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Evolution of development and the Ophiuroidea-revisited

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ABSTRACT: While evolutionary shifts in development in echinoids and asteroids can generally be characterised by transitions from feeding to non-feeding larval forms, in ophiuroids this dichotomy can be further categorized according to the phenotype of the metamorphic larval form. Ophiuroid developmental modes include feeding (planktotrophic) ophioplutei, and non-feeding (lecithotrophic) reduced ophioplutei, vitellariae and brooded larvae. The metamorphic stage is characterized by a distinct pattern of resorption of the ophiopluteal arms and re-arrangement of the ciliated band. The evolution of development in ophiuroids is thus manifested in two phenomena: the acquisition of lecithotrophy and a divergence in metamorphic phenotypes (Type I and Type II development). We have documented development from the families Ophiocomidae, Ophiodermatidae, Ophionereidae, Ophiotrichidae and Ophiactidae to elucidate how evolutionary changes in development through acquisition of lecithotrophy and divergent metamorphic phenotypes contributed to the developmental diversity in the Ophiuroidea. New data on development from twenty-three species, including species with planktotrophic ophioplutei and lecithotrophic vitellaria larvae is provided. Our results support the general dichotomy in development (Type I and Type II) proposed by Mladenov (1985). However, species with intermediate patterns of development among ophiotrichids and ophiactids, suggests that Type I and Type II development may represent two extremes of an evolutionary developmental continuum. Developmental data obtained from ten lecithotrophic developers of unrelated taxa revealed that a common pattern of morphogenesis underlined formation of vitellaria larvae, suggesting a common ancestor for Type II developers. We await molecular phylogenies to refine hypotheses on evolutionary pathways in development for the Ophiuroidea.

1 INTRODUCTION

One of the better-documented aspects in the evolution of development of echinoderms is seen in the multiple transitions in development from an ancestral-type feeding (or planktotrophic) larva to development via a non-feeding (or lecithotrophic) larva (Strathmann 1985). Like many other marine invertebrates, developmental modes in echinoderms display a high diversity in larval morphology that includes a range of feeding and non-feeding larval forms. This diversity in larval morphology is not only intriguing but has posed many challenges for understanding the evolution of development in the phylum.

Among the pioneers of echinoderm embryology, Mortensen (1921, 1931, 1937, 1938) was one of the first to recognize that in the Ophiuroidea there were certain features in larval morphology that could have important bearing for understanding the evolution of development in this class. However, our knowledge of the developmental diversity in the Ophiuroidea is limited, because development through to settlement is known for approximately thirty species (reviewed by Hendler 1975, 1991). Development through a feeding ophiopluteus includes most species studied to date (Hendler 1991). The discovery of a species, *Ophiocoma pumila* (Lükten 1856), with both a feeding ophiopluteus and a non-feeding vitellaria larva during development suggest that a biphasic mode of development also occurs in the Ophiuroidea (Mladenov 1985). The evolutionary significance of this dichotomy in developmental modes remains to be addressed. Nevertheless, Mladenov's discovery provides the basis for hypotheses on the evolution of development in ophiuroids. Thus patterns of development in the Ophiuroidea can be classified according to the main larval form that carries the developing juvenile during metamorphosis (Figure 1). In this scheme planktotrophy and lecithotrophy occur in association with two main modes of development, namely, Type I and Type II.

To elucidate how evolutionary changes in development may have contributed to the developmental diversity of the Ophiuroidea, we have documented development for a range of ophiuroid taxa that include members of the families Ophiothrichidae, (Ljungman 1867), Ophiactidae (Matsumoto 1915), Ophionereidae (Ljungman 1867), Ophiodermatidae (Ljungman 1867) and Ophiocomidae (Ljungman

