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A new viviparous species of asterinid (Echinodermata, Asteroidea, Asterinidae) and a new genus to accommodate the species of pan-tropical exiguoid sea stars

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Abstract

This paper describes a new species of viviparous, intragonadal brooder of asterinid sea star and clarifies the identities of *Patiriella pseudoexigua* Dartnall 1971, the species *Patiriella pseudoexigua sensu* Chen and Chen (1992) and *Patiriella pseudoexigua pacifica* (Hayashi, 1977). The latter is raised to specific rank. Analysis of mitochondrial DNA supports the concept of a pan-tropical assemblage of species for which a new genus, *Cryptasterina*, is created. All species in *Cryptasterina* are morphologically similar and comprise species with planktonic, lecithotrophic, non-feeding larvae, and viviparous outlier species with limited distributions. The full diversity of this species diaspora remains to be resolved.

Key words: Echinodermata; Asteroidea; Asterinidae; *Cryptasterina* new genus; new species; new combination; cryptic species; developmental biology; viviparity; tropical

Introduction

The sea star family Asterinidae has two species-rich genera, *Asterina* and *Patiriella* (Rowe and Gates 1996). Based on molecular and morphological evidence, these genera are now considered to be paraphyletic (Hart et al. 1997). In comparison with other asteroids the Asterinidae appear particularly prone to rapid change in life history, a feature that has played a major role in species divergence (Dartnall 1969, 1971; Hart et al. 1997; Byrne et

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al. 1999). Within *Patiriella*, the "*exigua*" group (*sensu* Dartnall 1971) has the most diverse life histories known for marine invertebrates including larval development in the plankton, the benthos and in the gonads (Dartnall 1969, 1971; Byrne 1995; Byrne and Cerra 1996).

The morphologically most homogeneous set of species in the sea star genus *Patiriella* (Verrill 1913) as it is currently understood, comprises those belonging to the "exigua" group (*sensu* Dartnall 1971) and referred to in this paper as the exiguoids. The exiguoids are small (rarely exceeding 20 mm R) asterinid sea stars the adults of which are phenotypically similar and reproductively diverse (Byrne et al. 1999; Hart et al. 2003). They can be distinguished most readily from other *Patiriella* species by the aspinous adradial row of actinal plates which abut the adambulacral plates of the skeleton. However, the species are cryptic and often difficult to distinguish from each other by traditional morphological means which has caused some authors to question criteria that may be difficult to observe in preserved specimens (see Clark and Downey 1992: 178–181). We can only observe here that museum collections can only be a reflection of the dynamics of species in their habitats. It is apparent also that poor collection data exacerbate this situation. For example at least some of the viviparous exiguoid species detected since 1969 are distinctively coloured in life (see Fig. 3).

Molecular phylogenetic analysis has demonstrated that the genus *Patiriella* is not monophyletic (Hart et al. 1997, and Fig. 1 herein) and that the tropical species group which contains viviparous brooding species and free spawning species all with large eggs and lecithotrophic development is distinct from the exiguoid species from SE Australia which exhibit viviparity and benthic development in egg masses (Byrne et al. 2003, Hart et al. 2003).

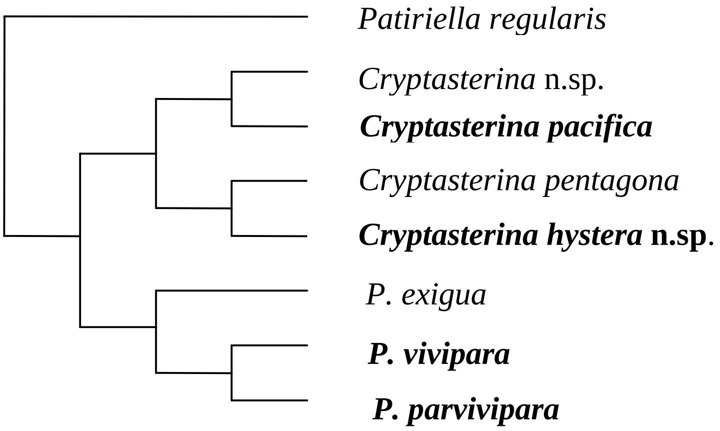

FIGURE 1. Molecular phylogeny of the 'exigua' group based on mtDNA sequence (updated from Hart et al. 1997) showing the pan-tropical species of *Cryptasterina* new genus. Viviparous brooding species names are shown in bold face.

