Life history diversity and evolution in the Asterinidae

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Synopsis Asterinid sea stars have the greatest range of life histories known for the Asteroidea. Larval form in these sea stars has been modified in association with selection for planktonic, benthic, or intergonadal developmental habitats. Life history data are available for 31 species and molecular data for 28 of these. These data were used to assess life history evolution and relationships among asterinid clades. Lecithotrophy is prevalent in Asterinidae, with at least 6 independent origins of this developmental mode. Morphological differences in the attachment complex of brachiolaria larvae were evident among species with planktonic lecithotrophy. Some features are clade specific while others are variable within clades. Benthic brachiolariae are similar in *Aquilonastra* and *Parvulastra* with tripod-shaped larvae, while the bilobed sole-shaped larvae of *Asterina* species appear unique to this genus. Multiple transitions and pathways have been involved in the evolution of lecithotropy in the Asterinidae. Although several genera have a species with a planktonic feeding larva in a basal phylogenetic position, relative to species with planktonic or benthic lecithotrophy, there is little evidence for the expected life history transformation series from planktonic feeding, to planktonic non-feeding, to benthic non-feeding development. Intragonadal development, a life history pattern unique to the Asterinidae, arose three times through ancestors with benthic or pelagic lecithotrophy. Evolution of lecithotrophy appears more prevalent in the Asterinidae than other asteroid families. As diverse modes of development are discerned in cryptic species complexes, new insights into life history evolution in the Asterinidae are being generated.

Introduction

The diversity of larval forms in marine invertebrates has long fueled discussion on evolutionary origins and pathways of evolutionary change (Gould 1977; Strathmann 1993; Raff 1996; McEdward 2000). In recent times these discussions have achieved a renewed rigor through use of the comparative approach where molecular phylogenies provide a robust framework with which to assess pathways of change (Ó Foighil and Smith 1995; Hart and others 1997; Duda and Palumbi 1999; Hart 2000; Collin 2001; McFadden and others 2001; Jeffery and Emlet 2003; Jeffrey and others 2003). Use of closely related species to investigate evolutionary pathways is particularly powerful because homologous features can be compared. In the Echinodermata this approach has been used to great effect with several asteroid and echinoid genera (Raff 1992; Smith and others 1995; Hart and others 1997, 2003; Jeffery and Emlet 2003; Jeffrey and others 2003; Raff and Byrne 2006).

While discussions on potential "indirect versus direct developing" ancestral states continues for some taxa (Haszprunar and others 1995; McHugh and Rouse 1998; Rouse 2000), for living Echinodermata, the feeding planktotrophic larva is considered to be a plesiomorphic character (Strathmann 1985; Raff 1992; Wray 1996; Smith 1997; but see Mooi and David 1998). In addition to the dichotomy of feeding versus non-feeding larvae, echinoderm developmental categories are also based on the number of larval stages present (McEdward and Miner 2001; Selvakumaraswamy and Byrne 2004, 2006). In the Asteroidea some major orders have only one larval stage (bipinnaria) while others have two (bipinnaria + brachiolaria), with various hypotheses proposed on the likely ancestral pattern (Chia and others 1993; McEdward and Janies 1993; McEdward and Miner 2001; McEdward and others 2002). The bipinnaria is shared by most asteroid orders, supporting the notion that this is the basal-type larval stage for the Asteroidea. Moreover, the bipinnaria is considered to represent the "dipleurula"-type larva ancestral for the Echinodermata. Brachiolariae present in the major orders Forcipulatida, Spinulosida, Velatida, and Valvatida might have evolved from the bipinnaria as settlement stage larvae (McEdward and Miner 2001). Brachiolariae have an attachment complex composed of three larval arms (brachia) and an adhesive disc. The morphology of this complex exhibits specializations for larval habitat and provides a useful landmark with which evolution of larval form can be assessed

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(Byrne, Cerra, Hart, and others 1999; McEdward and others 2002).

Among sea stars with bipinnaria and brachiolaria larvae, the Asterinidae, a species-rich valvatid family, is noted for its diverse life histories (Byrne and Cerra 1996; Hart and others 2004). These sea stars have the greatest diversity of life histories known for the Asteroidea. Most Australasian asterinids have lecithotrophic larvae that develop in planktonic, benthic, or intragonadal habitats (Lawson-Kerr and Anderson 1978; Hart and others 1997, 2003, 2004; Byrne, Cerra, Hart, and others 1999; Byrne and others 2003; Dartnall and others 2003). Life history evolution appears to have exerted a strong influence on speciation in these asteroids. The larvae have diverse phenotypes and ecologies while the adults are similar in both of these features (Hart and others 1997, 2003; Byrne, Cerra, Hart, and others 1999; Byrne and others 2003).

Although selection on larval phenotype has been strong, adult asterinids are often remarkably similar. As a result, cryptic morphospecies, not readily discerned by traditional taxonomy, have been detected (Dartnall 1969; Keough and Dartnall 1978; Hart and others 1997, 2003; Byrne and others 2003; Dartnall and others 2003; O'Loughlin and Waters 2004). Traditional systematics of the Asterinidae has been confounded by morphological characters of limited phylogenetic value (Clark and Downey 1992; Dartnall and others 2003; O'Loughlin and Waters 2004). Guided by molecular data, the taxonomy of the Asterinidae in Australasia has been revised and several new genera and species have been described (O'Loughlin 2002; O'Loughlin and others 2002, 2003; Dartnall and others 2003; O'Loughlin and Waters 2004; Waters and others 2004). This taxonomic revision provided an important opportunity to review the patterns of life history evolution in asterinid genera. Life history and/or molecular data available for 31 species from the present and previous studies (Byrne and Cerra 1996; Hart and others 1997, 2004; O'Loughlin and Waters 2004; Byrne 2005) were used for the phylogenetic comparisons. Some species in O'Loughlin and Waters (2004) were not included due to lack of life history data.

