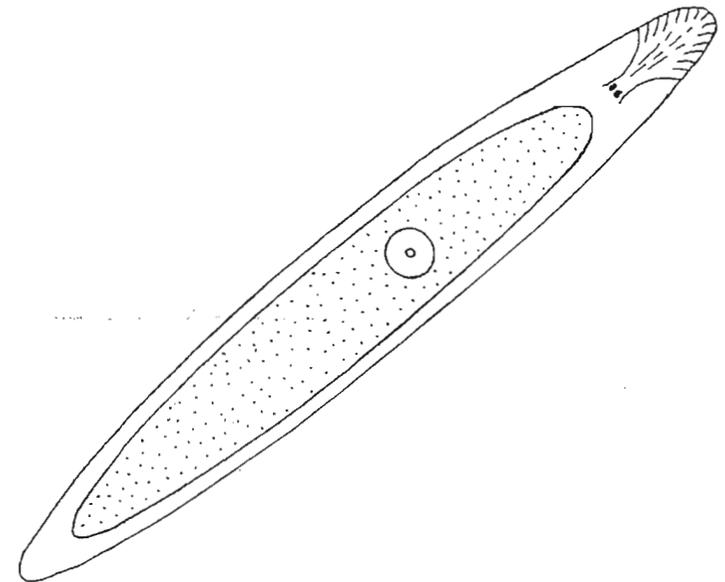


**KEYS TO THE
FRESHWATER
MICROTURBELLARIANS
OF BRITAIN AND IRELAND**
WITH NOTES ON THEIR ECOLOGY

J. O. YOUNG



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The Environment Agency is pleased to be associated with the publication of this key, the 59th in the FBA's series of Scientific Publications. The keys provide essential, authoritative information needed for both pure and applied freshwater ecologists.

This key is an invaluable source reference for the collection and identification of microturbellarians throughout the British Isles, and further advances our knowledge of this group of "flatworms". High quality information is required to underpin future advances in the assessment of the state of our fresh waters. The Environment Agency's aim is to achieve the best water environment for England and Wales. Accurate identification of lesser-known macroinvertebrates is essential with respect to the Agency's duties with regard to biodiversity and furthering conservation. Microturbellarians are not routinely used in the Agency's monitoring programmes, but our support of this publication is indicative of our belief in the better understanding of our native biota in order to manage the environment more sensitively.

Paul Logan
National Ecology Advisor
Environment Agency

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PREFACE

Our last Scientific Publication (No. 58) was a revised key to the freshwater triclads or free-living Turbellaria, written by Professor T. B. Reynoldson and Dr J. O. Young. Their key dealt with the twelve species of "flatworms" known to occur in Britain and Ireland. These macroturbellarians are relatively large in size, with adults ranging from about 8 mm to 35 mm in length, making them familiar animals to everyone who samples in fresh waters.

Now, in this latest Scientific Publication (No. 59), Dr Young has extended our coverage of the Turbellaria by producing a series of keys which, for the first time, enable the user to identify 56 species of free-living microturbellarians that currently have been recorded from Britain and Ireland. Like the larger triclads they occur in a wide range of freshwater and brackish habitats, but are less widely known, perhaps because of their small size. With a body length often less than 3 mm and a lanceolate shape, popular methods of collecting benthic macroinvertebrates may result in the escape of these small microinvertebrates through the relatively coarse meshes of most pond-nets. Unfortunately, preservation of pond-net samples results in microturbellarians being reduced to insignificant, dull-coloured masses. Hence this key includes informative and essential sections on collection, preservation (for histological examination) and methods of identifying live animals.

The occurrence of some species in temporary, brackish and polluted waters suggests that the group may be useful as part of a monitoring programme for water quality. The clearly illustrated keys provide biologists with one of the necessary tools to investigate this possibility as well as providing an incentive to look for previously undescribed species.

Dr Young has also produced a comprehensive summary of the literature on the general biology and ecology of the group, much of which is available only in German. All who are interested in microturbellarians will have cause to be grateful for the inclusion of this information.

It is hoped that publication of this volume will bring Microturbellaria to the attention of more freshwater biologists than hitherto and help to promote more research on this particular component of the benthic invertebrate fauna.

The Ferry House
March 2001

Roger Sweeting
Chief Executive

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INTRODUCTION

The Phylum Platyhelminthes, or Plathelminthes (see Ehlers & Sopott-Ehlers 1995), traditionally embraces three Classes: the predominantly free-living Turbellaria, and the parasitic Cestoda (tapeworms) and Trematoda (flukes), though in some classification schemes the Monogenea are split off the last group to form a separate Class. The Turbellaria have a ciliated epidermis, rhabdoids, an intestine (gut) without an anus and, usually, a complex reproductive system. Turbellarians conveniently can be divided into two groups, the Macroturbellaria (Polycladida and Tricladida) and the Microturbellaria, though these terms have no taxonomic status. Polyclads and triclads have a branched intestine, whereas microturbellarians have an unbranched sac-like intestine; exceptionally, the Order Acoela contains turbellarians that lack a distinct intestine.

As the name suggests, microturbellarian species are usually small, mostly up to 3 mm in body length, but some can reach 12 mm, e.g. *Mesostoma ehrenbergii*. Most microturbellarians are cylindrical, though a few are flattened (e.g. *Macrostomum* spp.), and some can form chains of zooids by asexual reproduction. They can glide over the surface of the substratum or on the underside of the water-surface, and most can swim though few habitually do so (Hyman 1951).

Microturbellarians occur in a wide variety of freshwater habitats (Bauchhens 1971; Young 1970, 1973a; Mack-Fira 1974; Schwank 1976, 1981a; Kolasa 1979, 1983; Heitkamp 1982). Many species can produce resistant eggs (cocoons), and are particularly well adapted to live in temporary habitats (Heitkamp 1988). Numerous freshwater species can also tolerate brackish water (Luther 1955, 1960, 1963; Kaiser 1974) whilst *Gyratrix hermaphroditus* occurs in the freshwater, brackish and marine environments (Curini-Galletti & Puccinelli 1994; Therriault & Kolasa 1999). Though little is known about the tolerance of microturbellarians to pollutants, some species appear to be more tolerant of organic pollution than others (Schwank 1982b), and Kolasa (2000) suggests that lotic microturbellarians have potential as indicators of water quality. Some microturbellarian species may have an important negative impact on their prey species. Thus, for example, *Mesostoma ehrenbergii* and *M. lingua* may play a role in structuring zooplankton communities, at least in small ponds (Blaustein & Dumont 1990). *Mesostoma* spp. also may have considerable potential for the biological control of mosquito populations (Blaustein 1990). A very few freshwater species are parasitic (Lanfranchi & Papi 1978).

In contrast to the considerable amount of knowledge available on the taxonomy and ecology of freshwater triclads in Britain and Ireland (Reynoldson 1966, 1983; Reynoldson & Young 2000), there is a paucity of such information on microturbellarians (Young 1970, 1975a, 1977a). This is undoubtedly due to their small size and difficulty of identification. Also, the fact that preservation of field samples in formalin or alcohol makes them mostly unrecognisable, compounds the problem. Reliable identification requires the examination of living specimens.

The first key to British and Irish freshwater microturbellarians was published by Young (1970) who listed 44 species. These comprised historical records, including Irish species reported by Southern (1936), and new records collected by the author. During the last 30 years, a further 12 species have been recorded, including one new to science (Young 1972a,b, 1985 and unpublished data; Schmidt & Schmid-Araya 1999). The keys presented here incorporate these additional species, and also incorporate suggestions for improvement of the keys made by students at Liverpool University and by workers at other establishments, over many years. In common with the situation regarding the freshwater triclads of the British Isles (Reynoldson & Young 2000), far fewer species of Microturbellaria have been recorded here than in continental Europe. However, in contrast to triclads, it seems likely that many microturbellarian species remain to be discovered. It is hoped that the publication of the keys and accompanying ecological notes will encourage future studies on this group of fascinating animals.

In recent years, two major publications have appeared concerning the identification of turbellarians from wide geographical regions. The first is a guide to the turbellarian genera of the world (Cannon 1986) and the second is a key to the freshwater turbellarian genera of North America (Kolasa 1991). Both include genera of microturbellarians.

CLASSIFICATION AND CHECKLIST OF SPECIES FOUND IN BRITAIN AND IRELAND

The phylogenetic relationships within the Platyhelminthes in general and Turbellaria in particular are controversial (Ehlers 1985a, b; 1986; Smith *et al.* 1986; Martens *et al.* 1989; Timoshkin 1991; Jondelius & Tholleson 1993; Mamkaev 1995). Earlier studies were based on morphological characteristics, ultrastructure features and developmental processes (Karling 1974; Rieger 1981, 1998; Ax 1984; Sopott-Ehlers 1985; Ehlers 1985b). More recently, whilst some workers still use such criteria (Gremigni 1997; Gremigni & Falleni 1998), most have focused on molecular characters, particularly the use of 18S ribosomal DNA (or 18S rRNA) sequences (Riutort *et al.* 1993; Rohde *et al.* 1993; Katayama *et al.* 1996; Carranza *et al.* 1997; Campos *et al.* 1998; Littlewood *et al.* 1998; Noren & Jondelius 1999).

The classification of microturbellarians is in a state of flux (Cannon 1986) but freshwater species are to be found in the Orders Catenulida, Macrostomida, Prolecithophora, Lecithoepitheliata, Proseriata and Rhabdocoela. Other Orders are solely marine although, exceptionally, the Acoela embraces the freshwater species *Limnoposthia polonica* (Kolasa & Faubel) and *Oligochoerus limnophilus* Ax & Dörjes. The first has been recorded from lakes in Poland (Faubel & Kolasa 1978) and the second from rivers, canals and lakes in continental Europe (Ax & Dörjes 1966; Dörjes & Young 1975) but not as yet from the British Isles. Illustrations of these European freshwater acoelans are given by Ax & Dörjes (1966) and Faubel & Kolasa (1978). An unidentified acoelan has also been recorded from fresh water in North America (Strayer 1985; Kolasa *et al.* 1987).

Again, the status of 'groups' within some of the Orders is uncertain and debated. For example, the Rhabdocoela can be subdivided into three Suborders: the Dalyellioida, Typhloplanoida and Kalyptorhynchia. However, some workers present the rhabdocoels as two 'groupings', the 'Dalyellioida' containing the 'sub-groupings' Dalyelliida and Temnocephalida (symbiotic animals not considered here), and the 'Typhloplanoida' containing the Typhloplanida and Kalyptorhynchia (see Cannon 1986). Kolasa (1991) retains the three Suborders Dalyellioida, Typhloplanoida and Kalyptorhynchia, and refers to the Dalyelliida, Temnocephalida and Typhloplanida as Superfamilies. The classification used in the present publication is given in Table 1, which lists the species found in the British Isles.

Table 1. Classification and checklist of microturbellarian species found in Britain and Ireland.

Order	Suborder	Family	Subfamily	Genus	Species
CATENULIDA					
CATENULIDAE					
				<i>CATENULA</i> Dugès 1832	<i>lemnae</i> Dugès 1832
				<i>SUOMINA</i> Marcus 1945	<i>turgida</i> (Zacharias 1902)
STENOSTOMIDAE					
				<i>RHYNCHOSCOLEX</i> Leidy 1851	<i>simplex</i> Leidy 1851
				<i>STENOSTOMUM</i> Schmidt 1848	<i>anatirostrum</i> Marcus 1945
				[Synonym <i>S. bryophilum</i> Luther 1960]	<i>grabbskogense</i> Luther 1960
					<i>leucops</i> (Dugès 1828)
					<i>unicolor</i> Schmidt 1848
MACROSTOMIDA					
MACROSTOMIDAE					
				<i>MACROSTOMUM</i> Schmidt 1848	<i>distinguendum</i> Papi 1951
					<i>johni</i> Young 1972
					<i>rostratum</i> Papi 1951
					<i>tuba</i> (Graff 1882)
MICROSTOMIDAE					
				<i>MICROSTOMUM</i> Schmidt 1848	<i>lineare</i> (Müller 1774)
PROLECITHOPHORA					
PLAGIOSTOMIDAE					
				<i>PLAGIOSTOMUM</i> Schmidt 1852	<i>lemani</i> (du Plessis 1874)
LECITHOEPITHELIATA					
PRORHYNCHIDAE					
				<i>GEOCENTROPHORA</i> de Man 1876	<i>baltica</i> (Kennel 1883)
					<i>sphyrocephala</i> de Man 1876
				<i>PRORHYNCHUS</i> Schultze 1851	<i>stagnalis</i> Schultze 1851
PROSERIATA					
BOTHRIOPLANIDAE					
				<i>BOTHRIOPLANA</i> Braun 1881	<i>semperi</i> Braun 1881
OTOMESOSTOMIDAE					
				<i>OTOMESOSTOMA</i> Graff 1882	<i>auditivum</i> (du Plessis 1874)
RHABDOCOELA					
DALYELLIOIDA					
DALYELLIIDAE					
				<i>CASTRELLA</i> Fuhrmann 1900	<i>truncata</i> (Abildgaard 1789)
				<i>DALYELLIA</i> Flemming 1822	<i>viridis</i> (Shaw 1791)
				<i>GIEYSZTORIA</i> Ruebush & Hayes 1939	<i>diadema</i> (Hofsten 1907)
					<i>expedita</i> (Hofsten 1907)
					<i>infundibuliformis</i>
					(Fuhrmann 1894)
					<i>rubra</i> (Fuhrmann 1894)
					<i>triquetra</i> (Fuhrmann 1894)

Order	Suborder	Family	Subfamily	Genus	Species
				<i>MICRODALYELLIA</i> Gieysztor 1938	<i>armigera</i> (Schmidt 1861)
					<i>brevimana</i>
					(Beklemischev 1921)
					<i>fairchildi</i> (Graff 1911)
					<i>schmidtii</i> (Graff 1882)
					[Synonym <i>M. kupelwieseri</i> (Meixner 1915)]
TYPHLOPLANOIDA					
TYPHLOPLANIDAE					
MESOSTOMINAE					
				<i>BOTHROMESOSTOMA</i> Braun 1885	<i>personatum</i> (Schmidt 1848)
				<i>MESOSTOMA</i> Ehrenberg 1837	<i>ehrenbergii</i> (Focke 1836)
					<i>lingua</i> (Abildgaard 1789)
					<i>platycephalum</i> Braun 1885
					<i>productum</i> (Schmidt 1848)
					<i>tetragonum</i> (Müller 1774)
OLISTHANELLINAE					
				<i>OLISTHANELLA</i> Voigt 1892	<i>obtusata</i> (Schultze 1851)
					<i>truncata</i> (Schmidt 1858)
OPISTOMINAE					
				<i>OPISTOMUM</i> Schmidt 1848	<i>pallidum</i> Schmidt 1848
PHAENOCORINAE					
				<i>PHAENOCORA</i> Ehrenberg 1835	<i>typhlops</i> (Vejdovsky 1880)
					<i>unipunctata</i> (Ørsted 1843)
RHYNCHOMESOSTOMINAE					
				<i>RHYNCHOMESOSTOMA</i> Luther 1904	<i>rostratum</i> (Müller 1774)
TYPHLOPLANINAE					
				<i>CASTRADA</i> Schmidt 1861	<i>armata</i> (Fuhrmann 1894)
					<i>intermedia</i> (Volz 1898)
					<i>lanceola</i> Braun 1885
					<i>luteola</i> Hofsten 1907
					<i>neocomensis</i> Volz 1898
					<i>stagnorum</i> Luther 1904
					<i>viridis</i> Volz 1898
				<i>LIMNORUANIS</i> Kolasa 1977	<i>romanae</i> Kolasa 1977
				<i>STRONGYLOSTOMA</i> Ørsted 1848	<i>elongatum</i> Hofsten 1907
					<i>radiatum</i> (Müller 1774)
				<i>TETRACELIS</i> Ehrenberg 1831	<i>marmorosa</i> (Müller 1774)
				<i>TYPHLOPLANA</i> Ehrenberg 1831	<i>viridata</i> (Abildgaard 1789)
KALYPTORHYNCHIA					
POLYCYSTIDAE					
				<i>GYRATRIX</i> Ehrenberg 1831	<i>hermaphroditus</i>
					Ehrenberg 1831
				<i>OPISTHOCYSTIS</i> Sekera 1911	<i>goettei</i> (Bresslau 1906)

It should be noted that *Macrostomum tuba* has been recorded only in warmed aquaria (Young & Young 1967) in the British Isles. It occurs in natural conditions in central and southern, but not northern, continental Europe (Lanfranchi & Papi 1978). Since the earlier key by Young (1970), *Microdalyellia schmidti* (Graff 1882) and *M. kupelwieseri* (Meixner 1915) are now considered to be synonyms (Bauchhenss 1971; Lanfranchi & Papi 1978). *Stenostomum bryophilum* Luther 1960, also included in the earlier key, is now considered to be a synonym of *S. anatirostrum* Marcus 1945b (Kolasa & Young 1974). Some workers have suggested that *Geocentrophora sphyrocephala* and *G. baltica* may be synonyms (e.g. Bauchhenss 1971), but in the absence of a comparative, definitive study to confirm this, the two species are retained here. Borkott (1970) suggested that *Stenostomum leucops* should be split into three species, namely *S. sthenum*, *S. plebejum* and *S. platycaudatum*, but this has not been widely adopted (Lanfranchi & Papi 1978). *Gyratrix hermaphroditus* is a species-complex represented in Western Europe by several sibling species that are karyologically and ecologically distinct. Species with $2n = 6$ chromosomes are marine, whereas species with $2n = 4$ chromosomes are found in fresh water. Freshwater populations from Russia and North Australia also have $2n = 4$, but in Puerto Rico and Bermuda both species groups with $2n = 4$ and $2n = 6$ have been found in intertidal areas (Puccinelli & Curini-Galletti 1987; Puccinelli *et al.* 1990; Curini-Galletti & Puccinelli 1990, 1994; Birstein 1991). Within the freshwater environment, a study of sixteen populations of *G. hermaphroditus* from small ponds in Germany indicated that the species comprised a group of at least five sibling species (Heitkamp 1978b, 1982).

Mesostoma lingua also may be composed of a complex of sibling species (Heitkamp 1972a, 1982; Heitkamp & Schrade-Mock 1977). Two different cytological and ecological 'strains' or 'races' have been found in *Tetracelis marmarosa*; a northern and boreo-alpine 'strain' with resting eggs (p. 110) and $2n = 8$ chromosomes, and a southern race with resting and subitaneous eggs (i.e. eggs develop inside the ovoviparous female; see p. 110) and $2n = 4$ chromosomes (Luther 1963; Papi 1952, 1954; Reisinger 1955; Heitkamp 1982). The karyotypes of other microturbellarians, including freshwater species, are given in Galleni & Canovai (1988), Birstein (1991) and Novikova (1999). Records of two species in the British Isles, *Gieysztoria triquetra* and *Mesostoma platycephalum*, should be regarded with caution (Young 1970). Perkins (1928) recorded the former (as *Dalyellia (Vortex) triquetra*) from Coe Fen, and the latter from Brick Pit Ponds, Wicken Fen, Cambridgeshire. Unfortunately, whole mount specimens of both species deposited in the British Museum are of poor quality and cannot be identified.

It is pertinent to mention that although *G. triquetra* has a wide distribution in continental Europe, *M. platycephalum* has only been recorded from Dorpat, Russia (Lanfranchi & Papi 1978). The anatomy of the latter species was described by Braun (1885).

Historical records of the various microturbellarian species found in the British Isles up to 1969 are detailed in Young (1970). For each species, he includes information on the location and type of habitat, time of collection and name of collector. These data, together with all post-1969 records, are also stored in the Biological Records Centre, CEH Monks Wood, Huntingdon, UK.

COLLECTION, EXAMINATION AND PRESERVATION

COLLECTION OF SPECIMENS

Because most microturbellarian species are tiny, a detailed account of their collection and examination is necessary. Most of them are too small to be collected by hand in the way that triclad flatworms can be removed from the under-surfaces of stones and leaves, and from the axils of leaves on plants (Reynoldson & Young 2000). Qualitative samples can be obtained using a fine-meshed sweep-net (Chodorowski 1959; Rixen 1961, 1968; Young 1970; MacIsaac & Hutchinson 1985). I have found that a bag-net with a mesh size of 300-400 μm , mounted on a square frame with a 1.5 m pole, is effective in sampling a wide variety of lentic and lotic habitats. Although some specimens may escape through this size of mesh, most of them will be trapped in the debris accumulating in the net. Excepting samples taken from open water, finer meshes, whilst retaining the smallest individuals, quickly clog with substratal materials. A hand-net can be used to sweep the water surface, open water and vegetation, and to scoop up the surface layers of substrata such as small stones, sand, mud, detritus and other debris. Larger stones can be picked up gently, holding the sweep-net underneath them, and washed thoroughly in a basin or bucket containing some water. The contents of the bag-net should be emptied periodically into transparent, plastic or glass collection vessels. Some workers (e.g. Kolasa *et al.* 1987) have collected surface sediments from springs and streams using a jar.

Groundwater microturbellarians have been sampled from the banks of lakes (e.g. Rixen 1961) and streams (e.g. Kolasa 1983; Kolasa *et al.* 1987) by digging a hole and allowing it to fill with water, and either sweeping the agitated water with a net or removing the contained water with a scoop or pump. A baiting technique has been used successfully by Maly *et al.* (1980) and Herbert & Payne (1985) to trap pond-dwelling *Mesostoma ehrenbergii* and *M. lingua*, respectively. The former used plastic ice-cream containers into which several holes had been cut and which contained pig-liver, whilst the latter used jars that had a piece of 1000 µm nylon mesh inserted in their lids. These jars were baited with heat-killed zooplankton (*Daphnia* and *Diatomus*) prior to being placed on their side in the pond for 24 hours. Pelagic microturbellarians can be collected by plankton tow-nets (Dumont *et al.* 1973; Roch *et al.* 1990). A variety of dredges and grabs have been used to collect samples from deeper waters (e.g. Young 1973a; Schwank 1976; Kolasa 1979).

Some workers have used the sweep-net technique to try and quantify samples by collecting a given area or volume of material such as algae, moss, etc. (e.g. Schwank 1981a,b) or by collecting for a given length of time, which provides relative, not absolute, abundances (Young 1973a). Strictly quantitative sampling in shallow waters can be obtained by the use of cylinders or boxes of various sizes to enclose a given volume/area of water and substratum from ponds and lakes (e.g. Young 1973a, 1975a, 1977a) and streams (e.g. Schwank 1981a,b; Kolasa 1983). Animals in the water column are removed by sweep-net, and from the substratum by a net or shovel. When small corers are used the core is ejected directly into the collection vessel (Young 1977a; Schwank 1981a,b). Boxes with their bottom covered by a fine mesh but open at the top, and filled with natural or sorted sediments, have been placed in streams and removed at timed intervals after colonisation by microturbellarians (Kolasa *et al.* 1987). An interesting quantitative method was used by Maly *et al.* (1980) to sample *M. ehrenbergii* from a pond. Pieces of cheesecloth covered by a layer of detritus were placed on the pond bottom and left for 7 to 10 days, after which they were lifted carefully and placed into trays. Palchick (1984) also used this method when examining the relationship between a species of *Mesostoma* and mosquitoes. In deeper lentic freshwaters, quantitative samples can be obtained using a variety of grabs (e.g. Kolasa 1979; Young 2001).

When collected, samples can be partly processed in the field by agitating the collected substratal material in a bucket and pouring the washings through sieves or nets (e.g. Kolasa 1983). This is only possible when the substratum consists mainly of mineral matter with little organic material, as is

found in mountain streams. Usually, the collected material is transported in the collection vessels directly back to the laboratory or place of study. Sometimes, however, it may be preferable to empty the contents of the bag-net into a basin, bucket or tray containing some water, in order to carefully remove large substratal items such as twigs, pebbles, etc. prior to transportation. Field collections should be returned fresh to the laboratory because most microturbellarian species will almost certainly be missed in preserved samples, and are difficult to identify in this state. Before transportation, the collection vessels should be three-quarters filled with water before closure. In very hot weather it is preferable to keep the samples cooled and/or aerated during transport (Young 1973a).

In the laboratory, it is sometimes possible to remove animals from field collections by carefully sifting through the substratal materials, particularly if the microturbellarians are large (Young 1975a, 1977a; Maly *et al.* 1980). Usually, however, the animals are too small to be processed in this way and the following procedure is necessary (Chodorowski 1959; Young 1970; Kolasa & Mead 1981). The samples either can be left in the collection vessels with lids removed, or poured into transparent perspex or glass aquaria topped up with water from the habitat from which the samples were taken or, less desirably, with tap water left to stand at least 24 hours before use. The samples should then be allowed to settle, when the water will clear and gradually stagnate as oxygen depletion occurs. The vessels are best kept in darkness or dim light. Every few hours for several days, the samples should be examined, with as little disturbance as possible, using illumination from a light source above or at various positions around the vessels. Microturbellarians may be found swimming in the open water, adhering or moving at the surface meniscus, on the surface of the collected materials, or on the sides of the vessel. The animals can be removed using a bulb-pipette with a bore diameter appropriate for the size of the species concerned and placed in a petri-dish with water from the sample vessel.

Different species of Microturbellaria may emerge from the collected materials at various time intervals as the stagnation process proceeds. The time taken to complete stagnation of the samples depends on the nature of the material and, particularly, on temperature; at normal room temperature, usually no more animals will emerge after 3 to 4 days. Sometimes the application of gentle heat to the bottom of the vessels containing the samples, using a hot plate, so that the surface of the sediment reaches about 30°C, encourages the emergence of turbellarians (Kolasa 1983). This works best if the samples contain little detritus, such as those obtained from mountain

streams. The samples are heated until the first animals appear, and the operation is repeated several times.

Methods developed for extracting microturbellarians from marine sands, which may be adaptable to freshwater samples, include the addition of sea-water ice to drive the animals from the sediment, or the addition of narcotics – such as magnesium chloride or ethanol – to the sample in order to anaesthetise the animals. This is followed by a vigorous stirring of the sample to separate mineral particles, and subsequently decanting the supernatant fluid through a fine mesh sieve (125 μm) to catch the animals (Martens 1984; Noldt & Wehrenberg 1984).

EXAMINATION OF LIVE SPECIMENS

It is emphasised that the isolated specimens should always be examined alive for identification. Most species are fairly transparent, allowing internal structures to be seen. Identification of preserved specimens is much more difficult. After noting the general shape, size, colour and movement of the animal, it is best studied using the 'squeeze preparation' technique which involves placing the specimen in a small drop of culture water on a microscope slide (Young 1970). A glass coverslip, which has had a thin layer of petroleum jelly (vaseline), or an equivalent substance, placed along the edges of its underside, is then lowered gently onto the animal. A small gap is left in the petroleum jelly to allow water to escape. Excess water is removed by absorbent paper or a fine pipette. The coverslip is pressed very lightly to immobilise the animal, which is then examined under a compound microscope at suitable magnifications. At intervals during examination of the appearance and arrangement of the internal organs, the degree of compression of the specimen may be increased, by applying pressure to the coverslip, to further flatten the animal and so obtain a clearer view of its anatomy. Eventually, the tissues may disrupt to produce so-called 'squash preparations' which are often necessary to study hard structures such as the penis stylet.

Although microturbellarians are best identified when alive, it sometimes may be necessary to examine whole mounts or histological sections to confirm identification, for example with typhloplanid species. If too much pressure has not been applied during the squeezing process, it may be possible to rescue the animal under observation; otherwise, fresh animals should be used.

PRESERVATION AND HISTOLOGICAL SECTIONS

Microturbellarian species are highly contractile and tend to shrink and distort on the addition of fixatives. Usually it is desirable to anaesthetise animals prior to fixing, using narcotics such as 7% ethanol, 0.1% chlorotone or 1% hydroxylamine hydrochloride (Kolasa 1991). However, some microturbellarians, for example *Phaenocora* spp., are satisfactorily killed, without relaxation, in Steinmann's fluid (1 part concentrated nitric acid, 1 part saturated solution of mercuric chloride in 5% sodium chloride, and 1 part distilled water). The fluid is dropped from a pipette onto the specimen moving in a shallow layer of water, after which the animal should be washed immediately in water or fixative before final preservation (Young 1970). Suitable fixatives include Bouin's fluid (15 parts saturated aqueous picric acid (1.22%), 5 parts formaldehyde and 1 part acetic acid), Stieve's fluid (19 parts mercuric chloride, 5 parts formaldehyde and 1 part acetic acid), or 70% ethanol (Kolasa 1991). Specimens should be stored in 70% ethanol.

Whole mounts can be examined unstained or stained in borax-carmin or aceto-carmin. For histological examination, animals are blocked in paraffin wax at 58°C and transverse or longitudinal sections are cut at 2–8 μm , with thickness depending on the size of the animal. The sections can be stained in Ehrlich's or Delafield's haematoxylin and eosin, or Mallory's triple stain. Whole mounts and sections can be mounted in any suitable mountant.

FEATURES USED FOR IDENTIFICATION

Distinguishing criteria that are seen in living whole-mounts include the type and position of the pharynx, the type of sexual reproduction, the structure and position of the reproductive organs, the number and position of the excretory ducts and pores, the presence or absence of eyes or pigment spots, a statocyst, light refracting organs and ciliated pits or grooves, and the size, shape and colour of the body. In some species, dark pigmentation (e.g. *Bothromesostoma personatum*) or the presence of green zoochlorellae (e.g. some *Castrada* spp., *Typhloplana viridata* and *Dalyellia viridis*) make some of these features difficult to see.

To assist users of the keys a brief summary of important features is provided here, and they are diagrammatically illustrated in Fig. 1 on page 21, and Figs 2 to 7 on pages 28–39. The illustrations given in Figs 2–7 are repeated at larger scales in the body of the keys, on pages 42 to 81. Some of the features have complex terminology, listed in the Figure legends.

PHARYNX

The pharynx is situated between the mouth and intestine, and its structure and position is of considerable use in separating microturbellarian species. Three basic types are found in freshwater species (Table 2): the pharynx simplex (Figs 2, 3A,B), pharynx plicatus (Fig. 3J,K) and pharynx bulbosus (Figs 3F–I, 4–7).

Table 2. Types of pharynx and distribution between Families of British and Irish Microturbellaria.

Type of pharynx	Families
Non-protrusible short tube: <i>simplex</i>	Catenulidae, Macrostomidae, Microstomidae Stenostomidae
Protrusible muscular cylinder: <i>plicatus</i>	Bothrioplanidae Otomesostomidae
Slightly protrusible, barrel-shaped: <i>bulbosus doliiformis</i>	Dalyelliidae
Slightly protrusible, variably shaped: <i>bulbosus variabilis</i>	Plagiostomidae Prorhynchidae
Slightly protrusible, globular/spherical: <i>bulbosus rosulatus</i>	Polycystidae Typhloplanidae

The *pharynx simplex* is a short tube of inturned, ciliated epidermis, without special musculature, but accompanied by the ordinary layers of subepidermal muscles.

