POLYCHAETES:

The Extraordinary World of Marine Segmented Worms

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Dedicated to the memory of Dr. Kristian Fauchald, 1935–2015.
Mentor, colleague, friend.

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Introduction

The ocean realm is often thought of as a vast, mysterious place with beautiful and bizarre creatures. As *the* largest contiguous habitat on the planet, and far less studied compared to terrestrial regions, the oceans continue to offer surprises. This brief account offers to the public a window into one of the fascinating groups of animals found throughout the world's oceans, including along the California coast, but which are largely unknown by most people: the segmented worms known as *polychaetes* (poly-keets).

Polychaete Worms and Their Evolutionary Cousins

The earliest formal classification of animals was developed in the 18th century. One of the groups recognized was Vermes, from the Latin *vermis* for 'worm.' Vermes included all worm-like creatures except for arthropods. As knowledge of these animals increased, it became apparent that the diversity of body forms and anatomies required more informative and accurate classifications. Early in the 19th century, members of the Vermes were split up, and worms were segregated into two classes, Worms and Annelids. Worms contained the flatworms and roundworms, while Annelids consisted of the segmented worms. Eventually the flatworms and roundworms were recognized as separate phyla, Platyhelminthes (from the Greek *platy*, 'flat' and *helminth*, 'worm') and Nematoda (from the Greek *nema*, 'thread' and -*odes*, 'like' or 'in the nature of'), respectively. The annelids now comprise the Phylum Annelida (from the Latin, *annellus*, 'a little ring' or 'annulation'). In this section we will look at some of the basic features of annelids.

The most distinctive feature of annelids, and what readily distinguishes them from other types of worms, is the segmented body plan (Figure 1). For instance, the only body cavity among flatworms is the gut. In addition to the gut, the roundworms have a continuous body cavity called a 'pseudocoel.' Unlike roundworms, the body cavity in annelids, called a 'coelom,' is divided into a linear series of compartments that make up the segments that are visible as rings or annulations along the outside of the body.

The Annelida includes two classes (Figure 1): Polychaeta, with over 10,000 species that are almost exclusively marine but with some brackish water and a few freshwater members; and Clitellata, the aquatic (marine and freshwater) and terrestrial earthworms and leeches, with about 8000 species. The word Polychaeta, pronounced 'poly-keeta,' is derived from two Greek words, *polys*, 'many,' and *chaite*, 'long hair,' referring to the distinct bundles of bristles or chaetae ('kee-tee') emerging from the lateral margins of segments. The term Clitellata comes from the Latin *clitella*, 'a pack saddle,' referring to the clitellum, which is a discrete glandular swelling or region of the epidermis that secretes a cocoon into which the eggs are deposited. Chaetae are also present among earthworms, but absent in leeches.

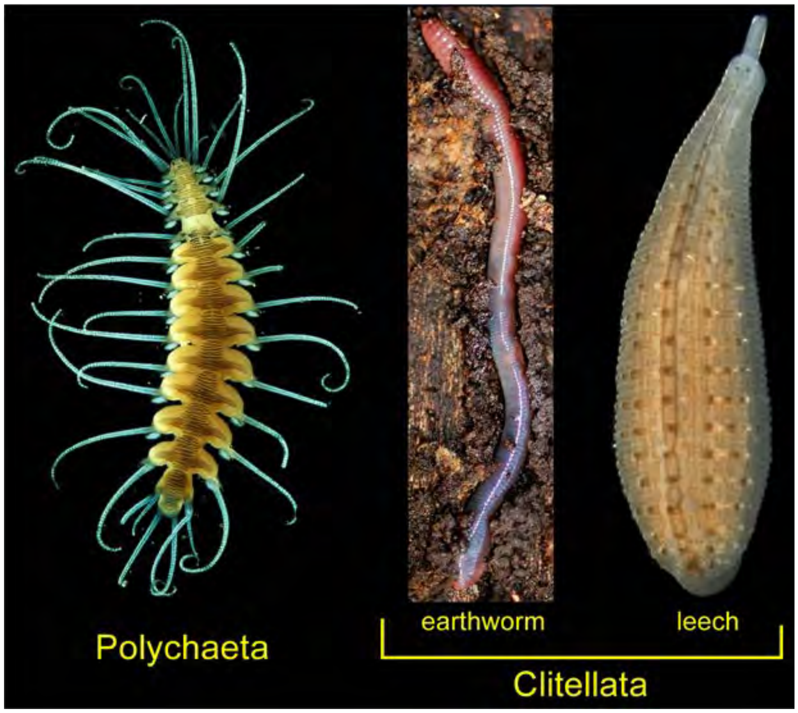

Figure 1. Evolutionary relationships among the major groups of Annelida. Photos by Leslie H. Harris (polychaete), William Vann (earthworm), Geoff Read (leech).

The Polychaete Body Plan – Magical Diversity

The general annelid body plan can be divided into three distinct regions: head, trunk, and pygidium. Unlike earthworms and leeches, these regions in polychaetes exhibit an amazing variety of shapes, sizes, and modifications of associated body parts. Thus only a very basic description of the polychaete body will be presented here. As will be seen later, in conjunction with talking about where polychaetes live and what they eat, the diversity of body forms will become more apparent.

Along with the variation in body forms, the size range of adult polychaetes is immense. There are members of some species with adults that are so small that they live between sand grains. The longest polychaetes have been known to be up to 200 feet long, although these are very threadlike. The vast majority of polychaetes, however, range from less than one-third of an inch to only several inches. This accounts for why polychaetes are so easily overlooked when one is casually exploring the sea shore.

Head region

The polychaete head region, or anterior end, comprises two distinct parts, the first called the prostomium, followed by the peristomium (Figure 2A, B). While prostomium and peristomium have the appearance of separate segments, they technically are not segmental in form, but instead are directly derived from the unsegmented larval polychaete body (see **Making New Polychaetes**, below). The prostomium is often conical or rectangular in shape, and usually of

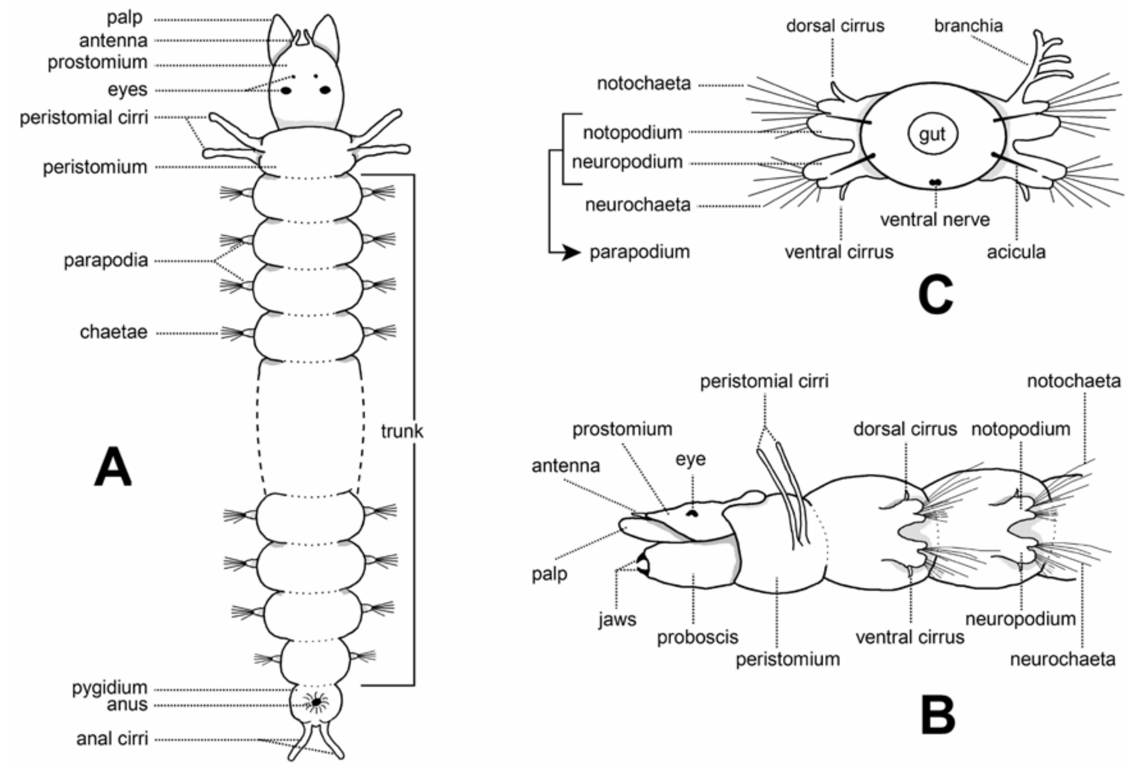

Figure 2. General polychaete morphology. **A.** Entire worm, dorsal (top) view. **B.** Cross section through a segment, showing parapodia and associated structures. **C.** Lateral (side) view of anterior (front) end.

similar dimensions as the peristomium and adjacent segments, although the prostomium can be much smaller and indistinct among some species (Fig. 3). Sensory appendages can include one to several pairs of eyes, especially among the more active species, as well as one or two pairs of antennae.

The peristomium often appears similar to adjacent segments, but dimensions can be variable. While the peristomium usually appears to lie behind the prostomium, in fact the prostomium usually is partially or almost entirely situated on top of the peristomium (Figures 2A, B, 3). The principle appendages on the peristomium are peristomial cirri and palps. Usually one to two pairs, peristomial cirri are typically slender and elongate, and serve a sensory function, thus are most prevalent on those polychaetes with an active and motile lifestyle. One pair of palps, when present, has two possible forms: lying below the prostomium or on top of the peristomium. Palps below the prostomium are sensory in function, usually conical, extending beyond the prostomium. Palps that originate on top of the peristomium are considerably longer, antenna-like, and serve both sensory and feeding functions (see **The Diets of Worms**, below). In some instances the peristomium may be fused with one to several adjacent body segments.

