



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

GERHARD HASZPRUNAR^{1,2} & MARTIN SPIES¹

¹SNSB - Zoologische Staatssammlung München, Münchhausenstr. 21, D-81247 München, Germany. E-mail: haszprunar@snsb.de

²Dept. Biology II and GeoBio-Center of LMU Munich, Germany

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

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.

Acknowledgements

We want to thank two anonymous reviewers for their helpful comments on an earlier draft of the manuscript.

References and annotations

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.

- Antonius, A. (1971) Das *Acanthaster* Problem im Pazifik (Echinodermata). *Internationale Revue der gesamten Hydrobiologie*, 56 (2), 283–319.
<http://dx.doi.org/10.1002/iroh.19710560209>
- Bahrom, N.A., Sirajudeen, K.N.S., Yip, G.W., Latiff, A.A. & Ghazali, F.C. (2012) Sulfated glycosaminoglycans from crown-of-thorns *Acanthaster planci*—extraction and quantification analysis. *Food Science & Nutrition*, 1 (1), 83–89.
<http://dx.doi.org/10.1002/fsn3.10>
- Baird, A.H., Pratchett, M.S., Hoey, A.S., Herdiana, Y. & Campbell, S.J. (2013) *Acanthaster planci* is a major cause of coral mortality in Indonesia. *Coral Reefs*, 32 (3), 803–812.
<http://dx.doi.org/10.1007/s00338-013-1025-1>
- Benzie, J.A.H. (1999) Major genetic differences between crown-of-thorns starfish (*Acanthaster planci*) populations in the Indian and Pacific Oceans. *Evolution*, 53 (6), 1782–1795.
<http://dx.doi.org/10.2307/2640440>
- Benzie, J.A.H. (2000) The detection of spatial variation in widespread marine species: methods and bias in the analysis of population structure in the crown of thorns starfish (Echinodermata: Asteroidea). *Hydrobiologia*, 420, 1–14.
<http://dx.doi.org/10.1023/A:1003943011631>
- Bianchi, G.—see Plancus, J. (1744)
- Birkeland, C. & Lucas, J.S. (1990) *Acanthaster planci: Major Management Problem of Coral Reefs*. CRC Press, United States, 267 pp. Available from: http://books.google.de/books?id=Z57rozbkLTAC&printsec=frontcover&hl=de&source=gbs_ge_summary_r&cad=0#v=onepage&q&f=false (accessed 4 July 2014) [Many pages are not shown, but the taxonomic part on pages 13–19 is available]
- Blake, D.J. (1979) The affinities and origins of the crown-of-thorns sea star *Acanthaster Gervais*. *Journal of Natural History*, 13 (3), 303–314.
<http://dx.doi.org/10.1080/00222937900770241>
- Bory de Saint-Vincent, J.B.G.M. (1827) *Tableau Encyclopédique et Méthodique des Trois Règnes de la Nature. Vers, Coquilles, Mollusques et Polypiers. Tome premier*. Paris, Agasse, viii (8) + 180 pp., pls. 1–95. [This is vol. 1 in a 3-volume re-edition (with modified title and content) of an earlier series edited by Bruguière (3 parts) and later Lamarck (2 parts) from 1791 to 1798. Page "(140)" —the brackets are critical—in Bory (1827) has the earliest known captions to "Tableau" plates 107A–107C on *Asterias echinites* (see Bruguière 1797). These plates were reproduced in vol. 2 ("Tome second") of Bory (1827).]