The *pharynx plicatus* is protrusible through the mouth. It is a muscular cylinder – lacking a delimiting septum – which is attached to the anterior end of, and projects downward and/or backward into, a large pharyngeal cavity.

The *pharynx bulbosus* is slightly protrusible. It is a glandulo-muscular bulb delimited by a muscular septum. There are three main types: the *pharynx doliiformis* (Fig. 4) which is barrel-shaped and horizontally orientated, the *pharynx rosulatus* (Figs 5–7) which is globular or spherical and dorso-ventrally orientated, and the *pharynx variabilis* (Fig. 3F–I) which has a variable shape and a weakly differentiated septum.

REPRODUCTIVE SYSTEM

The reproductive system in Microturbellaria is complex and varies between the different Orders (Fig. 1). Because reproductive features are used in certain parts of the keys, some descriptive detail of the system is required.

Catenulida and Macrostomida

Asexual reproduction by transverse fission occurs in the Catenulida, and in the Family Microstomidae (e.g. *Microstomum lineare*) of the Order Macrostomida, when a chain of two or more zooids is formed (see Figs 2 and 3A, pp. 28–31). With regard to sexual reproduction, the female gonad is simple and developing eggs are entolethical, i.e. yolk occurs within the oocytes (ova), in both the Catenulida and Macrostomida; there are no separate yolk cells or glands (Figs 1A and 3B, pp. 21 and 31). However, the occurrence of sexually mature animals can be rare in some populations of some species of Catenulida and in *M. lineare*.

In mature animals, the male system comprises a single testis, a sperm duct (vas deferens), a penis – which has a stylet (hard structure) in some species (e.g. *M. lineare*) – and a gonopore. The latter opens dorsally in the anterior half of the body in the Catenulida, and ventrally in the posterior part of the body in *M. lineare* (Marcus 1945a,b).

The female system includes an ovary (occasionally more than one) but no oviduct or permanent gonopore in the Catenulida, and there is a single ovary, oviduct and gonopore opening in the posterior half of the body in *M. lineare*.

In species of *Macrostomum*, a pair of ovaries and oviducts are connected to the female antrum and open via the female gonopore onto the ventral body surface (Fig. 1A, p. 21; Fig. 3B, p. 31). A pair of testes and sperm ducts (vasa deferentia), sometimes expanded proximally into a false seminal vesicle (spermiducal vesicle), are connected to the male copulatory complex, the lumen of which is called the ductus ejaculatorius (ejaculatory duct). The male complex comprises a vesicula seminalis (seminal vesicle), which receives and

stores sperm from the testes, a vesicula granulorum (prostatic or granular vesicle), which stores granular secretions from the prostatic glands, and the copulatory organ, which comprises a hard, tubular penis stylet that opens via a ventral male gonopore (Figs 1A, 3B). The female and male gonopores are situated near the hind end of the body, the latter more posteriorly than the former (Figs 1A, 3B).

Prolecithophora, Lecithoepitheliata and Proseriata

In these three Orders, and in the Rhabdoceola, the female gonad is heterocellular, with separate yolk- and oocyte-producing parts (eggs are ectolethical, i.e. yolk is not incorporated within the oocyte). The yolk is diffuse and either partially or fully separated from the oocytes in the Prolecithophora (Fig. 3F, p. 31), surrounds the oocytes in a single germovitelarium (organ containing ovary and yolk cells) in the Lecithoepitheliata (Fig. 3G), and is separate from the oocytes and usually in discrete parts or organs in the Proseriata, and in the Rhabdoceola (Figs 3J,K and 1B,C). In *Plagiostomum lemani* (Prolecithophora), the paired diffuse testes lie in the front part of the body. The paired ovaries and diffuse yolk glands (vitellaria) lie at the side of the pharynx and intestine (Fig. 3F). The common gonopore opens ventrally in the hind part of the body.

In *Prorhynchus stagnalis* and *Geocentrophora* spp. (Lecithoepitheliata), the single germovitelarium lies in the posterior half of the body and the female gonopore opens ventrally, just anterior to the middle of the body (Fig. 3G). The testes lie posteriorly, but the vesicula seminalis and vesicula granulorum lie in an anterior position, with the ejaculatory duct and penis stylet opening into the pharyngeal cavity (buccal tube) which opens at the front end of the body (Fig. 3G-I). In *Bothrioplana semperi* (Proseriata) there are a pair of small, usually non-functional testes, positioned dorso-laterally on either side of the pharynx (Fig. 3K), a pair of ovaries lying at each side of the atrium copulatorium (see below) and ventral to the intestine, and a pair of follicular yolk glands positioned along the sides of the body. A common gonopore opens in the posterior half of the body. In *Otomesostoma auditivum* (Proseriata), the paired lateral-lying follicular testes and yolk glands lie in the front half of the body and along the length of the body, respectively (Fig. 3J). The paired compact ovaries lie just behind the pharynx, and the male gonopore opens anterior to the female pore.

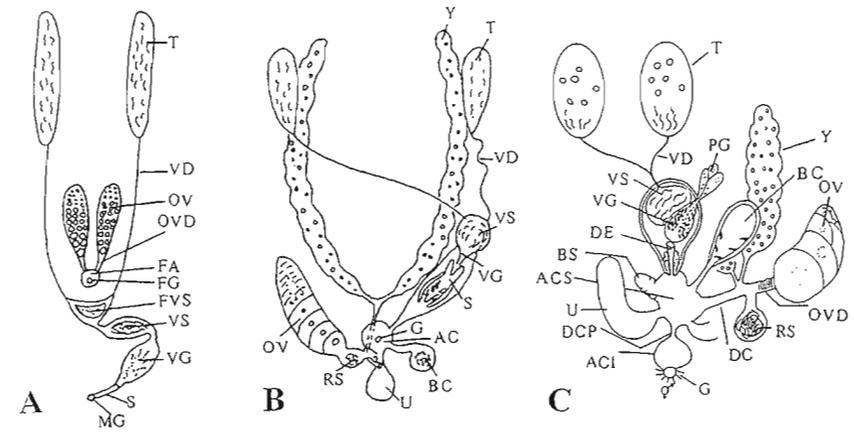


Fig. 1. A-C: Schematic representation of the main reproductive organs and structures of some freshwater microturbellarians.

A, Macrostomida, Macrostomidae.

B, Dalyellioida, Dalyelliidae (ventral view).

C, Typhloplanoida, Typhloplanidae. In some species, the relative arrangement of the structures and organs may be a little different or additional structures may be present. (C, reproduced with permission from Kolasa 1991).

AC	atrium copulatorium	MG	male gonopore
ACI	inferior atrium copulatorium	OV	ovary
ACS	superior atrium copulatorium	OVD	oviduct
BC	bursa copulatrix	PG	prostatic glands
BS	blind sac of atrium copulatorium	RS	receptaculum seminalis
DC	ductus communis (ovo-vitelline duct)	S	penis stylet (hard structure of the copulatory organ)
DCP	ductus copulatorius	T	testis
DE	ductus ejaculatorius	U	uterus
FA	female antrum	VD	vas deferens
FG	female gonopore	VG	vesicula granulorum
FVS	false vesicula seminalis	VS	vesicula seminalis
G	common gonopore	Y	yolk gland

Rhabdocoela

The Rhabdocoela have complex reproductive organs and these are shown schematically for the Suborders Dalyellioida (Family Dalyelliidae) and Typhloplanoida (Family Typhloplanidae) in Fig. 1B and 1C, respectively. The various structures have the same function as described above for the Macrostromida. Additionally, the receptaculum seminalis (seminal receptacle) and the bursa copulatrix (bursa or seminal bursa) store recipient sperm from a co-copulant, and the uterus stores fertilised eggs. The male and female systems open into an atrium copulatorium (atrium genitale or copulatory atrium) which opens ventrally via a common gonopore. One or two blind sacs (atrium pouches) opening into the atrium copulatorium may be present.

In the species of Dalyelliidae, the single ovary is usually situated in a caudal position towards the right side of the body (Fig. 4, p. 33). The yolk glands are situated in a dorso-lateral position and dorsal to the testes. The testes are usually situated in the anterior body half in the *Microdalyellia* spp., though in *M. fairchildi* and sometimes in *M. armigera* they occur in a caudal position (Luther 1955), in the hind part of the body in *Castrella truncata* and species of *Gieysztoria*, and along the side of the length of the gut in *Dalyellia viridis*. The penis stylet, the hard structure of the copulatory organ, has a complex shape (Fig. 4). There is a single, common gonopore in the caudal part of the body.

Within the Typhloplanidae there is one ovary, and paired testes and yolk glands; exceptionally, *Limnoruanis romanae* (Subfamily Typhloplaninae) has only a single line of large yolk cells above the intestine (Fig. 5C, p. 35). Whether or not the testes are ventral or dorsal to the yolk glands is a distinguishing feature used in the key to separate the typhloplanid species. The paired testes lie ventral to the paired yolk glands in species of the Subfamilies Rhynchomesostominae (*Rhynchomesostoma rostratum*) and Typhloplaninae (*Castrada* spp., *Strongylostoma* spp., *Tetracelis marmorosa* and *Typhloplana viridata*), and lie dorsal to the yolk glands in the Mesostominae (*Mesostoma* spp. and *Bothromesostoma personatum*), Olisthanellinae (*Olisthanella* spp.), Opistominae (*Opisthomum pallidum*), and Phaenocorinae (*Phaenocora* spp.). There is a single, common gonopore. In *Phaenocora* spp. the penis is replaced by a cirrus, which is the terminal part of the ejaculatory duct, often lined with spines, that is eversible to the exterior and acts as a copulatory organ (Fig. 5E,F). In the Kalyptorhynchia, the testes, ovary and yolk glands are paired in *Opisthocystis goettei* (Fig. 5B) but single in *Gyratrix hermaphroditus* (Fig. 5A). There is a single, common gonopore in the posterior half of the body in

O. goettei. In *G. hermaphroditus*, there are separate female and male pores, the former opening slightly anterior to the latter which opens at the posterior tip of the body.

ADDITIONAL NOTES ON THE MALE REPRODUCTIVE SYSTEM,
INCLUDING PENIS STYLETS

Immature animals of species that are identified using features of the reproductive system, for example the penis stylet, cannot be identified to specific level. However, usually, mature animals are also found in most samples. Because body shape and internal structure are fairly similar in species of *Macrostromum*, only *M. rostratum* is fully illustrated (Fig. 3B). However, the penis stylet, a most important distinguishing criterion, is shown for each of the other species (Fig. 3C-E). Likewise, for species of *Microdalyellia* and *Gieysztoria*, which have a similar appearance and internal anatomy (with the exception of the position of the testes), only *M. fairchildi* and *G. rubra*, which has characteristic, strongly papillate yolk glands, are illustrated (Fig. 4C,G). Again, only the penis stylet is shown for each of the other species (Fig. 4D-F, H-K). Also, because species of *Castrada* have a similar external appearance and internal structure, diagrams for only *C. armata* and *C. luteola* are presented (Fig. 6A,B). The male copulatory apparatus, important for separating species, is shown for each of the other species (Fig. 6C-G). However, the bursa copulatrix is not shown in diagrams of the male copulatory apparatus of *C. armata* and *C. luteola*; the bursa is very small in the latter species. The typical lay-out of the male and female reproductive organs in species of *Mesostoma* has been shown only for *M. tetragonum* and *M. ehrenbergii* (Fig. 7D,E), as they are particularly obvious in these transparent animals.

The average length or height of the penis stylet for all species, as found in British and Irish specimens, where possible, is given in the illustrations, whilst the range of measurements is indicated in the keys. The natural proportions of the penis stylet of each species of Dalyelliidae are shown in the diagrams (Fig. 4). The handle length is usually equal to the remaining portion of the stylet in *M. fairchildi* (Fig. 4C). However, occasionally, the handles can be much longer, indeed as much as twice as long as the remaining portion. In the illustration of *M. fairchildi* not all of the spines are indicated because the proximal spines are often 2 to 3 rows deep; the collateral branch (Luther 1955) is not evident in British material. In a very few specimens of *M. schmidtii* the handles are shorter than shown in the drawing (Fig. 4F). In *D. viridis* (Fig. 4B)

one or both pairs of double handles are sometimes seen to be fused together. In *Castrella truncata* (Fig. 4A) the exact number of spines is difficult to make out, but there are about 12 to 13 on each branch (Hofstein 1907).

EXCRETORY SYSTEM

The excretory system consists of protonephridia. The excretory (protonephridial) ducts open via an excretory pore (nephridiopore) directly onto the surface of the body, or into the gonopore or genital atrium (space into which male and female systems open), or into the mouth or buccal cavity (region behind the mouth but before the pharynx). In the Catenulida there is a single, central excretory duct which arises caudally, running dorsally forward and then ventrally backwards to discharge posteriorly onto the body surface (Fig. 2). In the Macrostromida there are a pair of main excretory ducts (Fig. 3B) which usually open separately onto the surface of the body just behind the mouth (Ferguson 1939). In *Plagiostomum lemani* (Prolecithophora) the paired nephridia, which have a dorsal and ventral branch in the front half of the body, do not have definite excretory pores (Hofsten 1907). In *Prorhynchus stagnalis* and *Geocentrophora* spp. (Lecithoepitheliata) the four lateral excretory tubes open onto the body surface by a pair of excretory pores situated in front of the female gonopore. In *Bothrioplana semperi* (Proseriata) the excretory pore of the paired tubes opens onto the surface in a ventral, mid-body position in front of the mouth. In *Otomesostoma auditivum* (Proseriata) three pairs of excretory tubes discharge onto the body surface through numerous pores.

The Dalyellioida (Family Dalyelliidae) have paired excretory ducts opening separately onto the surface, in the region of the gonads. The Typhloplanoida (Family Typhloplanidae) have paired excretory ducts but, exceptionally, *Limnoruanis romanae* has a single tube which opens ventrally on the body surface in front of the pharynx (Fig. 5C). In the Subfamilies Mesosotominae and Typhloplaninae (except *L. romanae*), the excretory pore of the combined ducts opens into the mouth (e.g. Figs 5H, 6A,B, 7). In the Subfamily Rhynchomesostominae the excretory ducts open into the gonopore (Fig. 6H). In the Subfamilies Olisthanellinae, Opistominae and Phaenocorinae the ducts open directly via pores onto the body surface; in the first, separately and posterior to the mouth, in the second by a single pore placed ventrally between the mouth and the gonopore, and in the last separately and ventrally about half or two-thirds of the way along the body. In the Kalypotorhynchia, the excretory ducts open into an excretory beaker (vesicle) in the rear end of the body in *Opisthocystis goettei* (Fig. 5B) but open directly on the body surface in a posterior position in *Gyratrix hermaphroditus* (Fig. 5A).

The excretory system is not easily seen in some microturbellarians, e.g. the Dalyellioida, and is only used in the key for groups in which it is fairly evident although, exceptionally, in *Macrostromum* spp. careful inspection is necessary.

SENSORY STRUCTURES AND SURFACE FEATURES

The presence or absence of a variety of sensory structures also assists in the separation of species. These include: eyes and pigment spots – pigmented light-sensitive structures (Fig. 3A,B,F,H,J; Fig. 4; Fig. 5A–C,E,G; Fig. 6H–J; Fig. 7); a statocyst – an organ of orientation comprising a space enclosing a granule and surrounded by sensory tissue (Figs 2B, 3J); light-refracting organs – perhaps with a photosensitive function, consisting of one or more refringent granules (Nuttymcombe & Waters 1938; Marcus & Marcus 1951) (Fig. 2D,E); and ciliated pits or grooves which are aggregations of sensory cells in lateral depressions situated in front of the brain (e.g. Fig. 2D–G; Fig. 3A,G–K).

Eyes and pigment spots are permanent features and easily seen, but in *Geocentrophora sphyrocephala* they are sometimes difficult to see or are lost in ageing specimens (Luther 1960).

The Kalypotorhynchia have a protrusible, glandulo-muscular adhesive organ called a proboscis, at the anterior end of the body, which is used in the capture of prey (Fig. 5A,B).

Rod tracks, consisting of aggregations of adenal rhabdoids (rod-like structures in the mesenchyme or parenchyma) are present in some species (e.g. all species of Typhloplanidae with the exception of *Opistomum pallidum*) (see, for example, Figs 5C,E–H, 6 and 7). Wrona (1986) provided evidence that they contribute to mucus production in triclads but their function in microturbellarians is uncertain. Though not used as a distinguishing feature in the keys, rod tracks are shown in the drawings of some species as they may assist identification. Caudal adhesive papillae, comprising gland cells which assist the animal to adhere to the substratum (Marcus & Marcus 1951; Tyler 1976), are conspicuous in some species (e.g. species of *Macrostromum* and Dalyelliidae) (Figs 3B and 4).

The microturbellarians have a ciliated epidermis, but cilia are not shown in the illustrations in Figs 2–7, except in the case of *Suomina turgida* (Fig. 2A₁) which demonstrates that the cilia can vary in length.

BODY SHAPE, SIZE AND COLOUR

Young animals hatch from eggs and resemble small adults. Exceptionally, *Ryhnhoscolex simplex* has a larval or juvenile stage which differs from the adult; for example, it has a statocyst.

Body shape can be useful in the identification of species; for example, the prostomium, the anterior end of the body in front of the intestine, is elongated in *R. simplex* (Fig. 2C), and the front tip of the body is retractable in *Ryhnhomesostoma rostratum* (Fig. 6H). Indeed, in the key to Typhloplanoida (pp. 62–81), the species of *Mesostoma* are separated entirely on body shape (Fig. 7D–H). Body lengths (mm) and colours quoted in the various keys refer to adult animals. For each species, adult size can be variable, and the quoted lengths are based mainly on British and Irish material. It should be noted that the scale of magnification used in Figs 2–7 is not constant for all species, a minimum of organs is shown to avoid confusion and, usually, a dorsal view of animals is given. Young individuals of some species are colourless and gain colour as they grow. Some microturbellarians (*Castrada* spp., *Dalyellia viridis*, *Phaenocora* spp. and *Typhloplana viridata*) may become green as they grow, due to the presence of algae (zoochlorellae) in their tissues (pp. 90–92).

CHECKING IDENTIFICATION AGAINST
FULL TAXONOMIC DESCRIPTIONS

Once a specimen has been identified using the following keys, it may be desirable to check it against a fuller taxonomic description available in other more detailed publications, such as Marcus (1945a,b, 1946), Luther (1955, 1960, 1963), Karling (1963), Kolasa & Young (1974) and Kolasa (1977b).

KEY TO ORDERS AND SUBORDERS

- 1 Pharynx simplex (PS, Figs 2A–G, 3A–E). Reproduction sexual or asexual by transverse fission when a chain of two or more zooids is formed (Figs 2A–G, 3A). If present, female gonad simple; developing eggs are entoethical (yolk contained within the oocytes; no separate yolk cells or glands) (Figs 1A, 3B)—

Orders **CATENULIDA** and **MACROSTOMIDA**

(page 42)

- Pharynx of other type (Fig. 3F–K and Figs 4–7). Sexual reproduction. Female gonad heterocellular with separate yolk- and oocyte-producing parts; developing eggs are ectoethical (yolk not incorporated within the oocytes)(Figs 1B,C, 3F–K, 4–7)—

2

- 2 Pharynx variabilis (PV, Fig. 3F–I). In the female gonad, yolk not contained in discrete organs, and is either diffuse (Fig. 3F) or surrounds the oocytes in a single germovitelarium (Fig. 3G–I)—

Orders **PROLECITHOPHORA** and **LECITHOEPITHELIATA**

(page 50)

- Pharynx of other type (Fig. 3J,K and Figs 4–7). In the female gonad, yolk is contained within discrete parts or organs (Figs 1B,C, 3J,K and 4–7)—

3

- 3 Pharynx plicatus, tubular and projecting ventrally or posteriorly (PP, Fig. 3J,K)—

Order **PROSERIATA**

(page 54)

- *EITHER*: Pharynx doliiformis, barrel-shaped and directed forward (PD, Fig 4)—

Order **RHABDOCOELA**

Suborder **DALYELLIODA**

(page 56)

OR: Pharynx rosulatus, usually globular and dorso-ventrally orientated (Figs 5–7) (exceptionally, elongated and directed posteriorly in *Opisthomum pallidum* (Fig. 5D) and more oval-shaped and directed forward in *Phaenocora* spp. (Fig. 5E,F))—

Order **RHABDOCOELA**

Suborders **KALYPTORHYNCHIA** and **TYPHLOPLANOIDA**

(page 62)

Fig. 2. A–G: Major features of species in the Families Catenulidae and Stenostomidae (Catenulida). The pharynx is simple – a short, non-protrusible tube of inturned, ciliated epidermis (pharynx simplex, PS).

A, *Suomina turgida*; A₁, showing cilia (after Kolasa 1991).

B, *Catenula lemnae*.

C, *Rhynchoscolex simplex*.

D, *Stenostomum leucops*.

E, *Stenostomum unicolor*.

F, *Stenostomum anatirostrum*.

G, *Stenostomum grabbskogense*.

- B brain (cerebral ganglia)
 C ciliated pit
 CA cilia
 CGP pre-oral ciliated groove
 EX excretory duct (protonephridial duct)
 F fission plane of zooids
 GP pharyngeal gland cells
 I intestine or gut
 LG longitudinal grooves
 LP long prostomium
 M mouth
 NP nephridiopore or excretory pore
 P prostomium
 PS pharynx simplex
 RB bowl-shaped, light-refracting organ
 RG globular, light-refracting organ
 SC sensory cells
 ST statocyst

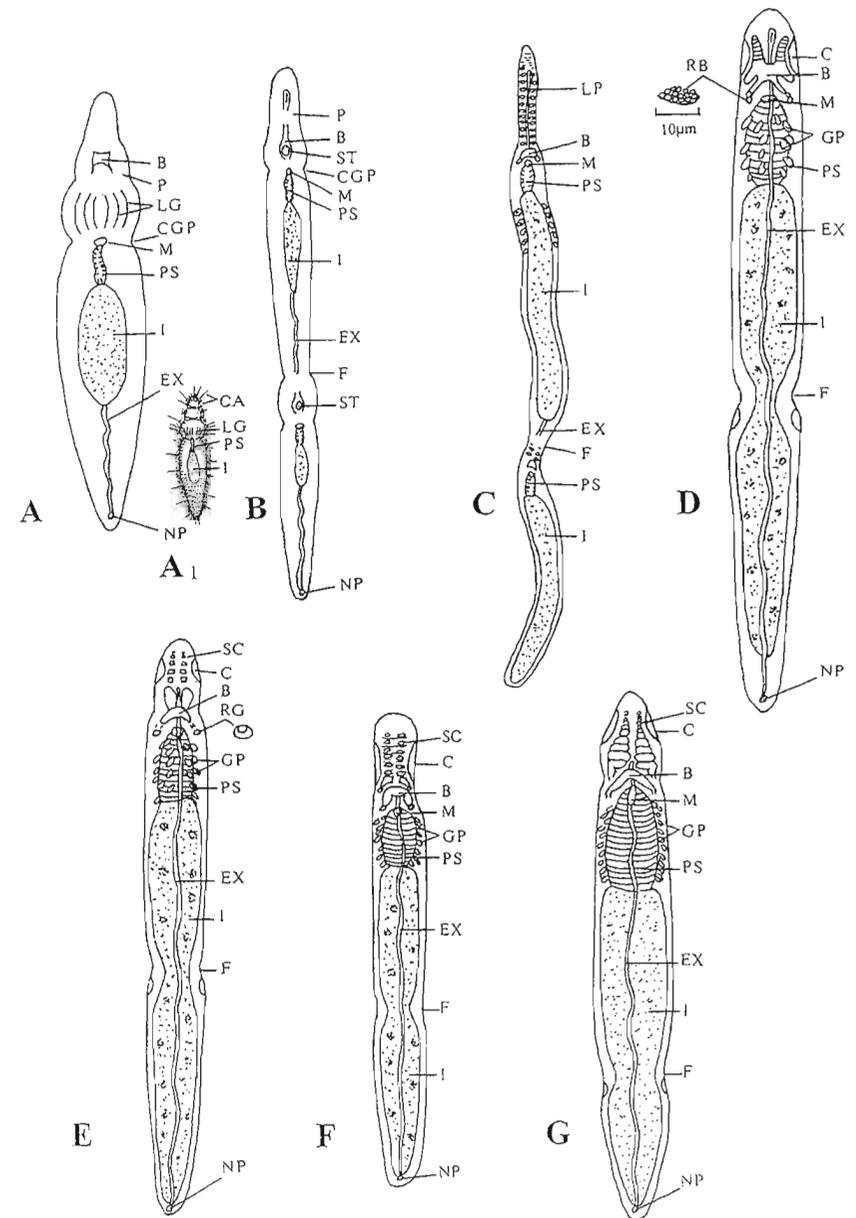


Fig. 3. A–E: Major features of species in the Families Microstomidae and Macrostomidae (Macrostomida). The pharynx is simple – a short, non-protrusible tube of inturned, ciliated epidermis (pharynx simplex, PS).

A. *Microstomum lineare*; A₁, side view of anterior end.

B. *Macrostomum rostratum*; B₁, penis stylet.

C. *Macrostomum distinguendum*; penis stylet.

D. *Macrostomum tuba*; penis stylet.

E. *Macrostomum johni*; penis stylet.

F–I: Major features of species in the Families Plagiostomidae (Prolethophora) and Prorhynchidae (Lecithoepitheliata). The bulbous pharynx is slightly protrusible, muscular and variable in shape (pharynx variabilis, PV).

F. *Plagiostomum lemani*.

G. *Prorhynchus stagnalis*.

H. *Geocentrophora sphyrocephala*.

I. *Geocentrophora baltica*.

J, K: Major features of species in the Family Otomesostomidae and Bothrioplanidae (Proseriata). The pharynx is muscular, cylindrical and protrusible (pharynx plicatus, PP).

J. *Otomesostoma auditivum*, showing testes (left side) and yolk glands (right side).

K. *Bothrioplana semperi*.

A	adhesive papillae	PC	pharyngeal cavity (buccal tube)
B	brain (cerebral ganglia)	PP	pharynx plicatus
C	ciliated pit	PS	pharynx simplex
E	dark eyes	PV	pharynx variabilis
EX	excretory duct (protonephridial duct)	RP	red pigment spot
EY	yellow/brown eyes	S	penis stylet (hard structure of copulatory organ)
F	fission plane of zooids	SP	protective sheath of stylet
FG	female gonopore	ST	statocyst
FVS	false vesicula seminalis (spermiducal vesicle)	T	testis
G	common gonopore	VG	vesicula granulorum (prostacic or granular vesicle)
GE	germovitellarium	VS	vesicula seminalis (seminal vesicle)
I	intestine or gut	Y	yolk glands (vitellaria)
M	mouth	YD	diffuse yolk glands (vitellaria)
MG	male gonopore		
O	opening of stylet		
OV	ovary		
PBS	pre-oral blind sac		

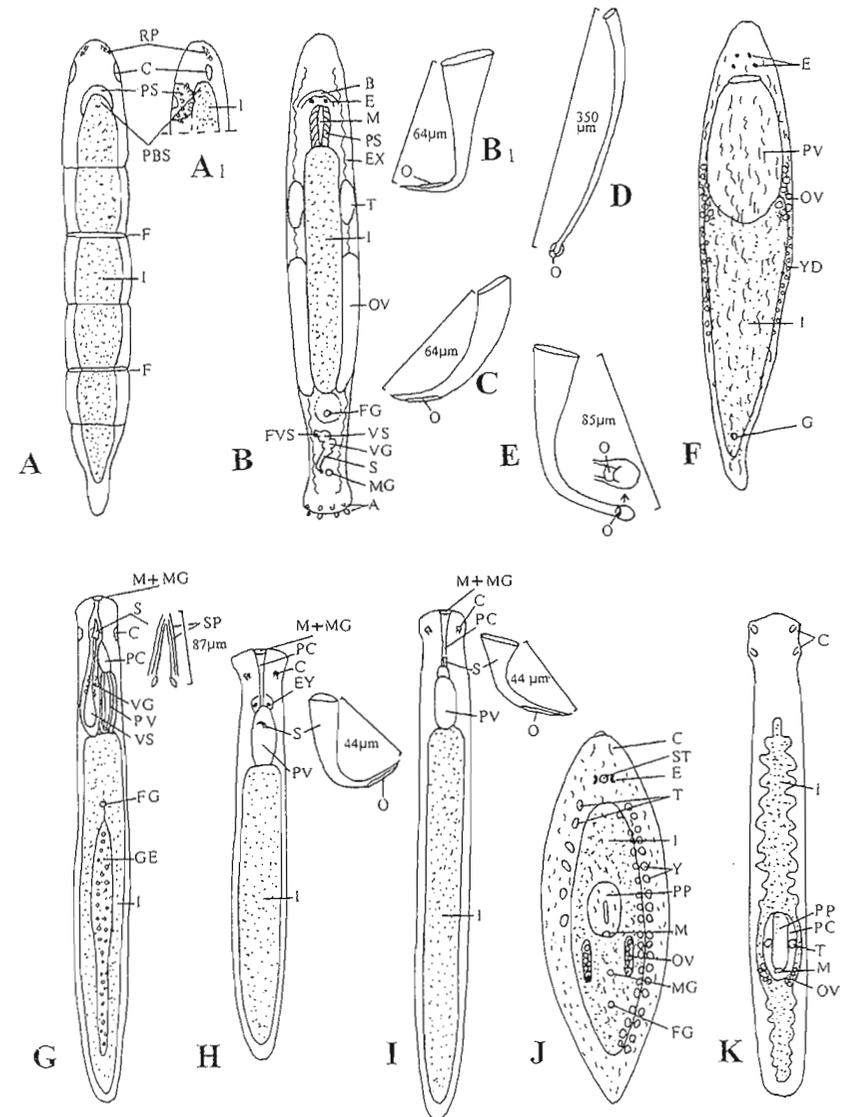


Fig. 4. **A–K**: Major features of species in the Family Dalyelliidae (Rhabdocoela: Dalyellioida). The bulbous pharynx is slightly protrusible, muscular, barrel-shaped and oriented horizontally (pharynx doliiformis, PD).

