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A new species of *Astrosarkus* from Western Australia including new Mesophotic occurrences of Indian Ocean Oreasteridae (Valvatida, Asteroidea)

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Abstract Mah, C.L. 2023. A new species of *Astrosarkus* from Western Australia including new Mesophotic occurrences of Indian Ocean Oreasteridae (Valvatida, Asteroidea). *Memoirs of Museum Victoria* 82: 143–165.

Astrosarkus lu n. sp. (Oreasteridae, Valvatida; Asteroidea) is described in addition to new *in situ* observations. Further occurrences of Indo-Pacific Oreasteridae are surveyed, with emphasis on distributions in the relatively poorly understood mesophotic zone.

Keywords Indian Ocean, deep-sea, Valvatida

Introduction

The mesophotic zone is a subject of increasing interest to conservation biology (e.g. Turner et al., 2019); evidence has been presented that this region is both a distinct, new zone with a distinctive fauna, as well as a possible refugia for shallow reefs (Semmler et al., 2017). The mesophotic zone has been delineated variously, but is defined herein as 30–150 m depending on region, a transition zone between shallow, reef ecosystems and deeper water habitats that historically has been difficult to investigate owing to being out of reach of shallow-water scuba diving and too shallow for conventional deep-sea sampling technology (e.g. large submersibles) (Baker et al., 2016).

Characterisation of the biological diversity in this newly discovered but poorly understood ecological zone is necessary to understand its impact on coral ecosystems (e.g. Turner et al., 2019). High diversity in coral species has been associated with mesophotic settings (Muir et al., 2018). Study of faunal composition of taxa in the mesophotic zone has suggested a mix of species from shallow and deeper waters (e.g. antipatharians in Bo et al., 2019). Numerous taxonomic studies have resulted in the discovery of undiscovered marine species, including corals (e.g. Breedy & Guzman, 2013), fishes (e.g. Tornabene et al., 2016) and other metazoans (e.g. Guerra Garcia & Ahyong, 2020). Echinoderm diversity shows high occurrence of potentially endemic mesophotic taxa and distinct species assemblages in the South Pacific (Mecho et al., 2019, 2021).

Within tropical reef settings, asteroids occupy prominent ecological roles, including those of predators affecting community structure, such as the crown-of-thorns sea star (*Acanthaster* spp.) (Birkeland and Lucas, 1990). Members of the Oreasteridae, which are sister taxa with *Acanthaster* (e.g., Yasuda et al., 2006; Mah and Foltz, 2011), are familiar in these habitats but are not well studied and many similarly occupy significant ecological roles. The cushion star *Culcita novaeguineae*, for example, can affect scleractinian coral community structure significantly (Glynn and Krupp, 1986). The shallow-water Indo-Pacific *Protoreaster nodosus* are known as important consumers and bioturbators in sedimentary habitats (e.g. Scheibling and Metaxas, 2008). Mesophotic observations of oreasterids, especially their diversity, is an important consideration within the context of coral reefs and related settings.

Among the most distinctive of mesophotic asteroids is the oreasterid *Astrosarkus*, which was one of the earliest known asteroids determined to specifically inhabit this depth zone. *Astrosarkus idipi* was first described by Mah (2003) from mesophotic settings in Palau (67 m), the Marshall Islands (125 m), and Reunion Island (Indian Ocean, 185–200 m). It has since been discovered in the Okinawa region of Japan and American Samoa (Kogure et al., 2009). Known specimens are large (up to 30 cm in diameter) and possess thick bodies with a soft but firm, fleshy body wall. They occur widely in the South Pacific and Indian Ocean, but have only been observed at mesophotic depths (67–210 m). One of the few other oreasterids present at mesophotic or deeper-water faunas is the South Pacific *Acheronaster tumidus* H.E.S. Clark 1982, which is known from 110–300 m from New Zealand, southern Australia and New Caledonia, with a possible second species observed from Rapa Nui at a depth of 269–300 m (Mah, 2021).

Recent exploration and sampling of deeper-water mesophotic habitats has revealed that in addition to *Astrosarkus*, multiple commonly encountered shallower-water oreasterid species are evident. New material discovered in the Museum Victoria during visits in 2017 and 2023, additional material from the National Museum of Natural History in Washington, DC (USNM), as well as newly acquired video imagery from multiple sources further elaborate on the unusual *Astrosarkus*, as well as mesophotic occurrences and other biology in the Oreasteridae. Occurrence and ecological observations will provide further insight into mesophotic asteroid faunas.

Materials and methods

Material referenced herein is deposited at the Museum Victoria (NMV) in Melbourne, Australia, the USNM, the California Academy of Sciences in San Francisco, CA (CAS) and the Muséum national d'Histoire naturelle in Paris, France (MNHN).

Systematics

OREASTERIDAE Fisher 1908

Diagnosis. Body variable, ranging from pentagonal, cushion-shaped round bodies to more strongly stellate forms. Disk and arms strongly arched, with large coeloms in large specimens (R>~4.0= cm). Abactinal skeleton reticulate papular regions well developed. Marginal plates well developed but variably obscured by heavily granulate dermal layer, well-developed body wall or other covering. Surface covered by large primary spines, tubercles and/or other accessory structures. Adambulacral plates tall, articular surfaces prominent. Ambulacral and adambulacral ossicles stout, closely spaced, forming diamond-shaped chamber over ambulacral groove. Actinal papulae absent. Calcareous interbrachial septum present. Coelomic openings large. Upturned, terminal arm tip. Spicules in tube feet. Modified from Marsh and Fromont (2020) and Mah (2003).

Comments. The Oreasteridae are among the most prominent of shallow-water tropical Indo-Pacific and tropical Atlantic Asteroidea, owing in part to their relatively large size (reaching approximate diameter of 30 cm), conspicuous spination and eye-catching coloration (e.g. *Pentaceraster* species) (Marsh and Fromont, 2020). Many shallow-water species, such as the tropical Atlantic *Oreaster reticulatus*, are endangered by tourist fisheries and other human-related activities (e.g. Scheibling and Metaxas, 2010). Many oreasterids are known from shallow-water settings, but the lower limits of their depth distributions are not well understood. Several shallow-water species, known best from reef habitats, display bathymetric distribution into mesophotic depths (e.g. Mah, 2017, and species herein).

Astrosarkus Mah 2003

Diagnosis. Body pentagonal to weakly stellate, R/r=1.25–1.4. Arms and disk confluent with rounded arm tips, with thick smooth, soft "flesh" imbued with channels through the body wall; highly modified abactinal, marginal and actinal plates. Surface has continuous granular cover. Larger accessory structures present or absent. Papular areas extensive on discrete mound-like regions on abactinal, lateral surface. Internal, fixed, spine-like processes on ambulacrals. Furrow spines 10–11, subambulacral spines, 2–5. Modified from Mah (2003).

Comments. This account reports on new specimens and observations from Australian as well as other Indian Ocean localities. At the time of description, known distribution was limited to the tropical South Pacific to Reunion Island. *Astrosarkus* is now known to be widely distributed at mesophotic depths throughout the tropical Indo-Pacific (30–150 m), including southern Japan and Guam (Kogure et al., 2009) to the Marshall Islands/South Pacific, the coast of northern Australia (Queensland and Western Australia) and the western Indian Ocean (Reunion Island, Mayotte, Maldives).

Astroksarkus idipi Mah 2003

Figure 1a–e, Figure 2a–d, Figure 3a–b

Mah 2003: 685; Kogure et al., 2009: 73; Wheeler and Pennak, 2013: 94; Conand et al., 2018: 114; Mulochau et al., 2019: 21; Mulochau et al., 2020: 17.

Diagnosis. Body massive, lateral edge rounded, outline weakly stellate, arm tips round. Thorny tubercles absent. Furrow spines 10–11, subambulacral spines 2–5, but only approximately 1.5–2 times the size of the adjacent furrow spines.

Comments. The collected specimen represents the first individual recovered from the Maldives and the first from the north Indian Ocean. The first such specimen from the Indian Ocean was the paratype from the Indian Ocean (Mah, 2003). The red/orange and white morphotype in Fig. 1 has been documented from Guam (Kogure et al., 2009). As summarised herein, this species is widespread throughout the Indo-Pacific, extending from southern Japan, Guam, New Caledonia and northern Australia to the western Indian Ocean (Mayotte, the Maldives, and Reunion Island). The observed colouration appears variable and may represent infraspecific variation. Further testing for cryptic species is desirable.

Australian individuals (based on video). The Cape York individual (referred to as Cape York video under Videos Referenced) displays a solid red-orange on the abactinal surface with large, mottled white patches along the lateral surface and smaller irregular patches present on each of the convex mounds on the abactinal surface. The video captures only two arms and the lateral surface (Fig. 3a).

Body shape stellate, or weakly so. Arms short, but relatively well developed. A species identified by the arms distinctly set off from the disk with the abactinal surface covered by pronounced tumid convexities covered by small, translucent papulae, approximately 500–700 per mound. Singular discrete irregular circular areas possibly pedicellariae, but exact determination is unclear. Ambulacral furrow upturned along arm radius extending to abactinal surface.

The Tegrosse Reef video (Fig. 3b) captured a view of the abactinal surface, but with no closeups. Appearance of this specimen was consistent with the description of this species as outlined in the type (Mah, 2003) with a massive body, short, thick arms with rounded tips and the surface covered by numerous shallow mound-shaped regions, developed in transverse series across the arms.

Colour trends. Colour variation in *A. idipi* follows two general trends. One color morph is solid orange variably with white highlights and/or mottling on the papular regions, especially on

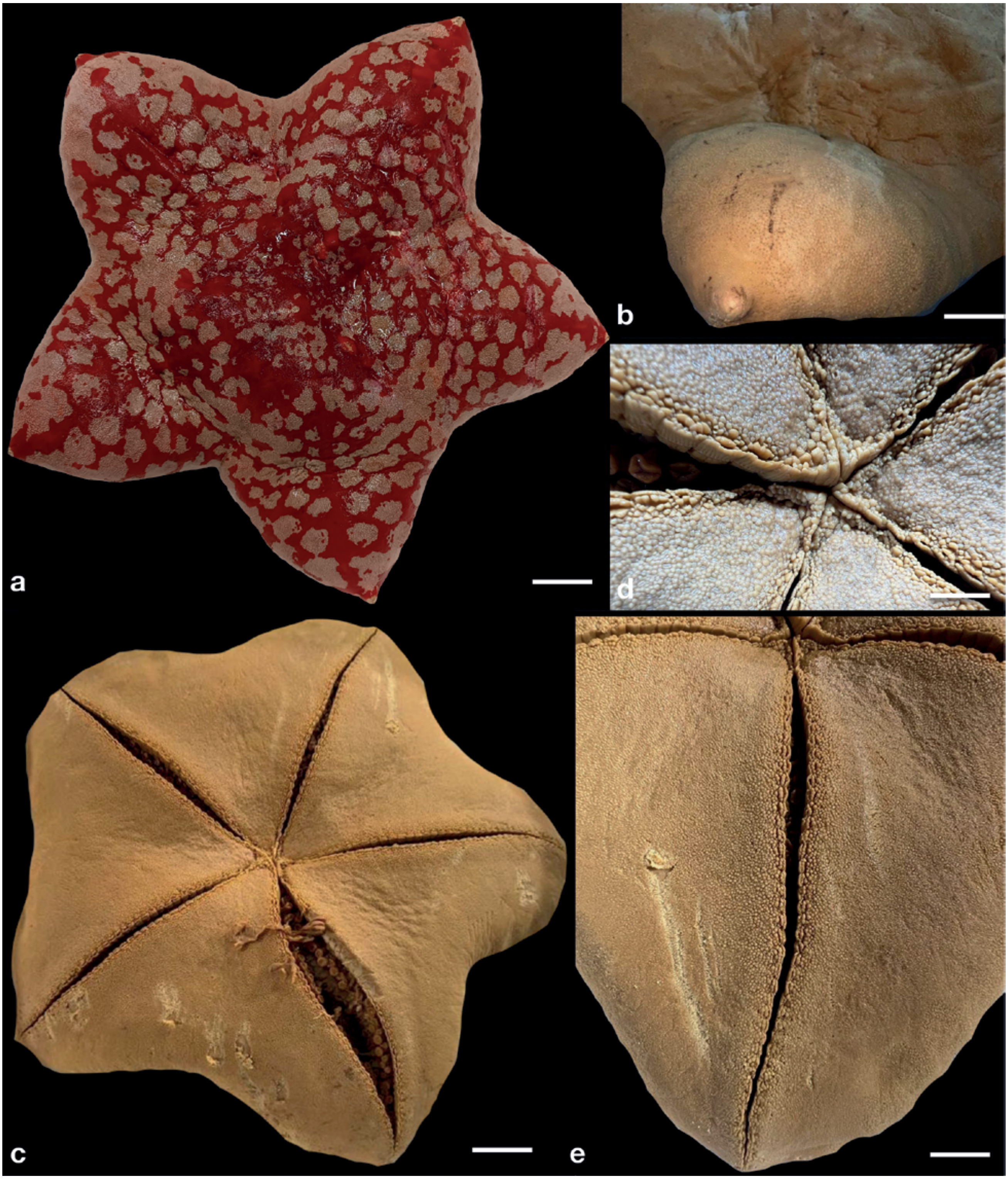

Figure 1. *Astrosarkus idipi* Maldives, specimen ID MAL1_330. a, Abactinal surface, specimen showing living coloration. Scale bar=4.0 cm; b, Abactinal surface of arm region. Scale bar=2.0 cm; c, Actinal surface, preserved specimen. Scale bar=4.0 cm; d, Actinal surface, oral region, closeup. Scale bar=1.0 cm; e, Actinal surface, showing furrow, adambulacral plates. Scale bar=2.0 cm.

