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How to assess the absence of a species? A revision of the geographical range of the horned sea star, *Protoreaster nodosus* (Echinodermata; Asteroidea)

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Abstract

Demonstrating the absence of a species has always been a challenge for natural sciences, which are more used to documenting their presence; however, both forms of data are of equal scientific significance. The horned sea star *Protoreaster nodosus* is said, in the scientific literature, to be present throughout the whole Indo-Pacific region, from eastern Africa to the Pacific Ocean islands. However, a review of the scientific literature, along with a critical bibliographical study, citizen science surveys, web-based pictures analyses, and field studies suggests that the presence of this species could instead be restricted to the western Pacific Ocean, from Thailand to Samoa and from Japan to New Caledonia, with no reliable record in the Indian Ocean. Such a huge and long-running mistake on a very common and conspicuous species exemplifies the importance of a critical approach towards species distribution data, which appears too often based on layers of reproduction of never-reassessed data, turning hypotheses into commonly shared truth.

Highlights

- This work aims to develop a method to assess the absence of a species in a large marine area despite widespread belief in the scientific literature.
- Mixed methods were used, including a bibliographical review, citizen science data, web-based pictures analyses and field studies.
- The horned sea star *Protoreaster nodosus*, appears to be absent from most of the Indian ocean, contrary to assertions within the scientific literature for more than a century.
- Such mixed method approaches can contribute to correcting similar long-running mistakes in the field of biogeography and raise awareness of potential major flaws in the scientific literature about species distribution.

Keywords: Assessing absence, Asteroidea, Biogeography, Citizen science, Distribution, Geographical range, Oreasteridae, *Protoreaster nodosus*.

Introduction

Sea stars play an important role within marine ecosystems as major predators of sessile fauna and opportunistic detritivores (Menge and Sanford 2013). Sea stars of the family Oreasteridae are relatively large-bodied species, with a robust shape characterized by a large central disc, covered by extensive papular areas that are often protected by hard tubercles, and usually five thickset arms (Clark and Rowe 1971). All but one species live in the tropical Indo-pacific, most of them in shallow waters, where they can easily be spotted thanks to their diurnal behavior, large size, and often bright colors. For these reasons, they constitute an important marine symbol but are threatened in some areas due to overfishing for the tourism and aquarium industries (Bos et al. 2008).

The “horned sea star” *Protoreaster nodosus* (L.) is one of the most conspicuous species in this family: this big sea star is distinctive due to its large, conical tubercles, and it can form important populations in many regions across the Pacific Ocean and purportedly also across the Indian Ocean, especially within silty beaches, seagrass beds and reef flats (Bos et al. 2008). This species was originally described by Johann Heinrich Linck in his pre-Linnean work *De Stellis marinis liber singularis* (Linck 1733) as *Pentaceros turritus* – already with a clear and illustrated distinction from *P. muricatus*, the future *P. lincki*, as well as *P. hiulcus*, currently another synonym of *P. nodosus* – and incorporated by Linnaeus in 1758 under the name *Asterias dorsatus*, amended for *Asterias nodosus* in 1759, later confirmed by Lamarck. It has been known under at least 20 synonyms throughout history (see

below), and has been part of the genera *Asterias*, *Oreaster*, *Pentaceros*, and finally *Protoreaster* Döderlein, 1916, within which we can also find *Protoreaster lincki* (Blainville, 1830), a western Indian Ocean endemic, *Protoreaster nodulosus* (Perrier 1875), a western Australia endemic, and *Protoreaster gotoi* Döderlein, 1936, seemingly restricted to Okinawa. See Fig. 1 for pictures and comparison.

In the field, *Protoreaster nodosus* is easily distinguished from *P. lincki* based on color patterns. The former is very variable, often plain sand-colored (varying from white to solid red or green), sometimes with an irregular and coarse tawny or red pattern (followed by a red oral face as well), often (but not always) with black or dark brown tubercles and arm tips – hence the popular nickname “chocolate-chips sea star” (See Fig. 1 for pictures and comparison). On the other hand, *P. lincki* has quite a consistent pattern, with a silver grey abactinal face adorned with a fine, bright red reticular pattern connecting the carinal rows of tubercles (often in three parallel lines) and red arm tips. In *P. lincki* the oral face is always plain burgundy red, and no third color has ever been observed in any of the pattern variations (however, once blunt the tubercle tips can appear orange or yellowish). Preserved specimens rapidly lose their

colors (be it by drying or conservation in ethanol or formalin), and are hence harder to tell apart. They are mostly distinguished by the presence in *P. lincki* of lateral tubercles on both side of the arm tips, on the distal superomarginal plates (from 0 to 7 per side). However, these tubercles can be reduced or even absent in some specimens, even at a mature stage (as in Fig. 1). Döderlein (1936) seemed unaware of this variation. *P. nodosus* generally bears larger and more conical tubercles, which are sometimes restricted to the five primary radial plates, and are usually in only one, carinal, row outside the disc. For both species, the abactinal tubercles shape can range from rounded bumps to elevated spines: they are always bumpy in young specimens and can taper or not with growth. However, *P. lincki* seems to have more often tapered tubercles. Both species have a similar size and shape: *P. lincki* is usually described with a ratio of arm length (R) to disc ray (r) of $R=2.3\sim 3r$, and *P. nodosus* $R=2\sim 3r$ (Marsh & Fromont 2020). Juveniles of both species are inconspicuous and nearly indistinguishable, both flattened, dull-colored with only 5 central short, blunt, bumpy tubercles at early stages. They both superficially look rather like *P. nodosus* (or even some goniasterids, despite extensive papular areas), which may cause confusion. Juvenile oreasterids are known



Figure 1. Comparison between *Protoreaster nodosus* (top left, 5 specimens from Vanuatu displaying color pattern variation, diameters around 25 cm), *P. lincki* (top right, diameter 20 cm), a juvenile *P. lincki* (bottom left, diameter 8 cm), and a *P. lincki* without superomarginal tubercles (bottom right, diameter 25 cm). All specimens were located at Mayotte Island. Photographs by the author.

to differ markedly from the adult stage, and many were historically described as separate species, such as *Goniodiscus sebae* (Müller & Troschel 1842), which have been found to be young *Calcita* spp. by Fisher (1919), or *Bothriaster primigenius* (Döderlein 1916), which appear to be juveniles of *Choriaster granulatus* (Lütken 1869).

As a common species with ecological importance, *Protoreaster nodosus* has been subject to many scientific studies, especially in the Philippines, Indonesia (Nakajima et al. 2013), Japan (Pan et al. 2012), and Singapore (Chim and Tan 2012). An alien population observed in the Mediterranean Sea was described by Alvarado et al. (1986), but it did not seem to thrive. As it frequently occurs on beaches and shallow waters, it is also well-known by divers and snorkelers under the common name “horned sea star” (sharing this name with many other oreasterids, including other *Protoreaster* and many *Pentaceraster*) or as the “chocolate-chip sea star”, due to the often-dark coloration of its tubercles. For these reasons, it is one of the main targets in the ornamental trade of sea stars, which has led to a strong decline of its population in some places (Bos et al. 2008) and even to its local disappearance in some places such as Guam (Scheibling and Metaxas 2008).

