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A systematic revision of the asterinid genus *Aquilonastra* O'Loughlin, 2004 (Echinodermata: Asteroidea)

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Abstract

O'Loughlin, P. Mark and Rowe, Francis W.E. A systematic revision of the asterinid genus *Aquilonastra* O'Loughlin, 2004 (Echinodermata: Asteroidea). *Memoirs of Museum Victoria* 63(2): 257–287.

The Indo-west Pacific Aquilonastra O'Loughlin is reviewed. Eleven species are retained in Aquilonastra: A. anomala (H.L. Clark); A. batheri (Goto); A. burtonii (Gray); A. cepheus (Müller and Troschel); A. corallicola (Marsh); A. coronata (Martens); A. iranica (Mortensen); A. limboonkengi (Smith); A. minor (Hayashi); A. rosea (H.L. Clark); A. scobinata (Livingstone). Asterina lorioli Koehler is reassigned to Aquilonastra. Thirteen new species are described: A. byrneae; A. colemani; A. conandae; A. doranae; A. halseyae; A. marshae; A. moosleitneri; A. oharai; A. richmondi; A. rowleyi; A. samyni; A. watersi; A. yairi. The four subspecies of Asterina coronata Martens are junior synonyms: Asterina coronata forma japonica Hayashi. The 13 fissiparous Red Sea specimens described by Perrier as Asteriscus wega are the syntypes. Asteriscus wega Perrier is a junior synonym of Asterina burtonii Gray. The provisional referral to Aquilonastra of three species is discussed: A. rosea; A. rowleyi; A. scobinata. No fissiparous species develops into a non-fissiparous pentaradiate form. A key to the species of Aquilonastra and map of type localities are provided.

Introduction

A revision of *Aquilonastra* O'Loughlin (in O'Loughlin and Waters, 2004) was anticipated by O'Loughlin and Rowe (2005), and its scope has grown through loans and donations of an abundant array of asterinid specimens and photos from the Indo-Pacific, Red Sea and Mediterranean regions.

This revision and description of 13 new species are based on morphological observations. O'Hara et al. (in preparation) are currently working on a molecular phylogeny analysis of species of *Aquilonastra*, and will examine congruity with the morphological observations. Byrne (2006) reported that for *Aquilonastra* a 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 clustered in *Aquilonastra* with *A. minor* a terminal taxon. Three species are referred to *Aquilonastra* provisionally: *A. rosea* (H.L. Clark, 1938), *A. rowleyi* sp. nov. and *A. scobinata* (Livingstone, 1933).

We recognize limitations in this revision. Images for fissiparous specimens on the Seychelles suggest another new species, but no material was available (see figs 3k,3l). Sloan et al. (1979) reported Asterina burtoni for Aldabra Atoll as a species with fissiparous and non-fissiparous forms. They described the non-fissiparous form as having five rays and single madreporite. We recognize throughout this work two such forms as distinct species. No material was examined to establish the status of these species. Indeed, we are unable to support the view that pluriradiate, fissiparous asterinids represent juveniles of larger, non-fissiparous pentaradiate adults (see Clark, 1967b for review). James (1975, 1982, 1985, 1989) reported Asterina burtoni from Lakshadweep (Laccadives) and Indian and Sri Lankan seas. Again, no material was examined to confirm systematic status. Sastry (1991) also reported Asterina burtoni from Lakshadweep, that appears to have represented nonfissiparous and fissiparous forms. No material was examined to confirm systematic status. The evidence in this paper indicates that Aquilonastra species have local geographical ranges. Thus some species reported here with extensive distributions (such as Oman to South Africa, and northern Australia to China) may prove with further analysis to be more than one species.

Body form, numbers of spinelets and spines per plate, and size of spinelets and spines are all related to specimen size for the 25 Aquilonastra species. And all of these characters show some variation for specimens of the same species at the same size, and on the same specimen. Preservation history is another factor affecting size and form of the various morphological characters. Species diagnostic characters are always given here for nominated specimen sizes, and for dried specimens. All of the Aquilonastra species show mottled live colour, and within a species the mottled colour can vary greatly. Colour is sometimes uniform on a specimen. However, some colours predominate in some species. Colour appears to vary with substrate colour. A full generic diagnosis for Aquilonastra is given, and these morphological characters are not repeated in each species diagnosis. Terminology follows O'Loughlin and Waters (2004).

Abbreviations for institutions are: AM—The Australian Museum, Sydney; HUJ—The Hebrew University of Jerusalem; MNHN—Muséum National d'Histoire Naturelle, Paris; MRAC—Museum of the Republic of Central Africa, Brussels; NHM—The Natural History Museum, London; NMV— Museum Victoria, Australia; NSMT—National Science Museum, Tokyo; TAU—Tel-Aviv University; TM—Tasmanian Museum, Australia; UF—The University of Florida; WAM— The Western Australian Museum. Specimen registration number prefixes are: AM J; MNHN EcA; NMV F; TM H; WAM Z. MAU is MNHN collection code for Mauritius.

Photography for many figures was performed using a Leica MZ16 stereomicroscope, DC300 Leica digital camera, and "Auto-Montage" software for composition of images.

Table 1. Species of Aquilonastra O'Loughlin, 2004, with type localities.

Species	Type localities
A. anomala (H.L. Clark, 1921)	Australia, Torres Strait, Murray I.
A. batheri (Goto, 1914)	Japan
A. burtonii (Gray, 1840)	Red Sea
A. byrneae sp. nov.	Australia, Great Barrier Reef, One Tree I.
A. cepheus (Müller and Troschel, 1842)	Indonesia, Jakarta (as Batavia)
A. colemani sp. nov.	SE Papua New Guinea, China Straits
A. conandae sp. nov.	W Indian Ocean, La Réunion I.
A. corallicola (Marsh, 1977)	W Pacific Ocean, Caroline Is., Palau
A. coronata (Martens, 1866)	Indonesia, Molucca and Flores Is.
A. doranae sp. nov.	S Japan, Ryukyu Is., Okinawa, Henza Island
A. halseyae sp. nov.	N Indian Ocean, Maldive Is.
A. iranica (Mortensen, 1940)	Iranian Gulf
A. limboonkengi (Smith, 1927)	China, Amoy
A. lorioli (Koehler, 1910)	Pakistan, Karachi
A. marshae sp. nov.	Red Sea
A. minor (Hayashi, 1974)	Japan, Honshu, Kushimoto
A. moosleitneri sp. nov.	N Indian Ocean, Maldive Is.
A. oharai sp. nov.	S Japan, Ryukyu Is., Okinawa, Seragaki
A. richmondi sp. nov.	Tanzania, Ras Kimbiji (central coast)
A. rosea (H.L. Clark, 1938)	SW Australia, off Perth, Rottnest I.
A. <i>rowleyi</i> sp. nov.	SE Africa, Sodwana Bay
A. samyni sp. nov.	Arabian Sea, Oman, Masirah I.
A. scobinata (Livingstone, 1933)	Tasmania
A. watersi sp. nov.	Arabian Sea, Oman, Masirah I.
A. yairi sp. nov.	E Mediterranean Sea, Israel, Michmoret

Key to Aquilonastra O'Loughlin species

- 1. Typically 5 equal or subequal rays, sometimes 6; form symmetrical; single conspicuous madreporite, rarely 2, very rarely 3 2
- Typically more than 5 rays, up to 9, in unequal size groups; form asymmetrical; always more than 1 inconspicuous madreporite
- 2. Gonopores actinal _____3
- Gonopores abactinal 5
- 3. Abactinal plates paxilliform; spinelets in dense, frequently crescentiform, clusters; spinelets pencil-like_____
- A. scobinata (SE Australia)
 Abactinal plates not paxilliform; spinelets not in dense clusters; spinelets not pencil-like
- 4. Abactinal plates with low rounded elevations; spinelets subpaxilliform; maximum R = 9 mm ______A. *minor* (Japan)
- Abactinal plates lacking rounded elevations; spinelets not subpaxilliform; maximum R = 15 mm
 - A. byrneae (NE Australia, Mariana Is.)
- 5. Abactinal spinelets in dense round paxilliform clusters _______. A. rosea (SW Australia)
- Abactinal spinelets not in dense paxilliform clusters _____6
- Projecting abactinal pedicellariae with conspicuous toothed valves, longer than spinelets; oral plate with up to 10 spines ________A. rowleyi (SE Africa)
- If abactinal pedicellariae present, valves not longer than spinelets; oral plate with up to 8 spines _____7
- Abactinal spinelets on rays differentiated on plates into apically thick and marginally thin; some irregularly distributed paxilliform plates ______8
- Abactinal spinelets may be of variable form, but not differentiated into two distinct forms; lacking paxilliform abactinal plates ______9
- 8. Abactinal radial plates with central subglobose spinelets, peripheral short conical to subgranuliform spinelets; lacking pedicellariae; actinal central interradial plates each with about 3 spines *A. lorioli* (N Indian Ocean)
- Abactinal radial plates with central digitiform spinelets, peripheral short conical spinelets; pedicellariae present; actinal central interradial plates each with about 5 spines ______A. coronata (Japan to N Australia)
- 9. Pedicellariae with differentiated valves in abactinal proximal interradii ______10
- Lacking pedicellariae 13
- 10. Abactinal spinelets thick, up to about 12 on each proximal carinal plate (at R = 21 mm) _____A. *iranica* (Persian Gulf)
- Abactinal proximal spinelets up to more than 40 per plate; superomarginal plates each with up to about 20 spinelets (at R = 19 mm) ________A. batheri (Japan)
- Abactinal proximal spinelets fewer than 25 per plate; superomarginal plates each with fewer than 10 spinelets (at R = 19 mm) ______12
- 12. Proximal abactinal spinelets small, thick, frequently of two forms, subgranuliform apically on plates; abactinal distal interradial plate spinelets splayed and overlapping adjacent

plate spinelets (at R = 20 mm); actinal interradial plates each with up to 5 spines (at R = 20 mm); size up to R = 25 mm

A. richmondi (E Africa coast, Madagascar, Mauritius)
 Proximal abactinal spinelets thin, similar form; abactinal distal interradial spinelets not overlapping adjacent plate spinelets if splayed; actinal interradial plates each with up to 10 spines (at R = 19 mm); size up to R = 19 mm

A. watersi (Arabian Sea, Mauritius)

- 13. Abactinal spinelets sacciform, short, wide globose basally, tapered to sharply pointed apically; up to about 12 spinelets on each proximal abactinal plate (at R = 19 mm); predominantly 2 actinal interradial spines on each plate _____ A. halseyae (Maldives)
- Abactinal spinelets not widely globose basally, not tapered to a sharp point apically; more numerous than 14 on each proximal abactinal plate (at R > 12 mm); predominantly > 3 actinal interradial spines on each plate ______14
- 14. Proximal abactinal spinelets short, thick, columnar or conical ______15
- Proximal abactinal spinelets long, thin, subsacciform _____16
- 15. Rays long, subdigitiform; spinelets mostly spread over exposed plate surface; predominantly 6 spines per actinal interradial plate (at R = 16 mm); actinal interradial spines short, thick, bluntly conical, sacciform. *A. samyni* (Arabian Sea to SE Africa, Madagascar, La Réunion)
- Rays short, strongly tapered; spinelets mostly concentrated over projecting proximal plate edge; predominantly 3 spines per actinal interradial plate (at R = 16 mm); actinal interradial spines conical to digitiform
- *A. marshae* (Red Sea, Gulfs of Aqaba and Suez) 16. Rays short, merging with disc: lacking doubly-papulate
- carinal plates; spinelets not clustered into groups on plates; spinelets frequently splay-pointed

A. oharai (Okinawa)

- Rays long, discrete; some doubly-papulate carinal plates present; spinelets frequently clustered into groups on plates; spinelets not splay-pointed ______17
- 17. Rays tapered; abactinal plates angled over papulae; spinelets long, thin, sub-sacciform to sacciform, tapering to fine point, rugose, subacicular; spinelets frequently projecting proximally over papulae

A. cepheus (Indonesia to N Australia)

 Rays digitiform; abactinal plates not angled over papulae; spinelets long, thick, conical to subsacciform, with numerous (5–6) points on distal sides and end of spinelets; spinelets not projecting proximally over papulae

A. limboonkengi (China)

- 18. Actinal interradial spines predominantly 1 per plate _______. A. conandae (Mascarene Is.)
- 19. Spinelets of 2 distinct forms, long thick digitiform apically on upper ray and marginal plates
 - A. corallicola (NE Indian to central W Pacific Oceans)
- Spinelets of one form _____ 20

- Spinelets long, frequently distinctly splay-pointed; pedicellariae present; size up to R = 12.5 mm
- A. anomala (central W Pacific)
 Spinelets not long, not distinctly splay-pointed; lacking pedicellariae; size up to R = 5 mm
- Rays wide at base, short, not elevated; spinelets thin digitiform or conical with distally long spines; actinal interradial spines up to 5 per plate
- A. doranae (Okinawa)
 23. Size up to R = 18 mm; some central abactinal plates atypically large and irregular
- *A. burtonii* (Red and Arabian Seas) — Size up to R = 9 mm; central abactinal plates not unusually
- large and irregular
 24

 24. Abactinal spinelets up to 16 per plate; spinelets splay
 - pointed; suboral spines up to 4 per plate __________. A. yairi (Red and Mediterranean Seas)
- Abactinal spinelets up to 10 per plate; spinelets not splaypointed; suboral spines up to 2 per plate

A. moosleitneri (Maldive Is.)

Asterinidae Gray, 1840

Remarks. For recent revision of Asterinidae see O'Loughlin and Waters (2004). For addition of new genus *Ailsastra* see O'Loughlin and Rowe (2005).

Aquilonastra O'Loughlin, 2004

Aquilonastra O'Loughlin, in O'Loughlin and Waters, 2004: 5 (key), 13–15, tables 1 and 2.—O'Loughlin and Rowe, 2005: 181.— Saba and Fujita, 2006: 270.—Byrne, 2006: 244, 245, 248, 250, 251.

Diagnosis (emended from O'Loughlin and Waters, 2004). Rays discrete, broad or narrow at base, tapering, rounded distally, interradial margin deeply incurved; fissiparous or non-fissiparous; fissiparous species with more than 1 inconspicuous madreporite, up to 9 rays, rays frequently unequal in length, form frequently asymmetrical; non-fissiparous species with 1 conspicuous madreporite, rarely 2, predominantly 5 rays, sometimes 6, form symmetrical, typically stellate; body flat actinally, high convex abactinally; disc variably distinct in non-fissiparous species, sometimes delineated by 5 transversely elongate radial and 5 short interradial plates; abactinal plates predominantly irregular on upper rays, in longitudinal series on sides of rays, series not perpendicular to margin; papulate areas extensive, plates predominantly with single notch for papula in papulate areas, papulae predominantly single per space, large, in longitudinal series along sides of rays; abactinal plates with glassy convexities; abactinal spinelets small, glassy, subgranuliform to digitiform, columnar or conical or sacciform or splay-pointed sacciform, in bands or tufts, numerous (10-40 per proximal abactinal plate); superomarginal and inferomarginal plates in regular series; actinal plates in longitudinal, not oblique, series; suboral spines present; adradial actinal spines in complete series; superambulacral plates present; superactinal plates present.

Type species. Asteriscus cepheus Müller and Troschel, 1842 (by original designation in O'Loughlin and Waters, 2004).

Other species. For all 25 species see Table 1 and Fig 1.

Remarks. O'Loughlin and Waters (2004) referred 12 species to the new genus *Aquilonastra*. They noted that *A. heteractis* had some characters that were exceptional to those shared by the other species of *Aquilonastra*. More recently O'Loughlin and Rowe (2005) reassigned this species to their new genus in the recombination *Ailsastra heteractis* (H.L. Clark, 1938). The remaining 11 original species are retained here in *Aquilonastra*. *Asterina lorioli* Koehler, 1910 was *incertae sedis* in O'Loughlin and Waters (2004). It is added here in the new combination *Aquilonastra lorioli* (Koehler, 1910). Thirteen new *Aquilonastra* species are described. The emended generic diagnosis refines the description but does not change any diagnostic characters.

Aquilonastra anomala (H.L. Clark, 1921)

Figures 1, 2a, 7a

Asterina anomala H.L. Clark, 1921: 95–96, pl. 7 fig. 8, pl. 23 fig. 5, pl. 26 figs 2, 3.—H.L. Clark, 1938: 143–144.—H.L. Clark, 1946: 133–134.—A.M. Clark and Rowe, 1971: 68, fig. 17g, tbl. 1.—Marsh, 1974: 92.—Marsh, 1977: 270–271, fig. 7, tbl. 2.—Oguro, 1983: 222–224, figs 5, 6, 12, 13.—A.M. Clark, 1993: 207.—Rowe and Gates, 1995: 33–34.—Waters et al., 2004: 874, 876, 877, tbl. 1, figs 1, 2.