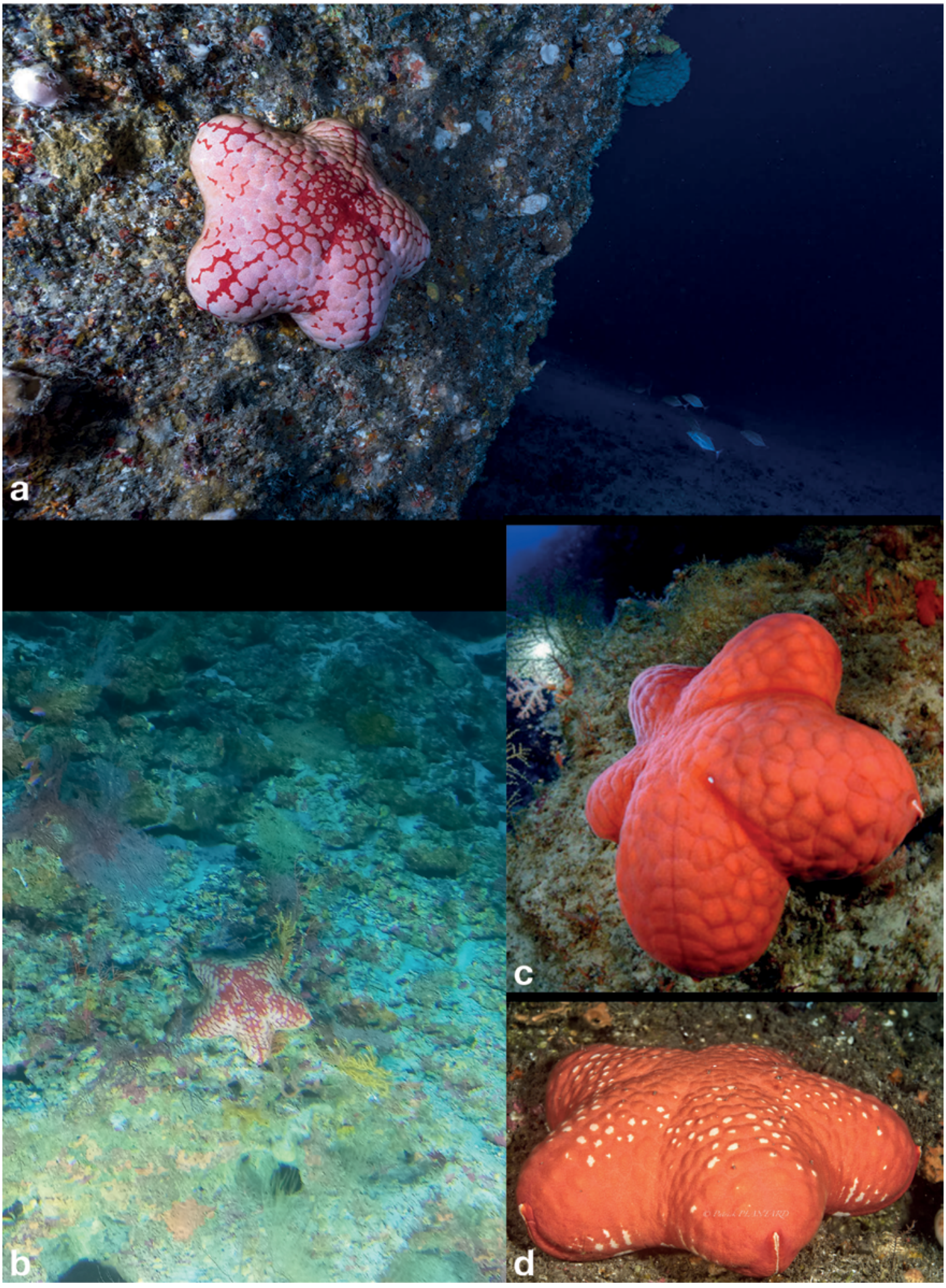

Figure 2. *Astrosarkus idipi*. Maldives/Mayotte. a, *Astrosarkus idipi* (white/red form) from Mayotte, 75 m. Photo courtesy Thierry Mayotte; b, *Astrosarkus idipi* (white/red form) from Maldives. Photo courtesy Paris Stefanopoulis; c, *Astrosarkus idipi* (orange form) from St. Leu, Reunion Island. Photo by Patrick Plantard; d, Orange form with white highlights from Lifou Island, New Caledonia. Photo courtesy Laurent Ballesta.

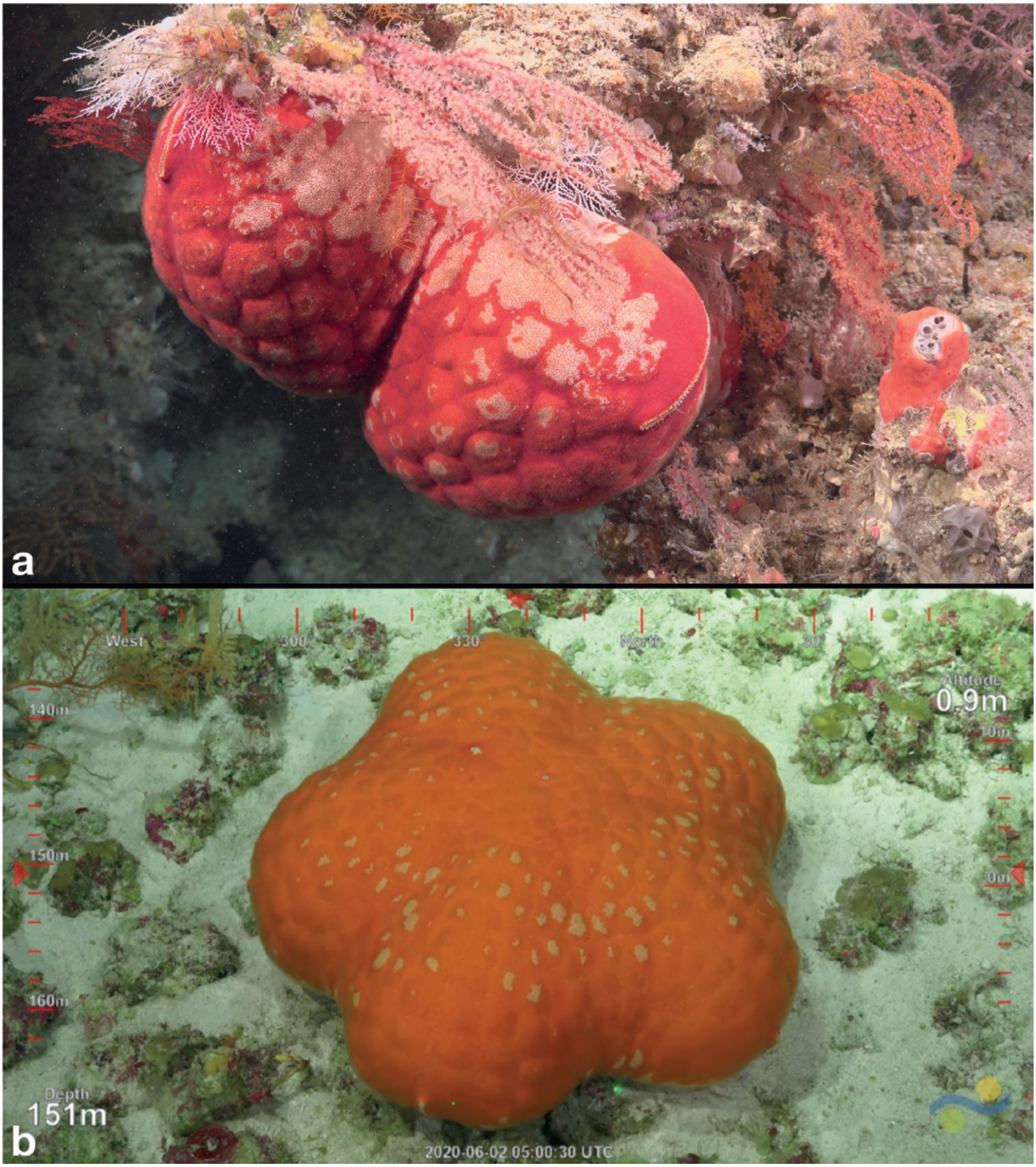

Figure 3. *Astrosarkus* spp. from Australia. a, *Astrosarkus* sp. Northern Depths, Great Barrier Reef; b, *Astrosarkus idipi* from Coral Sea Marine Park. Distance between lasers is 10.0 cm.

the actinal surface around the mouth. This form has been observed from New Caledonia, Palau, Enewetak, Okinawa, Cape York, and Tegrosse Reef in the Coral Sea, off Queensland, Australia. The second colour form is primarily bright orange or red with bright white papular regions, which are confluent and forming an almost mixed colouration. This latter form has been observed in Guam, Mayotte, Maldives and Reunion Island. Discerning trends with colouration is difficult, given the relatively few observations at hand, but most of the deeper water individuals seem to be the solid-orange colour variant.

Ecological comments. The Cape York, Australia, video observation shows this species *in situ* on a rocky underhang in close proximity to a cluster of abundant encrusting metazoans, including octocorals, hydroids, sponges and possibly stylasterid corals. While a clear predation event was not evident, it seems likely that one of these types of metazoans is/are a prey item for this species. This would be consistent with an image of *Astrosarkus* (Fig. 2b) with one arm over what appears to be sponges and other encrusting organisms in Mayotte at 91 m.

The specimen from South Diamond Islet/Tegrosse Reef, off Queensland, Australia was observed amidst a mixed field of rhodoliths (unattached algal nodules) and sandy sediment at 151 m. Its coloration, surface texture and absence of apparent spination or tubercles (although closeups were not obtained) suggested that this was *A. idipi*. Based on the laser scale of 10 cm, this individual was approximately R=20.0, r=15.0 cm, consistent with other occurrences of this species. A small unidentified pufferfish, *Canthigaster*, was observed adjacent to the animal during the video, but its relationship (which could simply be incidental) to *Astrosarkus* is unclear.

The individual observed on Lifou Island, New Caledonia (110 m) is consistent with the colour and overall shape (Mah, 2003) of individuals from Palau and the South Pacific. The degree of arm development seems slightly more pronounced in this individual than in others. This specimen was observed on hard substrate covered by epizoic and encrusting organisms.

