

Reproduction and Larval Morphology of Broadcasting and Viviparous Species in the *Cryptasterina* Species Complex

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Abstract. The *Cryptasterina* group of asterinid sea stars in Australasia comprises cryptic species with derived life histories. *C. pentagona* and *C. hystera* have planktonic and intragonadal larvae, respectively. *C. pentagona* has the gonochoric, free-spawning mode of reproduction with a planktonic lecithotrophic brachiolaria larva. *C. hystera* is hermaphroditic with an intragonadal lecithotrophic brachiolaria, and the juveniles emerge through the gonopore. Both species have large lipid-rich buoyant eggs and well-developed brachiolariae. Early juveniles are sustained by maternal nutrients for several weeks while the digestive tract develops. *C. hystera* was reared *in vitro* through metamorphosis. Its brachiolariae exhibited the benthic exploration and settlement behavior typical of planktonic larvae, and they attached to the substratum with their brachiolar complex. These behaviors are unlikely to be used in the intragonadal environment. The presence of a buoyant egg and functional brachiolaria larva would not be expected in an intragonadal brooder and indicate the potential for life-history reversal to a planktonic existence. Life-history traits of species in the *Cryptasterina* group are compared with those of other asterinids in the genus *Patiriella* with viviparous development. Modifications of life-history traits and pathways associated with evolution of viviparity in the Asterinidae are assessed, and the presence of convergent adaptations and clade-specific features associated with this unusual mode of parental care are examined.

Introduction

Speciation in marine invertebrate taxa is strongly influenced by the evolution of life-history traits. Evolutionary changes that influence speciation include modifications to gamete-binding proteins, oogenesis, larval nutrition (planktotrophic, lecithotrophic), and location (planktonic, benthic) of development (Strathmann, 1985; Reid, 1990; Palumbi, 1992; Vacquier *et al.*, 1995; Byrne *et al.*, 1999, 2003; Duda and Palumbi, 1999; ÓFoighil and Taylor, 2000; Villinski *et al.*, 2002). In a large number of these cases, the combination of rapid and diverse evolution of larval forms and stasis in adult stages has resulted in congeneric species with markedly different larval phenotypes and habitats but similar adult phenotypes and ecologies. This decoupling of larval and adult morphological evolution suggests that critical examination of suspected morphospecies will reveal undiscovered marine biodiversity. Molecular and developmental studies have shown that many problematic taxa include a suite of cryptic species (Reid, 1990; Knowlton, 1993; Degnan and Lavin, 1995; ÓFoighil and Smith, 1995; Arndt *et al.*, 1996; Huber *et al.*, 2000). Application of the comparative approach has made many of these taxa important models for the investigation of processes underlying evolution and development, and speciation in the sea (Hart *et al.*, 1997; Degnan and Lavin, 1995; Huber *et al.*, 2000).

The potential for species divergence through life-history evolution is common in some marine invertebrate taxa but rare in other, even closely related, taxa. Genera in which speciation is associated with evolution of development are found among gastropods (*Littorina*, *Conus*), clams (*Lasaea*), soft corals (*Alcyonium*), asteroids (*Asterina*, *Patiriella*), echinoids (*Heliocidaris*) and ascidians (*Molgula*) (Reid, 1990; ÓFoighil and Smith, 1995; Raff, 1996; Hart *et*

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al., 1997; Duda and Palumbi, 1999; Huber *et al.*, 2000; McFadden *et al.*, 2001). Why some taxa are prone to developmental evolution and not others is not known. In the Asteroidea, the Asterinidae is a species-rich family comprising species that share derived forms of reproduction, larval morphology, and brood protection (Byrne and Cerra, 1996; Byrne *et al.*, 1999b). Molecular phylogenetic analyses of these sea stars revealed many examples of convergence in which derived life-history traits have evolved through independent pathways (Hart *et al.*, 1997, 2003).

In temperate Australia, the *Patiriella exigua* species group includes three species: one benthic egg layer and two viviparous lineages (Dartnall, 1969, 1971; Keough and Dartnall, 1978). Until the observation of live birth, the viviparous species were considered to be morphs of *P. exigua*. Detailed analysis of mtDNA sequences revealed the presence of a second cryptic group of asterinids in the genus *Cryptasterina*, which occurs throughout Australasia (Hart *et al.*, 2003; Dartnall *et al.*, 2003). These sea stars, formerly in the *Patiriella pseudoexigua* species complex (Dartnall, 1971; Rowe and Gates, 1995), have been reassigned to *Cryptasterina* in a recent taxonomic review (Dartnall *et al.*, 2003). One lineage, *C. pentagona*, (formerly *P. pseudoexigua*) occurs in Queensland. A second lineage, *Cryptasterina* n. sp. (also formerly known as *P. pseudoexigua*) occurs in Wanlitung, Taiwan, and its planktonic lecithotrophic life history is well-documented (Chen and Chen, 1992). The viviparous species described by Hayashi (1977), *Patiriella pseudoexigua pacifica*, has been reassigned to *C. pacifica* (Dartnall *et al.*, 2003).