- Bruguière, J.-G. (1797) *Tableau Encyclopédique et Méthodique des Trois Règnes de la Nature. Dix-neuvième Partie. Vers Testacées, a Coquilles Bivalves*. Paris, Agasse, [2] pp., pls. 93–286. [According to Evenhuis & Petit (2003: 3), plates 96–289[sic!] were published in 1792 in another part of the same "Tableau" series (see the remarks on Bory 1827 above). We have seen copies of the relevant plates ("107A", "107B" and "107C") only behind title pages dated 1797, but cannot rule out errors in the digital versions or accompanying data. However, as the plates do not carry taxon names, the precise year of their publication is irrelevant to nomenclature. Plates "107A" to "107C" in Bruguière (1797) are reproductions of plates 61, 60 (in this order!) and 62 in Watt (1786), with new text added above and below the figures. For captions corresponding to the plates in Bruguière (1797), see Bory (1827). See also Lamarck (1816).]
- Caso, M.E. (1962) Estudios sobre Astéridos de México. Observaciones sobre especies pacíficas del género *Acanthaster* y descripción de una subespecie nueva, *Acanthaster ellisii pseudoplanci*. *Anales del Instituto de Biología, Universidad Nacional Autónoma de México*, 32 (1–2), 313–331. ["1961"]
- Caso, M.E. (1970) Morfología externa de *Acanthaster planci* (Linnaeus). *Anales del Instituto de Biología, Universidad Nacional Autónoma de México, Serie Ciencias del Mar y Limnología*, 41 (1), 63–78.
- Caso, M.E. (1972) El género *Acanthaster*. Su biología, ecología y su efecto destructor de los arrecifes. *Revista de la Sociedad Mexicana de Historia Natural*, 33, 51–83.
- Caso M.E. (1974) Morfología externa de *Acanthaster planci* (Linnaeus). Symposium on Indian Ocean and Adjacent Seas. *Journal of the Marine Biological Association of India*, 16 (1), 83–93.
- Clark, A.M. (1993) An index of names of recent Asteroidea—Part 2: Valvatida. In: Jangoux, M. & Lawrence, J.M. (Eds.), *Echinoderm Studies. Vol. 4*. Balkema, Rotterdam, pp. 187–366.
- Columna, F.—see Plancus, J. (1744)
- De'ath, G., Fabricius, K.E., Sweatman, H. & Puotinen, M. (2012) The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proceedings of the National Academy of Sciences of the U.S.A.*, 109 (44), 17995–17999.
<http://dx.doi.org/10.1073/pnas.1208909109>
- Döderlein, L. (1888) Echinodermen von Ceylon. Bericht über die von den Herren D^{res} SARASIN gesammelten Asteroidea, Ophiuroidea und Echinoidea. *Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere*, 3, 821–846, pls. 31–33. Available from: <https://archive.org/stream/zoologischesjahr03jena#page/820/mode/2up> (accessed 4 July 2014)
- Ellis, J. & Solander, D.—see Watt (1786)
- Evenhuis, N.L. & Petit, R.E. (2003) Corrections and additions to the dating of the "Histoire Naturelle des Vers" and the Tableau Encyclopédie[sic!] (Vers, coquilles, mollusques et polypiers) portions of the Encyclopédie Méthodique. *Zootaxa*, 207, 1–4.
- Fisher, W.K. (1917) New starfishes from the Philippines and Celebes. *Proceedings of the Biological Society of Washington*, 30, 89–93. Available from: <https://archive.org/stream/proceedingsofbio30biol#page/88/mode/2up> (accessed 4 July 2014)

