Rotifera

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2 authors:

Diego Fontaneto
Italian National Research Council

Willem H. De Smet
University of Antwerp

Diego Fontaneto and Willem H. De Smet

4 Rotifera

4.1 Introduction

Rotifera comprise about 2,000 species (Segers 2007) of microscopic animals, usually much less than 1 mm in length, characterized by the presence of a ciliated corona and a muscular pharynx called mastax (Wallace et al. 2006). Traditionally, 3 groups are recognized in Rotifera: Bdelloidea, Monogononta, and Seisonacea. Each group is peculiar for general morphology and ecology, but mostly for reproductive modes: Seisonacea are exclusively sexual and live as epibionts on the crustacean *Nebalia*; Monogononta are facultative cyclical parthenogens, free-living in freshwater and marine waters (Wallace et al. 2006); Bdelloidea are obligate parthenogens living in any wet or moist habitat, capable of surviving desiccation through dormancy (Ricci & Fontaneto 2009).

The position of Rotifera in the tree of life is clear: they belong to the spiralian clade Platyzoa, together with Platyhelminthes, Gnathostomulida, Gastrotricha, Micrognathozoa, and Acanthocephala (Dunn et al. 2008, Hejnol et al. 2009, Edgecombe et al. 2011). But the relationships among the groups of Rotifera, i.e., Bdelloidea, Monogononta, and Seisonacea, are not clear at all, as their relationships with Acanthocephala (see Section 4.5, Phylogeny).

Rotifera can be found in any habitat where water becomes available, even for short periods, due to their peculiar ability to produce dormant stages that resist absence of water (Gilbert 1974, Ricci 2001). The mechanisms through which resting stages are produced and survive in the absence of water are different between Bdelloidea and Monogononta, whereas no resting stages are known for Seisonacea. Dormancy makes these animals an interesting model system to understand the mechanisms of desiccation resistance, freeze tolerance, starvation, survival in extreme environmental conditions, and ageing (King 1969, Pouchkina-Stantcheva et al. 2007, Hilhorst 2008, Austad 2009, Snell et al. 2012). Moreover, the ability to recover after dormancy involves mechanisms that restore living conditions, including the potentials for repairing DNA and the resistance to ionizing radiation (Gladyshev & Meselson 2008).

Another very peculiar feature of Rotifera is their asexual reproduction (Schön et al. 2009); Monogononta are cyclical parthenogens, whereas Bdelloidea are strictly parthenogenetic. Bdelloidea have even been framed as “evolutionary scandal” because they evolved and diversified in the absence of sexual recombination (Maynard Smith 1986, Judson & Normark 1996). The aspects of asexuality are very intriguing (Fussmann 2011), and Bdelloidea are known to have rather peculiar mechanisms to counteract the problems of strictly asexual reproduction (Gladyshev et al. 2008, Wilson & Sherman 2010).

Rotifers are used in aquaculture (Lubzens 1987, Lubzens et al. 1989) where mass production has been developed (Hagiwara et al. 1997) to provide live food for fish fry, and as model organisms for ecotoxicology (Ramírez-Pérez et al. 2004, Dahms et al. 2011). Most of the experimental work performed on rotifers is based on species that have been cultured for aquaculture or for ecotoxicology, so that a great deal of information is available for the *Brachionus plicatilis* species complex, the most widely cultured of all rotifers.

Rotifer research started with the first microscopist, Anthony van Leeuwenhoek (1632–1723), who described a Bdelloidea in one of his letters from 1687 (Wallace et al. 2006). Since its origin, the history of rotifer research has had 2 main aspects. On the one hand, there are lines of research that focus on the organisms and try to understand rotifers in themselves; on the other hand, scientists from several branches of science work using rotifers as a model system to answer questions of broad interests. The history of rotifer research is, thus, a continuous mingling of these 2 complementary approaches. The rotifer meetings, held every 3 years since 1976, are a combination of different focuses and provide a great avenue for interaction among rather different scientists with different approaches, gathered together by the interest for this fascinating group of animals. The proceedings of these meetings are usually published in *Hydrobiologia*, and we will continuously refer to papers from such meetings throughout the text.

4.2 Morphology

While various investigators contributed to the knowledge of morphology and anatomy of rotifers following their description by van Leeuwenhoek, the start for the great advance in anatomy and histology was given by Zelinka (1886, 1888, 1891, 1892a, b), who introduced histological techniques, e.g., the use of microtome-cut sections. Zelinka studied different organ systems, especially the nervous system of bdelloids, discovered the mastax and caudal ganglion, and revealed the course of the major nerves and branching-off nerves until their endings. Superior pioneering anatomohistological work was done by de Beauchamp, dealing with the retrocerebral apparatus (de Beauchamp 1905, 1906), corona (de Beauchamp 1907a), integument, intestinal system (de Beauchamp 1907a, b, 1909), and mastax (de Beauchamp 1908, 1909) of all rotifer orders. Eutely was first demonstrated for the brain of *Epiphanes, Eosphora, Euchlanis*, and *Notommata* by Hirschfelder (1910) and later on for different organs in *Epiphanes senta* by Martini (1912) and *Asplanchna priodonta* by Nachtwey (1925). The latter authors and Hlava (1905), Lehmensick (1926), Seehaus (1930), Waniczek (1930), Peters (1931), Stossberg (1932), Remane (1933), Dehl (1934), Brakenhoff (1937), to mention a few (for a review of studies prior to 1929, see Remane 1933), made painstakingly detailed studies of the different organ systems that are still reliable at large. An important synoptic work on rotifer morphology and anatomy was presented by Remane (1929) and followed by his classical and impressive work published between 1929 and 1933 (Remane 1933). Further comprehensive reviews are by, e.g., Hyman (1951), de Beauchamp (1965), and Wallace et al. (2006). Specific morphoanatomical information on the different groups of rotifers are presented in the works dealing with taxonomy and identification keys (e.g., Bartoš 1951, Bdelloidea; Voigt 1957, Bdelloidea and Monogononta; Donner 1965, Bdelloidea; Kutikova 1970, Monogononta; Koste 1978, Monogononta; Kutikova 2005, Bdelloidea); an update for several families is presented in the more recent identification guides (Segers 1995, Nogrady et al. 1995, De Smet 1996, De Smet & Pourriot 1997, Nogrady & Segers 2002).

In the past 25 years, several new techniques were introduced for the study of rotifer organ and cellular organization. Ultrastructural investigations using transmission electron microscopy (TEM) and/or scanning electron microscopy (SEM) were performed on the different organ systems (e.g., Clément & Wurdak 1991, Clément 1993, Melone 1998, Riemann & Ahlrichs 2010). Detailed study of the structure of the trophi became possible by SEM (e.g., Markevich 1989, Kleinow et al. 1990, De Smet, 1998, Melone et al. 1998a). Immunohistochemistry, epifluorescence, and confocal laser scanning microscopy (CLSM) was used to investigate the nervous system (e.g., Kotikova 1995, 1998, Hochberg 2007, 2009, Leasi et al. 2009), and epifluorescence and CLSM were likewise used to study musculature (e.g., Hochberg & Litvaitis 2000, Santo et al. 2005, Sørensen 2005a, b, Hochberg & Ablak Gorbuz 2008, Leasi & Ricci 2010).

4.2.1 General and external morphology

Descriptions of rotifer species refer to the females (if not otherwise stated), as males are absent in Bdelloidea and are smaller and of much simpler organization in Monogononta, and moreover have been rarely investigated.

4.2.1.1 Morphology of the female

The body shape is enormously diverse, but generally bilaterally symmetrical, with a clear differentiation between both ends and between the ventral and the dorsal sides (Fig. 4.1). Usually, there is a head, trunk, and foot more or less clearly marked off by transversal folds. The foot is always located behind the cloacal aperture, which allows its localization even when the trunk grades imperceptibly into the foot. The body often appears segmented due to the presence of permanent transversal folds in the integument. These are considered pseudosegments, as there is no true segmentation in rotifers. A pseudosegment marked off between head and trunk, called neck, is often present. Head and foot are usually retractable into the trunk. The head bears the characteristic rotatory apparatus or corona, used for locomotion and/or food collection by its cilia, and the mouth and several sense organs, including sensory bristles and pits, eyespots, ciliated tentacles, and one or more dorsal antennae. The apical region can be provided with palps (e.g., *Gastropus*), ciliated auricles (e.g., *Notommata, Synchaeta*), a retractile (*Colurella, Lepadella*) or non-retractile shield (e.g., *Squatinella, Cotylegaleata*), a snout-like process or proboscis (*Rhinoglena*), apical tentacles (e.g., *Collotheca hoodi, Ptygura pectinifera*), a cup-shaped sucker-like structure (*Cotylegaleata*), a projecting rostrum, etc. The rostrum of the monogononts is a dorsal hood-shaped structure, usually offset by a fold, at the anterior end of the body (e.g., many Dicranophoridae); the apertures of the retrocerebral organ lie ventral to the rostrum. The rostrum (proboscis) of the bdelloids (Fig. 4.2) is a complex, unpaired and retractable, blunt-conical organ with ciliated tip provided with styli, and lamella(e). It is usually composed of 2 pseudosegments, often bearing the apertures of the retrocerebral organ and eyespots when present (e.g., most *Rotaria, Adineta oculata*). When

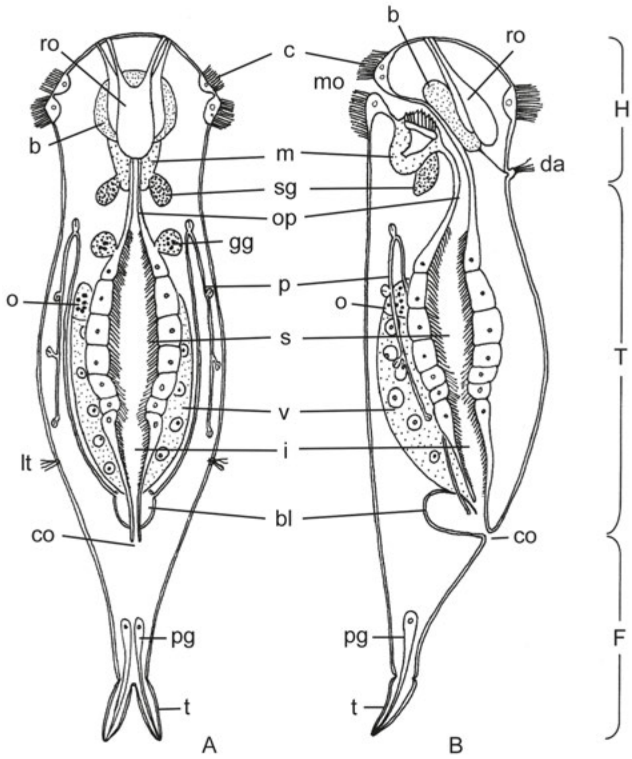

Fig. 4.1: Scheme of the rotifer anatomy. (A) Dorsal and (B) lateral. Abbreviations: H, head; T, trunk; F, foot; b, brain; bl, bladder; c, corona; co, cloacal opening; da, dorsal antenna; gg, gastric gland; i, intestine; lt, lateral antenna; m, mastax; p, protonephridium; o, ovarium; pg, pedal gland; ro, retrocerebral organ; s, stomach; sg, salivary gland; v, vitellarium. (Modified from Wallace & Ricci 2002.)

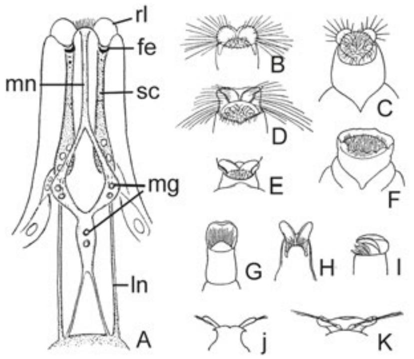

Fig. 4.2: The rostrum of Bdelloidea. (A) *Rotaria macroceros*, (B) *Philodina acuticornis*, (C) *Mniobia incrassata*, (D) *Philodina brevipes*, (E) *Adineta grandis*, (F) *Zelinkiella synaptae*, (G) *Macrotrachela natans*, (H) *Habrotrocha angusticollis*, (I) *Embata hamata*, (J) *Adineta* cf. *barbata*, and (K) *Adineta barbata*. Abbreviations: fe, frontal eye; ln, lateral rostral nerve; mg, medial rostral ganglion; mn, medial rostral nerve; rl, rostral lamella; sc, sensory cell. (Modified from Remane 1933.)

the corona is withdrawn, the rostrum is extended, forming the frontal part of the head; with unfolded corona, it is retracted, becoming dorsal. The bdelloid rostrum is involved in tactile perception and locomotion: during creeping, the rostrum is brought in contact with the substrate and used for adhesive attachment, producing leech-like movements (e.g., Hochberg & Litvaitis 2000).

The head encloses the brain, the glandular retrocerebral organ, and often part of the mastax. The trunk may be cylindrical, fusiform, sacciform, ovate, spherical, etc. In cross section, it is circular, triangular, laterally enlarged, or compressed to various degrees, both dorsoventrally or laterally. The ventral surface is often more or less flattened, and the dorsal one is mostly more or less strongly arched. In Trichocercidae, the cylindrical body is spirally twisted to the left. The posterodorsal end of the trunk is often extended into a more or less prominent projection or tail, overhanging the cloacal aperture. The tail may be unlobed, bilobed, trilobed, or extended into a conical (*Notommata tripus*) or spiniform process (*Proalinopsis staurus, Dorystoma caudatum*). The trunk bears the lateral antennae (lacking in bdelloids), usually situated distally on either side, but displaced to the coronal field in Conochilidae; in *Testudinella*, the trunk carries the dorsal antenna as well. The integument can be smooth, but in species with stiffened integument or lorica, it often exhibits a great variety of ornamentation, such as longitudinal or transversal ridges or furrows, punctuations, spines, pustules, tubercles, polygonal or circular fossettes, etc.; the different adornments can be arranged in a way to make larger polygonal (e.g., *Keratella, Platyias, Trichotria*), longitudinal (e.g., *Notholca*), or transversal (e.g., *Lophocharis*) patterns on the lorica. SEM of the tegument surface reveals numerous pores on small elevated areas (Ricci & Melone 1984, 1998a). The trunk of many species is provided with movable or nonmovable projections or appendages serving different functions. Projections occur at the anterior and posterior margins of the trunk, on the dorsal surface, or along the entire body (except the ventral surface), and less frequently on the head and foot. Spines enhance buoyancy of planktonic species (e.g., *Brachionus, Keratella, Kellicottia*) and serve as defense mechanism against being swallowed by predators (e.g., *Brachionus, Keratella*; see Section 4.4, Physiology). In bdelloids (e.g., *Pleuretra hystrix*), spines help to anchor to the substrate (Fontaneto & Melone 2003). Paddles (*Polyarthra*), arm-like appendages bearing stiff bristles (*Hexarthra*), and movable setae (*Filinia*), all with strong muscles inserted at their base, serve for jumping locomotion to escape predators, or for predator deterrence (e.g., Stemberger & Gilbert 1987, Gilbert 1999). *Asplanchna* enhances protection against gape-limited predators by an increase of size, expanding soft portions of its integument into lateral outgrowths, through an increase of the hydrostatic pressure of its pseudocoel. Two large, dorsal conical outgrowths behind the corona in *Synchaeta bicornis* and *S. fennica* are supposed to compensate, by an increase of their volume, for the increased internal pressure upon contraction of the body (Remane 1929). In *Philodina alata*, a similar function may be attributed to the paired muscularized lateral outgrowths, obvious only in contracted animals. The trunk contains the gastrointestinal, excretory, and reproductive organs.

A foot is usually present, and in most species, it is located at the end of the trunk, but it may be displaced ventrally (e.g., *Gastropus, Ploesoma, Testudinella*) or twisted out of the body axis (e.g., *Trichocerca*). In planktonic monogononts, the foot is mostly absent (e.g., *Asplanchna, Ascomorpha, Horaella, Notholca, Filinia, Keratella, Pompholyx, Trochosphaera*). The foot may be very short to very long and is usually composed of a few to many telescopically retractable pseudosegments, or it is cylindrical with a ringed or wrinkled appearance (e.g., *Brachionus, Ptygura, Testudinella*). The foot is generally partly to completely retractable in the trunk. In soft-bodied rotifers, it can be simply withdrawn into the body, or in species with a stiffened, almost inflexible lorica, the foot is retracted through the foot opening. In sessile species (Flosculariidae, Collothecidae), the foot of adult females is mostly very long and modified into a contractile stalk that may terminate in a non-contractile, narrow columnar pedicel. A short discoid foot is shown by *Cupelopagis*. In most Ploima, a caudal antenna is usually present dorsally on the distal pseudosegment. The foot contains the pedal glands producing adhesive secretions and terminates in the attachment organs, such as 1–4 toes, an adhesive disc, or a ciliated ring. Toes may be absent (e.g., *Asplanchna, Ascomorpha, Conochilus, Horaella, Notholca, Filinia, Keratella, Pompholyx, Trochosphaera*) or vestigial (e.g., *Proalides, Synchaeta monopus*), especially in the planktonic species. Size, shape, and structure of the toes show a huge range of morphological variation and adaptations in monogonont Ploima (Fig. 4.3). Most of the ploimid genera have 1 to 2 symmetrical toes; unequal toes are present in *Monommata* and *Trichocerca*. An additional spur can be present between the toes (e.g., *Squatinella rostrum, Trichotria pocillum*) or laterally from each toe (*Cotylegaleata*) and 2–8 needle-shaped substyli at the base of the toes are characteristic in *Trichocerca*. The toes may be very long and surpass the length of the body (*Beauchampiella, Monommata, Scaridium*). They may be conical, lanceolate, leaf-shaped, needle-shaped, etc., and straight or curved. They are generally not pseudosegmented but are often provided with an offset distal part, the claw (e.g., *Cephalodella, Dicranophorus, Lecane*); the toe(s) of some *Lecane* species show up to 3 pseudosegments. Depending on the stiffening of their integument, toes can be flexible (e.g., *Lindia, Notommata, Synchaeta*) or rigid (e.g., *Trichotria, Mytilina, Lecane*); in some species, there is a rigid basal part and a soft distal part (e.g., *Encetrum frenoti, Notommata pachyura*). Attachment of adults of the sessile Floscularidacea and Collothecacea is by an adhesive disc, or the end of the foot is undifferentiated, whereas their juvenile stages have a ciliated ring at the end of the foot; the foot of the adult free-swimming *Testudinella* bears a ciliated cup.

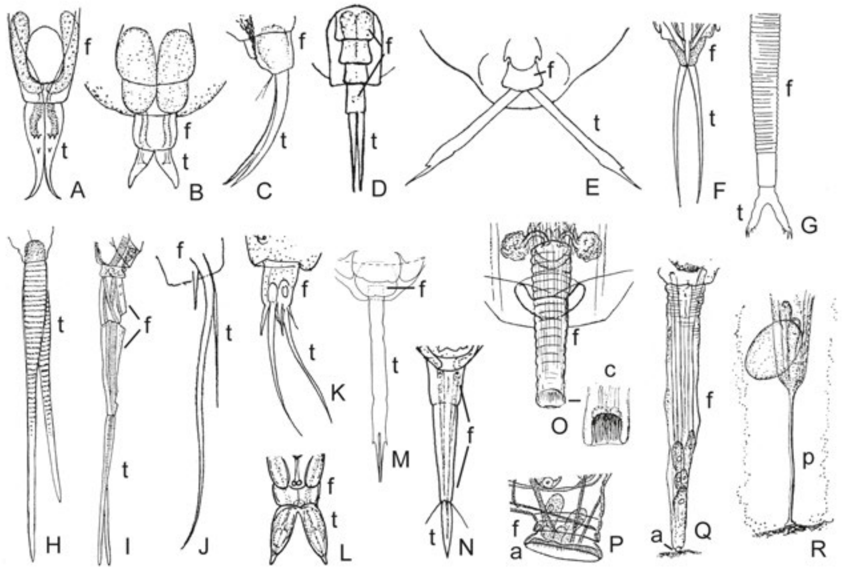

Fig. 4.3: Variation of the foot and toes in Monogononta. (A) *Cephalodella forficula*, (B) *Notommata voigti*, (C) *Cephalodella gibba*, (D) *Lepadella* sp., (E) *Lecane luna*, (F) *Dicranophoroides caudatus*, (G) *Brachionus diversicornis*, (H) *Monommata* sp., (I) *Scaridium longicaudum*, (J) *Trichocerca pusilla*, (K) *Trichocerca tigris*; (L) *Dicranophorus cambari*, (M) *Lecane bulla*, (N) *Microcodon clavus*, (O) *Testudinella* sp., (P) *Cupelopagis vorax*, larva, (Q) *Collotheca* sp., and (R) *Collotheca* sp. Abbreviations: a, adhesive disc; c, ciliated cup; f, foot; p, non-contractile pedicel; t, toe. (From Donner 1956, Koste 1978, Kutikova 1970, Wulfert 1957.)

Variation in morphology of the toes is lower in bdelloids (Fig. 4.4). Toes in bdelloids are generally short, conical, and flexible, and their number is 2, 3, or 4: a pair of ventral toes (*Didymodactylos*), a single dorsal toe, and a pair of ventral ones (e.g., *Macrotrachela, Rotaria, Adineta*), or a pair of smaller dorsal and a pair of larger ventral toes (e.g., *Dissotrocha, Philodina, Philodinavus*). Toes may be lacking, and attachment is by an undivided (e.g., *Anomopus, Zelinkiella*) or cleft adhesive disc (e.g., *Mniobia*). The penultimate foot pseudosegment carries dorsally or dorsolaterally 2 appendages, the spurs, characteristic of most bdelloids; *Henoceros* only shows a single dorsal spur. Depending on the structure and function of the foot and its toes, the following types are recognized in rotifers: creeping foot: foot and toes short, few pseudosegments (Notommatidae, Bdelloidea); swimming foot: foot long cylindrical and unsegmented or with several long pseudosegments (e.g., *Brachionus, Testudinella, Rotaria neptunia*) or foot short with long toes used for steering when swimming (e.g., *Euchlanis, Cephalodella*, Trichocercidae); jumping foot: pseudosegments and/or toes very long, provided with strong muscles (*Beauchampiella, Monommata, Scaridium*), used for, e.g., escape reactions; sessile foot: long retractile foot, often with adhesive disc (sessile Flosculariidae, Collothecidae).

Most rotifers are colorless and very transparent, but transparency may be reduced in species with a thick granulated lorica. Rotifers often appear colored by the content of the digestive system because of the pigments ingested with the food (brownish, greenish), or presence of symbiotic zoochlorellae (green). In a few species, whole animals or distinct organs are colored because of their own pigments. A red coloring is most common, especially in species inhabiting the Arctic-alpine environment (e.g., *Philodina gregaria*), and shades of yellow, brown, violet, and dark blue occur in the diverse taxa.

Several rotifers secrete protective sheaths or tubes (see Section 4.2.2, Integument).

4.2.1.2 Coloniality

Some 25 species belonging to 8 genera of mostly sessile monogononts (Flosculariidae, Conochilidae) form permanent colonies varying in size from a few individuals to 3,500 animals (see Wallace 1987, Wallace et al. 2006). Colony formation can be allorecruitive, autorecruitive, or geminative. In the allorecruitive colony formation, the free-swimming solitary juveniles settle on the tubes of conspecifics, forming an arborescent colony (e.g., *Limnias ceratophylli, Floscularia conifera, F. ringens*). When the juveniles remain within the parental colony, the latter will reach a critical size, and subsequently splits up into 2 or more daughter colonies (autorecruitive colony formation in, e.g., *Conochilus hippocrepis* and *C. unicornis*). The colonies are spherical, with the individuals radiating from the centre, each animal having its own mucous tube (*C. unicornis*), or the tubes coalescing into a single spherical mass (*C. hippocrepis*). In the geminative colony formation, newborns leave the parent colony together as a planktonic juvenile colony (e.g., *Lacinularia flosculosa, Sinantherina socialis*). The sheath-forming bdelloid *Rotaria macroceros* often aggregates in large numbers sticking together.

4.2.1.3 Corona

The basic organization of the corona was elucidated by light microscopy (LM) (de Beauchamp 1907a, 1908, 1965, Remane 1933) and later on largely confirmed

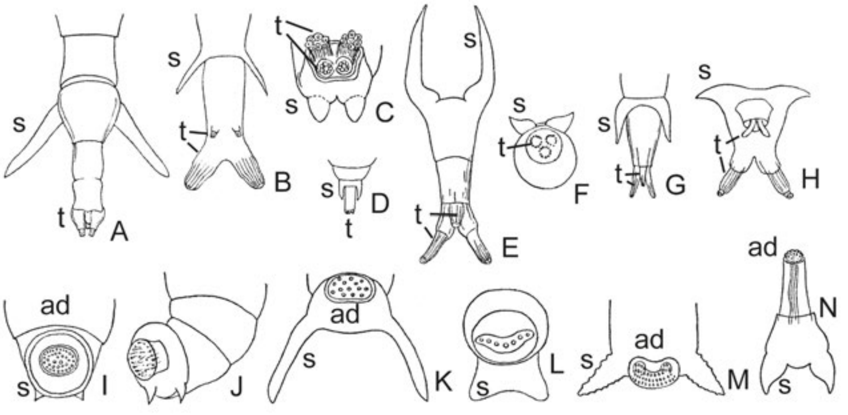

Fig. 4.4: Variation of the foot, toes (t), adhesive discs (ad) and spurs (s) in Bdelloidea. (A) *Rotaria socialis*, (B) *Philodina gregaria*, (C) *P. flaviceps*, (D) *Habrotrocha pavida*, (E) *Macrotrachela crucicornis*, (F) *M. asperula*, (G) *M. muricata*, (H) *Embata hamata*, (I, J) *Zelinkiella synaptae*, (K) *Mniobia circinata*, (L) *M. obtusicornis*, (M) *M. russeola*, and (N) *M. armata*. (From Remane 1933.)

by SEM in its essential outlines (e.g., Clément & Wurdak 1991, Melone & Ricci 1995, Melone 1998, Ricci & Melone 1998a). The ground plan of the corona (Fig. 4.5) comprises a ciliated area, the buccal field, surrounding the usually ventrally located mouth opening. The buccal field is evenly ciliated with short cilia. It extends upward around the head and forms a circumapical band, delimiting an unciliated apical field. The cilia of the ciliary ring at the anterior margin of the circumapical band are strong and form the preoral trochus – a ciliary row of usually finer cilia at the posterior margin forms the postoral cingulum. Between the trochus and the cingulum runs a finely ciliated groove. The apical field bears numerous sensory receptors and is often provided with setae and tufts or rows of cilia (styli, cirri, membranelles).

When the circumapical band consists only of a single row of cilia, forming a preoral or postoral ciliary ring with the anterior or posterior margin of the buccal field, it is called paratrochus and paracingulum, respectively. Ciliary rings or arcs formed only by the preoral part of the buccal field are called pseudotrochus. The corona is absent in the parasitic genus *Balatro*.

In many species, the marginal cilia of the circumapical band are elongated and often situated on a pair of lateral ear-like projections (Fig. 4.6), the auricles (e.g., *Lindia, Notommata, Synchaeta, Tetrasiphon*). Auricles are expanded and assist when swimming; they can be withdrawn in the head when creeping (*Notommata*). In monogononts, the distal part of the corona on which the cingulum inserts can be developed into a prominent pad or fold, the under lip (e.g., *Hexarthra, Filinia*); in bdelloids, both under and upper lips are present.

The ultrastructure of the cilia (Fig. 4.7) was described by, e.g., Lansing & Lamy (1961), Clément (1977), Clément & Wurdak (1991). The axoneme of the motile cilia shows the characteristic 9 peripheral doublets and 2 central tubules. The basal body consists of doublets or singlets instead of the classical triplets. Intramembranous particles are present (*Brachionus calyciflorus*) over the entire surface

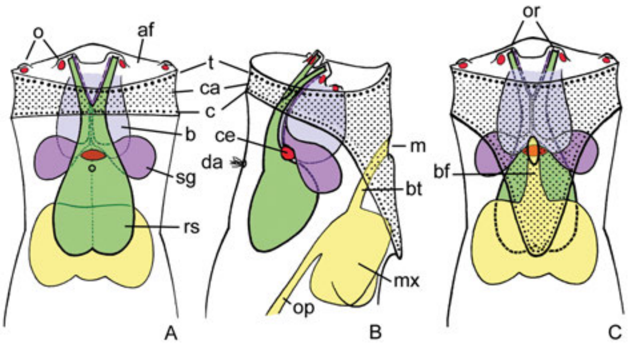

Fig. 4.5: Basic organization of the rotary apparatus and other organs of the head. (A) Dorsal, (B) lateral, and (C) ventral. Abbreviations: af, apical field; b, brain; bf, buccal field; bt, buccal tube; c, cingulum; ca, circumapical band; ce, cerebral eye; da, dorsal antenna; m, mouth; mx, mastax; o, ocellus; op, esophagus; or, orifice of retrocerebral organ; rs, retrocerebral sac; sg, subcerebral glands. (Modified from Donner 1956, de Beauchamp 1965, and Clément & Wurdak 1991.)

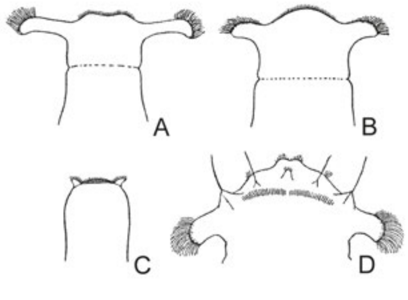

Fig. 4.6: Ciliated auricles. (A) *Notommata copeus*, (B) *Lindia fulva*, (C) *Tetrasiphon hydrocora*, and (D) *Synchaeta* sp. (From Remane 1933.)

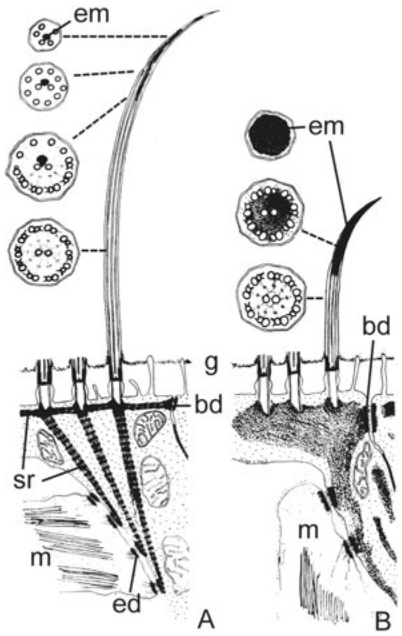

Fig. 4.7: Diagram of the cilia of the rotatory apparatus, in longitudinal and cross section. (A) cilia from the trochus and (B) cilia from the buccal field. Abbreviations: bd, belt desmosome; ed, epitheliomuscular desmosome; em, electron-dense material; m, muscle; sr, striated ciliary rootlet. (Modified from Clément & Wurdak 1991, with permission.)

of the cilia of the tactile bristles or are aligned along the cilia of the pseudotrochus and base of the motile cilia of the corona. In some cilia, an electron-dense material is present at the tip (*Notommata copeus, Trichocerca rattus, Philodina roseola*), or where doublets become singlets, it extends along the central doublets to the tip (*Brachionus sericus*). The ciliary rootlets are striated and occur in 2 types (Scholtyseck & Danneel 1962, Clément 1977, 1987, Clément & Amsellem 1989). The vertical rootlets penetrate into the cytoplasm, inserting on epitheliomuscular desmosomes, or to a fibrous intracytoplasmic layer, inserted itself on desmosomes between coronal cells and integument (the desmosomal belt). The horizontal rootlets interconnect the cilia at their base and insert upon the desmosomal belt. Horizontal ciliary roots may be absent (*Asplanchna*). The muscles inserted on the ciliary roots of the cingulum and pseudotrochus (*Brachionus calyciflorus, B. plicatilis*) may control the ciliary beat. They are innervated and show characteristics of very fast fibers.

Various modifications of the ground plan of the corona have been described, which grossly correlate with the mode of locomotion and feeding habits.

Corona types in Monogononta (see de Beauchamp 1907a, 1908, 1965, Remane 1933, Melone 1998) (Figs. 4.8 A–K and 4.9)

***Notommata* type.** Extensive buccal field around mostly ventral and central mouth opening. Circumapical band and apical field present; apical field fairly small; circumapical band laterally with paired tufts of stronger cilia; trochus and cingulum weakly developed. In creeping or slow-swimming animals (Notommatidae).

***Dicranophorus* type.** Corona almost exclusively composed of extensive buccal field surrounding central mouth opening. Circumapical band absent or reduced to paired tufts of stronger cilia laterally from buccal field. In creeping or slow-swimming animals (Dicranophoridae, some Notommatidae).

***Asplanchna* type.** Buccal field strongly reduced. Apical field large. Circumapical band an interrupted circle of cilia around the large apical field; trochus and cingulum not differentiated. Planktonic species (Asplanchnidae, Synchaetidae, Gastropodidae, Trichocercidae, several Notommatidae, e.g., *Eosphora, Sphyrias*).

***Euchlanis-Brachionus* type.** Only supraoral part of buccal field well developed; marginal cilia powerful, enlarged to stiff cirri, the rest of the buccal field with weak cilia, or transverse rows and arcs of cilia/cirri above and laterally from mouth opening, respectively, forming pseudotrochus; arcs and/or tufts of cirri, often set on cushions. Apical field small. Circumapical band present, often interrupted; cingulum not differentiated, may form paracingulum with posterior rows of buccal cilia. In planktonic and semi-planktonic species (Euchlanidae, Epiphanidae, Brachionidae).

***Conochilus* type.** Trochus and cingulum well developed, usually interrupted ventrally. Mouth displaced to the dorsal side. In free-swimming species (Conochilidae).

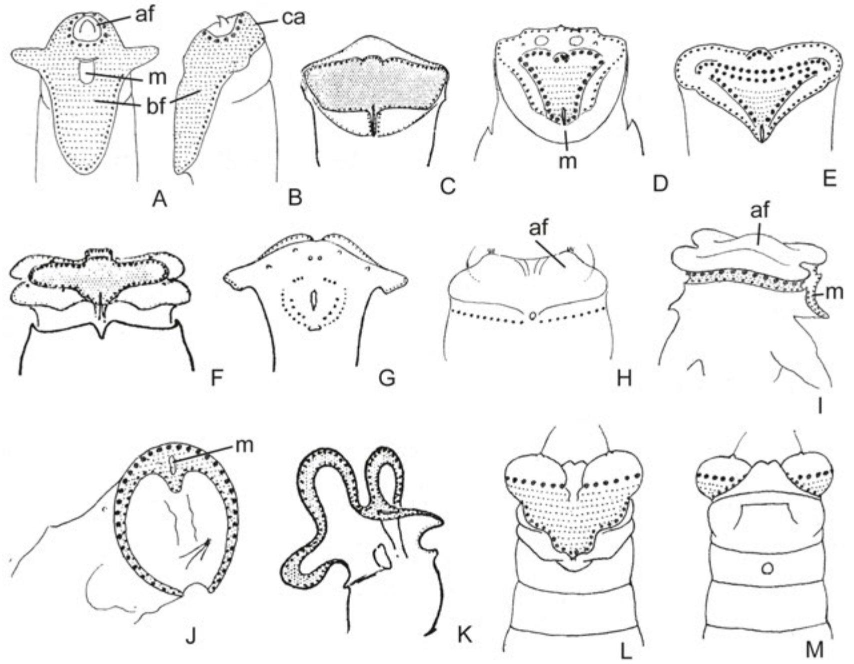

Fig. 4.8: Types of corona: (A–K) Monogononta, (L, M) Bdelloidea. (A) *Notommata*, ventral, (B) *Notommata*, lateral, (C) *Cyrtonia*, (D) *Euchlanis*, (E) *Epiphanes*, (F) *Brachionus*, (G) *Synchaeta*, (H) *Asplanchna*, (I) *Hexarthra*, (J) *Conochilus*, (K) *Floscularia*, (L) *Macrotrachela*, ventral, and (M) *Macrotrachela*, dorsal. Large dots indicate trochus, medium dots cingulum, small dots ciliation of circumapical band. Abbreviations: af, apical field; bf, buccal field; ca, circumapical band; m, mouth. (From de Beauchamp (1907, 1965.)

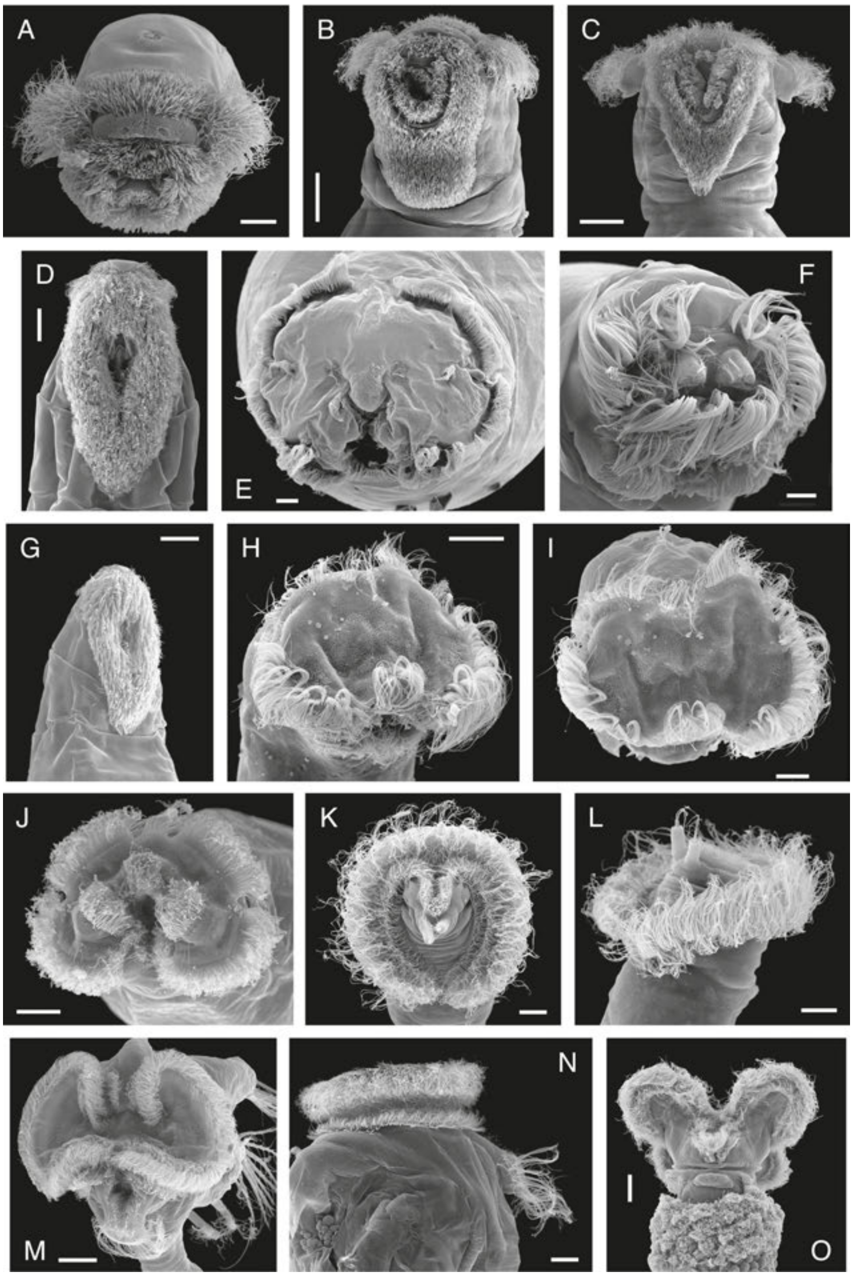

Fig. 4.9: SEM picture of the shape of the corona in different genera of Monogononta: (A–C) *Notommata*, (D, G) *Dicranophorus*, (E) *Asplanchna*, (F) *Euchlanis*, (H, I) *Cyrtonia*, (J) *Brachionus*, (K, L) *Conochilus*, (M, N) *Hexarthra*, and (O) *Floscularia*. Scale bar = 10 μm (A, D, F, I, K, L, N), 20 μm (B, C, E, G, H, J, M, O). (Photo courtesy of Giulio Melone.)

***Hexarthra* type.** Buccal field small. Circumapical band and apical field large; strongly developed trochus and weaker cingulum, not interrupted ventrally. In sessile (Flosculariidae), semi-planktonic (Testudinellidae), and free-swimming species (Hexarthridae).

***Collotheca* type.** Corona extended into 2–8 blunt or elongate lobes, forming funnel with mouth at center of the bottom. Edges of lobes with motionless cilia or setae or lobes apically with bundles of long setae. In sessile and planktonic species (Collothecidae). The corona of adult females of Atrochidae (*Acyclus, Atrochus, Cupelopagis*) lacks cilia or setae; a ciliated corona, used for swimming, is only present in their juveniles and males.

Corona types in Bdelloidea (see de Beauchamp 1907a, 1908, 1965, Remane 1933, Melone & Ricci 1995, Ricci & Melone 1998a) (Figs. 4.8 L–M and 4.10)

***Philodina* type.** Ventral mouth opening surrounded by buccal field. Buccal field anteriorly delimited by 2 individual retractable trochal disks elevated on pedicels, lined by C-shaped wreath of long cilia, the trochi, and posteriorly demarcated by a single wreath of long cilia, the cingulum. Each trochus is made of about 30 rows of

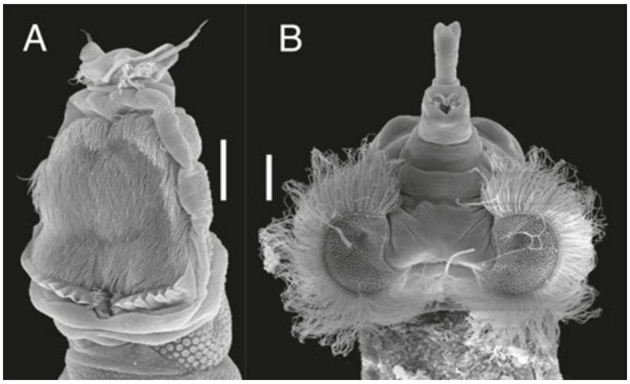

Fig. 4.10: SEM picture of the shape of the corona in 2 genera of Bdelloidea: (A) *Adineta* and (B) *Dissotrocha*. Scale bar = 10 μm. (Photo courtesy of Giulio Melone.)

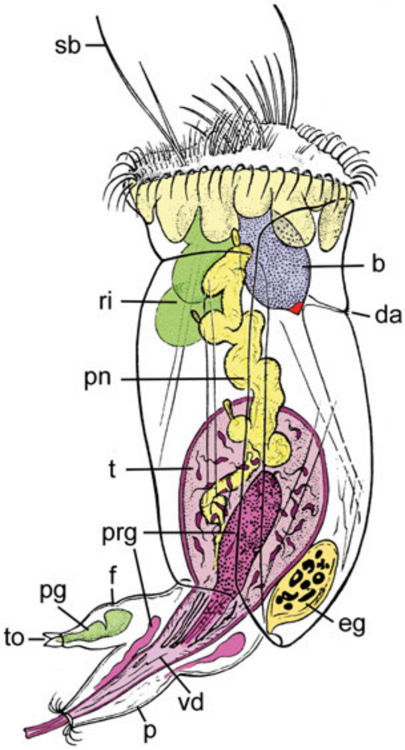

Fig. 4.11: Male of *Brachionus calyciflorus*. Abbreviations: b. brain with eyespot; da, dorsal antenna; eg, “excretion” granules; f, foot; p, penis; pg, pedal glands; pn, protonephrial apparatus; prg, prostate glands; ri, rudiments of intestinal system; sb, sensory bristles; to, toes; t, testis; vd, vas deferens. (Modified from de Beauchamp 1965.)

cilia. The cilia of the cingulum insert on a cingulum pad. Between the pedicels, the epidermis forms an upper lip; an epidermal lower lip lines the mouth opening ventrally. Cingulum and cingulum pad with whiskers bordering mouth opening. Corona used for swimming and capturing food; both actions possible at the same moment. In Philodinidae and Habrotrochidae.