Materials and methods

Meridiastra occidens, *Meridiastra gunnii*, and *Meridiastra mortenseni* were obtained from Perth (Western Australia), the Morninton Peninsula (Victoria), and Mission Bay, Auckland (New Zealand), respectively. *Meridiastra atyphoida* and *Meridiastra scobinata* were obtained from Tasmania. *Aquilonastra* new sp. and *Cryptasterina* new sp. #1 were collected from One Tree Island (Queensland). *Cryptasterina* new sp. #2 was collected from Bird Island (Queensland). Fertile eggs were obtained by placing the ovaries in the ovulatory hormone 1-Methyladenine in filtered seawater (FSW). For several species new data on egg size were determined by image analysis. Data on egg size for *Patiria chilensis*, *Paranepanthia grandis*, *Paranepanthia aucklandensis*, and *Stegnaster inflatus* were obtained by dissection (personal communications, M. Barker, M. Fernandez and D. McClary). Ova were fertilized and the larvae were reared in FSW as detailed in Cerra and Byrne (2004). For scanning electron microscopy (SEM), specimens were fixed in 2.5% glutaraldehyde in FSW for 30–60 min, rinsed in distilled water, dehydrated through graded ethanols, critical point dried, mounted on stubs, and viewed with a Joel JSM-354 SEM.

For maximum parsimony analyses the CO1 gene and adjacent tRNA sequences from the mtDNA of 28 asterinid species (Table 1) with known life history data (Table 2) were accessed from Genbank. Sequence data for *Asterinia stellifera* were provided by R. Ventura and H. Lessios. Dubious segments at the beginning and end of each sequence were removed, leaving a 1716 bp segment, which was aligned using ClustalX. Building the tree rooted with the asteriid species *Coscinasterias acutispina* or *Pisaster ochraceus* or unrooted with no out group resulted in the same tree topology.

The dataset was compiled in MacClade 4 (Maddison and Maddison 2000) and a cladistic analysis was performed using PAUP*4.0b10 (Swofford 2002). All characters were equally weighted with gaps treated as data missing. A stepmatrix was included to weight transversion:transition as 2:1 (as in Waters and others 2004). Heuristic searches and maximum parsimony analysis were used to find most parsimonious trees (MPTs). The analysis used tree-bisection-reconnection branch swapping and starting trees were obtained by random stepwise addition. Bootstrap values were calculated from 100 replicates and 50 stepwise additions. Bootstrap values >50 are shown.

Results

Phylogeny

The revised taxonomy of the Asterinidae (O'Loughlin and Waters 2004) presents six main clades encompassing several new genera, *Meridiastra*, *Aquilonastra*, and *Parvulastra*, and previously established genera, *Paranepanthia*, *Patiria*, *Asterina*, *Patiriella*, and *Cryptasterina*. A single MPT was identified here (Fig. 1) with a total length of 2911 (consistency index = 0.1616; retention index = 0.415).

Table 1 Sources of mtDNA sequence data used for phylogenetic analysis

Species	Location	CO1
Coscinasterias acutispina	Japan	AF485025[a]
Pisaster ochraceus	North America	X55514[e]
Paranepanthia grandis	Australia	AY370757[c]
Paranepanthia aucklandensis	Auckland Island	AY370751[c]
Stegnaster inflatus	New Zealand	AY370743[c]
Patiria pectinifera	Japan	D16387[d]
Patiria miniata	North America	U50056[e]
Patiria chilensis	Chile	AY370745[c]
Meridiastra atyphoida	Australia	AY370760[c]
Meridiastra calcar	Australia	U50046[e]
Meridiastra gunnii	Australia	U50049[e]
Meridiastra medius	Australia	AY370749[c]
Meridiastra occidens	Australia	U50048[e]
Meridiastra oriens	Australia	U50047[e]
Meridiastra mortenseni	New Zealand	AY370750[c]
Asterina gibbosa	Europe	U50058[e]
Asterina phylactica	Europe	AH011640[f]
Asterina stellifera	Brazil	—[g]
Parvulastra vivipara	Australia	U50054[e]
Parvulastra parvivipara	Australia	U50055[e]
Parvulastra exigua	Australia	U50053[e]
Aquilonastra scobinata	Australia	AY370755[c]
Aquilonastra burtoni	Red Sea	AY370752[c]
Aquilonastra coronata	Japan	AY370747[c]
Aquilonastra miner	Japan	AY370746[c]
Patiriella regularis	New Zealand	U50045[e]
Cryptasterina pentagona	Australia	AF509224[f]
Crypasterina hystera	Australia	AF509225[f]
Cryptasterina pacifica	Japan	U50057[e]
Cryptasterina sp.	Taiwan	PPU50051[e]

[a] Wada and colleagues (1996).
[b] Knott and Wray (2000).
[c] Waters and colleagues (2004).
[d] Asakawa and colleagues (1995).
[e] Hart and colleagues (1997).
[f] Hart and colleagues (2004).
[g] Ventura and Lessios, unpublished.