Occurrence/distribution. Palau, American Samoa, Southern Japan, Maldives, Mayotte, Reunion Island, 67–210 m

New occurrence. northeastern coast Australia (Queensland), 151 m.

New occurrence. Lifou Island, New Caledonia, 110 m

Specimen referenced. MAL1_330 (unique ID number), Addu, Maldives, 85 m. MAL 1 330, 22/9/2022, site D. 1 wet spec. R=~18.0, r=~12.5

Videos referenced. 1. Tregrosse Reef, South Diamond Islet Australia, -17.80118148° S, 150.63650088° E, 151 m. Observed by R/V *Falkor*, ROV SuBastian, dive 365. Video: https://www.youtube.com/watchv=Ll1Pt9v0URM&list=PLJGVqQI3okzah21Nq70K57SJs1D54QjkX&index=6&t=22855s

2. Cape York, 500 m-tall detached reef offshore of Cape York, off Queensland, Australia, -12.39211352° S, 143.85684846° E, 116 m. Observed by RV *Falkor* voyage FK200930, Northern Depths of the Great Barrier reef, ROV SuBastian, dive S0401. Video: https://www.youtube.com/watch?v=RnUVnNX7yrw&list=PLJGVqQI3okzbyfrJeAfGKLJ2SX-3fu4it&index=15&t=5731s

***Astrosarkus lu* nov. sp.**

urn:lsid:zoobank.org:act:0F642FA4-3A6C-4E4E-B07A-1E3AB371A96B

Figure 4a-g

Etymology. This species is named for Dr. Chung-Cheng Lu, curator emeritus at the Museum Victoria, who collected the specimen, in honour of his contribution to Australian invertebrate zoology. The surname Lu is held in apposition.

Diagnosis. Large pointed tubercles on the abactinal and lateral surface. Furrow spines thick, 4–7; subambulacral spines mostly 5–6, quadrate to round in cross-section in irregular series, each three times as thick as the furrow spines. Region adjacent to the adambulacral spination with numerous, relatively short bivalve pedicellariae.

Comments.This is the first specimen occurrence of *Astrosarkus* in Australia and as with *A. idipi*, *Astrosarkus lu* n. sp. occurs at mesophotic depths. This species shows small, thorn-like spines on the abactinal and lateral surfaces, as well as having differing numbers of adambulacral armaments, notably fewer furrow spines, 4–7 rather than 10–11 as in *A. idipi*, as well as having much larger and differently shaped subambulacral spines. These suggest a defensive function that might not apply to the more widespread *A. idipi*. Pedicellariae in *A. lu* n. sp. are similar in appearance but differ in having more elongate valves than *A. idipi*. Although a dissection of the holotype was not attempted, the fleshy material composing the body wall appears identical to the one present in *A. idipi*.

Although deck shots of this species were taken, colour was difficult to interpret, but appeared red to magenta on the abactinal surface with a white or light actinal surface. Other images of other *Astrosarkus* spp. studied herein showed no individuals with comparable colour or spination.

Occurrence. Off Western Australia in the Timor Sea, 83–84 m.

Description. Body pentagonal (R/r=1.25) thick (height=5.5 cm), stout, covered in smooth flesh which obscures all but adambulacral spination and abactinal tubercular spines. Body solid to the touch, with flesh pushed unevenly on surface. Arm terminus upturned.

Abactinal surface forming a reticulated pattern composed of smooth granule-infused dermis and large distinct papular regions, 100–1000 papulae per area (approximately 1–2 cm x 1–2 cm). Papular regions vary in size and extend onto lateral surface, with largest areas along peripheral disk region adjacent to periphery. Smaller, more discrete regions present more centrally on disk and arms. Distinct elongate papulae emerge from about half of papular pores examined. Non-papular regions composed of dense granule-infused dermis with approximately five granules on a 1.0 mm count. Single tubercular spines with pointed tips, interspersed throughout abactinal and lateral surfaces, most of these present on non-papular surface but with some papular pore regions bearing a single spine. Madreporite round, polygonal, sitting on raised area on abactinal surface, base surrounded by tissue. Sulci relatively shallow.

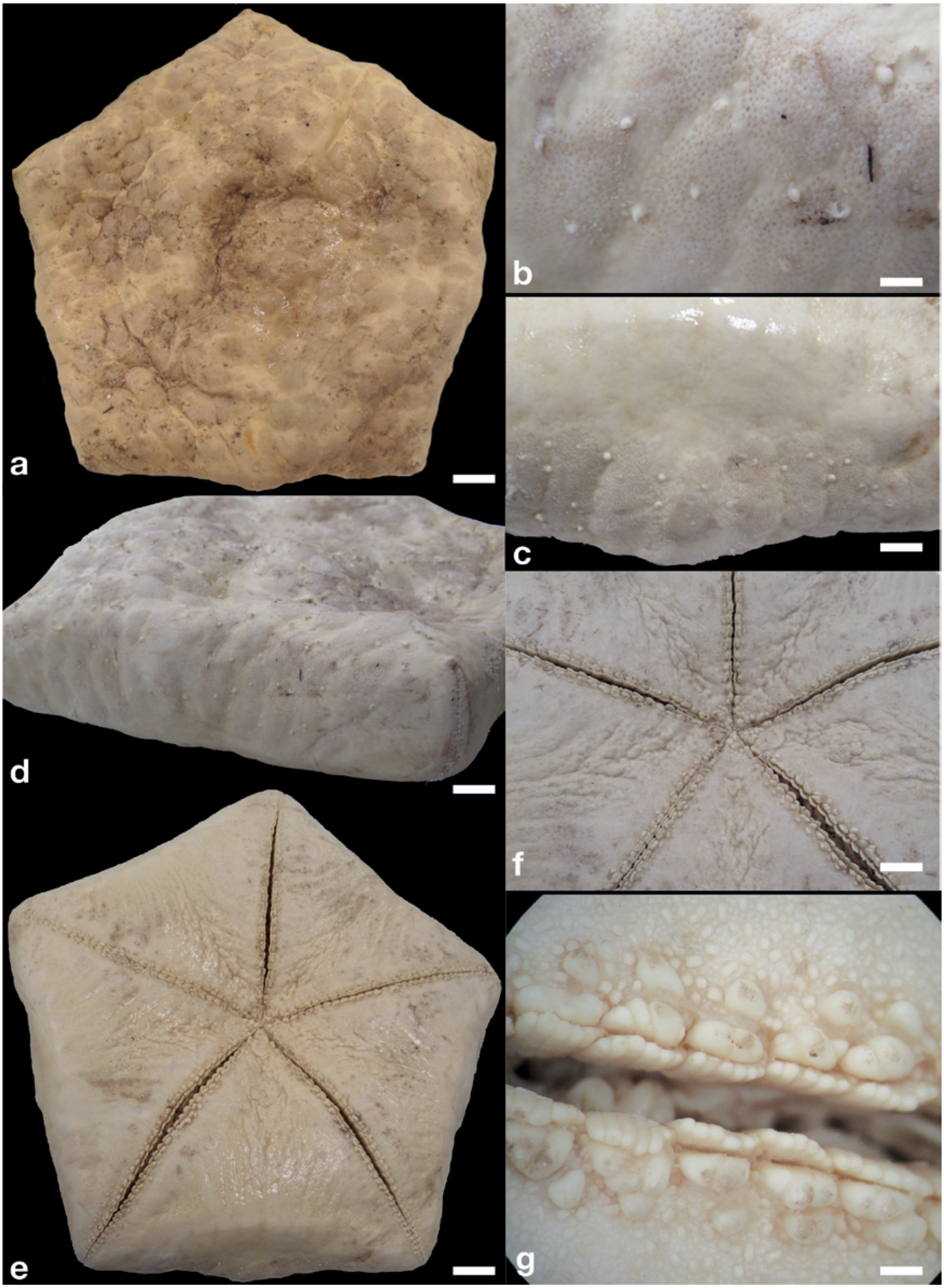

Figure 4. *Astrosarkus lu* n. sp. Scale unavailable. a, Abactinal view; b, Closeup showing spiny tubercles; c, Lateral view showing spiny tubercles on marginal plates; d, Lateral view; e, Actinal surface view; f, Closeup of oral region on actinal surface; g, Closeup of adambulacral armature, furrow spines, etc.

Marginal plates not evident from external surface but covered by thick tissue. Lateral surface appears to be distinguished by weakly expressed elongate segments, approximately 14 per interradius. Each segment covered with a similarly elongate papular region, containing 500–1000 papulae on each. Tubercle-like spines present along lateral surface with regular occurrence on both papular and non-papular areas. Terminal plate pronounced, triangular with rounded edges. Ambulacral grooves distinctly present along lateral surfaces on each radii.

Actinal surface demarcated by absence of papular regions, ostensibly beginning at lower end of marginal "segments" on lateral surface. Actinal intermediate area dominated by granule-infused dermis. Actinal–lateral areas relatively texture free but approaching midway to proximally, these areas have shallow grooves in addition to distinct valleys and dendritic indentions within each actinal intermediate region.

Furrow spines 4–7, mostly five or six, each spine blunt, thick, quadrate in cross-section with each array in straight to weakly concave formation. Subambulacral spines in two irregular rows, the one adjacent to furrow spines composed of two to three blunt spines each approximately three times the thickness of a furrow spine, the one proximal to the mouth with tapered tips, almost acorn-like in shape, these becoming more cylindrical in cross-section distally adjacent to the terminus. The second subambulacral spine mostly single but exceptionally with two, both of these adjacent to the actinal intermediate region. Region adjacent to the adambulacral spination with numerous, relatively small bivalve pedicellariae, approximately 1.0 mm in length, approximately 6–10 associated with each subambulacral spine. Coarse, larger quadrate to polygonal granules present, approximately three counted along a 1.0 mm line.

Oral plates with closely appressed furrow spines, nine per side, each with rounded, blunt tip, quadrate to round in cross-section, with some spines twice as thick as others. A single spine observed on the oral plate projecting into the mouth. Oral plate "surface" covered with irregularly large and thick spines, 10–15, similar in stature to subambulacrals but also irregular in size, shape, all closely appressed to one another. Actinal intermediate regions adjacent to adambulacral furrow spination with higher numbers of pedicellariae and greater numbers of larger granules.

Material described. Holotype, NMV F 242065 Australia, Western Australia, Timor Sea, North West Shelf, 12º 05' 12" S – 12º 54' S, 125º 37' E – 125º 35' E. 83–84 m. Coll. Chung Chen Lu. 1 April 1981. RV *Hai Kung*, Cruise number 70040102. 1 wet spec. R=16.5, r=~13.2, h=~5.5 cm (measured from underside).

Choriaster Lütken, 1869

Choriaster granulatus Lütken, 1869

Figure 5a–b

Lütken, 1869: 35; Goto 1914: 604; Fisher 1919: 367; Domantay and Roxas 1938: 217; Hayashi 1939: 424; Chang et al., 1964: 61; A.M. Clark 1967: 37; Liao 1980: 154; Marsh and Marshall 1983: 675; Jangoux 1986: 124; Marsh and Fromont 2020: 295

Diagnosis. Body stellate (R/r=2.6), strongly thickened, arms round in cross-section. Interradial arcs acute. Surface smooth covered by finely granulate dermal covering. Reticulate skeleton present but covered by a thick, dense fibrous tissue bearing minute plates. Although obscured by granulate dermal covering, abactinal, marginal and actinal plates well developed. Papular pores present only on abactinal surface, terminating at superomarginal plates. Furrow spines slender, 8–9; subambulacral spines large, flat and truncate, three to four (exceptionally five). Modified from Marsh and Fromont (2020), Mah (2003).

Comments. A readily recognizable species, primarily encountered in shallow-water coral-reef related habitats, depth range, 0–40 m (Marsh and Fromont, 2020). Recent ROV video accounts from the Indian Ocean discovered this species in the Maldives at 60–70 m and in the Comoros at a depth of 80 m, indicating that the lower limit of this species likely occurs at mesophotic depths. Mesophotic individuals were observed on rocky substrates covered by epizoic, encrustations adjacent to light, sandy sediment.

