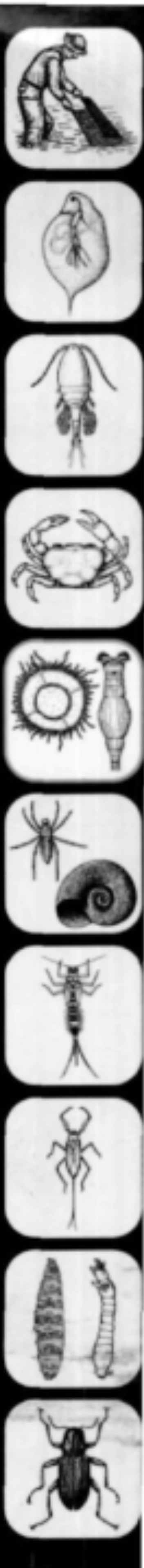
Guides to the

Freshwater Invertebrates of Southern Africa



Volume 5: Non-Arthropods

The Protozoans, Porifera, Cnidaria, Platyhelminthes, Nemertea, Rotifera, Nematoda, Nematomorpha, Gastrotrichia, Bryozoa, Tardigrada, Polychaeta, Oligochaeta and Hirudinea

Editors: JA Day & IJ de Moor

TT 167/02

Water Research Commission

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Prepared for the Water Research Commission

March 2002

WRC Report No. TT 167/02

Obtainable from:

Water Research Commission
PO Box 824
Pretoria
0001

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

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ISBN 1 86845 827 X

Printed in the Republic of South Africa

Cover photograph: '*The Olifants River, Mpumalanga, in the Lowveld Zone*' by F.C. de Moor.

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 in 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It is a truism that identification guides are perpetually out of date, particularly in terms of nomenclature, due to advances in systematics.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, and Irene de Moor was contracted to take on the job of 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 original authors were not paid for their efforts, which were given in the true spirit of science and a love of their work.

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 South African Museum and the WRC have given organizational support at various stages of the publication.

Three of the authors — John Day, Nancy Millard and Jan Oosthuizen — passed away some time before their manuscripts had been finalized, and Juan Heyns passed away suddenly in December 2001, at the time when this volume was in its final stages of production. Juan was able to see the final proofs of his chapter, but we are saddened by the thought that he did not live long enough to see this volume in print.

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 volume: Ferdy de Moor, Fred Gess, Sarah Gess and Helen James of the Albany Museum for providing constant advice on editorial and technical details relating to the systematics of freshwater invertebrates; Charmain Wynne for doing much of the page-setting; Nikki Köhly and Belinda Day for their excellent drawings of invertebrates and Nancy Bonsor for her assistance in tracing and touching up figures; Bronwyn Tweedie, Debbie Brody and John Keulder of the Graphics Services Unit, Rhodes University, for drawing the maps and producing bromides; Jenny Gon for compiling the index and for the use of her 'eagle eye' in spotting spelling discrepancies during this process, and Yuven Gounden of the WRC for his advice on printing and text layout.

Three of the original authors of chapters in this book — John Day, Nancy Millard and Jan Oosthuizen — passed away some time before their manuscripts had been finalized. We were fortunate in being able to call on the assistance of a number of authors — Jenny Day, Nancy Rayner, Chris Appleton and Mark Siddall respectively — who were able to 'fill in the gaps' in order to complete the chapters and prepare them for publication. Nancy Rayner and Jenny Day are also acknowledged for their willingness to take up the challenge and write outside their fields of expertise in order to cover little-known taxa such as the Nemertea, Nematomorphs and Tardigrada. The dedication of these authors is greatly appreciated.

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, 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 which often arises in association with regional names, a 'Glossary of place-names' has been compiled (see page 281), 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

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INTRODUCTION

'LOWER' INVERTEBRATES

by

J.A. Day

Although the majority of invertebrates that one is likely to encounter in inland waters are arthropods, many other taxa are also represented in these waters. They are generally less common than arthropods in terms of both numbers of taxa and numbers of individuals, although in some places certain species may occur in countless millions. While most aquatic arthropods are large enough to be readily visible at low magnification, some of the other forms are extremely small and cannot be seen, except with a good-quality compound microscope. For this reason, and because of the difficulties inherent in sampling and preserving many of them, the tinier forms are poorly known, particularly in regions like southern Africa, where the efforts of taxonomists have largely been directed towards the arthropods and molluscs.

Indeed, when discussing the contents of these volumes, the editors had to decide whether or not to attempt to cover all freshwater invertebrate taxa known to occur in the region, or whether to stick to those taxa for which experts (i.e. practising taxonomists) were prepared to write the chapters. We decided to cover all the taxa, even though we knew that coverage would be very uneven. In this way we could inform our readers about the state of the taxonomy of each group, even if that state was pretty poor. We are particularly grateful to the biologists who have contributed literature-based chapters on these poorly-known animal groups.

A NOTE ON THE TAXA TREATED IN THIS VOLUME

The taxa covered in this book include what zoologists sometimes call, rather unfairly, the 'minor phyla' and the 'lower' invertebrates as well as a number of 'major phyla'. The 'lower' invertebrates are so called because they are simpler in form than the 'higher' invertebrates (which include, among freshwater forms, the arthropods and the molluscs). The 'minor' phyla are those represented by few species, which occur only in obscure places, or are of uncertain affinities, or are difficult to study. In fresh waters these include the hydrozoans, the sponges, the nemertines, the nematomorphs, the tardigrads, the gastrotrichs, the bryozoans and the polychaetes, even though in the sea the sponges, the hydrozoans and the polychaetes are most definitely 'major' phyla. In contrast, the turbellarians, leeches, oligochaetes and rotifers are more speciose in, and probably contribute functionally far more to, inland waters than they do in the sea, while the nematodes and protozoans are ubiquitous and speciose in both environments.

A few words should be said about the systematic position of the protozoans. Although the phylum Protozoa used to be thought of as consisting of single-celled animals, these are now usually placed with other single-celled organisms, and the algae, in the Kingdom Protista. Some of them, particularly the ciliated forms, share important features with animals and so zoologists have tended to claim the animal-like forms. Thus the term 'protozoan' is still commonly used but has really become the common name for the animal-like protists and to most zoologists has no formal meaning.

IDENTIFYING THE TAXA TREATED IN THIS VOLUME

The key below serves to distinguish between the taxa treated in each of the chapters of this volume. For further information on the biology of these animals, the reader is referred to good invertebrate texts such as the earlier editions of Robert D. Barnes's *Invertebrate Zoology* (e.g. 1980), the more recent (but less detailed) *The Invertebrates: a New Synthesis* by Richard Barnes and co-authors, or the massive *Invertebrates* by Gary and Richard Brusca. Useful biological notes, as well as taxonomic information and keys, can be found in Pennak's invaluable *Freshwater Invertebrates of the United States*, particularly the third edition (1989).

Note that it is always difficult to provide a key that is technically correct in all details and at the same time is reasonably easy for non-specialists to use. Thus, this key is designed specifically to distinguish the members of each taxon that are known to occur in southern African inland waters. It will almost certainly not provide the right answers for certain taxa found outside of the region.

Protozoans

Protozoans occur wherever there is even the slightest film of water, so some are found in damp soil, others in inland waters and yet others in the sea. They are distinguished from all other organisms by the fact that each individual consists of a single cell, although they may form colonies of identical cells. While this distinction is clear from a functional point of view, without practice it is not always easy to tell by simple visual examination under a microscope whether an organism consists of one cell, or of many. This is at least partly because protozoans and other minute aquatic creatures are normally examined live, and it is not possible to see without staining them whether their bodies are divided up by cell membranes or not. In fresh waters, organisms most likely to be confused with protozoans are rotifers, some of the smaller turbellarian flatworms, and miracidium larvae of parasitic flukes. If a specimen that you are attempting to identify does not fit the protozoan key in Chapter 1, check on the figures in Chapter 4 and Chapter 6 to ensure that you are indeed dealing with a protozoan and not a minute multicellular animal.

Other minute ciliated forms

A number of minute ciliated creatures are not easily distinguished from each other because even though they may have very different internal structure, this is not easily discerned under the microscope. Thus, it is possible to confuse ciliates (i.e. ciliated protozoans) with rotifers, gastrotrichs and — most particularly — the miracidium larvae of flukes. The reader is advised to examine the diagrams in each of these chapters for confirmation of the identification of each of these forms. Generally, though, it is only some ciliates that can move by rotating the whole body, only the rotifers that have a 'crown' of strong cilia, and only miracidia that have a distinct pair of (usually bean-shaped), dark eyespots.

Worms

The worm-like (i.e. long and thin) creatures are usually fairly easy to tell apart, but very small ones *must* be examined under a compound microscope since this is the only way to see the segmental setae that are of diagnostic importance for the identification of oligochaetes.

KEY TO THE TAXA DESCRIBED IN THIS VOLUME

Many of the minute forms are best examined when still alive because their most characteristic features are aspects of their locomotion. Indeed, most of them become so distorted when preserved that it is difficult even for experts to be able to identify them.

1. Minute (0.01–1 mm)[1] single-celled organisms, details of structure visible only at magnification of 100x or more; movement by amoeboid creeping or by means of cilia or flagella[2]; occasionally colonial (e.g. Figs 1.3–1.31) (**protozoans**)[1] .... Kingdom PROTISTA (pp. 7–58)

– Multicellular organisms, usually somewhat larger (>0.5 mm) and often visible to the naked eye; moving by means of muscles (and/or cilia in the smaller forms); often wormlike or sessile 2

2. Sessile, entirely unable to move and stuck to the substratum, or able to move only by a very slow looping or creeping motion; not wormlike 3

– Free-living forms, mostly elongate, wormlike and benthic or interstitial, or radially symmetrical and planktonic (very occasionally minute forms inhabiting cases that limit movement) 5

3. Featureless or perforated by roughly equal-sized holes; encrusting on hard objects such as stems and stones (**sponges**) .... Phylum PORIFERA (pp. 59–73)

– Polypoid, often colonial, consisting of one to many individual polyps [tube-dwelling rotifers key out here: see couplet 8] 4

4. Polyps simple with about six to eight long, retractile tentacles; solitary, or forming a 'colony' consisting of a parent individual and up to four or five buds (**hydras**) .... Phylum CNIDARIA, Class HYDROZOA (pp. 74–87)

– Polyps numerous, small, complex, retractile (**bryozoans**) .... Phylum BRYOZOA (pp. 173–188)

5. Radially symmetrical, jelly-like, planktonic (**medusae**) .... Phylum CNIDARIA, Class HYDROZOA (pp. 74–87)

– Not radially symmetrical: usually wormlike, distinctly longer than wide and often with an obvious head end, or ovoid with a long, often forked, tail 6

6. Minute (<<1 mm), unciliated and planktonic with a long tail, or benthic or interstitial with four pairs of stubby 'legs' and usually a pair of eyes 7

– Variable in size; with neither four pairs of 'legs' nor a tail 8

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[1] Many of the organisms dealt with in this volume are extremely small and not only protozoans move by means of cilia; multicellular organisms usually show a clear gut and anterior and posterior end, however. Consult the figures in Chapters 4 (platyhelminthes), 6 (rotifers) and 9 (gastrotrichs) if you are in doubt.

[2] **Miracidium larvae** (Fig. 4.6) of flukes look very like ciliated protozoans but they are flattened and bilaterally symmetrical, they usually possess a pair of dark eyes and they glide along the bottom without rotating.

7. *Planktonic, with a flattened body and a long, sometimes forked, tail* (cercaria larvae of flukes) .... Phylum PLATYHELMINTHES, Class TREMATODA (pp. 92–110)

– Benthic or interstitial, with four pairs of stubby 'legs', and usually with a pair of eyes, giving the appearance of minute teddy bears; often in ephemeral waters (**water bears**) .... Phylum TARDIGRADA (pp. 189–192)

8. Minute (<2 mm); benthic or interstitial; body covered by a thin cuticle, apparently divided into sections, and/or in a tube, and/or covered with rows of spines or scales; usually with a short pair of projections forming a furca (tail fork) or a pair of 'toes' posteriorly 9

– Large or small; wormlike; body covering various; no posterior toes or furca 10

9. Anterior end bearing a whirling 'corona' of cilia used for feeding; locomotion by means of coronal cilia or leech-like creeping; posteriorly with a pair of toes whereby the individual attaches to the substratum when feeding or creeping; may live in a tube (**rotifers** or **wheel animalcules**) .... Phylum ROTIFERA (pp. 116–135)

– Body covered dorsally with rows of spines or scales; usually with a furca able to attach to the substratum; cilia anteriorly as tufts and ventrally as long rows; locomotion is smooth ciliary gliding; no tube (**gastrotrichs**) .... Phylum GASTROTRICHA (pp. 166–172)

10. Body elongate, usually many times longer than wide, tough and wiry, circular in cross-section, with a firm cuticle, usually entirely without ornamentation; movement confined to a writhing motion 11

– Body wormlike but not always many times longer than wide and not always circular in cross section, muscular rather than wiry, and not with an obvious cuticle; may be segmented and/or bear setae; forms of movement various 12

11. Large, elongate worms, >100 mm long and 2–3 mm wide, usually dark in colour, often found in tangles of two or more worms in swimming pools (**nematomorphs**) .... Phylum NEMATOMORPHA (pp. 162–165)

– Small worms, usually <10 mm long, spindle-shaped and transparent; usually interstitial or benthic (**nematodes**) .... Phylum NEMATODA (pp. 136–161)

12. Body divided into a number of repeated segments, each with two or four bundles of setae (NB: in smaller forms, segmentation and setae may be visible only under a compound microscope) 13

– Body unsegmented, or segmented but without segmental bundles of setae 14

13. Each segment with a pair of lateral parapodia bearing numerous setae and/or setal bundles, including hooded hooks (Fig. 12.1B,C); head usually bearing tentacles and often jaws; no clitellum; large worms (>10 mm) found in the upper reaches of estuaries and in coastal lakes (**polychaetes**) .... Phylum ANNELIDA, Class POLYCHAETA (pp. 193–202)
– Parapodia lacking; bundles with few setae and no hooded hooks; no tentacles or jaws; clitellum often present; very small (1mm) to large (up to 100 mm) (**oligochaetes**) .... Phylum: ANNELIDA, Class: OLIGOCHAETA (pp. 203–236)
14. A sucker present at both the anterior and the posterior end of the body; body may show traces of segmentation (**leeches**) .... Phylum ANNELIDA Class HIRUDINEA (pp. 237–263)
– No suckers; body may seem to be segmented but it is merely the diverticula of the gut showing through the unsegmented body wall 15

15. Body strongly muscular, pale in colour and oval in cross section; mouth anterior, sometimes with a long simple proboscis projecting from it; anus terminal; several small black eyes dorsolaterally on head (**proboscis worms**) .... Phylum NEMERTEA (pp. 111–115)
– Body muscular or not, flattened, variable in colour; mouth usually ventral with no proboscis; no anus; eyes one pair or absent (**flatworms, planarians**) .... Phylum PLATYHELMINTHES, Class TURBELLARIA (pp. 89–92)

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CHAPTER 1

THE PROTOZOANS

by

J. Heeg

Protozoans can conveniently be defined as single-celled eukaryotes: organisms that carry out all essential life activities within the confines of a single cell membrane enclosing one or more membrane-bound nuclei. They may form clonal colonies in which, with few exceptions, all individuals are identical and able to function as independent units.

Until recently, all organisms conforming to the above definition, whether autotrophic or heterotrophic, were included in a single phylum, the Protozoa, established by von Siebold in 1845. This tradition is followed in all older and several current school and elementary university textbooks. Studies since the advent of the electron microscope, and of more sophisticated light microscopy, have emphasized and re-evaluated differences between what were originally regarded as the four constituent classes (or later, sub-phyla) of the phylum Protozoa; today four (or six, depending on authority) distinct phyla, all conforming to the above definition, are recognized as constituting the sub-kingdom Protozoa of the kingdom Protista, which it shares with the 'algae'. The term 'protozoa' must therefore be accepted as merely a useful collective noun for these phyla, of which only two, the Sarcomastigophora and Ciliophora, are represented in freshwater habitats. The remaining phyla, the Apicomplexa and Cnidospora, previously regarded as sub-classes of the class Sporozoa, are entirely comprised of parasitic species.

BIOLOGY

Protozoans are ubiquitous; most, if not all, free-living genera and many species, although constrained by environmental factors, are thought to be cosmopolitan in their distribution (Lee et al., 1985). They are found in all natural and most man-made freshwater habitats. Their small size — freshwater species seldom exceed 1 mm in their greatest dimension — is a major factor in almost every aspect of their biology in that it imposes a very high surface:volume ratio on them, rendering them extremely sensitive to their physical and chemical environment, and placing constraints on the sizes of particles that they are able to ingest. Yet, despite this, protozoans exhibit all the major lifestyles found among multicellular organisms, making it impossible to generalize on all but a few aspects of the biology of the assemblage as a whole. Their nutrition can be autotrophic, heterotrophic or both; some species are microphagous, others macrophagous; they may be sedentary, epizoic or vagile; filter-feeders, detritivores or active predators. Bacteria are an important food source for heterotrophic protozoans; thus they play an important role in the decomposition of organic matter in aquatic environments; the microbial loop (detritus →minerals + bacteria →protozoans →detritus) may account for a large proportion of detritus breakdown and mineralization within the water column of both natural and man-made aquatic ecosystems. Sedentary filter-feeding ciliates, such as *Vorticella* and *Stentor* commonly form components of filter beds in sewage works. Autotrophic flagellated protozoans, as part of the phytoplankton, contribute to the productivity of the plankton community, particularly as food for planktonic crustaceans which, in turn, are fed upon by fish. Pelagic fisheries such as those targeting *Limnothrissa miodon* on Lakes Tanganyika and Lake Kariba are largely dependent upon such a food chain.

All protozoans are able to reproduce asexually by means of binary fission and are thus able to multiply rapidly under favourable conditions. Sexual reproduction is known to occur in at least some representatives of the Sarcomastigophora and Ciliophora. It is usually triggered by a change in environmental conditions such as a deterioration in the food supply, a temperature change or a spatial restriction and often precedes encystment. Conjugation, which broadly follows the animal pattern of sexual reproduction in that it involves an exchange of meiotically-produced, haploid pronuclei between two individuals, is known to occur in many Ciliophora and is probably common throughout that phylum. Among the haploid Phytomastigophorea of the phylum Sarcomastigophora, plant-like sexual reproduction, involving the fusion of mitotically-produced gametes, has been observed in all families of the order Volvocida. A few individual species scattered among the sub-phylum Sarcodina, particularly among the Foraminifera, are known to have alternating sexual and asexual generations, but information on the rest is sparse and often anecdotal: most seem to reproduce only asexually by binary or multiple fission.

Several environmental factors have been identified as determining the composition of the protozoan community in any particular water body. These include water movement, the nature and quantity of dissolved gases (e.g. oxygen, carbon dioxide, hydrogen sulphide etc.) and solids, pH, temperature, and the degree of enrichment (trophic status) among others. Generalizations can really only be made regarding the effect of water movements, all other factors apparently acting, either directly or indirectly, at the level of individual species. In terms of their life styles, protozoans may be divided broadly into swimming, creeping and sedentary forms. Because of their small size and consequent high surface:volume ratio, they inhabit an environment where frictional forces predominate and even the best swimmers among them rarely attain speeds exceeding 2 mm/s. Swimming forms are therefore severely restricted by current speed in running water where they are at a risk of being swept downstream, unless they inhabit the boundary layer close to the bank or bottom where friction causes a velocity gradient which falls to zero. Since the thickness of the boundary layer decreases as current speed increases, the rate of flow in a stream determines its potential species richness: the slower the rate of flow, the greater the number of species that can maintain their positions in the stream. It follows that water bodies, such as swamps, ponds and lakes, will support the greatest diversity of protozoans. In such environments one finds swimming forms throughout the water column as part of the plankton community, while creeping and sedentary forms occur on the substratum, on submerged plants and as part of the neuston, where the surface tension at the air-water interface provides an effective purchase. Each of these habitats is unlikely to be uniform in its physical, chemical and biotic conditions. Thus, within them one may find varying degrees of spatial heterogeneity in the protozoan community. A broad summary of the habitat preferences of the genera mentioned in this chapter is given in Table 1.1.

A further effect of their high surface:volume ratio is that protozoans are poorly buffered against physical and chemical conditions in their surroundings: while the comparatively large surface area permits ready ingress of such essentials as oxygen and dissolved nutrients, it renders them equally susceptible to toxic solutes. The plasma membrane must perforce be permeable to water, since oxygen and carbon dioxide need to pass through it in solution. Protozoans are, therefore, sensitive to osmotic pressure: freshwater species are typically hyperosmotic to their surroundings, and need to counter the influx of water by pumping out the excess by way of one or more contractile vacuoles. However, if the external osmotic pressure should increase, as would happen under conditions of sustained evaporation, they are prone to rapid water loss, and the final drying up of

Table 1.1: Summary of the occurrence in various freshwater habitats of the genera included in the key *

Genus	Habit	Benthic		Planktonic		Neuston
		Detritus & algal mats	Epiphytic on macrophytes	Vegetated margins	Open water, ponds, lakes	
Actinophrys				+++	+++	++
Actinosphaerium				+	+++	++
Amoeba		+++	++			
Arcella		+++	+++			++
Blepharisma				+++	+++	
Bodo		Common in bacteria-rich water with lowered oxygen levels				
Carchesium	Sed. Col.	++	++			
Carteria		++		++	++	
Centropyxis		++	++			+
Ceratium				+++	+++	
Chaos		See comment in key				
Chilomonas		++		+++	+++	++
Chlamydomonas				+++	+++	++
Chromulina				++	++	
Clathrulina		+	+			
Codonosigidae	Sed. Col.	++	++			++
Colacium	Sed. Col.	++	++	Epizoic, particularly on copepods		
Coleps		++		++	++	
Colpidium		++		++	++	
Colpoda		Common in bacteria-rich water				
Cryptomonas				++	++	++
Didinium		++		++	++	
Difflugia		++	++			++
Difflugiella		++	++			
Dileptus		++		++	++	
Dinamoeba		++	++			
Dinobryon		++	++			++
Epistylus		++	++			
Eudorina	Col.			+++	+++	
Euglena		++		+++	+++	
Euglypha		++	++			
Euplotes		++	++			++

* From personal observations and various literary sources.

Table 1.1 (cont.)

Genus	Habit	Benthic		Planktonic		Neuston
		Detritus & algal mats	Epiphytic on macrophytes	Vegetated margins	Open water, ponds, lakes	
Gonium	Col.			+++	+++	
Gymnodinium				++	+++	
Haematococcus				+++	++	++
Halteria		++		++		
Lacrymaria		++		++	++	
Loxodes		++		++		
Mallomonas				++	+++	
Mayorella		++	++			++
Ochromonas				++	+++	
Opercularia	Sed. Col.	++	++			
Pandorina	Col.			++	++	
Paradileptus				++	++	
Paramoecium		++		++	++	
Pelomyxa		+				
Peranema		++		++		
Peridinium				++	+++	
Phacus		++		++	++	++
Prorodon				++	++	
Salpingoecidae	Sed.	+	+			
Spirostomum		++		++		
Stentor	Sed.	++	++			++
Stylonychia		++	++	++		++
Synura	Col.			++	++	
Tetrahymena		++		++		
Trachelius				++		
Trachelomonas		++		++	++	
Vaginicola	Sed.	++	++			
Volvox	Col.			+++	+++	
Vorticella	Sed.	+++	+++			++

KEY: Col. = colonial; Sed. = sedentary; +++ = common; ++ = present; + = rare the habitat would result in almost immediate lethal desiccation. All freshwater species studied so far react to such adverse conditions by a process of encystment — the secreting of an enclosing impermeable shell. In the encysted state protozoans drastically reduce the rate of all metabolic processes and can survive most potentially lethal conditions, including the drying up of the habitat, changes in osmotic pressure, and high and low temperatures. Several species are known to survive in the encysted state for a number of years, and can be effectively dispersed by wind, or in mud and organic debris on water birds and other animals. This may account for the apparent worldwide distribution of so many well-known genera as well as their survival in temporary water bodies, even those that are inundated only once in several years.

As a result of their potential for rapid multiplication, together with their sensitivity to both favourable and adverse environmental conditions, protozoan communities are seldom static. Over a given period, resources at a particular trophic level may become depleted, predation from a higher level may be encouraged or conditions may be modified to favour a competing species, all of which may cause species to disappear from a community or to be replaced by others. Such effects may be localized through habitat heterogeneity and are likely to be short-term, or they may be sustained over longer periods where conditions are uniform. The result of this is a succession of dominance within the community. Lee et al. (1985) give a typical succession of protozoans associated with decaying organic matter: small zooflagellates and the ciliate *Colpoda* →small ciliates →large swimming and crawling ciliates and peritrichs →autotrophic flagellates and large swimming ciliates. This succession is accompanied by a succession of creeping amoeboid species. Different conditions will give rise to different succession patterns; one must expect both spatial and temporal differences in the structure of the protozoan community of any particular water body.

COLLECTING

The simplest method of collecting protozoans from shallow astatic waters such as a pond or a lake margin, is to fill a large, wide-mouthed glass jar (e.g. a 1 litre domestic preserve jar) with water from the habitat in such a way as to incorporate the full extent of the shallow water column in the sample. This is best achieved by scooping, and ensuring that some bottom debris and submerged plant material is incorporated in the sample. Care must be taken that strongly reducing sediments, characterized by the smell of hydrogen sulphide, are not included in the sample, as almost all protozoans are intolerant of low oxygen and high sulphide concentrations.

Allowing the jar to stand in a well-lit location, but not in direct sunlight, for three to four days results in a mixed culture in which the protozoans establish a distribution pattern, which presumably reflects that in the natural habitat. Samples for study can be withdrawn from various levels in the mixed culture by means of a Pasteur pipette, taking care to create as little disturbance as possible. Sampling a mixed culture over a period of time will usually show a succession, but whether this reflects succession in the natural habitat is debatable, since changes in the physical and chemical conditions in a jar are likely to be very different from those in the natural habitat.

The protozoan community of temporary water bodies can be effectively studied by collecting dry surface sediment samples, which include not only encysted protozoans, but also the resting eggs of rotifers, gastrotrichs and crustaceans, and resting spores of algae. These resting stages can all be activated by the addition of distilled water, or preferably rainwater where this is not likely to be contaminated by urban air pollution. Good results can be obtained by initially just moistening a 5 mm layer of the sediments in a 500 ml beaker, leaving it in a warm, well-lit position for one or two days, and then carefully adding water to a level of about 8–10 cm in stages over a period of three days. Frequent sampling of such a culture usually shows a marked succession of protozoan taxa over time.

Individual zones and specific substrata within shallow water bodies can be sampled by means of an aspirator or Noland's apparatus (Fig. 1.1). Controlled suction on the mouthpiece draws water, together with contained micro-organisms, into the aspirator via the intake nozzle, which can

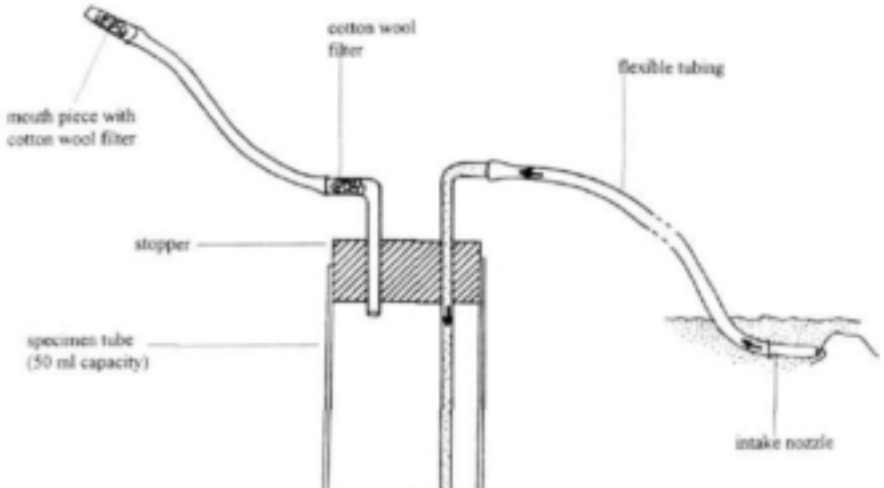


Fig. 1.1. Noland's apparatus: a simple aspirator for collecting protozoans from specific surfaces or at specific depths.

be directed at a specific micro-habitat. Cotton wool filters in the suction tube are necessary to prevent the possible intake of pathogens by the collector, and should be replaced after each collecting trip.

The vertical distribution of protozoans in large water bodies such as lakes can only be investigated by using specialized collecting equipment. A composite sample of at least the top few metres of the water column of a lake can be collected using a hose pipe sampler: a length of hose pipe with a stout cord fixed to one (distal) end is lowered vertically into the water column, distal end first. Once the full length of the hose pipe is submerged, the proximal end, which should be just below the surface, is closed by simply pressing the thumb firmly over the opening and the distal end is hauled in by means of the attached cord. The hose pipe now contains a composite sample of the water column, from the surface down to a depth equal to the length of the hose pipe, which can be poured into a suitable container through the distal end by releasing the thumb on the proximal end. Vertical descent of the hose pipe can be facilitated by the attachment of a suitable weight below the distal end. This sampling method is used to good effect by algologists and should work equally well for collecting protozoans. Small pieces of an artificial substratum such as foam rubber, suspended in the water column at different levels from an anchored float or buoy and left in place for a few days, can be used to concentrate those protozoans, transient in the water column, that prefer a solid substratum.

Quantitative analysis of communities requires bulk fixation and concentration of samples, both of which can cause considerable distortion of protozoans, rendering identifications difficult if not impossible. Specialist literature (e.g. Joska et al., In Press) should be consulted on the treatment of quantitative samples.

EXAMINATION

Freshwater protozoans range in size from less than 10 µm to 3 000 µm (3 mm), the majority of species falling between 30 and 150 µm. A compound microscope with a x 10 ocular lens and at least x 10 and x 40 objectives is required for their study; a x 3 objective is useful for scanning a sample, while a x 90 –100 oil-immersion objective is essential for discerning fine detail. Dark-field illumination, phase contrast and interference contrast are useful additions, but not essential except for the specialist researcher.

Wherever possible, protozoans should, at least initially, be viewed alive, since fixation and other preparative processes frequently distort specimens and obscure essential details, even when carried out by experienced technicians. Examination of living material, particularly swimming forms, is difficult because they are constantly moving into and out of the field of view; hence they need to be restrained. The following methods are simple and have proved to be consistently successful.

Trapping in cotton wool

Tease out a *small* quantity of cotton wool on a microscope slide. Ideally, there should be a criss-crossing layer, one to two strands thick, forming a meshwork with apertures 1.0 to 1.5 mm in diameter (i.e. approximating the field of view of the microscope with the x10 objective in place) and covering an area about equal to that of the coverslip to be used. Place a drop of culture on the cotton wool and cover with a coverslip.

Slowing with methyl cellulose

Prepare a 10% solution of methyl cellulose in distilled water. Using a thin glass rod, make a ring of this viscous solution on a slide; the *outside* diameter of the ring should equal the diameter of the coverslip to be used. Place a drop of culture in the centre of the ring, and cover with the coverslip. The methyl cellulose from the ring will slowly diffuse into the culture sample, rendering it more viscous and slowing down the protozoans, thus making observation easier.

Fine particle suspensions

Cilia and flagella cannot normally be seen in the living protozoan unless sophisticated light microscopy techniques such as interference contrast are used. Their presence can, however, readily be inferred by mixing a small quantity of a suspension of carmine particle, or even indian ink, with a drop of the culture and observing the movement of particles around the animals. Cilia create a streaming of particles over the surface of the animal, whereas waves travelling along the length of a flagellum show up as displacements of the particles conforming to the wave movement.

Many protozoans will ingest the suspended particles, taking them in through the *cytostome* or 'cell mouth' to form a food vacuole. Fine particle suspensions therefore also assist in identifying these organelles.

STAINING METHODS

Details not visible in the untreated living specimen can be shown by suitable staining. Many stains, specific for particular organelles, are used by protozoologists, but these fall beyond the scope of this chapter. The following simple methods are, however, useful aids in the identification of protozoans when using the keys provided here.

Vital staining

Mixing a small quantity of a 0.01% aqueous Neutral Red solution with a drop of the culture on a microscope slide will stain the nuclei and food vacuoles of most protozoans without killing them. Janus Green at the same concentration, and applied in the same way, will show up mitochondria. Nile Blue Sulphate is a useful general vital stain which slows down protozoans before killing them.

Methyl Green

Acetic Methyl Green (0.5% w/v in 1% acetic acid) is a useful nuclear stain. Place a small drop at the edge of the coverslip and allow it to diffuse into the sample of living protozoans. This method is particularly good for showing up the macronucleus of ciliates without the necessity for fixation and other pre-treatment, but it does kill them.

Nigrosin

In order to see surface structures of ciliates, particularly cilia, undulating membranes and membranelles, mix a *small* drop of the culture with an equal volume of a 10% w/v aqueous Nigrosin solution near one end of a microscope slide coated with a *thin* layer of human saliva. Spread the mixture thinly by dragging it over the slide as you would a blood smear, and allow it to dry thoroughly in air before mounting under a coverslip with DPX or any other suitable mountant. Alternatively, the slide may be left uncovered for direct viewing with an oil immersion objective.

The above techniques are sufficient for routine examination of protozoans and their identification using the keys provided in this chapter. The specialist literature should be consulted for further methods, particularly those pertaining to making permanent preparations.

IDENTIFICATION AND CLASSIFICATION

The identification keys included in this chapter are designed to identify those protozoan genera which, in the author's experience, occur at least regularly, if not commonly, in pond samples collected from the coastal regions and midlands of Kwa–Zulu Natal, and to a lesser extent, from the Eastern Cape and the south-western Cape. It must be stressed that genera which have only been encountered occasionally in these regions may well be common elsewhere and *vice versa.* Most genera included in the keys do, however, occur commonly in lakes and ponds in the Northern Hemisphere, suggesting that they are likely to be common everywhere. The number of described protozoan species is conservatively estimated by various authors as 50 000, a number exceeded only by that of the insects and possibly the molluscs. This, together with the apparent cosmopolitan distribution of most genera, makes it very likely that any sample will contain some genera not included in the key, which must be regarded as merely a first guide to the identification of common genera. In cases of doubt, or where accurate identification is crucial, more comprehensive works, of which there are many, should be consulted. Lee et al. (1985) is perhaps the most up-to-date comprehensive text, Corliss (1979) is an excellent synoptic work on the Ciliophora, and both Ward & Whipple (1959) and Pennak (1989) have the advantage of including only freshwater genera. Although much has been published on pathogenic/parasitic protozoans in South Africa, free-living forms have received little attention from researchers apart from the list of common taxa found in the Western Cape, compiled by Joska et al. (In Press).

The classification of protozoans has undergone considerable revision in recent years, the latest near-consensus version probably being that used in Lee et al. (1985). This classification, often based on observations made with highly sophisticated equipment and techniques, differs materially from that found in most school and university texts: it uses much new and unfamiliar terminology, and is extremely complex. Such a classification becomes both unwieldy and bewildering to the non-specialist. In the compilation of this chapter, I have tended towards conservatism: the classification scheme used in the keys is a modification of the older system of protozoan classification and the morphological terminology is, for the most part, that which is to be found in standard zoology texts. Users should be aware that this has been done for the sake of expediency, and that a given genus may well belong in a higher taxon different from that given here. This should further stress the need to consult more comprehensive literature where accurate up-to-date classification is important. It must also be pointed out that several taxa which fall within the definition of the phylum Sarcomastigophora, but include autotrophic species, are included in the botanical literature as 'algae', a term which, like 'protozoa', has now lost its systematic relevance. Where a taxon has, in the past, been commonly referred to in the botanical literature, the botanical equivalent of the zoological nomenclature used here is given in parenthesis following the name.

The references cited are but a few of the considerable number published. The choice is based solely on what I have found particularly useful among those available to me. Most guides to the freshwater faunas of the Northern Hemisphere include a section on protozoans, and their keys have, in many instances, been prepared by specialist protozoologists. These are, for the most part, much more inclusive than the keys in this chapter, as the protozoan fauna of southern Africa is almost unknown when compared to that of Europe and North America. A few of these more comprehensive guides have been included in the list of references: these, and others not mentioned but to which the user may have access, should be consulted where this chapter proves to be inadequate for the identification of a particular specimen.

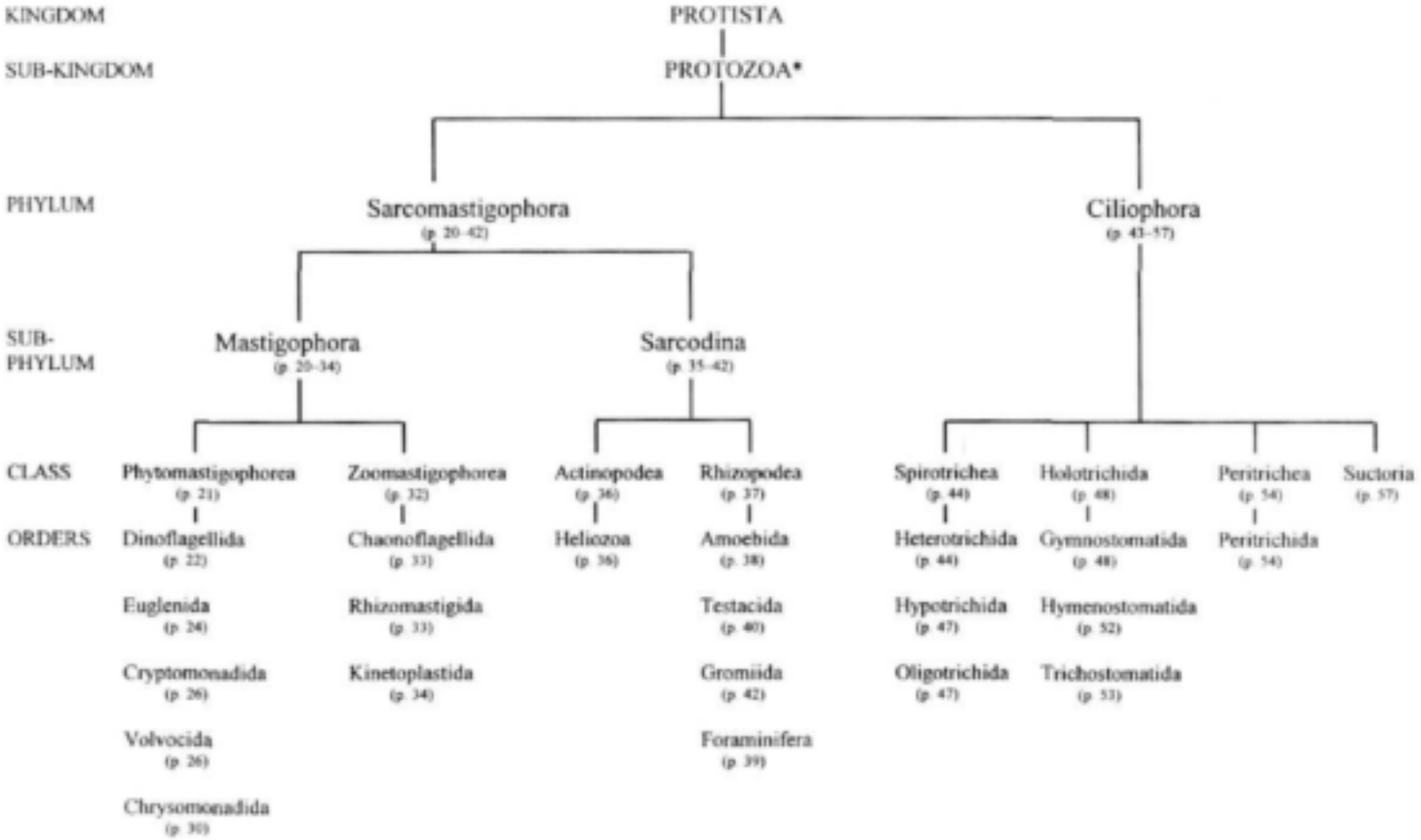
KEYS TO FRESHWATER PROTOZOANS

The following keys should enable the user to identify many of the commonly-occurring protozoan genera as well as a few which, while not necessarily common, are of special interest and are known to occur in southern Africa. They have been designed in such a way that, where a genus of a particular specimen is not included, it will in most cases be possible to assign it to its appropriate order, and sometimes family. The system of classification of protozoans used in the keys is summarized in Fig. 1.2.

PROTOZOA: KEY TO PHYLA

1. Cilia never present, movement by flagella or pseudopodia; usually a single nucleus but, where multinucleate, nuclei almost always monomorphic; may be autotrophic or heterotrophic .... **Sarcomastigophora** (Page 20)

– Movement by cilia or organelles derived from cilia; bi- or multinucleate; nuclei dimorphic with usually a single large polyploid macronucleus and one or more haploid micronuclei; typically heterotrophic, but may contain symbiotic, pigmented autotrophs enclosed in vacuoles .... **Ciliophora** (Page 43)



***Note**: The system of classification used here (including the taxon 'Protozoa') is no longer widely accepted, but it is used here for convenience (for reasons explained in the text).

Fig. 1.2: The higher classification of protozoans with cross references to pages where taxa are described in this chapter.

PHYLUM: SARCOMASTIGOPHORA

The Sarcomastigophora includes all amoeboid and flagellated protozoans previously included in the classes Sarcodina, Mastigophora and Opalinida of the phylum Protozoa. The existence of flagellated amoebae, as well as species that are able to change from a benthic amoeboid form to a pelagic flagellated form, has resulted in most authorities including these apparently very different organisms in a single phylum.

KEY TO THE SUB-PHYLA OF SARCOMASTIGOPHORA

1. Cell form fixed by an outer pellicle; one or more flagella present, or where flagella absent, chloroplasts present; binary fission in the longitudinal plane; autotrophic or heterotrophic; solitary or colonial.. **Mastigophora** (Page 20)
– Movement by pseudopodia even when a flagellum is present, hence cell form not fixed and fission plane indeterminate; never colonial; heterotrophic .... **Sarcodina** (Page 35)

SUB-PHYLUM MASTIGOPHORA

Includes all flagellated protozoans, whether autotrophic or heterotrophic, and as such is probably an artificial assemblage. Flagellates usually constitute the major part of any protozoan community and are, for the most part, difficult to identify beyond the level of order without resorting to ultrastructural features. This is particularly true for small colourless species. Many autotrophic flagellates can assume a palmella form in which the flagella are lost.

KEY TO THE CLASSES OF MASTIGOPHORA

1. Colourless flagellates 2
– Pigmented autotrophs with distinct chloroplasts .... **Phytomastigophorea** (part) (Page 21)

2. Solitary 3
– Colonial, sedentary, usually stalked .... **Zoomastigophorea** (part) (Page 32)

3. Distinct reservoir or gullet from which flagella arise .... **Phytomastigophorea** (part) (Page 21)
– No reservoir or gullet 4

4. Cingulum with transverse flagellum present (Fig 1.3A) .... **Phytomastigophorea** (part) (Page 21)
– No cingulum .... **Zoomastigophorea** (part) (Page 32)

CLASS: PHYTOMASTIGOPHOREA

Includes all autotrophic flagellates (phytoflagellates) with distinct chloroplasts, as well as related colourless heterotrophs. The orders included in the class are extremely diverse, particularly at the ultrastructural and biochemical levels, suggesting that the class is an artificial assemblage of distantly related taxa.

KEY TO THE ORDERS OF PHYTOMASTIGOPHOREA

1. Colonial 2
– Solitary 4

2. Flagella absent 3
– Flagella present 7

3. Individuals embedded in a simple mucilaginous matrix, usually arranged in pairs as a consequence of cell division .... 'palmella' stages of various orders (no further keys)
– Individuals, each with a flask-shaped reservoir, form a dendriform colony (Fig. 1.4B, C); colour grass-green; often epizoic .... **Euglenida** (part) (Page 24)

4. Cingulum and sulcus present (Fig 1.3A– C) .... **Dinoflagellida** (Page 22)
– Cingulum and sulcus absent 5

5. A distinct gullet or a reservoir from which the flagella arise 6
– No reservoir or gullet, flagella arise from the cell surface 7

6. Reservoir flask-shaped, small relative to cell body length (e.g. Fig 1.4A– D); cell body length usually > 50 μm; colour, when pigmented, grass green .... **Euglenida** (part) (Page 24)
– Prominent sac-like gullet, often extending half the cell body length (Figs 1.5A, B); cell body small, usually <40 μm, ovoid or barrel-shaped; colour, when pigmented, olive green to brownish .... **Cryptomonadida** (Page 26)

7. Cell body enclosed in a distinct cell wall through which the flagella pass; bright, grass-green colour may be masked by red carotenoid pigment .... **Volvocida** (Page 26)
– Cell body not enclosed in a cell wall but may have a covering of ornate scales up to 10 μm long, often with prominent projecting spines, or be enclosed in a lorica; colour, when pigmented, yellow-brown to golden .... **Chrysomonadida** (Page 30)

ORDER DINOFLAGELLIDA

(Dinophyceae in the botanical literature)

Unique features of the dinoflagellates include the cingulum with its transverse flagellum, the sulcus with its trailing flagllum, and features of the nucleus not normally visible through the light microscope. Although unarmoured genera occur in fresh waters, the common genera are readily distinguished from all other freshwater protozoans by the thick cellulose thecal plates that enclose the protoplast. Autotrophic and heterotrophic forms occur.

DINOFLAGELLIDA — KEY TO TAXA

1. Well-developed thecal plates enclose the cell (**Peridiniidae**) 2
– No thecal plates (**Gymnodiniidae**) .... *Gymnodinium* (Fig 1.3A)

2. Compressed; single prominent apical horn and one to three horns at the opposite end .... *Ceratium* (Fig. 1.3B)
– Form rounded; horns, if present, not prominent .... *Peridinium* (Fig. 1.3C)

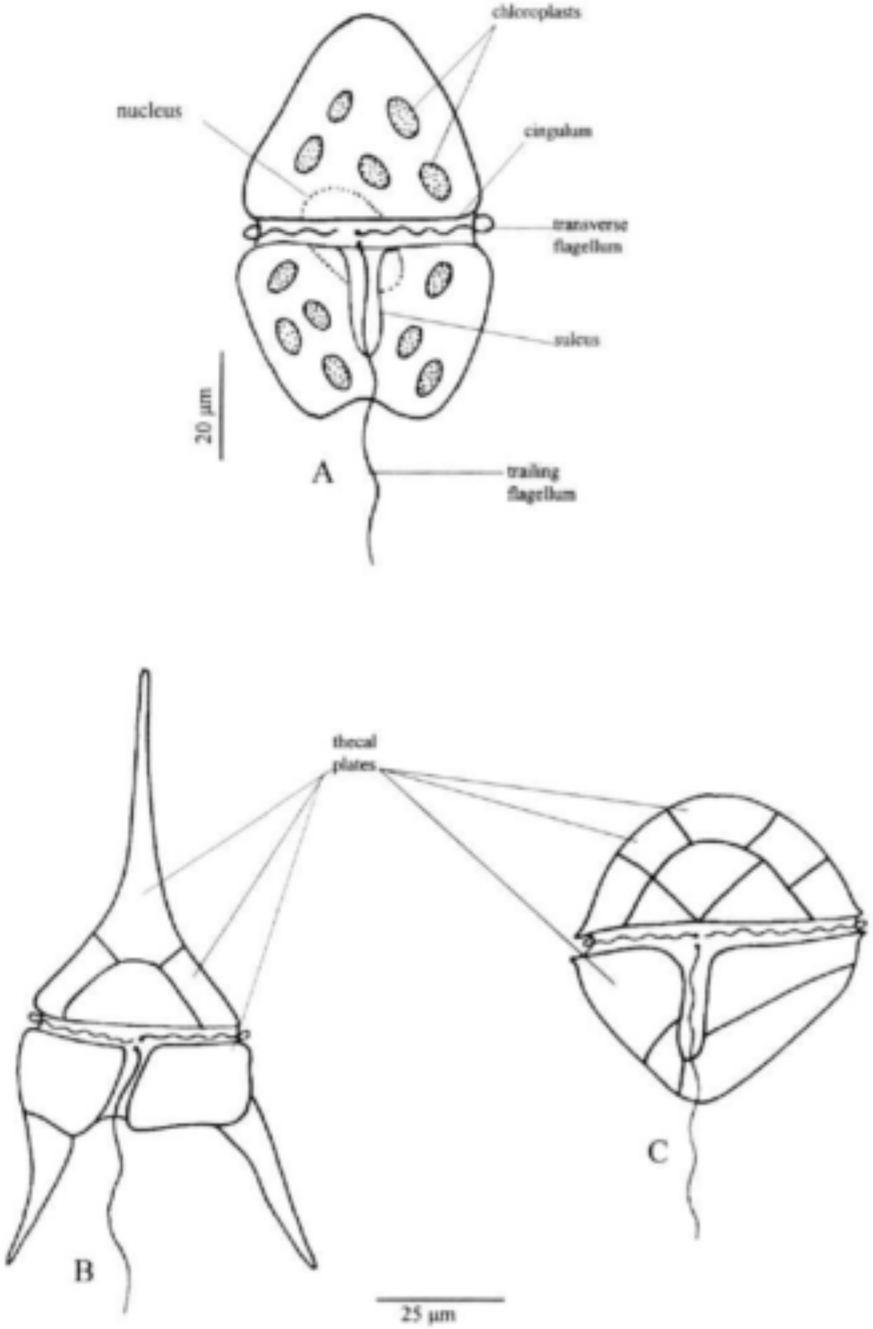


Fig. 1.3. Dinoflagellida. **A**, *Gymnodinium* sp. (Gymnodiniidae). **B–C**: Peridiniidae: **B**, *Ceratium* sp.; C, *Peridinium*.

ORDER EUGLENIDA

(Euglenophyceae the botanical literature)

This order includes both pigmented and colourless flagellates characterized by a flask-shaped reservoir from which two flagella arise. In pigmented forms, usually only one flagellum emerges from the reservoir, the second being small and wholly contained in the reservoir, often fused with the emergent flagellum. Several genera, notably *Peranema* and *Euglena* spp., are capable of temporarily changing shape by distorting the pellicle while creeping on the substratum (euglenoid movement). All pigmented forms and some colourless forms have a conspicuous red eye spot or stigma.

EUGLENIDA: KEY TO TAXA

1. Solitary 2
– Colonial, individuals attached to the stalks of the dendriform colony at the anterior (reservoir) end, suggesting that the stalks are modified, fused flagella embedded in a mucoid matrix; benthic, epiphytic, often epizoic on copepods .... (**Colacidae**) e.g. *Colacium* (Fig. 1.4B, C)

2. Pigmented (**Euglenidae**) 3
– Colourless .... (**Peranemidae**) e.g. *Peranema* (Fig 1.4A)

3. Cell body broad: length less than twice the width 4
– Cell body narrow: length approximately four or five times the width; cylindrical or flattened; green chlorophyll may be temporarily masked by red carotenoid in *E. rubra*; several species, separated on chloroplast shape and number .... *Euglena* (Fig. 1.4D)

4. Cell body ovoid, enclosed in a hyaline cup or lorica .... *Trachelomonas* (Fig. 1.4E)
– Cell body flattened, posterior end usually pointed; body twisted in some species .... *Phacus* (Fig. 1.4F, G)

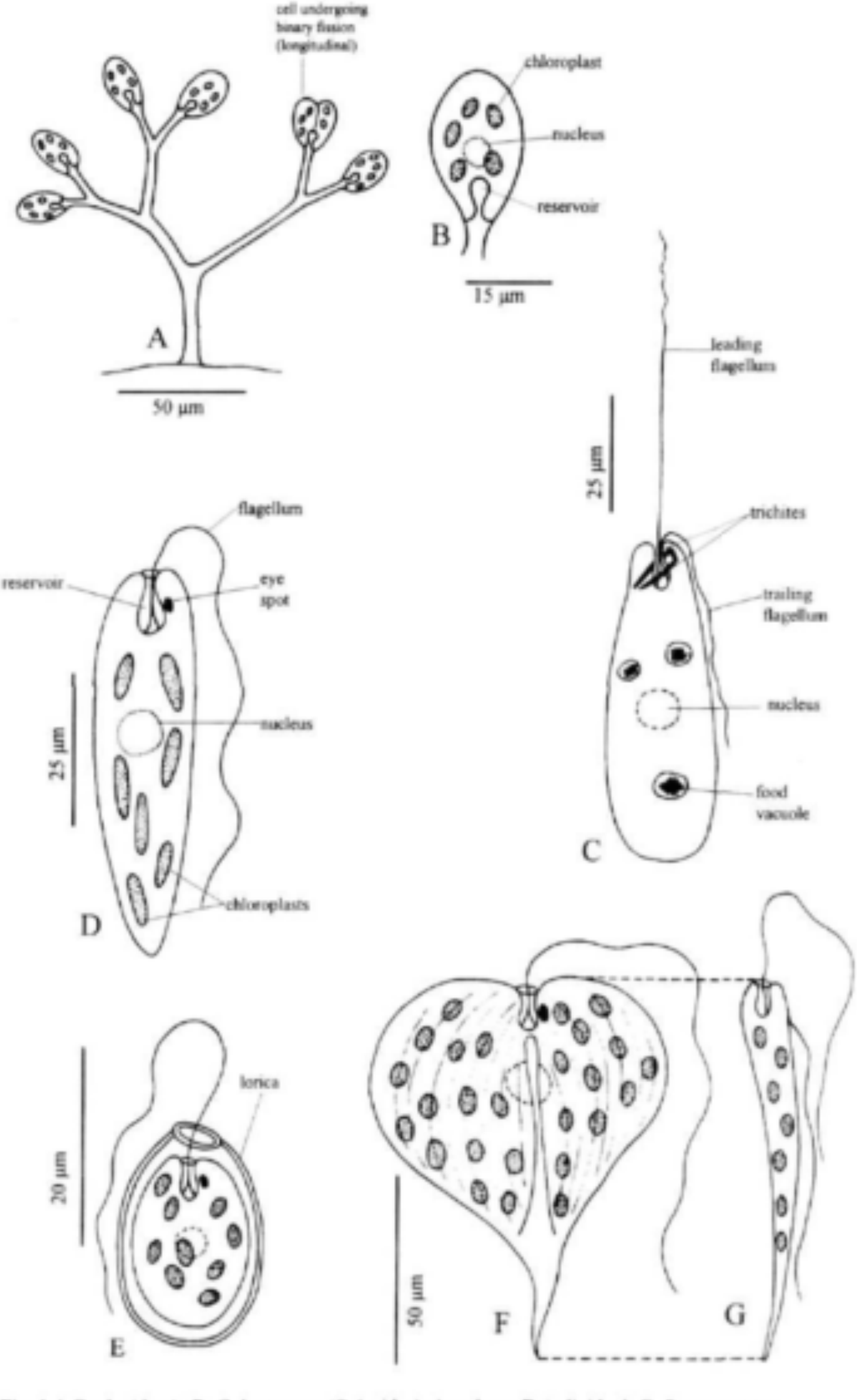


Fig. 1.4. Euglenida. **A–B**, *Colacium* sp. (Colacidae): **A**, colony; **B**, individual. **C**, *Peranema* sp. (Peranemidae). **D–G**, Euglenidae: **D**, *Euglena* sp.; **E**, *Trachelomonas* sp.; **F–G**, *Phacus* sp.: **F**, dorsal view; **G**, lateral view.

ORDER: CRYPTOMONADIDA

(Cryptophyceae in the botanical literature)

Small pigmented or colourless flagellates, the majority of which have a prominent sac-like gullet lined with trichocysts which extends half the length of the cell body. Two flagella of unequal length and furnished with stiff lateral projections (mastigonemes or 'flimmers'), arise from a small vestibule leading off the gullet. While most are less than 10 µm in length, the two common genera are larger (20–30 µm).

CRYPTOMONADIDA: KEY TO COMMON GENERA

1. Pigmented with two large chloroplasts ....*Cryptomonas* (Fig. 1.5A)
– Colourless ....*Chilomonas* (Fig. 1.5B)

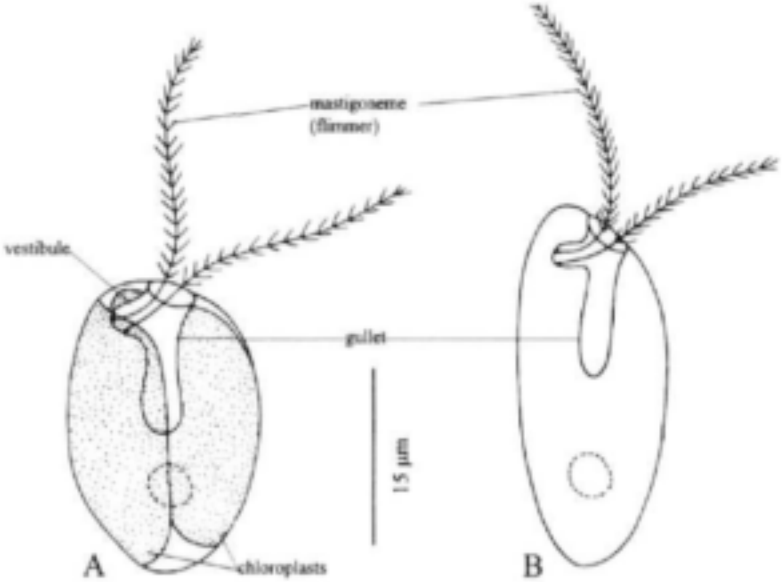


Fig. 1.5. Cryptomonadida: **A**, *Cryptomonas* sp.; **B**, *Chilomonas* sp.

ORDER VOLVOCIDA

(Volvocales in the botanical literature)

This order, sometimes called the Phytomonadida, is the only one comprised exclusively of haploid, obligate autotrophic flagellates with distinctly plant-like characteristics, notably a cellulose cell wall, post-zygotic meiosis, and a single, large, cup-shaped chloroplast. Chlorophyll a and b present, giving the cells their bright grass green colour which may be masked by red carotenoid pigments under conditions of bright light. Each cell has either two or four flagella and a prominent eyespot or stigma.

VOLVOCIDA: KEY TO TAXA

1. Solitary 2
– Colonial, cells embedded in a mucilagenous matrix (Fig. 1.7) (**Volvocidae**) 3

2. Four flagella .... (**Carteriidae**) e.g. *Carteria* (Fig. 1.6A)
– Two flagella (**Chlamydomonadidae**) 3

3. Protoplast separated from cell wall by hyaline mucilage; cytoplasmic extensions through mucilage from protoplast to cell wall; colour often red in bright light .... *Haematococcus* (Fig. 1.6B)
– Protoplast not separated from cell wall .... *Chlamydomonas* (Fig. 1.6C)

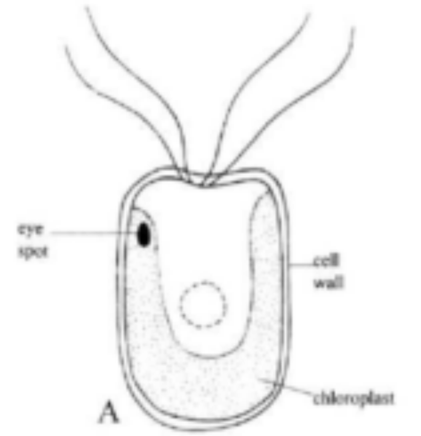


Fig. 1.6. Volvocida. **A**, *Carteria* sp (Carteriidae). **B–C**, Chlamydomonadidae: **B**, *Haematococcus* sp.; **C**, *Chlamydomonas* sp.

4. Colony a flat plate; four, eight, or more (usually 16) *Chlamydamonas*-like cells .... *Gonium* (Fig. 1.7A)
– Colony spheroid or ovoid 5

5. Colony with eight or 16 cells, spheroid to barrel-shaped; wedge-shaped cells allow for characteristic close packing; chloroplast with longitudinal striations .... *Pandorina* (Fig. 1.7B)
– Colony spheroid to ovoid with 16 or more cells; cells not closely packed; chloroplast without striations 6

6. Colony with 32 (occasionally 16) cells .... *Eudorina* (Fig. 1.7C)
– Colony with 128 to > 6 000 interconnected cells, arranged around the surface of a hollow sphere. Asexually produced daughter colonies often enclosed within the sphere .... *Volvox* (Fig. 1.7D, E)

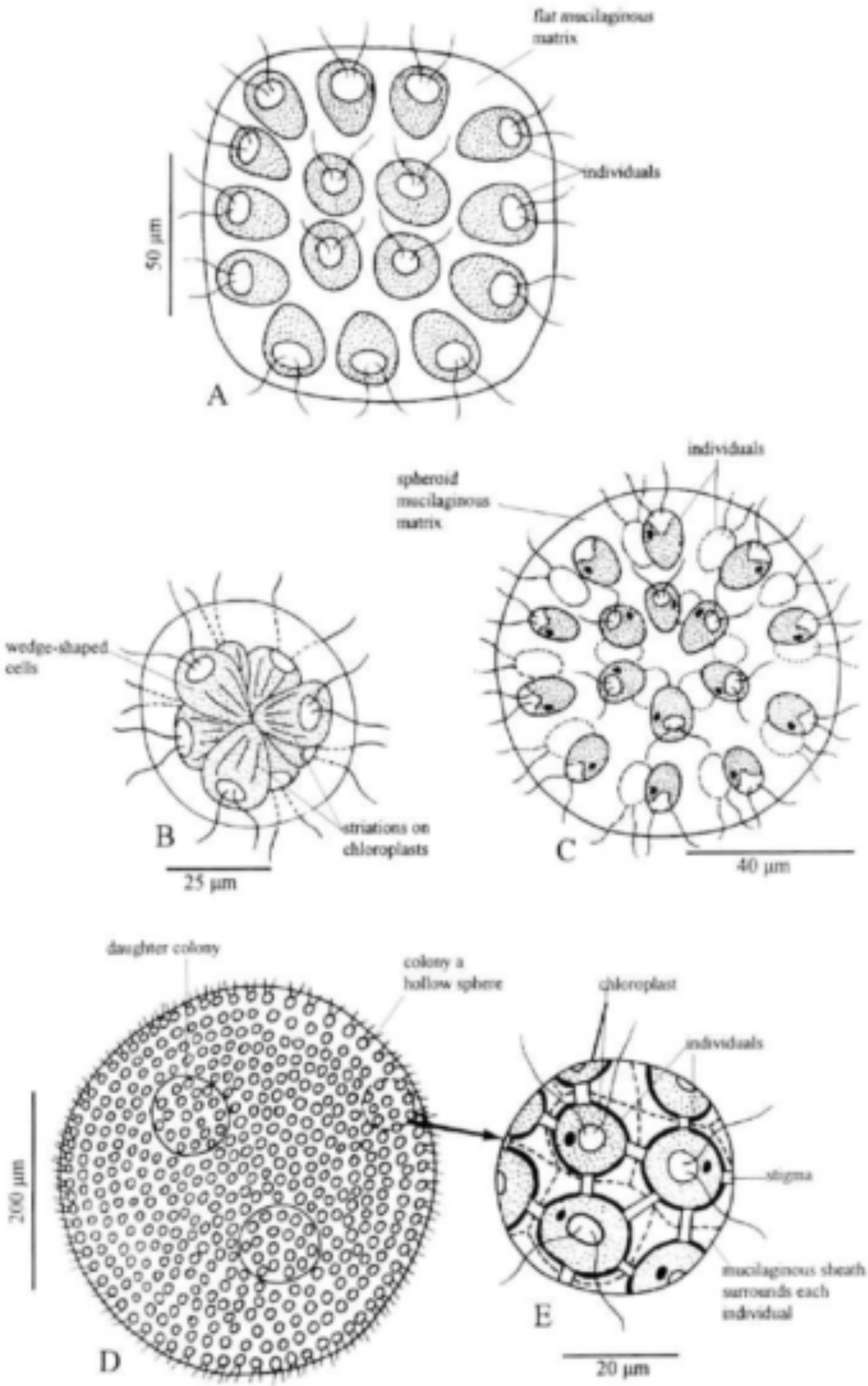


Fig. 1.7. Volvocida. **A**, *Gonium* sp. **B**, *Pandorina* sp. **C**, *Eudorina* sp. **D–E**, *Volvox* sp.: **D**, colony; **E**, surface detail (magnified). (Note that the individuals within colonies illustrated in (A), (C) & (E) resemble *Chlamydomonas*).

ORDER: CHRYSOMONADIDA

(Chrysophyceae in the botanical literature)

This order includes both pigmented and colourless phytoflagellates with one, or more usually two, flagella. Chloroplasts of pigmented species shades of yellow, yellow-brown or yellow-green, never grass green. Never enclosed in a cell wall, although several genera have a covering of secreted scales or plates, and some are enclosed in a hyaline cup or lorica.

CRYSOMONADIDA: KEY TO GENERA

1. Solitary 2
– Colonial.. 4

2. Uni-flagellate 3
– Bi-flagellate, flagella of unequal length .... *Ochromonas* (Fig. 1.8C)

3. Surface covered in scales, each scale with a prominent spine .... *Mallomonas* (Fig. 1.8A)
– Surface without scales .... *Chromulina* (Fig. 1.8B)

4. Loricate; colony branching .... *Dinobryon* (Fig. 1.8D)
– Without a lorica, colony spherical .... *Synura* (Fig. 1.8E)

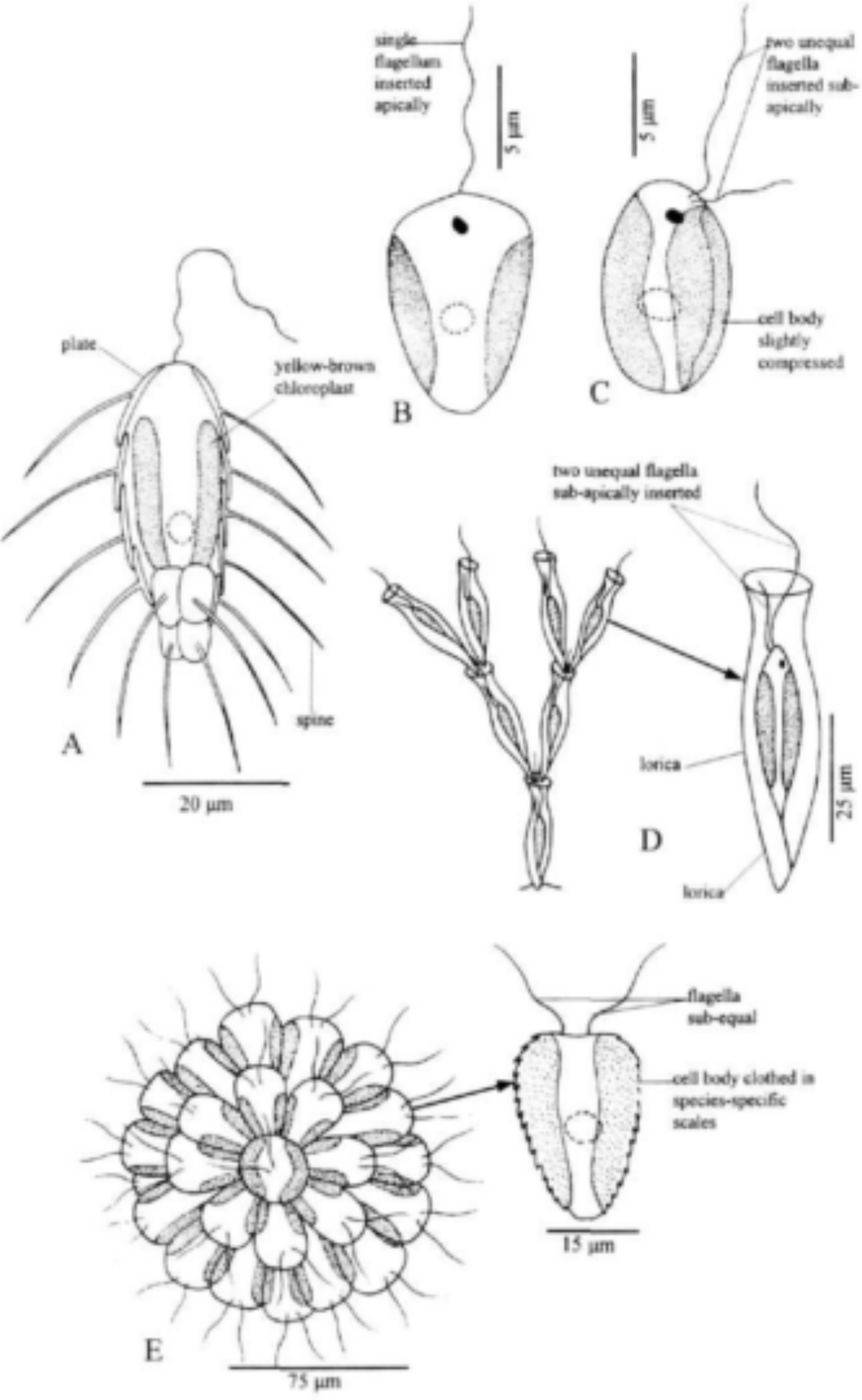


Fig. 1.8. Chrysomonadida: **A**, *Mallomonas* sp.; **B**, *Chromulina* sp.; **C**, *Ochromonas* sp; **D**, *Dinobryon* sp. (colony and individual); **E**, *Synura* sp. (colony and individual).

CLASS ZOOMASTIGOPHOREA

This class includes those orders of flagellated protozoans in which no autotrophic forms are known. Most of the orders are either largely or exclusively parasitic or endosymbiotic. Like the Phytomastigophorea, the class is almost certainly an artificial assemblage; in this connection see particularly comments on the order Rhizomastigida (Page 33).

ZOOMASTIGOPHOREA: KEY TO ORDERS

1. Never a collar surrounding the base of the flagellum; solitary 2
– Flagellum arises from the centre of a funnel-shaped collar; benthic or planktonic; solitary or colonial .... **Choanoflagellida** (Page 33)
2. Amoeboid; cell body shape plastic; single flagellum .... **Rhizomastigida** (Page 33)
– Cell body shape fixed by a pellicle; two flagella .... **Kinetoplastida** (Page 34)

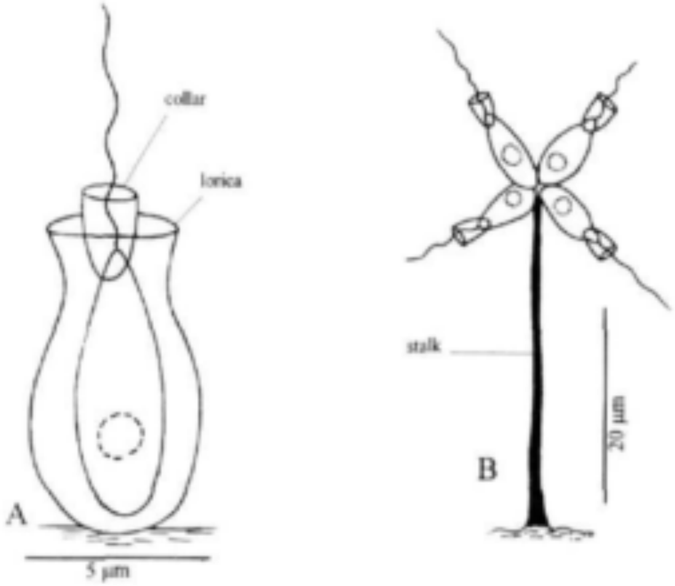


Fig. 1.9. Choanoflagellida: A, Salpingoecidae (generalized); B, Codonosigidae (generalized).

ORDER CHOANOFLAGELLIDA

Small (usually < 10 µm), colourless flagellates, easily recognized by the presence of a distinctive collar which surrounds the basal part of the single flagellum. Solitary forms and stalked colonies are sedentary, benthic, epiphytic or hyponeustic, while colonies lacking a stalk are planktonic. Two families are known to occur in fresh waters: the family *Salpingoecidae* (Fig. 1.9A) is characterized by individuals being enclosed in a thick-walled lorica, while the family *Codonosigidae* (Fig. 1.9B) is iloricate. I have seen representatives of both, though not commonly, and have not attempted further identification.

ORDER RHIZOMASTIGIDA

This order, which included all the flagellated amoebae, is no longer recognized but, since several of the families and genera previously included have not yet been satisfactorily assigned to other taxa, and such re-assignments as have been made rely on a detailed knowledge of life cycle stages and ultrastructure, the order is retained here. Flagellated amoebae are often seen in pond samples, but attempts at further classification and identification are fraught with difficulties.

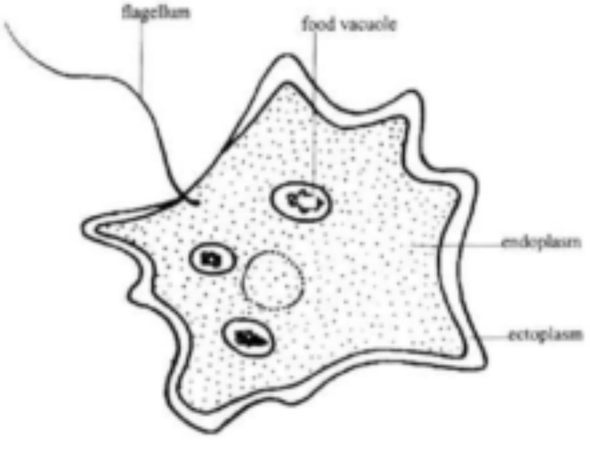


Fig. 1.10. Rhizomastigida: flagellated amoeba (generalized).

ORDER: KINETOPLASTIDA

A single large mitochondrion, visible on staining with Janus Green, is characteristic of this order. The mitochondrion extends over almost the whole length of the body and terminates in a kinetoplast at the base of the flagella. It includes only two families: the wholly parasitic Trypanosomatidae and the Bodonidae, with both free-living and parasitic genera. The genus *Bodo* (Fig. 1.11) comprises small (10–15 µm) colourless flagellates that are roughly bean-shaped and have a leading and a trailing flagellum. They often occur in large numbers in bacteria-rich waters.

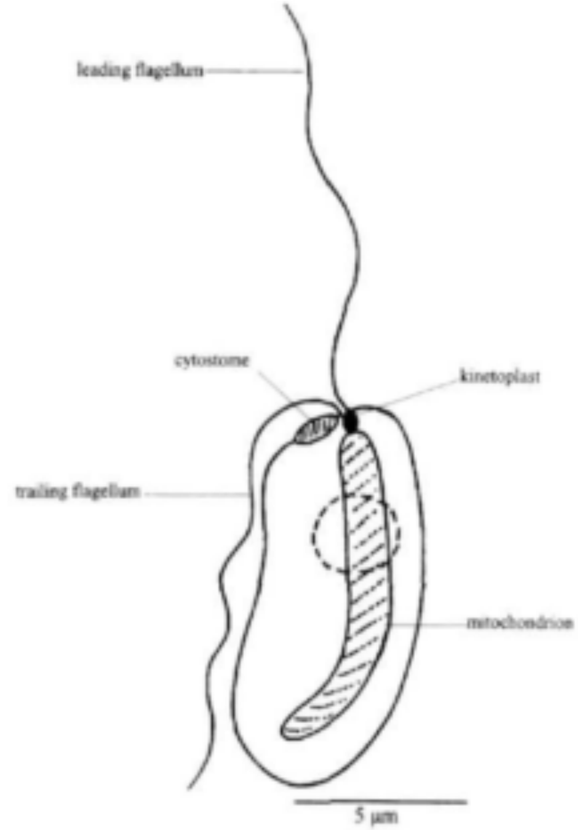


Fig. 1.11. Kinetoplastida: *Bodo* sp. (Bodonidae).

SUB-PHYLUM: SARCODINA

Includes all non-flagellated forms which move and/or gather and ingest food by means of pseudopodia. They may be enclosed in a test into which sand grains are sometimes incorporated, or in a perforated, often complexly-shaped, calcium carbonate shell. Four types of pseudopodia occur:

Lobopodia are finger-like blunt tipped lobes and may be granular with a hyaline cap or largely hyaline (Fig. 1.12A).

Filopodia are thin, pointed, often branching, hyaline pseudopodia (Fig. 1.12B)

Reticulopodia are long, thin, hyaline, branching pseudopodia similar to filopodia, but with frequent anastomoses between branches and between separate pseudopodia that form a net for food capture (Fig. 1.12C).

Axopodia are thin, stiff, projecting pseudopodia occupying fixed positions on the cell body surface. Each consists of a central axial filament composed of bundles of microtubules surrounded by a thin layer of clear cytoplasm (Fig. 1.12D).

While, for the purposes of this key, the absence of a flagellum and the presence of pseudopodia are used as key characteristics defining the Sarcodina, users must bear in mind that this is an oversimplification, particularly where the flagellated amoeboid genera are concerned (see Rhizomastigida, Page 33). An extreme example is the facultative pathogen, *Naegleria gruberi*,

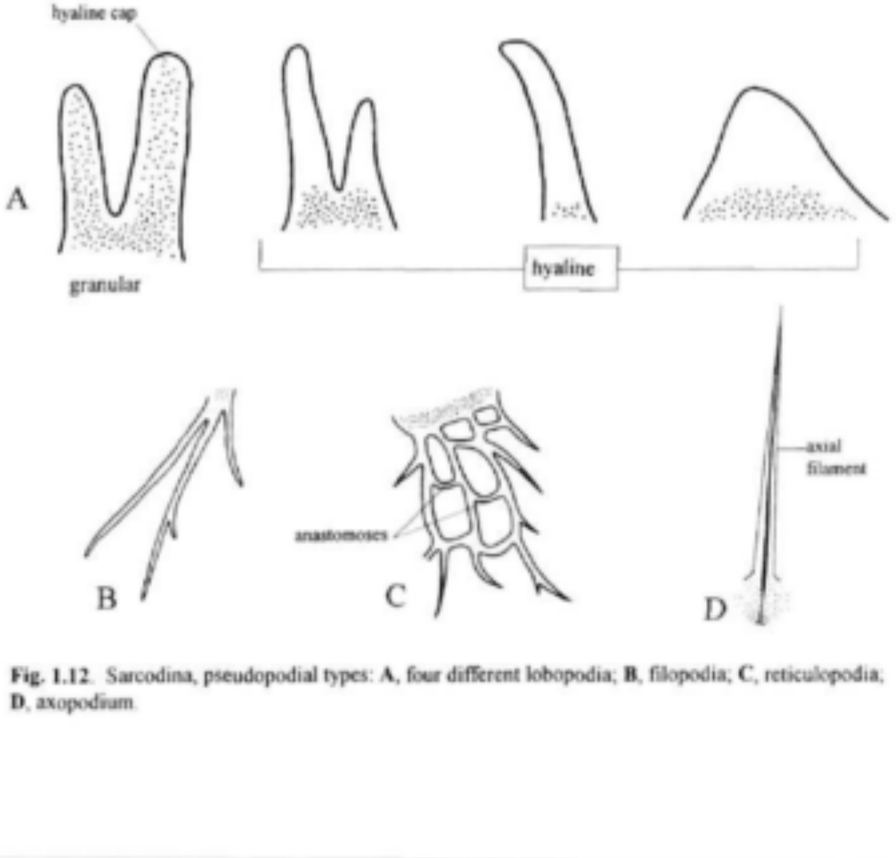


Fig. 1.12. Sarcodina, pseudopodial types: **A**, four different lobopodia; **B**, filopodia; **C**, reticulopodia; **D**, axopodium.

known from southern Africa. It can change from a nondescript benthic, or sometimes interstitial mud-dwelling, amoeboid form, to a typical colourless free-swimming flagellate and back again. It was previously included in the Rhizomastigida, but the family to which it belongs is now assigned to a separate order of the Sarcodina. Unless one is able to follow the change of form, correct identification is impossible. Where accurate identifications are important, it is essential that specialist literature is consulted. Lee et al. (1985) is probably the best starting point.

SARCODINA: KEY TO CLASSES

1. Cell body spherical, with stiffened, radially-projecting axopodia, often interspersed with temporary, flexible filopodia .... **Actinopodea** (Page 36)
– Cell body shape variable, usually not fixed, or body enclosed in a test or shell; axopodia never present .... **Rhizopodea** (Page 37)

CLASS: ACTINOPODEA

Includes all Sarcodina in which at least some pseudopodia are axopodia, having a fixed position and an axial filament comprising bundles of microtubules which extend into the endoplasm of the cell body. The two major orders in the class are the marine Radiolaria, characterized by an elaborate siliceous skeleton and an intracellular pseudochitinous central capsule, and the freshwater Heliozoa.

ORDER: HELIOZOA

Actinopodea which lack a central capsule demarcating ectoplasm from endoplasm and in which the siliceous skeleton, if present, is poorly developed. Includes both sedentary and free-living forms.

HELIOZOA: KEY TO TAXA

1. Sedentary; cell body enclosed in a stalked perforated capsule .... **(Clathrulinidae)** e.g. *Clathrulina** (Fig. 1.13A)
– Free living; no enclosing capsule, although cell body may be surrounded by a thick mucous layer **(Actinophryidae)** 2

2. Conspicuous vacuolated ectoplasm; multinucleate; large, usually > 200 µm ....*Actinosphaerium* (Fig. 1.13B)
– Ectoplasm not clearly distinguishable; single central nucleus; small, usually <50 µm ....*Actinophrys* (Fig. 1.13C)

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* To date only empty, stalked capsules have been found in a dam in the Vernon Crookes Reserve near Umzinto (KwaZulu–Natal).