***Abrochtha* type.** Similar to *Philodina* type, but with an unpaired trochus composed of a unique row of cilia, and encompassing the rudimentary pedicels and V-shaped cingulum; cingulum pad and whiskers bordering mouth opening lacking. Locomotion and capturing food are 2 separate actions. In *Abrochtha* and *Philodinavus*.

***Adineta* type.** The corona is a homogenous ventral field of undifferentiated cilia: trochus, cingulum, and cingulum whiskers absent; cingulum pad present. Posterior border of ciliated field with paired cuticular denticulate structures, the food rake. *Adineta* is unable to swim or to create water currents: the corona is used only for gliding and feeding by scraping the substrate; food is collected with the rake. In Adinetidae.

4.2.1.4 Morphology of the male

Males (Fig. 4.11) are usually much smaller than the females and of simpler structure (Wesenberg-Lund 1923, Remane 1933). The sexual dimorphism (Fig. 4.12) is almost a continuum ranging from very weak to very pronounced. Species of Ploima with males of similar appearance to the female and displaying a well developed head, trunk, foot, and toes (e.g., *Eosphora najas, Pourriotia werneckii*, formerly *Proales werneckii, Rhinoglena frontalis, Notommata copeus*) are usually slightly smaller (70%–90% of the length of the female) and/or slender, but often have a reduced corona. Melone (2001) studied the coronae of both sexes in *R. frontalis* by SEM and showed that they are organized in the same way, but the corona of the male is smaller by a reduction of the number of cilia present in its different parts. Other differences concerned the relatively longer foot, proboscis, and lateral antennae. In species with extremely reduced males (e.g., *Polyarthra, Trichocerca*), the length of the males is only about 15%–50% of the female, and the body is merely a conical or sac-shaped structure without foot, bearing a strongly reduced corona consisting of a terminal ciliated field or tufts of cilia. Spines and appendages of the body and lorica found in the female are lacking or reduced, e.g., the male of *Hexarthra* only has 3 reduced arms, 1 dorsal and 2 lateral ones, instead of the 6 arms in the female. In some species displaying strong sexual dimorphism, males may show characters absent in females (e.g., Remane 1933, Segers &

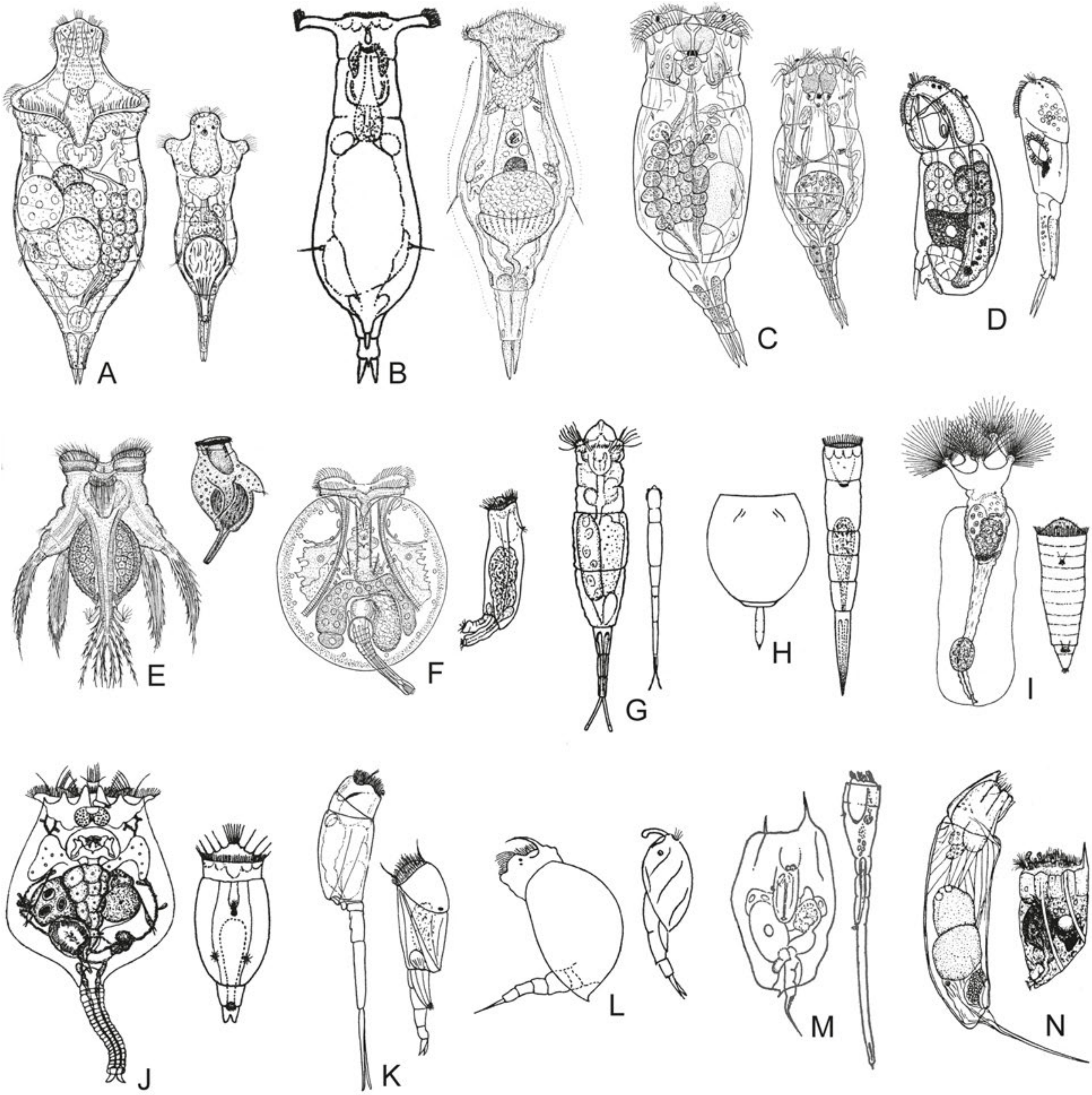

Fig. 4.12: Sexual dimorphism in Monogononta: (left) female and (right) male. (A) *Rhinoglena frontalis*, (B) *Notommata copeus*, (C) *Eosphora najas*, (D) *Cephalodella catellina*, (E) *Hexarthra mira*, (F) *Testudinella patina*, (G) *Wierzejskiella velox*, (H) *Lecane psammophila*, (I) *Collotheca ornata*, (J) *Brachionus urceolaris*, (K) *Scaridium longicaudum*, (L) *Colurella uncinata*, (M) *Trichocerca pediculus*, and (N) *Trichocerca capucina*. (From different authors.)

Rico-Martinez 2000): the males of *Lecane bulla* and *Synchaeta triophthalma* have 2 separate toes instead of the single toe in the female; the neck region in the male of *Pompholyx sulcata* consists of several plates that are absent in the female; in male Brachionidae, the neck is stiffened and the trunk often shows several plates.

In the sessile Flosculariidae and Collothecacea, the length differences between the sexes may be very great, the males only reaching 5%–10% of the length of the females, and resembling the free-swimming juvenile females. They often show a conical projection at the anterior end, bearing apical eyes, which is absent in the adult females; a foot with adhesive disc may be present (*Lacinularia*).

Males of most benthic monogononts show little or medium reduction in structure and length, unlike the ones of planktonic species, which are the most extremely reduced (Wesenberg-Lund 1923, Remane 1933, Riemann & Kieneke 2008). According to Ricci & Melone (1998b), this phenomenon suggests that the species in the 2 habitats are exposed to different selection pressures. Serra & Snell (1998) suggested that male dwarfism in rotifers could be the result of selection on females, to produce a high number of males in a short period with a minimum reproductive cost.

4.2.2 Integument

The integument is syncytial, and besides its function as an outer protective covering, it plays a role as peripheral skeleton, serves for muscle attachment, and has an endocrine and exocrine function. The skeleton function is provided by a dense intracytoplasmic lamina (ICL) (e.g., Clément 1969, Koehler 1965b, 1966, Dickson & Mercer 1967, Schramm 1978a, Clément & Wurdak 1991, Kleinow 1993), composed of 2 filamentous keratin-like proteins (molecular weight, 39 and 47 kDa, respectively), cross-linked by disulfide bonds (Bender & Kleinow 1988). The ICL lies just under the outer cell membrane of the syncytial integument and is regularly perforated by pores (Figs. 4.13 and 4.14). The cell membrane invaginates through these pores forming spherical bulbs within the cytoplasm. Clément (1969, 1980, 1985, 1993) recognizes 4 types of ICL according to the absence or presence of different layers, and the vertical or horizontal orientation of their composing structures. The bdelloid type ICL shows a thickened and uniformly electron-dense internal layer and a very thin external layer (*Philodina acuticornis odiosa, P. roseola, Rotaria* sp., *Habrotrocha rosa*). In monogononts, 3 types may be recognized, characterized by a thick external layer, and a thin or lacking electron-dense internal layer. The stacked lamella type shows several fibrous horizontal layers: 7 in *Notommata* and 3 in *Asplanchna* and *Synchaeta*; the internal layer is strongly reduced. The vertical tube type consists of a layer of juxtaposed vertical tubes and a well-developed thin internal layer (*Brachionus*, *Mytilina*). The uniformly dense type shows a dense homogenous layer that may be thick (*Trichocerca, Keratella*) or thin (*Filinia, Sinantherina*); the internal layer is absent.

The thickness of the ICL varies greatly within a single rotifer and between different species. Within the animal, the ICL is very thin in the apical region and thicker and more dense at the level of the trunk, foot, and spines, and thin and flexible at the articulation between the trunk and the corona and at the other joints of, e.g., the foot, toes, paddles, and movable spines (e.g., Clément 1987, Clément & Wurdak 1991). The stiffening can also be restricted to separate plates, e.g., a dorsal and ventral trunk plate in *Euchlanis*, or 3–5 trunk plates in *Cephalodella*. The plates are separated by a thin flexible ICL, with the integument taking the shape of a more or less deep invagination or sulcus between the plates. Species showing an extremely thick and stiffened ICL of the major body regions, hence becoming almost inflexible are called loricates (e.g., Brachionidae, Mytilinidae, Trichotriidae) and those with a thin and flexible ICL throughout are illoricates or semi-loricates

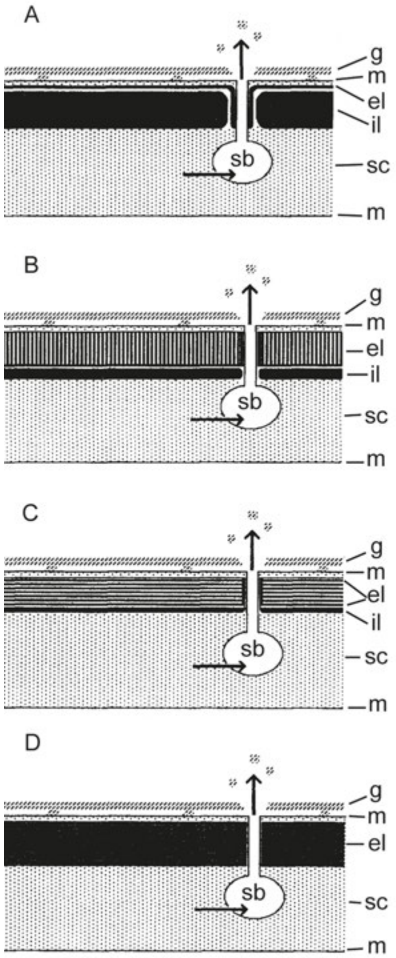

Fig. 4.13: Diagram of the 4 types of intracytoplasmic lamina. (A) *Philodina* type, (B) *Brachionus* type, (C) *Notommata* type, and (D) *Trichocerca-Filinia-Keratella* type. Abbreviations: el, external lamina; g, glycocalyx; il, internal lamina; m, membrane; sb, secretory bulb; sc, syncytial cytoplasm. (Modified from Clément 1993.)

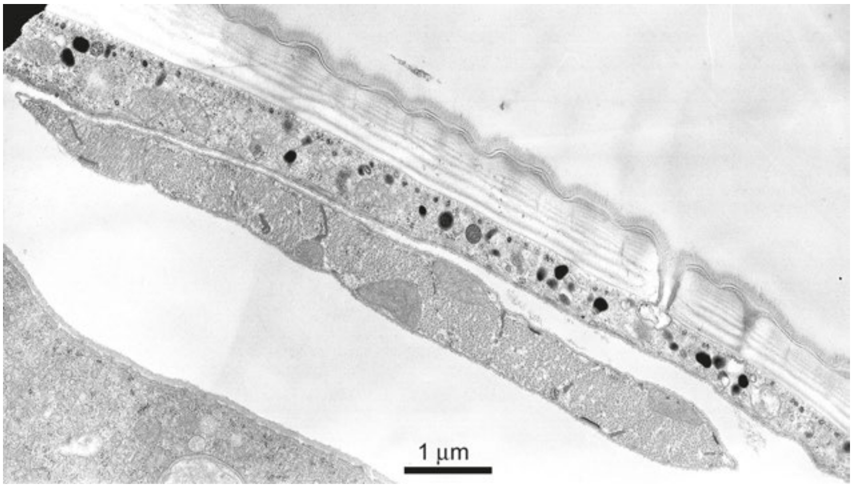

Fig. 4.14: TEM section of the integument of *Macrotrachela quadricornifera*. The ICL is visible, with several layers. The section of a pore crossing the lamina is also visible. (Photo courtesy of Giulio Melone.)

(e.g., Epiphanidae, Asplanchnidae, Lindiidae). All stages from illoricate to strongly loricate may occur within a single genus or family; therefore, the degree of stiffness of the ICL generally is of little taxonomic significance.

Secretions produced by the syncytial integument are expelled to the outside through secretory bulbs and pores traversing the ICL (e.g., Clément 1977, Clément & Wurdak 1991). These secretions form a very thin to thick extracellular “cuticle”, or glycocalyx, to which foreign particles may stick. Among the secreted substances are glycoproteins that play a role in male mate choice, discriminating females based on species, sex, age, and reproductive status (e.g., Snell et al. 1995). The integument also has an endocrine function, discharging its secretion products in the pseudocoel *via* secretory granules produced by the rough endoplasmic reticulum and Golgi apparatus (Clément 1977, Clément & Wurdak 1991).

The ICL also serves for the attachment of the body muscles and the cutaneovisceral muscles. Associated with the integument are several glands: pedal glands, the retrocerebral organ, ovifer glands to fix and carry eggs (*Sinantherina*), modulus glands in tube-forming Flosculariacea, etc.

4.2.2.1 Pedal glands

The foot contains the pedal glands and their reservoirs and ducts. They are unicellular or syncytial, and secrete cement to attach the animal on the substrate temporarily (Ploima, Bdelloidea) or permanently (sessile Flosculariacea and Collothecacea). In some species, the secretion of the pedal glands is also used to anchor eggs to the substrate. Monogononts generally have paired multinucleate pedal glands lying in the foot or extending into in the distal part of the trunk; smaller accessory pedal glands with an own aperture or an aperture in common with the main glands may be present. In bdelloids, from 2 to 15 pairs of mononucleate pedal glands can be found (Fig. 4.15). The ducts of the pedal glands may be widening locally into reservoirs. The secretion is discharged *via* apertures in the attachment organs at the end of the foot. In species with reduced or vestigial foot, pedal glands are usually lacking. The apertures of the pedal glands lie on or near the tip of the toes in most Ploima; in *Trichocerca*, they issue at the base of the toes and the secretion flows externally along the toe(s). In Flosculariacea and Collothecacea, the toes open at the adhesive disc or at the end of the foot. In bdelloids, the tips of both toes and spurs have openings for the ducts of the pedal glands; in the adhesive discs, the pedal glands issue by numerous openings (e.g., up to 14 in *Habrotrocha proxima*).

In monogononts, only one type of secretion is produced by the same animal, whereas in bdelloids, the same animal produces 2 types of secretion (Clément 1987, Clément & Wurdak 1991).

4.2.2.2 Retrocerebral organ

The retrocerebral organ (Figs. 4.5 and 4.16) is located dorsal to the brain and mastax and consists of the unpaired median retrocerebral sac and 2 lateral subcerebral glands (de Beauchamp 1905, 1906, 1965). From the anterior part of the sac, an unpaired duct runs toward the corona and bifurcates anteriorly into 2 ducts opening on the apical field; the openings often lie on a single or paired papilla. The subcerebral glands have ducts alongside those of the sac. In monogononts, the content of the sac often appears strongly vacuolated and may contain light refracting bodies

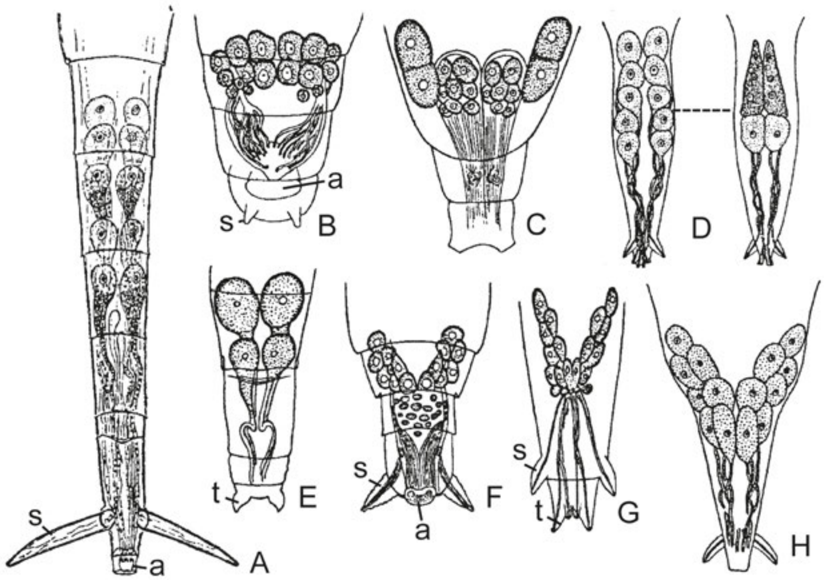

Fig. 4.15: Variation of the pedal glands in Bdelloidea. (A) *Rotaria socialis*, (B) *Zelinkiella synaptae*, (C) *Mniobia tetraodon*, (D) *Embata parasitica*, (E) *Mniobia armata*, (F) *M. russeola*, (G) *Philodina vorax*, and (H) *Adineta barbata*. Abbreviations: a, adhesive disc; s, spur; t, toe. (From Kutikova 2005.)

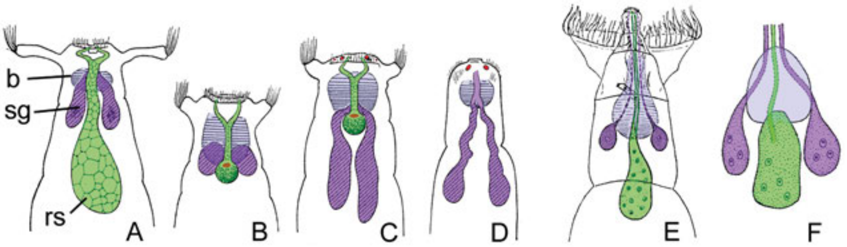

Fig. 4.16: Types of retrocerebral organs in Monogononta (A–D) and Bdelloidea (E, F). (A) *Notommata copeus*, (B) *Notommata aurita*, (C) *Itura myersi*, (D) *Erignatha clastopis*, (E) *Rotaria socialis*, and (F) *Embata parasitica*. Abbreviations: b, brain; rs, retrocerebral sac; sg, subcerebral glands. (Modified from Brakenhoff 1937 and de Beauchamp 1965.)

and red-colored pigment granules. The subcerebral glands are granular and often contain a light refracting globule in *Encentrum*. The size of sac and glands, and their contents, is highly variable: there may be a sac without glands or glands without a sac (Fig. 4.16). Variations of the subcerebral glands may be apparent also in different populations of the same species. In Ploima, the retrocerebral organ is mostly well developed, but lacking in some species; it is reduced or absent in Flosculariacea and Collothecacea. In bdelloids, the retrocerebral organ is especially developed in creeping species (Brakenhoff 1937), and the different glands produce only one type of secretion (Clément & Wurdak 1991).

Ultrastructural investigations show that the retrocerebral organ is made up of multinucleate mucous glands, and surrounded by a muscular sheath at its base. The muscle has long thick filaments surrounded by thin filaments. The ratio of thick to thin filaments is 1:6, which is characteristic of a slow and tonic contraction. The ducts are lined by longitudinal microtubules lying below the cell membrane and assisting in the discharge of mucous secretions (Clément 1977, 1980, Clément & Wurdak 1991).

The function of the retrocerebral apparatus is not well known. According to Clément & Wurdak (1991), it probably lubricates the cilia of the corona involved in creeping. In bdelloids, it may be responsible also for the adhesive attachment of the rostrum when creeping (Brakenhoff 1937). Clément et al. (1983) also noticed that the female of *Notommata copeus* envelopes new laid eggs with mucus secretions from the pedal glands and the retrocerebral organ.

The retrocerebral organ is also present in male rotifers (e.g., Wesenberg-Lund 1923, Riemann & Kieneke 2008) and apparently does not show sexual dimorphism.

4.2.2.3 Sheaths and tubes

Many rotifers, especially bdelloids (see Donner 1950) and sessile and planktonic monogononts (e.g., Remane 1933, Edmondson 1945, Wright 1950, Fontaneto et al. 2003), secrete or construct sheaths or tubes formed of mucus (e.g., *Conochilus* spp., *Gastropus stylifer, Lacinularia* spp., *Trichocerca cylindrica*), mucus and cemented detritus or fecal material (e.g., *Habrotrocha gracilis, H. pavida, H. pusilla*), gelatinous material (e.g., *Acyclus, Collotheca, Ptygura, Stephanoceros*), pellets made of bacteria and detritus (*Floscularia ringens*), fecal pellets (*F. janus, Ptygura pilula*), and rigid, often ringed material (*Habrotrocha angusticollis, Limnias melicerta*). The tubes may enclose the whole animal or the foot only. Eggs are laid inside. Some benthic-periphytic monogononts secrete close-fitting mucous coats, often containing foreign particles (e.g., *Encentrum umbonatum, Notommata copeus, Paradicranophorus hudsoni, Tetrasiphon). Cephalodella forficula* starts its life as a more or less planktonic form before constructing long (up to 5 mm), substrate-bound and detritus-covered mucous tubes, often closed at both ends, in which it swims around (Dodson 1984). Several bdelloids have an outer covering of secretion shaped as stiff platelets (e.g., *Mniobia incrassata, M. mirabilis*) or thin rods (e.g., *Rotaria socialis*). The mucous or gelatinous tubes appear to be secreted by the general body surface in *Ptygura* and bdelloids or glands near the mastax in bdelloids (Edmondson 1945, Donner 1950, Wulfert 1969) or they are formed by the pedal glands in, e.g., *Cephalodella forficula, Collotheca campanulata*, and *Limnias melicerta* (Dodson 1984, Wulfert 1969). The pellets composing the tube of *F. ringens* are formed in a ciliated groove below the lower lip, the modulus, by collecting and concentrating bacteria and detritus, and gluing them together with sticky secretion from the modulus glands (Fontaneto et al. 2003). For details on tube construction in *Collotheca campanulata, F. ringens, F. janus, Limnias melicerta* and *Stephanoceros fimbriatus*, see, e.g., Edmondson (1945), Wright (1950), Wulfert (1969), de Beauchamp (1965), Fontaneto et al. (2003), and Wallace et al. (2006). Sheaths and tubes may protect against predation and drying out and enhance buoyancy in planktonic species.

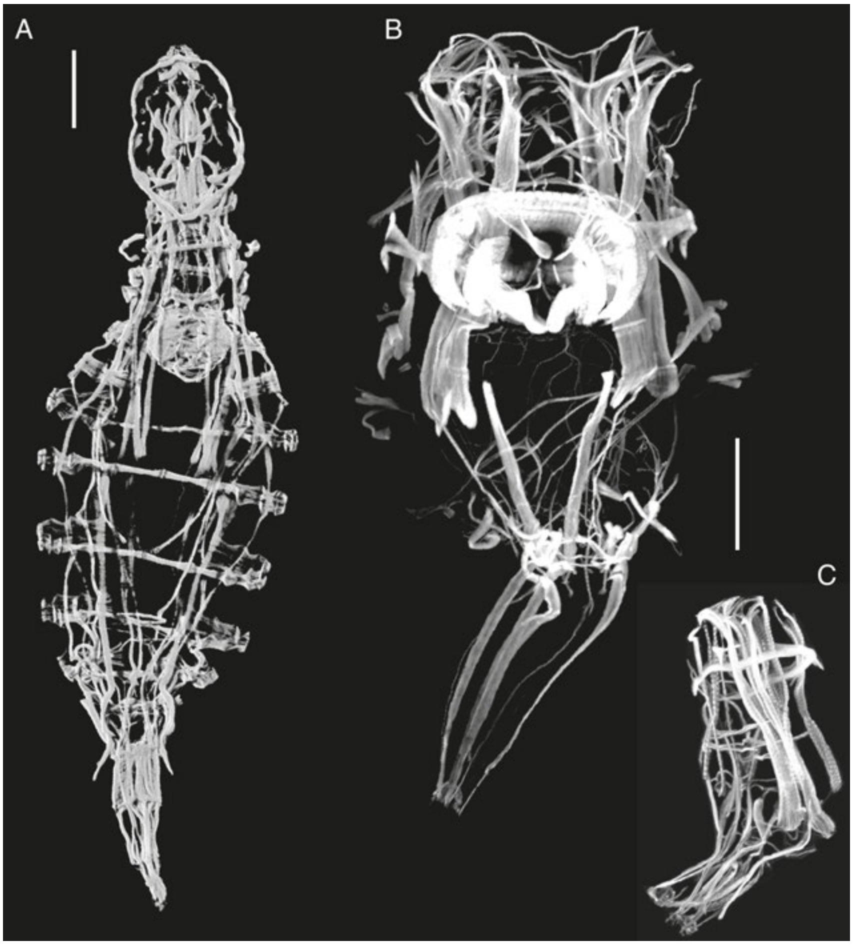

Fig. 4.17: CLSM of musculature. (A) *Adineta ricciae*, (B) *Brachionus manjavacas* female, and (C) *Brachionus manjavacas* male. Scale bar = 20 µm (A) and 50 µm (B, C). (Photo courtesy of Francesca Leasi.)

4.2.3 Musculature

4.2.3.1 Musculature of the female

The muscles of rotifers comprise smooth, cross-striated, or obliquely striated types, which can be monocellular or bicellular, phasic or tonic, strong or weak, and endurant or not (e.g., Amsellem & Clément 1977, Clément & Amsellem 1989), and occurring as thin filaments or arranged in separate small bands. They are organized into somatic muscles, controlling movement and changes of body form, and serving the head, foot, dorsal antenna, etc., the cutaneovisceral muscles connecting the internal organs with the integument, and the visceral muscles surrounding the digestive tract, cloaca, and reproductive apparatus.

The arrangement of the somatic component, studied by LM and histological techniques, received much attention in the past (e.g., Zelinka 1886, Martini 1912, Nachtwey 1925, Remane 1933, Seehaus 1930, Peters 1931, Stossberg 1932, Dehl 1934, Brakenhoff 1937). The results of these earlier observations were largely corroborated and refined by epifluorescence and CLSM (Fig. 4.17) of the phalloidin stained F-actin fibers (e.g., Kotikova et al. 2001, 2004, 2006, Santo et al. 2005, Sørensen et al. 2003, Sørensen 2005a, b, Hochberg & Ablak Gurbuz 2008, Hochberg et al., 2008, Riemann et al. 2008, Leasi & Ricci 2009, Wilts et al. 2009, Wilts & Ahlrichs 2010, Leasi et al. 2010). Comparison of the somatic muscular system among all rotifer taxa investigated to date reveals a common basic pattern (e.g., Santo et al. 2005, Leasi et al. 2012), consisting of 2 major groups: a system of outer circular bands and a system of inner, paired, and bilaterally symmetrical longitudinal bands (Figs. 4.18 and 4.19). Both circular and longitudinal muscles insert at their endings on the skeletal syncytial integument and sometimes at the level of muscle Z-elements (Clément & Amsellem 1989). Musculo-epithelial junctions are by desmosomes, joined to the ICL by dense material; musculomuscular junctions are by desmosomes and hemidesmosomes and gap junctions (e.g., Koehler 1965b, Clément 1969, Clément & Amsellem 1989). Somatic muscles of bdelloids are smooth or obliquely striated, whereas in monogononts, cross-striated muscles preponderate (Clément & Amsellem 1989, Clément 1993).

Circular muscles are localized in the head, trunk, and junction between trunk and foot. Strongly developed circular muscles in the head directly behind the corona form the coronal sphincter, able to contract tightly over the head after retraction of the corona, and thereby protecting the latter (Clément & Amsellem 1989).

The circular muscles of the trunk comprise several, mostly 3 to 7, separate muscles. Upon contraction, they exert pressure on the turgid pseudocoel, which results in the extension of the body. There is a great deal of variation in the circular muscle pattern of the trunk, supposed to reflect the ecology, mode of locomotion, shape of the body, and presence of integumentary plates (e.g., Remane 1933, Leasi & Ricci 2009). The circular muscle system may consist of closed muscular rings (*Asplanchnopus*

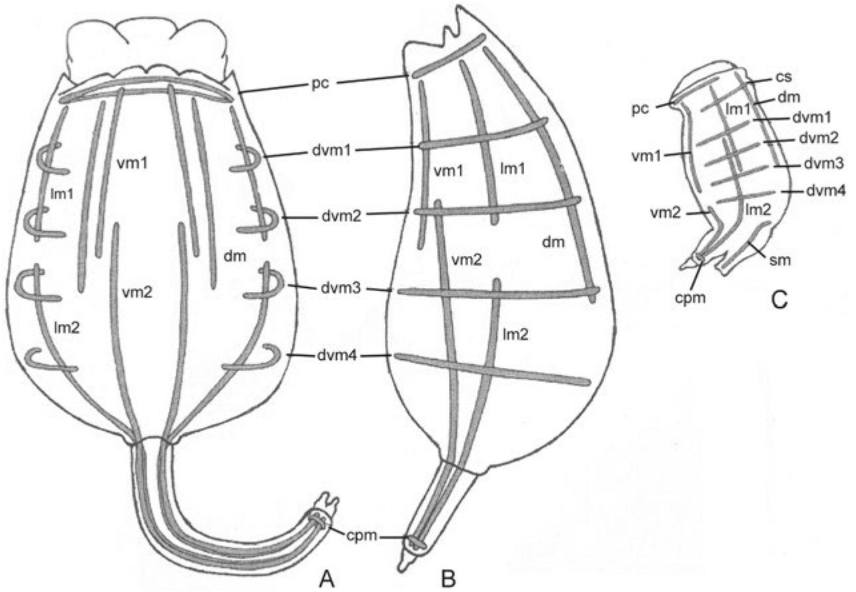

Fig. 4.18: Diagram of musculature in *Brachionus manjavacas.* (A) Female, ventral view, (B) female, lateral view, and (C) male, lateral view. Abbreviations: cs, corona sphincter; dm, dorsal longitudinal muscle; dvm, dorsoventral muscle; lm, lateral longitudinal muscle; pc, muscle pars coronalis; sm, splanchnic longitudinal musculature of the penis; vm, ventral longitudinal muscle. (From Leasi et al. 2010.)

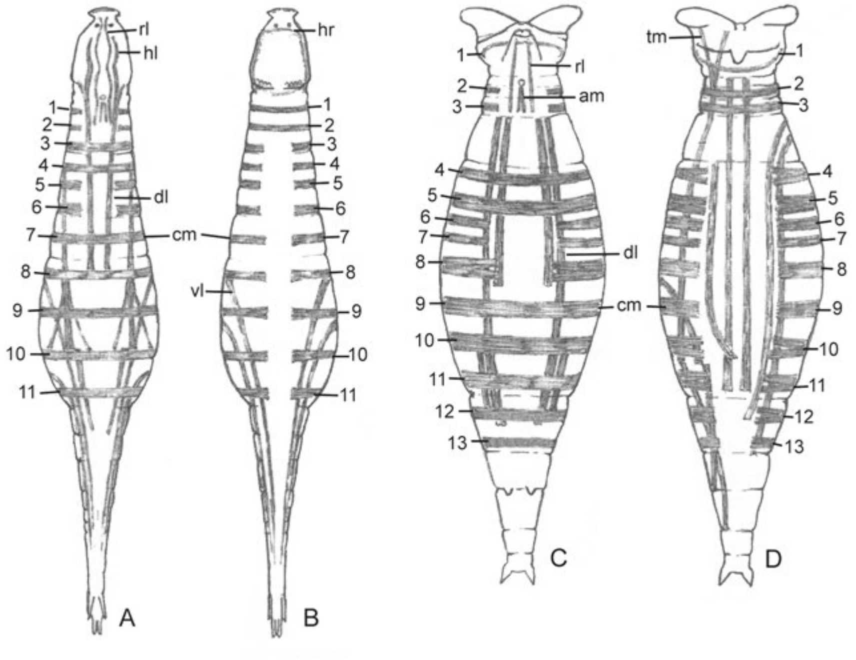

Fig. 4.19: Diagram of somatic musculature in *Adineta ricciae* (A, B) and *Macrotrachela quadricornifera* (C, D). (A, C) Dorsal view and (B, D) ventral view; Abbreviations: am, musculature of antenna; cm, circular muscles (1–13); dl, dorsal longitudinal muscles; hl, dorsal longitudinal muscles of the head; hr, ring muscle of the head; rl, longitudinal muscles of the rostrum; tm, musculature of the trochi; vl, ventral longitudinal muscles. (From Leasi & Ricci 2009.)

multiceps, Notommata glyphura) or semi-circular, and open configurations just beneath the integument. The interruptions of the semi-circular muscles may be ventral (e.g., *Adineta ricciae, Macrotrachela quadricornifera, Encentrum mucronatum, Epiphanes senta, Proales fallaciosa, Floscularia ringens*) or both dorsal and ventral (*Proales reinhardti*), or the muscles may be split into paired dorsolateral and paired ventrolateral bands connecting the different integumentary plates of the lorica (*Dicranophorus forcipatus*). In some species, the circular muscles are modified into strands that became free from the integument and only connected to it by their endings (e.g., *Testudinella, Euchlanis*). Complete or ventrally open muscle rings are mostly characteristic of soft-bodied monogononts and bdelloids. In loricates or semi-loricates, with stiffened integumentary plates, the circular muscles are generally less developed. They are reduced to short lateral dorsoventral strands connecting the dorsal and ventral parts of the tegument or lorica plates in dorsoventrally compressed species (e.g., *Brachionus* spp., *Euchlanis dilatata, Testudinella patina*). Transversal muscle bands are found in laterally compressed species (e.g., *Colurella, Mytilina*) and oblique lateroventral strands are present in species with triangular cross section (e.g., *Mytilina*). Circular muscles along the trunk are absent in species possessing movable appendages like spines (e.g., *Filinia novaezealandiae*), arms (e.g., *Hexarthra mira*) or paddles (e.g., *Polyarthra major*), but it has been suggested that some muscles serving these appendages are derived from the circular muscles (e.g., Levander 1894, Hochberg & Ablak Gurbuz 2007, 2008). A pedal sphincter is often present at the junction of the trunk and foot, and a circumpedalis muscle may encircle the junction between foot and toes.

The inner, longitudinal retractor muscles are present in the head, trunk, and foot (if present) and insert at different points of the integument; some may span the length of the animal inserting anteriorly in the head or neck region and posteriorly at the base of the trunk. They usually occupy a dorsal, lateral, and ventral position and permit bending of the body and withdrawal of head and foot into the trunk. In bdelloids, the longitudinal muscles are responsible also for the contraction into a tun-shaped stage during desiccation. The different insertion points of the respective head and foot retractors allow the muscles to withdraw these extremities independently. The number of longitudinal muscles as well as their length, width, and insertion points is variable between different taxa and even between closely related species. The longitudinal muscle pattern seems to be determined by different modes of locomotion and adaptation to a specific ecological niche.

Major anatomical changes in the somatic muscular system do not take place during the larval development and metamorphosis to the adult stage in *Acyclus inquietus*, a rotifer with free-swimming larvae and sessile adult females (Hochberg et al. 2010).

Information on the cutaneovisceral muscle system is restricted (e.g., Remane 1933, Kotikova et al. 2006). The number of muscles and position appears very variable, even within a single genus. They hold the organs in place, and are especially common at the level of mastax and cloaca. Others have a more specific function, e.g., the dilatator muscles of the mouth in raptorial species (*Asplanchna, Synchaeta*) allow for the swift opening of the mouth to engulf the prey.

Very little information is available on the visceral musculature (e.g., Remane 1933, Kotikova et al. 2006, Riemann et al. 2008, Wilts et al. 2009, Wilts & Ahlrichs 2010, Leasi et al. 2010). The corona, mastax, esophagus, salivary glands, stomach, intestine, cloaca, oviduct, retrocerebral organ, pedal glands and their reservoirs, and protonephridia may be provided with muscle cells or syncytial muscle fibers. Reticulate, circular, and longitudinal arrangements occur.

4.2.3.2 Musculature of the male

Little is known on the musculature of the male. The figures presented by Wesenberg-Lund (1923) should be interpreted cautiously, but circular and central, dorsal, and ventral longitudinal retractor muscles are definitely present in many males (Remane 1933, de Beauchamp 1965). Waniczek (1930) found no fundamental differences in body musculature between the sexes in *Asplanchna*. Comparison of the muscle organization by CLSM of the females and males of *Brachionus manjavacas* (Fig. 4.18 C) and *Epiphanes senta*, with different ecology and stiffness of the lorica, reveals an identical condition independent of their ecology and morphology, suggesting that evolution and development constrains the organization of the male muscular system (Leasi et al. 2010).

In *B. manjavacas* and *E. senta* visceral muscles are present in the reproductive apparatus but absent in the gastrointestinal system, which could be expected because the latter is lacking in these species (Leasi et al. 2010). The reproductive apparatus is supplied by several muscles in longitudinal and circular (*B. manjavacas*) as well as transversal arrangements (*E. senta*).

4.2.4 Nervous system

Information on the nervous system goes back to the LM and histological observations by, e.g., Zelinka (1888, 1891), Hlava (1905), Hirschfelder (1910), Martini (1912), Nachtwey (1925), Seehaus (1930), Peters (1931), Stossberg (1932), Remane (1933), and Dehl (1934). Additional details were revealed by TEM (e.g., Eakin & Westfall 1965, Clément 1977, Clément et al. 1991) and application of histochemical techniques (e.g., Nogradi & Alai 1983, Raineri 1984, Keshmirian & Nogradi 1987, 1988, Kotikova 1995, 1998). Immunochemistry and CLSM (e.g., Hochberg 2006, 2007, 2009, Leasi et al. 2009) demonstrated the presence of, among others, cholinergic, adrenergic, catecholaminergic, dopaminergic, and serotonergic systems.

The nervous system of only few species has been studied. The neuronal organization is fairly conservative in rotifers (e.g., Kotikova 1995, 1998, Hochberg 2006) and shows a basically bilateral symmetry (Fig. 4.20). It consists of a large cerebral ganglion, commonly called brain, located behind the corona dorsally to the mastax, and surrounded by either epithelial or muscular cells. The brain is of varying shape and size: rounded, sac-shaped, quadrangular, or triangular, etc. The number of cells is constant for each species (e.g., 183 in *Epiphanes senta* and 249 in *Synchaeta tavina*). The neuropilar core of *Philodina roseola* and *Trichocerca rattus* is central and surrounded by perikarya at its periphery (Clément 1977, Clément & Wurdak 1991). Perikarya and associated neurites, display a strong symmetry in number, size,

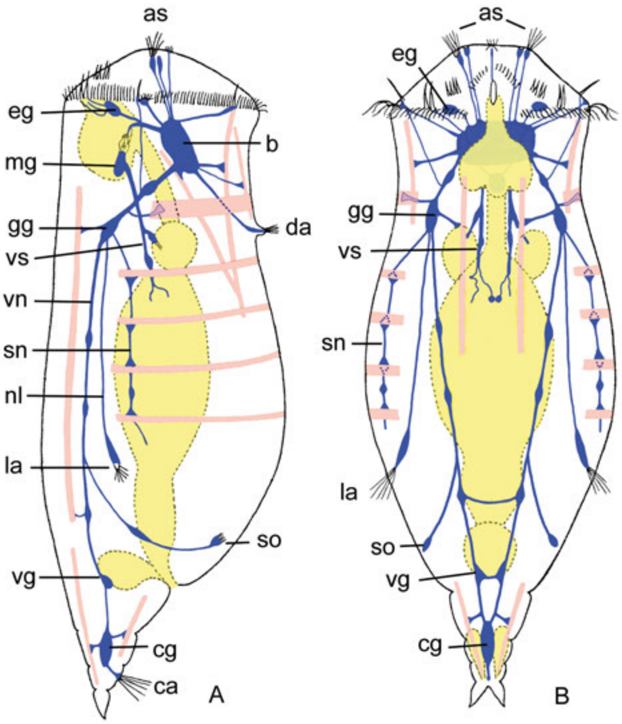

Fig. 4.20: Diagram of the nervous system of rotifers. (A) Lateral and (B) ventral. Dark grey, nervous system; light grey, intestinal system, bladder, and pedal glands; medium grey, muscles. Abbreviations: as, apical sense organs; b, brain; ca, caudal antenna; cg, caudal ganglion; da, dorsal antenna; eg, epipharyngeal ganglion; gg, geniculate ganglion; la, lateral antenna; mg, mastax ganglion; nl, nerve to lateral antenna; sn, scalar nerve; so, supra-anal sense organ; vn, ventral nerve; vg, vesicular ganglion; vs, visceral nerve. (Modified from Remane 1933.)

connections, and pathways between the cerebral hemispheres (e.g., Hochberg 2007, 2009). Two ventral main nerves, composed of a bundle of axons, proceed from the sides of the brain to the caudal or foot ganglion, branching of lateral nerves at secondary ganglia. The coronal region with its sensory structures and the dorsal antenna are innervated by a series of paired neurites issuing from the brain that may form neuronal rings (Kotikova 1998, Hochberg & Lilley 2010). The brain also sends nerves to the mastax, salivary glands, and the dorsal, lateral, and ventral retractor muscles. Neurites branching off from the ventral main nerves supply the dorsal, lateral, and ventral retractor muscles, internal organs, and lateral antennae. A pair of perikarya in the foot sends neurites to the caudal ganglion; an unpaired neurite connects the caudal antenna with the caudal ganglion. A transverse commissure between the lateral longitudinal neurites in the head or between the main nerve cords in the anterior and posterior regions of the trunk may be present.

In males, brain, nerves, and sensory organs appear well developed, but the mastax ganglion is usually absent in accordance with the reduced non-functional mastax (Remane 1933). In *Brachionus plicatilis*, Keshmirian & Nogrady (1988) demonstrated catecholaminergic innervation of all major organs and the male copulatory apparatus.

