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Larval budding, metamorphosis, and the evolution of life-history patterns in echinoderms

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Abstract. The oral surface and mouth of juvenile asteroids and echinoids with indirect development forms on the lower left side of the larval body, thus establishing a new axis of body symmetry. In contrast, the juvenile mouth of ophiuroids and holothuroids develops from the larval one, and the larval and adult body axes roughly coincide. Explaining how two such disparate modes of development arose in evolution has been a perennial problem for echinoderm biologists, but recent observations on larval budding in asteroids may provide an answer. The juvenile mouth of asteroids forms near the base of the left posterolateral lobe. The posterolateral lobes are also the principal site of bud formation in asteroid larvae that propagate asexually, and buds form mouths. By accelerating the development of oral and ectodermal structures belonging to the bud, and combining these with internal organs derived from the parent larva, a composite individual could be constructed with the same orientation and positioning as the juvenile rudiment in asteroids. Whether this also explains the position of the juvenile rudiment in echinoids is a more complex question, depending in part on whether asexual propagation is derived, and restricted to asteroids and ophiuroids, or is more primitive and hence widespread among stem echinoderms.

Echinoderm larvae have fascinated zoologists since their discovery by Johannes Müller, roughly 150 years ago (e.g., Müller 1853), and they figured prominently in academic debates on the relationship between evolution and development during the late 19th century (Winsor 1976). The metamorphosis of asteroids and echinoids is especially remarkable for producing a dramatic change in body symmetry. The rudiment of the juvenile in both groups develops on the left side of the larval body, with the oral surface facing out, so the oral/aboral axis of the juvenile and hence, the adult, is perpendicular to the bilateral plane of larval symmetry. Formative events involve a coelomic derivative, the left hydrocoel, which lies on the left side of the body near the junction between the stomach and esophagus (Fig. 1A,B). The hydrocoel develops into a ring that produces 5 radial projections, which become the circular and radial canals respectively of the juvenile water vascular system (reviewed by Dawydoff 1948a; Burke 1989). The definitive mouth is established when the developing juvenile esophagus, which includes part of the larval esophagus in some species, grows through the ring. The larval mouth and residual parts of the larval esophagus are then resorbed or histolysed (Chia & Burke 1978). Formative events in ophiuroid and holothuroid metamorphosis also involve the left hydrocoel, which again begins its development near the junction of the stomach and esophagus. However, as development proceeds, the hydrocoel moves to the ventral midline and grows around the esophagus (Fig. 1C). In consequence, in ophiuroids and holothuroids, the larval mouth and the adult mouth coincide.

The diversity of form and development exhibited by echinoderm larvae is difficult to interpret in a simple and consistent way. The 4 classes mentioned above, which together constitute the eleutherozoan echinoderms, are generally accepted as being more closely related to each other than any is to the other major group of modern echinoderms, the crinoids, which probably diverged earlier (Sprinkle 1992; Sumrall & Sprinkle 1998). The fossil record indicates that eleutherozoan echinoderms diversified during the early to middle Ordovician, and both the morphological and molecular evidence places asteroids and ophiuroids together as earlier offshoots of a lineage leading to echinoids and holothuroids (Wada & Satoh 1994; Littlewood et al. 1997). Each of the 4 classes has a distinctly different type of planktotrophic larva, whereas crinoids lack a feeding larva so far as is known. The larvae of ophiuroids and echinoids are superficially similar. They are called pluteus larvae for their shape, and both are supported internally by a framework of skeletal

