European Journal of Taxonomy 1022: 176–201
https://doi.org/10.5852/ejt.2025.1022.3087
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europeanjournaloftaxonomy.eu
ISSN 2118-9773
2025 · Stöhr S.

Received: 23 April 2025 • Accepted: 12 August 2025 • Published: 10 October 2025

Topic editor: Magalie Castelin • Section editor: Didier Van den Spiegel • Desk editor: Pepe Fernández

Research article

urn:lsid:zoobank.org:pub:B189BB0C-3060-4DC5-8F9B-35E8088DB699

Two new species of brittle stars (Echinodermata: Ophiuroidea), living epizoic on a stalked crinoid

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Abstract. Brittle star species with epizoic life-style are found in at least a dozen families and on a wide variety of host animals (Cnidaria, Porifera, Mollusca, other Echinodermata). An overview of epizoic brittle star species is provided. This study is the first account of brittle stars living epizoic on the crinoid *Neogymnocrinus richeri*. Two species were described as new to science, for one of them, a new genus, *Warenophis* gen. nov., was erected. "*Ophiomitrella*" *thuyi* sp. nov. is tentatively placed in the genus *Ophiomitrella*, because the genus is polyphyletic and its type species was here found not to concur with the generic characters. All species of *Ophiomitrella* and *Ophiosemnotes* were analysed, key characters are listed, and the taxonomic status of these genera is discussed. *Warenophis andersi* gen. et sp. nov. possesses an unusual combination of features that doesn't match any known genus, such as flat, serrated arm spines, large disc plates without granules or spines, arm spine articular structures with tongue-like extension, and it could not yet be placed in a family. Based on lateral arm plate characters, it has affinities with the Ophiacanthidae and Ophiotomidae.

Keywords. Taxonomy, Ophiacanthidae, Ophiotomidae, *Ophiomitrella*.

Stöhr S. 2025. Two new species of brittle stars (Echinodermata: Ophiuroidea), living epizoic on a stalked crinoid. *European Journal of Taxonomy* 1022: 176–201. https://doi.org/10.5852/ejt.2025.1022.3087

Introduction

Ophiuroidea Gray, 1840, generally known as brittle stars, include 2136 species according to the latest census, based on published descriptions and revisionary works (Stöhr *et al.* 2025). Among these, a small number are known to occur epizoic or endozoic on or in other animal hosts (Table 1). Most species of ophiuroid with the ability to curl the arms (e.g., Euryalida Lamarck, 1816, Hemieuryalidae Verrill, 1899) are expected to be epizoic, but the host species are yet unknown for many of these. The ophiuroids often prefer a specific taxonomic group of hosts, e.g., Euryalida often occur on corals (many are found only on black corals), Amphiuridae Ljungman, 1867 have so far only been found associated with sea urchins, and epizoic Ophiactidae Matsumoto, 1915 seem to occur mainly on and in sponges, whereas Ophiotrichidae Ljungman, 1867 have been found on a variety of hosts (Table 1). At least one fossil ophiuroid species has been found epizoic on a crinoid (Thuy *et al.* 2020), indicating that these associations have a long evolutionary history. Particularly common are ophiuroid–coral relationships, and the coral most likely

Table 1 (continued on next three pages). Non-exhaustive list of epizoic and endozoic species of Ophiuroidea Gray, 1840 and their host species. Compiled from the cited literature sources and museum collection specimens.

Family	Ophiuroid	Host	Source
		Cnidaria hosts	
Asteronychidae Ljungman, 1867	*Asteronyx loveni* Müller & Troschel, 1842	Pennatuloidea, Octocorallia	Buhl-Mortensen & Buhl-Mortensen 2004
Gorgonocephalidae Ljungman, 1867	*Gorgonocephalus caputmedusae* (Linnaeus, 1758)	Various corals, *Lophelia pertusa* (Linnaeus, 1758)	Buhl-Mortensen & Buhl-Mortensen 2004
	Gorgonocephalus eucnemis (Müller & Troschel, 1842)	*Gersemia* v. Marenzeller, 1878, *Eunephthya* Verrill, 1869	Mortensen 1927; Patent 1970; Buhl-Mortensen & Buhl-Mortensen 2004
	Gorgonocephalus lamarcki (Müller & Troschel, 1842)	Various corals, *Lophelia pertusa* (Linnaeus, 1758)	Buhl-Mortensen & Buhl-Mortensen 2004
	Astrogordius cacaoticus (Lyman, 1874)	*Antipathes* Pallas, 1766, *Ellisella barbadensis* (Duchassaing & Michelotti, 1864)	Buhl-Mortensen & Buhl-Mortensen 2004
	Astrothorax waitei (Benham, 1909)	Corals	Personal observation on museum specimen
	Asteroporpa annulata Örstedt & Lütken in Lütken, 1856	Various corals	Buhl-Mortensen & Buhl-Mortensen 2004
	Asteroporpa indicus (Baker, 1980)	Coral	Personal observation on museum specimen
	Astrothrombus rugosus H.L. Clark, 1909	Coral	Personal observation on museum specimen
Euryalidae Gray, 1840	*Asteromorpha tenax* Baker, 1980	Coral	Personal observation on museum specimen
	Asteroschema ajax A.H. Clark, 1949	*Pseudochrysogorgia bellona* Pante & France, 2010	Cook *et al*. 2023
	Asteroschema clavigerum Verrill, 1899	*Paramuricea biscaya* Grasshoff, 1977	Girard *et al*. 2016
	Asteroschema tenue Lyman, 1875	Corals	Buhl-Mortensen & Buhl-Mortensen 2004
	Asteroschema tubiferum Matsumoto, 1911	Coral	Personal observation on museum specimen
	Asteroschema tumidum Lyman, 1879	Coral	Personal observation on museum specimen
	Astroceras elegans (Bell, 1917)	Coral	Personal observation on museum specimen

Table 1 (continued).

Family	Ophiuroid	Host	Source
Euryalidae Gray, 1840	*Ophiocreas oedipus* Lyman, 1879	*Metallogorgia melanotrichos* (Wright & Studer, 1899)	Mosher & Watling 2009
	Ophiocreas sibogae Koehler, 1904	Coral	Personal observation on museum specimen
	Astrobrachion constrictum (Farquhar, 1900)	*Antipathella fiordensis* (Grange, 1990)	Grange 1991
Ophiomusaidae O'Hara, Stöhr, Hugall, Thuy & Martynov, 2018	*Ophiomusa lymani* (Wyville Thomson, 1873)	*Acanella arbuscula* (Johnson, 1862), gorgonians	Buhl-Mortensen & Buhl-Mortensen 2004
Ophiacanthidae Ljungman, 1867	*Ophiocanops felli* McKnight, 2003	*Antipathes* Pallas, 1766	McKnight 2003
	Ophiocanops multispina Stöhr, Conand & Boissin, 2008	*Antipathes* Pallas, 1766	Stöhr *et al.* 2008
	Ophioplinthaca citata Koehler, 1904	Primnoidae	O'Hara & Stöhr 2006
	Ophiomoeris obstricta (Lyman, 1878)	Soft corals, sponges	O'Hara & Stöhr 2006
	Ophiosemnotes clavigera (Ljungman, 1865)	*Lophelia pertusa* (Linnaeus, 1758), *Paramuricea placomus* (Linnaeus, 1758)	Buhl-Mortensen & Buhl-Mortensen 2004
	Ophiacantha abyssicola G.O. Sars, 1872	Various corals, *Lophelia pertusa* (Linnaeus, 1758)	Buhl-Mortensen & Buhl-Mortensen 2004
	Ophiosabine anomala (G.O. Sars, 1872)	Various corals, *Lophelia pertusa* (Linnaeus, 1758)	Buhl-Mortensen & Buhl-Mortensen 2004
	Ophiacantha bidentata (Bruzelius, 1805)	*Lophelia pertusa* (Linnaeus, 1758)	Allen Brooks *et al.* 2007
	Ophiacantha setosa (Bruzelius, 1805)	Corals	Tortonese 1965
	Ophiomitrella mensa O'Hara & Stöhr, 2006	Cnidaria	O'Hara & Stöhr 2006
Ophiotomidae Paterson, 1985	*Ophiotreta valenciennesi* (Lyman, 1879)	*Lophelia pertusa* (Linnaeus, 1758)	Stöhr & Segonzac 2005
Hemieuryalidae Verrill, 1899	*Astrogymnotes irimurai* Baker, Clark & McKnight, 2001	*Antipathes* Pallas, 1766	Baker *et al.* 2001; Buhl-Mortensen & Buhl-Mortensen 2004
	Hemieuryale pustulata v. Martens, 1867	*Nicella guadalupensis* (Duchassaing & Michelotti, 1860)	Gondim *et al.* 2015
	Sigsbeia murrhina Lyman, 1878	*Stylaster filogranus* Pourtalés, 1871	Lyman 1878

Table 1 (continued).