4.2.5 Sensory structures

Rotifers have a great variety of sensory cells and sensory organs, which can be classified as mechanoreceptors, photoreceptors, and chemoreceptors. However, many of them are sensory complexes having multiple functions; the function of several others is unknown or conjectural (e.g., Remane 1933, de Beauchamp 1965, Clément et al. 1983, Wurdak et al. 1983, Clément & Wurdak 1991). The presence and number of sensory structures vary greatly, even within a single genus or family (for a review, see Remane 1933).

The apical field and cingulum of the corona of monogononts are frequently provided with sensory bristles (styles or cirri, and membranelles), sensory papillae, chemoreceptive pores, sensory pits, etc., emanating from a single or a small number of nerve endings (Fig. 4.21). The sensory bristles apparently have a tactile function and participate in sensing water movement and contact with conspecifics and/or prey and male mate choice (e.g., Remane 1933, Clément et al. 1983, 1991, Snell et al. 1995, Joanidopoulos & Marwan 1998). They are composed of several cilia, the axoneme of which contains the characteristic 9×2+2 tubules. The sensory endings of their nerve fibers are usually surrounded by a supporting epithelial cell, which is protruding into the pseudocoelom.

Sensory papillae, with or without apical cilia, are often present in the apical field as well (Fig. 4.22). Each of the 2 palps of *Trichocerca rattus*, known as palpar organ, shows 6 symmetrically arranged nerve fibers enclosed at their base by 2 supporting epithelial cells. Within the palps are nerves terminating in microvilli and cilia containing the 9 peripheral doublets but lacking the 2 central tubules. Clément et al. (1983) suggest that the palpar organ is responsible for the recognition of the filamentous shape of the algae they feed on. The finger- to sickle-shaped palp in the apical field of *Ascomorpha ovalis* and *A. saltans* serves to hold the prey while its contents are being extracted. In several *Dicranophorus* species, the head bears 2 to 6 anterolateral palps, supposed to be tactile organs.

Chemoreceptive pores located in the anterior syncytial integument beneath the cingulum have been described in *Brachionus* and *Notommata* (Clément et al. 1983,

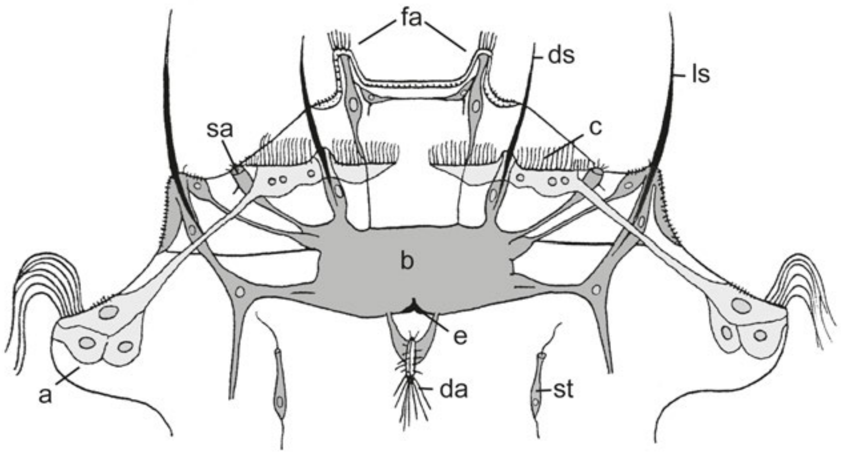

Fig. 4.21: Head of *Synchaeta* with antennae, sensory styles and brain. Abbreviations: a, auricle; b, brain; c, dorsolateral part of corona; ca. secondary coronal antenna; da, dorsal antenna; ds, dorsal coronal seta; e, cerebral eyespot; fa. frontal coronal antenna; ls, lateral coronal seta; st, dorsolateral sensory cell of trunk. (Modified from Kutikova 1970.)

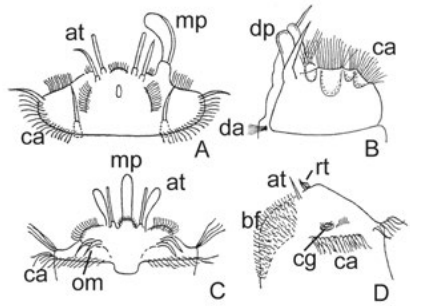

Fig. 4.22: Palps and sensory organs on apical field. (A) *Ascomorpha ovalis*, (B) *Trichocerca stylata*, (C) *Trichocerca capucina*, and (D) *Pleurotrocha petromyzon*. Abbreviations: at, apical tentacle; bf, buccal field; ca, circumapical band; cg, ciliated groove; da, dorsal antenna; dp, dorsal palp; mp, median palp; om, oral membranel. (A, C, D, From Remane 1933; B, from de Beauchamp 1965.)

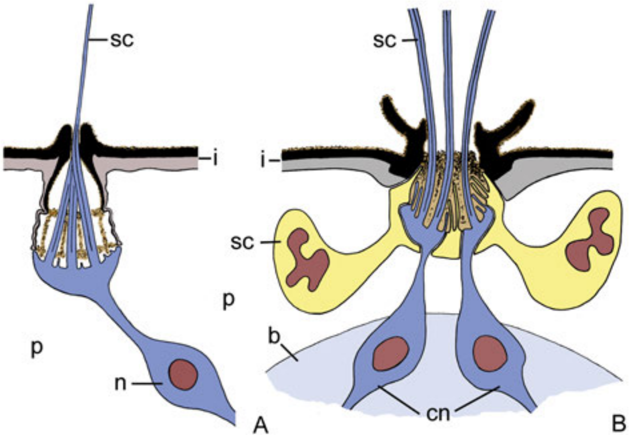

Fig. 4.23: Lateral (A) and dorsal antenna (B) in *Trichocerca rattus*. Abbreviations: b, brain; cn, cerebral neuron terminating at multinucleate, symmetrically arranged supporting cell (sc); i, integument; n, simple neuron in direct contact with integument; p, pseudocoelom. (Modified from Clément & Wurdak 1991, with permission.)

Clément & Wurdak 1991). Non-ciliary sensory endings in the form of microvilli are present inside the lumen underlying the pore (*Brachionus calyciflorus*, *B. sericus*) or the pore continues internally through a muff-shaped underlying epithelial cell, the cavity of which contains cilia and microvilli borne by a sensory nerve ending (*Brachionus plicatilis*, *Notommata copeus*).

Ciliated pits with chemoreceptor function and resembling chemoreceptive pores consist of an external cavity enclosing epithelial cilia, and an internal cavity lined with specialized cilia and sensory membranes (Clément et al. 1983, Wurdak et al. 1983). There are paired structures located on the apical field in, e.g., *Asplanchna*.

The prominent sensory organs of the body are mostly the dorsal and lateral antennae and to a lesser extent the caudal antenna. The dorsal antenna is found in all taxonomic groups of rotifer and generally situated medially on the head or neck but displaced to the anterior part of the trunk in *Testudinella*. In monogononts, it is a more or less long cylindrical projection bearing tufts of cilia or consists of tufts of cilia or styles projecting through a pore in the integument; occasionally, it is reduced to an unciliated pit. The dorsal antenna is paired in the embryonic stage, and becomes fused into an unpaired organ in most of the full-grown species; it is rarely absent (e.g., *Conochilus*). It consists of 2 cerebral nerve fibers with ciliated ends supported by an epithelial cell, which forms a subsurface pocket containing the bases of the sensory cilia (Fig. 4.23 B). The dorsal antenna is most prominent and of greater complexity in bdelloids, where it forms a long tube, telescopically retractable by paired muscles cells contained within it. The dorsal antenna of bdelloids has 3 pairs of nerve endings and several epithelial supporting cells (Clément 1977, Clément & Wurdak 1991).

Paired lateral antennae (Fig. 4.24) are present in monogononts, but lacking in bdelloids. They are usually situated laterally and symmetrically in the posterior half of the trunk but may be displaced ventrally or dorsally, or more anteriorly up to the apical field in *Conochilus*; in *Hexarthra*, they are situated on the ventral arms; they rarely lie on the caudal lorica spines (e.g., *Plationus patulus macracanthus)*. In numerous Trichocercidae, the lateral antennae are in very asymmetrical positions. Partial to complete fusion of the apically displaced antennae occurs in some *Conochilus*. The lateral antennae are of similar shape as the dorsal antenna, but usually smaller (Fig. 4.23 A). They consist of a single sensory neuron in direct contact with the integument, with which it forms a pocket containing the bases of the sensory cilia (Clément 1977, Clément & Wurdak 1991).

A single, rarely paired, small dorsal caudal antenna, consisting of a ciliated pit or a more or less shallow projection tipped with a tuft of cilia, is generally present on the distal foot pseudosegment, between or above the base of the toes in Ploima (Fig. 4.25). In some species (e.g., *Notommata, Proales*), there is an unciliated papilla between the toes, and the distal foot pseudosegment of Collurellidae and *Cotylegaleata* bears a dorsal sensory pit, apparently lacking cilia.

Photoreceptors, called eyes, eyespots, or ocelli, are commonly present in monogononts and bdelloids, which most of the species retaining the eyes throughout their life. Eyespots are often lacking in adults of sessile orders, but present in their free-swimming juvenile stages (e.g., Hlava 1908, Hochberg et al. 2010). Eyespots contain a red to black pigment; the intensity of the color largely

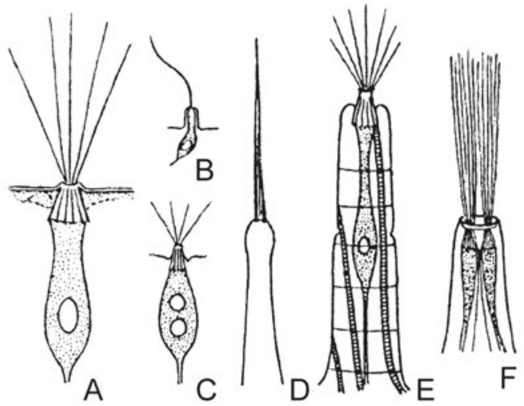

Fig. 4.24: Forms of lateral antennae in Monogononta. (A) Basic type, (B) *Lecane ligona*, (C) *Synchaeta tavina*, (D) *Tetrasiphon hydrocora*, (E) Flosculariidae, scheme, and (F) *Conochilus unicornis*. (From Remane 1933.)

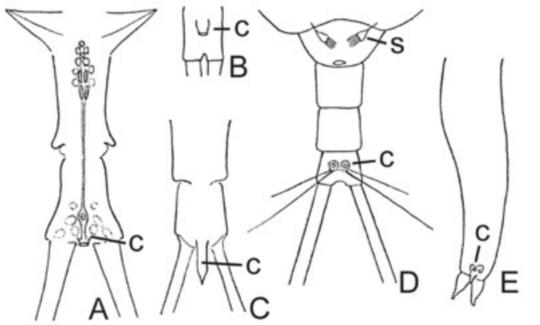

Fig. 4.25: Forms of caudal antennae in Monogononta. (A) *Trichotria tetractis*, (B) *Lepadella ovalis*, (C) *Trichotria pocillum*, (D) *Euchlanis*, and (E) *Brachionus*. Abbreviations: c, caudal antenna; s, sense organ. (Modified from Remane 1933.)

depends on the food, i.e., the carotenoids assimilated (Birky 1964). Light-refracting globules without pigment have been referred to colorless eyes (e.g., *Encentrum*) and may represent photoreceptive structures that lack a pigment cup containing screening pigment. The eyes are usually situated frontally or dorsally (rarely ventrally, e.g., *Hexarthra*) on the apical field, rostrum, and lateral sides of the corona or on the brain. According their specific location, they are called apical, frontal, rostral, or lateral eyespots, etc., and cerebral eyes. Cerebral eyes lie on the brain and are mostly single or sometimes paired but often fused (e.g., Notommatidae, Synchaetidae), unlike the other eye types, which are usually paired. Some species show a combination of frontal, lateral, and cerebral eyespots, e.g., *Eosphora najas* has 5 eyespots. The ultrastructure of the ocelli and cerebral eyes has been studied by, e.g., Clément et al. (1983) and Clément & Wurdak (1991). The frontal eyespots of *Rhinoglena frontalis* and apical eyespots of *Filinia longiseta* consist of anterior ciliated cells forming a cup with screen pigment, and enclosing a nerve ending from which microvilli containing the photosensitive pigment emanate. The paired lateral eyes of *Asplanchna brightwellii* and the paired median ones of *Trichocerca rattus* show sensory nerve endings bearing ampulla-shaped photoreceptive cilia (Fig. 4.26), separated from the outside medium by a thin cuticle. A light-refracting lipid globule in front of the microvilli of the ocelli is present in many species and referred to as lens in the older literature (Remane 1933).

The cerebral eye is integrated into the brain and associated with the epithelial cells surrounding the latter. The ultrastructure of the cerebral eyes (Fig. 4.27) of the 5 species studied to date is unique for each of them (Eakin & Westfall 1965, Clément 1980, Clément

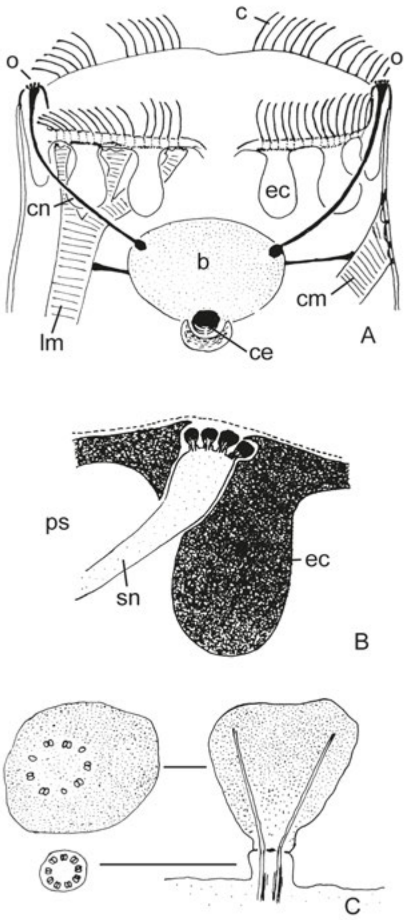

Fig. 4.26: Ocelli and cerebral eye of *Asplanchna brightwellii*. (A) General scheme of head, (B) Detail of ocellus, and (C) Detail of ampulla-shaped cilium with cross sections. Abbreviations: b, brain; c, corona; ce, cerebral eye; cm, circular skeletal muscle; cn, cerebral neuron; ec, epithelial socket cell; lm, longitudinla skeletal muscle; o, ocellus; sn, sensory nerve ending with ampulla-shaped cilia; ps, pseudocoel. (From Clément & Wurdak 1991, with permission.)

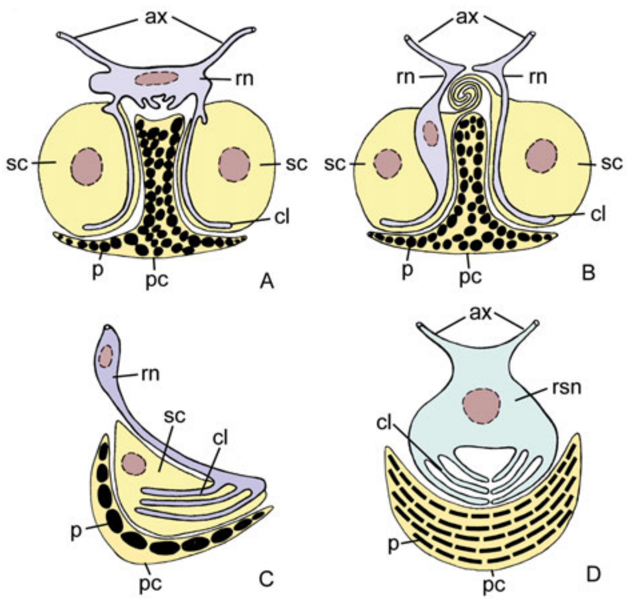

Fig. 4.27: Cerebral eyes of monogonont rotifers. (A) *Brachionus calyciflorus*, (B) *Brachionus plicatilis*, (C) *Trichocerca rattus*, and (D) *Asplanchna brightwellii*. Abbreviations: ax, axon; cl, cytoplasmic lamella of relay neuron; pc, epithelial cell with pigment cup or cavities containing pigment granules or platelets (p); sc, sensory neuron lacking axon; rn, relay neuron with axon leading to the neuropile of the brain; rsn, relay neuron becoming sensory neuron with stacked lamellae. (From Clément & Wurdak 1991, with permission.)

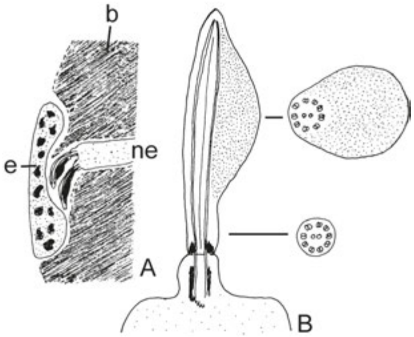

Fig. 4.28: Cerebral eye of the bdelloid *Philodina roseola*. (A) Location of the eye at periphery of brain and (B) detail of ampulla-shaped cilium in longitudinal and cross section. Abbreviations: b, brain, e, epithelial cell with pigment granules; ne, nerve ending with 2 ampulla-shaped cilia. (From Clément & Wurdak 1991, with permission.)

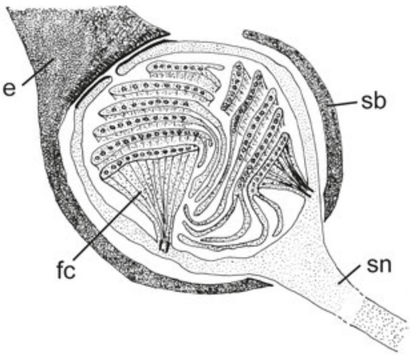

Fig. 4.29: Phaosome of the bdelloid *Philodina roseola*. Abbreviations: e, epithelial cell; fc, stacks of flattened cilia; sb, spherical bulb; sn, sensory nerve. (From Clément & Wurdak 1991, with permission.)

et al. 1983, Clément & Wurdak 1991). The monogononts (*Asplanchna brightwellii, Brachionus calyciflorus, B. plicatilis, Trichocerca rattus*) show an unpaired median epithelial cell containing the red screening pigment composed of pigment granules (*Brachionus, Trichocerca*) or platelets (*Asplanchna*). This epithelial cell is cup-shaped (*Trichocerca, Asplanchna*) or has 2 lateral cavities (*Brachionus*), which are responsible for its x-shape observed *in vivo*. The cavities and cup lodge a sensory neuron lacking axons (*Brachionus, Trichocerca*); they are connected to a single (*B. calyciflorus, T. rattus*) or 2 (*B. plicatilis*) relay neurons sending off axons to the brain. In *Brachionus*, each of the relay neurons sends a single cytoplasmic lamina into the sensory neuron; in *Trichocerca*, the relay neuron forms stacked lamellae penetrating into the unpaired sensory neuron. The structure of the cerebral eye of *Asplanchna* consists of a relay neuron that becomes the sensory neuron, forming stacked lamellae in the pigmented epithelial cup; 2 axons penetrate into the brain. A median cerebral eye is absent in bdelloids, but paired ones, located on either side of the brain, are present in, e.g., *Philodina, Dissotrocha, Embata, Habrotrocha collaris*, and *Abrochtha*. The ultrastructure of the cerebral eye of the only bdelloid studied (*Philodina roseola*) shows that it consists of a nerve ending bearing 2 ampulla-shaped cilia and lodged in an epithelial cell containing granules of screening pigment (Fig. 4.28). The presumed components for photoreception that contain the visual pigment of the above 5 species are different as well: tubular formations of the endoplasmic reticulum (*B. calyciflorus*), a stack of plasma and ER membranes (*B. plicatilis*), stacks of intracytoplasmic plasma membrane (*T. rattus*), lamellar rhabdomeres (*A. brightwellii*), and electron-dense ampulla-shaped cilia (*P. roseola*).

A photoreceptive function was also suggested for the phaosome (Fig. 4.29) of the bdelloid *Philodina roseola* (e.g., Clément 1980, Clément & Wurdak 1991). The unpaired phaosome is located at the base of the rostrum, near the outlets of the retrocerebral apparatus. It consists of a sensory nerve, ending in a spherical bulb containing a stack of fan-shaped flat cilia bearing lateral membrane expansions. The bulb is supported by an epithelial cell.

Other receptors, consisting of ciliated sensory cells, occur in the mouth region, buccal tube, mastax, pseudocoel, penis, cloaca, etc. (Clément et al. 1983, Clément & Wurdak 1991).

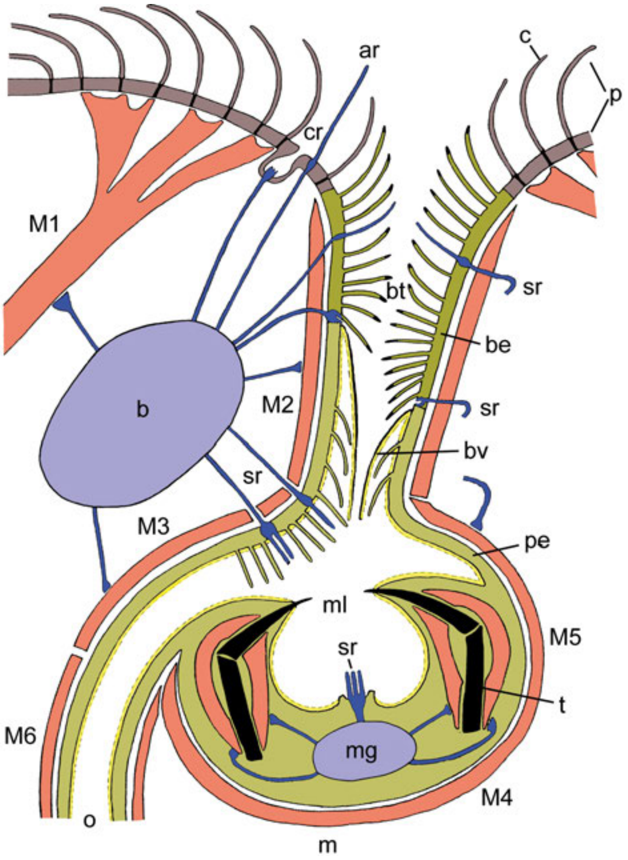

Fig. 4.30: Diagram of oral apparatus: mouth, mastax, and esophagus. Abbreviations: ar, anterior coronal mechanoreceptor; b, brain. be, buccal epithelium; bt, buccal tube; bv, buccal velum; c, cilium; cr, chemoreceptor; m, mastax; mg, mastax ganglion; ml, mastax lumen, M1–M6, muscles and their innervations; o, esophagus; p, pseudotrochus; pe, pharyngeal epithelium; sr, sensory receptor; t, trophi. (Modified from Clément & Wurdak 1991, with permission.)

4.2.6 Intestinal system

4.2.6.1 Intestinal system of the female

The anatomy of the intestinal system is thoroughly documented in Remane (1933). For studies of its ultrastructure relying on TEM, see, e.g., Clément et al. (1980a, b, c, 1983) and Clément & Wurdak (1991). The digestive system is similar in most bdelloids and monogononts and consists of a mouth, buccal tube, pharynx with mastax, esophagus, stomach, intestine, cloaca, and cloacal aperture or anus. In most species, the gastrointestinal system runs straight from mouth opening to anus but is U-shaped in species with anteriorly displaced anus (e.g., Conochilidae). The mouth commonly opens apically to ventrally in the centre of the buccal field and frequently at the base of a more or less strongly developed funnel (Fig. 4.30). Several sensory receptors, supposed to participate in food intake, are present in the mouth region (Wurdak et al. 1983). The mouth leads to the buccal tube or opens directly into the pharynx. The buccal tube is formed by a simple epithelium, consisting of mushroom-shaped cells with the caps organized in an imbricate way forming the tube wall, and the stalks representing the cell bodies containing nuclei and most of the cytoplasm (Clément et al. 1980b). Sheaths of circular and longitudinal muscles surround the buccal tube (e.g., Clément et al. 1980c). The buccal tube is short and devoid of cilia or absent in raptorial species (e.g., *Asplanchna*, *Dicranophorus*) and more or less long and cylindrical and covered with cilia in filter feeders (e.g., *Brachionus, Philodina*). The buccal cilia are characterized by an electron-dense tip. In many rotifers, the buccal tube ends in a supple myelin-like structure, the buccal velum, separating the buccal lumen from the pharynx or mastax lumen, thus preventing rejection of the ingested food (Clément et al. 1980a, 1983). The buccal epithelium is provided with several sensory receptors (Wurdak et al. 1983).

The pharynx is short and usually ciliated but may be lacking in species with trophi that can be thrust out through the mouth opening (e.g., Dicranophoridae). Pharyngeal cilia have a classical 9 × 2 + 2 configuration but are surrounded by a double membrane that is an extension of the double membrane around the pharyngeal lumen (Clément & Wurdak 1991). The pharynx leads to the cavity of a muscular masticatory apparatus, the mastax (Figs. 4.30 and 4.31). This cavity occupies the anterior, dorsal, or anterodorsal part of the mastax and opens posteriorly into to the esophagus. The epithelial wall of the mastax cavity is lined with a thin cuticle. The cuticle is lamellar (“myelinic cuticle”) and formed by the superimposition of cellular unit membranes coalescing in 2 to 30 and more bilayers (Clément 1993). The basal part of the mastax ventrally contains the sclerotized jaws or trophi and their associated muscles, epithelial cells, salivary glands, sensory receptors, and a small nerve ganglion.

The trophi comprise a set of hard, cuticularized extracellular elements formed by various epithelial cells

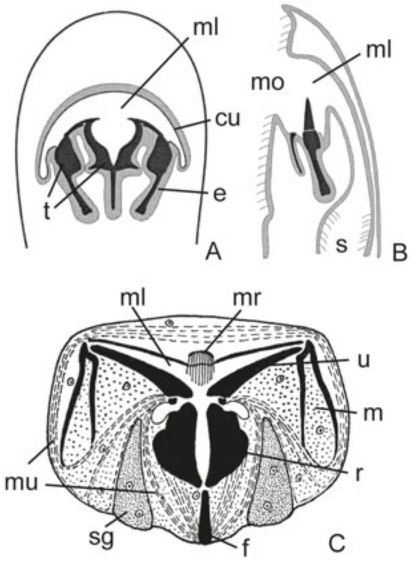

Fig. 4.31: Diagram of mastax. (A) Dorsal view, trophi forcipate, (B) lateral view, trophi forcipate, and (C) cross section, trophi malleate. Abbreviations: cu, cuticle; e, epithelium; f, fulcrum; m, manubrium; ml, mastax lumen; mo, mouth; mr, mastax sensory receptor; mu, muscles; r, ramus; s, stomach; sg, salivary gland; t, trophi; u, uncus. (Modified from de Beauchamp 1965 and Riemann & Ahlrichs 2008.)

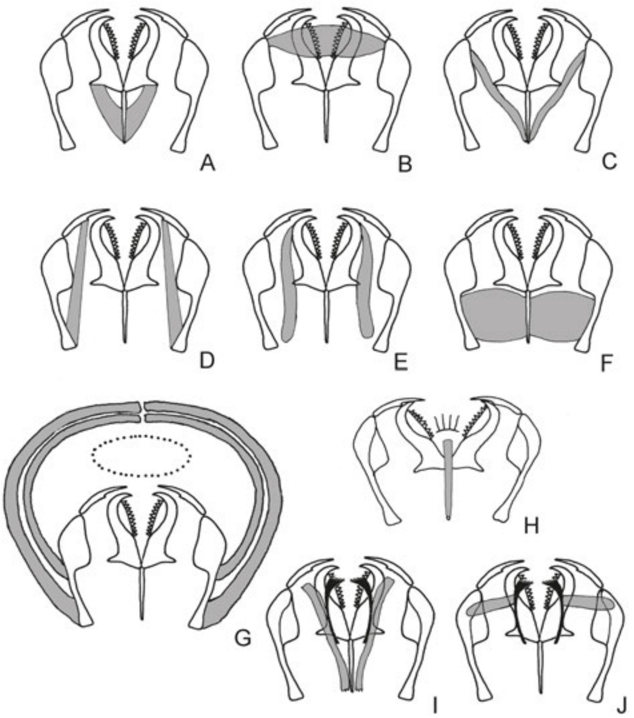

Fig. 4.32: Diagram of the musculature of the trophi apparatus of *Dicranophorus forcipatus*: (A–G) dorsal and (H–J) ventral. (A) Musculus fulcro-ramicus, (B) Musculus transversus manubrii, (c) musculus fulcro-manubricus, (d) musculus manubrico-uncus, (e) musculus caudo-ramicus, (f) musculus circumglandis, (g) musculus manubricus perioralis, (h) mastax receptor retractor, (i) musculus hypopharyngeus, and (j) musculus manubrico-hypopharyngeus. (Modified from Riemann & Ahlrichs 2008.)

(e.g., Koehler & Hayes 1969a, b, Clément & Wurdak 1991). Each element is build up of tubular sclerite bodies composed of an electron-dense core surrounded by electron-lucent material (e.g., Rieger & Tyler 1995). Some elements (ramus and manubrium) are hollow and contain the nucleus and perinuclear cytoplasm of an epithelial cell(s); others (uncus and fulcrum) are solid, lying next to their epithelial cell nucleus and cytoplasm. The main trophi elements (Fig. 4.31 C) consist of an unpaired median fulcrum, and 3 paired elements: ramus, uncus, and manubrium, connected by ligaments and moved by muscles connecting the different elements with each other and with the wall of the mastax. The development of the different elements and associated muscles is considerably modified in the different families or species, in relation to their mode of life and feeding habits (see below for a detailed description of the different trophi types).

The highly complex musculature of the different trophi types is poorly known and relies on histological observations (e.g., Martini 1912, Seehaus 1930, Stossberg 1932, Remane 1933, de Beauchamp 1909, 1965), and TEM and/or CLSM of the monogononts *Bryceella stylata, Dicranophorus forcipatus, Notholca acuminata, Pleurotrocha petromyzon, Proales tillyensis Trichocerca rattus, Asplanchna brightwellii, Notommata copeus, Brachionus calyciflorus*, and the bdelloid *Philodina roseola* (Clément 1987, Clément & Wurdak 1991, Sørensen et al. 2003, Riemann & Ahlrichs 2008, Wilts et al. 2010, Wulfken et al. 2010). There usually is a series of paired muscles (e.g., 13 in *T. rattus*, 6 in *B. stylata*) joining specifically paired trophi elements or trophi elements and mastax wall (Fig. 4.32). Paired muscles found in several mastax types studied to date are, e.g., abductor muscles interconnecting cauda of manubria with base of rami, muscles interconnecting the distal end of the fulcrum with the head of the manubria, malleus flexors interconnecting the cauda of the manubria with the unci, muscles connecting manubria to both the median and peripheral mastax floor, etc. The number of unpaired muscles is restricted: e.g., a strong hypopharynx muscle connects the enlarged dorsodistal end of the fulcrum with the opposite wall of the mastax lumen in species with virgate trophi; a weak retractor lies on the dorsal edge of the fulcrum and terminates in the mastax sensory receptor in species with forcipate and modified malleate trophi; the rami adductor muscle connects both rami distally in, e.g., malleate and incudate trophi, and a transversal manubrium adductor connects the heads of both manubria in, e.g., malleate, modified malleate, forcipate, and virgate trophi. Comparison of the musculature in different species, and identification of homologous muscles is difficult. Possible homologous muscles are: the paired muscle connecting fulcrum and caudal part of rami, the paired muscle attached to the caudal end of the fulcrum and the dorsal edge of the head of the manubria, the paired muscle joining the distal end of the manubria and the unci, the paired muscle interconnecting the distal end of the manubria with the anterolateral part of the rami, and the unpaired hypopharynx muscle/fulcrum sensory receptor retractor (e.g., Riemann & Ahlrichs 2008, Wilts et al. 2010, Wulfken et al. 2010).

In bdelloids, mastax muscles are often laminar, and short with few cross-striations, unlike the longer and regularly striated muscles observed in monogononts (Clément & Wurdak 1991, Clément 1993). In *T. rattus*, all muscles proved unicellular, except one. The attachment of the muscles to the trophi elements and their adjacent epithelial cells is by desmosomes. The flexible ligaments connecting the trophi elements contain electron-dense cuticular material. The muscles are innervated by the mastax ganglion situated at the mastax floor. Several sensory receptors, such as ciliated pits and ciliated cells, occur between the trophi and the mastax floor, and on the roof of the mastax (Clément et al. 1983, 1991, Wurdak et al. 1983).

A variable number of mononucleate or multinucleate salivary glands are generally present, closely associated with the mastax ventrolaterally (Fig. 4.33), or incorporated in the mastax wall (Fig. 4.31 C); apparently, they also may be lacking. Their anterior part is often transformed into a large reservoir (e.g., *Asplanchna*, Flosculariacea, median salivary gland of several bdelloids). The ducts open anterior to the trophi or in the buccal tube.

The esophagus is short to long. de Beauchamp (1909), and later confirmed by Clément et al (1980b, 1991), distinguished 2 sections: the cuticular and the ciliary esophagus. The cuticular esophagus is the tube emanating from the mastax toward the stomach. It is an expansion of the dorsal pharyngeal wall of the mastax, composed of a thin epithelial layer surrounded by a thicker muscular layer and lined by a fine cuticle. The ciliated esophagus is the section between the cuticular esophagus and the stomach and made of ciliated cells, the cilia of which end in the stomach lumen. The cilia are long and form a vibratile flame, helping to move down the food and preventing regurgitation. The periesophageal musculature may consist of longitudinal and circular muscles or a reticular muscle layer and appears correlated with different modes of feeding (Remane 1933). Several types of esophagus have been recognized, based on its total length, length and width of cuticular and ciliary sections, presence of a vibratile flame, etc. (Remane 1933).

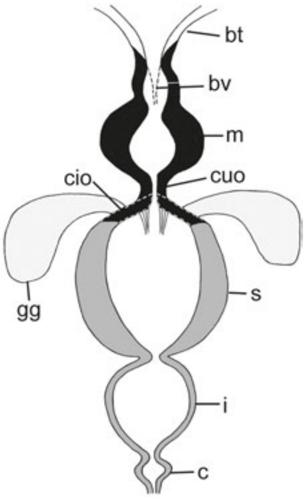

Fig. 4.33: Diagram of the intestinal system in rotifers. Abbreviations: bt, buccal tube; bv, buccal velum; c, cloaca; cio. ciliary esophagus; cuo, cuticular esophagus; gg, gastric gland; i, intestine; m, mastax; s, stomach. (Modified from Clément & Wurdak 1991, with permission.)

The stomach wall is syncytial in bdelloids and cellular with usually clearly defined cells in monogononts. In bdelloids (*Philodina roseola, Habrotrocha rosa*), the stomach lumen is lined by a thick, dense fibrillar terminal web (Fig. 4.34), lying directly under the plasma membrane (Mattern & Daniel 1966a, Schramm 1978a, Clément & Wurdak 1991). This web is perforated by large pores containing invaginations of the stomach cell membrane, pinching off digestive vesicles and vacuoles toward the cytoplasm. In monogononts, a thin fibrous terminal web, pierced by pores, may be present (*Asplanchna*) or lacking (*Brachionus, Filinia, Notommata copeus, Rhinoglena, Trichocerca rattus*). Digestive vacuoles are formed by endocytosis as well (Wurdak 1987, Clément & Wurdak 1991). The stomach is enveloped by a mesh of circular and longitudinal muscles or by syncytial muscle fibers. The anterior part of the stomach may be provided with an offset proventriculus (e.g., many *Encentrum* and *Proales*). Blind sacks of the stomach wall often occur in species showing intracellular digestion and/or symbiotic zoochlorellae (e.g., *Ascomorpha, Birgea, Dicranophoroides caudatus, Gastropus, Itura*).

Usually, there is a pair of syncytial gastric glands opening at the junction of ciliated esophagus-stomach by a pore directly or by a more or less long duct. The shape of the glands is variable and may be ovate, rounded, lobate, kidney-shaped, tubular, etc. The glands are rich in rough

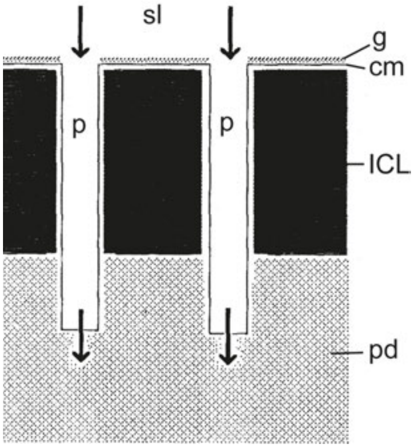

Fig. 4.34: Diagram of the apical part of the syncytial wall of the stomach in Bdelloidea. Abbreviations: cm, cell membrane; g, glycocalyx; ICL, intracytoplasmic lamina; p, pore; pd, part of cytoplasm with digestive vacuoles; sl, stomach lumen. (From Clément 1993, with permission.)

endoplasmic reticulum and Golgi complexes; secretory granules accumulate in the basal part of the glands next to the stomach (e.g., Clément & Wurdak 1991). The secretions of the gastric glands play a primary role in the extracellular digestion. Other gland-like structures of variable shape and number (Remane 1933), remembering gastric glands by structure and inclusions (de Beauchamp 1909), and mostly situated on the dorsal stomach wall occur in several species (e.g., *Enteroplea lacustris*, *Epiphanes clavulata*, *Microcodon clavus*, *Tetrasiphon hydrocora*). Gastric glands are rarely absent (e.g., *Albertia typhlina*), but mostly lacking in species with stomach blind sacks and/or symbiotic zoochlorellae.

The stomach either is distinctly constricted off from the intestine by a muscular sphincter, or merges gradually into it. The syncytial intestine is thin-walled and provided with motile cilia and microvilli; the latter may be replaced by atypical flattened cilia containing microtubules (Clément 1977, Clément & Wurdak 1991). In bdelloids, the microvilli show submembrane helicoidal filaments, which are lacking in monogononts. Externally, the intestine is provided with a continuation of the musculature of the stomach.

The intestine empties in a short, contractile cloaca, opening dorsally at the base of the foot. In species with ventrally displaced foot, it opens terminally or even ventrally (*Ploesoma*); in Flosculariidae, it opens on a papilla. The lumen of the cloaca is lined by a thin epithelial syncytium surrounded by a reticular muscle layer. The cloacal wall (*Asplanchna brightwellii*) includes a multicellulary sensory receptor, with cilia and microvilli projecting toward the cloacal opening. The sensory cells are near the cloacal ganglion innervating the cloacal muscles. The syncytial wall of the cloaca merges imperceptibly into the syncytial integument, and is seldom ciliated (e.g., Clément et al. 1983, Clément & Wurdak 1991, Ahlrichs 1993). Oviducts, bladder, or protonephridial ducts open in the cloaca as well. In some species, there is no cloaca or cloacal aperture, and fecal matter is ejected through the mouth (e.g., *Asplanchna*) or stored as defecation pellets in the stomach (e.g., *Ascomorpha*).

There are many variations (Fig. 4.35) on the general scheme of the intestinal system as outlined above (see Remane 1933). In Collothecacea, the anterior end is transformed into a large buccal funnel. A semicircle of cilia in this funnel separates an anterior part or vestibulum, from a posterior chamber, the infundibulum. The mouth is at the base of the infundibulum, and leads to a narrow esophagus hanging freely in a very large cavity, the proventriculus. The small trophi are situated at the bottom of the proventriculus. The proventriculus is homologous to the mastax with its lumen enlarged into a food-storage organ.

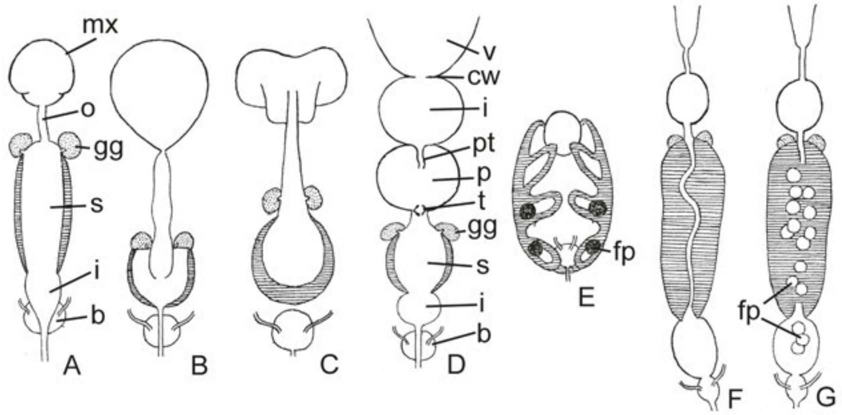

Fig. 4.35: Variation of the intestinal system in Monogononta (A–E) and Bdelloidea (F, G). (A) *Encentrum*, (B) *Synchaeta*, (C) *Asplanchna*, (D) *Collotheca*, (E) *Ascomorpha ecaudis*, (F) *Philodina*, and (G) *Habrotrocha*. Abbreviations: b, bladder; cw, ciliary wreath; fp, fecal pellet; gg, gastric gland; i, intestine; if, infundibulum; mx, mastax; o, esophagus; p, proventriculus; pt, pharyngeal tube; s, stomach; v, vestibulum. (From Donner 1956, 1965.)

Digestion is generally extracellular, although intracellular digestion can take place (*Asplanchna*) after an initial extracellular digestion (Wurdak 1987). In some monogonont genera (e.g., *Ascomorpha*) and the bdelloid family Habrotrochidae, digestion is intracellular. In Habrotrochidae, the stomach is a syncytial protoplasmic mass without lumen. The food is formed into pellets or food vacuoles in a short chamber behind the mastax; the vacuoles become digested when circulating in the stomach protoplasm.

4.2.6.2 Trophi

The trophi (Figs. 4.36–4.39) may be organized in a strictly bilaterally symmetrical (most species) to highly asymmetrical way (*Aspelta*, Trichocercidae). The fulcrum (absent in bdelloids) serves as an attachment for the 2 rami; together, these 3 elements are referred as incus. Adjoining them on each side are an uncus and manubrium, which hinging together form the malleus. The fulcrum is of variable length and can be plate- or rod-shaped and distally tapering, expanding, or forked, or provided with a basal plate. The rami are tall or flat in cross section, and their shape varies from roughly triangular to strongly elongate and almost parallel-sided. Their inner margin can be smooth or bears elongate sclerite bodies, the rami scleropili, which may fuse into a ridge and/or a series of tooth-like projections. At the outer part of their base, rami may show lateral projections, the alulae. Rami and fulcrum lie in the same plane, or form a more or less great angle with each other. The rami operate like a forceps with the fulcrum as the base. The unci consist of a single tooth, or few to many teeth, often firmly fused into rigid plates. Each uncinal tooth consists of a head and shaft; the teeth are mostly unequal. A subuncus, composed of minute teeth, rods, or plate-shaped elements, is mostly present, and situated distally beneath the uncus. The manubria are more or less triangular, or crescent- or rod-shaped supports of the unci. They are composed of an expanded head or clava, connected to the uncus, and a more or less strongly elongate shaft terminating in a handle-like distal end, the cauda, which is present in Ploima but absent in Gnesiotrocha and Bdelloidea. The head or clava is composed of 3 chambers that may be strongly reduced or absent. The malleus lies in the same plane as the incus, or the unci and manubria stand in different planes to each other and/or to the incus. A variable number of diverse accessory elements, e.g., epipharynx, hypopharynx, suprarami, etc., is often present in monogononts.

