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# Four new species and a new genus of Antarctic sea cucumbers with taxonomic reviews of *Cladodactyla*, *Pseudocnus*, Paracucumidae and *Parathyonidium* (Echinodermata: Holothuroidea: Dendrochirotida)

P. Mark O'Loughlin[1,*] (http://zoobank.org/urn:lsid:zoobank.org:author:97B95F20-36CE-4A76-9D1B-26A59FBCCE88), Melanie Mackenzie[2] (http://zoobank.org/urn:lsid:zoobank.org:author:5E3E21B9-E3DC-4836-8731-D5FD10D00CBF), Gustav Paulay[3] (http://zoobank.org/urn:lsid:zoobank.org:author:A2F155E4-7958-4E63-B36A-CAB23F190A07) and Didier VandenSpiegel[3] (http://zoobank.org/urn:lsid:zoobank.org:author:CE8C3D01-28AD-43F7-9D4F-04802E68CB1A)

[1] Marine Biology Section, Museum Victoria, GPO Box 666, Melbourne, Victoria 3001, Australia (pmoloughlin@edmundrice.org)
[2] Marine Biology Section, Museum Victoria, GPO Box 666, Melbourne, Victoria 3001, Australia (mmackenzie@museum.vic.gov.au)
[3] Florida Museum of Natural History, University of Florida, Gainesville, FL 32611–7800, USA (paulay@flmnh.ufl.edu)
[4] Biological Collection and Data Management Unit, Royal museum for central Africa, B–3080, Tervuren, Belgium (dvdspiegel@africamuseum.be)
[*] To whom correspondence and reprint requests should be addressed. E-mail: pmoloughlin@edmundrice.org

http://zoobank.org/urn:lsid:zoobank.org:pub:A7DD4099-9D59-44F5-81CB-4CD95CA1AFD5

**Abstract**

O'Loughlin, P. M., Mackenzie M., Paulay, G. and VandenSpiegel, D. 2014. Four new species and a new genus of Antarctic sea cucumbers with taxonomic reviews of *Cladodactyla*, *Pseudocnus*, Paracucumidae and *Parathyonidium* (Echinodermata: Holothuroidea: Dendrochirotida). *Memoirs of Museum Victoria* 72: 31–61.

Four new species of Antarctic sea cucumbers are described, three with author O'Loughlin: *Crucella susannae*, *Euthyonidiella huwi*, *Laevocnus katrinae*; and *Laevocnus leachmani* with authors Davey and O'Loughlin. *Pseudocnus* Panning is reviewed, and Antarctic species separated into new genus *Laevocnus* O'Loughlin. We raise the three subspecies of *Pseudocnus dubiosus*, viz. *dubiosus* (Semper), *koellikeri* (Semper) and *leoninus* (Semper), to species status. We refer *Cucumaria croceoida* Vaney to the synonymy of *Cladodactyla crocea* (Lesson). We synonymize *Dendrelasia* O'Loughlin with *Cladodactyla* Brandt, and re-describe the reassigned *Cladodactyla sicinski* (O'Loughlin). This species broods in a dorsal marsupium. The diagnoses of genus *Parathyonidium* Heding and species *Parathyonidum incertum* Heding are reviewed. The type specimens for *Parathyonidium incertum* are listed. *Parathyonidium incertum* Heding is the only known Antarctic holothuroid that is a coelomic brooder. The Paracucumidae Pawson and Fell is reviewed. Phylogenetic trees are given for species in the genera *Cladodactyla*, *Heterocucumis*, *Staurocucumis*, *Laevocnus*, *Crucella* and *Paracucumis*. Tables are provided for the species of *Cladodactyla* and *Pseudocnus*. Keys are included for the species of genus *Laevocnus* and family Paracucumidae.

**Keywords**

Bransfield Strait; South Shetland Islands; Shag Rock; South Georgia; Cladolabidae; Cucumariidae; Paracucumidae; *Cladodactyla*; *Crucella*; *Dendrelasia*; *Euthyonidiella*; *Laevocnus*; *Paracucumis*; *Pseudocnus*; coelomic brood protection; new genus; new species; synonym.

## Introduction

O'Loughlin *et al*. (2010) provided a comprehensive overview of the especially diverse Antarctic sea cucumber species with a list of 187 (including 51 until then not described). Three subsequent papers by O'Loughlin and VandenSpiegel (2010) on apodids, O'Loughlin and Whitfield (2010) on psolids, and O'Loughlin *et al*. (2013) on new species from Admiralty Bay in the South Shetland Islands have furthered our knowledge of Antarctic sea cucumbers. This fauna is predominantly endemic to south of the Antarctic Convergence. mtDNA sequence data are providing insight into additional cryptic species and synonymies, as evidenced in O'Loughlin *et al*. (2010). Recent Antarctic expeditions have continued to collect specimens of unknown species of sea cucumbers.

The BAS BIOPEARL I expedition in 2006, under the leadership of Katrin Linse on the RRS *James Clark Ross* (JR 144) to the Scotia Sea, sampled the shelf (200 and 500 m) and slope (1000 and 1500 m) of the Falkland Trough, Livingstone Island, Deception Island, Elephant Island, the South Orkney Islands, Southern Thule, South Georgia and Shag Rock. The

Linse *et al*. 2008 BIOPEARL II expedition (JR 179) sampled from 500 to 2500 m in the southern Bellingshausen and Amundsen Seas. The many sea cucumber specimens were sent on loan to Museum Victoria and were identified by Mark O'Loughlin, Melanie Mackenzie and Emily Whitfield. Two new Antarctic holothuroid species from these collections are described in this work.

An IPY–CAML expedition was conducted by NIWA from 29 January to 22 March 2008 on RV *Tangaroa* with expeditioner Niki Davey able to focus on sea cucumbers as part of her role. This voyage sampled in the Ross Sea and associated seamounts and abyssal plains. One of the new *Pseudocnus* Panning, 1949 species in this work (with authors Davey and O'Loughlin) was collected during this voyage and is included here because of our extensive review of genus *Pseudocnus*. A paper on other new sea cucumber species from this expedition and a comprehensive overview of Ross Sea holothuroids is in preparation (Davey *et al*.). A sea cucumber specimen was passed on to us from CEAMARC RSV *Aurora Australis* Voyage 3 off Adelie and George V Lands in 2007 / 2008. This single specimen is assigned to the same new *Pseudocnus* species found in the Ross Sea.

In March and April 2012 Susanne Lockhart (NOAA's US AMLR Program) participated in Expedition ANT–XXVIII/4 on RV *Polarstern* in the region of the Antarctic South Shetland Islands at shelf depths of about 50–500 m in support of the CCAMLR initiatives to detect Vulnerable Marine Ecosystems. The quantitative demersal finfish stock assessment survey provided Susanne with a rare opportunity for a quantitative assessment of Antarctic invertebrate abundance, distribution and biomass. Trawl net dimensions were measured *in situ* using a ScanMar net monitoring sonar system. A comprehensive invertebrate analysis from 64 successful trawls yielded 4,120 holothuroid specimens of which 217 lots with many hundreds of holothuroids were preserved and donated to Museum Victoria for determination. Up to 1425 sea cucumber specimens were taken per station indicating a density of up to 87,119 holothuroid specimens per square nautical mile. The subsequent identification of all specimens in Museum Victoria by Mark O'Loughlin, Melanie Mackenzie and Emily Whitfield revealed new species of which one is described here. Further papers will describe other new species and quantitative outcomes from this survey.

In O'Loughlin *et al*. (2013) new genus and species *Dendrelasia sicinski* O'Loughlin were described for a single specimen from Admiralty Bay in the South Shetland Islands. Amongst the many sea cucumbers collected by Susanne Lockhart around the South Shetland Islands (see above) there are many larger specimens that are conspecific with the smaller type specimen of *Dendrelasia sicinski* and that are also morphologically referable to *Cladodactyla* Brandt, 1835. We clarify these systematic issues.

O'Loughlin (1994) summarized knowledge on brood-protecting and fissiparous cucumariids, and O'Loughlin *et al*. (2009a) described additional examples. Reference was made in the recent paper to a species of brood-protecting *Parathyonidium* Heding, 1954 (in Heding and Panning, 1954) that is determined and discussed here as *Parathyonidium incertum* Heding, 1954 (in Heding and Panning, 1954).

We have reviewed the five relevant genera while describing new species of *Cladodactyla*, *Crucella* Gutt, 1990, *Euthyonidiella* Heding and Panning, 1954 and *Pseudocnus*, and report brood-protecting by *Parathyonidium incertum*. This systematic paper is based primarily on morphological observations, and shows generally good congruence and support from emerging genetic data. However, there are some conflicts between morphological indicators for generic referral and genetic data. We anticipate further genetic data and future comprehensive reviews of the relevant generic assignments, and await additional insight into morphology and genetic congruence before further generic re-assignments.

## Methods

Scanning electron microscope (SEM) images were taken by Didier VandenSpiegel after clearing the ossicles of associated soft tissue in commercial bleach, air-drying, mounting on aluminium stubs, and coating with gold. Observations were made using a JEOL JSM-6480LV SEM. Measurements were made with Smile view software. Tissues were sent to Gustav Paulay (UF) for sequencing and the specimen locations, tissue codes, catalogue numbers and GenBank Accession numbers are recorded in Appendix 1. A 655 bp portion of the mitochondrial gene cytochrome oxidase subunit 1 (COI) was sequenced from selected specimens using the echinoderm barcoding primers COIceF (5'-ACTGCCCACGCCCTAGTAATGATATTTTT-TATGGTNATGCC-3') and COIceR (5'-TCGTGTGTC-TACGTCCATTCCTACTGTRAACATRTG-3') (Hoareau and Boissin 2010), as described in Michonneau and Paulay 2014. Note that these echinoderm specific primers amplify positions 242 to 898 in COI compared with positions 74 to 733 amplified by Folmer primers. Sequences have been submitted to GenBank (See appendix). COI sequences were aligned by eye and analyzed using Maximum Likelihood with 100 bootstrap replicates, implemented in MEGA (Tamura *et al*. 2013).

Photos of most specimens were taken in Museum Victoria by Melanie Mackenzie, in collaboration with Mark O'Loughlin, using a Nikon D300S digital camera with 60 mm Nikkor macro lens for large specimens, and a Leica DC500 high resolution digital camera system with Auto Montage software for small specimens. The photo of *Laevocnus leachmani* Davey and O'Loughlin sp. nov. was taken by Peter Marriot (NIWA) using a Nikon DX camera with a 60 mm macro lens. The photo of a live *in situ* brood-protecting specimen of *Cladodactyla crocea* (Lesson, 1830) in the Falkland Islands was provided by Paul Brickle (SMSG). Photos of live specimens of *Cladodactyla sicinski* (O'Loughlin, 2013) and *Crucella susannae* O'Loughlin sp. nov. were taken on the RV *Polarstern* and provided by Susanne Lockhart (NOAA's US AMLR). The photo of a live *in situ* specimen of *Cladodactyla sicinski* in Fildes Bay in the South Shetland Islands was taken by Dirk Schories (UACh).

## Abbreviations

| | |
|---|---|
| AAD | Australian Antarctic Division |
| AMLR | Antarctic Marine Living Resources |

| | |
|---|---|
| ANARE | Australian Antarctic Research Expedition |
| BAS | British Antarctic Survey |
| BENTART | Integrated study of the benthonic biodiversity of Bellingshausen Sea and Antarctic Peninsula (Spain) |
| BIOPEARL | BIOdiversity dynamics: Phylogeography, Evolution And Radiation of Life |
| CCAMLR | Commission for the Conservation of Antarctic Marine Living Resources |
| CEAMARC | Collaborative East Antarctic Marine Census |
| ICZN | The International Commission on Zoological Nomenclature, or the International Code of Zoological Nomenclature, as appropriate. |
| IPY–CAML | International Polar Year–Census of Antarctic Marine Life |
| MNCN | Museo Nacional de Ciencias Naturales (Spain) |
| MNHN | Muséum national d'Histoire naturelle (Paris) |
| MOLAF | Prefix code for tissues taken from specimens at NMV |
| MOLG | Prefix code for tissues taken from NIWA specimens in the University of Genoa |
| MOLN | Prefix code for tissues taken from NIWA specimens |
| MOLSI | Prefix code for tissues taken from Smithsonian Institution specimens |
| NDMQ | Prefix code for tissues taken by Niki Davey from Macquarie Island specimens |
| NHMUK | British Museum of Natural History (registration number prefix NHMUK) |
| NIWA | New Zealand National Institute of Water and Atmospheric Research Ltd. (est. 1992) |
| NMV | Museum Victoria (registration number prefix F) |
| NOAA | United States National Oceanic and Atmospheric Administration |
| SMSG | Shallow Marine Survey Group (Falkland Islands) |
| UACh | Universidad Austral de Chile |
| UF | Florida Museum of Natural History, University of Florida |
| USNM | United States National Museum of Natural History, Smithsonian Institution |
| ZMUC | Natural History Museum of Denmark (Zoology); Zoological Museum, University of Copenhagen |

Numbers in brackets after registrations refer to numbers of specimens in lots.

Order **Dendrochirotida** Grube, 1840

*Remarks*. Smirnov (2012) established suborder Cucumariina for dendrochirotid families with the calcareous ring lacking segmented posterior prolongations. These included Cucumariidae Ludwig, 1894, Paracucumidae Pawson and Fell, 1965, and Thyonidiidae Heding and Panning, 1954 that was raised to family status by Smirnov (2012). No suborder was nominated for dendrochirotid families excluded from Cucumariina. These include Cladolabinae Heding and Panning, 1954 that was also raised to family status in Smirnov (2012). We do not nominate suborders of Dendrochirotida in this work.

Family **Cladolabidae** Heding and Panning, 1954 *sensu* Smirnov 2012

*Diagnosis (after Smirnov 2012)*. Tentacles 15–20 arranged in 2 or 3 circles (10+5, 10+10, 10+5+5); tube feet arranged along radii or scattered over entire body; calcareous ring segments usually entire, high, not subdivided into pieces; radial plates with forked prolongations, medium length or short, usually entire or sometimes subdivided into a few very short pieces; sometimes short forked prolongations on inter-radial segments; ossicles tables with 2 pillars, disc with few perforations and sometimes reduced making tables rod-like, convex cross-like spined plates, and rosettes.

*Remarks*. Smirnov (2012) raised the subfamily Cladolabinae Heding and Panning, 1954 to family status, and offered his opinion that "quite possibly the family is polyphyletic".

***Euthyonidiella*** Heding and Panning, 1954

*Diagnosis (after Heding and Panning 1954)*. Tentacles 15–20; tube feet in radial or scattered arrangement; calcareous ring radial plates with paired long undivided posterior prolongations; ossicles tables with 2 pillars.

*Type species*. *Euthyonidiella kyushuensis* Heding and Panning, 1954 (type locality southern Japan) (by original designation)

*Assigned species and type localities*. *Euthyonidiella ambigua* (Heding, 1942) (Tanzania); *E. dentata* Cherbonnier, 1961 (Brazil); *E. destichada* (Deichmann, 1930) (Caribbean Sea); *E. dubia* Cherbonnier, 1958 (Sierra Leone); *E. huwi* O'Loughlin sp. nov. (below; Shag Rock); *E. kyushuensis* Heding and Panning, 1954 (Kyushu); *E. trita* (Sluiter, 1910) (Caribbean Sea); *E. tungshanensis* (Yang, 1937) (Fujian Sea); *E. zacae* (Deichmann, 1938) (Galapagos).

*Remarks*. The species assigned to *Euthyonidiella* are quite similar morphologically with the exception of *Phyllophorus tungshanensis* Yang, 1937 (assigned to *Euthyonidiella* by Liao and Clark 1995), and *Euthyonidiella dubia* Cherbonnier, 1958. We question these two assignments. A specimen from NW Australia collected at 184–187 m depth (NMV F149748; UF tissue sequence code MOL AF 408) morphologically closely resembles both *Euthyonidiella kyushuensis* from south Japan and *Euthyonidiella ambigua* from east Africa. This specimen is provisionally determined as *Euthyonidiella kyushuensis*.

***Euthyonidiella huwi*** O'Loughlin sp. nov.

*Zoobank LSID*. http://zoobank.org:act:8DD8AA4E-E46C-4FDE-8A14-F796CA2B0427

Figure 1

*Material examined*. Holotype. Western Antarctica, Shag Rock, 53°38'S 40°54'W, 206 m, BAS BIOPEARL I stn SR–EBS–4, 11 Apr 2006, NMV F168650 (UF tissue sequence code MOL AF 816).

Paratypes. Type locality and date, NMV F189889 (3 small juveniles); NHMUK 2010.137–138 (2).

Other material (not *Euthyonidiella huwi*). *Euthyonidiella kyushuensis* Heding and Panning, 1954. NW Australia, 17°29'S 120°28'E, 184–187 m, RV *Southern Surveyor*, SS05/2007 stn 91, 20 Jun 2007, NMV F149748 (1) (UF tissue sequence code MOL AF 408).

*Description*. Body cylindrical, slightly pentagonal in transverse section, rounded anterior and posterior, up to 7 mm long (tentacles deeply withdrawn), up to 2 mm diameter; thin calcareous body wall with surface bristle of table spires; 20 dendritic tentacles, 5 pairs large, 5 pairs very small, latter probably in slightly inner ring; tube feet in irregular single to double radial series, some spread inter-radially; calcareous ring high, not segmented; anterior end of radial plates with deep division at muscle attachment and with lateral notch, posterior prolongations short, forked, not segmented (ring of 2 mm long paratype specimen lacking posterior prolongations); inter-radial plates with anterior taper, blunt posterior, lacking posterior prolongations; short stone canal with bean-shaped madreporite free in coelom; single tubular polian vesicle.

Body wall with abundant irregular tables: discs round to slightly oval, margins lobed around perforations, 2 large central perforations, frequently 6 (up to 14) additional perforations, perforations most numerous in smallest specimens, discs predominantly 70 $\mu$m long, up to 90 $\mu$m long; spires with 2 pillars up to 40 $\mu$m long, spinous distally, sometimes with connecting bridges distally, distal bridges sometimes with spines on mid-bridge. Tentacles with irregular thick elongate perforated plates, up to 88 $\mu$m long. Peri-anal body wall with abundant tables and internal thick knotted scale-like ossicles.

*Colour (preserved)*. White.

*COI DNA barcode of holotype:* AATAATGATCGGGGGGTTTGGGAACTGATTAATCCCACTAATGATTGGAGCACCAGACATGGCTTTTCCCCGAATGAAAAAAATGAGATTCTGACTAATCCCCCCCTCATTTATTTTACTCTTAGCTTCAGCAAGAGTAGAAAGAGGGGCAGGAACTGGTTGGACGGTATACCCCCCTCTTTCAAGAAAAATAGCTCACGCAGGAGGCTCAGTTGACTTAGCAATATTTTCCCTTCACCTAGCGGGAGCCTCATCAATTCTAGCTTCTATAAAATTTATAACTACAATAATAAAAATGCGAACCCCAGGGGTAAGTTTTGACCGACTATCCCTATTTGTGTGGTCAGTATTTATTACAGCCTTTCTTCTACTTCTGAGACTCCCAGTATTAGCCGGGGCTATAACCATGTTACTAACTGATCGTAATATTAATACAACGTTTTTTGACCCTGCGGGAGGGGGTGATCCCATATTATTTCAACATCTATTCTGATTCTTTGGTCATCCAGAAGTGTACATTCTAATCTTACCAGGCTTCGGTATGATTTCCCATGTCATTGCTCATTATAGAGGAAAGCAAGAACCCTTCGGATATTTAGGTATGGTCTATGCAATGGTAGCCATAGGTATTTTAGGATTTTTAGTTTGAGCCCAC

*Distribution*. Western Antarctica, Shag Rock, 54°S 41°W, 206 m.

*Etymology*. Named for Huw Griffiths (British Antarctic Survey), in appreciation of his role in the BAS BIOPEARL expeditions, his contribution to collecting the specimens studied here, and with gratitude for his gracious collaboration in Antarctic holothuroid research.

*Remarks*. *Euthyonidiella huwi* O'Loughlin sp. nov. is distinguished from the other species of *Euthyonidiella* by a combination of: predominantly radial occurrence of tube feet; table discs that sometimes have more than eight perforations; relatively short posterior prolongations on the radial plates of the calcareous ring. The provisionally determined specimen of *Euthyonidiella kyushuensis* from NW Australia and *Euthyonidiella huwi* from Antarctica are sister taxa among 19 sequenced sclerodactylids *sensu lato* based on CO1 sequences, although they are quite divergent from each other (K2P pairwise distance = 0.20). We observed that the calcareous ring of a 2 mm long juvenile of *Euthyonidiella huwi* lacked posterior prolongations. We recognize that the relatively short posterior prolongations in the 7 mm long holotype may represent ontogenetic change, as may the sometimes more numerous perforations in the table discs and predominantly ambulacral occurrence of the tube feet. We acknowledge the unsatisfactory element in describing a new species from a few small specimens that may represent developmental stages, but we judge that it is important to establish the occurrence of genus *Euthyonidiella* Heding and Panning in Antarctica.