Family	Ophiuroid	Host	Source
	Sigsbeia laevis Ziesenhenne, 1940	"red coral"	Ziesenhenne 1940
Ophiotrichidae Ljungman, 1867	*Macrophiothrix melanosticta* (Grube, 1868)	Pennatuloidea	Hoggett 1990
	Ophiothela danae Verrill, 1869	gorgonians	Fatemi & Stöhr 2019
	Ophiothela venusta (de Loriol, 1900)	*Suberogorgia suberosa* (Pallas, 1766)	Fatemi & Stöhr 2019
	Ophiothrix savignyi (Müller & Troschel, 1842)	*Suberogorgia suberosa* (Pallas, 1766)	Fatemi & Stöhr 2019
	Ophiocnemis marmorata (Lamark, 1816)	rhizostome jellyfish	Fujita & Namikawa 2006
Echinodermata hosts			
Gorgonocephalidae Ljungman, 1867	*Astrothorax waitei* (Benham, 1909)	Crinoidea	T. O'Hara, observation on museum specimen
Amphiuridae Ljungman, 1867	*Amphipholis linopneusti* Stöhr, 2001	*Linopneustes murrayi* (A. Agassiz, 1879)	Stöhr 2001
	Amphipholis conolampadis Kroh & Thuy, 2013	*Conolampas diomedeae* Mortensen, 1948	Kroh & Thuy 2013
	Ophiodaphne formata (Koehler, 1905)	*Astriclypeus manni* Verrill, 1867	Tominaga *et al.* 2004
	Ophiodaphne spinosa Tominaga, Hirose, Igarashi, Kiyomoto & Komatsu, 2017	*Clypeaster japonicus* Döderlein, 1885	Tominaga *et al.* 2017
	Nannophiura lagani Mortensen, 1933	*Laganum depressum* L. Agassiz, 1841	Mortensen 1933
Ophiotrichidae Ljungman, 1867	*Ophiomaza cacaotica* Lyman, 1871	Crinoidea, Comatulida	Potts 1915; Mekhova & Britayev 2015
	Gymnolophus obscura Ljungman, 1867	Crinoidea	Potts 1915
	Ophiolophus novarae Marktanner-Turneretscher, 1887	*Comanthus bennetti* (J. Müller, 1841)	Guille *et al.* 1986
	Ophiophthirius actinometrae Döderlein, 1898	*Actinometra solaris* (Lamarck, 1816)	Döderlein 1898
	Macrophiothrix melanosticta (Grube, 1868)	Crinoidea	Hoggett 1990
Ophiacanthidae Ljungman, 1867	*Ophiacantha pentacrinus* Lütken, 1869	*Endoxocrinus* (*Endoxocrinus*) *parrae parrae* (Gervais in Guérin, 1835)	Lütken 1869
	Ophiolebes comatulina McKnight, 2003	Comatulida	McKnight 2003
	Ophiolebes paulensis O'Hara & Thuy, 2022	Crinoidea	O'Hara & Thuy 2022

Table 1 (continued).

Family	Ophiuroid	Host	Source
Ophiacanthidae Ljungman, 1867	*Ophiomitrella floorae* Thuy, Numberger-Thuy & Jagt, 2020 (fossil)	Crinoidea	Thuy *et al.* 2020
	"*Ophiomitrella*" *thuyi* sp. nov.	*Neogymnocrinus richeri* (Bourseau, Améziane-Cominardi & Roux, 1987)	Present study
Ophiacanthida incertae sedis	*Warenophis andersi* gen. et sp. nov.	*Neogymnocrinus richeri* (Bourseau, Améziane-Cominardi & Roux, 1987)	Present study
	Porifera hosts		
Ophiactidae Matsumoto, 1915	*Ophiactis savignyi* (Müller & Troschel, 1842)	Porifera	Hendler *et al.* 1995; Fatemi & Stöhr 2019
	Ophiactis algicola H.L. Clark, 1933	Porifera, Bryozoa	Hendler *et al.* 1995
	Ophiactis quinqueradia Ljungman, 1872	Porifera	Hendler *et al.* 1995
	Ophiactis modesta Brock, 1888	Porifera	Peyghan *et al.* 2018
Ophiotrichidae Ljungman, 1867	*Ophiothrix angulata* (Say, 1825)	Porifera	Hendler *et al.* 1995
	Ophiothrix suensonii Lütken, 1856	Porifera	Hendler *et al.* 1995
	Ophiothrix lineata Lyman, 1860	Porifera	Hendler *et al.* 1995
	Ophiothrix oerstedii Lütken, 1856	Porifera	Hendler *et al.* 1995
	Mollusca hosts		
Amphilepidida O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017	*Ophienigma spinilimbatum* Stöhr & Segonzac, 2005	*Bathymodiolus* Kenk & B.R. Wilson, 1985	Stöhr & Segonzac 2005
Ophiuridae Müller & Troschel, 1840	*Ophioctenella acies* Tyler, Paterson, Sibuet, Guille, Murton & Segonzac, 1995	*Bathymodiolus* Kenk & B.R. Wilson, 1985	Tyler *et al.* 1995

functions as a perch for the (usually particle feeding) ophiuroid to reach higher water layers above the sea floor. In most cases, the ophiuroid-coral relationship is considered facultative, but a few species appear not to be able to live without their host, e.g., *Asteronyx loveni* Müller & Troschel, 1842 (Buhl-Mortensen & Buhl-Mortensen 2004). Among the more unusual relationships are ophiuroids riding on pelagic jellyfish (Fujita & Namikawa 2006), and the observation of *Ophiomusa lymani* (Wyville Thomson, 1873) on gorgonian corals (Buhl-Mortensen & Buhl-Mortensen 2004) is unexpected in a species with rather rigid arms that usually lives on the open bottom of the deep-sea plains (Gage & Tyler 1991).

Several species of ophiuroid are known to live on crinoids (Table 1), and this study reports two additional species that were found on the stalked cyrtocrinid *Neogymnocrinus richeri* (Bourseau, Améziane-Cominardi & Roux, 1987) in the Tonga Islands. As far as known, these are the first records of epizoic brittle stars from this species of crinoid. Both species of ophiuroid are new to science, and the aim of this study was to describe them and to understand their systematic relationships. One of these species has a highly unusual morphology that does not concur with any known genus, and it has uncertain affinities to higher taxa. The other species has affinities with the genus *Ophiomitrella* Verrill, 1899, a polyphyletic complex of morphologically highly similar species, from which one molecular clade was recently separated and placed in the genus *Ophiosemnotes* Matsumoto, 1917 (O'Hara & Thuy 2022). The discovery of the new species prompted an investigation into the taxonomic status of *Ophiomitrella*, attempting to find morphological characters that may be useful to delimit monophyletic clades, ideally in agreement with the molecular clades found by Christodoulou *et al*. (2019).

Material and methods

The ophiuroids were discovered on a specimen of *N. richeri* that was collected during the cruise Bordau 2 to the Tonga Islands in 31 Mar.–22 Jun. 2000 (Richer de Forges 2000). They were stored in 80% ethanol. The ophiuroids were clinging to the oral side of the crinoid, with their arms tightly wrapped around the crinoid arms (observation by the author). During removal of the ophiuroids, their arms broke, unfortunately. One specimen each was subjected to diluted household bleach, to gently remove the outer skin. They were then air-dried, mounted on aluminium stubs with spray glue, and coated with gold for examination in a scanning electron microscope Hitachi FE-S4300. After scanning the dorsal side, they were removed from the stubs by dissolving the glue in butyl acetate, turned over and re-attached with fresh glue, to scan also the ventral side of the animals. An arm piece of the unknown genus was dissolved in concentrated bleach to dissociate the ossicles. These were then glued to SEM stubs and examined in the instrument.

To identify the specimens of "*Ophiomitrella*", all species currently assigned to *Ophiomitrella* and *Ophiosemnotes* were analysed from their original descriptions and actual type specimens or digital photos of the type specimens, as available, and four key characters were compared (Table 2). Since the specimens did not match any of the known species, they are described as new. The second species did not match any known genus or species and both a new genus and a new species are described below. To place it in the ophiuroid classification, its lateral arm plates were compared with species across the whole Ophiuroidea. After its greatest similarities were found to be with Ophiacanthida O'Hara *et al.*, 2017, it was compared with several genera in the families Ophiacanthidae Ljungman, 1867 and Ophiotomidae Paterson, 1985.

The terminology for morphological characters follows common practice in the field (Stöhr *et al.* 2012). Terms for oral structures follow Hendler (2018) as far as they could be identified. The more generic term 'lateral oral papillae' was used for papillae that cannot be identified in the absence of ontogenetic series.

To understand the phylogenetic relationships of the new genus, a Bayesian phylogenetic analysis was performed using the software package MrBayes (Huelsenbeck & Ronquist 2001) with the same parameters and family level morphological characters as in Stöhr (2024), but with a partly different set of species. Particularly, two species of *Ophiolimna* Verrill, 1899, and *Ophiocopa spatula* Lyman, 1883, were added to the data matrix, since their spine articular structures on the lateral arm plates resemble the new genus. Also, these represent two different families and complete sets of characters were available. The dataset contained 153 characters and 71 species (Supp. file 1). To compare tree structures, the analysis was run without the new genus. In addition, an analysis with only the 46 characters from lateral arm plates was run, since these have been shown to be taxonomically highly informative (Thuy & Stöhr 2011), and for the new genus and species not all other structures were available. Only variable characters were sampled, and the coding parameter was set to variable in the Bayesian analysis. Character states were assumed to have equal frequency, and prior probabilities were equal for all trees. As outgroup, *Aganaster gregarius* (Meek & Worthen, 1869) was used. Evolutionary rates were assumed to vary between sites according to a discrete gamma distribution. Branch lengths were unconstrained. The average standard deviation of split frequencies stabilized at about 0.006–0.01 after nine million generations, sampled every 1000 generations. The first 25% of the trees were discarded as burnin. The resulting consensus trees were examined with the software FigTree ver. 1.4.4 by Rambaut (https://tree.bio.ed.ac.uk/software/figtree/).