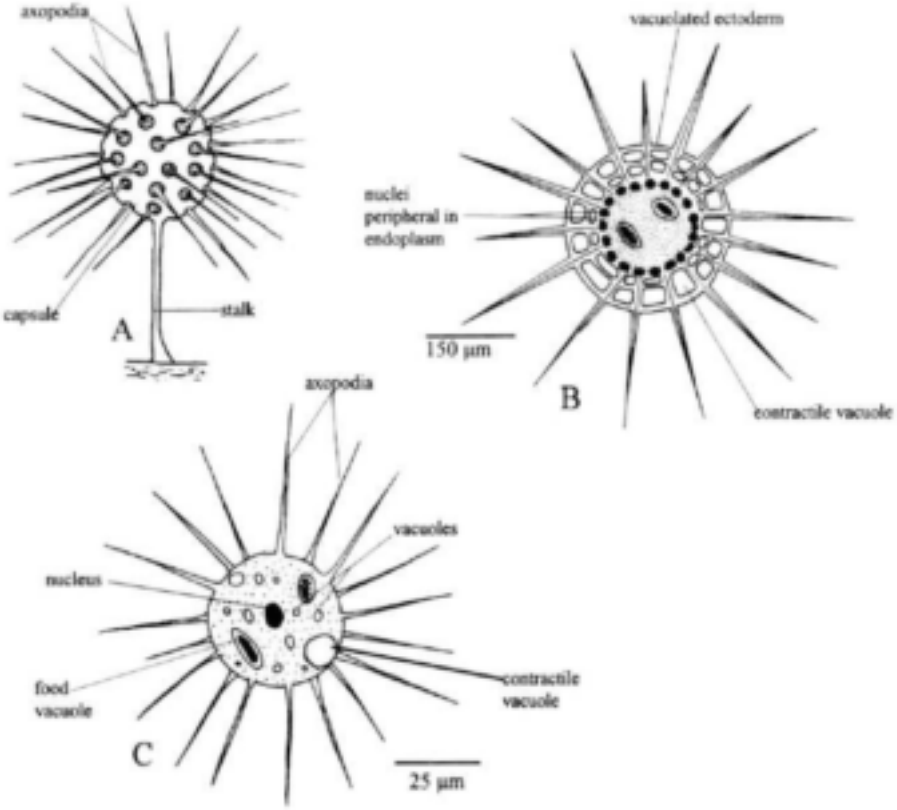

Fig. 1.13. Heliozoa. **A**, *Clathrulina* sp. (Clathrulinidae) (capsule 60–80 µm, stalk variable). **B–C**, Actinophryidae: **B**, *Actinosphaerium* sp (200–1000 µm); **C**, *Actinophrys* sp. (30–60 µm).

CLASS: RHIZOPODEA

Includes all amoeboid Sarcodina, whether enclosed in a test or naked. Pseudopodia are important for identification, so it is important to examine living material wherever possible.

RHIZOPODEA: KEY TO ORDERS

1. Cell body naked .... **Amoebida** (Page 38)
– Cell body enclosed in a test or perforated calcium carbonate shell 2

2. Cell body enclosed in a test, which may have sand grains or debris incorporated in it; pseudopodia either lobopodia or filopodia 3
– Cell body enclosed in a perforated calcium carbonate shell; pseudopodia are reticulopodia .... **Foramenifera** (Page 39)

3. Pseudopodia are lobopodia; test simple, discoid to spheroid or vase-shaped, not made up of separate plates or scales; with or without incorporated sand grains .... **Testacida** (Page 40)
– Pseudopodia are filopodia or reticulopodia; test simple or made up of separate plates or scales, some of which may bear projecting spines; with or without incorporated sand grains .... **Gromiida** (Page 42)

ORDER AMOEBIDA

Includes the typical amoebae, characterized by lobopodia. May be polypodial (having several pseudopodia at a given time) or monopodial (slug-like); uninucleate or multinucleate; cell body never enclosed in a test.

AMOEBIDA: KEY TO TAXA

1. Polypodial; uninucleate or multinucleate 2
– Monopodial, movement slug-like by means of cytoplasmic waves; multinucleate; large, 500–3 000 µm when active and contracting to a sphere 120–2000 µm in diameter sphere when at rest ....(**Pelomyxidae**) e.g. *Pelomyxa** (Fig.1.14A)

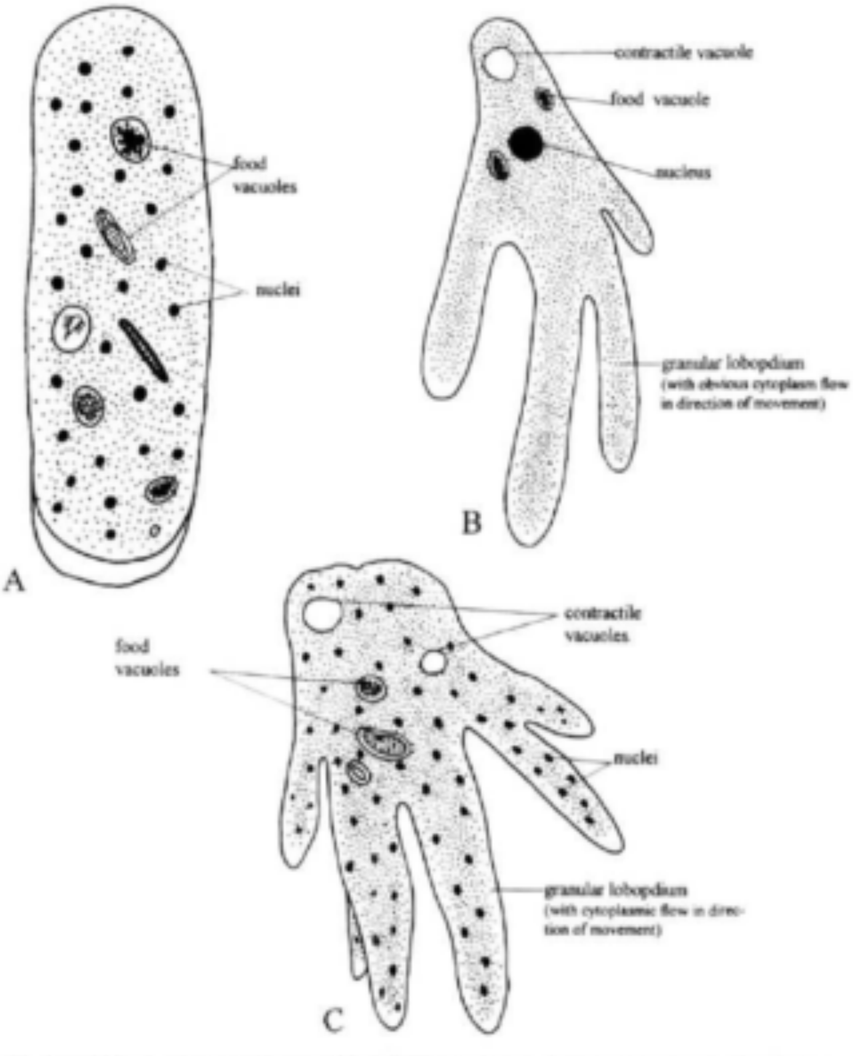

Fig. 1.14. Amoebida. **A**, *Pelomyxa* (Pelomyxidae) (500 µm – 3mm). **B–C**: Amoebidae: **B**, *Amoeba* sp. (50 – 600 µm); **C**, *Chaos* sp. (1 – 4 mm).

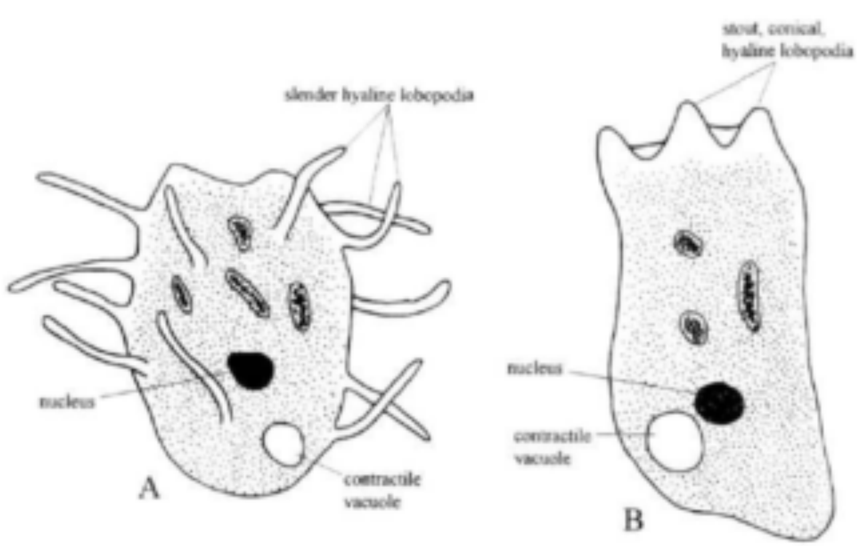

Fig. 1.15. Amoebida (Mayorellidae): **A**, *Dinamoeba* sp. (30 – 100 µm); **B**, *Mayorella* sp. (40 – 150 µm).

2. Pseudopodia granular; large, usually > 100 µm; uninucleate or multinucleate (**Amoebidae** — Fig. 1.14B,C) 3

– Pseudopodia hyaline, not used in locomotion; moves by cytoplasmic waves; small, < 40 µm; uninucleate (**Mayorellidae** — Fig. 1.15A,B) 4

3. Uninucleate; usually < 500 µm. Six genera differing in nuclear structure .... e.g. *Amoeba* (Fig. 1.14B)

– Multinucleate; large, usually > 1 000 µm .... *Chaos*** (Fig. 1.14C)

4. Numerous slender pseudopodia, some pointing upwards .... *Dinamoeba* (Fig. 1.15A)

– Few tapered pseudopodia with bluntly rounded tips in the direction of movement only .... *Mayorella* (Fig. 1.15B)

* *Pelomyxa*: only known from the Liesbeek River, Cape Town.

** *Chaos*: Author has only once found this genus in a culture of *Paramecium*, purchased from a Grahamstown supplier, so may not occur naturally in southern Africa.

ORDER FORAMENIFERA

This order is characterized by the cell body being enclosed in a calcium carbonate shell, which may be single- or many-chambered, with a single aperture and many minute perforations through which the thin pseudopodia project. The pseudopodia are reticulopodia, which resemble branching filopodia and which typically anastomose to form a net for food capture. Foramenifera are essentially marine, but do occasionally occur in coastal brackish waters. They are included here as they have been found in inland gypsous springs in the coastal Namib Desert in Namibia.

ORDER TESTACIDA

Includes most of the commonly-encountered testate amoebae. Easily confused with the Gromiida if the pseudopodia are not visible, particularly where sand grains or other debris is incorporated into the test. The presence of blunt-tipped lobopodia is the only reliable character.

TESTACIDA: KEY TO TAXA

1. Test smooth, chitinous; transparent, yellow-brown; shape discoid through sub-spherical to vase shaped; no embedded sand grains 2

– Test opaque with embedded sand grains 3

2. Test aperture invaginated; test of most species discoid to hemispherical, round when viewed from above/below; few species sub-spherical ....(**Arcellidae**) e.g *Arcella* (Fig. 1.16A, B)

– Test aperture not invaginated; tall, ovate to vase shaped .... **Hyalospheniidae** (Fig. 1.17)
(Several genera e.g. *Difflugiella, Leptochlamys*)

3. Aperture of test invaginated.. **Centropyxidae**
(Includes several genera e.g. *Centropyxis* which is characterized by an acentric test aperture —Fig. 1.18)

– Aperture of test not invaginated .... **Difflugidae**
(Few genera; includes several species of *Difflugia* (Fig. 1.19) which are characterized by a test which is ovate to tall and vase-shaped).

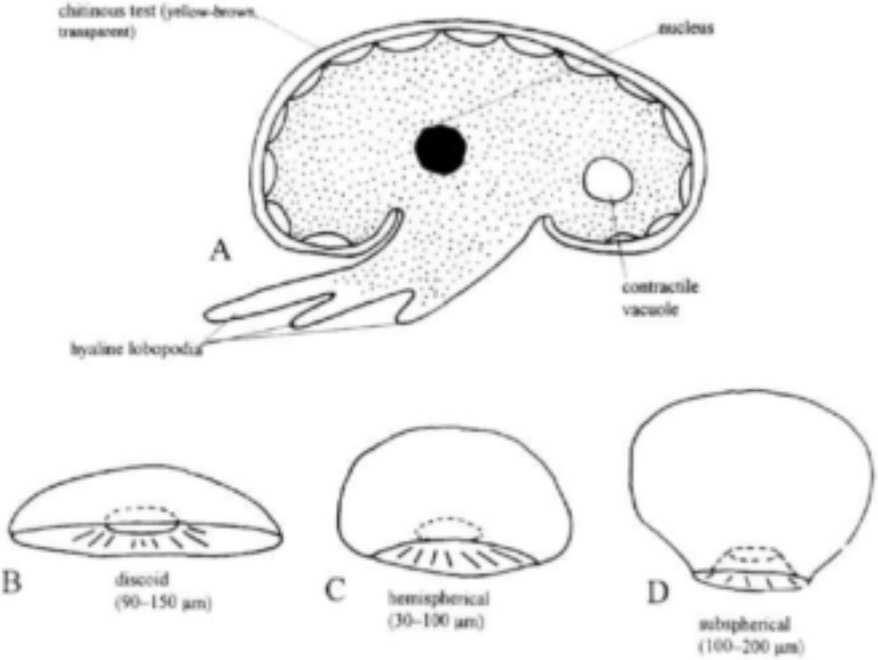

Fig. 1.16 Testacida, Arcellidae: **A**, *Arcella* sp., sagittal section; **B–D**, various test forms found in *Arcella* (diagrammatic, not of living animals)

Fig. 1.17. Testacida, Hyalospheniidae: generalised, similar to *Difflugiella* sp., sagittal section (15–40 µm).

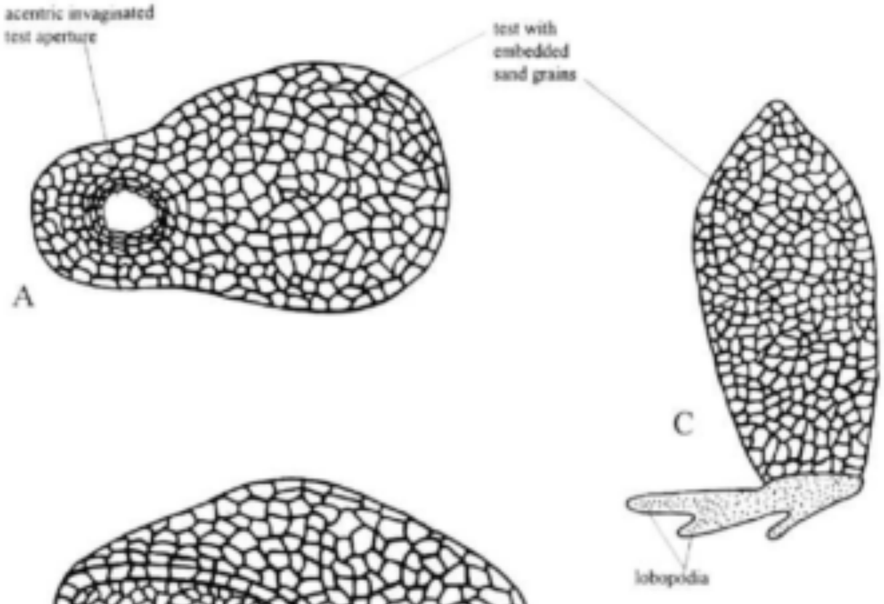

Fig. 1.18. Testacida. **A–B**, test of *Centropyxis* sp. (Centropyxidae) (50– 100 µm) : **A**, ventral view; **B**, lateral view. **C**, *Difflugia* sp. (Difflugidae) (100– 300 µm).

ORDER: GROMIIDA

Testate amoebae characterized by having filopodous pseudopodia. Easily confused with the Testacida, as one family comprising several genera incorporates sand grains and debris into the test.

GROMIIDA: KEY TO FAMILIES

1\. Test made up of regularly arranged, overlapping secreted scales .... **Euglyphidae**

(Includes several genera; where at least some scales have projecting spines, e.g. *Euglypha* —Fig. 1.19)

– Test without secreted scales; may have sand grains or debris incorporated into the test .... **Gromiidae**

(No genera identified from southern Africa).

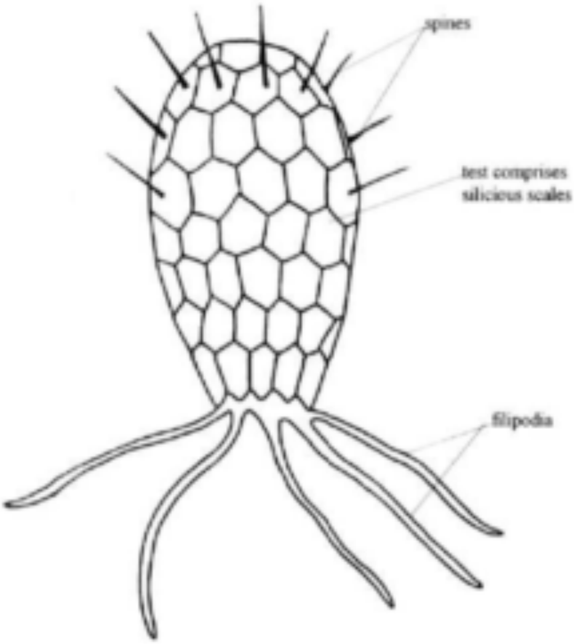

Fig. 1.19. Gromiida: *Euglypha* sp. (Euglyphidae) (50–150 µm).

PHYLUM CILIOPHORA

The phylum Ciliophora comprises a diverse assemblage of protozoans which are, nonetheless, all clearly related (see Corliss, 1979). Ciliates are characterized by the presence of cilia, and usually a single macronucleus, which is polyploid, and one or more diploid micronuclei. While these characteristics are manifest in most ciliates, there are exceptions: cilia are absent in adult suctorians, and more than one macronucleus may occur in a few genera, mainly in the order Gymnostomatida. One or other of the definitive characters is, however, always present. The most recent classification of the phylum divides it into three sub-phyla, eight classes and 48 orders, a system far too complicated for the purposes of this chapter. The classification employed here is based on that of Hyman (1940) and serves a useful 'pigeon hole' function, but users should be aware that it is very much out of date in a serious systematic context.

CILIOPHORA: KEY TO CLASSES

1 Peristome with a conspicuous adoral zone of well-developed membranelles .... **Spirotrichea** (Page 44)
– Membranelles absent or, where present, small, few, confined within a buccal cavity 2

2. Free-swimming; somatic ciliation usually conspicuous .... **Holotrichida** (Page 44)
– Sedentary, usually stalked; ciliation confined to the peristome, or absent; with or without lorica 3
3. Peristome with usually three semimembranes formed from rows of partially-fused cilia .... **Peritrichea** (Page 54)
– No cilia; large prey items captured by means of adhesive tentacles .... **Suctoria** (Page 57)

CLASS: SPIROTRICHEA

Includes those ciliates with a peristomal region bearing a tract of membranelles winding clockwise into the buccal cavity.

SPIROTRICHIA: KEY TO ORDERS

1. Body uniformly ciliated .... **Heterotrichida** (Page 44)
– Body ciliation (as opposed to buccal ciliation) reduced or absent; cirri often present 2

2. Dorso-ventrally flattened; peristomial membranelles extend from the anterior surface, following a clockwise curve into the buccal cavity; length > 100 µm; conspicuous ventral cirri .... **Hypotrichida** (Page 47)
– Cell body spheroid, small <50 µm; thin cirri project radially from body; peristomial field of membranelles very well developed .... **Oligotrichida** (Page 47)

ORDER HETEROTRICHIDA

Conspicuous ciliates with a uniform somatic ciliation in addition to the peristomial membranelles. Macronucleus often elongate.

HETEROTRICHIDA: KEY TO TAXA

1. Body trumpet-shaped when extended; peristome disc-like, apical, with a clockwise spiral of membranelles; usually sedentary, but may sometimes swim (**Stentoridae**) .... *Stentor* (Fig. 1.20)
– Body shape not as above; axis of peristomial ciliature straight to more or less helical, parallel to the long axis of the cell body; free swimming, sometimes creeping 2

2. Worm-like, usually large (> 1 000 µm); cell body highly contractile; body ciliature forms a helical pattern, particularly clear when cell body contracted; no undulating membrane (**Spirostomidae**) .... *Spirostomum* (Fig. 1.21A)
– Shape fixed, ovoid-elongate 150–200 µm long; peristomial membranelles straight, turning clockwise into buccal cavity; conspicuous undulating membrane projects from the buccal cavity; colour faintly pink (**Blepharismidae**) .... *Blepharisma* (Fig. 1.21B)

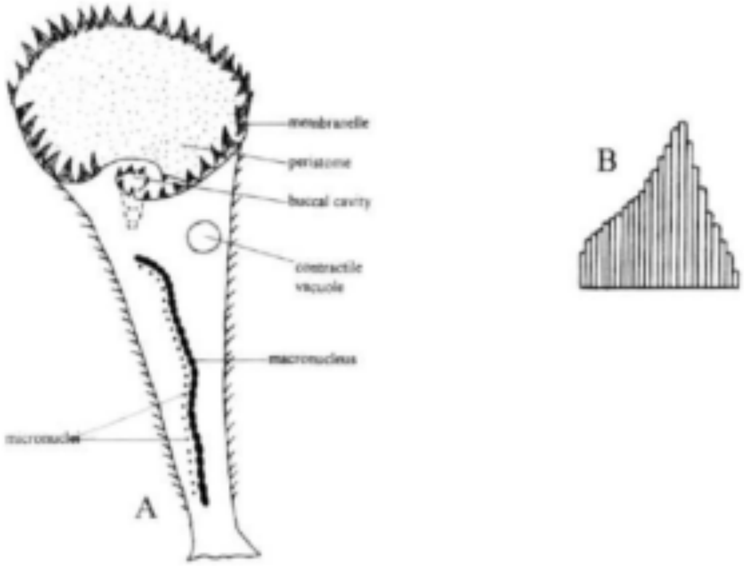

Fig. 1.20. Heterotrichida. **A– B**, *Stentor* sp., (Stentoridae): **A**, generalised structure (200µm – 2 mm); **B**, detailed structure of a membranelle.

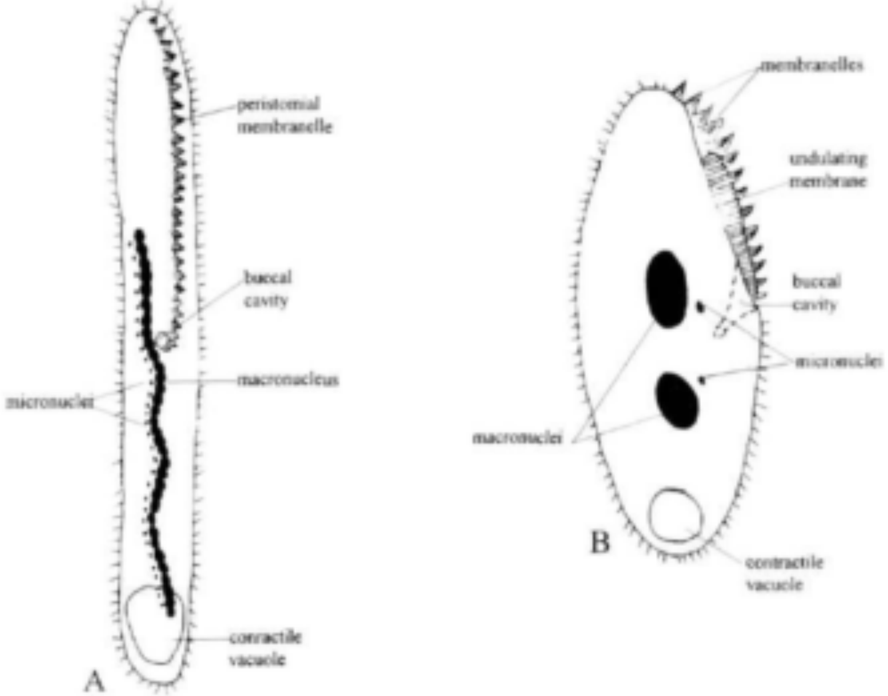

Fig. 1.21. Heterotrichida: **A**, *Spirostomum* sp. (Spirostomidae) (500µm–3 mm); **B**, *Blepharisma* sp. (Blepharismidae) (120–200 µm).

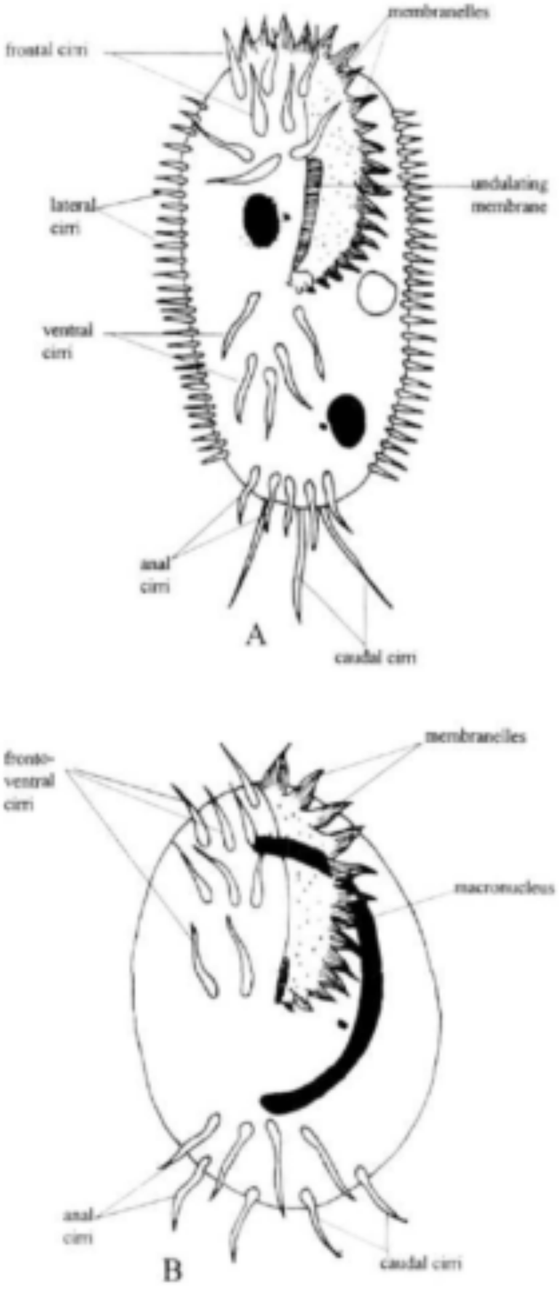

Fig. 1.22 Hypotrichida: **A**, *Stylonychia* sp. (Oxytrichidae) (100 –300µm) ; **B**, *Euplotes* sp. (Euplotidae) (70 –100µm)

ORDER HYPOTRICHIDA

Ciliates that spend much of their time crawling over vegetation and bottom debris, the characteristic ventral cirri functioning as legs, as well as being used in swimming.

HYPOTRICHIDA: KEY TO TAXA

1. A distinct row of thin cirri along lateral margins in addition to the stouter ventral and anterior cirri (**Oxytrichidae**) .... *Stylonychia* (Fig. 1.22A)
– No lateral marginal cirri (**Euplotidae**)................................ *Euplotes* (Fig. 1.22B)

ORDER OLIGOTRICHIDA

Small, near spherical, free-swimming ciliates with a disproportionately large peristomial zone of membranelles. No somatic cilia, the membranelles having taken over the swimming function. Two families, only one of which has been seen to date. *Halteria* (Fig. 1.23), an example of the family Halteridae, has seven triads of thin cirri projecting radially from the cell body. It swims with a distinctive 'bouncing' movement.

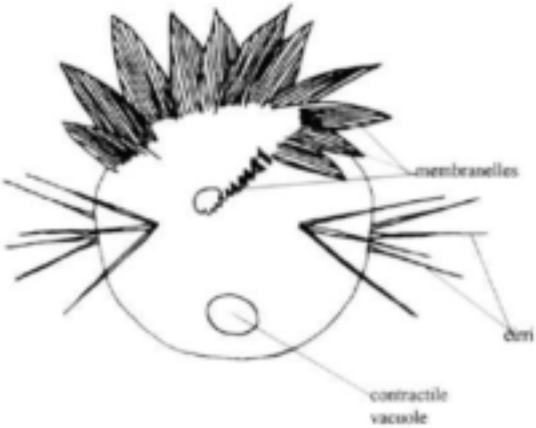

Fig. 1.23. Oligotrichida: *Halteria* sp. (Halteridae) (25–50μm).

CLASS HOLOTRICHIDA

Ciliates without specialized peristomial ciliature, i.e. they lack an adoral zone of membranelles or semimembranes, although membranelles and undulating membranes may form part of the buccal ciliature, being confined to a buccal cavity sunk below the surface of the cell body. Some somatic ciliature is always present, although it may be confined to specific areas of the body surface.

HOLOTRICHIDA: KEY TO ORDERS

1. Cytostome at, or very slightly below, body surface; no buccal cavity or oral vestibule (see *Loxodes*— Fig. 1.26A) .... **Gymnostomatida** (Page 48)
– Buccal cavity or vestibule present 2

2. Buccal cavity containing complex ciliary organelles (membranelles, undulating membranes); a distinct oral groove in larger forms, in which the buccal ciliature cannot be seen with the light microscope, gives them a slipper-like appearance; oral groove absent in smaller forms .... **Hymenostomatida** (Page 52)
– No complex ciliary organelles; cytostome located in a simple vestibule .... **Trichostomatida** (Page 53)

ORDER GYMNOSTOMATIDA

Holotrichous ciliates, which have the cytostome located at, or very near to, the cell body surface. They have no membranelles or undulating membranes for the creation of feeding currents. As several members of the order feed on large prey relative to their own size, the cytopharyngeal region is often provided with trichites — microtubular organelles which dilate the cytopharynx, enabling the engulfing of large food particles. Somatic ciliature is usually uniform, but may be concentrated in distinct bands in some genera. The Gymnostomatida include several families and genera, of which only a few have been identified with certainty from southern African fresh waters.

GYMNOSTOMATIDA: KEY TO TAXA

1. Cell body clothed in regularly-arranged calcium carbonate platelets located below the plasmamembrane; distinctly barrel shaped; eight spines present on the posterior (aboral) half of the cell body (**Colepidae**)......*Coleps* (Fig. 1.24)
– Body not clothed in platelets; variously shaped 2

2. Cytostome at the base of a trichocyst bearing proboscis-like extension of the anterior body; ventral cilia on the proboscis extend to and surround the cytostome (**Trachelidae**) 3
– Cytostome apical or sub-apical 5

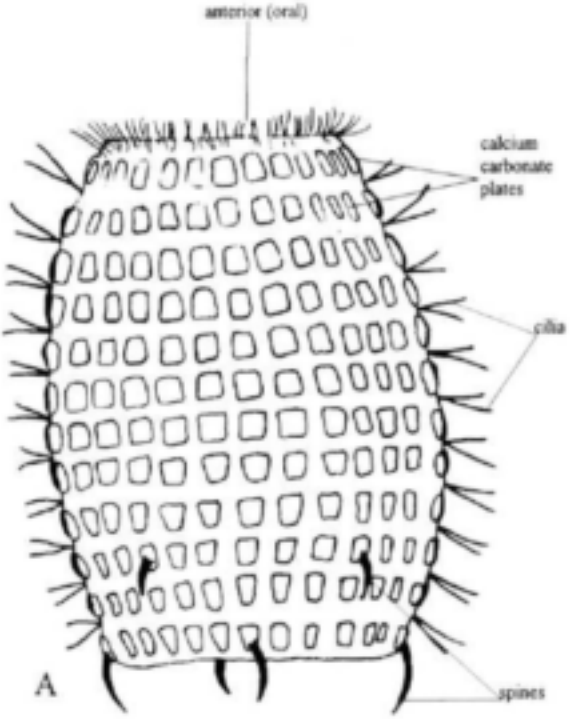

Fig. 1.24. Gymnostomatida. *Coleps* sp. (Colepidae) (80–120µm).

3. Cytoplasm highly vacuolated, containing a number of large, clear vacuoles in addition to several small contractile vacuoles; body ovoid; proboscis about 25% of total body length .... *Trachelius* (Fig. 1.25A)
– Cytoplasm not highly vacuolated, having several contractile vacuoles only; proboscis about 50% of total body length 4

4. Body slender, length about seven times width; usually two or more macronuclei ....*Dileptus* (Fig. 1.25B)
– Body length two to four times width; proboscis twisted in a loose helix in at least one species ....*Paradileptus* (Fig. 1.25C)

5. Anterior of body extended into a long, flexible 'neck' with the exerted cytostome at its tip (**Lacrymariidae**)......................... *Lacrymaria* (Fig. 1.26A–B)
– No flexible 'neck' 6

6. Cytostome sub-apical in a shallow groove; body laterally compressed, with cilia on right side only (**Loxodiidae**) .... *Loxodes* (Fig. 1.26C)
– Cytostome apical; body not compressed 7

7. Cytostome exerted; body ciliature in two transverse encircling bands (**Didiniidae**) ....*Didinium* (Fig. 1.26D)
– Cytostome slightly inverted; body ciliature uniform ....
.... **Prorodontidae** (Fig. 1.26E). e.g. *Prorodon*

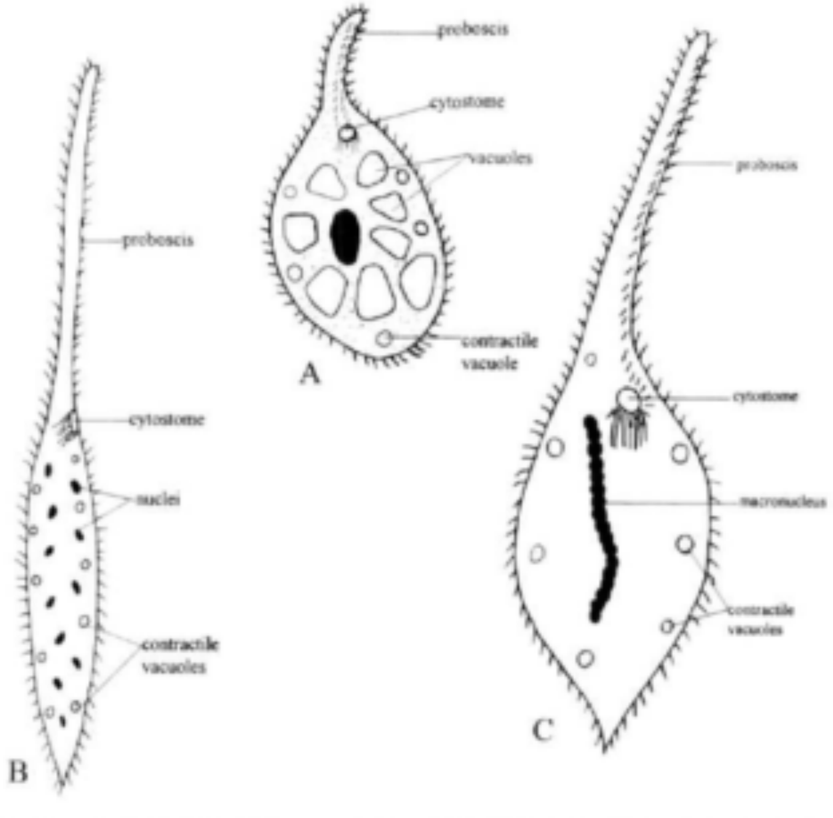

Fig. 1.25. Gymnostomatida, Trachelidae: **A**, *Trachelius* sp. (200–400 µm); **B**, *Dileptus* sp. (generalised); **C**, *Paradileptus* sp. (100–450 µm).

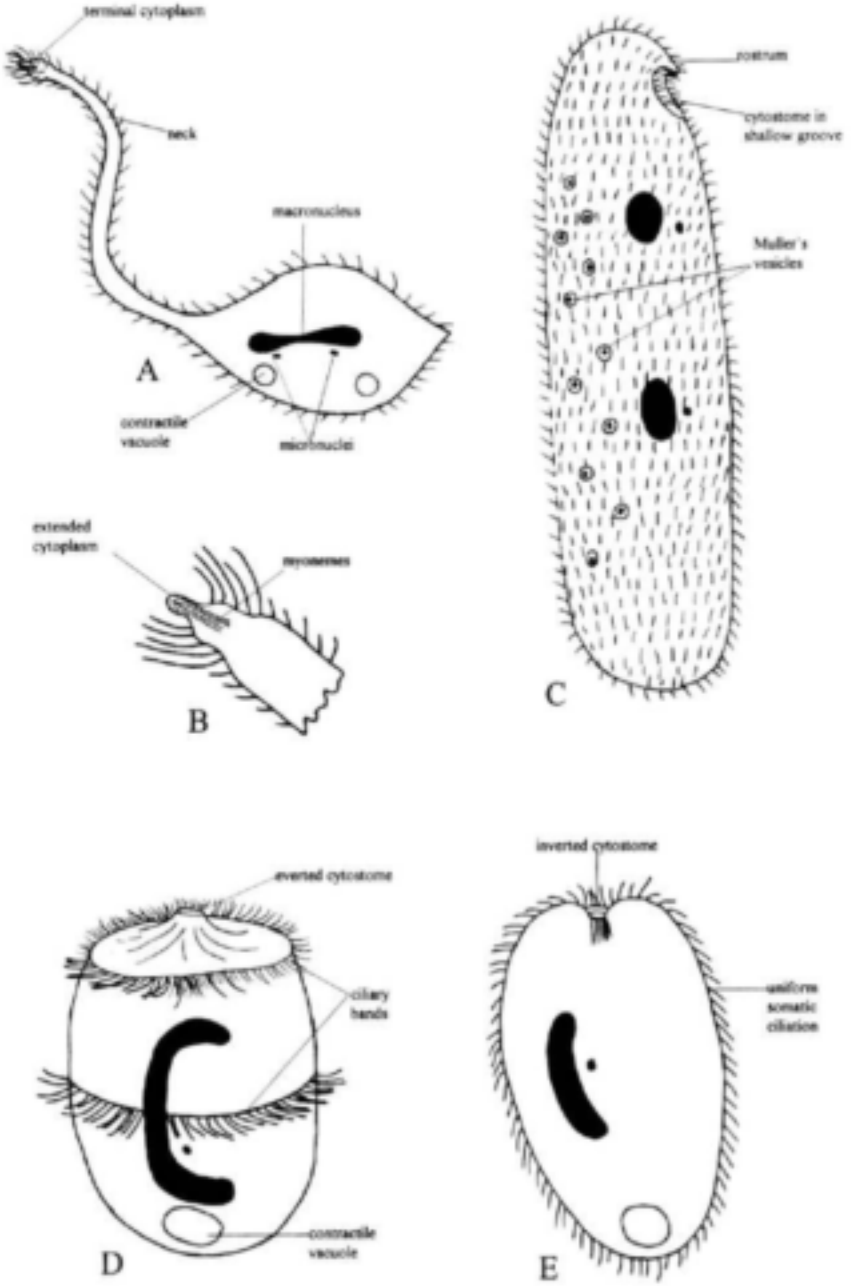

Fig. 1.26. Gymnostomatida. **A–B**, *Lacrymaria* sp. (Lacrymariidae) (500–1000+ µm extended): **A**, whole animal; **B**, detail of extended cytostome. **C**, *Loxodes* sp. (Loxodiidae) (125–700µm); **D**, *Didinium* sp. (Didiniidae) (100 –200µm); **E**, Prorodontidae (generalised) (100 + µm).

ORDER: HYMENOSTOMATIDA

Holotrichous ciliates with a complex buccal ciliature for feeding on small particles. These organelles are, unfortunately, difficult to see by conventional light microscopy in the large Paramoecidae, which were, until quite recently, included in the Trichostomatida. The Hymenostomatida include many small ciliates that are difficult to identify.

HYMENOSTOMATIDA: KEY TO TAXA

1. Large ciliates, >150 µm in length, with a distinct oral groove (**Paramoecidae**) .... *Paramoecium* (Fig. 1.27A)

– Small ciliates, <100 µm; no oral groove; buccal cavity typically with three membranelles and a paraoral undulating membrane; an anterior 'suture' separates left and right ciliary rows ....
.... **Tetrahymenidae** (e.g. *Tetrahymena* —Fig. 1.27B)
........................**Turaniellidae** (e.g. *Colpidium* — Fig. 1.27C)
.... **Glaucomidae**

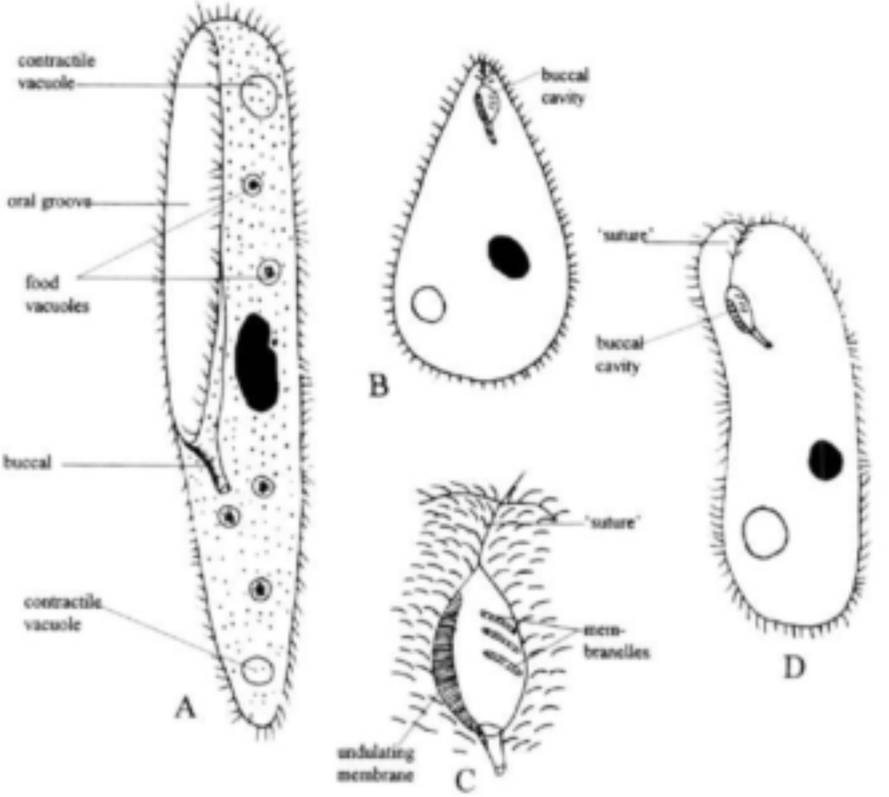

Fig. 1.27. Hymenostomatida: **A**. *Paramoecium* sp. (100–350 µm) (Paramoecidae); **B–C**, *Tetrahymena* sp. (30–60 µm) (Tetrahymenidae): **B**, whole animal; **C**, detail of buccal cavity; **D**, *Colpidium* sp. (50–60 µm) (Turaniellidae).

ORDER TRICHOSTOMATIDA

Holotrichous ciliates in which the cytostome is located in a vestibule without buccal organelles, although elongate oral cilia may be present. The genus *Colpoda* (Colpodidae—Fig. 1.28), characterized by its kidney shape, mid-ventral vestibule with elongate oral cilia and paired somatic cilia, occurs commonly, usually in stagnant water with decaying organic matter.

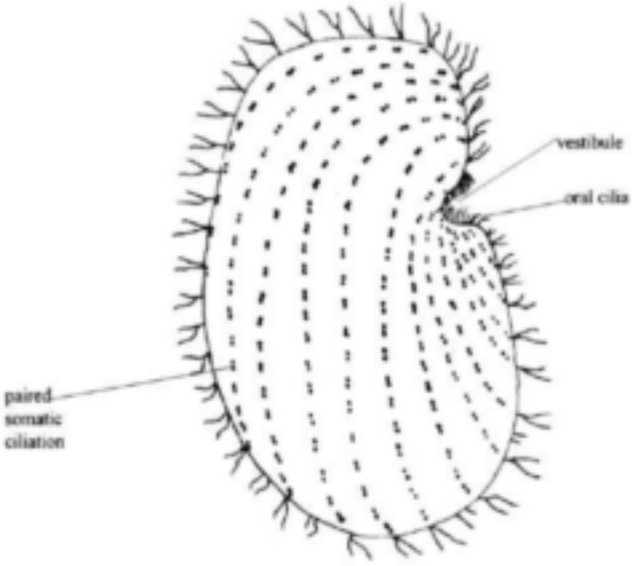

Fig. 1.28. Trichostomatida: *Colpoda* sp. (40–110 μm) (Colpodidae).

CLASS PERITRICHEA

Sedentary ciliates, solitary or colonial, with a number (usually three) of well-developed peristomial semi-membranes which wind anti-clockwise into a prominent buccal cavity. No somatic ciliature or membranelles. Includes a single order, *Peritrichida*, with the characteristics of the class.

PERITRICHIDA: KEY TO TAXA

1. Loricate .... **Vaginicolidae**.(e.g. *Vaginicola* —Fig. 1.29A)
– No lorica 2

2. Stalk contractile; solitary or colonial (**Vorticellidae**) 3
– Stalk non-contractile; colonial 4

3. Solitary, though may be densely packed, giving the impression of being colonial .... *Vorticella* (Fig. 1.29B)
– Colonial; colony dendriform, branching from a non-contractile stem; individuals contract independently ....*Carchesium* (Fig. 1.30)

4. A collar separates the peristome from the rest of the cell body .... **Epistylidae** (e.g. *Epistylus* —Fig. 1.31A)
– No collar between peristome and rest of cell body .... **Operculariidae** (e.g. *Opercularia* —Fig. 131B)

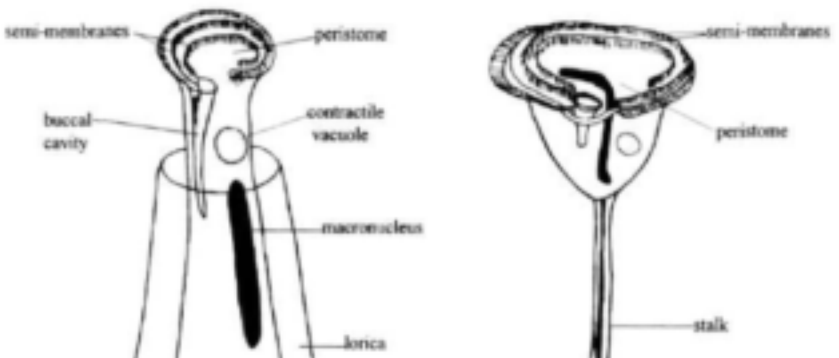

Fig. 1.29. Peritrichida: **A**, *Vaginicola* sp. (*ca.* 120 µm) (Vaginicolidae); **B**, *Vorticella* sp. (cell body 50 –100 µm) (Vorticellidae).

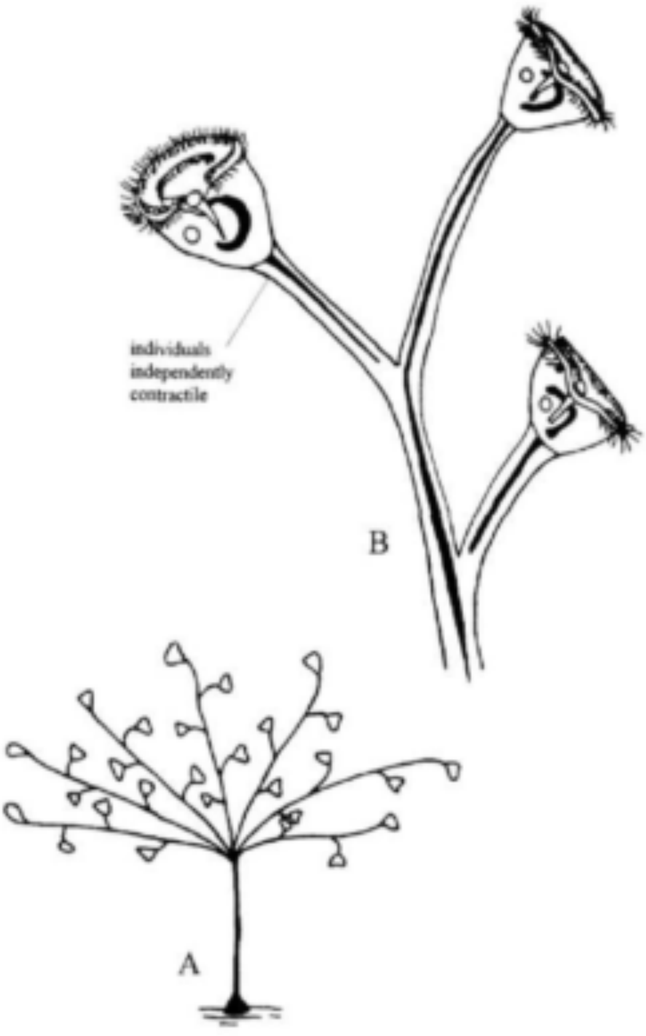

Fig. 1.30. Peritrichida, *Carchesium* sp. (Vorticellidae): **A**, colony form; **B**, detail of individuals (cell body *ca.* 100 µm).

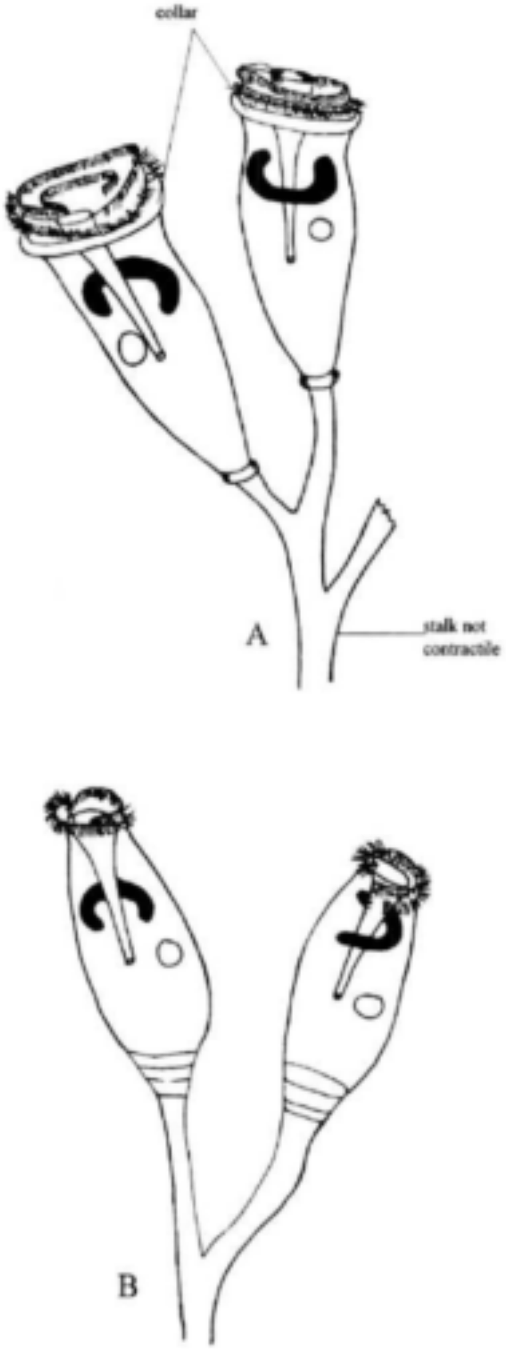

Fig. 1.31. Peritrichida: **A**, *Epistylus* sp. (Epistylidae) (cell body up to 160 µm); **B**, *Opercularia* (Operculariidae) (cell body up to 150 µm).

CLASS SUCTORIA

Sedentary ciliates with dimorphic nuclei in which cilia are only present in the 'swarmers' —free-swimming daughter individuals that are produced asexually by budding. These metamorphose into the adult form once settled. Adults capture prey by means of adhesive tentacles, through which digestive enzymes, and probably toxins, are injected into the prey, and the products of digestion are absorbed.

Classification into orders requires swarmer formation to be observed. The three families included below are said to occur commonly in freshwater in the Northern Hemisphere, usually associated with mosses and filamentous algae, or epizoic on animals ranging from planktonic crustaceans to fish and terrapins. The key below should be regarded as only the roughest of guides, and must be used with extreme circumspection. Where identification is important, a more comprehensive text should be consulted at the outset.

SUCTORIA: KEY TO FAMILIES

1. Loricate; usually stalked .... **Acinetidae**
– No lorica 2

2. Cell body spherical; usually stalked .... **Podophryidae**
– Cell body variously shaped, usually roughly triangular, never spherical; stalked or sessile .... **Tokophryidae**

ACKNOWLEDGEMENTS

Thanks are due to Jenny Day and Irene de Moor for helpful suggestions towards improving the format of this chapter, and to Nancy Bonsor for turning my sketches into acceptable illustrations.

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NOTES ON THE USE AND CONTENT OF SOME OF THE ABOVE REFERENCES

Corliss (1979): An excellent comprehensive work on the Ciliophora.

Curds et al. (1982): Volumes 22 and 23 of the series *Synopses of the British Fauna.* An excellent coverage of the Ciliophora, with keys and illustrated descriptions to the level of genera and a literature guide to keys and descriptions of species.

Hyman (1940): This well known text, though now outdated, is still a useful source of morphological and basic systematic information.

Jahn & Jahn (1940): A very useful beginners' guide, well illustrated and easy to use. Covers all the genera included here and more. Unfortunately, now out of print.

Lee et al. (1985): Probably the nearest to a comprehensive systematic treatment, representing the views of 12 leading protozoologists in a single volume. Profusely illustrated with both photographs and line drawings, it provides keys to, and describes, most recognized genera in a 'near consensus' systematic context, and includes a guide to all the important primary literature. Expensive, but essential for any serious researcher.

Pennak (1989): Includes a comprehensive key and line drawings.

Ward & Whipple (1959): Includes a comprehensive key and line drawings. Three chapters (described below) are devoted to protozoans.

Chapter 8. *Zooflagellates* by J.B. Lackey: 190–231.

Chapter 9: *Rhizopoda and Actinopoda* by G. Deflandre: 232–264.

Chapter 10: *Ciliophora* by L.E. Noland: 265–298.

CHAPTER 2

PORIFERA

by

J. Heeg

Sponges belong to the phylum Porifera, a name derived from the pores that perforate their outer surfaces. Most of the approximately 4 500 described species are marine. Only 22 genera, including approximately 110 species, have been recorded from fresh waters worldwide. The freshwater sponges comprise only four families in the order Haplosclerida of the Class Demospongia. Of these, two families—Lubomirskiidae and Adociidae — are monospecific and confined to the ancient Lake Baikal in Russia and one, the Potamolepidae with two genera and 11 species, seems to be confined to tropical Africa, extending at least as far south as the Zambezi and Kunene river systems and the coastal plain of northern KwaZulu–Natal. The remaining species all belong to the family Spongillidae, which has a worldwide distribution, and includes several genera and at least some species that appear to be cosmopolitan.

Freshwater sponges have not elicited much interest, particularly during the latter half of the twentieth century. Many species descriptions, involving numerous synonymies, date from the nineteenth century. The early decades of the twentieth century saw notable contributions from several workers, particularly Nelson Annandale, W. Arndt and N.G. Gee, which considerably extended our knowledge of freshwater sponges from localities other than Europe and North America. This more extensive knowledge, together with the widely dispersed early literature and the likelihood of many confusing synonymies, prompted Gee to initiate a revision of the Spongillidae, at that time the only generally recognized family of freshwater sponges. Gee amassed a very large collection of material from all over the world, but did not live to carry out the envisioned revision. His collection did, however, form the basis of a comprehensive revision by Penney & Racek (1968), which must now be regarded as the definitive work on the Spongillidae. A further notable and fundamental contribution to freshwater sponge systematics was that of Brien, who in several papers between 1966 and 1969, produced compelling evidence for their polyphyletic origin and inclusion in the four separate families mentioned above— see Brien (1969, 1970) for a summary and synthesis.

Seven species in five genera of Spongillidae have been recorded from southern Africa, and I have seen both genera of Potamolepidae, collected from the Okavango and Chobe rivers and Lake Nhlabane. This represents a very low species richness for the region as a whole. Focused collecting may well increase the number of species.

Morphology

The structure of a sponge is extremely simple, comprising a few unspecialised tissues and no recognizable organs. The cells of a sponge show a remarkable degree of plasticity, many being able to change their form and function depending on requirements at any particular time, and the degree of integration, though real, is low. This has led to a sponge being likened to a loosely integrated colony of protozoans.

Essentially, a sponge consists of a number of chambers lined by collared flagellated cells called choanocytes, which have a structure similar to that of the Choanoflagellida (see Protozoa, Chapter 1). These flagellated chambers are interconnected by a network of canals and are embedded in a jelly-like substance, the mesoglea or mesohyl. The whole structure is enclosed in a perforated outer membrane, the epidermis, and is supported internally by a skeleton comprising a meshwork of siliceous spicules and fibres of a keratin-like protein called spongin embedded in the mesoglea. In addition to those spicules that form the skeletal meshwork — known as megascleres — many species contain smaller, structurally distinct, spicules called microscleres, in the mesoglea. Microscleres seldom exceed 20% of the length of a megasclere, and are usually much smaller. The pores perforating the epidermis are of two distinct sizes: numerous very small perforations called ostia (sing. ostium) and fewer larger openings called oscula (sing. osculum). The mesoglea, although in itself acellular, contains a variety of amoeba-like cells or amoebocytes which move about within it and are responsible for most of the important life functions of the sponge. They digest food and distribute assimilated food to where it is needed; they produce skeletal spicules and spongin; they are also responsible for both sexual and asexual reproduction. Different types of amoebocytes are named according to their specialised functions. Sponge cells show a remarkable degree of plasticity in both form and function: not only can different amoebocytes change their functional roles, but amoebocytes may

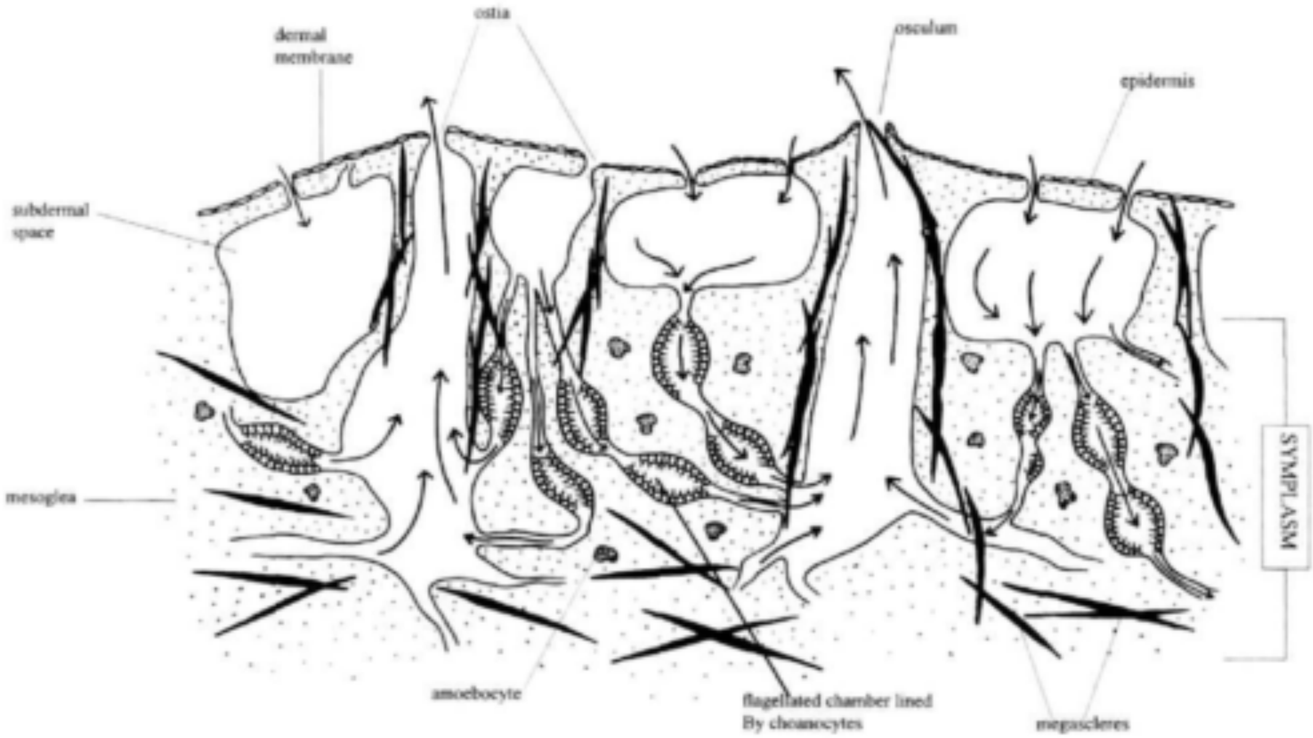

Fig. 2.1. Diagrammatic representation of the general structure of a freshwater sponge of the family Spongillidae, reconstructed from a series of sections through *Ephydatia fluviatilis*. Arrows show the paths of water currents through the sponge.

assume the form and role of choanocytes and *vice versa*.

Figure 2.1, a diagrammatic reconstruction of *Ephydatia fluviatilis*, illustrates the structure typical of the freshwater family Spongillidae. The ostia open into large cavities usually referred to as sub-dermal spaces, separated by columns of the spicular skeleton. The sub-dermal spaces are, in fact, cavities in the mesoglea, since a thin mesogleal layer remains attached to the inner surface of the epidermis to form a dermal membrane. The main body of the sponge, separated from the dermal membrane by the sub-dermal space, is referred to as the symplasm. Attachment of the sponge to the substratum is through the secretion of a basal cuticular membrane by the cells in contact with the substratum. Spongin maintains the integrity of the skeletal meshwork; amoebocytes secrete spongin around groups of skeletal spicules, binding them together in rows or groups, thus giving both form and resilience to the sponge as a whole.

GENERAL BIOLOGY

Studies on freshwater sponges have been almost entirely confined to taxonomy and their general biology is largely inferred from the better-studied marine sponges. Given their simple tissue grade structure and undoubted relationship to marine sponges, this inference seems provisionally valid in the absence of contrary evidence. The lack of organ systems particularly a nervous system, devolves most life activities to the level of individual cells, yet a sponge behaves as an integrated whole. This is largely attributable to the amoebocytes, of which there several forms, each performing a specific function.

Feeding

All sponges are filter feeders, extracting small organic particles (bacteria, small protozoans, and fine organic detritus) from the surrounding water. Water, together with suspended matter, is drawn into the sponge through the ostia by the combined action of the flagella of the choanocytes and external water movements such as currents and waves. Within the sponge, water is channelled through the flagellated chambers, and via the system of exhalent canals, to the oscula, where it is expelled (see Fig. 2.1). On passing through the flagellated chambers, organic particles are selectively filtered out of the water by the choanocytes and taken up in food vacuoles; these are later passed on to wandering amoebocytes, which digest contained food, assimilate the products of digestion and store them intracellularly for later distribution where needed. Thus, while the processes of feeding, digestion and assimilation are typically protozoan, the division of labour and the redistribution of nutrients reflect a degree of integration which clearly distinguishes sponges from colonial protozoans. Several species have been reported as harbouring autotrophic symbionts, but the degree of dependence of these species on their symbionts is not known.

Reproduction

Sponges reproduce both sexually and asexually. Sexual reproduction maintains genetic heterogeneity and facilitates dispersion within a water body. Groups of choanocytes or amoebocytes undergo meiotic division to form spermatids, which give rise to spermatozoa by mitosis. These leave the sponge through the oscula with the exhalent current. Female gametes arise from archaeocytes—very large, sedentary amoebocytes which have been charged with substantial quantities of stored food material by wandering amoebocytes called 'nurse cells'. The archaeocytes undergo meiosis to form ova. Sperm enter a sponge via the ostia with the inhalent current, are entrapped by the choanocytes, and are carried to unfertilized ova by amoebocytes. Larval development takes place within the parent sponge. Repeated mitotic divisions and differentiation of the daughter cells into a mass of amoebocytes, wholly or partially surrounded by flagellated cells, result in the formation of a free-swimming larva that is expelled with the exhalent current. After a brief planktonic existence the larva settles to undergo further differentiation and reorganization of the cells to form a new individual sponge.

Most sponges can reproduce asexually when fragments resulting from mechanical damage settle fortuitously in a locality where they can establish themselves and grow. Freshwater sponges, and a few marine species, have evolved specialised forms of asexual reproduction that enhance survival under adverse conditions such as seasonal drying up or freezing of the habitat. In freshwater species, these methods of asexual reproduction are thought to also facilitate wider dispersal between water bodies. Prior to the seasonal onset of adverse conditions, groups of amoebocytes, that have accumulated considerable food reserves and are known as thesocytes, become enclosed in a resistant cuticular envelope. Many such packages, known as a 'winter bodies', gemmules or statoblasts, remain enmeshed in the skeleton or attached to the basal membrane (and thus the substratum), after the death of the parent sponge. Some may also be carried to new localities. Being resistant to desiccation, winter bodies also provide a means for the wider dispersal of the species by wind (should the habitat dry out completely) or in mud on the legs of animals. They remain dormant until favourable conditions return, when the enclosed thesocytes emerge and differentiate to form a new sponge. Thesocytes from a number of winter bodies that have originated from the same parent sponge are known to contribute to the formation of a single new sponge if they come into contact during the differentiation process. This would facilitate the rapid reoccupation of the original, presumably favourable, site in successive seasons, since many winter bodies remain associated with the skeleton and basal membrane after the death of the parent sponge.

Brien (1969) draws a clear distinction between the winter bodies of the Spongillidae, to which he suggests that the term 'gemmule' should be confined, and those of the Potamolepidae to which he refers by the more general term 'statoblast'. Details of the structure of a gemmule of *Ephydatia* sp. are illustrated in Fig. 2.2 and are more or less representative of the

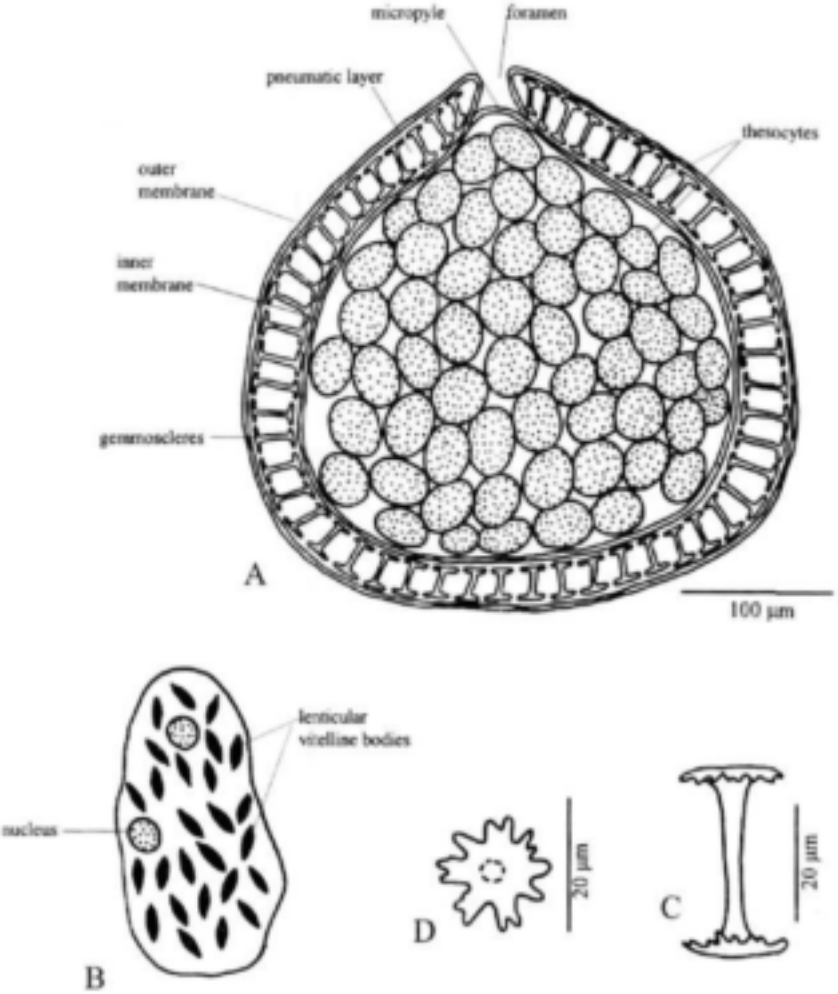

Fig. 2.2. Spongillid gemmule structure: **A**, diagrammatic representation of a section through the gemmule of *Ephydatia fluviatilis*; **B**, thesocyte detail; **C–D**, birotulate gemmosclere: **C**, lateral view; **D**, end view.

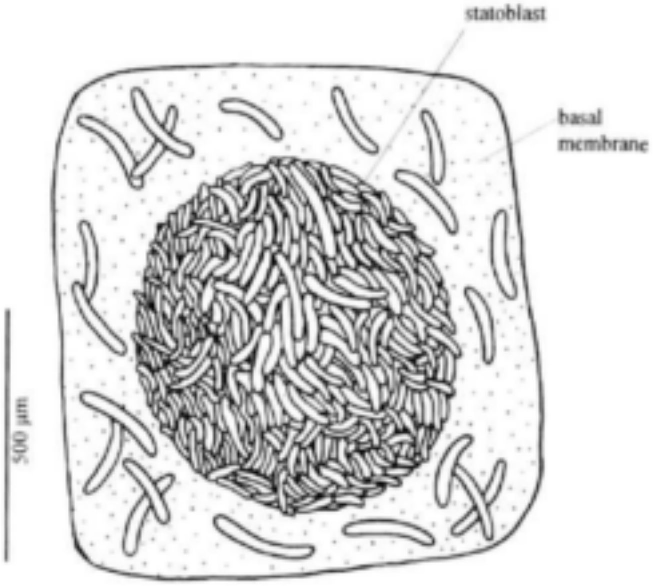

Fig. 2.3. Surface view of a statoblast (on basal membrane) of *Potamolepis* sp.

Spongillidae. A group of thesocytes is surrounded by a cuticular membrane, the inner membrane. Each thesocyte is bi- or multi-nucleate, and contains food reserves in the form of numerous lenticular vitelline bodies, all of approximately the same size. Surrounding the inner membrane is a thicker, non-living layer, generally referred to as the pneumatic layer, the name deriving from the presence in some species (though not in *Ephydatia*) of numerous small gas-filled alvaeoli or 'air spaces'. Embedded in the pneumatic layer are small spicules, structurally distinct from the microscleres, known as gemmoscleres, which presumably add to the mechanical strength of the gemmule. The micropyle, from which the thesocytes will ultimately emerge, is located below a foramen through the pneumatic layer. In several species, particularly those with a very well-developed pneumatic layer, the foramen is lined by a porous tube connecting the micropyle with the surface of the gemmule. A thin outer membrane encloses the whole structure. In contrast to the relatively complex structure of the spongillid gemmule, Brien (1969) describes the statoblast of the Potamolepidae as a group of uni-nucleate thesocytes, each containing irregular, variously-shaped, vitelline inclusions, enclosed in a cuticular envelope. There is no pneumatic layer nor micropyle, and mechanical reinforcement is by miniature versions of the megascleres, rather than distinct gemmoscleres, aggregated to form a mosaic on the surface of the statoblast (Fig. 2.3).

Habitat Preferences

Freshwater sponges are known to occur in both permanent and temporary running and standing waters worldwide. In spite of this, very little is known of their ecology. They need a solid, stable substratum for attachment, and are thus found on the surfaces of submerged rocks, logs and roots, in fact on anything firm and sufficiently raised above the substratum to ensure that the sponge is not covered by silt or detritus. Most species occur in shallow water, very few having been recorded from depths greater than four metres. This preference may reflect their dependence on wind-driven water currents to augment the action of the flagella in drawing feeding currents through the sponge. Species harbouring autotrophic symbionts would, of necessity, be confined to shallow waters where there is sufficient light for photosynthesis.

Aspects of water chemistry have been implicated in determining the distribution of a few spongillid species, including two apparently cosmopolitan species (*Ephydatia fluviatilis* and *Eunapius fragilis)* known to occur in southern Africa (Jewell, 1935, 1939, quoted in Pennak, 1989). Jewell's studies indicated that concentrations of calcium, inorganic carbon and silicon, as well as pH, were apparently important environmental factors governing the distribution of individual species, but that there were significant intra-generic differences. *Ephydatia fluviatilis* seemed to prefer alkaline conditions, whereas *Eunapius fragilis* tolerated a wide range of pH and dissolved solids, but was limited by calcium concentrations below 2.1 mg/litre.

COLLECTION AND PRESERVATION

Freshwater sponges are usually collected by chance rather than design, since we have only a rudimentary knowledge of their habitat requirements. Careful examination of suitable substrata may yield specimens. The use of a metal scoop might allow more effective sampling, but such a device is also likely to damage specimens as they are, for the most part, very fragile. Wherever possible, the sponge should be collected still attached to its substratum, since the removal of intact specimens from their substrata often proves to be difficult.

Collected specimens should be preserved in 70% alcohol. Wrapping individual specimens (together with their field labels) in soft tissue paper after preliminary fixation in alcohol, and storing these in alcohol between wads of cotton wool, provides adequate protection against mechanical damage during transportation. Intact specimens which have been carefully dried can usually still be identified, since spicules and winter bodies will have been preserved. They are, however, very prone to damage.

IDENTIFICATION

The identification of freshwater sponges requires microscopic examination of the spicules and winter bodies. Maceration by placing a small piece of sponge overnight in a 5% solution of either sodium or potassium hydroxide will leave a residue of spicules and winter bodies which must be carefully washed in several changes of distilled water, dehydrated and mounted in either balsam or Euparal for examination under the microscope. An alternative method for the rapid examination of spicules is given by Pennak (1989) who recommends maceration in hot concentrated (fuming) nitric acid. A small piece of sponge is placed on a microscope slide, covered with a few drops of nitric acid, heated to dryness over a flame in a fume cupboard, and mounted directly in balsam. This treatment destroys everything except spicules, and obviates the need for repeated washing and dehydration prior to mounting, but is apparently not suitable for permanent mounts of voucher specimens. Overnight maceration of gemmules in concentrated nitric acid at room temperature can also be used to reduce the opacity of the pneumatic layer. See Pennak (1989) for details on the use of nitric acid.

Microscleres, because of their small size, are easily lost in the processes described above. They are most abundant in the dermal membrane, fragments of which should be dehydrated, cleared and mounted to show the presence and structure of microscleres.

Three spicule types, illustrated in Fig. 4.4, occur in the genera recorded from southern Africa: amphioxeas (Fig. 2.4A–C) are characterised by both ends being pointed to various degrees, amphistrongyles (Fig. 2.4D–F) have rounded, blunted ends and birotulates (Figs 2.2C & 2.4G) have a rotule or disc, which may be variously ornamented with spines at each end. All spicule types may, depending on species, be furnished with granules or spines at various locations along their length.

KEY TO THE GENERA OF FRESHWATER SPONGES RECORDED FROM SOUTHERN AFRICA

Introduction

The following key to the genera recorded from the Zambezi and Kunene systems southward must be used with circumspection, since it is partly based on descriptions in the literature rather than on personal observations. Furthermore, there is every likelihood that the seven genera included here do not represent the total fauna. The species recorded from southern Africa, together with such distribution data as are available, are listed at the end of the key. Most recorded genera seem to be represented in the region by a single species, but this requires confirmation. In the genus *Eunapius*, where three species have been recorded from southern Africa, criteria for their initial separation are given, but, since identification is based on a suite of characters, further confirmation is required. It is therefore necessary to refer to the primary literature wherever accurate identification is important. Penney & Racek (1968) give comprehensive descriptions of the genera in the Spongillidae as well as of those species for which adequate type, or voucher study-material, was available; Brien's (1969, 1970) syntheses of the Potamolepidae provide references to the original descriptions of species included in this family. These references should be used as a first step in any attempt to identify specimens beyond the scope of this key. Using keys that antedate these publications is likely to land one in a mire of synonymies.

KEY TO THE GENERA

1. Winter bodies are of the gemmule type with pneumatic layer, foramen and micropyle; sponge usually soft to brittle; skeleton a loose reticulation of megascleres scattered throughout symplasm and/or arranged in radial and transverse bundles (Fig. 2.1); megascleres are slender amphioxeas (Fig. 2.4A–C) or amphistrongyles, (Fig. 2.4D), with a length:width ratio greater than 10:1 (usually much greater), but if the length:width ratio approximates 10:1 then birotulate microscleres are present; gemmules are located in the symplasm and/or on the basement membrane (**Spongillidae**) 2

– Winter bodies are simple statoblasts, lacking pneumatic layer, foramen and micropyle (Fig. 2.3); sponge robust, firm; skeleton a dense reticulation of megascleres aggregated in bundles of six to eight (Fig. 2.5); megascleres stout, distinctly curved amphistrongyles with a length:width ratio less than 10:1 and occasionally a few slender amphioxeas; microscleres never present; statoblasts attached to the basal cuticular layer, enclosed in lacunae in symplasm (**Potamolepidae**) 6

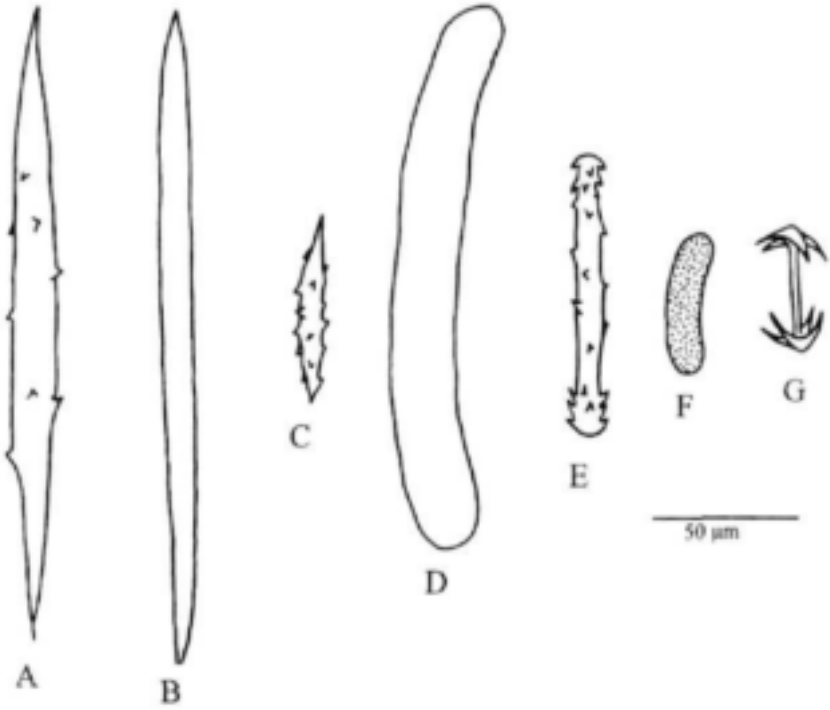

Fig. 2.4. Spicule types found in freshwater sponges. **A–C**, amphioxeas: **A**, megasclere of *Stratospongilla*; B, megasclere of *Ephydatia*; **C**, microsclere of *Stratospongilla*. **D–F**, amphistrongyles: **D**, megasclere of *Potamolepis*; **E**, gemmosclere of *Eunapius*; **F**, gemmosclere of *Stratospongilla*. **G**, birotulate microsclere of *Corvospongilla*. (G redrawn from Kirkwood 1906)

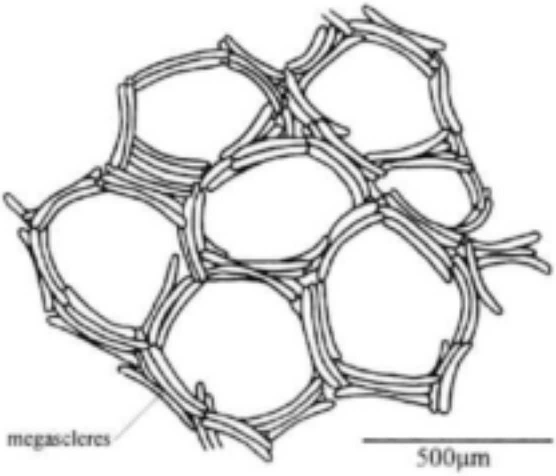

Fig. 2.5. Surface view of the skeletal network of *Potamolepis* sp. drawn from a dried specimen.

