



A new species of crown-of-thorns sea star, *Acanthaster benziei* sp. nov. (Valvatida: Acanthasteridae), from the Red Sea

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Abstract

A new species of crown-of-thorns sea star (CoTS), *Acanthaster benziei* sp. nov., is described based on four specimens collected from Saudi Arabia's Red Sea coast where it inhabits coral reefs. Species delimitation from congeners in the species complex, i.e., *Acanthaster planci*, *Acanthaster mauritiensis* and *Acanthaster* cf. *solaris*, is primarily based on distinct and diagnostic mitochondrial DNA sequence regions. Species separation of *Acanthaster benziei* is additionally justified due to diagnostic morphological characters: fewer arms; narrower and thinner spines; fanned spine tips in primary and latero-oral spines; a wider tip or tapering shape in circumoral spines; and rhombus-shaped oral pedicellariae.

Key words: Acanthasteridae, *Acanthaster*, morphology, taxonomy, Red Sea, coral reefs

Introduction

Acanthaster spp. are corallivorous sea stars that are widely distributed on tropical Indo-Pacific coral reefs, from the Red Sea and the East-African coast to Mexico, between a latitude of about 33° north and south (Fabricius 2013). The colloquial name ‘crown-of-thorns sea star’ (CoTS) refers to one of their most characteristic features, their large spines, which cover the aboral surface. The sea stars feed extraorally – predominantly on polyps of branching Acroporidae corals (Pratchett *et al.* 2014) – by exerting their stomach over the coral and secreting digestive enzymes (Fabricius 2013). CoTS are most infamous for their tendency to undergo rapid and massive increases in population size, referred to as ‘outbreaks’, whereby huge numbers of feeding adults can cause rapid and widespread depletion of live coral cover (Chesher 1969). For this reason, they are identified as one of the leading causes of coral reef decline in the Indo-Pacific region (De’ath *et al.* 2012; Traçon *et al.* 2011) and are consequently one of the best-studied coral reef invertebrates.

The taxonomic history of *Acanthaster* species spans more than 300 years, beginning with Rumphius' (1705) description of “Stella Marina Quindecim Radium” from Ambon Island, Indonesia. Later, Plancus & Gualtieri (1743) described “Stella marina echinata” (= lat. “spiny marine star”). However, it was Linnaeus (1767) in the appendix of the 12th edition of his famous “Systema naturae” who first formally described *Acanthaster planci* (as *Asterias planci*), the most famous representative of the genus, and honoured Janus Plancus (the pseudonym of Giovanni Bianchi, 1693–1775) with the species name. Several species have subsequently been described from different regions of the Indo-Pacific; however, for much of the last century, only two species – *A. planci* (crown-of-thorns sea star) and *Acanthaster brevispinus* (short-spined crown-of-thorns sea star; a non-coral predator that is not a threat to coral reefs) – were formally accepted (reviewed in Haszprunar & Spies 2014; Haszprunar *et al.* 2017).

It is only within the last thirty years that researchers began to suspect that the previously regarded Indo-Pacific species ‘*Acanthaster planci*’ may refer to multiple species or sub-species (reviewed in Haszprunar and Spies 2014). This notion is supported by DNA barcoding using partial mitochondrial DNA sequences of the Cytochrome c Oxidase subunit I (COI) gene, which indicates that *A. planci* encompasses four deeply divergent clades (Vogler *et al.* 2008). These four clades were proposed to represent four species, each with a distinct and largely non-overlapping distribution across the Indo-Pacific region: one from the Red Sea (RS), one from the southern Indian Ocean (SIO), one from the northern Indian Ocean (NIO), and one from the Pacific Ocean (PO) (Vogler *et al.* 2008, see also Vogler *et al.* 2012, 2013). This separation of the RS, NIO and PO species has also been confirmed using a nuclear genome-based analysis, however, the SIO could not be included due to sampling difficulties (Yuasa *et al.* 2021). An in-depth review of the original literature and species descriptions, which aimed to allocate species names to these four genetic clades (Haszprunar & Spies 2014), concluded that *A. planci* is the valid name for the northern Indian Ocean species, *Acanthaster mauritiensis* (de Loriol 1885) for the southern Indian Ocean species, and *Acanthaster cf. solaris* (Schreber 1793) for the Pacific Ocean species (see Haszprunar *et al.* 2017 for an in-depth discussion of species name allocation). However, a validation of any name for the Red Sea species was not possible. Here, we formally describe and name the Red Sea species for the first time.

Materials and methods

Collection, preparation and storage

The specimens have been assigned museum registration numbers, but referred to herein with an abbreviation of this number (e.g., SNSB-BSPG.GW.4081 is referred to as GW4081). The four specimens of the type series studied here (GW4081, GW4168, GW4202, GW4266; Table 1) were collected in 2017 by Sara Campana and Oliver Voigt on Saudi Arabia’s Red Sea coast at a depth between 2–10 m. The sea stars were narcotized with Menthol, fixed in 4% formaldehyde, and preserved in 70% ethanol in air-sealed plastic boxes. The specimens, i.e., their gross morphology, are overall intact, however many spines and pedicellariae are broken. Before narcotization and fixation, subsamples were taken for DNA analyses and preserved in 95% EtOH. Other material listed in Table 2 was investigated morphologically for comparative purposes.

The material of the type series (Tab. 1) was collected and exported in the framework and under permits of the Red Sea Biodiversity Project, a collaboration between the Senckenberg Research Institute and the King Abdulaziz University, Jeddah (Saudi Arabia), as well as under permits by the King Abdullah University of Science and Technology (KAUST). The comparative material listed in Table 2 was collected and exported by permits to the Australian Institute of Marine Science (AIMS, permit number G12/35236.1), Five Oceans Environmental Services (Oman, permit no. 01/2015 from the Ministry of Environment and Climate Affairs, now Environment Authority), and from the Maldives under permit number 30-D/INDIV/2016/420 (collection) and 30-D/INDIV/2016/702 (export).

TABLE 1. The type series investigated, including sampling location, details about preservation, and voucher location. BSPG refers to the ‘Bavarian State Collection for Palaeontology and Geology’ of the Bavarian Natural History Collections (SNSB). SNSB-BSPG.GW.4202 is designated as the holotype, all other individuals are paratypes.

Identification number	Sampling location	Latitude / longitude (WGS84)	Preservation	Whole specimen Voucher location	COI
SNSB-BSPG.GW.4202 (holotype)	Miskah Island, Farasan Banks, Saudi Arabia	18.84166667 / 40.78138889	70% Ethanol	BSPG	Yes
SNSB-BSPG.GW.4081 (paratype)	Coast guard reef, near Al-Lith, Saudi Arabia	20.124560 / 40.258746	70% Ethanol	BSPG	Yes
SNSB-BSPG.GW.4168 (paratype)	Mubarak, Farasan Banks, Saudi Arabia	19.09444444 / 40.37916667	70% Ethanol	BSPG	Yes
SNSB-BSPG.GW.4266 (paratype) subadult	Tidhkar Island, Farasan Banks, Saudi Arabia	19.12777778 / 40.6694444	70% Ethanol	BSPG	Yes

TABLE 2. Other material examined for comparative morphology. BSPG refers to ‘Bavarian State Collection for Palaeontology and Geology’ and ZSM to Zoological State Collection Munich, both of the Bavarian Natural History Collections (SNSB). All material was collected in shallow water, less than 20 m water depth.

