The Gnathifera

Phyla Gnathostomulida, Rotifera (including Acanthocephala), and Micrognathozoa

T he clade Gnathifera includes three phyla: Gnathostomulida, Microgna-thozoa, and Rotifera, with the latter including the parasitic acantho-cephalan worms (formerly a separate phylum). The name is derived from the Greek *gnathos*, "jaw" and the Latin *fera*, "to bear," and refers to the presence of pharyngeal hard parts, i.e., jaws that are either present or secondarily lost in all gnathiferan taxa. Despite their small size, gnathiferans show a remarkable complexity of anatomy, especially in their jaw structures (e.g., the mastax and trophi) and the organization of their muscular and ner-vous systems.

Until the mid-1990s, the Gnathostomulida and Rotifera were pooled together with other microscopic taxa in questionable groups such as "Aschelminthes" or "Nemathelminthes"—catchall group-ings that were more or less solely character-ized by hosting microscopic taxa with uncer-tain phylogenetic positions. At that time, the Acanthocephala was treated as a distinct phy-lum, but despite their macroscopic size and endoparasitic biology, they were already con-sidered to be closely related to the Rotifera, based on ultrastructural similarities in their integuments. During the 1990s, a number of re-searchers began to investigate the phylogenetic positions of the aschelminth phyla. In 1995, two important papers (by W. H. Ahlrichs, R. M. Rieger and S. Tyler) suggested a sister-group relationship between Gnathostomulida and Rotifera, based on a proposed homology be-tween the jaws in the two groups. The homol-ogy was supported by ultrastructural data from transmission electron microscopy, which dem-onstrated that jaws in both taxa are made up by rodlike elements that in cross section appear as translucent areas with a central, electron-dense core. Ahlrichs (1995) referred to this group as Gnathifera, and he further suggested that the

Classification of The Animal Kingdom (Metazoa)

Non-Bilateria*
(a.k.a. the diploblasts)
  PHYLUM PORIFERA
  PHYLUM PLACOZOA
  PHYLUM CNIDARIA
  PHYLUM CTENOPHORA

Bilateria
(a.k.a. the triploblasts)
  PHYLUM XENACOELOMORPHA

Protostomia
  PHYLUM CHAETOGNATHA

SPIRALIA
  PHYLUM PLATYHELMINTHES
  PHYLUM GASTROTRICHA
  PHYLUM RHOMBOZOA
  PHYLUM ORTHONECTIDA
  PHYLUM NEMERTEA
  PHYLUM MOLLUSCA
  PHYLUM ANNELIDA
  PHYLUM ENTOPROCTA
  PHYLUM CYCLIOPHORA

Gnathifera
  PHYLUM GNATHOSTOMULIDA
  PHYLUM MICROGNATHOZOA
  PHYLUM ROTIFERA

Lophophorata
  PHYLUM PHORONIDA
  PHYLUM BRYOZOA
  PHYLUM BRACHIOPODA

ECDYSOZOA
  Nematoida
    PHYLUM NEMATODA
    PHYLUM NEMATOMORPHA

  Scalidophora
    PHYLUM KINORHYNCHA
    PHYLUM PRIAPULA
    PHYLUM LORICIFERA

  Panarthropoda
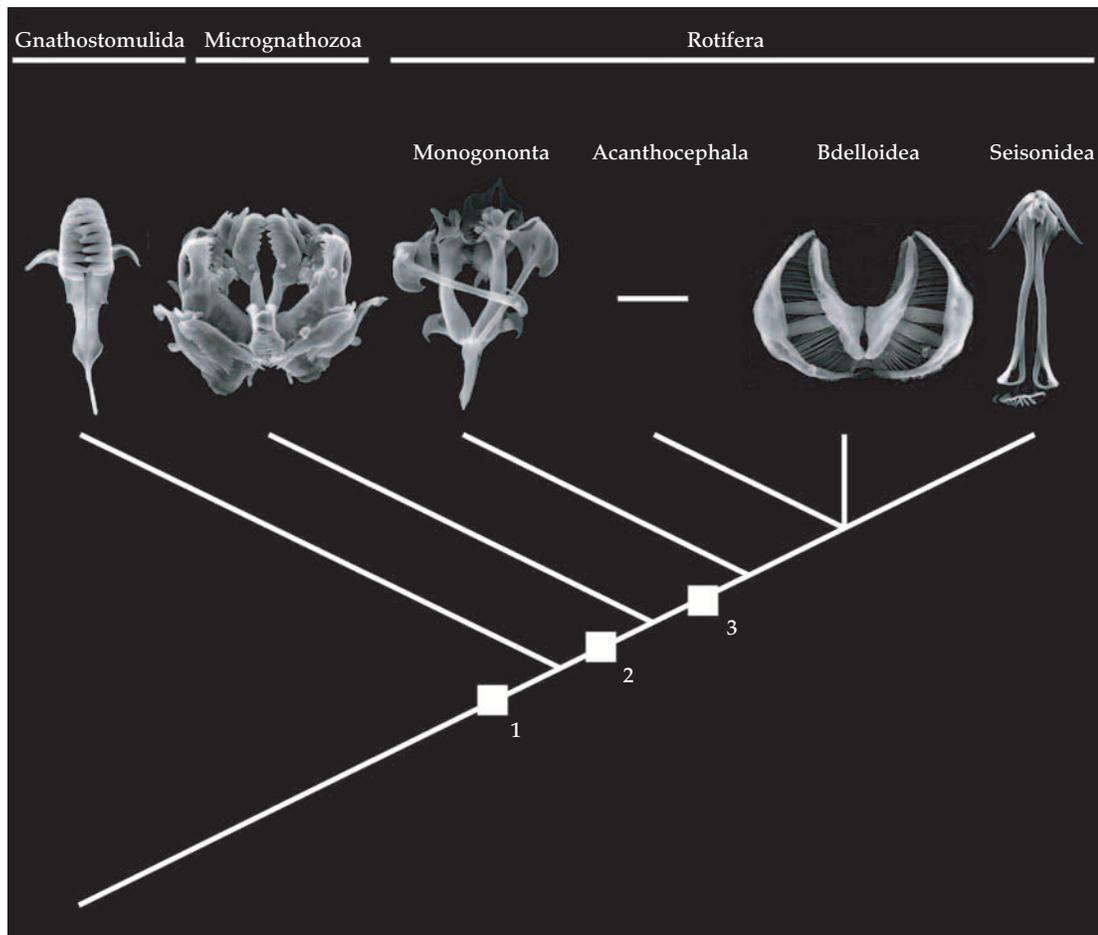   PHYLUM TARDIGRADA
    PHYLUM ONYCHOPHORA
    PHYLUM ARTHROPODA
      SUBPHYLUM CRUSTACEA*
      SUBPHYLUM HEXAPODA
      SUBPHYLUM MYRIAPODA
      SUBPHYLUM CHELICERATA

Deuterostomia
  PHYLUM ECHINODERMATA
  PHYLUM HEMICHORDATA
  PHYLUM CHORDATA

*Paraphyletic group

Martin V. Sørensen wrote the introduction and revised sections on phyla Gnathostomulida and Rotifera. Katrine Worsaae and Reinhardt Møbjerg Kristensen wrote the section on phylum Micrognathozoa.

Figure 16.1 Phylogenetic tree showing jaw structure and the relationships within Gnathifera. Synapomorphies for the major clades are marked on the tree: (1) pharyngeal hard parts/jaws composed of rods made of a translucent material with an electron-dense core, (2) cellular epidermis with intracellular protein lamina, (3) syncytial epidermis.

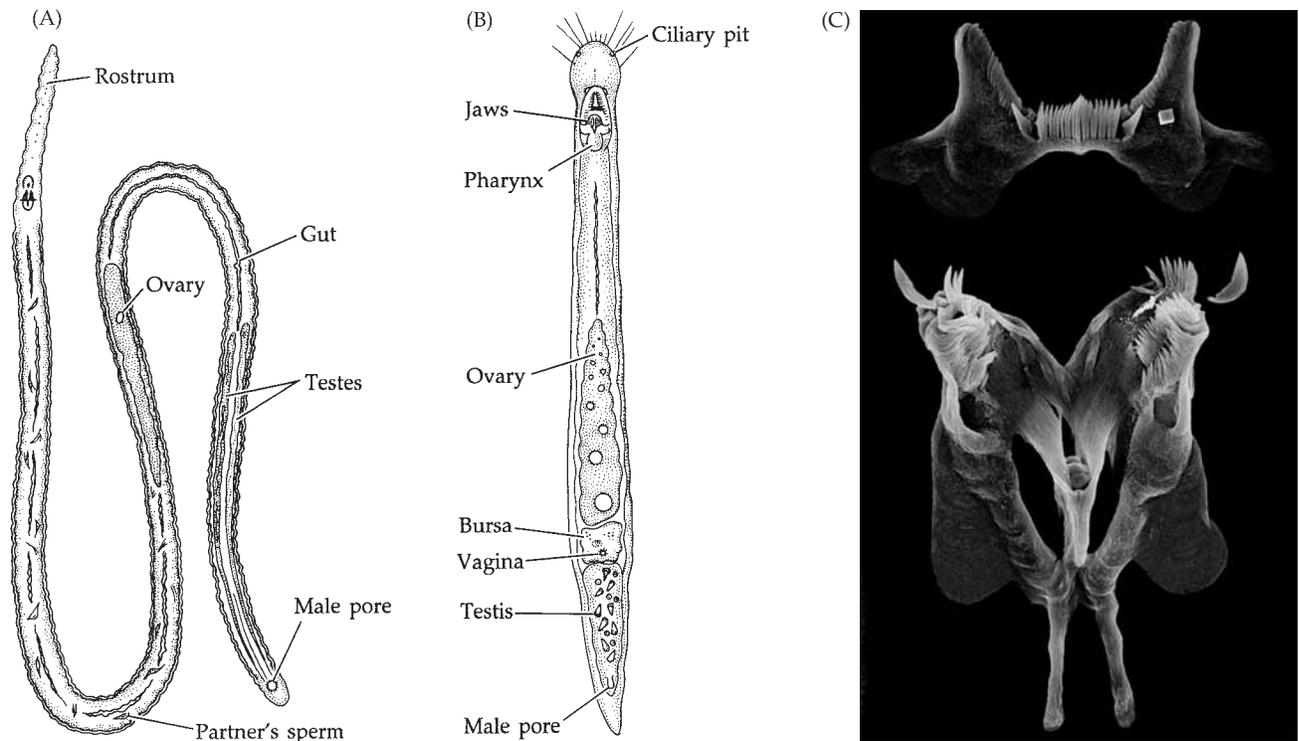endoparasitic acanthocephalans were actually no more than highly modified rotifers.

At the same time Gnathifera was taking its shape, another new animal was discovered in mosses from a cold spring in Greenland. It was a tiny, microscopic invertebrate that in some respects resembled a rotifer, and in other ways a gnathostomulid, but also possessed several characteristics that were not found in any other groups. The animal had jaws that were even more complex and numerous in elements than those found in the two other gnathiferan phyla. Transmission electron microscopy showed that the ultrastructure of the jaws was nearly identical with that of Rotifera and Gnathostomulida. Six years after its discovery, R. M. Kristensen and P. Funch (2000) named the animal *Limnognathia maerski*, and assigned it to a new animal group Micrognathozoa, which four years later was recognized as a third gnathiferan phylum.

Morphologically, Gnathifera appears to be a well-supported monophyletic group that is characterized by the presence of homologous pharyngeal hard parts, and at least one phylogenomic study has also found support for the clade Gnathifera.

Morphology-based phylogenies indicate that Gnathostomulida branches off as the most basal gnathiferan, whereas Micrognathozoa and Rotifera (including Acanthocephala) appear as sister-groups supported by similarities in the ultrastructure of their integuments (Figure 16.1). Both free-living Rotifera and Acanthocephala (see below) have a syncytial epidermis where the outer cuticle has been replaced by an intracellular protein lamina in the epidermal cells. Micrognathozoa has a regular non-syncytial epidermis, but a similar intracellular protein lamina is found in its dorsal epidermal plates, and the presence of this lamina is considered synapomorphic for Micrognathozoa and Rotifera-Acanthocephala.

Several molecular studies initially suggested a close relationship between Gnathostomulida and Rotifera–Acanthocephala, but then in 2015, using larger datasets, the Micrognathozoa began to appear as a sister group to the Rotifera–Acanthocephala.