2. Microscleres present. 3
– Microscleres absent (but see comment on gemmoscleres in *Radiospongilla* — couplet 5) 4
3. Microscleres are short, slender, sharply-pointed amphioxeas covered in small spines (Fig. 2.4C); gemmules usually flattened at base, with poorly-defined pneumatic layer, aggregated at the base of the sponge; gemmoscleres short, stout, finely- granulated amphistrongyles aggregated on the inner and outer membranes of the gemmule. .... *Stratospongilla*
– Microscleres are microbirotulates (Fig. 2.4G); gemmules oval or flattened at the base, usually located at base of sponge, enclosed in a cage formed by megascleres; pneumatic layer poorly developed or absent; gemmoscleres spined, distinctly-curved amphistrongyles ....*Corvospongilla*

4 Gemmoscleres are birotulates embedded radially in a moderately well-developed pneumatic layer (Fig. 2.2); gemmules numerous, sub-spherical, scattered throughout the symplasm; foramen without a porous tube .... *Ephydatia*
– Gemmoscleres are amphioxeas and/or amphistrongyles; gemmules either scattered in symplasm or basal; foramen with a porous tube. 5

5. Pneumatic layer of gemmule well developed, with large polygonal air spaces (Fig. 2.6A); foramen tubular; gemmoscleres are strongly-spined amphistrongyles with spines more numerous at the ends (Fig. 2.4E), embedded tangentially in pneumatic layer (Fig. 2.6A); gemmules often somewhat flattened, and may occur in large numbers; in some species gemmules often form a distinct pavement with a common pneumatic layer at the base of the sponge, or they may form aggregations of small groups with a common pneumatic layer .... *Eunapius*

– Pneumatic layer well developed but with minute, irregularly-shaped air spaces; gemmoscleres are slender, strongly-spined amphistrongyles, spines occurring in greater numbers at the tips, where they are markedly recurved; gemmoscleres embedded radially in the pneumatic layer. In the only species recorded from southern Africa the gemmoscleres occur in two series (biseriate) with only the inner series radially embedded, the outer series being arranged more or less randomly at the surface of the pneumatic layer (Fig. 2.6B); gemmules small, scattered throughout the sponge (*Note*: in the young, developing sponge, gemmoscleres may occur in the dermal membrane and symplasm; these should not be confused with microscleres) .... *Radiospongilla*

6. Sponge encrusting, cushion-like; surface smooth; oscula distributed in a regular fashion over surface .... *Potamolepis*
– Sponge forms a fusiform mass; surface rugose (rough), bark-like, often hispid (bristly); oscula irregularly distributed over surface, often located on raised protuberances .... *Potamophloios*

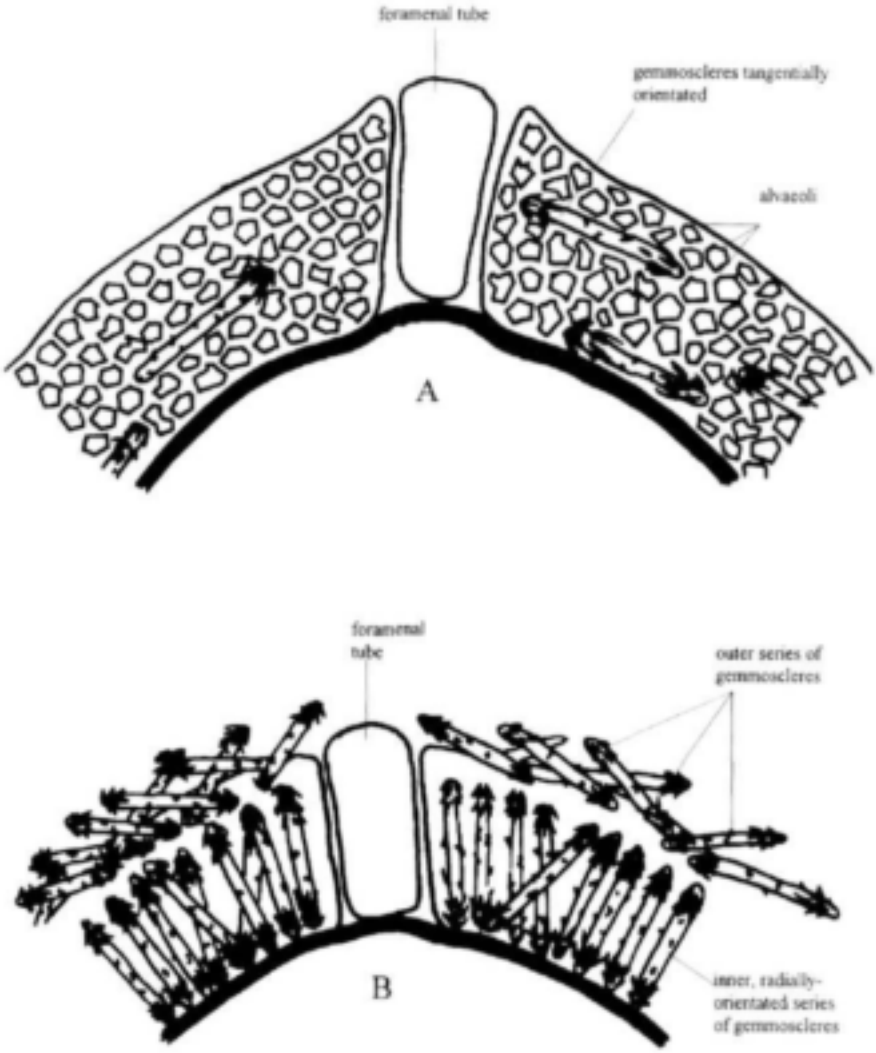

Fig. 2.6. Diagrammatic representation of the micropylar regions of gemmules of two spongillid species: **A**, *Eunapius* sp., showing the large alvaeoli and tangentially-orientated gemmoscleres; **B**, *Radiospongilla cerebellata*, showing the radial orientation of the inner series of biseriate gemmoscleres. (B from the description in Penney and Racek 1968).

LIST OF RECORDED SPECIES

CLASS: Demospongia

ORDER: Haplosclerida

Family: **Spongillidae**

Eunapius Gray, 1867

E. fragilis (Leidy, 1851): Zimbabwe, KwaZulu–Natal; cosmopolitan; a soft, fragile, flat, encrusting sponge with a smooth surface; colour light gray to white; gemmules usually form a pavement at base of sponge.

*E. michaelseni** (Annandale, 1914): Zambezi River; a moderately hard, brittle, encrusting sponge; colour light grey; gemmules occur in small groups with a common pneumatic layer near base of sponge.

*E. nitens** (Carter, 1881): Zambezi System; a massive, nodulose sponge; gemmules not in groups, scattered throughout sponge.

Stratospongilla Annandale, 1909

*S. bombayensis*** (Carter, 1882): Far East to central Africa, down to KwaZulu–Natal; a thin encrusting sponge; surface irregular; consistency brittle.

Corvospongilla Annandale, 1911

*C. zambesiana** (Kirkpatrick, 1906): Zambezi System; a thick, encrusting sponge with an irregular surface. Description lacking in essential details, particularly of gemmule.

Radiospongilla Penney & Racek, 1968

*R. cerebellata** (Bowerbank, 1863): cosmopolitan; Zambezi System; form varies from shallow cushions to large bulbous masses; surface brainlike; consistency soft; colour varied—yellow, grey, green.

Ephydatia Lamouroux, 1816

E. fluviatilis (Linneaus, 1758): temperate regions worldwide: Cape Flats, Free State, Northern Cape, KwaZulu–Natal, Namibia; form bulbous with corrugated surface; consistency brittle; colour brown; usually found on stems of emergent plants, often in temporary waters.

Family: **Potamolepidae**

Potamolepis Marshall, 1883

Although this genus is widespread in tropical Africa, it is only known in southern Africa from the Popa Rapids in the Okavango River (Namibia). Not identified to species-level.

Potamophloios Brien 1969

Distribution as for *Potamolepis*. Known in southern Africa only from unidentified specimens from the Chobe River (Namibia) and from Lake Nhlabane in northern KwaZulu–Natal.

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* Information from descriptions; actual specimens not seen.

** Information based largely on descriptions; only a small fragment without gemmules actually seen.

ACKNOWLEDGEMENTS

Thanks are due to Barbara Curtis (National Museum of Namibia) for the loan of the Namibian material and to Chris Appleton (University of Natal) and to Maitland Seaman (University of the Free State) for South African specimens. Janet Sheldon-Heeg (Technikon S.A.) assisted me by translating substantial portions of the French literature quoted, and Nancy Bonsor produced the illustrations from my often rough sketches.

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Note on References: Annandale (1914) includes distribution data for the whole of Africa.

CHAPTER 3

CNIDARIA

by

N.A. Rayner, C.C. Appleton & N.A.H. Millard†

The Phylum Cnidaria was formerly known as the Coelenterata (hollow intestine) but that term now refers collectively to two Phyla: the Cnidaria and the Ctenophora (comb jellies — all marine). Cnidarians are defined as being predaceous carnivores with a tissue level of organization. They utilize nematocysts (stinging cells), which are exclusive to the Cnidaria, for defence and to obtain prey. There are three well-defined cnidarian classes: the Hydrozoa (hydroids, siphonophores, hydrozoan medusae), the Scyphozoa (marine jellyfish) and the Anthozoa (corals, sea anemones, soft corals). These comprise about 11 000 species that occur in a wide variety of marine habitats and are often abundant.

Comparatively few cnidarians occur in freshwater. Species of *Hydra*, *Chlorohydra* and *Pelmatohydra* (all commonly known as 'hydras') are included in the Class Hydrozoa, Order Hydroida, and the freshwater jellyfish are classified in the Class Hydrozoa, Order Trachylina, Family Limnomedusae. Distribution of hydra is not well known outside of North America, probably mainly due to sporadic collection effort. *Chlorohydra viridissima* which has been recorded from North America, Europe, Greenland, South America and New Zealand (Pennak, 1978) probably occurs in South Africa. Of the Limnomedusae, two freshwater species (*Craspedacusta sowerbii* and *Limnocnida tanganjicae*) and one brackish-water species (*Ostroumovia inkermanica*) have been recorded in southern Africa. *Craspedacusta sowerbii* has been recorded extensively in northern temperate countries (Kramp, 1961) and more recently in temperate regions of South Africa (Rayner, 1988, 1997; Rayner & Appleton, 1989, 1992). *Limnocnida tanganjicae* is endemic to subtropical and tropical Africa (Rayner &

Appleton, 1989; Dumont, 1994). *Ostroumovia inkermanica* is known from the Black Sea (Kramp, 1961) and has also been recorded from lakes on the east coast of KwaZulu–Natal and Mozambique (Millard, 1975). This account relates to the freshwater cnidarians, namely species of *Hydra*, *Pelmatohydra*, *Chlorohydra* and the three species of Limnomedusae.

General morphology

Cnidarians are diploblastic, acoelomate, radially symmetrical invertebrates. There are two basic homologous body forms of the Cnidaria: the asexual, sessile polyp (also called a 'hydranth') (Fig 3.1A) and the sexual, motile (free-swimming) medusa (Fig 3.2F). The polyp is cylindrical, attached aborally, and is either solitary or colonial (in which case it is sometimes called a 'hydroid colony'). The medusa is bell- or saucer-shaped, with the mouth on the undersurface (it has been likened to an 'upside down polyp'). Both polyps and medusae are similar in terms of the structure of internal organs and the general organization of tissues. There is only one internal cavity, the gastrovascular cavity, with one opening, the mouth. The body wall consists of two cellular layers, the ectoderm and endoderm, separated by a jelly-like mesogloea which contains a few amoeboid cells and is of varying thickness and complexity. The endoderm lining the gastrovascular cavity is termed the gastrodermis. All cnidarians have nematocysts (stinging capsules – Fig. 3.1B & C), which are located in the ectoderm and are mainly concentrated on the tentacles (Fig. 3.1A). Each nematocyst contains a coiled thread, which is associated with paralysing substances and can be extruded explosively by turning inside out. Nematocysts are fired only once and replaced by new ones which form from interstitial cells in the ectoderm. Nematocysts enable cnidarians to capture relatively large prey or prey that would otherwise escape. Cnidaria are regarded as 'fishermen' as they do not actively pursue prey. Some organisms such as the marine opisthobranchian mollusc *Glaucus atlanticus* feed on cnidarians and after incorporating the nematocysts into their tissues, use them as a ' second-hand' defence mechanism. Cnidarian digestion is initially extracellular and later intracellular. Undigested material is extruded through the mouth.

HYDROZOA IN SOUTHERN AFRICA: KEY TO TAXA

1. Solitary polyps with tentacles; gonads directly on the body wall; without a medusoid stage (Figs 3.1A, D) 2

– Polyp small and inconspicuous; with or without tentacles; solitary or colonial (Figs 3.2 A–D, 3.3A–B, F); medusoid stage dominant (Figs 3.2F, 3.3E, H–F) (**Limnomedusae**) 3

2. Colour usually green; column 15–30 mm long; usually 4–12 tentacles; column uniform in width (Fig. 3.1D) .... *Chlorohydra viridissima*

– Colour brown, column up to 20 mm long; tentacles longer than body; basal part of the column forms a slender stalk (Fig. 3.1E) ....*Pelmatohydra oligactis*

3. Medusa almost spherical (Fig. 3.2F); gonads on the wall of the gastrovascular cavity and on its radial extensions; polyp with extensile tentacles (Fig. 3.2A–D) (Subfamily **Moerisiidae**) .... *Ostroumovia inkermanica*

– Medusa not spherical (Figs 3.3E, H); gonads as a ring around the mouth or suspended from the radial canals; polyp without tentacles (Figs 3.3A, F) 4

4. Medusa 5–10 mm in diameter; gonads suspended from the four radial canals (Fig. 3.3E) (Subfamily **Olindiadidae**) .... *Craspedacusta sowerbii*

– Medusa 20–25 mm in diameter; gonads as a ring around the mouth (Fig. 3.3H) (Subfamily **Limnocnididae**) .... *Limnocnida tanganjicae*

CLASS: HYDROZOA

Order Hydroida

Suborder: **Anthomedusae**

There are a number of records of hydras in southern Africa. Although these have not been authoritatively identified, they include a number of species of *Hydra* and probably at least two other cosmopolitan species – *Chlorohydra viridissima* and *Pelmatohydra oligactis*.

HYDRA

Morphology

Species of *Hydra* reach about 15 mm in height when expanded (Figs 3.1A, D, E). They attach loosely to the substratum by a pedal disc ('holdfast') and bear a circle of about 11 hollow tentacles around the mouth. The polyp is cylindrical, attached to the substratum at the aboral end, with a whorl of tentacles around the mouth. In the centre of the circlet of tentacles is a raised dome-like hypostome that bears a single opening, the mouth. Polyps are solitary or colonial. *Hydra* species do not have a medusoid stage and gonads develop externally on the body wall of the polyp.

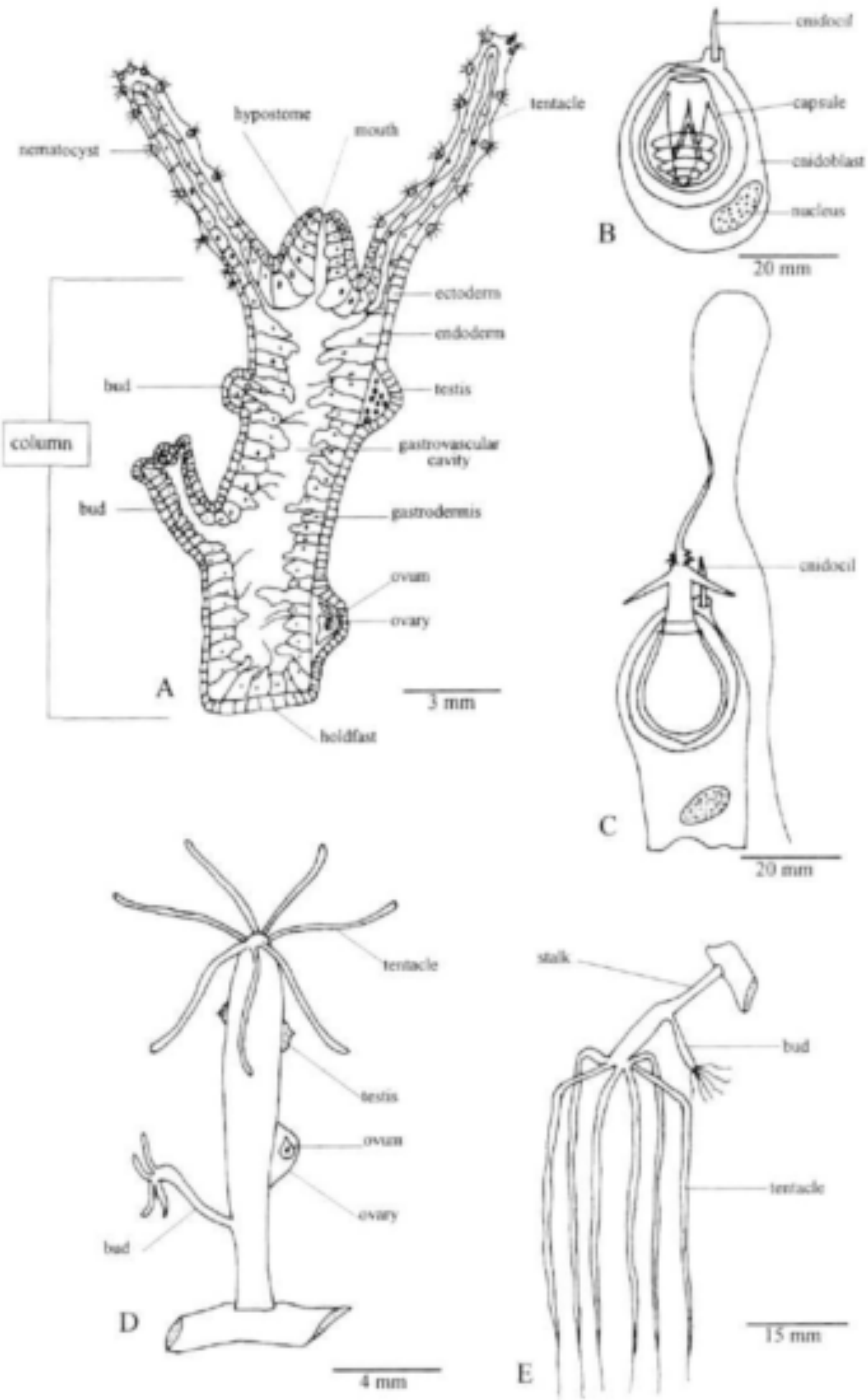

Fig. 3.1. Cnidarians. **A**, *Hydra sp.*, vertical section showing characteristic features of polyp. **B–C**, nematocysts: **B**, in undischarged state; **C**, in discharged state. **D**, *Chlorohydra viridissima*, habitus. **E**, *Pelmatohydra oligactis*, habitus.

Habitat preferences

Hydra species are common in freshwater ponds, streams, ornamental ponds and water tanks. They are sessile and may be found attached to stones, vegetation and the perimeter of the pond. They can, however, move along the substratum by gliding on the pedal disc or by means of looping movements, using the pedal disc and the tentacles alternately to attach themselves to the substrate. Possibly as a result of food shortage, *Hydra* may sometimes be seen to be inverted at the surface, attached to the surface film by mucus. Hydras are usually brown or green in colour, depending on their age and the coloration of ingested unicellular algae. Although there are few local records, it seems likely that they will be present in any suitable freshwater habitat.

Records

Species of *Hydra* have been recorded in standing waters in KwaZulu–Natal and in both slow-flowing and standing waters in the Western Cape. Although there are only a few definite records of *Hydra* spp. in southern Africa, their distribution in the region is probably widespread.

Feeding

Hydra species are carnivorous, feeding on small crustaceans, worms and insect larvae, which they capture with the extended tentacles. The prey is paralysed by the nematocysts (Fig. 3.1A–C) and transferred to the mouth. Glutathione (a peptide released by the wounded prey) stimulates *Hydra* to open its mouth. The body wall then contracts to force the food downwards. Food particles are engulfed by the pseudopodia of the gastrodermal cells and undigested particles are voided from the mouth. Digested food is stored in the gastrodermis as fat and glycogen or distributed to the epidermis.

Reproduction

The medusa of *Hydra* species is suppressed. The gonads are borne directly on the body wall (Fig. 3.1A). Asexual reproduction by budding of new polyps (Fig. 3.1A) is common when conditions are favourable. Each polyp detaches and develops into a new polyp. An environmental cue, such as decreasing daylight length or a reduction in water temperature, will stimulate sexual reproduction, which involves the formation of gonads on the outer surface of the body wall. Sexes are usually separate, but if the individual is hermaphroditic, the testes are higher up on the column (Fig. 3.1A). The ovary contains one or two large ova. After fertilization, the ovum is covered by a tough coat and will lie dormant as a cyst in the mud until conditions are

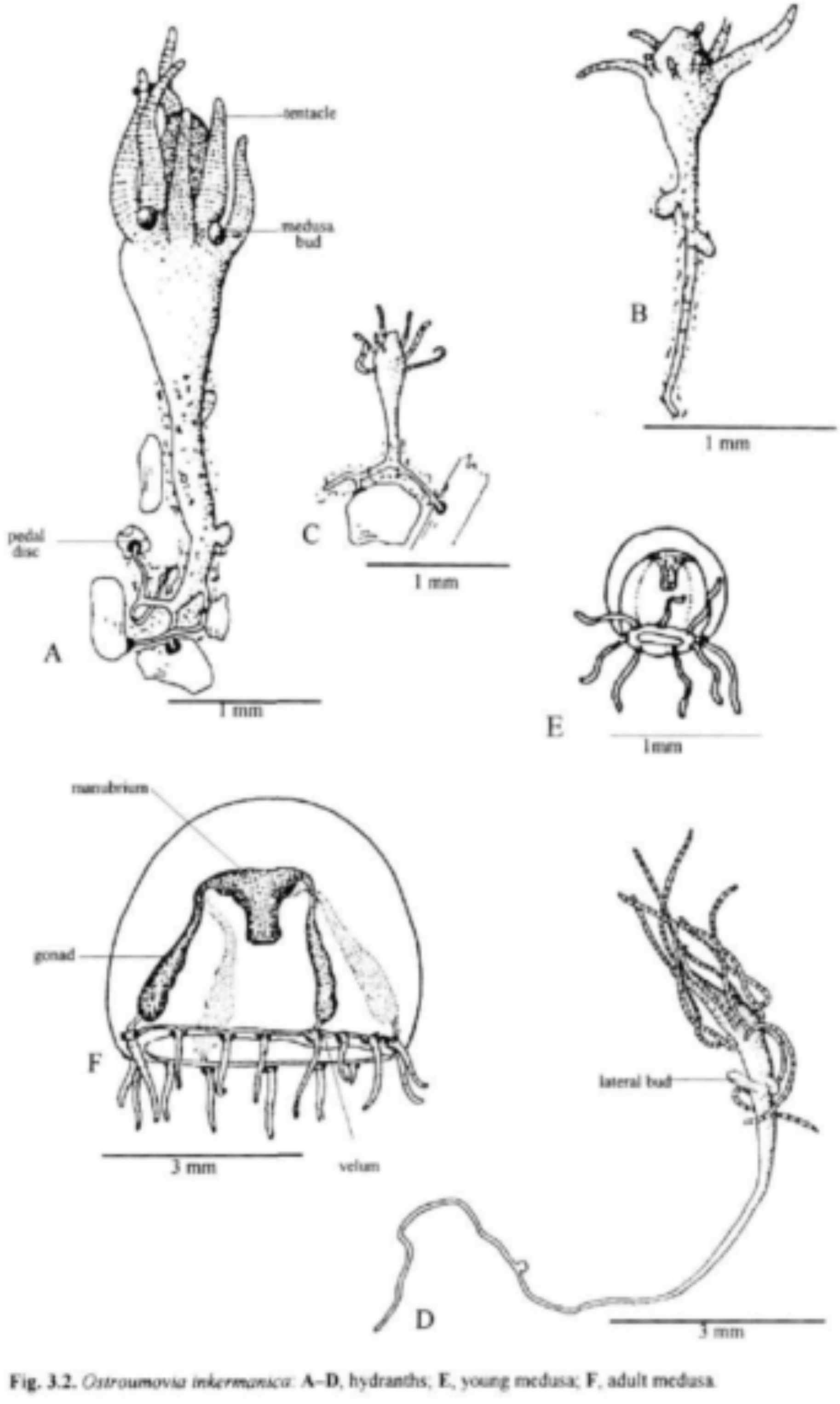

Fig. 3.2. *Ostroumovia inkermanica*: **A–D**, hydranths; **E**, young medusa; **F**, adult medusa.

favourable for hatching and growth, after which it will form a new polyp.

Chlorohydra viridissima (Pallas, 1766) (Fig. 3.1D)

Chlorohydra viridissima has a column, which may be up to 30 mm in length but is usually less than 15 mm. There are usually from four to 12 tentacles and ovaries and testes do not develop simultaneously. This species is sometimes called the 'green hydra' because of the abundant algal cells (probably mostly unicellular *Chlorophyta*) usually present in the gastrodermis. Such living algae probably have a true symbiotic relationship with the hydra, but dead and disintegrating algal cells are digested as food. The algae are passed from one generation to the next in the egg cytoplasm. *Chlorohydra viridissima* is widely distributed and common (Pennak, 1978).

Pelmatohydra oligactis (Pallas, 1766) (Fig. 3.1E)

Pelmatohydra oligactis has a column of up to 20 mm in length. The tentacles are longer than the body, and the basal part of the column forms a slender stalk. It is brown due to the presence of a symbiotic brown alga.

Order: Trachylina
Family: **Limnomedusae**

The Limnomedusae are of particular interest because they illustrate the phenomenon of a relatively coherent group, clearly of marine origin, which appears rather easily, though for no known physiological reason, to make the evolutionary transition to freshwater (Hutchinson, 1967). In all, there are about 10–14 freshwater species of Limnomedusae. This account relates to the three species recorded from southern Africa: *Ostroumovia inkermanica* (Subfamily: Moerisiidae), *Craspedacusta sowerbii* (Subfamily: Olindiadidae), and *Limnocnida tanganjicae* (Subfamily: Limnocnididae).

Taxonomic nomenclatural note

According to the rules of the International Code of Zoological Nomenclature, the specific epithets of '*sowerbii*' (not '*sowerbyi*') for *Craspedacusta* and of '*tanganjicae*' (not '*tanganyicae*') for *Limnocnida,* as designated by their original authors, Lankester (1880) and Günther (1893) respectively, must be adhered to. As will be noted from the references, this has not always been observed.

Morphology

Limnomedusae exhibit an alternation of generations between the dominant medusa and a reduced polyp of only a few millimetres in height. Medusae, which bear the gonads externally, are bell- or disc-shaped, with a variable number of tentacles around the margin of the bell. Depending on their age, they vary in size up to a maximum diameter of about 25 mm. Locomotion is by rhythmic contractions of the bell. It is important to note that in this account the words 'polyp' and 'polyp colony' are interchangeable with 'hydroid' and 'hydroid colony'. Millard (1975) introduced the term 'hydranth' for the polyps of *Ostroumovia inkermanica.*

Habitat preferences

Polyps are attached to vegetation or hard objects, making translocation easy (Rayner & Appleton, 1992). They are so small that they tend to be overlooked and their presence may only be detected when a swarm of medusae appear. The medusae are planktonic, occurring in ponds, small lakes and river margins. Large swarms may appear in one season and may not be seen again for years. They often multiply rapidly in dams and reservoirs to form swarms which may become a serious nuisance and have been known to block pipes and canals (for example, in Lake Kariba, Zimbabwe —Mills, 1973).

Feeding

Limnomedusae feed by capturing small prey items with their tentacles and paralysing their prey with the nematocysts. Prey include zooplankton such as rotifers, copepods and cladocerans. Payne (1926) mentioned turbidity and a poor food supply as factors that may limit the size of hydroid populations. A good supply of food may stimulate the budding of medusae.

Reproduction

Medusae are budded and detached from the polyp. In *Craspedacusta sowerbii,* the first buds released are very small (0.5 mm diameter) and bell-shaped with eight tentacles (Fig. 3.3D) (Rayner, 1988). Gonads develop on the medusa and the gametes, when released, fuse to produce a planula larva. This will settle on the substratum and give rise to a new polyp or colony of polyps. These polyp colonies are often referred to as a hydroid colony and the polyps as hydroids. It appears that medusae of only one sex are budded from a polyp colony which may explain why the medusae occur so sporadically. There are three types of asexual reproduction. In addition to the budding of medusae, the polyps (Fig. 3.3A, B) reproduce asexually by budding off planula-like buds called frustules which detach and give rise to a new polyp. They may also bud new polyps that do not detach from the parent and form a hydroid colony (Payne, 1924).

Ostroumovia inkermanica (Paltschikowa-Ostroumowa, 1925) (Figs 3.2A–F)

Morphology and Reproduction

The hydranth (Fig. 3.2A–D), which is slender at the base and widens distally, reaches 3 mm in height and is covered by a gelatinous sheath. It attaches to the substratum (usually sand-grains) by horny pedal discs borne on branching stolons. There are four to twelve tentacles on each hydranth. The hydranth produces asexual buds from the column and medusa buds from amongst the tentacles (Fig. 3.2A, E). The hydranth may be solitary with a single pedal disc at the base, or stolonization at or near the base may result in a branching hydrorhiza with four or more pedal discs (Figs 3.2A–D). The medusa (Fig. 3.2 F) which reaches 8 mm in diameter and 5.5 mm in height, is dome-shaped, has a very thick mesogloea and a very small gastrovascular cavity with radial lobes extending almost to the bell margin; the distal portions of the gonads on the radial lobes are sac-like and pendant. There are up to 32 tentacles of different lengths (Millard, 1975).

Distribution

In southern Africa this species is known from brackish lakes in — Lake Nhlange (Kosi Bay system) and Lake St Lucia (KwaZulu–Natal) and from Lagoa Poelela in Mozambique. Half-grown medusae (1.7 x 1.7 mm) have been found together with hydranths in Kosi Bay, and mature medusae (4.4 x 3.4 mm) with 16–18 tentacles, in Lake St Lucia. The known salinity regime in these habitats is 3 –10.8‰. Polyps have been recorded between depths of 2 m and 16 m. Also known from estuaries on the northern coast of the Black Sea (type locality), India, France and the Netherlands (Millard, 1975).

Craspedacusta sowerbii (Lankester, 1880) (Figs 3.3A–E)
Microhydra ryderi (Potts, 1906)

Morphology

The polyp of this species (Fig. 3.3A, B), originally known as *Microhydra ryderi* (Payne, 1924), lacks tentacles and produces asexual planula-like bodies (frustules) and medusa buds. The hydroid stage on which medusa buds are formed may occur as a single polyp or in a colony, and is only 2 mm in height. The polyp was called *Microhydra ryderi* until its relationship to *C. sowerbii* was realized (Payne, 1924). The mouth is surrounded by a battery of large nematocysts. When the medusa breaks away from the hydroid to become free-swimming, it is bell-shaped and has eight tentacles (Fig. 3.3D). The medusa is 15 – 20 mm in diameter and has 200 – 400 marginal tentacles of varying length, arranged in three sets. The gastrovascular cavity of the medusa is slender and reaches just beyond the margin of the bell. The four gonads are sac-like and suspended from the four radial canals (Fig. 3.3E).

Distribution

Craspedacusta sowerbii is the most abundant and widespread freshwater cnidarian. Except for Antarctica, it occurs on all continents and subcontinents, including major and minor islands, and now inhabits the subtropics and the warm-temperature belt of the entire planet (for details see Dumont, 1994: Fig. 1). *Craspedacusta sowerbii* was first recorded from Africa by Rayner (1988) in Lake Midmar (KwaZulu–Natal) and was subsequently recorded from Albert Falls Dam and Craigie Burn (Tugela catchment — KwaZulu–Natal), and the Theewaterskloof Dam and the Great Berg River in the Western Cape. *Craspedacusta sowerbii* probably formed part of a wave of introductions of freshwater organisms to South Africa after the Second World War. Although it has a cosmopolitan distribution, in South Africa it is classified as an introduced alien species. The distribution of this species appears to be slowly expanding, particularly in the Western Cape, probably as a result of inter-basin translocations of the dormant polyp on structures associated with recreation e.g. boats, or in vegetation (Rayner & Appleton, 1992).

Habitat preferences

Craspedacusta sowerbii has been found in rivers, lakes, impoundments, ponds, reservoirs and ornamental ponds (Rayner, 1988). It has not, however, been recorded from the mainstreams of rivers or from temporary pools. The sporadic appearance of *C. sowerbii* does not appear to be related to temperature. Medusae have been recorded from lily ponds at 32 °C and the cold artesian Bass lake, Indiana, USA (Payne, 1924). Payne (1926) mentioned turbidity and a poor food supply as limiting factors for hydroid populations. Observers have noted that the appearance of swarms of medusae seems to be associated with clear water conditions.

Feeding

A plentiful food supply may stimulate budding. Budding of medusae of *C. sowerbii* in Lake Midmar (Rayner, 1988) coincided with high diversity and numbers of zooplankters, which agrees with observations by Davis (1955) in Crystal lake, Ohio, USA.

Reproducton

Hydroids (Fig. 3.3 A,B) produce asexual, planula-like buds called frustules. These detach and move away from the parent colony and within 24 hours they attach to the substratum and become new polyps (Payne, 1924). Polyps also give rise to medusa buds and, on release as immature medusae (Fig. 3.3D), have eight tentacles. Sexual reproduction involves the formation of four ectodermally-derived gonads which are suspended from the four radial canals of the medusa. Each polyp colony produces medusae of one sex and this may be a factor in restricting dispersal — in cases where all the polyps in one water body produce medusae of the same sex. Fusion of gametes will produce a planula which when it settles, gives rise to a new polyp colony. During the winter, the polyp of *C. sowerbii* contracts into a solid mass of cells and secretes a chitinous-like covering around it (Payne, 1924).

Limnocnida tanganjicae (Günther, 1893) (Figs 3.3 F–H)

Morphology

The polyp (Fig. 3.3F), normally attached to macrophytes, reaches a length of about 0.5 mm. It branches to form a colony of two to seven individuals which is without tentacles, but has a terminal ring of large nematocysts around the mouth. The disc-shaped medusa reaches 25 mm in diameter and has about 300 marginal tentacles of different lengths. The gastrovascular cavity is short and wide with the gonads forming a ring on its walls (Fig. 3.3H).

Distribution

Limnocnida is a tropical genus which was first recorded from Tanzania (Tanganyika) (Günther, 1893) and is limited to Africa and the Indian subcontinent. (For details of its distribution, Dumont 1994: Fig. 1). Kramp (1961) recorded 31 occurrences of *L. tanganjicae* (or species which are now regarded as synonyms —*L. rhodesiae, L. congoensis, L. cymodoce*) in Africa between 1883 and 1958. Oldewage & Shafir (1991) summarized records relating to the occurrence of *L. tanganjcae* on the African continent. Since its description in 1893, this species has been recorded from rivers and impoundments associated with all the major African river systems including the Zambezi, Limpopo, Congo, Nile, Niger and lakes in the Rift Valley.

Habitat preferences

Limnocnida tanganjicae occurs in rivers in inconspicuous numbers, but

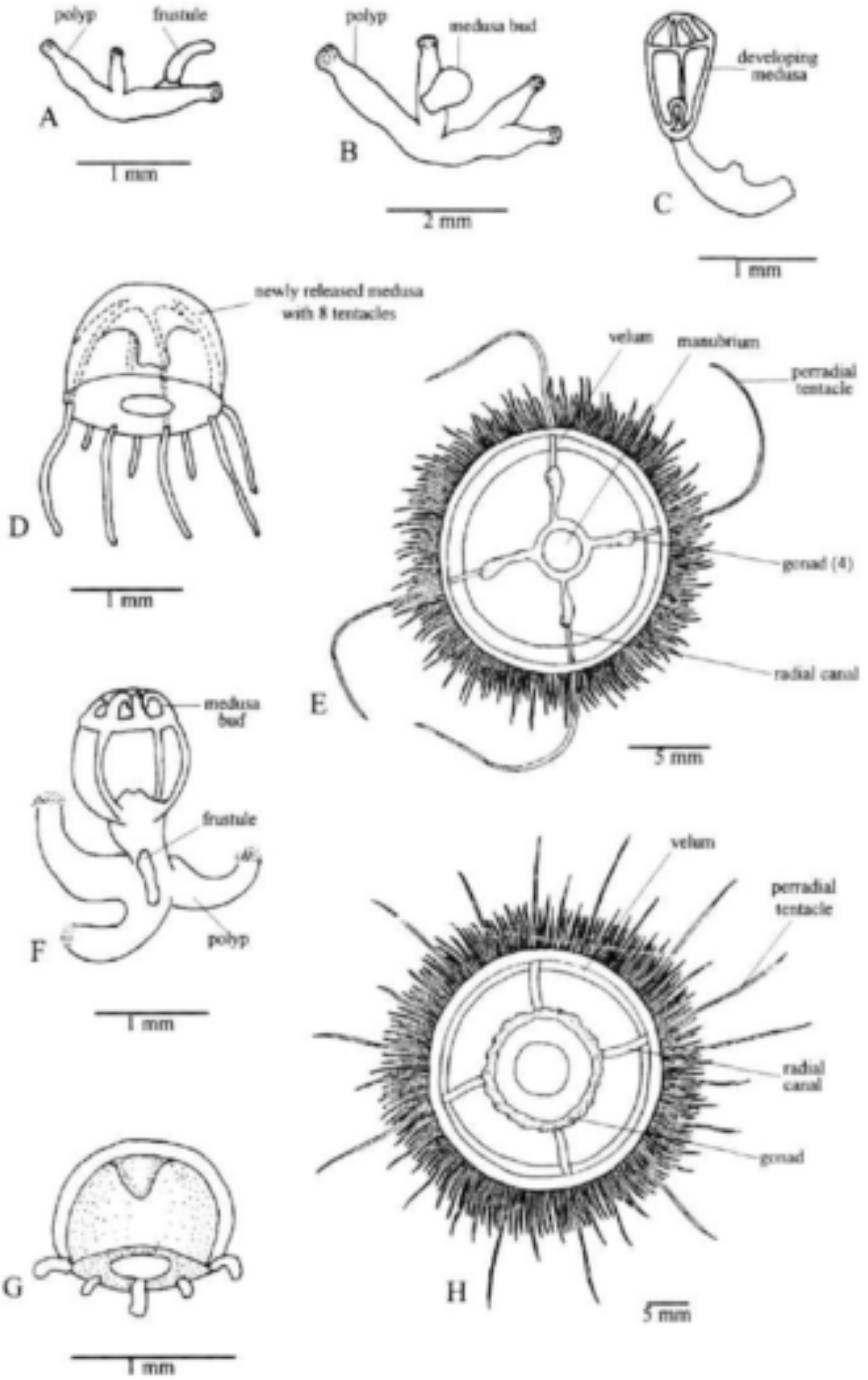

Fig. 3.3. **A–E**, *Craspedacusta sowerbii*: **A**, polyps with a developing frustule; **B**, polyp colony producing a medusa bud; **C**, a developing medusa before release; **D**, young medusa with eight tentacles; **E**, adult medusa. **F–H**, *Limnocnida tanganyicae*: **F**, polyp; **G**, young medusa; **H**, adult medusa. (A–D redrawn from Payne 1924; E & H reproduced with permission of Cambridge University Press from Rayner & Appleton 1989; F & G redrawn from Edney 1939).

builds up large populations in lakes, reservoirs, backwaters and sometimes in artificial habitats such as a goldfish pond in Johannesburg (Jordaan, 1934). Mills (1973) recorded a short-lived (August 4 to September 6, 1972) 'bloom' of this species in Lake Kariba. The medusa and hydroid stages of *L. tanganjicae* occupy different habitats. In Lake Lisikili (East Caprivi, Namibia) the medusae are concentrated in areas devoid of vegetation. This preference may be related to a vertical migratory pattern (medusae began surfacing at about 08h00 and remained there until about 14h00). Many medusae were seen to be resting on the lake bottom during late afternoon and evening (Oldewage & Shafir, 1991). In all cases polyps were found on the stems of macrophytes at about 5 m below the surface (Pitman, 1965).

Feeding

Sharma & Chakrabarti (2000) observed a significant reduction of biomass of zooplankton during a seasonal 'bloom' of *Limnocnida indica* medusae in a lake associated with the River Yamuna, India. Numbers of Cladocera (*Moina* sp.), Copepoda (*Mesocyclops* sp.) and rotifers (*Keratella* sp.) were reduced, but recovered when the medusae disappeared. Unpublished data indicate that the medusae may prey on larger organisms such as chironomids and tubificid worms as well.

Reproduction

Reproduction follows the general pattern given above for Limnomedusae with the branching of polyps and the production of frustules and medusa buds (Fig. 3.3 F, G). In *L. tanganjicae*, but not in other species, medusae are budded from the manubrium of the adult (Jordaan, 1935; Hutchinson, 1967).

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CHAPTER 4

PLATYHELMINTHES

by

C.C. Appleton

The Phylum Platyhelminthes or 'flatworms' comprises three classes of which one, the Turbellaria, contains free-living and commensal forms while the other two, the Trematoda (flukes) and Cestoda (tapeworms) are entirely parasitic, generally in the guts of vertebrates. Representatives of all three classes occur in fresh water, but the Turbellaria and Trematoda are most commonly encountered by field biologists. Turbellarians can be found 'gliding' over submerged surfaces or between the sand grains of the substratum. Trematodes are, as noted above, parasites, and most use a mollusc as the first intermediate host, and sometimes as a second intermediate host as well. Their free-living cercarial stages are often found emerging in large numbers from these infected molluscs. All tapeworms that are transmitted in freshwater belong to the subclass Cotyloda (false tapeworms). Their free-living larval stages, known as coracidia (singular coracidium), will not be seen unless specifically looked for. For example, the coracidium of the tapeworm *Cephalochlamys namaquensis*, a common parasite of the platanna, *Xenopus laevis*, is spherical and ciliated and because it mimics a colonial alga like *Volvox*, it improves its chances of being eaten by a foraging cyclopoid copepod and so continuing its life-cycle. It lives for only 4–5 hours. Tapeworms will not be considered further in this chapter.

As their phylum name (Grk *platus* = flat, *helmins* = intestinal worm) suggests, the Turbellaria and Trematoda are dorso-ventrally flattened, unsegmented worm-like (vermiform) animals. The freshwater forms range in length from a few millimetres in the case of many turbellarians to the largest trematodes which measure 40–50 mm. Although they have a number of common features such as the absence of an anus; a usually branched, blind-ending gut; an excretory system with prominent lateral canals ending in flame cells; a complex hermaphrodite reproductive system and the ability to reproduce asexually as well; they differ dramatically in their life-histories. Fresh water turbellarians develop directly from eggs whereas trematodes (and cestodes) undergo complex life-cycles which include a variable number of larval stages that do not resemble the adults at all.

TURBELLARIA

These are free-living, mobile flatworms, the largest freshwater species of which may grow up to 20 mm long. They vary in colour from pale and translucent to dark grey although this may vary within and between populations of the same species (Young & Young, 1974). Some of the smaller forms may have symbiotic chlorophyte algae in the parenchymatous tissue between the epidermis and the gut. They usually have a distinct head end, which is characterized by one or more pairs of dorsally-situated eyes. These eyes consist of light-receptor cells that respond to the intensity of light as well as its direction.

General Biology

Turbellarians are carnivorous animals, feeding on various invertebrates which they ingest through a muscular pharynx lying in a pouch in the ventral body wall and which, in the larger forms (i.e. the orders Tricladida and Polycladida), can be protruded to function as a prey-capturing device. Food is broken up, usually in the pharynx, and digestion may be entirely intracellular, entirely extracellular or a combination of both. Small forms (order Rhabdocoela) feed on protozoans and small invertebrates such as cladocerans while larger forms feed on larger prey such as oligochaetes, amphipods, molluscs, insect larvae and even small tadpoles. An African species, *Mesostoma zariae*, has been proposed as a potential biocontrol agent for the larvae of disease-carrying mosquitoes (Mead, 1978).

The epidermis of turbellarians is ciliated and movement of these cilia enables the animals to creep or 'glide' slowly over submerged surfaces such as stones or vegetation in both standing and flowing water or in interstitial habitats, i.e. between sand grains in the surface layer of the substratum. Wave-like undulations are visible along the bodies of the larger forms as they move. Turbellarians produce prodigious quantities of mucus from epidermal gland cells and this serves to facilitate locomotion and to protect the body surface as well as entangling prey. Since almost all flatworms are hermaphrodites, their reproductive systems consist of male and female parts, which join at a common genital opening on the ventral surface. Cross-fertilization is the rule. Many turbellarians are thought to produce two types of eggs: thin-shelled summer eggs which develop and hatch rapidly, and thicker-shelled winter eggs which are resistant to desiccation and low temperatures and undergo a period of diapause before they develop. This allows these species to survive times of drought when their habitats dry out. The eggs hatch into miniature flatworms. Some turbellarians also reproduce asexually by fission, which is believed to occur in response to changing environmental conditions such as rising temperatures and increasing food availability.

Classification

The guts of turbellarians vary greatly in design and this variation forms the basis for the more conservative classification of the class into five broadly-based orders, four of which occur in fresh water. In the order Rhabdocoela (Fig. 4.1A) the pharynx leads to an unbranched, sac-like gut cavity; in the order Tricladida (Fig. 4.1B) it leads into a tripartite cavity and in the order Polycladida into a many-branched cavity. The order Temnocephalida (Fig. 4.1C) comprises ectocommensals that are often found on the bodies of crustaceans. More modern classifications of the Turbellaria vary considerably but recognize 12 to 15 orders, most containing small animals of less than 5 mm in length which are collectively known as the 'microturbellaria'. The larger turbellarians (>5 mm) belong, as noted above, to the orders Tricladida and Polycladida. Most polyclads are marine and are not discussed further in this chapter.

Distribution

Turbellarians have been found in a wide variety of habitats across the subcontinent, from the coast to high-altitude mountain streams and from sub-tropical areas such as KwaZulu–Natal to semi-arid regions such as the Karoo and Namibia. Young & Young (1974) cited a record of *Dugesia* from an altitude of 4 000 m on Mt Kenya. Despite their widespread occurrence, knowledge of the southern African, and indeed the African freshwater turbellarian fauna is poor and there is thus no key to species or even to genera. Young (1976) reviewed the records from Africa and listed 80 species in 29 genera and seven orders. Of these 51 (64%) were considered to be confined to Africa and 29 (36%) were known from beyond the continent.

This relatively high 'cosmopolitan' component may owe its dispersal to migratory birds — certainly the resistant eggs or cysts of rhabdocoels could easily be incorporated into dried mud on birds' legs and feet and be distributed in this way. Freshwater triclads probably rely on active dispersal, with the result that some 82% of species reported from Africa are known only from the continent. Genera reported from southern Africa include *Bothrioplana, Castrada, Dugesia, Mesostoma, Neppia, Phaenocora* and *Prorhynchus.*

Ecology

Reynoldson (1981) identified interspecific competition as being more influential in determining turbellarian distribution patterns than either physiological factors such as water temperature or biological factors such as food availability, parasitism and predation. Predators include many insects, such as odonatan nymphs and plecopteran and trichopteran larvae, and their major parasites are protozoans, chiefly ciliates and sporozoans (Apicomplexa).

The ectocommensal *Temnocephala chaeropsis* from Australia, has been found on the exoskeleton of imported Australian crayfish, *Cherax tenuimanus*, being farmed in the Free State (Mitchell & Kok, 1988; Avenant-Oldewage, 1993). These turbellarians occurred mostly around the heads and mouths of the crayfish and readily infested the indigenous crab, *Potamonautes warreni*, in the laboratory. This serves to highlight the danger inherent in introducing exotic freshwater organisms. Temnocephalids show a moderate to high degree of host specificity but both temnocephalans and triclads have a propensity to become invasive when introduced to new areas.

Collection and Culture of Turbellaria

Large turbellarians such as triclads can be collected from submerged stones and vegetation by visual inspection. Submerged vegetation can also be sampled with a sweep-net and sedimentary substrata by means of a Surber Sampler. Stony or sandy areas are disturbed, for instance by kicking, and the dislodged material is collected in an open-mouthed bag placed a metre or so downstream. Debris collected in the sampler should be placed in a jar and left for up to eight hours under illumination after which many of the flatworms present move up the sides, out of the now oxygen-depleted water. These can be collected with a Pasteur pipette. Smaller forms can also be recovered using a flotation technique, immersing the debris in a magnesium sulphate ($MgSO_4$) solution and removing those that float to the surface. Turbellarians can be cultured in clean, boiled water and fed on water fleas (Cladocera) and/or chironomid or mosquito larvae. Food prepared from oligochaetes can also be used, but cultures fed on arthropods show the best growth rates.

Since the turbellarian fauna of Africa is so poorly known and modern classifications of the group are in a state of flux, it seems acceptable to compromise and follow the admittedly unnatural (but well known) classification of older texts, e.g. Marshall & Williams (1972), in the key to freshwater orders given below.

KEY TO FRESHWATER ORDERS OF TURBELLARIA

1. Free-living forms, lacking tentacles or suckers 2
– Ectocommensal forms, usually attached to crustaceans; up to 12 tentacles present at anterior end and a sucker at the posterior end; transparent .... **Temnocephalida** (Fig. 4.1C)

2. Gut straight and undivided, mouth at anterior end or in anterior half of body.... .... **Rhabdocoela** (Fig. 4.1A)
– Gut with diverticula (caeca) or branches; mouth not at anterior end, usually in posterior half of body 3

3. Gut with three main branches, one directed anteriorly and two directed posteriorly; each has numerous lateral diverticula; mouth in middle of body .... **Tricladida** (Fig. 4.1B)
– Gut with many-branched diverticula radiating from a main 'stem'; mouth at posterior end of body .... **Polycladida**

TREMATODA

The basic structure of trematodes is similar to that of the Turbellaria but, since they are parasites, they possess organs of attachment, usually suckers, and a powerful pharynx that helps them ingest liquified food. They lack eyes, although some have eyespots in their cercarial stage. There are two subclasses of trematodes, the Monogenea and the Digenea and both have aquatic life-cycles. Both are alike morphologically, but monogeneans are immediately recognizeable by their relatively large size (to 2–3 cm) and the conspicuous and unique opisthaptor at the posterior end of the body. This is an organ of attachment and is equipped with hooks and often with suckers as well.

TREMATODE LIFE-CYCLES

Monogenea

The Monogenea, which have a direct life-cycle without larvae and involving only one host, are ectoparasites of poikilotherm vertebrates: frogs (and their tadpoles) and fish. In southern Africa, the genera *Protopolystoma* and *Polystoma* have commonly been found infecting the nasal passages, bladders and cloacas of various species of frog. Several

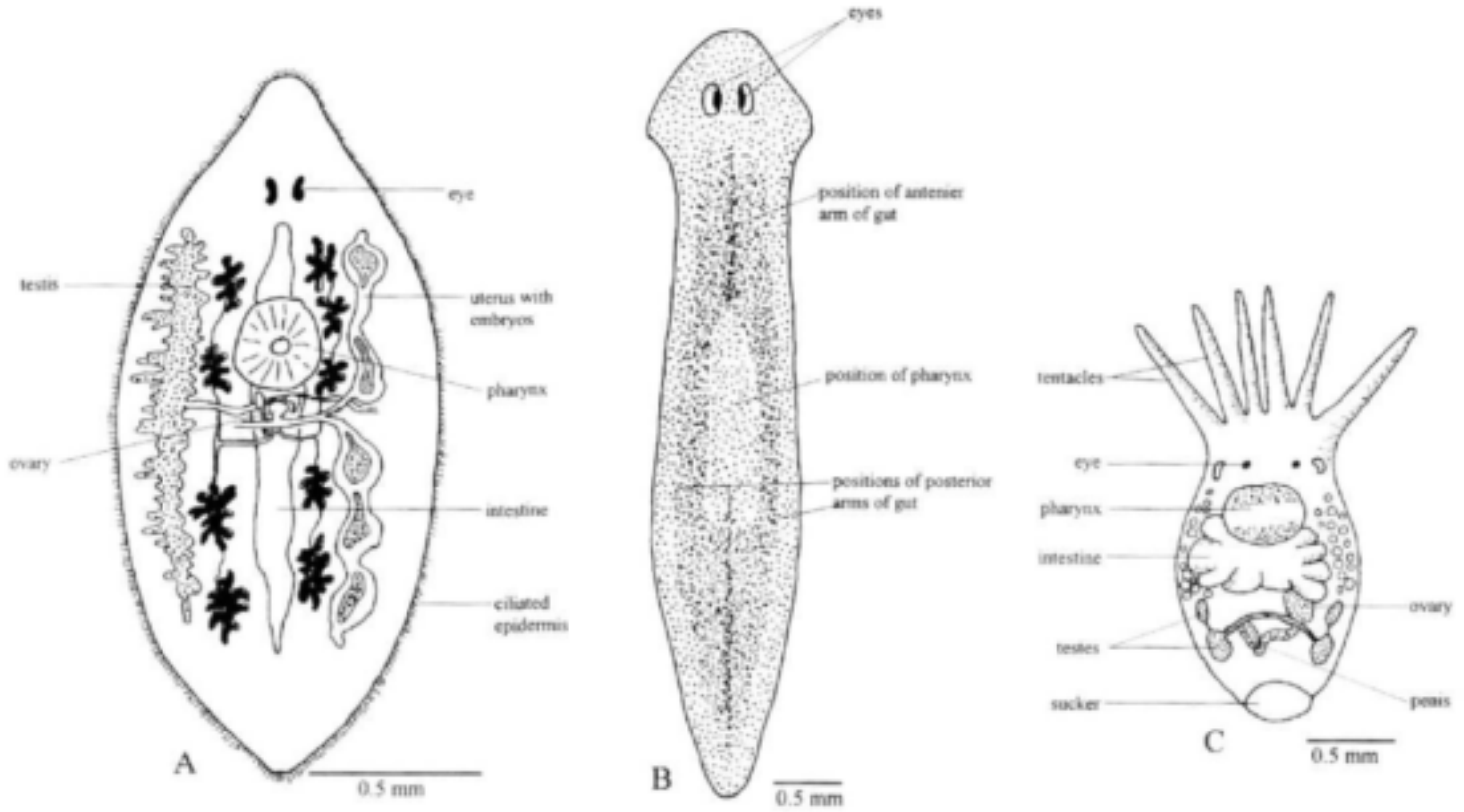

Fig. 4.1. Turbellarian worms: typical (generalized) drawings showing the main morphological features. **A**, typical rhabdocoel turbellarian (*Mesostoma* sp.); **B**, typical triclad turbellarian (*Dugesia* sp.) – note that the central pale area indicates the position of the pharyngeal cavity in the ventral body wall; C, typical temnocephalid turbellarian (*Temnocephala* sp.).

species of another genus, *Dactylogyrus* (Fig. 4.2), parasitize the skin and gills of fish, particularly of the family Cyprinidae. Heavy infestations cause considerable harm to their hosts and may become a problem in fish hatcheries. Mashego (1983) has provided a key to species of *Dactylogyrus* occurring in South Africa.

Digenea

The much more diverse Digenea have an indirect life-cycle involving several larval stages and two or more hosts. Their adults are endoparasitic in a variety of organs, chiefly the gut, of all types of vertebrates. They lay eggs which pass into water, usually in the host's faeces, and each hatches to release a microscopic, ciliated miracidium. This miracidium seeks out the first intermediate host, always a mollusc and usually a snail. Once inside this mollusc, the miracidium metamorphoses into a germinal sac, either a mother redia or a mother sporocyst, which multiplies asexually over a period of several weeks to produce daughter rediae or daughter sporocysts and eventually cercariae.

The cercaria is the second free-swimming larval stage of the digenean life-cycle (the first is the miracidium) and they are produced in large numbers via asexual reproduction inside the mollusc host's body. Once described as a 'tailed distributive and infective larva', the cercaria measures up to about 1.0 mm in length and usually comprises a 'head' or 'body' with a long tail attached. This 'head' is, in essence, a miniature fluke as it has suckers (usually two but sometimes only one), a well-developed excretory system and, in some cases, a stylet protruding through the oral sucker or a collar of spines around the head region. It also contains the rudiments of structures, i.e. gut and reproductive system, that become functional in the adult. The tail is purely a locomotory device that is able to propel the cercaria through the water in its quest for the next host in its life-cycle. In some families the tail is equipped with fin-folds or setae. A prominent excretory canal runs from the bladder down the length of the tail, opening to the exterior via a single pore at the tip or for only part of the tail's length, opening via a pair of pores closer to its base.

Because their guts are not fully developed, cercariae cannot feed. This means that their life-spans are short, measured in hours, and if they do not complete the next link in the life-cycle within say 10–15 hours, they will die. Adaptations allowing the cercariae to find the next host are usually of two kinds. In some the cercaria gets itself into the final hosts' food supply, using its cyst-secreting (cystogenous) glands to encyst as a metacercaria either *inside* a second intermediate host (e.g. an insect larva, another snail, a leech or even a fish) or *on* emergent vegetation. Then, in either

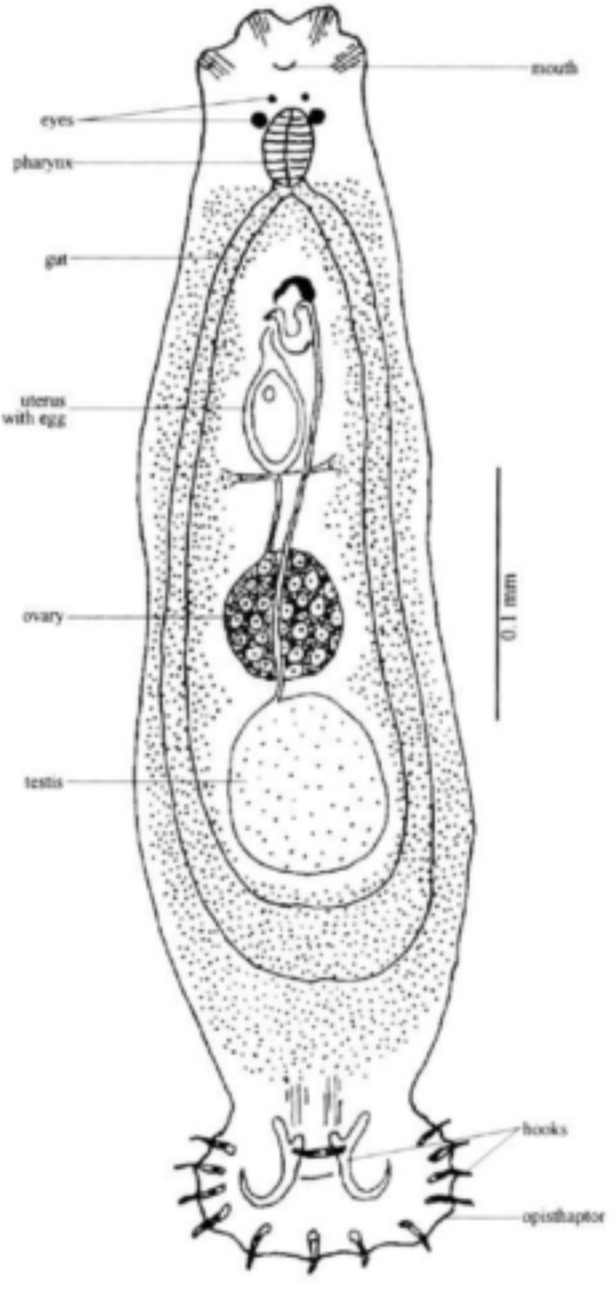

Fig. 4.2. Diagram of a monogenean trematode (*Dactylogyrus* sp.) showing its main morphological features. Note the absence of suckers in this genus, but the presence of both small and large hooks on the opisthaptor.

case, it waits to be eaten by the appropriate final host. This 'indirect infection' method is used by most trematodes. The other less common method is for the cercaria to penetrate its final host's skin directly, without going through any cyst stage. This requires the evolution of specific host-finding behaviour and the possession of specialized penetration glands which secrete histolytic enzymes to break down the host's epidermis at the point of contact and enable it to actively penetrate (infect) its final host. This 'direct infection' method is used by a group of bloodflukes which, in their adult stages, live in the final hosts' blood vessels, almost always in veins. Three families belong to this group: two, the Sanguinicolidae and Spirorchidae, parasitize fish and reptiles (i.e. cold-blooded vertebrates) respectively, while the third, the Schistosomatidae, parasitizes warm-blooded vertebrates (i.e. birds and mammals including man), causing bilharzia (schistosomiasis).

GROUPS OF CERCARIAE

Like the Turbellaria, the African trematode fauna is poorly known so that it is impossible to do more than refer cercariae to 'groups' or 'types' based on common morphological features rather than to families, genera or species. The most convenient way to classify cercariae is according to a scheme given by Dawes (1956). It is an artificial scheme which uses morphological characters of the cercariae which may or may not have taxonomic significance. Dawes (1956) recognized 10 groups of cercariae, each of which can be divided into sub-groups or sub-types. Representatives of nine of these groups are found in fresh water and all but one have been reported from Africa. These in turn formed the basis for the somewhat different nine groups (several with sub-types) used by Frandsen & Christensen (1984) to draw up a useful key to African forms and by Schell (1985) who recognized 25 groups in his key to cercariae developing in North American freshwater molluscs.

The following morphological and life-cycle characters are variable and were therefore used in the classifications by the above authors:

- the number of suckers: one sucker (monostome) or two suckers (distome)
- the position of the suckers: the oral sucker is usually anterior but the ventral sucker (acetabulum) may be situated midway along the body or posteriorly
- the presence or absence of eyespots (ocellate or non ocellate)
- the ratio of body length : tail length

- the type of excretory system, bladder and arrangement of flame-cells
- the presence or absence of finfolds, processes or setae on the tail (where they are present, their arrangement is important)
- the presence or absence of a row(s) of spines on an anterior collar or of a stylet inside the oral sucker
- the presence (and number) of penetration and cystogenous glands
- intra-molluscan development in sporocysts or rediae
- swimming, resting and encystation behaviour.

COLLECTION, PRESERVATION AND EXAMINATION

Snails can be screened for patent trematode infections by isolating them in small transparent containers such as test tubes (12.5 ml plastic vials are ideal) under strong overhead light. This strong light seems to override any intrinsic shedding pattern or rhythm and cercariae will emerge from infected snails after a few hours. Cercariae can be collected with a Pasteur pipette and examined on a slide under high power (x 400) or oil immersion (x 1000) of a compound microscope. They are best examined alive but they are highly contractile and move rapidly. If necessary, they can be immobilized by applying a drop of a 2.5% solution of methyl cellulose at the edge of the coverslip. Staining in a supravital stain such as 1% Neutral Red or Nile Blue Sulphate is a useful way of showing the cercaria's internal structures.

Individual snails may be infected by more than one species of larval trematode (called dual or multiple infections) and may thus shed cercariae of each species at the same time. Since many trematodes have seasonal transmission patterns, especially in temperate regions, shedding snails are most likely to be found during the warmer months of the year, i.e. September to April. Species of introduced snails, e.g. *Physa acuta*, have not been found shedding cercariae although they may carry metacercarial cysts in their pericardial sacs, i.e. around their hearts.

The study of the abundance, longevity and spatial distribution of cercariae already shed into the water, known as cercariometry, requires filtering large quantities of water. Cercariae collected are then stained and examined under a microscope. Cercariometry is used more for investigating the dynamics of trematode transmission than for qualitative collections.

Types of cercariae

The morphological features of the two main types of cercariae are shown in Figs 4.3 A & B; a simple-tailed cercaria (Fig. 4.3A) and a furcocercaria (Fig. 4.3B). Dawes' (1956) classification of cercariae occurring in freshwater can be summarized in eight groups as follows (a ninth group, the microcercous cercariae, is omitted because it has not been reported from Africa). Sub-groups have been described for many of these but only those of the three most commonly encountered groups, the echinostomes, xiphidocercariae and furcocercariae, are given here.

Amphistome cercariae (Fig. 4.4A)

Prominent body with pigmented eyespots; ventral sucker at or very near the posterior end; globular masses of highly refractile material fill the main (lateral) excretory canals which are typically looped. Develop in rediae. Born at a relatively early stage of development and 'mature' as free parasites in the snail's tissues. Weak swimmers with a short free life; they encyst on marginal vegetation where they can remain viable for several weeks. To become adult flukes, these metacercarial cysts must be eaten by herbivorous animals. An example is the conical fluke of cattle, *Calicophoron microbothrium*, which develops in the snail *Bulinus tropicus*.

Monostome cercariae (Fig. 4.4B)

Ventral sucker absent; eye-spots may be present; often with a pair of small adhesive glands just anterior to the base of the tail. Like amphistomes, these develop in rediae, are born immature and complete their development in the snail's tissues. Have a very short free life (several minutes only) after which, like the amphistomes, they encyst on submerged surfaces such as plants and even snail shells.

Gymnocephalous cercariae (Fig. 4.4C)

Anterior end rounded and lacking a piercing spine or stylet. Eye-spots absent; oral sucker may be protrusible; ventral sucker weak or absent. Pharyngeate, penetration glands present. Tail longer than body and a finfold may be present. Develop in rediae in either prosobranch or pulmonate snails. Rediae lack locomotor appendages. Weak swimmers which have a free life of only a few hours. They encyst on submerged vegetation. An example is the liver-fluke *Fasciola hepatica* which develops in the snail *Lymnaea truncatula* and probably *L. columella* as well.

Cystocercous cercariae (Fig. 4.4D)

A variable group of large (up to 2 mm), rather bizarre cercariae characterized by having a swollen tail which is sometimes longer than the body. This tail has a cavity in its base into which both the body, and sometimes a long, thin filament as well, can be retracted. This retractile filament, also called a 'delivery tube' (Schell, 1985) or 'tube protractile' (Fain, 1953), is

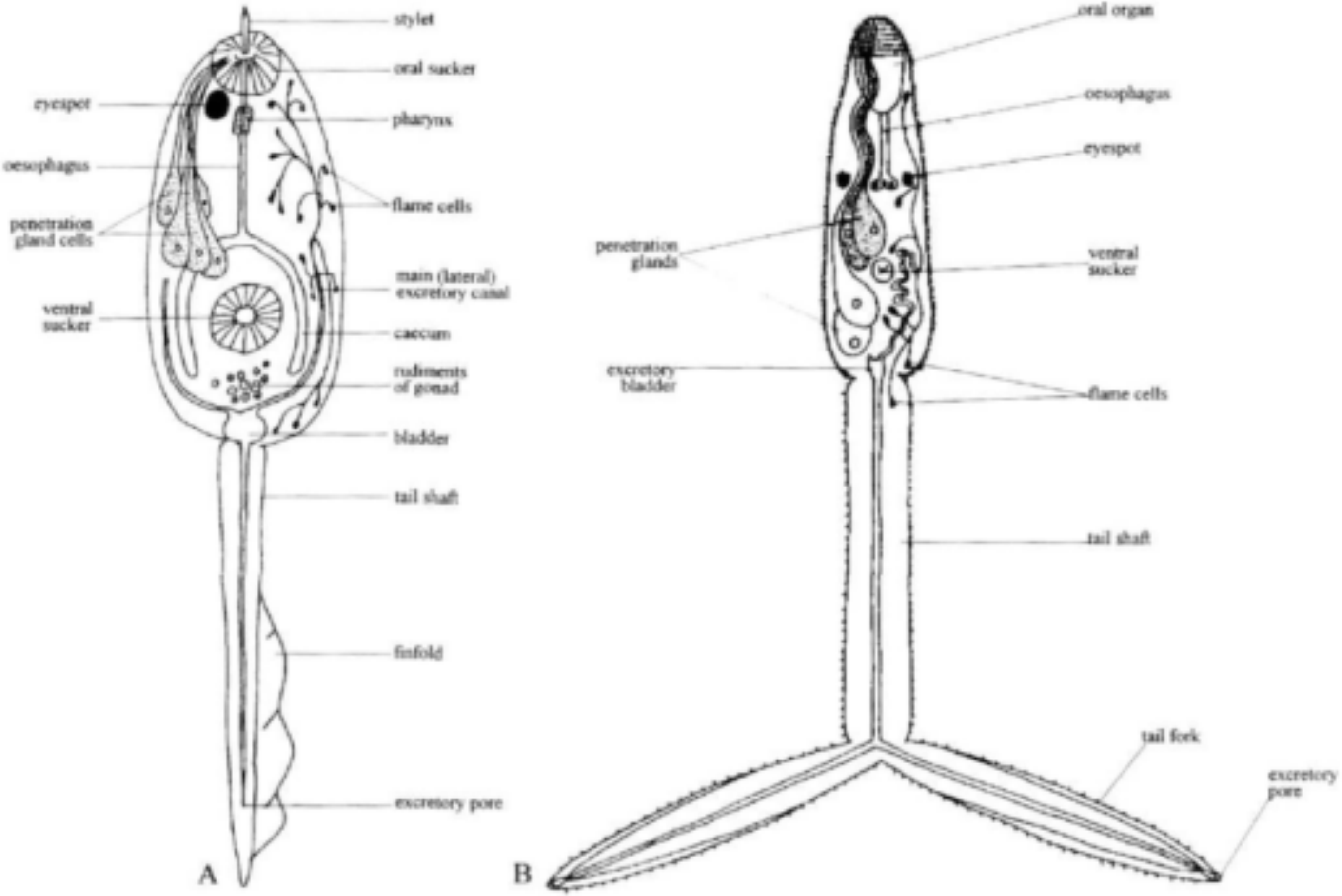

Fig. 4.3. Digenea: general morphological features cercariae: **A**, simple-tailed cercaria; **B**, furcocercaria.

thought to project the cercarial body through the intestine wall of the second intermediate host, possibly a copepod (Dawes, 1956). Some develop in sporocysts, others in rediae. Some have a forked tail and are included with the furcocercariae by some authors.

Echinostome cercariae (Fig. 4.4E)

A common group. Echinostome cercariae are generally recognizable by their relatively large size and the presence of a 'head' collar armed with one or more rows of spines. The gut is pharyngeate, the caeca long, easily visible and extending almost to posterior end of body; the main excretory canals thick and often filled with refractile granules; the ventral sucker is larger than the oral one and is situated in the posterior half of the body. The morphology of echinostome cercariae (particularly the pattern of collar spination; the presence/absence of a pre-pharyngeal sac and, if present, its contents; the presence/absence of finfolds on the tail and, if present, their arrangement) appears to provide more reliable taxomomic characters than adult morphology.

The 'collar spines' are arranged in a U-shaped pattern around the collar and Taplin (1964) proposed a useful nomenclature for different types of spines found. She recognized 'angle' or 'corner' spines (a) at either end of the collar, 'lateral' spines (*l*) on the inside of these and a single row (d) or alternating oral (do) and aboral (da) rows, of 'dorsal' spines in the middle – see Beaver (1937) and Taplin (1964) for useful illustrations of the arrangement of collar spines. The 'angle' or 'corner' spines are usually the largest. Since the numbers of these types vary among species, a formula was used to describe their arrangement: i.e. 'a + *l* + d + *l* + a' where, in species with alternating rows of dorsal spines, 'd' may comprise 'do + da'.

Cercariae are produced in rediae which are usually yellow/orange in colour but may be whitish. The morphology of the redia, particularly the shape and relative length of its gut, is also useful for classification. The rediae also have a collar and move actively amongst the snail's tissues.

Echinostome cercariae are strong swimmers, helped by their well-developed tails. About an hour after emergence, these cercariae usually move to the bottom of the waterbody and adopt a creeping movement. They are common parasites of pulmonate snails, less so of prosobranchs. They encyst in a wide variety of second intermediate hosts, mostly insect larvae and molluscs – sometimes in the same snail that served as the first intermediate host. The genera *Echinostoma* and *Echinoparyphium* commonly use snails of the genera *Bulinus*, *Biomphalaria* and *Lymnaea* as intermediate hosts and sometimes occur as dual infections with schistosomes or strigeids (see under furcocercariae).

Dawes (1956) recognized four sub-groups which are repeated below,

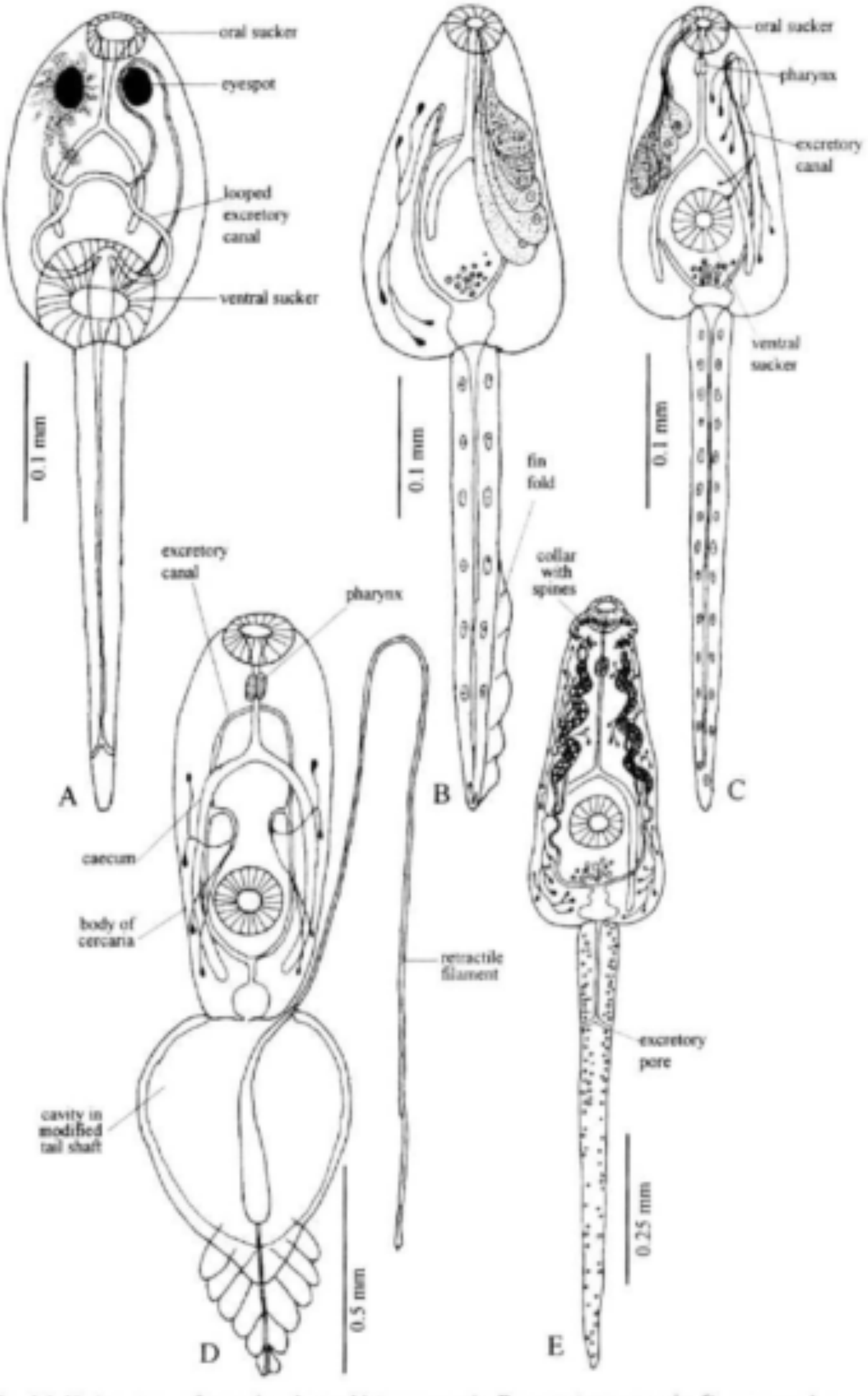

Fig. 4.4. Various types of cercariae: **A**, amphistome cercaria; **B**, monostome cercaria; **C**, gymnocephalous cercaria **D**, cystocercous cercaria; **E**, echinostome cercariae. (A, B & C from Porter, 1938; D from Fain, 1953; E from Taplin, 1964).

though it is doubtful if they are all valid for the South African fauna. For example the number of collar spines is used as a diagnostic character but only above 37 whereas Porter (1938), Taplin (1964) and King (1991) have all recorded cercariae with fewer than 30 spines. Dawes' scheme does not cater for these.

The four sub-groups are listed below:

'Echinata' group: collar well-defined with 37 spines arranged in a double row; four 'angle' or 'corner' spines on each side larger than the rest; many (about 50) small salivary gland cells arranged in two cords, one on each side (each cord consists of an inner and an outer part); excretory pores close to base of tail; tail with or without a finfold. Gut extends a quarter to two thirds of its length. Porter (1938) considered that most of the echinostome cercariae she found in South African snails belonged to this group.

'Coronata' group: collar generally well-defined; 43–45 collar spines arranged in a double row, the spines in both rows similar in size or those in oral row slightly smaller than in the aboral row; many (20–30) small salivary gland cells arranged as single clusters in two cords, one on each side; excretory pores close to base of tail; no finfold on tail. Gut of redia extends about a quarter to two thirds its length.

'Echinatoides' group: more than 40 collar spines, 'angle' or 'corner' spines slightly larger than others; many small salivary gland cells arranged in two cords, one on each side; excretory pores close to base of tail; both dorsal and ventral finfolds on tail.

'Subechinatoides' group: Porter (1938) did not find any cercariae from the 'Echinatoides' group in her monographic survey of South African freshwater cercariae but proposed this group to accommodate three apparently related species. Characters included a weakly defined collar and the absence of marked shoulders; relatively few collar spines which were fine and equal in size except for the 'angle' spines which were larger; three or four large salivary gland cells on each side; excretory pores near tip of tail (about one tenth of tail length from the tip); no finfolds on tail. Gut of redia extends for half or more of its length.

Xiphidocercariae (Fig. 4.5A)

A large but artificial grouping of small, pharyngeate cercariae generally less than 0.5 mm long, possessing a distinctive stylet inside the oral sucker. This stylet is associated with cystogenous glands; its shape varies and is used for further classification. The gut usually has well-developed caeca but these are vestigial in some cases. Development occurs entirely within branched sporocysts. Weak swimmers which soon resort to creeping. Encystment occurs in the body of a second intermediate host, usually an insect but may be a fish or even the snail in which it was formed. Five sub-groups have been recognized:

Cercariae microcotylae: very small (less than 0.2 mm long); body and tail of similar length, ventral sucker smaller than oral sucker and situated posterior to mid-body; four pairs of penetration glands; excretory bladder bicornuate ('two-horned'); tail without a finfold.

Cercariae virgulae: as above but characteristic 'virgula' organ present just posterior to stylet; lobes of excretory bladder deep ('V-shaped'). Schell (1985) included the Cercariae Microcotylae in this sub-group.

Cercariae ornatae: body longer than tail, ventral sucker smaller than oral sucker, characterized by having a terminal finfold on the tail.

Cercariae armatae: body and tail of similar lengths; ventral and oral suckers of roughly equal size; excretory bladder 'Y-shaped'; tail without a finfold.

Cercariae ubiquitae: body and tail of similar length; ventral sucker vestigial or absent; caeca vestigial or absent, tail without finfolds.

Cercariaea (Fig. 4.5B)

These cercariae do not develop tails. Some are produced in rediae and others in branched sporocysts. Since they lack a tail, they cannot swim but use their suckers to creep. They have also been observed to float. They encyst in other invertebrates.

Furcocercous cercariae (Figs. 4.5C–4.5G)

Possession of a forked tail is diagnostic for this large group although the relative development of the tail shaft and furcae varies. Some, such as the cercariae of the Clinostomatidae and Sanguinicolidae have prominent finfolds on the body and the latter on the tail furcae as well. Eye-spots may be present. Furcocercariae generally hang or rest motionless in the water with their forked tails pointing upwards. When they swim, they do so tail first. Furcocercariae are generally produced in sporocysts, but some develop in rediae. They can be divided into four sub-groups based on their morphology, i.e. whether or not they have a pharynx (pharyngeate/apharyngeate), whether the tail forks are long or short (longifurcous/brevifurcous) and whether they have both oral and ventral suckers (distome) or only the oral one (monostome). The sub-groups are:

a. Apharyngeal, brevifurcous, distome cercariae: (e.g. Schistosomatidae) (Fig. 4.5C–D) and Spirorchidae in part;

b. Apharyngeal, brevifurcous, monostome cercariae: (e.g. Spirorchidae in part — Fig. 4.5E — and Sanguinicolidae);

c. Pharyngeal, brevifurcous, monostome cercariae: (e.g. Clinostomatidae) Fig. 4.5F);

d. Pharyngeal, longifurcous, distome cercariae: (e.g. Strigeidae) (Fig. 4.5G).

Families in sub-group 'd' (Strigeidae and Diplostomatidae) and in sub-group 'c' (Clinostomatidae) are intestinal parasites of birds, while the bloodflukes of the families Schistosomatidae, Spirorchidae and Sanguinicolidae are included in sub-groups 'a' and 'b'. The absence of a muscular pharynx (apharyngeate condition) was recommended as the most useful diagonostic character for differentiating schistosomes from most other distome furcocercariae in the early days of bilharzia research and is still recommended today. The possession of a pair of eye-spots in cercariae of the Schistosomatidae readily distinguishes those that parasitize the veins of birds (ocellate) from those that parasitize mammals (non-ocellate). The arrangement of argentophilic papillae on the body of the cercariae also provides a useful tool for identifying schistosome cercariae (Knos & Short, 1979). These papillae have an affinity for silver stains and can be shown up by staining the cercariae with 2% silver nitrate ($AgNO_3$) —hence their name 'argentophilic'. Cercariae of *Schistosoma* spp. typically rest hanging in the water with their tail furcae at an angle of about 45° (Fig. 4.5C) while the furcae of *Trichobilharzia* sp. are curled (Fig. 4.5D).

Because of the medical and veterinary importance of those species of *Schistosoma* that cause human and bovine bilharzia, the Schistosomatidae has become the best-studied trematode family in Africa. These and the four other species of *Schistosoma* known from southern Africa are listed together with their intermediate and definitive (final) hosts in Table 4.1. These seven parasites use snails of the genera *Biomphalaria* or *Bulinus* as their intermediate hosts.