Bootstrap analysis revealed little support (<50%) for basal nodes, but provided strong support for most terminal modes (Fig. 1). The tree supports the monophyly of the genera as determined in Waters and colleagues (2004). It differs from the previous studies (O'Loughlin and Waters 2004; Waters and others 2004) in separating *Parvulastra* from the other Pacific asterinids and placing this genus in a basal position.

Distribution of life history patterns in the asterinid clades

Life history data are available for 31 asterinid species. Of these, 6 have planktotrophic development and the rest are lecithotrophs. The distribution of life histories varies across the asterinid genera (Table 1, Fig. 1). With the assumption that planktotrophy is the ancestral larval type for these asterinids, the MPT indicates that lecithotrophy arose independently at least six times in the asterinid clades. Most genera contain species with at least two developmental modes. The exceptions are *Patiria* from the north and south Pacific, where all the species ($n = 3$) investigated have planktotrophic development, and *Paranepanthia* from Australia and New Zealand with two planktonic lecithotrophs. *Patiriella* has one species (O'Loughlin and Waters 2004), *Patiriella regularis*, a planktotrophic developer. The type genus *Asterina* is represented by three species, one planktotroph (*A. stellifera*) and two species with benthic brachiolariae (*Asterina gibbosa* and *A. phylactica*).

Meridiastra from temperate Australia includes four species with planktonic lecithotrophy and one planktotroph, *M. mortenseni* (Table 2). *M. atyphoida* has a large egg and is expected to have lecithotrophic development. In the phylogeny, the planktotrophic developer *M. mortenseni* is basal to the lecithotrophic *Meridiastra*, but this node in the MPT has weak support.

Aquilonastra is largely Indo-Pacific in distribution. It includes two planktonic lecithotrophs, *Aquilonastra burtoni*, *Aquilonastra coronata*, *Aquilonastra batheri*, and two benthic lecithotrophs, *Aquilonastra minor* and *Aquilonastra* new sp. (Table 2). *Aquilonastra scobinata* has a large egg and is expected to have lecithotrophic development. In this clade planktonic lecithotrophy is likely to be the ancestral state for the species with benthic development.

Cryptasterina currently includes six species——three intragonadal brooders, two planktonic lecithotrophs, and a new species with an undetermined lecithotrophic larval form (Table 2). Both the Japanese and Taiwanese (*Cryptasterina* sp., *Cryptasterina pacifica*) and the Australian (*Cryptasterina* new sp. #1, *Cryptasterina* new sp. #2, *Cryptasterina pentagona*, *Cryptasterina hystera*) groups include species with intragonadal and planktonic development (Fig. 1). Intragonadal development has evolved twice in this group (Hart and others 2003). Planktonic lecithotrophy appears to be the ancestral-type life history for evolution of intragonadal development in *Cryptasterina*.

Parvulastra from temperate Australia comprises three species, a benthic developer and two intragonadal

Table 2 Developmental patterns and larval types in the Family Asterinidae[a]

Genus/species	Egg diameter (μm)	Spawning/fertilization	Dev. type	Larval type(s)
Asterina				
A. gibbosa	500	Benth. eggs	BL	Bilobed Brach.
A. phylactica	500	Broods benth. eggs	BL	Bilobed Brach.
A. stellifera	150	Broadcasts	Pt	Bip. and Brach.
Stegnaster				
S. inflatus	1000	—	L	—
Paranepanthia				
P. aucklandensis	400	—	L	—
P. grandis	800	—	L	—
Patiria				
P. miniata	169	Broadcasts	Pt	Bip. and Brach.
P. chilensis	160	—	Pt	—
P. pectinifera	170	Broadcasts	Pt	Bip. and Brach.
Meridiastra				
M. mortenseni	240	Broadcasts	Pt	Brach.
M. calcar	413	Broadcasts	PL	Brach.
M. oriens	400	Broadcasts	PL	Brach.
M. occidens	400	Broadcasts	PL	Brach.
M. gunnii	430	Broadcasts	PL	Brach.
M. atyphoida	400	—	L	—
Parvulastra				
P. exigua	390	Benth. eggs	BL	Tripod brach.
P. vivipara	150	Ig	IgL	Reduced
P. parvivipara	235	Ig	IgL	Reduced
Patiriella				
P. regularis	150	Broadcasts	Pt	Bip. and Brach.
Aquilonastra				
A. batheri	433	Broadcasts	PL	Brach.
A. burtoni	550	Broadcasts	PL	Brach.
A. coronata japonica	422	Broadcasts	PL	Brach.
A. minor	437	Benth. eggs	BL	Tripod brach.
A. scobinata	450	—	L	—
Aquilonastra new sp (Qld)	420[b]	—	L	—
Cryptasterina				
C. pacifica	400	Ig	IgL	Brach.
C. pentagona	413	Broadcasts	PL	Brach.
C. hystera	440	Ig	IgL	Brach.
Cryptasterina sp (Taiwan)	320	Broadcasts	PL	Brach.
Cryptasterina new sp #1 (Qld)	440[b]	Ig	IgL	Brach.
Cryptasterina new sp#2 (Qld)	380[b]	—	PL	—

[a] Data from MacBride (1896); James (1972); Komatsu (1975); Kano and Komatsu (1978); Komatsu and colleagues (1979); Marthy (1980); Emlet and colleagues (1987); Chen and Chen (1992); Chia and colleagues (1993); Byrne and Cerra (1996); and Byrne and colleagues (2003); personal communications from M. Barker, M. Fernandez, D. McClary, and R. Ventura.

