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Fossil Focus: Annelids

by Luke Parry*[1]

Introduction:

Annelids, whose name comes from the Latin meaning 'little ring', make up a phylum of invertebrates with a unique segmented body plan. They are important components of terrestrial and marine ecosystems, and form one of the most diverse invertebrate groups, including as many as 15,000 described species (Fig. 1). Their closest living relatives are the molluscs, brachiopods and nemerteans (proboscis worms). Annelids can broadly be split into two groups, the polychaetes and clitellates. These groups share many features, such as segmented bodies and paired bundles of bristles made of chitin, called chaetae or setae.

The most familiar annelids are the clitellates — the earthworms, leeches and their relatives — which have become adapted to a terrestrial lifestyle, possess relatively simple tube-like bodies and have greatly reduced bristles. Polychaete annelids, by contrast, are almost exclusively marine, and have various kinds of chaetae situated on outgrowths called parapodia (Fig. 2). These limb-like extensions of the body can have a variety of functions, including locomotion and anchoring inside dwelling tubes. Polychaetes have a range of lifestyles: they can be active predators, they can feed on organic matter that has settled on the sea floor, or they can be fixed in one place and filter nutrients from the sea water.

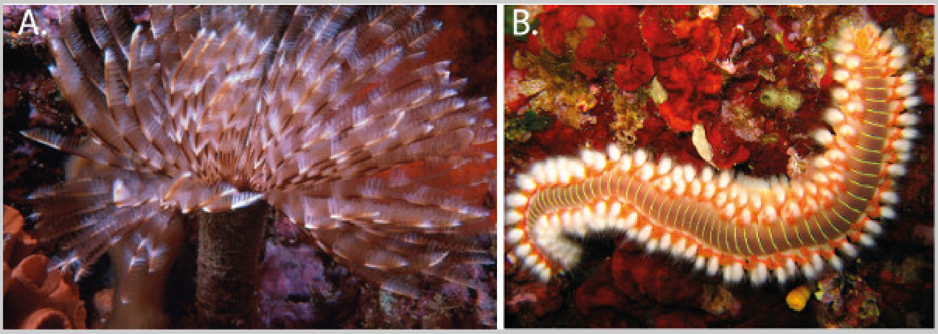

Figure 1 — A, *Sabellastarte spectabilis* a tube dwelling feather duster worm; B, *Hermodice carunculata*, a fireworm that preys on corals.

Anatomy:

Annelids have a body composed of many segments, capped at one end by the head and at the other by the pygidium. Often, the segments of their bodies are very similar, bearing repeated organ systems — an arrangement called homonymous segmentation. The body can also have regions with different types of external and internal structures, each performing specific functions. Chaetae emerge from the body wall in clitellates and from parapodia in polychaetes.

The head is composed of two components without bristles: the prostomium at the front and then the peristomium, which contains the mouth. The head can bear eyes and numerous appendages for sensing the environment and gathering food. Many annelids also have hardened jaws, and some polychaetes, such as glycerids (bloodworms), have a highly venomous bite.

The parapodia of polychaetes are diverse and often complex structures. They can bear gills, sensory tentacles called cirri, and various kinds of chaetae. Some chaetae have hooked ends that are used to anchor the animal inside a burrow or dwelling tube. Others have jointed ends that may be used to make movement more efficient. Unlike close relatives such as molluscs, annelids have a closed circulatory system for transporting blood, which is oxygenated either through gills or by gas exchange through the body wall.