- Fisher, W.K. (1919) Starfishes of the Philippine seas and adjacent waters. *Bulletin of the United States National Museum*, 100 (3), xii (12) + 712 pp., 156 pls. Available from: <http://archive.org/stream/bulletinunitedst10031919unit#page/n5/mode/2up> (accessed 4 July 2014)
- Gervais, P. (1841) Astérie. In: *"Plusieurs professeurs du Jardin du Roi"* (Eds.), (1840–1841) *Dictionnaire des sciences naturelles dans lequel on traite méthodiquement des différents êtres de la nature, ...; suivi d'une biographie des plus célèbres naturalistes. Supplément. Tome I*. Ch. Pitoit, Paris, pp. 461–481. Available from: <https://play.google.com/store/books/details?id=xJQ5AAAAcAAJ&rdid=book-xJQ5AAAAcAAJ&rdot=1> (Accessed 22 Jul. 2014) [This work is not part of the 61-volume dictionary series (1816–1845) with practically identical title. Instead, it represents the only volume ever published of a separate series intended to supplement the former. "Supplément Tome I" was published in two separately issued "livraisons". The first of these instalments covered dictionary terms starting with the letters A-ANT; the earliest known date of its existence as a publication is 24 October 1840; see Bibliographie de la France 29, Journal Général 43: 579. For the second part, covering letters APH-AYE, the earliest known date is 22 May 1841; see Bibliographie de la France 30, Feuilleton du Journal de la Librairie 21: 3.] [There are reports of the name *Acanthaster* from "Année" 8 (1841) of the serial "L'Écho du Monde Savant", but we have been unable to see this volume. However, as the journal reviewed references to scientific works published elsewhere, any mention in it of *Acanthaster* Gervais is expected to have followed rather than preceded Gervais' 1841 "Astérie" article in the dictionary supplement.]
- Gesner, J. [also cited as Gessner] (1758) *Tractatus physicus de petrificatis in duas partes distinctus, quarum prior agit de petrificatorum differentiis & eorum varia origine; altera vero de petrificatorum variis originibus, praecipuarumque telluris mutationum testibus*. Lugduni Batavorum, T. Haak, 136 pp. Available from: http://books.google.de/books/about/Tractatus_physicus_de_petrificatis.html?id=3vYTAAAAQAAJ&redir_esc=y (accessed 4 July 2014) [Requires registration with 'Google books']
- Gray, J.E. (1840) A synopsis of the genera and species of the class Hypostoma (*Asterias* Linn.). *The Annals and Magazine of Natural History*, 6 (36), 175–184 & 6 (37), 275–290. <http://dx.doi.org/10.1080/03745484009443296>
[As stated in a footer line on the respective first page of each journal issue ("number"), the first part of Gray's paper was published in number XXXVI (36; beginning on journal p. 161) on 1 November 1840, the second part, which includes the treatment of *Echinaster* Gray, in number XXXVII (37; beginning on p. 241) on 1 December 1840.]
