AMBULACRARIA

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Summary

The Ambulacraria is a major clade of invertebrates that are the immediate sister group to the chordates. It comprises the phyla Echinodermata and Hemichordata and the puzzling genus *Xenoturbella*, the latter being included on the basis of its molecular similarity. The morphological characters uniting Echinodermata and Hemichordata are listed, as are those that characterize each phylum separately. The five classes of echinoderm and two classes of hemichordate are brief described, and information is provided about their mode of life, development, geological history and current views on their phylogenetic relationships.

1. General Introduction

Ambulacraria is the formal name applied to a group of invertebrate animals that includes the echinoderms and hemichordates. They are exclusively marine and their origins extend back some 525 Ma to the Cambrian radiation when the earliest examples appear in the fossil record, although their actual origins probably lie slightly earlier, based on molecular clock studies. They encompass a surprisingly diverse array of animals (Figure 1). Echinoderms, with approximately 7,000 living species, are by far the largest group included here and can be stellate, globular, plant-like or worm-like in shape. All, however, display a five-fold radial symmetry and have a characteristic multiplated skeleton of calcite. Hemichordates are a much smaller group with just some 100 living species, and include both worm-like and polyp-like organisms. Finally there is the Plactosphaeroidea, a recently erected group that holds just one genus, *Xenoturbella*. *Xenoturbella* is an organism of extremely simple morphology but which has a strong molecular signature that show it belongs to the Ambulacraria.

With such a diversity of form it is not immediately obvious what unites these three groups. Nevertheless, hemichordates and echinoderms do have a remarkably similar larval stage, the larva having an anterior and two paired coeloms and a folded ciliary band that is used for feeding and locomotion. It was this similarity that first alerted biologists to their close relationship and which prompted Metschnikoff in 1881 to propose the name Ambulacraria for the grouping. A further similarity lies in the elaboration of the middle coeloms into hydraulic tentacular systems in both echinoderms and pterobranch hemichordates (the water vascular system and the paired feeding tentacles respectively). However, convincing support for uniting these animals only came when molecular phylogenetics demonstrated that all three shared many common genetic signatures.