The mouth is located on the peristomium, just below the prostomium (Figure 2B). Among many species, the front part of the gut can be extended out of the mouth as an eversible pharynx or

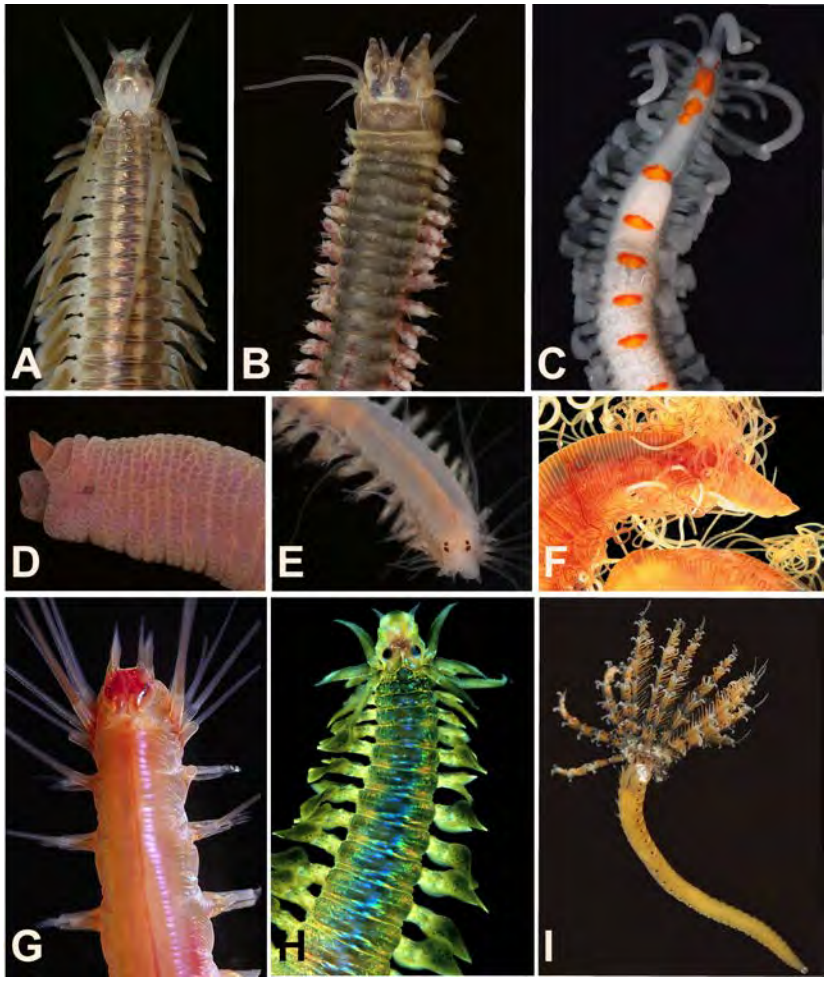

Figure 3. An overview of the diversity of anterior ends among polychaetes. **A, H.** Phyllodocidae. **B.** Nereididae. **C.** Syllidae. **D.** Capitellidae. **E, G.** Hesionidae. **F.** Cirratulidae. **I.** Sabellidae. Photos by David Fenwick (**A–E**, **I**), Leslie H. Harris (**F–H**).

proboscis. The pharynx can be tube-like or just an extension of the lower lip. The proboscis facilitates the consumption of food, so additional aspects of this structure will be mentioned below (see **The Diets of Worms**, below).

Trunk – body segments, parapodia, chaetae

The trunk comprises the region between prostomium/peristomium and pygidium, and is composed of the body segments (Figures 2A–C, 3). Consistent with the diversity of sizes and shapes of polychaetes, the number of segments is extremely wide ranging, from just a few to many hundreds. The most notable features of segments are the paired, fleshy appendages along the lateral margins, called parapodia, and the bristles or chaetae that extend from parapodia (Figure 2B, C). The parapodia, along with chaetae among many species of polychaetes give the appearance of a series of paddles or feet along the body (Figure 3A–C, E, G, H). Indeed, the parapodia and chaetae are crucial for enabling polychaetes to move over the surface of the sea floor, burrow into sand and mud, or live in tubes. The consequence is that the shapes of parapodia and chaetae often give clues of general habitat and motility, where the more active polychaetes tend to have well-developed parapodia and chaetae, while in more sedentary individuals the parapodia and chaetae are much shorter (Figure 4). In addition to chaetae, parapodia often have appendages, called cirri, or larger structures that function as branchiae or gills.

Parapodia can be subdivided into upper and lower components, called notopodia and neuropodia, respectively (Figure 2C). When a parapodium consists of notopodia and neuropodia it is said to be biramous. There are instances in which only notopodia or neuropodia are present, in which case the parapodium is uniramous. Chaetae extending from notopodia are collectively called notochaetae, and those in neuropodia as neurochaetae. Noto- and neuropodia among some polychaete species have internal supporting rods called aciculae (acicula, singular).

Figure 4. Comparisons of parapodia development among polychaetes with different levels of motility. **A.** Burrower (Capitellidae). **B.** Tube dweller (Ampharetidae). **C, D.** Highly mobile (Phyllodocidae, Polynoidae, respectively). Photos by David Fenwick.

Of the anatomical structures among polychaetes it is the diversity of forms and structural details of chaetae that are the most impressive, as well as critically important for ecological and evolutionary studies. Chaetae are vital for everyday functions, from motility to protection. Their chemical composition is similar to that of the exoskeleton of arthropods, thus chaetae are stiff yet pliable. Chaetae range in shape from very slender and elongate to very short, barely emerging beyond the body wall and with numerous teeth (Figure 5). This immense structural variety offers abilities for polychaetes to exploit every possible habitat in the world's oceans.

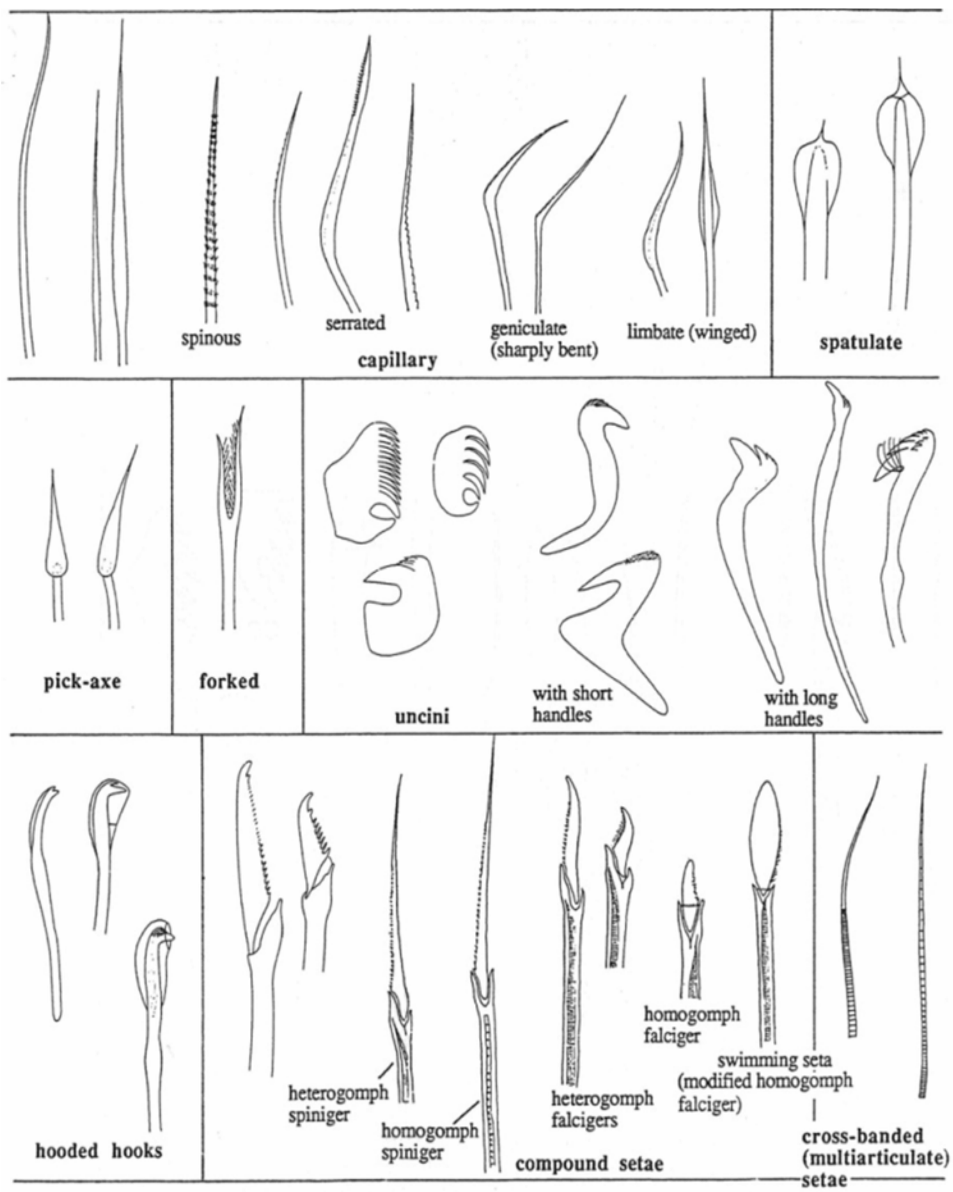

Figure 5. Representations of the diversity of polychaete chaetae. After Kozloff, 1987.

Pygidium
The posterior end of polychaetes is the non-segmental pygidium, which is usually conical or broadly rounded (Figure 2A). As noted earlier, the pygidium is part of the original unsegmented larva. As larval worms begin growing, segments are added to the trunk from a special tissue adjacent to the pygidium. The anus opens on the pygidium, usually on the upper surface. The pygidium among many polychaete species also have narrow, elongate fleshy extensions called anal cirri; the number of cirri can range from one to several pairs.

Polychaetes are Everywhere in the Oceans

Polychaete worms live in every type of habitat in the seas—they can be found in the intertidal sands of any beach, all the way down to the deepest depths of the oceans. And members of many species live in brackish waters as well as members of a few species in freshwater. Most polychaetes make the sea floor their home, where they burrow through sand and mud, or crawl over the sediment surface. There are members of some species that are fully pelagic, spending their entire life swimming in the water column. Because of their vast abundance, polychaetes comprise an extremely important link in ocean food chains. As a result, polychaetes are one of the most important groups of organisms for assessing the health of marine ecosystems.