Lineage/Species	Identification number	Sampling location	Latitude / longitude	Preservation	Voucher location
Pacific, <i>A. cf. solaris</i>	SNSB-BSPG. GW.31709	Australia: Great Barrier Reef (John Brewer Reef)	-18.633 / 147.067	Dried	BSPG
Pacific, <i>A. cf. solaris</i>	SNSB-BSPG. GW.31710 ZSM 20140115	Australia: Great Barrier Reef (John Brewer Reef)	-18.633 / 147.067	Dried	BSPG
Northern Indian Ocean, <i>A. planci</i>	SNSB-BSPG. GW.41290	Maldives: Fafuu Atoll, Magoodhoo Island	3.078402 / 72.964336	Dried	BSPG
Northern Indian Ocean, <i>A. planci</i>	SNSB-BSPG.GW.1900 ZSM 20160311	Oman: Muscat, Capital Area Yacht Club	23.588495 / 58.605517	Ethanol	ZSM
Northern Indian Ocean, <i>A. planci</i>	SNSB-BSPG.GW.1901 ZSM 20160312	Oman: DINR Police Island	23.858186 / 58.097445	Ethanol	ZSM
Northern Indian Ocean, <i>A. planci</i>	SNSB-BSPG.GW.1902 ZSM 20160313	Oman: DINR Police Island	23.858186 / 58.097445	Ethanol	ZSM
Northern Indian Ocean, <i>A. planci</i>	SNSB-BSPG.GW.1916 ZSM 20160327	Oman: DINR Police Island	23.858186 / 58.097445	Ethanol	ZSM
Southern Indian Ocean, <i>A. mauritiensis</i>	SNSB-BSPG.GW.1912 ZSM 20160323	Oman: DINR Police Island	23.858186 / 58.097445	Ethanol	ZSM
Southern Indian Ocean, <i>A. mauritiensis</i>	SNSB-BSPG.GW.1913 ZSM 20160324	Oman: DINR Police Island	23.858186 / 58.097445	Ethanol	ZSM

DNA Barcoding using partial mitochondrial cytochrome oxidase subunit I (COI) sequences

The distinction of a distinct Red Sea clade/species within the *Acanthaster 'planci'* species complex was primarily based on the analysis of partial mitochondrial cytochrome oxidase subunit I (COI) sequences in Vogler *et al.* (2008). In order to evaluate if the type series clusters in the Red Sea clade as in Vogler *et al.* (2008), and therefore can be assigned to this distinct species, we generated new COI sequences. To do so, we first extracted DNA from tube feet of the type series samples using the “DNA, RNA, and protein purification”-kit by Macherey-Nagel (Ref. 740952.50 Lot: 1707/002). We followed the manufacturer's “Genomic DNA from tissue” protocol with the following modifications: in step 2, the pre-lysing, the samples were left 1.5 hours in the Thermomixer by Eppendorf; at step 4, adjusting the conditions, 99 % Ethanol was used; and at step 8, for elution, 50 µl ddH₂O was used to unbind the DNA from the membrane of the spin-columns. A NanoDrop 2000 by Thermo Scientific™ was used to check DNA quality and quantity.

Partial COI sequences were amplified using primers and conditions as described in Vogler *et al.* (2008). Sanger sequencing was carried out at the Biozentrum of the Ludwig-Maximilians-Universität München in Planegg-Martinsried on an ABI 3730 capillary sequencer.

The original haplotype dataset of Vogler *et al.* (2008) was then supplemented with the new sequences from the type series of *A. benziei* sp. nov. from Saudi Arabia (Red Sea), as well as five samples from Israel (Red Sea) extracted from full mitochondrial genome sequences from Yuasa *et al.* (2021) (accession numbers LC566218–LC566222). The 632 bp alignment (available in the supplementary material) of 84 sequences was processed in Geneious Prime 2019 (<http://www.geneious.com>). A maximum-likelihood phylogeny was calculated in IQ-Tree v.1.6.12 (Nguyen *et al.*, 2015) using the best-fit evolutionary model Tamura-Nei+F+I, chosen according to BIC in IQ-Tree, with 1000 bootstrap replicates. In addition, a neighbour-joining (NJ) clustering of COI sequences with bootstrapping (1000 replicates) was performed in Geneious Prime 2019 using the best-fit Tamura-Nei model. Alignment positions of the partial COI sequences used here refer to positions in the full mitochondrial genome sequences from Yuasa *et al.* (2021). The four newly generated sequences of the *A. benziei* type series are deposited in the European Nucleotide Archive (Accession Numbers OW970326 – OW970329).

Morphometrics

The number of arms (rays) and madreporites were manually counted. A measuring band or mechanical calliper was used for size measurements. The radius from the middle of the disc to one arm tip (R), i.e., the length of one ray, was measured on the oral side of the individual (Figure S1). Likewise, the diameter of the disc (r) was measured from the centre to the interradial margin (Figure S1). The spines were distinguished by their position on the arm or disc and the symmetry they show within one arm.

Terminology

For the general and stereom (calcite skeleton of echinoderms) morphology we used the terminology of Walbran (1987) that followed the nomenclature established by Blake (1979). The nomenclature of Motokawa (1986) to describe the characteristics of the spines was applied (see also Fig. 1), and for the pedicellariae the one of Jangoux & Lambert (1988). To our knowledge, the works of Blake (1979), Motokawa (1986) and Walbran (1987), are to date the only ones specifically describing the morphological features of *Acanthaster* sea stars, hence we apply this terminology here (for some examples with respect to spines see Fig. 1).

