

Larval and life-cycle patterns in echinoderms¹

Larry R. McEdward and Benjamin G. Miner

Abstract: We review the literature on larval development of 182 asteroids, 20 crinoids, 177 echinoids, 69 holothuroids, and 67 ophiuroids. For each class, we describe the various larval types, common features of a larval body plan, developmental patterns in terms of life-cycle character states and sequences of larval stages, phylogenetic distribution of these traits, and infer evolutionary transitions that account for the documented diversity. Asteroids, echinoids, holothuroids, and ophiuroids, but not crinoids, have feeding larvae. All five classes have evolved nonfeeding larvae. Direct development has been documented in asteroids, echinoids, and ophiuroids. Facultative planktotrophy has been documented only in echinoids. It is surprising that benthic, free-living, feeding larvae have not been reported in echinoderms. From this review, we conclude that it is the ecological and functional demands on larvae which impose limits on developmental evolution and determine the associations of larval types and life-cycle character states that give rise to the developmental patterns that we observe in echinoderms. Two factors seriously limit analyses of larval and life-cycle evolution in echinoderms. First is the limited understanding of developmental diversity and second is the lack of good phylogenies.

Résumé : On trouvera ici une revue de la littérature sur le développement larvaire de 182 astéroïdes, 20 crinoïdes, 177 échinoïdes, 69 holothuroïdes et 67 ophiuroïdes. Pour chacune des classes, nous décrivons les divers types de larves, les caractères communs du plan général du corps de la larve, les patterns de développement, en particulier les différents états des caractéristiques du cycle biologique et les séquences de stades larvaires, enfin, la répartition phylogénétique de ces états des caractères; nous en déduisons les transitions évolutives qui peuvent expliquer la diversité existante. Les astéroïdes, les échinoïdes, les holothuroïdes et les ophiuroïdes, mais pas les crinoïdes, ont des larves qui se nourrissent. Les cinq classes possèdent aussi des larves qui ne se nourrissent pas. Le développement direct a été observé et décrit chez les astéroïdes, les échinoïdes et les ophiuroïdes. Les planctonophagie facultative n'est connue que chez les échinoïdes. Il est étonnant qu'aucune des classes d'échinodermes ne semble avoir de larves benthiques et libres qui se nourrissent. Cette révision indique que, dans les patterns de développement que nous observons chez les échinodermes, ce sont les besoins écologiques et fonctionnels des larves qui imposent des limites à l'évolution du développement et qui déterminent l'association entre le type de larve et les caractères du cycle biologique. Deux facteurs empêchent l'analyse adéquate de l'évolution des larves et des cycles biologiques chez les échinodermes : le premier est notre compréhension limitée de la diversité de leur développement, le second, le manque de bonnes études phylogénétiques.

[Traduit par la Rédaction]

Introduction

In this paper, we review the literature on the larval diversity and developmental patterns of the five classes of echinoderms (Appendix Table A1). For each class, we describe the various larval types, common features of a larval body plan, developmental patterns in terms of life-cycle character states

and sequences of larval stages, and the phylogenetic distribution of these traits, then we analyze the evolution of larvae and developmental patterns. A discussion of the hypotheses about adaptive and historical factors that drive the evolution of life cycles and explain patterns of development is beyond the scope of this review. Interested readers should consult recent echinocentric reviews (e.g., Strathmann 1985, 1993; Emler 1994; Wray 1995a; Hart et al. 1997; McEdward 1997; McEdward and Janies 1997; Byrne et al. 1999a; Byrne et al. 1999b; Levitan 2000).

A developmental pattern is a unique combination of life-cycle character states (McEdward and Janies 1993). Patterns here are evaluated with respect to three characters (Table 1): type of morphogenesis (complex larval, simple larval, direct), nutritional mode (planktotrophic or lecithotrophic), and developmental habitat (pelagic or benthic) (for a discussion of these and other life-cycle characters see McEdward and Janies 1997). Out of the 12 possible developmental patterns, we expect only 8 combinations of character states to be via-

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L.R. McEdward² and B.G. Miner.³ Department of Zoology,
 University of Florida, 223 Bartram Hall, P.O. Box 118525,
 Gainesville, FL 32611, U.S.A.

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²Deceased.

³Corresponding author (e-mail: miner@zoo.ufl.edu).

Table 1. Matrix of echinoderm life-cycle character states.

Morphogenesis	Nutrition	Habitat	Functional*	Traditional nomenclature
Complex larval	Planktotrophic	Pelagic	Yes	Planktotrophy
		Benthic	Yes	Demersal
	Lecithotrophic	Pelagic	Yes	Facultative planktotrophy
		Benthic	Yes	Demersal
Simple larval	Planktotrophic	Pelagic	No	
		Benthic	No	
	Lecithotrophic	Pelagic	Yes	Lecithotrophy or direct development
		Benthic	Yes	Lecithotrophy, brooding, viviparity, or direct development
Direct	Planktotrophic	Pelagic	No	
		Benthic	No	
	Lecithotrophic	Pelagic	Yes	Lecithotrophy or direct development
		Benthic	Yes	Brooding, viviparity, or direct development

Note: Each unique combination of states represents a developmental pattern.

*This column indicates combinations of characters that should or should not be viable.

ble. For example, simple larval morphology refers to cases where larvae lack elaborate external structures, especially those used in feeding. It is unlikely that such larvae are planktotrophic. Definitions of life-cycle stages, processes, and patterns follow those given by McEdward and Janies (1993, 1997). These categories work reasonably well for echinoderms but may not be suitable for other groups of marine invertebrates. Three aspects of evolution were analyzed: changes in larval types and developmental sequences, functional transitions among life-cycle character states, and the phylogenetic distribution of life-cycle changes. In this paper, we accept the argument that a pelagic planktotrophic larva with complex morphogenesis was plesiomorphic for each class (Jägersten 1972; Strathmann 1978; Wray 1995a).

Phylogenies for relationships of families within the classes were taken from the following sources: Blake (1987), Wada et al. (1996), and Lafay et al. (1995) for asteroids, Rasmussen (1978) and Ubags (1978) for crinoids, Littlewood and Smith (1995) and Young and George (2000) for echinoids, Kerr and Kim (1999) for holothuroids, and Smith et al. (1995) for ophiuroids. Note that while we recognize the highly variable quality of these trees, they represent the best hypotheses for the phylogenetic relationships within these classes at present. They are used here to illustrate the analysis of larval and life-cycle evolution. We hope that the inadequacy of some of these trees stimulates further phylogenetic work and generates robust species-level trees suitable for detailed analyses of echinoderm evolution.

Asteroids

Diversity of larval types

Starfish have five larval types: bipinnaria, brachiolaria, yolky brachiolaria, barrel-shaped larva, and yolky non-brachiolaria larva; they also have a nonlarval mesogen with direct development (see Fell 1967, p. S68; Oguro 1989; Chia et al. 1993; McEdward and Janies 1993).

Bipinnaria

The bipinnaria (Fig. 1A) is a complex, pelagic, feeding larva characterized by the bilateral arrangement of the pre-

and post-oral ciliated swimming and feeding bands that are borne on the arms (MacBride 1914, p. 464; Kume and Dan 1968, p. 306). The body is ovoid in shape with two ventral folds (oral and anal hoods), numerous lateral lobes, and arms. Bipinnarian arms are hollow extensions of the body wall (epidermis); they contain blastocoelic space but are not supported by calcareous skeletal rods (Hyman 1955). Although, the number and size of bipinnarian arms vary among species, the arms can be identified by their anatomical location using the nomenclature designated by Mortensen (1898, pp. 6–7). The bipinnaria possesses a complete, functional gut (e.g., *Asterias forbesi*, *Asterias vulgaris*, Agassiz 1877; *Luidia sarsi*, Wilson 1978; *Patiriella regularis*, Byrne and Barker 1991). Some species of asteroids undergo asexual reproduction during larval life (Bosch et al. 1989; Bosch 1992; Rao et al. 1993; Jaekle 1994). Bipinnaria are reported to occur in the following asteroid orders: Forcipulatida, Notomyotida, Paxillosida, and Valvatida (Table 2).

Brachiolaria

The brachiolaria also is a complex, feeding larva (Fig. 1B) but is characterized by the presence of specialized attachment structures on the preoral lobe: the brachiolar arms and attachment disk. Brachiolar arms are hollow but contain extensions of the larval anterior coelom, and are thereby distinguished from bipinnarian arms (Gemmil 1914; Barker 1978). Brachiolar arms are used by larvae to test the substratum and provide initial, temporary adhesion during settlement. The adhesive disk secretes cement and provides more permanent attachment for metamorphosis. In all asteroid species that develop via both bipinnarian and brachiolarian stages (e.g., *Asterias rubens*, Gemmill 1914; *P. regularis*, Byrne and Barker 1991), the only difference in larval morphology that distinguishes these stages is the presence of the brachiolar attachment structures. The brachiolaria is just a fully developed bipinnaria that has added structures for settlement to the benthos. Although these larvae are given different names, they are not independently evolved types of larvae but rather are sequential developmental stages. Planktotrophic brachiolaria occur in the Forcipulatida and the Valvatida (Table 2).

Table 2. Phylogenetic distribution of larval types among the asteroids.

Order and family	Bipinnaria	Brachiolaria	Yolky brachiolaria	Barrel-shaped	Yolky non-brachiolaria	Mesogen
Paxillosida						
Astropectinidae	✓			✓		
Luidiidae	✓					
Goniopectinidae					✓	
Forcipulatida						
Zoroasteridae						
Asteriidae	✓	✓	✓			
Valvatida						
Archasteridae	✓	✓				
Odontasteridae	✓	✓				
Ganeriidae						
Asterinidae	✓	✓	✓			
Poraniidae	✓	✓	✓			
Goniasteridae			✓			
Ophidiasteridae	✓	✓	✓			
Mithrodiidae	✓	✓				
Oreasteridae	✓	✓				
Acanthasteridae	✓	✓				
Notomyotida						
Benthopectinidae	✓					
Spinulosida						
Echinasteridae			✓			
Velatida						
Solasteridae			✓			
Pterasteridae			✓			✓

Yolky brachiolaria

Some asteroids (e.g., *Crossaster papposus*, Gemmill 1920; *Echinaster echinophorus*, Atwood 1973; *Solaster endeca*, Gemmill 1912; *Mediaster aequalis*, Birkeland et al. 1971) develop via a nonfeeding pelagic brachiolarian larva. Non-feeding brachiolarian larvae are morphologically simpler than planktotrophic brachiolarian larvae because they lack the ciliated swimming and feeding structures, bipinnarian arms, and a functional gut (Fig. 1C). The most conspicuous larval structures that characterize both feeding and nonfeeding brachiolarian larvae are the attachment structures (brachiolar arms and attachment disk) and bilateral symmetry. Some asteroids develop via a benthic brachiolaria that has reduced brachiolar structures. For example, in the intragonadal brooders *Patiriella vivipara* and *Patiriella parvivipara*, the brachiolar arms are reduced and are nonfunctional (Byrne and Cerra 1996). More typically, brooded brachiolariae retain well-developed and functional brachiolar arms and adhesive disks (e.g., *Henricia sanguinolenta*, Masterman 1902; *Leptasterias hexactis*, Osterud 1918; Chia 1968; *Henricia* sp., Chia and Walker 1991; variety F, *Henricia leviuscula*, Fisher 1911, p. 282, according to Strathmann et al. 1988) (Fig. 1D). Yolky brachiolariae are broadly distributed in the asteroids, occurring in the Forcipulatida, Spinulosida, Valvatida, and Velatida (Table 2).

Barrel-shaped larva

Barrel-shaped larvae are nonfeeding larvae with abbreviated development and simplified morphology (Fig. 1E). They are characterized by a large, transparent (i.e., non-yolky) preoral lobe and by the absence of larval arms, ciliated bands, mouth,

and anus (Komatsu 1982). The larval coelom does not extend anteriorly into the conspicuous preoral lobe. Barrel-shaped larvae occur in some species of paxillosids (e.g., *Astropecten latespinosus*, Komatsu 1975; Komatsu et al. 1988; *Ctenopleura fisheri*, Komatsu 1982; *Astropecten gisselbrechti*, Komatsu and Nojima 1985).

Yolky nonbrachiolaria larva

A yolky, nonfeeding larva of simple morphology was described in the brooding asteroid *Ctenodiscus australis* (Lieberkind 1926). This larva lacks bipinnarian arms, brachiolarian arms, and ciliated bands (Fig. 1F), but nothing is known about its internal morphology. It could be a yolky larva or a direct-developing mesogen.

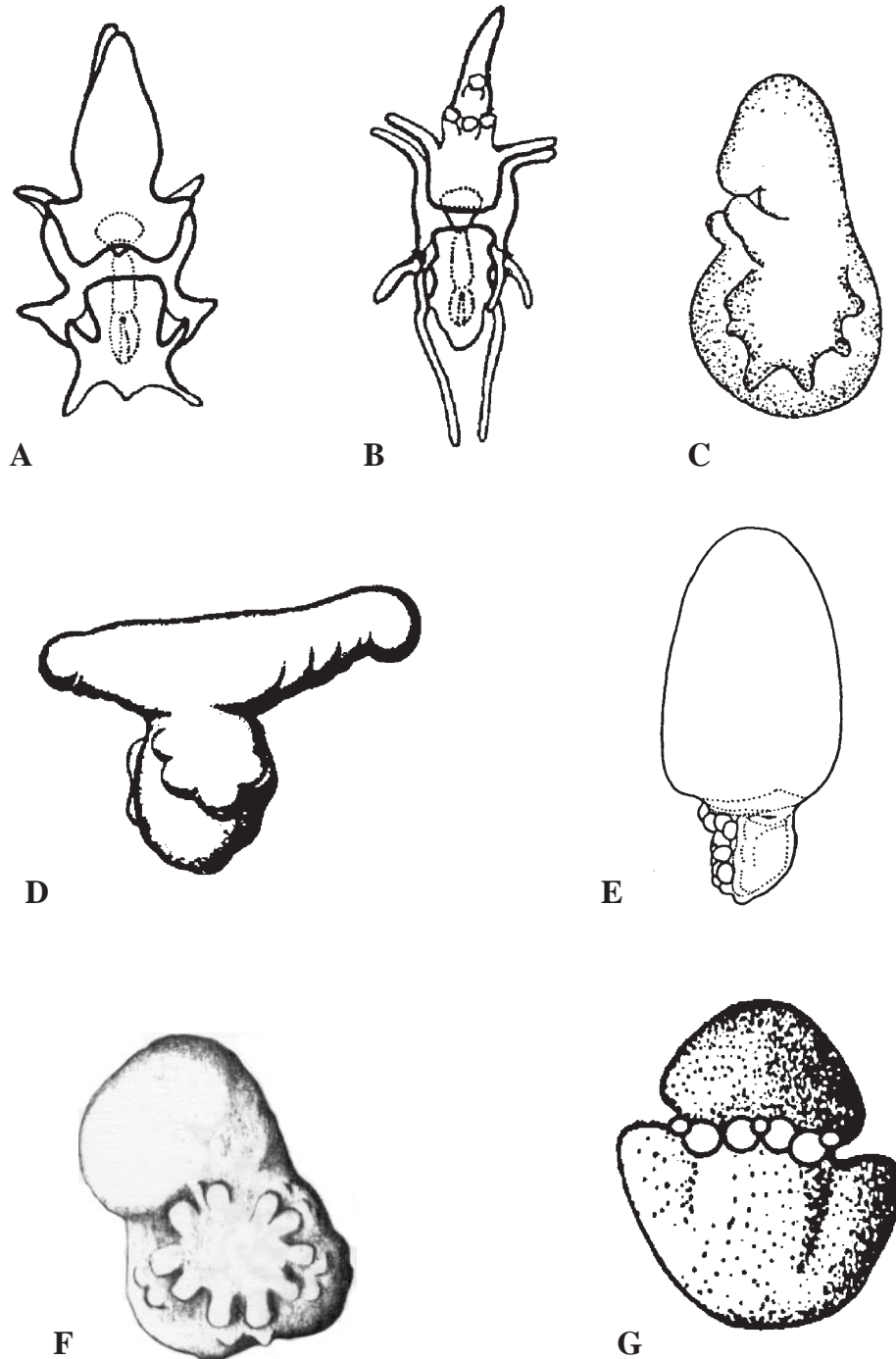
Mesogen

The velatid asteroid *Pteraster tessellatus* has pelagic, direct development (McEdward 1992; Janies and McEdward 1993; McEdward 1995). Direct development is characterized by the complete absence of the larval body plan and metamorphosis. Morphogenesis of adult structures is highly derived and is unlike anything that occurs in asteroid larvae. Direct development also occurs in several brooding *Pteraster* species (e.g., *Pteraster militaris*, Kaufman 1968; *Pteraster acicula*, *Pteraster temnochitin*, *Pteraster pulvillus*, *Pteraster stellifer*, Janies 1995) (Fig. 1G).

Asteroid larval body plan

Several morphological features are common to all starfish larvae and define a characteristic larval body plan (see Hyman 1955; Fell 1967; McEdward 1995). First, all asteroid

Fig. 1. Larval diversity of asteroids. (A) Bipinnaria of *Luidia foliolata*, modified from Strathmann (1974, p. 324). (B) Brachiolaria of *Pisaster ochraceus*, modified from Strathmann (1974, p. 324). (C) Pelagic yolky brachiolaria of *Solaster endeca*, modified from Hyman (1955, p. 298). (D) Brooded yolky brachiolaria of *Asterina gibbosa*, modified from MacBride (1896, plate 18). (E) Barrel-shaped larva of *Ctenopleura fisheri*, modified from Komatsu (1982, p. 202). (F) Yolky nonbrachiolaria of *Ctenodiscus australis*, modified from Lieberkind (1926, p. 193). (G) Mesogen of *Pteraster militaris*, modified from Kaufman (1968, p. 508).



larvae have bilateral symmetry. External features, such as bipinnarian arms, ciliated bands, and lateral brachiolar arms, if present are distributed symmetrically to the left and right sides of the midsagittal plane. The other external structures, such as mouth, anus, median brachiolar arm, and adhesive disk, if present lie on the midline of the larval body. The major internal larval structures likewise are arranged around (nervous system and paired coeloms) or on the midline (gut

and unpaired coeloms) (Gemmill 1914; Hörstadius 1939; Barker 1978; Burke 1983a; Lacalli et al. 1990; Komatsu et al. 1991). Second, the larval coeloms are always arranged as a set of three sacs from anterior to posterior and the post-metamorphic fates of the coeloms are highly conservative (Erber 1985; Hyman 1955). The anterior coelom (axocoel) is unpaired in all asteroid larvae, but it forms from a pair of sacs in some species. It becomes the axial coeloms in the

adult. The middle coeloms (hydrocoels) are paired, but the left sac becomes larger and develops into the water-vascular system of the adult. The posterior pair of sacs (somatocoels) gives rise to the perivisceral and perihemal coeloms after metamorphosis. Third, all asteroid larvae possess a homologous anterior region called the preoral lobe. This is a purely larval structure that generally contains an anterior extension of the unpaired coelom, bears brachiolar attachment structures (if present), serves as an attachment stalk, and is resorbed during metamorphosis. Fourth, the larva and adult are constructed using independent morphogenetic axes. The rudiment of the juvenile starfish develops as a disk that lies in a sagittal plane in the posterior of the larval body. The axis of radial symmetry of the juvenile and adult is orthogonal to the larval plane of bilateral symmetry, so that the oral surface of the juvenile corresponds to the left side of the larva. Nonfeeding larvae lack several features present in feeding larvae, such as ciliated bands and bipinnarian arms, and therefore have a simpler body form. Curiously, nonfeeding asteroid larvae never develop transverse bands of cilia, which are common in crinoid, holothuroid, and ophiuroid larvae, but rather they become uniformly ciliated (see Emler 1994). All nonfeeding larvae possess all of the characteristic features of the larval body plan and undergo metamorphosis to the adult form.

Diversity of developmental patterns

Five (possibly six) of the eight viable developmental patterns occur among the asteroids (Table 3). Three patterns are very widespread among the orders: pelagic planktotrophy with complex larval morphogenesis, and both pelagic and benthic lecithotrophy with simple larval morphogenesis (Table A1). Pelagic and benthic lecithotrophy with direct development is restricted to a single genus, *Pteraster*, in the Velatida (Janies 1995). There is one potential case of pelagic lecithotrophy with complex larval morphogenesis. *Porania antarctica* is described as having reasonably large (550 µm), yolky eggs that develop into bipinnaria larvae that are capable of ingesting particulate food (Bosch 1989). It is not known whether feeding is required for development to metamorphosis, but the juveniles retain substantial amounts of yolk after metamorphosis, so this might be a case of facultative planktotrophy. Benthic lecithotrophic larvae can be free-living (i.e., demersal) (e.g., *Porania* sp., Bosch 1989; *Asterina minor*, Komatsu et al. 1979) or brooded. Brooding occurs in a variety of locations including under the adult body (e.g., *Leptasterias polaris*, Himmelman et al. 1982), in the stomach (e.g., *C. australis*, Lieberkind 1926), in the gonads (e.g., *Asterina pseudoexigua pacifica*, Komatsu et al. 1990; *P. vivipara* and *P. parvivipara*, Byrne 1996), and in specialized brood chambers (e.g., *P. militaris*, McClary and Mladenov 1990).

