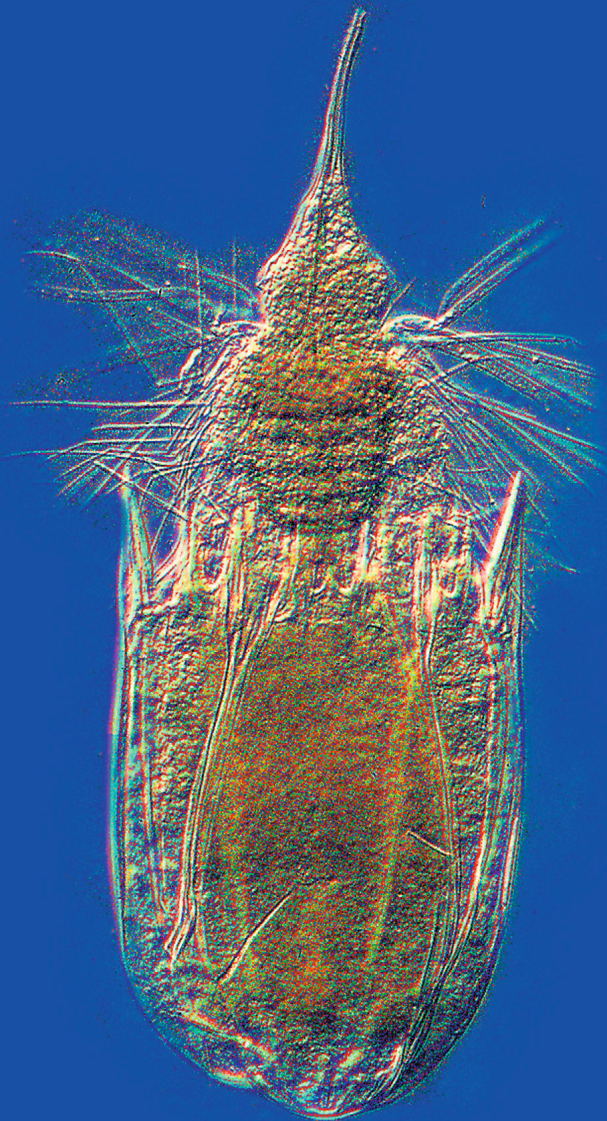


# MEIOFAUNA MARINA

Biodiversity, morphology and ecology  
of small benthic organisms

16



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## An overview and a dichotomous key to genera of the phylum Gastrotricha

M. Antonio Todaro\* and William D. Hummon\*\*

### Abstract

Gastrotricha are microscopic (0.06-3.0 mm in body length) free-living, acoelomate, aquatic worms, characterised by a meiobenthic life style. In marine habitats they are mainly interstitial, whereas in fresh waters they are ubiquitous as a component of periphyton and benthos and to a more limited extend also of the plankton. The phylum is cosmopolitan with about 700 described species grouped into two orders: Macrodasysida, with some 250 strap-shaped species, all but two of which are marine or estuarine, and Chaetonotida with some 450 tenpin-shaped species, two thirds of which are freshwater. Macrodasysida include 7 families and 32 genera, whereas Chaetonotida counts 8 families and 30 genera. This key includes several recently described taxa, namely Xenodasyidae, Muselliferidae, *Chordodasiopsis* and *Diuronotus*.

Keywords: meiofauna, invertebrates, benthos, teaching, taxonomy

### Introduction

Gastrotricha are microscopic (0.06-3.0 mm in body length) free-living, acoelomate, aquatic worms, characterised by a meiobenthic life style. In marine habitats they are mainly interstitial, whereas in fresh waters they are ubiquitous as a component of periphyton and benthos and to a more limited extend also of the plankton. In marine sediments, gastrotrich density may reach 364 individuals/10 cm<sup>2</sup>; typically they rank third in abundance following the Nematoda and the harpacticoid Copepoda, although in several instances they have been found to be first or the second most abundant meiofaunal taxon (Coull 1985, Todaro et al. 1995, Hochberg 1999).

In freshwater ecosystems population density may reach 158 ind./10 cm<sup>2</sup> making the taxon rank among the top 5 most abundant groups. In aquatic environments the ecological role of the gastrotrichs is realised within the microphagous, detritivorous, benthic community. Like free-living nematodes, gastrotrichs swallow their food, which is made up of microalgae, bacteria and small protozoans, by means of the powerful sucking action of the triradiate muscular pharynx, and in turn they are preyed upon by turbellarians and small macrofauna.

The phylum is cosmopolitan with about 700 described species grouped into two orders: Macrodasysida, with some 250 strap-shaped species, all but two of which are marine or estuarine, and

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Chaetonotida with some 450 tenpin-shaped species, two thirds of which live in freshwater. Macro-dasyida include 7 families and 32 genera, whereas Chaetonotida counts 8 families and 30 genera. However due to the numerous species, and at least three new genera that wait to be described, these statistics should be considered as very conservative, particularly for the Chaetonotida. Despite their diversity and abundance, the phylogenetic relationships of the Gastrotricha are still unclear. Based on morphology, most researchers, though considering the evolutionary connections of these worms to be quite obscure, regard them as close allies of the Gnathostomulida, the Rotifera, or the Nematoda. On the other hand, a re-examination of the “Aschelminthes” phylogeny based on the SSU rRNA gene sequence analysis showed the Gastrotricha as the sister taxon of the Platyhelminthes, while later studies placed them close to the Ecdysozoa, the Lophotrochozoa, or neither one. Such discrepancies between the traditional and the modern views on the gastrotrich phylogeny suggest that further research in this direction is necessary (see Todaro et al. 2006a). Unclear are also the in-group phylogenetic relationships; representative of the two orders Macro-dasyida and Chaetonotida are so different to cast doubt about their affiliation to the same phylum (Todaro et al. 2003a). Fortunately, relationships among taxa belonging to different families are becoming less obscure (Todaro et al. 2006b, Leasi & Todaro 2008).

An introduction to the gastrotrichs and their morphology can be obtained from several sources, e.g. d’Hondt (1971), Hummon (1982), Ruppert (1988, 1991) and Balsamo & Todaro (2002).

### Materials and methods

Sampling techniques in marine systems and freshwater habitats are generally similar; qualitative sampling involves the collection of sediment using a shovel, a jar or a corer, while quantitative work mostly uses a small corer (2-5 cm inner diameter), such as a syringe with the tip cut-off. The marine-estuarine species are mostly interstitial, living amid relatively clean, fine to coarse sands, although some are tolerant of high organic, sulfide or pollution loads, and a few even occur in mud and oozes (e.g. Hummon et al. 1990; Todaro & Rocha 2004, 2005; Hummon 2006; Todaro et al. 2006c; Balsamo et al. 2007).

Qualitative littoral samples are usually taken by digging holes in the beach and removing the sediment from the wall and the bottom of the hole with a scoop or spoon whereas bulk sublittoral sediments can be collected directly removing sediment from the top 10-cm layer with a 500-ml plastic jar. Replicated small samples are more representative of the community of a site than a single large sample, because the distribution of gastrotrichs, as most meiofaunal taxa, is patchy. Similar techniques apply to the interstitial forms of freshwater habitats. Periphytic and semipelagic freshwater species are collected by sampling clumps of vegetation mixed with sediment and by repeatedly filtering the water through a 30 µm mesh plankton net (Hummon 1981). Both marine and freshwater samples should be processed within a week to extract the living animals, which are generally more suitable than fixed specimens. For freshwater samples only, additional checks some time after collection are recommended, since as a result of resting eggs, species initially absent may be found later. Interstitial gastrotrichs can be extracted from the sediment by narcotisation with aqueous solution of MgCl<sub>2</sub> (7 % marine or 1 % freshwater); to this end place a spoonful of sand in a small jar, add enough narcotic solution to cover the sand, swirl, leave for 10 min, swirl, decant into a small Petri dish, add an equal amount of either seawater or freshwater and observe under a dissecting microscope at 40-50 × magnification. Periphytic species are extracted from the vegetation by repeatedly rinsing and squeezing the plants, and the supernatant is filtered through a 30 µm mesh sieve. For the qualitative extraction of epibentic freshwater forms, either stirring the sediment into a suspension and decanting the water through a fine mesh net or centrifugation using a density gradient are suitable methods. To study living specimens, use a micropipette for transfer to a slide, then use modelling clay posts beneath the corners of 15-18 mm square coverslips, and observe under a compound microscope using differential interference contrast optics (DIC). Cuticular details may require SEM survey, for which specimens are prepared by critical point drying or the hesamethildysilazane technique (e.g. Todaro 1992, Hochberg & Litvaitis 2000).