In most of the recent scientific publications (e.g., Alvarado et al. 1986, Bos et al. 2008, Chim and Tan 2012, Nakajima et al. 2013, Marsh and Fromont 2020) as well as marine life books and the World Asteroidea Database (Mah 2022), this species is uniformly described as common in the Indo-Pacific region from East Africa to New Caledonia and Japan. This description appears to be based generally on the classical *Monograph of shallow-water Indo-West Pacific echinoderms* (Clark and Rowe 1971), which summarizes statements from other papers to describe the distribution as including “Islands of western Indian Ocean” and “East Africa & Madagascar”. Linnaeus’ original type location was stated as “*M[ari] Indico*”, an expression which then actually fitted with the Indo-Pacific region in general. Nonetheless, some other classical references indicate very different geographical ranges (Alvarado et al. 1986). For example, Döderlein (1936), who revised the species and its synonyms and who had a good knowledge of common Indian Ocean species, reported it with certainty only for “Australia, Indonesia, New Caledonia, Philippines, Torres Strait.” Recently, only Jangoux (2021) followed this opinion.

Hence, given this discrepancy and the fact that no scientist or diver from the western Indian Ocean seems to have ever seen this species in the region, I led an extensive review of field inventories of sea stars of the Indian Ocean in order to check whether this species had ever been observed there. A critical analysis of the scientific literature about this genus was also undertaken, along with a review of Museum collections, internet-based research of pictures of *Protoreaster* from the Indian Ocean, a worldwide survey in divers’ communities, and targeted field studies.

Material & Methods

Study species

Systematic position and synonyms according to WoRMS (Mah 2022):

- Order VALVATIDA (Perrier 1884)
- Family OREASTERIDAE (Fisher 1911)
- Genus *PROTOREASTER* (Döderlein, 1916)
- Protoreaster nodosus*** (Linnaeus 1758)
- Asterias dorsatus* (Linnaeus 1753) (Protonym)
- Asterias nodosa* (Linnaeus 1758)
- Oreaster clouei* (Perrier 1869) (Synonym according to Bell (1884))
- Oreaster franklini* (Gray 1840) (Synonym according to Döderlein (1936))
- Oreaster hiulcus* (Müller and Troschel 1842) (Synonym according to Döderlein (1936))
- Oreaster hondurae* (Domantay and Roxas 1938)
- Oreaster intermedia* (von Martens 1866) (Synonym according to Döderlein (1936))
- Oreaster mammosus* (Perrier 1869) (Synonym according to Döderlein (1936))
- Oreaster modestus* (Goto 1914)
- Oreaster mutica* (von Martens 1866) (Synonym according to Döderlein (1936))
- Oreaster nahensis* (Goto 1914) (synonym according to Hayashi (1938))
- Oreaster nodosus* (Linnaeus 1758)
- Oreaster turritus* (Gray 1840) (Synonym according to Döderlein (1936))
- Pentaceros clouei* (Perrier 1869) (Synonym according to Döderlein (1936, index))
- Pentaceros franklini* (Gray 1840) (Synonym according to Fisher (1919))
- Pentaceros hiulcus* (Gray 1840) (Synonym according to Döderlein (1936))
- Pentaceros hiulcus* (Müller and Troschel 1842) (Synonym according to Döderlein (1936))
- Pentaceros modestus* (Gray 1866) (Synonym according to Döderlein (1936))
- Pentaceros nodosus* (Linnaeus 1758)
- Pentaceros turritus* (Gray 1840) (Synonym according to Döderlein (1936))
- Pentaceraster horridus* and *Pentaceraster multispinus* shared in their taxonomic history misleading synonyms with *P. nodosus*: respectively *Oreaster nodosus* (either Linnaeus 1758, or Michelin 1845) and *Pentaceros nodosus* (either Linnaeus 1758, or von Martens, 1866). Only *P. horridus* is both recorded in the Indian Ocean and similar enough to cause taxonomic confusion.

Bibliographical analysis

A total of 25 scientific publications containing sea star inventories for the Indian Ocean were identified and reviewed, dating from 1874 to 2020. These inventories include touristic countries such as the Maldives as well as uninhabited and nearly pristine reefs such as the French Scattered Islands. In all of these documents, we looked for *Protoreaster nodosus* and synonyms, comparing possible descriptions with modern knowledge about the species. We also

searched for mentions of the sister taxa *Protoreaster lincki*.

We examined the sources used by Clark and Rowe (1971), so as to check if they did actually mention this species for the region, paying particular attention to possible misleading synonyms. The 4 sources were: Gardiner (1909), Döderlein (1916), Herdman and Herdman (1904), and Hoffmann (1874).

Museum specimens

We searched for specimens in the world's main museum collections of Indian Ocean sea stars in order to check if there was any specimen of *P. nodosus* collected in the Indian Ocean or any ambiguous specimen of *P. lincki* or *Pentacaster* spp. (all formerly grouped under the obsolete genus *Pentaceros*). The list of Museum collections reviewed is the following: Paris MNHN, online collection databases of the London NHM, and Washington Smithsonian.

Material examined

Protoreaster nodosus: MNHN-IE-2014-1256, Malaysia, 1 specimen in alcohol; MNHN-IE-2014-559, labelled "individu nommé par Lamarck", type specimen of *Asterias nodosa* Lamarck, no provenance data, 1 dry specimen; MNHN-IE-2017-990, Catanduanes (Philippines), 1 dry specimen; MNHN-IE-2017-993, no provenance data, 1 dry specimen; "n°6" (unregistered specimen, Lerat 1910), New Caledonia, 1 dry specimen.

Protoreaster lincki: MNHN-IE-2014-476, Madagascar, 1 specimen in alcohol; MNHN-IE-2014-1250, Zanzibar, 4 specimens in alcohol; MNHN-IE-2014-1251, Zanzibar (col. Rousseau 1841), 1 specimen in alcohol; MNHN-IE-2014-1245, Zanzibar, 1 specimen in alcohol; MNHN-IE-2014-1246, Zanzibar 3 specimens in alcohol; MNHN-IE-2014-1247, Zanzibar, 1 specimen in alcohol; MNHN-IE-2017-966, Zanzibar, 1 dry specimen; MNHN-IE-2017-845, Reunion island ("Isle Bourbon"), 1 dry specimen; MNHN-IE-2017-856, Zanzibar, 1 dry specimen; 1 dry specimen; MNHN-IE-2014-1248, Aden, 1 specimen in alcohol; EcAs 11 132, Madagascar (Nosy Be), 1 dry specimen; "M. Geay n°26, 1906" (unregistered specimen), Madagascar, 1 dry specimen; "61" (unregistered specimen, Thomassin 1964), Madagascar (Tuléar), 1 dry specimen; "46" (unregistered specimen, Grandidier 1899), Madagascar, 2 dry specimen; unregistered specimen (labelled by C. Mah 23 May 2001), 1 dry specimen.