Abbreviations

ars = articular structure
AS = adoral shield
ASP = arm spine
CP = compartment plate
DAP = dorsal arm plate
dd = disc diameter
dist = distal
dl = dorsal lobe
dors = dorsal
IR = interradial plate
LAP = lateral arm plate
LOPa = lateral oral papillae
OS = ral shield
prox = proximal
RS = radial shield
SEM = scanning electron microscope
sp = spur
TP = tooth papillae
TS = tentacle scale
VAP = ventral arm plate
vars = vertebral articular structure
vent = ventral

Institutional acronyms

MNHN = Muséum national d'Histoire naturelle, Paris
SMNH = Swedish Museum of Natural History, Invertebrate collection, Stockholm

Results

Taxonomy

Class Ophiuroidea Gray, 1840
Superorder Ophintegrida O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017
Order Ophiacanthida O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017
Family Ophiacanthidae Ljungman, 1867

Genus ***Ophiomitrella*** Verrill, 1899
Fig. 1; Table 2

Type species

Ophiacantha laevipellis Lyman, 1883.

Material examined

ANTARCTICA – **Maria Island** • 1 spec., syntype of *Ophioripa conferta*; depth 1300 fathoms (2379 m); 13 Dec. 1912; Australasian Antarctic Expedition; MNHN, MNHN-IE-2013-10230 (formerly Ec Os 20388).

CHILE – **Gulf of Ancud** • 3 specs, syntypes of *Ophiomitrella chilensis*; Paso Tenaún, S of Punta Tenaún; 42°20′50″ S, 73°22′00″ W; depth 70 m; 24 Jan. 1949; Lund University Chile Expedition stn M42; triangular dredge; hard bottom; SMNH, SMNH-Type-2321.

INDONESIA – **Kei Island •** 1 spec., syntype of *Ophiacantha tenuis*; 5°48.2′ S, 132°13′ W; depth 304 m; 1899–1900; Siboga Expedition stn 253; MNHN Ec Os 2040.

NORWAY • 3 specs, syntypes of *Ophiactis clavigera*; depth 364–546 m; 22 Oct. 1864; Uggla Expedition; on *Gorgonia*; SMNH, SMNH-Type-3724.

SOUTH ATLANTIC OCEAN – **Gough Island •** 1 spec., syntype of *Ophiomitrella ingrata*; depth 100 fathoms (183 m); 23 Apr. 1904; Scotia Expedition; MNHN, MNHN-IE-2013-10308 (formerly Ec Os 20364).

WEST INDIES – **off St. Vincent •** 1 spec., paratype of *Ophiacantha laevipellis*; depth 88 fathoms (160 m); 21 Feb 1879; Blake stn 232; MNHN, MNHN-IE-2013-10160 (formerly Ec Os 20398).

Remarks

When Verrill (1899a) erected *Ophiomitrella*, he described it in a confusing dichotomous list, from which it is difficult to extract the characters that delimit this genus. Under section "*A*", he sorted species in which the adoral shields are restricted to the proximal part of the oral shield, but under "*A.A.*" they extend around the oral shield. *Ophiomitrella* is found under "*B.B.*", which doesn't mention adoral shields, but has uncovered radial shields, whereas "*B.*" is meant for species with covered radial shields. Finally, under "*n.n.*", *Ophiomitrella* has separated dorsal arm plates and thorny, slender arm spines that meet dorsally. The only species assigned to *Ophiomitrella* was *O. laevipellis*, making it the type species of the genus by monotypy. According to the redescription (Verrill 1899b), *Ophiomitrella* should have small, widely separated radial shields, not bearing granules or spines, adoral shields limited to the proximal part of the oral shield, disc with scattered granules or stumps. In the same work (Verrill 1899b), *O. laevipellis* is described as having long, narrow, covered radial shields, with only their distal part exposed, which was here confirmed by examination of publicly available photos of the holotype (MCZ:IZ:OPH-1957) and photos of a paratype taken by the author (Fig. 1I–J).

Verrill subdivided *Ophiomitrella*, based on differences in arm spines, and placed *O. laevipellis* in one subgroup, whereas *Ophiomitrella cordifera* (Koehler, 1896) and *Ophiomitrella globulifera* (Koehler, 1896) formed the other subgroup. The latter two species match the description of the genus *Ophiomitrella*, which is however still a polyphyletic genus (O'Hara *et al.* 2018), despite the recent transfer of a group of species to the morphologically highly similar genus *Ophiosemnotes* (O'Hara & Thuy 2022).

The necessary revision of these genera is far beyond the scope of this study, and as O'Hara & Thuy (2022) found, morphological characters that support the molecular clades have not been identified yet. In Table 2, the species were grouped by the nature of their disc spines (granules are considered homologous to spines). The majority of the species have more or less spherical (granule-like) disc spines, and the removal of *Ophiosemnotes brevispina* (H.L. Clark, 1911), that lacks disc spines, and *Ophiosemnotes diaphora* (H.L. Clark, 1911), that has granules, from the *Ophiosemnotes* group concurs with the latest published molecular phylogeny (Christodoulou *et al.* 2019). Thus, a revision of *Ophiosemnotes* appears necessary. However, on that tree, these two species are also in a separate clade from the remaining *Ophiomitrella*, and other members of this group are found in several clades on the molecular phylogeny (Christodoulou *et al.* 2019), which suggests that the granular disc spine group may be polyphyletic. Several of the species with stellate disc spines form a clade on the molecular tree, but the clade includes also *Ophiomitrella barbara* Koehler, 1904, which was here grouped as having elongated

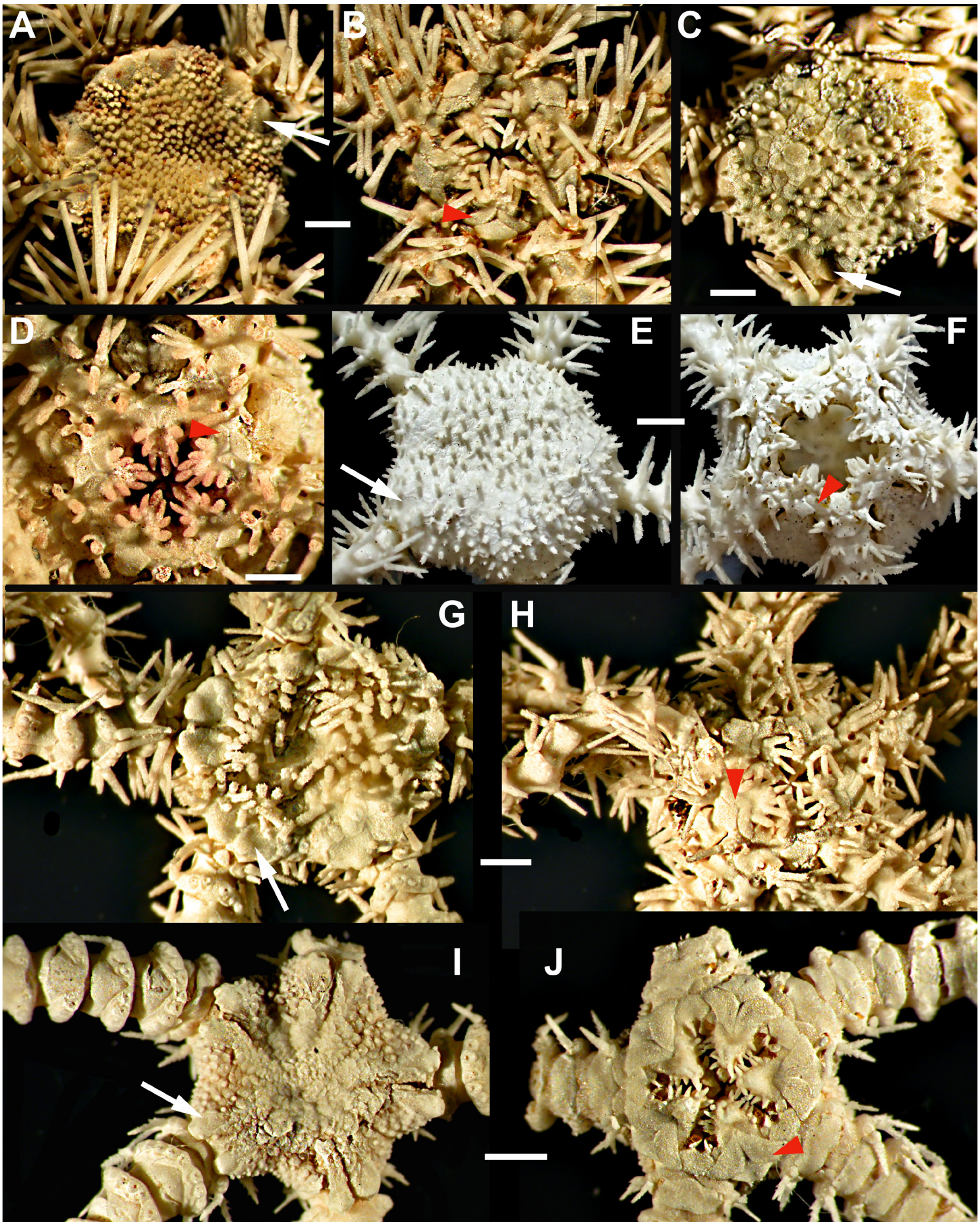

Fig. 1. Type specimens of some species currently placed in the genera *Ophiomitrella* Verrill, 1899 and *Ophiosemnotes* Matsumoto, 1917. **A–B**. *Ophiacantha tenuis* Koehler, 1904, syntype (MNHN Ec Os 20408). **A**. Dorsal disc. **B**. Mouth. **C–D**. *Ophiomitrella ingrata* Koehler, 1908, syntype (MNHN-IE-2013-10308). **C**. Dorsal disc. **D**. Mouth. **E–F**. *Ophiomitrella chilensis* Mortensen, 1952, syntype (SMNH-Type-2321). **E**. Dorsal disc. **F**. Mouth. **G–H**. *Ophioripa conferta* Koehler, 1922, syntype (MNHN-IE-2013-10230). **G**. Dorsal disc. **H**. Mouth. **I–J**. *Ophiacantha laevipellis* Lyman, 1883, paratype (MNHN-IE-2013-10160). **I**. Dorsal disc. **J**. Mouth. Arrows point to radial shields, arrowheads mark adoral shields. Scale bars = 1 mm.