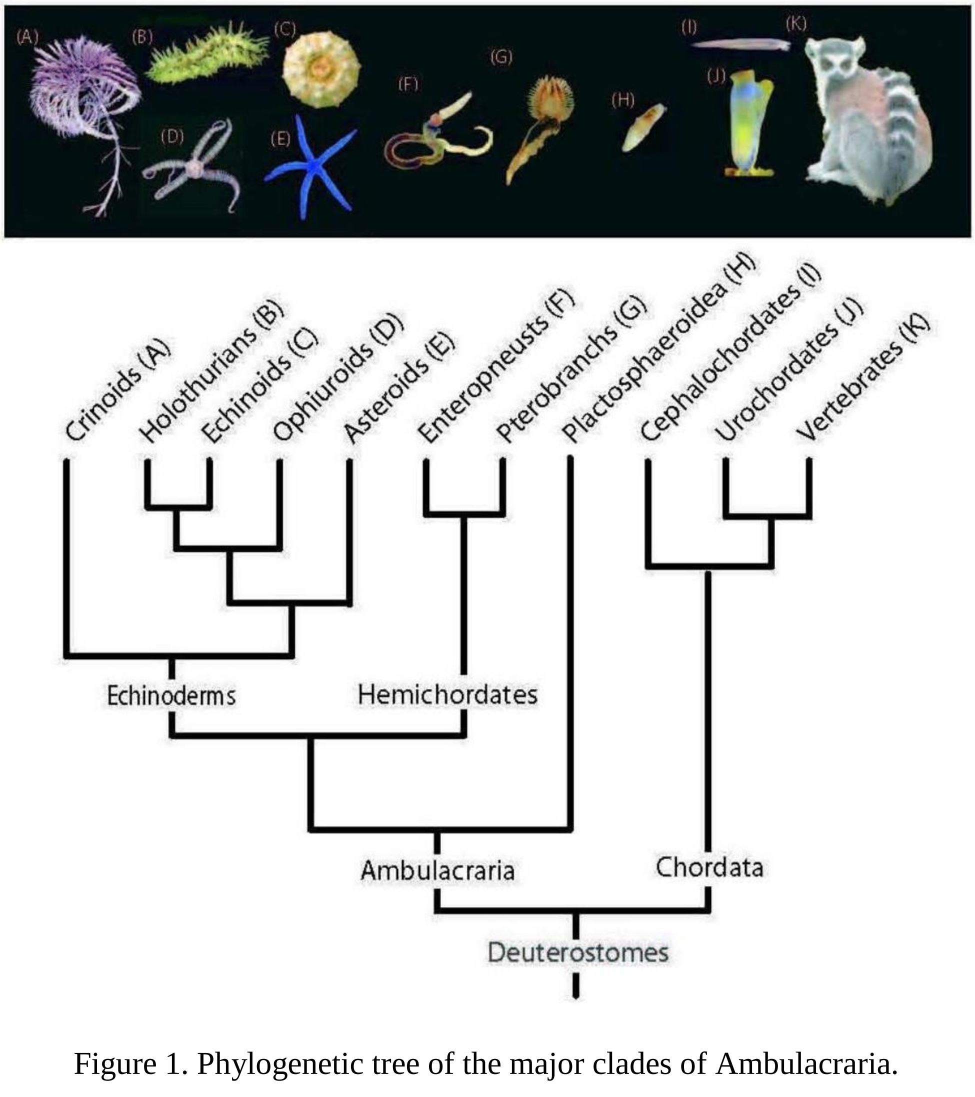

Figure 1. Phylogenetic tree of the major clades of Ambulacraria.

The ambulacraria are of very limited commercial interest as a food source, with only a few species of echinoderms (echinoids and holothurians) being seriously fished. However, they are a group of considerable scientific importance because they provide the closest invertebrate outgroup to the branch of the Tree of Life that includes ourselves. Because echinoderms have diverged further than any other animal phylum from the ancestral bilateral body plan, they provide an ideal group in which to explore the history and genetic basis for the origins of novel body plans.

2. The Echinodermata

2.1. General features

Echinoderms are an entirely marine group of invertebrates that includes such familiar animals as the starfishes and sea urchins. They are found living from the poles to the equator and from the intertidal zone to the deep-sea trenches at more than 8000 m water depth. Currently there are some 7,000 extant species, distributed amongst five classes, the Crinoidea (sea lillies), Asteroidea (starfishes), Ophiuroidea (brittle stars), Holothuroidea (sea cucumbers) and Echinoidea (sea urchins) (Figure 1). Because they mostly have a well-developed skeleton of calcite they have left a long and rich fossil record extending back 525 Ma. Echinoderms range in size from a few millimeters to over a meter, though some fossil crinoids grew to more than 26 m in length. They form a major component of the deep-sea macrofauna where their activities are important for carbon cycling, but are also a conspicuous element in many shallow water communities including reefs and algal meadows. They are mostly benthic, living on or buried within the sediment, although there is one species known to be pelagic. They adopt a variety of different feeding strategies - suspension feeding, deposit feeding, and active predation. Amongst their ranks are a number of ‘keystone’ taxa that play a critical role in maintaining the ecological balance of important communities. These include the echinod *Strongylocentrotus* that, through its grazing activities on macroalgae, is critical for maintaining diversity in kelp forests, and the starfish *Pisaster*, that acts as an important predator on mussel beds. In the geological past echinoderms have been so prolific that their skeletons are found in rock-forming abundance.

Key features of echinoderms (Figure 2) –

There are a number of features that are unique to echinoderms and set them appart from other animal phyla.

(i) Radiality. Most obviously, echinoderms have a very distinctive body plan that displays pentaradiate (five-fold) symmetry, a pattern that is unique amongst the animal phyla (Figure 2A-C). Whereas other higher metazoans have a body plan that is basically bilaterally symmetrical, echinoderms have radically departed from this, with a radial arrangement of appendages derived ultimately from a single larval coelom, originally one of a pair. This has resulted in some confusion about what corresponds to anterior and posterior or dorsal and ventral in an adult echinoderm, and for that reason workers usually orientate by referring to oral and aboral. While some groups such as irregular echinoids and holothurians, have a bilateral organization, this is clearly secondary and superimposed onto an original pentaradial body plan.