On the basis of the position of *C. pentagona* in the phylogenetic tree, nested between broadcasting and brooding species (Hart *et al.*, 1997), and in light of the very broad geographic range of this nominal species, it appeared likely that Australian morphs of *C. pentagona* would have interesting modes of development. A recent molecular study revealed the relationships among four lineages of this taxon recently called *P. pseudoexigua* (Hart *et al.*, 2003). In Queensland these lineages comprise two species with different life histories (Hart *et al.*, 2003). One of these species, *C. hystera*, is a recently described intragonadal brooder (Dartnall *et al.*, 2003). In this study we examined populations of *Cryptasterina* from the original type locality in Queensland and elsewhere along the coast to document details of their reproduction and development. We compared the life history traits of *C. hystera* to those of other viviparous asterinids in the genus *Patiriella* and closely related broadcasting species to assess the changes associated with the evolution of viviparity. This life history is at the extreme end of the broadcast-brooding modes of propagation in the Asteroidea. The pathways in the evolution of viviparity in the Asterinidae are assessed, and the potential for convergent adaptations in species with this unusual mode of parental care is examined.

Materials and Methods

Cryptasterina pentagona was collected from five locations along the Queensland coast (Fig. 1) at irregular intervals between 1996 and 2002. This included several sites in North Queensland (10/00; 11/00; 10/02), including Airlie Beach (20°30'S; 148°45'E); Rowes Bay, Townsville (19°15'S; 146°50'E); and Bingil Bay, Mission Beach (17°50'S; 146°06'E). *C. hystera* was collected from Statue Bay (23°15'S; 150°45'E) in central Queensland (8/96; 2/96; 9/97; 10/99). The samples were used to assess the condition of the gonads and preserve samples for histology. The type locality for *P. pseudoexigua* is Airlie Beach (Dartnall, 1971). In October 2002, the gonads of specimens from Airlie Beach and several sites in Bowen (20°1'S; 148°16'E)—Dalrymple Point, Rose Bay, and Murrays Bay (Fig. 1)—were examined and processed for histology. Isolated ovaries of females from these sites and from Rowes Bay, Townsville, were induced to spawn through the use of

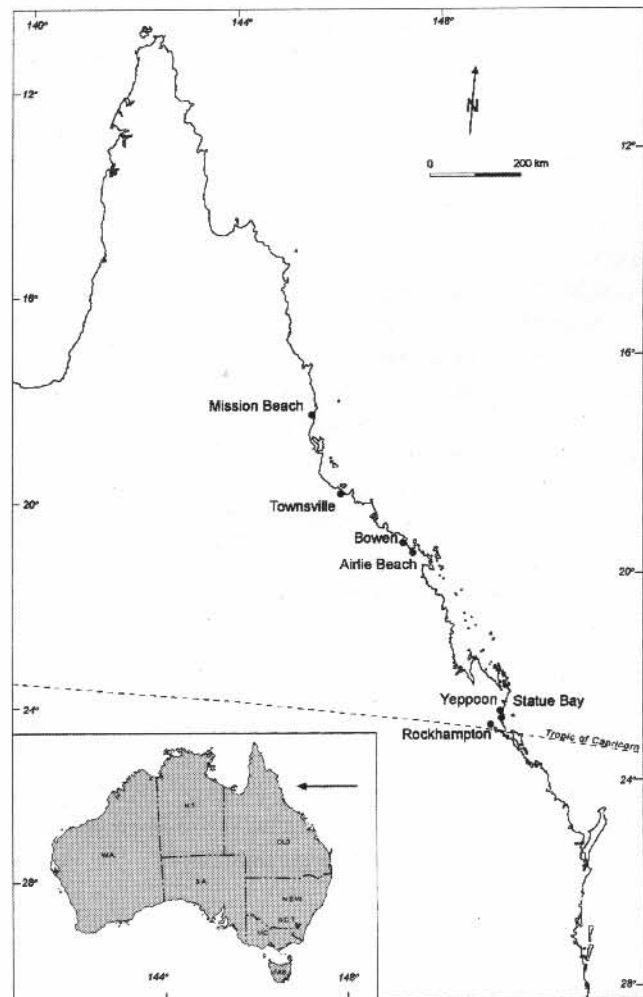


Figure 1. Map of Queensland showing sample locations and current known distributions of *Cryptasterina pentagona* and *C. hystera*.

the ovulatory hormone 1-methyladenine in filtered seawater (10^{-5} M in filtered seawater [FSW]). The eggs were fertilized with sperm removed from the testes, and the larvae were reared in FSW at 23–25 °C. Settlement substrata including glass slides aged in seawater and pieces of coralline algae were introduced into some culture dishes containing competent larvae. The gonads of the Statue Bay sea stars contained embryos. These were removed and reared *in vitro* in FSW (1.0 μ m) at 22 °C through metamorphosis.

For histology, the gonads were fixed in Bouin's fluid for 24 h, rinsed in distilled water, dehydrated in graded ethanols, and embedded in paraffin. Serial sections were stained with hematoxylin and eosin. For scanning electron microscopy, larvae and juveniles were fixed for 1 h in 2.5% glutaraldehyde in 0.45 μ m FSW. Use of a secondary fixative was found to be unnecessary (Byrne, pers. obs.). After fixation, the specimens were dehydrated, critical-point-dried, and viewed with a JEOL JSM-35C scanning electron microscope.