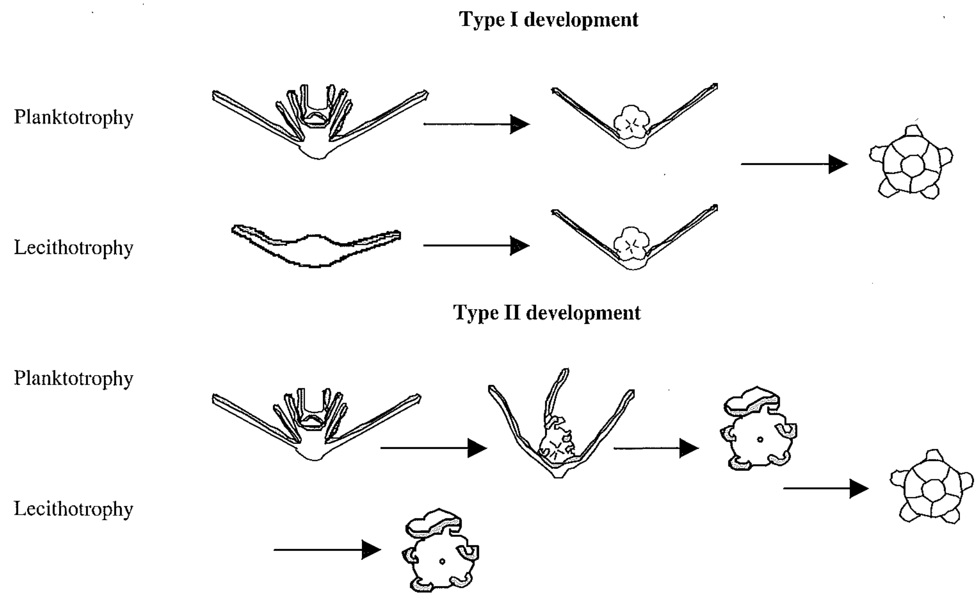

Figure 1. Modes of development in the Ophiuroidea. In this scheme planktotrophy can occur in two ways. In Type I development, the feeding ophiopluteus metamorphoses by complete resorption of all the larval arms (including the ciliated band), except the postero-lateral pair which supports the developing juvenile until settlement. In Type II development, the feeding ophiopluteus transforms into a secondary, non-feeding larval form, the vitellaria prior to metamorphosis. In this mode, all the larval arms are resorbed but associated fragments of the ciliated band are retained and remodelled into the transverse ridges of the vitellaria larva. Lecithotrophic development occurs in association with these two main modes of development. In Type I, a non-feeding ophiopluteus metamorphoses in the same manner as its planktotrophic counterpart. In Type II lecithotrophy, development occurs only via a vitellaria larva.

1867). These cosmopolitan taxa were chosen because they are large speciose families that contain species displaying all known modes of the development for the class. Accounts of development for species in each family, with particular attention to larval morphology and the metamorphic stage are presented to provide a modern synthesis on the evolution of development for the Ophiuroidea.

2 MATERIALS AND METHODS

Temperate and tropical species from Ophiothrichidae, Ophiactidae, Ophiocomidae, Ophionereidae, and Ophiodermatidae were collected from the Sydney region, the Great Barrier Reef (Lizard Island Research Station and Raine Island), the Atlantic coast of Panama (Galeta Research Station, Smithsonian Tropical Research Institute) and Pacific coast of Panama (Taboga Island, Bay of Panama). The following species were examined: *Ophiothrix caespitosa* (Lyman 1879), *O. ciliaris* (Lamarck 1816), *O. spongicola* (Stimpson 1855); *Ophiactis resiliens* (Lyman 1879); *Ophiocoma aethiops* (Lükten 1859), *O. alexandri* (Lyman 1860), *O. echinata* (Lamarck 1816), *O. erinaceus* (Müller & Troschel 1840), *O. dentata* (Müller & Troschel 1840), *O. pusilla* (Brock 1888), *O. schoenleinii* (Müller & Troschel 1840), *O. scolopendrina* (Lamarck 1816), *O. wendtii* (Müller & Troschel 1842), *Ophionereis schayeri* (Müller & Troschel 1840), *Clarkcoma pulchra* (Clark 1928), *Ophiarthrum pictum* (Müller & Troschel 1842), *Ophiomastix annulosa* (Lamarck 1816), *O. mixta* (Lükten 1869), *Ophioderma brevicaudum* (Lükten 1856), *O. appressum* (Say 1825), *O. cinereum* (Müller & Troschel 1842), *Ophiarachnella gorgonia* (Müller & Troschel 1842) and *O. ramsayi* (Bell 1888). Detailed accounts of development for all these species are given elsewhere (Selvakumaraswamy & Byrne 2004, 2000a, Selvakumaraswamy 2002, Cisternas & Byrne 2000, 2003, in press, and unpublished data by Cisternas). A summary of all spawning trials and developmental sequences obtained per species studied are given in Table 1.

