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An integrative approach to the taxonomy of the crown-of-thorns starfish species group (Asteroidea: *Acanthaster*): A review of names and comparison to recent molecular data

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Abstract

The scientific names published for species and subspecies in the genus *Acanthaster* Gervais (Asteroidea: Valvatida: Acanthasteridae) are reviewed, with particular attention to the *A. planci* species group (crown-of-thorn starfish, COTS). Several problems with earlier nomenclatural and bibliographic data are resolved. The available name for the type species of *Acanthaster* in the original combination is *Asterias echinites* Ellis & Solander in Watt, 1786; the often-cited "*Asterias echinus*" and "*Acanthaster echinus*" are incorrect subsequent spellings, therefore unavailable. The scientific names and taxonomic concepts for species and subspecies in *Acanthaster* are compared to recently published, robust COI-barcoding clades. Two of four clades in the *A. planci* group can be named unequivocally, a third requires a neotype designation to decide which of two available names will be valid, and the fourth clade necessitates a new species description and name. The References section includes annotations explaining bibliographical data important to the nomenclatural evaluations. Many hyperlinks interspersed with the paper's texts offer quick access to digital versions of the respective references.

Key words: nomenclature, sibling species, barcoding, linked references

Introduction

The "crown-of-thorns starfish" (COTS), *Acanthaster planci* (Linnaeus, 1758), with their corallivorous lifestyle arguably are a serious threat to coral reefs throughout the Indo-Pacific Ocean region. Episodic "mass outbreaks", during which tens of thousands of starfish devour most if not all corals on a reef, are one of the major causes of coral mortality in many countries. Especially on the Great Barrier Reef, COTS outbreaks have significantly contributed to coral reef decline in the last decades (e.g. De´ath *et al.* 2012). Consequently, COTS are among the most studied and abundantly cited marine organisms (e.g. Antonius 1971, Moran 1988, Baird *et al.* 2013). Moreover, the spines and pedicellaria of these large starfish can be quite harmful also to humans (e.g. Lee *et al.* 2013a, 2013b).

Since the 18th century, authors perceiving morphological differences among specimens or published descriptions have proposed and named a number of taxa, then variously united or divided them. In recent times at least one species other than *Acanthaster planci* has been accepted as valid, *A. brevispinus* Fisher, 1917, which does not feed on corals or threaten reefs. The two species may interbreed (Lucas & Jones 1976), but their separation is supported by molecular data (Yasuda 2006, Vogler *et al.* 2008).

During the last 25 years several authors have increasingly suspected that *Acanthaster planci* itself may warrant division in several (sub-)species (e.g. Nishida & Lucas 1990; Benzie 1999, 2000; Gérard *et al.* 2008; Yasuda *et al.* 2009). A recent molecular and biogeographic investigation that used samples covering the entire Indo-Pacific range of *A. planci* from the Red Sea to the eastern Pacific Ocean showed four deeply divided clades (Vogler *et al.* 2008). Indeed, the observed divergence (8.8–10.6 %) between clades compared to <0,7% within each clade in the "barcoding fragment" of the mitochondrial COI-gene strongly suggests that *A. planci* in the traditional, broad sense consists of four different species. These clades/species show distinct geographical distribution patterns across the

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Indo-Pacific, with one species restricted to the Red Sea, one each occurring in the northern and southern Indian Ocean, and the fourth showing pan-Pacific distribution (Vogler *et al.* 2008, 2012, 2013). Live animals representing corresponding populations and color variation have been photographed by Vogler (2010: p. 93).

Prior to the present study, none of the four molecular clades was correlated unequivocally with any scientific taxon name in the Linnean system. Possibly due to this absence of links to morphological data, which are possible but have not yet been analyzed, most recent authors have ignored the results by Vogler *et al.* (2008, 2012, 2013) and continued to refer to "*Acanthaster planci*" (e.g. Bahrom *et al.* 2012, Leray *et al.* 2012, Mills 2012, Rivera-Posada *et al.* 2012, Messmer *et al.* 2013). This situation is problematic, as data from an unpublished doctoral thesis suggest distinct differences between the clades concerning biological and ecological, but also pharmacological and medical aspects (Vogler 2010).