For quantitative studies, a treatment of the samples with an aqueous solution of MgCl<sub>2</sub> for 10 minutes is highly recommended prior to fixation. Preservation may be carried out in 10 % borax-buffered formalin with rose bengal

(1 %) to facilitate sorting. The gastrotrichs of the quantitative sample can be separated from the sediment, generally by flotation and multiple decantations. If samples are richer in detritus, extraction can be performed by using the silica gel gradient centrifugation technique (LUDOX AM,  $d=1.210$ ; Pfannkuche & Thiel 1988). The supernatant can be filtered using a 30  $\mu\text{m}$  mesh sieve or, better, poured directly into a Petri dish for locating gastrotrichs; identification can be performed on specimens mounted in water, or better, based on permanent mounts. These can be prepared in 10 % formalin or in a mixture of formalin-glycerol (3:1) and sealed with glyceel or nail polish. Gastrotrichs can also be mounted in pure glycerine on H-S slide after treatment in a solution of 5 % glycerine 95 % ethyl alcohol for 1-2 days (Lee & Chang 2003). However, in many cases permanent mounts do not allow a complete taxonomic study, as several diagnostic features deteriorate over time.

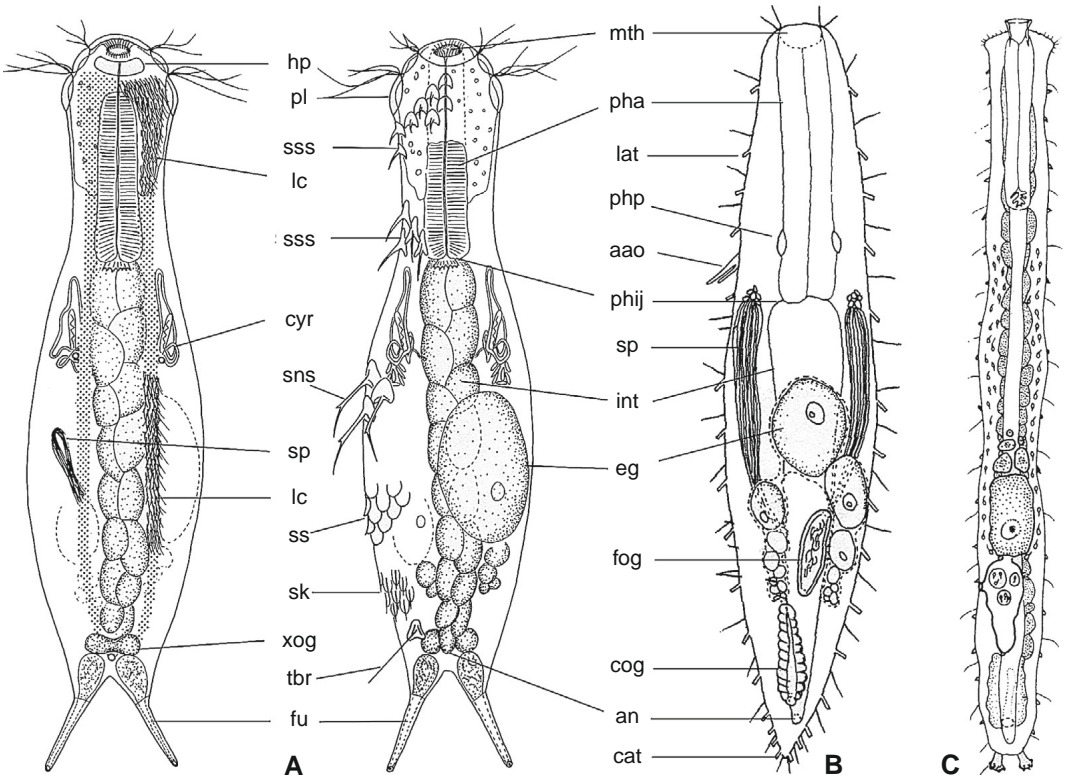
The following key (modified from Hummon 1973 & Balsamo & Todaro 2002) includes all of the genera of marine, brackish and freshwater gastrotrichs known all over the world. It is designed for use by biologists who identify animals as part of their normal work, but who may have little familiarity with the gastrotrich fauna. For the inclusion of Muselliferidae see Leasi & Todaro, (2008); for the exclusion of *Metadasydytes* see W. D. Hummon (this volume). Finally the readers should be informed that W. D. Hummon (this volume) is proposing a name change for the genus *Platydasys*.

The key is pragmatic in approach and is based on important discriminatory characters as seen in relaxed adult specimens. Where possible characters are those which are readily visible, using DIC optics, and which are quantifiable. Each member of a couplet is given the identifying number of the couplet and a letter, **a** or **b**; the number and letter in parenthesis refers to that member of a previous couplet from which a particular couplet was derived. Figures of genera are identified according to the couplet members to which they refer. Finally, nothing replaces experience, especially that gained by intensive study of as broad a range of genera and species as it is possible to obtain.

## Results

### Key to the genera of Gastrotricha

- |    |   |                           |
|----|---|---------------------------|
| 1a | Body tenpin-shaped; posterior end furcate (furca); anterior, lateral and dorsal adhesive tubes absent; posterior adhesive tubes numbering two (exceptionally four, or absent) at the tip of the furcal branches. Mouth opening narrow ( $<0.4 \times$ head width); pharyngeal pores absent. Mostly common; marine, brackish and freshwater: interstitial, epibenthic and periphytic; occasionally semiplanktonic. Order CHAETONOTIDA, Suborder PAUCITUBULATINA (Fig. 1A).....           | 34                        |
| 1b | These characteristics not combined.....   | 2                         |
| 2a | (1b) Body worm-shaped, anterior and dorsal adhesive tubes absent; lateral adhesive tubes, present, although often inconspicuous (in form of papillae), several per side; posterior adhesive tubes, several per side, fused at their bases forming two adhesive organs; mouth narrow ( $<0.4 \times$ head width), opens by means of a projecting cuticular tube, pharyngeal pores absent. Uncommon; marine: interstitial. Order CHAETONOTIDA, Suborder MULTITUBULATINA, NEODASYIDAE..... | <i>Neodasys</i> (Fig. 1C) |
| 2b | (1b) Body tenpin- or, more often, worm-shaped; anterior, lateral and posterior adhesive tubes present, usually numerous; dorsal adhesive tubes present in several taxa; mouth opening narrow to broad; pharyngeal pores usually present, though occasionally inconspicuous. Marine and brackish rarely freshwater: interstitial. Order MACRODASYIDA (Fig. 1B).....  | 3                         |
| 3a | (2b) Marine or brackish.....  | 4                         |
| 3b | (2b) Freshwater. INCERTAE SEDIS (Fig. 9).....   | 33                        |
| 4a | (3a) Body tenpin-shaped; head well defined, includes most ( $>0.8 \times$ length) of pharynx; dorsal adhesive tubes absent, posterior end lobed, furcate or bifurcate. Cuticle smooth, or forming crests and thickenings; musculature clearly cross-striated.....   | 5                         |
| 4b | (3a) Body worm-shaped, head usually not distinct or, when distinct, includes only part ( $<0.5 \times$ length) of pharynx; cuticle smooth or forming scales and/or spines. ....   | 9                         |



**Fig. 1.** **A.** Drawing of a hypothetical Chaetonotida Paucitubulatina. **B.** Drawing of a hypothetical Macrodasysida. **C.** *Neodasys* (Chaetonotida, Multitubulatina). **Aao**, accessory adhesive organs; **an**, anus; **cat**, caudal adhesive tubes; **cog**, caudal organ; **cyr**, cyrtocytes; **eg**, egg; **fog**, frontal organ; **fu**, furca; **hp**, hypostomion; **int**, intestine; **lat**, lateral adhesive tubes; **lc**, locomotor cilia; **mth**, mouth; **pha**, pharynx; **phij**, pharyngo-intestinal junction; **php**, pharyngeal pores; **pl**, pleuria; **sk**, keeled scale; **sns**, scales with notched spines; **sp**, sperm; **ss**, smooth scales; **sss**, scales with simple spines; **tbr**, tactile bristle; **xog**, X-organ. **A, B**, modified from Balsamo & Todaro (2003); **C**, Modified from Ruppert (1988).

- 5a (4a) Cuticle smooth; dorsal side of the trunk bare; chordoid organ absent. Common to rare; marine and brackish: interstitial. DACTYLOPODOLIDAE (Fig. 2). ..... 6
- 5b (4a) Cuticle forming crests and thickenings, if smooth dorsal side of the trunk bearing long rod-like structure; chordoid organ present. Rare; marine: interstitial. XENODASYIDAE (Fig. 3). ..... 8
- 6a (5a) Head simple or with a pair of laterally directed tentacles; cuticle smooth; posterior end bilobed. Lateral adhesive tubes present. Often common; marine: interstitial. .... *Dactylopodola* (Fig. 2A)
- 6b (5a) Head simple or with tentacles; cuticle smooth; posterior end bifurcate. Lateral adhesive tubes absent. .... 7
- 7a (6b) Head simple, without tentacles; cuticle smooth. Rare; marine: interstitial. .... *Dendropodola* (Fig. 2B)
- 7b (6b) Head with elongate crenulated lateral lobes. Uncommon; marine: interstitial. .... *Dendrodasys* (Fig. 2C)
- 8a (5b) Trunk lacking rod-like structure, but showing conspicuous indentations along the lateral margins; posterior end furcate, each branch ending with short adhesive tubes. Rare; marine: interstitial. .... *Xenodasys* (Fig. 3A)

