 1998.

Numerous authors, including those in this book, have contributed time and expertise towards the drafting of the keys. The authors have not been paid for their efforts, which were given in the true spirit of science and a love of their work. It is with regret that we have to note that two of the authors, Botha de Meillon and Willis Wirth, passed away some time before the publication of this volume.

A small donation from the Zoological Society of South Africa helped to initiate this project, but the series is largely a product of the Southern African Society of Aquatic Scientists (SASAQS), whose members are acknowledged for their support.

Umgeni Water, the Albany Museum, the Freshwater Research Unit (University of Cape Town), the South African Museum and the WRC have given organizational support at various stages of the publication.

Chris Dickens, Steve Mitchell & Irene de Moor

ACKNOWLEDGEMENTS

The publication of this series of guides would not have been possible without the enormous effort and dedication of a number of people and organizations who have been mentioned in the Preface.

The following people and organizations are also acknowledged for their assistance in the production of this book: Nikki Köhly, Belinda Day and Carryn Manicom for their excellent drawings; Bronwyn Tweedie, Debbie Brody and John Keulder of the Graphics Services Unit, Rhodes University, for drawing the maps and producing bromides; Ian Surridge and Warren de Moor for assisting with indexing, and Drinie van Rensburg of the WRC for her advice on printing and text layout.

Further acknowledgements pertaining to particular chapters in this volume are given at the end of the chapters concerned.

GEOGRAPHICAL REGION COVERED BY THIS GUIDE

This series of invertebrate guides covers the southern African region, defined as 'south of (and including) the Cunene Catchment in the west and the Zambezi Catchment in the east' (Fig. 1). Distribution records from further afield are, however, sometimes included for various reasons, particularly in cases where keys to particular groups have historically been composed to cover a wider region in Africa. The greatest collection effort has, however, focussed on catchments south of the Limpopo River, so the emphasis has fallen naturally on this region.

Collection efforts relating to most groups of freshwater invertebrates fall far short of adequate coverage. Consequently, locality records of many taxa are patchy and cannot be regarded as a good reflection of actual

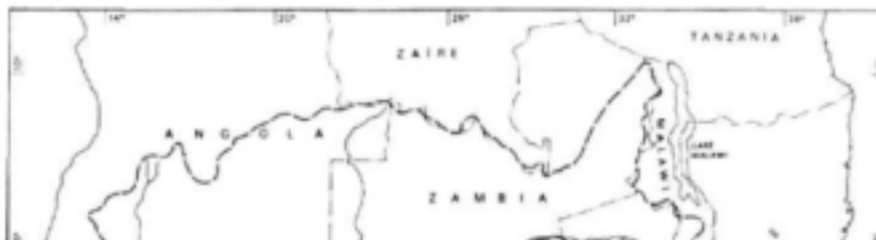


Fig. 1. Southern Africa: the region covered by this series of invertebrate guides.
KEY: The dark dashed line represents the northern boundary of the Cunene Catchment in the west and the Zambezi Catchment in the east.

distributions. For this reason the term 'records' has been used in preference to 'distribution'.

It is hoped that this series of guides will stimulate a greater collection effort, which will in turn lead to the upgrading of geographical information on the diversity of freshwater invertebrates in southern Africa. In order to avoid meaningless references to place-names such as the ubiquitous 'Rietfontein', all records are related to countries, provinces or acceptable regional names. To avoid the confusion that often arises in association with regional names, a 'Glossary of place-names' has been compiled (see page 189), and a map of the new provincial boundaries in South Africa is given below (Fig. 2).

Fig. 2. The new provincial boundaries of the Republic of South Africa

ABOUT THE AUTHORS AND EDITORS

Maureen Coetzee is head of the Department of Medical Entomology at the National Health Laboratory Service in Johannesburg.

Jenny Day is Director of the Freshwater Research Unit and Head of the Zoology Department, University of Cape Town, Western Cape.

Botha de Meillon (1902–2000) worked for many years on the taxonomy of biting flies at the South African Institute for Medical Research in Johannesburg.

Ferdy de Moor is the Head of the Department of Freshwater Invertebrates at the Albany Museum, Grahamstown, Eastern Cape.

Irene de Moor is a freelance scientific editor, currently working at the Albany Museum, Grahamstown, Eastern Cape.

Arthur Harrison was Professor of Zoology at the University of Waterloo in Ontario, Canada. Since he retired in 1986 and returned to his birth place, Cape Town, he has continued to work on chironomid taxonomy.

André Prins, now retired to Velddrif on the west coast of South Africa, was a dipteran systematist at the South African Museum in Cape Town.

Willis Wirth (1914–1994) was based in the Smithsonian Institution in Washington, D.C., and employed in the Systematic Entomology Laboratory of the US Department of Agriculture.

CHAPTER 1

INTRODUCTION

by

A.D. Harrison, A. Prins & J.A. Day

Members of the Order Diptera include insects such as mosquitoes, gnats and midges, as well as houseflies, craneflies and a host of less familiar forms. Most adult insects have two pairs of wings but, as the name 'Diptera' (Gr *dis*, two, *pteron*, wing) indicates, adult flies have but a single pair of membranous fore-wings, the hind wings being modified into knob-like structures known as halteres or balancers. Adult flies range in size from minute delicate midges hardly more than a millimeter in length to robust 'robber flies' of more than 70 mm in length. There are said to be more than 85 000 species of dipterans, which are abundant throughout the world from the tropics to the Arctic and from the seashore to high mountains — indeed, anywhere that their larvae can live and find food. Distribution ranges of some species are very narrow, while others are virtually cosmopolitan.

Adult dipterans are always terrestrial but the immature stages of many species are aquatic and grub-like, bearing no legs or other obvious identifying features. While some of the families with aquatic larvae have been thoroughly studied in southern Africa, many others are virtually unknown. As one might imagine, it is those families that pose a danger or nuisance to humankind that have been most extensively studied. Thus more-or-less complete species lists are available only for the Culicidae (mosquitoes), the Simuliidae (blackflies) and the Ceratopogonidae (no-see-ums), all of which contain blood-sucking pests, and for the houseflies and their allies. The only other groups that are reasonably well known are the Chironomidae (a family of midges), which are the commonest and most species-rich of all the families with aquatic larvae, the Blephariceridae (net-winged midges, found in mountainous regions), the Psychodidae (moth flies and sewage flies, usually associated with eutrophic waters), and the Ephydridae (shore flies and brine flies, usually found in brackish or saline waters).

Dipterans are traditionally divided into two suborders, mostly on adult characters. Immature stages of the two groups are distinctive, though. Details are given on page 8; for the moment, it is worth noting that in the Suborder Nematocera, the larval head and body segments are clearly distinguishable, whereas larval Brachycera are maggot-like. The families of Diptera with aquatic larvae that are dealt with in this book are as follows.

Suborder **Nematocera**

Tanyderidae	tipulid-like flies
Tipulidae	crane flies
Blephariceridae	net-winged midges
Psychodidae	moth flies, sand flies and sewage flies
Ptychopteridae	phantom crane flies
Dixidae	meniscus midges
Chaoboridae	phantom midges
Corethrellidae	(no common name)
Culicidae	mosquitoes
Thaumaleidae	solitary midges
Simuliidae	black flies
Ceratopogonidae (= Heleidae)	no-see-ums, biting midges
Chironomidae	non-biting midges

Suborder **Brachycera**

Tabanidae	horse flies
Athericidae	(no common name)
Stratiomyidae	soldier flies
Empididae	dance flies
Dolichopodidae	long-legged flies
Syrphidae	hover flies, drone flies (larvae are known as rat-tailed maggots)
Sciomyzidae	marsh flies
Ephydridae	brine flies, shore flies
Muscidae	house flies

The treatment of the different families varies widely in this book. In some cases, specialists have written relatively long sections on the families on which they are experts. In other cases, however, so little is known about the families that what appears here is no more than a brief and general introduction to the groups, relying mostly on information gleaned from other parts of the world. When the present work was first conceived more than ten years ago, Dr Andre Prins, who had recently retired from the Entomology Dept of the South African Museum, agreed to collate the section on dipterans, as well as to write short accounts of the poorer-known groups. He wrote every word of his manuscript by hand. Since then both Dr de Meillon and Dr Wirth have passed away, and Dr Prins has retired to Velddrift, Western Cape.

AQUATIC DIPTERA

Like many other insects, immature dipterans differ from the adults in structure, habits and habitat requirements. Larvae of some families live on land; in other families, at least some species live in water or other liquids. Generally, the requirements are similar for all the members of a particular family, though. Larvae of all members of the blackfly family (family Simuliidae) live in fast-flowing fresh waters, for instance, while those of the brine flies (family Ephydridae) are found in chemically harsh environments such as salt lakes or pools of brine; one remarkable Californian ephydrid, *Halaeomyia petrolei*, is confined to pools of crude petroleum. As a rule, of the 24 families with at least some aquatic larvae, those of the Blephariceridae, Chaoboridae, Corethrellidae, Thaumaleidae, Dixidae, Culicidae, Ptychopteridae, Tanyderidae, Simuliidae, Athericidae and Sciomyzidae always occur in water. In other families, however, only some species have aquatic larvae while others live in damp soil or, in the Psychodidae for instance, even in cow pats or other organically-rich habitats.

Because they are very adaptable, some larvae that are not normally aquatic are able to survive and breed in a variety of liquids, even if—sometimes particularly if—they are polluted with organic matter. Larvae of the Fanniidae (lesser houseflies and latrine flies), for instance, possess fleshy tubercles or protuberances that increase the surface areas of their bodies and allow them to float. The hind spiracles of the larvae of some dipterans may be withdrawn into the body or may even be closed by muscular contraction, preventing the larvae from drowning. The larvae of the Indian bazaar fly (*Chrysomya megacephala*, family Calliphoridae) are known to survive, together with the aquatic larvae of some psychodids, even in sewage tanks and cesspits, while larvae of the Piophilidae (cheese skippers) may inhabit the remains of carcasses when these occur in shallow waters. In this volume, though, we do not treat these normally-terrestrial families.

Not all dipteran larvae have unsalubrious habits. Many are found in rivers, from intermittent mountain streams to the large rivers of the plains, or in standing waters from temporary rock pools to the great lakes of the world; some are even found intertidally.

Habits

We tend to think of dipterans (flies, mosquitoes, etc.) mostly as pests. Indeed, particularly in tropical and subtropical regions, some mosquitoes are vectors of pathogenic organisms such as viruses and malarial parasites, while in West Africa blackflies (Simuliidae) carry the nematodes (filarial worms) that cause river blindness. Of the families with aquatic or semi-aquatic representatives in southern Africa, the Ceratopogonidae, Culicidae, Simuliidae and Tabanidae are of medical and veterinary importance because adult females are vectors of pathogenic organisms or they transmit parasitic diseases to humans and domestic animals. Some biting forms are serious irritants to humans and domestic animals while others, such as chironomid midges, may be a serious nuisance when vast numbers emerge from lakes, entering houses and even causing asthma as hairs, detached from their wings, fill the air.

On the other hand, even larvae of those species that carry pathogens in their adult stages may, as larvae, play important parts roles in the functioning of freshwater ecosystems. Many dipterous larvae feed on algae or other plant matter and so transfer energy through the food chain; others feed on dead organic matter, while others are predators.

Living in fast-flowing streams presents a problem that is solved by various dipteran larvae in a number of ways. A simuliid larva, for instance, will attach a mat of silken strands to the substratum and then attach itself to the silk by a ring of small hooks on the last segment; it will also use strands of silk as lifelines. Blephariccrid larvae, on the other hand, have several ventral suckers. They move by sidling sideways, very slowly and carefully, releasing three of the suckers each time and attaching them again before releasing the others. Some grub-like dipteran larvae move along the bottom by means of prolegs (false legs), or swim by means of clumps of spinules or specialized hair-like setae. In this way chaoborid (phantom midge) larvae, for instance, swim in the open waters of lakes.

All dipterans with aquatic immature stages have adaptations that allow the adult to emerge without drowning, but this is a particular problem for insects living in fast-flowing waters. When an adult simuliid escapes from its pupal case, for instance, it carries a bubble of air for support until it reaches a quiet place, whereas eclosing blephariccrids rely on their long legs for support while escaping from the pupal case.

Feeding

The adult females of many species need a meal rich in protein before they can lay their eggs but few of them are carnivorous. Instead, many flies are ectoparasitic, adults feeding on the blood of their hosts, or the larvae are saprophagous or coprophagous, living in protein-rich decaying organic matter, including carcasses and animal dung. Larvae are not only concealed and protected from the elements and from their natural enemies in such habitats, but they also act as decomposers of dead organic material, enriching their surroundings with nutrients. Adults of such dipterans are strictly terrestrial but the Syrphidae, Stratiomyidae, Psychodidae, Tipulidae, Ceratopogonidae, Tabanidae and Empididae all contain some species with aquatic larvae.

Most aquatic nematoceran larvae feed on organic matter, scraping it off the substratum or consuming the mud through which they burrow. Some, such as the blackflies, collect food by filtering it out of the water column, while some chironomids pump water through tubes they have constructed and trap particles on mucous secretions. Chaoboridae and Corethellidae, and some Culicidae, Chironomidae and Ceratopogonidae, are predatory. Aquatic brachyceran larvae are usually collectors of organic matter but some are predators: sciomyzids, for instance, feed on aquatic snails and *Limnophora* (Muscidae) is predatory on other aquatic insect larvae and also on oligochaetes.

Reproduction and life cycles

Diptera are generally dioecious (having separate sexes), although young are produced parthenogenetically in some Psychodidae and Chironomidae. In the Nematocera, which include most of those species with aquatic larvae, eggs (rather than live larvae) are usually produced. The incubation period varies from a few hours to a few days, depending on the species and on whether or not the eggs are enclosed in a protective cover, as well as on climatic factors such as temperature. In a few cases, the incubation period may be as long as a few months.

The larvae that hatch from the eggs are very different from the adults. They have no jointed legs; mouthparts may be complex and fairly typically insectan, or they may be greatly reduced and modified. The larva metamorphoses into a further immature stage, the pupa, which is very different in appearance from the adult and often also from the larva. Pupae may be entirely inactive or may be able to swim, but they do not feed.

Respiration

In aquatic larvae, respiration is effected in one of two ways: by direct intake of atmospheric oxygen through the spiracles, or by diffusion of dissolved oxygen into the body. In the first case air is breathed directly and at least one pair of normal insect spiracles is retained. Larvae of some groups live in aqueous media such as stagnant pools foul with rotting vegetation, or cesspits, in which there is a deficiency of oxygen. The larvae (rat-tailed maggots) of the Syrphidae (hover flies), for instance, have long, telescopic breathing tubes with spiracular openings at their tips that can 'pierce' the meniscus or surface of the water. In the Sciomyzidae (marsh flies), swallowed air in the gut enables the larvae to float or swim just under the surface, while processes between the spiracles prevent them from getting wet. Certain tabanid (horsefly) larvae live in mud, building mud cylinders that protect them from the elements when the water evaporates and the mud starts to dry out.

In the second type of respiration, which is found in larvae that are more completely adapted to life in water, respiration takes place by diffusion through the integument, often expanded in places to form gills, and no functional spiracles are present. The larvae of some species of *Chironomus* live in bottom muds that are poor in oxygen. They are known as 'blood worms' because they are bright red, due to the presence of haemoglobin in their body fluids that enables them to respire at low oxygen concentrations. (They also have what appear to be finger-like 'gills' at the posterior ends of their bodies but these tubercles are actually involved in osmoregulation.)

Distribution

Distribution records are based on collections made by individual scientists and housed in museums and other institutions. One should always bear in mind, therefore, that the apparent absence of a particular species from a particular area may be due not to its physical absence but to a lack of appropriate collections, or even to misidentification of specimens.

Southern Africa, as part of the sub-Saharan region, has its own zoogeographical fauna and South Africa, in particular, has a rich fly fauna. Introduction of foreign species also invariably occurs from time to time. A sufficiently large number of Palaearctic species has been recorded from the southern Cape Province to suggest that some elements of the fauna of Africa north of the Sahara may have had their origins in the southern parts of the continent. On the other hand, a number of different flies, particularly of the families Chironomidae, Ephydridae, Ceratopogonidae and Psychodidae, as well as of the Syrphidae and others, have been caught at high altitudes. It is thus possible that dispersal by wind may play a far greater role in intercontinental distribution of flies than is generally realized, and that the physical drifting of the continents may not have been entirely responsible for the present-day distribution patterns.

Most genera with aquatic larvae are probably represented in southern Africa, although we cannot be certain, since some families have been so poorly studied. Most of the families of aquatic dipterans that do occur in sub-Saharan Africa co-occur in all the major regions of the world, and many of the genera have worldwide distributions. The picture is different at species level, though; a few species are common to Africa and Eurasia, but most species found in sub-Saharan Africa are endemic.

Many species are limited to a single climatic zone, such as the tropics, but some are very widespread. Interestingly, some south-temperate forms may be found along the high peaks of the Afromontane mountain chain that runs from South Africa to Ethiopia—a distribution pattern by no means confined to invertebrates. Some groups, such as the chironomid sub-family Aphroteniinae, show a Gondwanan distribution, being found in South America, South Africa and Australia but nowhere in the northern hemisphere. The Ptychopteridae, whose larvae occur in saturated mud at the margin of streams, are absent from South America and the Australasian region, but are found (rarely) in South Africa. On the other hand, the Australasian region has the world's richest tanyderid fauna while the family is very poorly represented in sub-Saharan Africa. The Empididae are particularly well represented in southern Africa, with about 29 genera (*Empis* being the largest) and more than 200 species. The Blephariceridae are also widespread, but they are confined to montane areas where the rainfall is reliable; only about 20 species are known from southern Africa. The Thaumaleidae are even more limited in distribution, larvae being found in thin films of water on rocks in cool mountain streams and only two species being known from the region.

MORPHOLOGICAL CHARACTERISTICS OF IMMATURE DIPTERA

Adult dipterans, like all arthropods, have a hard, sclerotized, jointed exoskeleton and a segmented body. Like other insects, they have wings although, unlike most other insects, there is but a single pair. In both adults and larvae the body is divided into three regions or tagmata. The head bears a pair of sensory **antennae**, a pair of chewing or biting **mandibles**, a median **labrum**, a pair of **maxillae** and a pair of fused second maxillae called the **labium**. Each of these may be highly modified. In adults, but not in larvae, each of the three segments (more correctly 'somites') of the **thorax** bears a pair of jointed legs. The abdomen consists embryologically of 11 segments, although only 9 or 10 are usually visible. Diptera adults and larvae are also characterized by the absence of jointed appendages on the abdomen.

In this volume we divide the Order Diptera into two suborders, the Nematocera and the Brachycera, named because of the structure of the antennae in the adults of each group. Features that distinguish immatures of the two groups are discussed below.

The reader is warned that morphological terminology tends to vary from one family to the next. For instance, the word 'seta' normally refers to any bristle-like structure, but in chironomids the word has a far more specific meaning; the structures through which many pupae breathe are variously known as breathing horns, respiratory horns and trumpets; anal lobes are also known as anal paddles or anal fins. In the section that follows, and in the keys to families, we have tried to use all of the different terms as appropriate.

Larval morphology

Features of the head and mouthparts are important for distinguishing the larvae of the Nematocera (Figs 1.1F–1.3D) and the Brachycera (Figs 1.3E–1.4). The **antennae** (e.g. Figs 1.2A–C), which are rarely prominent in larval dipterans except in the predatory members of the Nematocera, consist of one to six segments. In many Brachycera they are reduced to small papillae or are virtually absent. Nematoceran larvae have a distinct, sclerotized **head capsule** (Figs 1.1A, C), which is large and obvious and, except in the Tipulidae (Fig. 1.1G), not retractable into the first thoracic segment. The antennae and mouthparts are well-developed and the mandibles bite horizontally towards each other (Fig. 1.1A). In filter-feeding families such as the simuliids (Fig. 1.3A) and culicids (Fig. 1.2A), the labrum may bear **labral fans** or **mouth brushes**.

In some brachyceran families (e.g. Fig. 1.3E) a sclerotized portion of the head capsule is present, and is usually partially exposed externally, while mouthparts such as the labrum, mandibles or maxillae are recognizable, although sometimes reduced, and the mandibles, which are hook- or sickle-shaped, move parallel one to another in the vertical plane (e.g. Fig. 1.1B). In others, the Muscomorpha (Figs 1.4C–H), the larvae are true maggots entirely lacking external evidence of a sclerotized head capsule. The normal mouthparts are absent or difficult to define, being replaced by characteristically-shaped **mouth hooks** (Figs 1.1D, 1.4F). The mouth hooks are the anterior, external tips of the **cephalo-pharyngeal skeleton**, which is a series of sclerotized bars hidden completely within the thorax, and which may be fairly solid or may be reduced to a series of narrow bars. Some authorities suggest that the mouth-hooks are modified mandibles, while others suggest that they are not derived from the mouthparts at all but from the outer covering of the larval body (i.e. they are cuticular outgrowths). In any event, they are not renewed after the last moult.

Behind the head the body consists of three thoracic and eleven abdominal segments. Three **thoracic** segments are normally distinguishable but in some families are characteristically fused to form a large, bulging, apparently single segment (e.g. Figs 1.2A–C). The **abdomen** consists of nine or ten visible segments, some of which may be adorned with setae or spines of various kinds. While dipteran larvae have no true jointed arthropod-like legs, they may be provided with soft, unjointed **prolegs** or parapods, which may be median (e.g. Fig. 1.3A) or paired, may occur on any (or many) of the body segments (e.g. Figs 1.3G, 1.4B) and may be furnished with claws or hooks, which are used for crawling and for clinging. In some families some of the abdominal segments are furnished with a circlet of prolegs (e.g. Fig. 1.3F), or a series of ventral **creeping welts** (Fig. 1.4A), which are also used in locomotion. A few forms have a series of mid-ventral suckers on the thoracic and/or abdominal segments. The last segment may variously be provided with lobes or tubercles, some of which are usually associated with the posterior spiracles (see below), some of which may be gills, and some of which are probably osmoregulatory in function. The thoracic and abdominal segments consist of a dorsal **tergum**, a ventral **sternum**, and lateral **pleura**. By convention, the abdominal segments are labeled with Roman numerals (i.e. I to XI).

Respiratory structures are often diagnostic for dipterous larvae. The number of openings to the respiratory tracheal system (known as **spiracles**) in 'primitive' Diptera was 10, but in most extant taxa the larvae show a considerable reduction in the number of functional spiracles. A pair of **anterior spiracles** is usually found on the prothorax, and pairs are often found on the abdominal segments too. In most Nematocera the last pair—the **posterior abdominal spiracles**—is present. These spiracles may be situated in a pit, or slit (Fig. 1.3F2) or on fleshy protuberances on the last abdominal segment. On the truncate terminal segment many tipulids have a **spiracular disc** that is usually surrounded by fleshy lobes, is often strengthened on its inner surface with black, sclerotized plates, and may be fringed with hairs (Figs 1.1E, H). The Dixidae have a pair of spiracles which is surrounded with hairs and situated dorsally on the eighth abdominal segment (Fig. 1.2D). In some other families the spiracles are borne on a posterior **respiratory siphon** that may be short (as in the psychodids: Fig. 1.3D) or long—as in mosquitoes (Fig. 1.2A). Spiracles are absent from the larvae of some families, for example the Blephariceridae, some Chaoboridae, the Simuliidae, the Ceratopogonidae and most Chironomidae.

Aquatic brachyceran larvae also show a reduction in the number of spiracles. Some have two pairs, anterior and posterior. The anterior spiracles may be found on fleshy lobes—sometimes with a fan-like tip—on each side of the prothorax (e.g. Fig. 1.4G), and the posterior abdominal spiracles are found on the posterior surface of the last body segment. These may be located in slits or on fleshy lobes (Fig. 1.4A), or borne on a respiratory siphon that may be short (as in the Ephydridae: Fig. 1.4G) or very long—as in rat-tailed maggots (Syrphidae: Fig. 1.4C). Spiracles are absent from the larvae of some brachycerid families, for example, the Atheridae (Fig. 1.3G) and some Empididae, but in all these taxa the tracheal systems are well developed.

MORPHOLOGICAL CHARACTERISTICS OF DIPTERAN PUPAE

In most aquatic members of the Nematocera, and some Brachycera, the larval skin is cast during pupation and the pupa looks quite different from the larva. (The Stratiomyidae—Fig. 1.5B—are exceptions: in this family the pupal skin remains behind and usually encloses the pupa). The pupae, which are green, brown or tan in colour, are recognized by the developing wings and appendages, which can be seen through the pupal exoskeleton. Some, including those of the Simuliidae, spin a **cocoon** (e.g. Fig. 1.5F), in which the pupa is formed and which is sometimes strengthened by tiny grains of sand. The head and thorax are fused to form a **cephalothorax** (Figs 1.6D1, E1), while the abdomen is free and sometimes bears terminal paddles (Figs 1.6D2, E2) used in swimming. In the some brachyderan families, however, the last larval skin is hardened or sclerotized to form a pupal shell or **puparium** (e.g. Figs 1.5C–E) in which the pupa remains throughout the process of metamorphosis. The puparium has much the same shape as the last larval instar and so pupae of this group can be identified by reference to the larval key.

Pupae of flies such as the Dolichopodidae, Dixidae and Culicidae have a pair of anterior spiracles forming **breathing horns**, **respiratory horns** or **trumpets** (e.g. Figs 1.6B, E1). The pupae of mosquitoes (Fig. 1.6D), which are air-breathing, are lighter than water so that when they rise to the surface, the respiratory horns automatically protrude into the air. In others, such as the Simuliidae (Fig. 1.5F) and most of the Chironomidae (e.g. Fig. 1.5G), the horns are closed and form physical gills. In orthoclad chironomids these are very small (e.g. Fig. 1.5G) or even absent but, since they live in fast-flowing water, respiration can take place through the whole integument of the body. In the Brachycera a single pair of spiracles is located on the hind part of the body, frequently on protuberances. The pupae of ptychopterids, whose larvae have long posterior siphons, are also provided with long respiratory horns on the thorax.

Unlike those of most dipterans, the pupae of the Culicidae, Dixidae, Chaoboridae and some tanypod chironomids are active, and bear a pair of flattened anal lobes, variously known as **paddles** or **fins** (e.g. Figs 1.6D2, E2), at the hind end of the body that assist in swimming. Most other pupae are motionless or move only when the adult is about to emerge.

IDENTIFICATION OF AQUATIC DIPTERANS

The keys to larvae and pupae (below) omit some rare forms that would make the keys more difficult to use. These are the Thaumaleidae, Ptychopteridae and Tanyderidae, which are discussed and illustrated in the notes on families in Chapter 2. For further details on these and the other families, refer to the later chapters in this book.

Although other useful references are available for the identification of immature stages of aquatic dipterans, some of them are very difficult to obtain, especially in Africa. Useful references to aquatic dipterans worldwide include Johannsen (1934, 1935, 1937a, 1937b), Thomsen (1937), Crosskey (1980) and McAlpine et al. (1981). Because most families and genera are virtually cosmopolitan, several works on North American insects are very useful. They include Usinger (1956), the second edition of Pennak (1978) (the third edition does not include the insects), McCafferty (1981) and Merrit & Cummins (1996). Various dipteran groups are dealt with in a series of volumes entitled *South African Animal Life* (Vol. 1 in 1956 to Vol. 15 in 1964) but no publications cover all the aquatic Diptera in southern Africa. The present volume represents a first attempt to provide such a coverage. References to individual families are given in Chapters 2–7.

KEY TO FAMILIES OF AQUATIC LARVAL DIPTERA KNOWN FROM SOUTHERN AFRICA

1. Mandibles moving against one another in a horizontal or oblique plane (Fig. 1.1A); head capsule usually complete and fully exposed (Figs 1.2A–H) but retractable and reduced in the Tipulidae; larvae usually not maggot-like: **Nematocera** (Figs 1.1E–1.3D) 2
– Mandibles or mouth hooks moving parallel to one another in a vertical plane (Figs 1.1B, D, 1.4F); head capsule variously reduced posteriorly and partially or almost completely retracted within thorax, even if such retracted portions comprise only a few slender rods; larvae maggot-like: **Brachycera** (Figs 1.3E–1.4H) 12

2. Head capsule partially to fully retracted into thorax, usually with longitudinal incisions of varying depth dorsolaterally (Fig. 1.1C); only the last pair of *spiracles (if any) open (Fig. 1.1G), usually bordered by one to three pairs of lobes,* often fringed with hairs (Figs 1.1E, F); mostly semi-terrestrial but true aquatics (e.g. Figs 1.1F–H) are found in torrents and backwaters in upper rivers .... **Tipulidae**: pp. 27–36
– Head capsule complete, not retracted into thorax, usually without longitudinal incisions; no spiracles open, or last pair open, or first and last pairs open; posterior ones usually without fringed lobes (Figs 1.1I–1.3D) 3

3. Body consisting of apparently only six divisions in all, anterior one consisting of fused head, thorax and first abdominal segment (Fig. 1.1I) and each division with a median suctorial disc ventrally; larvae on rocks in mountain torrents .... **Blephariceridae**: pp. 36–38
– Head distinct, constriction separating it from the thorax; no suctorial discs (Figs 1.2–1.3D) 4

4. All three thoracic segments fused and indistinctly differentiated (Figs 1.2A–C), forming a single unit wider than any abdominal segment; thoracic and abdominal segments with prominent lateral fan-like tufts of long setae, and/or terminal segment with a fan of anal setae 5
– Thoracic segments usually individually distinguishable; thorax and abdomen about equal in diameter, or abdomen wider; setae on thoracic and abdominal segments not tufted and no anal fan on terminal segment (Figs 1.2D–1.3D)..........7

5. Antennae prehensile (grasping: Fig. 1.2C) with long apical setae; mouth brushes lacking; sometimes posteriorly with a respiratory siphon; in lakes, ponds and very slow-flowing sections of large rivers 6
– Antennae not prehensile and with only short apical setae; prominent mouth brushes on either side of labrum; respiratory siphon always present; mostly found in still waters: mosquito larvae (Fig. 1.2A) ....**Culicidae**: Chapter 4

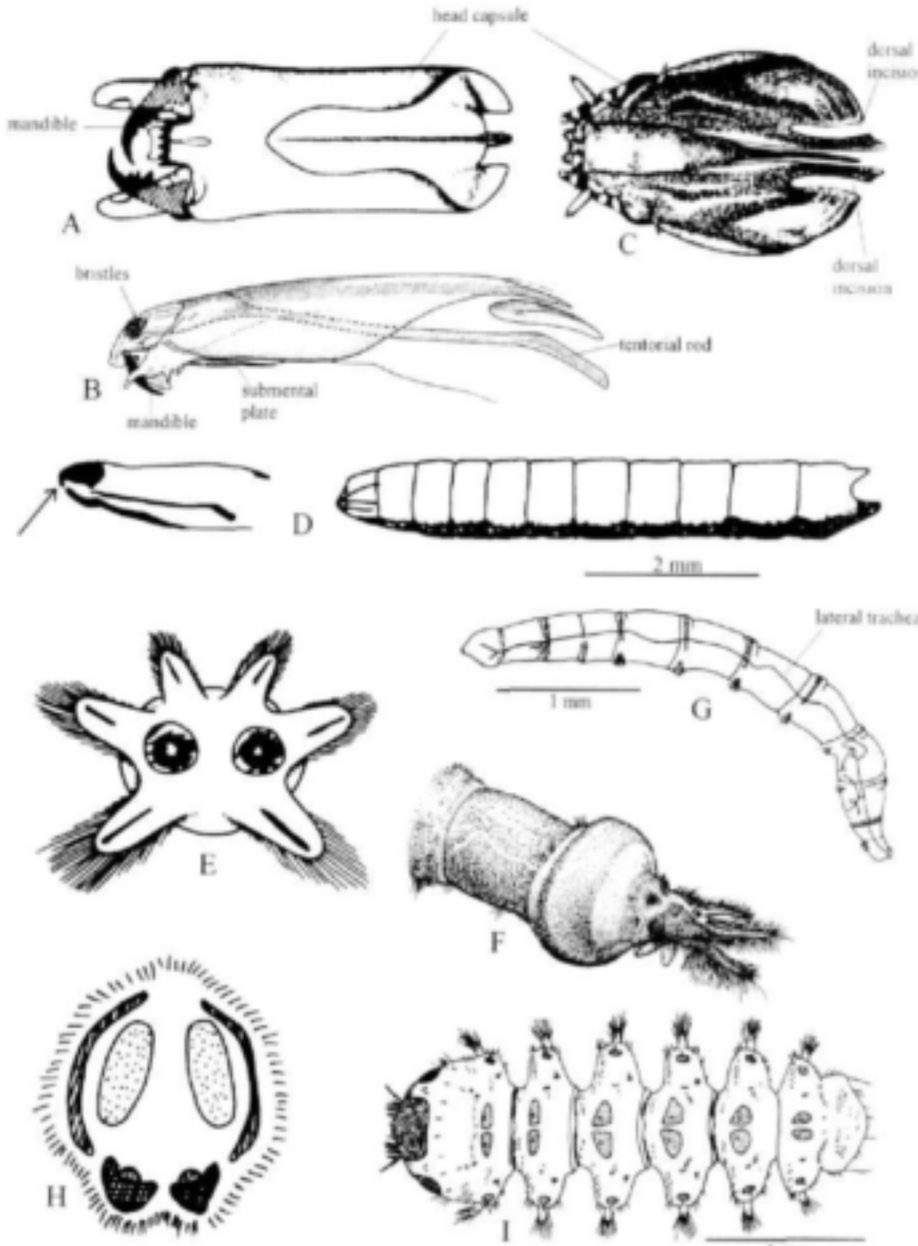


Fig. 1. 1. Dipteran larvae. **A**, head and mandibles of a tipulid larva in ventral view. **B**, left lateral view of mouthparts and cephalopharyngeal skeleton of a tabanid larva. **C**, dorsal view of the head of a tipulid larva showing posterior incisions. **D**, left lateral view of a dolichopodid larva (*Hydrophorus* sp.) with detail of the cephalopharyngeal skeleton. **E–H**, tipulids: **E**, posterior view of a spiracular disc; **F**, dorso-lateral view of the anal segment of *Limnophila* sp.; **G**, left lateral view of *Limonia tipulipes*, entire animal; **H**, posterior view of the spiracular disc of *L. tipulipes*. **I**, dorsal view of a larval blephariceid (*Elporia* sp.). A–C redrawn from Merrit & Cummins (1978); D–H redrawn from Usinger (1956); I redrawn from Edwards (1915).

6. Eighth abdominal segment with a single elongate respiratory siphon (Fig. 1.2B); rarely found ....**Corethrellidae**: pp. 45–46
– Eighth abdominal segment without such a respiratory siphon (Fig. 1.2C); common in lakes ....**Chaoboridae**: pp. 44–45

7. Body usually flexed to form a U-shape; paired hooklet-bearing prolegs on first and usually second abdominal segments; abdominal segments V–X each with dorsal shields fringed with setae; abdomen posteriorly with pair of flattened dorsolateral lobes fringed with setae; anus on conical terminal segment; marginal vegetation of streams, rivers and ponds (Figs 1.2D, E)..**Dixidae**: pp. 41–42
– Body not forming a U-shape; abdominal segment I with or without prolegs and segments 5–10 without dorsal shields; no flattened dorsolateral lobes; anal segment not conical (Figs 1.2F–1.3D)..8

8. Prothorax with a single proleg or a pair of prolegs ventrally (Figs 1.2F–G, 1.3A–C)....9
– Prothorax without prolegs (Figs 1.2H, 1.3D)..11

9. Head capsule with a pair of conspicuous folding labral fans dorsolaterally; abdominal segments V to VIII swollen, posterior segment ending in a circlet of numerous radiating rows of minute hooks (Fig. 1.3A); larvae sessile, usually in swiftly-moving streams..**Simuliidae**: Chapter 5
– Head capsule lacking folding labral fans; posterior abdominal segments neither conspicuously swollen nor with radiating rows of hooks posteriorly, although anal prolegs bearing claws may be present 10

10. All body segments dorsally with prominent tubercles and/or stout setae (Figs 1.2F–G)..**Ceratopogonidae** (part): Chapter 3
– Body segments lacking prominent dorsal tubercles and stout setae, although fine setae may be present (Figs 1.3B–C)..................**Chironomidae**: Chapter 6

11. Each body segment subdivided into two or three annulations, some or all bearing dorsal sclerotized plates; integument with numerous dark spots that, with the dorsal plates, give a greyish brown colour to the larvae; posterior spiracles usually at the apex of a short conical tube (Fig. 1.3D); in slow reaches of rivers, specially if polluted, and in sewage trickling filters (but *Pericoma* in mountain waterfalls)..**Psychodidae**: pp. 38–40
– Long thin larvae with body segments not annulated; integument smooth, shiny and creamy white (transparent in life), lacking all surface features except sometimes a few setae terminally and sometimes a retractile anal proleg bearing a few small hooklets (Fig. 1.2H); in streams, rivers, ponds and lakes ....**Ceratopogonidae** (part): Chapter 3

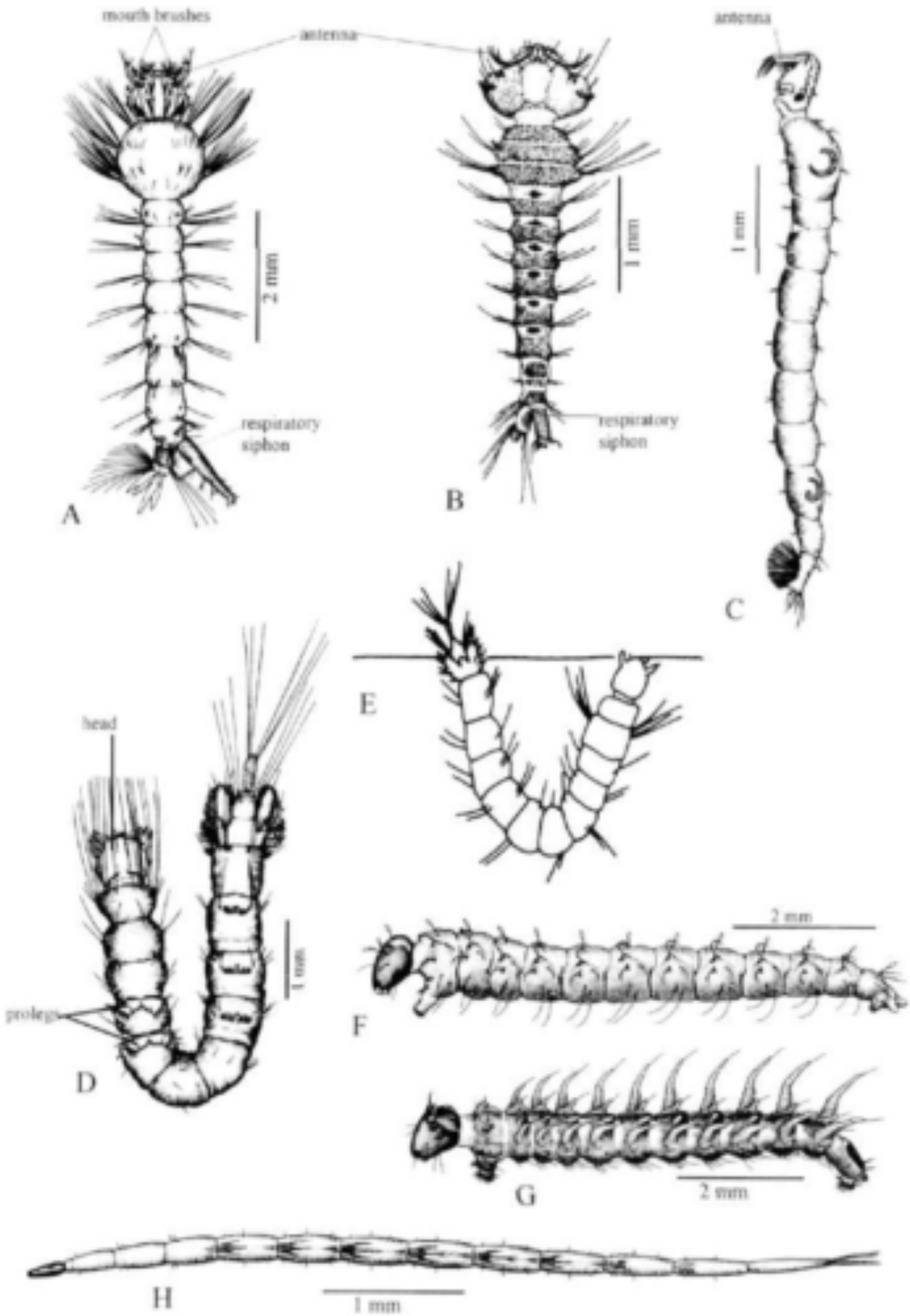


Fig. 1.2. Dipteran larvae. **A**, a culicid in dorsal view. **B,** a corythrellid in dorsal view. **C**, a chaoborid, in left lateral view. **D–E**, dixid larvae: **D**, in ventral view; **E**, in position at the meniscus. **F–H**, ceratopogonid larvae in left lateral view: **F**, *Forcipomyia* sp. (Forcipomyinae); **G**, *Atrichopogon* sp. (Forcipomyinae); **H**, *Bezzia* sp. (Ceratopogoninae). A–D redrawn from Johannsen (1934), F–H redrawn from McAlpine et al. (1981).

12. Sclerotized portions of head capsule exposed externally but sometimes greatly reduced with slender skeletal rods prominent internally (Fig. 1.1B): 13
– No evident external sclerotized head capsule, head being reduced to internal pharyngeal skeleton (Fig. 1.4D–F)..17

13. Body somewhat depressed, integument toughened and leathery; head capsule capable of only slight independent movement and usually with distinctive lateral eye prominences (arrowed in Fig. 1.3E2); in marginal vegetation in lower river zones or edges of small wetlands ...... **Stratiomyidae**: p. 163–164
– Larvae usually not obviously depressed and not with a toughened integument; head capsule capable of independent movement and lacking lateral eye prominences (Figs 1.3F–1.4B)..14

14. Head capsule well developed dorsally, closed ventrally by a submental plate; tentorial rods solidly fused with head capsule internally; a brush of backwardly-curved bristles usually present on each side of the clypeus above and near base of each mandible (Fig. 1.1B)... 15
– Head capsule reduced to a pair of slender rods; no submental plate and no brushes of bristles above the mandibles (Fig. 1.1D)............................ 16

15. Posterior spiracles opening within slits on either side of a vertical linear bar or a retractile, laterally-compressed spine; first seven abdominal segments girdled by three or four sets of fleshy pseudopods, giving the body a ringed appearance (Fig. 1.3F1); in streams, rivers, and margins of ponds and lakes .... **Tabanidae**: pp. 159–161
– Posterior spiracles absent or situated well within a small terminal cavity; all abdominal segments with a pair of ventral prolegs bearing hooklets; posteriorly often with a pair of fringed, elongate processes (Fig. 1.3G); in quieter spots in upper rivers ....**Athericidae**: pp. 161–162

16. Posterior spiracles at the base of the upper two of four smooth primary lobes on the last abdominal segment; abdominal segments ventrally with transverse creeping welts (Fig. 1.4A); in mountain streams, rare.............................. ....**Dolichopodidae**: pp. 166–167
– Larvae usually without spiracles; abdominal segments with paired prolegs bearing apical hooklets; terminal abdominal segment with one to four rounded lobes bearing apical setae (Fig. 1.4B); in runs in middle to lower zones of rivers ....**Empididae**: pp. 164–166

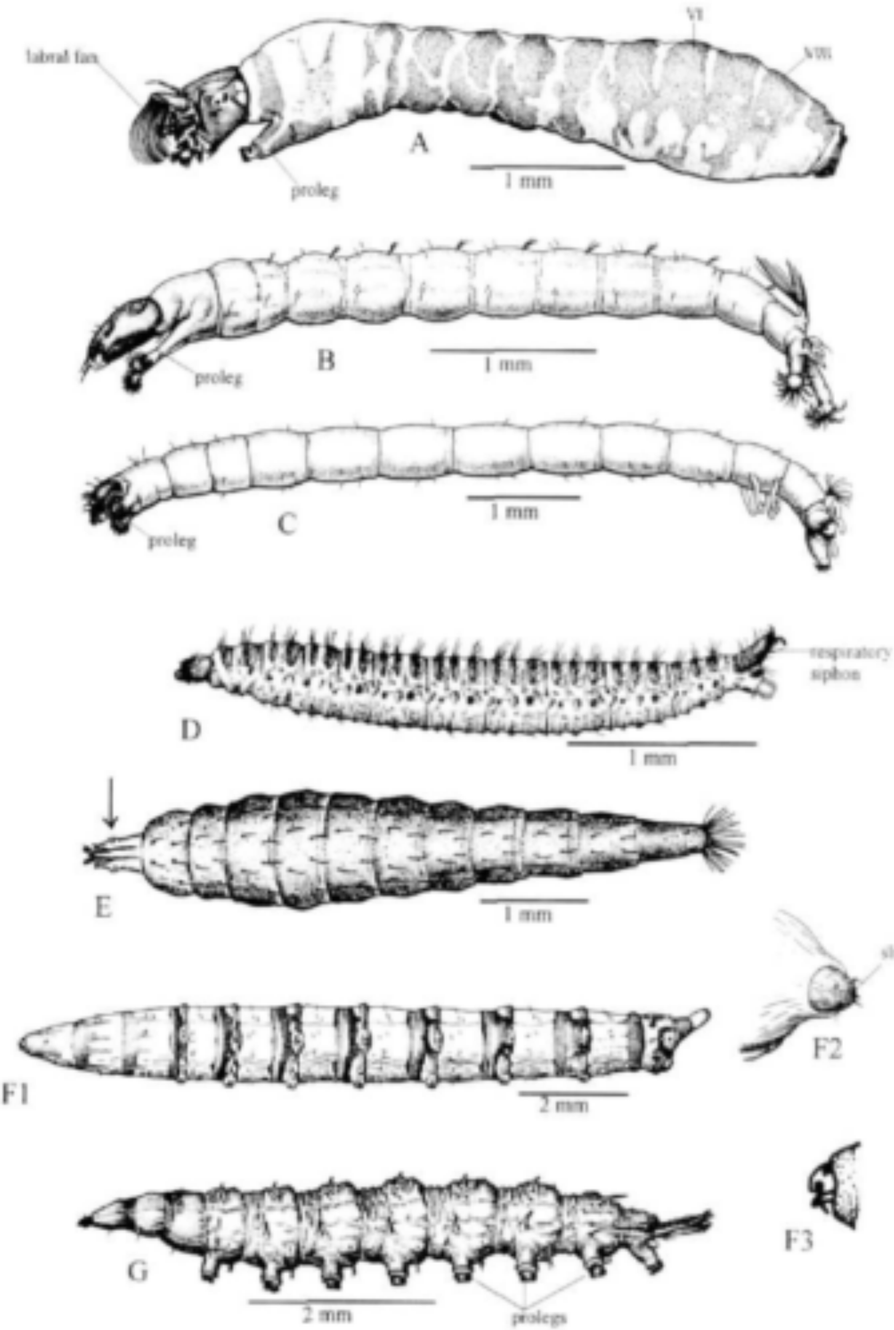


Fig. 1.3. Dipteran larvae in left lateral view (cont.). **A**, a simuliid. **B–C**, chironomids: **B**, a tanypod; **C**, a chironomine. **D**, a psychodid. **E**, a stratiomyid. **F**, a tabanid: F1, whole larva; F2, position of terminal spiracles; F3, head capsule. **G**, an athericid. A–D, F–G redrawn from McAlpine et al. (1981); E redrawn from Johannsen (1935).

17. Posterior spiracular plates fused and apparently single, or very closely approximated, usually on apex of a telescopic respiratory tube (Fig. 1.4C); in polluted waters ....**Syrphidae**: pp. *168–169*
– Posterior spiracular plates always distinctly separated, whether mounted on a respiratory tube or not 18

18. Cephalopharyngeal skeleton with a sclerotized ventral arch below the base of the mouth hooks (Fig. 1.4E), its anterior margin usually toothed; body segments often covered with short, fine hairs; terminal segment often somewhat tapered, its apex with tubercles surrounding posterior spiracles that are only slightly elevated (Fig. 1.4D); at margins of wetlands or slow-flowing sections of rivers; some are predators on aquatic snails.................. **Sciomyzidae**: pp. 169–170
– Cephalopharyngeal skeleton lacking a ventral arch (Fig. 1.4F); if the body is extensively covered with fine hairs then a respiratory siphon is present, or each spiracle is situated on a short tubular terminal projection 19

19. Posterior abdominal segments somewhat tapered, sometimes ending in a retractile respiratory tube, which may be forked; integument of posterior abdominal segments covered with setae or spinules or with setose tubercles on some segments (Fig. 1.4G); in brackish or saline water .... **Ephydridae**: pp. 171–172
– Posterior abdominal segments rather truncate; posterior spiracles may be on tubercles, but no other tubercles present (Fig. 1.4H); at margins of wetlands and in slow-flowing parts of rivers, or in stony torrents.........................
....**Muscidae**: pp. 172–174

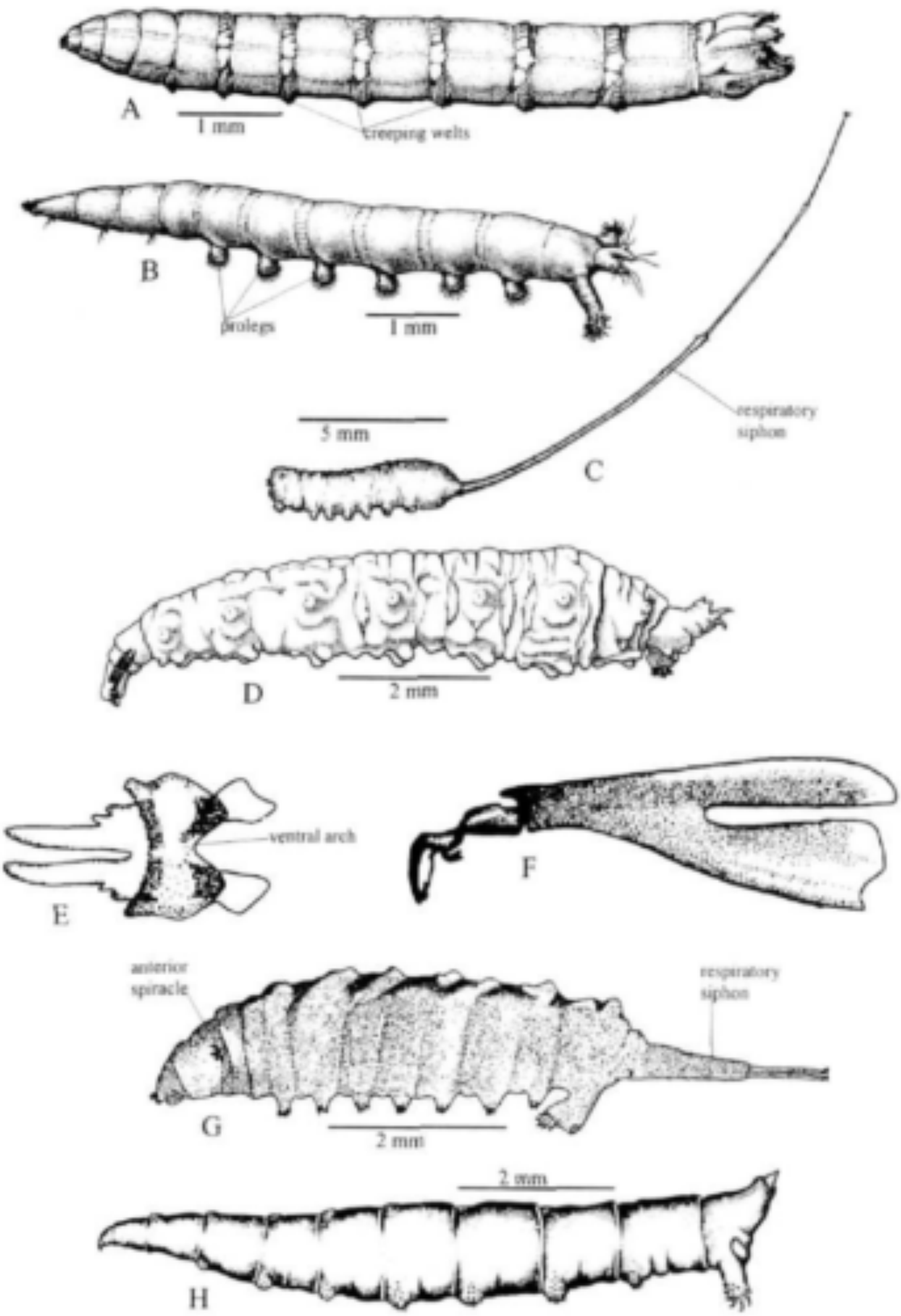


Fig. 1.4. Dipteran larvae (cont.). Entire animals shown in left lateral view (unless otherwise stated). **A**, a dolichopodid. **B**, an empidid. **C**, a syrphid;. **D**, a sciomyzid. **E–F**, cephalopharyngeal skeletons: E, of a sciomyzid in ventral view; **F**, of a muscid in lateral view. **G**, an ephydrid. **H**, a muscid. A, B redrawn from McAlpine et al. (1981); C–D, G–H redrawn from Johannsen (1935); E, F, redrawn from Usinger (1956).

KEY TO FAMILIES OF AQUATIC PUPAL DIPTERA KNOWN FROM SOUTHERN AFRICA

Introductory Note: This key is modified from Johannsen (1934–1937) and Thomsen (1937). Muscomorph pupae can be identified with reference to the larval key above. Note that pupae of the Athericeridae (larval key couplet 15) are not aquatic but are found in the soil of river banks.

1. Pupa free, not completely covered by the last larval skin, although it may be covered by a cocoon (Fig. 1.5A) ; developing limbs can be seen through the pupal integument (Figs 1.5F–1.7) 2
– Pupa remaining wholly within the last larval skin, the puparium, which is heavily sclerotized and may be shortened to form an ellipsoidal or egg-shaped body; no limbs visible (Fig. 1.5B–E)..3

2. Antennal sacs elongated, lying over the compound eyes and extending to or beyond the bases of the wing sheaths; prothoracic respiratory organs in most cases are conspicuous respiratory horns; head without spinose processes except in the Tipulidae: **Nematocera** (Figs 1.5F–1.6) 4
– Antennal sacs short, directed posterolaterally, not lying over the eyes; head usually with spinose processes; prothoracic respiratory horns usually rudimentary or lacking (Fig. 1.7): **Brachycera** (part) 13

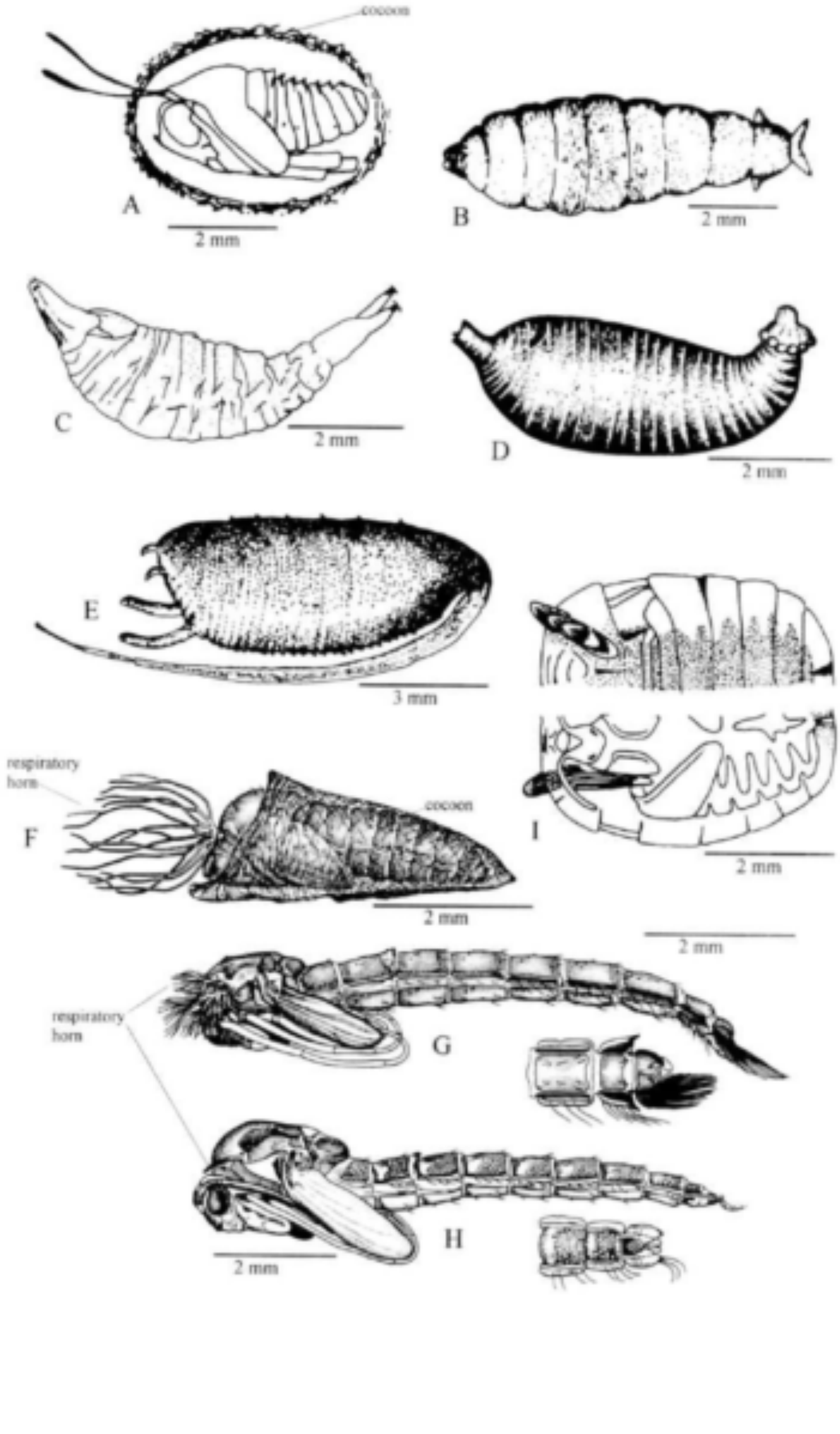
3. Puparium within the larval skin, which is unchanged in shape and with the larval head distinct (see larval key and Fig. 1.5B).......... **Stratiomyidae**: pp. 163–164
– Puparium without a distinct head, the larval skin modified in shape owing to the changed form of the pupa within (Figs 1.5C–E): **Brachycera** (part) .... go to larval key, couplet 17 (page 18)

4. Pupa (Fig. 1.5F–H) enclosed in a fibrous cocoon; always in running water.......5
– Pupa (Figs 1.5I, 1.6) without a cocoon although sometimes in a tube of silk covered with silt or algae; in running or standing waters 6

5. Cocoon slipper-shaped, projecting respiratory organs large, consisting of one to many fine or coarse filaments (Fig. 1.5F), sometimes like antlers.................. .... **Simuliidae**: Chapter 5
– Cocoon conical or cylindrical (often missing in preserved material); respiratory organ, if present, a slender, unbranched filament (Fig. 1.5H) or thick and branched (Fig. 1.5G) .... **Chironomidae** (in part): Chapter 6

6. Body of pupa more or less convex (Fig. 1.5I), hard-shelled, attached limpet-like to rocks in fast-running water ....**Blephariceridae**: pp. 36–38
– Body of pupa not so attached and not limpet-like (Figs 1.5J–1.6) 7

Fig. 1.5. Dipteran pupae: entire animals shown in left lateral view, unless otherwise stated. **A**, a dolichopodid in cocoon. **B**, a stratiomyid, in dorsal view. **C**, puparium of an ephydrid. **D**, puparium of a sciomyzid. **E**, puparium of a syrphid. **F**, a simuliid in cocoon. **G–H** chironomids: **G**, a chironomine. **H**, an orthoclad. **I**, composite diagram of a blephariceridid, in dorsal view above and in ventral view below. A–E redrawn from Usinger (1956); F redrawn from Johannsen (1937a); G redrawn from Johannsen (1937b); H, redrawn from McAlpine (1981).


cocoon
A
2 mm
B
2 mm
C
2 mm
D
2 mm
E
3 mm
respiratory horn
F
cocoon
2 mm
I
2 mm
2 mm
respiratory horn
G
H
2 mm

7. Leg sheaths long and straight, projecting beyond (sometimes far beyond) the ends of the wing sheaths; posterior end of body often forked or spined or with spiny lobes, not paddle-shaped nor adapted for swimming; head and bases of antennal sheaths often armed with tubercles or spines; respiratory horns equal (Fig. 1.6A) or very unequal (Fig. 1.6B) in length; thorax scarcely wider or thicker than abdomen; large, usually 8mm or more in length; pupation in mud, sand or earth, rarely in open water .... **Tipulidae**: pp. 27–36
– Leg sheaths projecting little if any beyond the wing sheaths, often much curved, undulating or folded; thorax usually thicker or deeper than abdomen, which often ends in a paddle; respiratory horns equal in length and plumose, branched or simple (Fig. 1.6C–I); length rarely over 8 mm; pupation usually in open water 8

8. Individuals small, straight and robust; leg sheaths short and straight, superimposed, easy discernable; tergites and sternites margined with spinules; last segment with a diverging pair of terminal spines and usually with one or more pairs of dorsal and ventral spines; respiratory horn more or less cylindrical, not flaring or funnel-shaped (Fig. 1.6C)...................... **Psychodidae**: pp. 38–40
– Leg sheaths undulating, curved or folded, or not easily discernable (Figs 1.6D–I).....9

9. Anal lobes consisting of two paddles, each with a midrib, which may end in a bristle; paddle at most finely serrate on margin (Figs 1.6D–E).......................
.................................**Culicidae** (Chapter 4) and **Chaoboridae**: pp. 44–45
– Paddle, if present, without a distinct midrib (Figs 1.6F–I) 10

10. Paddles narrow, completely fused basally, a strong hair on outer margin beyond middle and a stout spine at tip; individuals minute (Fig. 1.6F)...........
....**Corethrellidae**: pp. 45–46
– With other characters (Figs 1.6G–I) 11

11. Swimming paddles consisting of two large pointed lobes, fused basally, not moveable and without long hairs and spines; spiracle distal to the middle of respiratory horn; pupa normally lying motionless on its side in an arched position (Fig. 1.6G) .... **Dixidae**: pp. 41–42
– Swimming paddles absent or, if present, the pupa differs in other characters (Figs 1.6H–I) 12

12. Pupa rigid, well chitinized (usually brown except when recently moulted) inactive; with two spines terminally (Figs 1.6H–I). ....
....**Ceratopogonidae**: Chapter 3
– Pupa not rigid; chitin usually thin; anal end various (Fig. 1.5G, H) ....
....**Chironomidae** (part): Chapter 6

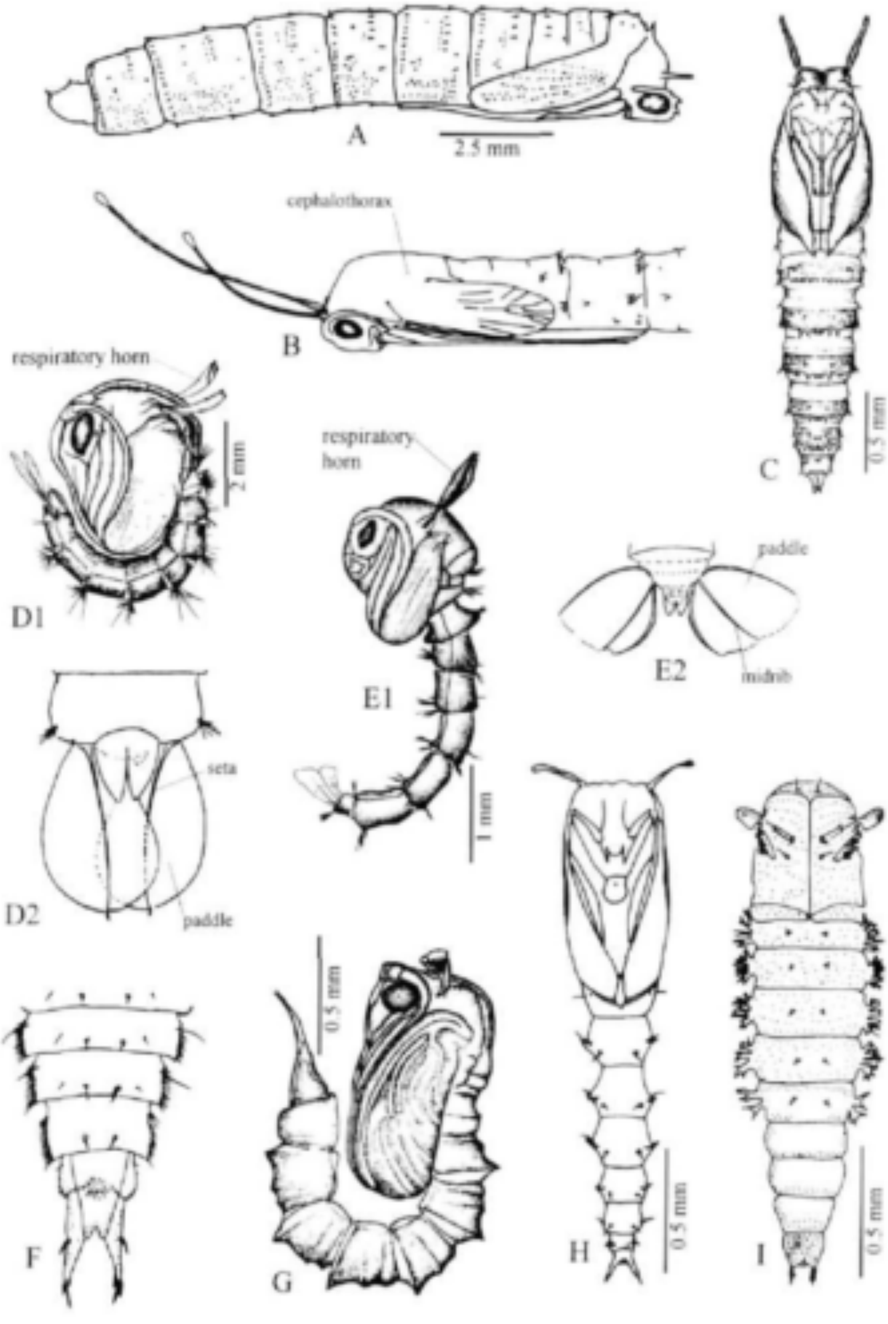


Fig. 1.6. Dipteran pupae (cont.): entire animals shown in left lateral view, unless otherwise stated. **A–B**, tipulids: **A**, form with even respiratory horns; **B**, form with uneven respiratory horns. **C**, a psychodid, in ventral view. **D**, culicids: D1, whole pupa; D2, anal lobes in dorsal view. **E**, chaoborids: E1, whole pupa; E2, anal lobes in dorsal view. **F**, posterior segments of a corethrellid in dorsal view. **G**, a dixid. **H–I**, ceratopogonids: **H**, *Bezzia*; **I**, *Atrichopogon*. A–G redrawn from Johannsen (1934); H, I redrawn from Thomsen (1937).