The purpose of this paper is to clarify the identities of the tropical exiguoids in order to allow other work to proceed, to record the discovery of a new viviparous species, and to record its limited occurrence on the Queensland coast where development of the littoral is already threatening known exiguoid habitats.

Systematic description

Nomenclature follows that of Clark and Downey (1992) and modifications following O'Loughlin (2002). Ambulacral index expresses the furrow armament as the mean number of furrow spines in relation to the total number of adambulacral plates, (x furrow/n amb) the latter chosen as a more consistent measure of operational body size than the greater radius R, which varies in response to relaxation and mode of preservation of specimens.

Abbreviations of institutional names are: BMNH, British Museum Natural History; MTQ, Museum of Tropical Queensland; NMV, Museum Victoria; RMHN, Naturalis, Leiden; TM, Tasmanian Museum.

Cryptasterina gen.nov.

Generic synonymy

Genus *Patiriella* Verrill, 1913 in part (for taxonomic history and diagnosis see Campbell and Rowe 1997 and references therein)
"*exigua*" group Dartnall, 1970, 1971 (in part)

Type species: *Asteriscus* (*Patiriella) pentagonus* Müller and Troschel 1842.

Etymology: The genus name is a combination of *crypta* (L, hidden) and *asterina* (little star) and refers to the cryptic species in the genus.

Diagnosis. A skeletally homogeneous group of Asterinidae with five rays; R up to about 20 mm; more or less pentagonal in outline (R:r ranging from 1.1–1.6 : 1); aborally arched.

Primary abactinal plates imbricate in two 'fields', a slightly irregular radial 'field' (usually the midradial and first dorsolateral series on either side) and a regular lateral 'field' on either side; mid-radial abactinal plates with proximal edge trilobed or often simply crescentic; the proximal concave edges of the abactinal plates subtend spaces with usually single papular pores with occasional secondary plates subdividing the papular spaces; low metapaxillar ridge carrying abactinal armament of coarse, granuliform spinelets.

Actinal plates aligned in oblique, overlapping series from between the second or third adambulacral plates and the inferomarginal plates and delimiting a membranous, triangular area behind the mouth plates which is usually filled by several rounded plates which can 'float' on the membrane or are loosely overlapping depending on their number and size; ventral lateral angle of the rays supported internally by abactinal, non-papulate plates the pennate 'tails' of which meet the actinal interradial plates; towards the ray base totally internalised secondary ossicles may complete the span between abactinal and actinal plates; internal, interradial pillar with secondary reinforcing ossicles; no interradial septum; lacking internal, bracing, superambulacral ossicles; actinal armament coarse, stout, tapering spines, mostly single; furrow spines usually in pairs, sometimes triplets proximally, often singletons distally; subambulacral spines are singletons; suboral spines one or none, occasionally pairs; oral spines 0–5; inferomarginal plates carry 5–7 webbed spinelets which overlap the neighbouring spine complements and comprise the body fringe; no pedicellariae.

Cryptasterina new genus can be distinguished from *Asterina*, as exemplified by *Asterina gibbosa* (Pennant), by the lack of pedicellariae, single spines on actinal interradial ossicles, shorter abactinal spinelets and the lack of a prominent ring of primary plates delineating the centre of the disc. *Patiriella*, as exemplified by *P. regularis* (Verrill), has longer abactinal spines (up to 0.6 mm long), is larger with R to 43 mm (Dartnall, 1969), has more pronounced metapaxillar ridges on the abactinal plates and more frequent secondary plates associated with extensive multi-papulate spaces (up to "c.12 plates and 12 papulae" ad-disc interradially, O'Loughlin 2002 p. 70).

The exiguoids of temperate SE Australia *(P. exigua, P. vivipara and P. parvivipara)* are a further distinct grouping (see Fig. 1; M.O'Loughlin pers.com.).