Based on ultrastructural similarities in their integuments, the microscopic rotifers and the macroscopic acanthocephalans have long been considered as likely sister taxa. However, more recently an increasing

(A)

(B)

(C)

Figure 16.2   Representative gnathostomulids.
(A) *Haplognathia simplex*. (B) *Austrognatharia kirsteueri*.
(C) Basal plate and jaws of *Gnathostomula armata*.

amount of evidence from molecular studies have un-ambiguously shown that Acanthocephala is not the sister of Rotifera, but actually evolved from within the Rotifera—presumably as a clade that became obligate endoparasitic, and subsequently went through a series of dramatic morphological modifications and changes. Modern acanthocephalans are so modified and adapt-ed to their endoparasitic lifestyle that it is hard to find comparative morphological characters that would place them inside Rotifera, but the molecular support is strong and includes studies based on selected target loci and expressed sequence tags, as well as the com-plete mitochondrial genomes.

Phylum Gnathostomulida: The Gnathostomulids

The phylum Gnathostomulida (Greek, *gnathos*, "jaw"; *stoma*, "mouth") includes about 100 species of minute vermiform hermaphroditic animals (Figure 16.2). These meiofaunal creatures were first described by Peter Ax in 1956 as turbellarians, but given their own phylum rank by Rupert Riedl in 1969. Gnathostomulids are found worldwide, interstitially in marine sands mixed with detritus, from the intertidal zone to depths of hundreds of meters. The tiny, elongate body (less than 2 mm long) is usually divisible into head, trunk, and in some species a narrow tail region. Distinguishing

features of this phylum include a unique jawed pha-ryngeal apparatus and monociliated epidermal cells (Box 16A). The currently described 100 species and 26 genera are divided between two orders.

GNATHOSTOMULID CLASSIFICATION

ORDER FILOSPERMOIDEA   Body usually very elongate, with slender rostrum; jaws relatively simple; male parts with-out injectory penis; sperm filiform (with one 9+2 flagellum);

BOX 16A   Characteristics of the Phylum Gnathostomulida

1. Triploblastic, bilateral, unsegmented, vermiform acoelomates
2. Epidermis monolayered; all epithelial cells are monociliated
3. Gut incomplete (anus rudimentary, vestigial, or absent)
4. Pharynx with unique, complex jaw apparatus
5. Without circulatory system or special gas exchange structures
6. Excretion through protonephridia with monociliated terminal cells
7. Hermaphroditic
8. Cleavage spiral and development direct
9. Inhabit marine, interstitial environments

female parts without vagina and bursa. (3 genera: *Cosmognathia*, *Haplognathia*, and *Pterognathia*)

ORDER BURSOVAGINOIDEA   Body usually not extremely elongate relative to width; head with shorter rostrum and often a constriction in the neck area; jaws complex; male parts with penis, with or without a stylet; sperm cells aflagellate, either dwarf cells or giant conuli; female parts with bursa and usually a vagina. (23 genera, including *Austrognatharia*, *Gnathostomula*, and *Onychognathia*)

The Gnathostomulid Body Plan

Body Wall, Support, and Locomotion

Each outer epithelial cell bears a single cilium by which the animal moves in a gliding motion. Movement is aided by body contortions produced by the contraction of thin strands of subepidermal (cross-striated) muscle fibers. These actions, plus reversible ciliary beating, facilitate twisting, turning, and crawling among sand grains, and allow limited swimming in some species. Mucous gland cells occur in the epidermis of at least some species. The body is supported by its more or less solid construction, with a loose mesenchyme filling the area between the internal organs.

Nutrition, Circulation, Excretion, and Gas Exchange

The mouth is located on the ventral surface at the "head–trunk" junction and leads inward to a complex muscular pharynx armed with pincerlike jaws and in some species an unpaired anterior basal plate (Figure 16.2). Curiously, the two known species of the genus *Agnathiella* have no jaws at all. Gnathostomulids ingest bacteria and fungi by snapping actions made by the jaws or scraping with the basal plate. The pharynx connects with a simple, elongate, saclike gut. A permanent, functional anus is not present, but in a few gnathostomulids a tissue connection between the posterior end of the gut and the overlying epidermis has been observed. This enigmatic feature has been variously interpreted as either a temporary anal connection to the exterior, as the remnant of an anus that has been evolutionarily lost, or as an incipient anus that has yet to fully develop.

These animals depend largely on diffusion for circulation and gas exchange. The excretory system is composed of serially arranged protonephridia that stretch from the pharyngeal region to the terminal end of the body. Like the epithelial cells, the protonephridial terminal cells are monociliated.

Nervous System

The nervous system is intimately associated with the epidermis and as yet is incompletely described. Various sensory organs, such as sensory ciliary pits and stiff sensoria formed by groups of joined cilia from monociliated cells are concentrated in the head region. Gnathostomulid specialists have attached a formidable array of names to these structures, which are of major taxonomic significance.

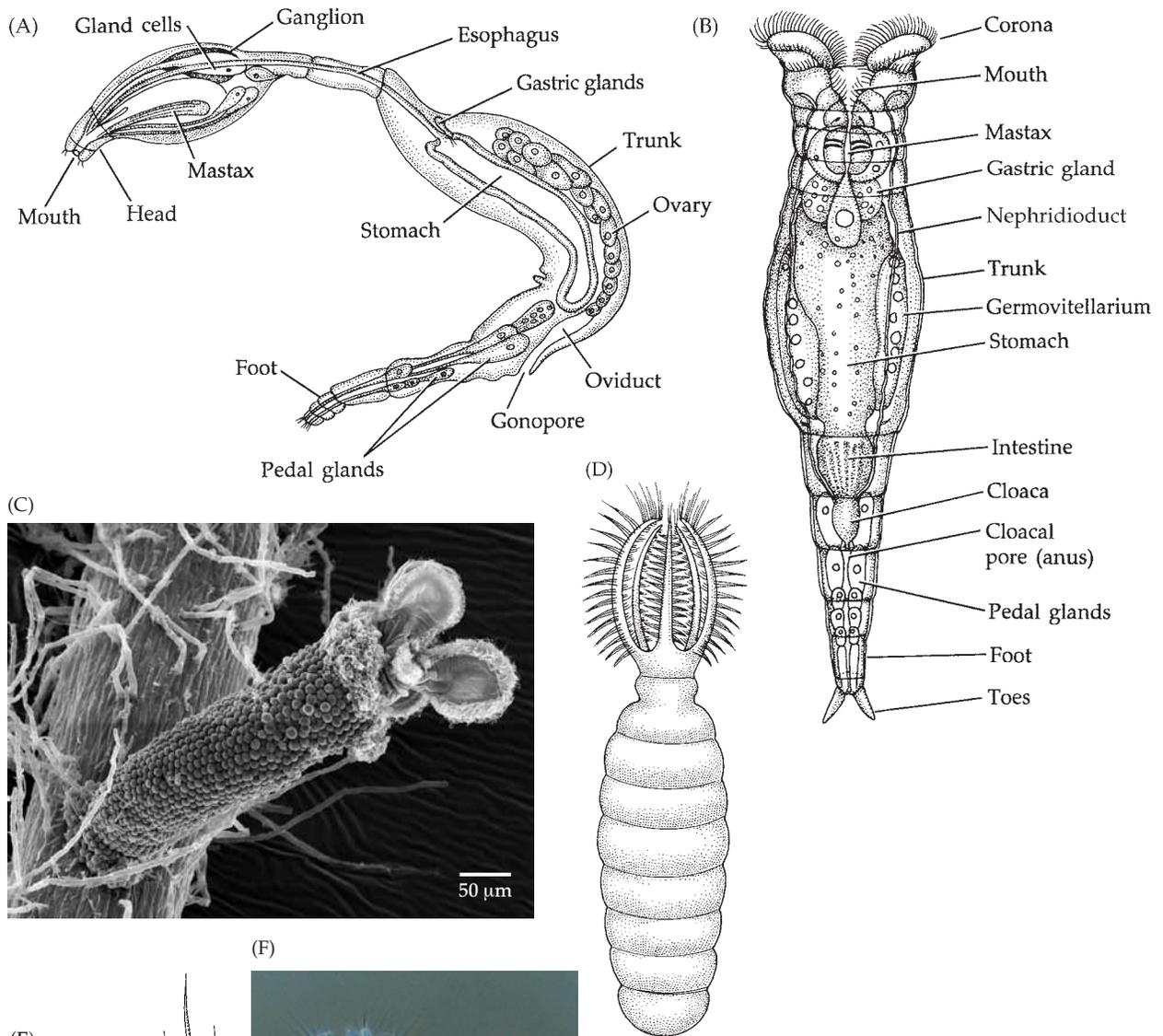### Reproduction and Development

Gnathostomulids are hermaphrodites. The male reproductive system includes one or two testes generally located in the posterior part of the trunk and tail; the female system consists of a single large ovary (Figure 16.2). Members of the order Bursovaginoidea possess a vaginal orifice and a sperm-storage bursa, both associated with the female gonopore, and a penis in the male system; members of the order Filospermoidea lack these structures.

Mating has been only superficially studied in gnathostomulids. Although the method of sperm transfer is not certain, suggestions include filiform sperm of filospermoid gnathostomulids boring through the body wall. Among some bursovaginoid gnathostomulids, sperm is transferred directly to the mating partner's bursa by hypodermic impregnation of the sclerotized penis stylet. In any case, these animals appear to be gregarious, to rely on internal fertilization, and to deposit zygotes singly in their habitat. Cleavage is reported as spiral and development is direct, but details on embryonic and juvenile development are generally scarce.

Phylum Rotifera: The Free-Living Rotifers

The phylum Rotifera (Latin *rota*, "wheel"; *fera*, "to bear") includes more than 2,000 described species of microscopic (about 100 to 1000 μm long), generally free-living animals. Furthermore, the parasitic, macroscopic acanthocephalan worms actually represent a rotifer in-group as well, but due to their considerable differences in biology and morphology, they will be discussed separately. Thus, in this section the name Rotifera refers to the microscopic, free-living rotifers only. The name "Syndermata" was proposed some time ago for a clade of Rotifera + Acanthocephala, but with the current understanding that these are not sister groups (the latter arose as a clade from within the former), that name is no longer useful.

Rotifers were discovered by the early microscopists, such as Antony van Leeuwenhoek in the late seventeenth century; at that time they were lumped with the protists as "animalcules" (mainly because of their small size). Besides the 2,050 or so known, morphologically recognizable species, complexes of cryptic speciation have been demonstrated for several morphospecies. For example, the species *Brachionus plicatilis* has been subject to intensive studies, and at least 22 cryptic species have been identified within this species group.

(A) Gland cells, Ganglion, Esophagus, Gastric glands, Trunk, Ovary, Oviduct, Gonopore, Pedal glands, Foot, Stomach, Mastax, Head, Mouth

(B) Corona, Mouth, Mastax, Gastric gland, Nephridioduct, Trunk, Germovitellarium, Stomach, Intestine, Cloaca, Cloacal pore (anus), Pedal glands, Foot, Toes

(C) 50 μm

(D)

(E)

(F)

Figure 16.3   Representative rotifers. (A) *Paraseison annulatus* (subclass Seisonidea), a marine ectoparasitic rotifer from the gills of *Nebalia*. (B) *Philodina roseola* (subclass Bdelloidea). (C–F) Members of the subclass Monogononta: (C) SEM of a sessile rotifer (*Floscularia*) that lives inside a tube that it constructs from small pellets composed of bacteria and detritus. (D) *Stephanoceros*, one of the strange collothecacean rotifers with the corona modified as a trap. (E) The loricae of two loricate rotifers. (F) Live specimens of *Stephanoceros*.

photo of *Conochilus*). They are most common in fresh water, but many marine species are also known, and others live in damp soil or in the water film on mosses. They often comprise an important component of the plankton of fresh and brackish waters.

Despite their small size, rotifers are actually quite complex and display a variety of body forms (Figure 16.3). Most are solitary, but some sessile forms are colonial, a few of which secrete gelatinous casings into which the individuals can retract (e.g., chapter opener

The body comprises three general regions—the head, trunk, and foot. The head bears a ciliary organ called the **corona**. When active, the coronal cilia often give the impression of a pair of rotating wheels, hence the derivation of the phylum name; in fact, rotifers

were historically called "wheel animalcules." Members of this phylum are further characterized by being blastocoelomate, having an integument without an outer cuticle, but instead with a supportive intracellular protein lamina. They have a complete gut (usually), protonephridia, show a tendency to eutely, and often have syncytial tissues or organs (Box 16B). The pharynx is modified as a **mastax** comprising sets of internal jaws called **trophi**. The morphology of the trophi is of great systematic importance and often the main character to identify species and genera.