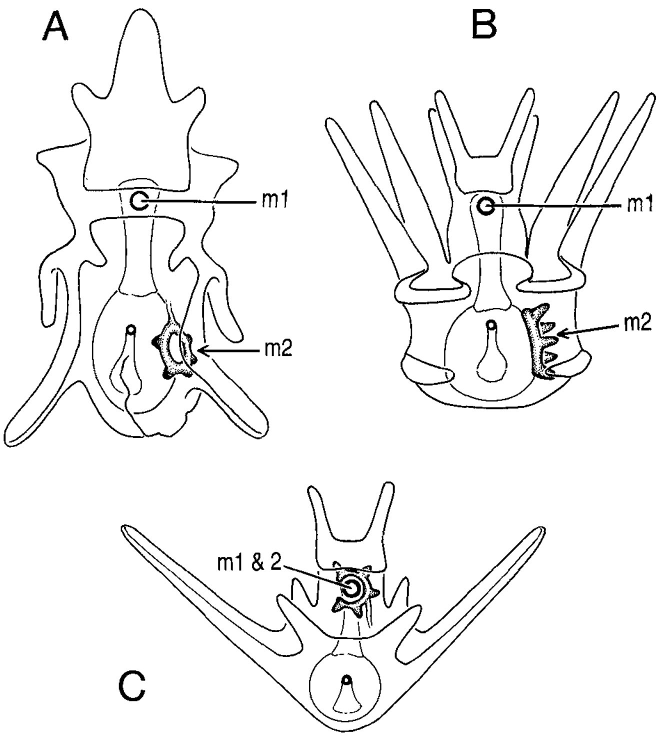

Fig. 1. Rudiment formation in the larvae of **(A)** an asteroid, **(B)** an echinoid, and **(C)** an ophiuroid, all in ventral view. The hydrocoel (shaded) develops first as a ring with radial projections to the primary podia. The larval mouth (m1) and juvenile mouth (m2) correspond in both ophiuroids and holothuroids (not shown), but are separate in asteroids and echinoids.

rods. Differences in larval morphology, most notably the arrangement of posterolateral structures, nevertheless support the idea that the two pluteus types are independently derived from something more like the larvae of asteroids or holothuroids.

The posterolateral elements are variously developed in echinoderm larvae, as elongate lobes in the bipinnaria, projecting ridges in the auricularia, and epaulets, vibratile lobes, or lateral spines in echinoid pluteus larvae (Lacalli 1993). The full range of variation in the latter can be appreciated in the excellent drawings of Mortensen (1921, 1931, 1937; reviewed by Pearse & Cameron 1991). The posterolateral elements in mature echinoid pluteus larvae are flanked on their dorsal and ventral side by larval arms with internal skeletal supports. In contrast, the posterolateral element in the ophiuroid pluteus is itself an arm that is flanked, in species that have them, by structures that resemble epaulets (cf. *Ophiocoma scolependrina* or *O. lineolata* in Mortensen 1937). Given these differences in structures that are key determinants of the hydrodynamic and swimming characteristics of the larvae, it is difficult to argue that the two pluteus types are any more closely related than either is to the bipinnaria or auricularia. The latter are, in any case, more similar to the tornaria larvae of enteropneust hemichordates (Nielsen 1998), which suggests that something broadly similar to the modern bipinnaria or auricularia was probably ancestral for echinoderms as a whole.

As a further complication, however, metamorphosis first converts the auricularia larva to a polytrochal doliolaria resembling the lecithotrophic polytrochal larvae of crinoids (Bury 1895; Smiley 1986; Lacalli & West 2000). Some ophiuroids pass through a similar polytrochal stage (the vitellaria) during metamorphosis (Grave 1903; Burke 1989), and tornaria larvae are also polytrochal if one takes into account the presence of both a primary and secondary telotroch in some species (Burdon-Jones 1957). It is thus very difficult to make a convincing case that polytrochal larvae are either more or less primitive than feeding larva. Both types of organization probably date from at least as far back as the common ancestor of echinoderms and hemichordates.

In summary, the patchy distribution of morphological characters among modern echinoderm larvae makes it difficult to distinguish ancestral characters from derived ones. This severely limits what one can say with certainty about the nature of the ancestral larva. Diversity of form among echinoderm larvae is generally thought to be due to both loss of characters and convergence, as each type of larva adapted to the demands of planktonic life (Fell 1948; Strathmann 1988; Strathmann & Eernisse 1994). In contrast, differences in the position and mode of formation of the juvenile rudiment have never been adequately explained. This paper examines whether the latter may be related to another developmental phenomenon observed in echinoderm larvae: their ability to regenerate and, in some taxa, to propagate asexually.