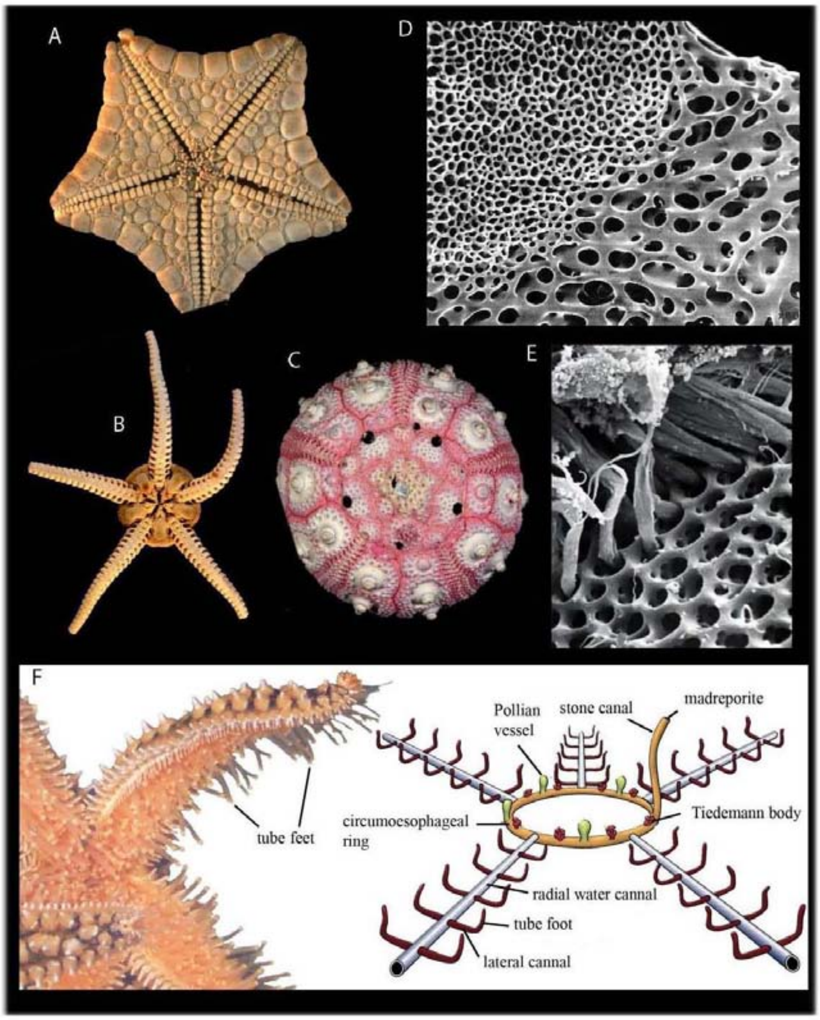

Figure 2. Echinoderm synapomorphies. A, B, Pentaradial symmetry, as shown by an asteroid (A) and ophiuroid (B). C, The skeleton of an echinoid showing the individual plates it is constructed of. D, E, Scanning electron micrographs of the skeleton of an echinoid showing the characteristic stereom structure (D) and the way in which soft tissue fills the pore space (E). F, The water vascular system in an asteroid. The left hand figure shows the external tube-feet and the right hand figure is a schematic diagram of the complete system (courtesy of Samuel Zamora).

(ii) Skeleton. Echinoderms have a calcitic skeleton that forms in the mesoderm and is therefore covered in skin throughout life. This skeleton is used for both support and protection. It is made up of a series of plates (Figure 2A, C) each of which acts as a single calcite crystal, yet has a unique three-dimensional mesh-like construction of interconnected rods termed stereom (Figure 2D). The family of genes responsible for controlling stereom production are unique to echinoderms. Calcite is deposited extracellularly in a syncitium of cells and the individual rods are built up of tiny nannoliths some 20 nm in size deposited in optical continuity and with almost no intervening organic matrix. The interconnected voids within each plate are filled with mesodermal tissue (termed stroma) including ligamental tissue that can bind plates together (Figure 2E). Stereom is thus a strong, lightweight material with a construction that inhibits crack propagation. Chemically it is a high Magnesium calcite, with usually around 8-15 % of Magnesium ion content. In places where the skeleton needs to be particularly strong and resistant to abrasion, as in the core to the teeth and at articulation surfaces, the Magnesium content can reach almost 50%. While most echinoderms have a fully formed interlocking skeleton of plates some have reduced their body-wall elements to microscopic spicules and a few holothurians are naked, without body-wall spiculation. A calcite skeleton is found in the larvae of echinoids, ophiuroids and some holothurians but is absent from the larvae of crinoids and asteroids.