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The tropical exiguoid species

Cryptasterina hystera sp. nov. Dartnall and Byrne

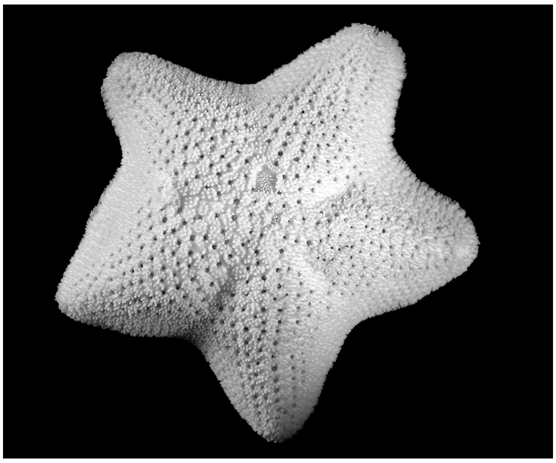

FIGURE 2. Abactinal surface of holotype of *Cryptasterina hystera* **sp.nov**. (R= 10.2 mm) Emergent young visible in the interradius to left of image.

Synonymy:

Patiriella pseudoexigua Dartnall, 1971 in part
Patiriella pseudoexigua Byrne *in* Prestedge, 1998
Patiriella pseudoexigua Byrne et al., 1999

Etymology: The species name (Gk *hystera* = womb) refers to the viviparous habit of this animal and maintains the reproductive metaphor (*vivipara*, *parvivipara*) used in naming other exiguoid species

Diagnosis. An exiguoid species of Asterinidae; abactinal plates of the papular areas mostly bi-lobed accommodating a single papula; few secondary abactinal plates present; hermaphrodite, viviparous, intragonadal brooder.

Holotype: MTQ collection number G2205, alcohol preserved specimen with part emergent juvenile, R = 10.2 mm collected 06.01.2003, S and R McKillup.

Type locality: Statue Bay, central Queensland, Australia, lat. 23°09'.997 S, long. 150° 46'.492 E.(fig. 3b) Beach number 1367 (Short, 2000). Habitat: mid intertidal under small rocks on mud and muddy sand (McKillup pers. com.)

Paratypes: collection data as for holotype; MTQ G2206 (3 specimens: R 9.5 mm, 9 mm, 10.5 mm); NMV F96255 (3 specimens : R 10 mm, 10.7 mm, 10.1 mm); TM 2987 (3 specimens: R 10 mm, 10.7 µm, 10 mm).

Other material examined. 10 specimens, data as for types; four specimens, Statue Bay, Queensland, coll. S McKillup, September, 2000 (authors' collection). One specimen Bargara, Queensland, Beach number 1502 (Short, 2000), coll R. Endean 10.1.1953, British Museum Natural History number 1953.5.18.8

Description

Up to 12 mm R; rays five (one specimen with 4 rays; n=24), form pentagonal to subpentagonal, R:r from 1.22–1.7); body thick, flat orally, flattened dome aborally, acute angle at margin; small subtriangular madreporite (about 1µm across at R = 11.5 mm).

Abactinal surface with papulate areas more extensive than non-papulate areas; few secondary plates; abactinal plates closely imbricate, rarely with more than one papular pore associated with each papular space; projecting proximal edges of plates mostly crescentic, lobed; metapaxillar ridge low, not prominent; disc not distinct; proximal interradial areas papulate similar to radial areas; distal interradial areas apapulate; abactinal spinelets granular, about 150 µm long, broader at base with constricted waist and capitate tip, terminally spinous; carinal and disc plates carry 7–12 spinelets in an irregular double row; distal interradial plates with a cluster of 5–7 spinelets; superomarginal plates elongate in the radial axis carrying a double row of up to eight spinelets; inferomarginal plates with a projecting flange of about seven webbed spinelets form the margin to the disc.

Actinal plates and spines in regular series from furrow to margin; first complete series runs from the third ambulacral plate distal to the mouth plates and comprises eight plates at R = 11.5 mm; interradial area proximal to the mouth plates carrying 2–5 loosely imbricate plates often aspinous; other actinal plates with a tapered conical spinelet up to 650 µm long: a very few plates may carry two spines close to the edge of the disc. Adambulacral plates with one subambulacral spine (occasionally two) 500 µm long proximally, reducing distally; furrow spines commonly in webbed pairs, occasional triplets near the mouth and unpredictably along the furrow and singletons distally ; furrow index 1.6–1.85. Five oral spines on each oral plate and one suboral spine on the actinal surface of the plate.

Intragonadal brooder; viviparous; no evidence of fissiparity; pedicellariae absent.