Family **Cucumariidae** Ludwig, 1894

Subfamily **Cucumariinae** Ludwig, 1894 *sensu* Panning 1949

*Diagnosis*. Ten dendritic tentacles; calcareous ring lacking segmented posterior prolongations; ossicles in the body wall perforated plates, sometimes rods, never cups or tables.

***Cladodactyla*** Brandt, 1835

= *Dendrelasia* O'Loughlin (in O'Loughlin *et al*., 2013): 69–70 (new synonymy)

Table 1; figure 2

*Diagnosis (sensu stricto – see Remarks)*. Ten equal tentacles; calcareous ring calcified and evident in small specimens but de-calcified and no longer evident in larger specimens; tube feet restricted to radii; dorso-lateral radial body wall thick, soft, "spongy"; external dorsal marsupium created by elongate indentation / invagination between dorso-lateral radii, radial edges may close over a protective chamber, anterior mid-dorsal gonoduct opening in marsupium; hermaphroditic; tube feet on bivium smaller and more numerous than on trivium; respiratory trees arise from 3–4 basal sources, each with dendritic branches; mid-body wall ossicles absent in larger specimens; peri-anal ossicles include prominently spinous, single-layered, perforated plates.

Table 1. Species currently assigned to *Cladodactyla*, occurrence, and contrasting morphological characters.

| Species | Occurrence | Dorsal marsupium | Tentacles | Calcareous ring | Body wall ossicles |
|---|---|---|---|---|---|
| C. *brunspicula* Thandar, 2008 | South Africa | Lacking | 10 equal; with rosettes | calcified | plates with small to filled perforations |
| C. *crocea* (Lesson, 1830) | Falkland Islands | Present | 10 equal, lacking rosettes | not calcified in larger specimens | lacking in larger specimens |
| C. *monodi* Cherbonnier, 1950 | Cameroon | Lacking | 2 small ventral, lacking rosettes | calcified | perforated plates |
| C. *senegalensis* Panning, 1940 | Senegal | Lacking | 2 small ventral; lacking rosettes | calcified | perforated plates |
| C. *sicinski* (O'Loughlin, 2013) | South Shetland Islands | Present | 10 equal, lacking rosettes | not calcified in larger specimens | lacking in larger specimens |

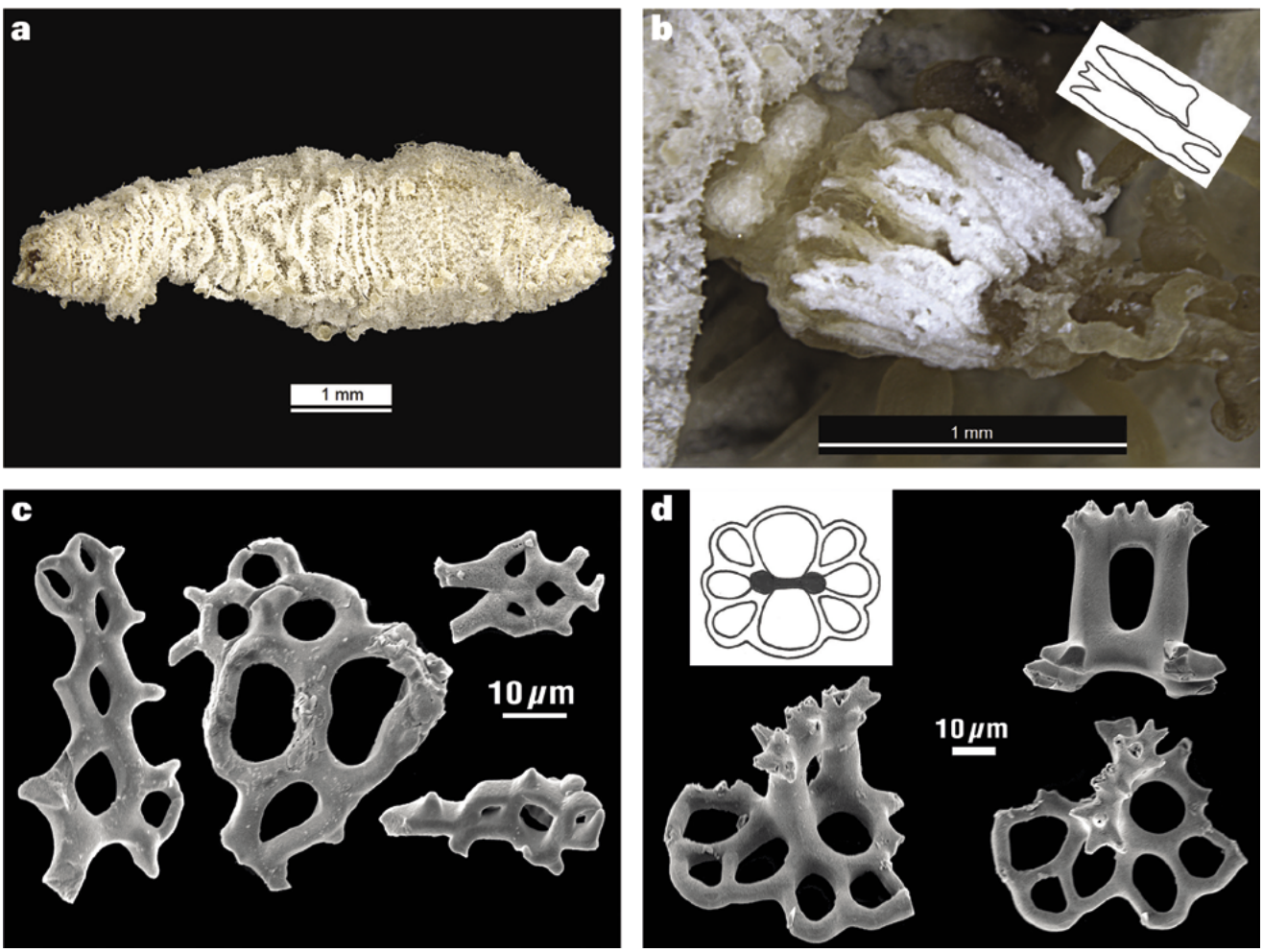


Figure 1. Holotype of *Euthyonidiella huwi* O'Loughlin sp. nov. (NMV F168650). a, preserved holotype; b, photo of calcareous ring, single polian vesicle (lower right), madreporite and stone canal (upper right) (insert: drawing of radial (bottom) and inter-radial (top) plates of the calcareous ring); c, SEM images of ossicles from the tentacles; d, SEM images of table ossicles from mid-body wall (insert: drawing of one common form of variable table discs).

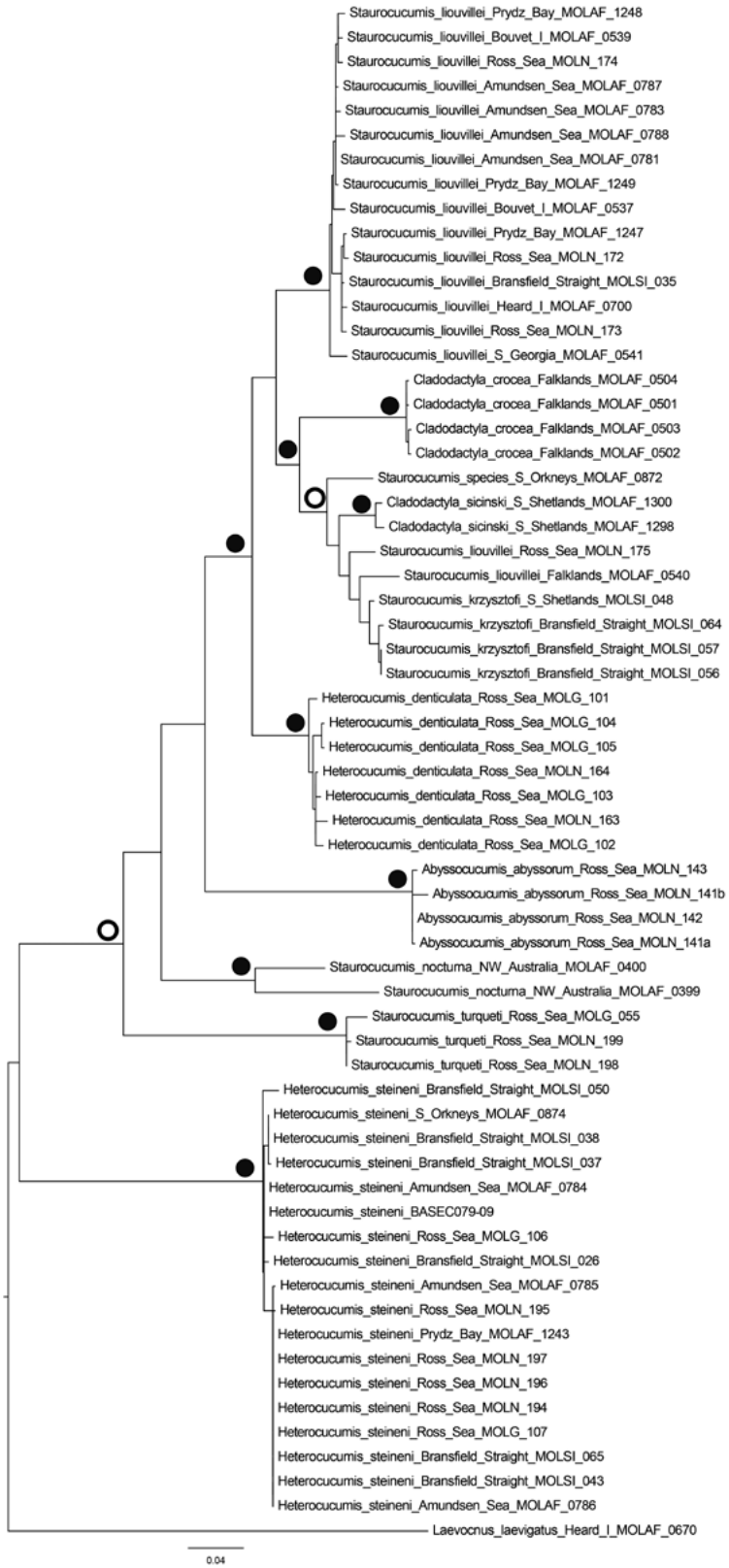


Figure 2. Maximum likelihood tree for *Cladodactyla–Heterocucumis–Staurocucumis* clade, based on COI sequences, T92+G+I model, 100 bootstrap replicates, *Laevocnus laevigatus* as outgroup. Filled circles >0.95 bootstrap support; hollow circles >0.70 bootstrap support.

*Type species*. *Holothuria crocea* Lesson, 1830 (type locality Falkland Islands (Malvinas)) (by subsequent designation (Panning 1940: 170))

*Remarks*. The availability of numerous larger specimens of *"Dendrelasia" sicinski* from the South Shetland Islands has enabled us to judge that *Dendrelasia* is a junior synonym of *Cladodactyla* (see below). We formalize the synonymy here. We base our *sensu stricto* diagnosis of *Cladodactyla* on the two species that we consider to be *Cladodactyla* in confidence: *C. crocea* and *C. sicinski*. The differences (Table 1) in the presence or absence of a dorsal external marsupium, tentacle arrangement, calcification in the calcareous ring, and ossicle forms, and the broad geographic distribution of the other included species, lead us to suspect that *Cladodactyla* as currently circumscribed may not be monophyletic.

COI sequence data from several hundred dendrochirotids (Michonneau *et al*. in prep.) recovers these two species of *Cladodactyla* in a clade with *Staurocucumis* (including *Abyssocucumis*, considered generically distinct by some (Hansen 1988, O'Loughlin 2002) but not others (Massin & Hendrickx 2011)) and *Heterocucumis*, with modest support. An analysis of this clade (Fig. 2), including samples of the type species of all four genera: *Cladodactyla crocea, Staurocucumis liouvillei, Abyssocucumis abyssorum, Heterocucumis steineni*, fails to recover these genera as monophyletic, and includes a subclade with 96% bootstrap support that has species of *Staurocucumis, Heterocucumis,* and *Cladodactyla* intermixed. Revising the generic limits of this lineage is beyond the scope of this paper. We note however that *Cladodactyla*, as the senior generic name in this assemblage, is clearly appropriate for *C. crocea* and *C. sicinski*.

***Cladodactyla crocea*** (Lesson, 1830)

Figures 2, 3, 4; table 1

*Holothuria (Cucumaria) crocea* Lesson, 1830: 153–154, pl. fig. 1.

*Cladodactyla crocea*.—Brandt, 1835: 43.—Wyville Thomson, 1878: 57–61, fig. 1.—Panning, 1957: 27–29, figs 10–13.

*Cucumaria crocea*.—Théel, 1886: 58–61, pl. 3 fig. 5, pl. 12 figs 1, 2 (see Remarks).—Ludwig, 1898: 15–24, pl. 1 figs 6–13.—Vaney, 1908a: 296.—1908b: 23–24.—Ekman, 1925: 75–81, figs 15, 16.

*Cucumaria croceoida* Vaney, 1908a: 299.—1908b: 31, pl. 5 figs 64–66.

*Cucumaria crocea* var. *croceoides*.—Ekman, 1925: 81–85, fig. 17.

*Material examined*. South-west Atlantic Ocean, Falkland Islands, *Discovery Expedition*, RRS *William Scoresby*, WS stn 231, 50°10'S 58°42'W, 159–167 m, 4 Jul 1928, NHMUK 2013.1 (1); W of Falkland Is, WS stn 867, 51°10'S 64°16'W, 148–150 m, 30 Mar 1932, NHMUK 2013.2 (1); WS stn 869, 52°16'S 64°14'W, 187 m, 31 Mar 1932, NHMUK 2013.3 (1); Falkland Is, US AMLR 2004 *Icefish* stn 17–OT20, 52°22'S 58°52'W, 78 m, S. Lockhart, 31 May 2004, NMV F105017 (4) (UF tissue sequence codes MOL AF 501, 502); *Icefish* stn 18–OT14, 52°08'S 58°05'W, 93 m, S. Lockhart, 28 May 2004, NMV F106967 (3) (UF tissue sequence code MOL AF 504); *Icefish* stn 21–OT16, 52°43'S 59°97'W, 120 m, S. Lockhart, 30 May 2004, NMV F105002 (3) (UF tissue sequence code MOL AF 503); Burdwood Bank, *Icefish* stn 5–BT4, 54°47'S 59°18'W, 303 m, S. Lockhart, 21 May 2004, NMV F160031 (1) (UF tissue code MOL AF542); Falkland Is, *Challenger* stn 315, 51°40'S 57°50'W, 9–22 m, 26–28 Jan 1876, USNM E10614 (2); Tierra del Fuego, Cape Penas, *Eltanin* stn 966, 53°40'S 66°20'W, 81 m, 10 Feb 1964, USNM E33519 (46).

*Description*. Body cylindrical, rounded orally and anally, up to 100 mm long 30 mm diameter (live, in Wyville Thompson 1878; 47 mm long preserved, in Ekman 1925); body wall soft, leathery, dorso-lateral radial body wall thick, soft, "puffy"; dorsal marsupium created by elongate indentation / invagination between dorsal radii; 10 equal tentacles; ring not calcified in larger specimens; tube feet restricted to radii in paired zig-zag rows, smaller and more numerous in dorso-lateral than in ventral radii, outer ventro-lateral rows of tube feet fewer and more spaced, dorsal tube feet absent in small specimens, often withdrawn into pits in preserved specimens; dorso-lateral radial tube feet do not cross inter-radius at anterior and posterior ends of marsupium; single polian vesicle; paired, unbranched tufts of hermaphroditic gonad tubules, genital papilla anterior mid-dorsal in marsupium; 2 respiratory trees, each divided basally into 2 sub-equal or unequal dendritic branches creating 4 trees, extending about two-thirds length of coelom.

Mid-body wall ossicles absent from largest specimens; in smaller specimens ossicles absent from marsupium wall but mid-lateral body wall with thick rods and spinous plates, rods frequently with single to numerous distal perforations, frequently with distal and lateral spines and branches, plates irregularly oval to round, with two larger central perforations, surface and margin with sharp spines, rods and plates intergrade, up to 296 $\mu$m long. Dorsal tube foot endplates up to 280 $\mu$m diameter, endplate support ossicles curved, distally perforate, spinous rods up to 136 $\mu$m long. Ventral tube feet endplates with irregular perforations, diameter about 360 $\mu$m, endplate support rods as in body wall but curved, about 168 $\mu$m long. Tentacle ossicles irregular thick rods with distal and sometimes lateral perforated extensions, with marginal denticulations around perforated parts, up to 272 $\mu$m long. Introvert lacking ossicles. Peri-anal body wall ossicles spinous rods and plates as in body wall, up to 176 $\mu$m long, and some larger oval plates with spinous margin, plates up to 240 $\mu$m long, no spinous crosses detected.

*Colour*. Live: body orange yellow, tentacles white. Preserved: body pale brown to grey to cream to pink with brown spots variably evident.

*Distribution*. South-west Atlantic Ocean, Falkland Islands (Malvinas), Burdwood Bank, Tierra del Fuego, 0–303 m.

*Remarks*. The synonymy above is selective and does not include the comprehensive list of early references provided by Ludwig 1898. Théel (1886) provided good illustrations (pl. 3 fig. 5) of the ossicles of *Cladodactyla crocea* but reported them as *Cucumaria laevigata*, and wrongly reported two small ventral tentacles for *Cladodactyla crocea*. Lampert (1886) was confused in his discussion of *Cucumaria crocea* and illustrated ossicles of *Pentactella laevigata* Verrill, 1876. *Cladodactyla crocea* is distinguished from the other *Cladodactyla* species by the combination of: presence of a

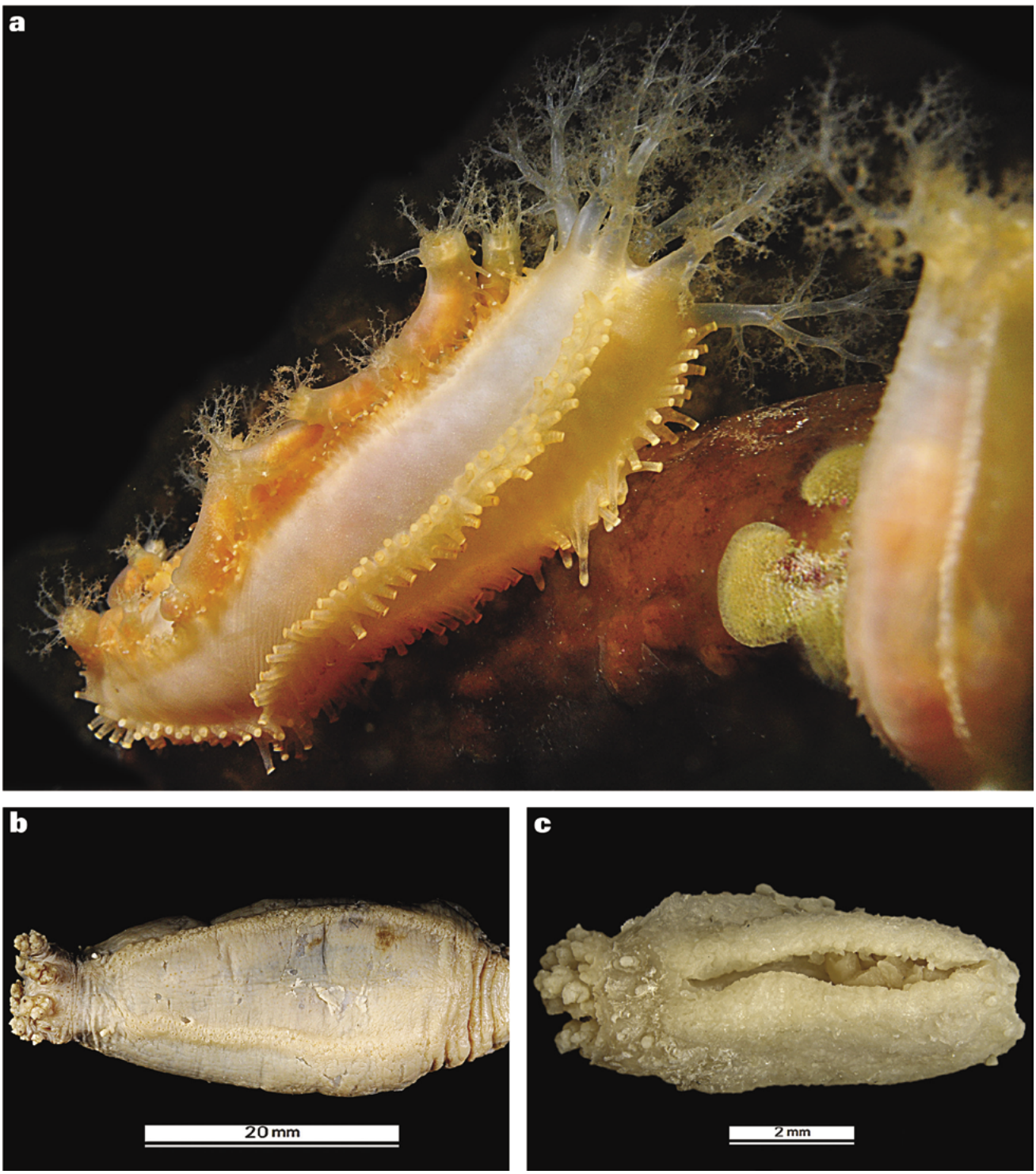


Figure 3. *Cladodactyla crocea* (Lesson, 1830). a, *in situ* photo of lateral view of live specimen with juveniles on the dorsal marsupium (Falkland Islands; photo by SMSG); b, dorsal view of 35 mm long preserved specimen showing thickened marsupial dorsal radial rims with numerous very small tube feet (NMV F105017); c, dorsal view of 8 mm long preserved specimen showing invaginated marsupium with enclosed embryos (NMV F160031).