Aquilonastra anomala.—O'Loughlin and Waters, 2004: 11, 13–15, fig. 1.

Material examined. N Australia, Torres Strait, Darnley I., 30 Apr 1977, WAM Z6849 (2); Kimberley, 17 Jul 1988, Z6843 (1); Papua New Guinea, Bismark Archipelago, 1–34 m, 29 Jun 2003, UF 2283 (1); 15–22 m, 26 Jun 2003, UF 2217 (1); West New Britain, 3–37 m, 17 Jun 2003, UF 2270 (1); Christmas I., 13 Feb 1987, Z6851 (1); Lord Howe I., AM J6169 (21); 15 Feb 1979, J16574 (2); H.L. Clark, Apr 1932, NMV F95593 (6); 20 May 2003, F97690 (6); 15 Mar 2002, F96699 (1); Solomon Is. 4–6 m, 20 Jun 2004, F94607 (1); 3–5 m, 26 Jun 2004, F94616 (3); Caroline Is. Z6845 (2); Palau, 26 Jul 1999, UF 1740 (3); Samoa, F96698 (2).

Diagnosis. Fissiparous *Aquilonastra* species; up to 8 rays, predominantly 7, broad basally, rounded distally; up to R = 12.5 mm (H.L. Clark, 1938); pedicellariae with differentiated conical valves larger than spinelets sometimes present in proximal interradial angle; up to 4 inconspicuous madreporites seen; abactinal gonopores present.

At R = 8 mm, r = 4 mm, lacking carinal series of plates, upper rays with 2 irregularly arranged longitudinal series of singly papulate plates; plates domed, angled over papulae more than notched; single papula per plate, rarely 2; some secondary plates intergrade with primary plates; spinelets long, thin conical pointed to prominently splay-pointed sacciform, up to about 20 spinelets over projecting surface of each proximal abactinal plate, predominantly in transverse double band, rare clustering of spinelets; distal interradial plates with up to about 6 sacciform splay-pointed spinelets; superomarginal and inferomarginal plates subequal; superomarginal plates each with up to about 8 spinelets, inferomarginal plates each with up to about 16 slightly larger spinelets, marginal spinelets long, splay-pointed sacciform. Spines per actinal plate up to: oral 7, suboral 5, furrow 6, subambulacral 5, actinal interradial 7 (variable, predominantly 3–4); interradial spines glassy, thin, conical, pointed, spinous, in transverse series or tufts on plates.

Colour (live). "Green, prettily variegated with white and rusky, with traces of red and yellow along the margins" (H.L. Clark, 1921); "green is common as a tinge, if not as a ground colour, and orange and brown are very generally evident; white blotches or markings may occur" (H.L. Clark, 1946); brown with reddish tinge apically, green tinge radially, white interradially, some orange marginally (photo by G. Paulay).

Distribution. N and NE Australia; Papua New Guinea; Lord Howe I.; Solomon Is.; Caroline Is., Palau; Marshall Is.; Fiji; Tonga; Samoa; Cook Is.; 0–37 m (Marsh, 1974; A.M. Clark, 1993; this work).

Remarks. A distinguishing character for the fissiparous *A. anomala* is the relatively long, frequently splay-pointed, abactinal spinelets. Green is commonly present in the mottled live colours.

Aquilonastra batheri (Goto, 1914)

Figures 1, 2b, 7b

Asterina penicillaris (part).—Sladen, 1889: 393 (two Challenger specimens from Kobé, Japan, non Asterina penicillaris (Lamarck, 1816), according to Goto (1914); Asterina penicillaris of uncertain identity and validity, according to A.M. Clark (1993)).

Asterina batheri Goto, 1914: 651–656, pl. 19 figs 275–278.— Hayashi, 1940: 119, pl. 13 figs 5, 6.—Hayashi, 1973: 71, pl. 12 fig. 2.—A.M. Clark, 1993: 207.—Fujita and Saba, 2000: 169, pl. 1C, pl. 3D, F.—Waters et al., 2004: 874, 876, 877, tbl. 1, figs 1, 2.

Aquilonastra batheri.— O'Loughlin and Waters, 2004: 11, 13–15, figs 1, 9e.—Saba and Fujita, 2006: 286.—Byrne, 2006: 245, tbl. 2.

Material examined. Japan, Toyama Bay, NMV F97441 (1); AM J11564 (2).

Diagnosis. Non-fissiparous *Aquilonastra* species; rays 5, broad basally, narrowly rounded distally; up to R = 34 mm, r = 14 mm (Goto, 1914); abactinal proximal interradial pedicellariae, pairs of tooth-like differentiated valves; gonopores abactinal; direct development into brachiolaria stage (Hayashi, 1973).

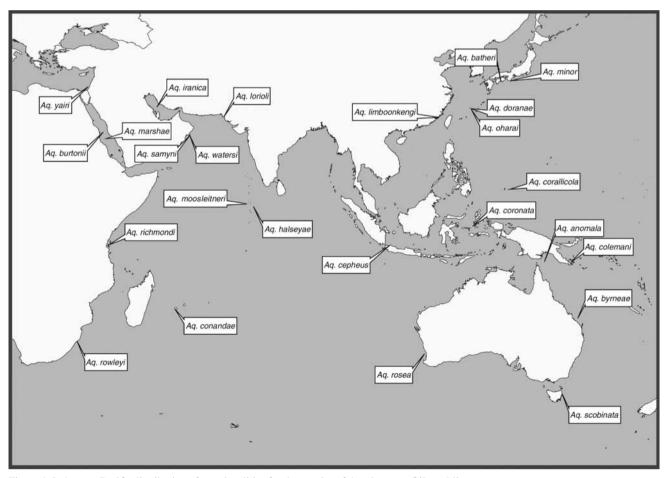


Figure 1. Indo-west Pacific distribution of type localities for the species of Aquilonastra O'Loughlin.



Figure 2. Photos of live colour and form of Aquilonastra species. a, A. anomala (H.L. Clark), Lord Howe I. (photo N. Coleman); b, A. batheri (Goto), Japan, Honshu, Hiroshima, Takehara (NSMT E–4136; photo T. Fujita, see Fujita and Saba, 2000); c, A. burtonii (Gray), Red Sea, Egypt (photo J. Hinterkircher); d, A. burtonii (Gray), Oman (photo G. Paulay); e, A. byrneae sp. nov., Qld, One Tree I. (photo M. Byrne); f, A. cepheus (Müller and Troschel), Papua New Guinea, Loloata I. (photo N. Coleman); g, A. cepheus (Müller and Troschel), Qld, Lady Elliot I. (photo N. Coleman); h, A. cepheus (Müller and Troschel), WA, Exmouth (photo N. Coleman); i, A. colemani sp. nov., Indonesia, Mayo I. (NMV F109374; photo S. Uthicke); j, A. colemani sp. nov., Papua New Guinea, Milne Bay (photo N. Coleman); k, A. conandae sp. nov., Indian Ocean, La Réunion I. (photo A. Barrere); l, A. coronata (Martens), Japan, Kyushu, Goto Is., Fukue I. (NSMT E–3683; photo T. Fujita).



Figure 3. Photos of live colour and form of *Aquilonastra* species. a, *A. doranae* sp. nov., Japan, Okinawa (UF 3913, holotype; photo G. Paulay); b, *A. halseyae* sp. nov., Indian Ocean, Maldive Is. (photo N. Coleman); c, *A. marshae* sp. nov., Red Sea, Egypt (photo J. Hinterkircher); d, *A. minor* (Hayashi), Japan, Honshu, Hiroshima, Takehara (NSMT E–4102; photo T. Fujita, see Fujita and Saba, 2000); e, *A. oharai* sp. nov., Japan, Okinawa (photo G. Paulay); f, *A. rosea* (H.L. Clark), WA, Ludlow (photo N. Coleman); g, *A. samyni* sp. nov., SE Africa, Sodwana Bay (photo Y. Samyn); h, *A. samyni* sp. nov., Oman (photo G. Paulay); i, *A. scobinata* (Livingstone), Victoria (photo L. Altoff); j, *A. watersi* sp. nov., Oman (photo G. Paulay); k, unidentified *Aquilonastra* fissiparous species, Indian Ocean, Seychelles Is. (photo N. Coleman); l, unidentified *Aquilonastra* fissiparous species, Seychelles Is., La Digue I. (photo M. Richmond).



Figure 4. Photos of live colour and form of *Aquilonastra* species. a, *A. conandae* sp. nov., Indian Ocean, La Réunion I., on under-surface of coral slab (photo A. Barrere); b, *A. corallicola* (Marsh), Indian Ocean, Cocos (Keeling) I. (photo N. Coleman); c, *A. lorioli* (Koehler), Pakistan (photo Qaseem Tahera); d, *A. marshae* sp. nov., Red Sea, Egypt (photo J. Hinterkircher); e, *A. richmondi* sp. nov., Tanzania, Mnazi Bay (photo M. Richmond); f, *A. yairi* sp. nov., Israel, Achziv (photo M. Tsurnamal, 5 July 1964).

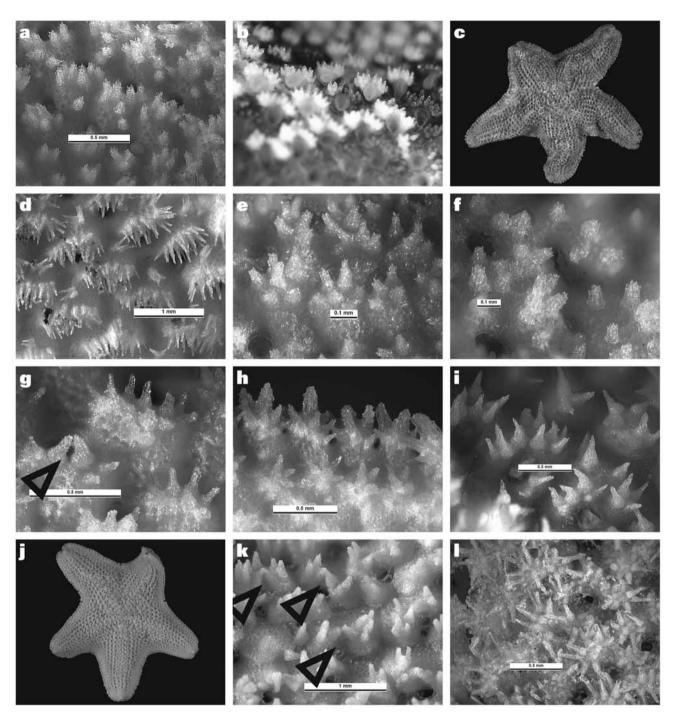


Figure 5. Photos of *Aquilonastra* species. a, *A. burtonii* (Gray), Zanzibar, spinelets (NHM 2004.2831); b, *A. byrneae* sp. nov., Qld, One Tree I., spinelets and papulae (photo M. Byrne); c, *A. cepheus* (Müller and Troschel), Jakarta (R = 20 mm; holotype MNHN EcAs1471); d, *A. cepheus* (Müller and Troschel), Papua New Guinea, spinelets (R = 17 mm; UF 2332); e, *A. colemani* sp. nov., Papua New Guinea, spinelets (UF 3284, holotype); f, *A. conandae* sp. nov., La Réunion I., spinelets (NMV F107414); g, *A. corallicola* (Marsh), Cocos (Keeling) I., pedicellaria (arrow) and spinelets (UF 745); h, *A. corallicola* (Marsh), Cocos (Keeling) I., marginal spinelets (UF 745); i, *A.halseyae* sp. nov., Maldive Is., spinelets (NHM 1965.6.1.84, holotype); j, *A. iranica* (Mortensen), Iranian Gulf (R = 13 mm; WAM Z6868); k, *A. iranica* (Mortensen), Iranian Gulf, spinelets and pedicellariae (arrows) (R = 14 mm; WAM Z6868); 1, *A. limboonkengi* (Smith), China, Amoy, spinelets (NHM 1926.12.22.35–36, syntype).

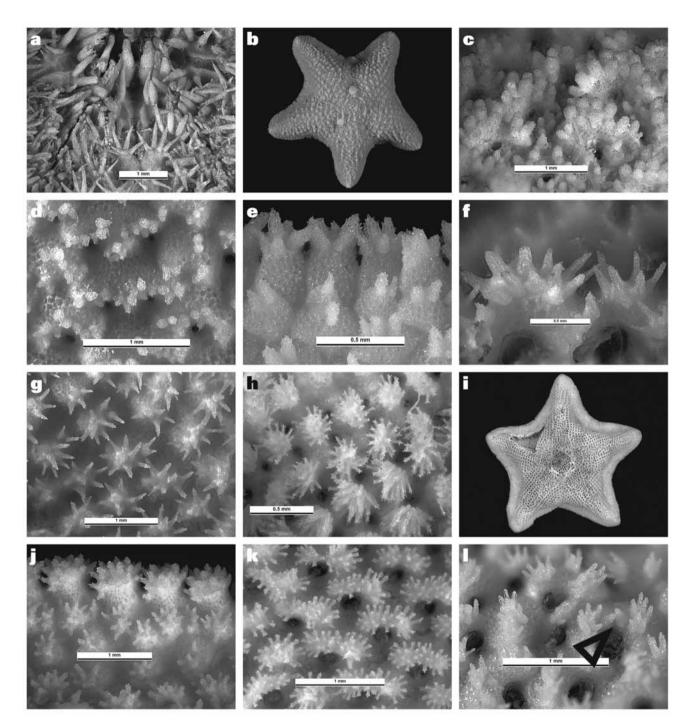


Figure 6. Photos of *Aquilonastra* species. a, *A. limboonkengi* (Smith), China, Amoy, spines (NHM 1926.12.22.35–36, syntype); b, *A. lorioli* (Koehler), Bombay, atypically two conspicuous madreporites, not fissiparous (R = 22 mm; NHM 1960.10.4.11–16); c, *A.lorioli* (Koehler), Pakistan, Karachi, spinelets (MNHN EcAs2662, syntype); d, *A. marshae* sp. nov., Red Sea, Egypt, spinelets (R = 13 mm; NMV F109382); e, *A. marshae* sp. nov., Red Sea, marginal spinelets (TM H1814); f, *A. richmondi* sp. nov., SE Africa, Sodwana Bay, spinelets (MRAC 1737); g, *A. richmondi* sp. nov., SE Africa, Sodwana Bay, distal interradial overlapping spinelets (R = 23 mm; MRAC 1737); h, *A. rosea* (H.L. Clark), WA, Jurien Bay, circular paxilliform spinelet clusters (R = 7 mm; WAM Z31162); i, *A. rowleyi* sp. nov., abactinal view (MRAC 1736, holotype, partly dissected, R = 23 mm); j, *A. samyni* sp. nov., SE Africa, Sodwana Bay, marginal spinelets (MRAC 1741); k, *A. scobinata* (Livingstone), Tasmania, Tamar R. mouth, crescentiform paxilliform spinelet clusters (R = 14 mm; NMV F112176); l, *A. watersi* sp. nov., Arabian Sea, Oman, spinelets and pedicellaria (arrow) (R = 15 mm; partly cleared paratype UF 3283).v

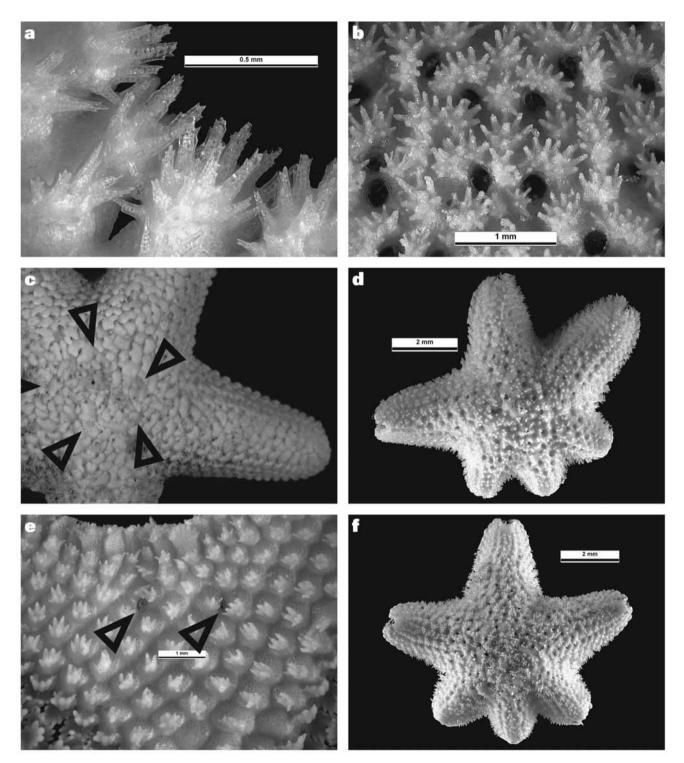


Figure 7. Photos of *Aquilonastra* species. a, *A. anomala* (H.L. Clark), Lord Howe I., marginal spinelets (NMV F97690); b, *A. batheri* (Goto), Japan, doubly papulate carinal plates with groups of spinelets (R = 19 mm; NMV F97441); c, *A. burtonii* (Gray), Red Sea, disc with five inconspicuous madreporites (arrows), five rays, large irregular proximal plates (R = 11 mm; lectotype NHM [18]40.3.23.54); d, *A. burtonii* (Gray), Oman (UF 1126); e, *A. byrneae* sp. nov., Qld, Tryon I., actinal interradius with two distal gonopores (R = 14 mm; NMV F109373); f, *A. colemani* sp. nov., Papua New Guinea (UF 3284, holotype).

