ANNELIDA

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Contents

Summary

Annelida contains a large assemblage of mainly marine animals that are commonly referred to as segmented worms. It also contains terrestrial groups such as earthworms.

There are about 15 000 described species, with more than half of this comprising the group Polychaeta. Polychaetes show a wide variety of forms and live in virtually all marine habitats. They represent an important component of marine biodiversity. The remaining annelids are referred to as Clitellata. Clitellata includes many marine worms, but is most well-known for containing earthworms and leeches. Annelids consist of three basic regions, with the majority of the body comprised of repeated units called segments. Most annelids also have hairlike structures called chaetae. The only parts of the annelid body that are not segmental are the head and a terminal post-segmental region called the pygidium. Most annelids have a distinct coelomic cavity that separates the body wall from the gut. In this cavity lie the internal organs, such as the excretory organs and gonads. Annelids show a wide variety of feeding and reproductive mechanisms. At present, our understanding of the evolution of annelids is poor and much more research is needed. Annelids have a fossil record that clearly dates back to the Cambrian period.

1. Introduction

Annelida is a substantial group of animals of about 15 000 described species, commonly referred to as segmented worms. The group is regarded as comprising two major groups referred to as Polychaeta and Clitellata, although this division is questioned. Polychaeta comprise the bulk of the diversity of Annelida, and are found in nearly every marine habitat, though they are rare in freshwater and virtually absent from land. Polychaetes are found from intertidal algal mats down to the deepest sediments. There are even pelagic polychaetes that swim or drift, preying on other plankton. Most polychaetes are cryptic, living under rocks or burying themselves in sediment. Some dig continuously through the sediment, while others make permanent burrows or tubes that they secrete or construct from gathered materials. Some polychaetes are more visible to humans and include mobile forms (Figure 1) crawling among algae or over sediment, while some of the tubicolous forms have spectacularly colored feeding appendages (Figure 2). While less diverse morphologically than Polychaeta, Clitellata are commonly found in marine, freshwater, and terrestrial environments. Almost all clitellates (Figure 3), except predatory or parasitic leeches (Figure 4), are burrowing detritus feeders, and few form any sort of permanent tube.

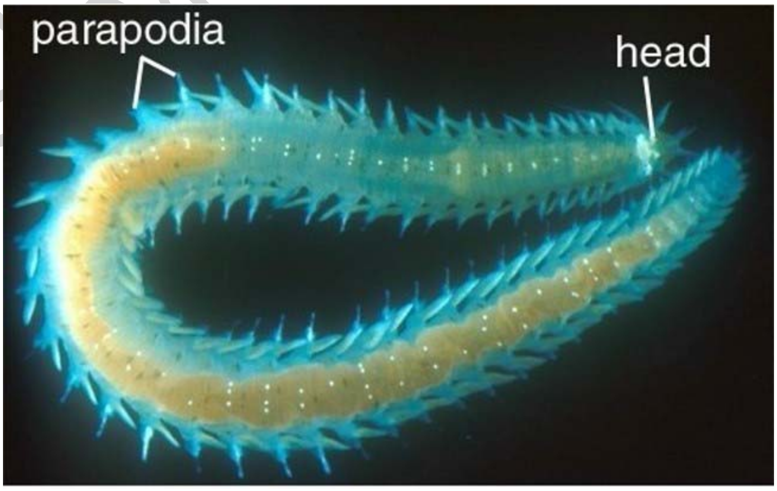

Figure 1. A mobile form of polychaete belonging to Phyllodocidae

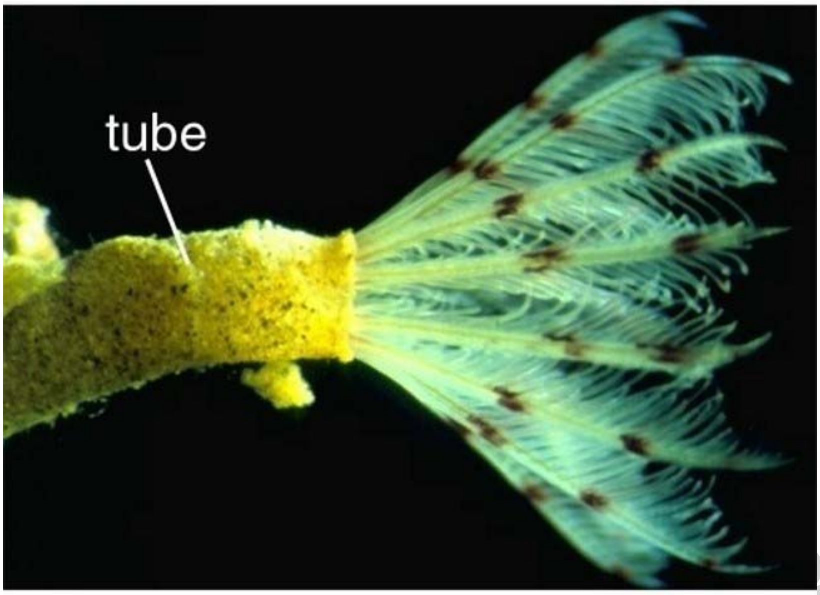

Figure 2. A tube-dwelling polychaete (Sabellidae) with only the head projecting from the tube. The head is transformed in this example into an elaborate food catching device.