- Harnack, A. (1900) *Geschichte der Königlich Preußischen Akademie der Wissenschaften zu Berlin. Erster Band—Zweite Hälfte. Vom Tode Friedrichs des Großen bis zur Gegenwart*. Berlin, Reichsdruckerei, pp. 493–1091. Available from: <http://bibliothek.bbaw.de/bbaw/bibliothek-digital/digitalequellen/schriften/anzeige?band=ak-gesch/harn-1-2> (accessed 4 July 2014)
- Houk, P. & Raubani, J. (2011) *Acanthaster planci* outbreaks in Vanuatu coincide with ocean productivity, furthering trends throughout the Pacific Ocean. *Journal of Oceanography*, 66 (3), 435–438. <http://dx.doi.org/10.1007/s10872-010-0038-4>
- International Commission on Zoological Nomenclature. (1999) *International Code of Zoological Nomenclature, Fourth Edition*. International Trust for Zoological Nomenclature, London, 306 pp. <http://dx.doi.org/10.5962/bhl.title.50608>
- Jangoux, M. & Aziz, A. (1984) Les astérides (Échinodermes) du centre-ouest de l'océan Indien (Seychelles, Maldives et îles Mineures). *Bulletin du Museum National d'Histoire Naturelle (Paris), 4^e série. Section A, Zoologie, biologie, et écologie animales*, 6 (4), 857–884. Available from: <http://bionames.org/bionames-archive/issn/0181-0626/6/857.pdf> (accessed 4 July 2014)
- Lamarck, J.B.P.A. (1816) *Histoire Naturelle des Animaux sans Vertèbres, Présentant les Caractères Généraux et Particuliers de ce[sic!] Animaux, ...: Tome second*. Paris, Verdière, 568 pp. [On pp. 559: Redescription of *Asterias echinites* with references to "Soland et Ell. tab. 60 à 62." and to "Encycl. pl. 107. A. B. C." See the remarks on Bory (1827) and Bruguière (1797) above.]
- Lane, D.J.W. (2012) *Acanthaster planci* impact on coral communities at permanent transect sites on Bruneian reefs, with a regional overview and a critique on outbreak causes. *Journal of the Marine Biological Association of the United Kingdom*, 92 (Special Issue 04), 803–809. <http://dx.doi.org/10.1017/S0025315411000890>
- Lee, C.-C., Tsai, W.-S., Hsieh, H.-J. & Hwang, D.-F. (2013a) Cytotoxicity of venom from crown-of-thorns starfish (*Acanthaster planci*) spine. *Molecular and Cellular Toxicology*, 9 (2), 1771–1784. <http://dx.doi.org/10.1007/s13273-013-0022-3>.
- Lee, C.-C., Tsai, W.-S., Hsieh, H.-J., & Hwang, D.-F. (2013b) Hemolytic activity of venom from crown-of-thorns starfish *Acanthaster planci* spines. *Journal of Venomous Animals & Taxons including Tropical Diseases*, 19 (22), 8 pp.
- Leray, M., Béraud, M., Anker, A., Chancerelle, Y. & Mills, S.C. (2012) *Acanthaster planci* outbreak: Decline in coral health, coral size structure modification and consequences for obligate decapod assemblages. *PLoS ONE*, 7 (4), e35456. [10 pp.] <http://dx.doi.org/10.1371/journal.pone.0035456>
- Leske, N.G. (1778) *Iacobi Theodori Klein naturalis dispositio echinodermatum*. Accesserunt lucubratiuncula de aculeis echinorum marinorum et spicilegium de belemnitis. Gleditsch, Lipsiae, 4 + xx (20) + 278 + 3 pp., pls. I–LIV (1–54).
- Linnaeus, C. (1758) *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata*. L. Salvius, Stockholm, [iv] + 824 pp.
- Linné, C. von (1767) *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus,*