Females and males were placed together and induced to spawn by a light/temperature shock method (Selvakumaraswamy & Byrne 2000b). Larvae from each spawning event were subsequently reared using standard culturing methods as described by Strathmann (1987). Development was documented

Table 1. Spawning trials and developmental series obtained for all ophiuroid species studied.

Species	Successful spawning events	Total no. of individuals spawned
Ophiothrix caespitosa	1/1	2(1♀/1♂)
O. ciliaris	2/2	4(2♀/2♂)
O. spongicola	8/8	64(48♀/16♂)
Ophiactis resiliens	4/7	42(28♀/14♂)
Ophiocoma aethiops	1/1	10(7♀/3♂)
O. alexandri	1/1	10(7♀/3♂)
O. dentata	1/1	9(6♀/3♂)
O. echinata	2/2	44(22♀/22♂)
O. erinaceus	2/2	23(16♀/7♂)
O. pusilla	1/2	11(7♀/4♂)
O. scolopendrina	2/2	32(21♀/11♂)
O. schoenleinii	1/2	18(9♀/9♂)
O. wendtii	2/2	35(14♀/11♂)
Ophionereis schayeri	5/10	60(40♀/20♂)
Ophioderma appressum	2/2	34(16♀/18♂)
O. brevicaudum	1/1	18(7♀/11♂)
O. cinereum	2/2	39(20♀/19♂)
Ophiarachnella gorgonia	3/3	33(23♀/10♂)
O. ramsayi	2/2	24(15♀/9♂)
Ophiomastix mixta	1/1	11(6♀/5♂)
O. annulosa	1/1	3(2♀/1♂)
Ophiarthrum pictum	1/1	4(3♀/1♂)
Clarkcoma pulchra	1/3	6(4♀/2♂)

using standard light and scanning electron microscopy (SEM) techniques. To determine developmental series, approximately 100 larvae per stage of development were examined by light microscopy and another 100 larvae were preserved for SEM.

3 RESULTS

Data on development for a total of twenty-three species were obtained from several spawning events as indicated in Table 1. Larval forms were previously unknown for nineteen of these species, except for accounts of larvae of *Ophiocoma echinata*, *O. erinaceus*, *O. scolopendrina* by Mortensen (1921, 1937) and *Ophioderma cinereum* by Hendler (1979).

3.1 *Type I planktotrophic development*

A feeding 8-armed ophiopluteus larva was characteristic of all *Ophiothrix* species studied as well as *Ophiactis resiliens* (Figure 2a). Development in *Ophiothrix* species displayed the typical Type I mode of development, except for *O. ciliaris*. *Ophiactis resiliens* also displayed an unusual mode of development. Metamorphosis in ophiotrichids was characterised by gradual and complete resorption of the larval arms and supporting skeletal rods, except for the

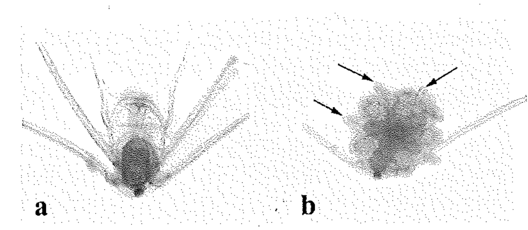

Figure 2. (a) Light micrograph of a fully developed 8-arm ophiopluteus of *Ophiactis resiliens* and (b) metamorphosing stage showing portions of ciliated bands (arrows) retained, while the corresponding larval arms were resorbed.