Table 2 (continued on next two pages). Key characters of all species currently placed in the genera *Ophiomitrella* Verrill, 1899 and *Ophiosemnotes* Matsumoto, 1917, compiled from original descriptions, examinations of type specimens or photos of type material, and Paterson (1985). Abbreviations: AS = adoral shield; DD = disc diameter; OS = oral shield. Generic type species indicated by asterisk.

Species	DD (mm)	Disc spines	Radial shields	Oral shields	Adoral shields
Group A: disc spines low, more or less spherical, or absent					
Ophiomitrella americana Koehler, 1914	6.5	small round, with thorny tips	small, 1/8 of dd, round, widely separated	rhombic, proximally acute, ~2× as wide as long, larger than AS	narrow crescent, proximal to OS
Ophiomitrella araucana Castillo-Alárcon, 1968	9	small granules	1/6 of dd, triangular, distally connected	rhombic, larger than AS	narrow crescent, proximal to OS
Ophiosemnotes brevispina (H.L. Clark, 1911)	8	none	~1/6 of dd, rounded, widely separated	rhombic to pentagonal	trapezoid
Ophiomitrella cordifera (Koehler, 1896)	4	few, low, globular, short peduncle	1/4 of dd, oval to triangular, distally connected	rhombic, proximally acute, larger than AS	crescent, extend barely around OS
Ophiosemnotes diaphora (H.L. Clark, 1911)	11	round granules	1/4 of dd, oval, widely separated	pentagonal, smaller than AS	trapezoid, proximal to OS
Ophiomitrella globulifera (Koehler, 1896)	11	large, globular	1/5 of dd, oval, widely separated	pentagonal to rhombic, large, distal projection	large, trapezoid, curved, proximal to OS
Ophiomitrella granulosa (Lyman, 1878)	9	dense, small granules	small, distally connected	rounded triangular, smaller than AS	large, trapezoid, proximal to OS
Ophiomitrella mensa O'Hara & Stöhr, 2006	10	capitate stumps	1/4 of dd, triangular, contiguous	small, wider than long, pentagonal	trapezoid, larger than OS, proximal to OS
Ophiomitrella nudextrema (H.L. Clark, 1939)	3	trifid stumps	1/6 of dd, triangular	diamond-shaped	trapezoid, large
Ophiomitrella parviglobosa O'Hara & Stöhr, 2006	4	spherical granules	1/9 of dd, triangular to circular	rhombic	crescent, proximal to OS
Ophiomitrella suspectus (Koehler, 1922)	8	dense, club-shaped, pediculate globules	1/5 of dd, triangular, connected	rhombic	trapezoid, large, proximal to OS
Ophiomitrella tenuis (Koehler, 1904)	5–6	dense, small, thorny, elongated granules	1/6 of dd, triangular, separated	rounded rhombic, larger than AS	crescent to trapezoid, proximal to OS
Ophiomitrella thuyi sp. nov.	4.2	smooth, spherical granules, variable size	1/4 of dd, rounded triangular, separated	rounded triangular, small distal lobe, smaller than AS	trapezoid, proximal to OS

Table 2 (continued).

Species	DD (mm)	Disc spines	Radial shields	Oral shields	Adoral shields
Group B: disc spines stellate					
Ophiomitrella mutata Koehler, 1904	10	dense, trilobed stumps	$^1/_{10}$ of dd, triangular, widely separated	rounded, rhombic, distal lobe	narrow crescent, proximal to OS
Ophiomitrella polyacantha (H.L. Clark, 1911)	6	stellate stumps, crown with perpendicular thorns	$^1/_6$ of dd, triangular, widely separated	rhomboid, proximally acute	trapezoid, proximal to OS
Ophiomitrella sagittata Koehler, 1922	9	dense, strong, trilobed head	$^1/_7$ of dd, triangular, widely separated	arrowhead-shaped, separating AS	crescent to trapezoid, proximo-lateral to OS
Ophiomitrella stellifera Matsumoto, 1917	4	stellate stumps, crown with 6 thorns	$^1/_{10}$ of dd, triangular, separated	rhombic to arrowhead-shaped, larger than AS	trapezoid, proximal to OS
Ophiomitrella subjecta Koehler, 1922	9	dense, short, club-shaped, thorny head	$^1/_9$ of dd, triangular, separated	rhombic, proximally acute	narrow crescent, proximal to OS
Group C: disc spines elongated stump-like with thorns					
Ophiomitrella barbara Koehler, 1904	7	long stumps with thorny crown	as disc scales, widely separated	rhombic, proximally acute	narrow crescent, proximal to OS
Ophiomitrella chilensis Mortensen, 1952	5	thorny stumps	~$^1/_8$ of dd, triangular, distally connected	rhombic, distal lobe	trapezoid, extending around OS
Ophiosemnotes clavigera (Ljungman, 1865)	6.5	long and short thorny stumps	rounded separated	rhombic	trapezoid
Ophiosemnotes conferta (Koehler, 1922)	6	elongated thorny stumps	$^1/_4$ of dd triangular, halfway connected	rounded rhombic, larger than AS	crescent, proximal to OS
Ophiosemnotes corynephora (H.L. Clark, 1911)	8	cylindrical stumps	~$^1/_6$ of dd, rounded triangular	rhombic	trapezoid, proximal to OS
Ophiosemnotes hamata (Mortensen, 1933)	4	cylindrical stumps	rounded triangular, distally connected	rhombic, larger than AS	crescent, proximal to OS
Ophiosemnotes ingrata (Koehler, 1908)	4	low stumps	$^1/_{10}$ of dd, round, widely separated	rounded rhombic	crescent, proximal to OS
Ophiosemnotes pachybactra (H.L. Clark, 1911)	11	club-shaped stumps	~$^1/_6$ of dd, rounded triangular, distally connected	rounded rhombic, as large as AS	crescent to trapezoid, proximal to OS
Ophiosemnotes paucispina (H.L. Clark, 1911)	10	rounded granules	$^1/_6$ of dd, oval, widely separated	rhombic	trapezoid

Table 2 (continued).

Species	DD (mm)	Disc spines	Radial shields	Oral shields	Adoral shields
**Ophiosemnotes tylota* (H.L. Clark, 1911)	10	stout thorny stumps	1/6 of dd, rounded triangular, distally connected	rhombic	trapezoid, proximal to OS
Group D: bar-like radial shields					
**Ophiomitrella laevipellis* (Lyman, 1883)	4.5	scattered low granules	pear-shaped (distal ends), bar-like ridge in disc	rhombic to triangular, smaller than AS	trapezoid to crescent, proximal to OS
Ophiomitrella porrecta Koehler, 1914	6.5	dense multifid spines	small as scales (distal ends), widely separated	pentagonal	crescent, proximal to OS

stumps, a character that is found in most of the species of *Ophiosemnotes* and in *Ophiomitrella chilensis* Mortensen, 1952 (see Fig. 2E), which has not been sequenced yet. Other characters, such as the shape of the adoral (trapezoid/crescent) and oral shields (rhombic, larger/smaller than adoral shields) and the size of the radial shields, vary between species without forming obvious groups. Thus, disc spines are the most promising phylogenetically informative character, but need to be differentiated in more detail, and additional characters need to be identified.

The issue is further complicated by the high similarity between *Ophiomitrella* and additional genera, which should also be re-assessed. *Ophiomitra* Lyman, 1869 shares with some *Ophiomitrella* not only the large adoral and small oral shield, but also the short, rounded radial shields. It was placed in Ophiotomidae Paterson, 1985 by O'Hara *et al*. (2018), but recent unpublished data (O'Hara pers. com.) suggest that its type species *Ophiomitra valida* Lyman, 1869 belongs in Ophiacanthidae instead. *Ophiomitra leucorhabdota* (H.L. Clark, 1911) falls into the Ophiotomidae clade, but several other species of *Ophiomitra* group with *Ophiosemnotes* (Christodoulou *et al.* 2019), which illustrates the genetic and morphological similarity between these genera. Last, but not least, the recently re-validated genus *Ophiophthalmus* Matsumoto, 1917 (Nethupul *et al.* 2022) is also rather similar to *Ophiomitrella*, having short rounded radial shields, small disc granules, and large crescent-shaped adoral shields proximal to the rhombic oral shield.

"*Ophiomitrella*" *thuyi* sp. nov.
urn:lsid:zoobank.org:act:BE331259-774D-4810-A3AE-E81A4234B406
Fig. 2

Diagnosis

The dorsal disc is densely covered by low round granules, except on the radial shields, which are ¼ as long as the disc diameter. There are three spiniform lateral oral papillae. The adoral shields are trapezoid, larger than the oral shield, positioned only proximal to the oral shield. There are up to eight arm spines that do not meet dorsally.

Etymology

The specific epithet honours palaeontologist Ben Thuy whose work has greatly advanced the understanding of ophiuroid evolution.

Type material

Holotype

TONGA – **N Ha'apai group** • 19°03.7′ S, 174°18.98′ E; depth 523–806 m; 14 Jun. 2000; Anders Warén leg.; Bordau stn DW1595; Warén dredge; on *Neogymnocrinus richeri* (SMNH-225978); MNHN, MNHN-IE-2023-165.

Paratype

TONGA – **N Ha'apai group** • 1 spec.; same collection data as for holotype; SMNH, SMNH-Type-10004.

