Introduction to Annelida and the Class Polychaeta

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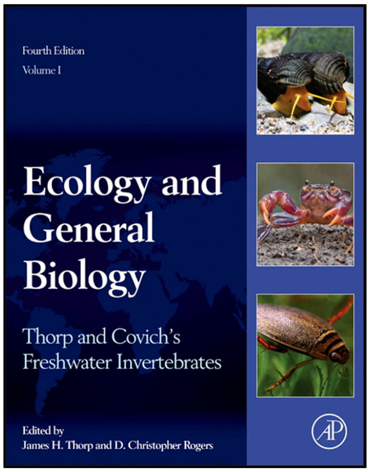

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Chapter 20

Introduction to Annelida and the Class Polychaeta

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Chapter Outline

INTRODUCTION TO INLAND WATER ANNELIDA

The annelids include terrestrial and aquatic (fresh and marine) earthworms, freshwater and marine worms, leeches, and branchiobdellids. They comprise the dominant invertebrates of the deep sea. Fresh or inland water annelids can be found in all kinds of aquatic and semi-aquatic environments, such as lakes, ponds, streams, rivers, groundwater, wet soils, and other wet habitats. Like terrestrial and marine annelids, they contribute importantly to the decomposition of organic material and as such provide an important ecosystem service. Some annelid groups, however, prey on other invertebrates, like the leeches, or are ectoparasitic or commensals, like the branchiobdellids and acanthobdellids. The latter are fish parasites. The second important ecosystem service is their role in the food web. Annelids can often be abundant and are an important food source for other invertebrates and fishes.

Annelids are discussed in four chapters of this book. The class Polychaeta, containing a large number of almost entirely marine worms, contains a few inland water species

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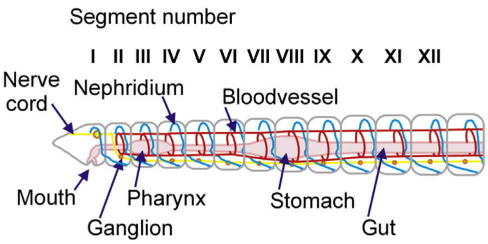

FIGURE 20.1 A typical annelid building plan.

and is dealt with separately in the second half of this chapter. Other members of the annelid group Clitellata are discussed in Chapter 21 (Oligochaeta), 22 (Branchiobdellida), and 23 (Hirudinea).

Except for the polychaetes (meaning 'many bristles'), the annelids have few bristles. There are somewhat fewer than 16,500 species presently known worldwide (Struck et al., 2007), and it is estimated that about 20,000–30,000 species exist in total. Of all annelids known today, 20–30% inhabit fresh and brackish inland waters.

All annelids can be recognized by their somewhat segmented bodies (Figure 20.1). These segments are formed by subdivisions that partially transect the body cavity. Each segment often contains the same body components, such as blood vessels, neural cords, excretion organs, and muscles. Segmentation improves the efficiency of body movement through contraction of muscles situated near the skin.

Annelids have a large and well-developed true coelom. Except in leeches, the coelom is partially subdivided by septa. The hydrostatic pressure in the coelom is maintained across segments and helps maintain body rigidity, allowing muscle contractions to bend the body without collapsing it. The internal organs of annelids are well developed and include a closed, segmentally arranged circulatory system. The digestive system is a complete tube with mouth and anus. Gases are exchanged through the skin, or sometimes through specialized gills or modified parapodia. Each segment typically contains a pair of nephridia. The nervous system includes a pair of cephalic ganglia attached to double nerve cords that run the length of the animal along the ventral body wall, with ganglia and branches in each segment. Annelids have some combination of tactile organs, chemoreceptors, balance receptors, and photoreceptors; some forms have fairly well-developed eyes, including lenses.

Annelids may be monoecious (with male and female reproductive organs) or dioecious (with male or female reproductive organs both not both). Some annelids, like the naidids, also reproduce asexually. Larva may or may not be present; but if present, they are of the trochophore type. Annelids egg development places them into the protostomes, where the spiral cleavage is determinate, meaning that the fate of the cells is determined as they are formed.

General Systematics

Annelida is an ancient and ecologically important animal phylum. In recent years several classifications have been proposed for annelids, including the division of the phylum Annelida into two subphyla, the Aclitellata (with the two classes Aphanoneura and Polychaeta [mostly marine worms]) and the Clitellata (including the classes Oligochaeta, Hirudinea, Acanthobdellida, and Branchiobdellida). Because the Aclitellata is a general term established only as an equivalent ranking to the Clitellata and is not based on phylogenetic studies, perhaps it would be best to refer to the two groupings as clitellates and non-clitellates (Wetzel and Kathman, 2002). The Clitellata and non-Clitellata are discussed in the first and last parts of this chapter, respectively. General information on this group relies heavily on material discussed in Wetzel and Kathman (2002).

The Clitellata include all segmented worms (Annelida) that possess a clitellum. This modification of the epidermis develops as a glandular girdle partly behind the female pores and secretes a cocoon in which eggs are laid (Martin et al., 2008). Among the annelids, they are commonly distinguished from the Polychaeta by their relative lack of chaetae (Brinkhurst, 1982a) and other distinctive features such as hermaphroditism, the organization of the reproductive system, and sperm ultrastructure (Westheide, 1997). Clitellates are most often divided into the oligochaetes (sludge worms, earthworms), branchiobdellids (ectoparasites/commensals of freshwater crayfish), and leeches (Brusca and Brusca, 2003).

Oligochaeta Sensu Stricto *(Sludge and Earthworms)*

Oligochaetes *sensu stricto* (=s.s.) are the most diverse and widely distributed group of annelids in all kinds of terrestrial and aquatic habitats. To date, approximately 5000 valid species of oligochaetes are described worldwide, of which about 1100 live in freshwaters. They represent more than 30 families of which about 23 occur in freshwaters. The Oligochaetes s.s. occur in marine, estuarine, freshwater, and terrestrial environments (Martin et al., 2008). About two-thirds of the species belong to the 'earthworm' families (Erseus, 2005) and are loosely termed 'megadriles' (Brinkhurst, 1982b). These earthworms all belong to the taxon Crassiclitellata (Jamieson, 1988), of which 10 families are predominantly terrestrial (the Terrimegadrili), and 4 families include species that occur in aquatic or semi-aquatic habitats (the Aquamegadrili with the families Almidae, Biwadrilidae, Lutodrilidae, and Sparganophilidae; Martin et al., 2008). One-third of the Oligochaeta s.s. species belong to the thin, slender, so-called 'microdriles' and comprise 13 families. Most microdriles are fully aquatic, with the exception of the Enchytraeidae, a family that is primarily terrestrial. Of the 650 described species in this family, 200 are aquatic, 150 are marine, and the remaining taxa are terrestrial (Martin et al., 2008).

Hirudinea (Leeches)

The Hirudinea, or true leeches, are highly specialized clitellates, separated from other annelid groups by the presence of an anterior circumoral sucker and a posterior ventral sucker. They represent a relatively small monophyletic group of annelids. They exhibit a marked scope of diversity, including ectocommensalism, parasitic sanguivory, and predatory life-history strategies, as well as a variety of reproductive behaviors (Apakupakul et al., 1999). The two orders Rhynchobdellida and Arhynchobdellida are distinguished by the possession of a protrusible muscular proboscis in the former and its absence in the latter. The order Arhynchobdellida comprises two suborders, Erpobdelliformes and Hirudiniformes, with the families Erpobdellidae, Haemopidae, and Haemadipsidae. The families Glossiphoniidae, Ozobranchidae, and Piscicolidae constitute the order Rhynchobdellida.

Leeches are characterized by 33 or 34 segments, no chaetae or septa, totally reduced parapodia, unpaired male and female genital openings in the region of the glandulose belt called the clitellum, two pairs of suckers, and other characteristics. Hirudinea are hermaphroditic. Each somite or primitive segment is superficially divided into usually 3–5, but sometimes more than 10, annuli. The coelomic cavity is transformed into a contiguous system of channels.

Although leeches primarily are restricted to freshwater, several species occur in estuarine, marine, and terrestrial environments, and they are found on all continents. They reproduce by eggs deposited in cocoons secreted by the clitellum. Their ontogeny is direct, without larval stages. Many leeches are blood-sucking on vertebrates or invertebrates; the others are mainly predators, rarely scavengers (Sket and Trontelj, 2008).

Acanthobdellida

Acanthobdellida consists of primitive leeches that possess a combination of oligochaetous- and hirudinean-like affinities (leeches with chaetae), suggesting their intermediate role between Oligochaeta and Euhirudinea. Some systematists consider this group to be an order within the class Hirudinea (Brinkhurst and Gelder, 1989). Acanthobdellidans are permanent parasites of coldwater fishes, especially salmonids and thymallids. The species all are restricted in their distribution to the extreme northern parts of the northern hemisphere. Two species are known from this group: *Acanthobdella peledina* and *Acanthobdella livanowi*. The latter is limited to the fresh waters of Kamchatka and Chukotka Peninsulas, and its biology is poorly studied (Kaygorodova et al., 2012). The former has a wide range of habitats at high latitudes of the Northern Palearctic, from Norway on the west to the Kolyma region on the east and in North America (Kaygorodova et al., 2012).

Branchiobdellae (or Branchiobdellida)

Branchiobdellidans are leech-like obligate ectosymbionts of primarily Holarctic crayfishes (Gelder, 1996) inhabiting either the host's external surface or, more rarely, its gill chambers. They currently comprise a single family-order (Branchiobdellida), although their taxonomic ranking has ranged from subfamily to class. Branchiobdellida contains one family, Branchiobdellidae, with four subfamilies, Branchiobdellinae, Bdellodrilinae, Cambarincolinae, and Xironodrilinae; 22 genera; and about 140 species (Gelder, in preparation). Some species are widely distributed while others are endemic to very small areas, often a single watershed.

Phylogenetic Relationships

The phylum Annelida is divided into two subphyla, the Aclitellata (with the two classes Aphanoneura and the mostly marine Polychaeta) and the Clitellata (including the classes Oligochaeta, Hirudinea, and Acanthobdellida, and the class or order Branchiobdellida). The Oligochaeta have long been suspected on morphological grounds to be a paraphyletic group, unless it includes branchiobdellids and leeches (Erseus, 1987; Martin et al., 2008). This paraphyly was recently confirmed by molecular analyses (Martin, 2001; Siddall et al., 2001), so that Clitellata has become synonymous with 'Oligochaeta.' The subphylum Oligochaeta thus includes the Oligochaeta *sensu stricto*, the branchiobdellids, the acanthobdellids, and the leeches (Sket and Trontelj, 2007).

The Clitellata are derived annelids, thus rendering 'Polychaeta' paraphyletic. In contrast, a different evolutionary scheme evolves based on morphological characters. In general, several studies have shown that the deep evolutionary relationships of diversified groups, such as Annelida, are hard to disentangle. Recent studies have not supported the monophyly of either Annelida or Polychaeta. The lack of a phylogenetic signal in the deepest part of the evolutionary tree supports the hypothesis that during the Cambrian, a period of fast diversification took place. This 'explosive radiation' of annelids is referred to by several authors (see among others Rousset et al., 2007). Such fast diversification results in very short branches, which in combination with differences in evolutionary rates in other parts of the tree, contribute to difficulties with the deepest clades of Annelida (Rousset et al., 2007).