A. *Castrella truncata*.

B. *Dalyella viridis*.

C. *Microdalyellia fairchildi*; C₁, showing position of the single egg.

D. *Microdalyellia brevimana*; penis stylet.

E. *Microdalyellia armigera*; penis stylet.

F. *Microdalyellia schmidtii*; penis stylet.

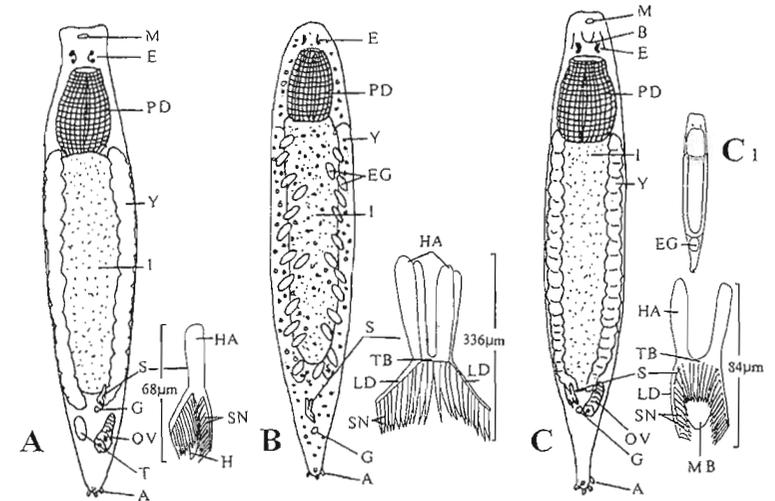
G. *Giaysztoria rubra*.

H. *Giaysztoria expedita*; penis stylet.

I. *Giaysztoria diadema*; penis stylet.

J. *Giaysztoria infundibuliformis*; penis stylet.

K. *Giaysztoria triquetra*; penis stylet (after Rixen 1961).



- A adhesive papillae
 B brain (cerebral ganglia)
 CR collar region
 E dark eyes
 EG egg capsule
 FE fenestrae region
 G common gonopore
 GL girdle
 H hook
 HA proximal handle or stalk
 I intestine or gut
 K keel
 LD lateral distal branch or end branch
 LS large spine
 M mouth
 MB median process, branch or piece
 MT median tube
 OV ovary
 PD pharynx doliiformis
 S penis stylet (hard structure of copulatory organ)
 SN spines
 T testis
 TB transverse bar or cross piece
 Y yolk glands (vitellaria)

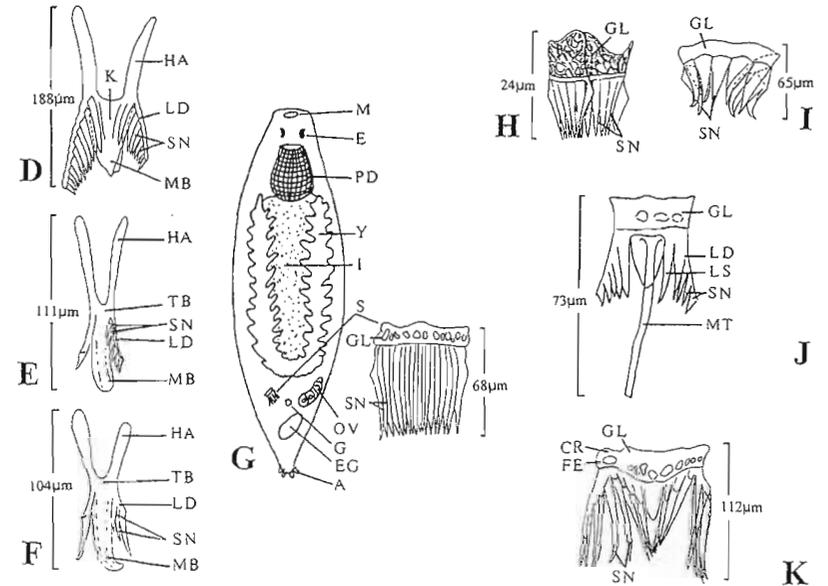


Fig. 5. **A–H**: Major features of species in the Families Polycystidae (A, B) and Typhloplanidae, Subfamilies Opisthominae, Phaenocorinae and Typhloplaninae (C–H) (Rabdocoela; Kalyptorhynchia and Typhloplanoida). The bulbous pharynx (pharynx rosulatus, PR) is slightly protrusible, dorso-ventrally oriented and globular or spherical (exceptionally, elongated and posteriorly directed in *Opisthomum* and more oval-shaped and directed forward in *Phaenocora*).

- A. *Gyratrix hermaphroditus*.
 B. *Opisthocystis goettei*.
 C. *Limnoruanis romanae* (after Kolasa 1991).
 D. *Opisthomum pallidum*.
 E. *Phaenocora unipunctata*.
 F. *Phaenocera typhlops*.
 G. *Tetracelis marmorosa*.
 H. *Typhloplana viridata*.

B	brain (cerebral ganglia)	T	testis
CI	cirrus (male copulatory organ)	U	uterus
CO	male copulatory organ	VG	vesicula granulorum (prostatic or granular vesicle)
DE	ductus ejaculatorius	VS	vesicula seminalis (seminal vesicle)
E	dark eyes	Y	yolk glands (vitellaria)
EV	excretory vesicle or beaker		
EX	excretory duct (protonephridial duct)		
FG	female gonopore		
G	common gonopore		
GN	glands		
GS	granular secretions		
I	intestine or gut		
M	mouth		
MG	male gonopore		
NP	nephridiopore or excretory pore		
OV	ovary		
PB	proboscis		
PR	pharynx rosulatus		
R	rod or rhabdoid tracks		
RS	receptaculum seminalis (seminal receptacle)		
S	penis stylet (hard structure of copulatory organ)		
SM	sperm		
SN	spines		

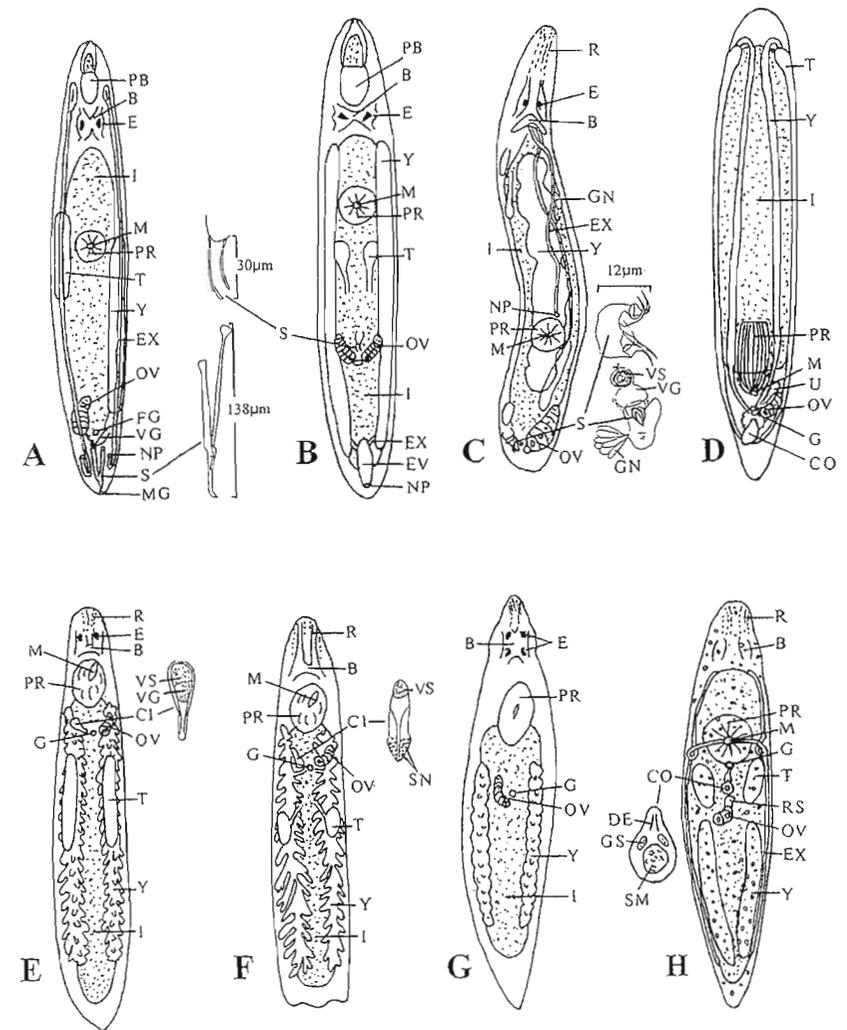
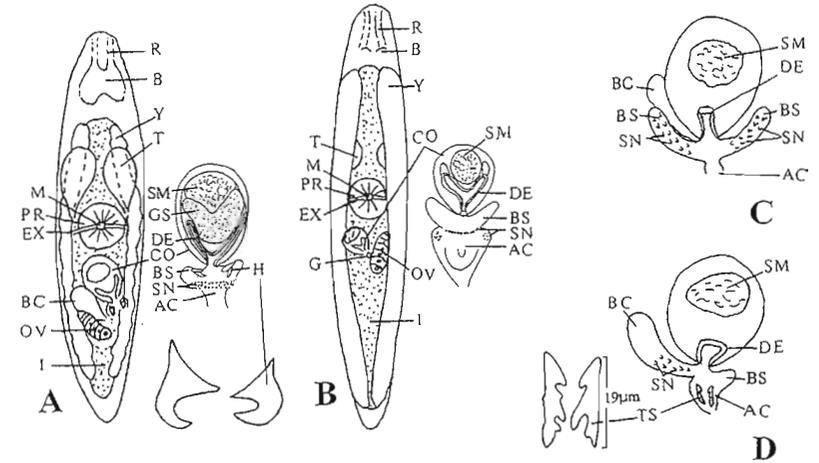


Fig. 6. A–J: Major features of species in the Family Typhloplanidae, Subfamilies Typhloplaninae (A–G), Rhynchomesostominae (H) and Olisthanellinae (I, J) (Rhabdocoela: Typhloplanoida). The bulbous pharynx is slightly protrusible, dorso-ventrally oriented and globular or spherical (pharynx rosulatus, PR).

- A. *Castrada armata* (ventral view).
 B. *Castrada luteola*.
 C. *Castrada intermedia*; copulatory apparatus.
 D. *Castrada neocomensis*; copulatory apparatus.
 E. *Castrada viridis*; copulatory apparatus.
 F. *Castrada stagnorum*; copulatory apparatus.
 G. *Castrada lanceola*; copulatory apparatus.
 H. *Rhynchomesostoma rostratum*.
 I. *Olisthanella obtusa*.
 J. *Olisthanella truncula*.



- AC atrium copulatorium (atrium genitale or copulatory atrium)
 B brain (cerebral ganglia)
 BC bursa copulatrix (bursa or seminal bursa)
 BS blind sac of atrium copulatorium
 CO male copulatory organ
 DE ductus ejaculatorius
 E dark eyes
 ER red eyes
 EX excretory duct (protonephridial duct)
 G common gonopore
 GS granular secretions
 H hook
 I intestine or gut
 M mouth
 NP nephridiopore or excretory pore
 OV ovary
 PGS pigment spot of irregular shape
 PR pharynx rosulatus
 R rod or rhabdoid tracks
 RAE retractile tip of body
 SM sperm
 SN spines
 T testis
 TS toothed structure
 Y yolk glands (vitellaria)

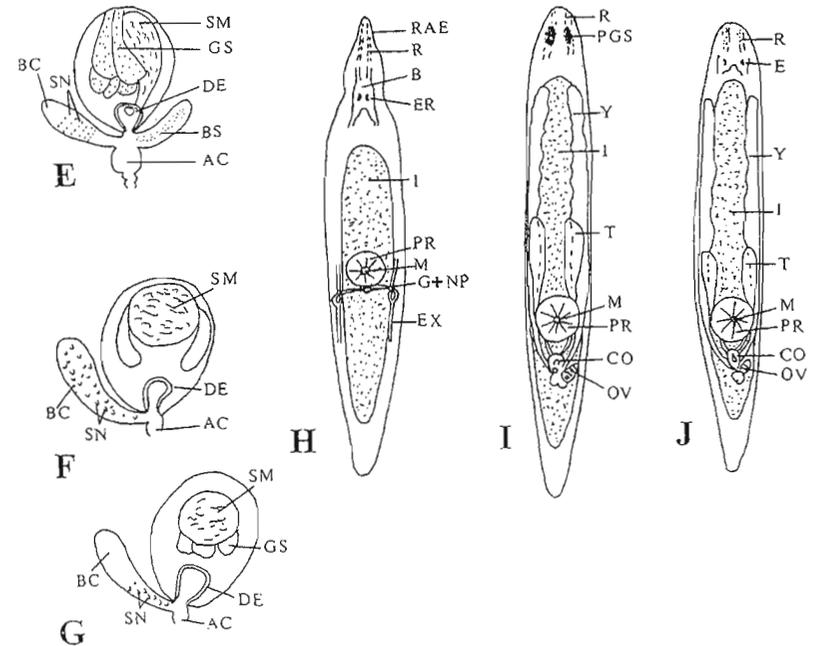


Fig. 7. A–H: Major features of species in the Family Typhloplanidae, Subfamilies Typhloplaninae (A, B) and Mesostominae (C–H) (Rhabdozoela; Typhloplanoida). The bulbous pharynx is slightly protrusible, dorso-ventrally oriented and globular or spherical (pharynx rosulatus, PR).

A. *Strongylostoma radiatum*.

B. *Strongylostoma elongatum*.

C. *Bothromesostoma personatum*.

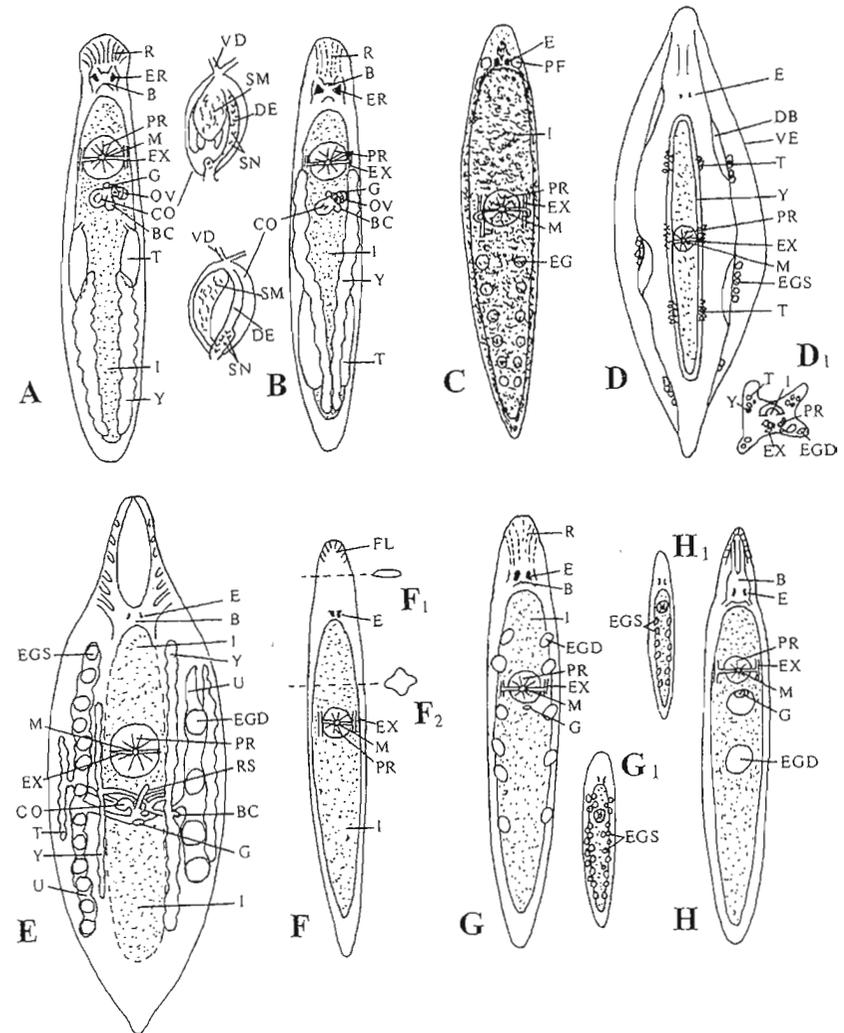
D. *Mesostoma tetragonum* (after Graff 1913); D₁, transverse section.

E. *Mesostoma ehrenbergii* (ventral view, after Graff 1913); the left side shows subitaneous eggs and the right side shows dormant eggs.

F. *Mesostoma platycephalum* (after Graff 1909); F₁ and F₂, transverse sections.

G. *Mesostoma lingua*; G₁, showing subitaneous eggs.

H. *Mesostoma productum*; H₁, showing subitaneous eggs.



- B brain (cerebral ganglia)
 BC bursa copulatrix (bursa or seminal bursa)
 CO male copulatory organ
 DB dorsal edge of body
 DE ductus ejaculatorius
 E dark eyes
 EG egg capsule
 EGD dormant egg(s)
 EGS subitaneous egg(s)
 ER red eyes
 EX excretory duct (protonephridial duct)
 FL flattened anterior end
 G common gonopore
 I intestine or gut
 M mouth
 OV ovary
 PF pigment free area
 PR pharynx rosulatus
 R rod or rhabdoid tracks
 RS receptaculum seminalis (seminal receptacle)
 SM sperm
 SN spines
 T testis
 U uterus
 VD vas deferens
 VE ventral edge of body
 Y yolk glands (vitellaria)

A LIST OF ABBREVIATIONS USED IN TEXT-FIGURES 8 TO 68 ON PAGES 43-81

A	adhesive papillae
AC	atrium copulatorium (atrium genitale or copulatory atrium)
B	brain (cerebral ganglia)
BC	bursa copulatrix (bursa or seminal bursa)
BS	blind sac of atrium copulatorium
C	ciliated pit
CA	cilia
CGP	pre-oral ciliated groove
CI	cirrus (male copulatory organ)
CO	male copulatory organ
CR	collar region
DB	dorsal edge of body
DE	ductus ejaculatorius
E	dark eyes
EG	egg capsule
EGD	dormant egg(s)
EGS	subitaneous egg(s)
ER	red eyes
EV	excretory vesicle or beaker
EX	excretory duct (protonephridial duct)
EY	yellow/brown eyes
F	fission plane of zooids
FE	fenestrae region
FG	female gonopore
FL	flattened anterior end
FVS	false vesicula seminalis (spermiducal vesicle)
G	common gonopore
GE	germovitellarium
GL	girdle
GN	glands
GP	pharyngeal gland cells
GS	granular secretions
H	hook
HA	proximal handle or stalk
I	intestine or gut
K	keel
LD	lateral distal branch or end branch
LG	longitudinal grooves
LP	long prostomium
LS	large spine

M	mouth
MB	median process, branch or piece
MG	male gonopore
MT	median tube
NP	nephridiopore or excretory pore
O	opening of stylet
OV	ovary
P	prostomium
PB	proboscis
PBS	pre-oral blind sac
PC	pharyngeal cavity (buccal tube)
PD	pharynx doliiformis
PF	pigment free area
PGS	pigment spot of irregular shape
PP	pharynx plicatus
PR	pharynx rosulatus
PS	pharynx simplex
PV	pharynx variabilis
R	rod or rhabdoid tracks
RAE	retractile tip of body
RB	bowl-shaped, light-refracting organ
RG	globular, light-refracting organ
RP	red pigment spot
RS	receptaculum seminalis (seminal receptacle)
S	penis stylet (hard structure of copulatory organ)
SC	sensory cells
SM	sperm
SN	spines
SP	protective sheath of stylet
ST	statocyst
T	testis
TB	transverse bar or cross piece
TS	toothed structure
U	uterus
VD	vas deferens
VE	ventral edge of body
VG	vesicula granulorum (prostatic or granular vesicle)
VS	vesicula seminalis (seminal vesicle)
Y	yolk glands (vitellaria)
YD	diffuse yolk glands (vitellaria)

KEY TO CATENULIDA AND MACROSTOMIDA

- 1 Pigment spots and eyes absent (Fig. 2A–G, p. 29). Reproduction asexual, when a chain of two or more zooids is formed (Fig. 2B–G), or sexual. Protonephridia with a single, central excretory duct (EX, Fig. 2A–G). Posterior end of body tapering and never spatulate (broadened) (Fig. 2A–G)— 2

CATENULIDA

- Pigment spots (RP, Fig. 3A, p. 31) or eyes (E, Fig. 3B) present. Reproduction sexual only (Fig. 3B) (exceptionally, *Microstomum* reproduces both asexually (Fig. 3A) and sexually). Protonephridia with a pair of excretory ducts (EX, Fig. 3B). Posterior end of body tapering (Fig. 3A) or, more usually, spatulate (Fig. 3B)— 8

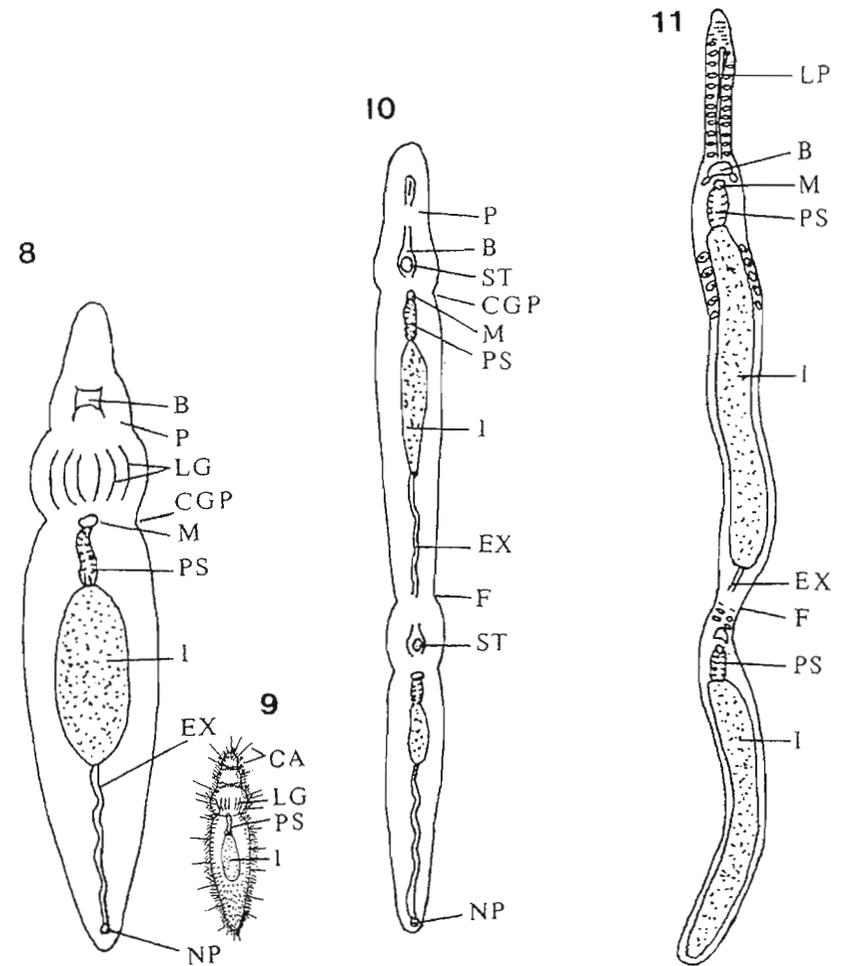
MACROSTOMIDA

- 2 Brain compact (B, Figs 8, 10). A pre-oral ciliated groove (furrow) is present, separating the prostomium (front end of body without the intestine) from the rest of the body (CGP, Figs 8, 10)— 3
Family Catenulidae

- Brain with anterior and posterior paired lobes; sensory cells in front of brain often in pseudometameric arrangement (parallel rows) (Figs 11–15). Pre-oral ciliated groove absent (Figs 11–15)— 4
Family Stenostomidae

- 3 Statocyst absent. A ring of ciliated longitudinal grooves present on prostomium (LG, Figs 8, 9). White/pale yellow. Length 0.3–0.4 mm—
Suomina turgida

- Statocyst present (ST, Fig. 10). Longitudinal grooves on prostomium absent (Fig. 10). Colourless/white. Length 0.8–1.0 mm (length of two zooids)—
Catenula lemnae



Figs 8–11. Major features of two species of Catenulidae (8–10) and one species of Stenostomidae (11).

8: *Suomina turgida*. 9: *S. turgida*, showing cilia (after Kolasa 1991). 10: *Catenula lemnae*. 11: *Rhynchoscolex simplex*. F is the fission plane of two zooids.

4 Ciliated pits and light-refracting organs absent. Prostomium elongated (Fig. 11). (A statocyst is present in the larval/juvenile stage). White/pale yellow. Length up to 6 mm—
Rhynchoscolex simplex

— Ciliated pits present (C, Figs 12–15). Light-refracting organs present or absent. Prostomium not elongated (Figs 12–15)— 5

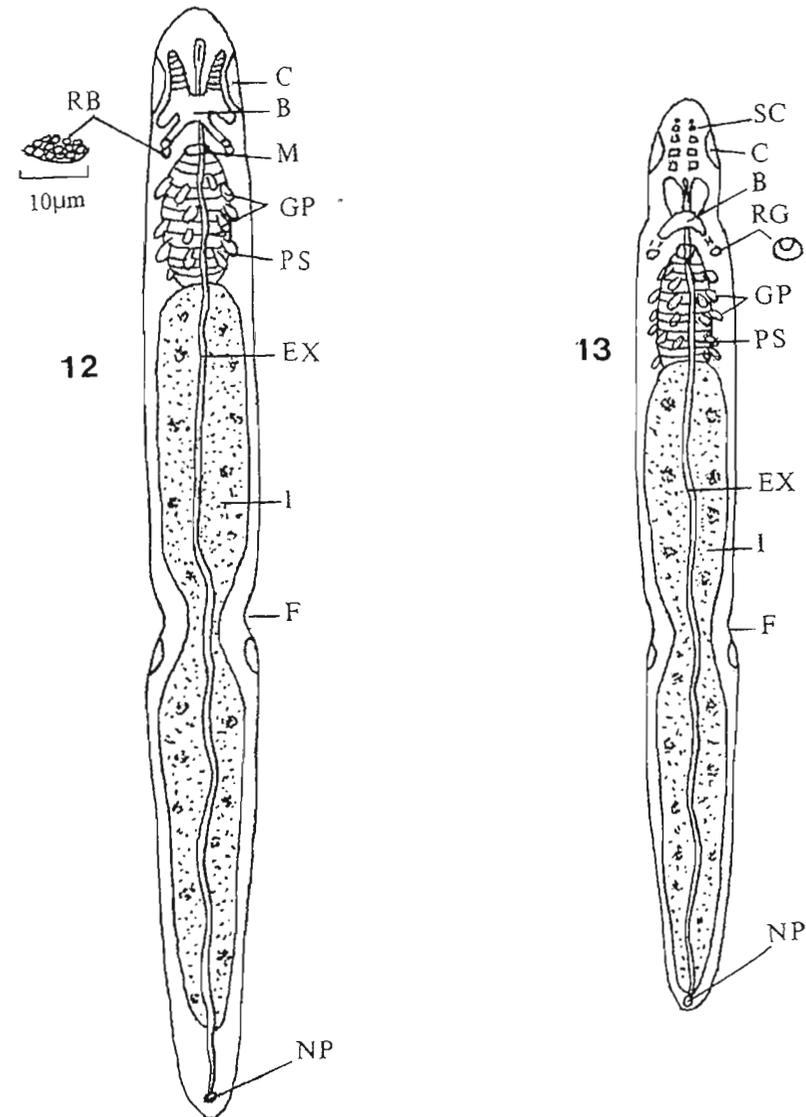
Genus *Stenostomum*

5 Light-refracting organs present (RB, Fig. 12; RG, Fig. 13)— 6

— Light-refracting organs absent (Figs 14, 15)— 7

6 Light-refracting organs bowl-shaped, comprising 20 or more granules (RB, Fig. 12). White/pale yellow. Length 0.7–1.7 mm (length of two zooids)—
Stenostomum leucops

— Light-refracting organs globular, comprising one or occasionally two granules (RG, Fig. 13). White/pale yellow. Length 0.5–1.3 mm (length of two zooids)—
Stenostomum unicolor



Figs 12–13. Major features of two species of Stenostomidae.

12: *Stenostomum leucops*, with bowl-shaped light-refracting organs (RB).

13: *Stenostomum unicolor*, with globular light-refracting organs (RG).

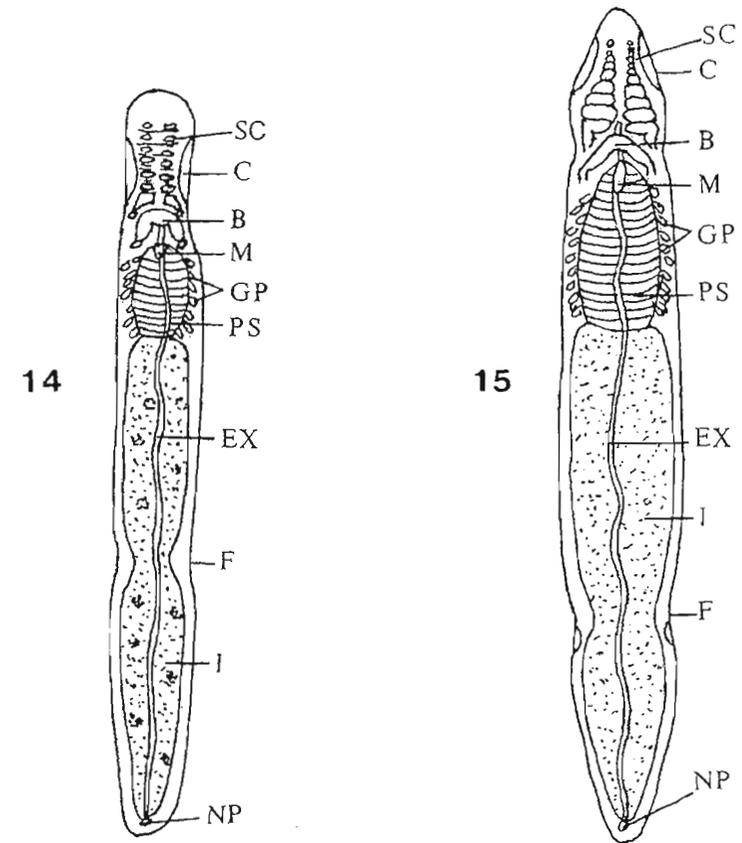
F is the fission plane of two zooids.

- 7 Front end of animal duck-billed in shape and searching in movement. Pharynx simplex about 1/8th of body length (PS, Fig. 14). Colourless/white. Length 0.5–1.0 mm (length of two zooids)—

Stenostomum anatrostrum

- Front end more pointed. Pharynx simplex about 1/5th of body length (PS, Fig. 15). Colourless/white. Length 0.4–0.8 mm (length of two zooids)—

Stenostomum grabbskogense



Figs 14–15. Major features of two species of Stenostomidae.

14: *Stenostomum anatrostrum*. 15: *Stenostomum grabbskogense*.

F is the fission plane of two zooids.