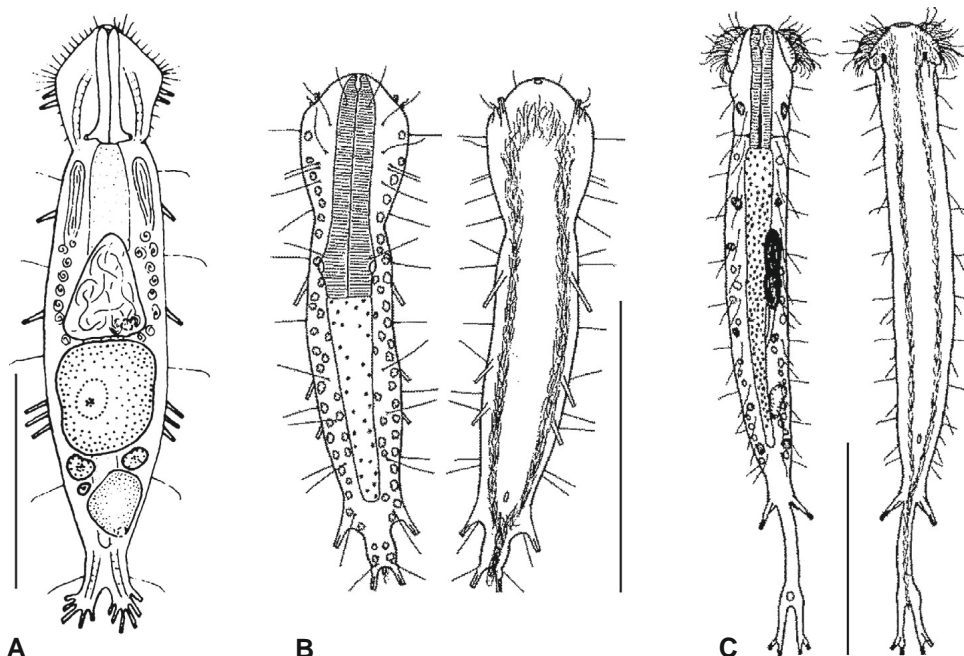


Fig. 2. Macrodasysida, Dactylopodolidae – Representatives of the genera *Dactylopodola* (A), *Dendropodola* (B), *Dendrodasys* (C). Scale bars = 100  $\mu$ m. A, modified from Ruppert (1988); B, modified from Hummon et al. (1998); C modified from Hummon et al. (1993).

- 8b (5b) Trunk showing several tentacles; lateral margins of the trunk parallel, without indentations; posterior end furcate; each branch ending with an adhesive pad. Rare; marine: interstitial. .... *Chordodasiopsis* (Fig. 3B)
- 9a (4b) Anterior adhesive tubes (generally 4 or more per side, occasionally 2 or 3) borne on extensible fleshy base; pharyngeal pores located at base of pharynx. .... 10
- 9b (4b) Anterior adhesive tubes borne more or less directly on ventral body surface (generally 1 to 3 per side (occasionally 4 or more); pharyngeal pores located at base of pharynx or in mid-pharyngeal region. .... 16
- 10a (9a) Head usually well delimited posteriorly by a constriction; posterior end broadly expanded, rounded, truncated, or tapered into a medial process, but not bilobed. LEPIDODASYIDAE (part) (Fig. 4). .... 11
- 10b (9a) Head usually not well delimited; posterior end bilobed. TURBANELLIDAE (part) (Fig. 5). .... 12

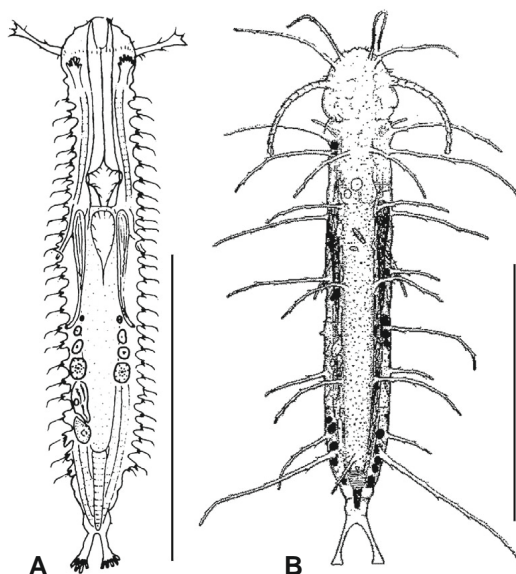


Fig. 3. Macrodasysida, Xenodasyidae – Representatives of the genera *Xenodasys* (A), *Chordodasiopsis* (B). Scale bars = 200  $\mu$ m. A, modified from Ruppert 1988; B, modified from Rieger et al. (1974).

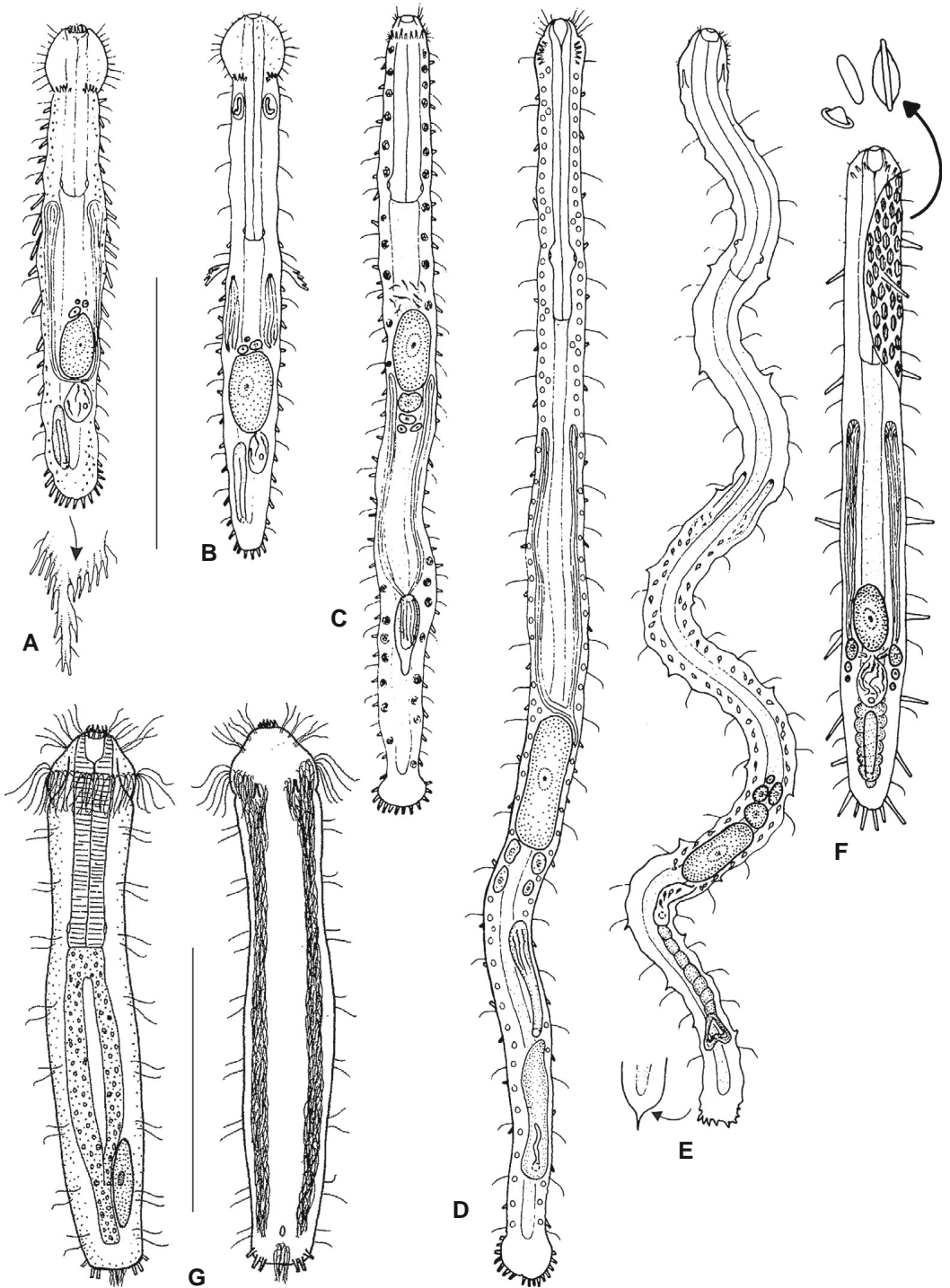


Fig. 4. Macrodasysida, Lepidodasysidae – Representatives of the genera *Cephalodasys* (A), *Pleudodasys* (B), *Mesodasys* (C), *Megadasys* (D), *Dolichodasys* (E), *Lepidodasys* (F), *Paradasys* (G). Scale bar = 200  $\mu$ m. A-F, modified from Ruppert (1988); G, original (W. D. Hummon).