Recent studies within the Clittelata suggested that (1) lumbriculids and branchiobdellidans may be a monophyly; (2) hirudineans and oligochaetes belong to a single taxon; (3) branchiobdellidans and hirudineans are a single group; (4) naidids are part of the tubificids; and (5) other possible similar relationships may exist. To date, nothing definitive has been established for these clitellate worms, but there

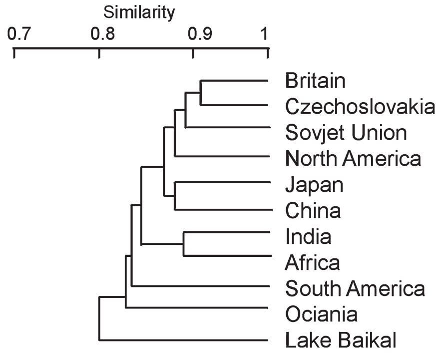

FIGURE 20.2 Faunal similarity of microdrile oligochaetes in different regions of the world. *Redrawn after Wang and Liang, 1997.*

is much ongoing research and debate about phylogeny (Wetzel and Kathman, 2002).

Struck et al. (2007) suggested that the previously considered separate phyla of Echiura and Sipuncula ('peanut worms') belong to the Annelida based on molecular data analysis.

Distribution and Diversity

Distribution

Wang and Liang (1997) performed an interesting analysis on the microdrile oligochaetes of the world. He used 'fuzzy clustering' to group 94 genera on the basis of their geographic distribution (Figure 20.2). About half of all genera appeared to be widely distributed while the other half was limited in their distribution. More specifically, Wang distinguished cosmopolitan genera, thermophilous forms (mainly tropical regions), Holarctic (including Lake Baikal), genera mainly occurring in America and Africa, and finally endemics that were restricted to North America, South America, Africa, Lake Baikal, Oceania, the former Soviet Union, and Japan. The microdile fauna of Lake Baikal is more or less independent due to its long existence and stability. In general, the naidids were more cosmopolitan in their distribution in comparison to all other, more geographically restricted families. He further showed a relationship between the number of genera and latitude as well as with area.

Omodeo (2009) distinguished three superfamilies within the megadrile oligochaetes: Lumbricoidea, Megascolecidae, and Eudriloidea. Within the Lumbricoidea, the aquatic genera are divided into the holarctic family Criodrilidae; the Glyphidrilidae inhabiting South Africa, southern Asia, and South America; and the Almidae with the Ethiopian genus *Alma*. The superfamily of Megascolecoidea comprises the four families Ocnerodrilidae, Acanthodrilidae, Octochaetidae, and Megascolecidae. The Ocnerodrilidae are comprised of small individuals that are mostly aquatic or semiaquatic and simply organized (Jamieson, 1974). The Eudriloidea inhabit intertropical Africa.

The Hirudinea comprises the taxa Achaetobdellae, Euhirudinea, and Hirudinida. About 15% of the 680 described species are marine and slightly fewer have switched to terrestrial life; the remainder are freshwater and are divided among 91 genera (Sket and Trontelj, 2008). They are globally distributed on all continents except Antarctica. The Hirudinea reach the highest diversity in the Holarctic region with one-half of all continental species. Known areas of local endemism are the ancient Siberian Lake Baikal and Lake Ohrid (about 10 species each) on the Balkan Peninsula, which is an endemicity area in itself (Sket and Trontelj, 2008). Species diversity is relatively evenly distributed among four major hirudinean clades, the proboscis-bearing Piscicolidae and Glossiphoniidae, the jawed Hirudiniformes, and the predaceous Erpobdelliformes (Sket and Trontelj, 2008).

Finally, the branchiobdellidans are primarily Holarctic distributed (Gelder, 1996), and the acanthobdellids occur in the Palaearctic and Nearctic Region. The Rhynchobdellida are cosmopolitan. The Arhynchobdellida families each have their own wider or smaller distribution.

Evolutionary Origin

The microdrile oligochaetes originated on the ancient supercontinent Laurasia (continents of Euro-Asia [including Japan] and North America), which did not differ much from the former supercontinent Gondwana, except for South America and Oceania (Figure 20.3). The reason is that each continent of Gondwana (except Oceania and South America) was connected to one continent of Laurasia, which enabled microdriles to migrate between both continents during a long period of time. Of the three superfamilies—Lumbricoidea, Megascolecoidea, and Eudriloidea—of the megadrile oligochaetes, the first is the most primitive one (Omodeo, 2009). The Lumbricoidea were limicolous and distributed over a broad territory corresponding to the northern and central regions of the Lower Triassic Pangaea. These megadriles may have been divided into a northern strain that originated in Laurasia, and a southern strain that originated in Gondwana. The Lumbricoidea differentiated at a time when the continental masses were separated during the Cretaceous. The most primitive among the Megascolecoidea are the Ocnerodrilidae, which were mostly limnic. The geographical range of the Octochaetidae suggests that they evolved in the central region of Triassic Pangaea. The distribution of the Acanthodrilidae supports the hypothesis that they originated in southern and eastern Gondwana and then spread into the western and northern regions, but the taxon is possibly polyphyletic. The Megascolecidae are native to Australia and New Zealand; they spread northwards to Indochina and the Asian Far East as well as to the Pacific coast of North America—possibly during the Cenozoic era. The

Eudriloidea, endemic to intertropical Africa, evolved more rapidly. More generally, the evolution of megadriles is characterized by numerous instances of convergence and remarkably slow speed, but speciation events in Megascolecidae and Eudrilidae were apparently very frequent (Omodeo, 2009).

The notorious ectoparasitic bloodsucking behavior of Hirudinea might be a sophistication of a less specialized commensalism or parasitism inherited from ancestors shared with branchiobdellids and acanthobdellids. There are two putative fossils from Bavarian deposits dating from the Upper Jurassic period, about 145 million years ago (*Epitrachys rugosus* and *Palaeohirudo eichstaettensis*); neither has both the definitive caudal sucker and the ring-shaped subdivisions of the body that would define them as leeches. For a long time it was assumed that the ancestral hirudinid was a blood feeder in a freshwater environment but that the ancestral hirudiniform unequivocally was terrestrial. This reflects the conclusions that the basal-most lineages in Erpobdelliformes were amphibious, the basal form in the Hirudiniformes was terrestrial, and the arhynchobdellid ancestor cannot be determined. Moreover, even though the hirudinids and macrobdellids are aquatic as adults, their cocoons are deposited on land (e.g., moist shorelines) and hatchling leeches must find their way to nearby water when they emerge (Borda and Siddall, 2004).

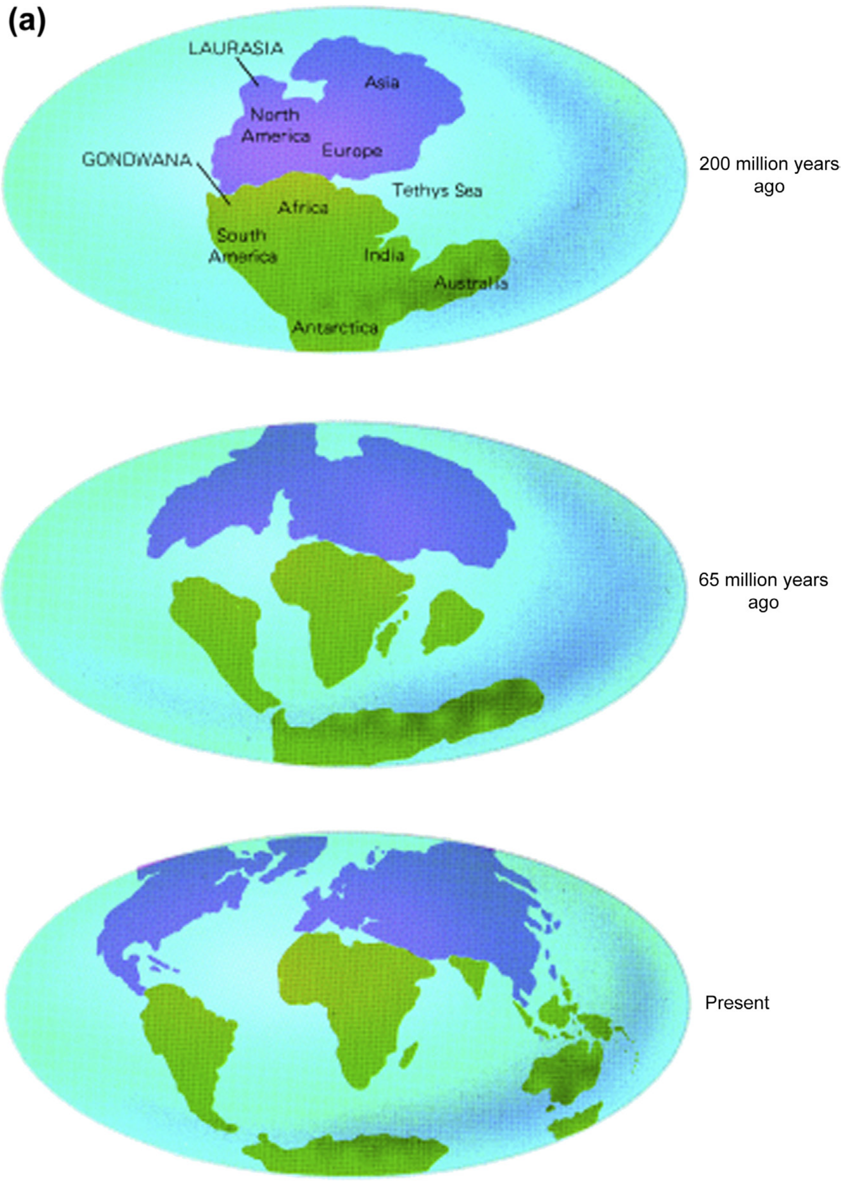

FIGURE 20.3 (a) The land masses of the earth as they may have appeared in the past and as they are today. (b) The breakup of Pangaea into Laurasia and Gondwana began about 200 million years ago. There is evidence for even earlier continental drift. *http://www.mcgraw-hill.com/site/tools/terms-of-use*.