Concerning nomenclatural matters, the latest detailed presentation (Birkeland & Lucas 1990: 13–19) clearly necessitated substantial additions and corrections. Therefore, as a basic step towards establishing a robust taxonomy of the *A. planci* species group, the present work reviews and evaluates the scientific taxon names and accessory data from the respective original and otherwise relevant references. The search for names to be checked was started using the World Register of Marine Species ("WoRMS"; Mah 2014).

In zoological nomenclature, some names at the species level constitute the typological foundation for names at the genus level, some of which then typify family-level names. Consequently, the following review sections A and B address the relevant species names, while the names at successively higher ranks are treated in review section C.

In the subsequent Discussion, we compare the recognized species names to the molecular data by Vogler *et al.* (2008, 2012, 2013) in order to determine whether clades may be assigned to valid species names and to identify any remaining obstacles to such solutions. Some bibliographic data important to the nomenclatural evaluations are given in annotations to the References section.

Readers are cautioned to note that the present review is not intended to preempt the necessary further work, and should not be mistaken as implementing any of the discussed possible consequences in taxonomy or nomenclature.

Review of names and taxa—Part A: The *Acanthaster planci* species complex

This part treats seven names on the species level in chronological order. The numbered section headings give the respective species epithet in combination with the genus name *Acanthaster*, where applicable.

(1) *Acanthaster planci* (Linnaeus, 1758)

Original combination. *Asterias planci*

Original source. Linnaeus (1758): p. 823, with references to "(p. 662. n. 8–9)" and "Column. phytob. app. t. 38. f. A."

https://archive.org/stream/carolilinnisys00linn#page/823/mode/1up

Nomenclatural status. Available name.

Type material. Holotype—the only specimen referred to by Linnaeus (1758), the one figured in Plancus (1744), plate XXXVIII (38), fig. A; see remark (2) below.

Type locality. Goa, West coast of (then Portuguese) India.

Remarks. (1) Linnaeus' (1758: Appendix p. 823) first reference under *A. planci* is to page 662 in the main part of his work, where he treated *Asterias laevigata* and *A. ophiura* as species numbers 8 and 9 under "VERMES, MOLLUSCA. Asterias." This reference is interpreted as indicating nothing more than a relative position in the numbered species sequence assigned by Linnaeus at the time of writing that Appendix. In fact, in the next major edition of "Systema naturae" (the twelfth, i.e. the last one he wrote himself) Linné (1767) followed hardly any of the position suggestions he had made for all species in the 1758 Appendix, and did not even mention *Asterias planci* anywhere. Instead he introduced a new species, *Asterias papposa,* as number 2 in the sequence (op. cit.: p. 1098), including a line "Column. phyt. t. 38 f. A?" (p. 1099) referring to the same figure in Plancus (1744) as given under *A. planci* in Linnaeus (1758). Regardless of Linnaeus´ reasons for this change, the "?" in the reference from

1767 makes the implied synonymy between *A. planci* and *A. papposa* a subjective and tentative one, thus does not affect separate availability for the two species names under the ICZN (1999) Code of nomenclature.

(2) The second reference under *A. planci* (Linnaeus 1758: 823) points to an illustration in Plancus (1744) that the latter had added to his re-edition of a 16th century work by F. Columna (= Colonna). The illustrated specimen was treated in more detail (not mentioned by Linnaeus) in corresponding text (Plancus 1744: second unpaginated page behind p. 134), as well as in the letters ("epistolae") by Plancus & Gualtierus (1743), who gave more descriptive data and a more comprehensive illustration than Plancus (1744).

(3) Concerning this holotype specimen Rowe & Gates (1995: 23) wrote "whereabouts undetermined", i.e. did not disclose whether they had tried to locate it anywhere. Searches on our behalf have not found any trace of it in relevant Italian collections in Pisa, Siena, Florence or Bologna (M. Dellacasa, G. Manganelli, G. Innocenti, B. Sabelli, pers. comms 2014). We have not received a reply from Rimini, but our Italian correspondents consider as highly unlikely that parts of the specimen have been preserved anywhere.

(4) The earliest published description of *A. planci* appears to be the one labeled “Stella Marina Quindecim Radiorum” in Rumphius (1705: book I, p. 39). Linnaeus (1758) referred to Rumphius (1705) under several of his other species names in *Asterias*, but not under *A. planci*.