Figure 3. A typical earthworm

Given their diverse habitats, it is not surprising that annelids vary greatly in form and size. Adults can range in length from a fraction of a millimeter to more than 6 m. Mobile polychaetes tend to have well-developed eyes and other sensory appendages. They can also have elaborate jaws for grasping and ingesting prey. Those that live in permanent tubes are basically sessile, projecting their feeding appendages from the tube and either collecting food from the surrounding surfaces or filtering it directly from the water. Clitellates are less diverse anatomically than polychaetes. Most are simple cylindrical shapes with no elaborations on the head or body.

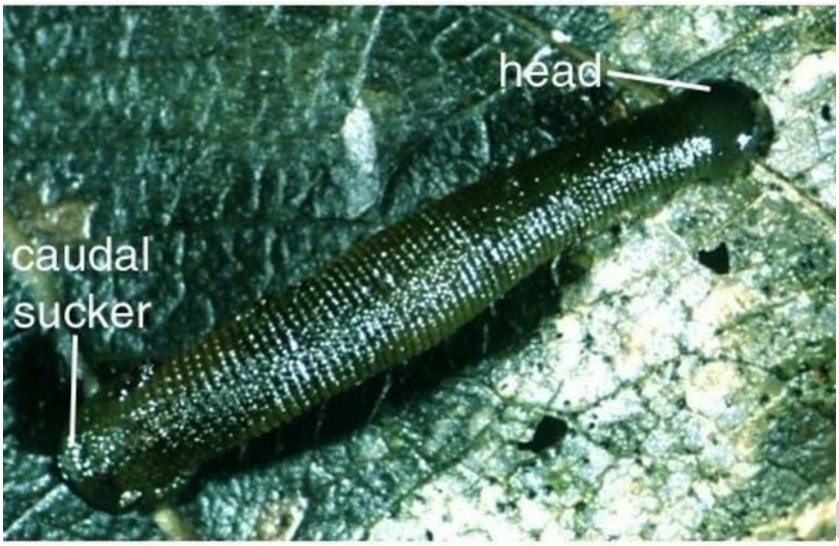

Figure 4. A terrestrial leech

2. Basic Annelid Organization

Annelid worms consist of three basic regions, with the majority of the body comprised of repeated units called segments. Each segment is, in principle, limited by septa dividing it from neighboring segments (Figure 5). Each segment usually carries parapodia (in many polychaetes, Figure 1) and chaetae, in addition to various, segmentally arranged internal organs, such as segmental organs and gonads. The only parts of the annelid body that are not segmental are the head and a terminal post-segmental region called the pygidium. The head is comprised of two units, the prostomium and the peristomium. The prostomium usually contains the brain and any sensory appendages, and the peristomium is the region surrounding the mouth opening. The postsegmental pygidium includes the zone from which new segments are proliferated forward during growth along its anterior edge.

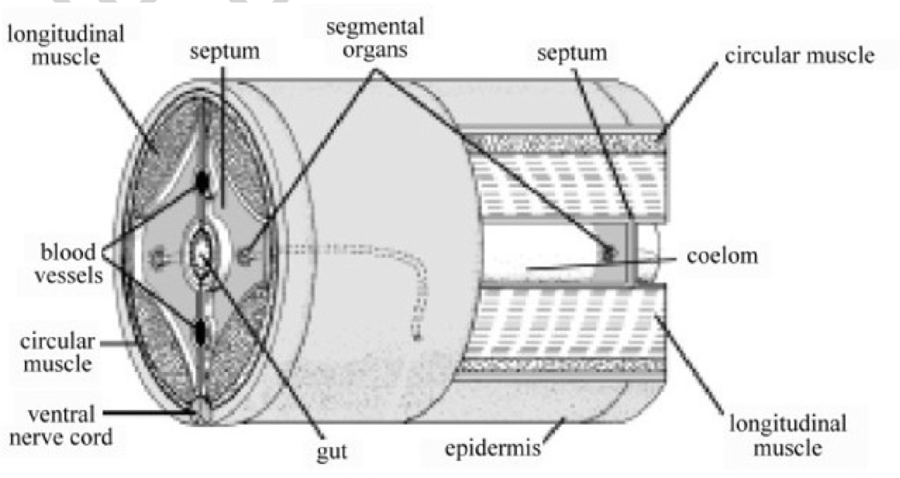

Figure 5. A schematic diagram showing two segments of an annelid in lateral view, (modified from Fransen, 1988)