Polychaete homes – burrows and tubes
Because polychaetes are soft-bodied animals, their main mode of defense is to remain hidden either by living in a burrow or crevices, or to produce some kind of tube. Especially among polychaetes that consume the sand or mud in which they live, they maintain a burrow that connects to the overlying water (Figure 6D). The integrity of burrows is maintained with the use of mucus secreted from glandular tissues in the body wall. When in contact with sea water, mucus stiffens into a thin layer along burrow walls, adhering to sediment particles. The tubes of most polychaetes are also formed from mucus secreted from the body surface, and with mud, sand, or shell fragments attached using the mucus, depending on the composition of the surrounding sediments in which individuals live (Figure 6A, B). In some instances, however, individuals of some species produce tubes only composed of mucus. Members of most species of polychaetes that produce tubes will exhibit very specific behaviors with regard to gluing particles to the outer surfaces of their tubes. Depending on how much mucus is produced, and what kinds of materials are added to them, tubes exhibit a wide range of flexibility and shapes. Indeed, the inner lining of mucus can be quite tough. Generally, tubes open at or just above the sea floor, with the remainder embedded in the surrounding sediment. There are, however, some polychaetes that have the ability to produce tubes composed of calcium carbonate (Figures 6C, 10F). In these instances, tubes are usually produced directly attached to the surfaces of rocks or other firm surfaces, and the worms remain in these structures their entire life.

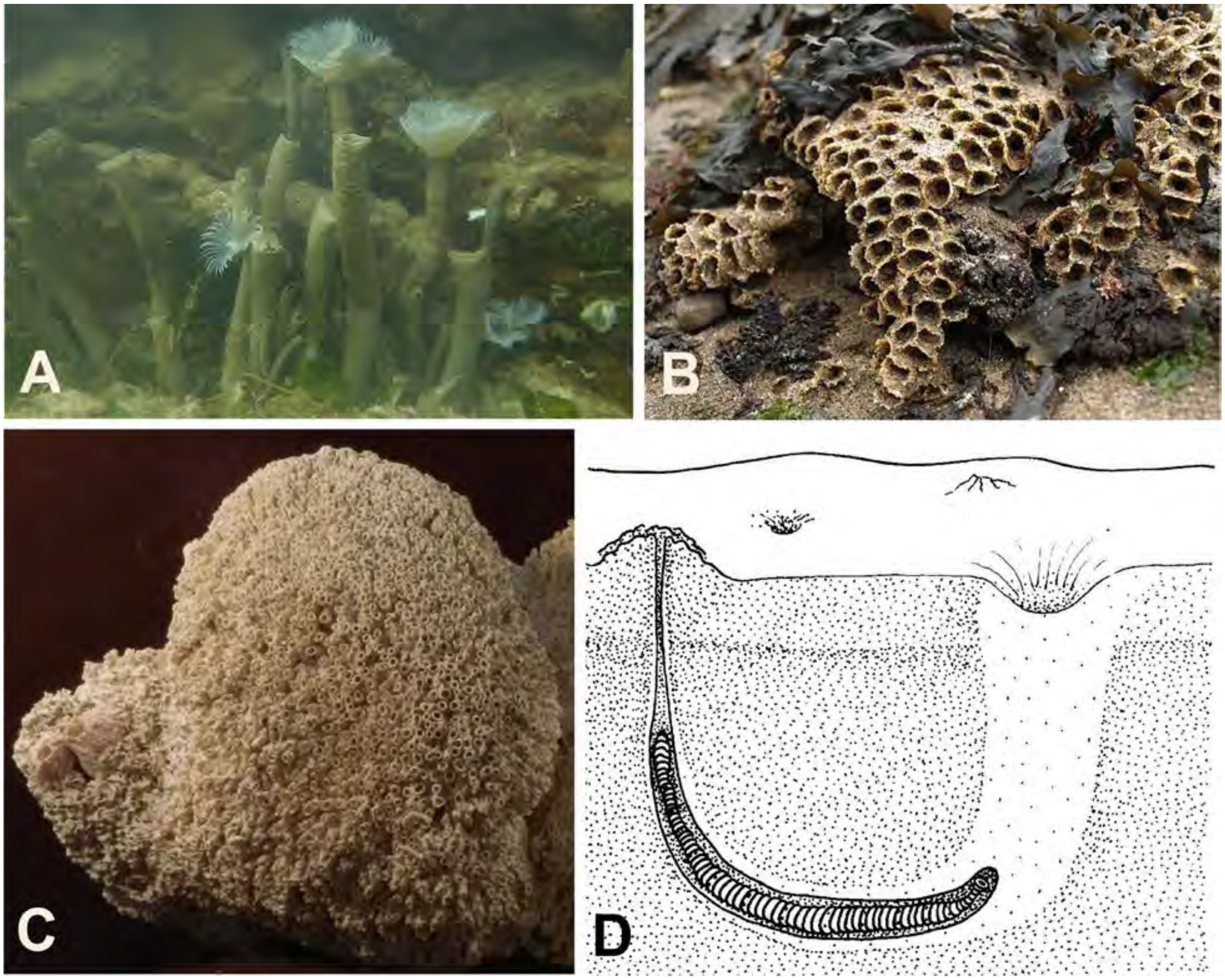

Figure 6. Common types of polychaete micro-habitats. **A.** Mud tubes (Sabellidae). **B.** Sand tubes (Sabellariidae). **C.** Calcareous tubes (Cirratulidae). **D.** Burrows in sand or mud. Photos by David Fenwick (A, B), J. Kirk Fitzhugh (C).

Food for others

Because polychaetes are a dominant part of the bottom fauna in any ocean ecosystem, most of which obtain their nutrition through the consumption of bacteria living on sediment particles, they are a fundamental link in marine food chains. Polychaetes are part of the diets of shrimps, crabs, other polychaetes, a variety of fishes, and even some shore birds.

"*Why should I care about polychaetes?*"

Our understanding of how the oceans operate and affect our very existence is dependent upon understanding the diversity of life in all marine and estuarine habitats. For instance, marine biologists monitoring the health of a particular region must rely on knowing what species occur in a given area and the role they play in the ecosystem. If we scoop up mud or sand from the sea floor on any part of the planet, regardless of depth, we find that polychaetes are usually the dominant organisms. As a consequence, marine biologists have found polychaetes to be excellent indicators of the effects of pollutants, as well as pointing to natural and human-induced changes in ecosystems. In order to accurately monitor the health of the world's oceans, marine biologists must be able to correctly identify the organisms they encounter. This is one of the reasons that the Natural History Museum of Los Angeles County maintains one of the world's largest polychaete collections, and why the collection receives so much use by researchers around the world.

The Diets of Worms

Polychaetes exhibit an array of novel strategies for acquiring food, and in order to accomplish that task, one will see diverse modifications of the head region. Examples of the five most common approaches to feeding will be mentioned here.

Sand and mud

Many burrowing polychaete species directly consume the sand or mud in which they live, much like the way earthworms feed (Figure 7). Some polychaete species with an eversible pharynx or proboscis will use that structure to collect sediments. The nutritional value of the consumed sand or mud comes from bacteria, protozoa, unicellular algae, and microscopic, multicellular organisms (e.g. roundworms) living on or in between sediment particles. The undigested sand or mud passes through the gut and is excreted, providing new real estate for microbial growth.

Figure 7. Examples of burrowing polychaetes. Notice that the anterior end is either pointed or rounded, without sensory appendages, and parapodia are poorly developed. **A.** Capitellidae. **B.** Arenicolidae. Photos by David Fenwick.

Surface deposit feeding
Rather than consume the sediment within which they live, some polychaetes are able to collect particles from the surrounding sea floor. This type of feeding is accomplished with several different types of head appendages among different polychaete groups.

A classic example of surface deposit feeding occurs among the ‘spaghetti’ or ‘medusa’ worms (Figure 8). These are a group of polychaetes with numerous, elongate tentacles that extend