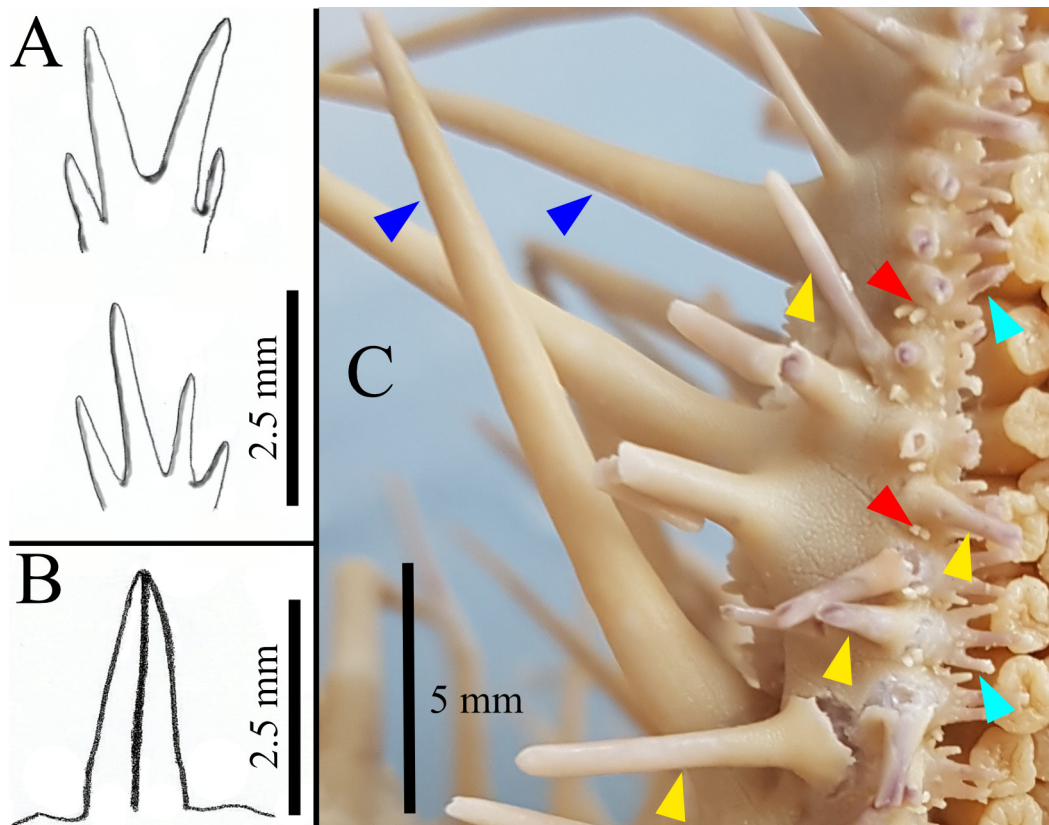


FIGURE 1. Illustrations of pedicellariae and spines (A–C). A: Subambulacral spines, top: bundle with two equally long spines each, bottom: bundle with four unequal long spines; B: Aboral pedicellariae with two valves; C: Close up of part of one arm of paratype GW4081, showing three different spine types indicated by arrows: latero-oral spines (dark blue), oral spines (yellow), subambulacral spines (turquoise). The actinal pedicellariae (red) are associated with the first row of oral spines.

Preparation of pedicellariae and spines

For each specimen, primary and secondary spines, as well as aboral pedicellariae were dissected from the aboral side, while subambulacral, oral, circumoral, and latero-oral spines, and oral pedicellariae were dissected from the oral side. Spines and pedicellariae were removed from different body parts, starting close to the centre of the disc and working towards the tips of the arms to obtain a more detailed picture of the different shapes of each spine or pedicellaria type. The samples were isolated and cleaned by digesting the soft tissue over approximately 72 hours with 5 % bleach with sodium hypochlorite (2,8 g / 100 g) as the active ingredient. When the soft tissue was dissolved, the samples were washed five times with double distilled water (ddH₂O) and ethanol (99 %), and finally dried. To confirm that spines and pedicellariae remained intact during the preparation process, they were checked constantly under a light microscope.

Digital microscopy

The overall shape of the spines and pedicellariae was examined and length (base to tip) of the samples was measured using a digital microscope (Keyence VHX-5000) at a magnification of 20× for primary and latero-oral spines, 30× for secondary, circumoral and oral spines, and 100× for oral and aboral pedicellariae. The Panorama function was used for very large spines with 100× magnification.

Results

Systematics

Class ASTEROIDEA de Blainville, 1830

Order VALVATIDA Perrier, 1884

Family ACANTHASTERIDAE Sladen, 1889

Genus *ACANTHASTER* Gervais, 1841

Gervais 1841: 461–481. Madsen 1955.

Diagnosis. Medium to large body discoidal, multi-radiate; skeleton surrounded by numerous bi-articulated spines on mammiform tubercles; madreporic tubercles numerous, conical, ten to 25 in number, arranged in a circle; ambulacral spines small, placed in a group beside them, a continuous small row of thin, enlarged spines. The spines are either long (up to ~3 cm) and venomous [*A. planci*-complex] or very short (up to 10 mm) [*A. brevispinus*]; they usually have a second joint about one third of the way down. They occur in tropical regions of the Indo-Pacific Ocean, including the Red Sea, and extend to the Eastern Pacific.

Acanthaster benziei sp. nov. Wörheide & Kaltenbacher

Zoobank LSID: urn:lsid:zoobank.org:act:4C462EF3-39AF-4767-96DF-C3B8CC5D9388

Formal name. *Acanthaster benziei* Wörheide & Kaltenbacher in Wörheide, Kaltenbacher, Cowan & Haszprunar 2022

Etymology. The species name pays tribute to Professor John Benzie, who has decisively promoted research on CoTS, with numerous publications and his own collection. He was among the first scientists to genetically analyse *Acanthaster* spp. and his collection was the basis of the work of Vogler *et al.* (2008), which represents a milestone in the species identification of these sea stars.

Holotype. SNSB-BSPG.GW.4202, adult individual (Fig. 2A), collected in 2017 by Sara Campana and Oliver Voigt at Miskah, Farasan, Saudi Arabia (18.84166667 / 40.78138889) in a water depth of 10 m. The sea star was narcotized with menthol, fixed in 4% formaldehyde, and preserved in 70% EtOH. Some tube feet for DNA analyses were preserved in 95% EtOH and are stored at SNSB-BSPG together with the specimens.

Paratypes. SNSB-BSPG.GW.4081, adult individual (Fig. 2B), collected from Coast guard reef, near Al-Lith, Saudi Arabia (20.124560 / 40.258746) in a water depth of <10 m, narcotized with menthol, fixed in 4% formaldehyde, and preserved in 70% EtOH. Some tube feet for DNA analyses were preserved in 95% EtOH and are stored at SNSB-BSPG together with the specimens.

SNSB-BSPG.GW.4168, adult individual (Fig. 2C), collected from Mubarak, Farasan Banks, Saudi Arabia (19.09444444 / 40.37916667) in a water depth of <10 m, narcotized with menthol, fixed in 4% formaldehyde, and preserved in 70% EtOH. Some tube feet for DNA analyses were preserved in 95% EtOH and are stored at SNSB-BSPG together with the specimens.

SNSB-BSPG.GW.4266, juvenile individual (Fig. 2D), collected from Tidhkar Island, Farasan Banks, Saudi Arabia (19.12777778 / 40.66944444) in a water depth of <10 m, narcotized with menthol, fixed in 4% formaldehyde, and preserved in 70% EtOH. Some tube feet for DNA analyses were preserved in 95% EtOH and are stored at SNSB-BSPG together with the specimens.