Description

Holotype

Dorsal disc. Rounded pentagonal, 4.4 mm dd, dorsal scales obscured by spherical granules of variable size. Radial shields bell-shaped, about ¼ as long as dd, not bearing granules, pairs of radial shields separated by single column of narrow scales bearing few granules.

Ventral disc. Covered by overlapping round scales, few scattered granules similar to dorsal ones. Three lateral oral papillae, two proximal ones spiniform pointed, distalmost one shorter, compressed, blunt, all roughly thorny. In mouth angle, an unidentified compartment plate (see Hendler 2018). Lyman's ossicle likely absent. Ventralmost tooth larger than papillae, flattened, pointed, roughly thorny. Upper teeth larger still, with increasingly rounded tip. Adoral shields limited to proximal edges of oral shield, trapezoid, with straight edges, proximal edge longer than distal edge, sides slanting. Oral shield rounded rhombic, about twice as wide as long, with small median process in distal edge, smaller than adoral shield. Madreporic shield longer, with central depression.

Arms. Dorsal arm plates fan-shaped, with convex distal edge, separated. Lateral arm plates arch around arm, meeting dorsally and ventrally. Up to eight conical, pointed, all over thorny, hollow arm spines, second dorsal spine longest, up to two arm segments long, ventral spines shorter than one arm segment. Spines do not meet across dorsal arm. Spine articular structures bordered by wavy ridge with unperforated stereom. First ventral arm plate narrow, extending into mouth slit, with median furrow. Other ventral arm plates rounded pentagonal, with strongly convex distal edge, acute proximal angle, slightly overlapping, distally a band of unperforated stereom. Single oval tentacle scale, closing tentacle pore completely.

Colouration. Dark green, similar to host *N. richeri*, faded in alcohol.

Paratype

Disc rounded pentagonal, 4.4 mm dd, fewer disc granules than holotype, interradially three columns of round scales, central column overlaps outer two. Other characters as in holotype.

Remarks

"*Ophiomitrella*" *thuyi* sp. nov. falls within the group of species with low round disc granules. It is closest to *O. tenuis* in its granule covered disc and same number of arm spines, but the granules in *O. tenuis* are smaller, slightly taller, less spherical, and somewhat thorny, and the arm spines form a continuous row across the dorsal arm. Its radial shields are smaller (1/6 of dd), the adoral shields are crescent-shaped, narrower, smaller than its oral shield, the madreporite is larger and has a domed centre. "*Ophiomitrella*" *thuyi* resembles *O. diaphora* (H.L. Clark, 1911) in the size of the radial shields, the large adoral shields and disc granules of variable size, but that species is considerably larger, the radial shields are widely separated, the dorsal arm plates are rhombic, it has up to seven arm spines and four lateral oral papillae, the distalmost one enlarged. Among other species with similar radial shields and large adoral shields, *O. mensa* O'Hara & Stöhr, 2006 has stump-like disc granules with widened head, in *O. globulifera*

(Koehler, 1896) the radial shields are widely separated by large scales and it reaches a larger size. All other species with round disc granules have smaller radial shields and/or crescent-shaped adoral shields (Table 2). There is some similarity to the specimens identified as *O. conferta* by O'Hara & Stöhr (2006), but they differ from the true *O. conferta* (Koehler, 1922) (Fig. 1G–H) and from *O. thuy* in having large

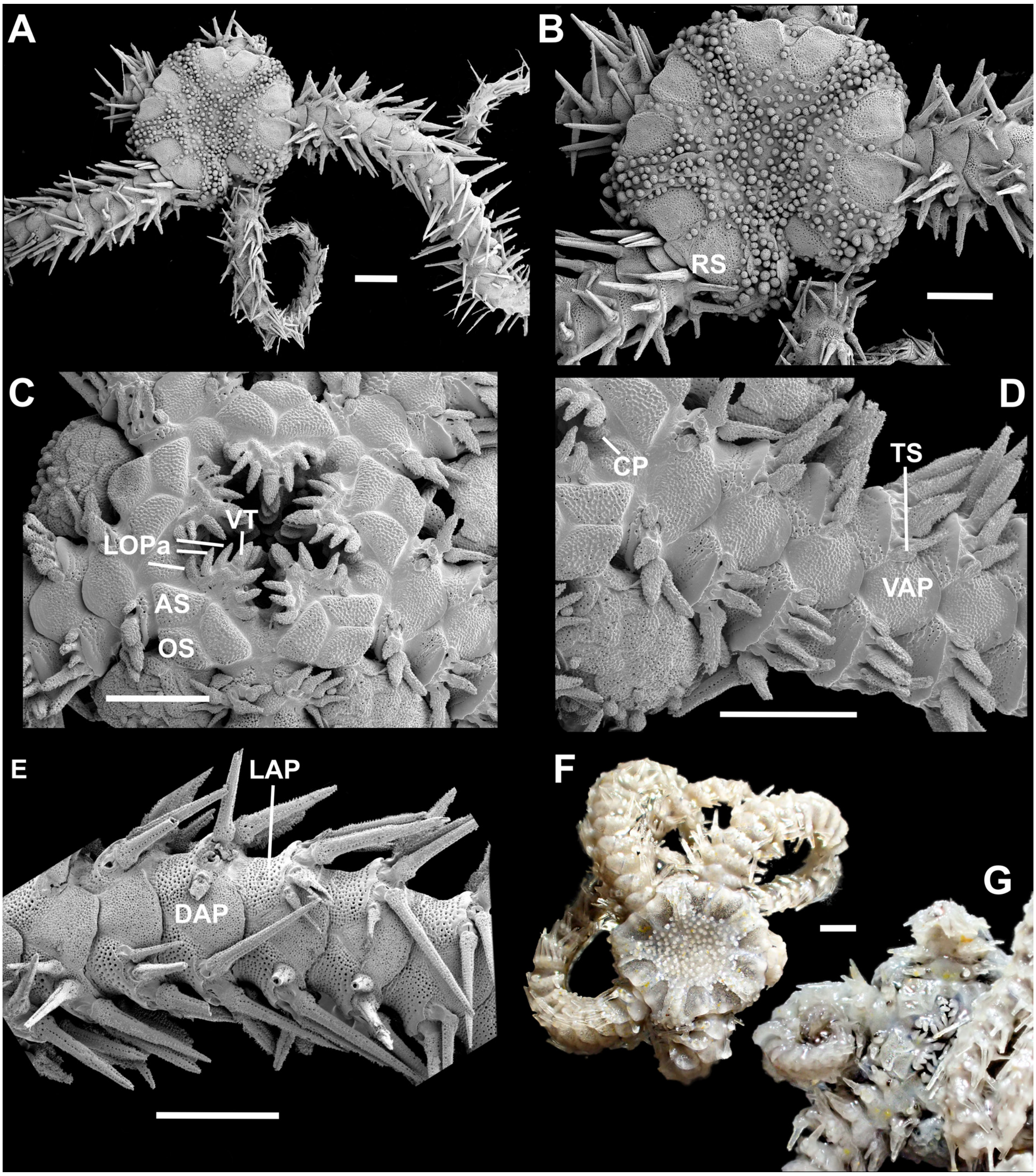

Fig. 2. "*Ophiomitrella*" *thuyi* sp. nov. **A–E**. Holotype (MNHN-IE-2023-165), SEM images. **A**. Dorsal overview. **B**. Dorsal disc. **C**. Mouth. **D**. Ventral arm. **E**. Dorsal arm. **F–G**. Paratype (SMHN-Type-10004), digital images. **F**. Dorsal aspect. **G**. Ventral aspect. Abbreviations: AS = adoral shield: CP = compartment plate; DAP = dorsal arm plate; LAP = lateral arm plate; LOPa = lateral oral papillae; OS = oral shield; RS = radial shield; TS = tentacle scale; VAP = ventral arm plate; VT = ventral tooth. Scale bars = 1 mm.

globular disc granules with short peduncle. Last but not least, none of the other species in *Ophiomitrella* and *Ophiosemnotes* are known to live on *N. richeri*, and the two new species described here may be the first records of epizoic ophiuroids on *N. richeri*.

Family Ophiacanthidae Ljungman, 1867 incertae sedis

Genus ***Warenophis*** gen. nov.
urn:lsid:zoobank.org:act:2691A6FF-A748-442D-BBEA-CAF345D2C153

Type species

Warenophis andersi sp. nov., here designated.

Diagnosis

As for type species.

Etymology

The name is a compound noun of masculine gender, honouring the eminent mollusc expert Anders Warén, who collected the species and is a mentor and long-time friend of the author, and '*ophis*' (meaning 'snake' in Greek), alluding to Ophiuroidea.

Warenophis andersi sp. nov.
urn:lsid:zoobank.org:act:D822AACB-B0DC-41F6-B53D-35454C9FE02B
Figs 3–4

Diagnosis

The disc is round, slightly domed, dorsally covered by large, irregular scales, with triangular, contiguous radial shields, that are ⅓ as long as the disc diameter. Granules and spines are completely absent from the disc. The dorsal arm plates are fan-shaped and contiguous. The ventral disc is covered by smaller round scales. At the apex of the jaw there are two elongated tooth papillae, along each jaw edge sit three small, round lateral oral papillae. The second tentacle pore is superficial outside the mouth slit. The up to four arm spines are flattened, wide, triangular, serrated, the dorsalmost spine is the largest. There is a single small, oval tentacle scale. The spine articulations on the lateral arm plate have a tongue-like dorsal extension.

Etymology

The specific epithet honours Anders Warén, who collected the species and is a mentor and long-time friend of the author.

Type material

Holotype
TONGA – **N Ha'apai group** • 19°03.7′ S, 174°18.98′ E; depth 523–806 m; 14 Jun. 2000; Anders Warén leg.; Bordau stn DW1595; Warén dredge; on *Neogymnocrinus richeri* (SMNH-225978); on SEM stub; MNHN, MNHN-IE-2023-164.

