ROTIFERA BDELLOIDEA

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Abstract
Bdelloid rotifers are microscopic aquatic animals, generally smaller than 1 mm. They can be found in any water body, but also in mosses, lichens and soil, due to their ability to survive desiccation entering dormancy. Dormant stages can also act as propagules for passive dispersal. These animals are very important in evolutionary biology, as they are the most diverse and old of the 'ancient asexuals'.

The following text is adapted from
Fontaneto, D. & Ricci, C. (2004) Rotifera: Bdelloidea. In: Yule C.M. & Yong H.S. (eds.), Freshwater invertebrates of the Malaysian Region. Academy of Sciences Malaysia, Kuala Lumpur, Malaysia, pp. 121-126.

Additional information on rotifers in general can be found in
Wallace R.L., Snell T.W., Ricci C. & Nogrady T., 2006. Rotifera. Volume 1: Biology, Ecology and Systematics (2nd edition). In: Dumont H.J.F., Guides to the identification of the microinvertebrates of the world. Kenobi Productions and Backhuys Publishers. 299 pp.

An online key for families and genera of monogonont rotifers, limited to the marine habitat is available from
http://www.pfeil-verlag.de/04biol/pdf/mm16_03.pdf

1. Introduction

The Bdelloidea is a class of rotifers that reproduce through ameiotic parthenogenesis only, and that are very common in several aquatic habitats (Donner 1965; Gilbert 1983; Ricci 1992; Mark Welch and Meselson 2000), and they have been named “evolutionary scandals” by Maynard Smith (1986), as they survived and speciated in the absence of sex. Bdelloids have rather uniform morphology and microscopic size (body length between 150–1500 µm). Almost all bdelloids are able to undergo a form of dormancy, called anhydrobiosis, to withstand unfavourable periods in their habitat (Gilbert 1974; Ricci 1987, 1998, 2001). Because of dormancy and parthenogenetic reproduction, several species are though to be cosmopolitan (Fontaneto et al. 2006, 2007a, 2008).

The class Bdelloidea consists of three orders (Adinetida, Philodinavida and Philodinida), four families, 19 genera and about 460 species recognized on morphology only (Donner 1965; Melone and Ricci 1995; Segers 2007).

The name bdelloids is derived from the Greek name for leeches (bdella) which they resemble when creeping on a substrate with leech-like movements. Their body consists of three regions: head, trunk and foot (Fig. 1). The head and foot appear segmented (pseudosegments) and are telescopically retractable into the trunk. A retractable rostrum is present on the head, that is clearly visible when the rotifer is creeping. A peculiar structure of bdelloids is the rotatory apparatus, called the corona, that in this class typically consists of two ciliated discs, the trochi, elevated on retractable pedicels. The cilia of each trochus are arranged along two parallel lines, and surround the ventral mouth opening. Bdelloids use their corona to create currents in water to convey food particles toward the mouth; ciliary beating also allows the rotifer to swim. The corona is developed in the order Philodinida, reduced in size and function in the Philodinavida, and transformed into a ventral ciliated field in the Adinetida (Melone and Ricci 1995). A dorsal antenna is present in all bdelloids. Eyes can be present on the rostrum or the head. A strong muscular pharynx forms the masticatory apparatus and is called the mastax; it consists of hard articulated pieces, trophi (Fig. 2), and the musculature connected to them. In contrast to monogonont rotifers, bdelloids present a unique trophi morphology, called ramate (De Beauchamp 1909; Melone et al. 1998; Melone and Fontaneto 2005). The trunk is the major region, and contains gonads, nephridia and gut, each connected to the dorsal cloaca. The reproductive apparatus consists of paired gonads (germarium), each embedded into a large gland, the vitellarium. Both germovitellaria are lateral to the gut, and eggs or embryos (in viviparous species) can be seen in the trunk. Caudally to it is the foot, with spurs and a number (2–4) of extensible toes, all bearing the openings of pedal glands.