Studies by SEM of the embryonic development of the malleate trophi (Fig. 4.37) show that the first observable

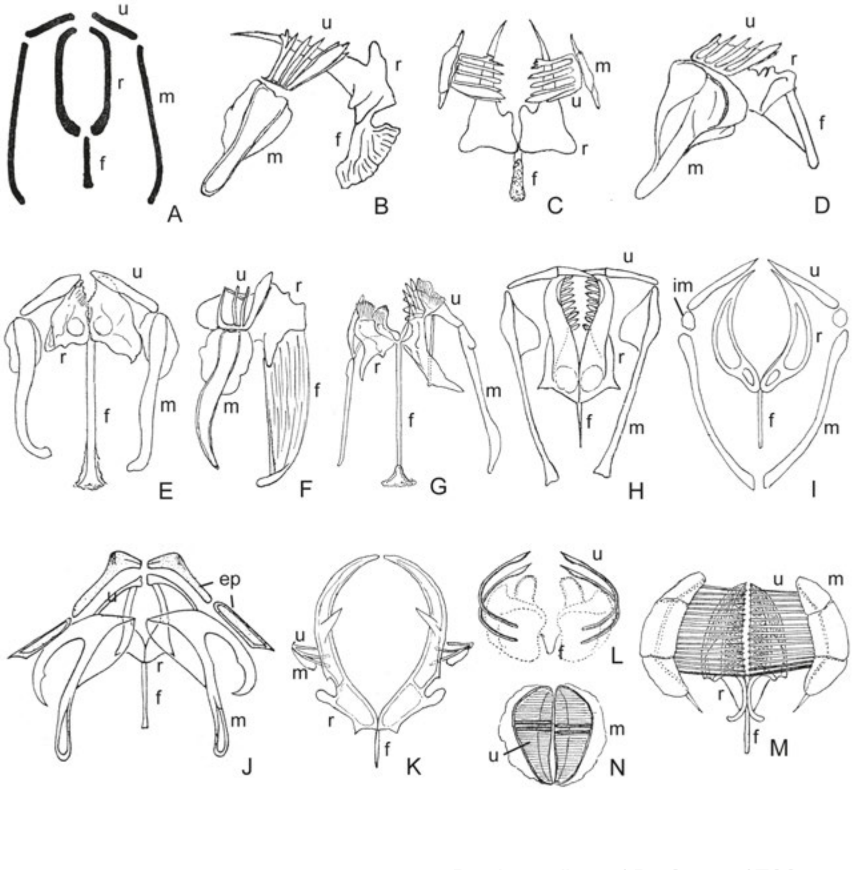

Fig. 4.36: The main trophi types. (A) Basic plan, (B–D) malleate (*Euchlanis*: B, right; C, ventral view); *Proales decipiens*, (D) right; (E–G) virgate (*Notommata copeus*: E, ventral; D, right; G, *Trichocerca rattus*, ventral), (H–I) forcipate (H, *Dicranophorus epicharis*, ventral; I, *Encentrum*), (J) cardate (*Lindia janickii*, ventral), (K) incudate (*Asplanchna*), (L) uncinate (*Collotheca*), (M) malleoramate (*Filinia*, ventral), and (N) ramate (*Macrotrachela*). Abbreviations: ep, epipharynx; im, intramalleus; f, fulcrum; m, manubrium; r, ramus; u, uncus.

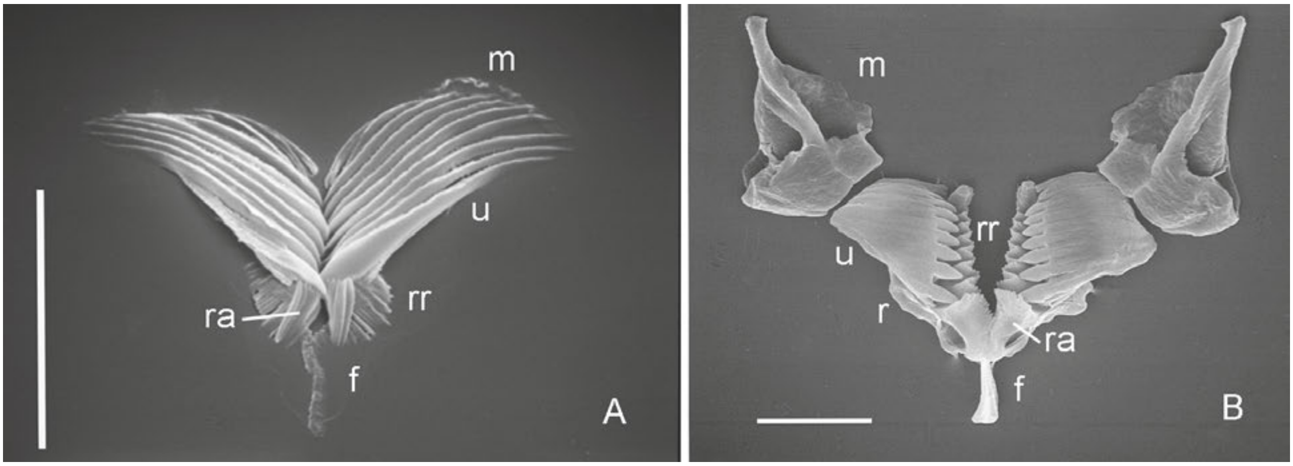

Fig. 4.37: Development of malleate trophi. (A) Early embryo and (B) adult. Abbreviations: f, fulcrum; m, manubrium; r, ramus, ra, rami apophysis; rr, reinforced ramus ridges; u, uncus. Scale bar=10 µm.

and distinctly sclerotized structures are a double row of elongate sclerite bodies along the longitudinal axis, wherein the future unci, reinforced ramus ridges, rami apophyses, and fulcrum are recognizable (De Smet, personal observation). By addition of sclerite bodies and apposition of amorphous sclerite material, the trophi attain their definitive shape and size in the fully grown embryo. After hatching ramate, malleate, virgate, forcipate, malleoramate, and uncinate trophi apparently do not change in size or shape and remain constant during the life of the rotifer (Fontaneto et al. 2003, Fontaneto & Melone 2005, 2006), although some post-embryonic growth cannot be ruled out in some taxa with incudate trophi, viz. *Asplanchna* (Fontaneto & Melone 2005).

Nine main types of trophi are recognized (Fig. 4.36), based on the shape and size of the elements, the presence of any accessory parts, and the way they operate. Several transitional types are known, and some other types are that specialized and modified that they cannot be classified into any of the main types. Shape of trophi is an utmost important character in rotifer taxonomy (Wallace et al. 2006), and even subtle differences in trophi shape may be useful in solving complexes of cryptic species; in monogononts, small details on the trophi shape can distinguish the species of the *Epiphanes senta* complex (Schröder & Walsh 2007) and between *Brachionus manjavacas* and *B. plicatilis* (Fontaneto et al. 2007). In bdelloids, the newly described *Abrochtha* from the USA have statistical differences in the number of minor teeth (Birky et al. 2011).

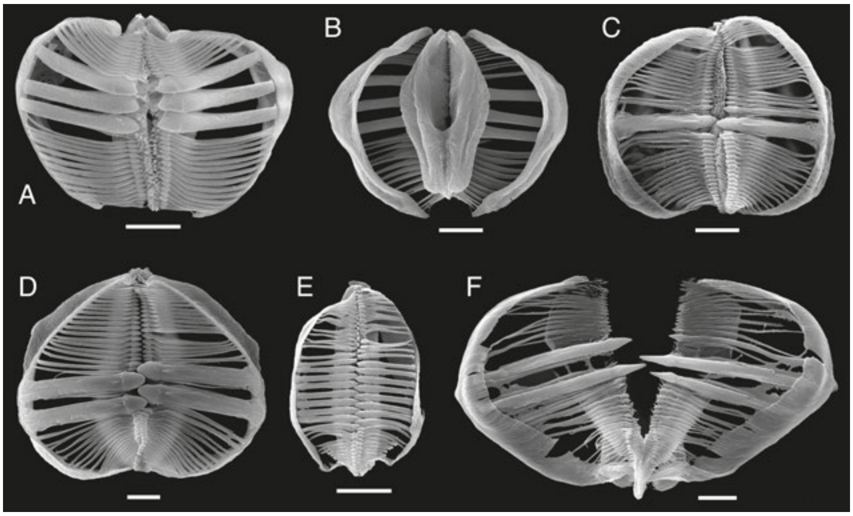

Fig. 4.38: SEM pictures of the ramate trophi in Bdelloidea. (A, B) *Dissotrocha aculeata*, (C) *Anomopus telphusae*, (D) *Rotaria tardigrada*, (E) *Otostephanos donneri*, (F) *Abrotrochtha carnivora*. (A, C–F) Dorsal view and (B) ventral view. Scale bar = 5 µm.

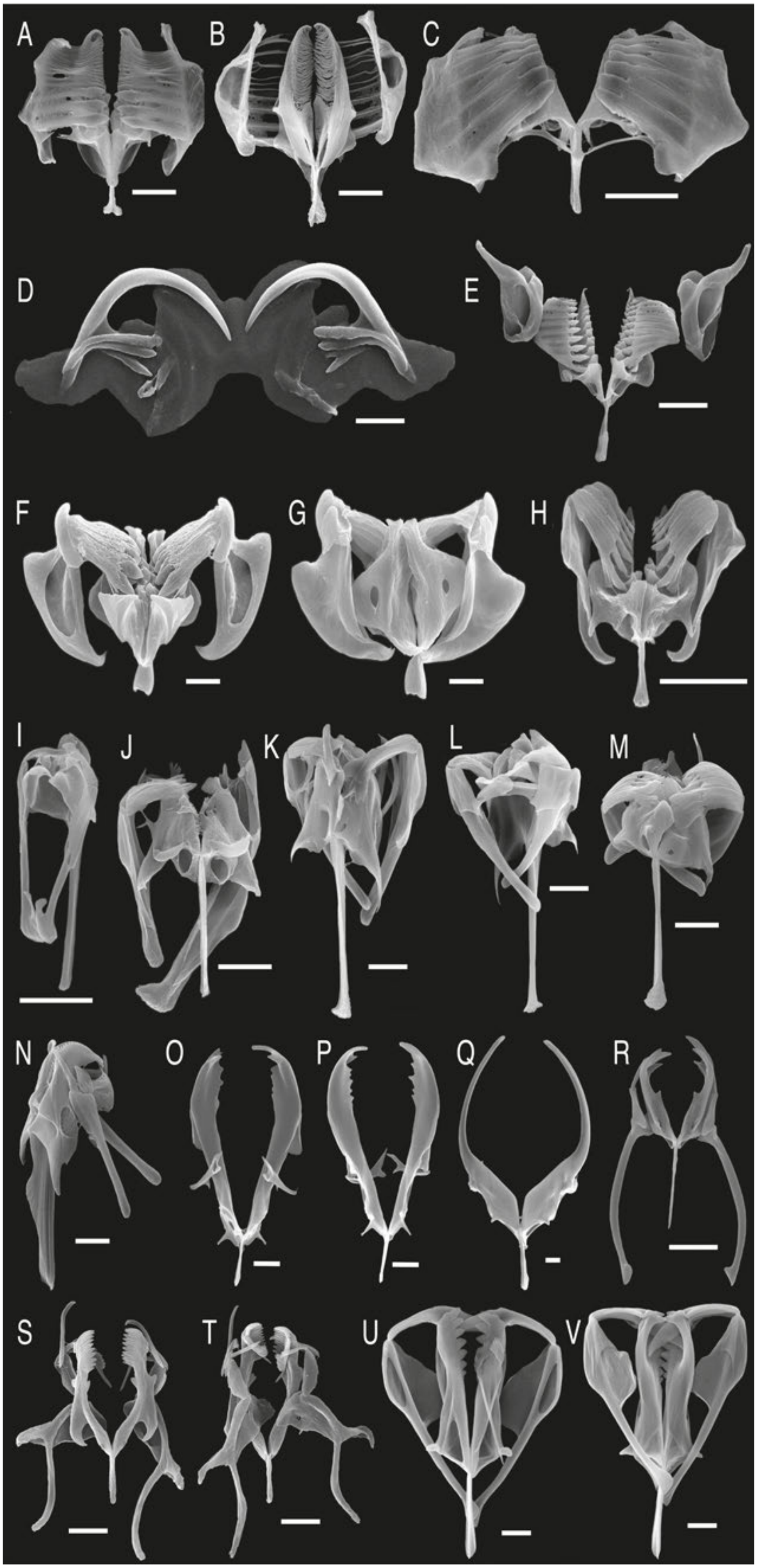

Fig. 4.39: SEM pictures of trophi types in Monogononta. (A, B) *Floscularia ringens*, (C) *Hexarthra* sp., (D) *Cupelopagis vorax*, (E) *Cyrtonia tuba*, (F, G) *Brachionus manjavacas*, (H) *Proales similis*, (I) *Cephalodella* sp., (J) *Pleurotrocha atlantica*, (K, L) *Notommata glyphura*, (M) *Notommata codonella*, (N) *Eothinia elongata*, (O, P) *Asplanchna priodonta*, (Q) *Asplanchnopus multiceps*, (R) *Encentrum algente*, (S, T) *Lindia deridderae*, and (U, V) *Dicranophorus forcipatus*. Scale bar = 10 µm.

SEM pictures of the trophi can be found in the references mentioned below for the different types and in Figs. 4.38 and 4.39.

Ramate. Rami sickle-shaped, flat. Fulcrum absent. Unci broad, usually with numerous teeth, occasionally broad semi-circular striated plates, usually with broad and narrow teeth. Manubria sickle-shaped, as lateral bands. Grinding. In subclass Bdelloidea only (e.g., Melone et al. 1998b, Melone & Fontaneto 2005).

Malleoramate. Rami more or less triangular, flat. Fulcrum short. Unci broad, with numerous teeth, occasionally resembling striated plates, proximal teeth usually enlarged. Manubria crescent-shaped with 3 superimposed major chambers, without shaft. Grinding. In order Flosculariacea only (e.g., Nogrady & Segers 2002, De Smet 2005a).

Uncinate. Similar to malleoramate type, but all trophi elements except unci strongly reduced. Unci teeth 2 or from 4 to 5, and only the first or first 2 of stout build, elongate and curved, forming supporting rods for mastax. Tearing. Only in Order Collothecacea: Atrochidae, Collothecidae.

Malleate. All parts of stout build. Rami more or less triangular, flat, inner margin usually toothed. Fulcrum short. Unci with several (4–12) firmly connected teeth, often fused into plate. Manubria provided with a fairly short shaft. The malleate trophi are adapted for gripping, grinding, and pumping. In Order Ploima: e.g., Epiphanidae, Brachionidae, Euchlanidae, Mytilinidae, Trichotriidae (e.g., Segers et al. 1994b, De Smet & Gibson 2008).

The submalleate type of Lecanidae is characterized by manubria showing a relatively long and incurved shaft (e.g., Segers 1995).

Virgate. All parts can be of slender build and/or thin. Rami broad, more or less triangular, recurved dorsally forming hemispherical dome. Fulcrum strongly elongated, distal end usually more or less expanded or strongly bent dorsally. Unci with few teeth, often only the first of stout build or teeth reduced. Manubria mostly with elongate shafts. Often strongly asymmetrical (e.g., *Trichocerca*). The virgate trophi type is the most variable of all. Used for swallowing food by pumping without crushing or piercing and sucking. The pumping action is produced by a powerful hypopharyngeal muscle. In Order Ploimida, e.g., Gastropodidae, Trichocercidae, Synchaetidae (e.g., Nogrady & Segers 2002).

The malleovirgate type showing many uncinal teeth is a transition between the malleate and virgate type. In Proalidae (e.g., De Smet 1996).

Incudate. Rami strongly elongate, curved, pincer-like. Fulcrum short. Unci and manubria strongly reduced. Specialized for seizing. Only in Asplanchnidae (e.g., Gilbert et al. 1979).

Cardate. Rami lyrate. Fulcrum medium long. Unci a few distinct teeth, first largest, or a striated plate. Manubria with well developed head and shaft, head with characteristic crescent- or rod-shaped ventral apophysis. Species-specific accessory trophi elements present, often numerous. Adapted for pumping; the pumping action is produced without the hypopharyngeal muscle: the lumen is widened by a rolling motion of the trophi. Only in Lindiidae (e.g., Nogrady & Segers 2002, De Smet 2005b).

Forcipate. Rami strongly elongate, straight, or curved, pincer-like, with toothed tips, inner margins often with few to numerous teeth. Fulcrum usually short to medium long. Unci strong, a single or few teeth only. Manubria rod-shaped, long, head reduced; often with intramalleus between uncus and manubrium. Seizing; rami and unci can be thrust out from mouth (Dicranophoridae). In Dicranophoridae and Ituridae (e.g., De Smet & Pourriot 1997).

In the hemiforcipate type, rami lack apical and medial teeth. In Asciaporrectidae (De Smet 2006).

Fulcrate. Fulcrum long, well developed. Rami short with strong, characteristic alulae. Unci small. Manubria absent. Pumping action performed by hypopharynx muscle attached to fulcrum. Only in Order Seisonacea (e.g., Segers & Melone 1998).

4.2.6.3 Intestinal system of the male

The intestinal system of the male shows transitions from fully developed to completely absent. To date, *Rhinoglena frontalis* is the only species studied in which the males possess a fully developed and functional system similar to the female (Melone 2001). The male trophi are similar to the female but display fewer uncinal teeth and a reduction of the size to about 70%. In several species, e.g., *Asplanchnopus multiceps*, *Eosphora najas*, and *Lacinularia flosculosa*, the male intestinal system is well developed, but trophi are apparently lacking (Hamburger 1907, de Beauchamp 1965). In other males, the digestive tract consists of a strand of stomach cells with distinct lumen and indications of gastric glands (e.g., *Mytilina*, *Synchaeta*) or it is a strand without lumen (e.g., *Asplanchna priodonta*); the cellular strand supports the testis. The digestive tract may be further reduced to a globular mass of cells without lumen (e.g., *Asplanchna brightwellii*, *Encentrum martes*), supposed to form an energy source. The intestinal system is completely absent in males of, e.g., *Conochilus*, *Filinia*, *Hexathra, Keratella, Polyarthra, Pompholyx*, and *Trichocerca* (e.g., Wesenberg-Lund 1923). The sensory receptors in the mouth region of the female, involved in feeding, are absent (Wurdak et al. 1983).

4.2.7 Body cavity

The body cavity of the rotifers is considered a pseudocoel, as it is not lined by an epithelium, but by extracellular matrix. It is usually a spacious cavity, apparently lacking fibrils or microfilaments of collagen (Clément & Wurdak 1991, Clément 1993). The pseudocoel of several taxa, e.g., *Asplanchna, Proales, Synchaeta*, and Collothecacea, contains free amoeboid cells or amoebocytes (Nachtwey 1925, Remane 1933, Baumann et al. 2000); these cells could not be demonstrated in *Brachionus, Notommata*, and *Trichocerca* (Clément 1980). The amoebocytes form a highly dynamic, 3-dimensional polygonal network of filopodia. The cytoskeleton of the filopodia contains F-actin and microtubules that are often organized in bundles. Filopodial motion types include lateral junction displacement, formation and extension of free-ending filopodia, and fusion of filopodial strands, resulting in enlargements, diminutions, and extinctions of the filopodial polygons, and in the formation of new polygons (Baumann et al. 2000). An intense and fast particle transport takes place in the filopodial strands. The amoebocytes are often vacuolated, and contain inclusions, "bacteroids", pigments, oil droplets, etc. In some species (e.g., *Cupelopagis vorax*, adult sessile *Collotheca, Proales*), specialized immobile amoeboid cells, the excretophores, apparently accumulate catabolites as excretion particles. The excretophores often pile up symmetrically near, e.g., the longitudinal and circular muscles, and the anterior part of the protonephridial tubule; their number and size increases with age (Remane 1933).

Salt composition and volume of the pseudocoelomic fluid are regulated by the protonephridia (e.g., Braun et al. 1966, Pontin 1966). The pseudocoel functions as a hydrostatic skeleton, and supposedly as respiratory and circulatory system, its pseudocoelomic fluid being replenished by the oxygen carrying water taken in by the digestive tract, and subsequently eliminated through the protonephridia.

4.2.8 Excretory system

4.2.8.1 Excretory system of the female

The excretory system of rotifers has been studied by LM (e.g., Remane 1933, Brakenhoff 1937, Pontin 1964) and TEM (e.g., Braun et al. 1966, Mattern & Daniel 1966b, Warner 1969, Schramm 1978b, Clément & Wurdak 1991, Ahlrichs 1993, Riemann & Ahlrichs 2010). It consists of 2 similar protonephridia lying ventrolaterally in the pseudocoel. The protonephridial apparatus is formed by 3–4 multinucleate cells and consists of few to several flame bulbs or terminal organs, attached to collecting tubules or capillary canals, which are connected to the main canals; the main canals discharge in an unpaired and contractile urinary bladder, or in a contractile cloaca (Fig. 4.40).

The flame bulbs (Fig. 4.41) are conical and laterally flattened, appearing cylindrical or fan-shaped depending on their orientation (e.g., *Asplanchna priodonta, A. brightwelllii, Dicranophorus forcipatus, Notommata copeus*) or almost cylindrical and round in cross section (e.g., *Encentrum mucronatum, Erignatha clastopis, Proales reinhardti*). They are hollow, and their lumen drains into the capillary canals of the syncytium. The distal end of each flame bulb is closed by a protoplasmic cap. In monogononts, the lateral wall of the flame bulb usually consists of cytoplasmic columns and electron-dense microvilli (pillars), arranged in concentric rings around a central

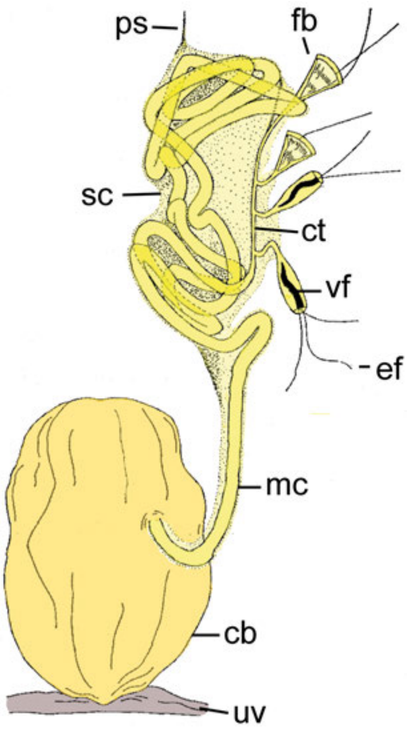

Fig. 4.40: Protonephridium and contractile bladder of *Asplanchna priodonta*. Top 2 flame bulbs shown frontally; other 2 shown from the side. Abbreviations: cb, contractile bladder; ct, collecting tubule; ef, external filament; fb, flame bulb; mc, main canal; ps, protoplasmic strand; sc. syncytial cytoplasm; uv, uterovesicular duct; vf, vibratile flame. (Modifed from Pontin 1964.)

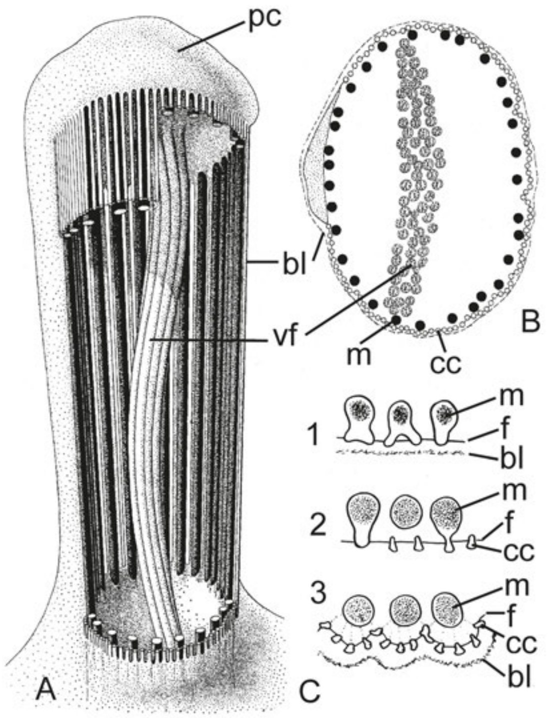

Fig. 4.41: Flame bulb. (A) Flame bulb partly opened to show internal organization, (B) cross section, and (C) detail of the filtering membrane in (1) bdelloids, (2) the monogonont *Trichocerca rattus*, (3) other monogononts (*Asplanchna, Brachionus, Notommata copeus, Rhinoglena*). Abbreviations: bl, basal lamina; cc, cytoplasmic columns; f, filtering membrane; m, microvilli; pc, protoplasmic cap; vb, vibratile flame. (A, B, From Braun et al. 1966; C, from Clément & Wurdak 1991, with permission.)

lumen with vibratile flame. Columns, and occasionally microvilli, are connected by a filtering membrane. In bdelloids and some monogononts (*Proales reinhardti*), microvilli are absent or not distinct from columns, and the filtering membrane is sustained by both. The cilia of the vibratile flame are connected with each other and inserted on the protoplasmic cap containing their basal bodies. Ciliary rootlets extending into the filter region are usually absent in monogononts, but present in bdelloids (see, e.g., Riemann & Ahlrichs 2010). The basal membrane is often present at the outside. The distal cap of the flame bulbs is connected to the integument by protoplasmic strands, maintaining the position of the protonephridial apparatus. The number of flame bulbs on each side of the body varies from 2 to 100 according to the species and appears positively correlated with the surface area of the species (Pontin 1964); the number is fairly constant for any one species.

The lumina of the flame bulbs are connected to the hollow cells of the protonephridial collecting tubule, and the latter joins with the intracytoplasmic lumen of the main canal syncytium. The intracytoplasmic lumen of the collecting tubules may be ciliated. The collecting tubules are mostly straight, whereas the main canals are straight, coiled, looped, or branched and often connected by a transversal canal, the Huxley anastomose, above the brain (e.g., *Epiphanes, Lacinularia, Stephanoceros*). Several protonephridium types (Fig. 4.42) have been described (for a review, see Remane 1933).

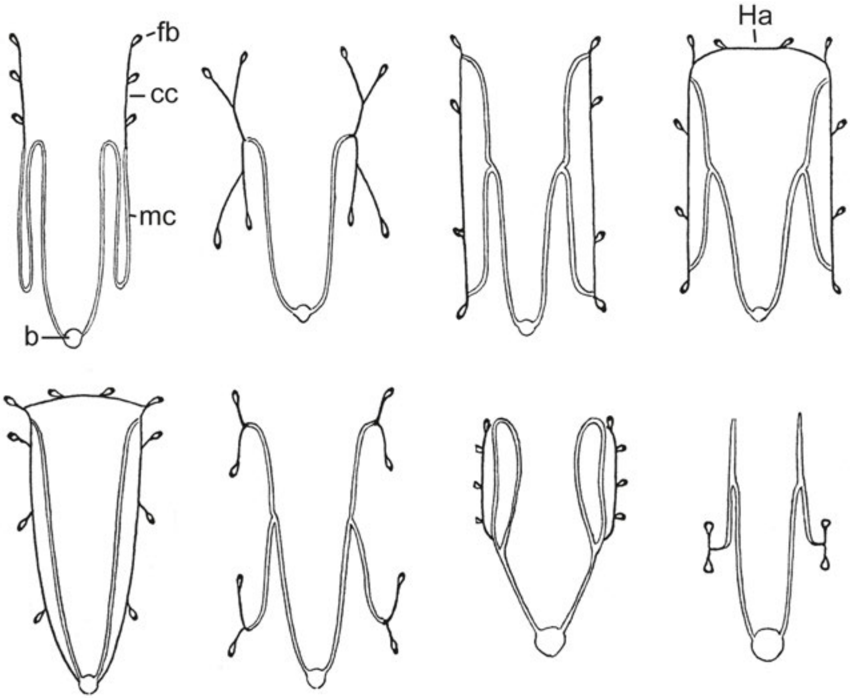

Fig. 4.42: Variation of the protonephridial system in Monogononta. Abbreviations: b, bladder; cc, capillary canal; fb, flame bulb; Ha, Huxley anastomose; mc, main canal. (From Remane 1933.)

A urinary bladder is only found in monogononts. It opens ventrally in the cloaca, or when occasionally absent, the protonephridia empty directly in the contractile cloaca (e.g., *Conochilus, Lacinularia, Testudinella*). The bladder syncytium is surrounded by a binuclear syncytial muscle, enabling the bladder to contract. In bdelloids, a separate urinary bladder is absent, and the protonephridia discharge in the terminal section of the intestine functioning as a bladder.

The protonephridial system of the rotifers has both an excretory and osmoregulatory function (e.g., Braun et al. 1966, Pontin 1966).

4.2.8.2 Excretory system of the male

Very little is known on the excretory system of the male (Wesenberg-Lund 1923), and results must be considered with caution (Remane 1933). Protonephridia have been found in most of the males described but appear absent in the strongly reduced ones. In several species flame bulbs, capillary ducts, and main canals are distinct (e.g., *Asplanchna, Asplanchnopus, Epiphanes*); the Huxley anastomose is present in male *Epiphanes*. The numbers of flame bulbs of the male and the female are identical (e.g., *Epiphanes senta, Asplanchna priodonta, Mytilina*) or apparently reduced in the male (Collothecacea). A contractile urinary bladder is usually absent but has been found in, e.g., *Asplanchna, Asplanchnopus, Cyrtonia, Stephanoceros*, and *Cupelopagis*. The protonephridia may discharge into the urinary bladder, into the vas deferens by a common duct, to the outside *via* separate pores near the genital opening, or into a bladder-like structure lying dorsally from the testis.

4.2.9 Reproductive organs

4.2.9.1 Reproductive organs of the female

The female reproductive system (Fig. 4.43) comprises the ovarium, the vitellarium, and a follicular layer surrounding both completely (bdelloids) or partly (monogononts) and continuing as an oviduct (e.g., Remane 1933, de Beauchamp 1965, Bentfeld 1971a, b, Amsellem & Ricci 1982, Clément & Wurdak 1991). In most species, the oviduct opens into the cloaca beyond the urinary bladder, or when the cloaca is reduced or absent, it directly leads to the outside. The female organs of monogononts consist of a single ovarium and vitellarium, whereas both organs are always paired in bdelloids, with the 2 oviducts joining into a single duct. They lie ventrally under the stomach and are mostly displaced to one side in monogononts.

The syncytial ovarium is small; it lies close to the vitellarium and contains the oocytes. In full-grown females, the syncytial vitellarium is a very large, yolk-producing gland with large polyploid nuclei, the number of which is usually constant within a species. The most frequently observed number is 8, but 4, and a multiple of 4 up to 32, occurs. Individual variations in number of nuclei in function of diet and doses of vitamin E have been described (e.g., Birky & Field 1966, Amsellem & Ricci 1982). The

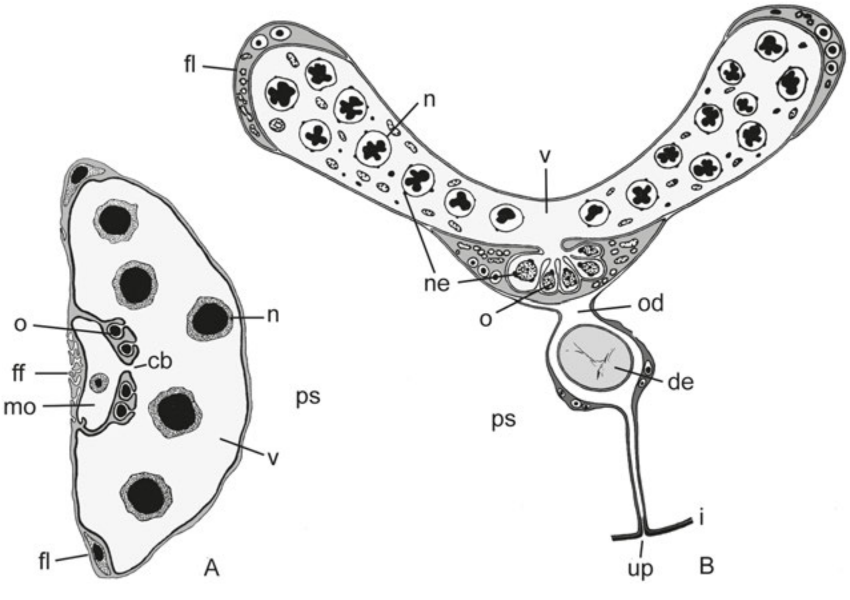

Fig. 4.43: Diagram of the female genital apparatus. (A) The bdelloid *Philodina roseola* and (B) the monogonont *Asplanchna brightwellii*. Abbreviations: cb, cytoplasmic bridge; de, developing embryo; ff, follicular folds; fl, follicular layer; i, integument; mo, maturing oocyte; n, nucleus with large nucleolus; ne, nucleolar extrusion; o, oocyte in ovarium; od, oviduct; ps, pseudocoelom; u, urogenital pore; v, vitellarium. (Modified from Clément & Wurdak 1991, with permission.)

shape of the vitellarium is rounded, lobed, band-shaped, horseshoe-shaped, cylindrical, etc., and often characteristic of the species.

4.2.9.2 Reproductive organs of the male

The male reproductive system (Fig. 4.44) consists of the unpaired, large, globular to pyriform testis, one to several accessory or prostate glands, the short to long, and mostly ciliated vas deferens, the copulatory organ or penis, and the dorsally lying genital aperture that is usually surrounded by a ring of cilia (e.g., Wesenberg-Lund 1923, Remane 1933, de Beauchamp 1965). If a digestive tract or its rudiments are present, the testis lies ventral to it. The wall of the testis is syncytial. The tip of the testis bears a wreath of cilia and often tufts of sensory cilia and several openings (*Brachionus, Asplanchna*); its inside is lined by integument (Aloia & Moretti 1974, Clément et al. 1983, Clément & Wurdak 1991). The testis is filled up with spermatids, spermatozoa, and testicular rods. The penis is protrusible (e.g., *Brachionus, Euchlanis, Gastropus*) or projecting continually (e.g., *Anuraeopsis, Keratella, Notholca*). In some species, the penis is absent, and the evertable vas deferens acts as penis (e.g., *Ascomorpha, Asplanchna, Epiphanes, Rhinoglena*), or the tube-shaped posterior extremity of the male is specialized for copulation (e.g., *Filinia, Hexarthra, Polyarthra*). Two pairs of cutaneovisceral muscles may insert on the vas deferens and act as retractores penis.

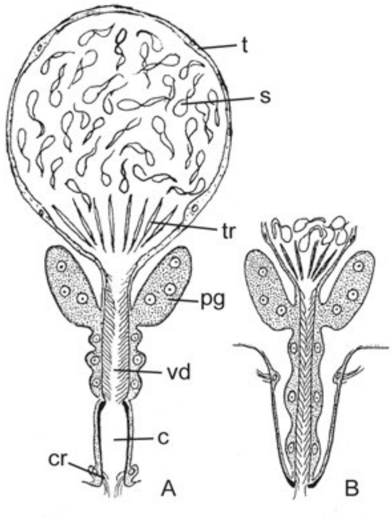

Fig. 4.44: Male reproductive system. (A) Scheme of male genital organ in Monogononta, penis redrawn and (B) penis everted. Abbreviations: c, cloaca; cr, ciliary ring at genital opening; pg, prostate glands; s, spermatozoa; t, testis; tr, testicular rods; vd, vas deferens. (Modified after Remane 1933 and Koste 1978.)

4.2.10 Gametes

Oogenesis was studied by, e.g., Nachtwey (1925), Lehmensick (1926), Bentfeld (1971a, b), and Clément & Wurdak (1991) for monogononts and by Hsu (1956a, b), Clément & Wurdak (1991), and Pagani et al. (1993) for bdelloids. The number of oocytes is fixed at birth (e.g., Buchner et al. 1965, Pagani et al. 1993). Maturation of the oocytes is by 2 subsequent equatorial divisions in bdelloids, with the extrusion of 2 polar bodies. Oogenesis of mononogonts is likewise by 2 equatioral divisions and extrusion of 1 polar body for the production of amictic eggs and 2 for the production of mictic ones (Gilbert 1993, Hsu 1956a, b). Important nucleolar extrusions are present in the cytoplasm of the immature oocytes of monogononts, but absent in bdelloids. During maturation, the volume of the oocyte increases considerably by the transfer of cytoplasm from the vitellarium through a cytoplasmic bridge; each oocyte has its own bridge (e.g., Bentfeld 1971b, Amsellem & Ricci 1982, Clément & Wurdak 1991). Subsequently, at the end of the growth period oocytes become detached from the ovary. After deposition of a shell in the oviduct, eggs are laid in oviparous species (most monogononts and bdelloids) or develop in the oviduct in ovoviviparous species. The term "viviparous" is often used for species who give live birth (e.g., the monogononts *Albertia, Asplanchna, Lindia, Rhinoglena, Trochosphaera*, and the bdelloids *Rotaria*), unlike the species who lay eggs enclosing a full-grown embryo that leaves the shell immediately after egg deposition. At hatching, juvenile females of free-swimming species usually have the adult shape. In sessile species, the females hatch as free-swimming larvae of typical rotifer appearance (Fig. 4.45), attaining the characteristic shape of the sessile stage after attachment and development into adults (e.g., Hochberg et al. 2010, Fontaneto et al 2003). Males are sexually mature at hatching and do not grow.

Three types of eggs are commonly produced in monogononts. The asexual or amictic egg (also called subitaneous egg) is a thin-shelled diploid egg produced by amictic females. The amictic egg develops into either amictic or mictic females. The sexual or mictic egg, also called male egg, is a small, thin-shelled haploid egg produced by mictic females; if unfertilized, it develop into males. Resting or dormant eggs are thick-shelled, fertilized mictic eggs, hatching into amictic females (Fig. 4.46). Resting eggs are actually resting embryos and not eggs (Boschetti et al. 2011a; see Section 4.3.3, Development). A fourth type of egg is the pseudosexual egg (e.g., in *Keratella hiemalis, Synchaeta*), an unfertilized resting egg produced *via* parthenogenesis in the absence of males (Ruttner-Kolisko 1946, 1974). Bdelloidea lack males, and their diploid eggs develop into females by parthenogenesis.

Eggs are spherical, ellipsoid, ovate, kidney-shaped, etc. They may be free floating, glued by a short stalk to the substrate, carried attached to the body of the female by a gelatinous thread, etc.; in several species, the resting egg is retained within the lorica. Amictic and mictic eggs are usually smooth, unlike the resting eggs, which are mostly ornamented with spines, ridges, pits, gas-filled vacuoles, etc. The ornamentation is often characteristic of the genus and/or species (e.g., Pourriot et al. 1983). The resting egg is mostly provided with a groove at one pole, where the shell opens on hatching of the young female. The shell of the amictic egg in *Trichocerca* consists of an external shell underlain by a thin internal envelope, joined to short microvilli at the periphery of the egg cytoplasm (Clément & Wurdak 1991). The shell of the resting egg of *Asplanchna* is composed of 3 coats: an external shell consisting of 2 coats separated by a space from an inner coat, which in its turn is separated by a space from the embryo (Wurdak et al. 1977).

During spermatogenesis, the primordial germ cells produce the spermatozoa, and atypical germ cells, which produce the testicular rods, formerly described as rudimentary, non functional, or atypical spermatozoa (e.g., Whitney 1917, 1918, Tannreuther 1919, Koehler 1965, Koehler & Birky 1966, Aloia & Moretti 1974).

The spermatozoa of a few monogononts, belonging to the genera *Asplanchna, Brachionus, Cephalodella,*

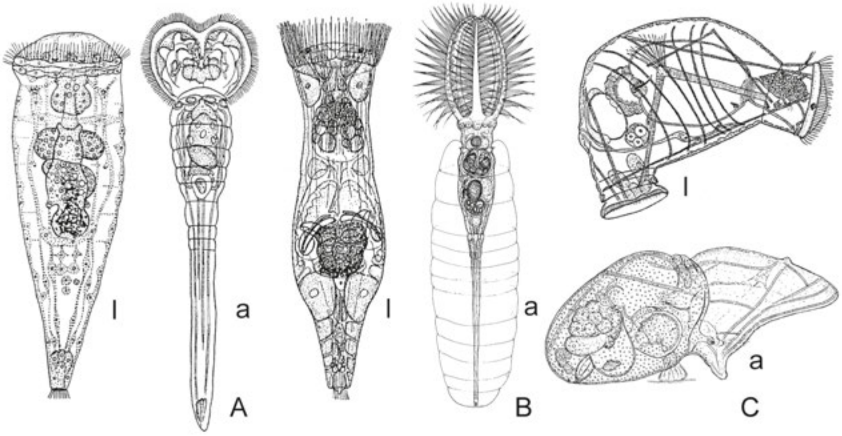

Fig. 4.45: Free-swimming larvae and sessile adults. (A) *Sinantherina socialis*, (B) *Stephanoceros fimbriatus*, and (C) *Cupelopagis vorax*. Abbreviations: a, adult female; l, larva. (From Remane 1933, Koste 1978, and Kutikova 1970.)

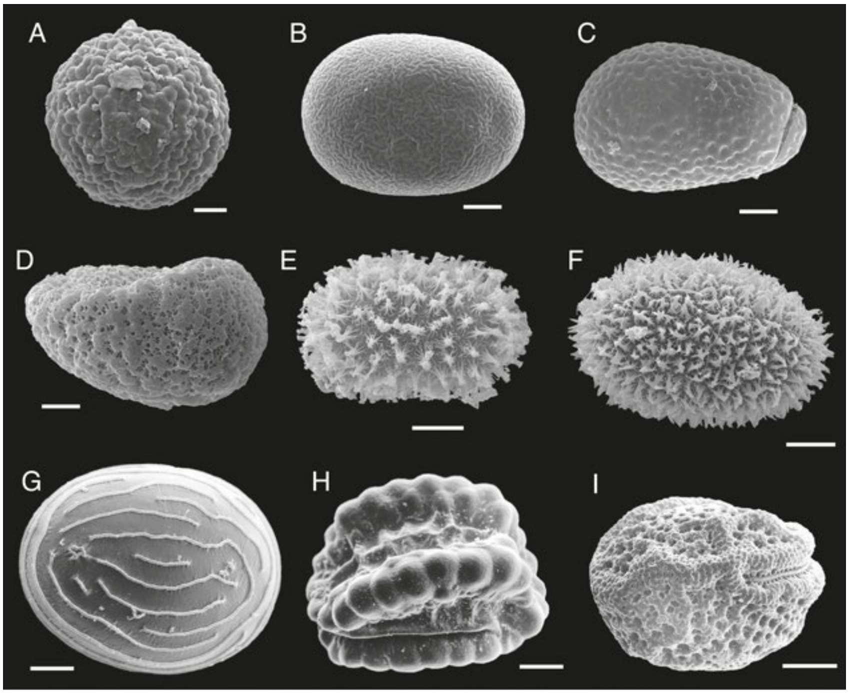

Fig. 4.46: SEM pictures of resting eggs of Monogononta: (A) *Asplanchna priodonta*, (B) *Brachionus plicatilis*, (C) *B. calyciflorus*, (D) *Epiphanes brachionus*, (E) *Rhinoglena frontalis*, (F) *Notommata codonella*, (G) *Conochilus natans*, (H) *Filinia longiseta*, and (I) *Hexarthra mira*. Scale bar = 20 µm, except for (G) 10 µm. (A–F, Photo courtesy of Giulio Melone; G–I, Photo courtesy of Hendrik Segers.)