At R = 19 mm, r = 10 mm, up to 4 proximal doubly-papulate carinal plates, each with up to 4 tufts each with 6-12 splayed spinelets, up to about 40 spinelets on proximal abactinal plates; plates with low domes for spinelets; few secondary plates; spinelets conical to digitiform, thick, subsacciform, splay-pointed; superomarginal plates smaller than inferomarginals, each series with up to about 20 spinelets per plate, slightly more stout on inferomarginals.

Spines per actinal plate up to: oral 7, suboral 5, furrow 7, subambulacral 9, actinal interradial 12 proximally 6 distally; interradial spines thin conical, to digitiform to subsacciform.

Colour (live). Disc and proximal apical area reddish-orange, madreporite white, proximal rays and interradii mottled with dark and light reddish-orange and white, distally pale reddish-orange (photo from M. Komatsu); disc and upper rays red, with sides of rays mottled mauve and brown, madreporite off-white (photo from T. Fujita).

Distribution. "Common in the middle and southern regions of Japan" (Hayashi, 1973); sublittoral (Hayashi, 1940) to 92 m (Sladen, 1889).

Remarks. O'Loughlin and Waters (2004) determined material from Oman (UF 70) as *A. batheri*. This material is redetermined in this work as *A. watersi* sp. nov. (below). The potentially large size, presence of numerous interradial pedicellariae with differentiated valves, and grouping of spinelets into tufts on proximal abactinal plates are distinguishing characters. Red is commonly present in the mottled live colours.

Aquilonastra burtonii (Gray, 1840)

Figures 1, 2c-d, 5a, 7c-d

Asterina burtonii Gray, 1840: 289.—Gray, 1866: 16.—Gray, 1872: 118.—H.L. Clark, 1923: 283 (status of species; possibly part).—Smith, 1927a: 641–645 (part).—A.M. Clark, 1952: 207 (possibly part; fissiparous; possibly *A. yairi* sp. nov. below).—Tortonese, 1960: 20–21 (probably part).

Asterina burtoni.—Tortonese, 1966: 3, fig. 1.—A.M. Clark, 1967a: 146, tbl. 1 (part; Red Sea material).—James and Pearse, 1969: 84–85 (part).—A.M. Clark and Rowe, 1971: 38 (part), 68, fig. 17a.—Tortonese, 1977: 281–282.—Price, 1983: 47–48, fig. 14 (part).—Archituv and Sher, 1991: 670.—Mladenov and Achituv, 1999: 152 (part).—Karako et al., 2002: 139–144 (part, El Fauz Red Sea population).

Asteriscus wega Perrier, 1869: 102.

Asterina wega.—Perrier, 1875: 318.—Achituv, 1969: 329–341 (part, "pluriradiate" form).—Achituv, 1973a: 333–336 (part, Akhziz lagoon and Haifa populations).

Asterinides burtoni.-Verrill, 1913: 482.

Asterina gibbosa.—Tortonese, 1957: 190 (non Asterina gibbosa Pennant, 1777; see Tortonese 1966).

Aquilonastra burtoni.— O'Loughlin and Waters, 2004: 11, 13 (part), 14.

Material examined. Lectotype (judged to be Gray's type by G.A. Smith, 1927a). Red Sea, NHM [18]40.3.23.54 (dry).

Asteriscus wega Val., Red Sea, M. Botta, 1837, MNHN EcAs2713 (1) (labelled "type"; see Remarks; not A. burtonii).

Red Sea, coll. Michelin, 1868, EcAs1566 (6); Ras Muhammad, 8 Aug 1968, HUJ SLR1917 (5); Gulf of Suez, Et Tur, 20 Sep 1967, HUJ SLR845 (2); 20 Sep 1967, TAU NS2090 (1, fissiparous form); 24 Dec 1965, TM H1815 (2); Île Abulat, *Calypso*, EcAs11842 (1); La Sicherie, EcAs11841 (1); S Sinai, El Fauz, Nov 2003, NMV F109383 (4); Gulf of Aqaba, near Dahab, 4 Nov 1981, TAU NS24408 (2, fissiparous forms); Sep 1976, TAU NS24501 (1); 18 Dec 1967, HUJ SLR1127 (1); 19 Feb 1968, SLR1341 (2).

Oman, Masirah I., Bar al Hikman peninsula, coral rubble, 3–4 m, 7 Nov 1999, UF 1126 (2); 0–1 m, 7 Nov 1999, UF 3280 (1); 3–4 m, 23 Jan 2005, UF 4240 (1); UF 4239 (2); 1–8 m, 18–24 Jan 2005, UF 4237 (1). Zanzibar, Prison I., seagrass bed, 6 Aug 1995, NHM 2004.2831 (1).

Diagnosis. Fissiparous *Aquilonastra* species; rays up to 8, frequently 7, form frequently asymmetrical post-fissiparity; form of larger specimens sometimes symmetrical with 5 equal rays; most interradii with inconspicuous madreporite; rays narrow basally, tapering, narrow rounded distally, digitiform; up to R = 18 mm; at R = 12 mm, r = 5 mm; gonopores not seen.

At R = 12 mm, lacking carinal plates; numerous secondary plates, intergrade with primary plates, frequently large irregular proximal abactinal plates; abactinal plates arched over papulae, rarely notched; spinelets small, variable in form, conical to columnar to digitiform, distally spinous, some splay-pointed, spread sparsely over plate surface, rarely up to about 15 spinelets on proximal plates, up to about 7 on midinterradial plates; superomarginal plates each with up to about 6 spinelets, inferomarginal plates each with up to about 12 larger spinelets.

Spines per actinal plate up to: oral 6, suboral 3 frequently 2, furrow 6, subambulacral 4, actinal interradial 1–4 (predominantly 3); interradial spines conical, sacciform.

Colour (live). "Greenish gray colour on the aboral side; a large and irregular, purplish brown blotch is on the centre, and is surrounded by red spots on the basal parts of the arms; the latter are usually darker (greenish) near their extremity, where a pale median line is to be observed" (Tortonese, 1966; Haifa specimens; the red spots are presumed here to be the madreporites); "variegated yellowish, brown and red" (Tortonese, 1977; Aqaba specimen); majority of 14 colour morphotypes from Elat were "mottled brown and orange" (pers. comm. Y. Achituv); Akhziz specimens were predominantly "mottled brown and orange" (pers. comm. Y. Achituv); "pale grey, mottled red and brown" (label with Zanzibar specimen); mottled browns, off-white (photos by G. Paulay).

Distribution. Eastern Mediterranean, Akhziz lagoon and Haifa populations; Red Sea, Gulf of Suez, Gulf of Aqaba; Arabian Sea, Oman; Arabian Gulf; NW Indian Ocean, Zanzibar; 0–8 m.

Remarks. Smith (1927a) discussed in detail the historical confusion surrounding Gray's *Asterina burtonii*, and gave a full synonymy. Gray's type was reported lost, but Smith asserted that he had found two of Gray's type specimens of *Asterina burtonii*. We follow Smith (1927a), and accept that the larger of these two specimens (NHM [18]40.3.23.54) is the type for *Asterina burtonii*. This lectotype for *Asterina burtonii* has five equal rays, but five small madreporites (R = 11 mm). We judge that the smaller of these two types (NHM [18]40.3.23.55) is conspecific with a second Red Sea fissiparous species *Aquilonastra yairi* sp. nov. (below).

A Paris Museum specimen of Asteriscus wega Val. (MNHN EcAs2713) labelled "type" was collected from the Red Sea by M. Botta in 1837. The Valenciennes manuscript name was not published, and this specimen has no type status. The name Asteriscus wega was published by Perrier who described (1869, 1875) 13 fissiparous specimens (syntype series) collected from the Red Sea by M. Botta in 1858. These fissiparous specimens, up to R = 15 mm (Perrier reported a diameter of 2-3 centimetres), are not conspecific with the Valenciennes non-fissiparous "type" specimen that has been examined here and has six equal rays and one conspicuous madreporite. It is referred below to Aquilonastra marshae sp. nov. Based on Perrier's 1869 and 1875 descriptions, Asteriscus wega Perrier, 1869 is judged to be conspecific with Asterina burtonii Gray, 1840, of which it becomes a junior synonym. This decision supports the opinion of a synonymy by A.M. Clark (1952, 1967b) and A.M. Clark and Rowe (1971).

Achituv (1973a) studied large numbers of four eastern Mediterranen populations of small fissiparous asterinids from Acre, Akhziz pool, Akhziz lagoon and Haifa. For the first two populations maximum R = 8 mm; for the latter two populations maximum R = 17 mm. These results are closely consistent with data for the two fissiparous species from the Red Sea, *A. yairi* sp. nov. with R up to 7 mm (below) and *A. burtonii* with R up to 18 mm. The invasion of the Mediterranean by both Red Sea fissiparous species is judged to be the best explanation for this data.

Mladenov and Achituv (1999, abstract) reported genetic studies of four populations of *Asterina burtoni*:

1. non-fissiparous Red Sea population from Elat

2. sympatric fissiparous Red Sea population from Elat

3. two allopatric fissiparous Mediterranean populations

They observed a high genetic difference between the fissiparous and non-fissiparous Elat populations, but not as high as between some fissiparous populations. On the assumption that the fissiparous populations were the same species, they concluded that there were not separate species in the four populations. We judge that there are two species represented by the fissiparous populations, and that both species occur in the eastern Mediterranean and one of them at Elat. This would explain the high genetic differences observed by Maldenov and Achituv (1999). To us, the Mladenov and Archituv (1999) evidence supports a conclusion of three species. This conclusion is congruent with morphological differences.

Karako et al. (2002) reported similar genetic studies and results for four fissiparous populations from Akhziv, Shikmona, and Mikhmoret on the coast of Israel, and El Fauz at the mouth of the Gulf of Aqaba, and a non-fissiparous population at Elat at the northern end of the Gulf of Aqaba. "Pentaradiate", rather than having a large conspicuous madreporite, was used to determine non-fissiparous specimens and can be misleading as the larger fissiparous specimens frequently have five equal rays but continue to have more than one inconspicuous madreporite. We judge, as above, that the Karako et al. results support an hypothesis of two fissiparous species and one non-fissiparous species. The three Mediterranean populations appear to us to be *Aquilonastra yairi* sp. nov. (below), and the El Fauz population *A. burtonii*. We refer the non-fissiparous species at Elat to *Aquilonastra marshae* sp. nov. (below). Specimens from all locations in the Karako et al. study, except Shikmona, were examined by us, and provide morphological support for the systematic decision that there are three separate species.

Tortonese (1936, 1966) first recorded *A. burtonii* in the Mediterrnean from Massawa (as *A. wega*) in 1936. Mortensen (1926) reported a fissiparous specimen from the Gulf of Suez as *Asterina burtonii*, but gave insufficient detail to judge here whether the specimen was *A. burtonii* or *A. yairi* sp. nov. In O'Loughlin and Waters (2004), material TM H1815 was referred to *A. burtoni* and that determination is confirmed here. A specimen TM H1814 was also assigned to *A. burtoni*, but is redetermined in this work as *Aquilonastra marshae* sp. nov. (below). There is no evidence in this study of a second smaller fissiparous species (*Aquilonastra yairi* sp. nov. below) in the Gulf of Aqaba.

Soliman (1999) reported studies of two asteroid populations in the Arabian Gulf, understanding them to be both *Asterina burtoni*. There is no indication in the report that either population had fissiparous individuals, and we assume that Soliman studied non-fissiparous populations that were thus not *A. burtonii*. In this review three other asterinid species occur in the region: *A. samyni* sp. nov. (below, Oman) reaches R = 27mm; *A. watersi* sp. nov. (below, Oman) reaches R = 19 mm; *A. iranica* (Mortensen, 1940, Arabian Gulf) reaches R = 35 mm. One Soliman (1999) population was up to R = 26 mm in size, and we hypothesize that it was *A. samyni*. The other was up to R = 16 mm, and we hypothesize that it was *A. watersi*. Soliman (1995) also reported an asterinid population study in the Arabian Gulf at Qatar. The largest individual was R = 26 mm. Again, we hypothesize that the population was *A. samyni*.

A.M. Clark (1974) and A.M. Clark and Courtman-Stock (1976) reported Asterina burtoni for SE Africa, and referred to both single madreporite pentamerous and fissiparous specimens from Mozambique. A. burtonii is reported here from Zanzibar, and possibly occurs off Mozambique. H.L. Clark (1923) reported Asterina burtonii in the fauna of South Africa, but referred only to a specimen from Mozambique. Non-fissiparous specimens are not A. burtonii. Jangoux (1984), and Jangoux and Aziz (1984, 1988) reported Asterina burtoni for New Caledonia, La Réunion, Seychelles, Mineures and Maldives. We found no evidence to confirm A. burtonii in any of these localities. Following many authors, Walenkamp (1990) listed A. cepheus Müller and Troschel, 1842, A. wega Perrier, 1869, A. cephea var iranica Mortensen, 1940 and ? A. anomala H.L. Clark, 1921 as junior synonyms of A. burtonii Gray, 1840. We consider only A. wega to be a junior synonym. Walenkamp's (1990) material is referred to A. richmondi sp. nov. (see below).

Perrier (1875), H.L. Clark (1923), Mortensen (1926), Smith (1927), A.M. Clark (1952) and Tortonese (1960) retained the original spelling of Gray (*burtonii*). Recent authors have used *A. burtoni*. Walenkamp (1990) argued for a restoration of the original spelling. We agree.

The characters distinguishing *A. burtonii* from *A. yairi* sp. nov. are detailed in the Remarks for *A. yairi* below. The mottled live colours for *A. burtonii* are red, orange, yellow, brown, grey, off-white.

Aquilonastra byrneae sp. nov.

Figures 1, 2e, 5b, 7e

Aquilonastra new. sp.-Byrne, 2006: 245, 248, 251, tbl. 2.

Material examined. Holotype. NE Australia, Great Barrier Reef, near Heron I., One Tree I., rocky shallows, Maria Byrne, Jan 2002, NMV F98748 (alcohol).

Paratypes. Type locality, Dec 2004, F98747 (1, alcohol); interridal, 12 Apr 2006, F111326 (2, alcohol); 27 May 2004, F109358 (1, dry, dissected).

Other material. Tryon I., 15 Sep 1970, F109373 (2, dry); Mariana Is., Guam I., Asan Point, reef flat, under rock, 11 Apr 1996, UF 894 (dry).

Diagnosis. Non-fissiparous *Aquilonastra* species; rays 5, narrow basally, broadly to narrowly rounded distally; up to R = 15 mm, r = 8 mm; gonopores actinal, interradial pairs frequently close, near margin; protandric hermaphrodite (Maria Byrne, pers. comm.).

At R = 15 mm, 0–3 proximal doubly-papulate carinal plates, each with up to 4 tufts with 3–5 spinelets per tuft; numerous proximal secondary plates, 0–3 per space; single large papula per space, rarely 2; disc variably distinctly bordered; spinelets small, short, form variable from conical to digitiform, distally pointed or blunt, some sacciform, not splay-pointed; up to about 16 spinelets across projecting edge of proximal abactinal plates, frequently 1–2 on bare distal mid-plate; up to 12 on proximal surface of distal interradial plates; superomarginal plates smaller than inferomarginals (subequal on Guam specimen), superomarginals with up to about 12 short conical pointed spinelets per plate, inferomarginals with up to about 20 spinelets, more stout and longer on inferomarginals.

Spines per actinal plate up to: oral 7, suboral 6, furrow 7, subambulacral 6, actinal interradial 8, predominantly 5; interradial spines thick, bluntly conical, subsacciform.

Colour (live). Disc sometimes cream centrally surrounded by dark brown ring, abactinally mottled with proximal upper rays predominantly olive-green to greenish-brown, interradii and distal rays predominantly cream; actinal surface cream with green patches (photo and pers. comm. M. Byrne); disc red or brown, thin boundary of white plates, proximal upper rays crimson red, remaining abactinal surface mottled with predominantly dark and pale brown, red and white (Guam photos by G. Paulay as *Asterina cepheus*).

Distribution. NE Australia, Great Barrier Reef, near Heron I., Tryon I. and One Tree I.; (possibly) W Pacific Ocean, Guam; rocky shallows.