postero-lateral arms which supported the developing juvenile until settlement. In contrast, metamorphosis in *O. ciliaris* and *O. resiliens* differed from other Type I developers in that portions of the ciliated band associated with the larval arms were retained and formed transverse ridges between the developing juvenile arms (Figure 2b). In these two species the postero-lateral arms were also fully or partially retained until settlement. Juveniles of *O. ciliaris* and *O. resiliens* settled with two arm segments plus the terminal arm plate. The juvenile mouth was fully opened by the time settlement occurred.

3.2. *Type II planktotrophic development*

Although most *Ophiocoma* species developed through an ophiopluteus larva, an 8-arm ophiopluteus was only observed for *O. echinata* and *O. wendtii* (results not shown). Other *Ophiocoma* species were raised only to the 4–6 armed stages. *Ophiocoma echinata* began to develop into a vitellaria-like larva prior to metamorphosis. In this species, the three anterior-most larval arm pairs (antero-laterals, post-orals and postero-dorsals) were gradually resorbed and the corresponding portions of the ciliated band were retained at the sites where the larval arms originally budded off the larval body. The postero-lateral arms were slowly resorbed into the larval body after all the other larval arms had been resorbed. A similar pattern was noted for *O. wendtii* though only at the early stages of resorption of the antero-lateral and post-dorsal larval arms. Although the linear hydrocoel had developed at this stage, differentiation of its five lobes and thus the start of metamorphosis (*sensu* Burke 1987) were not observed before the larvae died.

An unusual diversity in larval morphology at the early stages of development was noted for *Ophiocoma* species (Figure 3). For example, *O. dentata* and *O. pusilla* passed through a 'bipinnaria-like' stage before the first pair of larval arms, the postero-laterals, developed. *Ophiocoma wendtii* and *O. alexandri* developed into a broad prism stage with a wide pre-oral

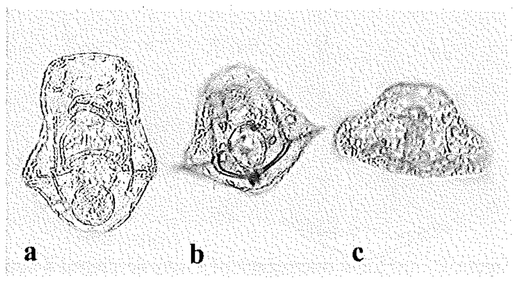

Figure 3. Early developmental stages of *Ophiocoma* species showing divergent larval morphologies:
(a) 4 day bipinnaria-like larva of *O. pusilla*,
(b) 3 day broad prism stage *O. wendtii*,
(c) 3 day prism of *O. scolopendrina*.

lobe and small, broad postero-lateral arm buds. In contrast, *Ophiocoma scolopendrina*, *O. echinata*, *O. aethiops*, *O. erinaceus* and *O. schoen-leinii* developed into typical prism stages with a reduced preoral lobe and elongated postero-lateral arm buds. Morphogenetic differences in these species also included differences in the extent to which the larval arms and supporting skeletal rods developed. The distribution of these 'clade'-specific pluteal characters in *Ophiocoma* is currently under investigation (Cisternas unpubl.).

3.3. *Type II lecithotrophic development*

Species from the genera *Ophioderma*, *Ophiarachnella*, *Ophionereis*, *Clarkcoma*, *Ophiarthrum* and *Ophiomastix* developed through a vitellaria larva (Type II Lecithotrophy). Early development of the vitellaria larva was characterised by differentiation of the anterior region (the pre-oral lobe), the mid-region (the ventral ridge, stomadeum and the juvenile rudiment), and the posterior region (Figure 4). These three larval regions underwent complex morphogenetic torsion events, which were in turn intimately associated with development of the transverse ciliated bands of the advanced vitellaria. The extensive morphogenetic movements that occurred in these species paralleled torsion events noted during the transition of the early bilateral larva to the vitellaria of *Ophionereis schayeri*. Unlike most of the vitellariae described here, the larva of *O. schayeri* had a continuous ciliated band. Subsequent torsion events involved fragmentation of the continuous ciliated band and remodelling of these fragments in the same fashion as the vitellariae of ophiodermatids and ophiocomids.