(5) The morphological features of *A. planci* evident from the plate in Plancus & Gualtierus (1743; see also Birkeland & Lucas 1990: fig. 4) and the plate in Plancus (1744) suffice to rule out species identity with *Acanthaster brevispinus* Fisher (see below) on account of the long aboral spines, but they are insufficient to assign the illustrated specimen to any of the clades derived from molecular data (see Discussion below). The original diagnosis of *A. planci* by Linnaeus (1758), “Asterias stellata lobis quindecim echinatis” [A star-like *Asterias* with 15 spiny arms] is not helpful here either.

(6) All specimens of the “electric blue” color variety (Vogler 2010: p. 93) which were checked by COI-barcoding belong to this species.

(2) *Acanthaster echinites* (Ellis & Solander in Watt, 1786)

Original combination. *Asterias echinites*

Original source. Watt (1786): p. 206, pls. 60–62.

http://archive.org/stream/naturalhistoryof00elli#page/206/mode/2up (text)

http://archive.org/stream/naturalhistoryof00elli#page/n341/mode/2up (plates)

Nomenclatural status. Available name. Fixed as the type species of *Acanthaster*; see Review Part C(1) below.

Type material. Holotype—the only specimen mentioned by Ellis & Solander in Watt (1786); see remark (1) below.

Type locality. Batavia (now Jakarta), Indonesia.

Remarks. (1) The text by Ellis and Solander states that the holotype specimen "was brought from Batavia by Captain W. Webber, and is in the possession of Dr. Fothergill" (Watt 1786: 206). Like Ellis and Solander, however, Fothergill had died before the work was published (op. cit.: vi). It remains to be determined whether any part of his collection has been preserved.

(2) The original description mentions very few characters and does not provide sufficient information about live color, details of spines or pedicellaria.

(3) Various subsequent works have misrepresented the name *Asterias echinites* by spelling it incorrectly and/or crediting its nomenclatural authorship to someone other than Ellis & Solander. These errors have caused considerable confusion; see under "*A. echinus*" (species section 4), and under *A. solaris* (species section 3, remark (4)).

(3) *Acanthaster solaris* (Schreber, 1793)

Original combination. *Asterias solaris*

Original source. Schreber (1793): p. 1–6, pls. I–II (1–2).

www.ub.uni-bielefeld.de/cgi-bin/neubutton.cgi?pfad=/diglib/aufkl/naturforscher/118931&seite=00000006.TIF (text)

www.ub.uni-bielefeld.de/cgi-bin/navtif.cgi?pfad=/diglib/aufkl/naturforscher/118931&seite=00000183.TIF&scale=8 (plates)

Nomenclatural status. Available name.

Type material. Holotype—the single specimen reported on by Schmidel (1781) and Schreber (1793); see remarks (2) and (3) below.

Type locality. Unknown; see remark (2) below.

Remarks. (1) The figures in Schreber (1793: plates I and II) clearly show a species of the *Acanthaster planci* species group.

(2) According to Schmidel (1781: 7) and Schreber (1793: 1, 5), Schmidel had bought two different starfish at a shop in Paris the owner of which had reported the source of both specimens as "die Magellanische Meerenge" (the Magellanic strait). Madsen (1955: 180) and others have argued that the material cannot have come from the Strait of Magellan in Tierra del Fuego, as members of *Acanthaster* occur in tropical waters only, and the second of Schmidel's specimens belonged to *Culcita schmideliana* (Retzius, 1805) [= *Asterias placenta* Schreber, 1793: 6, a junior primary homonym of *A. placenta* Pennant, 1777], which does not occur in South America. Therefore, the type locality of *Acanthaster solaris* (Schreber) has been assumed to be "one of the Philippine localities to which the name of Magellan is attached" (Madsen 1955). However, we have not found evidence of any sea strait in the Philippines ever having been named after Magellan (though there is a widely known "Magellan´s Cross" on a shore of Cebu island). Accordingly, we do not follow such unsupported assumptions here, and find it reasonable to doubt the dealer's locality information quoted by Schmidel (1781).

(3) The holotype has not been found in the two natural-history collections known to have acquired substantial amounts of Schreber's material after his death, namely at the University Erlangen-Nürnberg (U. Andraschke, pers. comm. 2014), and at the Zoologische Staatssammlung in Munich (ZSM).