Etymology. Named for Maria Byrne, Professor of Developmental and Marine Biology in the University of Sydney, and Director of One Tree Island Research Station on the Great Barrier Reef, in appreciation of her contribution of specimens for this work and her research on life history diversity and evolution in Asterinidae.

Remarks. A significant diagnostic character of *A. byrneae* is the presence of actinal gonopores. The dominant mottled live colours are green, brown and red, with cream or white. At R = 12 mm, the material from the Great Barrier Reef has

predominantly 5 actinal interradial spines per plate, the Guam specimen predominantly 3. This variation (on its own) is judged to be an inadequate basis for separating the material into two species, but this and colour differences suggest the possibility of two species. We identify the Guam specimen as *A. byrneae* with some hesitation.

Aquilonastra cepheus (Müller and Troschel, 1842)

Figures 1, 2f-h, 5c-d

Asteriscus cepheus Müller and Troschel, 1842: 41–42.—Dujardin et Hupé, 1862: 375–376.—Perrier, 1869: 99.

Asterina cephea.—Perrier, 1875: 315–317 (part; type).—Möbius, 1880: 50.—Döderlein, 1888: 825.—Sluiter, 1889: 307–308.

Asterina cepheus.—Martens, 1866: 85.—H.L. Clark, 1915: 95.— Fisher, 1919: 411, pl. 115 fig. 4.—Fisher, 1925: 79–80.—Liao and A.M. Clark, 1995: 130, pl. 15, figs 10, 11.—Rowe and Gates, 1995: 34.— A.M. Clark and Mah, 2001: 335.

Asterina burtoni.—H.L. Clark, 1921: 96–97, pl. 6 fig. 2.—Smith, 1927b: 276.—H.L. Clark, 1938: 144–145.—H.L. Clark, 1946: 133.— Marsh, 1974: 91–92 (non *Asterina burtonii* Gray, 1840).

Asterina burtoni cepheus.—A.M. Clark and Rowe, 1971: 68–69, fig. 17h, table 1, pl. 9 figs 4–5. —Liao, 1980: 171, figs 2:1, 2:2, 4, pl.4 figs 6–7.—A.M. Clark, 1993: 208 (non Asterina burtonii Gray, 1840) Aquilonastra cepheus.—O'Loughlin and Waters, 2004: 11, 13–15.

Material examined. Holotype. Indonesia, Jakarta (as Batavia), M. Reynaud, 1829, MNHN EcAs1471 (dry).

Other material. Indonesia, Sulawesi, 2 Jan 2000, UF 2623; New Guinea, Trobriand Group, AM J22934 (1); 1 Jun 1998, UF 2332 (1); 1 Jul 1998, UF 2415(1); Philippines, Bohol I., 25 Mar 2004, NMV F106973 (2); Australia, Queensland, Heron I., 14 Jul 1973, F95594 (2); One Tree I., J23331 (1); Tryon I., 15 Sep 1970, F95789 (4); Northern Territory, Darwin, 11 Oct 1976, F95799 (1); Western Australia, Abrolhos Is., 2 Sep 1972, WAM Z6778 (7); J8321 (5); 11 Mar 1972, F95793 (21); 12 May 1972, F95795 (6); Exmouth Gulf, F95794 (4); F95790 (2); F95792 (1); F95787 (1); F95788 (1); Aug 1972, F95790 (2); Quobba, 20 Jun 1972, F95791 (3).

Diagnosis. Non-fissiparous *Aquilonastra* species; rays 5, rarely 4 or 6, long, broad basally, strongly tapered, narrowly rounded distally, predominantly subequal, form sometimes asymmetrical; up to R = 25 mm; gonopores abactinal, some close pairs under same plate.

At R = 20 mm, r = 10 mm, abactinal plates angled up over papulae, crescentiform appearance; 0-3 proximal doubly papulate carinal plates; some large secondary plates, frequently 1 per space, up to 2; predominantly 1 papula per space, up to 3; disc frequently distinct, bordered by 5 large radial plates 5 small interradials; spinelets glassy, rugose, long, thin, finely pointed distally, not splay-pointed, subacicular, subsacciform to sacciform, up to about 32 spinelets in double series on large radial plates, up to about 24 in double series on proximal abactinal plates (frequently fewer), spinelets on anterior edge of plates, frequently angled over papula, sometimes in tufts; up to about 15 on mid-interradial plates; superomarginal plates with variably up to 8–10 spinelets per plate, inferomarginals with variably up to 16–24 thicker, longer spinelets per plate.

Spines per actinal plate variably up to: oral 6–9, suboral 2–8, furrow 6–8, subambulacral 4–8, actinal interradial 4–8; interradial spines thick, conical, blunt, subsacciform.

Colour (live). Wide range of mostly mottled colours with pink, mauve-red, grey, brown, grey-brown, reddish-brown, dark brown, black flecking, green, cream, white; disc frequently with broken white border (photos from N. Coleman).

Distribution. Indo-Malayan Region, Ceylon, Southern China, Philippines, Indonesia, W Pacific Ocean, northern Australia; 0–70 m (Liao and A.M. Clark, 1995; Marsh, 1974 as *Asterina burtoni*; Rowe and Gates, 1995).

Remarks. As noted in the diagnosis, the numbers of spinelets and spines per plate is more variable than in other Aquilonastra species. The distinctive diagnostic character of A. cepheus is the thin long finely-pointed subsacciform spinelets projecting over papulae. Smith (1927b), Liao (1980) and Liao and A.M. Clark (1995) all noted this as a distinguishing character. O'Loughlin and Waters (2004) redetermined as Aquilonastra cepheus a specimen from Hong Kong (NHM 1981.2.6.25). It is redetermined in this work as A. limboonkengi (below). In his comprehensive synonymy for A. burtonii, Walenkamp (1990) showed the position of many authors who considered A. cepheus to be a junior synonym of A. burtonii. Liao and A.M. Clark (1995) restored the species status of A. cepheus. Asterina cepheus was reported for Thursday I. (N Australia) by Bell (1884, Alert collections); for Zanzibar by Bell (1903); and for Saya de Malha and Seychelles Is. by Bell (1909). None of this material was examined. We found no evidence of A. cepheus in the western Indian Ocean. The live colour of A. cepheus is sometimes uniform, frequently mottled, and varies greatly.

Aquilonastra colemani sp. nov.

Figures 1, 2i-j, 5e, 7f

Material examined. Holotype. SE Papua New Guinea, China Straits, Samarai I., on rubble, 150°48'E, 9°40'S, 10 m, J. Starmer, 6 Jun 1998, UF 3284 (dry).

Paratypes. Type locality and date, UF 2419 (8, dry).

Other material. Indonesia, Flores Sea, West Sumbawa Regency, Mayo I., underside of coral rubble, shallow sublittoral, 14 Nov 2005, NMV F112173 (1); F109374 (4).

Diagnosis. Fissiparous *Aquilonastra* species; up to 7 rays, predominantly 6, narrow base, rounded distally, subdigitiform; up to R = 5 mm, r = 3 mm; high elevation apically, sides of rays steep; up to 2 inconspicuous interradial madreporites seen, up to 3 anal pores; gonopores not evident.

At R = 5 mm, upper ray plates irregular in size and form, longitudinal series of large papulae along sides of rays, single papula per plate; secondary plates present; spinelets thick short conical to columnar, spinous surface, not splay-pointed, up to about 12 spinelets on free surface of proximal abactinal plates; superomarginal and inferomarginal plates subequal; superomarginal plates each with up to about 8 spinelets, inferomarginal plates each with up to about 12 spinelets.

Spines per actinal plate up to: oral 6, suboral 3, furrow 5, subambulacral 3, actinal interradial 2; interradial spines glassy, rugose, bluntly pointed conical to digitiform.

Colour (live). Abactinally very dark brown on disc and upper rays, white margin (photos from N. Coleman, S. Uthicke).

Distribution. SE Papua New Guinea, China Straits; Indonesia, Flores Sea, Mayo I.; 0–10 m.

Etymology. Named for Neville Coleman, with gratitude for his generous assistance in making available to us his many live colour slides of Indo-Pacific asterinids.

Remarks. The distinguishing features of *A. colemani* are the small size (up to R = 5 mm), fissiparous habit, and dark brown with white margin colouration

Aquilonastra conandae sp. nov.

Figures 1, 2k, 4a, 5f, 8a-b

Asterina burtoni.—Kojadinovic et al., 2004: 225–229 (part, fissiparous specimens; non Asterina burtonii Gray, 1840).

'Asterina' sp. 2.—Rowe and Richmond, 2004: 3287–3288 (part, not Rivière Banane or Zanzibar specimens), fig. 5 (colour).

Material examined. Holotype (in alcohol). Indian Ocean, Mascarene Is., La Réunion I., Trou d'Eau, rocky shallows, C. Conand, 17 Sep 2004, MNHN EcAh11904.

Paratypes. Type locality and date, AM J24288 (23, in alcohol); EcAh11905 (26, in alcohol); NMV F107411 (1, dry, dissected); F107412 (29, in alcohol); F107413 (4, dry, dissected).

Other material. La Réunion I., type locality, Sep 2003, F107414 (5); 12 Jun 2002, NMV F109368 (2); 22 Mar 2003, F109366 (1); 16 Feb 2006, F109379 (1); Rodrigues I., Île aux Fous, coralline substrate, Shoals of Capricorn Programme, 21 Sep 2001, NHM 2004.2815–2824 (10); Antonio's Finger, 9 m, 21 Sep 2001, J24289 (1); Antonio's Finger Reef, off Grande Baie, NHM 2004.2826–2829 (4); Passe Coco, under rubble, 6 m, NHM 2004.2830 (1); Trou Malabar, coral rubble, 10 m, NHM 2004.2825 (1); Agalega Is., 25 Feb 1979, WAM Z6871 (1); Mauritius (Île Maurice), MAU–74, 27 lots, Peyrot-Clausade, 1974, EcAs11877–11903 (381); EcAs2578 (6); (Île Bourbon), Maillard, 1862, EcAs1563 (1).

Diagnosis. Fissiparous *Aquilonastra* species; rays 5–7, predominantly 6, largest specimens with 5; rays discrete, variably narrow to wide basally, tapering, rounded distally, sometimes digitiform; up to R = 10 mm, r = 5 mm (holotype, in alcohol); contiguous spinelets over papulae possibly act as pedicellariae, spinelets not differentiated as valves; abactinal gonopores.

At R = 8 mm, plates with proximal notch or indentation for papula, rarely doubly notched; secondary plates present; single large papula per papular space; 2 longitudinal series of single papulae along each side of rays; abactinal spinelets glassy, rugose, on upper rays short thick columnar to conical, subgranuliform, up to rarely 12 per plate, readily lost, on sides of rays short conical, in distal interradius thin, some splaypointed; marginal plates in regular series, subequal; superomarginal spinelets up to about 5 per plate, short conical; inferomarginal spinelets up to about 10 per plate, distal larger, some splay-pointed.

Spines per actinal plate up to: oral 6 (rare), suboral 3 (rare), furrow 4, subambulacral 2, actinal interradial 3 (predominantly 1); interradial spines short, thick, conical to subsacciform, pointed distally.

Colour (live). Variably mottled with red, cream, brown and green (photos from C. Conand).

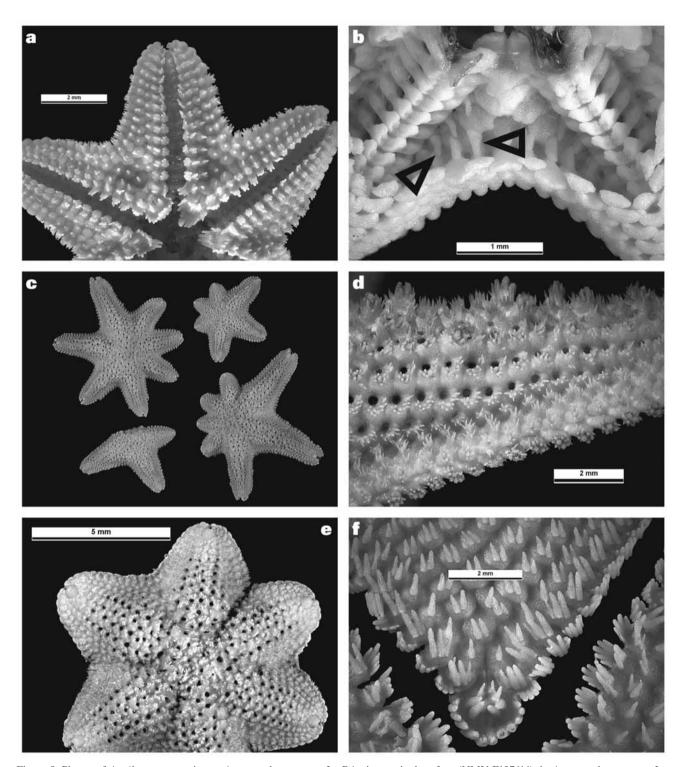


Figure 8. Photos of *Aquilonastra* species. a, *A. conandae* sp. nov., La Réunion, actinal surface (NMV F107414); b, *A. conandae* sp. nov., La Réunion, interior with superambulacral (left arrow) and superactinal (right arrow) plates (NMV F107414); c, *A. corallicola* (Marsh), Cocos (Keeling) I., fissiparous (up to R = 13 mm, UF 745); d, *A. coronata* (Martens), Australia, Darwin, side of ray, some paxilliform plates with differentiated spinelets (R = 22 mm; NMV F95796); e, *A. doranae* sp. nov., Okinawa (R = 5 mm; holotype UF3913); f, *A. halseyae* sp. nov., Maldive Is., actinal spines (NHM 1965.6.1.84, holotype).

Etymology. Named for Chantal Conand, Professor Emeritus, University of La Réunion, in appreciation of her considerable contribution to echinoderm research and this paper.

Distribution. Indian Ocean, Mascarene Is., Agalega Is., Mauritius, Rodrigues Is., La Réunion I., rocky and coralline substrate, 0–10 m.

Remarks. Kojadinovic et al. (2004) determined La Réunion material to be Asterina burtoni, and discussed both small asymmetrical fissiparous forms with more than one inconspicuous madreporite and slightly larger symmetrical pentaradiate sexual forms with a single madreporite. Maximum size was R = 9 mm, consistent with A. conandae material observed in this study. But none of the many specimens from La Réunion seen here had only a single madreporite. Some of the largest specimens were symmetrical and pentaradiate, but all had more than one inconspicuous madreporite. Only a few pentaradiate symmetrical specimens from La Réunion with a single conspicious madreporite have been seen in this study. Two are referred to Aquilonastra samyni sp. nov. (below), and a few to an undescribed species of Tegulaster. A specimen from Zanzibar (NHM 2004.2831), referred by Rowe and Richmond (2004: 3288) to 'Asterina' sp. 2, is determined here as Aquilonastra burtonii (above).

The distinguishing diagnostic characters for *A. conandae* amongst western Indo-Pacific fissiparous species of *Aquilonastra* are: predominantly single actinal interradial spine per plate; high proportion of specimens with fewer rays (80% with 5–6 rays); size difference. With R up to 10 mm, *A. conandae* is larger than *A. moosleitneri* sp. nov. below (R up to 9 mm) and *A. yairi* sp. nov. below (R up to 7 mm), and smaller than *A. burtonii* (R up to 18 mm) and *A. corallicola* below (R up to 16 mm).

Aquilonastra corallicola (Marsh, 1977)

Figures 1, 4b, 5g-h, 8c

Asterina corallicola Marsh, 1977: 271–275, figs 8, 9, tbls 1, 2.– Oguro, 1983: 224–225, figs 7–9, 14.–A.M. Clark, 1993: 208.

Asterina anomala.-Fujita et al. 2001: 319, pl. 2G (non Asterina anomala H.L. Clark, 1921).

Aquilonastra corallicola.-O'Loughlin and Waters, 2004: 11, 13-15.

Material examined. Paratypes. Caroline Is, Palau, 10 m, M. Yamaguchi, 9 Feb 1971, WAM Z1704 (3); AM J10257 (2).

