

Evolution Within a Bizarre Phylum: Homologies of the First Echinoderms¹

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SYNOPSIS. The Extraxial/Axial Theory (EAT) of echinoderm skeletal homologies describes two major body wall types: axial and extraxial. The latter is subdivided into perforate and imperforate regions. Each of the regions has a distinctly different source in early larval development. Axial skeleton originates in the rudiment, and develops in association with the pentaradially arranged hydrocoel according to specific ontogenetic principles. Perforate and imperforate extraxial regions are associated with the left and right somatocoels respectively, are not governed by ontogenetic principles of plate addition, and are products of the non-rudiment part of the larval body. The morphology of even the most bizarre of the earliest echinoderms can be explored using the EAT. Among these, edrioasteroid-like taxa best fit the idea that forms expressing archimery in the sequential arrangement of axial, perforate extraxial, and imperforate extraxial regions are the first echinoderms. Metamorphosis is especially marked in clades that have a high axial to extraxial skeleton ratio because structures developing from the non-rudiment part are suppressed in favor of the developing axial elements during this process. However, in early echinoderms, extraxial skeleton makes up a far larger proportion of the body wall than axial, implying that metamorphosis was not as significant a part of the developmental trajectory as it is in more recently evolved taxa. Echinoderm radiation consists of a succession of apomorphies that reduced the expression of extraxial components but increased the influence of axial ones, with a concomitant increase in the prominence of metamorphosis.

INTRODUCTION

The familiarity of a seastar or a sea urchin belies their overall weirdness. Not only are they quite different from each other, together with all the other members of the Echinodermata, they form a clade very disparate from all other phyla. Students of metazoan evolution learn that echinoderms can be distinguished by the possession of a water vascular system, mesodermally derived calcite plates with trabecular structure (stereom) in the body wall, and a distinctive embryology in which the typically bilateral larvae seem to be magically transformed into the pentaradial adults. The frequency and oddity of these patterns is impressive. But when echinoderms are viewed in the light of some overarching principles that in-

tegrate all of these and other characteristics, they form an excellent model for testing ideas about the origins of evolutionary novelty in general.

It is not surprising that the origin and subsequent radiation of the Echinodermata has become at once a compelling and perplexing research program. Even the briefest of surveys of adult echinoderms, fossil and extant, will reveal a clade rich in morphological disparity and unfamiliar structures. Such fertile ground has yielded a diverse crop of phylogenetic analyses drawn from morphological (*e.g.*, Paul and Smith, 1984; Smith, 1988*a, b*, 1990; Sumrall, 1997), molecular (*e.g.*, Raff *et al.*, 1988; Wada and Satoh, 1994), or total evidence data (*e.g.*, Littlewood *et al.*, 1997). Works dealing with morphology contain valuable data about possible synapomorphies of major echinoderm clades, but none of them incorporate the kind of overarching model of homologies that seems a necessary step in trying to sort out the confusion that still exists.

¹ From the symposium *Evolutionary Relationships of Metazoan Phyla: Advances, Problems, and Approaches* presented at the Annual Meeting of the Society for Integrative and Comparative Biology, 3–7 January 1998, at Boston, Massachusetts.

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Phylogenetic analyses are only as good as the characters they employ. They should rest on careful character analyses, taking advantage of all that we know about echinoderm anatomy, ontogeny, and paleontology to test homologies. Attempts to accomplish these analyses have been hampered by the lack of a detailed scheme of basic homologies such as the well-known model of cranial and post-cranial elements in the vertebrates.

Mooi *et al.* (1994) suggested a scheme within which homologies of skeletal elements of the echinoderms could be evaluated. Subsequent works (David and Mooi, 1996, 1998; Mooi and David, 1997) have elaborated on these ideas, including a synthesis with preliminary phylogenetic analyses (Mooi and David, 1997). It is the purpose of the present work to build on these concepts by focusing on the earliest events in the phylogeny of the Echinodermata. In this way, we should be able to develop a picture not only of how the phylum originated, but also of the salient features of the first echinoderms. To explore these points, we summarize the most significant parts of a model of skeletal homologies and the ways in which they relate to embryology. We then apply these principles to a variety of Cambrian taxa widely considered to represent the most basal members of the Echinodermata. We also use the model to draw some inferences about the significance of embryology in understanding the origin and diversification of the phylum.