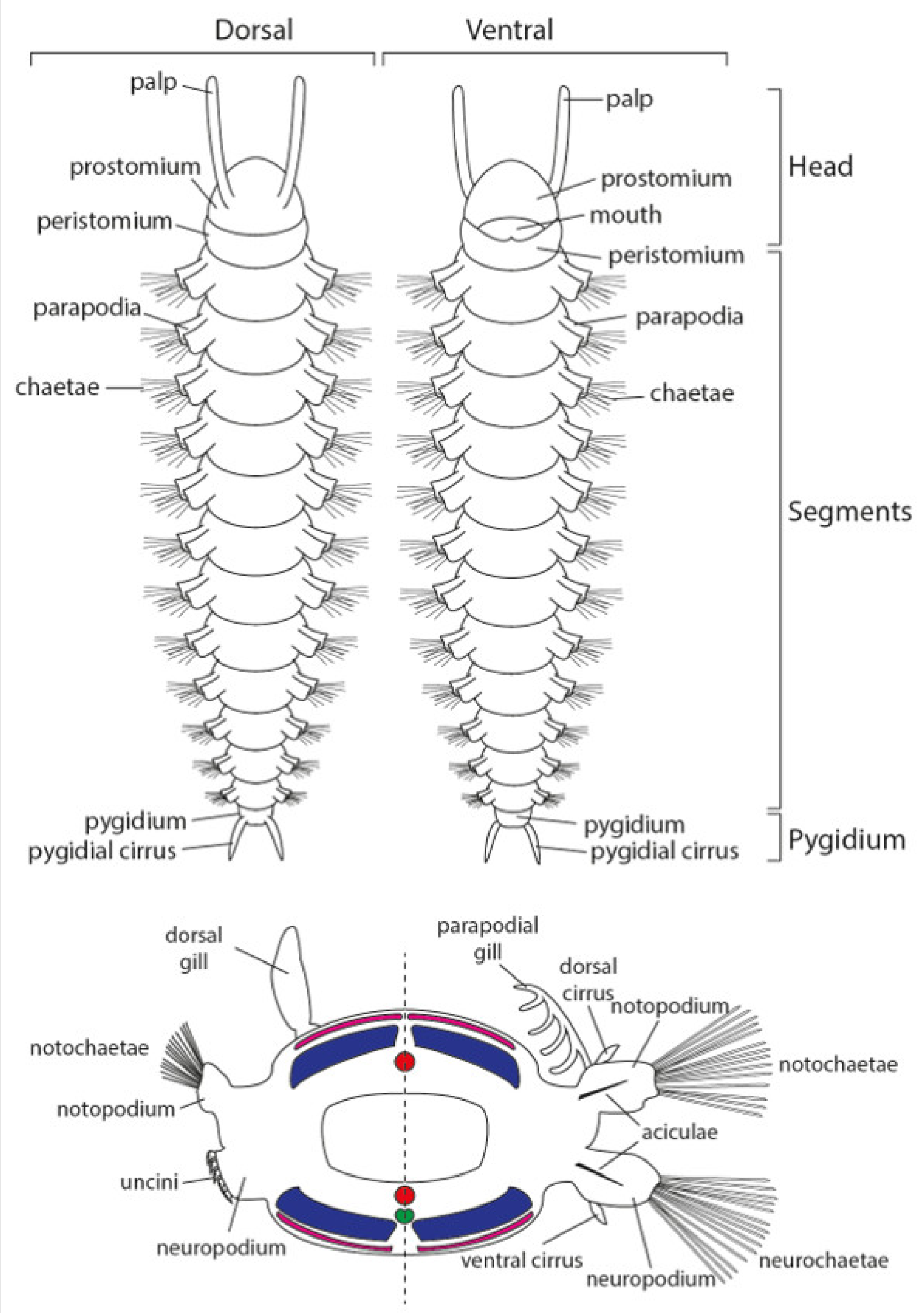

Figure 2 — Generalized polychaete anatomy: Top, dorsal (top) and ventral (bottom) view of a polychaete worm showing its segmented body, parapodia, chaetae and head and associated structures; Bottom, Cross-section showing the various external structures in polychaetes. The left view shows those that might be found in active polychaetes, whereas the right shows examples of structures in burrow- and tube-dwelling polychaetes. Red, blood vessel; green, double nerve cord; pink, circular muscle band; blue, longitudinal muscle band.

Unlike a lot of other organisms, including vertebrates, annelids have no hard parts for their muscles to act against when moving. Instead, they have what is known as a hydrostatic skeleton. They have two major muscle groups: longitudinal muscles act to shorten the body, and circular muscles act to extend it. These opposing muscles compress the fluid inside the worms' bodies, allowing them to move. The best example of this hydrostatic skeleton is found in earthworms, which use powerful peristaltic motions to burrow through terrestrial sediments. Clitellates can also be differentiated from polychaetes on the basis of their reproductive biology.ll clitellates are all hermaphrodites. The 'collar' seen on earthworms is the clitellum, a reproductive structure that gives the group its name. This secretes a cocoon, into which sperm and eggs are deposited and in which fertilization occurs. By contrast, polychaetes can reproduce asexually by budding off clones or through external fertilization, which sometimes involves a process called epitoky. In epitoky, the whole animal can transform into a swimming form capable of breeding, or clones can separate off from the back end of the worm. However they are produced, these swimming forms often have reduced digestive systems, because they live for only a short time. Their motor and sensory organs are enhanced. They swarm to the water's surface, where they shed eggs and sperm, and the eggs are fertilized.