Biology of this species is poorly understood. Spawning has been reported in April with planktotrophic larvae. They scavenge on dead fish and other animals, and likely feed on microbial biofilm (Marsh and Fromont, 2020).

Color variation ranges from pink with light to dark papular regions. Specimens from the Indian Ocean, especially Tanzania, Madagascar and adjacent areas, as well as those in the Red Sea, seem to show especially dark papular regions with strong contrast to the lighter surrounding pink to peach coloration.

Occurrence. Widely occurring throughout the Indo-Pacific. Southern China and Japan (Ryukyu Islands), Vietnam, Singapore, eastern Caroline Islands, New Caledonia, Fiji, Tonga, Australia on the Great Barrier reef and Ashmore reefs off Western Australia, Indonesia, Papua New Guinea, Philippines to the Red Sea, and east Africa. 0–40 m.

Depth/new occurrences. Maldives to 60–70 m
Moheli Island, Comoros at 80 m.

Material/video referenced. Comoros Video, Moheli Island (Comos) 12° 27.531" S, 43 38.286" E, 80 m. Observed 10 Oct 2018. Image by CEPF/ACEP Comoros Biodiversity Project.

Culcita Agassiz 1836

Diagnosis. Adults large with massive pentagonal, strongly arched body and confluent arms. Abactinal-lateral and actinolateral edges round, producing a nearly circular appearance. Marginal plate limits and body surface concealed by thickened, granule-invested dermis. Pore areas well developed but irregular to confluent. Actinal granules, granule-invested dermis dense, obscuring limits of the plates. Modified from Marsh and Fromont (2020).

Small individuals of *Culcita* are more flattened and pentagonal and appear more "goniasterid-like" (Kano et al., 1991).

Comments. *Culcita* includes three accepted species, *C. novaeguineae, C. coriacea* and *C. schmideliana*, known from Indo-Pacific, Red Sea and Indian Ocean habitats respectively.

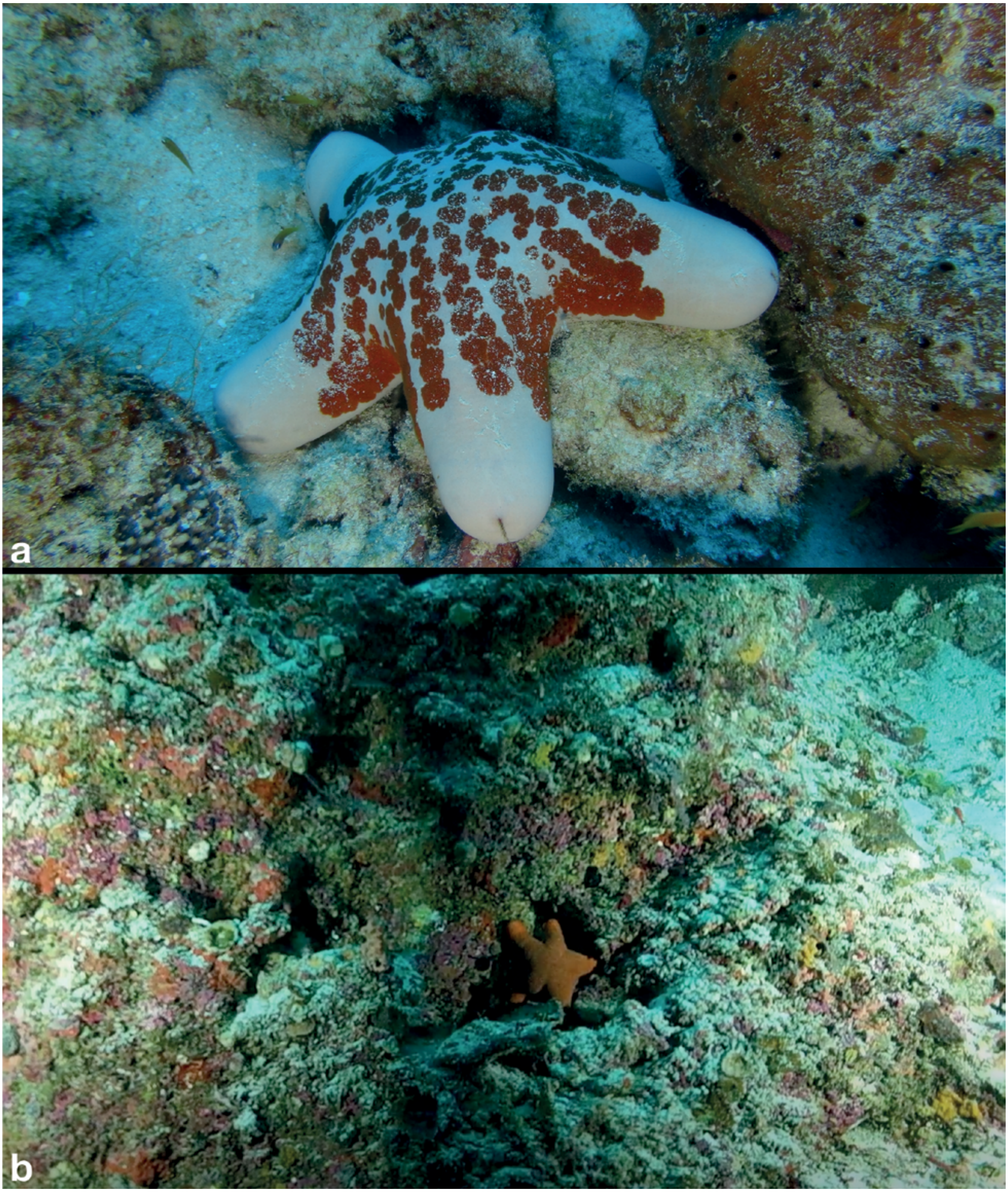

Figure 5. *Choriaster granulatus* a, *In situ* image from Comoros, 80 m. Image courtesy Comoros Biodiversity Project; b, *In situ* image from Maldives, 60–70 m. Image courtesy Maldives Ocean Research Expedition.

Culcita novaeguineae Müller and Troschel 1842

Figure 6a

Culcita novaeguineae Müller and Troschel 1842: 38; Sluiter 1895: 57; Döderlein 1896: 310; H.L. Clark 1908: 201; Goto 1914: 507; Fisher 1919: 360; H.L. Clark 1921: 32; Djakonov 1930: 247; Livingstone 1932: 265; Engel 1938: 10 (var. Leopold); Domantay and Roxas 1938: 215; A.M. Clark & Rowe 1971: 34, 54; Liao 1980: 154; Jangoux and deRidder 1987: 90. Marsh and Fromont 2020: 400.
Goniodiscus sebae Müller and Troschel 1842: 58.
Hosea spinulosa Gray 1847: 78.
Culcita pentangularis Gray 1847: 74.
Culcita pulverulenta Perrier 1869
Hippasteria philippiensis Domantay and Roxas 1938: 209.

Diagnosis. Body shape pentagonal disk, strongly arched, arms confluent. Abactinal and marginal plates concealed by thick granule-covered dermis. Papular regions large and variably confluent, with distinct papulae-free region laterally adjacent to contact with marginal plates. Spinelets or tubercles present on papular areas. Expression of spines and tubercles varied. Actinal region covered by dermis invested with coarse granules, tubercles and/or short, conical spines. Modified from Marsh amd Fromont (2020).

The mesophotic specimen observed was red with white mottled papular regions and dark colored tubercles (Fig. 6a).

Comments. *Culcita novaeguineae* is widespread. This species shows a wide range of variation consistent with its widespread distribution. Preliminary data suggests a cryptic complex within this species (G. Paulay, pers. comm).

Culcita novaeguineae is known primarily as a shallow-water reef species, with most occurrences under 30.0 m (e.g. Glynn and Krupp, 1986; Rowe and Gates, 1995; Marsh and Fromont, 2020). Video observations by the ROV SuBastian has shown this species at 99 m depth from off Queensland, occurring on a coarse, sandy bottom with rhodoliths and algal cover. No clear character differences in colour, spination, shape or size were observed on the individual imaged. No specimen was collected.

Occurrence. Widely distributed throughout the Indo-Pacific Ocean. Hawaiian Islands, southern Japan, southern China and Taiwan, southeastern Polynesia, Pitcairn Island to Philippines, Indonesia, north coast of Australia from Western Australia to Queensland, Papua New Guinea, east to east Africa, the Andaman Islands and southeast Asia.

New mesophotic occurrence. Off Queensland Australia 99.0 m depth.

Video observation. Bowl Slide Australia, 125 km offshore from Townsville, Queensland, Australia, -18.38805116° S, 147.66887222° E, 99 m. ROV SuBastian, dive 394, FK200930.

Culcita schmideliana (Bruzelius, 1805)

Figure 6b–c

Asterias schmideliana Bruzelius 1805: 11.
Culcita schmideliana Gray 1840: 276; Perrier 1875: 266 (74); Döderlein 1896: 315 (with varieties); Simpson and Brown 1910: 53; Clark and Rowe 1971: 41; Jangoux 1973: 18; A.M, Clark and Courtman-Stock 1976: 67; Marsh and Marshall 1983: 675; Jangoux 1985: 31; Rowe and Gates 1995: 99; Marsh and Fromont 2020: 402.

Diagnosis. Distinct papular free area laterally adjacent to the marginal plates. Distinct prominent tubercles and/or spines present on the skeletal ridges between the papular regions, lacking armament on the papular regions. Modified from Marsh and Fromont (2020).

Comments. Gates and Rowe (1995) and Marsh and Fromont (2020) have listed the bathymetric range of this species as extending into the mesophotic, see also below.

Prey includes hard and soft corals, echinoids, encrusting sponges, ascidians, and algal biofilm on reef sand or seagrass substrates (Marsh and Fromont, 2020, Thomassin, 1976). Unusual population densities in the Maldives have had an adverse affect on corals recovering from bleaching events (Bruckner & Coward, 2018).

Occurrence. Primarily Western Indian Ocean, east Africa, including Madagascar, Maldives, to the Lakshadweep Islands, Indonesia, north-east coast of Australia, Western Australia to New Townsland and Cocos (Keeling) Islands. 0–92 m.

Material examined. USNM E37276 Off Lagoon, Kendikolu Island, Miladummadulu Atoll, Maldives, Indian Ocean. 5.97° N, 73.32° E, 44–46 m. Coll. F.C. Ziesenhenne. 29 March 1964. 1 dry spec. R=10.7, r=8.3.

MNHN-IE-2007-3995 North of Sainte Luce, southern Madagascar, 24° 35' 52.2024" S, 47° 32' 6" E, 80–86–m. Coll. ATIMO VATAE, R/V Nosy Be, May 2 2010. 1 wet spec.

Halityle Fisher 1913

Halityle Fisher 1913: 211; 1919: 362
Culcitaster H.L. Clark 1914: 144

Diagnosis. Monotypic, as for species.

Halityle regularis Fisher 1913

Figure 7a–g, Figure 8a–f

Halityle regularis Fisher 1913: 211; James 1973: 557; Baker and Marsh 1976: 107; Rowe and Gates 1995: 102; Branch et al. 2010: 224; Marsh and Fromont 2020: 422
Culcitaster anamesus H.L. Clark 1914: 145

Diagnosis. Specimens massive, bodies pentagonal to weakly stellate, thickened (R/r=1.18–1.66) with distinct lateral surfaces, abactinal surface with distinctive reticulate pattern. Body surface covered by continuous fine granular cover. Up to 22 superomarginals and 40–50 inferomarginals in each interradius. Actinal surface with distinct rhombic plates with strikingly dark-coloured regions around mouth. Adambulacral plates with furrow spines, 8–11, closely adpressed, flat. Two to three subambulacrals, domed, tips wrinkled. Modified from Baker and Marsh (1976).

Colour ranges from orange to red, maroon or purple with white, yellow to orange papular areas. Actinal surface apricot to pink with adjacent actinal plates orange or violet outlined with orange granules (modified from Marsh and Fromont, 2020). Exceptionally with white to yellow coloration extending over arm tips from actinal surface. Smaller individuals with more mottled variable colouration, with darker irregular plates around the periphery of the abactinal surface.