Results

Our field survey of life-history traits in six populations of *Cryptasterina* provided data on the distribution of two lineages, one broadcasting species and one intragonadal brooder. *C. pentagona* from the type locality Airlie Beach (Fig. 1) was found to be a free-spawner with a short-lived planktonic larva. This species was found from Airlie Beach to Mission Beach in north Queensland (Fig. 1). Mission Beach is near the northern limit of the distribution of *C. pentagona* in Queensland (A.J. Dartnall, James Cook University, pers. comm.). This species was located under rocks high in the intertidal zone which dry out at low tide. Reports of *C. pentagona* south of Airlie Beach will have to be checked in light of the discovery of *C. hystera* in Statue Bay, Central Queensland (Fig. 1). *C. hystera* is an intragonadal brooder. Molecular data indicate that this new species also occurs in Yeppoon (Hart *et al.*, 1997). It occurs high in the intertidal under small rocks in mangrove habitats. The distribution of the two species may overlap south of Airlie Beach. A thorough search of the sites used in this study indicated that the two species do not co-occur in north Queensland.

Planktonic developer

C. pentagona is a dioecious free-spawner with a planktonic lecithotrophic brachiolaria larva (Figs. 2A, B, D; 3A–C). Ovaries of specimens collected in October and November 2000 and October 2002 were gravid (Fig. 2A). They contained large eggs dominated by large lipid droplets. Spawning eggs (413 μ m diameter; SE = 6.4 μ m, n = 20) were an amber-gold color. They were positively buoyant and floated to the surface as they emerged from the gonopore. Mature testes were typical of asteroids, having a layer

of spermatogenic columns along the germinal epithelium and a lumen filled with sperm (Fig. 2B).

Development of *C. pentagona* through the stages of holoblastic radial cleavage, early blastula, wrinkled blastula, and gastrula was typical of development in lecithotrophic sea stars (Byrne, 1995). At 23 °C the early larvae (2 days) had a large preoral lobe and developing larval arms (brachia) (Fig. 3A). The central brachium developed as a bulge that emerged from the preoral lobe, flanked posteriorly on either side by two lateral brachia (Figs. 2D, 3B). Advanced brachiolariae (5 days) had a prominent brachiolar complex comprising three brachia and a central adhesive disc (Fig. 3C). Early larvae swam at the surface propelled by their cover of cilia (Fig. 3A, B, F); but as the juvenile rudiment developed in the posterior region, they swam at the bottom of the culture dishes, anterior end up. An extracellular matrix with meshlike holes covered the surface of the larvae and juveniles (Fig. 3F). This feature was most evident over the brachia of the larvae and on the oral surface and tube feet of the juveniles. Advanced larvae adhered to surfaces using their brachia. As they explored the substratum, they flexed dorsally to bring the adhesive disc to the surface. Once they were committed to metamorphose, permanent benthic attachment was achieved by the adhesive disc assisted by the brachia. The larvae attached to a range of substrata including the walls of the culture dishes, although they appeared to favor coralline algae (Fig. 2F). Most larvae metamorphosed regardless of whether a specific settlement substratum was introduced into the culture dishes. Many of them settled on the walls of their containers. Newly metamorphosed juveniles (620 μ m diameter; SE = 11.8, n = 15) had two pairs of tube feet in each radius (Fig. 3D, E). They were a dark amber color, indicating the presence of extensive maternal nutritive reserves. The mouth did not open for 3 weeks after settlement (Fig. 3D). Development to the settled juvenile stage took 9 days at 23 °C, while at ambient temperatures (30 °C) in Queensland, development was completed in 6 days (Dartnall, pers. comm.).

Intragonadal developer

C. hystera had ovotestes that were a mosaic of oogenic and spermatogenic areas (Fig. 2C). Gravid specimens were present in all the samples obtained from September to November, indicating that the reproductive period lasts at least 3 months. In December 1999, the gonads contained juveniles and few gametes. The amount of spermatogenic tissue in the gonads varied among individuals (n = 20). In some specimens, sperm was only detectable histologically; in others, white testicular regions of the gonad were evident by direct examination. Like those of *C. pentagona*, the eggs were large (440 μ m diameter; SE = 6.0 μ m, n = 8) and contained abundant lipid droplets. They floated to the sur-