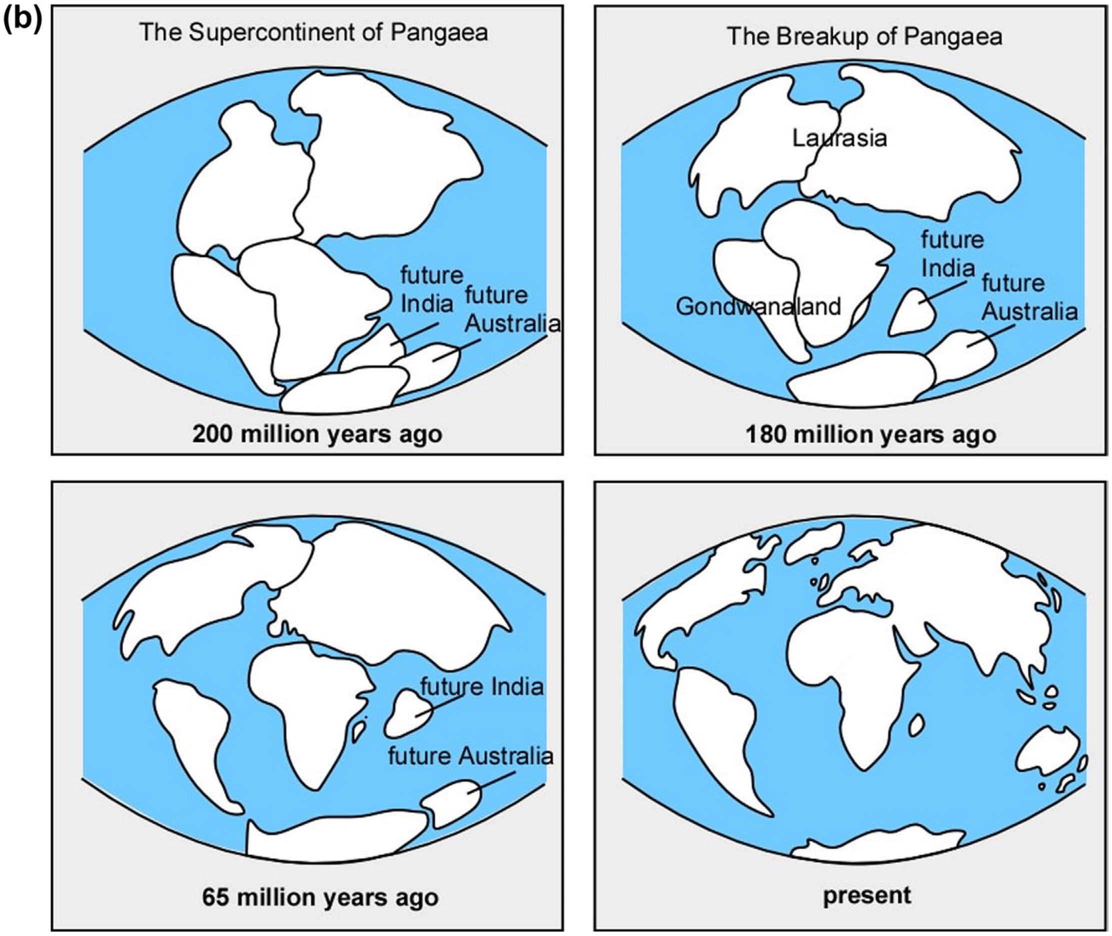

FIGURE 20.3 Cont'd

GENERAL BIOLOGY

External Anatomy

Most annelids are elongated, worm-like (vermiform), segmented animals which are cylindrical, and bilaterally symmetrical in cross-section. The prostomium is mostly small and pointed; the peristomium is sometimes fused with the prostomium. The segmentation, a serial repetition of internal and external body parts, includes a specialization of body segments for specific functions, like reproduction. The annelids range in size from much less than 1 mm in length to more than 3 m (Avel, 1959). All aquatic oligochaetes are usually very thin and small, ranging from about 1 mm to a few cm in length The smallest annelids described to date would appear to be *Neotenotrocha* (Dorvilleidae, Eunicida) reaching only a few 100 microns in length (Eibye-Jacobsen and Kristensen, 1994). Also within Eunicida may be found the largest annelid, which is ~3 m in length and ~5 cm in diameter. Some earthworms, such as the Giant Gippsland Earthworm (Megascolides australis), can reach 1 m in length. The largest leech in the world, *Haementeria ghilianii*, is found in South America and reaches more than 40 cm in length.

Members of the class Oligochaeta lack parapodia and have a reduced number of chaetae, whereas individuals in the class Hirudinea lack both lack parapodia and chaetae. The oligochaete chaetae are usually sigmoid with simple, bifid, or pectinate tips (Figure 20.4). Genital chaetae can have different and complex shapes. The length of the chaetae is higher in aquatic species. Chaetae occur in various numbers on each side of mostly all segments. Two groups of chaetae are ventral, and two groups are ventrolateral or dorsolateral in location. Chaetae arise from setal sacs, in which chaetae are secreted and from which they emerge. In these sacs, there are protractor and retractor muscles that allow the chaetae to be extended or withdrawn. The number of chaetae per bundle varies from 1 to about 25. In any case, both ventral and both dorsal bundles usually have the same number of chaetae, respectively. Genital chaetae are more often the more complex structures. Freshwater species normally have longer chaetae than terrestrial ones.

The head is positioned in the four anterior most segments. It is poorly developed and sometimes bears appendages as extension of the prostomium (in the first segment above the mouth). The head lacks sensory appendages. In

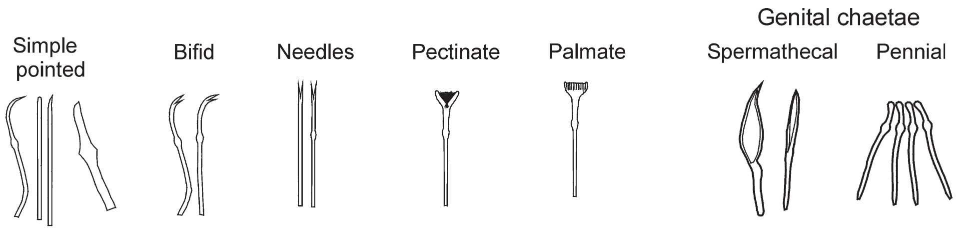

FIGURE 20.4 Oligochaeta types of chaetae.

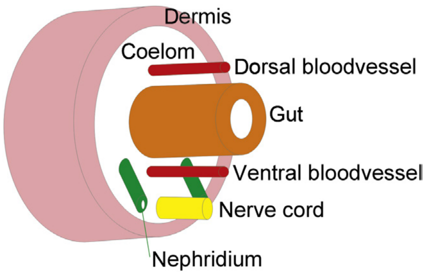

FIGURE 20.5 The oligochaete two-tube building plan.

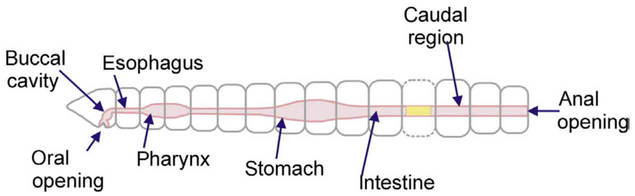

FIGURE 20.6 The oligochaete digestive track.

a few genera, like *Stylodrilus* and *Pristina*, the prostomium is drawn out into a tentacle or proboscis. The oligochaetes have a clear mouth in the first segment, and the hirudinids possess a sucker. The number of segments varies in the oligochaetes, whereas the hirudinids have 33 or 34. Apart from true segments, hirudinids bear minute annuli (one to five per segment) that should not be mistaken for additional segments. The last segment, or pygidium, bears the anus.

The structure of the body wall consists of a thin cuticle overlying an epidermal layer with mucus secreting gland cells. Circular muscles are positioned under this layer. Annelids have a body covered by an external cuticle that is never shed or molted. Epidermal microvilli secrete a network of fibers that are in part collagenous and also contain scleroprotein. Chaetae are also cuticular structures, but contain large amounts of chitin. Both classes have a clitellum in mature stage. This is a swollen region by glands that secrete mucus for copulation and cocoon formation. The position of the clitellum varies, though it is always in the anterior half of the trunk.

Internal Anatomy

Oligochaeta have a double-tube building plan (Figure 20.5). The coelom is located between the central gut and the outer skin, and is filled with fluid. As in molluscs, this coelom (fluid-filled body cavity) is divided into compartments due to segmentation. This cavity allows for increased hydrostatic pressure that is useful for locomotion, swimming, and burrowing. By shifting the coelomic fluid from segment to segment, different pressures can be effected that result in precise movements.

Beneath the epidermis and its basal lamina lies a layer of circular muscle. This muscle layer forms a nearly continuous sheath around the body, except in polychaetes with well-developed parapodia. Beneath the circular muscle layer lie thick longitudinal muscles. In many annelids the longitudinal muscles are present as four distinct bands.

The gut or digestive track is straight and relatively simple (Figure 20.6). The mouth opens into a small buccal cavity which in turn opens into a somewhat larger pharynx. In some species the pharynx can be everted to suck the food inside. The pharyngeal glands produce a salivary secretion that contains mucus and enzymes. The pharynx opens into the esophagus, a narrow tubular canal that sometimes forms a crop. In the esophagus, calciferous glands that are involved in ionic regulation are present. Their function is to regulate calcium content, carbonate concentration, and pH of the blood and coelomic fluid. The reminder of the digestive track is formed by the intestine. The anterior half of the intestine functions to promote secretion of enzymes and digestion of food, while the posterior half functions to absorb the food breakdown material and transport these to the blood. The blood vessels are situated between the intestine muscles and the epithelium. This circulatory system is present both ventrally and dorsally. Both are connected by a lateral vessel in each segment. Smaller branches transport blood into capillaries to supply organs. The dorsal vessels, which are contractile, receive blood from the intestinal sinus, and the segmented vessels and carry it anteriorly. The dorsal vessels are the principal 'engine' distributing the blood. The ventral vessels transport blood posteriorly toward the segmental vessels and the intestinal sinus. In oligochaetes, the hearts are commissural vessels in the anterior part of the body.

Two fused ventral nerve cords are located internal to the muscle layers of the body wall in most oligochaetes. Each segment has several pairs of lateral nerves which contain both sensory and motor components. Several giant nerve fibers connect in each ganglion with motor neurons that innervate the longitudinal muscles. The subpharyngeal ganglion is the principal center of movement control and dominates the succeeding ganglia. Movement is a consequence of signals from the ventral nerve cord and the sensory neurons in the body wall. The cerebral ganglion or brain is positioned further anteriorly and serves as central coordinating organ.

Though eyes are often lacking, the integument always contains isolated photoreceptors. Most oligochaetes are negatively phototactic to strong light and positively responsive to weak light. Annelids further bear chemoreceptors and tactile nerve endings.

Segments also contain metanephridia, which play an important role in water and salt balance, as described in the next section.

Physiology

Annelid respiration mainly goes through the body wall, often facilitated by a blood vessel network that sometimes contains small amounts of hemoglobin. Some groups, like tubificids and naidids, also use their alimentary canal for oxygen uptake. The sedentary living tubificids often inhabit substrates low in oxygen. In such habitats, these worms keep the anterior part of their body buried in the substrate, while the posterior part waves freely through the water column for the most oxygen uptake. In the alimentary canal, water is refreshed by cilia and gut movement. Some annelids bear external gill-like morphological structures well supplied with blood vessels.

A second adaptation to low oxygen levels is the tolerance for even prolonged periods of anoxic conditions. Tubificids then intensify the utilization of glycogen as a source of energy when the glycogen is transformed into lactic acid.

Oligochaetes excrete waste products and chemical substances using metanephridia, with ammonia being the primary nitrogenous waste. One pair of metanephridia typically occurs per segment, except at the anterior and posterior ends. The openings or nephridiopores are mostly situated at the ventrolateral side. Salt and water balances, which are particularly important in freshwater annelids, are regulated by the nephridia. Normally, the urine contains far lower concentrations of salts than do the coelomic fluid and blood. Thus, a considerable reabsorption of salts must take place in the nephridial system (Figure 20.7).

Physiological color change probably evolved de novo in the rhynchobdellid leeches. In the Hirudinea, physiological color change occurs only in certain species of the Piscicolidae and the Glossiphoniidae. The color change response normally takes about 15–30 min or longer and is profoundly affected by light in some leeches. They darken in the light and lighten in the dark. Leeches do not adapt to background colors. Temperature plays only a minor role in the color change process in leeches, and the effects vary among species. The nervous system is intimately involved in the color change process in at least some leeches. Participation by the nervous system in the color change response is probably via a neurohumoral mechanism (Sawyer and Dierst-Davies, 1974).

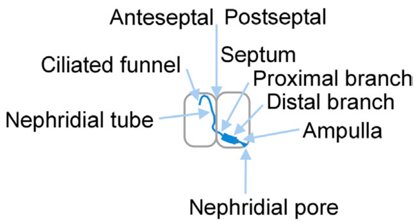

FIGURE 20.7 The oligochaete nephridial system.

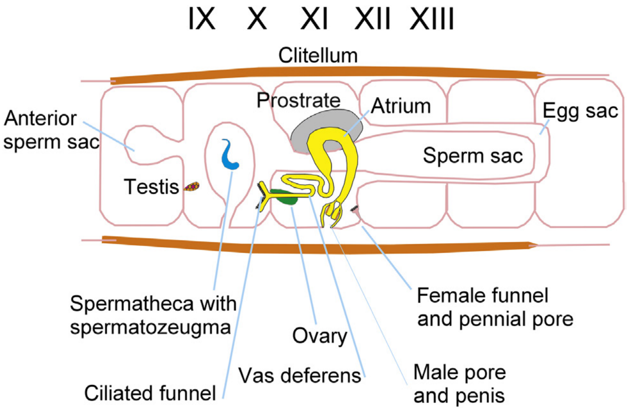

FIGURE 20.8 The Tubificidae sexual organs.