- differentiis, synonymis, locis. Tomus I. Pars 2. Editio duodecima, reformata.* L. Salvius, Stockholm, pp. 533–1327 + [36].
- Loriol, P. de (1885) Catalogue raisonné des Échinodermes recueillis par M. V. de Robillard à l'île Maurice. (II. Stellérides). *Memoires de la société de physique et d'histoire naturelle de Genève*, 29 (1^{re} Partie) (N^o 4), 84 pp., pls. VII–XXII (7–22). Available from: <https://archive.org/details/mmoiresdelasocit29soci> (accessed 4 July 2014)
- Lucas, J.S. & Jones, M.M. (1976) Hybrid crown-of-thorns starfish (*Acanthaster planci* X *A. brevispinus*) reared to maturity in the laboratory. *Nature*, 263 (5576), 409–412. <http://dx.doi.org/10.1038/263409a0>
- Lucas, J.S., Nash, W.J. & Nishida, M. (1985) Aspects of the evolution of *Acanthaster planci* (L.) (Echinodermata; Asteroidea). *Proceedings of the 5th International Coral Reef Congress*, 5, 327–332. Available from: http://www.reefbase.org/resource_center/publication/pub_17523.aspx (accessed 4 July 2014)
- Ludwig, H. & Hamann, O. (1899) Die Seesterne. In: *Bronn's Klassen und Ordnungen des Thier-Reichs in Wort und Bild*. 2. Band. 3. Abteilung: Echinodermen (Stachelhäuter), II. Buch, Akademische Verlagsgesellschaft, Leipzig, pp. 461–966, pls. I–XII (1–12). Available from: <https://archive.org/stream/drhgbronnklasse020302bron#page/n5/mode/2up> (accessed 4 July 2014)
- Lütken, Chr. (1871) Fortsatte kritiske og beskrivende Bidrag til Kundskab om Søstjernene (Asteridene). *Videnskabelige Meddelelser fra den naturhistoriske Forening i Kjöbenhavn. Tredje Aarties tredje Aargang [the third decade's third year; = overall vol. 33]*, 227–304, pls. IV–V (4–5). Available from: <http://www.biodiversitylibrary.org/item/110780#page/4/mode/1up> (accessed 4 July 2014)
- Madsen, F.J. (1955) A note on the seastar genus *Acanthaster*. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i København*, 117, 179–192, pls. I–VI (1–6).
- Mah, C.L. (2014) World Asteroidea database. Available from: www.marinespecies.org/asteroidea (accessed 1 July 2014)
- Messmer, V., Pratchett, M.S. & Clark, T.D. (2013) Capacity for regeneration in crown of thorns starfish, *Acanthaster planci*. *Coral Reefs*, 32 (2), 461. <http://dx.doi.org/10.1007/s00338-013-1017-1>
- Mills, S.C. (2012) Density-dependent prophylaxis in the coral-eating crown-of-thorns sea star, *Acanthaster planci*. *Coral Reefs*, 31 (2), 603–612. <http://dx.doi.org/10.1007/s00338-012-0883-2>
- Moran, P.J. (1986) The *Acanthaster* phenomenon. *Oceanography and Marine Biology—an Annual Review*, 24, 379–480. [Reprinted in Moran (1988)] <http://dx.doi.org/10.1002/iroh.19880730414>
- Moran, P.J. (1988) The *Acanthaster* phenomenon. *Australian Institute of Marine Science, Monograph Series*, 7, 178 pp. (ISBN 0-642-13250-X) Available from: <http://archive.org/stream/Acanthasterphen00Mora#page/n1/mode/2up> (accessed 4 July 2014) [A re-edition and bibliographic update to Moran (1986)]
- Moran, P.J. (1990) *Acanthaster planci*—biographical data. *Coral Reef*, 9 (3), 95–96. <http://dx.doi.org/10.1007/bf00258218>
- Müller, J. (1840) ... über den Bau des *Pentacrinus Caput Medusae*. *Bericht über die zur Bekanntmachung geeigneten Verhandlungen der Königlich Preussischen Akademie der Wissenschaften zu Berlin*, 1840 (April), 88–106. Available from: <http://bibliothek.bbaw.de/bbaw/bibliothek-digital/digitalequellen/schriften/anzeige?band=08-verh/1840> (accessed 4 July 2014) [The header information in Müller & Troschel (1840: 318)—see the next reference below—identifies that work as an "excerpt from the monthly report of the Royal Academy of Sciences in Berlin. Month of April 1840." Indeed, the paper's contents are almost identical to those beginning at the bottom of page 99 in Müller (1840). Müller & Troschel (1842: pp. X, 5) treated Müller (1840) as having been published before Müller & Troschel (1840). In a comprehensive monograph on the Academy's history Harnack (1900: 770) wrote that the monthly report issues were to be issued "generally upon completion of each month", in order to be able to "publish more quickly than in the Abhandlungen" series of the same academy, and that this "instrument proved to be very practical and to actually achieve its purpose". We conclude that Müller (1840) was published in May of 1840, i.e. not only prior to Gray (1840) but also before Müller & Troschel (1840).]
- Müller, J. & Troschel, F.H. (1840) Ueber die Gattungen der Asterien. *Archiv für Naturgeschichte*, 6 (1), 318–326. Available from: <https://archive.org/stream/archivfnaturg0601berl#page/318/mode/2up> (accessed 4 July 2014) [Previous opinion dating this work from June of 1840 looks questionable, as immediately below the paper's final lines on page 326 the header of the following work states that part of the latter had been presented at a meeting on "21 July 1840". However, in light of our findings on Müller (1840)—see the next reference above—the precise publication date of Müller & Troschel (1840) is no longer critical to nomenclature.]
- Müller, J. & Troschel, F.H. (1842) *System der Asteriden*. F. Vieweg & Sohn, Braunschweig, xx (20) + 134 + [1] pp., 12 pls. Available from: <https://archive.org/stream/systemderasterid00ml> (accessed 4 July 2014)
- Müller, J. & Troschel, F.H. (1844) Beschreibung neuer Asteriden. *Archiv für Naturgeschichte*, 10 (1), 178–185. Available from: <https://archive.org/stream/archivfnaturg1001berl#page/178/mode/2up> (accessed 4 July)
- Nash, W.J., Goddard, M. & Lucas, J.S. (1983) Population genetic studies of the crown-of-thorns starfish, *Acanthaster planci* (L.), in the Great Barrier Reef region. *Coral Reefs*, 7 (1), 11–18. <http://dx.doi.org/10.1007/bf00301976>
- Nishida, M. & Lucas, J.S. (1990) Genetic differences between geographic populations of the crown-of-thorns starfish