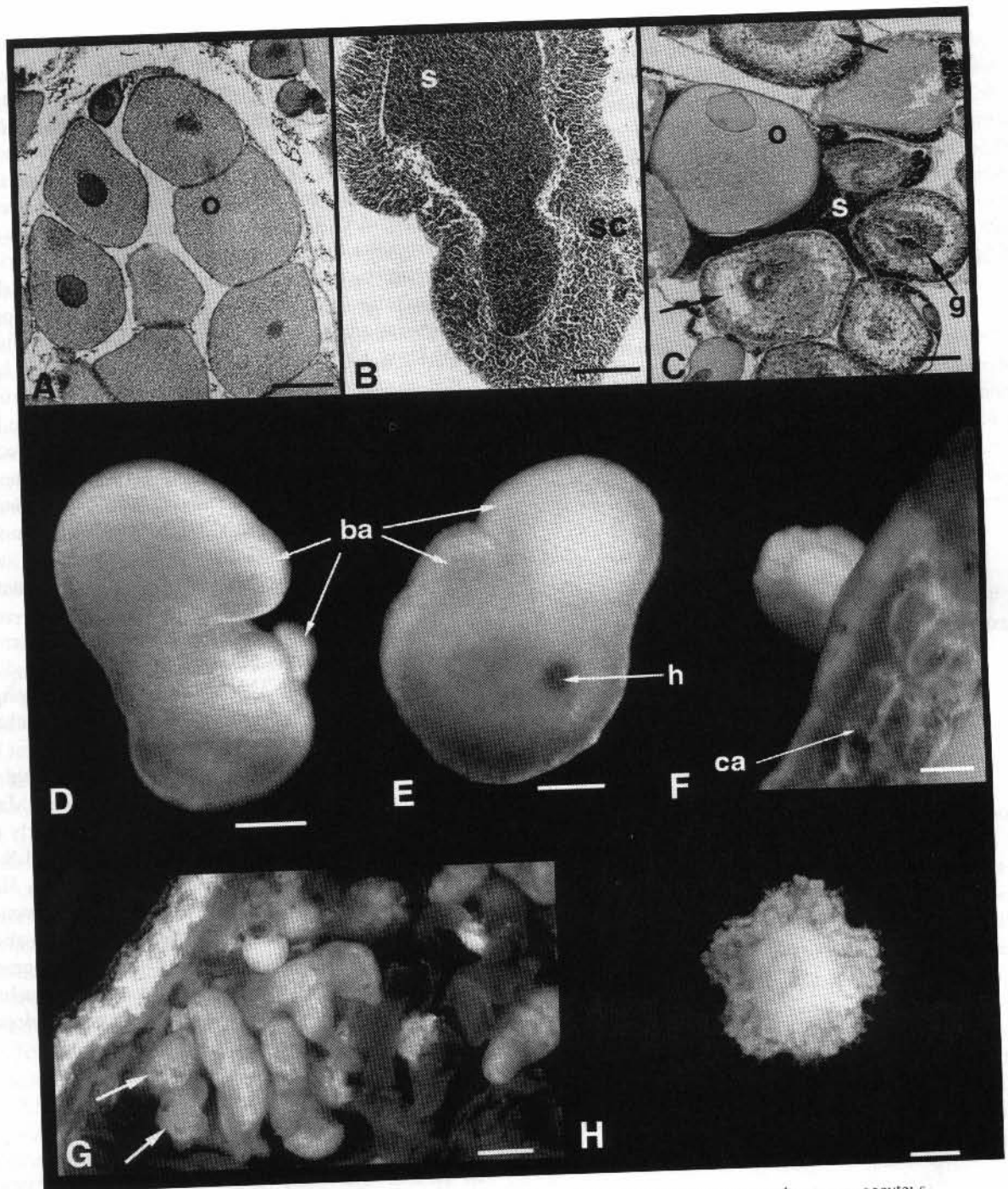


Figure 2. Histology and light microscopy. (A, B) *Cryptasterina pentagona* ovaries and testes. o, oocyte; s, spermatozoa; sc, spermatocyte columns. (C) *C. hystera*. The ovotestis contains lipid-rich eggs (o), sperm (s), and developing embryos (arrows); g, gastrula. (D, E) Brachiolaria larvae of *C. pentagona* and *C. hystera* respectively. ba, brachia; h, hydropore. (F) Metamorphosing juvenile *C. pentagona* on coralline algae (ca). (G) Dissected *C. pentagona* showing juveniles (arrows) in gonad. (H) Newly released *C. hystera*. Scales: A–E = 100 μm ; F, H = 200 μm ; G = 500 μm .

face when removed from the gonad and were gold-orange, with a dark vegetal pole.

Developing embryos and larvae were interspersed with gametes in the gonad (Fig. 2C, G). Embryos removed from

the gonad at the early blastula stage developed independently of the parent through the wrinkled blastula and gastrula stages into a planktonic highly buoyant brachiolaria. The developing brachia appeared as three bulges (Fig.