Reproduction

Annelids reproduce both sexually and asexually. Sexual reproduction is most common among all main families of Oligochaeta and Hirudinea. During copulation, two mature, hermaphroditic animals embrace in such a way that their heads face opposite directions. In this position the male genital pores are opposite to the spermathecal opening of the other (Figure 20.8). Copulatory structures, modified musculature of the body and genital chaetae, assist in the exchange of spermatozoa. In some families, accessory glands produce a secretion that 'glues' partners together. Copulation last about 5–10 min. The spermatozoa are stored in the spermatheca until the cocoons are laid. Cocoons are formed by a clitellar gland secretion produced in the clitellum that acts as cocoon membrane. The membrane initially is elastic and transparent. By contractions of the body wall musculature, the membrane slides toward the head. When passing the female genital pore, the eggs are pushed into it; and when passing the spermathecal opening, the spermatozoa are added. The fully formed cocoon is deposited in the upper layer of the substrate or attached to hard material, like macrophytes. After the cocoon is deposited, it hardens when the membrane becomes chitinous and takes a distinctive shape. Cocoons can include up to 40 eggs. The cocoons are deposited a considerable time period after copulation because the female reproductive system takes longer to develop. Cross-fertilization is common in annelids, but self-fertilization may also occur. The timing of sexual reproduction varies widely among annelid species in response to different environmental conditions. Some produce cocoons throughout the year, whereas others are limited to specific weeks.

In naidids, asexual reproduction (mostly by paratomy) is considered the dominant type, while sexual reproduction occurs rarely and then only sporadically. Early in the twentieth century, Piguet (1906) observed that sexual reproduction of some species occurred seasonally in certain sites. To survive periods of unfavorable conditions, especially droughts, protective cocoons allow populations to resist stress and recover once favorable environmental conditions return. The cocoon is an effective trait adaptation to survive adverse conditions. In this regard, the cocoons of naidids in extreme habitats are analogous to the gemmules of sponges, the resting eggs of rotifers, and the ephippia of cladocerans (Parish, 1981). Christensen (1984) showed that a great variety of asexual reproductive modes are known among aquatic oligochaetes. He distinguished four main types of asexual modes and indicated the genetic and ecological implications, as follows. First, the often expressed expectations of a strong predominance of one particularly adaptive genotype are not born out. Second, in most cases, a number of genetically distinct clones are present in each population, and they show a strong differential distribution in heterogeneous environments, indicating an effective exploitation of the available resources. Third, most cases of asexual propagation are reproductive strategies of their own and not escape mechanisms. And finally, the mechanisms underlying asexual propagation are complex and involve many aspects of the life history.

The ability of tubificids to reproduce parthenogenetically following, or in place of, bisexual reproduction has been shown (Poddubnaya, 1984). During parthenogenesis, the spermatogenesis ceases at an early stage of sexual cell development. Together with some peculiarities of the structure of the sexual system, this rules out the possibility of self-fertilization in this family of worms.

GENERAL ECOLOGY AND BEHAVIOR

Distribution and Habitat Selection

Annelids occur in all types of stable and unstable aquatic habitats except the deep sea, hot springs, and extreme high-saline reservoirs. They live in unstable environments, like intermittent, small streams, ditches, and ponds, or other water bodies that are subject to fast and strong fluctuations in environmental conditions, including temperature, acidity, salinity, or dissolved oxygen. They can also be abundant in permanent streams, rivers, and lakes where environmental conditions are relatively stable. Of course, the species occurring in each of these two groups are not mutually exclusive. In particular, species characteristic of unstable habitats can frequently be collected in stable situations. In contrast, however, species typically occurring in stable environments are seldom collected in unstable ones (Parish, 1981).

Oligochaetes are cold-blooded animals that possess life-history strategies that enable them to distribute over large geographical areas and over a huge variety of water types. The annelids from stable fluvial environments are mostly benthic. They inhabit the sandy and silty soils with lower flows. Stones, gravel, and organic hard substrates host many fewer annelid species. Macrophytes and habitats in backwaters sustain more species and higher numbers of individuals. These macrohabitats share many habitat characteristics with lakes and ponds. In general, littoral zones contain large numbers of species and have the highest diversity. Oligochaetes occur in lakes from the upper shore to the deep central bottom. Depth is not a limiting factor; e.g., *Rhynchelmis brachycephala* occurs at a depth of 1650 m in Lake Baikal (Chekanovskaya, 1962). Lake-inhabiting oligochaetes can be grouped into inhabitants of the littoral zone, sublittoral, and profundal. Typical planktonic species are lacking, but some species can swim and are, therefore, sometimes collected among plankton. In general, the annelid species composition of the littoral zone of lakes does not differ from that of pools, ponds, marshes, and ditches. Many species of Alluroididae and Enchytraeidae are amphibious and inhabit semi-aquatic to wet terrestrial habitats.

Water bottoms that contain considerable quantities of organic material maintain the highest densities of annelids, though often in lower species diversity. Abundance of different species of annelids can, therefore, serve as indication of water quality.

Some naidids are commensal or parasitic on snails. The naidid *Schmardaella* even lives in the ureters of tree frogs.

Most leeches inhabit freshwaters, although some are marine. Only few species tolerate high current velocities. Most species occur in the littoral zones of shallow vegetated waters, like lakes, ponds, pools, reservoirs, bogs, and marshes.

Physiological Constraints

Oligochaetes are known to survive long periods of anoxia by utilizing predominately the propionate-acetate or glycolytic pathway after short-term acclimation to anoxia.

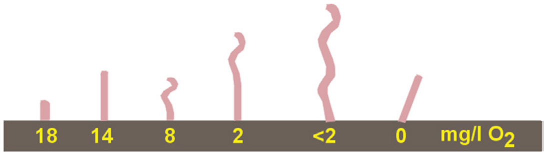

FIGURE 20.9 Wave activity of oligochaetes during decreasing oxygen concentration.

Anoxic metabolism, however, is not restricted to anoxia but can be invoked under oxic (hypoxic or aerobic) conditions and also during intense locomotory activity. The presence of hemoglobin in the blood increases the survival rate of many oligochaetes under low oxygen concentrations. Therefore, respiration is often used as a stress indicator (Figure 20.9).

Some annelids can survive drought conditions. The animal at such moments excretes a tough mucous cover that forms a cyst. This cyst can protect against both desiccation and freezing. Some leeches can burrow into the moist soil and lose as much as 90% of their body weight during dehydration and still survive.

Acid environments are more often unfavorable habitats, as worms generally need calcium to maintain a higher pH in the blood. Still, acid pools are inhabited by some specialists adapted to these extreme conditions, like the naidid *Vejdovskyella*. Leeches are also poorly represented in acid environments.

In order to survive droughts, some hirudinids will dig into the substrate, even though they may lose up to 90% of their body fluid.

Feeding Behavior

The majority of oligochaetes are scavenger feeders on dead organic matter, particularly vegetative detritus. Bottom-inhabiting oligochaetes selectively ingest particles silt- to clay-sized from the substrate, transport them vertically upward through their gut, and deposit them as feces at the sediment–water interface. This continuous activity (bioturbation) results in a change of the habitat. The top of the sediment becomes covered by fecal pellets; the underlying layer becomes more silt-clayish; and below that layer, the substrate becomes more sandy.

The tube-dwelling genus *Ripistes* feeds on fine detritus. This species has long chaetae on the sixth through eighth segments. In feeding, the anterior part of the body is extended from the tube, and the long chaetae are moved through the water column. Detritus collected on the chaetae is then periodically wiped off in the worm's mouth. Finally, the genus *Chaetogaster* has evolved several feeding modes. Some species live commensally in snails, while some others are predators on amebas, ciliates, rotifers, and trematode larvae. Predatory species suck in their prey through a pharynx contraction.

Predators and Parasites

Because annelids can occur in high numbers, they are often an important food source for macroinvertebrate and vertebrate predators. Fish that feed on annelids constitute the primary factor in population control. In the littoral zone, annelids are preyed upon by various predatory insects, flatworms, and so on. Among the annelids, the hirudinids feed on oligochaetes.

There are several parasites known to influence the life duration of oligochaetes. Among them are caryophyllaeid cestodes and the gregarinids (Sporozoa: Gregarina). All the parasites of the latter group have been found in the sperm sacs and spermiducal funnels, the coelom, and locally in the lumen of the digestive tract. Among the microsporidians (protozoa), some species of Sporozoa and Actinomyxidia parasitize oligochaetes. Of the holotrichous infusoria, *Astomata* can fill the worm body to the extent that the digestive tract is closed. The tapeworm *Archigetes* (Cestoda) can inhabit the lumen of oligochaetes. Some other oligochaetes are intermediate hosts for Cestoda. Also rotifers can be found within or on the outside of oligochaete worms. Sometimes oligochaetes are coated with infusoria (*Peritricha*) (Chekanovskaya, 1962). The actinospore infection of oligochaetes in natural waters and fish farms is related to the life-cycle of myxosporeans. Oligochaetes act as hosts for this myxosporean, which later kills the salmonid fish host.

Locomotion and Other Interspecific Interactions

Movement in oligochaetes is through peristaltic contractions. The burrowing species construct a tube of mucus-glued grains. The worms mostly are positioned upside down in this tube. Longitudinal muscle contraction is important in burrowing species when dilating the tube and anchoring the body against the tube wall. During longitudinal contraction, chaetae are extended. Circular muscle contraction and the consequent elongation of segments together with a coelomic fluid pressure pulse are most important in crawling. During circular contraction, the chaetae are retracted. Most oligochaetes can move forward and backward. The speed of movement strongly depends on the size of the animal. On average they glide 2–3 cm forward during one contraction and can move 15–30 cm/min.

Using laboratory measurements of respiration in *Tubifex tubifex*, *Limnodrilus hoffmeisteri*, and *Peloscolex multisetosus*, Chua and Brinkhurst (1973) demonstrated effects of interspecific interactions between two tubificid species. The same individuals in mixed species culture respired significantly less than in pure culture. The effector of the interaction in the one interaction between *T. tubifex* and *L. hoffmeisteri* is waterborne. Furthermore, *T. tubifex* and

L. hoffmeisteri are both attracted to the feces of *T. tubifex* rather than to those of *L. hoffmeisteri* or to a control sediment. This substantiates the hypothesis that lowered respiration and increased growth caused by mixing the two species could be due to an increase in time spent burrowing rather than feeding, when isolated species are removed from their preferred food (the feces of another species of worm). These experiments showed some of the interspecific relationships between oligochaetes.

COLLECTING ANNELIDS AND SPECIMEN PREPARATION

Collecting Annelids

Annelida can be collected with various quantitative and qualitative methods. They can be collected in qualitative numbers by using a dip- or kicknet or similar form of net, like a tea dipper or sieve. Non-swimming annelids can be collected by hand-picking with forceps from different kinds of substrates, like stones, logs, leaf packets, algal and moss clumps, or man-made items. To collect more mobile aquatic Annelida, any fine-meshed net can be drawn through a column of water either with or without submerged vegetation. The use of different techniques for collecting specimens of different substrates and habitats will yield the highest diversity of animals. The smaller the mesh size of the net, the smaller the specimens and the larger the number of annelids collected.

Quantitative collections can be performed using grabs (such as the Ekman, Ponar, Peterson, Van Veen grabs), box corers, pipe dredges, dredges, bottom samplers (like the Hess and Surber sampler), single and multiple bores, piston cores, and core samplers. Artificial substrates can be used to collect annelids, like the Hester-Dendy square or round multiple-plate samplers, and various stone or marbles basket samplers. The applicability, efficiency, effectiveness, and accuracy of each of these devices will vary between water and habitat types. Choice of sampling technique always depends on the objectives of the study.