Evolution of developmental patterns

There has been a long history of debate over the nature of the ancestral asteroid life cycle (reviewed by McEdward and Janies 1993). The ancestral life-cycle pattern probably consisted of pelagic planktotrophy with a bipinnarian larva (Oguro et al. 1988). This is different from the ancestral life cycle inferred by McEdward and Janies (1993) on the basis of Blake's (1987) phylogeny, but it now seems most likely

because recent molecular evidence supports a basal position for the Paxillosoida (Lafay et al. 1995; Wada et al. 1996). Given this assumption, then the brachiolaria stage most likely occurred as a secondary acquisition (Fig. 2d) in the lineage leading to all non-paxillosoid asteroids (Fig. 3). Alternatively, the ancestral life cycle could have consisted of both bipinnaria and brachiolaria stages, and the brachiolaria was then lost in the paxillosoid lineage. The inferred sequence of evolutionary changes in larval types, developmental sequences, and life-cycle character states is illustrated in Fig. 2. Note that some transitions are assumed to be reversible (habitat and nutrition), whereas changes in morphogenesis (e.g., complex-simple or simple-direct) are irreversible (McEdward and Janies 1997). The acquisition of larval stages such as the evolution of the brachiolaria stage is inferred to be reversible, but the loss of the bipinnaria (Figs. 2b, 2f) is probably irreversible.

The ancestral life cycle and the life cycles derived through changes 2a, 2b, and 2c (Fig. 2) occur only in the paxillosoids and represent all of the documented diversity within that order. Barrel-shaped larvae probably evolved from bipinnaria (Oguro 1989). The evolution of barrel-shaped larvae must have occurred at least twice, given the phylogeny suggested by Wada et al. (1996). Yolky nonbrachiolarian development might have evolved once, since it is known in only a single species. However, it is not clear whether this larva evolved from a nonfeeding barrel-shaped larva or directly from a feeding bipinnaria.

Life cycles with brachiolaria larvae characterize all asteroids in the orders Forcipulatida, Valvatida, and Spinulosida, and most of the species in the Velatida (Fig. 3). There is very little information about development in the orders Brisingida or Notomyotida. Direct development (Figs. 2h, 2i) has been documented only in one genus (*Pteraster*) in the Velatida. There are numerous variations on asteroid life cycles with brachiolaria stages (Fig. 2), including transitions between pelagic and benthic development and the evolution from feeding to nonfeeding larvae. The latter transition actually involves two sequential changes: planktotrophy-lecithotrophy and complex-simple larval morphogenesis (see McEdward and Janies 1997). The shift in nutritional mode is associated with changes in egg provisioning (Byrne et al. 1999a; Byrne and Cerra 2000; McEdward and Morgan 2001). Evolutionary changes 2f and 2g (and possibly 2e; Fig. 2) have occurred repeatedly in the asteroids (Hart et al. 1997). In some very specialized (i.e., intragonadal) brooders, such as *P. vivipara* and *P. parvivipara*, there has been the evolution of reduced egg size (135–148 µm) in spite of lecithotrophic development. This apparently occurred in association with very small juvenile size at metamorphosis (244–314 µm) followed by extensive cannibalistic post-metamorphic juvenile growth (1–5 mm) prior to release from the parent (Byrne and Cerra 1996).

Crinoids

Diversity of larval types

Doliolaria and *vitellaria*

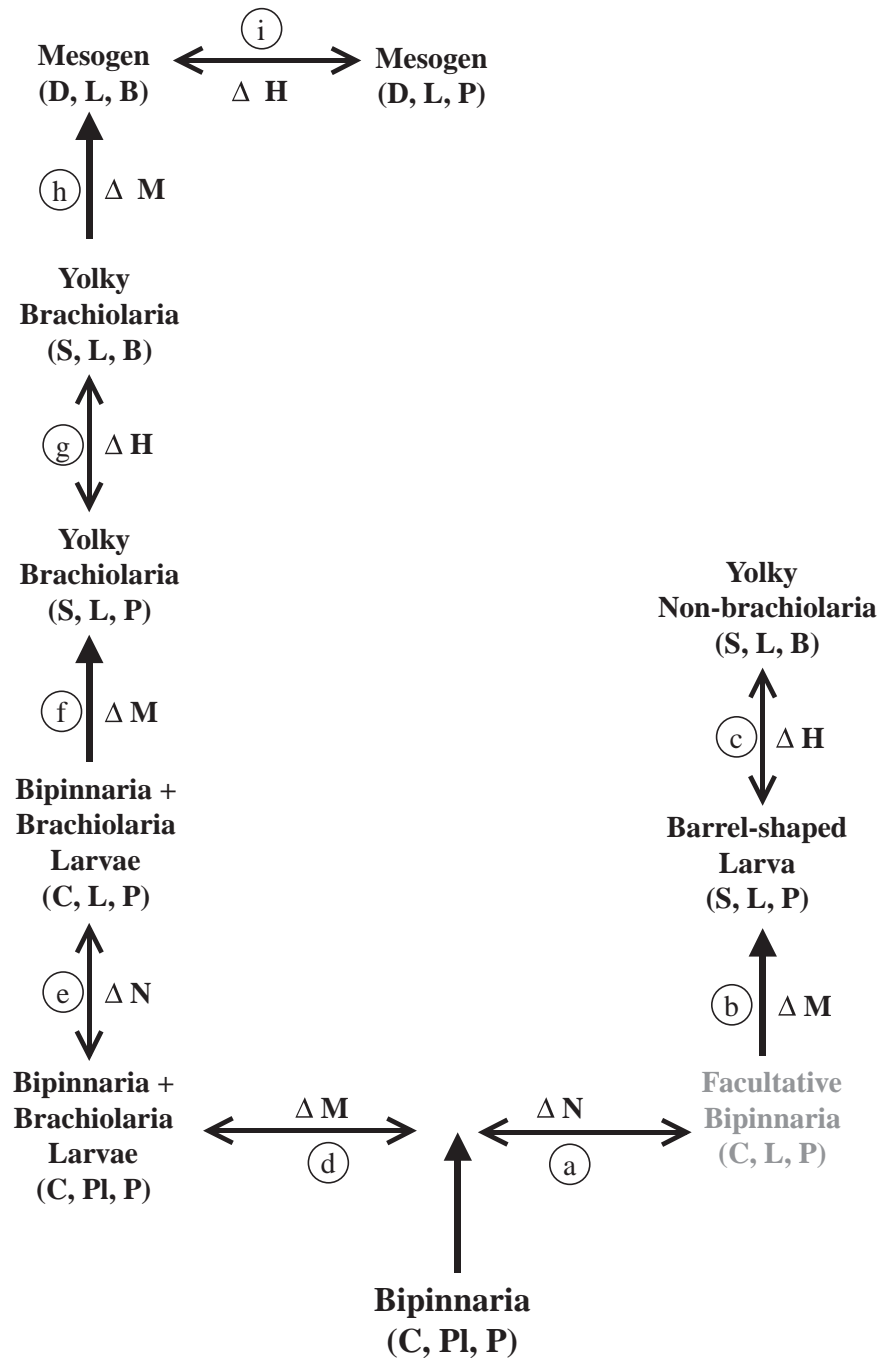
The majority of crinoids have only a doliolaria larva (Holland 1991). This larva is ovoid with 4–5 transverse bands of cilia and a tuft of apical cilia (Fig. 4). One species is known

Table 3. Phylogenetic distribution of developmental patterns among asteroids.

Order and family	Complex				Simple				Direct			
	Planktotrophy		Lecithotrophy		Planktotrophy		Lecithotrophy		Planktotrophy		Lecithotrophy	
	Pelagic	Benthic	Pelagic	Benthic	Pelagic	Benthic	Pelagic	Benthic	Pelagic	Benthic	Pelagic	Benthic
Paxillosida												
Astropectinidae	✓						✓	✓				
Luidiidae	✓											
Goniopectinidae							✓	✓				
Forcipulatida												
Zoroasteridae							✓					
Asteriidae	✓						✓	✓				
Valvatida												
Archasteridae	✓							✓				
Odontasteridae	✓											
Ganeriidae								✓				
Asterinidae	✓						✓	✓				
Poraniidae	✓		?					✓				
Goniasteridae							✓					
Ophiasteridae	✓						✓					
Mithrodiidae	✓											
Oreasteridae	✓											
Acanthasteridae	✓											
Notomyotida												
Benthopectinidae	✓						✓					
Spinulosida												
Echinasteridae							✓	✓				
Velatida												
Pterasteridae								✓			✓	✓
Solasteridae							✓					

Note: Functional developmental patterns are in boldface type.

Fig. 2. Evolutionary changes in asteroids. The hypothetical ancestor is shown at the base of the diagram with changes in habitat (ΔH), morphology (ΔM), and nutrition (ΔN) leading to different life-cycle patterns. Single-headed arrows represent non-reversible changes and double-headed arrows represent reversible changes. Gray text indicates required intermediates that have not been reported. Abbreviations in parentheses represent the morphology (C, complex; S, simple; D, direct), nutrition (Pl, planktotrophy; L, lecithotrophy), and habitat (P, pelagic; B, benthic) of that larval type.

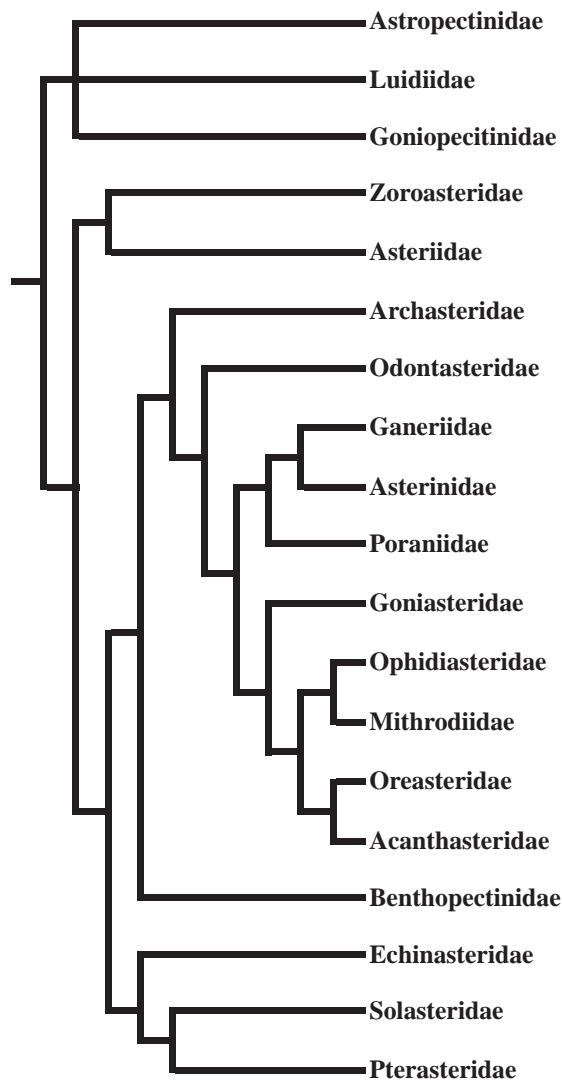


to have an internally brooded vitellaria larva (e.g., *Notocrinus virilis*, Mortensen 1920), which lacks both ciliated bands and general surface ciliation. Late in larval life, an antero-ventral adhesive pit and a ventral vestibule form. The formation of these structures alters the arrangement of the ciliated bands of the doliolaria. The first (most anterior) band becomes discontinuous in the ventral region between the pit and the vestibule. The second band is displaced posteriorly, on the ventral surface, by the vestibule and it

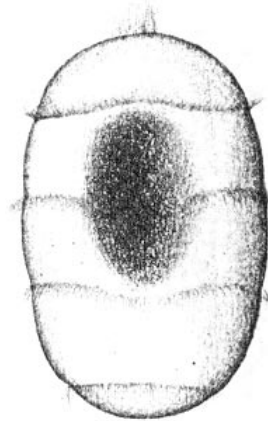
merges with the third band. The adhesive pit serves to attach the larva to the substratum at settlement by forming the attachment disk of the juvenile. The vestibule is an ectodermal invagination that closes to become an internal sac during the early stages of metamorphosis, soon after settlement.

Crinoid larval body plan

There are only minor variations in the characteristics of the doliolaria and vitellaria larvae among crinoid species

Fig. 3. Phylogeny of asteroid families.

(Mortensen 1920; Holland 1991). External features of the larval body plan are the pattern of ciliation, the adhesive pit, and the vestibule. Internal larval features include the following division of the archenteron into two internal sacs. The anterior sac is the entero-hydrocoel, which develops into the gut and the water-vascular system. The posterior sac is the coelomic vesicle, which gives rise to the rest of the coelomic structures (Mortensen 1920). The somatocoels arise as left and right extensions from the coelomic vesicle, imparting a fundamental bilateral symmetry on the larva. However, the subsequent development of these coeloms rapidly shifts the left coelom ventrally and the right coelom dorsally. Later, the left coelom rotates posteriorly to become the oral perivisceral coelom and the right coelom becomes the aboral perivisceral coelom (Mortensen 1920). The only other indications of bilateral organization in the larva are the nervous system and the original location of the vestibule (on the midventral side, defined relative to the plane of symmetry established by the somatocoels). During metamorphosis, the vestibule and associated ventral structures, such as the mouth and arms, rotate towards the oral pole of the juvenile

Fig. 4. Larval diversity of crinoids: doliolaria of *Tropiometra carinata*, modified from Mortensen (1920, plate X).**Table 4.** Phylogenetic distribution of larval types among the crinoids.

Order and family	Doliolaria only	Vitellaria only
Comatulida		
Comasteridae	✓	
Mariametridae	✓	
Himerometridae	✓	
Thalassometridae	✓	
Tropiometridae	✓	
Antedonidae	✓	
Notocrinidae		✓
Aporometridae	✓	
Unknown		
Unknown	✓	

(= posterior end of the larva). At no point is there a distinct juvenile rudiment oriented orthogonally to the larval plane of symmetry.

Diversity of developmental patterns

All crinoids develop via a short-lived nonfeeding larva, followed by a benthic, nonfeeding, stalked, cystidean stage that undergoes a prolonged metamorphosis into the benthic, feeding, pentacrinoid juvenile (Tables 4, 5). Larval development in crinoids can be either pelagic or benthic. *Florometra serratissima* free-spawns and their eggs, embryos, and larvae develop in the plankton (Mladenov and Chia 1983). Other species brood eggs and embryos, and then release fully formed, pelagic, doliolaria larvae (e.g., *Antedon bifida*, Lahaye and Jangoux 1985). Other species release larvae that have begun the early stages of metamorphosis, which settle and transform immediately into the cystidean stage (e.g., *Isometra vivipara*, Mortensen 1920). The paedomorphic species *Comatilia iridometrifformis* broods in the ovary and releases late-stage larvae (Messing 1984).

Evolution of developmental patterns

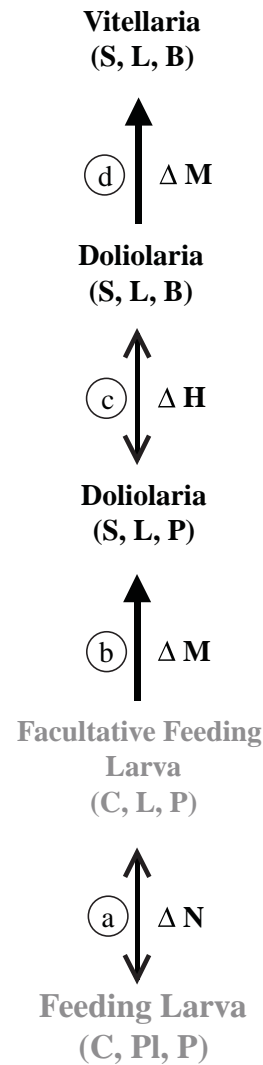
Given the assumption that the ancestral echinoderm life cycle involved a pelagic, planktotrophic larva with complex morphogenesis (Strathmann 1987; Wray 1995a), then there must have been at least one transition to simple morpho-

Table 5. Phylogenetic distribution of developmental patterns among crinoids.

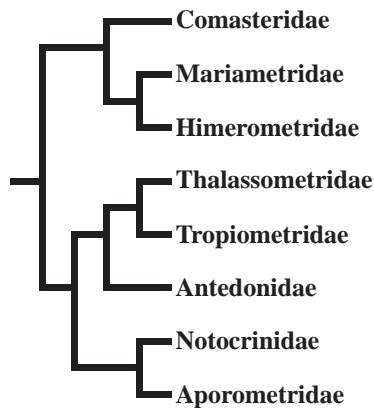
Order and family	Complex			Simple			Direct		
	Planktotrophy		Lecithotrophy	Planktotrophy		Lecithotrophy	Planktotrophy		Lecithotrophy
	Pelagic	Benthic	Pelagic	Benthic	Pelagic	Benthic	Pelagic	Benthic	
Comatulida									
Comasteridae			✓						
Mariametridae			✓						
Himerometridae			✓						
Thalassometridae				✓					
Tropiometridae				✓					
Antedonidae									
Notocrinidae									
Aporometridae									
Unknown									
Unknown									

Note: Functional developmental patterns are in boldface type.

Fig. 5. Evolutionary changes in crinoids. The hypothetical ancestor is shown at the base of the diagram with changes in habitat (ΔH), morphology (ΔM), and nutrition (ΔN) leading to different life-cycle patterns. Single-headed arrows represent non-reversible changes and double-headed arrows represent reversible changes. Gray text indicates required intermediates that are unknown. Abbreviations in parentheses represent the morphology (C, complex; S, simple; D, direct), nutrition (Pl, planktotrophy; L, lecithotrophy), and habitat (P, pelagic; B, benthic) of that larval type.



genesis and lecithotrophy in the crinoids (Fig. 5). It is not possible to rule out the existence of other life cycles in extinct lineages nor the possibility that lecithotrophy evolved multiple times within the class. Only in cases where retention of brooded young involves loss of larval structures (i.e., ciliated bands) can we infer that brooding is the derived condition. In all cases where fully formed larvae are brooded, it is very possible that pelagic development could easily re-evolve. Hence, most cases of pelagic development could represent secondary transitions in life cycles and need not represent the unmodified ancestral state. Benthic development must have evolved at least 1–4 times in the class (Fig. 6, Table 5).

Fig. 6. Phylogeny of crinoid families.

Echinoids

Diversity of larval types

Echinoids have two larval types: echinopluteus and non-feeding larva; they also have a nonlarval mesogen.

Echinopluteus

The echinopluteus (Fig. 7A) is a complex, pelagic, feeding, larva characterized by anteriorly directed arms that are supported by calcareous skeletal rods (Okazaki 1975). The larva is bilaterally symmetrical with the arms arranged as left-right pairs, except in some cases where there is a medial, unpaired, posterior arm (e.g., *Lovenia elongata*, Mortensen 1937; *Aspidodiadema jacobyi*, Young and George 2000) (see Mortensen 1898 for nomenclature). The body forms of plutei are very diverse, as a result of variation in the number (2–13, typically 8) and the relative size of the larval arms (Mortensen 1921, 1931, 1937, 1938; Onoda 1936, 1938; Pearse and Cameron 1991; Wray 1992). The arms are hollow extensions of the body wall that contain blastocoelic space and bear the ciliated feeding-band structure. The band traces a convoluted loop around the larval body. In the late-stage larvae of some species, parts of the ciliated band become isolated from the loop and become specialized for locomotion (Pearse and Cameron 1991, p. 591). The larval skeleton consists of arm rods, which can be solid or fenestrated, and other skeletal pieces that support the posterior part of the larval body (Pearse and Cameron 1991, p. 590). In some species (e.g., *Lytechinus variegatus*, McEdward and Herrera 1999), late-stage larvae possess well-developed pedicellariae. Echinoplutei possess a complete gut consisting of a tubular esophagus, bulbous stomach, short tubular intestine, and an anus opening on the posterior ventral side (Burke 1981). Nerves run along the ciliated band and the muscular esophagus. A neuropile occurs at the anterior end of the oral hood (Burke 1978, 1983b). The vestibule is an ectodermal invagination, located on the left side of the larva, which forms in late-stage plutei and is associated with the developing juvenile rudiment (Okazaki 1975). Plutei have been documented in 8 of the 11 echinoid orders (Table 6).

Nonfeeding larvae

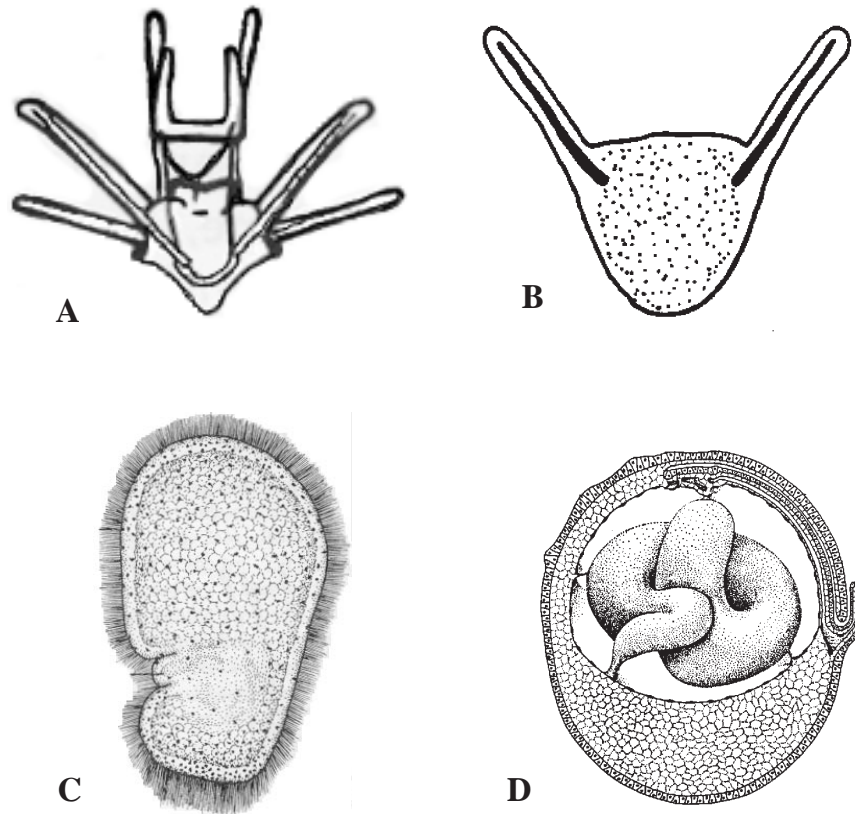
Yolky, nonfeeding echinoid larvae have much simpler

Table 6. Phylogenetic distribution of larval types among the echinoids.