- throughout the Pacific Ocean. *Marine Biology*, 98 (3), 359–368.
<http://dx.doi.org/10.1007/bf00391112>
- Petit, R.E. (2011) Reprint of Lamarck's 1816 "Liste des objets". *Conchologia ingrata*, 3, 1–18. Available from: http://conchologia.com/publication_pdf/3.pdf (accessed 4 July 2014)
- Plancus, J. (a pseudonym of Bianchi, G.) (1744) Appendix ad Φυτοβασανov. P. [136], pl. XXXVIII (38). In: Plancus, I. & Columna, F.† (Eds.), *Fabi Columnae Lyncei Φυτοβασανov cui accessit vita Fabi et Lynceorum notitia adnotationesque in Φυτοβασανov Iano Planco Ariminensi auctore et in Senensi academia anatomes publico professore. [The Lyncean Fab(i)us Columna's 'Phytobasanos', to which have been added a biography of Fab(i)us and an appraisal of the Lynceans, as well as notes on the 'Phytobasanos', by Ianus Plancus of Rimini, the author and a public professor at the anatomical academy of Siena.]*. I.P. Aeris, Florence; lii (52) + 134 + [2] pp., 38 pl. Available from: http://books.google.de/books?id=Le5v5sSQDiC&printsec=frontcover&hl=de&source=gbs_ge_summary_r&cad=0#v=onepage&q&f=false (accessed 4 July 2014) [In this digital version, the bottom of the page with plate XXXVIII shows three lines of text. As evidenced by their references to names and pages in Linné (1767), these text lines are not parts of the printed original from 1744 but were entered later on the digitized copy.]
- Plancus, J. & Gualtierus, N. [= Bianchi, G. & Gualtieri, N.] (1743) *De stella marina echinata quindecim radiis instructa epistolae binæ quarum altera ad Carolum Antonium Iulianum a Iano Planco, altera vero ad ipsum Plancum a Nicolao Gualtiero, conscriptæ. [Two letters on a spiny starfish equipped with fifteen arms, one written to Carolus Antonius Julianus by Janus Plancus, the other to that same Plancus by Nicolaus Gualtierus.]* Preprinted separate, 12 pp., 1. pl. Florence. Available from: <https://play.google.com/store/books/details?id=s1VQXBasaalC&rdid=book-s1VQXBasaalC&rdot=1> (1743, separate; plate incompletely visible; access requires registration with 'Google books') [As far as known, this work was published first in 1743 as a preprinted separate, then in 1744 in *Memorie sopra la Fisica e Istoria naturale di diversi Valentuomini*, 2, 283–288 + 289–294 (digitized pages 307–312, 313–318), 1 pl. (on p. XV of this journal volume, some corrections to the texts are proposed). The "1 January 1743" date given for the separate by Google books cannot be correct, as the letters by Gualtierus and Plancus are signed with "September" and "October" 1743, respectively.]
- Rivera-Posada, J., Owens, L., Caballes, C.F. & Pratchett, M.S. (2012) The role of protein extracts in the induction of disease in *Acanthaster planci*. *Journal of Experimental Marine Biology and Ecology*, 429, 1–6.
<http://dx.doi.org/10.1016/j.jembe.2012.06.008>
- Rivera-Posada, J.A., Pratchett, M., Cano-Gómez, A., Arango-Gómez, J.D. & Owens, L. (2011) Injection of *Acanthaster planci* with thiosulfate-citrate-bile-sucrose agar (TCBS). I. Disease induction. *Diseases of Aquatic Organisms*, 97 (2), 85–94.