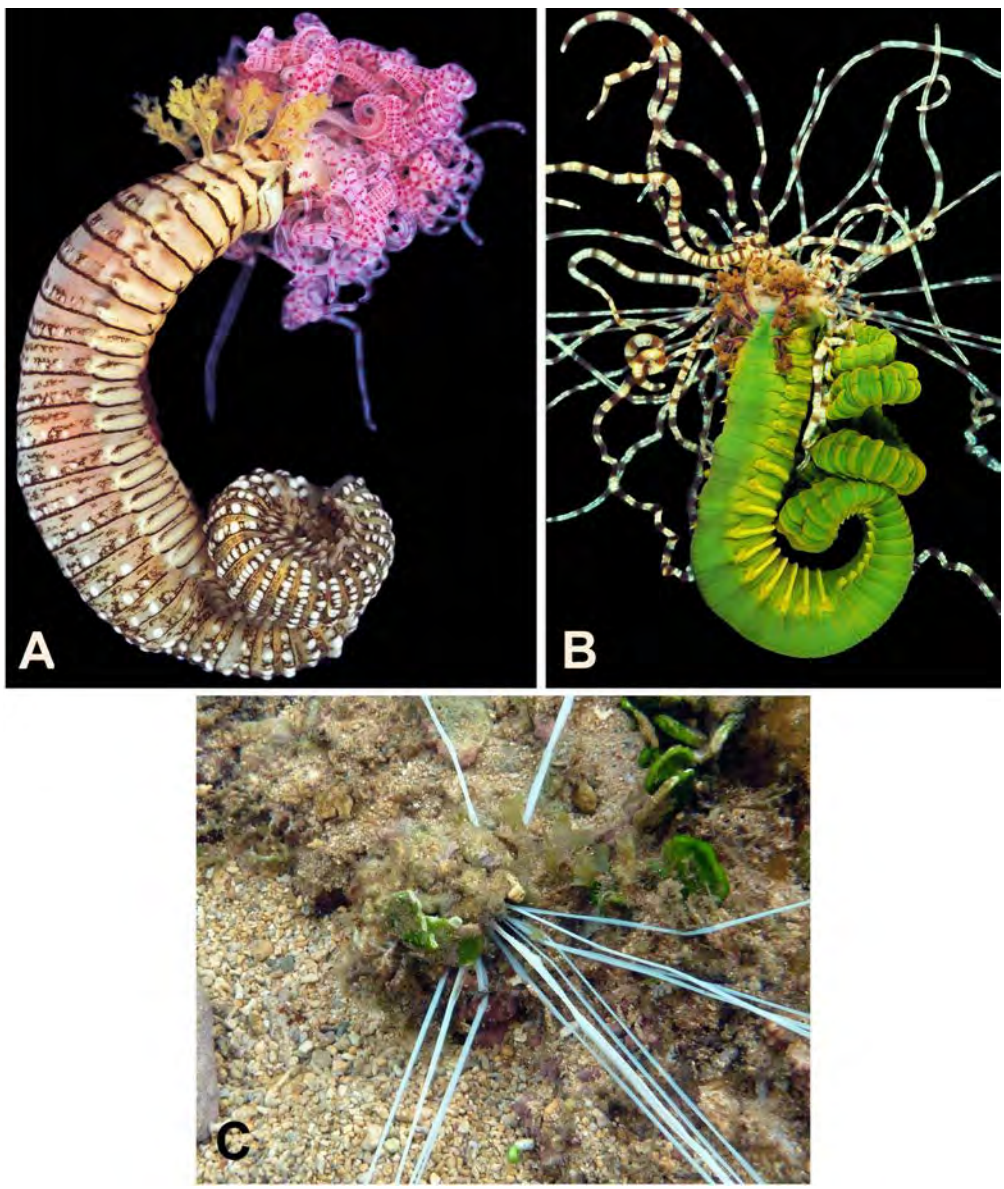

Figure 8. A, B. ‘Spaghetti worms’ (Terebellidae) are good examples of surface deposit feeding polychaetes. Note the numerous feeding tentacles from the upper lip. **C.** Typical feeding position, with tentacles extending from the tube and spread over the sea floor. Photos by Alexander Semenov (**A**, **B**), Susan Scott (**C**).

from the worm's upper lip, giving the appearance of spaghetti. Spaghetti worms are sedentary and live their lives in sand or mud tubes buried in the sediment, beneath rocks, or in crevices. They extend their tentacles, which are capable of moving independently, out of the tube opening and over the sediment surface. Tentacles can be easily stretched over several times the length of the body. Each tentacle has a shallow groove running its entire length and these grooves are covered with microscopic hairs called cilia. The cilia convey collected sediment particles back to the worm's mouth, where it can sort and selectively consume items. Spaghetti worms also use their tentacles to collect the sand, shell, or mud that goes into construction of their tubes. Snorkelers and divers often see spaghetti worms by way of their white tentacles spreading out from the tube opening. Fortunately for the worm, if tentacles are bitten off by predators, such as fishes or crabs, they can be regenerated.

We pointed out earlier that paired palps located on the upper surface of the peristomium often function in feeding. The spionid polychaetes (Family Spionidae) are good examples (Figure 9). Most spionids are sedentary, living in mucous or sediment tubes. Their palps are long and uniformly slender, with distinct arrangements of cilia along their length. Extending out of the tube, the palps can be directed to the sea floor and moved over the sediment. The cilia then convey particles back to the mouth where the worm can selectively consume items.

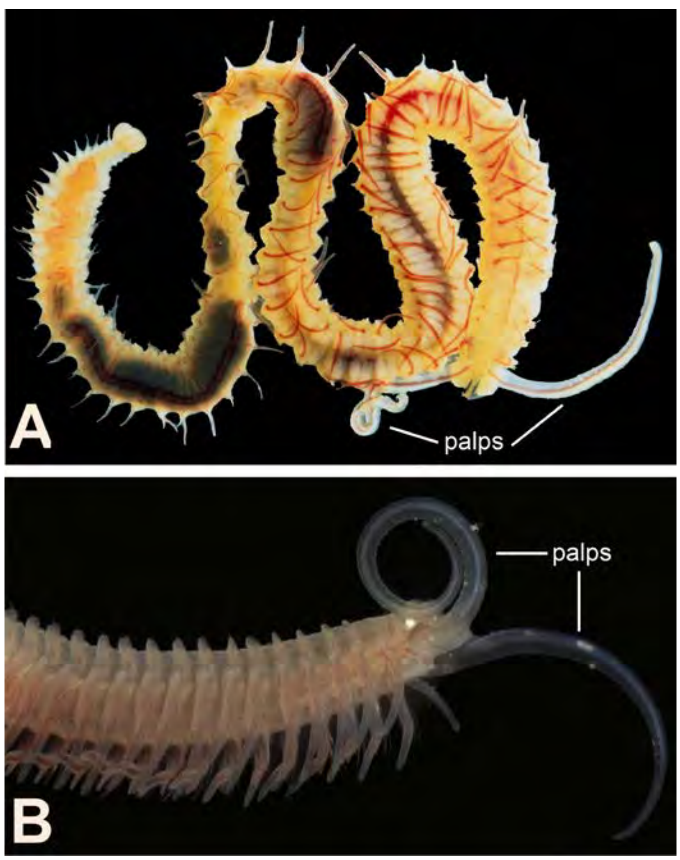

Figure 9. A, B. Spionidae palps. Photos by Leslie H. Harris (**A**), David Fenwick (**B**).

Filter feeding
There are several intriguing means by which some polychaetes filter food particles from the surrounding water. These occur among species that live very sessile lives in tubes. Three examples offer insight into the diversity of this feeding strategy.

Two closely related groups, the fan worms (families Sabellidae and Fabriciidae) and feather duster worms (family Serpulidae), are experts at filtering food out of water (Figure 10). The head region is highly modified into what is called a 'branchial crown.' While the name implies that the structure is used in gas exchange, it's more important function is feeding. The crown is composed of two semi-circular bases, from which extend a series of tentacles, called radioles. Each radiole has a ciliated groove along its length and on either side of that groove are

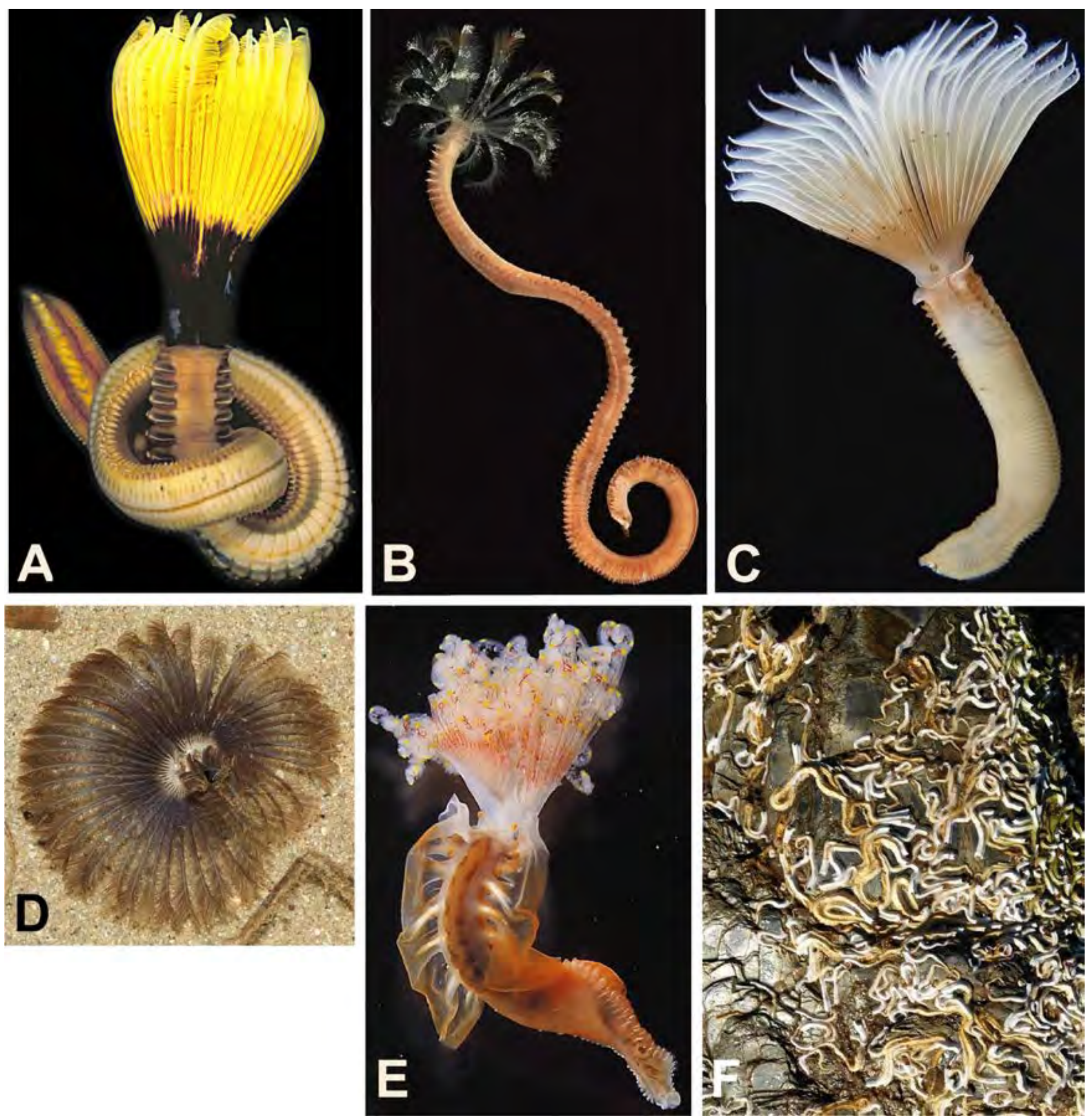

Figure 10. Examples of branchial crowns used for filter feeding. **A–D.** Sabellidae. **E.** Serpulidae. **F.** Calcareous tubes of serpulids. Photos by Leslie H. Harris (A, E), David Fenwick (**B–D**, **F**)

numerous, evenly-spaced side branches called pinnules, each with three sets of cilia. When the branchial crown is extended out of the tube, it has the shape of a funnel. The cilia on the pinnules beat in unison to create a current that draws water between the radioles. Suspended particles of sediment and plankton can be collected by the pinnules, transported to the radioles, and ultimately to the mouth at the base of the crown. The mouth is surrounded by a pair of large, ciliated lips that carefully sort the particles, selecting those that are to be eaten, while others are either discarded or attached with mucus for the worm's tube.