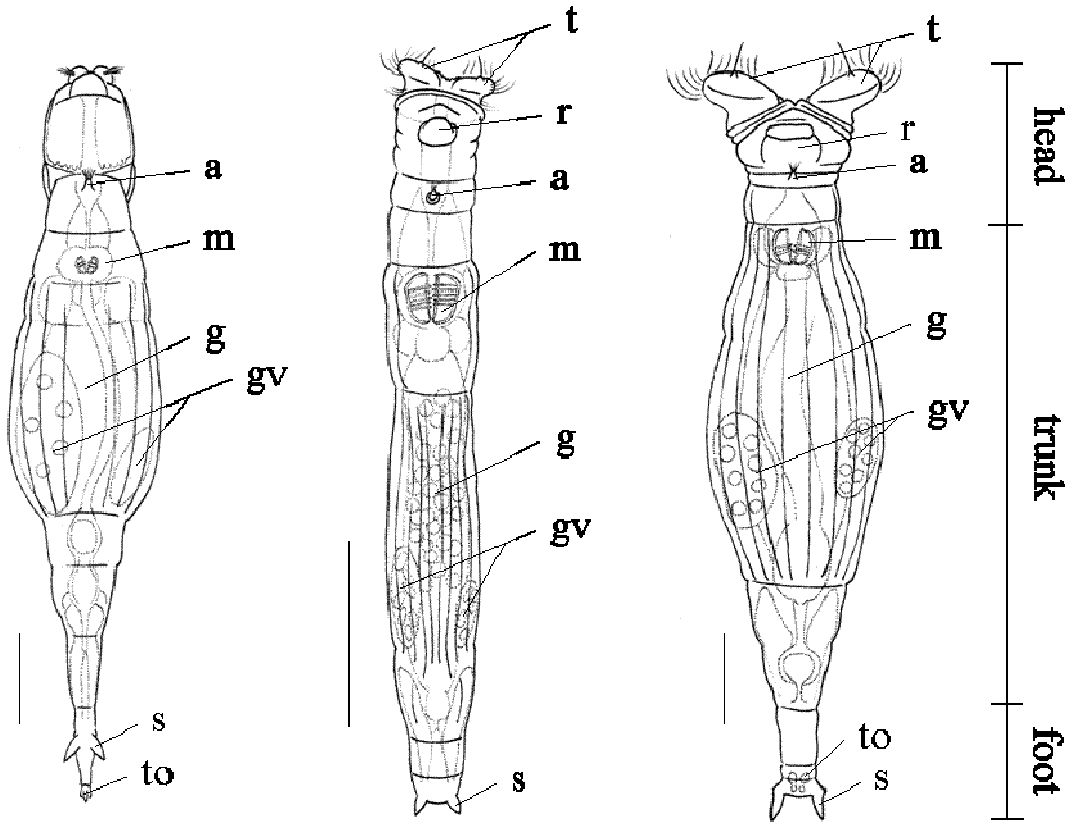

Fig. 1 Examples of bdelloid species: A) *Adineta vaga*, B) *Habrotrocha gracilis*, C) *Philodina vorax*; a, dorsal antenna; g, gut; gv, germovitellaria; m, mastax; r, rostrum; s, spurs; t, trochi; to, toes. Scale bars, 50 µm. (A, C modified from Donner 1965; B modified from Song and Kim 2000).

2. General Biology

Except for one species, *Abrochtha carnivora*, which preys upon other rotifers (Ricci *et al.* 2001), bdelloids feed by filtering or scraping or browsing small food items, such as bacteria, unicellular algae, yeasts or particulate organic matter (Ricci 1984).

Bdelloid rotifers dwell on the bottom of lotic and lentic waters, as well as in the thin water film surrounding soil particles, mosses or lichens. Many bdelloids can swim, but in general only occasionally and for short distances, thus some species can be occasionally found in plankton samples (Pejler and Berzinš 1993). Few bdelloids are epizoic and only one, *Zelinkiella synaptae*, is strictly marine.