Epiphanes, and *Lacinularia*, have been described with LM (Hamburger 1907, Whitney 1917, 1918, Tannreuther 1919, Tauson 1927). Ultrastructural studies are limited to *Asplanchna brightwellii* (Koehler 1965, Koehler & Birky 1966, Aloia & Moretti 1974), *A. sieboldii* (Koehler 1965), *Brachionus plicatilis* (Melone & Ferraguti 1994), *B. sericus* (Clément 1977, Clément & Wurdak 1991), and *Epiphanes senta* (Melone & Ferraguti 1999). The general organization of the spermatozoon is similar for the species studied, except for some minor differences concerning shape and size (Fig. 4.47). The spermatozoon is an elongated cell with a posterior cell body containing the nucleus and an anterior complex composed of a flagellum and undulating membrane; an acrosome is absent. The single axoneme is intracellular and shows the usual 9 × 2 + 2 tubules, in which the inner dynein arms only are present (Melone & Ferraguti 1994, 1999). The elongate nucleus is lobate and located anteriorly behind the flagellar region (Koehler 1965, Melone & Ferraguti 1994, 1999). The cytoplasm contains randomly distributed elongate mitochondria, different types of vesicles, free ribosomes, dense granules, etc.

The shape and length of the spermatozoa studied by EM is as follows: *Asplanchna*: gourd-shaped, 15–20 µm; *Brachionus plicatilis*: filliform, 70–80 µm (flagellum 40–45 µm, cell body 30–35 µm); *Epihanes senta*: sausage-shaped, bent, and weakly twisted, 12–15 µm (cell body 8–10 µm).

The testicular rods are rod-shaped structures developing late in embryonic life, i.e., in essentially mature males, from atypical germ cells showing intense secretory activity (Koehler 1965, Koehler & Birky 1966, Clément 1977, Melone & Ferraguti 1994). The rods contain dense material originating from Golgi vesicles and are organized as densely packed microtubules; a nucleus and flagellum are lacking. They are extruded from the cell within 2 membranes, one derived from the Golgi vesicle and one from the cell membrane. Testicular rods occur in almost all monogonont families and are supposed to assist, mechanically or enzymatically, in the penetration through the female integument during copulation (Remane 1933, Koehler 1965). They are always much smaller than the spermatozoa, e.g., 15 × 2 µm in *Asplanchna*, 16 × 1.5 µm in *Brachionus plicatilis*, and 14 × 1 µm in *Epiphanes senta* (Melone & Ferraguti 1999).

4.3 Reproduction and development

4.3.1 Reproductive biology

Rotifers are a textbook example of the different types of reproduction in animals. Seisonacea are characterized by sexual reproduction, which is in common with most animals (see chapter on Seisonacea). Monogononta can

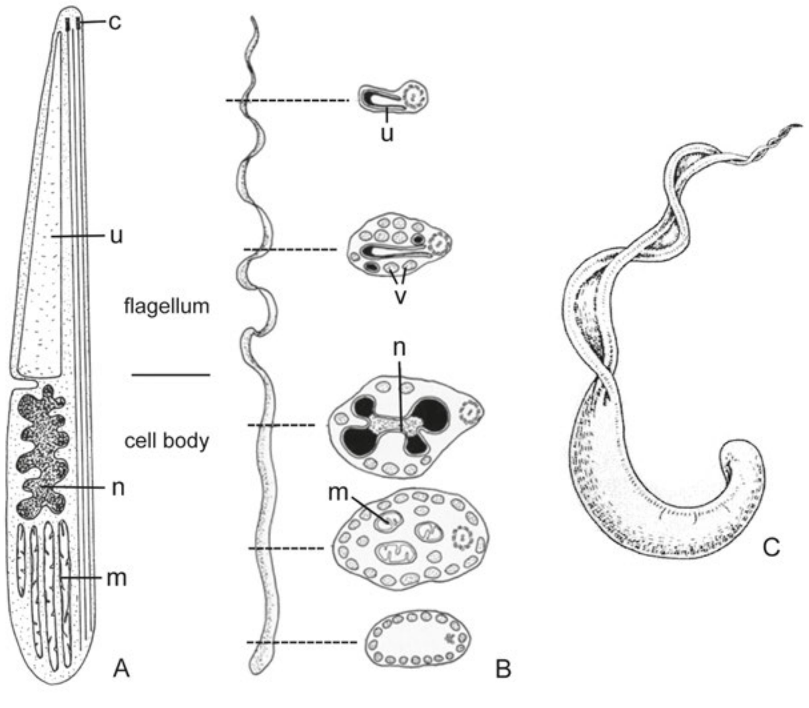

Fig. 4.47: Spermatozoon. (A) Diagram of spermatozoon of Monogononta, (B) spermatozoon of *Brachionus plicatilis* with representative cross sections, and (C) Spermatozoon of *Epiphanes senta*. Abbreviations: c, centriole; m, mitochondrion; n, nucleus; u, undulating membrane; v, vesicles containing tubules. (A, Modified from Melone & Ferraguti 1999; B, C, modified from Melone & Ferraguti 1994.)

alternate parthenogenesis, both through the development of diploid eggs producing females and through the development of haploid eggs producing males, to sexual reproduction (Serra & Snell 2009). Bdelloidea are the most famous case of ancient asexuals and the whole group diversified and persisted in the absence of any known form of sexual reproduction (Mark Welch et al. 2009).

Clear absence of sex in Bdelloidea cannot be proven unambiguously, as hidden sex may always occur. Yet, a large amount of observation on Bdelloidea never produced any evidence of meiosis, males, hermaphrodites, or vestigial genital structures (Birky 2010). Moreover, all the available indirect cytological and genetic evidence concurs in supporting their actual asexuality (Normark et al. 2003, Mark Welch et al. 2009): high sequence divergence between gene copies, functional divergence of former alleles, and multiple functionally divergent and conserved copies have been found (Mark Welch & Meselson 2000, Pouchkina-Stantcheva et al. 2007, Eyres et al. 2012), there is lack of high-copy-number retrotransposons (Arkhipova & Meselson 2000, 2005), an accumulation of deleterious mutations has been found (Barraclough et al. 2007, Swanstrom et al. 2011), and the diversification rates in Bdelloidea are clearly different from those in Monogononta (Fontaneto et al. 2012b). According to our current knowledge, Bdelloidea produce only diploid eggs that hatch into females that can lay eggs that hatch into females, without any form of sexual recombination. Thus, the whole genome of the mother is inherited by all the daughters, producing clonal lines. Because of the evolutionary success of Bdelloidea in the absence of sexual reproduction, Maynard Smith (1986) dubbed them as an "evolutionary scandal". This makes bdelloids an excellent study system for the origin of sex in animals (Bell 1982) by understanding how these peculiar organisms thrive in the absence of sex. One caveat is nevertheless present due to the possibility of horizontally transferred genes, which are abundant and functional in Bdelloidea (Boschetti et al. 2012) and may represent an alternative mechanism to sexual recombination to maintain genetic variability (Gladyshev et al. 2008).

A rather peculiar reproductive behavior is present also in the other group of Rotifera, the Monogononta, characterized by cyclical parthenogenesis. Cyclical parthenogenesis is a combination of asexual, parthenogenetic, and sexual reproduction (Serra & Snell 2009). The conditions thought to favor cyclical parthenogenesis are seasonal and/or unpredictable temporal heterogeneity (Carmona et al. 1995, Serra et al. 2003, Ricci 2001), typical of the ephemeral habitats where most Monogononta thrive. In Monogononta, asexual females, called amictic females, produce asexual daughters by ameiotic (apomictic or amictic) parthenogenesis. In response to certain environmental cues such as population density, photoperiod, or chemical triggers (Pourriot & Clément 1981, Stelzer & Snell 2003, Snell 2011), asexual females produce sexual daughters, called mictic females (Gilbert 1963b). These sexual females produce meiotic eggs, which, if not fertilized, develop into haploid males. If fertilized by a male, eggs develop into cysts, called resting eggs, which undergo diapause. When resting eggs hatch, the cycle starts again and asexual females reproduce by parthenogenesis until the next round of sexual reproduction. Variations to this life cycle have been described, including amphoteric females producing both ameiotic and meiotic eggs (Gilbert 1974, King & Snell 1977), parthenogenetic resting eggs (Gilbert 1995, Gilbert & Schreiber 1998), and sexual females hatched from resting eggs (Schröder et al. 2007). The mechanisms involved in mating behavior in monogononts has been studied mostly for those species used in aquaculture (Hagiwara et al. 1995b, Rico-Martínez & Snell 1996, 1997), and a set of molecules potentially involved in mate recognition have already been tested and described (Snell 2011) (see Section 4.4, Physiology).

4.3.2 Cleavage

Most Rotifera are oviparous, but several ovoviviparous species retain the developing embryos inside the body (Gilbert 1989). Oviparous species may carry the eggs, attach them to the substrate, or simply release them in the water column (Wallace et al. 2006).

Rotifera possess a deterministic cleavage that follows a modified spiral pattern (Gilbert 1989). The fate of the cells is established very early in the development (Pray 1965). Moreover, Rotifera are eutelic (Clément & Wurdak 1991); cell divisions occur only during embryogenesis, whereas the newborn already possesses the same number of cells of the adult. Embryo development follows the 3 typical steps of cleavage, gastrulation, and organogenesis (Boschetti et al. 2005).

Eggs are poor in yolk; they are laid unsegmented and extrude the polar body before undergoing cleavage (Hsu 1965a, b, Gilbert 1989). During cleavage, subsequent divisions produce smaller and smaller cells of unequal size and amount of cytoplasm, called blastomeres. Cleavage is holoblastic and cell divisions are unequal. For a review of the current knowledge on cleavage, see Boschetti et al. (2005). A typical 16-blastopore stage is present with 4 rows of 4 cells each, and at this stage, gastrulation starts (Gilbert 1989, Boschetti et al. 2005).

4.3.3 Development

Gastrulation in Rotifera occurs by epibolic movements and consequent involution; the resultant gastrula is a stereogastrula without a recognizable internal cavity. Lechner (1966) described 2 stages in the gastrulation process, a first epibolic growth of the blastoderm cell and a second stage with a further epibolic growth coupled with the involution of the blastoderm to form the blastopore. Not all authors agree on this 2-stage process, on the position of the blastopore and the origin of the mouth, and on the origin on the digestive system (Boschetti et al. 2005). Modern analyses should be performed to obtain a clear description of the embryo development in Rotifera.

Cell lineage mapping has been performed only on few species (Zelinka 1892b, Pray 1965, Lechner 1966), and organogenesis is not well known, with discrepancies in the scattered available information. The main differences concern the origin of the digestive and the reproductive systems (Boschetti et al. 2005). According to Gilbert (1989), the stomodaeum, the pharynx, the nervous system, the excretory system, and the muscles originate from the ectoderm; the reproductive system, the germarium, and the vitellarium from the mesoderm; the digestive system from the endoderm.

It has to be reminded that Rotifera are eutelic (Clément & Wurdak 1991) and possess a constant number of cells (or better, of nuclei) throughout all life because several tissues are syncytial. Cell divisions occur during embryogenesis only, and the fixed number of cells is supposed to be species specific (Boschetti et al. 2005). The newborn possesses the same number of cells of the adult, and the cells will only increase in size during life.

In sessile Rotifera, the juveniles that hatch from the eggs are very different from the adults, and undergo radical developmental changes (Fontaneto et al. 2003, Wallace et al. 2006). Such changes include formation of the adult corona and elongation of the foot (see Section 4.2.1.2, Coloniality).

Development of resting eggs is also poorly understood (Wurdak et al. 1978, Hagiwara et al. 1995a, Boschetti et al. 2011a). The so-called resting eggs are actually diapausing embryos that will resume their development after being activated by external and/or internal stimuli (Gilbert 1974, Pourriot & Snell 1983, García-Roger et al. 2006).

4.4 Physiology

Very few studies deal with the general physiology of Rotifera. For example, almost nothing is known on the digestive system; we only know some of the enzymes involved and the absorptive process (Lindemann et al. 2001). More efforts have been implemented to analyze the triggers of the switch between sexual and asexual reproduction in Monogononta (Snell 2011), the physiological aspects of dormancy in Bdelloidea (Tunnacliffe & Wise 2007), hormone-induced phenotypic plasticity (Gilbert 1999), and the ecotoxicological and ecophysiological mechanisms (Dahms et al. 2011).

No rotifer hormones have been yet described (Snell 2011), but the rotifers that have been tested respond to a variety of hormones and neurotransmitters from vertebrates and insects (Gallardo et al. 1997, 1999, 2000, Snell & DesRosiers 2008), including growth hormone, human chorionic gonadotropin, triiodothyronine, juvenile hormone, serotonin, GABA, and progesterone. Several putative endocrine disruptors, sufficiently similar to hormones that they interfere with normal endocrine signaling in aquatic animals have effects on rotifers (Snell & Joaquim-Justo 2007). Moreover, rotifers indeed produce growth-promoting substances (Ohmori et al. 2011).

Evidence that rotifers use chemical signals as pheromones is available in rotifers, especially to regulate their reproduction (Snell 2011). These include compounds excreted in the medium that trigger the switch from sexual to asexual reproduction (Gilbert 1963a, Stelzer & Snell 2006), and mate recognition pheromones (Snell et al. 1995, Snell & Stelzer 2005, Snell et al. 2009). Also, environmental triggers have been described, such as dietary α-tocopherol, photoperiod, and crowding (Gilbert 1981, Pourriot & Clément 1981, Stelzer & Snell 2003).

The mechanism that switches asexual to sexual reproduction in Monogononta is controlled by the accumulation of a signaling molecule produced by the rotifers themselves (Gilbert 2004). Such population-level metabolic synchrony, regulating gene expression in response to fluctuations in population density, is similar to what known as quorum sensing in bacteria (Miller & Bassler 2001).

Rotifera, together with other microscopic aquatic animals such as tardigrades and nematodes, are able to withstand lack of water, in a desiccated and/or frozen state, entering dormancy. Bdelloidea may enter dormancy in any stage of their life cycle (Ricci & Fontaneto 2009), whereas Monogononta produce resting eggs that can remain dry and/or frozen for extended periods before hatching (Gilbert 1974, Schröder 2005). In the dry state, there is little or no evidence of metabolic activity (Clegg 1986, 2001). The desiccating process in Bdelloidea is influenced by the nature of the substrate and the humidity; the process involves morphological changes such as the contraction of the body into a tun shape and the packing of internal structures (Ricci et al. 2003, 2008).

The biochemical mechanisms used to survive by microscopic animals during dormancy are not fully understood (Clegg 2001, Oliver et al. 2005, Tunnacliffe & Wise 2007, Lubzens et al. 2010), but the main actors are thought to be specific molecules that protect the intracellular and extracellular environment against the various damages induced by the lack of water (Crowe et al. 1998, Rebecchi et al. 2007). Sugars such as trehalose and sucrose were, for a time, considered the main molecules involved in the process in plants and animals (Alpert 2006). Yet, trehalose, present in nematodes and tardigrades, is absent in Bdelloidea (Lapinski & Tunnacliffe 2003) and found only in traces in Monogononta (Caprioli et al. 2004). It has been recognized that other molecules are important as well in the physiology of dormancy (Tunnacliffe & Lapinski 2009): these include heat shock proteins, late embryogenesis abundant proteins, chaperones, antioxidants, and others (Goyal et al. 2005, Denekamp et al. 2009, Clark et al. 2012). Intriguingly, even foreign genes, acquired through horizontal gene transfer, seem to be involved in the desiccation response of Bdelloidea (Boschetti et al. 2011b).

Whereas Bdelloidea recover from their dormant stage as soon as water becomes available (Ricci 1998a), hatching of resting eggs of Monogononta is triggered by a more complex mechanism, with temperature and/or light conditions, interacting with the length of desiccation (Minkoff et al. 1983, Schröder 2005).

Several planktonic rotifers exhibit considerable environmentally controlled variation in spine development and body size. The most striking case is the elongation of spines in loricated rotifers in response to the presence of specific predators (Gilbert 1999, 2011). Such elongation of spines occurs due to chemical compounds, called kairomones, identified in the environment by rotifer mothers, which produce daughters with longer spines (Gilbert 1967).

The physiological response to chemical changes in the environment is studied in detail in Rotifera, and ecotoxicological analyses have been performed both in the laboratory and in the field (Snell & Janssen 1995). Rotifers are used in the risk assessment of pharmaceuticals, endocrine disruptors, and heavy metal pollution, through whole-animal bioassays and gene expression studies (Dahms et al. 2011). Responses regarding growth condition, reproduction, population dynamics, and toxicity are well known, especially for the laboratory model of the genus *Brachionus* (Yúfera 2001, Sarma et al. 2001, 2005, 2009).

4.5 Phylogeny

The close relationship between the 3 traditional groups of Rotifera (Bdelloidea, Monogononta, and Seisonacea) and Acanthocephala is well accepted in traditional morphological studies; Rotifera and Acanthocephala share a peculiar syncytial epidermis with an ICL (Clément 1993, Wallace et al. 1996, Garey et al. 1998) and a similar morphology of the sperm cell (Melone & Ferraguti 1994, Ferraguti & Melone 1999). In addition, phylogenetic analyses using several molecular markers support their close relationship (Garcia-Varela & Nadler 2006), so that they have been grouped in the taxon Syndermata (Ahlrichs 1997).

The monophyly of the 3 major groups of Rotifera is not debated (Herlyn et al. 2003, Sørensen & Giribet 2006). Nevertheless, their evolutionary relationships are still unclear, and different analyses usually provide discordant results regarding their position and the position of Acanthocephala (Lasek-Nesselquist 2012). This latter group can be supported either as a sister group of monophyletic Rotifera, or at different positions within Rotifera (Herlyn et al. 2003, Sørensen & Giribet 2006, Fontaneto & Jondelius 2011). The 6 hypotheses regarding the possible phylogenetic relationships within the clade Rotifera+Acanthocephala (Syndermata) are, in historical order,

(a) Bdelloidea, Monogononta, and Seisonacea (traditionally named Rotifera) as a monophyletic clade, sister to Acanthocephala (Fig. 4.48 A): This hypothesis is based on general morphological similarities and supported by morphological cladistic analyses (Melone et al. 1998b, Sørensen & Giribet 2006), but never supported by molecular phylogenies.

(b) Lemniscea (Fig. 4.48 B): The hypothesis of Bdelloidea and Acanthocephala as sister groups is based on the supposed presence of a proboscis and lemnisci in Bdelloidea (Lorenzen 1985). Ricci (1998b) argued that the morphological basis of the hypothesis was false, due to a misinterpretation of the rostrum and the hypodermic cushions of Bdelloidea as homologous to the proboscis and lemnisci of Acanthocephala. Notwithstanding the unreliability of the morphological basis, this first analysis brought attention to the Rotifera+Acanthocephala relationship. Moreover, the first phylogenetic studies on

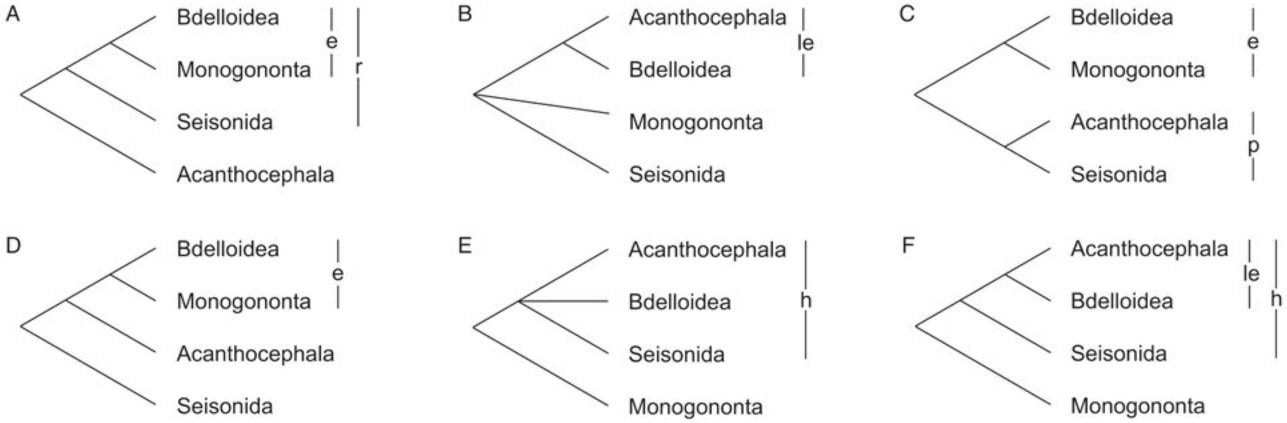

Fig. 4.48: Alternative phylogenetic hypotheses for the clade Rotifera+Acanthocephala: (A) classic theory of a monophyletic origin of the Rotifera, (B) Lemniscea hypothesis, (C) Pararotatoria hypothesis, (D) Acanthocephala as Eurotatoria sister group, (E) Hemirotifera hypothesis, and (F) Seisonacea as Lemniscea sister group. Abbreviations: e, Eurotatoria; h, Hemirotifera; le, Lemniscea; p, Pararotatoria; r, Rotifera. (Modified from Fontaneto & Jondelius 2011.)

16S and 18S rDNA supported such relationship (Garey et al. 1996). The position of Seisonacea and Acanthocephala was not included in the discussion on Lemniscea.

(c) Pararotatoria (Fig. 4.48 C): The hypothesis of Eurotatoria (Bdelloidea+Monogononta) as a sister group of Pararotatoria (Acanthocephala+Seisonacea) is based on morphological characters such as sperm morphology and epidermal ultrastructure (Ahlrichs 1997). Moreover, this relationship was supported by the inclusion of Seisonacea in the 18S molecular data set (Herlyn et al. 2003).

(d) Acanthocephala as a sister group to Eurotatoria (Bdelloidea+Monogononta) (Fig. 4.48 D): This hypothesis is supported by a phylogenetic analysis of the nuclear gene hsp82 (Mark Welch 2000) and from a combined analysis of hsp82+18S (Mark Welch 2005). Seisonacea were not included, as no hsp82 was available for them.

(e) Hemirotifera (Fig. 4.48 E): In this hypothesis, Monogononta are the sister group of Hemirotifera (Acanthoc ephala+Bdelloidea+Seisonacea), based on combined molecular and total evidence analyses of 74 morphological characters and DNA sequence data from 18S, 28S, histone H3, and COI (Sørensen & Giribet 2006).

(f) Monogononta as a sister group of the other 3 groups, and Seisonacea as a sister group of Lemniscea (Fig. 4.48 F), inferred from a phylogenetic analysis of concatenated 18S+28S+COI (Garcia-Varela & Nadler 2006) and supported by EST phylogenomics (Witek et al. 2008).

Almost any plausible relationship among Acanthocephala, Bdelloidea, Monogononta, and Seisonacea has been suggested, with no agreement between different analyses (Fontaneto & Jondelius 2011, Lasek-Nesselquist 2012). Two main patterns emerge from all the analyses performed until now: (i) the traditional hypothesis of Acanthocephala as a sister clade of monophyletic Rotifera has never been supported by molecular phylogenies and (ii) the most recent analyses even split the clade Eurotatoria (Min & Park 2009, Witek et al. 2009). Nevertheless, Seisonacea, Bdelloidea, and Monogononta share many morphological and ecological features, and there is no morphological support for the splitting of Eurotatoria (Melone et al. 1998b). The only unambiguous pattern is that each of the 3 groups of Rotifera (Bdelloidea, Monogononta, and Seisonacea) is a monophyletic clade. But the relationships between them are still not clear.

4.6 Systematics

Classically, 3 groups are recognized within Phylum Rotifera: Seisonacea, Bdelloidea, and Monogononta. The classification we report here is that of Segers (2002), based on morphology alone, given that the phylogenetic relationships have not been solved yet for rotifers using molecular approaches (see Section 4.5, Phylogeny).

4.6.1 Classification

Class Pararotatoria Sudzuki, 1964
    Order Seisonacea Wesenberg-Lund, 1899
Class Eurotatoria De Ridder, 1957
  Subclass Bdelloidea Hudson, 1884
    Order Adinetida Melone & Ricci 1995
    Order Philodinavida Melone & Ricci 1995
    Order Philodinida Melone & Ricci 1995

Subclass Monogononta Plate, 1889
  Superorder Pseudotrocha Kutikova, 1970
    Order Ploima Hudson & Gosse, 1886
  Superorder Gnesiotrocha Kutikova, 1970
    Order Flosculariacea Harring, 1913
    Order Collothecacea Harring, 1913

Subclass Bdelloidea (Fig. 4.49) is a group of completely asexual animals, reproducing by apomictic thelytoky. Ovaries and vitellaria paired. Body composed of telescopically retractable pseudosegments. Usually illoricate. Corona characteristic, composed of 2 trochal discs, may be reduced to buccal field. Head bears dorsal antenna and ciliated rostrum. Lateral antennae lacking. Number of toes 2, 3, or 4 or adhesive disc. Penultimate pseudosegment with spurs. Stomach syncytial. Trophi ramate.

The bdelloids comprise 4 families in 3 orders (Melone et al. 1998b), to accommodate 19 genera and about 460 species (Segers 2007): order Adinetida with family Adinetidae (2 genera), order Philodinida with families Habrotrochidae (3 genera) and Philodinidae (11 genera), and order Philodinavida with family Philodinavidae (3 genera). Species count for bdelloids is done considering all subspecies as valid species; given the problems in defining species in asexual taxa, we here follow the rule that every morphological variability described at the subspecies level has the validity of species.

Order Adinetida is a group of bdelloids with fusiform to vermiform body, mostly compressed dorsoventrally, characterized by a corona of the *Adineta* type, without trochus and with a ventral ciliated field with rake of teeth at its base or at its lateral sides. Only 1 family, Adinetidae, with 20 species.

Order Philodinavida is a group of bdelloid rotifers characterized by trophi close to the mouth opening and extruded when animal is feeding. The corona is poorly developed, reduced to small ciliated field. Only 1 family, Philodinavidae, with 9 species.

Order Philodinida is the richest and most diverse group of bdelloids, characterized by a *Philodina*-type corona, deep and not protrusible trophi. Two families with about 435 species.

Subclass Monogononta shows cyclic parthenogenesis, interrupted by sexual reproduction. Males usually strongly reduced. Fertilization internal, resulting in dormant (resting) eggs. Single ovary, vitellarium, and testis. Body pseudosegmented, shape very various, usually with distinct head, trunk, and foot. Loricate or illoricate. Foot and

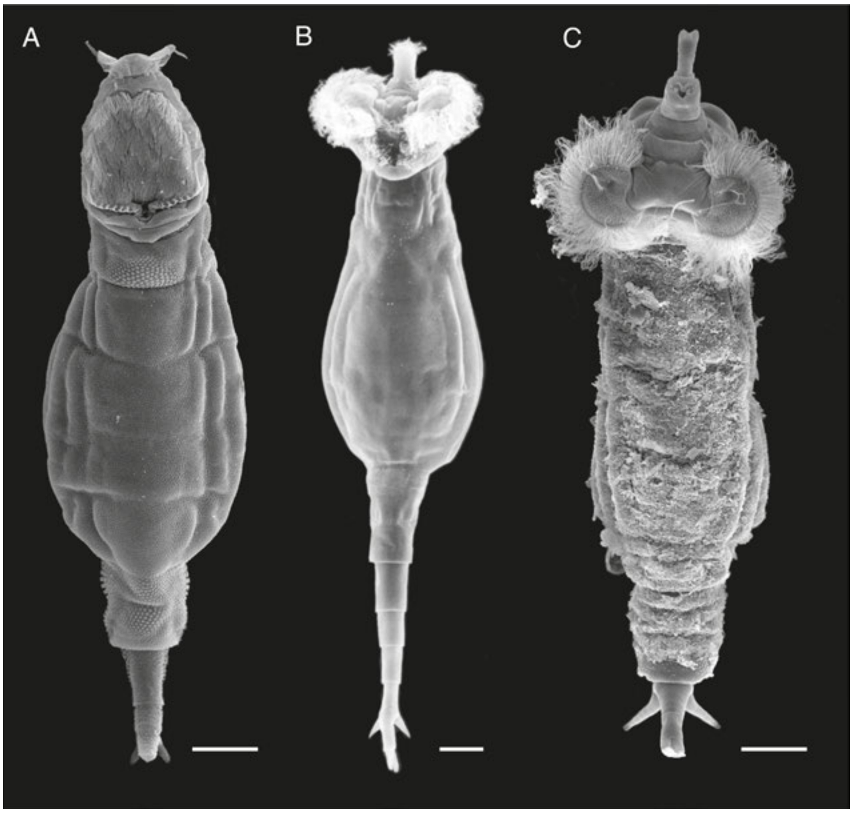

Fig. 4.49: SEM pictures of Bdelloidea. (A) *Adineta tuberculosa*, (B) *Rotaria macrura*, and (C) *Dissotrocha aculeata*. Ventral view. Scale bar = 20 µm. (Photo courtesy of Giulio Melone.)

toes very various, usually 2 toes, or adhesive disc; toes may be absent. Lateral antennae always present. Corona and trophi of various types. Dorsal antenna present, ciliated rostrum absent. Stomach cellular.

About 1,600 species are recognized in 3 orders: Ploima, Flosculariacea, and Collothecacea, comprising 23 families and 113 genera.

Order Ploima (Fig. 4.50) is extremely varied in body plan, corona, toes, and trophi. Never sessile permanently. Trochus never surrounding apical field; corona often with pseudotrochus differentiated by the buccal field. Usually 2 toes, rarely single toe, toes often absent in planktonic species. Trophi forcipate, incudate, malleate, or virgate. About 1,410 species.

Order Flosculariacea (Fig. 4.51) is a group of monogonont rotifers, characterized by malleoramate trophi. Body plan variable; free-swimming juveniles differ in shape from adult females. Foot, if present, without toes; in juveniles and free-swimming species terminating in ring of cilia or ciliated cup. Loricate or illoricate. Corona of *Hexarthra* or *Conochilus* type. About 140 species.

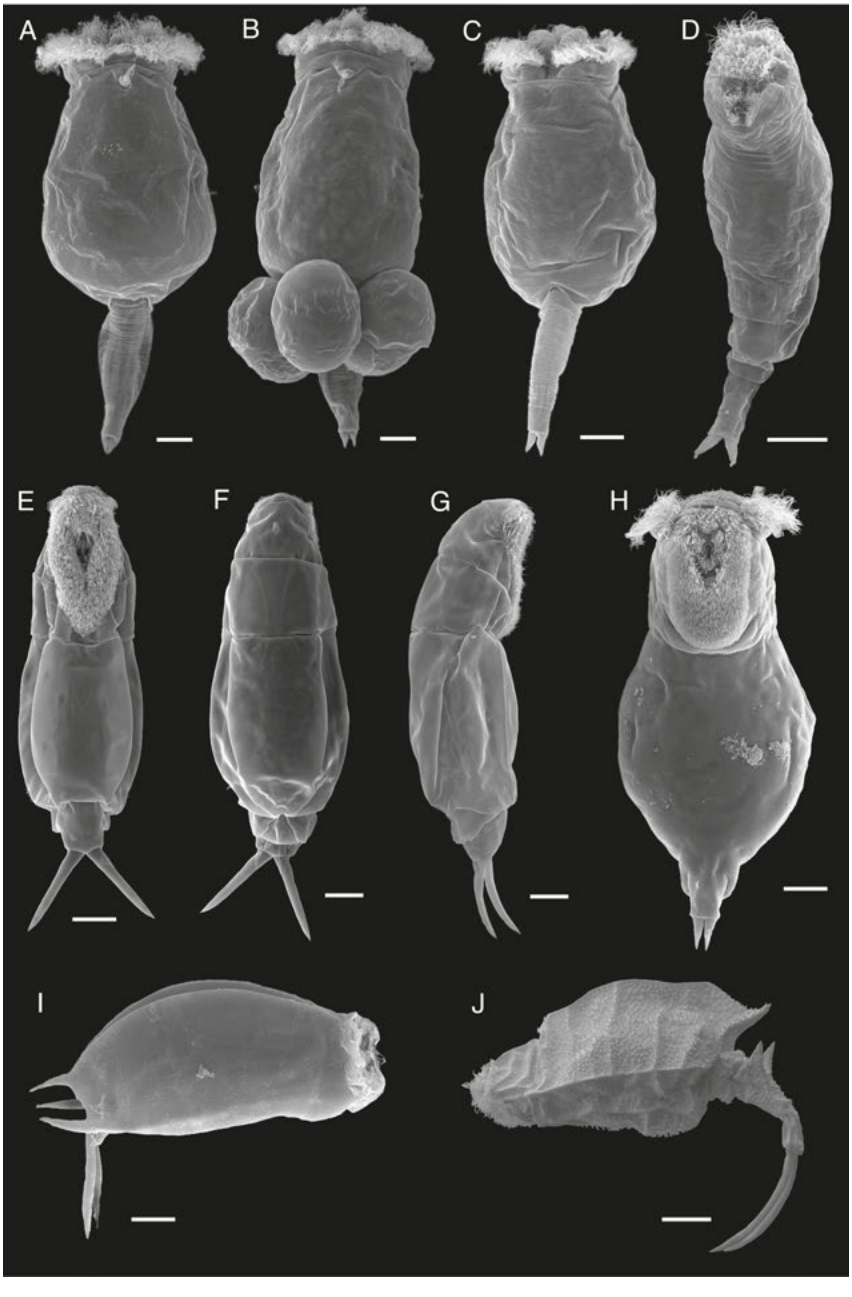

Fig. 4.50: SEM pictures of Ploima. (A–C), *Brachionus manjavacas*, (D) *Proales theodora*; E–G, *Dicranophorus forcipatus*, (H) *Notommata glyphura*, (I) *Mytilina ventralis*, and (J) *Trichotria tetractis*. Scale bar = 25 µm. (A–I, photo courtesy of Giulio Melone; J, photo courtesy of Eike F. Wiltz.)

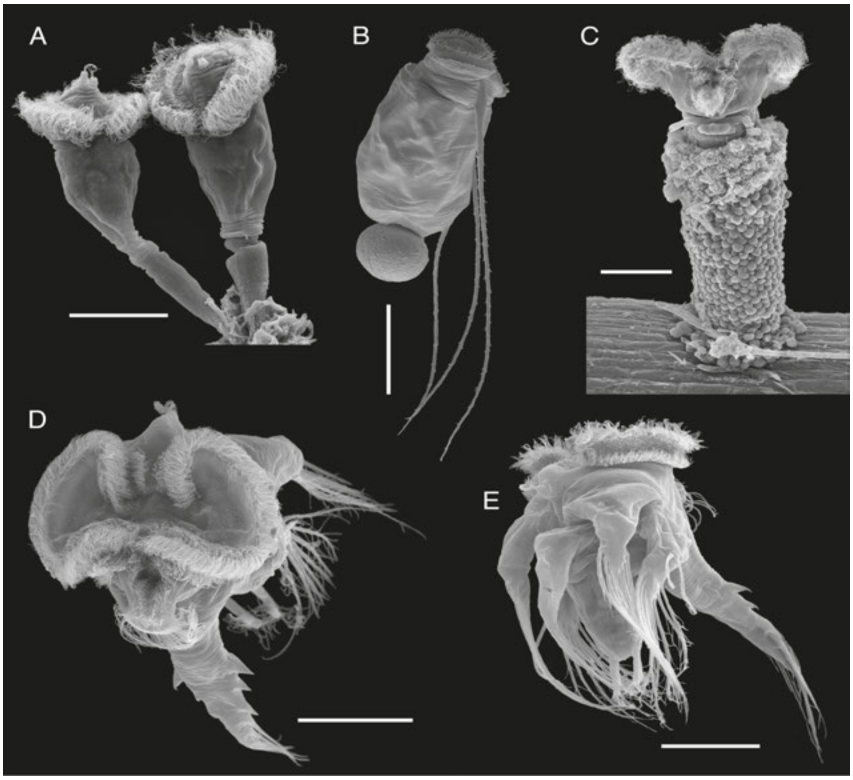

Fig. 4.51: SEM pictures of Flosculariacea, (A) *Conochilus hippocrepis*, (B) *Filinia longiseta*, (C) *Flosculariacea ringens*, and (D, E) *Hexarthra mira*. Scale bar = 50 µm. (A, C–E, photo courtesy of Giulio Melone; B, photo courtesy of Eike F. Wiltz.)

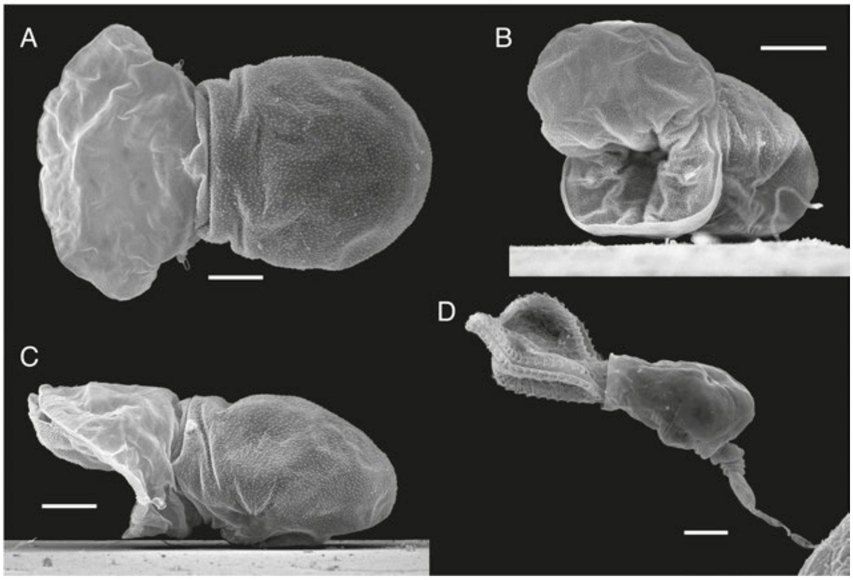

Fig. 4.52: SEM pictures of Collothecacea. (A–C) *Cupelopagis vorax* and (D) *Stephanoceros fimbriatus*. Scale bar = 50 µm. (Photo courtesy of Giulio Melone.)

Order Collothecacea (Fig. 4.52) is a group of rotifers characterized by uncinate trophi. Body elongate conical or saccate; foot always without toes, long with small adhesive disc, or modified into ventral adhesive disc, or reduced; foot of free-swimming juveniles with ciliary ring. Illoricate. Corona of *Collotheca* type, a modified funnel with or without long setae, and often lacking cilia. Most species are sessile, but several live in the plankton. About 51 species.