Comments. Although readily recognisable, relatively little is known about the biology and ecology of *H. regularis*. Numerous taxa are associated with this species, including parasitic cyclopodid copepods from Madagascar (Humes, 1971), the symbiotic shrimp and polychaete (*Periclimenes* and *Hololepidella*, respectively)in Vietnam (Antokhina and Kritayaev, 2012), pontoniine shrimp in Australia and New Caledonia (Bruce, 1980, 1983), and parasitic eulimid snails (Gosliner et al., 1996).

Size changes in Halityle regularis. Several if not all members of the Oreasteridae possess a dramatic shift in body morphology and colour as the individual develops from a relatively small to larger body size. This smaller size is similar to body forms observed in the Goniasteridae, with a more pentagonal to weakly stellate shape (R/r= approximately 1.0), as well as a more flattened abactinal surface with more weakly developed features, such as spines, granules, relative to the

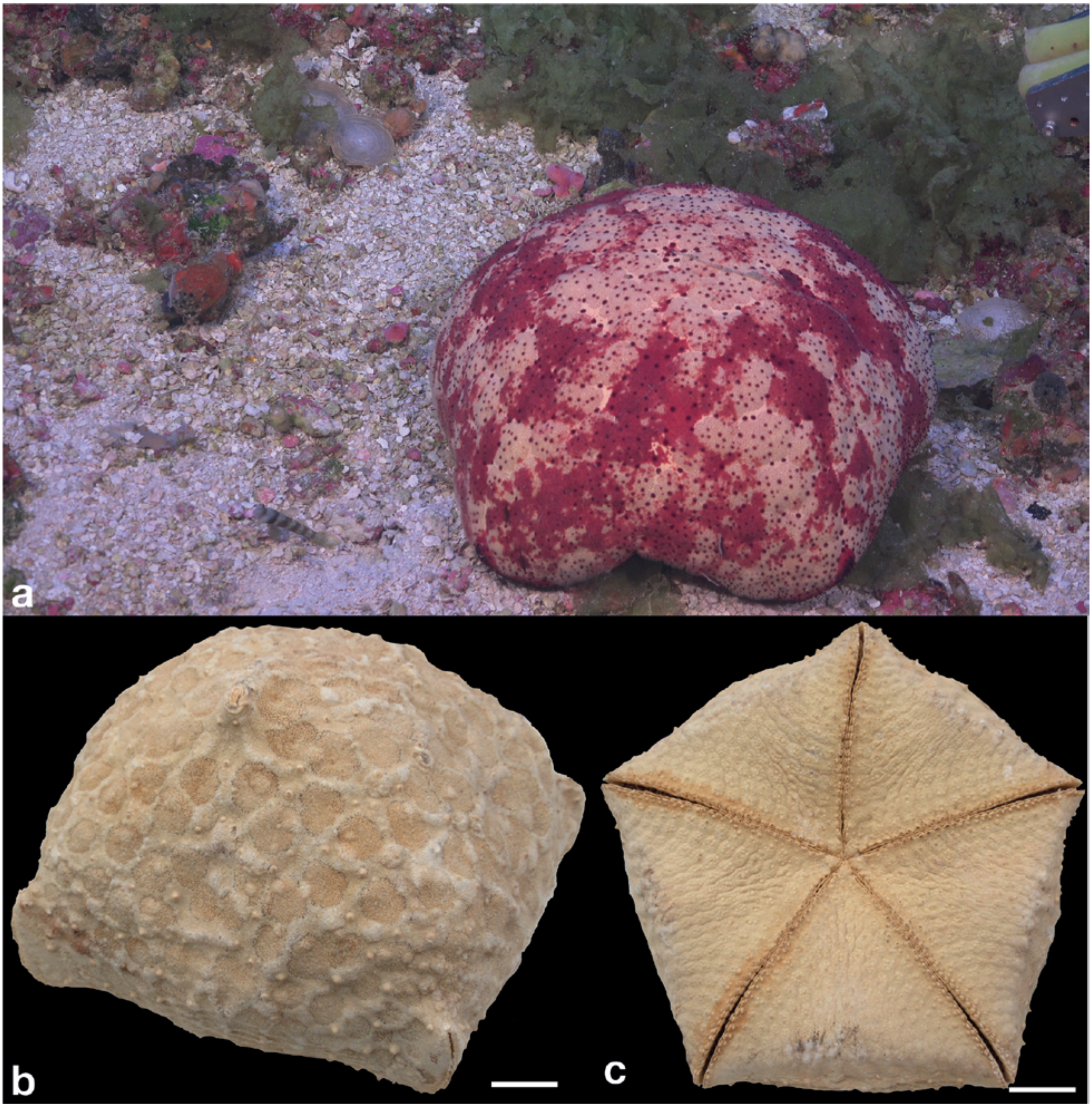

Figure 6. *Culcita* spp. a, *Culcita novaeguineae* in situ from Bowl Slide, Australia, 99 m. Courtesy of R/V *Falkor*, Schmidt Ocean Institute; b, *Culcita schmideliana*, USNM E37276, Abactinal view. Scale bar=2.0 cm; c, Actinal view. Scale bar=2.0 cm.

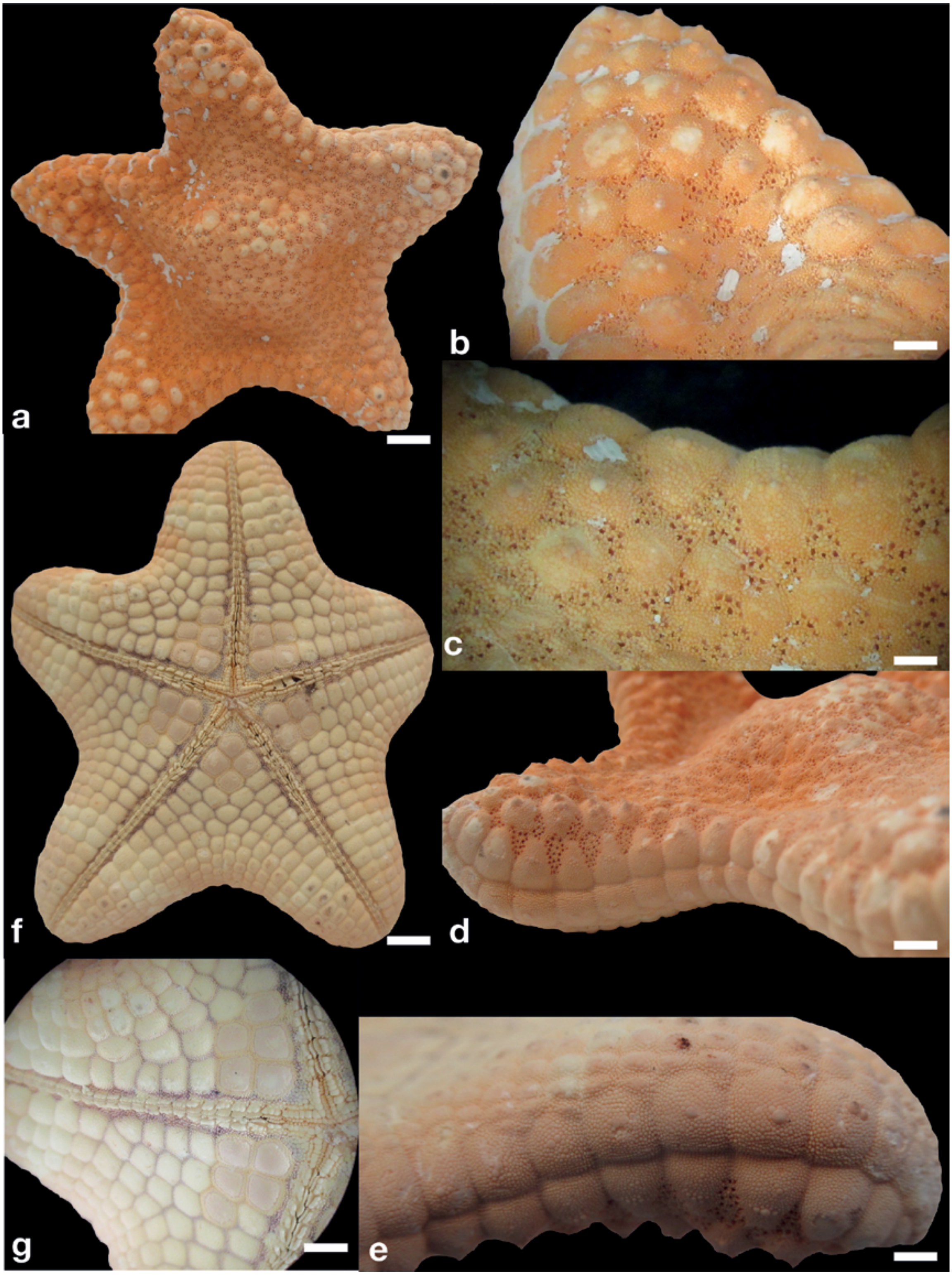

Figure 7. *Halityle regularis* USNM 1688944, Philippines, small individual. a, Abactinal view. Scale bar=0.5 cm; b, Close-up on armtips showing enlarged distal and superomarginal plates. Scale bar=0.2 cm; c, Close-up on abactinal-superomarginal contact showing spiny tubercles on superomarginals. Scale bar=0.2 cm; d, Lateral view showing spiny tubercles and large spines on superomarginal, inferomarginal plates. Scale bar=0.2 cm; e, Inferomarginal and superomarginal plates. Scale bar=0.2 cm; f, Actinal view. Scale bar=0.5 cm; g, Closeup oral region, adambulacral furrow. Scale bar=0.2 cm.