A notable group of polychaetes, honey-comb worms (family Sabellariidae), are named for their sometimes massive colonies or reefs of sand-grain tubes in rocky intertidal zones (Figure 6B). Honey-comb worms are sedentary, spending their entire adult lives in their individual tubes that are cemented together. The head region contains numerous ciliated filaments around the mouth. During high tides, honey-comb worms extend their heads out of their tubes and the tentacles collect unicellular algae (phytoplankton). The tentacles also function to collect suspended sand grains that are cemented with the worm's mucus to form its tube.

One of the most peculiar polychaetes hidden away in shallow waters is the parchment worm (Chaetopteridae; Figure 11A). The common name derives from the leathery tube that is

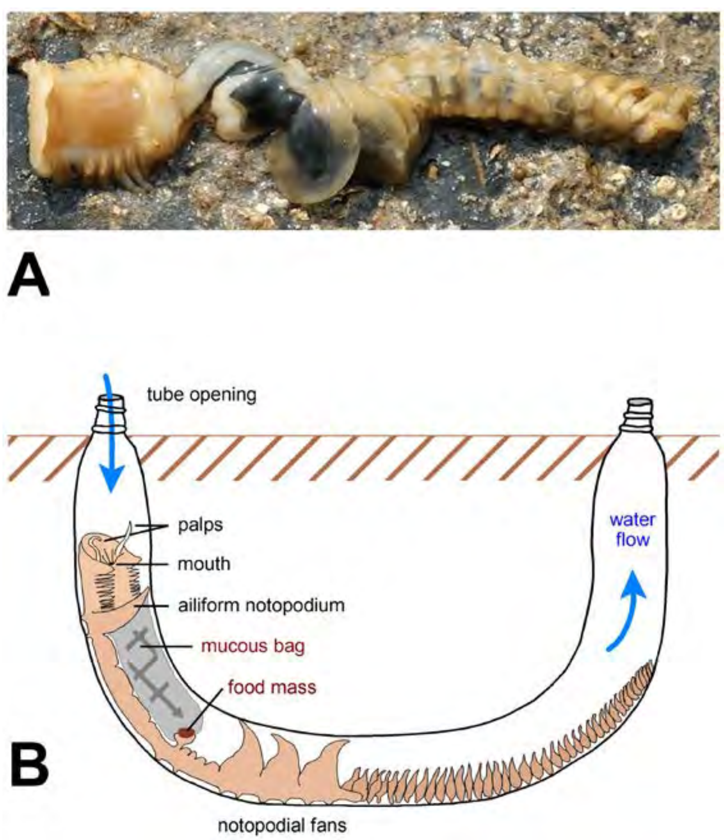

Figure 11. Parchment worm, *Chaetopterus* sp. **A.** Entire individual removed from tube. **B.** Feeding orientation of worm in its tube. Photo by David Fenwick.

produced from mucus secreted by the worm. Tubes are U-shaped, with openings at both ends much narrower than the space in which the worm resides (Figure 11B). The tube is buried in sand or mud, with tube openings exposed above the sediment. The worm spends its entire adult life in the tube. To obtain food, parchment worms rely on a unique mechanism for filtering food from the water. A pair of enlarged, ailiform parapodia near the head end secretes a mucous net in the form of an elongate bag. Several fan-like parapodia behind the bag rhythmically move to draw water into the tube closest to the head, through the tube and out the other opening. In the process, the mucous bag collects planktonic organisms and detritus. The bag is then gathered up as a small rounded mass and moved to the mouth, where it is eaten.

Carnivores

In contrast to the various approaches to obtaining food from the sediment in which they live or the surrounding water, some polychaetes are, or have the capacity to be carnivorous, feeding on other polychaetes, small crustaceans, and in some instances larger prey in the form of fish. As we will see, however, many groups of polychaetes that can accommodate a predatory lifestyle tend to be omnivorous, feeding on animals as well as algae, including diatoms, and detritus. How is it possible that a soft-bodied worm can capture live prey? The solution is the ability to extend either the lower lip or the front part of the gut, a tubular or axial pharynx, out of the mouth. In most of these instances, the lower lip or pharynx is equipped with one to many pairs of jaws that facilitate feeding by grasping prey. There are, however, some predatory polychaetes with an eversible pharynx that lack jaws. Some examples of the variation in carnivorous polychaetes are presented next.

A group of polychaetes commonly used in introductory biology classes as well as for fish bait, the sandworms or ragworms (Nereididae), have one pair of sharp, pincher-like jaws (Figure 12). Depending on the species, sandworms inhabit mucous tubes but are motile. In addition to some being carnivorous, others are herbivores and some feed on detritus. In a predatory capacity, the jaws are exposed at the end of the fully everted pharynx, and in contact with a prey item the jaws will close as the pharynx is withdrawn, pulling the prey into the gut. Fishermen who use sandworms as bait are familiar with the painful pinch the jaws can inflict on exposed skin.

The bloodworms (Glyceridae), a name derived from the pinkish-red color caused by the worm's blood pigment (Figure 13A), are the only known venomous polychaetes. While some are known to be predatory, members of other species feed on bottom sediments and detritus. Predatory species are known to occupy a system of burrows, but other species can be found beneath rocks or among algae. Bloodworms are notable for having a long eversible pharynx that leads to an expanded end with four jaws arranged in a square pattern (Figure 13B). At least in the case of some predatory bloodworms, each jaw has a narrow canal opening to the outside, through which venom, a neurotoxin, is released from venom glands associated with each jaw. Studies have shown that predatory bloodworms wait at one of the openings of their burrows and when they sense the presence of prey, usually a worm or crustacean, the pharynx is rapidly everted

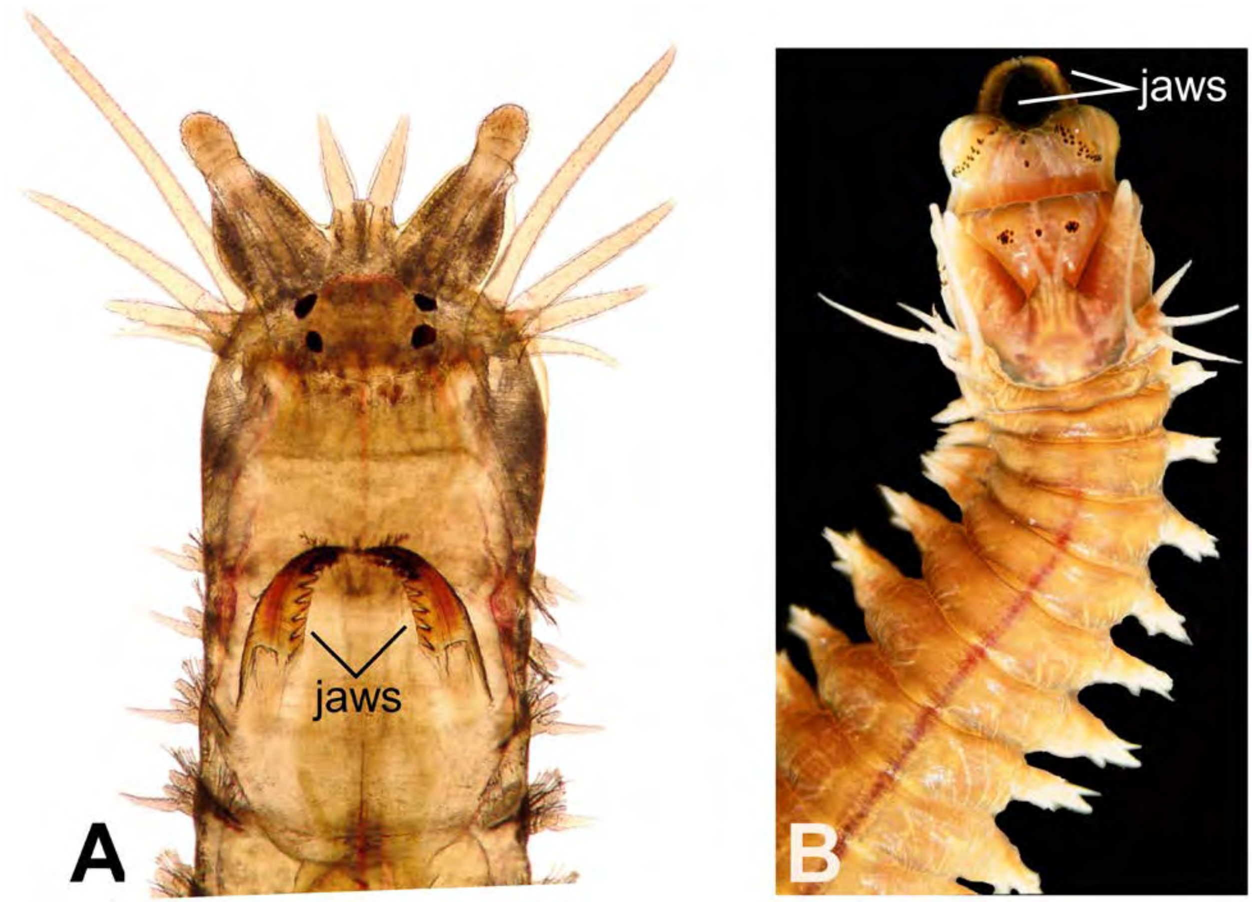

Figure 12. Examples of the one pair of jaws found among members of Nereididae. **A.** Jaws within body. **B.** Jaws at the end of the everted pharynx. Photos by Leslie H. Harris.

and venom injected through the jaws, paralyzing the prey, and then withdrawing it into the mouth as the pharynx is retracted.

Another group of polychaetes with a number of predatory representatives is the highly diverse scaleworms (Polynoidae). The common name refers to the presence of flat, overlapping protuberances on the back of the worm that have the appearance of fish scales (Figure 4D). Scaleworms are highly motile, living on sand, mud, under rocks, or in crevices, as well more sedentary species that live commensally in the burrows or tubes of other polychaetes, in association with sea stars, and in the shells used by hermit crabs. Scaleworms have an eversible pharynx, at the end of which are four jaws arranged as closely-spaced top and bottom pairs that have the form of a beak (Figure 14). Predatory scaleworms feed on other polychaetes and crustaceans, while those that are commensal usually feed on detritus brought in by the host.