The stages in the life cycles of *Schistosoma mansoni* and *S. haematobium* are illustrated clockwise in Fig. 4.6. The cercariae of schistosomes are the infective stage for humans. About 0.5 mm long, they are produced in large numbers in sporocysts inside the snail intermediate host and released into the water, mostly between 10h00 and 14h00. Because they cannot feed and have only a limited supply of food, they live for only about 48 hours. If they do not find a human host within 10–12 hours, they will die. Cercariae penetrate unbroken skin quickly and then travel via the bloodstream to the liver, where they develop into adult worms within 6–8 weeks. When mature they pair up and migrate to the target organs, the veins draining

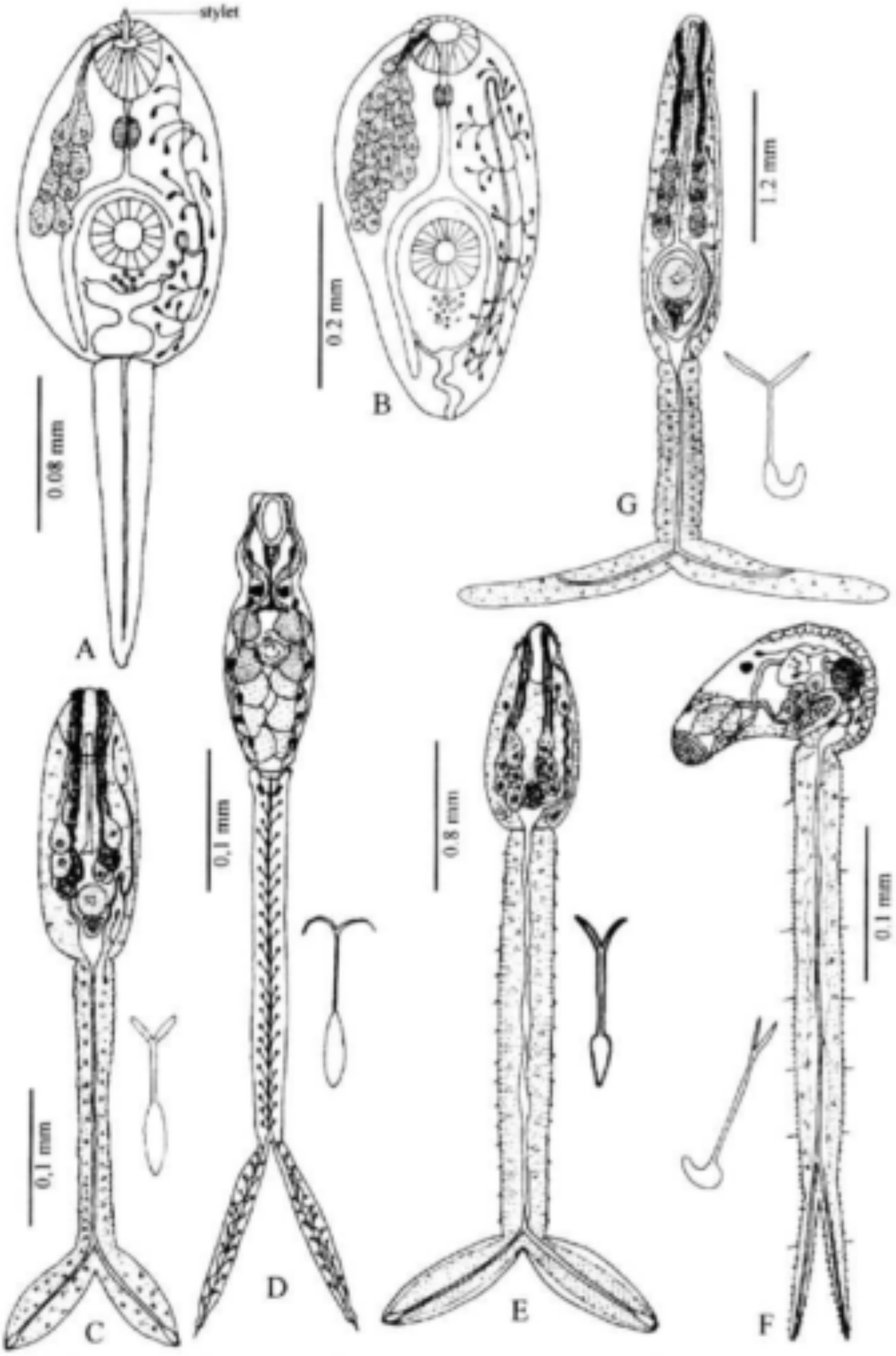

Fig. 4.5. Various types of cercariae. **A**, xiphidocercaria. **B**, cercaraeum. **C–D**, schistosome cercaria with small diagrams showing resting positions of cercariae: **C**, *Schistosoma* (resting postion hanging in the water with tail furcae at an angle of about 45°); **D**, *Trichobilharzia* sp. (resting position with furcae curled). **E**, spirorchid cercaria (resting position unknown). **F**, clinostomatid resting cercaria (identified by the typical 'hammer-shaped' head and tail shaft held at an angle of 45–55°). **G**, strigeid cercaria, showing resting, 'U-shaped' position of the cercariae with the tail held vertically and the head held downwards. (C from Porter, 1938; F from Fain, 1953; G from Vercammen-Grandjean, 1960).

the bladder in the case of *S. haematobium* and those draining the intestine and rectum in the case of *S. mansoni*. Adult worms normally live for three to five years but some are known to have lived for as long as 30 years.

The distributions of the two species overlap in southern Africa. *Schistosoma haematobium* (urinary bilharzia) occurs over most of Zimbabwe, Swaziland, Mozambique, Gauteng, Northwest Province, Northern Province, Mpumalanga and KwaZulu–Natal. It extends down the south-eastern seaboard below approximately 1 000 m altitude into the Eastern Cape. Several foci of transmission in the Eastern Cape seem to have disappeared during the past five or six decades and the southern limit of the parasite now lies in the former Transkei. It is not found in the Western Cape because its snail host does not occur there. *Schistosoma haematobium* also occurs in the northern parts of Namibia and Botswana. The distribution of *Schistosoma mansoni* is more restricted than that of *S. haematobium*. It is confined to the easternmost parts of Northern Province and Mpumalanga and KwaZulu–Natal below about 1 000 m altitude. As with *S. haematobium*, highest prevalences and intensities of infection occur in the extreme eastern parts of the sub-continent. The disease is patchy in KwaZulu–Natal. One of the few places in Africa where bilharzia infection has recently spread is in the seasonal part of the Okavango delta in northern Botswana. Here *S. mansoni* infection rose dramatically from zero in the 1960s to around 80% in the 1980s. In southern Africa, *S. haematobium* is carried by the pulmonate snails *Bulinus africanus* and *B. globosus*, while *S. mansoni* is carried by *Biomphalaria pfeifferi*. The distributions of

Table 4.1. Species of *Schistosoma* reported from southern Africa together with their intermediate and final hosts.

Species	**Snail intermediate host(s)**	**Mammalian final (definitive) host**
Schistosoma haematobium	*Bulinus africanus & B. globosus*	man
Schistosoma mansoni	*Biomphalaria pfeifferi*	man, vervet monkey, baboon
Schistosoma mattheei	*Bulinus africanus & B. globosus*	waterbuck, buffalo, cattle, sheep
Schistosoma edwardiense	*Biomphalaria pfeifferi*	hippopotamus
Schistosoma leiperi	*Bulinus globosus*	lechwe, sitatunga, waterbuck
Schistosoma margrebowiei	*Bulinus forskalii*	lechwe, sitatunga, waterbuck
Schistosoma rodhaini	*Biomphalaria pfeifferi*	not known – probably a nocturnal rodent

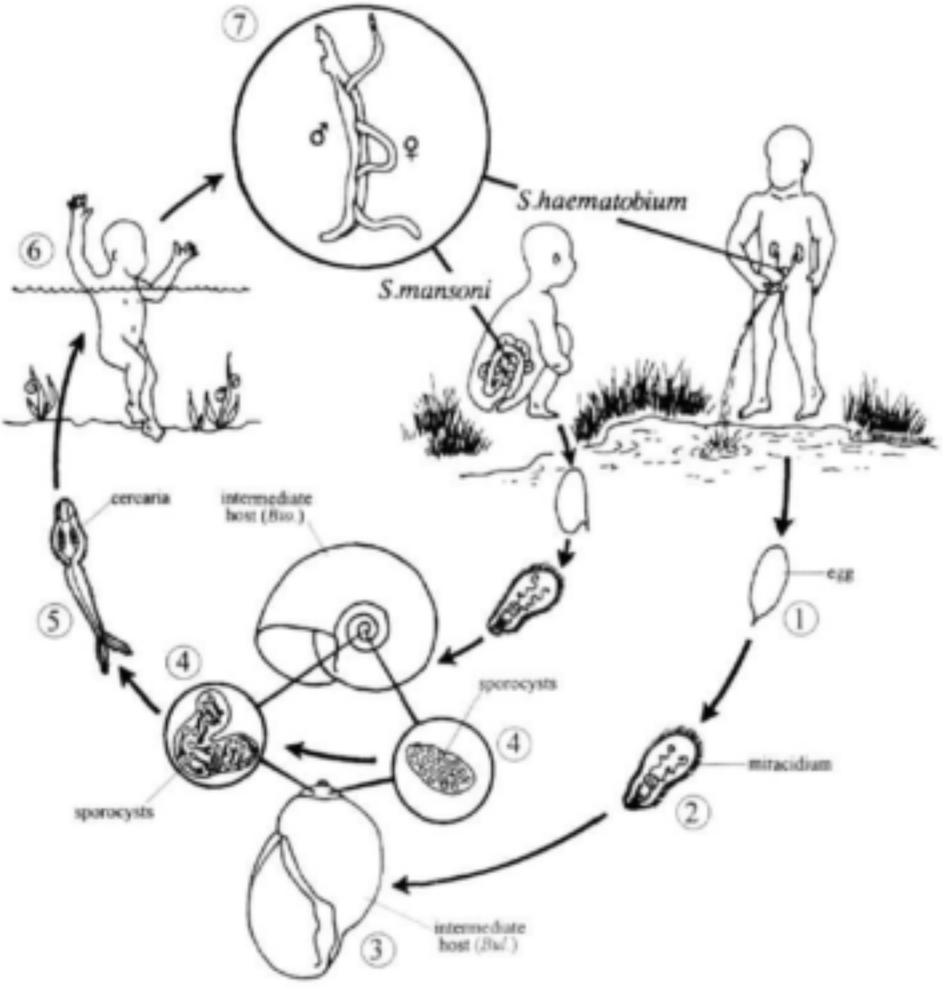

Fig. 4.6. Phases in the life-cycle of the bilharzia flukes, *Schistosoma haematobium* and *S. mansoni*: (1) eggs are voided from the human host (usually children) in urine (*S. haematobium*) or faeces (*S. mansoni*). Only if they are passed into freshwater will they hatch to release a miracidium (2) which infects a snail intermediate host, *Bulinus africanus* or *B. globosus* for *S. haematobium* (*Bul.*) and *Biomphalaria pfeifferi* (*Bio.*) for *S. mansoni* (3). Once inside the snail the miracidium becomes a mother sporocyst which multiplies asexually to produce many daughter sporocysts (4). Several generations of daughter sporocysts are produced in this way before they form large numbers of cercariae (5) which leave the snail and infect a human host (6). They do this by using the secretions of their penetration glands to enable them to pass through human skin at the point of contact. When inside a human host, they enter the blood stream and are carried to the liver where they grow into mature worms, pair-up and migrate to the veins draining the bladder in the case of *S. haematobium* and small intestine and rectum in the case of *S. mansoni*. Once they have reached their target organs, they mate (7) and the female lays eggs which make their way into the bladder or intestine to start the cycle again.

these snail species, all three of which belong to the family Planorbidae, are wider than those of the diseases caused by the parasites they carry. Readers wanting more information on bilharzia in southern Africa should consult the useful booklet by Gear & Pitchford (1977).

Several species of schistosomes have been recorded from water birds in southern Africa but the adult of only one has been identified, *Bilharziella polonica* from the coot, *Fulica cristata* (Porter, 1938). Its snail host is not known. Five other avian schistosomes have been identified from their eggs in birds' droppings (Appleton, 1986), and probably belong to the large and widespread genus *Trichobilharzia*. The cercariae of at least one of these, a common parasite of waterfowl, particularly the Spurwing Goose (*Plectropterus gambensis*), and transmitted by the snail *Lymnaea natalensis*, cause 'swimmer's itch' or 'cercarial dermatitis' in people after contact with infested water. These cercariae readily penetrate human skin but usually die there after about 72 hours, causing an itchy dermatitis (Appleton & Brock, 1986). The cercariae of other species of avian schistosomes can probably also cause 'swimmer's itch'.

ACKNOWLEDGEMENTS

I am grateful to the University of Natal Press (Pietermaritzburg) for permission to reproduce material previously published in *Freshwater Molluscs of Southern Africa* (1996). The illustrations of the different types of cercariae were redrawn from various publications dealing with African, mostly South African, cercariae by Nikki Köhly (Figs. 4.3B, 4.5C & 4.5E–G), Marlies Craig (Fig. 4.6) and the author (4.1–4.3A, 4.4A–4.5B). Figure 4.15D, by Ingrid Eriksson, was drawn from life.

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CHAPTER 5

NEMERTEA

by

J.A. Day

The Nemertea, also known as the Nemertina or the Rhynchocoela, is a small phylum of about 900 species of unsegmented worms. While most members are benthic or bathypelagic marine organisms, a few species are known to be widespread in fresh waters. The genus *Prostoma* seems to be more or less cosmopolitan, with about six species presently recognized, mostly known from single localities. Five other monospecific genera have been described relatively recently, each from a single locality in Europe, Asia, Australasia or South America.

Freshwater nemerteans from Africa are very poorly known, to the extent that it is not even certain which species of *Prostoma* most commonly occur here. The information in this chapter is taken almost entirely from textbook accounts of northern hemisphere forms, so surprises no doubt await biologists who examine our freshwater nemerteans in detail.

GENERAL BIOLOGY

Morphology

Nemerteans (Fig. 5.1) are long, thin, unsegmented worms with a ciliated epidermis and a through gut, but no body cavity. They are very similar to the turbellarian platyhelminthes in body form but, while an anus is present in nemerteans, it is absent from platyhelminthes. Nemerteans are sometimes known as 'proboscis worms' because they possess an eversible proboscis (Figs 5.1A–C) that shoots out from the head to capture prey. A proboscis of this type, lying in a cavity dorsal to, and separate from, the gut is unique to this phylum.

It is not easy to identify worms definitively as nemerteans without dissecting them, and it is impossible to identify them to species without preparing thin sections for histological examination. Nonetheless, in inland waters, the only worms that are entirely unsegmented and virtually featureless are the nemerteans and the nematomorphs (see Chapter 8). Nematomorphs are relatively long worms, often 50 mm or more in length, with wiry, cylindrical brown or blackish bodies and no eyes. In contrast, freshwater nemerteans are no more than a few millimetres long. When preserved, the body is a pale, slightly flattened, muscular cylinder. Close examination under the microscope should reveal a flattened head end with (usually) six minute, dark eyes on the dorsal surface (Fig. 5.1A, B), but individuals lacking eyes, or with four or eight eyes, are known. Sometimes the common opening of the mouth and proboscis can be seen anteriorly as a tiny pore. (Interestingly, and in contrast, some species of marine nemerteans are very brightly coloured and a few reach lengths of several metres.)

Classification

The Phylum Nemertea consists of two classes, each with two orders. The major differences between these taxa concern the arrangement of the muscle layers and nerves in the body wall. *Prostoma*, the only freshwater genus known from Africa, belongs to the Class Enopla and the Order Hoplonemertea. Members of the Enopla are characterized by the mouth being anterior to the cerebral ganglia and the central nervous system internal to the two-layered body musculature. The proboscis of hoplonemerteans is armed with a hardened stylet; the mouth and proboscis emerge from a common pore, and the intestine is straight, with lateral diverticula.

Distribution and habitat preferences

Most nemerteans are burrowers, but a few live under stones or in vegetation. The North American species of *Prostoma* are said to prefer sluggish shallow streams or the littoral regions of small ponds and lakes. In South Africa they have been recorded from rivers throughout the country, mostly in Mpumalanga and KwaZulu–Natal but also along the south coast and as far west as the Berg River (Western Cape). They have seldom been recorded from wetlands, but whether this is because wetlands have not been extensively sampled in the region, or because the local species have a real preference for rivers, is not known.

Feeding

Nemerteans are normally predatory, preferring to feed on living chironomid larvae, but they are also known to take copepods. A nemertean is

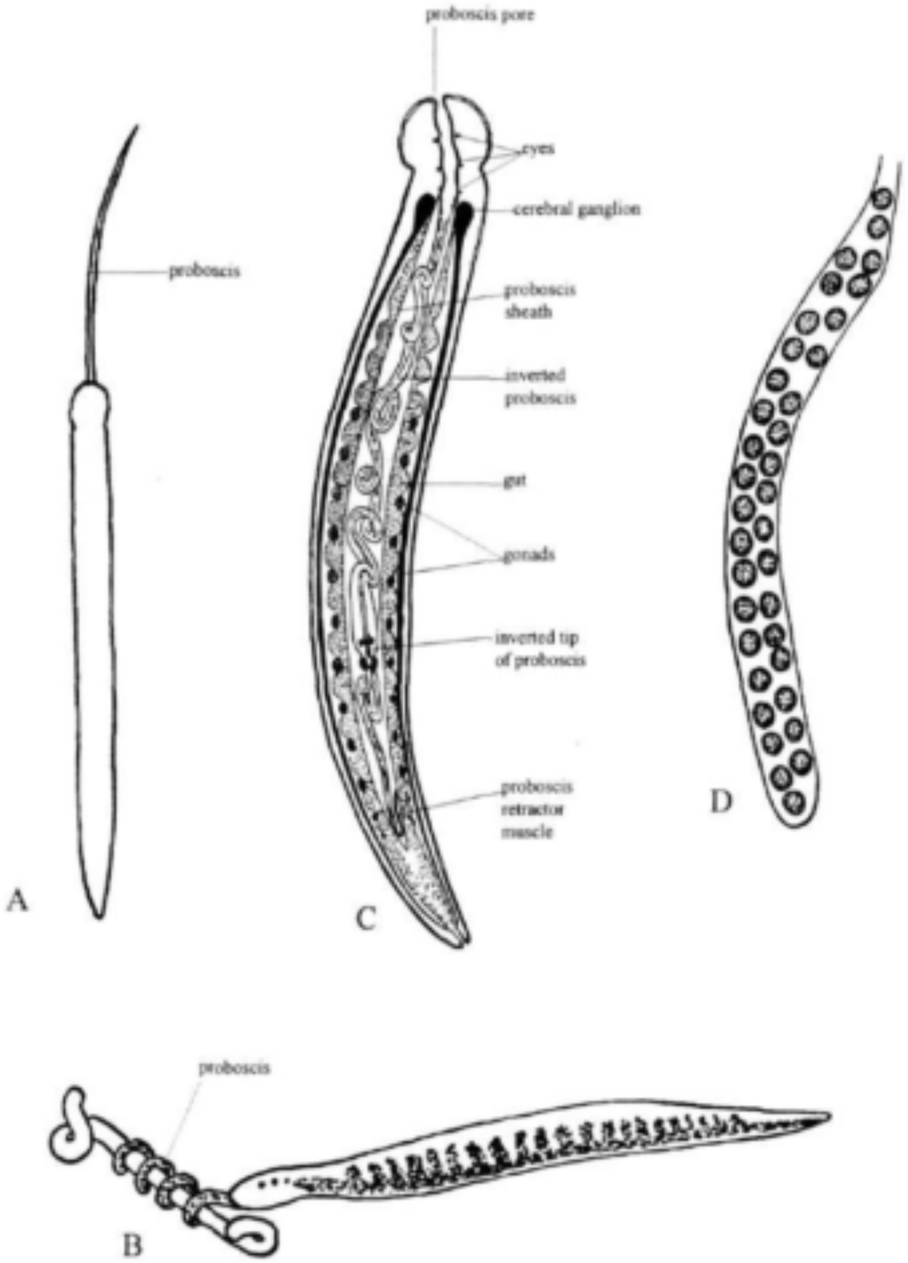

Fig. 5.1. *Prostoma* spp. **A– B**, whole animal with extended proboscis; **C**, dorsal view showing the proboscis in its sheath overlying the gut; **D**, eggs in a mucous sheath. (B–D from Hyman, 1951).

apparently able to sense the presence of a prey item from a distance of several centimetres. When it senses that food is available, the worm moves forward and shoots out its proboscis, so that the prey is impaled upon the sharp stylet at the tip of the proboscis. The worm then throws several coils around its prey (see Fig. 5.1B), rather as a constricting snake does, before engulfing the entire body.

Reproduction

Marine nemerteans are usually dioecious (have separate sexes) and undergo external fertilization, resulting in the formation of a free-swimming planktotrophic larvae called pilidia. *Prostoma*, on the other hand, is a protandrous hermaphrodite. Pairs of ovotestes lie between the gut diverticula down the length of the body and each produces many sperm, but just a single egg. From the literature, the extent of self-fertilization is not clear, but reports suggest that when reproduction occurs, an individual secretes a mucous sheath around itself and exudes into this the single egg, and many sperm, from each ovotestis. Pennak (1989) also notes that two individuals, one of which is functionally male and the other functionally female, may secrete a mutual sheath (Fig. 5.1D) into which they secrete the gametes, some of which are likely to be fertilized by sperm from the partner.

Pennak also reports that, under adverse conditions, individuals may secrete layers of mucus that become covered with debris and harden to form resting cysts. Since the cysts are not resistant to desiccation, however, they cannot provide long-term protection against dry conditions, although the animals may survive for a number of weeks in this way. Experiments have also shown that nemerteans can survive starvation for long periods, losing more than nine-tenths of their body volumes, and still be able to survive when provided with food.

Phylum NEMERTEA
Class Enopla
Order Hoplonemertini
Family **Tetrastemmatidae**
Prostoma Dugés, 1828

Individuals in the genus *Prostoma* are hermaphrodite and have two muscle layers in the walls of the body and proboscis; the proboscis, which is shorter than the body when extruded, bears a single stylet; usually four to eight eyes are present; body length is less than 35 mm (presumably in the living animal).

Two species are known from southern African fresh waters but cannot be separated without histological sectioning. This means that most specimens have not been identified to species, although the genus has been recorded in virtually all of the coastal rivers of South Africa from northern KwaZulu–Natal to the Berg River in the Western Cape and in the Vaal Catchment. The most recent reference specifically to the southern African forms is Correa (1951), while Gibson & Moore have somewhat more recently (1976) synthesized information on freshwater nemerteans worldwide.

Prostoma graecense (Böhmig, 1892)

Body length 0.4–14mm; oesophageal wall thick and ciliated. Kenya, Tanzania, South Africa and widespread elsewhere.

Prostoma eilhardi (Montgomery, 1894)

Body length 1.5–12mm; oesphageal wall thin and unciliated. Kenya, Tanzania, South Africa and widespread elsewhere.

ACKNOWLEDGEMENTS

The drawings in this chapter were scanned and prepared by Belinda Day, who is thanked for her assistance.

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CHAPTER 6

ROTIFERA

by

*C. K. Brain**

With about 1 800 species in 120 genera world-wide, rotifers are not prominent in the animal kingdom as a whole, but they do have an important place among microscopic freshwater invertebrates. For nearly two hundred years they have been favourite objects of study among microscopists, professional and amateur, due largely to the ubiquitous presence of rotifers in fresh waters and damp mosses of all kinds, their beauty, and their ceaseless motion. For these reasons, rotifers are better known than are representatives of other 'minor' invertebrate phyla.

Rotifers, or 'wheel-bearers', derive their name from the fact that the synchronized beating of their ciliated head-crowns have the appearance of turning wheels. Rotifers are acoelomate worms between 40 µm and 2 mm in length with affinities to turbellarians, gastrotrichs and nematodes. Like nematodes, the number of cell nuclei produced during ontogenetic development is fixed with no further cell divisions occurring once the embryo is fully developed. The great majority of rotifers seen under the microscope are females — in fact, among bdelloid rotifers males have never been seen at all — so descriptions and keys provided here refer to females.

The Phylum Rotifera contains two classes, the Digononta and the Monogononta. Digonont rotifers, characterized by paired ovaries, are further divided into two orders, the Seisonidea with its single genus *Seison* which occurs as commensals on marine Crustacea, and the Bdelloidea, found typically in fresh water and mosses. In bdelloids, males are unknown and reproduction is by parthenogenesis, while, as the name implies, females creep around on the substrate in a leech-like manner. By contrast, the Monogonont rotifers, making up 90% of known species, have single

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* Illustrations by Pascalle Chesselet.

ovaries and males are typically small and degenerate; there are three orders: Ploima, Flosculariacea and Collothecacea.

Ecology

Rotifers are found in a great variety of water sources while damp moss habitats are much favoured by many of the bdelloids. Such habitats are prone to periodic desiccation and rotifers have two means of overcoming the problem: bdelloid rotifers have the ability, through a process known as cryptobiosis, to slowly dry out and then to come to life again when water returns. Monogonont rotifers lack this facility but can survive as resting eggs, blown about by the wind, as do desiccated bdelloids (see Fig. 6.3G). For this reason many rotifer species are cosmopolitan, to be found wherever suitable conditions prevail.

As a group, rotifers have a strong preference for fresh water, in which most of the species are found. However, in southern Africa, brak water sources also harbour rotifers, particularly of the genera *Brachionus* and *Hexarthra*. Rotifers with the highest known salinity tolerance occur in Namib desert springs where *Proales similis* has been found to tolerate a salinity of almost three times that of seawater (Brain & Koste, 1993), while a marine species of *Synchaeta* has recently been described from the Benguela Current off the south-western Cape (Brownell, 1988).

Many rotifers are benthic, living on the substratum or among submerged vegetation. These tend to have long, mobile feet and thick loricas. Others are sessile, living in sheaths or gelatinous tubes and making use of special food-catching mechanisms. Of the 120 rotifer genera known worldwide, about 30% live constantly or occasionally in the plankton where population numbers tend to be much higher than they are for benthic rotifers. Densities of 200–300 rotifer individuals per litre are not unusual for planktonic rotifers and numbers may be much higher. Because of their small size, rotifers constitute a minor part of the zooplankton biomass — for instance the dry weight of a single *Daphnia* may be equivalent to that of 300–500 rotifers. But the part played in the production cycle is certainly important, since many rotifers feed on bacteria and detritus and have a rapid turnover.

Five rotifer adaptations to planktonic life can be mentioned:

- A lowered specific gravity through reduction of the lorica (e.g. *Brachionus calyciflorus*), inflation of the body (*Asplanchna, Synchaeta*) or the production of gelatinous material (*Conochilus, Collotheca, Gastropus*).
- Partial or complete atrophy of the attachment organs, such as a shortening of the foot (*Synchaeta, Epiphanes*) or loss of the foot and toes as in many planktonic forms.

- Development of swimming and floating appendages such as mobile bristles (*Filinia, Hexarthra, Polyarthra*) or rigid spines (*Keratella).*
- Protection of eggs against sinking by attaching them to the mother (e.g. *Brachionus, Filinia, Keratella*) or by floating devices such as oil droplets (*Polyarthra*) or spines (*Synchaeta*).
- Linking up of individual rotifers in chains (*Hexarthra)* that promote flotation (see Heeg & Rayner, 1988).

Collection, preservation and examination

Freshwater rotifers can be collected conveniently with a small plankton net made of fine-mesh gauze, typically 70 meshes/cm, conical in shape, with a tube or vial tied into the pointed end of the net. The contents of this vial can then be poured into a shallow petri dish for examination with transmitted light under a stereo microscope. Individual rotifers are picked up with a micropipette and transferred to a flat or hollow-ground microscope slide, for examination with a compound microscope, with magnifications generally between x 100 and x 250, after the water drop has been covered with a cover-slip. In cases where the rotifers are present among dense algae or other water plants, it is convenient to examine a sample of the vegetation in water with a stereo microscope and to pick individual rotifers up with a micropipette. Some species of rotifer tend to be very active, making examination difficult and, in such cases, the addition of a few drops of local anaesthetic, such as 4% Procaine, to the water sample containing the rotifers, serves to slow them down. For permanent preservation, rotifers should be transferred via micropipette to a 4% formalin solution, or 70% alcohol in a small vial. Where examination of the rotifer's mastax structure is needed, the dead body of a rotifer is usually placed on a microscope slide and is dissolved through the addition of a drop or two of household bleach or sodium hypochlorite. The mastax structure will resist this treatment and can be examined under a cover-slip with a high-magnification compound microscope. The microscopic examination of other internal organs can usually be done on complete rotifers with transmitted light, as these minute animals are generally transparent.

The morphology of female rotifers

The body consists typically of a head, trunk and foot (Fig. 6.1). The head bears the ciliated rotatory organ or 'corona', which serves the purpose of bringing food to the mouth (or 'oral aperture') and of locomotion. One may assume that ancestral rotifers had a uniformly ciliated head, an apical

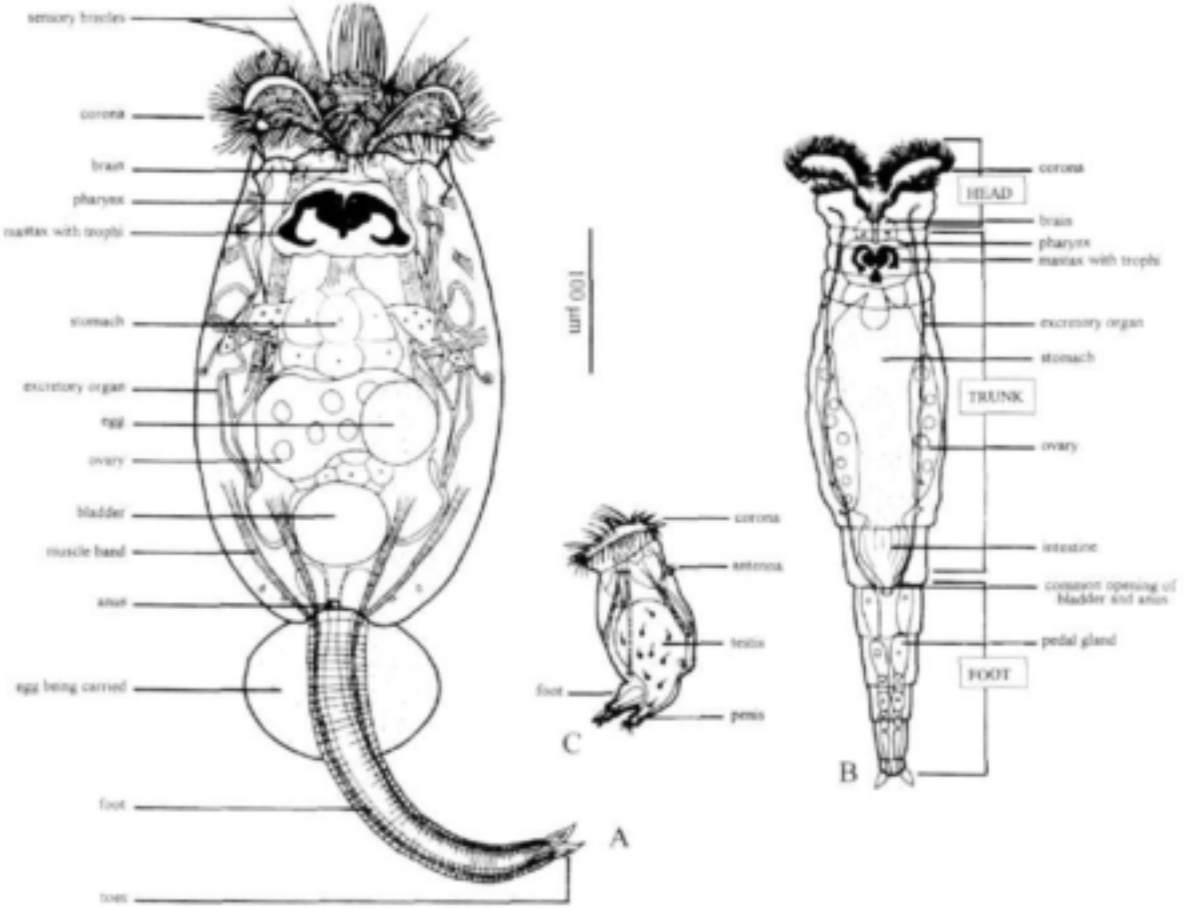


Fig. 6.1. Diagrams showing the structure of typical rotifers with various characteristics indicated: **A**, female monogonont rotifer (*Brachionus*), ventral view; **B**, female digonont or bdelloid rotifer (*Philodina*), ventral view; **C**, male rotifer (*Brachionus*), lateral view. (Redrawn from Koste, 1978 and Pennak, 1978)

field, and a buccal field surrounding the mouth. The form of these various ciliated areas on the corona is useful in placing a particular rotifer in its correct family. Sense organs for light and touch are present in many rotifers. Although eyes are typically placed immediately above the 'brain', or cerebral ganglion, eye-spots are more widely distributed while tactile organs may be in the form of sensory hairs, ciliated pits or dorsal and lateral antennae. Nerves connect these antennae to the brain.

The cavity of the trunk is filled with fluid, as there is no circulatory system, and it contains the following organs (Fig. 6.1A & B): the digestive tract including the pharynx, mastax, oesophagus, salivary glands, stomach, gastric glands and intestine; the excretory system consisting of flame bulbs, ducts and a bladder; the brain, mentioned above, and circular and longitudinal muscles extending into the head and foot. The anus marks the junction between the trunk and the foot and serves as the combined dorsal opening for the rectum, bladder and oviduct. The segmented foot typically has two toes, containing pedal glands with outlets at their tips.

A rotifer's body surface is covered with a cuticle, which is either thin and flexible or thickened and more or less rigid, in which case it is termed a lorica. The lorica can consist of several plate-like sections of the trunk cuticle, or it may be rigid and sculptured.

The trunk may carry prominent lateral appendages, as in *Polyarthra* (Fig. 6.4A), or muscular appendages, as in *Hexarthra* (Fig. 6.4K), which allow rapid swimming movements, or long movable spines, as in *Filinia* (Fig. 6.4L), presumably useful in defence against predators.

Features of taxonomic importance

The mastax

Ventral to the pharynx is a crop-like pouch, the mastax, containing a number of hard parts called trophi (Fig. 6.2A), which are used for grinding food. Trophi can be studied in preserved specimens and so they are of particular taxonomic importance. They consist of an unpaired fulcrum with an adjoining pair of rami, flanked on either side by one of a pair of unci and manubria. Fulcrum and rami together form the incus, which is ventro-caudal and set at an oblique angle to the dorso-cranial part, the malleus, in such a way that the teeth of the unci grind against each other and also against the surface of the rami. Movement is made possible by muscles connecting the individual parts and walls of the mastax.

The basic elements described above may be distinguished in the trophi of any rotifer but they are considerably modified in the various families according to feeding habits. Five important types of rotifer trophi are used as distinguishing characters in identification keys (Fig. 6.2B–F).

Malleate trophi (Fig. 6.2B): the fulcrum and manubria are small, but the unci and rami are well-developed. Food particles are held and ground between unci and rami. This arrangement is commonly found in the Brachionidae.

Ramate trophi (Fig. 6.2C): a modification of the malleate trophi, found in bdelloid rotifers as well as in representatives of the Testudinellidae, Conochilidae and Hexarthridae. The unci form large grinding plates with many toothed ridges; the rami are large, but the fulcrum and manubria are much reduced.

Uncinate trophi (Fig. 6.2D): an arrangement found only in the Collothecidae where the trophi lie freely at the bottom of a large funnel-shaped proventriculus, homologous to the mastax. The trophi are probably not of much importance as the food is predigested.

Virgate trophi (Fig. 6.2E): the long fulcrum and manubria are often asymmetrical with pointed rami and slightly toothed unci. The trophi are used for piercing and sucking, the food being swallowed uncrushed by means of pumping motions of the mastax. This arrangement is found in the Notammatidae, Trichocercidae, Gastropodidae and Synchaetidae.

Forcipate trophi (Fig. 6.2F): large pincers are formed by the toothed rami, but other parts are considerably reduced. The rami can be extruded through the mouth to grip prey, an arrangement found in the Asplanchnidae and Dicranophoridae.

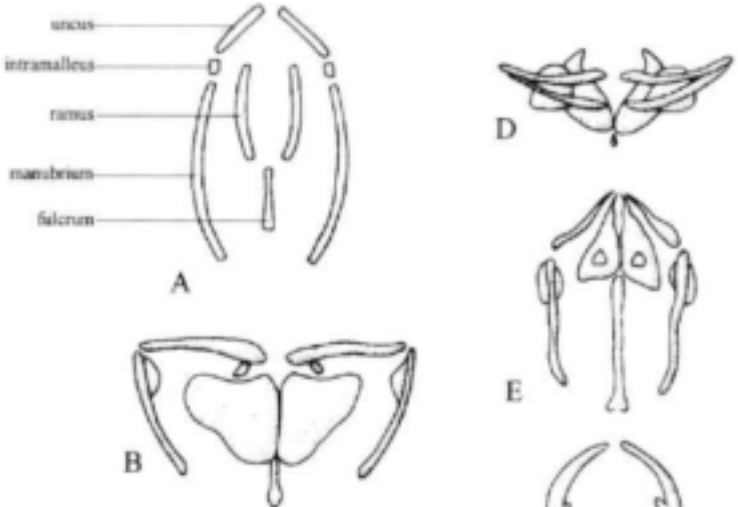


Fig. 6.2: Rotifer mouthparts or trophi (dorsal views). **A**, schematic diagram of generalised rotifer mastax. **B–F**, types of trophi found in various rotifer taxa: **B**, malleate type; **C**, ramate type; **D**, uncinate type; **E**, virgate type; **F**, forcipate type. (Redrawn from Ruttner-Kolisko, 1978).

Male morphology

Among monogonont rotifers, sexual dimorphism is extreme with males (Fig. 6.1C) being invariably much smaller than corresponding females. The lifespan of males tends to be very short and, as the digestive system is degenerate, feeding usually does not occur. In this case the ciliated corona is used purely for locomotion and the small conical males can swim with great speed and agility in their search for females. The male gonad consists of a very large testis in which mature sperm swim freely; it opens into a prominent penis which is dorsal to the foot and is used to penetrate the female's body wherever the male is able to strike.

Reproduction

Rotifers reproduce entirely by means of eggs or living young while vegetative proliferation, common in primitive worms, does not occur. In bdelloid rotifers, in which only females are known, reproduction is parthenogenic, whereas in monogont rotifers there is an alternation between parthenogenic and sexual reproduction modes. In monogononts, varying numbers of successive generations reproduce by means of diploid parthenogenic cells, termed amictic eggs. In certain conditions, often at the end of summer, mictic eggs are produced by means of two meiotic divisions in which the chromosome set is reduced to the haploid number. If these haploid eggs are fertilized, they produce resting eggs with highly resistant shells that are able to survive desiccation and unfavourable conditions for long periods; if they remain unfertilized, they develop into haploid dwarf males. The individual emerging from a resting egg is invariably an amictic female which then completes the reproductive cycle.

CLASSIFICATION AND IDENTIFICATION OF ROTIFERS IN SOUTHERN AFRICA

An outline of the classification of southern African rotifers is given in Table 6.1.

The keys and illustrations (given below) are based on Koste (1978), Pennak (1978), Ruttner-Kolisko (1974) and other sources which are gratefully acknowledged. The great majority of rotifers seen under the microscope are females — in fact among bdelloid rotifers, males have never been seen at all — so descriptions and keys provided here refer to females.

Table 6.1. Checklist of rotifer genera in southern Africa

	CLASS: Digononta
Order: Bdelloidea	
Adinetidae	*Adineta* (Fig. 6.3A)
Habrotrochidae	*Habrotrocha* (Fig. 6.3B)
Philodinidae	*Dissotrocha* (Fig 6.3C) *Macrotrachela* (Fig. 6.3D) *Mniobia* (Fig. 6.3E) *Philodina* (Fig. 3F & G) *Pleuretra* (Fig. 6.3H) *Rotaria* (Fig. 6.3I & J)
	CLASS: Monogononta
Order: Ploima	
Ephphanidae	*Cyrtonia* (Fig. 6.6A) *Epiphanes* (Fig. 6.6B)
Brachionidae	*Anuraeopsis* (Fig. 6.6C) *Brachionus* (Fig. 6.6D) *Keratella* (Fig. 6.6E) *Platyias* (Fig. 6.6F)
Euchlanidae	*Euchlanis* (Fig. 6.6G & H)
Mytilinidae	*Dipleuchlanis* (Fig. 6.7A) *Mytilina* (Fig. 6.7 B & C)
Trichotridae	*Lophocharis* (Fig. 6.7D) *Macrochaetus* (Fig. 6.7E) *Trichotria* (Fig. 6.7F)
Colurellidae	*Colurella* (Fig. 6.7G) *Lepadella* (Fig. 6.7H) *Squatinella* (Fig. 6.7I)
Lecanidae	*Lecane* (Fig. 6.5A)
Proalidae	*Proales* (Fig. 6.5B)
Notommatidae	*Cephalodella* (Fig. 6.5C) *Eosphora* (Fig. 6.5D) *Monommata* (Fig. 6.5E) *Notommata* (Fig. 6.5F) *Scaridium* (Fig. 6.5G) *Taphrocampa* (Fig. 6.5H)
Trichocercidae	*Trichocerca* (Fig. 6.5I)
Gastropodidae	*Ascomorpha (*Fig. 6.5J) *Gastropus* (Fig. 6.5K)
Synchaetidae	*Ploesoma* (Fig. 6.5L) *Polyarthra* (Fig. 6.4A) *Synchaeta* (Fig. 6.4B)
Asplanchnidae	*Asplanchna* (Fig. 6.4C)
Dicranophoridae	*Encentrum* (Fig. 6.4D)
Order: Flosculariacea	
Testudinellidae	*Pompholyx* (Fig. 6.4E) *Testudinella* (Fig. 6.4F)
Flosculariidae	*Limnias* (Fig. 6.4G) *Sinantherina* (Fig. 6.4H)
Conochilidae	*Conochilus* (Fig. 6.4 I, J)
Hexarthridae	*Hexarthra* (Fig. 6.4K)
Filiniidae	*Filinia* (Fig. 6.4L)
Order: Collothecacea	
Collothecidae	*Collotheca* (Fig. 6.4M)

Class: DIGONONTA, Order: **Bdelloidea**

Rotifers of the Class Digononta are characterized by paired ovaries, a ramate mastax (Fig. 6.2C) and the absence of a lorica or secreted tube. All freshwater digonont rotifers belong to the Order Bdelloidea in which only females are known and reproduction is entirely by parthenogenesis. The cylindrical body is highly contractile and telescopic allowing leech-like locomotion or active swimming, propelled by the coronary cilia.

BDELLOIDEA IN SOUTHERN AFRICA: KEY TO GENERA (FEMALES)

1. Rostrum incomplete and corona absent (Fig 6.3A) .... *Adineta*
– Rostrum well-developed; corona present, can be retracted into mouth (Figs 6.3B–J) 2

2. Stomach filled with protoplasm, in which food vacuoles are formed; intestine not ciliated; oviparous (Fig. 6.3B) .... *Habrotrocha*
– Stomach hollow and intestine ciliated; viviparous or oviparous (Figs. 6.3C–J) (Philodinidae) 3

3. With four toes, of which two are dorsal and two terminal 4
– Toes not of this pattern 6

4. Cuticle smooth (Fig. 6.3F) (but this is not obvious in desiccated specimens) (see Fig 6.3G) .... *Philodina*
– Cuticle rough or folded 5

5. Cuticle coarse but without many transverse folds; with or without spines; viviparous (Fig. 6.3C) .... *Dissotrocha*
– Cuticle leathery, with many transverse folds; viviparous (Fig. 6.3H) .... *Pleuretra*

6. Toes with cup-like suckers or fused into one or two discs (Fig. 6.3E) .... *Mniobia*
– Three toes, one dorsal and two terminal (Figs 6.3D, I) 7

7. Eyes absent; oviparous (Fig. 6.3D) .... *Macrotrachela*
– Two eyes usually present on the proboscis (Fig. 6.3J); viviparous; some species very elongated, up to 1,5 mm long (Fig. 6.3I) .... *Rotaria*

Class: MONOGONONTA. Orders: **Ploima, Flosculariacea & Collothecacea**

As the name implies, monogonont rotifers have unpaired ovaries, a variety of mastax-types and the presence, or absence, of loricas and secreted tubes. Representatives of 39 genera are known at present from southern Africa.

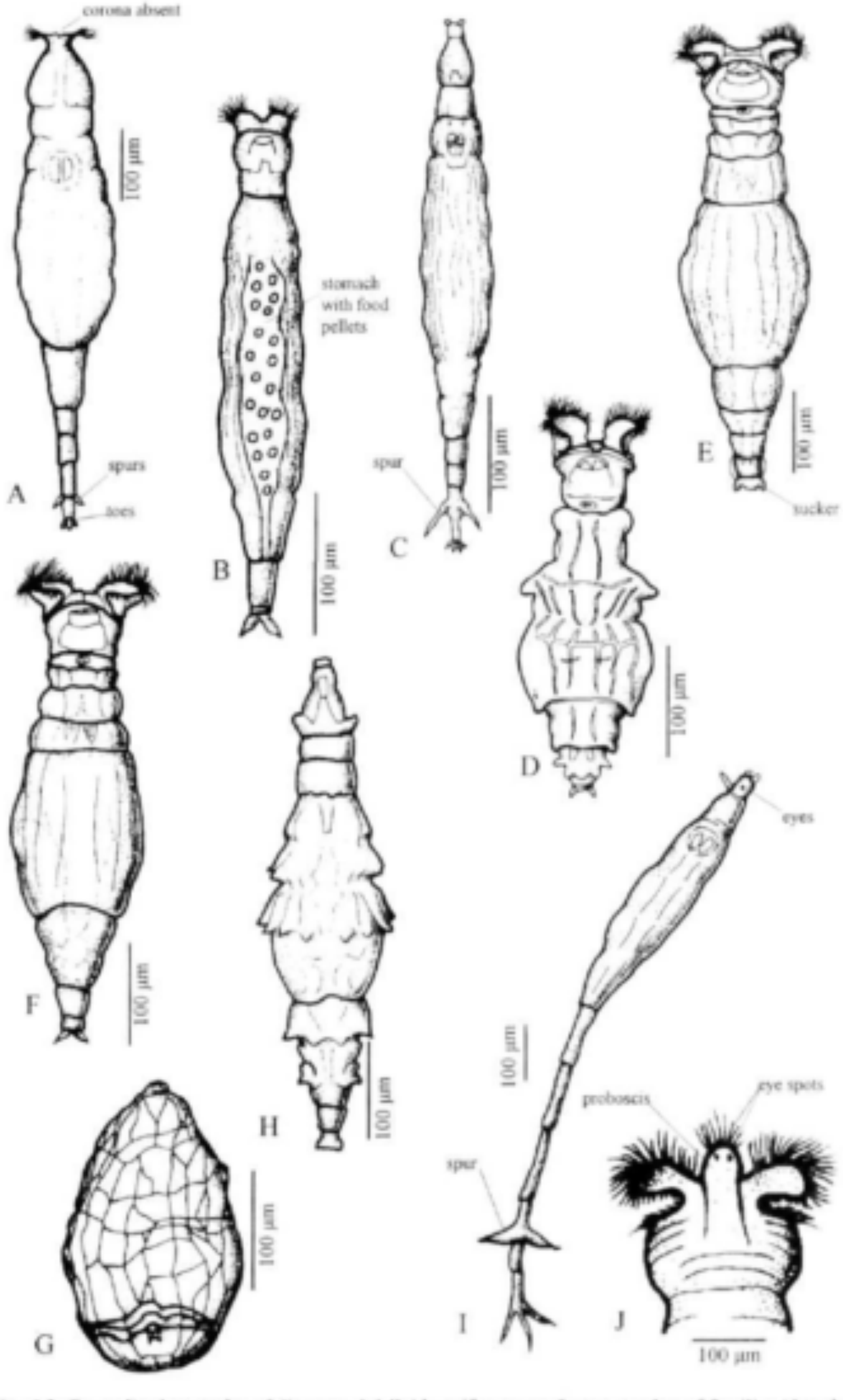


Fig. 6.3: Generalized examples of digonont, bdelloid rotifer genera from a number of families (dorsal views): **A**, Adinetidae: *Adineta*. **B**, Habrotrochidae: *Habrotrocha*. **C–J**, Philodinidae: **C**, *Dissotrocha*; **D**, *Macrotrochela*; **E**, *Mniobia*; **F**, *Philodina* (undesiccated); **G**, *Philodina* (in desiccated form); **H**, *Pleuretra*. **I–J**, *Rotaria*: **I**, dorsal view of whole animal; **J**, detail of corona
(Drawings based on the following: Donner, 1968; Pennak, 1978 and other sources.)

MONOGONONTA IN SOUTHERN AFRICA: KEY TO GENERA (FEMALES)

1. Female nearly always free-swimming or creeping; lorica present or absent; no secreted tube; corona not especially large; foot, when present, typically with two toes; solitary 3

– Female usually sessile, without a lorica but often in a secreted tube; corona large; foot, when present, long, annulated, without toes but with a termina attachment disc; solitary or colonial 2

2. Corona surrounded by concentric wreaths of cilia, with a furrow between the wreaths; outer cilia shorter than inner; mouth offset; usually one or two antennae; mastax malleo-ramate; solitary or colonial (**Flosculariacea**) 38

– Corona very large, without a double wreath of cilia; no well-developed antennae; mouth central; mastax uncinate or poorly developed; buccal field horse shoe-shaped with the mouth at the bottom of a large concave infundibulum; solitary and often sessile (Fig. 6.4M) (**Collothecacea**) .... *Collotheca*

3. Foot and toes always absent 4

– Foot always present; toes usually present 11

4. With 12 lateral appendages; body short and more or less cylindrical (Fig. 6.4A) .... *Polyarthra*

– Not with 12 such appendages 5

5. With six muscular appendages; body conical with a double ciliary wreath and a ciliated groove between; common in alkaline waters (Fig. 6.4K) (Hexarthridae) .... *Hexarthra*

– Without such appendages 6

6. No lorica but three or four long movable spines (Fig. 6.4L) (**Flosculariacea**) .... *Filinia*

– Lorica present or absent; spines, if present, confined to the anterior and posterior margins of the lorica 7

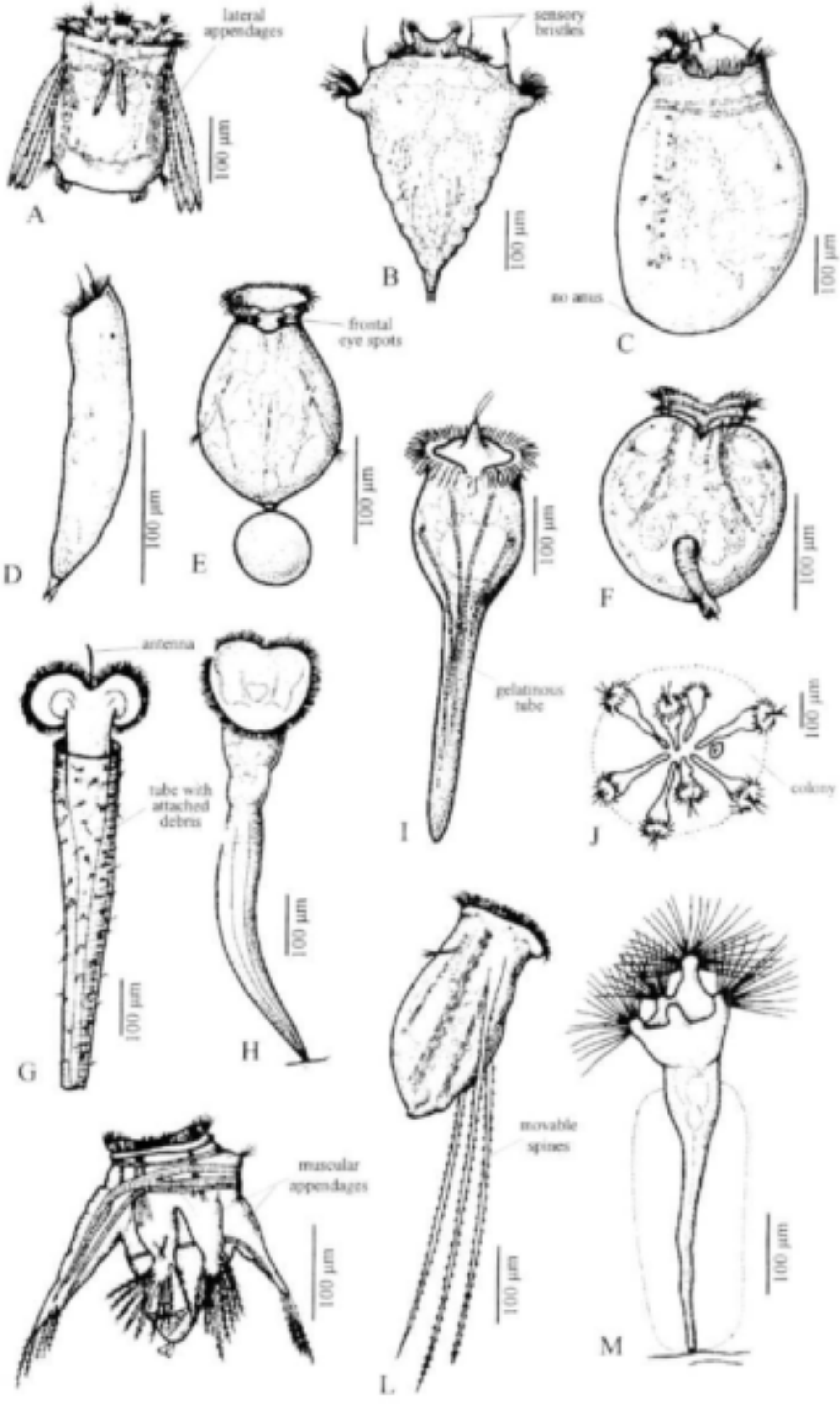
7. Lorica spinous and made up of two plates fused laterally; dorsal surface of lorica with a pattern of polygonal facets (Fig. 6.6E) .... *Keratella*

– Lorica present or absent and not spinous 8

8. Large transparent rotifers, over 400µm long, sac-shaped with a well-developed corona; intestine and anus absent; mastax incudate; often viviparous; predatory (Fig. 6.4C) .... *Asplanchna*

– Smaller and more opaque; less than 200µm 9

Fig. 6.4. Generalized examples of monogonont rotifer genera from a number of families:
A–B, Synchaetidae: **A**, *Polyarthra*, dorsal view; **B**, *Synchaeta*, dorsal view; **C**, Asplanchnidae: *Asplanchna*, lateral view. **D**, Dicranophoridae: *Encentrum*, lateral view. **E–F**, Testudinellidae: **E**, *Pompholyx*, ventral view; **F**, *Testudinella* (ventral view). **G–H**, Flosculariidae: **G**, *Limnias*, dorsal view; **H**, *Sinantherina*, ventral view. **I–J**, Conochilidae: *Conochilus*: **I**, lateral view; **J**, dorsal view of several individuals in a colony. **K**, Hexarthridae: *Hexarthra*, lateral view. **L**, Filiniidae: *Filinia*, lateral view. **M**, Collothecidae: *Collotheca*, lateral view. (Drawings based on the following sources: Donner, 1968; Koste, 1978; Pennak, 1978; Pontin, 1978 and Ruttner-Kolisko, 1974).


lateral appendages
100 µm
A
sensory bristles
100 µm
B
no anus
100 µm
C
frontal eye spots
100 µm
D
100 µm
E
100 µm
I
100 µm
F
antenna
tube with attached debris
100 µm
G
100 µm
H
gelatinous tube
100 µm
colony
J
muscular appendages
100 µm
K
movable spines
100 µm
L
100 µm
M

9. Lorica thin or absent; sac-shaped; a very large lobed stomach filling most of the body; anus absent; mastax virgate (Fig. 6.5J) .... *Ascomorpha*
– With a thick lorica; not sac-like 10

10. Lateral edges of dorsal and ventral plates of lorica closely confluent, flat or four-lobed in cross section; two frontal eyespots; mastax malleo-ramate (Fig. 6.4E) .... *Pompholyx*
– Lateral edges of lorica plates connected by infolded cuticle; ventral plate of lorica flat, dorsal plate arched; mastax malleate (Fig. 6.6C) .... *Anuraeopsis*

11. With a well-developed rigid lorica 12
– Lorica absent or poorly developed and flexible 29

12. Foot typically annulated and attached to the ventral surface; lorica one rigid piece; mastax virgate 13
– Foot terminal or subterminal 14

13. Foot with one or two toes emerging from a small ventral opening; lorica surface plain, body laterally compressed (Fig. 6.5K) .... *Gastropus*
– Foot annulated with two toes; lorica surface marked with ridges or vesicles; body not laterally compressed; lorica open along midventral line; mastax virgate (Fig. 6.5L) .... *Ploesoma*

14. Cylindrical body curved and asymmetrical; lorica a single cylindrical piece; toes unequal in length and spike-like; creeping or free-swimming; mastax virgate; trophi asymmetrical (Fig. 6.5I) .... *Trichocerca*
– Toes not spike-like 15

15. Foot long, retractile, annulated and ending in a tuft of cilia; lorica almost circular and flattened dorsoventrally with dorsal and ventral plates fused laterally; mastax malleo-ramate (Fig. 6.4F) .... *Testudinella*
– Foot ending in one or two toes 16

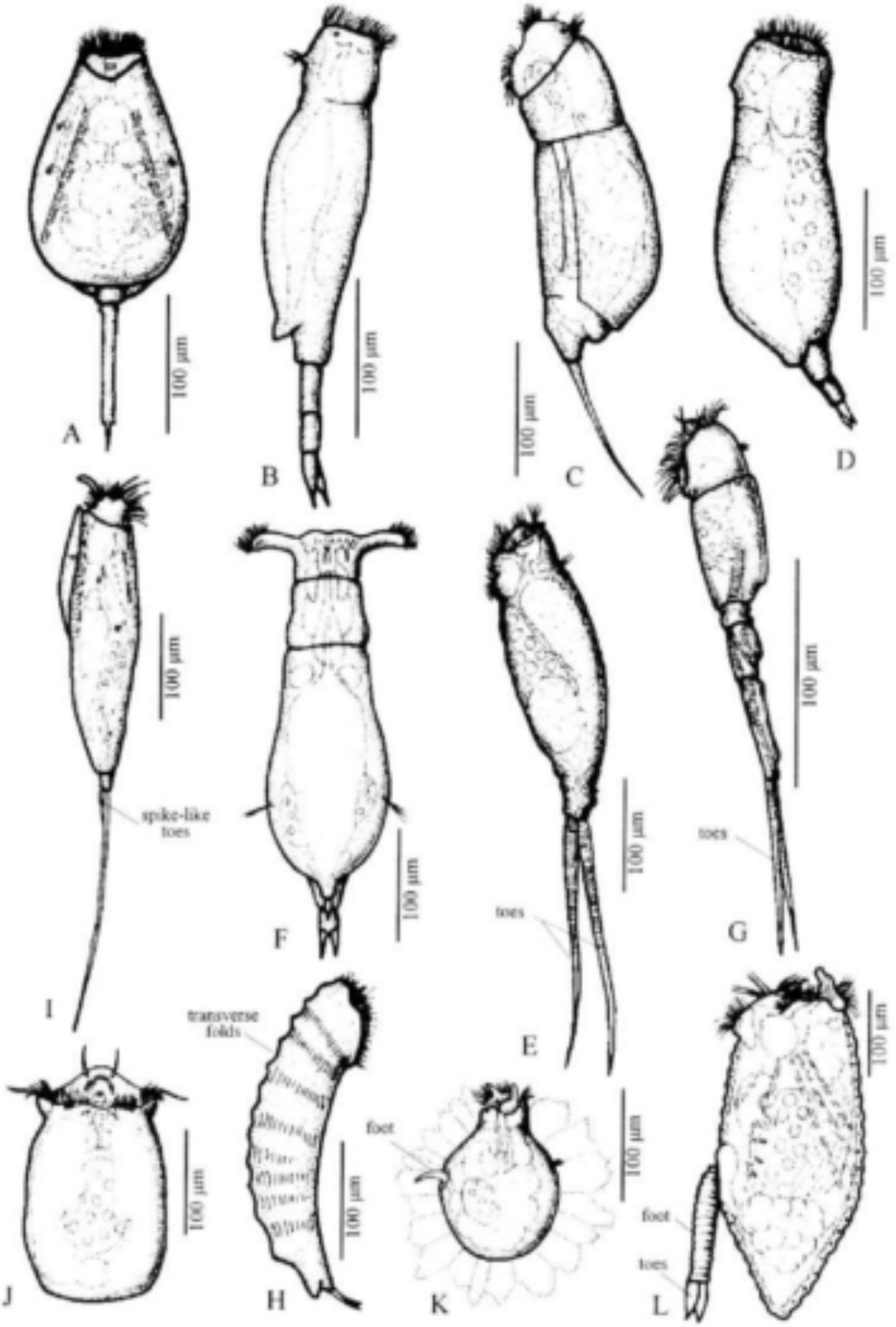


Fig. 6.5. Generalized examples of monogonont rotifer genera from a number of families. **A**, Lecanidae: *Lecane*, dorsal view. **B**, Proalidae: *Proales*, lateral view. **C–H**, Notommatidae: **C**, *Cephalodella*, lateral view; **D**, *Eosphora*, lateral view; **E**, *Monommata*, lateral view; **F**, *Notommata*, dorsal view; **G**, *Scaridium*, lateral view; **H**, *Taphrocampa*, lateral view. **I**, Trichocercidae: *Trichocerca*, lateral view. **J–K**, Gastropodidae: **J**, *Ascomorpha*, dorsal view; **K**, *Gastropus*, dorsal view. **L**, Synchaetidae: *Ploesoma*, lateral view. (Drawings based on on the following: Donner, 1968; Koste, 1978; Pennak, 1978; Pontin, 1978 and Ruttner-Kolisko, 1974).

16. Entire margin spiny; lorica heavy with 4–10 long dorsal and six posterior spines; foot short; mastax malleate (Fig. 6.7E) .... *Macrochaetus*
– Entire body-margin not spiny 17

17. Head with a wide circular shield; lorica cylindrical or pyriform, often with one or two median dorsal spines or several on the posterior margin of the lorica; a spine sometimes at the base of the toes; mastax malleate (Fig. 6.7I) .... *Squatinella*
– Head without a wide circular shield 18

18. Two spines at the base of the foot or occasionally two posterior dorsolateral spines on the lorica; lorica thick, with large facets in one boxlike piece; mastax malleate (Fig. 6.7F) .... *Trichotria*
– Without two such spines 19

19. Body moderately flattened dorsoventrally; dorsal and ventral lorica plates fused laterally; anterior dorsal margin of lorica usually with four to six spines, posterior margin with or without spines; two toes; mastax malleate 20
– Another combination of characters; mastax usually malleate or sub-malleate; body never dorsoventrally flattened and never with four to six spines on the anterior dorsal lorica margin 21

20. Foot segmented and retractile (Fig. 6.6F) .... *Platyias*
– Foot long, annulated, retractile and not segmented (Fig. 6.6D) .... *Brachionus*

21. Strongly compressed laterally; lorica composed of two lateral plates; frontal hood present on the head; toes long and tapering; lorica open along anterior, ventral and posterior margins; terminal foot segment short (Fig. 6.7G) .... *Colurella*
– Not strongly compressed laterally; lorica of a different construction, frontal hood absent 22

22. Foot and toes long, lorica without spines or plates; lorica vase-shaped and thin; toes shorter than rest of body; mastax virgate (Fig. 6.5G) .... *Scaridium*
– Foot short, toes short or long 23

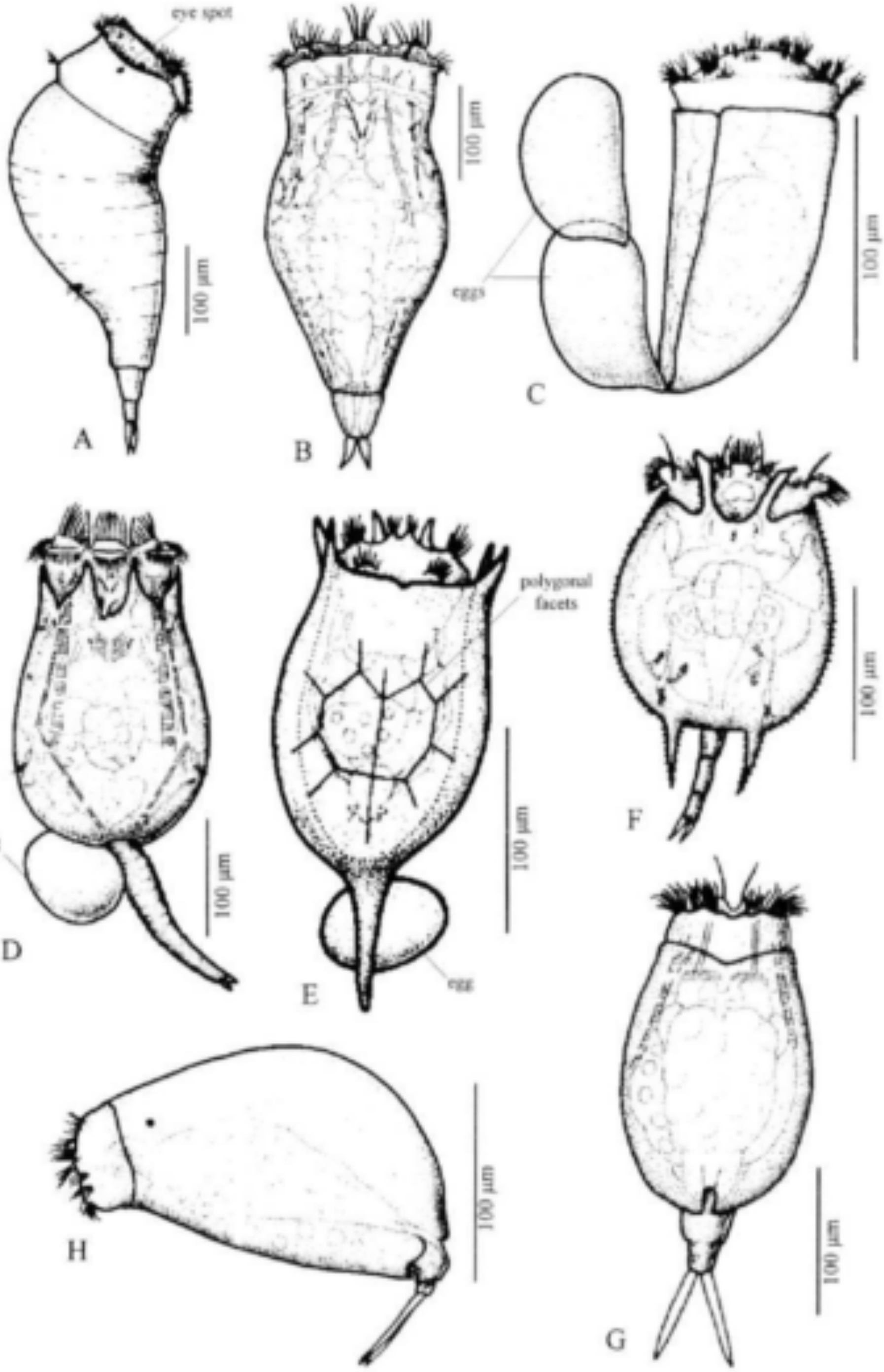


Fig. 6.6: Generalized examples of monogonont rotifer genera from a number of families.
A–B, Epiphanidae: **A,** *Cyrtonia*; **B**, *Epiphanes*. **C–F**, Brachionidae: **C**, *Anuraeopsis* (lateral view); **D**, *Brachionus* (dorsal view); **E**, *Keratella* (dorsal view); **F**, *Platyias*. (dorsal view). **G–H**, Euclanidae: **G,** *Euchlanis* dorsal view; **H**, *Euchlanis*, lateral view. (Drawings based on the following sources: Donner, 1968; Koste, 1978; Pennak 1978; Pontin, 1978; Ruttner-Kollisko, 1974).

23. Lorica consisting of a ventral plate and two lateral plates, edges of which form two dorsal ridges; often with anterior and posterior spines (Fig. 6.7B,C) .... *Mytilina*

– Lorica constructed differently 24

24. Lorica in one rigid box-like piece with a prominent dorsal keel or low ridge extending the entire length of the lorica (Fig. 6.7D) .... *Lophocharis*

– Lorica usually composed of a dorsal and ventral plate 25

25. Lorica with dorsal and ventral plates rigidly joined at the edges with an anterior opening for the head and a posterior one for the foot; foot well developed (Fig. 6.7H) .... *Lepadella*

– Lorica with dorsal and ventral plates not united at the edges; foot not well developed; benthic or occasionally in the plankton 26

26. Body spindle- or prism- shaped; two tapering and curved toes; lorica thin and poorly developed (Fig. 6.5C) .... *Cephalodella*

– Lorica rigid and well-developed, more or less flattened dorsoventrally; toes long; mastax malleate or submalleate 27

27. Lorica with dorsal plate much smaller than ventral plate; cuticle connecting the plates forms a deep groove dividing the body cavity into two unequal parts (Fig. 6.7A) .... *Dipleuchlanis*

– Lorica with dorsal plate the same size as, or larger than, the ventral plate 28

28. Foot with two rudimentary segments; toes parallel-sided; strongly compressed dorsoventrally (Fig. 6.5A) .... *Lecane*

– Foot with two or three indistinct segments; toes usually slightly fusiform; ventral plate flat, dorsal plate arched and convex, sometimes keeled (Fig. 6.6G, H) .... *Euchlanis*

29. Corona with four long sensory bristles; body conical; toes small; mastax virgate (Fig. 6.4B) .... *Synchaeta*

– Corona without such bristles 30

30. Corona complex, with outer and inner bands of cilia, sometimes with accessory rows of cilia and ciliated protuberances; mastax malleate; large species 31

– Corona simple with a single peripheral band of cilia; general surface of corona without cilia or with scattered cilia; corona occasionally with two slight sensory protuberances 32

31. Eyespot absent; body not strongly tapered posteriorly (Fig. 6.6B) .... *Epiphanes*

– Eyespot present; body strongly tapered posteriorly (Fig. 6.6A) .... *Cyrtonia*

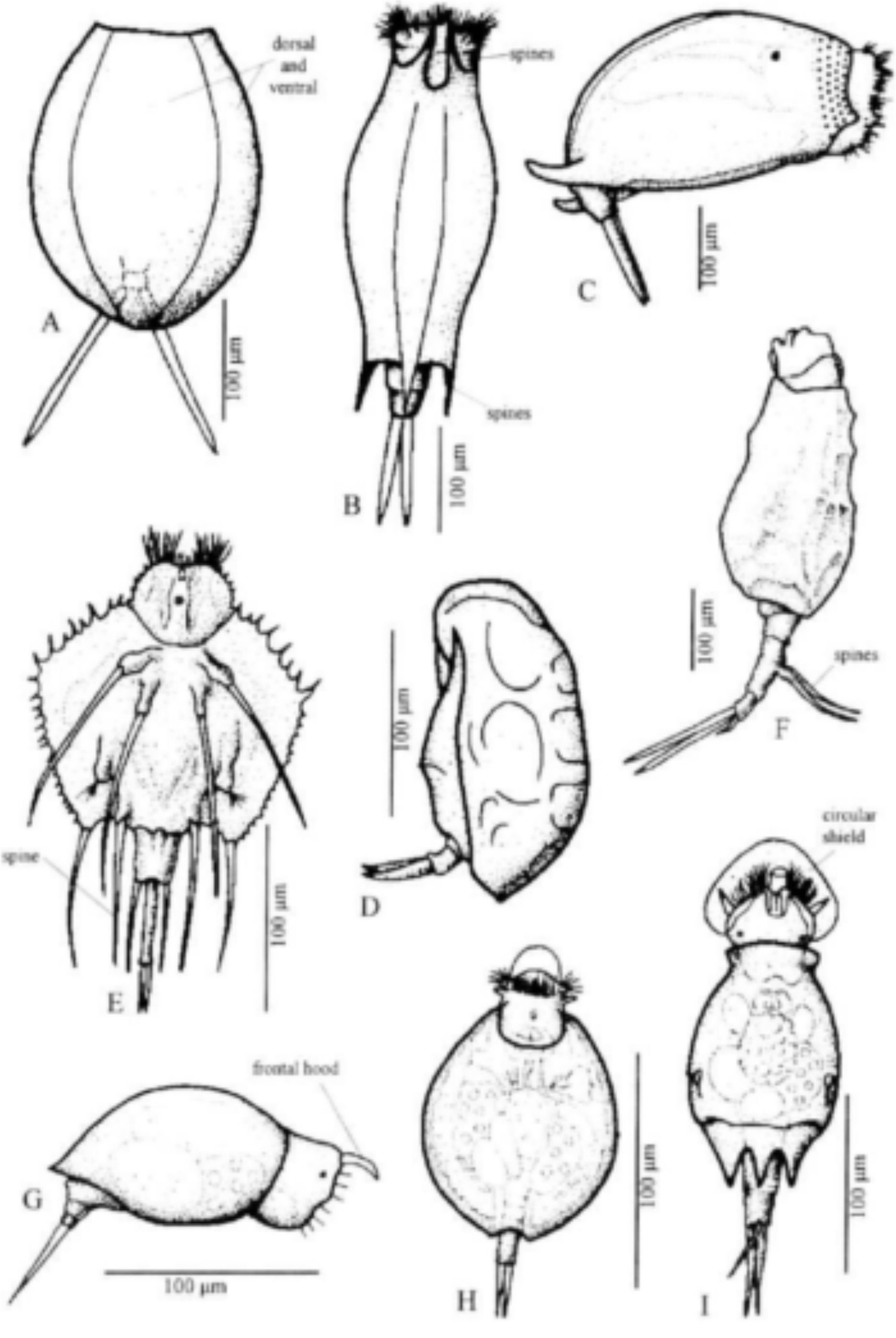


Fig. 6.7. Generalized examples of monogonont rotifer genera from a number of families. **A–C**, Mytilinidae: **A**, *Dipleuchlanis*, (dorsal view); **B**, *Mytilina*, dorsal view; **C**, *Mytilina*, lateral view. **D–F**, Trichotridae: **D**, *Lophocharis*, lateral view; **E**, *Macrochaetus*, dorsal view; **F**, *Trichotria*, lateral view. **G–I**, Colurellidae. **G**, *Colurella*, lateral view; **H**, *Lepadella*, dorsal view; **I**, *Squatinella*, dorsal view. (Drawings based on the following sources: Donner, 1968; Koste, 1978; Pennak, 1978; Pontin, 1978 and Ruttner-Kollisko, 1974).

32. Mastax forcipate; trophi strongly compressed dorsoventrally and adapted for protrusion and tearing prey; unci weak and needle-like; corona oval and ventral, or subcircular and strongly oblique; marginal cilia short, with the exception of two lateral auricle-like tufts of cilia; rostrum large; buccal field evenly ciliated (Fig. 6.4D) .... *Encentrum*
– Mastax not forcipate; corona frontal or oblique 33

33. Mastax virgate or virgate-forcipate, adapted for sucking out contents of plant cells and animals 34
– Mastax modified malleate; unci adapted for crushing and grinding; corona oblique with two lateral tufts of cilia but no auricles (Fig. 6.5B) ....*Proales*

34. Toes longer than rest of body, usually unequal in length (Fig. 6.5E)..........
....*Monommata*

35. Body marked with transverse folds or annuli; foot rudimentary (Fig. 6.5H)....
....*Taphrocampa*
– Body not with transverse folds or annuli 36

36. Toes relatively long, pointed and usually curved; foot rudimentary and unjointed; body prismatic or spindle-shaped; lorica present, more or less sclerotized and made up of a dorsal and ventral plate; rami and unci of very simple construction (Fig. 6.5C) ....*Cephalodella*
– Toes comparatively short; rami and unci more complicated 37

37. Rami roughly hemispherical; cervical eyespot only; some species covered by a gelatinous secretion (Fig. 6.5F) ....*Notommata*
– Each uncus with a single simple tooth; rami bent at right angles with teeth (Fig. 6.5D) ....*Eosphora*

38. Ciliary wreath with a ventral gap; mouth on the corona, near the dorsal edge; one or two antennae on the corona; colonies composed of radiating individuals inhabiting coherent gelatinous tubes (Fig. 6.4I, J) ....*Conochilus*
– Ciliary wreath with or without a dorsal gap; mouth ventral to the corona; eyespots usually present, adults usually sessile.................................39

39. Adults in spherical sessile colonies attached to aquatic plants; colonies without tubes; corona kidney shaped (Fig. 6.4H) ....*Sinantherina*
– Tube composed of a chitin-like substance, often opaque and covered with debris; corona of two distinct lobes or nearly circular; dorsal antenna present (Fig. 6.4G) ....*Limnias*

ACKNOWLEDGEMENTS

My thanks are due to Jenny Day for initially proposing the compilation of this illustrated key to rotifers and for her editorial help. More recently, Irene de Moor has taken this process further, for which I am very grateful. Various colleagues in the rotifer-research fraternity, such as Claudia Ricci, Russ Shiel, Eric Hollowday and Walter Koste have been generous with their advice and encouragement.

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CHAPTER 7

NEMATODA

by

J. Heyns[†]

The Nematoda form one of the largest groups in the animal kingdom, in terms of numbers of species and of individuals. There are more than 15 000 known species, and most authorities estimate that the actual number of species may be in excess of 80000. They occur on land, in fresh water and in the ocean. Nematodes are regarded as freeliving when they feed on bacteria, fungi or other micro-organisms, or when they are predators on other small animals. Others are parasites of plants or of nearly all other animal groups.

Nematodes that are normally encountered in freshwater habitats are all microscopic, wormlike creatures, ranging from about 0,25 mm to (at most) 8–10 mm in length. Even though some specimens may be several mm in length, they are seldom more than 30 or 40 μm in diameter, so that they are normally not visible to the naked eye.

Nematodes reproduce sexually, normally producing eggs after copulation. Sexes are separate in most nematodes, but hermaphrodites also occur, and parthenogenesis is common in some groups. Most nematodes go through four moults to become sexually mature, and immature forms basically resemble adults except for size and the lack of gonads and a sexual apparatus.

The construction of a key to freshwater nematodes occurring in southern Africa is complicated by two factors: firstly by the lack of information, since very little research has been done thus far on freshwater nematodes in this region, and secondly, by the fact that not all nematodes collected among the benthos can automatically be regarded as aquatic organisms. Terrestrial nematodes, both free living and plant parasitic forms, are frequently found in large numbers in the bottom sediment or mud after being washed into streams and other waterbodies, where they can survive for long periods. Moreover, many families and genera contain both terrestrial and aquatic species. When one of these is found in water, it is particularly difficult to decide whether or not it is a truly aquatic form.

CLASSIFICATION OF FRESHWATER NEMATODES

The policy followed during the construction of the present key was to include all freshwater genera which have been recorded from southern Africa, as well as those known to occur here from unpublished records. Also included are several cosmopolitan genera that have been recorded from elsewhere in Africa, even though they have thus far not been found in southern Africa. Lastly, a few representative genera have been included of those terrestrial and plant parasitic groups (of the orders Rhabditida, Tylenchida and Dorylaimida) which are most frequently encountered among the benthos in freshwater habitats.

No attempt has been made to include an outline of the classification of the Nematoda, since this is impractical in a work of such limited scope. According to one system of classification (Maggenti, 1981) the Phylum Nematoda comprises two classes, some eighteen orders, 184 families and several thousand genera. Even if we ignore the numerous taxa that are parasitic on animals, the so-called freeliving nematodes still account for far more than a thousand genera classified into some 140 families.

For additional information and possible identification of forms not included in this key, the reader is referred to Goodey's 1963 book on soil and freshwater nematodes (which is unfortunately out of print and not readily available in libraries) or the book by Heyns (1971) on plant and soil nematodes of South Africa. Keys designed specifically for freshwater nematodes are those by Ferris et al. (1973), Tarjan et al. (1977), Zullini (1982) and Pennak (1989).

MORPHOLOGY

Information on the general morphology and biology of nematodes in general can be found in any good textbook on Zoology. Pennak (1989) includes a brief account of the morphology and biology of nematodes and a useful illustrated glossary of the more common morphological terms used in nematology can be found in Heyns (1971).

Figures 7.1 and 7.2 illustrate most of the morphological characters used in the keys. A few other less common characters, which are useful for the identification of some groups or genera, are illustrated in Figs 7.4, 7.5, 7.6 & 7.7. A more detailed explanation of certain taxonomically-important characters is given below.

The outer layer of the body wall is called the cuticle, and this may be either smooth, radially striated (Fig. 7.1H) resulting in more or less distinct annules, or punctated in various ways (Figs 7.1F, 7.3U & 7.4B). The lateral lines are minute longitudinal lines on the sides of the body that may vary in number from one to several, but are usually constant within a species (see Fig. 7.4).

The anteriormost part of the nematode body, which in its primitive form is radially symmetrical and bears six distinct lips, is called the lip region. This area is often demarcated by a constriction (Figs 7.1G, 7.6H & 7.7H & K) or in some groups by an internal sclerotized framework (Figs 7.1H & 7.5H). Each lip may carry an inner (nearer to the mouth opening) and an outer (further from the mouth opening) labial papilla or labial seta (Figs 7.1F, G). There are also four cephalic papillae or cephalic setae (Figs 7.1F & 7.5S).

In the Cephalobidae there are cuticular extensions of the lip region called probolae. Those nearest to and surrounding the mouth opening are called labial probolae, while those further back are called cephalic probolae. The probolae may assume different shapes (as shown in Figs 7.4M, X, Y) that are useful generic characters.

The amphids are a pair of laterally situated sense organs on or near the lip region. Their apertures may assume various shapes, as shown in Figs 7.1B–E. Phasmids likewise are paired lateral organs, but these are normally found on the tail —in nematodes the tail is defined as that part of the body posterior to the anus —though sometimes somewhat anterior to the anus (Fig. 7.4U, W).

There is some confusion in the nematological literature concerning the various parts of the anterior feeding apparatus. For the purpose of this chapter we can regard stoma and pharynx as synonymous, to indicate the anteriormost, either narrow or broader, part of the alimentary canal. Often, when the stoma is appreciably broader, it is referred to as a buccal cavity, or vestibule, and when the walls of this cavity become strongly sclerotized, as a buccal capsule. The 'teeth' (or 'mural teeth') are sclerotized tooth-like outgrowths from the wall of the stoma (see Fig. 7.1F), found in some predatory groups such as the Mononchida.

The anterior feeding apparatus is followed by the oesophagus, the muscular part leading from the stoma to the intestine. Both the stoma and the oesophagus assume many different shapes, and are of great diagnostic value in nematodes. Various stoma and oesophagus shapes are depicted in Figs 7.1 and 7.2, as well as in the relevant illustrations in Figs 7.3–7.7.