- 8 (1) One pair of anterior red pigment spots (RP), ciliated pits (C) and a pre-oral blind sac (PBS, intestine extension in front of mouth) are all present (Fig. 16). Reproduction sexual (hooked penis stylet may be present) or, more usually, asexual when zooids separated by division planes are apparent (F, Fig. 16). Body cylindrical with pointed posterior end which lacks adhesive papillae (Fig. 16). White/pale yellow. Length 1.0–1.8 mm (length of two zooids)—
Microstomum lineare

- One pair of dark eyes present (E, Fig. 17). Ciliated pits and pre-oral blind sac absent. Sexual reproduction only. Body flattened with spatulate posterior end which has adhesive papillae (A, Fig. 17)— 9

Genus *Macrostomum*

- 9 Distal end of penis stylet sharp (S, Figs 17–19)— 10

- Distal end of penis stylet blunt, with either thickened walls or cowl-(hood)-shaped (Figs 20, 21)— 11

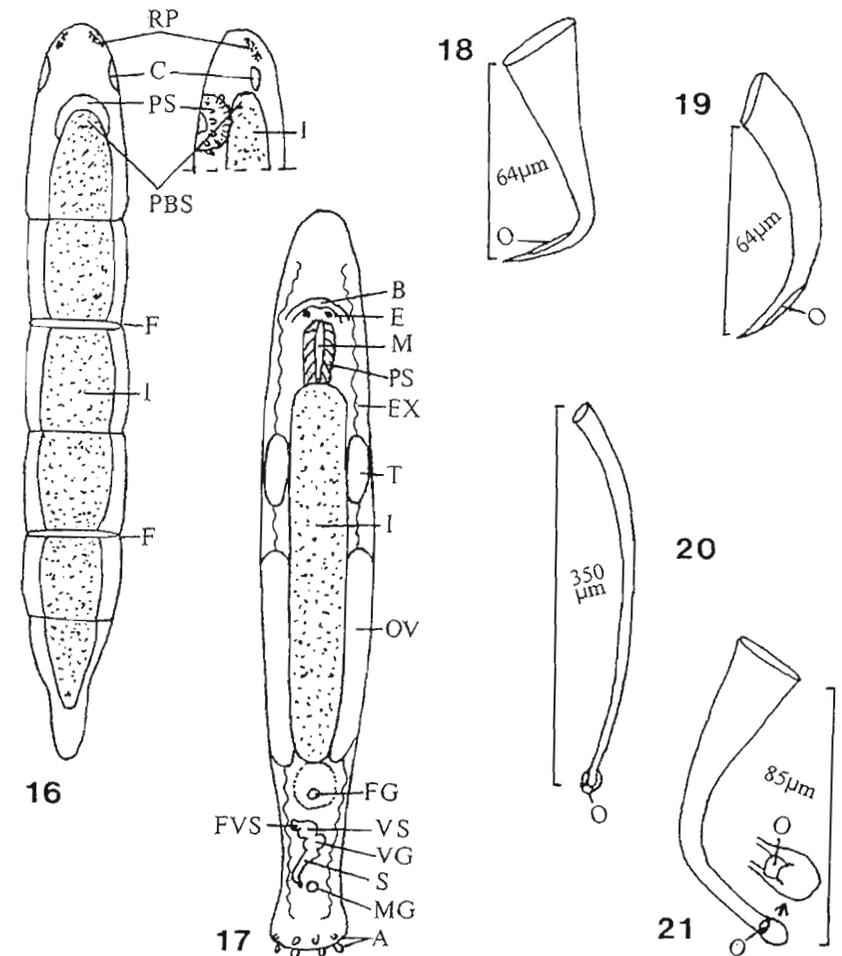
- 10 Penis stylet very slightly spiralled (S, Fig. 17); distal end opening superior, i.e. on concave side (O, Fig. 18). Colourless/white. Length 0.8–1.5 mm—
Macrostomum rostratum

- Penis stylet not spiralled; distal end opening inferior, i.e. on convex side (O, Fig. 19). Colourless/white. Length 0.8–1.5 mm—

Macrostomum distinguendum

- 11 Penis stylet not curved in two planes and 280–420 μm in length; distal end with thickened walls, and terminal opening (O, Fig. 20). Colourless/white. Length 1.0–2.2 mm. Only recorded from warmed freshwater aquaria—
Macrostomum tuba

- Penis stylet curved in two planes and 80–90 μm in length; distal end cowl shaped, and with sub-terminal opening (O, Fig. 21). Colourless/white. Length 1.0–1.3 mm—
Macrostomum johni



Figs 16–21. Major features of the single species in the Microstomidae and four species in the Macrostomidae.

16: *Microstomum lineare*, with a side view of the anterior end; RP, red pigment spot; C, ciliated pit; PS, pharynx simplex; PBS, pre-oral blind sac; I, intestine.
17: *Macrostomum rostratum*. 18: *M. rostratum*, penis stylet and opening (O).
19: *Macrostomum distinguendum*, penis stylet and opening (O).
20: *Macrostomum tuba*, penis stylet with opening (O). 21: *Macrostomum johni*, penis stylet with opening (O).

KEY TO PROLECITHOPHORA AND LECITHOEPITHELIATA

- 1 Yolk cells are diffuse and separate from the oocytes; paired yolk glands (YD) and paired ovaries (OV) lie at the sides of the intestine and pharynx (Fig. 22)—

PROLECITHOPHORA

*Plagiostomum lemani**

*This is the only prolecithophoran species recorded in Britain. Two pairs of dark eyes are present (E, Fig. 22). The pharynx variabilis is large (PV, Fig. 22). White to yellow/pale brown; brown lines of pigmentation on the dorsal side. Length up to 6 mm.

- Yolk surrounds the oocytes in a single germovitellarium (organ containing ovary and yolk cells) (GE, Fig. 23). A penis stylet is present, near the pharynx (S, Figs 23–25); a male gonopore (MG) opens into the pharyngeal cavity (PC) which opens at front end of the body (M) (Figs 23–25)—

2

LECITHOEPITHELIATA

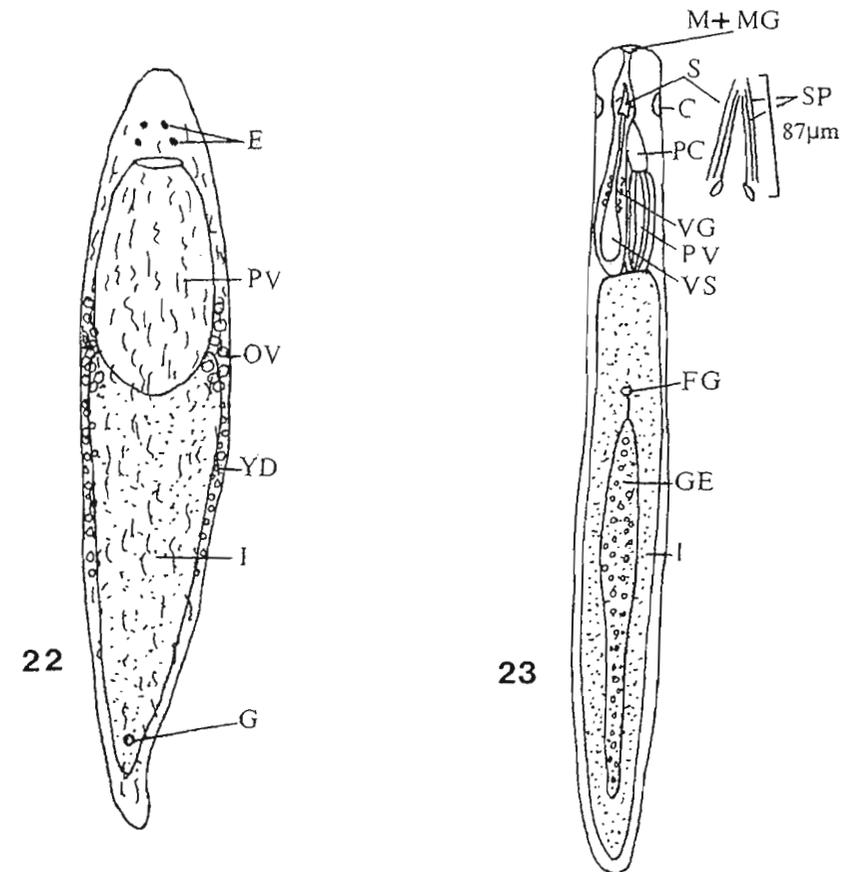
- 2 Penis stylet straight and 78–96 μm in length (S, Fig. 23). No eyes (Fig. 23). White/pale yellow. Length up to 6 mm—

Prorhynchus stagnalis

- Penis stylet curved and 38–50 μm in length (S, Figs 24, 25). Eyes present or absent—

3

Genus *Geocentrophora*

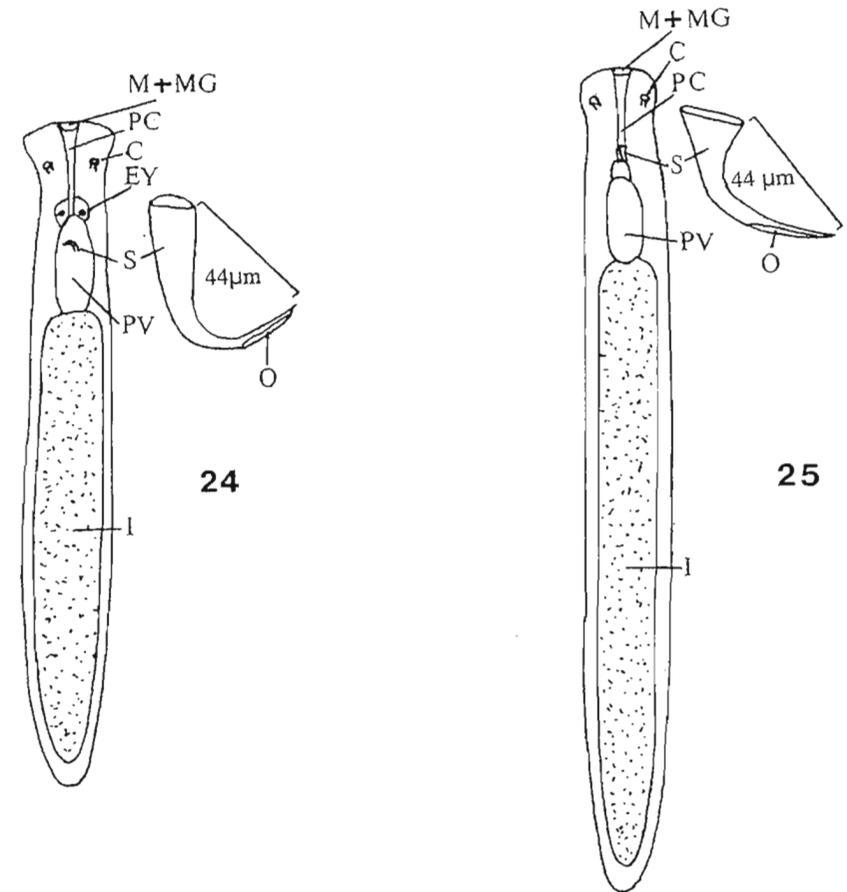


Figs 22–23. Major features of the single British species of Plagiostomidae (Prolecithophora), and a species of Prorhynchidae (Lecithoepitheliata).

22: *Plagiostomum lemani*. 23: *Prorhynchus stagnalis*, with details of the straight penis stylet (S) surrounded by a protective sheath (SP).

3 One pair of yellow-brown eyes (Fig. 24). White/pale yellow. Length up to 4 mm—
Geocentrophora sphyrocephala

— Eyes absent (Fig. 25). White/pale yellow. Length up to 7 mm—
Geocentrophora baltica



Figs 24–25. Major features of two species of *Geocentrophora* in the Prohynchidae (Lecithoepitheliata).

24: *Geocentrophora sphyrocephala*, with details of the penis stylet (S) and opening (O). 25: *Geocentrophora baltica*, with details of the penis stylet (S) and opening (O).

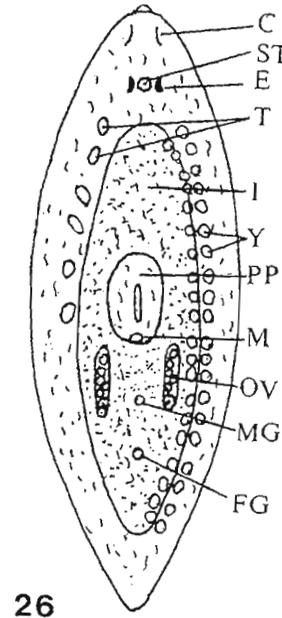
KEY TO PROSERIATA

- 1 Statocyst (ST) and one pair of dark eyes (E) present (Fig. 26). Short pharynx plicatus (PP) directed ventrally. Intestine (I) not split around pharynx (Fig. 26). Pale brown with paler ventral surface, and mesenchyme faintly reticulated. Length 2.5–3.5 mm—

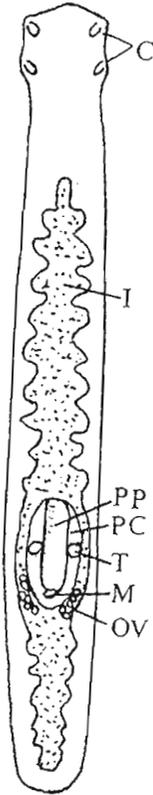
Otomesostoma auditivum

- Statocyst and eyes absent. Longer pharynx plicatus (PP) directed posteriorly. Intestine split around pharynx (Fig. 27). White/pale yellow. Length 2.0–3.0 mm—

Bothrioplana semperi



26



27

Figs 26–27. Major features of the two British species of Otomesostomidae and Bothrioplanidae (Proseriata).

26: *Otomesostoma auditivum*, depicting testes (T) on the left side and ovaries (OV) on the right side. 27: *Bothrioplana semperi*.

KEY TO RHABDOCOELE: DALYELLOIDA

1 Penis stylet (S) 52–84 μm in length, hooked (H, Fig. 28), with one handle (HA, Fig. 28) and located in a separate pocket adjacent to the bulb of the copulatory organ. (In *Dalyellia*, *Gieysztoria* and *Microdalyellia* the penis stylet is directly attached to the rest of the copulatory organ). One pair of dark eyes each consisting of an anterior and posterior part connected by a pigment band (E, Fig. 28). Mature animals with a single stalked egg in posterior position (OV, Fig. 28). Light to dark red-brown (sometimes almost black). Length 0.8–1.2 mm— *Castrella truncata*

— Penis stylet (S) with a pair of handles (HA) or without handles (Figs 29–39). One pair of dark eyes not comprising anterior and posterior parts (E, Figs 29, 30, 35)— 2

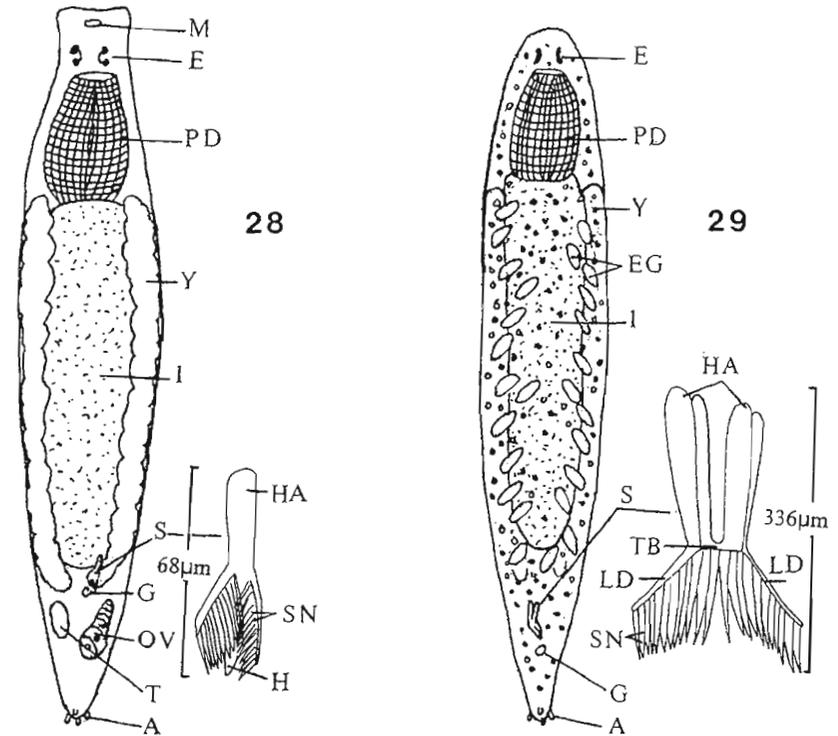
2 Penis stylet (S) with a pair of handles (HA, Figs 29–34). Mature animals with numerous eggs (EG, Fig. 29) or a single egg (EG, Fig. 31)— 3

— Penis stylet (S) a spiny girdle with no handles (SN, Fig. 35–39). Mature animals with a single egg in posterior part of body (EG, Fig. 35)— 7
Genus *Gieysztoria*

3 Penis stylet (S) with one pair of broad handles, each of which is usually cleft longitudinally into two parts, 292–380 μm in length (HA, Fig. 29). Mature animals with many eggs distributed along length of the animal (EG, Fig. 29). Green (with zoochlorellae); young animals are colourless/white. Length 2.5–4.0 mm— *Dalyellia viridis*

— Penis stylet (S) with a pair of intact handles (HA, Figs 30, 32–34). Mature animals with a single egg in posterior part of the body (EG, Fig. 31)— 4

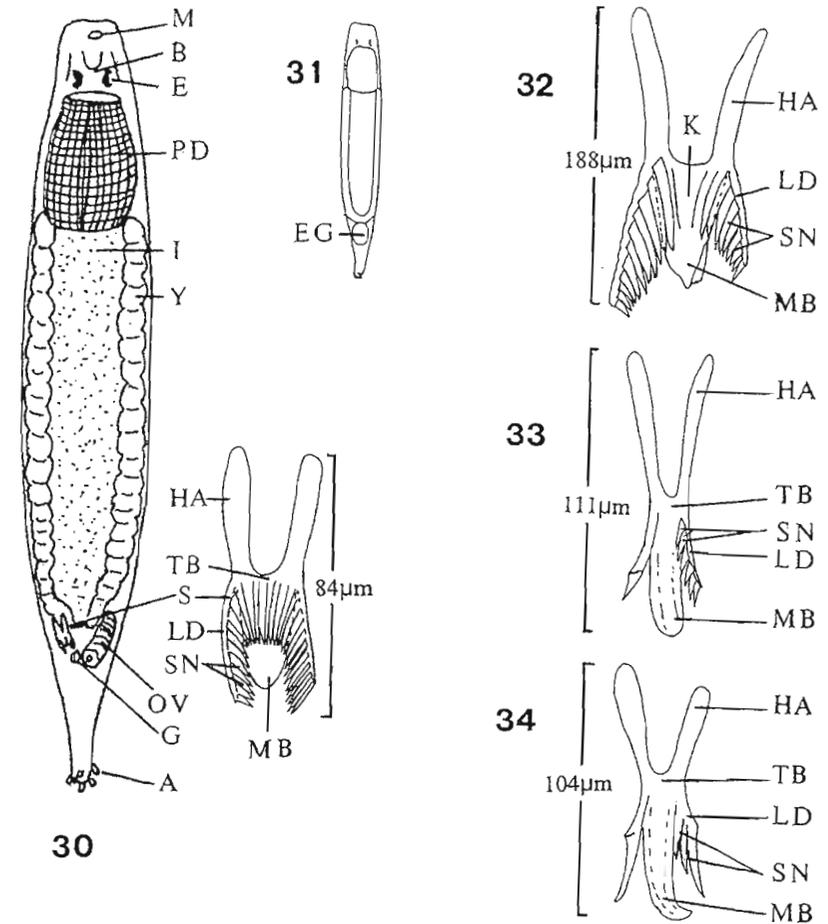
Genus *Microdalyellia*



Figs 28–29. Major features of two species of Dalyellidae (Dalyelloida).

28: *Castrella truncata*, with a penis stylet (S), single handle (HA), spines (SN) and a hook (H). 29: *Dalyellia viridis*, with a penis stylet (S), broad handles cleft in two (HA), a transverse bar (TB) and lateral distal branches (LD) carrying spines (SN).

- 4 Penis stylet with numerous spines on both of the lateral distal branches (left branch 15–25 and right branch 14–30 spines) and on the transverse bar (8–12 spines); stylet 68–100 μm in length (Fig. 30). Colourless/pale brown; sometimes anterior tip of body is reddish. Length 0.8–1.1 mm—
Microdalyellia fairchildi
- Penis stylet with only a few or numerous spines on both of the lateral distal branches, but none on the transverse bar (Figs 32–34)— 5
- 5 Penis stylet with numerous spines on both of the lateral distal branches (left branch 7–12 and right branch 8–12 spines), and with a keel (K) extending from the transverse bar part way down the median branch; stylet 128–248 μm in length (Fig. 32). Colourless/pale brown-red; sometimes anterior tip of body is reddish. Length 0.9–1.4 mm—
Microdalyellia brevimana
- Penis stylet with fewer spines on the lateral distal branches and without a keel (Figs 33, 34)— 6
- 6 Penis stylet with 1 spine (occasionally 2 or 3) on one lateral distal branch and 6 spines (occasionally 4, 5, 7 or 8) on the other; end of median branch rounded, and straight or only slightly bent; 85–137 μm in length (Fig. 33). Colourless/pale brown-red; sometimes anterior tip of body is reddish. Length 0.8–1.4 mm—
Microdalyellia armigera
- Penis stylet with 1 spine (rarely 2 or 3) on one lateral branch and 1–3 spines on the other; end of median branch more pointed, and bent sideways, often hook-shaped; 80–128 μm in length (Fig. 34). Colourless/pale brown-red. Length 0.8–1.0 mm—
Microdalyellia schmidtii

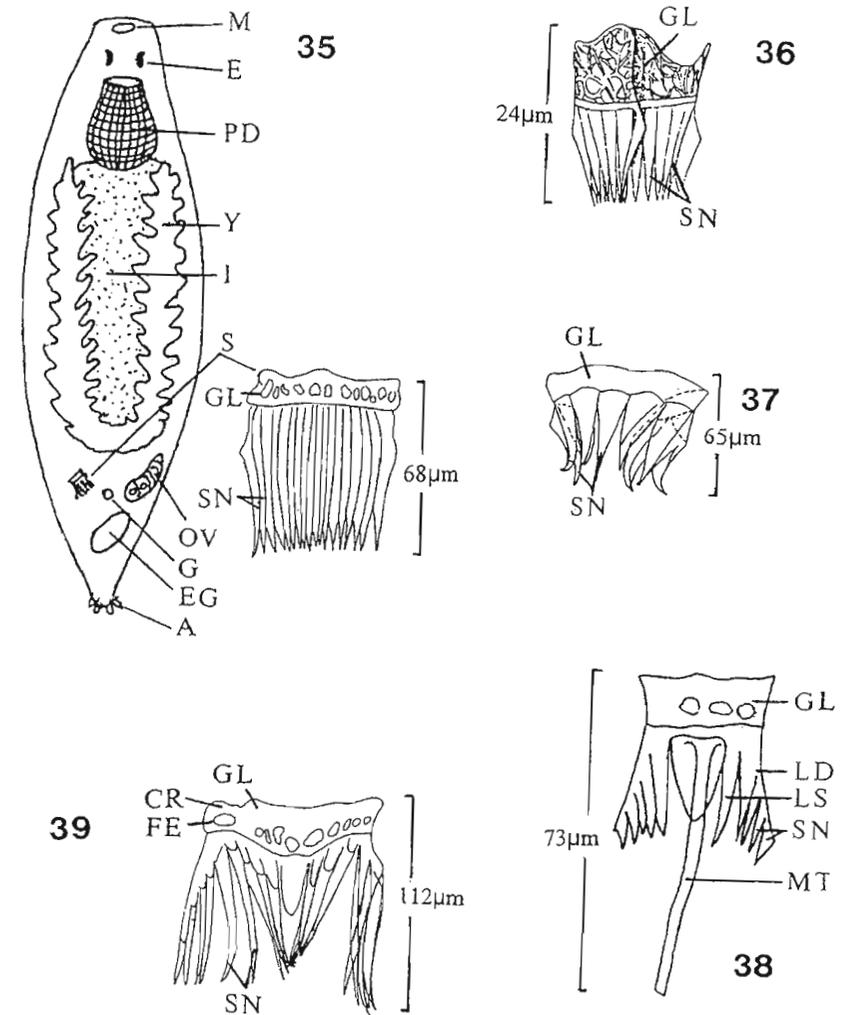


Figs 30–34. Major features of four species of Dalyelloida (Dalyelloida).

30: *Microdalyellia fairchildi*, with a penis stylet (S), two handles (HA), transverse bar (TB), lateral distal branches (LD) with spines (SN), and a median process (MB).
31: *M. fairchildi*, showing position of the single egg (EG) at the hind end of the body.
32: *Microdalyellia brevimana*, penis stylet with a median keel (K).
33: *Microdalyellia armigera*, penis stylet.
34: *Microdalyellia schmidtii*, penis stylet. Abbreviations as for *M. fairchildi*.

- 7 Penis stylet with spines of fairly similar appearance and length (SN, Figs 35–37)— 8
- Penis stylet with spines not all of similar appearance and length (SN, Figs 38, 39)— 9
- 8 Penis stylet 60–76 μm high and with 16–24 spines: height of girdle (GL) much less than half of the length of the spines (SN) (Fig. 35). Yolk glands strongly papillate (Y, Fig. 35). Yellow/brown-red. Length 1.0–1.5 mm—
Gieysztoria rubra
- EITHER: Penis stylet 20–28 μm high and with about 18–26 spines; height of girdle equal to or more than half the length of the spines (GL, Fig. 36). Yolk glands faintly incised or smooth. Colourless/pale brown. Length 0.7–1.0 mm—
Gieysztoria expedita
- OR: Penis stylet 60–70 μm high and with 8–11 spines; height of girdle much less than half the length of the spines (GL, Fig. 37). Yolk glands faintly incised. Colourless/pale brown. Length 0.9–1.3 mm—
Gieysztoria diadema
- 9 Penis stylet 64–82 μm high, with 2–4 spines on each lateral distal branch, and with a long median tube with one larger spine on either side (MT, Fig. 38). Pale brown/dark brown-red. Length 0.8–1.0 mm—
Gieysztoria infundibuliformis
- Penis stylet about 100–125 μm high and with about 18 spines; no long median tube (Fig. 39). Colourless/pale brown. Length 1.1–1.5 mm—
*Gieysztoria triquetra**

*There is only one doubtful record from Britain; see p. 12.

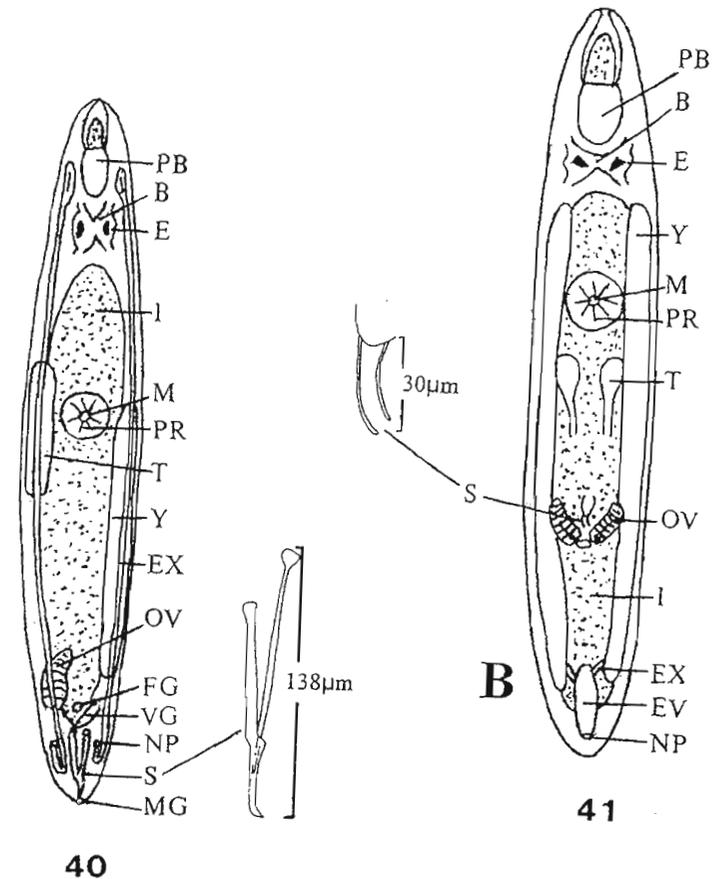


Figs 35–39. Major features of five species of Dalyellidae (Dalyelloida).

- 35: *Gieysztoria rubra*, with a penis stylet (S), girdle (GL) and spines (SN).
 36: *Gieysztoria expedita*, penis stylet with a deep girdle (GL) and spines (SN).
 37: *Gieysztoria diadema*, penis stylet with a shallow girdle (GL) and relatively few spines.
 38: *Gieysztoria infundibuliformis*, penis stylet with a long median tube (MT).
 39: *Gieysztoria triquetra*, penis stylet with a collar region (CR) and fenestrae region (FE) (after Rixen 1961).

KEY TO RHABDOCOELA: KALYPTORHYNCHIA AND TYPHLOPLANOIDA

- 1 With a proboscis (PB, Figs 40, 41)— 2
KALYPTORHYNCHIA
- Without a proboscis (Figs 42–68)— 3
TYPHLOPLANOIDA
- 2 Penis stylet wishbone-shaped and 111–165 μm in length (S, Fig. 40). Unpaired ovary (OV), testis (T) and yolk gland (Y). Female gonopore (FG) anterior to male gonopore (MG) which opens at posterior tip of body (Fig. 40). Excretory ducts (EX) open directly onto body surface; excretory vesicle absent (Fig. 40). Colourless/pale yellow. Length 1.5–2.0 mm—
Gyratrix hermaphroditus
- Penis stylet a simple tube and 20–38 μm in length (S, Fig. 41). Paired ovaries, testes and yolk glands. Single gonopore. Excretory ducts open into an excretory vesicle (EV) at rear end of body (Fig. 41). Colourless/pale yellow. Length 1.6–2.5 mm— *Opisthocystis goettei*



Figs 40–41. Major features of two species of Polycystidae (Kalyptorhynchia).
 40: *Gyratrix hermaphroditus*, with a wishbone-shaped penis stylet (S).
 41: *Opisthocystis goettei*, with a simple penis stylet (S).