[b] Data from unspawned eggs in gonad. BL, Benthic lecithotroph; Benth, benthic; Bip, bipinnaria; Brach, brachiolaria; Dev., development; Ig, intragonadal; IgL, intragonadal lecithotroph; L, lecithotroph; Pt, planktotroph; PL, planktonic lecithotroph; Dashed line, no data.

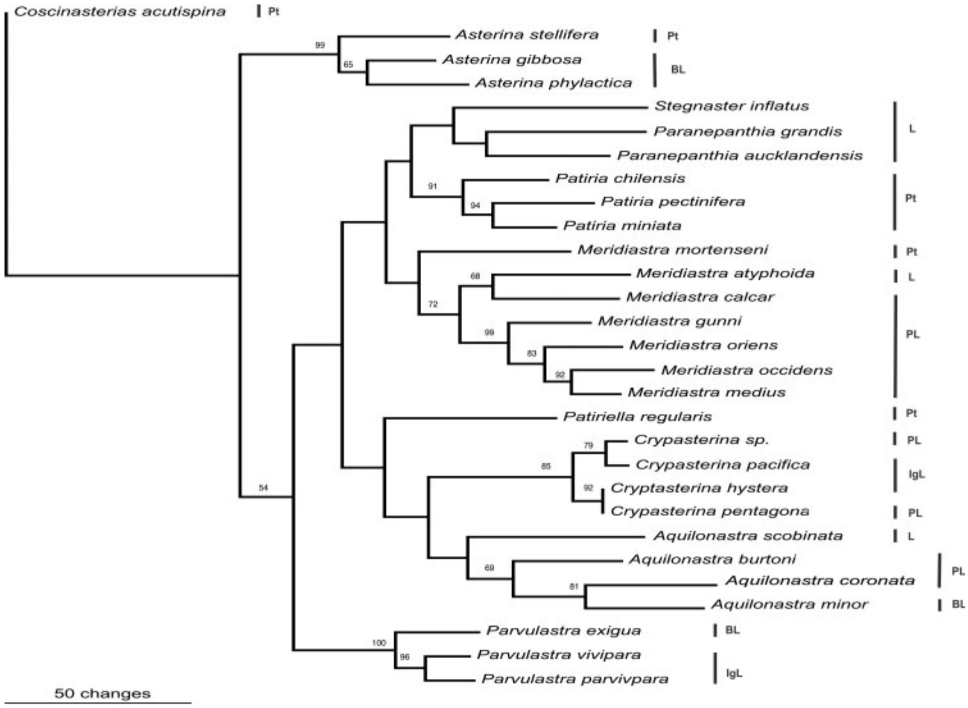

Fig. 1 MP phylogenetic tree showing relationships of asterinid mtDNA sequences (see Table 1). Bootstrap values >50% are indicated. Abbreviations for developmental mode as in Table 2.

developers. Benthic development in egg masses appears to be the ancestral state for evolution of intragonadal brooding in this genus (Fig. 1) (Hart and others 1997).

Life history traits and larval forms

The main dichotomy in life history in the asterinids is the possession of (1) a small egg and development through feeding bipinnaria and brachiolaria larvae or (2) a large egg and development through a lecithotrophic brachiolaria only (Table 2, Figs. 2–4). Asterinids with planktotrophic larvae (*Patiria pectinifera*, *Patiria miniata*, *P. chilensis*, *P. regularis*, *M. mortenseni*, *A. stellifera*) have small (150–170 μm diameter) negatively buoyant eggs (Fig. 1, Table 2). They develop through typical feeding bipinnaria and brachiolaria larvae (Fig. 3A and B).

Most of the other asterinids have large (320–1000 μm diameter) eggs and lecithotrophic development (Table 2, Figs. 3 and 4). The exception is the brooding *Parvulastra* species that have small, secondarily reduced eggs (135–150 μm diameter) that support development to a minute 200 μm diameter juvenile (Fig. 3H). Asterinid eggs vary greatly in composition and buoyancy (Byrne, Cerra, and others 1999; Villinski and others 2002). The eggs of planktonic developers have a range of buoyancies, while the benthic developers have negatively buoyant eggs that adhere to the substratum with their sticky jelly coat. Variation in egg buoyancy between closely related lecithotrophs is exemplified by *Meridiastra*. *M. gunnii* and *M. occidens* have buoyant eggs that float immediately to the air–water interface after release, while eggs of *Meridiastra calcar* and *Meridiastra oriens* are negative to neutrally buoyant, eventually sinking to the substratum. A strongly buoyant egg is characteristic of the *Aquilonastra* and *Cryptasterina* species known to have planktonic or intragonadal larvae, while the benthic developers *A. minor* and *Parvulastra exigua* have negatively buoyant eggs (Komatsu and others 1979,

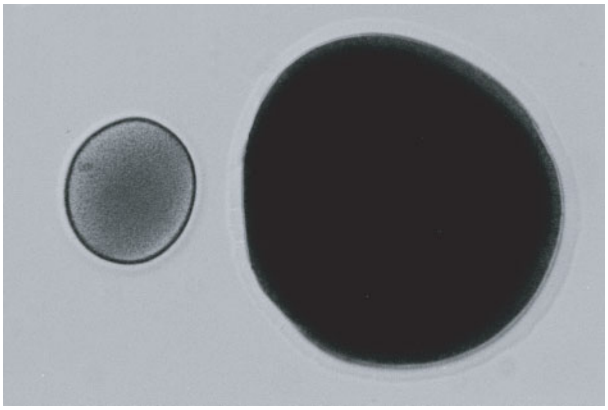

Fig. 2 Contrasting small and large eggs from a planktotroph, *Patiriella regularis*, and a lecithotroph, *Meridiastra calcar*, respectively. Scale bar = 100 μm.