Physical and chemical requirements are not well known and spatial and temporal distribution of bdelloids is often patchy and probably depends on food sources (Ricci and Balsamo 2000).

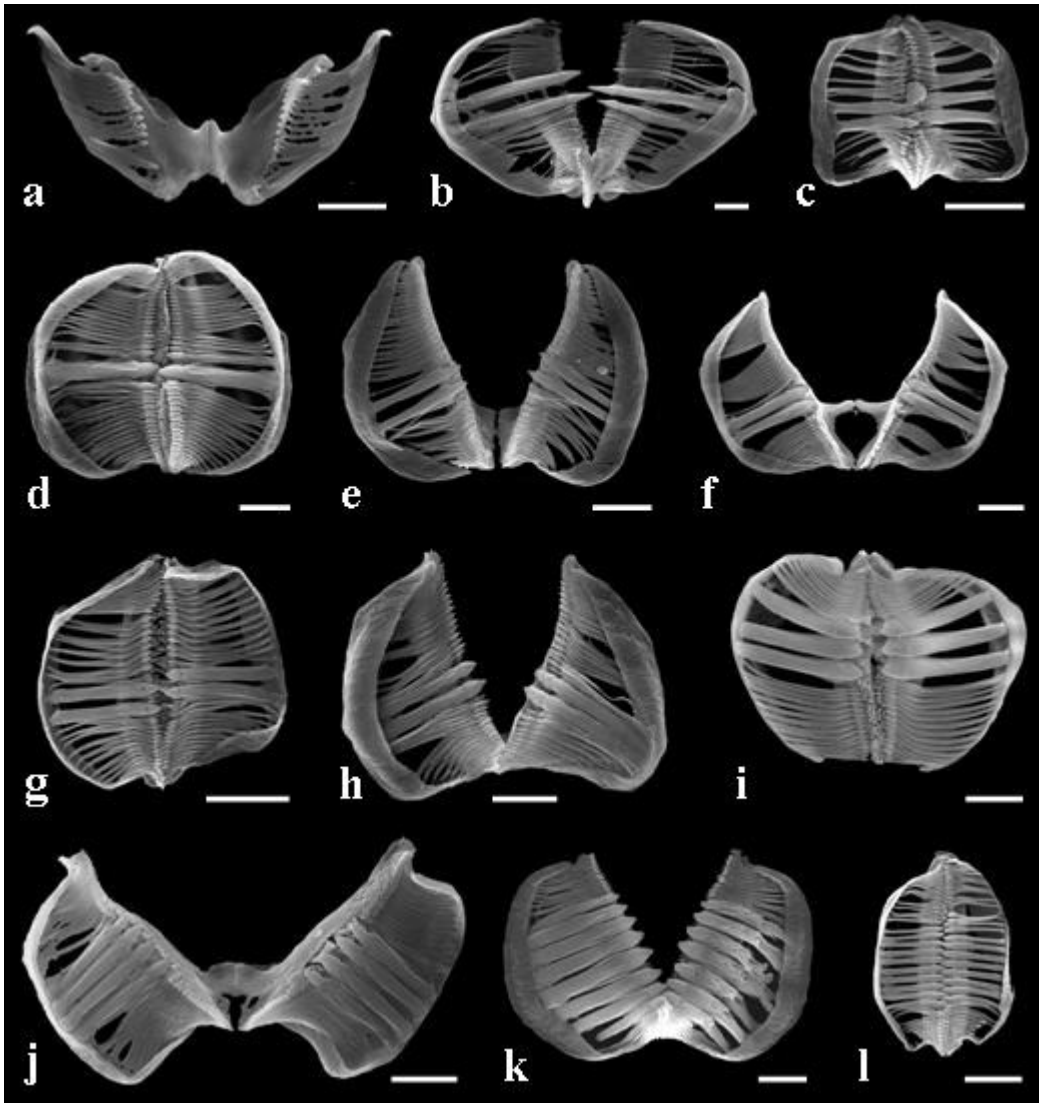

Fig. 2 SEM pictures of trophi of bdelloid rotifers in cephalic view: a-b, Philodinavida; c, Adinetida; d-l, Philodinida; a, *Henoceros falcatus*; b, *Abrochtha carnivora*; c, *Adineta steineri*; d, *Anomopus telphusae*; e, *Macrotrachela crucicornis*; f, *Philodina citrina*; g, *Pleuretra reticulata*; h, *Zelinkiella synaptae*; i, *Dissotrocha aculeata*; j, *Didymodactylos carnosus*; k, *Mniobia magna*; l, *Otostephanos donneri*. Scale bar = 5 µm. (Modified from Melone and Fontaneto 2005)

3. Life Cycle

Under laboratory conditions, their life cycle is about 30 days, during which they can lay 30–40 eggs (Ricci 1983). Life span in the field is unknown. In response to disturbance (e.g. evaporation of environmental water) bdelloids enter anhydrobiosis, and will resume activity when the habitat conditions become suitable again. The rate of recovery depends upon species (Ricci 1998), length of desiccation period (Caprioli and Ricci 2001) and rotifer age

(Ricci 1987; Örstan 1995; Orsenigo *et al*. 1998). In any case, dormancy represents a blind period in the bdelloid life, because they will resume their life without considering the time spent dormant. It seems that some species do really need to become dormant from time to time: constantly stable conditions seem to drive laboratory cultures to decline (Ricci 2001).

4. Collection and Specimen Preparation

Bdelloid rotifers may be found in the plankton and periphyton, and as interstitial fauna or psammon. Planktonic and littoral bdelloids are collected by dragging a plankton net (mesh size: 25-50 µm) through the open water, submerged vegetation, littoral macrophytes or algae. Bdelloids inhabiting periphyton may be collected using a flexible collecting