Paratypes
TONGA – **N Ha'apai group** • 2 specs; same collection data as for holotype; in ethanol, arm ossicles on SEM stub; SMNH, SMNH-Type-10005.

Description

Holotype

Dorsal disc. 4.8 mm dd, pentamerous. Round, domed disc, centre with irregular scales of variable size, no granules or spines. Radial shields scalene triangular, about as long as ⅓ of dd, completely contiguous. Primary rosette not distinguishable. Large rectangular interradial scale separates pairs of radial shields.

Ventral disc. Covered by scales smaller than on dorsal disc. Oral shield rhombic, 1.5 times as wide as long, distal edge convex, madreporite larger, no hydropore visible. Adoral shields crescent-shaped, proximal edge slightly concave, restricted to proximal edges of oral shield. Short jaws with two finger-like tooth papillae, teeth wide, rounded. Three minute, round granule-like lateral oral papillae. Large superficial second tentacle pore outside mouth slit, with oval, scale-like adoral shield spine at edge of adoral shield.

Arms. Dorsal arm plates fan-shaped, as long as wide, contiguous. Lateral arm plates forming part of dorsal arm. Up to four arm spines, two dorsal spines largest, flat, triangular, proximal edge convex, distal edge straight, perpendicular to arm, imbricated, roof-like horizontal. Spines smaller on distal arm, but same flat shape throughout arm. Two ventral spines shorter, narrower, flattened. All arm spines with serrated edges. Ventral arm plates widely axe-shaped, twice as wide as long, lateral edges deeply excavated, distal edge straight, proximal edge wide flat angle, barely contiguous. Single round tentacle scale, not completely closing pore.

Colouration. Dark green, similar to host *N. richeri*, faded in alcohol.

Ossicles

Lateral arm plates. Outer side with three to four spine articular structures on elevated part, shaped as two lobes, almost vertical in position, dorsal lobe tongue-shaped widened, ventral lobe short, muscle opening larger than nerve opening. Proximal outer edge of LAP with median process (spur). Stereom finely porous, along proximal edge a finer meshed band. Vertebral articular structures on inner side as angled flat ridge with finer pores than surrounding stereom, and round low knob on ventro-proximal part. Large pores distal to ridge, flat spur median on distal part.

Arm spines. Articular structures as oval, flat, smooth knob with median slit and deep groove dorsodistal to knob. On largest spine, articular structures offset to distal part of lateral edge.

Vertebrae. Zygospondylous articulation with zygosphene as long as zygocondyles, extending beyond lower ends of zygocondyles. No dorsal keel-like structure.

Paratypes

Specimen A: 4.1 mm dd, disc damaged, but plates and scales similar to holotype. Two arms completely broken off, three at distance from disc. Arms and ventral disc like holotype. Tentacle scale smaller than in holotype. Arm pieces present in sample.

Specimen B: juvenile of 2.2 mm dd, dorsal disc with pentagonal central primary plate, slightly smaller, rounded square radial primary plates, small pentagonal proximal interradial plate, larger rectangular distal interradial plate. Radial shields scalene triangular, contiguous. Oral papillae as in other paratype and holotype. Large tentacle pores with single minute scale. Small arm pieces in sample, all but one arm broken off close to disc.

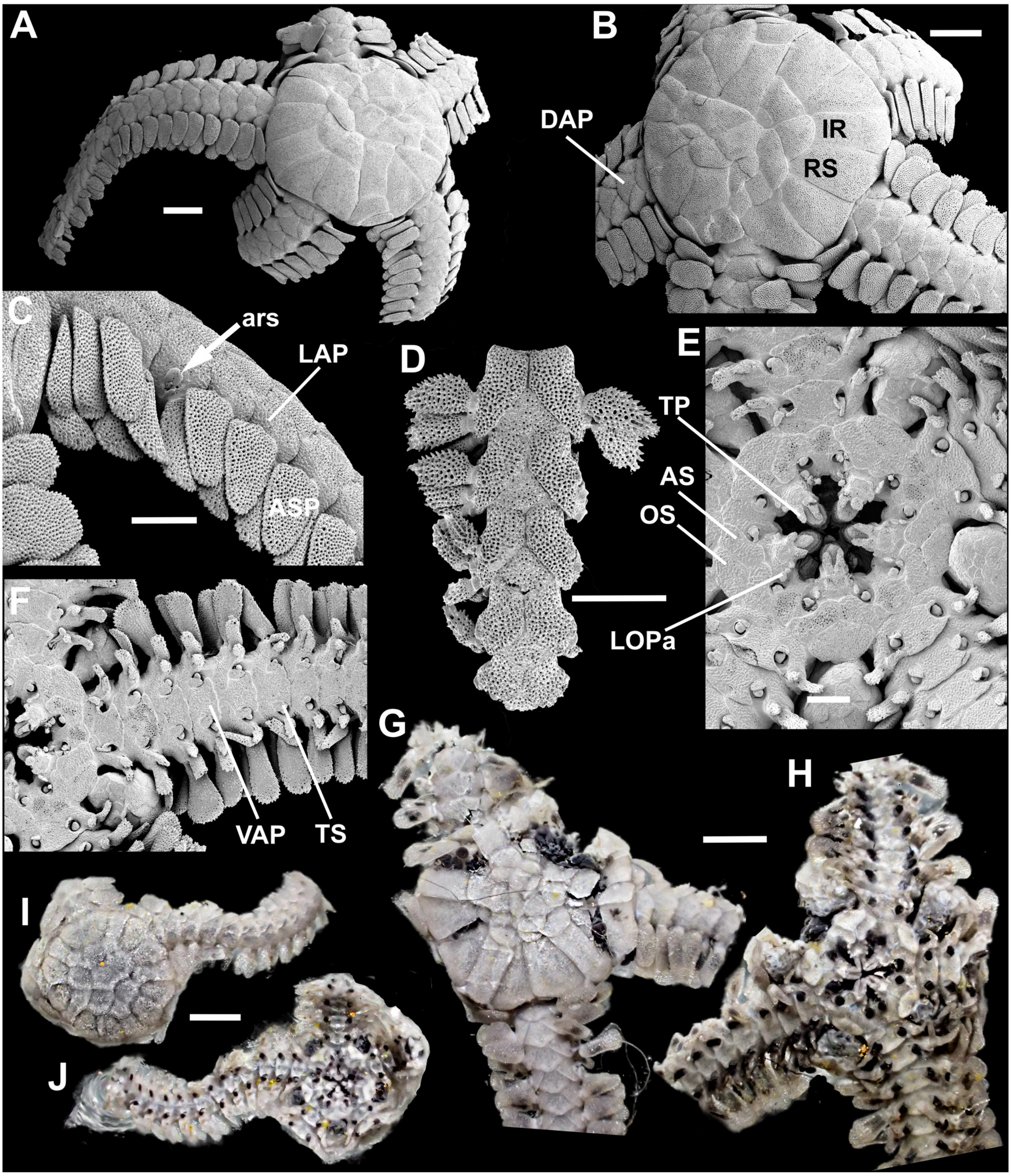

Fig. 3. *Warenophis andersi* sp. nov. **A–E**. Holotype (MNHN-IE-2023-164), SEM images. **A**. Dorsal overview. **B**. Dorsal disc and arms. **C**. Proximal arm, laterally. **D**. Distal arm, dorsally. **E**. Mouth. **F**. Ventral arm. **G–J**. Paratypes (SMNH-Type-10005), digital photos. **G, I**. Dorsal aspects. **H, J**. Ventral aspects. Abbreviations: ars = articular structure; AS = adoral shield; ASP = arm spine; DAP = dorsal arm plate; IR = interradial plate; LAP = lateral arm plate; LOPa = lateral oral papillae; OS = oral shield; RS = radial shield; TP = tooth papillae; TS = tentacle scale; VAP = ventral arm plate. Scale bars: A–B, F–J = 1 mm; C–E = 0.5 mm.