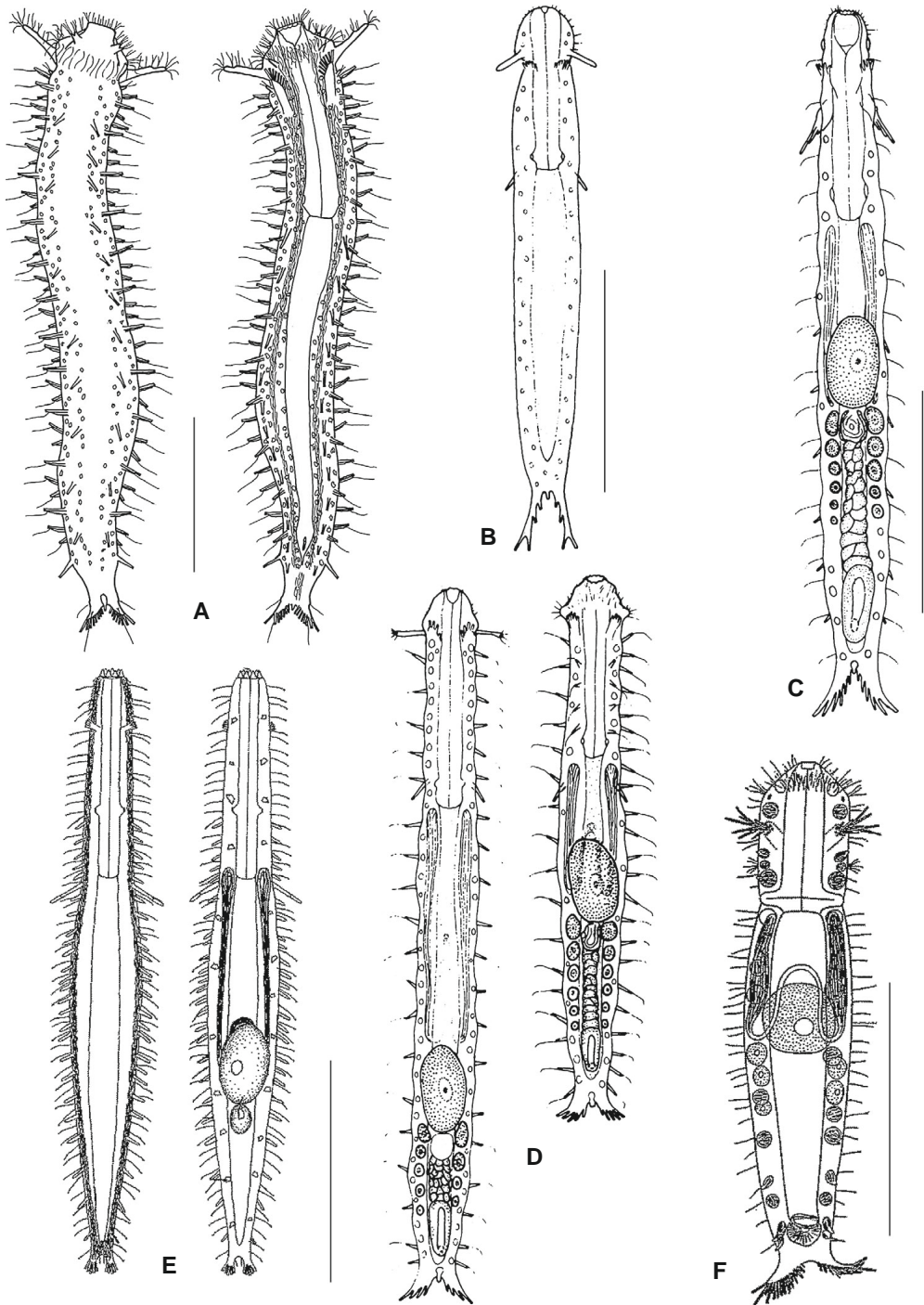


Fig. 5. Macrodasyida, Turbanellidae – Representatives of the genera *Dinodasys* (A), *Pseudoturbanella* (B), *Paraturbanella* (C), *Turbanella* (D), *Prostobuccantia* (E), *Desmodasys* (F). Scale bars = 200  $\mu$ m. A, original (W. D. Hummon); B-D, modified from Ruppert (1988); E, modified from Evans & Hummon (1991); F, modified from Clausen (2000).

- 11a (10a) A pair of laterally directed accessory adhesive organs present near the pharyngo-intestinal junction, each comprised of four adhesive tubes; a pair of drumstick-like organs on the dorsal side of the pharyngeal region. Rare, marine: interstitial. ....  
..... *Pleurodasys* (Fig. 4B)
- 11b (10a) Laterally directed accessory adhesive and drumstick-like organs, such as those described above, absent. Regionally common; marine and brackish: interstitial. ....  
..... *Cephalodasys* (Fig. 4A)
- 12a (10b) Head bearing elongate (>0.5 × head width) lateral tentacles. ....13
- 12b (10b) Head perhaps bearing conical lobes (<0.5 × head width), but not tentacles. ....14
- 13a (12a) Lateral adhesive tubes numerous. Uncommon; marine: interstitial. ....  
..... *Dinodasys* (Fig. 5A)
- 13b (12a) Lateral adhesive tubes absent, a single pair of ventral adhesive tubes inserting just behind pharyngo-intestinal junction. Rare; marine: interstitial. ....  
..... *Pseudoturbanella* (Fig. 5B)
- 14a (12b) A pair of posteriorly directed ventrolateral accessory adhesive organs present in the anterior portion of the pharyngeal region, each organ comprising 2 adhesive tubes of unequal lengths. Common; marine and brackish: interstitial. ....  
..... *Paraturbanella* (Fig. 5 C)
- 14b (12b) Ventrolateral accessory adhesive organs such as those described above absent, or located in different region of the body. ...  
.....15
- 15a (14b) Accessory adhesive organs, absent. Common; marine and brackish: interstitial. ....  
..... *Turbanella* (Fig. 5D)
- 15b (14b) Accessory adhesive organs arising near the pharyngo-intestinal junction. Rare; marine: interstitial. ....*Prostobuccantia* (Fig. 5E)
- 16a (9b) Pharyngeal pores located in mid-pharyngeal region, posterior end of body tapered into a medial process. MACRODASYIDAE (Fig. 6). ....17
- 16b (9b) Pharyngeal pores located at base of pharynx; posterior end of body not tapered into a medial process. ....18
- 17a (16a) Posterior process short (<0.2 × length of head, trunk). Common; marine: interstitial. ....*Macrodasys* (Fig. 6A)
- 17b (16a) Posterior process elongate (>0.8 × length of head, trunk). Regionally common; marine: interstitial and epibenthic. ....  
.....*Urodasys* (Fig. 6B)
- 18a (16b) Cuticular structure present in the form of thickenings, scales, papillae or hooks. ....  
.....19
- 18b (16b) Cuticle naked, lacking armature. ....25
- 19a (18a) Mouth opening narrow (<0.4 × head width); cuticular armature of elongate, keeled thickenings. Uncommon; marine: interstitial. LEPIDODASYIDAE (part). ....  
.....*Lepidodasys* (Fig. 4F)
- 19b (18a) Mouth opening-broad (>0.6 × head width); cuticular armature of broadened scales, papillae or variously spined hooks. THAUMASTODERMATIDAE (part) (Fig. 7). ....20
- 20a (19b) Cuticular armature with broadened scales or papillae. ....21
- 20b (19b) Cuticular armature with uni- or multi-spined hooks. ....22
- 21a (20a) Cuticular scales present, but not papillae; a single row of wide spines present on either side of body; testes paired. Uncommon; marine: interstitial. ....  
..... *Diplodasys* (Fig. 7A)
- 21b (20a) Cuticular papillae present, but not scales or spines; testis present on right side only. Uncommon; marine: interstitial. ....  
..... *Platydasys* (Fig. 7B)
- 22a (20b) Cuticular armature with uni-spined hooks; testes paired. Common; marine: interstitial. ....*Acanthodasys* (Fig. 7C)
- 22b (20b) Cuticular armature with multi-spined hooks; testis present on right side only. ....  
.....23
- 23a (22b) Buccal palps (flashy grasping structures preceding on either sides the mouth basket), present; hooks 3-, 4- or 5-spined (triancres, tetrancres and pentancre). Common; marine: interstitial. .... *Pseudostomella* (Fig. 7D)
- 23b (22b) Buccal palps absent; hooks 3-, 4- or 5-spined (tri-, tetra- or pentancre). ....24