2.1. Coelom

Nearly all annelids have a fluid-filled cavity between the outer body wall and the inner gut, and this is referred to as a coelom (Figure 6). The advantages of having a coelom are thought to be as follows:

1. The gut is separated from the body wall and with its own musculature can move independently.
2. The coelom provides a space where gametes (sperm and eggs) can mature and where nutrients and waste products can be moved or stored.
3. The coelom provides a hydrostatic skeleton upon which muscles can act.

Because the coelom is filled with incompressible fluid, contraction of muscles in one part of the body causes expansion in another part of the body. The extent of this reaction is in part determined by the division of the coelom by septa separating the segments. Physiological problems associated with the evolution of the coelom are related to the expansion of the body and the distance of the gut from the outer surface. This means that transport of respiratory gases and nutrients cannot be accomplished by diffusion through the tissues alone, as in Platyhelminthes. Most taxa with a coelom therefore have a circulatory system, though a number of annelid groups also rely on movement of the coelomic contents to facilitate gas exchange.

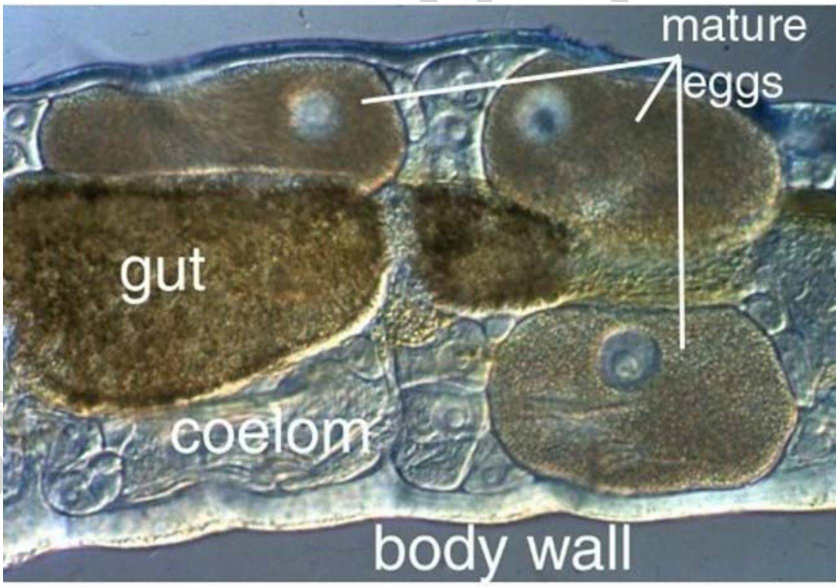

Figure 6. Light micrograph of the midbody of a female sabellid polychaete. The coelom of this specimen is filled with developing eggs, three of which are near maturity

The coelom in many annelids is organized as a series of compartments divided by intersegmental septa. This compartmentalization means that if the worm is damaged or severed the coelomic contents will only be lost from a few segments and locomotion can be maintained. In other annelids there may only be a few septa dividing the coelom. Under these circumstances much more coelomic fluid is lost with injury, and locomotion is severely affected. However, there are advantages in having large coelomic compartments, particularly for burrowing polychaetes. A number of annelid, groups, particularly leeches, myzostomes, and a number of small polychaetes, have little or no coelomic space in the body. This may be a secondary phenomenon in each group. In leeches the role of the coelom in locomotion has been replaced by a sucker-based mode of movement. Of the polychaetes with small adult size, those with no coelom tend to use ciliary movement.

2.2. Metamerism

The serially repeated segmentation seen in annelids is known as metamerism. Each segment is a unit isolated from adjacent segments by membranous septa. In addition to the septa in each segment, there are usually dorsal and ventral mesenteries that separate a pair of coelomic compartments. Segments are formed sequentially in annelids and are established during development from paired growth zones at the posterior end of the body. This means that the youngest segment in the body of an annelid is always the most posterior. Many annelids, such as leeches, have a fixed number of segments, but in others segments continue to be added throughout life. Structures such as the excretory, locomotory, and respiratory organs are generally repeated in each segment (Figures 5 and 6). However, all segments are basically united by the digestive, vascular, muscular, and nervous systems and so have little autonomy. The septa separating each segment can be virtually complete, as in most clitellates, but in many polychaetes the septa are incomplete or even absent, resulting in coelomic continuity along much of the body.