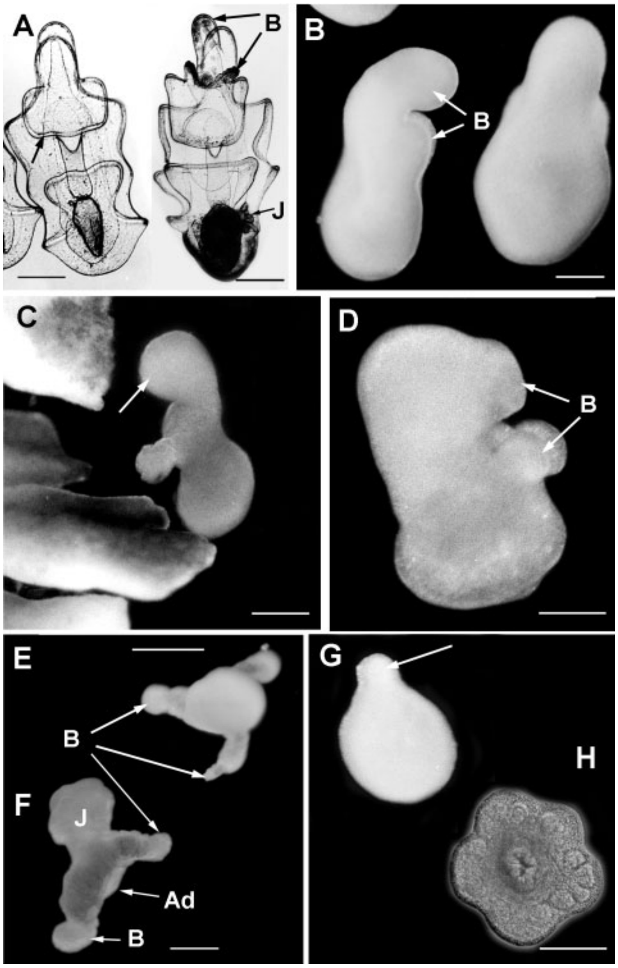

Fig. 3 Light microscopy of asterinid larvae shown in orientation in life. **A:** Bipinnaria and brachiolaria of the planktotroph *Patiriella regularis*. **B–D:** Planktonic lecithotrophic developers; note the hook-like anterior brachium of *Meridiastra oriens* (B) and the lobe-like anterior region of *Meridiastra gunnii* (arrow, C). The anterior brachium of *Cryptasterina pentagona* (D) develops as a protrusion of the preoral lobe. The juvenile rudiment develops in the posterior region. **E and F:** Benthic larvae: tripod larva of *Parvulastra exigua* (E) and bilobed larva of *Asterina gibbosa* (F). **G:** Pear-shaped intragonadal larva of *Parvulastra vivipara*. **H:** Intragonadal juvenile of *P. parvivipara*. Ad, adhesive disc; B, brachium; J, juvenile rudiment. Scale bars: A, Bipinnaria, = 100 μm, brachiolaria, = 200 μm; B, D, G and H = 100 μm; C, E and F = 200 μm. A, from Byrne and Barker (1991); E, from Byrne (1995); F, courtesy D. Haesaerts.

1990; Chen and Chen 1992; Byrne 2005; Byrne and others 2003).

Several species with large eggs have not been reared, but based on egg size (Table 2) are assumed to have lecithotrophic development. *Paranepanthia* species, *Stegnaster inflatus*, *M. atyphoida*, and *Cryptasterina* new sp. #2, have large 400–1000 μm diameter eggs (Table 1). They have aboral gonopores, indicating that they are probably broadcasters with a planktonic larva. *A. scobinata* has oral gonopores (O'Loughlin and Waters 2004) and 400 μm diameter eggs, indicating that their progeny develop in benthic egg masses. *Aquilonastra* new sp. has oral gonopores and 400 μm diameter eggs and is likely to have benthic larvae.

Planktonic lecithotrophic brachiolariae have a well-developed attachment complex with a large central brachium flanked by two smaller brachia (Figs. 3B–D and 4A–D). The adhesive disc is centrally located at the base of the arms. The benthic lecithotrophs develop in egg masses and the larvae have a hypertrophied attachment complex modified for permanent attachment (Figs. 3E, F and 4E, F).

Brachiolaria morphology varies within and among the asterinid clades. The profile of planktonic larvae differs in the shape of the arms and the adhesive disc. In most *Meridiastra* species (*M. oriens*, *M. occidens*, *M. calcar*) the anterior brachium develops as a hook-like structure forming a ventrally directed bend in the anterior lobe (Figs. 3B and 4A). The adhesive disc is round and is obscured by the brachia. The anterior brachium of *M. gunnii* also forms a ventrally directed bend, but has a more lobe-like appearance (Figs. 3C and 4B and C). The brachia of this species are covered with prominent bump-like papillae, and the triangular-shaped adhesive disc is evident on surface view (Figs. 3C and 4B and C). The brachiolaria of *M. gunnii* has a more elongate profile than those of the other *Meridiastra* species (Fig. 3C). The anterior brachium of the brachiolariae of *Cryptasterina* and *Aquilonastra* species develops as a lobe-like protrusion of the preoral lobe (Figs. 3D and 4D) (see also Komatsu 1975; Kano and Komatsu 1978).