The rhabdions (see Fig. 7.1I), are sclerotized sections of the wall of the stoma, that appear as a series of short rods when seen in optical section,

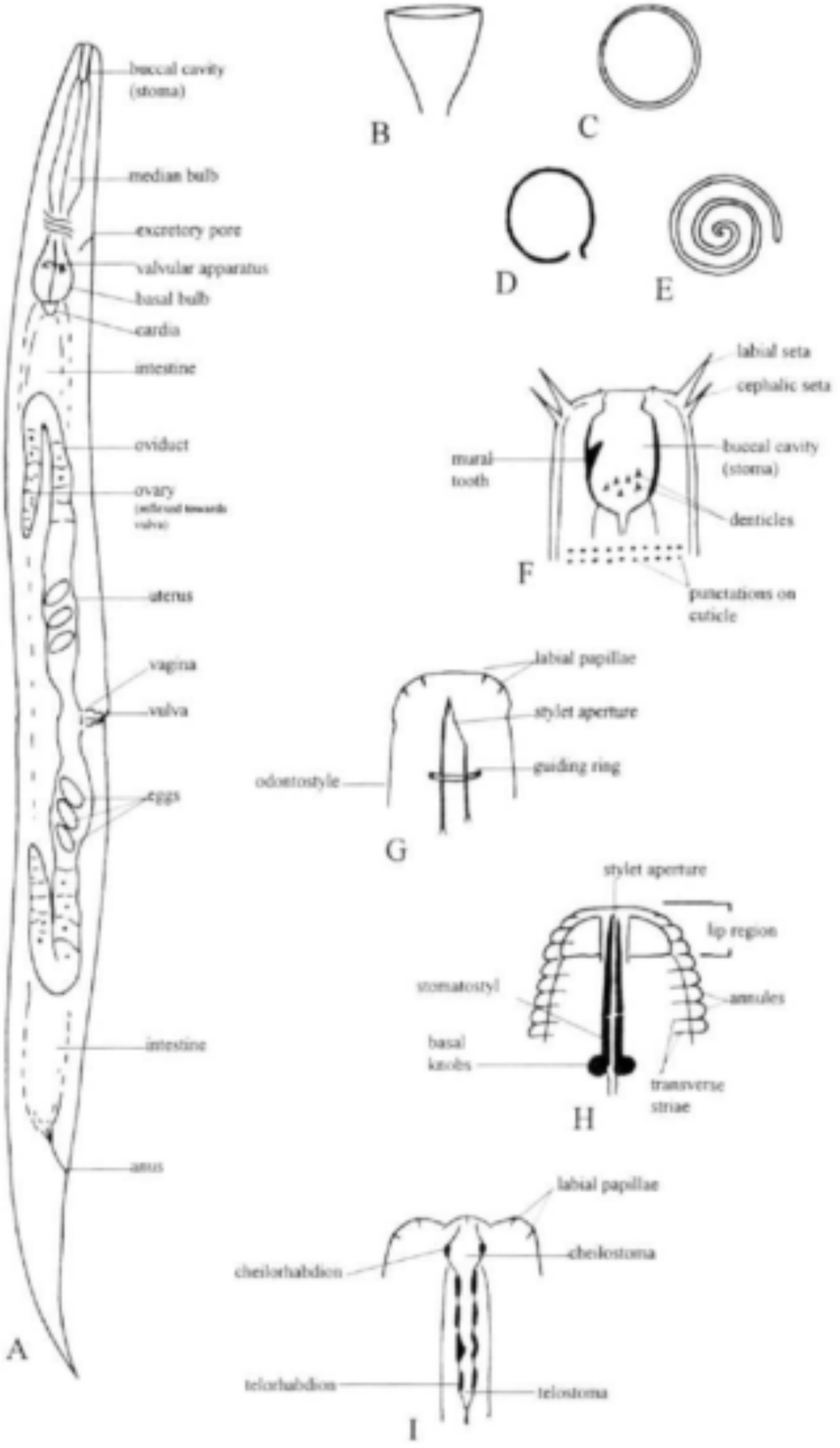


Fig. 7.1. Schematic figures illustrating some of the morphological characters used in the keys. **A**, generalised nematode. **B–E**, various amphid shapes: **B**, stirrup-shaped; **C**, circular; **D**, open circle; **E**, multi-spiral. **F–I**, hypothetical nematode heads showing detail of several anatomical features such as papillae, setae, mural tooth, denticles, odonto- and stomatostyles (protusible stylets) and rhabdions.

under high magnification. (Note that the cheilorhabdion and telorhabdion are those sclerotized parts of the stoma associated with the cheilostoma and telostoma respectively —Fig. 7.1I).

In two groups there is a protrusible stylet in the stoma. In the Tylenchida this stylet is referred to as a stomatostyle (Figs 7.1H & 7.5A, C, H, I), since it originates *in situ* in the stoma, supposedly by a hardening of the stoma wall, while in the Dorylaimida it is called an odontostyle (Figs 7.1G & 7.7D, G, H, K, M) since it is formed more posteriorly in a special cell in the wall of the oesophagus.

At the base of the oesophagus, and projecting into the anterior end of the intestine is a heart-shaped muscular structure, serving as a valve to prevent reflux of food from the intestine to the oesophagus. This oesophago-intestinal valve is usually referred to as the cardia (Figs 7.1A, 7.2A–C).

In female nematodes the reproductive system may have either one or two branches, each consisting of an ovary, oviduct and uterus (Fig. 7.1A). Nematodes with two ovaries are called didelphic. Normally these are opposed, i.e. one ovary being anterior, and the other posterior to the vulva, this condition being referred to as amphidelphic. Species with only one ovary are referred to as being monodelphic. In these cases the ovary may either be anterior (i.e. prodelphic) or posterior (i.e. ophisthodelphic).

The protrusible sclerotized paired copulatory organs of the male are called spicules (Fig. 7.2F), and the more or less immovable guide through which they slide when they are extruded, is called the gubernaculum (Fig. 7.2F). In many groups the male has a bursa (or 'copulatory bursa') which consists of paired lateral extensions of the cuticle surrounding the cloaca (Fig. 7.2F). (Note that female nematodes have an anus, separate from the vulva, while in males the reproductive and digestive systems open via a common pore, the cloaca). The bursa is used to clasp the body of the female during copulation. In other groups there are 'genital papillae' anterior to the cloaca. These are usually referred to as 'ventromedian supplements' or 'supplementary organs' (Figs 7.2G & 7.6M, N).

COLLECTION AND PRESERVATION

Since nematodes cannot be seen with the naked eye, special methods have to be used to extract specimens from samples. The simplest of these is to fit a piece of rubber tubing onto the stem of a glass funnel, close it tightly with a screw clamp, partly fill the funnel with tap water, and stand the funnel on a rack. A platform of rough-meshed wire is then fitted into the funnel, and some tissue paper placed on top of the platform. Mud or sand from the bottom of a dam or stream is then gently placed on top of

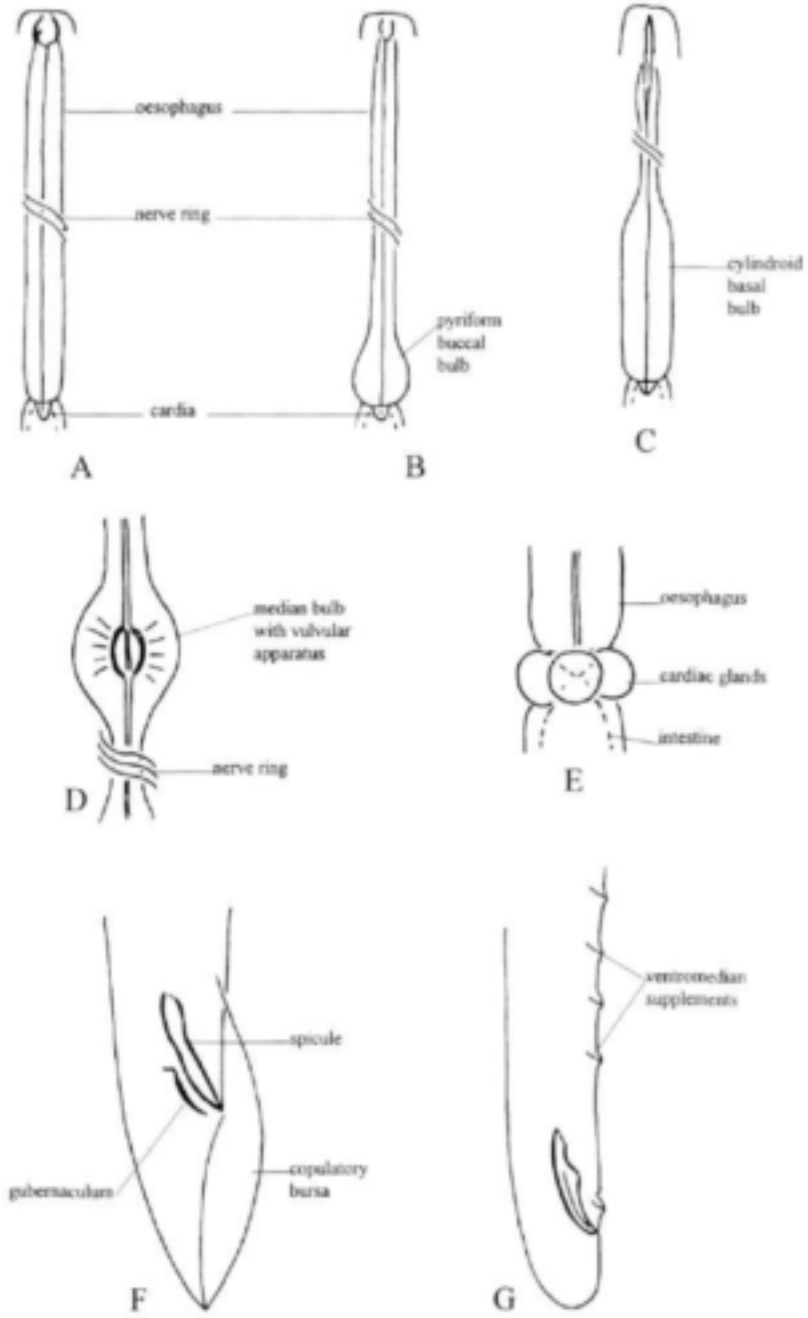


Fig. 7.2. Schematic figures illustrating morphological characters used in the keys:
A, cylindrical oesophagus; **B**, cylindrical oesophagus with basal swelling (basal bulb or terminal bulb); **C**, oesophagus with cylindroid basal bulb (dorylaimoid oesophagus); **D**, muscular median oesophageal bulb with valvular apparatus; **E**, junction between oesophagus and intestine showing three cardiac glands; **F**, male tail with copulatory bursa; **G**, male tail with genital papillae (supplementary organs).

the tissue paper, so that it is just above water level and in contact with the water in the funnel. After 24 to 48 hours nematodes will have moved into the water column and can be collected by means of drawing a few millilitres from the bottom of the rubber tubing. This solution can then be examined under a stereoscopic dissecting microscope and individual nematodes picked out with a fine needle. These are then placed in a drop of water on a specimen slide prior to more detailed examination. To relax the nematodes they may be heated over a small flame until all movement stops. To see most of the features described in the accompanying keys, the nematodes have to be covered with a thin coverslip and viewed under the highest powers of a compound microscope, preferably under oil immersion at x1 000 magnification. Note that in nearly all nematodes, the head, when relaxed by heat, curves towards the ventral side. This means that they lie on their sides when secured between a slide and a coverslip. Therefore, unless otherwise stated, all views of the head are understood to be lateral views. The term 'dorso-ventral' view is also used to indicate that the external appearance from the dorsal and ventral view is the same. Lack of space prevents the inclusion of more detailed information on methods of collecting, preparing and studying nematodes. For this the reader is referred to the comprehensive work edited by Southey (1970) on methods for work with plant and soil nematodes, or the more compact guide by Koen & Furstenberg (1970). The key by Ferris et al. (1973) also contains a useful section on techniques for collecting, isolating and preparing nematodes for identification.

KEY TO THE ORDERS OF NEMATODA THAT MAY OCCUR IN SOUTHERN AFRICAN FRESH WATERS

1. Cephalic or cephalic plus labial setae present (Fig. 7.1F); amphids spiral (Fig. 7.1E) or circular (Fig. 7.1C) (except transverse, slit-like apertures in all (Enoplida— see couplet 2 —and in of Chromadorida —see couplet 3) 2

– Without cephalic or labial setae (Fig. 7.1G); amphid apertures minute pores or transverse slits 5

2. Amphids with inconspicuous, slit-like apertures .... ENOPLIDA (p. 151)

– Amphids spiral or circular 3

3. Buccal cavity funnel-shaped, with denticles; cuticle punctate (Fig. 7.3U).......... .... CHROMADORIDA (p. 146)

– Buccal cavity usually small, unarmed, or narrowly tubular (rarely with denticles in Araeolaimida); cuticle annulated or smooth 4

4. Usually with two reflexed ovaries; cuticle annulated; buccal cavity tubular, rarely with denticles; oesophagus usually cylindrical with a basal swelling (Fig. 7.2B) .... ARAEOLAIMIDA (p. 143)

– Mostly with one outstretched ovary; cuticle smooth or annulated; buccal cavity inconspicuous, unarmed (Fig. 7.3A); oesophagus cylindrical (Fig. 7.2A) or cylindrical with a basal swelling (Fig. 7.2B) ........MONOHYSTERIDA (p. 143)

5. Oesophagus cylindrical; buccal cavity large, barrel-shaped, with sclerotized walls, with one to three teeth, or one dorsal tooth plus several small denticles (Figs 7.6A, C, E, F, G) .... MONONCHIDA (p. 154)

– Oesophagus with distinct basal or median bulb, or both, never cylindrical; buccal cavity narrow, with protrusible stylet, or variable, with or without one or more teeth and/or denticles 6

6. Amphids stirrup-shaped (Figs 7.1B & 7.3T), with slit-like apertures usually at base of lip region; oesophagus with cylindroid or rarely pyriform basal bulb (Figs 2B, C), without valvular apparatus; male usually without copulatory bursa, but with ventromedian supplements (Fig. 7.2G) .... DORYLAIMIDA (p. 156)

– Amphids minute, situated on lip region, and normally not visible under the light microscope; oesophagus usually with valvular apparatus in median (Fig. 7.2D) or basal bulb (Fig. 7.1A); male usually with a copulatory bursa (Fig. 7.2F) and without ventromedian supplements 7

7. Buccal cavity with protrusible stylet, usually with basal knobs (Fig. 7.1H) .... TYLENCHIDA (p. 150)

– Buccal cavity cylindroid or variable, its walls composed of various sclerotized rhabdions (Fig 7.1I), with or without tooth or teeth but never with a protrusible stylet .... RHABDITIDA (p. 146)

Order MONOHYSTERIDA (Figs 7.3A, B)

This order contains marine, brackish water, freshwater and soil forms. Only the genus *Monhystera sensu lato* is known from freshwater in southern Africa, where it is especially prevalent in polluted waters (Heyns, 1976). Five South African freshwater species of *Monhystera* (Figs 7.3A, B) have been described by Joubert & Heyns (1980). They are non-selective deposit or bacterial feeders.

Order ARAEOLAIMIDA (Figs 7.3C–T)

This order contains mostly marine and brackish water forms, with some freshwater and a few soil forms. Nothing is known about the feeding habits of many of the genera, while some are known or suspected to feed on micro-organisms. Of the seven genera included in the key, only *Chronogaster* has been studied taxonomically in South Africa (Heyns & Coomans, 1980). Three of the *Chronogaster* species known from South Africa occur only in aquatic habitats, while *C. africana* occurs in both fresh water and soil. *Chronogaster* is known to feed on diatoms. Of the other genera included in the key, *Cylindrolaimus* is suspected of being microbivorous. *Plectus* and *Anaplectus* probably feed on bacteria, while nothing definite is known about the feeding habits of *Aphanolaimus, Paraphanolaimus* or *Rhabdolaimus*.

KEY TO SOME COMMON GENERA OF ARAEOLAIMIDA

1. Spinneret absent or obscure ....*Chronogaster* (Figs 7.3C–G)
– Spinneret present (Figs 7.3J, M, S) 2

2. Oesophagus cylindrical without basal bulb 3
– Oesophagus with basal bulb 5

3. Stoma distinct, elongate and cylindrical; cuticle with weak annulations; ovary single ....*Cylindrolaimus* (Fig. 7.3K)
– Stoma a short broad cylinder or obscure; cuticle with fairly strong annulations; two ovaries 4

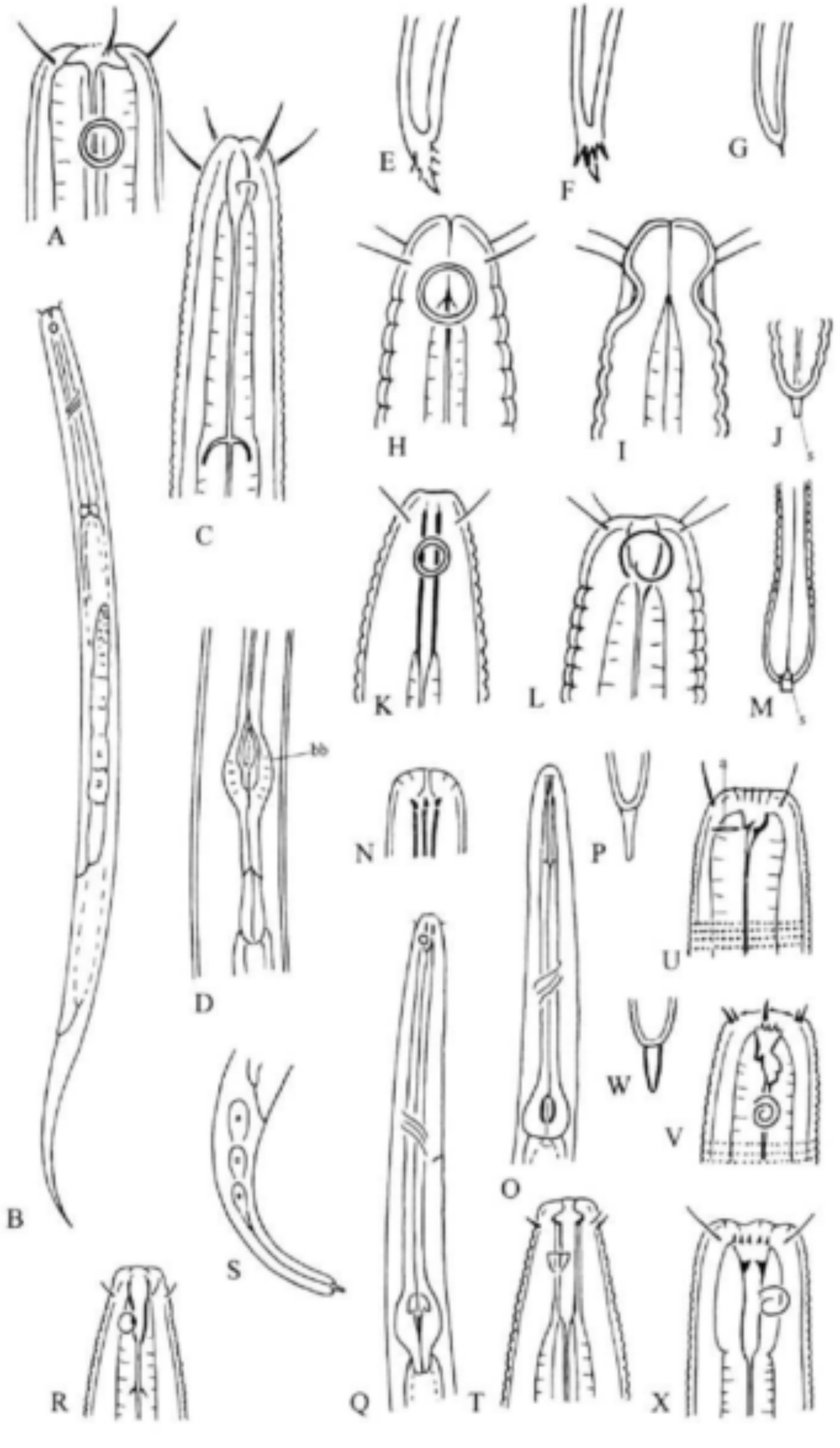
4. Stoma obscure; amphid circular (Fig. 7.1C) ....*Aphanolaimus* (Figs 7.3H–J)
– Stoma a short broad cylinder; amphid unispiral or an open circle (Fig. 7.1D) ....*Paraphanolaimus* (Figs 7.3L, M)

5. Amphid a closed circle .... *Plectus* (Figs 7.3Q–S)
– Amphid slit-like or obscure 6

6. Cephalic setae present; cuticle distinctly annulated ....*Anaplectus* (Fig. 7.3T)
– Cephalic setae absent; cuticle weakly annulated ....*Rhabdolaimus* (Figs 7.3N–P)

Fig 7.3. **A–B**, *Monhystera*: **A**, head; **B**, female, whole animal. **C–D**, *Chronogaster*: **C**, head; **D**, cardiac region. **E–G**, *Chronogaster*, tail terminus in various species. **H–I**, *Aphanolaimus*, head in lateral and dorsoventral view. **J**, *Aphanolaimus*, tail terminus with spinneret. **K**, *Cylindrolaimus* head, lateral view. **L–M**, *Paraphanolaimus*: **L**, head, lateral view; **M**, tail terminus; **N–P**, *Rhabdolaimus*: **N**, head; **O**, oesophageal region; **P**, tail terminus. **Q–S**, *Plectus*: **Q**, oesophageal region; **R**, head; **S**, tail. **T**, *Anaplectus*, head; **U**, *Chromadorita*, head; **V–W**, *Achromadora*: **V**, head; **W**, tail terminus. **X**, *Ethmolaimus*, head

KEY: am = amphid; bb = basal bulb of oesophagus; s = spinneret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Order CHROMADORIDA (Figs 7.3U–X)

This large order, with numerous families, contains primarily marine forms, with some representatives in fresh water and soil. Little is known about the feeding habits of these nematodes. Only three genera have been recorded from freshwater habitats in southern Africa. *Chromadorita*, which is mainly marine, also has some freshwater species which are known to feed on diatoms; *Ethmolaimus* occurs in freshwater bodies and their sandy shores as well as in moist soil (feeding habits unknown), and *Achromadora* occurs in fresh water and moist soil, and feeds on algae and diatoms.

KEY TO SOME GENERA OF CHROMADORIDA

1. Amphid aperture a transverse slit; depth of stoma much less than width of lip region .... *Chromadorita* (Fig. 7.3U)
– Amphid spiral (Fig. 7.1E); depth of stoma equal to or longer than width of lip region 2

2 Stoma roughly cycindrical, with three similar, anteriorly placed teeth .... *Ethmolaimus* (Fig. 7.3X)
– Stoma irregularly funnel-shaped, with a larger dorsal tooth and two smaller, more posterior, subventral teeth .... *Achromadora* (Figs 7.3V, W)

Order RHABDITIDA (Fig. 7.4)

This is one of the largest orders of almost exclusively terrestrial nematodes, with some rare freshwater forms. Many of the common soil forms, such as the Cephalobidae, however, are often found in aquatic habitats, and it is difficult to determine whether some species are truly aquatic, or have accidentally washed into streams where they then survive on the bottom for long periods. Most of the Rhabditida are probably microbivorous, and many probably feed on bacteria since they are commonly found in large numbers wherever decaying organic matter occurs. Some groups are predaceous, and others are parasites of vertebrates and invertebrates. Only four families, which include those genera most often encountered in freshwater habitats, are included in this key.

KEY TO SOME FAMILIES OF RHABDITIDA

1. **Walls of stoma with small rhabdions (Fig. 7.1I); stoma usually small and cylindrical; oesophagus without median bulb; females usually monodelphic; males without copulatory bursa (Fig. 7.2G)** 2
– Stoma long, tubular, or broad and with teeth or denticles; oesophagus often with median bulb; female mostly didelphic; male with copulatory bursa, which may be reduced (Fig. 7.2F) 3

2. Head with six incisures or six appendages (Figs 7.4A, B); amphids posterior to head .... **Teratocephalidae** (p. 147)
– Head smooth or with three appendages (probolae) (Figs 7.4M, X, Y); amphids at base of lips .... **Cephalobidae** (p. 150)

3. Oesophagus with a muscular valvated median bulb (Fig. 7.2D) and glandular basal bulb; stoma mostly with conspicuous teeth; bursa mostly reduced .... **Diplogasteridae** (p. 147)
– Oesophagus with a muscular valvated basal bulb; stoma tubular without prominent teeth; bursa mostly strongly developed .... **Rhabditidae** (p. 148)

Family **Teratocephalidae**

A small group of rare nematodes found in fresh water and wet soil; probably microbivorous. Heyns (1977) described two *Euteratocephalus* species from freshwater habitats in South Africa.

KEY TO THE COMMON GENERA OF TERATOCEPHALIDAE

1. Amphids small, pore-like; head without setae; monodelphic, prodelphic .... *Teratocephalus* (Fig. 7.4A)
– Amphids large, spiral; head with four slender setae (but only two visible in dorsal or ventral view); didelphic .... *Euteratocephalus* (Fig. 7.4B)

Family **Diplogasteridae**

A relatively large group of which the representatives are usually found wherever there is an accumulation of decaying organic matter, where they probably feed on bacteria, although some species with larger teeth in the stoma are undoubtedly predacious. Five genera have been found in freshwater habitats in South Africa, viz. *Metadiplogaster, Anchidiplogasteroides, Paroigolaimella, Acrostichus* and *Mononchoides.* Dassonville (1981) and Dassonville & Heyns (1984) reported on South African species belonging to these genera.

KEY TO SOME GENERA OF DIPLOGASTERIDAE

1. Monodelphic and prodelphic .... *Metadiplogaster* (Figs 7.4G–I)
– Didelphic and amphidelphic 2

2. Stoma about five times as long as broad ....
.... *Anchidiplogasteroides* (Figs 7.4C, D)
– Stoma about as long as broad, or slightly longer 3

3. Stoma shorter than broad; dorsal tooth opposed by two rasp-like areas ....
.... *Paroigolaimella* (Figs 7.4E, F)
– Stoma longer than broad; dorsal tooth not opposed by two rasp-like areas 4

4. Cheilostoma without conspicuous ribs; telostoma small, funnel-shaped ....
.... *Acrostichus* (Fig. 7.4J)
– Cheilostoma surrounded by twelve to eighteen longitudinal ribs; telostome long, cylindrical .... *Mononchoides* (Figs 7.4K, L)

NOTES ON SELECTED SPECIES OF DIPLOGASTERIDAE IN SOUTHERN AFRICA

Metadiplogaster: only *M. secundus* positively identified from South Africa.

Anchidiplogasteroides (Figs 7.4C, D): only *A. stigmatus* positively identified from South Africa.

Paroigolaimella (Figs 7.4E, F): only *P. bernensis* known from South Africa. In this species the vagina is flask-shaped and sclerotized, with a sac-like spermatheca attached to it anteriorly.

Acrostichus (Fig. 7.4J): only *A. nudicapitatus* positively identified from South Africa.

Mononchoides (Figs 7.4K, L): several species occur in South Africa, of which *M. aquaticus*, *M. changi* and *M. gracilis* have been positively identified.

Family **Rhabditidae**

This is another large group of predominantly terrestrial bacterial feeders found in all soils, and often in large concentrations, where decaying vegetable matter occurs. Fairly large numbers of individuals of some species are sometimes found in aquatic habitats, indicating that they may live as truly aquatic organisms. It is impracticable to include these in the key, but examples of three of the more common genera (*Rhabditis, Mesorhabditis* and *Diploscapter*) are illustrated in Figs 7.4O–S.

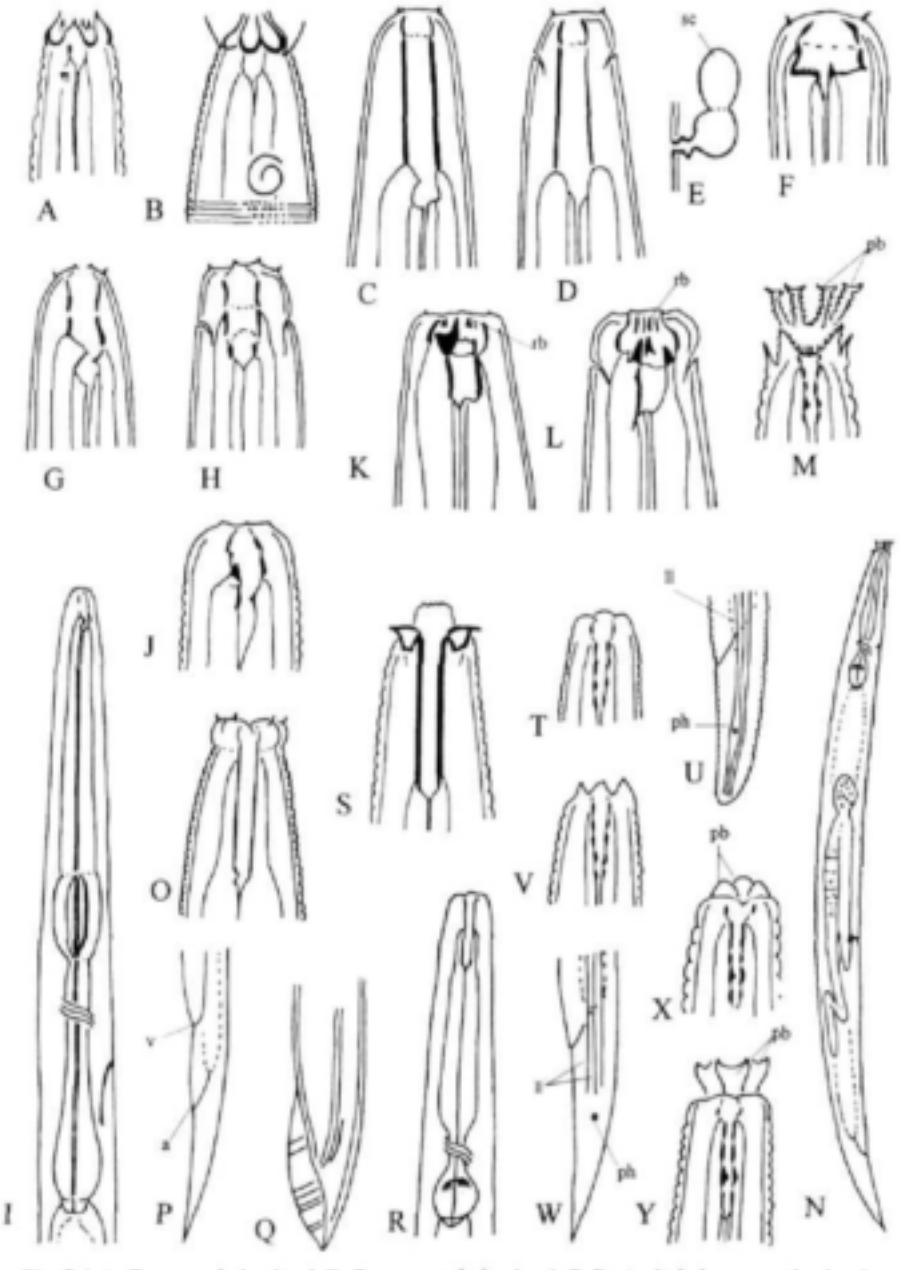

Fig. 7.4. **A**, *Teratocephalus*, head. **B**, *Euteratocephalus*, head. **C–D**, *Anchidiplogasteroides*, head: **C**, lateral view; **D**, dorsoventral view. **E–F**, *Paroigolaimella*: **E**, vagina with spermatheca; **F**, head; **G–I**, *Metadiplogaster*: **G**, head lateral view; **H**, head, dorsoventral view; **I**, oesophageal region. **J**, *Acrostichus*, head; **K–L**, *Mononchoides* head: **K**, lateral view; **L**, dorsoventral view. **M–N**, *Acrobeles*: **M**, head; **N**, entire female. **O–Q**, *Mesorhabditis*: **O**, head; **P**, female tail; **Q**, male tail. **R**, *Rhabditis*, oesophageal region. **S**, *Diploscapter*, head. **T–U**, *Cephalobus*: **T**, head; **U**, tail. **V–W**, *Eucephalobus*: **V**, head; **W**, tail. **X**, *Acrobeloides*, head. **Y**, *Chiloplacus*, head.

KEY: a = anus; ll = lateral lines; sc = spermatheca; pb = probolae; ph = phasmid; rb = ribs; v = vulva.

Family **Cephalobidae**

Nematodes of this family, and especially of the genera *Acrobeles* and *Eucephalobus*, are very common inhabitants of all soils, including cultivated soil, in southern Africa. They are suspected of being saprophagous or microbivorous. It is doubtful whether any of the species are truly aquatic, although there is no proof of this. Since they are so frequently found among the benthos, five of the more common and easily recognizable genera are included in the key. Terrestrial species of *Acrobeles* were studied by Heyns & Hogewind (1969) and Heyns (1969).

KEY TO THE MORE COMMON GENERA OF CEPHALOBIDAE IN SOUTHERN AFRICA

1. Head without probolae 2
– Head with three labial and six cephalic probolae (Figs 7.4M, X, Y) 3

2. Tail blunt and rounded, lateral lines extending to the tip of the tail .... *Cephalobus* (Figs 7.4T, U)
– Tail attenuated, usually pointed; lateral lines not extending beyond phasmid .... *Eucephalobus* (Figs 7.4V, W)

3. Labial probolae long and slender, furcate at tip, and elaborately fringed .... *Acrobeles* (Figs 7.4M, N)
– Labial probolae short, rounded or furcate plates 4

4. Labial probolae, or at least the dorsal one, furcate, the submedian ones usually asymmetrical .... *Chiloplacus* (Fig. 7.4Y)
– Labial probolae rounded, not furcate .... *Acrobeloides* (Fig. 7.4X)

Order TYLENCHIDA (Figs 7.5 A–L)

In a recent monograph of this huge order of almost exclusively terrestrial nematodes, Siddiqi (1986) recognized five suborders, numerous superfamilies, some 30 families and 216 genera, excluding the Aphelenchina, which are traditionally regarded as belonging to the Tylenchida. Most of these nematodes feed on the roots or aerial parts of higher plants or on fungi, while others are parasites on insects. As is the case with other terrestrial nematodes, many Tylenchida are frequently found among the benthos. Some of these may be true aquatic organisms, either feeding on fungi — e.g. *Aphelenchus* (Figs 7.5C–E) and *Aphelenchoides* (Figs 7.5F, G) of the suborder Aphelenchina, or on submerged roots of plants — e.g. *Hirschmaniella* (Figs 7.5A, B) of the suborder Tylenchina, and *Hemicycliophora* (Fig. 7.5I, J) of the suborder Criconematina. Other species of these same genera are found in wet or, more usually, in drier soil. These four genera are illustrated in Fig. 7.5, since they are frequently found in fairly large numbers in aquatic habitats in South Africa. Also shown in Fig. 7.5 is *Pratylenchus* (Fig. 7.5H), a well-known plant parasite, as well as *Scutellonema* (Figs 7.5K, L), a representative of a large group of plant parasites, the so-called spiral nematodes (Hoplolaimidae). All of these are commonly found on the bottoms of streams in South Africa. It is not practical or useful to supply a key to the genera in this order since many other terrestrial Tylenchida may also accidentally find their way into the benthos, making any key to this group of little value.

In most species of the superfamily Hemicycliphoroidea, the final larval cuticle is retained by the adult female after the last moult, as a protective body sheath (Fig. 7.5J).

Order ENOPLIDA (Figs 7.5 M–V)

This is a large order of primarily marine nematodes, with some representatives in fresh water and soil. Most species are probably predacious although some feed on diatoms, algae and/or organic detritus. Of the genera included in the key, *Ironus* is probably just as common in soils in South Africa as in freshwater. South African species of this genus were studied by Argo & Heyns (1972). *Oncholaimus* represents a large group of predacious, primarily marine nematodes, of which two freshwater species have been described from South Africa — *O. deconincki* by Heyns & Coomans (1977) and *O. jessicae* by Coomans & Heyns (1986)— while *Prismatolaimus*, *Tobrilus*, *Tripyla* and *Trischistoma* occur mainly in freshwater but also in soil. Several species of the genera *Tobrilus*, *Neotobrilus*, *Macrotobrilus*, *Brevitobrilus* and *Eutobrilus* have been reported from southern Africa (Joubert & Heyns, 1979). They are grouped together as *Tobrilus sensu lato* in the key.

KEY TO THE MORE COMMON GENERA OF ENOPLIDA IN SOUTHERN AFRICA

1. Stoma cylindrical, its length equal to several times the width of the lip region, and with three large claw-like teeth anteriorly .... *Ironus* (Figs 7.5M, N)
– Stoma at most slightly longer than the width of the lip region, with three large teeth, or with one or two small teeth in its base or in anterior part of oesophagus 2

2. Stoma strongly sclerotized and with three strong, anteriorly-directed teeth .... *Ocholaimus* (Figs 7.5O,P)
– Stoma less strongly sclerotized and with one or two small teeth in its base or in the anterior part of the oesophagus 3

3. Stoma a simple unsclerotized tube 4
– Stoma a large, sclerotized cavity 5

4. Cephalic setae shorter than half width of lip region (Fig. 7.5S), cuticle annulated; didelphic .... *Tripyla* (Fig. 7.5S)
– Cephalic setae longer than width of half lip region (Fig. 7.5T); cuticle smooth; monodelphic, prodelphic .... *Trischistoma* (Fig. 7.5T)

5. Stoma barrel-shaped, the walls distinctly sclerotized, often with small teeth in its base .... *Prismatolaimus* (Figs 7.5U, V)
– Stoma funnel-shaped, the walls weakly sclerotized, with small teeth in its base or in small 'pockets' in anterior part of oesophagus .... *Tobrilus sensu lato* (Fig. 7.5Q)

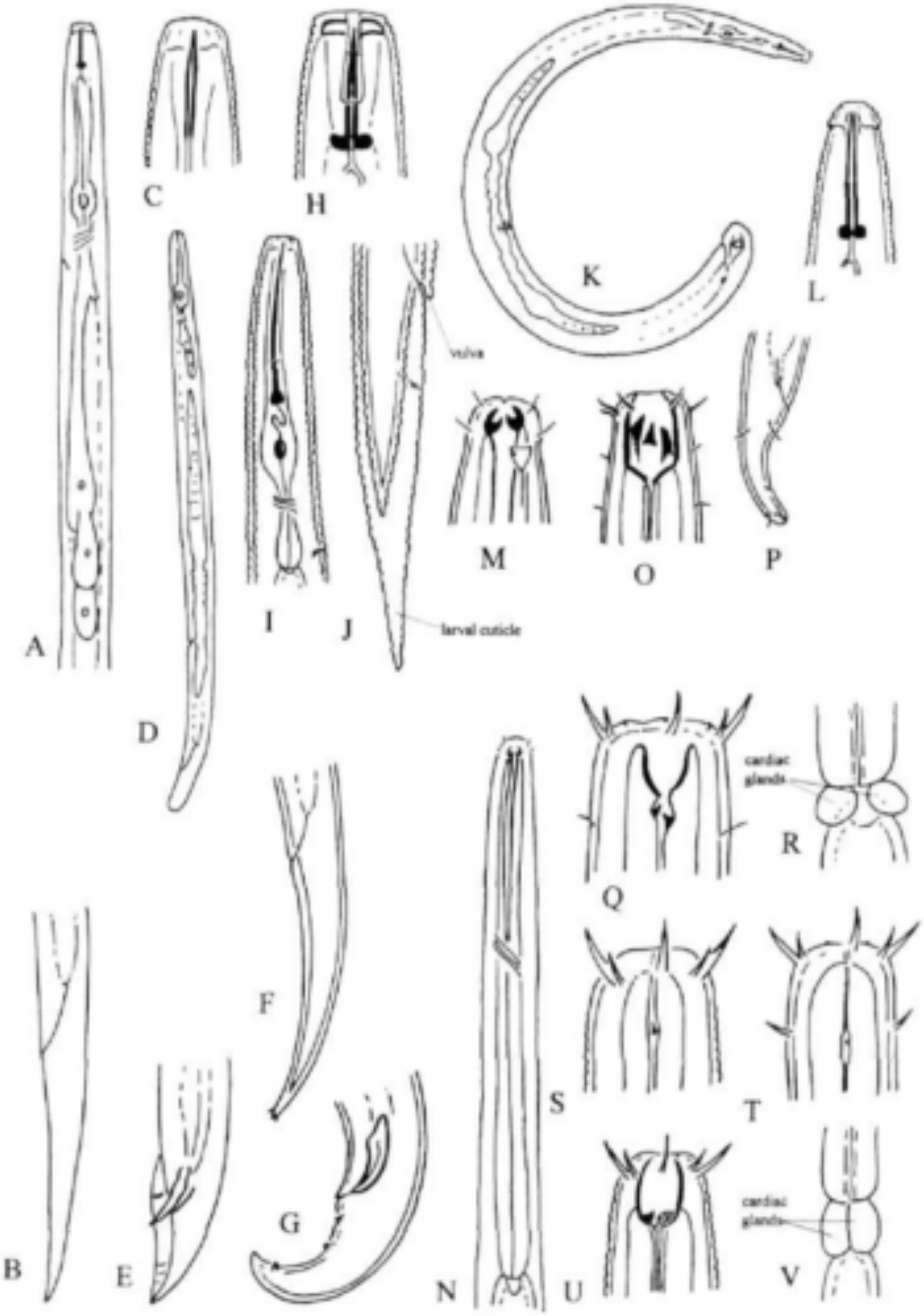

Fig. 7.5. **A–B**, *Hirschmaniella*: **A**, oesophageal region; **B**, tail; **C–E**, *Aphelenchus*: **C**, head; **D**, entire female; **E**, male tail; **F–G**, *Aphelenchoides*: **F**, female; **G**, male tail. **H**, *Pratylenchus*, head. **I–J**, *Hemicycliophora*: **I**, oesophageal region; **J**, tail. **K–L**, *Scutellonema*: **K**, entire female; **L**, head. **M–N**, *Ironus*: **M**, head; **N**, oesophageal region. **O–P**, *Oncholaimus*: **O**, head; **P**, tail. **Q**, *Tobrilus sensu lato*, head. **R**, cardiac region as it appears in *Tobrilus*, *Tripyla* and *Trischistoma*. **S**, *Tripyla*, head. **T**, *Trischistoma*, head. **U–V**, *Prismatolaimus*: **U**, head; **V**, cardiac region.

Order MONONCHIDA (Figs 7.6A–G)

The Mononchida are a large group of predacious nematodes feeding on protozoons, nematodes, rotifers, tardigrades and small oligochaetes. They are usually easily recognizable among other nematodes on account of the conspicuous, barrel-shaped and strongly sclerotized stoma, mostly with several large mural teeth. They occur in soil as well as in aquatic habitats. The group is well represented in South Africa and a series of papers (published between 1965 and 1968) by Coetzee and by Heyns & Lagerwey, give reports on local species. Since most of the species in this order are from terrestrial habitats, these papers have not been included in the list of references.

KEY TO THE MORE COMMON GENERA OF MONONCHIDA IN SOUTHERN AFRICA

1. Single large dorsal tooth in stoma not opposed by other teeth or denticles (Figs 7.6A, C) 2
– Single large dorsal tooth in stoma opposed by other teeth or denticles (Figs 7.6E, F, G) 3

2. Apex of dorsal tooth in anterior half of stoma; oesophago-intestinal junction non-tuberculate (Fig. 7.6B) .... *Mononchus* (Figs 7.6A, B)
– Apex of dorsal tooth usually in posterior half of stoma; oesophago-intestinal junction tuberculate (Fig. 7.6D) .... *Iotonchus* (Figs 7.6C, D)

3. Dorsal tooth opposed by two smaller subventral teeth .... *Cobbonchus* (Fig. 7.6E)
– Dorsal tooth opposed by numerous denticles 4

4. Denticles opposing dorsal tooth arranged in several transverse rows .... *Mylonchulus* (Fig. 7.6F)
– Denticles opposing dorsal tooth arranged in two longitudinal ventral rows (but note that, when examined in lateral view under high magnification, only one row of denticles can be seen at any level of focus) .... *Prionchulus* (Fig. 7.6G)

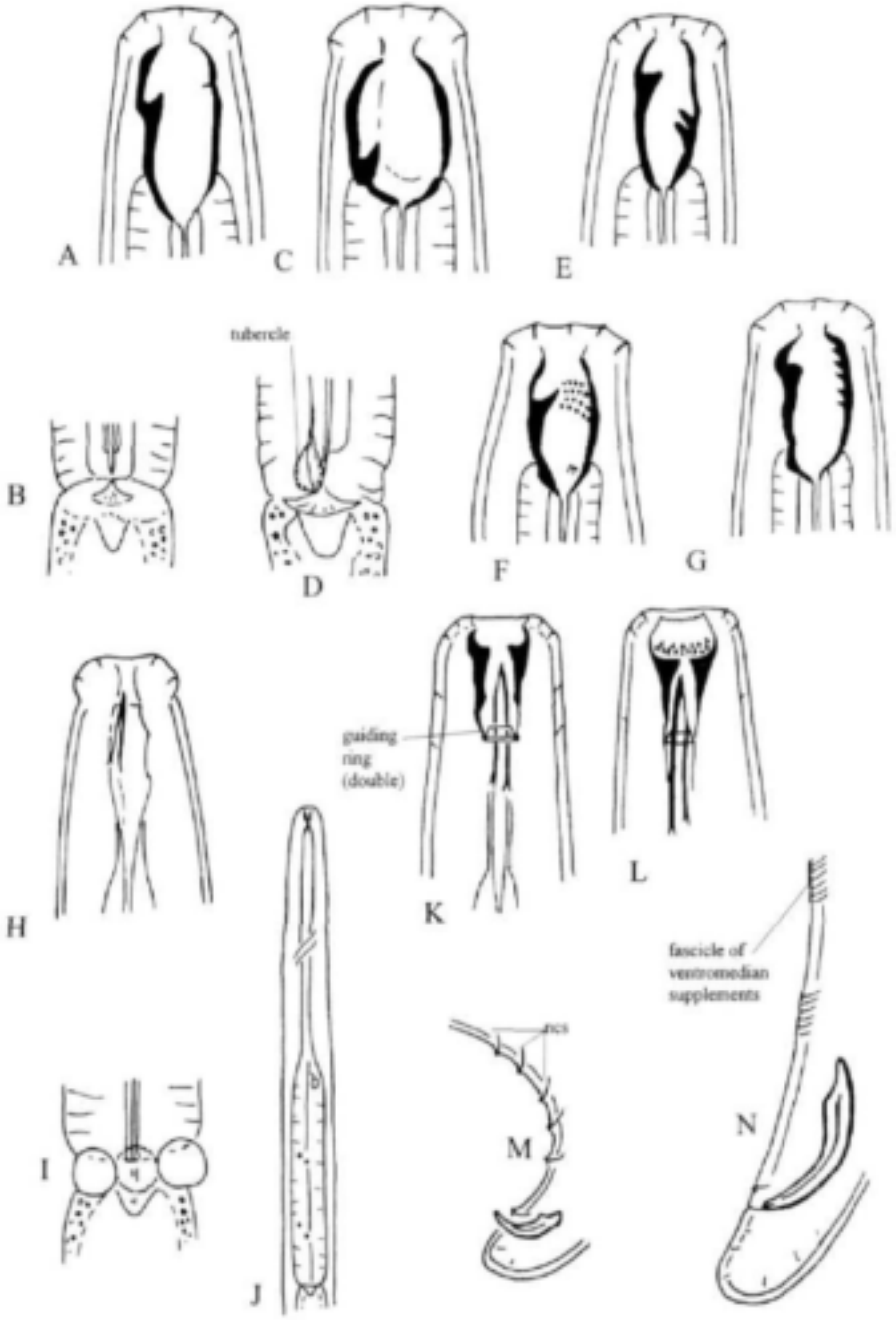

Fig. 7.6. **A–B**, *Mononchus*: **A**, head; **B**, non-tuberculate cardiac region. **C–D**, *Iotonchus*: **C**, head; **D**, tuberculate cardiac region. **E**, *Cobbonchus*, head. **F**, *Mylonchulus*, head. **G**, *Prionchulus*, head. **H–I**, *Nygolaimus sensu lato*: **H**, head; **I**, cardiac region. **J–K**, *Actinolaimus*: **J**, oesophageal region; **K**, head. **L–M**, *Paractinolaimus*: **L**, head; **M**, tail (male). **N**, *Afractinolaimus*, tail (male).

KEY: ncs = non-contiguous ventromedian supplements.

Order DORYLAIMIDA (Figs 7.6H–N & 7.7 A–M)

In terms of numbers of species and individuals, the Dorylaimida probably surpass all other nematode groups in the soil, and are rivalled only by the Tylenchida and Rhabditida. In contrast to these two groups, however, the Dorylaimida also contain a considerable number of aquatic species. Although some genera in the order (e.g. *Dorylaimus* and *Ischiodorylaimus*) and many genera of the superfamily Actinolaimoidea, appear to be almost exclusively aquatic, other aquatic species belong to genera which contain both aquatic and terrestrial species (e.g. *Mesodorylaimus*), or are predominantly terrestrial. The feeding habits of most dorylaims are still unknown and, although some are known to be plant parasites and others predators, the majority probably feed on algae and fungi. On the whole, dorylaims are relatively large compared with other free-living forms, with species of *Dorylaimus, Afractinolaimus* and many Longidoridae attaining lengths of up to, and in excess of, 8 mm. Where available, more information on feeding habits and ecology is given under superfamily and family headings.

A number of reports on South African freshwater dorylaimid species have been published: Heyns & Argo (1969) and Vinciguerra & Heyns (1984) on Actinolaimoidea; Basson & Heyns (1974) and Heyns & Kruger (1983) on Mesodorylaimus, and Kleynhans (1970) on Dorylaimus, Ischiodorylaimus and Prodorylaimus. A more comprehensive study by Andrássy (1970) dealt with freshwater species of the above-mentioned genera as well as with Laimydorus and Afractinolaimus.

KEY TO THE SUBORDERS OF THE DORYLAIMIDA

1. With mural tooth in left subventral wall of stoma (Fig. 7.6H); three conspicuous gland cells surrounding cardia (Fig. 7.6I) .... Suborder NYGOLAIMINA

– With protrusible axial stylet (Figs 7.1G; 7.6K, L; 7.7D, G, H, K, M); mostly without gland cells surrounding cardia ....Suborder DORYLAIMINA

Suborder NYGOLAIMINA (Figs 7.6H, I)

This suborder is composed of one superfamily with two families of mostly terrestrial nematodes. The family Nygolaimidae contains several genera, of which *Nygolaimus sensu lato* (Figs 7.6H, I) is sometimes found in fresh water. Nygolaimids are predators on small oligochaetes.

Suborder DORYLAIMINA (Figs 7.6J–N & 7.7A–M)

KEY TO SOME SUPERFAMILIES OF THE DORYLAIMINA

1. Stoma with distinctly sclerotized buccal cavity, usually with four large mural teeth (Figs 7.6K, L) .... **Actinolaimoidea**
– Stoma without sclerotized walls and without mural teeth 2

2. Basal bulb surrounded by conspicuous spiral muscle sheath (Fig. 7.7A) .... **Belondiroidea**
– Basal bulb without spiral muscle sheath (Fig. 7.6J) .... **Dorylaimoidea**

Superfamily **Actinolaimoidea** (Figs 7.6J–N)

Many Actinolaimoidea are aquatic and considered to be predators on other small organisms.

KEY TO SOME GENERA OF THE ACTINOLAIMOIDEA

1. Cuticle with several conspicuous longitudinal ridges .... *Actinolaimus*
– Cuticle without longitudinal ridges, but with minute transverse striae 2

2. Stoma without rasp-like denticles (Fig. 7.6K) .... *Neoactinolaimus*
– Stoma with several rasp-like denticles (Fig. 7.6L) 3

3. Medium-sized (up to 5 mm in length); female gonads with single flexure; male supplements evenly spaced (Fig. 7.6M) .... *Paractinolaimus*
– Very large, 5–7 mm in length; female gonads with multiple flexures; male supplements in two fascicles (Fig. 7.6N) .... *Afractinolaimus*

Superfamily **Belondiroidea** (Figs 7.7A–D)

This is a large superfamily of predominantly terrestrial nematodes, containing several families and numerous genera. Illustrated here are just two genera frequently encountered in fresh water in southern Africa: *Oxydirus* (Figs 7.7A–C) of the family Oxydiridae and *Dorylaimellus sensu lato* (Figs 7.7D) of the family Dorylaimellidae.

Superfamily **Dorylaimoidea** (Figs 7.7E–M)

This is one of the predominant groups of terrestrial nematodes, encompassing numerous families and genera. Species of some genera appear to be truly aquatic, while others favour wet soil and many others are probably encountered among the benthos after having been accidentally washed into streams from their terrestrial habitats. Only those most commonly found in freshwater habitats in southern Africa are included here.

KEY TO SOME FAMILIES OF THE DORYLAIMOIDEA

1\. Odontostyle long and slender, its length several times the width of the lip region (Fig. 7.7E) .... **Longidoridae**

– Odontostyle shorter, and mostly rather stout, its length at most twice the width of the lip region (Figs 7.7G, H, K, M) 2

2 Tails of both sexes similar 3

– Sexual dimorphism in tail: female tail long, attenuated (Fig. 7.7F), often filiform; male tail short, conoid to bluntly rounded (Figs 7.7J, L) .... **Dorylaimidae**

3\. Tails of both sexes long, filiform (as in Figs 7.7 B, C) .... **Prodorylaimidae**
(e.g. *Prodorylaimus* —often found in fresh waters)

– Tails of both sexes short, at most three times as long as body diameter at the level of the anus, conoid to bluntly rounded (Figs 7.7I, J) 4

4\. Stylet with large aperture, at least one half or more the odontostyle length; without a sclerotized guiding ring, the anterior edge of the guiding sheath an irregular fold (Figs 7.7H) .... **Aporcelaimidae**
(e.g. *Aporcelaimellus* — Figs 7.7H–J)

– Stylet with smaller aperture, less than half the odontostyle length; with a distinct, sclerotized guiding ring (Fig. 7.7K) .... **Qudsianematidae**
(e.g. *Eudorylaimus*, the most commonly-found genus of this family in South Africa —Fig. 7.7K)

Family: **Dorylaimidae** (Figs 7.7 F, G, L, M)

KEY TO SPECIES OF DORYLAIMIDAE

1\. Guiding ring usually appearing single (as in Fig. 7.7G); body length mostly less than 2 mm .... *Mesodorylaimus* (Figs 7.7F, G)

– Guiding ring usually appearing double (as in Figs 7.6K & 7.7M); body length mostly more than 2 mm 2

2\. Cuticle without longitudinal ridges .... *Laimydorus*

– Cuticle with longitudinal ridges 3

3\. Male ventromedian supplements in a single, contiguous series (as in Fig. 7.7L); medium to large, body length mostly more than 3 mm .... *Dorylaimus* (Figs 7.7L, M)

– Male ventromedian supplements in two fascicles (as in Fig. 7.6N); very large, body length up to 7 mm .... *Ischiodorylaimus*

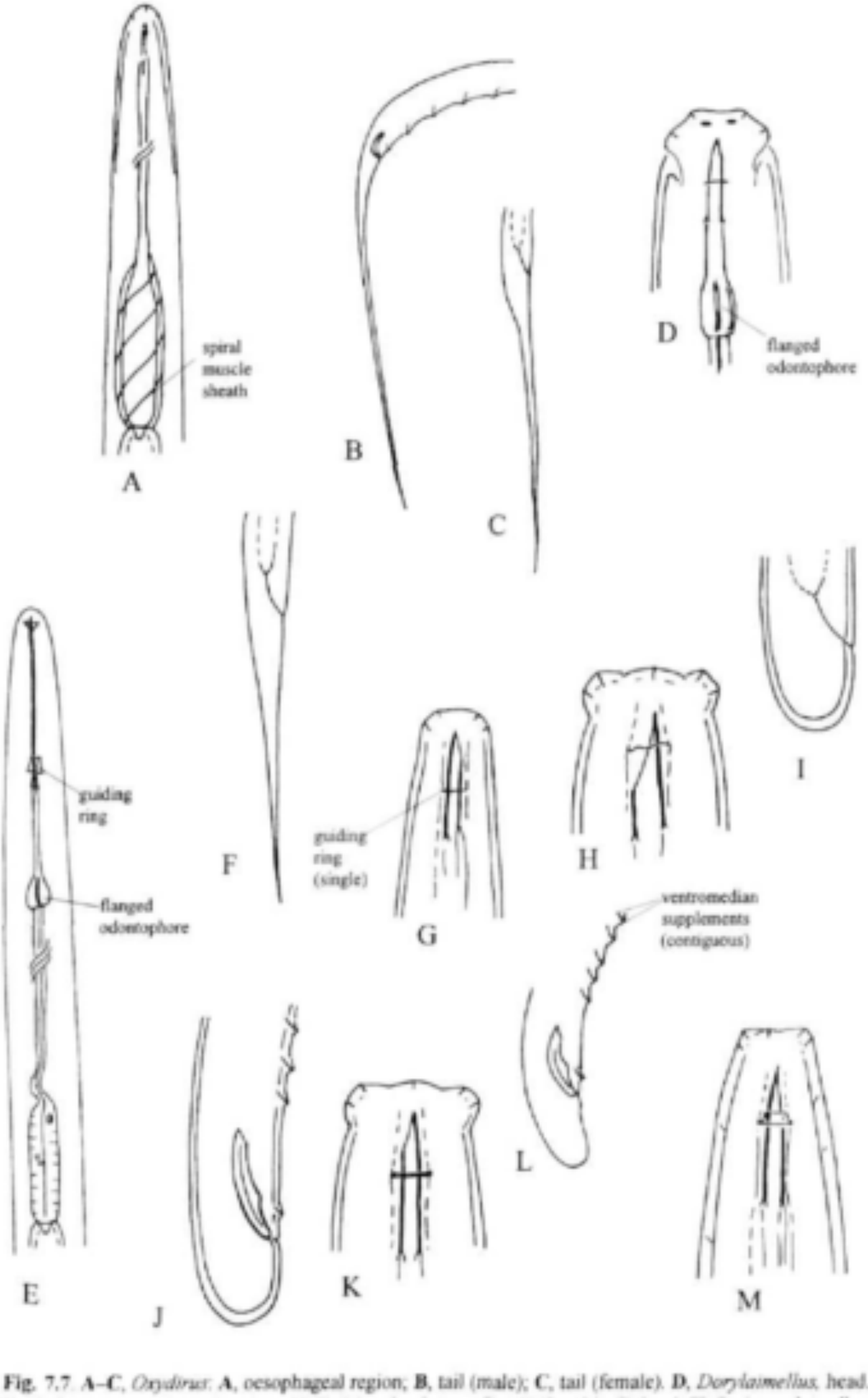

Fig. 7.7. **A–C**, *Oxydirus*: **A**, oesophageal region; **B**, tail (male); **C**, tail (female). **D**, *Dorylaimellus*, head. **E**, *Xiphinema*, oesophageal region. **F–G**, *Mesodorylaimus*: **F**, tail (female); **G**, head. **H–J**, *Aporcelaimellus*: **H**, head; **I**, tail (female); **J**, tail (male). **K**, *Eudorylaimus*, head. **L–M**, *Dorylaimus*: **L**, tail (male); **M**, head.

Family: **Longidoridae** (Fig. 7.7E)

Medium to large (up to 10 mm), relatively slender nematodes. They feed on plant roots, and often cause considerable damage to crops. Some species can also transmit plant viruses. Specimens of *Xiphinema* (Fig. 7.7E) and *Longidorus* are often found among the benthos, where they can apparently survive for long periods after being washed into streams. Some species of *Xiphinema* are frequently found in wet habitats along stream banks.

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CHAPTER 8

NEMATOMORPHA

by

N.A. Rayner & C.C. Appleton

The Nematomorpha (horse hair worms or hairworms) are a small pseudocoelomate phylum significantly resembling the Nematoda. Some authors consider them to be a class of the phylum Aschelminthes. They are often referred to as the Gordiacea as they can tie themselves into a knot of Gordian proportions. There are two orders, the Gordioidea and Nectonematoidea. The larvae of the Gordioidea are parasites of insects and emerge as adult worms in freshwater or on damp soil. About 320 species have been described globally. The Nectonematoidea are marine and there is only one genus, *Nectonema* which parasitizes crabs in the juvenile stages.

Morphology

Adult worms are long (5–100 cm), slender (1–3 mm) and unsegmented (Fig. 8.1A). They vary in colour from light to dark brown, and the mouth opening is located terminally or ventro-terminally at the simple anterior end but may be absent. The posterior end may be lobed or grooved (Fig. 8.1A) and the cloacal pore is located ventro-terminally or, like the mouth, it may be lacking. The body surface may be smooth or, more frequently, roughened and the worm may resemble a piece of fine wire or a tough root fibre. Nematomorphs are so opaque that little or no internal structure is visible. The epidermis is syncytial and is covered by an elastic cuticle which is moulted during growth. This cuticle may be decorated with papillae (warts) and areolae (areas of thickening) of various shapes, sometimes with setae, bristles or pores. These are useful diagnostic features. Movement is muscular and the muscle cells are large with contractile processes below the epidermis. There are no cilia. There is a through gut but it tends to be become degenerate. The nervous system comprises a thick circum-oesophageal ring and a single ventral nerve cord. The sexes are separate but males are usually shorter than females. Nematomorphs differ from the nematodes in having no excretory system. The adults do not feed, are inactive, and females devote most of their energy to egg production.

Habitat preferences

Nematomorphs are often found in drinking troughs, ponds or any body of freshwater. The second author records the following: "While working in the Bilharzia laboratory in Nelspruit (Mpumalanga) in the 1980s, members of the public brought in several live adult nematomorphs which had *come through taps in houses and offices from the municipal water supply*. The specimens were uniform dark brown in colour, about 200–250 x 1–1.5 mm in size. Subsequently in 1998, second year zoology students from the University of Natal (Durban) found three nematomorph worms, measuring 140–201 x 0.25–0.4 mm inside two adults of the elegant grasshopper, *Zonocerus elegans* (Pyrgomorphidae). These grasshoppers which are very common, were collected in the grounds of the University of Natal in Durban in early spring. As there was no evidence of lobes at the posterior end, the worms were presumably all juveniles. The label in the bottle stated 'in gut' but it is more likely that juvenile worms of this size would have left the gut and were probably in the body cavity or haemocoel."

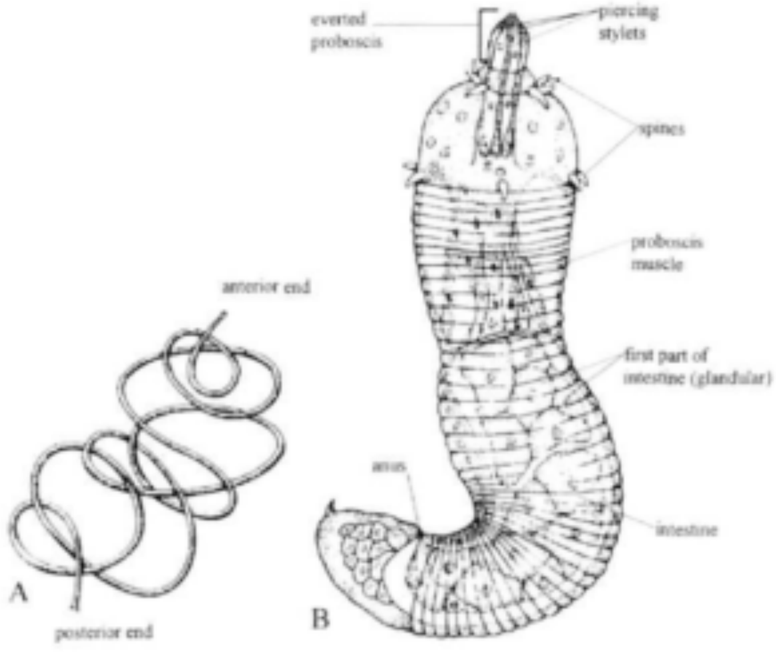

Fig. 8.1: **A**, male horsehair worm (length up to 100 cm; width 1–3 mm). **B**, *Gordius aquaticus*, infective gordioid larva. A after Noble & Noble (1982); B adapted from Pechenik (1991).

Feeding

The mouth of the adult worm, if present, is small and functionless for they do not feed, metabolising nutrients acquired as juveniles. The larvae lack a functional digestive system and as internal parasites absorb nutrients from the host's tissues and fluids.

Reproduction

Males have a pair of long tubular testes that open independently into the cloaca through short sperm ducts. A seminal vesicle sometimes lies at the end of the testis. The cloacal wall of some species is armed with bristles and may serve as a cirrus. Young ovaries resemble the testes, but as they mature, form lateral diverticula in which the ova ripen. As many as 4 000 diverticula may occur. The ovary is empty and serves as a uterus, storing ripened ova. The two oviducts combine to form a common atrium from which a seminal receptacle arises. The atrium opens into the cloaca. The male wraps his body around the female and deposits sperm near the female cloacal opening. Sperm migrate into the seminal receptacle. When the ova are mature they emerge in long strings which may contain several million eggs. Cloacal secretions provide the binding material for the strings. The gordioid larva (Fig. 8.1B) which develops is sometimes referred to as an echinoderid larva (Meglitsch, 1972). This larva, which measures 0.05 –0.15 mm, is equipped with a proboscis and hooks at the anterior end. Within 24 hours after hatching, it either encysts on vegetation and waits to be eaten by an insect host such as a beetle, cricket or grasshopper, or it may use its armed proboscis to bore into the insect. How it locates this host is not clear, but once inside the body cavity, the larva develops into a juvenile worm. After about four months, the nearly-mature juvenile worm moults to lose the last traces of its larval structure, and breaks through the host's body wall, killing it in the process. This emergence occurs in spring or early summer and, unless the host is close to water at the time, the larva will die. It has been suggested that larval nematomorphs may somehow manipulate their host's behaviour so that they actively search for water when the parasite is ready to emerge.

Identification and distribution

Three well-known genera have been recorded from North America: *Chordodes* (two species), *Paragordius* (one species) and *Gordius* (seven species). Males and females require separate keys. There is no information regarding the genera or species in southern Africa, but the few records that are available suggest a wide distribution. Nematomorphs are seldom seen and are probably more common than generally realized. The presence of a dark band just behind the head, coupled with a pattern of areolae resembling a honeycomb in the cuticle, and the absence of any evidence of lobes at the posterior end, suggest that the juvenile worms recovered from the grasshopper *Z. elegans* belong to the genus *Gordius* (van Heerden, 2001; von Fintel, 2001).

Human infection

Textbooks (e.g. Faust et al., 1975) note that there are many records of nematomorphs 'parasitizing' people on several continents. These include worms being passed in faeces and vomitus and emerging from the urethra. Generally, these infections (e.g. Pippet & Fernando, 1961) are considered to be the result of worms being accidentally swallowed together with drinking water. Another source of infection may be the consumption of aquatic insects. It should be emphasized that hairworms are not true parasites of humans, but may be ingested accidentally and only seen when eventually voided. There are no records of hairworms being recorded from man in South Africa though their presence may have been overlooked or confused with other species of worms which are common parasites of children.

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CHAPTER 9

GASTROTRICHA

by

J. Heeg

Gastrotrichs are microscopic (50–1 000 µm) vermiform or fusiform psuedocoelomate metazoans found among filamentous algae, mosses, the periphyton on macrophytes, the organic debris on the substratum and as shallow infauna in most aquatic habitats. Because of their small size and the fact that they are often collected in protozoan samples, they were originally thought to be ciliates ('infusoria'), until Ehrenberg recognized their metazoan nature in 1838, considering them to be rotifers. Metschnikoff, while recognising their similarity to the Rotifera in many features, proposed the name Gastrotricha in 1864, in reference to their ventral ciliation, a character not shared by rotifers. The first detailed study of their anatomy was undertaken by Zelinka (1889), whose illustration of *Chaetonotus* is still to be found in almost every general zoology textbook today. Gastrotrichs share a number of features with both the Rotifera and the Nematoda; consequently, several authors (notably Hyman, 1951) have grouped them with these and other pseudocoelomates (Nematomorpha, Echinodera and Priapulida) as classes of a single phylum, the Aschelminthes. The more conservative view, which regards each of these taxa as a separate phylum, is still held by some.

Two orders are recognized. The vermiform, flatworm-like Macrodasyoidea are, with the exception of the Brazilian genus *Redudasys* (Kisielewski, 1987), exclusively marine. All freshwater species, together with some marine and brackish water forms, are included in four families in the order Chaetonotoidea. They are generally fusiform, some superficially resembling rotifers, from which they are readily distinguishable by the lack of a mastax and corona (see chapter 6). About 250 freshwater species, included in 14 genera, have been described world wide (Pennak, 1989), but none from southern Africa to date. They are nevertheless known to occur in several localities in South Africa and Namibia (personal

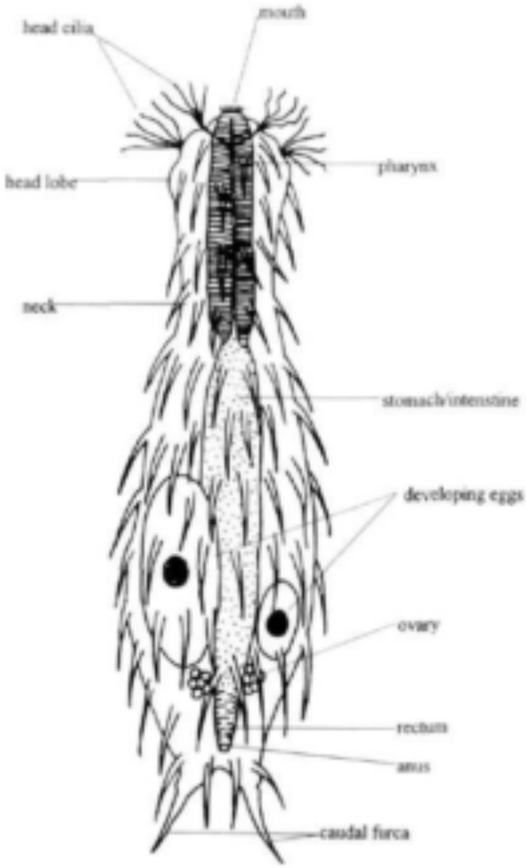

Fig. 9.1. A generalized chaetonotoid gastrotrich, based largely on the commonly-occurring genus, *Chaetonotus* (Chaetonotidae).

communications and observations) suggesting that they are widespread throughout the sub-continent.

Morphology

Most chaetonotoid gastrotrichs are readily recognised by their body shape and movement. An anterior head lobe, separated from the rest of the body by a neck-like constriction, is characteristic, while all except the few genera in the families Neogosseidae and Dasydytidae have a distinct caudal furca. The ventral surface bears tracts of locomotory cilia which impart a gliding movement, reminiscent of that of a flatworm. Elongate cilia, occurring either singly or in tufts, are located on the head lobe. The body surface is covered in a cuticle that is almost invariably elaborated into spines, plates or scales.

The internal anatomy is simple. The alimentary canal comprises a terminal or sub-terminal mouth, a well-developed tri-radiate pharynx, very similar to that of nematodes (see Chapter 7), a tubular stomach/intestine and a short rectum leading to a postero-dorsal anus. In freshwater species a single pair of protonephridia possibly serves an osmoregulatory function. The saddle-shaped brain is large, almost filling the head lobe, and two lateral nerve trunks extend almost the whole length of the body. All freshwater Chaetonotoidea are thought to be parthenogenetic, a single pair of ovaries being located posteriorly, lateral to the gut. Eggs are extruded through a ventral gonopore, which also leads to a sac-like structure, the X– organ, of unknown function.

Biology

Despite their common and widespread occurrence, freshwater gastrotrichs have hardly been studied beyond their basic taxonomy. Very little is known of their biology, and even much of this requires confirmation through further investigation, it being largely superficial, anecdotal or simply inferred from morphology.

Members of the family Chaetonotidae, which includes some 90% of all known freshwater species, are essentially benthic or epiphytic. Feeding seems to be on small organic particles (detritus, small protozoans, bacteria), the animals apparently browsing unselectively as they move over the substratum. The head cilia aid in the concentration of food particles in the region of the mouth (Pennak, 1989). There is no buccal cavity, the mouth leading directly into the muscular pharynx which provides the force necessary for the passage of food through the alimentary canal, there being no other gut musculature in pseudocoelomates. The families Neogosseidae and Dasydytidae are considered by Hyman (1951) to be pelagic. If confirmed, this would imply different food sources and food-gathering mechanisms from those of the Chaetonotoidae. Pennak (1989) doubts the planktonic nature of these two families, but the extraordinarily long spines in several species lend support to Hyman's suggestion that at least some species are planktonic.

The reproductive biology of freshwater gastrotrichs, where studied, is reminiscent of that of the Rotifera. Although the Macrodasyoidea and some marine and brackish water Chaetonotoidea are known to be hermaphrodites, all freshwater chaetonotoids are considered to be parthenogenetic females. Each ovary consists of a few oocytes, an individual producing only a limited number of eggs (<5) during its lifetime. The eggs mature in the pseudocoel; they are oval in shape and very large, reaching a length exceeding one third of the total body length of the parent in most species. Each egg is extruded through the ventral genital pore and a cuticle covering its outer surface quickly hardens on contact with the surrounding water. In most species, the surface of the egg bears some cuticular elaboration in the form of bristles or blunt spines. The eggs are laid singly in selected protected locations such as the axils of macrophytes or the shed exoskeletons of small crustaceans, and are attached to some solid object or to the substratum.

Two types of egg are known to be produced by at least some chaetonotoid species (Hyman, 1951; Pennak, 1989). Tachyblastic or subitaneous eggs commence cleavage as soon as they are laid, and hatch within 12 to 70 hours. Opsiblastic or dormant eggs are slightly larger than tachyblastic eggs and have thicker shells. They are produced in response to deteriorating environmental conditions and can survive freezing and desiccation in a state of dormancy that can last for at least two years (Pennak, 1989). Weiss and Levy (1979) reported the presence of 'packets' of sperm in the common freshwater *Lepidodermella squamata*. These were located in a position where testes would be expected and occurred in only a small proportion of a very large, randomly collected sample from a number of cultures. If the occasional presence of hermaphrodites is found in other species, it would suggest a heterogonous sequence of generations in which opsiblastic eggs result from fertilized ova. Should further, particularly cytogenetic, studies confirm this, the reproductive biology of freshwater gastrotrichs would parallel that of the ploimate rotifers (see Chapter 6).

Distribution

Studies on freshwater gastrotrichs have been almost entirely confined to Europe and, to a lesser extent, to North America. The only genera recorded from the southern hemisphere are *Redudasys* (Macrodasyoidea) and the chaetonotoids—*Arenotus* from Brazil, *Proichthyidium* from Argentina, and the aberrant *Kijanebalola* from East Africa. The indications are that a number of the common genera are cosmopolitan in their distribution, but our present limited knowledge precludes any generalization.

EXAMINATION AND IDENTIFICATION

Although common, the Gastrotricha, particularly the freshwater Chaetonotoidea, are poorly known. The most recent taxonomic syntheses are those of Remane (1927, 1935-36). Pennak (1989) gives a key to recorded North American genera, all of which occur in Europe. *Kijanebalola* is the only genus recorded from Africa (de Beauchamp, 1965). I have frequently collected gastrotrichs in freshwater samples and have, on the basis of superficial examination, tentatively identified some of them as species of *Chaetonotus* and *Lepidodermella*, two genera which are common in the northern hemisphere.

The following key to, and notes on, the four families of freshwater chaetonotoids recognized by Pennak is largely based on information in Hyman (1951) and Pennak (1989) and relies on external characters readily observable in the living animal through a light microscope. For identification beyond this level it will be necessary to refer to Remane's monographs, although Pennak (1989) should prove a useful intermediate step.

KEY TO THE FRESHWATER FAMILIES OF CHAETONOTOIDEA

1. Paired post-anal processes form a caudal furca 2
– Caudal furca absent but paired small rounded lobes, tufts of elongated spines or peg-like styloid processes may be present post-anally; commonly with very long spines on the body 3

2. Caudal furca simple (Fig. 9.1) ....**Chaetonotidae**
– Processes forming the caudal furca bifurcate ....**Dichaeturidae**

3. Head with a pair of club-shaped tentacles (Fig. 9.2) ....**Neogosseidae**
– Head without tentacles (Fig. 9.3) ....**Dasydytidae**

ADDITIONAL NOTES ON FAMILIES

Chaetonotidae (Fig. 9.1)

By far the largest family, including seven genera with some 90% of all recorded freshwater species, many of which are distributed throughout the northern hemisphere and may well prove to be cosmopolitan. The commonly-occurring genera, *Chaetonotus* and *Lepidodermella,* together make up about half the known freshwater gastrotrich fauna. In *Chaetonotus* (comprising about 110 described species) the body is covered in short cuticular spines or spine-bearing scales, while *Lepidodermella* (comprising 15 species) is clothed in cuticular plates or scales. Other genera in this family are *Arenotus* from Brazil, *Aspidiophorus* known only from Europe, and *Polymerus*, *Ichthyidium*, and *Heterolepiderma* from Europe and North America.

Dichaeturidae

According to Pennak (1989), this family comprises a single genus, *Dichaetura,* to date only known from Europe. De Beauchamp (1965), however, includes *Dichaetura* and the Argentinian genus *Proichthyidium* (in which the furcal process is not forked) in the family Proichthyididae, a family not mentioned by other authors consulted and for which no clear key characters are given. Both genera are rare, and are mentioned here because of their possible Southern Hemisphere/ Gondwanaland connection.

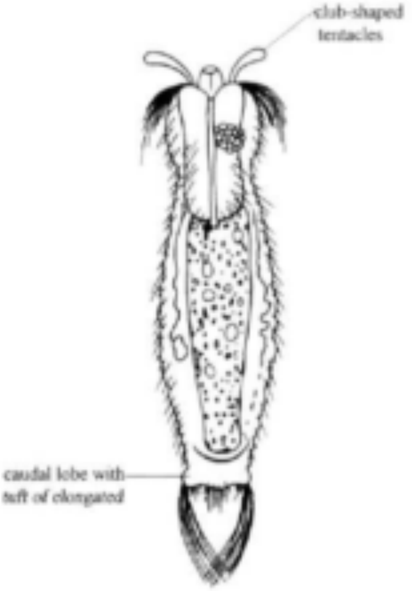

Fig. 9.2. *Neogossea* (generalized) showing the club-shaped tentacles characteristic of the family Neogosseidae (redrawn from Hartog, 1896).

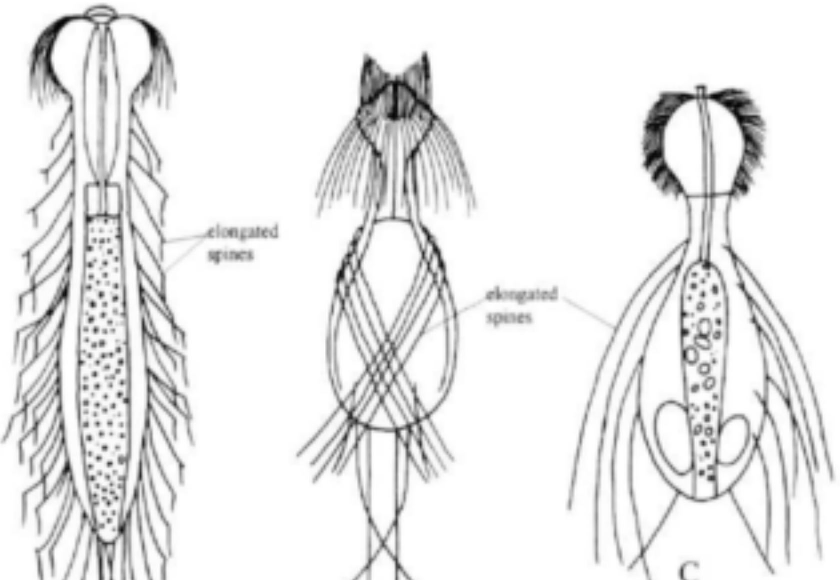

Fig. 9.3. Different forms in the genus *Dasydytes* (Dasydytidae): **A**, *D. goniathrix*; **B**, *D. saltitans*; **C**, *D. longisetosum* (redrawn from Hartog, 1896)

Neogosseidae (Fig. 9.2)

The family Neogosseidae comprises only the northern hemisphere genus *Neogossea*. De Beauchamp (1965) includes *Dasydytes* as well as *Kijanebalola*, the only genus recorded from Africa, in this family. The need for revision of the former (see below) and the seemingly aberrant form of the latter, as illustrated in de Beauchamp (1965), suggest that their inclusion here may be premature, but worth mentioning in case the latter genus occurs further south.

Dasydytidae (Fig. 9.3)

The genus *Dasydytes*, with several sub-genera and 25 species, seems from illustrations to be extremely variable; Pennak (1989) considers it to be in urgent need of revision. Judging from their body form and extremely long setae, some of the included species, such as *D. saltitans* (Fig. 9.3B) and *D. longisetosum* (Fig. 9.3C), are likely to prove to be pelagic, whereas others resemble typical benthic chaetonotoids.

ACKNOWLEDGEMENTS

Thanks are due to Nancy Bonsor for the final preparation of the illustrations.

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CHAPTER 10

BRYOZOA

By

J. Heeg

The phylum Bryozoa, also commonly referred to as Polyzoa, previously included two classes of colonial polyp-like animals, the Entoprocta and Ectoprocta, superficially similar in that both possess a conspicuous crown of ciliated tentacles known as a lophophore. The main criterion for separation of the classes was the position of the anus: in the Entoprocta both mouth and anus open on the lophophore, whereas in the Ectoprocta the anus opens dorsally outside the ring of tentacles. Subsequent, more detailed studies, encompassing the morphology and embryology of both classes, provided good grounds for elevating the Entoprocta to the status of a separate phylum, which is now generally accepted. The phylum Entoprocta has few freshwater species, none recorded from southern Africa. Hyman (1959) proposed that the older names—Bryozoa and Polyzoa — be abandoned in favour of the name Ectoprocta which would clearly distinguish the ectoprocts as constituting a newly-defined phylum, distinct from the Entoprocta. This proposal has not met with general acceptance, while the name 'Bryozoa' is still a widely accepted alternative to Ectoprocta,

Most Bryozoa are marine. The phylum is divided into three classes and includes approximately 4 000 species. The few species of the predominantly marine class Gymnolaemata that are known to inhabit freshwater have not been recorded from Africa, and the class Stenolaemata is exclusively marine. About 50 species which are exclusively freshwater, make up the class Phylactolaemata, the focus of this chapter. Depending on the authority, 10–12 genera and four or five families are recognized, while the morphological and biological similarities between phylactolaemate species do not justify systematic categories higher than family (Hyman, 1959).