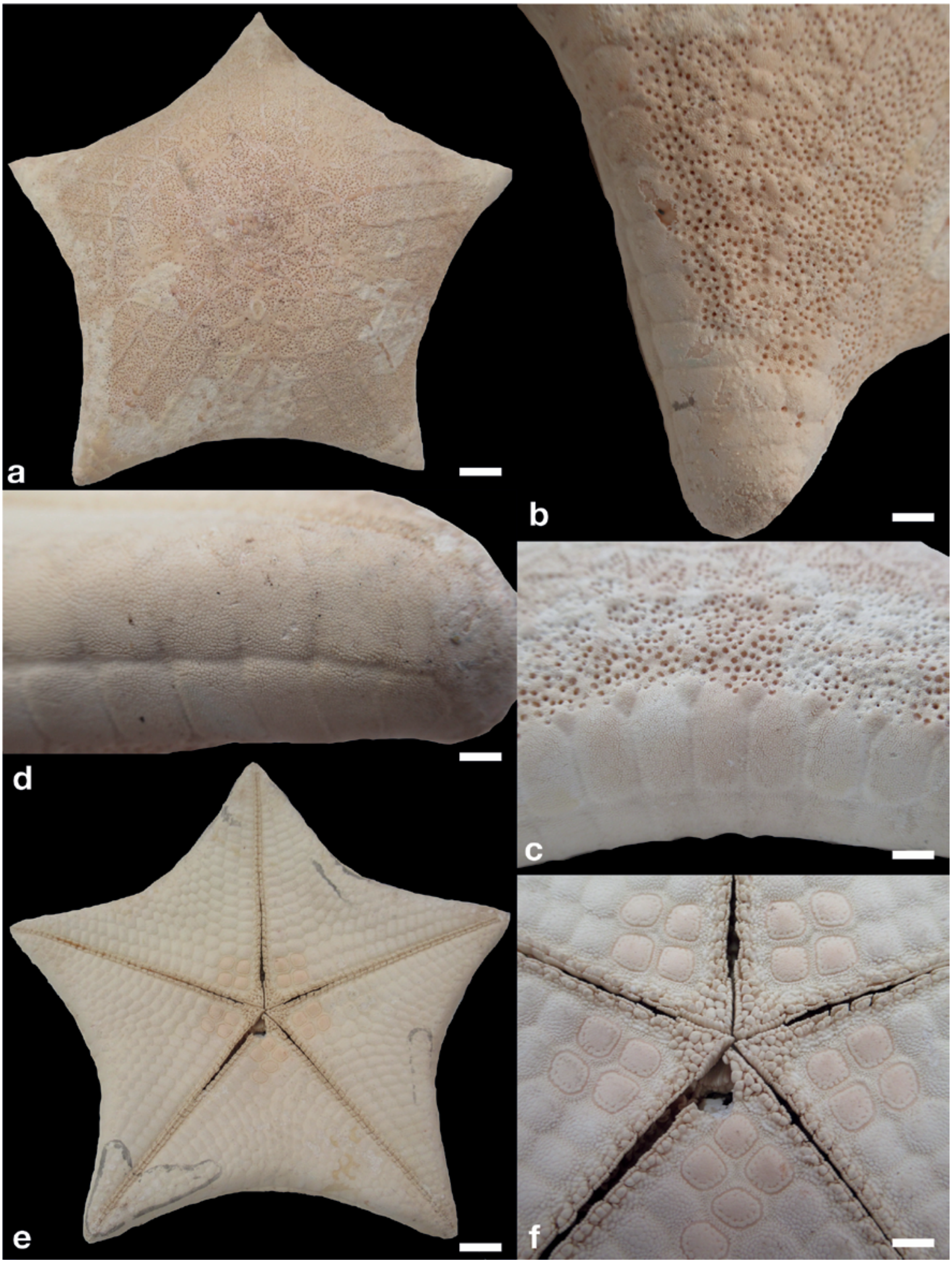

Figure 8. *Halityle regularis* USNM E45474, Somalia, larger individual. a, Abactinal view. Scale bar=1.5 cm. b, Closeup of armtip showing low tubercles on distal surface. Scale bar=0.8 cm; c, Lateral view showing superomarginal plates and low tubercles. Scale bar=0.5cm; d, Lateral view of armtip showing marginal plates, inferomarginal, superomarginal surface. Scale bar=0.5 cm; e, Actinal view. Scale bar=1.5 cm; f, Closeup of oral and adambulacral furrow. Scale bar=0.5 cm.

strongly arched larger forms. This change has been observed most notably in *Culcita* species (Döderlein, 1917; Kano et al., 1991) whose adult form is relatively large and strongly arched (approximately 20–30 cm in diameter, 10-20 cm in height) relative to the smaller form (at approximately 0.5–4.0 cm), which is pentagonal in outline with a flattened abactinal surface, displaying few if any of the tubercles, spines or other characters observed in the larger forms. The differences were so pronounced that this smaller form was identified as a separate genus until intermediate sizes were recognised. Other oreasterids with documented changes of this kind include the tropical Atlantic *O. reticulatus*, which undergoes both a morphological but also colour change (Hendler et al., 1995) as it approaches a larger size. Although this morphological change is thought to be present throughout the Oreasteridae, size-related data across all genera remains incomplete, especially for those genera with more unusual, large-sized forms, such as *Halityle*.

USNM 1688944 is one of the smallest of reported *Halityle* specimens, and was compared with descriptions in Baker and Marsh (1976) as well as with other specimens at R=5.9, 9.1 and 13.0 cm. This specimen was recognised as *Halityle* based on its distinctive actinal plate pattern as well as the distinctive scalar granules covering the plate surface. It shares other recognisable features such as a consistent number of furrow spines, as well as the enlarged and identical number of subambulacral spines, the intercalated 22opular pores with the superomarginal plates, as well as the marginal plate shape. Nearly all the superomarginal plates, as well as numerous enlarged, strongly convex abactinal plates present on the distal surface of the arm, display pronounced tubercles or short, pointed spines. Inferomarginals also display 1–4 enlarged round tubercles or spines centrally on the plate surface.

Numerous differences between USNM 168894 and the other, larger specimens are apparent. Note, however, that individuals from different areas may also show variation in morphological character development as they increase in size. Perhaps the most distinct difference is the presence of tubercles with spiny tips on distalmost abactinal and superomarginal plates. Tubercles/spines seem to be, at first, distinctly at odds with the morphology of adult specimens, because nearly every detailed description of *H. regularis* notes the complete absence of spines or similar accessories on the abactinal and marginal plate surfaces. However, careful examination of the sequentially larger specimens, USNM E45474 with R=9.1 and USNM E13719, R=5.9, 6.4, shows very small, low, mound-like tubercles present in the distal and lateral regions on the disk and arms, sitting on the plates between the papular areas. These tubercles appear lower and broader as the animal becomes larger among the Somalian specimens studied herein. Among the larger specimens available (USNM 40867, no data) and the holotype (USNM 32634, which have R>13.0 cm, there appear to be minute, weakly expressed rugosities in these areas. This implies that these more acutely pointed tubercles are covered over by the granular cover or the plates are expanded as the animal grows. Prior accounts, such as Fisher (1919), have not mentioned these rugose projections, likely owing to their small size and relatively nondescript appearance consistent with the granular surface. The spine-like tubercles on the superomarginal plates appear to be displaced to a location above the contact between superomarginal plates in each interradius. Curiously, although abactinal and superomarginal tubercle/spines appear to be compensated for on larger specimens, these structures do not show relictual presence on the inferomarginal plates.

Pedicellariae were not observed in USNM 1688944 but are present in specimens with R>5.9 on the adambulacral plates, with descriptions mentioning further pedicellariae in large specimens, suggesting they emerge in larger individuals. Papular regions show an increase in the number of papular pores between the specimen showing R=4.5 and r=5.9. These areas become more triangular and better developed in larger individuals. The substantial changes to body shape occur between R=4.5 and R=5.9: the disk begins developing the strong arched convex shape, arms become more lateral facing, and the reticulate pattern in the adult forms takes on its more distinct appearance.

USNM 1688944 is otherwise consistent with prior descriptions of this species (Baker and Marsh, 1976). This includes a similar granular covering, rhombic actinal plates, a consistent number of furrow spines (8–11), domed subambulacral spines (two to three), and identical pedicellariae.

Occurrence. Widely distributed throughout the Indo-Pacific. Southern Japan, Enewetak Atoll, New Caledonia, the Philippines, Lembeh Strait, Indonesia, Vietnam, the Lakshadweep Archipelago, southern India, east Africa, Madagascar; Ningaloo Reef, Exmouth Gulf, North West Shelf, Western Australia; Keppel Bay and Heron Island, Queensland. 3–275 m.

Material examined. USNM E13719 SW of Gas Jinnah, Somalia, Indian Ocean. 9.68° N, 51.05° E, 60–70 m. Coll. R/V *Anton Bruun*, 16 Dec 1964. 2 dry specs. R=5.9, r=3.7; R=6.4 r=3.9.

USNM E45470 Off NE coast, Somalia, Indian Ocean. 10.3843° N, 51.2517° E, 26–37 m. Coll. R/V *Anton Bruun*, 8 Jan 1987.1 dry spec. R=13.0 r=8.0.

USNM E45474 Off NE coast, Somalia, Indian Ocean. 10.3843° N, 51.2517° E, 40–49 m. Coll. R/V *Anton Bruun*, 8 Feb 1987. 1 dry spec. R=9.1, r=5.5.

USNM 168894 Balut Island, Philippines, North Pacific Ocean. 50–150 m. 1 dry spec. R=4.5, r=2.5.

Pentaceraster Döderlein, 1916

Döderlein, 1916: 424; 1936: 331; Clark and Rowe 1971: 55; A.M. Clark 1993: 310 (checklist)

Diagnosis. Body stellate (R/r=2.0–3.0, seldom >3.0) with strongly arched disk, elongate, triangular arms. Distal abactinal, actinal and especially marginal plates covered with distinct, even-sized, projecting granules. Abactinal–lateral regions with distinctly reticulate plates showing well-defined pore areas. Primary plates with spines or conical tubercles arranged in longitudinal series in most species. Distal inferomarginal plates with an enlarged spine or conical projection in most species. Intermarginal pore areas weakly developed or absent. Modified from Marsh and Fromont (2020).

Comments. *Pentaceraster* includes 15 species that occur widely throughout the Indo-Pacific. The diagnosis follows Marsh and Fromont (2020), but boundaries for the concept of *Pentaceraster* have not been tested or reviewed since their establishment (Döderlein, 1916, 1936). Other oreasterid genera, such as *Poraster*, and the typological *Oreaster*, differ from *Pentaceraster* by relatively few characters and invite additional scrutiny, especially as further data on variation among species within these genera has produced taxonomic overlap. For example, Doderlein's key (1936) differentiates the Atlantic *Oreaster* from *Pentaceraster* by the presence of low dorsal spines, a character observed in highly variable Indo-Pacific species, such as *Pentaceraster alveolatus* or *Pentaceraster mammilatus*. Character variation among *Pentaceraster* species is similarly problematic, with several species displaying character variation that is at odds with established species concepts, particularly as outlined by Döderlein (1916, 1936).

Pentaceraster alveolatus (Perrier 1875)

Figure 9a–f

Pentaceros Perrier 1875: 243 (1876: 59); Koehler 1910: 95
*Oreaste*r Bell 1884: 73; Domantay and Roxas 1938: 212
Pentaceraster Döderlein, 1916: 428; Jangoux 1986: 126; Kohtsuka et al. 2020: 58

Diagnosis. Primary circlet and carinal series bearing large, conical spines, dorsolateral armament present primarily on the disk. Superomarginals and inferomarginals with prominent spines. Spination on disk and arms variably absent to abundant with lateral regions on disk and arms. Arms slender and elongate. Based on Marsh and Fromont (2020), Clark and Rowe (1970).

Comments. *Pentaceraster alveolatus* is a widely occurring and highly variable species, which apparently displays a significant amount of morphological overlap with other *Pentaceraster* species within its range. Although an identification has been made with the surest possible accounting, boundaries for differing species and variation observed in the specimens themselves present difficulty. Identification was based on the relatively few spines present along dorsal surfaces along the disk and arms, as outlined by Clark and Rowe (1970), but variation is inconsistent with published taxonomic definitions, as are other instances outlined herein. Revision is desirable.

USNM E37286 is most similar to a large specimen (R=13 cm) figured by Doderlein (1936: Fig. XXV, Figs.2 & 3) identified as *P. alveolatus*, from the Philippines, showing pronounced spination on the lateral sides of the disk but more weakly on the mid to distal arm regions. However, Doderlein (1936) shows a wide range of spine expression for *P. alveolatus* from the Philippines to southern Japan, including several individuals with much less spinose abactinal surface and starkly different appearance.

USNM E37286 also shows one to few spines on the superomarginal plates of each interradius, which conflicts with the diagnostic keys in Clark and Rowe (1971). This result would suggest *Pentaceraster horridus* or *Pentaceraster tuberculatus*. Neither of these species concepts as outlined by Doderlein (1936) appears consistent with USNM E37286.

If correctly identified, USNM E327286 represents the first occurrence of this species from the African coast and one of the few records of this species from the Indian Ocean. Marsh and Fromont (2020) reported one specimen of this species from Western Australia, from 35 m depth. It is possible that this species only occurs at mesophotic depths in the Indian Ocean. If so, the morphology could be phenotypically variable owing to depth or indicative of a cryptic species.

Occurrence. Widely occurring throughout the Indo-Pacific. Southern Japan, China, Guam, New Caledonia, Samoa, Indonesia, Philippines, Western Australia (single occurrence), 1–54 m.

Range & depth extension. Somalia, 60–70 m.

Material examined. USNM E37286 SW of Gas Jinnah, Somalia, Indian Ocean. 9.68° N, 51.05° E, 60–70 m. Coll. R/V Anton Bruun, 16 Dec. 1964. 1 dry spec. R=12.1, r=3.9.

Poraster Döderlein, 1916

Döderlein, 1916: 438; 1936: 364.