Pentacaster spp. (most often labelled as "*Pentaceros hiulcus*"): MNHN-IE-2014-1243, Mauritius, 2 specimens in alcohol; MNHN-IE-2017-769, Zanzibar, 1 dry specimen; MNHN-IE-2017-841, Zanzibar, 1 dry specimen; MNHN-IE-2017-842, Mauritius, 1 dry specimen; MNHN-IE-2017-843, no geographical data, 1 dry specimen; MNHN-IE-2017-844, no geographical data, 1 dry specimen; MNHN-IE-2017-987, no geographical data, 1 dry specimen; MNHN-IE-2014-393, Zanzibar, 1 dry specimen; "E406" (unregistered

specimen, labelled *Pentaceros hiulcus*), Zanzibar, 2 dry specimens.

All these specimens, along with a sample of live specimens from the field (3 *P. lincki* from Mayotte and 30 *P. nodosus* from the south Pacific), were examined and measured in order to confirm the accuracy of the current determination key and to search for unpublished specific characteristics or specimens adding new evidence about the distribution of these species.

Web-based picture analysis

We carried out different picture searches via Google using the word "*Protoreaster*" along the countries and main regions of the Indian Ocean (Australia, Bangladesh, Chagos, Comoros, Djibouti, India, Kenya, Madagascar, Malaysia, Maldives, Mauritius, Mayotte, Mozambique, Myanmar, Oman, Pakistan, Réunion, Seychelles, Somalia, South Africa, Sri Lanka, Tanzania, Thailand, Yemen, Zanzibar). Given the number of results and their rapidly decreasing relevance, we restricted our analysis to the 10 first result pages. We used occurrences of the close and common Indian species *Protoreaster lincki* as a control for detection probability. Another search was done using all the known popular, common names for *Protoreaster nodosus* (chocolate-chip sea star, horned sea star, knobby star). Analyzed pictures were selected based on two criteria: the credibility of the geographical origin provided and the lack of identification issues. Observations in Singapore, Philippines, and Indonesia were used as "control" or proof of the validity of the method, as this species is known to be abundant there.

A refined search was undertaken using GPS-located pictures on the specialized websites FlickrR and iNaturalist (see Michonneau & Paulay, 2014 for more information about this collaborative project). Both are important photographic databases; the latter includes many photographs taken or identified by professional scientists. These identifications were checked again within the scope of the present study.

Diving community surveys

Two calls for observation were sent within various internet communities, beginning in January 2015, asking users if they had observed any *Protoreaster nodosus* west of Sumatra, along with pictures and a short description of the species. The first one was posted on the French speaking "Forum photo-mystère" of DORIS¹ (curated by the French diving federation and sponsored by the MNHN), an important community that gathers more than 2800 registered attendees and many more readers, including many professional scientists. The second survey was sent by e-mail to the *Biosub*² mailing list an academic network of marine biologists. Relevant personal relationships (professional divers, underwater photographers, and marine scientists) were also systematically asked from 2014 to 2022.

1 <http://doris.ffessm.fr/>, last accessed 02/05/2022

2 <http://www.biosub-5962.fr/>, last accessed 02/05/2022

Field work

The authors led echinoderm field studies in the following countries (Fig. 2): Reunion Island (2011), Kenyan coast (2012), Maldives (Baa, Malé and Ari atolls, 2014–2015), Oman (2016) and Mayotte (2016–2021), along with two Pacific Ocean surveys from New Caledonia and Vanuatu (2019–20).

The main reef habitats (beaches, reef flats, seagrass beds, reef crests, reef walls, channels, with a particular emphasis on shallow, silted lagoons) were investigated by snorkeling or scuba diving both day and night, multiple times during the day and across the season, and on multiple sites, including hiding places such as beneath rocks and inside reef cavities. See Ducarme (2018) for a more detailed example of the protocol.

Results

Bibliographical analysis

Among the 24 Indian Ocean field inventories retrieved (Table 1), only 6 cited *P. nodosus* (three of them using an ambiguous synonym, and two of them being older than Döderlein's description of the genus), whereas all (3/3) inventories from the central Indo-Pacific recorded the species. In comparison, *Protoreaster lincki* was mentioned in 10/24 inventories from the Indian Ocean, and never in the Pacific Ocean.

Museum specimens

Among all the specimens examined, we found no reliable record of *P. nodosus* from the Indian ocean.

MNHN-IE-2014-476 – type of “*Oreaster clouei*”

Perrier (1869) described *Oreaster clouei* from this juvenile specimen from Madagascar (MNHN-IE-2014-476), insisting on the fact that some of the distal superomarginal plates wore tubercles, but Döderlein (1936) seemed to neglect this information (given in French) and placed the species in synonymy with *Protoreaster nodosus* without any comment. The specimen is similar to juvenile *P. lincki* observed in the Indian Ocean (see fig. 1), and it displays small buds of disto-lateral tubercles, as already stressed by Perrier, which clearly identifies it as a *P. lincki*.

MNHN-IE-2017-856 – type of “*Oreaster mammosus*”

In the same work, Perrier also describes *Oreaster mammosus*, which he compares to *O. turritus* and *O. hiulcus* (two synonyms of *P. nodosus*), but considers it as another species. The record for this species is based on this small (R=4cm) specimen from Zanzibar (Louis Rousseau collection, 1841), which lacks lateral tubercles. The specimen possesses large carinal tubercles, similar in appearance to those in the *P. nodosus* specimens from the Pacific Ocean; nonetheless it can correspond equally well to a young *P. lincki* that has yet to develop lateral tubercles. This record is considered odd by Döderlein (1936), who put a question mark on Perrier's Zanzibar record since he considers it (and remains) a doubtful record.

Based on marginal tuberculation, all other Indian Ocean *Protoreaster* specimens from MNHN (MNHN-IE-2014-476, MNHN-IE-2014-1250, MNHN-IE-2014-1251, MNHN-IE-2014-1245, MNHN-



Figure 2. Location of field study sites (red circles) in the Indo-Pacific domain (darker blue). Map from Eric Gaba (CC-by-sa), Winkel Tripel projection.

Table 1. Results of bibliographical analysis of field surveys for *Protoreaster* spp.