<http://dx.doi.org/10.3354/dao02401>
- Rowe, F.W.E. & Gates, J. (1995) Echinodermata. In: Wells, A. (Ed.), *Zoological Catalogue of Australia*, 33, xiii (13) + pp. 1–510 pp. [CSIRO Australia, Melbourne]
- Rumphius [= Rumph], G.E. (1705) *D'Amboinsche Rariteitkamer*. F. Halma, Amsterdam, 539 pp. Available from: <http://gdz.sub.uni-goettingen.de/dms/load/img/?PPN=PPN372428037&IDDOC=279913> (accessed 4 July 2014)
- Schmidel, K.C. (1781) Beschreibung eines Seesternes mit rosenförmigen Verzierungen. *Der Naturforscher (Halle a. d. Saale)*, 16, 1–7, pl. I (1). Available from: <http://www.ub.uni-bielefeld.de/cgi-bin/neubutton.cgi?pfad=/diglib/aufkl/naturforscher/118812&seite=00000006.TIF> (accessed 4 July 2014)
- Schreber, J.C.D. von (1793) Beschreibung der Seesonne, einer Art Seesterne, mit 21 Strahlen. *Der Naturforscher (Halle a. d. Saale)*, 27: 1–6, pls. I–II (1–2). Available from: <http://www.ub.uni-bielefeld.de/cgi-bin/neubutton.cgi?pfad=/diglib/aufkl/naturforscher/118931&seite=00000006.TIF> (accessed 4 July 2014)
- Sladen, W.P. (1889) Report on the Asteroidea (starfish) collected by H.M.S. Challenger during the years 1873–1876. *Report on the Scientific Results of the Voyage of H.M.S. Challenger 1873–76. Zoology*, Vol. XXX (30). Text, [6] + xlii (42) + 893 pp. Available from: <http://www.biodiversitylibrary.org/item/43777> (accessed 4 July 2014) [Illustrations for this work were issued separately in *Zoology* — Vol. XXX (30). Plates.]
- Studer, Th. (1885) Verzeichniss der während der Reise S.M.S. Gazelle um die Erde 1874–76 gesammelten Asteriden und Euryaliden. *Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin. Aus dem Jahre 1884. Abhandlungen nicht zur Akademie gehöriger Gelehrter. Physikalische Abhandlungen, Abh. II*, pp. 1–64, pls. I–V (1–5). Available from: http://bibliothek.bbaw.de/bbaw/bibliothek-digital/digitalequellen/schriften/anzeige/index_html?band=07-abh/1884&seite:int=602 (accessed 4 July 2014)
- Stump, R.J.W. & Lucas, J.S. (1990) Linear growth in spines from *Acanthaster planci* (L.) involving growth lines and periodic pigment bands. *Coral Reefs*, 9 (3), 149–154.
<http://dx.doi.org/10.1007/bf00258227>
- Vogler, C. (2010) *Phylogeography and evolution of the crown-of-thorns starfish Acanthaster planci*. PhD-Thesis, University of Munich (LMU), Faculty of Geo-Sciences, 138 pp.
- Vogler, C., Benzie, J.A.H., Barber, P.H., Erdmann, M.V., Ambariyanto, Sheppard, C., Tenggardjaja, K., Gérard, K. & Wörheide, G. (2012) Phylogeography of the Crown-of-Thorns starfish in the Indian Ocean. *PLoS ONE*, 7 (8), e43499. [10 pp.]
<http://dx.doi.org/10.1371/journal.pone.0043499>
- Vogler, C., Benzie, J.A.H., Lessios, H., Barber, P. & Wörheide, G. (2008) A threat to coral reefs multiplied? Four species of crown-of-thorns starfish. *Biology Letters*, 4 (6), 696–699.
<http://dx.doi.org/10.1098/rsbl.2008.0454>