- 3 Yolk gland (Y) comprised of a single line of large cells above the intestine (I) (Fig. 42). Single excretory duct (EX) opening ventrally at the nephridiopore (NP) in front of the pharynx rosulatus (PR) (Fig. 42). Eyes (E) present. Colourless/white. Length 0.4–0.5 mm—

Limnoruanis romanae

- Yolk glands (Y) paired, situated on both sides of the intestine (I) (shown in Figs 43–49, 56–59, 61, 64). Paired excretory ducts (EX) (shown in Figs 47–49, 55, 58–61, 63–65, 67). Eyes present or absent— 4

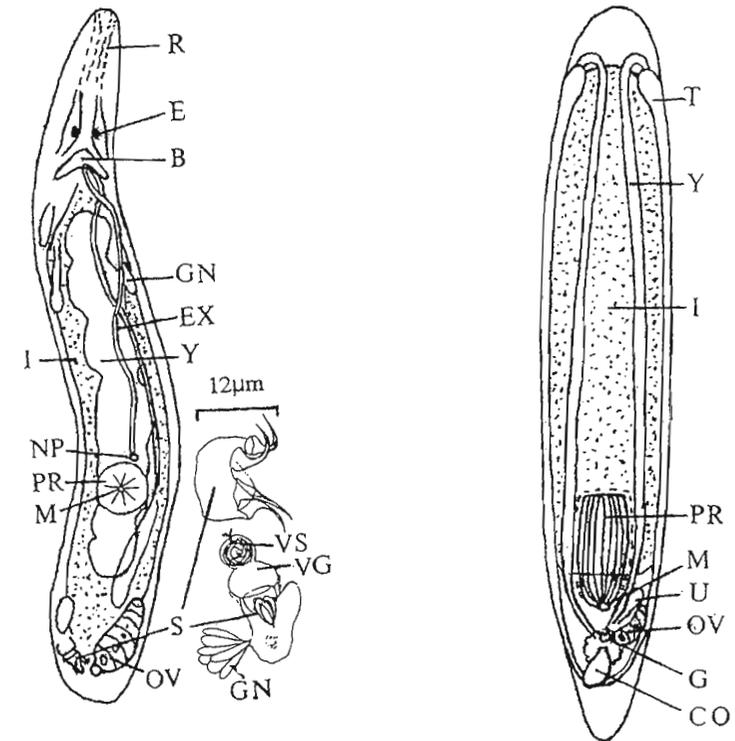
- 4 Pharynx rosulatus (PR) elongated, directed posteriorly, and situated near the hind end of the body (Fig. 43). Excretory ducts open by a single nephridiopore ventrally between the mouth (M) and common gonopore (G) (Fig. 43). Eyes absent. Pale yellow/white; mesenchyme often pale pink and body fluid greenish. Length 2.0–4.5 mm—

Opistomum pallidum

- EITHER: Pharynx rosulatus (PR) slightly oval-shaped, directed anteriorly, and situated near the front end of the body (Figs 44, 45). Excretory ducts open separately and ventrally onto the body surface about half-way or two-thirds down the body. Eyes (E) present or absent— 5

Genus *Phaenocora*

OR: Pharynx rosulatus (PR) directed ventrally, typically round (slightly elongated in *Tetracelis marmorosa*, Fig. 46) and situated nearer the middle of the body (Figs 48, 49, 55, 60–67), although it can be distinctly in the anterior half (*Tetracelis marmorosa*, Fig. 46), *Typhloplana viridata*, Fig. 47, and *Strongylostoma* spp., Figs 58, 59), or in the posterior half (*Olisthanella* spp., Figs 56, 57). Excretory ducts either open into the mouth (buccal cavity) or gonopore (genital atrium), or open separately onto the body surface. Eyes present or absent— 6



42

43

Figs 42–43. Major features of two species of Typhloplanidae (Typhloplanoida).

42: *Limnoruanis romanae*, showing a penis stylet (S) (after Kolasa 1991).

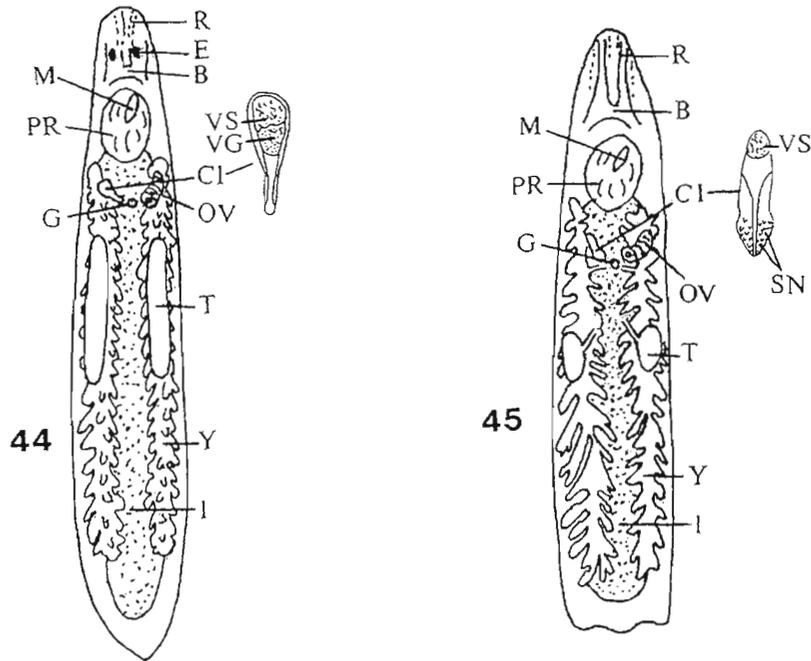
43: *Opistomum pallidum*.

- 5 Pair of yellow/brown eyes (E) (rarely absent) (Fig. 44). Copulatory organ (cirrus) without spines (CI, Fig. 44). Pale yellow/brown; sometimes green with zoochlorellae. Length 2.5–3.5 mm—

Phaenocora unipunctata

- Eyes absent (Fig. 45). Copulatory organ (CI) with spines (SN, Fig. 45). Pale yellow/brown; sometimes green with zoochlorellae. Length 2.5–3.5 mm—

Phaenocora typhlops



Figs 44–45. Major features of two species of Typhloplanidae (Typhloplanoida).

44: *Phaenocora unipunctata*, showing the male copulatory organ (cirrus, CI).

45: *Phaenocora typhlops*, showing the male copulatory organ (cirrus, CI) with spines (SN).

- 6 Pharynx rosulatus slightly elongated and situated distinctly in anterior half of the body (PR, Fig. 46). Two pairs of dark eyes (E, Fig. 46). Small testes ventral to yolk glands (Y). Excretory ducts open into the mouth. White/pale yellow or pale grey/brown. Length 1.0–1.5 mm—

Tetracelis marmorosa

- Pharynx typically round and usually situated nearer to the middle of the body (Figs 47–49, 55–68), though distinctly in anterior half in *Typhloplana viridata* (Fig. 47) and *Strongylostoma* spp. (Figs 58, 59) and in posterior half in *Olisthanella* spp. (Figs 56, 57). Eyes present or absent. Testes ventral or dorsal to yolk glands. Excretory ducts open into the mouth or gonopore, or separately onto the body surface— 7

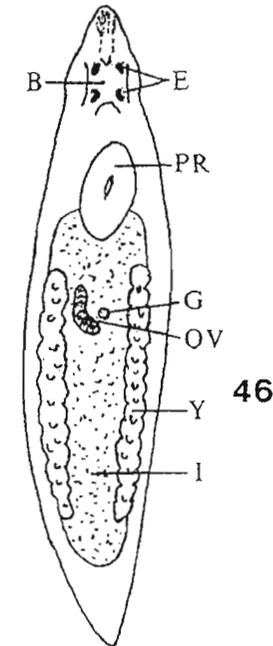


Fig. 46. Major features of *Tetracelis* in the Typhloplanidae (Typhloplanoida).

46: *Tetracelis marmorosa*.

- 7 Eyes or pigment spots absent. Testes ventral to yolk glands. Excretory ducts (EX) open into the mouth (M) (Figs 47-49)— **8**
- Eyes or pigment spots (E) present (Figs 55-68). Testes dorsal or ventral to yolk glands. Excretory ducts open into the mouth (M) or gonopore (G), or separately onto the body surface— **15**
- 8 Atrium copulatorium and bursa copulatrix are absent. Testes (T) lie posterior to the pharynx rosulatus (PR) (Fig. 47). Green (with zoochlorellae); young animals colourless/white. Length 0.8-1.0 mm—
Typhloplana viridata

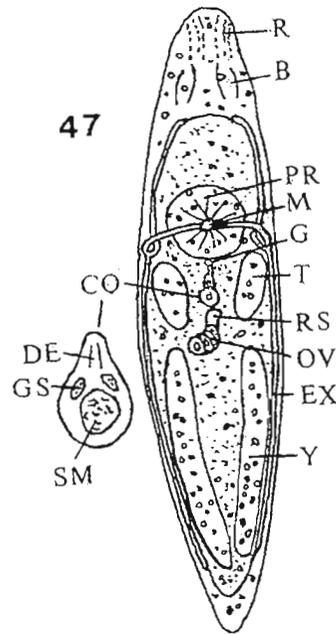
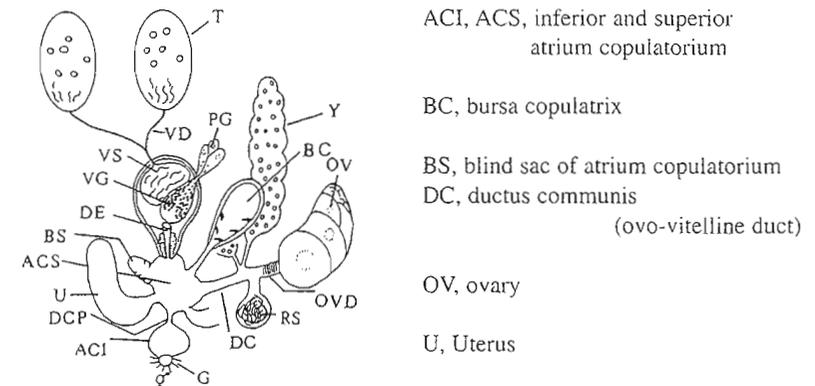


Fig. 47. Major features of *Typhloplana* in the Typhloplanidae (Typhloplanoida).
47: *Typhloplana viridata*, showing the male copulatory organ (CO), with a ductus ejaculatorius (DE), granular secretions (GS) and sperm (SM). Also depicted are rod or rhabdoid tracks (R), brain (B), pharynx rosulatus (PR), mouth (M), common gonopore (G), testis (T), receptaculum seminalis (RS), ovary (OV), excretory ducts (EX) and yolk glands (Y).

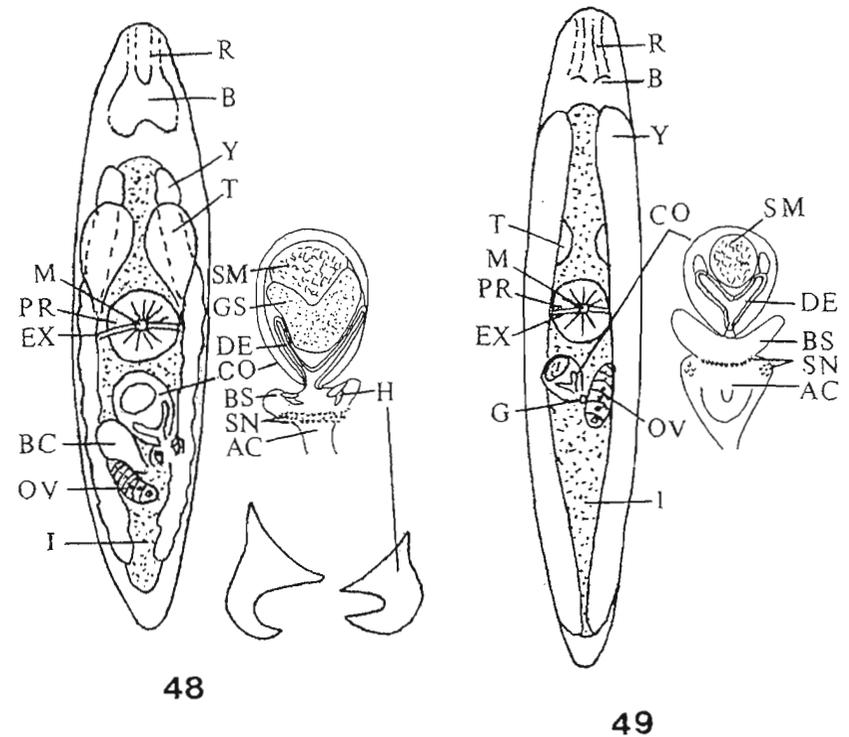
- Atrium copulatorium (AC) and bursa copulatrix* (BC) are present. Testes extend anterior to or lie at each side of the pharynx rosulatus (PR) (Figs 48-54)— **9**
Genus *Castrada*
- 9 Atrium copulatorium (AC) with one or two blind sacs* (BS) with spines (SN) (Figs 48-52)— **10**
- Atrium copulatorium relatively narrow, without blind sacs (Figs 53, 54)— **14**

*It is important to distinguish between the single bursa copulatrix and one or two blind sacs that are adjacent when present. These structures are part of the posterior part of the male copulatory apparatus; details are shown in Figs 48-54. The bursa copulatrix and copulatory organ are enclosed in a common sheet of muscle, whereas the blind sacs are extensions of the atrium copulatorium. The general arrangement of reproductive organs in the Family Typhloplanidae, with one ovary and two testes, is illustrated in Fig. 1C (p. 21) and described on page 22; the text-figure is reproduced below to assist users of this key.



DCP, ductus copulatorius; DE, ductus ejaculatorius; G, common gonopore; OVD, oviduct; PG, prostatic gland; RS, receptaculum seminalis; T, testis; VD, vas deferens; VG, vesicula granulorum; VS, vesicula seminalis; Y, yolk gland.

- 10 Ductus ejaculatorius (DE) bifurcated (Figs 48, 49) — 11
- Ductus ejaculatorius simple and not bifurcated (Figs 50–52)— 12
- 11 With one hook (H) in each of the two blind sacs (BS) (Fig. 48).
White/pale yellow colour (sometimes tinged green with zoochlorellae).
Length 0.8–1.5 mm— *Castrada armata*
- Without hooks in the two blind sacs (Fig. 49). White/pale yellow.
Length 0.8–1.1 mm— *Castrada luteola*

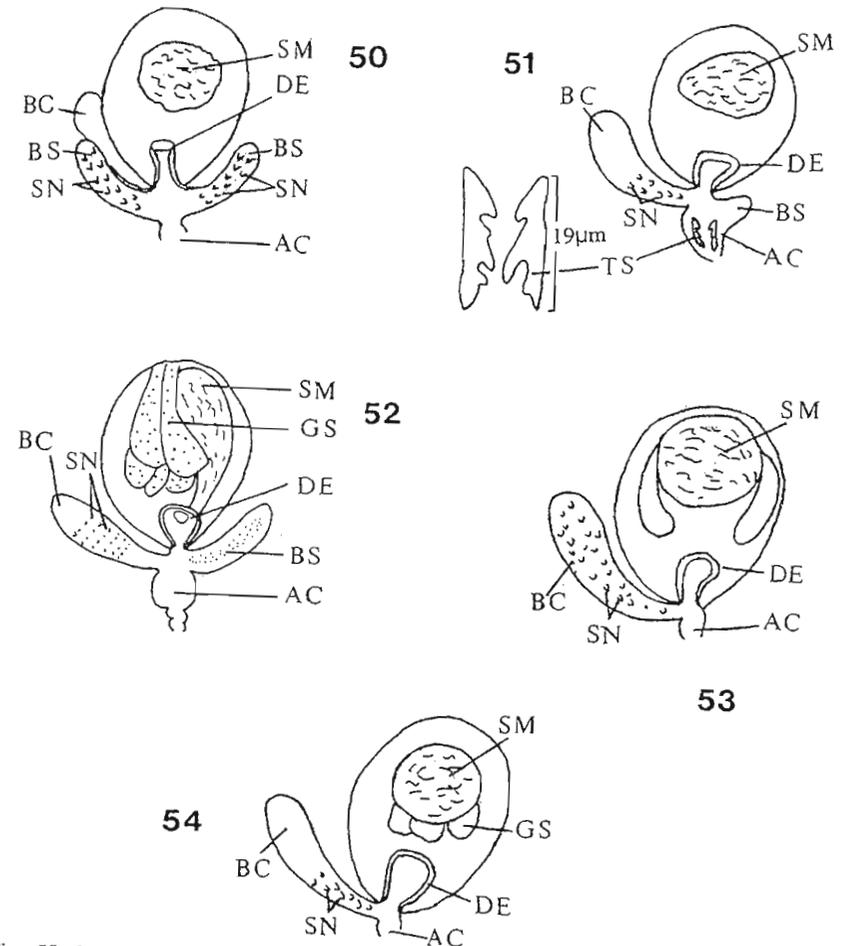


Figs 48–49. Major features of two species of *Castrada* in the Typhloplanidae (Typhloplanoida).

48: *Castrada armata* (ventral view), showing the male copulatory apparatus with the male organ (CO), atrium copulatorium (AC), two blind sacs of the atrium (BS) with spines (SN) and hooks (H), ductus ejaculatorius (DE), granular secretions (GS) and sperm (SM). **49:** *Castrada luteola*, showing the male copulatory apparatus with the male organ (CO), atrium copulatorium (AC), two blind sacs of the atrium (BS) with spines (SN), ductus ejaculatorius (DE), granular secretions (GS) and sperm (SM). Note that the bursa copulatrix is not shown for either species: the bursa copulatrix is very small in *C. luteola*.

Also depicted are rod or rhabdoid tracks (R), brain (B), pharynx rosulatus (PR), mouth (M), common gonopore (G), testis (T), receptaculum seminalis (RS), ovaries (OV), excretory ducts (EX) and yolk glands (Y).

- 12 Atrium copulatorium (AC) with two blind sacs (BS) which have spines (SN) (Fig. 50). Usually green (with zoochlorellae). Length 1.0–1.5 mm—
Castrada intermedia
- Atrium copulatorium with only one blind sac (Figs 51, 52)— 13
- 13 Atrium copulatorium with two large toothed structures (TS) of complicated form, 17–21 μm in length (Fig. 51) (not distinct hooks as found in the blind sacs of *Castrada armata*; see Fig. 48). Usually green (with zoochlorellae). Length 0.9–1.5 mm—
Castrada neocomensis
- Atrium copulatorium without such structures (Fig. 52). Green (with zoochlorellae). Length 0.5–0.6 mm—
Castrada viridis
- 14(9) Entire bursa copulatrix with spines (Fig. 53). Usually green (with zoochlorellae). Length 0.6–0.8 mm—
Castrada stagnorum
- Only stalk of bursa copulatrix with spines (Fig. 54). Pale yellow/grey colour. Length 2.0–3.5 mm—
Castrada lanceola



Figs 50–54. Major features of the male copulatory apparatus of five species of *Castrada* in the Typhloplanidae (Typhloplanoida).

50: *Castrada intermedia*. 51: *Castrada neocomensis*. 52: *Castrada viridis*. 53: *Castrada stagnorum*. 54: *Castrada lanceola*.

Atrium copulatorium (AC), one or two blind sacs of the atrium (BS) with spines (SN), bursa copulatrix (BC), ductus ejaculatorius (DE), granular secretions (GS) and sperm (SM), toothed structure (TS) in *C. neocomensis*.

15(7) Anterior tip of body retractable (RAE, Fig. 55). Testes ventral to yolk glands. Excretory ducts (EX) open into a common gonopore and nephridiopore (G+NP) (Fig. 55). Colourless/pale yellow/pale red. Length 1.5–3.5 mm—
Rhynchomesostoma rostratum

— Anterior tip of body not retractable (Figs 56–68). Testes dorsal or ventral to yolk glands. Excretory ducts (EX) open into the mouth (M) (Figs 58–68) or separately onto body surface (not illustrated in Figs 56, 57)—
16

16 Pharynx rosulatus (PR) distinctly in posterior half of body (Figs 56, 57). Testes (T) dorsal to yolk glands (Y) (Figs 56, 57). Excretory ducts open separately onto the body surface, posterior to the mouth and pharynx—
17

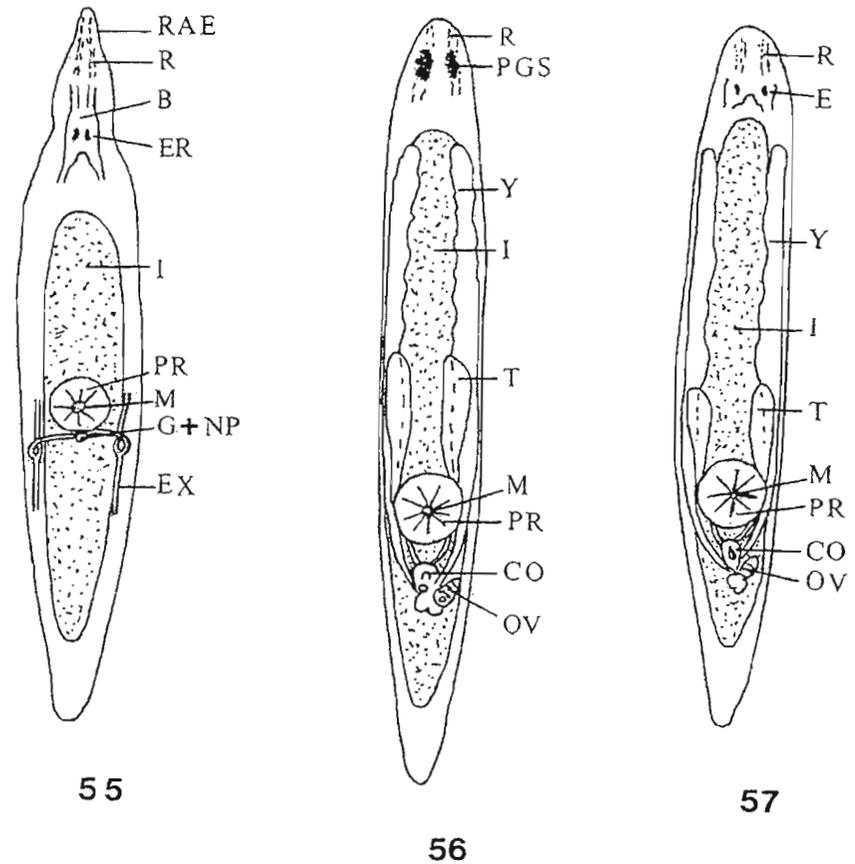
Genus *Olisthanella*

— Pharynx rosulatus in anterior half or middle of the body (Figs 58–68). Testes dorsal or ventral to yolk glands. Excretory ducts (EX) open into the mouth (M) (Figs 58–68)—
18

17 Anterior end with large pigment spots of irregular shape; usually 1–3 in number but sometimes fused into one mass; dark in transmitted light (PGS, Fig. 56). Pale yellow/brown. Length 1.1–1.5 mm—

Olisthanella obtusa

— Pigment spots absent. One pair of dark–red to black eyes (E, Fig. 57). Colourless/pale yellow. Length 1.0–1.3 mm—
Olisthanella truncula



Figs 55–57. Major features of three species of Typhloplanidae (Typhloplanoida).
55: *Rhynchomesostoma rostratum*. 56: *Olisthanella obtusa*. 57: *Olisthanella truncula*.

- 18 Pharynx rosulatus (PR) distinctly in anterior half of the body (Figs 58, 59). Testes (T) ventral to yolk glands (Y) (Figs 58, 59)— **19**

Genus *Strongylostoma*

- Pharynx rosulatus (PR) nearer to the middle of the body (Figs 60–68). Testes (T) dorsal to yolk glands (Y) (shown in Figs 61, 62, 64)— **20**

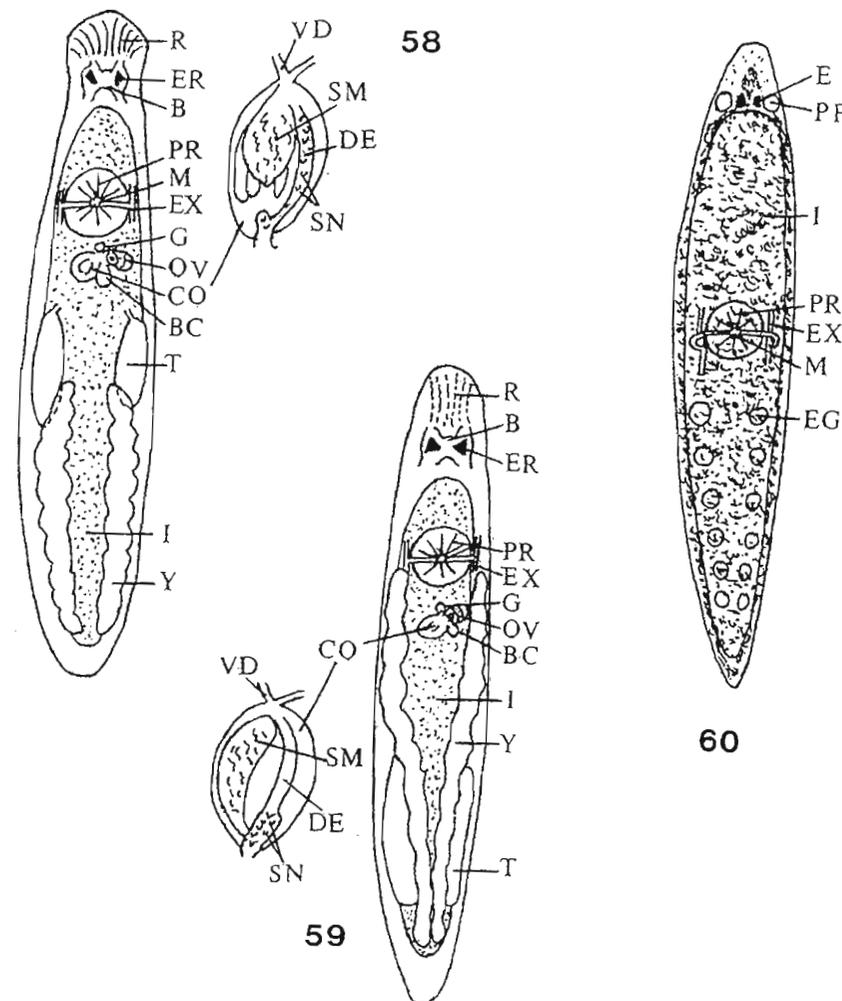
- 19 Whole length of ductus ejaculatorius (DE) with spines (SN) (Fig. 58). Anterior tip of body slightly spatulate or fan-shaped (Fig. 58). Pale red: yellow and red oil droplets in gut and mesenchyme. Length 0.7–1.5 mm—
Strongylostoma radiatum

- Only distal part of ductus ejaculatorius (DE) with spines (SN) (Fig. 59). Anterior end of body not widened (Fig. 59). Pale yellow/grey to red/dark brown; oil droplets and dark concretions may be present. Length 0.9–1.5 mm—
Strongylostoma elongatum

- 20 With a ventral pit in anterior part of body, and a canal (ductus spermaticus) directly connecting the bursa copulatrix to the ductus communis (ovo-vitelline duct) (see p. 69 for locations of BC and DC). Dark chocolate brown/black with paler front end, and two pigment-free areas (PF) in the region of the eyes (E) (Fig. 60). Length 4.0–5.0 mm—
Bothromesostoma personatum

- Without such a pit and canal. Colour of body much paler (Figs 61–68)— **21**

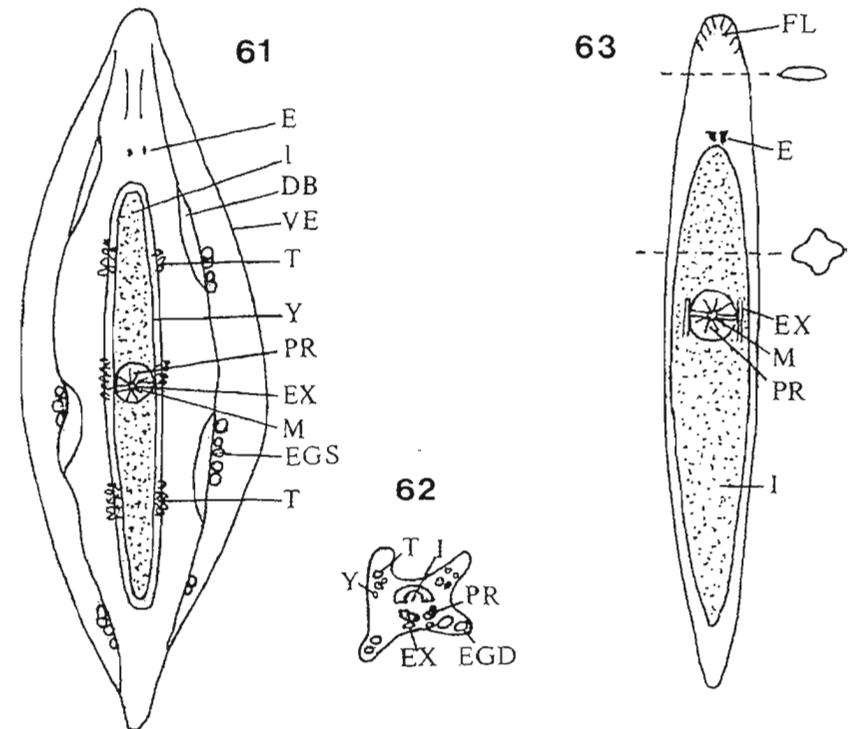
Genus *Mesostoma*



Figs 58–60. Major features of three species of Typhloplanidae (Typhloplanoida).
58: *Strongylostoma radiatum*, showing the male copulatory organ (CO), with spines (SN) along the length of the ductus ejaculatorius (DE). **59:** *Strongylostoma elongatum*, showing the male copulatory organ with spines along the distal part of the ductus ejaculatorius (abbreviations as above). **60:** *Bothromesostoma personatum*.

- 21 At least part of the body is ridged or keeled in cross section (Figs 61–63)— 22
 — Body not ridged or keeled as above (Figs 64–68)— 23
- 22 Sides of body drawn out into four longitudinal ridges (Figs 61, 62). Colourless/pale yellow-red. Length up to 10 mm—
Mesostoma tetragonum
- Body with a dorsal and a ventral keel though anterior end is dorso-ventrally flattened (Fig. 63). Pale yellow/brown. Length 4.0–4.5 mm—
*Mesostoma platycephalum**

*There is only one doubtful record from Britain; see p. 12.



Figs 61–63. Major features of two species of Typhloplanidae (Typhloplanoida).

61: *Mesostoma tetragonum* (after Graff 1913), showing ventral edge of body (VE) and dorsal edge (DB) viewed through the animal, excretory duct (EX), eyes (E), subitaneous eggs (EGS), mouth (M), pharynx rosulatus (PR), testis (T) and yolk glands (Y). **62:** *Mesostoma tetragonum*, transverse section showing the four longitudinal ridges of the body and dormant eggs (EGD), excretory duct (EX), intestine (I), pharynx rosulatus (PR), testis (T) and yolk glands (Y). **63:** *Mesostoma platycephalum* (after Graff 1909), with two transverse sections depicting the presence and absence of dorsal and ventral keels.