THE EXTRAXIAL-AXIAL THEORY (EAT)

The EAT encompasses two main sources of data from both fossil and extant taxa. The first concerns body wall morphology and the contained skeletal elements. The second concerns embryological patterns. The following is an abbreviated account of these main aspects of the EAT.

Skeletal homologies

The EAT grew out of observations of basic ontogenetic differences in two main types of echinoderm skeleton: extraxial and axial (Mooi *et al.*, 1994). In extraxial skeleton, new skeletal elements can be added anywhere within the extraxial region. There

are no ontogenetic organizing principles applicable to all echinoderms that govern the timing and pattern in which extraxial elements are added during growth. Extraxial skeleton can be further subdivided into two recognizable portions. Perforate extraxial skeleton is pierced by several types of orifices not found in any other type of skeleton. These openings include epispires, hydrospores, gonopores, and the periproct (which contains the anus). Because of great variation among echinoderm clades, a large number of plate systems have been named that fall under the general category of perforate extraxial skeleton. The most important of these are thecal plates such as the radials and basals of some pelmatozoans, and plates associated with the aboral surfaces of arms such as the abactinals of asterooids and the brachials of crinoids. An expanded list can be found in Mooi and David (1997, Table 1). Imperforate extraxial skeleton is virtually absent in the living taxa except crinoids. It appears to be restricted to stems, holdfasts, and the surface opposite the mouth in earlier forms such as edrioasteroids.

In contrast to extraxial skeleton, axial skeletal elements are added according to an empirically derived set of principles gathered under the Ocular Plate Rule (OPR). The OPR embodies a number of broad concepts applicable to all members of the phylum: 1) axial elements form in association with the growing radial canals of the water vascular system; 2) new axial plates are added in a blastema at the end of growing ambulacral series (this can occur in association with an ocular, or terminal plate, but this region is not calcified in all clades); 3) the newest plates in the series are at the tip of the ambulacrum, and the oldest are adjacent to the mouth (in taxa with a calcified ocular or terminal, this axial element always appears before the first ambulacral elements proper); 4) in almost all echinoderms, the new plates form a biserial sequence of ambulacral plates, and each ambulacral is associated with a tube foot (departures from this pattern, such as uniseriality or multiple podia per plate, are demonstrably derived); 5) the paired columns of each axial series are staggered, so that

there is a zig-zag suture separating the 2 columns in the biserial sequence; 6) a very important consequence of the OPR-driven, staggered addition of plates in each biserial ray of the axial system is that one of the two first plates must appear before the other in the early juvenile. This creates a strongly canalized pattern in all echinoderms in which this phenomenon has been investigated, and is known as Lovén's Rule. The implications of Lovén's Rule have been discussed in the context of echinoderm evolution by David *et al.* (1995) and Hotchkiss (1995). Axial skeleton includes all elements in the body wall added according to the OPR, such as terminals (oculars), ambulacral flooring plates, cover plates, basicoronal (=mouth frame) plates, and adambulacral plates (Mooi and David, 1997, Table 1).

Embryological homologies

The morphological criteria for recognizing the major skeletal types in echinoderms are grounded in underlying embryological patterns that are correlated with these body wall regions (David and Mooi, 1996, 1998). So much has been written on echinoderm embryology (summarized in Hyman, 1955; Giese *et al.*, 1991, *inter alia*) that we cannot hope to produce a better précis here except to highlight events relating to the EAT.

The generalized pattern of development for echinoderms can be summarized as follows: 1) the zygote passes through typical deuterostome blastula and gastrula stages; 2) three pairs of coelomic compartments appear along the longitudinal axis of the gastrula, the first pair forming a prosome, the second a mesosome represented most conspicuously by a hydrocoel on the left side of the larva, and the third a metasome consisting of left and right somatocoels (archimery of Nielsen, 1995); 3) the hydrocoel forms a torus (which becomes the ring canal in adults) around the larval esophagus; 4) five primary lobes appear along the perimeter of the hydrocoel ring, elongating to form the five radial canals of the adult; 5) the left somatocoel, which comes to lie under the hydrocoel, interacts with the latter to produce the rudiment; 6) the rudiment evaginates and interacts to varying degrees with the non-rudiment part of the larval

body to produce the adult morphology (metamorphosis).