A highly surprising discovery about rotifers was made in 2008, when it was found that bdelloid rotifers have incorporated large numbers of genes from diverse foreign sources into their genomes, including bacteria, fungi, and plants. These foreign genes have accumulated mainly in the telomeric regions at the ends of chromosomes, and at least most of them seem to retain their functional integrity.

ROTIFER CLASSIFICATION

CLASS HEMIROTATORIA   Endoparasites, ectoparasites, or free-living; this group is recognized only by molecular data.

SUBCLASS ACANTHOCEPHALA   Macroscopic endoparasites; see chapter section below.

SUBCLASS BDELLOIDEA   (Figure 16.3B) Found in freshwater, moist soils, and foliage (also marine, and terrestrial); corona typically well developed; trophi ramate (grinding). (20 genera, e.g., *Adineta*, *Embata*, *Habrotrocha*, *Philodina*, *Rotaria*)

SUBCLASS SEISONIDEA   (Figure 16.3A) Epizoic on the marine leptostracan crustacean *Nebalia*; corona reduced to bristles; trophi fulcrate (piercing); males fully developed and considered to have diploid chromosome numbers; sexual females produce only mictic ova. (2 genera: *Paraseison* and *Seison*)

CLASS EUROTATORIA

SUBCLASS MONOGONONTA   (Figure 16.3C–F) Predominately freshwater, some are marine; swimmers, creepers, or sessile; corona and trophi variable; males typically short lived, haploid, and reduced in size and complexity; sexual reproduction probably occurs at some point in the life history of all species; mictic and amictic ova produced in many species; single germovitellarium. (121 genera, e.g., *Asplanchna*, *Brachionus*, *Collotheca*, *Dicranophorus*, *Encentrum*, *Epiphanes*, *Euchlanis*, *Floscularia*, *Lecane*, *Notommata*, *Proales*, *Synchaeta*, *Testudinella*)
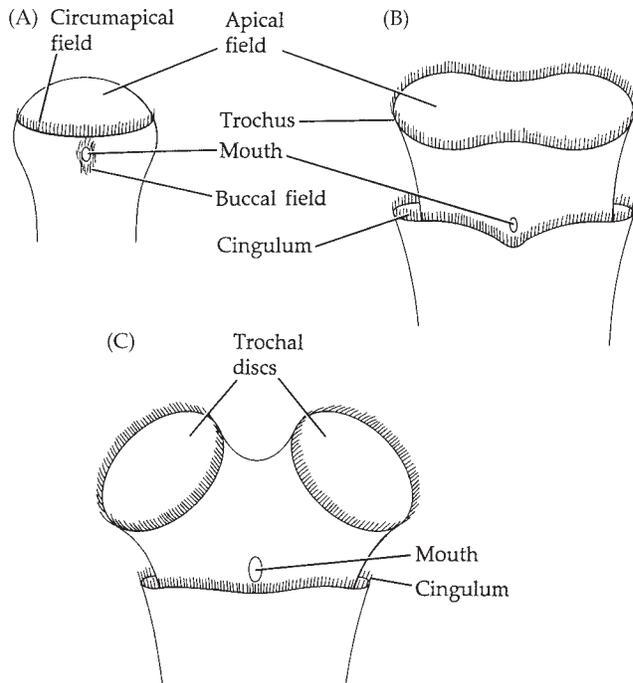
The Rotifer Body Plan

Body Wall, General External Anatomy, and Details of the Corona

Most rotifers possess a soft, gelatinous glycocalyx outside their epidermis, but unlike many other invertebrates, they have no external cuticle. Instead they have an intracellular protein lamina located inside the epidermis, for protection and stabilization of the body. This protein lamina may vary considerably in thickness and flexibility among the genera and families. Species with a very thin protein lamina are called "illoricate rotifers," and they often appear as very flexible and hyaline animals that contract completely when disturbed. In other species, the intracellular protein lamina is much thicker and forms a body-armor, called a **lorica**, and these species are referred to as "loricate rotifers." Another special condition of the rotifer epidermis regards the absence of walls between the epidermal cells, meaning that the epidermis is a syncytium with about 900 to 1,000 nuclei.

The body surface of many illoricate rotifers is annulated, allowing flexibility. The surface of loricate species often bears spines, tubercles, or other sculpturing (Figure 16.3E). Many rotifers bear single dorsal and paired lateral sensory antennae arising from various regions of the body. A foot is not present in all species, but when present it is often elongate, with cuticular annuli that permit a telescoping action. The distal portion of the foot often bears spines, or a pair of "toes" through which the ducts from pedal glands pass. The secretion from the pedal glands enables the rotifer to attach temporarily to the substratum. The foot is absent

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BOX 16B   Characteristics of the Phylum Rotifera

1. Triploblastic, bilateral, unsegmented blastocoelomates
2. Gut complete and regionally specialized
3. Pharynx modified as a mastax, containing jawlike elements called "trophi"
4. Anterior end bears variable ciliated fields as a corona
5. Posterior end often bears toes and adhesive glands
6. Epidermis syncytial, with fixed number of nuclei; secretes extracellular glycocalyx and intracellular skeletal lamina (the latter forming a lorica in some species)
7. With protonephridia, but no special circulatory or gas exchange structures
8. With unique retrocerebral organ
9. Males generally reduced or absent; parthenogenesis common
10. With modified spiral cleavage
11. Inhabit marine, freshwater, or semiterrestrial environments; sessile or free-swimming

Figure 16.4   Modifications of the corona among selected rotifer types. (A) The presumed plesiomorphic condition has buccal and circumapical fields. (B) The circumapical field is separated into trochus and cingulum. The trochus is lobed, like that of *Floscularia*. (C) The trochus is separated into two trochal discs, as found in many bdelloid rotifers.

from some swimming forms (e.g., *Asplanchna*) and is modified for permanent attachment in sessile types (e.g., *Floscularia*).

The **corona** is the most characteristic external feature of rotifers. Its morphology varies greatly and, in some groups, the corona is an important taxonomic character. The presumed primitive condition is shown in Figure 16.4A. A well-developed patch of cilia surrounds the anteroventral mouth. This patch is the buccal field, or circumoral field, and it extends dorsally around the head as a ciliary ring called the circumapical field. The extreme anterior part of the head bordered by this ciliary ring is the apical field. The corona has evolved to a variety of modified forms in different rotifer taxa. In some species, the buccal field is quite reduced, and the circumapical field is separated into two ciliary rings, one slightly anterior to the other (Figure 16.4B). The anteriormost ring is called the trochus, the other the cingulum. In many bdelloid rotifers the trochus is a pair of well-defined anterolateral rings of cilia called trochal discs (Figure 16.4C), which may be retracted or extended for locomotion and feeding. It is the metachronal ciliary waves along these trochal discs that impart the impression of rotating wheels.

Many organs and tissues of rotifers display eutely: cell or nuclear number constancy. This condition is
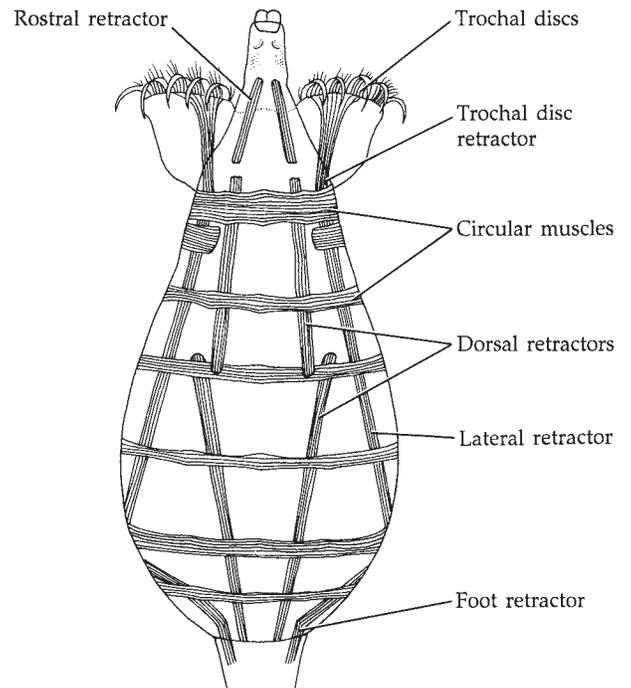
established during development, and there are no mitotic cell divisions in the body following ontogeny.

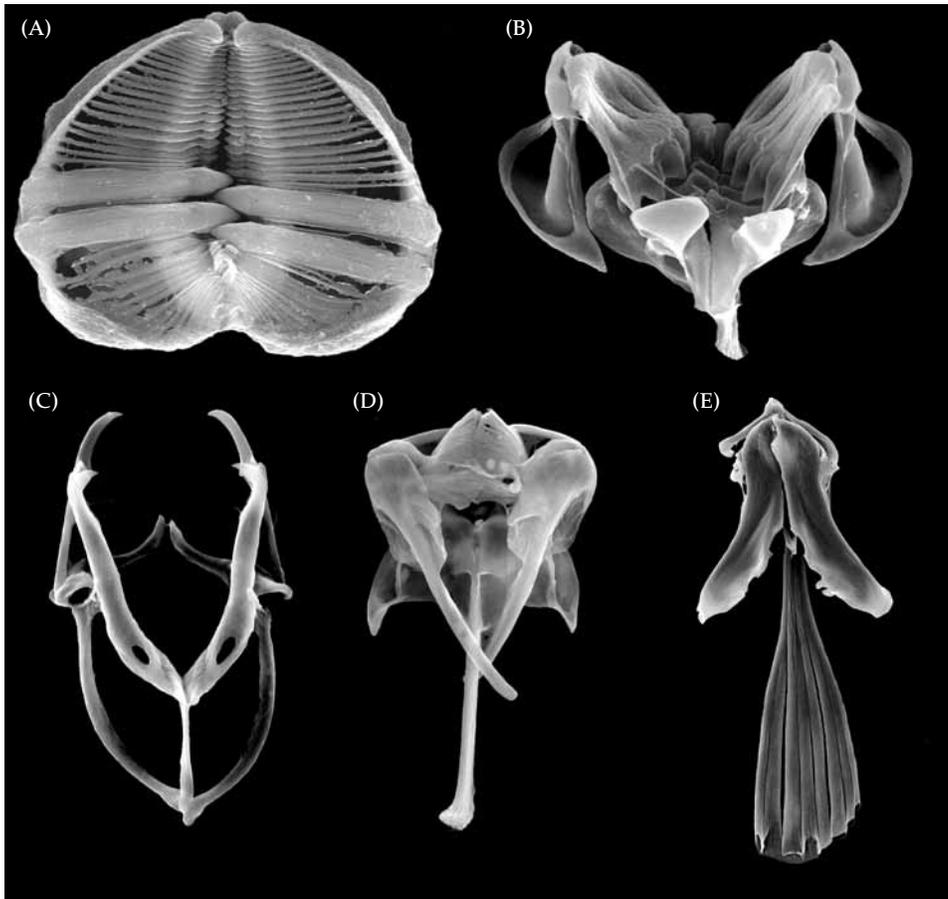## Body Cavity, Support, and Locomotion

Beneath the epidermis are various circular and longitudinal muscle bands (Figure 16.5); there are no sheets or layers of body wall muscles. The internal organs lie within a typically spacious, fluid-filled blastocoelom.

In the absence of a thick, muscular body wall, body support and shape are maintained by the intraepidermal skeletal lamina and the hydrostatic skeleton provided by the body cavity. In loricate species the integument is only flexible enough to allow slight changes in shape, so increases in hydrostatic pressure within the body cavity can be used to protrude body parts (e.g., foot, corona). These parts are protracted and retracted by various muscles (Figure 16.5), each consisting of only one or two cells.

Although a few rotifers are sessile, most are motile and quite active, moving about by swimming or creeping like an inchworm. Some are exclusively either swimmers or crawlers, but many are capable of both methods of locomotion. Swimming is accomplished by beating the coronal cilia, forcing water posteriorly along the body, and driving the animal forward, sometimes in a spiral path. When creeping, a rotifer attaches its foot with secretions from the pedal glands, then elongates its body and extends forward. It attaches the extended anterior end to the substratum,

Figure 16.5   Major muscle bands of the bdelloid rotifer, *Rotaria* (dorsal view).