Source	Area	<i>P. nodosus</i> or synonym	<i>P. lincki</i> or synonym
Hoffmann 1874	Madagascar and surroundings	<i>Oreaster nodosus</i> + <i>Oreaster muricatus</i> <i>var. mutica</i>	<i>Oreaster muricatus</i>
Herdman and Herdman 1904	South-East India	<i>Pentaceros nodosus</i>	<i>Pentaceros lincki</i>
Gardiner 1909	Seychelles	<i>Pentaceros nodosus</i>	<i>Pentaceros lincki</i>
Macnae and Kalk 1958	Inhaca (Mozambique)	X	<i>Protoreaster lincki</i>
James & Pearse 1969	Red sea	X	X
Sloan et al. 1979	Aldabra (Seychelles)	X	<i>Protoreaster lincki</i>
Humphreys 1981	Kenya and surroundings	<i>Protoreaster nodosus</i>	<i>Protoreaster lincki</i>
D B James 1983	East India	X	X
Jangoux and Aziz 1984	Seychelles, Maldives, and Indian Ocean islands	X	<i>Protoreaster lincki</i>
Walenkamp 1990	Mozambique	X	<i>Protoreaster lincki</i>
Rowe and Richmond 2004	Rodrigues (Mascarenes)	X	X
James 2004	Maldives	X	X
Putchakarn and Sonchaeng 2004	Thailand	<i>Protoreaster nodosus</i>	<i>Protoreaster lincki</i>
Mulochau et al. 2007	Mayotte (Comoros archipelago)	X	X
Mulochau and Conand 2008	Glorieuses (Scattered Islands)	X	X
Sadhukhan and Raghunathan 2011	Rutland Island (south Andaman Sea)	X	X
Andréfouët et al. 2012	Baa atoll (Maldives)	X	X
Sadhukhan and Raghunathan 2012a	North Andaman Sea	X	X
Sadhukhan and Raghunathan 2012b	South Andaman Sea	<i>Protoreaster nodosus</i>	<i>Protoreaster lincki</i>
Conand et al. 2013	Europa (Scattered Islands)	X	X
Sakthivel and Fernando 2014	South-East India	X	X
Rao and Kumar 2014	Port Blair Bay, South Andaman Island, India	X	X
Conand et al. 2015	Scattered islands	X	X
Conand et al. 2018	Reunion Island (Mascarenes)	X	X
Lane et al. 2000	South China Sea	<i>Protoreaster nodosus</i>	X
Améziane 2007	New Caledonia	<i>Protoreaster nodosus</i>	X
Tuapattinaja et al. 2014	Ambon, Indonesia	<i>Protoreaster nodosus</i>	X

IE-2014-1246, MNHN-IE-2014-1247, MNHN-IE-2017-856, MNHN-IE-2017-966, MNHN-IE-2017-845, EcAs 11 132, "M. Geay n°26, 1906", "61", "46", and unregistered specimen "C. Mah 23/05/2001") fitted in *Protoreaster lincki*, including specimens labelled as "*Pentaceros hiulcus*" that did not belong to the genus *Pentaceros* (which is the case for MNHN-IE-2017-769, MNHN-IE-2017-841, MNHN-IE-2017-842, MNHN-IE-2017-843, MNHN-IE-2017-844, MNHN-IE-2017-987, MNHN-IE-2014-393 and "E406"). This

includes both registered and unregistered collections and all potentially synonymous combinations. Likewise, all Pacific Ocean specimens examined fitted in *Protoreaster nodosus*. Results are presented in Table 2.

USNM 19698 Putative *P. nodosus* from Seychelles

This specimen from the Smithsonian Institute was recorded as *P. nodosus* from the Seychelles and was

Table 2. Result of MNHN specimen examination. Changes are indicated in bold.

Museum ID/label	Label	Origin	Proposed identification
MNHN-IE-2014-476	<i>Oreaster clouei</i>	Madagascar	<i>Protoreaster</i> sp. (juv.)
MNHN-IE-2014-1243	<i>Pentaceros mammillatus</i>	Mauritius	<i>Pentaceraster mammillatus</i>
MNHN-IE-2014-1245	<i>Pentaceros muricatus</i>	Zanzibar	<i>Protoreaster lincki</i>
MNHN-IE-2014-1246	<i>Pentaceros muricatus</i>	Zanzibar	<i>Protoreaster lincki</i>
MNHN-IE-2014-1247	<i>Pentaceros muricatus</i>	Zanzibar	<i>Protoreaster lincki</i>
MNHN-IE-2014-1248	<i>Pentaceros muricatus</i>	Aden	Oreasteridae (juv.)
MNHN-IE-2014-1250	<i>Pentaceros muricatus</i>	Zanzibar	<i>Protoreaster lincki</i>
MNHN-IE-2014-1251	<i>Pentaceros muricatus</i>	Zanzibar	<i>Protoreaster lincki</i>
MNHN-IE-2014-1256	<i>Pentaceros turritus</i>	Malaysia	<i>Protoreaster nodosus</i>
MNHN-IE-2014-393	<i>Pentaceros hiulcus</i>	Zanzibar	<i>Pentaceraster</i> sp.
MNHN-IE-2014-559	<i>Asterias nodosa</i>	(Lamarck)	<i>Protoreaster nodosus</i>
MNHN-IE-2017-769	<i>Protoreaster nodosus</i>	Zanzibar	<i>Pentaceraster</i> sp.
MNHN-IE-2017-841	<i>Protoreaster nodosus</i>	Zanzibar	<i>Pentaceraster</i> sp.
MNHN-IE-2017-842	<i>Protoreaster nodosus</i>	Mauritius	<i>Pentaceraster</i> sp.
MNHN-IE-2017-843	<i>Protoreaster nodosus</i>	?	<i>Pentaceraster</i> sp.
MNHN-IE-2017-844	<i>Protoreaster nodosus</i>	?	<i>Pentaceraster</i> sp.
MNHN-IE-2017-845	<i>Pentaceros muricatus</i>	Réunion	<i>Protoreaster lincki</i>
MNHN-IE-2017-856	<i>Oreaster mammosus</i>	Zanzibar	<i>Protoreaster</i> sp. (juv.)
MNHN-IE-2017-966	<i>Pentaceros muricatus</i>	Zanzibar	<i>Protoreaster lincki</i>
MNHN-IE-2017-987	<i>Protoreaster nodosus</i>	?	<i>Pentaceraster</i> sp.
MNHN-IE-2017-990	<i>Pentaceros turritus</i>	Philippines	<i>Protoreaster nodosus</i>
MNHN-IE-2017-993	<i>Pentaceros</i>	?	<i>Protoreaster nodosus</i>
"46 Grandidier"	<i>Protoreaster lincki</i>	Madagascar	<i>Protoreaster lincki</i>
"61 Thomassin"	<i>Protoreaster lincki</i>	Madagascar	<i>Protoreaster lincki</i>
"C. Mah 23/05/2001"	<i>Protoreaster lincki</i>	Madagascar	<i>Protoreaster lincki</i>
"E406"	<i>Pentaceros hiulcus</i>	Zanzibar	<i>Pentaceraster</i> sp.
"M. Geay n°26, 1906"	<i>Pentaceros turritus</i>	Madagascar	<i>Protoreaster lincki</i>
"n°6" (Lerat 1910)	<i>Protoreaster nodosus</i>	New Caledonia	<i>Protoreaster nodosus</i>
EcAs 11 132	<i>Protoreaster lincki</i>	Madagascar	<i>Protoreaster lincki</i>

called into question by Yamaguchi (1977). According to Smithsonian asteroid expert Christopher Mah who examined it (pers.com.), it was actually another misidentified *P. lincki* specimen, and its identification has now been corrected. All the other registered *P. nodosus* specimens within the Smithsonian Institute collection came from the Pacific Ocean, and all *P. lincki* from the Indian Ocean.

One last specimen not examined here, MNHN-IE-2017-837 (labelled as "*Asterias nodosa* Lamarck 1816 var. 3"), from the Baudin expedition in Mauritius (1800–1804) and drawn by Péron & Lesueur, was recently synonymized with *Protoreaster lincki* by Jangoux (2021).