Axial skeleton is strictly associated with the rudiment. The first skeletal elements of the axial system appear adjacent to the primordial lobes. New plates in the developing ambulacral system are laid down according to the OPR in the zig-zag pattern described above. As plates are added, the radial canals elongate, increasing the distance between the base of the primordial lobe (the terminal tentacle in the adult) and the ring canal.

During metamorphosis of living taxa much of the non-rudiment portion of the body is lost or histolyzed. However, significant portions of non-rudiment coelomic and skeletal components are retained into adulthood in some clades, such as crinoids and asteroids. Calcified portions of the larval body wall develop into the extraxial skeleton. Therefore, the two major divisions of echinoderm body wall, axial and extraxial, are derived from the rudiment and the non-rudiment parts of the larva, respectively, indicating that the two skeletal types are distinguished by early ontogenetic divergences (David and Mooi, 1996).

THE EARLIEST ECHINODERMS

Previous works on the morphology and relationships of early echinoderms have greatly expanded our knowledge of these enigmatic forms. Smith (1985, 1988a, b, 1990) provided cladistic treatments and carefully rendered reconstructions. Sprinkle (1992) reviewed features of the early radiation of echinoderms, and Sumrall (1997) published comments and provided a tree for many taxa, including the earliest forms. The EAT has been used to construct a basic phylogeny upon which more focused analyses can be based (Mooi and David, 1997; David and Mooi, 1998). Here we integrate earlier works with that scheme in order to comment on specific taxa of early echinoderms, and to elucidate some of the homologies that are revealed through application of the EAT.

Some taxa thought to be basal echinoderms are not considered so here. For example, homalozoans are frequently placed in a sister clade to the rest of the echinoderms (*e.g.*, Paul and Smith, 1984; Sprin-

kle, 1992). The strangeness of the homalozoans has made it difficult to find homologies shared with other echinoderms. The absence of recognizable synapomorphies is frequently responsible for the removal of odd taxa from a given group, so the homalozoans have, almost by default, been placed basally in echinoderm phylogeny. Like Sumrall (1997), we feel that homalozoans originate higher up in the tree, and that their morphology, interpreted through the EAT, is much better understood as highly specialized rather than as indicative of basal forms. They are clearly a very old group, but evidently no older than other early echinoderms (*e.g.*, Smith, 1988*b*), so their removal from the base of the tree does not introduce significant stratigraphic gaps. We have been able to use the EAT to make some sense of these bizarre fossils and have found that our interpretation is largely in accord with that of Ubaghs (1968) and Parsley (1997). The EAT provides no support for the calcichordate scenario (see, for example, Jefferies, 1997), nor does it suggest that homalozoans shed light on the origins of the phylum itself.

"Edrioasteroid-like taxa"

The Edrioasteroidea is an extinct class of echinoderms that had relatively small, flattened, disk-shaped bodies. They were sessile, with the aboral surface attached to a hard substrate. The mouth, with five, often curved ambulacra radiating from it, faced upwards (Fig. 1). The Edrioasteroidea have been considered to include taxa such as *Camptostroma*, *Stromatocystites*, *Edriodiscus*, and *Cambraster* (Sprinkle, 1992; Guensburg and Sprinkle, 1994). Smith (1985) showed phylogenetically that the first two of these taxa should be excluded from the Edrioasteroidea, and placed more basally than the rest of the edrioasteroids. Although we agree with this assessment, Mooi and David (1997) question the placement of *Edriodiscus* in a position that would imply its involvement in the origin of the seastars and would remove *Cambraster* from this position as well. The synapomorphies that link *Edriodiscus* and *Cambraster* to the seastars (Smith, 1985) are undermined by the application of the

EAT, particularly those concerning the possession of a marginal ring (Mooi and David, 1997; see below).