Order and family	Pluteus	Nonfeeding larva	Mesogen
Cidaroida			
Cidaridae	✓	✓	
Echinothurioida			
Echinothuriidae		✓	
Phormosomatidae		✓	
Diadematoidea			
Diadematidae	✓		
Aspidodiadematidae	✓		
Clypeasteroida			
Clypeasteridae	✓		
Arachnoididae	✓		
Fibulariidae	✓	✓	
Echinarachniidae	✓		
Astriclypeidae	✓		
Mellitidae	✓		
Dendrasteridae	✓		
Laganidae	✓	✓	
Cassiduloida			
Echinolampadidae	✓		
Cassidulidae		✓	
Aptopygidae	✓		
Neolampadidae		✓	
Spatangoida			
Schizasteridae	✓	✓	✓
Brissidae	✓		
Loveniidae	✓		
Spatangidae	✓		
Phymosomatoida			
Arbaciidae	✓		
Stomopneustidae	✓		
Glyptocidaridae	✓		
Temnopleuroida			
Temnopleuridae	✓	✓	
Echinoida			
Echinidae	✓		
Strongylocentrotidae	✓		
Toxopneustidae	✓		
Echinometridae	✓	✓	
Paraechinidae	✓		
Holasteroida			
Urechinidae		✓	
Holectypoida			
Holectypidae	✓		

morphology than echinoplutei. These larvae range in form from reduced plutei (Fig. 7B) that have 2–4 larval arms, but lack ciliated bands and a functional gut (e.g., *Phyllacanthus imperialis*, Olson et al. 1993; *Peronella japonica*, Okazaki and Dan 1954; Pearse and Cameron 1991, p. 618) to very simple ovoid larvae (schmoos; Fig. 7C) that lack arms, ciliated bands, gut, and have only a vestigial skeleton (e.g., *Asthenosoma ijimai*, Amemiya and Tsuchiya 1979; Amemiya and Emler 1992; *Heliocidaris erythrogramma*, Williams and Anderson 1975; Raff 1987; Emler 1995; *Phyllacanthus parvispinus*, Parks et al. 1989). Nonfeeding larvae are wide-

Fig. 7. Larval diversity of echinoids. (A) Echinopluteus of *Echinolampas crassa*, modified from Wray (1992, p. 260). (B) Reduced echinopluteus of *Peronella japonica*, modified from Raff (1987, p. 8). (C) Schmoos of *Heliocidaris erythrogramma*, modified from Williams and Anderson (1975, p. 387). (D) Mesogen of *Abatus cordatus*, modified from Schatt and Féral (1996, p. 37).



spread in the class, occurring in eight of the 10 orders (Table 6).

Mesogen

The subantarctic brooder *Abatus cordatus* has direct development and lacks all features of the echinoid larval body plan (Schatt and Féral 1996). The mesogen is unlike any echinoid larva (Fig. 7D), including even the most simplified schmoos. Nearly every aspect of development from embryonic cleavage, through gastrulation, to coelom formation is markedly different from that of all other echinoids. Although brooding occurs in several groups of echinoids, direct development has been documented in only a single species. It is not clear if there are common features of direct-developing mesogens.

Echinoid larval body plan

Body symmetry, morphogenetic axes, coelomic organization, nervous system, vestibule, and metamorphic fates of larval structures are common to all echinoid larvae, both echinoplutei and nonfeeding larvae, and define the larval body plan. Larvae show bilateral symmetry around a midsagittal plane. External structures, such as the larval arms, ciliated band, gut openings, and pedicellaria, if present are arranged either as left–right pairs or, if unpaired, lie along the midline of the body. Likewise, internal structures are bilateral (nervous system, coelomic sacs) or on the midline (gut). The rudiment of the juvenile develops around an independent set of morphogenetic axes from those of the larva.

The juvenile is radially symmetrical around an oral–aboral axis that is oriented orthogonal to the plane of larval symmetry. Hence, the oral side of the juvenile develops on the left side of the larval body and requires considerable rearrangement of larval structures at metamorphosis (Hyman 1955; Okazaki 1975; Pearse and Cameron 1991).

Initially the coeloms consist of two lateral outpockets of the invaginating archenteron. These coelomic spaces elongate and lie laterally beside the esophagus. Later they constrict and divide into anterior and posterior parts. The posterior coelomic sacs are the left and right somatocoels. The anterior coelom on the right side divides again to form an anterior axocoel and middle hydrocoel. On the left side, the latter two sacs remain connected by a tube (Hyman 1955). The basic organization of the larval nervous system is the same in echinoplutei and greatly simplified schmoos (Bisgrove and Raff 1989). All euechinoid larvae develop an ectodermal invagination on the left side of the larva that associates with the hydrocoel and contributes to the formation of the juvenile rudiment. The metamorphic fates of many larval structures are highly conserved among echinoid larvae (Gordon 1929; Hyman 1955; Chia and Burke 1978). The following larval structures are not incorporated into the juvenile structures: epidermis, ciliated bands, arm rods (although skeletal plates of juveniles often form at the base of larval arm rods), mouth, esophagus, anus, and the right axocoel. The larval stomach and intestine contribute to the development of the juvenile gut. The left axocoel becomes the axial coelom, the left hydrocoel becomes the entire water-vascular system, and

the right hydrocoel becomes the madreporic vesicle. The left and right somatocoels become the perivisceral coelom of the adult.

Diversity of developmental patterns

Five of the eight viable developmental patterns occur among the echinoids (Table 7). Three patterns are phylogenetically widespread: pelagic planktotrophy with an echinopluteus larva, pelagic lecithotrophy with simplified nonfeeding larvae, and benthic lecithotrophy with simplified nonfeeding larvae. In addition, there are two documented examples of pelagic lecithotrophic development (facultative feeding) with echinoplutei (*Clypeaster rosaceus*, Emler 1986; *Brisaster latifrons*, Hart 1996). There is also a single documented case of benthic lecithotrophic direct development (*Abatus cordatus*), but Schatt and Féral (1996) have identified several other brooding species that potentially have direct development. In echinoids, broods are generally held among the spines (e.g., *Cassidulus caribbearum*, Gladfelter 1978), under the body near the mouth (e.g., *Goniocidaris umbraculum*, Barker 1985), or in depressions of the test (marsupia) (e.g., *A. cordatus*, Hyman 1955; Schatt and Féral 1996).

Evolution of developmental patterns

Echinoids differ from asteroids, holothuroids, and ophiuroids because there is only a single larval stage, never a sequence of stages during pre-metamorphic development. The ancestral echinoid life cycle probably consisted of a pelagic planktotrophic echinopluteus larva (see Jägersten 1972; Strathmann 1978; Wray 1995a, 1996). This life cycle persists in the majority of echinoid species. The subsequent evolution of other larval types and developmental patterns occurred repeatedly but presumably followed the same sequence of changes (Fig. 8). The shift from planktotrophy to lecithotrophy (Fig. 8a) preceded the transition in morphology from feeding echinopluteus to nonfeeding schmoo (Fig. 8b) (Hart 1996). Although only two extant species are known to be facultative feeders, it is inevitable that all transitions to nonfeeding larvae passed through this developmental pattern. However, it is not inevitable that once having evolved lecithotrophy, morphology would be altered and feeding capability lost. The transition between planktotrophy and lecithotrophy is based largely on differences in egg provisioning. We expect such differences to reflect adaptive fine-tuning to food conditions in the plankton and to be common, rapid, and reversible because they do not involve changes in larval morphology (see McEdward and Janies 1997).

In contrast, the loss of larval feeding involves considerable morphological and developmental changes that result in the reduction and eventual loss of the echinopluteus larva. This evolutionary transition (Fig. 8b) has been studied in considerable detail in the Australian sea urchins *Heliocidaris tuberculata* (echinopluteus) and *H. erythrogramma* (schmoo). Derived features of development that accompanied the loss of the pluteus are numerous and extensive (Wray 1995b, 1996): changes in oogenesis and egg provisioning; early specification of the dorsal–ventral axis; altered cleavage geometry (equals 4th cleavage yields 16 cells without micromeres); changes in cell lineage, especially dorsal–ventral asymmetry in vegetal cell fates and greatly increased contribution of animal hemisphere blastomeres to the vestibule; wrinkled

blastula with an extremely small blastocoel; changes in timing of gene expression (e.g., absence of msp130 protein, which is associated with calcium deposition in skeletons, along with absence of primary mesenchyme cells and drastic reduction of the larval skeleton); changes in morphogenesis, such as extensive mesenchyme cell proliferation in blastocoel (1700–2200 vs. 30–60 in the pluteus), which then form adult rather than larval skeleton; modifications of gastrulation; reduction or elimination of many larval structures; and a gradual metamorphosis (Raff 1987; Bisgrove and Raff 1989; Parks et al. 1989; Wray and Raff 1989; Henry et al. 1990; Scott et al. 1990; Wray and Raff 1991; Emler 1995; Byrne et al. 1999b). These differences evolved quickly, within 5–8 mega-annum (Ma) (mtDNA) or 10–13 Ma (DNA hybridization) (Smith et al. 1990; McMillan et al. 1992). The widely conserved features of pluteus development and morphology undergo extensive changes rapidly when permitted by a shift in nutritional mode (Wray 1995b). This is surprising if early development is highly constrained, but not if stabilizing selection is the cause of evolutionary stasis.

The nutritional shift from planktotrophy to lecithotrophy has occurred repeatedly in the echinoids (Fig. 9, Table 7). It has evolved at least twice (*C. rosaceus* and *B. latifrons*), possibly many more times, without leading to loss of the echinopluteus. It also must have preceded every instance of the evolution of nonfeeding larval development, since lecithotrophy is a necessary precondition for the loss of feeding capability (Wray 1995a; McEdward and Janies 1997). Feeding plutei have been lost at least 20 times in the echinoids (Fig. 9, Table 7), yet have not re-evolved once (Wray 1996). Loss of feeding has been accompanied by substantial increases in egg provisioning beyond that necessary for lecithotrophic development (McEdward and Janies 1997; McEdward and Morgan 2001). The transition from pelagic to benthic development must have occurred at least 8 times to account for the distribution of brooding species within the class (Fig. 9, Table 7). The reverse transition need not be inferred to have taken place to account for pelagic development in any family of echinoids. Since direct development is known in only a single species, it is not necessary to postulate that it has evolved more than once.

Holothuroids

Diversity of larval types

Holothuroids have at least three larval types: auricularia, doliolaria, and vitellaria; some species might have direct development via a mesogen.

Auricularia

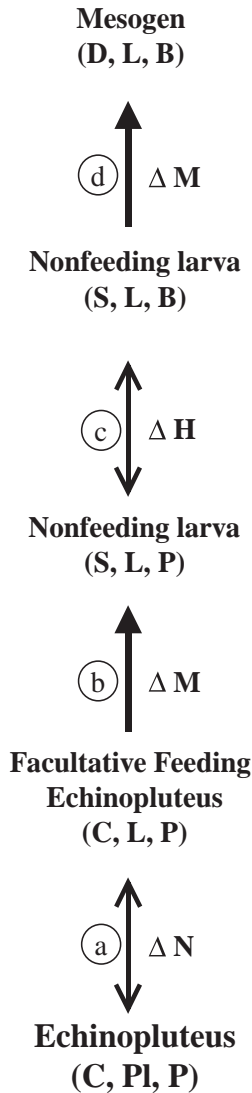
The auricularia (Fig. 10A) is a complex, bilaterally symmetrical, planktotrophic larva. The basic body shape is ovoid, with two ventral folds, an oral hood, and an anal hood (Hyman 1955). The single ciliated band (contrast with the bipinnaria) traces a convoluted loop around the margin of the body, extending along lobes that project from the body. The lobes never develop into distinct larval arms, such as those of bipinnaria or plutei. However, the lobes can become very numerous and exceptionally elaborate, as in the giant larvae of the apodid holothuroids *Auricularia nudibranchiata* and *Auricularia bermudensis* (Fig. 10B) (Garstang 1939;

Table 7. Phylogenetic distribution of developmental patterns among echinoids.

Order and family	Complex				Simple				Direct			
	Planktotrophy		Lecithotrophy		Planktotrophy		Lecithotrophy		Planktotrophy		Lecithotrophy	
	Pelagic	Benthic	Pelagic	Benthic	Pelagic	Benthic	Pelagic	Benthic	Pelagic	Benthic	Pelagic	Benthic
Cidaroida												
Cidaridae	✓						✓	✓				
Echinothurioida												
Echinothuriidae							✓					
Phormosomatidae							✓					
Diadematoidea												
Diademataidae	✓											
Clypeasteroidea												
Clypeasteridae	✓		✓									
Arachnoididae	✓											
Fibulariidae	✓							✓				
Echinarachniidae	✓											
Astriclypeidae	✓											
Mellitidae	✓											
Dendrasteridae	✓											
Laganidae	✓		✓									
Cassiduloidea												
Echinolampadidae	✓											
Cassidulidae											✓	
Echinobrissidae	✓											
Neolampadidae											✓	
Spatangoidea												
Schizasteridae	✓		✓								✓	
Brissidae	✓											
Loveniidae	✓											
Spatangidae	✓											
Phymosomatoida												
Arbaciidae	✓											
Stomopneustidae	✓											
Glyptocidaridae	✓											
Temnopleuroidea												
Temnopleuridae	✓						✓	✓				
Echinoida												
Echinidae	✓											
Strongylocentrotidae	✓											
Toxopneustidae	✓											
Echinometridae	✓						✓	✓				
Paraechinidae	✓											
Holasteroidea												
Urechinidae											✓	
Holectypoida												
Holectypidae	✓											

Note: Functional developmental patterns are in boldface type.

Fig. 8. Evolutionary changes in echinoids. The hypothetical ancestor is shown at the base of the diagram with changes in habitat (ΔH), morphology (ΔM), and nutrition (ΔN) leading to different life-cycle patterns. Single-headed arrows represent non-reversible changes and double-headed arrows represent reversible changes. Abbreviations in parentheses represent the morphology (C, complex; S, simple; D, direct), nutrition (Pl, planktotrophy; L, lecithotrophy), and habitat (P, pelagic; B, benthic) of that larval type.

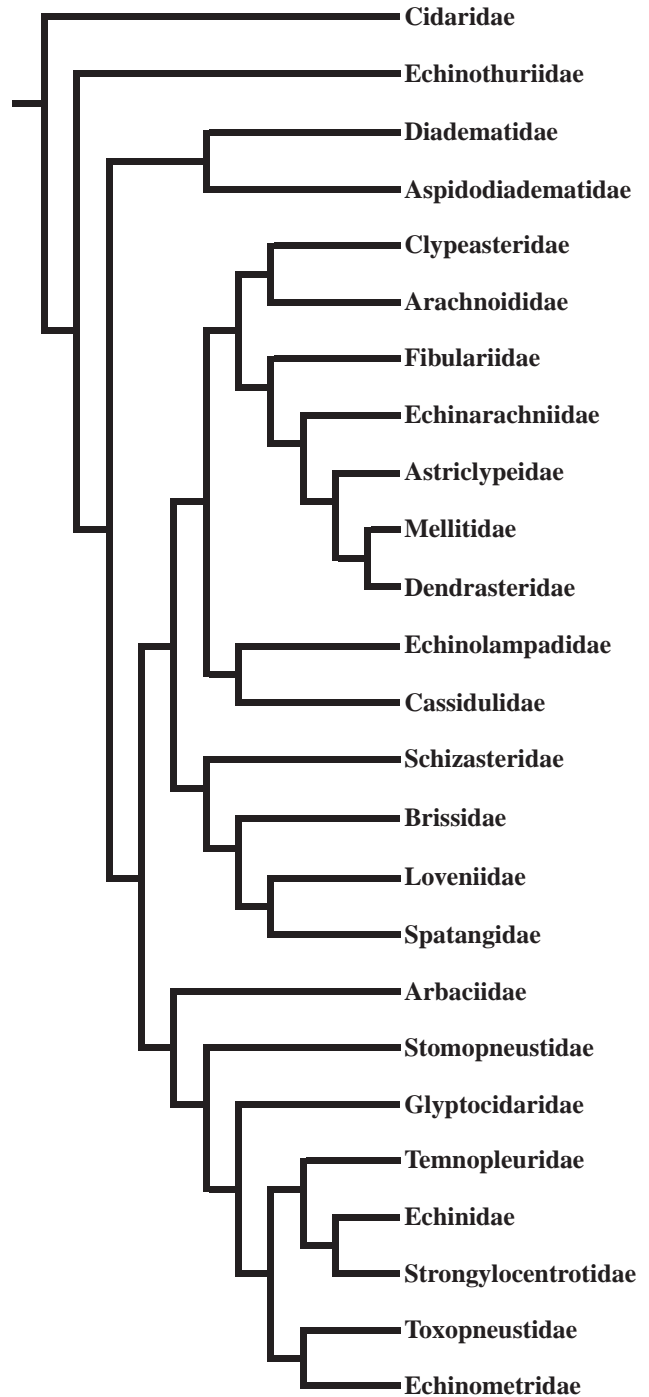


Pawson 1971). The auricularia possesses a complete, functional gut consisting of a mouth located on the ventral surface but under the oral hood, esophagus, bulbous stomach, tubular intestine, and an anus that opens midventrally on the anal lobe. In contrast to all other complex feeding larvae of echinoderms, a juvenile rudiment does not develop in the holothuroid auricularia (Smiley 1986), but rather it develops in the subsequent larval stage. The auricularia occurs in only two of the six orders, Apodida and Aspidochirotida (Table 8).

Doliolaria and vitellaria

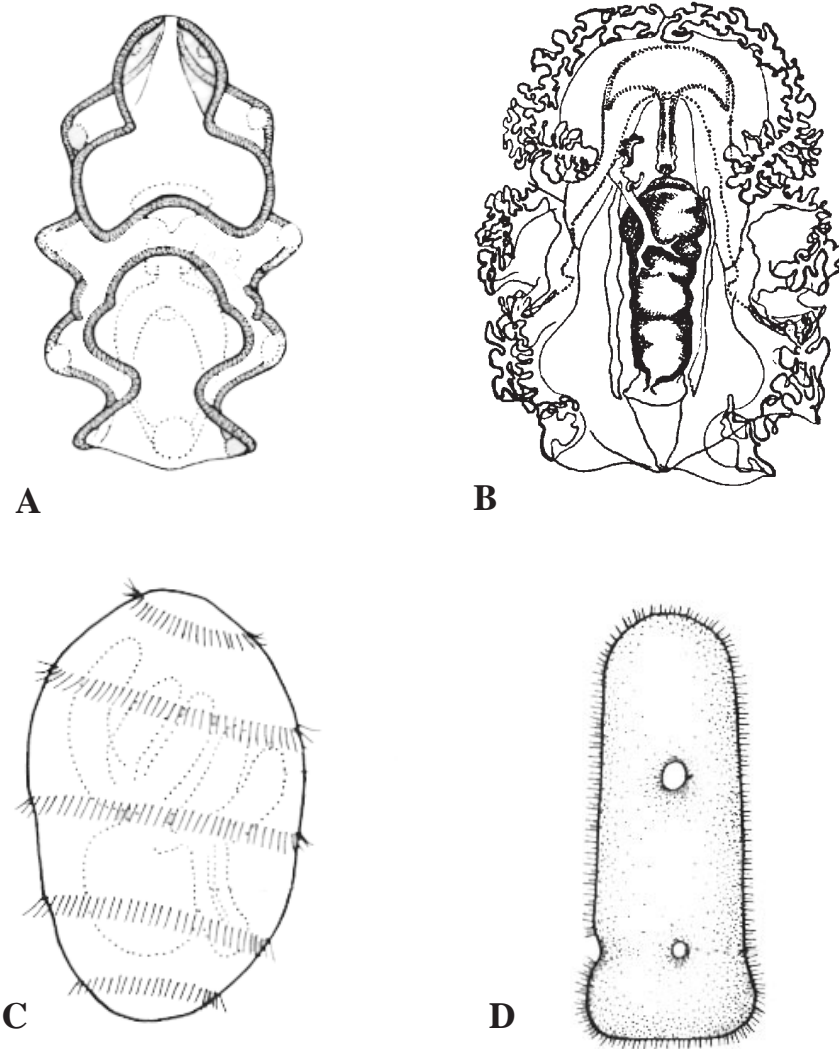
The doliolaria and vitellaria larvae are simple, nonfeeding larvae that are characterized by an ovoid body shape, and

Fig. 9. Phylogeny of echinoid families.



in the case of the doliolaria, by transverse ciliated bands (Figs. 10C, 10D). These larval types develop in two different ways depending on the developmental pattern. In the case of pelagic, planktotrophic development via an auricularia larva, a doliolaria is formed late in larval life and represents a transitional, metamorphic stage. The transformation of the auricularia into the doliolaria involves the simplification of body shape, breakup of the convoluted ciliated band, formation of transverse ciliary rings (Lacalli 1988, 1993), histolysis of the larval gut, and transformation of the oral cavity into the vestibule (Smiley 1986). Meta-

Fig. 10. Larval diversity of holothuroids. (A) Auricularia of *Parastichopus californicus* modified from Strathmann (1987, p. 577). (B) Giant auricularia of *Auricularia bermudensis*, modified from Garstang (1939, p. 324). (C) Doliolaria of *Parastichopus californicus*, modified from Strathmann (1987, p. 577). (D) Vitellaria of *Eupentacta quinquesemita*, modified from Strathmann (1987, p. 577).



morphosis involves development of the juvenile structures within the doliolaria larva to produce a pelagic juvenile called the pentactula (Smiley et al. 1991).