Evolutionary relationships

Until the past decade, the relationship between the two annelid groups remained obscure, and there were two competing hypotheses about what the ancestor of all living annelids looked like. The first hypothesis suggested that the clitellate body plan evolved first, and that the annelid ancestor was a simple burrowing organism. The second hypothesis argued that polychaetes have the most primitive body plan, and that the annelid ancestor was active and lived on the sea floor, using parapodia and chaetae to move around.

DNA evidence now suggests that clitellates are more closely related to some polychaetes than to others (Fig. 3), implying that the most recent common ancestor of all annelids had a polychaete-like body plan. Fortunately, the fossil record corroborates this, and the oldest annelid fossils are polychaetes.

Evidence from DNA and body shape also suggests that polychaetes are divided into two natural groups or clades.

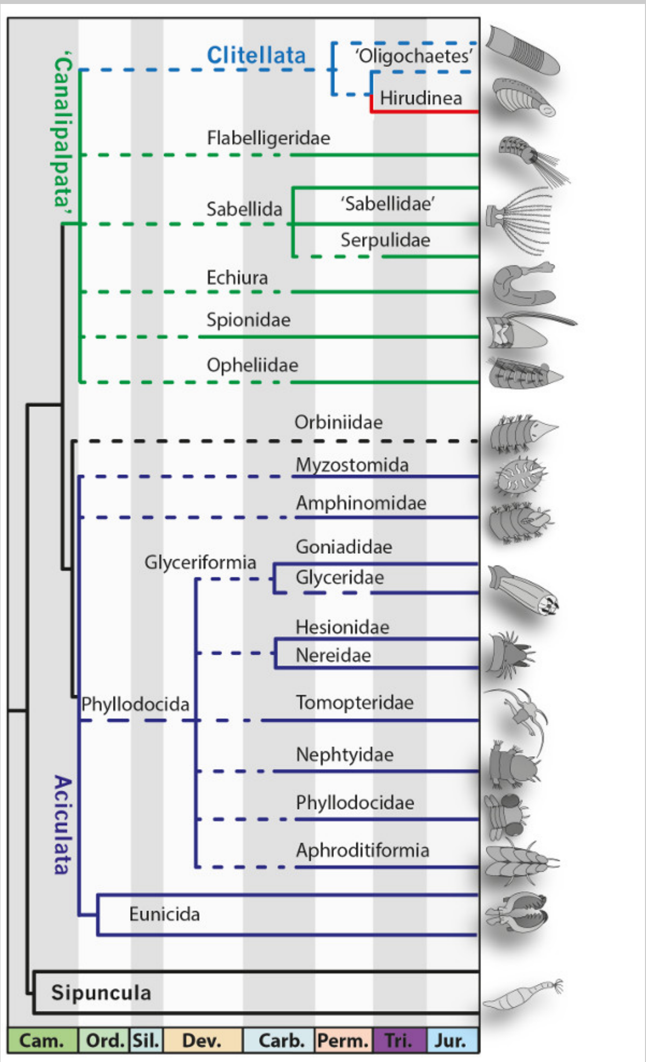

Figure 3 — Relationships of major groups of annelid worms.

The first group includes worms with active and often predatory lifestyles, which have diverse head appendages such as palps and antennae, for sensing their environment. They also have robust chaetae called aciculae inside their parapodia that aid their locomotion, as bones do in vertebrates. It is from these chaetae that the group gets its name, the Aciculata. The second group comprises more sedentary animals with palps adapted for feeding. These give the group their name, the Canalipalpata (Fig. 3).