Figure 16.6 SEMs showing different rotifer trophi types. (A) *Dissotrocha aculeata* with the ramate trophus type, found in all bdelloids. (B) *Brachionus calyciflorus* with the malleate trophus type that characterizes several monogonont families. (C) *Encentrum astridae* with forcipate trophi, found in the monogonont family Dicranophoridae. (D) *Resticula nyssa* with its virgate trophi, typical for Notommatidae and several other monogonont families. (E) *Paraseison kisfaludyi*, fulcrate trophi of the ectoparasitic Seisonidea.

releases its foot, and draws its body forward by muscular contraction.
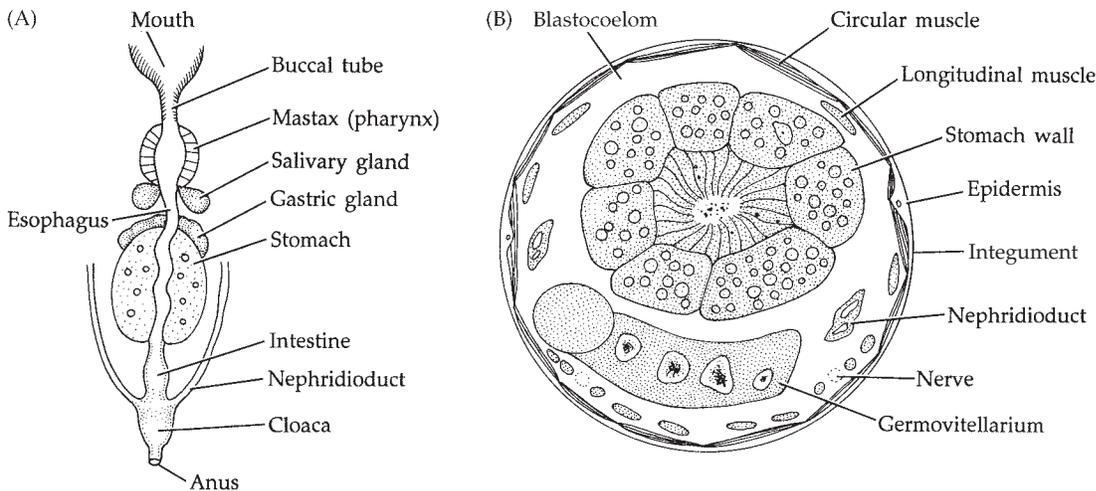
Feeding and Digestion

Rotifers display a variety of feeding methods, depending upon the structure of the corona (Figure 16.4) and the mastax trophi (Figure 16.6). Ciliary suspension feeders have well-developed coronal ciliation and a grinding mastax. These forms include the bdelloids, which have trochal discs and a ramate mastax (Figure 16.6A), and a number of monogonont rotifers, which have separate trochus and cingulum and a malleate mastax (Figure 16.6B). These forms typically feed on organic detritus or minute organisms. The feeding current is produced by the action of the cilia of the trochus (or trochal discs), which beat in a direction opposite to that of the cilia of the cingulum. Particles are drawn into a ciliated food groove that lies between these opposing ciliary bands and are carried to the buccal field and mouth.

Raptorial feeding is common in many species of Monogononta. Coronal ciliation in these rotifers is often reduced or used exclusively for locomotion. Raptorial feeders obtain food by grasping it with protrusible, pincerlike mastax jaws; most possess either a forcipate mastax (non-rotating) (Figure 16.6C) or an incudate mastax (rotating 90–180° during protrusion). Raptorial rotifers feed mainly on small animals but are known to ingest plant material as well. They may ingest their prey whole and subsequently grind it to smaller particles within the mastax, or they may pierce the body of the plant or animal with the tips of the mastax jaws and suck fluid from the prey (Figure 16.6D).

Some monogonont rotifers have adopted a trapping method of predation. In such cases the corona usually bears spines or setae arranged as a funnel-shaped trap (Figure 16.3D,F). The mouth in these trappers is located more or less in the middle of the ring of spines (rather than in the more typical anteroventral position); thus, captured prey is drawn to it by contraction of the trap elements. The mastax in trapping rotifers is often reduced.

A few rotifers have adopted symbiotic lifestyles. As noted in the classification scheme, seisonids live on

Figure 16.7 (A) Digestive system of a rotifer. (B) Cross section through the trunk.

marine leptostracan crustaceans of the genus *Nebalia*. These rotifers (*Seison* and *Paraseison*) crawl around the base of the legs and gills of their host, feeding on detritus and on the host's brooded eggs. It has been suggested that species of the predatory *Paraseison* may use the anterior tip of the fulcrum of its fulcrate trophi (Figure 16.6E) to pinch the cuticle of its leptostracan host and feed on its haemolymph. Some bdelloids (e.g., *Embata*) also live on the gills of crustaceans, particularly amphipods and decapods. There are isolated examples of endoparasitic rotifers inhabiting hosts such as *Volvox* (a colonial protist), freshwater algae, snail egg cases, and the body cavities of certain annelids and terrestrial slugs. Little is known about nutrition in most of these species.

The digestive tract of most rotifers is complete and more or less straight (Figure 16.7A). (The anus has been secondarily lost in a few species, and some have a moderately coiled gut.) The mouth leads inward to the pharynx (mastax) either directly or via a short, ciliated buccal tube. Depending on the feeding method and food sources, swallowing is accomplished by various means, including ciliary action of the buccal field and buccal tube, or a pistonlike pumping action of certain elements of the mastax apparatus. The mastax is ectodermal in origin. Opening into the gut lumen just posterior to the mastax are ducts of the salivary glands. There are usually two to seven such glands; they are presumed to secrete digestive enzymes and perhaps lubricants aiding the movement of the mastax trophi.

A short esophagus connects the mastax and stomach. A pair of gastric glands opens into the posterior end of the esophagus; these glands apparently secrete digestive enzymes. The walls of the esophagus and gastric glands are often syncytial. The stomach is generally thick walled and may be cellular or syncytial, usually comprising a specific number of cells or nuclei
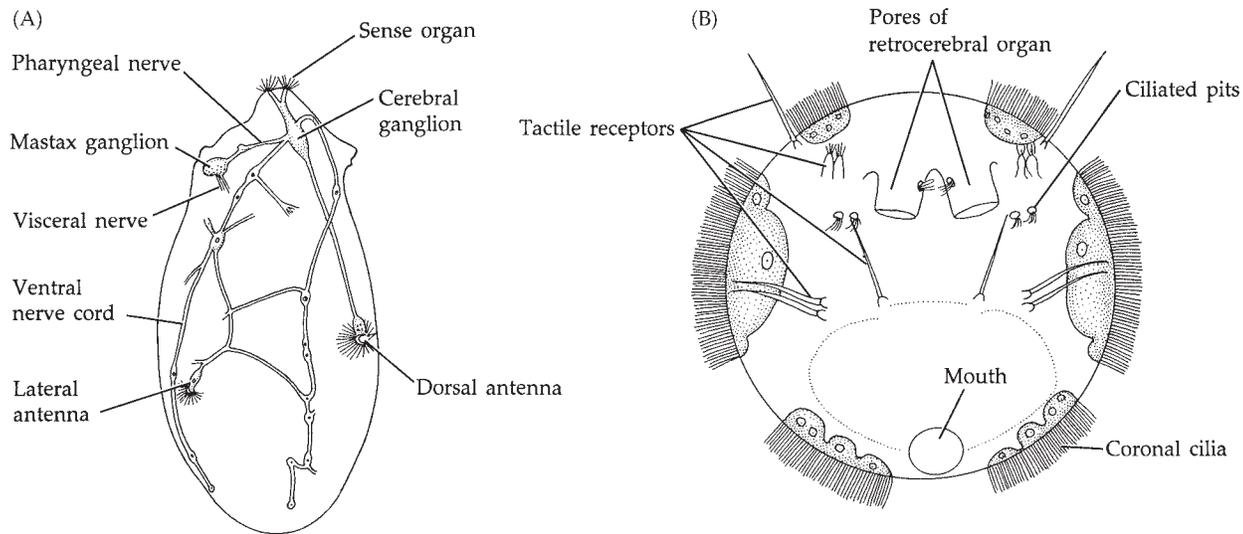
in each species (Figure 16.7B). The intestine is short and leads to the anus, which is located dorsally near the posterior end of the trunk. Except for *Asplanchna*, which lacks a hindgut, an expanded cloaca connects the intestine and anus. The oviduct and usually the nephridioducts also empty into this cloaca.

Digestion probably begins in the lumen of the mastax and is completed extracellularly in the stomach, where absorption occurs. In one large and enigmatic group of bdelloids the stomach lacks a lumen. Although much remains to be learned about the digestive physiology of rotifers, some experimental work indicates that diet has multiple and important effects on various aspects of their biology, including the size and shape of individuals as well as some life cycle activities (see Gilbert 1980).

Circulation, Gas Exchange, Excretion, and Osmoregulation

Rotifers have no special organs for internal transport or for the exchange of gases between tissues and the environment. The blastocoelomic fluid provides a medium for circulation within the body, which is aided by general movement and muscular activities. Small body size reduces diffusion distances and facilitates the transport and exchange of gases, nutrients, and wastes. These activities are further enhanced by the absence of linings and partitions within the body cavity, so the exchanges occur directly between the organ tissues and the body fluid. Gas exchange probably occurs over the general body surface wherever the integument is sufficiently thin.

Most rotifers possess one or several pairs of flame bulb protonephridia, located far forward in the body. A nephridioduct leads from each flame bulb to a collecting bladder, which in turn empties into the cloaca via a ventral pore. In some forms, especially the bdelloids, the ducts open directly into the cloaca, which is enlarged to act as a bladder (Figure 16.7A). The protonephridial system of rotifers is primarily osmoregulatory in function, and is most active in freshwater forms.

(A)

(B)

Figure 16.8 (A) The nervous system of *Asplanchna*. (B) The coronal area of *Euchlanis* (apical view). Note the various sense organs.

Excess water from the body cavity and probably from digestion is also pumped out via the anus by muscular contractions of the bladder. This "urine" is significantly hypotonic relative to the body fluids. It is likely that the protonephridia also remove nitrogenous excretory products from the body. This form of waste removal is probably supplemented by simple diffusion of wastes across permeable body wall surfaces.

Some rotifers (especially the freshwater and semiterrestrial bdelloids) are able to withstand extreme environmental stresses by entering a state of metabolic dormancy. They have been experimentally desiccated and kept in a dormant condition for as long as four years—reviving upon the addition of water. Some have survived freezing in liquid helium at –272°C and other severe stresses dreamed up by biologists.

Nervous System and Sense Organs

The cerebral ganglion of rotifers is located dorsal to the mastax, in the neck region of the body. Several nerve tracts arise from the cerebral ganglion, some of which bear additional small ganglionic swellings (Figure 16.8A). There are usually two major longitudinal nerves positioned either both ventrolaterally or one dorsally and one ventrally.

The coronal area generally bears a variety of touch-sensitive bristles or spines and often a pair of ciliated pits thought to be chemoreceptors (Figure 16.8B). The dorsal and lateral antennae are probably tactile. Some rotifers bear sensory organs, which are arranged as a cluster of micropapillae encircling a pore. These organs may be tactile or chemosensory. Most of the errant rotifers possess at least one simple ocellus embedded in the cerebral ganglion. In some, this cerebral ocellus is accompanied by one or two pairs of lateral ocelli on

the coronal surface, and sometimes by a pair of apical ocelli in the apical field. The lateral and apical ocelli are multicellular epidermal patches of photosensitive cells. Pierre Clément (1977) described possible baro- or chemoreceptors in the body cavity that may help regulate internal pressure or fluid composition.
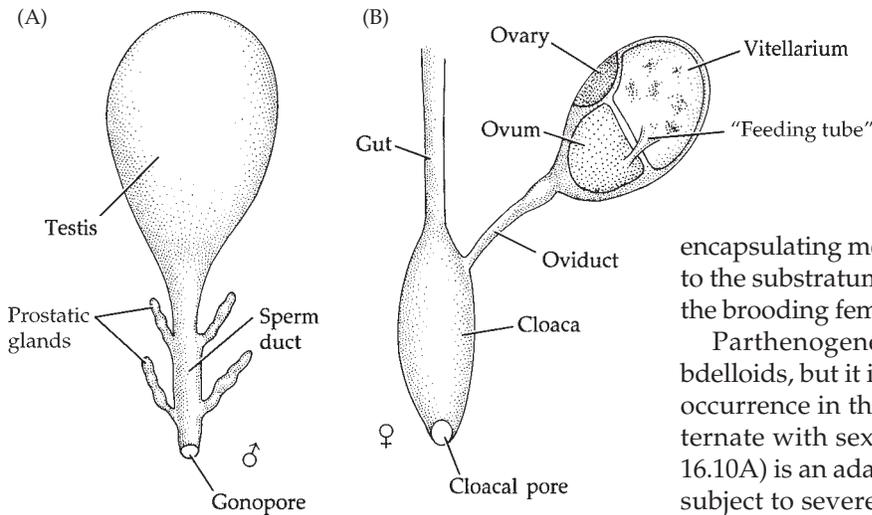
Associated with the cerebral ganglion is the so-called **retrocerebral organ**. This curious glandular structure gives rise to ducts that lead to the body surface in the apical field (Figure 16.8B). Once thought to be sensory in function, more recent work suggests that it may secrete mucus to aid in crawling.