Colour: In life dark olive green above and paler green underneath (MB personal observation; Fig. 3a).

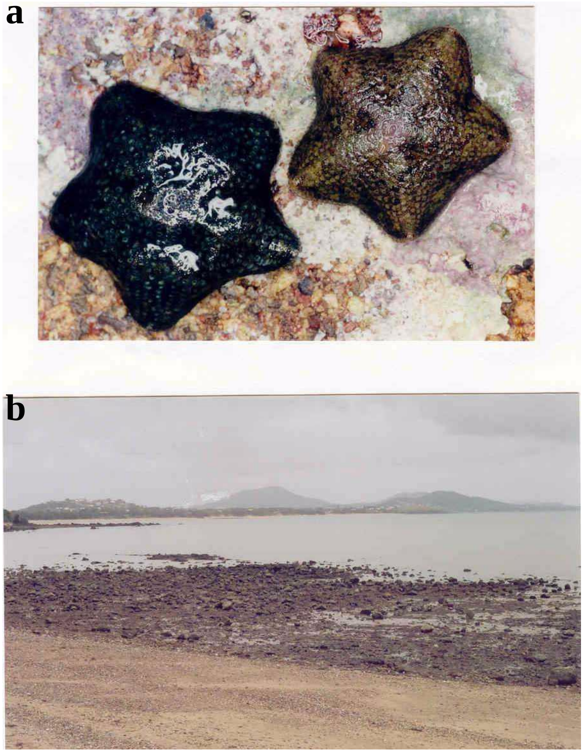

FIGURE 3. a) Colour in life *Cryptasterina hystera* n.sp. (at left) and *Cryptasterina pentagona* (at right) Photograph. M Byrne. b) Statue Bay, central Queensland. Boulder and cobble beach. Type locality for *C. hystera* n. sp. Photograph. S McKillup.

Distribution: Currently known only to these authors from the type locality and Bargara and Kinka Beaches, central Queensland, despite extensive searches northward along the Queensland coast.

Developmental biology: *Cryptasterina hystera* **sp.nov.** had ovotestes with oogenic and spermatogenic regions and the gonads are gravid from September to November . The gonads contained juveniles (Fig. 3) in December and January. This sea star has large buoyant eggs (440 µm diameter; SE= 6.0 µm, n=8) that are a gold/orange colour with a dark vegetal pole.

Developing embryos and brachiolaria larvae were interspersed with gametes in the gonad. The larvae are highly buoyant with a well developed brachiolar complex of 3 brachia and an adhesive disc. In the laboratory the larvae exhibited typical settlement behaviour exploring the substratum and adhered to the substratum with their brachia and adhesive disc.

Newly settled juveniles were an amber colour due to the presence of yolk reserves. It took three weeks for the mouth opening to develop and by this time these juveniles had a well developed skeleton.

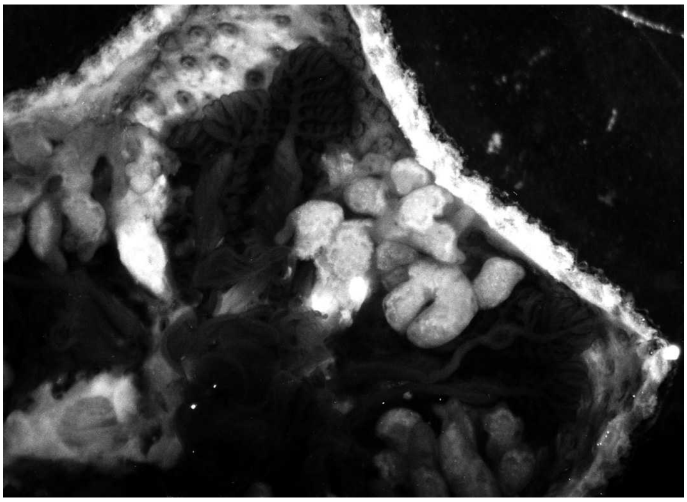

FIGURE 4. Aboral view of the gonads of *C. hystera* n. sp. filled with late stage juveniles just prior to leaving the parent, Juveniles about 500 µm.

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. These juveniles had a mouth opening, a functional digestive tract and a well-developed skeleton. Newly released juveniles were white, due to the colour of the skeleton and appeared to lack residual maternal nutrients.