tube attached to a large syringe. Alternatively, plant material, debris and algae can be squeezed over a plankton net. Creeping animals can be collected by scraping various substrata. Psammon is collected with coring devices, dredges etc., or simply by scraping the uppermost centimetres of sand with a vial. The sand is consequently mixed with water, and after momentary settling the water is decanted through a plankton net. At the shore, samples taken below the mean water level, and especially in the intertidal zone, will yield some bdelloid rotifers. Quantitative sampling is possible, although difficult, and we suggest to follow the recommendations by Wallace & Ricci (2002). Higgins & Thiel (1988) and Giere (1993) can also be consulted, as methods developed for other microscopic or small organisms can be applied to rotifers as well. After collection, samples have to be quickly transferred unaltered to the laboratory for examination.

Many bdelloid rotifers live among mosses, lichens, roots and soil. Samples can be collected dry, stored for a long time, and then re-hydrated in the lab to obtain living animals. Recovery success after long periods of dehydration may be scarce; thus, it is always better to look at the samples as soon as possible. To re-hydrate dry samples, put a small piece of moss in a petri dish and add distilled water; after few minutes some bdelloids will start moving, recovering from anhydrobiosis. These animals can be collected and analysed.

Trophi can be observed by microscope at high magnification, squeezing the animals under a coverglass. However, for a more detailed examination preparation of trophi is necessary. This can be done by adding a small drop of NaOCl, which will dissolve soft tissues and enhance recognizability of trophi features. For details on SEM preparation follow De Smet (1998) and Segers (2004), or consult the rotifer trophi web page (http://users.unimi.it/melone/trophi).