Other material. Caroline Is, Palau, 6 m, 7 Sep 1995, UF 3209 (1); 0–4 m, 6 Mar 2003, UF 1715 (1); 6 m, 7 Sep 1995, UF 3223 (1); 2 m, 6 Jun 1995, UF 324 (1); 23 m, 8 Jun 1995, UF 2440 (2); Jun 1975, Z6845 (2); Marianas Is, Guam, 2–4 m, 11 Sep 1997, UF 895 (7); 2–3 m, 27 Nov 1998, UF 862 (12); 10–15 m, 14 Jan 2000, UF 678 (1); 18 m, 30 May 1997, UF 1119 (1); 1–2 m, 16 Apr 1999, UF 864 (6); 2 m, 5 Nov 1998, UF 827 (4); 10 m, 20 Jan 2000, UF 675 (1); Saipan I., 3–12 m, 18 Aug 2003, UF 3528 (1); Singapore, 1–3 m, 3 Nov 2000, UF 2714 (1); Indonesia, Sulawesi, 4–32 m, 26 Sep 1999, UF 1827 (1); Indian Ocean, Cocos (Keeling) I., under dead coral rubble, 15 m, 8 Dec 1999, UF 745 (7); 10–20 m, 6 Dec 1999, UF 750 (3); 1–2 m, 8 Dec 1999, UF 768 (2); UF 1648 (1); NE Australia, Great Barrier Reef, One Tree I., NMV F98746 (6); Fiji, 5–8 m, 11 Oct 2001, UF 1007 (1). *Diagnosis.* Fissiparous *Aquilonastra* species; up to 8 rays, predominantly 6 or 7, rays elongate, wide basally, tapered, narrowly rounded distally; up to R = 16 mm (Sulawesi), 12 mm (Palau), 13 mm (Cocos); some abactinal pedicellariae, with 2–3 differentiated thick valves; abactinal gonopores.

At R = 12 mm, r = 5 mm; upper ray plates irregular in arrangement, rarely a few doubly papulate carinal plates proximally; 1–3 papulae per papular space, 3 rare; papulae in 2 longitudinal series along each side of ray; 0–2 secondary plates per papular space proximally; upper ray plates paxilliform with 2 forms of spinelets; 1–3 thick, digitiform, blunt apical spinelets on each plate, up to about 12 thin conical pointed spinelets peripherally on each plate, spinelets not splay-pointed; superomarginal plates each with up to about 6 thin pointed spinelets; inferomarginal plates each with 1–4 thick digitiform apical spinelets.

Spines per actinal plate up to: oral 6, suboral 6, furrow 5, subambulacral 5, actinal interradial 5; interradial spines rugose, some digitiform, most thin conical pointed; actinal spines generally of 2 forms, tall digitiform, short thin.

Live colour. Mottled red and yellow (photos from G. Paulay).

Distribution. W Pacific Ocean, Marianas Is., Caroline Is., Fiji, NE Australia; E Indian Ocean, Cocos (Keeling) I.; Sulawesi; Singapore; 0–32 m.

Remarks. The distinugishing characters for this large fissiparous species are the long tapering rays, two forms of spinelets on paxilliform upper ray plates, and golden red mottled colour. Three small specimens from Madagascar (MNHN EcAs11876; R = 4 mm), collected by Cherbonnier on 6 April 1960, are damaged but appear to have the diagnostic characters of *A. corallicola.* The colour and form of the material from Malaysia referred to *Asterina anomala* by Fujita et al. (2001) indicate that it is *A. corallicola.*

Aquilonastra coronata (Martens, 1866)

Figures 1, 21, 8d

Asterina coronata Martens, 1866: 73–74.—Fisher, 1918: 108– 110.—A.M. Clark and Rowe, 1971: 68, pl. 9 fig. 6.—VandenSpiegel et al., 1998: 452–453, fig. 37A–D, pl. 3 fig. 8.—A.M. Clark, 1993: 208.— Rowe and Gates, 1995: 34.—Chao, 1999: 407–408.—Fujita et al., 2001: 319–320, pl. 2H.—Waters et al., 2004: 876–877, tbl. 1, figs 2, 3.

Asterina spinigera Koehler, 1911: 20–21, pl. 4 figs 11, 12 (junior synonym by VandenSpiegel et al., 1998).

Asterina novae-zealandiae.—Goto, 1914: 643, pl. 19 figs 279–281 (non *Asterina novae-zelandiae* Perrier, 1875 = *A. coronata* Martens, 1866, according to Fisher, 1919: 413).

Asterina cristata Fisher, 1916: 27-28.

Asterina cristata euerces Fisher, 1917: 91.

Asterina coronata cristata Fisher, 1918: 111, pl. 13.—Fisher, 1919: 411–414, pl. 115 fig. 3, pl. 131 figs 4, 4a.—Fisher, 1925: 80.—A.M. Clark, 1993: 208–209.—O'Loughlin and Waters, 2004: 15 (junior synonym, this work).

Asterina coronata euerces Fisher, 1918: 110.—Fisher, 1919: 414– 416, pl. 115 figs 1–2, pl. 116 figs 1–2, pl. 131 figs 5, 5a.—A.M. Clark, 1993: 209.—O'Loughlin and Waters, 2004: 15 (junior synonym, this work). Asterina coronata fascicularis Fisher, 1918: 110.—Fisher, 1919: 414.—H.L. Clark, 1928: 390.—H.L. Clark, 1938: 145–148, pl. 12 fig. 1.—A.M. Clark, 1993: 209 (junior synonym by Rowe and Gates, 1995).

Asterina coronata coronata.—Fisher, 1918: 110.—Fisher, 1919: 414.—A.M. Clark, 1993: 208.

Asterina coronata forma japonica Hayashi, 1940: 119–120, pl. 11 figs 5–7, pl. 13, fig. 7.—Hayashi, 1973: 72, pl. 12 fig. 3 (junior synonym, this work).

Aquilonastra coronata.—O'Loughlin and Waters, 2004: 11, 13–15.—Byrne, 2006: 245, tbls 1, 2, fig. 1.

Material examined. Australia, NT, Darwin, H.L. Clark, Jul 1929, NMV F95797 (2); 11 Jun 1976, F95798 (1); 13 Jun 1976, F95796 (4); AM J6188 (10); J6613 (18); J8206 (2); Caroline Is., J13660 (1); Taiwan, Sanshi, 28 Feb 2003, UF 1425 (2); J19956 (1); Japan, F96700 (1); Kushimoto, J11563 (2).

Diagnosis. Non-fissiparous *Aquilonastra* species; rays 5, broad basally, tapering, narrowly rounded distally; up to R = 32 mm; gonopores abactinal; numerous abactinal pedicellariae frequently present, 2–4 curved pointed differentiated valves.

At R = 30 mm, r = 14 mm; abactinal surface very uneven with irregularly distributed high paxilliform plates; abactinal spinelets of 2 forms on paxilliform plates, up to about 6 thick long digitiform or pointed spinelets on apex of each plate, up to about 10 thin short pointed spinelets around margin of plate; thin spinelets subacicular, not splay-pointed; disc clearly delineated by 5 radial 5 interradial plates; lacking doublypapulate carinal plates; upper ray with irregular zig zag series of small primary and secondary plates, lacking papulae; 0-4 secondary plates per papular space on upper rays, intergrade with primary plates; 1-4 papulae per papular space; plates smaller than superomarginal inferomarginals, superomarginals with up to about 10 thin, rugose, pointed, not splay-pointed spinelets per plate; inferomarginals with up to about 4 thick long digitiform or pointed spinelets on apex of each plate, up to about 12 thin spinelets around margin of plate.

Spines per actinal plate variably up to: oral 8, suboral 8, furrow 7, subambulacral 7, actinal interradial 7, predominantly 5; interradial spines conical, pointed, frequently two forms on each plate, thick centrally thin peripherally.

Colour (live). "The normal coloration is mottled olive-greens, light and dark, with more or less dark dull red, usually in irregular blotches. One specimen was very largely bright rustred, over most of the dorsal surface. Some specimens occur with no trace of green dorsally; these are more or less fawncolour mottled with brown and have a distinct red tinge. Most secimens have red markings but the shade may be very deep; in a few cases it was replaced by black. A common feature is a blotch of carmine at the base of each arm; in one specimen this was nearer vermilion." (H.L. Clark, 1938); mottled grey-brown, with orange and white markings (photo from M. Komatsu); mottled grey-brown, with dark brown, orange and white markings (photo from T. Fujita).

Distribution. Northern Australia to Japan, Singapore to Caroline Is.

Remarks. Fisher (1916, 1917, 1918, 1919, 1925) established and maintained three subspecies of *Asterina coronata*, but stated

his own uncertainty. H.L. Clark (1928) recorded his doubt about the subspecies. Hayashi (1940) added a fourth subspecies from Japan. Rowe and Gates (1995) made *A. coronata fascicularis* a junior synonym of *A. coronata*. Material from Taiwan and northern Australian are morphologically conspecific, including the presence of abundant pedicellariae. In his key to four subspecies Fisher (1919) used the presence of pedicellariae to key *A. coronata euerces* from the other three. This is erroneous, since abundant pedicellariae are present in the northern Australian and northern Pacific material. These pedicellariae closely resemble those illustrated by Fisher (1919, pl. 131 fig 5a) for *A. coronata euerces*. Variation in spine number per plate is not an adequate basis for upholding the subspecies. All are judged here to be junior synonyms.

O'Loughlin and Waters (2004) redetermined two specimens from Bombay (NHM 1960.10.4.11–16), previously identified as *Asterina lorioli*, as *Aquilonastra coronata*. That decision is reversed here.

The distinguishing character of *A. coronata* is the irregularly distributed high paxilliform abactinal plates with two forms of spinelets.

Aquilonastra doranae sp. nov.

Figures 1, 3a, 8e

Material examined. Holotype (in alcohol). Japan, Okinawa, Yonashiro Marine Road causeway to Henza I., 26°20'N, 127°56'E, intertidal seagrass, 25 Jul 2004, G. Paulay, UF 3913.

Diagnosis. Fissiparous *Aquilonastra* species; rays 6, subequal, short, broad basally, narrowly rounded distally; R = 5 mm, r = 3.5 mm; 3 inconspicuous interradial madreporites; gonopores not evident.

Abactinal plates strongly imbricate, notched for papula; upper ray plates with 1 papula, 2 irregular longitudinal series; plates on sides of rays with 1 papula, 1 longitudinal series, beginnings of second longitudinal series (0–3 plates); spinelets conical or digitiform, distally spinous, up to about 10 spinelets across raised proximal edge of proximal abactinal plates, plate surfaces bare distally; superomarginal plates each with up to about 6 spinelets, inferomarginal plates each with up to about 12 longer splay-pointed spinelets.

Spines per actinal plate up to: oral 5, suboral 3, furrow 4, subambulacral 3, actinal interradial 5 (predominantly 3); interradial spines conical, long, thin, finely tapered.

Colour (live). Mottled red, green, grey, white abactinally; proximal disc area crimson red; proximal rays and interradii dark grey-green to yellow-green; distal abactinal surface mottled pale green, mauve grey, white (photo by G. Paulay).

Distribution. Japan, Okinawa, Henza I., seagrass shallows.

Etymology. Named for Ruth Doran, with gratitude for her assistance in providing asterinid distribution maps.

Remarks. Although only one specimen is available, the fissiparous habit, geographical isolation, green colouration, short rays, thin digitiform or conical spinelets with long spines distally, and up to five actinal interradial spines per plate together support the erection of a new species.

Aquilonastra halseyae sp. nov.

Figures 1, 3b, 5i, 8f

Asterina burtoni.—A.M. Clark and Davies, 1966: 599, 603.— Jangoux and Aziz, 1984: 861, 872, 873 (part; non Asterina burtonii Gray, 1840).

Asterina cepheus.—Moosleitner, 1997: 12–13, fig. 23b (only) (fig. 23a is a photo of a Red Sea Aquilonastra sp., pers. comm. H. Moosleitner (= A. marshae sp. nov., see below); non Asteriscus cepheus Müller and Troschel, 1842).

Asterina burtoni cepheus.—A.M. Clark and Rowe, 1971: 68–69, fig. 17, tbl. 1.—A.M. Clark, 1993: 208 (non Asteriscus cepheus Müller and Troschel, 1842).

Material examined. Holotype (in alcohol). Indian Ocean, Maldives, Addu Atoll, Gan I., lagoon reef, 10 m, P. Spencer Davies, 11 Feb 1964, NHM 1965.6.1.84.

Paratypes. Type locality and date, NHM 1965.6.1.85a (1, dry); NHM 1965.6.1.85b (1, part dissection, in alcohol).

Diagnosis. Non-fissiparous *Aquilonastra* species; rays 5, broad basally, narrowly rounded distally; up to R = 19 mm, r = 9 mm; gonopores not seen.

At R = 19 mm, rare proximal doubly papulate carinal plates; rarely 1 secondary plate per papular space; spinelets distinctly sacciform, sharp point distally; up to about 15 spinelets per proximal plate, sometimes in discrete groups; primary superomarginal plates frequently separated by smaller plate; superomarginals with 2–4 thin, sacciform pointed spinelets; inferomarginal plates with up to about 12 spinelets, proximally similar to superomarginal spinelets, more stout and longer distally.

Spines per actinal plate up to: oral 6, suboral 5, furrow 6, subambulacral 4, actinal interradial 4 (predominantly 2); interradial spines stout, short, subsacciform, pointed distally, on raised proximal edge of plates.

Colour (live). "Various shades of brown, sometimes with darker or lighter spots" (Moosleitner, 1997; fig. 23b); disc variably outlined in white; abactinally mottled pink, pale red-brown, white, with dark red-brown flecks; or mottled dark and light redbrown, white, bright red star apically (photos by N. Coleman).

Distribution. Indian Ocean, Maldives, 1–30 m (Moosleitner, 1997).

Etymology. Named for Sheila Halsey of the Natural History Museum in London, who has graciously assisted the authors with literature searches and facilitated the loan of materials for echinoderm research.

Remarks. The distinguishing character of *A. halseyae* is the distinctive sacciform, conical, sharply-pointed form of the abactinal spinelets. A.M. Clark and Rowe (1971) judged that the fissiparous and non-fissiparous asterinds occurring in the Maldives were *Asterina burtoni* Gray, 1840, and referred the fissiparous form to the subspecies *A. burtoni burtoni* and the non-fissiparous form to the subspecies *A. burtoni cepheus.* We refer the non-fissiparous Maldives asterinid to *A. halseyae* sp. nov. (here), and the fissiparous Maldives asterinid to *A. moosleitneri* sp. nov. (below).

Aquilonastra iranica (Mortensen, 1940)

Figures 1, 5j-k

Asterina cephea var. iranica Mortensen, 1940: 65–66, pl. 1 figs 1–4. Asterina burtoni.—A.M. Clark and Rowe, 1971: 68, 69, tbl. 1.—

Price, 1983: 47–48, fig. 14 (part, non-fissiparous). Asterina burtoni burtoni var. iranica.—A.M. Clark, 1993: 207, 208. Aquilonastra iranica.—O'Loughlin and Waters, 2004: 11, 13–15.

Material examined. Syntype, Iranian Gulf, S of Bushire, coral reef, 18 Feb 1937, AM J17891 (1, dry). Other material. Bahrain, Jufair, mudflat, WAM Z6868 (6); W Pakistan, Balochistan coast, Gwader, 25°N62°E, 2 Dec 1977, NMV F112182 (1); F112183 (2).

Diagnosis. Non-fissiparous *Aquilonastra* species; rays 5, long, broad basally, tapering, rounded distally; up to R = 35 mm, r = 15 mm (Mortensen, 1940); abactinal proximal interradial pedicellariae, pairs of tooth-like differentiated valves; abactinal gonopores.

At R = 20 mm, r = 11 mm, from 0 to 5 proximal doubly papulate carinal plates; lacking secondary plates; spinelets on abactinal plates in small groups, up to 4 per group, or in transverse single or double series; up to about 12 spinelets on proximal abactinal plates; spinelets short, thick, conical to subsacciform; distal interradial plates with 4–6 splayed spinelets; superomarginal plates smaller than inferomarginals, up to about 6 spinelets per superomarginal plate, up to about 12 thicker spinelets per inferomarginal plate.

Spines per actinal plate up to: oral 8, suboral 5, furrow 7, subambulacral 9 (sometimes in 2 series), actinal interradial 5 (predominantly 3); interradial spines long, conical.

Colour (live). "Grayish, with reddish or bluish-gray spots; oral side lighter, uniformly coloured" (Mortensen, 1940).

Distribution. Iranian Gulf; Arabian Sea, W Pakistan, soft and hard substrate.

Remarks. O'Loughlin and Waters (2004) raised *A. cephea* var. *iranica* to species status. *A. iranica* is distinguished by: large size (up to R = 35 mm); pedicellariae with differentiated valves; few short thick conical to subsacciform spinelets on proximal abactinal plates.

Aquilonastra limboonkengi (Smith, 1927)

Figures 1, 51, 6a, 9a

Asterina limboonkengi Smith, 1927b: 273–276, figs 1–3.—Liao, 1980: 171, figs 3:1, 3:2, 5.—A.M. Clark, 1982: 490–491.—A.M. Clark, 1993: 211.—Liao and A.M. Clark, 1995: 66, 130–131, pl. 18 figs 6–7.

Aquilonastra limboonkengi.—O'Loughlin and Waters, 2004: 11, 14, 15.

Material examined. Syntypes. China, Amoy, C. Ping, NHM 1926.12.22.35–36 (2, alcohol; very damaged).

Other material. SE Hong Kong, North Rocks, near Ninepins I., 15 m, NHM 1981.2.6.23–25 (1).