(4) Müller & Troschel (1842: 25) treated a species under the name "*Echinaster solaris* Nobis", even though their synonymic listing referred to several earlier works that had used the same or a different species name, among them "Soland. et Ellis tab. 60–62" (i.e. *Asterias echinites* Ellis & Solander in Watt, 1786) and "Asterias solaris. Naturforscher Stück 27, tab. 1. 2." (i.e. *Asterias solaris* Schreber, 1793). Later, Müller & Troschel (1844: 180) proposed a new genus to be called *Echinites* and to receive *A. solaris* as the only species mentioned, but both proposals are invalid; see section C(2) below.

(5) The species epithet was misspelled as "*solans*" by Ludwig & Hamann (1899: 711). This incorrect subsequent spelling does not constitute an available name (ICZN 1999: Art. 33.3).

(4) "*Asterias echinus*" and "*Acanthaster echinus*"

Original combination. Not applicable.

Sources. See remarks.

Nomenclatural status. Unavailable names (incorrect subsequent spellings); see remarks.

Type material and type locality. Not applicable.

Remarks. (1) Schreber (1793: 5) compared his "*Asterias solaris"* to the starfish description by Ellis and Solander (in Watt 1786) but unfortunately misquoted several data from that earlier work. The most significant of these errors was the introduction of an incorrect subsequent spelling of the species name *Asterias echinites* Ellis & Solander (see species section (2) above), which Schreber gave as "*Asterias Echinus*".

(2) Lamarck (1816: 559) spelled *Asterias echinites* correctly, and referred to "Soland. et Ell. tab 60 à 62." (i.e. to the plates in Watt 1786) as well as to "Encycl. pl. 107. A. B. C." (i.e. to the plates in Bruguière 1797).

(3) Gray (1840: 281) cited "Asterias Echinites, *Lam.*" but right next to it also "Asterias Echinus, *Solander and Ellis*, t. 60, 61, 62", as if he had not read Lamarck (1816). Gervais (1841: 474) repeated this double listing, except for changing the latter combination to *Acanthaster* "*echinus*, Ellis et Soland.". Although the correct combination, *Acanthaster echinites*, was recognized at least as early as by Lütken (1871: 292), some more recent authors have gone farther in the wrong direction with "*Acanthaster echinus* Gervais" (e.g. Birkeland & Lucas 1990: 17, Rowe & Gates 1995: 23).

(4) Incorrect subsequent spellings like "*Asterias echinus*" and "*Acanthaster echinus*" in the works cited above do not constitute separately available names (ICZN 1999: Art. 33.3). One important consequence of this fact concerns the type species of *Acanthaster* Gervais; see Review Part C, section (1).

(5) ***Acanthaster ellisii*** (Gray, 1840) [often misspelled *ellisi*]

Original combination. *Echinaster ellisii*

Original source. Gray (1840): p. 281.

http://archive.org/stream/annalsmagazineof06londuoft#page/281/mode/2up

Nomenclatural status. Available name; see remark (2) below.

Type material. Unknown number of specimens from the collection of "H. Cuming, Esq." (Gray 1840: 281); see remark (3) below.

Type locality. "South America" (Gray 1840: 281); further details unknown.

Remarks. (1) Gray's (1840: 281) proposal of the new name reads "Echinaster Ellisii, *Gray.* Asterias Echinus, *Solander and Ellis*, t. 60, 61, 62. Asterias Echinites, *Lam.*". Apparently Gray thought that the South American material from the Cuming collection belonged to the same taxonomic species as the Indonesian specimen described and named by Ellis and Solander in Watt (1786), and cited by Lamarck (1816). Nevertheless Gray proposed a new name, *Echinaster ellisii,* and used it as valid in place of *Asterias echinites* Ellis & Solander. This substitution was treated as unjustified by Gervais (1841), who used *Acanthaster echinites* (Ellis & Solander) as the valid name, with *Echinaster ellisii* as a junior synonym.

(2) According to the Code of nomenclature in effect today, the "unnecessary substitute name" *Echinaster ellisii* was invalid originally (ICZN 1999: Art. 10.6), but has been available from Gray (1840) nonetheless (ICZN 1999: Art. 12). It is not unavailable under Code Art. 11.6, as Gray published it in senior rather than junior synonymy with *Asterias echinites* Ellis & Solander. Consequently, the available name *Acanthaster ellisii* (Gray) may be used as a valid name—at species or subspecies rank—by anyone not considering it as a junior synonym of any other available name.