5. Key to Bdelloidea Families and Genera

Only careful observation of living specimens allows appropriate identification of bdelloid species. Most of the taxonomically important features are poorly detectable, or not visible, in contracted specimens and can only be seen in active animals. Thus the use of preserved samples for listing bdelloid species is useless. Two keys to species are available (Bartoš 1951; Donner 1965); other keys relate to generic identification, and among them a useful pictorial key has been produced recently (Ricci and Melone 2000).

Because of obligate parthenogenesis, the species of bdelloids are strictly 'morphospecies', even if, quite surprisingly for such a group of understudied animals, clusters from molecular analyses and from geometric morphometrics analyses of the shape and size of trophi well match traditional species (Fontaneto et al. 2007b). In contrast to monogonont rotifers, trophi morphology of bdelloids is rather uniform and cannot be used for species identification. No extensive revision of the established bdelloid taxonomy has been done so far.

The following taxonomic key considers all bdelloid families and genera known in freshwater habitats.

1. Trophi (jaws) close to mouth opening; can be extruded when the animal is feeding……..……..**Philodinavidae 2**
   Trophi deep in the oesophagus, not extruded when feeding……..……..…...**4**

2.(1) Corona with trochi (ciliated discs) elevated on pedicels…..…….....*Abrochtha*
   Corona reduced to small ciliated field, no trochi visible…….……...**3**

3.(2) Foot with 2 short spurs…...…….....*Philodinavus*
   Foot with 1 spur and 4 big toes……..*Henoceros*

4.(1) Corona modified to a ventral ciliated field with no trochi…..……..**Adinetidae 5**
   Corona with trochi elevated on pedicels……..……..……**6**

5.(4) Foot long and extensible, with 3 toes and 2 spurs……..……..*Adineta*
   Foot short with several papillae on the posterior border of the penultimate pseudo-segment……..……..……*Bradyscela*

6.(4) Stomach without visible lumen and with round pellets within its wall. Pedicels of trochi are often very close each other……..…….....**Habrotrochidae 7**
   Stomach with thick walls, with a lumen and not completely filled with round pellets…….....**Philodinidae 9**

7.(6) Upper lip with remarkably large lobe, that partially covers the trochi……..……..*Scepanotrocha*
Upper lip normally developed, trochi visible……...**8**

8.(7) Each trochus has a transversal cuticular ring, ventrally and dorsally incomplete...……..……*Otostephanos*
Trochi without cuticular ring..……*Habrotrocha*

9.(6) Foot without toes……...……**10**
Foot with toes……...……..**11**

10.(9) Foot shorter than one half as trunk length……*Mniobia*
Foot longer than one half as trunk length; often epizoic…..…….*Anomopus*

11.(9) Foot with 2 toes……..……*Didymodactylos*
Foot with 3 toes……..…….…….....**12**
Foot with 4 toes……..…….....**14**

12.(11) Corona with horn-shaped lateral projections..……..…..…..*Ceratotrocha*
Otherwise……..…….……**13**

13.(12) Viviparous, often eye-spots on rostrum; rostrum extended also when swimming…..……..*Rotaria*
Oviparous, eye-spots commonly absent.……*Macrotrachela*

14.(11) Viviparous……...…….……...**15**
Oviparous……..……...…….……**16**

15.(14) Integument sculptured……..……...……..……..*Dissotrocha*
Integument smooth…….……*Embata*

16.(14) Integument thick and sculptured; eye-spots not evident...……..*Pleuretra*
Integument thin and smooth; eye-spots, when visible, on brain……*Philodina*