Reproduction and Development

Parthenogenesis is probably the most common method of reproduction among rotifers. Other forms of asexual reproduction are unknown, and most groups show only very weak powers of regeneration. Most rotifers are gonochoristic; however, other than the Seisonidea, males are either reduced in abundance, size, and complexity, and with haploid chromosome numbers (Monogononta), or are still unknown (Bdelloidea). If you find a rotifer, the chances are good that it is a female.

The male reproductive system (Figure 16.9A) includes a single testis (paired in Seisonidea), a sperm duct, and a posterior gonopore whose wall is usually folded to produce a copulatory organ. Prostatic glands are sometimes present in the wall of the sperm duct. The males are short lived and possess a reduced gut unconnected to the reproductive tract.

The female system includes paired (Bdelloidea) or single (Monogononta) syncytial germovitellaria (Figure 16.9B). Eggs are produced in the ovary and receive yolk directly from the vitellarium before passing along the oviduct to the cloaca; in those forms that have lost the intestinal portion of the gut (e.g., *Asplanchna*), the oviduct passes directly to the outside via a gonopore. In the Seisonidea, there are no yolk glands.
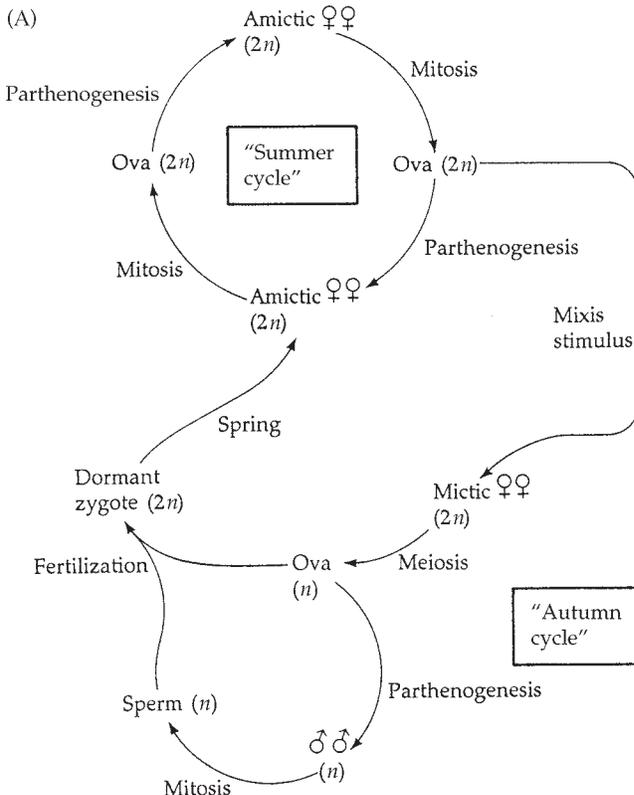
(A)

(B)

Figure 16.9   Male and female reproductive systems from a generalized monogonont rotifer.

encapsulating membranes and are then either attached to the substratum or carried externally or internally by the brooding female.

Parthenogenesis is generally the rule among the bdelloids, but it is also a common and usually seasonal occurrence in the monogononts, where it tends to alternate with sexual reproduction. This cycle (Figure 16.10A) is an adaptation to freshwater habitats that are subject to severe seasonal changes. During favorable conditions, females reproduce parthenogenetically through the production of mitotically derived diploid ova (amictic ova). These eggs develop into more females without fertilization. However, when ova from amictic females are subjected to particular environmental conditions (so-called mixis stimuli), they develop into mictic females, which then produce mictic (haploid) ova by meiosis. The exact stimulus apparently varies among different species and may include such factors as changes in day length, temperature, food resources, or increases in population density. Although these cycles are commonly termed "summer" and "autumn cycles," this is a bit misleading because mixis can also occur during warm weather and many populations have several periods of mixis each year. Mictic ova require fertilization by male gametes to develop a new female individual, but if no males are present, the unfertilized mictic ova will instead develop into haploid males, which produce sperm by mitosis. These sperm fertilize other mictic ova, producing diploid, thick-walled, resting zygotes. The resting zygotic form is extremely resistant to low temperatures, desiccation, and other adverse environmental conditions. When favorable conditions return, the zygotes develop and hatch as amictic females (Figure 16.10B), completing the cycle.

In rotifers with a male form, copulation occurs either by insertion of the male copulatory organ into the cloacal area of the female or by hypodermic impregnation. In the latter case, males attach to females at various points on the body and apparently inject sperm directly into the blastocoelom (through the body wall). The sperm somehow find their way to the female reproductive tract, where fertilization takes place. The number of eggs produced by an individual female is determined by the original, fixed number of ovarian nuclei—usually 20 or fewer, depending on the species. Once fertilized, the ova produce a series of

(A)

(B)

Figure 16.10   (A) Mictic/amictic alternation in the life cycle of a monogonont rotifer. (B) Micrograph of an amictic female hatching from an overwintering phase.

Bdelloids are prone to infection by an aggressive fungus, *Rotiferophthora angustispora*, that eats them from the inside out. Experiments have recently shown that the longer the rotifers remain dry and in a state of dormancy, the more likely they are to avoid infection by *R. angustispora*, suggesting that their adaptation for quiescence may also be an adaptation to avoid fungal predation.

Only a few studies have been conducted on the embryogeny of rotifers (see especially Pray 1965). In spite of the paucity of data, and some conflicting interpretations in the literature, it is generally thought that rotifers have modified spiral cleavage. However, detailed analyses of cell lineages are still needed to determine if the typical spiral pattern persists past the first couple of cell divisions in rotifers, especially with regard to the origin of the mesoderm. The isolecithal ova undergo unequal holoblastic early cleavage to produce a stereoblastula. Gastrulation is by epiboly of the presumptive ectoderm and involution of the endoderm and mesoderm; the gastrula gradually hollows to produce the blastocoel, which persists as the adult body cavity. The mouth forms in the area of the blastopore. Definitive nuclear numbers are reached early in development for those organs and tissues displaying eutely.

Errant rotifers undergo direct development, hatching as mature or nearly mature individuals. Sessile forms pass through a short dispersal phase, sometimes called a larva, which resembles a typical swimming rotifer. The "larva" eventually settles and attaches to the substratum. In all cases, there is a total absence of cell division during postembryonic life (i.e., they are eutelic).

Many rotifers exhibit developmental polymorphism, a phenomenon also seen in some protists, insects, and primitive crustaceans. It is the expression of alternative morphotypes under different ecological conditions, by organisms of a given genetic constitution (the differentiation of certain castes in social insects is one of the most remarkable examples of developmental polymorphism). In all such animals studied to date, the alternative adult morphotypes appear to be products of flexible developmental pathways, triggered by environmental cues and often mediated by internal mechanisms such as hormonal activities. In one well-studied genus of rotifers (*Asplanchna*), the environmental stimulus regulating which of several adult morphologies is produced is the presence of a specific molecular form of vitamin E—α-tocopherol. *Asplanchna* obtains tocopherol from its diet of algae or other plant material, or when it preys on other herbivores (animals do not synthesize tocopherol). The chemical acts directly on the rotifer's developing tissues, where it stimulates differential growth of the syncytial hypodermis after cell division has ceased. Predator-induced morphologies also occur among rotifers. *Keratella slacki* eggs, in the presence of the predator *Asplanchna* (both are rotifers), are stimulated to develop into larger-bodied adults with an extra long anterior spine, thus rendering them more difficult to eat.

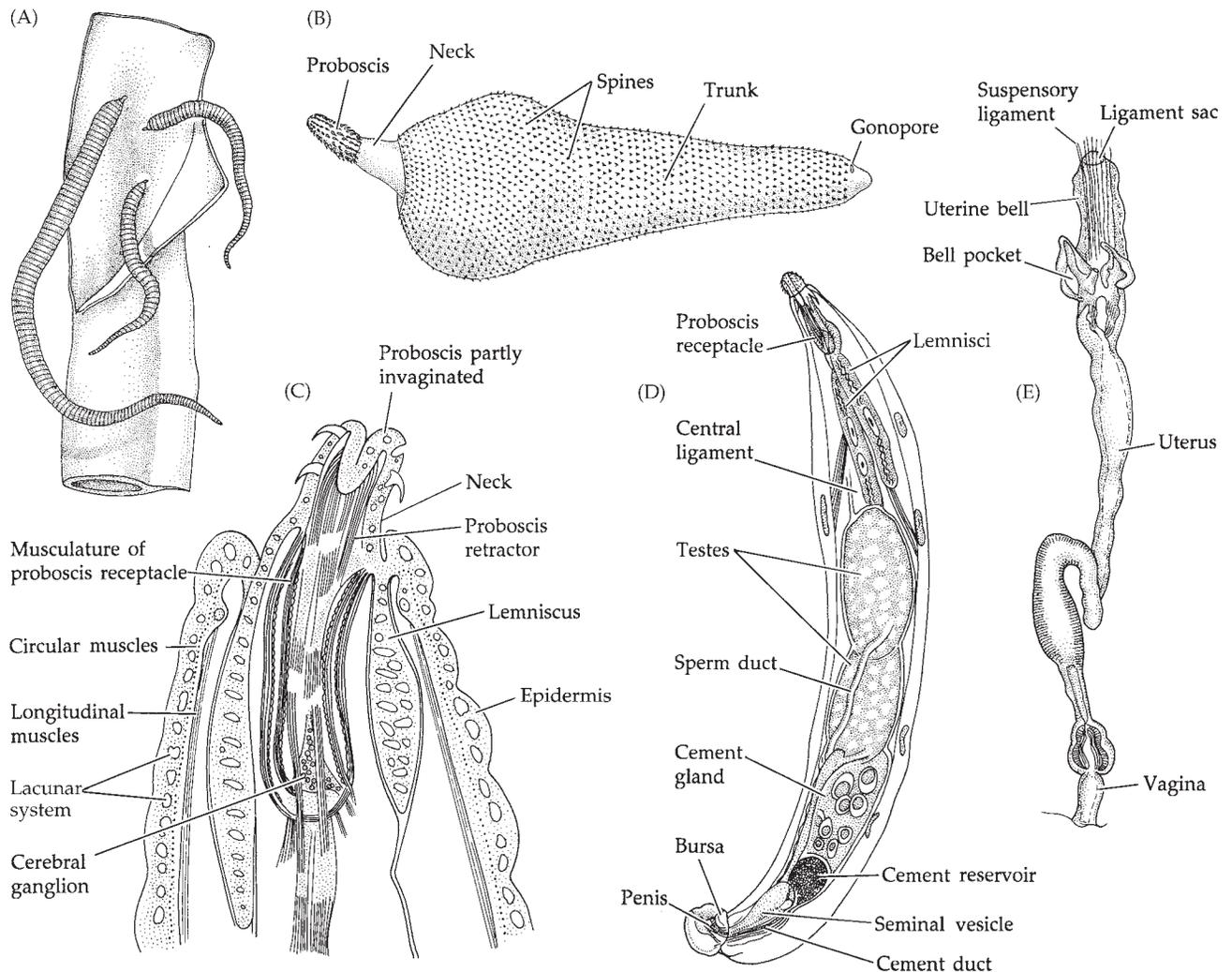# Phylum Rotifera, Subclass Acanthocephala: The Acanthocephalans

As adults, the 1,200 or so described species of acanthocephalans are obligate intestinal parasites in vertebrates, particularly in birds and freshwater fishes. Larval development takes place in intermediate arthropod hosts. The name Acanthocephala (Greek *acanthias*, "prickly"; *cephalo*, "head") derives from the presence of recurved hooks located on an eversible proboscis at the anterior end. The rest of the body forms a cylindrical or flattened trunk, often bearing rings of small spines. Most acanthocephalans are less than 20 cm long, although a few species exceed 60 cm in length; females are generally larger than males. The digestive tract has been completely lost, and, except for the reproductive organs, there is significant structural and functional reduction of most other systems, a condition related to the parasitic lifestyles of these worms (Box 16C). The persisting organs lie within an open blastocoelom, partially partitioned by mesentery-like ligaments.