- 24a (23b) Head with 2 pairs of laterally directed tentacles; hooks 4-spined. Common; marine: interstitial..... *Thaumastoderma* (Fig. 7E)
- 24b (23b) Head with 0 or 1, pair of laterally directed tentacles; hooks 3- 4- or 5-spined. Very common; marine: interstitial. ....  
..... *Tetranchyroderma* (Fig. 7F)
- 25a (18b) Anterior adhesive tubes several to many, borne in a tuft; lateral adhesive tubes absent. Rare; marine: interstitial. TURBANELLIDAE (part) (Fig. 5).....  
..... *Desmodasys* (Fig. 5H)
- 25b (18b) Anterior adhesive tubes few to many, but not borne in a tuft; lateral adhesive tubes usually present or, if absent, then anterior adhesive tubes few.....26
- 26a (25b) Anterior, lateral and posterior adhesive tube groups with many tubes each (>10 per side); mouth narrow (<0.4 × head width) and posterior end distinctly bilobed. PLANODASYIDAE (Fig. 8). ....27
- 26b (25b) At least one group with few to several adhesive tubes (<6 per side); mouth narrow to broad, if narrow, then posterior end not distinctly bilobed.....28
- 27a (26a) Tail lobes form oval appendages on the posterior end; most anterior adhesive tubes arranged transversely; bursa elongate. Rare; marine: interstitial.....  
..... *Planodasys* (Fig. 8A)
- 27b (26a) Tail lobes form furcate extensions on the posterior end; most anterior adhesive tubes arranged longitudinally; bursa ovate. Uncommon; marine: interstitial. ....  
..... *Crasiella* (Fig. 8B)
- 28a (26b) Mouth narrow (<0.4 × head width); testes paired. LEPIDODASYIDAE (part) (Fig. 4). ....29
- 28b (26b) Mouth broad (>0,6 × head width) or, if narrow, leading to a large buccal cavity surrounded by an oral hood; testis present on right side only. THAUMASTODERMATIDAE (part). ....32
- 29a (28a) fully grown adults (both sexual apparatus and mature gametes present) usually less than 1 mm in total length.....30
- 29b (28a) fully grown adults up to 3.5 mm in total length, always exceeding 1 mm.....31

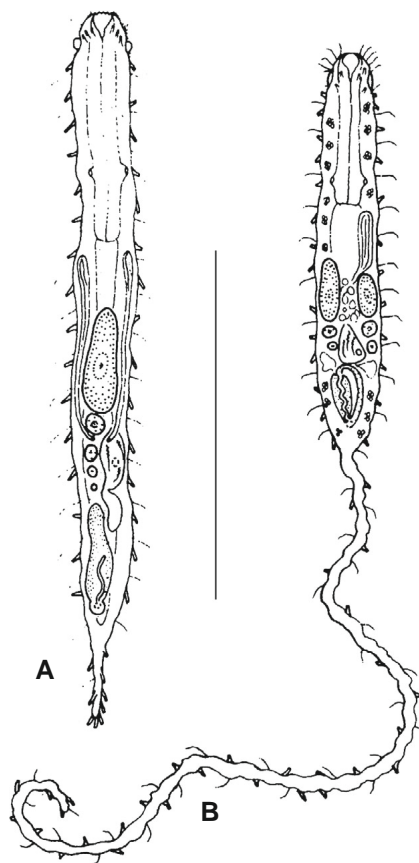
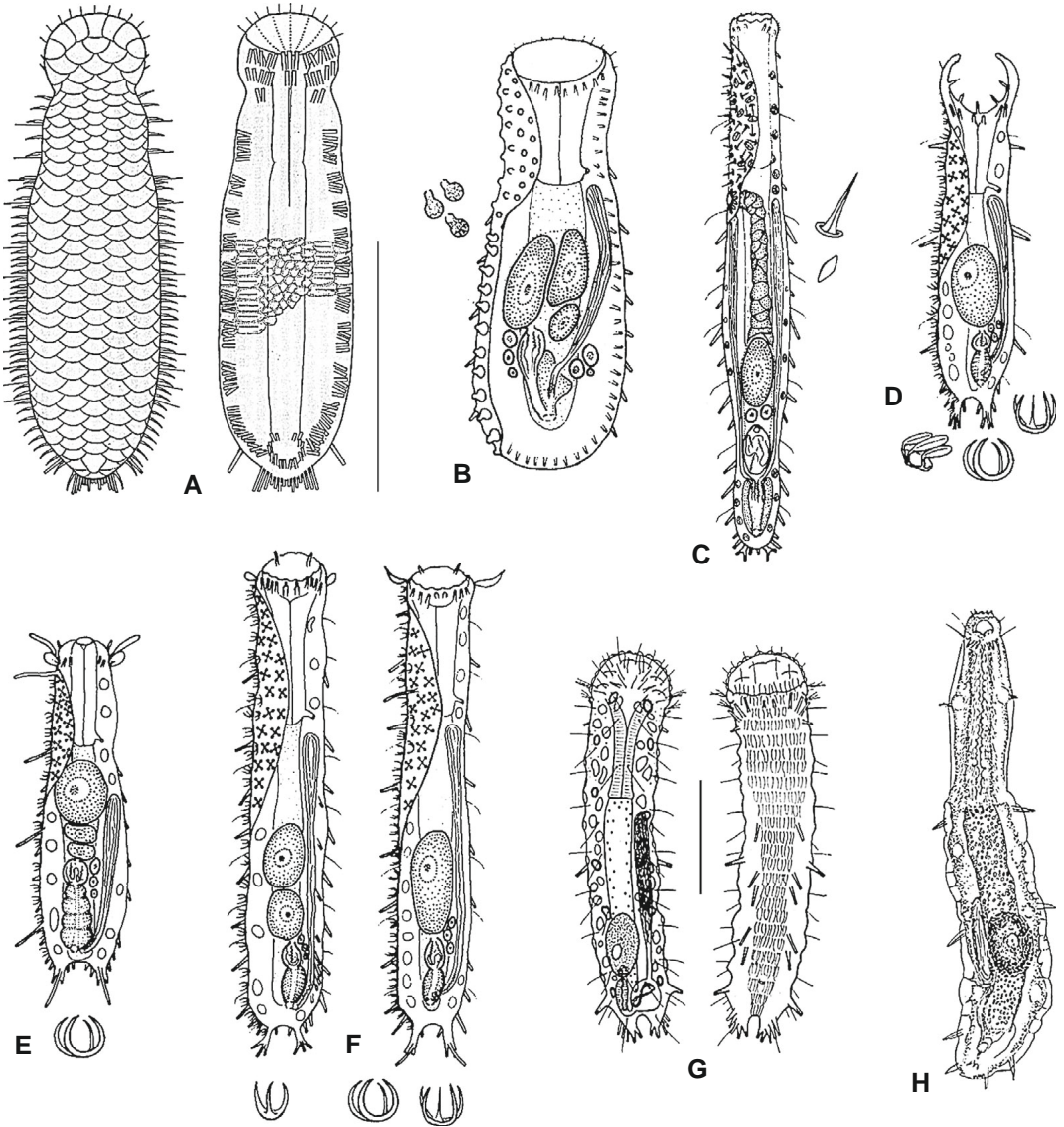


Fig. 6. Macrodasysida, Macrodasysidae – Representatives of the genera *Macrodasys* (A), *Urodasys* (B). Scale bar = 200  $\mu$ m. A, B, modified from Ruppert (1988).

- 30a (29a) Anterior adhesive tubes in two groups of 1-4 tubes per side; lateral adhesive tubes absent or less than 6 per side. Uncommon; marine: Interstitial..... *Paradasys* (Fig. 4G)
- 30b (29a) Anterior adhesive tubes few to several; lateral adhesive tubes several to many per side. Common; marine: interstitial. ....  
..... *Mesodasys* (Fig. 4C)
- 31a (29b) Anterior adhesive 1 per side; lateral adhesive tubes inconspicuous (in form of papillae). Uncommon; marine: interstitial. .  
..... *Dolichodasys* (Fig. 4E)
- 31b (29b) Anterior adhesive few to several; lateral adhesive tubes distinct, many per side. Uncommon; marine: interstitial. ....  
..... *Megadasys* (Fig. 4D)



**Fig. 7.** Macrodasysida, Thaumastodermatidae – Representatives of the genera *Diplodasys* (A), *Platydasys* (B), *Acanthodasys* (C), *Pseudostomella* (D), *Thaumastoderma* (E), *Tetranchyroderma* (F), *Ptychostomella* (G), *Hemidasys* (H). A-F,H, bar scale = 200  $\mu$ m, G, bar scale = 50  $\mu$ m. A, Modified from Luporini et al. (1973); B-F, modified from Ruppert (1988); G, modified from Hummon et al. (1993); H, modified from Claparéde (1864).