The sample should preferably be returned to the laboratory unprocessed (live or fixed) for sorting. Sorting is done by bare eye or by use of a dissecting microscope (magnification 50×). The latter usually yields a higher diversity and number of specimens. Field sorting will yield much fewer species and specimens. This especially applies to small annelids. The use of screen-bottomed wash sieves will speed up sorting but introduces the risk of physically damaging the specimens. The use of an elutriating technique, like careful swirling and rinsing the sample, provides better results. After rinsing a sample in a bucket or container (>5 l) of water, the rinse water should be filtered through a fine mesh net or sieve. This procedure should be repeated four to nine times, depending on the amount and composition of the material. It reduces the amount of mineral and coarse organic material. The method is less appropriate to obtain quantitative results.

Some groups can best be observed alive. After collection, the annelids should be placed in a small container (cooled, except for collections from warm water habitats) for return to the laboratory. Additionally, live samples often yield whole individuals or zooid chains of naidids that often are lost when fixed. Observation of live individuals can provide a clear view of internal structures and can be a learning experience for students.

Preparation for Identification

Samples can be fixed, preferably immediately after collection, particularly in warm weather conditions or when samples contain larger amounts of degradable material. The samples and local conditions decide the usage of preservatives or fixatives. Small annelids can be preserved with ethanol. Larger annelids are fixed using a 10% end-solution of formalin, preferably buffered with something like borax or calcium or magnesium carbonate. Bouin's fluid is less widely used than formalin, but it is one of the best fixatives to use if staining and sectioning of annelid tissue is planned.

Except for the larger worms (Lumbriculidae, Sparganophilidae, and Lumbricidae), the aquatic oligochaetes should be identified using whole slide mounts and a compound microscope. The mounting media can vary, but could include Canada balsam or Amman's lactophenol.

INTRODUCTION TO THE INLAND WATER POLYCHAETA

General Introduction

Inland water (fresh and brackish water) polychaetes are, like all polychaetes, easy to recognize by the paddle-like appendages that protrude from the lateral sides of each body segment. These appendages are covered by numerous tiny hairs that contribute to movement and, in some groups, create water currents for feeding. These numerous hairs give the polychaetes their name (*poly* = many; *chaeta* = hairs).

A literature review for this chapter of Polychaeta (Annelida) including Aphanoneura (the oligochaete-like Aeolosomatidae and Potamodrilidae) living in freshwater yielded records of 168 species, 70 genera, and 24 families representing all of the major polychaete clades, but less than 2% of all species (Glasby and Timm, 2008). Worldwide, the number of real freshwater polychaetes is very low. It is estimated that fewer than 50 species seem to be restricted to freshwater habitats (Pennak, 1989). Of the 85 families of polychaetes known to occur worldwide, freshwater polychaetes can be found in the families of Nereididae, Sabellidae, Spionidae, and Histriobdellidae, as well in the former

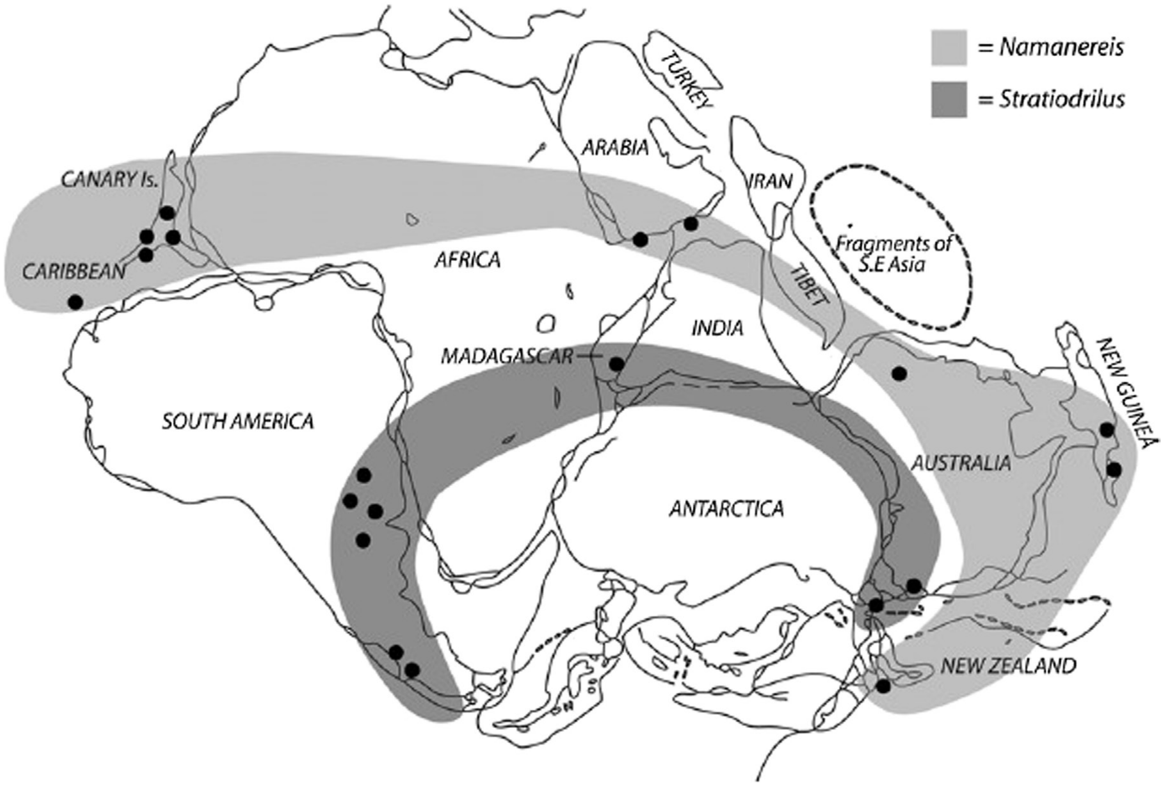

FIGURE 20.10 Distribution of species of Namanereis (Nereididae) and Stratiodrilus (Histriobdellidae) across Gondwana before its breakup in the mid to late Jurassic. *Reproduced with kind permission of Chris Glasby.*

oligochaete family, Aeolosomatidae. Most of these belong to the Nereididae, a primarily marine family. The Nereidae are known to be tolerant for high salinity fluctuations. The family Nereidae (Phyllodocida) includes 55 freshwater species, over half of which are in the subfamily Namanereinae. Fourteen other families are represented by a single species and genus. The freshwater polychaete fauna is more diversified in warmer regions than in temperate zones. More than half the nonmarine nereidids occur in the tropical and subtropical regions of the western Pacific. Higher numbers of nonmarine species are also found in Asia and South America. One remarkable feature of freshwater polychaetes is their small size. This could also be reason that they are sometimes overlooked.

Polychaetes are an ancient group dating back to the Middle Cambrian (540 million years ago), and possibly earlier. However, because they do not fossilise well—usually only the jaws, chaetae, tubes and burrows leave imprints—there are large gaps in the fossil record. Still, at least three distinct processes appear to account for the colonization of inland waters: (1) invasion of a clade prior to the break-up of Gondwana, as in *Aphanoneura*, *Namanereis*, *Stratiodrilus*, and *Caobangia*; (2) relatively recent stranding of individual species (relicts); and (3) the temporary visitation of euryhaline species (Glasby and Timm, 2008). In the latter category are several marine species that have extended their distribution range into brackish and freshwater but are unable to reproduce there. Again, the largest numbers stem from the families Nereidae and Sabellidae (Figure 20.10).

The prevailing theory is that most freshwater or brackish polychaete habitats were once geographically connected or are presently connected to the ocean (Hartman, 1959). In addition, almost all freshwater polychaetes have been collected within a range of 32 km of the ocean (Pennak, 1989), supporting a theory of recent evolution into freshwater.

More than half of all species and genera inhabit lakes and rivers, followed by lagoons, estuaries (which have a high proportion of euryhaline species), and inland seas. Less common, atypical polychaete habitats include subterranean waters, the hyporheic zone of rivers, and plant container habitats (phytotelmata) (Glasby and Timm, 2008).

In general, the non-Clitellata can be grouped into the Polychaeta and Aphanoneura, as described next.

General Systematics

Polychaeta

Three major clades of the Polychaeta (sand worms, tube worms, or clam worms) are recognized: Scolecida, Aciculata (among them Amphinomida, Eunicida, and

Phyllodocida), and Canalipalpata (with Terebellida, Spionida, Pogonophora, and Sabellida).

Polychaetes, like other members of the Annelida, have two pre-segmental regions (the prostomium and peristomium), a segmented trunk (metastomium), and a post-segmental pygidium. The nuchal organs, a pair of chemosensory structures on the posterolateral margin of the prostomium, are apparently the only synapomorphy of the Polychaeta that distinguishes them from other Annelida (Rouse and Fauchald, 1995). Nuchal organs vary from well-developed posteriorly projecting loops to inconspicuous pits or grooves. The largest nuchal organs are found in the Amphinomidae and the Euphrosinidae, where the ciliated folds on the caruncle represent the nuchal organs; in many other families nuchal organs are not easily seen.

Polychaetes exhibit a wide range of feeding strategies, ranging from those that are carnivorous predators, deposit feeders, suspension feeders, herbivores, and opportunistic feeders. A few species are parasitic, and some are commensal. Still, most inland water species are deposit feeders or scavangers (Nereididae) or suspension feeders or grazers (Sabellidae).

Polychaetes are tolerant of reduced oxygen levels or of toxic pollutants, like heavy metals. Therefore, they can be useful pollution indicators, as are the oligochaetes.

Aphanoneura

The Aphanoneura, which are head-crawling or suction-feeding worms, are regarded as aberrant canalipalpatans (a taxon of Polychaeta). They include the Aeolosomatidae, formerly aligned with the Oligochaeta, and the Potamodrilidae (Fauchald and Rouse, 1997). Aeolosomatids are minute oligochaete-like ciliated worms with no clear affinity to other polychaetes; they mostly inhabit freshwater. Like the similar potamodrilids, they lack head appendages and parapodial lobes, but may be distinguished from them by the presence of colored epidermal glands all over the body surface. The Aeolosomatidae is the only Aphanoneura family that has epidermal glands present as discrete colored spots.

Phylogenetic Relationships

For a long time the most commonly used division of the polychaetes was the separation of the 'Errantia' from the 'Sedentaria.' This division was based on a system of convenience without any evolutionary argumentation (Fauchald and Rouse, 1997). Recent cladistic analyses of Annelida and other groups have provided a new division of polychaetes into two main clades (Rouse and Fauchald, 1997): Scolecida and Palpata. The small group of Scolecida, with less than 1000 named species, composes burrowing worms with bodies reminiscent of earthworms. The majority of polychaetes belong to the Palpata. The Palpata are divided into Aciculata and Canalipalpata. Half of the polychaete species belong to the Aciculata—the group that largely comprises the former taxonomic group Errantia. The group includes major subgroups, such as Phyllodocida and Eunicida, which tend to be mobile forms with well-developed eyes and parapodia with internal supporting chaetae, or aciculae, for rapid locomotion. The Canalipalpata, a group with more than 5000 named species, is distinguished by having long grooved palp structures that are used for feeding. Canalipalpata is divided into Sabellida, Spionida, and Terebellida. Members of most of these groups live in tubes and use their palps to feed in various ways.