13. Pupa robust, short, with greatly elongated prothoracic respiratory horns (Fig. 1.7A) .... **Dolichopodidae**: pp. 166–167
– Pupa elongate, prothoracic respiratory organs not conspicuous (Figs 1.7B–D) 14

14. Leg sheaths no longer than wing cases (Figs 1.7B) ....**Tabanidae**: pp. 159–161
– Leg sheaths longer than wing cases (Figs 1.7C–D)..................................... ....**Empidae**: p. 164–166

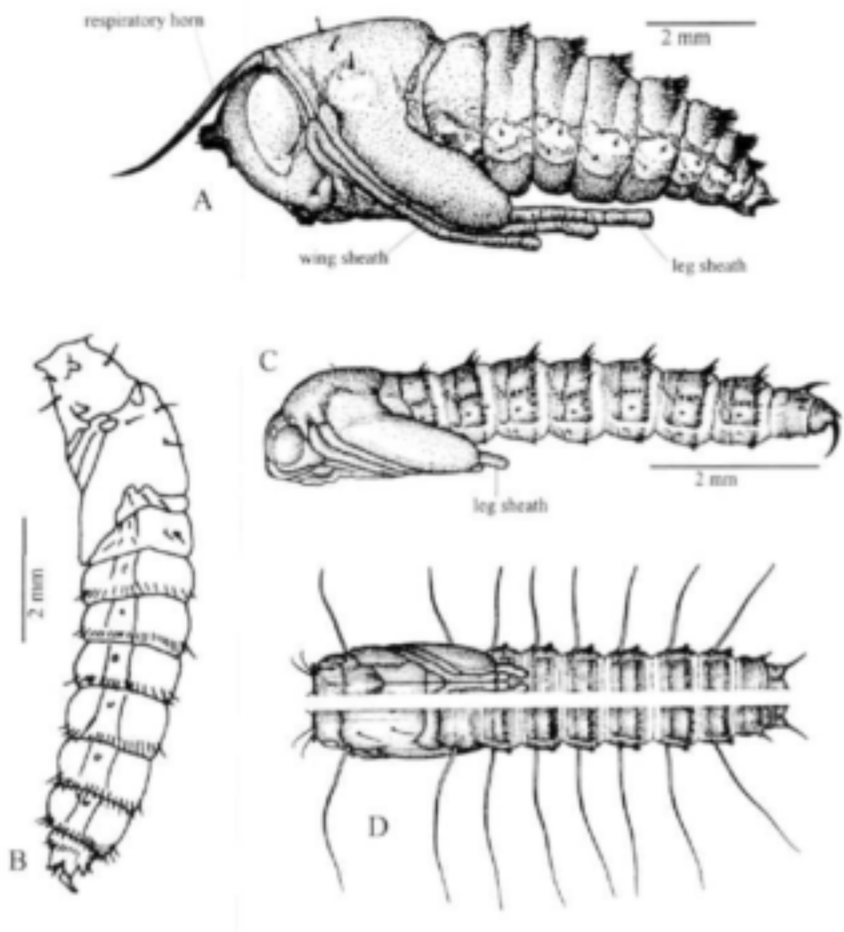


Fig. 1.7. Diptera pupae (cont.): entire animals shown in left lateral view, unless otherwise stated. **A**, a dolichopodid. **B**, a tabanid. **C–D**, empidids: **C**, *Clinocera* sp., entire animal in lateral view; **D**, *Hemerodroma* sp., composite diagram indicating the ventral view above and the dorsal view below. A, C, D redrawn from McAlpine et al. (1981); B redrawn from Johannsen (1935).

USEFUL REFERENCES

CROSSKEY, R.W. (Ed.) 1980. *Catalogue of the Diptera of the Afrotropical Region.* British Museum (Natural History), London: 1437 pp.

*JOHANNSEN, O.A. 1934. Aquatic Diptera Part I. Nemocera, exclusive of Chironomidae and Ceratopogonidae. *Agricultural Experiment Station, Cornell University.* Memoir **164**, Ithaca, New York.

*JOHANNSEN, O.A. 1935. Aquatic Diptera Part II. Orthorrhapha-Brachycera and Cyclorhapha. *Agricultural Experiment Station, Cornell University.* Memoir **177**, Ithaca, New York.

*JOHANNSEN, O.A. 1937a. Aquatic Diptera Part III. Chironomidae: subfamilies Tanypodinae, Diamesinae and Orthocladinae. *Agricultural Experiment Station, Cornell University.* Memoir **205**, Ithaca, New York.

*JOHANNSEN 1937b. Aquatic Diptera Part IV. Chironomidae: subfamily Chironominae. *Agricultural Experiment Station, Cornell University.* Memoir **210**, Ithaca, New York.

McCAFFERTY, W.P. 1981. Aquatic Entomology. Jones & Bartlett, Boston.

McALPINE, J.F., PETERSON, B.V., SHEWELL, G.E., TESKEY, H.J., VOCKEROTH, J.R. & WOOD, D.M. (Eds) 1981. Manual of Nearctic Diptera Vol. I. *Research Branch, Agriculture Canada*, Monograph **27**, Quebec.

MERRIT, R.W. & CUMMINS, K.W. (Eds) 1996. *An Introduction to the Aquatic Insects of North America.* Kendall/Hunt, Dubuque.

PENNAK, R.W. 1978 (2nd ed.). *Freshwater Invertebrates of the United States.* Wiley-Interscience, New York.

*THOMSEN, L.C. 1937. Aquatic Diptera Part V. Ceratopogonidae. *Agricultural Experiment Station, Cornell University.* Memoir **210**, Ithaca, New York.

USINGER, R.L. (Ed.) 1956. *Aquatic Insects of California with Keys to North American Genera and Californian Species.* University of California Press, Berkley.

* reprinted as a collected volume by Entomological Reprint specialists, East Lonsing, Michigan, in 1969.

CHAPTER 2

LESSER-KNOWN NEMATOCERA

by

A.D. Harrison, A. Prins & J.A. Day

The nematocerans include both some very well known families of dipterans with aquatic larvae—the Chironomidae, the Simuliidae, the Culicidae and the Ceratopogonidae—and several uncommon or poorly-known families. The Ceratopogonidae are dealt with in Chapter 3, the Culicidae in Chapter 4, the Simuliidae in Chapter 5 and the Chironomidae in Chapter 6. The present chapter deals with the smaller families (the Tanyderidae, Psychodidae, Ptychopteridae, Dixidae, Chaoboridae, Corethrellidae, and Thaumaleidae) as well as those larger families (the Tipuliidae and Blephariceridae) for which no expert was available to write an account. To identify an immature dipteran to family, the reader is referred to Chapter 1.

Tanyderidae

primitive craneflies

Figs 2.1A–F

According to Alexander (1964), the family Tanyderidae is one of the most primitive in the Diptera. Worldwide, the family is known from only 33 species in ten genera. The majority of species (19) are known from the Australasian region but only one species has been recorded from southern Africa. This is *Peringueyomyina barnardi*, the only species in the genus. It is known only from the Franschoek, Palmiet and Hottentots–Holland areas of the Western Cape.

Adult tanyderids are tipulid-like flies, rather similar to phantom craneflies (family Ptychopteridae: see p. 40) but differing slightly in wing venation and recognisable because the head is drawn out into a long proboscis (Fig. 2.1A). They generally occur in shady places and among vegetation along the banks of streams. The larvae (e.g. Fig. 2.1B) are elongate and cylindrical, with a number of filaments terminally on the abdomen.

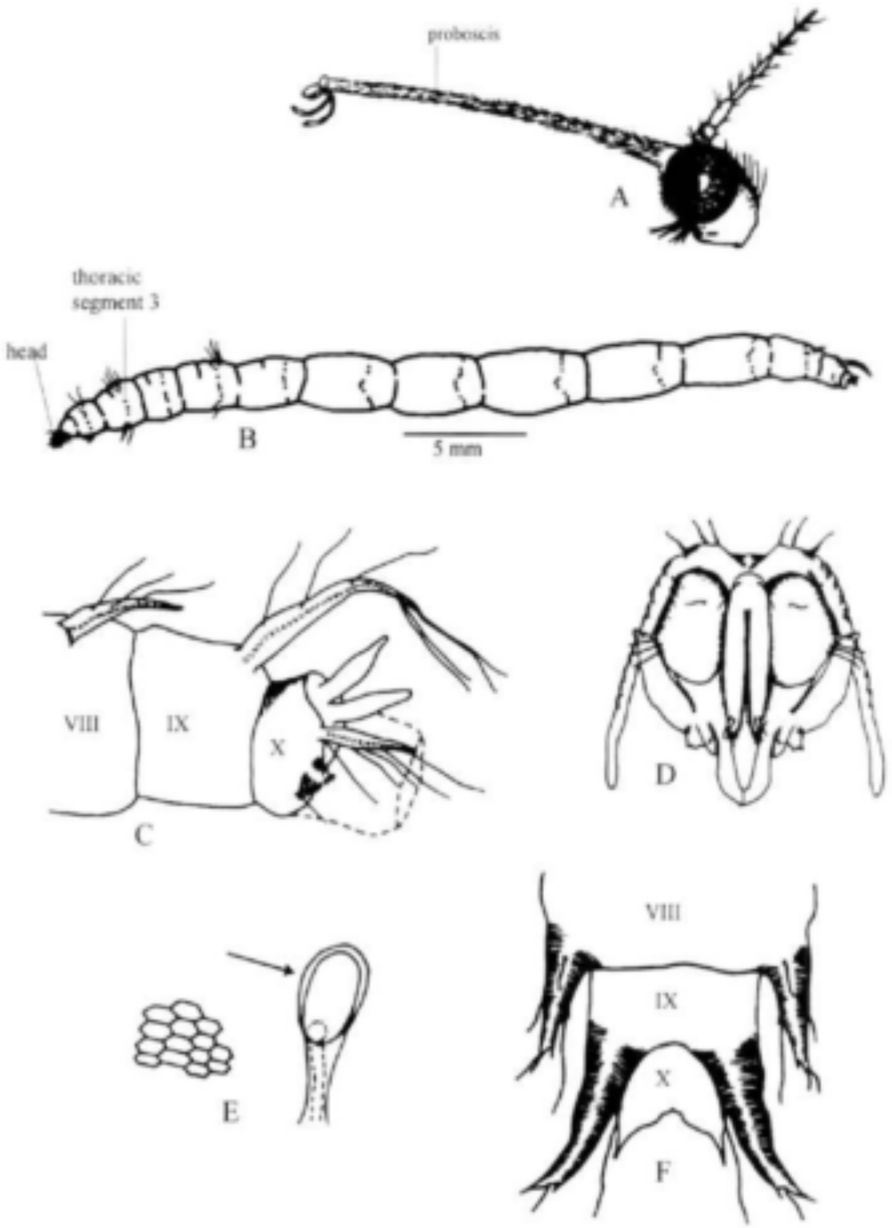


Fig. 2.1 Tanyderidae. **A**, head of an adult *Peringueyomyia barnardi* in lateral view; **B**, left lateral view of a larval *P. barnardi*; **C**, enlarged right lateral view of the terminal abdominal segments of a larva of *P. barnardi*; **D**, anterior view of the head of a pupa of *P. barnardi*; **E**, detail of a thoracic horn of a pupal *P. barnardi*; **F**, dorsal view of terminal abdominal segments of pupal *P. barnadi*. (A redrawn from Alexander (1964); B–F redrawn from Wood (1952).

Biology

Wood (1952) reports the larvae of *P. barnardi* in the white gravelly sand spits along the edge of forested streams in shady spots in the western Cape mountains. When mature, the larvae migrate to drier areas along the margins of streams to pupate.

Aquatic stages

Mature larvae of *P. barnardi* (Fig. 2.1B) are elongate, about 25 mm long and dirty white in colour. The body segments lack creeping welts and prolegs but thoracic segments 2 and 3, and abdominal segment II, bear lateral spines. The abdomen does not end in a spiracular disc but in a number of conspicuous filaments, which may be gills or osmoregulatory organs.

Pupae of *P. barnardi* (Fig. 2.1C–F) resemble those of the Tipulidae. They measure about 14 mm in length and are pale yellowish-brown in colour, except for the thorax and respiratory horns, which are dark brown. The antennal sheaths extend to the bases of the wing-pads; the thorax is depressed and practically flat; the respiratory horns (Fig. 2.1E) are short with funnel-shaped apices; and dorsolaterally the last three abdominal segments end in a pair of darkened projections (Figs 2.1C, F).

Useful references to the tanyderids are Wood (1952) and Alexander (1964).

Tipulidae

craneflies

Figs 2.2–2.4

The family Tipulidae is the largest in the Diptera with about 14 000 species worldwide. Adult craneflies are well-known because they often turn up in houses, attracted by lights. They are easily recognized by their long legs, for which reason they are also known as daddy-long-legs—and are also sometimes mistaken for 'giant mosquitoes'. Most do not seem to feed as adults, although on rare occasions individuals have been seen apparently feeding from long tubular flowers. Mandibles are apparently wanting, but modified maxillae with palps are present. Adults of some species are large (wing-span 75 mm or more) and, since these insects are vulnerable to wind action, some are wingless. Alexander & Byers (1981) observe that 'because many species of Tipulidae are so abundant, they are extensively preyed upon by birds, mammals, fishes and other vertebrates, as well as by spiders and predatory insects. The Tipulidae are therefore of tremendous ecological importance'.

Larvae have reduced, retracted heads (Figs 2.2B–C) but normal, horizontally-biting mandibles (Figs 2.2A, E, F–I). The posterior spiracles

(Figs 2.2D, 2.3) are surrounded by one to three pairs of lobes, which are often setose. Larvae of many species are found in moist places such as damp moss, holes in trees, and rotting vegetation, but others occur in drier places. In the northern hemisphere the larvae of *Tipula paludosa* are important pests of pasture grasses and commercial crops. Larvae of a few species are found in freshwater habitats, even in fast-flowing streams.

The pupa forms within the last larval skin, which is then shed. Most pupae have a pair of respiratory horns but this is a variable character, as is evident in the key below. In some aquatic forms, such as *Antocha*, the pupa is enclosed in a silken case that must be removed before identification is possible.

Southern African tipulid fauna

Hutson (1980b) reports that about 1300 species in 55 genera and numerous subgenera are known from the Afrotropical Region. Many of the 340 or so species known from southern Africa seem to be endemic. 'As generic concepts stand at present there are relatively few groups unique to the Afrotropical Region, but conversely there are several major groups that are unrepresented in it', says Hutson. The larger members belong to the long-palped craneflies (subfamily Tipulinae). In southern Africa the largest genus in the subfamily is *Nephrotoma*, with about 27 species, none of which has aquatic larvae, although larvae of some species of the related genus *Tipula* are aquatic. The smaller, short-palped, forms constitute the largest subfamily (the Limoniinae), with about 30 South African genera comprising at least 167 species. Those genera with aquatic larvae are indicated in the larval key below.

Biology

Aerial swarms of mating tipulids are often seen, although spider webs are sometimes used by males to hang from or even to vibrate upon. In species with aquatic larvae, eggs are apparently laid during up-and-down flights of females, their ovipositors now and then touching the water. In some members of the Tipulinae, particularly those that lay in wet places, the eggs possess filaments that can attach to a hard surface. In those Limoniinae that have aquatic larvae, no filaments have been found, however, and the eggs, which are spindle-shaped and dark in colour, are mostly placed on the leaves of water plants, where they adhere by means of a sticky substance (Hemmingsen 1952).

Cranefly larvae, particularly those that live in waterlogged places, have large open spiracles on a spiracular disc at the hind end of the body, forcing the larvae to reach the air periodically. In certain members of the subfamily Limoniinae, the tracheal system can be closed completely and breathing is effected by tracheal gills at the tip of the abdomen (e.g. Fig. 2.2C). In these species the pupae (Fig. 2.4C) also have elongate branched filaments arising from the thoracic spiracles.

Larvae of aquatic forms usually occur in water that is well aerated and fast-flowing. As in the case of the blackflies, larvae living in these conditions are able to produce silk. Some live in silken tubes, open at both ends, while others are found in silken cases, which may be constructed just before pupation begins. Larvae of some of the predatory Limoniinae have sharp, curved mandibles (see Fig. 2.2E) and feed on the larvae of other insects such as flies and dragonflies, or on small worms. They may also be cannibalistic. Such larvae are mostly active, and are usually elongate and slim; some are said to produce a painful bite when handled carelessly.

Identification of immature tipulids

Much of the information in this section comes from Hutson (1980b). Other useful references are Alexander (1920) and Wood (1952).

The larvae of the South African species *Limonia (Dicranomyia) tipulipes* (Fig. 2.2B–C), described by Wood (1952), may be taken as an example of an aquatic tipulid. They are about 12 mm long, cylindrical, and dirty white in colour. In their natural habitat they build slime tubes, covered by moss and other particles, which render them inconspicuous and from which they must be removed if they are to be identified.

The **head capsule** of a tipulid larvae is retractile, in that it can be pulled backwards within the thorax (e.g. Fig. 2.2A). In some it forms a complete covering; in others, the head is slit postero-dorsally by one or more incisions (Figs 1.1C, 2.1A); and in yet others, the posterior part of the head capsule is reduced to a series of chitinized rods (Fig. 2.2E). The **antennae** (Fig. 2.2A) are two-segmented and short, each with an apical papilla surrounded by about three smaller papillae; the **mandibles** (Figs 2.2A, E) are broad, with about three apical teeth; the **maxillae** are well-developed, with well defined palps and about five apical papillae. In some species the paired tracheal tubes can clearly be seen through the body wall (Fig. 2.2B, 2.3D), commencing at the hind spiracles with four small lobes visible around the **spiracular disc** on the last segment of the abdomen (Fig. 2.3). The spiracular disc forms the posterior face of the last abdominal segment in many tipulids. In *Limonia tipulipes* it is small and surrounded by short stiff hairs (Fig. 2.2D); the two oval spiracles, flanking stripes and two semi-circular areas are all dark brown. The size of the spiracular disc, the lengths of the surrounding lobes and the degree of setation vary from group to group.

Tipulid pupae (Fig. 2.4) are elongate; they are commonly brownish in colour and devoid of setae, but they may bear spines. Thoracic **respiratory horns** are often present. In *Limonia tipulipes* these are somewhat

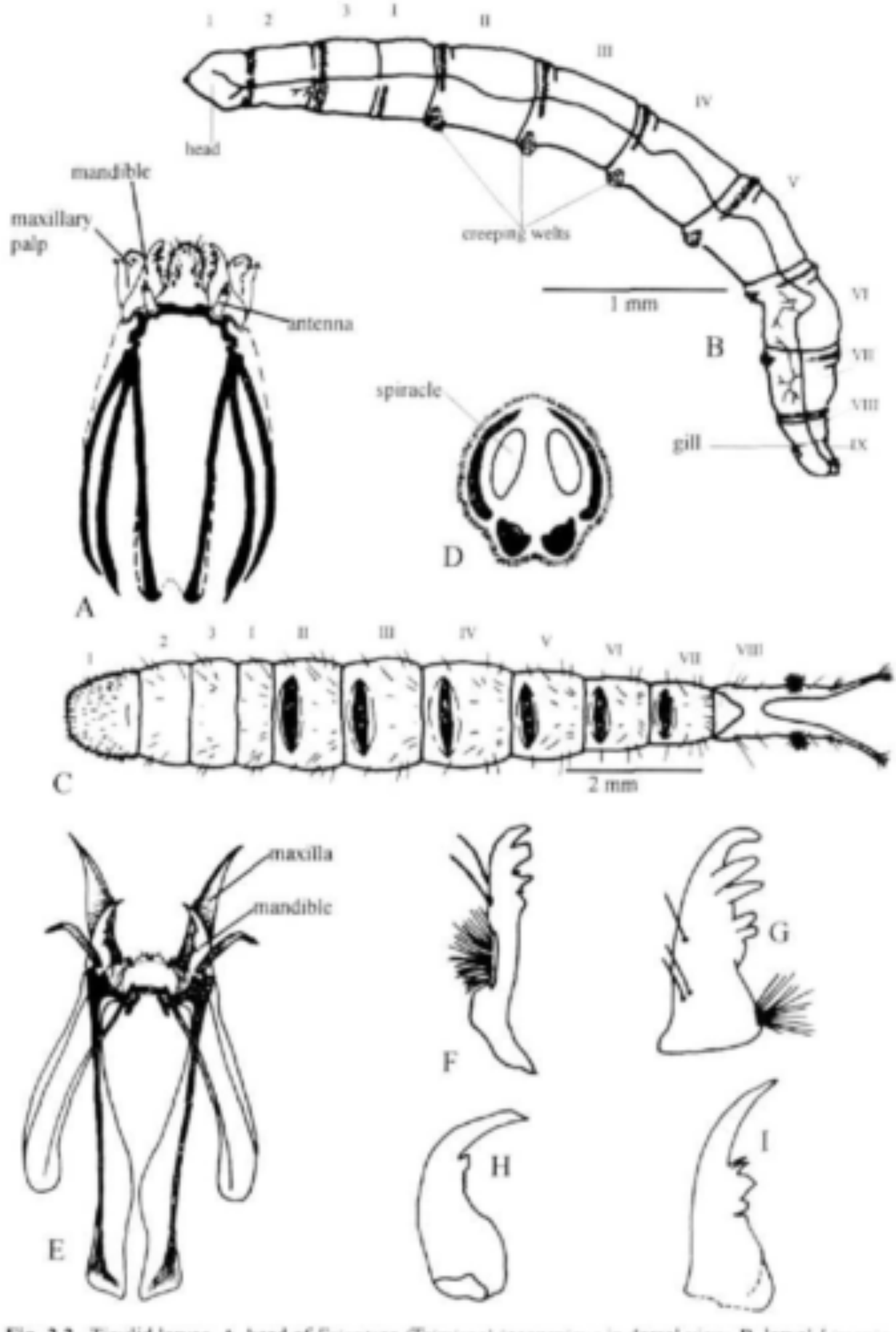


Fig. 2.2. Tipulid larvae. **A**, head of *Erioptera (Trimicra) inconspicua* in dorsal view; **B**, larval *Limonia tipulipes* in lateral view; **C**, larval *Antocha* sp. in dorsal view; **D**, spiracular disc of *Limonia tipulipes*; **E**, head of *Limnophila dubiosa* in ventral view; **F–I**, right mandibles in ventral view: **F**, *Gonomyia sulphuroides*, **G**, *Erioptera (Trimicra) inconspicua*; **H**, *Conosia irrorata*; **I**, *Limnophila dubiosa*. A–B, D-I redrawn from Wood (1952): C redrawn from McAlpine et al. (1981).

flattened, each with a slit-like pore apically, while each abdominal segment is often subdivided into two **annuli**, and transverse pads of spines and hooklets occur on both dorsal and ventral surfaces. The last body segment usually has spine-like processes that differ in male and female pupae.

TIPULID GENERA WITH AQUATIC STAGES KNOWN FROM SOUTHERN AFRICA: KEY TO LARVAE

Note: This key, modified from Wood (1952), separates the more common genera of Tipulidae whose larvae have been recorded in inland waters in southern Africa.

1. Border of spiracular disc divided into six to eight (commonly six) short lobes (Fig. 2.3A) (subfamily **Tipulinae**)..2
– Spiracular disc, if present, divided into fewer than six lobes of varying length (Figs 2.3B–I) (subfamily **Limoniinae**)..3

2. Anal lobes small and inconspicuous; larvae dwelling in moss.....*Dolichopeza*
– Anal lobes large and conspicuous (Figs 2.3A); not moss dwellers: if aquatic then in mud or beneath mats of *Juncus* or near streams or springs ....*Tipula*

3. No spiracles or spiracular disc but a single pair of long processes on terminal segment (Fig. 2.2C) .... *Antocha*
– Not a single pair of long processes on terminal segment; spiracular disc present or absent 4

4. Spiracular disc absent or lobeless; terminal segment short, tapering sharply to a blunt apex bearing the two spiracles (e.g. Fig. 2.3C, D)..........................5
– Spiracular disc surrounded by distinct lobes, which may be small or large (Fig. 2.3E–I) 6

5. Creeping welts or pedal warts present (as in Fig. 2.2B); terminal segment as in Figs 2.3C, D .... *Limonia (Dicranomyia) capicola*
– No pads, welts or warts ....*Rhabdiomastix* (*Sacandaga*)

6. Spiracular disc squarely truncate, edge divided into five lobes (Fig. 2.3F, I) of which the dorsal one may be very small 7
– Spiracular disc surrounded by four lobes (Figs 2.3B, E, H) 8

7. Spiracular disc without a fringe of hairs along the margins of the lobes; inner surfaces of lobes with a conspicuous pattern of dark markings (Fig. 2.3F); mandibles uniformly narrow, apically divided into teeth (Fig. 2.2F); in gravelly sand on stream margins .... *Gonomyia*
– Lobes of disc fringed with moderately long hairs along outer margins; inner surfaces of lobes clear, without dark markings (Fig. 2.3I); mandibles broad at base, tapering gradually to a large apical hooked tooth (Fig. 2.2G) ....*Erioptera* (*Trimacra*)

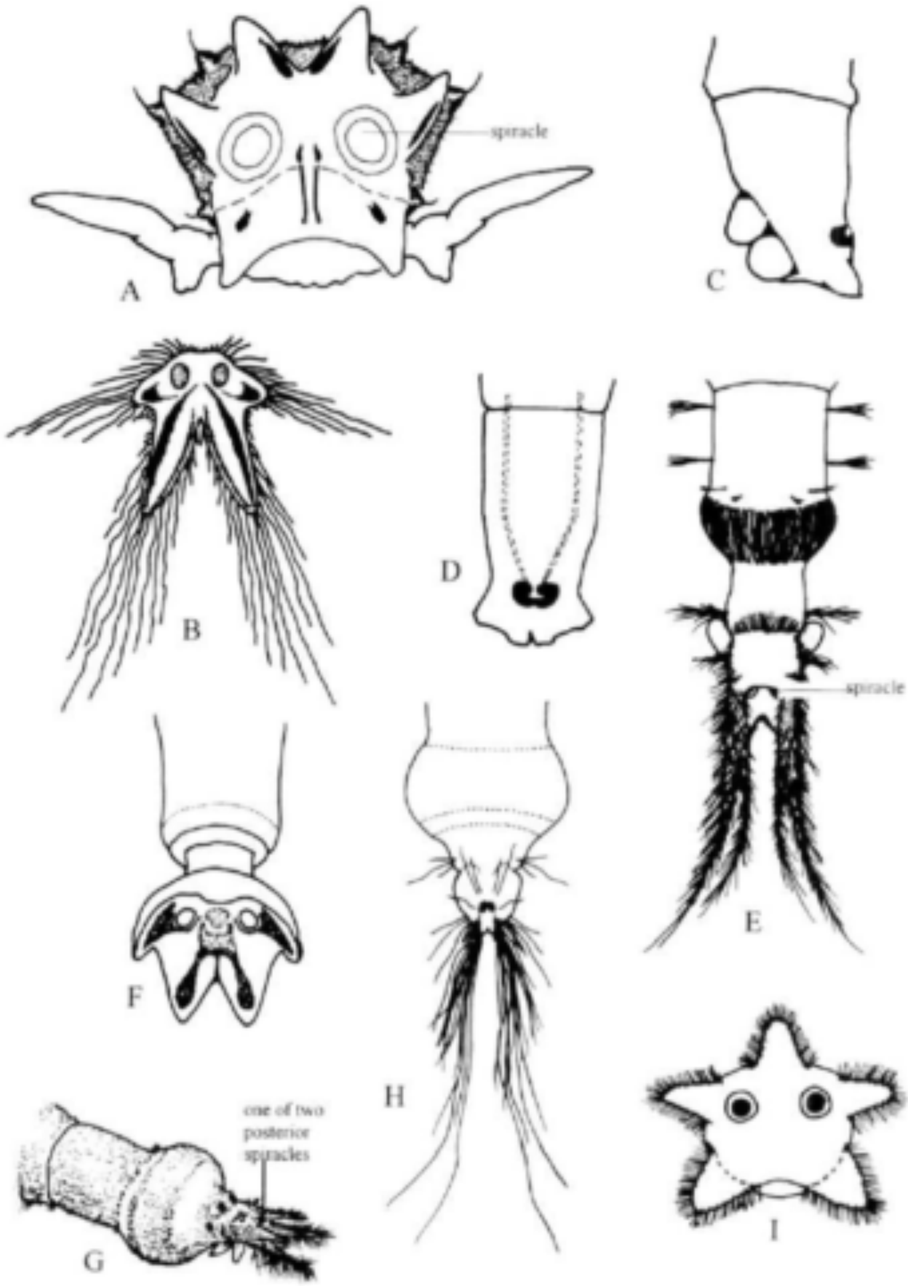


Fig. 2.3. Tipulid larvae (cont.): posterior segments and spiracular discs. **A**, *Tipula pomposa* in posterior view; **B**, *Conosia irrorata* in posterior view; **C**, *Limonia capicola* in lateral view; **D**, *L. capicola* in dorsal view; **E**, *Limonia dubiosa* in dorsal view; **F**, *Gonomyia sulphurelloides* in postero-dorsal view; **G**, *Limnophila* sp. in dorso-lateral view; **H**, *Limnophila crepusculum* in dorsal view; **I**, *Erioptera (Trimacra) inconspicua* in posterior view. A–F, H–I redrawn from Wood (1952), G redrawn from McAlpine et al. (1981).

8. Head capsule entire, compact, often minute; creeping welts dorsally on abdominal abdominal segments II–VII and ventrally on abdominal segments I–VII (Fig. 2.2B); abdominal segments not swollen anterior to disc; larvae in silt-covered gelatinous tubes in moss or on rocks .... *Limonia* spp.
– Head capsule (when dissected) consisting posteriorly of only four chitinous rods (Fig 2.2E); creeping welts absent; subterminal abdominal segment may be expanded to form a bulbous swelling (Fig. 2.3E, G, H); larvae in gravelly sand or mud spits, not in moss or on rocks..9

9. Maxilla (Fig. 2.2E) an elongate, flattened blade projecting antero-laterally...... 10
– Maxilla (e.g. Fig. 2.2A) not an elongate blade and not extending antero-laterally .... *Erioptera*

10. Mandible with a single ventral cutting tooth (Fig. 2.2H); ventral lobes of spiracular disc much longer than dorsal pair (Fig. 2.3B); larvae living at the edges of small trickles .... *Conosia*
– Mandible with three to four ventral cutting teeth (Fig. 2.2I); spiracular disc with microscopic lobes (Fig. 2.3H) or with lobes greatly elongated but of equal length (Fig. 2. 3E, G) .... *Limnophila*

TIPULID GENERA WITH AQUATIC STAGES KNOWN FROM SOUTHERN AFRICA: KEY TO PUPAE

Note: This key, also modified from Wood (1952), separates the more common genera of Tipulidae whose pupae are known from inland waters in southern Africa. Note that some tipulid pupae are found not in water but in damp places, usually close to waterbodies.

1. Sheaths of maxillary palps strongly curved or recurved at tips (Fig. 2.4D) (subfamily Tipulinae)..2
– Maxillary palps not recurved at tips (e.g. Fig. 2.4E) 3

2. Moss dwellers...Dolichopeza
– Living in mud, or beneath mats of *Juncus*, in or near streams or springs ....*Tipula*

3. Respiratory horns divided into eight long filaments (Fig. 2.4C)....... *Antocha*
– Respiratory horns undivided or minute 4

4. Basal transverse welt of hooks and spines on tergites 3–7 and sternites 5–7; pupae in silt-covered gel tubes in moss or on rocks ....*Limonia*
– No welts on tergites or sternites; pupae in gravelly sand or mud spits 5

5. Respiratory horns large, conspicuous (Figs 2.4B, E).................................6
– Respiratory horns microscopic, mere raised tubercles (e.g. Fig. 2.4F)...........9

6. Respiratory horns wide basally, twisted into flattened blades (Fig. 2.4E) ....*Erioptera* (subgenus *Trimicra*)
– Respiratory horns not twisted (Figs 2.4A, D), (if slightly twisted, as in Fig. 2.4B, the twisting is apical and not basal and the horns are not flattened) 7

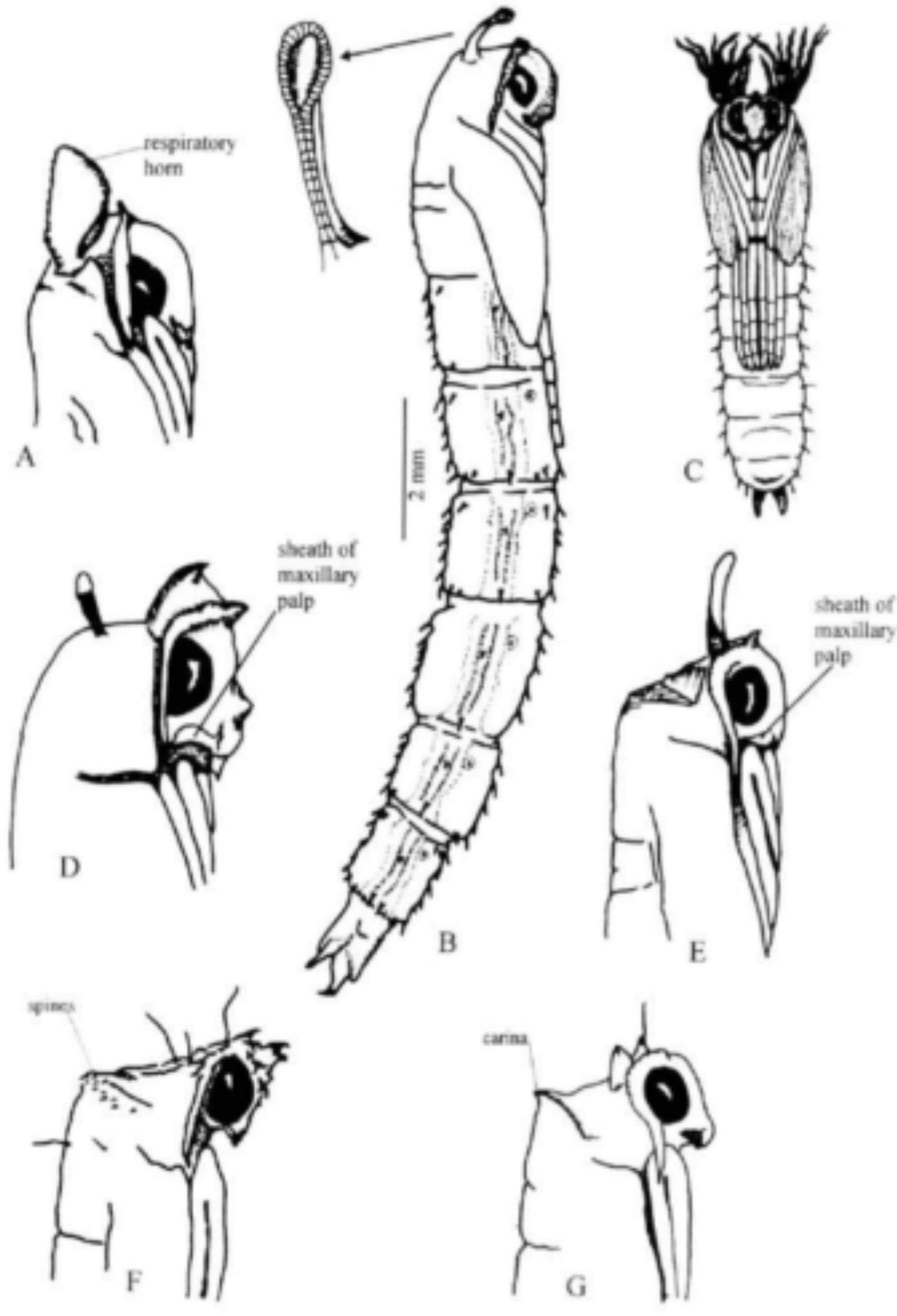


Fig. 2.4. Tipulid pupae, in right lateral view, unless otherwise stated. **A**, *Limonia tipulipes*; **B**, *Conosia irrorata*; **C**, *Antocha* sp. in ventral view; **D**, *Tipula coronata*; **E**, *Erioptera (Trimacra) inconspicua*; **F**, *Rhabdomastix afra*; **G**, *Goniomyia nigrobimbo*. A–B, D–G redrawn from Wood (1952); C redrawn from McAlpine et al. (1980).

7. Thorax immediately behind head deeply concave, bounded posteriorly by a transverse carina (Fig. 2.4G) .... *Gonomyia*
– No concave area or carina on thorax, which is entirely convex (e.g. Fig. 2.4A, B) 8

8. Respiratory horn slightly twisted apically into a funnel-shaped opening (Fig. 2.4B) .... *Conosia*
– Respiratory horn not twisted or dilated apically but cylindrical or tapering gradually to a narrow apex .... *Limnophila*

9. Cephalic crest conspicuous, consisting of numerous acute spines (Fig. 2.4F)..... .... *Rhabdomastix*
– Cephalic crest absent .... *Erioptera*

All of the genera mentioned above, some with a number of subgenera, are known from southern Africa. Most of the species that Wood placed in *Erioptera* are now placed on other genera, mainly in *Baeoura* (Hutson, 1980a) in the tribe Eriopterini. It is probably better to take the key entries to *Erioptera* as applying to the whole tribe.

Blephariceridae

net-winged midges

Figs 2.5A–B

The family Blephariceridae is small, with about 25 genera and 200 species widely distributed throughout the world. With minimal powers of dispersion, and the immature stages being dependent on the rushing water of rocky streams or the spray of waterfalls, many species are endemic to relatively small areas. Adult blephariceridss are slender, long-legged, often colourful, flies resembling small craneflies but with the wings held upwards when at rest. Shortly after they emerge and copulate, females glue their eggs, either singly or in small groups, to rock surfaces in the river bed. In some species this happens during the dry season, the eggs hatching only when the water level in the river rises. Both larvae and pupae are usually very dark in colour, sometimes almost black.

The larvae (Fig. 2.5A) are all aquatic and flattened. Segments are coalesced so that the entire animal appears to consist of only seven segments in all, including the head. Each 'segment' is furnished with a mid-ventral sucker, used for attachment to rocks in fast-flowing mountain streams and rivers. Locomotion is slow and is accomplished in two ways. Sideways progression, which occurs when the larva is alarmed, is done by releasing the terminal suckers at one end, rotating the body, reattaching the suckers, then repeating the action at the opposite end. Forward motion is by leech-like undulation. Larvae are browsers, feeding on diatoms and other algae on the rocks. There are four larval instars. The pupae (Fig. 2.5B) are also flattened and attached firmly to rocks in rivers.

Southern African blephariceridfauna

According to Stuckenberg (1980a), 19 species have been described from South Africa, all belonging to the genus *Elporia* in the subfamily Paltostomatinae. Except for one or two species in West Africa, and another in Argentina, all are endemic to southern Africa. We cannot be sure that this represents a gondwanian distribution, but we do know that within sub-Saharan Africa blephariceridss have been found only in South and West Africa. Species of *Elporia* are found in the Cape Fold Mountains, including Table Mountain (which is home to what appears to be a Cape Peninsula endemic), and in the Great Escarpment and the Drakensberg Mountains from the Eastern Cape to the Northern Province. A single species, *E. flavopicta*, occurs in both areas. Stuckenberg found none in the Zoutpansberg or in the eastern mountains of Zimbabwe, nor have any been recorded from the Rift Valley mountains of east African or Ethiopia. In Madagascar a group of at least eight species belongs to another genus, *Paulianina*, in the subfamily Edwardsininae.

Biology

According to Barnard (1947), at least one South African species, *Elporia barnardi* on Table Mountain, lays its eggs in a manner typical for the genus. Eggs are to be found during the dry season, from January to May, laid singly on rocks covered with a thin film of water or kept damp with spray. They adhere very firmly to a rock, are oval in shape, 0.2 x 0.25 mm, and blackish in colour. It appears that some of the rocks may become dry and yet the eggs still survive. Larvae appear in the river with the onset of rains.

Pupae adhere to rocks in the same situations as their larvae. Adults emerge from the pupal skins under water, their long legs allowing them to hold on to the pupal cases before escaping to the surface. Because the pupal case is anchored to the substratum under water, the emerging fly may not be able to harden quickly and one might therefore expect it to be swept away. This does not happen, though, because whereas most flies take a few minutes to harden, blepharicerids are almost immediately ready to fly, the wings being fully adjusted but neatly folded within the pupal skin.

Adults often congregate on the banks of streams or over foaming water at the base of cascades; when in the air they fly with an undulating movement. Males of some South African species swarm; they are also known to suck nectar from flowers. Females may or may not have mandibles but it is not clear to what use they are put when they are present (Stuckenberg 1980a).

Identification of immature blephariccerids

Blephariccerid larvae (Fig. 2.5A) are very characteristic, being limpet-shaped and bearing a mid-ventral row of suckers. The body appears to consist of only seven segments. The head, the three thoracic segments and the first abdominal segment are usually fused to form the cephalothorax; the next five abdominal segments are free and the last four (VII–X) also unite to form a single unit. All body segments have small lateral lobes that act as pseudopods. They respire through five pairs of tufted tracheal gills on the ventral surface.

Pupae (Fig. 2.5B) are flattened and anchored permanently to a rock by three pairs of ventral abdominal suckers. Antero-dorsally they bear a pair of structures, each consisting of four thin transverse plates, that are sometimes called 'respiratory horns'. They are not, in fact, equivalent to the true respiratory organs of other dipteran pupae but they apparently protect a pair of spiracles that open at their bases.

Psychodidae

moth flies, sewage flies

Figs 2.5C–G

The family Psychodidae is small but representatives occur almost worldwide. It is divided into several subfamilies (some authorities recognize as many as six), but only three are common in sub-Saharan Africa. Of these the Phlebotominae, a group of small biting flies (sandflies) of medical importance, do not have aquatic larvae, and the Bruchomyiinae are non-biting flies whose larvae are not aquatic. Larvae of most of the Psychodinae, which are not biting flies, feed on decaying matter such as droppings of herbivorous mammals, but some live in aquatic systems, particularly where there is gross organic pollution. They are usually abundant in the trickling filters of sewage purification works, so the adults are often called 'sewage flies'. Others, of the genus *Pericoma*, are found in mountain waterfalls; adults are known as moth flies because of their hairy wings.

Adult psychodids are small, brownish, hairy flies with broad, almost pointed wings. The larvae (Figs 2.5C–F) are characterized by one or (usually) more dorsal plates on most segments, and a short posterior siphon. Some (e.g. Fig. 2.5F) that live in fast currents have a midventral row of suckers. The tips of the legs of the pupae (Fig. 2.5G) do not extend posteriorly beyond the apices of the wing covers; the prothoracic respiratory horns are usually long and slender and the abdominal segments have one or more rows of short spines dorsally and ventrally.

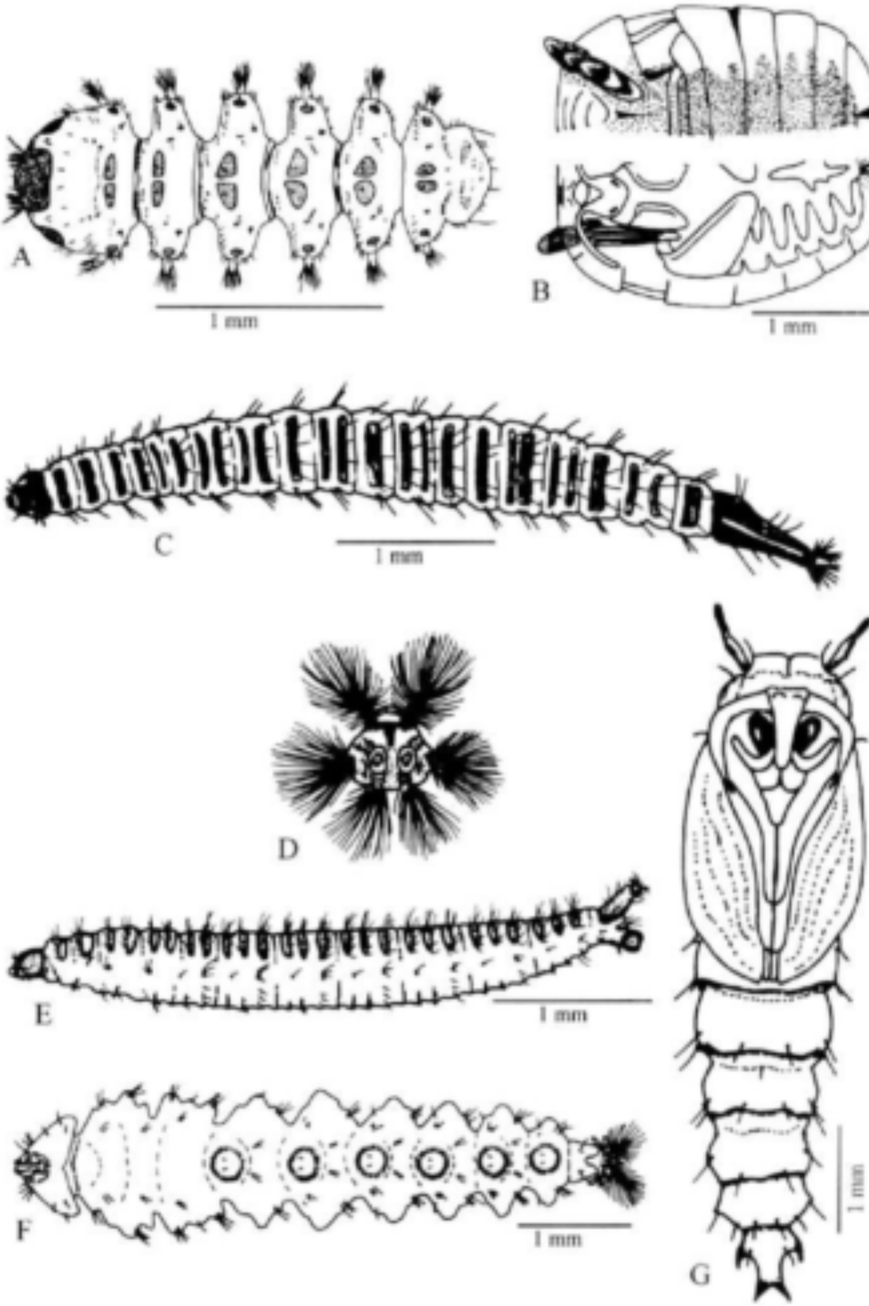


Fig. 2.5. A–B, Blephariceridae. **A**, larva of *Elporia* sp. in dorsal view; **B**, pupa of *Elporia* sp. in dorsal (upper) and ventral views. **C–G**, Psychodidae: **C–F**, larvae: **C**, *Clogmia albopunctata* in dorsal view, with **D**, spiracular disc in posterior view; **E**, *Pericoma* sp. in lateral view; **F**, *Telmatoscopus* sp. in ventral view; **G**, pupa of *Clogmia albipunctata* in ventral view. A redrawn from Stuckenberg (1955); B original; C, D, F, G redrawn from Hennig (1950); E redrawn from McAlpine et al. (1981).

Southern African psychodid fauna

Sixteen genera of Psychodinae are known from sub-Saharan Africa, represented in South Africa by twenty-three species, but probably many more await discovery. Duckhouse & Lewis (1980) comment that some South African species may show an affinity with far southern species in Australia and South America, but the bulk of the fauna is closer to that of the Palaearctic region. Of 20 recognized genera only three are endemic. Two of these genera fall within the Psychodinae. The largest genus is the cosmopolitan *Psychoda*, of which at least two species, *Psychoda alternata* and *P. severini*, are found in South African sewage purification works, together with the cosmopolitan *Clogmia albipunctata* (also known as *Telmatoscopus albipunctatus*). Large masses of sewage flies shedding wing hairs have been held responsible for causing asthma in sewage workers. *C. albipunctata* is also attracted to decaying carcasses and has been involved overseas in human myiasis (disease or injury caused by infestation by larval dipterans that are not necessarily parasitic (Smith & Thomas 1979).

Larvae of the genus *Pericoma* are found in mountain waterfalls in both the Cape Fold Belt and Drakensberg mountain ranges.

Biology

The eggs of only a few species have been described. In the genus *Psychoda* the number of eggs laid in a mass varies from 20 to more than 100. The rate of hatching varies greatly, probably depending on water temperature. Reported rates vary from 34–48 hours to 6–14 days. Larval development is rapid and the pupal stage lasts for only a few days. Thus populations can build up very quickly in sewage filters and other grossly polluted waters.

Identification of larvae and pupae

No keys are available to aquatic larvae and pupae. The most useful reference to the southern African representatives of the group is Duckhouse & Lewis (1980).

Ptychopteridae

phantom craneflies

Figs 2.6A, B

The Ptychopteridae form a very small family, similar to the true craneflies, except for a detail of the venation of the wings. Adults are usually 10–15 mm long and pale-coloured with darker wing markings. The larvae (Fig. 2.6A) are elongate and bear an unsegmented respiratory siphon posteriorly; the body segments have serially arranged hairs and abdominal segments I–III have a pair of small ventral prolegs, each with a single hook-like spine.

The pupae (Fig. 2.6B) have unequally developed thoracic horns, one very long and slender, exceeding the body length, and the other very short. Some of the leg sheaths are longer than the wing pads. Abdominal segments have transverse rows of spicules.

Southern African ptychopterid fauna

According to Alexander (1964) the family includes a total of 3 genera with 60 species worldwide, mostly in the genus *Ptychoptera*, which is the only genus found in South Africa so far. No ptychopterids have been discovered in Neotropical or Australasian regions. These flies are not common in South Africa or anywhere else.

Biology

Larvae are aquatic or semi-aquatic, living in shallow water or in saturated mud at the side of streams, or even in semi-liquid media, usually foul with decaying organic matter and often teeming with maggots of other flies. As this type of medium is generally deficient in oxygen, the respiratory tube is used for obtaining oxygen from the surface of the water.

Identification of immature ptychopterids

Superficially the larvae (Fig. 2.6A) resemble the rat-tailed maggot larvae of certain drone flies (Syrphidae), in that they also possess a long telescopic respiratory siphon. Ptychopterids, though, have a distinct (if small) head, while in syrphids no head is visible at all. There are no keys to the immature stages of the southern African forms. Of the eight species recorded from Africa, only two are known from southern Africa: *Ptychoptera capensis* from KwaZulu–Natal and Mpumalanga, and *P. stuckenbergi* from the Inyanga region of Zimbabwe. The most useful reference is Alexander (1964). Hutson (1980c) lists the species known from the Afrotropical region.

Dixidae

meniscus midges or—in the USA—dixa midges

Figs 2.6C–H

The family Dixidae is small and distributed worldwide. There seems to be very little endemism at generic level, the genera *Dixa* and *Dixella* being cosmopolitan. Adult dixids are non-biting flies, very similar to mosquitoes but lacking wing and body scales, and the antennae of males are not plumose.

All dixids have aquatic larvae and pupae. Larvae (Figs 2.6C–G), which usually take a U-shape when at rest (and when preserved), have a pair of ventral prolegs on each of the first two abdominal segments. The pupae (Fig. 2.6H) are generally similar to those of the Culicidae but the respiratory horns are short and widely separated, and lack long hairs and spines.

Southern African dixid fauna

There are about 200 species known worldwide. According to Freeman (1956b), eight species are known from, and endemic to, sub-Saharan Africa, seven in the genus *Dixa* and one in the genus *Dixella* (subgenus *Paradixa*). All are endemic to sub-Saharan Africa; of these, three are known only from South Africa. They are *Dixa capensis*, *Dixa bicolor* and *Dixella harrisoni*.

Biology

Adults gather in cool wet places near water, where males swarm in the evenings to mate. Eggs are laid in a gelatinous mass on a solid substratum in very shallow water in quiet pools, or at the edge of streams where the water is fairly still. Although the larvae can swim actively, they mostly crawl about on vegetation or over rocks at the water's edge, often adopting an inverted U-shape (Fig. 2.6G) in the meniscus, and filter minute organisms from the water by means of their mouth brushes. Before pupation, the larvae usually fix themselves to stones or plants in a damp shady place a few centimetres above the water level. The pupae rest just beneath the surface film of water for three or four days before the adults emerge.

Identification of immature dixids

Larvae of the genus *Dixa* bear crowns of feathered setae (Fig. 2.6E) on abdominal segments I–VII, distinguishing them from those of *Dixella*, from which these setae are absent (Hutson 1980d). Wood (1934), describing the larvae of *Dixa bicolor*, states that they are dark brown, about 6–6.5 mm long, with dorsal hair-crowns on abdominal segments III–VII; abdominal segments V–VII bear ventral locomotory plates with spines; the antennae have only microscopic spinules; the mandibles are well-developed and almost sickle-shaped; the labrum bears two well developed hair brushes; the front part of the prothorax below the head bears some stout bristles; the two circular posterior spiracles are situated below six branched bristles and each spiracular plate has a hair fringe, as does a pair of lateral plates; the body ends in a caudal appendage with six long, microscopically plumose, setae.

Freeman (1956a) provides a key to adult dixids from sub-Saharan Africa but no keys are available to immature stages.

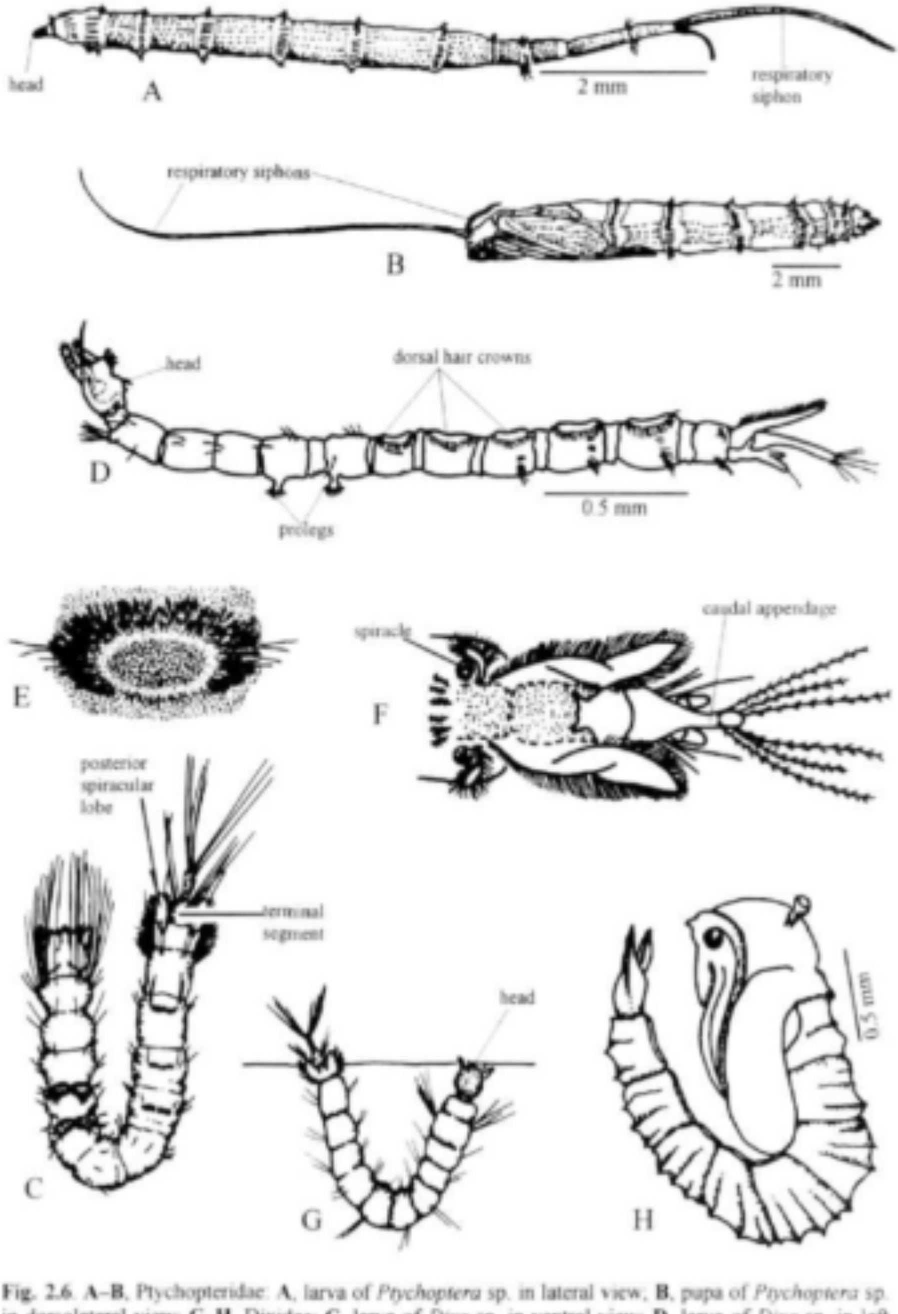


Fig. 2.6. **A–B**, Ptychopteridae: **A**, larva of *Ptychoptera* sp. in lateral view; **B**, pupa of *Ptychoptera* sp. in dorsolateral view; **C–H,** Dixidae: **C**, larva of *Dixa* sp. in ventral view; **D**, larva of *Dixa* sp. in left lateral view; **E**, crown of setae from a tergum of a *Dixa* larva; **F**, posterior segments of *Dixa* sp. in dorsal view; **G**, position of a *Dixa* larva hanging from the meniscus; **H**, dixid pupa in left lateral view. A, B redrawn from McAlpine et al. (1981); C redrawn from Usinger (1956); D, F redrawn from Wood (1934); E redrawn from Merrit & Cummins (1978); G, original, H redrawn from Hennig (1950).

Chaoboridae

phantom midges, lake flies

Figs 2.7A, B

The Chaoboridae is a small family of mosquito-like flies with a world-wide distribution. Hutson (1980e) estimates that the family consists of a few more than 100 species. Until recently the chaoborids were included as a subfamily within the Culicidae but the two differ in that in adult chaoborids, scales are confined to the wing margins and the veins are beset with long dense hairs, while in culicids scales are found on both wing margins and the upper surface of the wing; in chaoborids, too, although a short proboscis is present, adults apparently do not feed.

Adults are small to medium flies, 1.4–10 mm in length, delicate, usually pale yellow, gray or brown, and often occurring in huge swarms consisting mostly of females. In Central Africa the local people collect them under these conditions and compress them into a cake known as 'Kungu Cake'.

As in the culicids, all three thoracic segments are united but the larvae of chaoborids (Fig. 2.7A) are carnivorous, the antennae being large and prehensile and used for catching prey. A spiracle is borne at the apex of a respiratory siphon of varying length on segment VIII, except in *Chaoborus*, (the commonest species in lakes), which has neither a spiracle nor a respiratory siphon. Since most chaoborids spend some time in mid-water, they are almost totally transparent, which is why they are known as 'ghost larvae' or 'phantom midges'.

Pupae (Fig. 2.7B) generally resemble culicid pupae but in chaoborids the thorax is less than a third of the total length of the pupa (more than a third in culicids), and the abdomen hangs straight down instead of curving forwards beneath the cephalothorax, as it does in culicids.

Southern African chaoborid fauna

Only eight sub-Saharan species are known and of these only one, *Chaoborus* (*Sayomyia) microstictus*, occurs in South Africa. Although the larvae and pupae are very common in lakes, reservoirs and other bodies of standing water, not much is known about their taxonomy and there is no key. They are all very typical of the genus.

Biology

The eggs of *Chaoborus* are laid on the water surface and are enclosed in a gelatinous mass. In other genera they are deposited in the debris at the edges of pools. According to Hutson (1980e), the immature stages of all species are carnivorous and fully aquatic. The elongate transparent larvae

(Fig. 2.7A) of the genus *Chaoborus* have two pairs of kidney-shaped air sacs, one pair on the thorax and one towards the end of the abdomen. They use the air in these sacs to rise in the water column, where they hang horizontally. At night they slowly descend to the substrate where they lie concealed in the mud. Their food consists of a variety of invertebrates, particularly mosquito larvae and copepods. They have no spiracles and oxygen is absorbed through the skin.

The pupae (Fig. 2.7B), like those of the mosquitoes, can move actively in the water. Their abdominal paddles are not movable, whereas those of the culicids are.

Hutson (1980e) deals with the Afrotropical chaoborids but no keys exist to immature forms.

Corethrellidae

Fig. 2.7C

The Corethrellidae is a small family of midges, very close to the Chaoboridae. According to Borkent (1993) the family includes only 62 extant species, all in the genus *Corethrella*. Most species are tropical and only three have been recorded from the Afrotropical region. Adults are small (1.3–2.5 mm), delicate, and usually gray, brown or blackish. They are distinguished from adult Chaoboridae in the structure of the mouthparts, in that those of female corethrellids are functional and of female chaoborids are not.

The larvae (Fig. 2.7C), which are all aquatic, are predatory with strong mandibles and prehensile antennae, and spiracles borne on the end of a rather short siphon. According to Borkent (1993) their prehensile antennae are not used for feeding and are not strictly homologous with those of the Chaoboridae. Corethrellid larvae lack the air sacs of chaoborids.

The pupae differ from those of chaoborids in that they are rather sharply tapered posteriorly with very narrow swimming paddles that are completely fused basally (Fig. 1.6F).

Southern African corethrellid fauna

Of the three species known in sub-Saharan Africa, only one is known from South Africa. This is *Corethrella harrisoni*, a few adults of which have been caught at Magoebaskloof in the Northern Province. They were described by Freeman (1956b).

Biology

All corethrellid larvae prefer large bodies of standing water. They are predators, feeding on other aquatic organisms. Nearly all adult females have functional mouthparts that seem to be used for blood-sucking. Apart from one species found feeding on a frog, their preferred hosts are unknown. Not much else seems to be known about the biology of the larvae.

Identification of immature corethrellids

Since only a single species (*Corethrella harrisoni*) is known from the area, the main key will suffice to identify larvae and pupae.

Very little has been written about the group but Freeman (1956b) and Borkent (1993) provide an introduction to the literature.

Thaumaleidae

solitary midges

Figs 2.7D–E

The Thaumaleidae is a small family with worldwide distribution. Only two genera, *Thaumalea* and *Trichothaumalea*, are known from the Northern Hemisphere. According to Stuckenberg (1980b), the family is of great zoogeographical interest. *Afrothaumalea*, the only Afrotropical genus, appears to be a palaeogenic, austral element of the fauna, sharing features of wing venation with the New Zealand type species of *Austrothaumelea* Tonnoir, a genus recorded also from temperate Australia and South America. They seem, therefore, to represent a true gondwanian connection.

Adults are small flies, about 2 mm long, rather similar to psychodids but without hairs. They are not active fliers and, according to Oldroyd (1964), tend to occur in cool regions such as higher altitudes in mountainous areas.

The larvae (Fig. 2.7D) are elongate and cylindrical with a broad, unpaired proleg on the prothorax and another at the end of the abdomen, each proleg being armed with a series of stout, curved hooks. The head is well-developed and non-retractile. Each thoracic and abdominal segment is sclerotized dorsally and body segments bear dark setae laterally. The prothorax has a pair of short respiratory tubes dorsally and abdominal segment VIII has a transverse respiratory opening near the hind margin, flanked by a pair of sclerotized finger-like processes with dark setae apically.

Pupae (Fig. 2.7E) resemble those of the Tipulidae and have short thoracic respiratory organs.

Southern African thaumaleid fauna

Only about 50 species are known worldwide. The only Afrotropical species named so far, which is found in South Africa, is *Afrothaumelea pamelae*, although Stuckenberg (1980b) mentions a second unnamed species from South Africa.