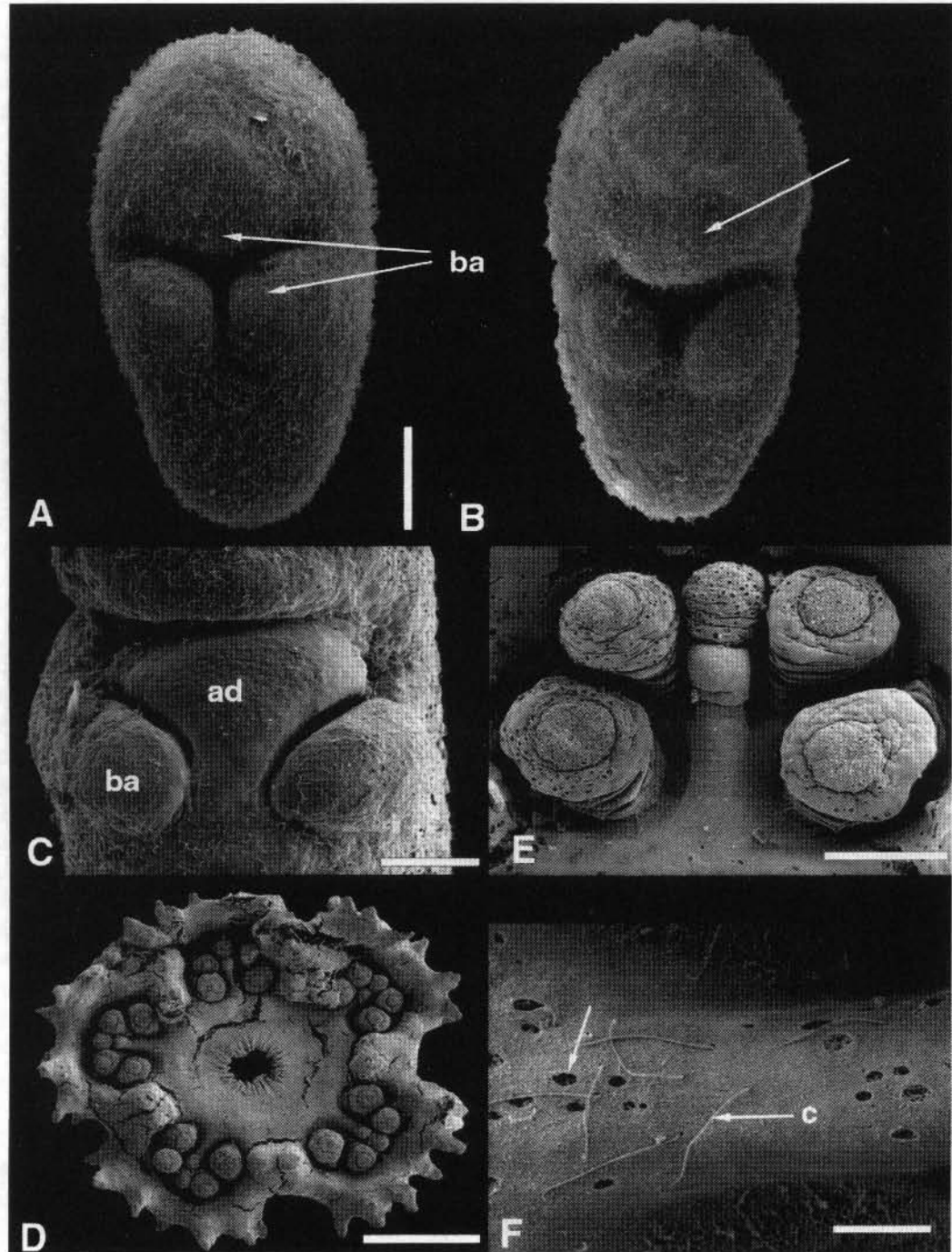


Figure 3. Scanning electron microscopy, *Cryptasterina pentagona*. (A, B) Brachiolaria larvae have a uniform cover of cilia. The central brachium (arrow) develops as a protrusion of the preoral lobe. (C) Advanced larva with a well-developed adhesive disc (ad) at the base of the brachia (ba). (D, E) Recently metamorphosed juvenile with two pairs of tube feet in each radius and with a mouth opening. (F) Detail of cilia (c) and meshlike matrix on larval surface. Scales: A, B = 100 μ m; C, E = 50 μ m; F = 4 μ m.

and independent brachiolaria and brachiolaria (Fig. 4A), and the adhesive disc developed between the arms (not illustrated). As in *C. pentagona*, advanced larvae had a well-developed preoral lobe from which the central brachium emerged as a bulge-like protrusion (Fig. 4B, C). They

swam anterior end up with their ciliary cover (Fig. 4F). Advanced larvae (10 days) had a well-developed brachiolar complex which was used for benthic attachment. They exhibited typical settlement behavior while exploring the