Web-based picture analysis

Picture search of *in-situ* images using country names within the Indian Ocean provided credible pictures of *P. lincki* or other misidentified species, but no credible observation of *P. nodosus* (Table 3). There was no significant difference when common names were used.

Exhaustive search of geolocated pictures on Flickr did not show any occurrence of *P. nodosus* west of Singapore, most pictures were taken in Singapore, Indonesia, and the Philippines.

We searched for geolocated and peer-reviewed observations in iNaturalist and retrieved a total of 926 reliable observations, mostly located in Indonesia, the Philippines, New Caledonia, and Singapore. Interestingly enough, some observations from Western Australia (the classical geographical location of the endemic species *P. nodulosus*) display *P. lincki*, making it the easternmost observation of this species by several thousands of kilometers and representing a whole new population. During the elaboration of the present work, this observation was finally confirmed by Marsh & Fromont (2020).

Diving community survey

The two diving community surveys did not retrieve any evidence for the presence of *P. nodosus* west of Thailand. More than 50 respondents just answered to say that they knew the species very well from diving

Table 3. Results of the internet pictures survey as for the end of 2021. The presence of data is indicated in bold.

	Google pictures search	FlickrR map search	iNaturalist observations
Seychelles	0 <i>Protoreaster nodosus</i> >10 <i>Protoreaster lincki</i>	0 <i>P. nodosus</i> 0 <i>P. lincki</i>	0 <i>P. nodosus</i> 3 <i>P. lincki</i>
Mascarenes (Réunion, Mauritius, Rodrigues)	0 <i>P. nodosus</i> 1 <i>P. lincki</i>	0 <i>P. nodosus</i> 0 <i>P. lincki</i>	0 <i>P. nodosus</i> 0 <i>P. lincki</i>
East Africa (Kenya, Tanzania, Mozambique, South Africa)	0 <i>P. nodosus</i> >10 <i>P. lincki</i>	0 <i>P. nodosus</i> 5 <i>P. lincki</i>	0 <i>P. nodosus</i> 147 <i>P. lincki</i>
Red Sea (Egypt, Arabia, Israel)	0 <i>P. nodosus</i> 0 <i>P. lincki</i>	0 <i>P. nodosus</i> 0 <i>P. lincki</i>	0 <i>P. nodosus</i> 0 <i>P. lincki</i>
Madagascar	0 <i>P. nodosus</i> >10 <i>P. lincki</i>	0 <i>P. nodosus</i> 1 <i>P. lincki</i>	0 <i>P. nodosus</i> 8 <i>P. lincki</i>
Mozambique Channel & Comoros	0 <i>P. nodosus</i> 7 <i>P. lincki</i>	0 <i>P. nodosus</i> 0 <i>P. lincki</i>	0 <i>P. nodosus</i> 2 <i>P. lincki</i>
Maldives	0 <i>P. nodosus</i> 0 <i>P. lincki</i>	0 <i>P. nodosus</i> 0 <i>P. lincki</i>	0 <i>P. nodosus</i> 0 <i>P. lincki</i>
India / Sri Lanka	0 <i>P. nodosus</i> >10 <i>P. lincki</i>	0 <i>P. nodosus</i> 0 <i>P. lincki</i>	0 <i>P. nodosus</i> 4 <i>P. lincki</i>
Andaman Sea	0 <i>P. nodosus</i> 0 <i>P. lincki</i>	0 <i>P. nodosus</i> 0 <i>P. lincki</i>	8 <i>P. nodosus</i> 0 <i>P. lincki</i>
Thailand	0 <i>P. nodosus</i> 1 <i>P. lincki</i>	0 <i>P. nodosus</i> 0 <i>P. lincki</i>	23 <i>P. nodosus</i> 0 <i>P. lincki</i>
Singapore	>10 <i>P. nodosus</i> 0 <i>P. lincki</i>	>10 <i>P. nodosus</i> 0 <i>P. lincki</i>	310 <i>P. nodosus</i> 0 <i>P. lincki</i>
Indonesia	>10 <i>P. nodosus</i> 0 <i>P. lincki</i>	>10 <i>P. nodosus</i> 0 <i>P. lincki</i>	452 <i>P. nodosus</i> 0 <i>P. lincki</i>
Philippines	>10 <i>P. nodosus</i> 0 <i>P. lincki</i>	>10 <i>P. nodosus</i> 0 <i>P. lincki</i>	133 <i>P. nodosus</i> 0 <i>P. lincki</i>

trips in the Pacific but had never seen it in the Indian Ocean. Most of them also reported that they had observed *P. lincki* very often but had never encountered any *P. nodosus* in the Indian Ocean. Answers came from the Mascarenes, South Africa, Madagascar, the Maldives, Thailand, Comoros archipelago, Tanzania and Kenya, and the respondents included several professional marine biologists and taxonomists.

Field studies

None of the Indian Ocean field studies (Oman, Reunion Island, Kenyan coast, Maldives, Mayotte) could retrieve any evidence of the presence of *P. nodosus* in the areas investigated, both during the day and at night, on any of the main habitat types, and even from local scientists, divers and sea-goers (Ducarme 2016, Ducarme 2018). *P. lincki* was found to be conspicuous on the Kenyan coast, and more occasionally in Mayotte, always on shallow seagrass beds or silted lagoons, both during the day and at night.

In the two western Pacific countries (New Caledonia and Vanuatu), *P. nodosus* was easily found in great abundance in very shallow waters (often several

individuals per square meter, sometimes so shallow that the tubercles emerged from the water), in seagrass beds and silted beaches and channels, both during the day and at night.

Based on 52 specimens examined (15 *P. lincki* and 37 *P. nodosus*), we established that both species show a mean disc ray to arm ray ratio (r/R) of 0.4 (ranging from 0.25 to 0.5), a result similar to the values found by Marsh & Fromont 2020 (0.3–0.5) and Bell 1884 (0.3–0.4). *Protoreaster lincki* has an average of 14.3 superomarginal plate per arm versus 16.9 for *P. nodosus* (15 in Bell 1884), but the difference is not significant ($p=0.69$ with a χ^2 test) and both species can reach 18 plates per arm. The disposition of disc tubercles seems to follow specific patterns, but here again the intraspecific variation is too important to provide any sound taxonomic signal, just like tubercle size and shape: *P. lincki* had a mean of 13,3 disc tubercles (ranging between 5 to 21, with a multimodal distribution peaking at 5, 10 and 21, the latter displaying an arrangement of 4 per ray with a central one), and *P. nodosus* showed a mean of 17,9, ranging from 5 to 26, with one aberrant specimen wearing 46