A number of other features characterised development through a vitellaria larva. Firstly, rapid skeletogenesis of juvenile structures at the early vitellaria stage occurred. Juvenile spicules (terminals, radials,

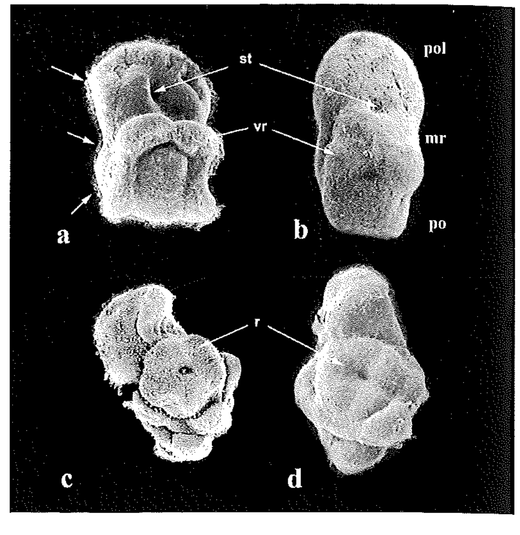

Figure 4. (a–b) SEM of a 2.5 day early vitellaria stage of *Ophionereis schayeri* and a 3 day *Ophiarachnella ramsayi* showing differentiation of the three main larval regions- the pre-oral lobe (pol), mid-region (mr) and posterior region (po). A continuous ciliated band (arrows) is present in *O. schayeri*. (c–d) vitellariae of *O. schayeri* (3.5) and *O. ramsayi* (4 day) showing the complex morphogenetic movements of the larval body. Vr = ventral ridge, st = stomadeum, r = rudiment.

first inter-radials and paired oral plates) originated in a radial fashion except in *O. schayeri*. In the latter species, juvenile spicules first developed in a linear fashion along the right and left somatocoels. Secondly, one pair of juvenile buccal podia (feeding structures) developed before settlement. The number of buccal podia pairs varied among species and according to egg size. Vitellariae derived from smaller eggs ($<300\,\mu m$), such as *O. schayeri* and *C. pulchra* developed two pairs before settlement. In contrast, species derived from larger eggs ($>300\,\mu m$) settled with only one pair. Similarly, the juvenile mouth (feeding competency) opened earlier in species from smaller eggs ($<300\,\mu m$) than in species from larger eggs ($>300\,\mu m$). Feeding competency was achieved post-settlement, ranging from two to at least ten days after settlement. Newly settled juveniles of all species also lacked arm segments and settled with a partially developed terminal arm plate. The first arm segment developed ten to twenty days post-settlement.

4 DISCUSSION

Developmental data presented in this study suggest that the metamorphic stage appears to be the most informative phase of development for elucidating evolutionary processes that give rise to the array of developmental modes in the Ophiuroidea. Further, our results support Mladenov's notion that two main modes of development, Type I and Type II exist in the Ophiuroidea (1985).