Larval regeneration, budding, and the role of the posterolateral lobes

The eggs and embryos of echinoderms have remarkable abilities to reorganize after experimental disturbances and form normal larvae (Hörstadius 1928, 1973), including the abilities to reconstitute the body from disaggregated cells. The latter has been studied extensively in echinoids (Guidice & Mutolo 1970; Freeman 1988), but asteroids seem to have an even greater capacity for reconstitution and reorganization (Dan-Sohkawa et al. 1986; Yamanaka et al. 1986). In addition, fully formed asteroid larvae will regenerate after transsection or removal of body parts (Hörstadius 1973, pp. 112–133; Vickery & McClintock 1998). The

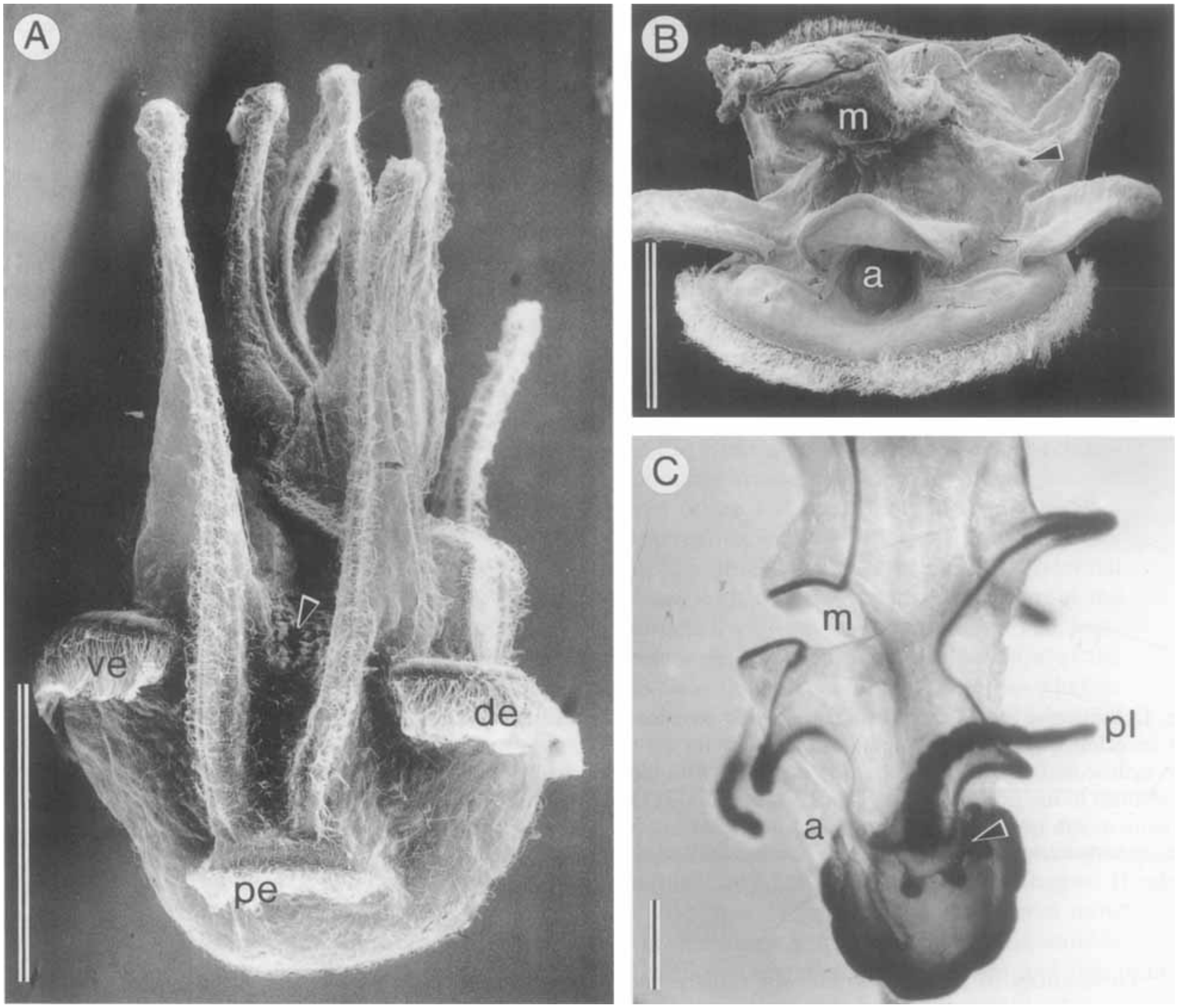

Fig. 2. Late-stage echinoid and asteroid larvae showing the position of the developing rudiment. See Lacalli (1993) for rearing and specimen preparation methods. Scale bars, 200 μm.

(A) Lateral view of a pluteus of *Strongylocentrotus franciscanus* seen from the left side, showing the dorsal (de), ventral (ve), and posterior (pe) epaulets. The opening to the vestibule is visible as a small pore (arrowhead) just forward of the posterior epaulet.

(B) Ventral view of a pluteus of *Lytechinus pictus*. The right side of the photo is the left side of the larva; the mouth (m) and anus (a) are indicated. The opening to the vestibule is visible as a small pore (arrowhead). The posterior epaulet is not visible from this angle; it lies between the two large larval arms.

(C) Osmium-stained brachiolaria larva of *Pisaster ochraceus* seen from the left side, showing the developing hydrocoel (arrowhead) just below the base of the left posterolateral lobe (pl). The latter has contracted on fixation and arcs forward in this specimen, but would trail behind in live larvae. See Lacalli (1996) for a stereo view that shows the spatial relationships between structures somewhat better.

regenerative capabilities of the coelomic system are especially well developed. In bipinnaria larvae, after removal of one or more of the coeloms, the larva compensates by forming new ones from the coeloms that remain, or from generalized mesenchyme, the gut, or from sites in the ectoderm near the hydropore. Similar replacements occur in the larvae of holothuroids and echinoids, in both feeding and lecithotrophic larvae. Generally, however, the regenerative abilities of lecithotrophic larvae, including crinoid larvae (e.g., Lacalli & West 1987), are more limited.

Besides its plasticity in experimental situations, the process of coelom formation has also been subject to considerable change during evolution. The basic pat-