FIGURE 20.11 *Aeolosoma hemprichi. http://animalkingdom.su/books/item/f00/s00/z0000048/st052.shtml.*

The families Aeolosomatidae (Figure 20.11) and Potamodrilidae were placed in the subclass Aphanoneura by Timm (1981). Brinkhurst (1982) then elevated this subclass to a class, maintaining parity with the class Oligochaeta, while noting that the Oligochaeta and Hirudinea both are often considered to be subclasses of the Clitellata (Brinkhurst and Wetzel, 1984). Singer (1978) addressed the biology, ecology, physiology, and systematics of the aeolosomatids and discussed their phylogenetic affinities with other annelids. More recently, polychaete systematists have included the aeolosomatids in the Polychaeta (Fauchald and Rouse, 1997; Rouse and Fauchald, 1997). Suffice it to say that the taxonomy of the species of Aeolosoma currently needs attention. Members of the family Aeolosomatidae are widely distributed, although the difficulties encountered in the study of this family have restricted the documentation of species. Potamodrilidae is represented by a single monotypic genus, *Potamodrilus*.

Distribution and Diversity

Of the subfamily Namanereidinae (Nereididae), most of the 37 species (including three species groups) in three genera (*Lycastoides*, *Namanereis* and *Namalycastis*) are reported from habitats with reduced salinity, freshwater, or even semi-terrestrial environments (Glasby, 1999). These include *Namanereis catarractarum* from water-filled tree holes in Papua New Guinea and moist leaf axils of Pandanus trees in Fiji. Another polychaete, *Namanereis cavernicola*, occurs in a freshwater pool in a Mexican cave 1650 m above sea level and 176 km from the Pacific coast. Also, *Namanereis araps* Glasby, 1997 has been collected from groundwater in the Sultanate of Oman.

The Aeolosomatidae have a worldwide distribution and mainly are freshwater inhabitants, but can also be found in shallow brackish waters (Jørgensen and Jensen, 1978). They have been collected from ponds, lakes, and rivers from decaying plant materials (Niederlehner et al., 1984).

GENERAL BIOLOGY OF POLYCHAETA

External Anatomy

The head of a polychaete is composed of the prostomium, peristomium, and pharynx. The prostomium is the most anterior pre-segmental part of the body to the mouth, which may or may not be retractile and often bears antennae, eyes, tentacles, and palps. The antennae have sensory organs, and the palps may be sensory or can be used as feeding appendages. Some species have one or two pairs of eyes on the prostomium. The peristomium, which is the first distinct post-prostomal region or segment around the mouth, includes the tentacular cirrus (especially in ciliary feeders, which may bear a crown of tentacles that can be opened like a fan or withdrawn into the tube) and the proboscis. The latter may bear chaetae, pals, and sometimes chitnous jaws. The pharynx, which is mostly eversible, is the anterior part of digestive tract for feeding and is sometimes used for burrowing.

The body or trunk is segmented. Each segment generally has its own local nerve center called a ganglion and a pair of nephridia for excretion (Figure 20.12). Each segment also has a pair of flatlike projections, the parapodia, on both sides of each segment. The parapodia are used for locomotion and gas exchange. Parapodia are unjointed segmental extensions of the body wall found in many polychaetes, though many lack these features. They are also absent in Clitellata and Echiura. Parapodia are equipped with musculature derived mainly from the circular muscle layer and usually carry chaetae. Parapodia vary in structure but basically can be considered to consist of two elements: a dorsal notopodium and a ventral neuropodium. In addition to bundles of chaetae, notopodia and neuropodia can also have a variety of cirri and gills. The movement of the parapodia is controlled by oblique muscles that run from the midventral line to the parapodia in each segment. They are most elaborate in actively crawling or swimming species, where they form large fleshy lobes that act as paddles. Parapodia of burrowing or tubicolous polychaetes can be slightly raised ridges carrying hooked chaetae called uncini. Each parapod bears chitinous bristle-like chaetae that are used in locomotion, feeding, and tube-building. The chaetae can vary strongly and can be simple, compound, capillary, limbate, bifurcate, trifurcate, pinnate, harpoon, pectinate, or spatulate. The tail (posterior body section) is truncated or tapered and contains a dorsal or terminal anus. Cirri may also be present.

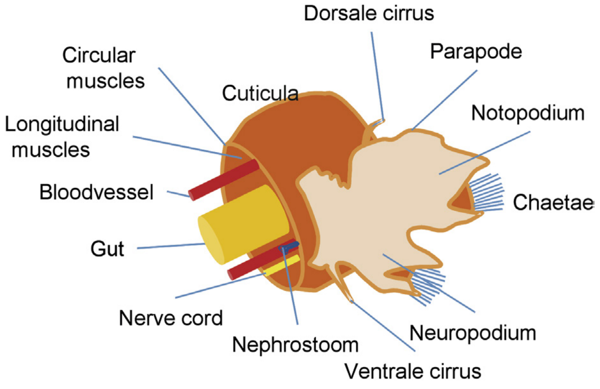

FIGURE 20.12 Anatomy of a polychaete segment.

Some polychaetes have gills. For example, the marine genus *Amphitrite* has three pairs of branched gills and long extensible tentacles, and the marine genus *Arenicola*, the burrowing lugworm, has paired gills on certain segments.

The Aeolosomatidae have a large, lobe-like prostomium that is almost completely ciliated ventrally and has lateral ciliated grooves that have been interpreted as nuchal organs. The muscular pharynx lies in the peristomium. The constrictions along the trunk give the appearance of external segmentation, but they actually represent a chain of zooids produced by fragmentation (paratomy). Parapodia are absent, and chaetae are usually present as four bundles per segment and are rarely absent. They comprise usually only capillaries, or sometimes sigmoid hooks or, rarely, only hooks. The body is often brightly colored due to the epidermal gland cells. Each gland cell consists of a vacuole, filled with red, green, blue-green, yellow, or sometimes colorless liquid; the function of the gland cells is unknown (Bunke, 1988).

The Potamodrilidae are similar to the Aeolosomatidae. In the Potamodrilidae, the prostomium fused to the peristomium, flattened, is frontally blunt, and is the peristomial part limited to lips. Antennae and palps are absent, and nuchal organs present as paired sensory papillae. All segments are similar and segmented, with parapodial structures that lack tentacular, dorsal, and ventral cirri. Also absent are gills, epidermal papillae, pygidial cirri, lateral organs, and dorsal cirrus organs. All are hair-shaped chaetae.

Internal Anatomy

Besides being segmented, the body wall of polychaetes is characterized by the presence of both circular and longitudinal muscle fibers surrounded by a moist, cellular cuticle that is secreted by an epidermal epithelium. Polychaetes have, like all annelids, a brain or cerebral ganglion that originates and usually resides in the head. The brain varies in structure, with more mobile active forms having the most complex brains, and sessile or burrowing forms having simple brains with little differentiation. The brain is connected to the ventral nerve cord by the circumpharyngeal connectives, which run down each side of the pharynx. The ventral nerve cord runs the length of the body and is usually composed of a pair of cords that are bound together. The nerve cord varies in thickness and dilates into a ganglion in each segment; from there, pairs of segmental nerves pass out to the body wall, muscles, and gut.

The polychaetes' digestive system consists of a foregut, a midgut, and a hindgut (Figure 20.13). The foregut includes a stomodeum, pharynx, and anterior esophagus. It is lined with cuticle, and the jaws, where present, are constructed of cuticular protein. The more anterior portions of the midgut secrete digestive enzymes, but absorption takes place toward the posterior end. A short hindgut connects the midgut to the exterior via the anus, which is on the pygidium.

There are six major kinds of sensory structures found in polychaetes. These include palps, antennae, eyes, statocysts, nuchal organs, and lateral organs. Palps and antennae are located on the head of many polychaetes. In some groups both are sensory, while in others the palps are used for feeding. Satocysts are balance sensory receptors. Nuchal organs are ciliated, paired, chemosensory structures, innervated from the posterior part of the brain. They are present in nearly all polychaetes, and Rouse and Fauchald (1997) suggested that they may represent an apomorphy for Polychaeta. This has been challenged by other authors, who suggest that nuchal organs may be an apomorphy for Annelida as a whole and have been lost in Clitellata/Oligochaeta (Purschke et al., 2000). Polychaetes also have various epidermal sensory cells that may be responsive to light or touch (such as lateral organs).

Most polychaetes have two fluid systems: the coelom and the circulatory system; and both (if present) are involved in excreting waste products. To achieve this excretion, there must be ducts to the exterior, and these are generally referred to as nephridia. Ducts, known as gonoducts or coelomoducts, are also required for the transfer of gametes that develop in the coelom to the outside of the body on maturity. The two different kinds of ducts are often simply referred to as segmental organs, since determining what kind of duct is present is problematic.

The circulatory system is closed in most polychaetes and Echiura, as it is in many clitellates. In some polychaete groups, however, the closed circulatory system is limited to major blood vessels and the distal capillary vessels are missing. A circulatory system is absent in many small polychaetes.

The polychaete excretory organs consist of protonephridia and mixed proto- and metanephridia in some taxa. Most polychaetes, however, have metanephridia, with one pair per segment; their interior end (nephrostome) opens into a coelomic compartment. The coelomic fluid passes into the nephrostome, and selective resorption occurs along the nephridial duct.

The families of Aeolosomatidae and Potamodrilidae have a more simple internal anatomy. As in oligochaetes, their building plan consists of a double-tube structure. The outer longitudinal muscles are grouped in bundles. The stomodaeum, at the anterior end of the middle gut, has a structure resembling a ventral buccal organ. For example in *Aeolosoma hemprichi*, it comprises the widened part of the gut in segments two to five. For the remaining species, the gut consists of a straight tube. A

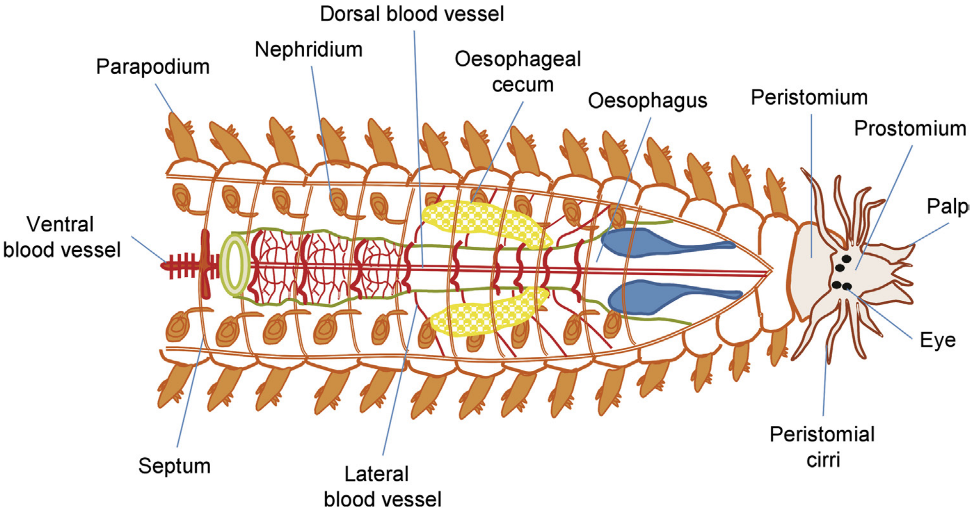

FIGURE 20.13 Dorsal view of a polychaete internal building plan. *Hartman, 1959; Kasprzak, 1984; Rouse and Pleijel, 2001.*

diaphragm or gular membrane is absent. The number of nephridia is limited to the first segments, specifically segments one and two in *Potamodrilus* and segments two to five in *A. hemprichi*. A connection between the nephridia and coelomoducts is absent. The circulatory system is closed, and a heart-like organ is absent. In *Potamodrilus*, the female gonads are situated in segment five and male gonads in segment six.

Physiology

The guts of most polychaetes are adapted anatomically and physiologically to obtain the maximum extraction of the very small proportion of organic matter from the mineral material which is often their diet. This process of food intake was well described for the marine worm *Arenicola marina* by Kermace (1955) as follows.