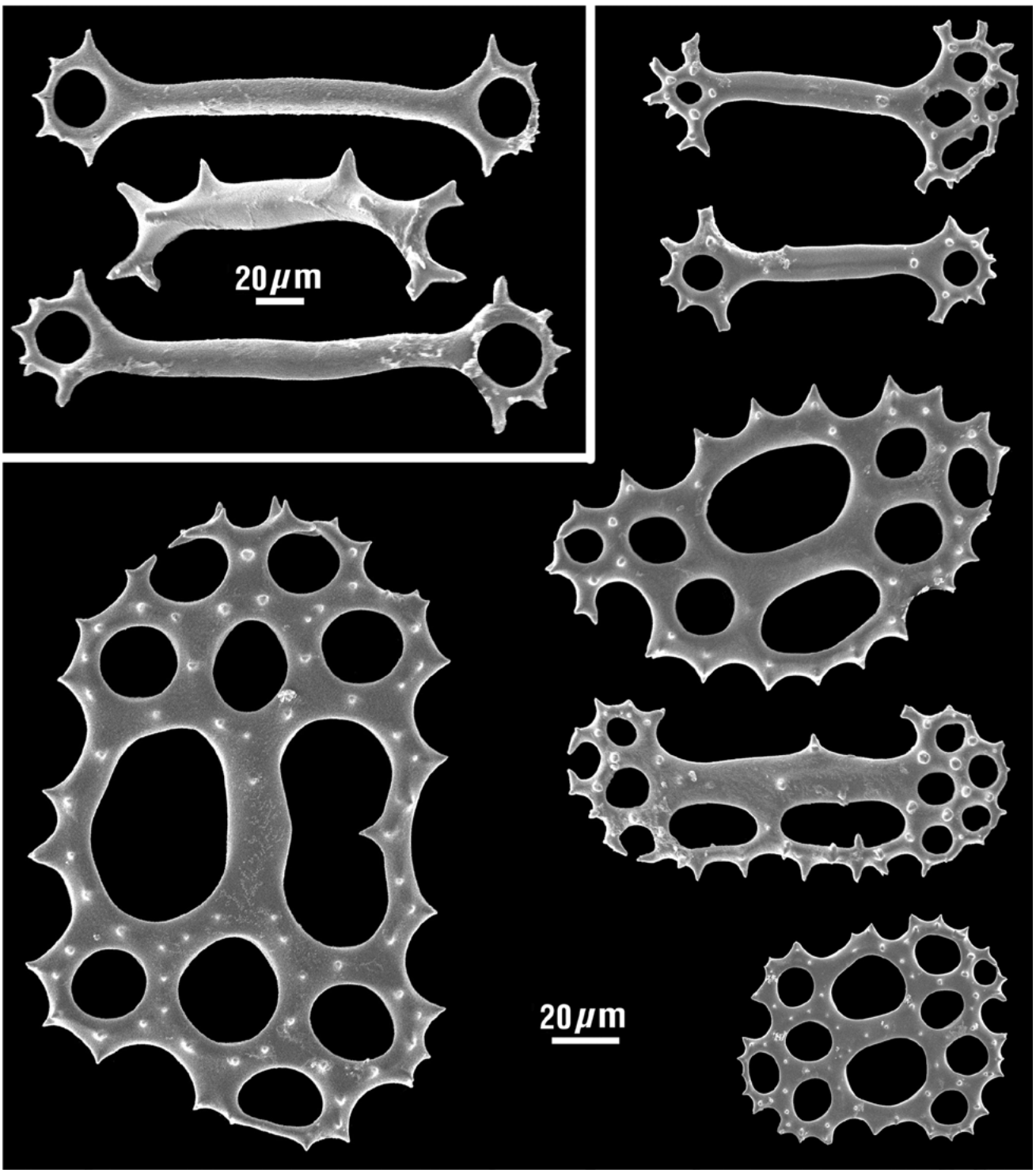


Figure 4. SEM images of ossicles from specimens of *Cladodactyla crocea* (Lesson, 1830). Main figure with spinous rods and plates from the dorso-lateral body wall of a 15 mm long specimen (NMV F105002); top left box with spinous rods from the lateral body wall of a 28 mm long specimen (NMV F106967).

dorsal external marsupium; dorso-lateral radial tube feet series not continuous anteriorly and posteriorly across the dorsal inter-radius to create a complete border to the marsupium; 10 equal tentacles; tentacle ossicles rods not plates; absence of introvert ossicles; presence of tube feet support rod ossicles; lack of spinous crosses in the peri-anal body wall.

Ekman (1925) found variations in body wall ossicle form, and in the presence or absence of ossicles, in specimens that he judged to be *Cucumaria crocea* and *Cucumaria croceoida* Vaney, 1908. Ekman could distinguish two groups, but acknowledged that there was an overlap, and thus relegated Vaney's species to a variety of Lesson's. We observed similar variations among specimens of *Cladodactyla crocea*, and thus judge that the variety *croceoides* should not have formal status and refer it to the synonymy of *Cladodactyla crocea*.

***Cladodactyla sicinski*** (O'Loughlin, in O'Loughlin et al., 2013)

*Dendrelasia sicinski* O'Loughlin (in O'Loughlin *et al*.), 2013: 70–73, figs 1–3.

Figures 2, 5, 6, 7, 8; table 1

*Material examined*. Holotype of *Dendrelasia sicinski*. Western Antarctica, South Shetland Islands, King George Is, Admiralty Bay, 200–250 m, P. Presler and J. Siciński, 1 Mar 1980, NMV F189855.

Other material. Western Antarctica, Elephant I., 61.26°S 54.90°W, 158 m, RV *Polarstern* ANT–XXVIII/4 stn 191, 18 Mar 2012, NMV F193767 (1); 61.20°S 54.90°W, 63 m, *Polarstern* ANT–XXVIII/4 stn 190, 18 Mar 2012, NMV F193770 (1); 61.34°S 55.49°W, 155 m, stn 195, 19 Mar 2012, NMV F193768 (1); 60.88°S 55.45°W, 243 m, stn 208, 21 Mar 2012, NMV F193769 (1); 60.98°S 55.69°W, 92 m, stn 229, 24 Mar 2012, NMV F193771 (5); 61.14°S 55.69°W, 78 m, stn 230, 24 Mar 2012, NMV F193766 (1) (UF tissue sequence code MOL AF 1298); South Shetland Is, 62.33°S 60.49°W, 119 m, stn 253, 29 Mar 2012, NMV F193772 (3) (UF tissue sequence code MOL AF 1300).

*Description (emended)*. Body fusiform, cylindrical in mid-body, tapers roundly at both ends; preserved body up to 70 mm long, 28 mm diameter; body wall thin to thick, soft, leathery; 10 equal dendritic tentacles; calcareous ring evident and calcified in small specimens, but becoming decalcified in 15 mm long specimen, and thus no longer evident in larger specimens; dorso-lateral radial body wall thick, soft; tube feet on dorso-lateral radii in paired close zig-zag rows on each radius, series extended across dorsal inter-radius anteriorly and posteriorly to border an external brood-protecting marsupium, dorso-lateral radial tube feet smaller and more numerous than ventral tube feet, tube feet on dorso-lateral radii may be withdrawn into pits; tube feet on trivium larger and fewer than on bivium, ventral radial series in paired zig-zag rows, fewer in outer rows of ventro-lateral series; shallow median groove in flat longitudinal muscles; single polian vesicle; paired, un-branched tufts of hermaphroditic gonad tubules, gonoduct opens at pore in mid-anterior marsupium; lacking male genital papilla; respiratory trees arise from 3–4 basal sources, each with dendritic branches, extending about half length of coelom.

Larger specimens lack mid-dorsal and mid-ventral body wall ossicles; 15 mm long specimen with prominently spinous rod, X-shape, Y-shape and branched forms up to 136 $\mu$m long. Tentacle ossicles predominantly perforated plates, some rods; plates thin, irregular, with denticulate margins, sometimes with fine surface spines, and larger central perforations; rods frequently with distal and lateral perforate developments and denticulate margin; plates and rods both up to 200 $\mu$m long. Introvert lacking ossicles. Dorsal tube feet endplates up to 480 $\mu$m diameter; tube foot support plates oval to sub-rectangular to pear-shaped to half-moon shaped, 2 large perforations centrally, margin denticulate to spinous to smooth, some with fine surface spines, up to 160 $\mu$m long. Ventral tube foot endplates up to 960 $\mu$m diameter, outer rim of endplate comprises fused irregular branched rods, not perforations, central perforations slightly larger than outer ones, tube foot support plates oval with surface and marginal spinelets, surface sometimes smooth, 4 large central perforations, 2 largest perforations adjacent, 2 smaller distal perforations, up to 208 $\mu$m long. Peri-anal body wall with plates, crosses, rods; single-layered perforated anal plates up to 320 $\mu$m wide, plates irregularly oval with marginal spines or denticulations, with or lacking surface spines, frequently 4 large central perforations in cross formation as described above; amongst the body wall ossicles small clusters of irregular distally spinous crosses of variable rod thickness, arms frequently bifid, sometimes with branches joined to create 8 perforations and slightly concave sub-rectangular plates, crosses up to 112 $\mu$m long; rare spinous or denticulate rods, with or without distal perforations, up to 96 $\mu$m long; all three peri-anal ossicle forms inter-grade.

*Colour*. Live: body and tentacles pale yellow, oral disc red. Preserved: body variably off-white to pale grey-brown; tentacle discs with paired brown markings anterior to each tentacle, sometimes fine brown spotting on the oral disc.

*Distribution*. Western Antarctica, South Shetland Is, Elephant I., 63–250 m.

*Remarks*. The SEM images of peri-anal ossicles in the recent Susanne Lockhart collection of larger specimens of a species of *Cladodactyla* from the South Shetland Islands are distinctive. They are identical in general shape and form with the peri-anal ossicles from a smaller specimen from Admiralty Bay in the South Shetland Islands illustrated in O'Loughlin *et al*. 2013 for the new genus and species *Dendrelasia sicinski* O'Loughlin, 2013. The small specimen from Admiralty Bay is morphologically conspecific with the larger specimens of the recent Lockhart collection. *Dendrelasia* is a junior synonym of *Cladodactyla*.

In specimens of *Cladodactyla sicinski* there is a distinct dorsal external marsupium. Indentations present in the soft inter-radial dorsal body wall within the marsupium suggest a prior presence of embryos or juveniles. *Cladodactyla sicinski* is distinguished from the other *Cladodactyla* species by the combination of: presence of a dorsal external marsupium; dorso-lateral radial tube feet series continuous anteriorly and posteriorly across the dorsal inter-radius to create a complete border to the marsupium; 10 equal tentacles; tentacle ossicles predominantly plates; absence of ossicles in the introvert; presence of tube feet support plate ossicles; presence of spinous crosses in the peri-anal body wall.

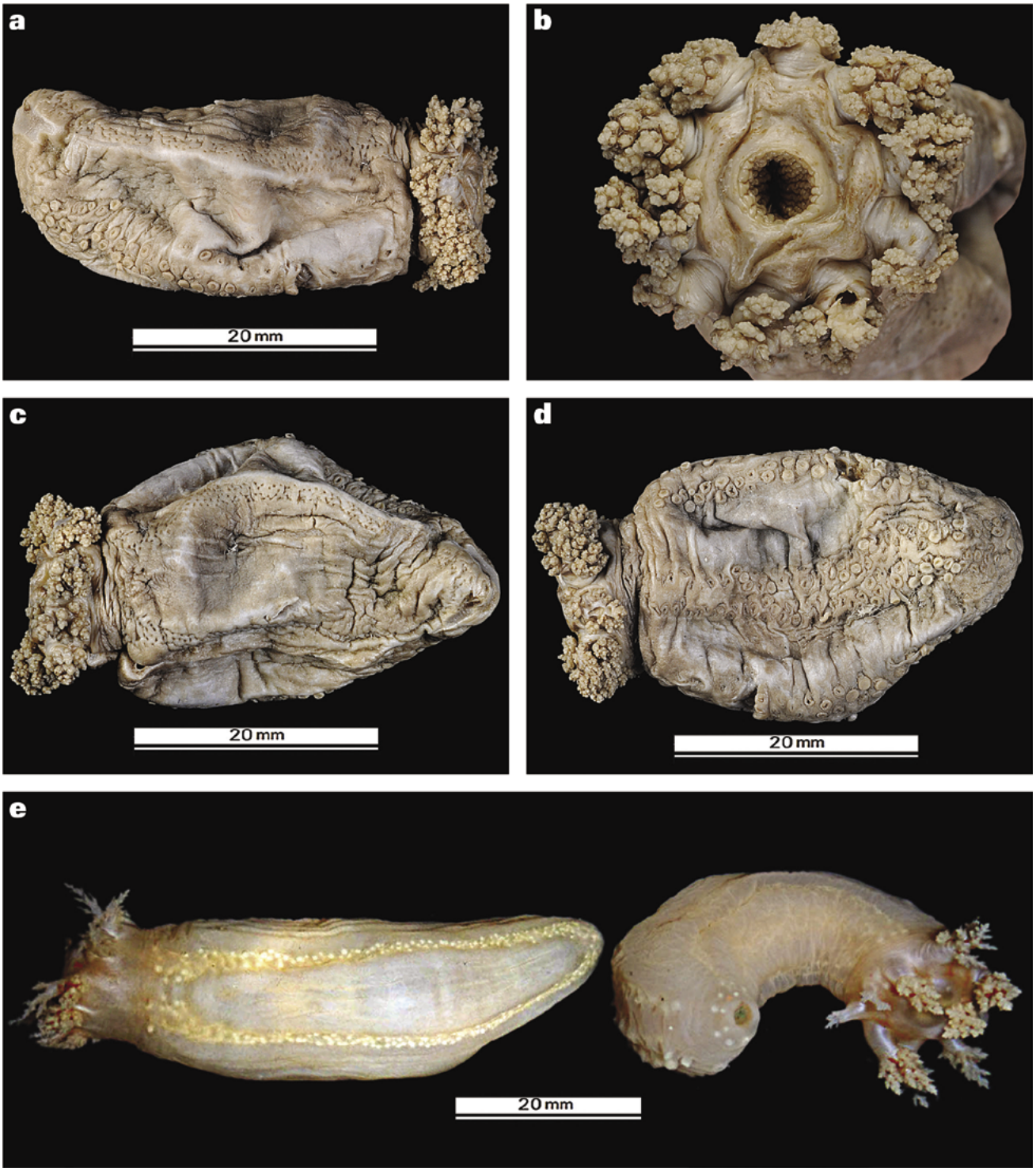


Figure 5. *Cladodactyla sicinski* (O'Loughlin, 2013) (preserved specimen, NMV F193767). a, right lateral view; b, tentacles; c, dorsal view (marsupium surface); d, ventral view; e, photos of two live specimens (South Shetland Islands; NMV F193772; photos by Susanne Lockhart).

***Pseudocnus*** Panning, 1949

Figure 9; table 2

*Pseudocnus* Panning, 1949: 422–425.—Panning, 1951: 73–80.—Panning, 1962: 57–80.—Thandar, 1987: 288–289.—Lambert, 1998: 474–476.—O'Loughlin and Alcock, 2000: 4.

*Diagnosis (sensu stricto* – see Remarks). Ten equal dendritic tentacles; tube feet in radial series, additional smaller tube feet scattered in inter-radii; ossicles in body wall of two forms, knobbed buttons typically regular in form with four perforations and lacking marginal spines at one end, and single-layered knobbed plates with spines at one tapered end; tentacles with perforated plates, rod-like plates and rosettes.

*Type species*. *Cucumaria koellikeri* Semper, 1868 (type locality Mediterranean Sea) (original designation by Panning 1949). Panning (1962) proposed an invalid re-designation of *Cucumaria dubiosa* Semper, 1868 as type.

*Remarks*. Panning (1949) designated *Cucumaria koellikeri* Semper, 1868 (type locality Mediterranean Sea) as type species of his new genus *Pseudocnus*. Subsequently Panning (1962) came to believe that his re-description (Panning 1949) of *Cucumaria dubiosa* Semper, 1868, as another species of *Pseudocnus*, was based on a specimen also belonging to *C. koellikeri*. This was rectified in Panning (1962) when synonymies and full descriptions of both *P. dubiosus* and *P. koellikeri* were given and Panning proposed, invalidly, to change the type of *Pseudocnus* to *Cucumaria dubiosa* (type locality Peru). The diagnostic description in Panning (1949) of

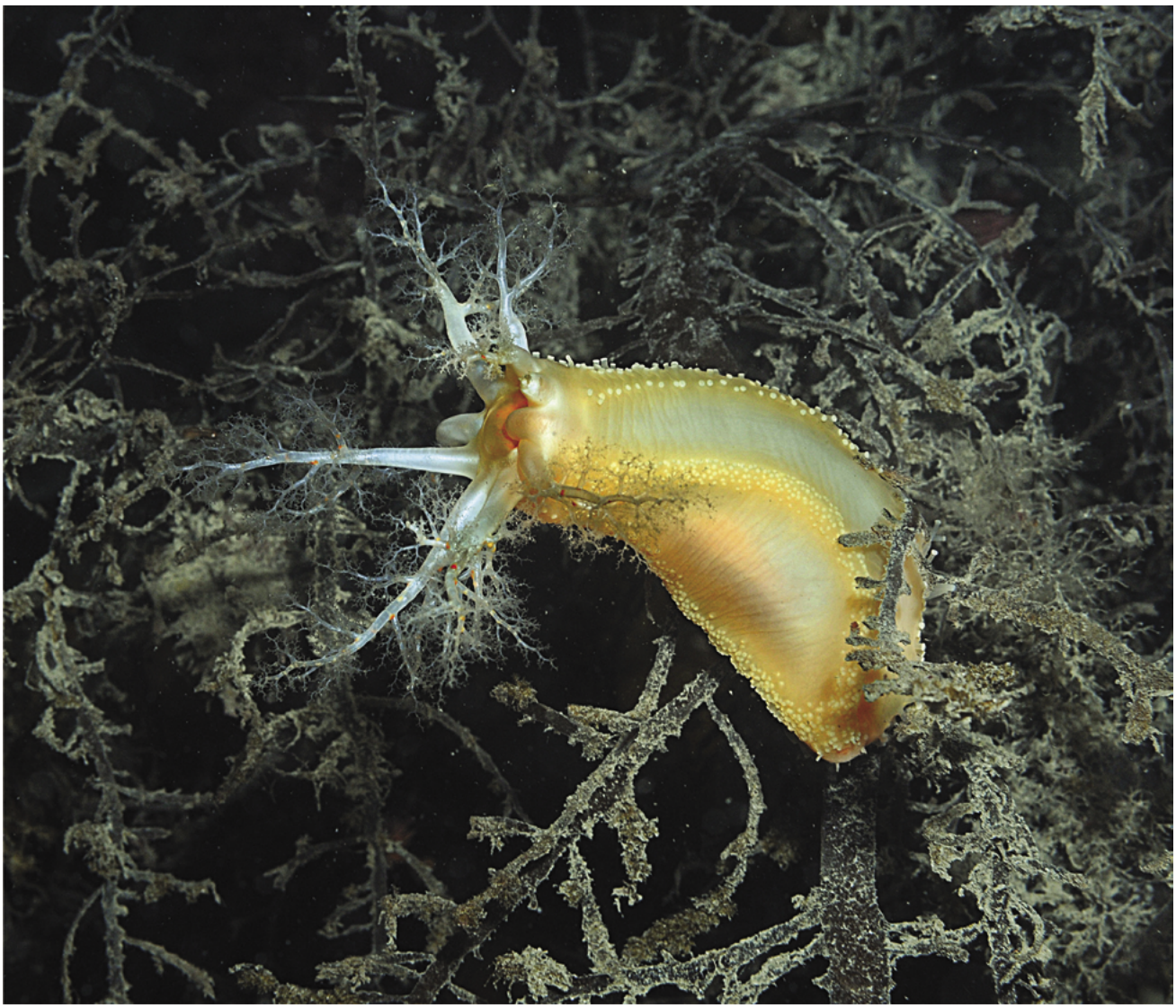

Figure 6. Photo of a live specimen of *Cladodactyla sicinski* (O'Loughlin, 2013) *in situ* in Fildes Bay on King George Island in the South Shetland Islands (photo taken by Dirk Schories (UACh) and used with permission).