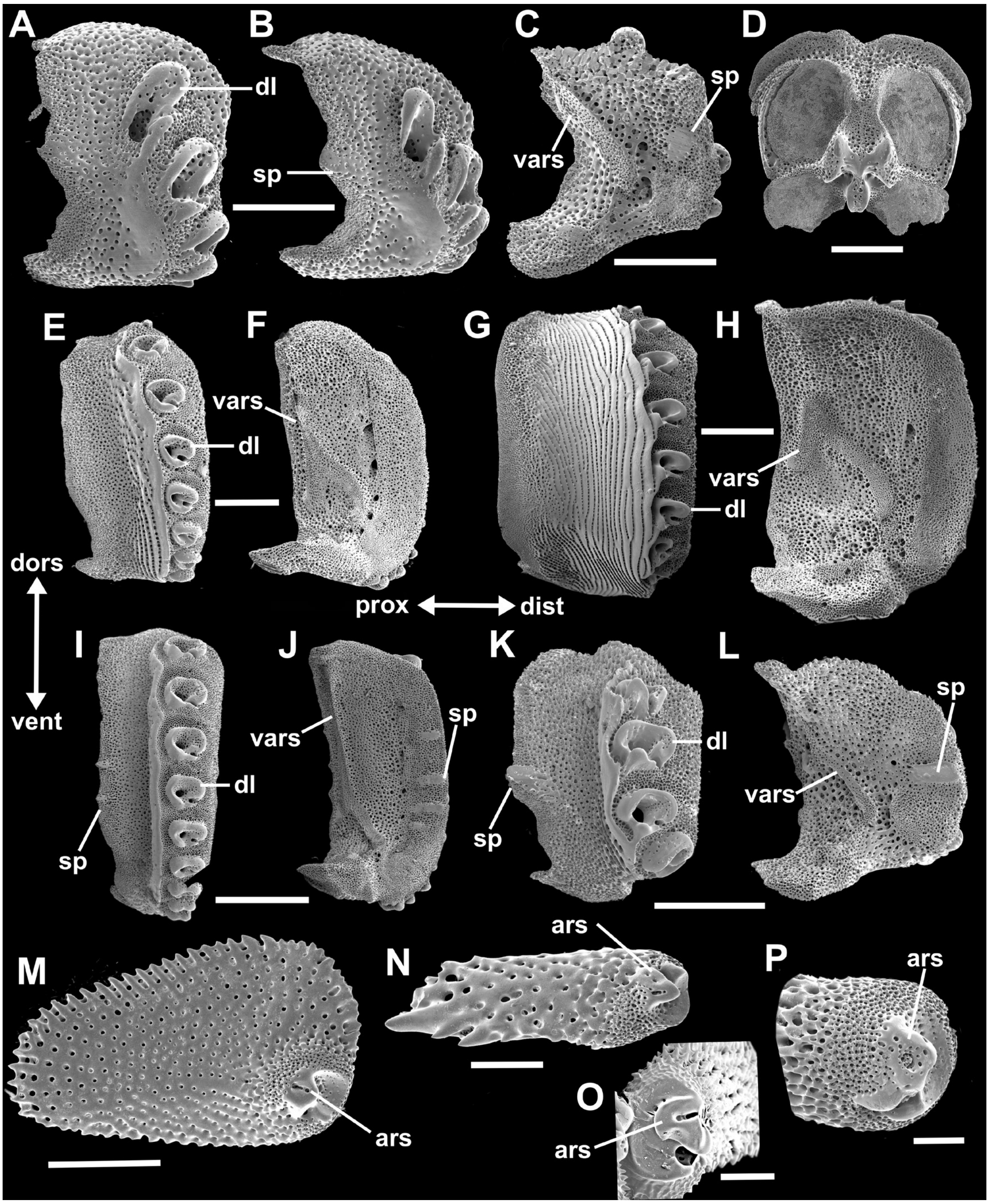

Fig. 4. Arm ossicles, SEM images. **A–D, M–N**. *Warenophis andersi* gen. et sp. nov. (SMNH-Type-10005). **A–C**. LAP. **A**. External aspect. **B**. External aspect, slightly angled. **C**. Internal aspect. **D**. Vertebra, distal face. **E–F, P**. *Ophiacantha bidentata* (Bruzelius, 1805) (SMNH-111042), LAP. **E**. External aspect. **F**. Internal aspect. **G–H**. *Ophiolimna antarctica* (Lyman, 1879) (SMNH-127060), LAP. **G**. External aspect. **H**. Internal aspect. **I–J**. *Ophiomitra leucorhabdota* (H.L. Clark, 1911) (SMNH-90622), LAP. **I**. External aspect. **J**. Internal aspect. **K–L, O**. *Ophiocopa spatula* Lyman, 1883 (SMNH-131566), LAP. **K**. External aspect. **L**. Internal aspect. **M**. Dorsal spine. **N**. Ventral spine. **O**. Arm spine. **P**. Arm spine. Abbreviations: ars = articular structure; dist = distal; dl = dorsal lobe; dors = dorsal; LAP = lateral arm plates; prox = proximal; sp = spur; vars = vertebral articular structure; vent = ventral. Scale bars: A–D, M = 250 µm; E–J = 1 mm; K–L = 0.5 mm; N–P= 100 µm.

Remarks

The taxonomic affinities of *Warenophis andersi* gen. et sp. nov. can be narrowed down to two families, Ophiacanthidae and Ophiotomidae. These are closely related and share numerous characters. All known ophiotomid genera have disc spines or granules, but the ophiacanthid genus *Ophiohamus* O'Hara & Stöhr, 2006 completely lacks disc armament, thus resembling the new species (O'Hara & Stöhr 2006). The flat, serrated arm spines of *W. andersi* are similar to those of Ophiotomidae, particularly *Ophiocopa* Lyman, 1883 and *Ophiopristis* Verrill, 1899. The analysis of the lateral arm plates showed that both families have a tendency to a tongue-like extension of the dorsal lobe of the spine articular structures (Fig. 4E, G, I, K), particularly obvious in *Ophiolimna* (Fig. 4G). The sigmoidal fold that is typical for the order Ophiacanthida is weakly expressed in the new species. The LAP of *W. andersi* has a proximal spur, which is more similar to Ophiotomidae than to Ophiacanthidae. Ophiotomidae LAPs have less conspicuous striations than those of Ophiacanthidae or they are limited to a small area, the new species lacks striations. The wavy border along the row of spine articulations on the LAPs is missing in *W. andersi*, but a slight elevation is present. The vertebral articular structure on the inner surface of the LAPs has the shape of a digit one (Numberger-Thuy & Thuy 2020) or an upside down check mark in Ophiacanthidae (Fig. 4F, H), but has an elongated dorsal extension in some Ophiotomidae, e.g., in *Ophiomitra leucorhabdota* (Fig. 4I), and in the new species it is a diagonal ridge, similar to *Ophiocopa spatula* (Fig. 4C, L). This ridge could be homologous to the long part of the digit one or a shortened version of the ophiotomid ridge, with the short downwards pointing proximal part missing. The articular structures on the arm spines are similar between the new species and *Ophiacantha* and *Ophiocopa* (Fig. 4M–P), perhaps slightly more similar to *Ophiocopa*. The evidence gathered from the new species is inconclusive, but Ophiacanthida is the most likely order. Ophiacanthidae is polyphyletic, and Ophiotomidae may need to be revised due to its type species appearing to be an ophiacanthid (O'Hara, unpubl. data). Family placement is proposed as incertae sedis until more data are available and the taxonomic issues with these families have been resolved.

The Bayesian phylogenetic inference places *W. andersi* gen. et sp. nov. on the same major branch as Ophiacanthida, but not close to Ophiacanthina O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017 (Fig. 5). The tree is more comb-shaped within the clade that holds the Ophiacanthina and its allies, compared to the tree inferred from the dataset excluding *W. andersi* (Fig. 6). The addition of the new species to the dataset has caused Ophioleucida O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017 to form a sister group to the rest of the clade, albeit still paraphyletic for Ophiernidae O'Hara, Stöhr, Hugall, Thuy & Martynov, 2018, and the Ophiodermatina Ljungman, 1867 are left paraphyletic for Ophiomyxidae Ljungman, 1867. *Ophiocopa spatula* is morphologically similar to *Ophiocamax vitrea* Lyman, 1878 and thus clusters with Ophiocamacidae O'Hara, Stöhr, Hugall, Thuy & Martynov, 2018, leaving the Ophiotomidae paraphyletic. The addition of more species (*Ophiactis profundi* Lütken & Mortensen, 1899, two *Ophiolimna*, and *O. spatula*) has caused small changes in the tree structure and node support values, compared to previously published versions of the dataset (Thuy & Stöhr 2016; Stöhr 2024), but the division into major clades is the same. The dataset for *W. andersi* is incomplete and lacks all inner disc skeletal characters, because a lack of material did not allow the sacrifice of a specimen for dissociation of the disc ossicles. The homologies of the oral papillae could not be assessed, since the necessary ontogenetic series is not available, but the proximal papillae below the teeth were interpreted as tooth papillae and it is assumed that there should be infradental papillae and an adoral shield spine at the second tentacle scale. Incomplete data can have a negative effect on the analysis, as was also observed in the test run with only LAP characters (Supp. file 2), which resulted in a comb-shaped tree structure with broken up Amphilepidida O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017. Only the Ophiacanthida still formed a clade similar to the complete analysis, and *W. andersi* is confirmed in the clade that contains the Ophiacanthida, but not within that order. Molecular data may also be needed, but the type material is suspected to have been preserved in denatured ethanol originally and none of the unique specimens could be sacrificed with such uncertain expected outcome.

Discussion

Reconciling the phylogeny of the Ophiuroidea, mostly inferred from molecular data, with its classification into formal taxon categories such as genera and families, is difficult and still highly incomplete. Placing new species in badly delimited higher taxa would add unnecessary confusion. *Warenophis* gen. nov. shares characters with two polyphyletic families (Ophiacanthidae, Ophiotomidae) and molecular data may be needed to resolve its phylogenetic position. "*Ophiomitrella*" *thuyi* sp. nov. could not be placed