Diagnosis. Body strongly stellate (R/r=2.7–4.5), disk thick, arms elongate, tapering. Adult sizes approximately R=24.0–30.0 cm. Abactinal surface coarsely granulated, lacking primary accessories (i.e. spines, tubercles) save for a prominent row of large, conical tubercles present along the carinal series of each arm. Well-defined, interradial, intramarginal region present, spanning approximately 10–16 supero-inferomarginal plate pairs. Spine-bearing plates present, transversely bisecting the contacts between the marginal plate pairs intramarginally. Furrow spines 5–7, subambulacral spines three to four. Papulae confluent on abactinal surface and present intermarginally but absent from the actinal surface (modified from ; Döderlein, 1916; Marsh and Fromont, 2020).

Poraster superbus (Möbius, 1859)

Figure 10a-e

Oreaster superbus Möbius, 1859: 5; Bell 1884: 81.
Oreaster productus Bell 1884: 74
Pentaceros superbus Sladen 1889: 345; Simpson and Brown 1910: 51; Brown 1910: 33.
Pentaceros indicus Koehler 1910: 110.
Poraster productus Döderlein, 1916: 438
Poraster superbus Döderlein, 1916: 440; 1936: 364; Humes and Cressey 1958: 395; Clark and Rowe 1971: 34, 54; Bruce 1974: 485; Jangoux 1984: 280; A.M. Clark 1993: 317 (checklist with synonymies); Kogure and Igei 2013: 33; Marsh and Fromont 2020: 432
Poraster superbus var. bengalensis Döderlein, 1936: 367

Diagnosis. Monotypic, as for genus.

Comments. Occurrences of *P. superbus* have been observed from Madagascar indirectly, primarily from records of various parasitic and associated crustacean species (e.g. Humes and Cressey, 1958; Bruce, 1974). Uncertainty was reflected by Clark and Rowe (1971), who qualified its occurrence in

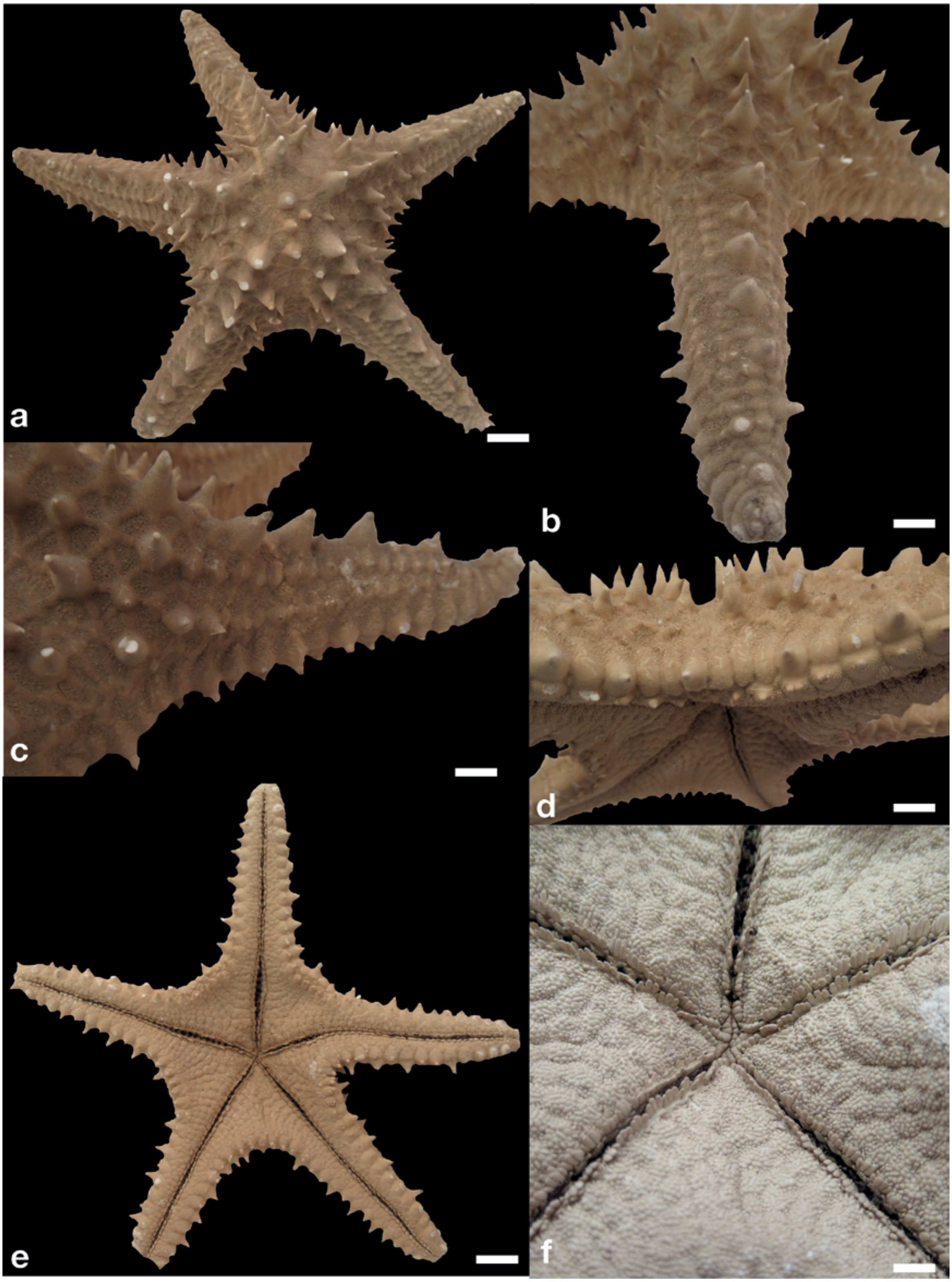

Figure 9. *Pentaceraster alveolatus* USNM E37286 a, Abactinal view. Scale bar=2.0 cm; b, Abactinal-lateral view showing degree of spination along arm. Scale bar=0.5 cm; c, Abactinal-lateral view showing spination and superomarginal surface. Scale bar=0.5 cm; d, Actinal-lateral view showing marginal spination. Scale bar=0.5 cm; e, Actinal view. Scale bar=2.0 cm; f, Closeup of oral region and ambulacral spination. Scale bar=0.5 cm.

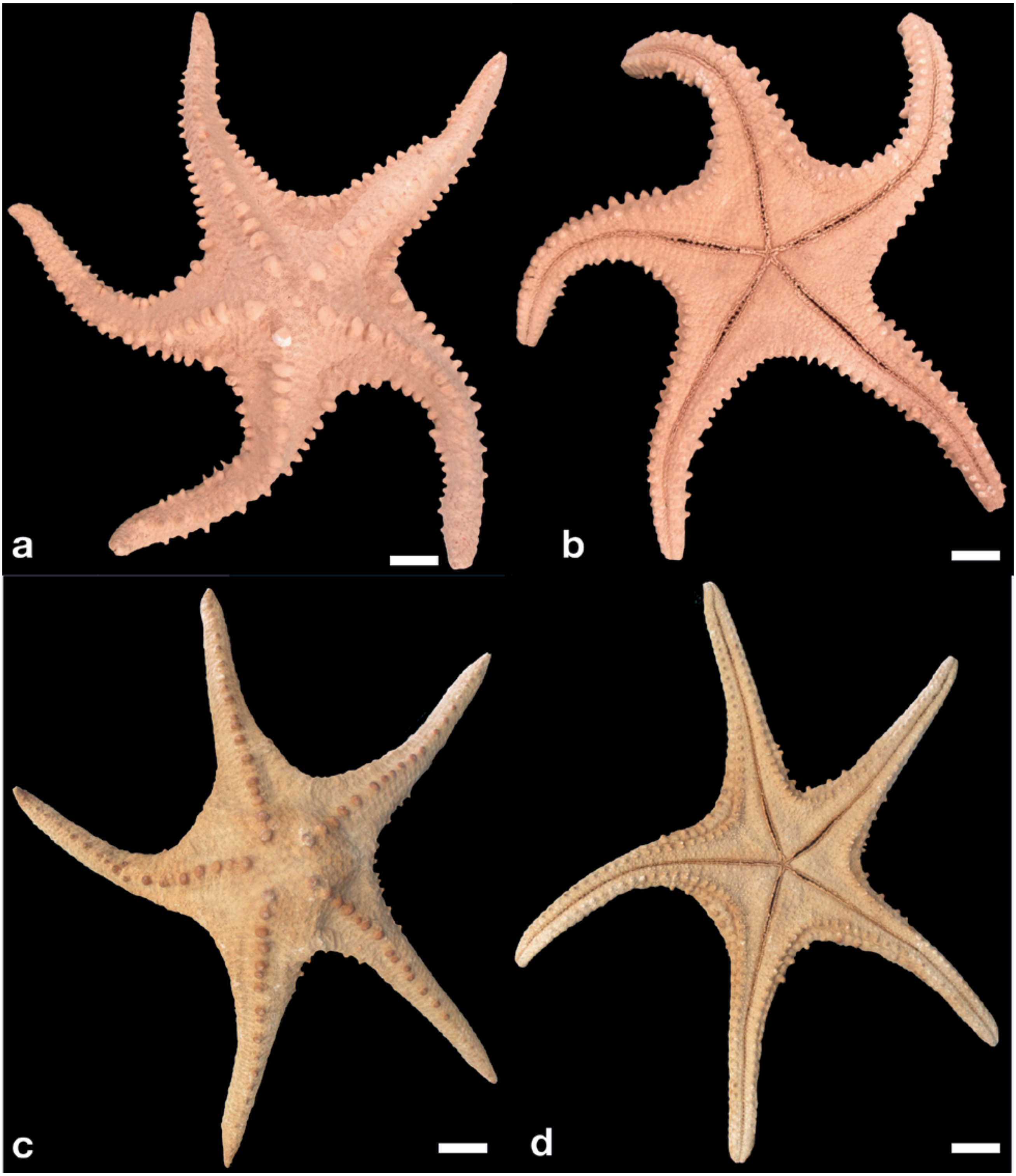

Figure 10. *Poraster superbus* variation. All scale bars=1.5 cm. a, USNM E45289 Abactinal; b, Actinal; c, USNM E 47401, Abactinal; d, Actinal.

Madagascar and east Africa with a "?", as well as by Marsh and Fromont (2020), who listed the species as present on the north-east coast of Africa but not further south. Multiple specimen records as well as imagery from iNaturalist confirm its presence in the Madagascar region.

Most recent accounts of *Poraster* reflect a single, wide-ranging species, *P. superbus*. The synonymy, however, reflects at least four morphotypes throughout its range. Two of those species, *P. superbus var. benegalensis* Döderlein, 1936 and *Poraster productus* (Bell, 1884) display small abactinal and carinal tubercles/spination compared to *Poraster indicus* (Koehler, 1910) and *P. superbus* itself. These latter two variants are apparently distinguished by the extent of superomarginal spination. Of the specimens examined, E47401 is more consistent with the *indicus* variant, whereas E45289 is more consistent with the description by Möbius (1859).

Few data are available on the biology of *P. superbus*. This species has been reported feeding on shelly sand with its stomach everted on a sand-encased solitary ascidian, as well as scavenging on moribund echinoids (Marsh and Fromont, 2020). Several parasitic and associated crustacean species have been reported (e.g. Humes and Cressey, 1958, Bruce, 1974). One observation (Derleisereiter, 2020) shows an individual in a spawning position with arms suspending the disk into the water column above a sandy substrate.

Occurrence. North-east coast of Africa to Zanzibar. Bay of Bengal to New Caledonia, southern China and north to Japan. 20–55 m. iNaturalist observations also show this species in Sri Lanka (Laccadive Sea), Singapore and in the Seychelles.

New records. Madagascar, Mozambique Channel, 30 m. Tanzania, Mergui Archipelago, Burma, Andaman Sea to 96 m (new depth record).

Material examined. USNM E 45289 Mozambique Channel, Madagascar, Indian Ocean, -15.87° S, 44.38° E, 30 m. Coll. R/V *Anton Bruun*, International Indian Ocean Expedition, 19 Oct 1964. 1 dry spec. R=16.2 cm, r=4.7.

USNM E 47401 Lord Loughborough Island, Mergui Archipelago, Andaman Sea, Burma. 10.62° N, 97.57° E, 96 m. Coll. R/V *Anton Bruun*, International Indian Ocean Expedition, 24 March 1963. 1 dry spec. R=21.4, r=6.5.