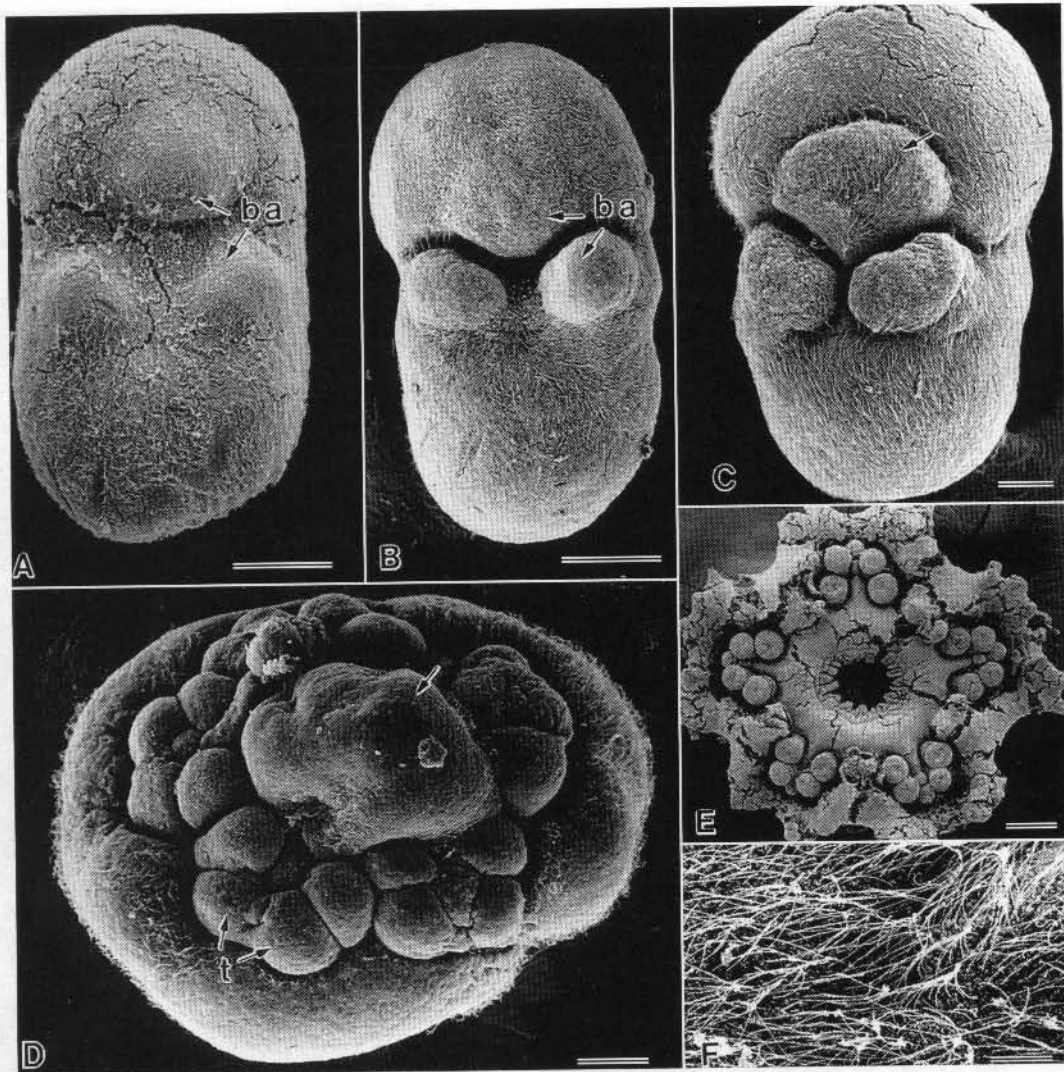


Figure 4. Scanning electron microscopy, *Cryptasterina hystera*. (A, B) Early larvae with developing brachia (ba). (C) Advanced larva. The central brachium (arrow) develops as a posterior protrusion of the preoral lobe. (D) Metamorphosing larva with resorbing larval body (arrow) and developing tube feet (t). (E) Recently metamorphosed juvenile with two pairs of podia in each radius and with a mouth opening. (F) Detail of cilia on larval surface. Scales: A, B, E = 100 μm ; C, D = 50 μm ; F = 12 μm .

substratum and adhered to the surface of the culture dishes either with the tips of the brachia or by flexing the body to attach the adhesive disc. The juvenile rudiment developed in the posterior region as the larval body was resorbed (Fig. 4D). Development *in vitro* to the juvenile stage took 16 days. Newly settled juveniles had a dark amber pigment due to the presence of maternal nutritive reserves. It took 3 weeks for the mouth opening to develop, and by this time maternal reserves were no longer evident (Fig. 4E). Three-week-old juveniles had a well-developed skeleton.

In aquaria, juveniles (800 μm diameter, SE = 6.3, $n = 10$) with two pairs of tube feet in each radius emerged from the gonopore on the aboral surface of the adults (Fig. 2H). These juveniles had a mouth opening, a functional digestive

tract, and a well-developed skeleton. Newly released juveniles were white due to the color of the skeleton, and they appeared to lack residual maternal nutrients.

Discussion

Recent discoveries of cryptic species in a range of taxa have been facilitated by investigation of developmental evolution and molecular phylogeny (Reid, 1990; Degnan and Lavin, 1995; ÓFoighil and Smith, 1995; Williams, 2000; Flowers and Foltz, 2001; McFadden *et al.*, 2001). Observations of juvenile birth resulted in the description of new viviparous *Patiriella* in the *P. exigua* group (Dartnall, 1969, 1971; Keough and Dartnall, 1978), and our investi-

gation of cryptic biodiversity in *Cryptasterina* was prompted by the results of molecular phylogeny (Hart *et al.*, 1997). The Asterinidae are a taxonomically difficult group and detection of the cryptic species investigated here would have been difficult with traditional taxonomy because adult forms appear very similar even to taxonomic experts (Dartnall, 1971; Rowe and Gates, 1995). Once specific status has been determined, however, close examination of cryptic species may reveal the presence of diagnostic morphological traits (Dartnall, pers. comm.). Indeed, life-history and molecular data have guided taxonomic effort in the discovery and description of several cryptic *Patiriella* species in New Zealand and Australia (O'Loughlin *et al.*, 2002; Dartnall, pers. comm.). Molecular data revealed that *C. pentagona*, the broadcasting species, occurs from the type locality Airlie Beach north to Townsville (Fig. 5; Hart *et al.*, 2003). *C. hystera* is known only from two locations, about 10 km apart. An extremely limited distribution is also characteristic of the viviparous *Patiriella* (Byrne *et al.*, 1999b). A survey of mangrove habitats along the central Queensland coast will be required to determine the distribution of *C. hystera*. The nominal taxon *C. pentagona* occurs through Asia (Marsh, 1977; VandenSpiegel *et al.*, 1998), and it is likely that other divergent lineages will be found (Dartnall *et al.*, 2003). Other widely distributed asterinids such as *Patiriella exigua*, which occurs from South Africa to Australia, also appear to be a suite of cryptic species (Dartnall, pers. comm.).

The life-history traits and phylogenetic relationships of species in the *Cryptasterina pentagona* group and the *Patiriella exigua* group are shown in Table 1 and Figure 5. The gonochoric, free-spawning mode of reproduction seen in *C. pentagona* and *Cryptasterina* n. sp. is ancestral for the Echinodermata, while acquisition of hermaphroditism, a derived character, is exhibited by most echinoderms that brood their young (Strathmann *et al.*, 1984; Byrne, 1991, 1999; Hendler, 1991). Like those of the other viviparous

species (Table 1), the gonads of *C. hystera* were ovotestes. This indicates the potential for self-fertilization, as appears to be the case for *P. vivipara* (Byrne, 1996). The amount of sperm in the gonads of *C. hystera* is more than sufficient to fertilize all the eggs produced, and so it is likely that some individuals release sperm. For out-crossing to occur, the sperm would have to gain access to eggs by swimming through the gonopore. A genetic study is required to determine if progeny in the gonads of the viviparous *Cryptasterina* and *Patiriella* are full siblings or half siblings. The diversity of the fertilization biology in these asterinids with complete out-crossing in the free-spawners, partial self-fertilization in the benthic egg layers, and potential for selfing in viviparous forms provides a useful model in which to investigate the relationships between the evolution of mating systems and the genetic structure of sea star populations (Byrne, 1995, 1996).