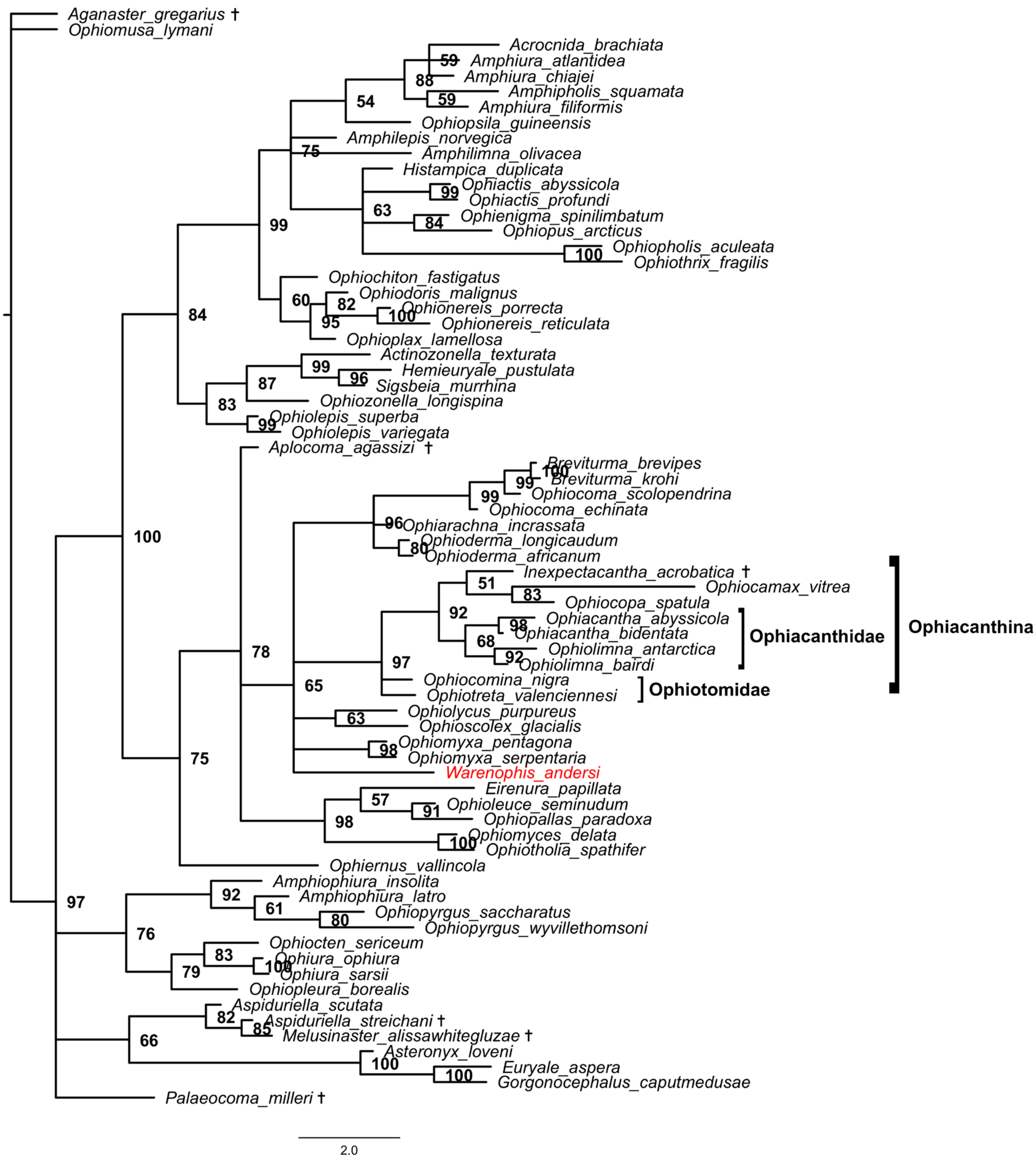

Fig. 5. Bayesian phylogenetic tree of Ophiuroidea Gray, 1840, based on morphological family level characters, showing the position of *Warenophis andersi* gen. et sp. nov. (red). Fossil species are marked by a cross. Node support values are posterior probabilities.

in a genus, because its affinities are with a genus that is both polyphyletic and invalid, since the generic type species does not show the characters that delimit *Ophiomitrella*, and it cannot at present be decided to which genus the type species belongs, due to the polyphyly of *Ophiomitrella* and Ophiotomidae. More specimens of both new species are needed to allow dissection for internal structures of the disc (e.g., genital plates) and molecular analysis. It would also be interesting to study how many specimens of *N. richeri* carry these brittle stars by examining a larger sample of crinoids.

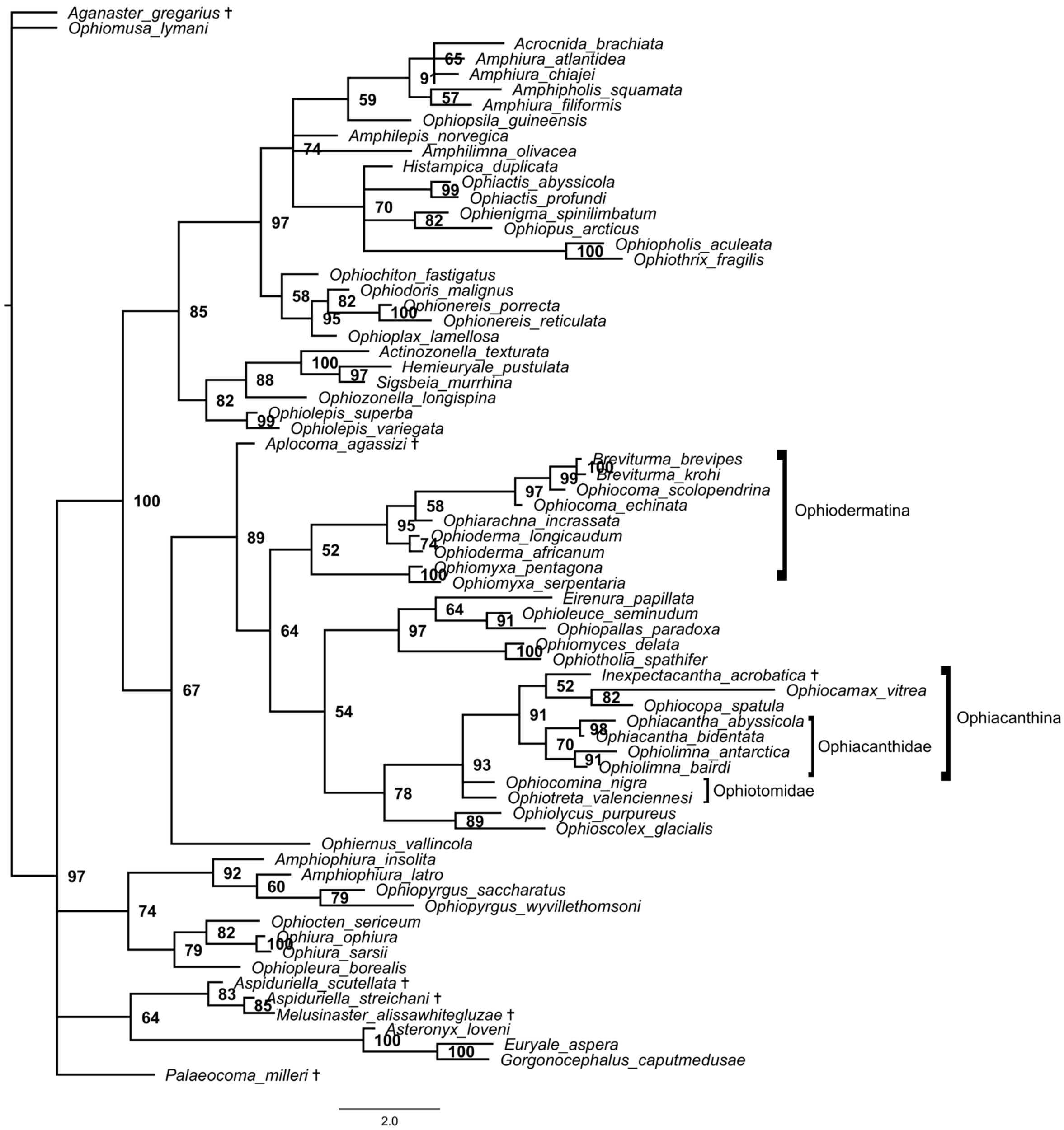

Fig. 6. Bayesian phylogenetic tree of Ophiuroidea Gray, 1840, based on morphological family level characters, *Warenophis andersi* gen. et sp. nov. omitted. Fossil species are marked by a cross. Node support values are posterior probabilities.

The possible benefits of an epizoic life-style to the ophiuroid are badly known for most species. Living on a sessile stalked crinoid limits movement for the ophiuroids, but it is currently unknown, if they can leave their host and move to a new host or live independently. Both brittle star species had the same colour as the crinoid and were thus well camouflaged, which might suggest that they are adapted to this particular host. All epizoic brittle star species found on crinoids belong to the families Ophiacanthidae or Ophiotrichidae (Table 1). Both families are generally known to be suspension feeders (Metaxas & Giffin 2004; Calero *et al.* 2018), and clinging to the crinoid arms, they may benefit from the particle flow down the arms generated by the feeding crinoid. In this context, it is surprising that two different species of ophiuroid co-exist on the same host specimen, and with several individuals each. Their reproduction mode is unknown, but there was no evidence of brooding, and the presence of different size individuals, including a juvenile, suggests several recruitment events. It would be helpful to know the occurrence frequency of the ophiuroids on the crinoids. More research is needed to understand the function or evolutionary advantage of the flat, serrated arm spines of *W. andersi* gen. et sp. nov., which would promote secure attachment to the crinoid, provide armour-like protection or even aid in filter-feeding.

Acknowledgements

I'm very grateful to Anders Warén for collecting the specimens and bringing them to my attention. The Bordau 2 research cruise took place on board RV *Alis*, May 30–June 22, 2000, led by principal investigator Bertrand Richer de Forges, in the Tonga archipelago as part of the Tropical Deep-Sea Benthos program. It operated under a permit delivered by the Kingdom of Tonga. Many thanks also to Marc Eléaume for supplying catalogue numbers for the holotypes. I'm grateful to two referees, who helped improve the manuscript.

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Supplementary files

Supp. file 1. Morphological character matrix of Ophiuroidea Gray, 1840, with commands for MrBayes. Nexus file. https://doi.org/10.5852/ejt.2025.1022.3087.13759

Supp. file 2. Bayesian phylogenetic tree of Ophiuroidea Gray, 1840, based on morphological family level characters from only lateral arm plates. Fossil species are marked by a cross. Node support values are posterior probabilities. https://doi.org/10.5852/ejt.2025.1022.3087.13761