The acanthocephalans are usually divided into three groups based upon the arrangement of proboscis hooks, the nature of the epidermal nuclei, spination patterns on the trunk, and nature of the reproductive organs: Palaeacanthocephala (e.g., *Polymorphus, Corynosoma, Plagiorhynchus, Acanthocephalus*), Archiacanthocephala (e.g., *Moniliformis*), and Eoacanthocephala (e.g., *Neoechinorhynchus, Octospiniferoides*) (see Figure 16.11).

The Acanthocephalan Body Plan

Body Wall, Support, Attachment, and Nutrition

Adult acanthocephalans attach to their host's intestinal wall by their proboscis hooks, which are retractable into pockets, like the claws of a cat (Figure 16.11). The chemical nature of the hooks is not yet known. In nearly all species, the proboscis itself is retractable into a deep proboscis receptacle, enabling the body to be pulled close to the host's intestinal mucosa. Nutrients are absorbed through the body wall, and a gut is absent. The outer body wall is a multilayered, syncytial, living tegument, which overlies sheets of circular and longitudinal muscles. The tegument includes layers of dense fibers as well as what appear to be sheets of plasma membrane, and an intracellular protein lamina, such as the one found in free-living rotifers. The tegument is perforated by numerous canals that connect to a complex set of unique circulatory channels called the **lacunar**

(A)

(B)

Proboscis   Neck

Spines   Trunk

Gonopore

Suspensory
ligament   Ligament sac

Uterine bell

Bell pocket

Proboscis partly
invaginated

(C)

Proboscis
receptacle   Lemnisci

(D)   (E)

Neck

Proboscis
retractor

Central
ligament

Uterus

Musculature of
proboscis receptacle

Lemniscus

Testes

Circular muscles

Epidermis

Sperm duct

Longitudinal
muscles

Lacunar
system

Cement
gland

Cerebral
ganglion

Bursa

Vagina

Penis

Cement reservoir

Seminal vesicle

Cement duct

Figure 16.11   Representative acanthocephalans.
(A) *Macracanthorynchus hirudinaceus*, an archiacantho-
cephalan, attached to the intestinal wall of a pig.
(B) *Corynosoma*, a palaeacanthocephalan found in aquatic
birds and seals. (C) Longitudinal section through the ante-
rior end of *Acanthocephalus* (class Palaeacanthocephala).
(D) An adult male eoacanthocephalan (*Pallisentis frac-
tus*). (E) The isolated female reproductive system of
Bolbosoma.

**BOX 16C   Characteristics
of the Subclass
Acanthocephala
(Phylum Rotifera)**

1. Triploblastic, bilateral, unsegmented
   blastocoelomates

2. Gut absent

3. Anterior end with hook-bearing proboscis

4. Tegument and muscles contain a unique system of
   channels called the lacunar system

5. Protonephridia absent except in a few species

6. With unique system of ligaments and ligament sacs
   partially partitioning the body cavity

7. With unique hydraulic structures called lemnisci that
   facilitate extension of proboscis

8. Gonochoristic

9. With acanthor larva

10. With modified spiral cleavage

11. All are obligate parasites in guts of vertebrates;
    many have complex life cycles.

system (Figure 16.11C). The tegumental channels near
the body surface may facilitate pinocytosis of nutrients
from the host. The body wall organization is such that
each species has a distinct external appearance; some
even appear to be segmented, but they are not.

At the junction of the proboscis and trunk, the epi-
dermis extends inward as a pair of hydraulic sacs
(**lemnisci**) that facilitate extension of the proboscis, as
in free-living rotifers; the proboscis is withdrawn by
retractor muscles. The lemnisci are continuous with
each other and with a ring-shaped canal near the an-
terior end of the body, whereas their distal ends float
free in the blastocoelom. This arrangement may help
to circulate nutrients and oxygen from the body to the

proboscis, although the actual function of the lemnisci is not known.

One or two large sacs lined with connective tissue arise from the rear wall of the proboscis receptacle and extend posteriorly in the body. These structures support the reproductive organs and divide the body into dorsal and ventral **ligament sacs** in the archiacanthocephalans and eoacanthocephalans, or produce a single ligament sac down the center of the body cavity in the palaeacanthocephalans (Figure 16.11D,E). Within the walls of these sacs are strands of fibrous tissue—the ligaments—that may represent remnants of the gut. The space between these internal organs is presumably a blastocoelom.

The body is supported by the fibrous tegument and the hydrostatic qualities of the blastocoelom and lacunar system. The muscles and ligament sacs add some structural integrity to this support system and canals of the lacunar system penetrate most of the muscles.

Circulation, Gas Exchange, and Excretion

Exchanges of nutrients, gases, and waste products occur by diffusion across the body wall (some Archiacanthocephala possess a pair of protonephridia and a small bladder). Internal transport is by diffusion within the body cavity and by the lacunar system, the latter functioning as a unique sort of circulatory system, which permeates most body tissues. The lacunar fluid is moved about by action of the body wall muscles.

Nervous System

As in many obligate endoparasites, the nervous system and the sense organs of acanthocephalans are greatly reduced. A cerebral ganglion lies within the proboscis receptacle (Figure 16.11C) and gives rise to nerves to the body wall muscles, the proboscis, and the genital regions. Males possess a pair of genital ganglia. The proboscis bears several structures that are presumed to be tactile receptors, and small sensory pores occur at the tip and base of the proboscis. Males have what appear to be sense organs in the genital area, especially on the penis.

Reproduction and Development

Acanthocephalans are gonochoristic and females are generally somewhat larger than males. In both sexes, the reproductive systems are associated with the ligament sacs (Figure 16.11E). In males, paired testes (usually arranged in tandem) lie within a ligament sac and are drained by sperm ducts to a common seminal vesicle. Entering the seminal vesicle or the sperm ducts are six or eight cement glands, whose secretions serve to plug the female genital pore following copulation. When nephridia are present, they also drain into this system. The seminal vesicle leads to an eversible penis, which lies within a genital bursa connected to the gonopore. This gonopore is often called a cloacal pore, because the bursa appears to be a remnant of the hindgut.
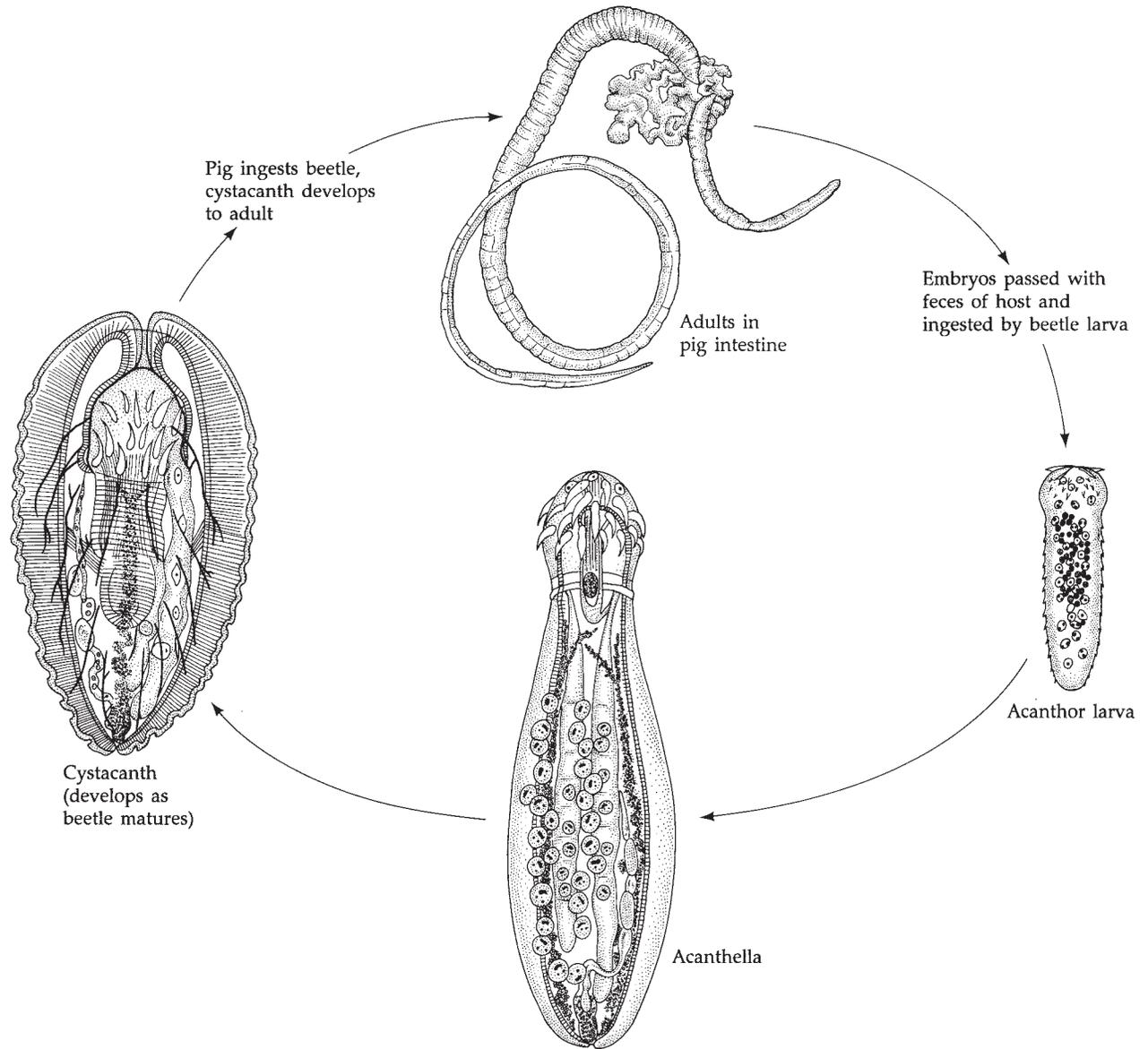
In females, a single mass of ovarian tissue forms within a ligament sac. Clumps of immature ova are released from this transient ovary and enter the body cavity, where they mature and are eventually fertilized. The female reproductive system comprises a gonopore, a vagina, and an elongate uterus that terminates internally in a complex open funnel called the **uterine bell** (Figure 16.11E). During mating the male everts the copulatory bursa and attaches it to the female gonopore. The penis is inserted into the vagina, sperm are transferred, and the vagina neatly capped with cement. Sperm then travel up the female system, enter the body cavity through the uterine bell, and fertilize the eggs.

Much of the early development of acanthocephalans takes place within the body cavity of the female. Cleavage is holoblastic, unequal, and likened to a highly modified spiral pattern. A stereoblastula is produced, at which time the cell membranes break down to yield a syncytial condition. Eventually, a shelled **acanthor larva** is formed (Figure 16.12). The embryo leaves the mother's body at this (or an earlier) stage. Remarkably, the uterine bell "sorts" through the developing embryos by manipulating them with its muscular funnel; it accepts only the appropriate embryos into the uterus. Embryos in earlier stages are rejected and pushed back into the body cavity, where they continue development. The selected embryos pass through the uterus and out the genital pore and are eventually released with the host's feces.

Once outside the definitive host, the developing acanthocephalan must be ingested by an arthropod intermediate host—usually an insect or a crustacean—to continue its life cycle. The acanthor larva penetrates the gut wall of the intermediate host and enters the body cavity, where it develops into an **acanthella** and then into an encapsulated form called a **cystacanth** (Figure 16.12). When the intermediate host is eaten by an appropriate definitive host, the cystacanth attaches to the intestinal wall of the host and matures into an adult.