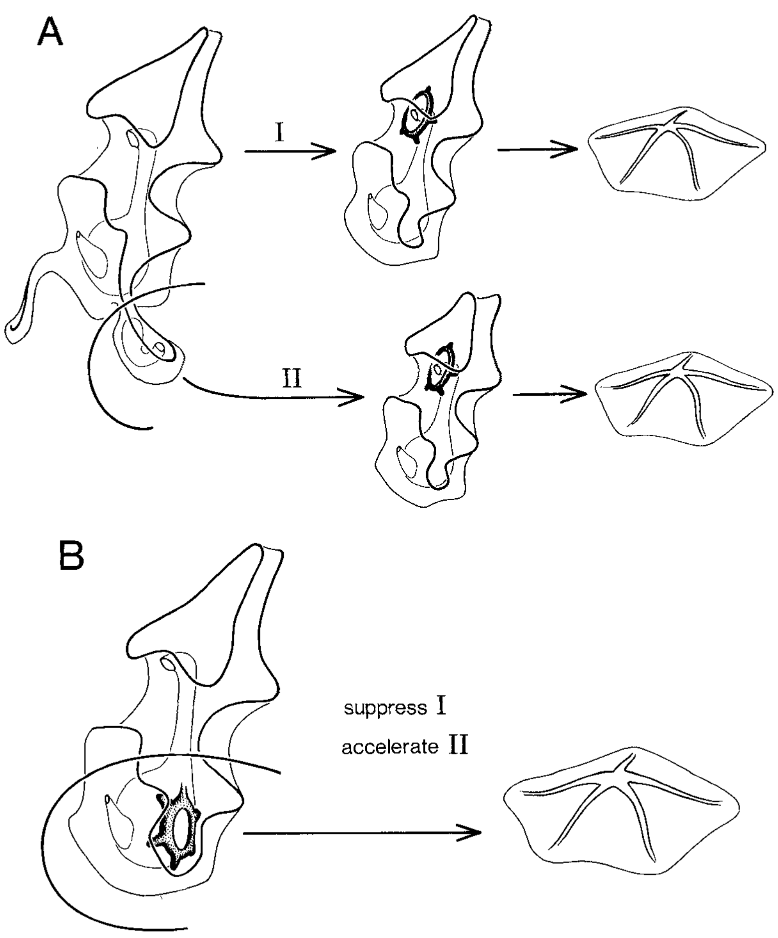

Fig. 3. A proposal for how the juvenile rudiment in asteroids may have evolved to incorporate structures derived by heterochrony from a bud.

(A) A hypothetical ancestral larva releasing a bud from its posterolateral lobes, as described by Bosch et al. (1989) and Jaeckle (1994). These detach and develop independently. Assuming both the parent larva and its buds metamorphose and settle (Pathways I and II), the simplest method is for both to retain the larval esophagus and mouth to the adult stage, which is presumably the primitive pattern.

(B) A later modification in which rudiment formation is suppressed in the parent larva, and the hydrocoel completes its development near the site where the mouth of the bud will form. The latter then becomes incorporated into the developing rudiment. The result is a composite individual that combines internal structures derived from the parent larva with oral structures induced precociously from presumptive bud tissue. There are thus two principal body axes and two mouths, just as in modern asteroids at metamorphosis.

tern in lower deuterostomes is for 3 pairs of coelomic cavities to form from the archenteron. These can all form from the tip of the archenteron, as in echinoids, ophiuroids, and most asteroids, or from various points along its sides or base, as in crinoids and some asteroids (Janies & McEdward 1993; Nielsen 1995). A similar variability is seen in enteropneust embryos and larvae (Dawydoff 1948b; Nielsen 1995). To a degree, this violates the usual criteria for assigning homology, since anatomical structures that are apparently homologous are being generated from different parts of the archenteron in different species, and from different sites yet again during regeneration. This demonstrates quite clearly the inherent plasticity of mesodermal morphogenesis throughout the lower deuterostomes and, at the same time, shows the problem inherent in assessing the homology of mesodermal structures in these taxa based on site of origin.

Scattered references to larval autotomy and budding occur in the older literature (e.g., Mortensen 1921), but these have recently been confirmed and extended in observations on asteroid and ophiuroid larvae. In ophiuroids, metamorphosis may leave behind the posterior larval arms, which then swim away and regenerate (Balser 1998). Asteroids are more versatile: they can autotomize the preoral lobe, which then regenerates a normal larva, or buds can form from the posterodorsal, posteroventral, or posterolateral lobes (Bosch et al. 1989; Jaeckle 1994). While not common in asteroid species generally, such processes may be quite important in the life history of species with long-lived oceanic larvae.

From the observations currently available, the posterolateral lobes are the most common site for bud formation in asteroids. The lobes swell, and gastrulation then occurs by means of a fairly typical blastopore that forms on the underside of the lobe. The archenteron extends to the flattened upper surface and breaks through to form the mouth, after which the bud can separate from the parent larva and develop independently in the plankton. The topological relationship between the bud and its parent is not entirely clear. The distal tip of the lobe becomes the apical pole of the developing bud, and the oral surface of both the lobe and bud appear to coincide, which means that the mouth of the bud probably develops in what is essentially an extension of the parent oral field. However, because the ciliary band disappears from the posterolateral lobe shortly after bud formation (Bosch et al. 1989), the precise relation of the parent oral field to that of the bud is a matter of conjecture. The problem is more pronounced in the case of posterodorsal and posteroventral buds. They detach at an earlier developmental stage, as rudimentary blastulae (Jaeckle 1994), so there is no easy way to relate their organization to the body axes of the parent larva.