Diagnosis. Non-fissiparous *Aquilonastra* species; rays 5, long, narrow to broad basally, tapering, rounded distally (rays digitiform on syntypes), up to R > 25 mm (Liao and A.M. Clark, 1995); gonopores abactinal.

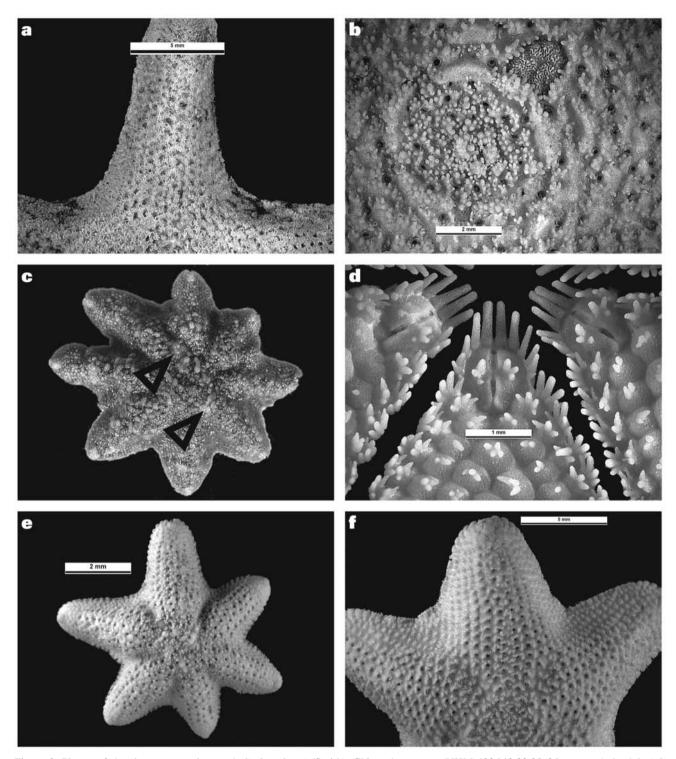


Figure 9. Photos of *Aquilonastra* species. a, *A. limboonkengi* (Smith), China, Amoy, ray (NHM 1926.12.22.35–36, syntype); b, *A.lorioli* (Koehler), Pakistan, Karachi, disc (MNHN EcAs2662, syntype); c, *A. lorioli* (Koehler), Pakistan, New Pachha, atypically eight rays, two conspicuous madreporites (arrows), asymmetrical (non-fissiparous; photo Qaseem Tahera); d, *A. marshae* sp. nov., Red Sea, actinal (TM H1814); e, *A. moosleitneri* sp. nov., Maldive Is. (R = 7 mm; holotype NHM 1902.3.13.27); f, *A. oharai* sp. nov., Okinawa (R = 12 mm; holotype UF 3285).

At R = 18 mm, r = 7 mm (larger syntype), from 0 to 4 proximal doubly-papulate carinal plates; 0-1 secondary plates per papular space; disc bordered with 5 radial 5 smaller interradial plates; spinelets on proximal abactinal plates in up to 4 groups, up to 10 spinelets per group, up to more than 30 spinelets on proximal abactinal plates; spinelets long, thick, conical to subsacciform, with numerous (5–6) points on distal sides and end of spinelets, not splay-pointed; mid-interradial plates with up to about 20 long, thin, pointed spinelets, sometimes larger group over anterior edge of plate, smaller group distally, groups splayed and overlapping spinelets on adjacent plates; superomarginal plates with up to about 12 thin spinelets per plate, up to about 24 thick spinelets per inferomarginal plate.

Spines per actinal plate up to: oral 7, suboral 6, furrow 7, subambulacral 7, actinal interradial 10 (frequently about 6); interradial spines long, conical.

Colour (live). "Dark brown with irregular red, purple or light brown spots" (Liao and A.M. Clark, 1995).

Distribution. SE coastal China, Guangdong and Fujian Provinces (Liao and A.M. Clark, 1995).

Remarks. Liao (1980) and Liao and A.M. Clark (1995) distinguished Asterina limboonkengi from Asterina burtoni cepheus (= A. cepheus here) by: abactinal spinelets squat, opaque with 5–6 terminal points (not slender, transparent with 1-3 terminal points); actinal spines stout, rugose with many points distally (not slender, smooth with few points distally); thin abactinal plates with large papular spaces with numerous secondary plates in large specimens (not thick with small papular spaces lacking secondary plates). We do not agree with all of these distinctions. We considered the actinal spines on the type specimen of A. cepheus to be short, thick, conical, blunt, and those on the syntypes of A. limboonkengi to be long, conical, finely tapered. We observed secondary plates on the types of both species. We thus have some uncertainty about the status of A. limboonkengi in China waters. O'Loughlin and Waters (2004) determined material from Oman (UF 68, UF 246, UF 1645) to be Aquilonstra limboonkengi. This material is referred here to the new species Aquilonastra samyni (below).

Aquilonastra lorioli (Koehler, 1910) comb. nov.

Figures 1, 4c, 6b–c, 9b–c

Asterina lorioli Koehler, 1910: 129–131, pl. 19 figs 5–8.–H.L Clark, 1915: 95.–A.M. Clark and Rowe, 1971: 38, 67.–A.M. Clark, 1993: 211.–O'Loughlin and Waters, 2004: 11, 37.

Palmipes sarasini de Loriol, 1897: 12.-Koehler, 1910: 129 (part; non Palmipes sarasini de Loriol, 1897).

Material examined. Syntypes. Pakistan, Karachi, MNHN EcAs2662 (1, dry, ray broken off); Mergui Archipelago, Cheduba I., WAM Z6848 (1, dry).

Other material. Bombay, BMNH 1960.10.4.11–16 (2); Native Jetty, Karachi, BMNH 1967.11.1.4 (2); Pakistan, Buleji, 24°N, 66°E, 9 Sep 2006, NMV F112184 (9).

Diagnosis. Non-fissiparous *Aquilonastra* species; rays 5, rarely 6 (Koehler, 1910, pl. 19 fig. 7), broad basally, narrowly rounded distally, up to R = 22 mm, r = 13 mm; gonopores abactinal.

At R = 22 mm, variable series of doubly-papulate carinal plates from none to half ray length, each with one cluster or up to 4 tufts of spinelets, up to about 20 spinelets on proximal carinal plates; disc defined by 5 transversely elongate series of subpaxilliform spinelets on radial plates, 5 small interradial plates; some high paxilliform clusters of spinelets on rays; spinelets vary significantly in form from large globose to thick digitiform apically on plates, to small pointed conical on margin of plates and on secondary plates; papular spaces large, predominantly single large papula per space, frequently 2 per space, up to 5 small secondary plates per space; superomarginal plates with up to about 10 short conical spinelets per plate, inferomarginal plates with up to about 20 spinelets.

Spines per actinal plate up to: oral 7, suboral 4, furrow 6, subambulacral 5, actinal interradial 6, predominantly 3; interradial spines thick, digitiform to bluntly conical.

Colour (live). Abactinal colour variably mottled with greybrown, green-brown, yellow-brown, red-brown, red, brown (photos from Qaseem Tahera).

Distribution. Arabian Sea, Karachi, Bombay, Ceylon.

Remarks. Specimen EcAs2662 (R = 18 mm) is from the type locality (Karachi), and the label is written in Koehler's handwriting (Tim O'Hara pers. comm.). It is judged here to be a syntype. Specimen WAM Z6848 (R = 7 mm) is from the type locality (Cheduba I.), and the label records "Exchange Zoological Survey India". It is judged to be one of the small specimens (7-11 mm) referred to by Koehler (1910), and also a syntype.

O'Loughlin and Waters (2004) listed Asterina lorioli as incertae sedis, because type material and information about internal skeletal structure were not available. Type material is available for this study, and the species is reassigned as the new combination Aquilonastra lorioli (Koehler, 1910). The variety of spinelet form, and paxilliform clusters of spinelets along rays, are similar to the spinelet arrrangement in Aquilonastra coronata (Martens, 1886). A. lorioli is distinguished by the globose to subgranuliform spinelets. A specimen (photo from Qaseem Tahera, figure 9c) has eight rays and two conspicuous madreporites, but the spinelets are distinctively those of A. lorioli.

Aquilonastra marshae sp. nov.

Figures 1, 3c, 6d-e, 9d

Asterina cephea.—Perrier, 1875: 315–317 (part, Red Sea; non Asteriscus cepheus Müller and Troschel, 1842).

Asterina burtonii.—Mortensen, 1926: 121 (part).—A.M. Clark, 1952: 207 (part; non-fissiparous).—Tortonese, 1960: 20–21 (part; non Asterina burtonii Gray, 1840).

Asterina burtoni.—Achituv, 1969: 329–341 (part, "pentaradiate" form).—James and Pearse, 1969: 84–85 (part).—A.M. Clark and Rowe, 1971: 68, tbl. 1 (part, Red Sea non-fissiparous).—Achituv, 1973b: 547-553.—Tortonese, 1977: 281–282 (part).—Price, 1982: 7 (part, Red Sea non-fissiparous).—Mladenov and Achituv, 1999: 152

(part).—Karako et al., 2002: 139–144 (part, Elat Gulf of Aqaba non-fissiparous population; non *Asterina burtonii* Gray, 1840).

Asterina cepheus.—Moosleitner, 1997: 12–13, fig. 3a (only) (non Asteriscus cepheus Müller and Troschel, 1842).

Material examined. Holotype. Red Sea, Jousseaume, 1892, MNHN EcAs11907 (dry).

Paratypes. Type locality and date, EcAs10316 (7, dry).

Other material. Red Sea, M. Botta, 1837, EcAs2713 (1; labelled as "type" of *Asteriscus wega* Val.; discussed under *A. burtonii* above); NMV F112169 (12); S Sinai, El Fauz, Nov 2003, F109382 (5); Ras el Misalla, 22 Sep 1970, HUJ SLR3030 (3); Ras Matarma, 31 Jan 1969, SLR2199 (1); 22 Sep 1981, TAU NS24413 (1); Egypt, under rocks, shallows, 15 Jul 2005, F107430 (1); Feb 2003, F109362 (1); 15 Jul 1966, TM H1814 (1); Gulf of Suez, Mission Dollfus, 1928, EcAs11839 (1); 27 Oct 1971, NS8560 (1); et Tur, 11 Sep 1968, HUJ IEC.57/141–198 (11); Gulf of Aqaba, 8 Oct 1968, TAU NS4130 (5); Jez Tiran, 25 Sep 1981, WAM Z6877 (1).

Diagnosis. Non-fissiparous *Aquilonastra* species; rays 5, sometimes 6, short, broad basally, tapered, narrowly rounded distally; up to R = 16 mm, r = 7 mm; predominantly 1 conspicuous madreporite, sometimes 2; gonopores abactinal; some paired thick spinelets probably act as pedicellariae, not differentiated as valves.

At R = 16 mm, 0–3 doubly-papulate carinal plates; plates angled over papulae, proximally crescentiform, 1 papula per space, frequently 1 secondary plate per papular space; disc bordered or not by 5 radial 5 interradial plates; spinelets thick, short, conical to subdigitiform, rugose, distally with multiple long fine points and frequently splay-pointed; up to about 14 spinelets across raised proximal edge of abactinal plates and angled over papula, frequently 1–2 on central bare distal surface of plate; up to about 8 spinelets per plate in mid-distal interradius; up to about 7 conical pointed spinelets per superomarginal plate, up to about 16 digitiform spinelets per inferomarginal plate, thick distally on plates.

Spines per actinal plate up to: oral 7, suboral 3, furrow 6, subambulacral 5, actinal interradial 5, predominantly 3; actinal interradial spines thick, sacciform, conical to digitiform.

Colour (live). Variably mottled with combinations of dark and pale mauve, dark brown to black, pale brown, red, green, white; sometimes predominantly pink-mauve or white (photos from H. Moosleitner and J. Hinterkircher; Moosleitner (1997)).

Distribution. Red Sea, Gulfs of Suez and Aqaba.

Etymology. Named for Loisette Marsh, Western Australian Museum, with appreciation of her generous assistance with loan material and her significant research into echinoderm systematics in the Indo-Pacific region.

Remarks. Two fissiparous species occur in the Red Sea, and are recognized in this work as *Aquilonastra burtonii* (above) and *Aquilonastra yairi* sp. nov. (below). *Aquilonastra marshae* has frequently been reported in the literature as a larger nonfissiparous pentaradiate growth stage of *Asterina burtonii* (see synonymy). Achituv (1973b) reported on the genital cycle of *Asterina burtoni* from the Gulf of Elat. Fissiparous and nonfissiparous forms were not distinguished. Maximum R was 14 mm. We judge that the material was probably principally *A*. *marshae*. Aquilonastra samyni sp. nov. (below) occurs on the coast of the Arabian Sea and is morphologically similar to A. *marshae*. The diagnostic characters that distinguish A. *marshae* from A. samyni are discussed in the Remarks for A. samyni below.

Aquilonastra minor (Hayashi, 1974)

Figures 1, 3d

Asterina minor Hayashi, 1974: 41–44, fig. 1.–A.M. Clark, 1993: 211.–Fujita and Saba, 2000: 169–170, pl. 3E.–Waters et al., 2004: 873, 876, 877, tbl. 1, figs 1, 2.

Aquilonastra minor.—O'Loughlin and Waters, 2004: 11, 13–15, fig. 1.—Saba and Fujita, 2006: 270–272, 286, fig. 15.—Byrne, 2006: 245, 251, tbls 1, 2, fig. 1.

Material examined. Japan, NMV F96697 (2).

Diagnosis. Non-fissiparous *Aquilonastra* species; rays 5, short, broad basally, narrowly rounded distally; up to R = 9 mm; gonopores actinal; direct development into brachiolaria stage (Hayashi, 1974).

At R = 7 mm, r = 5 mm, rare proximal doubly papulate carinal plates, rare secondary plates, abactinal plates with low domes, spinelets in tufts or bands, subpaxilliform, described as "paxilliform" by Hayashi (1974); up to about 20 spinelets on proximal abactinal plates; spinelets thin, columnar, distally spinous; superomarginal plates smaller than inferomarginals, up to about 8 spinelets per superomarginal plate.

Spines per actinal plate up to: oral 6, suboral 4, furrow 5, subambulacral 3, actinal interradial 3; interradial spines digitiform.

Colour (live). "Pale greenish white, pale green or brownish grey with small greenish white patterns and small dark brown scattering spots, and reddish colour intermixed in the marginal zone; madreporite yellowish orange" (Hayashi, 1974); disc cream, rays and interradii pale mottled pink, brown, cream white (photo from M. Komatsu).

Distribution. Japan, southern Honshu, Kushimoto, littoral (Hayashi, 1974).

Remarks. The largest of the many specimens observed by Hayashi (1974) were up to R = 6 mm. The two specimens donated by Mieko Komatsu to Jon Waters, and subsequently to Museum Victoria, are up to R = 7 mm (preserved). Fujita and Saba (2000) reported R up to 9.4 mm for Takehara (assumed not dried). Saba and Fujita (2006) reported R up to 7.7 mm for Sagami Bay. We wonder whether there is more than one species being referred to *A. minor*. Distinctive characters for *A. minor* are: rounded low domes on some abactinal plates; actinal gonopores.

Aquilonastra moosleitneri sp. nov.

Figures 1, 9e

Asterina burtoni.—A.M. Clark and Davies, 1966: 599.—A.M. Clark, 1967b: 146, fig. 1B.—Jangoux and Aziz, 1984: 861, 872, 873 (part; non Asterina burtonii Gray, 1840).

Asterina burtoni burtoni.—A.M. Clark and Rowe, 1971: 68, fig. 17e.—A.M. Clark, 1993: 207–208 (non Asterina burtonii Gray, 1840).

Asterina anomala.—Moosleitner, 1997: 12, fig. 22 (non Asterina anomala H.L. Clark, 1921).

Material examined. Holotype. Maldive Is., Male, Hulule, J.S Gardiner, 1899–1900, NHM 1902.3.13.27 (alcohol). Paratypes. Type locality and date, NHM 1902.3.13.28–33 (30).

Other material. Maldive Is., Eryadoo I., WAM Z6854 (1; photo in Moosleitner, 1997).

Diagnosis. Fissiparous *Aquilonastra* species; rays up to 7, predominantly 6, form frequently asymmetrical post-fissiparity, form of larger specimens sometimes symmetrical with 5 equal rays, most interradii with inconspicuous madreporite; rays narrow basally, tapering, narrow rounded distally; up to R = 9 mm, r = 4 mm; abactinal gonopores on largest pentaradiate specimens.

At R = 9 mm, lacking carinal plates; some secondary plates; 3 longitudinal series of papulae on sides of mid-ray; spinelets granuliform, short conical to columnar, rugose, blunt; up to about 10 spinelets over each plate, readily detached; superomarginal plates each with up to about 5 spinelets, inferomarginal plates each with up to about 10 larger spinelets.