Mooi and David (1997, Fig. 7) use the term "edrioasteroid-like taxa" to refer to early echinoderms with a basic edrioasteroid body plan, but that are not necessarily part of the more crownward Edrioasteroidea. In addition to crownward edrioasteroids, taxa such as *Cambraster* and *Edriodiscus* fall into this category, as do *Camptostroma* and *Stromatocystites*. Although we do not consider the latter two as members of the Edrioasteroidea, their morphology and age suggest that they are among the earliest echinoderms (Smith, 1988*a, b*, 1990; Sumrall, 1997). Here we examine aspects of the major skeletal types of the EAT that support this assertion.

Axial skeleton in basal echinoderms

The axial skeleton of the earliest echinoderms is relatively poorly expressed when compared to that of extant taxa such as asteroids and echinoids. In edrioasteroid-like taxa, the rays are very narrow, and their surface area is only a small percentage of the oral region (Fig. 1). However, axial elements of these basal forms are subject to the same principles that govern ontogenetic patterns of living echinoderms, as exemplified by *Stromatocystites* depicted in Paul and Smith (1984) and Smith (1985). The rays are made of flooring plates laid down in a biserial, zig-zag pattern according to the OPR, with the oldest plates adjacent to the mouth, and the youngest at the tips of the rays. The flooring plate series was embedded in the surrounding body wall that constitutes the rest of the oral surface (Fig. 1). The radial water vessel lay externally along the perradial suture of the flooring plates and evidently terminated adjacent to the youngest plates in each ray (Fig. 1). Because the ring canal of the water vascular system encircles the esophagus internal to the axial system, the radial canals must have passed through the proximal notches between the first pair of axial plates that constitute the circum-oral mouth frame ("primordial ambulacral plates" of Smith [1985, Text-Fig. 7]). The flooring plates of edrioasteroid-like taxa are homologous with

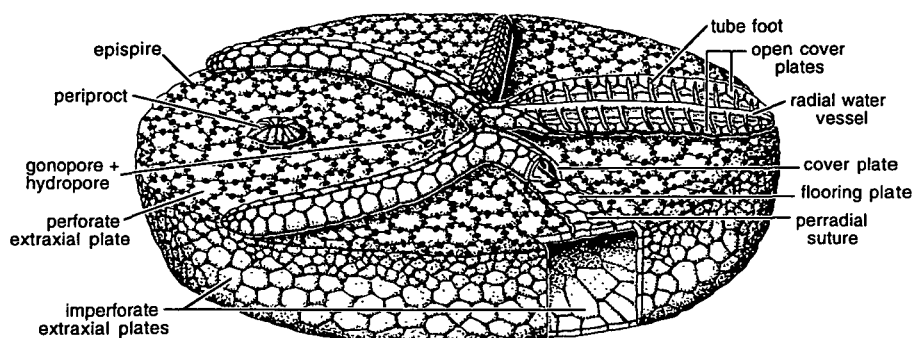


FIG. 1. Morphology of an edrioasteroid-like early echinoderm (based primarily on *Stromatocystites*). Extraxial elements are labeled on the left side of the figure, axial elements on the right.

the ambulacral plates of asteroids and echinoids, and the zig-zag suture is homologous with the perradial suture of extant forms. The outer edges of the flooring plates supported 2 series of cover plates forming thin, contiguous sets that could be folded to meet over the center of the flooring plates (Paul and Smith, 1984) (Fig. 1). Their association with tube feet (Paul and Smith, 1984, Fig. 13) further supports the axial nature of cover plates. The axial rays of the earliest echinoderms were not perfectly pentaradial, exhibiting instead a bilateral arrangement known as the 2-1-2 pattern (Sprinkle, 1973, Text-Fig. 16, 1992). This pattern appears to be plesiomorphic for the echinoderms in general. It is modified into a more perfectly stellate, pentaradial pattern in later taxa such as blastoids and independently in the clade containing asteroids and echinoids.