Sipunculans, commonly known as peanut worms, are unsegmented worms that are closely related to annelids. Some studies from genetic data place them within the annelid group, whereas others place them as annelids' closest relative. The relationship remains controversial, because sipunculans have no features that would link them exclusively to annelids. If they do indeed belong inside the annelid group, they have lost segmentation, chaetae and a closed circulatory system.

The fossil record of annelids:

When organisms are fossilized, hard parts are more likely to survive than soft tissues. As a result, most annelid fossils consist of jaws and calcified dwelling tubes (Fig. 4). Under special conditions, for example when decay is suppressed or organic materials are replaced with minerals, whole annelids can be found as fossils. Such conditions, although rare, have occurred many times during the history of Earth. Figure 4A shows examples from the Carboniferous period (approximately 300 million years ago), and Fig. 5 some from the Cambrian period (approximately 500 million years ago).

Figure 4 — A, Whole-body polychaete fossil *Esconites zelus*, Upper Carboniferous, Illinois, Royal Ontario Museum 47521. Figure copyright of host institution.

The oldest polychaetes are found in early Cambrian mudstones (520 million years old) from the Sirius Passet deposit of North Greenland. Slightly younger, but equally important, early annelid fossils are found in the Burgess Shale of British Columbia, Canada, dating from the middle Cambrian (505 million years old). These fossils predate the most recent common ancestor of all living annelids, and so demonstrate features that are primitive for annelids.

The early Cambrian species *Phragmochaeta* had no head appendages; instead, it had an array of bristles around its head, which may have performed a sensory function. This fossil contains rare preservation of muscle bands in a mineral called calcium phosphate, demonstrating that paired muscle bands developed early in annelids' evolution. The heads of *Canadia* and *Burgessochaeta* from the Burgess Shale possess paired sensory palps, representing the next step in the assembly of the annelid body plan. *Pygocirrus*, from Sirius Passet, is the Cambrian fossil most closely related to living annelids, because it has sensory tentacles at the end, a common feature of many major groups of polychaetes.