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Cryptasterina pentagona (Muller and Troschel, 1842) new combination

Synonymy

Asteriscus pentagonus Muller and Troschel, 1842
Asterina pentagona von Martens, 1866
Asterina exigua HL Clark, 1908
Patiriella exigua Verrill, 1913 (in part)

Asterina exigua Fisher, 1919
Asterina exigua HL Clark, 1921
Patiriella exigua HL Clark, 1921
Patiriella exigua HL Clark, 1938 (in part)
Patiriella exigua HL Clark, 1946 (in part)
Patiriella exigua Endean, 1956 (in part)
Patiriella pseudoexigua Dartnall, 1971(in part)
Patiriella obscura Dartnall 1971
Patiriella pseudoexigua Rowe and Gates, 1995

Material examined: RMHN Ech Coll Nr 687 Indonesia, Java, coll. H Boie, syntype of *Asteriscus pentagonus*, dry broken specimen; RMHN Ech Coll Nr 3010, Ambon, Indonesia, Snellius Expedition, coll 11–17 Sept 1930 (2 specimens in alcohol); RMNH Ech Coll Nr 3005, Paleleh Beach, Sulawesi, Indonesia, Snellius Expedition, coll 21 Aug 1929 (2 specimens in alcohol).

Other material (locality records): **Authors' collection**: three specimens, Rowes Bay, Townsville, coll. AJ Dartnall, 31.12.2002.; 16 specimens, Bingil Bay, Queensland, coll. J Lacey 8.8.2000; Nine specimens, Dalrymple Point, Bowen, coll J Lacey 7.8.2000.

Description: Up to c 20 mm R; rays five, form pentagonal to subpentagonal, R:r from 1.22–1.7; body thick, flat orally, flattened dome aborally, acute angle at margin; small subtriangular madreporite (about 1 mm across at R = 11.5 mm).

Abactinal surface with papulate areas more extensive than non-papulate areas; few secondary plates; abactinal plates closely imbricate, rarely with more than one papular pore associated with each papular space; projecting proximal edges of plates mostly crescentic, lobed; metapaxillar ridge low, not prominent; disc not distinct; proximal interradial areas papulate similar to radial areas; distal interradial areas apapulate; abactinal spinelets granular, about 150 µm long, broader at base with constricted waist and capitate tip, terminally spinous; carinal and disc plates carry 7–12 spinelets in an irregular double row; distal interradial plates with a cluster of 5–7 spinelets; superomarginal plates elongate in the radial axis carrying a double row of up to eight spinelets; inferomarginal plates with a projecting flange of about seven webbed spinelets form the margin to the disc.

Actinal plates and spines in regular series from furrow to margin; first complete series runs from the third ambulacral plate distal to the mouth plates and comprises eight plates at R = 11.5 mm; interradial area proximal to the mouth plates carrying 2–5 loosely imbricate plates often aspinous; other actinal plates with a tapered conical spinelet up to 650 µm long. Adambulacral plates with one subambulacral spine (occasionally two) 700 µm long proximally, 300 µm long distally; furrow spines commonly in webbed pairs, occasional triplets near the mouth and unpredictably along the furrow; furrow index 1.2–2. Five oral spines on each oral plate and one suboral spine on the actinal surface of the plate.

Distribution: locality records (from Dartnall 1971 and recent observations by authors unless referenced otherwise). **Tropical Queensland, Australia** (Airlie Beach; Rose Bay, Kings Beach and Dalrymple Point, Bowen; Rowes Bay, Townsville; Bingil

Bay; Low Island; Erub (Darnley) Is, Torres Strait. **Papua New Guinea**, Bora Bada. **Vanuatu.** Espiritu Santo. **Philippines**, Zamboanga.; Port Binang; Bataan; Port Galera Bay. **Solomon Islands**, Aola, Guadalcanal. **Palau,** Koror Is (Marsh 1977). **BMNH**: Russell Island, Solomon Islands, 19.10.1965; Mersing, east coast Malaysia 1.2.1957. **RMNH Naturalis, ex Snellius Expedition-Indonesian locations**: Kisar, 2.11.1930; Koepang, Timor, 8.112. 1929;Taliaboe, Soela Islands, 19.3.1930; Tidore, 24–29.9.1929; Paternoster Island, 8.2.1930; Kafal, Misool Group 3–5.10.1929; Bongao, Tawitawi, Sulu Islands, 16.9.1929; Maratoea, 3–10.6.1930; Endeh, Flores, 6–8.11.1930; Ambon, 11–17.9.1930; Leti, 31.10.1930; Merampi, Nenoesa Is, 20.6.1930, Talaud Is, 14–21.6.1930; Batoe Ata, 6.3.1930.