In the benthic developers the brachiolar complex develops as a tripod-like structure in *Parvulastra* and *Aquilonastra* or as a bilobed sole-like structure in *Asterina* and serve as a tenacious attachment device (Figs. 3E, F and 4E, F). The tripod larval form of *P. exigua* results from hypertrophic development of the lateral brachia. The adhesive disc forms early in the development, is well developed, and has a round profile (Fig. 4E). In *Asterina* the brachiolar complex is bilobed, formed by two asymmetric brachia (Figs. 3F and 4F) and a round adhesive disc (MacBride 1896; Haesaerts and others 2006).

The intragonadal brooders have the most derived mode of development and their egg size and larval form varies greatly. *Parvulastra* species have small (135–150 μm diameter), secondarily reduced, negatively buoyant eggs. Their brachiolariae, when present, are highly reduced with minimal or no development of the attachment complex (Figs. 3G and 4G, H). In the intragonadal environment the brachiolar complex is

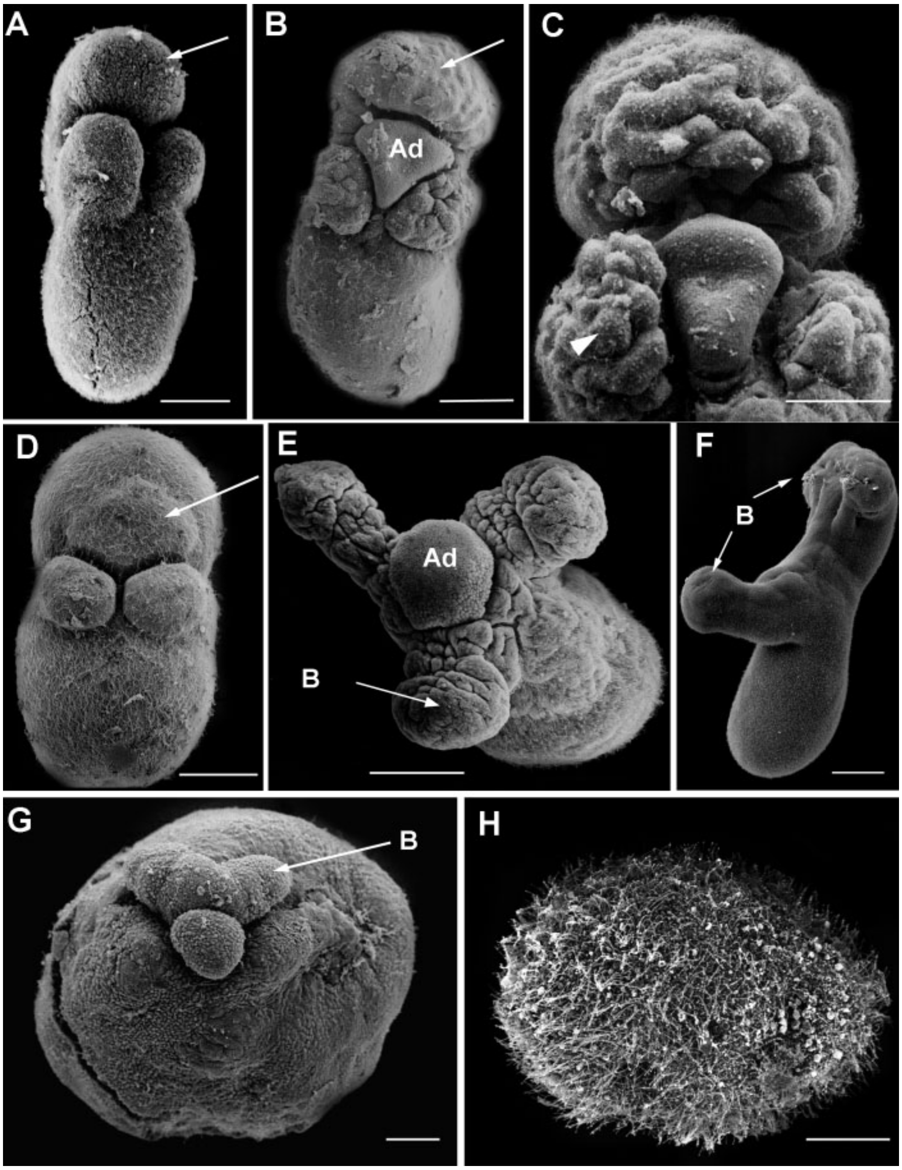

Fig. 4 Scanning electron microscopy of lecithotrophic asterinid larvae anterior end up. **A:** Brachiolaria larvae of *M. oriens* with hook-shaped anterior brachium (arrow). **B and C:** Brachiolaria of *M. gunnii* with the brachial surface covered in papillae (arrowhead). The anterior brachium (arrow) is a lobe-like structure. **D:** Brachiolaria of *Cryptasterina pentagona*. The anterior brachium (arrow) develops as a protrusion of the preoral lobe. **E and F:** Benthic larvae of *P. exigua* (E) and *Asterina gibossa* (F). **G and H:** Intragonadal larvae of *Parvulastra vivipara* (G) and *Parvulastra parvivipara* (H). Ad, adhesive disc; B, brachium. Scale bars: A–F = 100 μm; G = 20 μm. D, from Hart and colleagues (2003); F, courtesy D. Haesaerts; G, from Byrne and Cerra (1996).