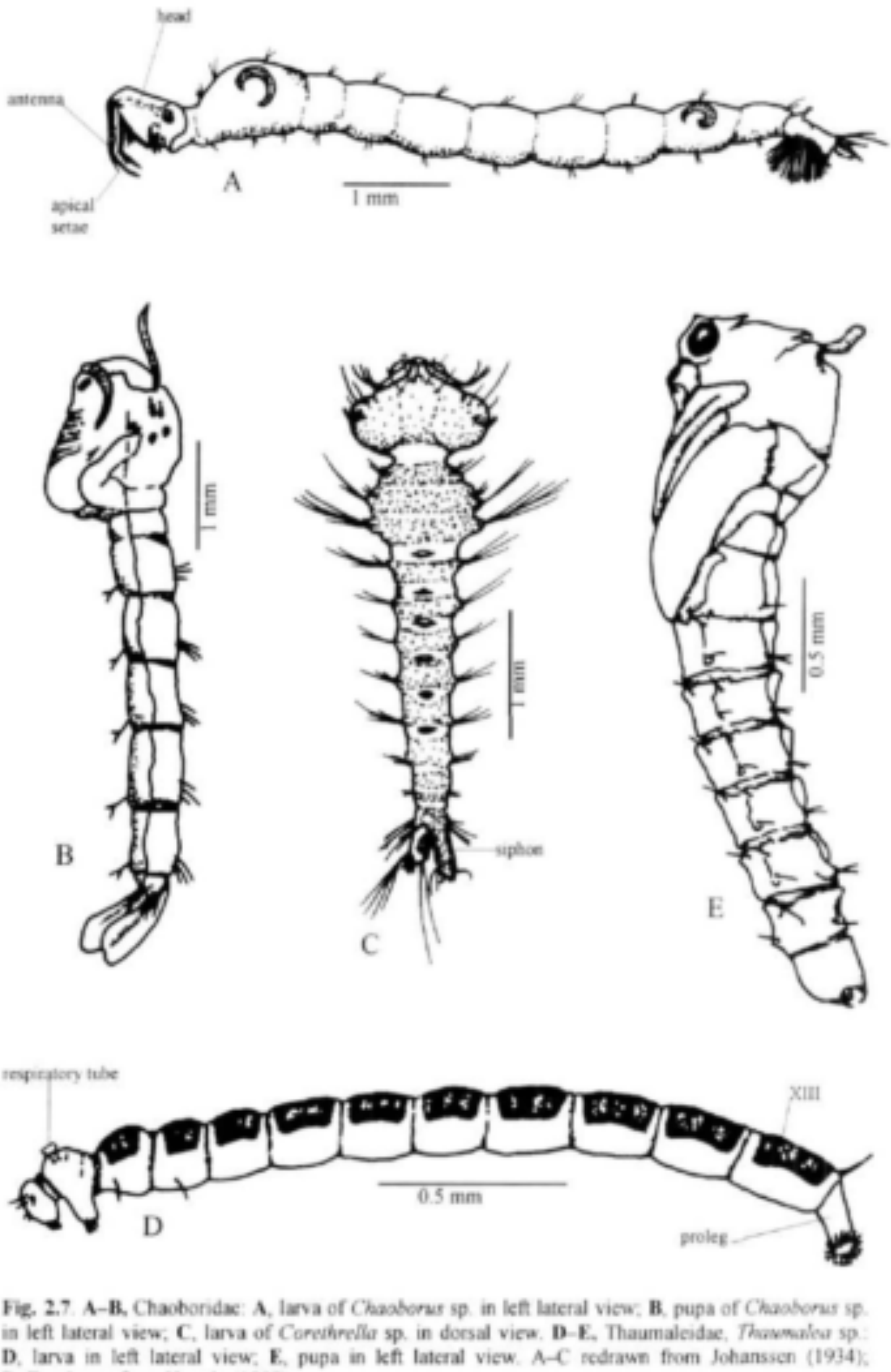


Fig. 2.7. **A–B**, Chaoboridae: **A**, larva of *Chaoborus* sp. in left lateral view; **B**, pupa of *Chaoborus* sp. in left lateral view; **C**, larva of *Corethrella* sp. in dorsal view. **D–E**, Thaumaleidae, *Thaumalea* sp.: **D**, larva in left lateral view; **E**, pupa in left lateral view. A–C redrawn from Johanssen (1934); D–E redrawn from Hennig (1950).

Biology

Larvae of all thaumeliids are aquatic and live partly submerged in a thin layer of water flowing over rocks in cool mountain streams (Stuckenberg, 1980b). The pupae are found in mud or wet moss near water (Oldroyd, 1964).

Identification of immature thaumaleids

Immatures thaumaleids have been described only by (Oldroyd, 1964) and Stuckenberg (1980b).

USEFUL REFERENCES

ALEXANDER, C.P. 1913. A revision of the South American dipterous insects of the family Ptychopteridae. *Proceedings of the United States National Museum* **44**: 331–334.

ALEXANDER, C.P. 1920. The craneflies of New York, Part II. Biology and phylogeny. *Cornell University Agricultural Experimental Station Memoirs* **38**: 691–1133.

ALEXANDER, C.P. 1964. Diptera (Nematocera) Tanyderidae, Ptychoptoridae, Tipulidae. *In*: Hanström, B., Brink, P. & Rudebeck, G. (Eds) *South African Animal Life* **10**: 229–441.

ALEXANDER, C.P. & BYERS, W. 1981. Tipulidae. *In*: McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R. & Wood, D.M. (Eds) *Manual of Nearctic Diptera*, Vol. 1. Agriculture Canada Monograph 27, Ottawa: 153-190.

BARNARD, K.H. 1947. The Blephariceridae (Diptera) of the S.W. Cape. *Journal of the Entomological Society of Southern Africa* **10**: 1–15.

BOWDEN, J. 1978. Diptera. *In*: Werger, M.J.A. (Ed.) *Biogeography and Ecology in Southern Africa* **2**: W. Junk, The Hague: 775–796.

BORKENT, A. 1993. A world catalogue of fossil and extant Corethellidae and Chaoboridae (Diptera) with a listing of reference keys, bionomic information and descriptions of each known life stage. *Entomologica Scandinavia* **24**: 1–24.

CROSSKEY, R.W. 1980. (Ed.) *Catalogue of the Diptera of the Afrotopical Region.* British Museum of Natural History, London.

DOWNES, J.A. 1969. The swarming and mating flight of Diptera. *Annual Review of Entomology* **14**: 271–298.

DUCKHOUSE, D.A. & LEWIS, D.J. 1980. Family Psychodidae. *In*: Crosskey, R.W. *Catalogue of the Diptera of the Afrotropical Region*. British Museum of Natural History, London: 93–105.

FREEMAN, P. 1956a. A revision of the species of *Dixa* (Diptera: Culicidae) from Africa South of the Sahara. *Proceedings of the Royal Entomological Society* (London) (B) **25**: 163–170.

FREEMAN, P. 1956b. Notes on Chaoboridae (Diptera: Nematocera) with descriptions of a new genus and two new species from Australia and Africa. *Proceedings of the Royal Entomological Society of London* (B) **31**: 41–43.

HEMMINGSEN, X.M. 1952. The oviposition of some cranefly species (Tipulidae) from different types of localities. *Videnskabelige Meddelelser fra Dansk*

Naturhistorisk Forening i Kjobenhavn: 365–320.
HENNING, W. 1950. *Die Larvenformen der Dipteren*, 2 Teil, Berlin.
HUTSON, A.M. 1980a. Family Tipulidae. *In*: Crosskey, R.W. (Ed.) *Catalogue of the Diptera of the Afrotropical Region*. British Museum of Natural History, London: 47–91.
HUTSON, A.M. 1980b. Family Tanyderidae. *In*: Crosskey, R.W. (Ed.) *Catalogue of the Diptera of the Afrotropical Region*. British Museum of Natural History, London: 92.
HUTSON, A.M. 1980c. Family Ptychopteridae. *In*: Crosskey, R.W (Ed.). *Catalogue of the Diptera of the Afrotropical Region*. British Museum of Natural History, London: 106–107.
HUTSON, A.M. 1980d. Family Dixidae. *In*: Crosskey, R.W. *Catalogue of the Diptera of the Afrotropical Region*. British Museum of Natural History, London: 110–111.
*HUTSON, A.M. 1980e. Family Chaoboridae. *In*: Crosskey, R.W. *Catalogue of the Diptera of the Afrotropical Region*. British Museum of Natural History, London: 112–113.
JOHANNENSEN, O.A. 1934. Aquatic Diptera. Part I. Nematocera exclusive of Chironomidae and Ceratopogonidae. *Cornell University Agricultural Experimental Station*, Memoir no. 164
MCALPINE, J.F., PETERSON, B.V., SHEWELL, G.E., TESKEY, H.J., VOCKEROTH, J.R. & WOOD, D.M. 1981. (Eds) *Manual of Nearctic Diptera*, Vol. 1. Agriculture Canada Monograph 27, Ottawa.
MERRIT, R.W. & CUMMINS, K.W. 1978. *An Introduction to the Aquatic Insects of North America*. Kendall/Hunt, Dubuque.
OLDROYD, H. 1964. *The Natural History of Flies*. Weidenfeld & Nicoloson, London.
SCHOLTZ, C. & HOLM, E. 1985. *Insects of Southern Africa*. Butterworths, Durban.
SCOTT, H. 1915. The early stages of *Paltostoma schineri* Will. (Diptera: Blepharoceridae). *Annals and Magazine of Natural History* **15**:181–202.
SMITH, K.G.V. & THOMAS, V. 1979. Interstitial myiasis in man caused by *Clogmia albipunctatus* (Psychodidae: Diptera). *Transactions of the Royal Society of Tropical Medicine and Hygiene* **73**: 349–350.
STUCKENBERG, B.R. 1955. New Blepharoceridae from South Africa. *Annals of the Natal Museum* **13**: 175–208.
STUCKENBERG, B.R. 1980a. Family Blepharoceridae. *In*: Crosskey, R.W. (Ed.) *Catalogue of the Diptera of the Afrotropical Region*. British Museum of Natural History: 108–109.
STUCKENBERG, B.R. 1980b. Thaumaleidae. *In*: Crosskey, R.W. (Ed.) *Catalogue of the Diptera of the Afrotropical Region*. British Museum of Natural History: 149.
WIRTH, W.W. & STONE, A. 1956. Aquatic Diptera. *In*: Usinger, R.L. (Ed.) *Aquatic Insects of California*. University of California Press, Berkeley: 372–482.
WOOD, H.G. 1934. Notes on the life history of *Dixa bicolor* Wood (Diptera). *Stylops* **3**: 205–208.
WOOD, H.G. 1952. The craneflies of the South West Cape (Diptera: Tipulidae). *Annals of the South African Museum* **39**: 1–327.

* **Note**: Hutson (1980e) includes a note on the genus *Corethrella*

CHAPTER 3

CERATOPOGONIDAE

by

*B. de Meillon† & W. W. Wirth† **

The Ceratopogonidae, commonly known as 'biting midges', 'no-see-ums' or 'punkies', form a very large family of midges. According to de Meillon & Wirth (1991) the family includes 89 genera and some 4732 species throughout the world, with 703 species in 50 genera recorded from the Afrotropical Region.

Ceratopoghonids are typical members of the Nematocera and are closely related to the Chironomidae, with which they share many characters. Adults of the two families can be distinguished from each other by details of the veins of the wings and also by the mouthparts. While ceratopogonids have biting mouthparts (many feed on mammalian blood), adult chironomids do not feed and so their mouthparts are not functional. Adult ceratopogonids are small flies, 1–4 mm in length, and are not often collected. Except for those that have attained importance because they bite humans, the family is poorly known.

The larvae of most species bear a sclerotized head capsule, although in a few the sclerotization is not obvious. Their cylindrical bodies are usually entirely unadorned with setae or protuberances (e.g. Figs 3.1C–E), although some have an anterior proleg and bodies are adorned with hairs and other protuberances (Figs 3.1A–B). Relatively few species have aquatic larvae.

Southern African ceratopogonid fauna

De Meillon & Wirth (1991), in a monograph on elements of the Afrotropical Ceratopogonidae, do not separate the South African species from those of the whole region, but it is clear that most of the species they record have been found in some part of South Africa. They state that of the 50 genera and 19 subgenera known in the region, 15 genera of the tribe Ceratopogonini and one subgenus of *Forcipomyia* are endemic to the region, also that the tribe Ceratopogonini has evolved to a remarkable degree in the region, exhibiting strong Gondwanaland affinities with the

* This chapter, which was originally written in 1988, has been modified and updated by AD Harrison.

faunas of southern South America and the Australasian region.

The family is represented in southern Africa by four subfamilies: the Leptoconopinae, whose larvae are found in saline to alkaline wet sand or soil; the Forcipomyiinae, whose larvae are aquatic or semi-aquatic; the Dasyheleinae with aquatic larvae, most of which live in small temporary habitats; and the Ceratopogoninae, whose larvae swim.

Biology

Habits of adult ceratopogonids are diverse, but most species are adapted to some type of bloodsucking. Species of *Culicoides, Lasiohelea* and *Leptoconops* suck vertebrate blood and some are notorious pests, especially in beach or mountain resort areas. Some species of *Culicoides* are known vectors of diseases, including onchocerciasis of horses and cattle, blue tongue of sheep, cattle horse-sickness, several human viruses and filariases, and *Haemoproteus* and *Leucocytozoon* diseases of birds. Females of most of the aquatic genera prey on small soft-bodied insects, such as adult aquatic midges and mayflies. Some species of *Atrichopogon* and *Forcipomyia* are ectoparasitic on larger insects. Many genera, for example *Dasyhelea*, visit flowers, feeding on nectar; some species of such genera either do not suck blood at all, or supplement their diets with nectar.

Ceratopogonid larvae are found in large numbers in nearly every aquatic or semi-aquatic habitat in every region of the world. The immature stages of the southern African Ceratopogonidae are found mostly in damp or wet places. Some are found under bark or on wet wood (e.g. *Forcipomyia*); in animal manure and wet decomposing plant material such as rotting banana stalks (e.g. some species of *Culicoides*); in damp sand along the sea shore or in desert oases (*Leptoconops*); in mud or wet sand at the margins of ponds, lakes, or streams; in and around moss and leaves floating on or dipping into water; and in the water itself. Those living in water may occur in leaf axils or flower bracts, in rock pools and tree holes, at the margins of ponds, lakes and slow-flowing streams with vegetation, or in seepages over mossy rocks and stones. The pupae of each species occur in the same environments as the larvae. They are mainly inactive, but work their way to the surface to breathe and for eclosion of the adult stage.

Identification of immature ceratopogonids

The immature stages of aquatic Ceratopogonidae from southern Africa, and indeed from the whole of the sub-Saharan region, are not well known. The last attempt to deal with them was by Mayer (1955), from whom the following account is drawn.

The eggs are usually somewhat elongate and taper to each end, but some modifications occur at subfamilial and tribal level. The larvae (Figs 3.1A–F), being typical nematocerans, usually have a sclerotized head capsule bearing mandibulate mouthparts and short antennae, and an elongate, poorly-sclerotized body consisting of three thoracic segments and nine abdominal segments. Spiracles and segmented legs are absent and the characteristic feature of many ceratopogonid larvae is the lack of spines and setae, and indeed of any ornamentation except perhaps a few fine terminal setae. Details of larval structure vary with the subfamily, the Forcipomyiinae (Figs 3.1A–B) being small caterpillar-like forms with prolegs that enable them to move around in comparatively dry situations, in contrast to the slender eel-like structure of other subfamilies (Figs 3.1C–F).

The pupae (Figs 3.1G–J) are more or less conical in shape and do not vary between subfamilies to the same extent that the larvae do, merely showing differences in some structures such as the bristles of the thoracic and abdominal tubercles, the shape of the respiratory horns, the number of spiracular openings, and shape of the terminal abdominal segment.

KEY TO THE SUBFAMILIES OF CERATOPOGONIDS WITH AQUATIC LARVAE

1. Anterior and posterior prolegs present (Figs 3.1A–B).. Subfamily **Forcipomyiinae**
– No prolegs (Fig. 3.1C–F) 2

2. Head capsule strongly sclerotized (Fig. 3.1C) Subfamily .... **Dasyheleinae**
– Head capsule weakly, or not, sclerotized (Figs 3.1D–F) 3

3. Body segments with secondary divisions, thus appearing to consist of more than 14 segments, including the head (Fig. 3.1D) .... Subfamily **Leptoconopinae**
– Body segments not divided, body seeming to consisting of 14 or fewer segments, including the head (Figs 3.1E–F)......Subfamily **Ceratopogoninae**

NOTES ON THE SUBFAMILIES OF CERATOPOGONIDAE*

These notes are taken mostly from de Meillon & Wirth (1991). Note that as well as the four cosmopolitan subfamilies mentioned below, a fifth, the monospecific Austroconopinae, is known from Australia.

Subfamily **Forcipomyiinae**
Figs 3.1A–B, G

The larvae are flattened dorso-ventrally and the mouthparts point ventrally. Body segments usually bear well-developed hairy or spiny processes. Anterior and posterior prolegs are present, distinguishing them from larvae of all

* Details of individual species and their distributions can be found at http://www.ru.ac.za/academic/departments/zooento/Martin/aceratopogonidae.html

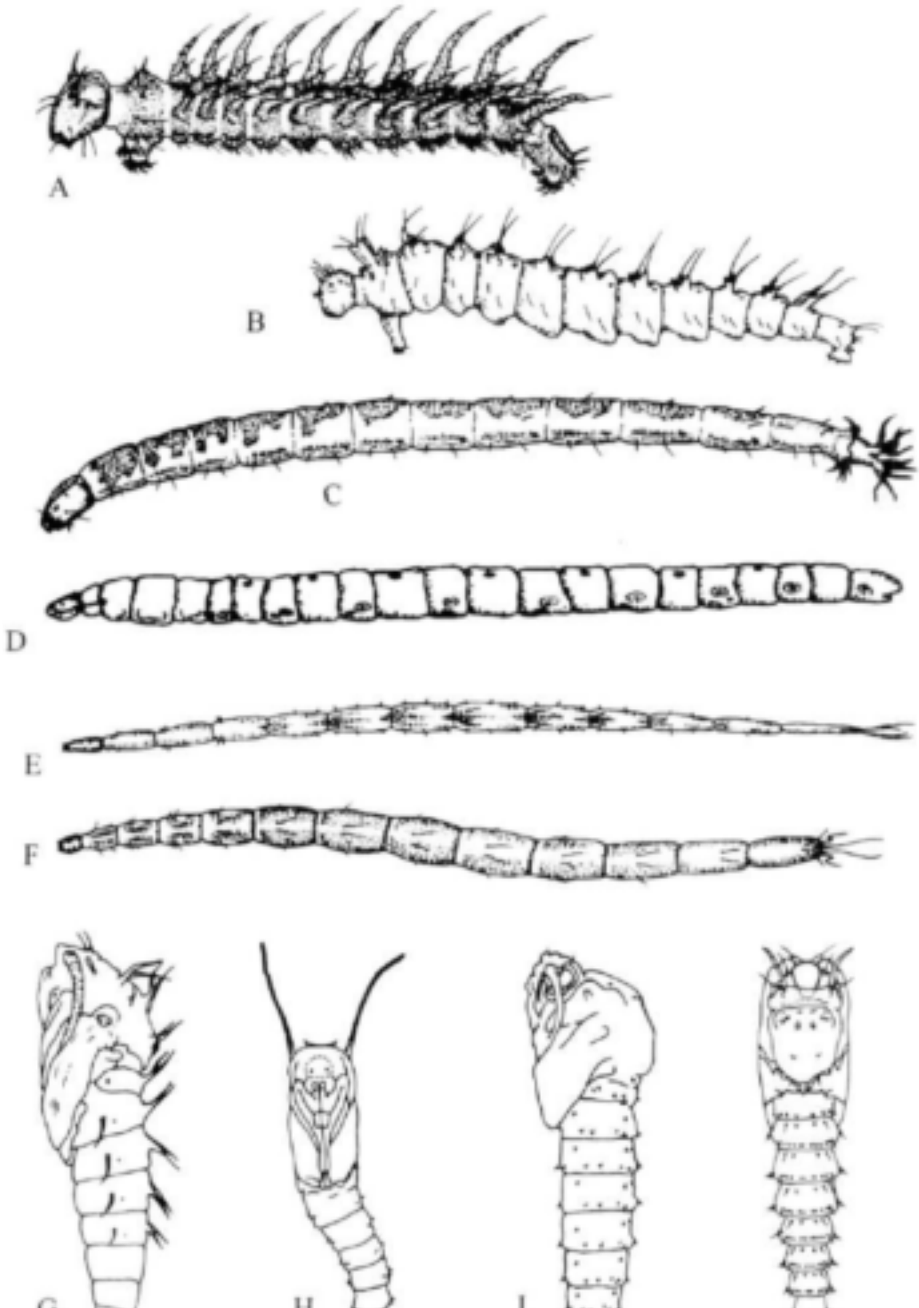


Fig. 3.1. A–F, Larval ceratopogonids in left lateral view. **A**, *Forcipomyia* sp. (Forcipomyinae); **B**, *Atrichopogon* sp. (Forcipomyinae); **C**, *Dasyhelea* (Dasyheleinae); **D**, *Leptoconops* (Leptoconopidae); **E**, *Bezzia* (Culicoidinae); **F**, *Culicoides* (Culicoidinae). **G–J**, pupal ceratopogonids: **G**, *Atrichopogon*; **H**, *Dasyhelea*; **I**, *Leptoconops*; **J**, *Culicoides*. A–C, E–J redrawn from McAlpine et al. (1981), D redrawn from de Meillon & Wirth (1991).

other subfamilies. Pupae (Fig. 3.1G) are stout and taper posteriorly, the last larval exuviae being retained on the tail (but not shown in the figure). Larvae are aquatic or semi-aquatic. Immature stages are usually found on the surfaces of wet wood or stones, the larvae feeding mainly on diatoms and other micro-flora. The subfamily consists of two genera, *Forcipomyia* with close to 100 species, and *Atrichopogon*, with 55. Most of the aquatic species belong to *Atrichopogon*, nine species of which are known from southern Africa.

Subfamily **Dasyheleinae**

Figs 3.1C, H

Larvae are aquatic, often being found in small temporary habitats. The larval body is curved, the head capsule short and stout, and the mouth directed ventrally. The last segment has terminal hooks. The pupae (Fig. 3.1H) are somewhat similar to those of the Ceratopogoninae but the last pupal segment has a pair of extra lateral processes, each bearing a seta. Eggs are of an unusual U-shape and are deposited in small clusters. Immature stages are often found in or on mats or masses of algae. The phytophagous larvae do not swim but creep, using their mouthparts and the terminal hooks on the abdomen. The only genus is *Dasyhelea*, with 79 species known worldwide; thirteen of these have been recorded in southern Africa.

Subfamily **Leptoconopinae**

Figs 3.1 D, I

The head capsule of leptoconopid larvae is not sclerotized but is supported by internal sclerotized rods and levers. The body is often yellowish to pinkish in colour. Eggs are slender. Immature stages are found not in water but in wet saline to alkaline sand or soil, the larvae often burrowing to considerable depths. Pupae (Fig. 3.1I) are stout-bodied. Nine species are known worldwide, of which six have been recorded from southern Africa.

Subfamily **Ceratopogoninae**

Figs 3.1 E, F, J

The subfamily Ceratopogoninae is a large diverse group known from six tribes, some 89 genera and nearly 5000 species. The five tribes with aquatic larvae are particularly well represented in the Afrotropical region and the southern hemisphere. (The sixth tribe, the Culicoidini, does not have aquatic larvae. It comprises two genera and some 1200 species, 150 or so of which are known from southern Africa). Of the remaining 88 genera, 50 (and some 700 species) are known from the Afrotropical region; 15 of these genera are endemic to the Afrotropical region and another 11 are cosmopolitan, while only seven genera are exclusively northern.

The larvae of the five tribes are the most aquatic in the family, being elongate and straight-bodied and swimming with an eel-like motion. They lack prolegs; the body bears no setae except for a terminal circle around the anus; the head is pear-shaped or oval and often very elongate; and the mouth is directed anteriorly. Eggs are elongate and often deposited in long ribbons. The larvae are important predators of other small aquatic animals.

Tribe **Ceratopogonini**

Larval habits are various, some sluggish and crawling through damp moss or algae in semi-aquatic habitats, some swimming vigorously at water surface or in deeper waters, others creeping though algal mats or wet soil' (De Meillon & Wirth, 1991). Most larvae are predacious.

The tribe is known from 45 genera and 854 species; of these, 15 genera are Afrotropical endemics, mostly from southern Africa, and another 11 genera have Afrotropical representatives. The Afrotropical endemic genera are listed below. Where a specific epithet is provided, the genus is monospecific.

Afrohelea capensis (South Africa)
Ankylohelea montana (South Africa)
Bothahelea (three species, one from South Africa and two from Zimbabwe)
Bothamia demeilloni (South Africa)
Calcarhelea bimater (South Africa)
Capehelea steli (South Africa)
Ceratohelea advena (Zimbabwe)
Congohelea fulgipennis (Congo)
Fanthamia (14 species, 13 from South Africa and one from the Congo)
Luciamyia biloba (South Africa)
Metacanthohelea cogani (Kenya, Aldabra)
Neohelea pastoriana (Guinea)
Notoceratopogon (four species, all from South Africa)
Paralluaudomyia maculata (Congo)
Stiloculicoides ugandae (Uganda)

The genera *Allohelea*, *Alluaudomyia*, *Brachypogon*, *Ceratopogon*, *Kolenohelea*, *Monohelea*, *Neurobezzia*, *Parabezzia*, *Pellucidomyia* and *Stilobezzia* are represented both within the Afritropical region and elsewhere.

Tribe **Heteromyiini**

Nine genera and 73 species are known, four genera and 45 species of these having been recorded only from the southern hemisphere. Fourteen species are Afrotropical. It seems that no species is endemic to the region and even the genera are fairly widely scattered. The genera with the greatest number of African species are *Clinohelea* (seven of the 35 species, but only two of those seven in southern Africa) and *Tetrabezzia* (four of the six species but only one of the four in southern Africa).

Tribe **Sphaeromiini**

This tribe is fairly large, with 21 genera and 321 species. It is best represented in the Old World tropics. No genera are confined to the Afrotropics although 73 species in 12 genera are known from the region. *Homohelea, Mackerrasomyia, Jenkinshelea* and *Neosphaeromias* are all circum-Indian-Ocean genera with representatives in southern Africa; of the cosmopolitan genera, 12 of the 49 species of *Mallochohelea* are African, as are eight of the 64 species of *Nilobezzia* and eight of the 37 species of *Sphaeromias*.

Tribe **Palpomyiini**

The Palpomyinae is a cosmopolitan tribe of six genera and 555 species, most of which occur in the neotropics. Three genera are represented in southern Africa: eleven of a total of 22 species of *Palpomyia*; six of a total of ten species of *Phaenobezzia*; and 36 of a total of 262 species of *Bezzia*.

Tribe **Stenoxenini**

The Stenoxenini form a small tribe of two genera and 56 species. Of these, three species of *Stenoxenus* have been recorded from southern Africa.

REFERENCES

DE MEILLON, B. 1956. Diptera (Nematocera): Ceratopogonidae. *In*: Hanström, B., Brinck, P. & Rudebeck, G (Eds) *South African Animal Life* **6**: 325–355.

DE MEILLON, B. & WIRTH, W.W. 1991. The genera and subgenera (excluding *Culicoides*) of the Afrotropical biting midges (Diptera: Ceratopogonidae) 1991. *Annals of the Natal Museum* **32**: 27–147.

DOWNES, J.A. & WIRTH, W.W. 1981. Ceratopogonidae. *In*: McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R. & Wood, D.M. (Eds) Manual of Nearctic Diptera Volume 1. Research Branch, Agriculture Canada, Quebec. Monograph **27**: 393–421.

FIEDLER, O.G.H. 1951. The South African biting midges of the genus *Culicoides* (Ceratopogonidae, Diptera). *Onderstepoort Journal of Veterinary Research* **25**: 3–33.

MAYER, K. 1955. Beitrag zur Ökologie und Morphologie afrikanischer Heleiden (Diptera). *Archiv für Hydrobiologie* **51**: 98-117.

WIRTH, W.W. & STONE, A. 1956. Aquatic Diptera. *In*: Usinger, R.L. (Ed.) *Aquatic Insects of California*. University of California Press, Berkeley: 372–482.

WIRTH, W.W., DE MEILLON, B. & HAESELBARTH, E. 1980. Family Ceratopogonidae. *In*: Crosskey, R.L. (Ed.) *Catalogue of the Diptera of the Afrotropical region*. British Museum of Natural History, London: 150–174.

CHAPTER 4

CULICIDAE

by

M. Coetzee

The mosquitoes belong to the family Culicidae of the suborder Nematocera. Adults can be distinguished from other similar flies by the conspicuous, forwardly-projecting proboscis, numerous appressed scales on the body, legs and wing veins, and a fringe of scales along the posterior margins of the wings (Service, 1980). Mosquitoes play an important role in the transmission of human diseases such as malaria, filariasis and various arboviruses. Hence they are one of the best studied families within the Diptera. Only female mosquitoes suck blood as they need the protein to develop their eggs. Not all species are blood-suckers, however, and indeed, all females of the subfamily Toxorhynchitinae need only the nectar of flowers in order to develop egg batches. Male mosquitoes do not have mouthparts that are adapted for piercing skin and therefore do not suck blood. Males can be distinguished from females by their very hairy antennae. Mosquito larvae are recognized by having a distinct head, thorax and segmented abdomen.

THE SOUTHERN AFRICAN CULICID FAUNA

Mosquitoes are classified into the Order Diptera, Family Culicidae and three subfamilies —Anophelinae, Toxorhynchitinae and Culicinae (Knight & Stone, 1977). In southern Africa (i.e. south of the Zambezi River) there are more than 220 species of mosquitoes belonging to 13 genera arranged in all three subfamilies (Gillies & Coetzee, 1987; Jupp, 1996). This is fairly well representative of the general mosquito fauna in the African region. There are no genera endemic to southern Africa and only about 30 species endemic to the sub-region. Adult females are easily identified to subfamily by posture, the shape of the proboscis and the length of the maxillary palps (Figs 4.1A–C).

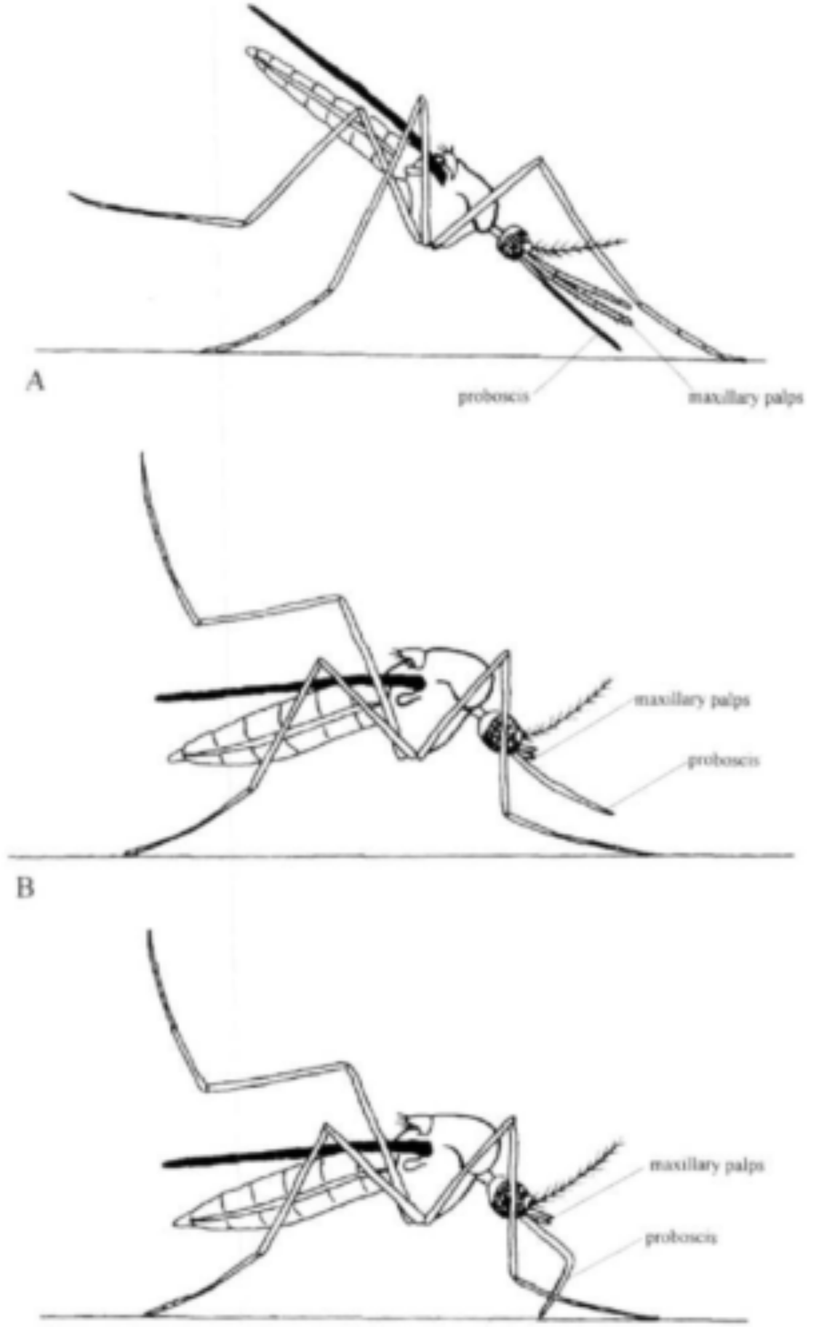


Fig. 4.1. Typical body shapes and resting positions of adult mosquitoes. **A**, anopheline—with abdomen at an angle of 45° to substrate and maxillary palps as long as proboscis; **B**, culicine—with abdomen parallel to substrate and maxillary palps shorter than proboscis; **C**, toxorhynchitine—posture similar to that of culicinines, but proboscis distinctly bent in the middle.

BIOLOGY

Some species of *Culex* can survive for long periods without laying eggs, e.g. when over-wintering. The occasional blood meal will be taken but the female will only venture out of her refuge once the environmental conditions are conducive to egg-laying. Some species of mosquitoes can lay their first batch of eggs without taking a blood meal but thereafter need a blood meal for every egg-laying. Mosquitoes of the genus *Malaya* have a curious feeding behaviour: they suck honey-dew from cocktail ants (*Crematogaster* spp.) by inserting their proboscides into the mouths of these ants when they open their jaws (Service 1990). Like *Toxorhynchites* adults, they do not need blood to develop their eggs.

Female mosquitoes can lay from 30 to 300 eggs at a time, depending on the species. Some species (e.g. of *Culex* and *Anopheles*) deposit their eggs directly onto the surface of the water (Figs 4.2A & C), while others, such as *Aedes* spp., lay their eggs just above the water level on damp substrates (Figs 4.2B). Such eggs can usually withstand desiccation. Eggs (Fig. 4.2A–C) are normally blackish in colour and ovoid, but there is considerable variation: for example, *Toxorhynchites* eggs do not turn black after being laid (Muspratt 1951), while some species of *Mansonia* have skittle-shaped eggs (Service l980).

Mosquito larvae live in a wide range of habitats including temporary rain pools, artificial water containers, reservoirs, swamps and slow-moving streams. They are filter feeders, feeding on yeasts, bacteria, protozoans and other micro-organisms. Larvae go through four moulting stages and development from first instar larva to pupa may last from seven to 30 days depending on the species and temperature. Living larvae

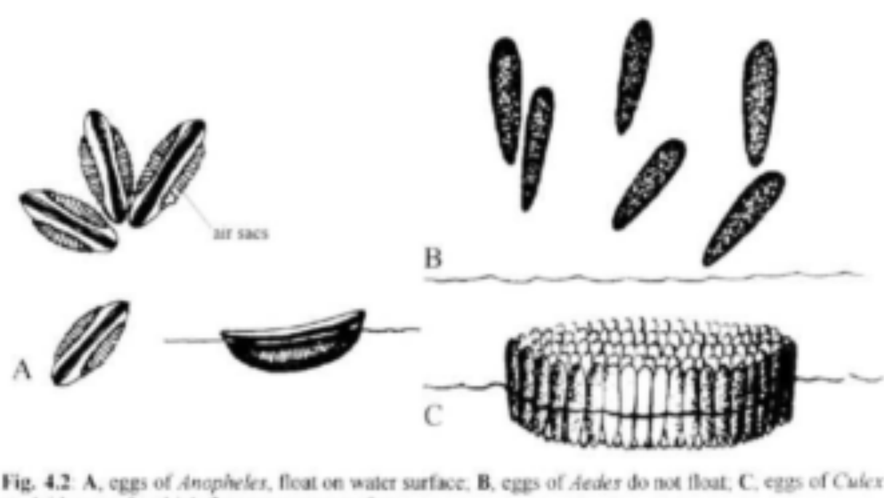


Fig. 4.2: **A**, eggs of *Anopheles*, float on water surface; **B**, eggs of *Aedes* do not float; **C**, eggs of *Culex* are laid as a raft, which floats on water surface.

of *Anopheles* can be recognized by their feeding and breathing positions at the surface of the water (Fig. 4.3A): they are surface feeders, lacking a breathing tube or siphon, and therefore lie parallel with the meniscus of the water. Culicine larvae usually browse over the substratum looking for food and only come to the surface of the water to breathe (Fig. 4.3B). Species of the genera *Mansonia* and *Coquillettidia* have highly specialized respiratory siphons (Fig. 4.6G) that pierce roots or stems of aquatic vegetation to obtain oxygen from air cells in the aerenchyma tissue of the plants.

Pupae of all mosquitoes are comma-shaped (Fig. 4.4A) and capable of brisk movement, using the paddles at the tip of the abdomen. They do not feed during this stage. They breathe through respiratory trumpets on the cephalothorax (Fig. 4.4A), pupae of *Mansonia* and *Coquillettidia* having modified trumpets (Fig. 4.8F) for breathing through plant stems. The pupal stage usually lasts two to three days.

IDENTIFICATION OF IMMATURE CULICIDAE

Larvae

Mosquito larvae (Fig. 4.5A) can be distinguished from all other dipterous larvae because they have a thorax in which all three segments are fused and which is wider than either the head or the abdomen. They also have a complete head capsule and only one pair of functional spiracles at the tip of the siphon or, in the case of the Anophelinae, at the tip of the last abdominal segment.

The head bears a pair of one-segmented lateral **antennae** (Fig. 4.5A) with an apical brush of six setae and one or more **subapical setae** (Figs 4.6D & F) that sometimes define a stouter basal portion from a more

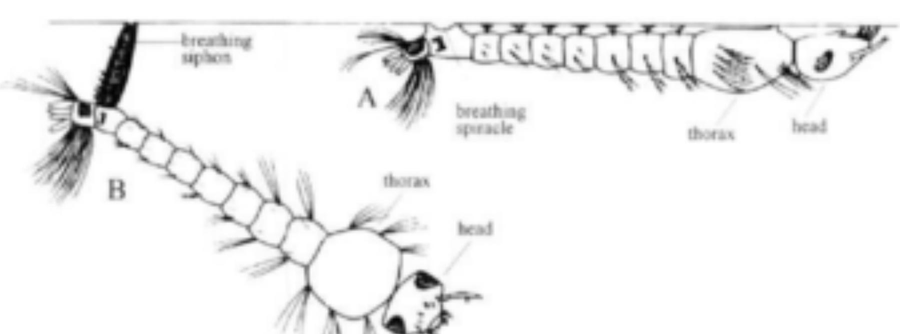


Fig. 4.3 Mosquito larvae: posture and feeding behaviour. **A**, anopheline: lying parallel with the meniscus of the water and feeding from the surface. **B**, culicine: breathing through a siphon, with head hanging downwards and feeding from deeper waters.

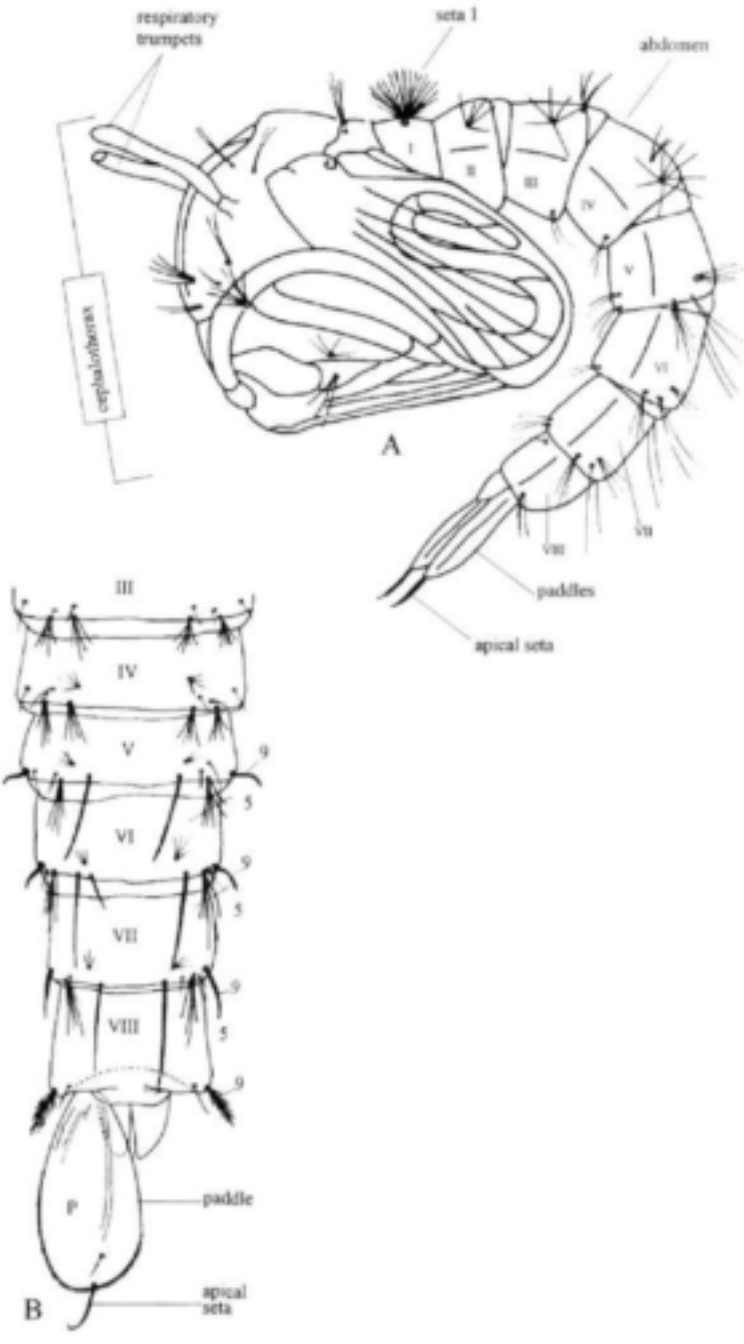


Fig. 4.4. Typical mosquito pupa: **A**, whole animal (lateral view); **B**, abdomen (dorsal view).

flexible distal portion. Mosquitoes are particle/filter feeders, the mouthparts bearing lateral **palatal brushes** (Fig. 4.5A) that may be modified to form a series of stout teeth (Fig. 4.6C) in predatory forms. Setae on the dorsal surface of the head may be well- (Fig. 4.6D) or poorly- (Figs 4.6F & 4.6H) developed, and may be single or branched, sometimes being many-branched (e.g. Figs 4.6D, F & H). The positions of setae are described by numbers, as indicated in Fig. 4.6F.

The **thorax** (e.g. Fig. 4.5A) consists of three fused segments.

The **abdomen** consists of ten apparent segments—the ninth being fused with the eighth—and numbered with Roman numeral I–X. The posterior end is usually asymmetrical, with a **respiratory siphon** (called the **spiracular apparatus** in Anophelinae) extending dorsally from segment VIII (Figs 4.5B, 4.5C). On the siphon, setae of taxonomic significance include the **subdorsal** and **subventral tufts** (Figs 4.7B–4.7D) and on segment X, setae, or groups of setae, numbered 1–4 (see Figs 4.7E–4.7G).

Segment VIII may bear a series of setae forming a **comb** laterally (Fig. 4.5C), while the inner (ventral) surface of the siphon usually bears another series of setae known as the **pecten** (e.g. Fig. 4.5C). The abdominal segments bear a number of setae, annotated in Arabic numerals, of which those occurring postero-laterally on the dorsal surface that are numbered '1' (e.g. Figs 4.5A & 4.6A) are of taxonomic significance at the generic level, particularly if they are **palmate** (shaped like a palm-leaf: Figs 4.5A & 4.6A). A **chitinous plate** (Fig. 4.6A) may be present on the dorsal surface of one or more abdominal segments.

Pupae

The head and thorax are united to form the **cephalothorax**, bearing a pair of **respiratory trumpets** (Fig. 4.4A), which may be flared (Fig. 4.8B) or parallel (Fig. 4.8E) at the tip. The length of the trumpet is divided into a distal **pinna** and a proximal **meatus**. The pinna is the part of the trumpet from the apex to an imaginary line drawn more or less perpendicular to the longitudinal axis at the most proximal margin of the spiracular opening, and may be modified (Fig. 4.8F). The meatus (e.g. Fig. 4.9E) is the part of the trumpet from the base to the imaginary line. The basal portion may be tracheated, i.e. have distinct transverse striations on the external surface (Fig. 4.8F, 4.9E).

The **abdomen** consists of eight obvious segments, the ninth and tenth being much reduced, sometimes visible as small lobes fused to segment VIII. Segments IX and X are usually indistinct and are normally ignored for taxonomic purposes, except in the case of *Toxorhynchites* spp. in which two distinct setae are found on Segment X (Fig. 4.8C). The positions of abdominal setae of taxonomic significance are numbered 1, 5 and 9 (Fig 4.4B). Setae 5 on segments IV to VI may be finely setose, giving the

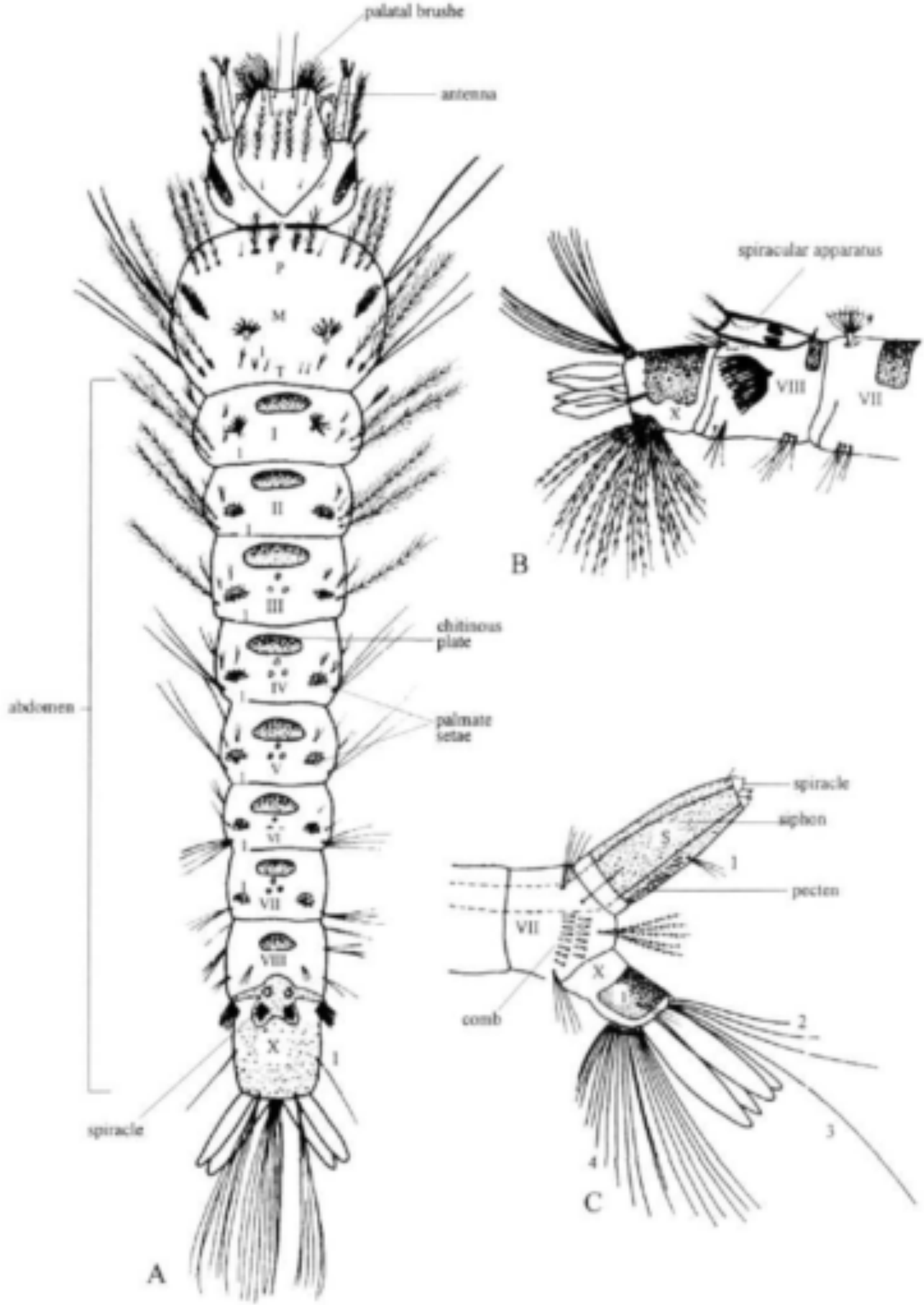


Fig. 4.5. Mosquito larvae. **A**, typical anopheline, whole animal (dorsal view). **B**– **C**, terminal segments of abdomen showing breathing apparatus and salient features (note that abdominal segment IX is fused to segment VIII and is never indicated in illustrations): **B**, typical anopheline; **C**, typical culicine.

appearance of being 'frayed' (Fig. 4.8J). Posteriorly, the abdomen bears a pair of **paddles** (e.g. Figs 4.4A, 4.4B), used in swimming. Each of these may or may not bear a single large **apical seta** (e.g. Figs. 4.4B, 4.8A), have a border of fringing setae (e.g. Fig. 4.8C, 4.9B) be **cleft** (indented) at the tip (e.g. Figs. 4.8H, 4.8I) and/or be **excavated** medially near the base (e.g. Figs 4.8K, 4.9K).

KEY TO THE GENERA OF FOURTH-STAGE SOUTHERN AFRICAN CULICID LARVAE

Note: Except where specified, the genera are well represented over the whole southern African region (i.e. south of the Zambezi River). *Anopheles, Culex* and *Aedes* have the greatest number of species. The recent revision of the Culicinae and Toxorhynchitinae by Jupp (1996) is recommended for further information and that of Gillies & de Meillon (1968) and Gillies & Coetzee (1987) for the Anophelinae.

Keys and illustrations used here are adapted from Edwards (1941), Hopkins (1952) and Mattingly (1971).

SOUTHERN AFRICAN CULICID LARVAE: KEY TO TAXA

1 Respiratory siphon absent (Figs. 4.3A, 4.5B); seta 1 on most abdominal segments palmate (Figs 4.5A, 4.6A) (Subfamily **Anophelinae**) .... *Anopheles* (*c.* 50 species)

– Siphon present (Figs 4.3B, 4.5C); seta 1 never palmate 2

2. Large lateral chitinous plate present on abdominal segment VIII (Fig. 4.6B) 3

– No such plate present (Subfamily **Culicinae**) 5

3. Palatal brushes comprise about ten strong curved spines (Fig. 4.6C); abdominal comb and pecten absent (Fig. 4.6B) (Subfamily **Toxorhynchitinae**) .... *Toxorhynchites* (two species)

– Palatal brushes not modified as above, consisting of a large number of very fine setae (e.g. Fig. 4.5A); comb set on edge of lateral chitinous plate; pecten present or absent (Subfamily **Culicinae**) 4

4. Antennae very large, greatly flattened, about a quarter as wide as long (Fig. 4.6D); siphon with a pair of long curved spines apically (Fig. 4.6E) .... *Aedeomyia* (two species)

– Antennae neither large nor flattened; siphon without spines apically .... *Uranotaenia* (16 species)

5. All head setae poorly developed (Figs 4.6F, 4.6H); siphon conical with serrated saw-like processes towards the apex (Fig. 4.6G) 6

– Head setae well developed (Fig. 4.6D); siphon lacking serrated, saw-like processes towards the apex 7

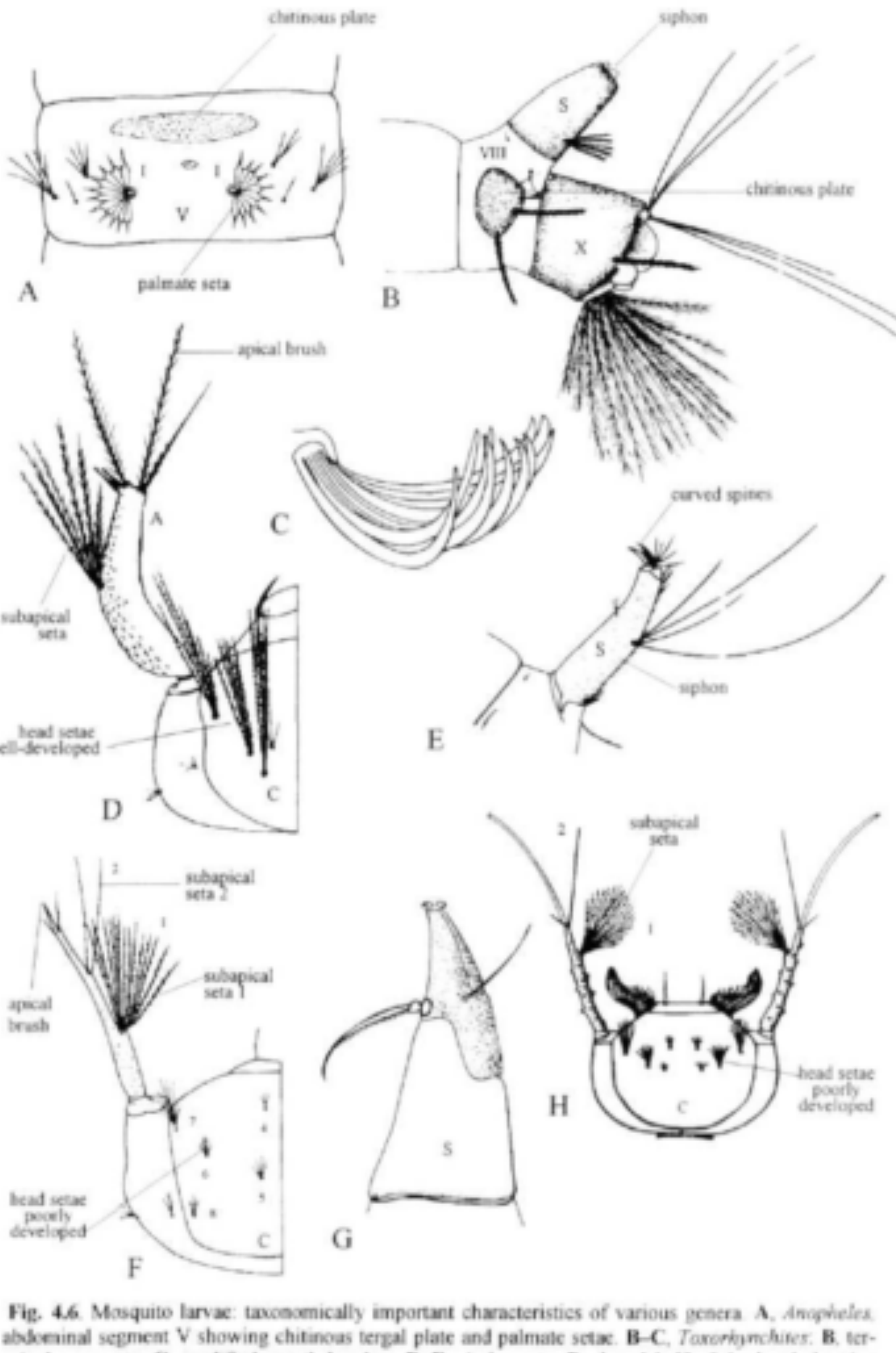


Fig. 4.6. Mosquito larvae: taxonomically important characteristics of various genera. **A**, *Anopheles*, abdominal segment V showing chitinous tergal plate and palmate setae. **B–C**, *Toxorhynchites*: **B**, terminal segments; **C**, modified mouth brushes. **D–E**, *Aedeomyia*: **D**, dorsal half of the head showing typical development of antennae and head setae; **E**, siphon with curved spines. **F–G**, *Mansonia*: **F**, half of the head in dorsal view; **G**, siphon showing adaptations for piercing hollow plant stems. **H**, *Coquillettidia*, head (dorsal view) showing distinctive antennae.

6. Portion of antenna beyond subapical setae about as long as basal portion, and flexible (Fig. 4.6H); comb of four to ten sharp pointed spines .... *Coquillettidia* (nine species)
– Portion of antenna beyond subapical setae much shorter than basal portion (Fig. 4.6F), and rigid; comb of two to three blunt-ended spines (Fig. 4.7A)... .... *Mansonia* (two species)

7. Siphon with a dorsal or subdorsal row of four or five multiple-branched tufts of setae (Fig. 4.7B) .... *Malaya* (one species)
– Siphon with at most two such tufts, of which one, if present, is subdorsal and the other is lateral (Fig. 4.7C) 8

8. Siphon with more than one subventral tuft (Fig. 4.7C): usually numerous tufts present but may be very small and inconspicuous or consist of single hairs (Fig. 4.7C) .... *Culex* (*c.* 45 species)
– Siphon with only one subventral tuft (Fig. 4.7D)..9

9. Seta 1 of siphon placed much before one-third of length from base (Fig. 4.7D)....10
– Seta 1 of siphon at least a third of distance from base (Fig. 4.7G)........11

10. Comb forming a patch of numerous small teeth (Fig. 4.7D)............................ .... *Culiseta* (two species)
– Comb forming a single row of not more than about ten teeth (Fig. 4.7G)....... .... *Ficalbia* (two species)

11. Seta 3 of abdominal segment X with at least three branches (Fig. 4.7E).......... .... *Mimomyia* (seven species)
– Seta 3 of abdominal segment X single (Fig. 4.7G) or (rarely) double (Fig. 4.7F) 12

12. Setal region 4 of segment X with four setae that are single or branched and whose bases do not form a barred area (Figs 4.7E, 4.7G); pecten reduced with at most four spines (Fig. 4.7F) .... *Eretmapodites* (three species)
– Setal region 4 of segment X often with more than four setae that are usually branched and whose bases always form a conspicuous barred area; pecten of at least eight spines (Fig. 4.7G) .... *Aedes* (*c.* 80 species)

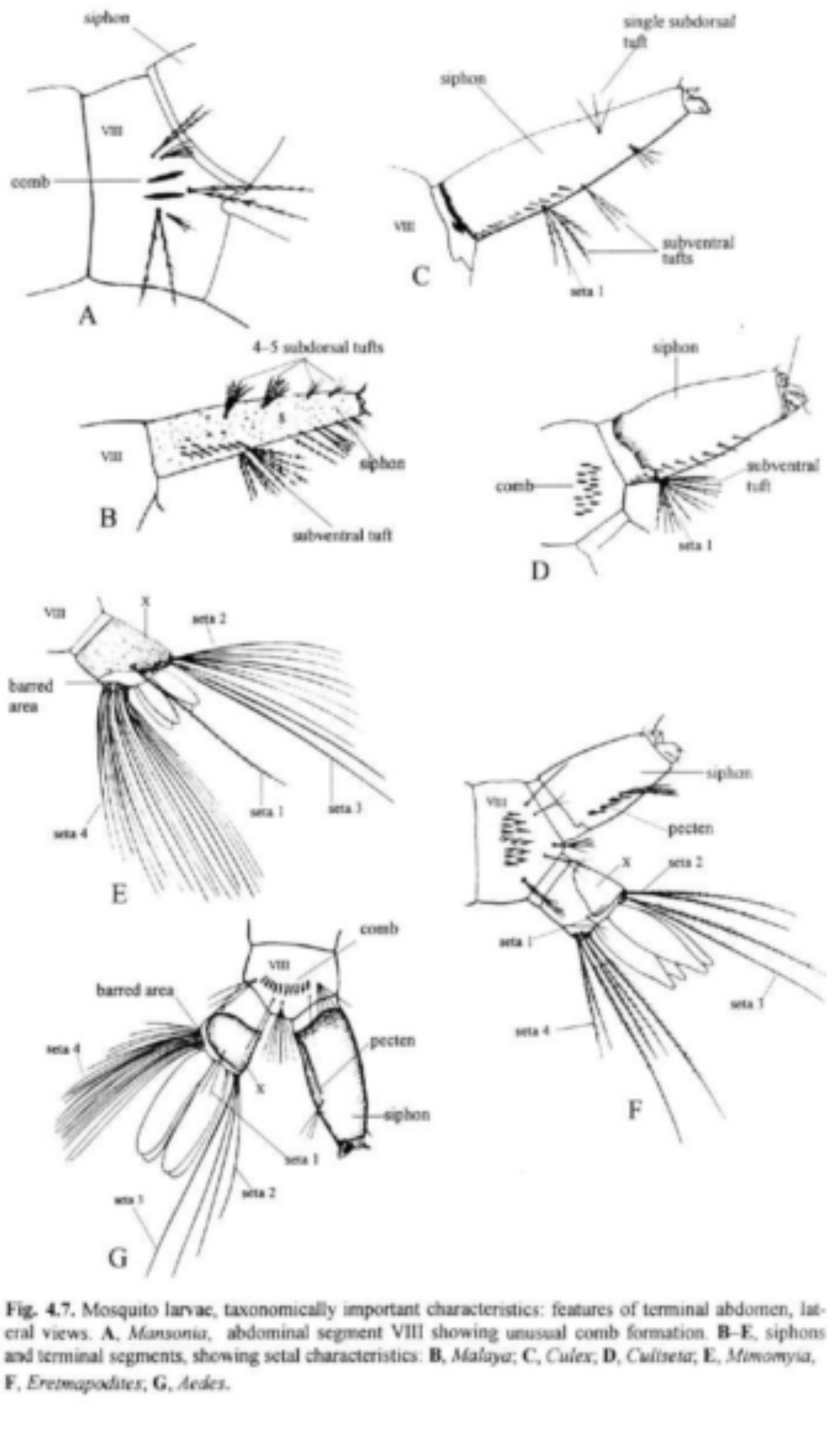


Fig. 4.7. Mosquito larvae, taxonomically important characteristics: features of terminal abdomen, lateral views. **A**, *Mansonia*, abdominal segment VIII showing unusual comb formation. **B–E**, siphons and terminal segments, showing setal characteristics: **B**, *Malaya*; **C**, *Culex*; **D**, *Culiseta*; **E**, *Mimomyia*, **F**, *Eretmapodites*; **G**, *Aedes*.

KEY TO THE GENERA OF SOUTHERN AFRICAN CULICID PUPAE[1]

1. Respiratory trumpets short, about twice as long as broad and widely flared; seta 9 of abdominal segments I–VIII more or less spine-like, quite conspicuous and placed exactly at the posterior corner of the segments (Figs 4.8A, 4.8B) .... *Anopheles*
– Trumpets long, more than twice as long as broad and flared (Fig. 4.8L) or relatively short but tubular (e.g. Fig. 4.8E); seta 9 of abdominal segments I–VII nearly always very small and somewhat removed from the posterior corner of the segments (Fig. 4.8H)........ 2

2. Abdominal segment X with conspicuously branched setae dorsally; seta 9 of abdominal segment VIII greatly reduced; paddles broad and without a pair of apical setae (Fig. 4.8C) .... *Toxorhynchites*
– Abdominal segment X without setae; seta 9 of abdominal segment VIII and paddles various 3

3. Trumpets with inner wall well separated from outer wall (Fig. 4.8E); paddles small and pointed, without apical setae (Fig. 4.8D) .... *Malaya*
– Trumpets with inner wall in contact with outer wall; characters of paddles not combined in this way 4

4. Trumpets with feathery processes at apex, modified for piercing plant tissue (Fig. 4.8F); seta 1 of abdominal segment I (Fig. 4.4A) absent (Fig. 4.8G)..... 5
– Trumpets lacking feathery processes at apex and/or seta 1 of abdominal segment I well developed (Fig. 4.4A) 6

5. All abdominal setae very small; no long, stout, bristles (Fig. 4.8H) .... *Coquillettidia*
– Two pairs of long, stout bristles posteriorly on abdominal segments I–VII (Fig. 4.8I) .... *Mansonia*

6. Paddles without spines or setae on both inner and outer borders, deeply cleft at apex; apical seta at least half as long as paddle; setae 5 of abdominal segments IV–VI with long, frayed median branch and short lateral branches (Fig. 4.8J).. .... *Aedeomyia*
– Paddles, and setae 5 of abdominal segments IV–VI not as above.......... 7

7. Trumpets at least about ten times as long as their breadth at mid point (Fig. 4.8L); paddles fringed, usually with irregular spicules, on both inner and outer borders, apical seta minute or absent (Fig. 4.8K) .... *Mimomyia*
– Characters not combined in this way 8

8. Paddles with inner half deeply excavated towards base and usually much broader than outer half; paddles fringed or toothed, usually extensively, on inner and outer borders; (Fig. 4.9A) .... *Uranotaenia*
– Characters not combined in this way 9

[1] Pupal characteristics are sometimes indistinct or show considerable overlap, even between genera, and this life stage of the Culicidae is usually not used for identification of taxa. It is more reliable to keep the pupae for two to three days until the adults emerge, and then identify the adults.