David *et al.* (1995) and Hotchkiss (1995) virtually simultaneously discovered compliance with Lovén's Rule in *Stromatocystites*. Lovén's Rule appears to represent deep-seated expression of a pattern fundamental to the OPR. The discovery that it operates in basal taxa as well as in most crownward extant forms suggests that it should also be expressed in some way or another in intervening clades such as crinoids and cystoids. That it has not yet been found in these groups underscores the pragmatic difficulties of a search that needs to be conducted in precisely the right place. Lovénian patterns must be sought in the order in which flooring plates are laid down. This is es-

pecially problematic for the crinoids, in which flooring plates of modern species are evidently uncalcified, and for cystoids in which the pattern is obscured by cover plates, extraxial elements, or by reduction in the number of rays. The report by Hotchkiss (1995, Fig. 3) that Lovén's Rule occurs in the cover plates of the edrioasteroid *Astrocystites* may or may not be a valid expression of the Rule. Until flooring plates of *Astrocystites* are observed, adherence to Lovén's Rule cannot be proven. In contrast, cover plate or brachiole origination patterns in cystoids cannot be used to falsify the occurrence of Lovén's Rule in these taxa without determining the pattern of formation of the first flooring plates.

Extraxial skeleton in basal echinoderms

In the earliest echinoderms, extraxial skeleton is by far the greatest constituent of the body wall, and the distinction between perforate and imperforate extraxial regions is more clearly expressed (Fig. 1). The boundary between the two extraxial regions can be marked by a change in the type of plating, as beautifully reconstructed in *Camptostroma* and *Stromatocystites* by Paul and Smith (1984, Figs. 5, 6), or by a distinct marginal ring as shown in *Cambraster* (Smith, 1985, Text-Fig. 2).

The perforate extraxial skeleton of edrioasteroid-like taxa surrounds the axial skeleton on the oral surface. In *Camptostroma*, it is constructed of two major plate types: stellate elements and secondary elements (Paul and Smith, 1984). These plates

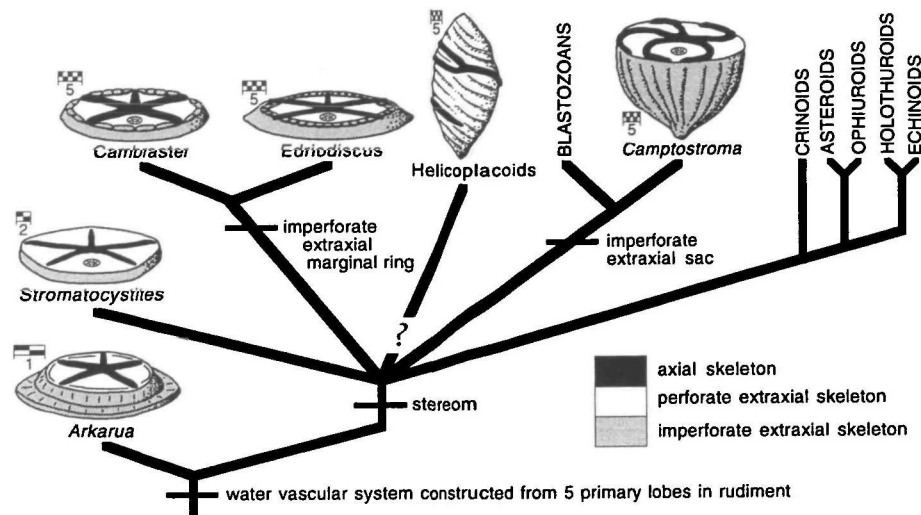


FIG. 2. Morphology of basal echinoderms mapped onto a provisional phylogeny of these forms and selected major clades. Pending further analysis, helicoplacoids are provisionally shown without shading except for axial skeleton. Topology adapted from Mooi and David (1997). Scale bars in mm.

form a monolayered lattice with sutural pores known as epispires that probably supported respiratory "soft, papulae-like extensions" (Sprinkle, 1973, p. 30) similar to those of modern seastars. In early forms, the hydropore and gonopore were situated near the mouth, and the periproct near the edge of the oral surface, all in the same posterior interradius (Fig. 1).

Previous surveys of the relative expression of body wall regions in all the Echinodermata (e.g., Mooi *et al.*, 1994), suggest that an enhanced capability to modify degree of expression is a hallmark of extraxial skeleton. Imperforate extraxial skeleton is particularly variable in the degree to which it is expressed, even among the Cambrian taxa discussed so far. In *Camptostroma*, it is strongly developed, extending as an aboral sac composed of numerous, isotropically arranged platelets (Fig. 2). In *Stromatocystites*, the plates are larger and tessellate, and the entire imperforate extraxial skeleton makes up a smaller percentage of the overall body wall (Fig. 2). As Paul and Smith (1984) implied, it is relatively easy to move from the morphology of *Stromatocystites* to that of *Camptostroma*. The EAT supposes that this transition occurred by enhancing the production of imperforate extraxial skeleton. Other differences among

the early echinoderms can be ascribed to alterations in the expression of perforate and imperforate extraxial regions.