In the case of lecithotrophic development via a simple larva, the initial larval stage is a uniformly ciliated vitellaria. In some species, the larvae remain uniformly ciliated (e.g., *Eupentacta fraudatrix*, Dolmatov and Yushin 1993; *Aslia lefevrei*, Costelloe 1988; *Cucumaria frondosa*, Hamel and Mercier 1996). In other species, the cilia become organized into 2–5 transverse rings to yield a doliolaria larva (e.g., *Chiridota rotifera*, Clark 1910; *Molpadia intermedia*, McEuen and Chia 1985). Intermediate conditions occur in some species, such as *Psolus chitinoides* (McEuen and Chia 1991), in which three transverse rings form in the posterior region of the body, but the preoral lobe remains uniformly ciliated. The conspicuous external features of the vitellaria are a vestibule and podial pits. The vestibule (not homologous with the echinoid vestibule) is located on the ventral surface just posterior to the preoral lobe and near the anteriormost ciliated ring. Podial pits are indentations on the surface that mark the site of emergence of the first ambulacral podia

(Dolmatov and Yushin 1993). Doliolaria larvae occur in four of the six holothuroid orders from which there are published descriptions of development (Table 8). Life cycles with only vitellaria larvae are known in four of the six orders (Table 8).

Holothuroid larval body plan

The common features of holothuroid larvae include bilateral symmetry, a preoral lobe, coelom formation and arrangement, a midventral vestibule, and aspects of metamorphosis. The axis of symmetry is the midsagittal plane. In the auricularia, the body lobes, ciliated bands, nervous system (Burke et al. 1986), and coeloms are symmetrically arranged with respect to the midsagittal plane. The gut and vestibule lie on the midline. The preoral lobe is the region of the body anterior to the vestibule in the vitellaria or doliolaria, or anterior to the oral cavity in the auricularia, which is the developmental precursor of the vestibule. Unlike asteroid larvae, there is no anterior extension of the coeloms into the preoral lobe (Smiley 1986). A single enterocoel arises from the gut and then splits to yield the definitive arrangement of coelomic

Table 8. Phylogenetic distribution of larval types among the holothuroids.

Order and family	Auricularia + doliolaria	Doliolaria only	Vitellaria only	Mesogen
Elasipoda				
Deimatidae			?	?
Apodida				
Synaptidae	✓		✓	?
Chiridotidae	✓	✓		
Molpadiida				
Molpadiidae		✓		
Caudinidae		✓		
Aspidochirotida				
Synallactidae		?	?	
Stichipodidae	✓			
Holothuriidae	✓		✓	?
Sclerodactylidae		?	?	?
Dendrochirotida				
Cucumariidae		✓	✓	?
Phyllophoridae		?	?	?
Psolidae		✓	?	?
Dactylochirotida				
Ypsilothuriidae			?	?

sacs: paired (left and right) somatocoels adjacent to the stomach and a left hydrocoel. Axocoels and the right hydrocoel are absent (Smiley 1986). The vestibule is an invagination on the surface of vitellaria or doliolaria, which opens at the time of emergence of the primary tentacles. It arises in a midventral location in doliolaria that develop from embryos rather than auricularia (*M. intermedia*, McEuen and Chia 1985; *E. fraudatrix*, Dolmatov and Yushin 1993; *C. frondosa*, Hamel and Mercier 1996; *P. chitinoides*, and *Psolidium bullatum*, McEuen and Chia 1991). In species that develop via an auricularia, the vestibule is derived from the oral cavity, which is midventral in the auricularia stage, but is directed anteriorly after transformation to the doliolaria. The pentactula stage (early post-metamorphic juvenile) is characterized by the presence of five primary tentacles (= buccal podia) (Smiley 1986). These primary tentacles arise from the initial five anterior outgrowths from the hydrocoel and emerge through the vestibule. The ambulacral (locomotory) podia arise from a subsequent set of five outgrowths from the posterior side of the hydrocoel and emerge through podial pits. During metamorphosis, the larval gut is histolyzed and replaced, the ciliary bands are lost, the hydrocoel becomes the water-vascular system, and the somatocoels become the perivisceral coelom (Chia and Burke 1978; Smiley 1986).

Diversity of developmental patterns

Given the limited number of detailed studies of holothuroid larval development (Table A1), the phylogenetic distribution of developmental patterns is not well known (Table 9). Three larval patterns have been documented and there are suspected cases of non-larval direct development as well. Pelagic, planktotrophic development with a complex auricularia larva and a doliolaria is known from only two orders but is the most common developmental pattern in the aspidochirotidids. Pelagic, lecithotrophic development is documented in the dactylochirotidids, dendrochirotidids, and molpadids, involving either doliolaria or vitellaria larvae or possibly mesogens

(Tables 8, 9). *Holothuria floridana* (Edwards 1909) and *Sclerodactyla (Thyone) briareus* (Ohshima 1925) might represent cases of pelagic, lecithotrophic, direct development (Table 9).

Benthic, lecithotrophic development involving doliolaria or vitellaria larvae occurs in four orders: Apodida, Aspidochirotida, Dendrochirotida, and Elasipoda (Tables 8, 9). Several species with brooded development (reviewed in McEuen 1986) might represent cases of direct development via a mesogen, but none are sufficiently well described to allow a definitive determination of the nature of morphogenesis or the presence of larval body plan features (Tables 7, 8, A1). Brooding of offspring occurs in various locations on or in the adult body: underneath the adult against the substratum (*Cucumaria lubrica*, Engstrom 1982), in depressions of the dorsal body wall, in brood pouches in the tentacle crown (*Psolus dubiosus*, Gutt 1991), in the coelom (synaptids), and in the ovaries (*Oneirophanta mutabilis*, Hansen 1968; *Leptosynapta clarki*, Sewell and Chia 1994).

Coelomic brooding involves retention of different larval types in different species. Among synaptids, *Synaptula hydriformis* broods vitellaria larvae, *Trochodota dunedinensis* broods doliolaria with five ciliary rings, and *C. rotifera* (Clark 1910) broods reduced auricularia followed by doliolaria with four ciliary rings. Some internal brooders clearly derive substantial nutrition from extra-embryonic sources during brooding of the pentactula stage (e.g., *L. clarki*, Sewell and Chia 1994).

Evolution of developmental patterns

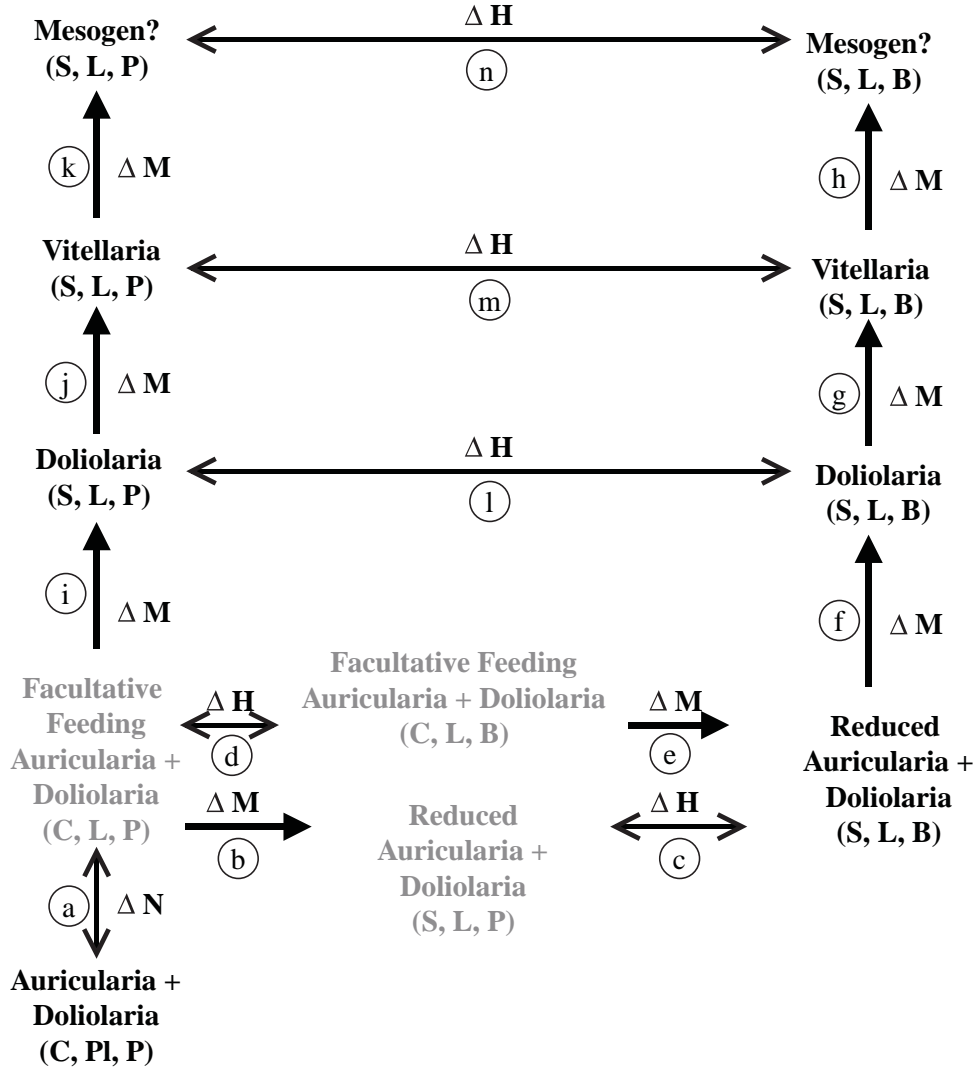
The ancestral holothuroid life cycle involved pelagic, planktotrophic development via an auricularia larva that metamorphosed via a pelagic, lecithotrophic doliolaria with five ciliary rings into a pentactula juvenile (McEuen 1986). We suggest that the pentactula was originally pelagic as well, given the widespread occurrence of pelagic juveniles in holothuroids. This reflects dissociation of settlement and

Table 9. Phylogenetic distribution of developmental patterns among holothuroids.

Order and family	Complex				Simple				Direct			
	Planktotrophy		Lecithotrophy		Planktotrophy		Lecithotrophy		Planktotrophy		Lecithotrophy	
	Pelagic	Benthic	Pelagic	Benthic	Pelagic	Benthic	Pelagic	Benthic	Pelagic	Benthic	Pelagic	Benthic
Elasipoda												
Deimatidae								?				?
Apodida												
Synaptidae	✓											?
Chiridotidae												✓
Molpadiiida												
Molpadiidae								✓				
Caudinidae								✓				
Aspidochirotida												
Synallactidae												✓
Stichipodidae	✓											
Holothuriidae	✓											?
Sclerodactylidae								?	?		?	?
Dendrochirotida												
Cucumariidae								✓	?		?	?
Phyllophoridae												?
Psolidae								✓	?			?
Dactylochirotida												
Ypsilothuriidae								?			?	

Note: Functional developmental patterns are in boldface type.

Fig. 11. Evolutionary changes in holothuroids. The hypothetical ancestor is shown at the base of the diagram with changes in habitat (ΔH), morphology (ΔM), and nutrition (ΔN) leading to different life-cycle patterns. Single-headed arrows represent non-reversible changes and double-headed arrows represent reversible changes. Gray text indicates required intermediates that have not been reported. Abbreviations in parentheses represent the morphology (C, complex; S, simple; D, direct), nutrition (Pl, planktotrophy; L, lecithotrophy), and habitat (P, pelagic; B, benthic) of that larval type.

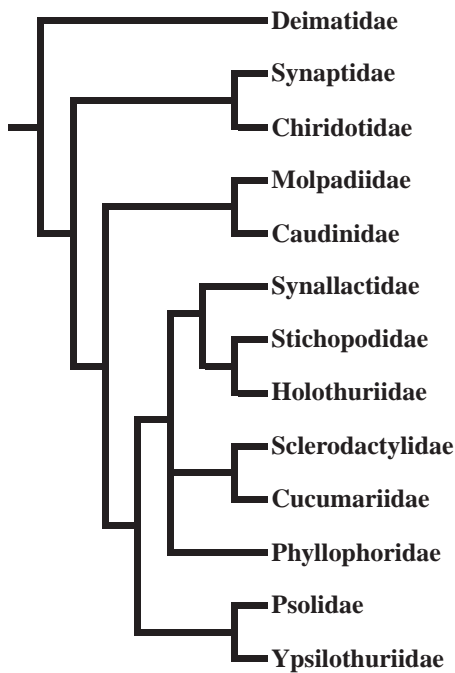


metamorphosis, probably because holothuroid metamorphosis is a gradual process that is relatively simple compared with the metamorphosis in other echinoderm classes (Smiley 1986).

The sequences of evolutionary transitions in life-cycle characters that could account for the diversity of developmental patterns in holothuroids are complex (Fig. 11). From the ancestral life cycle, the auricularia larval stage was lost (Fig. 11). In most species without an auricularia, it is tempting to infer the occurrence of changes shown in Figs. 11a and 11i, which are similar to the changes that are thought to have occurred in the other classes during the loss of feeding larvae: first the nutritional change to lecithotrophy then the alterations of morphology to simplify the larva, both occurring with pelagic development. There are no documented cases of facultative feeding or reduced pelagic auricularia stages in holothuroids, but reduced auriculariae do occur in brooders. This would require, first, the nutritional switch to lecitho-

trophy (Fig. 11a) and then the changes in morphology and habitat, presumably in either order (Figs. 11b, 11c or 11d, 11e). The evolution of benthic development with doliolaria larvae could evolve from either a life cycle with pelagic larvae via a reversible change in habitat (Fig. 11l) or from brooding through further changes in morphology that lead to the complete elimination of the auricularia stage (Fig. 11f). The net changes from the ancestral life cycle are the same and the two postulated evolutionary routes might be distinguished by embryology, larval morphology, and phylogenetic analysis (Fig. 12) (Strathmann and Eernisse 1994).

The evolution of vitellaria larvae is presumed to occur by changes in morphology to eliminate the development of ciliary rings, either in pelagic larvae (Fig. 11j) or in benthic brooders (Fig. 11g). We consider this morphological change to be reversible because (i) the developmental alterations required to rearrange cilia should be minor, (ii) doliolaria develop from an initially uniformly ciliated embryo, and

Fig. 12. Phylogeny of holothuroid families.

(iii) transverse rings have evolved repeatedly among echinoderms and represent convergence on an effective locomotory design, given relaxation of the need to feed (Emler 1994). Shifts in habitat (Fig. 11m) could account for pelagic or benthic vitellaria from benthic or pelagic ancestors, respectively.

The evolution of direct development (sensu McEdward and Janies 1997) has not been documented in holothuroids but has been suggested (see above). The morphological changes that lead to the loss of the larval body plan are expected to be sufficiently extensive as to be irreversible (Figs. 11h or 11k). Again, given a simple shift in habitat, there could be evolution, in either direction, between pelagic and benthic direct development (Fig. 11n).

Derived life cycles occur in all holothuroid orders (Tables 8 and 9, Fig. 12). Life cycles characterized by only a doliolaria larva must have evolved at least 4–5 times (Table 8, Fig. 12). Likewise, vitellaria (non-doliolaria) evolved a minimum of 3–6 times in the class. There is considerable uncertainty whether the many holothuroids that brood morphologically simple offspring have nonfeeding larvae or direct development via mesogens (Tables 8 and 9). Minimum estimates for the independent evolution of direct development range from 0 to 5 times (Table 8, Fig. 12). The loss of larval feeding occurred at least 8 times and benthic development evolved at least 6 different times in the holothuroids (Tables 8 and 9, Fig. 12).

Ophiuroids

Diversity of larval types

Ophiuroids have three larval types: ophiopluteus, doliolaria, and vitellaria; they also have direct development via a mesogen.

Ophiopluteus

The ophiopluteus (Fig. 13A) is a complex, bilaterally symmetrical, feeding larva characterized by anteriorly directed arms that are supported by calcareous skeletal rods (Hyman 1955; Yamashita 1985; Hendler 1991). The larval arms are not homologous to the larval arms of echinoplutei but share some common names resulting from a similarity of location (Mortensen 1898). There seems to be less variation in body form and number of larval arms among ophioplutei than in echinoplutei (Hendler 1991). Most planktotrophic ophioplutei have four pairs of larval arms: posterolaterals, anterolaterals, postorals, and posterodorsals (e.g., *Ophiopholis aculeata*, Olsen 1942; *Ophiothrix suenisoni*, Mladenov 1985). Arms are hollow extensions of the body wall that contain blastocoelic space and bear the ciliated feeding-band structure. The ciliated band of late-stage larvae does not give rise to localized regions that are specialized for locomotion. The larval skeleton consists of solid (never fenestrated) rods. Ophioplutei possess a complete gut consisting of mouth, esophagus, bulbous stomach, recurved, tubular intestine, and anus. Ophioplutei lack a vestibule. Metamorphosis occurs by one of two patterns (Mladenov 1985). In type I metamorphosis (e.g., *Ophiothrix fragilis*, MacBride 1907), the anterolateral, postoral, and posterodorsal arms are resorbed into the juvenile rudiment in the center of the pluteus body. A rapid metamorphosis of the rudiment occurs while it is pelagic and is supported by the ciliary activity of the posterolateral arms, which are cast off at settlement. In some species (e.g., *O. aculeata*), the posterolateral arms of the ophiopluteus remain functional after loss of the juvenile, and later a new larval body and a second juvenile develop (Balsler 1998). In type II metamorphosis (e.g., *Ophiocoma pumila*, Mladenov 1985), all four pairs of larval arms are resorbed and the larva transforms into a doliolaria during metamorphosis. Ophioplutei occur only in the order Ophiurida (Table 10).

Doliolaria and vitellaria

Nonfeeding larvae of ophiuroids are very diverse. Some yolky, nonfeeding, reduced ophioplutei (Fig. 13B) have one pair of larval arms (posterolaterals) (e.g., *Ophiothrix oerstedii*, Mladenov 1979), yet others have only rudimentary arms (e.g., *Amphipholis abditus*, Hendler 1977). Some very simple, ovoid larvae lack all larval arms, yet have vestigial pluteus structures (e.g., *Ophioneries schayeri*, Selvakumaraswamy and Byrne 2000). Doliolaria larvae typically have four transverse ciliary rings (e.g., *Ophiolepis elegans*, Stancyk 1973; *Ophioplocus japonicus*, Komatsu and Shōsaku 1993) (Fig. 13C), although some species possess only three (e.g., *Ophionereis annulata*, Hendler 1982). The simplest form that retains elements of the larval body plan (paired enterocoels and bilateral symmetry) is a vitellaria that lacks ciliated bands (*Amphipholis japonica*, Oguro et al. 1982). Reduced plutei metamorphose via the type I pattern. Vitellaria larvae are widespread throughout the class (Table 10), but in many cases it is not clear whether nonfeeding larvae possess transverse ciliated bands and are doliolariae.

Mesogen

The Australian brooder known as Kirk's ophiuroid has direct development (Fell 1941). The mesogen is unlike any ophiuroid larva (Fig. 13D), including even the most simpli-

Fig. 13. Larval diversity of ophiuroids. (A) Ophiopluteus of *Ophiothrix* sp. modified from Mortensen (1921, plate XIX). (B) Reduced ophiopluteus of *Amphiplus abditus*, modified from Hendler (1977, p. 55). (C) Doliolaria of *Ophionereis* sp. Mortensen (1921, plate XXXI). (D) Mesogen of Kirk's ophiuroid, modified from Fell (1941, plate XXI).