- 32a (28b) Mouth broad; ventral locomotor cilia not restricted to pharyngeal region; male genital pore lacking cuticular plates. Common; marine: interstitial.....  
.....*Ptychostomella* (Fig. 7G)
- 32b (28b) Mouth narrow, leading to a large buccal cavity surrounded, by an oral hood; ventral locomotor cilia restricted to pharyngeal region; male genital pore surrounded by cuticular plates. Very rare (possibly extinct); marine: interstitial.....  
.....*Hemidasys* (Fig. 7H)
- 33a (3b) Body length from 300 to 400  $\mu$ m; two pairs of anterior ventral adhesive tubes. Rare, interstitial.....  
.....*Redudasys* (Fig. 9B)

- 33b (3b) Body length up to 220 µm; one pair of anterior (possibly ventral) adhesive tubes. Rare, interstitial. ....*Marinellina* (Fig. 9A)
- 34a (1a) Locomotor cilia beneath pharyngeal region inserted as tightly-packed “hypotrichous” cirri, occurring in two longitudinal rows. Marine and brackish. XENOTRICHULIDAE (Fig. 10).....35
- 34b (1a) Locomotor cilia beneath pharyngeal region inserted individually, occurring in longitudinal rows, loose tufts or as a uniform field, never organised in cirri. Marine, brackish and freshwater.....37
- 35a (34a) Locomotor cirri of two or more sizes, generally with 1-2 transverse rows of tiny cirri anteriorly and two isolated tufts of cirri in the mid-trunk region; pharynx bearing a bulb anteriorly. Common; marine and brackish: interstitial.....  
.....*Heteroxenotrichula* (Fig. 10A)
- 35b (34a) Locomotor cirri of nearly the same size; two isolated tufts of cirri in the mid-trunk region present or absent (not seen); pharynx cylindrical, without bulb. ....36

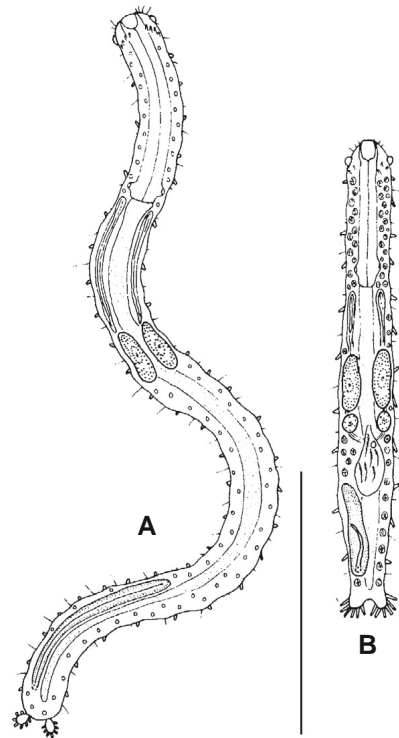


Fig. 8. Macrodasysida, Planodasyidae – Representatives of the genera *Planodasys* (A), *Crasiella* (B). Scale bar = 200 µm. A, B, modified from Ruppert (1988).

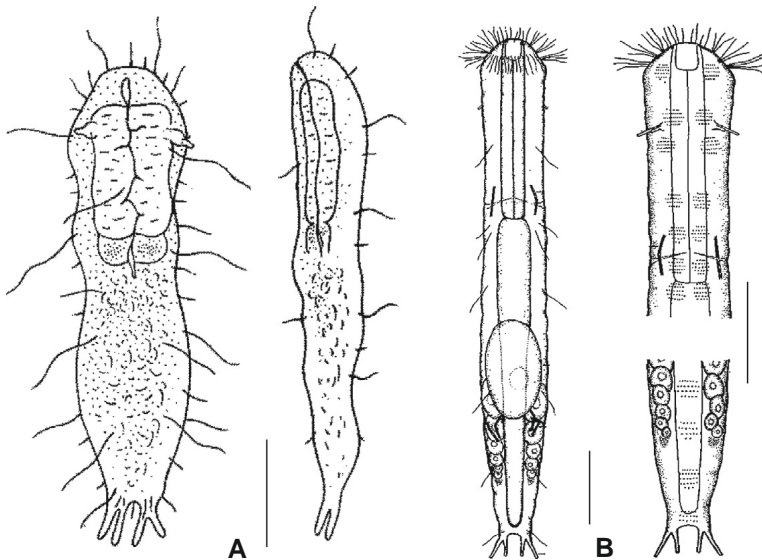
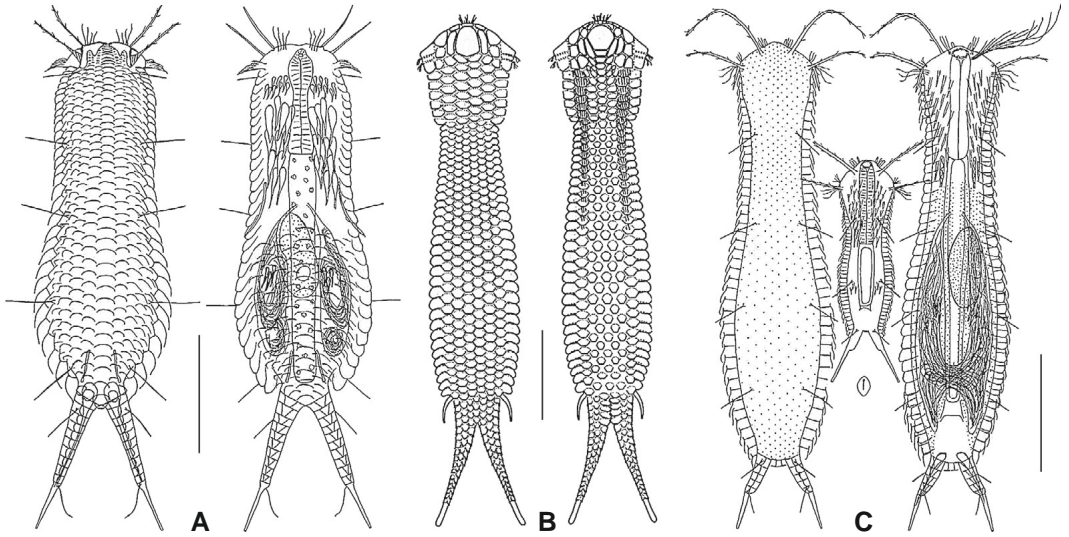


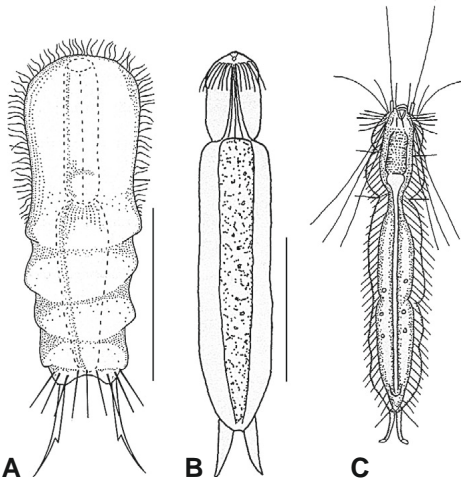
Fig. 9. *Incertae sedis* – Representatives of the genera *Marinellina* (A), *Redudasys* (B). Scale bars = 50 µm. A, Modified from Ruttner-Kolisko (1955); B, modified from Kisielewski (1987).



**Fig. 10.** Chetonotida, Xenotrichulidae – Representatives of the genera *Heteroxenotrichula* (A), *Draculiciteria* (B), *Xenotrichula* (C). Scale bars = 50 µm. A, C, original (W. D. Hummon); B, modified from Luporini et al. (1973).

36a (35b) Male apparatus absent; head well defined; dorsal scales flat; lateral mid-trunk scales peduncolated; single spine on either side of the base of the caudal furca. Common; marine: interstitial. ....  
 ..... *Draculiciteria* (Fig. 10B)

36b (35b) Male apparatus present; pharynx without anterior bulb; head usually indistinct; lateral mid-trunk scales simple, flat, or pedunculated; if pedunculated, similar to dorsal mid-trunk scales. Common; marine and brackish: interstitial. ....  
 ..... *Xenotrichula* (Fig. 10C)



**Fig. 11.** Chetonotida: A, Dichaeturidae – Representative of the genus *Dichaetura*, B, C, Proichthydiidae – Representatives of the genera *Proichthydiium* (B), *Proichthydioides* (C). Scale bars = 50 µm. A, modified from Balsamo (1983); B, modified from Cordero (1918); C, Redrawn from Suzuki (1971).