Forms such as *Edriodiscus* and *Cambraster* evolved a specialized set of extraxial plates called marginals by Smith (1985) and Smith and Jell (1990) who homologized them with similar structures in *Archegonaster* and certain seastars. The EAT does not support this proposed homology (Mooi and David, 1997) because the rings of edrioasteroid-like taxa appear to be derived from imperforate extraxial elements. As such, the ring forms a boundary between perforate and imperforate regions (Fig. 2). In asteroids, the ring is derived from perforate extraxial elements, and is wholly enclosed by perforate extraxial plates. The strong negative correlation between the thickness of an echinoderm's body and the degree to which marginal rings are expressed suggests selection for peripheral elements that contribute to the structural integrity of a flattened body. Edrioasteroid-like echinoderms also seem to be subject to this phenomenon.

Arkarua and the helicoplacoids: Even earlier echinoderms?

Arkarua is a poorly preserved, tiny Precambrian (Ediacaran) fossil that has been

described as an echinoderm (Gehling, 1987; Smith, 1990; Smith and Jell, 1990; Mooi and David, 1997; David and Mooi, 1998; but see Sprinkle and Guensburg, 1997). However, it appears to have lacked one of the synapomorphies most often used to support monophyly of the Echinodermata: the presence of calcium carbonate stereom. This does not negate the possibility that *Arkarua* is a basal edrioasteroid-like taxon that has a water vascular system, but falls below the node supported by the appearance of the stereom (Mooi and David, 1997, Fig. 7).

Arkarua exhibits features like those of other early echinoderms. There seems to be an axial region expressing pentaradial symmetry (although the existence of the 2–1–2 pattern is as yet undetermined) embedded within an oral region of what could be interpreted as perforate extraxial skeleton (Fig. 2). Gehling (1987, Fig. 3) depicted serial elements in his reconstruction, but it is difficult to say that these elements were laid down according to the OPR. Positional criteria of homology suggest a perforate extraxial region in *Arkarua*, but the fossils show insufficient detail to reveal any openings. Finding the periproct in one of the “interradial” regions of this surface would be a major step in determining the affinities of *Arkarua*. The aboral side corresponds to the imperforate extraxial body wall of other edrioasteroid-like taxa.

The presence of a pentaradial axial component and perforate and imperforate extraxial elements in the earliest verifiable edrioasteroid-like taxa is remarkably concordant with the morphology of *Arkarua*. The above discussion would be much less tenable if *Arkarua* had some echinoderm features such as pentaradiality, but a radically different body wall configuration from that seen in the earliest Cambrian edrioasteroid-like taxa. The supposition of Fortey *et al.* (1996) that crucial innovations in body plans occurred in tiny taxa before the increase in disparity at the base of the Cambrian partially fits the idea that *Arkarua* is a stem lineage of small echinoderms that evolved before the appearance of stereom (Fig. 2). The evolution of stereom in echinoderms greatly enhanced their fossiliza-

tion potential, but does not rule out the possibility that rarely-preserved, soft-bodied echinoderms originated in the Precambrian.

The Early Cambrian helicoplacoids have also been placed at or near the base of the echinoderm clade (Paul and Smith, 1984; Holland, 1988). We follow Paul and Smith's (1984, Fig. 4) reconstruction of helicoplacoids as triradiate echinoderms (Fig. 2). The flooring and cover plates of helicoplacoids are homologous with the same axial elements seen in edrioasteroid-like taxa, with the oldest elements near the mouth, and the youngest at the ends of the helical rays coiling around the elongate body. The rest of the plates in the body are likely extraxial, but the lack of orifices makes it impossible to say more. Ascertaining the position of the anus, hydropore, or gonopore would assist in differentiating the two main extraxial regions.