(iii) Water vascular system (Figure 2F). The water vascular system is a series of fluid-filled tubes that function as a hydraulic system and which include the tube-feet, one of the most versatile and important organs in the echinoderm body. Tube feet are blind-ending tubes that protrude from the body and which usually end in a small disc. They can be extended by pumping water into them from internal fluid reservoirs (ampullae) and are contracted by muscles in their stalk. They serve a variety of important functions, being used in feeding (particle capture and manipulation), adhesion and locomotion across the sea floor, and for effecting gaseous exchange. The system originates from the middle of the three sets of larval coeloms, with the right axocoel giving rise to a ring around the mouth from which radial tubes emerge, one to each of the five ambulacral rays [in multiarmed echinoderms each arm has its own radial water vessel]. It is from these radial vessels that the tube-feet branch. The left axocoel is very much reduced by comparison, giving rise to only a short tube (the stone canal) that runs from the circumoesophageal ring to the exterior (Figure 2F). Ciliary activity through this opening keeps the fluid level in the system topped up.

(iv) Development (Figure 3). Echinoderms undergo a complete metamorphosis during development. While this is not unusual by itself, the path that is followed is unique. After fertilization, which in almost all cases occurs externally after release of egg and sperm into the water column, a bilateral larva develops that migrates into the water column to feed. These larvae show a diversity of structure but all have a folded ciliary band, which is used for both locomotion and feeding. Larvae have a mouth, anus and simple digestive tract, but there is also a cluster of some 200 set aside cells that are not used. After feeding for a few weeks the set aside cells begin to form the adult, while the larval features start to be resorbed, with typically just part of the larval stomach being retained into the adult. It is at this stage that the left hydrocoel begins to develop outpouches, establishing a pentaradial pattern of growth. Echinoderms thus start life with bilateral symmetry and during metamorphosis pass through an asymmetric stage that involves torsion and the resultant suppression of the left-hand coeloms, before finally pentaradiality comes to dominate. Thus the echinoderm water vascular system is homologous to just one of the pair of pterobranch hemichordate tentacles.

(iv) Hox gene expression. Linked to their unusual development echinoderms are one of the few groups know to have broken the direct association between Hox-gene expression and the morphological anterior-posterior axis. Hox genes are an important family of genes responsible for primary body patterning in animal phyla. In all bilaterian animals there is a direct co-linearity between the position where specific Hox genes are expressed and the primary body axis, with anterior Hox genes being expressed towards the anterior of the animal and posterior hox genes towards its posterior. This arrangement is also true for larval echinoderms, but with metamorphosis and the resulting torsion of organs, this colinearity breaks down and the adult rudiment develops under a complex mixture of Hox gene signals. By breaking the colinearity of Hox-gene expression and morphological anterior-posterior development, echinoderms have been freed from the usual constraints that control bilateral development.