*Pseudocnus koellikeri* (Semper, 1868) was accurate. A significant diagnostic difference between these two species is that *Pseudocnus dubiosus* has eight large and two small tentacles, while *Pseudocnus koellikeri* has 10 equal tentacles. Our *sensu stricto* diagnosis of *Pseudocnus* is based on the descriptions of the type species *Cucumaria koellikeri* by Koehler (1921, 1927) and Panning (1949, 1962).

Panning (1949) described, then revised (1962), *Pseudocnus*. In his revision he considered five taxa to be sub-species, all within his "*dubiosus* group": *Pseudocnus dubiosus africanus* (Britten, 1910) (junior synonym of *Pseudocnella insolens* (Théel, 1886) by Thandar 1987); *Pseudocnus dubiosus dubiosus* (Semper, 1868); *Pseudocnus dubiosus jaegeri* (Lampert, 1885) (junior synonym of *Pseudocnella sykion* (Lampert, 1885) by Thandar 1987); *Pseudocnus dubiosus koellikeri* (Semper, 1868); *Pseudocnus dubiosus leoninus* (Semper, 1867). On the basis of significant morphological differences (see Table 2 and new genus below) we raise three of these sub-species to species status: *P. koellikeri*, *P. dubiosus* (s.s.), and *P. leoninus*. As noted above Thandar (1987) transferred the remaining two to *Pseudocnella* Thandar, 1987.

Deichmann 1941 stated that *Cucumaria salmini* Ludwig, 1875 (type locality: Sulawesi, Indonesia) was probably a junior synonym of *Cucumaria leonina* Semper, 1867 (assumed type locality: "Singapore"), because of their similarity and presumed proximity of occurrence, rejecting Ekman's 1925 conclusion that the type locality for *Cucumaria leonina* was in error. Panning 1962 however, reaffirmed Ekman's 1925 conclusion, noting that the type was preserved in "rum from Singapore", and considered the type locality for *C. leonina* to be around the Falkland Islands (Malvinas). Ludwig (1875) likened the ossicles of his *C. salmini* to Semper's 1868 *C. dubiosa*, and referred to the illustration of a distally spinous plate and knobbed button in Semper's figures. *C. leonina* also has this ossicle combination. While we have not restudied the type of *C. salmini* we consider it unlikely that this tropical Pacific species would be conspecific with a sub-antarctic South American species. We thus raise *Pseudocnus salmini*

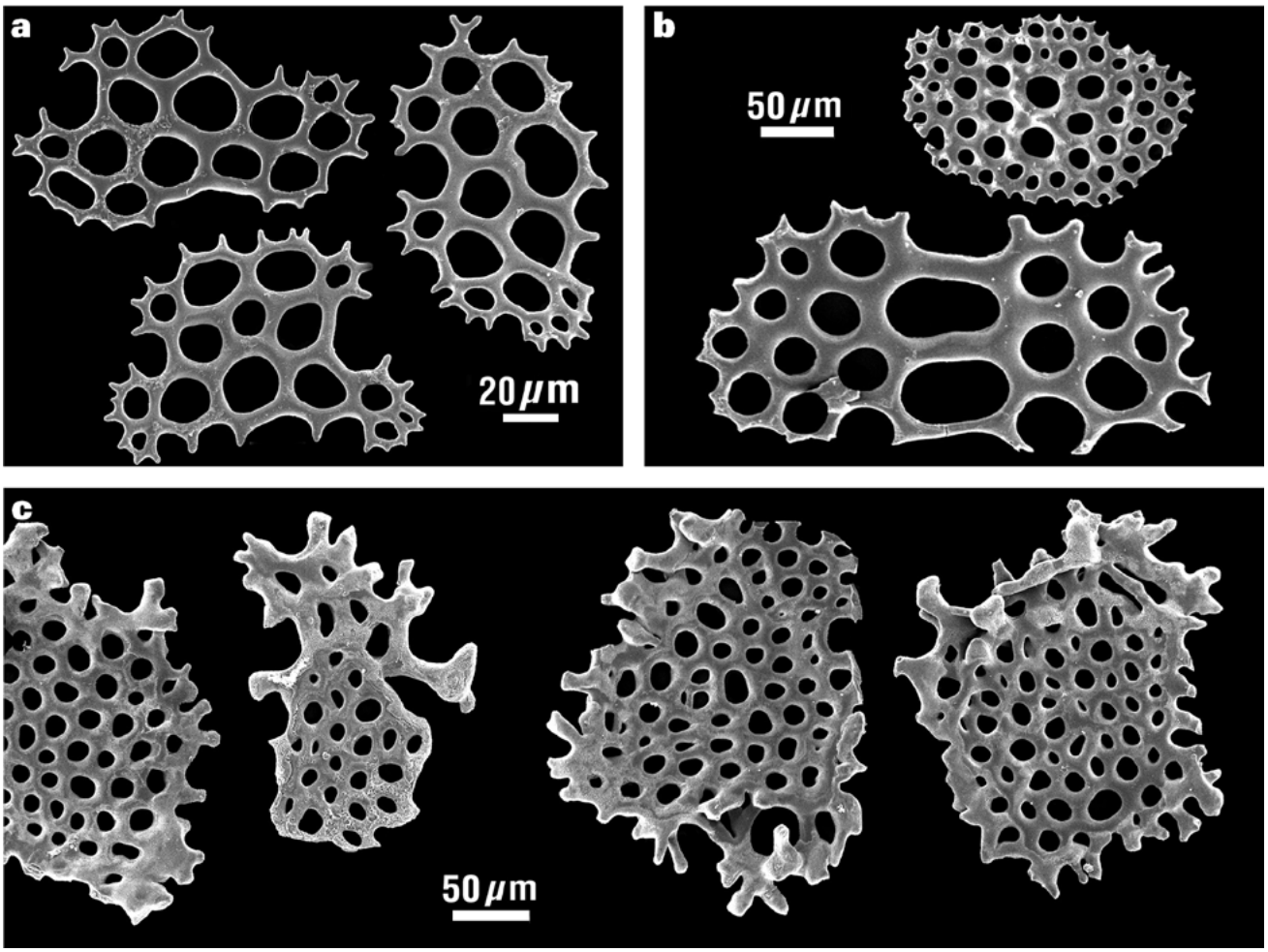


Figure 7. SEM images of ossicles from specimen of *Cladodactyla sicinski* (O'Loughlin, 2013) (NMV F193767). a, tentacle ossicles; b, ventral tube foot ossicles with presumed to be residual body wall plate (top) and tube foot support plate (bottom); c, ventral tube foot endplate fragments with rim of fused outer marginal support rods.

out of synonymy (by Deichmann 1941) with *Pseudocnus leoninus*. We provisionally refer *P. leoninus* to the new genus (below) on the bases of supportive genetic data and sub-Antarctic occurrence. We do not refer *P. salmini* to the new genus for three reasons: Ludwig (1875) likened the ossicles to those of *C. dubiosa*; tropical occurrence; absence of any indicative genetic data.

Panning (1962) created two groups of species assigned to *Pseudocnus* Panning, 1949: those with both distally spinous pine-cone-shaped knobbed plates and knobbed buttons in the

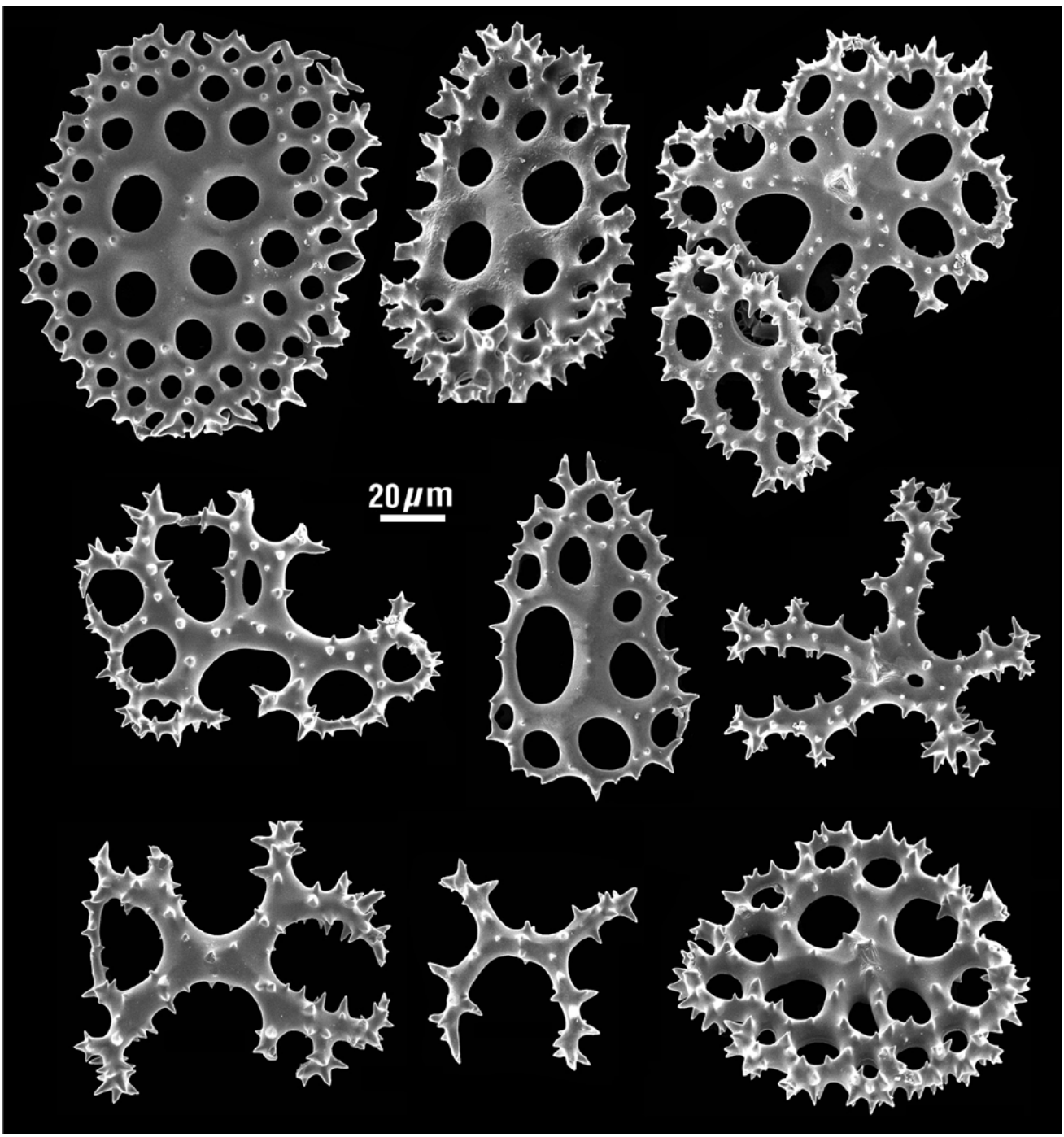


Figure 8. SEM images of peri-anal spinous cross and spinous plate ossicles from specimen of *Cladodactyla sicinski* (O'Loughlin, 2013) (NMV F193771).

body wall were assigned to the "*dubiosus* group"; those that lacked knobbed buttons were assigned to the "*laevigatus* group". We agree with this distinction between two morphologically distinct groups. Our limited genetic data support a "*laevigatus* group" clade (Fig. 9), and this clade shows geographic cohesion; all species live in the sub-antarctic – Antarctic region. *Pseudocnus leoninus*, the only sub-antarctic member of Panning's "*dubiosus* group" (with a complete cover of tube feet and numerous knobbed buttons in the body wall), genetically groups with Panning's "*laevigatus* group" (Fig. 9). We describe a new genus below, *Laevocnus* O'Loughlin gen. nov., that includes most species of Panning's "*laevigatus* group", and provisionally includes *P. leoninus*.

In contrast, North Pacific species assigned to *Pseudocnus* (including *P. curatus, P. lubricus, P. californicus*) are closely related to North Pacific species of *Cucumaria* (Arndt *et al*. 1996, Michonneau *et al*. in prep.), and do not cluster near the *Laevocnus* clade. Lambert (1998) judged that sub-species *Cucumaria fisheri astigmata* Wells, 1924 is conspecific with *Pseudocnus lubricus* (H. L. Clark, 1901). Lambert (1998) further judged that *Cucumaria curata* Cowles, 1907 should be retained in *Pseudocnus* and proposed a third "*curatus* group" for *Pseudocnus* species. *Pseudocnus curatus* (Cowles) has smooth buttons, with a few perforations only, in the body wall.

Thandar (1987) transferred four species from *Pseudocnus* to his new genus *Pseudocnella* Thandar, 1987: *Cucumaria sinorbis* Cherbonnier, 1952 (type species), *Cucumaria insolens* Théel, 1886 (junior synonym *Cucumaria leonina* var. *africana* Britten, 1910), *Semperia sykion* Lampert, 1885 (junior synonym *Cucumaria jaegeri* Lampert, 1885), and *Cucumaria syracusana* Grube, 1840.

*P. cornutus* (Cherbonnier, 1941) (Patagonia) was included in the "*laevigatus* group" by Panning and fits geographically there also. It differs from *Pseudocnus* species *sensu stricto* by having two smaller ventral tentacles, having tube feet radial only, and lacking buttons. It groups with species of the new

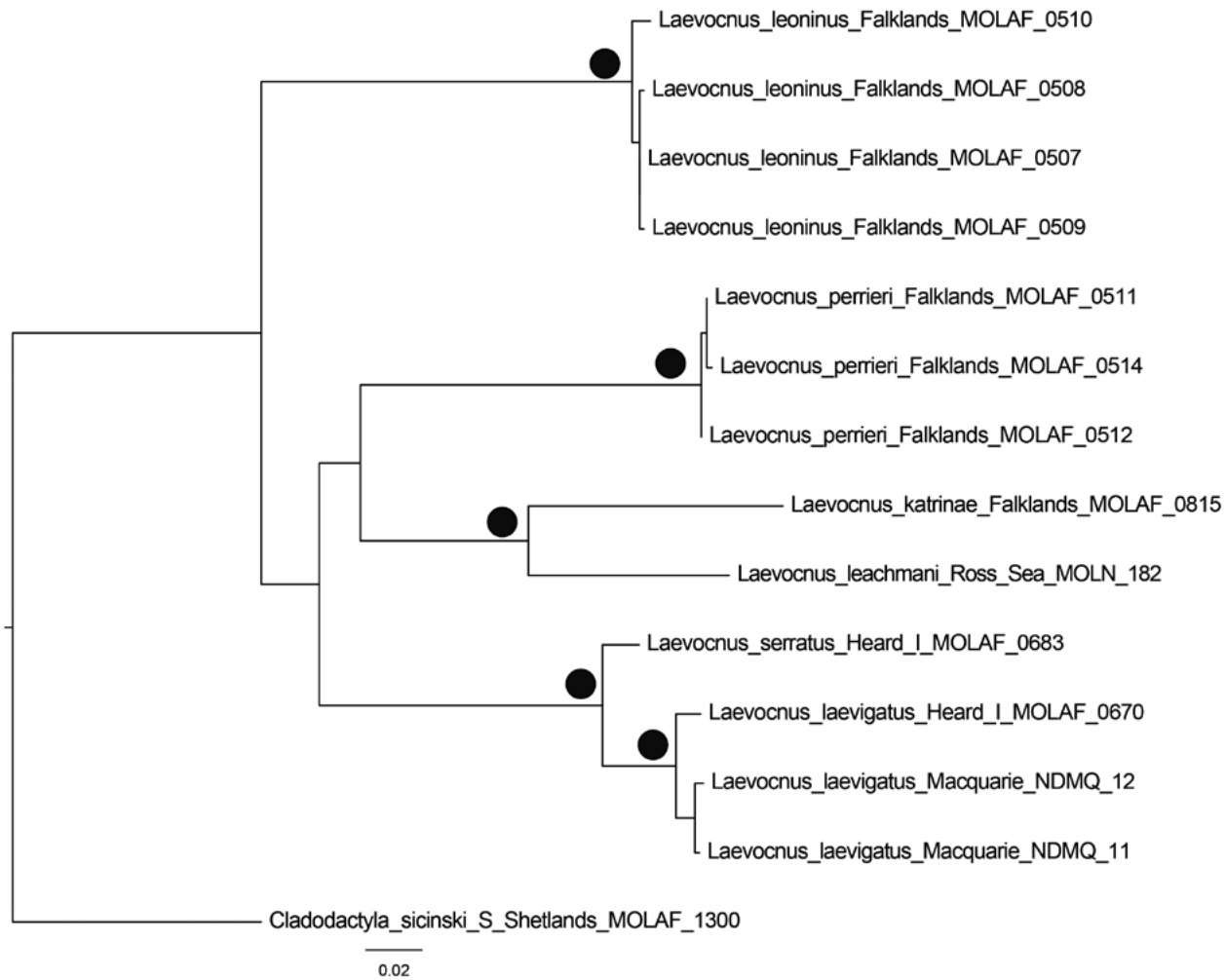


Figure 9. Maximum likelihood tree for *Laevocnus* clade, based on COI sequences, GTR+I model, 100 bootstrap replicates, *Cladodactyla sicinski* as outgroup. Filled circles >0.95 bootstrap support.

Table 2. Species remaining assigned to *Pseudocnus* in this work, most atypical for the genus *sensu stricto*, with the appropriate exception of *P. koellikeri* and the possible exception of *P. salmini* (see Remarks).

| **Species of *Pseudocnus*** | **Occurrence** | **Morphological characters** |
|---|---|---|
| *P. alcocki* (Koehler and Vaney, 1908) | Andaman Islands | 2 smaller ventral tentacles; tube feet radial only; body wall with small smooth buttons only |
| *P. californicus* (Semper, 1868) | California | 2 smaller ventral tentacles; tube feet radial only; body wall lacking knobbed buttons |
| *P. curatus* (Cowles, 1907) | California | body wall with thick smooth buttons with few perforations only, lacking distally spinous plates |
| *P. dubiosus* (Semper, 1868) | Peru | 2 smaller ventral tentacles |
| *P. echinatus* (von Marenzeller, 1881) | Japan | 2 smaller ventral tentacles; tube feet radial only; body wall with knobbed plates with long pointed spire |
| *P. goreensis* (Cherbonnier, 1949) | Senegal | 2 smaller ventral tentacles; multi-layered plates present in body wall |
| *P. grubei* (von Marenzeller, 1874) | Adriatic Sea | 2 smaller ventral tentacles; tube feet radial only; body wall with *curatus*-like and multi-layered ossicles |
| *P. koellikeri* (Semper, 1868) | Mediterranean Sea | 10 equal tentacles and as diagnosed |
| *P. lamperti* (Ohshima, 1915) | Aleutian Islands | 2 smaller ventral tentacles; tube feet radial only; body wall lacking knobbed buttons |
| *P. lubricus* (H. L. Clark, 1901) (= *C. fisheri astigmata* Wells, 1924 (by Lambert 1998)) | Puget Sound | tube feet scattered dorsally; body wall with distally spinous plates and knobbed buttons |
| *P. pawsoni* Won and Rho, 1998 | Korea | 2 smaller ventral tentacles; inter-radial tube feet small, scattered; body wall with *curatus*-like and multi-layered ossicles |
| *P. rhopalodiformis* (Heding, 1943) | Congo | rhopalodinid body form; 2 smaller ventral tentacles; tube feet radial only |
| *P. rugosus* Cherbonnier, 1957 | Sierra Leone | 2 smaller ventral tentacles; tube feet radial only; body wall with multi-layered ossicles |
| *P. salmini* (Ludwig, 1875) | Indonesia | as for P. *dubiosus* |
| *P. sentus* O'Loughlin and Alcock, 2000 | New Zealand | 2 smaller ventral tentacles; body wall with multi-layered distally spinous ossicles |
| *P. spinosus* (Ohshima, 1915) | Japan | 2 smaller ventral tentacles; tube feet radial only; body wall lacking knobbed buttons |
| *P. thandari* Moodley, 2008 | South Africa | 2 smaller ventral tentacles; tube feet radial only |

genus (below) by having tube feet confined to the radii and lacking buttons, but differs by having two smaller tentacles and having rod-plate ossicles and not plates in the tentacles. We provisionally refer *P. cornutus* to *Laevocnus* (below).

The species that remain assigned to *Pseudocnus* exhibit a range of contrasting morphological characters: 10 dendritic tentacles that may be equal or eight large and two small ventral; tube feet completely restricted to radii, largely restricted to radii, or uniformly distributed around body; macroscopic external anal scales present or absent; 'calcareous' ring calcified or not; body wall ossicles in different combinations with single-layered perforated knobbed plates with one end tapered and distally spinous (pine cone shape, pear shape) present or absent, knobbed buttons present or absent, multi-layered perforated knobbed plates present or absent, incomplete baskets present or absent, thick smooth buttons with few perforations only present or absent. We judge that species with such different combinations of morphological characters are not congeneric (see Table 2). None occurs in southern cold temperate to Antarctic waters. A further review of the species that remain assigned to *Pseudocnus* is needed.