As characteristic of echinoderms, the evolution of lecithotrophy in *Cryptasterina* species involved acquisition of a large egg (Table 1). The increase in egg size from what would have been an ancestral form with a small egg and planktotrophic development is considered to have been necessary to sustain development without feeding (Mortensen, 1921; Strathmann, 1978; Emler *et al.*, 1987). The presence of extensive nutritive reserves in newly metamorphosed juveniles, however, shows that a considerable portion of maternal reserves in the eggs of the two *Cryptasterina* species investigated here is allocated to the perimetamorphic postlarval period. A substantial proportion of the maternal provisions in their large eggs is stored through larval development to support development of the postlarval stages, a feature seen in other lecithotrophic echinoderms (Emler and Hoegh-Guldberg, 1997; Hoegh-Guldberg and Emler, 1997; Byrne *et al.*, 1999a, 2003; Villinski *et al.*, 2002). In contrast, the small eggs (135–150 μm diameter) of *P. vivipara* and *P. parvivipara* are similar in size to those (150 μm diameter) of their planktotrophic congener *P.*

Table 1

Life-history traits of the Cryptasterina pentagona and Patiriella exigua species groups

Species*	Location†	Gonad structure	Egg size (diam in μm)	Larval habitat
<i>C. pentagona</i> group				
<i>C. pentagona</i>	Qld	Dioecious	413	Planktonic
<i>C. hystera</i>	Qld	Hermaphrodite	440	Intragonadal
<i>C. pacifica</i> (1)	Japan	Hermaphrodite	450	Intragonadal
<i>C. n. sp.</i> (2)	Taiwan	Dioecious	320	Planktonic
<i>P. exigua</i> group				
<i>P. exigua</i> (3)	NSW, Tas, SA	Dioecious	360	Benthic
<i>P. vivipara</i> (4)	Tas	Hermaphrodite	150	Intragonadal
<i>P. parvivipara</i> (4)	SA	Hermaphrodite	135	Intragonadal

* (1) Komatsu *et al.* (1990); (2) Chen and Chen (1992); (3) Byrne (1995); (4) Byrne (1996).

† NSW, New South Wales; Qld, Queensland; SA, South Australia; Tas, Tasmania.

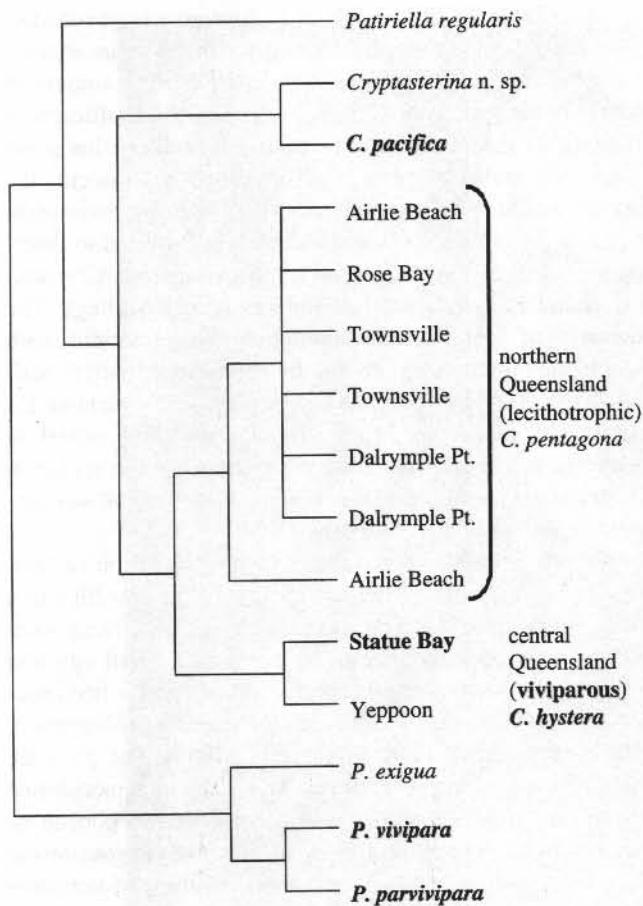


Figure 5. Phylogenetic tree based on branch-and-branch searching of mtDNA sequences (COI and 5 tRNA genes) from the *Cryptasterina pentagona* and *Patiriella exigua* groups (after Hart *et al.*, 1997, 2003). Species in bold are known to be viviparous. Bootstrapping produced strong support ($\geq 92\%$) for monophyly of the six northern Queensland lineages, for two southern Queensland lineages, and for all these lineages as a clade separate from *P. regularis*. The Yeppoon specimen was from a museum collection and the presence of intragonadal embryos could not be confirmed.

regularis and represent a secondary reduction in size (Byrne and Cerra, 1996; Hart *et al.*, 1997). The eggs of *P. vivipara* and *P. parvivipara* support intragonadal lecithotrophic development to a very small postlarva (200–300 μm diameter), indicating that the maternal reserves in these eggs may be near the limit required to support development through metamorphosis in the absence of feeding (Byrne, 1996).