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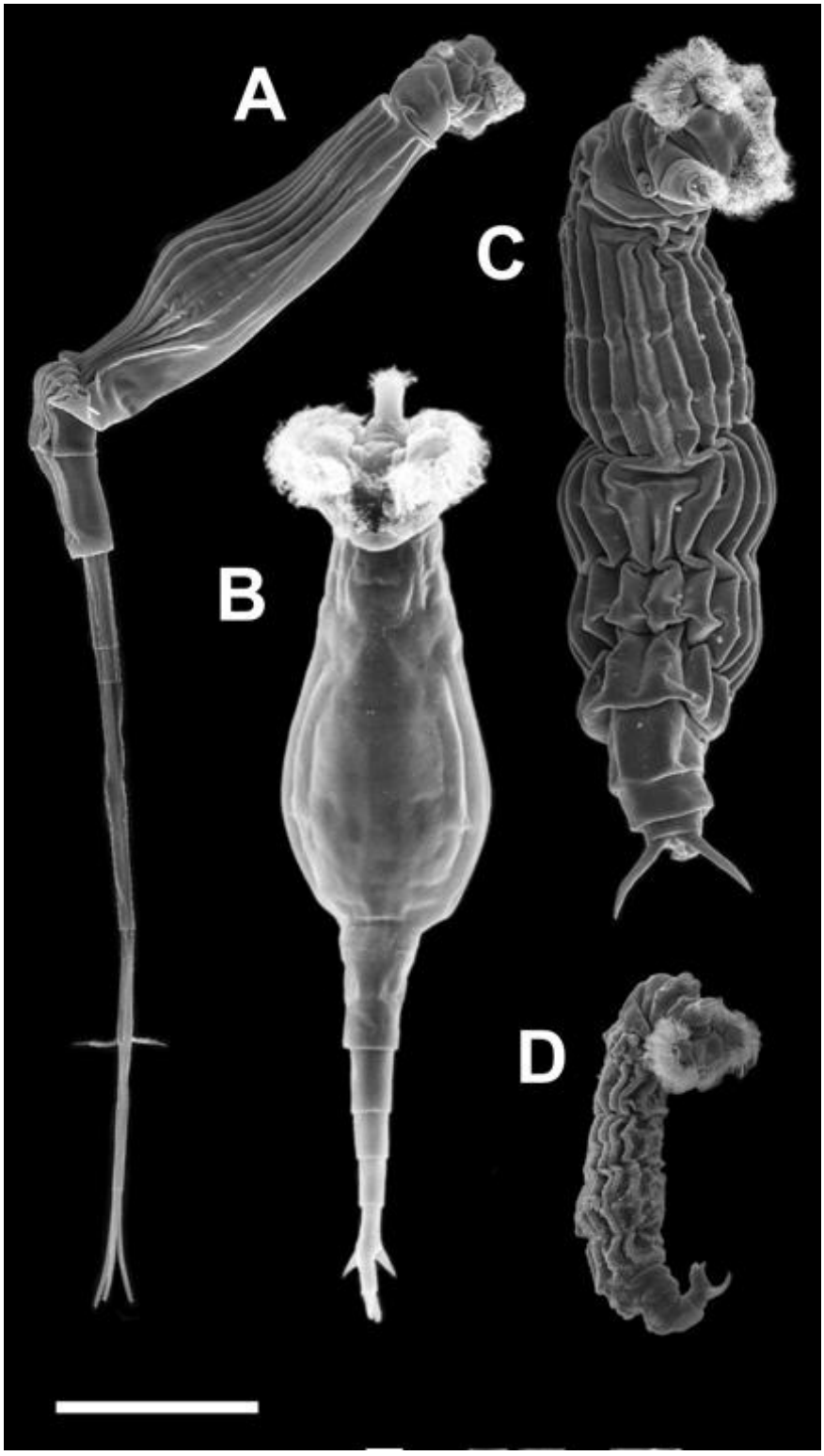
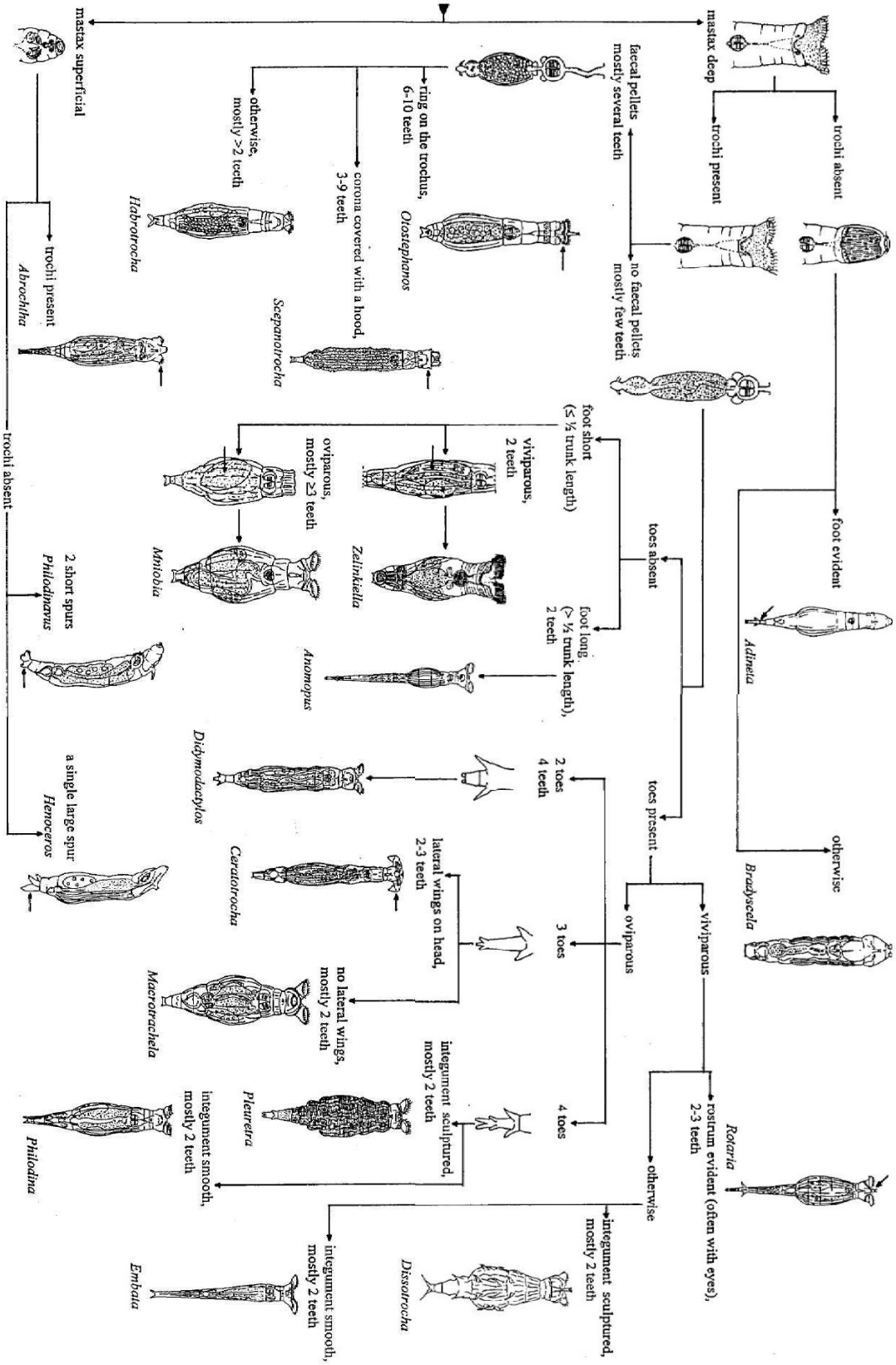


Scanning Electron Microscopy pictures of animals of the genus *Rotaria*: (A) *R. neptunia*, (B) *R. macrura*, (C) *R. tardigrada*, (D) *R. sordida*. (Modified from Fontaneto et al., 2007b).



Pictorial key to the genera of bdelloid rotifers (modified from Ricci & Melone, 2000)