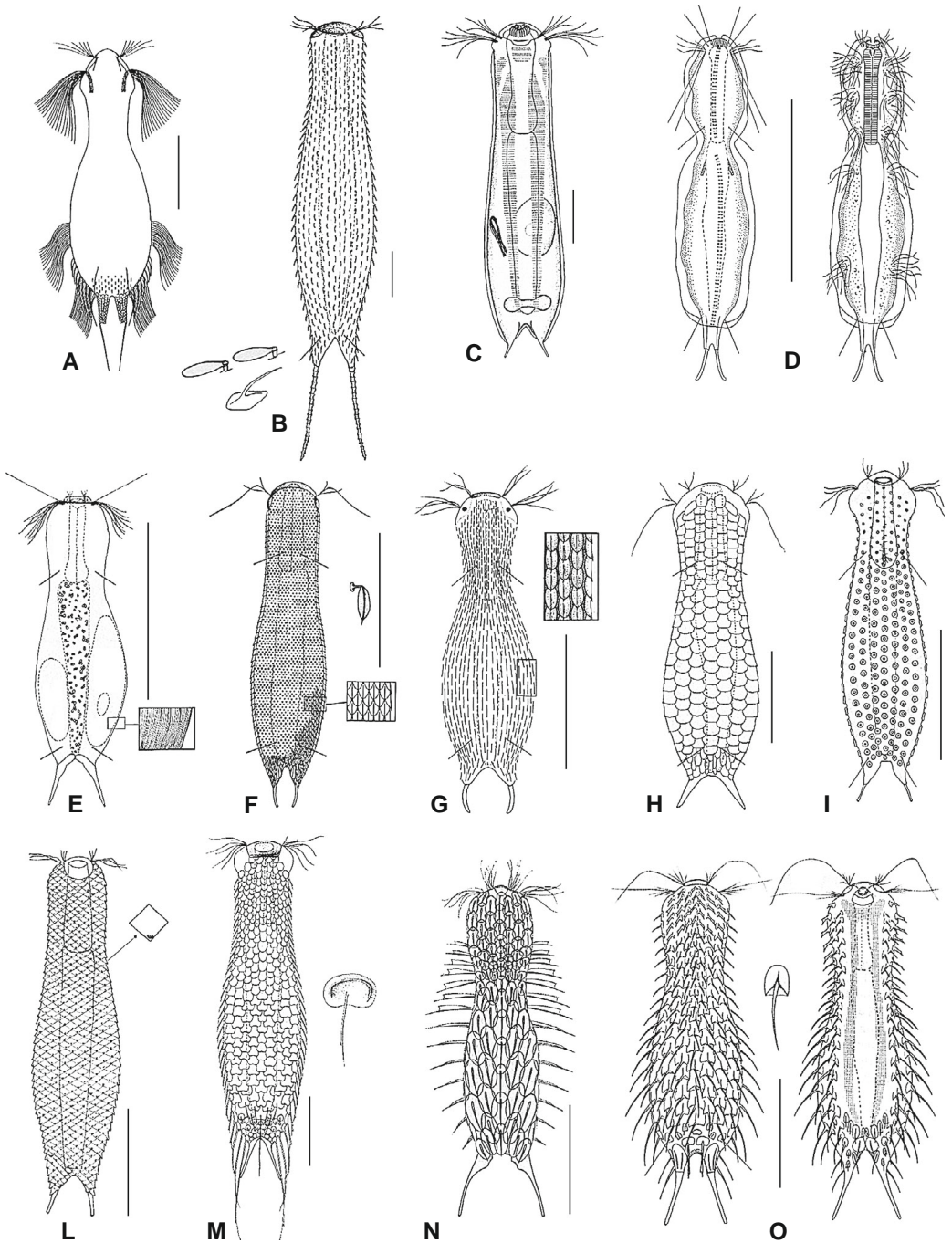
37a (34b) Furcal branches present, with or without adhesive tubes. .... 38  
 37b (34b) Furcal branches absent; posterior body end truncated or rounded with possible presence of two protuberances or spines. .... 54

38a (37a) Posterior end bifurcate, with 4 adhesive tubes or 2 adhesive tubes and 2 spiny processes; cuticle naked, lacking armature. Rare; freshwater: interstitial. DICHAETURIDAE. .... *Dichaetura* (Fig. 11A)

38b (37a) Posterior end truncated, bilaterally projected into protuberances, or furcate, with 0, 2 or 4 adhesive tubes; cuticular armature in form of scales and/or spines present or absent. .... 39

39a (38b) Cuticular armature absent; caudal adhesive tubes sickle-shaped; cephalic cilia not grouped into tufts. Very rare; freshwater: hyperbenthic or semiplanktonic. PROICHTHYIDIIDAE (Fig. 11B,C). .... 40

- 39b (38b) Cuticular scales and spines generally present; if present caudal adhesive tubes mostly straight, long to very short; cephalic cilia grouped into tufts or in a band encircling a muzzle-like anterior projection of head, which bears the mouth.....41
- 40a (39a) A transverse row of short dorsal cephalic cilia; ventral cilia arranged in tufts, only present on the head and neck regions. Fresh water: hyperbenthic. ....  
.....*Proichthyidium* (Fig. 11B)
- 40b (39a) No dorsal cephalic cilia; ventral cilia arranged in two longitudinal bands. Fresh water: semiplanktonic. ....  
.....*Proichthydioides* (Fig. 11C)
- 41b (39b) Cephalic cilia in 1 or 2 pairs of tufts, inserting dorso- or ventro laterally on head. Common (except *Arenotus* and *Undula*); marine, brackish and freshwater: periphytic, epibenthic and interstitial CHAETONOTIDAE (Fig. 12). ....42
- 41a (39b) Cephalic cilia in a band, encircling a muzzle-like anterior projection of head, which bears the mouth; two or four posterior adhesive tubes. Uncommon to rare, marine: interstitial or infaunal. MUSELLIFERIDAE (Fig. 15).....61
- 42a (41b) Caudal appendages with adhesive tubes. ....43
- 42b (41b) Caudal appendages without adhesive tubes. Rare; fresh water: epibenthic. ....  
.....*Undula* (Fig. 12A)
- 43a (42a) Caudal furca very long (up to  $\frac{1}{3}$  of the total length), segmented, naked or bearing very small scales or spines. Common; freshwater: epibenthic, periphytic.....  
.....*Polymerurus* (Fig. 12B)
- 43b (42a) Caudal furca from mid length to very short, unsegmented, without scales or spines.....44
- 44a (43b) Body cuticle smooth or with numerous, non-spined scales; occasionally a few spines at the furcal base. ....45
- 44b (43b) Body cuticle covered with numerous spined and/or keeled scales; short to very long spines, simple or with 1-2 lateral notches. ....52
- 45a (44a) Body cuticle smooth.....46
- 45b (44a) Body cuticle with non-spined scales. ....  
.....48
- 46a (45a) Thin, smooth cuticle which may show very tiny, longitudinal lines; rarely a few spines at the furcal base. Common; freshwater, rarely marine or brackish-water: epibenthic, periphytic, interstitial.....47
- 46b (45a) Very thick, smooth, cuticle clearly distinguishable from the epidermis. Rare; freshwater: interstitial... *Arenotus* (Fig. 12C)
- 47a (46a) Furcal base pedunculate; ventral locomotory cilia arranged in tufts. Uncommon; marine: interstitial. ....  
.....*Caudichthyidium* (Fig. 12D)
- 47b (46a) Furcal base not pedunculate; ventral locomotory cilia arranged in two longitudinal bands. Common; freshwater, rarely marine or brackish-water.....  
.....*Ichthyidium* (Fig. 12E)
- 48a (45b) Scales small with a stalk or a keel. 49
- 48b (45b) Scales large, flat, polygonal, rhomboidal or circular in shape.....50
- 49a (47a) Scales with a stalk. Common; freshwater, brackish-water, marine: epibenthic, periphytic, interstitial. ....  
.....*Aspidiophorus* (Fig. 12F)
- 49b (47a) Scales with a keel. Common; freshwater, brackish-water, marine: epibenthic, periphytic, interstitial. ....  
..... *Heterolepidoderma* (Fig. 12G)
- 50a (48b) Numerous polygonal scales. Common; freshwater, rarely brackish-water and marine: epibenthic, periphytic, interstitial.....  
.....*Lepidodermella* (Fig. 12H)
- 50b (48b) Scales rhomboidal or circular in shape. ....51
- 51a (50b) Few circular scales. Rare; freshwater: periphytic. ....*Fluxiderma* (Fig. 12I)
- 52b (50b) Numerous rhomboidal scales. Rare; freshwater: periphytic. ....  
.....*Rhomballichthys* (Fig. 12L)
- 52a (44b) Dorsal scales with a double anterior edge, lacking a keel but with or without a spine; ventral, interciliary scales similar in shape to the dorsal scales; some pairs of long



**Fig. 12.** Chaetonotida, Chaetonotidae—Representative of the genera *Undula* (A), *Polymerurus* (B), *Arenotus* (C), *Caudichthyidium* (D), *Ichthyidium* (E), *Aspidiophorus* (F), *Heterolepidoderma* (G), *Lepidodermella* (H), *Fluxiderma* (I), *Rhomballichthys* (L), *Lepidochaetus* (M), *Halichaetonotus* (N), *Chaetonotus* (O). Scale bars = 50  $\mu$ m. A, modified from Kisielewski (1991); B, E-H, M, Modified from Balsamo (1983); C, Modified from Kisielewski (1987); D, Modified from Mock (1979); I, L, modified from Swank 1991; N, Modified from Schrom (1972); O, modified from Hummon et al. (1992).



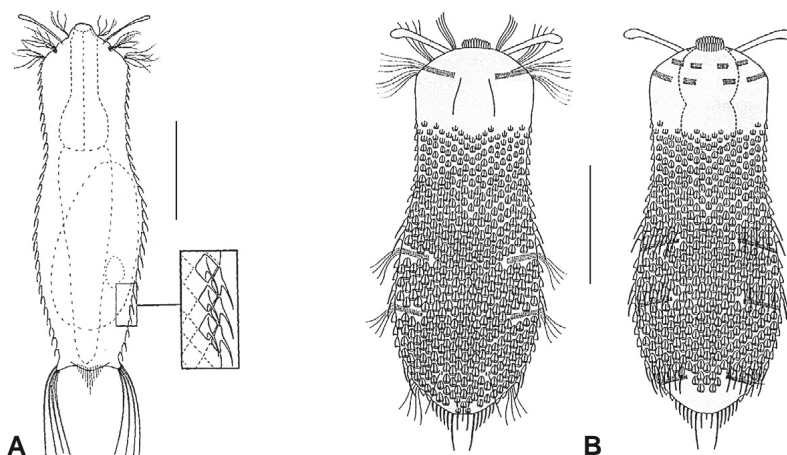


Fig. 13. Chetonotida, Neogosseidae – Representative of the genera *Neogosseia* (A), *Kijanebalola* (B). Scale bars = 50  $\mu$ m. A, modified from Balsamo (1983); B, modified from Kisielewski (1990).