At metamorphosis, the posterolateral lobes are again a site of special significance in both echinoids and asteroids. The future oral surface of the juvenile echinoid develops from the floor of an invagination, the vestibule, that remains open to the outside in at least some species, e.g., of *Stongylocentrotus, Arbacia, Lytechinus* and *Dendraster* (Burke 1989). The site of mouth formation in relation to other landmarks on the larval surface can thus be determined precisely. Based on my own specimens, the opening is located in the oral field, upstream of the ciliary band, directly above (anterior to) the posterior epaulet (Fig. 2A,B). In positional terms, the posterior epaulets are the closest counterpart of the posterolateral lobes in asteroids, and the developing hydrocoel in the latter lies just at the base of the left posterolateral lobe (Fig. 2C, see also Mortensen 1937, 1938). Precisely where the mouth breaks through in asteroids, whether on the oral or aboral side of the ciliary band, is less certain. This is because most larval structures, including the ciliary bands, are resorbed by the time the mouth forms (e.g., Gemmill 1914). The close association of the hydrocoel with the base of the left posterolateral lobe during its early development is nevertheless clear.

Positioning the juvenile rudiment: two alternatives

Examples of left/right asymmetry occur during development throughout the lower deuterostomes. Various scenarios have been proposed to explain this phenomenon (e.g., Jefferies et al. 1996), but there is no general agreement on its significance. The asymmetries are particularly pronounced in echinoderm embryos; usually the left side of the body is favored at the expense of the right, e.g., in the formation of the coeloms or the positioning of the juvenile rudiment. The retention of the larval axis as an axis of adult symmetry is generally considered to be primitive, and Smiley (1986) has argued that the auricularia larva is closest to the ancestral pattern. Whether or not this is strictly true, it is the case that retaining the larval mouth and the original axis of bilateral symmetry allows the metamorphosing larva to use the residual ciliary bands temporarily for locomotion. This may be the primitive condition judging from crinoids, which also have a polytrochal larva. The establishment of a secondary mouth and a new symmetry axis in asteroids and echinoids thus appears to be an evolutionary novelty that needs explanation.

The simplest way to do this is to assume that the rudiment has shifted position and reoriented, but is otherwise the same, i.e., it contains no new structures derived from other sources. Experimental work shows that rudiment development requires the presence of the hydrocoel, which is apparently responsible for the induction of the mouth and associated oral structures (Runnström 1917; Hörstadius 1973, pp. 114–118). In all 4 eleutherozoan classes, the hydrocoel begins its development on the left side of the body near the site that, in echinoids, will form the vestibule. To generate a normally positioned echinoid rudiment, the hydrocoel would need to do no more than complete its development without moving, meanwhile inducing a vestibule, mouth, and associated oral structures in the usual way. This could have evolved as a way of simplifying development, or because it allows the larva to continue feeding without interference from the developing rudiment.

In the above scenario, the vestibule is the only entirely novel structure. Experiment shows that it can form at the normal position even in the absence of the hydrocoel (Hörstadius 1973). One therefore needs to explain, without invoking the hydrocoel, how a specific site on the body surface forward of the posterior epaulets becomes the site of vestibule formation. Assuming that the ancestral condition was for all oral structures to form exclusively from tissue near the larval mouth, one could envisage the location of this zone being gradually respecified over time, so that it moved progressively closer to the site of initial hydrocoel differentiation. The same process could have occurred independently in echinoids and asteroids, yielding a similar result because the hydrocoel rudiment occupies an approximately similar position in both.