Thus far, we have referred to those polychaetes with an eversible pharynx armed with jaws. There are several evolutionarily-related polychaete groups that have a muscular, eversible pharynx that lacks jaws, yet are predatory. One example includes the phyllodocids

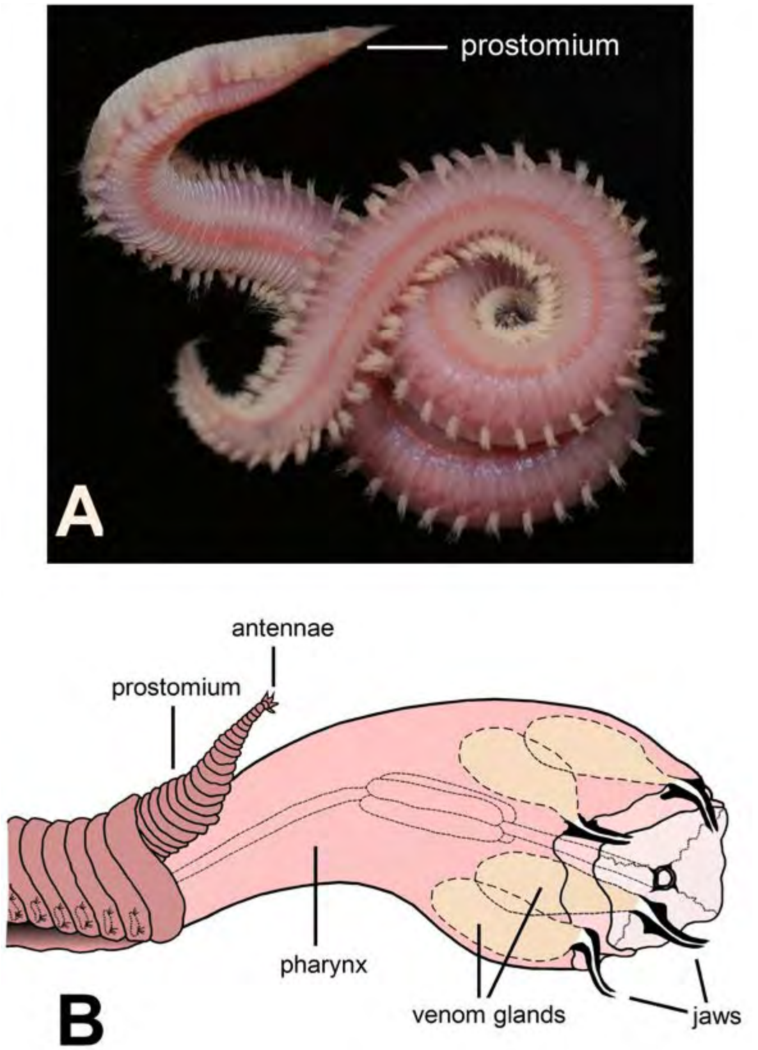

Figure 13. Bloodworms (Glyceridae). **A.** Individual with withdrawn pharynx. **B.** Everted pharynx, showing the four jaws and associated venom glands used in prey capture. Photo by David Fenwick.

(Phyllodocidae), which are elongate, slender worms (Figure 15). Phyllodocids are active hunters, feeding on other polychaetes.

In contrast to the eversible, axial pharynx discussed earlier, there is a large group of polychaetes in which the eversible pharynx is a well-developed lower lip on which are a series of jaws in the form of a pair of pincher-like mandibles and five or more pairs of plate-like maxillae (Figure 16). The group comprises the Order Eunicida, which contains five families. The eunicids range from slender to thick, elongate worms with numerous segments, often living in burrows or tubes, or among rocks. Some are highly motile, with a varied diet ranging from facultative carnivores to herbivores, as well as consuming detritus. A notable member of the Family Eunicidae has gained widespread notoriety in the press and on the internet: the 'Bobbit' worm (Figure 16C). Bobbit worms live in burrows, reaching lengths over six feet long. At night,

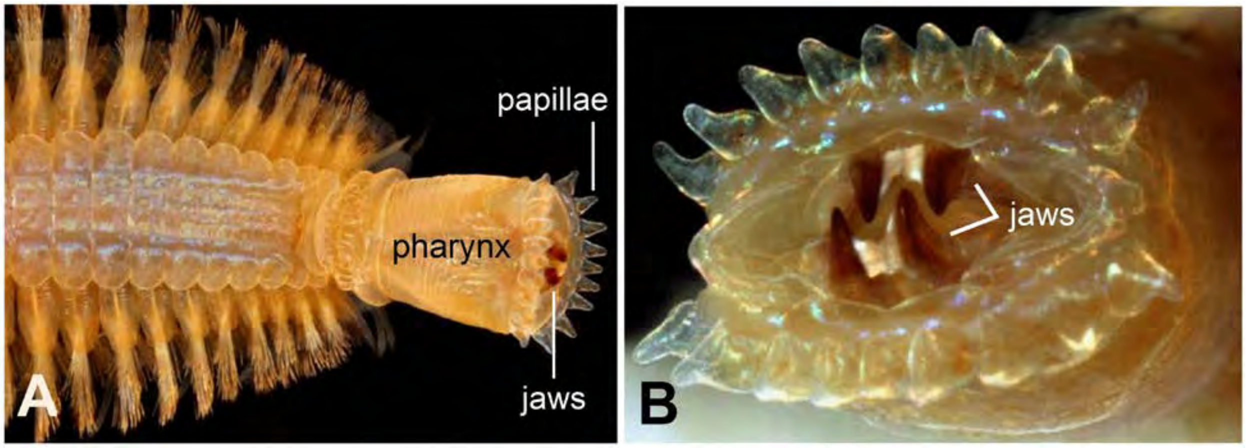

Figure 14. A, B. Everted scaleworm (Polynoidae) pharynx with four terminal jaws. Photos by Denis Riek.

the worm exhibits a novel sit-and-wait predatory behavior. The front end of the body is extended out of the burrow, and the pharynx protruded out of the mouth such that the mandibles and five pairs of maxillae are fully opened. The worm waits in this position until a fish or crab are within striking distance and the mandibles quickly close on the prey, withdrawing back into the burrow.

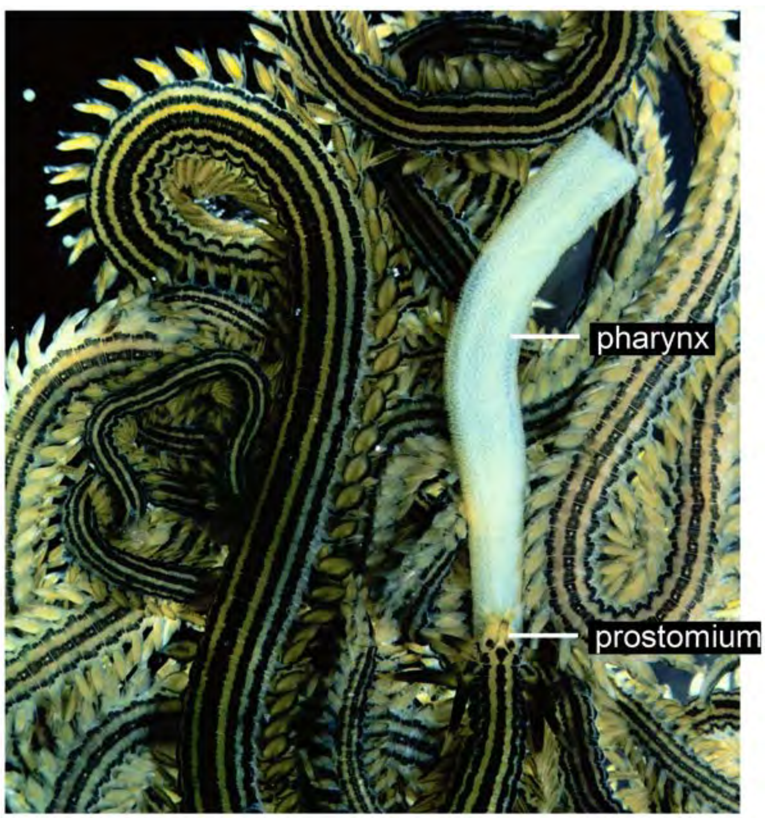

Figure 15. A member of Phyllodocidae with the very long pharynx extended out of the mouth. Photo by Leslie H. Harris

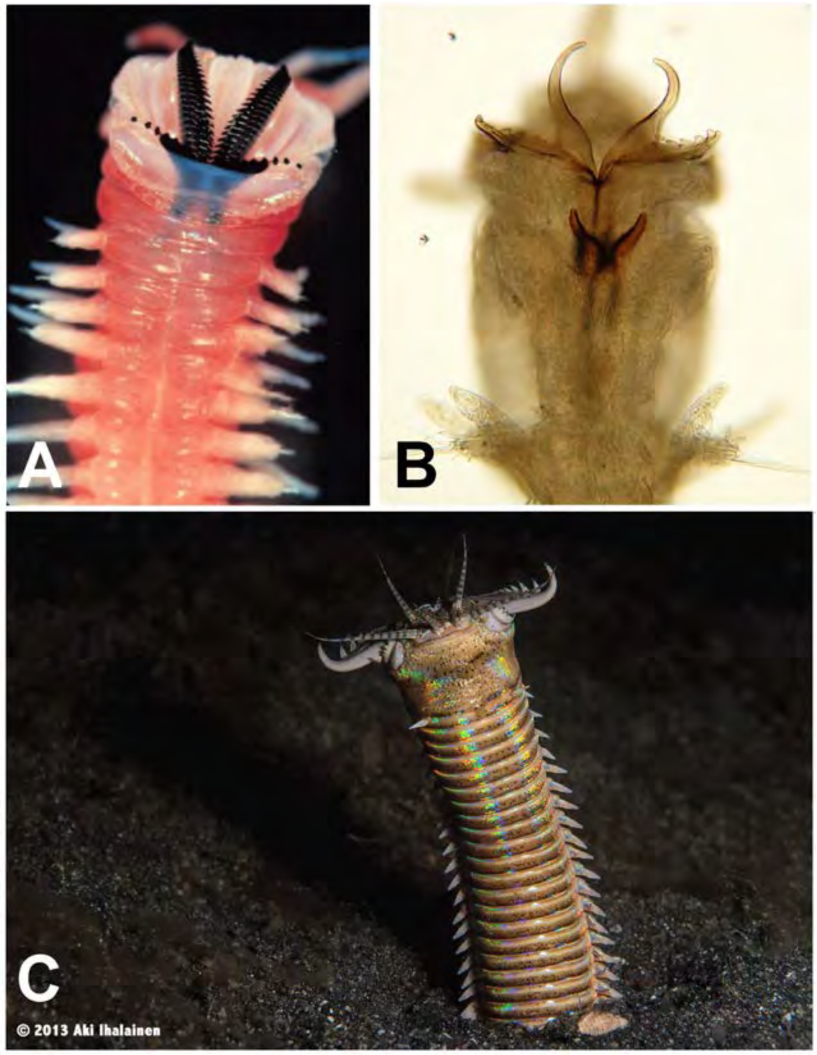

Figure 16. Multiple pairs of jaw pieces typical of members of the group Eunicida. **A.** Dorvilleidae. **B, C.** Eunicidae. Photos by Leslie H. Harris (**A**), Kelvin Barwick (**B**), Aki Ihalainen (**C**).