> *The diet contains a large inorganic indigestible portion and as is to be expected. In as far as the digestive processes of other soil eating animals are known, e.g., oligochaetes, the polychaetes share the characteristic that a large amount of digestion occurs intracellularly in wandering amoebocytes, thus leaving the gut lumen free to deal with the vast quantities of indigestible siliceous material. Therefore, the gut wall consists of four layers; (1) the outer peritoneal covering, (2) a longitudinal muscle layer, (3) a circular muscle layer and (4) an inner epithelium. There is a system of ciliary tracts, which in the glandular region of the esophagus is associated with the longitudinal ridges of the lining epithelium; and which consists of the ciliated ventral groove and lateral tracts arising from it in the post-cardiac region of the stomach, the intestine and the rectum. There are isolated patches of cilia on the walls of the cardiac region of the stomach. Movement of the cilia in these tracts is believed to keep the contents of the stomach mixed and in suspension, thus ensuring that the food particles are brought into contact with the entire epithelium. The cilia also assist the passage of food through the gut, although this is mainly brought about by the rhythmic contractions of the body wall impinging upon the latter. The esophagus is capable of a considerable amount of muscular activity and initiates some of the gut movements. Parts of the blood system of the animal lie in close proximity to the gut and as the blood system plays a part in digestion. The food passes through the trunk gut, i.e., the proboscis, esophagus, stomach and intestine, to the rectum in about 14 min in an actively feeding worm. Food is taken into the esophagus from the base of the funnel of the burrow by the constantly everting and inverting proboscis, without any preliminary sorting. It is temporarily stored in the muscular region of the esophagus, but eventually it passes to the stomach through the glandular region of the former, where mucus and a little enzyme material is poured onto it by the unicellular glands in the walls. At the junction of the esophagus and the stomach there are the openings of the esophageal pouches, the secretion from which contains mucus and Qestive enzymes. While in the stomach food particles in the sand are digested both intra- and extra-cellularly, the epithelial cells engang the food particles thus leaving the lumen of the gut filled with the large residual mass of indigestible, mostly siliceous, material. These food particles are taken from the epithelial cells by amoebocytes, which while digesting them, wander to all parts of the body in the blood and coelomic fluid. The indigestible remains of these particles are deposited by the amoebocytes in the epidermis, peritoneal cells, intravasal tissue, coelom and in the lumen of the gut…. pH values are given for different parts of the gut, only that of the stomach (pH 5.4–6.0) differing appreciably from neutrality. Changes in pH affect the viscosity of the mucus, which is least viscous in the stomach where the pH is lowest. This aids the cilia and the movements of the gut in keeping the contents of this region in suspension. Elsewhere in the gut, the mucus is more viscous and acts as a lubricant, protecting the gut wall from the abrasive action of the sand grains. An actively feeding worm defaecates at intervals of approximately 45 min.*

Diffusion of gas through the body wall accounts for part of the gas exchange. Gills are common among polychaetes and mostly associated with the parapodia. Most polychaetes have a well-developed blood–vascular circulation system. The circulation is relatively simple, as blood flows in the anterior direction through the dorsal vessel, which goes over ventral vessels on the anterior side of the body. In most segments, lateral vessels transport part of the blood toward the ventral vessel. The ventral vessel carries the blood posteriorly. Smaller vessels carry blood to the parapodia, nephridia, body wall, and gut. Polychaete blood is mostly colorless or has respiratory pigments such as hemoglobin, chlorocruorin, or hemerythrin.

Coelomic fluid that contains wastes passes through a funnel into the tubule of the metanephridia. This funnel penetrates the membrane between two segments, and then the remaining part of the metanephridia opens at the base of the neuropodium on the ventral side of the segment anterior of the funnel.

The osmoregulatory ability of polychaetes is great, especially in the Nereididae. In these tolerant species, the blood and tissue fluids are isotonic with the surrounding environment. In freshwater, however, these species remain at an internal salt concentration higher than the surrounding freshwaters. Under these conditions, the nephridia produce a urine that is hyposmotic to the coelomic fluid. The chloragogen tissue, coelomocytes, and gut wall play a supporting role in excretion.

Reproduction

Although many marine polychaetes reproduce asexually, all freshwater species reproduce sexually. Most polychaetes have separate sexes, but some crawling and swimming species are hermaphroditic. A free-swimming larval stage is typical of marine forms, but is absent in all freshwater species. The freshwater polychaetes have no permanent sex organs, and they usually have separate sexes. The reproductive system is simple with gonads that appear as temporary swellings of the peritoneum and shed their gametes into the coelom. The gametes are then carried to the outside through gonoducts, through the metanephridia, or by rupture of the body wall. Fertilization is external.

Generally, aeolosomatids reproduce by asexual transversal fission (paratomy). Reproduction begins when the worm reaches a determined number of metameres (depending on the species). This stage gives rise to the clonal production of a chain of filial zooids that detach themselves from the parental zooid in a few days (fragmentation). The doubling time of Aeolosomatidae is short and usually lies between one and four days (Inamori et al., 1990). This mode of reproduction can lead rapidly to high population densities. Sexual reproduction has been reported in only a few species (Christensen, 1984). Only one species, *Aeolosoma singulare*, is known to reproduce exclusively by sexual reproduction (Marotta et al., 2003).

GENERAL ECOLOGY AND BEHAVIOR OF POLYCHAETA

Polychaetes are often divided into two groups based on their activity: sedentary (benthic) polychaetes and errant (free-moving) polychaetes. Sedentary polychaetes spend much or all of their lifetime in tubes or permanent burrows and many of them, especially those that live in tubes, have special adaptations for respiration and feeding. Errant polychaetes include different locomotion groups: free-swimming pelagic forms, active burrowers, crawlers, and tube worms that temporarily leave their tubes for feeding or breeding. Most of these, like species of the genus *Nereis*, are predatory and equipped with jaws or teeth. Predaceous polychaetes have an eversible, muscular pharynx armed with jaws that can be thrust out with surprising speed to capture prey.

Distribution and Habitat Selection

The regions supporting the highest diversity of freshwater polychaetes are, in order, the Palaearctic, Neotropical, Oriental, Nearctic, Australasian, and Afrotropical regions. They rarely occur on oceanic islands (only Nereididae). They are essentially absent from the Antarctic region, except for *Namanereis quadraticeps*, a circum-subantarctic species found in the freshwater seep zones of the upper shores. Three further species are found in the Arctic. The species *Marenzelleria wireni*, *Manayunkia speciosa*, and *Chone* sp. have occasionally been found in tundra lakes. Note that all three arctic freshwater polychaetes are also widespread south of the Arctic. *M. wireni* is a tolerant species that occurs in a wide range of conditions. It is found in both fresh and marine waters, although it usually inhabits the less brackish part of estuaries of rivers. It also tolerates a wide range of oxygen levels and survives temporarily without oxygen. *Chone* sp. and *M. speciosa* are more restricted to freshwater habitats.

The species of the family Namanereidae are highly variable in their habitat (Williams, 2004). The occurrence in brackish water areas is common, although the range of salinity tolerated is high. The species generally prefer shallow waters and soft, calcareous fine-grained substrate, often rich in decaying plant detritus. However, as predatory worms, this detritus is not a food source.

Aeolosoma maritimum is the only marine representative of the family Aeolosomatidae. They occur in the mesopsammal of a sandy beach at the Gulf of Tunis. The salinity of the habitat ranged from 29.2‰ to 34.6‰.

Potamodrlilus fluviatilis is a typical rheophilic inhabitant of the mesopsammal. Its epidermal glands enable this species to stick itself to the substrate in high current velocities.

Physiological Constraints

The optimal temperature for growth and reproduction of *A. hemprichi* and *Aeolosoma variegatum* is 20–30 °C, and at 10 °C reproduction stops (Kamemoto and Goodnight, 1956). Various authors recorded mass presences of Aeolosomatidae, especially *A. hemprichi*, in wastewater treatment plants for sludge reduction (Liang et al., 2006).

Feeding Behavior

Polychaetes have diverse feeding habits, depending on their lifestyle. Most errant polychaetes are typically predators or scavengers, and most sedentary polychaetes feed on suspended particles, or are deposit feeders that consume sediment particles. Some species dip into the substrate with feeding tentacles, scoop up some muck, and draw it into their mouths to digest any edible particles. This occurs predominately in the tube-living polychaetes, which are primarily filter feeders. By moving their appendages within these tubes, they create a water current that draws smaller particles to their mouths. The predaceous polychaetes are often active hunters, swimming through the water and grasping prey, such as small worms or algae, with an extendible, jaw-like structure.

Little is known about the specific feeding habits of namanereidid polychaetes, but it is usually assumed they most are predatory or omnivorous. Most predaceous species have a muscular, eversible pharynx equipped with a pair of toothed, opposing jaws. The jaws of some phyllodocid polychaetes are used to capture and hold prey or to tear off pieces of algae and decaying matter, while those of some Eunicida are used for scraping food particles from hard substrates.

Aeolosomatidae feed on plant tissue, detritus, protozoa, bacteria, and algae. The particles are swept toward the mouth by ciliary currents set up at the anterior end and by a type of suction feeding. *Aeolosoma* suck fine material by placing their mouth on the substrate.

When lifting the center of the prostomium by muscular contraction, a partial vacuum is created that dislodges particles from the substrate. Potamodrilidae worms mainly feed on dead organic plant material. Their eversible pharynx bulb also provides a comparable kind of suction apparatus.

Locomotion

Polychaetes' locomotion traits, which involve extension/retraction of parapodia and chaetae, are burrowing, slow creeping (six to eight segments in one 'wavelength'), fast crawling (14 segments), and swimming.

Some *Aeolosoma* species swim with the aid of beating the cilia at the head end of the body. *Aeolosoma* forms a resistant mucous cyst stage that can easily be transported from one place to another. Potamodrilidae do not use body muscles to move; the only active movement is provided by moving cilia on the head.

Predators and Parasites

The freshwater polychaete *Manayunkia speciosa* serves as the obligate intermediate host for the myxosporean parasites *Ceratomyxa shasta* and *Parvicapsula minibicornis*, which adversely affect the survival and freshwater production of juvenile salmon in the Klamath River and elsewhere in the Pacific Northwest of the USA.

Invasive Tendencies

An interesting example of an invasive freshwater polychaete is *Hypania invalida*. This species is native in the Ponto-Caspian range, in both fresh and brackish waters. It tolerates a wide range of salinity (0–12 S), temperature (2–25 °C), and depth (from the shore line up to more than 400 m depth). *H. invalida* penetrates the European waters from three directions, using northern (the Volga catchment), central (Dnepr and Vistula catchments), and southern (the Danube catchment) corridors (Bij de Vaate et al., 2002).

COLLECTING POLYCHAETES AND SPECIMEN PREPARATION

Freshwater polychaetes are collected in much the same manner as other annelids. As with most invertebrates, searching individually for the small freshwater polychaetes in the field is not productive. If representative samples of a polychaete fauna are required, it is necessary to collect a sample of the substrate (e.g., sand, mud, algae). A grab, shovel, or corer (a cylinder that is pushed into the sediment) are mostly used to collect sediment. To facilitate sorting, Rose Bengal, which stains all living material pink, can be added to the sample. The sediment is carefully washed through a sieve, and the specimens are picked off the sieve with a forceps or the material is poured into a white tray. Next, the worms and other organisms are separated from the sediment. At this point, it is advisable to use a dissecting microscope to ensure all specimens in the sample are found.