- Vogler, C., Benzie J.A.H., Tenggardjaja, K., Ambariyanto, Barber, P.H. & Wörheide, G. (2013) Phylogeography of the crown-of-thorns starfish: genetic structure within the Pacific species. *Coral Reefs*, 32 (2), 515–525.
<http://dx.doi.org/10.1007/s00338-012-1003-z>
- Walbran, P.D. (1987) *Technical Memorandum: An atlas of the skeletal components of the crown-of-thorns starfish (Acanthaster planci (L.))*. Annual Report of the Great Barrier Reef Marine Park Authority (GBRMPA-TM-11), Townsville, 42 pp, incl. 13 pls. (ISSN 0817-6094, ISBN 0-642-52641-9). Available from: http://www.gbrmpa.gov.au/__data/assets/pdf_file/0005/9752/gbrmpa-tm11.pdf (accessed 4 July 2014)
- Waters, J., O'Loughlin, P.M. & Roy, M.S. (2004) Cladogenesis in a starfish species complex from southern Australia: evidence for vicariant speciation? *Molecular Phylogenetics and Evolution*, 32 (1), 236–245.
<http://dx.doi.org/10.1016/j.ympev.2003.11.014>
- Watt, M. (Ed.) (1786) *The natural history of many curious and uncommon zoophytes, collected from various parts of the globe by the late John Ellis, Esq. F. R. S. Soc. Reg. Upsal. Soc. author of the natural history of English Corallines, and other works. Systematically arranged and described by the late Daniel Solander, M. D. F. R. S. & c.. With sixty-two [sic] plates engraven by principal artists*. B. White and Son + P. Elmsly, London, xii (12) + 208 pp., 63 + [2] pls. Available from: <https://archive.org/details/naturalhistoryof00elli> (accessed 4 July 2014) [This work was published on the initiative of Sir Joseph Banks by Ellis' daughter years after the deaths of Ellis (†1776) and Solander (†1782); thus, for the purposes of nomenclature Ellis and Solander cannot be cited as the authors of the publication (ICZN 1999: Art. 50.1.1). However, contents of the work show clearly that Ellis had collected the material and closely overseen the production of the plates by various artists (Watt 1786, editor's introductory "Advertisement", p. vi), with the possible exception of the two unnumbered plates, which appear to be reproductions of older originals. The work's contents also show that Solander had "arranged and described" (op. cit.: title) the taxa treated in the text, including data "found in Mr. Ellis's papers" (op. cit.: p. 198). Consequently, we continue to credit Ellis & Solander with the nomenclatural authorship of all taxon names newly proposed in Watt (1786).]
- Yasuda, N., Hamaguchi, M., Sasaki, M., Nagai, S., Saba, M. & Nadaoka, K. (2006) Complete mitochondrial genome sequences for crown-of-thorns starfish *Acanthaster planci* and *Acanthaster brevispinus*. *BMC Genomics*, 7 (17), 10 pp.
- Yasuda, N., Nagai, S., Hamaguchi, M., Okaji, K., Gérard, K. & Nadaoka, K. (2009) Gene flow of *Acanthaster planci* (L.) in relation to ocean currents revealed by microsatellite analysis. *Molecular Ecology*, 18 (8), 1574–1590.
<http://dx.doi.org/10.1111/j.1365-294x.2009.04133.x>