The larvae and juveniles of *C. pentagona* have a meshlike extracellular matrix covering regions of the body, similar to that described for *P. regularis* (Byrne and Barker, 1991). Preservation of this matrix depends on fixation method, suggesting it may be an artifact (Byrne, pers. obs.). Alternatively, its presence in some regions of larvae and juveniles such as the brachiolar arms and oral surface indicates that the extracellular matrix may have regional differences.

Newly settled juveniles of *C. pentagona* (612 μm diam-

eter) and *C. hystera* (600 μm diameter) reared *in vitro* were supported by maternal nutrients for several weeks until the digestive tract became functional and juveniles could feed. Juveniles of *C. hystera* (2–3 weeks old, 800 μm diameter) left the parent with a functional gut. Similarly, newly metamorphosed juveniles of *C. pacifica* (650 μm diameter) emerge from the gonopore (900 μm diameter) with a functional gut (Komatsu *et al.*, 1990). The juveniles of *P. vivipara* and *P. parvivipara* continue their growth in the gonads to become the largest recruiting juveniles (1.0–5.0 mm diameter) known for the Asteroidea (Byrne, 1996). They spend up to a year in the gonads preying on their siblings, an unconventional source of maternal nutrients. There may be selection for extended brood care in the viviparous species. Intragonadal brooding of progeny through the vulnerable early postlarval stages and their release at a large size undoubtedly conveys a survival advantage for the juveniles. Mortality of the early settlement stages of marine invertebrates is usually high (Gosselin and Qian, 1997). Interestingly, the gonads of *C. hystera* contained a few large juveniles (1–2 mm diameter), indicating that brood cannibalism occasionally occurs in this species (Byrne, pers. obs.).

The eggs of species in the *Cryptasterina* group have conspicuous lipid reserves, a feature characteristic of echinoderms with planktonic lecithotrophy (Emlet *et al.*, 1987; Emlet and Hoegh-Guldberg, 1997; Hoegh-Guldberg and Emlet, 1997; Byrne *et al.*, 1999a, 2003; Villinski *et al.*, 2002). Their brachiolariae are also similar in appearance, with a prominent preoral lobe and a central brachium that develops as a bulge-like protrusion (Komatsu *et al.*, 1990). Possession of a buoyant egg and a functional larva in *C. hystera* and *C. pacifica* would not be expected in viviparous asterooids. These features and the morphological similarity of their larvae to those of congeners with planktonic development suggest that viviparity in these sea stars evolved through retention and fertilization of a large egg by a *C. pentagona*-like ancestor. This suggestion is supported by molecular phylogenetic data (Fig. 5; Hart *et al.*, 2003).

The intragonadal brachiolariae of *P. vivipara* and *P. parvivipara* are vestigial, unlike those of *C. hystera*. Their minute larvae have a reduced brachiolar complex comprising three small nonsticky protrusions that cannot function in attachment, and some embryos do not develop brachia at all. Intragonadal development in *P. vivipara* and *P. parvivipara* is thought to have evolved through a *P. exigua*-like ancestor that laid benthic egg masses and had highly modified benthic nondispersive larvae (Fig. 5; Byrne, 1995; Hart *et al.*, 1997). Evolution of viviparity through retention of eggs by an ancestor with benthic egg masses is suggested to have been a likely pathway for the acquisition of this form of brooding in asterinids (Strathmann *et al.*, 1984; Byrne, 1996).

Despite their intragonadal location, the larvae of *C. hys-*

tera exhibited exploratory settlement behavior and attached to the substratum with their brachia and adhesive disc prior to metamorphosis, in a manner typical of planktonic asteroid larvae. This behavior is unlikely to serve any function in the intragonadal environment. A reversal to a planktonic larva is readily envisaged for *C. hystera* and *C. pacifica*, a suggestion also made for *Pteraster tesselatus* (McEdward, 1992). These species could potentially use two modes of development, releasing some progeny as dispersive larvae and others as juveniles. By contrast, *P. vivipara* and *P. parvivipara* are committed to intragonadal development. A reversal to reacquire a large egg and functional larva appears unlikely for *P. vivipara* and *P. parvivipara*.

Intragonadal development is rare in the Echinodermata. Among asteroids, intragonadal development and live birth is known for only three genera, *Cryptasterina*, *Patiriella* (Table 1), and the aberrant *Xyloplax medusifformis* from the deep sea (Rowe *et al.*, 1987). Morphological and molecular evidence supports the conclusion that viviparity evolved independently three times in *Patiriella* and *Cryptasterina* (Fig. 5; Hart *et al.*, 1997, 2003). Parallel evolution of derived lecithotrophic life histories is common in echinoderms and is often associated with a suite of convergent phenotypes (Strathmann, 1985; Emler *et al.*, 1987; Wray, 1996; Hart *et al.*, 1997). For asterinids, some convergent adaptations associated with viviparity are evident in all brooding species, while other features follow phylogenetic lines (Table 1, Fig. 5). With respect to adult traits, convergence is seen in possession of ovotestes and the potential for self-fertilization in both *Cryptasterina* and *Patiriella*. Egg type and composition, however, is similar within these genera, but not between them. With respect to developmental phenotype, *Cryptasterina* and *Patiriella* differ in the presence of functional or nonfunctional larvae. Regardless of the pathways involved in evolution of viviparity, however, the probability of making the evolutionary switch to intragonadal development appears high in the Asterinidae. Selection for viviparity may be associated with colonization of marginal habitats along the upper fringe of the intertidal, a habitat not generally utilized by sea stars. Why this unusual form of parental care evolved in *Cryptasterina* and *Patiriella* and not in other asteroid taxa is not known.

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