***Laevocnus*** O'Loughlin gen. nov.

*Zoobank LSID*. http://zoobank.org:act:6A6572E8-B33F-4200-80F8-5963E557DE65

Key 1; figure 9

*Diagnosis*. Ten equal dendritic tentacles; tube feet on radii only, radial series cross introvert to base of tentacles; 'calcareous' ring lacking posterior prolongations; ring sometimes not calcified in larger specimens; gonad tubules not branched; body wall ossicles single-layered perforated knobbed plates with one end tapered and distally spinous; lacking four-holed knobbed buttons; tentacles ossicles perforated plates, rarely rods, never rosettes.

*Type species*. *Pentactella laevigata* Verrill, 1876a, b (type locality Kerguelen Islands)

*Assigned species and occurrence*. *Laevocnus cornutus* (Cherbonnier, 1941) (Patagonia); *L. intermedius* (Théel, 1886) (Heard and Kerguelen Islands); *L. katrinae* O'Loughlin sp. nov. (Shag Rock); *L. laevigatus* (Verrill, 1876a, b) (Kerguelen Is); *L. leachmani* Davey and O'Loughlin sp. nov. (Ross Sea); *L. leoninoides* (Mortensen, 1925a) (New Zealand sub-antarctic islands); *L. leoninus* (Semper, 1867) (Falkland Is); *L. marionensis* (Théel, 1886) (Marion I.); *L. perrieri* (Ekman, 1927) (Falkland Is, South Georgia); *L. serratus* (Théel, 1886) (Heard I.).

*Etymology*. Formed from a combination of "*laev*" from *laevigata* (the species name of the type for the new genus), with the established and related generic name *Ocnus* (masculine).

*Remarks*. We judge that having 10 equal tentacles or eight large and 2 small ventral ones is a significant distinguishing generic character. Cherbonnier 1941 reported that his species *P. cornutus* had two slightly small ventral tentacles. No other *Laevocnus* species has other than 10 equal tentacles. *Laevocnus* species are distinguished from *Pseudocnus* species (*sensu stricto*) by: lacking inter-radial tube feet; having ossicles in the body wall limited to single-layered knobbed plates with spines at one end; rarely having rods and never rosettes in the tentacles.

As noted above in the previous Remarks *Laevocnus leoninus* is an anomalous inclusion in *Laevocnus*, having: a uniform cover of tube feet; numerous buttons in the body wall; and tentacle rods. It does have 10 equal tentacles. *Laevocnus leoninus* is sympatric with *Laevocnus perrieri* as a cold temperate species of the new genus. Also noted above is the provisional inclusion of *Laevocnus cornutus* that has two smaller tentacles and rod-plates in the tentacles.

*Laevocnus marionensis* is also a somewhat anomalous inclusion as it has body wall ossicles with slightly developed tapered spinous ends inter-grading with knobbed buttons that usually show some distal development.

O'Loughlin (2009) assigned *Cucumaria serrata* var. *intermedia* Théel, 1886 (Heard and Kerguelen Islands) and *Cucumaria serrata* var. *marionensis* Théel, 1886 (Marion Island) to *Pseudocnus* and raised them to species status. We now reassign these species to *Laevocnus*.

O'Loughlin (1994) reported that *Laevocnus laevigatus* exhibited brood-protection in "two ventral invaginated marsupia that opened through a common mid-body vestibule". In some female specimens (NMV F165742 (6)) of *Laevocnus serratus* we observed two ventral brood pouches invaginated into the coelom, with one or two ventral inter-radial external openings. There were up to 40 brood juveniles in one individual, each up to 3 mm long, sub-equal in size, and with their tentacle crowns developed. Two ventral openings but no internal pouches were observed (specimen NMV F84982) for *Laevocnus intermedius* and it is assumed that this species also has this brood-protecting adaptation.

COI sequence data from several hundred dendrochirotids (Michonneau *et al*. in prep) recovers *Laevocnus* as a single clade, albeit poorly supported, that includes *L. katrinae* sp. nov., *L. laevigatus, L. leachmani* sp. nov., *L. leoninus, L. perrieri* and *L. serratus* (Fig. 9).

Key (1) to the species of ***Laevocnus*** O'Loughlin gen. nov.

1. Tube feet cover the body uniformly ..... ***Laevocnus leoninus*** (Falkland Is)

— Tube feet restricted to the radii ..... **2**

2. Tube feet in single well-spaced series in mid-body on all radii ..... **3**

— Close zig-zag or paired series of tube feet on all radii, may be more scattered on dorso-lateral radii ..... **5**

3. Body up to 40 mm long; tube feet in paired series anteriorly; body wall ossicles with long, narrow "goose neck", ending in a sparsely perforated and spinous taper ..... ***Laevocnus serratus*** (Heard I.)

— Body up to 15 mm long; single series of tube feet anteriorly; body wall ossicles with short tapered spinous end ..... **4**

4. Calcareous ring thin and indistinct; two polian vesicles; body wall ossicles smaller, up to 208 $\mu$m long ..... ***Laevocnus katrinae*** sp. nov. (western Antarctica, Shag Rock, 206 m)

— Calcareous ring distinct; single polian vesicle; body wall ossicles larger, up to 280 $\mu$m long ..... ***Laevocnus leachmani*** sp. nov. (eastern Antarctica, Ross Sea and off King George V Land, 299–1645 m)

5. Body wall ossicles with spinous end predominantly rounded or not significantly elongate and tapered; body wall ossicles small, up to 160 $\mu$m long ..... **6**

— Body wall ossicles with distal spinous end typically elongate and tapered; largest body wall ossicles longer than 180 $\mu$m long ..... **7**

6. Body wall ossicles irregularly oval, predominantly with one end rounded and closely spinous, up to 140 $\mu$m long; tentacles ossicles large smooth perforated plates; preserved specimens smaller, up to 35 mm long ..... ***Laevocnus leoninoides*** (New Zealand sub-antarctic Is)

— Body wall ossicles with slightly developed tapered spinous ends, inter-grading with knobbed buttons usually showing some distal development, up to 160 $\mu$m long; tentacles ossicles perforated plates with surface spines; preserved specimens larger, up to 55 mm long ..... ***Laevocnus marionensis*** (Marion I.)

7. Two smaller tentacles; rod-plate ossicles in the tentacles ..... ***Laevocnus cornutus*** (Patagonia, Falkland Is)

— Equal tentacles; plate ossicles in the tentacles ..... **8**

8. Preserved specimens small, up to 40 mm long; tentacle plates with some surface spines; lacking ventral coelomic brood sacs and openings ..... ***Laevocnus perrieri*** (Falkland Is, South Georgia)

— Largest preserved specimens up to at least 60 mm long; tentacle plates with knobs or smooth, not with surface spines; females with ventral coelomic brood sacs and openings ..... **9**

9. Preserved body up to 115 mm long; body wall ossicles up to 220 $\mu$m long; tentacles ossicles smooth plates ..... ***Laevocnus laevigatus*** (Kerguelen Is)

— Preserved body up to 65 mm long; body wall ossicles up to 185 $\mu$m long; tentacle ossicles plates with surface knobs ..... ***Laevocnus intermedius*** (Heard I.)

***Laevocnus katrinae*** O'Loughlin sp. nov.

*Zoobank LSID*. http://zoobank.org:act:AC9E8725-E167-405E-BCAA-3904F35161D6

Key 1; figures 9, 10

*Material examined*. Holotype. Southern Atlantic Ocean, Western Antarctica, Shag Rock, 53.63°S 40.91°W, 206 m, BAS BIOPEARL 1 stn SR–EBS–4, 11 Apr 2006, NMV F168836 (UF tissue sequence code MOL AF 815).

Paratypes. Type locality and date, NMV F 189886 (9); type locality and date, NHMUK 2010.139–142 (4).

*Description*. Up to 14 mm long, 4 mm diameter (tentacles deeply withdrawn); body cylindrical, rounded orally and anally; thin, semi-translucent, calcareous body wall; 10 equal dendritic tentacles; calcareous ring present, indistinct, thin sinusoidal cucumariid-like, lacking posterior prolongations; tube feet extended, rigid, about 0.3 mm diameter, restricted to single well-paced radial series, up to 7 tube feet per series externally, plus up to 9 per series on withdrawn introvert; 5 small anal papillae; lacking macroscopic anal scales; 2 polian vesicles; 2 tufts of un-branched gonad tubules.

Ossicles in body wall similar in smallest (2 mm long) and largest specimens, elongate to irregularly-oval perforated plates, with marginal and surface knobs, tapered at one end, there bearing distal spines, plates up to 208 $\mu$m long. Ossicles in tentacles irregularly rectangular to triangular perforated plates with denticulate to spinous margins and few small surface granulations, up to 180 $\mu$m long. Ossicles in tube feet endplates with small irregular perforations; tube feet support ossicles irregularly-curved, perforated plates, frequently with distally-spinous mid-plate projection, plates up to about 200 $\mu$m long. Peri-anal ossicles distally spinous knobbed plates as in mid-body wall.

*Colour (preserved)*. Body and tentacles white.

*COI DNA barcode of holotype:* AATTATGATAGGAGGCTTTGGAAACTGATTAATACCTTTAATGATAGGAGCCCCCGATATGGCTTTCCCACGAATGAACAATATGAGATTCTGATTAATACCCCCTTCTTTTATTTTACTATTGGCTTCTGCTGGAGTAGAAGGAGGTGCAGGAACAGGATGAACTATTTACCCACCTTTATCCAGAAAAATAGCTCATGCAGGAGGATCTGTAGATTTAGCTATATTTTCCCTACACTTAGCAGGTGCCTCCTCAATACTTGCATCTATTAAATTTATTACTACTATTATAAATATGCGAGCACCAGGAGTTTCATTTGATCGTTTACCACTATTTATTTGATCAGTTCTAATAACCGCCTTTCTTTTACTTCTAAGTCTTCCTGTTTTAGCAGGTGCTATTACAATGTTATTAACAGACCGAAATATAAAAACAACTTTTTTTGATCCATCAGGAGGAGGAGACCCTATACTATTTCAACACTTATTTTGATTTTTTGGACACCCTGAAGTTTATATTTTGATTCTACCAGGATTTGGAATGATATCACACGTAATTACTCATTATAGAGGTAGACAAGAACCATTTGGATATTTAGGAATGGTTTATGCTATGATAGCTATAGGTATTTTAGGTTTTATCGTGTGAGCACAC

*Distribution*. Southern Atlantic Ocean, Western Antarctica, Shag Rock, 206 m.

*Etymology*. Named for Katrin Linse (British Antarctic Survey), in appreciation of her role in the BAS BIOPEARL expeditions and the collection of specimens studied here, and with gratitude for her gracious collaboration in making BAS specimens available for this study and providing relevant data.

*Remarks*. *Laevocnus katrinae* is distinguished from other species of *Laevocnus* by the morphological characters detailed in the key above, as well as by >17% pair-wise K2P divergence in CO1 sequence.

***Laevocnus leachmani*** Davey and O'Loughlin sp. nov.

*Zoobank LSID*. http://zoobank.org:act:DD44CDAF-F84B-4D6F-B979-FCB0EBD60015

Key 1; figures 9, 11

*Pseudocnus* species (Ross Sea) O'Loughlin *et al*., 2010: table 1.

*Material examined*. Holotype. Eastern Antarctica, Ross Sea, 72.08°S 175.55°E, 1620 m, stn TAN0802/139, N. Davey, 22 Feb 2008, NIWA 42203 (UF tissue sequence code MOL N 182).

Paratype. Type locality and date, NIWA 61890 (1).

Other material. Ross Sea, 72.07°S 175.59°E, 1629–1645 m, stn TAN0802/135, 22 Feb 2008, NIWA 61100 (4 juvenile specimens); off George V Land, 66.57°S 142.00°E, 299–521 m, CEAMARC RSV *Aurora Australis* Voyage 3, stn 9EV117, 26 Dec 2007, NMV F189887 (1).

*Description*. Body up to 15 mm long (preserved, tentacles withdrawn), 6 mm diameter; body fusiform; body wall thin, calcareous, with a rugose surface created by a close cover of projecting spinous ossicle ends; 10 equal dendritic tentacles; 5 oral papillae, 5 anal papillae, lacking anal scales; tube feet projecting, not withdrawn, about 0.4 mm in diameter, restricted to a single, well-spaced series in all radii, extending across the introvert; calcareous ring distinct, calcified, cucumariid-like, lacking posterior prolongations; single polian vesicle; two tufts of unbranched gonad tubules; 3 embryos in withdrawn oral cavity in one specimen.

Body wall ossicles irregularly oval to oblong, single-layered, perforated, knobbed plates, with one end of plate always sharply spinous and frequently narrowed into a short distally-spinous neck, spinous apex frequently upturned, plate perforations smaller at ends, sometimes with two large perforations centrally separated by a narrow knobbed bridge, plates up to 280 $\mu$m long; lacking knobbed buttons. Tentacle ossicles perforated plates of variable form and size, up to 240 $\mu$m long, marginally

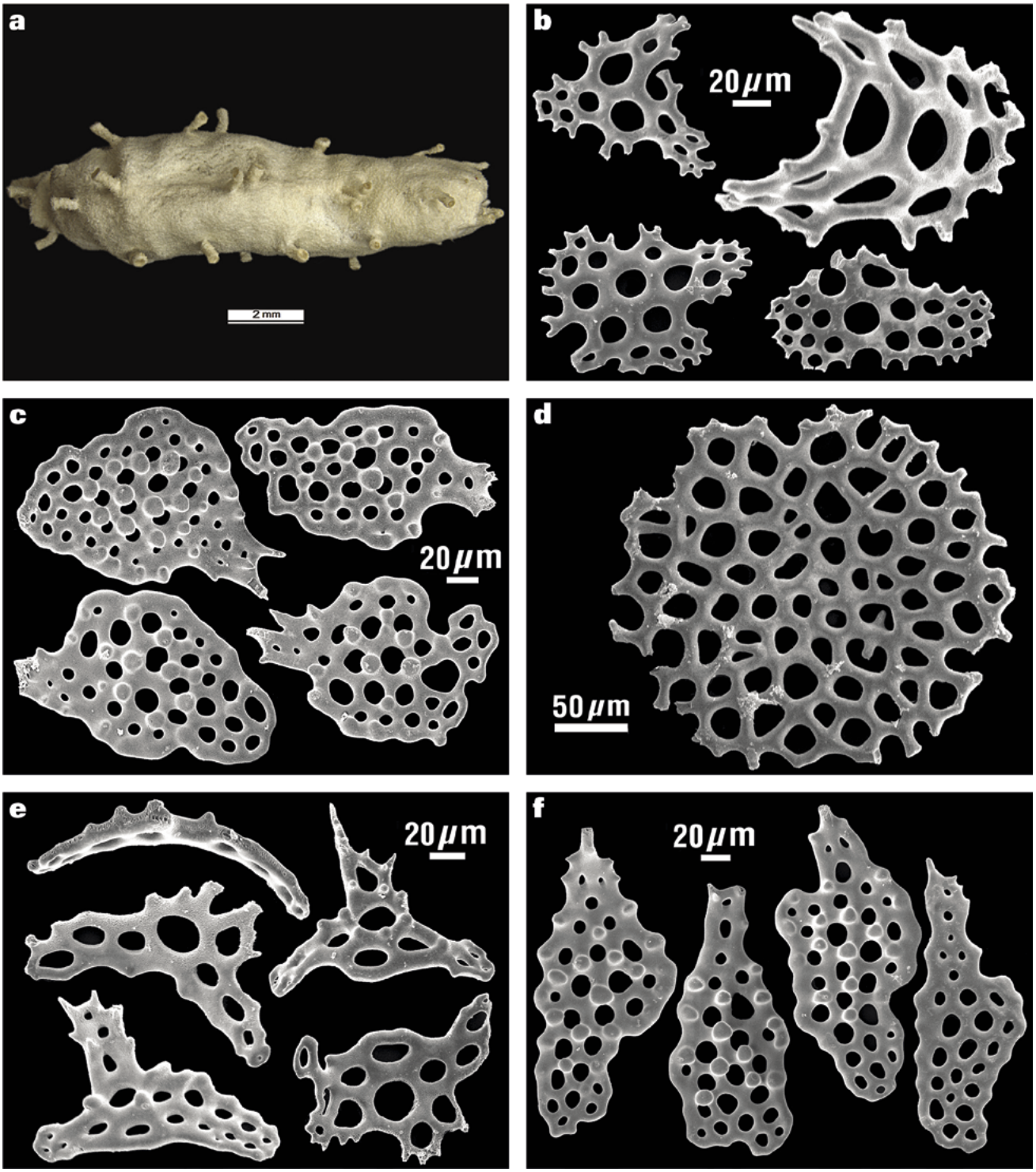


Figure 10. *Laevocnus katrinae* O'Loughlin sp. nov. holotype (NMV F168836). a, preserved holotype; b–f, SEM images of ossicles from the holotype – b, tentacle plates; c, mid-body wall plates with one end distally spinous; d, tube foot endplate; e, endplate support ossicles with distally spinous lateral projection; f, peri-anal plates with one end distally spinous.

spinous, sometimes with surface knobs or spines; no rods or rosettes. Tube feet endplate support ossicles bent and curved plates with apically spinous mid-plate projection.

*Colour (preserved).* White.

*COI DNA barcode of holotype:* TAACTGATTAATACCTTTAATGATTGGAGCCCCTGACATGGCTTTCCCACGAATGAACAATATGAGATTCTGATTAATACCCCCATCCTTTCTTTTACTACTAGCTTCTGCTAGTGTAGAAAGAGGTGCAGGAACAGGATGAACTATTTACCCCCCCTTATCTAGAAAAATAGCCCATGCAGGAGGATCTGTAGATCTAGCTATTTTTTCACTTCACCTAGCAGGTGCCTCTTCAATTCTTGCAGCTATAAAATTTATAACTACTATAATAAAAATGCGAGCACCAGGTATTTATTTTGACCGTCTATCATTATTTATCTGATCCGTCTTTATTACTGCTTTTCTATTACTCTTAAGTCTTCCAGTATTAGCAGGTGCTATTACAATGTTATTAACAGATCGAAACATAAACACTACCTTCTTTGATCCATCAGGTGGAGGAGATCCTATATTATTCCAACACTTATTCTGATTTTTTGGACACCCAGAAGTATATATTCTTATTTTACCAGGATTTGGTATGATATCTCATGTAATTACACATTATAGAGGAAGACAAGAACCCTTTGGATATTTAGGTATGGTTTATGCTATGATATCTATAGGTATTTTAGGTTTCCTAGTATGAGCTCACCACATGTTTACTGTAGGA

*Distribution*. Eastern Antarctica, Ross Sea and off George V Land, 299–1645 m.

*Etymology*. Named for Andrew Leachman, skipper of the RV *Tangaroa* for 38 years, that included seven marine research voyages to Antarctica.

*Remarks*. *Laevigatus leachmani* is distinguished from other species of *Laevocnus* by the morphological characters detailed in the key above, as well as by >17% pair-wise K2P divergence in CO1 sequence. This species is listed as *Pseudocnus* species (Ross Sea) by O'Loughlin *et al*. (2010) (Table 1).