Reproduction and development: This species is a dioecious free spawner with a planktonic lecithotrophic larva. The gonads are gravid from October to November (Gist, 1993; personal observations AJD and JC). The eggs are 413 µm in diameter (SE=6.4, n= 20).

In the laboratory development to settled juvenile stage took five days.

Newly metamorphosed juveniles were orange in colour due to the presence of yolk in the gut but by eight days post-settlement this material was reduced and the mouth became visible. Ten days old juveniles were about 750 µm diameter and had two or three pairs of tube feet. Settlement and metamorphosis were still occurring in the laboratory cultures 21 days after settlement was first noted. By day 34 the largest star attained 1.85 mm diameter and four pairs of tube feet

Ontogeny of the juvenile skeleton. After 45 days the first subambulacral spines and first orals were visible and by day 58 a second oral spine had been added; the first paired furrow spines were present at the adambulacral between tube feet one and two; two inferomarginal plates in each half interradius each carried five fringing spines which are not noticeably webbed and were separated from the neighbouring set by an interradial fringing notch. At this stage the first ambulacrals link to the projection from the oral plate; a pigmented eyespot became visible; plates of the aboral surface carry from one to three spinelets; no noticeable aboral imbrication visible.

80 days after initial settlement post-settlement stars ranged from 1.5–2 mm diameter but there was little visible change in spinulation and plate development. Actinal intermediate plates were not present and the abactinal plates were not noticeably imbricate but carried up to eight (8) granular spinelets. Individuals were variously pigmented: some were almost colourless and translucent, others showed dark, greenish pigmentation mostly confined to the abactinal spinelets.

It has not been possible to find post-settlement stars of this size in the field (AJD and JC, pers obs) this year (2002–3). Juveniles may be cryptic and thus difficult to find. The smallest individuals collected have a diameter of about 10 mm. At this size the animals have a full oral spine complement; about 13 adambulacral plates mostly carrying two furrow spines (furrow index 1.62); and a full actinal interradial ossicle complement with seven plates in the first complete chevron. Currently, we are unable to document this developmental gap.

Colour in life: Abactinal colouration variable green, red, black in mottled combinations, often a stellate darker pattern is superimposed incorporating the areas of the central disc and the top of the rays. (Fig. 3a).

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Patiriella pseudoexigua Dartnall, 1971

Status: See *C. pentagona* (above)

Patiriella obscura Dartnall, 1971

Status: See C. *pentagona* (above). This species was placed in the synonymy of *P. pseudoexigua* by Rowe and Gates (1995) but those authors gave no reason for that decision. Comparative studies show that the original material of *P. obscura sensu* Dartnall, 1971 comprises a sample from a population of larger individuals than the specimens which were the basis for *P. pseudoexigua* (Dartnall, unpub.obs.). Their distinction was a product of limited sampling. This has caused problems for workers over the years since 1971 but data from studies by others (Ottesen 1976, Gist 1993 and Lacey 2000) and more recent observations (Dartnall, unpub. obs.) have shown that the two "species" are two dimensions of a growth series and are conspecific. Whether "*obscura*" includes animals which are older (perhaps second year breeders) than "*pseudoexigua*" (current year breeders) warrants further investigation.

Cryptasterina (*Patiriella) " pseudoexigua*" Chen and Chen, 1992

Synonymy: non *P. pseudoexigua* Dartnall

Material examined: four specimens, Taiwan, coll. Chao, 2000

The pattern of flattened and closely appressed abactinal plates distinguishes this species from its mirror image congener ("*P. pseudoexigua"* in Australia). In addition molecular data have supported its distinctiveness (Hart et al. 1997). It is the sister species to *C. pacifica* (n. comb; see below and Fig. 1) and referred to here as *Cryptasterina* n.sp.

Distribution: southern Taiwan (Wanlitung) (Chen and Chen 1992).