MORPHOLOGY

Bryozoans are clonal colonies of interconnected, coelomate, polyp-like zooids. Each zooid has arisen from a bud on another individual, thus all the zooids in a colony are intimately connected to one another, both internally through a common coelom, and externally by a continuous body wall.

The zooid

Observed through a stereo microscope, a living, undisturbed phylactolaemate zooid (Fig. 10.1) will be seen to have a horse-shoe shaped (or in one genus oval/circular) organ fringed with ciliated tentacles, the lophophore, carried on a short, flexible neck, called the tentacle sheath. Any disturbance will cause retraction of the lophophore and tentacle sheath into the protection of the more-or-less rigid, cylindrical, proximal part of the zooid. The internal anatomy of a zooid is simple, comprising a U-shaped alimentary canal suspended in the coelom, an ovary located on the ventral body wall, and a simple nervous system with a dorsal cerebral ganglion. Extending from the base of the U-shaped gut is a string of mesodermal tissue, the funiculus, on which the testis is located and the statoblasts develop; the funiculus connects with a mesodermal strand joining it to those of surrounding zooids. The musculature comprises circular and longitudinal smooth muscles in the body wall and a pair of striated retractor muscles in the coelom, which arise proximally from a common base. There are no respiratory, circulatory or excretory organs, nor coelomducts of any description, including gonoducts. The lophophore and tentacle sheath of the zooid, together with the associated musculature, alimentary canal and cerebral ganglion, are collectively referred to as a polypide, while the basal portion, which includes the reproductive organs and body wall musculature, is known as a cystid. Figure 10.1 shows the essential morphology of a generalized phylactolaemate zooid. A more detailed account of bryozoan morphology is given in Hyman (1959).

Retraction of the polypide is effected by the pair of retractor muscles which have their origin in the body wall of the proximal region of the cystid and their insertion in the base of the lophophore. Their contraction pulls the lophophore downward and results in introversion of the neck region to now form a sheath around the lophophore. The lophophore and tentacle sheath are pulled into the cystid and occlusion of the retracted polypide is completed by contraction of the atrial sphincter muscle. Eversion of the polypide involves dilation of the atrium, relaxation of the retractor muscles, and contraction of the muscles in the body wall. Protection of the delicate, retracted polypide is enhanced by an external cuticula

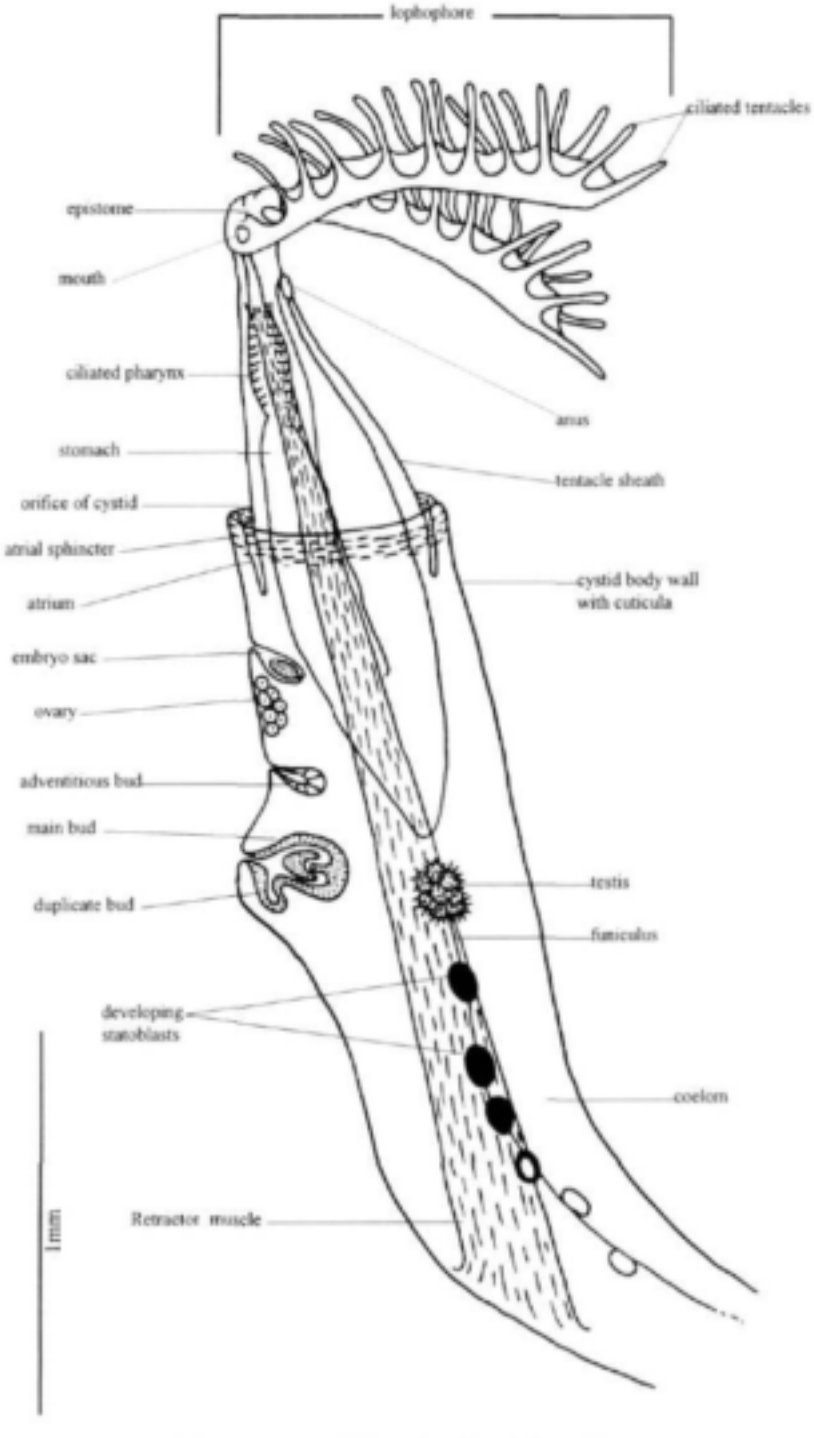

Fig. 10.1. Generalized phylactolaemate zooid, based largely on *Plumatella repens.*

or zooecium, secreted by the epidermal cells of the cystid body wall. The nature of the zooecium varies from species to species, ranging from thin and transparent, through opaque to thick and gelatinous. Although some authorities such as Ryland (1970) have reservations about the use of the term 'zooecium', it is a convenient name for the non-living, secreted part of the zooid which functions as an exoskeleton, and which is the sense in which it is used in such texts as Hyman (1959) and Pennak (1989).

Colony formation and growth

Colony formation is by budding from a region of blastogenic tissue on the ventral body wall of the cystid where, in the newly mature zooid, sequentially developing bud rudiments are located (see Fig. 10.1). In the families Fredericellidae and Plumatellidae, development of the main bud gives rise to a daughter zooid in which the duplicate bud, which will become its main bud, already begins development. The adventitious bud now becomes the new maternal main bud, and a new adventitious bud forms between it and the orifice. Further growth of the daughter zooid by elongation of its basal region now forms a stolon-like connection between the coeloms of maternal and daughter zooids. This succession may be repeated for a limited number of generations before the maternal polypide degenerates, leaving only its cystid and zooecium. The colony therefore consists of both degenerated and functional zooids: the latter, with their actively feeding polypides, being concentrated in the regions of growth. Since the bud rudiments are located mid-ventrally with the adventitious bud lying between the main bud and the orifice, and there is a dichotomy at every zooid with every successive cycle, the resulting colony is a complex system of uniserial branches that either ramify over the substratum or, by growing at right angles to the substratum, form bushy growths. Such colonies are referred to as being of the *plumatellid type* (Fig. 10.2A). In the family Lophopodidae, the bud rudiments are located bilaterally on either side of the median sagittal plane, the main bud to the left and the adventitious bud to the right. This results in a fan-shaped growth pattern. Such *lophopodid type* colonies (Fig. 10.2B) have a thick gelatinous zooecium that is continuous between adjacent cystids, and polypides that are confined to the region near the edge of the colony.

The potential for rapid colony growth under favourable conditions is enormous. Bushnell (1966) has studied the population dynamics of *Plumatella repens* in two North American lakes. Colonies were found to show a geometric rate of increase in zooid numbers, generally doubling every 3.4 to 5.4 days, but slowing down to a doubling rate of 7.4 days during lower spring temperatures. The mean longevity of a polypide was

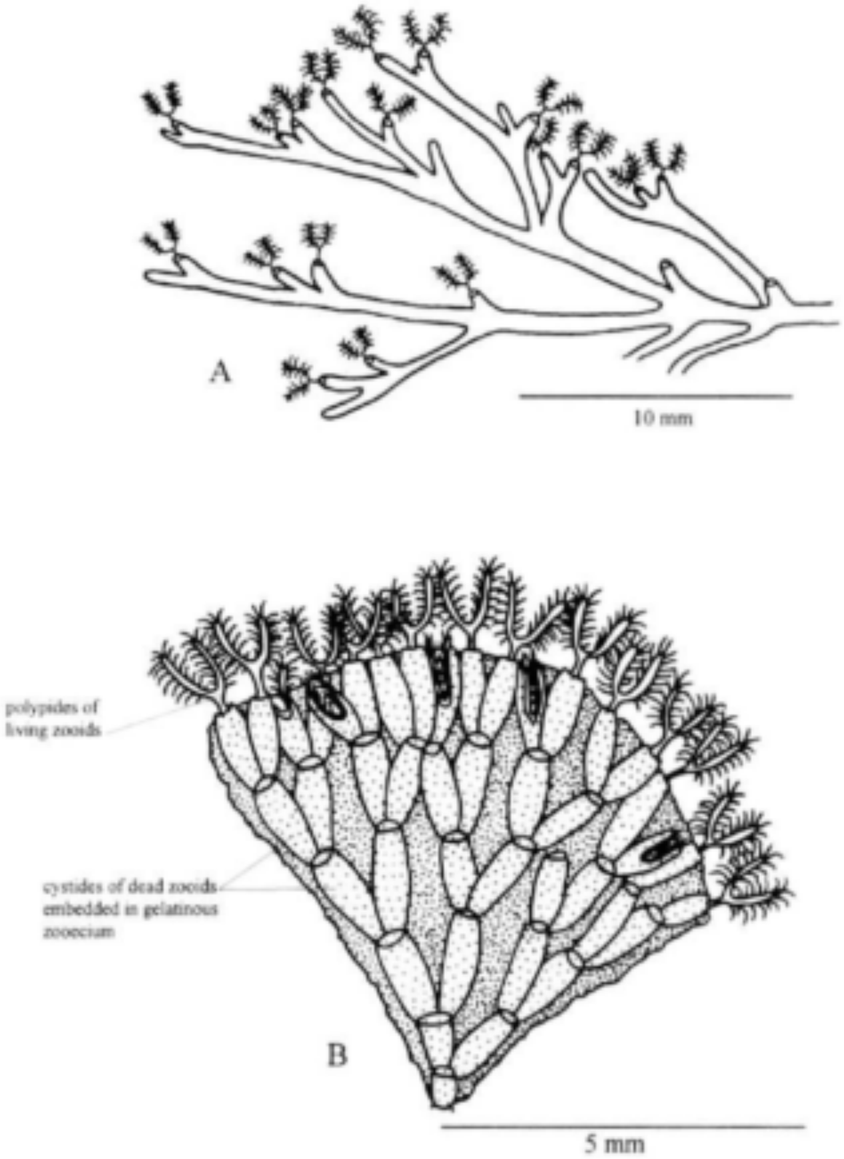

Fig. 10.2. Phylactolaemate colony forms. **A**, plumatellid type; *Plumatella repens*. **B**, lophopodid type: young colony of *Lophopodella capensis*.

about 20 days, with 47% and 20% of polypides surviving for 21 and 28 days respectively.

GENERAL BIOLOGY

While marine bryozoans, with their considerable diversity and long fossil record, have been quite extensively studied, the same cannot be said for the Phylactolaemata, studies on freshwater bryozoans having gone little beyond taxonomy and reproductive biology. Their economic importance is limited to the clogging of water mains, a problem largely eliminated by improved filtration methods (Harmer, 1913, quoted in Ryland, 1970). Bushnell (1966) has carried out a field study on the ecology of freshwater bryozoans in Michigan, covering such aspects as substratum preferences, interspecific interactions, plant and animal associations, and a study of the population dynamics of *Plumatella repens*. Other studies of phylactolaemate biology have mainly focused on individual species. In southern Africa there have been no investigations into either their ecology or aspects of their biology. The account of bryozoan biology in this chapter should therefore be viewed as a compilation of generalizations extracted from various sources. The most accessible and comprehensive source of information on the biology and ecology of the Phylactolaemata still seems to be Hyman (1959).

Food and feeding

Phylactolaemata, like all Bryozoa, are filter feeders. Cilia located on the lateral surfaces of the tentacles create a water current towards the lophophore, part of which is directed by a ciliary tract on the inner surface of each tentacle into a ciliated groove leading to the mouth. Planktonic organisms caught up in this feeding current, ranging in size from bacteria to rotifers and small crustaceans, are drawn into the pharynx by the pharyngeal cilia and swallowed. Hyman (1959) quotes studies by Rüsche (1938) in which a single polypide of *Plumatella fungosa* swallowed 25 large planktonic flagellates and a large number of smaller plankters in 20 minutes, and, in a rich culture of *Chlamydamonas*, filled the pharynx and swallowed the contents every 20 to 25 seconds. Considering the size which *Plumatella* colonies can reach and their potential for forming new colonies (described below), their localized impact on a littoral plankton community might be substantial.

Sexual reproduction

Sexual reproduction in phylactolaemates is unusual in that it apparently involves self-fertilization, a condition rare in the Animal Kingdom. Each zooid is hermaphrodite, both ovary and testis being located in the coelom, but there are no coelomoducts through which sperm can leave or enter. Fertilization takes place in the coelom, perhaps while the egg is still in the ovary. The fertilized egg comes to be located in an invagination of the cystid body wall, the embryo sac, where it develops into an oval ciliated larva. The larva has a structure similar to a cystid, consisting of an outer ectoderm and inner peritoneum, surrounding a coelom. By a complex process of invaginations, reminiscent of bud development during colony formation, one to four primary polypides are produced within the coelom. Each primary polypide becomes surrounded by a double layer of cells that will form the associated cystids to give rise to a primary zooid. Formation of a primary zooid follows a similar pattern to the development of new individuals in colony formation by budding: the larva is, therefore, already a young colony in which the larval body is the maternal cystid. Maturation of the gonads is usually followed by degeneration of the maternal polypide, facilitating the release of the fully-developed larva which remains free-swimming for only a short period before settling to found a new colony, of which the primary zooid is the ancestrula. Newly settled young colonies are able to move over the substratum to a limited extent, and may remain motile for a short time while selecting a site for permanent settlement.

Asexual reproduction and dispersal by statoblasts

Phylactolaemata survive adverse conditions, such as fluctuations in temperature and water levels, by the production of statoblasts. A statoblast is an asexually produced cell mass enclosed in a protective sclerotized shell and is capable of undergoing a prolonged period of dormancy. In most genera, each zooid produces a single statoblast which is released upon degeneration of the polypide, but in some Plumatellidae several statoblasts may develop sequentially along the funiculus at any given time (see Fig. 10.1) to be extruded through an atrial pore when fully developed (Hyman, 1959).

Four types of statoblast, differing in their capsule form (see Fig. 10.3), are generally recognized:

Sessoblasts, regarded as the simplest type, remain permanently attached to the basal region of the parent cystid after degeneration of the polypide. The bivalved capsule is simple, lacking a flotation device or spines of any description.

Piptoblasts, have a similar simple structure to sessoblasts, but do not remain permanently attached to the parent cystid.

Floatoblasts and *spinoblasts* float upon release from the parent. The junction between the two valves extends outwards to form a flattened ring, the pneumatic annulus, that contains small air-filled spaces to provide buoyancy. Where the pneumatic annulus bears spines, the statoblast is known as a *spinoblast*; where such spinous armature is lacking, it is called a *floatoblast*.

Germination of a statoblast is always preceded by a period of dormancy, the duration of which depends on season and physical environmental conditions. In northern temperate climates, statoblasts produced and released in summer germinate in one to two weeks, whereas those produced in autumn remain dormant until the following spring. Drying prolongs the dormancy period, dry statoblasts remaining viable for several months: an extreme case is known in *Lophopodella carteri*, which has been recorded as having survived out of water at room temperature for four-and-a-half years. The number of statoblasts produced in a favourable habitat can be enormous: Brown (1933, quoted in Hyman, 1959) calculated that the colonies present in association with a single square metre of aquatic plants in Lake Douglas, Michigan, would release 800 000 statoblasts on disintegration in autumn. Brown also reports drifts of statoblasts and statoblast shells of up to 1.5 m wide along the lake shore. Statoblasts therefore not only provide the means for local dispersion and for surviving adverse seasonal conditions within a particular habitat; they can also play a role in the wider dispersal to new habitats by wind or in mud on the feet of wading birds and other animals.

HABITAT AND DISTRIBUTION

Phylactolaemates have been recorded from both permanent and temporary lentic and lotic habitats worldwide. Very few species have been recorded from fast-flowing water, and even these occur more commonly in slow-flowing and astatic waters. Acid and brackish waters also appear to be unsuitable habitats, as are those high in inorganic suspended solids. Most genera occur in shallow water and appear to establish themselves preferentially on submerged aquatic plants, particularly the undersides of water lily leaves. Bushnell (1966) reports a significantly higher mortality, presumed to be due to predation by snails and trichopteran larvae, in young colonies that settled on the lake bottom when compared to those that settled on plants. *Fredericella sultana* is the only species known to occur in deep water, having been recorded at depths of 30 and 170 m in Lake Lucerne (Switzerland).

With the exception of *Stephanella* and *Gelatinella*, which seem to be

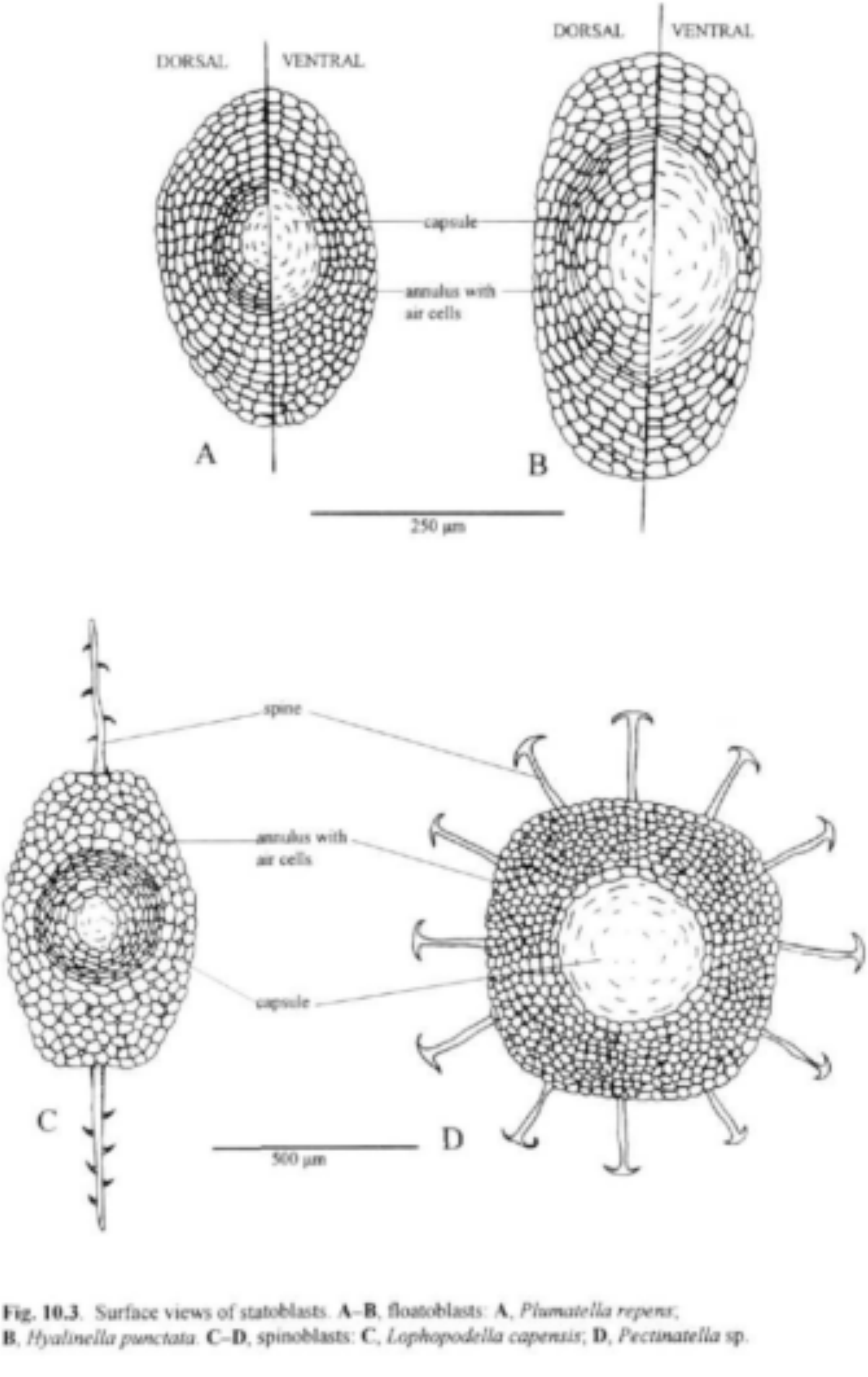

Fig. 10.3. Surface views of statoblasts. **A–B**, floatoblasts: **A**, *Plumatella repens*; **B**, *Hyalinella punctata*. **C–D**, spinoblasts: **C**, *Lophopodella capensis*; **D**, *Pectinatella* sp.

endemic to Japan, all genera have a widespread distribution. The family Cristatellidae, with a single species—the uniquely motile *Cristatella mucedo*— is confined to the northern temperate zone, but all other families occur in both hemispheres and all species recorded from the Southern Hemisphere are assignable to Northern Hemisphere genera. Four species, *Fredericella sultana, Plumatella repens, Plumatella emarginata* and *Lophopodella carteri,* are regarded by Hyman (1959) as truly cosmopolitan. Considering the potential for wide dispersal afforded by the statoblasts, the genetic conservatism resulting from self fertilization, and the paucity of studies, particularly in the Southern Hemisphere, this list might well prove to be incomplete.

COLLECTION, PRESERVATION AND EXAMINATION

Phylactolaemata are likely to be more common in southern Africa than records would imply, the meagre records probably reflecting a lack of interest in the animals rather than their scarcity. Examination of submerged aquatic plants and other suitable substrata should significantly increase the number of recorded species.

Colony form, shape of the lophophore, nature of the zooecium and structure of the statoblasts are all important characters in the identification of phylactolaemates. As in most soft-bodied invertebrates, many details are seen more clearly in the living animal. Initial observation through a dissecting microscope, while the animal is still alive and immersed in water from its habitat (and preferably still attached to its substratum), is therefore recommended.

Voucher specimens must be narcotized prior to preservation, since direct fixation will invariably result in the polypides retracting into the cystids before they are killed. Place the colony (which is still attached to its substratum) in a shallow dish containing sufficient water from its habitat to amply cover it, and leave it undisturbed until the polypides emerge. Gently sprinkle a few menthol crystals onto the surface of the water and leave overnight. This should fully narcotize the polypides, which will prevent them from retracting in response to mechanical disturbance. Decant the water and replace it with 40% formalin for about ten minutes, after which the specimen may be washed and preserved in a 5% solution of glycerin in 70% alcohol.

Statoblasts in the colony are usually clearly visible under a dissecting microscope. For a more detailed examination, remove the statoblasts from the zooecium by tearing the tissue with a pair of fine-pointed insect mounting pins and allowing them to float or fall out. These can then be collected, dehydrated and mounted on a microscope slide for examination through a compound microscope.

IDENTIFICATION

Six genera, including some ten species, are known to occur in Africa, but only two species—*Plumatella emarginata* and *Lophopodella capensis*—have been recorded from southern Africa (Hastings, 1929). *Plumatella repens*, *Hyalinella punctata* and an unidentified species of *Pectinatella* are added to this list in this chapter. As it is unlikely that this represents the whole southern African phylactolaemate fauna, the key provided includes all genera recorded from the African continent.

KEY TO THE GENERA OF PHYLACTOLAEMATA RECORDED FROM AFRICA

Notes on this key:

Details of species, where known, appear at the end of the key.

* Indicates genera known to occur in southern Africa.

1. Colony form plumatellid-type (Fig. 10.2A); repent, ramifying over the substratum or more or less erect, bushy; zooecium tubular, thin and membranous to moderately thick and gelatinous but always leaving the cystids of adjacent zooids more or less discreet; statoblasts are piptoblasts or oval to subcircular floatoblasts (Fig. 10.3A,B); sessoblasts may be present 2

– Colony form lophopodid-type (Fig. 10.2B), an unbranched sheet or mound comprising a continuous gelatinous zooecium in which the cystids are embedded (Fig. 10.2B, 10.4); statoblasts are spinoblasts (Figs 10.3C, D) or spindle-shaped floatoblasts, sessoblasts never present (**Lophopodidae**) ... 5

2. Lophophore round or broadly elliptical; zooecium a thin cuticula; statoblasts are oval to kidney-shaped piptoblasts (**Fredericellidae**) ....*Fredericella*

– Lophophore horseshoe-shaped; statoblasts are oval floatoblasts with or without sessoblasts (**Plumatellidae**) 3

3. Zooecium a thick, gelatinous, hyaline cuticula; colony broadly branching; sessoblasts never present ....**Hyalinella*

– Zooecium obviously tubular, thin, firm to horny, transparent to opaque (Fig. 10.1); sessoblasts may be present 4

4. Membranous extension of the edge of the orifice closes over the polypide when retracted .... *Afrindella*

– Retracted polypide not so covered .... **Plumatella*

5. Statoblast ellipsoid, with one or more barbed spines at each pole (Fig.10.3C); individual colonies small (10–30 mm), fan-like, lobulate .... **Lophopodella*

– Statoblasts circular to sub-rectangular, with a marginal ring of anchor-like hooked spines arising from the edge of the float (Fig. 10.3D); colony large (up to 600 mm in diameter) mound shaped, comprising a massive gelatinous zooecium with small, polygonal groups of zooids embedded in its surface (Fig. 10.4) .... **Pectinatella*

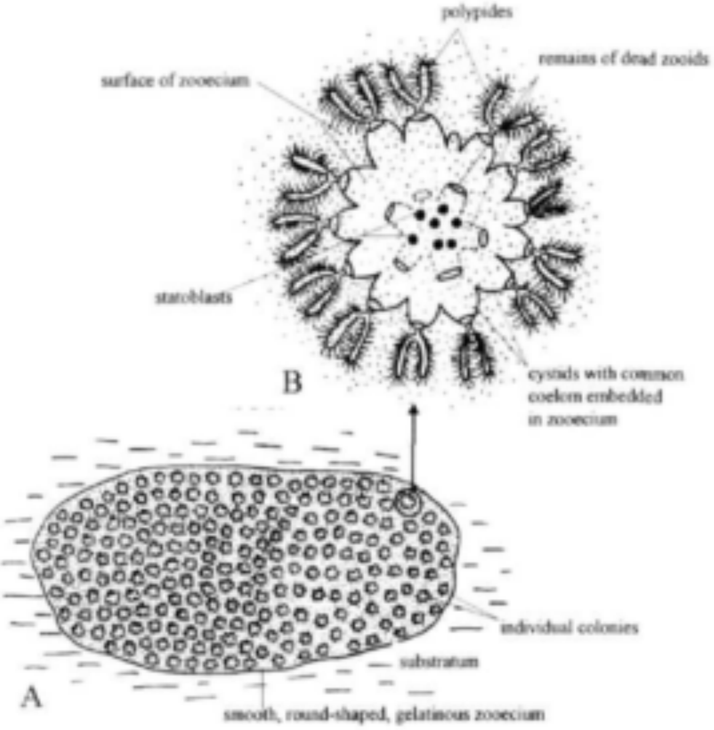

Fig.10. 4. *Pectinatella* sp: **A**, aggregation of individual colonies in a common gelatinous zooecium, surface view; **B**, detail of an individual colony.

CLASS PHYLACTOLAEMATA

ANNOTATED LIST OF RECORDED GENERA AND SPECIES

Fredericellidae

Fredericella Hyatt

The only genus in the family Fredericellidae, *Fredericella* is readily distinguished from all other Phylactolaemata by its broadly oval to reniform lophophore. The only two species in the genus differ in the number of their lophophore tentacles and the shapes of their statoblasts. The genus has not, as yet, been recorded from southern Africa, but its wide distribution suggests that its presence here is likely.

F. sultana (Blumenbach)

Characteristic features

Zooids have long, slender cystids resulting in the colony resembling a tangle of tubes ramifying loosely over the substratum. Lophophore reniform in young polypides, tending to broadly oval in older individuals (Hyman, 1959). Lophophore with 17–27 tentacles. Piptoblasts typically reniform.

Distribution:

Cosmopolitan: recorded from all continents and through a latitudinal range from Greenland in the North to Tierra del Fuego in the South.

F. australiensis Goddard

Characteristic features

This species, which differs from *F. sultana* in having 24–30 tentacles, does not have particularly slender cystids, and its piptoblasts are broadly oval to circular. It is included here as its presence in Australia suggests a possibly wider distribution in the Southern Hemisphere.

Distribution

Australia, Mexico, with a single record from Wyoming, U.S.A.

Plumatellidae

Plumatella Lamarck

This genus is characterized by the presence of oval floatoblasts, often present in considerable numbers, and distinct tubular cystids with a thin chitinous cuticula forming the zooecium. Colony form is typically a branching tangled mass of zooids, repent and/or bushy. Sessoblasts may be present. The genus is distributed world-wide and includes several species, only two of which are at present known to occur in southern Africa.

Plumatella emarginata Allman

Characteristic features

Characteristic of this species are a distinct notch in the dorsal margin of the orifice, a well developed keel on the dorsal surface of the cystid, and broadly oval floatoblasts in which the air cells of the annulus partially cover the dorsal surface of the capsule. The colony form is open and bushy (Hyman, 1959) and the colour of the cuticula is dark (Pennak, 1989).

Distribution

The only southern African record to date is from Florida Lake in Gauteng (Hastings, 1929), but the species is cosmopolitan, so its distribution in the sub-continent is likely to be more extensive.

Plumatella repens (Linnaeus)

Characteristic features

Cystids with an entire orifice margin, a very light yellowish cuticula, and no keel. Floatoblasts broadly oval with air cells of the annulus extending to partially cover the dorsal surface of the capsule. Colony repent, loosely branching.

Distribution

Cosmopolitan, but not recorded from southern Africa in the literature. A specimen from an aquarium in the Zoology Department, University of the Orange Free State (Bloemfontein, FS), which conforms to this species in all important characteristics, has been examined by the author. The cosmopolitan distribution of this species suggests that it will be found elsewhere in southern Africa.

Afrindella Annandale

This genus, represented by a single species, *A. tanganyikae*, is described as differing from *Plumatella* in having a stiffer, horny cuticula and a membranous extension of the orifice which closes over the retracted polypide. It is known from East Africa and India, so may extend into southern Africa.

Hyalinella Jullien

The genus is characterized by a hyaline gelatinous cuticula, which may incorporate exogenous material (diatom frustules, fine sediment particles etc.) giving the colony a thickly branching form. Branching may be obscured in older parts of the colony through the cuticulae of adjacent branches overlapping or coalescing, but typical plumatellid growth is always evident in younger parts. Floatoblasts, always present in mature zooids, are taxonomically important for separating species.

Hyalinella punctata (Hancock)

Characteristic features

This species is characterized by its narrowly oval floatoblasts, in which the air cells of the annulus partly cover the dorsal surface of the capsule (Fig. 10.3B).

Distribution

Cosmopolitan. Although recorded from many localities in both hemispheres, including north and central Africa, this species has not been reported from southern Africa apart from a single specimen from the mSundusi River near Pietermaritzburg (KZN) (pers. obs.). Given its cosmopolitan distribution, it is likely to occur throughout the region.

Family Lophopodidae

Lophopodella Hyatt

Zooids form a fan-shaped colony, embedded in a continuous lobate, gelatinous zooecium in which the polypides are confined to the outer edge, all facing the same direction. Young colonies, comprising a few polypides, are mound shaped and motile, capable of moving some 20 mm per day. Each polypide produces a single spinoblast bearing one or more barbed spines at each pole. The genus is represented in all continents and at all latitudes world-wide. To date, only one species recorded from southern Africa.

Lophopodella capensis (Sollas)

Characteristic features

This species, characterized by a single barbed spine at each pole of the spinoblast (Fig. 10.3C), appears to be endemic to southern Africa. Individual colonies are small: specimens from the Friedenau and Lichtenstein Dams near Windhoek rarely exceeded 12 mm, but fusion of adjacent colonies to form larger units, as suggested by Hastings (1929), seems to occur on crowded substrata. Specimens of 200–300 mm from Rietfontein, reported to Hastings, almost certainly represent such fusion. The typical colony form illustrated in Fig. 10.2B may be obscured in cases where several colonies fuse.

Lophopodella carteri (Hyatt), which differs from *L. capensis* in having six short barbed spines at each pole of the spinoblasts, has a widespread distribution, and is known from East Africa (Brien, 1960); it could well extend into southern Africa. Hyman (1959) mentions *L. thomasi* and *L. stuhlmani* as being endemic to Africa, but I have been unable to trace further details on these species.

Distribution

Southern Africa: Valkenberg Vlei (WC), Lake Chrissie (MPL), Rietfontein (GT), Florida Lake (GT), Avenue Pan (Benoni) (GT), Windhoek (NAM).

Pectinatella Leidy

Colony forms a thick, smooth, cushion-like gelatinous mass in which the zooids are aggregated in small groups of 12 to 18 embedded in the surface (Fig. 10.4). *P. magnifica* is reported to reach a size of 600 mm. In this species the colony does not originate from a single ancestrula; small motile colonies, each originating from a separate statoblast, come together and secrete the communal zooecium. Within each individual constituent colony, the body walls of the cystids partially break down, so the polypides arise from a common coelom. This mode of colony formation seems not to occur in all species of *Pectinatella* (Hyman, 1959). Each zooid produces a single circular/sub-rectangular spinoblast with a marginal ring of anchor-shaped spines (Fig. 10.3D). Not previously recorded from Africa.

Pectinatella sp

Characteristic features

Specimens from the localities mentioned below were sent to the author for identification some years ago. No attempt was made to identify the specimens to species.

Distribution

Leeupan (Kruger National Park), Fern Cliff (Pietermaritzburg) (KZN).

ACKNOWLEDGEMENTS

Thanks are due to Barbara Curtis (National Museum of Namibia) for the loan of the Namibian material, to Maitland Seaman (University of the Free State) and three anonymous collectors for specimens from various South African localities, and to Nancy Bonsor for the final preparation of illustrations.

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CHAPTER 11

TARDIGRADA

by

N.A. Rayner

Tardigrades are soft-skinned, minute animals that seldom exceed one millimetre (Fig. 11.1). Commonly known as 'water bears', the Tardigrada are sometimes classified with the arthropods, but their phylogenetic status is not clear. Several tardigrade characteristics such as the non-chitinous cuticle and the unjointed appendages are decidedly different from those of arthropods and some authors link tardigrades to the Aschelminthes (round worms).

Morphology

The Tardigrada possess a cuticle that is moulted, but in contrast to that of arthropods, the tardigrade cuticle is thought to be proteinaceous rather than chitinous. About 400 tardigrade species have been described and all are small —between 0.5–1.2 mm in length (Pechenik, 1991). The body appears to consist of four segments but is not divisible into regions, except that in some species a slight constriction separates off an anterior part or 'head' from the rest of the body. The mouth is provided with a sucking proboscis. There are four pairs of short unjointed legs (I–IV) each of which is provided with four claws. The last pair of legs is terminal.

The mouth is surrounded by papillae and the buccal cavity contains a pair of horny, sometimes calcified, stylets. The ducts of a pair of what are possibly salivary glands open into the cavity of the mouth. There is a muscular pharynx, a narrow oesophagus and an extensive stomach. The anus is sub-terminal, being situated in front of the last pair of limbs.

There are no organs of respiration, nor heart nor blood vessels. Gaseous exchange takes place across the body surface via a permeable cuticle.

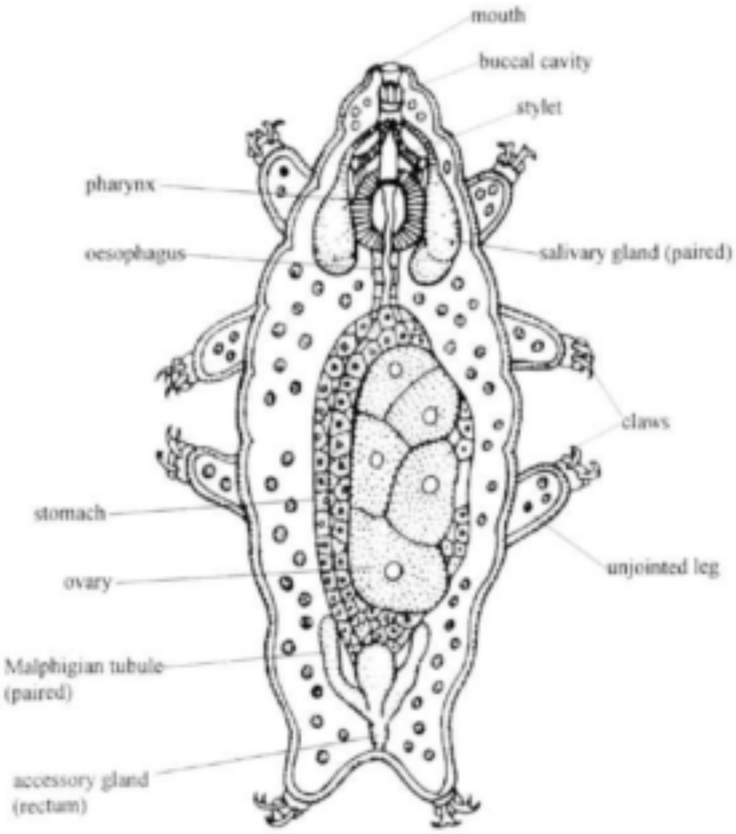

Fig. 11.1: *Macrobiotus hufelandi* (modified from Marshall & Williams 1972)

Muscles of the body wall are single, smooth, and occur in bands. The nervous system consists of pre-oral ganglia joined by circum-oesophageal commissures linked to a double ventral nerve cord which has four ganglia along its length. Two eye spots are situated at the anterior end. Details of the osmo-regulatory system are not well known: some glands appear to resemble Malphigian tubules, although their function has not been established.

Habitat preferences

A few tardigrades are marine, but most species live in freshwater habitats, in bottom detritus or attached to freshwater plants. The majority are semi-aquatic, living on mosses, lichens, and liverworts. Tardigrades are slow-moving animals. Even aquatic species cannot swim, but creep awkwardly over plants or on the sediment, using their claws to cling to surfaces.

Tardigrades spend most of their lives in a desiccated cryptobiotic state during which time they are resistant to unfavourable conditions such as low or high temperatures and pollutants, and may be dispersed by air currents. As soon as water becomes available they rehydrate and become active. Some aquatic tardigrades may enter cryptobiosis when desiccated, but others secrete a thick-walled cyst under the cuticle. A tardigrade may live up to 10 years in this cryptobiotic state; the total life span, including episodes of cryptobiosis, may be up to 70 years in some species, although life spans of less than one year are more common (Pechenik, 1991).

Feeding

Tardigrades take no solid food. Many pierce plant cells and suck out the contents, using a complex feeding apparatus with sharp stylets. A few tardigrade species use their stylets to attack small animals. Some may be true carnivores, but the majority appear to be herbivores. The mouth opens into a short buccal cavity that is stiffened by cuticular rings.

Reproduction

Sexes are separate and gonads in both sexes are saccular. The products of the gonads are shed through the terminal part of the intestine. Females are often more numerous than males and mating and egg-laying take place at the time of moulting. In the majority of species, sperm are deposited into an old female skin containing eggs, but in some species the sperm are deposited into the female tract before the cuticle is completely shed. Depending on the species, one to 30 eggs are laid at a time. In aquatic tardigrades, the eggs may be either deposited in the old cuticle or attached singly or in groups to various objects. Parthenogenesis is common. Development is direct and rapid and completed in 14 days or less. The young tardigrades resemble the adults and they hatch by breaking the shell with their stylets. Further growth is attained by increase in the size of cells rather than by the addition of cells. As many as 12 moults may take place during the life cycle.

Identification

Very little is known about tardigrades in southern Africa as there has been no definitive study on this group. They are seldom encountered and are probably overlooked because of their very small size.

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CHAPTER 12

POLYCHAETA

by

J.H. Day[†] & J.A. Day

While most species of Oligochaeta occur in moist soil, many others are found in fresh water and relatively few occur in the sea. The reverse is true for the Polychaeta, almost all of which are marine or estuarine. These two classes of Annelida may be distinguished externally by the fact that the Polychaeta usually have segmental, flaplike parapodia bearing numerous setae (bristles), and a head with appendages and sometimes with jaws. The Oligochaeta lack these features but many have a 'saddle' or clitellum—a thickened part of the body that secretes the cocoon around the eggs. A few species of polychaetes appear similar to oligochaetes, in that they lack parapodia and head appendages, but they also lack a clitellum.

GENERAL BIOLOGY

Distribution and habitat requirements

As noted, polychaetes are most common in the sea, where the salinity is about 35. Where salinities are greatly reduced in the upper reaches of estuaries, and in coastal lakes, polychaete diversity is very low. Although inland waters worldwide support only a handful of species of polychaetes, various species of the family Nereidae have been reported from entirely fresh waters. While four species are known from very dilute coastal and estuarine waters in southern Africa, only one, *Ceratonereis keiskama*, is known from truly fresh waters. Four other species of polychaete, each belonging to a different family, are also known from practically fresh waters at the upper ends of southern African estuaries.

Most of the species have well-developed gills, which allow them to survive where oxygen tensions are low, as they often are in estuarine muds. *Capitella capitata* (Fig. 12.1A), which can live in very anoxic conditions, is dark red because of the haemoglobin in its blood. The only polychaetes with no apparent respiratory adaptations are the two species of *Ceratonereis*, which tend to live in cleaner and less anoxic sands.

Feeding

Different species of polychaetes feed on a wide range of materials from mud to plants and animals. Although no specific studies have been done on the local species, it is likely that *Capitella capitata* ingests the mud itself; that *Cauleriella alata* selectively picks particles of organic material from the surface of the mud using its palps; that *Desdemona ornata* and *Ficopomatus enigmaticus* are filter feeders; and that the nereids feed on a variety of organic particles, including small living animals.

Reproduction

With few exceptions, polychaetes have separate sexes. They undergo broadcast spawning, releasing eggs or sperm into the sea, where fertilization takes place. The fertilized eggs develop into small larvae that live and feed in the plankton, gradually taking on adult features and eventually settling to the bottom as miniature adults. Fresh or very brackish waters are harsh places for eggs and sperm, and so broadcast spawning as a means of reproduction is extremely uncommon in fresh waters. How the southern African polychaetes from fresh- and brackish-waters are able to cope with these conditions is not known. It may be that the estuarine forms reproduce at the time of year when salinities are likely to be highest; it is even possible that they cannot breed at all under these conditions but that the headwaters of estuaries are colonized anew by each new generation. Reproductive adaptations of *Ceratonereis keiskama* to the virtually fresh water of the land-locked Lake Sibaya (KwaZulu–Natal) would repay study.

Collection and preservation

Fresh- and brackish-water polychaetes are known to occur in southern Africa only in estuaries and a few coastal lakes. Most occur in sandy or muddy substrata, often in anaerobic conditions, but *Ficopomatus enigmaticus* occurs on any reasonably hard surface, including submerged macrophytes. *Ceratonereis keiskama* can also live on the fronds of submerged macrophytes, but more commonly it burrows into sandy muds. Burrowing polychaetes can be collected by sieving mud collected approximately to spade depth, or by examining the fronds of macrophytes from suitable localities. They are best fixed in 4% formaldehyde and transferred to 70% ethyl alcohol for examination and storage (see Vol. 1 —Day In Prep).

Systematics

The class Polychaeta is divided into two orders, the Errantia and the Sedentaria. As their names suggest, errant polychaetes tend to be active animals, while 'sedentary' polychaetes are usually sedentary and usually dwell in tubes or burrows. Each of the orders is divided into a series of different families, but polychaete systematists often disagree about the number of families and which genera should be included in them.

Morphology of polychaetes

Every polychaete worm has a distinct head end and a segmented body (e.g. Figs 12.1A, 12.2H). In most species, each body somite (segment) has a pair of lateral flaps, called parapodia (Figs 12.2I–L), which are used for crawling and sometimes even for swimming. The structure of the head end and of the parapodia are important for identification even to family level. The head itself is usually small (e.g. Figs 12.1F, 12.2I) and may be entirely obscured by the anterior appendages (Figs 12.1H, I). The number and arrangement of these appendages are important in distinguishing families from each other. Errant polychaetes usually have well-developed sensory structures on the head (Figs 12.2E, I, K), including eyes, thin, mobile antennae and tentacles, and short, stout palps. Sedentary polychaetes, on the other hand, are more likely to bear on their heads structures used in feeding. These include a single pair of long, grooved palps (e.g. Figs 12.1E, F) or a number of radioles (Figs 12.1H, I), which are whorls of long, finger-like, ciliated tentacles used in filter-feeding. Among its radioles, the Serpulidae, one of the filter-feeding families, also bear a characteristic operculum (Fig. 12.1I) that closes the mouth of the tube (Fig. 12.1J). Animals bearing large crowns of tentacles can also use them as gills, but others may have specialized respiratory structures. The cirratulids, for instance, have long gill filaments along the length of the body (Figs 12.1E, F), while the parapodia of some nereids are divided (Figs 12.2J, L), forming a large surface area that can be used for gas exchange.

The parapodia vary from being almost-indistinguishable flaps (e.g. Figs 12.1D, G) to large, elaborate structures (e.g. Fig. 12.2J). One of the most characteristic features of polychaetes are the setae, which are inserted into the parapodia and give them purchase for crawling or burrowing. The setae may be simple (eg Figs 12.1B, 12.2B) or compound (consisting of more than one section: Figs 12.2C, F) and may occur singly or in bundles. The parapodia are separated into a doral flap, the notopodium, and a ventral flap, the neuropodium. Since notopodal and neuropodal setae may differ from each other, as may those towards the anterior and posterior parts of the body, it is important when identifying to species level to examine parapodia from the appropriate part of the body, as indicated in the key.

Identification of polychaetes

It is often necessary to examine setae under a compound microscope in order to identify a polychaete to species or even to genus. Use a sharp, fine blade to slice off a parapodium from the appropriate part of the body and mount it in glycerine under a coverslip on a microscope slide. Polychaetes of the family Capitellidae have no anterior appendages and their parapodia are much reduced. In order to distinguish them from oligochaetes, use a compound microscope to check the setae from the middle part of the body. If they are hooked at the tip and covered by a delicate hood (Figs 12.1B, C), then they belong to a capitellid polychaete and not to an oligochaete. When identifying polychaetes, bear in mind that they are very delicate creatures and easily lose their slender appendages, particularly gills and sometimes palps too. If it has received rough treatment when being collected and preserved, a delicate worm like *Cauleriella alata* may lose all of its appendages and may initially be mistaken for a capitellid or even for an oligochaete, unless the setae are examined microscopically.

KEY TO THE BRACKISH- AND FRESHWATER POLYCHAETES OF SOUTHERN AFRICA

The key that follows is suitable *only* for low or very variable-salinity waters in southern Africa. It does not apply to polychaetes living in the sea or at the seaward ends of estuaries, or in other parts of the world.

1. Head and anterior end without appendages; body as a long, threadlike earthworm (Fig. 12.1A) without projecting parapodia or gill filaments (Fig. 12.1D) but with numerous setae, including hooded hooks (Figs 12.1B, C) on each segment .... *Capitella capitata*
– Head and anterior end with one or more pairs of appendages (palps, Fig. 12.1F; tentacles, Figs 12.2E, I, K; or radioles, Figs 12.1H, I); body segments with parapodia (e.g. Fig 12.2D, G) and/or gill filaments (Figs 12.1E, 12.2J) 2

2 Head obscured by a crown of feathery radioles (Figs 12.1H, I); no jaws; body in a tube 3
– Head evident (e.g. Figs 12.1F, 12.2A, H); anterior end with paired tentacles (Figs 12.2E, I, K) and/or palps (Figs 12.1F, 12.2E, I, K); mouth with jaws; not living in a tube 4

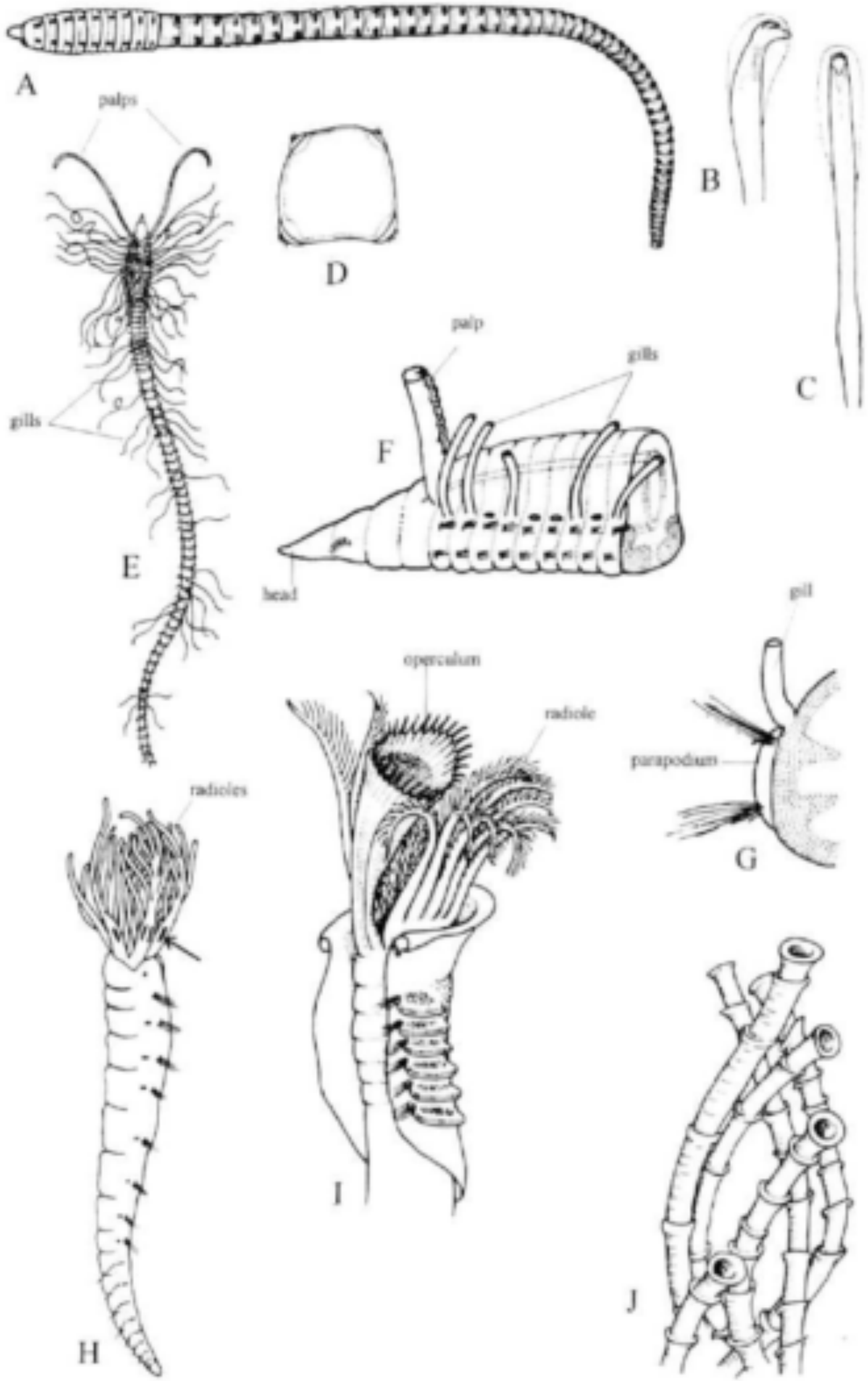

Fig. 12.1. **A–D**, *Capitella capitata*: **A**, whole animal, x 4; **B**, hooded hook in side view; **C**, hooded hook in front view; **D**, diagrammatic cross-section of a somite near the middle of the body. **E–G**, *Cauleriella alata*: **E**, whole animal (x 2); **F**, head end, palps and gills trancated; **G**, anterior view of a parapodium from the mid-section of the body. **H**, *Desdemona ornata*, whole animal (x 5). **I–J**, *Ficopomatus enigmaticus*: **I**, head end (x 5); **J**, tubes.

3. Tubes soft, muddy, separate and fragile; no operculum; three pairs of radioles form a plume on the head (Fig. 12.1H) .... *Desdemona ornata*

– Tubes hard, calcareous and entwined, tube mouth trumpet-shaped (Fig. 12.1J); operculum present with short spines; many radioles (Fig. 12.1I).......................... ....*Ficopomatus enigmaticus*

4. Head without antennae but with one pair of long, grooved palps (Figs 12.1E, F); parapodia reduced to ridges (Fig. 12.1G) and irregularly bearing long, thin dorsal gill filaments (Fig. 12.1E) .... *Cauleriella alata*

– Head with paired antennae, short, stout ungrooved palps and tentacles (Figs 12.2E, I, K); parapodia large and flap-like (Figs 12.2D, G, J) 4

5. Notopodia of some anterior parapodia bearing branching gills (Figs 12.2 H, J, L) ..6

– All parapodia without gills (Figs 12.2A, D, G) 7

6. Gills arising as numerous filaments from the dorsal cirrus (Fig. 12.2J), roughly on somites 12–24 (Fig. 12.2H) .... *Dendronereis arborifera*

– Gills arising as several short filaments directly from the dorsal lobes of parapodia (Fig. 12.2L), roughly on somites 8–30 .... *Dendronereides zululandica*

7. Posterior parapodia (Fig. 12.2D) bearing one large simple seta (Fig. 12.2B) among many compound setae (Fig. 12.2C) in the lower (neuropodial) bundle ....*Ceratonereis erythraeensis*

– Posterior parapodia (Fig. 12.2G) with compound setae (Fig. 12.2F) but with no large simple setae .... *Ceratonereis keiskama*

BIOLOGICAL NOTES

Class Polychaeta
Order Sedentaria
Family **Capitellidae**
Capitella capitata (Fabricius, 1780)
Figs 12.1A–D

This species is common in estuaries, particularly those used as harbours, burrowing in mud that may be foul-smelling, with a high organic content. Individuals contain haemoglobin in the blood, thus appearing dark red when alive. As might be expected, they tolerate low oxygen tensions and a wide range of conditions. Cosmopolitan. Length 20–30 mm.

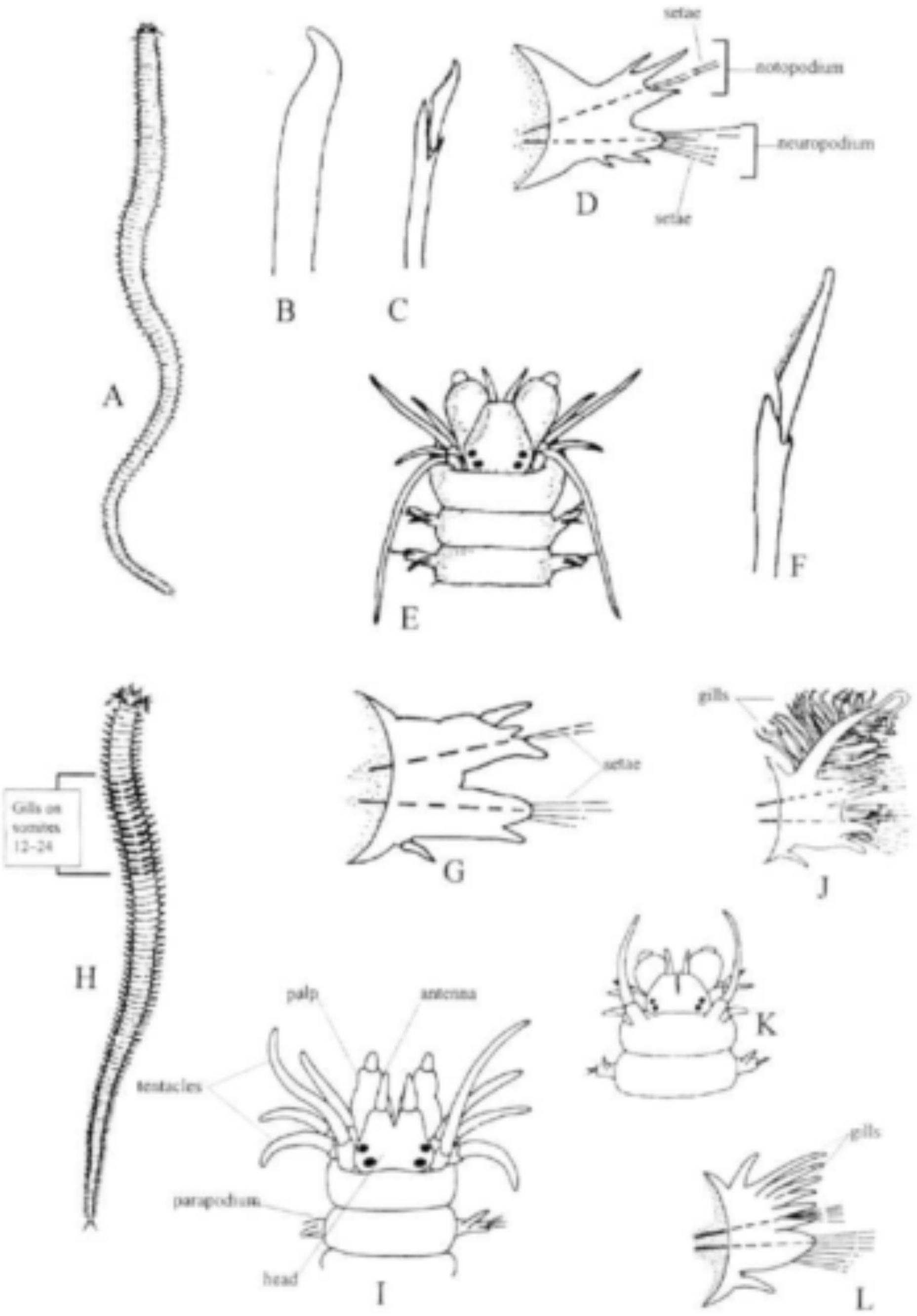

Fig. 12.2. A–D, *Ceratonereis erythraeensis*: **A**, whole animal (x 2); **B**, simple giant seta from a posterior notopodium; **C**, a normal seta from a posterior neuropodium; **D**, a posterior parapodium, anterior view. **E–G**, *Ceratonereis keiskama*: **E**, head, dorsal view; **F**, a seta from a posterior neuropodium; **G**, a posterior parapodium, anterior view. **H–J**, *Dendronereis arborifera*: **H**, whole animal (x 2); **I**, head, dorsal view; **J**, a gill-bearing parapodium. **K–L**: *Dendronereides zululandica*: **K**, head, dorsal view; **L**, gill-bearing parapodium.

Family **Cirratulidae**

Cauleriella alata (Southern, 1914)

Figs 12.1E–G

Cauleriella alata was originally found in a brackish lake in India but it is now known to extend along the African coast as far south as Knysna Estuary (Western Cape), where individuals live in sandy mud and gather surface particles with their grooved tentacles. Gill filaments allow them to live in conditions low in oxygen. Length 20–30 mm.

Family **Sabellidae**

Desdemona ornata Banse, 1957

Fig. 12.1H

Desdemona ornata was first described from the Klein River Estuary near Hermanus (Western Cape). Known in estuaries from Namibia to KwaZulu–Natal, this species may be a southern African endemic. Individuals are filter- (and possibly detritus-) feeders, living on the surface of sandy mud. Black marks at the bases of the radioles (arrowed in Fig. 12.1H) are diagnostic. Length up to 20 mm.

Family **Serpulidae**

Ficopomatus enigmaticus (Fauvel, 1923)

Figs 12.1I, J

Ficopomatus enigmaticus (*Mercierella enigmatica* in the older literature) was originally recorded from an estuary in France, but is now known in temperate and subtropical estuaries worldwide. A filter feeder, it is abundant in some estuaries but not in the sea. It is easily kept in the laboratory and is the subject of much experimental work (e.g. Davies et al., 1989). Milnerton Lagoon and Zandvlei in the south-western Cape both support large populations of this species, as do Swartvlei and the Wilderness Lakes in the southern Cape (e.g. Davies, 1982). Individuals are gregarious, building calcareous tubes twisted together and attached to bridge pilings, artificial banks and even to hard lumps of mud. *Ficopomatus enigmaticus* is also known from many other warm estuaries around the world; a related species replaces it in the tropics. Length up to 50 mm.

Order Errantia

Family **Nereidae**

Ceratonereis erythraeensis Fauvel, 1918

Figs 12.2A–D

Ceratonereis erythraensis is widely distributed in warm and tropical Indo–West Pacific seas and estuaries. Individuals burrow into muddy sand and are common in beds of the sea grass, *Zostera*. They are probably omnivorous. Length 80–160 mm.

Ceratonereis keiskama Day, 1953

Figs 12.2E–G

Ceratonereis keiskama is possibly a southern African endemic, being known from estuaries from the Western Cape to KwaZulu–Natal, and from coastal lakes such as Lake Sibaya (KZN), where it is abundant in sand and on macrophytes (Boltt, 1969). Similar to *C. erythraensis*, this species occurs at even lower salinities. Length usually 10–20 mm, occasionally up to 70 mm.

Dendronereis arborifera Peters, 1854

Figs 12.2H–J

Dendronereis arborifera is an Indo–Pacific species known from the eastern Cape to Mozambique and Madagascar. Individuals are common at the mouth of St Lucia Bay (KZN) and in mangrove swamps, where they are found in soft mud. The large gills suggest that they are adapted to living in conditions where oxygen tensions are low. They extend their heads onto the mud surface, feeding on particulate material drifting by. Length up to 100 mm.

Dendronereides zululandica Day, 1951

Figs 12.2K–L

Dendronereides zululandica has so far been recorded only from Zululand and Mozambique, so may be a southern African endemic. It is known from estuaries and mangrove swamps, but is not common. Presumably its habits are similar to those of *Dendronereis arborifera*. Length up to 80 mm.

ACKNOWLEDGEMENTS

Notes for this chapter were made by the senior author, John Day, before he died. The chapter was completed by the second author based on JHD's manuscript notes and also on his handwritten notes in a copy of Day (1967), a second and revised edition of which he was preparing for publication by the British Museum (Natural History) when he died. The British Museum never did publish this second edition, so some of the records cannot be confirmed. Drawings were scanned and prepared by their daughter, Belinda Day, mostly from Day (1967).

The second author thanks Fiona Mackay, Grazyna Marska and Michelle van der Merwe for providing some of the southern African records of polychaetes from fresh and brackish waters.

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CHAPTER 13

OLIGOCHAETA

by

W. van Hoven & J.A. Day

The Class Oligochaeta in the Phylum Annelida contains about 3000 species of earthworms and their allies. Unlike the more familiar earthworms, which are commonly found in soil, most of the oligochaetes dealt with in this chapter are truly aquatic, about 500 species being found in rivers and wetlands throughout the world; a further 200 or so species are marine or estuarine. Defining an 'aquatic' oligochaete is not easy. While many of these species are always aquatic, various earthworms are also found fairly commonly in water, especially at times when water levels rise after extended rainy periods. What is more, the biogeography of the group is complex. Based on morphological evidence, it would seem that many species are widespread or even cosmopolitan. The extent to which this is true will only become clear when adequate genetic studies have been done on some apparently cosmopolitan species and we can see if forms from different regions of the World are genetically related as well as being morphologically similar. Human-induced translocations of oligochaetes further complicate the situation. In many cases it is not at all clear whether the present distribution of a species of oligochaete is an artefact of collecting effort, a natural phenomenon, or the result of translocation. It is easy to understand, however, how the shipping of plants in soil is likely to result in the spread of common earthworms and other oligochaetes.

Habitat Preferences

Oligochaetes are found in all kinds of inland waters from mountain streams to estuaries and from coastal lakes to man-made reservoirs. In fact, the only waters that they seem unable to penetrate are temporary ones, because they have no ability to withstand desiccation. On the other hand, many oligochaetes carry haemoglobin in the blood and so are able to live in virtually anoxic conditions. In this way they are able to tolerate extreme levels of organic pollution and are sometimes the only macroinvertebrates that are able to survive in grossly polluted waters. Aquatic oligochaetes such as *Tubifex* spp., *Limnodrilus* spp. and *Branchiura sowerbyi* (which has long gills on the posterior part of the body — Fig. 13.8E), are thus important indicators of poor water quality. It is interesting that several other African species have gills (see Figs 13.5H–N), perhaps because anoxic conditions are particularly common in warm waters.

Feeding

Despite their apparent similarities, oligochaetes feed in a variety of ways. Members of the family Tubificidae feed much as earthworms do, ingesting mud containing detritus and digesting the organic material. *Tubifex* itself lives head-down in a muddy tube, feeding on organically-rich mud, while its rear end is wafted around in the water. The tiny aeolosomatids use cilia on the prostomium to generate feeding currents, picking up loose particles from the substratum.

Feeding habits are particularly varied in the Naididae. In most species, a mucus-covered dorsal diverticulum of the pharynx is everted and picks up food particles, which are then retracted into the mouth. Both *Dero digitata* and *Nais variabilis*, naidids commonly found in South Africa, graze on algae affixed to small twigs and the like. The protruded part of the pharynx forms an oval trumpet with the lateral parts functioning as lips that hold the food in place. Thus the food does not merely adhere to the pharynx by means of mucus, but is also actively tugged loose. Members of the naidid genus *Chaetogaster*, commensals on snails, are carnivorous, sucking tiny animals into the pharynx. Individuals of some species of *Ripistes* live in fixed mucous tubes, from which they protude. When undisturbed, the worm stretches out the foremost part of its body, swinging rhythmically to and fro. Small food particles in the water adhere to long sticky hair chaetae, which are licked off at intervals by being pulled through the mouth.

Reproduction

Most aquatic oligochaetes reproduce sexually in much the same way as earthworms do. The worms are hermaphroditic, having both testes and ovaries. Two worms copulate by surrounding themselves with mucous secretions from the clitellum. Some taxa have paired penes that can insert sperm into the female genital openings of the partner but in others the sperm travels along a groove on the outside of the body from the male opening of one worm to the female opening of its partner. In either case, after cross-fertilization has taken place in the female part of the genital tract, the eggs are extruded into the mucous secretion and the worms withdraw, leaving the eggs in the mucus, which hardens to form a cocoon in which the eggs develop.

Naidids and aeolosomatids commonly also reproduce asexually by budding, a new head being developed part way along the body (Fig. 13.1D), while regeneration of lost anterior or posterior parts of the body is common, mostly in naidids and tubificids. It is thus important when identifying oligochaetes to ensure that one is dealing with whole specimens and not fragments!

Taxonomy

The class Oligochaeta is usually divided into three orders. The order Lumbriculida, said to be the most primitive, has a single monogeneric family, the Lumbriculidae, and occurs strictly in fresh waters. The order Tubificida includes about seven families, which together form the bulk of the aquatic oligochaetes. Members of these two orders are together commonly called the 'microdrile' oligochaetes. The third order, the Haplotaxida, has about 18 families, of which about eight are small (i.e. have few species) and aquatic. The other ten families or so include all of the typically large terrestrial earthworms, although some of these families have one or two facultatively aquatic representatives.

Note that the family Aeolosomatidae is something of a taxonomic mystery, being excluded from the Oligochaeta by some authorities. When included, it is usually placed close to the Tubificida.

Aquatic oligochaetes of Africa

Thanks mainly to the massive work on the aquatic oligochaetes of the World, written by Brinkhurst & Jamieson (1971), we have a fair idea of the taxonomy of the group at least up to that time. The African aquatic oligochaete fauna is relatively well known, several papers being available, particularly on South African forms. Of the 500 or so species known worldwide in the microdrile taxa, about 50 have been recorded from southern Africa, and a somewhat greater number for the whole of Africa. Most species are cosmopolitan, or with widespread but scattered distribution records, while two of the twelve or so families have Gondwanan distributions. About 20 species of megadrile oligochaetes are both aquatic and known from Africa. Most of them seem to be African endemics and one, *Eukerria saltensis*, is known only from southern Africa.

Morphology

Superficially the aquatic oligochaetes resemble their bigger terrestrial counterparts, the earthworms, but they are usually much smaller and more slender. Most reach a length of about 10–30 mm although in some species the individuals are scarcely 1 mm long, and others may attain lengths of 300 mm or more.

The body of an oligochaete consists of a large number of more- or-less identical segments or somites. The most anterior structure is the prostomium (Fig. 13.1A), which is not a true segment but protrudes in a roof-like fashion above the mouth and bears the cerebral ganglia internally. In a few species the prostomium may be drawn out to form a long proboscis. It is customary to designate the true body segments serially by Roman numerals, beginning at the anterior end. Thus the first true segment, the peristomium, is designated as 'I' (Fig. 13.1A). The peristomium lies just behind the prostomium and is the segment through which the mouth opens. It is devoid of the chaetae (called 'setae' in polychaetes) that are usually present on all other segments. The chaetae are arranged in four bundles, two dorso-laterally and two ventro-laterally. In some groups the chaetae may be absent from the first few segments. Simple eyespots are located on the peristomium of some species (Fig. 13.1D).

It is usually essential to clear specimens (see below) and mount them for viewing under a compound microscope if they are to be correctly identified, because the number and position of external genital openings (Figs 13.1B–C), and of the clitellum (Figs 13.3A–B, K–M), are often diagnostic but are sometimes difficult to pinpoint. The clitellum is a saddle- or ring-shaped swelling situated on a number of adjacent segments, often well behind the gonadal segments. This organ is responsible for producing the mucus that is used in copulation and that forms the cocoon in which the eggs are deposited. It is present in all oligochaetes but is very much thinner and less obvious in the microdriles. The paired male and female genital ducts lead to external pores located either in the same segment as the gonads they serve, or in the segment immediately behind them. Associated with the female openings is one or more pairs of sac-like spermathecae (Fig. 13.1B), in which sperm from the partner is stored; their positions, and those of the spermathecal pores, may be diagnostic. There may be one or more pairs of these structures located in or near the gonadal segments, commonly in front of, or in, the testicular segments. The spermathecal pores and the male and female gonopores (sometimes just called 'pores') usually open in the longitudinal line of the ventro-lateral bundles of chaetae. When a penis is present, it may be surrounded by a penis sheath (Figs 13.10F–H), which is also diagnostic in some species. In some

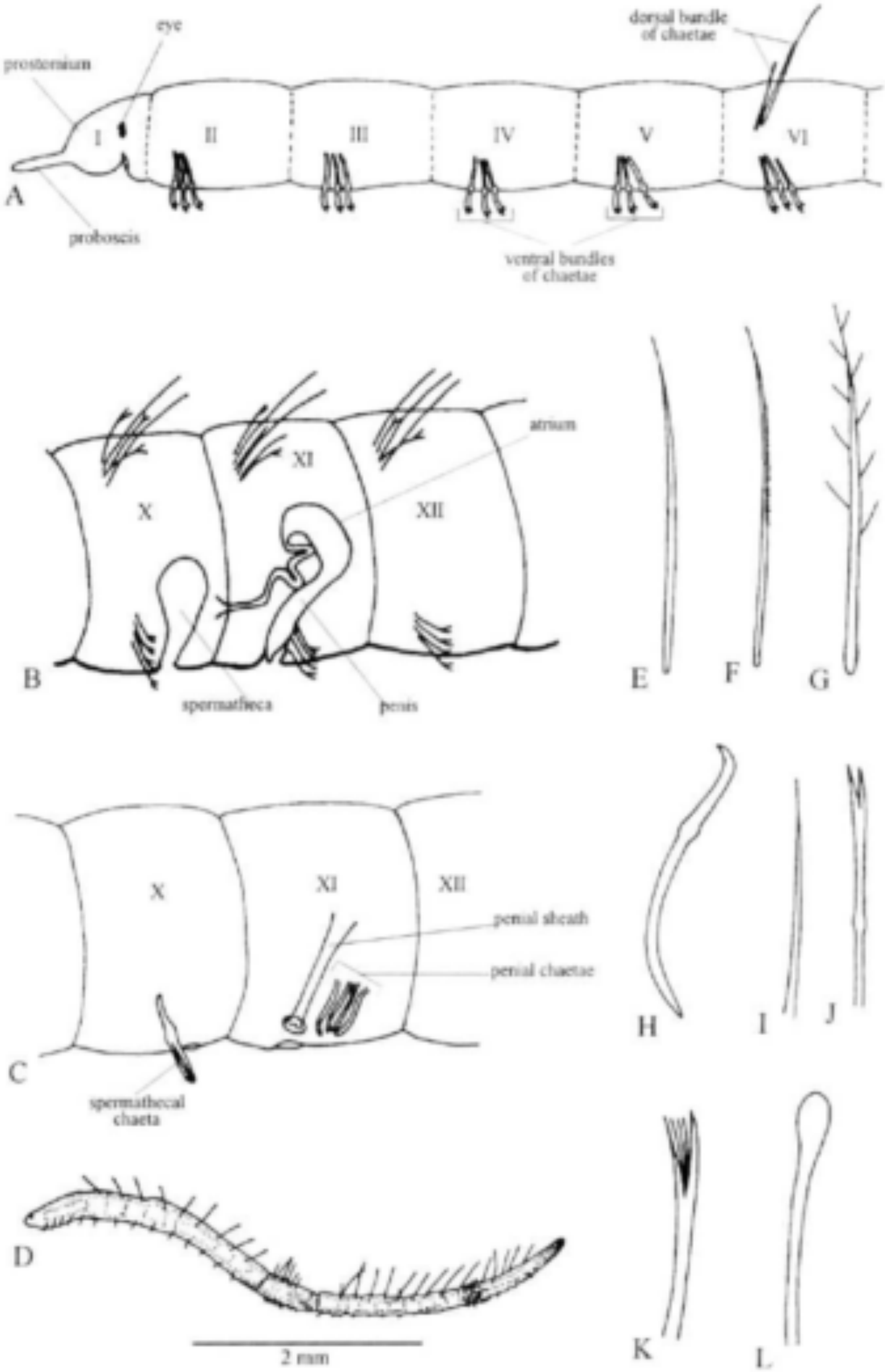

Fig. 13.1. **A**, generalized naidid, left lateral view of anterior somites. **B–C**, left lateral views of the genital somites of a generalized tubificid. **D**, a naidid undergoing fission. **E–G**, hair chaetae: **E**, simple; **F**, serrate; **G**, feathery. **H–L**, crochets: **H**, hooked; **I**, simple-pointed; **J**, bifid; **K**, pectinate; **L**, paddle-shaped. (A redrawn from Hiltunen & Klemm, 1980; B–C redrawn from Hiltunen et al., 1982).
(Note that in Figs A–C the Roman numerals refer to segment numbers).

megadriles the skin in the region of the clitellum is ridged or otherwise differentiated from the skin of the rest of the body. These areas are said to possess 'genital markings'. A single megadrile family, the Almidae, has a pair of elongated flaps called claspers that project from the body near the clitellum and are said to be involved in mating.

Important features in classifying microdrile worms are the chaetae, which may be of several types (Figs 13.1E–K). They are arranged in four bundles, two dorsolateral and two ventrolateral. The number and type of chaetae in each bundle are diagnostic. All chaetae can be divided into one of two types: hair chaetae and crochets. Crochets (Figs 13.1H–K) are sigmoid (S-shaped), usually stout, and swollen at some point along their lengths, while hair chaetae (Figs 13.1E–G) are more or less slender, elongated filaments, with no bulge in the shaft. They may be feathery (Figs 13.1F–G), bearing fine lateral hairs. Bifid crochets (Fig. 13.1J) are crochets whose distal ends are bifurcate. The form of the bifurcate teeth and their relative lengths are commonly used in identification to species. The teeth sometimes become worn or reduced so that they appear to be simple-pointed, occasionally with a trace of the reduced tooth visible. Pectinate chaetae (e.g. Figs 13.1K & 13.10A–B) are essentially bifid crochets with a series of fine intermediate teeth between the two outer teeth. The intermediate spines may be as large as the outer teeth so that the distal end is broadly palmate. Oar chaetae (e.g. Figs 13.1L & 13.8I) are flattened and paddle-shaped. All of the chaetae mentioned so far are somatic chaetae, since they have nothing to do with reproduction. In contrast, genital chaetae (Fig. 13.1C), often associated with the spermathecal or penial segments, are used to anchor the two animals in place during copulation.

COLLECTION, PRESERVATION AND EXAMINATION

Collection

Worms are easiest to see, and so to pick out from debris and sediment, when they are alive. For this reason it is advisable to leave newly-collected sediment, debris or algae in a flat white collecting dish until the worms emerge, and then pick them out with tweezers or a Pasteur pipette. Use a dissecting microscope to find small specimens. *Tubifex* and its allies usually live in foul mud. If a sample of mud containing *Tubifex* is left overnight in a container covered with a few millimetres depth of water from the site, the worms will rebuild their burrows and next morning can be seen wafting their rear ends in the water. It sometimes helps, when sorting dead specimens from dense debris, to stain the sample in 1% Rose Bengal, which stains animal tissue pink.

Preservation

Worms may be killed and preserved in 70% alcohol, although some will fragment or lose their gills. For identification, worms should be transferred to 30% alcohol, then to water and then placed on a slide in a few drops of Amman's lactophenol (prepared by adding 40g of carbolic acid to 40 ml of lactic acid, then adding 80 ml glycerol and 40 ml water). The worms should be covered with a coverslip and left in this fluid for several hours before being examined. Slight pressure on the coverslip will flatten the specimen and clear it, making the important internal features relatively easily visible under the microscope. To identify the various types of chaetae of a specimen, it is necessary to examine both the dorsal and the ventral bundles from several regions of the body. Note that it is greatly preferable to examine live specimens if possible. In particular, it is almost impossible to kill and preserve specimens of *Dero* (Figs 13.5H–N) with the gills extended, so the genus is virtually unrecognizable without reference to living specimens.

Since genital structures are found only in mature specimens, it is advisable to attempt to identify only adult worms. In this regard, Thorp & Covich (1991) note that "The various reproductive organs and modified setae that may develop close to the genital pores can best be found by looking carefully in the correct segment. ….In contrast to immature specimens, a mature worm will have an external clitellum (though this is not as prominent as that of an earthworm), and the egg and sperm sacs are full and therefore visible. The worm is often distended in the genital region."

KEY TO THE FAMILIES OF AQUATIC OLIGOCHAETES KNOWN FROM AFRICA

Sections dealing with the Naididae and Tubificidae are slightly modified from Brinkhurst (1966).

Introductory Notes

- The key to families is an artificial one. It is impossible to identify microdriles accurately without clearing them and using a compound microscope, or megadriles without cutting serial sections. This key is designed to allow separation of taxa as far as possible without sectioning and with as little dissection as possible. For this reason it will separate ONLY those species already recorded from the region. It is likely to be very misleading outside of southern Africa and for species not previously recorded in the region.

- While some oligochaetes regularly undergo asexual reproduction by fission, most are also able to regenerate after they have been damaged. Look out for specimens where heads have been regenerated because the count of somites may be abnormal.
- Where only a single species is known for the region, contents of square brackets indicate species-specific features in the key below.