Polychaetes should initially be preserved in 5–10% formalin (2–4% formaldehyde) or in other histological fixatives, such as Bouins fluid. Afterward, specimens should be transferred to 70% ethanol, although material preserved in high-strength (94%) alcohol is normally adequate, especially if bulk samples are elutriated to remove sediment before preservation. As color, presence of eyes, and other features are best recognized in live specimens, specimens should be observed live whenever possible. Free-living or swimming species can be collected using a hand net or by collecting macrophytes and algae, which can be placed immediately into a bag and sealed. These samples are sorted in the laboratory in the same way the sediments were sorted.

Quantitative studies of polychaete communities often involve the use of quadrats, corers, or comparable equipment that collects a specific volume of sediment. The sediment with the often-hidden fauna should then be placed in a container and returned to the laboratory for examination.

All samples should be labeled using waterproof paper and ink. When the entire sample is fixed for later sorting, such labels should be placed within the sample.

Aeolosomatids can be very small and pelagic and can be collected using plankton nets. When studying swamps, aeolosomatids can be collected by squeezing moss tufts.

When studying live specimens, one can use narcotics to relax the animal. Magnesium chloride is an effective narcotic for invertebrates at a concentration of about 7% in freshwater. Also carbonized drinking water is a cheap and effective option. Another advantage of the latter is a quick recovery from the anesthetic.

REFERENCES

Apakupakul, K., Siddall, M.E., Burreson, E.M., 1999. Higher level relationships of leeches (Annelida: Clitellata: Euhirudinea) based on morphology and gene sequences. Mol. Phylogenet. Evol. 12, 350–359.

Avel, M., 1959. Classe des anne´lides oligoche`tes. In Grasse´, P.P, (Ed.), Traite´ de Zoologie, vol. 5, No. 1. Paris, 224–462.

Bij de Vaate, A., Jazdzewski, K., Ketelaars, H.A.M., Gollasch, S., Van der Velde, G., 2002. Geographical patterns in range extension of Ponto-Caspian macroinvertebrate species in Europe. Can. J. Fish. Aquat. Sci. 59, 1159–1174.

Borda, E., Siddall, M.E., 2004. Arhynchobdellida (Annelida: Oligochaeta: Hirudinida): phylogenetic relationships and evolution. Mol. Phylogenet. Evol. 30, 213–225.

Brinkhurst, R.O., 1982. Evolution in the Annelida. Can. J. Zool. 60, 1043–1059.

Brinkhurst, R.O., 1982a. British and Other Marine and Estuarine Oligochaetes. Freshwater Biological Association. 127 pp.

Brinkhurst, R.O., 1982b. Evolution in the Annelida. Can. J. Zool. 60, 1043–1059.

Brinkhurst, R.O., Gelder, S.R., 1989. Did the lumbriculids provide the ancestors of the branchiobdellidans, acanthobdellidans and leeches? Hydrobiologia 180, 7–15.

Brinkhurst, R.O., Wetzel, M.J., 1984. Aquatic Oligochaeta of the world, supplement: a catalogue of new freshwater species, descriptions, and revisions. Suppl. Can. Tech. Rep. Hydrogr. Ocean. Sci. 44, 1–101.

Brusca, R.C., Brusca, G.J., 2003. Invertebrates, second ed. Sinauer Associates, Sunderland, Massachusetts.

Bunke, D., 1988. Aeolosomatidae and potamodrilidae. In: Higgins, R.P., Thiel, H. (Eds.), Introduction to the Study of Meiofauna. Smithsonian Institution Press, Washington, DC, pp. 345–348.

Chekanovskaya, O.V., 1962. Aquatic Oligochaeta of the USSR. Keys Fauna USSR 78, 1–513.

Christensen, B., 1984. Asexual propagation and reproductive strategies in aquatic Oligochaeta. Hydrobiologia 115, 91–95.

Chua, K.E., Brinkhurst, R.O., 1973. Evidence of interspecific interactions in the respiration of tubificid oligochaetes. J. Fish. Res. Board Can. 30, 617–622.

Eibye-Jacobsen, D., Kristensen, R.M., 1994. A new genus and species of Dorvilleidae (Annelida, Polychaeta) from Bermuda, with a phylogenetic analysis of Dorvilleidae, Iphitimidae and Dinophilidae. Zool. Scr. 23, 107–131.

Erséus, C., 1987. Phylogenetic analysis of the aquatic Oligochaeta under the principle of parsimony. Hydrobiologia 155, 75–89.

Erséus, C., 2005. Phylogeny of oligochaeteous Clitellata. Hydrobiologia 535, 357–372.

Fauchald, K., Rouse, G., 1997. Polychaete systematics: past and present. Zool. Scr. 26, 71–138.

Gelder, S.R., 1996. A review of the taxonomic nomenclature and a checklist of the species of the Branchiobdellae (Annelida: Clitellata). Proceedings of the Biological Society of Washington, 109, 653–663.

Gelder, S.R. Monograph of the Branchiobdellida (Annelida: Clitellata) or Crayfish Worms, in preparation.

Glasby, C.J., 1999. The Namanereidinae (Polychaeta: Nereididae) part 1 taxonomy and phylogeny, part 2 cladistic biogeography. Rec. Aust. Mus. Suppl. 25, 1–144.

Glasby, C.J., Timm, T., 2008. Global diversity of polychaetes (Polychaeta; Annelida) in freshwater. Hydrobiologia 595, 107–115.

Hartman, O., 1959. Capitellidae and Nereididae (marine annelids) from the Gulf side of Florida with a review of freshwater Nereidae. Bull. Mar. Sci. Gulf Caribb. 9, 153–168.

Inamori, Y., Kuniyasu, Y., Hayashi, N., Ohtake, H., Sudo, R., 1990. Monoxenic and mixed cultures of the small metazoa *Philodina erythrophthalma* and *Aeolosoma hemprichi* isolated from a waste-water treatment process. Appl. Microbiol. Biotechnol. 34, 404–407.

Jamieson, B.J.M., 1974. The zoogeography and evolution of Tasmanian Oligochaeta. In: Williams, W.D. (Ed.), Biogeography and Ecology in Tasmania. Junk, The Hague, pp. 195–228.

Jamieson, B.G.M., 1988. On the phylogeny and higher classification of the Oligochaeta. Cladistics 4, 367–410.

Jørgensen, K.F., Jensen, K., 1978. Mass occurrence of the oligochaete *Aeolosoma hemprichi* Ehrenberg in activated sludge. Biokon Reports 7, 9–11.

Kamemoto, F.I., Goodnight, C.J., 1956. The effects of various concentrations of ions on the asexual reproduction of the oligochaete *Aeolosoma hemprichi*. Trans. Am. Microsc. Soc. Invertebr. Biol. 75, 219–228.

Kasprzak, K., 1984. The previous and contemporary conceptions on phylogeny and systematic classifications of Oligochaeta (Annelida). Ann. Zool. Warszawa 38, 205–223.

Kaygorodova, I.A., Dzyuba, E.V., Pronin, N.M., 2012. Leech-like parasites (Clitellata, acanthobdellida) infecting native and endemic eastern Siberian Salmon fishes. Scientific World J. 2012, 1–8.

Kermace, D.M., 1955. The anatomy and physiology of the gut of the polychaete *Arenicola marina* (L.). Proc. Zool. Soc. Lond. 125, 347–381.

Liang, P., Huang, X., Qian, Y., 2006. Excess sludge reduction in activated sludge process through predation of *Aeolosoma hemprichi*. Biochem. Eng. J. 28, 117–122.

Marotta, R., Ferraguti, M., Martin, P., 2003. Spermiogenesis and seminal receptacles in *Aeolosoma singolare* (Annelida, Polychaeta, Aeolosomatidae). Italian J. Zool. 70, 123–132.

Martin, P., Martinez-Ansemil, E., Pinder, A., Timm, T., Wetzel, M.J., 2008. Global diversity of oligochaetous clitellates (“Oligochaeta”; Clitellata) in freshwater. Hydrobiologia 595, 117–127.

Martin, P., 2001. On the origin of the Hirudinea and the demise of the Oligochaeta. Proceedings of the Royal Society of London, Series B 268, 1089–1098.

Niederlehner, B.R., Buikema Jr., A.L., Pittinger, C.A., Cairns Jr., J., 1984. Effects of cadmium on the population growth of a benthic invertebrate *Aeolosoma headleyi* (Oligochaeta). Environ. Toxicol. Chem. 3, 255–262.

Omodeo, P., 2009. Evolution and biogeography of megadriles (Annelida, Clitellata). Italian J. Zool. 67, 179–201.

Parish, J., 1981. Reproductive ecology of Naididae (Oligochaeta). Hydrobiologia 83, 115–123.

Pennak, R.W., 1989. Fresh-water Invertebrates of the United States, third ed. John Wiley and Sons, Inc., New York, NY. 628 pp.

Piguet, E., 1906. Observations sur les Naididtes. Rev. suisse Zool. 14, 185–315.

Poddubnaya, L.L., 1984. Parthenogenesis in tubificidae. Hydrobiologia 115, 97–99.

Purschke, G., Hessling, R., Westheide, W., 2000. The phylogenetic position of the Clitellata and the Echiura – on the problematic assessment of absent characters. J. Zool. Syst. Evol. Res. 38, 165–173.

Rouse, G.W., Fauchald, K., 1995. The articulation of annelids. Zool. Scr. 24, 269–301.

Rouse, G.W., Pleijel, F., 2001. Polychaetes. Oxford University Press, London.

Rouse, G.W., Fauchald, K., 1997. Cladistics and polychaetes. Zool. Scr. 26, 139–204.

Rousset, V., Pleijel, F., Rouse, G.W., Erseus, C., Siddall, M.E., 2007. A molecular phylogeny of annelids. Cladistics 23, 41–63.

Sawyer, R.T., Dierst-Davies, K., 1974. Observations on the physiology and phylogeny of colour change in marine and freshwater leeches (Annelida: Hirudinea). Hydrobiologia 44, 215–236.

Siddall, M.E., Apakupakul, K., Burreson, E.M., Coates, K.A., Erséus, C., Gelder, S.R., Källerjö, M., Trapido-Rosenthal, H., 2001. Validating Livanow: molecular data agree that leeches, branchiobdellidans and *Acanthobdella peledina* form a monophyletic group of oligochaetes. Mol. Phylogenet. Evol. 21, 346–351.

Singer, R., 1978. Suction feeding in *Aeolosoma* (Annelida). Trans. Am. Microsc. Soc. 97, 105–111.

Sket, B., Trontelj, P., 2007. Global diversity of leeches (Hirudinea) in freshwater. In: Balian, E.V., Lévêque, C., Segers, H., Martens, K. (Eds.), Freshwater Animal Diversity Assessment. Hydrobiologia. http://dx.doi.org/10.1007/s10750-007-9010-8.

Sket, B., Trontelj, P., 2008. Global diversity of leeches (Hirudinea) in freshwater. Hydrobiologia 595, 129–137.

Struck, T.H., Schult, N., Kusen, T., Hickman, E., Bleidorn, C., McHugh, D., Halanych, K.M., 2007. Annelid phylogeny and the status of Sipuncula and Echiura. BMC Evol. Biol. 57, 1–11.

Timm, T., 1981. On the origin and evolution of aquatic Oligochaeta. Eesti NSV Eaduste Akad. Toim. Biol. Seer. 30, 174–181.

Wang, H.Z., Liang, Y., 1997. Analyses of distribution and faunal relationship of inland-water microdrile Oligochaeta (Annelida) in the world and China. Acta Hydrobiol. Sin. 21, 91–102.

Westheide, W., 1997. The direction of evolution within the Polychaeta. J. Nat. Hist. 31, 1–15.

Wetzel, M.J., Kathman, R.J., 2002. North American Freshwater Oligochaeta. An introduction. 16 pp.

Williams, D.D., 2004. Review of the polychaete genus *Namanereis* (Nereididae) in the Caribbean region, with a record of *N. hummelincki* from deep freshwater wells in Barbados. Caribb. J. Sci. 40, 401–408.