Most ophiotrichids for which development has been documented through metamorphosis display Type I planktotrophic development (reviewed by Byrne & Selvakumaraswamy 2001). The metamorphic stage of these species was characterised by a juvenile suspended between the postero-lateral arm pair of the former ophiopluteus larva until settlement. In comparison, the metamorphic stages of *O. ciliaris* and *O. resiliens* deviated from the typical Type I development in that portions of the ciliated band were retained to late stages of metamorphosis and resembled the transverse ridges of vitellaria larvae. An intermediate mode of metamorphosis has also been documented for another ophiactid species *Ophiodaphne formata* (Tominaga et al. 2004). Whether the presence of ciliated ridges represents a functional advantage to the pre-settlement stage in these species, or is merely an alternative mode of development is not known. Earlier studies by Mortensen on a series of unidentified ophioplutei (*Ophiopluteus formosus*, *Ophiopluteus undulatus*, *Ophiopluteus pusilus* and *Ophiopluteus spp.*), *Ophiura albida* and *Amphiura filiformis* revealed that additional intermediate metamorphic stages occur in other ophiuroids (Mortensen 1920, 1921, 1931). Unfortunately, detailed accounts of metamorphosis to settlement are not available for these species, preventing their divergent metamorphic patterns from being placed in an evolutionary context. However, these divergent modes of metamorphosis provide a link for elucidating possible evolutionary routes in the mode of development in ophiuroids. That is, they may represent a transitional stage in the evolution of either Type I from Type II development or Type II from Type I. Alternatively, this may indicate a plasticity retained from an ancestor with Type I and Type II capabilities. Comparative studies of metamorphic stages of species with planktotrophic development and a robust phylogenetic framework may provide the basis to elucidate the polarity of this change in development.

Data on development of *Ophiocoma* species suggests that Type II planktotrophic development may be more widespread in the genus than Type I development. To date, Type II planktotrophic development is not known from any other ophiuroid, except in *Ophiocoma pumila* (Mladenov 1985). Thus the question as to whether the divergence of Type I and Type II development may also define certain phylogenetic lines remains unanswered. Of particular interest is the unusual diversity in early pluteal morphology displayed by the *Ophiocoma* species reported here. Differences in larval morphogenesis suggest that selection on the early stages of development may have important consequences for the overall morphology of the fully formed ophiopluteal stage. Further studies on development of *Ophiocoma* species may provide a useful model for understanding how functional constraints may have shaped the evolution of the ophiopluteus from a dipleurula-like larva. In *Ophiocoma dentata* and *O. pusilla*, the early larva has a bilaterally symmetrical morphology with a simple circumoral ciliated band which resembles the asteroid bipinnaria larva. Subsequent development of small tetra-radiate spicules eventually gives rise to the larval arms of the pluteal form.

The results from the Type II lecithotrophs (*Ophioderma appressum*, *O. cinereum*, *O. brevicaudum*, *Ophiarchanella ramsayi*, *O. gorgonia*, *Ophiomastix annulosa*, *O. mixta*, *Ophiarthrum pictum*, *Ophionereis schayeri* and *Clarkcoma pulchra*) showed that there are some common underlying developmental features in vitellariae from unrelated taxa. The striking morphogenetic events of the larval body and subsequent development of the transverse ciliated ridges suggests that either remarkable convergence in developmental mechanisms has occurred or that these taxa may have shared a common ancestral mode of development. The similar remodelling of the ciliated band in the auricularia-doliolaria transition and that seen in crinoids (Nakano et al. 2003, Lacalli 1993, Lacalli & West 2000) suggests that a common ancestor is more likely. Additional studies on development of other vitellariae may reveal whether this trend is prevalent in other ophiuroid taxa.

Although lecithotrophy is often associated with accelerated development to the juvenile stage, newly settled juveniles of Type II developers are comparatively less-structurally developed than the newly settled stages of Type I developers. Juveniles from Type I developers settle with 3 arm segments (including the terminals) and a fully functional mouth. In contrast, the juveniles of Type II developers settle with a partially developed terminal arm plate, and a non-functional mouth. Juveniles of Type II developers reach a comparable stage of growth ten to thirty days after settlement. In the latter group, the extent and timing of juvenile feeding competency and development of locomotory structures appear to be influenced by the amount of maternal provisioning in the egg. Interestingly, the disc diameter of newly settled juveniles from Type I and Type II developers are similar, ranging between 200–300 μm (Hendler 1991, Selvakumaraswamy 2002, Cisternas pers. obs.). This suggests that in ophiuroids there is selection for settlement to occur at a certain juvenile size. However, differences in the extent of juvenile development at settlement appear to be constrained by the main mode of development (either Type I or II) for the taxa in which they occur.

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