KEY TO THE FAMILIES OF AQUATIC OLIGOCHAETES KNOWN FROM AFRICA

1. More than two chaetae per bundle (e.g. Fig 13.1A–C), dorsally at least (some may be very short); hair chaetae (Fig 13.1E–G) usually present but sometimes absent; worms often relatively delicate, not typically earthworm-like 2*

– One or two crochets per bundle; no hair chaetae; mostly large (>30 mm long), often sturdy, earthworm-like forms 6

2. Reproduction often asexual, resulting in chains of individuals (Fig. 13.2A), each <5 mm in length; body wall with red, greenish or yellow pigmented oil droplets; prostomium (Fig. 13.2B) ciliated **(Aelosomatidae)** (prostomium twice width of more posterior somites; 3–5 long, and 3–5 short, straight hair chaetae in each bundle) .... *Aeolosoma hemprichi* (Figs 13.2A–C)

– Reproduction sexual or asexual; length of individual usually >5 mm; body without oil droplets; prostomium not ciliated; hair chaetae in dorsal bundles, otherwise absent 3

3. Prostomium elongate; body with one median and two lateral processes terminally (Figs 13.2E–G): **Opistocystidae** [dorsal bundles with 2–4 simple hair chaetae and 2–4 feathery hairs; ventral bundles with 3–5 bifid crochets] ....
.... *Opistocysta funiculus* (Figs 13.2D–G)

– Prostomium long or short; body not terminating in one median and two terminal processes 4

4. Dorsal bundles start on somite III with 1–3 long hair chaetae and sometimes with two crochets so short that they do not emerge from the chaetal sacs; ventral chaetae start on somite II, each with a simple-pointed sigmoid crochet and a bifid crochet with a rudimentary upper tooth; adult worms 15–30 mm in length .... **Phreodrilidae** (Fig. 13.2H)

– Chaetae not arranged as above; size variable 5

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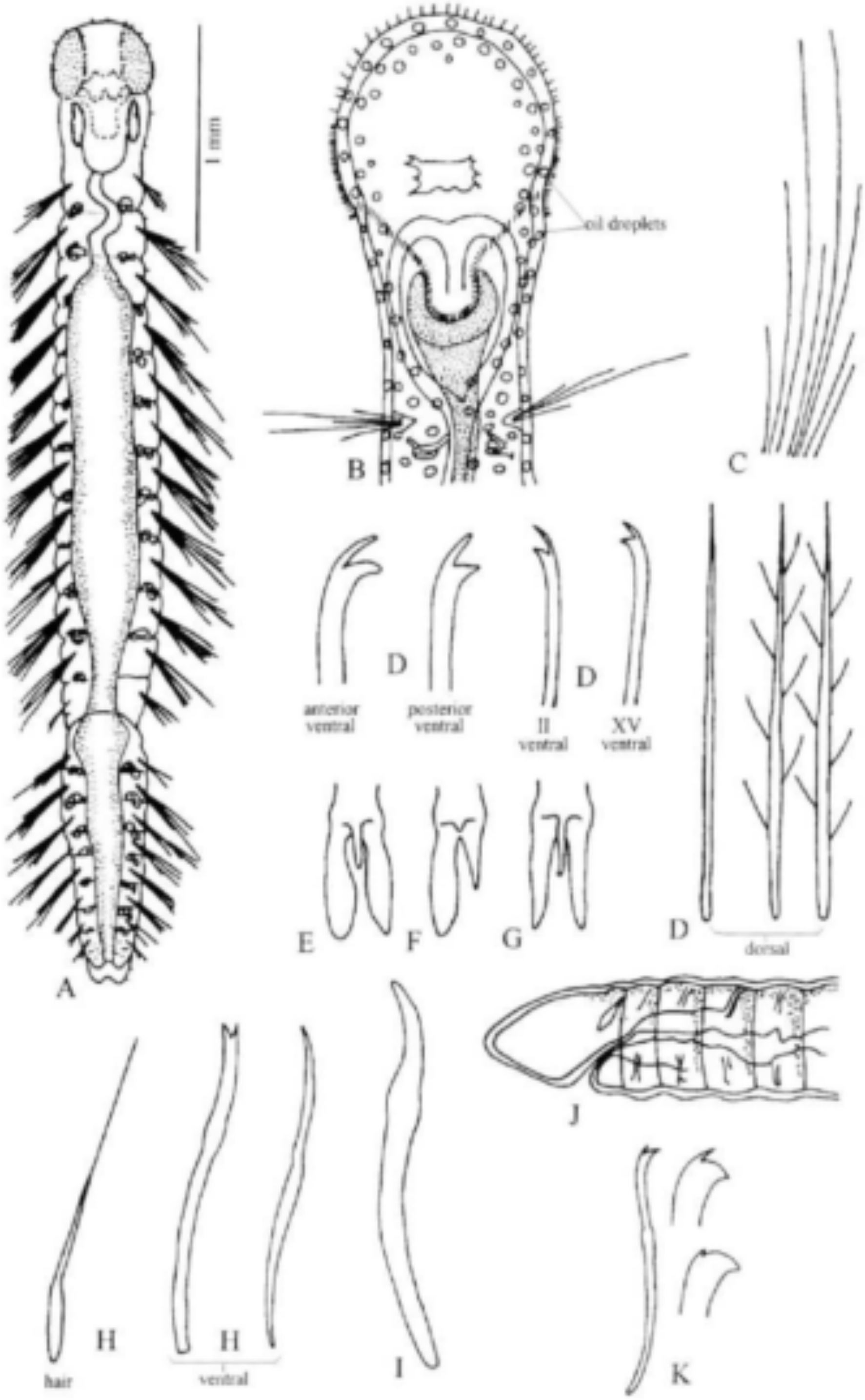
* The Family **Enchytraeidae** is not strictly aquatic but tends to inhabit stream banks, etc. Individuals are white or pink worms with two to six similar crochets per bundle (simple-pointed and sigmoid or straight) and the spermathecae opening on somite IV or V. They have not yet been recorded from southern Africa.



Fig, 13.2. A–C, Aeolosomatidae, *Aeolosoma* sp.: **A**, dorsal view of whole animal; **B**, ventral view of anterior end; **C**, dorsal bundle of chaetae. **D–G**, Opistocystidae, *Opistocysta funiculus*: **D**, chaetae; **E–G**, variation in posterior appendages. **H**, Phreodrilidae: chaetae. **I**, Haplotaxidae: larger chaetae of *Haplotaxis* sp. **J–K**, Lumbriculidae, *Lumbriculus variegatus*: **J**, anterior end in left lateral view; **K**, chaetae. (A–C redrawn from Pennak, 1989; D–K redrawn from Brinkhurst & Jamieson, 1971).

5. Reproduction often asexual, resulting in chains of individuals (e.g. Fig. 13.1D); pectinate chetae (Fig. 13.1K) rarely present in dorsal bundles; male gonopores opening between somites V and VIII; not tube-dwelling and not obviously re in colour ....**Naididae** (Figs 13.1A, 13.1D, 13.4D–13.7H

– Chains of individuals never formed; dorsal bundles usually with pectinate chaetae; male gonopores usually open on somite XI (Figs 13.1B, C); may b tube-dwelling and often red in colour when alive ....**Tubificidae** (Figs 13.1B–C, 13.8A–13.10H)

6. Claspers (Fig. 13.3G), genital markings (Fig. 13.3A–B, H, I, K–M) and/or genital chaetae (Figs 13.3D–F) present; clitellum (Figs 13.3A–B, K) extensive, usually stretching about from somite XIV to XXIV; somatic chetae simple, sigmoid (e.g. Fig. 13.1H), two per bundle ....**Glossosomatidae**, Subfamily **Alminae** (Figs 13.3A–G)

– No claspers; genital setae present or absent; clitellum and somatic chaetae variable 7

7. Gut with an eversible pharynx; clitellum extending over somites XI to XIII or XIV: **Haplotaxidae** [male pores on XI and XII; prostomium short and broad; chaetae simple-pointed, all similar] ....*Haplotaxis africanus* (Fig. 13.2I)

– Pharynx not eversible; clitellum variable 8

8. Body wall transparent, showing bright red blood vessels in living specimens; crochets (Fig.13.2K) bifid, two per bundle; male gonopores open on somite X; eggs large and yolky: **Lumbriculidae** [thin, elongate worms to 100 mm long and 1–2 mm wide; dark green pigment in anterior body wall] ....*Lumbriculus variegatus* (Figs 13.2J–K)

– Blood vessels usually not visible; crochets simple-pointed; clitellum and male gonopores variable 9

9. Clitellum extending over somites XII to XVI or XVII and including male and female gonopores; eggs large and yolky; no gizzard ....**Alluroididae** (Figs 13.3H–K)

– Clitellum extending from somites XIII to XIX or starting at or behind XXII; male pores on somite XIII, XIV or XVII 10

10. Clitellum extending from XIII to XIX or XX; male gonopores on XVII; no gizzard ....**Ocnerodrilidae** (Figs 13.3L–M)

– Clitellum extending from somites XXII to XXVI, XXVI to XXXII or XXVII to XXXIV; male gonopores on somites XIII or XV; gizzard present ....**Lumbricidae** (Figs 13.4A–C)

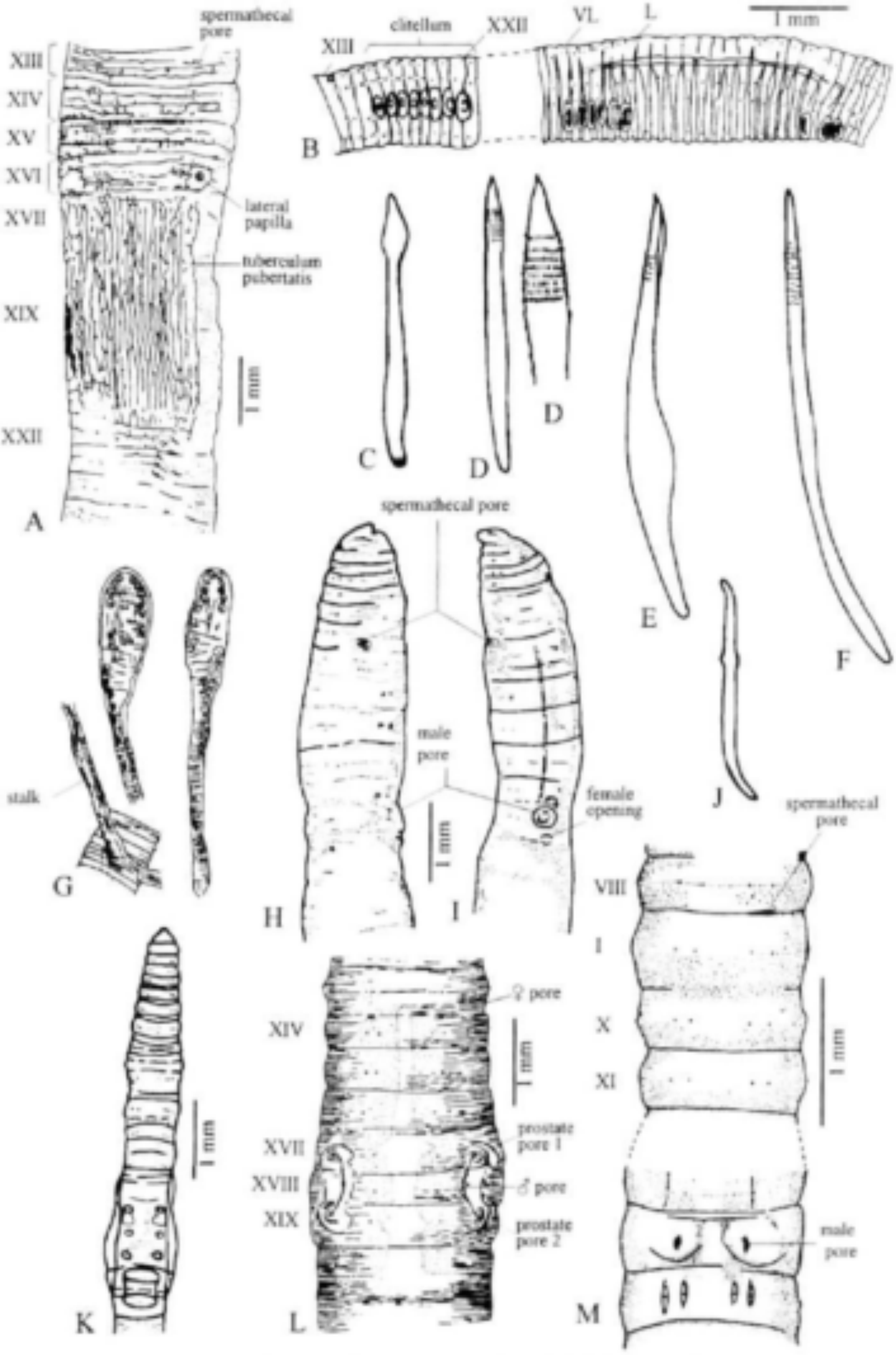


Fig. 13.3. **A–G**, Alminae (Glossosomatidae): **A**, genital field of *Callidrilus ugandensis* in ventral view; **B**, mid-body segments of *Glyphidrilus stuhlmanni* in lateral and ventro-lateral view. **C–F**, genital chaetae: **C**, *Alma emini*, **D**, *A. nilotica*, **E**, *A. millsoni*, **F**, *A. togoensis*. **G**, claspers of *Alma emini*. **H–K**, Alluroididae, *Alluroides brinkhursti*: **H**, anterior end in dorsal view; **I**, anterior end in lateral view; **J**, lateral chaeta from somite XX. **K**, anterior of *Standeria transvaalensis* in dorsal view. **L–M**, Ocnerodrilidae: **L**, genital somites of *Eukerria saltensis* in ventral view; **M**, genital somites of *Pygmaeodrilus arausiensis* in ventral view. (A–K redrawn from Brinkhurst & Jamieson, 1971; L–M redrawn from Jamieson, 1967).

KEY TO THE NAIDIDAE RECORDED FROM SOUTHERN AFRICA

This key, which is taken from Brinkhurst (1966), separates the genera and indicates which species are known from the region. A question mark in the species name indicates that the specific identity of the taxon is not confirmed. Brinkhurst also provides keys to the local species of *Pristina*, *Dero*, *Nais*, *Allonais* and *Branchiodrilus*.

1. No dorsal chaetae (three species recorded from southern Africa) .... *Chaetogaster* (Figs 13.4D–F)
– Dorsal chaetae present 2

2. Hair chaetae absent 3
– Hair chaetae (Figs 13.1E–G) present 4

3. Dorsal chaetae beginning in II; 4–12 chaetae per bundle .... *Homochaeta setosa*
– Dorsal chaetae beginning in V (*P. litoralis* and *P. frici*).................... *Paranais* (Fig. 13.4G)

4. Dorsal chaetae beginning in II 5
– Dorsal chaetae beginning in IV, V or VI (or even more posteriorly — often XVIII, XIX or XX in full-grown specimens) .... *Haemonais waldvogeli* (Fig. 13.4H)

5. Body wall covered with foreign matter adhering to secretions from cutaneous glands .... *Stephensoniana trivandra* (Fig. 13.4I)
– Body wall without foreign matter; proboscis present in several species (eight species known from southern Africa) .... *Pristina* (Figs 13.5A–G)

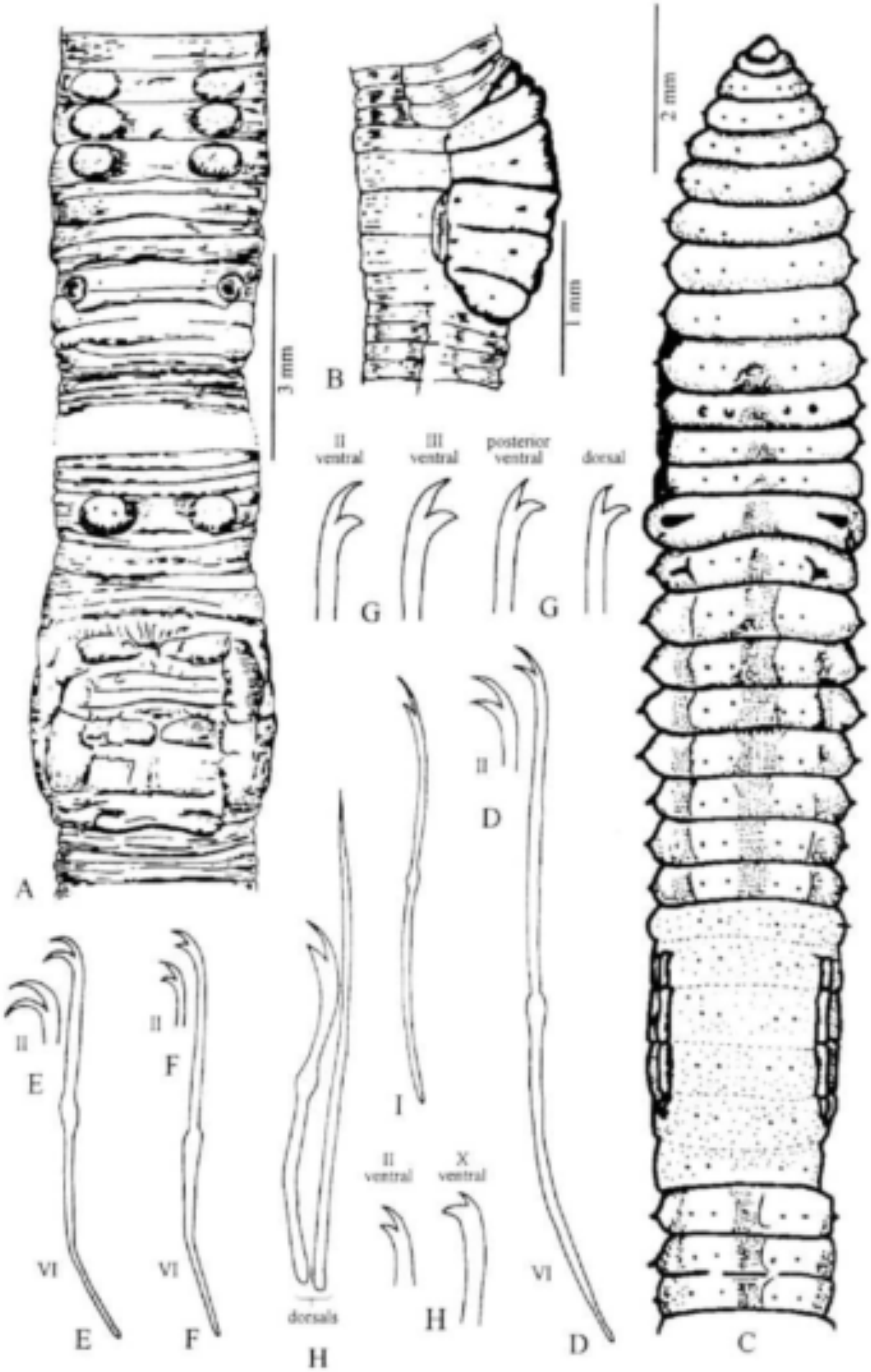


Fig. 13.4. **A–C**, Lumbricidae: **A**, genital somites of *Allolobophora caliginosa* in ventral view; **B**, clitellar somites of *Dendrobaena rubida* in ventro-lateral view; **C**, anterior somites of *Eiseniella tetraedra* in ventral view; **D–G**, chaetae of Naididae: **D**, *Chaetogaster cristallinus*; **E**, *C. limnaei*; **F**, *C. langi*; **G**, *Paranais litoralis*; **H**, *Haemonais waldvogeli*; **I**, *Stephensoniana trivandra*. (A–C from Jamieson, 1967; D–G redrawn from Brinkhurst, 1971; H redrawn from Brinkhurst & Jamieson, 1971; I redrawn from Hiltunen & Klemm, 1980).

6. Gills present (except in species parasitic on frogs' eyes) (Figs 13.5H–I, K–L, N, 13.6A) 7
– No gills 8

7. Anal gills present (Figs 13.5H–I, K–L, N) except in parasites; NB: gills usually retract and are not visible in dead animals (eight species known from southern Africa) ..... *Dero* (Figs 13.5H–P)
– Gill filaments on most segments from VI, enclosing dorsal chaetae anteriorly ..... *Branchiodrilus* (Figs 13.6A–B)

8. Prostomium extended into a long proboscis ... *Stylaria fossularis* (Fig. 13.6C)
– No proboscis 9

9. Hair chaetae of VI very long (Fig. 13.6E); body covered with a crust of foreign matter ..... *Slavina appendiculata* (Figs 13.6E–F)
– No elongate hair chaetae or crust of foreign matter 10

10. Hair chaetae stout, rigid, and at least some strongly serrated ..... *Vejdovskyella comata* (Fig. 13.6D)
– Hair chaetae smooth (e.g. Figs 13.1E, 13.7G) 11

11. Eyes usually present (e.g. Fig. 13.7A); anterior ventral chaetae of II–V often somewhat different from the rest (seven species recorded from southern Africa) ..... *Nais* (Figs 13.7A–H)
– Eyes absent; anterior ventral chaetae differ little from the rest (four species recorded from southern Africa) ..... *Allonais* (Figs 13.8A–D)

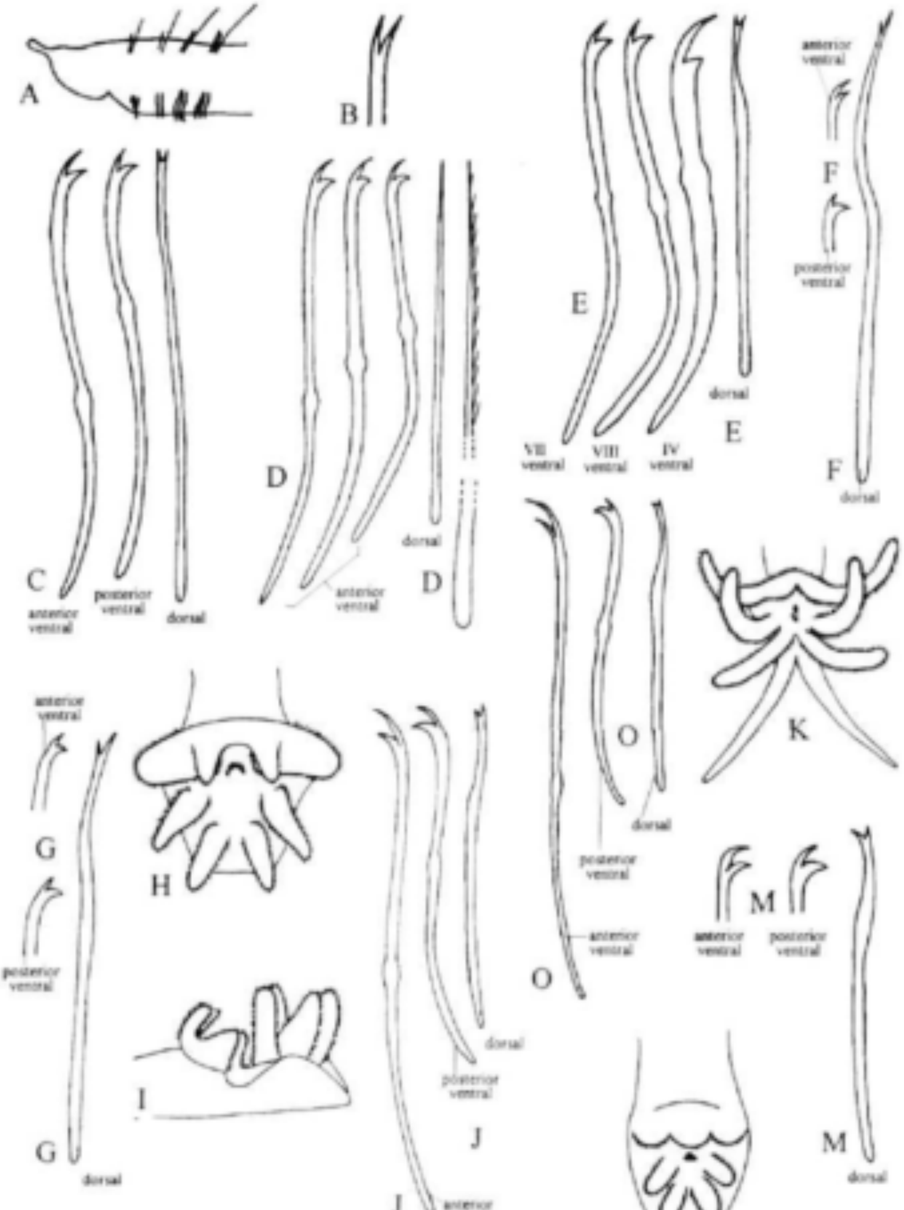


Fig. 13.5. Naididae: **A–G** *Pristina*: **A**, generalized worm with proboscis, lateral view; **B–G** chaetae: **B**, *P. bilobata*; **C**, *P. foreli*; **D**, *P. longiseta*; **E**, *P. aequiseta*; **F**, *P. menoni*; **G**, *P. amphibiotica*; **H–P**, *Dero* spp. **H–J**, *D. digitata*: **H**, posterior end in dorsal view; **I**, posterior end in lateral view; **J**, chaetae. **K–M**, *D. furcatus*: **K**, posterior end in dorsal view; **L**, posterior end in lateral view; **M**, chaeta. **N–O**, *D. obtusa*: **N**, posterior end in dorsal view; **O**, chaetae. **P**, *D. flabelliger*, chaeta. (A–G, J, M, O redrawn from Brinkhurst, 1971; H–I, K, L, N redrawn from Pennak, 1989; P redrawn from Brinkhurst & Jamieson, 1971.

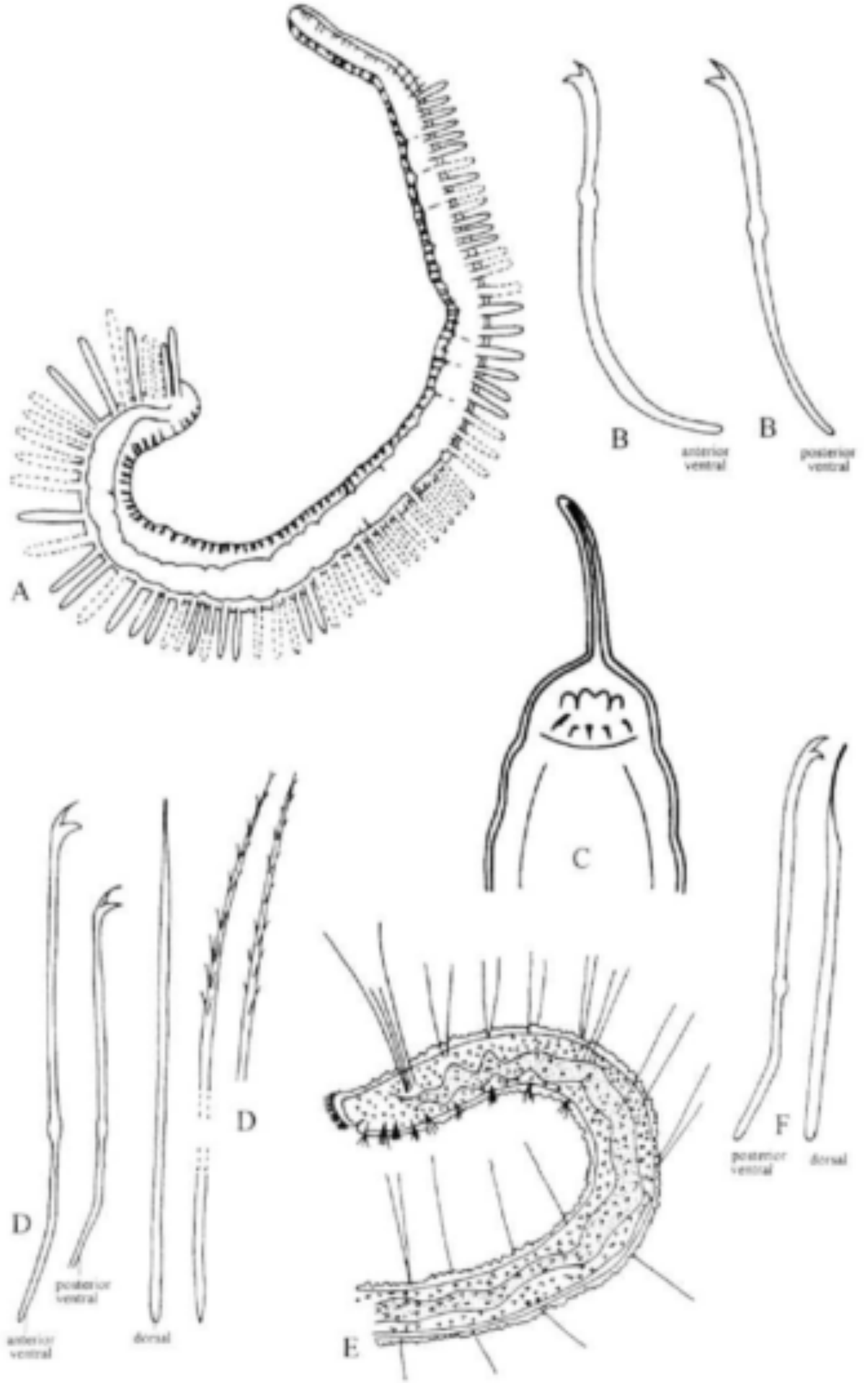


Fig. 13.6. Naididae. **A–B**, *Branchiodrilus cleistochaeta*: A, whole worm in lateral view; **B**, chaetae; **C**, *Stylaria fossularis*, anterior somites in dorsal view; **D**, chaetae of *Vejdovskyella comata*; **E–F**, *Slavina appendiculata*: **E**, anterior somites in lateral view; **F**, chaetae.
(A, B, E, F, redrawn from Brinkhurst & Jamieson, 1971; D, K redrawn from Brinkhurst, 1971).

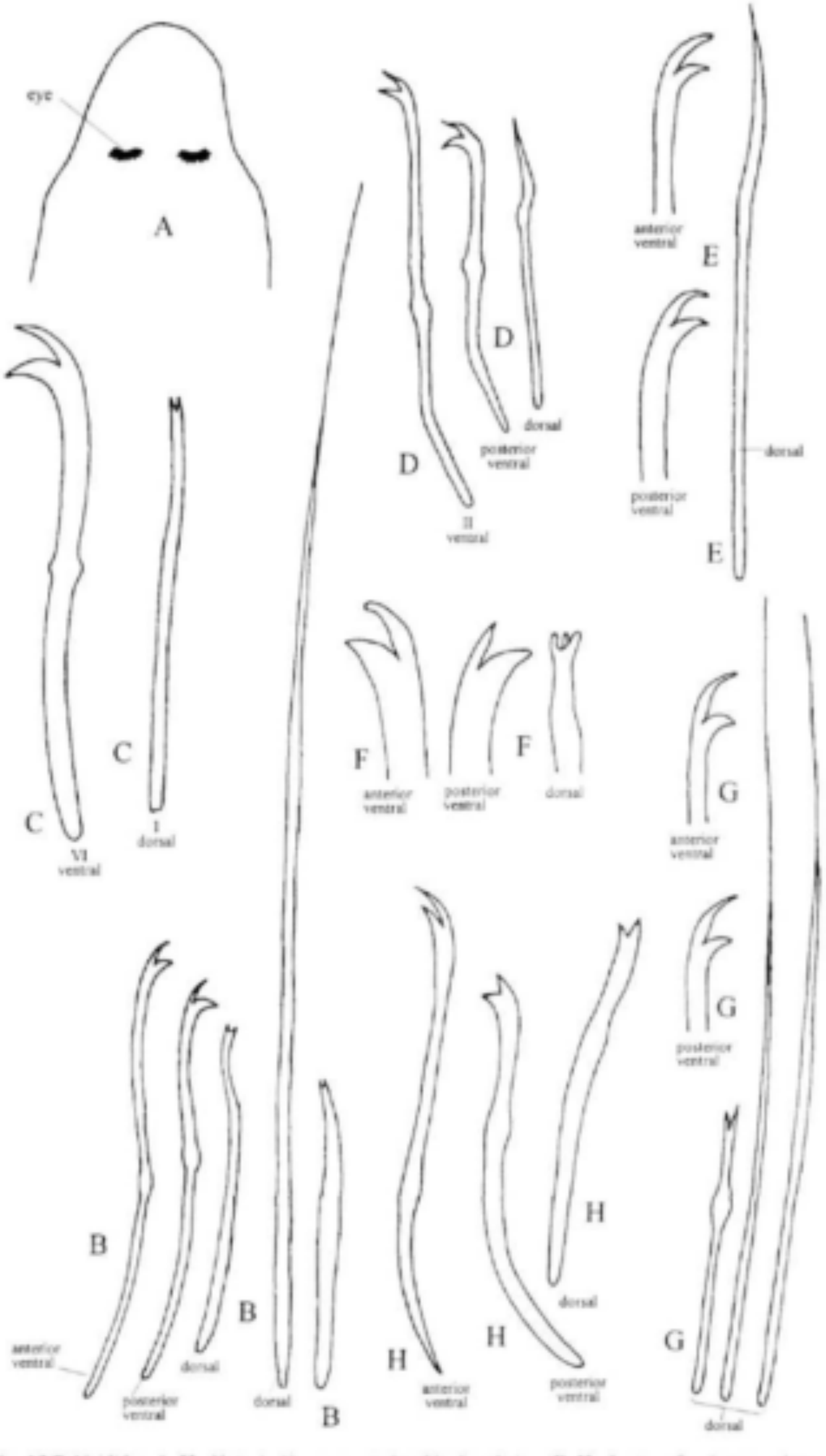


Fig. 13.7. Naididae. **A–H**, *Nais*: **A**, *N. communis*, head in dorsal view; **B–H**, chaetae of various species: **B**, *N. communis*; **C**, *N. variabilis*; **D**, *N. pseudobtusa*; **E**, *N. simplex*; **F**, *N. africana*; **G**, *N. elinguis*; **H**, *N. raviensis*. (D, F, H redrawn from Brinkhurst & Jamieson, 1971; E redrawn from Brinkhurst, 1971; B, G redrawn from Pennak, 1989; C redrawn from Hiltunen & Klemm, 1980).

KEY TO THE SPECIES OF TUBIFICIDAE RECORDED FROM SOUTHERN AFRICA

(Taken from Brinkhurst, 1966)

1. Hair chaetae present 2
– Hair chaetae absent 11

2. A fan of dorsal and ventral gill filaments on posterior segments (Fig. 13.8E); hair chaetae short, all other chaetae varying from simple-pointed to bifid or even slightly pectinate dorsally .... *Branchiura sowerbyi* (Figs 13.8E–F)
– No gill filaments; chaetae not as above 3

3. Posterior dorsal crochets between the short hairs are oar- or paddle-shaped (Fig. 13.8G), the distal ends being flattened in the plane of the teeth .... *Aulodrilus pigueti* (Fig. 13.8G)
– No paddle-shaped dorsal crochets 4

4. Dorsal (and sometimes ventral) crochets with short, thin, sometimes rudimentary upper teeth (Fig. 13.8H), sometimes duplicated .... *Aulodrilus pluriseta* (Fig. 13.8H)
– Dorsal crochets simply bifid (e.g. Fig. 13.1J) or clearly pectinate (Fig. 13.1K) 5

5. Dorsal crochets simply bifid 6
– Dorsal crochets clearly pectinate 7

6. Hair chaetae characteristically twisted distally (Fig. 13.8J); in brackish water .... *Monopylephorus irroratus* (Fig. 13.8J)
– Hair chaetae straight; in fresh water .... *Tubifex natalensis* (Fig. 13.9C–D)

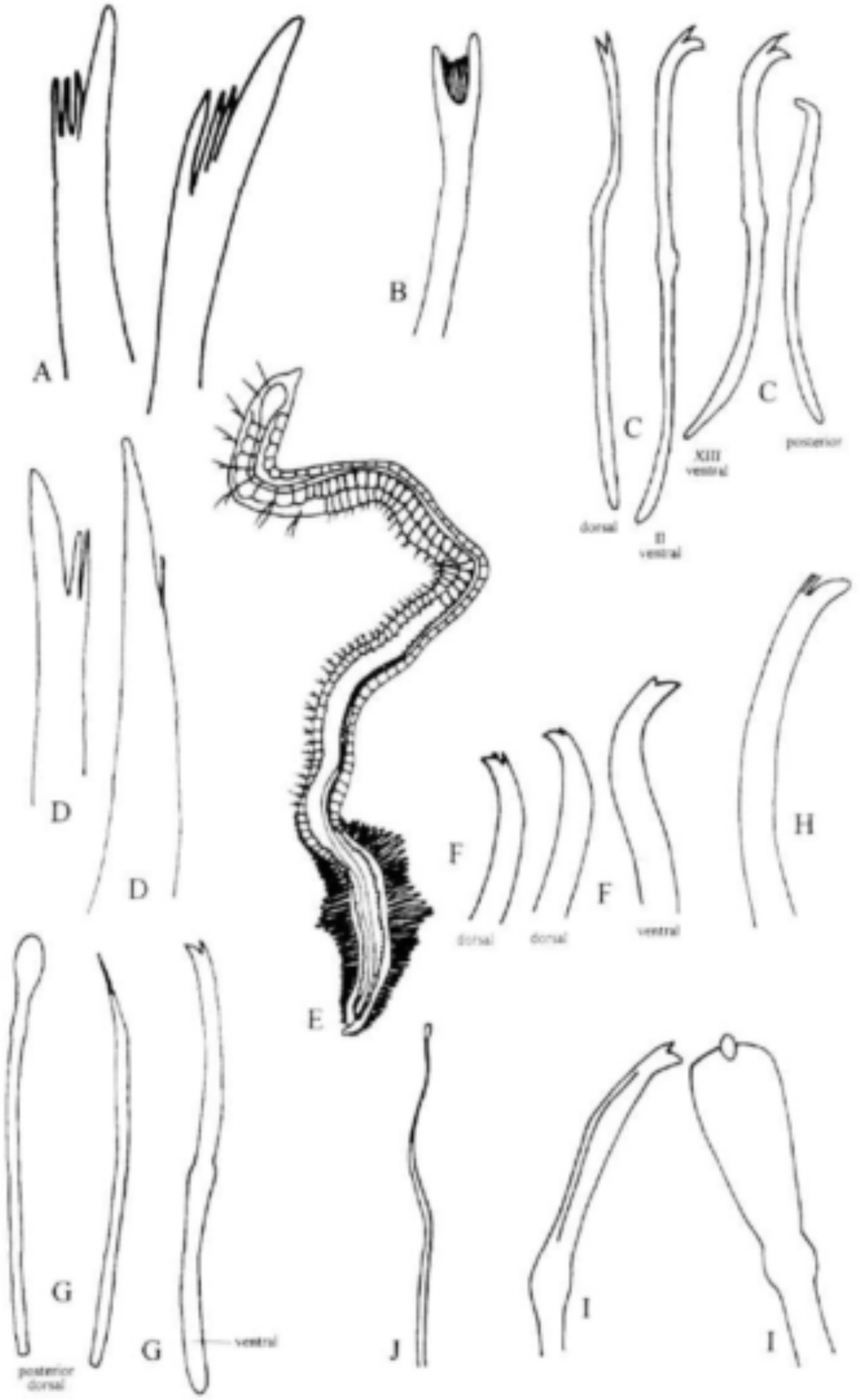


Fig. 13.8. A–D, chaetae of *Allonais* (Naididae): **A**, *A. inaequalis*; **B**, *A. pectinata*; **C**, *A. gwaliorensis*; **D**, *A. paraguayensis*; **E–J**, Tubificidae: **E–F**, *Branchiura sowerbyi*: **E**, whole worm in dorsal view; **F**, chaetae; **G–I**, chaetae of *Aulodrilus* spp.: **G**, *A. pigueti*; **H**, *A. pluriseta*; **I**, *A. limnobius*. **J**, chaetae of *Monopylephorus irroratus*. (A, B, D, H, I, redrawn from Brinkhurst & Jamieson, 1971; C, E, J, redrawn from Brinkhurst, 1966; F redrawn from Brinkhurst & Jamieson, 1971; G redrawn from Pennak, 1989).

7. Worms exceptionally thin with long hair chaetae; pectinate crochets with small U–shaped tips with only one or two intermediate teeth ....*Tubifex ignotus* (Fig. 13.9E)
– Worms broader, hair chaetae not exceptionally elongate; pectinate crochets not of this form 8

8. Anterior ventral chaetae a mixture of simple-pointed and bifid crochets; pectinate chaetae distinctive, hand-like with spaces between the teeth (Fig. 13.10A)..... ....*Epirodrilus allansoni* (Fig. 13.10A)
– Anterior ventral crochets all bifid; pectinate chaetae not as in Fig. 13.10A....9

9. Anterior ventral crochets frequently with upper tooth thinner and hardly longer than the lower tooth (Fig. 13.9F); cuticular penis sheaths conical (Fig. 13.9G)....... ....*Tubifex templetoni* (Fig. 13.9F–G)
– Anterior ventral crochets with upper tooth thinner and clearly longer than the lower (e.g. Fig. 13.9A); cuticular penis sheaths short and tub-shaped (Fig. 13.9B) or absent 10

10*. Spermathecal chaetae broad, hollow-ended (Fig. 13.10B); no cuticular sheaths on penis ....*Potamothrix hammoniensis* (Fig. 13.10B)
– Spermathecal chaetae unmodified; cuticular penis sheaths thin, tub-shaped (Fig. 13.9B) ....*Tubifex tubifex* (Figs 13.9A–B)

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*From this point onwards, only mature specimens can satisfactorily be identified with this key.

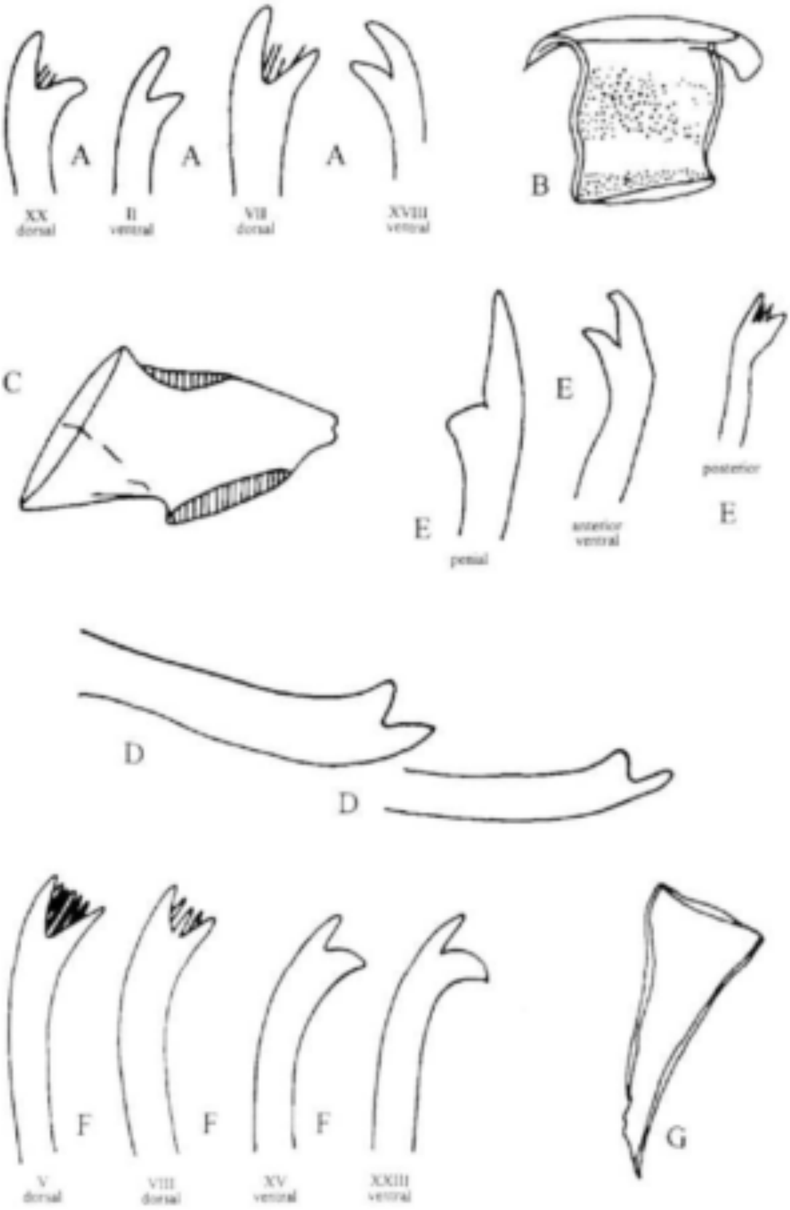

Fig. 13.9 **A–G**, *Tubifex* spp. (Tubificidae). **A–B**, *T. tubifex*. **A**, chaetae; **B**, penis sheath. **C–D**, *T. natalensis*. **C**, penis sheath; **D**, chaetae. **E**, *T. ignotus*, chaetae. **F–G**, *T. templetoni*. **F**, chaetae; **G**, penis sheath. (D redrawn from Brinkhurst & Jamieson, 1971); (A, C, F redrawn from Brinkhurst, 1966; B, G redrawn from Brinkhurst & Jamieson, 1971; G redrawn from Pennak, 1989, P redrawn from Brinkhurst, undated).

11. Penes absent 12
– Penes present, with cuticular penis sheaths (Figs 13.10F-H) 16

12. Penial chaetae absent; in freshwater 13

– Penial chaetae (e.g. Fig. 13.10D) present 14

13. Crochets with the upper tooth shorter than the lower; posterior chaetae with the shaft flattened laterally, forming wings at right angles to the (reduced) teeth (Fig. 13.8I); spermathecae paired.. *Aulodrilus limnobius*
– Crochets with upper tooth longer than the lower; no wings on the posterior chaetae; only left-hand spermatheca present.. *Monopylephorus parvus*

14. Prostomium with a dorsal pit opening to the exterior by a median dorsal pore; spermathecae absent, spermatophores attached externally to the body wall .... *Bothrioneurum vejdovskyanum* (Fig. 13.10D)
– No prostomial pit; spermathecae present 15

15. Penial chaetae with knobbed tips grouped closely; vasa deferentia short, entering atrium laterally, atrium broadly pear-shaped; freshwater species .... *Rhyacodrilus stephensoni* (Fig. 13.10C)
– Penial chaetae not well known; vas deferens short, atrium tubular; in brackish water .... *Monopylephorus africanus*

16. Crochets with the upper tooth longer and broader than the lower tooth (Fig. 13.10E); penis sheaths (Fig. 13.10F) short, one to four times longer than broad with a simple flange distally.................... *Limnodrilus udekemianus* (Figs 13.10E–F)
– Crochets with upper tooth longer or shorter than the lower tooth but no broader; penis sheaths more than one to four times as long as broad (Figs 13.8G–H) 17

17. Penis sheaths 1–14 times as long as broad (Fig. 13.10G), tip variable but commonly with the distal aperture at right angles to the shaft .... *Limnodrilus hoffmeisteri* (Fig. 13.10G)
– Penis sheaths 17–43 times as long as broad (Fig. 13.10H), tip basically triangular with the distal aperture in line with the shaft .... *Limnodrilus claparedianus* (Fig. 13.10H)

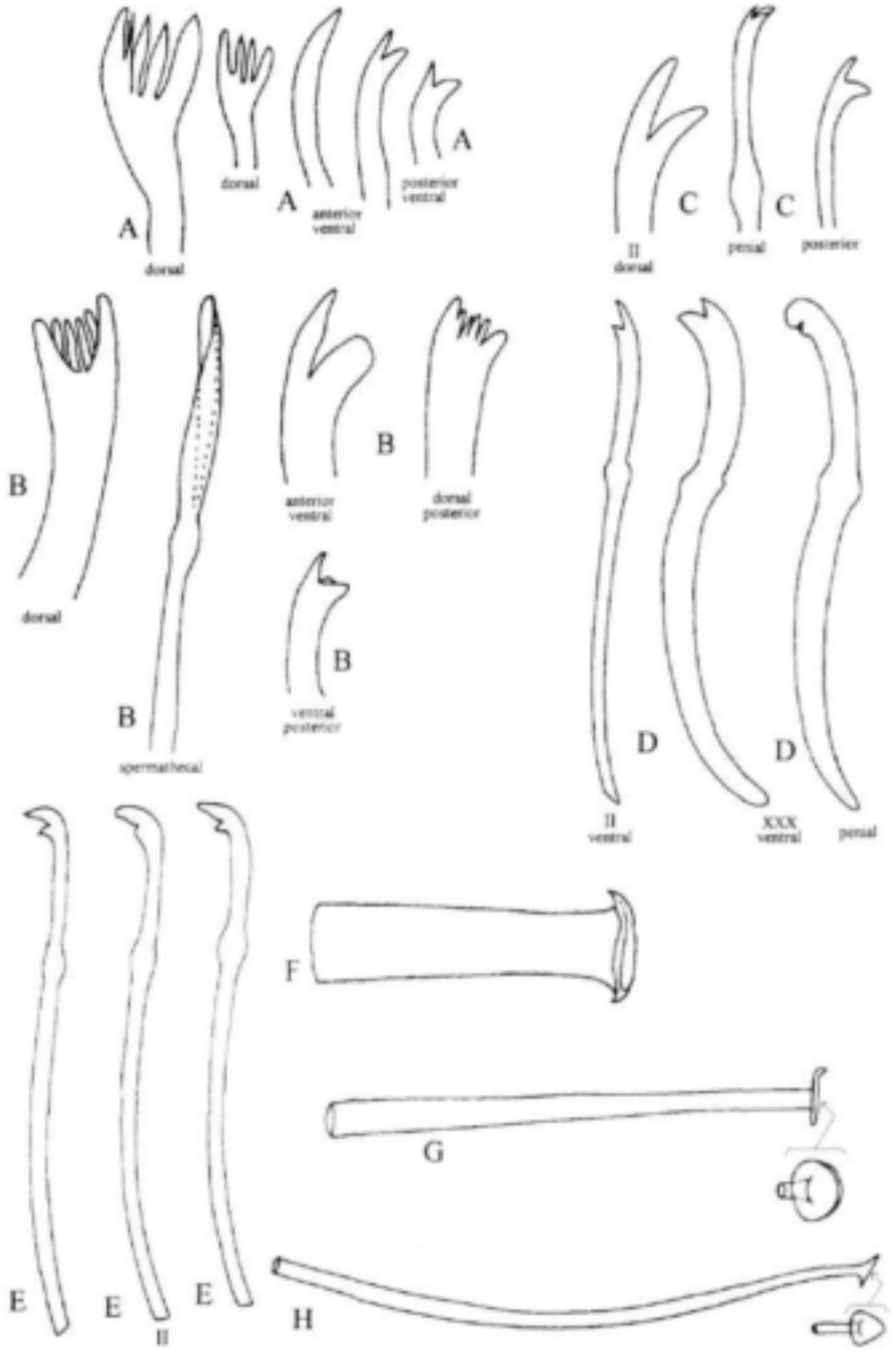

Fig. 13.10. Tubificidae. **A**, chaetae of *Epirodrilus allansoni*; **B**, chaetae of *Potamothrix hammoniensis*; **C**, chaetae of *Rhyacodrilus stephensoni*; **D**, chaetae of *Bothrioneurum vejdovskyanum*; **E–H**, *Limnodrilus* spp.: **E**, ventral chaetae of *L. udekemianus*; **F–H**, penis sheaths: **F**, *L. udekemianus*; **G**, *L. hoffmeisteri*; **H**, *L. claparedianus*. (A, C redrawn from Brinkhurst & Jamieson, 1971; B redrawn from Brinkhurst (undated); D–H redrawn from Hiltunen et al., 1982).

NOTES ON SOUTHERN AFRICAN OLIGOCHAETES

The following are the species of African freshwater oligochaetes listed by Brinkhurst (1966), Jamieson (1967) and Brinkhurst & Jamieson (1971). Brinkhurst identified material collected by the Council for Scientific & Industrial Research (CSIR) (Pretoria) in the 1950s and 1960s from a number of rivers throughout South Africa but in his publications he seldom indicates the exact localities from which the species were recorded. He indicates that his type material was deposited in the Transvaal Museum (Pretoria, Gauteng), so the reader interested in detailed distribution records will need to consult that institution. Geographical localities have been given present-day names (see the list of abbreviations on page 280) except where this might be misleading because the positions of political boundaries have changed. Uncertain identifications are not listed here.

Collecting efforts to the north of South Africa have been sporadic, so some records appear to indicate rather haphazard distributions throughout the continent. This phenomenon is probably an artefact of patchy collecting effort and, in some cases, also the effect of accidental introductions of northern-hemisphere species.

NOTE: the term 'megadrile' is sometimes used to refer to the larger, more terrestrial and more earthworm-like oligochaetes of the suborder Lumbricina and 'microdrile' to the others, which are generally smaller, more delicate, and more likely to be aquatic. Sciacchitano (1960) records a number of species of megadriles from wet but not waterlogged habitats. These are not listed below.

Family **Aeolosomatidae**

Figs 13.2A–C

A small cosmopolitan family of about 20 species of tiny, ciliated, strictly aquatic worms, possibly not even true annelids. Few species have been described but Brinkhurst (1966) considered that many further species are to be found in Africa and elsewhere. *Aeolosoma hemprichi* Ehrenberg, 1831, a cosmopolitan species with individuals up to 2 mm in length, was recorded many years ago from the Sudan, East Africa and the Congo. It is known from fresh and brackish water.

Order **LUMBRICULIDA**

Family **Lumbriculidae**

Figs 13.2J–K

Small, slender worms, mostly < 40 mm long; body more or less transparent when alive, showing bright red blood vessels. Mostly a northern-hemisphere family, semi-aquatic to aquatic, with about 12 genera and many species. Only one species has been recorded from the southern hemisphere, and that only from southern Africa: *Lumbriculus variegatus* (Müller, 1774), from Gauteng, the Eastern Cape and the Western Cape; it may well be a vagrant, introduced accidentally.

Order **TUBIFICIDA**

Several families of mostly small, slender, aquatic 'microdrile' oligochaetes.

Family **Enchytraeidae**

'Potworms': a large cosmopolitan family, with more than 20 genera, most species of which are marine or terrestrial. The taxonomy of the freshwater forms, at least, requires revision. No African records are easily available.

Family **Naididae**

Figs 13.1A, D, 13.4D–13.8D

The naidids form a large and important family of about 20 genera of small worms. Most do not reach a length of 10 mm, although adults of a few species may reach 75–80 mm. Reproduction may be by budding, the resulting specimens not always having complete heads; chains of budding individuals may be found. Many, if not most species, are cosmopolitan.

Chaetogaster

Figs 13.4D–F

A cosmopolitan genus of six species, including the mostly northern-hemisphere *C. cristallinus* Vejdovsky, 1883 and *C. langi* Bretscher, 1896, both of which are also known from Ethiopia; and the minute (<2.5 mm), cosmopolitan *C. limnaei* von Baer, 1827, which lives commensally on snails; in Africa it has been recorded from the Durban area (KZN).

Paranais

Fig 13.4G

A cosmopolitan genus of five species, some of which seem to prefer the brackish water of estuaries. Both species recorded from South Africa are also known from Europe and North America. *Paranais littoralis* (Müller, 1784) occurs in southern and eastern Cape estuaries and *P. frici* Hrabě, 1941 in the lower Zinkwazi River (KZN) and the Umhlatazana Estuary (KZN) in fresh and brackish water.

Nais
Figs 13.7A–H

A large cosmopolitan genus with about 15 species, seven of which have been recorded from Africa. Their distributions are listed in Table 13.1.

Table 13.1. Distribution records for species of *Nais* from Africa

Species	**Global distribution**	**African records**
N. communis Piguet, 1906* Figs 13.7A–B	cosmopolitan	SA (widespread), Mt Kenya, Lake Volta
N. variabilis Piguet, 1906* Fig. 13.7C	cosmopolitan	SA (widespread), Mt Kenya
N. simplex Piguet, 1906 Fig. 13.7E	Europe, N. America	Madagascar, Lake Volta, GT
N. elinguis Müller, 1773 Fig. 13.7G	cosmopolitan	MPL, WC, KZN, GT, common in polluted water
N. raviensis Stephenson, 1914 Fig. 13.7H	Asia	Kenya, Zimbabwe
N. pseudobtusa Piguet, 1906 Fig. 13.7D	Europe, N. America	Namibia
N. africana Brinkhurst, 1966 Fig. 13.7F	southern Africa	eastern parts of South Africa to Port Elizabeth (EC)

* Of *N. communis* Piguet, 1906, Brinkhurst notes that "many specimens observed by the CSIR collections belong to this species or to *Nais variabilis* Piguet, 1906, which are very difficult to separate in preserved materials".

Slavina
(Figs 13.6E–F)

A small genus of four species, mostly from South America, and characterized by papillae covering the body. *Slavina appendiculata* (Udekem, 1855) is cosmopolitan but in Africa has been recorded only from Berg River (WC), where it is common.

Vejdovskyella
(Fig. 13.6D)

A small genus of two species. *Vejdovskyella comata* (Vejdovsky, 1883) is known from Europe, Asia and North America, and has been recorded from the middle Berg River (WC) (*V. hellei* Brinkhurst & Jamieson, 1971, occurs in brackish water in Alaska).

Stylaria

(Fig. 13.6C)

Stylaria is one of the relatively few genera of oligochaete with an elongate proboscis. One species is recognized: *S. fossularis* Leidy, 1852, known from Asia and North America, and from the lower Berg River (WC).

Branchiodrilus

(Figs 13.6A–B)

Three species are recognized, from Asia, Africa and Australasia. *B. hortensis* (Stephenson, 1910), from Asia, Australia and the Sudd region of the Nile River in Sudan, has gills on most segments. Brinkhurst suggests that material from Lakes Kariba (ZIM) and Volta may belong to this species. *Branchiodrilus cleistochaeta* Dahl, 1957, from Cameroon, has gills on most segments.

Dero

Figs 13.5H–P

Dero is a large cosmopolitan genus of some 40 species, several of which (subgenus *Allodero*) are commensal or parasitic on or in amphibians; several others (subgenera *Dero* and *Aulophorus*) construct tubes, which may be clear or have foreign material adhering to them. Several species bear one or more pairs of gills in the posterior branchial fossa. Some information on African species is given in Table 13.2.

Table 13.2. Notes on the species of *Dero* recorded from Africa

Species	**Global distribution**	**African records**	**Comments**
D. (Allodero) bauchiensis (Stephenson, 1930)	Africa	Nigeria and Mozambique	parasitic on frogs (*Phrynomerus* spp.)
D. digitata (Müller, 1773) Figs 13.5H–J	cosmopolitan	Sudd region of the Nile in Sudan; Lakes Volta and Kariba; many records from SA	usually 4 pairs of gills
D. cooperi Stephenson, 1932	? (synonmy confused)	Abyssinia	4 pairs of small gills
D. nivea Aiyer, 1930	Europe, Asia	Free State, Vaal River	3 pairs of small gills
D. obtusa Udekem, 1855 *Figs 13.5N–O*	cosmopolitan	MPL, Swartkops River (EC)	2–3 pairs of gills
D. (Aulophorus) furcatus Schmarda, 1861 Figs 13.5K–M	cosmopolitan	Lakes Kariba and Volta; widespread in SA	3–4 pairs of gills
D. (Aulophorus) tonkinensis (Vejdovsky, 1894)	S & E Asia	Kenya, Madagascar	2 pairs of long, cylindrical gills
D. (Aulophorus) flabelliger Stephenson, 1931 Fig 13.5P	Australia, China	Kenya, Lake Volta	3 pairs of long cylindrical gills, 1 pair of palps

Allonais

(Figs 13.8A–D)

A genus of six species, found on all continents but Europe. Four of the six species are represented in Africa and/or Madagascar: *A. inaequalis* (Stephenson, 1911) from Asia, South America, KwaZulu–Natal and Mpumalanga; *A. pectinata* (Stephenson, 1910) from Asia, Abyssinia, the Sudan, Madagascar and, in South Africa, the Swartkops River (EC) and Vaal Dam (GT); *A. paraguayensis* (Michaelsen, 1905) from Asia, North and South America, Madagascar and widespread in Africa from Egypt to the Western Cape, including Lakes Volta and Kariba; and *A. gwaliorensis* (Stephenson, 1920) from Asia and Madagascar.

Stephensoniana

Fig 13.4I

A monospecific genus, *S. trivandra* (Aiyer, 1926) is known from India, the Middle East and KwaZulu–Natal.

Pristina

Figs 13.5A–G

A large cosmopolitan genus of more than 20 species of tiny worms, usually less than 10 mm long. Individuals of many species are characterized by a proboscis formed by the elongation of the prostomium. Some details of the 11 species recorded from Africa are given in Table 13.3.

Family **Tubificidae**

Figs 13.1B–C, 13.8E–13.10H

A large and important family with more than 20 genera and some hundreds of species. Most are freshwater forms but some are marine. Certain freshwater species are able to thrive in waters grossly polluted by organic matter.

Tubifex

Figs 13.9A–G

The genus *Tubifex* is commonly found in organically polluted waters. Three species are known from South Africa: *Tubifex tubifex* (Muller, 1774) from the former Transvaal and KwaZulu–Natal; *T. ignotus* (Štolc, 1886) a single record from KZN; and *Tubifex natalensis* Brinkhurst, 1966, known only from the Umhloti River (KZN). The specific identity of specimens resembling *T. templetoni* from Gauteng and the Western Cape is not certain.

Table 13.3. Notes on the species of *Pristina* recorded from Africa

Species	Global distribution	African records	Comments
P. minuta (Stephenson, 1914)	India, Brazil	Vaal River; KZN	length 2 mm; no proboscis
P. jenkinae (Stephenson, 1931)	S. America	Kenya, Abyssinia	2–3 mm; no proboscis
P. synclites Stephenson, 1925	S. Asia	KZN; Lakes Kariba and Volta	5–7 mm; short proboscis
P. foreli (Piguet, 1906) Fig. 13.5C	Europe, Turkestan	GT, KZN, WC	2–7 mm; proboscis present
P. aequiseta Bourne, 1891 Fig. 13.5E	cosmopolitan	Madagascar; eastern parts of SA	2–8 mm; proboscis present
P. longiseta Ehrenberg, 1828 Fig. 13.5D	Europe, Asia	Madagascar, E. Africa, WC, KZN	3–5 mm; proboscis present
P. proboscidea Beddard, 1896	S. America, Asia	Zanzibar	2–5 mm; proboscis present
P. bilobata (Bretscher, 1903) Fig. 13.5B	Europe, Middle East	Cameroon	1–4 mm; no proboscis
P. amphibiotica Lastočkin, 1927 Fig. 13.5G	Europe	Cameroon	3–6 mm; no proboscis
P. menoni (Aiyer, 1930) Fig. 13.5F	India, Europe	Cameroon	7 mm; no proboscis

Limnodrilus

Figs 13.10E–H

Limnodrilus consists of about 12 species, most of which are cosmopolitan in distribution. Three of the cosmopolitan species are known from southern Africa: *L. hoffmeisteri* Claparède, 1862, one of the commonest oligochaetes in the world and widespread in South Africa; *L. udekemianus* Claparède, 1862, less common but still widespread in South Africa; and *L. claparedianus* Ratzel, 1868, recorded from the Vaal Dam catchment and KwaZulu–Natal.

Potamothrix

Fig. 13.10B

A genus of about ten species of small individuals, mostly Holarctic, but one species is also known from Australasia and two from Africa: *P. heuscheri* (Bretscher, 1900), also known from Europe and Israel, and *P. hammoniensis* (Michaelsen, 1901), an Holarctic species also found in the Vaal River.

Rhyacodrilus

Fig. 13.10C

A cosmopolitan genus of about 12 species. *R. stephensoni* Černosvitov, 1942 has been found in Sirkelsvlei on the Cape Peninsula, the only record from Africa; the only other record for the same species is from Tibet.

Branchiura

Figs 13.8E–F

Branchiura is a monotypic genus, cosmopolitan in distribution, and characterized as the only tubificid bearing gills. *B. sowerbyi* Beddard, 1892 is common throughout South Africa.

Monopylephorus

Fig. 13.8J

A cosmopolitan genus of about seven species, mostly from brackish waters. Those recorded from Africa are the northern-hemisphere *M. parvus* Ditlevsen, 1904, found in the Swartkops Estuary; and the cosmopolitan brackish-water species *M. irroratus* (Verrill, 1873), found in an estuary in Morocco. The generic position of '*Monopylephorus*' *africanus* Michaelsen, 1913, originally described from 'Witpoort' in the former Transvaal, is uncertain.

Bothrioneurum

Fig. 13.10D

A cosmopolitan genus of about four species, seemingly commonest in South America. *B. vejdovskyanum* Štolc, 1888, a cosmopolitan species, is widespread in streams in South Africa and has also been recorded from Kenya. *B. aequatorialis* (Michaelsen, 1935) has been recorded only from the Congo.

Aulodrilus

Figs 13.8G–I

A small cosmopolitan genus of five species. Both species known from Africa have cosmopolitan distributions, *A. limnobius* Bretscher, 1899 also being recorded from several coastal rivers in KwaZulu-Natal and *A. pigueti* Kowalewski, 1914 from lagoons near Durban (KZN), from swamps on the upper Nile, and from Lake Kariba (ZIM).

Epirodrilus

Fig. 13.10A

A small genus of only four species, two from Europe, one from lake Titicaca in South America, and *E. allansoni* Brinkhurst, 1966 from the Vaal River near Warrenton (NC).

Limnodriloides

A genus of only four marine species, adults small, <20 mm in length. The genus is mentioned here because *L. winckelmanni* (Michaelsen, 1914) is known only from the intertidal of Swakopmund in Namibia.

Family **Phreodrilidae**

Fig. 13.2H

A monogeneric southern hemisphere family with fewer than 20 species; also known from Sri Lanka. Two species are known from Africa. *Phreodrilus niger* (Beddard, 1891) is known from Tierra del Fuego and the Falkland Islands, and in South Africa is widespread in the Western Cape; also found in the catchment of the Vaal Dam. *Phreodrilus africanus* (Goddard & Malan, 1913) is known only from the mountains above Stellenbosch (WC).

Family **Opistocystidae**

Figs 13.2D–G

This family is also monogeneric, with fewer than 10 species, all bar one species apparently confined to the Americas, where they are rare. The genus has been recorded from Africa but its specific status is questioned. *Opistocysta funiculus* Cordero, 1948, with a long prostomium, is known from Argentina and Brazil, and may be the species recorded from the White Nile.

Order **HAPLOTAXIDA**

This order contains the earthworm-like forms, sometimes called the 'megadriles', which are mostly large, terrestrial forms.

Family **Haplotaxidae**

Fig. 13.2I

A cosmopolitan freshwater and semi-terrestrial family with one genus and about 15 species, mostly Eurasian and Australasian. A single species, *Haplotaxis africanus* (Michaelsen, 1905), is known from Simonstown (WC) and Australasia.

Family **Alluroididae**

Figs 13.3H–K

This small family, which consists of three genera and a handful of species, seems to be confined to Africa south of the Sahara, and to South America.

Alluroides

Figs 13.3H–J

The genus *Alluroides*, with four species, seems to be an African endemic. *A. pordagi* Beddard, 1894 has been recorded from several countries in

Central Africa, *A. brinkhursti* Jamieson, 1968 from Ethiopia, *A. ruwenzoriensis* Brinkhurst, 1964 from Uganda and *A. tanganyikae* Beddard, 1906 from Lake Tanganyika.

Standeria

Fig. 13.3K

The only species is *Standeria transvaalensis* Jamieson, 1968, known only from Lake Chrissie (MPL).

Syngenodrilus

The only species is *Syngenodrilus lammensis* Smith & Green, 1919 from Kenya.

Subfamily **Alminae**

This subfamily, which seems to be represented mostly in the tropics, consists of five genera from tropical Africa and the Nile basin, Central and South America, and south-east Asia. They are largely or entirely aquatic.

Callidrilus

Fig. 13.3A

Individuals are fairly large, reaching 200 mm or more. Two species are known in the genus, both from Africa: *C. scrobifer* Michaelsen, 1890, from Mozambique, Tanzania and Malawi; and *C. ugandensis* (Jamieson, 1963) from Kenya and Lake Victoria.

Glyphidrilus

Fig. 13.3B

Glyphidrilus contains 15 species, all but one of which is known only from south-east Asia. *G. stuhlmanni* Michaelsen, 1935, though, has been recorded only from Tanzania.

Alma

Figs 13.3C–G

Thirteen species, all from Africa north of the Zambezi. Adult individuals of most species are relatively large (>100 mm). *Alma emini*, which is widespread in Central Africa, is the only species to reach as far south as the Zambezi River.

Family **Lumbricidae**

Figs 13.4A–C

The family Lumbricidae is essentially terrestrial but a few species (three in South Africa) have been collected often enough to suggest that they occur routinely in aquatic ecosystems. Other species will, of course, be found sporadically on ephemerally flooded lands.

Eiseniella

Fig. 13.4C

Eiseniella tetraedra (Savigny, 1826), a small cosmopolitan earthworm, has been recorded in rivers in the Port Elizabeth district (EC), the Cape Flats (WC) and the Jukskei River (GT). Specimens measured 34–59 mm in length.

Dendrobaena

Fig. 13.4B

Dendrobaena rubida (Savigny, 1826), a very common earthworm worldwide, is known from terrestrial localities in South Africa and also occasionally from aquatic biotopes, having been found in the Berg River (WC), and the Umgeni River (KZN).

Allolobophora

Fig. 13.4A

Allolobophora caliginosa (Savigny, 1826), said by Jamieson to be 'probably the most widespread and abundant earthworm', is widespread in South Africa, and known from Namibia, but has been collected from aquatic ecosystems only in the Eerste River catchment (WC) and the Umgeni River (KZN).

Family: **Ocnerodrilidae**

Figs 13.3L–M

A circumtropical family of earthworms, mostly terrestrial.

Eukerria

Fig. 13.3L

Eukerria saltensis (Beddard, 1895) is seemingly a Gondwanan endemic earthworm, found in both aquatic and terrestrial ecosystems, and known from South America (mostly), southern Asia and Australia; in South Africa it is widespread in rivers of the Western Cape and is known from the Vaal River Catchment.

Pygmaeodrilus

Fig. 13.3M

Pygmaeodrilus arausiensis Michaelsen, 1910 is known only from southern Africa, having been recorded from the Grootfontein region (NAM), the Sabie River (MPL), the Free State and the Vaal River Catchment.

ACKNOWLEDGEMENTS

We are grateful to Caryn Manicom for redrafting all the figures in this chapter.

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CHAPTER 14

HIRUDINEA

by

J. H. Oosthuizen† & M. E. Siddall

The leeches of southern Africa received very little attention from taxonomists and limnologists until the latter part of the 20th Century. The principal reason for this is not entirely clear, because leeches are by no means uncommon in southern African waters, and it has long been known that they are potential indicator species for certain water quality parameters such as heavy metal contamination and dissolved oxygen content. That being said, there are not many leech systematists in the world to draw upon for knowledge, and without a thorough grasp of the internal and external distinguishing characteristics, identifying leeches to species, or even to genus, can be a daunting task. A major reason for this is the relatively uniform external appearance of leeches particularly when specimens are not properly prepared for examination. It is, therefore, not surprising that very little published information was available on the representatives of this group in southern Africa prior to Oosthuizen's work (cut short by his untimely death).

Leeches were well known for their 'medicinal' uses in the 18th and 19th centuries when they were used for many purposes, such as alleviating headaches and reversing obesity. It is unlikely that any of these treatments were successful, but leeches are now experiencing a renaissance in medicine and pharmacology: they are the tools of choice for treating post-operative haematomas in microsurgery, and their powerful salivary anticoagulants are being studied for uses in heart disease and even cancer treatments.

There are approximately 50 species of leeches in four families in southern Africa and it comes as a surprise to many people that most bloodfeeding (haematophagous) leeches are not parasitic on humans. Most species feed on frogs, turtles, fishes, or wading birds.

Leeches are found in almost any aquatic habitat in southern Africa except in extremely fast-flowing water (as in the Drakensburg) or seasonally intermittent water (as in Namaqualand). Their favoured habitats (where they may sometimes be found in abundance) are lakes, ponds, swamps and shallow, slow–moving streams.

COLLECTION, FIXATION AND PRESERVATION OF LEECHES

Collection

It is advisable to concentrate collection effort on bodies of water known to host vertebrate fauna, such as fish, frogs and waterbirds, that are normally preyed on by leeches.

The best method of collecting leeches in almost any body of water is to turn over rocks, stones, and other submerged debris like dead branches, in still or slow-moving bodies of water. Most leeches are nocturnal in their habits and so are usually found hiding under such items during the day. Moreover, the glossiphoniid leeches (which are abundant in southern Africa) can often be found brooding their young on the underside of smooth surfaces. Decaying or rotting wood is a poor substrate for leeches, whereas freshly waterlogged wood, and smooth stones are ideal. This makes sense if one considers that leeches maintain their position using a caudal sucker, which needs smooth surfaces to hold on to.

For successful sampling, it is preferable to wade, knee-deep into water, and enthusiastic naturalists may choose to carry out this exercise barelegged, in order to collect those few species that are haematophagous on humans. A simple leg-check every few minutes will reveal whether there are any large hirudinid leeches in the area. (It is worth noting that, to date, there have been no records of the transmission of human diseases by leeches, and the avid hirudinologist quickly sees his aversion grow into curiosity.) Of course, this type of collecting should not be done in water that is home to crocodiles or bilharzia.

Most leeches will remain alive for days or weeks if placed in sufficient amounts of fresh water (but not tap water). A 50 ml screw-cap plastic container is normally used for storage of virtually all species encountered. Some features need to be observed on the living animal, so it is advisable to photograph the living specimen for a record of colour (see page 244) and to note the crop morphology (see page 246).

Anaesthetization

It is very important that special care be taken when leeches are prepared for study. They should always be anaesthetized before fixation as opposed to simply immersing them alive in a preservative. Either 5–15% ethanol (final concentration) or carbonated water (soda water) will usually suffice. If neither is available it is probably best to leave the leeches alive for a few days prior to fixation. Menthol, magnesium chloride, and even tobacco crushed in water have been tried, but none of these allow the controlled anaesthesia needed to prepare a superb specimen.

If one is using a 50 ml container for collecting purposes in which there is about 35–40 ml (of water and leeches), the initial anaesthetization is achieved by the addition of 1–2 ml of 96% ethanol followed by vigorous shaking. Small specimens of less than 1 cm will immediately go into torpor and let go of the walls of the container, while larger specimens may require the addition of up to 6–8 ml of ethanol before they let go. Either way, once the leeches have released from the walls of the container, an additional 5 to 15 minutes may be required before they are fully anaesthetized. A properly anaesthetized leech will not respond to pinching with forceps or similar stimulation. If after 15 minutes the leech is still responding to stimuli, an additional increment of ethanol is in order. Depending on the size and species of leech, it may take from 5 minutes to 30 minutes for proper relaxation.

Leeches are not normally 'slimy', but if annoyed (e.g. by exposure to ethanol) they may produce copious quantities of polysaccharides (mucus). This can be partially removed by laying the leech on a damp cloth or paper-towel. Any remaining mucus can be lifted off later (after fixation) with a small paintbrush during microscopic examination.

Fixation

It is advisable to separate worms into morphospecies (i.e. individuals that look alike externally) prior to fixation. One half of the collection is then fixed in 95–100% ethanol while the other half is fixed in 10% formalin. The rationale for this is that leeches fixed in ethanol are unsuitable for histological sectioning, whereas those fixed in formalin are unsuitable for DNA isolation and genetic characterization. Moreover, different pigments will fade or dissolve differently in different fixatives. If there is only one representative of a morphospecies, it should be fixed in ethanol because dissections are still possible in this medium.

Leeches should be fixed in a relaxed state: that is, with the exception of the long hirudinids and salifids, specimens should not necessarily be placed flat on a surface like a pertri dish as this may alter diagnostic characters like the position of the caudal sucker. In the case of glossiphoniid leeches that are less than 3 cm in length, the anaesthetized specimens should be placed in a properly labelled storage jar in fixative that is at least three times the volume occupied by the leeches themselves.

Larger or more vermiform leeches (like the salifids or hirudinids), are preferably fixed in a flat (but not flattened) position. The leeches should be laid out on a dish and a small volume of fixing fluid poured over the specimen (not enough to cover or to float the specimens, but enough to begin hardening the surfaces). After a few minutes, the leeches should be turned over and a little more fixative applied. In this way one will ensure that the surfaces of the leeches are fixed evenly. At no time should the leeches be allowed to dry out. Scanning electron microscopy can be performed on formalin-fixed leeches as long as the surfaces have never been allowed to desiccate. Once the leeches appear to retain their straight and flat form they can be completely immersed in fixative. Specimens fixed in ethanol will become stiff within a few minutes and can be transferred to a storage container. Formalin-fixed leeches will require up to 20 minutes or more before it is safe to transfer them without fear of bending or damaging specimens.

Preservation

During collecting trips it is normally convenient to wait until the end of the expedition before transferring leeches to a permanent storage medium. However, if the opportunity permits, after a period of one week, ethanol-fixed leeches should be transferred to fresh 95–100% ethanol (in order to maintain integrity of the DNA) and if it is certain that the material will be used for molecular studies these should be kept in a refrigerator, a –20 °C freezer (not the self-defrosting variety) or at –80 °C, and formalin-fixed leeches should be transferred to 70% ethanol. This will prevent bleaching and will allow the material to be housed in any natural history collection that conforms to worker-safety standards.

GENERAL BIOLOGY

MORPHOLOGY

Leeches are segmented worms characterized by division of the body into 34 segments, of which the seven segments at the posterior end are fused to form a large, powerful caudal sucker (Figs 14.1A & 14.3B). The mouth is surrounded by an anterior or cephalic sucker formed by the fused ventral surfaces of the first few segments (Fig 14.1C). The possession of a constant number of body segments and these anterior and posterior suckers distinguishes leeches from the closely-related Oligochaeta which are also found in fresh waters in southern Africa (see Chapter 13). Most leeches, especially the glossiphoniids, are dorso-ventrally flattened.

Body shape

Members of the Salifidae are characterized by having a very slender body with the sides about parallel, a tapered anterior end (Fig. 14.2G) and a tendency towards dorsoventral flattening at the posterior (caudal) sucker. The Hirudinidae, Haemopidae and Haemadipsidae of southern Africa, on the other hand, all have a more or less robust, sub-fusiform body with the sides nearly parallel and the anterior end widely rounded (e.g. Fig. 14.2H).

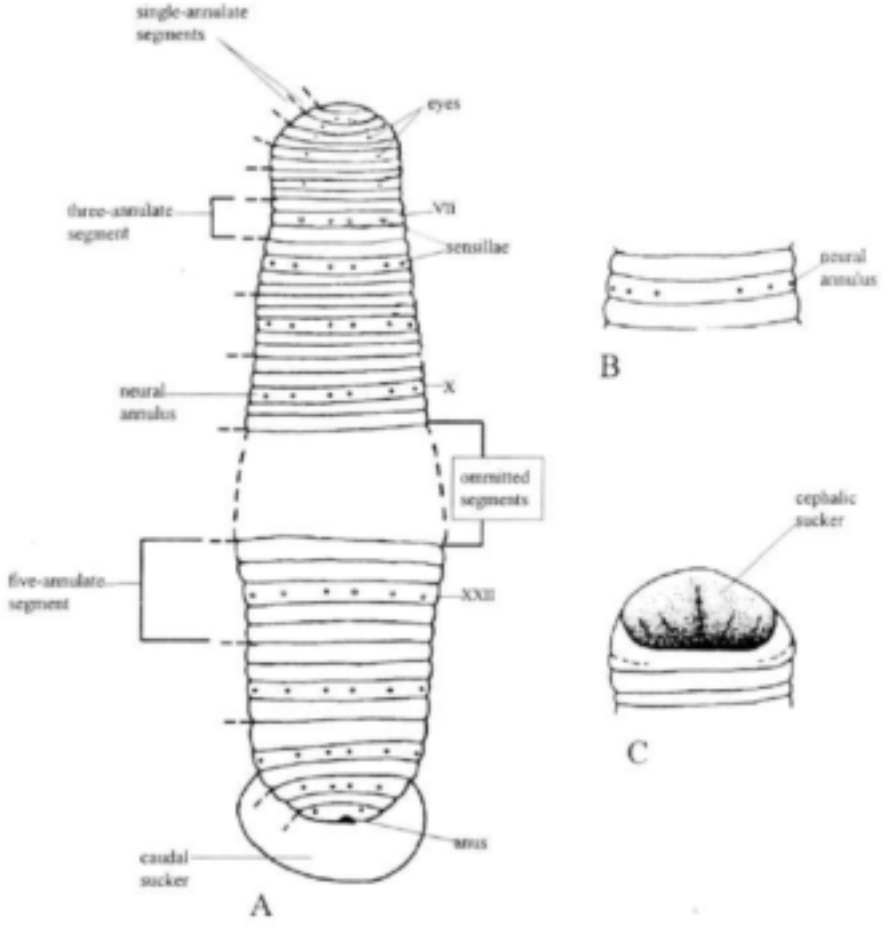

Fig. 14.1. External features of typical leeches: **A**, five-annualate leech, showing the division of segments (dorsal view); **B**, single segment of a tri-annulate leech (dorsal view); **C**, anterior end of a hirudinid (ventral view).

In the Glossiphoniidae, shape varies markedly between species (Figs 14.2A–F) and in some instances it is so typical that it allows a trained eye to recognize species without further examination. The shapes depicted in Fig. 14.2 are those of moderately-fed individuals in a natural resting pose. When leeches move, their shape changes continuously as a result of stretching and contracting movements. Furthermore, the 'typical' body shape of haematophagous glossiphoniids is altered considerably when they feed because of their habit of ingesting large quantities of blood. Some species exhibit a marked difference in body shape in the non-breeding and breeding conditions. For example, the posterior region of breeding individuals of *Batracobdelloides tricarinata* (Fig. 14.2B) is markedly expanded sideways (to provide sufficient room for the large number of attached young) in comparison with that of non-breeding individuals (Fig. 14.2A).

Annulation

Although not a feature unique to them, leeches are characterized by the external subdivision of the segments into rings or annuli (Figs 14.1A, B & 14.3B). The number of annuli per segment in the middle region of the body (from the seventh segment — denoted VII) is characteristic for different family-groups (or even genera and sometimes species). These are usually referred to as 'complete' segments. The number of annuli per segment becomes progressively reduced towards both ends of the body (Fig. 14.1A). The relative number of annuli in each of the first six segments (I through VI) can be species-specific. Although leeches are known in which complete segments consist of as many as 14 annuli (Harding & Moore, 1927; Mann, 1962), the freshwater leeches known in southern Africa are either triannulate (three annuli per segment — Fig. 14.1B), five-annulate (five annuli per segment — Fig. 14.1A), or seven-annulate (seven annuli per segment). It is not always clear how to count the number of annuli per segment. Determining the position of papillae or sensillae (see below) or, in the case of larger species, the ventral nephropores can be useful for this assessment. If papillae are present, they will predominate on one annulus (called the 'neural' annulus) in each segment and one can determine the number of annuli per segment by counting the number of annuli between each of these 'neural' annuli (see below).