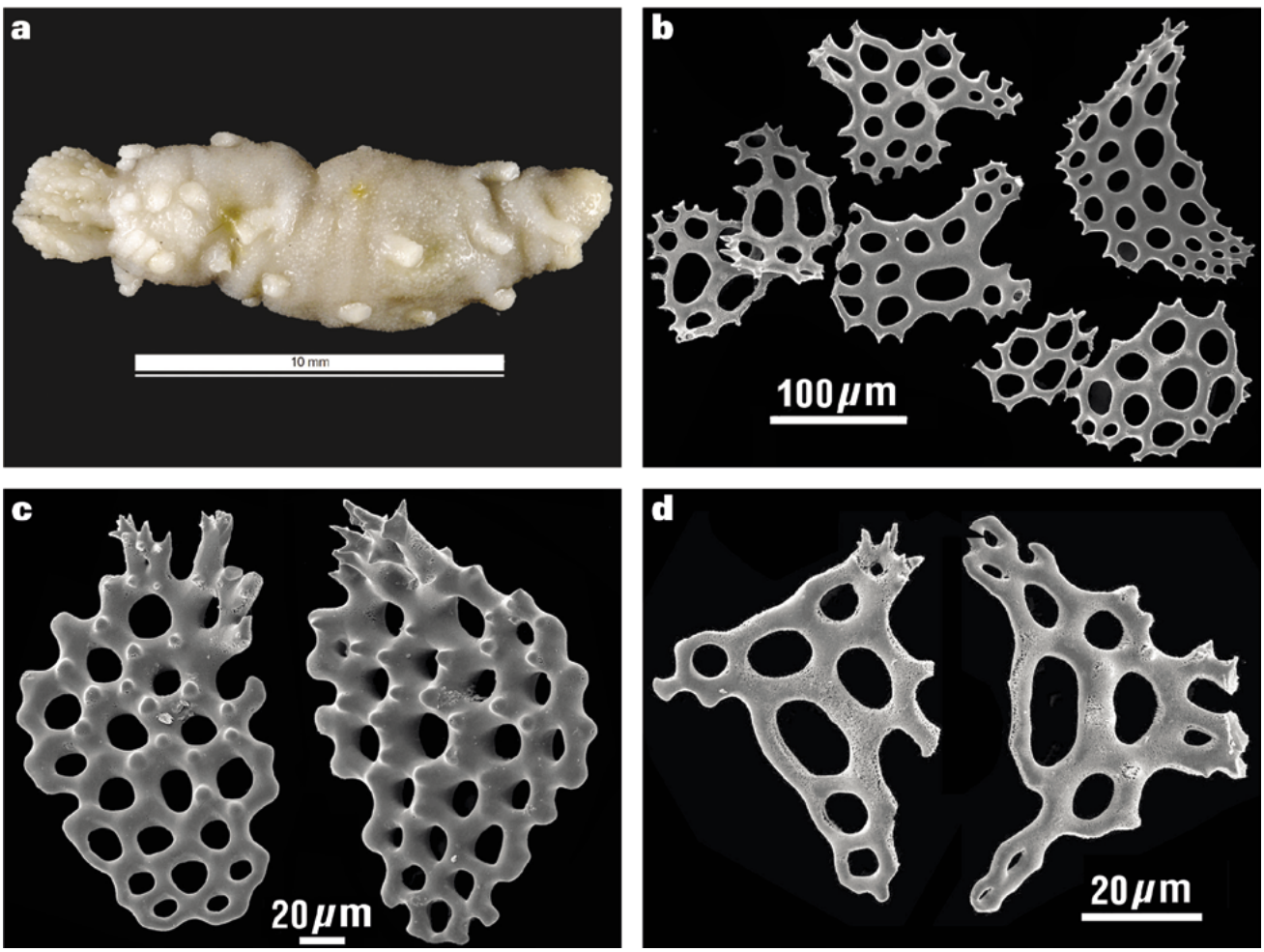


Figure 11. *Laevocnus leachmani* Davey and O'Loughlin sp. nov. a, preserved holotype (NIWA 42203; photo by Peter Marriot (NIWA)); b–d, SEM images of ossicles from a paratype (NIWA 61890) – b, tentacle plates; c, mid-body wall plates with one end distally spinous; d, tube foot endplate support ossicles, one with distally spinous lateral projection.

Family **Paracucumidae** Pawson and Fell, 1965

Key 2; figure 12

*Diagnosis*. Body cylindrical, posterior taper; body wall thin; tube feet distributed around body; 10–15 dendritic or sub-digitiform tentacles, ventral pair usually small; mid-body wall ossicles perforated plates, some with knobs, some with secondary layer developments from one or a few layers to dome-like stacks or spines, sometimes in cross form.

*Included genera*. *Paracucumis* Mortensen, 1925b; *Crucella* Gutt, 1990

*Remarks*. Gutt (1990) referred his new genus *Crucella* to the Paracucumidae, and O'Loughlin (2002) and O'Loughlin *et al*. (2009b) maintained this referral. O'Loughlin *et al*. (2009b) discussed *Crucella*, judged that *Caespitugo citriformis* Gutt, 1990 is a junior synonym of *Thyone scotiae* Vaney, 1906 and referred *Thyone scotiae* to *Crucella*. Currently the family has three recognized species: *Paracucumis turricata* (Vaney, 1906) (junior synonym *Paracucumis antarctica* Mortensen, 1925b by O'Loughlin 2002), *Crucella scotiae* (Vaney, 1906), and *Crucella hystrix* Gutt, 1990. We add a fourth species *Crucella susannae* O'Loughlin sp. nov. Phylogenetic analysis based on CO1 sequence data recovers a monophyletic Paracucumidae among 200 species of dendrochirotids sequenced to date, but shows *Crucella*, as currently defined, to be paraphyletic (Fig. 12), with *C. scotiae* sister to the new species *C. susannae* and *P. turricata* sister to these two species. However *P. turricata* has what we judge to be two significant morphological characters (up to 15 tentacles and body wall plates imbricating or contiguous) that are not shared with *C. scotiae* and *C. susannae*. We acknowledge this anomaly for generic assignment, but on primarily morphological grounds maintain *Thyone scotiae* in *Crucella* and maintain *Paracucumis* as a monotypic genus. CO1 data indicate further cryptic, geographical divergence within *C. hystrix* and *C. scotiae* as previously indicated by O'Loughlin *et. al*. (2010). We note in relation to the 2010 paper and relevant tree (page 8) that the South Shetland specimen (green) of *C. scotiae* is re-identified here as our new species *C. susannae*.

Key (2) to the species of Paracucumidae (Antarctica)

1. Body form elongate, narrow, vermiform; plates covering body wall imbricate or contiguous; body cover of high domes on plates; tube feet around body mostly inconspicuous; up to 15 dendritic tentacles ..... ***Paracucumis turricata***

— Body form not elongate, narrow, vermiform; plates in mid-body wall not imbricate, some contiguous; body with or lacking domes or fine spines on plates; tube feet around body conspicuous; 10 tentacles ..... **2**

2. Preserved body up to 30 mm long; finely spinous surface appearance; tentacles sub-digitiform; knobbed perforated cross ossicles in mid-body wall, some with narrow spires ..... ***Crucella hystrix***

— Preserved body up to at least 50 mm long; wide blunt domes or smooth surface appearance; tentacles dendritic; mid-body plate ossicles never in cross form ..... **3**

3. Uniform cover of tube feet; mid-body wall ossicles include large irregular plates (up to 600 $\mu$m long), some with secondary layering and central elevation forming a low dome ..... ***Crucella scotiae***

— Tube feet closer together and larger ventrally than dorsally; mid-body wall ossicles round to oval single-layered perforated plates (up to 170 $\mu$m long), never with secondary layering ..... ***Crucella susannae***

***Crucella*** Gutt, 1990

Key 2; figure 12

*Diagnosis (emended)*. Body cylindrical, not vermiform, with narrowed tail; body wall thin; 10 dendritic or sub-digitiform tentacles, ventral pair small; tube feet distributed around body, sometimes unevenly; body wall ossicles perforated plates, some with knobs, some with low secondary layering forming domes, some with spires; mid-body plates generally spaced apart, some plates possibly contiguous but not imbricating.

*Type species*. *Crucella hystrix* Gutt, 1990 (type locality Weddell Sea)

*Assigned species and type locality*. *Crucella hystrix* Gutt, 1990 (Weddell Sea); *C. scotiae* (Vaney, 1906) (Antarctic Peninsula); *Crucella susannae* O'Loughlin sp. nov. (South Shetland Islands)

*Remarks*. *Crucella* is reviewed above in the Remarks and Key for Paracucumidae.

***Crucella susannae*** O'Loughlin sp. nov.

*Zoobank LSID*. http://zoobank.org:act:962A6E3A-4177-4585-A1BB-A4AC17FD1E90

Key 2; figures 12, 13, 14

*Material examined*. Holotype. Antarctica, South Shetland Islands, off King George Island, 61.83ºS 58.63ºW, 191 m, CCAMLR RV *Polarstern* ANT–XXVIII/4 stn 79/264, S. Lockhart, 31 Mar 2012, NMV F193782.

Paratypes. Off Elephant Island, 60.98ºS 55.69ºW, 92 m, CCAMLR RV *Polarstern* ANT–XXVIII/4 stn 79/229, 24 Mar 2012, NMV F193784 (17) (UF tissue sequence code MOL AF1293); Bransfield Strait, 62.45ºS 055.27ºW, 244 m, CCAMLR RV *Polarstern* ANT–XXVIII/4 stn 79/269, 1 Apr 2012, NMV F198491 (1); South Orkney Islands, 60.59ºS 45.15ºW, AMLR 2009 stn 78/8, 92–105 m, 11 Feb 2009, NMV F169315 (1).

*Description*. Up to 52 mm long, 28 mm diameter (strongly contracted, tentacles deeply withdrawn); body bluntly rounded and upturned orally, tapered upturned cone-shaped anally; body wall thin, firm, parchment-like to soft leathery; 8 large, 2 small ventral, dendritic tentacles; solid typical cucumariid calcareous ring present, lacking any posterior prolongations; completely covered with small tube feet, close-set and about 0.4 mm diameter ventrally, scattered and about 0.2 mm diameter dorsally; with numerous small peri-anal papillae; lacking macroscopic anal scales; 2 tufts of gonad tubules, not branched; respiratory trees present; 1 polian vesicle.

Dorsal body wall with scattered, not imbricating or contiguous, thick, single-layered, oval to round plates, with up to 22 perforations, irregular margins sometimes with blunt denticulations, sometimes with surface knobs, up to 168 $\mu$m long. Ventral body wall ossicles similar to dorsal. Tentacles with perforated plates and long, narrow, perforated, rod-like plates, with marginal digitiform and blunt denticulations, plates smooth or with some surface knobs, up to 560 $\mu$m long. Ventral tube feet with endplates with rounded margin, large and small perforations irregularly arranged, up to 360 $\mu$m diameter; lacking tube foot support ossicles. Peri-anal ossicles include plates as in body wall; numerous larger, oval, perforated plates with low secondary layering, up to 280 $\mu$m long; and pyramidal multi-layered anal scales, about 360 $\mu$m high and wide at base.

*Colour.* Live: Body pale brown and blue-grey. Preserved: pale brown to grey to off-white.

*COI DNA barcode of paratype:* TATTATGATAGGAGGTTTTG-GTAATTGGTTAATTCCATTAATGATAGGAGCACCAGA-CATGGCCTTCCCTCGAATGAATAAAATGAGATTCTGAT-TAATTCCCCCTTCTTTTGTGCTTCTGCTTACCTCCGCAA-GAATAGAAAATGGGGCTGGTACAGGTTGAACTTTATAC-CCCCCTCTTTCAAGAAAAATAGCTCACGCAGGAA-GATCAGTAGATCTTGCTATTTTTTCGCTACATCTAGCAG-GAGCCTCCTCTATTCTTGCCTCCATAAAATTTATAAC-TACCATAATAAAAATGCGAACCCCAGGAATTTCATTT-GACCGTCTACCACTTTTTGTCTGATCCGTTTTTATAACA-GCCTTCCTATTAGTATTAAGCCTCCCAGTTTTAGCAGGT-GCTATAACAATGTTATTAACCGACCGAAAAAT-TAAAACAACCTTCTTTGACCCAGCAGGAGGAGGAGACC-CCATTTTATTTCAACACTTATTCTGATTCTTTGGACATC-CAGAAGTTTATATACTTATTTTACCAGGGTTCGGAATGA-TATCTCACGTTATTGCACACTATAGAGGAAAGCAA-GAACCATTTGGGTACTTAGGAATGGTTTACGCTATGG-TAGCAATAGGAGTATTAGGCTTCCTAGTATGAGCTCAC

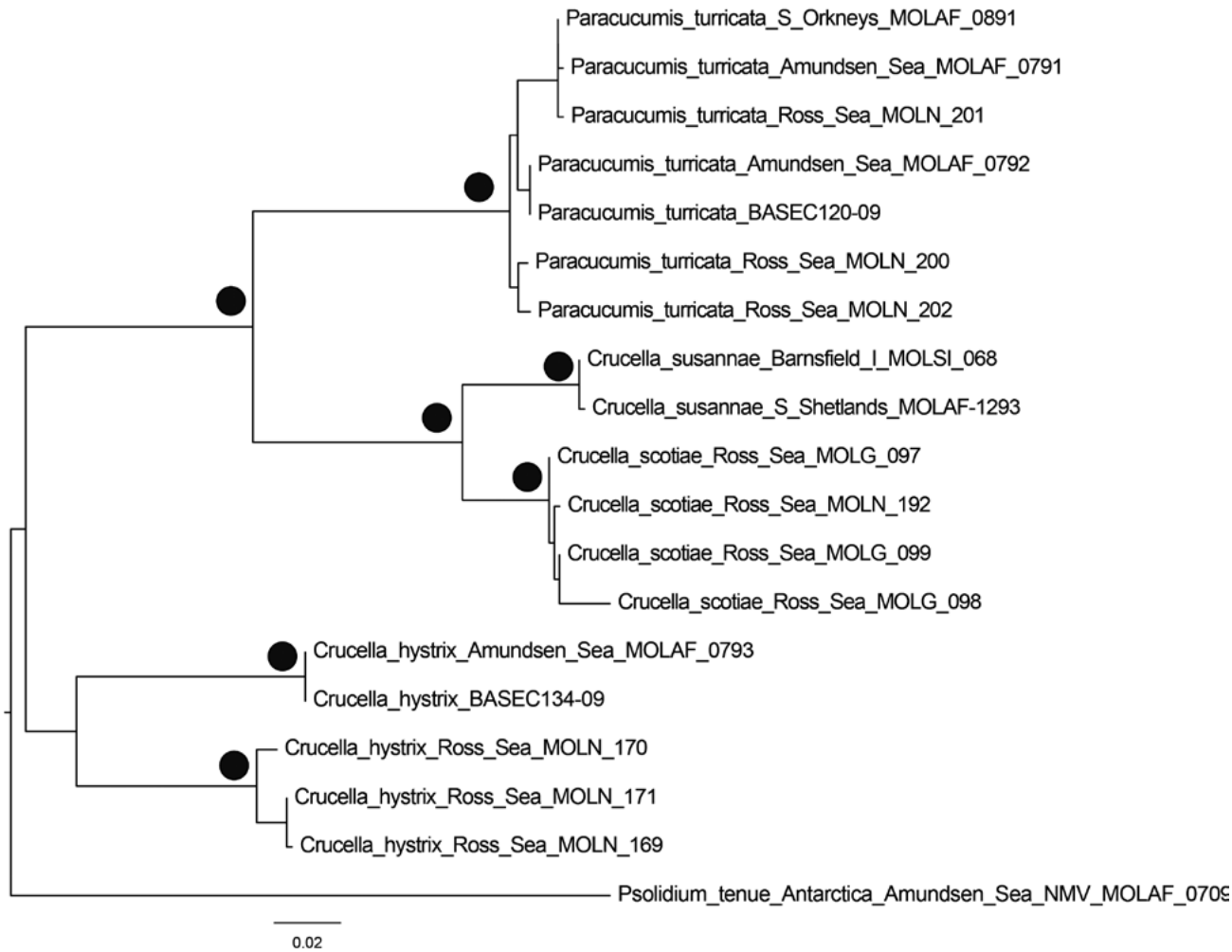


Figure 12. Maximum likelihood tree for Paracucumidae, based on COI sequences, GTR+G model, 100 bootstrap replicates, *Psolidium tenue* as outgroup. Filled circles >0.95 bootstrap support.

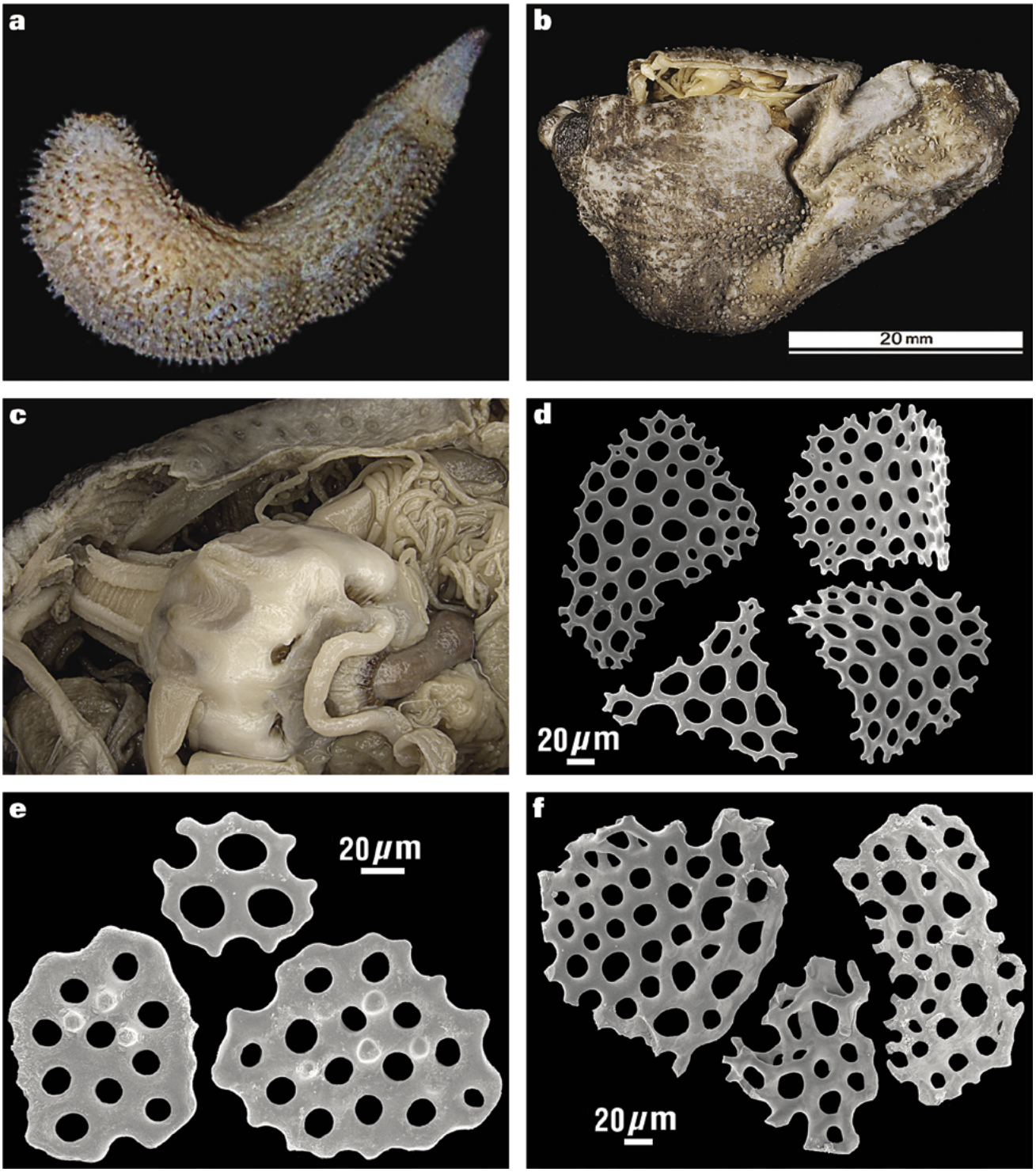


Figure 13. *Crucella susannae* O'Loughlin sp. nov. a, photo of live specimen of a paratype (Elephant I.; NMV F193784; photo by Susanne Lockhart); b–f, holotype (NMV F193782) – b, left lateral view of preserved body of holotype; c, calcareous ring, polian vesicle, gonad tubules; d, SEM images of tentacle ossicles; e, SEM images of body wall ossicles; f, SEM images of fragments of endplate.