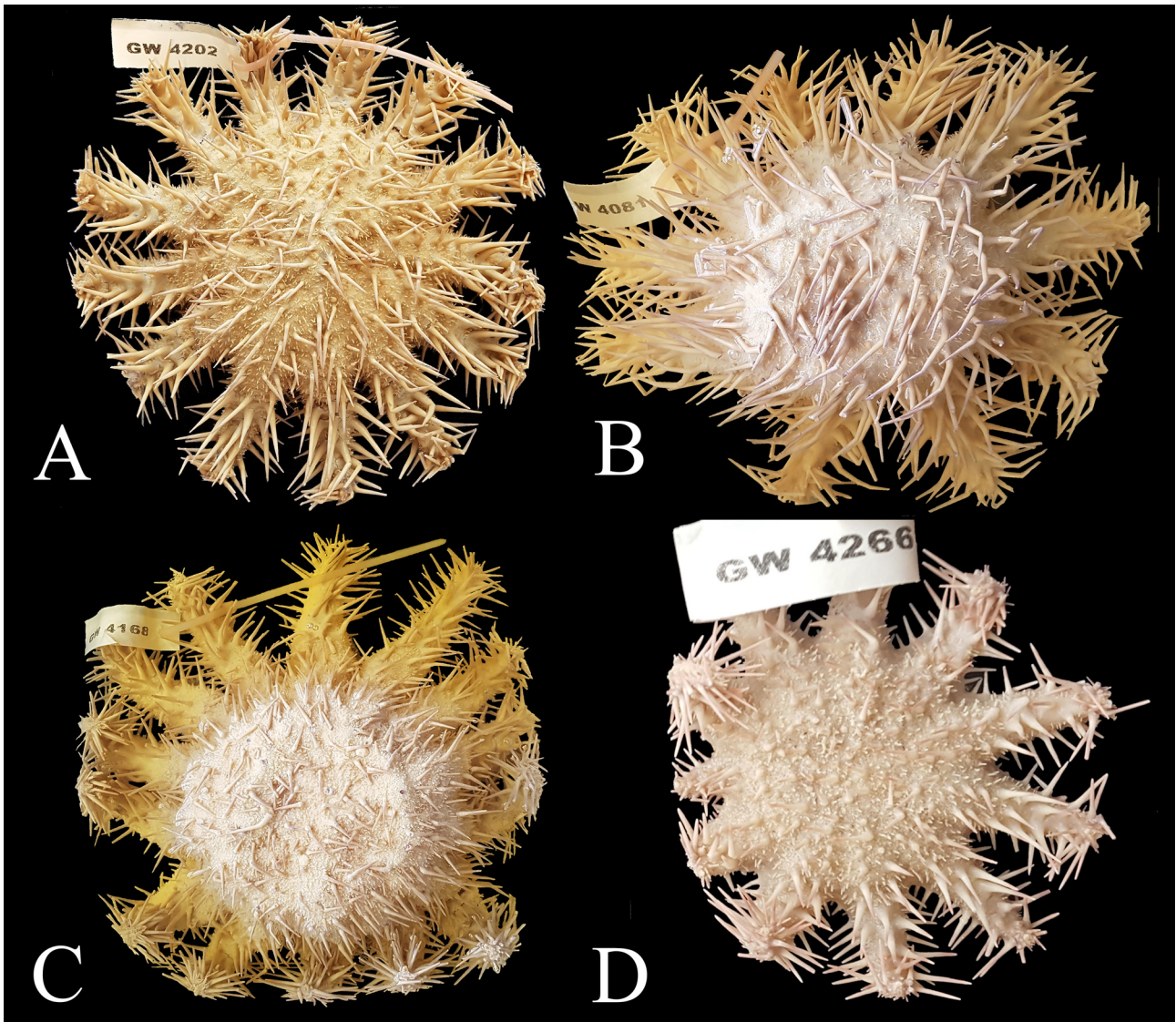


FIGURE 2. Ethanol-preserved specimens of the type series. GW4202 (A) is the holotype, all the others (B–D) are paratypes. Note that individual GW4266 is a juvenile specimen. Size of labels 6×2 cm.

Diagnosis. DNA barcoding analysis of partial COI sequences reasserted *Acanthaster benziei* as a deeply divergent clade (Fig. 3, see also Vogler *et al.* [2008]) with distinct geographic distribution (Red Sea). *Acanthaster benziei* possesses diagnostic mutations in its partial mitochondrial COI gene sequenced here that are unique for the Red Sea and not shared with any other species of the species' complex, i.e., *A. planci*, *A. mauritiensis* and *A. cf. solaris*. Specifically, mutations in the following positions are diagnostic for *A. benziei* (the position refers to the position in the COI gene extracted from the mitochondrial genome of a specimen from Israel [GenBank accession number LC566218]; the first nucleotide is the one in *A. benziei*, the second one in the other three species): 150 (T / C), 426 (G / A), 495 (T / C), 504 (G / A), 555 (T / C), 585 (G / A), 588 (T / C), 612 (G / A), 711 (T / C), 714 (C / T). All these are silent third-codon mutations.

The following diagnostic morphological characters differentiate *A. benziei* from its congeners, and were assessed from the type series at size measured (see Table 3): fanned spine tips in primary and latero-oral spines; a wider tip or tapering shape in circumoral spines; and rhombus-shaped oral pedicellariae. Additionally, *A. benziei* has fewer arms than its congeners (up to 14 in *A. benziei* vs. up to 23 in *A. cf. solaris* from the Pacific).

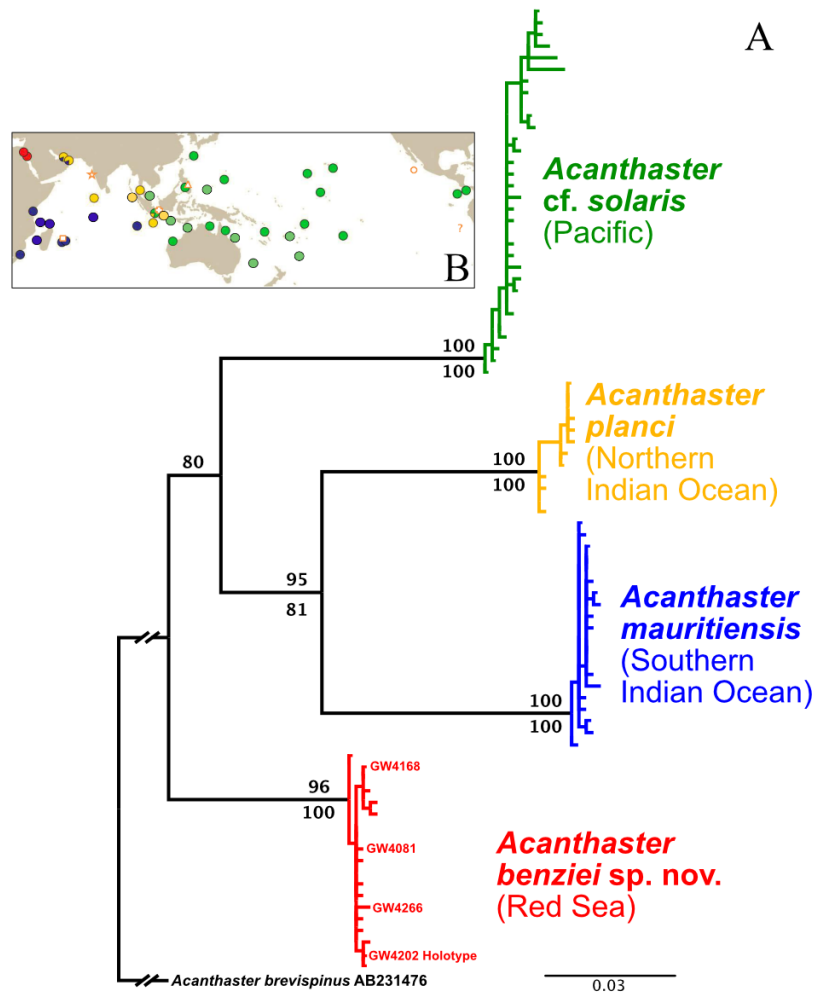


FIGURE 3. A: Indo-Pacific ‘*Acanthaster planci*’ species complex, COI ML tree based on the haplotype alignment of Vogler *et al.* (2008), supplemented with five samples from Israel (see text for details) extracted from full mitochondrial genome sequences from Yuasa *et al.* (2021) and four sequences of the type series of *Acanthaster benziei* sp. nov. (GW4xxx, highlighted in bold). The tree was rooted with *Acanthaster brevispinus* (accession number AB231476), showing the deep divergence among, and little diversity within, species/geographic clades. ML bootstrap values are above branches, bootstrap values of the NJ clustering of haplotypes below branches.