- 23 Body flattened and leaf-like (Fig. 64). Colourless/pale yellow. Length up to 12 mm—
Mesostoma ehrenbergii
- Body rounder in cross-section (Figs 65–68)— 24

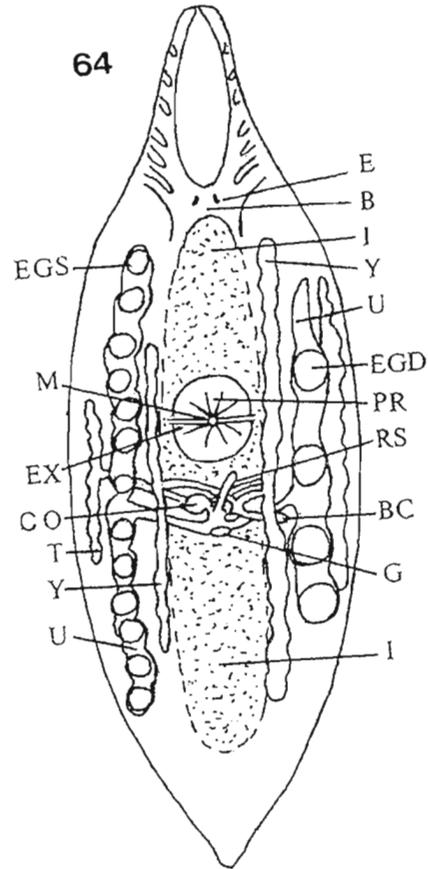
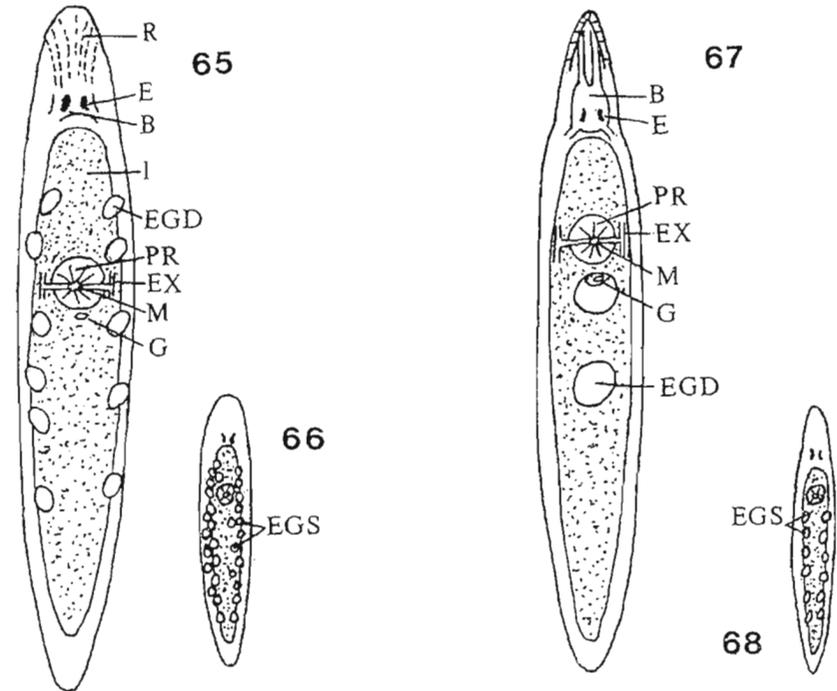


Fig. 64. Major features of *Mesostoma ehrenbergii* in the Family Typhloplanidae (Typhloplanoida).

64: *Mesostoma ehrenbergii* ventral view (after Graff 1913), left side showing subitaneous eggs (EGS; see p. 110) and right side showing dormant eggs (EGD). Other abbreviations are listed on pp. 40–41.

- 24 Anterior tip of body rounded (Figs 65, 66). Pale yellow/brown. Length up to 7 mm—
Mesostoma lingua
- Anterior tip more acuminate (Figs 67, 68). Body more darkly pigmented; yellow/brown with ventral side darker than dorsal side. Length 2.5–3.0 mm—
Mesostoma productum



Figs 65–68. Major features of two species of Typhloplanidae (Typhloplanoida).

65: *Mesostoma lingua*, with dormant eggs (EGD), a common gonopore (G), mouth (M), pharynx rosulatus (PR) and excretory ducts (EX). 66: *Mesostoma lingua*, depicting the presence of subitaneous eggs (EGS) (see p. 110). 67: *Mesostoma productum*; abbreviations as above. 68: *Mesostoma productum*, depicting the presence of subitaneous eggs (EGS).

BIOLOGY

FEEDING BEHAVIOUR AND FOOD

Hyman (1951) states that microturbellarians detect the presence of intact prey (i.e. not emitting body fluids) either by direct contact with chemoreceptors or by the disturbance created in the water by the prey. The chemical perception of fluids from damaged or recently dead prey is by chemoreceptors, particularly those in sensory areas such as the ciliated pits of *Stenostomum* and the ciliated grooves of *Phaenocora* and *Bothromesostoma*. More recently, Wrona & Koopowitz (1998) carried out a detailed study of *Mesostoma ehrenbergii*, and concluded that mechanical rather than chemical stimuli are likely to be the primary cues responsible for prey recognition and initiation of capture and feeding behaviour.

Capture of prey

In catenulid microturbellarians such as *Stenostomum* and *Macrostomum*, which possess a pharynx simplex (p. 18), small food items are swept back into the pharynx by the large cilia surrounding the mouth; this is capable of great distension, and food is engulfed whole. The more complex types of pharynx (pp. 18–19) are equally adept at seizing small food items and also can penetrate the integument of larger prey. Thus the pharynx doliiformis of the Dalyellioida can be distended but is not very protrusible, and there is a tendency for food items to be swallowed whole. The pharynx rosulatus of the Typhloplanoida is not very distensible but is partly protrusible. Whilst small items are ingested intact, the protruded pharynx is applied to the body wall of larger prey and pushed through some weak spot; the body fluids and tissues are then sucked up into the gut; Wrona & Koopowitz (1998) provide a comprehensive account of prey capture and feeding by *M. ehrenbergii*. The highly protrusible pharynx plicatus of the Proseriata is inserted into prey and contents are sucked out by peristaltic action. Microturbellarians attack larger prey individually but, sometimes, the initial attack is followed by a mass attack by numerous individuals (Mead 1978).

Some species of typhloplanid rhabdocoels, e.g. *Mesostoma lingua* and *M. ehrenbergii*, use different strategies to capture prey (Blaustein & Dumont (1990)). (a) *Trapping by mucus*: as the rhabdocoel moves along the substratum, mucus is deposited and entraps prey (Steinmann & Bresslau 1913; Graff 1913). Also, microturbellarians that glide along the underside of the water surface in small waterbodies, such as ponds and pools, may slowly sink in the

water column, depositing a mucous thread or web which traps open-water prey (Schwartz & Hebert 1982). (b) *Active searching*: microturbellarians moving along the substratum or dropping at the end of a mucous thread detect and orientate towards a prey organism (Bauchhenss 1971; Schwartz & Hebert 1982, 1986). (c) *Sit-and-wait or ambush predation*: rhabdocoels remain suspended in the water by their mucous thread or wait in cover, such as vegetation, to attack prey as it passes by (Steinmann & Bresslau 1913; Bresslau 1933). (d) *The use of a toxin*: the mucus produced by *M. lingua* is poisonous and prey can be overcome on direct contact with the rhabdocoel (Schwartz & Hebert 1986) or by diffusion of the poison from mucous webs (Case & Washino 1979). Dumont & Carels (1987) have demonstrated, in the laboratory, that the substance diffusing from mucus is a neurotoxin which can paralyse prey. The toxin decomposes rapidly and its inactivation rate is strongly temperature-dependent. The effect of the toxin on prey communities in field conditions remains uncertain. Interestingly, Wrona & Koopowitz (1998) found no evidence for a special chemical paralysis of prey by *M. ehrenbergii*. The apparent paralysis seen in cladocerans and mosquito larvae was partly a behavioural response of the prey in 'playing possum', and partly by immobilization of the prey by mucus produced by the rhabdocoel.

Species of Kalyptorhynchia use the anterior proboscis to capture their prey (Karling 1963). Also, *Prorhynchus stagnalis* and *Gyratrix hermaphroditus* use the penis stylet to stab prey. In the latter species, the proboscis momentarily adheres to the prey whilst the stylet is protruded and pushed into the prey (Mead & Kolasa 1984).

Digestion

Jennings (1957, 1968, 1974) studied digestion in two unidentified species of *Stenostomum* and *Macrostomum*, and in *Mesostoma tetragonum*. In the last two microturbellarians, digestive enzymes initiate extracellular (intraluminal) proteolysis, although this was not proven unequivocally for *M. tetragonum*. In *Stenostomum*, the extracellular disintegration of food is largely mechanical through contraction of the gut and entire body. In all three species, the extracellular process reduces the food to a particle size available for phagocytosis and intracellular digestion.

Diet

With a few exceptions, details of the diet of freshwater microturbellarians are poorly known. Most information is based on incidental observations of the gut contents of animals collected from the field for taxonomic or other types of investigation, or on items eaten in laboratory cultures. Although they feed mostly on intact, living organisms, microturbellarians have been observed feeding on damaged or dying prey (Anderson 1970), and some workers claim that dead prey, if not excessively decomposed, is also eaten by some species (e.g. *Microstomum lineare*, *Plagiostomum lemani*, *Bothrosostoma personatum*, *Olisthanella truncula* (Jennings 1957; Luther 1960; Schwank 1981b; Heitkamp 1982)). However, consumption of live prey is likely to predominate. The food eaten by the microturbellarian species that occur in the British Isles is presented in Table 3, which has been compiled from information appearing in scattered publications dealing with animals from continental Europe, North and South America, and, to a limited extent, the British Isles (Reisinger 1923; Haffner 1925; Ruhl 1927; Marcus & Marcus 1951; Luther 1955, 1960, 1963; Jennings 1957, 1968; Rixen 1961, 1968; Karling 1963; Borkott 1970; Bauchhenss 1971; Heitkamp 1972a, 1978a, 1982; Young 1973b, 1978 and unpublished; Watson 1976; Göltenboth & Heitkamp 1977; Collins & Washino 1979; Maly *et al.* 1980; Schwank 1981b; Schwartz & Hebert 1982, 1986; Mac Isaac & Hutchinson 1985; Ingole 1988; Blaustein 1990; Blaustein & Dumont 1990; Dumont & Schorreels 1990; Schmid-Araya & Schmid 1995, 2000; Beisner *et al.* 1996, 1997a,b; Wrona & Koopowitz 1998). For five of the species the food eaten by animals in laboratory studies is also shown.

Bacteria are eaten mainly by the Catenulida though they also feature in the diet of small individuals of other species, such as *Geocentrophora* spp., *Prorhynchus stagnalis*, *Olisthanella truncula* and *Limnoruanis romanae*, and probably others. The catenulids also consume single-celled algae, protozoans, rotifers and other small animals. Macrostomid species appear to eat algae such as diatoms and desmids, protozoans, rotifers, nematodes, small oligochaetes, turbellarians, crustaceans and insect larvae. *Microstomum lineare* is known to eat *Hydra* and to use the hydroid's nematocysts, placed in the microturbellarian's epidermis, to capture prey (e.g. Kepner *et al.* 1938; Karling 1966). Little is known about the food eaten by *Plagiostomum lemani*, *Bothrioplana semperi* and *Otomesostoma auditivum*; they appear to be carnivorous, including small oligochaetes or crustaceans in their diet. *Geocentrophora* and *Prorhynchus* eat algae, rotifers and other small

invertebrates such as oligochaetes; *G. sphyrocephala* is reported to consume protozoans, rotifers, microturbellarians and cladocerans. Dalyelliid species include mainly algae, protozoans and rotifers in their diet, although nematodes, oligochaetes and microturbellarians are eaten by some species. Typhloplanid rhabdocoels are mainly carnivorous, eating a variety of small invertebrates although some, for example *Castrada viridis*, *Limnoruanis romanae*, *Stongylostoma* spp. and *Typhloplana viridata*, also consume algae. The ventral surface of *Bothrosostoma personatum* is flattened and this allows the animal to cling to the undersurface of the water-film, where it feeds on trapped terrestrial insects. Kalyptorhynchian species are carnivorous, with small crustaceans dominating the diet.

A few detailed investigations on diet have been made. Young (1973b) studied the food eaten by *Phaenocora typhlops* living in a small English pond. In laboratory experiments, potential food organisms held in dishes were exposed to attack by rhabdocoels. The gut contents of field-collected animals were identified by microscopy and by a serological technique, the precipitin test. Tubificid oligochaetes were the main prey of the rhabdocoel. A similar study of *Phaenocora unipunctata*, living in a temporary English pond, again revealed that tubificids, followed by lumbriculids, were the main component in its diet, though cladocerans and chironomid larvae were eaten to a limited extent (Young 1978).

The most detailed laboratory studies on diet and feeding preferences have been carried out on *Mesostoma* spp. Mac Isaac & Hutchinson (1985) found that *M. lingua* from a Canadian tundra pond fed heavily on the cladoceran *Daphnia pulex* and the chironomid *Chironomus riparius*, but not on the fairy shrimp *Branchinecta paludosa* or the copepod *Diaptomus arctica*. Interestingly, the addition of vegetation, which provided habitat complexity, resulted in increased predation rates on their prey, contrary to what might be expected. This was explained in terms of the entanglement of prey which, when dying or dead, would be accessible to the microturbellarian. Schwartz & Hebert (1986), using *M. lingua* from a low arctic Canadian pond, also found that cladocerans (*Daphnia pulex* and *Simocephalus vetulus*) were the preferred food, but the small copepod *Diaptomus tyrrelli* was also eaten. Larger copepods (*Diaptomus* spp.) and the chironomid *Anatopynia* sp. were scarcely eaten. The rate of feeding by *M. lingua* is temperature-dependent (Dumont & Schorreels 1990). *Mesostoma ehrenbergii* collected from Canadian ponds fed on six different cladoceran species (Schwartz & Hebert 1982), and on the cladoceran *Daphnia magna*, larval mosquitoes (*Aedes*) and the annelid *Tubifex tubifex* (Wrona & Koopowitz 1998).

Table 3. The food of microturbellarian species that occur in Britain and Ireland, based mainly on studies of populations in continental Europe and America.

Species	Food
CATENULIDA	
<i>Catenula lemnae</i>	Bacteria
<i>Suomina turgida</i>	Bacteria
<i>Rhynchoscolex simplex</i>	Bacteria, tubificid oligochaetes, dipteran larvae
<i>Stenostomum anatrostrum</i>	Bacteria, algae, rotifers
<i>Stenostomum grabbskogense</i>	Bacteria, algae, flagellates, rotifers
<i>Stenostomum leucops</i>	Bacteria, green algae, desmids, diatoms, rhizopods, flagellates, ciliates, rotifers, microcrustaceans and microturbellarians (e.g. catenulids, <i>Castrada</i> , <i>Gyratrix</i>)
<i>Stenostomum unicolor</i>	Bacteria, green algae, flagellates, rotifers
MACROSTOMIDA	
<i>Macrostomum distinguendum</i>	Green algae, desmids, diatoms, rhizopods, ciliates, flagellates, rotifers, microturbellarians, small oligochaetes, small cladocerans
<i>Macrostomum jolani</i>	Green algae, desmids, diatoms, ciliates, flagellates, rotifers
<i>Macrostomum rostratum</i>	Green algae, desmids, diatoms, rhizopods, ciliates, rotifers, microturbellarians, small oligochaetes, small cladocerans
<i>Macrostomum tuba</i>	Green algae, desmids, diatoms, ciliates, flagellates, rotifers, small oligochaetes, small cladocerans
<i>Microstomum lineare</i>	<i>Hydra</i> , microturbellarians (e.g. <i>Gieysztor</i> , <i>Microdalyellia</i> , <i>Gyratrix</i>), rotifers, nematodes, oligochaetes, copepods, cladocerans, ostracods, insect larvae and nymphs (e.g. chironomids, ceratopogonids, ephemeropterans)
PROLECITHOPHORA	
<i>Plagiostomum lemnae</i>	Oligochaetes, microcrustaceans
LECITHOEPITHELIATA	
<i>Geocentrophora baltica</i>	Bacteria, algae, small oligochaetes
<i>Geocentrophora sphyrocephala</i>	Bacteria, green algae, desmids, diatoms, rhizopods, microturbellarians, rotifers, nematodes, small oligochaetes, cladocerans
<i>Prorhynchus stagnalis</i>	Bacteria, algae, microturbellarians, oligochaetes
PROSERIATA	
<i>Bothrioplana semperi</i>	Oligochaetes
<i>Otomesostoma auditivum</i>	Oligochaetes, microcrustaceans
RHABDOCOELA: DALYELLIODA	
<i>Castralla truncata</i>	Green algae, diatoms, ciliates, flagellates, rotifers, nematodes
<i>Dalyellia viridis</i>	Algae, animals (e.g. microturbellarians); (in the laboratory, freshly dead oligochaetes, molluscs)
<i>Gieysztor</i>	Algae, flagellates, rotifers
<i>Gieysztor</i>	Algae
<i>Gieysztor infundibuliformis</i>	Algae, flagellates and other protozoans, rotifers, microturbellarians.
<i>Gieysztor rubra</i>	Green algae, diatoms, flagellates, rotifers
<i>Gieysztor triquetra</i>	Diatoms, flagellates, rotifers

<i>Microdalyellia armigera</i>	Green algae, desmids, diatoms, flagellates, rhizopods, ciliates, rotifers, microturbellarians, small oligochaetes
<i>Microdalyellia brevimana</i>	Green algae, diatoms, rotifers
<i>Microdalyellia fairchildi</i>	Green algae, diatoms, ciliates, rotifers
<i>Microdalyellia schmidti</i>	Green algae, diatoms, rotifers
RHABDOCOELA: TYPHLOPLANOIDA	
<i>Bothromesostoma personatum</i>	Naidid oligochaetes, cladocerans, Collembola, ephemeropteran nymphs, mosquito larvae, terrestrial dipterans trapped at water surface
<i>Mesostoma ehrenbergii</i>	Mainly cladocerans but also naidid and tubificid oligochaetes, large rotifers, fairy shrimps, mosquito larvae
<i>Mesostoma lingua</i>	Mainly cladocerans and copepods (including larval stages) but also oligochaetes, ostracods, small insect larvae (chironomids and mosquitoes)
<i>Mesostoma platycephalum</i>	Unknown
<i>Mesostoma productum</i>	Small cladocerans, copepods (particularly larval stages)
<i>Mesostoma tetragonum</i>	Small oligochaetes, microcrustaceans, insect larvae
<i>Olisthanella obtusa</i>	Ciliates, rotifers, oligochaetes
<i>Olisthanella truncula</i>	Bacteria, rotifers, nematodes, oligochaetes
<i>Opisthomum pallidum</i>	Naidid and tubificid oligochaetes: (in the laboratory, freshly dead crustaceans, molluscs, insect larvae)
<i>Phaenocora typhlops</i>	Tubificid oligochaetes: (in the laboratory, squashed lumbricid oligochaetes, cladocerans, chironomids, chaoborids; occasional ostracods, snails)
<i>Phaenocera unipunctata</i>	Mainly tubificid and lumbricid oligochaetes, but also flagellates, cladocerans, chironomid larvae, microturbellarians (dalyellioidan species, <i>Rhynchomesostoma</i> , <i>Gyratrix</i>)
<i>Rhynchomesostoma rostratum</i>	Oligochaetes, cladocerans, copepods (including larval stages), microturbellarians, mosquito larvae, other aquatic insects: (in the laboratory, additionally, ostracods)
<i>Castrada armata</i>	Flagellates, rotifers
<i>Castrada intermedia</i>	Ciliates, rotifers; (in the laboratory, additionally, cladocerans, larval stages of copepods)
<i>Castrada lanceola</i>	Ciliates, rotifers
<i>Castrada luteola</i>	Ciliates, flagellates, rotifers
<i>Castrada neocomensis</i>	Flagellates, rotifers
<i>Castrada stagnorum</i>	Rotifers, nematodes, small oligochaetes (<i>Aelosoma</i>), rarely single-celled algae
<i>Castrada viridis</i>	Diatoms, ciliates, flagellates
<i>Limnoruanis romanae</i>	Bacteria, diatoms, rotifers
<i>Strongylostoma elongatum</i>	Desmids, diatoms, cladocerans
<i>Strongylostoma radiatum</i>	Diatoms, cladocerans
<i>Tetracelis marmorosa</i>	Rotifers, small oligochaetes, small cladocerans and copepods
<i>Typhloplana viridata</i>	Green algae, rotifers
RHABDOCOELA: KALYPTORHYNCHIA	
<i>Gyratrix hermaphroditus</i>	Copepods (including larval stages), some cladocerans
<i>Opisthocystis goettei</i>	Copepods (including larval stages), some cladocerans

In general, laboratory studies have shown that *Mesostoma* spp. feed more on cladocerans than on copepods, and they particularly eat cyclopoids, large calanoids and ostracods (Rocha *et al.* 1990). The reason for this food preference is uncertain and controversial, with prey size, behaviour and morphology being implicated. For example, Schwartz & Hebert (1982) found size-dependent predation for *M. ehrenbergii* feeding on cladocerans (see above); small animals were ignored and it was unable to catch large prey. MacIsaac & Hutchinson (1985) claim that the low predation rate by *M. lingua* on fairy shrimps and copepods in their experiments was due to vigorous escape mechanisms, including violent jerks and hops. Rocha *et al.* (1990) found that an unidentified *Mesostoma* sp. was able to eat an ostracod species that had a smooth carapace and a wide gap between its valves, but not a species with a spiny carapace and a narrow gap. The fact that *M. lingua* can paralyse its prey with a neurotoxin (p. 83) would suggest the potential to capture all types and sizes of prey. It is possible, however, that the effect of the toxin might vary according to prey type. Interestingly, high densities of *Mesostoma lingua* sometimes have been found coexisting with favoured prey organisms such as *Daphnia*, which might suggest the occurrence of toxin-resistant 'strains' of *Daphnia* or that some 'strains' of *M. lingua* do not produce toxin (Blaustein & Dumont 1990).

Impact of microturbellarians on populations of prey organisms

Mesostoma species are voracious predators on crustacean zooplankters, particularly cladocerans, and individual specimens of *M. lingua* and *M. ehrenbergii* respectively can consume more than 5 and 10 waterfleas per day (Schwartz & Hebert 1982; Dumont & Schorrells 1990). When these species occur at high natural densities (Maly *et al.* 1980; MacIsaac & Hutchinson 1985), this genus of rhabdocoels may have an impact on zooplankton communities. Based on laboratory and field studies, Maly *et al.* (1980) suggest that *M. ehrenbergii* might affect the population dynamics of zooplankters, particularly cladocerans, in small ponds, especially those with a high surface to volume ratio and a moderately high turbellarian density (more than 200–300 per m²). From laboratory experiments, Schwartz & Hebert (1986) concluded that the influence of *M. lingua* might be important in pond zooplankton communities, producing a shift in dominance away from cladocerans such as *Daphnia* towards larger calanoid copepods. Densities of *M. lingua* regularly were negatively correlated with those of cladocerans, but not with copepods, in Californian rice-field enclosures (Blaustein 1990). In

laboratory experiments, a high temperature (25°C) destabilised the population dynamics of *M. ehrenbergii* and *Daphnia pulex*, with eventual extinction of the cladoceran. At a lower temperature (18°C), the *Daphnia* population persisted, and the rhabdocoel induced changes only in age structure of the cladoceran, rather than affecting overall biomass (Beisner *et al.* 1996). In a further sophisticated experiment using the same two temperatures and five different food levels, Beisner *et al.* (1997a) concluded that the differential effects of *M. ehrenbergii* on the dynamics and structure of its prey could be attributed to changes in life-history, physiological rates and reproductive strategy (production of subitaneous or dormant eggs – see p. 110) employed by the rhabdocoel at the different temperatures.

Another example of the negative effect that rhabdocoel predation can have on prey densities includes the evidence obtained by Young (1975a; 1977a) that *Phaenocora typhlops* (p. 105) and, perhaps, *Ph. unipunctata*, control or have a severe impact on their oligochaete prey in ponds. Finally, Kusch & Kuhlmann (1994) and Kusch (1998) provide a good example of how the severity of predation pressure by microturbellarians manifests itself in a prey organism. The presence of *Stenostomum unicolor* (referred to as its synonym *S. sphagnetorum* in the publications) induces morphological changes in the ciliate *Euplotes octocarinatus*, which alters from a typical ovoid form into an enlarged 'winged' form. This diminishes the risk of predation on the ciliate but incurs a demographic cost; generation times are increased and population growth rate is reduced. *Stenostomum* releases a 17.5 kDa peptide in the surrounding medium, which activates the morphological transformation of *Euplotes* (Kusch 1993).

Effects on mosquito larvae – biological control

Several studies have shown that *Mesostoma*, a worldwide genus (Hyman & Jones 1959; Young 1976a; Lanfranchi & Papi 1978) eat mosquito larvae (Kolasa 1978; Kolasa *et al.* 1985), and their use in the biological control of the insects, which are agents of various human diseases, has been investigated. Based on laboratory and field studies, *Mesostoma lingua* has been shown to eat mosquito larvae (*Culex* and *Anopheles*) and has a negative correlation with their numbers in commercial rice-fields in California (Collins & Washino 1978, 1979; Case & Washino 1979; Legner 1979a; Palchick 1984). Blaustein (1990) provided direct experimental evidence for an impact of the rhabdocoel on larval mosquito populations. *Mesostoma* depressed numbers of larvae but

predation pressure changed seasonally, being low in autumn.

Other species of *Mesostoma* also may have potential as biological control agents of mosquito larvae (*Aedes*, *Anopheles*, *Culex*, *Culiseta* and *Toxorhynchites*). These include *Mesostoma appinum* Kolasa & Schwartz from Australia, *M. timbunke* Kolasa & Mead and *M. wanum* Kolasa & Mead, both from Papua New Guinea, and *M. zariae* Kolasa & Mead from Africa (Mead 1978; Kolasa 1984, 1987). In laboratory experiments, Kolasa (1984) found there were differences in the efficiency of *Mesostoma* species at capturing prey, attributed to different sizes of the predator species and to their behavioural and structural characteristics.

Detailed laboratory studies have shown that *Mesostoma* species have great potential as biological control organisms. They have a high intrinsic reproductive rate (R_0) and innate capacity to increase in numbers (r_m) (Kolasa 1987). Their overall growth is several times faster than that of triclad flatworms, such as *Dugesia dorotocephala*, which also have been studied as potential biological control agents of mosquitoes (e.g. Yu & Legner 1975; Tsai & Legner 1977; Legner & Tsai 1978). *Mesostoma zariae* has a high feeding rate on mosquito larvae, consuming 10 to 14 fourth-instar larvae per individual each day; it has relatively few predators and a reasonably long life-span, averaging 70–80 days, with the longest span at 143 days (Mead 1978). Juvenile *Mesostoma* readily eat mosquito larvae and, interestingly, Kolasa (1984) observed that in field situations there is a high percentage of juvenile worms in populations of multivoltine *Mesostoma*. This may be a crucial factor in reducing mosquito populations, particularly in temporary habitats where only one or a few generations of the turbellarian and univoltine species of mosquito develop. In such circumstances, only the juveniles of *Mesostoma* may have an opportunity to feed on mosquitoes before the insects complete their life cycle. Lastly, *Mesostoma* produces resting eggs (p. 110) which can resist desiccation and adverse conditions, and assist in the dispersal of the species (p. 95).

SYMBIOTIC ZOOCHLORELLAE

Several species of marine turbellarians contain endozoic algae, and the symbiotic relationship between alga and animal has been studied in some detail for the acoelans *Amphiscolops* and, particularly, *Convoluta* (e.g. Provasoli *et al.* 1968; Taylor 1971; Nozawa *et al.* 1972; Muscatine *et al.* 1974; Holligan & Gooday 1975; Douglas 1983). In the freshwater environment, many workers have reported the presence of zoochlorellae in the tissues of

microturbellarians including *Castrada*, *Dalyellia*, *Phaenocora* and *Typhloplana* (e.g. Sekera 1904; Couvreur 1915; Limberger 1918; Reisinger 1923; Chodat 1924; Genevois 1924; Haffner 1925; Gelei 1927; Middelhoek 1948; Luther, 1963). However, very few studies have examined the alga-animal relationship.

Eaton & Young (1975) and Young & Eaton (1975) carried out detailed field and laboratory studies of the symbiotic relationship between the alga *Chlorella vulgaris* var. *vulgaris* (Chlorococcales) and the rhabdocoel *Phaeonocora typhlops*, in a small English pond. The alga exists in a free-living state in the pond. The microturbellarian is present in the pond for most of the year but overwinters in the cocoon phase (p. 105). The source of algae infecting *Ph. typhlops* was tubificid worms eaten by the rhabdocoel. The initial infection of hatchlings by algae occurred in the pharyngeal region, and subsequently spread posteriorly. The rate of infection of the population was rapid, being complete in 4 to 5 weeks after animals had hatched from cocoons. An average of 76,000 algal cells per animal was recorded at 36 days after hatching but this value had halved by 66 days. The decline was attributed to digestion of algae by the host during a period of acute food (tubificids) shortage in the host's life (p. 105). The symbiotic relationship is not obligate for either partner.

Both partners benefit from the algal-invertebrate symbiotic relationship. For the rhabdocoels, the presence of algae leads to reduced body shrinkage rates, compared with uninfected animals, during periods of food (tubificid) shortage (p. 105). The microturbellarian may utilise substances secreted by the algae and/or actually digest its symbiont (see above). There also may be increased survival in conditions of oxygen depletion, as experienced in mud where the animal lives. For the algae, the pond environment is unfavourable for free-living cells as they sink in the anoxic mud, where they are also deprived of light. But the presence of *Ph. typhlops* allows the size of the total algal population in the pond to be increased over a limited period of the year.

The contribution by the algae to the microturbellarian host's nutrition, by providing photosynthetic carbon, and its respiration, by producing oxygen, was confirmed in later studies on other microturbellarian species. In laboratory experiments, Heitkamp (1979a) found that both *Dalyellia viridis* and *D. penicilla* (Braun) respire oxygen produced by their *Chlorella* symbionts. The consumption of oxygen in darkness by *D. penicilla* is lower in specimens with symbionts than in those without. Up to 50% of the oxygen

consumed by *D. viridis* can be provided by its algae. *Dalyellia viridis* with zoochlorellae endured anaerobic conditions for a longer time than *Mesostoma lingua* and *Opisthomum pallidum*, which lack the algae. Interestingly, in another paper, Heitkamp (1979b) found that *D. viridis*, possessing zoochlorellae, had a higher respiration rate than another three species – *Mesostoma ehrenbergii*, *M. lingua* and *O. pallidum*, which did not have endozoic algae; the symbiotic algae may contribute to the observed high rate.