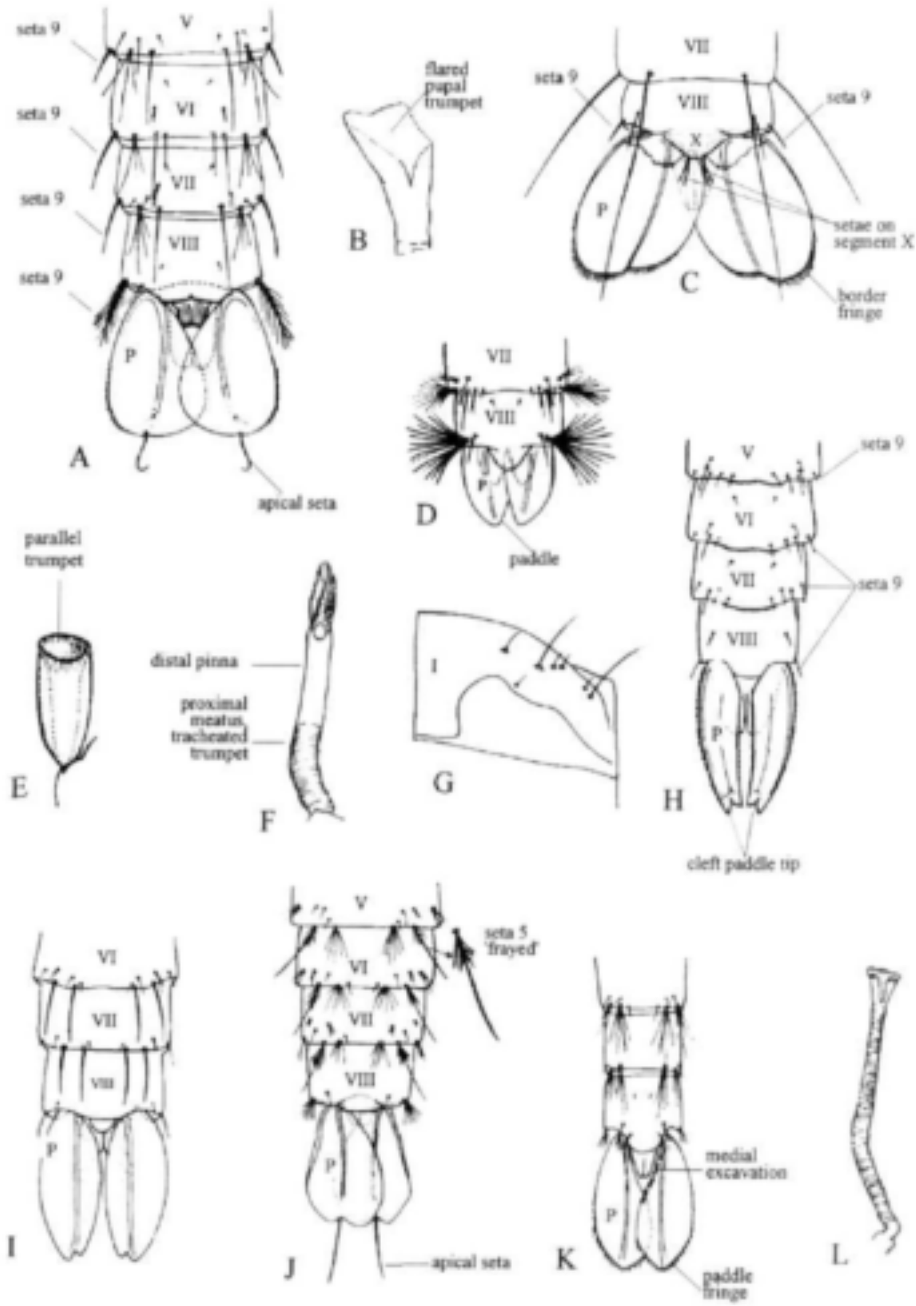


Fig. 4.8. Mosquito pupae: taxonomically important characteristics. **A–B**, *Anopheles*: **A**, terminal segments; **B**, flared breathing trumpet. **C**, *Toxorhynchites*, terminal segments. **D–E**, *Malaya*: **D**, terminal segments; **E**, breathing trumpet. **F–G**, *Coquillettidia*: **F**, breathing trumpet; **G**, abdominal segment I (note absence of distinct setal tuft). **H–K**, terminal segments: **H**, *Coquillettidia*; **I**, *Mansonia* **J**, *Aedeomyia*, **K**, *Mimomyia*. **L**, elongated trumpet of *Mimomyia*.

9. Paddles with long delicate fringe on both borders, apical setae long and stout (Fig. 4.9B); cephalothoracic seta 8 much longer and stouter than cephalothoracic seta 9 (Fig. 4.9C) .... *Eretmapodites*
– Characters not combined in this way 10

10. Trumpets at least seven times as long as their breadth at half way, the pinna occupying at least half the length and the meatus entirely or almost entirely tracheoid (Fig. 4.9E); seta 9 of segment VIII very feebly developed; paddle edge strongly serrated on outer half; inner half smooth (Fig. 4.9D) .... *Ficalbia*
– Characters not combined in this way 11

11. Cephalothoracic seta 8 anterior to, or at most slightly posterior to, base of trumpet and very much anterior to cephalothoracic seta 9; trumpets nearly always with only rudimentary basal tracheation (Fig. 4.9F); seta 9 of abdominal segment VIII nearly always positioned on the posterior border of the segment (Fig. 4.9G) .... *Aedes*
– Cephalothoracic seta 8 level with, or posterior to, the base of the trumpet and nearly level with cephalothoracic seta 9; trumpets frequently with sub-basal tracheation (Fig. 4.9H); seta 9 of abdominal segment VIII various.......... 12

12. Trumpets with well-developed sub-basal tracheation (Fig. 4.9H), or seta 9 of abdominal segment VIII distinctly removed from the posterior border of the segment (Fig. 4.9I), or (usually) both .... *Culex*
– Trumpets with rudimentary basal tracheation at most (Fig. 4.9J); seta 9 of abdominal segment VIII always arising from the posterior border of the segment (Fig. 4.9K).. *Culiseta*

NOTES ON THE GENERA

Subfamily **Anophelinae**

Anopheles

This is the only genus containing vectors of malarial parasites. Three of the approximately 50 species occurring in southern Africa are major vectors. Some species are also able to transmit filarial parasites and arboviruses. Larval habitats range from high-salinity waters on the coastal planes to freshwater streams and mineral springs. All but two species possess well-developed abdominal palmate setae with which they maintain the horizontal position in the water.

Subfamily **Toxorhynchitinae**

Toxorhynchites

Two species are found in southern Africa, over most of the region. Adult females feed on nectar or fruit-juices. They do not possess piercing mouthparts and are therefore of no medical importance. The larvae prey on

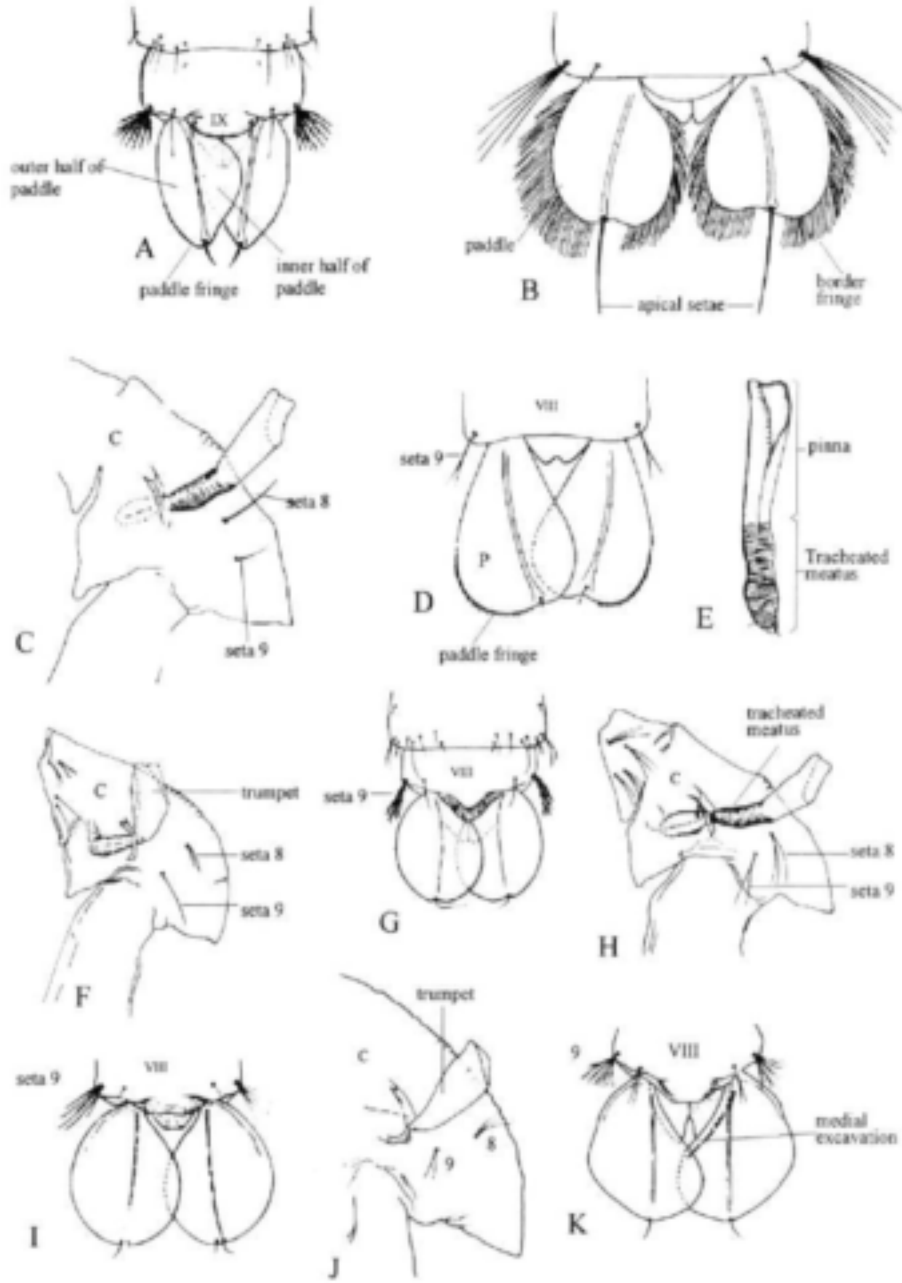


Fig. 4.9. Mosquito pupae: taxonomically important characteristics. **A**, *Uranotaenia*, terminal segments. **B–C**, *Eretmapodites*: **B**, paddles; **C**, cephalothorax showing setae and breathing trumpet. **D–E**, *Ficalbia*: **D**, terminal segments: **E**, breathing trumpet. **F–G**, *Aedes*: **F**, cephalothorax showing setae and breathing trumpet; **G**, terminal segments. **H–I**, *Culex*: **H**, cephalothorax showing setae and breathing trumpet; **I**, terminal segments. **J–K**, *Culiseta*: **J**, cephalothorax showing setae and breathing trumpet; **K**, terminal segments.

the larvae of other mosquitoes, however, and have been tested as a means of biological control in some areas of the world, although without much success. They are mainly found in container habitats such as tree-holes, bamboo-stumps, discarded tins and tyres, which are not the preferred habitats of most of the medically important species.

Subfamily **Culicinae**

Aedeomyia

Larvae are found in swamps or abandoned borrow-pits in association with living vegetation.

Uranotaenia

Larvae possess a relatively short siphon and so adopt an almost horizontal position at the surface of the water, somewhat as *Anopheles* larvae do. This may cause confusion between the two genera. Larval habitats are mainly shaded pools and swamps with vegetation.

Coquillettidia

Larvae and pupae require aquatic vegetation, either rooted or floating, in swamps and marshes. They remain attached to plant stems and are very rarely collected in nets or scoops. They only leave the plant during moulting and on emergence of the adult.

Mansonia

Adults of some species may be important vectors of filaria parasites but this has not yet been proven in southern Africa. Larval habits are the same as those of *Coquillettidia*.

Malaya

Only one species is known to occur in southern Africa. It has been found breeding in plant axils in KwaZulu–Natal and Mpumalanga.

Culex

A large genus containing efficient vectors of filarial parasites and many arboviruses affecting humans and stock animals. *Culex* larvae breed in a great variety of aquatic habitats, from natural pools to pit latrines and blocked drains. *Culex tigripes* has predatory larvae and is quite common in southern Africa.

Culiseta

Only two species are known to occur in southern Africa, but are widespread in the region. Larvae have been found in pools, barrels and cattle dips.

Ficalbia

Two species are known, from Mozambique and Zimbabwe. Larvae are found in clear, stagnant water with vegetation: in swamp margins and ditches.

Mimomyia

Larval habitats are the same as for *Ficalbia*. Seven species are known, occurring all over the southern region, except for the Western Cape, Eastern Cape, Northern Cape and the Free State.

Eretmapodites

This genus is unique to Africa. Larvae can be found in small collections of water in fallen leaves, old tins, snail shells, plant-axils and, rarely, tree-holes. Some species have larvae that are predatory on other mosquito larvae.

Aedes

A very large genus containing the efficient urban Yellow Fever virus vector *Aedes aegypti*. Although Yellow Fever virus does not occur in southern Africa, *Ae. aegypti* is nevertheless a very common human-biting mosquito. Many species of *Aedes* are vectors of filarial parasites (in other parts of Africa) and various arboviruses. Larval habitats are usually temporary water bodies, since the eggs rely on direct rainfall or river flooding to hatch, many being tree-hole breeders. Larvae are primarily bottom-feeders and browse over the mud or debris. Some species have predatory larvae and others can tolerate high salinities. The eggs can withstand desiccation, sometimes for years, between rains.

ACKNOWLEDGEMENTS

Dr P. Jupp and Prof R.H. Hunt are thanked for comments on the manuscript. The Natural History Museum, London, is thanked for permission to reproduce illustrations from Edwards (1941) and Hopkins (1952). Prof M.W. Service is thanked for permission to reproduce, wholly or in part, figures from Service (1980) and for comments on the manuscript.

USEFUL REFERENCES

EDWARDS, F.W. 1941. *Mosquitoes of the Ethiopian Region. III. Culicine adults and pupae.* British Museum (Natural History), London: 499 pp.

GILLIES, M.T. & DE MEILLON, B. 1968. *The Anophelinae of Africa South of the Sahara.* Publication of the South African Institute for Medical Research, no. 54: 343 pp.

GILLIES, M.T. & COETZEE, M. 1987. *Supplement to the Anophelinae of Africa South of the Sahara.* Publication of the South African Institute for Medical Research, no. 55: 143 pp.

HOPKINS, G.H.E. 1952. *Mosquitoes of the Ethiopian Region. I. Larval Bionomics of Mosquitoes and Taxonomy of Culicine Larvae.* British Museum (Natural History), London: 355 pp.

JUPP, P.G. 1996. *Mosquitoes of Southern Africa. Culicinae and Toxorhynchitinae.* Ekogilde Publishers, South Africa: 156 pp.

KNIGHT, K.L. & STONE, A. 1977. *A Catalog of the Mosquitoes of the World.* Thomas Say Foundation, Maryland: 611 pp.

MATTINGLY, P.F. 1971. Contributions to the mosquito fauna of Southeast Asia. XII. Illustrated keys to the genera of mosquitoes (Diptera: Culicidae). *Contributions of the American Entomological Institute* 7(4): 1–84.

MUSPRATT, J. 1951. The bionomics of an African *Megarhinus* (Dipt. Culicidae) and its possible use in biological control. *Bulletin of Entomological Research* **42**: 355–370.

SERVICE, M.W. 1980. *A Guide to Medical Entomology.* Macmillan Press, Ltd., London: 226 pp.

SERVICE, M.W. 1990. *Handbook to the Afrotropical Toxorhynchitine and Culicine Mosquitoes, excepting* Aedes *and* Culex. British Museum (Natural History), London: 207 pp.

CHAPTER 5

SIMULIIDAE

by

F.C. de Moor

Blackflies, buffalo gnats, reed smuts or river midges are some of the names commonly applied to the family of two-winged flies scientifically known as Simuliidae. This family includes many species of economic, veterinary and medical importance such as the notorious (and aptly-named) *Simulium damnosum*, the carrier of a filarial worm that infects humans and causes river blindness in many regions of West Africa. The cattle-biting pest, *S. chutteri*, is of some economic importance in parts of southern Africa, as it causes a serious deterioration in the condition of cattle, and may carry diseases such as rift-valley fever.

Adult simuliids (Fig. 5.1A), which are about the size of a match-head, have a sturdy body, and a head slung low on a humped thorax. The head bears a pair of eleven-segmented, cigar-shaped antennae, and short, toothed, downwardly-pointing mouthparts. The thorax bears one pair of large, rounded wings that fully overlap the abdomen when at rest. Larvae (Fig 5.1B) have the following characteristics: an absence of segmented legs; a characteristic, club-shaped outline with a posteriorly swollen abdomen; a pair of large, fan-shaped filtering fans on a helmet-shaped, fully-sclerotized head capsule; a small midventral thoracic proleg, and a subterminal, posterior abdominal proleg that bears a circlet of hooks used for attachment to the substratum. Pupae (Fig. 5.1C) are embedded in shoe- or slipper-shaped silken cocoons and have characteristically shaped thoracic respiratory organs that are often branched.

Simuliids have a worldwide distribution but are excluded from certain oceanic islands and the polar regions. There are currently 1720 validly-named species (including 10 fossil species) in 25 genera and 53 subgenera (Crosskey & Howard, 1996; Crosskey, 1999). Because many species of blackfly are important bloodsucking pests of man and his livestock, they are a well-studied group and, until recently, were considered to be reasonably well known taxonomically. In the 1960s, however, systematists studying pest species of blackfly, using the banding characteristics of the giant polytene chromosomes of the salivary glands of larvae, came to realize that certain species were in fact complexes consisting of many morphologically-indistinguishable 'sibling species' (Crosskey, 1981, 1987a; Rothfels, 1979; Steyskal, 1972). As a result of this research it has now been realized that there are many new species, some tentatively described and others still awaiting discovery.

THE SOUTHERN AFRICAN SIMULIID FAUNA

In the southern African region described in this volume (see Fig. 1, page 77), there are about 65 species of blackfly (see list at the end of this chapter). Freeman & de Meillon (1953) and Crosskey (1960, 1969) covered the Afrotropical Simuliidae in detail and the majority of southern African species (aside from sibling species) are now known in the adult and pupal stages. Larvae of a number of species are undescribed, although research efforts are presently increasing our knowledge of them (Palmer, 1991). All eight species of *Paracnephia* and 15 of the 57 species of *Simulium*, or 35% of the Simuliidae, are endemic to the region.

BIOLOGY

Adults

Adults (Fig. 5.1A) are small (3–6 mm long), stout-bodied flies and are almost always visibly sexually dimorphic. The males have eyes that meet together in the centre of the head with large facets on the top half and smaller facets on the bottom half, while the females have well-separated eyes with uniformly-sized facets. The enlarged facets allow for acute resolution of moving objects. During calm windless days, blackflies orientate and hover around some physical object, forming an almost stationary column of flies. Depending on the species such swarms, composed almost entirely of the males of a single species, are formed directly above rapids or at some prominent feature on a hill near the water or even around the host animals on which the females feed. These male mating-swarms may comprise anything between a few and many thousands of individuals. If a female flies into the field of vision of males in the swarm she is instantly followed, clasped and mated by a male.

After mating, the female fly either nourishes the developing eggs directly from fat-body reserves accumulated during her larval life or else seeks out a host to obtain a blood meal that will provide additional

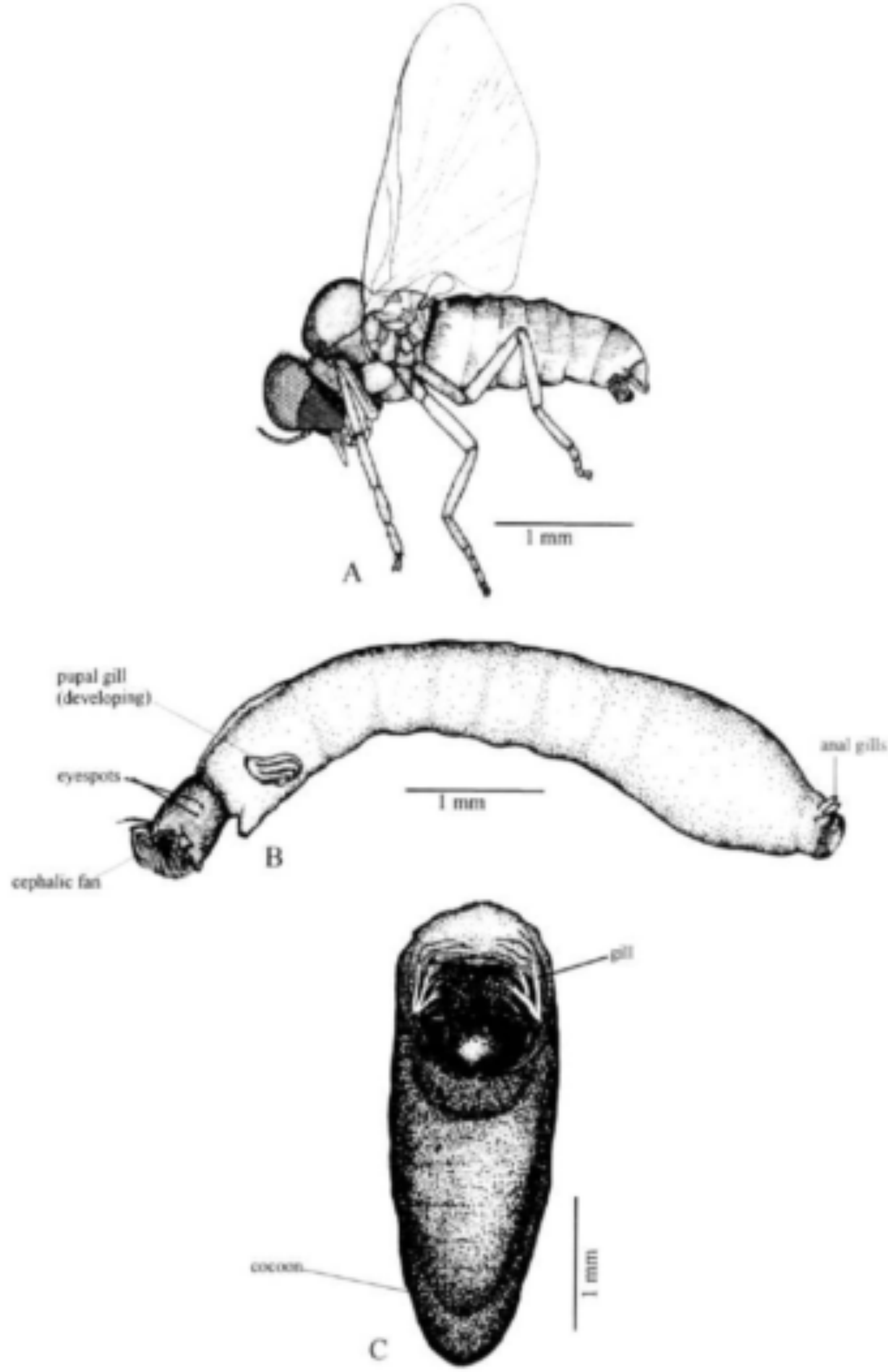


Fig. 5.1. Larval, pupal and adult characters of Simuliidae: **A–C**, *Simulium (Metomphalus) chutteri*: **A**, adult male (right lateral view); **B**, larva (lateral view); **C**, pupa in silken cocoon (dorsal view).

protein for the development of the eggs. After a period of egg maturation the female returns to the water to deposit her eggs. Ovipositing habits vary from species to species and can entail the scattering of eggs loosely onto the water surface, laying eggs on reeds or other submerged plant matter, or laying eggs on partially-submerged stones in shallow riffles (de Moor 1989).

Adult blackflies show a wide variety of feeding adaptations, although only female flies feed on blood. Unlike a mosquito, which punctures a small hole in the skin of its host prior to sucking blood, a blackfly chews a gaping wound in the skin and laps up the blood that is exuded. Secondary infections in wounds are therefore frequently the most serious aspects of blackfly attacks. While many species of blackfly do not feed as adults, some of those that do will feed on the blood of mammals, while others are specialized for feeding on birds. Species that feed on birds can usually be recognized by the shape of the tarsal claws (found terminally on each leg), which have an extra tooth used for hooking onto feathers (Crosskey, 1990).

Larvae and pupae

The larval and pupal stages of blackflies are among the animals best adapted to life in fast-flowing water and the absence of suitable running water is, in most cases, a limiting factor in their regional distribution. They have limited locomotory powers and rely on flowing water to provide food and to maintain dissolved oxygen at the required high levels. All species of blackfly are found in flowing fresh water, although *Simulium adersi*, a widespread species in southern Africa, has also been recorded from highly saline and even brackish estuarine waters, while another common species, *Simulium ruficorne*, has been recorded from very small trickles of water with temperatures up to 35°C. As they spend all of their lives in running water, larvae of blackflies lead an almost entirely sedentary existence.

Larvae of various species can usually be found on stones or submerged vegetation (Fig. 5.2) or on any other hard substrata in moderately-swift to swiftly-flowing water. A larva will attach itself to the substratum by embedding the circlet of hooks on the posterior proleg (Fig. 5.4B) into a patch of silk that it has spun and attached to the substratum. It will remain in a semi-upright position when feeding, retracting into a more horizontal position closer to the substratum when at rest. In the feeding position the cephalic fans (Figs 5.3A–B) are extended with their concave surfaces facing the current. A fine layer of sticky mucus, continuously secreted into the fans, collects fine particulate matter from the water. The fans are periodically retracted and the mandibles, which have a terminal brush of hairs, are used to scrape off the attached particles. Larvae of blackflies are

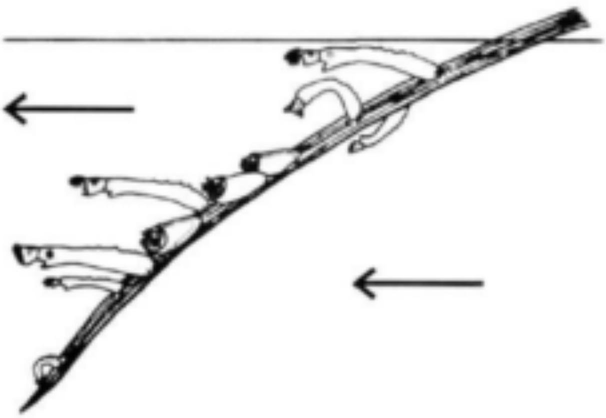


Fig. 5.2. Larvae and pupae on a submerged grass blade (arrow indicates the current direction)

extremely efficient biological filterers and have been recorded extracting particles from 350 µm to as little as 0.1 µm in diameter from the water. Their food, extracted from suspended detritus in the water column, is comprised of diatoms, algae, microscopic invertebrates and even bacteria.

At certain stages of their life cycles, or when disturbed, the larvae leave the substratum and become part of the organic drift in rivers. When a larva moves into an area with a suitable current flow, it usually spins a small patch of silk onto the substratum immediately in front of it. Moving around on the substrate to find a suitable position is a slow and deliberate process. By hooking the anterior proleg into a newly-secreted patch of silk, releasing hold of the patch of silk into which the posterior proleg was attached, and then looping the posterior proleg forward to grip the newly-spun patch of silk, the larva is able to move slowly around the substratum by means of a tedious looping form of locomotion. Evasive escape locomotion can also be achieved by releasing the hold on the substratum, but at the same time leaving an anchor-line of silk attached. The water current carries the larva downstream away from immediate danger but keeps it within reach of the more favoured, swift-flowing habitat.

The larvae of most species go through seven instars before pupating. The final-instar larva (Fig. 5.1B), which has a pair of clearly-visible developing pupal gills (sometimes called 'respiratory histoblasts'), is actually a functional pupa within a larval skin. This so-called 'pharate pupa' spins a silken cocoon before it completes pupation. The cocoon can vary from an open-ended 'slipper' shape (Figs 5.8E, F) to a 'shoe' shape with a closed protective ridge (Figs 5.8A–D). Pupae are firmly attached to various substrates (such as rocks or trailing vegetation) in flowing waters. Species whose pupae have slipper-shaped cocoons are generally found in slower-flowing waters than those with shoe-shaped ones. The development of the 'neck' on shoe-shaped cocoons is variable within a species and is determined by the current velocity to which the larvae is exposed during development, the neck becoming more extensive in stronger currents (e.g. Figs 5.8C, D). Within the cocoon, the pupa is immobile and has a number of little hooks on its abdomen (Figs 5.7B, C) that keep it firmly embedded inside the case. At the front end of the pupa is a pair of simple or branched **plastron gills** (Figs 5.1C, 5.9A–J, 5.10A–N). They are remarkable organs that extract dissolved oxygen directly from the water and will remain functional even under a pressure of 10 metres of water (Hinton 1964). The shape of these pupal gills is frequently species-specific and provides one of the quickest and easiest methods for identifying blackfly pupae.

On completion of metamorphosis the adult blackfly, encased in the pupal skin, accumulates air between the body and the pupal skin. During emergence the skin splits lengthwise dorsally between the head and thorax, and the adult rises head-first to the water surface, enclosed in a bubble of air. On reaching the surface the bubble bursts, releasing a completely dry adult that flies off into the air.

ECOLOGY

Southern African blackflies are less well known than those of West Africa, where a great deal of effort has gone into studying the blackfly transmitters of the parasitic filarial nematode worm, *Onchocerca volvulus*, which causes river blindness in people living near streams and rivers in that region. According to Crosskey (1987b) there are more than 40 cytologically-distinct species within the *Simulium (Edwardsellum) damnosum* sensu lato complex, some of which have been identified as carriers of the filarial parasite. In southern Africa there are at least six recognized species of this complex (Crosskey & Howard, 1999), but so far river blindness has not been recorded in the region. Several species of blackfly in southern Africa are known to become pests when populations get large. Adult females of some species feed on mammals (particularly cattle and sheep) while ornithophilic species feed on poultry (particularly chickens and turkeys). The main culprits are *Simulium chutteri*, *S. nigritarse*, *S. adersi*, and *S. damnosum* s.l.. The latter two species have also been observed feeding on humans (personal observation; Jupp & Palmer, 1999).

Blackflies can form 95% or more of the total number of individual invertebrates collected from stones in rapids and hence they can truly be considered to be specialists of that swift-flowing aquatic biotope. Because of their abundance, blackflies form an important component of the aquatic food chain in swift-flowing water. They are important primary consumers of planktonic plant matter and detritus held in suspension by the flowing water. In turn, they are preyed on in their aquatic stages by secondary consumers such as fish, crabs, leeches and other aquatic insects and in the adult stage by fish, birds, spiders and dragonflies, as well as by other predatory dipterans (de Moor, 1992).

COLLECTION, REARING AND PRESERVATION

Larvae and pupae can be collected from almost any form of substratum in flowing water. To obtain a representative (qualitative) sample of as many species as possible, it is advisable to collect from a wide range of biotopes within flowing sections of rivers, i.e. from various substrates (including stones and trailing vegetation) and at various current speeds. If it is possible to remove the substrate (e.g. stones, vegetation or snagged wood), then a hand net of 250 μm mesh size is held downstream of the collection point prior to the removal of stones from the water. The stone or plant is then carried in the net to the river bank where attached larvae and pupae are removed with a fine pair of tweezers. These, and any larvae adhering to the net, are then placed in a container together with water from the river. In the case of substrates (such as large boulders or bedrock) that cannot be removed from the stream, the collector may run his/her hand across the rock surface while holding the collection net slightly downstream of the collection point in order to trap larvae that will release their hold and drift into the net.

Pupae are usually firmly fixed to their substrata and, if wanted for rearing, have to be very carefully removed. This is best done with a sharp scalpel-blade or pen-knife, which is scraped under the cocoon, loosening the attachment. Once detached the cocoon is gently lifted, care being taken to handle the pupa as little as possible.

Sampling methods used for estimating population densities of simuliids are described in Chutter (1968); de Moor (1982a) and Palmer (1994).

Live larvae and pupae can be transported to the laboratory in containers of natural water maintained on ice in a cool-box. The animals will survive for several days if not too crowded. Larvae placed on wet tissue paper in petri dishes on ice survive very well. Pupae for rearing can be stored individually, either on short lengths of the vegetation on which they are naturally found, or on narrow strips of absorbent paper such as filter paper or blotting paper. These are then placed in small specimen tubes or pill vials with a few drops of water on the bottom to ensure that the paper remains moist. The tubes can be sealed with a wad of cotton wool. Tubes must be kept in a cool, shaded place. Adults should emerge in one to five days. Larvae, depending on the species, can be maintained for several weeks in an aquarium with a bubbling air stone in a cool room (preferably below 22 °C). More elaborate rearing techniques are reviewed by Mokry et al. (1981).

Larvae and pupae collected for preservation can be stored in 5% formaldehyde (about 12% formalin) or 80% ethyl alcohol. Specimens stored in formaldehyde retain colour and pigmentation patterns better than those preserved in alcohol, which tends to leach out pigments. Larvae killed in >90% alcohol show important diagnostic features such as extended cephalic fans and extruded ventral papillae and anal gills.

Adult flies are best killed with ethyl acetate or ether and pinned on 'minuten' insect pins. Alternatively, material can be stored in 70–80% ethyl alcohol but this makes material less accessible for reference purposes and also tends to alter coloration when observed in the liquid medium. If adults are reared from pupae they should be allowed to mature and harden for at least 24 hours after emergence before they are killed. Teneral (not fully hardened and developed) adults tend to be very soft and details of sclerotized parts do not show up clearly.

PREPARATION OF SPECIMENS FOR EXAMINATION

Many features are best seen when examining whole animals preserved in ethanol under a dissecting microscope at about 10–100 x magnification. Details of the larval head and its appendages need to be examined under a compound microscope at about 400 x magnification using prepared slides. For this the head of a larva is removed and left in a 10% potassium hydroxide solution for several hours. After periodic examination to determine that the soft tissues have been sufficiently dissolved, the head capsule is immersed for about five minutes in glacial acetic acid to clear. It is then placed in clove oil on a microscope slide, manipulated with a micro-needle until in a suitable position for viewing, and a coverslip is then placed over the slide, making it ready for viewing under a compound microscope. Permanent slide mounts can be made with Euparol, Canada Balsam or some other suitable mounting medium.

IDENTIFICATION

The identification of simuliids to species level is not always easily accomplished. Pupal stages of the subgenus *Pomeroyellum* are easily identified to species level on the basis of their characteristic pupal respiratory organs, whereas adult females of different species remain indistinguishable. In other instances larvae and pupae of different species are identical, while adults show clear specific characters. Identification to species level should ideally take into account all of the larval, pupal and adult characters as well as ecological criteria such as descriptions of the larval and pupal habitat, and adult activity times and places, as well as behaviour.

The terminology used here is explained in detail by Crosskey (1960, 1990). Blackfly larvae are elongated and pear-shaped with the hind part wider than the head end (Figs 5.1B, 5.4 A–C). The **head** (Figs 5.3A–B) consists of an elongated, open-ended, barrel-shaped and fully sclerotized **capsule** with a large frontal aperture, the **oral cavity**, around which the mouth-parts are attached, and a large posterior opening, the **occipital foramen**, behind which the thorax is attached. The head capsule is made up of two large plates: a lower hull-shaped one that forms the floor and sides of the head, and an upper, slightly convex, dorsal **cephalic apotome** also known as the **fronto-clypeus**. The lower plate is divided into two lateral **postgenae** and an anteromedian plate, the **hypostomium**, which are all fused together. The paired postgenae are usually incompletely fused ventrally, leaving a membrane-filled, variously shaped **postgenal cleft** open to the hind margin. The shape and size of this cleft is diagnostic for different species. The region of the postgenae behind the hypostomium and before the postgenal cleft forms the **postgenal bridge**. The hind margin of the postgenae is narrowly rimmed along each side from the dorsal edge to the ventral postgenal cleft by a darkly pigmented **postocciput**. Dorsolaterally the postgenae are adorned with a pair of pigmented, light-sensitive eyespots on either side. As the larvae grow, develop and moult through seven instars, a pair of tiny oval **cervical sclerites** become differentiated from the upper ends of the postocciput and either remain connected (as in *Paracnephia*, Fig 5.5A) or become separated and free on the 'neck' membrane (as in *Simulium*, Fig 5.5B) in the final instar. The hypostomium forms an anteromedial, raised projection from the floor of the head capsule and bears a terminal row of non-socketed teeth. The hypostomium broadens posteriorly and gently tapers to fuse with the postgenae. Behind the tapered margin there is a row of **hypostomial setae**. The front margin of the postgenal plate is strengthened by two strongly-sclerotized, vertically-orientated, X-shaped buttresses. The lower pair provides pivots for the mandibles and the upper pair supports the stems of the **cephalic fans** and the bases of the antennae. Prominent retractable fan-shaped organs, the cephalic fans (Figs 5.3A–B) can be extended in front of the head. These are made up of a number of concave, rod-like rays, each with **microtrichia** (minute cross hairs) which are used to sieve particles of food carried by the flowing water.

The cephalic apotome and postgenae are frequently adorned with differing patterns of pigmentation useful for species identification (Figs 5.6A–F). Immediately behind the head on the underside of the body is a single finger-like **proleg** with a terminal circlet of little hooks. The posterior end of the larva has a large sucker-like proleg with several circles of hooks (Figs 5.4 A–D). The position and details of the hooks of the posterior proleg are diagnostic for different species. A pair of posterior ventral protrusions or papillae are present in some species (Fig. 5.4B). A hollow extension of the rectal floor forms blind, haemolymph-filled tubules, the **anal gills**, which can be extruded from, or withdrawn into the anus (Fig. 5.4A–C). It was originally assumed that these rectal gills served the function of oxygen exchange but recent studies in other Diptera indicate that they are osmoregulatory in function. Larvae can range in size from a total length of less than 2 mm for first instars to 13 mm for the final instars of some of the larger forms.

Figs 5.3–5.6 illustrate the characters used in the key to larval subgenera and Figs 5.1C and 5.7–5.10 show details of some of the characters used in the key to pupal subgenera. A 'positive' pattern of head pigmentation means that the basic pigmentation pattern is uniformly dark (e.g. Figs 5.6C & E); a 'negative' pattern means that there is a central unpigmented area surrounded by dark pigmentation (e.g. Figs 5.6B & F). Final instar larvae can be recognized by the presence (laterally on the second abdominal segment) of pupal gills, which first appear small and pale but become progressively larger and more darkly pigmented just prior to pupation (as in Figs 5.4A–C).

Simuliid pupae are **obtect**, meaning that they have the developing adult legs, wings, antennae and mouthparts all firmly glued to the body during development. Male and female pupae can be easily recognized by the developing compound eyes: in males the eyes have large dorsal facets that meet in the midline of the head whereas the eyes of the female have smaller facets and are clearly separated from each other. Paired thoracic gills (Figs 5.1C, 5.9 & 5.10) connect to the developing adult fly via spiracles. The hollow respiratory gills, which are filled with water, have a plastron surface composed of fine interlaced filaments that entrap air and form a functional physical gill. A thickened plastron surface at the base of the gill comes into direct contact with the adult spiracle so that exchange of oxygen takes place directly between the plastron surface and the adult spiracle. The water-filled gill tubules serve to equilibrate pressure under the water, preventing collapse of the gills even under pressure of 10 m of water (Hinton, 1964). The size, shape and structure of the gills differ enormously between species. The abdomen of the pupa is adorned dorsally and ventrally with an armature of forwardly turned hooks, combs and scattered hair-like setae (Figs 5.7B–C). Functionally, the large hooks are the most important as they keep the pupa firmly embedded in its silken cocoon. The structure of the cocoon varies from species to species and is usually indicative of the preferred strength of current in which the larvae and pupae of particular species live.

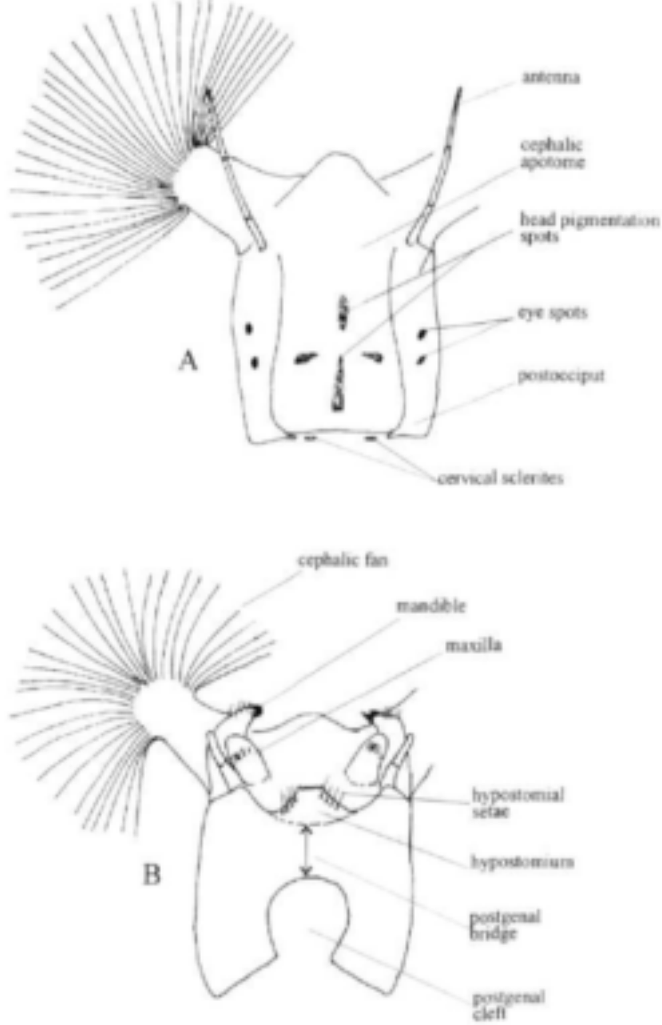


Fig. 5.3 **A–B**, head capsule of a typical *Simulium* larva (cephalic fans not shown in full extent): **A**, dorsal view; **B**, ventral view.

KEYS TO THE IMMATURE STAGES OF SOUTHERN AFRICAN SIMULIIDS

Note: this key is primarily for the identification of final or penultimate instars, although earlier instars can be identified in many cases. The effectiveness of the key is enhanced if used in conjunction with the key to pupae. In many instances the dissection and examination of gills in final-instar larvae will greatly aid identification.

No satisfactory characters separating the larvae of the subgenera *Paracnephia (Paracnephia)* and *Paracnephia (Procnephia)* have been found in the literature or from the limited material available.

Keys to species, mostly for adults and pupae but also for a number of larvae, can be found in de Carvalho (1962), Freeman and de Meillon (1953), Lewis (1965a, 1965b) and Crosskey (1960, 1969).

KEY TO GENERA, SUBGENERA AND SPECIES GROUPS OF SIMULIIDAE IN SOUTHERN AFRICA (LARVAE)

1. Cervical sclerites (Fig. 5.3A) merged with upper ends of postocciput (Fig 5.5A) in final instars; hypostomium (Fig. 5.3B) with large fusiform teeth aggregated in three separate groups (Figs. 5.5C); cephalic apotome widest at about a third of the distance from the posterior margin (Fig. 5.6A) .... *Paracnephia*

– Cervical sclerites separated from upper ends of postocciput (Fig 5.5B) in final instars; hypostomium with simple teeth not aggregated into three separate groups (Fig. 5.5D–H); cephalic apotome widest near the posterior margin (Figs 5.6B–F): *Simulium* 2

2. Larvae attached to river crabs; hypostomium with an even row of 13 apical teeth (Figs 5.5D); head elongated, cephalic apotome rounded posteriorly (Fig. 5.6B); so far recorded only from Malawi.................. *S. (Lewisellum)*

– Larvae not attached to river crabs; hypostomium and shape of cephalic apotome not as above 3

3. Larvae attached to mayfly nymphs; posterior abdominal proleg and circlet of hooks in a ventral position (Fig. 5.4D)........................ S. (*Phoretomyia*)

– Larvae not attached to mayfly nymphs; posterior abdominal proleg in a subterminal position (Figs 5.1C, 5.4B & C) 4

4. First five abdominal segments with paired dorsolateral subconical tubercles (anteriormost arrowed in Fig. 5.4C); cuticle of entire body, including anterior proleg, covered with elongated scale-like setae............. *S (Edwardsellum)*

– No paired dorsolateral swellings on abdomen (at most slightly produced bumps not covered with dense setae); if cuticle has conspicuous simple scales these do not extend onto the anterior proleg 5

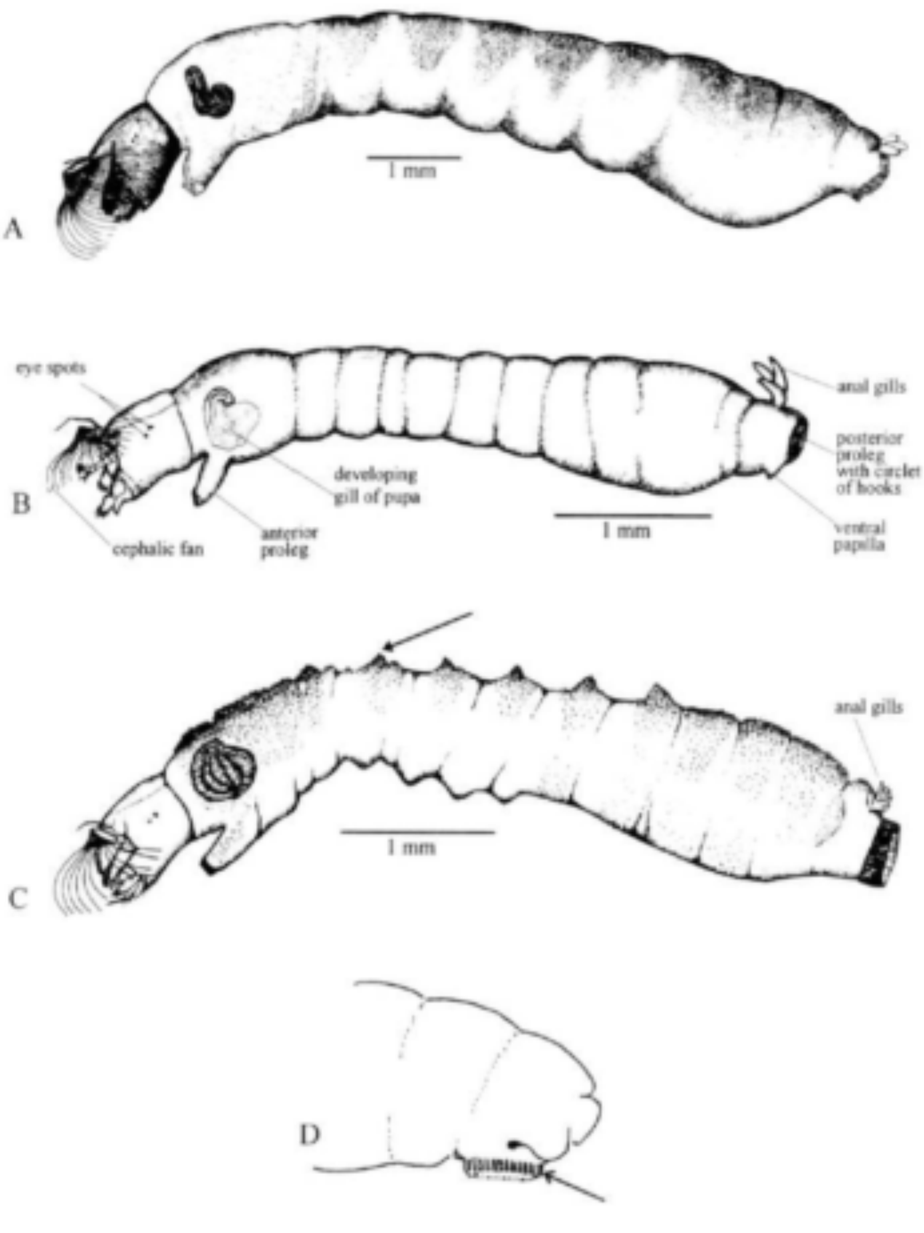


Fig. 5.4. Final instar larvae, lateral views: **A**, *Paracnephia* sp.; **B**, *Simulium (Nevermannia)* sp.; **C**, *S. (Edwardsellum)* sp. **D**, posterior segments of larva of S. *(Phoretomyia)* sp. showing the ventral posterior proleg (arrowed).

5. Dorsal cuticle of body adorned with large flat scales; postgenal cleft elongated and subelliptical (Fig. 5.6I) .... *S. (Metomphalus) albivirgulatum*
– Body cuticle bare, or with a sparse covering of scales, or with abundant minute, hair-like or fan-shaped setae; large fan-like setae, if present, confined to posterodorsal part of the abdomen; postgenal cleft of various shapes but not as in Fig 5.6I 6

6. Ventral papillae (as in Fig. 5.4B) absent (Figs 5.1B, 5.4C); rows of hypostomal setae diverging posteriorly from lateral margins of hypostomium; median and corner teeth of hypostomium not strongly prominent (Figs 5.5E–H); head pigmentation pattern always positive or not distinctive (Figs 5.6C–E).........7
– Ventral papillae present (Fig. 5.4B), subconical, sometimes small and rounded; rows of hypostomial setae lying nearly parallel to lateral margins of hypostomium; median and corner teeth of hypostomium strongly prominent (Figs 5.5I–J); head pigmentation pattern negative (Fig. 5.6F) or positive (Fig. 5.6E)..11

7. Postgenal cleft (Fig. 5.3B) small, much shorter than postgenal bridge, and forming a square or rounded notch (Fig. 5.6J); anal gills with secondary lobules (see Fig. 5.4C); hypostomial setae numerous, 8–24 in each row but usually 12–18 (Fig. 5.5E) .... *S. (Anasolen)*
– Postgenal cleft large, rounded (Figs 5.6M–N), sagittate (Figs 5.6H, O), subcordate (Fig. 5.6L) or elongate (Fig. 5.6K) but always much longer than postgenal bridge; anal gills simple (Fig. 5.4B) or with secondary lobules (Fig. 5.4C); hypostomial setae various but never more than 10 per row....... 8

8. Postgenal cleft large, elongated and mitre-shaped (Fig. 5.6K); anal gills with many finger-like secondary lobules; pigmentation of head capsule positive and usually dark; hypostomial setae eight to ten (rarely 11) per row (Fig. 5.5F) .... *S. (Freemanellum)*
– Postgenal cleft large, rounded, sagittate or sub-cordate; anal gills simple or with secondary lobules; pigmentation of head capsule positive (Fig. 5.6C), often faint and indistinguishable (Fig. 5.6D); usually fewer than eight hypostomial setae per row 9

9. Postgenal cleft sub-cordate, postgenal bridge minute (Fig. 5.6L); anal gills simple; head capsule faintly pigmented posteriorly; hypostomial setae four per row (Fig. 5.5G) .... *S. (Afrosimulium) gariepense*
– Postgenal cleft rounded or sagittate; anal gills simple or with secondary lobules; pigmentation of head capsule positive or not discernable (Figs 5.6C–D); hypostomial setae usually three to eight per row 10

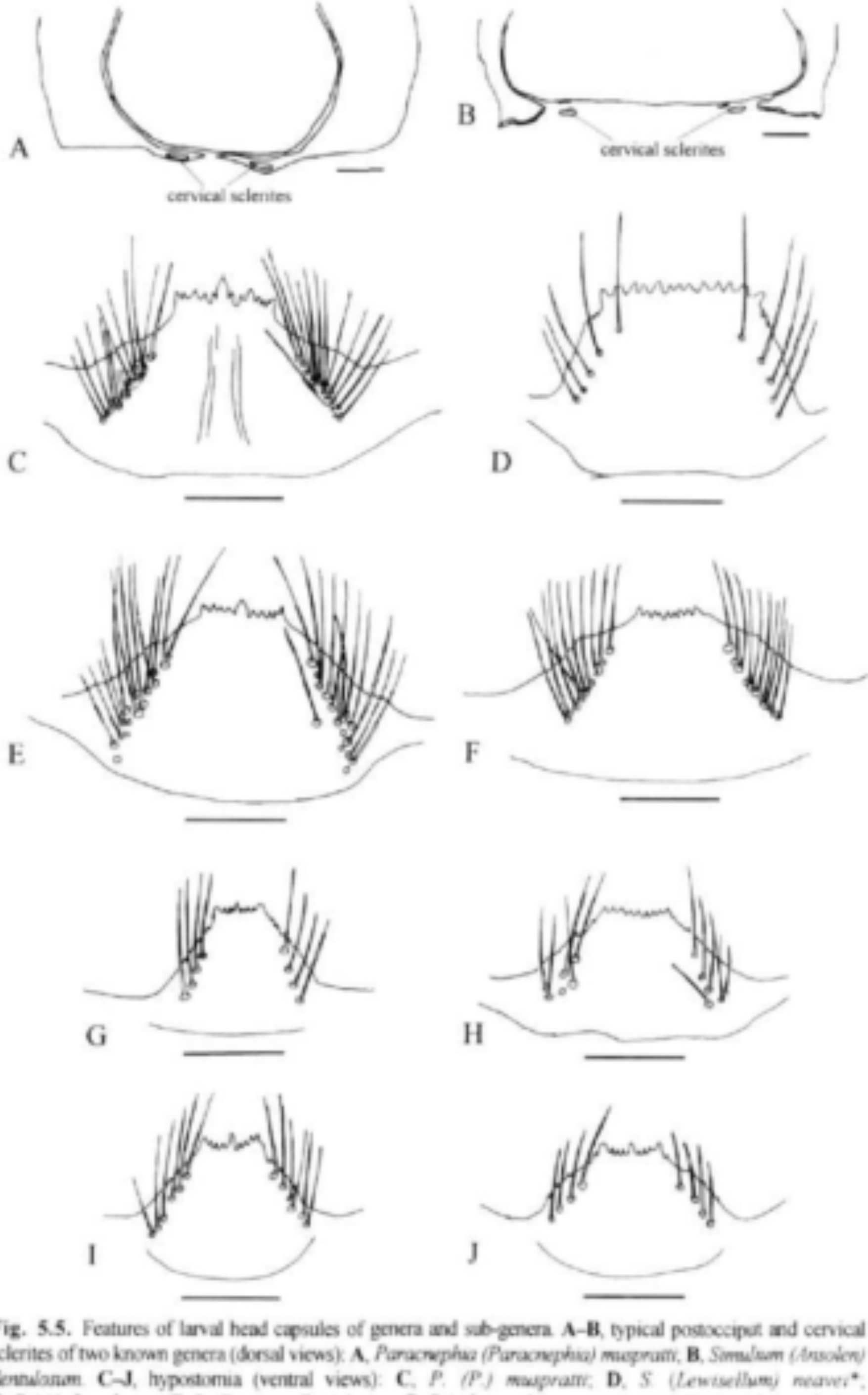


Fig. 5.5. Features of larval head capsules of genera and sub-genera. **A–B**, typical postocciput and cervical sclerites of two known genera (dorsal views): **A**, *Paracnephia (Paracnephia) muspratti*; **B**, *Simulium (Anasolen) dentulosum*. **C–J**, hypostomia (ventral views): **C**, *P. (P.) muspratti*; **D**, *S. (Lewisellum) neavei**; **E**, *S. (A.) dentulosum*; **F**, *S. (Freemanellum) hessei*; **G**, *S. (Afrosimulium) gariepense*; **H**, *S. (Metomphalus) chutteri*; **I**, *S. (Nevermannia) nigritarse*; **J**, *S. (Meilloniellum) adersi*. Scale Bar: A–J = 0.1 mm.

* **Note**: *S. (L.) neavei* does not occur in the region, but is included to demonstrate features of the sub-genus.

10. Three (or occasionally four) hypostomial setae per row; postgenal cleft large and sub-circular (Fig. 5.6M); anal gills with finger-like secondary lobules .... *S. (Byssodon)*
– Four to eight hypostomial setae (rarely up to ten) per row (Fig. 5.5H); postgenal cleft large and sub-circular or sagittate (Figs 5.6N–O); anal gills simple or with secondary lobules .... *S. (Metomphalus)*

11. Head pigmentation pattern positive (Fig. 5.6E) (NB: positive head pigmentation also occurs in some members of the subgenus *Pomeroyellum* so it is advisable to examine pupal gills to confirm identification); postgenal cleft very small, much smaller than postgenal bridge (Fig. 5.6P). (In the *loutetense* group the postgenal cleft is narrow and elongated and similar to Fig. 5.6K but not as pronounced as in Fig. 5.6I) .... *S. (Nevermannia)*
– Head pigmentation pattern usually negative (but positive in some species of *S.* (*Pomeroyellum*), forming an H–shape on the cephalic apotome (Fig. 5.6F); postgenal cleft longer than or equal to the length of postgenal bridge...... 12

12. Postgenal cleft medium sized and rounded (Fig. 5.6Q); ventral papillae (Fig. 5.4B) rounded and small, rather inconspicuous; cuticle of abdomen adorned with small simple or slightly fusiform setae.......... *S. (Meilloniellum)*
– Postgenal cleft of various shapes (e.g. Fig. 5.6R); ventral papillae subconical and well developed; cuticle of abdomen posterodorsally adorned with large scales or small divided setae (no setae in the *kenyae* species group)........ .... *S. (Pomeroyellum)*

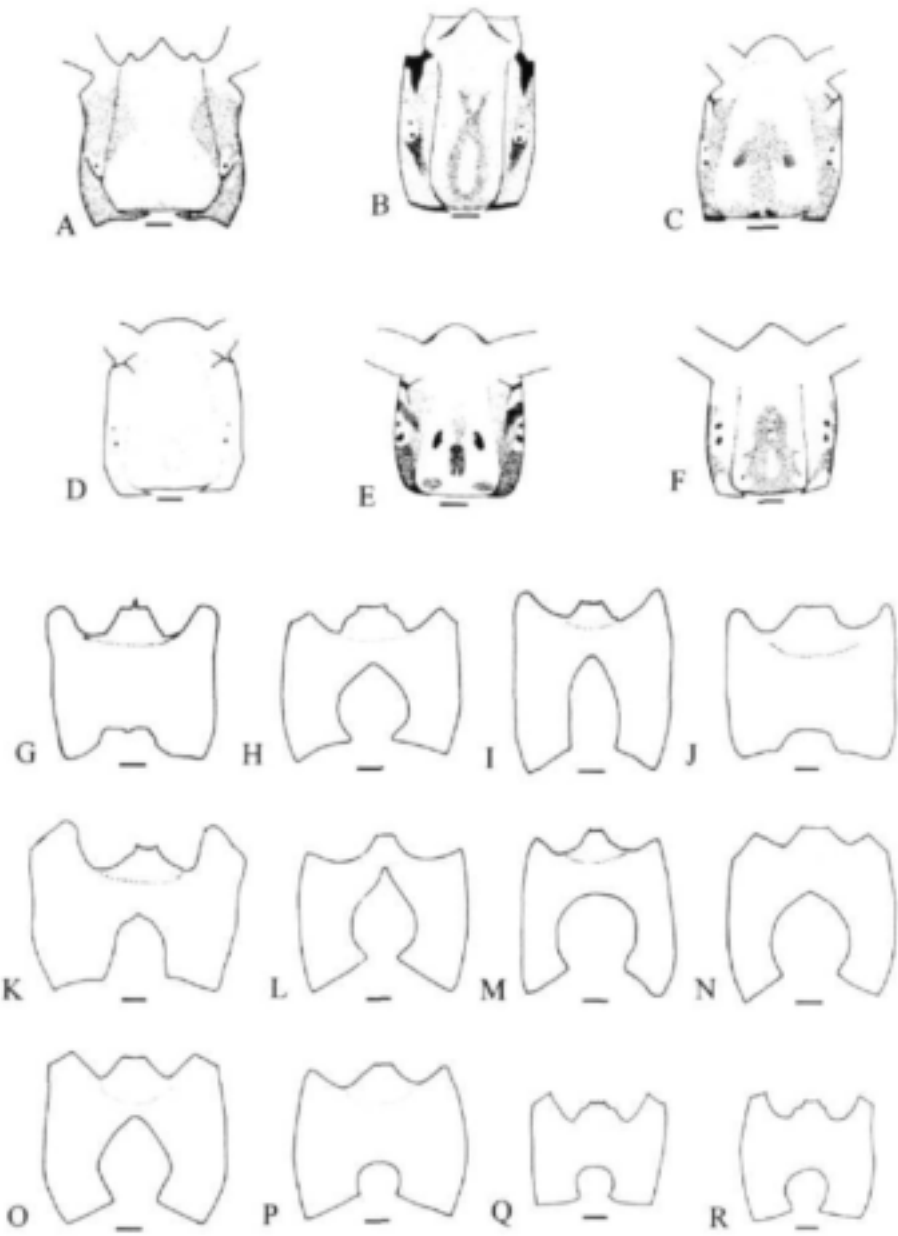


Fig. 5.6. Shapes of larval head capsules and patterns of pigmentation. **A–F**, dorsal views: **A**, *Paracnephia (Paracnephia) muspratti*; **B**, *S.* (*Lewisellum*) *neavei*; **C**, *S.* (*Metomphalus*) *hargreavesi*; **D**, *S.* (*Metomphalus*) *chutteri*; **E**, *S.* (*Nevermannia*) *nigritarse*; **F**, *S.* (*Meilloniellum*) *adersi*. **G–R**, ventral views showing postgenal cleft and bridge. **G**, *P.* (*P.*) *muspratti*; **H**, *S.* (*Edwardsellum*) *damnosum*; **I**, *S.* (*Metomphalus*) *albivirgulatum*; **J**, *S.* (*Anasolen*) *dentulosum*; **K**, *S.* (*Freemanellum*) *hessei*; **L**, *S.* (*Afrosimulium*) *gariepense*; **M**, *S.* (*Byssodon*) *griseicolle*; **N**, *S.* (*M.*) *chutteri*; **O**, *S.* (*M.*) *hargreavesi*; **P**, *S.* (*N.*) *nigritarse*; **Q**, *S.* (*M.*) *adersi*; **R**, *S.* (*Pomeroyellum*) *bequaerti*. Scale bar = 0.1 mm.

KEY TO GENERA, SUBGENERA AND SPECIES GROUPS OF SIMULIIDAE IN SOUTHERN AFRICA (PUPAE)

Note: pupae with eight-filamented respiratory gills are found in the subgenera *Lewisellum*, *Meilloniellum* and *Pomeroyellum*, and some careful discretion is needed to separate these groups. Examination of larval material from the same collection site will help.

As identification to species level is relatively easy, this key will distinguish animals to the level of species or species group in many instances.

1. Last abdominal segment with a pair of strong, elongated terminal hooks (Fig. 5.7A); cuticle of abdomen with well sclerotized tergal and sternal plates: *Paracnephia* 2
– Last abdominal segment with a pair of small blunt or slightly thorn-like tubercles (Fig. 5.7C); cuticle of abdomen not strongly sclerotized (*Simulium*) 3

2. Gill with six to seven filaments, with apically converging intertwined tips (Fig. 5.9B) .... *P. (Procnephia)*
– Gill with 10-22 filaments, or with six apically divergent filaments .... *P. (Paracnephia)*

3. Pupae attached to river crabs; gill with eight long slender filaments (Fig. 5.9A), usually longer than length of body; recorded only from Malawi .... *S. (Lewisellum)*
– Pupae not attached to river crabs; gill various: if with eight filaments, then shorter than body length 4

4. Gill with three robust, tapering, flattened, leaf-like or rounded branches (Figs 5.9C–D) 5
– Gill a single stem with or without terminal branches (Figs 5.10F & G) or with four or more slender unbranched filaments (Figs 5.9E, 5.10A, B, J, K) or else with numerous branched filaments (Figs 5.9H, 5.10E) or with more than one type of filament, which may or may not branch (Figs 5.9I–J)........6

5. Gill with three strongly tapering, tube-like branches with nodular sculpturing (Fig. 5.9C) .... *S. (Afrosimulium) gariepense*
– Gill with three leaf-like, flattened branches with smooth unsculptured walls (Fig. 5.9D) .... *S. (Byssodon)*

6. Pupal cocoon shoe-shaped with a 'heel' and a well developed neck (Figs 5.8A–D) (except *S. albivirgulatum*, which has an inconspicuous neck); dorsally abdominal segments III–IV with a row of hooks, VI–VIII with no spine combs (Fig. 5.7B) 7
– Pupal cocoon slipper-shaped (Figs 5.8E–F), sometimes with an indistinct neck; dorsally abdominal segments III–IV with a row of hooks and VI–VIII with well developed, backward-directed spine combs (Fig. 5.7C) 12

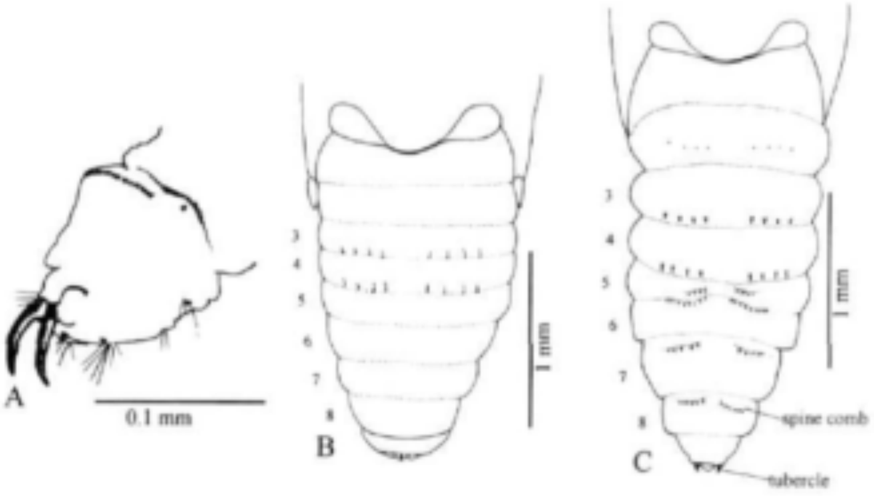


Fig. 5.7. Details of pupal features: **A**, terminal abdominal segment of a typical pupa of *Paracnephia damarense*; **B–C**, dorsal views of pupae: **B**, *S. (Metomphalus) chutteri*, **C**, *S. (Nevermannia) nigritarse*.