(3) Gray (1840: 178) wrote that "specimens discovered by Mr. Cuming" were "in the collection ... of the Zoological Society" of London. According to information on wikipedia.org, "In 1866 after Cuming's death, the Natural History Museum of London purchased 82,992 of his specimens" (https://en.wikipedia.org/wiki/Hugh_Cuming, visited 21 February 2014). However, Madsen (1955: 188) reported that two earlier attempts to locate Gray's material of *Echinaster ellisii* had failed and thus concluded that "it has been lost". Caso (1962) did not refer to original type material of *Acanthaster ellisii* when she described a subspecies, *A. ellisii pseudoplanci* (see species section (7) below). In summary, barring any rediscovery at the NHM or in other collections, the original type material of *Echinaster ellisii* Gray, 1840 appears to be lost.

(4) Madsen (1955) referred to several earlier works in considering *Acanthaster ellisii* (Gray) as a valid species, and gave morphological characters as well as a differential diagnosis.

(6) ***Acanthaster mauritiensis*** de Loriol, 1885

Original source. Loriol (1885): p. 6–10, pl. XII (12), figs. 1, 1a–e, 2, 2a, 3, 3a–i.

http://archive.org/stream/mmoiresdelasocit29soci#page/n323/mode/2up (text)

http://archive.org/stream/mmoiresdelasocit29soci#page/n411/mode/2up (plate)

Nomenclatural status. Available name.

Type material. An unknown number of syntypes from collections by V. de Robillard; see remark (1) below.

Type localities. Various unspecified collecting sites of Robillard's around Mauritius Island.

Remarks. (1) According to Loriol (1885: 9) "Mr de Robillard ... sent this species quite frequently"; thus, the original description was based on an unknown number of syntypes. At least two of these appear to have been preserved at the Department of Invertebrates of the Muséum d'histoire naturelle de la Ville de Genève (Switzerland) (collection codes MHNG-INVE-70565, -70566; J. Mariaux, pers. comm. 2014).

(2) Loriol (1885) described and illustrated many details of his species.

(7) ***Acanthaster ellisii pseudoplanci*** Caso, 1962

Original source. Caso (1962): p. 322–330, text-figs. 3–4, pl. 3: figs. 1–29, pl. 5: figs. 3–9, 17.

Nomenclatural status. Available name.

Type material. 16 syntypes (Caso 1962: 327); see remark (1) below.

Type localities. "al Sureste y Oeste de la bahía Rafael Castelán Orta y al Oeste de la bahía Vargas Lozano" (Caso 1962: 327), Socorro Island, East Pacific off Mexico; see remark (2) below.

Remarks. (1) At least eleven syntypes have been preserved in the Colección Nacional de Equinodermos "Dra. Ma. E. Caso Muñoz" in Mexico City (F.A. Solís-Marín, pers. comm. 2014); collection codes: ICML-UNAM 2.73.0 (6 dry specimens), ICML-UNAM 2.73.1 (5 specimens in alcohol).

(2) Caso (1962) based her subspecies distinction on a detailed morphological comparison of the hard parts of specimens of "*A. ellisii pseudoplanci*" from an Universidad Nacional expedition (op. cit.: p. 327) with others she had received under the name "*A. ellisii* (Gray)" from F.C. Ziesenhenne of the Allan Hancock Foundation (p. 322) at the University of Southern California in Los Angeles. Parts of the latter material had been collected near the southern tip of Socorro Island. Although Caso reported the Socorro bays involved in both sample sets with different names, the latter appear to reflect nothing but contemporary U.S. (English) versus Mexican (Spanish) usage. In fact, some of the Socorro localities for Caso's (1962) "*A. ellisii* (Gray)" appear to be practically identical to the type localities of *A. ellisii pseudoplanci*, or at least so close that geographic separation of the respective populations is highly unlikely.

Review of names and taxa—Part B: *Acanthaster brevispinus*

Acanthaster brevispinus Fisher, 1917

Original source. Fisher (1917): p. 92.

http://archive.org/stream/proceedingsofbio30biol#page/92/mode/1up

Nomenclatural status. Available name.