With or without the EAT, certain lines of investigation must be followed to clear up some inconsistencies in previous arguments concerning helicoplacoids and *Arkarua*. In previous phylogenetic analyses of echinoderms, both helicoplacoids and *Arkarua* are seldom, if ever, shown simultaneously in the tree. For example, in works such as Paul and Smith (1984, Fig. 19) that predate the discovery of *Arkarua*, helicoplacoids are depicted in the evolutionary tree. However, when *Arkarua* is added to such a tree (Smith and Jell, 1990, Fig. 53; Smith, 1990, Fig. 12.3), helicoplacoids are curiously omitted from the explicit scenario. The question is, where would they go if both taxa were included? If triradiality is plesiomorphic for the phylum (Paul and Smith, 1984; Holland, 1988; Smith, 1988a), then helicoplacoids should fall below the node that joins the pentaradial *Arkarua* to the rest of the Echinodermata. However, if the lack of stereom is plesiomorphic for the phylum, then *Arkarua* falls below the node that links the helicoplacoids to the rest of the echinoderms (Fig. 2), a position that is also more congruent with the stratigraphic record. One way out of this conundrum is to suggest that helicoplacoids represent derived, aberrant forms that have secondarily lost rays, and that the consistency with which they find themselves at the base of

the tree in most previous analyses is at least partially a result of the same “forcing” phenomenon noted above for homalozoans. That is, the obfuscation of obvious synapomorphies with other echinoderm taxa by the adoption of an unusual morphology erroneously forces helicoplacoids downward and out of the more crownward clade.

THE EARLIEST DEVELOPMENTAL PATTERNS

The consequences of developmental studies for our understanding of echinoderm evolution have been discussed in many contexts (*e.g.*, Strathmann, 1988; Holland, 1988; Nielsen, 1995), but the most common approach has been to explore larval characters separately from those of the adults. However, David and Mooi (1996, 1998) noted a correlation between overall developmental pattern (especially in degree of metamorphosis) and the ratio of axial to extraxial skeleton in the body wall of the adult. In spite of a wide variety of developmental trajectories (reviewed in Hyman, 1955; Giese *et al.*, 1991), events in the early ontogeny of all echinoderms suggest fundamental characteristics that illuminate this correlation.

Echinoids, in which the body wall is almost entirely axial in origin (Mooi *et al.*, 1994), undergo pronounced metamorphosis. We ascribe this to the fact that in echinoids, the non-rudiment part of the larval body contributes virtually nothing to the body wall of the adult. The rudiment is then pressed into rapid construction of the adult body during the act of metamorphosis (David and Mooi, 1996, 1998). Because echinoids are derived relative to the rest of the Echinodermata, choosing them as paradigms for “maximal indirect” development (Peterson *et al.*, 1997) yields a skewed picture of the role of metamorphosis in the origin and radiation of the Echinodermata. However, it is this very trait of the echinoids (the “exception that proves the rule”) that represents the point of departure for any extrapolation down the tree towards features that might characterize the development of the earliest echinoderms.

The most likely sister group to echinoids, the sea cucumbers (Fig. 2), displays a radical truncation of the developmental trajec-

tory shown by the other extant classes (David and Mooi, 1996). Their lack of distinct metamorphosis reflects paedomorphic retention of non-rudiment components into adulthood—components that give the holothuroids a morphology almost diametrically opposed to that of echinoids, considering that holothuroids are almost entirely extraxial skeleton. Because this is derived in holothuroids, it is not indicative of plesiomorphic morphologies in the first echinoderms.

Asteroids and ophiuroids lack imperforate extraxial skeleton, but retain the perforate extraxial as a major component of the adult body wall (Mooi *et al.*, 1994). Although metamorphosis can be significant in some asteroids and ophiuroids, the rudiment evaginates far less than in echinoids (David and Mooi, 1996), and the non-rudiment part of the larva plays a larger role in construction of the adult body wall than in echinoids. However, crinoids continue to express imperforate extraxial skeleton in the form of the stem (Mooi and David, 1997). All crinoids in which development has been studied have non-feeding larvae, introducing uncertainty concerning how much this affects the applicability of crinoid developmental patterns to questions of phylogeny (Strathmann, 1988). Crinoids exhibit reduced metamorphosis partly as a result of their lecithotrophic reproduction, but largely because they have plesiomorphically retained so much extraxial skeleton into adulthood. Because extraxial body wall comes from the non-rudiment larval body, metamorphosis does not need to occur to the same degree as in forms such as echinoids and asteroids.