compound tubercles; the arrangement was similar in both species, but with more variability and more chaotic specimens in *P. nodosus*. Tubercles were often slenderer in *P. lincki* and more rarely reduced to buttons or enlarged to wide conical growths, but both species seem to exhibit the whole range of tubercle shapes and sizes, ranging from blunt buttons to tapering spines. Some ectopic tubercles (not aligned with the carinal row) were rarely present on the distal part of the arms in both species. The oral face did not show any notable difference between the two species either, be it for ambulacral armament or pedicellariae. The color pattern of *P. lincki* was remarkably consistent in all specimens, regardless of morphological variability: always a pale silver (sometimes yellowish) background color striated with a bright red reticulated pattern connecting the tubercles, and a darker red oral face. When eroded, the tubercle tips can appear orange to golden yellow. On the contrary, the color pattern of *P. nodosus* was extremely variable, with solid-colored specimen (from pure white to dark brown), bicolor ones (solid-colored with darker tubercles and arm tips) and multicolored specimens (usually two colors on the body such as grey and red with black tubercles and arm tips; the tip of the tubercles and sometimes of the arms can exhibit a bluish tinge). The oral face usually shares the darkest color of the body (but not of the tubercles when they are black). Quite often, the body of multicolored specimens is pale (from white to red through pink, tawny or brown, sometimes green), with dark tubercles circled with another color (tawny, red or brown), which can be restricted to a narrow zone around the tubercles or can extend to cover a large part of the dorsal surface, sometimes most of the body except some actinal regions between the arms. The latter color pattern appears quite similar to the one exhibited by *Pentaceraster alveolatus* in New Caledonia (see Guille et al. 1986), although the tuberculation differs.

Discussion

No new record of *Protoreaster nodosus* from the Indian Ocean could be retrieved by any of the methods used here. Hence, the only source of record remains the scientific literature, which is discussed below.

Bibliographical analysis

Only six field inventories mention the presence of *P. nodosus* in the Indian Ocean. Nevertheless, these observations must be interpreted with caution. The three earliest ones Hoffmann (1874), Herdman and Herdman (1904), and Gardiner (1909) were written before Döderlein's description and revision of the genus and used, respectively, the obsolete ambiguous synonyms "*Oreaster nodosus* (Gray)", "*Pentaceros nodosus*", and "*Pentaceros nodosus* (Gray)". The first synonym clearly refers to *Pentaceraster horridus* (Gray 1840), which is known from this region, and the two others could refer to *Pentaceraster multispinus* (von Martens 1866), also said by some sources to be a species from this region (Clark and Rowe 1971), or

maybe some other species of oreasterids from the *Pentaceros* group, as it was still weakly defined at that time. Herdman and Herdman (1904) refer to "*Pentaceros nodosus* (Gray)", which is an incorrect combination, the species having been described by Linnaeus. Hence, this mention can't be trusted as a true record of the actual *P. nodosus*, all the more so given that the depth indications (between 10 and 70m deep) appear deeper than the classical habitat of *P. nodosus*. Gardiner 1909 records both *Protoreaster* from only one site (Saya de Malha) and adds that "a very large number of the specimens were immature", which suggests that a misidentification may have occurred due to the ambiguity of juveniles. The mention of *Pentaceraster gracilis*, another species that is not known from the Indian Ocean, may suggest that the taxonomic accuracy of this paper may not be fully consistent with the established taxonomy.

Hence, there is no sound evidence that any of these three studies actually refer to *P. nodosus*. Hoffmann (1874) also mentions *Oreaster muricatus* var. *mutica* von Martens (an actual and non-ambiguous synonym of *P. nodosus*), illustrated with a clear picture of the species, but does not provide any location for it. We can then consider these mentions as potential false positives. The fourth mention (Humphreys 1981) does not come from a direct observation but from a report by external observers of Watamu Marine Park in the south of Kenya. The description of the material given does not correspond to any known morph of this species. The description would instead better fit a *Pentaceraster* sp., and fieldwork within this station found no *Protoreaster* but many specimens of *Pentaceraster* sp. The fifth mention (Putchakarn & Sonchaeng 2004) comes from Thailand, quoting a training course in Phuket from 1987, not involving the authors, and an oral presentation from 1998: the study reports both species of *Protoreaster* in the same sites (*P. lincki* being doubtful, see below). Hence, we have to consider the possibility of the westernmost limit of *P. nodosus* being in Phuket Bay. The last record (Sadhukhan and Raghunathan 2012b) is also from south Andaman Sea and reports again both species of *Protoreaster* within same sites. However, this observation must be interpreted with caution as it is contradictory with another article of the same authors published the same year (Sadhukhan and Raghunathan 2012a), as well as with another source about the south Andaman Islands, which recorded a wider number of species (Rao and Kumar 2014). Sastry, Scheibling, & Metaxas's (2007) mention of the species in the Nicobar Islands appears more credible, making this archipelago another possible western boundary of this species' distribution, and thus needing further confirmation.

We advocate to move the synonymy of *Pentaceros hiulcus* Gray 1840 (the description which was based on Linck's description and picture), from *Protoreaster nodosus* to *Pentaceraster* spp. Although Gray's description fits ambiguously with both species, Linck clearly describes and draws a characteristic *Pentaceraster*, and most historical specimen under

this name belong to this genus. Before the distinction between *Pentacaster* and *Protoreaster* was made (in Döderlein 1936), all “*Pentaceros*” species were mostly defined based on very weak characters such as size or shape of the tubercles, hence several different species from both genera were assigned to each species. Therefore Gray (1840) incorrectly merged *P. hiulcus* with “*Ast. nodosa, a. Lamk*”, whereas Linck’s original distinction between *Pentaceros hiulcus*, *P. muricatus*, and *P. turritus* appears to still be sound and valid, referring respectively to *Pentacaster sp.*, *Protoreaster lincki* and *Protoreaster nodosus*.

If we focus only on the contemporary bibliography, Clark and Rowe’s book appears as the most cited source for the geographical range of *P. nodosus*, and the source used by all subsequent works. But this work mostly consists of a review of many previous surveys, with little first-hand information. Four references are cited for the presence of *P. nodosus* in the Indian Ocean: Gardiner (1909) for “Western Indian Ocean”, Hoffman (1874) for “East Africa & Madagascar”, and Döderlein (1916) along with Herdman & Herdman (1904) for Ceylon (Sri Lanka). We have already commented on Gardiner (1909) and Herdman & Herdman (1904) and observed that Hoffman (1874) actually does not make reference to this species or any of its synonyms. The last reference (Döderlein, 1916) is not a survey report but a taxonomy synthesis, which states that “This species is widespread on a large part of the Indo-Pacific tropical coasts, from north Australia to Ceylon, and eastward to Samoa at least”. But the same author described 20 years later (Döderlein 1936) another geographical range for this species, restricted to Australia, Indonesia, New Caledonia, Philippines and Torres Strait, clearly expressing his doubts about an observation in Zanzibar (the juvenile specimen MNHN-IE-2017-856, see above), and stating that “data outside from this zone, such as Isle de France [Mauritius] need confirmation” (Döderlein 1936). We have already

seen above that Perrier’s two specimens (*O. clouei* and *O. mammosus*) can’t be considered as records of *P. nodosus*. In his review of the species, Döderlein (1936) ignores the former and puts a question mark on the latter, which remains for him the only potential record in the Indian Ocean; yet he finally limits his description of the geographical range of the species to the Pacific Ocean. We therefore prefer to follow this more recent version as it is consistent with our other results and invalidates Clark & Rowe’s last source for the western Indian Ocean.