USNM E47402 East of Phuket Island, Thailand, Andaman Sea, Indian Ocean. 7.92347° N, 98.8363° E, 16–20 m. Coll. RV *Gallardo*, Fifth Thai Danish Expedition, 15 Feb 1966. 2 dry specs. R=20.0 r=5.0; R=22.0 r=4.8.

CASIZ 30883 South Tanzania, Menai Bay, -6.408° S, 39.4106667° E, 18 m. Coll. Coral Reef Research Foundation, 3 Feb 1996. 1 wet spec.

MNHN-IE-2007-1000, South of Cape Saint Sebastian, Madagascar, Indian Ocean. -12.61717° S, 48.505° E, 59–60 m. Coll. Bouchet, Puillandre and Richer, MIRIKY. 29 June 2009. 1 wet spec. R=14.4, r=5.2.

MNHN-IE-2007-1090, South of Cape Saint Sebastian, Madagascar, Indian Ocean. -12.62733° S, 48.43317° E, 60–63 m. Coll. Bouchet, Puillandre and Richer, MIRIKY. 29 June 2009. 2 wet specs. R=4.3, r=1.2; R=1.3, r=0.6.

Protoreaster Döderlein, 1916

Protoreaster lincki (de Blainville, 1830)

Figure 11a–e

Asterias lincki de Blainville 1830: 238; 1834: 219
Pentaceros muricatus Gray 1840: 277
Oreaster muricatus Dujardin and Hupe 1862: 383
Oreaster reinhardti Lütken 1864: 159; Bell 1884: 74.
Oreaster lincki Lütken 1864: 156; Bell 1884: 72; H.L. Clark 1923: 273.
Pentaceros reinhardti Perrier 1878: 24; Sluiter 1895: 56; Koehler 1910: 101.
Protoreaster lincki Döderlein 1916: 423; 1936: 328; Tortonese 1949: 33; Kalk 1954: 113; Macnae and Kalk 1962: 108; Balinsky 1958: 1969; Kalk 1958: 215; 1959: 21; Day 1969: 182; A.M. Clark and Rowe 1971: 54; Jangoux 1973: 23; A.M. Clark and Courtman-Stock 1976: 68; Julka and Das 1978: 346; Marsh 1976: 222; Sloan et al. 1979: 722; Ebert 1979: 72; Tortonese 1980: 11; Aziz and Jangoux 1984: 137; A.M. Clark 1984: 90; Jangoux and Aziz 1984: 860; Walenkamp 1990: 51; Aziz 1986: 323; Marsh and Fromont 2020: 435.

Diagnosis. Body strongly stellate (R/r=2.3–3.0), arms triangular in shape, disk and arms thick, strongly arched, triangular in cross-section. Surface covered by smooth pavement of flat, polygonal granules. Primary circlet on disk with prominent spines, this area divided into five triangular regions. Reticulation across abactinal surface with well-developed reticulation surrounding areas with numerous papular pores, including five triangular regions on disk. Distal superomarginal plates with prominent laterally projecting tapering spines or knobs. Inferomarginal spines/tubercles absent. Bivalve pedicellariae present on a minority of marginal plates. Modified from Marsh and Fromont (2020).

Comments. Although recognised primarily as a near-shore, shallow-water species, previously documented at 0–10 m depth (Marsh and Fromont, 2020), one specimen collected from Madagascar was recorded from 40 m, a mesophotic and currently the deepest-known occurrence.

Marsh and Fromont (2020) indicated that it feeds on microbial biofilms and opportunistic scavenging. Ebert (1976) reported this species spawning in the Seychelles in early May and in northwestern Australia during November.

Shrimp associates such as *Zenopontonia* (formerly *Periclimenes*) have been observed in association with this species (Bruce, 1982).

Occurrence. Western Indian Ocean. Red Sea, Sri Lanka, Mozambique, Java, Indonesia. Northwest Australia, 0–40 m.

Material examined. IE-2007-3947, Madagascar, 25° 45.7" S, 44° 52.0" E. 41.0 m. Coll. N/O *Nosy Be*, 13 May 2010. 1 wet spec. R=8.8, r=3.3.

Discussion. The Oreasteridae surveyed herein as well as many other asteroid species in the Indo-Pacific region (e.g. Mah, 2017, 2018, 2021) are present at much deeper depths than recorded previously (e.g. 0–10 m for *P. lincki* [Marsh and Fromont, 2020] versus 40 m herein). The oreasterids surveyed here are widespread, ranging from the Indian Ocean (e.g. *P.*

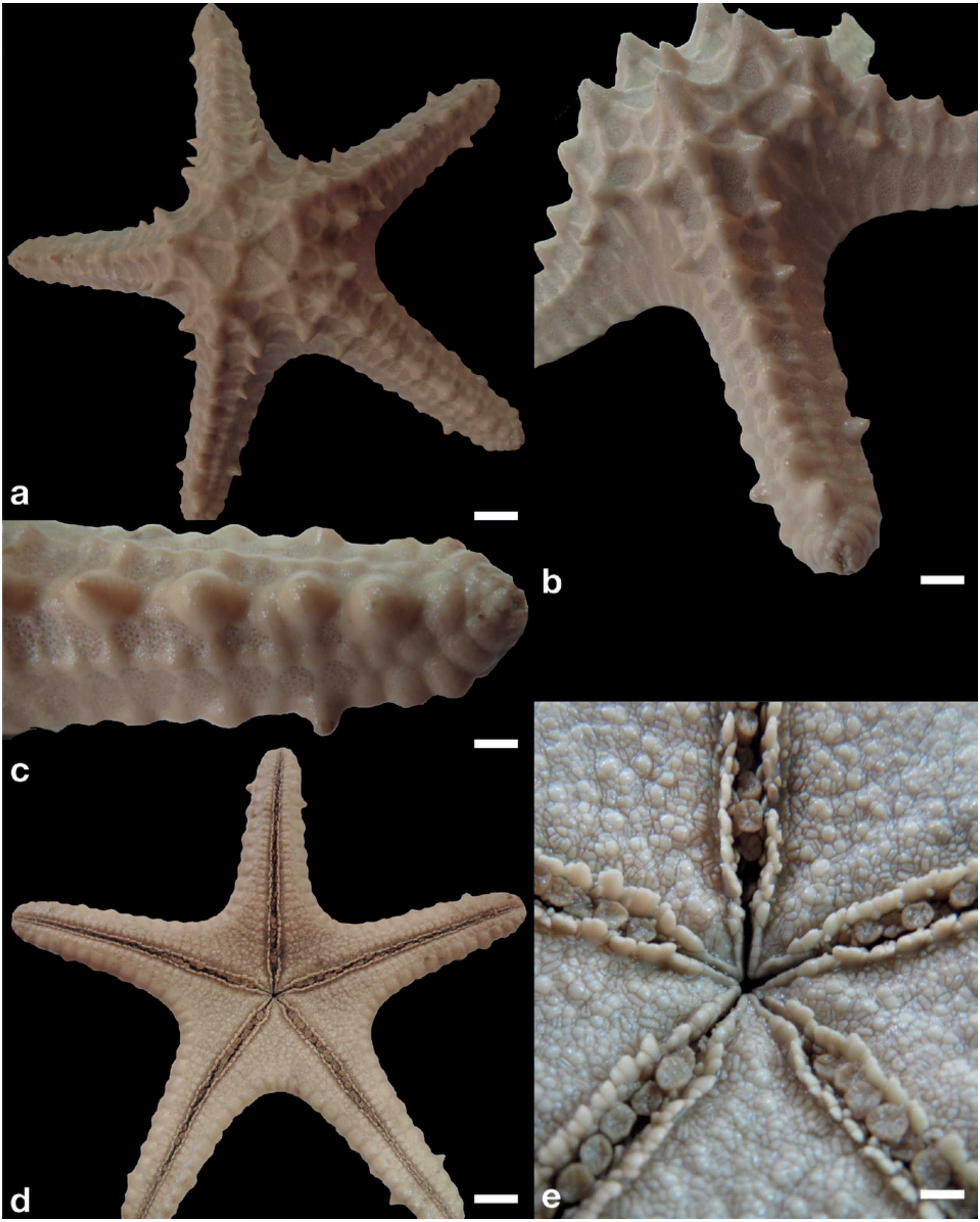

Figure 11. *Protoreaster lincki*. MNHN IE-2007-3947. a, Abactinal view. Scale bar=1.5 cm; b, Abactinal-lateral view showing degree of spination and disk and arms. Scale bar=0.5 cm; c, Armtip showing carinal and superomarginal spines. Scale bar=1.0 cm; d, Actinal view. Scale bar=1.5 cm; e, Closeup of oral region and adambulacral spination. Scale bar=0.5 cm.

lincki or *C. schmideliana*) to throughout the Indo-Pacific (e.g. *A. idipi, P. alveolatus*). This combination of widespread distribution and extending into the mesophotic is a trend observed in other shallow-water tropical asteroid Valvatida, such as in the Goniasteridae (e.g. *Fromia*), the Ophidiasteridae (e.g. *Linckia*) and the Asterodiscididae (e.g. *Asterodiscides*) (Mah, 2021). Distributions of these taxa remain largely shallow (< 200 m), with only some taxa exceptionally extending much deeper (e.g. *Asterodiscides* can occur to 800 m).

Most oreasterids surveyed here appear to be extensions of shallow-water asteroid faunas, that is, species displaying a wide bathymetric range, a pattern also observed in other taxa, such as corals and fishes (Kahng et al., 2016). Food may be one important consideration, as numerous accounts have observed the widespread presence of benthic communities dominated by algae, sponges, cnidarians and other encrusting or colonial organisms (e.g. Harris et al., 2021; Bell et al., 2022). Observations of shallow-water oreasterid taxa, including *C. granulatus*, *Protoreaster,* and *Culcita* spp. have indicated food preferences consistent with bottom fauna observed at these depths, particularly sponges and microalgal biofilms, all of which appear to be tied to the lower limit of photosynthesis.

Astrosarkus (Fig. 2a–d, 3a–b) has been observed in close proximity to multiple sessile taxa, including cnidarians and sponges (Fig. 3a).

Bathymetrically, *Astrosarkus* stands apart in occurring at greater depths (67–210 m) than other mesophotic Oreasteridae (0–100 m, only exceptionally to 275 m). The most prominent feature that sets *Astrosarkus* apart from other oreasterids is its thick, soft body wall, which is unique within the Oreasteridae. Members of the family Poraniidae display a similar type of strongly developed soft-tissue body wall (Mah and Foltz, 2014). This character is poorly understood, but all living poraniids are known from cold-water settings (Mah and Blake, 2012) suggesting that this character could be constrained or influenced by colder-water habitats. *Astrosarkus*' unusual body wall could be influenced by its depth, because the mesophotic zone is cooler than shallow tropical settings in the 0–100 m zone.

Based on the taxa surveyed herein, oreasterids appear similar to other mesophotic faunas (e.g. fishes, sponges, gorgonians; Baldwin et al., 2018, Idan et al., 2018, respectively) in being a mix of shallow-water taxa with a minority of taxa, in this case *Astrosarkus* spp., that are limited to a mesophotic distribution (Breedy and Guzman, 2013). Other asteroid groups, including the Ophidiasteridae, Goniasteridae, and Asterodiscididae, with similar mesophotic distributions (i.e. they do not occur in shallow, surface-level habitats), have been reported from the South Pacific (Mah, 2021). As further taxonomic groups are surveyed, it is hoped that better understanding of mesophotic species will provide a stronger basis for understanding diversity and establishing marine conservation in this setting.

List of mesophotic Oreasteridae treated here

Astrosarkus idipi Mah 2003

***Astrosarkus lu* n. sp.**

Culcita novaeguineae Müller and Troschel, 1842

Culcita schmideliana (Bruzelius, 1805)

Halityle regularis Fisher, 1913

Pentaceraster alveolatus (Perrier, 1875)

Poraster regularis (Möbius, 1859)

Protoreaster lincki (de Blainville, 1830)

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