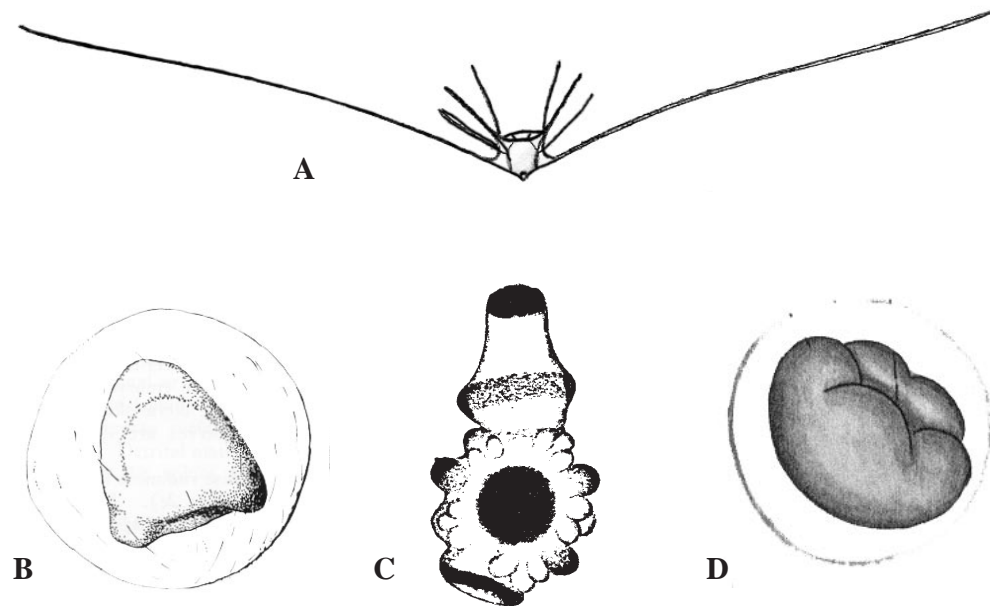


Table 10. Phylogenetic distribution of larval types among the ophiuroids.

Order and family	Pluteus + Doliolaria	Pluteus only	Vitellaria only	Doliolaria only	Mesogen
Phrynophiurida					
Gorgonocephalidae			?	?	
Ophiurida					
Ophiomyxidae			?	?	
Ophiacanthidae			?	?	
Hemieuryalidae			?	?	
Ophiodermatidae			✓	✓	
Ophiuridae		✓	✓	✓	
Ophionereididae			✓	✓	
Ophiocomidae	✓	✓	?	?	
Amphiuridae		✓	✓		✓
Ophioactidae		✓			
Ophiothricidae		✓	✓	?	
Unknown					
Unknown (Kirk's ophiuroid)					✓

fied vitellaria (e.g., *A. japonica*, Oguro et al. 1982) because of the lack of bilateral symmetry, orientation of the hydrocoel, and novel patterns of morphogenesis of the coeloms, gut, and skeleton (Fell 1941). Nearly every aspect of development from embryonic cleavage, through gastrulation, to coelom formation is markedly different from that of all other ophiuroids. *Amphipholis squamata* also has highly derived development (e.g., coelom formation entirely by schizocoely, without any trace of enterocoels) (Fell 1946).

Ophiuroid larval body plan

Ophioplutei share a common set of features that define the larval body plan. All larvae are bilaterally symmetrical. In plutei, the arms are present as left-right pairs and the ciliated band traces a loop around the body that is symmetrical with respect to the midsagittal plane. Internal larval structures are

also bilaterally symmetrical (coeloms) or lie on the midline of the body (gut). In vitellaria larvae, it is the arrangement of archenteron and paired larval coeloms that defines the plane of symmetry. As in asteroids and echinoids, the morphogenetic axis around which the juvenile rudiment initially develops is oriented orthogonal to the plane of larval symmetry, with the future adult oral side corresponding to the left side of the larva. However, during type I metamorphosis of ophioplutei, the hydrocoel rotates 90° around the anterior–posterior axis of the larva, bringing the oral surface to the ventral side of the pluteus body and placing the plane of hydrocoel disk parallel to the plane of the posterolateral arms (Olsen 1942; Hyman 1955). Thus the juvenile mouth develops at the site of the larval mouth. Although the juvenile rudiment appears first in the post-rotational position in some reduced plutei and doliolaria larvae (Stancyk 1973;

Table 11. Phylogenetic distribution of developmental patterns among ophiuroids.

Order and family	Complex				Simple				Direct				
	Planktotrophy		Lecithotrophy		Planktotrophy		Lecithotrophy		Planktotrophy		Lecithotrophy		
	Pelagic	Benthic	Pelagic	Benthic	Pelagic	Benthic	Pelagic	Benthic	Pelagic	Benthic	Pelagic	Benthic	
Phryngosphiurida													
Gorgonocephalidae													
Ophiurida													
Ophiomyxidae												✓	
Ophiacanthidae												✓	
Hemiteuryalidae												✓	
Ophiodermatidae												✓	
Ophiuridae												✓	
Ophionereididae												✓	
Ophiocomicidae												✓	
Amphiuridae												✓	
Ophioactidae												✓	
Ophiothricidae												✓	
Unknown													✓
Unknown (Kirk's ophiuroid)													✓

Note: Functional developmental patterns are in boldface type.

Mladenov 1979; Komatsu and Shōsaku 1993), it is not certain whether hydrocoel rotation occurs or if coelomogenesis has been modified so that the hydrocoel develops in the definitive location and orientation. The left and right axocoels give rise to the adult axial coelom (= ampulla of the stone canal), the left hydrocoel forms the water-vascular system, the somatocoels give rise to the perivisceral coelom, the skeletal plates arise independently from the larval skeletal rods, and the mouth, esophagus, and stomach are retained in the juvenile, whereas the intestine and anus are lost (Hyman 1955; Chia and Burke 1978). Larval skeletal rods are discarded, but in some species, part of the larval body persists and a second larva and juvenile are cloned (Balsler 1998). In species with pelagic development, metamorphosis occurs in the plankton and settlement takes place after the juvenile has well-developed arms with skeletal plates and several sets of podia.

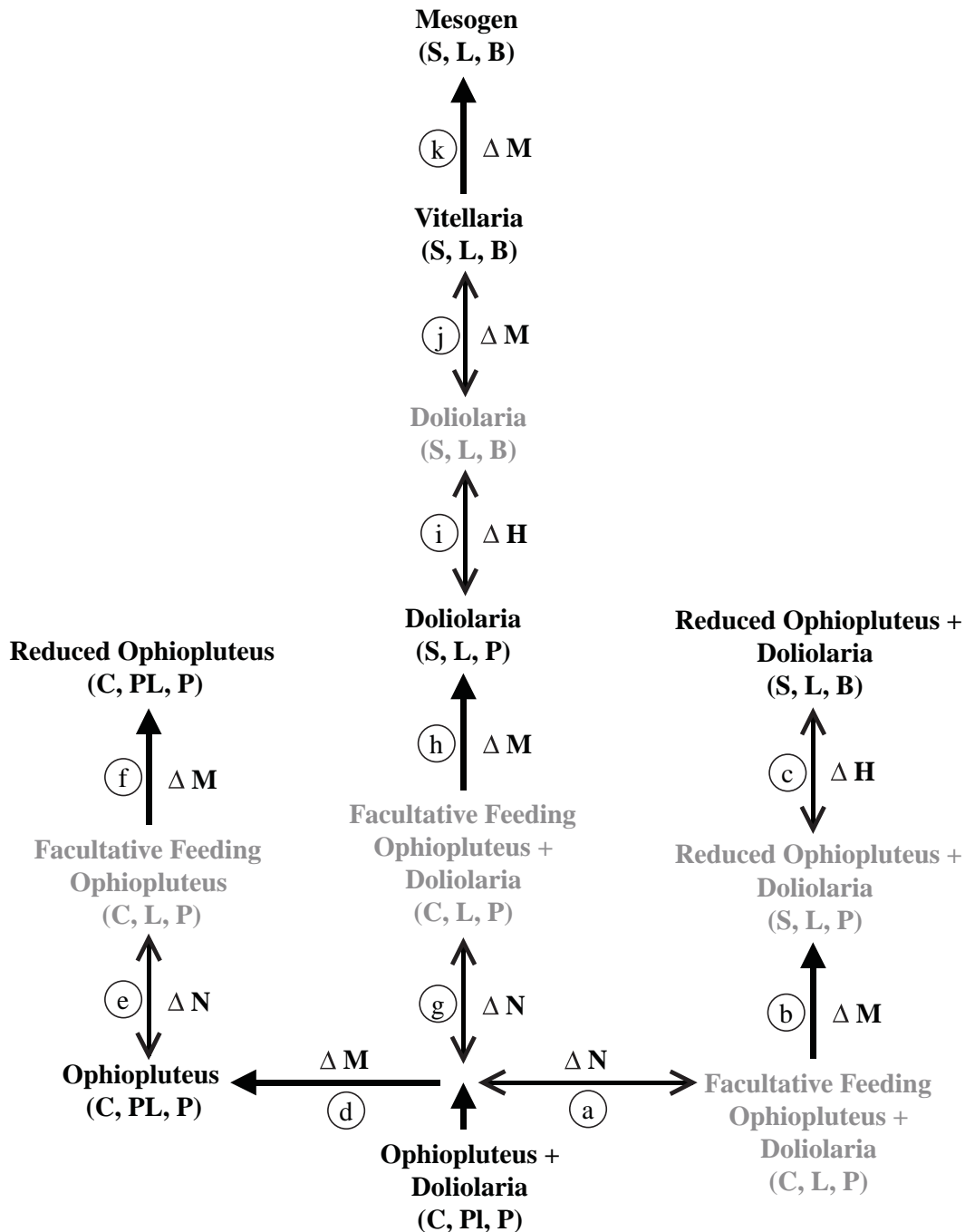
Diversity of developmental patterns

Four of the eight viable developmental patterns occur in ophiuroids (Table 11). Lecithotrophic development, both in the plankton and on the benthos, is phylogenetically widespread and occurs in more families than does planktotrophy via an ophiopluteus (Table 10). In most species with planktotrophic development, the pluteus is the final larval stage, but in one species, *O. pumila* (Mladenov 1985), the ophiopluteus transforms into a pelagic, nonfeeding doliolaria at the onset of metamorphosis. Pelagic lecithotrophic development occurs via reduced plutei (e.g., *O. oerstedii*, Mladenov 1979) or a doliolaria larva (e.g., *O. japonicus*, Komatsu and Shōsaku 1993). Benthic development involves reduced plutei that metamorphose before hatching, or brooded vitellaria, or mesogens. Demersal (non-brooded benthic) development occurs within tough, adhesive vitelline envelopes that adhere to the substratum (e.g., *A. abditus*, Hendler 1977). Brooding typically occurs in the genital bursae of the adult and in some cases there is a tissue connection between the bursal wall and the developing larva (*A. japonica*, Oguro et al. 1982). Extra embryonic nutrition can support growth to a very large size prior to emergence of the juveniles (e.g., *Ophionotus hexactis*, Turner and Dearborn 1979; *A. squamata*, Fell 1946; Walker and Lesser 1989; Byrne 1991).

Evolution of developmental patterns

The ancestral ophiuroid life cycle (Fig. 14) probably involved planktotrophic development via an ophiopluteus larva, followed by a pelagic, lecithotrophic doliolaria larva, and type II metamorphosis (Mladenov 1985). Some ophiuroid specialists argue that life cycles characterized by only a doliolaria larva evolved by progressive reduction of the pluteus and retention of the ancestral, terminal doliolaria stage (see Fell 1948, p. 97; Mladenov 1985, p. 293). This could account for demersal development with a reduced pluteus and a doliolaria (Figs. 14a, 14b, 14c), pelagic development via a doliolaria (Figs. 14g, 14h), brooded development with vitellaria (Figs. 14i, 14j), and brooding with direct development (Fig. 14k). However, this hypothesis is insufficient to account for all larval patterns in the ophiuroids. Loss of the doliolaria (Fig. 14d) must have occurred to give rise to life cycles in which there is only a pluteus larval stage with type I metamorphosis (planktotrophic or lecithotrophic;

Fig. 14. Evolutionary changes in ophiuroids. The hypothetical ancestor is shown at the base of the diagram with changes in habitat (ΔH), morphology (ΔM), and nutrition (ΔN) leading to different life-cycle patterns. Single-headed arrows represent non-reversible changes and double-headed arrows represent reversible changes. Gray text indicates required intermediates that are unknown. Abbreviations in parentheses represent the morphology (C, complex; S, simple; D, direct), nutrition (PL, planktotrophy; L, lecithotrophy), and habitat (P, pelagic; B, benthic) of that larval type.



Figs. 14e, 14f). Most of the transitions illustrated in Fig. 14 involve multiple evolutionary events and link only patterns of development that have been documented in the ophiuroids. We strongly advocate considering the functional requirements and options that accompany the evolution of larval characters in evaluating the possible routes from ancestral to derived life cycles. There is a confusing array of possible evolutionary transitions that could account for the diverse derived life cycles and larval stages of ophiuroids, if all transitions are

assumed to involve only a single character change and all hypothesized intermediate patterns are considered. Some hypothesized intermediates are clearly necessary (Fig. 14). The transition to lecithotrophy must precede the loss of complex larval morphology or the evolution of encapsulated development. Several developmental patterns could have evolved by alternative routes and if evolved repeatedly, by multiple routes. For example, pelagic, lecithotrophic development via a reduced pluteus could have evolved from a planktotrophic

pluteus that lacked a doliolaria stage or could have evolved from a reduced pluteus with a doliolaria. Unfortunately, the developmental diversity of the ophiuroids is too poorly known to confirm or eliminate most of these possibilities. Given the current understanding of ophiuroid development, it is important to recognize the range of possible evolutionary routes to different larval patterns, rather than to rely on seductively simple hypotheses that account for only a subset of the patterns.

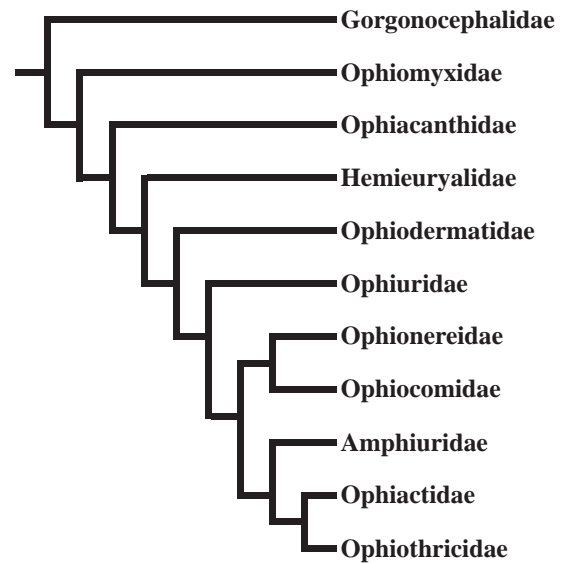
Nonfeeding larval development is much more widespread among ophiuroid families than is planktotrophic larval development (Table 11). Given that the ancestral ophiuroid life cycle involved a planktotrophic ophiopluteus larva and assuming that the loss of a feeding larval stage is irreversible (Strathmann 1978; McEdward and Janies 1997), then non-feeding larval development must have evolved at least 10 times (Table 11, Fig. 15). Benthic development must have evolved at least eight times. Direct development has evolved at least twice in the class.

Summary and conclusions

The familiar larval stages of the echinoderms, such as bipinnaria, auricularia, echinopluteus, and ophiopluteus, are characterized by many features that do not define the larval body plans for their respective classes. The structures that make these larvae so visually striking and identifiable are specializations for life in the plankton, providing these larval forms with adaptations to effectively capture particulate food. Once the transition to lecithotrophy occurs, then it is possible, and very common, for substantial changes to occur in the external morphology of these larvae. Both functional analyses of larval design for swimming and feeding, and developmental studies of the changes that underlie shifts in morphology, illustrate that these changes occur in features associated with the capture of particulate food by larvae. Many other features of larval organization remain unaltered in the evolution of nonfeeding larvae and it is these that comprise the larval body plan. It is tempting to interpret these fundamental features of larval morphology and metamorphosis (e.g., morphogenesis, organization, and post-metamorphic fates of coeloms) as conserved because of developmental constraints (i.e., features so intimately associated with the construction of the adult body plan that evolutionary change is not feasible). Yet the recent discovery of highly derived, direct development in asteroids and echinoids demonstrates without question how radically even the most basic features of development can be altered and still give rise to the same adult morphology. The only conclusion that can be supported from these observations is that it is life-history ecology (i.e., the functional demands on larvae) that imposes limits on developmental evolution and determines the associations of larval types and life-cycle character states that gives rise to the developmental patterns that we observe in marine organisms.

The evolutionary transition from complex larval morphology (feeding larvae) to simple larval morphology (nonfeeding larvae) requires that increased levels of yolk or lipid be provisioned in the eggs (Byrne and Cerra 2000; McEdward and Morgan 2001). Initial increases in egg provisioning result in lecithotrophic larvae that can feed but do not need to

Fig. 15. Phylogeny of ophiuroid families.



do so (facultative planktotrophy; e.g., *C. rosaceus*, Emlet 1986; *B. latifrons*, Hart 1996). Subsequent increases in egg provisioning allows simplification of larval morphology with loss of larval feeding capability (Strathmann 1978; Wray 1995a; Hart 1996; McEdward and Janies 1997). The selective factors that drive the evolution of very large, energy-rich eggs or the evolution of simple larval morphology have not been systematically investigated. It seems likely that independence from the risk of food limitation and advantages of building larger juveniles could favor very large eggs. Simple larval morphology might be advantageous because time and energy could be saved if larval feeding structures are not built. Simple nonfeeding larvae occur in all classes of echinoderms (Table 12) in spite of inconsistent terminology for these larval stages: yolky brachiolaria, barrel-shaped larva, and non-brachiolaria larva for asteroids; doliolaria and vitellaria for crinoids; reduced pluteus and schmoo for echinoids; vitellaria and doliolaria for holothuroids; and reduced pluteus, vitellaria, and doliolaria for ophiuroids.

Striking convergence is observed in the morphology of nonfeeding larvae both within and among classes. There are three reasons for this. First, simplification (i.e., loss of elaborate, conspicuous, unique structures) of feeding larvae inevitably reduces the perceived morphological disparity among derived larval types. Second, the less conspicuous structures (e.g., coeloms, nervous systems) are the only features by which to describe these larvae. This leads to the perception of greater similarity, even though the same similarities exist among feeding larvae. Third, real convergence in larval body form (ovoid shape) and external features (transverse ciliated bands) occur as a result of common functional requirements (swimming) and a lack of need for structures for conflicting demands (feeding, defense) (Emlet 1991, 1994).

The nomenclature for nonfeeding larvae with simple morphology is not consistent among echinoderm classes. The term doliolaria was used by Bury (1895) to describe the late developmental stage with transverse ciliary rings, distinguishing it from the holothuroid auricularia larva with convoluted ciliated bands. In some holothuroids, doliolaria has the connotation of being a pupal stage, intermediate between

Table 12. Phylogenetic distribution of larval types among the echinoderm classes.

Class	Planktotrophic larva	Vitellaria	Doliolaria	Mesogen
Asteroidea	✓	✓		✓
Crinoidea		✓	✓	
Echinoidea	✓	✓		✓
Holothuroidea	✓	✓	✓	
Ophiuroidea	✓	✓	✓	✓

larva and juvenile. Fell (1945) used the term vitellaria (= yolk-larva) for all echinoderm larvae that were simple (i.e., lacked arms or projections), ovoid or barrel-shaped, yolky, free-swimming, and provided with transverse ciliary rings. This is consistent with modern usage of the term by ophiuroid workers. Hendler (1982) used the term vitellaria as a general name for all simple, yolky, echinoderm larvae (including crinoids and holothuroids), without drawing distinction for larvae with transverse rings. Wray (1995a) used the term schmoo to refer to simple echinoid larvae. Many of these larvae have the same features as vitellaria.

We agree with Hendler (1982) that the term vitellaria should refer to any nonfeeding, endotrophic larva, regardless of body form. Whereas lecithotrophy refers to "yolk-feeding," endotrophy covers a broader range of larvae including nonfeeding larvae that do not depend on yolk-derived energy (e.g., post-planktotrophic auricularia stage in holothuroids and the post-pluteus stage in some ophiuroids). Most nonfeeding larvae are morphologically simple (i.e., ovoid), but in some cases, especially in the echinoids and ophiuroids, they can retain aspects of the pluteus form, such as larval arms. Our suggestion is consistent with recent usage by holothuroid workers (e.g., Dolmatov and Yushin 1993; Hamel and Mercier 1996). By our definition, vitellaria larvae occur in asteroids, echinoids, crinoids, holothuroids, and ophiuroids. Some vitellaria larvae possess transverse ciliary rings, presumably as an adaptation for effective locomotion (Emlet 1994). We recommend retaining the term doliolaria to refer to larvae with one or more transverse ciliated bands. Some examples of vitellaria larvae that are not doliolariae include yolky brachiolariae and barrel-shaped larvae of asteroids, reduced plutei and schmoos of echinoids, uniformly ciliated barrel-shaped larvae of crinoids and holothuroids, and reduced plutei and uniformly ciliated, barrel-shaped larvae of ophiuroids.

It is important to recognize that nonfeeding larvae have evolved independently and repeatedly in each class and the use of a common name does not imply homology. Rather, the term vitellaria recognizes their convergent structural and nutritional attributes. Likewise the few documented cases of mesogens in the asteroids, echinoids, and ophiuroids, and the many potential cases in the holothuroids represent the independent evolution of direct development. The selective factors that account for the widespread morphological convergence of developmental stages in derived life cycles of echinoderms have not been investigated in detail and clearly deserve attention.