Spines per actinal plate up to: oral 5, suboral 2, furrow 5, subambulacral 3, actinal interradial 3 (predominantly 3); interradial spines short, conical, pointed.

Colour (live). "Reddish, speckled with darker and lighter spots" (Moosleitner, 1997).

Distribution. Maldive Is.

Etymology. Named for Horst Moosleitner, with gratitude for his assistance in providing photos and specimens for this work, and with appreciation of his work on the asteroids of the Maldives.

Remarks. Moosleitner (1997) noted that in the absence of a connecting growth series this small fissiparous species was probably a separate species from the non-fissiparous asterinid on the Maldives. We agree that there are two species. A.M. Clark (1967b) determined the small fissiparous asterinid from the Maldive Is as *Asterina burtoni*. The 31 specimens (NHM 1902.3.13.27–33) are similar to *Aquilonastra conandae* in size, number of rays, and spinelet and spine form, but are similar to *Aquilonastra burtonii* in frequently having more than one interradial actinal spine per plate. The species size (up to R = 9 mm) is significantly smaller than *A. burtonii* (up to R = 18 mm).

Aquilonastra oharai sp. nov.

Figures 1, 3e, 9f

Material examined. Holotype. Japan, Okinawa, Seragaki, under rock on reef, 1–2 m, G. Paulay, 26 Jul 2004, UF 3285 (alcohol).

Paratypes. Type locality and date, UF 3916 (1, alcohol); Kunigami, reef flat, under rock, G. Paulay, J. Geller, M. Malay, Y. Hiratsuka, 4 Jul 2004, UF 3914 (1, alcohol; BOKI–14, d GP 595, 596).

Diagnosis. Non-fissiparous *Aquilonastra* species; rays 5, wide basally, tapered, rounded distally; up to R = 12 mm, r = 7 mm; gonopores abactinal.

At R = 12 mm, lacking proximal doubly papulate carinal plates; some secondary plates, frequently 1 per proximal papular space; single large papula per space; spinelets conical, thin, fine point to splay-pointed, subsacciform, in double splayed series across proximal edge of plates, rarely in tufts, up to about 14 spinelets on proximal abactinal plates, up to about 8 on distal interradial plates; superomarginal plates smaller than inferomarginals, superomarginals with up to about 14 spinelets per plate, inferomarginals with up to about 14 spinelets, more stout on inferomarginals.

Spines per actinal plate up to: oral 6, suboral 2, furrow 4, subambulacral 4, actinal interradial 6, predominantly 4–6 proximally; interradial spines conical, thick basally, pointed distally.

Colour (live). Variable, disc dark brown, mottled abactinally with mauve-violet, dark and pale brown, greenish brown, off-white; or disc dark brown, mottled abactinally with pale and dark green, and off-white (photos by G. Paulay).

Distribution. Japan, Okinawa, 0-2 m.

Etymology. Named for Tim O'Hara, Senior Curator of Marine Invertebrates, Museum Victoria, in appreciation of his contribution to this work and to echinoderm systematics and biogeography.

Remarks. A. oharai is distinguished from *A. cepheus* and *A. limboonkengi* by the shorter rays, absence of any proximal doubly papulate carinal plates, absence of clustering of the abactinal spinelets on the plates, and the splay-pointed form of some abactinal spinelets. *A. oharai* is described from only three specimens, with R up to 12 mm. The morphological characters used to distinguish the new species may be variable within the species, and size related. In the absence of adequate comparative material we have some uncertainty about the status of *A. oharai* in relation to *A. cepheus* and *A. limboonkengi*.

Aquilonastra richmondi sp. nov.

Figures 1, 4e, 6f,g, 10a

Asterina burtoni.—Jangoux, 1973: 35–38, fig. 13 (probably part, Mozambique material; non Asterina burtonii Gray, 1840).

Asterina burtonii.-Walenkamp, 1990: 67-72, figs 30, 31 (part, Mozambique material; non Asterina burtonii Gray, 1840).

Asterina coronata.—Jangoux, 1973: 38–39 (part, 3 Mozambique specimens; non Asterina coronata Martens, 1866 according to Walenkamp, 1990; non Asterina burtonii Gray, 1840).

'Asterina' sp. 1.—Rowe and Richmond, 2004: 3287 (part, Grand Paté specimen), fig. 4 (colour).

Material examined. Holotype. Tanzania, Ras Kimbiji, lower littoral, under boulders, M. Richmond, 4 Sep 2004, NHM 2005.37 (alcohol).

Paratypes. Type locality and date, NHM 2005.35 (1); NHM 2005.36 (1).

Other material. Côtes d'Arabie, St. XLVII, 1901–1904, MNHN EcAs11043 (1); Kenya, Kiunga Marine Reserve, 8 m, Apr 1999, MRAC 1739 (1); Zanzibar, Rousseau, 1841, EcAh3884 (1); Tanzania, Mnazi Bay, Ruvula Peninsula, rocky, lower littoral, 3 Feb 2004, NHM 2004.2832 (1); Mombassa, NHM 1972.8.22.3–17 (2 of 14 seen); Comoros, Mayotte, Mission Cherbonnier 25, littoral reef, 1959, MNHN EcAs11862 (1); Mission Cherbonnier 27, 1959, EcAs11863 (1);

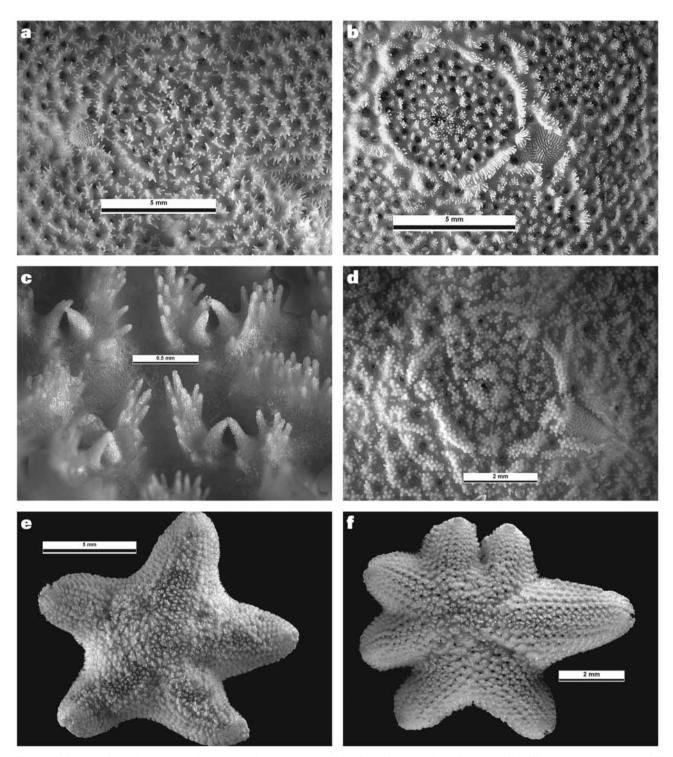


Figure 10. Photos of *Aquilonastra* species. a, *A. richmondi* sp. nov., SE Africa, Sodwana Bay, disc (MRAC 1737); b, *A. rowleyi* sp. nov., SE Africa, Sodwana Bay, disc (MRAC 1736, holotype); c, *A. rowleyi* sp. nov., SE Africa, Sodwana Bay, pedicellariae (MRAC 1736, holotype); d, *A. samyni* sp. nov., SE Africa, Sodwana Bay, disc (MRAC 1741); e, *A. watersi* sp. nov., Rodrigues I. (NHM 2004.2813–2814); f, *A. yairi* sp. nov., Mediterranean Sea, Israel, Michmoret (R = 7 mm; holotype NMV F112174).

NW Madagascar, Nossi-Bi I. (Nosy Bé), Plante Collection, 1965– 1970, EcAs11865 (2); littoral reef, 2 Dec 1959, EcAs11858 (5); Cherbonnier, 6 Oct 1959, EcAs11859 (7); SW Madagascar, Mission Cherbonnier 201, Station Platier, 1962, EcAs11861 (2); NE Madagascar, Ile Sainte Marie, Ile aux Nattes, 26 Jun 1960, EcAs11860 (1); SE Madagascar, Fort Dauphin, Mission Decary, 1932, EcAs11864 (1); Madagascar, Gruvel Collection, 1923, EcAs10379 (1); Mauritius, Rodrigues I., Grand Paté, on coral, 20 m, 23 Sep 2001, AM J24287 (1); E South Africa, Sodwana Bay, 11 m, 10 Feb 2001, MRAC 1737 (1); 14 m, Aug 1999, MRAC 1738 (1).

Diagnosis. Non-fissiparous *Aquilonastra* species; rays 5, rarely 6, broad to narrow basally, tapered, narrowly rounded distally; up to R = 25 mm, r = 12 mm; form frequently asymmetrical, one ray shorter than other 4; gonopores abactinal; pedicellariae sometimes evident on upper rays and in interradii, 2–3 short, thick valves not significantly differentiated from adjacent spinelets.

At R = 20, r = 10 mm, abactinal plates closely imbricate, proximal edge projecting, spinelets subpaxilliform; 0-5 proximal doubly-papulate carinal plates; few proximal secondary plates, 0-2 per space; predominantly single large papula per space, sometimes 2; spinelets short, conical, bluntly pointed, subsacciform, not splay-pointed, frequently of two forms, thin on outer margin of plates, thick short on apex of plates (columnar to subgranuliform); up to about 20 spinelets on each proximal abactinal plate, predominantly over surface of plate, some in clusters of 3-4; distal interradial plates with up to about 8 long, thin, pointed spinelets, frequently splayed in distinctive widely radiating cluster per plate, overlapping spinelets of adjacent plates on larger specimens; superomarginal plates smaller than inferomarginals, superomarginal plates with up to about 7 spinelets per plate, inferomarginals with up to about 14 spinelets per plate, thin proximally thick distally.

Spines per actinal plate up to: oral 8, suboral 4, furrow 7, subambulacral 5, actinal interradial 5, predominantly 2; interradial spines thick, rugose, bluntly conical, subsacciform.

Colour (live). Sharply mottled with green, maroon, pale brown, pink, white, black (photos by M. Richmond); variable and changeable, mottled with red, pink, orange, white, grey, blue (Walencamp, 1990; with colour photos).

Distribution. Côtes d'Arabie, E Africa, Kenya, Tanzania, Comoros, Madagascar, Mauritius, E South Africa; under boulders and in crevices in rocks and live coral; 0–20 m.

Etymology. Named for Matt Richmond, with appreciation of his contribution of material from Tanzania and Rodrigues I.

Remarks. Two distinctive features of *A. richmondi* are: frequently two forms of spinelets on the abactinal plates, thicker apically; splayed overlapping spinelet clusters on the distal abactinal plates. The detailed description and colour photos of *A. burtonii* by Walenkamp (1990) indicate that the Mozambique Inhaca material was not *A. burtonii* and is conspecific with *A. richmondi*. Ludwig (1899) reported *Asterina cepheus* for Zanzibar. There is no evidence in this study of *A. cepheus* occurring in the western Indian Ocean, but the morphologically similar *A. richmondi* is reported here for Zanzibar.

Aquilonastra rosea (H.L. Clark, 1938)

Figures 1, 3f, 6h

Paranepanthia rosea H.L. Clark, 1938: 161–162, pl. 22 fig. 8.– H.L. Clark, 1946: 137.–A.M. Clark, 1993: 223.–Marsh and Pawson, 1993: 285.–Rowe and Gates, 1995: 39.

Asterinopsis rosea.-Cotton and Godfrey, 1942: 203.

Aquilonastra rosea.—O'Loughlin and Waters, 2004: 11, 13-15.

Material examined. Paratypes. SW Western Australia, Rottnest I., AM J6171 (3).

Other material. Rottnest I., 18 Aug 2004, WAM Z31171 (1); Perth, 4 Aug 2004, Z31174 (1); Jurien Bay, J7437 (4); 13 m, 27 Apr 2005, Z31162 (1); Abrolhos Is., 110 m, 6 Dec 1970, Z21265 (1).

Diagnosis. Non-fissiparous *Aquilonastra* species; rays 5, long (at R = 17 mm), wide basally, tapering to narrowly rounded distally, up to R = 17 mm, r = 9 mm.

At R = 17 mm, regular doubly papulate carinal plates proximally; abactinal plates not in 2 "fields"; abactinal plates with high raised rounded column or ridge, concave papular notch; longitudinal series of plates and papulae along sides of rays; predominantly single large papula per space; very few secondary plates; disc delineated by 5 wide radial plates, 5 short interradial plates; spinelets sacciform, long, splaypointed; spinelets in paxilliform dense splayed round tufts of more than 30 per plate; superomarginal and inferomarginal plates with subequal tufts of spinelets.

Spines per actinal plate up to: oral 9; suboral 12; furrow 7; subambulacral 12; actinal interradial 20; spines on subambulacral and actinal plates in tufts; interradial spines sacciform, splay-pointed.

Colour (live). "Rose-red, more or less variegated with creamcolour" (H.L. Clark, 1938).

Distribution. SW Australia, Abrolhos I. to Rottnest I.; 0-110 m.

Remarks. O'Loughlin and Waters (2004) reassigned *Paranepanthia rosea* to *Aquilonastra*. This reassignment is upheld here provisionally on the basis of the arrangement of abactinal plates and papulae, the presence of internal superambulacral plates, and the arrangement of actinal plates. However, the paxilliform tufts of long thin abactinal spinelets and actinal spines, and high numbers of spinelets and spines per plate, are atypical of *Aquilonastra*. *A. scobinata* (below) is morphologically similar to *P. rosea* in having paxilliform tufts of numerous long thin abactinal spinelets, superambulacral plates in series parallel to the furrow. The paxilliform tufts of spinelets in *A. rosea* are round, those in *A. scobinata* are frequently crescentiform.

Aquilonastra rowleyi sp. nov.

Figures 1, 6i, 10b, c

Material examined. Holotype (dry). South Africa, KwaZulu Natal, Sodwana Bay, 11 m, Y. Samyn and I. Tallon, 10 Feb 2001, MRAC 1736.

Diagnosis. Non-fissiparous *Aquilonastra* species; rays 5, not discrete or elongate, wide basally, narrowly to broadly rounded distally, R = 23 mm, r = 14 mm; form shallow concave

interradially; pedicellariae present in proximal interradii, 2 valves differentiated with inner teeth, taller than adjacent spinelets; abactinal gonopores.

At R = 23 mm, lacking abactinal carinal series of plates, broad band of upper ray plates irregularly arranged, longitudinal and transverse series along sides of rays creating lattice-like appearance, plates with concave papular notch; single small papula per space; 6 longitudinal series of papulae along each side of mid-ray; secondary plates numerous on irregular upper ray; disc delineated by continuous curved dense band of spinelets on 5 wide radial plates, each with up to about 100 spinelets, 5 small interradial plates; spinelets glassy, elongate, thin, pencil-like; up to about 30 spinelets in short crescentiform band across projecting edge of each plate on proximal ray; irregular lumpiness more than glassy convexities on plates; superomarginal and inferomarginal plates subequal, in regular series; superomarginal plates with up to about 8 pencil-like spinelets; inferomarginal plates with up to about 16 spinelets, proximally subequal with superomarginal spinelets, distally longer and thicker.

Integument evident actinally; non-plated area in one proximal actinal interradius.

Spines per actinal plate up to: oral 10 long, thin; suboral 5 long, 5 short; furrow 7; subambulacral 7; actinal interradial 4, predominantly 3; interradial spines glassy, long, sacciform, in webbed combs.

Colour (live). No record.

Distribution. East African coast, KwaZulu Natal, Sodwana Bay, 11m.

Etymology. Named for Chris Rowley (Marine Biology Section, Museum Victoria), in appreciation of the photography and curatorial assistance that have been graciously provided in support of asterinid systematic research.

Remarks. The new species has many of the diagnostic characters of *Aquilonastra*, but is assigned with reservations because the numerous spinelets are pencil-like and not typical of *Aquilonastra*. They resemble those of *Patiriella oliveri* (Benham, 1911), *Callopatiria granifera* (Gray, 1847), and *Aquilonastra scobinata* (below). The rays are distinct, but the form is closer to subpentagonal than the discrete-rayed form of *Aquilonastra*. In an absence of adequate material we are unwilling to erect another asterinid genus. The tall pedicellariae with distinctive innertoothed valves are unique amongst asterinids.

Aquilonastra samyni sp. nov.

Figures 1, 3g, h, 6j, 10d

Material examined. Holotype. Oman, Masirah I., 1–7 m, under rocks, G. Paulay, 6 Nov 1999, UF 246 (alcohol).

Paratypes. Type locality, 15–18 m, G. Paulay, 5 Nov 1999, UF 68 (8, alcohol); Bar al Hikman, under rocks, 0–1 m, M. Bouchard, 7 Nov 1999, UF 1645 (2).