On top of that, the main historical specialist of Indian Ocean shallow sea stars, Michel Jangoux, never recorded the presence of *P. nodosus* in any of his numerous fieldwork-based publications throughout the whole ocean, such as Jangoux and Aziz (1984).

Our morphological study did not retrieve any new morphological traits to distinguish *Protoreaster nodosus* from *P. lincki* specimens without marginal tubercles once dried. Hence, color pattern remains the most relevant character, followed by distal superomarginal tubercles (which range from 0 to 7 in *P. lincki* with a mean of 2,4, and nearly never exceed the distal half of the arm). None of the species exhibited inferomarginal or marginal actinolateral tubercles, which distinguish this genus from *Pentacaster*. The possibility of confusion between the two species appears only one-way, as some specimens of *P. lincki* can happen to be deprived of superomarginal tubercles, whereas no specimen of *P. nodosus*, even the most aberrant ones (e.g., 7-armed, with ectopic, chaotic or branching tuberculation), seems able to develop such appendages. In some rare cases, the color pattern of *P. nodosus* could come close to that of *P. lincki*, and this also holds true for some *Pentacaster regulus* from New Caledonia, although the marginal tuberculation remains clearly different.

A synthetic summary of our results is presented in Table 4. The three methods used are congruent

Table 4. Synthetic table of results for *Protoreaster nodosus* from the present study.

	Literature & collections	Diver observations	Internet pictures	Field studies
Seychelles	No reliable record	Absent	Absent	-
Mascarenes	Absent	Absent	Absent	Absent
Comoros Archipelago	Absent	Absent	Absent	Absent
East Africa & Madagascar	No reliable record	Absent	Absent	Absent
Red Sea	Absent	Absent	Absent	-
South-east Arabia	Absent	Absent	Absent	Absent
Persian Gulf	No data	Absent	Absent	-
Maldives area	Absent	Absent	Absent	Absent
Sri Lanka & southern India	No reliable record	Absent	Absent	-
North Andaman Sea	Absent	Absent	Absent	-
South Andaman Sea	Present	Present	Absent	-
South China Sea	Present	Present	Present	-
New Caledonia	Present	Present	Present	Present
Philippines	Present	Present	Present	-

with each other and with field observations. These results suggest that *Protoreaster nodosus* is restricted westward to south-western Thailand (around the Phuket Bay). Southward of Timor. It is then replaced by *Protoreaster nodulosus* along the Australian west coast (of which it is considered endemic), and westward by *Protoreaster lincki*, widespread in the Seychelles, Madagascar, East Africa, and Sri Lanka, and featuring an isolated population in north-western Australia. All the species in this genus seem to share a similar ecology, and there might be some buffer zones of sympatry, such as in the Andaman Sea (and maybe Western Australia).

Possible bias

Assessing the absence of a species from an area is always more difficult than assessing its presence, as the species might just be too scarce or cryptic to be noticed, or the researcher may not look in the right place, at the right time, or the right way. However, this particular species is known as a species with abundant populations in the areas where it lives and is among the most conspicuous, easily spotted and readily identified shore animals in the Pacific Ocean, as evidenced by the thousands of records we easily retrieved throughout the different methods used here. Hence, there is little chance that this species could have a cryptic presence in the Indian Ocean and avoid all observers and investigative methods. The fact that the same abundance, ecology, and behavior was observed in the alien population introduced in the Mediterranean helps supporting the idea that it has a consistent conspicuousness and ecology across its geographical distribution.

One obvious bias in our method could be due to the use of data from non-professional recreative photographers. But the consistency in results between a peer-reviewed naturalist website such as iNaturalist and results from Flickr and Google prove that such method appears quite reliable, at least for such conspicuous and photographic species. Of course, less beautiful, less common, or smaller species would not be able to be surveyed this way, which works mostly for conspicuous and charismatic species (Ducarme et al. 2012).

The recent disappearance of the species could also be a hypothesis to explain its absence, as most ambiguous observations recorded in the literature date back from 35 to 140 years. This shallow shore species is heavily fished in the Pacific and is already known to have disappeared in some isolated places such as Guam (Scheibling and Metaxas 2008) – this extinction being confirmed by our results. But the disappearance of a widespread Indo-Pacific species from a whole ocean without significant population change in the other one and in the absence of a significant fishery or ecological perturbation seems unlikely, and we know no historical record of such an event. Moreover, such species would still be expected to be found in uninhabited or preserved regions such as the French Scattered Islands, Outer Seychelles, or Baa atoll in the Maldives, where no significant trade, tourism or

echinoderm fishery took place before the mid-1980s (James and Manikfan 1994). On top of that, even in the case of a recent extinction, old museum specimens would still be found (the MNHN collection began in the 18th century, hence predating the ambiguous records and including many now-extinct species and several thorough collections from the Indian ocean). The fact that the species is still present (and photographed) in countries like Philippines or Indonesia despite well-documented heavy fishing and ecological forcing there renders the overfishing hypothesis even less likely (Bos et al. 2008).

Another hypothesis explaining the sudden disappearance of this species could be a disease, as has been extensively studied in the US west coast in connection with the sea star wasting disease. However, even such events are not known to completely eradicate a species on such a large zone, and populations eventually recover after some decades (Miner et al. 2018). The low connectivity of the alleged zones (Madagascar, Seychelles, Kenya, and India) and the presence of isolated islands and archipelagos also tends to rule out the epidemic hypothesis. Moreover, such an event has never been recorded in the Indian Ocean to our knowledge and should have left traces in the scientific literature, especially when involving conspicuous littoral species. Given the range and timespan studied here, life-history traits and odd population dynamics, events don't seem likely to have such wide-ranging effects either. Nevertheless, science is always a work in progress, and any sighting of this species in the Indian Ocean from now on would then challenge the conclusions of the present paper and open up even more fascinating scientific questions.

Lessons learned from using a partially citizen-science, web-based methodology

This study used a mixed method in order to cover the required geographic scale, a database big enough to span nearly a whole ocean, and the precision of field observations. As artifacts or errors were observed in both scientific literature and non-professional web-based documents, crossing these two sources along with field experience and observations proved of great interest. Tourists constitute an unprecedented population of marine observers and data collectors and can hence provide a high quality geolocated database that no scientific project could ever hope to produce. The development of hybrid tools such as iNaturalist.org and semi-professional networks can also come closer to reaching the aim of unifying a huge number of citizen-based observations with professional identification (Michonneau and Paulay 2014). Citizen science is already well-developed in a few other scientific fields and taxonomic groups (such as cetaceans, birds or gastropods, cf. Bouchet et al. 1993), and could be put to better use within the marine sciences (Dickinson et al. 2010), as is already the case in some regions (Bourjon et al. 2018). However, some countries or regions totally lacking tourists (as well as scientists), such as Somalia, remain as large gaps in every case.