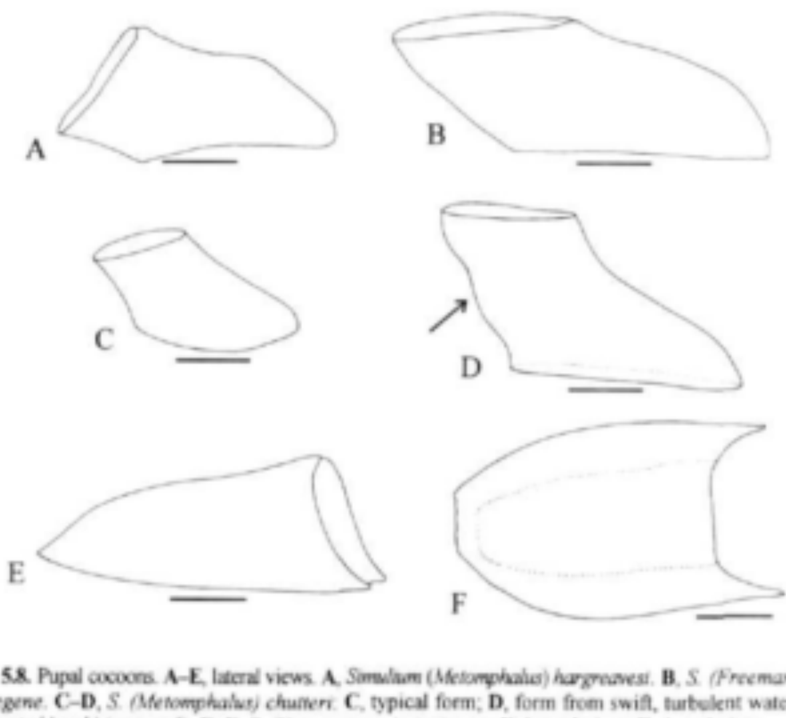


Fig. 5.8. Pupal cocoons. **A–E**, lateral views. **A**, *Simulium (Metomphalus) hargreavesi*. **B**, *S. (Freemanellum) debegene*. **C–D**, *S. (Metomphalus) chutteri*: **C**, typical form; **D**, form from swift, turbulent waters with elongated 'neck' (arrowed). **E–F**, *S. (Nevermannia) nigritarse*: **E**, lateral view; **F**, dorsal view.
Scale Bar = 1 mm.

7. Gill with four filaments (Fig. 5.9E) .... *S. (Freemanellum)*
– Gill with more than four filaments 8

8. Gill with 8–19 sharp pointed filaments with blackened tips (Fig. 5.9F) and of one type only... *S. (Anasolen)*
– Gills not with sharp darkened tips, usually robust, branched and frequently with secondary filaments (Figs 5.9G–J) 9

9. Gills consisting of six or nine large, thin-walled tubular branches arising between a pair of large curved basal arms, all branches pale and essentially of the same form (Fig. 5.9G) .... *S. (Edwardsellum)*
– Gills consisting of stout or tubular primary branches, often with basal arms, and thinner secondary filaments (Figs 5.9H–J): *S. (Metomphalus)* 10

10. Gill ending in a large number of equally sized filaments arising from five basal branches (Fig. 5.9H); pupal cocoon with indistinct neck .... *S. (M.) albivirgulatum*
– Gill with stout primary branched filaments and variously sized thinner secondary filaments, or rounded tubular branches (Figs 5.9I, J); pupal cocoon with distinct neck (e.g. Figs 5.8A, C, D) 11

11. Gill with distinct basal arms and large central branches without terminal filaments (Fig. 5.9J); fifth segment of abdomen with a pair of hooks on each side .... *S. (M.) medusaeforme* group
– Gill without basal arms; large central branches usually with terminal filaments (Fig. 5.9I); fifth segment of abdomen with or without a single minute ventral hook but not with a pair of ventral hooks on each side .... *S. (M.) bovis* group

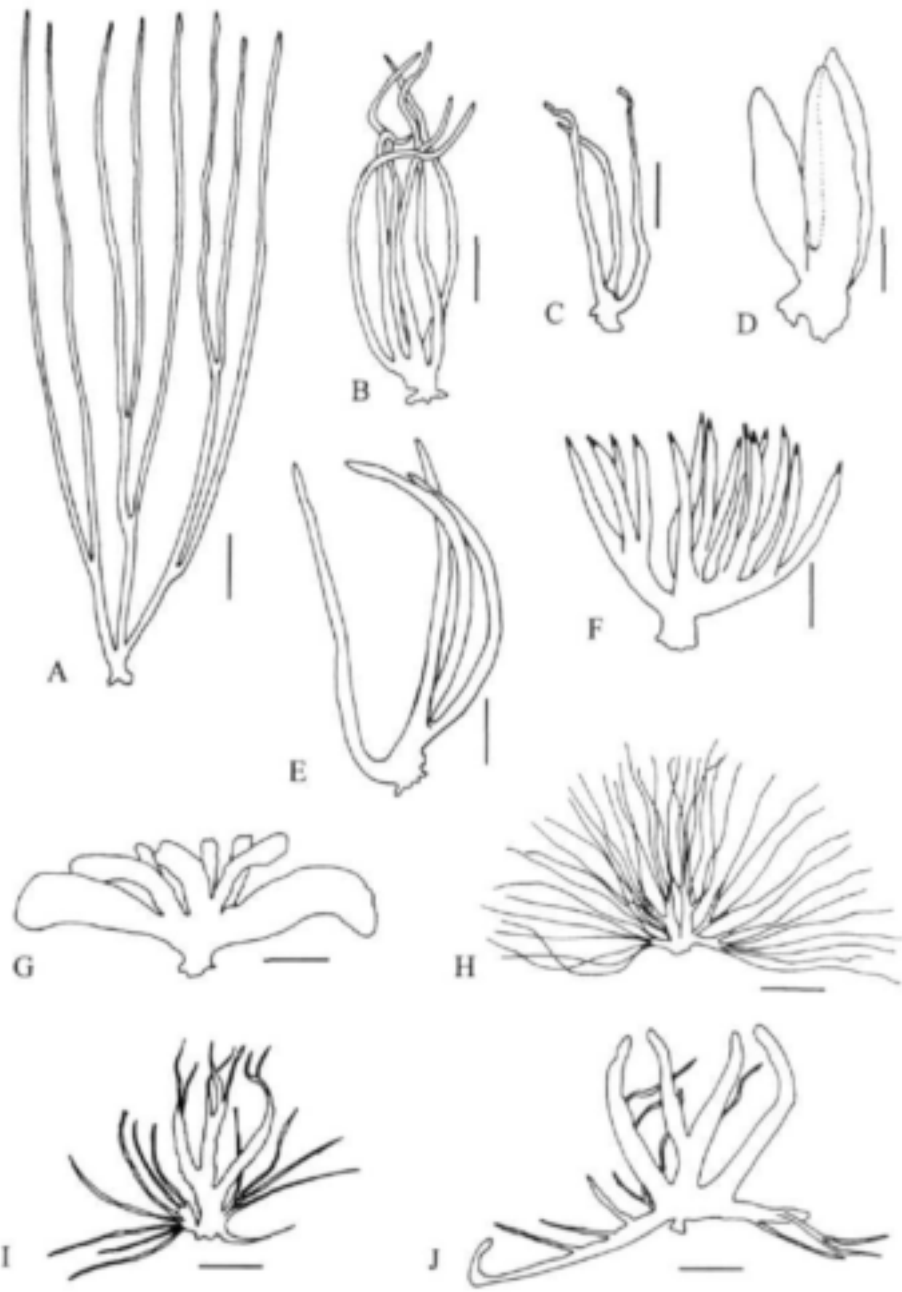


Fig. 5.9. *Simulium* pupal gills. **A**, *S.* (*Lewisellum*) *woodi*; **B**, *Paracnephia* (*Procnephia*) *damarense*; **C**, *S.* (*Afrosimulium*) *gariepense*; **D**, *S.* (*Byssodon*) *griseicolle*; **E**, *S.* (*Freemanellum*) *debegene*; **F**, *S.* (*Anasolen*) *dentulosum*; **G**, *S.* (*Edwardsellum*) *damnosum* s.l.; **H–J**, *S.* (*Metomphalus*) spp.: **H**, *S.* (*M.*) *albivirgulatum*; **I**, *S.* (*M.*) *chutteri*; **J**, *S.* (*M.*) *hargreavesi*. Scale bar = 0.1mm.

12. Gill variously branched with four or six filaments (Figs 5.10A–C)........... .... *S. (Nevermannia)*
– Gill various, but never with four to six filaments..............................13

13. Gill with either eight or eleven filaments (Figs 5.10D–E).....*S. (Meilloniellum)*
– Gill of varied form (Figs 5.10F–N) but never with six or eleven filaments and if with eight filaments, never with multiple branching as in Figs 5.9A & 5.10..14

14. Gill with 25–41 slender filaments arising from a common base and arranged in a semicircular fashion (Fig 5.10N); pupa attached to mayfly nymphs; abdomen with more than 20 blunt hooks around each segment V–VII dorsally; cocoon much reduced, covering only the abdomen........... ..*S. (Phoretomyia)*
– Gill with 18 or fewer filaments and of varied form but never arranged in a semicircular fashion (Figs 5.10F–M); pupa attached to submerged substrate often on leaf litter or trailing plant matter; abdomen with hooks and spine combs as in Fig. 5.7C....*S. (Pomeroyellum)*..15

15. Gill a single, long, forward-directed tube or a tube branching into eight apical thread-like filaments taking up less than half the length of the entire tube (Figs 5.10F, G)..*S. (Pomeroyellum) kenyae* group
– Gill not as described above 16

16. Gill with 7–20 filaments, sometimes arising from a common basal stem; if with eight filaments, then *not* arising only from a common stem (Figs 5.10H–J)...... .... *S. (Pomeroyellum) alcocki* group
– Gill with long common basal stalk or of varied form but not with sub-basal filaments 17

17. Gill with eight filaments arising from a common stem about half way along its length (Fig. 5.10K) ....*S. (Pomeroyellum) mcmahoni*
– Gill arising from a base and dividing into two simple arms or else branching off a secondary series of short, stout arms (Figs 5.10L–M) .... *S. (Pomeroyellum) cervicornutum* group

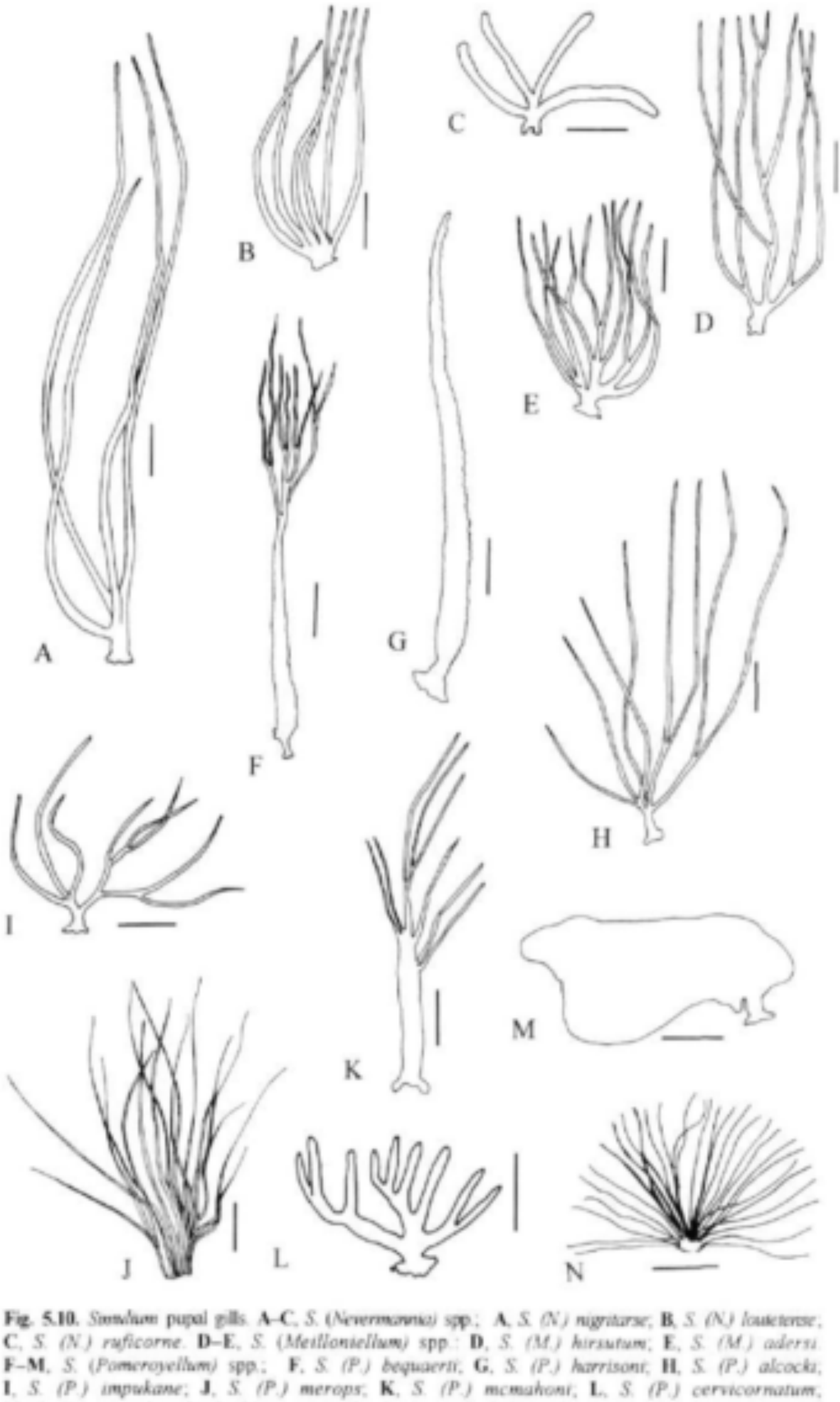


Fig. 5.10. *Simulium* pupal gills. **A–C**, *S.* (*Nevermannia*) spp.; **A**, *S.* (*N.*) *nigritarse*; **B**, *S.* (*N.*) *louketense*; **C**, *S.* (*N.*) *ruficorne*. **D–E**, *S.* (*Meilloniellum*) spp.; **D**, *S.* (*M.*) *hirsutum*; **E**, *S.* (*M.*) *adersi*. **F–M**, *S.* (*Pomeroyellum*) spp.; **F**, *S.* (*P.*) *bequaerti*; **G**, *S.* (*P.*) *harrisoni*; **H**, *S.* (*P.*) *alcocki*; **I**, *S.* (*P.*) *impukane*; **J**, *S.* (*P.*) *merops*; **K**, *S.* (*P.*) *mcmahoni*; **L**, *S.* (*P.*) *cervicornatum*; **M**, *S.* (*P.*) *rotundum*. **N**, *S.* (*Phoretomyia*) *lumbwanum*. Scale bar = 0.1 mm.

NOTES ON GENERA AND SUBGENERA

Southern African species of blackfly fall into several ecological categories, which are closely reflected in the subgeneric divisions of the family. The distribution and ecology of many southern African species, as recorded in the list on pages 104–106, are discussed by Palmer & de Moor (1998).

Paracnephia

Species of the genus *Paracnephia* are usually found in streams on outcrops of ancient geological formations such as the granite outcrops near Harare, Zimbawe or inselbergs such as the Brandberg in the Namib desert in Namibia. In the south-western Cape, some sedimentary deposits of Table Mountain Sandstone, where streams may only flow intermittently, also support several species of *Paracnephia*. Larvae and pupae are found in mosses attached to rocks in swift-flowing waters and pupae form a communal silken mat. This genus has ancient linkages with species on other southern landmasses and can be considered to comprise Gondwanaland relics. The genus also shows morphological and ecological similarities with European *Prosimulium* species. Mature larvae, pupae and adults have been collected in late spring to early summer (September–December) in the south-western Cape. Very little is known about the biology and ecology of the species found in southern Africa. There are two subgenera, *Paracnephia (Paracnephia)* (with six species divided into two species groups), and *Paracnephia (Procnephia)* with two species found in southern Africa.

Simulium (Afrosimulium) gariepense

Simulium (Afrosimulium) gariepense, the sole representative of the subgenus, is adapted to slow-flowing regions of large, turbid rivers such as the Orange. It may in fact be one of the few species that is able to survive on muddy substrata. Following the construction of dams and development of larval blackfly population control programmes along the Orange River this species has become rare and should be considered threatened (Palmer 1997). Palmer and Palmer (1995) have recommended measures to protect this species.

Simulium (Anasolen) and *S. (Freemanellum)*

The majority of species in these two subgenera are cascade-inhabiting, favouring cool, clear mountain streams. They are found in the swiftest of flows, sometimes even clinging to rock surfaces and trailing roots in waterfalls. Species of *S.* (*Anasolen*) are recorded from glacier-melt streams in Kenya at altitudes up to 5000 m above sea-level (Crosskey, 1969). They include species with some of the largest individuals in this family, larvae growing to 13 mm in length and adults occasionally attaining a wingspan of 20 mm. There are two species of *Simulium (Anasolen)* recorded from southern Africa. *S. (A.) dentulosum* is widespread, while *S. (A.) rhodesiense* is recorded only from Zimbabwe.

The subgenus *S. (Freemanellum)* is represented by four species in southern Africa. *Simulium (F.) debegene*, which is the most common, is restricted to cascades and waterfalls where water quality is excellent. Two other species, *S. (F.) hirsutilateris* and *S. (F.) empopomae*, have similar ecological requirements but are more restricted in distribution. All three species occur along the eastern parts of the country and are absent from the southern and south-western Cape, where *S. (F.) hessei* is endemic.

Simulium (Byssodon)

Members of the subgenus *Byssodon* live in very large rivers. They have an almost continuous distribution throughout the Afrotropical region, North Africa the middle East and Europe. Crosskey (1969) considers that Simuliidae adapted to very large rivers, such as the Nile, have thereby maintained a dispersal route between Europe and Africa even during extreme drought conditions, which would have created severe ecological and geographical barriers to other simuliid species that are not adapted to conditions in large rivers. Two species in this subgenus have been recorded from southern Africa, while in West Africa *S. griseicolle* has been recorded as a pest on poultry (Crosskey, 1960).

Simulium (Edwardsellum)

The *S. (Edwardsellum) damnosum* s.l. complex of species is represented by six described species in southern Africa, as well as at least four further undescribed species in this complex (Palmer & de Moor, 1999). It is one of the most common and widespread blackflies in southern Africa (Palmer & de Moor, 1998, 1999). Population densities in medium-sized rivers and below impoundments are often high. Regulation of rivers by man has favoured this species, causing a considerable increase in its distribution in recent times (Palmer & de Moor, 1999). The larvae and pupae of this complex of species are found on stones and trailing vegetation in the swift-flowing waters of medium-sized rivers. The adults have been recorded biting humans, poultry and livestock but have so far not been recorded as transmitters of onchocerciasis.

Simulium (Metomphalus)

Species belonging to the subgenus *Metomphalus* are most frequently found on stones and trailing vegetation in the swift turbulent waters of medium to large rivers. The *Simulium (Metomphalus) bovis* group has six species, of which four can be considered as large-river species. *Simulum chutteri*, a species which is found in the swiftest of currents in rapids on the Vaal and Orange Rivers, can at certain times of the year be found at densities up to 400 000 individuals or 700 g dry weight mass of blackfly m^{-2} of river bottom (de Moor, 1982a). This species can be regarded as one of the most serious pest simuliids in southern Africa and a great deal of research and effort has gone into devising methods for control and eradication (Chutter, 1968; Howell & Holmes, 1969; Howell et al., 1981; de Moor, 1982a, 1982b; Car & de Moor, 1984; de Moor & Car, 1986; de Moor et al., 1986; Palmer & Palmer, 1995; Palmer, 1997). With the advent of transfers of water from the Orange River to the Great Fish River in the Eastern Cape, conditions in the receiving river have been altered to the advantage of this species. While it was rare in the Great Fish River before the transfer of Orange River water, it is now a pest in this region (O'Keeffe, 1986; O'Keeffe & de Moor, 1988). *Simulium bovis*, a voracious cattle pest, occurs in the middle to lower reaches of large warm, alkaline rivers. It is absent from the Vaal and Orange Rivers and appears to have a disjunct distribution with one population in the more tropical northern and eastern regions of South Africa and further northward and a second population in the south-western Cape (Palmer & de Moor, 1998). The other two large- river species, *S. fragai* and *S. arnoldi*, are recorded from the Cunene and Zambezi Rivers respectively.

The *S. medusaeforme* group is represented by eight species in southern Africa. The larvae of these species are often not easy to distinguish from each other and pupae often reveal better diagnostic characters. *Simulium medusaeforme* is one of the most widespread and common blackflies in southern Africa and is found in a wide range of stream and river types in water quality ranging from excellent to poor (Palmer & de Moor, 1998). It has adapted to river regulation and is frequently common below impoundment outlets and in artificial waterways. It is usually found in the upper to middle reaches of medium size rivers. *Simulium hargreavesi* is not as widespread as *S. medusaeforme* but prefers similar flow and water conditions. *Simulium vorax* is restricted to fast-flowing rivers and to water of moderate to excellent quality; it is also widespread and is often found together with *S. medusaeforme* in large rivers (Palmer & de Moor, 1998). The species *S. natalense, S. letabum, S. africanum* and *S. zombaense* are all confined to cool, clear, swift-flowing mountain streams.

Simulium (Meilloniellum)

Two species of this subgenus have been recorded from southern Africa. *Simulium adersi* is a widespread, adaptable species common in small- to medium-sized rivers and favouring slow-flowing water. Because ecological conditions in large rivers vary widely, *S. adersi* is frequently found coexisting with many of the other *Simulium* species in medium to large rivers. It has also been recorded from regions where wave action occurs in lakes and on a few occasions even from saline waters, showing a tolerance of, or adaptability to, a range of ecological conditions. *Simulium adersi* is a pest on poultry and has been recorded as biting farm workers (Palmer & de Moor 1998). *Simulium hirsutum* is common in mountain streams where water quality is excellent. Because it is almost indistiguishable from *S. adersi*, its occurrence may be more common than estimated at present (Palmer & de Moor, 1998).

Simulium (Nevermannia)

Members of the subgenus *Nevermannia* are the most widespread of all simuliids on the African continent and two groups (*ruficorne* and *loutetense*) with seven species have been recorded from southern Africa. The *ruficorne* group comprises four species. *Simulium nigritarse* s.l. is considered to comprise a complex of 19 or more sibling species (Fain & du Jardin, 1983) of which at least three are known from southern Africa (Palmer & de Moor, 1998). As a colonizer of newly formed streams, and also able to tolerate a wide variety of polluted waters, it is the most widely distributed species in South Africa. It is found in a wide spectrum of flowing waters, from the smallest of trickles to large rivers, but favours slow to moderate currents. It is recorded as a pest on poultry (Palmer & de Moor, 1998). *Simulium ruficorne* is adapted to survival in conditions of little or no flow, even in desert regions, and can be found in the most stagnant of water bodies. It is also one of the first colonizers of newly-inundated streams (Harrison, 1966). Of the other two species *S. brachium* has been recorded from below impoundment outlets or in mountain streams with fast-flowing currents, and *S. katangae* is rare, but has been recorded from three widely separated localities in South Africa.

The *loutetense* group comprises three species, all of which are usually found in cool, clear mountain and foothill streams with excellent to good quality water, *S. loutetense* and *S. narcaeum* in swiftly-flowing water and *S. rutherfoordi* in slower-flowing stretches. *Simulium rutherfoordi* is widespread in South Africa and *S. narcaeum* has been recorded only from the Drakensberg Mountains (Palmer & de Moor, 1998).

Simulium (Pomeroyellum)

The subgenus *Pomeroyellum* is the most species-rich of all the subgenera in the Afrotropical region and has 15 recognized species in southern Africa. In the majority, the larvae and pupae attach themselves to dead leaves, trailing roots and grasses in slow-flowing waters of small streams although some species can be found in rapids and in the swift waters of large rivers. The subgenus is divided into three groups. The *kenyae* group, with five species, is characterized by pupae having long, forward-directed tubular gills, which may branch into terminal filaments from about one third along its length (Figs 5.10F, G & K). *Simulium harrisoni* is restricted to the south-western Cape. *Simulium bequaerti*, a warm-water species, is common in small and temporary streams in the eastern sub-tropical regions of South Africa. *Simulium mcmahoni* is widespread in slow-flowing water of small to very large rivers but is absent from the southern and south-western regions. The other two species, *S. schoutedeni* and *S. awashense*, are known only from Angola and Botswana.

The *cervicornutum* group comprises three species which, in the pupal stages, have gills that branch into two robust arms, each of which may have secondary branching (Figs 5.10 L, M). *Simulium rotundum* is a widespread species common in warm alkaline streams and medium-sized rivers. It is often associated with other species, such as *S. nigritarse* and *S. damnosum* s.l., found near impoundment outlets. The closely related *Simulium unicornutum* is widespread, found in the headwaters of streams in the eastern part of the country, and is common in the south-western Cape at lower altitudes. The third species of the group, *Simulium cervicornutum*, is common in small to medium-sized, clear alkaline streams and can tolerate moderate pollution.

The *alcocki* group comprises seven species with complex filamentous branching of the gills in the pupae (Figs 5.10H–J). *Simulium alcocki* and *S. impukane* are widespread in mountain foothill and temporary streams, and both are tolerant of moderate pollution. *S. merops* is restricted to cool acidic waters of the southern and south-western Cape and is common in small forested streams. The four other species (*S. evillense, S. johannae, S. schwetzi* and *S. tentaculum*) are found in small streams, larvae and pupae often on leaf litter or trailing vegetation in mountainous regions of tropical countries to the north of South Africa, but these species are too poorly known to make further suggestions as to their ecological requirements.

Simulium (Lewisellum) and *S. (Phoretomyia)*

The subgenus *Lewisellum* has larval and pupal stages that attach to river crabs living in small streams. This probably assists in avoiding predators but can also be considered as an adaptation to being 'piggy-backed' in and out of small bodies of water that periodically dry up. In the southern African region, species belonging to this subgenus have so far been recorded only from Malawi. The subgenus *Phoretomyia*, which has larval and pupal stages that attach to mayflies living in small streams and rivers, is represented by larvae and pupae recently collected by the author in South Africa, Swaziland and Zimbabwe. The larvae of *S. (P.) lumbwanum* were collected in mountain foothill streams, attached to heptageniid mayfly nymphs (de Moor, 1999). They show specialization for attachment to host insects with the posterior abdominal proleg in the larvae being situated ventrally and the pupae having modified spine combs on the abdomen that increase purchase inside the much-reduced pupal cocoon.

ACKNOWLEDGEMENTS

I would like to thank Nikki Köhly and Helen Barber-James who assisted with drawing some of the figures. Helen Barber-James, Roger Crosskey, Rob Palmer, Marjorie Scott and Brian Wilmot all read through and commented on drafts of the manuscript. Rob Palmer provided larvae of some species for the figures drawn. The National Research Foundation is thanked for providing funds for and encouraging the research on which this chapter is based. The Directorate of Museums and Heritage, Eastern Cape, are thanked for providing research facilities.

SIMULIIDAE: CHECKLIST OF SPECIES AND NOTES ON SOUTHERN AFRICAN DISTRIBUTION

TRIBE PROSIMULINI

Paracnephia (Paracnephia) Rubtsov

brincki group

P. (P.) brincki (de Meillon) South Africa (WC)

***muspratti* group**

P. (P.) barnardi (Gibbins) South Africa (WC)
P. (P.) harrisoni (Freeman and de Meillon) South Africa (WC)
P. (P.) herero (Enderlein) Namibia
P. (P.) muspratti (Freeman and de Meillon) South Africa (WC)
P. (P.) thornei (de Meillon) South Africa (WC)

Paracnephia (Procnephia) Crosskey

P. (P.) damarense (de Meillon and Hardy) Namibia
P. (P.) rhodesianum (Crosskey) Zimbabwe

TRIBE SIMULIINI

Simulium (Afrosimulium) Crosskey

S. (A.) gariepense de Meillon: South Africa (FS, EC, NC), Namibia

Simulium (Anasolen) Enderlein

S. (A.) dentulosum Roubaud: South Africa (EC, WC, MP, G, KZN, NP), Angola, Lesotho, Malawi, Zimbabwe
S. (A.) rhodesiense de Meillon: Zimbabwe

Simulium (Byssodon) Enderlein

S. (B.) griseicolle Becker: South Africa (EC, NC, FS, MP), Botswana
S. (B.) tridens Freeman and de Meillon: Malawi, Zambia

Simulium (Edwardsellum) Enderlein

S. (E.) damnosum s.l. Theobald: South Africa (all provinces) Angola, Lesotho, Malawi, Mozambique, Namibia, Swaziland, Zimbabwe
S. (E.) kilibanum Gouteux: Malawi
S. (E.) latipollex Enderlein: South Africa (MP)
S. (E.) machadoi Luna de Carvalho: Angola
S. (E.) 'Sanje' cytoform Dunbar: Malawi
S. (E.) vilhenai Luna de Carvalho: Angola

Simulium (Freemanellum) Crosskey

S. (F.) debegene de Meillon: South Africa (EC, FS, MP, G, KZN, NW), Zimbabwe
S. (F.) empopomae de Meillon: South Africa (KZN)
S. (F.) hessei Gibbins: South Africa (WC, EC)
S. (F.) hirsutilateris de Meillon: South Africa (KZN, NP)

Simulium (Lewisellum) Crosskey

S. (L.) nyaslandicum de Meillon: Malawi
S. (L.) woodi de Meillon: Malawi

Simulium (Meilloniellum) Rubtzov

S. (M.) adersi Pomeroy: South Africa (all provinces), Angola, Botswana, Malawi, Mozambique, Namibia, Swaziland, Zambia, Zimbabwe

S. (M.) hirsutum Pomeroy: South Africa (WC, EC, MP, KZN, NP) Angola, Malawi, Mozambique, Zimbabwe

Simulium (Metomphalus) Enderlein

***albivirgulatum* group**

S. (M.) albivirgulatum Wanson & Henrard: South Africa (KZN), Angola, Botswana, Zambia, Zimbabwe

Simulium (Metomphalus) Enderlein

***bovis* group**

S. (M.) arnoldi Gibbins: Zambia, Zimbabwe

S. (M.) bovis de Meillon: South Africa (WC, EC, KZN, MP, NP), Angola, Malawi, Mozambique, Namibia, Zimbabwe

S. (M.) chutteri Lewis: South Africa (EC, NC, FS, NW), Namibia

S. (M.) fragai Marini de Araujo Abreu: Angola, Namibia

S. (M.) janzi Marini de Araujo Abreu: Angola

S. (M.) wellmanni Roubaud: South Africa (EC, FS, MP, KZN, NP), Angola, Zambia

***medusaeforme* group**

S. (M.) africanum Gibbins: Lesotho

S. (M.) colasbelcouri Grenier and Ovazza: Angola

S. (M.) hargreavesi Gibbins: South Africa (WC, EC, NC, MP, KZN, NW), Angola, Malawi, Mozambique, Zambia, Zimbabwe

S. (M.) letabum de Meillon: South Africa (WC, EC, MP, KZN, NP)

S. (M.) medusaeforme Pomeroy: South Africa (all provinces), Angola, Lesotho, Malawi, Mozambique, Swaziland, Zambia, Zimbabwe

S. (M.) natalense de Meillon: South Africa (EC, KZN)

S. (M.) vorax Pomeroy: South Africa (WC, EC, FS, KZN, MP, NP), Angola, Lesotho, Malawi, Mozambique, Swaziland, Zambia, Zimbabwe

S. (M.) zombaense Freeman and de Meillon: Malawi

Simulium (Nevermannia) Enderlein

***loutetense* group**

S. (N.) loutetense Grenier and Ovazza: Angola, Zambia

S. (N.) narcaeum de Meillon: South Africa (KZN)

S. (N.) rutherfoordi de Meillon: South Africa (WC, EC, FS, KZN, MP, NP, NW), Zimbabwe

***ruficorne* group**

S. (N.) brachium Gibbins: South Africa (WC, EC, NW)

S. (N.) katangae Fain: South Africa (EC, KZN, G)

S. (N.) nigritarse Coquillett: South Africa (all provinces), Angola, Lesotho, Mozambique, Swaziland, Zambia, Zimbabwe

***S. (N.) ruficorne* group (cont.)**

S. (N.) ruficorne Macquart: South Africa (all provinces), Angola, Malawi, Mozambique, Namibia, Swaziland, Zambia, Zimbabwe

Simulium (Phoretomyia) Crosskey

S.(P.) lumbwanum de Meillon: South Africa (MP), Swaziland, Zimbabwe

Simulium (Pomeroyellum) Rubtzov

***alcocki* group**

S. (P.) alcocki Pomeroy South Africa (WC, EC, FS, G, MP, KZN, NP), Angola, Malawi, Mozambique

S. (P.) evillense Fain, Hallot & Bafort: Botswana, Zambia

S. (P.) impukane de Meillon: South Africa (all provinces), Angola, Malawi, Mozambique

S. (P.) johannae Wanson: Zambia

S. (P.) merops de Meillon: South Africa (WC, EC)

S. (P.) schwetzi Wanson: Angola

S. (P.) tentaculum Gibbins: Malawi

***cervicornutum* group**

S. (P.) cervicornutum Pomeroy: South Africa (EC, KZN, MP, NP, G), Angola, Malawi, Mozambique, Zambia

S. (P.) rotundum Gibbins: South Africa (EC, KZN, MP, NP, G), Angola, Malawi, Mozambique

S. (P.) unicornutum Pomeroy: South Africa (WC, EC, FS, KZN, MP, G, NP), Angola, Malawi, Mozambique, Zambia

***kenyae* group**

S. (P.) awashense Uemoto, Ogata and Mebrahtu: Botswana

S. (P.) bequaerti Gibbins: South Africa (EC, KZN, FS, MP, NP), Angola, Lesotho, Zimbabwe

S. (P.) harrisoni Freeman and de Meillon: South Africa (WC)

S. (P.) mcmahoni de Meillon: South Africa (EC, NC, FS, MP, G, NW, NP), Angola, Botswana, Malawi, Mozambique, Namibia

S. (P.) schoutedeni Wanson: Angola

USEFUL REFERENCES

CAR, M. & DE MOOR, F.C. 1984. The response of Vaal River drift and benthos to *Simulium* (Diptera: Nematocera) control using *Bacillus thuringiensis* (H–14). *Onderstepoort Journal of Veterinary Research* **51:** 155–160.

CHUTTER, F.M. 1968. On the ecology of the fauna of stones in the current in a South African river supporting a very large *Simulium* population. *Journal of Applied Ecology* **5:** 531–561.

CROSSKEY, R.W. 1960. A taxonomic study of the larvae of West African *Simuliidae* (Diptera: Nematocera) with comments on the morphology of the larval black-fly head. *Bulletin of the British Museum (Natural History) Entomology* **10**(1): 1–74.

CROSSKEY, R.W. 1969. A re-classification of the Simuliidae (Diptera) of Africa and its islands. *Bulletin of the British Museum (Natural History) Series B. Supplement* **14:** 1–195.

CROSSKEY, R.W. 1981. Simuliid taxonomy — the contemporary scene. *In*: Laird, M. (Ed.) *Blackflies: the Future for Biological Methods in Integrated Control*. Academic Press, London: 3–18.

CROSSKEY, R.W. 1987a. The future of black fly taxonomy. pp. 11–23. *In*: Kim, K. C. & Merritt, R.W. (Eds.) *Black flies: Ecology, Population Management, and Annotated World List, USA*. The Pennsylvania State University, Pennsylvania: 528 pp.

CROSSKEY, R.W. 1987b. A taxa summary for the *Simulium damnosum* complex, with special reference to distribution outside the control areas of West Africa. *Annals of Tropical Medicine and Parasitology* **81**(2): 181–192.

CROSSKEY, R.W. 1990. *The Natural History of Blackflies*. John Wiley and Sons, Chichester: 711 pp.

CROSSKEY, R.W. 1999. *First Update to the Taxonomic and Geographical Inventory of the World Blackflies (Diptera: Simuliidae)*. The Natural History Museum, London: 10 pp.

CROSSKEY, R.W. & HOWARD, T.M. 1996. *A Taxonomic and Geographical Inventory of the World Blackflies (Diptera: Simuliidae)*. The Natural History Museum, London: 144 pp.

DE CARVALHO, L. 1962. Dados para o conhecimento dos Simulidos de Angola (Diptera Simuliidae). *Publicacoes Culturais da Companhia de Diamantes de Angola* **60**: 13–56.

DE MOOR, F.C. 1982a. *A community of Simulium species in the Vaal River near Warrenton*. Ph.D Thesis, University of the Witwatersrand, Johannesburg: 317 pp.

DE MOOR, F.C. 1982b. Determination of the Number of Instars and Size Variation in the Larvae and Pupae of *Simulium chutteri* Lewis 1965 (Diptera: Simuliidae) and some possible bionomical implications. *Canadian Journal of Zoology* **60**(6): 1374–1512.

DE MOOR, F.C. 1989. Alternative life-history styles in Simuliidae (Insecta: Diptera). *In*: Bruton, M.N. (Ed.) *Alternative Life-History Styles in Animals*. Kluwer Academic Press, Dordrecht: 293–316.

DE MOOR, F.C. 1992. Parasites, generalist and specialist predators and their role in limiting the population size of blackflies and in particular *Simulium chutteri* Lewis (Diptera: Simuliidae) in and along the Vaal River, South Africa. *Annals of the Cape Provincial Museums (Natural History)* **18**: 271–291.

DE MOOR, F.C. 1999. Phoretic association of blackflies (Diptera: Simuliidae) with heptageniid mayflies (Ephemeroptera: Heptageniidae) in South Africa. *African Entomology* 7(1): 154–156.

DE MOOR, F.C. & CAR, M. 1986. A field evaluation of *Bacillus thuringiensis* var. *israelensis* as a biological control agent for *Simulium chutteri* (Diptera: Nematocera) in the middle Orange River. *Onderstepoort Journal of Veterinary Research* **53**: 42–50.

DE MOOR, F.C., CHUTTER, F.M. & DE MOOR, I.J. 1986. Drift behaviour and microhabitat selection in the preimaginal stage of *Simulium chutteri* (Diptera: Simuliidae). *Hydrobiologia* **133**: 143–154.

FAIN, A. & DU JARDIN, J.P. 1983. The *Simulium nigritarse* complex (Diptera: Simuliidae). *Revue de Zoologie Africaine* **97**: 379–452.

FREEMAN, P. & DE MEILLON, B. 1953. *Simuliidae of the Ethiopian Region.* London, London British Museum (Natural History): 224 pp.

HARRISON, A.D., 1966. Recolonisation of a Rhodesian stream after drought. *Archiv fur Hydrobiologie* **62**: 405–421.

HINTON, H.E. 1964. The respiratory efficiency of the spiracular gill of *Simulium*. *Journal of Insect Physiology* **10**(1): 73–80.

JUPP, P.G. & PALMER, R.W. 1999. Blackflies (Diptera: Simuliidae) biting a resident of suburban Johannesburg. *South African Medical Journal* **89**(4): 388–389.

HOWELL, C.J., BEGEMAN, G.J., MUIR, R.W. & LOUW, P. 1981. The control of Simuliidae (Diptera: Nematocera) in South African rivers by modification of the water flow volume. *Onderstepoort Journal of Veterinary Research* **48**(1): 47–49.

HOWELL, C.J. & HOLMES, G.W. 1969. The control of Simuliidae in the Vaalharts irrigation complex. *Journal of the South African Veterinary Medical Association* **40**: 59–67.

LEWIS, D.J. 1965a. On the *Simulium medusaeforme* complex (Diptera, Simuliidae). *Entomologist's Monthly Magazine* **100**: 183–187.

LEWIS, D.J. 1965b. On the *Simulium bovis* complex (Diptera, Simuliidae). *Annals and Magazine of Natural History* **13**(7): 449–455.

MOKRY, J.E., COLBO, M.H. & THOMPSON, B.H. 1981. Laboratory colonization of blackflies. pp. *In*: Laird, M. (Ed.) *Blackflies: the Future for Biological Methods in Integrated Control*. Academic Press, London: 299–306.

O'KEEFFE, J.H., 1986. The Blackfly problem in the Great Fish River. *The Naturalist* **29**(3): 3–8.

O'KEEFFE, J.H. & DE MOOR, F.C. 1988. Changes in the physico-chemistry and benthic invertebrates of the Great Fish River, South Africa, following an interbasin transfer of water. *Regulated Rivers Research and Management* **2**: 39–55.

PALMER, R.W. 1991. Description of the larvae of seven species of blackflies (Diptera: Simuliidae) from southern Africa, and a regional checklist of the family. *Journal of the Entomological Society of southern Africa* **54**(2): 197–219.

PALMER, R.W. 1994. A rapid method of estimating the abundance of immature blackflies (Diptera: Simuliidae). Onderstepoort Journal of Veterinary Research **61**: 117–126.

PALMER, R.W. 1997. *Principles of Integrated Control of Blackflies (Diptera: Simuliidae) in South Africa.* Water Research Commission Report No 650/1/97 Pretoria: 307 pp.

PALMER, R.W. & DE MOOR, F.C. 1998. Annotated records of blackfly (Diptera: Simuliidae) distribution in southern Africa. *African Entomology* **6**(2): 223–251.

PALMER, R.W. & DE MOOR, F.C. 1999. *Simulium damnosum* s.l. complex widespread in southern Africa. *British Simuliid Group Bulletin* **14**: 10–14.

PALMER, R.W. & PALMER, A.R. 1995. Impacts of repeated applications of *Bacillus thuringiensis* var. *israelensis* de Barjac and temephos used in blackfly (Diptera: Simuliidae) control, on macroinvertebrates in the middle Orange River, South Africa. *Southern African Journal of Aquatic Sciences* **21**: 35–55.

ROTHFELS, K.H. 1979. Cytotaxonomy of blackflies (Simuliidae). *Annual Review of Entomology* **24**: 507–539.

STEYSKAL, G.C., 1972. The meaning of the Term 'Sibling Species'. *Systematic Zoology* **21**(4): 446.

WALLACE, J.B. & MERRITT, R.W. 1980. Filter-feeding ecology of aquatic insects. *Annual Review of Entomology* **25**: 103–132.

CHAPTER 6

CHIRONOMIDAE

by

A.D. Harrison

Chironomids often constitute 50% or more of the total number of species of macro-invertebrates present in inland waters. Some authorities have calculated that there are 10 000 to 15 000 species worldwide, but there are probably not more that 300 to 400 species in southern Africa. The larvae constitute a large part of the biomass of aquatic macroinvertebrates, often between 10% and 50%, and form important links in the food chain, as they feed directly on algae or detritus and then are eaten by most aquatic predators. They are an important food of young fish in lakes and rivers.

Unlike many other taxa of aquatic insects, the chironomid fauna of southern Africa, indeed of Africa generally, does not display much local endemism. Of the seven subfamilies of chironomids only one, the Aphroteniinae, is a Gondwanan endemic, the other six all being widespread throughout the world. (For further information on distribution, see 'Notes on subfamilies' on pages 156–158).

Like all other Diptera, chironomids are holometabolous insects with separate egg, larval, pupal and adult stages. They spend most of their lives in the larval stage, which may last for several months in species of genera such as *Clinotanypus*, *Chironomus*, *Nilodorum*, *Cryptochironomus* and *Kiefferulus*, with large individuals, but only two or three weeks in species with smaller individuals. There are four larval instars.

Habitat requirements

Chironomid larvae are found in both running and standing fresh waters. They occur in stony torrents, in waterfalls and in all riverine habitats from the mountains to the sea. Some are found on the bottoms of deep lakes while others are very abundant in the aquatic vegetation fringing lakes of all kinds. Chironomids are among the main inhabitants of ponds and wetlands and are found even in water retained in small depressions in rocks, and in tree holes. A few exploit other wet and damp habitats such as rich soils (especially in forests), and even cow pats.

Some chironomids, such as *Baeotendipes* (Chironominae), are found in brackish water and chironomids are among the few insect groups that have invaded truly marine habitats. The world-wide intertidal genera, *Telmatogeton* and *Thalassomyia* (subfamily Telmatogetoninae), are found in southern Africa. In addition, the genus *Clunio* is found all over the world in marine to brackish environments, and *Semiocladius* is found intertidally on Indian Ocean shores and also in the Pacific. Both belong to the subfamily Orthocladiinae.

In many parts of Africa where there are long dry seasons, a number of species are adapted to life in transient habitats such as rain pools in rocks, and in the footprints of large animals. The duration of the temporary habitats may be close to the life span of the chironomids inhabiting them. Larvae of *Chironomus pulcher* and *C. imicola* are found in rain pools on rocks in most of Africa, as well as in other very temporary habitats; their larval stages last for as short a time as ten days before metamorphosis. In pools of even shorter duration, larvae of the extraordinary West African species, *Polypedilum vanderplanki*, are able to survive complete desiccation of their habitat, quickly reviving when it fills up with water again. This species has not yet been found in southern Africa.

Interestingly, the specialized larvae of the subfamily Podonominae are found in small seasonal streams and trickles in mountain regions. How and where they complete their life cycles is not yet fully understood, as some of these habitats may be completely dry for four or five months at a time.

Food and feeding

Most chironomid larvae feed on algae or detritus, obtaining food mainly by scraping the substratum. Other larvae have specialized feeding habits. Those of *Stenochironomus*, for instance, mine tunnels in dead leaves that have fallen into the water; larvae of *Xenochironomus* burrow into freshwater sponges, and of *Collartomyia* burrow into the pupae of hydropsychid caddis flies. All of the Tanypodinae are predatory, at least in their later instars; they mostly feed on small chironomid larvae, other aquatic insects, nematodes and oligochaetes.

Reproduction

Eclosion (emergence as an adult) usually takes place in late afternoon or early evening and the newly moulted (teneral) adults fly to sheltered spots while their cuticles harden. Adults of many species have been found feeding on honeydew, the sugary secretion of aphids, but it is not known what proportion of species do this.

The flying males of most species form mating swarms. Some (such as *Chironomus* spp.) in the evening, but others some time during the day, usually in the early morning. The swarms often appear over the tops of bushes or other objects. A female flies into a swarm and is grasped by a male and the pair fly to a sheltered spot to mate. The male usually dies soon after mating but the female waits until late afternoon or dusk to lay her eggs. Those from stony torrents (such as species of *Cricotopus* and *Orthocladius* — Orthocladiinae), fly in a zig-zag manner over the surface of the torrent and drop their egg masses right into it. These sink quickly and stick onto stones. Others lay their eggs in the water as they sit on some object at the surface. The eggs are enclosed in a jelly-like muco-polysaccharide so that the egg mass soon absorbs water and becomes greatly enlarged.

Development of the embryos is usually very rapid and first-instar larvae hatch within a few days of the egg being laid. When the larva is ready to pupate the thoracic region becomes swollen and soon ecdysis occurs. Chironomid pupae superficially resemble mosquito pupae but do not curl themselves into the well-known comma-shape. Pupae of most chironomids live either in the larval tube or in a tube constructed by the larvae prior to pupation, but pupae of the Tanypodinae are free-swimming and are found at, or near, the surface of the water. Within the pupa the adult develops until it is fully formed but still within the pupal cuticle. The pharate adult leaves its tube and swims actively to the surface, where it emerges from its pupal skin and flies away. This is a very rapid process in torrential streams.

The adults, commonly known as non-biting midges, resemble mosquitoes but do not have biting mouthparts. The males usually have plumose antennae, but the females do not. Most adults, especially the males, are very short-lived, some of the smaller ones living for only a few hours. Adults vary in length from about 20 mm or more (*Chironomus*) to as little as 2 or 3 mm (*Nilotanypus, Corynoneura, Thienemanniella, Nanocladius* and some species of *Cladotanytarsus*).

BIOLOGY OF IMMATURE CHIRONOMIDS

The best known chironomid larvae are the red 'blood-worms' of *Chironomus* (Fig. 6.1B), found in the mud at the bottom of ponds and muddy streams, especially in polluted waters. Most other larvae have the same general appearance but are smaller, those in well-aerated habitats and running waters often being greenish in colour. The minute first-instar larvae differ markedly in structure from the other three instars and are very difficult to identify; those of some lake-dwellers are found in the water column because they form a planktonic or dispersal phase.

Most chironomid larvae construct tubes, made of salivary secretions and debris, which are usually attached to the substratum or buried in the mud. The inmates reach out to grab food, such as algal cells and organic debris, but retreat back very rapidly into the tube when danger threatens. Others have portable cases (Figs 6.8L–P) similar to those of the Trichoptera (see Volume 8), whereas others, including the predatory Tanypodinae (Fig. 6.1A), are free-living.

Bottom dwellers, such as *Chironomus* and *Nilodorum*, have a form of haemoglobin in their blood that assists in respiration when the oxygen content of the water is low. Tube dwellers in still or slow-flowing water also execute pumping respiratory movements that keep water circulating through their tubes.

COLLECTION AND IDENTIFICATION OF CHIRONOMIDS

Larvae should be collected with a hand-net of very fine mesh. This can be swept through the aquatic vegetation of lakes, ponds, rivers or streams, or held in stony torrents below stones disturbed by hand or kicked with the foot. Chironomid larvae also turn up in grab samples from lake bottoms and in samples from other aquatic habitats.

Samples taken in the field may be preserved in 10% formalin but in the laboratory they should be transferred to 70% alcohol, in which they can be kept indefinitely. Identification of larvae to species requires mounting them on a microscope slide for examination under a compound microscope. Euparal is a good mounting medium. Before mounting, the head (or the 'head capsule' as it is usually called: Figs 6.2C–E), should be separated from the body and mounted ventral-side up. It is usually necessary to press down on the coverslip, carefully, to flatten the capsule and to spread out the mouth-parts. The body should be mounted separately; it usually lies in a lateral position.

Pupae are collected in the same way as larvae (above) but collections specifically for pupae can be made in the late afternoon, in backwaters in rivers and streams or in quiet areas at lake shores amongst vegetation. At this time pupae will be seen rising to the surface to eclose and can be netted. It is more valuable, however, to allow eclosion to occur and then to collect moulted adults as well as pupal skins (exuviae), which may also have the last larval moult attached. The new adults should not be preserved immediately but should be allowed to harden off in a vial overnight. Pupae and adults should be preserved in 70% alcohol.

Dr. Peter Langton writes: "The recently deposited strand on the shore of a lake or river is often a good source of chironomid pupal exuviae and is simply scraped up and placed in plastic bags. In streams, flotsam trapped on emergent vegetation or amongst rocks is also likely to be rich in exuviae and can be collected in a similar way, though a 'skim net' held just downstream of the obstruction during collection will pick up any disturbed exuviae. These collections may be sorted in white plastic trays late that day and the exuviae transferred to specimen tubes containing 70% isopropanol (or 70% ethanol). Alternatively, the alcohol can be added to the plastic bags in sufficient quantity to cover all the enclosed flotsam, which will keep in this condition for months until it is sorted".

(CAUTION! All pupae, as well as their moulted 'skins' or exuviae, should be examined first under a dissecting microscope, using a black background and incident (top) light, to determine the structure of the thoracic horn. The plumose thoracic horns (Figs 6.9B, 6.10Aa) of the Chironominae may be invisible on mounted specimens. The **cephalothorax** of the whole pupa should be mounted on its side and the abdomen mounted dorsal-side up. Exuviae (the word has the same form in the singular and the plural) should not be dissected but should be mounted dorsal-side up in Euparal or some similar medium.

Identification of immature chironomids

In order to identify larval and pupal chironomids, the reader should be familiar with the basic structure of immature dipterans, as described on pages 8–11. Further morphological details, used specifically in the identification of immature chironomids, are described below.

Larvae

Larvae (Figs 6.1A–C) are elongate, cylindrical and usually slender with a hardened, non-retractile **head capsule** (Fig. 6.2D–E). A feature of taxonomic significance is the appearance of the **frons**, or **frontal apotome** (Fig. 6.1E, H), which is that part of the front of the head extending from the base of the antennae to the frontal base of the head. (Note that Fig. 6.1H is drawn as if the head has been split open horizontally from inside and flattened out to show the relationship between the frontal apotome, clypeus, labrum and mouthparts).

The **antennae** (Figs 6.1G, 6.3C–M) consist of four to seven segments, but the apical three are often small and difficult to see. In most genera they bear **Lauterborn organs**. These paired compound organs, consisting of a peg sensillum and two series of digitiform, thin-walled extensions, usually occur at or near the apex of the second antennal segment (e.g. Figs 6.3I, J), but one of the pair may be subapical and/or on the third segment. The antenna is usually divided into a basal **pedestal** and a thinner **flagellum** (Figs 6.3C, J, K).

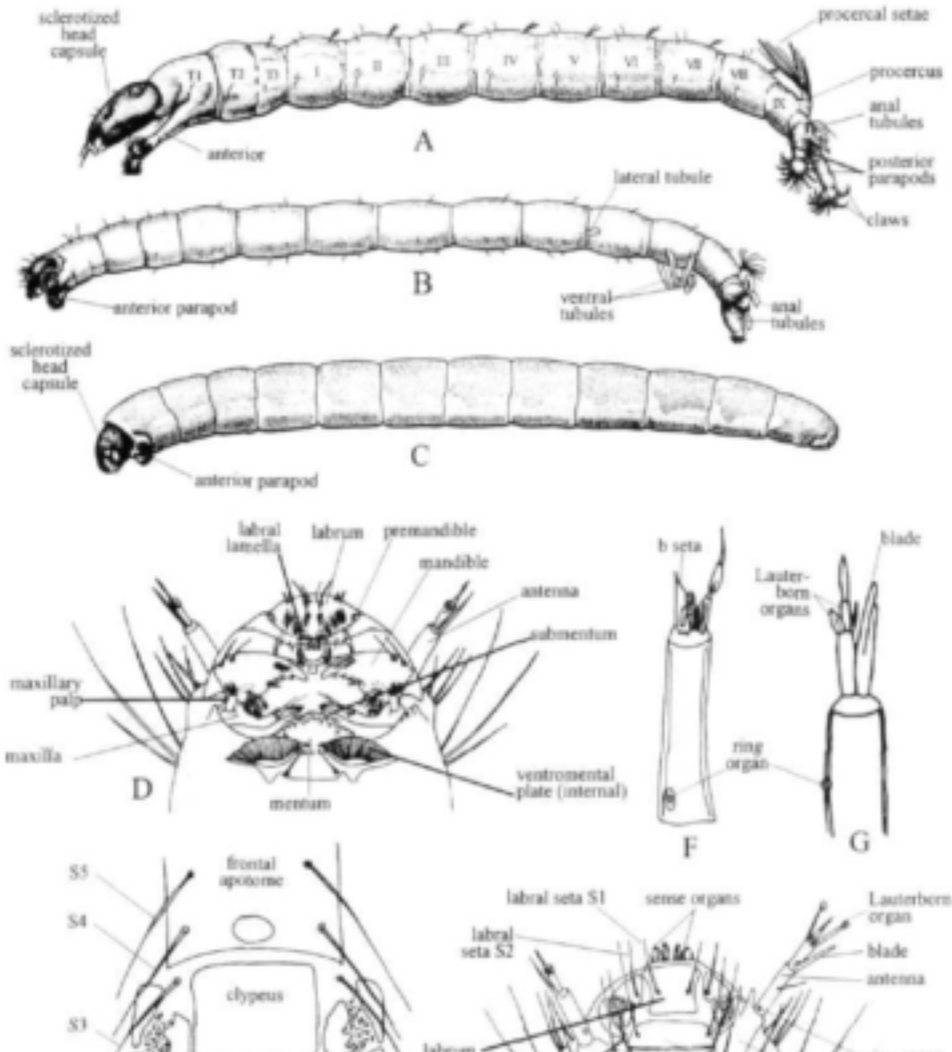


Fig. 6.1. General features of chironomid larvae. **A–C**, entire larvae in left lateral view: **A**, Tanypodinae; **B**, Chironominae; **C**, Orthocladiinae. **D**, generalised chironomid head in ventral view. **E**, generalized chironomid head in dorsal view. **F**, maxillary palp. **G**, antenna. **H**, generalised head as if slit horizontally and flattened, showing the relationship between the major apotomes and anterior appendages. A–C redrawn from McAlpine et al. (1981); D–H redrawn from Wiederholm (1983).

The **feeding apparatus** (Figs 6.1D, 6.1H, 6.2) consists of both unpaired mid-line structures and paired mouthparts. Of the unpaired structures, anteriormost is the **labrum**, the upper 'lip', which lies between the clypeus and the mouth (Fig. 6.1E). The labrum is beset with a number of paired setae, outside of which are one or more smooth to pectinate lamellae or sheets, the **labral lamellae** (Figs 6.4C–F). In the Tanypodinae the floor of the mouth (i.e. not visible externally) bears the sclerotized **ligula**, a conspicuous toothed plate flanked by a pair of small **paraligulae** (Figs 6.2G, 6.5G–J). In the other sub-families the ligula is much smaller and less obvious. Immediately behind the mouth is the **hypopharynx,** a median lobe that does not bear appendages, and that in larval tanypods is called the **pecten epipharyngis** (i.e. the comb-like part of the hypopharynx: (Figs 6.1H, 6.2G, 6.5L). The hypopharynx is followed posteriorly by the labium, parts of which in chironomids fuse with the hypopharynx to form the **premento-hypopharyngeal complex**. The labium consists of the **submentum**, the **mentum** and the **prementum**, the submentum being the basal part by which it is attached to the head. The mentum forms the sclerotized medioventral floor of the head capsule and is usually visible as a toothed ventral plate. The **ventromentum**, which is internal and therefore visible only through the integument of the head, is often expanded laterally to form two **ventromental plates** (Figs 6.2E, 6.6, 6.7). The prementum is the soft ventral lobe of the premento-hypopharyngeal complex separated from the hypopharynx by the salivary outlet and bearing the ligula and the paraligula (see above).

Starting anteriorly, the paired appendages are as follows. The **premandibles** (Figs 6.1H, 6.4G–K), a pair of ventral structures attached to the labrum, take the form of toothed plates or processes that may bear brushes of setae (e.g. Fig. 6.4G). These are followed posteriorly by the paired mandibles, of which the **seta interna**, the **basal tooth** and the **apical tooth** (Figs 6.2A–B) are of taxonomic significance. Posteriormost of the paired appendages are the **maxillae** (Figs 6.1F, 6.3 N–Q), the **palps** of which may bear a **ring organ**, a small circular sensory structure on the basal segment.

Thorax and abdomen (Figs 6.1A–C) are not clearly differentiated from each other. The **thorax** consists of three separate somites, the first of which bears a pair of **parapods** or prolegs that often fuse to form a single median appendage under the 'chin'. The **abdomen** consists of nine visible somites, labelled with Roman numerals I–IX. In a few genera segment VIII bears one or more pairs of **ventrolateral tubules** (Fig. 6.1B). Ventrally, segment IX usually bears ventrally a pair of parapods (recognizable by the terminal hooks or claws), 1–3 pairs of anal papillae, and a pair of procerci. The **anal papillae** (sometimes called anal tubercles) are oblong, ovoid or tapering appendages of the anal segment above and between the posterior

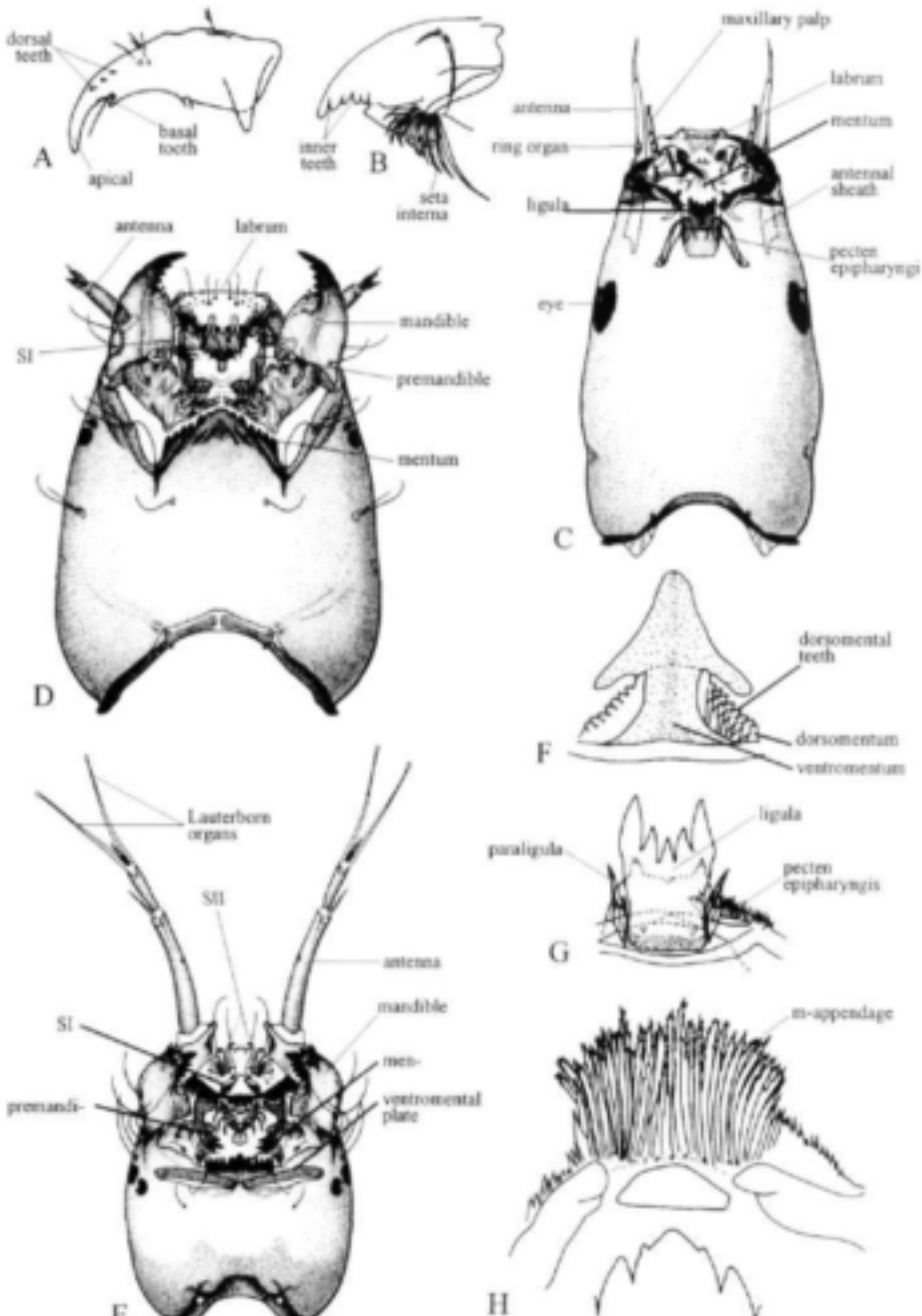


Fig. 6.2. Chironomid larvae. **A**, generalised mandible. **B**, Diamesinae: mandible of *Harrisonina*. **C–E**, head capsules, ventral views: **C**, Tanypodinae; **D**, Orthocladiinae; **E**, Chironominae (Tanytarsini). **F–G**, distinguishing characteristics of Tanypodinae; **F**, mentum; **G**, ligula, paraligulae and pecten hypopharyngis. **H**, M-appendages of prementum of Telmatogetoninae. A, F–H from Wiederholm (1983); B from Brundin (1966); C–E from McAlpine et al. (1981).

parapods; the **procerci** (singular '**procercus**') are a pair of dorsal preanal tubercles carrying 1–20 apical setae and usually two lateral setae.

Most chironomid larvae have no open spiracles but those of the Gondwanan subfamily Podonominae have a single pair of spiracles dorsally on the abdomen (Fig. 6.3B).

Pupae

Whole pupae (Figs 6.9A–C) can be identified, and so can the cast skins, or exuviae, based largely on details of the setation and other ornamentation of the body segments.

The head and thorax, together with the developing legs and wings, are united in the **cephalothorax** (Fig. 6.9E), which bears a pair of respiratory **thoracic horns**. These horns (Fig. 6.10A), which may be in the form of simple lobes or many-branched plumose tufts, are equivalent to the structures called respiratory horns, trumpets, breathing horns or cephalic horns in other dipteran families. A thoracic horn is attached to the cepahlothorax at the **basal ring**, the shape of which may be diagnostic. It connects to the outside either by means of an **aeropyle** (Fig. 6.10Ad), which is a tiny pore, or by means of a **plastron plate**, which is a much larger, porous apical plate (e.g. Fig. 6.10Ah). The head (Fig. 6.9D) bears some diagnostic characters: the **frontal apotome**, a plate in front of and between the **antennal sheaths** (Fig. 6.9D), often carries **frontal setae**, **cephalic tubercles** and/or **frontal warts**. Cephalic tubercles bear setae on raised projections, while frontal warts are wartlike tubercles. Important features of the thorax are the **wing sheaths**, which are often ornamented with a **pearl row** of tiny teeth or denticles, and the **nose** (Fig. 6.9E), a small projection posterodorsally on the wing sheath.