4.6.2 Keys

4.6.2.1 Key to higher taxa

01a – Trophi fulcrate. Corona rudimentary. Body with small oval head, long slender neck, fusiform trunk, and stalk-like foot terminating in adhesive disk. Epizoic on marine crustaceans of the genus *Nebalia*. Males and females in equal numbers. Paired ovaries … **Class Pararotatoria, Order Seisonacea**

01b – Trophi not fulcrate. Corona mostly well developed. Body not as above. Not epizoic on *Nebalia*. Mostly or only females. Ovaries paired or single ovary ………………………………… **02**

02a – Paired ovaries. Trophi ramate …… **Class Eurotatoria, Subclass Bdelloidea**

02b – Single ovary. Trophi not ramate (Class Eurotatoria, Subclass Monogononta) …………………………… **03**

03a – Trophi malleoramate. Corona elliptical to round, heart-shaped, horseshoe-shaped, or 4-lobed, without long setae. Free-swimming or sessile ……………………… **Order Flosculariacea**

03b – Trophi uncinate. Corona funnel-like with tentacles, lobes, or knobs bearing long setae; there may be cilia between the tentacles, lobes, etc. Usually sessile, a few planktonic species ……………………… **Order Collothecacea**

03c – Trophi otherwise: cardate, forcipate, incudate, malleate, or virgate …………… **Order Ploima**

4.6.2.2 Key to families of Bdelloidea

01a – Esophagus short; trophi usually close to the mouth opening, generally extruded when animal is feeding. Proximal minor teeth of uncus plate usually reduced or absent. Corona reduced to small ciliated field, trochi absent, or small …… **Philodinavidae**

01b – Esophagus long, trophi deeper, never extruded. Proximal and distal minor teeth of uncus plate always present. Corona otherwise, with trochi absent or present …………………………… **02**

02a – Corona modified to a ventral ciliated field, no trochi. Foot long and extensible, with 3 toes and 2 spurs, or short and plump, with disc-shaped distal pseudosegment, and spurs absent. Common behavior is scraping and browsing the substratum …………… **Adinetidae**

02b – Corona frontal, with trochi, mostly elevated on pedicels. Foot with 2 spurs of variable length. Toes present (2, 3, or 4) or absent. Vortex feeding …………………………… **03**

03a – Stomach without recognizable lumen, with round pellets in its wall …… **Habrotrochidae**

03b – Stomach with thick wall and visible lumen, not filled with round pellets ……….. **Philodinidae**

4.6.2.3 Key to families of Ploima

01a – Anterior half of body composed of 16 pseudosegments with finely denticulate distal margin. Endoparasitic in earthworm *Pheretima* ……………… **Clariaidae**

01b – Anterior half of body not composed of 16 pseudosegments. Not parasitic in *Pheretima* ………………………… **02**

02a – Vitellarium strongly elongate, cylindrical, wound around intestine, with 20–30 nuclei. Connection between stomach and intestine narrow, surrounded by wreath of ca. 6 spherical glands …… **Tetrasiphonidae**

02b – Vitellarium spherical, ovate, U-shaped, lobed, etc., not cylindrical and wound around intestine, usually with 8 nuclei. No wreath of glands between stomach and intestine ………… ……………… **03**

03a – Mouth opening ventral, surrounded by hollow cup-shaped structure. Head covered by non-retractile shield. Trophi specialized virgate with 2 stiletto-shaped elements …… **Cotylegaleatidae**

03b – Not as above …………………………… **04**

04a – Trophi highly modified, manubria heart-shaped, 2 large hook-shaped accessory elements. Stomach with blind sacks, stomach wall with green zoochlorellae. Gastric glands absent ……………… **Birgeidae**

04b – Not as above …………………………… **05**

05a – Trophi hemiforcipate, manubria with long rod-shape shaft and small axe-shaped head. Free-living or symbiotic in shells of testate amoebae …… **Asciaporrectidae**

05b – Trophi not hemiforcipate with long manubria, if hemiforcipate with medium long manubria with broad head, and 2 trapezoid epipharyngeal plates. Free-living or symbiotic with organisms other than testate amoebae …………………………… **06**

06a – Trophi cardate. Illoricate ……………… **Lindiidae**

06b – Trophi not cardate. Loricate or illoricate …………………………… **07**

07a – Trophi forcipate or hemiforcipate with medium long manubria. Illoricate …………………………… **08**

07b – Trophi not forcipate. Loricate or illoricate …………………………… **09**

08a – Trophi with hook-shaped alulae, not protrusible. Stomach and intestine mostly greenish, filled with zoochlorellae ………………… **Ituridae**

08b – Trophi without alulae or with differently shaped alulae, protrusible. Stomach and intestine rarely with zoochlorellae …… **Dicranophoridae**

09a – Trophi incudate. Illoricate ……… **Asplanchnidae**

09b – Trophi otherwise. Loricate or illoricate ………………………… **10**

10a – Trophi virgate ………………………… **11**

10b – Trophi strictly malleate, submalleate, or malleovirgate ………………………… **16**

11a – Foot and toes very long, combined longer than body …………… **Scaridiidae**

11b – Foot shorter, toes variable, combined shorter than or as long as body ………………………… **12**

12a – Body more or less strongly asymmetrical. Trophi very asymmetrical, asymmetry concerns all trophi elements. Foot terminally, a short single pseudosegment bearing several bristles (substyli) and elongate spine-like toe(s) of unequal length. Trunk usually cylindrical with dorsal crest (usually asymmetrical); ventral fissure absent ……… **Trichocercidae**

12b – Body symmetrical. Trophi usually symmetrical, sometimes weakly asymmetrical (asymmetry most pronounced in rami and unci). Toes absent or present and usually of equal length, never substyli; occasionally, a single toe. Body sacciform, fusiform, conical, etc., never with dorsal crest, or if indication of dorsal, crest lorica with ventral fissure ………………………… **13**

13a – Stomach colored yellowish or brownish, with blind sacs. Body saccate to ovate, weakly loricate ……… **Gastropodidae**

13b – Stomach without blind sacs. Trunk fusiform, conical, vasiform, or cylindrical and illoricate, or ovate to bean-shaped and distinctly loricate ……………………………… **14**

14a – Corona with stiff setae and sensory palps. Strongly developed V-shaped hypopharynx muscles. Illoricate or loricate. With or without 6 sword-shaped paddles .... **Synchaetidae**

14b – Not as above **15**

15a – Body conical, dorsum strongly arched, head continuous with trunk. Foot long, narrow. Single toe. Mouth opening bordered by long stiff cilia forming pseudotrochus ...... **Microcodonidae**

15b – Body more or less strongly fusiform, head usually distinctly offset. Foot usually short and broad. Toes usually paired, rarely a single toe. Corona of *Notommata*-type ...... **Notommatidae**

16a – Trophi submalleate, number of unci teeth reduced, usually composed of 3 stout subequal fused teeth, shaft of manubria elongate. Foot short, a single pseudosegment, inserted ventrally on ventral plate. Toes 2 or fused (partly or completely) to 1. Usually loricate with dorsal and ventral plate separated by lateral furrows (sulci); dorsal and ventral plate not distinguishable in illoricate species .... **Lecanidae**

16b – Trophi strictly malleate, or malleovirgate, unci with many teeth, gradually decreasing in length, shaft of manubria not particularly elongated; when number of teeth reduced, foot absent or composed of 2–5 pseudosegments in line with trunk. Loricate or illoricate. Dorsal, ventral and/or lateral sulci present or absent **17**

17a – Head shield present, retractile or non-retractile .... **Lepadellidae**

17b – Head shield absent **18**

18a – Loricate, lorica of 1 piece with longitudinal dorsal sulcus or dorsal keel (not part of polygonal facets). Foot present .... **Mytilinidae**

18b – Loricate or illoricate, without dorsal sulcus or keel (if present part of polygonal facets). Foot absent or present **19**

19a – Illoricate or very weakly loricate **20**

19b – Distinctly loricate **21**

20a – Mouth set at end of shallow or deep, large funnel-shaped buccal field. Corona usually with conspicuous series of tufts of long cirri. Foot distinct with 1 or 2 toes or rudimentary and toes lacking. Trunk occasionally with several protruding transversal folds; without lateral sulci. Trophi strictly malleate .... **Epiphanidae [illoricate Brachionidae may key out here]**

20b – Mouth superficial, no large funnel-shaped buccal field. Corona usually without tufts of long cirri [except in *Bryceella*]. Foot distinct with 1 or 2 toes. Trunk without protruding transversal folds; usually without lateral sulci [shallow ones in *Bryceella*]. Trophi malleate to malleovirgate .... **Proalidae**

21a – Conspicuous lateral sulci present. Foot with 2 stout toes .... **Euchlanidae**

21b – Lateral sulci absent, shallow, or inconspicuous. Foot absent or present; toes absent or present **22**

22a – Lorica covering clearly defined head, trunk, and foot .... **Trichotriidae**

22b – Lorica only covering trunk and occasionally foot. Foot absent or present .... **Brachionidae**

4.6.2.4 Key to families of Floscularicea

01a – Body loricate. Free-swimming …………… **Testudinellidae**

01b – Body illoricate. Free-swimming or sessile in tubes of mucus, pellets, or rigid material …………………………………… **02**

02a – Body with 6 arm-like appendages with fanwise arranged setae. Free-swimming ………………… **Hexarthridae**

02b – Body without arm-like appendages. Free-swimming or sessile …………………………………… **03**

03a – Apical field dome-shaped. Body with or without 2 long lateral movable setae and 1 caudal seta. Foot absent. Free-swimming ………… **Trochosphaeridae**

03b – Apical field not dome-shaped. Movable setae always absent. Foot present. Free-swimming or sessile …………………………………… **04**

04a – Corona round, horseshoe- to U-shaped. Teeth of left uncus longer than those of right one. Free-swimming, often colonial ………………… **Conochilidae**

04b – Corona round, heart-shaped, or with 2–8 lobes, not horseshoe- or U-shaped. Teeth of left and right uncus equally long. Adults sessile or swimming in colonies ……………… **Flosculariidae**

4.6.2.5 Key to families of Collothecacea

01a – Corona funnel-shaped without lobes or cilia …………………… **Atrochidae**

01b – Corona with lobes, tentacles, or points bearing long setae and cilia ……………… **Collothecidae**

4.6.3 Characterization of families

Subclass Bdelloidea Hudson, 1884
Order Adinetida Melone & Ricci, 1995
Family Adinetidae Hudson & Gosse, 1886 (Figs. 4.49 A and 4.53 A, B)

Body fusiform to vermiform, mostly compressed dorsoventrally. Esophagus long, trophi deep, not protrusible. Stomach tube-shaped with lumen. Corona a ventral ciliated field with rake of teeth at its base (*Adineta*) or at its lateral sides (*Bradyscela*), trochi absent; rostrum terminal, not retractile. Eyespots usually absent. Foot narrow, 3 toes, 2 spurs (*Adineta*), or foot short, plump, distal foot pseudosegment disc-shaped with papillae, spurs absent (*Bradyscela*). Proximal and distal minor teeth of uncus always present. Oviparous, rarely viviparous. Gliding movement. Feeding by scraping and browsing.

Two genera: *Adineta* Hudson & Gosse, 1886 (18 spp.) and *Bradyscela* Bryce, 1910 (2 spp.).

Limnoterrestrial, in aerophytic mosses, leaf litter, soil, *Sphagnum*, hygropsammon, and littoral submerged vegetation.

Order Philodinavida Melone & Ricci, 1995
Family Philodinavidae Harring, 1913 (Fig. 4.53 C–E)

Esophagus short. Stomach tube-shaped with lumen. Corona poorly developed, reduced to small ciliated field, trochi absent or small, cheeks present, stout non-retractable rostrum, short dorsal antenna (Ricci & Melone 1998a). The trophi are close to the mouth opening, and extruded when animal is feeding. Proximal minor teeth of uncus plate reduced or absent. Foot with 4 toes, and 2 spurs. Oviparous. The aberrant carnivorous *Abrochtha carnivora* has a long pharynx that can be widened to become a large funnel, used in combination with the mouth cone to envelop the prey (rotifers); its trophi are not protrusible, and the uncus shows numerous minor teeth (Ricci et al. 2001).

Three genera: *Abrochtha* Bryce, 1910 (5 sp.), *Henoceros* Milne, 1916 (2 spp.), and *Philodinavus* Harring, 1913 (2 sp.).

Benthic-periphytic in stagnant and running waters.

Order Philodinida Melone & Ricci, 1995
Family Habrotrochidae Bryce, 1910 (Fig. 4.53 F–I)

Body fusiform to vermiform. Esophagus long, trophi deep, not protrusible. Stomach without recognizable lumen, with round pellets in its wall. Corona frontal, with small but well developed trochi, mostly elevated on pedicels. Upper lip not extending beyond ciliary disc, or hood-shaped. Eyespots present or absent. Foot with 2 spurs of variable length. Toes present (2, 3, or 4) or absent. Proximal and distal minor teeth of uncus plate always present.

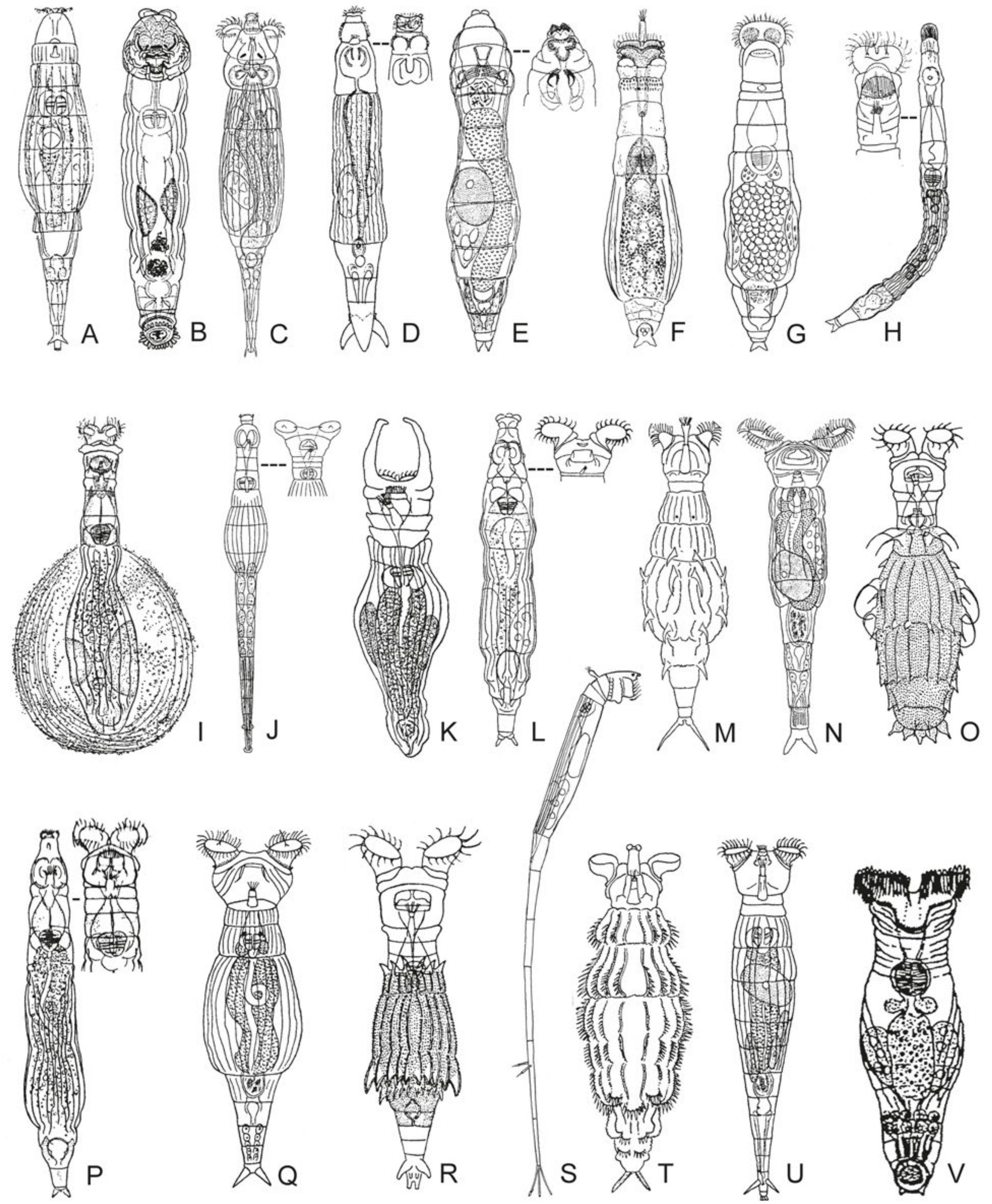

Fig. 4.53: Bdelloidea. (A) *Adineta vaga*, (B) *Bradyscela clauda*, (C) *Abrochtha intermedia*, (D) *Henoceros falcatus*, (E) *Philodinavus paradoxus*, (F) *Otostephanos monteti*, (G) *Scepanotrocha rubra*, (H) *Habrochtha serpens*, (I) *Habrotrocha pusilla textrix*, (J) *Anomopus telphusae*, (K) *Ceratotrocha cornigera*, (L) *Didymodactylos carnosus*, (M) *Dissotrocha a. aculeata*, (N) *Embata laticeps*, (O) *Macrotrachela multispinosa*, (P) *Mniobia orta*, (Q) *Philodina citrina*, (R) *Pleuretra brycei*, (S) *Rotaria neptunia*, (T) *Rotaria sordida fimbriata*, (U) *Rotaria citrina*, and (V) *Zelinkiella synaptae*. (After different authors.)

Oviparous, rarely viviparous. Vortex feeding. Some *Habrotrocha* species form secretions and more or less bottle-shaped shells or occupy shells of testate amoebae (*Centropyxis, Nebela*) or the cups (amphigastrae) under the leaflets of hepatic mosses (*Frullania, Lejeunia*); others reported from empty *Sphagnum* and plant (*Typha*) cells (Donner 1950).

Three genera: *Habrotrocha* Bryce, 1910 (128 sp.), *Otostephanos* Milne, 1916 (13 spp.), and *Scepanotrocha* Bryce, 1910 (11 spp.).

Limnoterrestrial, in aerophytic mosses and lichens, leaf litter, wet soil, *Sphagnum*, hygropsammon, and littoral submerged vegetation; occasionally epizoic on insect larvae, molluscs, etc.

Family Philodinidae Ehrenberg, 1838 (Figs. 4.49 B, C and 4.53 J–V)

Shape of body variable, fusiform, vermiform, cylindrical, etc. Integument soft or stiffened and often ornamented with grooves, spines, platelets, warts, etc. Esophagus long, trophi deep, not protrusible. Tube-shaped stomach with lumen. Corona frontal, well developed, with trochi mostly elevated on pedicels. Rostrum retractile. Eyespots present or absent. Foot with 2, 3, or 4 toes, or with adhesive disc and toes absent. Two spurs of variable length. Proximal and distal minor teeth of uncus plate always present. Vortex feeding. Oviparous and ovoviviparous.

Eleven genera: *Anomopus* Piovanelli, 1903 (2 spp.), *Ceratotrocha* Bryce, 1910 (4 spp.), *Didymodactylos* Milne, 1916 (1 sp.), *Dissotrocha* Bryce, 1910 (34 spp.), *Embata* Bryce, 1910 (5 spp.), *Macrotrachela* Milne, 1886 (97 spp.), *Mniobia* Bryce, 1910 (49 spp.), *Philodina* Ehrenberg, 1830 (50 spp.), *Pleuretra* Bryce, 1910 (14 spp.), *Rotaria* Scopoli, 1777 (27 spp.), and *Zelinkiella* Harring, 1913 (1 sp.).

Limnoterrestrial, in aerophytic mosses and lichens, *Sphagnum*, leaf litter, soil, dung; in benthos, periphyton, hygropsammon and hydropsammon of freshwaters, rarely planktonic; a few species in brackish and marine environments. Several species epizoic on crustaceans: *Mniobia branchicola* on gill plates of terrestrial isopods (*Ligidium); Embata commensalis, E. laticeps, E. parasitica, Rotaria magnacalcarata, R. murrayi, R. socialis* on freshwater isopods and amphipods, e.g., *Asellus, Gammarus; Anomopus telphusiae* and *Embata parasitica* in gill chamber of freshwater crayfish, e.g., *Astacus, Austropotamobius*, and crab (*Potamon*), and *Anomopus chasmagnathi* in gill chamber of brackish-water crab (*Chasmagnathus); Zelinkiella synaptae* on body surface and tentacles of sea cucumbers (Synaptidae) and polychaetous annelids (Terebellidae); several freshwater species have been reported epibiotic on insect larvae, molluscs, etc.

Subclass Monogononta Plate, 1889
Order Ploima Hudson & Gosse, 1886
Family Asciaporrectidae De Smet, 2006 (Fig. 4.54 A)

Illoricate. Body fusiform with offset head, trunk, and foot. Foot short to fairly long, broad. Two short toes. Trophi hemiforcipate organized for grasping, with long rod-shaped manubria bearing axe-shaped head, long fulcrum, and 2–3 large uncinal and 3–5 subuncinal teeth pivoting on the broad tips of the flat rami. Oviparous.

Three species: the free-living benthic-periphytic *Asciaporrecta hyalina* (formerly *Pleurotrocha hyalina*), and *A. difflugicola* and *A. arcellicola* inhabiting shells of live testate amoebae of the genus *Difflugia* and *Arcella*, respectively. Probably parasites, feeding on the protoplasm of their hosts (De Smet 2006).

Family Asplanchnidae Eckstein, 1883 (Fig. 4.54 B, C)

Body sac-shaped, sometimes with lateral protuberances, head differentiated, foot and toes present or absent, hyaline. Illoricate. Corona *Asplanchna* type, a single ring of cilia. Eyespot cerebral or absent. With or without intestine and anus. Vitellarium spherical, saccate, or horseshoe-shaped. Gastric glands on esophagus. Trophi incudate. Oviparous and ovoviviparous.

Three genera: *Asplanchna* Gosse, 1850 (9 spp.), *Asplanchnopus* Guerne, 1888 (4 spp.), and *Harringia* de Beauchamp, 1912 (2 spp.).

Planktonic (*Asplanchna*), semi-planktonic (*Asplanchnopus*), and benthic-periphytic (*Harringia*) species.

Family Birgeidae Harring & Myers, 1924 (Fig. 4.54 D)

Illoricate. Body plump, vase-shaped, head separated from trunk by neckfold. Foot extremely slender, 3 pseudosegments. Two lanceolate short toes. Corona frontal, circumapical band interrupted dorsally, passing laterally to auricle-like area of strong cilia, buccal field close-set with short cilia. Stomach with 10 blind sacks, stomach wall crowded with zoochlorellae. Gastric glands absent. Large eyespot ventrally on small brain. Trophi unique, highly specialized with large, hooked pseudunci expanded at their proximal ends into broad laminae; at rest hooks protrude slightly through mouth opening. Fulcrum long, rod-shaped, directed toward mouth. Rami elongate, narrow, attenuated toward tiops. Unci with 4–5 linear teeth. Manubria heart-shaped with very short cauda.

Monotypic family, with a single species: *Birgea enantia* Harring & Myers, 1922, reported from freshwater swampy pond (Wisconsin and New Jersey, USA).

Family Brachionidae Ehrenberg, 1838 (Figs. 4.50 A–C and 4.54 E–L)

Loricate, occasionally very weakly loricate. Lorica usually more or less dorsoventrally depressed, angular, rectangular, or hexagonal; anterior margins of lorica often with spines, caudally with or without spines or extensions; head and foot retractable in lorica. Foot present or absent, if present long and wrinkled or with pseudosegments; 2 small toes. Corona *Brachionus* type, frontal with reduced ciliation, pseudotrochus with 3–5 humps with short cilia on top and cirri between. Eyespots frontal, cerebral, or lacking. Trophi malleate. Oviparous.

Seven genera: *Anuraeopsis* Lauterborn, 1900 (5 spp.), *Brachionus* Pallas, 1766 (55 spp.), *Kellicottia* Ahlstrom, 1938 (2 spp.), *Keratella* Bory de St. Vincent, 1822 (45 spp.), *Notholca* Gosse, 1886 (42 spp.), *Plationus* Segers, Murugan & Dumont, 1993 (3 spp.), and *Platyias* Harring, 1913 (3 spp.).

Planktonic and semi-planktonic in littoral, temporarily attached to substrate; *Brachionus rubens* and *B. sessilis* epizoic on cladocerans, occasionally on *Corixa* sp. Freshwater, a few species in brackish and marine environments.

Family Clariaidae Kutikova, Markevich & Spirodonov, 1990 (Fig. 4.54 M)

Illoricate. Body elongate fusiform, anterior half with 16 pseudosegments, showing longitudinal striations and finely denticulate distal margin. Toes very long, weakly inflated. Trophi aberrant with thin elongate forceps-like rami, inner margin of rami lined with numerous, and loosely bound short teeth, rami with set of 4 small apical teeth. Single uncus tooth, short manubria, and long fulcrum.

Monotypic family, with a single species: *Claria segmentata* Kutikova, Markevich & Spirodonov, 1990, parasitic in earthworm *Pheretima modigliani* Rosa, 1889 (Megascolecidae).

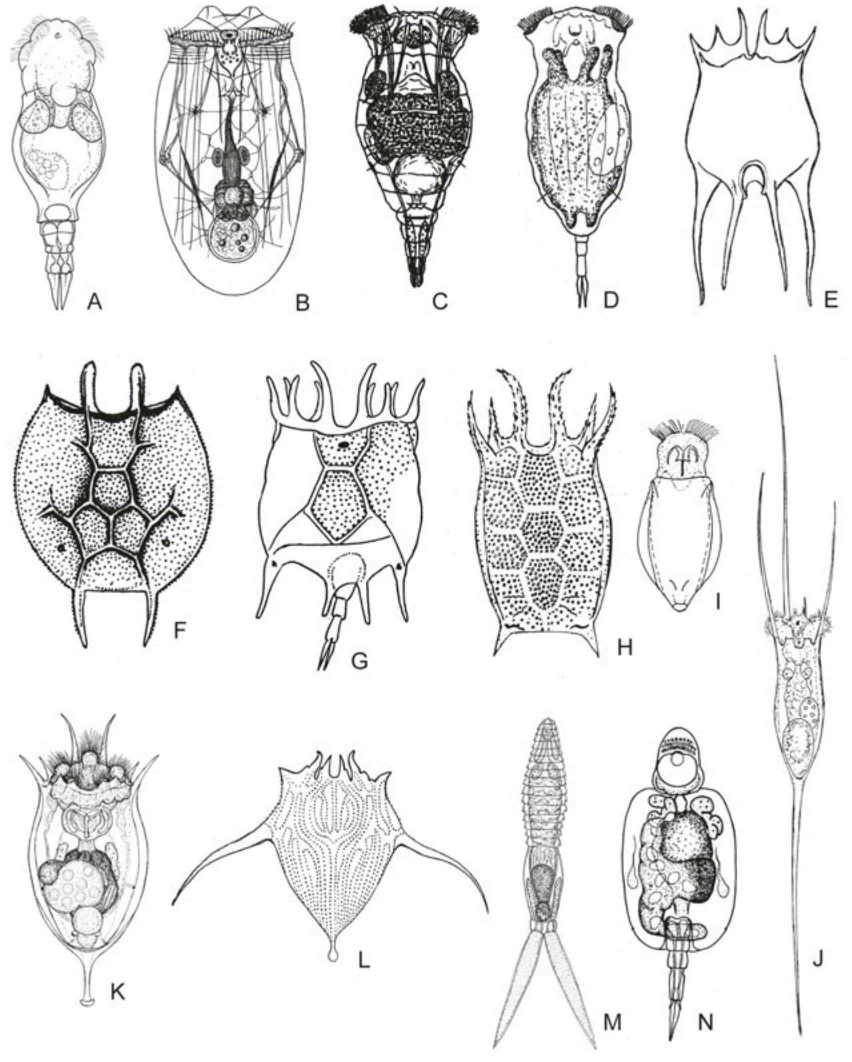

Fig. 4.54: Monogononta. (A) *Asciaporrecta arcellicola*, (B) *Asplanchna priodonta*, (C) *Harringia eupoda*, (D) *Birgea enantia*, (E) *Brachionus mirabilis*, (F) *Platyias quadricornis*, (G) *Plationus patulus*, (H) *Keratella serrulata*, (I) *Anuraeopsis fissa*, (J) *Kellicottia longispina*, (K) *Notholca kozhovi*, (L) *Notholca olchonensis*, (M) *Claria segmentata*, and (N) *Cotylegaleata perplexa*. (After different authors.)

Family Cotylegaleatidae De Smet, 2007 (Fig. 4.54 N)

Loricate. Head relatively small, covered by non-retractile head shield, offset from rectangular, and slightly dorsoventrally compressed trunk. Foot long, 4 pseudosegments, distal by one longest, bearing 2 toes, and 2 ventrolateral spurs. Corona reduced, ventral; mouth opening surrounded by large, shallow cup-shaped structure with stiffened wall. Trophi modified virgate, with small unci composed of 5–6 teeth, short manubria, long fulcrum, and 2 relatively long stilletto-shaped epipharyngeal elements.

Monotypic family, with a single species: *Cotylegaleata perplexa* De Smet, 2007, found in benthos of freshwater lake at 8–9 m depth; ectoparasite? (De Smet 2007).

Family Dicranophoridae Harring, 1913 (Figs. 4.50 E–G and 4.55 A–F)

Illoricate or semi-loricate. Body elongate cylindrical, fusiform, usually with offset head, trunk, and foot. Head usually with dorsofrontal rostrum. Trunk mostly with dorsal fold or tail, covering foot more or less. Foot and toes (2) usually short. Corona of *Dicranophorus* type, ventral or oblique, often 2 lateral ciliary tufts of longer cilia; corona absent in parasitic genus *Balatro*. Eyespots frontal, 2, rarely 4, or absent. Trophi forcipate, protrusible. Oviparous, ovoviviparous.

The family comprises 19 genera: *Albertia* Dujardin, 1838 (7 spp.), *Aspelta* Harring & Myers, 1928 (21 spp.), *Balatro* Claparède, 1867 (4 spp.), *Dicranophoroides* De Smet, 1997 (4 spp.), *Dicranophorus* Nitzsch, 1827 (52 spp.), *Donneria* De Smet, 2003 (1 sp.), *Encentrum*, Ehrenberg, 1838 (subgenera *Encentrum, Isoencentrum*, and *Pseudencentrum* De Smet, 1997, 105 spp.), *Dorria* Myers, 1933, *Erignatha* Harring & Myers, 1928 (5 spp.), *Glaciera* Jersabek, 1999 (1 sp.), *Inflatana* Kutikova, 1985 (1 sp.), *Kostea* De Smet, 1997 (1 sp.), *Myersinella* Wiszniewski, 1936 (4 spp.), *Paradicranophorus* Wiszniewski, 1929 (5 spp.), *Parencentrum* Wiszniewski, 1936 (2 spp), *Pedipartia* Myers, 1937 (1 sp.), *Streptognatha* Harring & Myers, 1928 (1 sp.), *Wierzejskiella* Wiszniewski, 1934 (2 spp.), *Wigrella* Wiszniewski, 1932 (2 spp.).

Benthic-periphytic, and psammic in freshwater, brackish, and marine environments; the most diverse rotifer family in saline waters. Several species live epizoically on freshwater crustaceans. *Encentrum grande* and *E. kulmatyckii* live on the thoracal and abdominal appendages, and the gills of *Asellus aquaticus* and *Gammarus pulex; Dicranophorus siedleckii* is also found on the gills and pleopods of *G. pulex*. *Dicranophorus hauerianus* and *D. cambari* inhabit the branchial cavities of several species of freshwater crayfish. Nearly all *Albertia* and *Balatro* species are obligatory parasites of terrestrial and aquatic oligochaetes. *Albertia* species live in the intestine of Naididae, Lumbricidae, and Lumbriculidae; *Balatro* is parasitic in the intestine or on the exterior of Lumbriculidae and Enchytraeidae. *Encentrum kozminskii* lives ectoparasitic on the skin and gills of carp (*Cyprinus carpio*).

Family Epiphanidae Harring, 1913 (Fig. 4.55 G-J)

Illoricate, occasionally weakly stiffened. Body fusiform, cylindrical, or conical to vase-shaped. Foot short to long, mostly indistinctly offset from trunk. Toes short and small, 2 or 1. Mouth set in funnel-shaped ventral buccal field with short cilia. Corona of *Euchlanis-Brachionus* type, a circumapical band of cilia; apical field with tufts of cilia, buccal field with short cilia; apical field can be elongated to form broad proboscis. Eye(s) pigmented or colorless; a single cerebral eye, or 2 eyes on proboscis. Trophi malleate. Oviparous or ovoviviparous.

Five genera: *Cyrtonia* Rousselet, 1894 (1 sp.), *Epiphanes* Ehrenberg, 1832 (6 spp.), *Mikrocodides* Bergendal, 1892 (3 spp.), *Proalides* de Beauchamp, 1907 (2 spp.), and *Rhinoglena* Ehrenberg, 1853 (4 spp.).

Planktonic and semi-planktonic, periphytic. Freshwater and brackish waters. *Epiphanes daphnicola* (formerly *Proales daphnicola*) is epibiotic on *Daphnia* spp., rarely on other cladocerans, copepods, amphipods, and oligochaetes.

Family Euchlanidae Ehrenberg, 1838 (Fig. 4.55 K, N)

Loricate. Body usually oval; trunk usually depressed, composed of 2–3 plates connected by thin membranes forming longitudinal sulci; head offset from trunk by constriction, foot well-differentiated with 2 stout, more or less long toes. Single cerebral eyespot. Corona *Euchlanis* type, with interrupted ciliary band, apical field with several tufts of cilia. Trophi malleate. Oviparous.

The family comprises 5 genera: *Beauchampiella* Remane, 1929 (1 sp.), *Dipleuchlanis* de Beauchamp, 1910 (3 spp.), *Diplois* Gosse, 1886 (1 sp.), *Euchlanis* Ehrenberg, 1832 (14 spp.), *Tripleuchlanis* Myers, 1930 (2 spp.).

Benthic-periphytic, littoral of freshwaters, rarely brackish and marine.

Family Gastropodidae Harring, 1913 (Fig. 4.55 L, M)

Loricate. Body ovate to sac-shaped, more or less compressed laterally and/or dorsoventrally. Lorica smooth, transparent, with or without longitudinal folds. Foot absent or present, more or less placed ventrally, retractable, usually annulated. Occasionally surrounded by mucus

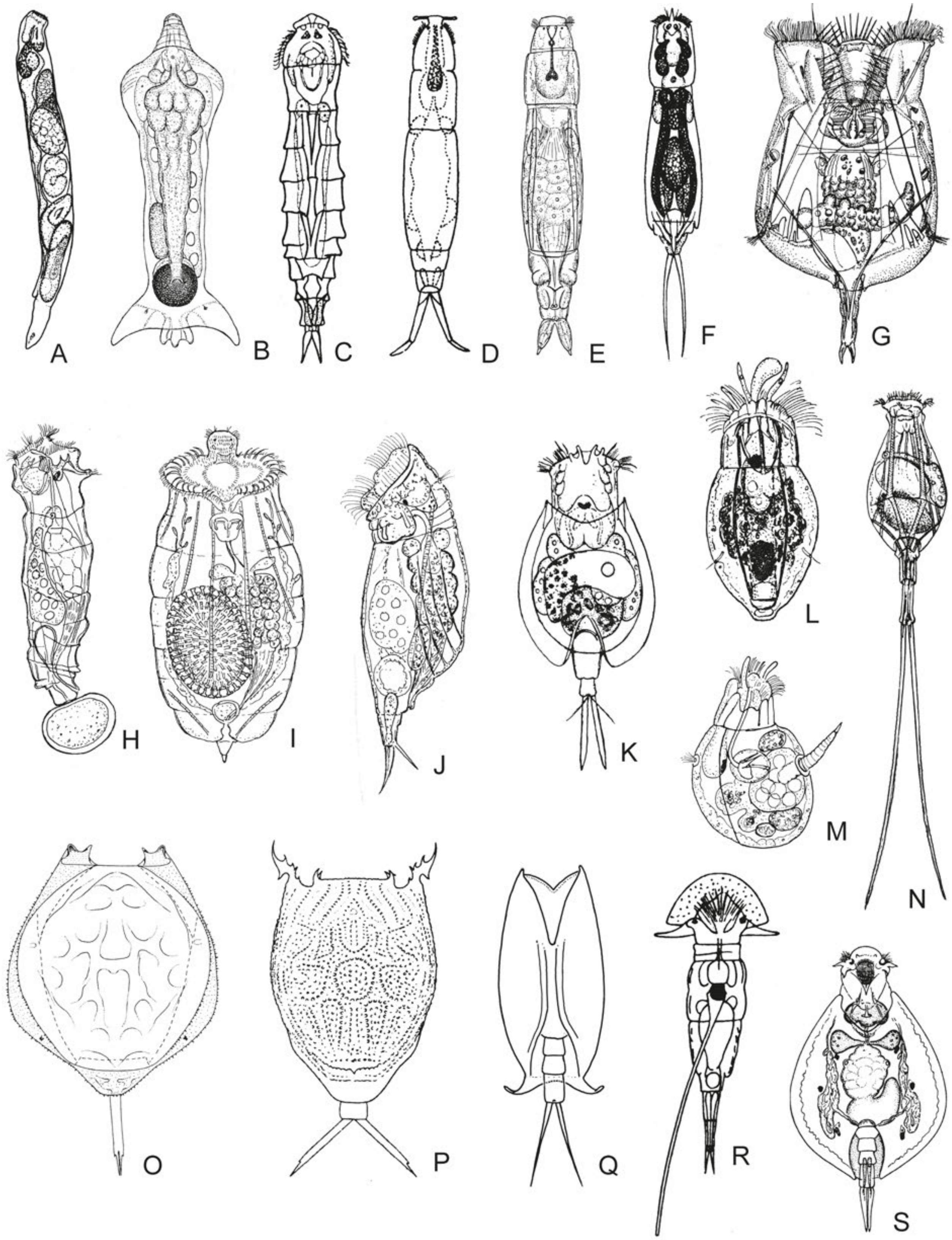

Fig. 4.55: Monogononta. (A) *Albertia vermiculus*, (B) *Balatro calvus*, (C) *Encentrum plicatum*, (D) *Dicranophorus hercules*, (E) *Dicranophorus cambari*, (F) *Dicranophoroides caudatus*, (G) *Epiphanes brachionus*, (H) *Proalides tentaculatus*, (I) *Rhinoglena fertoeensis*, (J) *Mikrocodides robustus*, (K) *Euchlanis meneta*, (L) *Ascomorpha saltans*, (M) *Gastropus stylifer*, (N) *Beauchampiella eudactylota*, (O) *Lecane sylvae*, (P) *Lecane satyrus*, (Q) *Colurella halophila*, (R) *Squatinella longispinata*, and (S) *Lepadella ovalis*. (After different authors.)

sheath. Stomach lobate or with blind sacks containing dark-colored defecation pellets; stomach wall often with zoochlorellae. Corona with well developed cingulum, apical field with sensory organs, e.g., styli, palps, tufts of bristles. Cerebral eyespot present. Trophi virgate. Oviparous.

The family comprises 2 genera: *Ascomorpha* Perty, 1850 (9 spp.) and *Gastropus* Imhof, 1888 (3 spp.).

Planktonic and semi-planktonic in littoral vegetation of freshwaters, rarely in brackish habitats.

Family Ituridae Sudzuki, 1964 (Fig. 4.56 A)

Illoricate. Body fusiform. Head more or less widening laterally; usually neck distinct. Foot short, 2 pseudosegments. Stomach with blind sacks; stomach and intestine with green zoochlorellae. Gastric glands absent. Corona reduced to a buccal field with 2 lateral, non-retractable ciliated auricles. Two frontal and single cerebral eyespot. Trophi similar to forcipate type of genus *Dicranophorus*. Oviparous.

A single genus *Itura* Harring & Myers, 1928, with 6 species.

Benthic-periphytic in freshwater habitats, occasionally in brackish environment.

Family Lecanidae Remane, 1933 (Fig. 4.55 O, P)

Loricate, rarely illoricate. Lorica cylindrical when extended; outline truncate-oval or shield-shaped; flattened dorsoventrally when contracted; with dorsal and ventral plates separated by lateral sulcus. Head opening of lorica slit-like, broad and shallow, often with the lateral corners forming angles or spines. Anterior margin of dorsal and ventral plate straight or with more or less deep sinus. Foot subdistally, very short, a single pseudosegment. Two separate or partly fused toes, or a single toe; tips of toes simply acute, or with completely or incompletely separated claws or incompletely separated pseudoclaws. Corona *Euchlanis* type. Single cerebral eyespot. Trophi submalleate. Oviparous.

A single genus *Lecane* Nitzsch, 1827, with about 170 spp.

Benthic-periphytic in littoral of freshwaters, several species in brackish environment, rarely marine. *Lecane branchicola* lives in the gill chambers of the freshwater crab *Potamon fluviatile*.

Family Lepadellidae Harring, 1913 (Fig. 4.55 Q–S)

Loricate. Lorica compressed dorsoventrally, composed of firmly joined dorsal and ventral plate, or a laterally compressed plate with ventral slit; lorica spines may be present. Head usually with retractile or non-retractile, semi-circular shield or membranous cap. Foot with 3–4 pseudosegments. Toes slender, acutely pointed, occasionally partly or completely fused. Corona *Euchlanis*-like, frontal, a single ciliary band. Two lateral eyespots, or eyes absent. Trophi malleate, occasionally modified. Oviparous.

Five genera: *Colurella* Bory de St. Vincent, 1824 (21 spp.), *Halolepadella* De Smet, 2012 (1 sp.), *Lepadella* Bory de St. Vincent, 1826 (subgenera *Heterolepadella* Bartoš, 1955; *Xenolepadella* Hauer, 1926, 80 spp.), *Paracolurella* Myers, 1936 (2 spp.), and *Squatinella* Bory de St. Vincent, 1826 (6 spp.).

Littoral, benthic-periphytic, occasionally in plankton and psammon. Freshwater, rarely in brackish or marine waters. *Lepadella astacicola, L. borealis, L. branchicola, L. lata*, and *L. parasitica* live in the gill cavities of freshwater crayfish (*Astacus* spp.).

Family Lindiidae Harring & Myers, 1924 (Fig. 4.56 B)

Illoricate. Body vermiform or fusiform, head, trunk, and foot generally distinct; tail usually present. Foot short, a single rudimentary pseudosegment or 2–3 pseudosegments. Two small, short toes. Corona *Notommata* type, a simple narrow ciliated field, ventral or strongly oblique; 2 lateral ciliary tufts, usually on auricles. Cerebral eye present, rarely absent. Trophi cardate, usually with complicated accessory trophi elements. Oviparous and ovoviviparous.

A single genus, *Lindia* Dujardin, 1841 (subgenus *Halolindia* Harring & Myers, 1924, *Neolindia* Segers, 2002) with 16 species.

Benthic-periphytic, among cyanobacteria, littoral, also in psammon and *Sphagnum*. Mainly freshwater, 4 brackish-marine species.

Family Microcodonidae Hudson & Gosse, 1886 (Fig. 4.56 C)

Illoricate. Body conical, tapering to long foot with single lanceolate toe. Corona large, heart-shaped; paracingulum with dorsal and ventral interruption; mouth opening central, bordered by long stiff membranelles forming pseudotrochus. Single, large red cerebral eyespot. Trophi virgate, manubria and unci reduced; epipharynx plate-shaped, often colored red to purple. Oviparous.

A single genus, *Microcodon* Ehrenberg, 1830 (1 sp.).

Semi-planktonic in vegetation rich littoral, occasionally in *Sphagnum*.

Family Mytilinidae Harring, 1913 (Figs. 4.50 I and 4.56 D, E)

Loricate. Lorica thick or thin, often ornamented, elongate, in cross section mostly triangular or rhomboid; ventral plate and dorsolateral plates firmly fused; often with longitudinal dorsal furrow flanked by lateral ridges, or single,

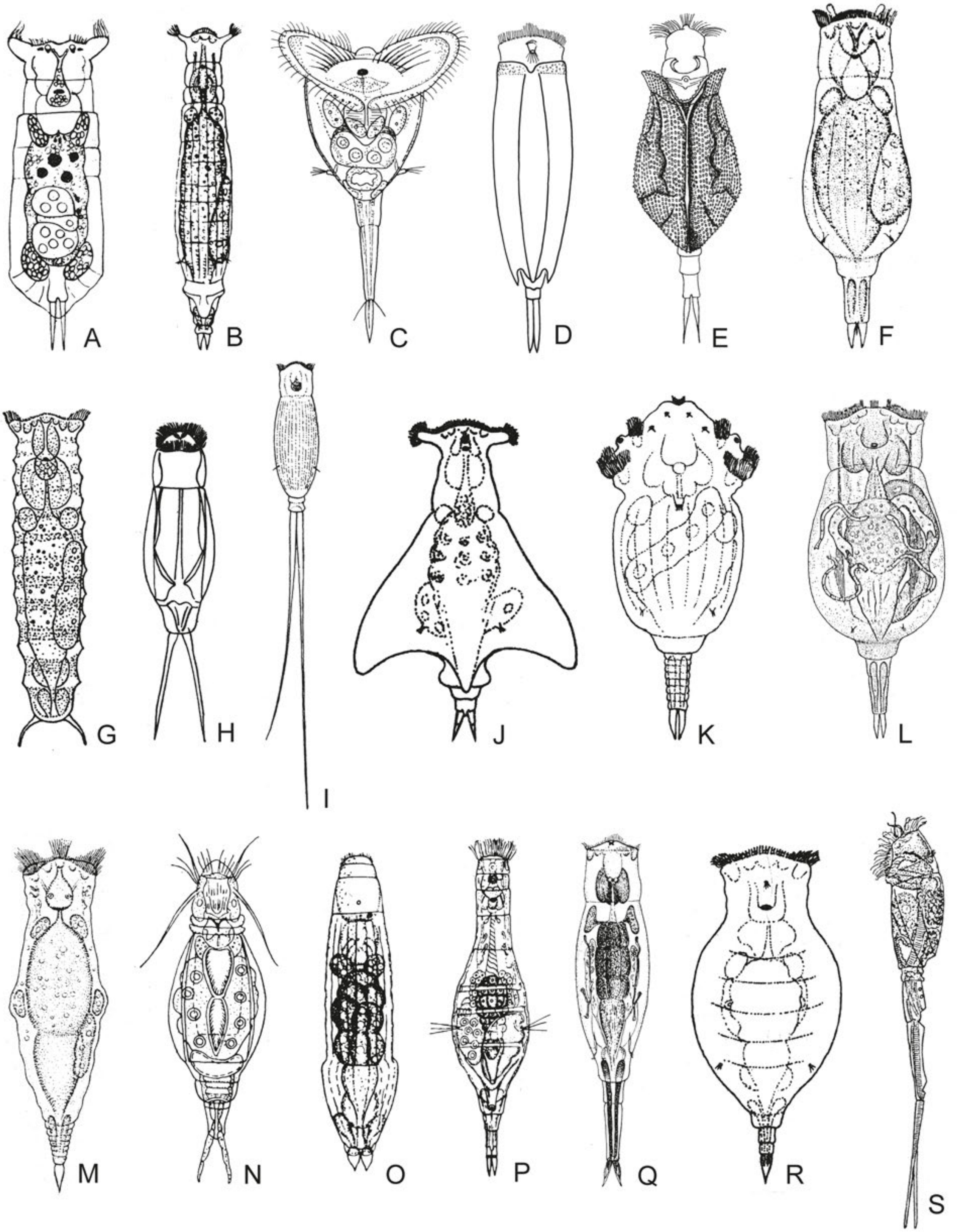

Fig. 4.56: Monogononta. (A) *Itura viridis*, (B) *Lindia pallida*, (C) *Microcodon clavus*, (D) *Mytilina brevispina*, (E) *Lophocharis rubens*, (F) *Rousseletia corniculata*, (G) *Taphrocampa selenura*, (H) *Cephalodella misgurnus*, (I) *Monommata maculata*, (J) *Notommata pachyura*, (K) *Sphyrias lofuana*, (L) *Enteroplea lacustris*, (M) *Tylotrocha monopus*, (N) *Bryceella stylata*, (O) *Wulfertia ornata*, (P) *Proalinopsis caudatus*, (Q) *Proales reinhardti*, (R) *Proales doliaris*, and (S) *Scaridium longicaudum*. (After different authors.)

rarely 3 ridges; anterior lorica margin often with spines. Foot short, 2–3 pseudosegments. Two toes. Corona *Euchlanis*-type. Single cerebral eye. Trophi malleate. Oviparous.