Type material. Holotype (United States National Museum; nr. 37,027).

Type locality. Sirun Island near Siasi, Sulu Archipelago, southwestern Philippines.

Remarks. (1) A detailed morphological redescription was provided by Fisher (1919: 442–443, pls. 117, 118, 131). The holotype has been figured by Birkeland & Lucas (1990: 15, fig. 5C,D).

(2) Morphology, molecular data (Yasuda *et al.* 2006; Vogler *et al.* 2008, 2012), and distinct autecology (these starfish are not a coral pest) clearly support separation of *A. brevispinus* from the *A. planci* group, although members of the two species groups may interbreed (Lucas & Jones 1976).

Acanthaster brevispinus seychellensis Jangoux & Aziz, 1984

Original source. Jangoux & Aziz (1984): p. 868–869, pl. 4: figs. C–D.

Nomenclatural status. Available name.

Type material. Holotype (Muséum national d'Histoire naturelle, Paris; nr. EcAs 2968).

Type locality. "Coriolis" campaign station C 26 (08.ix.1980), 4º57.5´ S, 55º10.6´ E, 63 m, Seychelles, western Indian Ocean.

Remarks. Jangoux & Aziz (1984) based their diagnosis on several morphological characteristics. However, subspecies status remains to be tested with molecular data, as no specimen from the type locality has been sequenced.

Review of names and taxa—Part C: Genus and family levels

Acanthaster Gervais, 1841

Original source. Gervais (1841): page 474.

https://play.google.com/books/reader?id=xJQ5AAAAcAAJ&printsec=frontcover&output=reader&authuser=0&hl=de&pg=GBS.PA474

Nomenclatural status. Available name. Replacement name for *Echinaster* Gray, 1840 [December]: 281, which is permanently unavailable due to junior primary homonymy with *Echinaster* Müller & Troschel in Müller, 1840 [May]: 102.

Type species. "*Acanthaster echinus* Ellis et. Soland." (Gervais 1841: 474) [= *Asterias echinites* (Ellis & Solander in Watt, 1786)], by subsequent designation of Fisher (1919: 441); see remarks (1)–(2) below.

Remarks. (1) Gervais (1841: 474) listed the species he included in *Acanthaster*, as follows: "*A. echinus*, Ellis et Soland., pl. 60–62; *A. echinites*, Lamk.; *Echinast. Ellisii*, Gray, *loc. cit.* (Amérique du Sud.)—*A. solaris*, Naturforcher[sic!], xxviii[sic!], pl. , f. 2." In this, Gervais treated as valid only the two names "*A. echinus*" and *A. solaris*, the former of which was listed with three 'synonyms'. The general arrangement and some of the erroneous data in it followed those in Gray (1840)—see Review Part A, species (4), remark (3)—but with the justified correction that "*A. Echinus*" (= *A. echinites*) enjoyed nomenclatural priority over *Echinaster ellisii*.

(2) To the present authors' knowledge, the earliest published statement concerning the type species of *Acanthaster* Gervais is by Fisher (1919: 441), who wrote "Type, *A. echinus* (=*A. planci* Linnaeus.)", and in his synonymic listing under *A. planci*, "*Acanthaster echinus* Gervais, Dict. sci. nat., suppl., vol. 1, 1841, p. 474." These statements of Fisher's were made at a time when guidelines for zoological nomenclature were not nearly as settled and widely observed as they became some decades later. Examined today, *A. echinus* as mentioned in Gervais (1841) does not qualify as a separately available name, and the use of such names, e.g. in type-species designations, can lead to serious complications. Fortunately, the current Code of nomenclature (ICZN 1999) allows the essence of Fisher's (1919) statements to be accepted as a valid fixation of the type species. The involvement of the incorrect subsequent spelling *Acanthaster echinus* is ruled immaterial by Code Art. 67.6, other misquoted data (e.g., authorship credit to Gervais) are permissible under Art. 67.7.

Consequently, the available name for the type species of *Acanthaster* is *A. echinites* (Ellis & Solander). The valid name to be used for this taxonomic species can depend on synonymy, if a senior synonym is determined either objectively (e.g. if two species names are based on one and the same name-bearing type specimen), or subjectively by any author arguing taxonomically for *A. echinites* being the junior synonym of an earlier available name.