Phylum Micrognathozoa: The Micrognathozoans

A new microscopic animal, *Limnognathia maerski,* was described in 2000 by Reinhardt Kristensen and Peter Funch from a cold spring at Disko Island, West Greenland. Due to the numerous unique features of this new microscopic animal, a new monotypic class, Micrognathozoa (Greek, *micro,* "small," *gnathos,* "jaw"; *zoa,* "animal") was erected. Though *L. maerski* shows

Figure 16.12   Life cycle of *Macracanthorhynchus hirudinaceus*, an intestinal parasite in pigs. The adults reside in the intestine of the definitive host and embryos are released with the host's feces. The encapsulated embryos are ingested by the secondary host, in this case, beetle larvae. Within the secondary host, the embryo passes through the acanthor and acanthella stages while the beetle grows, eventually becoming a cystacanth. When the beetle is ingested by a pig, the juvenile matures into an adult, thereby completing the cycle.

a superficial resemblance to microscopic annelids, its affiliation with Gnathostomulida and Rotifera was quickly established based on ultrastructural similarities of the epidermis and jaws. Jawlike structures are also found in other protostome taxa, such as the proboscises of kalyptorhynch turbellarians, in dorvilleid annelids, and aplacophoran molluscs, but studies of their ultrastructure show that none of these jaws are homologous with those of *L. maerski*. Early molecular phylogenetic studies showed that Micrognathozoa did not nest within either the two other gnathiferan phyla (Gnathostomulida and Rotifera), but next to them. For this reason, Micrognathozoa was given phylum status (Giribet et al. 2004). A later phylogenetic analysis based on transcriptomic data placed Micrognathozoa as the sister group to Rotifera (including Acanthocephala), with these two comprising the sister clade to Gnathostomulida. Micrognathozoa still includes only the single described species from Greenland, but

two later records of morphologically similar micrognathozoans from geographically widely separated freshwater creeks in Antarctica and Great Britain will most likely prove to be distinct, cryptic species when DNA analyses have been completed. In the southern Indian ocean on Ile de la Possession (Crozet Islands) micrognathozoans were found to be numerous in

Figure 16.13 Micrognathozoa:
Limnognathia maerski. (A) Ventral view.
(B) Lateral view.

lakes and rivers, whereas in the United Kingdom only a few animals have been found from a stream in southern Wales (and only in winter), as well as an animal found on a single sand grain of river sediment in Lambourn Parish, Berkshire.
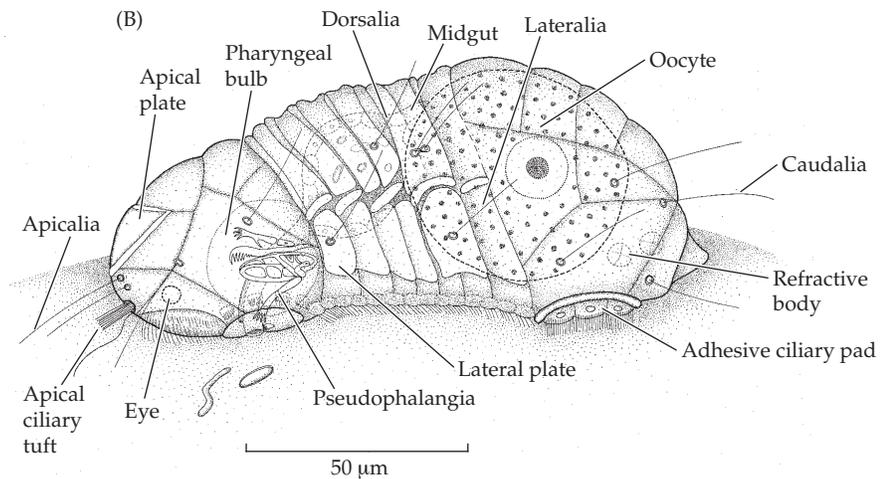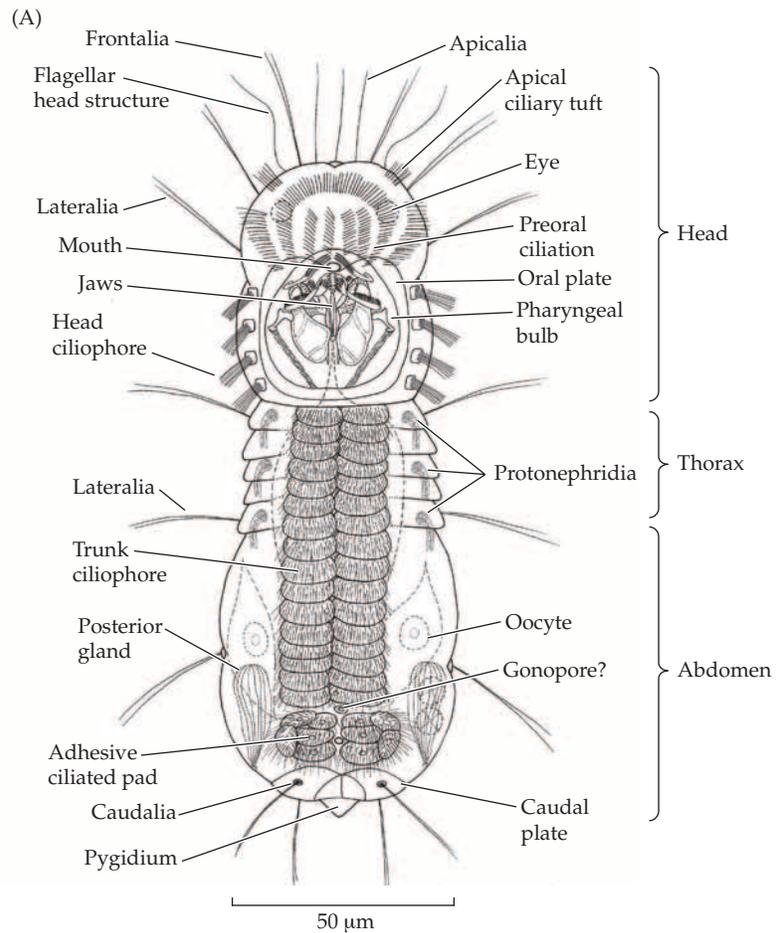
The Micrognathozoan Body Plan

Limnognathia maerski is an acoelomate animal ranging from 101 µm to 152 µm in adult length (juveniles measuring 85–107 µm in length). The adult body can be divided into three main regions: a head, an accordion-like thorax, and an abdomen (Figures 16.13 and 16.14); the head contains the prominent jaw apparatus (Box 16D).

Epidermis, Ciliation, and Body Wall Musculature

Despite their small size, micrognathozoans have a complex support system and body musculature. *Limnognathia maerski* has dorsal and lateral **epidermal plates** formed by an intracellular matrix as in rotifers and acanthocephalans (Figures 16.13 and 16.14). Ventral plates are lacking, but the "naked" epidermis has a thin extracellular glycocalyx layer and a true cuticular oral plate (described below). The animal lacks syncytia, a key character of Rotifera (and Acanthocephala); however, it possesses a unique form of gap junctions showing transverse electron dense bands in a zipper-like pattern (we call these **zip-junctions**) between the dorsal epidermal cells.

The ventral ciliation consists of an arched preoral ciliary field, four pairs of head **ciliophores** (synchronously beating multiciliated cells) surrounding the pharyngeal bulb, 18 pairs of ventral ciliophores located at the thorax and abdomen, and a posterior adhesive ciliary pad (Figure 16.13). The ventral paired ciliophores form the locomotory organ and are characterized by very long ciliary roots, originally mistaken for cross-striated muscles. These cells are highly similar to ciliophores found in the interstitial microscopic annelids *Diurodrilus* and *Neotenotrocha*. An adhesive ciliary pad consisting of five pairs of multiciliated cells is located posteriorly on the ventral side. A midventral pore exists between the clusters of ciliated cells, which may represent the female gonopore of the paired oviducts seemingly having a midventral common opening. The ciliary pad is very different from the adhesive toes of rotifers, gastrotrichs, and annelids, and the structure may be a unique synapomorphy for Micrognathozoa.

As in many marine interstitial animals (e.g., gnathostomulids, gastrotrichs, microscopic annelids), special forms of tactile bristles or sensoria are found on the body. The tactile bristle may consist of a single sensory

BOX 16D   Characteristics of the Phylum Micrognathozoa

1. Triploblastic, bilateral, unsegmented, acoelomate
2. Epidermis with supporting dorsal and lateral plates (intracellular matrix)
3. Without a syncytial epidermis
4. Ventral ciliation consisting of preoral ciliary field and paired ciliophores (synchronously beating multiciliated cells) around mouth and along midline of thorax and abdomen
5. Sensory organs in the form of stiff monociliated cells supported by microvilli (collar receptors) and nonciliated internal eyes (phaosomes)
6. Posterior end with ciliated pad and one pair of glands
7. Mouth opening ventral, gut incomplete (the dorsal anus being temporary)
8. Pharyngeal apparatus containing complex jaw apparatus with four sets of jaw-like elements and several sets of striated muscles largely related to the fibularium and the main jaws
9. Three pairs of protonephridia with monociliated terminal cells
10. Without circulatory system or special gas exchange structures
11. Males unknown; probably parthenogenetic
12. Two female gonads in close contact with the midgut

Figure 16.14   Micrognathozoa: *Limnognathia maerski*, light micrographs. (A) Adult female with mature egg (length 0.14 mm). (B) Juvenile with relatively large thorax/smaller abdomen and immature oocyte (length 0.09 mm).

cell, the **collar receptor**, with a single cilium in the middle surrounded by 8 or 9 microvilli. Two large, posterior glands were recently revealed by immunostaining (Figures 16.13 and 16.15), which by their simple configuration and homogenous content resemble mucus-secreting glands. They might have an adhesive function, together with the ciliary pad, but they do not resemble the more complex adhesive duo gland system found in the posterior end of gastrotrichs and the interstitial annelid *Diurodrilus*. Otherwise, no epidermal glands are known from micrognathozoans.

Limnognathia maerski has an elaborate body wall musculature, comprising seven main pairs of longitudinal muscles extending from head to abdomen, and 13 pairs of oblique dorsoventral muscles localized in the thoracic and the abdominal regions (Figure 16.16). The musculature further comprises several minor posterior muscles and fine anterior forehead muscle, as well as the prominent pharyngeal muscular apparatus (Figure 16.17B). Cross-striated muscles are found in both the body wall and the jaw musculature. The three main ventral longitudinal pairs and one dorsal pair of muscles (green and turquoise muscles, Figure 16.16) span
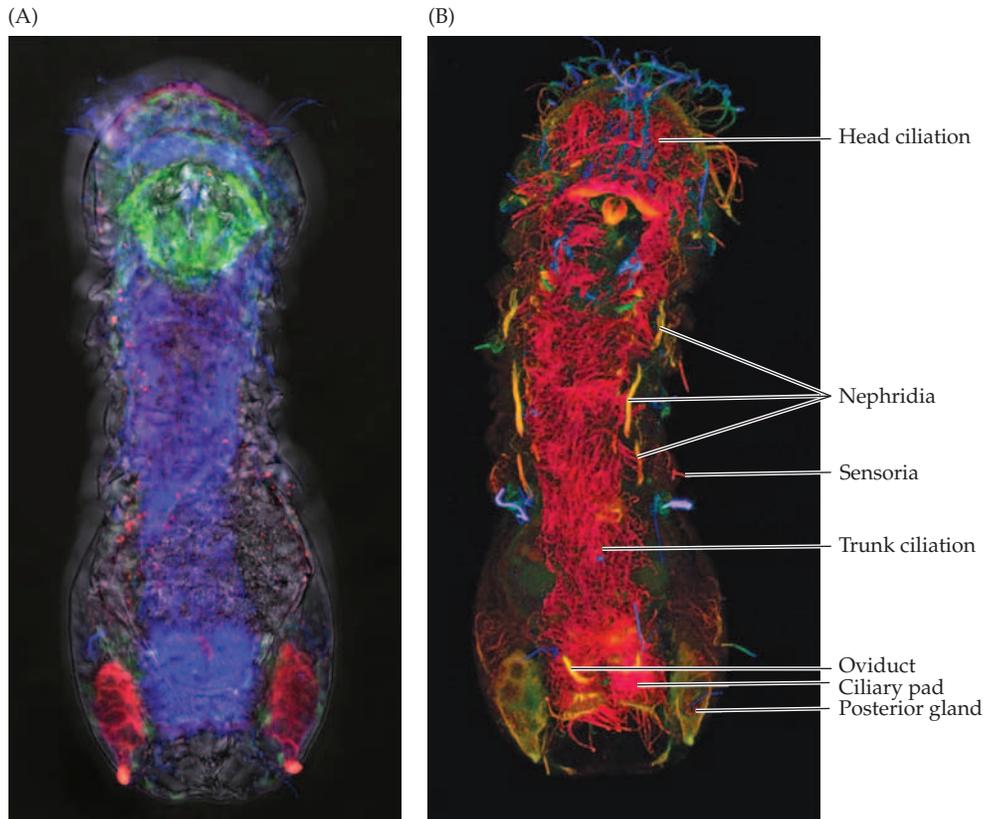
the entire length of the body, and some fibers even branch off to continue anteriorly into the head and posteriorly into the abdomen, forming a fine muscular diversification. These muscles seemingly aid longitudinal contraction and ventral bending of the body. The 13 oblique dorsoventral muscles may function together with the longitudinal muscles as supporting semicircular body wall musculature. Their close approximation to the gut further suggests they may act as gut musculature, thus possibly compensating for the lack of outer or inner circular musculature in Micrognathozoa.