Symbiotic relationships

The topic of polychaete feeding would not be complete without mentioning one group that has forsaken acquiring nutrition on its own. These are members of the Family Siboglinidae, commonly referred to as 'vent worms,' 'bone-eating worms,' and 'zombie worms' (Figure 17). The common names are associated with some of the habitats occupied. While siboglinids have been known since 1900, mainly consisting of very small individuals, their notoriety with the public began in the late 1970's with the discovery of deep sea hydrothermal vents and giant tube worms living in close proximity. Subsequent discoveries have been made in association with methane seeps and most recently on whale bones in deep water. Siboglinids are entirely sessile, living in tubes formed from secreted mucus. Regardless of size among the 100 or so known species, adult siboglinids lack a mouth and digestive system. Nutrition is obtained through the commensal relation with chemoautotrophic bacteria living inside the worms. The

Figure 17. Members of the Siboglinidae. Polychaetes that obtain nutrition from commensal bacteria. **A.** *Riftia pachyptila* from eastern Pacific, . **B.** *Lamellibrachia luymesi* from Gulf of Mexico.

bacteria metabolize carbon dioxide and sulfur compounds supplied by the worm from the surrounding water, and in turn provide nutrition to the worm.

Making New Polychaetes

Reproduction among polychaetes is quite varied. While their relatives, the clitellates – earthworms and leeches – are all hermaphroditic, the majority of polychaetes have separate sexes, although hermaphroditism does occur. Some species of polychaetes are capable of undergoing asexual reproduction by fragmenting the body (Figure 18). For instance, an

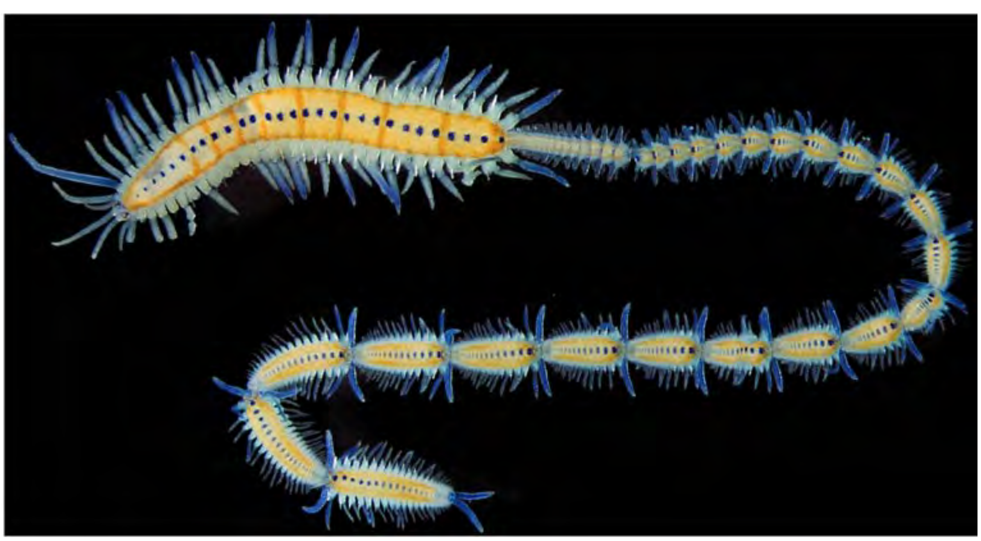

Figure 18. Asexual reproduction by way of budding in a member of *Myrianida pachycera*. Photo by Leslie H. Harris.

individual might separate into anterior and posterior halves. The posterior end of the front half will regenerate to form new segments, complete gut, and anus, while the back half will regenerate new anterior segments, head region, and mouth. Interestingly, these same individuals usually are also capable of reproducing sexually. Another type of asexual reproduction occurs when clones bud off the adult and eventually detach and crawl away.

Many polychaete species release eggs and sperm directly into the water, where fertilization takes place. Embryos then develop into a ciliated trochophore larva that will remain in the water column for hours to weeks depending on the species. The trochophore is an important stage in the life history because it facilitates dispersal. The trochophore eventually metamorphoses into a juvenile that settles to the sea floor, where it will continue to grow to maturity. An alternative to dispersing eggs is the brooding of eggs, embryos, and trochophore larvae by the female. Young then crawl away from the parent when they are juveniles. As a consequence, dispersal is more limited.

While most polychaetes that release eggs and sperm into the water do so while remaining in their burrows, tubes, or otherwise from the sea floor, there are some species that develop modified bodies filled with gametes that can swim up into the water column, called swarming. These modified individuals are called epitokes, and once in the water column the bodies burst open, releasing their gametes (Figure 19).

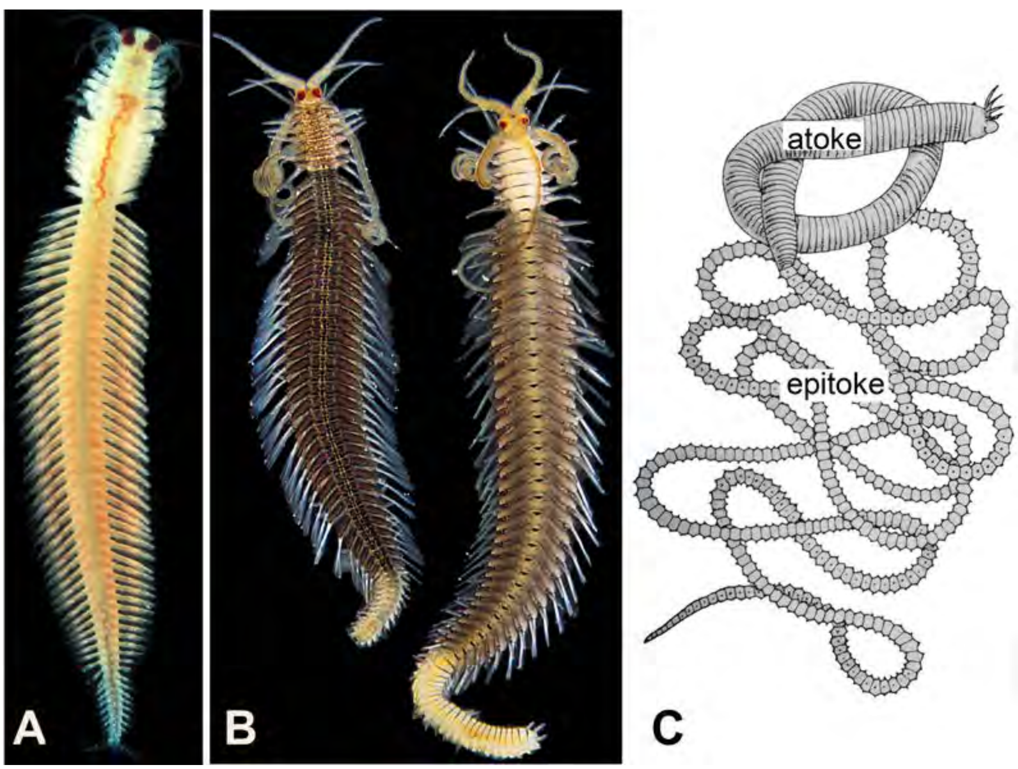

Figure 19. Examples of epitokous polychaetes. **A.** A member of Nereididae. **B.** Members of Syllidae. **C.** Member of Eunicidae, *Palolo viridis*. Photos by Leslie H. Harris.

Epitokes can be of several forms. Among some ragworm species (Nereididae, see **The Diets of Worms**, *Carnivores*; Figures 3B, 12), sexually mature adults will undergo an overall body change. The two pairs of eyes on the head enlarge; the posterior half of the body expands, and associated parapodia become broader and the normally slender chaetae are replaced with numerous, elongate, paddle-shaped chaetae (Figure 19A). The body wall becomes thinner, the gut and other tissues in the modified segments disintegrate and the body cavities become engorged with eggs or sperm. After sunset, epitokes swarm toward the surface, the bodies burst open, releasing gametes. The adults die afterwards.

Another form of epitokes occur among some members of the Eunicidae, the 'Palolo worms.' In preparation for reproduction, the back half of the body transforms into the epitoke, becoming filled with gametes (Figure 19C). The unmodified anterior end is known as the atoke. During Spring and early Summer, when the moon is waning, the epitokous part of the body detaches from the worm and swarms to the water surface where it breaks open to release gametes. The atokous body remains on the sea floor and can regenerate the posterior end.

Fossil Polychaetes – Millions of Years of Success

Polychaete fossils are known from rocks dated as far back as the mid-Cambrian period (500 million years ago), such as from the famous Burgess Shale Formation in British Columbia, Canada. Another famous locality is the Francis Creek Shale Formation in Illinois, with Mazon Creek fossils from the Pennsylvanian period (300 million years ago). What is especially fascinating about Mazon Creek polychaetes, like the ones shown in Figure 20, is that they contain members of species that can be assigned to families of polychaetes that have members in existence to this day. Clearly, the remarkable evolutionary longevity of polychaetes has been due to their success at being able to exploit every possible type of habitat in the world's oceans and at all depths.