While Fisher (1919) may be pardoned for any lack of 'nomenclatural awareness' reflected in his type-species designation, the same cannot be said of recent authors repeating those errors and even adding new ones. For example, Birkeland & Lucas (1990: 13) failed to understand the data explained in remark (1) above, and mistakenly claimed that in Gray (1840) and Gervais (1841) "there were already five species names, *planci, echinus, echinites, solaris,* and *ellisii*". Rowe & Gates (1995) made yet another unfortunate addition by claiming that the type-species of *Acanthaster* had been established "by monotypy". If only to avoid potential threats to the stability of nomenclature arising from the perpetuation of such flawed data, the corresponding entries on the WoRMS website (http://www.marinespecies.org/aphia.php?p=taxdetails&id=205212), so far misleading, should be corrected as soon as possible in light of our findings.

Many papers mentioning starfish now placed in *Acanthaster* were published prior to the 20th century already, some in places so remote that we have not been able to access them yet. Therefore, it is conceivable that a valid type-species designation could still surface which predates that of Fisher's (1919). However, any such discovery could have more than minor consequences to nomenclature only if it fixed as the type species of *Acanthaster* the other one of Gervais' (1841) originally included species, *A. solaris* (Ellis & Solander). Judging from the body of literature examined in the present study, we consider as negligible both, the likelihood of that happening and the effect it might have.

Echinites Müller & Troschel, 1844

Original source. Müller & Troschel (1844): page 180.

https://archive.org/stream/archivfrnaturg1001berl#page/180/mode/1up

Nomenclatural status. Unavailable name; see remark (1) below.

Type species. Not applicable.

Remarks. (1) The name is permanently unavailable due to junior primary homonymy with *Echinites* Gesner, 1758 (p. 35: Echinoidea) and with *Echinites* Leske, 1778 (p. xviii (18) and 157: Echinoidea).

(2) The incorrect subsequent spelling "*Echinetes*" by Ludwig & Hamann (1899: 710) does not constitute a separately available name (ICZN 1999: Art. 33.3).

Acanthasteridae Sladen, 1889

Original source. Sladen (1889): page 536 (as subfamily Acanthasterinae in family Echinasteridae).
http://www.biodiversitylibrary.org/item/43777#page/590/mode/1up
Nomenclatural status. Available name.
Type genus: *Acanthaster* Gervais, 1841.

Discussion

Comparison with COI-barcoding clades. As presented in the Review section Parts A and B above, a number of names have been published for taxa in the genus *Acanthaster*. The four COI-barcoding clades distinguished by Vogler *et al.* (2008, 2012) in the *A. planci* species group show significant genetic divergence and quite distinct geographical patterns (Fig. 1), thus can be compared to the species and subspecies concepts and names, as follows.

(1) *Acanthaster planci* (Linnaeus, 1758) with the type locality Goa, West India, corresponds to the Northern Indian Ocean (NIO) clade.

(2) "*Acanthaster echinus*", as explained above, is an unavailable name that must not be used.

(3) The name *Acanthaster echinites* (Ellis & Solander in Watt, 1786) cannot be referred to a barcoding clade with sufficient confidence, as its type locality off Jakarta (Indonesia) is currently inhabited by members of the two clades called *A. planci* and *A. solaris* here. Animals assigned to the latter two species have been found even at the same location, "Pulau Seribu", Seribu Island, about 40 km NW of Jakarta (Benzie 1999, fig. 1; Vogler *et al.* 2008, supplement T1; Vogler 2010. p. 119, 123). A neotype designation—see the Prospect section below—in accordance with ICZN regulations should result in one of two alternative solutions, fixing *A. echinites* (Ellis & Solander, 1786) either as a junior synonym of *A. planci* (Linnaeus, 1758) or as a senior synonym of *A. solaris* (Schreber, 1793).

FIGURE 1. Geographic distribution of COI-barcoding clades and of type localities of names (modified from Vogler *et al.* 2008): red—Red Sea (RS) clade; blue—South Indian Ocean (SIO) clade; yellow—North Indian Ocean (NIO) clade; green—Pacific Ocean (PO) clade.
Location of type localities of nominal species: asterisk—*A. planci*; cross—*A. echinites*; triangle—*A. solaris* (with doubts, see text), square—*A. mauritiensis*; circle—*A. ellisii pseudoplanci*; "?"—the type locality of *A. ellisii* was not specified: in South American waters of the East Pacific.