The **abdomen** (Figs 6.1B, C & D) consists of nine visible segments, the last of which is known as the **anal somite**. The anal somite often bears a pair of **anal lobes**, as well as the **genital sacs**, which cover the adult sex organs. Male pupae have larger antennal and genital sacs than female pupae do. The anal lobes may bear **anal spurs** (Fig. 6.10C) or an **anal comb** (Fig. 6.10B), consisting of groups spines consisting of postero-lateral groups of spines.

Taxonomically significant features of the abdominal somites (Figs 6.10B, C) include the following. **Conjunctives** are the thin dorsal intersegmental membranes that sometimes bear small setae. **Points** are the minute spinules or tubercles that form **point patches** (literally, patches of points) or a sharkskin-like pattern called **shagreen**. **Pedes spurii** A and B are 'false legs' on the pupal abdomen**. Pedes spurii A** form a whorl of spinules at the posterolateral corners of segments IV to VIII (often only IV), while **pedes spurii B** form a posterolateral hump on abdominal segment II and sometimes also on III.

The number and arrangement of some setae (e.g. Figs 6.10B, C) are of taxonomic significance. Normal thin **lateral setae** on the posterior somites are labelled L1–L3, while setae on the posterior segments (labelled LS1–LS4) are the specialized broad, ribbonlike **taeniate setae** or **swim setae** that enable the pupa to swim at eclosion. **D setae** are dorsal. Spines and spurs, which are rigidly attached, should not be confused with setae and macrosetae, which are in sockets.

KEYS TO THE LARVAE OF CHIRONOMIDS KNOWN FROM SOUTHERN AFRICA

These keys are based on fourth-instar larvae but in most cases can be used for third instar larvae also.

CHIRONOMID SUBFAMILIES: KEY TO LARVAE

1. Antennae retractile; conspicuous toothed ligula (Figs 6.2C, G) present; mentum largely membranous (Fig. 6.2C) or with teeth arranged in conspicuous plates or longitudinal rows (Fig. 6.2F); mentum various...... **Tanypodinae**
– Antennae non-retractile; no conspicuous toothed ligula (Figs 6.1D, H, 6.2D, E) 2

2. Body partly covered with plates of different shape and size (Fig. 6.3A), which carry most of the strongly developed setae; mentum lacking teeth; very small larvae in mountain streams and rivers .... **Aphroteniinae**
– Body without setigerous plates; mentum usually entirely toothed (Figs 6.2D, E), occasionally with weakly chitinized or translucent portions, but never membranous 3

3. Dorsal spiracles present on segment VIII (Fig. 6.3B); premandibles absent; larvae on rocks in intermittent mountain streams .... **Podonominae**
– No spiracle on segment VIII; premandibles (Figs 6.1H, 6.2D–E) present, usually well-developed and conspicuous 4

4. Ventromental plates well developed with conspicuous striations for half their width or more (Figs 6.1D, 6.2E) (*Kribiothauma* (Fig. 6.8D) and *Stenochironomus* (Fig. 6.6J) have reduced striations) .... **Chironominae**
– Ventromental plates vestigial (Fig. 6.2D) to well-developed (Fig. 6.6B): when well-developed, never with striations but occasionally with setae underneath (Fig. 6.6A) 5

5. Mentum with eight teeth per side, the second lateral tooth being very small; seta interna of mandible fan-shaped (Fig. 6.2B); larvae from intermittent mountain streams .... **Diamesinae** (*Harrisonina*)
– Mentum with fewer than eight lateral teeth (e.g. Fig. 6.2D); seta interna not fan-shaped 6

6. M-appendage of prementum conspicuous, divided into many fine, often serrate, branches resembling a single brush (Fig. 6.2H); antennae short with four segments; larvae marine, intertidal .... **Telmatogetoninae**
– Prementum variably developed, never with a brush; antennae usually with more than four segments (Fig. 6.3E), each of which may be very tiny (Fig. 6.2D), those with only four segments being long (Fig. 6.3C); mostly freshwater larvae but *Clunio* and *Semiocladius* are marine .... **Orthocladiinae**

Subfamily **Tanypodinae**

TANYPODINAE: KEY TO SOUTHERN AFRICAN GENERA

1. Body segments relatively broad, each with a midlateral longitudinal fringe of broad swim setae (most easily seen in unmounted specimens); head rounded to oval; anal tubules mostly twice as long as wide 2
– Body segments relatively slender, without a fringe of swim setae; head longer than wide, oval to narrow; anal tubules at least three times as long as wide (Fig. 6.1A) 9

2. Cephalic Index (width:length of head capsule) 0.65–0.70; head gradually tapered anteriorly in dorsal view; sensory organs of labrum clearly visible at anterior margin of head (see Fig. 6.1E); dorsomental teeth not located on a distinct plate (unlike the condition in Fig. 6.2F); anal tubules situated at the tip of the abdomen; live specimens always red 3
– Cephalic index 0.75–1.00; head rounded anteriorly in dorsal view; sensory organs of labrum not distinctly noticeable, lying ventral to anterior margin of head; dorsomental teeth located on a clearly defined plate (Fig. 6.2F); anal tubules situated at base of posterior parapod; live specimens not always red 4

3. Mandible strongly hooked, with large pointed basal tooth (arrowed in Fig. 6.4L); antenna at least four times as long as mandible; first inner tooth of ligula not, or only slightly, bent towards outer tooth .... *Clinotanypus*
– Mandible not strongly hooked, without large pointed basal tooth (Fig. 6.4N); antenna about three times as long as mandible; first inner tooth of ligula strongly bent towards outer tooth .... *Coelotanypus*

4. Cephalic index about 1.0; mandible widely expanded in basal half; apical tooth (arrowed in Fig. 6.4M) short, less than a fifth the total length of the mandible; pecten epipharyngis much reduced, scarcely noticeable .... *Tanypus*
– Cephalic index <0.95; mandible smoothly curved from base to apex; apical tooth at least a fifth the length of the mandible (Figs 6.4P, Q); pecten epipharyngis (e.g. Fig. 6.2G) not reduced, clearly recognizable 5

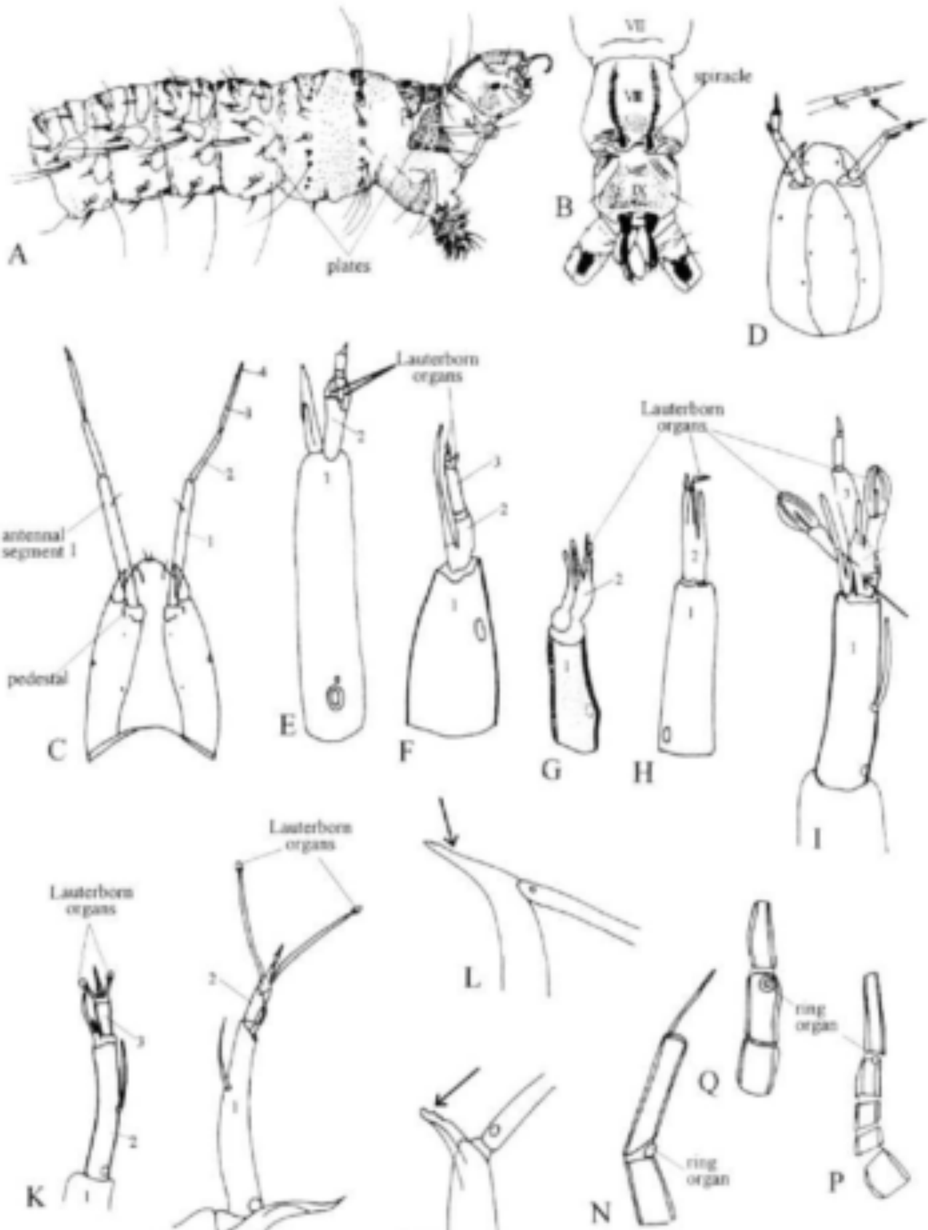


Fig. 6.3. Chironomid larvae. **A**, larva of *Aphrotenia* in right lateral view. **B**, posterior segments of *Archeochlus* (Podonominae) showing dorsal spiracles on 8th somite. **C**, head capsule of *Corynoneura* in dorsal view. **D**, head capsule of *Thienemanniella*, dorsal view. **E–M**, antennae: **E**, *Orthocladius* sp.; **F**, *Harnischia* sp.; **G**, *Cyphomella* sp.; **H**, *Paracladopelma* sp.; **I**, *Cladotanytarsus* sp.; **J**, *Tanytarsus* sp.; **K**, *Rheotanytarsus* sp.; **L**, *Zavrelia* sp.; **M** , *Stempellina* sp. **N–Q**, maxillary palps: **N**, *Paramerina* sp.; **P–Q**, *Ablabesmyia* spp. A, B, redrawn from Brundin (1966); C–F, H–Q redrawn from Wiederholm (1983); G redrawn from Saether (1977).

5. Mandible with relatively large, blunt, basal tooth (arrowed in Fig. 6.4P); apical half of ligula black 6
– Mandible without a basal tooth or with a pointed basal tooth or teeth (Figs 6.4Q, 6.5A); teeth of ligula pale or dark brown 7

6. Main point of paraligula short, at most twice as long as accessory points (in contrast to Fig. 6.5G); accessory points of equal size, twice as numerous on outer as on inner side; pecten epipharyngis with ten short teeth in a sparse row .... *Procladius* (*Psilotanypus*)
– Main point of paraligula (arrowed in Fig. 6.5G) at least three times as long as accessory points, which are exceptionally large; none or a few present on inner side; pecten epipharyngis with a close row of more than ten normal teeth and some short teeth nearby; mandible as in Fig. 6.4P .... *Procladius (Holotanypus)*

7. Ligula with four teeth; mandible with several large, prominent, simple basal teeth (arrowed in Fig. 6.4Q) .... *Psectrotanypus*
– Ligula with five teeth; mandible with a small pointed basal tooth (arrowed in Fig. 6.5A) or basal tooth bifid 8

8. Dorsomentum with four large teeth and one very small tooth; outermost tooth may be absent; ring organ of maxillary palp (e.g. Fig. 6.1F) located in the middle of, or somewhat proximal to the middle of, the basal segment .... *Apsectrotanypus*
– Dorsomentum with six to eight large inner teeth and a very small outer tooth (Fig. 6.2F); ring organ of maxillary palp located about a third of the length from the base; mandible illustrated in Fig. 6.5A .... *Macropelopia*

9. All body segments with setae at least as long as half the width of the segments; maxillary palp illustrated in Fig. 6.4B and ligula and paraligulae in Fig. 6.5J .... *Conchapelopia*
– Most body segments without long setae 10

10. Basal segment of maxillary palp subdivided into two to five segments (Figs 6.3N, P, Q) 11
– Basal segment of maxillary palp single, undivided (Fig. 6.1F) 12

11. Basal segment of maxillary palp divided into two subsegments, intrasegmental membrane with ring organ in proximal third of basal segment (Fig. 6.3N); paraligula slender (Fig. 6.5H) .... *Paramerina*
– Basal segment of maxillary palp subdivided into two to five segments (Figs 6.3P–Q); intersegmental region with ring organ in middle of, or distal to middle of, basal segment; paraligula broadened in basal half .... *Ablabesmyia*

12. Inner teeth of ligula (arrowed in Fig. 6.5I) smaller and shorter than middle tooth; middle tooth larger than, or as large as, the outer teeth....... *Nilotanypus*
– Inner teeth of ligula larger than or approximately equal in length to middle tooth (Figs 6.5J, K)..13

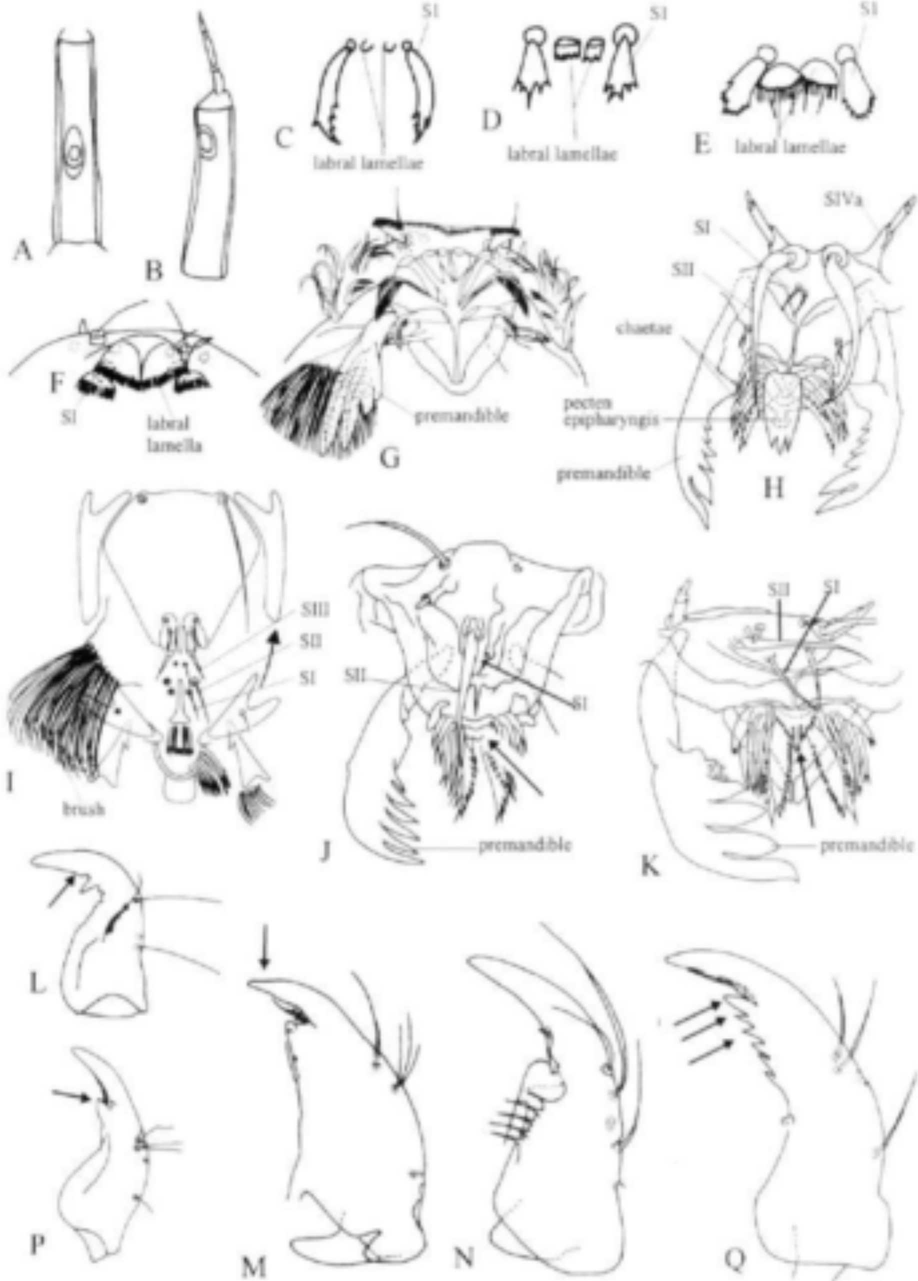


Fig. 6.4. Chironomid larvae. **A–B**, maxillary palps: **A**, *Trissopelopia* sp. (truncated); **B**, *Conchapelopia trifascia*. **C–F**, paired labral lamellae between bases of palmate SI setae: **C–E**, *Chaetocladius* spp.; **F**, *Metriocnemus* sp. **G–K**, labro-hypopharyngeal regions, ventral views: **G**, *Metriocnema* sp.; **H**, *Harnischia* sp.; **I**, *Xenochironomus* sp.; **J**, *Gillotia* sp.; **K**, *Cryptochironomus* sp. **L–Q** left mandibles, ventral views: **L**, *Clinotanypus claripennis*; **M**, *Tanypus* sp.; **N**, *Coelotanypus* sp.; **P**, *Procladius (Holotanypus) brevipetiolatus*; **Q**, *Psectrotanypus* sp. All figures redrawn from Wiederholm (1983).

13. Points of inner teeth of ligula straight; area of muscle attachment a narrow basal stripe (arrowed in Fig. 6.5K) .... *Larsia*
– Points of inner teeth of ligula curved outwards; area of muscle attachment not as above (e.g. Fig. 6.5J) 14

14. Ring organ of maxillary palp situated in middle third of basal segment (Fig. 6.4A); pecten epipharyngis with a strong corner tooth and long teeth in middle of row (Fig. 6.5L) .... *Trissopelopia*
– Ring organ of maxillary palp situated in distal third of basal segment (as in Fig. 6.4B); pecten epipharyngis with neither a strong corner tooth nor with long teeth in the middle of the row ....*Thienemannimyia*

NOTE. The larvae of *Cantopelopia* and *Chrysopelopia* are not known. Larvae of *Apsectrotanypus* have not yet been collected in southern Africa although the adults are known to occur in mountain regions. Genera keying out in couplets 3–6 live mainly in standing water or in pools in rivers and streams. *Macropelopia* and those keying out in couplets 9–14 live mainly in running water.

Subfamily **Orthocladiinae**

Most Orthocladiinae live in running water but some live in lake margins, in damp soil or even in the marine intertidal region. They are characteristic of stony runs in streams and rivers.

ORTHOCLADINAE: KEY TO SOUTHERN AFRICAN GENERA

1. Anal end without procerci (as in Fig. 6.1C) or with procerci, but with neither distinct procercal setae nor posterior parapods 2
– Procerci present, setae variable in number 6

2. Preanal and anal segments, and posterior parapods, bent at right angles to axis of rest of body (Fig. 6.8H); larvae terrestrial .... *Bryophaenocladius*
– Preanal and anal segments in same axis as rest of body 3

3. Anal tubules absent; larvae from the marine intertidal. 4
– Anal tubules (see Fig. 6.1B) present; larvae never marine, mostly terrestrial 5

4. Antennae with five segments .... *Clunio*
– Antennae with three segments .... *Semiocladius*

5. SI and SII setae (see Fig. 6.1H) both bifid; larvae usually in damp soil.......... .... *Pseudosmittia*
– SII setae never bifid; larvae usually found in damp soil, greenhouses, etc. (Fig. 6.1C)..*Smittia*

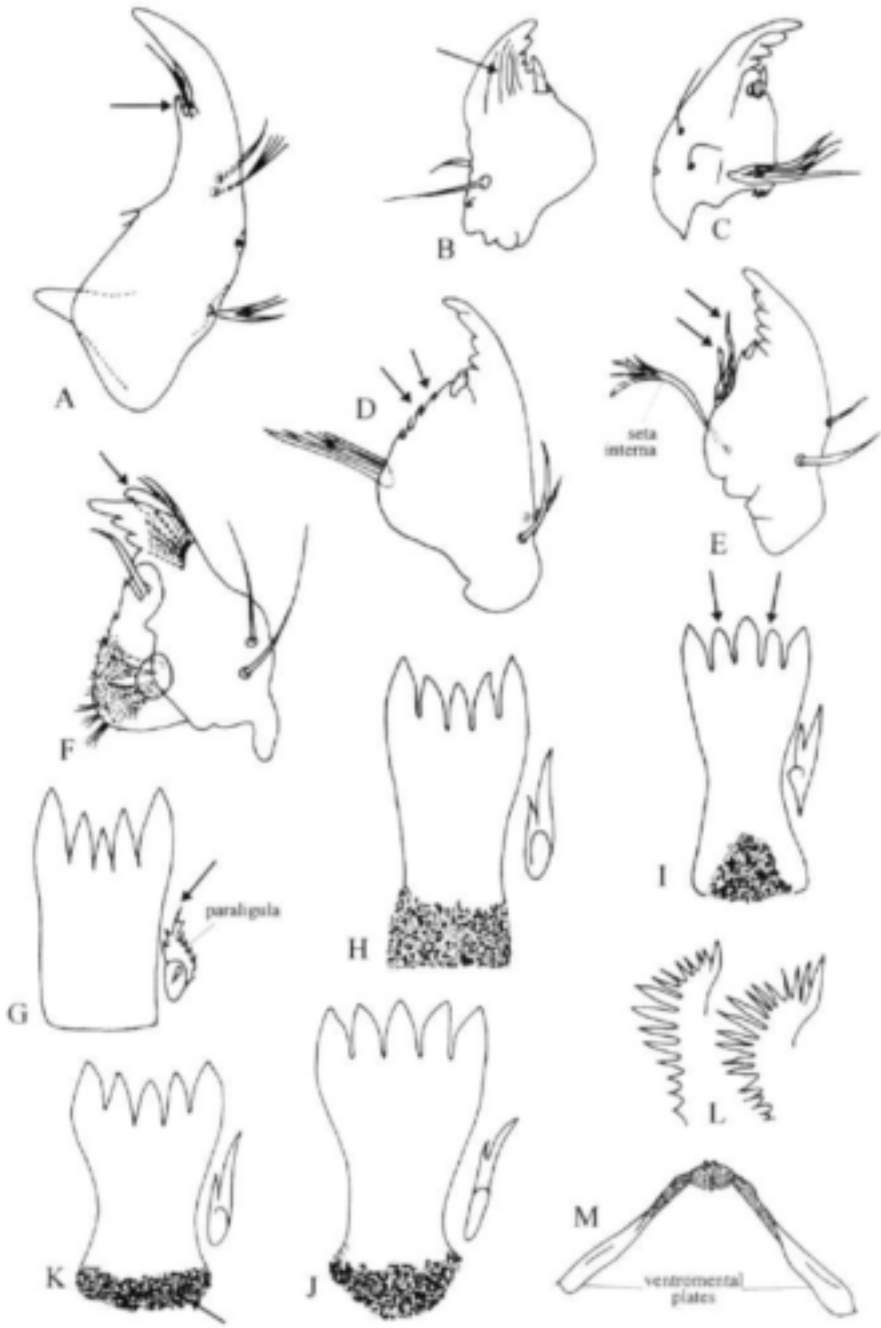


Fig. 6.5. Chironomid larvae. **A–F**, mandibles, ventral views (A, D–F, left mandibles; B–C, right mandibles). **A**, *Macropelopia* sp.; **B**, *Cricotopus dibalteatus*; **C**, *Cricotopus flavozonatus*; **D**, *Eukiefferiella* sp.; **E**, *Cardiocladius* sp.; **F**, *Zavreliella* sp. **G–K**, ligulae and paraligulae (Tanypodinae): **G**, *Procladius (H.) brevipetiolatus*; **H**, *Paramerina* sp.; **I**, *Nilotanypus comatus*; **J**, *Conchapelopia trifascia*; **K**, *Larsia* sp. **L**, pecten epipharyngis of *Trissopelopia* sp. **M**, mentum of *Nanocladius* sp. All figures redrawn from Wiederholm (1983).

6. Antenna, including flagellum, at least half length of head, often more (Figs 6.3C, D) 7
– Antenna shorter than half length of head (e.g. Fig. 6.2D).......... 8

7. Antenna longer than head, four-segmented (Fig. 6.3C) .... *Corynoneura*
– Antenna shorter than head, usually five-segmented, but the three distal segments may be very tiny (Fig. 6.3D).......... *Thienemanniella*

8. One anal seta as long as quarter the length of the body.......... 9
– No anal seta as long as a quarter the length of the body.......... 10

9. Mandible with three inner teeth .... *Pseudorthocladius*
– Mandible with one to two inner teeth .... *Parachaetocladius*

10. All body segments with long coarse setae; mentum with two median teeth; known only from the Western Cape mountains .... 'hairy orthoclad'
– Body setae very short, or long and fine, on some or all segments; mentum various 11

11. Preanal segment IX extending backwards over anal segment with procercal setae directed backwards (Fig. 6.8I) .... *Paraphaenocladius*
– Posterior segments normal, anal setae directed dorsally (as in Fig. 6.1A)... 12

12. Ventromental plates (see Fig. 6.5M) conspicuous, extending lateral to the outer teeth of the flattened mentum; no beard 13
– Ventromental plates usually weak or vestigial (Figs 6.2D, 6.6D, F) or if large, then beard present (arrowed on Fig. 6.6A), or SI bifid, or both.......... 15

13. All S setae (see Fig. 6.1H) simple, fine and difficult to see; ventromental plates narrow and elongate (Fig. 6.5M) .... *Nanocladius*
– SI seta never simple; ventromental plates not narrow and elongate.......... 14

14. Ventromental plates pointed laterally and extending to edge of head capsule (Fig. 6.6B); SI bifid; antenna with five segments; mentum with one median tooth .... *Paradoxocladius*
– Ventromental plates not extended to edge of head capsule; SI apparently simple but apically split; antenna seven-segmented, segment 7 vestigial; mentum with two median teeth; larvae in long tubes in sand and mud of streams. (The only species known so far from southern Africa is *P. natalensis* from the Drakensberg) .... *Paratrissocladius*

15. Beard (arrowed in Fig. 6.6A) present beneath ventromental plates 16
– Beard absent 18

16. SI seta (see Fig. 6.1H) simple; body segments 7–10 may bear plumose setae .... *Synorthocladius*
– SI seta bifid, plumose or palmate.......... 17

17. SI bifid; mentum with two median teeth and beard consisting of many setae (Fig. 6.6A) .... *Rheocricotopus*
– SI palmate with three to ten subequal lobes; mentum with one or two median teeth and beard consisting of a few large setae .... *Psectrocladius*

18. SI simple, or with very weak apical bifurcation or dentation 19
– SI clearly bifid, palmate or comb-like 20

19. Inner margin of mandibles with simple spines (arrowed in Fig. 6.5D) .... *Eukiefferiella*
– Inner margin of mandibles with large serrate or branched spines (arrowed in Fig. 6.5E) (head almost black and difficult to dissect) .... *'Cardiocladius' hessei* (Western Cape)

20. SI bifid; labral lamellae (see Fig. 6.1H) absent 21
– SI palmate, pectinate or simple; labial lamellae present or absent 27

21. Mentum with paired median teeth ....*Mesocricotopus*
– Mentum with a single median tooth 22

22. Some body segments with tufts of setae .... *Cricotopus* (part)
– Body segments with simple setae only 23

23. Median tooth of mentum (Fig. 6.6C) much shorter than the first laterals; mandible short with prominent longitudinal ridge lines (arrowed in Fig. 6.5B) .... *Cricotopus dibalteatus* (and related species)
– Median tooth of mentum longer than, or equal to, first laterals; mandible not as above 24

24. First lateral mental tooth bulbous, broader at middle than at base (arrowed in Fig. 6.6D); larvae rare in normal stream samples .... *Paratrichocladius*
– First lateral mental tooth widest at base (e.g. Figs 6.6E, F) 25

25. Larvae shaped like very small (< 1.5 mm) green commas with black heads; bifid SI often not obvious as branches may adhere together; larvae on surfaces of rocks in fast current; in W. Cape Fold Belt mountains ... *Notocladius*
– Larvae not shaped like green commas, heads usually light; bifid SI obvious; microhabitats various 26

26. Mentum longer than broad, ventromental plates long (arrowed in Fig. 6.6F); antenna as in Fig. 6.3E......... .... *Orthocladius bergensis*
– Mentum about as long as broad (Fig. 6.6E), ventromental plates short; mandible as in Fig. 6.5C .... *Cricotopus* (part)
(One species, *C. kisantuensis*, that keys here, has long setae on all body segments; it can be separated from *Tvetenia*, couplet 28, by its bifid seta SI.)

27. Inner margin of mandible with one to five long, large serrate or branched spines (Fig. 6.5E); seta SI palmate; head brown to almost black, depending on species (black heads heavily chitinized and difficult to dissect).......... .... *'Cardiocladius'* (part)
– Inner margin of mandible with small or no spines; SI variable; head never black 28

28. Setae on all abdominal segments at least half the length of the segments that bear them; SI palmate ....*Tvetenia*
– No abdominal setae as long as this on any segment 29

29. Premandibles without brush but with one to six teeth; labral lamellae absent or weak 30
– Premandibles with brush and two to four teeth (as in Fig. 6.4G); labral lamellae, when present, distinct and paired, separate or fused at base (e.g. Fig. 6.4F) 32

30. Ventromental plates weak; base of mentum with rounded tooth (arrowed in Fig. 6.6G); larvae usually found in small trickles .... *Limnophyes*
– Ventromental plates distinct; no tooth at base of mentum 31

31. Ventromental plates (arrowed in Fig. 6.6H) often extending to outer mental tooth but not beyond; outer mental teeth arranged regularly ....*Parakiefferiella*
– Ventromental plates (arrowed in Fig. 6.6I) extending beyond outer mental tooth; outer mental teeth arranged irregularly or clumped .... *Parametriocnemus*

32. Anal setae short; labral lamellae bell-shaped (Fig. 6.4F); antennae often strongly reduced; labro-hypopharyngeal region illustrated in Fig. 6.4G; larvae tend to be found in water in leaf axils and tree holes or in moss ....*Metriocnemus*
– Anal setae long; labral lamellae absent or paired, with separate bases (Figs 6.4C–E); antennae never strongly reduced; many species found in damp soil.. *Chaetocladius*

NOTE. Many of the genera listed in this key appear to be rare or to have specialized habitats. Samples from mountain streams and the upper parts of rivers usually consist mostly of *Cricotopus* (often *C. dibalteatus*), *Rheocricotopus*, *Parametriocnemus*, *Tvetenia*, *Eukiefferiella* and the very small larvae of *Corynoneura*, *Thienemanniella* and *Notocladius*, the latter in the Cape Fold Belt Mountains. In the lower zones of rivers the stony-run orthoclads are mainly *Cricotopus*, *Rheocricotopus*, *Corynoneura* and *Thienemanniella*. Larvae of *Polypedilum* spp. (subfamily Chironominae, usually light-coloured with yellowish heads) are common in stony runs and marginal vegetation of streams and rivers and should not be confused with orthoclads.

Subfamily **Chironominae**

Larvae normally live in non-transportable cases, exceptionally in transportable cases similar to those of trichopterans. Larvae of the *Harnischia* complex are free-living. Most Chironominae live in slow-flowing or standing water. Exceptions are some species of *Polypedilum* and all species of *Rheotanytarsus*.

Two types of larvae do not fit into any of the categories below. They can be identified as follows.

A. Very small larvae in which the mentum (Fig. 6.8D) has numerous fine teeth and the ventromental plates lack striations, SI is branched, and the mandible has a needle-like apical tooth: *Kribiothauma*.

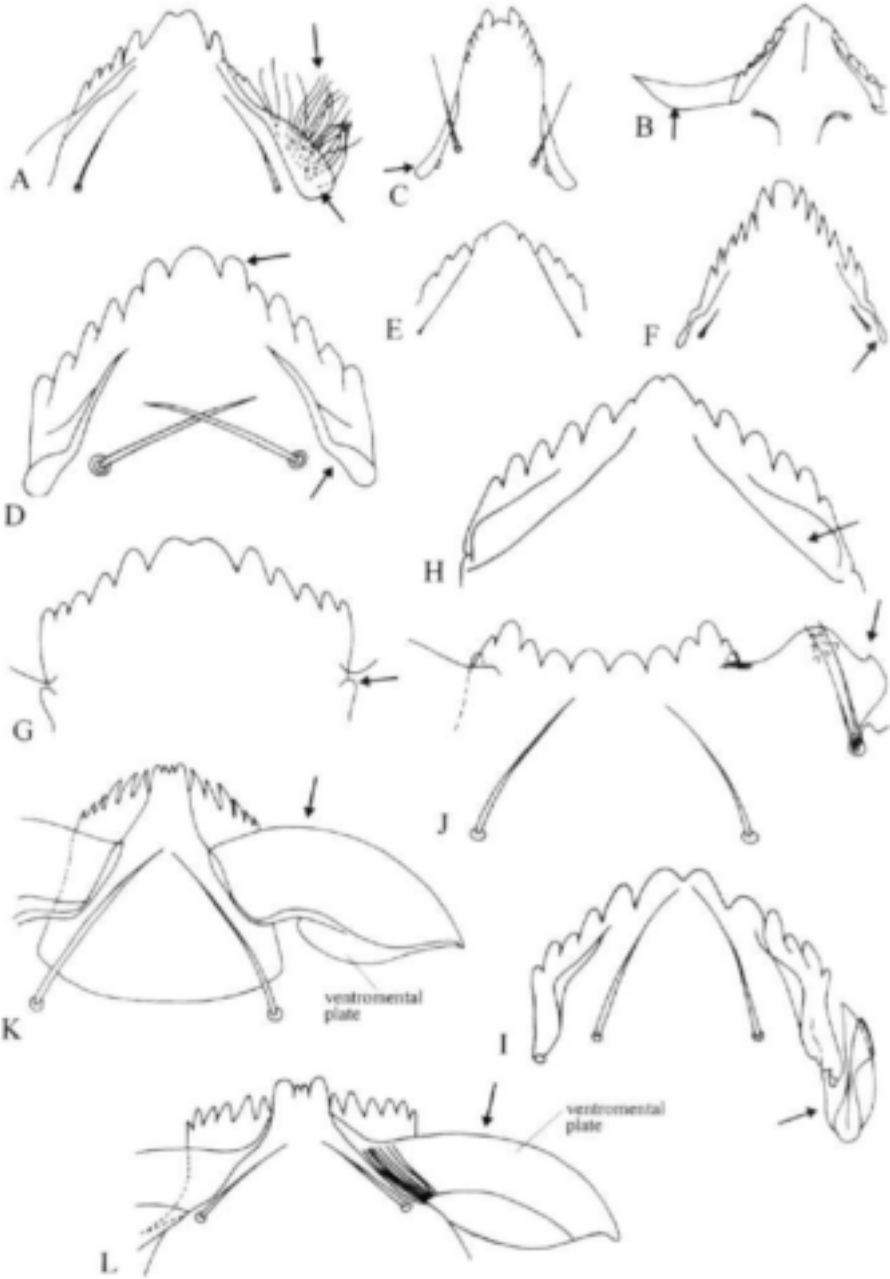


Fig. 6.6. Chironomid larvae. Menta: **A**, *Rheocricotopus* sp.; **B**, *Paradoxocladius* sp.; **C**, *Cricotopus dibalteatus*; **D**, *Paratrichocladius* sp.; **E**, *Cricotopus bizonatus*; **F**, *Orthocladius bergensis*; **G**, *Limnophyes* sp.; **H**, *Parakiefferiella* sp.; **I**, *Parametriocnemus* sp.; **J**, *Stenochironomus* sp.; **K**, *Nilothauma* sp.; **L**, *Stictochironomus* sp. All figures redrawn from Wiederholm (1983).

B. Larvae (Fig. 6.8Q) that feed as parasitoids in cases of hydropsychid caddis pupae. The anterior parapods are strongly reduced with minute claws and all S–setae are simple. In life the larvae are creamy-red: *Collartomyia*.

CHIRONOMINAE LARVAE: KEY TO SOUTHERN AFRICAN GENERA

1. Bases of SI usually not fused, but may lie on a single plate-like base, SII not on a long pedestal; antennae with five to seven segments, Lauterborn organs without stalks at tip of segment 2 (Fig. 6.3F), or alternate on segments 2 and 3; ventromental plates present, usually distinctly separated medially (e.g. Fig. 6.1D) but may be reduced (in *Stenochironomus*): Tribe **Chironomini** 2

– Bases of SI fused (see Fig. 6.2E), setae SII situated on long pedestals; antennae always five-segmented with one seta on basal segment (Fig. 6.3I), Lauterborn organs (e.g. Figs 6.2 E, 6.3I), often on long stalks, usually arising distally on segment 2; ventromental plates always present, usually separated medially by less than the width of the median mental tooth (Tribe **Tanytarsini**) 33

2. SI plumose to some extent (see Fig. 6.1H), SII never blade-like; labral lamellae present and usually well-developed; pecten epipharyngis a wide, distally-toothed plate, or divided into three plates, usually toothed and (rarely) finger-like (in *Paratendipes)*; dorsal tooth of mandible (arrowed in Fig. 6.5F) usually present, but may be small or absent: **Tribe Chironomini**, excluding the *Harnischia* complex 3

– SI and SII simple, frequently blade-like, SI rarely (some *Parachironomus* spp.) divided into three to five slender lobes; labral lamellae usually absent; pecten epipharyngis a single plate or scale, sometimes large and distinctly toothed (*Harnischia* —Fig. 6.4H —and *Parachironomus*) but more commonly small, without distinct teeth (arrowed in Fig. 6.4J) although sometimes lobed or serrated; dorsal tooth of mandible always absent: **Tribe Chironomini**, *Harnischia* complex.. 23

3. Larvae with transportable cases[1] (e.g. Fig. 6.8L) with circular openings; abdominal segment VII with a pair of long, broad ventrolateral appendages produced below abdominal segment VIII, which has a dorsal hump (Fig. 6.8R); mandible illustrated in Fig. 6.5F .... *Zavreliella*

– Larvae with fixed cases or free-living; abdominal segments VII and VIII without appendages or hump...4

4. Two pairs of ventral tubules; lateral tubules (see Fig. 6.1B) present or absent 5

– Never more than one pair of ventral tubules, usually none; lateral tubules always absent 6

5. Two pairs of well-developed anal tubules (Fig. 6.1B); lateral tubules present; premandibles (see Fig. 6.1H) mostly with two teeth .... *Chironomus*[1]

– Anal tubules reduced to flat humps; lateral tubules absent; premandibles with five teeth; larvae in saline to very saline waters....................... *Baeotendipes*

[1] Some species of *Chironomus* (e.g. *C. satchelli*) with green larvae have transportable cases but in other respects the larvae key out to *Chironomus*.

6. Head dorsoventrally flattened, distally tapered, wedge-shaped; anterior edge of mentum strongly concave with characteristic arrangement of teeth, ventromental plates reduced (arrowed in Fig. 6.6J); thoracic segments strongly thickened, not only in prepupal stage; abdomen narrowing anally, posterior parapods reduced; larvae mine leaves recently fallen into water .... *Stenochironomus*
– Head not flattened dorso-ventrally and not tapering to a wedge-shape; menta of different forms; thoracic segments not thickened except in prepupal stage; abdomen and posterior parapods normal 7

7. Labrum with a dense brush of flattened setae (Fig. 6.4I) on each side; miners of fresh-water sponges .... *Xenochironomus*
– Labrum without a brush of setae 8

8. Median tooth of mentum deeply sunken (as in Fig. 6.7B)........................ 9
– Median tooth or teeth of mentum not deeply sunken 10

9. Mandible normal, with inner teeth (as in Fig. 6.2B) .... *Stelechomyia*
– Mandible with one fang-like apical tooth .... *Zuluchironomus*

10. All mental and mandibular teeth pale; arrangement of teeth on mentum characteristic (Fig. 6.6K); larvae small, reaching only 4–5 mm................11
– Mental and mandibular teeth brown or black, in part at least, and not arranged as in Fig. 6.6K; larvae usually >5 mm 12

11. Eyespots on each side touching each other; basal segment of antenna shorter than flagellum; median tooth of mentum in four parts, two broad outer points and two small points centrally, ventromental plate striated only in basal half (Fig. 6.6K).. *Nilothauma*
– Eyespots on each side widely separated; basal segment of antenna about twice as long as flagellum; outer of four median mental teeth very narrow; ventromental plates completely striated .... *Pagastiella*

12. Antenna six-segmented, Lauterborn organs large, alternately placed on segments 2 and 3 13
– Antenna five-segmented, Lauterborn organs sometimes difficult to discern, but always opposite on segment 2 (as in Fig. 6.1G) 18

13. Median tooth of mentum simple, broadly rounded and pale; SII on a long cylindrical stalk; mandible without a dorsal tooth (see Fig. 6.2A) .... *Paralauterborniella*
– Median tooth of mentum with three to four parts, pale or dark; SII without a stalk; mandible with or without a dorsal tooth 14

14. All mandibular and mental teeth brown, the three to four median teeth protruding beyond the remainder (Fig. 6.6L) 15
– Dorsal tooth of mandible pale; the three to four median teeth of mentum pale or dark but always projecting less than the second lateral teeth, and the first lateral teeth always shorter than the second 16

15. Mandible with dorsal tooth (see Fig. 6.2A); central pair of median mental teeth considerably smaller than outer pair, mentum often badly worn and occasionally with only three median teeth .... *Stictochironomus*
– Mandible without a dorsal tooth; the three median mental teeth resemble one trifid tooth .... *Stictochironomus caffrarius*

16. Mentum (Fig. 6.7A) with three, mostly pale, median teeth; mandible with three inner teeth; pecten epipharyngis (see Fig. 6.1H) consisting of a plate divided into three or more branches .... *Microtendipes*
– Mentum with four median teeth; mandible with only two inner teeth; pecten epipharyngis consisting of three separate platelets 17

17. The four median teeth of the mentum always pale and of equal height, or central pair higher; platelets of pecten epipharyngis mostly not serrated distally .... *Paratendipes*
– The four median teeth of the mentum dark, occasionally somewhat paler than the lateral teeth, central pair narrow and depressed, outer pair broad, tall and sloping inwards (Fig. 6.7B); platelets of pecten epipharyngis always serrated distally .... *Omisus*

18. Frontal apotome (see Fig. 6.1H) with a depression or variably-formed mark distally (arrowed in Figs 6.8E–G) 19
– No depression or mark on frontal apotome 22

19. Ventromental plates each distinctly narrower than mentum; frontal apotome illustrated in Fig. 6.8E .... *Dicrotendipes*
– Ventromental plates as wide as, or wider than, mentum 20

20. Ventromental plates touching or almost touching medially; larvae in acid standing waters, Western Cape and Okavango Delta.. *Acinoretracus*
– Ventromental plates clearly separated medially 21

21. Ventromental plates separated medially by a third the width of the mentum; frontal apotome with an elliptical depression anteromedially (Fig. 6.8F); SI setae (see Fig. 6.1H) finely plumose on both sides .... *Kiefferulus*
– Ventromental plates separated medially by an eighth the width of the mentum (Fig. 6.7C); frontal apotome anteromedially with a reticulated mark (arrowed in Fig. 6.8G); SI deeply palmate .... *Nilodorum*

22. Mentum in three parts, the four median teeth set off from rest of mentum and in contact with the anteriorly-produced median ends of the ventromental plates (Fig. 6.7D) .... *Endochironomus*
– Mentum undivided, median ends of ventromental plates pointing posteriorly or towards each other (Fig. 6.7E) (note mental teeth may be even, or uneven as in Fig. 6.7E).. *Polypedilum*

23. Pecten epipharyngis with numerous transparent teeth .... *Parachironomus*
– Pecten epipharyngis not as above: scale-like, may or may not be partially divided into two (or three) lobes or teeth, often much reduced..................24

24. Outer two (or three) pairs of mental teeth usually forming a distinct group, set forward in relation to slope of remaining teeth (Figs 6.7F–G); premandble bifid (Fig. 6.1H).. 25
– Mentum usually not as above; premandible with at least three teeth, usually more 27

25. Median tooth of mentum usually double, or at least notched medially (Fig. 6.7F): if simple, then median part of mentum not very steeply sloping ....*Cladopelma*
– Median tooth simply rounded, laterally notched, or distinctly trifid: when simple, median part of mentum slopes much more than lateral regions (e.g. Fig. 6.7G) 26

26. Median tooth broad, simple, laterally-notched or trifid; second lateral tooth placed well posterior to first lateral tooth so that central part of mentum slopes very steeply (Fig. 6.7G) .... *Cryptotendipes*
– Median tooth of mentum trifid; mentum very gently sloping (Fig. 6.7H)... .... *Microchironomus*

27. Antenna seven-segmented 28
– Antenna five- or six-segmented 29

28. Mentum with a broad, pale median area and seven pairs of oblique brown lateral teeth (Fig. 6.7I) .... *Demicryptochironomus*
– Mentum not as above, all one colour (Fig. 6.7J) .... *Beckidia*

29. Anterior border of mentum concave, with broad pale median area and several pairs of dark, obliquely placed lateral teeth (Fig. 6.7K) 30
– Mentum not as above (e.g. Figs 6.8A–C) 31

30. Pecten epipharyngis (arrowed in Fig. 6.4J) is a small scale with three weakly-defined distal lobes; SI very small, seta-like; mentum illustrated in Fig. 6.7L .... *Gillotia*
– Pecten epipharyngis (arrowed in Fig. 6.4K) is a triangular serrated scale; SI well developed, more than half the length of SII; mentum illustrated in Fig. 6.7K; larvae very common.................................. *Cryptochironomus*

31. Antenna five-segmented, segments 2 and 3 subequal (Fig. 6.3F); pecten epipharyngis with three subequal teeth distally (Fig. 6.4H); mentum illustrated in Fig. 6.8A .... *Harnischia*
– Antenna five (or six)-segmented, segment 2 much longer than segment 3; pecten epipharyngis never with three equal teeth distally 32

32. Mentum with one median tooth (Fig. 6.8B); antennal segment 2 with basal two-thirds weakly chitinized (Fig. 6.3G) .... *Cyphomella*
– Mentum with two median teeth (Fig. 6.8C); antennal segment 2 fully chitinized (Fig. 6.3H) .... *Paracladopelma*

33. Ventromental plates almost in contact medially (as in Fig. 6.2E), separated by less than the width of the median mental tooth; larvae in fixed cases 34
– Ventromental plates separated medially by at least the width of the three median mental teeth; larvae in transportable cases (Figs 6.8L–N) 38

34. Premandible with three to five teeth 35
– Premandible bifid (as in Fig. 6.1H) 37

35. Antennal segment 2 (arrowed in Fig. 6.3I) wedge-shaped, no longer than segment 3; Lauterborn organs large, situated on stalks shorter than the organs themselves; some claws of posterior parapods with fine internal serrations (arrowed in Fig. 6.8J) .... *Cladotanytarsus*
– Antennal segment 2 cylindrical, distinctly longer than segment 3; Lauterborn organs small, situated on long stalks (Figs 6.3J, K); claws of posterior parapods all simple, or some with a pad or row of hooklets but never with fine serrations 36

36. Claws of posterior parapods all in the form of simple hooks; antenna illustrated in Fig. 6.3J .... *Tanytarsus*
– Some claws of posterior parapods with a row or pad of robust hooklets (Fig. 6.8K) .... *Virgatanytarsus*

37. Lauterborn organs situated on stalks at least twice the length of antennal segments 3–5 combined (as in Fig. 6.2E); cases without arm-like extensions (only adults found so far in S. Africa) .... *Micropsectra*
– Lauterborn organs situated on stalks no more than one-and-a-half times the length of segments 3–5 combined (Fig. 6.3K); cases with arm-like extensions (Fig. 6.8P); in fast-flowing water ....*Rheotanytarsus*

38. One Lauterborn organ arising in proximal half of antennal segment 2, the other apically on the same segment; case as illustrated in Fig. 6.8M ....
.... *Stempellinella*
– Both Lauterborn organs arising apically on antennal segment 2 39

39. Antennal pedestal with a conspicuous, rather transparent, palmate process mesially (arrowed in Fig. 6.3M); cases as illustrated in Fig. 6.8L................
....*Stempellina*
– Antennal pedestal with simple apical spur (arrowed in Fig. 6.3L) but lacking palmate process 40

40. Distal spur on antennal pedestal short and blunt .... *Constempellina*
– Distal spur on antennal pedestal long and pointed, somewhat expanded at tip (arrowed in Fig. 6.3L); the only known southern African species does not conform to northern hemisphere species; case illustrated in Fig. 6.8N ......
.... *Zavrelia kribensis*

Note: the larvae of *Skusella* are not known.

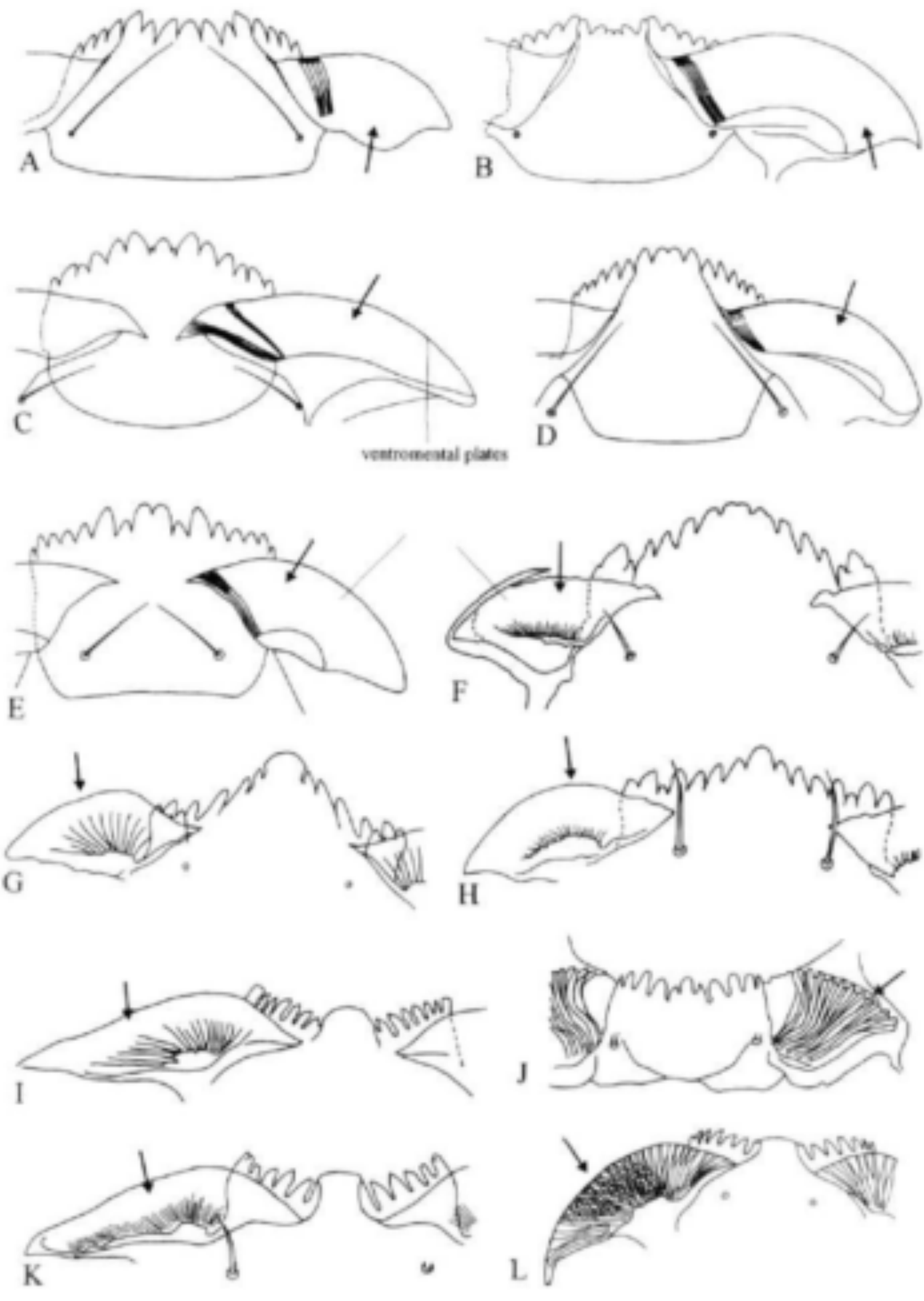


Fig. 6.7. Chironomid larvae. Menta with ventromental plates arrowed: **A**, *Microtendipes* sp.; **B**, *Omisus* sp.; **C**, *Nilodorum* sp.; **D**, *Endochironomus* sp.; **E**, *Polypedilum* spp; **F**, *Cladopelma* sp.; **G**, *Cryptotendipes* sp.; **H**, *Microchironomus* sp.; **I**, *Demicryptochironomus* sp.; **J**, *Beckidia* sp.; **K**, *Cryptochironomus* sp.; **L**, *Gillotia* sp. All figures redrawn from Wiederholm (1983).

KEYS TO THE PUPAE OF CHIRONOMIDS KNOWN FROM SOUTHERN AFRICA

NOTE. The author acknowledges the valuable help of Dr Peter H. Langton in constructing this key.

Users of this key must pay attention to the 'caution' on page 114 and examine all pupae under a dissecting microscope with incident light before mounting them on slides.

CHIRONOMID *PUPAE*: KEY TO SOUTHERN AFRICAN SUBFAMILIES

1. Tergites VIII and IX developed as a circular terminal disc (Fig. 6.12F); marine, intertidal .... **Telmatogetoninae**
– Tergites VIII and IX not combined to form a circular terminal disc (Figs 6.9A–C, 6.10B–D); habitats various 2

2. Thoracic horns with a conspicuous plastron plate (Fig. 6.10Ah, arrowed in Figs 6.11F–J) 3
– Thoracic horns, when present, without a conspicuous plastron plate (Figs 6.10Aa–g, 6.11B–E) 4

3. Anal lobes each with two large macrosetae inserted approximately in the middle third of th e lobe margin and/or with a fringe of small setae or spines along the margins (e.g. Figs 6.9A, 6.14E-K).................. **Tanypodinae** (part)
– Macrosetae of anal lobes often more distal than the middle third of the lobe margin, small, spinelike and greater than two in number; anal lobe never with fringe (Fig. 6.13B).. **Podonominae**

4. Thoracic horns large, at least a third as long as the cephalothorax, with a subsurface meshwork (Figs 6.11B–C) or slender without a meshwork but with small surface spines (Figs 6.11D–N); anal lobes with two lateral macrosetae (Fig. 6.10D) .... **Tanypodinae** (part)
– Thoracic horns not large and with no meshwork, or large but branched or plumose (Figs 6.9B, 6.10Aa-b) or (frequently) absent; anal segment not lobed (Figs 6.13A, B) or anal lobes with zero to many lateral macrosetae (if only two macrosetae on each side, then these are terminal — e.g. Fig. 6.10B)...... 5

5. Thoracic horns, when present, unbranched 6
– Thoracic horns with two or more (often many) branches, or plumose (Figs 6.9B, 6.10 Aa, b).. **Chironominae** (part)

6. Posterolateral angles of segment VIII almost always with a spine or groups of spines (the anal spur or comb: Figs 6.10B, C); anal lobe usually fringed (fringe may be reduced or absent) but never with terminal macrosetae.......... .... **Chironominae** (part)
– Posterolateral angles of segment VIII without a spine or spines, but setae may be present (e.g. Figs 6.15A, C, E); anal lobes with or without fringe, but terminal macrosetae may be present 7

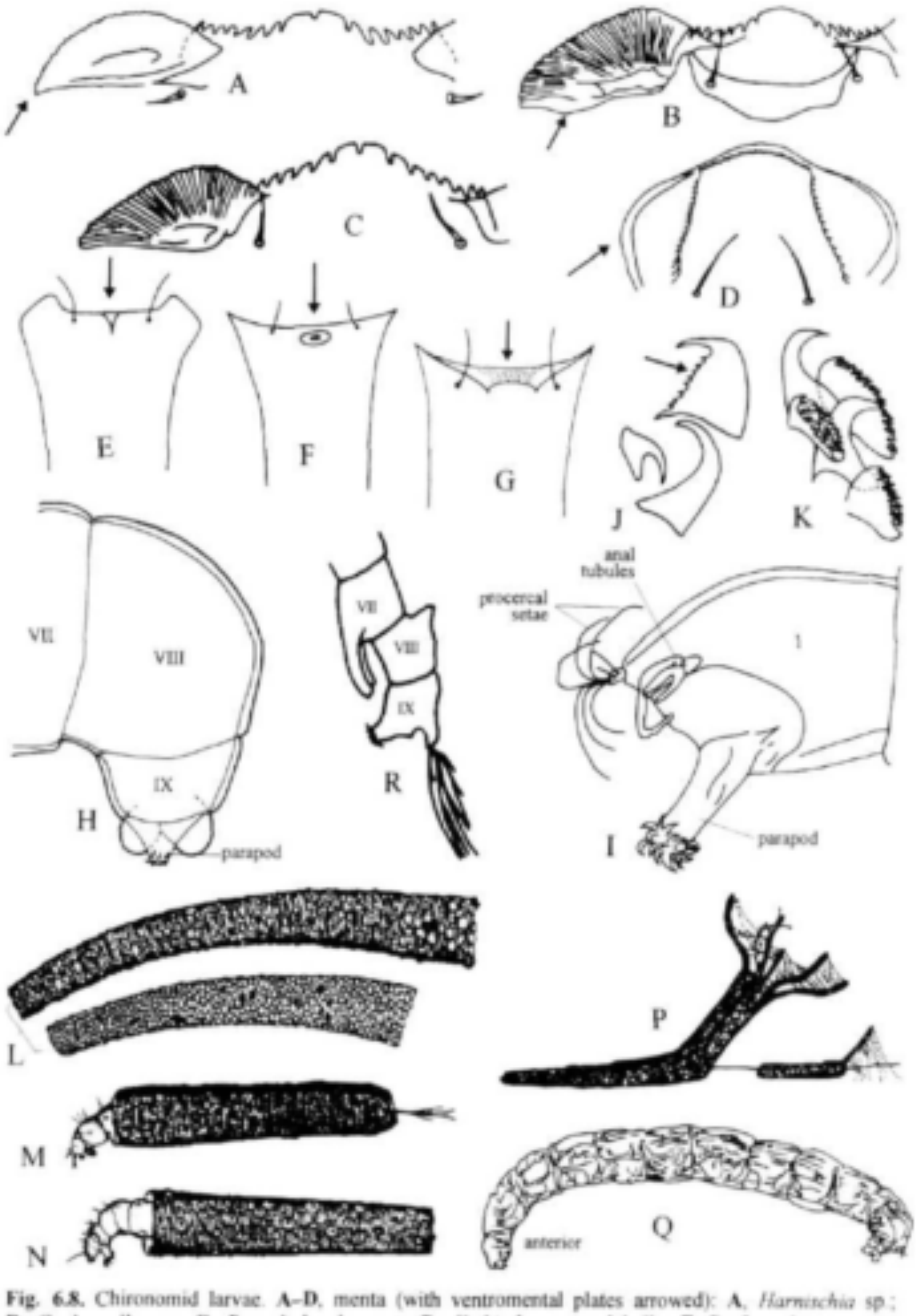


Fig. 6.8. Chironomid larvae. **A–D**, menta (with ventromental plates arrowed): **A**, *Harnischia* sp.; **B**, *Cyphomella* sp.; **C**, *Paracladopelma* sp.; **D**, *Kribiothauma pulchella*. **E–G**, frontal apotomes: **E**, *Dicrotendipes pilosimanus*; **F**, *Kiefferulus chloronotus*; **G**, *Nilodorum brevipalpis*. **H–I**, posterior somites: **H**, *Bryophaenocladius* sp.; **I**, *Paraphaenocladius* sp.; **J–K**, claws of posterior parapods: **J**, *Cladotanytarsus* sp.; **K**, *Virgatanytarsus* sp.; **L–P**, larval cases: **L**, two species of *Stempellina*; **M**, *Stempellinella*; **N**, *Zavrelia*; **P**, *Rheotanytarsus* sp.; **Q**, left lateral view of larval *Collartomyia* sp. **R**, posterior somites of *Zavreliella* sp. A–C, H–K, R redrawn from Wiederholm (1983); L–P redrawn from Thienemann (1974); Q redrawn from Amakye & Saether (1992).

7. Fore- and mid-leg sheaths directed straight backwards, only the tarsal section of the hind-leg sheaths recurved under the wing sheaths 8
– All leg sheaths recurved under the wing sheaths (Fig. 6.9C) .... **Orthocladiinae**

8. Fore- and mid-leg sheaths clearly longer than the wing sheaths; from intermittent rocky mountain streams: **Diamesinae** .... *Harrisonina petricola*
– Fore- and mid-leg sheaths only reaching the tips of the wing sheaths; very characteristic arrangements of macrosetae on segment VIII and anal segment (as in Fig. 6.13A); very small pupae in mountain streams.......................... .... **Aphroteniinae**

Subfamily **Telmatogetoniinae**

TELMATOGETONIINAE PUPAE: KEY TO SOUTHERN AFRICAN GENERA

Note: only adults have been found in Southern Africa so far but a search of rocky intertidal zones on the coast, especially the east coast, should reveal pupae.

1. Ventral surface of terminal disc (Fig. 6.12F) with at least seven long setae on each side of the genital sacs .... *Telmatogeton*
– Ventral surface of terminal disc with only two setae on each side of the genital sacs ....*Thalassomyia*

Subfamily **Tanypodinae**

Note: the pupae of of *Cantopelopia* and *Chrysopelopia* are unknown.

TANYPODINAE PUPAE: KEY TO SOUTHERN AFRICAN GENERA

1. Outer borders of anal lobes with a dense fringe of hair-like spinules (Figs 6.14A, D–G) 2
– Outer borders of anal lobes without a fringe of hairlike spinules, or with a weak fringe (Figs 6.14C, H–K) 6

2. Each anal lobe tapering to a point posteriorly (e.g. Figs 6.14A, E, F) and with a fringe of hair-like setae 3
– Each anal lobe broadly rounded externally, without a sharp posterior point (Figs 6.14C, D, G); setae of fringe taeniate 5

3. Anal lobes with a fringe on both outer and inner borders (Figs 6.14E, F) 4
– Anal lobe with a fringe only on the outer border, inner border minutely armed with short spinules (Fig. 6.14A); thoracic horn illustrated in Fig. 6.14B .... *Macropelopia*

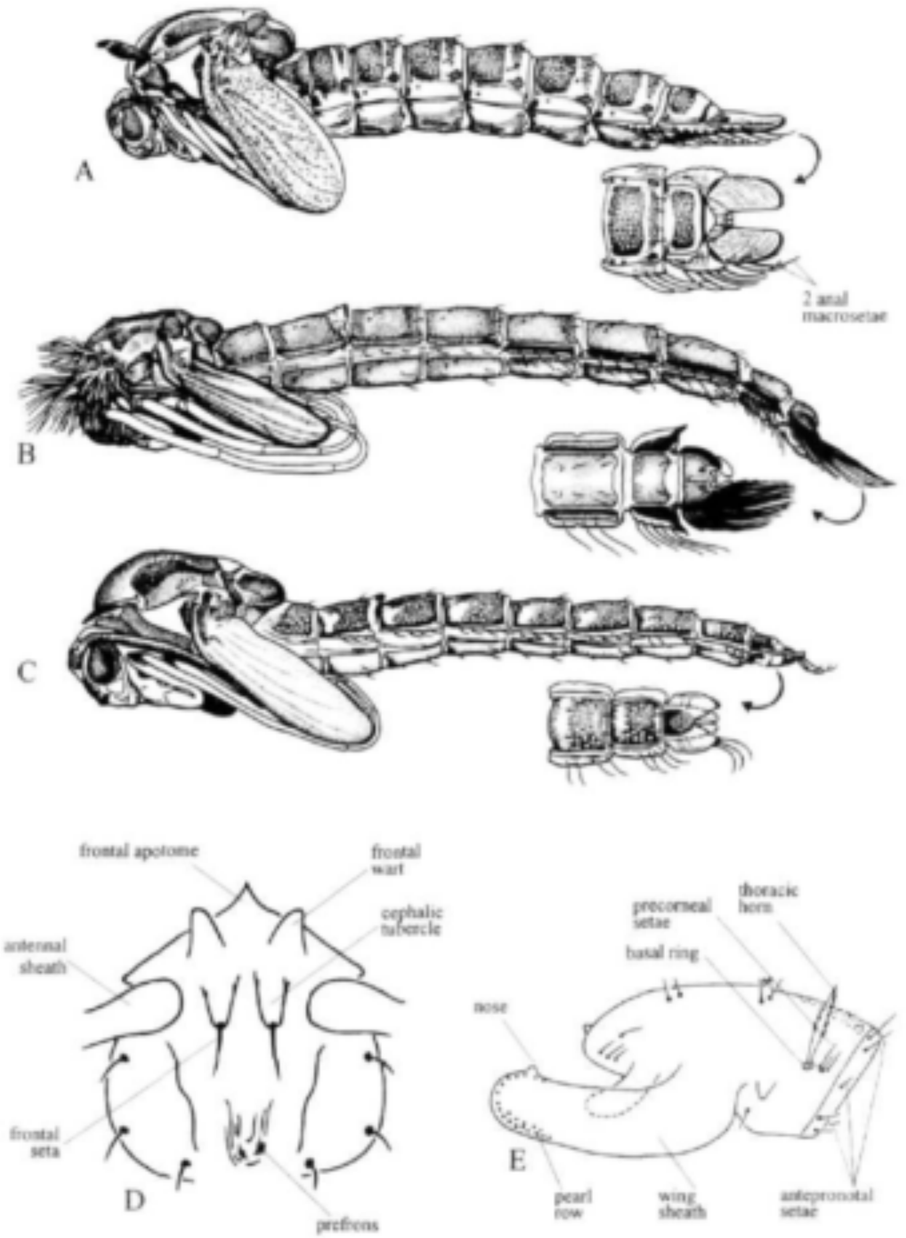


Fig. 6.9. General features of chironomid pupae. **A–C**, entire pupae in left lateral view: **A**, Tanypodinae; **B**, Chironominae; **C**, Orthocladiinae. **D**, generalized head in dorsal view; **E**, right lateral view of thorax, leg sheaths not included. A–C redrawn from McAlpine et al. (1981); D–E redrawn from Wiederholm (1983).