Two genera: *Lophocharis* Ehrenberg, 1838 (6 spp.), *Mytilina* Bory de St. Vincent, 1826 (12 spp.).

Benthic-periphytic, occasionally in plankton; freshwater, rarely in brackish environments.

Family Notommatidae Hudson & Gosse, 1886 (Figs. 4.50 H and 4.56 F–M)

A taxonomically unsatisfactory assemblage of diverse taxa (see Nogrady et al., 1995). Illoricate to partly loricate. Body plan various, mostly fusiform, with offset head, trunk, and foot; often with tail. Foot usually short, composed of single or few pseudosegments. Toes short to long. Corona *Notommata, Dicranophorus*, and *Asplanchna* type, often with ciliated auricles. Eyespots present or absent, frontal or cerebral. Trophi virgate. Oviparous.

The family comprises 17 genera: *Cephalodella* Bory de St. Vincent, 1826 (191 spp.), *Dorystoma* Harring & Myers, 1922 (1 sp.), *Drilophaga* Vejdovsky, 1883 (3 spp.), *Enteroplea* Ehrenberg, 1830 (1 sp.), *Eosphora* Ehrenberg, 1830 (6 spp.), *Eothinia* Harring & Myers, 1922 (7 spp.), *Monommata* Bartsch, 1870 (18 spp.), *Notommata* Ehrenberg, 1830 (53 spp.), *Pleurotrocha* Ehrenberg, 1830 (8 spp.), *Pleurotrochopsis* Berzins, 1973 (2 spp.), *Pseudoharringia* Fadeew, 1925 (2 spp.), *Pseudoploesoma* Myers, 1938 (1 sp.), *Resticula* Harring & Myers, 1924 (7 spp.), *Rousseletia* Harring, 1913 (1 sp.), *Sphyrias* Harring, 1913 (1 sp.), *Taphrocampa* Gosse, 1851 (3 spp.), *Tylotrocha* Harring & Myers, 1922 (1 sp.), and *Pleurata* Nogrady & Pourriot, 1995 (6 spp.). Position of *Pourriotia werneckii* (formerly *Proales werneckii*) and *P. carcharodonta* uncertain (De Smet 2003, 2009).

Most species benthic-periphytic or semi-planktonic in littoral of freshwater habitats, rarely in brackish waters; few marine species. *Cephalodella crassipes* lives in the branchial chambers of freshwater crayfish (*Astacus* spp.). Several species are ectoparasites or endoparasites. Ectoparasitic: *Cephalodella parasitica* on oligochaetes; *Drilophaga bucephalus* and *D. delagei* on oligochaetes and leeches. Endoparasitic: *Cephalodella volvocicola* in *Volvox* colonies; *C. edax* and *Pleurata uroglenae* in *Uroglena volvox; Pourriotia* spp. in *Vaucheria* spp. and *Dichotomosiphon tuberosus*.

Family Proalidae Harring & Myers, 1924 (Figs. 4.50 D and 4.56 N–R)

A taxonomically unsatisfactory assemblage of diverse taxa. Illoricate to semi-loricate. Body cylindrical, fusiform, or swollen. Head, trunk, and foot usually clearly defined; foot short to very long. Two toes or single. Corona simple, mostly supraoral, with oblique buccal field and lateral parts of circumapical band. Eyespot(s) cerebral, frontal, lateral, or absent. Trophi malleate, virgate, or a modification of one of these types; epipharynx usually present. Oviparous.

Four genera: *Bryceella* Remane, 1929 (3 spp.), *Proales* Gosse, 1886 (43 spp.), *Proalinopsis* Weber, 1918 (6 spp.), and *Wulfertia* Donner, 1943 (3 spp.).

Benthic-periphytic, planktonic, and semi-planktonic, psammic. In freshwater, brackish, and marine environments. Several parasitic species; ectoparasitic: *Proales christinae* and *P. gonothyraeae* on hydroid polyps, *P. paguri* on *Eupagurus bernhardus*; endoparastic: *P. gigantea* in eggs of several species of freshwater snail, *P. parasita* in colonial algae (*Volvox, Uroglena, Uroglenopsis*).

Family Scaridiidae Manfredi, 1927 (Fig. 4.56 S)

Loricate or semi-loricate. Body fusiform to cylindrical, with stiffened longitudinal plates. Foot very long, 3 pseudosegments, with strong transversally striated muscles. Two very long, equal toes. Corona oblique, a dorsally interrupted band of cilia, and ventral trochus with stiff cilia surrounding mouth opening. Unci projecting through mouth opening. Eyes absent. Mastax with apical red spot. Trophi modified virgate; epipharynx weak, consisting of horseshoe-toothed anterior part and pair of elongate dorsal projections. Oviparous.

A single genus *Scaridium* Ehrenberg, 1830 (7 spp.).

Periphytic in freshwaters.

Family Synchaetidae Hudson & Gosse, 1886 (Fig. 4.57 A–D)

Illoricate and loricate. Body of different shape, rectangular, sac-shaped, bell-shaped, ovate. Anterior of genus *Polyarthra* with 6 serrated paddles. Head usually set off from trunk by fold or fissure, with or without ciliated lateral auricles. Rigid lorica ornamented. Foot absent, short, or long and annulated. Toes short, 2, single, or absent. Corona *Asplanchna* type, frontal, with sensory setae, tufts of cilia, ciliated palps, etc. Cerebral eye usually present, single or paired. Trophi virgate, hypopharynx muscle mostly prominent. Oviparous and ovoviviparous.

Three genera: *Ploesoma* Herrick, 1885 (7 spp.), *Polyarthra* Ehrenberg, 1834 (11 spp.), and *Synchaeta* Ehrenberg, 1832 (39 spp.).

Mostly planktonic, rarely semi-planktonic and periphytic in freshwaters. Genus *Synchaeta* with several marine species.

Family Tetrasiphonidae Harring & Myers, 1924 (Fig. 4.57 M)

Illoricate, but integument stiff. Body cylindrical, head, and trunk not separated by transversal folds. Foot short, 2 pseudosegments. Two fairly long, slender, acute

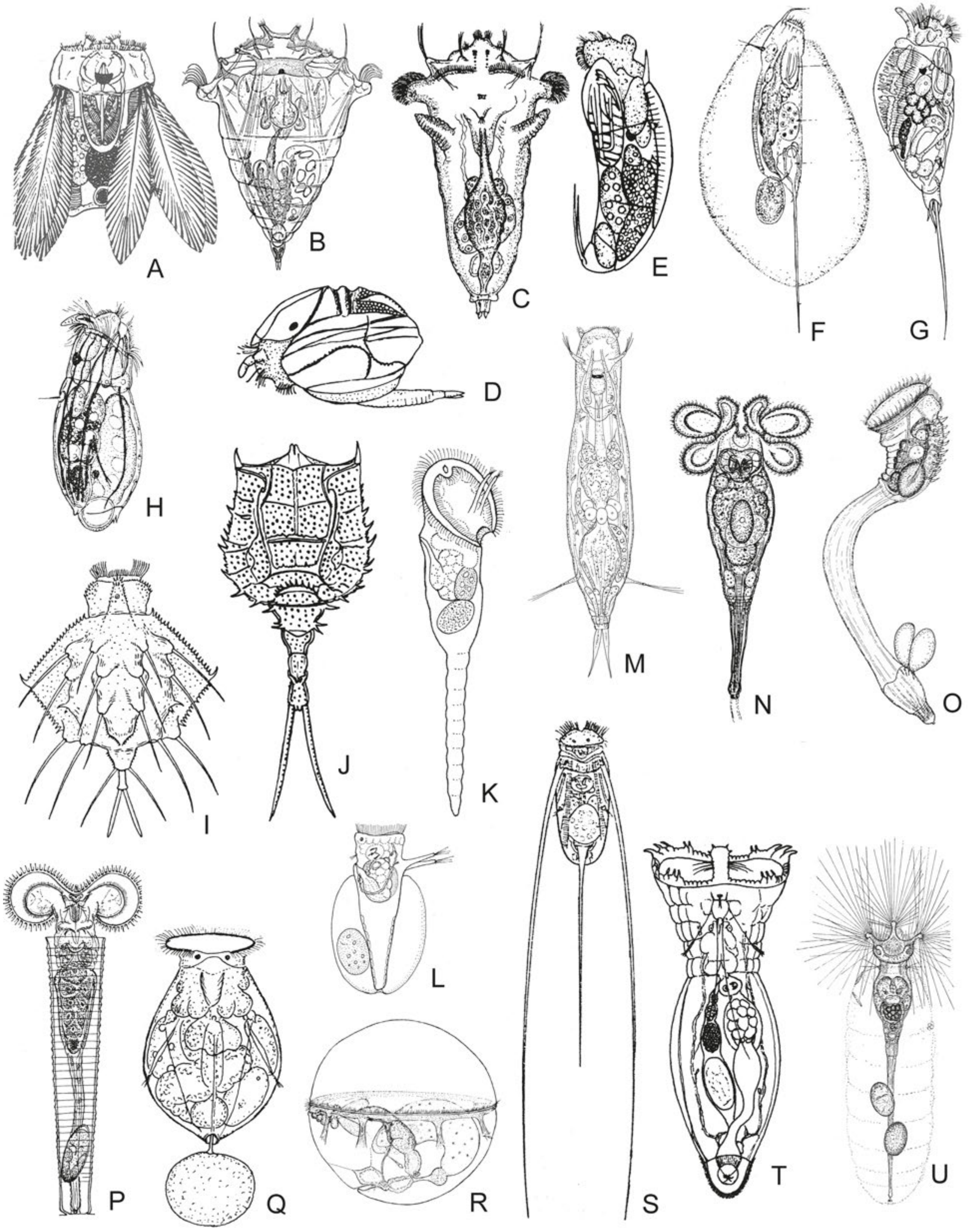

Fig. 4.57: Monogononta. (A) *Polyarthra major*, (B) *Synchaeta pectinata*, (C) *Synchaeta bicornis*, (D) *Ploesoma lenticulare*, (E) *Trichocerca weberi*, (F) *Trichocerca cylindrica*, (G) *Trichocerca rattus*, (H) *Ascomorphella volvocicola*, (I) *Macrochaetus multispinosus*, (J) *Trichotria truncata*, (K) *Conochilus hippocrepis*, (L) *C. natans*, (M) *Tetrasiphon hydrocora*, (N) *Octotrocha speciosa*, (O) *Sinantherina spinosa*, (P) *Limnias melicerta*, (Q) *Pompholyx sulcata*, (R) *Trochosphaera aequatorialis*, (S) *Filinia limnetica*, (T) *Atrochus tentaculatus*, and (U) *Collotheca coronetta*. (After different authors.)

toes. Dorsal antenna double, 2 fairly large, conical tubules with tuft of long sensory setae. Lateral antennae near posterior, very long, tubular with few very long setae. Corona oblique, ciliation very faint, anterolaterally 2 V-shaped, concave ciliated appendages; post-oral margin projecting as fairly prominent chin. Single cerebral eyespot. Connection between stomach and intestine narrow, surrounded by wreath of ca. 6 spherical glands. Vitellarium strongly elongate, cylindrical, wound around intestine, with 20–30 nuclei. Trophi unique. Rami elongate lyrate, recurved dorsally, with large alulae. Fulcrum short, lamellar. Unci with single tooth, and thin crescent-shaped basal lamella. Manubria complex, rod-shaped, curved, with appendages, connected to unci and rami. Accessory trophi elements present. Adults usually covered with firm jelly case. Oviparous.

Monotypic family, with single species: *Tetrasiphon hydrocora* Ehrenberg, 1840 (1 sp.)

Periphytic in soft acid wates, *Sphagnum* pools.

Family Trichocercidae Harring, 1913 (Fig. 4.57 E–H)

Loricate, rarely illoricate. Body ovate, cylindrical, fusiform, often twisted and asymmetrical, often with dorsal crest. Head usually with closing plates. Foot present and short, or absent. Toes if present 1–2, short to long, seta-like, usually of different length and left longest; often bristles or substyli at base of toes. Single cerebral eyespot. Corona *Asplanchna* type, frontal, circumapical band weakly developed. Trophi virgate, strongly asymmetrical.

The family comprises 3 genera: *Ascomorphella* Wiszniewski, 1953 (1 sp.), *Elosa* Lord, 1891 (2 spp.), *Trichocerca* Lamarck, 1801 (75 spp.). Oviparous.

Planktonic and periphytic, rarely psammic; predominantly freshwater, a few marine species only. *Ascomorphella volvocicola* lives endoparasitic in colonies of *Volvox aureus, V. globator*, and *Uroglena volvox*.

Family Trichotriidae Harring, 1913 (Figs. 4.50 J and 4.57 I, J)

Loricate. Lorica very rigid, ornamented with pustules and spines; spines movable in *Macrochaetus*; often with plates covering head. Head, trunk, and foot clearly defined. Foot usually 2–4 pseudosegments. Toes 2, often very long. Single cerebral eyespot. Corona frontal, weakly developed, incomplete ring of cilia. Trophi malleate. Oviparous.

The family comprises 3 genera: *Macrochaetus* Perty, 1850 (11 spp.), *Trichotria* Bory de St. Vincent, 1827 (7 spp.), and *Wolga* Skorikov, 1903 (1 sp.).

Periphytic in littoral vegetation and *Sphagnum* puddles; freshwater, occasionally in brackish waters.

Order Flosculariacea Harring, 1913

Family Conochilidae Harring, 1913 (Figs. 4.51 A and 4.57 K–L)

Illoricate. Adult females free-swimming, solitary, or colonial (5 to >400 individuals per colony) and clustered within gelatinous mass produced by pedal glands. Body conical, long, unsegmented foot, toes absent. Intestine U-shaped. Corona *Conochilus* type, horseshoe-shaped, U-shaped, or circular. Antennae apically inside coronal field or dorsally outside coronal field. Two dorsal eyes beneath corona. Trophi malleoramate, weakly to very asymmetrical; left uncinal teeth longer. Oviparous, ovoviviparous.

Two genera: *Conochilus* Ehrenberg, 1834 (type genus), and subgenus *Conochiloides* Hlava, 1904 (6 spp.), and *Conochilopsis* Segers & Wallace, 2001 (1 sp.).

Planktonic, freshwater, rarely in brackish water.

Literature: Segers & Wallace (2001).

Family Flosculariidae Ehrenberg, 1838 (Figs. 4.51 C and 4.57 N, O)

Illoricate. Adult females sessile, solitary in tubes of mucus, pellets, or rigid material, or free-swimming in spherical colonies. Larvae free-swimming, foot with ciliated cup. Body conical, foot unsegmented, long to very long, often with pedicel. Dorsal antenna small to very long, single or paired. Elongate, hook-shaped, etc. stiff lorica elements in neck region present or absent. Corona *Hexarthra* type, heart-shaped, circular, or 2- to 8-lobed. Trophi malleoramate, symmetrical. Oviparous.

The family comprises 9 genera: *Beauchampia* Harring, 1913 (1 sp.), *Floscularia* Cuvier, 1798 (10 spp.), *Lacinularia* Schweigger, 1820 (8 spp.), *Lacinularoides* Meksuwan, Pholpunthin & Segers (1 sp.), *Limnias* Schrank, 1803 (6 spp.), *Octotrocha* Thorpe, 1893 (1 sp.), *Pentatrocha* Segers & Shiel, 2008, *Ptygura* Ehrenberg, 1832 (28 spp.), and *Sinantherina* Bory de St Vincent, 1826 (6 spp.).

Attached to submerged aquatic vegetation, *Sphagnum*, and other substrates, and planktonic (*Lacinularia, Sinantherina, Ptygura libera*). Freshwater, rarely brackish, or marine.

Family Hexarthridae Bartoš, 1959 (Fig. 4.51 D, E)

Illoricate. Body conical, with 6 thick arm-like appendages: 1 dorsal, 1 ventral, 2 laterodorsal, and 2 lateroventral, bearing pinnate bristles arranged fanwise at their tips; bristles inserted singly or in pairs; ventral arm longest with series of lateral spines. Foot absent. Some species with 2 dorsocaudal club-shaped appendages bearing distal tuft of cilia or caudal spine. Dorsal antenna on prominence above dorsal arm; lateral antennae on ventral arms. Corona *Hexarthra* type, an undulate double band of cilia; in some species, with outward bend ventral lip. Two red eyespots on apical field ventrally near corona. Trophi malleoramate. Oviparous.

A single genus, *Hexarthra* Schmarda, 1854 (13 spp.).

Planktonic in freshwater, brackish, marine, and inland saline waters.

Family Testudinellidae Harring, 1913 (Fig. 4.57 Q)

Loricate. Body more or less oval, more or less compressed dorsoventrally; head and trunk differentiated, foot absent or long, cylindrical ending in ciliated cup; lorica hyaline, usually smooth; anterodorsal margin often with median expansion; anteroventral margin with median incision. Foot opening ventral, from median to terminal. Lateral and dorsal antennae more or less in line, usually near middle of lorica. Corona *Hexarthra* type, a simple circumapical band of cilia. Two eyespots, sometimes absent. Trophi malleoramate. Oviparous.

The family comprises 3 genera: *Anchistestudinella* Bērziņš, 1973 (1 sp.), *Pompholyx* Gosse, 1851 (3 spp.), *Testudinella* Bory de St. Vincent, 1826 (45 spp.).

Benthic-periphytic, semi-planktonic in littoral. Predominantly freshwater, but also in brackish and marine environment. *Testudinella caeca* and *T. elliptica* periphytic but also epizoic on *Asellus aquaticus*.

Family Trochosphaeridae Harring, 1913 (Figs. 4.51 B and 4.57 R, S)

Illoricate. Body spherical or sac-shaped, with or without 2 movable anterolateral setae and 1 or 2 posterior setae. Foot absent. Dorsal antenna reduced, posterior to dorsal gap. Lateral antennae occasionally on papillae. Corona simple, a ciliary band with dorsal gap and ciliated buccal field; ventrally drawn out into more or less distinct lip. Apical field bare, domed. Two anterior red eyespots. Trophi malleoramate. Oviparous, ovoviviparous.

Three genera: *Filinia* Bory de St. Vincent, 1824 (15 spp.), *Horaella* Donner, 1949 (2 spp.), and *Trochosphaera* Semper, 1872 (2 spp.).

Planktonic, freshwater, and occasionally brackish waters.

Order Collothecacea Harring, 1913

Family Atrochidae Harring, 1913 (Figs. 4.52 A–C and 4.57 T)

Illoricate. Body elongate conical, anterior part funnel-shaped, distinctly offset or not by constriction. Sessile or creeping. Foot unsegmented, long with small adhesive disc, contained in gelatinous sheath, or very short without sheath and adhesive disc, or modified into ventral sucker-like attachment organ without sheath. Lateral antennae near base of coronal funnel. Corona a large buccal funnel without cilia, with or without lobes and/or marginal tentacles; opening of funnel more or less apical or oblique ventral. Eyespots absent or only obvious in juveniles. Ciliated corona, used for swimming, present in juveniles. Trophi uncinate. Oviparous and ovoviviparous.

Three genera: *Acyclus* Leidy, 1882 (2 spp.), *Atrochus* Wierzejski 1893 (1 sp.), *Cupelopagis* Forbes, 1882 (1 sp.).

Periphytic, freshwater. Predatory; *Acyclus inquietus* lives in colonies of *Sinantherina socialis*, feeding on eggs and larvae.

Family Collothecidae Harring, 1913 (Figs. 4.52 D and 4.57 U)

Illoricate. Sessile, rarely free-swimming; mostly with mucous or gelatinous case or tube. Body plan various, ovate, spherical, elongate conical, etc.; foot unsegmented, long without toes, tip mostly undifferentiated, or with small adhesive disc. Lateral antennae absent. Dorsal antenna reduced. Corona *Collotheca* type, funnel-shaped with vestibulum and infundibulum; a single ring of mobile, often strongly reduced cilia; margin of coronal funnel smooth, or with lobes, tentacles, or knobs bearing long motionless setae. Eyespots present, 2, rarely 3, often disappearing in adults, or absent. A ciliated corona, used for swimming, present in juveniles. Trophi uncinate. Oviparous and ovoviviparous.

The family comprises 2 genera: *Collotheca* Harring, 1913 (45 spp.), and *Stephanoceros* Ehrenberg, 1832 (2 spp.).

Predominantly benthic-periphytic, a few planktonic species. Freshwater, less frequent in brackish water.

4.7 Biogeography

Due to the presence of resting stages (Hairston & Kearns 2002), all Rotifera, both Bdelloidea and Monogononta, have, in principle, the potential for cosmopolitan distribution (Artois et al. 2011). Nevertheless, data on their distribution is really scarce; thus, no reliable inference can be reliable for Bdelloidea (Ricci 1987, Ricci & Fontaneto 2009), whereas for Monogononta our biogeographical knowledge reflects the distribution of rotifer scientists (Fig. 4.58) more than that of rotifers themselves (Dumont 1983, Segers & De Smet 2008, Fontaneto et al. 2012a). The information for Seisonacea is even scantier (see chapter by Ahlrichs & Riemann).

Notwithstanding such difficulties in analyzing biogeography of understudied animals with too few data on their distribution (Artois et al. 2011), some Rotifera are known to have very limited distribution. For species that are locally common and that are easy to identify, such

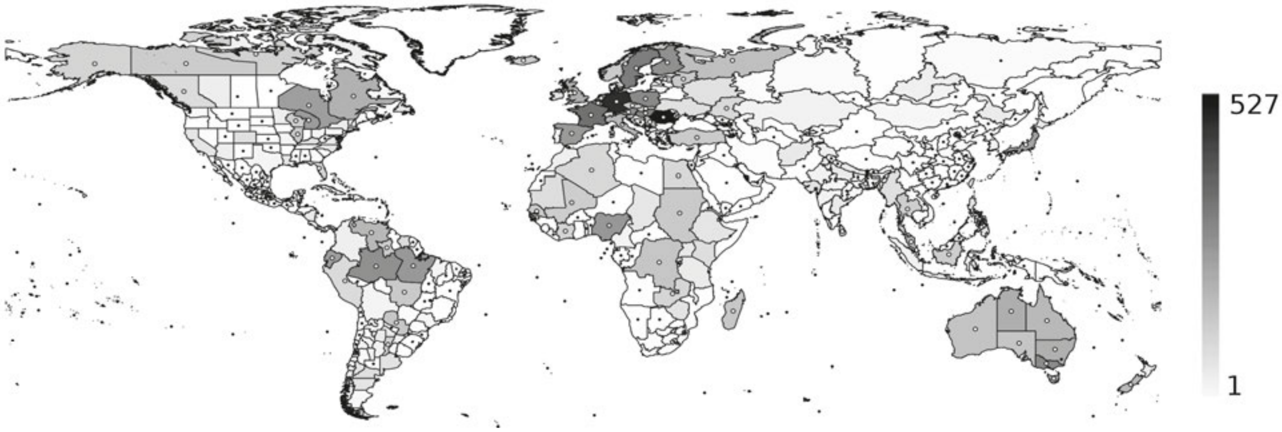

Fig. 4.58: Global species richness of Monogononta at the finest resolution scale of the Biodiversity Information Standards (Taxonomic Database Working Group) records published between 1960 and 1992. The gray gradient of the scale bar indicates species richness. Black dots mark geographical units with no rotifer records; white circles mark geographical units with at least 100 species. (Modified from Fontaneto et al. 2012a.)

narrow distribution can be considered reliable (Segers & De Smet 2008). Hotspots of diversity and with high number of endemic species for Rotifera exist in Australia, China, North America, and tropical South America, whereas few endemics are present in Africa and in the Indian subcontinent (Segers & De Smet 2008).

Environmental variables, linked to niche conservatism and geological history, are known to shape biogeographical patterns in larger organisms (Cox & Moore 2010), but no studies have successfully attempted yet to disentangle these variables at the global scale for Rotifera (Fontaneto et al. 2012a). At smaller scale, distribution and richness of Rotifera are known to be correlated to environmental variables such as altitude (Obertegger et al. 2010), temperature (Bērziņš & Pejler 1989), salinity (Kaya et al. 2010b), and trophic state (Obertegger & Manca 2011).

Latitude is only a description of position, but it often correlates with ecological variables that are biologically relevant and shape the biogeographical patterns in species richness (Hawkins & Diniz-Filho 2004). As in other microscopic animals (Maraun et al. 2007, Artois et al. 2011), it seems that no latitudinal gradient in species richness is present in Rotifera (Fontaneto et al. 2012a). For Bdelloidea, polar areas such as Svalbard islands are at least as rich as temperate ones (Kaya et al. 2010a); meanwhile, for Monogononta, although a global analysis revealed no latitudinal gradients (Fontaneto et al. 2012a), detailed studies focusing on specific taxa described latitudinal gradients in species richness, for example, in Brachionidae (Pejler 1977), in Lecanidae (Segers 1996), and in *Trichocerca* (Segers 2003). Also, the species composition of communities in Monogononta is known to change with latitude (Green 1972).

Detailed lists of rotifer species exist for several parts of the world, and the geographical distribution of most species is rather well known (recent reviews in Segers 2007, 2008). Nevertheless, much work still needs to be performed, new species are often found even in well-studied areas, and the geographical ranges of most species are often widened.

Biogeographical studies using phylogenetic information (=phylogeography) have been performed only for few species, mostly of the *Brachionus plicatilis* species complex (e.g., Gómez et al. 1995, 2000, 2002a, 2002b, 2007, Mills et al. 2007, Campillo et al. 2011). Recently, additional model taxa have been used, including the *B. calyciflorus* species complex (e.g., Xiang et al. 2011a, b), but also *Testudinella clypeata* (Leasi et al. 2013) and several *Synchaeta* (Obertegger et al. 2012). The consensus of these analyses is that rotifers, as other microscopic organisms with high potential for passive dispersal, are indeed widely distributed, but they still experience the constraints of geography in their distribution (Fontaneto 2011). Thus, the occurrence of refugia can be analyzed as in larger organisms (Gómez & Lunt 2006), biogeographical patterns exist, with evidence of enclave distribution, founder events, and localized genetic differentiation (De Meester et al. 2002).

4.8 Paleontology

As for all the Platyzoa clade, the fossil record is almost non-existent. The few proper fossil records of rotifers have been found in amber and are limnoterrestial Bdelloidea (Poinar & Ricci 1992, Waggoner & Poinar 1993). More numerous are the records for subfossil rotifers from the Holocene in peat bogs and other kind of deposits, both of Bdelloidea (e.g., Warner & Chengalath 1988, 1991) and of Monogononta (e.g., Swadling et al. 2001, Turton & McAndrews 2006).

Resting eggs of rotifers are also known to occur as subfossil in different sediments (Van Geel 2001). Interestingly, some records of unidentified palynomorphs may actually be rotifer resting eggs (Van Geel 1998). Subfossil resting eggs may hatch after up to a century in the sediments (Piscia et al. 2012), as it happens for ephippia of cladoceran crustaceans (Caceres 1998). Thus, they do not represent true fossils, but a genetic legacy from the past that can still "invade" the present time.

4.9 Ecology

The rotifer species are conditioned by the classical abiotic and biotic variables, such as temperature, pH, ions, organic compounds, prey-predator relationships, competition, food supply, and parasites (see Wallace et al. 2006). Many species play an important role in the food webs because of their large population size and rapid turnover rate. Rotifers serve as food for, e.g., copepods, oligochaetes, raptorial cladocerans, chironomids, chaoborids, fish larvae, and planktivorous and benthivorous fish (e.g., Schmid-Araya & Schmid 1995, Monakov 2003).

Rotifers are ubiquitous components of the aquatic biocoenoses, both freshwater and saline. The great majority (~85%) of the species known to date, both bdelloids and monogononts, occur in freshwater environments; the others are inhabitants of athalassic, inland saline waters, and the true thalassic, brackish, and marine, environments (e.g., Fontaneto et al. 2006a, 2008). Most species are free-living, while others are sessile, epibiotic, ectoparasitic or endoparasitic; free-living or sessile taxa may be solitary or colonial. Bdelloids are predominantly semi-aquatic, whereas monogononts are mostly found in truly aquatic environments. Species diversity of monogononts is smallest in the polar regions, whereas bdelloids are rarer in the subtropics and tropics (Donner 1956).

4.9.1 Feeding ecology

The food and way of feeding depend on the structure and function of the corona and trophi. As a group, bdelloid rotifers are primary consumers and microphagous, feeding on bacteria, yeasts, and small algae, by filtering, scraping, or browsing (Melone et al. 1998a). Many species are exclusively feeding on bacteria and yeasts (*Habrotrocha thienemanni*) and some feed on chlorophytes in particular (*Philodinavus paradoxus, Habrotrocha tridens); Macrotrachela fungicola* feeds on a mushroom, and a single species, *Abrochtha carnivora*, preys on other bdelloids and monogononts (Ricci et al. 2001).

The feeding habits of monogononts are enormously varied, as reflected by the variation in trophi and corona types. Both primary and secondary consumers, microphagous and macrophagous taxa, as well as omnivorous, herbivorous, and carnivorous species occur (see, e.g., Pourriot 1977, Monakov 2003). Monogonont rotifers with a well developed corona may be microphagous or macrophagous, consuming detritus, tripton, bacteria, yeasts, protozoans, and algae. They are usually planktonic, collecting food by currents generated through the coronal cilia, and grinded by the unci of the malleate or malleoramate trophi (e.g., Brachionidae, Conochilidae, Trochosphaeridae). Free-living herbivorous benthic-periphytic and semi-planktonic taxa mostly have a less developed corona and virgate trophi specialized for piercing and pumping. For example, *Ascomorpha ovalis* (Gastropodidae) feeds preferentially on dinoflagellates (*Ceramium*, *Peridinium*), by piercing the cells and sucking their content; it has special coronal palps to grasp the cell and to hold it in place when feeding (Stelzer 1998). Another species of the latter family, *Gastropus hyptopus*, grasps a cell of a *Synura* colony (xanthophyte) and swallows it whole. Members of the Notommatidae and Trichocercidae (e.g., *Notommata copeus*, *Trichocerca rattus*) move along the algal filaments of *Spirogyra* and *Mougeotia*, and feed by piercing the cells and sucking their content. Creeping species with in general ventrally situated mouth opening browse the epiphytic algae and bacteria (Proalidae, Lecanidae, Lepadellidae). In the sessile *Collotheca* spp. and *Stephanoceros fimbriatus*, the anterior part is transformed into a broad funnel or vestibulum, with arms that draw together to trap the prey (flagellates, ciliates) when it enters the infundibulum. Food selectivity is evident for several other taxa, e.g., *Lindia* spp., and *Brachionus diversicornis* preferentially feeds on cyanobacteria; *Notommata collaris* typically feeds on a single desmid genus (*Closterium*), whereas *N. pachyura* shows a preference for different genera (*Closterium, Penium, Staurastrum*), and *Trichocerca elongata* is feeding on Oedogoniales.

Carnivory is quite common in Asplanchnidae, Dicranophoridae, Notommatidae, Synchaetidae, and Atrochidae. Among the prey eaten are protozoans, rotifers, nematodes, small crustaceans, and their juveniles; cannibalism has been reported in *Asplanchna* (Gilbert 1976a, b, 1980). The prey may be grasped by the forcipate trophi (e.g., *Dicranophorus*) or swallowed after contact with the corona and help of the incudate trophi (*Asplanchna*) or its contents are sucked out using virgate trophi (*Synchaeta*). The sessile *Cupelopagis vorax* (Atrochidae) has a very large anterior funnel devoid of coronal cilia that envelops the prey, which is lacerated by the uncinate trophi. Selectivity for prey is also evident for the raptorial species. For example, *Notommata glyphura, N. aurita*, and *Ploesoma hudsoni* feed on other rotifers; *N. pseudocerberus* feeds exclusively on the ciliates *Stentor niger* and *S. polymorphus*, but avoids *S. coerulaeus; Trichocerca capucina* sucks out eggs of other planktonic rotifers; *Dicranophorus isothes* penetrates between the valves of cladocerans and eats the cladoceran from within. Although prey selectivity is evident in many species, populations of the same species may differ in their preferences (Gilbert 1980). *Proales fallaciosa* and *Dicranophorus isothes* are known as scavengers, feeding on dead oligochaetes, microcrustaceans, and macroinvertebrates. For the hosts and feeding habits of parasitic rotifer species, see Section 4.9.2.3, Symbiotic Associations.

4.9.2 Habitat

4.9.2.1 Freshwater and limnoterrestrial habitats

Lentic free water. The euplanktonic rotifers of lentic waters are independent of substrate, and able to dwell at the surface or at determined depths. The rotifer fauna of the pelagial of lakes and large water bodies almost exclusively consists of euplanktonic species, while plankton of ponds and shallow water bodies is composed of euplanktonic and semi-planktonic species characteristic of the littoral and submerged vegetation. Many benthic species may be found swimming around in shallow waters as well. The rotifer species richness of the pelagic zone is lower than for the littoral region and psammon habitat. For instance, Muirhead et al. (2006) estimated species richness for 3 temperate freshwater lakes in Poland, and found total species numbers ranging from 167 to 205 species, with 44–65 for the pelagic, 137–162 for the littoral, and 100–135 for the psammon habitat. Rotifer densities may vary from a few individuals per liter in oligotrophic waters to >10,000 ind L^{-1} in nutrient-enriched waters.

Among the freshwater bdelloids, only a single species, *Rotaria neptunia*, is truly planktonic in eutrophied waters. Several others are often semi-planktonic in the littoral region or in shallow waters (e.g., *Rotaria macrura, Philodina citrina, P. megalotrocha*). All other euplanktonic rotifers belong to the monogononts, in particular to the Asplanchnidae, Brachionidae, Conochilidae, Synchaetidae, and Trochosphaeridae.

The rotifer communities are influenced by physical, chemical, and biological factors, whose relative role in structuring assemblages and controlling seasonal dynamics may vary within or between aquatic systems (Hunter & Price 1992). To mention are temperature, oxygen concentration, light intensity, and pH (e.g., Hofmann 1977), food quality and quantity (Dumont 1977), exploitative and interference competition (May & Jones 1989, MacIsaac & Gilbert 1991, Fussmann 1996), predation (Williamson 1983, Neill 1984), and parasitism (Ruttner-Kolisko 1977).

The rotifer fauna can be divided into perennial, and seasonal taxa, with or without distinct maxima, and species with erratic occurrence. The seasonal succession and maxima of the different species is in general fairly constant, and characteristic of the water body, although variations related to the climatological conditions may occur. Seasonal succession in temperate regions is primarily driven by temperature, and related food supply (e.g., seasonal development of phytoplankton); the major determinant involved in the tropics is apparently the alternation of wet and dry seasons (e.g., Apstein 1904, Green 1960).

Although most rotifers have a wide tolerance range for temperature (Bērziņš & Pejler 1989), many species show a distinct seasonality in occurrence (May 1983). Three main categories in response to water temperature can be distinguished: eurythermous species able to maintain a dense population over a wide range of temperatures (e.g., *Keratella cochlearis, K. quadrata*), and stenothermous species unable to maintain populations outside a well-defined range, i.e., warm stenothermous species preferring warm water (e.g., *Anuraeopsis fissa, Pompholyx sulcata, Trichocerca pusilla*), and cold stenothermous taxa exclusively found in winter and in cold hypolimnion (e.g., *Kellicottia* spp., *Keratella hiemalis, Notholca* spp.). Some species are eurytherm (*Synchaeta kitina*), but cold or warm adapted, showing high population development at low or high temperatures, respectively (May 1983).

Light, food, temperature, oxygen, and predation are among the influences responsible, directly or indirectly, for the vertical distribution of planktonic rotifers. In stratified lakes, the vertical distribution of rotifers is strongly related to the season, and the thermal and oxygen gradients, with some species also showing diurnal vertical migrations (e.g., Larsson 1971, Ruttner-Kolisko 1980b, Armengol-Díaz et al. 1993, Miracle & Armengol-Díaz 1995). Rotifer populations concentrate at the depths with pronounced gradients. For example, in Lake La Cruz, Armengol-Díaz et al. (1993) found that when stratification develops from winter to summer, some rotifers (*Anuraeopsis fissa, Keratella quadrata, Polyarthra dolichoptera*) show a downward migration following the thermocline to produce extremely dense populations near the oxic-anoxic boundary, whereas others (*Anuraeopsis miraclei, Filinia hofmanni*) migrated upward following the oxycline. The vertical segregation of *Cephalodella acidophila* and *Elosa woralii*, dominant in the hypolimnion and the epilimnion of acid mining lakes, respectively, is attributed to specific differences in efficiency for using the autotrophic or mixotrophic form of *Chlamydomonas acidophila* as food. *Elosa* shows a higher efficiency in using the autotrophic form, whereas *Cephalodella* feeds on the mixotrophic form of the flagellate occurring in the deeper water under low light. The mixotrophic form proved a poor food source for *Elosa* (Weithoff & Wacker 2007, Hartwich et al. 2010).

Active diurnal vertical migrations of rotifers have been described for several species (see, e.g., Miracle 1977, Magnien & Gilbert 1983). Migration tends to be different for different species and time of the year, and the same species may show upward nocturnal migration at one season, and the reverse at another, or no migration at all (e.g., George & Fernando 1970, Miracle 1977). The amplitude of diurnal migration ranges from 0.2 to 8 m. Variables triggering migration are temperature, oxygen concentration, competition for food resources, avoidance of predation, mechanical interference competition, etc. For example, George & Fernando (1970) found that light was controlling the migration and vertical distribution of *Filinia terminalis, Keratella quadrata*, and *Polyarthra vulgaris*. Food resource, both its quality and quantity, apparently determined the diurnal migrations to the surface at night of *Synchaeta pectinata* (8 m) and *Trichocerca simoneae* (6 m) in a Polish dystrophic lake (Karabin & Ejsmont-Karabin 2005). In a study on rotifer water layer preferences (0–2 m, and 5–35 m) in an oligotrophic mountain lake at midday and midnight during summer, Obertegger et al. (2008) found the vertical distribution related to temperature, food availability, presence of predators, and exposure to UV radiation. Some species (*Keratella quadrata, Synchaeta pectinata*) showed a population maximum in the deeper layer during midday, and in the upper layer during midnight, whereas others always remained in the lower layer (*Asplanchna priodonta, Filinia terminalis, Synchaeta kitina*) or upper layer (*Polyarthra dolichoptera, S. grandis*). Migrating species apparently favored the higher temperatures in the upper layer, while non-migrating ones seemed restricted by, e.g., food supply. Positioning in the deeper layer during midday seemed a strategy for UV avoidance; moreover, the possession of photoprotective compounds probably played a role in UV tolerance as well. In a shallow (1.5 m) pond at Vermont, USA, Gilbert & Hampton (2001) found a possible predator avoidance-response cascade induced by notonectids. A reverse diurnal migration was noted for a single rotifer species, *Polyarthra remata*, but not for 6 other co-occurring rotifers, and the copepod *Tropocyclops extensus*, which is an important predator of *Polyarthra*. During the day when *Tropocyclops* is most abundant near the bottom, *Polyarthra* is most abundant near the surface. The diurnal migration of *Tropocyclops* itself to the deeper layers during the day was supposed to be an avoidance response to the notonectid *Bueno*, preying on the copepod during the day.

Examining diurnal cycles of reproduction and vertical migration of *Keratella crassa*, Magnien & Gilbert (1983) found a differential migration of ovigerous and non-ovigerous females, the ovigerous ones reaching their lowest and highest positions in the water column about 4 and 6 h later than non-ovigerous females.

Lotic free water. Swift flowing mountain waters cannot maintain downstream-directed rotifer plankton populations: species found in such habitat originate from vegetation, benthos, and hyporheos. In rivers and streams, however, rotifers usually form the dominant component of the potamoplankton (e.g., Shiel et al. 1982, Walz 1995, Zimmermann-Timm et al. 2007, Bertani et al. 2011). For example, the number of species amounts to 61 for the Middle Loire, France (Lair 2005), to 27, 53, and 74, respectively, for 3 Masurian streams (Ejsmont-Karabin & Kruk 1998), and up to 51 taxa for the freshwater reach of the river Scheldt, Belgium (Azémar et al. 2010). Planktonic loricate species usually predominate, followed by epibenthic and littoral species, and last by illoricate rotifers, which are the least diverse and abundant (Lair 2005, Azémar et al. 2010). However, land-use activity can influence this sequence, with the littoral and benthic species becoming dominant in streams draining agriculturally developed catchments (Ejsmont-Karabin & Kruk 1998). The loricate planktonic species appear better adapted to the current than the soft-bodied ones. Densities can be >10,000 ind L^{-1} (e.g., Zimmermann-Timm et al. 2007). Brachionidae belonging to the genera *Keratella* and *Brachionus* usually dominate numerically. This can be explained by their ability of rapid reproduction and the capacity of several species to continue growing at currents of 0.2 m sec^{-1} (Lair 2005). The main factors controlling rotifer abundance are temperature and water transport time.

Macrophytes. Aquatic macrophytes create an enormous increase in habitat complexity, food availability, and shelter for the fauna. As such, rotifers are known to show a greater diversity and mostly higher densities in stands of aquatic vegetation than in the adjacent pelagic zone (e.g., Pennak 1966, Duggan 2001, Duggan et al.

2001, Kuczyńska-Kippen et al. 2003, Kuczyńska-Kippen & Cerbin 2003, Kuczyńska-Kippen 2005). The rotifer assemblages are dominated by Lecanidae, Lepadellidae, Notomatidae, and Trichocercidae. The periphytic community comprises (1) plant browsers rarely leaving the substrate (e.g., *Colurella colurus*), (2) browsing species that leave the substrate frequently, and swim around in the spaces between the vegetation (e.g., *Lecane lunaris*), (3) sessile species, (4) planktonic species that browse occasionally (e.g., *Brachionus calyciflorus*), and (5) chiefly planktonic taxa (e.g., *Filinia, Hexarthra, Kellicottia*). Several species, especially sessiles, favor particular or few plant species and/or specific zones on the plants (e.g., Edmondson 1944, Wallace 1977a, b, Wallace & Edmondson 1986). For example, *Stephanoceros fimbriatus* is predominantly found on *Utricularia, Cupelopagis vorax* favors submersed plants with broad flat or very gently convex leaves (*Potamogeton, Ranunculus*), and *Collotheca gracilipes* selects leaflets of *Elodea canadensis*.

Species richness and abundance of periphytic rotifers are generally related to macrophyte architecture, and greater among plants with a greater structural complexity providing a greater variety of habitats, and a larger quantity or variety of food (e.g., Duggan et al. 2001, Kuczyńska-Kippen & Nagengast 2006, Lucena-Moya & Duggan 2011). An increasing structural complexity apparently does not affect species richness and abundance of the planktonic taxa. A greater architectural complexity likewise stands for more opportunities for refuge from predators. Kuczyńska-Kippen (2007) found several planktonic rotifers to seek anti-predator refuge in the macrophyte stands during the daytime. Walsh (1995) assessed habitat-specific predation susceptibilities for *Euchlanis dilatata* in the presence of *Myriophyllum exalbescens, Elodea canadensis*, and *Ceratophyllum demersum* and 2 predators (damselfly nymphs and *Hydra*). Rotifer survival was greatest on *Myriophyllum* in the presence of both predators, and conversely, the presence of the *Elodea* and *Ceratophyllum* increased rotifer susceptibility to predation by the damselfly nymphs, by increasing their foraging ability. Decreasing the macrophyte complexity by, for example, removing leaves, resulted in a lower survival of *Euchlanis*.

In her study on rotifer body size and macrophyte architecture, Kuczyńska-Kippen (2005) found that the size distribution of the rotifer assemblages was directly related to the morphological and spatial structural complexity of the substrates. Densities of rotifers were also higher in the more heterogeneous habitats, probably by an increase of the potential refugia.