B: Geographic distribution of COI-barcoded clades and of type localities of names (Figure 1 from Haszprunar *et al.* 2017): red—Red Sea (RS) species; blue—Southern Indian Ocean (SIO) species (*A. mauritiensis*); yellow—Northern Indian Ocean (NIO) species (*A. planci*); green—Pacific Ocean (PO) species (*A. cf. solaris*). Location of type localities of nominal *Acanthaster* species: asterisk—*A. planci*; cross—*A. echinites*; triangle—*A. solaris*, square—*A. mauritiensis*; circle—*A. ellisii pseudoplanci*; “?” - the type locality of *A. ellisii* was not specified: in South American waters of the East Pacific.

Morphological description. Applies to the holotype, except otherwise noted. Large sea star with a convex disk and 13 arms (number of arms across type series 11–14, Table 3), which have a subcylindrical cross section. Each arm tapers to an acute point and the arms are slightly variable in length. The mean disk radius (*r*) measures 58 mm, the mean length of rays (*R*) is 91 mm (*R/r* ratio = 1.57).

There are two rows of ambulacral tube feet (approximately 1–3 mm in diameter, with flattened tips and no sucker) in the ambulacral groove in the midline of the oral side of each arm. The stereom on both the oral and aboral side consists of a mesh of ossicles, concealed by soft tissue and a large number of spines and pedicellariae, both of which are sheathed in tissue, typically labyrinthic or elongated trabeculated. The aboral disc surface has many papulae with no clear arrangement. The tissue here is relatively soft and compressible. The anus – in the centre of the disc – has no papulae, is harder, and is spaciouly encircled by six madreporites on the disk.

TABLE 3: Basic measurements of type specimens, including number of arms and madreporites, mean length of arms (R) and radius of disk (r). Note that GW4266 is a juvenile specimen.

	GW4202	GW4081	GW4168	GW4266
Number of Arms	13	11	14	11
Mean R (length of arm)	91 mm	106 mm	125 mm	50 mm
Mean r (radius of disc)	58 mm	51.5 mm	65 mm	28 mm
R:r ratio	1.57	2.06	1.92	1.79
Number of Madreporites	6	4	4	4

Six spine types are distinguished: primary and secondary spines on the aboral side, and subambulacral, circumoral, oral, and latero-oral spines on the oral side (see Fig. 1 for definition). The primary and the secondary spines, that cover the aboral surface, differ in size and supporting ossicle (the pedicle), which is shorter and supported by a secondary ossicle in the secondary spines (Motokawa 1986; Walbran 1987). Subambulacral spines are very short and occur next to the ambulacral groove or furrow. Long latero-oral spines intercross with those of the adjacent arm, while the oral spines are shorter, with a blunt tip, positioned in one or two rows next to the subambulacral spines. Most circumoral spines are longer than the oral spines and are located in a single row at the mouth opening. One group of circumoral spines is part of two adjoining rays. Spines on the oral side may have a bend in the lower quarter of the shaft, are more irregular than the aboral spines, and either lack or have a less dominant pedicle. The oral and circumoral row of spines is continuous throughout all of the arms. They fringe the ambulacral spines from the tip of one arm to the mouth opening, turning to the next arm, where they also fringe the ambulacral spines, remaining symmetrical on both sides of the ambulacral groove. Variations and intermediate forms of one or more of the spine tip shapes within one individual are possible, however, the pointed tip is common in any sea star studied from the type series.

Primary spines (Figs. 4A, 6) are the longest spines on the aboral surface, ranging between approximately 6–33 mm in length. They are straight and slender, slightly shorter (approx. 6–27 mm) on the disc and longer (approx. 27–33 mm) on the arms, consist of one to two parts and are supported by a basal/primary ossicle (= pedicle). The shape of spine tips is variable, but most common is a fanned spine tip with several small furrows (Fig. 6A). The spines can be granulated in the upper half.

Secondary spines (Fig. 4B) are found mainly on the disc, but also on the arms. They are less numerous and shorter than the primary spines, ranging between approximately 8–11 mm in length. Secondary spines always consist of one part, but otherwise reflect the appearance of primary spines, also regarding granulation.

Latero-oral spines (Figs. 4C, 7) are similar in size to the primary spines, ranging between approximately 4–20 mm in length. They are located on marginal ossicles, forming no or short pedicles, compared to primary spines. Spine tips have similar shapes to primary spines: pointed to fanned or flat with a slight furrow in the middle, rounded tip with small furrows, mostly broader than tips of aboral spines, can be asymmetrical, can widen or taper upwards. Granulation may be present.

Circumoral spines (Figs. 4D, 8) form a single row surrounding the mouth, and range in length between approximately 9 and 11 mm. Groups of 8–12 spines are associated with two large oral ossicles and every ray has two oral ossicles (occurring symmetrically, one on each side of a ray), each with the same number of spines. One group of circumoral spines is part of two adjoining rays. Within each group, the spine that is closest to the mouth is the terminal spine. There are always two terminal spines, which are the longest, and the spines become shorter towards the adambulacral ossicles. All spines are wider and mostly flattened towards the tip, with the flat side facing either the ambulacral furrow or, if terminal, the mouth opening. Spine tips are mostly flat and may have furrows or be smooth; a pointed tip is rare. Granulation may be present.

Oral spines (Fig. 4E) are very abundant, occurring in one or two rows on the oral-intermediate ossicles and in

one row on the adambulacral ossicles, with a flat side facing the ambulacral furrow. They are similar to circumoral spines, but smaller, in the range of 4–7 mm length, and with deeper furrows. The upper outline can show a depression in the middle.

Subambulacral spines (Fig. 4F) fringe the margin of the ambulacral grooves. They are the most abundant and smallest, ranging between 2–11 mm in length, becoming shorter towards the tip of the arm. Three to four spines are grouped in an adambulacral comb on one ossicle, which is connected by tissue at the base; the outer spines within the grouped spines are always the smallest. Each group of spines is associated with one tube foot. Most spine tips are pointed; however, larger spines can have a flattened tip with slight furrows. The shaft of the spines can be bulbous on one side, increasing the width at the middle of the spines.

All **pedicellariae**, aboral and oral, are straight, bivalved, and alveolar, positioned over a small cavity, or cupule in the underlying ossicle (see Gale 2011).