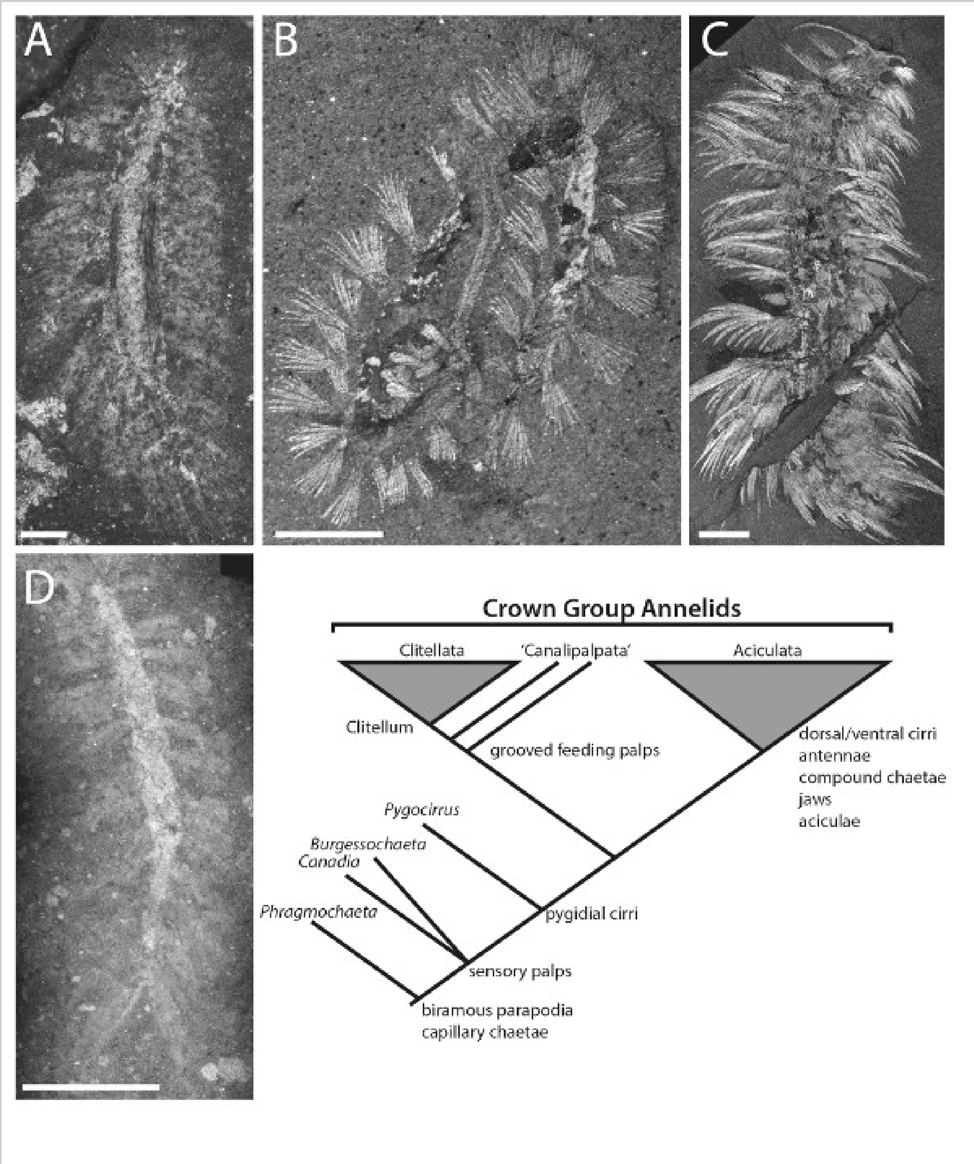

Figure 5 — Cambrian fossil polychaetes and their relationships. A, *Phragmochaeta canicularis*, Geological Museum of Copenhagen MGUH 30888, scale bar 1.5 mm; B, *Burgessochaeta setigera*, Smithsonian Museum of Natural History 198705, scale bar 2 mm; C, *Canadia spinosa*, SMNH57654, scale bar 2 mm; D, *Pygocirrus butyricampum*, MGUH 29288, showing pygidial cirri, scale bar 5 mm. All figures copyright of host institution.

These very ancient fossils show us the order in which the key components of the annelid body plan developed. They also suggest that the annelid ancestor was probably an active organism that lived on top of the sea-floor. Since the Cambrian, annelids have evolved many more modes of life, such as filter-feeding in feather duster worms, ambush predation in eunicid worms and land-dwelling in earthworms and leeches.

The machaeridian mystery

Machaeridians are a puzzling group of fossils with repeated shell plates made of calcium carbonate. They are split into three distinct families, all of which are now extinct: the plumulitids, which have armour on their top surface, and the turiliepadids and lepidocoleids, whose bodies are entirely enclosed by their shell plates. Machaeridians are rarely recovered as complete fossils, and so the majority of their fossil record is made up of individual shell plates (Fig. 6).