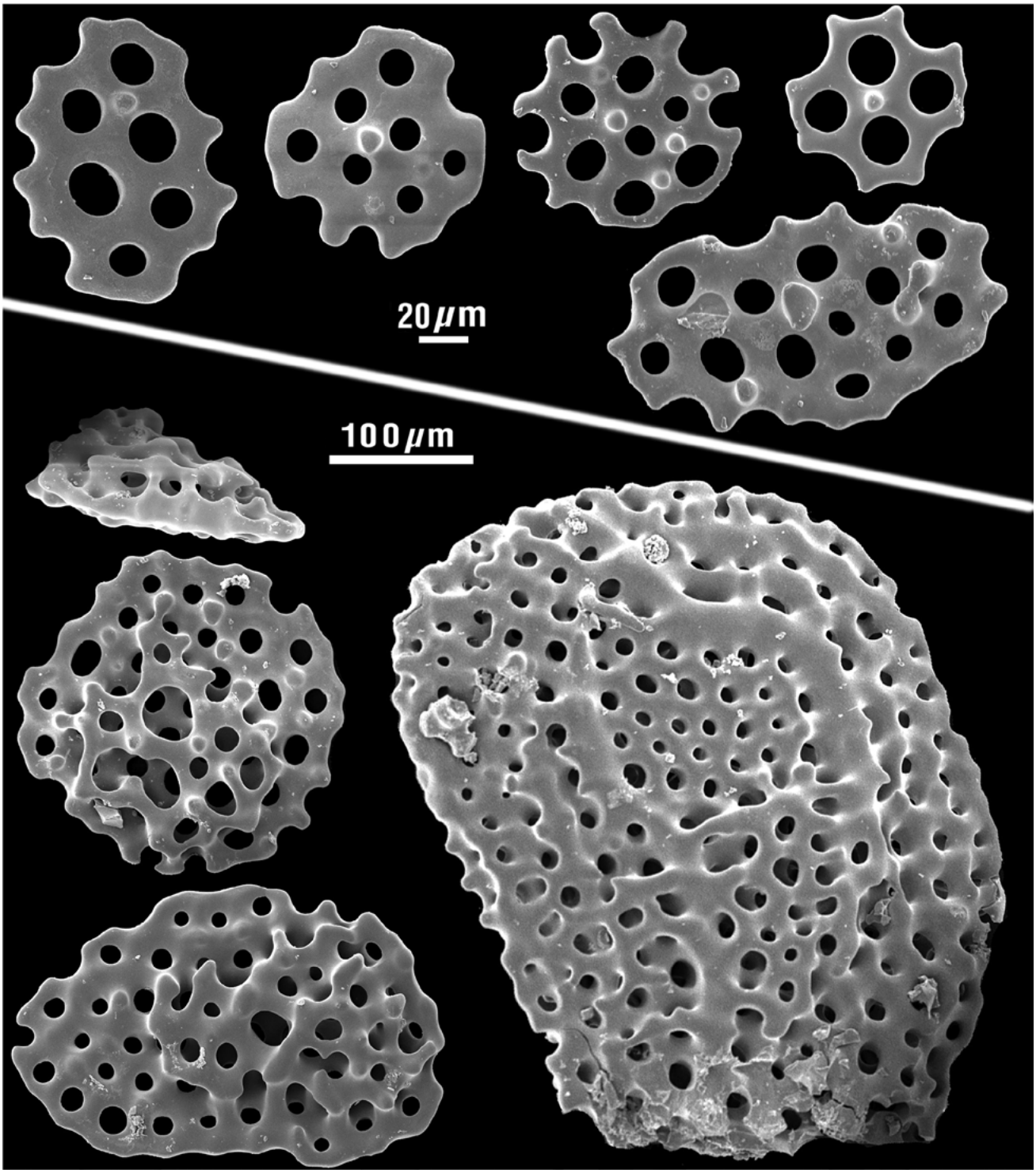


Figure 14. SEM images of peri-anal body wall ossicles from holotype of *Crucella susannae* O'Loughlin sp. nov. (holotype NMV F193782). Top: typical mid-body wall ossicles in the peri-anal region. Bottom: fragment of peri-anal scale with some secondary layer development, and perforated plates with secondary layer developments.

*Distribution*. Western Antarctica, South Shetland, Elephant, South Orkney Islands, 92–244 m.

*Etymology*. Named for Susanne Lockhart (National Oceanic and Atmospheric Administration's US AMLR Program), in appreciation of her initiative and hard-working role in quantitatively collecting, preserving, documenting and donating to Museum Victoria many hundreds of specimens of sea cucumbers from the 2012 CCAMLR demersal finfish trawl survey.

*Remarks*. *Crucella susannae* is distinguished from other species in family Paracucumidae in the key. We judge that the preserved dark brown colour of the holotype (NMV F193782) is a result of discolouration from trawl contents.

***Paracucumis*** Mortensen, 1925b

Key 2

*Diagnosis (emended)*. Body form cylindrical, elongate, narrow, vermiform, posterior tapered; body cover of high domed plates; up to 15 dendritic tentacles, ventral pair and possibly some others small; tube feet distributed around body, may be rudimentary and inconspicuous; plates covering body wall imbricate or contiguous, some multi-layered into a high dome-like elevation.

*Type species*. *Thyone turricata* Vaney, 1906 (= *Paracucumis antarctica* Mortensen, 1925b by O'Loughlin 2002) (type locality South Orkney Islands) (monotypic)

*Remarks*. *Paracucumis* is reviewed above in the Remarks and Key for Paracucumidae.

Family **Thyonidiidae** Heding and Panning, 1954

*Diagnosis (Smirnov 2012)*. Tentacles 15–25; plates of calcareous ring lacking segmented posterior extensions; ossicles tables with 2, 3 or 4 pillars, or plates (*Parathyonidium*), or reduced (*Patallus* and *Athyonidium*).

*Remarks*. Thyonidiinae Heding and Panning, 1954 was raised to family status by Smirnov (2012) who understandably suspected that the Thyonidiidae is polyphyletic, those genera with tables not related to those lacking tables.

***Parathyonidium*** Heding, 1954

*Parathyonidium* Heding, 1954 in Heding and Panning 1954.

*Diagnosis* (see *Description* of *Parathyonidium incertum* Heding, 1954 below)

*Type species*. *Parathyonidium incertum* Heding, 1954 (type locality South Georgia) (monotypic)

*Remarks*. Albert Panning (in Heding and Panning 1954) noted that his Copenhagen friend and colleague Sven Heding died before the publication of their anticipated *Discovery Report*, where he planned to describe the new genus *Parathyonidium* and species *Parathyonidium incertum*. Albert further noted that Elizabeth Deichmann had taken over work on the *Discovery* specimens, but had agreed that Albert would publish the description as written by Sven. Albert assigned the authorship of the new taxa to Heding, and the descriptions were published in Heding and Panning (1954). A *Discovery Report* on holothuroids was never published. The *Discovery* holothuroid collection is currently in Museum Victoria where most specimens have now been determined. Mark O'Loughlin and his colleagues hope to complete a *Discovery Report* on holothuroids. Here we have emended the diagnosis of *Parathyonidium* Heding, 1954 to more fully describe the tentacle form and arrangement, calcareous ring, gonad tubule arrangement, and ossicles.

***Parathyonidium incertum*** Heding, 1954

Figure 15

*Parathyonidium incertum* Heding, 1954 in Heding and Panning 1954: 37–39, text fig. 3.—O'Loughlin *et al*., 2009b: 5–6, table 1, fig. 1d–f.—O'Loughlin *et al*., 2010: table 1.

*Parathyonidium* Heding species.—O'Loughlin *et al*., 2009a: 217, fig. 2c.

*Parathyonidium* species.—O'Loughlin *et al*., 2010: 4, table 1.

*Material examined*. Holotype. West of Shag Rock, South Georgia, *Discovery Expedition*, RRS *Discovery II* stn 474, 199 m, 12 Nov 1930, no registration found (data from Heding and Panning 1954; specimen not located).

Paratypes. South Shetland Islands, Clarence Island, Discovery Expedition, *Discovery* stn D170, 61°26'S 53°46'W, 342 m, 23 Feb 1927, NHMUK 2011.171–173 (3); ZMUC–HOL–300 (3) (confirmed by Tom Schioette ZMUC; specimens not seen here); Elephant I., 600 m, MNHN–IE–2013–2479 (2) (previously EcHh250, confirmed by Sébastien Soubzmaigne MNHN; specimens not seen here).

Other material. South Atlantic Ocean, South Georgia, US AMLR 2004, *Icefish* stn 47–BT25, 55.06°S 35.24°W, 116 m, 12 Jun 2004, NMV F104998 (1); Antarctic Peninsula, Low I., BENTART–2006, R/V *Hesperides*, stn LOW47, 63.47°S, 62.22°W, 115 m, 12 Feb 2006, MNCN 29.04/126 (1 specimen), body wall ossicles slide NMV F161525; MNCN 29.04/127 (2 specimens), posterior body ossicles slide NMV F161526, tentacle ossicles slide NMV F161527; Eastern Antarctica, off Enderby Land, *Nella Dan*, ANARE stn HRD010, 65°56'S 50°52'E, 386–400 m, M. Norman, 15 Nov 1985, NMV F84983 (15), NMV F165585 (1), NMV F189876 (4); stn HRD011, 65°50'S 50°35'E, 540 m, M. Norman, 20 Nov 1985, NMV F189880 (2).

*Description (emended from O'Loughlin et al. 2009b)*. Specimens up to 35 mm long preserved (tentacles partly extended, NMV F104998), sub-cylindrical, elongate, widest diameter 5 mm; soft thick body wall; lacking distinct ventral sole; oral end sometimes upturned, slightly tapered and rounded distally when tentacles withdrawn; anal end slightly tapered and rounded distally; 13 to 16 dendritic tentacles (holotype with 13; NMV F104998 with 16; one paratype NHMUK 2011.171–173 with 15), typically in a single circle of 5 single, smaller, radial and 5 pairs of larger, inter-radial tentacles; long digitiform genital papilla posterior to dorsal tentacle pair immediately distal to tentacle crown in male specimen (suggesting internal fertilization and brood protection); female genital pore posterior to dorsal tentacle pair; tube feet large, confined to radii, spaced in single series

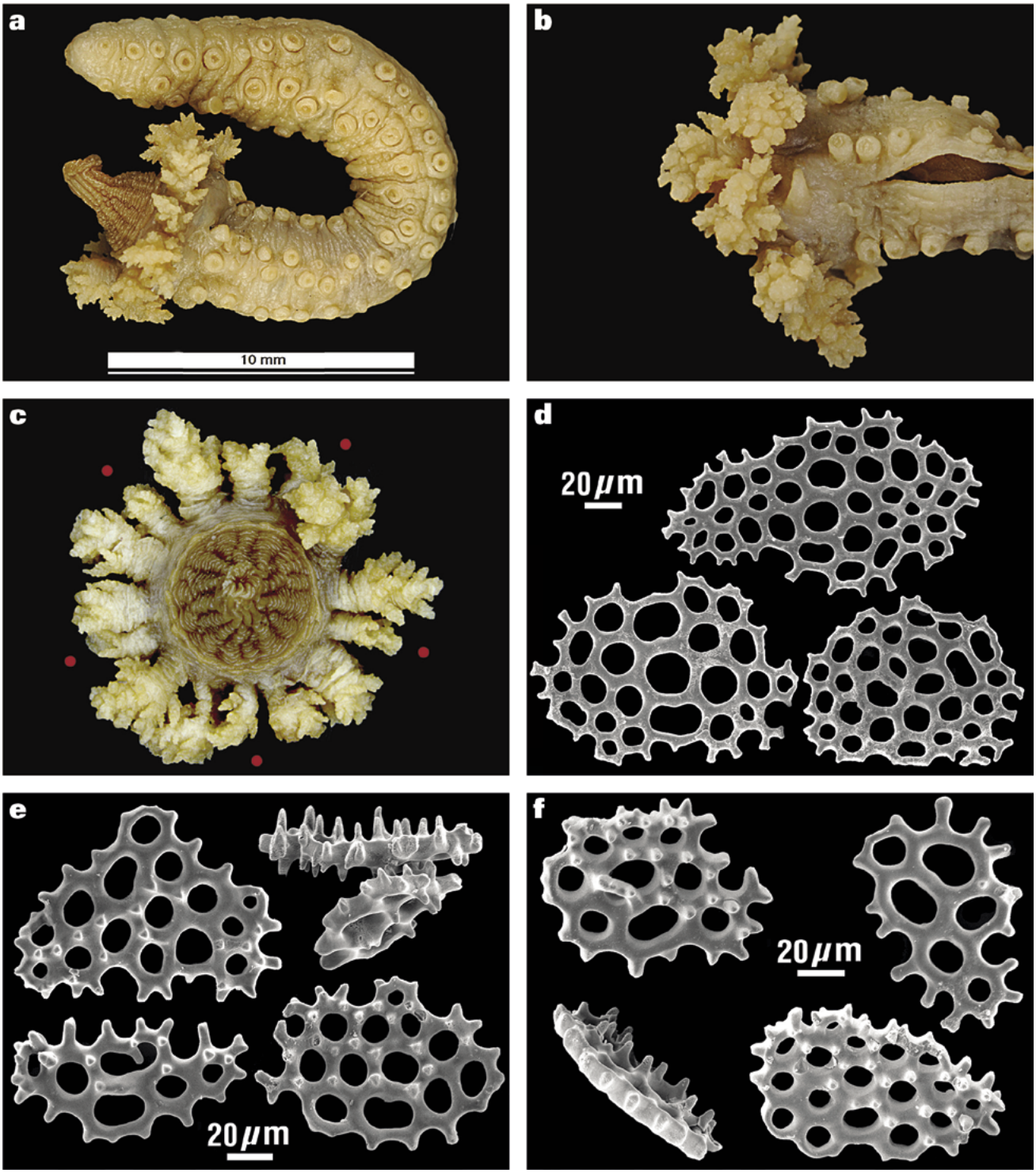


Figure 15. *Parathyonidium incertum* Heding, 1954. a–c, paratypes NHMUK 2011.171–173. a, specimen showing large radial tube feet, and smaller tentacle aligned with radius / ambulacrum (oeophagus everted); b, dorsal inter-radial male genital papilla immediately distal to tentacle crown; c, view of tentacle crown with smallest tentacles aligned with radii / ambulacra (denoted by red spot; top right small tentacle obscured by larger tentacle). d–f, specimen NMV F104998. d, SEM images of ossicles from tentacles; e, SEM images of ossicles from dorsal mid-body wall; f, SEM images of ossicles from ventral mid-body wall.

from base of tentacles to anus; calcareous ring with radial plates only, sub-rectangular, elongate, wide anteriorly and posteriorly, narrowed mid-plate, deep posterior notch; 1–2 long, tubular polian vesicles; no respiratory trees; gonad tubules in two tufts, not in series along gonoduct, one tuft on each side of dorsal mesentery, tubules not branched; brood-protection of free juveniles in the coelom.

Body wall ossicles two types of plates: abundant, thin, lattice-like, smooth to knobbed, single-layered, irregular plates, with bluntly denticulate margins, and with few to many perforations, similar dorsally and ventrally; and additional thin, elongate, plates, with 2 large central perforations, 2 small distal perforations, with one end extended with few small perforations, and with short blunt denticulations on surface and around margin, typically 100 $\mu$m long, but up to 160 $\mu$m long; these small plates intergrade with the larger smooth to knobbed, marginally denticulate plates, that are up to 200 $\mu$m long. Tube foot with large (up to 360 $\mu$m diameter) endplates, few perforated support plates. Tentacle ossicles perforated round to oval, slightly concave plates, with blunt marginal denticulations, some with central knob, some fine surface spines, plates up to 280 $\mu$m long; rods absent. Peri-anal body wall with incipiently multi-layered, thick, round, perforated plates / scales, 440 $\mu$m diameter.

*Colour (preserved).* Yellow-white, some specimens with a violet hue; purple internally (Heding 1954), pale grey (this work).

*Distribution*. South Atlantic, South Georgia, Shag Rock; Western Antarctica, Elephant I., South Shetland Is, Antarctic Peninsula; Eastern Antarctica, Enderby Land; 115–600 m.

*Remarks*. Heding and Panning (1954) makes clear reference to a "Type" from Shag Rock, and also refers in the description to additional specimens. This holotype has not been located in any of the European or United States museums. There are paratypes so labelled in the MNHN and ZMUC. Amongst the *Discovery Expedition* specimens there are three from Clarence Island in the South Shetland Islands (NHMUK 2011.171–173) that are from the same original lot as the labelled paratypes in Copenhagen (ZMUC–HOL–300 (3)). We have labelled and listed these NHMUK specimens as paratypes. We have found numerous specimens from off Enderby Land in Eastern Antarctica in the collections of Museum Victoria (NMV). These coelomic brood-protecting specimens were first thought to represent a new species (see O'Loughlin *et al*. 2009a, 2010), but we now judge that they are conspecific with *Parathyonidium incertum*. This is the only Antarctic coelomic brood-protecting species reported to date (see O'Loughlin *et al*. 2009a).

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## References

Arndt, A., C. Marquez, P. Lambert and Smith M. J. 1996. Molecular phylogeny of eastern Pacific sea cucumbers (Echinodermata: Holothuroidea) based on mitochondrial DNA sequence. *Molecular Phylogenetics and Evolution* 6: 425–437.

Brandt, J. F. 1835. *Prodromus descriptionis animalium ab H. Mertensio in orbis terrarum*. Petropoli.

Britten, M. 1910. Echinodermata: A)Holothuroidea. In *Zoologische und Anthropologische Ergebnisse einer Forschungsreise im Westlichen und Zentralen Südafrika Ausgeführt in den jahren 1903–1905* 4(14): 239–243. Jena.

Cherbonnier, G. 1941. Note sur une nouvelle Holothurie antarctique: *Cucumaria cornuta* nov. sp. *Bulletin Sociétè Zoologique France* 66: 271–270.

Cherbonnier, G. 1949. Note sur une holothurie nouvelle des côtes du Sénégal: *Hemioedema goreensis* n. sp. *Bulletin Muséum National Histoire Naturelle Paris* 2 série 21(5): 585–589.

Cherbonnier, G. 1950. Une nouvelle holothurie dendrochirote des côtes du Cameroun: *Cladodactyla monodi* n. sp. *Bulletin Muséum National Histoire Naturelle Paris* 2 série 22(3): 375–377.

Cherbonnier, G. 1952. Contribution à la connaisance des holothuries de l'Afrique du Sud. *Transactions of the Royal Society of South Africa* 33: 469–509, 16 pls.

Cherbonnier, G. 1957. Holothuries des côtes de Sierra-Leone. *Bulletin Muséum National Histoire Naturelle Paris* 2 série 29(6): 485–492.

Cherbonnier, G. 1958. Holothuries des côtes de Sierra-Leone. (4e note). *Bulletin Muséum National Histoire Naturelle Paris* 2 série 30(3): 294–299.

Cherbonnier, G. 1961. Deux nouvelles espèces d'holothuries dendrochirotes des côtes Brésiliennes. *Bulletin Muséum National Histoire Naturelle Paris* 2 série 33(6): 611–615.

Clark, H. L. 1901. Echinoderms from Puget Sound: Observations made on the Echinoderms collected by the parties from Columbia University, in Puget Sound in 1896 and 1897. *Proceedings Boston Society Natural History* 29: 323–337.

Cowles, R. P. 1907. *Cucumaria curata* sp. nov. *Johns Hopkins University Circular* 195: 8–9, pl. 2 figs 2, 3, 5, 6, pl. 4 fig. 7.

Deichmann, E. 1930. The Holothurians of the Western Part of the Atlantic Ocean. *Bulletin of the Museum of Comparative Zoology, Harvard University* 71: 43–236.

Deichmann, E. 1938. Eastern Pacific Expeditions of the New York Zoological Society. XVI. Holothurians from the western coasts of Lower California and Central America, and from the Galapagos Islands. *Zoologica, New York* 23: 361–387.

Deichmann, E. 1941. The Holothurioidea collected by the Velero III during the years 1932 to 1948. Part I, Dendrochirota. *Allan Hancock Pacific Expeditions* 8: 61–153, pls 10–30.

Ekman, S. 1925. Holothurien. *Further zoological results of the Swedish Antarctic Expedition 1901–1903* 1(6): 1–194.

Ekman, S. 1927. Holothurien der deutschen Südpolar–Expedition 1901–1903 aus der Ostantarktis und von den Kerguelen. *Deutsche Südpolar–Expedition* 19 (Zoology 11): 359–419.

Grube, A. E. 1840. *Aktinien, Echinodermen und Würmer des Adriatischen und Mittelmeeres*. pp. 33–43, 1 pl. Königsberg.

Gutt, J. 1990. New Antarctic holothurians (Echinodermata). I. Five new species with four new genera of the order Dendrochirota. *Zoologica Scripta* 19: 101–117.

Hansen, B. 1988. The genus *Staurocucumis* Ekman and its possible affinity with *Echinocucumis* Sars (Holothuroidea, Dendrochirota). In: R. D. Burke, P. V. Mladenov, P. Lambert and R. L. Parsley (eds.) Echinoderm biology. Proceedings of the Sixth International Echinoderm Conference, Victoria, 23-28 August 1987. p 301-308.

Heding, S. G. 1942. Über *Cucumella triplex* und zwei neue Holothurien der Deutschen Tiefsee–Expedition. *Zoologischer Anzeiger* 137: 217–220.

Heding, S. G. 1943. Deux nouvelles holothuries dendrochirotes du Congo et quelques remarques au sujet de *Halodeima coluber* (Semper). *Bulletin du Musée royal d'Histoire naturelle de Belgique* 19(34): 1–8.

Heding, S. G. and Panning, A. 1954. Phyllophoridae. Eine bearbeitung der polytentaculaten dendrochiroten holothurien des zoologischen museums in Kopenhagen. *Spolia Zoologica Musei Hauniensis* 13: 209 pp.

Hoareau, T. and Boissin, E. 2010. Design of phylum-specific hybrid primers for DNA barcoding: addressing the need for efficient COI amplification in the Echinodermata. *Molecular Ecology Resources* 10: 960–967.

Koehler, R. 1921. *Faune de France. 1. Échinodermes*. 210 pp., 153 figs. Le Chevalier: Paris.

Koehler, R. 1927. *Les Échinodermes des mers d'Europe*. 2. 339 pp. Librarie Octave, Gaston Doin: Paris.

Koehler, R. and Vaney, C. 1908. *Holothuries recuielles par l'Investigator dans l'Ocean Indien. 2. Les Holothuries Littorales*. 54 pp., 3 pls. Trustees Indian Museum: Calcutta.

Lambert, P. 1998. A taxonomic review of five northeastern Pacific sea cucumbers (Holothuroidea). Pp. 473–477 in: Mooi, R. and Telford, T. (eds). *Echinoderms: San Francisco. Proceedings of the Ninth International Echinoderm Conference*. Balkema: Rotterdam.