Other material. Oman, Bar al Hikman peninsula, 1–3 m, under rocks, 18–20 Jan 2005, UF 4210 (2); 2–3 m, UF 4201 (3); 2–4 m, under rocks, Jan 2005, UF 4143 (3); Muscat, Qurm, intertidal, 26 Jan 2005, UF 4147 (6); UF 4251 (1); UF 4252 (1); Bandar Khayran, under rocks, 0–5 m, 29 Oct 1999, UF 1378 (1); Madagascar, MNHN EcAs11853 (1);

NW Madagascar, Nossi Be (Nosi Bé), littoral reef, 24 Sep 1964, EcAs11848 (1); 2 Dec 1959, EcAs11849 (5); 1962, EcAs11850 (1); 6 Oct 1959, EcAs11851 (3); 3 Dec 1959, EcAs11852 (2); SW Madagascar, Tuléar, EcAs11847 (1); Ile Sainte-Marie, 11 Feb 1979, WAM Z6870 (2); La Réunion I., Tobogan, 10 Sep 2001, NMV F109365 (1); South Africa, Sodwana Bay, 10 m, Jul 2000, MRAC 1741 (1); 13 m, Aug 1999, MRAC 1740 (1); MRAC 1743 (1); Bangha Nek, 16 m, Aug 1999, MRAC 1742 (1).

Diagnosis. Non-fissiparous *Aquilonastra* species; rays predominantly 5, rarely 6, narrow basally, slight taper, rounded distally, subdigitiform, up to R = 27 mm, r = 11 mm; single conspicuous madreporite, 2 rare, 3 very rare; gonopores abactinal.

At R = 23 mm, r = 9 mm, 0–3 proximal doubly papulate carinal plates; disc frequently well-delineated by 5 radial 5 interradial plates; up to about 30 spinelets in irregular double transverse series across proximal abactinal plates, some spinelets in poorly defined clusters (spinelets granuliform on small specimens); 0–2 secondary plates per papular space proximally, rarely 2 papulae per space; spinelets small, short, thick, conical to columnar, sometimes splay-pointed, sometimes with long thin distal point; up to about 14 on distal interradial plates, not overlapping adjacent plate spinelets if splayed; superomarginal plates smaller than inferomarginals, superomarginals with up to about 12 spinelets per plate.

Spines per actinal plate up to: oral 8, suboral 6, furrow 7, subambulacral 8, actinal interradial 14, predominantly 8–12; interradial spines short, thick, rugose, sacciform, bluntly conical (lower spine numbers per plate on South Africa material).

Colour (live). Variable; disc white, apically around disc bright red, rays mottled mauve, brownish-red, off-white, brown (photos from G. Paulay and Y. Samyn).

Distribution. Oman (Masirah I.); Madagascar; La Réunion I.; E South Africa (Sodwana Bay); 0–18 m.

Etymology. Named for Yves Samyn, of the Royal Belgian Institute of Natural Sciences, for his contribution of specimens used in this work and in appreciation of his research on echinoderm systematics.

Remarks. Pentaradiate, single madreporite, non-fissiparous specimens as small as R = 6 mm have been examined, evidence that this species does not have a small pluriradiate fissiparous growth stage. Large specimens have mostly come from the deeper sublittoral (3–18 m), while the numerous small specimens have mostly come from the intertidal and shallow sublittoral (0–2 m). If this species occurs in deeper sublittoral habitats this might account for the absence of the species in collections from most of the eastern African coast. It might also account for the absence of large specimens from Madagascar, as the collecting appears to have been littoral.

A. samyni is morphologically similar to A. marshae (above), but is distinguished from A. marshae (characters in brackets) by: rays long, mostly subdigitiform, only slightly tapered (not short, mostly strongly tapered); abactinal surface is predominantly flat (plates not raised proximally and angled over papulae); spinelets are predominantly spread over plate surface (not predominantly concentrated over raised proximal plate edge); distal plate surfaces with spread spinelets (not bare with 1–2 central spinelets); at R = 16 mm, predominantly 6 spines per actinal plate (not 3); actinal spines short, blunt, sacciform (not conical to digitiform).

For population studies by Soliman (1995, 1999) see Remarks under *A. burtonii* above.

Aquilonastra scobinata (Livingstone, 1933)

Figures 1, 3i, 6k

Asterina scobinata Livingstone, 1933: 1–2, pl. 5 figs 9–12, 15.— H.L. Clark, 1938: 149–150.—Cotton and Godfrey, 1942: 201.—H.L. Clark, 1946: 132.—Dartnall, 1969: 55.—Dartnall, 1970a: 73, 76.— Dartnall, 1970b: 19–20, figs 1, 2.—Dartnall, 1980: 8, 34, 66.—Zeidler and Shepherd, 1982: 412, fig. 10.6e.—O'Loughlin, 1984: 134.—A.M. Clark, 1993: 213.—Rowe and Gates, 1995: 35.—Waters et al., 2004: 873, 876, figs 1, 2.

Aquilonastra scobinata.—O'Loughlin and Waters, 2004: 11, 13–14, fig. 1.—Byrne, 2006: 245, 248, tbls 1, 2, fig. 1.

Material examined. Holotype. Tasmania, AM J1241.

Other material. Tas., Port Arthur, 25 Nov 1968, NMV F112178 (2); Eaglehawk Neck, J9060 (3); Tamar R. mouth, North Head, 28 Oct 1978, F112176 (1); King I., 10 Mar 1980, F112177 (1); Vic., Inverloch, 28 Mar 1981, F72975 (1); Point Leo, 20 Apr 1935, F58683 (1); Phillip I., NMV F72998 (1); Flinders ocean platforms, 7 Sep 1994, F112180 (3); Cape Otway, 3 Apr 1983, F58682 (2); Killarney, F72997 (10); Port Fairy, F72985 (2); SA, Port MacDonnell, 8 Jan 1988 F112179 (1).

Diagnosis. Non-fissiparous *Aquilonastra* species; rays 5, wide basally, tapered, narrowly rounded distally, up to R = 18 mm, r = 8 mm; form frequently asymmetrical with one ray shorter; actinal gonopores, hermaphrodite.

At R = 14 mm, r = 7 mm, proximal ray with zig-zag carinal series of singly papulate plates, bordered laterally by subequal non-papulate plates; singly papulate plates in longitudinal series along sides of rays; papulate plates not notched, slightly crescentiform, non-papulate plates round to oval to irregular; rarely 2 papulae per space; secondary plates rare; disc small, variably delineated by 5 long radial 5 short interradial plates; spinelets elongate, thin, pencil-like, splay-pointed sacciform; up to more than 30 per plate, in splayed tuft or crescentiform or straight band across plate; superomarginal and inferomarginal plates subequal, in regular series; superomarginal plates with up to about 10 pencil-like splaypointed spinelets; inferomarginal plates with up to about 20 paxilliform similar spinelets.

Spines per actinal plate up to: oral 7; suboral 6; furrow 6; subambulacral 6; actinal interradial 7; interradial spines long, rugose, digitiform, some pointed distally.

Colour (live). Dark brown to greyish-brown to cream, with some dark flecking (O'Loughlin, 1984).

Distribution. Tas., Bass Strait, Cape Conran (eastern Vic., NMV collections) to Port MacDonnell (SA); rocky lower littoral and shallow sublittoral.

Remarks. A. *scobinata* is provisionally maintained in *Aquilonastra* because of the arrangement of abactinal plates and papulae, the presence of internal superambulacral plates, and the arrangement of actinal plates. The paxilliform tufts of

long thin pencil-like abactinal spinelets and actinal spines, and high numbers of spinelets and spines per plate, are atypical of *Aquilonastra*. Morphological similarities of *A. scobinata* to *A. rosea* and *A. rowleyi* have been noted above.

Dartnall (1970b) reported actinal gonopores and hermpahrodite reproduction. Mieko Komatsu (pers. comm.) confirmed that a specimen (F112180) was hermaphroditic.

Aquilonastra watersi sp. nov.

Figures 1, 3j, 6l, 10e

'Asterina' sp. 1.—Rowe and Richmond, 2004: 3287 (part, Trou Malabar specimens).

'Asterina' sp. 2. —Rowe and Richmond, 2004: 3287 (part, Rivière Banane specimen).

Asterina cephea.—Loriol, 1885: 69–71, pl. 21 figs 1–5 (non Asteriscus cepheus Müller and Troschel, 1842).

Material examined. Holotype. Oman, Masirah I., shore, under rocks, G. Paulay, 5 Nov 1999, UF 3282 (alcohol).

Paratypes. Type locality and date, UF 70 (5, alcohol); UF 3283 (1, dry, dissected); Masirah I., reef slope, under rocks, 1–5 m, G. Paulay, 1 Nov 1999, UF 356 (1, alcohol).

Other material. Oman, Bar al Hikman peninsula, under rocks, 0–6 m, Jan 2005, UF 4142 (10); UF 4148 (1); UF 4144 (1); UF 4192 (2); Red Sea, Egypt, near Qusier, 2002, NMV F106970 (1); Mauritius, MNHN EcAs11866 (1); ex MAU 74–6, EcAs11867 (1); ex MAU 74–20, EcAs11868 (1); ex MAU 74–23, EcAs11869 (1); ex MAU 74–24, EcAs11870 (1); ex MAU 74–33, EcAs11871 (2); ex MAU 74–36, EcAs11872 (1); ex MAU 74–40, EcAs11873 (1); ex MAU 74–38, EcAs11874 (1); ex MAU 74–40, EcAs11875 (1); Mauritius, Robillard, NHM [18]89.3.11.7–9 (3); Cape Malheureux, Coin de Mire I., 24 m, 15 Nov 1999, UF 3281 (1); Rodrigues I., Rivière Banane, in algae, 21 Sep 2001, AM J24290 (1); Trou Malabar, coral rubble, 10 m, 22 Sep 2001, NHM 2004.2813–2814 (2); Madagascar, Nossi-Bi, littoral reef, 2 Dec 1959, EcAs11906 (1).

Diagnosis. Non-fissiparous *Aquilonastra* species; rays 5, broad basally, tapering, rounded distally, up to R = 19 mm, r = 11 mm; gonopores abactinal; few pedicellariae in abactinal interradii, each with 2 thick curved pointed differentiated valves, not evident on small specimens.

At R = 16 mm, r = 9 mm, 0–10 proximal doubly papulate carinal plates, each with up to 4 spinelet clusters each cluster with up to 7 spinelets; up to about 20 spinelets on proximal abactinal plates, in clusters or band across proximal edge of plate; rare small secondary plates; spinelets small, thin, long, digitiform to predominantly bluntly conical, sometimes subsacciform, rarely splay-pointed; up to about 8 in tufts on distal interradial plates, not overlapping adjacent plate spinelets if splayed; superomarginal plates smaller than inferomarginals, superomarginals with up to about 14 larger spinelets per plate.

Spines per actinal plate up to: oral 7, suboral 6, furrow 6, subambulacral 6, actinal interradial 8, predominantly 5–6; interradial spines thick basally, conical, subsacciform.

Colour (live). Mottled pale brown, red-brown, grey-brown, blue-grey, off-white (photo by G. Paulay).

Distribution. Arabian Sea, Oman; Red Sea, Egypt; W Indian Ocean, Mauritius, Rodrigues I.; 0–24 m.

Etymology. Named for Jon Waters, of the University of Otago in New Zealand, in appreciation of his significant contribution to our understanding of the molecular phylogeny of Asterinidae.

Remarks. Two of the larger specimens from Mauritius (UF 3281, MNHN EcAs11868) have the characteristic pedicellariae of the types from Oman. For population studies by Soliman (1999) see *Remarks* under *A. burtonii* above. *A. watersi* is distinguished by differentiated thick pedicellariae, and small, thin, long, subacicular spinelets.

Aquilonastra yairi sp. nov.

Figures 1, 4f, 10f

Asterina wega.—Achituv, 1973a: 333–336 (part, Acre and Akhziz pool populations).

Asterina burtonii.—Smith, 1927a: 641–645 (part).—Tortonese, 1960: 20–21 (probably part).

Asterina burtoni.—Price, 1983: 47–48, fig. 14 (part).—Achituv and Sher, 1991: 670 (part).—Mladenov and Achituv, 1999: 152 (part).— Karako et al., 2002: 139–144 (part, Akhziv, Shikmona, and Mikhmoret Mediterranean populations).—Waters et al., 2004: 874, 876–877, figs 1, 2, tbl. 1 (non Asterina burtonii Gray, 1840; see above).

Asterina burtoni burtoni.—A.M. Clark and Rowe, 1971: 68, fig. 17c (Acre), tbl. 1 (part).—A.M. Clark, 1993: 207–208 (part; non Asterina burtonii Gray, 1840).

Aquilonastra burtoni.— O'Loughlin and Waters, 2004: 11, 13 (part), 14, fig. 1.—Byrne, 2006: 245, tbls 1, 2, fig. 1 (non Asterina burtonii Gray, 1840).

Material examined. Holotype. Mediterranean Sea, Israel, Michmoret, Y. Achituv, 11 Jun 2005, NMV F112174 (alcohol). Paratypes. Type locality and date, F107434 (18, alcohol).

Other material. Israel, Akhziv, 25 Oct 1966, MNHN EcAs11042 (67, dry); Gulf of Suez, A.P. Dollfus, 25 Dec 1928, EcAs11840 (1, dry); AM J17892 (2, dry); Red Sea, NHM [18]40.3.23.55 (1, dry); don. J. Waters, F104975 (22, alcohol); F104974 (2, alcohol).

Diagnosis. Fissiparous *Aquilonastra* species; rays up to 8, predominantly 6, form frequently asymmetrical post-fissiparity; form of larger specimens sometimes symmetrical with 5 equal rays, most interradii with inconspicuous madreporite; rays narrow basally, tapering, narrow rounded distally, digitiform; up to R = 7 mm, r = 4 mm; gonopores not seen.

At R = 7 mm, lacking carinal plates; lacking large irregular proximal abactinal plates; 2 irregular longitudinal series of papulae on each side of rays; spinelets subgranuliform, short thick conical to columnar, splay-pointed, cover plates closely, frequently clustered in groups of up to 8 per group, up to about 16 spinelets on proximal plates, up to about 14 on midinterradial plates; superomarginal plates each with up to about 7 spinelets, inferomarginal plates each with up to about 14 taller spinelets.

Spines per actinal plate up to: oral 5, suboral 4 (frequently 3), furrow 4, subambulacral 4, actinal interradial 4 (predominantly 3); interradial spines conical, thin, pointed.

Colour (live). Specimens from Shikmona were all "mottled brown and orange" (pers. comm. Y. Achituv).

Distribution. Eastern Mediterranean, Acre, Akhziz pool populations, Michmoret, Shikmona; Red Sea, Gulf of Suez.

Etymology. Named for Yair Achituv (Bar-Ilan University, Israel), with appreciation of his contribution of material for this study and his research on the asternids of the eastern Mediterranean and Red Sea.

Remarks. At R = 7 mm, *A. yairi* is distinguished from *A. burtonii* by: having more actinal spines per plate (up to four not two suboral; up to four not two interradial); close cover of spinelets on abactinal plates, frequently clustered into groups (not covering plates sparsely); smaller and more regular abactinal plates; more numerous papulae.

Achituv (1969) studied "pentaradiate and pluriradiate" forms of an asterinid from Elat in the Gulf of Aqaba, and referred the pentaradiate form to *Asterina burtoni* and the pluriradiate form to *Asterina wega*. We support his conclusion that there are two discrete species. But we refer the nonfissiparous pentaradiate form to *Aquilonastra marshae* sp. nov. (above). The fissiparous pluriradiate form had R up to 12 mm, and is judged here to be *Aquilonastra burtonii* (Gray, 1840) and not conspecific with the smaller fissiparous species *A*. *yairi*. We have seen no evidence that *A*. *yairi* occurs in the Gulf of Aqaba. The use of "pentaradiate" to determine nonfissiparous specimens can be misleading as the larger fissiparous specimens frequently have five equal rays but continue to have more than one inconspicuous interradial madreporite.

For evidence from Achituv (1973) that both *A. burtonii* and *A. yairi* occur in the eastern Mediterranean, see Remarks under *A. burtonii* above.

Specimens (NMV F104974, F104975) were assumed to be *A. burtoni* and reported in the molecular phylogenetic work of Waters et al. (2004), and represented in the phylogenetic tree of O'Loughlin and Waters (2004). Both lots are redetermined in this work as *A. yairi*. In O'Loughlin and Waters (2004), the material AM J17892 (2) was assigned to *A. burtoni*. It is redetermined here as *A. yairi*.

The discovery of two type specimens of *Asterina burtonii* by Smith (1927a) is discussed above under *A. burtonii*. The smaller of these two types is assigned here to *A. yairi*.

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