Of the five classes that we have analyzed in this paper, only the crinoids lack a feeding larval stage (Table 12). All classes have nonfeeding vitellaria larvae. Doliolaria larvae are absent in the asteroids and echinoids. It is not at all clear why the nonfeeding larvae in these two classes would lack

transverse ciliated rings, especially given that feeding echinoplutei have regions of the ciliated band that are specialized for locomotion and are arranged transversely on or around the larval body. Direct development has been documented in three classes (Table 13), but in very few species so far, and only quite recently in asteroids and echinoids. We suspect that multiple, independent cases of direct development occur in all classes of echinoderms.

Although six of the eight viable developmental patterns have been reported in echinoderms (Table 13), only four patterns occur in more than a single class, and of those, direct development is restricted to one or a very few species in echinoids and ophiuroids. Facultative planktotrophy has been documented in only two species of echinoids. It is very likely that many more unrecognized cases exist in each of the four classes with feeding larvae. Examination of larval morphology is not sufficient to distinguish facultative from obligate planktotrophy; nutritional experiments are necessary.

It is not surprising that pelagic direct development is rare. So far, it has been reported in only one species of asteroid. Direct development is expected to evolve mostly in brooding species but only under special conditions (McEdward 1995; McEdward and Janies 1997). Although it does not preclude the re-evolution of pelagic development, we expect benthic, direct development to be relatively rare, and hence pelagic direct development to be even less common.

It is surprising that benthic, free-living, feeding larvae have not been reported in the echinoderms (Table 13). Complex feeding larvae are very common in echinoderms, but regardless of whether they are obligately or facultatively planktotrophic, all are pelagic and none are benthic. Since benthic development in simple nonfeeding larvae or direct-developing mesogens usually involve brooding rather than free-living larvae, it is unlikely that nutritional limitation accounts for the rarity of benthic, free-living larvae; more likely it is predation risk. The absence of benthic, free-living larvae is striking and deserves attention by marine ecologists.

Two factors seriously limit the usefulness of analyses of larval and life-cycle evolution in echinoderms. First is the limited understanding of developmental diversity. Many of the descriptive and comparative reports are quite old and are in need of reexamination to provide definitive answers to modern questions. Coincident with increased interest in larval ecology over the past three decades, descriptions and analyses of ecological patterns of larval development have become common and studies documenting the morphological development of larvae have become relatively rare. In spite of this trend, much of the diversity in echinoderm development has been documented in the past 20 years. The important point is that we are far from understanding the full

Table 13. Phylogenetic distribution of developmental patterns among the echinoderm classes.

Class	Complex				Simple				Direct			
	Planktotrophy		Lecithotrophy		Planktotrophy		Lecithotrophy		Planktotrophy		Lecithotrophy	
	Pelagic	Benthic	Pelagic	Benthic	Pelagic	Benthic	Pelagic	Benthic	Pelagic	Benthic	Pelagic	Benthic
Asteroidea	✓						✓				✓	
Crinoidea							✓					✓
Echinoidea	✓			✓			✓					✓
Holothuroidea	✓						✓					✓
Ophiuroidea	✓						✓					✓

Note: Functional developmental patterns are in boldface type.

extent of larval types and developmental patterns in echinoderms and more descriptive and comparative work is greatly needed. We hope that the growth of interest in the field of evolutionary developmental biology will stimulate renewed attention to the question of larval and developmental diversity. The second, and more serious, limitation on the study of larval and life-cycle evolution is the lack of good phylogenies for echinoderms. There are useable, but controversial and incomplete, family-level trees for asteroids, echinoids, holothuroids, and ophiuroids. What is needed for many evolutionary questions is a solid species-level tree. Given that phylogenetic information is crucially important, and that sequencing methods are becoming faster, cheaper, and easier, it is our hope that good trees will be available in the near future for all of the echinoderm classes.

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Appendix

Table A1. Developmental patterns of species within the Asteroidea, Crinoidea, Echinoidea, Holothuroidea, and Ophiuroidea.

Class, order, family	Species	Developmental pattern			Larval type	Sources
		Morphogenesis*	Nutrition [†]	Habitat [‡]		
Asteroidea						
Forcipulatida						
Asteroidea						
	<i>Anasterias antarctica</i>	S	L	B		Arnaud 1974
	<i>Anasterias directa</i>	S	L	B		Simpson 1982
	<i>Anasterias mawsoni</i>	S	L	B		Simpson 1982
	<i>Anasterias minuta</i>	S	L	B		Fisher 1940
	<i>Anasterias perrieri</i>	S	L	B		Arnaud 1974; Lawrence et al. 1984
	<i>Anasterias rupicola</i>	S	L	B		Lawrence et al. 1984
	<i>Anasterias sphaerulata</i>	S	L	B		Arnaud 1974
	<i>Anasterias studeri</i>	S	L	B		Fisher 1940; Hayashi 1972
	<i>Aphelasterias japonica</i>	C	Pl	P	Bipinnaria and brachiolaria	Davydov and Vassetsky 1994
	<i>Asterias amurensis</i>	C	Pl	P	Bipinnaria and brachiolaria	Kume and Dan 1968
	<i>Asterias brandtii</i>	S	L	B		MacBride and Simpson 1908

Table A1 (continued).

Class, order, family	Species	Developmental pattern			Larval type	Sources
		Morphogenesis*	Nutrition [†]	Habitat [‡]		
	<i>Asterias calamaria</i>	C	Pl	P		Mortensen 1921
	<i>Asterias forbesi</i>	C	Pl	P	Bipinnaria and brachiolaria	Galtsoff and Loosanoff 1939; Costello et al. 1957
	<i>Asterias lincki</i>	S	L	P		Falk-Petersen 1982
	<i>Asterias rubens</i>	C	Pl	P	Bipinnaria and brachiolaria	Thorson 1946
	<i>Asterias vulgaris</i>	C	Pl	P	Bipinnaria and brachiolaria	Field 1892; Goto 1898; Costello et al. 1957
	<i>Brisinga endecacnemos</i>	S	L	P		Tyler et al. 1984
	<i>Brisingella coronata</i>	S	L	P		Tyler et al. 1984
	<i>Calvasterias laevigata</i>	S	L	B		Fell 1953
	<i>Calvasterias suteri</i>	S	L	B		Fell 1967
	<i>Coscinasterias calamaria</i>	C	Pl	P	Bipinnaria and brachiolaria	Barker 1978
	<i>Cryptasterias turqueti</i>	S	L	B		Hyman 1955
	<i>Diplasterias brandti</i>	S	L	B		Hyman 1955
	<i>Diplasterias brucei</i>	S	L	B		Fisher 1940; Hyman 1955
	<i>Diplasterias meridionalis</i>	S	L	B		Fisher 1940; Lawrence et al. 1984
	<i>Diplasterias octoradiata</i>	S	L	B		Fisher 1940; Hayashi 1972
	<i>Diplasterias radiata</i>	S	L	B		Arnaud 1974
	<i>Distolasterias nipon</i>	C	Pl	P	Bipinnaria and brachiolaria	Wada et al. 1996
	<i>Evasterias troscheli</i>	C	Pl	P	Bipinnaria and brachiolaria	Mortensen 1921
	<i>Freyella spinosa</i>	S	L	P		Tyler et al. 1984
	<i>Granaster nutrix</i>	S	L	B		Hyman 1955
	<i>Leptasterias aequalis</i>	S	L	P		Gordon 1929
	<i>Leptasterias arctica</i>	S	L	B		Hyman 1955
	<i>Leptasterias compta</i>	S	L	B		Verrill 1914
	<i>Leptasterias cribaria</i>	S	L	B		Verrill 1914
	<i>Leptasterias epichlora</i>	S	L	B		Verrill 1914
	<i>Leptasterias groenlandica</i>	S	L	B		Lieberkind 1920; Hayashi 1972
	<i>Leptasterias hexactis</i>	S	L	B	Brachiolaria	Osterud 1918; Chia 1966, 1968
	<i>Leptasterias littoralis</i>	S	L	B		Verrill 1914; O'Brien 1976
	<i>Leptasterias muelleri</i>	S	L	B		Thorson 1946
	<i>Leptasterias ochotensis</i>	S	L	B	Brachiolaria	Kubo 1951; Kano et al. 1974
	<i>Leptasterias polaris</i>	S	L	B	Brachiolaria	Emerson 1977; Himmelman et al. 1982
	<i>Leptasterias pusilla</i>	S	L	B		Hyman 1955
	<i>Leptasterias tenera</i>	S	L	B	Brachiolaria	Worley et al. 1977
	<i>Lysasterias adeliae</i>	S	L	B		Arnaud 1974
	<i>Lysasterias belgicae</i>	S	L	B		Hyman 1955
	<i>Lysasterias chirophora</i>	S	L	B		Hyman 1955
	<i>Lysasterias hemiora</i>	S	L	B		Arnaud 1974
	<i>Lysasterias heteractis</i>	S	L	B		Arnaud 1974
	<i>Lysasterias joffrei</i>	S	L	B		Arnaud 1974
	<i>Lysasterias perrieri</i>	S	L	B		Hyman 1955
	<i>Marthasterias glacialis</i>	C	Pl	P	Bipinnaria and brachiolaria	Thorson 1946
	<i>Neosmilaster georgianus</i>	S	L	B		Arnaud 1974
	<i>Neosmilaster steineri</i>	S	L	B		Hyman 1955
	<i>Notasterias armata</i>	S	L	B		Arnaud 1974
	<i>Odinella nutrix</i>	S	L	B		Hyman 1955
	<i>Orthasterias koehleri</i>	C	Pl	P	Bipinnaria and brachiolaria	Strathmann 1987
	<i>Pisaster brevispinus</i>	C	Pl	P	Bipinnaria and brachiolaria	Strathmann 1987
	<i>Pisaster ochraceus</i>	C	Pl	P	Bipinnaria and brachiolaria	Mortensen 1921; Strathmann 1987
	<i>Pycnopoida helianthoides</i>	C	Pl	P	Bipinnaria and brachiolaria	Greer 1962; Strathmann 1987
	<i>Sclerasterias richardi</i>	C	Pl	P		Falconetti et al. 1977
	<i>Stichaster australis</i>	C	Pl	P	Bipinnaria and brachiolaria	Barker 1978
	<i>Stichaster roseus</i>	C	Pl	P	Bipinnaria and brachiolaria	Gemmill 1916; Mortensen 1920c
Zoroasteridae	<i>Zoroaster fulgens</i>	S	L	P		Tyler et al. 1984
Notomyotida						
Benthopectinidae	<i>Benthopecten armatus</i>	S	L	P		Tyler et al. 1982a
	<i>Benthopecten simplex</i>	S	L	P		Pain et al. 1982a
	<i>Cheiraster gerlachei</i>	C	Pl	P	Bipinnaria only	MacBride 1910
	<i>Pectinaster filholi</i>	S	L	P		Pain et al. 1982a; Tyler et al. 1982a
	<i>Pontaster tenuispinus</i>	S	L	P		Pain et al. 1982a
Paxillosida						
Astropectinidae	<i>Astropecten auranciacus</i>	C	Pl	P	Bipinnaria only	Hörstadius 1939
	<i>Astropecten gisselbrechti</i>	S	L	P	Barrel-shaped larva	Komatsu and Nojima 1985
	<i>Astropecten irregularis</i>	C	Pl	P	Bipinnaria only	Thorson 1946; Tyler et al. 1982a

Table A1 (continued).

Class, order, family	Species	Developmental pattern			Larval type	Sources
		Morphogenesis*	Nutrition [†]	Habitat [‡]		
	<i>Astropecten latespinosus</i>	S	L	P	Barrel-shaped larva	Komatsu 1975
	<i>Astropecten polyacanthus</i>	C	Pl	P	Bipinnaria only	Oguro et al. 1975
	<i>Astropecten scoparius</i>	C	Pl	P	Bipinnaria only	Oguro et al. 1976
	<i>Astropectin velitaris</i>	C	Pl	P	Bipinnaria only	Mortensen 1937
	<i>Bathybiaster vexillifer</i>	S	L	P		Tyler et al. 1982b
	<i>Ctenopleura fisheri</i>	S	L	P	Barrel-shaped larva	Komatsu 1982
	<i>Dytaster insignis</i>	C	Pl	P		Tyler and Pain 1982a; Tyler et al. 1982a
	<i>Leptychaster almus</i>	S	L	B		Hyman 1955
	<i>Leptychaster kerguelensis</i>	S	L	B		Hyman 1955
	<i>Leptychaster uber</i>	S	L	B		Hyman 1955
	<i>Plutonaster bifrons</i>	C	Pl	P		Tyler and Pain 1982a; Tyler et al. 1982a
	<i>Psilaster andromeda</i>	S	L	P		Tyler and Pain 1982a; Tyler et al. 1982a
Goniopectinidae	<i>Ctenodiscus australis</i>	S	L	B	Yolky non-brachiolaria	Lieberkind 1926
	<i>Ctenodiscus crispatus</i>	S	L	P		Shick et al. 1981
Luidiidae	<i>Luidia ciliaris</i>	C	Pl	P	Bipinnaria only	Mortensen 1913; Wilson 1978; Domanski 1984
	<i>Luidia clathrata</i>	C	Pl	P	Bipinnaria only	Dehn 1980
	<i>Luidia foliata</i>	C	Pl	P	Bipinnaria only	Strathmann 1987
	<i>Luidia maculata</i>	C	Pl	P	Bipinnaria only	Komatsu et al. 1994
	<i>Luidia quinaria</i>	C	Pl	P	Bipinnaria only	Komatsu et al. 1982
	<i>Luidia sarsi</i>	C	Pl	P	Bipinnaria only	Thorson 1946; Wilson 1978
	<i>Luidia savignyi</i>	C	Pl	P	Bipinnaria only	Mortensen 1938
	<i>Luidia senegalensis</i>	C	Pl	P	Bipinnaria only	Komatsu et al. 1991
Spinulosida						
Echinasteridae	<i>Echinaster echinophorus</i> (type 1)	S	L	P	Brachiolaria	Atwood 1973; Scheibling and Lawrence 1982
	<i>Echinaster echinophorus</i> (type 2)	S	L	P	Brachiolaria	Kempf 1966; Scheibling and Lawrence 1982
	<i>Echinaster purpureus</i>	S	L	P	Brachiolaria	Mortensen 1938
	<i>Echinoaster sepositus</i>	S	L	P	Brachiolaria	Nachtsheim 1914
	<i>Henricia leviuscula</i>	S	L	P	Brachiolaria	Verrill 1914; Strathmann 1987
	<i>Henricia parva</i>	S	L	B		Arnaud 1974
	<i>Henricia sanguinolenta</i>	S	L	P	Brachiolaria	Masterman 1902
	<i>Henricia smilax</i>	S	L	B		Arnaud 1974
	<i>Henricia</i> sp.	S	L	P	Brachiolaria	Komatsu et al. 1995
	<i>Henricia tumida</i>	S	L	B		Verrill 1914
	<i>Rhopiella hirusta</i>	S	L	B		Arnaud 1974
	<i>Rhopiella koehleri</i>	S	L	B		Fisher 1940
Valvatida						
Acanthasteridae	<i>Acanthaster brevispinus</i>	C	Pl	P	Bipinnaria and brachiolaria	Lucas and Jones 1976
	<i>Acanthaster planci</i>	C	Pl	P	Bipinnaria and brachiolaria	Henderson and Lucas 1971; Lucas 1973; Yamaguchi 1977
Archasteridae	<i>Archaster andromeda</i>	S	L	B		Thompson 1878
	<i>Archaster excavatus</i>	S	L	B		Thompson 1878
	<i>Archaster typicus</i>	C	Pl	P	Bipinnaria and brachiolaria	Yamaguchi 1977; Komatsu 1983
Asterinidae	<i>Asterina batheri</i>	S	L	P	Brachiolaria	Kano and Komatsu 1978
	<i>Asterina burtoni</i>	S	L	P		James 1974
	<i>Asterina coronata</i>	S	L	P	Brachiolaria	Komatsu et al. 1979
	<i>Asterina gibbosa</i>	S	L	B	Brachiolaria	MacBride 1896; Emson and Crump 1976; Marthy 1980
	<i>Asterina minor</i>	S	L	B	Brachiolaria	Komatsu et al. 1979; Soliman and Nojima 1984
	<i>Asterina pectinifera</i>	C	Pl	P	Bipinnaria and brachiolaria	Kume and Dan 1968; Soliman and Nojima 1984
	<i>Asterina phylactica</i>	S	L	B	Brachiolaria	Emson and Crump 1979
	<i>Asterina pseudoexigua</i>	S	L	B		Matsuoka 1981
	<i>Asterina pseudoexigua pacifica</i>	S	L	B	Brachiolaria	Komatsu et al. 1990
	<i>Asterina scobinata</i>	S	L	B		Soliman and Nojima 1984
	<i>Kampylaster incurvatus</i>	S	L	B		Fisher 1940
	<i>Nepanthia belcheri</i>	S	L	P	Brachiolaria	Kenny 1969; Otteson and Lucas 1982

Table A1 (continued).

Class, order, family	Species	Developmental pattern			Larval type	Sources
		Morphogenesis*	Nutrition [†]	Habitat [‡]		
	<i>Patiria miniata</i>	C	Pl	P		Heath 1917; Cameron and Holland 1983
	<i>Patiriella brevispina</i>	S	L	P	Brachiolaria	Byrne 1996
	<i>Patiriella calcar</i>	S	L	P	Brachiolaria	Lawson-Kerr and Anderson 1978; Byrne 1991
	<i>Patiriella exigua</i>	S	L	B	Brachiolaria	Mortensen 1921; Lawson-Kerr and Anderson 1978; Byrne 1991
	<i>Patiriella gunnii</i>	S	L	P	Brachiolaria	Byrne 1996
	<i>Patiriella obscura</i>	S	L	P	Brachiolaria	Lawson-Kerr and Anderson 1978
	<i>Patiriella parvivipara</i>	S	L	B	Brachiolaria	Byrne 1996
	<i>Patiriella pseudoexigua</i>	S	L	P	Brachiolaria	Lawson-Kerr and Anderson 1978; Chen and Chen 1992
	<i>Patiriella regularis</i>	C	Pl	P	Bipinnaria and brachiolaria	Keough and Dartnall 1977; Byrne and Barker 1991
	<i>Patiriella vivipara</i>	S	L	B	Brachiolaria	Dartnall 1971; Byrne 1996
Ganeriidae	<i>Cyethra macquariensis</i>	S	L	B		Simpson 1982
Goniasteridae	<i>Hippasteria spinosa</i>	S	L	P	Brachiolaria	Lambert 1981
	<i>Iconaster longimanus</i>	S	L	P	Brachiolaria	Lane and Hu 1994
	<i>Mediaster aequalis</i>	S	L	P	Brachiolaria	Birkeland et al. 1971
	<i>Paragonaster subtilis</i>	S	L	P		Tyler and Pain 1982b; Tyler et al. 1982a
	<i>Pseudarchaster parelii</i>	S	L	P	Brachiolaria	Tyler and Pain 1982b; Tyler et al. 1982a; Wada et al. 1996
Mithrodiidae	<i>Mithrodia clavigera</i>	C	Pl	P	Bipinnaria and brachiolaria	Yamaguchi 1975
Odontasteridae	<i>Odontaster validus</i>	C	Pl	P	Bipinnaria and brachiolaria	Pearse 1965, 1969; Pearse and Bosch 1986
Ophidiasteridae	<i>Certonardoia semiregularis</i>	S	L	P	Brachiolaria	Hayashi and Komatsu 1971
	<i>Fromia ghardaqana</i>	S	L	P	Brachiolaria	Mortensen 1938
	<i>Gomophia egyptiaca</i>	S	L	P	Brachiolaria	Yamaguchi 1974
	<i>Leiaster leachi</i>	C	Pl	P	Bipinnaria and brachiolaria	Yamaguchi 1975
	<i>Linckia laevigata</i>	C	Pl	P	Bipinnaria and brachiolaria	Mortensen 1931; Yamaguchi 1973
	<i>Linckia multifora</i>	C	Pl	P	Bipinnaria and brachiolaria	Mortensen 1938
	<i>Linckia pacifica</i>	C	Pl	P	Bipinnaria and brachiolaria	Yamaguchi 1975
	<i>Ophidiaster granifer</i>	S	L	P	Brachiolaria	Yamaguchi 1975; Yamaguchi and Lucas 1984
	<i>Ophidiaster guildingii</i>	C	Pl	P	Bipinnaria and brachiolaria	Mortensen 1921
	<i>Ophidiaster robillardi</i>	C	Pl	P	Bipinnaria and brachiolaria	Yamaguchi and Lucas 1984
	<i>Ophidiaster squaneus</i>	C	Pl	P	Bipinnaria and brachiolaria	Yamaguchi 1975; Yamaguchi and Lucas 1984
Oreasteridae	<i>Choriaster granulatus</i>	C	Pl	P	Bipinnaria and brachiolaria	Yamaguchi 1975
	<i>Culcita novaguineae</i>	C	Pl	P	Bipinnaria and brachiolaria	Yamaguchi 1973, 1975, 1977
	<i>Culcita schmiedeliana</i>	C	Pl	P	Bipinnaria and brachiolaria	Mortensen 1931
	<i>Pentaceraster mammillatus</i>	C	Pl	P	Bipinnaria and brachiolaria	Mortensen 1938
	<i>Protoreaster nodosus</i>	C	Pl	P	Bipinnaria and brachiolaria	Yamaguchi 1977
Poraniidae	<i>Asteropsis carinifera</i>	C	Pl	P	Bipinnaria and brachiolaria	Mortensen 1937
	<i>Dermasterias imbricata</i>	C	Pl	P	Bipinnaria and brachiolaria	Strathmann 1987
	<i>Porania antarctica</i>	C	L?	P	Facultative planktotrophy?	Bosch 1989
	<i>Porania pulvillus</i>	C	Pl	P	Bipinnaria and brachiolaria	Gemmill 1915
	<i>Porania</i> sp.	S	L	P	Brachiolaria	Bosch 1989
Velatida						
Pterasteridae	<i>Diplopteraster verrucosus</i>	S	L	B		Fisher 1940
	<i>Hymenaster gennaeus</i>	S	L	P		Pain et al. 1982b
	<i>Hymenaster membranaceus</i>	S	L	P		Pain et al. 1982b
	<i>Hymenaster nobilis</i>	S	L	B		Thompson 1878
	<i>Hymenaster pellucidus</i>	S	L	B	Brachiolaria	Janies 1995
	<i>Hymenaster praecoquis</i>	S	L	B		Arnaud 1974
	<i>Pteraster (Marsipaster)</i> sp.	D	L	B	Mesogen	Janies 1995
	<i>Pteraster acicula</i>	D	L	B	Mesogen	Janies 1995
	<i>Pteraster militaris</i>	D	L	B	Mesogen	Kaufman 1968; Janies 1995
	<i>Pteraster obscurus</i>	D?	L	B	Mesogen?	Verrill 1914; Janies 1995
	<i>Pteraster pulvillus</i>	D	L	B	Mesogen	Janies 1995
	<i>Pteraster stellifer</i>	D	L	B	Mesogen	Janies 1995
	<i>Pteraster temnochiton</i>	D	L	B	Mesogen	Janies 1995
	<i>Pteraster tessellatus</i>	D	L	P	Mesogen	McEdward 1992; Janies and McEdward 1993

Table A1 (continued).