2.3. Chaetae

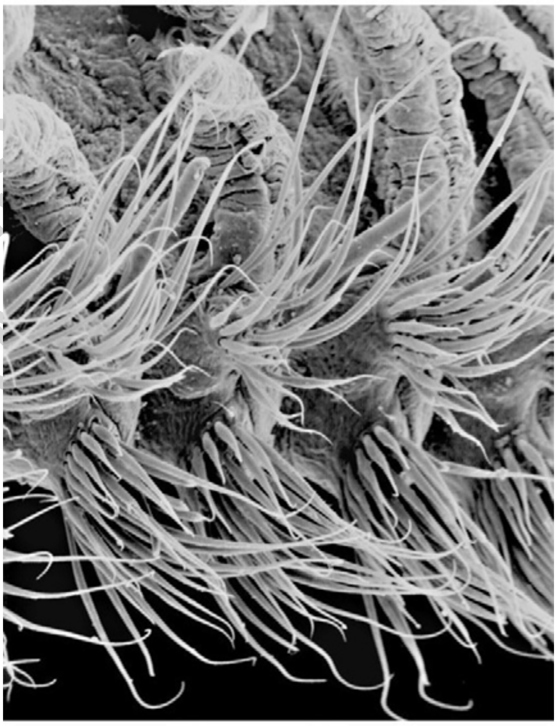

Figure 7. Numerous chaetae projecting from the body wall of a paranoid polychaete

Chaetae (also called setae) are bundles of chitinous, thin-walled cylinders held together by sclerotinized protein. They are produced by a microvillar border of certain invaginated epidermal cells and so can be defined as cuticular structures that develop within epidermal follicles. Chaetal ultrastructure is similar in all cases, but there is considerable diversity of form. Chaetae can be long thin filaments (Figure 7) or stout multihooked structures. In some cases they form compound structures with ligaments. In polychaetes there are often numerous chaetae in each segment, usually emerging in two bundles on each side of the body. Chaetae are a feature that can be regarded as uniting annelids as a group, though similar structures are found in another group known as Brachiopoda. It is possible that Brachiopoda should be considered as closely related to annelids. Chaetae have been lost in leeches and a few polychaete groups.

3. Annelid anatomy

3.1. Body Wall

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. The epidermis is usually a columnar epithelium, ciliated in certain areas of the body. Beneath the epidermis and its basal lamina lies a layer of circular muscle. The circular 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 virtually all annelids the longitudinal muscles are present as four distinct bands. In addition to the circular and longitudinal muscle layers, there can be series of “oblique” muscle fibers that join the ventral area of the body with the midlateral region. The final body wall component in most, but not all annelids, is a thin peritoneal layer lining the coelom (Figures 5 and 6).

3.2. Parapodia

Parapodia are unjointed extensions of the body wall found in many polychaetes (Figures 1 and 7), though many do 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. They may be supported internally by one or more larger, thick chaetae called aciculae. Parapodia vary in structure but basically can be considered to consist of two elements; a dorsal notopodium and a ventral neuropodium. In addition to various kinds of chaetae, notopodia and neuropodia can also have a variety of cirri and gills. They are most elaborate in actively crawling or swimming forms where they form large fleshy lobes that act as paddles. Parapodia of burrowing or tubicolous polychaetes can simply be slightly raised ridges carrying hooked chaetae called uncini.

3.3. Nervous System

Annelids have a brain or cerebral ganglion that originates and usually resides in the head. The brain varies in structure, with mobile active forms having the most complex brains, and sessile or burrowing forms having simple brains with little differentiation. This variation in brain morphology is correlated with the degree of sensory input the brain receives, because burrowing sedentary forms tend to have few sensory appendages. In all cases the brain is dorsal and is connected to a ventral nerve cord by two circumoesophageal connectives. In polychaetes with a complex brain, there are three distinct divisions: forebrain, midbrain, and hindbrain. In clitellates and polychaetes with simple brains, there are no obvious subdivisions. The ventral nerve cord, usually made up of a pair of cords that are bound together, runs the length of the body. It varies in thickness and dilates into a ganglion in each segment, from which pairs of segmental nerves pass out to the body wall, muscles, and gut.

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Biographical Sketch

Greg Rouse is an Australian Research Council QEII Fellow based in the School of Biological Sciences, University of Sydney. He has also worked at the University of Queensland and the Smithsonian Institution. His major research interest is the evolution of life histories in marine invertebrates, particularly polychaete annelids. This involves study of anatomy and development of the groups under study, and the theoretical aspects of phylogeny reconstruction.