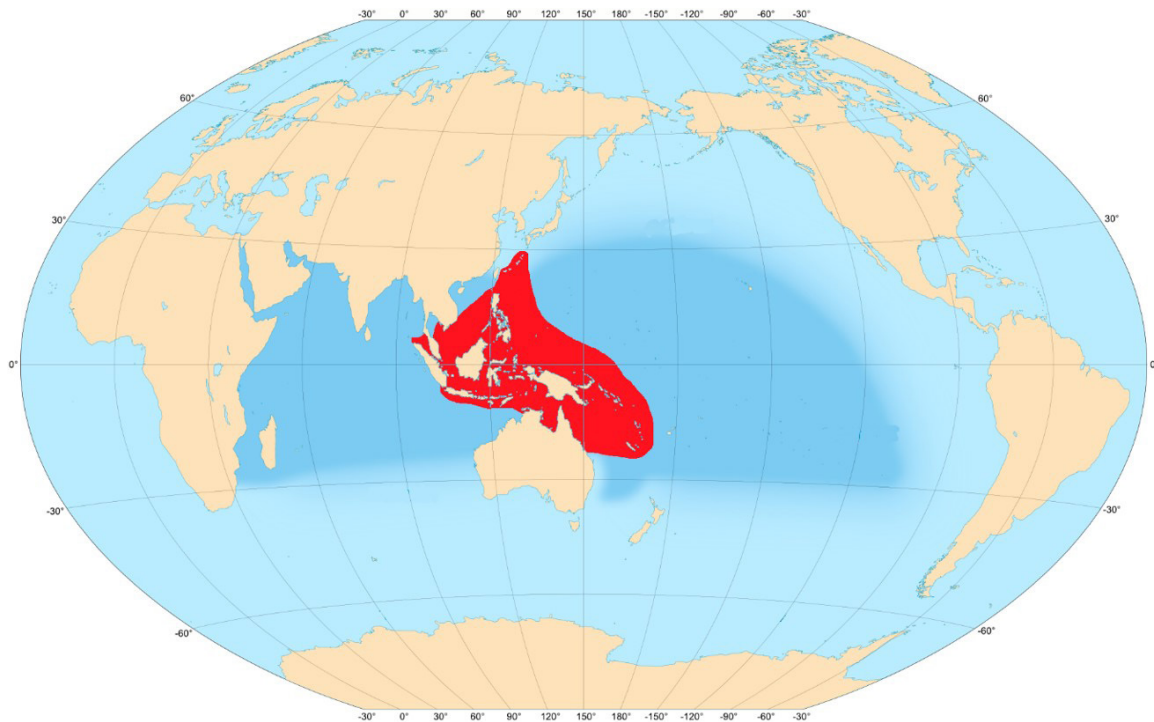


Figure 3. Re-assessed distribution map of *Protoreaster nodosus* (red area). The deep blue area, representing the “Indo-Pacific domain”, can be seen as the previously estimated distribution map, showing the extent of the reduction. Map from Eric Gaba (CC-by-sa), Winkel Tripel projection.

Here, the web project DORIS (above) allowed confirmation of the first record of *P. lincki* from Reunion Island, whereas it had never been reported from central Indian Ocean islands (Conand et al. 2018) – not counting the presence of a long-unregistered Reunion Island specimen in the MNHN collection (MNHN-IE-2017-845, Lantz collection from 1865). However, due to the scarcity of its main habitat (intertidal seagrass beds) in this island, the species is probably rare and inconspicuous. iNaturalist observations also provided the first records of *P. lincki* in Western Australia, in Coral Bay, as later confirmed by Marsh and Fromont (2020).

This study also adds another case where color patterns prove to be a more consistent and reliable characteristic than morphology, just like for species of sea cucumbers of the genus *Bohadschia* (Kim et al. 2013), which may challenge classical taxonomic conceptions about “hard” and “soft” criteria. It also stresses the issues related to species described on the sole basis of poorly preserved specimens in insufficient number, which is still the case of nearly all the species of the close genus *Pentaceraster*. Community-based data appears extremely helpful in addressing such issues. Genetic analyses may also help us understand better the complicated “*Pentaceros*” group, but consideration of such data is beyond the scope of the present paper.

Conclusion

The different approaches used in this study all suggested that the horned sea star *Protoreaster nodosus* is probably absent from most of the Indian

Ocean, contrary to a widespread and never assessed scientific assumption, seemingly stemming from incorrect synonymies and preserved specimens that were either juvenile, aberrant or just misidentified. Since there is no reliable mention in any field inventory, no observation by professional researchers and divers, and no picture taken by tourists could be found on the whole World Wide Web, this study provides compelling evidence that the western limit of this species occurs in western Thailand (probably between Phuket bay and Nicobar islands, Sastry et al. 2017), with other bounds being north to Okinawa (where the limits with *P. gotoi* needs further research), east to Vanuatu, and south to Timor and Brisbane, Australia (Fig. 3). These boundaries fit roughly with what is often called the “coral triangle”. Our results also suggest that the *P. nodosus* population from Guam has seemingly not recovered (which would need field-based confirmation) and that the Mediterranean alien population probably collapsed (there are no recent observations on citizen science programs and no scientific record since 1986). No observation from Polynesia is recorded by any method, which is consistent with the literature.

On the other hand, *Protoreaster lincki* seems to be present from South Africa to Kenya, around Madagascar and the Seychelles but rare in central Indian Ocean islands (only one record from Reunion Island, none from the Maldives and Mauritius), and absent from the Red Sea (as already stated by Döderlein (1936)). The observations in Tamil Nadu confirm the records from India and Sri Lanka by Herdman and Herdman (1904), and Döderlein (1936). This species also appears

to be present in at least one site in Western Australia (sympatric with *P. nodulosus*). We have no evidence that the African, Indian, and Australian populations are connected (as hypothesized in Marsh and Fromont (2020)). However, a sound redescription of all the former “*Pentaceros*” oreasterid sea stars appears to be needed (especially for *Pentaceraster* spp.), as classical diagnoses appear insufficient and often misleading, mostly based on very variable traits such as tubercle number, size, and shape.

Such investigation is also of conservation concern as it divides by more than three the supposed geographical range of this species. The horned sea star *Protoreaster nodosus* would then be restricted mostly to densely populated regions where it is already often overfished (especially Indonesia and Philippines) and could then become much more easily threatened than previously believed: similar misbelief about more fragile or targeted species may then jeopardize them seriously. The present study also underlines the need for implementing sound methodologies for assessing geographical ranges, rather than just adding up records regardless of their age, accuracy, and credibility at the risk of overestimating the size of animal distributions and populations. It is then difficult but probably paramount to identify the number of species suffering from similar mistakes regarding their geographical range, as in the case of tropical species that are easily assigned as present throughout the whole Indo-Pacific based on very limited evidence and neglecting poorly investigated dispersion barriers. We encourage future workers to voucher specimens in museums in order to make such investigation easier and testable in future studies. To conclude, our results showed the relevance of citizen science data as a complement to more traditional scientific data and methods, and the mixed method used here could be extended to other taxa with similar features to help reduce the classical difficulty of assessing the presence or absence of conspicuous species in large areas. We hope to have stressed the importance of reassessment of species distribution data, a step which is of paramount importance for conservation, biogeography, ecology, and taxonomy.

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Data Availability Statement

All data from web-based citizen sciences programs used here (iNaturalist, DORIS) is public, and iNaturalist data is free of use under the Creative Commons license. Registered Museum collections are available for consultation on the relevant websites.

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