Locomotion

Micrognathozoans swim in a characteristic slow spiral motion when moving freely in the water column. It is a slow movement, very different from the rotifers. From video recordings, it seems that the trunk ciliophores are used both in swimming and in epibenthic crawling or gliding motions on the substrate. Gliding is accomplished by the rows of motile ciliophores, each with multiple cilia beating in unison, in the same way as seen in the annelid *Diurodrilus*. However, the preoral ciliary field does not seem to be involved in either swimming or gliding. *Limnognathia maerski* has never been observed moving backwards (as is common among gnathostomulids), not even when they reverse

(A)

(B)

Head ciliation

Nephridia

Sensoria

Trunk ciliation

Oviduct
Ciliary pad
Posterior gland

Figure 16.15   Micrognathozoa: confocal laser scanning microscopy images of *Limnognathia maerski*, maximum intensity projection of Z-stacks. (A) Antibody staining showing ventral ciliation in blue, pharyngeal musculature in green, posterior glands in red. (B) Depth coded projection of anti-acetylated α-tubulin immunoreactivity showing the ventral ciliation (red) and the ciliated three anterior pairs of nephridial ducts and one pair of posterior oviducts beneath the ciliary field (yellow).
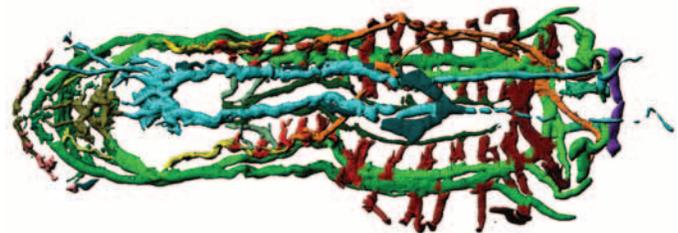
the beating of their long cilia. In addition, an escape motion has been observed where contraction of trunk muscles creates rapid jerky movements.

Pharyngeal Apparatus, Feeding, and Digestion

The mouth opens ventrally on the anterior margin of the cuticular, nonciliated oral plate and leads into the pharyngeal cavity, followed by a short esophagus dorsal to the paired jaw apparatus, then continuing into the undifferentiated, nonciliated gut. The temporary anus is located dorsally and opens only periodically, as also seen in all gnathostomulids and in some gastrotrichs.
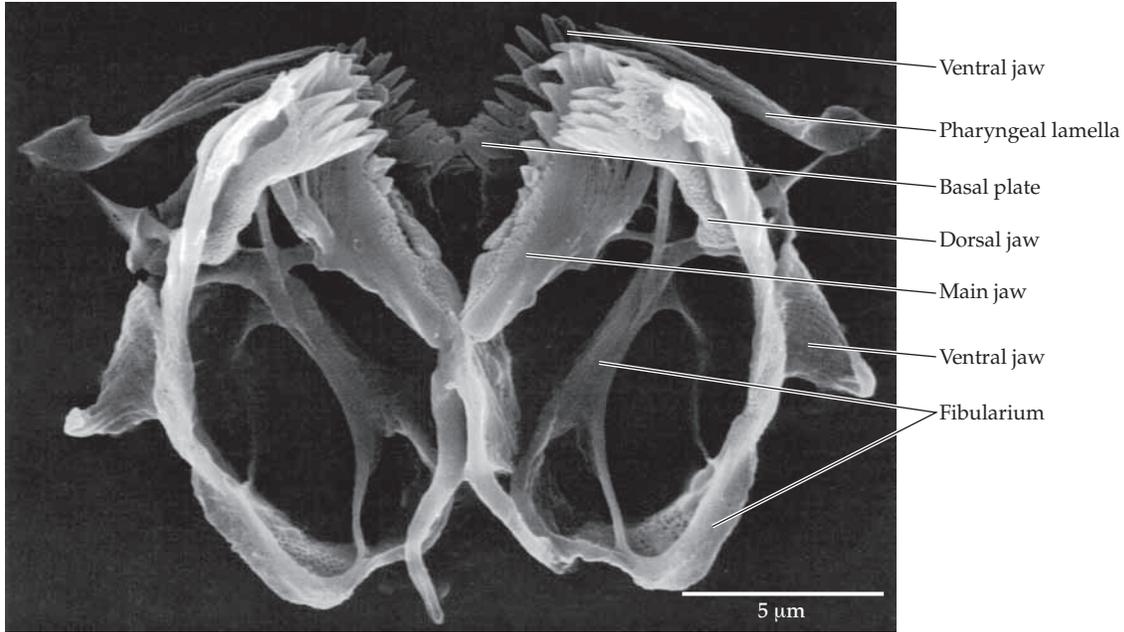
The less than 30 μm wide pharyngeal apparatus shows a complexity unseen in any other microscopic taxon, comprising numerous hard jaw parts and intricate musculature (Figure 16.17), as well as a buccal ganglion. The jaw parts comprise four main sets of sclerotonized, denticulated, hard elements (sclerites): the large paired **fibularium**, the **main jaws**, the **ventral jaws**, and the **dorsal jaws**. The largest sclerite in each jaw is the fibularium and it plays a central role in supporting the pharynx. Several subparts of the main sclerites have been described, including the anterior region of the ventral jaws called the **pseudophalangia**. So far, little is known about the functionality of this complex apparatus or the possible independent movement of all these parts, and only the pseudophalangia has been observed protruding from the mouth in fast snapping movements, possibly grasping food. The pharyngeal musculature is similarly complex and includes a major
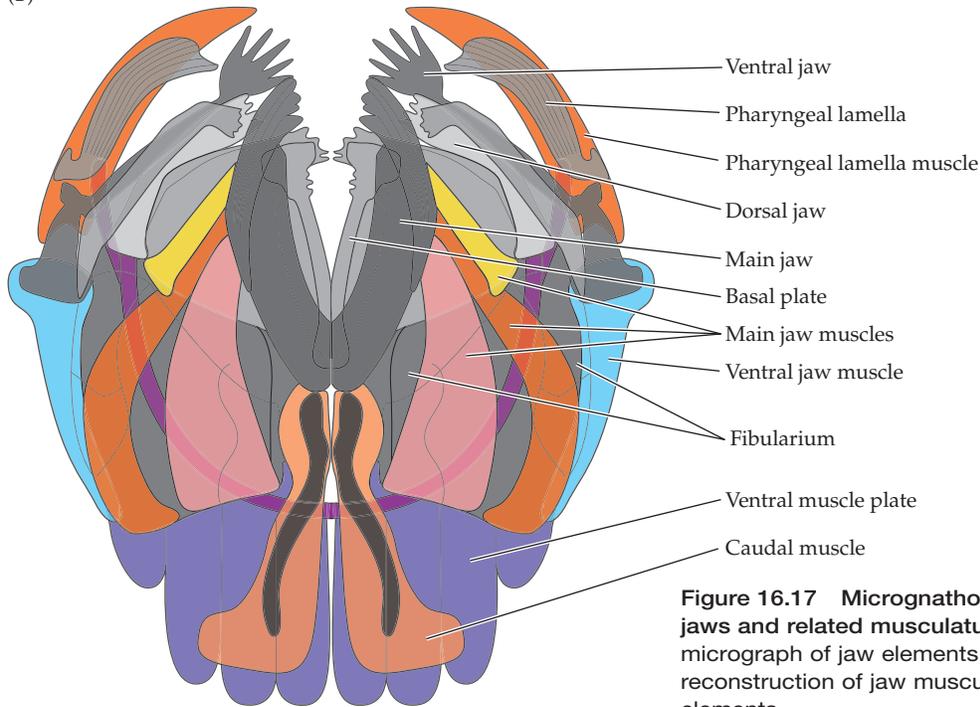

Figure 16.16   Micrognathozoa: *Limnognathia maerski* isosurface reconstruction of body wall musculature from confocal microscopy of phalloidin staining. Reconstruction showing 13 oblique dorsoventral pairs of muscles (red) and seven main pairs of longitudinal muscles: three ventral (green), two lateral (yellow and orange), and two dorsal pairs (blue) as well as additional minor muscles.
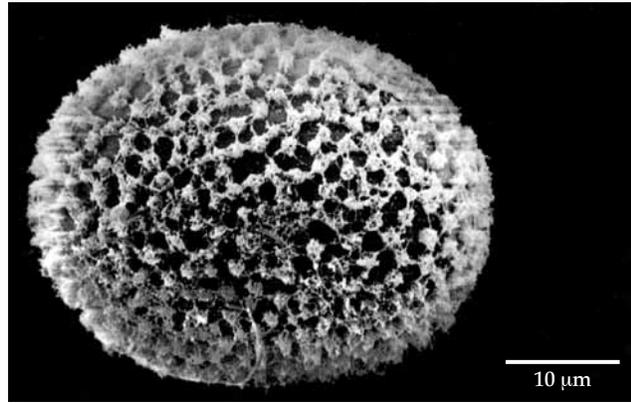
(A)

Ventral jaw
Pharyngeal lamella
Basal plate
Dorsal jaw
Main jaw
Ventral jaw
Fibularium

5 µm

(B)

Ventral jaw
Pharyngeal lamella
Pharyngeal lamella muscle
Dorsal jaw
Main jaw
Basal plate
Main jaw muscles
Ventral jaw muscle
Fibularium
Ventral muscle plate
Caudal muscle

Figure 16.17   Micrognathozoa: *Limnognathia maerski* **jaws and related musculature.** (A) Scanning electron micrograph of jaw elements, dorsal view. (B) Schematic reconstruction of jaw musculature related to specific jaw elements.

ventral muscle plate supporting (and moving) the entire jaw apparatus, as well as several other paired and unpaired striated muscles (Figure 16.17B). The ventral muscle plate is formed by 8–10 longitudinal cross striated muscle fibers (purple muscles, Figure 16.17B) underlying the fibularium and enveloping the jaws laterally and caudally. This large muscle is unique to the Micrognathozoa, being absent in other gnathiferan phyla. The many paired and unpaired muscles seem mainly related to the fibularium and the main jaws, moving the jaws as well as supplying some of the minor jaw elements such as the accessory sclerites and the pharyngeal lamellae and allowing for the extrusion of the ventral jaws. The feeding biology of micrognathozoans is not well known. The animals are found on mosses or in the sediments, and video recordings have shown the animal eating bacteria on the surfaces of mosses and sand grains.

Figure 16.18 Micrognathozoa: scanning electron micrograph of *Limnognathia maerski* sculptured winter egg.

10 μm

Circulation, Gas Exchange, and Excretion

Micrognathozoans are acoelomates with no circulatory system, and gas exchange takes place by diffusion across the epidermis. There are three pairs of protonephridia, two pairs in the thorax and one pair extending into the abdomen. The terminal cells are monociliated in contrast to the multiciliated terminal cells of Rotifera, but similar to those found in Gnathostomulida. It has been suggested that the monociliated condition is plesiomorphic within Protostomia.

Nervous System and Sense Organs

Micrognathozoa possess a seemingly simple nervous system consisting of an anterior, slightly bilobed, dorsal brain and two ventral nerve cords, extending from each of the lobes to the posterior abdomen. A large buccal ganglion is found within the pharyngeal apparatus, which may control the movement of jaw elements, and is possibly followed by a few indistinct posterior ganglia. Peripheral nerves extend from the cords, connecting to the sensory cilia. Some of these cilia are clearly monociliated collar receptors (one cilium surrounded by 8–9 microvilli), whereas others are more complex with several sensory cells involved. The terminology of the sensory structures is, from anterior to posterior: apicalia, frontalia, lateralia, dorsalia, and caudalia (Figure 16.13). In the anterior end of the animal, a pair of lateral hyaline vesicles is present. They may be unpigmented, inner eyes of the annelid type, the so-called phaosomes, and like these contain a dense layer of microvilli, but no ciliary structures.

Reproduction and Development

Only the female reproductive system has been found, suggesting the *Limnognathia maerski* is parthenogenetic. The reproductive system is anatomically simple, and it seems that the two ovaries obtain nutrition directly from the midgut, a feature also reported from freshwater chaetonotoid gastrotrichs. Though collecting has been done year round in Greenland, the species is only found during the short summer. Two egg types have been found, as in limnic gastrotrichs and rotifers, where the smooth egg may be a quick-developing summer egg and the strongly sculptured winter egg (Figure 16.18) may be a resting egg, not developing during the ten-month-long Arctic winter.

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