Aboral pedicellariae (Fig. 4G) are located among the primary spines, secondary spines and papulae, and are mostly very frequent, giving the aboral side of the sea stars a hairy appearance. They are very common on the disc, but less frequent on the arms; however, abundance differs between individuals. They consist of two equally sized valves, ranging between approximately 2–3 mm in length, are long and slender, and are nearly symmetrical with a tapering tip. The outer rim of the valves has a fine, tooth-like structure that is uniform but can be more prominent on one side.

Oral pedicellariae (Figs. 4H, 8) occur at two locations: most commonly next to oral spines or the group of subambulacral spines on the adambulacral ossicle; or more rarely, between the oral spines on the oral ossicles, or exceptionally found on marginal ossicles. The valves are mostly of the same length, ranging between approximately 1.5–2 mm in length. The overall shape is very variable, however there are two main shapes: i) smaller and irregularly formed with a hook-shaped tip, wide from the side, slender from the front, rounded shaft under the “hook” which may have small, asymmetrically-arranged teeth; or ii) flatter, largely resembling the shape of a rhombus due to a widening in the middle part and a pointed tip, with teeth occurring asymmetrically on the outer rim and occasionally on the inner surface, if the area is large enough.

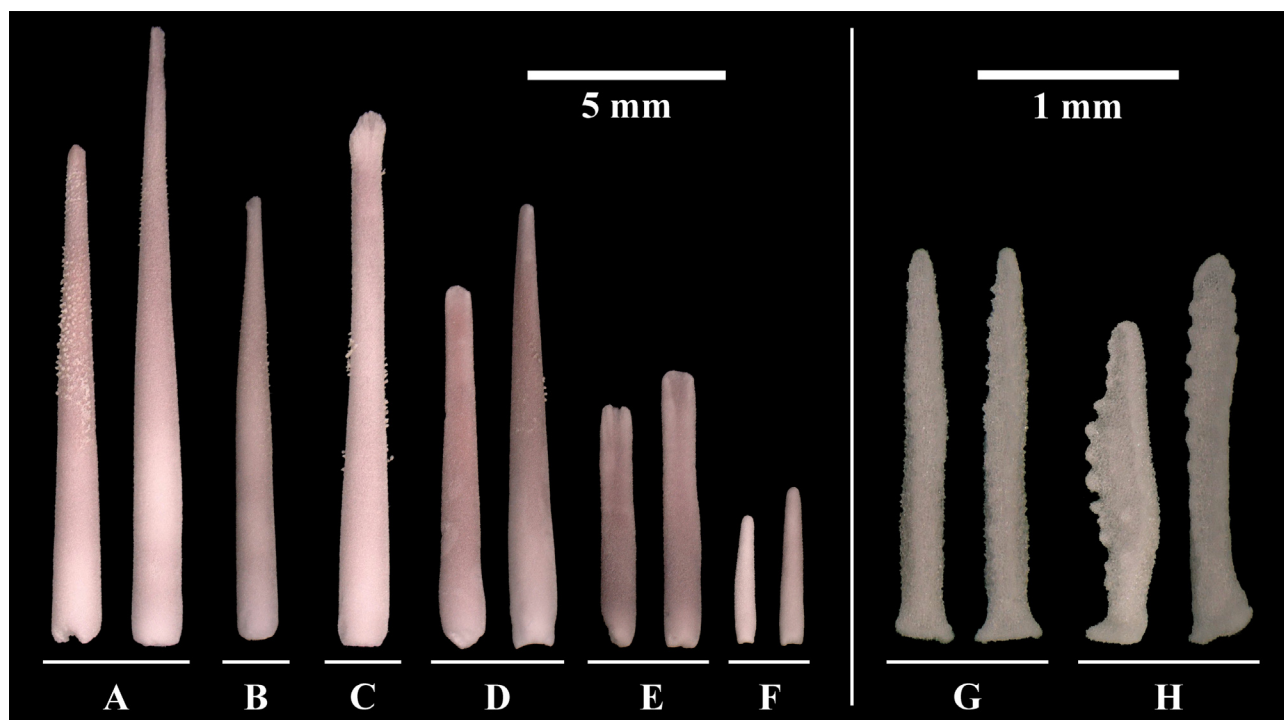


FIGURE 4. *Acanthaster benziei* sp. nov. (holotype GW4202) (A-B) Aboral spines, (C-F) oral spines and (G-H) pedicellariae of four adult specimens of *Acanthaster benziei* sp. nov.: (A) Primary spines, (B) Secondary spines, (C) Latero-oral spines, (D) Circumoral spines, (E) Oral spines, (F) Subambulacral spines, (G) Aboral pedicellariae, (H) Oral pedicellariae.

Colour. The colouration of live adult specimens is grey-green to grey-purple, with aboral spines that can be orange to reddish in colour (Fig. 5). Reddish papulae on the aboral surface may also give a bulls-eye appearance due to the formation of two darker rings (Birkeland & Lucas 1990) (Fig. 5 B, D).