no longer used for benthic attachment. Reduced selection to maintain a functional attachment complex in *Parvulastra* has resulted in variable larval morphologies. Embryos (180–300 μm diameter/length) swim out of dissected gonads. They range in shape from oval to pear or peanut-shape and only a few of these have identifiable brachiolaria features (Figs. 3G and 4G and H). Despite the unusual variety of larval forms, development proceeds to a normal juvenile. In *Parvulastra parvivipara* some embryos appear to metamorphose after gastrulation, indicating that this species may be evolving complete direct development. The suggestion from the phylogeny (Fig. 1) that the viviparous *Parvulastra* had a *P. exigua*-like ancestor is supported by the structure of the vestigial brachiolaria of *Parvulastra vivipara* (Fig. 4F). These larvae have three brachia. They are equal in length and appear as a miniature version of the attachment complex of *P. exigua*, but lack an adhesive disc. Due to the reduction in maternal provisioning, the intragonadal juveniles of *Parvulastra* cannibalize their clutch-mates as a food source to support growth to term. The juveniles emerge from the parent's gonopore as large, near-sexually mature sea stars.

In contrast, intragonadal brooders in the genus *Cryptasterina* have large (400–440 μm diameter), strongly buoyant eggs and typical brachiolariae, similar to those of their congeners with planktonic lecithotrophy (Figs. 3D and 4D). The brachiolariae of these species are fully functional and develop *in vitro* to the juvenile stage independent of the parent. Development is fully supported by egg reserves and the progeny leave the parent as small juveniles.

Discussion

The phylogenetic tree in this study is similar to that produced by Waters and colleagues (2004) using the same parsimony methods, supporting the generic distinctions of O'Loughlin and Waters (2004). As in the previous studies (Hart and others 1997, 2004; Waters and others 2004), the Atlantic *Asterina* are placed as a sister clade to the Indo-Pacific asterinids by MP. The deeper generic relationships within the Asterinidae however are not resolved. Our understanding of the molecular phylogenetics of the Asterinidae remains preliminary until sequence data become available for a broader suite of taxa. Internal nodes were found to have low bootstrap values (<50%), leading to uncertainty about generic relationships. The MP and ML trees generated by Waters and colleagues (2004) shared this variability in internal node position. The position of *Parvulastra* basal to the other Pacific genera is different in the present study. The position of *Cryptasterina* as a distinct clade separate from *Aquilonastra* is also different in the present analysis and may be influenced by the addition of two more *Cryptasterina* species. It is not clear whether the contradictions identified in asterinid phylogeny are a product of taxon selection, rapid evolution of the CO1 gene, or a high degree of homoplasy. The analyses by Waters and colleagues (2004) included 37 species, while the present analysis of species with known life history data involved 28 species, 3 of which were not included in the earlier study.

Within the Asteroidea, the Asterinidae presents a variety of fertilization strategies, larval forms, and developmental habitats. With the assumption that planktotrophy is ancestral, for these sea stars, the phylogeny indicates that lecithotrophy has arisen many times, as is the case for other echinoderm groups (Emlet and others 1987; Wray 1996). Among the lineages examined here, lecithotrophy was more prevalent than planktotrophy, indicating a general selection toward this developmental mode in most asterinid clades. As noted for Australian temnopleurid echinoids (Jeffery and others 2003), however, the dominance of lecithotrophy in the Asterinidae may be influenced by the unidirectional nature of the switch to non-planktonic development and by the characteristic that non-planktotrophs can only produce descendants with non-feeding larvae.

The transition to planktonic lecithotrophy across all asterinid clades involved complete loss of the bipinnaria larva. Unlike that seen in some lecithotrophic echinoids and ophiuroids (Emlet 1995; Byrne, Emlet, and others 2001; Selvakumaraswamy and Byrne 2004), there are no remnants of the feeding larval stage (aside from the closed archenteron). There are no traces of the ciliated bands or the elaborate bipinnarial nervous system prompting the suggestion that the bipinnaria, as a developmental module, has been completely deleted from the ontogenetic program of the lecithotrophs (Byrne, Cisternas, and others 2001; Byrne and Cisternas 2002).

Differences in the buoyancy of the eggs and larvae within and among genera may reflect different selection for the location of fertilization, dispersal, and post-larval provisioning, among a range of factors that are likely to influence egg development (Byrne, Cerra, and others 1999; Byrne and Cerra 2000; Styan and others 2005). In particular, there seems to be a fine-tuning in lipid composition of the eggs with respect to developmental habitat (Villinski and others 2002). Some clades of planktonic lecithotrophs have distinct egg traits. *Aquilonastra* and *Cryptasterina* species have buoyant eggs while *Meridiastra* species have eggs of variable buoyancy. *Meridiastra* is also characterized by atypical syncytial cleavage, the presence of which is suggested to be influenced by phylogenetic history (Cerra and Byrne 2004).

With numerous independent origins for planktonic lecithotrophy in the Asterinidae, it is not surprising that brachiolar anatomy and microstructure differ among clades. The brachiolariae of *Meridiastra* species with a hook-shaped anterior brachium can be distinguished from those of *Cryptasterina* and *Aquilonastra* with a lobe-like anterior brachium. Interestingly, the most derived benthic and intragonadal developers have strikingly different larval forms. The tripod larva of *Parvulastra* and *Aquilonastra* contrasts with the bilobed sole-shaped larva of the two *Asterina* species (MacBride 1896; Haesaerts and others 2006). Similarly, the vestigial intragonadal brachiolaria of *Parvulastra* contrasts with the functional intragonadal brachiolaria of *Cryptasterina*.