In a laboratory study, Douglas (1987) found cells of the alga *Chlorella vulgaris* in the mesenchyme tissue below the epidermis in the rhabdocoels *D. viridis* and *Typhloplana viridata*. When both microturbellarians were cultured for 15 days in either continuous illumination or in darkness, the dark-treated animals were 30–60% shorter. The algae in both species fixed carbon-14 by photosynthesis, 30–40% of which was transported to animal tissue. Freshly isolated algal cells released photosynthate, predominantly as maltose.

PARASITES

Little is known about the occurrence of parasites in freshwater microturbellarians. An early publication by Graff (1903) considered the turbellarians as both parasites and hosts. General statements are sometimes made about their presence but these lack specific detail. For example, Pennak (1978) states that ciliates, gregarines and nematodes are found in microturbellarian hosts.

Unidentified sporozoans have been observed in *Catenula lemnae*, *Microstomum lineare*, *Gieysztoria expedita*, *Rhynchomesostoma rostratum*, *Mesostoma ehrenbergii*, *M. lingua* and *Gyratrix hermaphroditus* (Meixner 1926; Luther 1955; Schwank 1981b; Young unpublished data). Microsporidians occur in *Microdalyellia armigera* and *M. schmidtii*, ciliates in *M. lineare* (Luther 1960), holotrichous ciliates, including *Holophyra* and *Ophyroglena*, occur in *Stenostomum leucops*, (Kepner & Carroll, 1923; Luther 1960), and gregarines and polymastigine flagellates were found in *G. hermaphroditus* (Karling 1963). A non-photosynthetic flagellate, *Desmomonas prorhynchi*, was found in an unidentified species of *Prorhynchus* from Australia (Williams 1999). Euglenoid flagellates occur in *C. lemnae* and several species of *Stenostomum*. With regard to the last type of parasite, *Astasia captiva* has been recorded from *Catenula lemnae* (Beauchamp 1911), and *Euglena leucops* from *Stenostomum leucops* (Hall 1931; Kolasa 1973) and from four other species of *Stenostomum* not found in the British Isles (Marcus 1945b; Kolasa 1982a). Kolasa (1991) states that

ciliates and flagellates also occur in typhloplanoidan rhabdocoels, and that he has recorded nematodes in *Prorhynchus* (Lecithoepitheliata). Nematodes have also been found in *Macrostomum rostratum*, *M. lineare*, and *Microdalyellia brevinana* (Luther 1955, 1960). Larval trematodes have been found in *Phaenocora unipunctata* and *Gieysztoria triquetra* (Dorner 1902; Chodorowski 1959), and larval cestodes (*Hymenolepis* sp.) in *M. lineare* (Rixen 1961).

The effect of parasites on freshwater microturbellarian hosts is unknown.

PREDATORS

There is a dearth of information on the predators of, and intensity of predation upon, freshwater microturbellarian species. The sparse literature suggests that they are eaten by other turbellarians, nematodes, annelids, crustaceans and insects, but specific detail is lacking (e.g. Pennak 1978; Kolasa 1991). Further available information is usually derived from laboratory observations.

Interspecific predation by microturbellarians

There are several reports in the literature of interspecific microturbellarian predation. Species of Catenulida, *Castrada* spp. including *C. intermedia*, *Gyratrix hermaphroditus*, and *Mesostoma lingua* are eaten by *Stenostomum leucops* (Luther 1960, 1963; Heitkamp 1972a). *Microstomum lineare* consumes *Gieysztoria*, *Microdalyellia* and *G. hermaphroditus*. *Phaenocora unipunctata* eats various dalyelliids, *Rhynchomesostoma rostratum* and *G. hermaphroditus* (Meixner 1926; Luther 1963; Heitkamp 1982). *Macrostomum distinguendum*, *M. rostrata*, *Geocentrophora sphyrocephala*, *Dalyellia viridis*, *Gieysztoria infundibuliformis*, *Microdalyellia armigera* and *Rhynchomesostoma rostratum* consume other unspecified microturbellarians (Luther 1955, 1960, 1963; Heitkamp 1982; see also Table 3, pp. 86–87). Heitkamp (1982) suggested that *Dalyellia viridis* and *D. penicilla* (Braun) may have depressed numbers of *Mesostoma lingua*, *R. rostratum* and *Ph. unipunctata* in small ponds in Germany, but the evidence is circumstantial. Several microturbellarians from Nigeria, including *Macrostomum*, *Stenostomum*, and *Phaenocora*, feed on other species of microturbellarians (Mead & Kolasa 1984).

Predation by other animals

Gastropod snails (*Lymnaea stagnalis* and *Planorbarius corneus*), oligochaetes (*Chaetogaster diaphanus*), copepods (*Macrocyclops albidus* and *Cyclops strenuus*), salamanders, and young fish, all fed upon *Microstomum lineare* (Heitkamp 1982). Ingole (1987, 1988) believes that the euryhaline *Macrostomum orthostylum* (Braun) has considerable potential as live food for the larval stages of commercially important fish and prawns reared in mass culture. Rixen (1961) observed *Macrostomum distinguendum* in the gut of *Chlorohydra viridissima*. *Phaenocora typhlops* and *Ph. unipunctata* from English ponds were preyed upon by the chironomid *Anatopynia varia*, and larvae and adults of the dytiscid beetle *Dytiscus marginalis*, respectively (Young 1973b, 1978).

Various predators feed on young and adult *Mesostoma lingua*. These include the oligochaete *Chaetogaster diaphanus*, the fairy shrimp *Branchineta paludosa*, copepods, including *Cyclops vicinus*, *Mesocyclops leuckarti* and *Cyclops vernalis* (*Acanthocyclops robustus*), the anuran *Triturus* (larvae) and, perhaps, fish, including the mosquitofish *Gambusia affinis* and the green sunfish *Lepomis cyanellus* (Heitkamp 1972a; MacIsaac & Hutchinson 1985; Blaustein & Dumont 1990). *Mesostoma ehrenbergii* was eaten by the fish *Gasterosteus aculeatus* and *Carassius*, and by salamanders (Göntenboth & Heitkamp 1977). With regard to species not recorded in the British Isles, an unidentified pelagic *Mesostoma* in Brazil was eaten readily by the copepod *Mesocyclops longisetus* and *Chaoborus* (Rocha *et al.* 1990). *Mesostoma appinum* Kolasa & Schwartz, *M. timbunke* Kolasa & Mead and *M. zariae* Kolasa & Mead from Nigeria were fed upon by large mosquito larvae (*Aedes*, *Anopheles*, *Culiseta* and *Culex*). *Mesostoma zariae* was also preyed upon by an unidentified *Phaenocora* (Microturbellaria) and unnamed anisopteran and zygopteran nymphs (Odonata).

Impact of predation on microturbellarian populations

It has not been demonstrated that any predator is able to affect, directly or indirectly, densities of microturbellarian populations in the field. Rocha *et al.* (1990) suggest that turbellarians could well be excluded from small ponds and lakes where combined vertebrate and invertebrate predation is severe, and suggest that the absence of *Mesostoma ehrenbergii* from American ponds containing the 'axolotyl' *Ambystoma tigrinum*, as reported by Maly *et al.* (1980), might be due to predation by this salamander. However, these statements are speculative.

DISPERSAL

The possibility that microturbellarians disperse within and between waterbodies by their own movements, as in the case of triclads (Reynoldson 1966), is unlikely but cannot be discounted. Also, it is possible that man may assist their distribution by, for example, the transport of water for drinking purposes, by fish stocking, and by keeping aquaria. A good example of the last is the occurrence of *Macrostomum tuba* in warmed aquaria in northern Eurasia, where it has not been recorded in natural habitats (Young & Young 1967). The passive transport, by some agency, of live microturbellarians, which are soft-bodied and subject to desiccation on removal from water, seems less likely than dissemination by a resistant phase. However, Kolasa (1991) reports that in an experiment conducted by Jan Ciborowski at the University of Windsor, North America, artificial pools on the roof of a building were colonised within a few weeks by six species of microturbellarians, five of which do not produce resistant disseminules. Resistant (dormant or resting) eggs or cocoons are produced by many microturbellarian species (p. 110). Survival of these cocoons in harsh conditions, such as low temperature, low oxygen levels or drought, can be good. For example, Heitkamp (1972a, 1977) found that, at high temperatures, dormant cocoons of *Mesostoma lingua* and *M. ehrenbergii* survived in moist mud for 3–4 and 2 months, respectively. At low temperatures, cocoons of the latter species survived for more than 6 months. Some species, for example *Bothrioplana semperi*, *Geocentrophora sphyrocephala*, *Prorhynchus stagnalis* and, perhaps, *Stenostomum unicolor* and *Phaenocora unipunctata*, also form cysts by surrounding their bodies with mucus, and endure desiccation for a short time (Sekera 1906, 1926; Reisinger 1923; Dahm 1951; Schwank 1981b). Therefore it seems likely that most microturbellarians are dispersed by the transport of these resistant phases, particularly cocoons, by some agency. Indeed it has been suggested that cocoons are distributed by wind (Reisinger & Steinböck 1927), by floating on ice or driftwood in transoceanic distribution (Steinböck 1931), or by adherence to the feathers, beaks and feet of birds such as waterfowl (Steinböck 1926, among others). With regard to the last agency, the fact that Europe and Africa have many microturbellarian species in common (Young & Kolasa 1974; Young 1976a, 1977b) may be a consequence of the extensive bird movements between these two areas (Young 1976b; Young & Young 1976; Mead & Kolasa 1984). Transport of cocoons in the digestive tract of birds or by other animals such as insects, at least over short distances, is also feasible, as other aquatic

organisms are dispersed in this way (Maguire 1963). Dahm (1951) suggests that the good dispersal powers of *B. semperi*, mainly through cocoons but also through cysts transported by wind or water birds, coupled with its ability to reproduce by parthenogenesis (p. 108), explains the wide geographical distribution of the species. Dormant cocoons (p. 110) of *Bothromesostoma personatum* can sometimes rise to the surface of the water where they float in contact with air, and Luther (1963) suggests that this would assist the distribution of the species within and between waterbodies.

Contrary to usual opinion, Herbert & Payne (1985) claim that dispersal between waterbodies by some microturbellarian species may be low. They surveyed enzyme variability at two polymorphic loci in populations of *Mesostoma lingua* in arctic ponds, many of which were intermittent in years of low rainfall, in Manitoba, Canada. Considerable gene frequency divergence was found between populations only a few metres apart, indicating that gene flow is low. The calculation of inbreeding coefficients suggested that existing populations receive an average of only one new migrant per generation. Consequently, they argue that dispersal may be low between ponds, especially permanent ones.

HABITAT

Microturbellarians are typically benthic animals, living on the surfaces of plants and other substratal materials, or burrowing into mud or the interstices of coarser substrata. Most species, however, can swim and periodically may be found in the water column, at least in still waterbodies. Indeed a few species, e.g. *Bothromesostoma personatum*, *Mesostoma lingua*, *M. productum* and *Strongylostoma radiatum*, are sometimes found in the plankton of ponds and small lakes (Gieysztor 1939; Luther 1963; Bauchhenss 1971). True pelagic species, including unidentified *Mesostoma* spp., occur in some lakes in North and Central Africa, Indonesia and Brazil (Ruttner 1952; Beauchamp 1954; Dumont *et al.* 1973; Rocha *et al.* 1990), and it has been shown that these perform diurnal vertical movements in the water column (Meester & Dumont 1990).

Information on the potential range of habitats occupied by the microturbellarian species found in Britain and Ireland (Table 1, pp. 10–11) has been derived from studies carried out mainly on continental Europe, but also in the British Isles (Nasanov 1926; Steinböck 1926, 1932; Weise 1942; Chodorowski 1959; Luther 1950, 1955, 1960, 1963; Karling 1963; Rixen 1961, 1968; Kraus 1965; Pörner 1966; Bauchhenss 1969, 1971; Young 1970,

1972b,c, 1973a, 1985; Kaiser 1974; Schwank 1976, 1981b; Kolasa 1977a, 1979, 1983; Lanfranchi & Papi 1978; Heitkamp 1982). Most species occur in a wide variety of habitats, including pools, ponds, lakes, ditches, canals, springs, streams and rivers. However, some groups tend to be absent from streams and rivers, including about half of the Dalyellioida (*Dalyellia viridis*, *Gieysztoria diadema*, *G. infundibuliformis*, *G. rubra*, *G. triquetra* and *M. fairchildi*), three species of *Castrada* (*C. armata*, *C. intermedia* and *C. luteola*), all of the genus *Mesostoma* (excepting *M. lingua*) and a few other species of Typhloplanoida (*Opisthomum pallidum*, *Rhynchomesostoma rostratum* and *S. radiatum*). Additionally, *Plagiostomum lemani*, *Otomesostoma auditivum*, *Bothromesostoma personatum*, *Mesostoma ehrenbergii*, *Strongylostoma elongatum*, *Tetracelis marmorosa* and *Typhloplana viridata*, that are typical of lakes (first two species) or ponds and lakes (other species), have been recorded very occasionally in slow-flowing waters (e.g. Steinböck 1926) and, in the case of *O. auditivum* and *T. viridata*, in streams (Schmid & Schmid-Araya 1999). Many species occurring in flowing waters tend to occur in the interstitial micro-habitat, e.g. catenulids. Others, including larger forms, tend to occupy vegetation, particularly in slow-moving water, e.g. *M. lingua*.

Most of the pool- and pond-dwelling species can occur in both temporary and permanent waters (p. 102). *Prorhynchus stagnalis*, *Geocentrophora sphyrocephala*, *G. baltica* and *Bothrioplana semperi* can be found in damp conditions, including moss and soil, at the edge of freshwater habitats (Reisinger 1925; Steinböck 1927, 1928). The last species and, sometimes, *Rhynchoscolex simplex*, can occur in groundwater (Hofsten 1907, 1912; Dahm 1951; Luther 1960; Rixen 1961; Schwank 1981b, 1986). A few species have restricted distributions: *Limnoruanis romanae* is recorded only from springs and streams, *Macrostomum johni* occurs in a single lake, and *M. tuba* has been found only in warmed aquaria, although it occurs naturally in standing and flowing waters in other countries, including some in central and southern Europe (Lanfranchi & Papi 1978). In Britain, *Stenostomum leucops*, *G. sphyrocephala* and *Phaenocora unipunctata* have been found in percolating filters in sewage works (Young 1970).

DISTRIBUTION AND ABUNDANCE IN LAKES

British lakes

The only detailed study of microturbellarians in British lakes is that of Young (1973a), who investigated their occurrence in calcium-rich, productive lakes in Cheshire and Shropshire, England, and calcium-poor lakes in Snowdonia, North Wales. Thirty-one species were collected. Twenty species occurred in calcium-rich lakes and 22 species in calcium-poor lakes. Three groups of species were identified: 11 occurred in both categories of lake, 9 only in calcium-rich lakes and 11 only in calcium-poor lakes. Total numbers of specimens collected in the same number of samples over the same time interval were 50% higher in the calcium-poor lakes. Most species, and certainly those recorded most frequently, were not confined to a particular habitat, viz., vegetation, stones or other substratum typical of the remaining littoral zone, and there were no seasonal changes in distribution between these habitats. An investigation of the occurrence of microturbellarians in deeper waters was made in one calcium-rich lake, where only a small number of species was found in the profundal zone. Peak numbers of specimens were recorded in midsummer in calcium-poor lakes and from late spring to early summer in calcium-rich lakes.

Large continental lakes

All other studies of lake-dwelling microturbellarians have been carried out in continental Europe (e.g. Meixner 1915; Reisinger & Steinböck 1925; Gięsztor 1938, 1939; Steinböck 1949, 1951; Reisinger 1955; An der Lan 1961; Rixen 1961; Schwank 1976; Holopainen & Paasivirta 1977; Kolasa 1977a), though Nalepa & Quigley (1983) and Strayer (1985) included microturbellarians in their investigation of the meiobenthos/micrometazoans in American lakes. In the European investigations, collections were of a qualitative nature, and in some cases were gathered from only a few habitats, or were made on only one occasion, or irregularly, or over a short time-interval. The most comprehensive studies based on quantitative information include Chodorowski (1959, 1960, in mesotrophic Harszsee, Poland), Rixen (1968, in oligotrophic Bodensee (Lake Constance), Germany), and Kolasa (1979, in eutrophic Lake Zbechy, Poland). Thirty-three, 38 and 53 microturbellarian species were recorded in the first, second and third of these studies. The greater number of species found in these investigations compared with Young's (1973a) study may be explained in terms of the relatively larger

size of these continental lakes and, in general, to the fact that far more microturbellarian species have been recorded in mainland Europe than in Britain (Lanfranchi & Papi 1978).

The studies revealed the following main points. (1) Many more species were found in the littoral than profundal zones. (2) Whilst many species occurred across the range of habitats examined, some tended to be associated with a particular habitat or micro-habitat. (3) As a consequence of (2), a number of habitats or microhabitats had a characteristic faunal community. (4) The littoral zone harboured the highest density of animals. (5) The number of species and total abundance of specimens peaked in the spring and late summer. For example, using Kolasa's (1979) intensive study to provide more detail, the greatest number of species and total number of animals occurred in shallow waters of 0.1 m to over 1 m; at 2 m there was a sharp decrease in the number of species and specimens, whilst at depths of 3 to 5 m turbellarian variety and numbers were poor. In other studies, particularly of oligotrophic lakes, the profundal zone is richer in species and abundance than in Kolasa's eutrophic lake (e.g. Steinböck 1932; Holopainen & Paasivirta 1977). Indeed, microturbellarians have been recorded at considerable depths in some continental European lakes, and many of the species occurring in the British Isles (e.g. *Catenula lemnae*, *Plagiostomum lemani*, *Prorhynchus stagnalis*, *Bothrioplana semperi*, *Otomesostoma auditivum*, *Castrella truncata*, *Gięsztoria diadema*, *Microdalyellia armigera*, *Rhynchomesostoma rostratum*, *Castrada armata*, *C. lanceola*, *C. luteola*, *C. viridis*, *Strongylostoma elongatum* and *Gyratrix hermaphroditus*) have been recorded at depths of 20 or more metres (Le Roux 1907-1908; Ekman 1915; Monard 1919; Reisinger & Steinböck 1925; Steinböck 1926, 1932, 1949; Luther 1960; Rixen 1968; Holmquist 1972). In Kolasa's (1979) study, within the shallow littoral zone, the largest numbers of species and animals were found in sand. The lowest number of species, comprising a relatively large number of specimens, was found in sedge-beds. The lowest number of specimens, represented by a fairly low number of species, was recorded in reed-beds. Though some species occurred in a wide variety of substrata, a number of habitats or sub-habitats with characteristic microturbellarian faunas were identified: sand, mud, sedge-beds, reed-beds, and submerged vegetation. The lack of evidence for distinct communities or assemblages associated with particular habitats or sub-habitats in the British lakes that have been studied, again may be a consequence of their relatively small size compared with continental lakes (see above). It is difficult to extract precise information on

the density of microturbellarians in lakes, due to the different ways in which data have been presented in publications, the use of different sampling techniques, and the heterogeneous nature of the substratum in the littoral zone of lakes. Holopainen & Paasivirta (1977) recorded a lake-wide annual mean of 3100 individuals per m² in Lake Paajarvi, Finland, Kolasa (1979) found an annual mean of 3500 per m² in shallow littoral areas in Zbechy Lake, Poland. Nalepa & Quigley (1983) found a mean (April–November) of 800 per m² in nearshore (11–23 m) Lake Michigan, USA, and Strayer (1985) found a lake-wide mean (July–October) of 27,000 per m² in Mirror Lake, North America.

Assemblages/communities

In conclusion, it would seem that the small size of microturbellarians may permit substantial numbers of species, and individuals, to coexist in lakes. The few available studies have suggested that, at least for large lakes, some spatial separation may occur, with habitats or sub-habitats having characteristic microturbellarian communities, though numbers of species and specimens are still relatively high in these areas. Spatial separation also has been found in brackish and marine environments (e.g. Karling 1974; Mack-Fira 1974; Reise 1984; Jouk *et al.* 1988), and this also results in the recognition of communities of species and assemblages associated with particular types of substrata and parts of the littoral zone. However, it will be difficult to disentangle the role of spatial and temporal separation, life-cycles, abiotic factors and biotic factors such as interspecific competition and predation, in determining the distribution and abundance of freshwater microturbellarian species. Despite a greater number of studies on microturbellarians in the marine environment, again there is uncertainty about the variables involved in their abundance and distribution (Boaden 1995; Dittmann 1998; Armonies & Reise 2000). Many sandy-shore turbellarians have spatial and migration patterns that are at least partly mediated by abiotic factors such as sediment type, depth of sediment, height on beach, temperature, fluctuations in the groundwater table, salinity, pore-water content, tidal or mechanical disturbance, and light intensity.

Despite the fact that different micro-assemblages in lakes each contain a large number of species and individuals, it is possible that microturbellarians may contribute little to the overall biomass or metabolism of the invertebrate benthic community (Strayer 1985; Kolasa *et al.* 1987), but much further work is required to clarify the situation.

DISTRIBUTION AND ABUNDANCE IN PONDS

British ponds

Young (1970) included small still waterbodies in his survey of microturbellarians in the British Isles. Lowland, hard-water pools and ponds with aquatic vegetation supported more species than those without vegetation, which were often situated in deciduous woodland. The fewest species were found in soft-water pools and ponds situated at a higher altitude, often containing peaty-brown water in moorland areas. Two common species in English ponds are *Phaenocora typhlops* and *Ph. unipunctata* (Young 1975a, 1978) which burrow in the mud where reduced oxygen conditions occur, and, interestingly, both species contain haemoglobin (Young & Harris 1973).

Continental ponds

The most comprehensive study in continental Europe is that of Heitkamp (1982), though Dorner (1902), Rixen (1961) and Bauchhenss (1971) also provide useful information. Heitkamp (1982), based on his own study of ponds in Germany, and those of previous workers, produced tolerance ranges for individual species with regard to temperature, pH, calcium content, alkalinity, oxygen content, water level, and occurrence in relation to aquatic flora and other types of substratum. In his own study, he found that the number of species ranged from 4 to 24 per pond, and the total number of individuals was higher in ponds in open land and with much vegetation than in woodland ponds without aquatic plants, a finding in agreement with Young (1970). Numbers of individuals of certain species were extremely high at several thousand per m² (e.g. *Microstomum lineare*); the average yearly production of microturbellarian individuals in ponds was between 150 and 80,000 per m². The maximum number of species in all of the small waterbodies examined, occurred in May. This contrasts with the two peaks of abundance found by Rixen (1961) (May and August) and Bauchhenss (1971) (June and August–October), and a single peak in August recorded by Dorner (1902). Other studies have also revealed high densities of microturbellarians in ponds and pools. For example, Maly *et al.* (1980) found a peak density of 2644 *Mesostoma ehrenbergii* per m² in a small Colorado pond, and Heitkamp (1972a) found a peak of 3500 *Mesostoma lingua* per m³ in a German pond.

Temporary habitats

Most of the species living in small, permanent waterbodies also occur in temporary ponds and pools, though some species, for example, *Dalyellia viridis*, are more commonly recorded in the latter. Characteristics that enable microturbellarian species to colonise and survive in temporary habitats include good powers of dispersal (p. 95), a versatile life-cycle (p. 113), the production of resting eggs (or less commonly, cysts) resistant to adverse environmental conditions (p. 110), and high reproductive and development rates. With regard to the last phenomenon, Heitkamp (1972a) observed that in the laboratory, *Mesostoma lingua* could produce a maximum of 170 subitaneous eggs (see p. 110) or 181 resting eggs per individual. He also found that in the laboratory the development time for one generation, from the hatching of an individual to the hatching of juveniles from subitaneous eggs produced by that individual, is 20 days at 25°C and 52 days at 10°C. Field observations are in accord with these findings. In German ponds the first generation in spring hatches at an average temperature of 8–10°C at the end of March, and juveniles of the second generation hatch after 6–7 weeks in the middle of May. Heitkamp (1972b, 1977) also found high reproductive and development rates in *Mesostoma productum* and *M. ehrenbergii*.

DISTRIBUTION AND ABUNDANCE IN STREAMS AND RIVERS

Continental streams and rivers

The composition and ecology of microturbellarians in lotic waters in the British Isles is poorly known (Young 1970; Schmid & Schmid-Araya 1999). In contrast, several studies on the taxonomy and occurrence of microturbellarian species have been carried out in continental Europe (e.g. Sibriakova 1929; Gieysztor 1938; Gieysztor & Szydal 1939; Husmann 1966; An der Lan 1967; Tilzer 1968; Kolasa 1982a; Schwank 1985). However, only a few investigations have been intensive and of a quantitative nature. Bauchhens (1971), Kaiser (1974) and Kolasa (1974) examined a number of springs in Germany and Poland, Schwank (1981a,b, 1982a,b) investigated highland streams in Hesse, Germany, and Kolasa (1983) collected from the Fosso Contesora, a small montane stream near Pisa, Italy. More recently, Kolasa *et al.* (1987) investigated springs, interstitial waters and streams in Southeastern New York, USA, and Kolasa (1989, 2000) studied the experimental colonisation of substrata in Wappingers Creek, North America. In her examination of the meiofauna in the gravel of the Oberer Seebach, an

Austrian stream, Schmid-Araya (1997) provided some information on the microturbellarian fauna.

Continental European streams harbour relatively large numbers of species and individuals. For example, Schwank (1981a) recorded 94 species of turbellarians (including 8 triclad species), and densities of more than 1000 specimens per litre of sediments from streams in Germany. Kolasa (1983) obtained 61 species (including 4 triclads), some with densities exceeding 7000 specimens per m² and a minimum of 2000 per m² at each site, from the Fosso Contesora stream in Italy. A mean density of 1280 individuals per m² was recorded by Kolasa (1989, 2000) in Wappingers Creek, in artificial substrata after a week of colonisation.

Factors affecting distribution and abundance in streams

The most important factors determining the abundance and distribution of stream-dwelling microturbellarians are claimed to be the structure of the substratum and the presence of varied microhabitats (Schwank 1982b; Kolasa 1983); the number of species found is directly correlated with the variety of available microhabitats. Thus, within a small section of a stream, Schwank (1981b) observed that microhabitats such as gravel, sand, moss, vascular plants and organic sediments, each differed in the number and composition of microturbellarian species inhabiting them. Kolasa *et al.* (1987) found that the greatest variety and highest abundance of microturbellarians occurred in sand with a grain-size of 425–700 µm. The lowest abundance and species richness was observed in substrata of small stones or large gravel. Schmid-Araya (1997) observed that microturbellarians had their maximum abundance at a depth of 20–40 cm in the gravel of the Oberer Seebach, with some differences between seasons and between pools and riffles. The disturbance of microhabitats by high water in spring, and autumnal stagnation and sedimentation, were the main cause of drastic changes in abundances and distribution of microturbellarians in streams in Eastern Hesse, Germany (Schwank 1981a). Certainly, as in littoral marine sands (p. 100), the interstitial microturbellarian community of streams is rich in species and numbers of animals. Nevertheless, Kolasa *et al.* (1987) suggest that, as in lakes (p. 100), the fauna may not contribute significantly to the overall biomass or metabolism of the invertebrate benthic community. Also, Schwank (1982b) concluded from his studies that microturbellarians are of secondary importance, compared with oligochaetes that are of paramount importance, as consumers in stream ecosystems. In both lotic and lentic habitats there is a

paucity of information on the role of microturbellarians in community energetics.

Due to a scarcity of information, little comment can be made on spatial patterns along the length of streams. In small second- and third-order montane streams, the greatest density is found in the upper reaches (epirhithron) and high densities occur in the lower stretches (metarhithron and hyporhithron) (Kolasa 1983). Bauchhenss (1971) and Schwank (1985) recorded differences in faunal composition in different sections of streams and rivers, again associated with differences in habitat or microhabitat. In continental Europe, Kolasa (1982b, 1983) observed that microturbellarian communities comprise species of different ecological origin, including terrestrial, marine, underground, running, limnetic and eurytopic elements, and the contribution of these elements to assemblages changes along the stream or river. Thus, for example, semi-terrestrial and terrestrial species, clean running water and marine elements contribute to the microturbellarian fauna of springs and upper reaches of streams (Kolasa 1977a, 1983; Schwank 1982a) whilst lower regions are dominated by eurytopic species (Kaiser 1974). In stream ecosystems, only a few ubiquitous species (e.g. *Microstomum lineare*, *Stenostomum leucops*, *S. unicolor*) are found in strongly organically polluted waters, and most species tolerate only clean to slightly polluted conditions (Schwank 1982b).

With regard to temporal occurrence, Schwank (1981b) found 9 winter species, 35 non-winter, 16 summer and 34 all-year turbellarian species in German streams. Kolasa (1983) and Kolasa *et al.* (1987) recorded a spring peak in density and an autumnal peak in diversity of microturbellarians in Italian and American streams. Schmid-Araya (1997) found two peaks of abundance, during summer and autumn, in an Austrian stream. However, seasonal occurrences of species and relative abundances of species would seem to vary according to geographical location (Schwank 1981b; Kolasa 1983), probably linked to temperature.

Schwank (1982b) concludes that factors influencing the standing crop and distribution of lotic microturbellarians include temperature, oxygen content and supply of food. However, as for lentic waters, precise, intensive studies examining the effects of abiotic variables (such as temperature, oxygen and pH) and biotic variables (such as competition and predation) on abundance and distribution of microturbellarians in lotic freshwaters, are lacking.

POPULATION DYNAMICS IN ENGLISH PONDS

Little is known about factors regulating and controlling abundance in microturbellarian populations. Exceptionally, Young (1973b, 1974, 1975a) carried out a detailed study of the population dynamics of *Phaenocora typhlops* living in a small English pond. The rhabdocoel lives on and in the mud, and is present from May to September. The remainder of the life-cycle is spent in the egg stage (cocoon) which has an obligatory diapause. Low temperature (5°C and lower) is required to stimulate egg development (p. 109). Survival of cocoons overwinter is high. Annual fecundity is just over one viable egg per adult. Recruited young grow rapidly in size at first, but growth-rate slackens as numbers and average size increase. After a peak in abundance in the second half of June, numbers decrease to zero.

The rhabdocoel has no major predators in the pond. Laboratory experiments, in which potential prey species were exposed to attack by the microturbellarian in dishes, and microscopical and serological examination of the gut contents of field-collected animals, indicated that *Ph. typhlops* feeds mainly on tubificid oligochaetes. In the field, as the numbers of the rhabdocoel increase, the numbers of tubificids decrease rapidly (Fig. 69). An increasing proportion of rhabdocoels is also found with an empty gut. Microturbellarian population events are explained in terms of the development of an acute food shortage and severe competition for food as the numbers of rhabdocoels increase. This results in a low fecundity and the shrinkage and death of many individuals. Subsequently, there is a natural senescence of survivors and elimination of the live population. Thus population regulation is achieved through intra-specific competition for food.