Class, order, family	Species	Developmental pattern			Larval type	Sources
		Morphogenesis*	Nutrition [†]	Habitat [‡]		
Solasteridae	<i>Crossaster papposus</i>	S	L	P	Brachiolaria	Gemmill 1920; Hayashi 1972
	<i>Solaster dawsoni</i>	S	L	P	Brachiolaria	Strathmann 1987
	<i>Solaster endeca</i>	S	L	P	Brachiolaria	Gemmill 1912
	<i>Solaster stimpsoni</i>	S	L	P	Brachiolaria	Strathmann 1987
Crinoidea						
Comatulida						
Antedonidae	<i>Antedon adriatica</i>	S	L	B, P	Doliolaria	Clark 1921
	<i>Antedon bifida</i>	S	L	B, P	Doliolaria	Lahaye and Jangoux 1985
	<i>Antedon mediterranea</i>	S	L	B, P	Doliolaria	Clark 1921
	<i>Antedon petasus</i>	S	L	P		Mortensen 1920b
	<i>Antedon rosacea</i>	S	L	B, P	Doliolaria	MacBride 1914
	<i>Florometra serratissima</i>	S	L	P	Doliolaria	Mladenov and Chia 1983
	<i>Isometra vivipara</i>	S	L	B	Doliolaria	Mortensen 1920a
	<i>Kempometra grisea</i>	S	L	B		Holland 1991
Aporometridae	<i>Phrixometra nutrix</i>	S	L	B		Holland 1991
	<i>Aporometra occidentalis</i>	S	L	B		Holland 1991
Comasteridae	<i>Capillaster multiradiatus</i>	S	L	P		Rutman and Fishelson 1985
	<i>Comatilia iridometriformis</i>	S	L	B	Doliolaria	Messing 1984
	<i>Oxycomathus japonicus</i>	S	L	P	Doliolaria	Kume and Dan 1968; Holland 1978
Himerometridae	<i>Heterometra savignii</i>	S	L	P	Doliolaria	Mortensen 1938
Marianetridae	<i>Lamprometra zlunzingeri</i>	S	L	P	Doliolaria	Mortensen 1937
Notocrinidae	<i>Notocrinus virilis</i>	S	L	B	Vitellaria	Mortensen 1920a
Thalassometridae	<i>Thaumatometra nutrix</i>	S	L	B		Mortensen 1920a
Tropiometridae	<i>Tropiometra audouini</i>	S	L	P		Mortensen 1937
	<i>Tropiometra carinata</i>	S	L	P	Doliolaria	Mortensen 1920a
Unknown						
Unknown	<i>Compsometra serrata</i>	S	L	B	Doliolaria	Mortensen 1920a
Echinoidea						
Cassiduloidea						
Cassidulidae	<i>Cassidulus mitis</i>	S	L	B		Gladfelter 1978; Emler et al. 1987
Echinobrissidae	<i>Apatopygus recens</i>	C	Pl	P	Pluteus	Mortensen 1948; Emler et al. 1987
Echinolampadidae	<i>Echinolampas crassa</i>	C	Pl	P	Pluteus	Cram 1971b; Emler et al. 1987
Neolampadidae	<i>Anochanus sinensis</i>	S	L	B		Grube 1868; Emler et al. 1987
	<i>Tropholampas loveni</i>	S	L	B		Clark 1923; Emler et al. 1987
Cidaroida						
Cidaridae	<i>Aporocidaris antarctica</i>	S	L	B		Mortensen 1909; Emler et al. 1987
	<i>Aporocidaris imilleri</i>	S	L	B		Emler 1989
	<i>Aporocidaris incerta</i>	S	L	B		Dell 1972; Poulin and Féral 1996
	<i>Austrocidaris canaliculata</i>	S	L	B		Mortensen 1928; Emler et al. 1987
	<i>Austrocidaris spinulosa</i>	S	L	B		Mortensen 1928; Emler et al. 1987
	<i>Cidaris cidaris</i>	C	Pl	P	Pluteus	Prouho 1887; Emler et al. 1987
	<i>Ctenocidaris geliberti</i>	S	L	B		Mortensen 1928; Emler et al. 1987
	<i>Ctenocidaris nutrix</i>	S	L	B		Hesse and Doflein 1910–1914; Emler et al. 1987
	<i>Ctenocidaris perrieri</i>	S	L	B		Mortensen 1928; Emler et al. 1987
	<i>Ctenocidaris polyplax</i>	S	L	B		Dell 1972; Poulin and Féral 1996
	<i>Ctenocidaris rugosa</i>	S	L	B		Dell 1972; De Ridder et al. 1993; Poulin and Féral 1996
	<i>Eucidaris metularia</i>	C	Pl	P	Pluteus	Mortensen 1937; Emler et al. 1987
	<i>Eucidaris thouarsi</i>	C	Pl	P	Pluteus	Emler et al. 1987; Emler 1988; Parks et al. 1989 (Table 1)
	<i>Eucidaris tribuloides</i>	C	Pl	P	Pluteus	Emler et al. 1987; Emler 1988; Parks et al. 1989 (Table 1)
	<i>Goniocidaris parasol</i>	S	L	B		Barker 1985
	<i>Goniocidaris umbraculum</i>	S	L	B	Schmoo	Barker 1985
	<i>Histocidaris elegans</i>	S	Pl	P		Mortensen 1928; Emler et al. 1987
	<i>Notocidaris gaussensis</i>	S	L	B		Mortensen 1909; Emler et al. 1987
	<i>Notocidaris hastata</i>	S	L	B		Dell 1972; Poulin and Féral 1996
	<i>Notocidaris remigera</i>	S	L	B		Dell 1972; Lockhart et al. 1994; Poulin and Féral 1996
<i>Notocidaris spinosa</i>	S	L	B		Dell 1972; Arnaud 1974; De Ridder et al. 1993; Poulin and Féral 1996	
<i>Phyllacanthus imperialis</i>	S	L	P	Reduced pluteus	Mortensen 1938; Emler et al. 1987	
<i>Phyllacanthus parvispinus</i>	S	L	P	Schmoo	Mortensen 1921; Emler et al. 1987; Parks et al. 1989	

Table A1 (continued).

Class, order, family	Species	Developmental pattern			Larval type	Sources	
		Morphogenesis*	Nutrition [†]	Habitat [‡]			
Clypeasteroidea	<i>Prionocidaris baculosa</i>	C	Pl	P	Pluteus	Mortensen 1938; Emlet et al. 1987	
	<i>Rhynchocidaris triplopora</i>	S	L	B		Mortensen 1909; Emlet et al. 1987	
	<i>Stylocidaris affinis</i>	C	Pl	P	Pluteus	Holland 1967; Emlet et al. 1987	
	<i>Stylocidaris lineata</i>	C	Pl	P	Pluteus	Young et al. 1992	
Arachnoididae	<i>Arachnoides placenta</i>	C	Pl	P	Pluteus	Emlet et al. 1987; Wray 1992; Feliciano 1933	
Astricypeidae	<i>Astricypeus manni</i>	C	Pl	P	Pluteus	Mortensen 1921; Harvey 1956; Emlet et al. 1987	
Clypeasteridae	<i>Echinodiscus auritus</i>	C	Pl	P	Pluteus	Mortensen 1938; Emlet et al. 1987	
	<i>Clypeaster humilis</i>	C	Pl	P	Pluteus	Mortensen 1937; Emlet et al. 1987	
	<i>Clypeaster japonicus</i>	C	Pl	P	Pluteus	Harvey 1956; Emlet et al. 1987	
	<i>Clypeaster rosaceus</i>	C	L	P	Pluteus	Emlet 1986	
	<i>Clypeaster subdepressus</i>	C	Pl	P	Pluteus	Emlet et al. 1987; R.B. Emlet, personal observation	
Dendrasteridae	<i>Dendraster excentricus</i>	C	Pl	P	Pluteus	Emlet et al. 1987; R.B. Emlet, personal observation	
	<i>Dendraster laevis</i>	C	Pl	P	Pluteus	Emlet et al. 1987; R.B. Emlet, personal observation	
Echinarachniidae	<i>Scaphechinus mirabilis</i>	C	Pl	P	Pluteus	Mortensen 1921; Emlet et al. 1987	
	<i>Scaphechinus tenuis</i>	C	Pl	P	Pluteus	Onoda 1938; Emlet et al. 1987	
	<i>Echinarachnius parma</i>	C	Pl	P	Pluteus	Harvey 1956; Emlet et al. 1987; R.C. Highsmith, personal communication	
Fibulariidae	<i>Echinocyamus pusillus</i>	C	Pl	P	Pluteus	Théel 1892; Emlet et al. 1987	
	<i>Fibularia nutrients</i>	S	L	B		Clark 1909; Emlet et al. 1987	
Laganidae	<i>Fibularia ovulum</i>	C	Pl	P	Pluteus	Mortensen 1937; Emlet et al. 1987	
	<i>Laganum depressum</i>	C	Pl	P	Pluteus	Mortensen 1938; Emlet et al. 1987	
	<i>Laganum fudsiyama</i>	C	Pl	P	Pluteus	Mortensen 1921; Emlet et al. 1987	
Mellitidae	<i>Peronella japonica</i>	C	L	P	Reduced pluteus	Okazaki 1975	
	<i>Encope aberrans</i>	C	Pl	P	Pluteus	Herrera 1998	
	<i>Encope michelini</i>	C	Pl	P	Pluteus	Eckert 1995	
	<i>Encope micropora</i>	C	Pl	P	Pluteus	Mortensen 1921; Emlet et al. 1987	
	<i>Encope stokesii</i>	C	Pl	P	Pluteus	Emlet et al. 1987; H.A. Lessios, personal observation	
Diadematoidea	<i>Leodia sexiesperforata</i>	C	Pl	P	Pluteus	Emlet et al. 1987; H.A. Lessios, personal observation	
	<i>Mellita quinquiesperforata</i>	C	Pl	P	Pluteus	Caldwell 1972; Emlet et al. 1987	
	Aspidodiadematae	<i>Aspidodiadema jacobyi</i>	C	Pl	P	Pluteus	Young et al. 1989; Young and George 2000
	Diadematae	<i>Aspidodiadema mejirei</i>	C	Pl	P	Pluteus	Mortensen 1940; Emlet et al. 1987
		<i>Astropyga pulvinata</i>	C	Pl	P	Pluteus	Mortensen 1921; Emlet et al. 1987
<i>Diadema antillarum</i>		C	Pl	P	Pluteus	Amy 1983; Emlet et al. 1987	
<i>Diadema mexicanum</i>		C	Pl	P	Pluteus	Emlet et al. 1987; R.B. Emlet, personal observation	
Echinoida	<i>Diadema savignyi</i>	C	Pl	P	Pluteus	Mortensen 1931; Emlet et al. 1987	
	<i>Diadema setosum</i>	C	Pl	P	Pluteus	Harvey 1956; Emlet et al. 1987	
	<i>Echinothrix diadema</i>	C	Pl	P	Pluteus	Mortensen 1931; Emlet et al. 1987	
	Echinidae	<i>Echinus acutus</i>	C	Pl	P	Pluteus	Lönning and Wennerberg 1963; Emlet et al. 1987
Echinometridae	<i>Echinus affinis</i>	C	Pl	P	Pluteus	Tyler and Gage 1984; Emlet et al. 1987	
	<i>Echinus alexandri</i>	C	Pl	P	Pluteus	Mortensen 1943b; Emlet et al. 1987	
	<i>Echinus esculentus</i>	C	Pl	P	Pluteus	MacBride 1903; Emlet et al. 1987	
	<i>Loxechinus albus</i>	C	Pl	P	Pluteus	Emlet 1989	
	<i>Sterechinus neumayeri</i>	C	Pl	P	Pluteus	Pearse and Giese 1966; Bosch et al. 1984; Emlet et al. 1987	
	<i>Anthocidaris crassispina</i>	C	Pl	P	Pluteus	Onoda 1931; Emlet et al. 1987	
	<i>Colobocentrotus atratus</i>	C	Pl	P	Pluteus	Emlet et al. 1987; L.R. McEdward, personal observation	
<i>Echinometra lucunter</i>	C	Pl	P	Pluteus	Emlet et al. 1987; R.B. Emlet, personal observation		

Table A1 (continued).

Class, order, family	Species	Developmental pattern			Larval type	Sources	
		Morphogenesis*	Nutrition [†]	Habitat [‡]			
	<i>Echinometra mathaei</i>	C	Pl	P	Pluteus	Hinegardner 1975; Emler et al. 1987	
	<i>Echinometra vanbrunti</i>	C	Pl	P	Pluteus	Emler et al. 1987; R.B. Emler, personal observation	
	<i>Echinometra viridis</i>	C	Pl	P	Pluteus	Emler et al. 1987; H.A. Lessios, personal communication	
	<i>Echinostrephus aciculatus</i>	C	Pl	P	Pluteus	Onoda 1936; Emler et al. 1987	
	<i>Evechinus chloroticus</i>	C	Pl	P	Pluteus	Dix 1969; Emler et al. 1987	
	<i>Helicoidaris erythrogramma</i>	S	L	P	Schmoo	Williams and Anderson 1975	
	<i>Helicoidaris tuberculata</i>	C	Pl	P	Pluteus	Raff 1987; Parks et al. 1988; Scott et al. 1990	
	<i>Heterocentrotus mammilatus</i>	C	Pl	P	Pluteus	Mortensen 1937; Emler et al. 1987	
	<i>Pachycentrotus bajulus</i>	S	L	B		Dartnall 1972; Emler et al. 1987	
Paraechinidae	<i>Parasalenia gratiosa</i>	C	Pl	P	Pluteus	Onoda 1938; Emler et al. 1987	
	<i>Paracentrotus lividus</i>	C	Pl	P	Pluteus	Lønning and Wennerberg 1963; Emler et al. 1987; Wray 1992	
	<i>Parechinus angulosus</i>	C	Pl	P	Pluteus	Cram 1971a; Emler et al. 1987; Wray 1992	
	<i>Psammechinus microtuberculatus</i>	C	Pl	P	Pluteus	Lønning and Wennerberg 1963; Emler et al. 1987; Wray 1992	
	<i>Psammechinus miliaris</i>	C	Pl	P	Pluteus	Lønning and Wennerberg 1963; Emler et al. 1987; Wray 1992	
	Strongylocentrotidae	<i>Allocentrotus fragilis</i>	C	Pl	P	Pluteus	Emler et al. 1987; R.R. Strathmann, personal observation
		<i>Hemicentrotus pulcherrimus</i>	C	Pl	P	Pluteus	Dan 1952; Harvey 1956; Emler et al. 1987
		<i>Strongylocentrotus droebachiensis</i>	C	Pl	P	Pluteus	Emler et al. 1987; R.R. Strathmann, personal observation
		<i>Strongylocentrotus echoides</i>	C	Pl	P	Pluteus	Mortensen 1943b; Emler et al. 1987
		<i>Strongylocentrotus franciscanus</i>	C	Pl	P	Pluteus	Emler et al. 1987; R.B. Emler, personal observation
<i>Strongylocentrotus intermedius</i>		C	Pl	P	Pluteus	Kawamura 1970	
<i>Strongylocentrotus nudus</i>		C	Pl	P	Pluteus	Kawamura 1970	
<i>Strongylocentrotus pallidus</i>		C	Pl	P	Pluteus	Emler et al. 1987; R.R. Strathmann, personal observation	
<i>Strongylocentrotus purpuratus</i>		C	Pl	P	Pluteus	Strathmann 1978; Emler et al. 1987	
Toxopneustidae		<i>Cyrtechinus verriculatus</i>	C	Pl	P	Pluteus	Mortensen 1921; Emler et al. 1987
	<i>Lytechinus anamesus</i>	C	Pl	P	Pluteus	Harvey 1956; Emler et al. 1987	
	<i>Lytechinus panamensis</i>	C	Pl	P	Pluteus	Mortensen 1921; Emler et al. 1987	
	<i>Lytechinus pictus</i>	C	Pl	P	Pluteus	Harvey 1956; Emler et al. 1987	
	<i>Lytechinus semituberculatus</i>	C	Pl	P	Pluteus	Mortensen 1943a; Emler et al. 1987	
	<i>Lytechinus variegatus</i>	C	Pl	P	Pluteus	Mazur and Miller 1971; Emler et al. 1987	
	<i>Lytechinus williamsi</i>	C	Pl	P	Pluteus	Emler et al. 1987; H.A. Lessios, personal communication	
	<i>Nudechinus scotiopremnus</i>	C	Pl	P	Pluteus	Mortensen 1937; Emler et al. 1987	
	<i>Pseudocentrotus depressus</i>	C	Pl	P	Pluteus	Giudice 1973; Emler et al. 1987	
	<i>Sphaerechinus granularis</i>	C	Pl	P	Pluteus	Endo 1952; Harvey 1956; Lønning and Wennerberg 1963; Emler et al. 1987	
	<i>Toxopneustes pileolus</i>	C	Pl	P	Pluteus	Onoda 1936; Emler et al. 1987	
	<i>Toxopneustes roseus</i>	C	Pl	P	Pluteus	Emler et al. 1987; Emler personal observation	
	<i>Tripneustes gratilla</i>	C	Pl	P	Pluteus	Onoda 1936; Emler et al. 1987	
	<i>Tripneustes ventricosus</i>	C	Pl	P	Pluteus	Lewis 1958; Emler et al. 1987; H.A. Lessios, personal communication	
Echinothurioida							
Echinothuriidae	<i>Araeosoma fenestratum</i>	S	L	P		Tyler and Gage 1984; Emler et al. 1987; Cameron et al. 1988	
	<i>Asthenosoma ijimai</i>	S	L	P	Schmoo	Amemiya and Tsuchiya 1979; Emler et al. 1987	
	<i>Asthenosoma varium</i>	S	L	P		Mortensen 1938; Emler et al. 1987	

Table A1 (continued).