While the transition from planktotrophic to lecithotrophic planktonic development appears similar across the asterinid clades, we do not have good understanding of the pathway(s) involved in benthic lecithotrophy and evolution of larvae with a tripod or bilobed attachment complex. The benthic tripod larvae of *P. exigua* and *A. minor* are strikingly similar to the benthic larvae of the asteriid, *Leptasterias hexactis* (Chia 1968), an example of convergent phenotypes in unrelated taxa. This larval form results from hypertrophic growth of the lateral brachia (Byrne 1995). The relationships between the bilobed attachment complex of *Asterina* and the three brachia that would have been present in the ancestral-type brachiolaria are not known. Interestingly, a small proportion (<1%) of *A. gibbosa* larvae develop three brachia, providing a link to the ancestral state (Haesaerts and others 2006). The large brachium may have originated from fusion of the two lateral brachia, although histology indicates that the large brachium of *A. gibbosa* has a single coelomic compartment (MacBride 1896). Detailed microscopic examination of the developing attachment complex of the benthic larvae of *Asterina* species may indicate how its bilobed form relates to the three-brachium ancestral state.

For *Aquilonastra*, the phylogeny potentially provides evidence of a life history transformation series, from planktonic feeding to planktonic non-feeding to the benthic non-feeding mode of development. All three modes of development are clustered in *Aquilonastra*, with *A. minor* being a terminal taxon. The position of *P. regularis*, the planktotroph, at the base of this clade, however, is weakly supported in the phylogeny. A brooding species is yet to be found in *Aquilonastra*, although this would be expected from the presence of brooders in the other genera that have species that develop in benthic egg masses (*Asterina*, *Parvulastra*).

In the Asteroidea, intragonadal brooding is known for only two asterinid taxa, *Parvulastra* and *Cryptasterina*. This most derived life history is associated with some unusual features including life in the high intertidal zone, diminutive size, and restricted distributions (Byrne 1996; Byrne and Cerra 1996; Byrne, Cerra, Hart, and others 1999; Byrne and others 2003). Intragonadal development has arisen three times, once in *Parvulastra* and twice in *Cryptasterina* (Hart and others 1997, 2003). For these species the phylogeny provides a good understanding of the pathways involved in evolution of development. *P. vivipara* and *P. parvivipara* appear to have had an ancestral *P. exigua*-like species that developed in benthic egg masses (Byrne 1995). This is supported by the structure of the vestigial brachiolariae possessing three miniature brachia that are equal in length. The ultrastructure and cytoplasmic contents of the reduced egg of *P. vivipara* and *P. parvivipara* are also similar to the ovum of *P. exigua* (Byrne, Cerra, and others 1999). The transition from benthic lecithotrophy to brooding is suggested to be the likely pathway involved in evolution of intragonadal development (Strathmann and others 1984). In contrast, evolution of intragonadal development in the three *Cryptasterina* species involved an ancestral form with a planktonic non-feeding brachiolaria (Byrne and others 2003; Hart and others 2003, 2004; Byrne 2005). This suggestion is supported by the presence of a functional intragonadal brachiolaria and a highly buoyant lipid-rich egg similar to those of congeners with a planktonic stage (Byrne, Cerra, and others 1999; Byrne and Cerra 2000; Byrne 2005). The larvae of the brooding *Cryptasterina* species are identical to those of their congeners with planktonic development (Byrne and others 2003; Byrne 2005).

This comparative approach to investigation of life history diversity within a suite of closely related asterinids has allowed unraveling of some of the complexity of developmental evolution. Some indications of transformation series in life history evolution are present in some clades but not others. Further phylogenetic analyses and increased taxonomic sampling are needed to assess evolutionary pathways of life history change in the Asterinidae (Keever and others, in progress). As we assimilate more information for asterinid species, we are gaining a greater understanding of life history evolution in these sea stars. The Asterinidae is a species-rich cosmopolitan sea star family and more species will be discovered as morphospecies complexes are divided into their individual lineages. Like that noted for temnopleurid sea urchins (Jeffery and Emlet 2003; Jeffrey and others 2003), southern Australia has been a hot spot for evolution of lecithotrophy in the Asterinidae. Northern Australia and the Indonesian Archipelago also appear to have a number of asterinids with lecithotrophic development and many of these are cryptic species. Indeed, the new intragonadal brooder (*Cryptasterina* new sp. #1) and benthic developer (*Aquilonastra* new sp.) were recently discovered on the Great Barrier Reef. Around the Southern Ocean, the distribution of asterinids is producing interesting insights into the biogeography of the region (Fell 1962; Waters and Roy 2004; Colgan and others 2005; Hart and others 2006).

There have been multiple transitions and pathways involved with the switch to different modes of lecithotrophic development in the Asterinidae. Life history traits appear to have evolved freely, contrary to previous notions of conservatism in early development (Raff 1996; Cerra and Byrne 2004). Thus far, the species known to have planktotrophic development ($n = 6$) are far outnumbered by the lecithotrophs ($n = 25$).

The rationale for the selection of lecithotrophy is not known but this life history mode appears more prevalent in the Asterinidae compared with other asteroid families.

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