The lowest branches of echinoderm phylogeny contain groups in which the rudiment contributes less to the body wall of the adult than the non-rudiment part of the larva (Fig. 3). This agrees well with a decrease in the amount of axial skeleton relative to extraxial as we move down the tree towards the earliest edrioasteroid-like taxa (Fig. 2). In these forms, the non-rudiment part of the larva contributed much more extraxial material to the adult body wall. This in turn implies that metamorphosis in the earliest echinoderms was virtually absent

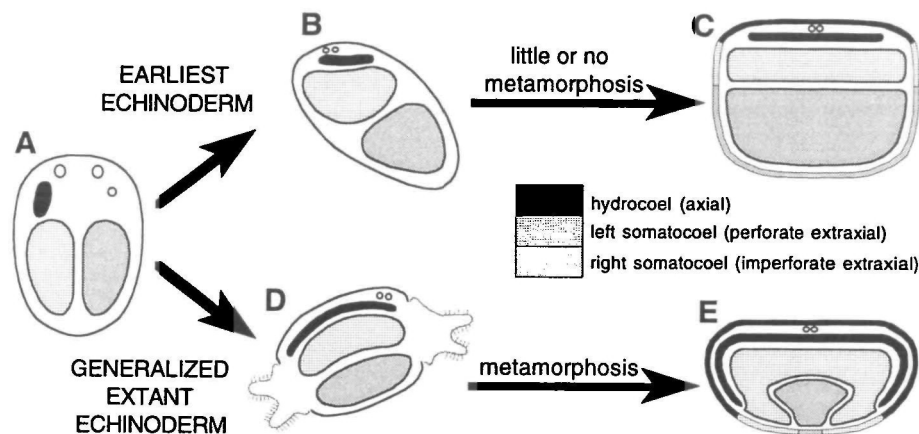


FIG. 3. Generalized schematics of basal and extant echinoderms showing expression of body wall types. A, larva showing archimery; B, pre-metamorphic larva of basal echinoderm; C, adult basal echinoderm; D, pre-metamorphic larva of extant echinoderm, specialized larval structures in light outline; E, adult extant echinoderm. In all figures, axocoels are represented by small, open circles.

(Fig. 3). The predominance of the axial skeleton observed in crownward taxa such as asteroids and echinoids is a product of apomorphies that suppressed the extraxial skeleton in favor of axial. Another product of these apomorphies is more pronounced pentaradiality, as axial skeleton increasingly constrained the shape of the remaining extraxial component of the body wall.

Study of extant forms with recently acquired dominance of the pentaradial axial skeleton has obscured the primordial linearity still exhibited in larval development and adult edrioasteroid-like fossil taxa (Mooi and David, 1997; David and Mooi, 1998). Therefore, a basic attribute of the earliest echinoderms was not pentaradiality per se, but an essential linearity in coelomic archimery (Nielsen, 1995) reflected by the sequence of axial (hydrocoel), perforate extraxial (left somatocoel), and imperforate extraxial (right somatocoel) regions (Fig. 3). Although all of these elements correspond to set-aside cells (reviewed in Peterson *et al.*, 1997), it would appear that the origin of echinoderms lies in the way that these set-aside cells were themselves apportioned into axial and extraxial components. Later radiation of the echinoderms rests in part on how the axial component comes to dominate most aspects of the adult morphology, thereby making metamorphosis a more and more conspicuous part of

early ontogeny (Fig. 3). This makes sense given that axial skeleton has become one of the most important elements in interactions between an echinoderm and its environment.

ACKNOWLEDGMENTS

Support to Mooi was provided by California Academy of Sciences In-house Funds and a CNRS Associate Researchship. Additional support came from a Smithsonian Research Opportunities Fellowship to David, and a NATO Collaborative Studies grant to both authors. This paper is a contribution of the theme "Signal morphologique de l'Évolution" of the UMR CNRS 5561 "Paléontologie Analytique and Géologie Sédimentaire."

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Corresponding Editor: Douglas H. Erwin