Body surface features

Each segment in the body is provided externally with a single, transverse row of sensory structures, called sensillae, on both the dorsal and

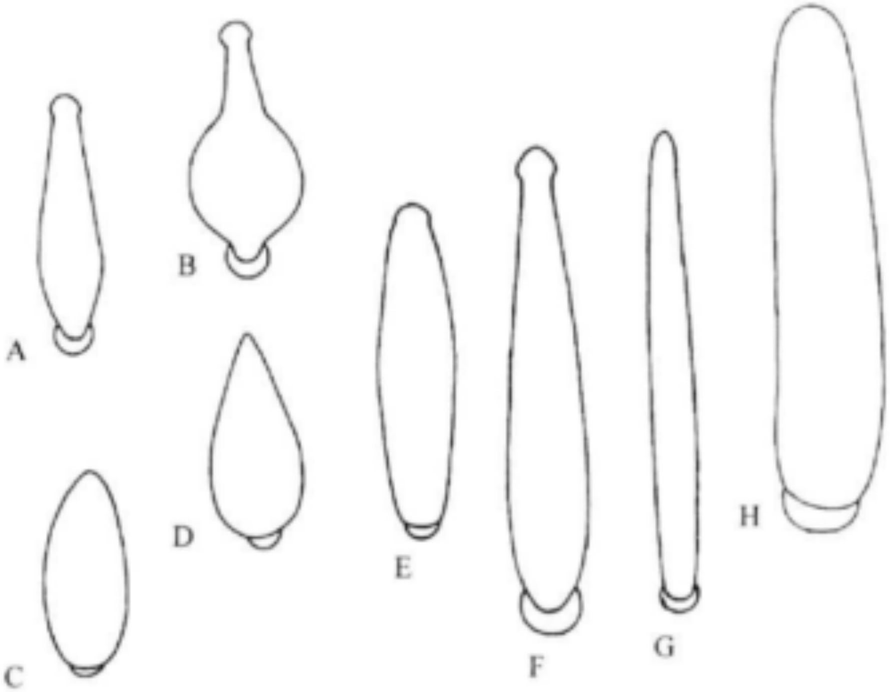

Fig. 14.2. Body profiles of various leeches (relaxed specimens); **A–F**, various glossiphoniids: **A–B**, non-breeding and breeding *Batracobdelloides tricarinata*; **C**, *Alboglossiphonia* spp.; **D**, *Helobdella* spp.; **E**, *Theromyzon* spp.; **F**, *Placobdelloides* spp.; **G**, Salifidae; **H**, Hirudinidae (Figures not drawn to scale).

ventral sides except in the regions of the suckers, where they are present on the dorsal side only. Whereas sensillae are always present, they are very difficult to locate and are even undetectable in some species, particularly in the Salifidae and some glossiphoniids where segmental limits can be determined only by dissection or by serial histological sectioning. In most other families there are three or four pairs of sensillae dorsally (Figs 14.1A, B) and three pairs ventrally (which are more difficult to visualize) and these are arranged in an orderly manner along the body. In all southern African leeches the neural annulus bearing the sensillae is the middle annulus of the segment (Figs 14.1A, B).

Apart from the very small and flat sensillae, the dorsal surfaces of the annuli may have a conspicuously rough appearance due to the presence of cutaneous elevations (Figs 14.7F, G, I, J), of which two categories are distinguished in the key: papillae are dome-shaped elevations with a smooth top (e.g. Figs 14.7G, I); tubercles are usually very large, cone-like structures with a variable number of papillae on the summit (Figs 14.7J, K).

Eyes

In the head region, photoreceptive cells are aggregated into dense groups in the deeper tissues, each group being surrounded by a cup-shaped layer of pigmented cells, to form ocelli or 'eyes'. Although the number and pattern of arrangement of the eyes are stereotyped in the families Hirudinidae, Haemopidae and Haemadipsidae (in which five pairs of eyes are arranged in a parabolic arch —Fig. 14.6A), southern African representatives of the families Glossiphoniidae and Salifidae exhibit great variation in ocular pattern amongst the different genera and species (Fig. 14.6). Not only does the number of eyes vary from one to four pairs (i.e. two to eight eyes) in different taxa, but their arrangement also makes the ocular pattern a very important criterion for the identification of species.

Colour pattern

Unlike many other freshwater invertebrates, leeches are often brightly coloured or elaborately patterned creatures. Although variations of intensity may occur in different individuals of a given species, the basic colour pattern for that species is usually recognizable. A few southern African species are characterized by two (Oosthuizen, 1978b) or three distinctly different colour patterns and in some cases there are even infraspecific differences in the colour of markings (Oosthuizen, 1978b, 1982). Unfortunately, the lustre of the colours of specimens is lost over time in specimens immersed in preservatives. Whenever possible, photographs should be taken of living specimens in order to provide a permanent record of the live colour state. Patterns may be spotted, longitudinally striped, or transversely banded (Fig. 14.8). Notwithstanding the relatively unstable nature of colour patterns in preservatives, they are reliable criteria for identification as far as the leeches of southern Africa are concerned and must, therefore, be carefully noted shortly (within a few months) after specimens have been killed.

DIGESTIVE SYSTEM

There are three basic units to the alimentary tract of leeches: the foregut, the midgut and the hindgut. Except for the Glossiphoniidae, the system consists of a buccal cavity which leads to a muscular pharynx provided with three jaws at its entrance (Fig. 14.3A); or jaws may be lacking. The pharynx is followed by the crop which constitutes the major part of the gut and from which extends one, ten or 20 pairs of laterally-directed branches or caeca. The crop serves as a storage place of food and at its posterior end it joins a short tubular intestine where both digestion and absorption take place. The intestine is followed by a short, tubular rectum which opens to the exterior via the anus which is situated on the mid-dorsal line anterior of the caudal sucker (Fig. 14.1A).

In the glossiphoniids (Fig. 14.3B), the foregut includes a muscular protusible proboscis with salivary cells attached at the base of the proboscis where it meets the oesophagus. These salivary cells may be arranged diffusely in the parenchyma (Fig. 14.3B) where they appear as large whitish globules with salivary ductules inserting into the base of the proboscis, or as compact salivary glands (Fig. 14.5) occurring in the open coelomic space next to the base of the proboscis. In some species the proboscis is of peculiar size, shape or structure (Oosthuizen 1978a, 1982) and of great diagnostic value but, due to its translucent nature, it is not always perceptible without dissection. The proboscis of the glossiphoniids is protrusible through a small pore situated within the cephalic sucker (Fig. 14.3B) and its position varies interspecifically. The only exception amongst the glossiphoniids in which this pore is not visible in surface view, is *Marsupiobdella africana* in which the cephalic sucker surrounds a large 'mouth' (Fig. 14.3C), leading to an oral chamber in the floor of which the proboscis pore is situated.

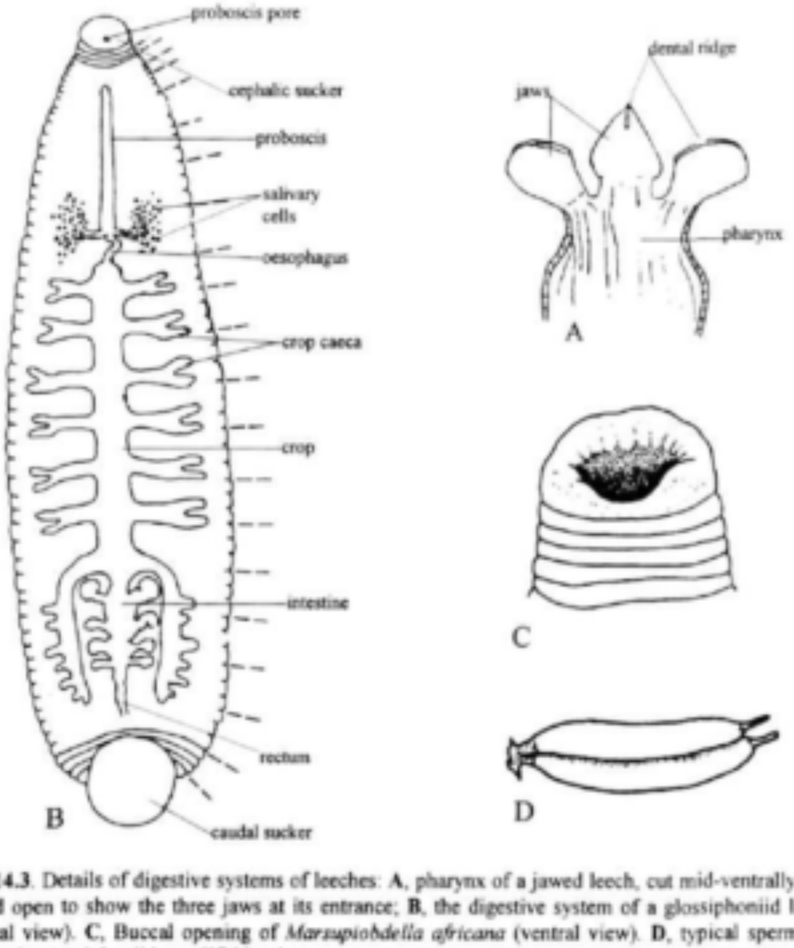

Fig. 14.3. Details of digestive systems of leeches: **A**, pharynx of a jawed leech, cut mid-ventrally and spread open to show the three jaws at its entrance; **B**, the digestive system of a glossiphoniid leech (ventral view). **C**, Buccal opening of *Marsupiobdella africana* (ventral view). **D**, typical spermatophore of a glossiphoniid or salifid leech.

In the blood-feeding hirudinids, the pharynx is equipped with three muscular jaws (Fig. 14.3A), each of which is armed with a row of tiny but sharp denticles or 'teeth'. The non-haematophagous salifids (which consume chironomid larvae) lack the pronounced jaws of the hirudinids and in their place have three slightly-raised ridges at the opening of their pharynx, each equipped with a pair of small denticles or 'stylets'.

In most taxa the mid-gut (or crop) of leeches is unremarkable and comprised of a large gastric sac (between segments X and XIX) where blood (or digested prey) is stored for long periods between feedings. In the glossiphoniids, the mid-gut is modified with five to seven pairs of bilateral sacs (gastric caeca) that expand and fill when the leech feeds (Fig. 14.3B). In all of these glossiphoniids, the most posterior pair originates in segment XIX and then extends posteriorly under the intestinal caeca to XIV; these are often referred to as 'diverticula' or 'postcaeca'. Because of the translucency of the body wall (especially on the ventral side) of live glossiphoniids, it is possible to recognize (in living specimens) details of the crop in a ventral surface view under specific circumstances. When the crop is filled to capacity, the contents allow determination of the total number and shape of its caeca. In most of the local glossiphoniids, the translucent empty crop is not perceptible in whole specimens. It is for this reason that the number and shape of the crop caeca are in some cases not included in the key. If visible, they may, however, assist in the identification process. In *Oosthuizobdella garoui, Oosthuizobdella stuhlmanni* and *Placobdelloides multistriata,* the wall of the crop contains large, green pigment cells (Oosthuizen, 1979, 1982), which allow one to determine the number and the shape of the caeca even in starved specimens (Figs 14.6A, B). Before collected leeches are killed they should be placed in a glass container and observed for details of the crop morphology (as described previously, under 'Collection'). The hindgut is comprised of an intestinal tube in the hirudinids and the salifids or a quadricaecate intestine in the glossiphoniids. The intestine invariably originates in segment XIX and continues posteriorly, where it is followed by a short rectal tube that exits through an anal pore just anterior and dorsal to the caudal sucker. The number of segments between the anus and the edge of the caudal sucker may be diagnostic in some groups.

REPRODUCTION

Leeches are hermaphroditic animals with separate male and female reproductive systems. Although the basic structural patterns differ in the major groups, marked interspecific variations are of great taxonomic importance. Even in the glossiphoniids, however, very little of the reproductive anatomy is visible in whole specimens. Proper characterization of the internal anatomy of leeches requires careful dissection and the teasing away of tough connective and parenchymal tissues, so characteristics of the reproductive systems are not included in the key. Only the externally visible features of these systems (such as the ventral position of gonopores) will be discussed. The interested reader is referred to the listed references for detailed descriptions.

In all of the species of southern Africa, the male and female systems open independently to the exterior, each by means of a small pore (the female gonopore) situated on the mid-ventral line, roughly one-third of the way back from the head (Fig. 14.4A). The male pore is always anterior of the female pore and both are usually situated within the furrows separating two consecutive annuli (Figs 14.8D, E) in segment XII. In some species, however, one (Fig. 14.4B) or both pores may be positioned on, and not between, annuli. Species of *Barbronia* possess two additional pores, called accessory copulatory pores, one anterior to the male gonopore and one posterior to the female gonopore (Fig. 14.4B).

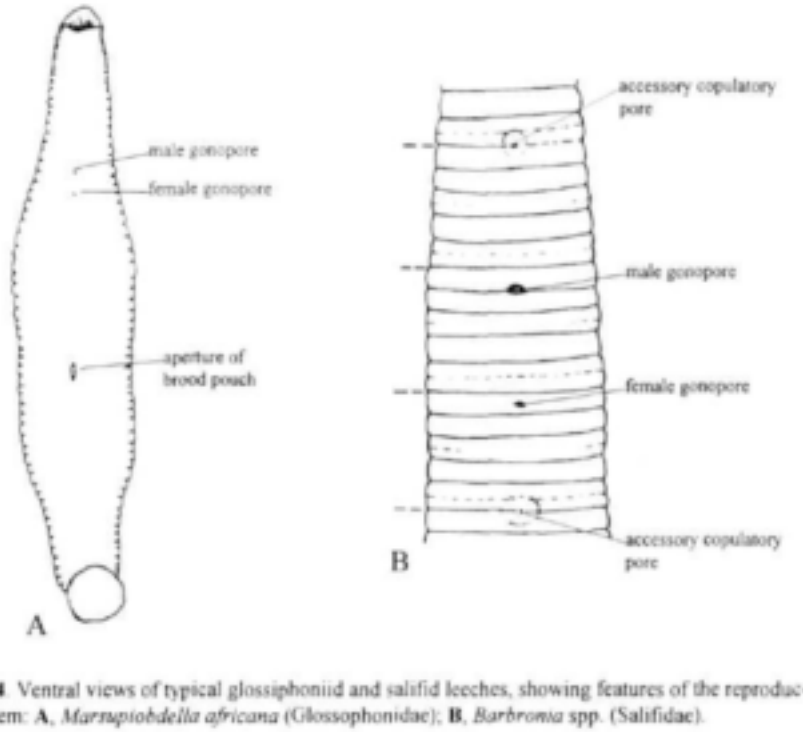

Fig. 14.4 Ventral views of typical glossiphoniid and salifid leeches, showing features of the reproductive system: **A**, *Marsupiobdella africana* (Glossophonidae); **B**, *Barbronia* spp. (Salifidae).

Reproducing individuals are usually distinguishable by the swelling of a certain number of annuli in the region that includes the gonopores. This swollen area constitutes the clitellum, which secretes the cocoons (egg cases). Unlike the homologous structure in terrestrial earthworms, the degree of prominence of the clitellum varies considerably in leeches. It may be very conspicuous in the Salifidae, but tends to be imperceptible in the Glossiphoniidae.

All glossiphoniids exhibit marked parental care with adults brooding their young between their ventral surfaces and a substrate (*Marsupiobdella africana* even holds them in a ventral fold) until such time as they are ready for their first feeding. The young then attach themselves to their parent, which carries them to their first blood meal.

Reproduction in leeches includes several specializations not equalled in the related Oligochaeta. Leeches are hermaphrodites and cross-fertilization is probably the rule. In the families Hirudinidae, Haemopidae and Haemadipsidae, spermatozoa are transferred from one individual directly into the female pore of the partner by means of a protrusible penis. In the Glossiphoniidae and Salifidae spermatozoa are enclosed in hardened spermatophores (Fig. 14.3D) which are secreted from the terminal portion of the male duct and injected into the body surface of a recipient leech either in the clitellar region (Salifidae) or virtually anywhere on the body (Glossiphoniidae). Spermatozoa are forced out of the spermatophore by hydrostatic shrinkage of its wall, whereupon the spermatozoa pass through the body wall and find their way into the ovarian system. Attached spermatophores are more frequently encountered in the Glossiphoniidae than in other kinds of leeches.

Except for the brooding glossiphoniids, leeches, like earthworms, form hardened egg cases ('cocoons'). The cocoons are either attached to a solid object in the water (e.g. in the Salifidae) or they are deposited in damp soil and under dead plant material near the water's edge (e.g. in the Hirudinidae, Haemopidae and Haemadipsidae). The glossiphoniids, however, exhibit highly specialized brooding behaviour: they either form membranous cocoons containing several eggs, e.g. in *Helobdella conifera*, or lay eggs singly, each being surrounded by its own membranous capsule, e.g. in *Batracobdelloides tricarinata*. The cocoons or eggs are either attached to the ventral surface of the body, or kept there by the inward folding of the sides of the body to form a temporary, tubular brood pouch that enables the leech to move around freely.

Young glossiphoniids attach themselves to the ventral surface of the parent by means of their caudal suckers and are carried around until ready to take their first meal after which they usually leave the parent. In some species, the young remain attached for longer periods and do not leave the parent until after several meals.

This type of care for the progeny reaches its most specialized development in *Marsupiobdella africana* in which a completely enclosed brood pouch or marsupium is formed, the aperture of which (Fig. 14.4A) can be closed or opened by means of a sphincter, thus allowing the parent to control the vagility of its young (van der Lande & Tinsley, 1976).

LOCOMOTION

The typical manner in which all of the locally-occurring species move about on a smooth solid substrate is through extension of the body in an anterior direction, attachment of the oral sucker to the substrate, release of the caudal sucker and then bringing the caudal sucker up towards the head before re-attachment. Most aquatic leeches are excellent swimmers that move through water with a coordinated vertical sinusoidal wave motion. With the exception of *Placodelloides jaegerskioeldi* though, glossiphoniids are incapable of swimming.

ECOLOGY

Heavy infestations of haematophagous leeches can cause high mortality amongst vertebrate populations. Contrary to what is generally believed, however, not all leeches are blood-sucking creatures. Although the majority of the southern African species feed on the blood of vertebrates, some are exclusively predators on other invertebrates. Some of these leeches are macrophagous, swallowing their prey whole (Salifidae, for instance, consume chironomid larvae) whilst others suck body fluids and soft parts from invertebrates (e.g. *Helobdella* spp. feed on oligochaetes and *Alboglossiphonia* spp. feed on snails).

Some species of leech feed exclusively on animals of a particular group —for instance, *Theromyzon cooperi* feeds only on birds and *Placobdelloides multistriata* on reptiles. Other leeches, like *Placobdelloides jaegerskioeldi* which feed on hippopotamuses, are restricted to a single host species. Several species exploit a wide range of hosts. Examples include *Oosthuizobdella garoui,* which feeds on turtles, birds and mammals, and *Hirudo michaelseni,* which feeds on the blood of fish, amphibians or mammals, but is also satisfied by a meal of freshwater snails. The predatory species generally include a variety of invertebrates in their diet.

Sawyer (1986) lists, in approximate order of significance, eleven environmental factors that determine the number and kinds of leeches in a given habitat. He places the availability of food at the top of the list. Observations of the leeches of southern Africa endorse this view and although it is likely that other factors listed by Sawyer (1986) do play a role in this regard, the diversity and abundance of food animals in a given habitat are very good indicators of the composition of the leech fauna.

Some leeches use other freshwater animals exclusively for transport. *Placobdelloides multistriata,* for instance, attaches to large aquatic insects like the giant waterbug (*Belostoma niloticum)* and water-scorpions (*Nepa* spp.) and is carried to other waterbodies by these night-flying insects (Oosthuizen, 1979). *Marsupiobdella africana* uses freshwater crabs both for shelter and to bring them into contact with their amphibian hosts (Dick, 1959). Haematophagous leeches are often carried from one habitat to another while attached to their hosts. This particularly applies to those leeches that encounter their hosts temporarily; examples are *Theromyzon cooperi* and *Oosthuizobdella garoui* from the nasal cavities of birds (Oosthuizen & Fourie, 1985), *Placobdelloides jaegerskioeldi* from the rectums of hippopotamuses, and hirudinids from the nasal and buccal cavities of game and domestic mammals. An important and interesting means by which glossiphoniids disperse within a given habitat is their ability to move upside-down, using the surface tension of water. The haematophagous glossiphoniids *Theromyzon cooperi* and *Oosthuizobdella garoui* use this method to find host individuals that would otherwise be outside their immediate reach.

Leeches are nocturnal animals and during the day they hide in any secure place, like the underside of solid objects in the water or amongst aquatic plants. It is only starved individuals of haematophagous species that will quickly come into the open in the daylight when they become aware of a potential host in the immediate vicinity. The availability of hiding places is probably the most important abiotic environmental factor determining the abundance and variety of leeches.

KEY TO THE FRESHWATER LEECHES OF SOUTHERN AFRICA

Introductory comments

All the features mentioned in couplets must be taken together when deciding which part of a couplet to select. Complementary information, which is included in parenthesesis, is of assistance to the identification process but may not always be available.

The key includes only external features, except for two instances when it is necessary to examine the internal morphology of specimens. To separate the jawless *Semiscoloides congolensis* from the jawed leeches (Hirudinidae), the specimen must be pinned on its back and a median ventral incision made posteriorly from the posterior lip of the oral sucker through the first nine or ten annuli, exposing the pharynx which must be split open to expose the inner surface (Fig. 14.3A). This permits determination of whether or not jaws are present on the pharynx. The closely related *Oosthuizobdella garoui* and *O. stuhlmanni* can only be reliably separated on the basis of the shape of the first pair of crop caeca (Fig. 14.5). As noted above, this can be determined without dissection by placing the leeches (preferably when blood-fed) in a transparent container and tracing the outlines of the filled gastric caeca.

The system of delimitation of genera followed here is that proposed by Sawyer (1986). Generic combinations accepted prior to publication of Sawyer's work, as well as synonyms, where applicable, are provided in parentheses. The generic position of *Mesobdella lineata* is probably erroneous. Until its phylogenetic position can be determined, the original combination is retained here. Finally, dimensions provided are those of the largest specimens so far recorded for respective species and indicate, unless otherwise stated, the lengths of straight, moderately-stretched, preserved specimens. These longitudinal measurements are very similar to the lengths of the leeches when they are alive and at rest.

KEY TO THE FRESHWATER LEECHES OF SOUTHERN AFRICA

1. Total number of annuli less than 80; (complete segments three-annulate; young carried on ventral side of parent; with protrusible proboscis, no jaws; not normally found swimming; dorsoventrally flattened) (**Glossiphoniidae**).. 5

– Total number of annuli more than 80; (complete segments five- or seven-annulate; young not carried by parent; without proboscis; with or without jaws; usually very good swimmers; vermiform shape) 2

2. Five pairs of eyes arranged in a parabolic arch (Figs 14.1A, 14.6A) 3

– Less than five pairs of eyes (Figs 14.6L, M) with or without accessory ocelli (Fig. 14.6N); dorsal side uniformly coloured without markings; (without jaws) (**Salifidae**) 19

3. Dorsal side with banded colour pattern, alternating dark green and yellowish green bands (Fig. 14.8A); (amphibious) .....*'Mesobdella' lineata* (Fig. 14.8A)

– Dorsal side uniformly coloured with or without numerous, small, black spots or with longitudinally striped pattern 4

4. With jaws (**Hirudinidae**) 21

– Without jaws; uniformly pearl grey without black spots, ventrally much paler than on dorsal side and having two areas separated by a wide, yellow stripe laterally .... *Semiscoloides congolensis*

5. Four pairs of eyes (Figs 14.6B, C) 6
– One to three pairs of eyes (Figs 14.6D, E, F, G, H, I, J, K & 14.7H) 8

6. Eyes arranged in two subparallel rows (Fig. 14.6B) .... *Theromyzon cooperi*
– First three pairs of eyes arranged in two subparallel rows, fourth pair (buccal eyes) on lateral margins of head (Fig. 14.6C) 7

7. First pair of crop caecae with anteriorly-directed lobes (Fig. 14.5A); dorsal surface of the body mostly distinctly marked with two (Fig. 14.7A) or four rows of dark spots .... *Oosthuizobdella garoui*
– First pair of crop caecae without anteriorly-directed lobes (Fig. 14. 5B); dorsal surface of the body without dark spots (Fig. 14.7B).................... *Oosthuizobdella stuhlmanni*

8 Eyes three pairs (Figs 14.6D, E, F), (caution: the anterior pairs may be coalesced, in which case they would appear as one pair; close examination will reveal a bilobed character confirming that these constitute two of three pairs (Figs 14.6D, E) 9
– Eyes one or two pairs (Figs 14.6G, H, I, J, K & 14.7H) 13

9. Eyes arranged in two rows (Fig. 14.6F); second and third pairs of eyes large, about equal in size, members of each pair approximately equidistant, thus representing the four corners of a square; first pair very small; head region conspicuously dilated into a circular sucker, distinct from body; dorsal side without striped pattern; (ten pairs of crop caecae) .... *Hemiclepsis quadrata*
– Eyes paired in three groups corresponding with the three corners of a triangle (Figs 14.6D, E); eyes of second and third pairs of each side coalesced (see caution in 8A); head region not conspicuously dilated; dorsal side finely striped (Fig. 14.7C) or finely mottled (Fig. 14.7D); (six or seven pairs of crop caecae) 10

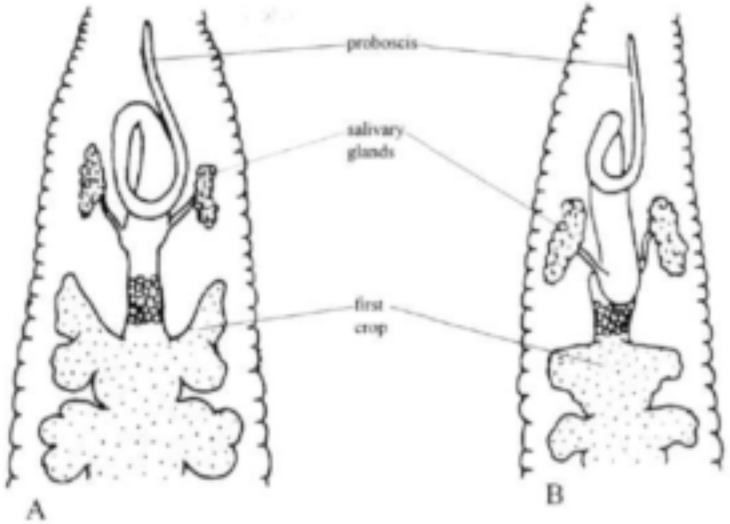

Fig 14.5. Outlines of the foregut and midgut in two different species of *Oosthuizobdella* (dorsal views): **A**, *O. garoui*; **B**, *O. stuhlmanni*.

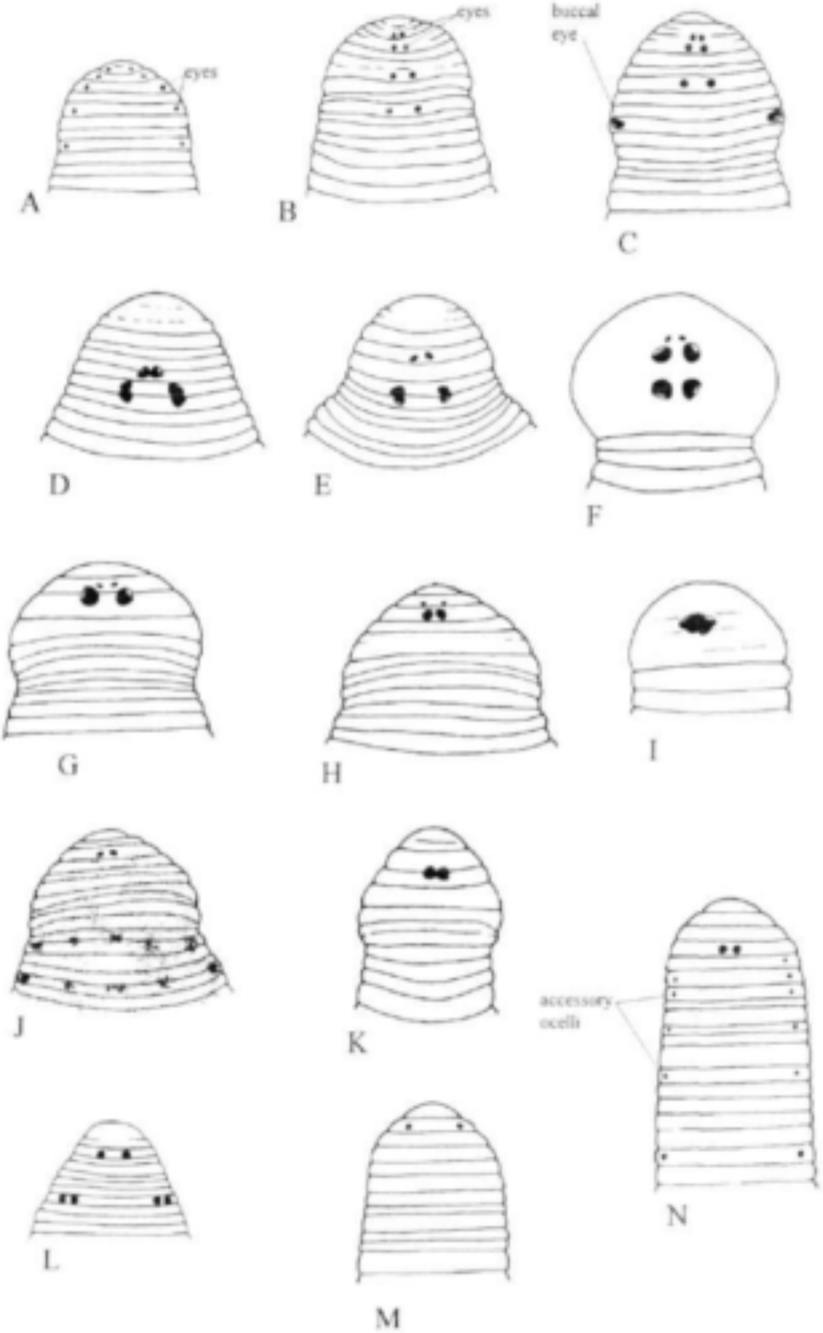

Fig. 14.6: Cephalic segments of various leech taxa showing arrangement and other features of eye spots (dorsal views). **A**, hirudinid leech. **B–K**, glossophonid leeches: **B**, *Theromyzon cooperi*; **C**, *Oosthuizobdella* species; **D**, *Alboglossiphonia* spp. **E**, *Alboglossiphonia disjuncta*; **F**, *Hemiclepsis quadrata*, (also showing pronounced dilation of the cephalic segments); **G**, *Batracobdelloides tricarinata*; **H**, *Oosthuizobdella aspera*; **I**, *Marsupiobdella africana* showing large coalesced eyes; **J**, *Placobdelloides multistriata*; **K**, *Placobdelloides jaegerskioeldi*. **L–N**, salifid leeches: **L**, *Barbronia* species; **M**, *Salifa africana*; **N**, *S. perspicax*.

10. Gonopores separated by one annulus; dorsally 34 or 36 narrow, longitudinal green or brown stripes at widest region of body; (seven pairs of crop caecae) .... *Alboglossiphonia conjugata*

– Gonopores separated by two annuli 11

11. Dorsal side with 14–20 narrow, longitudinal, brown stripes at widest region of body and roughened by papillae (Fig. 14.7F) ; each annulus in middle region of body with about 12 large and several much smaller papillae .... *Alboglossiphonia macrorhyncha*

– Dorsal side with more than 20 narrow, longitudinal stripes at widest region of body, or finely mottled; (seven pairs of crop caecae) 12

12. Dorsal side with 28 or 30 narrow, dark green or brown stripes, not roughened by papillae; cephalic sucker deep and cup-shaped (Fig. 14.7E); (first six pairs of crop caecae bilobed) .... *Alboglossiphonia cheili*

– Dorsal side with 34 or 36 green or light brown, narrow stripes or finely mottled and roughened by 15 to 18 large papillae and numerous smaller papillae in middle region of body (Fig. 14.7F); cephalic sucker not deeply cup-shaped .... *Alboglossiphonia disjuncta*

13. Two pairs of eyes, first pair very small, about a quarter to a third the diameter of second pair (Figs 14.6G, H) 14

– One pair of eyes (Figs 14.7H, 14.6I, J, K) 15

14. First pair of eyes close together, between and in line with antero-medial corners of second pair (Fig. 14.6G); proboscis pore in centre of sucker; dorsal side of body with three or five rows of large papillae forming ridges, especially distinct posteriorly (Fig. 14.7G), sometimes perceptible only in dead animals; posterio- dorsal surface with four or six rows of bright yellow spots (Fig. 14.7G) .... *Batracobdelloides tricarinata*

– First pair of eyes more widely separated than second pair and in front of, and nearly opposite to, outer margins of second pair (Fig. 14.6H); proboscis pore at anterior edge of oral sucker; dorsal side without ridges or yellow spots .... *Oosthuizobdella aspera*

15. With brown chitinoid plaque dorsally in neck region (Fig. 14.7H) (six pairs of crop caecae) .... *Helobdella stagnalis*

– Without chitinoid plate 16

16. Dorsal side of every third annulus with up to eight large, dark-coloured tubercles, tipped with black, in a transverse row (Fig. 14.7I); gonopores separated by one annulus; (five pairs of crop caecae) .... *Helobdella conifera*

– Dorsal side without tubercles or with large tubercles, not arranged as above; gonopores separated by two annuli; (seven pairs of crop caecae) 17

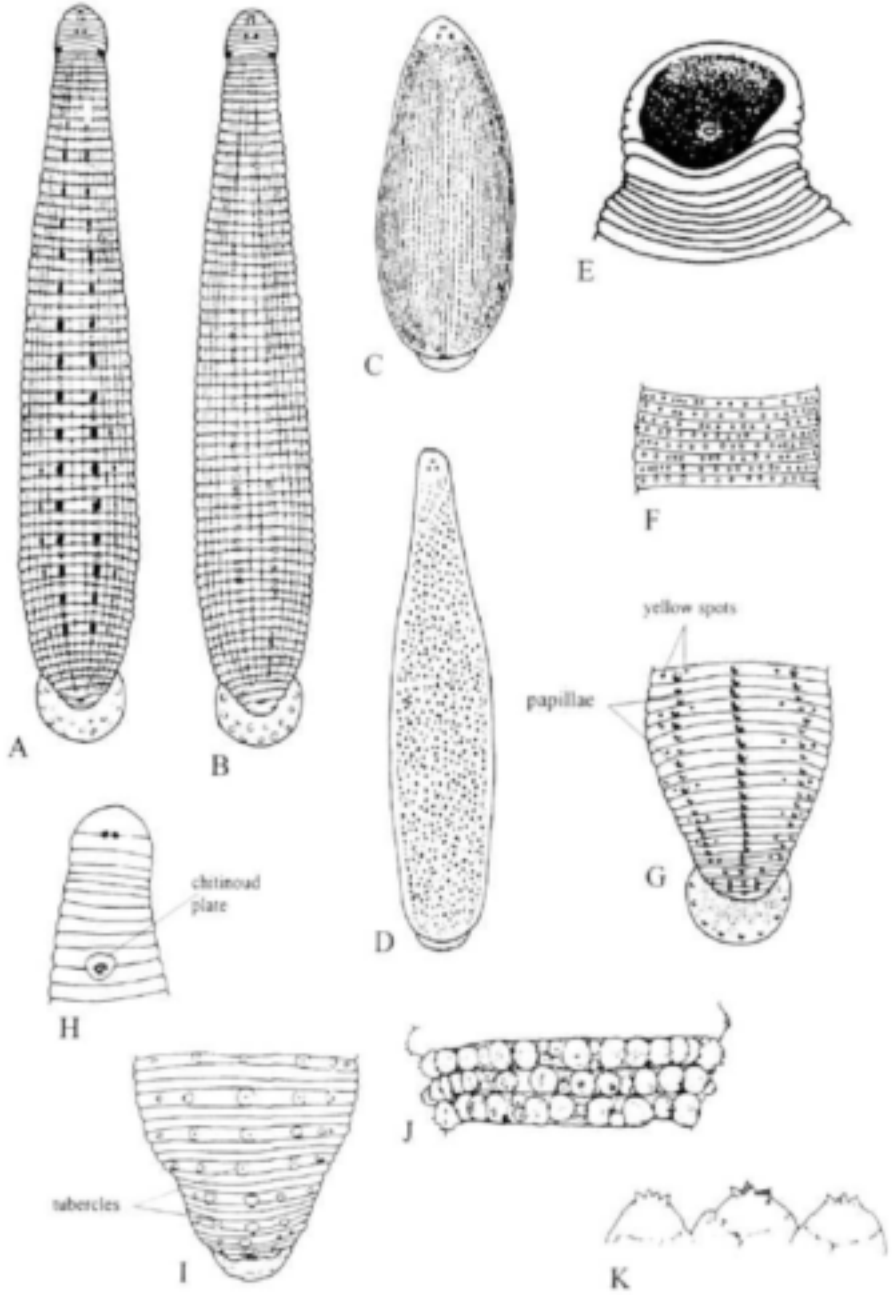

Fig. 14.7. Characteristic shapes and patterns of papillae, tubercles and other surface features of various leech species. **A**, *Oosthuizobdella garoui* (dorsal view); **B**, *O. stuhlmanni* (dorsal view); **C–D**, two different surface patterns of *Alboglossiphonia* (dorsal views); **E**, *A. cheili* (ventral view of the buccal region); **F**, *A. disjuncta* (dorsal view of mid-body segments); **G**, *Batracobdelloides tricarinata* (dorsal view showing dorsal pigmentation and papillary pattern). **H**, *Helobdella stagnalis* (dorsal view of cephalic segments showing characteristic chitinoid plaque); **I**, *H. conifera* (showing black-tipped papillae on every third annulus); **J–K**, *Placobdelloides jaegerskioeldi*: **J**, complete triannulate segment; **K**, section of segment under high-magnification showing detail of dorsal tubercules

17. Mouth opening large (Fig. 14.3C); eyes coalesced (Fig. 14.6I); dorsal side with 11 pairs of dark green patches (Fig. 14.8A). (Reproducing individuals with enclosed brood pouch and aperture on mid-ventral line in posterior half of body — Fig. 14.4A) .... *Marsupiobdella africana*

– Proboscis pore small, at anterior margin of cephalic sucker (Figs 14.6J, K) 18

18. Dorsal side with an interrupted, golden-yellow median stripe from between eyes to just in front of posterior sucker and five series of dark, irregularly-shaped blotches (Fig. 14.6J) and roughened by irregularly-arranged papillae of various sizes; eyes well separated (Fig. 14.6J) .... *Placobdelloides multistriata*

– Uniformly flesh-coloured to olive brown; dorsal side of each annulus extremely roughened by large tubercles (Fig. 14.7J), each with a rosette of pointed papillae on summit (Fig. 14.7K); each annulus in mid-body region with transverse row of 15 to 24 tubercles (Fig. 14.7J); eyes touching (Fig. 14.6K) .... *Placobdelloides jaegerskioeldi*

19. Two accessory copulatory pores present, one anterior and one posterior to the male and female gonopores respectively (Fig. 14.4B); two 'pairs' of eyes in which the posterior pair are doublets (Fig. 14.6L) ...... *Barbronia* spp.

– Accessory copulatory pores absent 20

20. One pair of eyes (Fig. 14.6M); gonopores separated by seven annuli .... *Salifa africana*

– One pair of eyes with six or seven accessory pairs of ocelli (Fig. 14.6N); gonopores separated by five annuli .... *Salifa perspicax*

21. Dorsal side with longitudinally-striped colour pattern; sides of body yellow or orange 22

– Dorsal side uniformly coloured, with or without small black spots 28

22. Ventral side heavily maculated (spotted/ blotched) with black (Fig. 14.8B); six dark bands dorsally, with large, black maculations (Fig. 14.8C) .... *Asiaticobdella fenestrata*

– Ventral side with a few black maculations or lacking pigment 23

23. Dorsal side with a dark median stripe (Figs 14.8F–K) 24

– Dorsal side without a dark median stripe (Figs 14.8L, M) 27

24. Ventral side without marginal black stripes (Fig. 14.8D); dorsally five or seven dark stripes (Figs 14.8F, G) or with median black stripe only (Fig. 14.8H) .... *Hirudo hildebrandti*

– Ventral side with black marginal stripes (Fig. 14.8E) 25

25. Dorsal side with 11 narrow black stripes, first two pairs on each side of median stripe segmentally merged to form a chain-like pattern (Fig. 14.8I) .... *Aliolimnatis africana*

– Dorsal side with seven dark stripes alternating with six light-coloured stripes (Figs 14.8J, K) 26

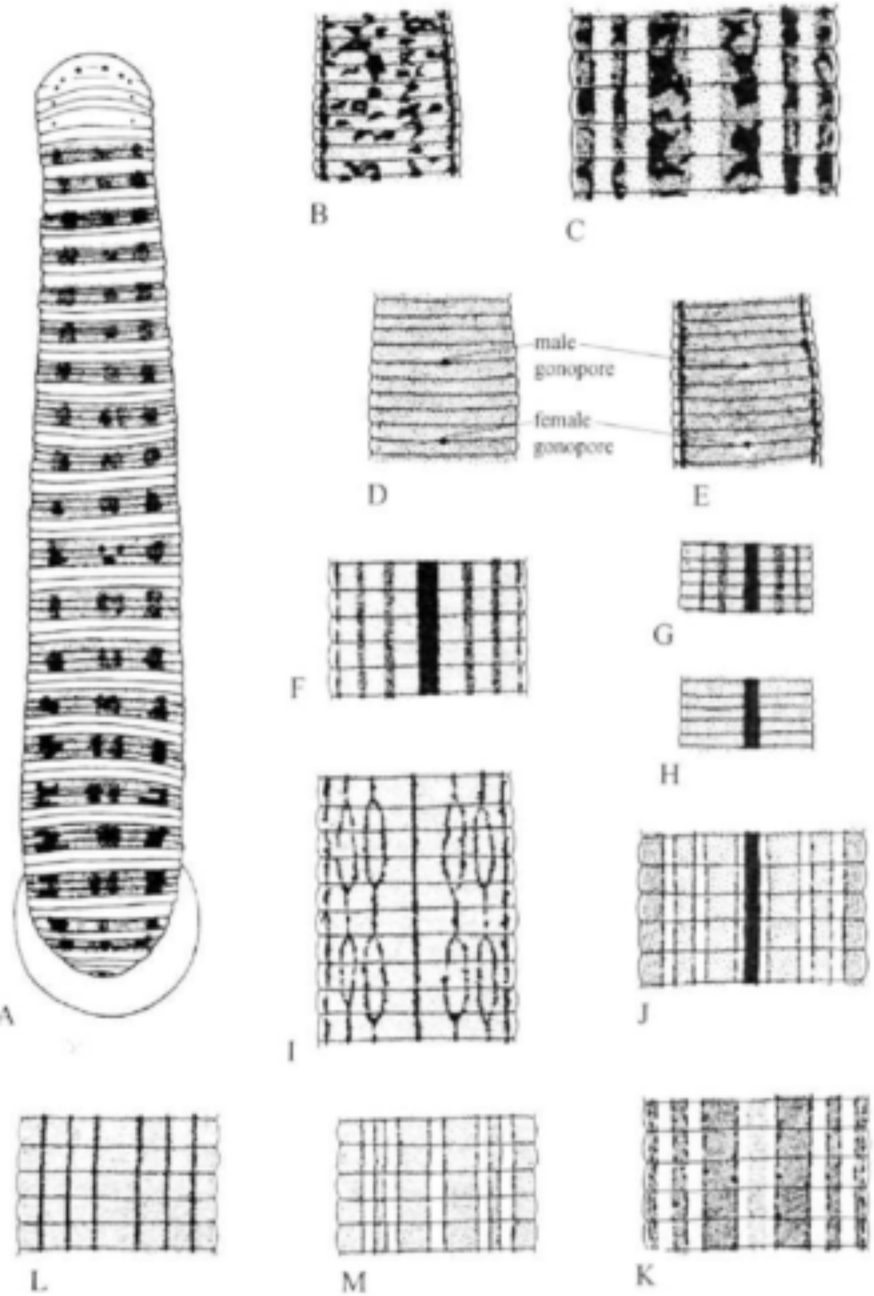

Fig. 14.8. Characteristic colour patterns of various leech species: **A**, *Mesobdella lineata*, dorsal colour pattern; **B**, *Asiaticobdella fenestrata*, ventral colour pattern; **C**, *A. fenestrata*, dorsal colour pattern; **D**, *Hirudo hildebrandti* showing relatively uniform ventral colour pattern; **E**, typical ventral colour pattern of most southern African blood-feeding Hirudinidae; **F–H**, *Hirudo hildebrandti*, dorsal colour pattern, showing variation within the species; **I–M**, dorsal colour patterns of various species: **I**, *Aliolimnatis africana*; **J**, *A. oligodonta*; **K**, *A. buntonensis*; **L**, *A. obscura*; **M**, *Hirudo michaelseni*.

26. Median stripe black, light-coloured stripes yellow (Fig. 14.8J) .... *Aliolimnatis oligodonta*

– Median stripe light brown, remaining light-coloured stripes olive green (Fig. 14.8K) .... *Aliolimnatis butonensis*

27. Dorsal side with six narrow, dark-brown stripes (Fig. 14.8L) .... *Aliolimnatis obscura*

– Dorsal side with five yellow stripes bordered with black (Fig. 14.8M) .... *Hirudo michaelseni*

28. Gonopores separated by eight annuli; dorsally and ventrally uniformly spotted with small, black blotches .... *Praobdella maculata*

– Gonopores separated by five annuli; without black spots .... *Praobdella radiata*

NOTES ON SPECIES

Haemadipsidae

The Haemadipsidae are strictly terrestrial leeches more commonly known from the Australasian tropics. It is not presently clear whether or not the South American and African *Mesobdella* species are actually the closest relatives of those haemadipsids in India and Asia, but their ecology is essentially the same.

'Mesobdella' lineata (Sciacchitano): found in forest streams in KwaZulu-Natal and Mpumalanga. Probably haematophagous; not common; when out of the water, keeps to wet rocks and vegetation close to stream; 14 mm.

Haemopidae

Haemopid leeches are macrophageous, i.e. they feed on earthworms and other invertebrates, having given up the blood feeding habits of their ancestors. They are usually fairly sluggish worms found in detritus or mud. *Semiscoloides congolensis* (Sciacchitano, 1959) (=*Semiscolex congolensis*) Known only from Victoria Falls. (Zimbabwe); probably terrestrial. 45 mm.

Glossiphoniidae

Glossiphoniids are strongly dorso-ventrally flattened. They exhibit a form of marked parental care in which the young attach themselves to the ventral surface of their parent after hatching and are transported to their first blood meal when the parent seeks its next.

Theromyzon cooperi (Harding, 1932) (=*Theromyzon lineatum*) (Fig. 14.6B): fairly common to abundant in pans, dams and vleis inhabited by waterbirds; haematophagous; feeds exclusively on birds; 26 mm.

Oosthuizobdella aspera (Moore, 1939) (= *Placobdella aspera*) (Fig. 14.6H): extremely rare in southern Africa, only one record from Kruger National Park; haematophagous on crocodiles; 14,9 mm (contracted).

Oosthuizobdella garoui (Harding, 1932) (=*Placobdella garoui*) (Figs 14.5A, 14.6C, 14.7A): common in eastern parts of southern Africa. Rare in dry western parts, but fairly common in the northern parts of Namibia; occurs in various types of habitats, particularly pans and vleis, in which the leeches are often present in very large numbers; haematophagous on reptiles, birds and mammals; 38 mm.

Oosthuizobdella stuhlmanni (Blanchard, 1897) (=*Placobdella stuhlmanni*) (Figs 14.5B, 14.6C, 14.7B): common throughout southern Africa but only in habitats where there are amphibians; haematophagous on amphibians; 33 mm.

Hemiclepsis quadrata (Moore, 1924) (=*Batracobdella quadrata*) (=*Alboglossiphonia quadrata* Sawyer, 1986) (Fig. 14.6F): apparently rare, known only from coastal areas in KwaZulu–Natal; probably haematophagous on fish; 7,6 mm.

Alboglossiphonia conjugata (Oosthuizen, 1978) (= *Batracobdella conjugata*) (Figs 14.6D, 14.7C–D): throughout southern Africa, very common in north-western parts but not common in other parts; liquidosomatophagous; 9 mm.

Alboglossiphonia macrorhyncha (Oosthuizen, 1978) (=*Glossiphonia macrorhyncha*) (Figs 14.6D, 14.7C–D): very common in most eastern parts of southern Africa, progressively less so westeward and not yet recorded in western half or region; liquidosomatophagous; 10 mm.

Alboglossiphonia cheili (Oosthuizen, 1978) (=*Batracobdella cheili*) (Figs 14.6D, 14.7C–D): throughout southern Africa, very common in north-western parts but not common elsewhere; liquidosomatophagous; 3 mm.

Alboglossiphonia disjuncta (Moore, 1939) (=*Glossiphonia disjuncta* = *Batracobdella disjuncta*) (Figs 14.6E, 14.7E & F): very common throughout southern Africa; liquidosomatophagous; 12 mm.

Batracobdelloides tricarinata (Blanchard, 1897) (= *Batracobdella tricarinata* = *Batracobdella nilotica* = *Batracobdella amnicola*) (Figs 14.6H, 14.7G): very common throughout the region, present in any body of water inhabited by fish; haematophagous on fish, especially catfishes (Clariidae); 20 mm.

Helobdella stagnalis (Linnaeus, 1758) (Fig. 14.7H): fairly common in eastern parts but apparently not present in western, drier parts; liquidosomatophagous on oligochaetes; 13 mm.

Helobdella conifera (Moore, 1933) (Fig. 14.7I): very common in eastern and northern parts of southern Africa and extremely abundant in some habitats; apparently not present in drier western parts; liquidosomatophagous; 14 mm.

Marsupiobdella africana Goddard & Malan, 1912 (Figs 14.3C, 14.4A, 14.6I & 14.8A): common throughout southern Africa in bodies of water inhabited by *Xenopus* spp.; often found on freshwater crabs which serve as transport hosts; haematophagous, apparently exclusively on *Xenopus* spp.; 12 mm.

Placobdelloides multistriata (Johansson, 1909) (= *Placobdella multistriata* = *Placobdella pulchra* = *Placobdella auroguttata* = *Placobdella unita*) (Fig. 14.4J): very common throughout southern Africa; haematophagous on terrapins and crocodiles; 40 mm.

Because of its habit of using large, freshwater hemipterans (waterscorpions and waterbugs) as transport hosts, this species is often found in bodies of water not inhabited by the hosts on which it feeds, occurring even in swimming pools and temporary pools of rain water, to which it is introduced by these night-flying insects.

Placobdelloides jaegerskioeldi (Johansson, 1909) (= *Placobdella jaegerskioeldi*) (Figs 14.4K, 14.7J–K): restricted to habitats inhabited by hippopotamuses; haematophagous; host specific; 62 mm.

Salifidae

Salifids are thin and mostly without color. They can often be found in aerated streams where their favorite food is chironomid larvae. The obserservation of numerous oval chitnoid 'cocoons' (egg cases) cemented to the undersides of rocks and debris also provided evidence of the presence of these leeches.

Barbronia spp. (Figs 14.4B & 14.6C): this genus is represented by two undescribed species, both of which are fairly common in the south–eastern region, less so westward; not yet recorded in the dry, western and northern areas; macrophagous; 22 mm (both).

Salifa africana (Moore, 1939) (= *Mimobdella africana*) (Figs 14.4M & 14.2G): known only from one locality in the most North-easterly part of southern Africa; macrophagous; 33,3 mm.

Salifa perspicax Blanchard, 1897 (Figs 14.2G & 14.4N): common throughout southern Africa; macrophagous; 40 mm.

Hirudinidae

These are the true 'medicinal' leeches which subsist almost exclusively on blood acquired from amphibians and other vertebrates. In the fully adult state they are large (up to 10 cm) and excellent swimmers exhibiting rather ornate color patterns on their dorsal surface.

Asiaticobdella fenestrata (Moore, 1939) (= *Limnatis fenestrata*) (Figs 14.8B, C): restricted to but common in north-western part of southern Africa; haematophagous on mammals; 60 mm.

Hirudo hildebrandti Blanchard, 1897 (=*Aliolimnatis hildebrandti* Sawyer, 1986) (Figs 14.1C, 14.2H, 14.6A & 14.8D, E, F–H): common in eastern parts, not present in western parts; haematophagous on mammals; 35 mm.

Hirudo michaelseni Augener, 1936 (= *Aliolimnatis michaelseni* Sawyer, 1986) (Figs 14.8E, M): very common throughout southern Africa; haematophagous on mammals but also on amphibians and fish; immature leeches also feed on freshwater snails; 65 mm.

Aliolimnatis africana (Blanchard, 1897) (= *Limnatis africana*) (Fig. 14.8I): restricted to most northerly parts; haematophagous on mammals; 40 mm.

Aliolimnatis oligodonta (Johansson, 1913) (=*Limnatis oligodonta*) (Fig. 14.8J): common in eastern parts, not present in western parts; haematophagous on mammals; 58 mm.

Aliolimnatis butonensis (Meyer, 1951) (= *Limnatis butonensis*) (Fig. 14.8K): very common in eastern parts of southern Africa from KwaZulu–Natal northwards, not present in southern and western parts; haematophagous on mammals; 85 mm.

Aliolimnatis obscura (Moore, 1939) (= *Limnatis obscura*) (Fig. 14.8L): common in western part of southern Africa and from southern parts of Namibia and Botswana northwards; haematophagous on mammals.

Praobdella maculata (Moore, 1939) (= *Myxobdella maculata*): in eastern parts of southern Africa from KwaZulu–Natal northwards; not common; haematophagous in nasal cavities of mammals; 52 mm (contracted).

Praobdella radiata Moore, 1958: in eastern parts of southern Africa from KwaZulu–Natal northwards; not common; haematophagous in nasal cavities of mammals; 61 mm.

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GLOSSARY OF TERMS

aboral	the surface of an animal away from the mouth
abyss	the deepest parts of the ocean
acellular	not composed of cells
acentric	not in the centre
acoelomate	any animal that does not possess a coelom (q.v.)
acute	sharply pointed
adult	a sexually mature individual that is able to breed
alien	of plants and animals, introduced from elsewhere, neither endemic or indigenous
alimentary canal	(= gut): a tubular organ divided into a series of zones specialized for the ingestion, digestion and absorption of food
ambulatory	walking
amictic	of rotifer eggs, produced parthenogenetically and not able to diapause (q.v.)
Amman's lactophenol	a substance used for clearing nematodes before viewing them microscopically
amoebocyte	one of the types of cell making up the body of a sponge; moves by means of pseudopodia as an amoeba does
amoeboid	moving by means of pseudopodia (q.v.)
amphibious	able to live in both water and air
amphidelphic	having two ovaries, one anterior to the vulva (q.v) and the other posterior
amphids	a pair of sense organs situated laterally on or near the lip region of nematodes
amphimixis	sexual reproduction: the fusion of male and female gametes (ova and spermatozoa) to form a zygote
amphioxea	a sponge spicule pointed at both ends
amphistome	of cercariae, with the ventral sucker situated at the posterior end
anastomosing	forming a network
anoxic	lacking oxygen
atrium	in oligochaetes, a chamber between the vas deferens (q.v.) and the male genital pore, sometimes containing a penis
annulated	with regular ring-shaped constrictions or markings
annule	he interval between two annulations
antenna	a thin, elongate, anterior sensory appendage
anterior	towards the head end of an animal
apical	at the tip
appendage	an structure such as an antenna or limb attached to the main body
archaeocyte	in sponges, a cell that gives rise to an egg

argentophilic	having an affinity for silver stains
artesian	of ground waters, under pressure
asexual reproduction	a mode of reproduction in which new individuals are produced from a single parent without the formation of gametes
aspirator	a piece of collecting equipment for sucking up small organisms
astatic	not constant: of aquatic ecosystems, those in which the water level fluctuates
autotrophic	not dependent upon organic material for food
axial stylet	a spear or stylet situated centrally in the lumen of the stoma of a nematode
axopod	(= axopodium): in protozoans, a thin, stiff, projecting pseudopod with a central axial filament composed of microtubules around which a thin layer of cytoplasm flows
basal knobs	(= stylet knobs): tripartate thickenings at the base of the stomatostylet (q.v.), or at the base of the extension of the odontostylet (q.v.) in nematodes
basal bulb	(= terminal bulb): part of the oesophagus of a nematode
bathypelagic	living in the water column deep in the sea
bell margin	the margin of the 'bell' or 'umbrella' of a medusa
benthic	pertaining to the bottom of a river, lake or wetland
bifid	split in two: bifurcate
bifurcate	forked: split in two
binary fission	the division of a cell (usually refers to a protozoan) into two identical daughter individuals following mitosis (q.v.)
biocontrol	control, usually of a kind of living organism, using another biological agent such as a predator or parasite
birotulate	a sponge spicule in which each end is disc-shaped
bladder	the internal organ in which urine is stored
blood fluke	a trematode fluke that lives in the bloodstream of its primary host
brackish	of water, salty but not as salty as sea water
branchial	concerning the gills
brevifurcous	with a short fork
brood pouch	(= marsupium): in leeches, a pouch in the mother's body in which eggs develop
buccal cavity	in ciliates, a depression leading to the cytostome and containing specialized ciliature
buccal cavity	(Nematodes) See *stoma*
buccal capsule	(Nematodes) see *stoma*
buccal field	in rotifers, the cilia around the mouth
budding	reproducing asexually by production of outgrowths from the body

bursa	one of a pair of lateral extensions of the cuticle posteriorly in some male nematodes
calcareous	chalky
cardia	in nematodes, a muscular, heart-shaped, conoid or elongate structure at the base of the oesophagus, projecting into the intestine and serving as a valve
caudal furca	a tail-fork
cell wall	in plants, the rigid, non-living structure enclosing the contents of each cell
cephalic	related to the head
cercariometry	measurement of the abundance, longevity and spatial distribution of platyhelminth cercariae
cerebral ganglion	the 'brain' of an invertebrate
chaeta	in oligochaetes, a chitinous bristle embedded in the body wall (= seta in polychaetes)
chaetal bundle	any of the four bunches of chaetae in a segment of an oligochaete
claspers	in almid oligochaetes, a pair of lateral flaps apparently used in copulation
clitellum	a saddle-shaped or ring-like swelling of a number of contiguous segments of the body of an oligochaete
cocoon	in oligochaetes, a protective case housing the eggs
crochet	in oligochaetes, a sigmoid (S-shaped) chaeta thickened in the middle of the shaft (contrast *hair chaeta*)
chelorhabdion	see *rhabdion*
chironmid	a midge whose larva are very common in fresh waters
chloroplast	an organelle containing chlorophyll
choanocyte	a filter-feeding, flagellated 'collar cell' in a sponge
cilia (sing. cilium):	fine, hairlike organelles projecting from the cell body, invariably in large numbers
ciliated	bearing cilia
ciliates	Ciliatea or Ciliophora: the ciliated protists
cingulum	a shallow groove encircling the cell body of a dinoflagellate and containing a transverse flagellum
cirri	(sing. *cirrus*): in ciliates, fused tufts of cilia forming stout, stiff, locomotory organelles
cladoceran	a branchiopod crustacean characterized by the presence of a bivalved carapace (see Vol. 2)
class	a taxon above order and below phylum
clavate	club-shaped
claw	a stout, hooked seta or bristle
cleft	split
clitellum	a saddle-shaped or ring-like nodule or swelling of certain adjacent segments in many non-polychaete annelids
cloaca	a common cavity into which the alimentary canal and the ducts of the urinogenital system open

cloaca (nematodes)	the joint terminal duct formed by the fusion of the vas deferens with the rectum in most male nematodes
clonal	genetically identical
cocoon	a protective case covering eggs or other immature stages of invertebrates
coelom	a body cavity formed within the mesoderm and lined by the peritoneal membrane: the main body cavity in most metazoan animals
coelomoducts	ducts connecting the coelom of an animal with the exterior
colonial	forming a colony consisting of a number of individuals
column	the cylindrical body of a hydroid polyp
commensal	a member of an association between organisms of two different species in which neither partner suffers any disadvantage
compressed	flattened (laterally compressed = flattened from both sides)
confluent	running together
conjugation	the complex and unusual process of sexual reproduction in cileates
conoid	shaped like a cone
contiguous	touching
contractile vacuole	in protists, a small spherical vesicle that regularly discharges water
copepod	a small, usually planktonic, crustacean (see Vol. 3)
corona	in rotifers, the apical ciliated band, characteristically composed of two rings called the 'trochus' (q.v.) and the 'cingulum' (q.v.)
cosmopolitan	occurring throughout the world
coverslip	a thin square of glass placed on a specimen on a slide under a microscope before viewing
crenate	having a margin formed of notches
crochet	a slender, S-shaped seta (q.v.)
cryptobiosis	a latent state in which metabolism comes to a reversible halt
cuticle	a non-living external protective layer produced by the ectoderm
cuticular membrane	in sponges, the membrane that adheres to the substratum
cyst	a protective capsule containing a dormant egg or larva
cystogenous	in cercariae, cyst-forming cells
cytopharynx	in ciliates the region, immediately below the cytostome, where food vacuoles are formed
cytoplasm	the material that forms the contents of a cell
cytostome	literally the 'cell mouth': in ciliates, a fixed location for the ingestion of food particles (see *buccal cavity, oral vestibule, oral groove*)
dendriform	branched like a tree
denticle	a small tooth
depressed	flattened (dorsoventrally depressed = flattened as if from above)
dermal membrane	in sponges, the outer 'skin'

dermatitis	inflammation of the skin
desmoneme	a nematocyst in which the distal end of the discharged thread coils around the prey
detritivore	an animal that feeds on detritus (q.v.)
didelphic	of a nematode, having two ovaries
detritus	in an ecological sense, the remains, often fragmentary, of dead plants and animals
diagnostic	of a character, one that defines the difference between a taxon and other similar ones
diapause	a period of slowed or arrested growth and development
digitiform	finger-like
dimorphic	of two distinct forms
dioecious	having separate males and females
diploblastic	of an animal, having a body wall composed only of two cell layers
diploid	having two sets of chromosomes per cell
distal	of an appendage, the end furthest from the midline of the body or the point of attachment(contrast *proximal*)
distome	of trematode platyhelminthes, having two suckers
diverticulum	(pl. diverticula): a sac-like outgrowth from a hollow internal organ
dorsal	the upper surface of an animal - usually the surface away from the substratum
dorso-ventrally flattened	flattened from above: depressed
DPX	a substance used as a mountant to make permanent slide preparations

ectocommensal	commensal animal living on the outside of its partner's body
ectoderm	the layer of cells in an embryo that will develop into the epidermis and nervous system of the adult
ectoparasite	a parasite living on the outside of its host's body
encystment	retreating into an impermeable shell (cyst) when environmental conditions deteriorate
endemic	restricted to, and native to, a particular area
endoderm	the layer of cells in an embryo that will line the alimentary canal and other internal organs of the adult
entire	of a margin, complete, without notches or slits
epidermis	the skin
epiphytic	living physically on the outer surface of a plant
epizoic	living attached to the body of another animal (or some times pertaining to one animal living attached to another)
eukaryote	an organism with a membrane-bound nucleus containing the nuclear DNA; all organisms except for bacteria and bluegreens are eukaryotic

euryhaline	able to thrive in a wide range of salinities
eurythermal	able to thrive in a wide range of temperatures
eutrophic	rich in nutrients
eutrophication	the process whereby high concentrations of nutrients result in the excessive growth of plants
excretion	(adj. = excretory): the elimination from an organism of waste products that arise as a result of metabolic activity
exoskeleton	the external covering of certain animals that protects and supports the body
exotic	see 'alien'
eye spot	a minute spot of pigment indicating a region of light-sensitivity in lower invertebrates
facultative	optional, hence able to survive in more than one habitat or life style
family	the taxon higher than genus and lower than order
fascicle	a small bundle or tuft
filament	a long, thread-like structure
filiform	slender, like a thread
filopod	(= filopodium) in protozoans, a long, thin, pointed pseudopodium with clear non-granular cytoplasm and lacking an axial filament
filter-feeder	an organism that feeds by filtering fine organic particles from the water
fission	asexual division of an organism into more-or-less-equal daughter cells
fixation	the chemical treatment of tissues to preserve intracellular structure and to facilitate subsequent staining
flagellated chamber	in sponges, a tiny chamber, lined by choanocytes, though whihc water is filtered
flagellum	(pl. flagella): a threadlike locomotory organelle projecting from the cell body
flame cells	ciliated cells at the ends of the distal tubules of the excretory systems of worms such as platyhelminths
flame bulb	flagellated cells that form part of the excretory and osmoregulatory system of platyhelminthes, rotifers and nemertines
flimmer	see *mastigoneme*
fluke	common name for a parasitic adult trematode flatworm
foot	in rotifers, the posterior part of the body
forcipate	forceps-like
Friedinger bottle	a device for taking water samples at predetermined depths
frustule	the siliceous capsule enclosing the cell body of a diatom or, in cnidarians, a planula-like bud (see *planula*)
furcate	forked

fusiform	spindle-shaped
gamete	a sex cell: spermatozoan or ovum (egg)
gastrodermis	layer of endoderm lining the inside of the gastrovascular cavity of cnidarians
gastrovascular	in cnidarians, the gut
gemmosclere	in sponges, the spicules in the wall of a gemmule
gemmule	(= statoblast) in sponges, an 'overwintering' body
genital	reproductive
genus	the taxon above species and below family
germinal sac	in trematodes, a sac-like structure in which germinal cells develop into further generations of germinal sacs or into cercariae (see *redia*, *sporocyst*)
gill	in aquatic organisms, a filamentous or platelike outgrowth through which gas exchange occurs
gonad	reproductive organ
gonochoristic	of an individual, of one sex only
gonopore	the pore through which gametes are released to the outside of an animal
gubernaculum	in nematodes, a grooved sclerotized structure in the dorsal wall of the spicular pouch (q.v.) that acts as a guide for the spicules
gullet	in flagellated protozoans, a sac-like depression extending into the cytoplasm
gut	alimentary canal (q.v.)
hair chaeta	in oligochaetes, a slender, hair-like chaeta with no swelling in the middle of the shaft (contrast *crochet*)
hair setae	very fine hair-like setae (q.v.)
haploid	having only one set of chromosomes per cell
head	the anteriormost tagma (q.v.) of the body of a bilaterally symmetrical animal, usually bearing the mouth, the brain and sense organs
hermaphrodite	of an individual, having both male and female gonads
hermaphrodite, sequential	of an individual, being first of one sex and later of the other
heterotrophic	requiring food in the form of organic material
histology	the study of the structure of cells and tissues
histolytic	able to destroy or disrupt tissue
homologous	of morphological features, of similar evolutionary origin
hooded hook	in polychaetes, a hooked seta (q.v.) with a thin membranous cover
host	an organism in or on which a parasite lives
hyaline	clear, transparent (cartilage-like)
hydranth	see *polyp* (Cnidaria)

hydroid	(adj.) e.g. *hydroid polyp*: referring to cnidarian polyps—see *polyp* (Cnidaria) (q.v.)
hydroid colony	see *polyp colony* (q.v.)
hyperosmotic	of body fluid, with a higher concentration of salts than the surrounding medium
hyponeuston	organisms floating at or immediately below the water surface
hypostome	a raised part around the mouth of a hydroid polyp (q.v.)
incisure	a notch, slit or cleft
infauna	the animals living within a soft substratum
inflated	as if blown up: greatly expanded
infundibulum	a funnel-shaped structure
intermediate	of hosts, one in which a parasite undergoes asexual but not sexual reproduction
interstitial	of animals, living between sand grains
intestine	a major part of the alimentary canal, posterior to the stomach and anterior to the rectum
invaginated	introverted
isorhiza	a type of nematocyst (q.v.) in cnidarians
jellyfish	a medusa (q.v.)
labial	related to the lip region
lamella	a sheet
lamellar	sheet-like
larva	a juvenile stage in the life cycles of many invertebrates
lateral	on the side (of an animal)
lobate	lobe-like
lobopod	(= lobopodium) in protozoans a blunt, finger-like pseudopod containing both ectoplasm and endoplasm
lobulate	having a lobed margin
lorica	a loose-fitting, non-living case surrounding the cell body of some mastigophorans, ciliophorans (see *test*) and rotifers
lumen	the cavity inside a hollow structure
macronucleus	in ciliates, a large polyploid nucleus
macrophagous	feeding on large particles of food
macrophyte	a large plant, usually found in or near water
maculated	spotted
maculations	spots
malleate	hammer-shaped
manubrium	the soft tissue hanging down round the mouth of a medusa
marginal	of vegetation, growing at the edge of the water
mastax	in rotifers and gastrotrichs, the muscular pharynx containing a set of jaws called *trophi* (q.v.)

mastigoneme	a stiff lateral projection set at right angles to the long axis of the flagellum in some flagellated protozoans (also called 'flimmer fibres' or simply 'flimmers')
medial/median	towards the middle
median bulb	in nematodes, the median bulb of the oesophagus, bearing sclerotized valve-plates
median sagittal plane	the plane dividing a bilaterally symmetrical animal into two halves
medusa	the free-swimming jellyfish stage in the life cycle of cnidarians
megadrile	of oligochaetes, the large, generally terrestrial, earthworm-like forms (order Lumbricida)
microdrile	of oligochaetes, the aquatic, non-earthworm-like forms (orders Lumbridulida and Tubificida)
monogeneric	of a family, having a single genus
megasclere	a large sponge spicule
meiosis	a type of cell division in which haploid gametes (q.v.) are produced from diploid cells (contrast *mitosis)*
membranelle	in ciliates, an organelle formed by the fusion of a short transverse row of cilia to form a fin-like structure that creates feeding currents
mesoglea	the gelatinous, non-cellular layer between the endoderm and ectoderm in the body wall of cnidarians
mesorhabdion	see *rhabdion*
metacercaria	an encysted cercaria (q.v.)
metarhabdion	see *rhabdion*
metazoa	(sing. metazoan): multi-cellular animals
methyl cellulose	a glutinous substance that slows down movement of microcroscopic organisms
microbivorous	feeding on microbes, mainly bacteria
micronucleus	in ciliates, the small diploid nucleus
microphagous	feeding on small particles
microsclere	a small sponge spicule
mictic	of rotifer eggs, produced by sexual reproduction and parthenogenetically and able to undergo diapause (q.v.)
miracidium	the ciliated, often free-swimming, first larval stage of trematodes
mitosis	the process of division into identical daughters (cf. meiosis)
moniliform	like a string of beads
monodelphic	having one ovary
monomorphic	having a single shape or form
monospecific	'one species': a genus (usually) that contains only one species
monostome	in trematodes, lacking the ventral sucker, so bearing only one sucker
morphological	concerning external form and structure

motile	able to move
moulting	shedding of the exoskeleton or cuticle
mountant	a liquid used for mounting biological material on a microscope slide
mural tooth	a tooth in the wall of the pharynx of nematodes

natatory	concerned with swimming
nematocyst	a cnidarian stinging cell
neuropodium	in polychaetes, the ventral flap of the parapodium (q.v.)
neutral red	a vital stain (q.v.)
Nile blue sulphate	a vital stain (q.v.)
nodule	a node or swelling
notopodium	in polychaetes, the dorsal flap of the parapodium (q.v.)
nuclear stain	a dye that shows up details of the nucleus

oar chaetae	in oligochaetes, flattened, blade-like crochets (q.v.)
obligate	not optional, hence limited to one habitat or life style
organic enrichment	(= organic pollution): of surface waters, containing much organic matter, usually of faecal origin
obligate	not optional: of parasites or commensals, those that cannot exist without the host
occlusion	closing off
ocellus	(= eye spot): a simple eye, typically consisting of some light-sensitive and some pigment cells
odontostyle	a toothed stylet (q.v.) in nematodes
oesophagus	the portion of the alimentary canal between the mouth and the intestine (in nematodes between stoma and intestine)
oesophagealthat intenstinal junction:	part of the alimentary canal where the oesophagus joins the intestine
oil immersion	a technique for viewing minute structures under a microscope using 'immersion oil' between objective lens and object to be viewed. to view specimens under oil immersion (for better resolution) a drop of immersion oil is placed between the 100x oil immersion objective of the microscope and the coverslip
oocyte	a cell that will give rise to an ovum
operculum	a lid: in some polychaetes, the structure that closes the mouth of the tube
opisthaptor	an posterior organ of attachment in monogenean trematodes
opisthodelphic	having a single ovary, situated posterior to the vulva
optical section	under the microscope, the section of the specimen that is in focus
oral	of the mouth: in cnidarians, the surface on which the mouth occurs (contrast *aboral*)

oral groove	in ciliates, a more-or-less-longitudinal groove leading to the buccal cavity
oral sucker	*in trematodes, the sucker around the mouth*
organelle	a part of a cell that carries out a specific function; analogous to an organ in a multicellular organism
oral vestibule	in the body surface of a ciliate, a ciliated depression leading to the cytostome
order	the taxon higher than family and lower than class
osculum	on the surface of a sponge, one of the small pores through which water enters a sponge (contrast *ostium*)
ostium	on the surface of a sponge, one of the numerous minute pores through which water leaves a sponge (cf. *osculum*)
ovary	the female reproductive organ
ovigerous	egg-bearing
ovotestisa	gonad (q.v.) producing both eggs and sperm
ovoviviparous	of female animals, those that retain their eggs in the body and give birth to live young
ovum	an egg cell
palmate	like a palm leaf
pectinate	comb-like; of oligochaete chaetae, with a number of small teeth between the main outer teeth of a bifid crochet (q.v.)
penial	*referring to the penis*
palmella	a non-motile 'larval' stage of some normally motile autotrophic flagellates
palp	a short, stubby tactile anterior sense organ in some polychaetes
papilla	a small, soft nipple-like protrusion
paraoral	near the cytostome of ciliates
parapodium	(pl. parapodia): one of paired lateral flaps on most segments of polychaetes
parenchyma	the ground tissue of animals such as platyhelminths
parthenogenesis	development of an ovum into a new individual without fertilization
Pasteur pipette	a pipette with a fine nozzle and a rubber bulb for creating suction
patent infection	infection of a host from which cercariae are being shed (see *pre-patent*)
pathogen	a disease-causing organism
pectinate	comb-like; of setae, having a bifurcate tip with smaller spinules between the two prongs
pedal disc	in hydroids, the basal part of the column (q.v.) that attaches to the substratum
peduncle	stalk
pelagic	living in the water column (usually implies an ability to swim against the current - see *plankonic*)

pellicle	in protozoans, the outermost living layer that incorporates the plasma membrane and gives the body a characteristic shape
periphyton	the community of microscopic organisms living on the surfaces of plants (see *epiphyton*)
peristome	an area on the surface of a ciliate bearing an extension of the specialized buccal ciliature
peristomium	in annelids, the first segment, immediately behind the prostomium (q.v.), surrounding the mouth and containing the cerebral ganglion (the 'brain')
pharynx	the gullet: the part of the alimentary canal immediately behind the mouth
phasmid	one of a pair of papillae on the tails of nematodes
phreatic	interstitial: living between sand grains
phylum	the highest taxon in the classification of animals
pinnate	feathery
planktonic	floating in the water column and at the mercy of the current (contrast *pelagic*)
planula	the minute, ciliated firtst larval stage of most cnidarians
plasma membrane	the cell membrane: in protozoans, usually the outermost 'skin' of the body
plumose	feathery
pneumatic layer	in sponges, the subsurface layer containing minute air spaces
polyp	an individual zooid of a colonial animal
polyp (Cnidaria)	(=hydranth): sessile stage in life cycle of cnidarians that typically reproduce asexually by budding. Some polyps are single, others form colonies (also called *hydroid colonies* or *polyp colonies*)
polyphyletic	of a taxon, arising from different ancestral groups
posterior	towards the tail end of an animal
pre-patent infection	infection before the time at which cercariae are released
prostomium	the presegmental part of the body of an annelid
protrusible stylet	(in nematodes) (=extrusible stylet) a stylet that can be protruded (extruded) through the mouth opening (used to pierce plant cells and suck out the contents)
prehensile	grasping
proboscis	a trunk-like moveable extension of the head
prodelphic	having a single ovary
produced	extended, elongated
prolobae	cuticular extensions on the lip region of certain nematodes
prorhabdion	see 'rhabdion'
Prosobranchia	a taxon of aquatic snails
prostomium	in annelids, a dorsal part of the head anterior to the first somite

protogynous	of sequential hermaphrodites (q.v.), those that are first female and then male
protoplast	the living part of a cell, excluding the cell wall, test, lorica etc.
protrandric	of sequential hermaphrodites (q.v.), being first male and later female
proventriculus	a part of the gut, usually anterior to the stomach and acting as a storage and/or grinding organ
proximal	of an appendage, the end nearest to the body
pseudocoelomate	the condition in which the body cavity (the pseudocoel) *derives from the embryonic blastocoel*
pseudopodium	(= pseudopod, pl. pseudopodia): a protrusion of a cell body, usually in the direction of movement, usually temporary, and usually locomotory in function
Pulmonata	a taxon of snails, usually terrestrial or freshwater
pyriform	pear-shaped
radial canal	one of a series of canals radiating from the mouth of a cnidarian medusa (q.v.)
radial symmetry	with a number of planes of symmetry around a central axis
rhabdion	in nematodes, a series of sclerotized sections of the wall of the stoma (mouth), appearing like a series of rods
radiole	in some polychaetes, one of the whorls of anterior tentacles
ramus	(pl. rami): a branch
rectum	the terminal part of the digestive tract
redia	in trematodes, a type of germinal sac, with a muscular pharynx and intestine, which can move within the host's tissues
reniform	kidney-shaped
repent	extending over a surface; creeping
reservoir	in flagellates, a localized depression in the pellicle forming a cavity from which the flagella arise
reticulopod	(= *reticulopodium*) a long, thin, branching pseudopod similar to a filopod but with frequent anastomoses between branches and between separate pseudopodia forming a filter-feeding net
robust	strong, stout
rostrum	a beak-like anterior process
rotatory organ	see *corona*
saprophagous	feeding on dead or decaying organic matter
sclerotized	tanned and hardened
sedentary	not freely-moving: attached to the substratum
segment	(more properly, *somite*): any of the individual sections making up the body of a segmented animal

semi-membrane	a membrane-like structure formed from a row of partially joined cilia that are free at their distal ends
sensilla	a small sense organ
sessile	attached or stationary, and without a stalk
seta	(= chaeta): a fine hair or bristle; a *compound* seta appears to be made up of more than one element
seta (in nematodes)	a slender to stout hairlike outgrowth from the cuticle, with a sensory function
setiform	seta-like
sexual reproduction	reproduction that involves the fusion of haploid gametes to form a diploid zygote
spermathecal chaetae	in oligochaetes, specialized chaetae in the ventral bundles of the spermathecal segment
siliceous	composed of silica or a related silicon compound
somatic	pertaining to the body as opposed to the gonads (q.v.)
somite	any of the individual sections making up the body of a segmented animal (= segment)
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
spermatheca	a sac that receives sperm from the copulating partner and stores it
spermatid	a stage in the development of a spermatozoan (q.v.)
spermatophore	a 'package' containing sperm
spermatozoon	a sperm cell
spicule	a small needle; in nematodes, the sclerotized male copulatory organ
spinnaret	(= terminal duct): the terminal opening of the caudal glands in nematodes
spinule	a small (usually thin) spine
sporocyst	in trematodes, a type of germinal sac (q.v.) in which there is no pharynx or intestine
spur	a stout spine
statoblast	(= gemmule): in sponges, an overwintering body
statocyst	a sense organ that indicates the horizontal plane
stenohaline	of organisms, those unable to thrive outside a narrow range of salinities
stenotele	a type of cnidarian nematocyst
stigma	a pigmented granule overlying the 'eyespot' in many autotrophic flagellates
stolon	the creeping >stem= that joins polyps in some cnidarians
stoma	in nematodes, the mouth (but sometimes called the pharynx)
stria	(pl. striae): elongate depressions or grooves

stylet	a hard, slender, bristle-like structure; in nematodes, a heavily sclerotized organ in the stoma
sub-fusiform	almost spindle-shaped
sub-acute	almost forming an acute angle: pointed but not sharp
sub-cylindrical	almost cylindrical
subequal	almost equal
subitaneous eggs	commence cleavage as soon as they are alid
succession	a sequence of species assemblages replacing one another over time
sulcus	a shallow longitudinal groove extending posteriorly from the cingulum of a dinoflagellate
supplement	one of a series of copulatory papillae in the males of some nematodes
supravital stain	a dye used to colour the internal organs of small organisms while they are still alive
symplasm	the main tissue forming the body of a sponge
synonymy	the names by which a species has been called
systematics	the study of the evolutionary relationships between organisms
tagma	one of the major divisions of the body (eg. head, thorax)
tentacle	a slender, flexible, sensory organ (used for prey-capture
in	hydroids)
test	a non-living case enclosing the cell body of some animals; may incorporate substances like sand
testate	enclosed in a test
testis	(pl. testes): the male reproductive organ
thecal plate	one of a series of cellulose plates covering the surface in some dinoflagellates
thesocyte	the cells of a sponge that form a gemmule (q.v.)
toes	in rotifers, the divided posterior extremity of the body
tri-radiate	radially symmetrical (q.v.) with three planes of symmetry
triad	a group of three
trichite	one of many rod-like structures in the cytopharyngeal region of some Mastigophora and Ciliophora
trichocyst	an extrusible sub-pellicular dart-like organelle found in many ciliates
trichopteran	a stonefly
truncate	cut off bluntly
trunk	the posteriormost tagma (q.v.) in many animals
tubercle	a small knob-like outgrowth or projection
turbidity	murkiness of water

ultrastructure	structural details too small to be seen except through an electron microscope
uncus	a hook
undulating membrane	a membrane formed by the fusion of (usually) two longitudinal rows of cilia; part of the buccal ciliature, located on the right of the cytostome
vacuole	a fluid-filled space in the cytoplasm of a cell
vagile	able to move freely
vas deferens	the duct that carries sperm from the testis
ventral	the lower surface of an animal - normally the surface closest to the substratum
ventral sucker	the more posterior of the two suckers of trematode parasites
vermiform	worm-like
vestigial	small and imperfectly developed
virgula	organ in platyhelminthes, an organ in which mucoid secretions are produced
vital stain	a substance that stains small organisms while they are still alive
viviparous	bearing live young
voucher specimen	an identified specimen, pertaining to a specific project, housed in a properly curated collection together with full bionomic notes
vulva	in nematodes, the external opening of the female reproductive system
zygote	the fertilized egg resulting from the fusion of egg and sperm

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.
Northern Province (NP)	formerly the 'northern Transvaal'.
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.
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 northern 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