However, the position of the developing hydrocoel in asteroids also corresponds quite closely with the site of secondary mouth formation in those species that bud, which raises another possibility: that some parts of the juvenile rudiment may be derived by heterochrony from a bud. I propose an evolutionary scenario that shows how the two might be linked (Fig. 3). The starting point is a hypothetical ancestral larva, portrayed as being basically bipinnaria-like, with a prolonged planktonic phase that includes repeated cycles of budding (Fig. 3A). The posterolateral lobes are assumed to be the preferred site for bud formation, as in modern asteroids. When either the parent larva or its buds eventually metamorphose (Pathways I and II respectively), the mode of rudiment formation is assumed to be that used by holothuroids and ophiuroids, i.e., the larval mouth and esophagus are retained.

If budding became less advantageous at some point in evolution, the budding cycle could have been truncated so that only one juvenile would develop from each developing embryo. There are two ways this could happen. The most direct would be to suppress budding altogether, leaving the rudiment to form as before around the esophagus of the primary larva (Pathway I in Fig. 3A). Alternatively, the hydrocoel could remain near the site of bud formation. Then, by accelerating the development of juvenile bud structures at the expense of larval ones, a composite juvenile combining parent and bud tissues could be produced (Fig. 3B). The larger internal structures of such a construct, e.g., gut and coelom, would derive from the parent larva in this scenario. The mouth and associated ectodermal structures, perhaps with some underlying mesenchyme, would derive from cells that originally were part of the bud. There would be little overt evidence of the prior existence of such buds except for the position of the juvenile mouth.

Is budding primitive or derived?

Asexual reproduction by autotomy and budding of larvae has so far been observed only in asteroids and ophiuroids. These are closely related taxa (Littlewood et al. 1997), so despite the much wider distribution of regenerative capabilities among echinoderms, it is possible that asexual propagation by larvae is a derived character restricted to just the two classes. If this is the case, the above proposal relating budding sites to rudiment position would apply only to asteroids. A separate explanation would be needed for why the rudiment is laterally positioned in echinoids. However, asexual propagation may have been more widely distributed among early metazoans, including early echinoderms, than it is today (Rieger 1994; Lacalli 1997). One can therefore not rule out the possibility that the life cycle of ancestral echinoderms included a larval stage that propagated asexually. Autotomy and budding could have evolved and then been lost in various lineages, without necessarily altering the basic form of the larva. If so, current interpretations of the evolutionary relationships between larvae would need to be reexamined with this in mind.

If asexual propagation was widespread among larvae of ancient echinoderms, its absence in most modern forms would be an indication that the selective advantage of this particular life-history strategy changed significantly at some point in the past. This could, for example, have been due to increased predation. Among the invertebrates that appeared as part of the Cambrian "explosion," there are a number of armored echinoderms, mainly low-level suspension and deposit feeders, including a few primitive crinoids (Sprinkle 1992). Protective armour is generally considered a response to increased activity by predators, and increased predation was probably a major factor driving evolutionary change during the early Cambrian (Conway Morris 1989, 1993; Vermeij 1990). Changes in adult morphology need not be accompanied by changes in the larva, since the two life-history stages are typically subject to quite different selective pressures. A general increase in predation in the marine environment could, however, have affected both.

Signor & Vermeij (1994) argue quite persuasively that the plankton prior to the Cambrian would have been a niche of low nutrient content but comparative safety. A prolonged pelagic larval stage that propagated by budding could have been a widespread and successful evolutionary strategy until well into the Cambrian. By that time, increasing numbers of actively swimming pelagic organisms had begun to appear, including predators with eyes (e.g., *Anomalocaris, Opabinia*). New kinds of predators, especially active visual predators able to seek out slow-swimming larvae, could have substantially increased selective pressure to metamorphose and settle as rapidly as possible. If this was the case, the diversity of surviving larval types suggests that the problem was solved by stem species of each echinoderm class in a slightly different way.

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