Interestingly, the lower numbers of tubificids in the pond during 1970 (Fig. 69) was due to the pond drying up in October–early November 1969, resulting in substantial mortality in the tubificid population (Young 1975a,b). The drought did not seriously affect the cocoons of *Ph. typhlops*, which hatched to produce high numbers of rhabdocoels as in the previous years. In 1970, competition for tubificids would have been more severe than in previous years and fewer cocoons would have been produced. Indeed, this was reflected in the lower ceiling in numbers of *Ph. typhlops* in 1971 compared with those of 1968, 1969 and 1970 (not shown in Fig. 69, but see Young 1975a).

The presence of symbiotic algae in the rhabdocoel reduces the animal's shrinkage rate under conditions of food shortage (p. 91), but this is thought to be an unimportant phenomenon in the population dynamics of the microturbellarian.

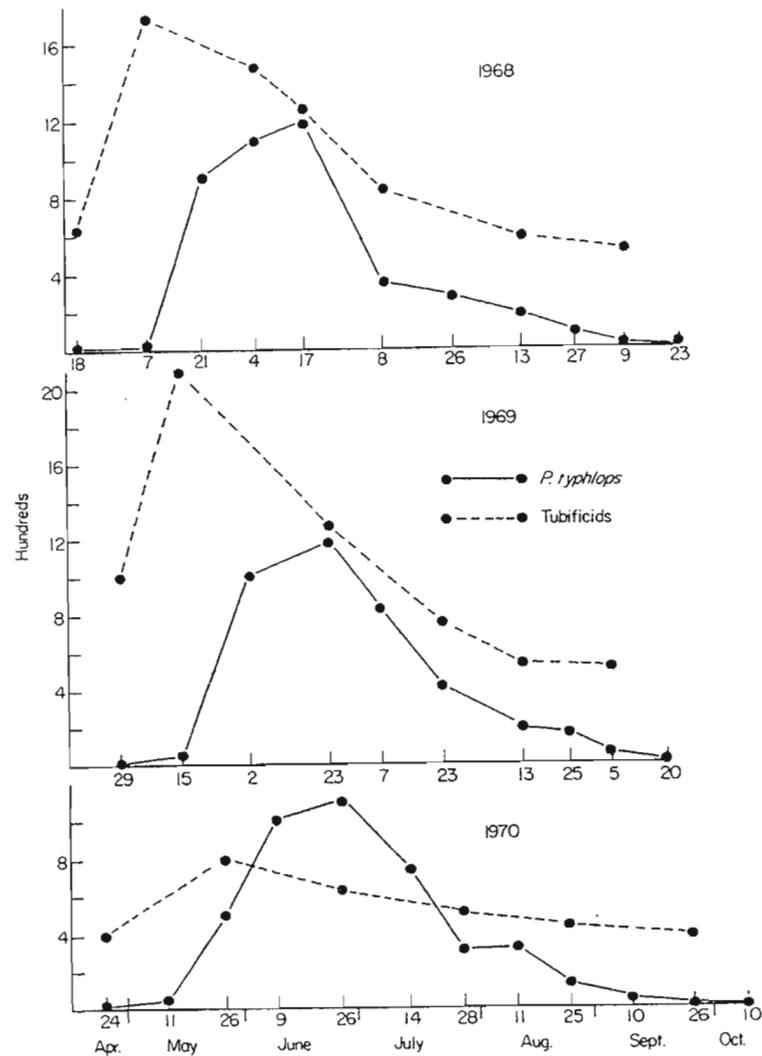


Fig. 69. Numbers of *Phaenocera typhlops* and tubificid oligochaetes obtained in samples (9240 cm²) from Little Crosby Pond, Liverpool, England, during April to September/October in 1968–1970. (Reproduced with permission from Young 1975a).

Evidence for the occurrence of intraspecific competition for food was also obtained from a detailed investigation of a population of *Phaenocera unipunctata* living in another small English pond which dries up each autumn (Young 1977a, 1978). The numbers of rhabdocoels, recruited from cocoons hatching after re-flooding of the pond in late autumn, declined to extinction in late winter. They reappeared in May–June from overwintering cocoons and numbers increased until the pond dried out, when all microturbellarians perished. Cocoons do not have an obligate diapause as in *Ph. typhlops*. Factors opposing numerical increase in *Ph. unipunctata* are low temperature, which inhibits cocoon deposition and hatching during late winter–early spring, intraspecific competition for food (tubificid and lumbricid oligochaetes), which depresses cocoon production when peak numbers are recorded in the summer months, and drought conditions that wipe out the active phase and kill some cocoons.

In the laboratory, Fiore (1971) and Heitkamp (1972a) found that a species-specific chemical substance produced by adults has an adverse effect on subitaneous egg production in *Mesostoma ehrenbergii* and *M. lingua*, respectively (p. 110). Fiore (1971) suggests that small ponds containing these rhabdocoels would provide a suitable habitat for this phenomenon to occur. Whether this is so, and if it assists population regulation, remains speculative.

REPRODUCTION

Asexual reproduction

The catenulid species and *Microstomum lineare* reproduce asexually, although sexual reproduction occurs rarely in some populations of these species (p. 19). Species that reproduce asexually regenerate readily (Hyman 1951; Moraczewski 1977; Palmberg & Reuter 1983; Reuter & Palmberg 1983), whereas sexually reproducing species have no or limited regenerative capability (Hein 1928; Ruhl 1927; Hyman 1951). Exceptionally, *Macrostomum* can regenerate its extremities, though not anterior to the brain (Ingole & Shirgur 1985).

Sexual reproduction

The environmental conditions influencing the development of sexual organs in the catenulids and *M. lineare* are controversial (e.g. Kepner *et al.* 1933; Hyman 1951). In European and North American populations of *Stenostomum* spp. and *M. lineare*, sexually mature animals have been reported mostly in the

autumn (Luther 1960). Borkott (1970) studied reproduction in a German population of *Stenostomum sthenum*, a sibling species in the *S. leucops* complex. The species shows protandry (see below), and both temperature and pH are involved in the differentiation of male and female reproductive organs. Oogenesis exhibited a temperature-dependent diapause. Eggs were laid in autumn and hatched in spring when the temperature approached 10°C.

Sexual reproduction in freshwater microturbellarians usually involves internal, cross-fertilisation (Hyman 1951). Normal, mutual copulation is the rule, where the penis is inserted into the female or common gonopore of the partner. However, in some species, e.g. *Stenostomum* spp. and *Gyratrix hermaphroditus*, hypodermic impregnation has been observed whereby sperm is injected, by means of the penis stylet, through the partner's epidermis, to migrate through the mesenchyme to the ovaries. Self-fertilisation is rare but has been observed occasionally in some species, e.g. *Otomesostoma auditivum*, *Castrella truncata*, *Gieysztoria rubra*, *Microdalyellia armigera*, *Opisthomum pallidum* and *Mesostoma* spp. (Sekera 1906; Ruhl 1927; Luther 1960; Fiore & Ioalé 1973; Heitkamp 1978a). In *B. semperi*, the male reproductive system is reduced and parthenogenetic dioecy occurs, i.e. one egg from each ovary fuse to give a single embryo (Dahm 1951; Sluys & Ball 1985; Smith 1991). Parthenogenesis also may occur in *Rhynchoscolex simplex*, where the testis is sometimes reduced or absent and, at times, in *Tetracelis marmorosa* (Reisinger 1924; Marcus 1945a,b; Luther 1960, 1963). Some species (e.g. *Stenostomum* spp., *Microstomum* spp., *Strongylostoma radiatum* and *G. hermaphroditus*) are protandrous, where the testes develop before ovaries (Hyman 1951; Luther 1960; Karling 1963; Rieger 1981).

Eggs and cocoons

Fertilised eggs are enclosed in a cocoon or capsule before being released into the environment. Each cocoon usually contains a single egg, although in some species, e.g. *Plagiostomum lemani*, *Dalyellia viridis*, *Castrella truncata* and *Opisthocystis goettei*, more than one egg has been reported in some populations (Berg 1938; Middelhoek 1948; Luther 1955; Karling 1963). The shape of a cocoon is usually spherical or oval, and in *P. lemani*, *C. truncata*, *Gyratrix hermaphroditus* and *O. goettei* it possesses a stalk. Many have an operculum through which the young escape on hatching (e.g. species of *Dalyelliidae* and *Phaenocora* spp.) but some rupture (e.g. *Mesostoma* spp.). Cocoon colour can be yellow, yellow-brown, red-brown, brown or dark brown. Details of colour, shape and size of cocoons for many of the species

listed in Table 1 (pp. 10–11) appear in scattered literature (e.g. Hofsten 1911; Ruhl 1927; Berg 1938; Luther 1955, 1960, 1963; Karling 1963; Rixen 1961; Papi 1954; Bauchhenss 1971; Young 1973a; Cox & Young 1974). Some species contain only one egg at a time, which is laid before another one can form (e.g. the *Catenulida*, *Macrostomida*, *Dalyelliidae* (with the exception of *Dalyellia*) and *Kalyptorhynchia*). Other species contain several eggs (e.g. the *Typhloplanoida*). Cocoons are deposited freely on or, more unusually, fastened to the substratum. They are usually laid through the gonopore, but in some species (e.g. *Stenostomum* spp., *D. viridis*, *Typhloplana viridata*, *Tetracelis marmorosa* and sometimes *Mesostoma* spp.) cocoons are released by rupture and death of the parent (see below).

Cocoons are resistant – in varying degrees according to species – to harsh environmental conditions such as low temperature and drought. Young (1974; 1977a) has studied in detail the survival and development of eggs in *Phaenocora typhlops* and *Ph. unipunctata*, respectively living in a permanent pond and a temporary pond in England. In *Ph. typhlops*, present in the living phase from May to September, overwintering eggs (cocoons), deposited in mud have an obligatory diapause. Low temperature (5°C or lower) is the only environmental feature that stimulates egg development and cumulative periods of this are adequate. At 3.5°C, the exposure period required is 4 weeks or more, though a minority of cocoons require only 2–3 weeks. A temperature of 9°C or more is required for hatching after the necessary low temperature stimulus. Hatching rates increase with rising temperature. Survival of cocoons is good, and viability is not affected by low dissolved oxygen content of the mud or absence of water; cocoons survived in damp mud for 3 months at a temperature of 14.5°C. The habitat of *Ph. unipunctata* dried up in the autumn and living rhabdocoels were absent until the spring. Cocoons released into the environment in autumn survived the drought and the overwintering low temperature when the pond refilled. Eggs do not have an obligatory diapause. They require a temperature above 6°C to hatch; the rate increases with rising temperature (9 to 23°C). Cocoons that were kept at low temperatures (1.5–6.0°C) for periods of up to 14 weeks, hatched on transference to higher temperatures (16 to 23°C).

Subitaneous and dormant eggs

In the family Typhloplanidae, species of *Mesostoma*, *Tetracelis marmorosa* and *Typhloplana viridata* produce two types of egg: subitaneous and dormant (resting) (Bresslau 1903; Graff 1904–1908, 1909; Sekera 1904; Steinman & Bresslau 1913; Beauchamp 1924, 1926a,b; Ruebush 1940; Ferguson & Hayes 1941; Mahan 1956; Legner 1979b).

Subitaneous eggs are enclosed in a thin covering or capsule and the embryos develop rapidly inside the mother (ovoviviparous), either in the uterus (e.g. *Mesostoma* spp.) or in the mesenchyme (e.g. *Typhloplana viridata*). Studies on *Mesostoma ehrenbergii* indicate that the capsule is proteinaceous in composition, is permeable to the passage of parental nutrients, and stretches for growing embryos (Fiore & Ioalé 1973; Gremingi & Domenici 1976, 1977). Subitaneous eggs may be self-fertilised (Fiore & Ioalé 1973; Heitkamp & Schrade-Mock 1977; Dumont & Schorreels 1990) or cross-fertilised (Heitkamp 1972a; Hebert & Payne 1985), and the young are released by the rupture and death of the parent (Heitkamp 1972a) or they pass through the gonopore (Fiore & Ioalé 1973). The production of this type of egg allows rapid population growth.

Dormant eggs are enclosed by a thicker, more resistant, protective shell, presumably composed of sclerotin (Domenici & Gremingi 1977). Developing embryos utilise nutrients accumulated in the yolk of vitelline cells (Bresslau 1903; Domenici & Gremingi 1977). Eggs are cross-fertilised (Hebert & Payne 1985; Dumont & Schorreels 1990) though self-fertilisation is possible (Sekera 1906; Fiore & Ioalé 1973). Eggs are released on death of the parent (Fiore & Ioalé 1973) or can be extruded through the gonopore (Heitkamp 1972a). Dormant eggs remain in their cocoons during harsh conditions such as low temperature and drought, and hatch when conditions ameliorate.

Within particular species, the production of the two types of egg can vary among populations (e.g. Heitkamp 1972a,b, 1977; Heitkamp & Schrade-Mock 1977). For example, in *Tetracelis marmorosa*, one cytological and ecological 'strain' or 'race' occurring in north and boreo-alpine continental Europe, produces only dormant eggs, whereas a second southern 'strain' produces both types of egg (Papi 1952, 1954; Reisinger 1955; Luther 1963; Heitkamp 1982). Also, Heitkamp & Schrade-Mock (1977) report a spectrum of populations of *Mesostoma lingua*. These range from, at one extreme, cold, high alpine locations where there is one generation each year, producing only dormant (resting) eggs, to, at the other extreme, North Africa, where many generations produce only subitaneous eggs. In between are found north, middle and south

European populations producing more than one generation per year and both types of egg. Thus the production of resting eggs tends to increase at higher latitudes. Interestingly, Kolasa (1987) reports that *Mesostoma timbunke* from a seasonally submerged aquatic habitat in Papua New Guinea produces only resting eggs, and in this respect resembles *Mesostoma* from high latitudes. He speculates that this convergence may be an adaptation to the restricted time available for reproduction in short-lived environments, and to the harsh environmental conditions that the dormant eggs need to survive between seasons.

Variables that determine production of the two types of egg and the hatching of resting eggs have been studied in detail for *Mesostoma ehrenbergii*, *M. lingua* and *M. productum*.

In *M. ehrenbergii*, Fiore & Ioalé (1973) found no evidence for endogenous determination of the life-cycle, but relative numbers of subitaneous and dormant eggs produced by the typhloplanid may be influenced by genotype. Several environmental factors have been implicated in determining which type of egg is produced, e.g. dissolved oxygen levels and a chemical produced by adults which inhibits the production of subitaneous eggs (Fiore 1971). However, reproductive strategy is influenced chiefly by temperature, amount of food, generation number, and the type of egg from which an individual arises (Fiore & Ioalé 1973; Heitkamp 1977; Beisner *et al.* 1996, 1997a). In laboratory experiments, Heitkamp (1977) found that individuals of *M. ehrenbergii* derived from dormant eggs produce subitaneous eggs independently of temperature (10 to 25°C). In contrast, animals derived from subitaneous eggs produce subitaneous eggs, dependent on temperature. When he incubated cocoons at room temperature (20°C), the hatching success of dormant eggs was increased by a period of exposure to low temperature. To obtain maximum hatching success, at least 30 and 90 days at 3.5°C is necessary for cocoons with water, and cocoons covered with mud and water, respectively. Hatching success decreases with longer exposure time at low temperature.

Beisner *et al.* (1997a) determined the most favourable conditions for subitaneous egg production in laboratory experiments in which *M. ehrenbergii* was cultured at two temperatures (18 and 24°C) and five food levels. Low temperature and a low food level were most favourable for individuals hatching from dormant eggs. The most favourable conditions for animals hatching from subitaneous eggs were either a high temperature and any food level (but especially low), or a lower temperature and a high food level only.

In experimental studies on four populations of *M. lingua* from Germany and Finland (Heitkamp 1972a), determination of the two types of egg is especially influenced by the density of animals kept in small containers, and changes in temperature. Sexually mature animals produce an unknown substance that causes the formation of dormant eggs. In the laboratory, the production of dormant eggs began at a population density of 15–20 animals per 1250 ml of water (20°C). With increasing density the percentage of animals carrying dormant eggs increased. This effect of crowding is dependent on temperature; smaller numbers of animals produce the same effect at lower temperatures. The type of egg produced by individuals hatching from either subitaneous or dormant eggs differed between the four populations, and the type of egg produced varied with temperature. For example, in three populations, individuals hatching from dormant eggs produced individuals that formed only subitaneous eggs at all experimental temperatures (within the range 4–9 and 22–30°C); the fourth population also produced a small proportion of dormant eggs, the ratio varying with temperature. In one population, individuals hatching from subitaneous eggs produced individuals which formed only dormant eggs at all temperatures; in the other populations, a varying proportion of subitaneous and dormant eggs were formed in the first set of eggs and this was temperature-dependent. The influence of other environmental factors is of little importance, though in one population an increase in dormant eggs during the summer months was probably due to increasing oxygen deficiency, or other factors. Heitkamp (1972a) found that in one population of *M. lingua*, a high hatching success was obtained by keeping dormant cocoons at 4°C for 3 months. However, Heitkamp & Schrade-Mock (1977) report that the dormant eggs of an Italian population have no dormancy period, whilst in other European populations dormancy is facultative or partial.

In laboratory experiments, Dumont & Schorreels (1990) found that fertility parameters (clutch size, total offspring, daily offspring) in *M. lingua* all depended on temperature rather than on food, and all showed a maximum value as well. For clutch size and total offspring, this occurred at 20°C, whereas for daily offspring it was 25°C. Thus, the trade-off between higher productivity but shorter life-span was such that 20°C was the optimum temperature for the population of *M. lingua* under study. In nature, such temperatures occur in May–June, while in July–August they overshoot the optimum. This may be the signal required by the animal to start producing dormant eggs.

In a population of *M. productum* with a living phase of 3–4 months, temperature again was implicated in production of the two types of egg (Heitkamp 1972b). The first generation hatching from dormant eggs produced only subitaneous eggs, and all subsequent generations hatched from subitaneous eggs. Under optimum conditions of 20°C the population produced subitaneous eggs. Average temperatures below (15°C) or above (25°C) this temperature caused dormant egg formation by a high percentage of animals. The majority of eggs formed towards the end of the life-cycle were dormant.

LIFE-CYCLES

Most of the information on life-cycles of freshwater microturbellarians has been derived from studies in continental Europe, particularly Germany (Chodorowski 1959; Luther 1955, 1960, 1963; Rixen 1961, 1968; Karling 1963; Kraus 1965; Pörner 1966; Bauchhenss 1971; Kaiser 1974; Schwank 1976, 1981b; Kolasa 1979; Heitkamp 1978a, 1982; Smith 1991). Heitkamp (1982) is particularly informative. The life-cycle of many species is flexible and can vary according to geographical location and type of habitat, e.g. if the waterbody is permanent or temporary. Also, the existence of species with a complex of sibling species or 'races' (e.g. *Mesostoma lingua*, *Tetracelis marmorosa* and *Gyratrix hermaphroditus* (p. 12) may contribute to a variable life-cycle.

Life-cycles of the fifty-five species that occur in the British Isles, based mainly on continental European studies, are summarised in Table 4. The information in this table should be regarded as tentative until further detailed studies in Britain and Ireland have been carried out. Twelve species listed in Table 4 have been recorded throughout the year, and no alternative life-cycles have been reported. Another eleven species have been found all year or for a specific part of a year. The remaining species have been recorded in spring-summer-autumn and/or summer-autumn and/or summer only. Exceptionally, *Dalyellia viridis* and *Opisthomum pallidum* occur during the autumn-winter-spring, or in periods within this time-span. Populations of *G. hermaphroditus* can also exhibit this last type of life-cycle.

Table 4. The seasonal occurrence of microturbellarian species. Information is based mainly on studies of populations in continental Europe.

Species	Seasonal occurrence
CATENULIDA	
<i>Catenula lemnae</i>	All year
<i>Suomina turgida</i>	All year
<i>Rhynchoscolex simplex</i>	All year
<i>Stenostomum anatrostrum</i>	?All year?
<i>Stenostomum grabbskogense</i>	?Spring-summer-autumn?
<i>Stenostomum leucops</i>	All year or spring-summer-autumn, or summer
<i>Stenostomum unicolor</i>	All year or spring-summer-autumn
MACROSTOMIDA	
<i>Macrostomum distinguendum</i>	Spring-summer-autumn or all year
<i>Macrostomum johni</i>	Unknown (only recorded in February and December)
<i>Macrostomum rostratum</i>	Spring-summer-autumn or all year
<i>Macrostomum tuba</i>	Unknown (only found in aquaria in Britain and North Europe)
<i>Macrostomum lineare</i>	All year or spring-summer-autumn
PROLECITHOPHORA	
<i>Plagiostomum lemani</i>	All year
LECITHOEPITHELIATA	
<i>Geocentrophora baltica</i>	All year
<i>Geocentrophora sphyrocephala</i>	All year
<i>Prorhynchus stagnalis</i>	All year
PROSERIATA	
<i>Bothrioplana semperi</i>	All year
<i>Otomesostoma auditivum</i>	All year
RHABDOCOELA: DALYELLIODA	
<i>Castrella truncata</i>	All year or spring-summer-autumn
<i>Dalyellia viridis</i>	Autumn-winter-spring (varies according to period when habitat is without water)
<i>Gieystoria diadema</i>	Unknown
<i>Gieystoria expedita</i>	Summer-autumn
<i>Gieystoria infundibuliformis</i>	Summer-autumn
<i>Gieystoria rubra</i>	Spring-summer-autumn
<i>Gieystoria triquetra</i>	Summer-autumn
<i>Microdalyellia armigera</i>	All year
<i>Microdalyellia brevimana</i>	Spring-summer-autumn or summer-autumn
<i>Microdalyellia fairchildi</i>	Spring-summer-autumn, or summer-autumn, or summer or, sometimes, all year
<i>Microdalyellia schmidtii</i>	All year, but other periods possible
RHABDOCOELA: TYPHLOPLANOIDA	
<i>Bothromesostoma personatum</i>	Summer-autumn or summer
<i>Mesostoma ehrenbergii</i>	Summer-autumn or summer

<i>Mesostoma lingua</i>	Summer-autumn or spring-summer-autumn or, occasionally, all year
<i>Mesostoma plarycephalum</i>	?Summer or summer-autumn?
<i>Mesostoma productum</i>	Summer-autumn or summer
<i>Mesostoma tetragonum</i>	Summer-autumn or summer
<i>Olisthanella obtusa</i>	All year or spring-summer-autumn
<i>Olisthanella truncata</i>	Spring-summer-autumn or summer-autumn
<i>Opisthomum pallidum</i>	Autumn-winter-spring or, sometimes, winter-spring, or spring
<i>Phaenocora typhlops</i>	Spring-summer-autumn
<i>Phaenocera unipunctata</i>	Spring-summer-autumn or all year
<i>Rhynchomesostoma rostratum</i>	All year or, occasionally, summer-autumn, or summer
<i>Castrada armata</i>	?Summer-autumn?
<i>Castrada intermedia</i>	Spring-summer-autumn or summer
<i>Castrada lanceola</i>	Summer-autumn or spring-summer-autumn
<i>Castrada luteola</i>	?Spring-summer-autumn?
<i>Castrada neocomensis</i>	?Spring-summer-autumn?
<i>Castrada stagnorum</i>	Spring-summer-autumn
<i>Castrada viridis</i>	All year
<i>Limmoruanis romanae</i>	All year
<i>Strongylostoma elongatum</i>	?Spring-summer-autumn or summer-autumn?
<i>Strongylostoma radiatum</i>	Spring-summer-autumn, or spring-summer, or summer-autumn
<i>Tetracelis marmorosa</i>	Spring-summer-autumn
<i>Typhloplana viridata</i>	Summer-autumn or spring-summer-autumn
RHABDOCOELA: KALYPTORHYNCHIA	
<i>Gyratrix hermaphroditus</i>	All year or, occasionally, spring-summer-autumn, spring-summer, or autumn-winter-spring, or spring
<i>Opisthocystis goettei</i>	Spring-summer-autumn or all year

Most species produce several generations within a year or part of a year when they are active. The number of generations is determined by several variables, such as temperature, food and the presence of water in the habitat. Single generations have been reported for populations of *Rhynchoscolex simplex*, *Prorhynchus stagnalis*, *D. viridis*, *Olisthanella obtusa*, *Opisthomum pallidum*, *Phaenocora typhlops*, *Ph. unipunctata* and *G. hermaphroditus*.

The life-cycles of microturbellarians have rarely been studied in detail. Exceptionally, *Mesostoma ehrenbergii*, *M. lingua* and *M. productum*, all of which can produce subitaneous and dormant eggs (p. 110), have been studied extensively in German ponds (Heitkamp 1972a,b, 1977, 1988; Heitkamp & Schrade-Mock 1977). All three species have a living phase from spring or summer to autumn (Fig. 70). *Mesostoma ehrenbergii* has six generations per life-cycle. The first generation hatches from resting eggs in May.

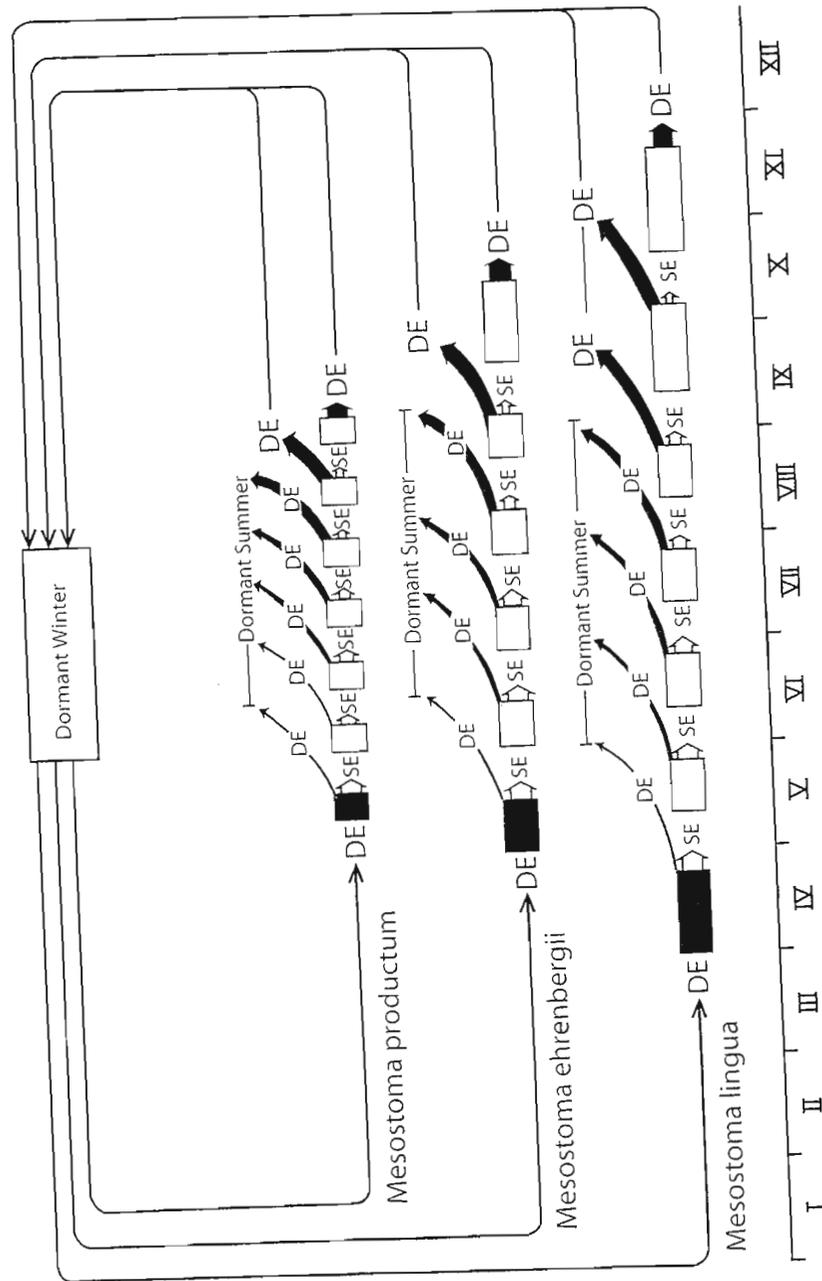


Fig. 70. Life-cycles of three species of *Mesostoma* in German ponds. In spring, the first generation of young animals (dark blocks) hatch from overwintering, dormant eggs (DE). The following generations (grey blocks) are produced from subitaneous eggs (SE). However, these successive generations produce a few eggs which undergo a period of dormancy before hatching. In late summer and autumn, a rising number of overwintering, dormant eggs are produced (increasing width of arrows), and the final autumn generation produces only dormant eggs. (Reproduced with permission from Heitkamp 1977).

Animals from resting eggs produce subitaneous eggs. All other generations up to October hatch from subitaneous eggs. A small proportion of dormant eggs may be produced by animals during summer but are produced mainly in the autumn. The dormant eggs survive cold and/or dryness over winter. The life-cycles of *M. lingua* and *M. productum* differ from that of *M. ehrenbergii* in the length and number of generations. In these, seven generations occur over periods of 7.5–8 months in *M. lingua* and 4 months in *M. productum* (Fig. 70).

In Britain, the life-cycles of only three species, namely *D. viridis*, *Ph. typhlops* and *Ph. unipunctata*, have been studied in detail, though information on seasonal occurrences also has been obtained from general collections of microturbellarian species (Young 1970, 1973a). Bevercombe *et al.* (1973) and Cox & Young (1974) investigated populations of *D. viridis* in a temporary pond and a ditch that were without water for several months in the summer/early autumn. After re-flooding in late autumn, resting cocoons did not hatch until February because the overwintering temperature was too low. Animals continued to grow and mature until the habitats dried up in May–June when the microturbellarians died, releasing their cocoons. Young (1975a) studied a population of *Ph. typhlops* in a permanent pond. The active phase spanned May to September and the rest of the year was spent in the resting cocoon stage. The eggs entered an obligate diapause which was released by a period of low temperature (5°C or lower) followed by a higher temperature (9°C or above) (p. 109). Young (1977a) investigated a population of *Ph. unipunctata* inhabiting a pond that dried up in the autumn. The cocoons survived the drought conditions and low winter temperature. They hatched in spring when the temperature exceeded 6°C. All three species produced a single generation during their active phase.

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Permission has been kindly granted to reproduce the following text-figures: Fig. 1C, Fig. 2A₁ (and Fig. 9), Fig. 5C (and Fig. 42) – Academic Press Inc.; Fig. 4K (and Fig. 39) – Archiv für Hydrobiologie; Fig. 69 – Blackwell Scientific Publications; Fig. 70 – Hydrobiologia.

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