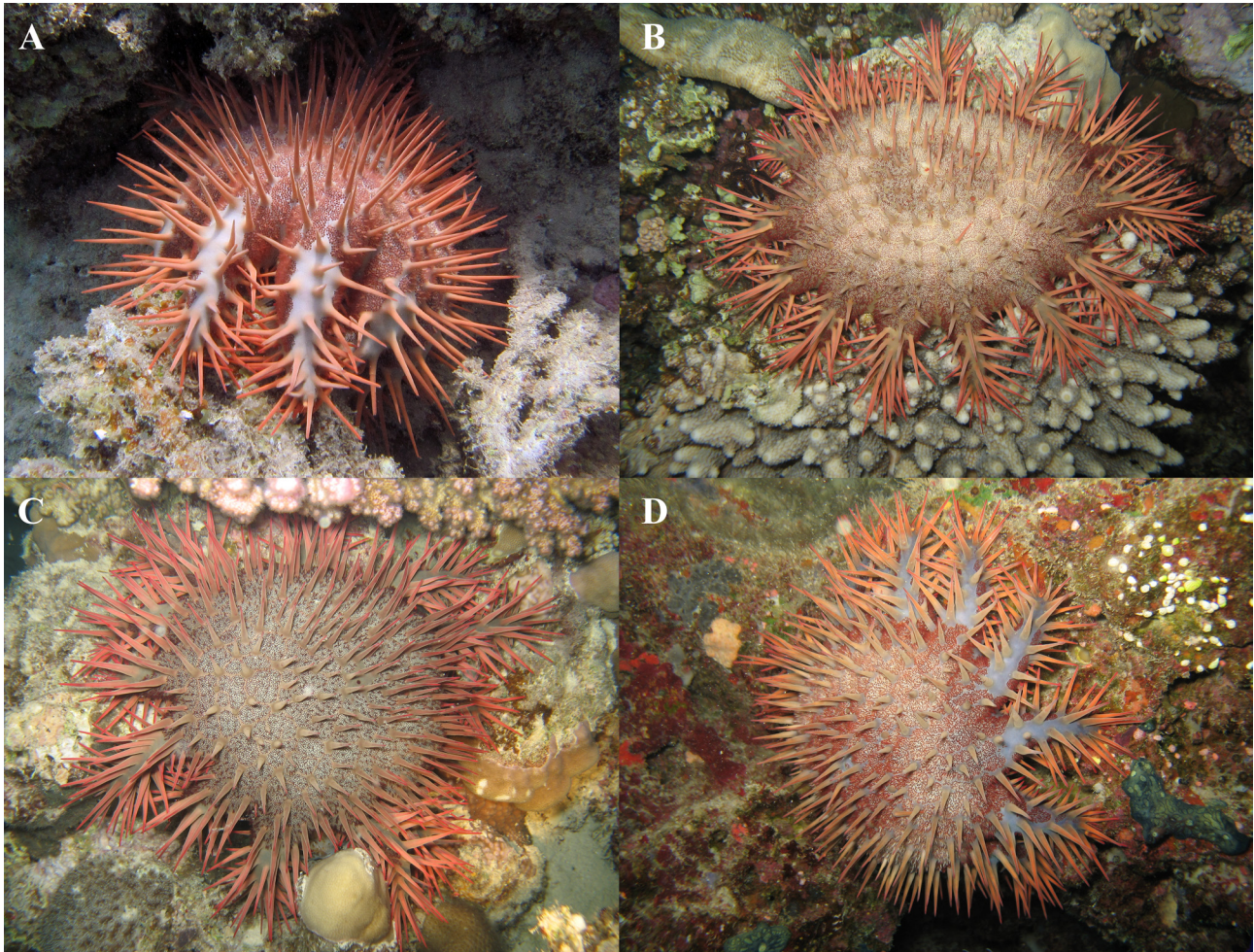


FIGURE 5. Typical colouration of *Acanthaster benziei* sp. nov. (A) GW4081 (Paratype, hiding during the day under a crevice), Al-Lith, Saudi Arabia, (photo credit: Oliver Voigt), (B–D) Thuwal Reefs, Saudi Arabia (photo credit: Gert Wörheide). Approximate diameter of specimens is 25–30 cm.

Distribution and habitat. So far known *Acanthaster benziei* is restricted to the Red Sea, where it inhabits coral reefs, predominantly the outer reef surfaces where it mostly hides in crevices during the day and feeds nocturnally.

Differential diagnosis. *Acanthaster benziei* sp. nov. can clearly be distinguished by diagnostic mutations in the partial COI gene sequences analysed, all material examined fall within the deeply divergent monophyletic group of CoTS from the Red Sea (see Fig. 3). There is full agreement with initial results that proposed species distinction of the Red Sea clade based on COI data alone (Vogler *et al.* 2008), recently corroborated by nuclear genome analyses (Yuasa *et al.* 2021). The molecular-based species distinction of *A. benziei* sp. nov. is also substantially supported by diagnostic morphological characters.

Acanthaster benziei has fewer arms than congeneric sea stars of comparable size from the other geographic regions/species. Our reported range between 11 and 14 arms in the type series (Tab. 3) is consistent with values previously reported for other individuals from the Red Sea (mean of 13 arms [Campbell and Ormond 1970]; maximum of 13–14 arms [Haszprunar *et al.* 2017]). By contrast, the number of arms reported for sea stars from India (= *A. planci*) was 15 (Linnaeus 1758) and for *A. mauritiensis* 13–16 (de Loriol 1885), with a maximum of 23 arms reported for *A. planci*, *A. mauritiensis* and the Pacific species *A. cf. solaris* (Haszprunar *et al.* 2017) (see Supp. Tab. 1).

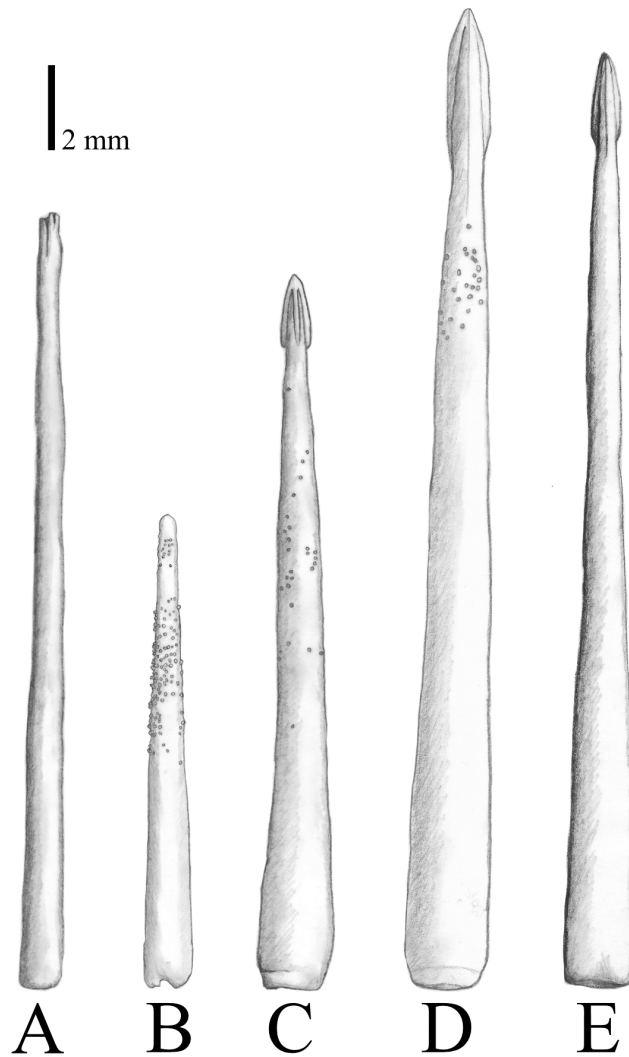


FIGURE 6. Typical primary spines, showing species-specific variation among (A, B) *Acanthaster benziei* sp. nov., (C) *A. planci*, (D) *A. mauritiensis*, and (E) *A. cf. solaris*.

The spines and pedicellariae of *A. benziei* are more variable, and spines are narrower and thinner than in its congeners. The pointy spine type was not found in such high abundance in specimens outside the Red Sea (Fig. 6, Suppl. Fig. S2–4). Unique for *A. benziei* are the fanned primary spines (Fig. 4A, 6A) and the distally fanned latero-oral spines, which can also be granulated (Fig. 4C, 7A). The granulation of the latero-oral spines is rare, and may also be found in *A. mauritiensis*, where the longest spines have an arrow-head tip (Fig. 7C; Suppl. Fig. S3C).

Compared to spines of its congeners, there are some key differences: primary spines of *A. planci* show only one tip-shape, which resembles an arrowhead (Fig. 6C; Suppl. Fig. S2A) – this was not found in *A. benziei*; secondary spines are longer compared to primary spines in *A. benziei* than in *A. mauritiensis* (around half to three quarters the size of the primary spines), *A. planci* and *A. cf. solaris* (around one quarter to half the size of primary spines); and the second articulation of primary spines is only found in *A. benziei*. Primary spines in CoTS from the Red Sea are also considered to be less harmful than spines of other regions, which could be connected to the shape, and they seem to have less toxins (Campbell & Ormond 1970).

Some shapes of the circumoral spines are unique for *A. benziei* (Fig. 8A). While the common shape of these spines in the species complex is straight, flattened, and with a blunt tip (e.g., in *A. planci* [Fig. 8C; Suppl. Fig. S2D] and *A. mauritiensis* [Fig. 8D; Suppl. Fig. S3D]), the spines of *A. benziei* (Figs. 4D, 8A) may have a wider tip or the tip is tapering and more pointed with some granules present on the shaft of the spine (Fig. 8B). Both shapes are only found in this spine type of *A. benziei*. The other oral spines are very similar to the corresponding spines of specimens examined from the other three species (Suppl. Figs. S2–4).