Benthos. Rotifers living on and in the sediment of bottoms of both lentic and lotic habitats have hardly been studied, because of difficulties with isolation of the specimens from the substrate (e.g., Carlin 1939, Pejler 1962, Donner 1970, Hoebel 1978, Anderson & De Henau 1980, Nalepa & Quigley 1983, Ricci & Balsamo 2000). The rotifer fauna is apparently less diverse and dominated by Dicranophoridae and Notommatidae (*Cephalodella* spp.), with some species, e.g., *Atrochus tentaculatus, Mytilina crassipes, Paradicranophorus hudsoni* characteristic of the habitat. Most species dwell at the sediment surface or mainly in the upper 1 cm of substrate. Densities are variable and low in oxygen poor environments; under favorable conditions a high density of 77,300 ind m^{-2} was found by Nalepa & Quigley (1983) in nearshore Lake Michigan.

Arenal. The interstitial of sandy sediments on the shores and the bottom of lentic and lotic waters is inhabited by a psammon community, of which rotifers may form an important component. For example, Wiszniewski (1934a) recorded 82 species in Lake Wigry (Poland), Myers (1936) found 145 species in Lenape and Union Lakes (Virginia, USA), Turner & Palmer (1996) found 77 taxa in Goose Creek (USA), and Muirhead et al. (2006) recorded 119 species in Lake Mikolajskie (Poland). The rotifers can be divided into psammobiotic or almost exclusively found in sandy sediment (e.g., *Lecane psammophila, Myersinella* spp., *Trichocerca taurocephala*), psammophilic or living in sand preferentially, but also in other habitats (e.g., *Lecane closterocerca, L. lunaris, Colurella colurus*), and psammoxenic or accidental components of sand (e.g., Wiszniewski 1937, 1947). Three zones can be distinguished in the psammolittoral region with reference to their relative degree of saturation with water, and each inhabited by its own community of organisms (e.g., Wiszniewski 1934b, 1947). The hydropsammon is found in the hydroarenal or permanently submerged sand, the hygropsammon occurs in the hygroarenal or sand above and adjacent to the water level and saturated by wave action and capillarity and the eupsammon living in the moist, partially saturated euarenal situated above the hygroarenal. The hydropsammon experiences less stress in comparison to the other zones and usually shows a lower species richness and lower density of rotifers (Wiszniewski 1947, Pennak 1940,, Bielañska-Granjer 2004, Kalinowska et al. 2012), whereas the hygropsammon in general yields the highest number and density of rotifers (e.g., Wiszniewski 1947, Evans 1982, Bielañska-Granjer 2001, Bielañska-Granjer & Molanda 2008). Total rotifer density and density of the different species in general is very variable, differing over time, among sites and between depths in the sand (e.g., Evans 1982, Bielañska-Granjer 2001, Ejsmont-Karabin 2005); reported total densities range from 0.0 to >1,200 ind cm^{-3} or amount to >1,500 ind 100 cm^{-2}. The structure and density of the psammon rotifer assemblages apparently depend primarily on sand grain size (Ejsmont-Karabin 2004, Bielańska-Granjer & Molanda 2008). In general, psammobiotic monogononts prefer the sand grain size fraction 0.5–1.0 mm, a fraction avoided by psammophiles and psammoxenes; bdelloids only prefer the smallest (<0.125 mm) sand grain fraction (Ejsmont-Karabin 2004). The width of the inhabitable zone depends on the slope of the littoral area, with rotifers reported up to 20 m above the water edge (Whitman et al. 1994). They are mostly concentrated in the upper 1 or 2–3 cm of sand but may occur up to 8 cm deep (e.g., Pennak 1940, 1951, Ruttner-Kolisko 1954, Evans 1982). Among the variables determining the vertical and horizontal distribution are wave action, temperature, oxygen content, abiotic and biotic (phytopsammon) nutrients, with each rotifer species being affected differently (Evans 1982, Ejsmont-Karabin 2005, 2006, Bielańska-Granjer & Molanda 2008).

Hyporheal. The porous hyporheic zone of the stream bed of running waters, formed by the interstices of a mixture of coarse sand or gravel and bordered by the benthos and surface water of the stream above and the true groundwater below, harbors a meiofaunal community, the hyporheos, of which rotifers may be an abundant and species-rich component (e.g., Palmer 1990a, b, Schmid-Araya 1998b). Palmer (1990a, b) found rotifers to comprise 35%–85% of the hyporheos, with densities up to 4.10^6 ind m^{-2} in a fourth-order stream in Virginia (USA), and Schmid-Araya (1998a) reports 11.5×10^6 ind m^{-2} in a mountain gravel stream in Austria. Rotifers were recorded as deep as 50–60 cm. Their vertical distribution is mainly related to sediment depth, mean water temperature, mean current velocity, oxygen, detritus content, and surface discharge (e.g., Palmer 1990a, Schmid-Araya 1998a, b).

Species richness is moderate: Ferrarese & Sambugar (1976) found 48 taxa (6 bdelloids, 39 monogononts) in the interstitial (0–40 cm) of the river Adige (Italy), and Schmid-Araya (1993, 1998a) recorded 53 taxa (16 bdelloids, 37 monogononts) in the hyporheal (0–40 cm) of a mountain gravel stream, the Oberer Seebach (Austria). The rotifer assemblages are generally dominated by a large number of rare species (Schmid-Araya 1998a). Bdelloids showed the highest densities between 0 and 30 cm, whereas monogononts were more abundant at greater depths.

Species composition and/or dominant species differ between the hyporheic zone and the surface benthos of the stream bed (Braioni & Gottardi 1979, Schmid-Araya 1998a). For example, of the 69 rotifers found in the surface bed sediment and hyporheal of Oberer Seebach, 10%–12% are exclusive inhabitants of the hyporheic interstitial up to a depth of 40 cm (Schmid-Araya 1993, 1998a).

Rotifers in gravel streams are important in the food webs as food items of other predatory meiofaunal taxa (microturbellaria, nematodes, oligochaetes, rotifers), and larval tanypodine chironomids (e.g., Schmid-Araya & Schmid 1995, Schmid 1994).

Soil. Notwithstanding that rotifers occur in almost every type of soil, this habitat has been hardly studied in the temperate region (e.g., Donner 1949, 1951, 1952, Schulte 1954, Pourriot 1979, Anderson et al. 1984, Błędzki & Ellison 2002, Devetter 2009). Of the more than 150 species of soil rotifer recorded, 95% are bdelloids. Most of them usually belong to the genus *Habrotrocha*, and to a lesser extent *Macrotrachela*, with the latter commonly developing the highest densities. *Bryceella stylata* and *Encentrum mustela* are among the most frequently reported monogonont species. Soil and litter rotifer communities represent an important part of soil fauna in most types of soil habitat. Rotifer densities are usually highest in the upper 3–6 cm (Pourriot 1979, Devetter 2009). As a group, bdelloids can occur at densities ranging from about 67,000 up to more than 2.1 million ind m^{-2}. Densities of monogononts are usually much lower, with up to 34,000 ind m^{-2} reported in a climax beech forest (Devetter 2009). The variables determining presence and abundance are moisture content (whether constant or not), porosity of soil, oxygen and carbon dioxide concentrations, pH, food resources, and the content and nature of the humus fraction, such as deciduous leafs, coniferous needles, fresh vs. decomposed litter, etc. (e.g., Schulte 1954, Pourriot 1979, Devetter 2007). The high rotifer densities suggest that they may play a significant role in nutrient cycling in the soil community (Anderson et al. 1984).

Wulfert (1944) described a new species, *Cephalodella clara*, from compost and bovine manure and moreover found *Adineta, Habrotrocha, Macrotrachela*, and *Encentrum* in the latter substrate as well as. A number of ectoparasites and endoparasites of the genera *Albertia, Balatro*, and *Claria* infest oligochaetes dwelling in soil and terrestrial moss (see Section 4.9.2.3, Symbiotic Associations).

Moss and lichen. Mosses, liverworts, and lichens are the habitat of a diverse rotifer fauna, mostly dominated by bdelloid species. Humidity was recognized as the primary regulating factor of rotifer species composition (e.g., Burger 1948, Ricci 1987). The presence of permanent water favors the colonization by monogononts. Depending upon whether there is constant or periodic water present, the moss will be inhabited by bdelloid species more or less tolerant to desiccation, allowing for a distinction among hydrophile, xerophile, or indifferent species (Pourriot

1979). Species living in habitats with intermittent wetting are able to enter anhydrobiosis and often secrete sheaths that protect them against too rapid drying (Donner 1950), whereas species living in permanent aquatic environments apparently are less capable of forming viable anhydrobiotic stages than those from terrestrial habitats (Ricci 1998a, Ricci & Caprioli 2005).

Data on the relationship between rotifer composition and moss or lichen are conflicting. There is no clear evidence of a species-specific relationship (e.g., Burger 1948, Francez 1980, Fontaneto & Ricci 2006) between bdelloid species and a peculiar moss species, and Kaya et al. (2010a) neither found a relationship between bdelloid species composition and life form of moss, viz. carpet, mat, or turf. On the contrary, in monogonont assemblages, Hájková et al. (2011) found that most of the variation was explained by moss species composition and recognize 4 functional moss groups, i.e., crawling dense, crawling loose, erect (mostly acrocarpous) moss, and tufts of *Sphagnum*. Investigating bdelloid rotifers in aerophytic moss on roofs, aged 3–92 years, Hirschfelder et al. (1993) suggested that age and structure of the moss may determine species composition. Comparing the upright moss *Ceratodon purpureus* with the mat-forming *Brachythecium glareosum*, with a higher moisture capacity and higher structural complexity, they found that bdelloid species richness increased with increasing age of roofs for both moss species, with *Brachythecium* containing significantly more species and individuals than *Ceratodon*. In their study on bdelloids inhabiting foliose lichen species, Fontaneto et al. (2011) found a significant, although weak association between bdelloids and lichen species, a wide overlap in bdelloid species composition between the lichens, and a wide ecological tolerance for most species.

Qualitative and quantitative differences in the distribution of rotifers along the moss shoot have been described. For example, on *Sphagnum erythrocalyx*, the sessile *Ptygura velata* settles only, but in large numbers, near the leaf tips at the concave sides of the leaves, so that they are almost entirely enclosed, their anterior part projecting above the edges (Edmondson 1944). Studying rotifers in mosses from Tatra streams, Madaliński (1961) recorded higher numbers of species and individuals, both bdelloids and monogononts, in the lower parts of the moss, whereas in the upper parts, only bdelloids were present, suggesting that water current may limit occurrence of some species. In a detailed study on the zonal distribution of rotifers on *Calliergon*, Priddle & Dartnall (1978) observed 6 species more or less permanently attached to the moss and distributed in relation to epiphyte growth. *Collotheca gracilipes* and *C. ornata cornuta* were found on the underside of the leaf with lowest epiphyte cover, while *Ptygura melicerta*, *P. crystallina*, and unidentified bdelloids preferred the leaf axil and the part of the middle stem zone with greatest epiphyte growth. Some bdelloids occupy the water-filled lobules of liverworts (see Phytotelmata).

The rotifer fauna of aerophytic mosses and lichens is very similar to the soil biocoenosis and comprises more than 200 species. The bdelloids account for more than 95% of the taxa and may build up large populations of 60–1,108 ind g^{-1} of different bryophyte species (Fantham & Porter 1945). Among the bdelloids, the genera *Habrotrocha* and *Macrotrachela* are the most diverse and abundant. The few monogononts recorded mostly belong to the genera *Bryceella, Colurella, Encentrum*, and *Lecane*. Comparing bdelloid assemblages from dry mosses and submerged mosses from lotic and lentic waters, Fontaneto et al. (2006b) found only few species in each single assemblage and recorded a strong habitat selection, with higher number of species in dry than in aquatic mosses. A comparison of bdelloid species assemblages in aerophytic mosses and lichens from the Alps revealed that both habitats significantly differed in both species number and composition; an altitudinal gradient in species richness was limited to a decrease in α diversity, but not in γ diversity (Fontaneto & Ricci 2006).

The rotifer fauna of submerged mosses is characterized by a moderate diversity with monogononts usually representing more than 65% of the taxa (e.g., Madaliński 1961, Donner 1970, 1972a). In mosses (exclusive *Sphagnum*), the bdelloid genera *Philodina, Rotaria, Macrotrachela*, and *Habrotrocha* are often the most species rich, whereas among the monogononts, the most diverse are *Colurella, Proales, Cephalodella*, and *Lecane*. The rotifers can form an important portion of the meiofauna of submerged mosses, e.g., in 2 rivers from the Czech Republic, Vlčková et al. (2002) found from 261,660 to 498,948 ind g^{-1} dry weight of *Fontinalis*, with monogononts and bdelloids contributing 11%–16% and 28%–76% respectively of the total number of all meiofaunal groups. In lotic environments, increasing flow velocity increases the relative bdelloid densities compared with monogononts (Linhart 2002, Linhart et al. 2002), apparently without changing the species composition of the rotifer fauna (Madaliński 1961).

The rotifer diversity of *Sphagnum* vegetation is dominated by monogononts of the genus *Lecane* and comprises several acidophilous and acidobiontic species (e.g., *Elosa woralii, Keratella serrulata, Lecane elasma, L. galeata, Trichotria caudata*) (e.g., Pawłowski 1938, de Graaf 1956, Francez 1981, Pejler & Bērziņš 1993, Błędzki & Ellison 2003, Bielańska-Granjer et al. 2011). Bdelloids are less species-rich but dominate quantitatively. Total rotifer densities reported for *Sphagnum* range from 30 to 1,160 ind g^{-1}, with bdelloids accounting for 56%–85% of the total density (Fantham & Porter 1945, Bielańska-Granjer et al. 2011). In a series of samples taken from completely submerged to nearly dry *Sphagnum*, rotifers show a succession in community composition, with the share of the bdelloids increasing with decreasing humidity and increasing acidity (de Graaf 1956). Characteristic bdelloid species for wet and moist *Sphagnum* are *Dissotrocha macrostyla, Habrotrocha constricta, H. roeperi, Macrotrachela quadricornifera, M. plicata*, and *Habrotrocha angusticollis*.

The Antarctic microfauna of terrestrial mosses, and mineral and ornithogenic soil typically consists of up to 3 groups of micrometazoa: nematodes, rotifers (bdelloids), and tardigrades (e.g., Petz 1997, Porazinska et al. 2002). Water and organic matter are the principal controlling factors for the presence and abundance of these groups. The highest rotifer abundances are usually reported in moss, e.g., Petz (1997) counted up to 5,260 ind g^{-1} dry moss samples from Wilkes Land, East Antarctica. Bdelloids also may be the most frequently occurring metazoan group in moss and fellfield soil of habitable patches of mountain penetrating the ice sheath (nunataks) (e.g., Sohlenius & Boström 2008). In polar desert ecosystems, bdelloid abundances declined from hundreds of thousands of individuals m^{-2} in lake sediment, to 100 ind m^{-2} in soils 10 m from shore, without change in taxa occurrence, suggesting that the extreme low diversity of the ecosystem limits competition and thus promotes broad ecological niches, or alternatively, a selection for species with broad ecological niches (Ayres et al. 2007).

In lakes of sub-Antarctic South Georgia, Hansson et al. (1996) found that rotifers were only occasionally present in the open water but in general were restricted to the vegetation (mainly mosses) in shallow areas and to the sediment surface. The dominant taxa were *Cephalodella gibba, Lecane closterocerca, Lepadella patella, Resticula* sp., and unidentified bdelloids. In Antarctic and sub-Antarctic areas, the bright red endemic *Philodina gregaria* is famous for its development into enormous densities, producing red patches on the bottom of pools often extending over many square meters, for example, Dartnall (1992) reports densities exceeding 20 million ind m^{-2}.

Ice habitats (see also Section 4.9.2.2 Saline Environments: Sea Ice). In the cyanobacteria-dominated microbial mat communities, growing in melt pools and ponds on the surface of ice shelves of both the High Arctic (Vincent et al. 2000) and the Antarctic (e.g., Suren 1990) rotifers, especially bdelloids may be the most abundant invertebrates. In benthic algal mats in melt ponds of the Ross Shelf, Antarctica, Suren (1990) found 7 species belonging to *Adineta, Habrotrocha, Philodina*, and a single monogonont, *Epiphanes senta*, and reported average densities of $4.26.10^5$ ind m^{-2}. Cryoconite holes, i.e., water-filled holes on glaciers and ice sheets, containing solid mineral, organic matter, and microbiota, and occurring in both polar regions, as well as in some alpine environments at lower latitudes also may serve as a habitat for rotifers. De Smet & Van Rompu (1994) report *Macrotrachela insolita, Philodina acuticornis odiosa, Encentrum permolle, E. mucronatum, Keratella cochlearis, K. quadrata*, and *Lecane closterocerca* from cryoconite holes on a Spitsbergen glacier (Arctic). Porazinska et al. (2004) found *Philodina gregaria* and *Cephalodella catellina* in southern Victoria Land (Antarctic), and Christner et al. (2003) identified *Philodina acuticornis* by rDNA amplification from Canada Glacier, McMurdo. The latter author showed that cryoconite preparations of bacteria and eukarya had sequences similar to rDNA molecules of species present in adjacent lake ice and microbial mat environments, suggesting that the cryoconite hole community was most likely seeded from these local environments.

Phytotelmata. Rotifers occur commonly in all main types of phytotelmata or plant container habitats, such as water-filled tree holes, pitcher plants, bromeliad tanks, bamboo internodes, and axils of leaves, bracts, or petals (Kitching 2000). They are frequently encountered in tree holes and may develop very dense monospecific populations or discrete communities that are mostly subsets of the larger soil and leaf litter communities. Species recorded from European tree holes include the bdelloids *Habrotrocha thienemanni, H. tripus, Macrotrachela quadricornifera, M. ehrenbergi, Philodina* sp., and the monogononts *Asplanchna* sp., *Brachionus* sp., *Colurella hindenburgi, C. uncinata, Encentrum* sp., *Lecane arcuata, Lecane* sp., *Lepadella patella, Squatinella stylata*, and *Trichocerca* sp. (e.g., Thienemann 1934, Röhnert 1950, Devetter 2004a). *Habrotrocha thienemanni* is a typical inhabitant occurring in almost every tree hole, and often developing into high densities up to tens of thousands per liter (Devetter 2004b). The other species must be considered ubiquitous accidental introductions.

Extensive work by Koste et al. (1991) on bromeliad tanks from Jamaica revealed a diverse fauna of 42 species (10 bdelloids, 32 monogononts) composed of *Habrotrocha* 3 spp., *Macrotrachela* 2 spp., *Philodina* 2 spp., *Rotaria* 3 spp., *Collotheca* 4 spp., *Colurella* 2 spp., *Lecane* 15 spp., *Lepadella* 5 spp., *Limnias* 1 sp., *Proales* 1 sp., *Ptygura* 1 sp., and *Trichocerca* 3 spp. The species composition suggests a biotic exchange with the surrounding freshwater systems.

In the water-filled leaf axils of plants with sheathing leaf bases, such as *Angelica, Dipsacus, Ravenala, Scirpus, Silphium*, etc. (e.g., Van Oye 1923, Varga 1928, Wallace et al. 2006), unnamed bdelloids, *Adineta vaga, Habrotrocha tridens, Mniobia symbiotica, Philodina roseola, Rotaria citrina, R. rotatoria*, and the monogononts *Encentrum mustela, Euchlanis dilatata*, and *Eosphora najas* have been recorded. Rotifers are also found in the water-filled pitcher leaves of the carnivorous *Nepenthes* spp. from Southeast Asia (Thienemann 1932), and *Sarracenia purpuraea* from northeast America (e.g., Bateman 1987, Petersen et al. 1997). Rotifers recorded associated with *Sarracenia* are the bdelloids *Adineta steineri, Habrotrocha rosa*, and *Macrotrachela quadricornifera quadricorniferoides*, and the monogononts *Cephalodella anebodica, Keratella mixta, Lecane lunaris, Notholca acuminata*, and *Polyarthra vulgaris*. About 70% of all pitchers are inhabited by *Habrotrocha rosea* (Petersen et al., 1997), a species also reported from moss, leaf litter, and soil; the other rotifer species are rare and probably occasional introductions. Błędzki and Ellison (1998) found that *H. rosea* is a reliable food source for the co-occurring larvae of the pitcher plant mosquito *Wyeomyia smithii*, and *Blaesoxipha fletcheri*, which consume *Habrotrocha* in direct proportion to the rotifer density. In the absence of these dipteran larvae, the density of *Habrotrocha* can reach about 900,000 ind L^{-1}. Colonization of new pitchers is probably by transport on migrating larvae and/or females of the pitcher plant mosquito (Bateman 1987). The species may also account directly for most of the plant's supply of N and P, and the association can thus been considered mutualistic. Błędzki & Ellison (2002) found that *H. rosa* alone accounted for 31% of the rotifer abundance in the bogs *Sarracenia* grows and estimated that it probably contributes more than 50% of the N and more than 75% of the P regenerated by rotifers in these bogs.

Additional types of phytotelmata include the hyaline *Sphagnum* cells inhabited by *Habrotrocha reclusa, H. roeperi*, and a small insufficiently described *Encentrum bryocola* (e.g., Donner 1965). Bdelloids also dwell in empty plant (*Typha*) cells (Donner 1965). The water-filled lobules or amphigastrae under the leaflets of liverworts (e.g., *Frullania, Lejeunia*) host the bdelloid *Mniobia symbiotica* (e.g., Zelinka 1886). Puterbaugh et al. (2004) studied the distribution of an unidentified bdelloid in the lobes of *Frullania eboracensis* and found at least 1 rotifer in 13%–71% of the lobes per moss plant, with up to 7 in an individual lobe. Rotifer distribution on a moss plant proved non-random, with higher occupation rates at the edges of the plant and the non-sex-expressing plants tending to have the greatest proportion of occupied lobules.

4.9.2.2 Saline environments

Some 450 rotifer taxa have been recorded from athalassic inland saline and thalassic, both strictly marine and brackish, environments (e.g., Fontaneto et al. 2006a, 2008). These rotifers comprise haloxenous elements, i.e., accidental introductions of freshwater species, euryhaline elements, and strictly haline species. Bdelloid and monogonont species are unevenly represented in the saline environments with an overall ratio of 1:83, compared with a ratio of 1:3 in freshwater habitats. This observation suggests that bdelloids may be "physiologically incompatible" with the saline environment. Generally speaking, rotifer species richness is decreasing with increasing salinity (e.g., Ruttner-Kolisko 1980a, Egborge 1994). The boundary at which the freshwater rotifer biocoenosis changes characteristically lies at 1.5‰ according to Ruttner-Kolisko (1971). In the lower salinity ranges, Kaya et al. (2010b) found drastic changes in rotifer species richness at the boundary between freshwater and subsaline waters (0.5‰) and between subsaline and hyposaline waters (3‰). Saline rotifers occupy a diverse range of habitats, behaviors, and trophic levels at all latitudes.

Athalassic environments. Some 172 taxa have been reported from athalassic waters, with to date only *Brachionus asplanchnoides, Cephalodella gisleni, C. mineri, Encentrum pachypus, H. jenkinae, H. polyodonta, Lecane abanica, L. inconspicua, Rhinoglena fertoensis*, and *Synchaeta cylindrica* apparently restricted to this environment (e.g., Fontaneto et al. 2006a). The other taxa are mostly euryhaline (104 taxa), whereas few are strictly haline and recorded also in thalassic waters (*Brachionus plicatilis, Colurella salina, Encentrum rousseleti, Hexarthra fennica, H. oxyuris, Lecane grandis, L. lamellata, Synchaeta elsteri*). The athalassic systems show a smaller number (~115 taxa) of haline rotifer taxa than the thalassic ones (~190 taxa), undoubtedly resulting from environmental stress, due to the often high salinities, the ionic composition, the high pH values, and the unstable character of these systems. A few species, *Cephalodella fluviatilis, Brachionus dimidiatus, B. plicatilis, Hexarthra jenkinae*, and *H. polyodonta*, dwell in the highly alkaline soda lakes characterized by temporal discontinuity. In the East African Lake Nakuru, a hypereutrophic soda lake (alkalinity 150–400 meq L^{-1}, pH ~10.5, conductivity $10–28 \times 10^3$ µS cm^{-1}, salinity ~11‰–32‰), Vareschi & Jacobs (1985) found that *B. dimidiatus* and *B. plicatilis* are the most productive primary consumers (1.7 kJ m^{-3} per day), contributing about 50% to the total consumption, and some 75% to the total secondary production of the lake.

The most ubiquitous and often most abundant rotifer in athalassic waters is *Brachionus plicatilis* reported from habitats with salinity ranging from 1‰ to 250‰ (Walker 1981, Hammer 1986). DNA taxonomy revealed that this morphospecies comprises more than 20 cryptic species (Gómez 2005, Suatoni et al. 2006, Gribble & Welch 2012). Salinity was shown to differentially affect life history traits and reproduction rates in the different species of the complex (Campillo et al., 2011) and was consequently considered one of the major determinants creating and maintaining local co-existence of multiple cryptic species. Because of being potentially adapted to a narrower ecological range (Gómez et al. 1997, Ortells et al. 2003, Campillo et al. 2011), the cryptic species succeed to co-exist by avoiding competition through temporal and spatial displacement, correlating with variation in salinity (Gómez et al. 1997, Ortells et al. 2003). The putative euryhaline status of several other species is probably often due to the former inability in recognizing cryptic species with narrow salinity ranges, but even in cases with hidden diversity, several of the cryptic species may still be truly euryhaline as it has been shown for *Testudinella clypeata* by Leasi et al. (2013).

Thalassic environments. To date, some 345 rotifer taxa have been recorded from thalassic (brackish and marine) environments, comprising 145 euryhaline taxa and 141 strictly thalassic ones, the remaining being haloxenous (e.g., Fontaneto et al. 2006a, 2008).

A few bdelloid species only have been reported from brackish and marine environments almost all over the world. Free-living species are usually found among vegetation, benthos, and dense growths of filamentous cyanobacteria. Their vertical distribution extends from the littoral until the bathyal zone (Higgins in Turner 1988). The symbiotic *Zelinkiella synaptae* (epibiont of sea cucumbers) and *Rotaria laticeps* are the only genuine marine species known to date; the latter has been reported in psammon up to a depth of 70 m in the Mediterranean. The symbiotic *Anomopus chasmagnathi* living on an estuarine brackish-water crab (*Chasmagnathus granulata*) is a strictly brackish element (Mañé-Garzón & Montero 1973). Among the euryhaline species, *Philodina roseola* and *Rotaria rotatoria* are commonly found in the intertidal and infralittoral vegetation and *Mniobia symbiotica* is the most abundant rotifer in the cyanobacteria and lichen (*Lichina pygmaea*) associations of the supralittoral fringe of rocky shores (Kronberg 1988).

Monogononts occur in all type of environments, including the open ocean, the coastal pelagial, seascapes such as estuaries, lagoons, bays, etc., intertidal and sublittoral biotopes, as well as the supralittoral, and other coastal environments occasionally exposed to seawater such as salt marshes. The benthic-periphytic Dicranophoridae is the most diverse family, represented by 11 genera and 81 species. Of all rotifer families, it also shows the highest number of species (53) confined to the truly marine habitat. In Synchaetidae, with only 3 genera, the planktonic genus *Synchaeta* is predominantly thalassic with 27 of the 47 species known worldwide found in brackish to marine waters. The other families characterized by considerable numbers of thalassic, mainly benthic-periphytic species are Brachionidae with *Notholca* (13 species thalassic out of 45), Lindiidae with *Lindia* (5 species thalassic of 17), and Proalidae with *Proales* (12 species thalassic of 47).

Pelagic zone. The rotifer plankton of the open oceans is characterized by its poor species richness and low population densities. Presently only 15 species have been reported, restricted to Brachionidae (*Notholca japonica*), Synchaetidae (*Synchaeta* spp.), and Trichocercidae (*Trichocerca marina, Trichocerca* sp.) (e.g., Smirnov 1933, Hada 1939, Bērziņš 1952, Dvoretsky & Dvortesky 2010).

Neritic zone. Information on rotifer diversity of continental shelf waters is restricted to few observations from the Atlantic, North Sea, and northeast Pacific. Of the 137 species reported, only 43% are thalassic, and the others are haloxenous (38%) or euryhaline (19%) elements. The neritic rotifer community is dominated by Synchaetidae, genus *Synchaeta*, both in species richness and abundances. Other frequently reported taxa belong to Trichocercidae (*Trichocerca marina*) and to a lesser extent Brachionidae (*Brachionus, Keratella*, and *Notholca*) (e.g., Lauterborn 1905, Remane 1929b, Bērziņš 1952, Fradkin 2001, Kogan 2005). Abundances are low with maximum densities of 64 ind L^{-1}, and <1 ind L^{-1} reported, respectively, for *Synchaeta* sp. and *Trichocerca* sp. in the northeast Pacific, off southern Oregon (Fradkin 2001). Compared with the pelagic zone, the neritic zone shows a greater rotifer species diversity, likely attributable to the proximity of land, and consequent nutrient input as well as the result of export of euryhaline and haloxenous species into coastal surface waters.

Benthos and psammon. Rotifers are found at the surface and in the interstices of the sediment, from the intertidal and sublittoral down to the abyssal (0–200 m). Their vertical distribution in the sediment is restricted to the oxygen-rich layer (Tzschaschel 1980, 1983). The typical fauna of both the intertidal and sublittoral is dominated by the Dicranophoridae (*Aspelta* spp., *Dicranophorus bulgaricus, Encentrum* spp., *Erignatha* spp., *Myersinella* spp., *Paradicranophorus* spp., *Wierzejskiella* spp., *Wigrella amphora*). Other characteristic taxa are *Colurella* and *Lepa-*

della pontica (Lepadellidae), *Lindia* (Lindiidae), *Notholca* (Brachionidae), *Proales* (Proalidae), *Testudinella bicorniculata, T. elongata*, and *T. obscura* (Testudinellidae), and *Trichocerca taurocephala* (Trichocercidae). A few species belonging to *Albertia* and *Proales*, infesting annelids and hermit crab, respectively, have been reported from benthic habitats (see Section 4.9.2.3, Symbiotic Associations).

Vegetation. Some 100 species have been reported from the algal vegetation of the sublittoral fringe, and the intertidal including its tide puddles and rock pools. The majority of the periphytic rotifers belong to the Dicranophoridae (*Aspelta* spp., *Encentrum* spp.), Lepadellidae (*Colurella* spp.), Brachionidae (*Notholca* spp.) and Proalidae (*Proales* spp.). Other typical periphytic taxa are *Testudinella clypeata* and *Pleurotrocha atlantica*. Species richness and abundances are usually low on the wave-exposed shores, with only few taxa managing to live in the dense growths of cyanobacteria and tuft-forming seaweeds. Sheltered tide pools and lagoons may show a greater rotifer diversity and development of periphytic species and enrichment by planktonic elements (e.g., *Keratella* spp., *Notholca* spp., *Synchaeta* spp.). The rotifer community in tide pools is apparently also negatively influenced by sediment loading and determined by the type of algal vegetation, with some rotifers showing a significant preference for brown or green algae (Saunders-Davies 1995, 1998). Proalidae with 2 *Proales* species have been found symbiotic on hydroids from the littoral (see Section 4.9.2.3, Symbiotic Associations).

Estuaries. Studies dealing with rotifers from estuaries are mostly restricted to plankton (e. g., Bakker & De Pauw 1975, Saunders & Lewis 1988, Dolan & Gallegos 1992, Holst et al. 1998, Park & Marshall 2000, Kogan 2005, Azémar et al. 2010). The typical estuarine systems, with a salinity gradient extending from the point of river entry with low salinity to the estuary outlet with salinity of the sea, are characterized by a dominance of freshwater species, with only few thalassic elements (*Synchaeta, Hexarthra, Trichocerca*) occurring in the brackish reach. For example, Holst et al. (1998) identified some 70 planktonic rotifer taxa in the Elbe estuary and found only *Synchaeta bicornis* as brackish element; Azémar et al. (2010) recorded 52 taxa in plankton of the Scheldt estuary with *S. bicornis* and *Keratella cruciformis* as the sole typical brackish water rotifers. Rotifer diversity, density, and biomass are usually negatively correlated with salinity.

Salt marsh. Pools and ditches of salt marsh, brackish retrodunal ponds, etc. revealed 195 species (e.g., De Ridder 1960, 1962), with a slight preponderance of the freshwater ones over the thalassic, mostly euryhaline taxa. Species records are highest for thalassic Dicranophoridae and Synchaetidae and freshwater and euryhaline Brachionidae, Lecanidae, Lepadellidae (*Colurella* spp., *Lepadella* spp.), and Notommatidae (*Cephalodella* spp.). Species composition and abundance is highly variable for the habitats studied, reflecting the great fluctuations of environmental conditions and possible freshwater inflow that characterize these habitats.

Sea ice. The brine channels permeating the sea ice of both polar and temperate regions make up a habitat of ice-associated or sympagic organisms consisting of viruses, prokaryotes, protists, algae, fungi, and metazoans. Environmental conditions are extreme, with strongly fluctuating temperatures always below the freezing point of pure water and salinities ranging from brackish to hypersaline. The sympagic rotifer community of the pack and land-fast ice of the Baltic Sea (e.g., Meiners et al. 2002, Werner & Auel 2004) is composed of at least 6 planktonic species (*Keratella cochlearis, K. cruciformis, K. quadrata, Synchaeta* cf. *baltica, S.* cf. *littoralis, Synchaeta* spp.) that dominate the metazoan biomass, indicating that this community is recruited from the plankton.

Rotifers are also commonly found in Arctic sea ice but are apparently lacking in the otherwise diverse and complex Antarctic sympagic community. Rotifers often dominate the sea ice meiofauna by abundance reaching up to 69,100 ind m^{-2} (e.g., Friedrich 1997, Schünemann & Werner 2005). To date, at least 9 species have been reported (Chengalath 1985, Friedrich & De Smet 2000): *Cephalodella* sp., *Encentrum graingeri, Proales reinhardti, Synchaeta bacillifera, S. glacialis, S. cecilia, S. hyperborea, Synchaeta* sp., and *S. tamara*. The genus *Synchaeta* is generally planktonic, whereas *Cephalodella, Encentrum*, and *Proales* are benthic-periphytic inhabitants of the intertidal and sublittoral. The Arctic pack ice is dominated by the planktonic *Synchaeta* spp., indicating that its rotifer fauna is mainly drawn from the underlying water column. The land-fast ice is dominated by the benthic-periphytic species, which may originate from the marine sediments or sublittoral vegetation.

Sea ice conceivably plays an important role in the colonization of the pelagial each year, when during ice melt in spring resting eggs are released in the underlying water mass.

4.9.2.3 Symbiotic associations

Several bdelloid and monogonont species live in close association with other organisms, such as cyanobacteria, protists, mosses, vascular plants, Hydrozoa, Rotifera, Ectoprocta, Mollusca, Annelida, Echinodermata, Arthropoda, and vertebrates (e.g., Budde 1924, May 1989). The nature of the symbiotic associations involved, whether commensalism, mutualism, or parasitism, is not always clear. Some of these rotifer-host associations appear relatively non-selective, whereas others have evolved a completely obligate species-specific or species-organismal group relationship.

Pleurata trypeta is apparently an obligate endoparasite in colonies of the cyanobacterium *Gomphosphaeria* (Nogrady et al. 1995). Species of *Ascomorphella, Cephalodella, Pleurata*, and *Proales* live endoparasitic in several species of the freshwater colonial green alga *Volvox* and the golden algae *Uroglena* and *Uroglenopsis*. They feed on the algal cells, which may lead to the destruction of the algal colony and collapse of the algal populations (Ganf et al. 1983, Van Donk & Voogd 1998). *Pourriotia* species (formerly *Proales werneckii*) live inside the siphonous filaments of various species of the yellow-green algae *Vaucheria* and in *Dichotomosiphon tuberosus* (e.g., Spooner 1994). Individual females of the species induce the formation of characteristic galls on the filaments where they remain, feeding on the cytoplasm and plastids and once adult start producing eggs (e.g., Wallace et al. 2001, De Smet 2009).

The bdelloid *Macrotrachela fungicola* is considered to be an ectoparasite of the mushroom *Dacrymyces deliquescens* (Garner 1937).

Dicranophorus difflugiarum lives parasitic within the shell of the testate amoeba *Difflugia acuminata* (De Smet & Pourriot 1997). *Asciaporrecta difflugicola* and *A. arcellicola* inhabit the shells of species belonging to the genus *Difflugia* and *Arcella*, respectively. It apparently are parasites, feeding on the protoplasm of their hosts (De Smet 2006).

Lecane clara and *L. triba* have occasionally been reported feeding on the upper layers of the freshwater sponge *Spongilla lacustris* (Bērziņš 1950). *Proales christinae* and *P. gonothyraeae* live within the hydrothecae of marine Hydrozoa, both as commensals and ectoparasites, respectively (De Smet 1994).

Symbiotic associations between rotifers are rare. Interspecific colony formation in colonial rotifers may be mutualistic, the individuals in a colony interacting in ways that could increase filtering efficiency (Wallace et al. 2006). The sessile monogonont *Acyclus inquietus* establishes itself within colonies of *Sinantherina socialis* and feeds on the newly hatched juveniles of its host. Parasitic behavior is also known for *Proales decipiens*, which enters the tube of *Stephanoceros fimbriatus* and feeds on the adult and its developing eggs (May 1989).

Oligochaetes have rotifer ectoparasites and endoparasites and serve as occasional basibiont for *Epiphanes daphnicola*. Nearly all *Albertia* and *Balatro* species are obligatory parasites, living on the epidermis or in the intestine of terrestrial and freshwater oligochaetes (Enchytraeidae, Naididae, Lumbricidae, Lumbriculidae); a single species, *A. crystallina*, is reported from a brackish water oligochaete (*Paranais litoralis*). They feed on the body fluids, and/or epidermal cells or intestinal mucosa (De Smet & Pourriot 1997). *Claria segmentata* lives in the gut of the earthworm *Pheretima modigliani* (Megascolecidae) (Kutikova et al. 1990). *Cephalodella parasitica* is an ectoparasite of freshwater *Stylaria lacustris* and *Vejdovkyella comata* (Koste 1972). *Drilophaga bucephalus* and *D. delagei* are ectoparasites of oligochaetes and leeches (Nogrady et al. 1995).

The marine bdelloid *Zelinkiella synaptae* lives on the body surface and tentacles of sea cucumbers (Synaptidae) and polychaetous annelids (Terebellidae) (e.g., de Beauchamp 1965). *Proales gigantea* is parasitic in eggs of several species of pulmonate freshwater snail. It feeds on the snail embryo and its surrounding fluid, invariably killing the embryo (e.g., De Smet 1996, Rao 1993). The species is also ovipositing in egg masses of chironomids and feeding on the eggs (Koreneva 1958). Molluscs and insects are often colonized by a very large number of bdelloids and a diverse community of monogononts not different from that of the habitat the host lives in (e.g., May 1989, Whiteley 1989, Bołtruszko 2010). These associations are probably purely commensal, the rotifer benefiting from the food carried toward it by the feeding currents of the host or by feeding on the host's excrement.

Only 1 rotifer, *Encentrum kozminskii*, is reported as a parasite of vertebrates, living on the skin and gills of carp (*Cyprinus carpio*), and feeding on the mucus and probably the epithelium (Wiszniewski 1948).

The only rotifer reported living on Ectoprocta in an apparently commensal association is the bdelloid *Philodina megalotrocha* (May 1989). The species attaches in clusters around the upper parts of the freshwater bryozoan *Lophopus crystallinus* and benefits from the feeding currents of the basibiont.

Most of the symbiotic rotifers, both bdelloids and monogononts, have been reported from crustaceans, especially freshwater ones (e.g., Budde 1924, Wiszniewski 1953, Hauer 1959, May 1989, Fontaneto et al. 2004). The only species reported from marine crustaceans are *Proales paguri*, which lives parasitic on the gills of the hermit crab *Eupagurus bernhardus* and feeds on the epithelium tissue, and *Anomopus chasmagnathi*, which is a symbiont in the gill chamber of an estuarine brackish-water crab (*Chasmagnathus granulata*).

Mniobia branchicola is the only rotifer that has been reported as living on terrestrial crustaceans (Němec 1895). The species is found on the gill plates of the isopod *Ligidium hypnorum* living in damp places. Among the freshwater crustaceans inhabited by rotifers are Branchiopoda, Copepoda, Isopoda, Amphipoda, and Decapoda. *Brachionus charini* is a commensal reported from the gills of the clam shrimp *Caenestheria* (Spinicaudauta) (Koste 1978), and *B. rubens* may be found on the gills of *Brachinella* (Anostraca) (Sharma 1979). *Brachionus rubens, B. sessilis*, and to a lesser extent *B. variabilis* and *Epiphanes daphnicola* are commonly reported as epibionts of several species of the different orders of Cladocera; the latter species is also the only epibiotic rotifer recorded from copepods (*Cyclops*). *Epiphanes daphnicola* is feeding on the sessile unicellular euglenaceans (e.g., *Colacium vesiculosum*) and ciliates living on the carapace of their host (Matveeva 1989). The freshwater louse *Asellus aquaticus* serves as substrate for at least 10 rotifer species, of which the bdelloids *Embata commensalis, E. laticeps, E. parasitica, Philodina convergens, Rotaria magnacalcarata, R. murrayi*, and *R. socialis*, and the monogononts *Encentrum hofsteni, E. kulmatyckii, Testudinella caeca*, and *T. elliptica* are among the most typical (e.g., Budde 1924, Wiszniewski 1953, May 1989, Cook et al. 1998, Fontaneto & Ambrosini 2010). Their association with *Asellus* varies from very strict (*Rotaria* spp.) to rather loose, with the species (e.g., *Encentrum* spp.) also occurring on other species of crustaceans, insects, or free-living (*Testudinella* spp.). Both species richness and individual numbers of rotifer proved highest on the ventral surface of the *Asellus* (Cook et al. 1998, Fontaneto & Ambrosini 2010). Detailed analysis of the spatial localization on the basibiont (Fontaneto & Ambrosini 2010) demonstrated that the different species consistently and significantly partition the space available, both by habitat selection and species interactions. The thoracal and abdominal appendages, and the gills of several Gammaridae may be inhabited by *Embata laticeps, E. parasitica, Philodina convergens, Cephalodella jakubskii, Dicranophorus siedleckii, Encentrum hofsteni, E. kulmatyckii*, and *Epiphanes daphnicola* (e.g., Budde 1924, May 1989, Boshko 1994). Data on rotiferan epibionts of freshwater shrimp are restricted to *Embata laticeps*, which was the only and rather common rotifer on *Caridina ensifera* (Fernandez-Leborans & von Rintelen 2007). The gill chamber of freshwater crayfish such as *Astacus* and *Austropotamobius* show a diverse rotifer fauna and may be inhabited by the bdelloid *Embata parasitica* and the monogononts *Cephalodella crassipes, Dicranophorus hauerianus, D. cambari, Lepadella astacicola, L. borealis, L. branchicola, L. lata*, and *L. parasitica* (e.g., Wiszniewski 1939, Hauer 1959). *Anomopus telphusiae* is to date restricted to the freshwater crabs *Potamon fluviatile, P. ibericum*, and *Socotrapotamon socotrensis* (Fontaneto et al. 2004, Van Damme & Segers 2004). The gill chamber of *Potamon fluviatile* also hosts *Lecane branchicola, Embata parasitica*, and *Macrotrachela cancrophila*.

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