Venomous & Poisonous Polychaetes

For all the diversity of forms among polychaetes and the formidable appearance of chaetae and jaws, there is only one group that can be considered poisonous to humans: the 'fireworms.' And only one group of polychaetes, the 'bloodworms,' are known to produce venom, used to subdue prey.

Fireworms

The fireworms are members of the Amphinomidae. Especially in subtropical and tropical waters, fireworms can grow to several inches up to one foot in length. They are very apparent because the body is thick and robust, usually with bright red branchiae on the notopodia and dense bundles of long, white chaetae (Figure 21). Add to this the fact that fireworms feed on corals and seem to have no natural enemies, they are often seen crawling over the surfaces of rocks, coral, or sand. The white color of the chaetae is due to a distinctive characteristic of fireworms: unlike other polychaetes, the chaetae contain calcium carbonate, making them very

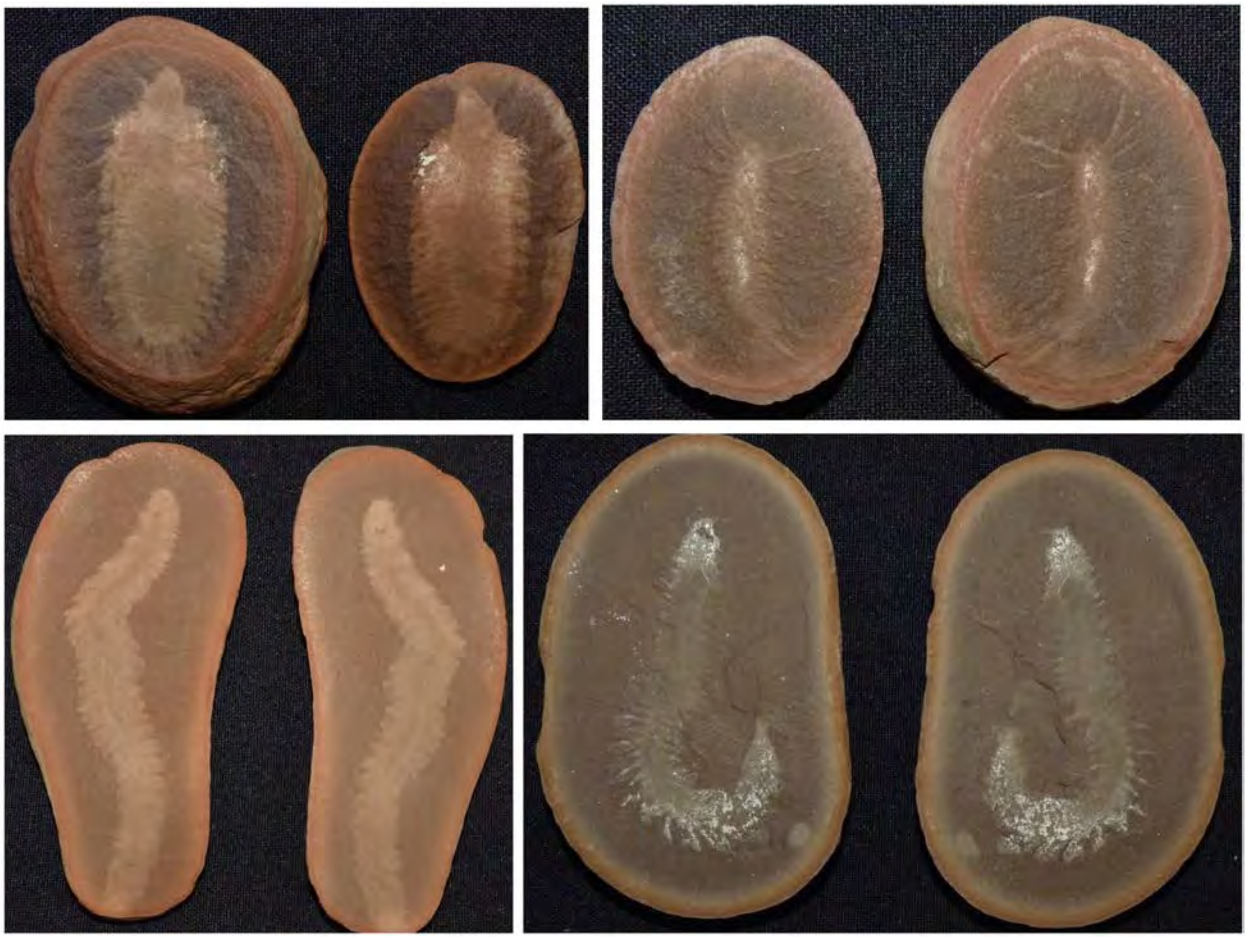

Figure 20. Fossil polychaetes from Mazon Creek, Illinois. Pennsylvanian Period, about 325 million years ago. Mazon Creek fossils are unusual because they occur in nodules, and are revealed by splitting into left and right halves. Photos by J. Kirk Fitzhugh.

stiff and brittle. The chaetae are hollow and filled with liquid, and the tips have barbs, giving them the appearance of harpoons.

If an unsuspecting swimmer picks up a fireworm with their bare hand, bundles of chaetae are embedded in the skin, breaking off like little splinters. Because the interior of the chaetae are hollow, the liquid inside causes an immune reaction in victims, resulting in swelling, blistering of the skin, and inflammation; hence reference to these polychaetes as ‘fireworms.’

Bloodworms

The presence of a neurotoxin released through the jaws of bloodworms that can incapacitate their prey was presented above (see **The Diets of Worms**: *Carnivores*: Figure 13). In terms of impacts on humans, bloodworms are commonly used as fish bait. If the jaws penetrate the skin, there can be a localized reaction to the venom in the form of swelling that can last for several days.

Figure 21. Fireworms (Amphinomidae). Note the dense bundles of calcareous chaetae. Photos by Leslie H. Harris.

Yummy! Polychaetes as Food for Humans

In the South Pacific islands, such as Vanuatu, Samoa, and Indonesia, islanders use nets to scoop up thousands of swarming epitokes of Palolo worms (see **Making New Polychaetes** above; Figure 19C), and prepare them alive for meals (Figure 22). A video of the process is available at https://www.youtube.com/watch?v=s74IEsoeH5E&feature=youtu.be.

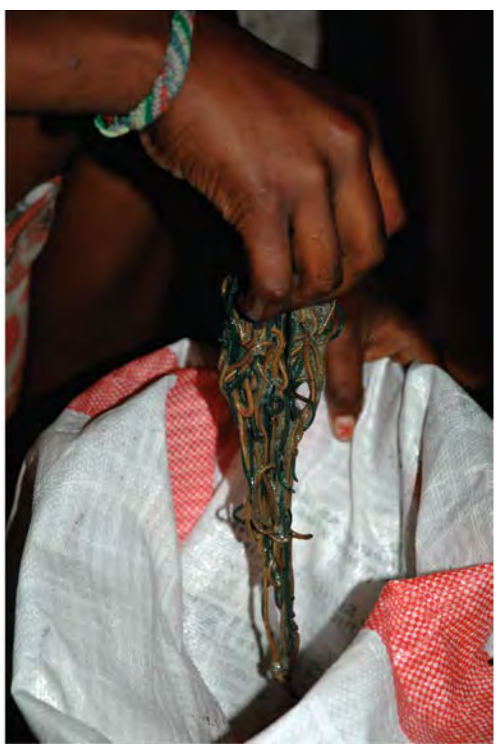

Figure 22. Freshly collected swarming epitoke polychaetes (Eunicidae, *Palolo* sp.) from Vanuatu, South Pacific. Photo by Angel Valdes.

The Polychaete Collection at the Natural History Museum of Los Angeles County

The Museum's polychaete collection represents one of the world's most important repositories for this group of organisms. Begun in 1940 at the Allan Hancock Foundation on the campus of the University of Southern California, Dr. Olga Hartman (1900–1974), one of the twentieth-century's preeminent polychaete researchers, grew the collection for over 30 years. Upon Dr. Hartman's retirement in 1969, Dr. Kristian Fauchald (1935–2015) maintained the tradition of expanding the collection from 1969–1977. Subsequent curators of the collection included Dr. John Pilger, Dr. Jerry Kudenov, Susan Williams and Leslie H. Harris. The Allan Hancock polychaete collection was transferred to the Natural History Museum of Los Angeles County in 1988, and in 1990 Dr. J. Kirk Fitzhugh, a former student of Dr. Fauchald, became Curator of the collection (Figure 23).

With over 200,000 containers holding several million specimens, the collection maintains the most comprehensive coverage of eastern Pacific polychaete species in the world. Because of its world-class status, the collection receives near-constant use by marine biologists from the west coast, and specimens are routinely lent to specialists all over the world. There is unparalleled breadth of coverage of eastern Pacific habitats, both in terms of depth (intertidal to abyssal) and volume of readily available material, as well as world-wide representation especially from Indian, Pacific, and Antarctic oceans. The collection also includes polychaetes from numerous environmental surveys from over the past 40 years in a range of depths along the coasts of Oregon, California, and Mexico.

Figure 23. A. Drs. Olga Hartman and Kristian Fauchald, 1969, at Dr. Fauchald's ph.d. graduation. **B.** Drs. Kristian Fauchald and J. Kirk Fitzhugh in Brazil, 2006. **C.** The polychaete collection room in the Natural History Museum of Los Angeles County. Photos by Daniel Dauer (**A**), J. Kirk Fitzhugh (**B**, **C**).

Suggested Reading

Books:

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Wittry, J. 2012. *The Mazon Creek Fossil Fauna*. Earth Science Club of Northern Illinois, Downers Grove.

Web sites:

Encyclopedia of Life, Polychaeta, Bristle worms: http://eol.org/pages/84/overview

BBC Nature Wildlife: http://www.bbc.co.uk/nature/life/Polychaete

Polychaetes: The Marine Worms: http://lkcnhm.nus.edu.sg/polychaete/Introworms.html

About Polychaetes: http://researchdata.museum.vic.gov.au/polychaetes/about.htm

Segmented Worms – The Polychaetes: http://australianmuseum.net.au/segmented-worms-the-polychaetes

About the author:

J. Kirk Fitzhugh, Ph.D., is Curator of Polychaetous Annelids at the Natural History Museum of Los Angeles County. His research focuses on the study of the evolutionary history of polychaetes, as well as philosophical issues regarding evolutionary biology.