4. Pointed apices of anal lobe approximately median on posterior margin of lobe (Fig. 6.14E); spines on tergite IV long, sometimes as long as somite...... .... *Psectrotanypus*
– Pointed apices of anal lobe positioned towards inner margin (Fig. 6.14F); spines on tergite IV small, much shorter than length of somite..................... .... *Apsectrotanypus*

5. Anal lobes pressed together forming a large single paddle-like swim plate (Fig. 6.14G); anal macrosetae lying dorsal to the fringe ....*Coelotanypus*
– Anal lobes diverging slightly posteriorly, each with a small inner apical projection bearing a group of long, recurved setae; anal macrosetae hidden within the fringe (Fig. 6.14D) ....*Clinotanypus*

6. Anal lobes quadrate with rounded outer and/or inner borders, together forming a large, almost semicircular, paddle (Fig. 6.14C) ....*Procladius*
– Anal lobes triangular (e.g. Figs 6.10D & 6.14J, K) or somewhat reduced (e.g. Fig. 6.14I), not together forming a large swimming paddle 7

7. Anal lobes distinctly less than twice as long as broad (Fig. 6.14I); thoracic horn illustrated in Fig. 6.11B .... *Tanypus*
– Anal lobes longer, usually at least twice as long as broad (Figs 6.14H, J, K) 8

8. Thoracic horns (Fig. 6.11C) large and bulbous, globular or elongate, horn sacs more or less filling the entire lumen; plastron plate very reduced and joined to the horn by a somewhat sinuous neck ....*Ablabesmyia*
– Thoracic horns variable, trumpet-shaped or tube-like or obviously expanded and flattened but horn sac not filling the entire lumen, plastron plate present or absent (Figs 6.11D–N) 9

9. Abdominal segments with a dense shagreen of longish, upright, mostly multi-branched or bifid spinules 10
– Abdominal segments either without shagreen or with a dense covering of normal, simple spines, spinules or tubercles, occasionally serially arranged in transverse rows 12

10. Thoracic horns with large plastron plate (arrowed in Fig. 6.11F)....... ....*Conchapelopia*
– Thoracic horns without plastron plate 11

11. Thoracic horns with aeropyle and corona (see Fig. 6.10Ah); segments II–VI without lateral taeniae, VII with four taeniae on each side and VIII with five taeniae ....*Hayesomyia*
– Thoracic horns without aeropyle or corona (Figs 6.11D–E); segments II–VI with six lateral taeniae on each side ....*Thienemannimyia*

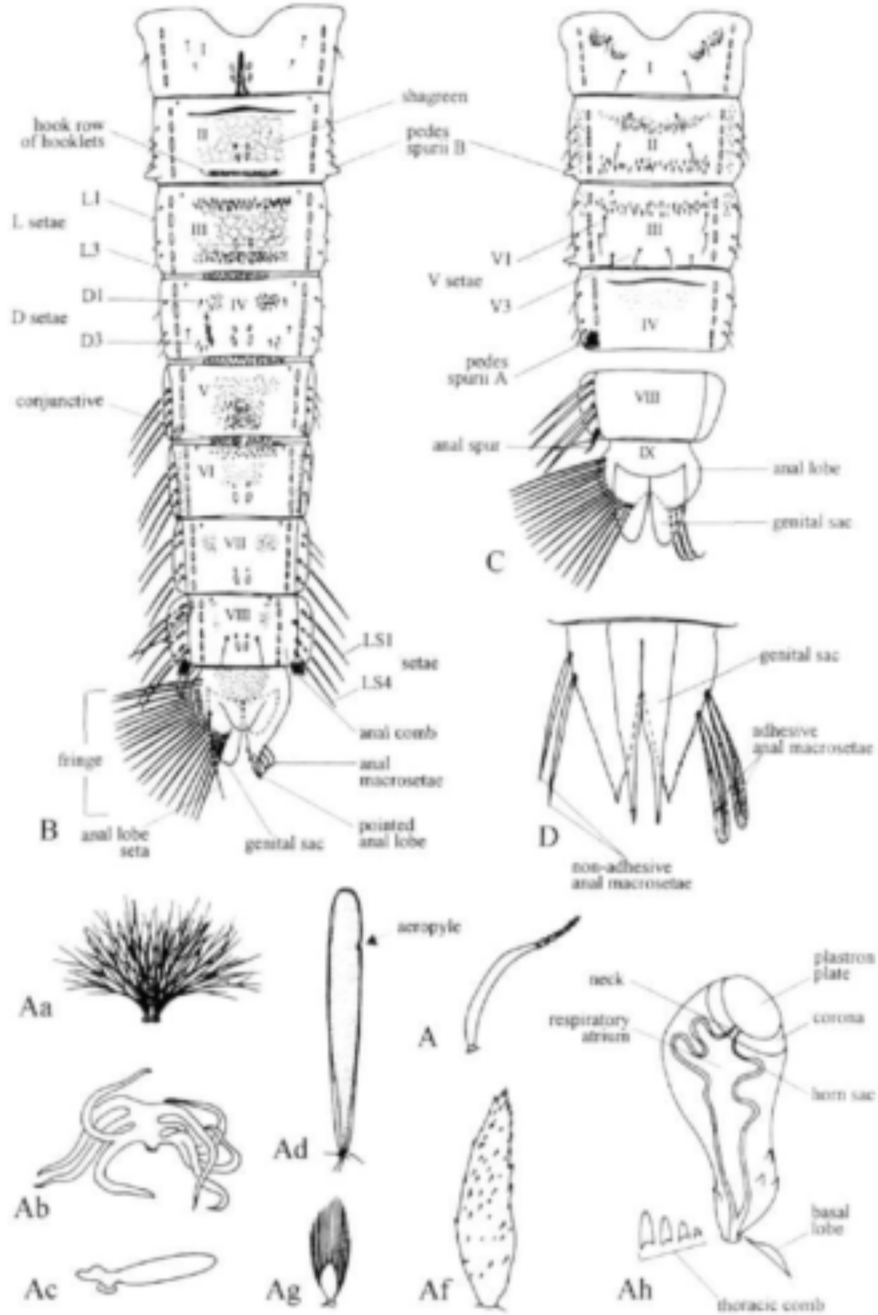


Fig. 6.10. General features of chironomid pupae. **Aa–h**, features of thoracic horns. **B–D**, composites: **B**, abdomen in dorsal view; **C**, abdomen in ventral view; **D**, anal lobes of some tanypods in ventral view. Aa–D redrawn from Wiederholm (1983).

12. Segment VII with at most 1 short lateral taenia; posterior borders of tergites with one or two rows of points or tubercles; thoracic horn with no plastron plate but with a large corona (arrowed in Fig. 6.11G) .... *Nilotanypus*
– Segment VII with more than one lateral taenia; posterior borders of tergites with no strong row of points or tubercles; thoracic horns with plastron plate (e.g. Figs 6.11H–N)..1

13. Anal macrosetae without adhesive sheaths (see Fig. 6.10D, left); thoracic horn straight, more or less symmetrical but flattened (Figs 6.11H, I)............. ....*Monopelopia*
– Anal macrosetae with adhesive sheaths (see Fig. 6.10D, right); thoracic horn (Figs 6.11J–N) mostly arched and asymmetrical 14

14. Horn sacs moderately to strongly lobed (Fig 6.11N); anal lobes illustrated in Fig. 6.14J .... *Larsia*
– Horn sac not lobed (Figs 6.11J–M) 15

15. Tergites with grouped point shagreen serially arranged in arched rows; horn atrium expanded beneath plastron plate and attached directly to it with no neck (Fig. 6.11J); anal lobes as illustrated in Fig. 6.14H ....*Trissopelopia*
– Tergites with solitary, very small spinulated shagreen not serially arranged in arched rows; horn atrium not suddenly expanded at apex, attached to plastron plate by a narrow neck (Figs 6.11K–M); anal lobes illustrated in Fig. 6.14K....... ....*Paramerina*

Subfamily **Orthocladiinae**

ORTHOCLADIINAE PUPAE: KEY TO SOUTHERN AFRICAN GENERA

1. Anal lobes with a full or partial fringe of setae, which may be sparse or dense, short or long (Fig. 6.10B, left) 2
– Anal lobes without a fringe of setae (Fig. 6.10B right) *or* anal lobes greatly reduced or absent 11

2. Anal lobes each with one macroseta ....*Paradoxocladius*
– Anal lobes each with three macrosetae, usually all long and hair-like but sometimes short, spine-like or unequal in length 3

3. Thoracic horns absent; pupae very small (<3 mm)..................................4
– Thoracic horns present; size of pupae variable 5

4. Anal macrosetae taeniate, resembling the setae of the lateral fringe; wing sheaths with pearl rows (see Fig. 6.9E) .... *Corynoneura*
– Anal macrosetae cylindrical; wing sheaths usually without pearl rows ....*Thienemanniella*

5. Most of the lateral setae on segment VIII are taeniate LS setae (see Fig. 6.10B)..... 6
– All lateral setae on segment VIII are hair-like L setae (or, rarely, narrowly taeniate)..10

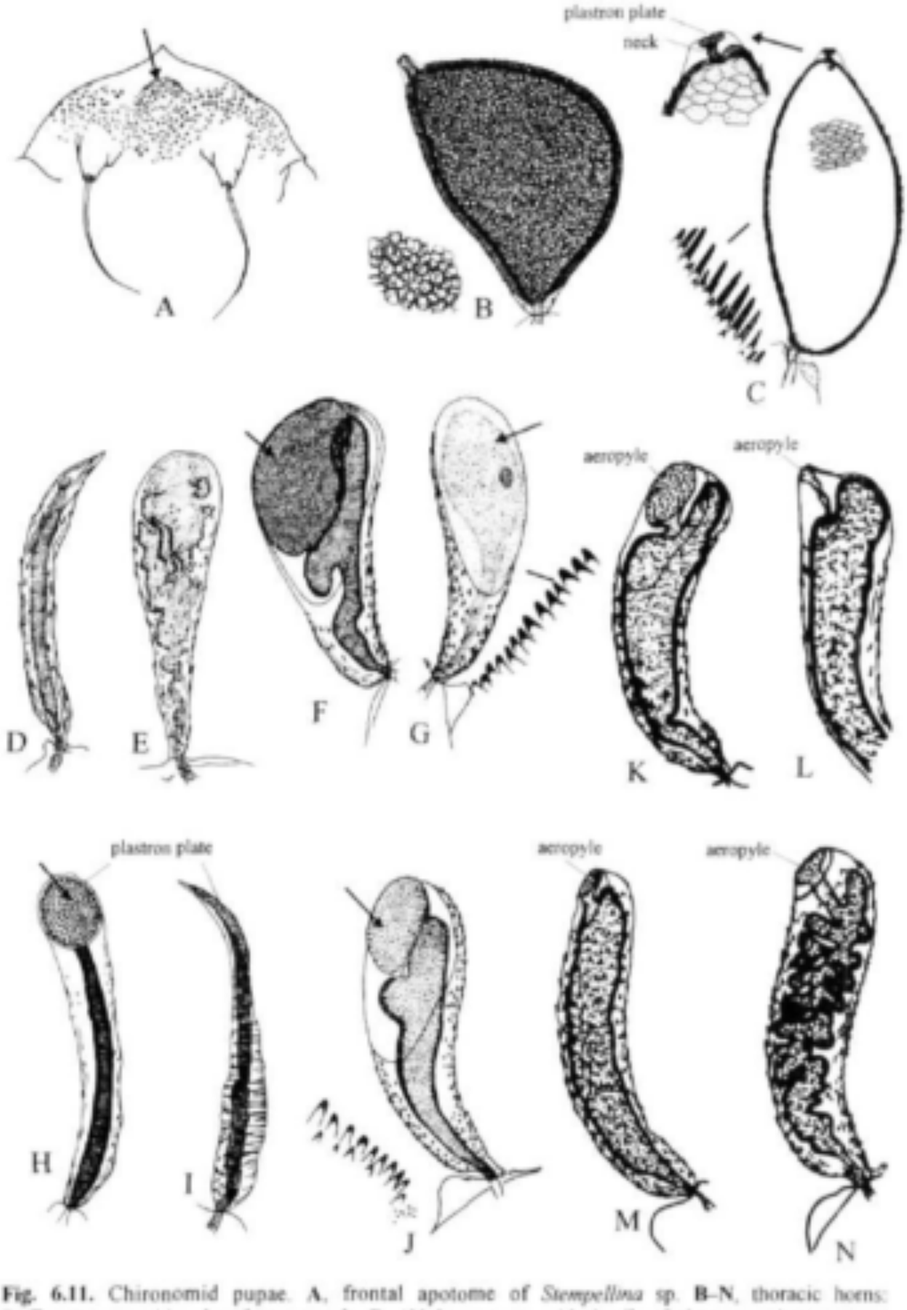


Fig. 6.11. Chironomid pupae. **A**, frontal apotome of *Stempellina* sp. **B–N**, thoracic horns: **B**, *Tanypus* sp. with subsurface network; **C**, *Ablabesmyia* sp. with details of plastron and ornamentation; **D–E**, *Thienemannimyia* spp.; **F**, *Conchapelopia* sp.; **G**, *Nilotanypus* sp. with details of ornamentation; **H–I**, *Monopelopia* spp; **J**, *Trissopelopia* sp. with details of ornamentation; **K–M**, *Paramerina* spp.; **N**, *Larsia* sp.; (All figures redrawn from Wiederholm (1983).

6. Tergite IV with simple shagreen only, but the shagreen points may be somewhat larger in the median field and/or along the posterior margins; discrete point patches or rows never present 7
– Tergite IV with discrete point patches or rows in the median field and/or along the posterior margins; shagreen may also be present 8

7. Pedes spurii B (see Figs 6.10B, C) present on segment III .... *Mesocricotopus*
– Pedes spurii B absent from segment III .... *Paratrissocladius*

8. Antepronotal and/or precorneal setae (see Fig. 6.9E) conspicuously large, longer than the thoracic horns and usually set on tubercles (Fig. 6.12B); pedes spurii B (see Figs 6.10B, C) usually large and strongly projecting (occasionally absent); pupae small (2–4 mm) ....*Nanocladius*
– Antepronotal and/or precorneal setae shorter than thoracic horn (Fig. 6.13D); pedes spurii B weak or absent 9

9. Centres of tergites IV–VI bare, tergites III–VIII with a double row of points on posterior margins (Fig. 6.13C) .... *Rheocricotopus*
– Centres of tergites IV–VI with a discrete patch of points and tergites III–VIII, with a single row of points on posterior margins.................. *Psectrocladius*

10. Wing sheaths with pearl rows (see Fig. 6.9E); pedes spurii B (see Fig. 6.10B) on segment II long and tapering to a point; note polygon pattern in conjunctives .... *Parametriocnemus*
– Wing sheaths without pearl rows; no pedes spurii B on segment II; no polygon pattern on conjunctives; W. Cape ....new genus near *Eurycnemus*

11. Anal lobes folded inwards to form a dorsal longitudinal ridge which may be crested posteriorly with strong points (arrowed in Fig. 6.15I, left); tergites II–VIII with a posterior transverse row or narrow band of strong points, with or without an anterior transverse band of points or shagreen; thoracic horns absent ....*Pseudorthocladius*
– If anal lobes folded inwards, they do not form a crest or ridge and the tergites are extensively armed with small points; thoracic horns present or absent 12

12. Anal lobes always well developed with three terminal or lateral macrosetae (see Fig. 6.10C, right), not including any setae on inner margin, which may be hairlike or spinelike 13
– Anal lobes sometimes absent or greatly reduced but if present with fewer than or more than three lateral macrosetae, not including those on the inner margin, which may be hairlike or spinelike.. 25

13. Thoracic horns present (e.g. Figs 6.15B, D, F) 14
– Thoracic horns absent 21

14. Tergite II without a hook row (see Fig. 6.10B) posteriorly, but III–V, or IV and V, or V alone with a posterior hook row which may be narrowly to widely broken medially 15
– If tergites III–V have a posterior hook row, then so do tergites VI and VII.... 17

15. Wing sheaths with a pearl row; anal lobes each with a submedian seta (arrowed in Fig. 6.15A) .... *Tvetenia*
– Wing sheaths without a pearl row; anal lobes without a submedian setae... 16

16. D4 setae on tergites VII and VIII small and light (arrowed in Fig. 6.15C).. *Eukiefferiella*
– D4 setae on tergites VI–VIII long and dark (arrowed in Fig. 6.15E).. *'Cardiocladius'*

17. Anal lobes forming a pair of pointed terminal projections, each with three anal macrosetae laterally along sides or at base of the anal projections (Fig. 6.15M).. *Parakiefferiella*
– Anal lobes without pointed posterior projections 18

18. Hooklets absent from posterior margin of tergite II, although rows of anteriorly-directed spinules may be present .... *Chaetocladius*
– Hooklets present on posterior margin of tergite II (Fig. 6.10B)................19

19. Tergite I extensively armed with small points; frontal setae (see Fig. 6.9D) absent; thoracic horns variable: small, smooth, oval (Fig. 6.12A) to elongate, somewhat club-shaped and toothed apically.................... *Paratrichocladius*
– Tergite I with at most a posterior band of small points; setae usually present on frontal apotome or praefrons; thoracic horns very elongate............... 20

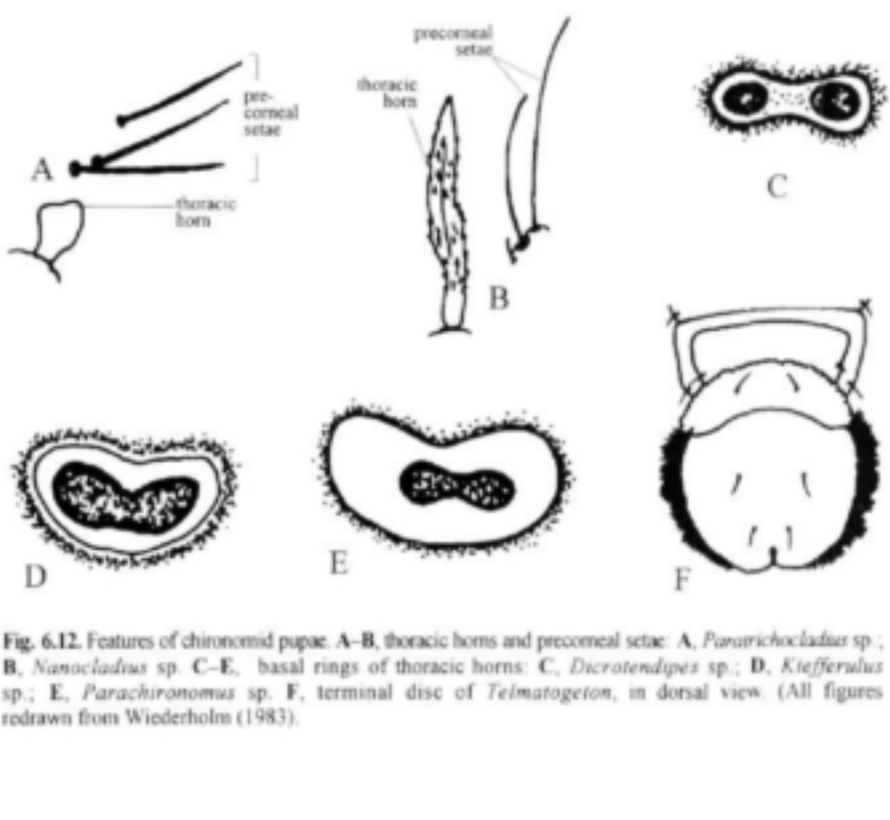


Fig. 6.12. Features of chironomid pupae. **A–B**, thoracic horns and precorneal setae: **A**, *Paratrichocladius* sp.; **B**, *Nanocladius* sp. **C–E**, basal rings of thoracic horns: **C**, *Dicrotendipes* sp.; **D**, *Kiefferulus* sp.; **E**, *Parachironomus* sp. **F**, terminal disc of *Telmatogeton*, in dorsal view. (All figures redrawn from Wiederholm (1983).

20. Hooklets on posterior margin of tergite II usually in two distinct rows extending along half or more of the margin .... *Cricotopus* (part)
– Hooklets on posterior margins of tergite II usually in three or more irregular rows, often limited to the median third of the margin .... *Orthocladius*

21. Macrosetae of the anal lobe spine-like, terminal, and differing in length and thickness: the medial macroseta is much larger than the other two and small additional points are present at the tip of the lobe (Fig. 6.15G) .... *Synorthocladius*
– Macrosetae of anal lobes spine- or hair-like: if spine-like, all three are about the same size (e.g. Fig. 6.15H); anal lobes with or without accessory points 22

22. Tergites I–VIII or II–VIII with posterior rows of very long, needle-like spines (arrowed in Fig. 6.15H) .... *Limnophyes*
– Tergites I–VIII or II–VIII without posterior rows of needle-like spines 23

23. Tergites III–VI with three separate transverse fields of shagreen, the anterior two fields with posteriorly-directed points and the posterior field with anteriorly-directed points; pupae marine, intertidal .... *Semiocladius*
– Tergites III–IV with uniform shagreen 24

24. Anal lobes with small spines on lateral borders and two submedian setae (Fig. 6.15J); pupae very small (<3 mm), often in silken cases on top of rocks in current; known so far only from the Western Cape .... *Notocladius*
– Anal lobes without small lateral spines or submedian setae........................ .... *Metriocnemus* (part)

25. Anal lobes each with at least one macroseta 26
– Anal lobes without macrosetae, but two spines may be present; anal lobes sometimes absent or greatly reduced 27

26. Thoracic horns absent .... *Metriocnemus* (part)
– Thoracic horns present ....*Paraphaenocladius*

27. Thoracic horns present but may be very small 28
– Thoracic horns absent 29

28. Tergite II with hooklets on the posterior margin; thoracic horns small, somewhat rounded .... *Cricotopus dibalteatus*
– Tergite II without hooklets on the posterior margin; thoracic horns long, digitiform .... *Paraphaenocladius* (part)

29. Each of conjunctives III/IV to VII/VIII with rows of hooklets; pupae marine...... .... *Clunio*
– Hooklets not present on conjunctive VII/VIII but may be present on others; some conjunctives may have bands of fine spinules; pupae mostly terrestrial 30

30. Distinct bands of tiny spinules present on some conjunctives...................... .... *Pseudosmittia* (part)
– No distinct bands of tiny spinules on any conjunctives, or bands may be present as a continuation of the tergal shagreen 31

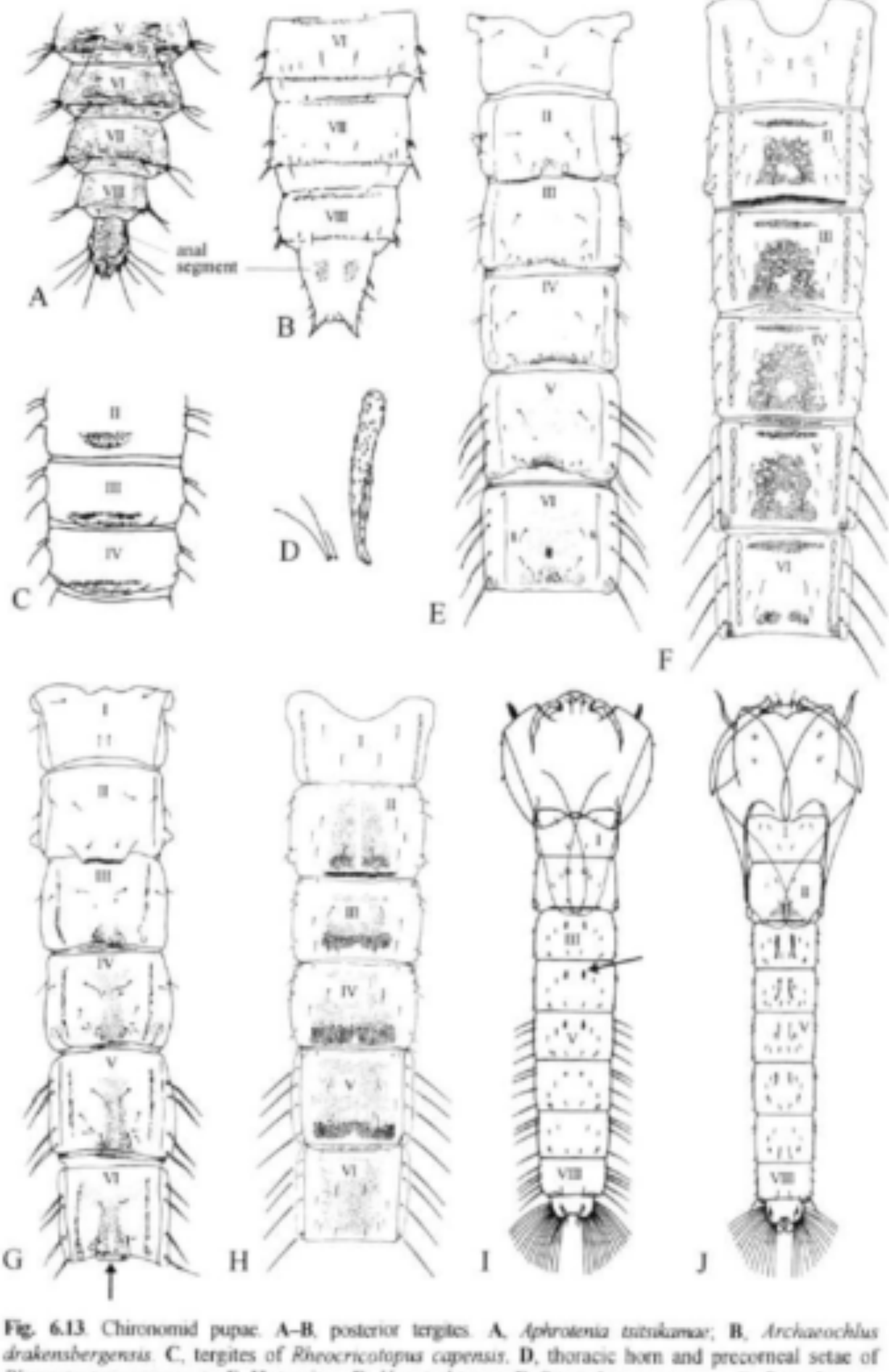


Fig. 6.13. Chironomid pupae. **A–B**, posterior tergites. **A**, *Aphroteniia tsitsikamae*; **B**, *Archaeochlus drakensbergensis*. **C**, tergites of *Rheocricotopus capensis*. **D**, thoracic horn and precorneal setae of *Rheocricotopus capensis*. **E–H**, tergites: **E**, *Harnischia* sp.; **F**, *Stictochironomus* sp.; **G**, *Parachironomus* sp.; **H**, *Chironomus* sp. **I–J**, exuviae in dorsal view: **I**, *Cladotanytarsus* sp.; **J**, *Tanytarsus* sp. A, B redrawn from Brundin (1966); D–H redrawn from Wiederholm (1983); I–J redrawn from Langton (1984).

31. No antepronotal setae or a single antepronotal seta (see Fig. 6.9E)...... *Smittia*
– Two to three antepronotal setae 32

32. Anal lobes of unusual shape: oblong or wider in middle and truncated terminally (Figs 6.15K, L)....................................*Bryophaenocladius* (part)
– Anal lobes usually weakly developed or absent or, if present, then not of an unusual shape 33

33. All cephalothoracic setae weak; anterior thorax may be weakly spinulose; tergite I without shagreen or with weak anterior fields ....*Pseudosmittia* (part)
– At least some thoracic setae moderately strong; anterior thorax often rugulose; tergite I with at least some posterior shagreen ....
.... *Bryophaenocladius* (part)

Subfamily **Chironominae**

NOTE. Many African species of *Polypedilum* have yet to be associated with their pupae, so a few may not key out to this genus. Nevertheless, most will key out to couplet 15.

CHIRONOMINAE PUPAE: KEY TO SOUTHERN AFRICAN GENERA

1. Thoracic horns (see Fig. 6.9B), with at least two branches, usually plumose with up to several hundred branches, base not dome-shaped individual branches sometimes with spines but never with long chaetae; abdominal tergites with variable arrangement of points or shagreen, seldom with distinct paired point-patches (except in *Zavreliella*, *Omisus* and *Acinoretracus*); wing sheaths (see Fig. 6.9E) almost invariably without a nose, never with pearl rows: Tribe **Chironomini** 2
– Thoracic horns simple: bare or with short spines or long chaetae and dome-like base; abdominal tergites (II)III–(V)VI usually with paired (Figs 6.13I, J) or unpaired point or spine patches; wing sheaths usually with nose and/or pearl rows: Tribe **Tanytarsini** 32

2. Thoracic horns exceedingly long, about as long as the whole pupa, narrow, the long branches sparsely divided beyond half way 3
– Thoracic horns without conspicuously long branches sparsely divided beyond half way 4

3. Each thoracic horn with only two branches near base, both long and dividing to three sub-branches beyond half way; no fine branches around base..............
.... *Paracladopelma graminicolor*
– One branch of each thoracic horn exceedingly long, branching to more than 3 sub-branches beyond half way and with fine branches around base........
.... *Cryptotendipes*

4. Abdominal tergites II–V or II–VI or III–VI with paired point-patches 5
– Abdominal tergites without paired point-patches 7

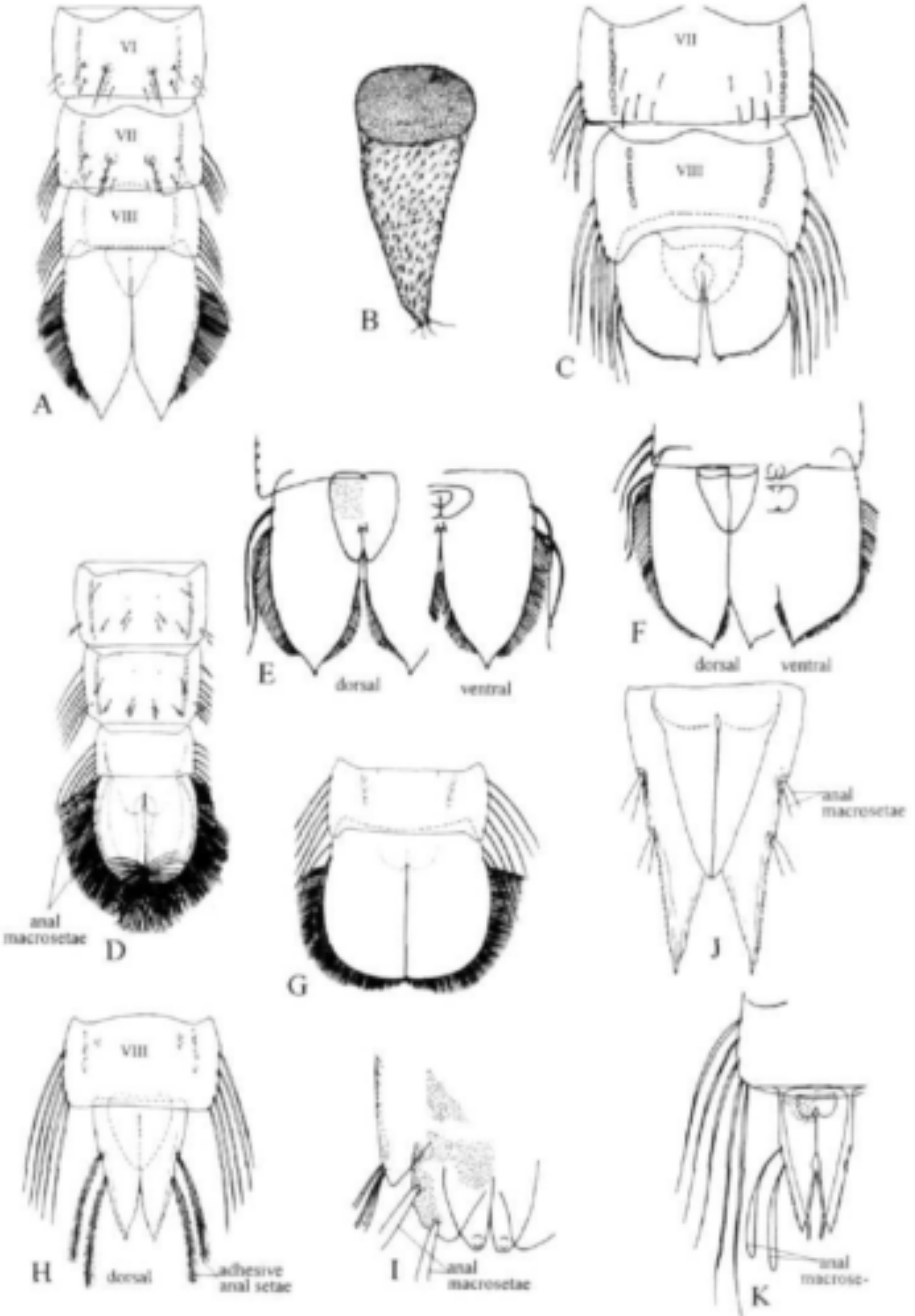


Fig. 6.14. Chironomid pupae. **A**, posterior tergites and anal lobes of *Macropelopia* sp. in dorsal view. **B**, thoracic horn of *Macropelopia*. **C–K**, anal lobes in dorsal view (but in figures with two views the one on the left shows the dorsal aspect and the one on the right the ventral aspect): **C**, *Procladius* sp.; **D**, *Clinotanypus* sp.; **E**, *Psectrotanypus* sp.; **F**, *Apsectrotanypus* sp.; **G**, *Coelotanypus* sp.; **H**, *Trissopelopia* sp.; **I**, *Tanypus* sp.; **J**, *Larsia* sp.; **K**, *Paramerina* sp. A–J redrawn from Wiederholm (1983); K redrawn from Langton (1984).

5. Dark, paired point-patches on tergites II–V; conjunctive IV/V with a pair of dark, anteriorly-directed hooks ....*Omisus*
– Pale, paired point-patches on tergites II–VI or III–VI; conjunctives IV/V bare 6

6. Point patches on tergites II–VI .... *Zavrelliella*
– Point patches on tergites III–VI; from acid waters in the W. Cape....... .... *Acinoretracus penicillatus*

7. Abdominal tergite VI with a posteromedial mound of spines ...... *Cladopelma*
– Tergite VI without a posteromedial mound of spines 8

8. Pedes spurii B (see Figs 6.10B, C) of segment II spinose .... *Beckidia*
– Pedes spurii B of segment II not spinose, or may be absent or weakly developed 9

9. Anal segment with forked dorsal posteromedian process (arrowed in Fig. 6.16A); exuviae mostly large, uniformly yellowish-brown to dark brown; abdomen often with surface network .... *Cryptochironomus*
– Anal segment without strong, forked process 10

10. Tergites II–V(VI) each with pair of patches of dark spines (pairs on II and III may be joined medially); dark spines arise from brown pits forming a network surrounded by dense shagreen; living in sponges ...... *Xenochironomus*
– Tergites II–V(VI) without dark spine patches or network 11

11. Thoracic horn forms a brush of about 30 to several hundred fine branches (as in Fig. 6.10Aa) 18
– Thoracic horn with at most 20 coarse branches (as in Fig. 6.10Ab).............12

12. Frontal setae absent; frontal warts (see Fig. 6.9D) dorsally curved .... *Microtendipes*
– Frontal setae (see Fig. 6.9D) present; frontal warts, if present, not dorsally curved 13

13. Wing sheaths (see Fig. 6.9E) with a blunt nose; abdominal segments II–IV each with four lateral L setae .... *Paralauterborniella*
– Wing sheaths without a blunt nose; abdominal segments II–IV each with three lateral L setae... 14

14. Tergite VIII with central field of coarse shagreen and a pair of very small anterolateral patches; segment IV with one taeniate LS seta (See Fig. 6.10B, right) ....*Nilothauma*
– Tergite VIII with only two anterolateral patches of fine shagreen, often difficult to see; segment IV without taeniate LS setae...........................15

15. Abdominal tergites II(III)–VI with an anterior transverse band of shagreen, stronger than and mostly separated from remaining shagreen; anal lobes without setae 16
– Tergites without an anterior transverse band of shagreen; one or more setae always present on anal lobes (as Fig. 6.10C, right).............................. 17

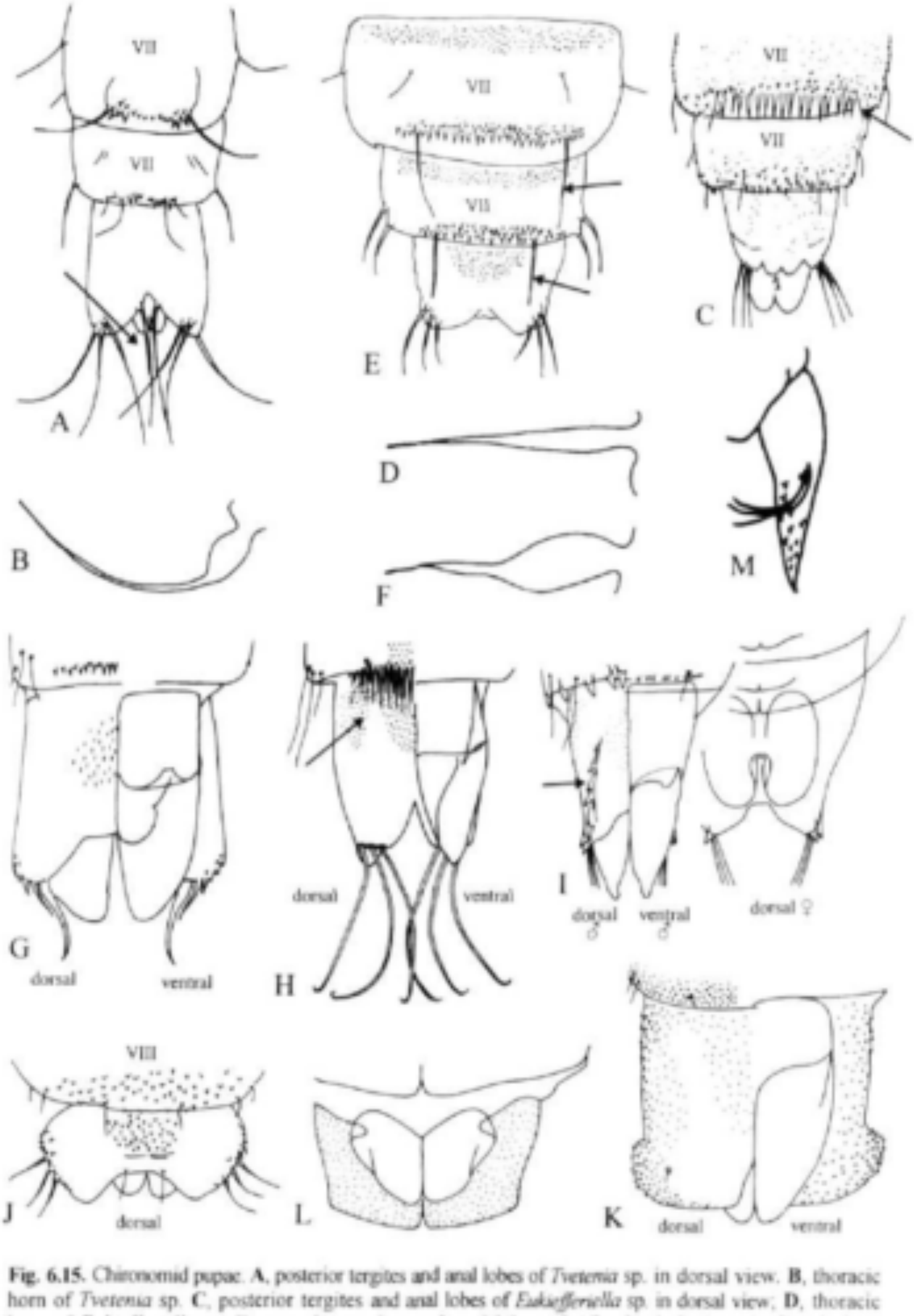


Fig. 6.15. Chironomid pupae. **A**, posterior tergites and anal lobes of *Tvetenia* sp. in dorsal view. **B**, thoracic horn of *Tvetenia* sp. **C**, posterior tergites and anal lobes of *Eukiefferiella* sp. in dorsal view; **D**, thoracic horn of *Eukiefferiella* sp; **E**, posterior tergites and anal lobes of *'Cardiocladius'* sp. in dorsal view; **F**, thoracic horn of *'Cardiocladius'* sp. **G–L**, anal lobes (in figures with two views, the one on the left shows the dorsal aspect and the one on the right the ventral aspect): **G**, *Synorthocladius* sp.; **H**, *Limnophyes* sp.; **I**, *Pseudorthocladius* sp. (male on left and female on right); **J**, *Notocladius capicola*; **K**, *Bryophaenocladius* sp. male; **L**, *Bryophaenocladius* sp. female; **M**, external lateral view of left lobe of *Parakiefferiella* sp. A–F, I–J redrawn from Wiederholm (1983); G–H, L redrawn from Langton (1984).

16. Tergites III–VI with an anterior transverse band of point shagreen and a posterior transverse mound of shagreen; conjunctives bare .... *Pagastiella*
– Tergites II–VI with an anterior band of strong points, often separate from the median patch of smaller points; posterior patches not set on a mound; conjunctives IV/V and sometimes III/IV usually with a transverse band of points .... *Polypedilum* (part)
17. Thoracic horn with 6 or 8–12 branches; cephalic tubercles or warts (see Fig. 6.9D) usually present; large pedes spurii B (see Fig. 6.10B, C) on segment II .... *Paratendipes*
– Thoracic horn with four branches; cephalic tubercles and frontal warts absent; pedes spurii B absent .... *Stelechomyia*

18. Pedes spurii A (see Fig. 6.10C) of segment IV absent .... *Stenochironomus*
– Pedes spurii A of segment IV well developed 19

19. Frontal setae absent; thorax with a cone-like dorsal projection bearing a strongly sclerotized depression at its apex; pupae in pupal cases of hydropsychid caddis on which the larvae feed .... *Collartomyia*
– Frontal setae present; thorax without cone-like projection of this type; not in caddis cases 20

20. Genital sacs of male with five to ten short, strong spines ventrally (Fig. 6.16B) (female exuviae with an extremely long, conical postero-median process between anal lobes — arrowed in Fig. 6.16C — are tentatively associated with this genus) .... *Gillotia*
– Genital sacs of male bare; postero-median process of female short or scarcely reaching beyond anal lobes 21

21. Anal combs (see Fig. 6.10B) consisting of a row of separate, slender teeth mostly rounded at apex and parallel-sided (Fig. 6.16D)........... *Cyphomella*
– Anal combs, if present, not as above 22

22. Inner borders of anal lobes with 20–25 short, spinose setae (Fig. 6.16E) continuous with, and at most only a quarter the length of the taeniate setae fringing entire outer border of lobe (in some species these short setae may be apical and spread back along the inner surface of the anal lobes to about half-way along the length of the anal lobe); only tergite II with anterior transverse band of stronger points .... *Nilodorum*
– Anal lobes with a uniform fringe of setae; either all tergites lack anterior transverse bands of shagreen or tergites II–V(VI) all have such bands 23

23. Tergites II(III)–VI with a narrow posterior transverse band of broad, short, pale points; hook row widely divided medially (Fig. 6.13E); no anal combs or spurs .... *Harnischia*
– Tergites II(III)–VI with hook row usually entire, rarely narrowly-divided medially and armament differing from above; anal combs or spurs present or absent 24

24. Points of the anterior transverse bands on tergites III to VI stronger than those of the median patches (Fig. 6.13F) .... *Stictochironomus*
– Points of the anterior transverse band, where present, no stronger than those of the median patch (e.g. Fig. 6.13H)...25

25. Segment II without pedes spurii B (see Figs 6.10B–C)............................ 26
– Segment II with pedes spurii B.. 28

26. Hook row of tergite II clearly divided centrally .... *Kloosia*
– Hook row of tergite II undivided (as in Fig. 6.13F).....................................27

27. Hook row occupying more than half the width of segment II; segment VIII with five taeniate setae on either border; sternite VIII of female produced into a pair of triangular processes posteriorly (arrowed in Fig. 6.16F, right), male more rounded .... *Demicryptochironomus*
– Hook row occupying less than half the width of segment II; segment VIII may have four or five taeniate setae; sternite VIII of female not produced......... .... *Paracladopelma*

28. Characteristic anal spur (Fig. 6.10C) arising ventrally on segment VIII (Fig. 6.16G) as a longitudinal ventral mound that becomes creased when collapsed, the projecting part armed apically with a brush of narrow teeth with hair-like apices or a few sturdy spinous points; conjunctives III/IV and/or IV/V with a pair of short, slender lateral (L) setae visible only on careful examination (Fig. 6.13H).......................... *Chironomus* and *Baeotendipes*
(*Chironomus* in fresh waters; *Baeotendipes* in saline to very saline waters)
– Anal spur, if present, not a brush (e.g. Fig. 6.16I); conjunctives III/IV and IV/V without lateral (L) setae 29

29. Hook row on tergite II broken in centre .... *Microchironomus*
– Hook row on tergite II continuous 30

30. Segment I without lateral (L) setae; basal ring (see Fig. 6.10Ac) of each thoracic horn large, strongly constricted medially and with two completely or almost completely separate tracheal branches (see Fig. 6.12C); anal spur usually present; simple, slender or cleft, S–shaped, curved outwards and apically produced into a fine hair-like point, or short and broad but occasionally an anal comb of slender spines instead ....*Dicrotendipes*
– Segment I with 1 lateral (L) seta; basal ring large or small with one or two tracheal branches; anal combs variable 31

31. Anal comb of brown, mostly large, teeth with paler 'windows' basally (see Fig. 6.16H); basal ring large, kidney-shaped with two fused tracheal branches (see Fig. 6.12D); tergite VI without a postero-median swelling armed with strong points; sternite VIII with one pair of short, soft ventral tubules.................... *Kiefferulus*
– Anal comb of at most eight colourless spines, or absent; basal ring small, elliptical or elongate with one or two fused tracheal branches (see Fig. 6.12E); tergite VI usually with a postero-median swelling bearing strong points (arrowed in Fig. 6.13G) (species without anal combs always possess this swelling); sternite VIII without ventral tubules .... *Parachironomus*

32. Segment VIII with anal spur, sometimes cleft or with one or two additional small spurs basally (Fig. 6.16I); pedes spurii A (see Fig. 6.10C) present on sternite IV 33
– Segment VIII with distinct anal comb (arrowed in Fig. 6.16M); pedes spurii A absent 37
33. Tergites II–IV (or V or VI) with distinct paired, anterior point patches (Fig. 6.16J); anal spurs illustrated in Fig. 6.16I .... *Rheotanytarsus*
– Tergites without paired, anterior point patches 34

34. Tergites III–VI each with a pair of narrow longitudinal bands of points, the bands becoming broader and the points larger posteriorly (Fig. 6.16K); frontal apotome and anterior half of thorax strongly granulose (see Fig. 6.11A) 35
– Tergites III–VI with fine spinules not arranged as above; frontal apotome (see Fig. 6.9D) and anterior half of thorax smooth or only weakly granulose 36

35. Frontal setae (see Fig. 6.9D) robust, thorn-like; frontal apotome without a median granulose mound .... *Constempellina*
– Frontal setae slender; frontal apotome with a median granulose mound (arrowed in Fig. 6.11A); tergites II–V illustrated in Fig. 6.16K.................... .... *Stempellina*

36. Thoracic horns with no spines but a fine roughness .... *Zavrelia*
– Thoracic horns with small spines .... *Stempellinella*

37. Tergite IV with a single anteromedian point patch .... *Paratanytarsus*
– Tergite IV with a pair of anterior point patches or longitudinal bands of point spines (arrowed in Figs 6.13I, J) 38

38. Segment VIII with posterolateral combs very wide and posterior margin almost straight (Fig. 6.16L)... *Virgatanytarsus*
– Each posterolateral comb composed of a clump of teeth or spines and confined to the posterolateral corners of segment VIII (Fig. 6.16M) 39

39. Precorneal setae (see Fig. 6.9D) set on a bulbous mound; tergites II–VI with paired circular to oval point patches anteriorly (Fig. 6.13I) .... *Cladotanytarsus*
– Precorneal setae not set on a bulbous mound; few species with paired circular or oval point patches on tergites II–VI: III–VI usually armed with anterior oval patches or longitudinal bands of points or spines (Fig. 6.13J); anal lobes illustrated in Fig. 6.16M .... *Tanytarsus*

NOTE. The pupae of *Kribiothauma* and *Skusella* are unknown.

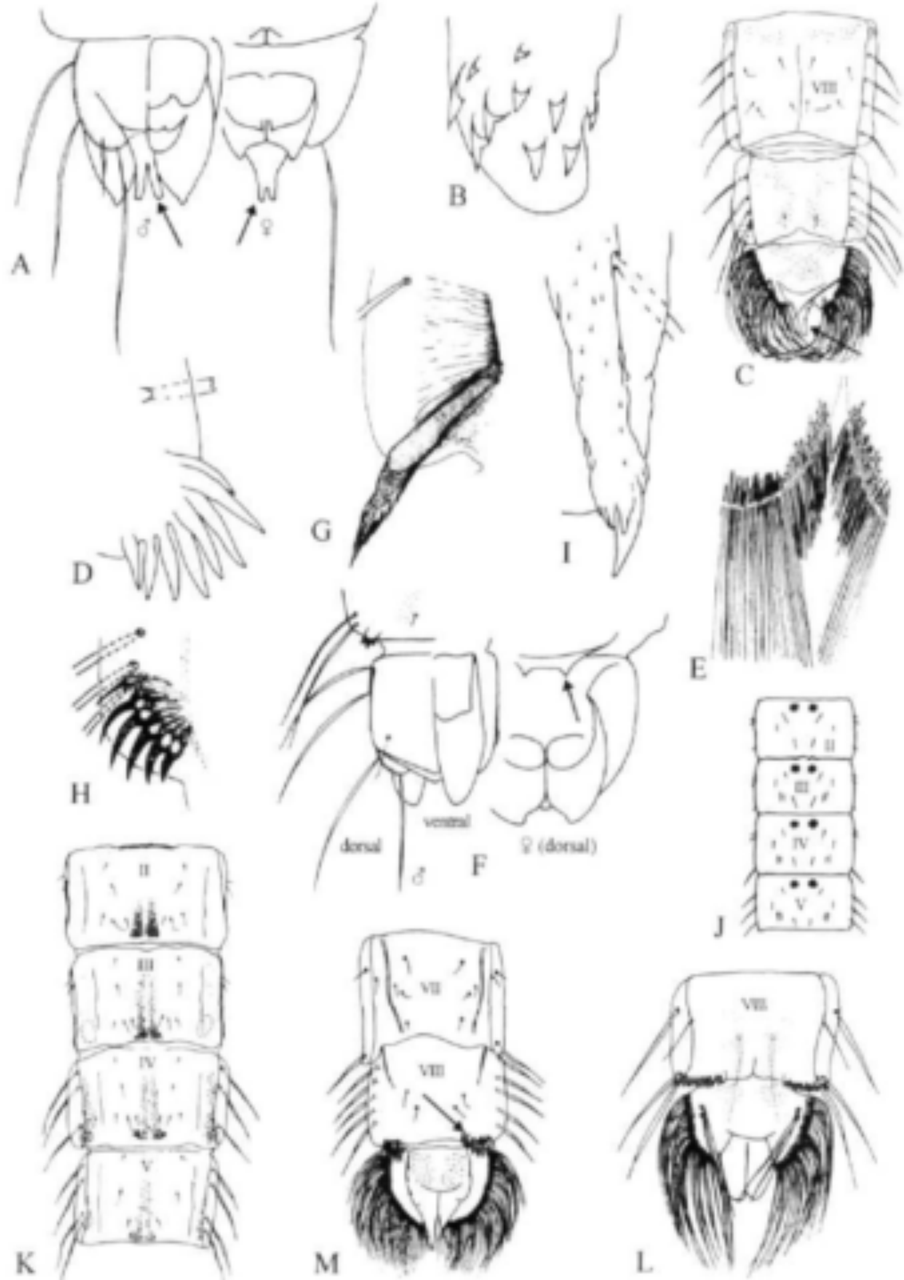


Fig. 6.16. Chironomid pupae. **A**, anal lobes of *Cryptochironomus* sp., male left (dorsal and ventral), female right (ventral). **B**, male genital sac of *Gillotia* sp. **C**, anal lobes of female *Gillotia* sp. **D**, anal comb on tergite VIII of *Cyphomella* sp. **E**, mid-region of anal lobes of *Nilodorum* sp. **F**, anal lobes of *Demicryptochironomus* sp. (male left, female right). **G**, anal spur of *Chironomus* sp. **H**, anal comb of *Kiefferulus* sp. **I**, anal spur of *Rheotanytarsus* sp. **J**, tergites II–V of *Rheotanytarsus* sp. **K**, tergites II–V of *Stempellina* sp. **L**, anal lobes of *Virgatanytarsus* sp., dorsal. **M**, anal lobes of *Tanytarsus* sp., dorsal. A, F, J redrawn from Langton (1984); B–E, G–I, K–M redrawn from Wiederholm (1983).

NOTES ON SUBFAMILIES

Family **Chironomidae**
Subfamily **Telmatogetoninae**

This is a marine intertidal group, the two species known from our coasts having a world-wide distribution. Records are skimpy, however, since no systematic collections have been made.

Subfamily **Podonominae**

Species of this world-wide subfamily occur typically in cold mountain regions. The southern hemisphere is richer in species than the northern hemisphere with numerous species in the Andes, southern Chile and Argentina, the sub-Antarctic islands, Australasia and southern Africa. The southern African and some Australian species are atypical, living in vegetation or moss or on open rock faces in temporary trickles over rocks and boulders. Their ability to survive during the dry season, when no water is present, has not yet been explained. In southern African species of *Archaeochlus* are found in the KwaZulu–Natal Drakensberg and Namibia, while *Afrochius harrisoni* is found on granite inselbergs near Dombashawa, north of Harare in Zimbabwe.

Subfamily **Aphroteniinae**

This subfamily of very small midges, with wing lengths of hardly more than 1 mm, is found only on the southern tips of the southern continents. It is a true Gondwanan group. The two South African species, *Aphrotenia tsitsikamae* and *A. barnardi*, are limited to the Cape Fold Belt Mountains (Western and Southern Cape), *A. tsitsikamae* being known from Bettys Bay to the Tsitsikama Forest, where it is particularly common, and *A. barnardi* from Table Mountain to the Hottentots Holland mountains (Western Cape). The minute larvae are found in stony runs, usually in small streams.

Subfamily **Tanypodinae**

Larvae of tanypods, which are found worldwide, are predatory in the later instars. Tropical Africa is richer in species than is the more southern part of the continent. Two genera, *Macropelopia* and *Apsectrotanypus*, show an interesting distributional discontinuity: both are found in the Cape Fold Belt mountains and both are widespread in the northern hemisphere but there are no records from anywhere in between.

Subfamily **Diamesinae**

Members of this subfamily are typical of very cold conditions, one species of *Diamesa* from Canada emerging and mating in air spaces under the ice. Typical species of *Diamesa* are found in glacial melt water on Mount Kenya and the Ruwenzoris. The only southern African species, *Harrisonina petricola,* is atypical in that the larvae live in warm conditions in intermittent mountain streams that run only during the wet season. Nothing is known about where or how this species survives during the dry season when no water is present. It is found from Zimbabwe to the Eastern Cape Province, the most southerly record being from the upper Kowie River near Grahamstown.

Subfamily **Orthocladiinae**

This large group is typical of fast-flowing rivers and streams, especially in rocky torrents. In cold climates orthoclads are also found lakes. Individuals are mostly small, half the size of a mosquito or less. Small midges of the large *Smittia* group are found in damp soils. Two marine genera, *Clunio* and *Semiocladius*, are both found on southern African coasts.

The group is most species-rich in the northern hemisphere, especially in colder climates. In southern Africa most species occur in mountain regions, but there are always some, especially species of *Orthocladius*, *Cricotopus* and *Thienemanniella*, in stony runs in lower river zones. Many of the species that occur in mountainous regions are found along the southern and eastern mountain ranges into east Africa and some even into the Ethiopian Highlands. A number of species appear to be endemic in South Africa, but this could be an artefact of poor collecting in mountains to the north. At least one species, *Notocladius capicola*, seems to be endemic to the mountains of the western and southern Cape.

Subfamily **Chironominae**

This, the largest subfamily of the Chironomidae, includes the large midge *Chironomus*, the type genus for the whole family. The subfamily has a world-wide distribution, except for the sub-Antarctic islands. Most species live in standing waters such as lakes, ponds, rock pools and even tree holes, but they are also abundant in the slower reaches of rivers. The large genus *Polypedilum* includes a few species found in mountain torrents and stony runs of rivers, although most species live in standing waters.

Africa is very rich in genera and species of Chironominae but many of these are limited to the tropics and sub-tropics. For instance, species of the genus *Nilodorum* are found in lakes, large rivers and ponds all over tropical Africa, Egypt and even into Israel, but are only found in the warmer parts of South Africa and not in the Western Cape. This pattern is repeated in a number of species of other genera. Some species show large geographic discontinuities, probably due to the lack of suitable habitat in the intervening countryside.

The subfamily is divided into two tribes, the Chironomini and the Tanytarsini. The Chironomini are mostly larger midges, many the size of mosquitoes, but some somewhat larger and some much smaller. Most larvae live in mud tubes on bottom substrates or attached to various underwater surfaces. Some species, including some of *Dicrotendipes*, have spotted wings and are found in lakes and ponds from the southernmost tip of the continent to Egypt and beyond. This illustrates another distribution pattern: species found in all climatic zones.

The Tanytarsini are all rather small, half the size of a mosquito or less. Larvae are all tube-dwellers, some making moveable cases. Adults have hairs on their wings that become detached as they fly. In some lakes, such as Zeekoevlei on the Cape Peninsula (Western Cape), and in large rivers such as the Nile at Khartoum, the larvae occur in vast numbers and the emerging males form huge mating swarms; the atmosphere can be full of their wing hairs, resulting in asthma attacks in the human population.

One genus, *Rheotanytarsus*, is typical of stony torrents and makes a case with prongs on which it spins a net to catch small food particles drifting in the current.

USEFUL REFERENCES

AMAKYE, J.S. & SÆTHER, O.A. 1992. Immatures and imagines of the Afrotropical species *Microtendipes lentiginosus* Freeman and *Collartomyia hirsuta* Goetghebuer (Diptera: Chironomidae). *Entomologica Scandinavica* **23**: 429–442.

BRUNDIN, L. 1966. Transantarctic relationships and their significance, as evidenced by chironomid midges. *Kungl. Svenska Vetenskapsakademiens Hanglingar, fjärde serien.* **11**:1– 472.

LANGTON, P.H. 1984. A key to pupal exuviae of British Chironomidae. Privately published by P.H. Langton. 324 pp.

MCALPINE, J.F., PETERSON, B.V., SHEWELL, G.E., TESKEY, H.J., VOCKEROTH, J.R. & WOOD, D.M. (Eds). 1981. Manual of Nearctic Diptera, Volume 1. *Agriculture Canada* Monograph **27**: 1–674.

SÆTHER, O.A. 1977. Taxonomic studies on Chironomidae. *Bulletin of the Fisheries Research Board of Canada* **196**: 1–143.

THIENEMANN, A. 1974. *Chironomus. Die Binnengewässer* **20:** 1–843. Stuttgart.

WIEDERHOLM, T. (Ed.). 1983. Chironomidae of the Holarctic Region. Part 1. Larvae. *Entomologica Scandinavica* Suppl. **19**: 1–457.

WIEDERHOLM, T. (Ed.) 1986. Chironomidae of the Holarctic region. Keys and diagnoses. Part 2 Pupae. *Entomologica Scandinavica* Suppl **28**: 1–482.

CHAPTER 7

BRACHYCERA

by

A.D. Harrison, A. Prins & J.A. Day

The suborder Brachycera corresponds more or less with the 'higher' flies: those with maggot-like larvae, and pupae that form within the old larval skin. The suborder includes some very well-known families of dipterans—the housflies and horseflies, for instance—as well as several uncommon or poorly-known families. The aquatic brachycerans of the southern African region are generally not well known and no experts were available to write account of the more important families. Thus, while this chapter provides an introduction to the major families with aquatic larvae, the authors make no claim to expertise in the group.

To identify an immature dipteran to family, the reader is referred to Chapter 1.

Family **Tabanidae**

horseflies and clegs: Figs 7.1A–C

The Tabanidae is a cosmopolitan family of about 3000 species of stout-bodied flies 10–25 mm in length. The adults can be recognized by the third antennal segment, which is elongate and bears an annulated style or **arista** apically. Males are harmless to other animals, sucking nectar from flowers, while females suck blood, mostly from mammals. Thus a less formal, but more rapid and painful means of identification, lies in the fact that most relatively large flies that bite are tabanids: they are aptly named 'horse flies' because they do not seem to be particularly fussy about which particular mammals they bite. The mouthparts form a piercing-and-sucking proboscis, which varies considerably in length from taxon to taxon. An interesting endemic group of tabanids is important as pollinators of the flowers of certain plants in the south-western Cape.

Tabanid larvae (Fig. 7.1A) are stout and sub-cylindrical with reduced heads. Circlets of prolegs and/or tubercles on the first seven abdominal segments give the body a ringed appearance. At the tip of the siphon is the **spiracle**, consisting of a vertical slit (Fig. 7.1B) or ending in a freely-extensible, sharply-compressed spine. Larvae mostly live in damp soil but those of a few species are fully aquatic. Of these, most live on the margins of ponds or streams but some are restricted to sand or gravel in the beds of swiftly-flowing streams. Some larvae apparently prey on small invertebrates, but the feeding habits of others are unknown. Larvae of most species crawl out of the water to pupate.

Pupae (Fig. 7.1C) are obtect, in that the sheaths of the wings, legs and mouthparts are fused to the exoskeleton of the rest of the body. A heavy transverse ridge of chitin usually covers the tapering antennal sheaths. The thoracic spiracles are prominent, each with a sclerotized marginal ridge above and behind it. Each abdominal segment, except the first, bears a more-or-less-complete transverse row of spines and, laterally, a short truncate spiracular tubercle. The anal segment may or may not bear spines, but the posterior part of the last segment is provided with six sharp projections.

The southern African tabanid fauna

Of the 700 or so species of tabanid known from the Afrotropical Region, about 250 have been recorded from southern Africa (Chainey & Oldroyd, 1980). In South Africa the species with the largest adults are the short-tongued, brownish *Tabanus biguttatus*, the brown *T. ustus*, the long-tongued, greyish, *Philoliche rostrata*, and the brownish *P. aethiopica*. Adults of all of these species reach lengths of about 23 mm. Most southern African species belong to world-wide genera but *Oldroydiella* and *Stuckenbergina* are apparently endemic to the region.

As is usually true for larval tabanids, few southern African species are fully aquatic; those that are aquatic mostly belong to common world-wide genera such as *Chrysops*, *Haematopota* and *Tabanus*.

Biology

In his discussion of the early stages of the tribe Tabanini, the larvae of which are closely associated with water, Oldroyd (1954) noted that females lay their eggs in masses on the leaves of water plants, or on grass or stones close to the water. The newly-hatched larvae drop into the water or burrow into the damp soil at the water's edge. It has been observed in some species that, when the egg mass has been laid, the female covers it with a creamy white secretion, which later hardens.

Some tabanid larvae, particularly those of the genera *Tabanus* and *Haematopota*, are voracious carnivores and most of them are cannibalistic, although a few feed on vegetable matter in shallow waters. Some tropical species that live in deep water apparently feed on the leaves of plants, attested to by the fact that the larvae of *Ancala fasciata*, from West Africa, are bright green in colour. Chainy & Oldroyd (1980) mention that larvae of *Tabanus biguttatus* and *T. fraternus*, which live in dry areas, construct mud cylinders that protect them from desiccation both as larvae and as pupae. Tabanid larvae pass through up to nine instars and may persist for nine months or more, although some develop far more rapidly than this, specially in warm conditions. Pupal stages usually last three weeks to a month.