Class, order, family	Species	Developmental pattern			Larval type	Sources
		Morphogenesis*	Nutrition [†]	Habitat [‡]		
Holasteroidea						
Urechinidae	<i>Plexechinus nordenskjoldi</i>	S	L	B		Mortensen 1909; Emlet et al. 1987
	<i>Urechinus mortenseni</i>	S	L	B		De Ridder et al. 1993; Poulin and Féral 1996
Holoelectypoida						
Holoelectypidae	<i>Echioneus cyclostomus</i>	C	Pl	P	Pluteus	Mortensen 1948; Emlet et al. 1987
Phymosomatoida						
Arbaciidae	<i>Arbacia dufresneii</i>	C	Pl	P	Pluteus	Bernasconi 1942; Emlet 1989
	<i>Arbacia lixula</i>	C	Pl	P	Pluteus	Harvey 1956; Emlet et al. 1987
	<i>Arbacia punctulata</i>	C	Pl	P	Pluteus	Harvey 1956; Emlet et al. 1987
	<i>Arbacia stellata</i>	C	Pl	P	Pluteus	Emlet et al. 1987; H.A. Lessios, personal communication
	<i>Coelopleurus floridanus</i>	C	Pl	P	Pluteus	Emlet 1989; J.E. Miller and D.L. Pawson, personal communications
	<i>Tetrapygyus niger</i>	C	Pl	P	Pluteus	Emlet 1989; Fuentes and Barros 2000
Glyptocidaridae	<i>Glyptocidaris crenularis</i>	C	Pl	P	Pluteus	Fukushi 1960; Emlet et al. 1987
Stomopneustidae	<i>Stomopneustes variolaris</i>	C	Pl	P	Pluteus	Mortensen 1931; Emlet et al. 1987
Spatangoida						
Brissidae	<i>Brissopsis lyrifera</i>	C	Pl	P	Pluteus	Lönning and Wennerberg 1963; Emlet et al. 1987
	<i>Brissus agassizii</i>	C	Pl	P	Pluteus	Mortensen 1921; Emlet et al. 1987
	<i>Brissus obesus</i>	C	Pl	P	Pluteus	Mortensen 1921; Emlet et al. 1987
	<i>Meoma grandis</i>	C	Pl	P	Pluteus	Mortensen 1921; Emlet et al. 1987
	<i>Meoma ventricosa</i>	C	Pl	P	Pluteus	Emlet et al. 1987; H.A. Lessios, personal observation
	<i>Metalia nobilis</i>	C	Pl	P	Pluteus	Emlet et al. 1987; R.B. Emlet, personal observation
	<i>Plagiobrissus grandis</i>	C	Pl	P	Pluteus	Emlet et al. 1987; H.A. Lessios, personal observation
Loveniidae	<i>Echinocardium cordatum</i>	C	Pl	P	Pluteus	MacBride 1914; Emlet et al. 1987
	<i>Echinocardium flavescens</i>	C	Pl	P	Pluteus	Mortensen 1951; Emlet et al. 1987
	<i>Echinocardium mediteraneum</i>	C	Pl	P	Pluteus	Hamann 1887; Emlet et al. 1987
	<i>Echinocardium mortenseni</i>	C	Pl	P	Pluteus	Fenaux 1969a; Emlet et al. 1987
	<i>Lovenia elongata</i>	C	Pl	P	Pluteus	Mortensen 1937; Emlet et al. 1987
Schizasteridae	<i>Abatus agassizii</i>	S	L	B		Mortensen 1951; Emlet et al. 1987
	<i>Abatus bidens</i>	S	L	B		Poulin and Féral 1996
	<i>Abatus cavernosus</i>	S	L	B		Mortensen 1910; Emlet et al. 1987
	<i>Abatus cordatus</i>	D	L	B	Mesogen	Schatt 1984; Schatt and Féral 1996
	<i>Abatus curvidens</i>	S	L	B		Mortensen 1936; Emlet et al. 1987
	<i>Abatus elongatus</i>	S	L	B		Mortensen 1951; Emlet et al. 1987
	<i>Abatus ingens</i>	S	L	B		Koehler 1926; Emlet et al. 1987
	<i>Abatus nimrodi</i>	S	L	B		Koehler 1926; Emlet et al. 1987
	<i>Abatus philippii</i>	S	L	B		Mortensen 1951; Emlet et al. 1987
	<i>Abatus schackletoni</i>	S	L	B		Poulin and Féral 1996
	<i>Amphipneustes bifidus</i>	S	L	B		Poulin and Féral 1996
	<i>Amphipneustes brevisternalis</i>	S	L	B		Poulin and Féral 1996
	<i>Amphipneustes koehleri</i>	S	L	B		Mortensen 1910; Emlet et al. 1987
	<i>Amphipneustes lorioli</i>	S	L	B		Mortensen 1936; Emlet et al. 1987
	<i>Amphipneustes marsupialis</i>	S	L	B		Koehler 1926; Emlet et al. 1987
	<i>Amphipneustes rostratus</i>	S	L	B		Koehler 1926; Emlet et al. 1987
	<i>Amphipneustes similis</i>	S	L	B		Mortensen 1936; Emlet et al. 1987
	<i>Amphipneustes tumescens</i>	S	L	B		Poulin and Féral 1996
	<i>Brachysternaster chesheri</i>	S	L	B		Schatt and Féral 1991; Poulin and Féral 1996
	<i>Brisaster fragilis</i>	C	Pl?	P	Pluteus	Runnström 1929; Emlet et al. 1987
	<i>Brisaster latifrons</i>	C	L	P	Pluteus	Hart 1996
	<i>Delopatagus brucei</i>	S	L	B		De Ridder et al. 1993; Poulin and Féral 1996
	<i>Parapneustes abatoides</i>	S	L	B		De Ridder et al. 1993; Poulin and Féral 1996
	<i>Parapneustes reductus</i>	S	L	B		De Ridder et al. 1993; Poulin and Féral 1996
	<i>Tripylus abatoides</i>	S	L	B		Mortensen 1951; Emlet et al. 1987
	<i>Tripylus cordatus</i>	S	L	B		Mortensen 1936; Emlet et al. 1987
	<i>Tripylus excavatus</i>	S	L	B		Mortensen 1951; Emlet et al. 1987
Spatangidae	<i>Spatangus purpureus</i>	C	Pl	P	Pluteus	Mortensen 1913; Emlet et al. 1987

Table A1 (continued).

Class, order, family	Species	Developmental pattern			Larval type	Sources
		Morphogenesis*	Nutrition [†]	Habitat [‡]		
Temnopleuroidea						
Temnopleuridae						
	<i>Amblypneustes ovum</i>	S	L	P		Emler 1989
	<i>Genocidaris maculata</i>	C	Pl	P	Pluteus	Mortensen 1943a; Emler et al. 1987
	<i>Holopneustes inflatus</i>	S	L	P		Mortensen 1943a; Emler et al. 1987
	<i>Hypsiechinus coronatus</i>	S	L	B		Mortensen 1943a; Emler et al. 1987
	<i>Mespilia globulus</i>	C	Pl	P	Pluteus	Onoda 1936; Harvey 1956; Emler et al. 1987
	<i>Pseudechinus huttoni</i>	C	Pl	P	Pluteus	Emler 1989; M.F. Barker, personal communication
	<i>Salmacis bicolor</i>	C	Pl	P	Pluteus	Aiyar 1935; Emler et al. 1987
	<i>Temnopleurus alexandri</i>	C	Pl	P	Pluteus	Tennent 1929; Emler et al. 1987
	<i>Temnopleurus hardwickii</i>	C	Pl	P	Pluteus	Harvey 1956; Osanai 1975; Emler et al. 1987
	<i>Temnopleurus scillae</i>	C	Pl	P	Pluteus	Mortensen 1937; Emler et al. 1987
	<i>Temnopleurus toreumaticus</i>	C	Pl	P	Pluteus	Onoda 1936; Emler et al. 1987
Holothuroidea						
Apodida						
Chiridotidae						
	<i>Chiridota rotifera</i>	S or D	L	B	Reduced auricularia and doliolaria	Engstrom 1980
	<i>Taeniogyrus contortus</i>	S	L	B	Doliolaria	Ludwig 1897 (cited in McEuen 1986, p. 215)
	<i>Taeniogyrus dunedimensis</i>	S	L	B	Doliolaria	McEuen 1986
Synaptidae						
	<i>Auricularia bermudensis</i>	C	Pl	P	Auricularia	Garstang 1939
	<i>Labidoplax buskii</i>	C	Pl	P	Auricularia and doliolaria	McEuen 1986
	<i>Labidoplax digitata</i>	C	Pl	P	Auricularia and doliolaria	McEuen 1986
	<i>Leptosynapta clarki</i>	D?	L	B		Sewell and Chia 1994
	<i>Leptosynapta gallieni</i>	C	Pl	P	Auricularia and doliolaria	McEuen 1986
	<i>Leptosynapta inhaerens</i>	C	Pl	P	Auricularia and doliolaria	McEuen 1986
	<i>Leptosynapta minuta</i>	S	L	B	Vitellaria?	McEuen 1986
	<i>Opheodesoma grisea</i>	C	Pl	P	Auricularia and doliolaria	Mortensen 1938
	<i>Synaptula hydriformis</i>	S	L	B	Vitellaria	McEuen 1986
	<i>Synaptula reciprocans</i>	C	Pl	P	Auricularia and doliolaria	Mortensen 1937; McEuen 1986
	<i>Synaptula vittata</i>	C	Pl	P	Auricularia and doliolaria	Mortensen 1937, 1938; McEuen 1986
	<i>Synaptula vivipara</i>	D?	L	B	Vitellaria	Clark 1896
Aspidochirotida						
Holothuriidae						
	<i>Actinopyga echinites</i>	C	Pl	P		Chen and Chian 1990
	<i>Actinopyga mauritiana</i>	C	Pl	P	Auricularia (and doliolaria?)	Mortensen 1937
	<i>Actinopyga serratidens</i>	C	Pl	P	Auricularia and doliolaria	Mortensen 1937
	<i>Holothuria arenicola</i>	C	Pl	P	Auricularia and doliolaria	Mortensen 1937
	<i>Holothuria difficilis</i>	C	Pl	P	Auricularia (and doliolaria?)	Mortensen 1938
	<i>Holothuria floridana</i>	D?	L	B	Vitellaria	McEuen 1986
	<i>Holothuria impatiens</i>	C	Pl	P	Auricularia and doliolaria	Mortensen 1938
	<i>Holothuria marmorata</i>	C	Pl	P	Auricularia (and doliolaria?)	Mortensen 1937
	<i>Holothuria mexicana</i>	C	Pl	P	Auricularia and doliolaria	Lacalli 1988
	<i>Holothuria nobilis</i>	C	Pl	P	Auricularia (and doliolaria?)	Mortensen 1938
	<i>Holothuria papillifera</i>	C	Pl	P	Auricularia (and doliolaria?)	Mortensen 1938
	<i>Holothuria pardalis</i>	C	Pl	P	Auricularia (and doliolaria?)	Mortensen 1938
	<i>Holothuria scabra</i>	C	Pl	P	Auricularia (and doliolaria?)	Mortensen 1937
	<i>Holothuria spinifera</i>	C	Pl	P	Auricularia (and doliolaria?)	Mortensen 1937
Stichopodidae						
	<i>Stichopus californicus</i>	C	Pl	P	Auricularia and doliolaria	Smiley 1986
	<i>Stichopus variegatus</i>	C	Pl	P	Auricularia and doliolaria	Mortensen 1937
Synallactidae						
	<i>Bathylotes natans</i>	S	L	B		Ohshima 1915 (cited in McEuen 1986, p. 206)
Dactylochirotida						
Ypsilothuriidae						
	<i>Ypsilothuria talismani</i>	S or D	L?	P?		Tyler and Gage 1983; Smiley et al. 1991
Dendrochirotida						
Cucumariidae						
	<i>Aslia lefevrei</i>	S	L	P	Vitellaria	Costelloe 1988
	<i>Cucumaria curata</i>	S or D	L	B		Turner and Rutherford 1976
	<i>Cucumaria echinata</i>	S	L	P	Doliolaria	Ohshima 1921 (cited in McEuen 1986, p. 133)
	<i>Cucumaria elongata</i>	S	L	P	Doliolaria	Chia and Buchanan 1969
	<i>Cucumaria frondosa</i>	D?	L	P	Vitellaria	Hamel and Mercier 1996
	<i>Cucumaria lubrica</i>	D?	L	B		Clark 1910; Engstrom 1982; McEuen 1986
	<i>Cucumaria miniata</i>	S	L	P	Doliolaria	McEuen 1986

Table A1 (continued).

Class, order, family	Species	Developmental pattern			Larval type	Sources
		Morphogenesis*	Nutrition [†]	Habitat [‡]		
Phyllophoridae Psolidae	<i>Cucumaria piperata</i>	S	L	P	Doliolaria	McEuen 1986
	<i>Cucumaria pseudocurata</i>	D?	L	B		Rutherford 1973; McEuen 1986
	<i>Eupentacta fraudatrix</i>	S	L	P	Vitellaria	Dolmatov and Yushin 1993
	<i>Eupentacta quinquesemita</i>	S	L	P	Vitellaria	McEuen 1986
	<i>Ocnus planci</i>	S	L	P	Doliolaria	McEuen 1986
	<i>Pentamera populifera</i>	S	L	P	Doliolaria	McEuen 1986
	<i>Pseudopsolus macquariensis</i>	S	L	B		Simpson 1982
	<i>Phyllophorus urna</i>	S	L	B	Vitellaria	McEuen 1986
	<i>Lissothuria antillensis</i>	S	L	B		Miller 1985
	<i>Lissothuria nutriens</i>	S	L	B		Wootton 1949 (cited in McEuen 1986, p. 122)
	<i>Psolidium bullatum</i>	S	L	P	Doliolaria	McEuen and Chia 1991
	<i>Psolidium incbans</i>	S	L	B		Ekman 1925 (cited in McEuen 1986, p. 122)
	<i>Psolus antarcticus</i>	S	L	B		Ludwig 1897 (cited in McEuen 1986, p. 122)
	<i>Psolus charcoti</i>	S	L	B		Ekman 1925 (cited in McEuen and Chia 1991)
	<i>Psolus chitonoides</i>	S	L	P	Doliolaria	McEuen and Chia 1991
	<i>Psolus dubiosus</i>	D?	L	B		Gutt 1991
	<i>Psolus ephippifer</i>	S	L	B		Théel 1886 (cited in McEuen 1986, p. 122)
	<i>Psolus fabricii</i>	S	L	P		Agassiz 1864 (cited in McEuen 1986, p. 125)
	<i>Psolus figulus</i>	S	L	B		Ekman 1925 (cited in McEuen 1986, p. 122)
	<i>Psolus granulatus</i>	S	L	B		Vaney 1907 (cited in McEuen 1986, p. 122)
<i>Psolus koehleri</i>	S	L	B		Vaney 1914 (cited in McEuen 1986, p. 122)	
<i>Psolus patagonicus</i>	S	L	B		Hernandez 1981 (cited in McEuen and Chia 1991)	
<i>Psolus phantapus</i>	S	L	P		Thorson 1946 (cited in McEuen 1986, p. 125)	
<i>Psolus punctatus</i>	S	L	B		Eckman 1925 (cited in McEuen 1986, p. 122)	
Sclerodactylidae	<i>Pachythyone rubra</i>	D?	L	B		Chaffee 1982
	<i>Sclerodactyla briareus</i>	D?	L	P		Ohshima 1925 (cited in McEuen 1986, p. 206)
Elasipoda						
Deimatidae	<i>Oneirophanta mutabilis</i>	D?	L?	B		Hansen 1968
Molpadiida						
Caudinidae	<i>Paracaudina chilensis</i>	S	L	P	Doliolaria	Inaba 1930 (cited in McEuen 1986, p. 94)
Molpadiidae	<i>Molpadia intermedia</i>	S	L	P	Doliolaria	McEuen and Chia 1985
Ophiuroidea						
Ophiurida						
Amphiuridae	<i>Amphiodia occidentalis</i>	C	Pl	P	Pluteus only	Strathmann 1987
	<i>Amphiodia pulchella</i>	C	Pl	P		Hendler and Littman 1986
	<i>Amphiophiura rowetti</i>	S	L	B		Hendler 1975
	<i>Amphioplus abditus</i>	S	L	B	Reduced pluteus	Hendler 1973, 1975, 1977
	<i>Amphipholis japonica</i>	S	MN?	B	Vitellaria	Oguro et al. 1982
	<i>Amphipholis kochii</i>	C	Pl	P	Pluteus only	Yamashita 1985
	<i>Amphipholis squamata</i>	S	L	B	Mesogen	Fell 1946
	<i>Amphipholis torelli?</i>	S	L	B		Hendler 1975
	<i>Amphiura belgicae</i>	S	L	B		Hendler 1975
	<i>Amphiura chiajei</i>	C	Pl	P	Pluteus only	Fenaux 1963
	<i>Amphiura filiformis</i>	C	Pl	P		Mortensen 1920c
	<i>Amphiura monorima</i>	S	L	B		Hendler 1975
	<i>Amphiura stimpsonii</i>	S	L	B		Hendler 1975
	<i>Amphiura vivipara</i>	S	L	B		Hendler 1975
	<i>Ophiophragmus wurdemani</i>	S	L	B		Hendler 1973, 1975
Hemieuryalidae	<i>Sigsbeia conifera</i>	S	L	B		Hendler and Littman 1986
Ophiacanthidae	<i>Ophiacantha vivipara</i>	S	L	B		Hendler 1975
Ophiactidae	<i>Ophiactis balli</i>	C	Pl	P		Mortensen 1913

Table A1 (concluded).

Class, order, family	Species	Developmental pattern			Larval type	Sources	
		Morphogenesis*	Nutrition [†]	Habitat [‡]			
Ophiocomidae	<i>Ophiactis quinqueradia</i>	C	Pl	P		Hendler and Littman 1986	
	<i>Ophiopholis aculeata</i>	C	Pl	P	Pluteus only	Olsen 1942; Balsler 1998	
	<i>Ophiocoma echinata</i>	C	Pl	P		Hendler 1975	
	<i>Ophiocoma erinaceus</i>	C	Pl	P		Hendler 1975	
	<i>Ophiocoma pica</i>	C	Pl	P		Mladenov and Emson 1984	
	<i>Ophiocoma pumila</i>	C	Pl	P	Pluteus and doliolaria	Mladenov 1985a	
	<i>Ophiocomella ophiactoides</i>	C	Pl	P		Mladenov and Emson 1984	
	<i>Ophiocomina nigra</i>	C	Pl	P	Pluteus only	Narasimhamurti 1933; Mladenov and Emson 1984; Yamashita 1985	
Ophiodermatidae	<i>Ophiopsila riisei</i>	S	L	P		Hendler and Littman 1986	
	<i>Cryptopelta granulifera</i>	S	L	B		Hendler 1975	
	<i>Ophiocoris vivipara</i>	S	L	B		Hendler 1975	
	<i>Ophioderma brevispinum</i>	S	L	P	Doliolaria	Grave 1900, 1916; Hendler 1975	
	<i>Ophioderma cinereum</i>	S	L	P	Vitellaria?	Hendler 1979b	
	<i>Ophioderma longicaudum</i>	S	L	P	Vitellaria	Fenaux 1969b; Hendler 1975	
	<i>Ophioderma rubicundum</i>	S	L	P	Vitellaria	Hendler and Littman 1986	
Ophiomyxidae	<i>Ophiurochaeta</i> sp.	S	L	B		Hendler and Littman 1986	
	<i>Ophiomyxa brevirima</i>	S	L	B		Garrett et al. 1997	
Ophionereididae	<i>Ophiomyxa flaccida</i>	S	L	P		Hendler and Littman 1986	
	<i>Ophionereis annulata</i>	S	L	P	Doliolaria	Hendler 1982	
	<i>Ophionereis olivacea</i>	S	L	B	Vitellaria	Byrne 1991	
	<i>Ophionereis reticulata</i>	S	L	P		Hendler and Littman 1986	
Ophiothricidae	<i>Ophionereis squamulosa</i>	S	L	P	Doliolaria	Mortensen 1921; Hendler 1975; Hendler and Littman 1986	
	<i>Ophionereis vivipara</i>	S	L	B		Hendler 1975	
	<i>Ophimaza cacaotica</i>	C	Pl	P	Pluteus only	Mladenov 1985a	
	<i>Ophiothrix angulata</i>	C	Pl	P		Hendler and Littman 1986	
	<i>Ophiothrix fragilis</i>	C	Pl	P	Pluteus only	MacBride 1907; Hendler 1975	
	<i>Ophiothrix oerstedii</i>	S	L	P	Reduced pluteus	Mladenov 1979	
	<i>Ophiothrix savignyi</i>	C	Pl	P	Pluteus only	Mortensen 1938	
	<i>Ophiothrix suensonii</i>	C	Pl	P	Pluteus only	Mladenov 1985b	
	<i>Ophiothrix triloba</i>	C	Pl	P	Pluteus only	Mortensen 1937	
	Ophiuridae	<i>Ophiocten gracilis</i>	C	Pl	P		Tyler and Gage 1982
		<i>Ophiolepis cincta</i>	S	L	P	Vitellaria	Mortensen 1938; Hendler 1975
		<i>Ophiolepis elegans</i>	S	L	P	Doliolaria	Stancyk 1973; Hendler 1975
		<i>Ophiolepis impressa</i>	S	L	P		Hendler and Littman 1986
		<i>Ophiolepis kieri</i>	S	L	B		Hendler 1979a
<i>Ophiolepis paucispina</i>		S	L	B		Hendler and Littman 1986	
<i>Ophionotus hexactis</i>		S	L	B		Mortensen 1920a, 1921, 1936; Hendler 1975	
<i>Ophiophycis gracilis</i>		S	L	B		Hendler 1975	
<i>Ophioplocus esmarki</i>		S	L	B		Hyman 1955; Hendler 1975	
<i>Ophioplocus japonicus</i>		S	L	P	Doliolaria	Komatsu and Shōsaku 1993	
Phrynophiurida	<i>Ophiura albida</i>	C	Pl	P		Mortensen 1931; Mladenov 1985a	
	<i>Ophiura carnea</i>	C	Pl	P		Tyler and Fenaux 1994	
	<i>Ophiura meridionalis</i>	S	L	B		Hendler 1975	
	<i>Ophiura sarsi</i>	C	Pl	P	Pluteus only	Strathmann 1987	
	<i>Stegophiura sculpta</i>	S	L	B		Hendler 1975	
	<i>Stegophiura vivipara</i>	S	L	B		Hendler 1975	
	Gorgonocephalidae	<i>Astrotoma waitei</i>	S	L	B		Hendler 1975
		<i>Gorgonocephalus eucnemis</i>	S	L	B, P		Strathmann 1987
Unknown							
Unknown	"Kirk's ophiuroid"	D	L	B	Mesogen	Fell 1941	

Note: Species are arranged by class, order, and family. See text for descriptions of developmental patterns and larval types.

*S, simple; C, complex; D, direct.

[†]L, lecithotrophic; Pl, planktotrophic.

[‡]B, benthic; P, planktonic.

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