(4) *Acanthaster solaris* (Schreber, 1793) corresponds to the Pacific Ocean (PO) clade of Vogler *et al.* (2008, 2012), specifically to the West Central Pacific haplotype of Vogler *et al.* (2013). The mitochondrial genome of specimens from Fiji was characterized by Yasuda *et al.* (2006), who also described microsatellites from various Pacific populations and found them to be distinctly different from those in *A. mauritiensis* (see below).

Caso (1970, 1974) described and depicted in detail the morphology of specimens assigned to this clade from Hawaii. A detailed SEM study of hard parts from Australian material was provided by Walbran (1987). The growth of spines on specimens from the Great Barrier Reef was described by Stump & Lucas (1990). Photographs of live animals belonging to this clade can be found in Vogler (2010: 93).

(5) *Acanthaster ellisii* (Gray, 1840) also corresponds to the PO clade, specifically to the East Pacific haplotype of Vogler *et al.* (2013). According to these data *A. ellisii* is a junior synonym of *A. solaris* (and possibly of *A. echinites*, see above). However, the divergence of haplotypes observed within this clade (op. cit.) and the separation in western and eastern Pacific populations may indicate that subspecies should be distinguished, one of which might then be called *A. solaris ellisii* (or *A. echinites ellisii*). More sampling in East Pacific waters is necessary to clarify the matter, including possible morphological differences. For example, Schreber (1793: pl. II) depicted spines in *A. solaris* as granulated, Studer (1884: 27) described smooth spines for *A. ellisii*, whereas the detailed morphological description by Caso (1962) did not reproduce that difference. Photographs of live animals considered as *A. ellisii* (because of their locality) are shown at

http://www.desertmuseumdigitallibrary.org/public/results.php?sc=Acanthaster%20ellisii and

http://www.ryanphotographic.com/asteroidea.htm

(6) *Acanthaster mauritiensis* de Loriol, 1885, was considered as a local variety of *A. echinites* (with *A. ellisii* as another synonym) by Döderlein (1888: 822–824), as he saw no discrete morphological differences among specimens from Mauritius and two other localities in the western or northern Indian Ocean, and from three localities in the western Pacific. However, microsatellites from various Indo-Pacific populations showed distinct differences between *A. mauritiensis* and "*A. ellisii"* (i.e. the Pacific clade) (Yasuda *et al.* 2009). According to the barcoding data, *A. mauritiensis* is a distinct species and corresponds to the South Indian Ocean (SIO) clade of Vogler *et al.* (2008, 2012). Photographs of live animals assigned to this clade (based on COI-sequences) are given in Vogler (2010: 93).

(7) *A. ellisii pseudoplanci* Caso, 1962 also corresponds to the Pacific Ocean (PO) clade, and specimens from the type locality even show the same (East Pacific) haplotype as *A. ellisii* (Vogler *et al.* 2013).

(8) The Red Sea (RS) clade of Vogler *et al.* (2008, 2012) cannot be assigned an available name and needs to be formally described. For photographs of live animals, see Vogler (2010: 93; based on COI-sequence) and (based on the locality in the Red Sea) http://www.fotosearch.com/photos-images/acanthaster-planci.html.

(9) *Acanthaster brevispinus* Fisher, 1917 is clearly separated from all species of the *Acanthaster planci* species complex in both, morphological and molecular features. Additional work is needed to decide whether or not the subspecies division in *A. brevispinus brevispinus* and *A. b. seychellensis* should be upheld.

Prospect. As mentioned in the individual nomenclature sections above, attempts to locate original type material for the species names in question are continuing. Fresh collecting at the respective type localities to allow designations of fully informative neotypes is in progress by the present senior author and collaborators, as is the formal description of the species represented by the RS-clade.

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General remarks. A number of the following bibliographical citations are accompanied by commentary or supplementary information, usually set between angular brackets.

In addition, aside from DOI links one or more hyperlinks to digitizations of the respective title are offered, wherever applicable, to facilitate access via online viewing or downloading. Unless stated otherwise these internet resources are available free of charge, but some of them require user registration. Note that the present authors do not endorse any product offered on or associated with any website referred to, nor do we guarantee that all corresponding data presented there are correct.

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