As they are not fully adapted to an aquatic existence, tabanid larvae come up to the surface of the water periodically to breathe air, which they do through the open spiracles at the hind end of the body. These spiracles are often placed on a respiratory siphon (Fig. 7.1B), which varies in length from species to species. In members living between tide marks on the seashore, the hind spiracles are usually provided with a ring of branched hairs. On the other hand, the larvae of the local *Philoliche caffra* develop in decaying kelp just above the high-water mark, or even between the tide marks, or on vegetable detritus at the edges of inland pools. Their bilobed spiracles, which are situated on an oval swelling, normally lack filaments, but can be closed tightly when the larvae submerge.

Identification of immature tabanids

Keys (Oldroyd, 1952, 1954, 1957) are available for adults of African species but not for immature stages.

Family **Athericidae**
Fig. 7.1D

The Athericidae, a small family of horse-fly-like flies with aquatic larvae, was separated from the family Rhagionidae (the snipe-fly family) by Stuckenberg in 1973. Adult rhagionids are similar to horse flies (Tabanidae) but have a long, slender, non-annulated style on the antenna. They are mainly found in the vegetation surrounding the edges of streams or on rocks in river beds. Females of some species are known to be blood-suckers, feeding on frogs, birds or mammals.

The larvae (Fig. 7.1D), which are found in rivers—mostly in fast-flowing streams—are elongate and taper anteriorly. The head capsule is small and retractable. The first seven abdominal segments bear pairs of prolegs with an apical and a subapical semicircle of curved claws, while segment 8 has a single proleg. The body ends posteriorly in two elongate caudal projections bearing fine filamentous setae. Between them is a single dorsomedial spiracle.

Pupae are not aquatic, larvae crawling out of the water to pupate in the soil in river banks.

The southern African Athericid fauna

The following information is taken from Stuckenberg (1960, 1980b). The genus *Atherix* is not found in the Afrotropical Region, the South African fauna consisting only of the genera *Suragina, Pachybates* and *Trichacantha,* all in the subfamily Athericinae. *Pachybates* and *Trichacantha* are entirely endemic to the mountains of the western and southern Cape (Stuckenberg 1960). *Suragina* has a worldwide distribution and is widespread in southern Africa, species being known from the Free State, Kwazulu-Natal, Mpungalanga, North-West Province, Limpopo, Zimbabwe and Gorongoza (Mozambique). The genus is also known from West and Central Africa; indeed, Stuckenberg considers the southern African members of the genus to be invasive elements from the tropics. He has found some in montane gallery forest but adults of others 'in riverine bush adjacent to muddy and even stagnant streams and rivers', so presumably their larvae are to be found in adjacent aquatic habitats. Stuckenberg (1980b) states that "South Africa has an unrivalled assemblage of endemic taxa" including both primitive and specialized forms.

Little work has been done on the larvae but they are common in mountain streams and rivers. Stuckenberg (1980b) notes that the predatory larvae are morphologically similar throughout the family.

Biology

Very little is known about the biology of the southern African species. Adults of some species, particularly in the genera *Pachybates* and *Trichacantha*, are socially inclined and participate in communal egg-laying. This was noticed in 1915 when Brauns collected *Pachybates braunai* at Stellenbosch in the Western Cape Province (Bequaert 1921). It is not known if adult females of Afrotropical species have the same blood-sucking habits as those of species from other parts of the world.

According to Oldroyd (1964), the eggs of European and North American species are laid on the leaves of plants overhanging water. In at least one European species, *Atherix marginata*, the young larvae live on the leaves and drop into the water only when they are ready to change into the second larval stage.

Identification of immature athericids

Stuckenberg (1960) gives keys to the adults of the genera found in South Africa, but no keys are available for immature stages.

Family **Stratiomyidae**
soldier flies: Figs 7.1E–F

The Stratiomyidae is a big cosmopolitan family of fairly large, wasp-like flies. Adults of most species are drab but some are black and yellow, while others are metallic blue, green or purple. They do not bite but are often found on flowers and are said to feed on flowers or over-ripe fruit and decaying material. Although they are found in a variety of places, they are seldom seen on the wing. In some members the thorax is armed with strong spines. When at rest the wings are closed over each other on the body, concealing the more conspicuous abdominal patterns and thus probably minimizing attention from predators. Small dancing swarms occur in some species.

The family has several subfamilies but only two, the Clitellariinae and the Stratiomyiinae, have aquatic or semi-aquatic larvae. Larvae (Fig. 7.1E) are very characteristic, being tough and flattish, with retractile heads and a roughened surface reminiscent of the skin of a shark. The pupae remain within the last larval skin, which thus becomes a puparium.

The southern African stratiomyid fauna

It is estimated that about 1500 species of stratiomyids are distributed throughout the world (Oldroyd 1964) and according to James (1980) at least 374 species occur in the Afrotropical Region. South Africa is represented by 37 genera and about 90 species many of which are endemic, although most genera are not. Both sub-families with aquatic larvae are found in southern Africa.

James (1980) lists the following stationmyid genera as having been recorded from southern Africa: in the subfamily Stratiomyinae, *Stratiomyia*, *Afrodontomyia*, *Dischizomyia*, *Oplodonta* (five species), *Zulumyia* and *Odonotomyia* (subgenus *Odontomyia*) (ten species); and in the subfamily Clitellariinae, *Nemotelus* (26 species) and *Oxycera*. A great deal of work remains to be done to correlate larvae and adults of southern African species.

Biology

Most stratiomyid larvae are characterized by their sharkskin-like skins. The roughness is due to deposition of calcium carbonate in the cuticle, particularly in the torpedo-shaped larvae of the larger forms that live in mud or around the edges of ponds and streams. Larvae of some members of the subfamily Stratiomyiinae have been found to breed in hot springs, or in fairly acid, or very saline, waters.

The biology of South African species is not well known. Eggs of one species of *Odontomyia*, found breeding in wet cow dung, are shiny and almost transparent, oblong, and with microscopic punctation. Prins (pers. obs.) has observed them to be laid in clusters of three or more and to require an incubation period of about six days during early winter. The young, newly-hatched larvae closely resemble the mature larvae.

Fully grown larvae pupate within the last larval skin (Fig. 7.1F). Most of them pupate out of the water in mud or soil, but some aquatic larvae do pupate in water. The air trapped between the pupa and the larval skin causes it to float at the surface, which exposes it to predators as well as to hazards such as being swept away or being trapped in a place where it is difficult for the adult to emerge (Oldroyd 1964).

Identification of immature stratiomyids

There is no key to southern African larvae but Johannsen (1933) gives a key to North American genera, all but one of which are known to occur in southern Africa as well.

Family **Empididae**
dance flies: Figs 7.1G–H

The Empididae is a large family of small, predatory flies of sparsely bristly appearance with powerful grabbing legs and conspicuous dagger-shaped proboscides. They are found worldwide. Members of some species have very long proboscides used for probing flowers for nectar. Larvae (Fig. 7.1G) have paired ventral prolegs on the abdominal segments and the terminal abdominal segment has one to four rounded lobes bearing apical setae. Not many species have aquatic larvae. Pupae are very variable and not well known.

The southern African empidid fauna

Of the 2000 or so recorded species of dance flies, more than 300 are known from the Afrotropical region and of these about 220 species in 33 genera are known from southern Africa. Immature forms are common in our rivers but simple means of identification are not readily available. Of the known aquatic forms in southern African, *Wiedemannia* has four species, *Clinocera* has two species (both in the subgenus *Hydrodromia*) and *Hemerodromia* has nine species (Smith, 1980). Representatives of the *Hybos, Ocydromia, Clinocera, Empis, Rhamphomyia* and *Hilaria* genera have also been recorded from southern Africa.

Biology

Adults of some species, particularly of the genera *Hybos*, *Ocydromia* and *Hemerodromia* prefer to run rather than to fly and usually catch their

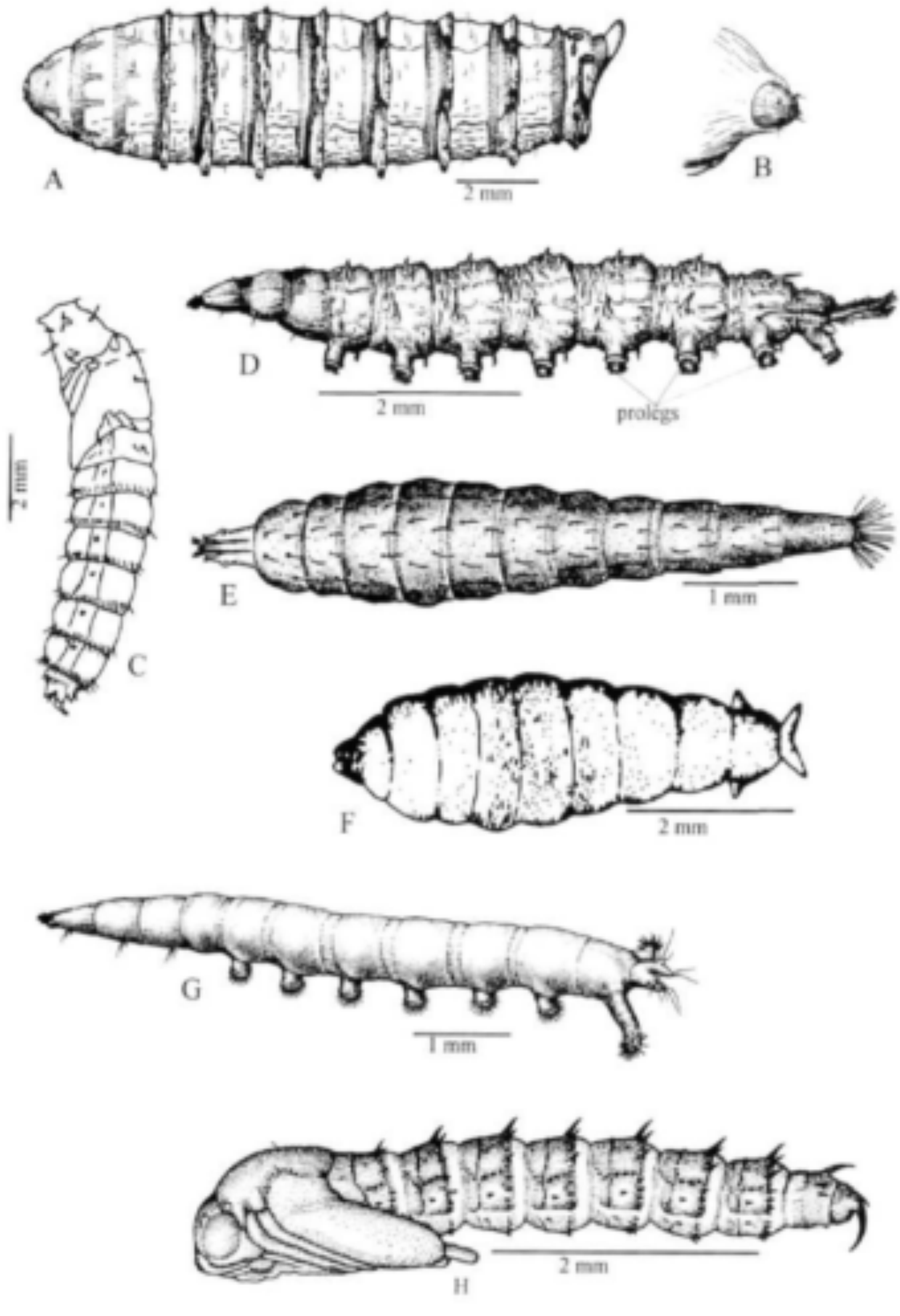


Fig. 7.1. Immature Brachycera, in left lateral view unless otherwise indicated. **A**, larval tabanid; **B**, respiratory siphon of a tabanid larva in posterodorsal view; **C**, a tabanid pupa; **D**, an athericid larva; **E**, a stratiomyid larva; **F**, a stratiomyid pupa; **G**, an empidid larva; **H**, an empidid pupa. A, B, D, G, H redrawn from McAlpine (1981); C, E, redrawn from Johannsen (1935); F redrawn from Usinger (1956).

prey on foot. Members of the genus *Clinocera* catch insects trapped in the surface film of water. In certain genera, such as *Empis* and *Rhamphomyia*, dancing swarms occur mostly over land, whereas in species of *Hilara* these swarms occur over water.

The immature stages of southern African species are poorly known, but have been found in various materials such as soil, decaying wood, and dung. Some may occur in mud or water, or even intertidally, although in most cases they are not fully aquatic. They are apparently predatory but may also exploit carrion at times.

According to Oldroyd (1964), larvae of the genus *Hemerodromia* (Fig. 7.1G) are perhaps the most completely aquatic, having prolegs with hooked crotchets for crawling under water. Steyskal & Knutson (1981) mention that empidid larvae prey on simuliid larvae while Oldroyd indicates that members of *Wiedemannia*, which is represented in South Africa, prey on simuliid pupae.

Empidid pupae (Fig. 7.1H) are also aquatic, being found on submerged stones or pupating in empty simuliid cocoons, or in stony crevices. Empidid pupae apparently do not produce cocoons.

Identification of immature empidids

Although some keys do exist (e.g. Smith, 1967; 1969), none are available for southern African species with aquatic larvae. Of the aquatic forms, the larvae of *Hemerodromia* (Fig. 7.1G) have seven pairs of abdominal prolegs and a pair of long tracheal filaments on the prothorax and on each of the first seven abdominal segments. The larvae of *Clinocera* have eight pairs of abdominal prolegs and bear numerous spinules on the abdominal segments; spiracles are located near the lower lateral margin of each abdominal segment except the last. The larvae of *Wiedemannia* have eight pairs of abdominal prolegs but lack setose appendages on the last segment.

Family **Dolichopodidae**

long-legged flies: Figs 7.2A–B

The Dolichopodidae is a fairly large world-wide family of small-, to medium-sized predatory flies, often with bright metallic green or coppery coloration. Although their wings are well-developed, they usually prefer to walk, catching their prey mostly on foot. Some have aquatic larvae.

The predatory larvae are usually whitish, cylindrical and slightly tapered anteriorly (Fig. 7.2A). The head capsule is small and unsclerotized externally, while the internal parts, including the mandibular-maxillary sclerites, are brown or black (see Fig. 1.1D). The posterior surface of the terminal segment is crossed with vertical and horizontal furrows, resulting in four or more lobes, not much produced and having a truncate appearance. Dorsal lobes usually bear a posterior spiracle fringed with a series of branched setae. Abdominal segments 1–7 each bear a pair of creeping welts ventrally on the anterior margins.

A dolichopodid pupa (Fig. 7.2B) is enclosed in a loose cocoon, to which debris often adheres. A pair of respiratory horns arise from the dorsal surface of the thorax just behind the eyes, while functional spiracles also occur on the first seven abdominal segments. Abdominal tergites usually have a row of dorsal spines. The respiratory horns sometimes protrude through a hole in the cocoon, the hole being big enough for the later escape of the adult fly during eclosion. In other forms the pupa wriggles out of the cocoon before the adult emerges.

The southern African dolichopodid fauna

About 6000 species have been described worldwide; of these, about 116 in 31 genera have been recorded from South Africa (Dyte & Smith 1980). Members belonging to the subfamilies Aprosylinae, Diaphorinae and Hydrophorinae contain species with aquatic larvae. Afrotropical species have not recently been revised and most of our knowledge comes from fragmentary reports contained in the results of various expeditions (Dyte & Smith, 1980). There is no key to the larvae.

Biology

Long-legged flies mostly frequent waterside vegetation. Mating usually takes place on the ground, often involving a colourful display as males wave their conspicuously-marked antennae, legs and wings in the air. In some species, the females station themselves on specific objects such as the trunks of trees, wet soil, wet rocks or dry rocks, where they wait for the males to display.

Most larvae are predatory and occur in the soil or in decaying vegetation, or are stem-borers. Aquatic forms may live in shallow water, in mud, on wet rocks covered with moss and other plant life, or at the edges of streams. Some even live between the tide marks on the seashore. They are not fully aquatic and, although they are normally predatory, they may from time to time feed on decaying materials and even on dead insects.

Identification of immature dolichopodids

There are no keys available for the southern African forms.

Family **Syrphidae**

hover flies and droneflies; rat-tailed maggots

Figs 7.2C–D

The Syrphidae is one of the largest and most sharply defined families in the Diptera. Adult syrphids are medium to large, brownish-yellow to blackish flies. They often frequent flowers and are characterized by their habit of hovering, hence the name 'hover flies'. Some species also visit carcasses and cadavers for moisture, and the cosmopolitan *Eristalis tenax*, whose larvae resemble male honey bees, often live in carcasses. The larvae are extremely varied in their habits. Larvae (Fig. 7.2C) of the aquatic species are known as 'rat-tailed maggots' because they have long telescoping posterior respiratory siphons with tiny fused spiracular plates at the tips. The head is virtually non-existent: the mouthparts are replaced by mouth hooks, and the segmentation of the body is often obscured. The genera *Eumerus* and *Ceriana* in the subfamily Melesiinae have larvae with short non-contractile siphons, while *Eristalis* (Fig. 7.2C) and other members of the tribe Eristalini mostly have aquatic larvae with long contractile siphons.

The larvae crawl out of the water to pupate. Pupae (Fig. 7.2D) are similar to the rat-tailed larvae but with shorter 'tails'.

The southern African syrphid fauna

Of the 500 or so species of syrphids known from the sub-Saharan region, 32 genera—with some 165 species—have been recorded from southern Africa. A large number are endemic but only a small minority has aquatic or semi-aquatic larvae. The genera *Chrysogaster*, *Myolepta*, *Eumeris*, *Ceriana*, *Eristalinus*, *Eristalis* and *Mallota* in the sub-family Melesiinae contain species with aquatic larvae in other parts of the world. Although these genera occur in southern Africa, but not much is known of the biology of their larvae. Two genera are particularly species-rich: *Eumeris*, with approximately 44 species, and *Eristalinus*, with approximately 17 species; only one species of *Eristalis* (the widespread *E. tenax*) has been reported from southern Africa (Smith & Vockeroth, 1980).

Biology

According to Skaife (1953), female droneflies lay their white, oval, eggs in small clusters at the edges of pools in slight hollows in the mud. The newly-hatched larvae creep into the water. The slender 'tail' of the larva is actually a long telescopic respiratory siphon, so that when the larva crawls along the bottom by means of ventral warts or prolegs, the long siphon can reach the surface even if the larva is feeding in water several centimeters deep. The larva is therefore able to survive in the shallow ooze at the edge of manure heaps. The gut has a filtering apparatus consisting of a number of parallel V-shaped plates, with which they filter organic fragments from the water. When humans drink foul water, they may accidentally imbibe young syrphid larvae, which could cause intestinal myiasis.

The larvae of two syrphid species (*Eristalinus taeniops* and *E. nigricans*) are very similar to, and are found under similar conditions as, the rat-tailed maggot larvae of *E. tenax*. The larvae of *Eristalinus taeniops* are a brownish colour, while those of *E. nigricans* are relatively dark. Adults of *E. taeniops* have transversely-striated eyes. The larvae of *Chrysogaster*, with at least four South African species, have sharp posterior spiracles that are hardened and able to pierce the stems of aquatic plants to obtain oxygen.

When mature, the larvae of most syrphids leave the water, bury themselves in damp soil and change into brownish pupae. The adult flies emerge within three weeks to a month.

Identification of immature syrphids

There are no comprehensive keys for the identification of southern African syrphids with aquatic larvae.

Family **Sciomyzidae**
marsh flies: Figs 7.2E–F

The Sciomyzidae consists of about 600 species, mostly found in the Holarctic Region of the northern hemisphere. Adult sciomyzids are medium-sized to large flies, brownish to yellowish in colour, often with spotted wings. They are characterized by the presence of a long seta in the middle of the front part of the middle femora. The antennae are usually long and project horizontally. The terminal segment of the larva (Fig. 7.2E) is usually tapered but not drawn out into a siphon, and the body is usually covered with short, fine hairs. Prolegs are present in some species. The pupae are yellowish to brownish and oval, and in most cases curve upwards at both ends; the larval structures are still visible on the integument (Fig. 7.2F)

Knutson made the following observations on the feeding behaviour of sciomyzid larvae: "The larvae are mainly predators or internal parasitoids of freshwater or terrestrial non-operculate snails, but a few feed on slugs, small sphaeriid clams or eggs of snails. The three Afrotropical species that have been reared, and for which the larvae are described.....feed on snails of the genera *Succinea**..., *Lymnaea* ...and *Physa*..." (Knutson, 1980).

* **Note**: it is likely that Knutson was referring to *Oxyloma patentissima*, the only freshwater succineid species found in southern Africa (C. Appleton pers. comm.).

The southern African sciomyzid fauna

Only three genera (*Salticella, Ethiolimna* and *Sepedon*), comprising about 23 species, occur in South Africa. Of these, *Sepedon* dominates with about 15 species (Knutson 1980).

Biology

The adults occur near ponds and streams and in muddy places. The eggs are laid separately or in groups on grasses and the newly-hatched larvae drop into the water. The incubation period varies from four to seven days at 24°C. According to Barraclough (1983), who describes the biology of various species of *Sepedon*, the eggs are oval, creamish to greyish in colour, and have dorsal and lateral ridges. (Barraclough also reports that the larvae of *Sepedon neavei,* from southern Africa, are dark brown in colour and may reach a length of about 11 mm). The larvae move about just under the surface of the water, seeking out pulmonate snails of the families Lymnaeidae, Physidae and Planorbidae, on which they feed. Barraclough notes that they are also known to feed on insect carrion. It has been suggested that these larvae might be useful in ridding aquatic habitats of planorbid snails, some of which are hosts to the parasites that cause human schistosomiasis (bilharzia), but sciomyzid larvae thrive only when snail populations are very dense.

Identification of immature sciomyzids

Mature larvae (Fig. 7.2E) are elongate. The thoracic segments are more slender than those of the abdomen. Each spiracle of the posterior siphon has three spiracular slits surrounded by hydrofuge hairs, which together form the spiracular disc, and which help the larva to maintain contact with the surface of the water. The spiracular disc is also used to grip the shell surface of the snails on which the larva feeds. The mouth opening is indicated by paired, curved mouthhooks. In the larvae of genera such as *Sepedon*, the body segments are provided with integumentary folds and tubercles used in locomotion; in other cases the tubercles may be produced into small pseudopods, so that these larvae resemble those of the tabanids. The lobes on the spiracular disc may be ventrolaterally bilobed.

The puparia of *Sependon nevei* (Fig. 7.2F) are dark or reddish brown and measure 7–8 mm in length. The anterior ends are bluntly tapered. Puparia may be found either in or out of the water; if in the water, they usually float just beneath the surface with the posterior spiracles in contact with the surface film (Barraclough, 1983). According to Barraclough, the pupal stage lasts 11 to 15 days.

Family **Ephydridae**

shore flies and brine flies: Fig. 7.2G–H

The Ephydridae is a large family of relatively small, mostly blackish flies, well represented in most parts of the world. According to Cogan (1980) the colloquial name 'shore fly' is applicable only to a small section of the family, as the majority of species are found in inland waters, either as aquatic larvae or attached to aquatic or semi-aquatic plants. The adults vary from very small (<2 mm) to about the size of a horsefly (10 mm). Some ephydrids are very similar to the dolichopodids and can easily be mistaken for them. Females of the genus *Nostima*, which has representatives in South Africa, are wingless, while species belonging to the genus *Ochthera*, with at least three South African species, have enormously developed forelimbs, which they use for capturing prey. The larvae (Fig. 7.2G) usually have several pairs of ventral prolegs, the last pair of which are much larger than the others, and a posterior respiratory siphon, WHICH IS often forked.

The southern African ephydrid fauna

Some 1000 species have been described world-wide, with 32 genera and about 57 species known from South Africa and some 250 species from the Afrotropical Region as a whole (Cogan, 1980). The almost cosmopolitan urine fly (*Scatella fusca*) has now been discovered in rock pools among the guano on several off-shore islands around the South African coast (the late R.K. Brook, pers. comm.).

Biology

According to Cogan (1980), ephydrids are found in a wide variety of habitats and some species show a remarkable tolerance to environmental extremes. Larvae of some species of *Scatella* are found in pools around hot springs, and larvae of *Halaeomyia petrolei*, the Californian petroleum fly, occur in natural pools of crude petroleum. Although many have freshwater larvae, larvae of others can tolerate very high salt concentrations and are to be found in in hypersaline lakes and in the upper parts of estuaries, where their pupae can be found attached to salt-tolerant grasses. Cogan reports that the large numbers of ephydrid larvae in alkaline and saline lakes provide an important source of food for water fowl. Yet other species are terrestrial: some are leaf-miners of agricultural importance; larvae of some species of *Actocetor*, a genus represented in South Africa, live in the egg-pods of locusts; others are free-living, some being aquatic or semi-aquatic. Some shorefly larvae are carnivorous, while others feed on algae in the water.

Some members of the genus *Hydrellia*, represented in South Africa by at least two species, produce larvae that mine into water plants and obtain their oxygen by inserting their spiracles, situated near the tips of two sharp hollow spines, into the tissues of the plants. Pupae of these species are similar to the larvae and form within the cavities created by the mining activities of the larvae. According to Oldroyd (1964), the eggs of species of *Notiphila*, another genus known from South Africa, are laid on water plants. Like *Hydrellia*, the hind spiracles of the larvae open below spines that seem able to penetrate into plant tissue, but the larvae actually live on the bottoms of ponds and streams. Their food is unknown.

Larvae of *Scatella fusca*, the urine fly are commonly found in places such as sewage filters with a high urine content. As is the case with many other species in this family, they are gregarious and may develop in such vast numbers that they block drainpipes.

Identification of immature ephydrids

There are no comprehensive keys to either the adults or the immature stages of South African aquatic ephydrids. The family is represented in South Africa by four subfamilies, of which the larvae belonging to the Notiphilinae are metapneustic, only the last pair of spiracles are open; all the other known larvae are amphipneustic, both anterior and posterior spiracles being open. The two posterior spiracles, each with three to five openings, are usually placed at the tip of a forked process, the siphon, which may vary in length (and which may even be absent). The head is greatly reduced, with no sclerotized parts, and the cephalo-pharyngeal skeleton is completely retracted into the thorax. Some members have prolegs provided with hooks, the posterior pair being the largest. In others the prolegs are weakly developed and sometimes only the last pair is visible. The larval integument is usually provided with short spines or spinules. In members of genera such as *Ephydra*, sensory papillae (Fig. 7.2G) armed with strong spines appear on some segments.

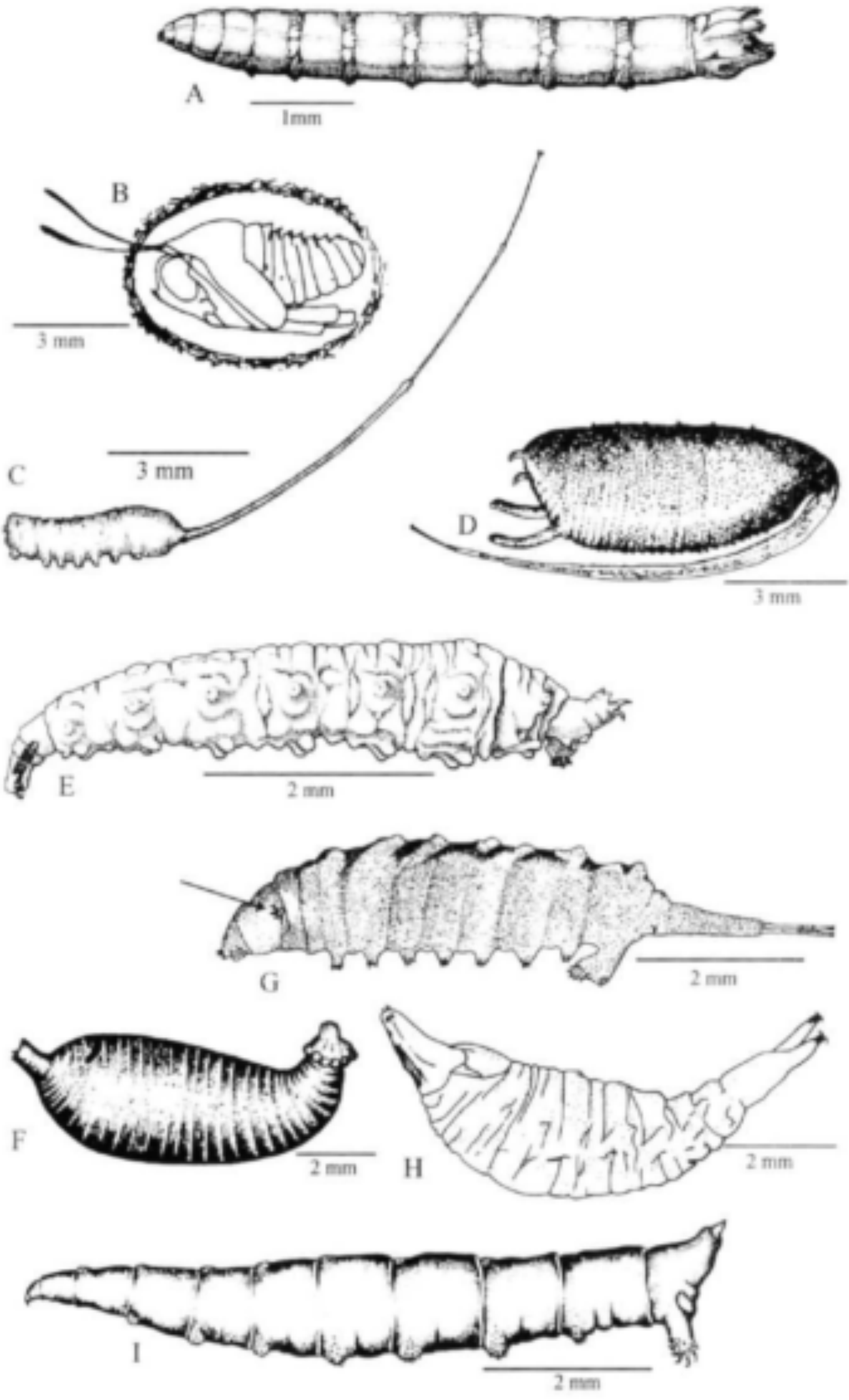
The pupae are formed within the larval integument. Tracheal gills, which have developed into respiratory horns (Fig. 7.2H), are present in pupae of the genus *Scatella*, with two southern African species, and *Brachydeutera*, with at least three.

Family **Muscidae**

house flies: Fig. 7.2I

The Muscidae is a very large family, the housefly, *Musca domestica*, being the best known representative. Most members of the family resemble

Fig. 7.2. Immature Brachycera, in left lateral view, unless otherwise indicated. **A**, a dolichopodid larva; **B**, a dolichopodid pupa; **C**, a syrphid larva; **D**, a syrphid pupa; **E**, a sciomyzid larva; **F**, a sciomyzid pupa; **G**, an ephydrid larva; **H**, an ephydrid pupa; **I**, a muscid larva. A redrawn from McAlpine (1981); B, D, F redrawn from usinger (1956); C, E, G-I redrawn from Johannsen (1935).


A
1mm
B
3 mm
C
3 mm
D
3 mm
E
2 mm
G
2 mm
F
2 mm
H
2 mm
I
2 mm

houseflies in appearance but some differ very much in biology. Some, like the biting housefly, *Stomoxys calcitrans*, and tsetseflies of the genus *Glossina*, have biting mouthparts and feed on blood. Larvae of most forms feed on decaying matter or plants but some, including those of the aquatic subfamily Limnophorinae, are carnivorous.

Sub-family **Limnophorinae**

The sub-family Limnophorinae is the only muscid family known to have fully aquatic larvae. Best known is *Limnophora*, a world-wide genus whose larvae live in running water. Other genera with aquatic larvae are *Lispe*, found in standing waters world-wide, and *Lispocephala* and *Lispoides* found in running waters in the Northern Hemisphere. The pale yellow larvae of *Limnophora* (Fig. 7.2I) have been observed among algae and moss growing on the margins of small streams, on waterfall cliffs and in the stony runs of larger rivers. They usually reach a length of about 14 mm and the body is very distinctly striated with a pointed anterior end. The head is greatly reduced. With the exception of the last segment, each abdominal segment has a belt of small setae composed of six to ten transverse rows. Ventrally, on each side of the median line on this belt, is a low protuberance on which the setae are longer and stronger. On the last segment, near the anterior margin on each side of the mid-ventral line, is a larger retractile proleg provided with about 14 large hooks. The terminal segment, which tapers slightly, ends in a pair of somewhat retractile conical projections, contiguous at the base, which bear a pair of black spiracles. The puparium is reddish brown, ovoid, and formed within the larval integument.

Twenty-six species of *Limnophora* are known from southern Africa but only from adults. The larvae are common in rivers, notably in stony runs, in most regions with permanent rivers. Eleven species of the genus *Lispe* have been described from southern Africa (Pont 1980), but no information is available on the larvae, except that they are usually found at the margins of ponds and lakes or other standing or slow-flowing waterbodies.

Biology

Limnophorine larvae are predatory, feeding on small aquatic animals such as oligochaetes, and simuliid and tipulid larvae. Apparently they crawl out of the water to pupate.

Identification of immature muscids

There are no keys to the larvae or pupae of aquatic muscids in southern Africa.

REFERENCES

BARRACLOUGH, D.A. 1983. The biology and immature stages of some *Sepedon* snail-killing flies in Natal. (Diptera: Sciomyzidae). *Annals of the Natal Museum* **25**: 293–317.

BEQUAERT, J. 1921. *Atherix braunsi* nov. sp., a South African leptid with gregarious habits (Diptera). *Psyche* **28**:1–7.

BERG, C.O. & KNUTSON, L.V. 1978. Biology and systematics of the Sciomyzidae. *Annual Review of Entomology* **23**: 239–258.

CHAINEY, J.E. & OLDROYD, H. 1980. Family Tabanidae. *In*: Crosskey, R.L. (Ed.) *Catalogue of the Diptera of the Afrotropical Region*. British Museum of Natural History, London: 275–305.

COGAN, B.H. 1980. Family Ephydridae. *In*: Crosskey, R.L. (Ed.) *Catalogue of the Diptera of the Afrotropical Region*. British Museum of Natural History, London: 655–669.

CROSSKEY, R.W. (Ed.) 1980. *Catalogue of the Diptera of the Afrotopical Region*. British Museum of Natural History, London.

DYTE, C.E. 1967. Some distinctions between the larvae and pupae of the Empididae and Dolichopodidae (Diptera). *Proceedings of the Royal Entomological Society of London (A)*. **42**: 119–128.

DYTE, C.E. & SMITH, G.V. 1980. Family Dolichopodidae. *In*: Crosskey, R.L. (Ed.) *Catalogue of the Diptera of the Afrotropical Region*. British Museum of Natural History, London: 443–463.

HENNIG, W. 1968. *Die Larvenformen der Diptera. 3 Teil.* Akademie Verlag, Berlin.

JAMES, M.T. 1980. Family Stratiomyidae. *In*: Crosskey, R.W. (Ed.). *Catalogue of the Diptera of the Afrotropical Region*. British Museum of Natural History, London: 253–274.

JOHANNSEN, O.A. 1935. Aquatic Diptera Part II. Orthorapha-Brachycera and Cyclorrapha. *Cornell University Agircultural Experimental Station Memoir* **177**: 1–62, plates I–XII.

KNUTSON, L.V. 1980. Family Sciomyzidae. *In*: Crosskey, R.L. (Ed.) *Catalogue of the Diptera of the Afrotropical Region*. British Museum of Natural History, London: 597–599.

OLDROYD, H. 1952. *The horseflies (Diptera: Tabanidae) of the Ethiopian Region. I. Haematopota* and *Hippocentrum*. British Museum of Natural History, London.

OLDROYD, H. 1954. *The horseflies (Diptera: Tabanidae) of the Ethiopian Region. II. Tabanus related genera.* British Museum of Natural History, London.

OLDROYD, H. 1957. *The horseflies (Diptera: Tabanidae) of the Ethiopian region. III. Chrysopinae, Scepsidinae and Pangoniinae, and a revised classification.* British Museum of Natural History, London.

OLDROYD, H. 1964. *The Natural History of Flies.* Weidenfeld & Nicoloson, London.

PONT, A.C. 1980. Family Muscidae. *In:* Crosskey, R.L. (Ed.) *Catalogue of the Diptera of the Afrotropical Region.* British Museum of Natural History, London: 721–753.

SCHOLTZ, C. & HOLM, E. 1985. *Insects of Southern Africa.* Butterworths, Durban.

SMITH, K.G.V. 1967. Diptera (Brachycera): Empididae. *In:* Hanström, B., Brinck, P. & Rudebeck, G. (Eds) *South African Animal Life* **13**: 217–233.

SMITH, K.G.V. 1969. The Empididae of southern Africa (Diptera). *Annals of the Natal Museum* **19**: 1–342.

SMITH, K.G.V. 1980. Family Empididae. *In:* Crosskey, R.W. (Ed.) *Catalogue of the Diptera of the Afrotropical Region.* British Museum of Natural History, London: 431–442.

SMITH, K.G.V. & VOCKEROTH, J.R. 1980. Family Syrphidae. *In:* Crosskey, R.L. (Ed.) *Catalogue of the Diptera of the Afrotropical Region.* British Museum of Natural History, London: 488–509.

STEYSKAL, G.C. & KNUTSON, L.V. 1980. Family Empididae. *In: Manual of Nearctic Diptera Vol 1.* Agriculture Canada, Ottawa: 607–624.

STUCKENBERG, B.R. 1960. Diptera (Brachycera) Rhagionidae. *In:* Hanström, B., Brinck, P. & Rudebeck, G. (Eds) *South African Animal Life* **7**: 216–308.

STUCKENBERG, B.R. 1973. The Athericidae, a new family in the lower Brachycera. *Annals of the Natal Museum* **21**: 649–673.

STUCKENBERG, B.R. 1980. Family Athericidae. *In:* Crosskey, R.W. (Ed.) *Catalogue of the Diptera of the Afrotropical Region.* British Museum of Natural History, London: 312–313.

GLOSSARY OF TERMS[1]

abdomen	the posteriormost, legless division of an insect's body, primitively with 11 segments but with 9 or 10 in most extant forms
acute	sharp-pointed
adhesive sheath	the sheath around the adhesive anal macrosetae (q.v.)
adhesive anal macrosetae	in pupal chironomids, sticky filamentous setae fringing the anal lobes
aeropyle	in pupal chironomids, a fine pore on the thoracic horn
Afrotropical	the biogeographic region of Africa south of the Sahara desert, not just the tropics
anal comb	in pupal chironomids a group of spurs (q.v.) or spines forming a comb postero-laterally on abdominal segment VIII
anal fin	see *anal lobe*
anal gill	see *anal tubule, anal papilla*
anal lobe	in chironomid pupae, the swimming paddle (q.v.)
anal papilla	in larval nematocerans, any of the pairs of soft appendages of the anal segment, seemingly of osmoregulatory function
anal projection	the pointed anal lobes of some chironomid pupae
anal segment	the segment bearing the anus
anal seta	one of the apical setae of the procercus (q.v.) of a chionomid larva
anal spur	in pupal chironomids, one of a pair of postero-lateral spurs on abdominal segment VIII
anal tubule	(= anal papilla): in larval nematocerans, any of the pairs of soft appendages of the anal segment, seemingly of osmoregulatory function
annulated	with rings or annuli
antenna	(pl. antennae): either of the anteriormost pair of segmental appendages, borne one on each side of the head and functioning as sense organs
antennal sac	the part of the pupa in which the adult antenna is formed
antepronotal setae	setae on the anterior part of the pronotum (q.v.)
alien	of plants and animals, introduced from elsewhere, neither endemic nor indigenous
anterior	at the front end of an animal
apical	at the tip

[1]**Note**: These definitions have been taken mainly from the 1989 edition of the *Torre-Bueno Glossary of Entomology* (Revised Edition 1989, compiled by S.W. Nichols: New York Entomological Society with the American Museum of Natural History). Many of the definitions regarding chironomids in Torre-Bueno were provided by Dr O.A. Sæther.

apotome	a single plate or sclerite (q.v.)
appendage	formally, any of the paired structures attached serially to the body segments of an arthropod; also any structure attached to another by a joint
arista	the bristle-like flagellum (q.v.) of the antenna in some adult dipterans
arthroideal membrane	(= arthrodial membrane): the soft membrane forming a hinge between sclerites (q.v.)
Australasian Region	the biogeographic region that includes Australia, New Zealand and nearby islands, New Guinea and parts of Indonesia (see Oriental Region)
basal ring of thoracic horn	the circular depression in which the thoracic horn is attached in chironomid pupae
beard	a beard-like group of setae on a sclerotised plate
benthic	pertaining to the bottom of a river, lake or wetland
bifid	divided into two branches
biotope	the smallest geographical unit of the biosphere or of a habitat that can be delimited by convenient boundaries and is characterized by its biota
brack(ish)	somewhat salty but less so than sea water
breathing horn	see *thoracic horn*
buccal cavity	see *oral cavity*
caudal	pertaining to the posterior, anal or 'tail' end
cephalic	belonging to or attached to the head
cephalic apotome	see *frontoclypeal apotome*
cephalic fan	a brush of filtering setae on the labrum of some aquatic dipteran larvae
cephalic horn	see *thoracic horn*
cephalic index	ratio of width to length of head capsule
cephalic tubercle	in pupal chironomids, any of the tubercles, mostly on the frontal apotome carrying frontal setae
cephalic wart	see frontal wart
cephalopharyngeal skeleton	in muscomorphs, the portion of head forming a heavily sclerotized, internal pharyngeal skeleton
cephalothorax	the united head and thorax (e.g. in dipteran pupae)
cervical	relating to the cervix or neck
chaeta	(pl. chaetae): usually an alternative term for 'seta' (q.v.) but in the entomological literature (and therefore in this volume) a non-articulated spine
chiton	(adj. = chitinous) a tough organic polymer that forms the basic structure of an arthropod cuticle
cleft	split

clypeus	that part of the insect head below the frons (q.v.) to which the labrum (q.v.) is attached anteriorly; in chironomid larvae, the part of the head carrying the S3 setae
cocoon	in many insects, a covering of the pupa, composed partly or wholly of silk
comb	a comb-like row of stiff setae or spicules
compound eye	an arthropod eye composed of many similar but separate light-sensitive facets
conjunctive	intersegmental (arthroideal) membrane
coprophagy	feeding on excrement
corona	a crown or crown-like process
coverslip	a thin square of glass placed over a specimen in a mounting medium on a microscope slide
creeping welt	one of the swollen transverse ridges on the anteroventral margins of abdominal segments I-VII (usually) with rows of minute sclerotized hooks, used for crawling
crest	a raised mid-dorsal ridge
cuticle	a secretion of the epidermis, covering the entire body of the insect: the exoskeleton
D seta	a dorsal seta on the tergite of a chironomid pupae
detritus	dead, broken up (usually organic) material
digitiform	finger-like
dioecious	having distinct sexes
distal	towards the free end of an appendage: that part furthest from the body
dorsal	the upper surface or 'back' of an animal
dorsomentum	see *mentum*
ecdysis	the process of moulting
eclosion	escape of the adult insect from the pupa, cocoon or puparium
ectoparasite	an external parasite
endemic	of a taxon, biogeographic distribution restricted to a particular given region
eutrophic	nutrient-rich
excavated	hollowed or scooped out
exoskeleton	the hard outer covering of an arthropod's body
extant	existing, living
exuviae	the cast skin of a larva or pupa (the word does not follow the usual Latin rules and is both singular and plural)
facet	one of the parts, areas or lens-like divisions of the compound eye of an insect

fenestra	literally a window: a transparent part of a membrane or sclerite (q.v.)
filarial worm	(= filaria): blood-dwelling parasitic nematodes
filiariasis	disease caused by filiarial worms (q.v.), often transmitted by blood-sucking dipterans
filter-feeder	an organism that feeds by filtering fine organic particles from the water
food chain	a sequence of organisms on successive trophic levels within a community, through which energy is transferred by feeding. Energy enters the food chain during fixation by primary produces (mainly green plants) and passes to the herbivores (primary consumers) and then to carnivores (secondary and tertiary consumers).
flagellum	the whip-like end of an antenna, consisting of few to many joints or segments
formalin	an aqueous solution of the gas, formaldehyde; full-strength formalin is 40% formaldehyde
frons	in dipterans, that part of the head extending from the base of the antennae to the upper base of the head; in larval chironomids this is called the frontal apotome
frontal apotome	in chironomid pupae, the plate in front of and covering the bases of the antennae, usually carrying frontal setae and often cephalic tubercles
frontal seta	S4 and S5 setae on the frontal apotome in larval chionomids
frontal wart	a wart-like tubercle on the frontal apotome of pupal chironomids (in addition to cephalic tubercles)
frontoclypeal apotome	in larval Diptera, fused clypeus (q.v.) and frontal apotome (q.v.)
frontofacial suture	in pupal dolichopodids, a suture or groove starting ventrally but visible behind the eye and antenna
gena	the part of the cranium on each side of the eye; in larval chironomids, the large sclerite on each side of the head (makes up the larger portion of the head except for the frontal apotome and the postmentum)
genital sac	in pupal chironomids, the sac covering the adult sex organs
gill	an external respiratory organ, usually finger- or plate-like structures offering a large surface area for gas exchange
Gondwanaland	during much of the Mesozoic Era (225-70 m years ago), a southern supercontinent consisting of continental blocks of South America, Africa, Madagascar, India, Antarctica and Australia
Gondwanian distribution	distributed throughout those continents or land masses that were originally part of Gondwanaland (q.v.)
granulose	covered with small, grain-like elevations
grub	(= maggot): a rounded, legless insect larva

gula	the fused lower ends of the postocciput (q.v.) forming a ventral plate
hair	a slender, flexible seta
haltere	in adult dipterans, the modified hind wings concerned with the maintenance of stability in flight
head	the first of the three tagmata or regions that make up the body of an arthropod, the other two being the thorax and the abdomen (q.v.)
head capsule	the fused sclerites of the head
Holarctic Region	biogeographic region combining the Palaearctic and Nearctic regions (q.v.)
holometabolous	of insects, having a life cycle with complete metamorphosis from larva through pupa to adult
homologous	of common evolutionary origin
hook row	in pupal chironomids, a row of hooklets (q.v.)
hooklet	(= hamulus): a tiny recurved spine
honey dew	sugary secretions of aphids (plant bugs)
horn sac	a long, apical diverticulum in the respiratory atrium of some chironomid pupae
hydrofuge hairs	water-repelling hairs at the tip of a respiratory siphon (q.v.) that break the surface tension and pierce the water surface
hypopharynx	a median lobe immediately behind the mouth; in larval chironomids it forms the dorsal part of the premento-hypopharyngeal complex, separated from the prementum by the salivary openings and part of the gena and in larval tanypod chironomids called the pecten hypopharyngis
hypostoma	in larval chironomids the anterior, more ventral part of the subgenal margin against the maxilla
hypostomium	see *mentum*
instar	a stage between moults in a nymph or larva
integument	(adj. integumentary): the outer layer of an insect comprising the living epidermis and the non-living cuticle
intestinal myasis	a disease caused by the infestation of dipterous larvae (which are not necessarily parasitic)
L seta	any of the lateral setae on the abdominal segments of chironomid larvae
labial palp	one of a pair of segmented appendages of the labium
labium	the fused second maxillae forming the floor of the mouth; in larval chironomids the mentum (q.v.) or premento-hypopharyngeal complex (*see* hypopharynx)
labral fan	paired, stalked fanlike bunches of setae laterally on the labrum in filter-feeding aquatic larval insects

labral lamella	one of several smooth to pectinate lamellae (sheets) between the setae anteriores (SI) on the labrum of larval chironomids
labrum	in insects, the upper 'lip', abutting the clypeus in front of the mouth
larva	an immature stage different in structure and habits from the adult
lateral tubule	one of the small, soft tubules projecting laterally on either side of segment X in some aquatic nematoceran larvae (cf. *ventral tubule*)
Lauterborn organ	in larval chironomids, paired compound organs at or near the apex of the second antennal segment, consisting of a peg sensillum (q.v.) and two series of digitiform, thin-walled extensions
leg sheath	the sheath around each leg of a dipteran pupa
leg	one of three pairs of jointed walking appendages in insects (lacking in immature diperans)
ligula	a sclerotized, toothed internal plate mid-dorsally on the floor of the mouth, conspicuous in in tanypod larvae but smaller in other chironomid sub-families
limpet	a flattened gastropod mollusc that adheres tightly to rocks
LS seta	specialized flattened taeniate (q.v.) setae on the posterior abdominal segments that enable chironomid pupae to swim at eclosion
M appendage	the medioventral appendage of the prementum in larval chironomids
macroseta	a seta conspicuously larger than adjacent setae
maggot	(= grub): a legless, apparently headless, larva
mandible	a jaw: either of the first pair of mouthparts in insects
maxilla	(pl. maxillae): either of the second pair of mouthparts in insects, usually with a jointed palp attached
maxillary palp	a jointed appendage of the maxilla
meatus	a channel or duct
mental	pertaining to the mentum (q.v.)
mentum	in larval chironomids a usually toothed, sclerotized, double-walled medioventral plate of the head capsule consisting of dorsomentum and ventromentum, which is often expanded into ventromental plates (q.v.)
mesial	towards the middle
mesothorax	in insects, the middle of three thoracic segments, bearing a pair of legs and the forewings (the true wings of Diptera) (see *prothorax* and *metathorax*)
metamorphosis	transformation: the drastic changes in form during development of a holometabolous (q.v.) insect from egg to adult

metathorax	the third thoracic segment, which bears the hind wings in most insects (but the halteres in Diptera) (see *prothorax* and *mesothorax*)
midrib	of a leaf, the central longitudinal rib; of aquatic dipteran pupae, the analogous structure on a swimming paddle
mitre-shaped	shaped like a bishop's hat
mouth hook	one of a pair of vertically-operating claw- or jaw-like structures of ectodermal origin in the mouth of a muscomorph dipteran larva; analagous to but probably not homologous with the mandibles of other insects
mouth brush	see *labral fan*
mouthparts	a collective term for the head appendages involved in feeding (ie the mandibles, maxillae and labrum)
myiasis	an infestation by larval dipterans, even if not normally parasitic
Nearctic Region	biogeographically the region including Alaska, Canada, Greenland, the continental United States and the Central Mexican Plateau (see Neotropical and Holarctic Regions)
negative pigmentation	a pale pattern on a dark background
nose	in some chironomid pupae, a distolateral projection of the wing sheath
notum	the dorsal surface of a thoracic segment
obtect	covered, concealed: of pupae, with the legs and wings adpressed to the body and unmovable
occipital arch	the area of the cranium between the occipital and postoccipital sutures, its dorsal part being the occiput and its lateral parts being the postgenae
occipital foramen	the opening at the back of the head through which the alimentary canal, the nerve chord, and some muscles, pass
occipital foramen	the passage between the back of the head and the thorax
Oriental Region	the biogeographic region that encompasses all of Asia and its islands, east of the Indus River and south of the Himalayas and south of the Palaearctic Region (q.v.) down to Wallace's Line, a hypothetical boundary between the Oriental and Australasian faunal regions proposed by Alfred Russell Wallace in the 19th century
oligochaete	earthworms and their allies
onchocerciasis	(= 'river blindness'): disease that can cause blindness in humans; caused by filarial nematode parasites, which are transmitted by blood-sucking blackflies
oral cavity	(=buccal cavity): the mouth
osmoregulation	maintenance of water and ionic balance
oviposition	egg-laying

paddle	one of the flattened anal lobes used for swimming in many pupal dipterans
Palaearctic Region	the biogeographical area encompassing Europe, Africa north of the Sahara, and Asia as far south as the Yangtze-kiang watershed and the Himalayas
Palaeogenic	a period roughly equivalent to the first two-thirds of the Tertiary period (about 66 m years ago), signifying of ancient origins.
palatal brush	see *labral fan*
palate	see *hypopharynx*
palmate	like the frond of a palm tree or the palm of a hand with finger-like processes
palp	an articulated branch, usually of a mouthpart
papilla	a soft, minute projection
paraligula	one or more sclerotised plates, rods or scales flanking the ligula (q.v.) at the ventral apex of the prementum in chironomid larvae
parapod	the term usually used for the prolegs (q.v.) in larval chironomids
parasitoid	an animal parasitic only in its immature stages
parthenogenesis	the development of an egg without fertilization
pathogenic	disease-producing
pearl row	a row of small blunt tubercles on the margin of the wing sheath in chironomid pupae
pecten	a comb-like series of setae, for instance on the siphon of culicid larvae
pecten hypopharynx	see *hypopharynx*
pedes spurii	'false legs' on the pupal abdomen
pedes spurii A	(in chironomids): a whorl of spinules at the posterolateral corners of segments IV to VIII (often only IV) in chironomid pupae
pedes spurii B	a posterolateral hump on abdominal segment II and sometimes also on III in chironomid pupae
pedicel	the second segment of the antenna, the segment that supports the flagellum
peg sensillum	of the Lauterbron organ (q.v.) of larval chironomids, a stiff, thick-walled peg at the apex of the second antennal segment
penultimate	next to the last
pinna	the 'ear-like' thoracic horns (q.v.) of some dipteran pupae
pharate	cloaked: within the cuticle of a preceding stage
pharyngeal	referring to the pharynx (q.v.)
pharynx	the part of the foregut between the buccal cavity and the oesophagus
physical gill	a bubble or film of air acting as a gill (also see *plastron*)
plastron	in aquatic insects, a film of air on the outside of the body, providing an extensive interface for gas exchange

plastron plate	a porous, apical plate on the thoracic horn of some chironomid pupae
pleuron	(Pl. = peura): the lateral part of a segment
pleurite	a sclerotized (q.v.) part of the pleuron (q.v.)
plumose	feather-like
point	in chironomid pupae, a minute spinule
point patch	(= shagreen): in chironomid pupae, a patch of minute spinules (points)
polytene	of chromosomes gigantic, containing many identical sets of DNA
positive pigmentation	a dark pattern on a pale background
posterior	towards the rear or tail of an animal
posteromedial	in the middle towards the rear
postgena	the lateral part of the occipital arch
postgenal bridge	a ventral bridge formed by the ventromedial fusion of the postgenae (q.v.)
postgenal cleft	an excavation in the postgenal bridge (q.v.)
postocciput	the extreme posterior rim of the cranium or head capsule
preanal segment	penultimate segment, often X in larvae and VIII in pupae
precorneal	in chironomid pupae, in front of the thoracic horn
predacious	predatory
prehensile	able to grasp, hold or seize
premandible	in some larval nematocerans, a pair of ventral structures attached to the labrum (q.v.) taking the form of toothed plates or processes
primary consumer	see *food chain*
prementum	in larval chironomids, the soft ventral lobe of the premento-hypopharyngeal complex (see *hypopharynx*)
prepupa	the active but non-feeding final instar of a pharate (q.v.) pupa
proboscis	an extended mouth structure or extensible mouth parts
procercus	a preanal tubercle, in larval chironomids carrying a number of apical and usually two lateral setae
process	an extension of a surface or margin
proleg	a soft, unsegmented leglike structure (=parapod)
pronotum	the dorsal surface of the prothorax (q.v.)
protozoans	single-celled organisms
prothorax	(adj. prothoracic): the first thoracic segment, bearing the anterior legs but no wings
proximal	that part of an appendage nearest to the body (cf. *distal*)
pseudopod	(= pseudopodium): in larval muscomorph dipterans, ventral locomotory welts (q.v.) produced into distinct protuberances covered with claw-like spines
punctation	pits or depressions in the cuticle
pupa	the inactive, non-feeding stage between larva and adult
pupal aster	in tabanids, the three pairs of large terminal spines froming a star shape

puparium	(pl. puparia): in some dipterans the sclerotized 'skin' (exuviae) of the last larval instar within which the pupa is formed
pupation	the act of becoming a pupa (q.v.)
qualitative sampling	see *sampling*
quantitative sampling	see *sampling*
rectal gill	see *anal gill*
respiratory siphon	the breathing tube of a culicine larva
respiratory horn	see *thoracic horn*
ring organ	in chironomid larvae, a circular campaniform sensillum on the basal segment of the antenna, mandible or maxilla
river blindness	see *onchocerciasis*
rugose	wrinkled
rugulose	minutely wrinkled
S seta	in chironomid larvae, any of the paired setae (usually labelled SI-SIV) on the labrum
sagittate	shaped like an arrowhead
saprophagous	feeding on fluids
sclerite	any plate of the body wall bounded by membrane or sutures
sclerotization:	hardening of the cuticle involving the development of crosslinks between protein chains
sclerotized	of the insect integument, hardened in definite areas by deposition or formation of other substances than chitin in the cuticula (see *sclerotization*)
sampling	the process of taking a sample: in ecological studies the purpose of sampling is often to obtain a subset of a population in a particular biotope (q.v.); the aim of qualitative sampling is to obtain a representative set of specimens (usually from particular taxa) present in the biotope; the aim of quantitative sampling is to obtain a numerical estimate of population levels of particular taxa in the biotope
secondary consumer	see *food chain*
sedentary	not freely-moving: attached to the substratum
segment	one of a series of repeated body units (strictly speaking, a somite)
sensillum	(pl. sensilla): a simple sense organ
serrate	with notched edges like the teeth of a saw
sessile	attached or fastened to the substratum and incapable of moving from place to place
seta	(pl. setae): a fine hair or bristle
seta interna	in larval chironomids, a pectinate (q.v.) seta on the inner dorsomedial edge of the mandible

setigerious	bearing setae (q.v.)
sexual dimorphism	the phenotypic (physical) differences between male and female of a single species
shagreen	in pupal chironomids, the pattern of spinules (points) on the abdominal segments
sheath	a structure enclosing other structures
sibling species	(= cryptic species): species with few or no morphologically distinct characters
siphon	in dipteran larvae, a long respiratory tube
somite	the correct technical term for a segment (q.v.)
species	for sexually reproducing organisms, a group of individuals that can interbreed with each other but are reproductively isolated from individuals of other populations: in general, individuals sharing a common gene pool
species complex	see *sibling species*
spinules	small spines
spiracle	an external opening to the tracheal system (q.v.)
spiracular	pertaining to the spiracles (q.v.)
spiracular apparatus	respiratory apparatus of anopheline mosquitoes
spiracular disc	posteriorly on the last segment, the disc-like area bearing the respiratory openings
spur	a large jointed spine
sternite	a sclerotized (q.v.) part of the sternum (q.v.)
sternum	(pl sternal, adj. sternal): the entire ventral surface of a segment
striation	stripes
sub-	almost
subcordate	more or less heart-shaped
subequal	almost equal
submental plate	see ventromental plate
submentum	the basal part of the labium by which it is attached to the head
sucker	an adhesive disc
supra-anal seta	in chironomid larvae, the seta dorsally on either side of the anal segment dorsal to the anal tubules
swim setae	the fringe of hairs on the anal lobes of some nematoceran pupae
swimming paddle	see *anal paddle, anal lobe*
taenia	(pl. taeniae): a ribbon-like seta
taeniate	flattened and ribbon-like
taxonomy	the theory and practice of classifying organisms
teneral	of an adult insect, after eclosion (q.v.) and before sclerotization and darkening occurs
tentorial rod	one of the rods making up the cephalopharyngeal skeleton of the head in muscomorph larvae

tergite	dorsal sclerite or the dorsal exoskeleton of a segment
tergum	(pl. terga): the upper or dorsal surface of a thoracic or abdominal segment of an insect
terminal disc	in some chironomids pupae, a disc formed from tergites VIII and IX
thoracic	of the thorax
thoracic horn	(= respiratory horn): in dipteran pupae, the variously-shaped and ornamented respiratory organ anterior on each side of the cephalothorax
thorax	the middle of the three tagma or regions making up the body of an insect and consisting of three segments: the prothorax, the mesothorax and the metathorax
trachea	(pl. tracheae): a spirally ringed, internal air tube, an element of the respiratory system
tracheal system	the respiratory system of insects (see *trachea*)
tracheal gill	a gill containing a trachea
trifid	split into three
truncate	cut off squarely at the tip
trumpet	in pupal Culicidae, the paired, usually moveable, dorsolateral appendage of the cephalothorax containing the mesothoracic spiracle
tubercle	a small protuberance
venation	the arrangement of veins in the wing of an insect
ventral tubule	(= ventral papilla): in chironomid larvae, any of one or two pairs of soft tubules on the last abdominal segment
ventral	of the lower or under surface of an animal's body
ventromental plate	the free lateral part of the ventromentum (q.v.)
ventromentum	the ventral wall of the mentum: lower and more proximal of the two transverse, usually projecting, subdivisions of the divided mentum (q.v.)
vibrissa	(pl. vibrissae): literally, whiskers: stiff, tactile hairs in adult dipterans on the facial ridge, which extends from the base of the antennae to the proboscis
wing sheath	the covering of the wing pad (q.v.)
wing pad	the encased developing wings in an insect pupa
yellow fever	an infectious tropical disease, affecting humans, that causes the skin to turn yellow
zoophilic	having an affinity for animals.

GLOSSARY OF PLACE NAMES

NEW PROVINCIAL NAMES IN SOUTH AFRICA TOGETHER WITH ABBREVIATIONS USED IN THE TEXT

Eastern Cape (EC)	formerly the eastern part of the Cape Province.
Free State (FS)	formerly the Orange Free State.
Gauteng (GT)	formerly the Pretoria/Witwatersrand/Vereeniging complex: part of the Transvaal.
KwaZulu–Natal (KZN)	formerly Natal, which included Zululand.
Mpumalanga (MPL)	formerly the 'eastern Transvaal'.
Northern Cape (NC)	formerly the north-western part of the Cape Province.
Limpopo (LIM)	formerly the 'northern Transvaal' (prior to 1994) and 'Northern Province' (from 1994–2002).
North West (NW)	formerly the 'western Transvaal'.
Western Cape (WC)	formerly the 'western Cape'.

ABBREVIATIONS OF OTHER COUNTRIES IN SOUTHERN AFRICA

BOTS	Botswana
LES	Lesotho
MWI	Malawi
MOZ	Mozambique
NAM	Namibia
SWZ	Swaziland
ZAM	Zambia
ZIM	Zimbabwe

REGIONAL NAMES

Bushmanland	(= Boesmanland): The north-eastern parts of Namibia, the south-western parts of Botswana and the drier northern areas of the Northern Cape.
Cape	One of the four former provinces of South Africa now named as follows: the north-western part is now the Northern Cape; the south-western part is now the Western Cape ; the eastern part, together with the former Ciskei and Transkei (qv), is now the Eastern Cape.
Caprivi	The north-eastern 'panhandle' of Namibia.
Damaraland	The west-central region of Namibia.
Delgoa Bay	(= Baia de Maputo): large bay on east coast of Mozambique, site of Maputo Harbour
Drakensberg Mountains	The mountain range stretching from the northern regions of the Eastern Cape through the highlands of KwaZulu–Natal, Lesotho and the eastern Free State to Mpumalanga.
Greater Namaqualand	The south-eastern part of Namibia (also see 'Namaqualand').
Griqualand East	Border region between the Transkei (qv) and KwaZulu–Natal.
Griqualand West	Arid region from Bloemfontein (Free State) westwards into the North West Province.
Highveld	High-altitude inland plateau characterized by grassland vegetation. Predominantly in Gauteng and the Free State.
Kalahari	The desert region of the northern North West Province, southern Botswana and south-eastern Namibia.
Karoo	Arid central region of southern Africa characterized by low scrub vegetation and very little grass cover: predominantly in the southern Northern Cape, the western parts of the Eastern Cape, the former Transkei (qv) and the northern border of the Western Cape.
Kaokoveld (Kaokoland)	The arid north-western coastal regions of Namibia.
Kruger National Park	Large nature reserve in the north-eastern region of Mpumalanga on the Mozambique border.
Makatini Flats	Pongola River floodplain, north-east of Jozini, Maputaland (q.v.)

Maputaland	Coastal plain in the north eastern region of KwaZulu–Natal and southern Mozambique, bounded by the Lebombo Mountains in the west and the Indian Ocean in the east.
Namaland	The coastal areas of the central Namib (qv) in Namibia.
Namaqualand	Arid region along the western parts of the Northern Cape and continuing into Namibia, where it is known as Greater Namaqualand (qv).
Namib Desert	The coastal desert of south-western Africa, extending roughly from the Orange River to Benguela in Angola.
Natal	One of the four former provinces of South Africa, which previously included the region variously known as Zululand and KwaZulu, now re-named KwaZulu–Natal.
Northern Province	One of the nine provinces of South Africa, now called 'Limpopo'.
Orange Free State	One of the four former provinces of South Africa, now known as the Free State.
Owamboland	(=Ovamboland): Northern region of Namibia.
Southern Cape	The southern coastal strip from Cape Agulhas in the west to Cape St Francis in the east.
Transkei	The region colloquially known as the Transkei is now part of the Eastern Cape Province, stretching from the Kei River to Port Edward on the KwaZulu–Natal border.
Transvaal	One of the four former provinces of South Africa: the north ern part is now the Northern Province; the eastern part is now Mpumalanga; the southern part is now Gauteng and the western region is now part of the North West Province.
Zululand	in KwaZulu–Natal, the eastern coastal belt and adjacent interior from the Tugela River to the Mozambique border .

INDEX OF SCIENTIFIC AND COMMON NAMES