Lampert, K. 1885. Die Seewalzen. Holothurioidea. Eine Systematiche Monographie. In Semper, C. (ed.) *Reisen im Archipel der Philippinen* 4(3): 312 pp., 1 pl., 3 figs. Wiesbaden.

Lampert, K. 1886. Die Holothurien von Süd-Georgien. *Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten* 3: 10–22, 1 pl.

Lesson, R. P. 1830. *Centurie Zoologique on Choix D'animaux Rares, Nouveaux ou Imparfaitement Connus*. Levrault, Paris. 244 pp., 80 pls.

Liao, Y. and Clark, A. M. 1995. *The Echinoderms of Southern China*. 614 pp., 338 figs, 23 pls. Science Press: Beijing and New York.

Ludwig, H. 1874 (1875). Beiträge zur Kenntniss der Holothurien. Arbeiten aus dem Zoologisch-Zootomischen Institut in Würzburg 2: 77–120, pls 6–7.

Ludwig, H. 1894. Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands, in charge of Alexander Agassiz, by the U.S. Fish Commission steamer *Albatross*, during 1891. XII. The Holothurioidea. *Memoirs of the Museum of Comparative Zoology, Harvard University* 17(3): 1–183, pls 1–19.

Ludwig, H. 1898. Holothurien. In: *Ergebnisse der Hamburger Magalhaensischen Sammelreise 1892/1893. Herausgegeben Naturhistorischen Museum Hamburg* 1. 98 pp., 3 pls.

Marenzeller v. E. 1874. Kritik adriatischer Holothurien. *Verhandlungen zoologisch-botanischen Gesellschaft in Wien* 24: 299–320.

Marenzeller v. E. 1881. Neue Holothurien von Japan und China. *Verhandlungen zoologisch-botanischen Gesellschaft in Wien* 31: 121–140, pls 4, 5.

Massin, C. and Hendrickx, M. E. 2011. Deep-water Holothuroidea (Echinodermata) collected during the TALUD cruises off the Pacific coast of Mexico, with the description of two new species. *Revista Mexicana de Biodiversidad* 82: 413–443.

Michonneau, F. and Paulay, G. 2014. Revision of the genus *Phyrella* (Holothuroidea: Dendrochirotida) with the description of a new species from Guam. *Zootaxa* 3760(2): 101–140.

Moodley, M. N. 2008. A new dendrochirotíd sea cucumber from the west coast of South Africa (Echinodermata: Holothuroidea: Cucumariidae). *African Zoology* 43(1): 61–65.

Mortensen, T. 1925a. Echinoderms of New Zealand and the Auckland-Campbell Islands. III–V. Asteroidea, Holothurioidea, Crinoidea. *Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i Kobenhavn* 79: 261–420, text figs 1–70, pls 12–14.

Mortensen, T. 1925b. On a small collection of Echinoderms from the Antarctic Sea. *Arkiv för Zoologi*. 17A 31: 1–12.

Ohshima, H. 1915. Report of the Holothurians collected by the United States Fisheries Steamer *Albatross* in the Northwestern Pacific during the summer of 1906. *Proceedings United States National Museum* 48: 213–291, pls. 8–11.

O'Loughlin, P. M. 1994. Brood-protecting and fissiparous cucumariids (Echinodermata, Holothurioidea). Pp. 539–547, 1 tbl., 6 figs *in* David, B., Guille, A., Féral, J-P. and Roux, M. (eds). *Echinoderms through Time. Proceedings of the Eighth International Echinoderm Conference, Dijon, France, 6–10 September, 1993*. Balkema: Rotterdam.

O'Loughlin, P. M. 2002. Report on selected species of BANZARE and ANARE Holothuroidea, with reviews of *Meseres* Ludwig and *Heterocucumis* Panning (Echinodermata). *Memoirs of Museum Victoria* 59(2): 297–325.

O'Loughlin, P. M. 2009. BANZARE holothuroids (Echinodermata: Holothuroidea). *Zootaxa* 2196: 1–18.

O'Loughlin, P. M. and Alcock, N. 2000. The New Zealand Cucumariidae (Echinodermata: Holothuroidea). *Memoirs of the Museum of Victoria* 58(1): 1–24, figs 1–6.

O'Loughlin, P. M., Eichler, J., Altoff, L., Falconer, A., Mackenzie, M., Whitfield, E. and Rowley, C. 2009a. Observations of reproductive strategies for some dendrochirotid holothuroids (Echinodermata: Holothuroidea: Dendrochirotida). *Memoirs of Museum Victoria* 66: 215–220.

O'Loughlin, P. M., Manjón-Cabeza, M. E. and Ruiz, F. M. 2009b. Antarctic holothuroids from the Bellingshausen Sea, with descriptions of new species (Echinodermata: Holothuroidea). *Zootaxa* 2016: 1–16.

O'Loughlin, P. M., Paulay, G., Davey, N. and Michonneau, F. 2010. The Antarctic region as a marine biodiversity hotspot for echinoderms: Diversity and diversification of sea cucumbers. *Deep-Sea Research II* 58 (2011): 264–275.

O'Loughlin, P. M., Stępień, A., Kuźniak, M., and VandenSpiegel, D. 2013. A new genus and four new species of sea cucumbers (Echinodermata) from Admiralty Bay, King George Island. *Polish Polar Research* 34(1): 67–86.

O'Loughlin, P. M. and VandenSpiegel, D. 2010. A revision of Antarctic and some Indo-Pacific apodid sea cucumbers (Echinodermata: Holothuroidea: Apodida). *Memoirs of Museum Victoria* 67: 61–95.

O'Loughlin, P. M. and Whitfield, E. 2010. New species of *Psolus* Oken from Antarctica (Echinodermata: Holothuroidea: Psolidae). *Zootaxa* 2528: 61–68.

Panning, A. 1940. Dendrochirote Holothurien von Dakar. *Videnskabelige meddelelser fra Dansk naturhistorisk forening* 104: 169–178.

Panning, A. 1949. Versuch einer Neuordnung der Familie Cucumariidae (Holothurioidea, Dendrochirota). *Zoologische Jahrbücher Abteilung für Systematik, Ökologie Geographie Tiere* 78: 404–470.

Panning, A. 1951. Über *Pseudocnus leoninus* (Semper) und verwandte Arten. *Zoologische Anzeiger* 146: 73–80.

Panning, A. 1957. Bemerkungen über die holothurian familie Cucumariidae (Ordnung Dendrochirota). 2. Die gattungen *Cladodactyla, Hemioedema* und *Psolidiella*. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 55: 25–38.

Panning, A. 1962. Bemerkungen über die holothurian familie Cucumariidae (Ordnung Dendrochirota). 3. Die gattung *Pseudocnus* Panning 1949. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 60: 57–80.

Pawson, D. L. and Fell, H. B. 1965. A revised classification of the dendrochirote holothurians. *Breviora* 214: 1–7. Museum Comparative Zoology: Harvard.

Semper, C. 1868 (1867). Holothurien. *Reisen im Archipel der Philippinen* 1: 1–288, pls 1–40.

Sluiter, C. P. 1910. Westindische Holothurien. *Zoologische Jahrbücher Supplement* 11(2): 331–342.

Smirnov, A. V. 2012. System of the class Holothuroidea. *Paleontological Journal* 46 (8): 793–832.

Tamura K., Stecher G., Peterson D., Filipski A., and Kumar S. 2013. MEGA6: Molecular Evolutionary Genetics Analysis Version 6.0. *Molecular Biology and Evolution* 30: 2725–2729.

Thandar, A. S. 1987. The status of some southern African nominal species of *Cucumaria* (s.e.) referable to a new genus and their ecological isolation. *South African Journal of Zoology* 22(4): 287–296.

Thandar, A. S. 2008. Additions to the holothuroid fauna of the southern African temperate faunistic provinces, with descriptions of new species. *Zootaxa* 1697: 1–57.

Théel, H. 1886. Report on the Holothurioidea dredged by H.M.S. *Challenger* during the years 1873–1876. *Report on the scientific results of the voyage of H.M.S.* Challenger, *Zoology* 14 (39): 1–290, 16 pls.

Vaney, C. 1906. Deux nouvelles Holothuries du genre *Thyone* provenant des Orcades du Sud. *Bulletin du Muséum d'Histoire naturelle, Paris* 12(6): 400–402.

Vaney, C. 1908a. Les Holothuries recueillies par l'Expédition antarctique écossaise. *Zoologischer Anzeiger* 33 (10): 290–299.

Vaney, C. 1908b. Les Holothuries de l'Expédition Antarctique National Ecossaise. *Transactions of the Royal Society of Edinburg* 6(1): 1–37, 5 pls.

Verrill, A. E. 1876a. Annelids and Echinoderms. Holothuroidea. *Pentactella* g. n. Pp. 68–69 in Kidder, J. H. (ed.). *Contributions to the Natural History of Kerguelen Island*. Harvard University Herbarium.

Verrill, A. E. 1876b. Annelids and Echinoderms, and Anthozoa in *Contributions to the Natural History of Kerguelen Island*. *Bulletin of the United States National Museum* 3: 64–77.

Wells, H. 1924. New Species of *Cucumaria* from Monterey Bay California. *Annals of the Magazine of Natural History* 9(14): 113–121, 1 pl.

Won, J. H. and Rho, B. J. 1998. Two new species and four new records of Holothuroidea from Korea. *Korean Journal Biological Sciences* 2: 9–20.

Wyville Thomson, C. 1878. Notice of some peculiarities in the mode of propagation of certain echinoderms of the Southern Sea. *Journal of the Linnean Society of London (Zoology)* 13: 55–79.

Yang, P. F. 1937. Report on the holothurians from the Fukien Coast. *Bulletin Marine Biology, Amoy, China* 2: 1–46.

Appendix 1. List of species, tissue sample code numbers, specimen repositories, specimen registration numbers, and GenBank Accession numbers.

| Genus | species | Sample number | Voucher repository | Catalog number | Location | GenBank Accession number |
|---|---|---|---|---|---|---|
| Heterocucumis | steineni | MOLN_195 | NIWA | 35396 | Ross Sea | HM196616.1 |
| Heterocucumis | steineni | MOLAF_0785 | NHM | 2010.125-130 | Amundsen Sea | HM196617.1 |
| Heterocucumis | steineni | MOLSI_043 | USNM | 1132662 | Bransfield Strait | HM196618.1 |
| Heterocucumis | steineni | MOLN_194 | NIWA | 36744 | Ross Sea | HM196619.1 |
| Heterocucumis | steineni | MOLN_196 | NIWA | 42196 | Ross Sea | HM196620.1 |
| Heterocucumis | steineni | MOLN_197 | NIWA | 35675 | Ross Sea | HM196621.1 |
| Heterocucumis | steineni | MOLAF_0786 | NHM | 2010.125-130 | Amundsen Sea | HM196622.1 |
| Heterocucumis | steineni | MOLG_107 | NIWA | 60846 | Ross Sea | HM196623.1 |
| Heterocucumis | steineni | MOLSI_065 | USNM | 1132677 | Bransfield Strait | HM196624.1 |
| Heterocucumis | steineni | MOLG_106 | NIWA | 60855 | Ross Sea | HM196625.1 |
| Heterocucumis | steineni | MOLSI_026 | USNM | 1132644 | Bransfield Strait | HM196626.1 |
| Heterocucumis | steineni | MOLAF_0784 | NHM | 2010.124 | Amundsen Sea | HM196627.1 |
| Heterocucumis | steineni | MOLSI_037 | USNM | 1132658 | Bransfield Strait | HM196628.1 |
| Heterocucumis | steineni | MOLSI_050 | USNM | 1132668 | Bransfield Strait | HM196629.1 |
| Heterocucumis | steineni | MOLSI_038 | USNM | 1132658 | Bransfield Strait | HM196630.1 |
| Staurocucumis | liouvillei | MOLAF_0541 | NMV | F104802 | South Georgia | HM196658.1 |
| Staurocucumis | liouvillei | MOLN_172 | NIWA | 36028 | Ross Sea | HM196659.1 |
| Staurocucumis | liouvillei | MOLSI_035 | USNM | 1132656 | Bransfield Strait | HM196660.1 |
| Staurocucumis | liouvillei | MOLN_173 | NIWA | 42158 | Ross Sea | HM196661.1 |
| Staurocucumis | liouvillei | MOLAF_0700 | NMV | F165748 | Heard Island | HM196662.1 |
| Staurocucumis | liouvillei | MOLAF_0537 | NMV | F160028 | Bouvet Island | HM196663.1 |
| Staurocucumis | liouvillei | MOLAF_0788 | NHM | 2010.168-173 | Amundsen Sea | HM196664.1 |
| Staurocucumis | liouvillei | MOLN_174 | NIWA | 36562 | Ross Sea | HM196665.1 |
| Staurocucumis | liouvillei | MOLAF_0539 | NMV | F104986 | Bouvet Island | HM196666.1 |
| Staurocucumis | liouvillei | MOLAF_0783 | NHM | 2010.158-163 | Amundsen Sea | HM196667.1 |
| Staurocucumis | liouvillei | MOLAF_0781 | NHM | 2010.158-163 | Amundsen Sea | HM196668.1 |
| Staurocucumis | liouvillei | MOLAF_0787 | NHM | 2010.168-173 | Amundsen Sea | HM196669.1 |
| Staurocucumis | liouvillei | MOLAF_0540 | NMV | F104800 | Falkland Islands | HM196670.1 |
| Staurocucumis | liouvillei | MOLN_175 | NIWA | 36904 | Ross Sea | HM196671.1 |
| Staurocucumis | krzysztofi | MOLSI_056 | USNM | 1132671 | Bransfield Strait | HM196672.1 |
| Staurocucumis | krzysztofi | MOLSI_057 | USNM | 1132671 | Bransfield Strait | HM196673.1 |
| Staurocucumis | krzysztofi | MOLSI_048 | USNM | 1132667 | South Shetlands | HM196674.1 |
| Crucella | hystrix | MOLAF_0793 | NHM | 2010.118 | Amundsen Sea | HM196710.1 |
| Crucella | hystrix | MOLN_170 | NIWA | 38641 | Ross Sea | HM196711.1 |
| Crucella | hystrix | MOLN_169 | NIWA | 42202 | Ross Sea | HM196712.1 |
| Crucella | hystrix | MOLN_171 | NIWA | 37784 | Ross Sea | HM196713.1 |
| Paracucumis | turricata | MOLAF_0791 | NHM | 2010.156 | Amundsen Sea | HM196714.1 |
| Paracucumis | turricata | MOLN_201 | NIWA | 36025 | Ross Sea | HM196715.1 |
| Paracucumis | turricata | MOLAF_0792 | NHM | 2010.157 | Amundsen Sea | HM196716.1 |
| Paracucumis | turricata | MOLN_200 | NIWA | 36490 | Ross Sea | HM196717.1 |
| Paracucumis | turricata | MOLN_202 | NIWA | 36007 | Ross Sea | HM196718.1 |
| Crucella | susannae | MOLSI_068 | USNM | 1132679 | Bransfield Strait | HM196719.1 |
| Crucella | scotiae | MOLG_098 | NIWA | 60742 | Ross Sea | HM196720.1 |
| Crucella | scotiae | MOLN_192 | NIWA | 36602 | Ross Sea | HM196721.1 |
| Crucella | scotiae | MOLG_097 | NIWA | 60730 | Ross Sea | HM196722.1 |

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|---|---|---|---|---|---|---|
| Crucella | scotiae | MOLG_099 | NIWA | 60732 | Ross Sea | HM196723.1 |
| Psolidium | tenue | MOLAF_0709 | NHM | 2010.151 | Amundsen Sea | HM196735.1 |
| Abyssocucumis | abyssorum | MOLN_141a | NIWA | 37727 | Ross Sea | KP165441 |
| Abyssocucumis | abyssorum | MOLN_141b | NIWA | 37727 | Ross Sea | KP165442 |
| Abyssocucumis | abyssorum | MOLN_142 | NIWA | 38038 | Ross Sea | KP165443 |
| Abyssocucumis | abyssorum | MOLN_143 | NIWA | 38033 | Ross Sea | KP165444 |
| Cladodactyla | crocea | MOLAF_0501 | NMV | F105017 | Falkland Islands | KP165445 |
| Cladodactyla | crocea | MOLAF_0502 | NMV | F105017 | Falkland Islands | KP165446 |
| Cladodactyla | crocea | MOLAF_0503 | NMV | F105002 | Falkland Islands | KP165447 |
| Cladodactyla | crocea | MOLAF_0504 | NMV | F106967 | Falkland Islands | KP165448 |
| Cladodactyla | sicinski | MOLAF_1298 | NMV | F193766 | South Shetlands | KP165449 |
| Cladodactyla | sicinski | MOLAF_1300 | NMV | F193772 | South Shetlands | KP165450 |
| Crucella | hystrix | BASEC134-09 | NHMUK | 2010.118 | Amundsen Sea | KP165451 |
| Crucella | susannae | MOLAF_1293 | NMV | F193784 | South Shetlands | KP165452 |
| Heterocucumis | denticulata | MOLG_101 | NIWA | 60822 | Ross Sea | KP165453 |
| Heterocucumis | denticulata | MOLG_102 | NIWA | 60824 | Ross Sea | KP165454 |
| Heterocucumis | denticulata | MOLG_103 | NIWA | 60794 | Ross Sea | KP165455 |
| Heterocucumis | denticulata | MOLG_104 | NIWA | 60784 | Ross Sea | KP165456 |
| Heterocucumis | denticulata | MOLG_105 | NIWA | 60799 | Ross Sea | KP165457 |
| Heterocucumis | denticulata | MOLN_163 | NIWA | 42174 | Ross Sea | KP165458 |
| Heterocucumis | denticulata | MOLN_164 | NIWA | 35932 | Ross Sea | KP165459 |
| Heterocucumis | steineni | BASEC079-09 | NHMUK | 2010.124 | Amundsen Sea | KP165462 |
| Heterocucumis | steineni | MOLAF_0874 | NMV | F169300 | South Orkneys | KP165461 |
| Heterocucumis | steineni | MOLAF_1243 | AAD BRC | 525 | Prydz Bay | KP165460 |
| Laevocnus | katrinae | MOLAF_0815 | NMV | F168836 | Falkland Islands | KP165463 |
| Laevocnus | laevigatus | MOLAF_0670 | NMV | F165738 | Heard Island | KP165464 |
| Laevocnus | laevigatus | NDMQ_11 | NIWA | 40109 | Macquarie Seamount | KP165465 |
| Laevocnus | laevigatus | NDMQ_12 | NIWA | 40205 | Macquarie Seamount | KP165466 |
| Laevocnus | leachmani | MOLN_182 | NIWA | 42203 | Ross Sea | KP165467 |
| Laevocnus | leoninus | MOLAF_0507 | NMV | F104820 | Falkland Islands | KP165468 |
| Laevocnus | leoninus | MOLAF_0508 | NMV | F106960 | Falkland Islands | KP165469 |
| Laevocnus | leoninus | MOLAF_0509 | NMV | F106962 | Falkland Islands | KP165470 |
| Laevocnus | leoninus | MOLAF_0510 | NMV | F161500 | Falkland Islands | KP165471 |
| Laevocnus | perrieri | MOLAF_0511 | NMV | F106964 | Falkland Islands | KP165472 |
| Laevocnus | perrieri | MOLAF_0512 | NMV | F104844 | Falkland Islands | KP165473 |
| Laevocnus | perrieri | MOLAF_0514 | NMV | F104844 | Falkland Islands | KP165474 |
| Laevocnus | serratus | MOLAF_0683 | NMV | F165742 | Heard Island | KP165475 |
| Paracucumis | turricata | BASEC120-09 | NHMUK | 2010.157 | Amundsen Sea | KP165477 |
| Paracucumis | turricata | MOLAF_0891 | NMV | F169314 | South Orkneys | KP165476 |
| Staurocucumis | krzysztofi | MOLSI_064 | USNM | 1132676 | Bransfield Strait | KP165478 |
| Staurocucumis | liouvillei | MOLAF_1247 | AAD BRC | 512 | Prydz Bay | KP165479 |
| Staurocucumis | liouvillei | MOLAF_1248 | AAD BRC | 513 | Prydz Bay | KP165480 |
| Staurocucumis | liouvillei | MOLAF_1249 | AAD BRC | 524 | Prydz Bay | KP165481 |
| Staurocucumis | nocturna | MOLAF_0399 | NMV | F149749 | NW Australia | KP165482 |
| Staurocucumis | nocturna | MOLAF_0400 | NMV | F151833 | NW Australia | KP165483 |
| Staurocucumis | species | MOLAF_0872 | NMV | F169307 | South Orkneys | KP165484 |
| Staurocucumis | turqueti | MOLG_055 | NIWA | 61055 | Ross Sea | KP165485 |
| Staurocucumis | turqueti | MOLN_198 | NIWA | 35782 | Ross Sea | KP165486 |
| Staurocucumis | turqueti | MOLN_199 | NIWA | 42169 | Ross Sea | KP165487 |