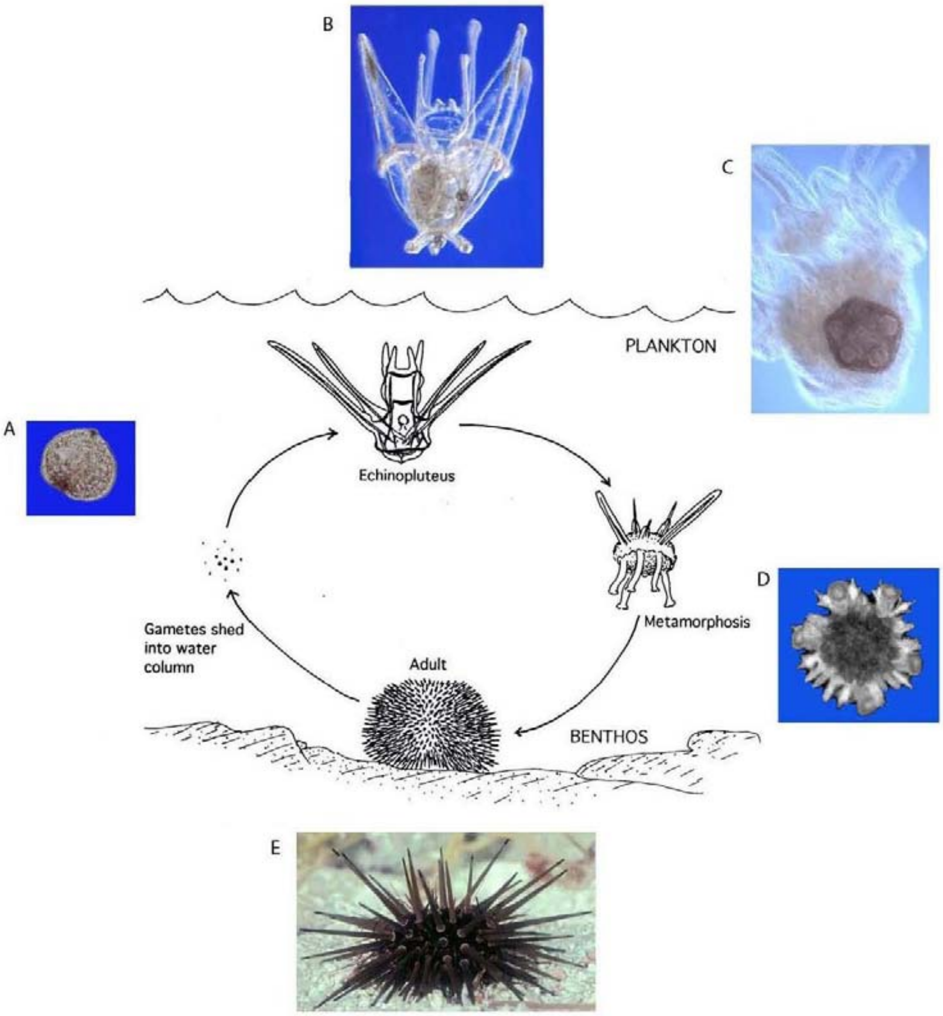

Figure 3. Life history cycle for an indirect developing sea urchin. A, fertilized egg; B, echinopluteus larva; C, late stage larva with adult rudiment clearly visible; D, immediately post-metamorphic juvenile; E, adult (larval photographs courtesy of Greg Wray).

(v) Nervous system. Despite being rather advanced organisms, nested high within the Bilateria, echinoderms have a remarkably simple nervous system. There is no centralized brain or ganglion complex that controls the animal's behavior. Rather the nerve plexus spread across the body acts as a diffuse control system.

(vi) Mutable collagenous tissue. Echinoderms have a unique collagen-based tissue that can change its mechanical properties under nervous control over a matter of seconds. This Mutable Collagenous Tissue (MCT) forms a number of important roles in all classes, and unlike muscle, in its stiffened state provides rigidity at no expense of energy. MCT also allows autotomy of body parts and the spectacular ‘melting’ of holothurian dermis.

Evolutionary relationships - The evolutionary relationships of the five extant classes of echinoderm are now largely resolved. Morphological and molecular evidence both point to crinoids as being the sister group to other echinoderms and to the echinoids and holothurians being sister groups. More uncertain has been the relationships of asteroids, ophiuroids and the clade echinoids+holothurians (=Echinozoa). Morphological arguments have been put forward both for pairing asteroids and ophiuroids, and for pairing ophiuroids and echinozoans, while molecular evidence has come up with a range of different topologies depending upon the gene examined and method of analysis used. The most recent analysis shows that the most reliable molecular signal supports an ophiuroid+echinozoan pairing while the signals for asteroid+echinozoan or asteroid+ophiuroid largely come from fast evolving and thus largely unreliable sites. Our best current estimate of class relationships is shown in Figure 1.

For the most part homology of the major body regions of echinoderms is fairly straight forward and is tied to development of the radial water system (e.g. EAT theory). The globular echinoids for example have evolved by drastically curtailing development of their aboral (extraxial) surface, which in starfishes forms the upper half of the body. By contrast the aboral surface in crinoids is hugely extended to form the long stalk.

Echinoderms have a rich fossil history that reveals a diverse set of body plans existed in the past. Most interesting are the asymmetric and near bilaterally symmetric stem-group fossils of the early Palaeozoic informally known as carpoids (see below). These fossils reveal a stage in echinoderm evolution that preceded the acquisition of radial symmetry and show that these early forms, like other deuterostomes, primitively had pharyngeal slits.

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Bibliographical sketch

Andrew B. Smith studied Geology at the University of Edinburgh and then completed a Ph. D. in Biological Sciences on echinoid structure and function in 1978. After a short spell as a post-doctoral researcher at the University of Liverpool he joined the Natural History Museum, London in 1981 where remains to this day. He is currently an individual merit promotion researcher in the Department of Palaeontology and is a fellow of the Royal Society and Royal Society of Edinburgh. His work encompasses all aspects of echinoderm biology and evolution, from their earliest fossil record to their molecular phylogeny. Much of his work focuses on the evolutionary history of echinoids.