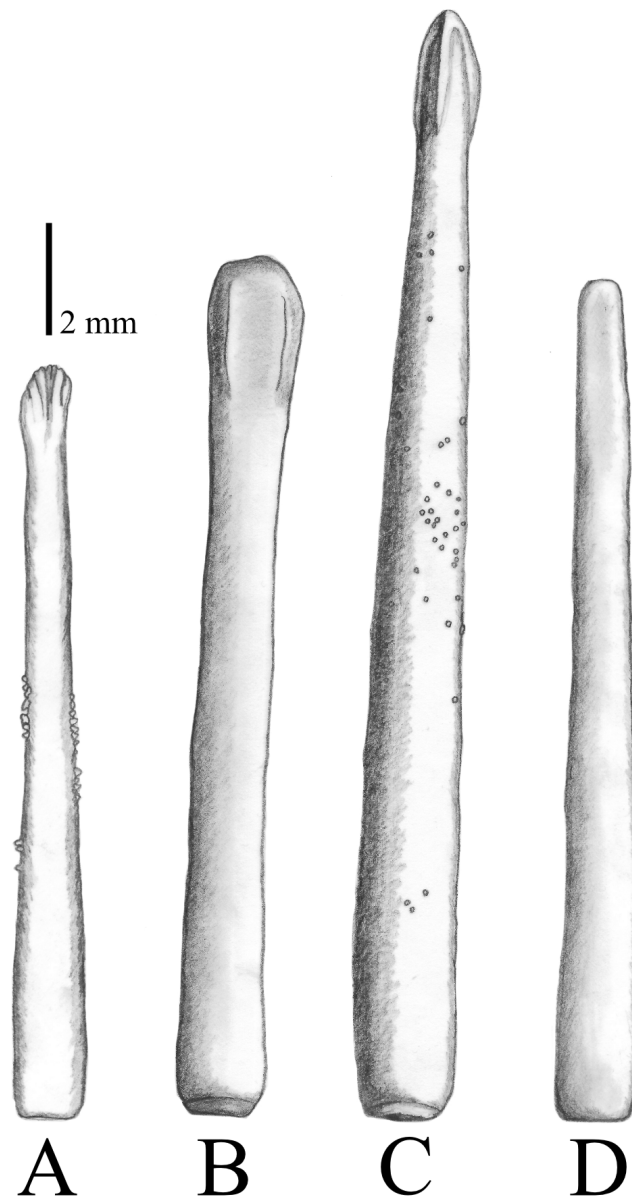


FIGURE 7. Typical latero-oral spines, showing species-specific variation among (A) *Acanthaster benziei* sp. nov., (B) *A. planci*, (C) *A. mauritiensis*, and (D) *A. cf. solaris*.

Aboral pedicellariae are more numerous in *A. benziei* than in the two Indian Ocean species *A. planci* and *A. mauritiensis*. The oral pedicellariae of *A. planci* (Fig. 9B; Supp. Fig. S2H) are mostly wider and straighter than those of *A. benziei* (Figs. 4H, 9A), which are the smallest among the four species, and are not as deeply curved as the pedicellariae of *A. mauritiensis* (Fig. 9C; Supp. Fig. S3H). The valves of the flat oral pedicellariae, which resemble the shape of a rhombus, with a widening at the middle, a pointed tip and teeth on the inner surface, were additionally only found in specimens from the Red Sea (Figs. 4H, 9A).

In summary, the main distinguishing morphological characters of *A. benziei* considered to be species-specific are the fanned spine tips in primary (Figs. 4A, 6) and latero-oral spines (Figs. 4C, 7), the wider tip or the tapering-pointed shape in circumoral spines (Figs. 4D, 8), as well as the rhombus-shaped oral pedicellariae with occasionally internal teeth (Figs. 4H, 9).

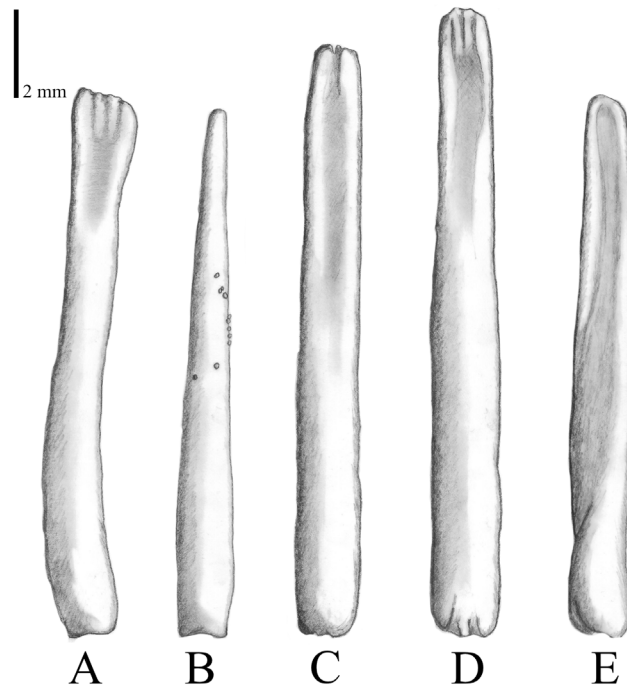


FIGURE 8. Circumoral spines, showing species-specific variation among (A, B) *Acanthaster benziei* sp. nov., (C) *A. planci*, (D) *A. mauritiensis*, and (E) *A. cf. solaris*.

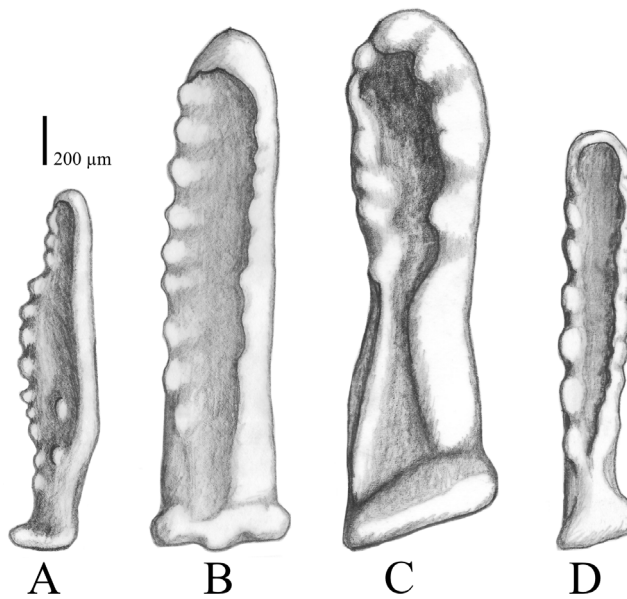


FIGURE 9. Oral pedicellariae, showing species-specific variation among (A) *Acanthaster benziei* sp. nov., (B) *A. planci*, (C) *A. mauritiensis*, and (D) *A. cf. solaris*.

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