Reproduction and development: Planktonic lecithotroph (detailed reproductive biology studies reported in the seminal paper of Chen and Chen, 1992)

"*Patiriella pseudoexigua*" VandenSpiegel et al., 1998

Status: The identity of a single specimen from West Pulau Semakau, Singapore attributed to *P. pseudoexigua* by Vanden Spiegel and colleagues is not clear. The specimen (not seen by these authors) is described as large for an exiguoid with R = 20 mm, with four oral spines , and apparently does not have actinally directed gonopores. The absence of this latter characteristic is not evidence of abactinally directed gonopores. Actinally directed gonopores are comparatively easy to discern and their absence is recordable, whereas evidence of abactinally directed gonopores may require dissection. Further to this discussion the nature of the adradial plates bordering the adambulacrals, which is significant in the exiguoids, is not apparent in either the description or figures. The presence of only four oral spines at the size stated reflects the condition in *Patiriella paradoxa* Campbell and Rowe, 1997 from Oman. It is to be hoped that more material becomes available though it seems unlikely given intensive land reclamation activity in Singapore.

Cryptasterina pacifica (Hayashi, 1977) new combination

Synonymy

Asterina pseudoexigua pacifica Hayashi, 1977
Asterina pseudoexigua pacifica Komatsu et al., 1990
Patiriella pseudoexigua pacifica AM Clark, 1993

Material examined: Kushimoto, Wakayama Prefecture, coll. Mioko Matsubara, 20 Nov. 2002

Distribution: Known from Kushimoto, Wakayama Prefecture, Japan.

Reproduction and development: viviparous lecithotroph with intragonadal fertilisation (Komatsu et al. 1990).

Colour in life: Abactinal colouration variable green, brown and yellow in mottled combinations (Saba et al., 2002 p.021); actinal surface blue green (Dartnall personal observation).

Discussion

Extraction of the new genus *Cryptasterina* does not solve the chequered generic relationships of the Asterinidae but can help pose some ideas for testing. *Patiriella regularis* Verrill is the type species of genus *Patiriella* and may well be grouped with *P. paradoxa* Campbell and Rowe, and *P. oliveri* (Benham,1911) including *nigra* HL Clark 1938. These species attain a larger size than the exiguoids, do not have an aspinous actinal adradial row of ossicles parallel to the adambulacrals, and carry an abactinal armament of longer but still granular spines. It is striking that *Patiria miniata* (Brandt 1835) and *Patiria pectinifera* (Muller and Troschel, 1842) show common features with the species associated with *P. regularis* and one can argue that genus *Patiria* is the logical placement for these species. However, AM Clark (1983) synonymised *Patiria* Gray, 1840 with *Asterina* Nardo, 1834 which, given the distinctive features of *Asterina gibbosa* Pennant, 1777, especially the pattern of plates bordering the central disc and the presence of pedicellariae, appears unlikely.

The remaining *Patiriella* species of interest are the southern Australian multi-armed species which may require a new genus. In addition the southeastern Australian species *P. exigua, P. vivipara* and *P. parvivipara* probably deserve generic isolation. We await work in progress by O'Loughlin and colleagues to test these suppositions.

In the exiguoids the portion of the interradial area proximal to the oral plates and bordered by the first entire chevrons of actinal plates running from furrow to fringe is often covered in membrane carrying a variable number of loosely overlapping "floating" plates. This was reported earlier for *Patiriella exigua* (Dartnall, 1971), and has been observed variably in the suite of species reported on herein. The characteristic was used, by Livingstone (1933) to distinguish *Disasterina* Perrier but we must now consider whether its variable expression is a function of growth.

The extensive distribution of these cryptic asterinid species coupled with discrete and limited locations where they occur has implications for both life history studies and conservation management. Cryptic species "with inherently low gene flows, inhabiting island-like habitats" (Proudlove and Wood 2003) (in these cases highly permeable boulder and cobble reflective beaches which are rare on tropical coasts (Short, 2000) may well show remarkable levels of local endemism and it is likely that further species may be detected as investigations proceed. Further to this some of the species considered herein appear to have undergone punctuate evolution (<0.5 Mya) of a highly derived, viviparous mode of reproduction (Dartnall,1969; Keough and Dartnall 1978; Hart et al. 1997, 2003; Byrne et al. 1999, 2003) and acquisition of this life history mode appears to have occurred on the periphery of parental species distributions.

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