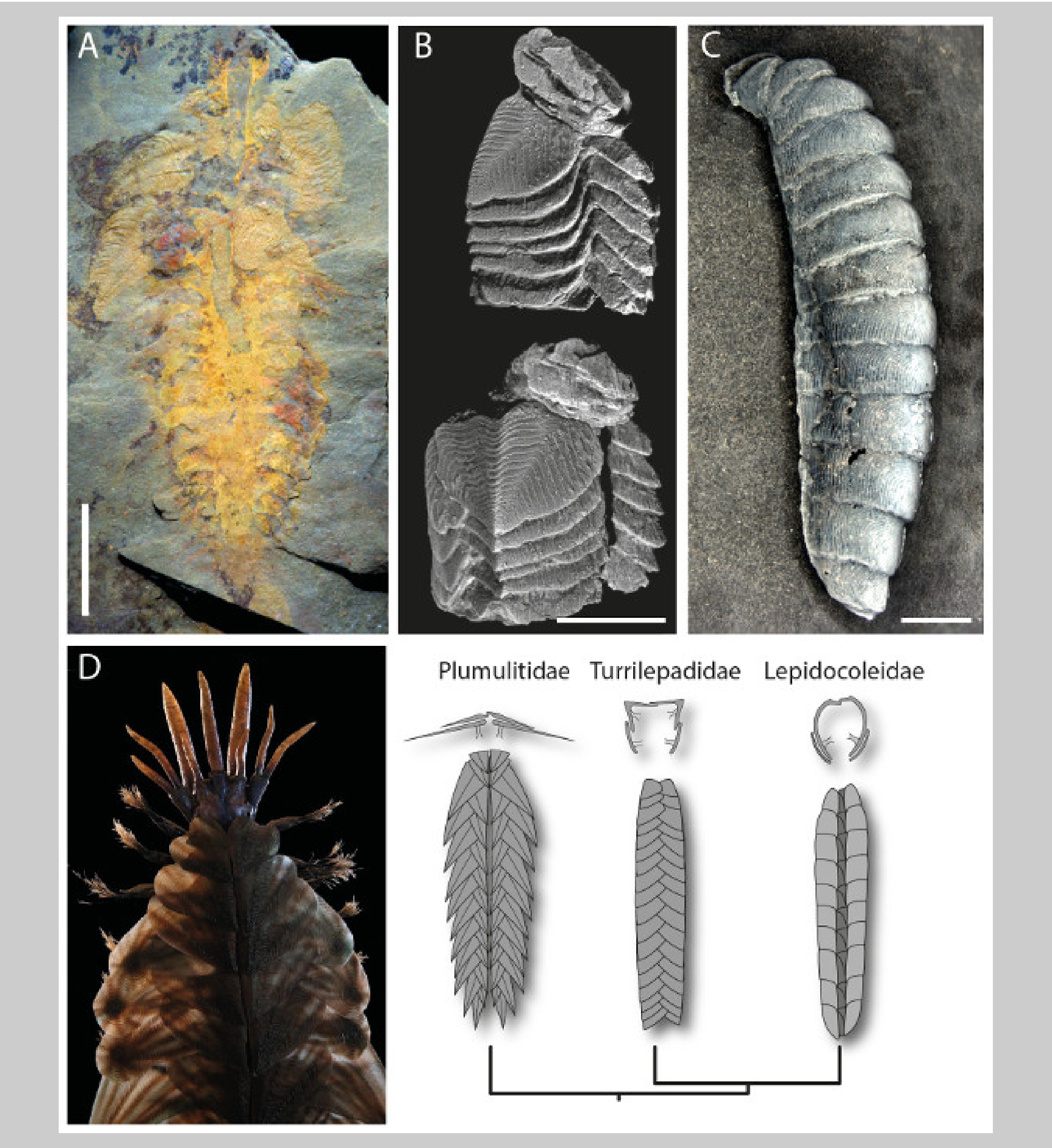

Figure 6 (previous page) — A, *Plumulites bengtsoni* showing preservation of soft tissue; scale bar 5 mm. B, *Turrilepas wrightiana*, Silurian, Gotland, Sweden, Naturhistoriska Riksmuseet 3852, incomplete specimen in different views; scale bar 5 mm. C, *Lepidocoleus sarlei*, middle Silurian, Wenlock, Rochester Shale, New York, Yale Peabody Museum IP227508; scale bar 5 mm. D, Reconstruction of *Plumulites bengtsoni* showing its shell plates and soft anatomy. Image A courtesy of Peter Van Roy, B and C courtesy of Jakob Vinther, D courtesy of Esben Horn, 10 Tons.

Since their discovery more than 150 years ago, machaeridians have been compared to many groups of invertebrates, including barnacles, echinoderms, molluscs and annelids. Without the preservation of soft parts, it proved impossible to confirm or disprove the placement of machaeridians in any of these groups. In 2007, however, a machaeridian fossil with parapodia and chaetae was discovered from the Early Ordovician period (approximately 480 million years old; Fig. 6A), confirming that machaeridians are an extinct group of armoured annelid worms. The fossils from all three subgroups can now be interpreted in light of an annelid body plan. The plumultids, with their passive armour and well-developed parapodia, are clearly the most primitive, and the turrilepadids and lepidocoleids have adapted to burrowing.

In turrelipadids, the shell plates have rib-like ornaments that are thought to have aided burrowing, like the ribs of the cockle shells that are common on modern beaches. Some lepidocoleids developed a tongue-and-groove hinge between their shell plates that would also have been aided burrowing.

Some polychaetes, such as serpulid worms, secrete calcium carbonate skeletons, but these are passive and unattached to the organism. The armour of machaeridians is therefore an entirely unique innovation early in the history of annelids, which survived for hundreds of millions of years before the group ultimately became extinct in the Permian period, by 250 million years ago.

Further reading

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