- and very thin spines at the sides of the furcal base. Quite common; freshwater: epibenthic, periphytic.....  
 .....*Lepidochaetus* (Fig. 12M)  
 52b (44b) Dorsal scales with a single anterior edge and a keel or a keel and/or a spine; ventral, intercalary scales different in shape from the dorsal scales. Very common; marine, brackish-water and freshwater: interstitial, epibenthic, periphytic.....53
- 53a (52b). Ventrolateral scales adjacent to locomotor ciliary tract with spines bearing lamellae (hydrofoil scales); dorsal scales with a keel; if present spines restricted to 1-3 scales. Common; marine and brackish-water: interstitial.....*Halichaetonotus* (Fig. 12N)
- 53a (52b). Hydrofoil scales usually absent; if present dorsal scales with spines. Very common; marine, brackish-water and freshwater: interstitial, epibenthic, periphytic.....  
 .....*Chaetonotus* (Fig. 12O)
- 54a (37b) Two club-shaped, cephalic tentacles; small scales with very short spines on the trunk; truncated or rounded body end bearing several spines. Rare; freshwater: epibenthic and semipelagic. NEOGOSSEIDAE (Fig. 13). .....55
- 54b (37b) No cephalic tentacles; scales reduced or absent; very long and motile spines arranged into groups on the trunk; truncated or rounded body end which may show bristly protuberances or spines. Rare; freshwater: epibenthic, periphytic, hyperbenthic and semipelagic. DASYDYTIDAE (Fig. 14). .....56
- 55a (54a) Truncated body end showing two protuberances, each with a tuft of long spines; fine spined scales. Epibenthic and semipelagic.....*Neogosseia* (Fig. 13A)
- 55b (54a) Rounded body end with a central group of spines and no protuberances; keeled scales. Epibenthic and semipelagic. ....  
 .....*Kijanebalola* (Fig. 13B)
- 56a (54b) Several long spines, up to  $\frac{1}{4}$  of the body length, scattered on the dorsal trunk region, or only two caudal spines; two longitudinal, ventral ciliary bands; pharynx with two bulbs. ....*Anacanthoderma* (Fig. 14A)
- 56b (54b) Long, lateral spines arranged into groups or longitudinal rows; tufts of ventral cilia; pharynx with one or no bulbs. ....57
- 57a (56b) Lateral spines with or without one lateral denticle; few large and elliptic scales, if present; pharynx with no bulb. ....58
- 57b (56b) Lateral spines with bifurcate apex and one lateral denticle, or with a sharp apex and 2-3 lateral denticles; if present, numerous, small, keeled scales; pharynx with one bulb.....59

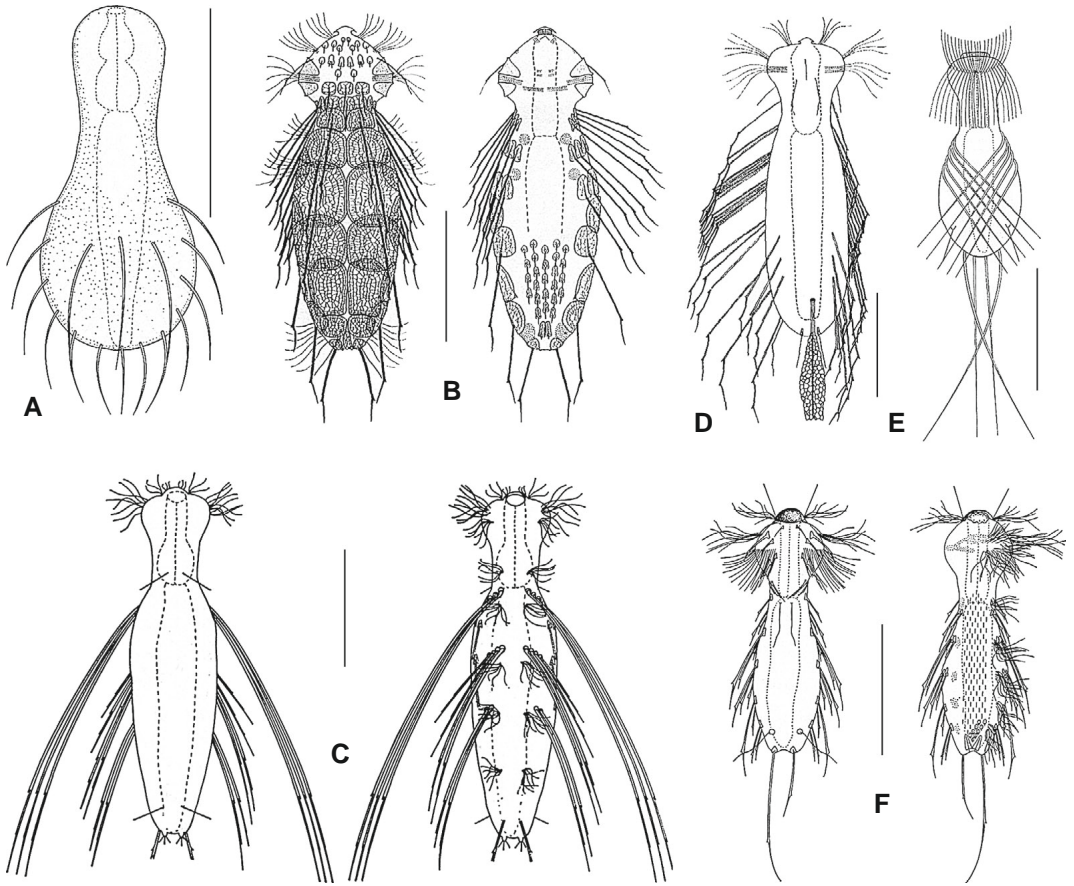


Fig. 14. Chetonotida, Dasydytidae – Representative of the genera *Anacanthoderma* (A), *Ornamentula* (B), *Stylochaeta* (C), *Dasydytes* (D), *Haltidytes* (E), *Setopus* (F). Scale bars = 50  $\mu$ m. A, F, modified from Balsamo (1983); B-E, modified from Kisielewski (1990).

- 58a (57a) Dorsal spines; two caudal spines per side; thick trunk and caudal spines with an evident lateral denticle; a few large dorsal scales with a lace-like surface. .... *Ornamentula* (Fig. 14B)
- 58b (57a) No dorsal spines; one caudal spine per side or none; if very long, the lateral spines are strongly bent at the base gradually becoming thinner up to a hair-like apical portion; spines with or without a lateral denticle. If present, small and weakly keeled scales. .... 60
- 59a (57b) Lateral spines with a sharp apex and 2-3 lateral denticles; scales absent; body end extending into two bristled protuberances. .... *Stylochaeta* (Fig. 14C)
- 59b (57b) Lateral spines with a bifurcate apex and one lateral denticle; scales present; rounded body end. .... *Dasydytes* (Fig. 14D)
- 60a (58b) Caudal spines present or absent; straight, lateral spines of medium length; ventral saltatorial spines absent..... *Setopus* (Fig. 14F)
- 60b (58b) Caudal spines absent; very long, strongly bent lateral spines extending up the dorsal side; ventral saltatorial spines present..... *Haltidytes* (Fig. 14E)
- 61a (41a) Posterior end furcated with two adhesive tubes; cuticular armature made up of keelless spinate scales. Rare, marine: interstitial or infaunal. Uncommon: interstitial or infaunal. .... *Musellifer* (Fig. 15A)

- 61b (41a) Posterior end furcate with four adhesive tube; cuticular armature made up of keel scales. Rare, marine; interstitial. ....  
 ..... *Diuronotus* (Fig. 15B)

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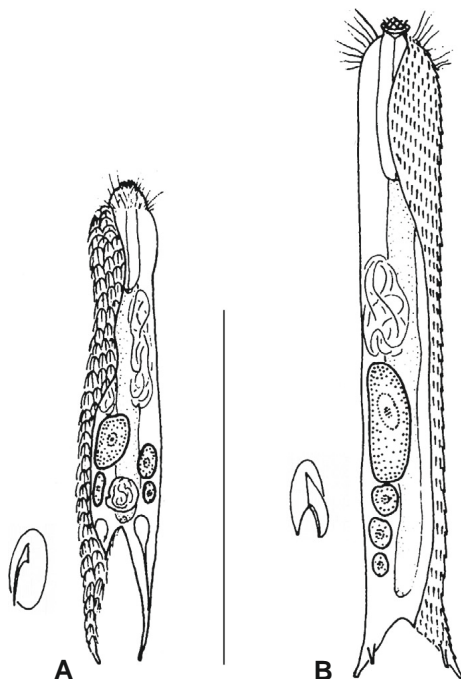


Fig. 15. Chaetonotida, Muselliferidae – Representative of the genera *Musellifer* (A), *Diuronotus* (B). Scale bar = 200  $\mu$ m. A, B, modified from Ruppert (1988).

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# MEIOFAUNA MARINA

Biodiversity, morphology and ecology  
of small benthic organisms

Volume 16

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