A re-appraisal of the holothuroid genera *Pseudocnus* Panning, 1949 and *Pseudocnella* Thandar, 1987 based on morphological and, for the latter, also molecular evidence (Echinodermata: Holothuroidea: Dendrochirotida: Cucumariidae)

by

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PREFACE

The research embodied in this thesis was completed by the candidate in the Discipline of Biology and Conservation in the School of Life Sciences of the College of Agriculture, Engineering and Science, University of KwaZulu-Natal, Westville Campus, Durban, South Africa. The research was financially supported by the National Research Foundation (NRF).

The contents of this work have not been submitted in any form to another university and, except for the observation and conclusions of other workers which are acknowledged in the text, the results reported are due to investigations by the candidate himself.

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Signed: A.S. Thandar (supervisor)

Date:

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Date:

DECLARATION 1: PLAGIARISM

I, Sifiso Mjobo, declare that:

(i) the research reported in this dissertation, except where otherwise indicated or acknowledged, is my original work;

(ii) this dissertation has not been submitted in full or in part for any degree or examination to any other university;

(iii) this dissertation does not contain other persons' data, pictures, graphs or other information, unless specifically acknowledged as being sourced from other persons;

(iv) this dissertation does not contain other persons' writing, unless specifically acknowledged as being sourced from other researchers. Where other written sources have been quoted, then:

a) their words have been re-written but the general information attributed to them has been referenced;

b) where their exact words have been used, their writing has been placed inside quotation marks, and referenced;

(v) where I have used material for which publications followed, I have indicated in detail my role in the work;

(vi) this dissertation is primarily a collection of material prepared by myself, and includes that submitted for publication as a journal article or presented as poster and/or oral presentations at conferences or meetings. In some cases, additional material has been included;

(vii) this dissertation does not contain text, graphics or tables copied and pasted from the Internet, unless specifically acknowledged, and the source being detailed in the dissertation and in the References section.

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Signed: S. Mjobo (candidate)

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DECLARATION 2: PUBLICATION

My role in this submitted paper is indicated. The * indicates senior and corresponding author.

Mjobo, S. * and Thandar, A. S. submitted. A new genus and a new species in the cucumariid subfamily Colochirinae (Echinodermata: Holothuroidea: Dendrochirotida: Cucumariidae).

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Signed: S. Mjobo

Date:

ABSTRACT

After the erection of the genus *Pseudocnella* by Thandar (1987) to accommodate three southern African Cucumariids and a Mediterranean form, then classified in *Pseudocnus,* certain problems still remained. In addition to this the recent revision of the Antarctic-Subantarctic species of *Pseudocnus* by O'Loughlin *et* al. (2014) left the remaining world species unattended to. Due to the above, both these genera (*Pseudocnus* and *Pseudocnella*) were looked at critically in order to determine whether all species assigned to them are congeneric. As far as the genus *Pseudocnus* is concerned those species excluded from O'Loughlin *et al* (2014) revision are looked at only morphologically by examining available materials and literature. Species belonging to the genus *Pseudocnella* are examined from both morphological and molecular aspects. O'Loughlin *et al*. (2014) restriction of the genus *Pseudocnus* was accepted and hence two new genera *Panningocnus* and *Thandarocnus* are diagnosed for those species with unequal tentacles and body wall deposits respectively made up of a single or more than a single layer of calcareous material. On this basis only three species now remain in *Pseudocnus*, with *Cucumaria koellikeri* Semper, 1868 as type species, nine species are transferred to *Panningocnus*, with *Cucumaria dubiosa* Semper, 1868 as type species and the remaining six species transferred to *Thandarocnus* with *Pseudocnus sentus* O'Loughlin & Alcock, 2000 as type species. A new genus *Hemiocnus* is erected for *Cladodactyla syracusana* Grube, 1840 (=*Pseudocnella syracusana*) as type species and to this is also transferred *Pseudocnella insolens* (Théel, 1886). The genus *Pseudocnella* now appears to accommodate only two South African nominal species with *Cucumaria sinorbis* Cherbonnier, 1952 remaining as type species. All species dealt with are diagnosed, keyed and their geographical distributions mapped, except those dealt with by O'Loughlin *et al*. (2014) and Thandar (1987).

Key words: Colochirinae, Cucumariinae, *Pseudocnus*, *Pseudocnella*, *Panningocnus*, *Thandarocnus*, *Hemiocnus,* new genera.

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I owe special gratitude to the curators of the following museums: MNHN, NMNH, ZMH, MCZ, ZMC, CAS, FMNH, MV, and USNM for loan of their invaluable materials.

I owe sincere gratitude to my family, especially my sisters Bulelwa Mjobo and Portia Myolwa, and my fiancé Phumlile Mbewu for their financial support and my mom Ntombizonke Dludla for her great motivation to complete my work.

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ABBREVIATIONS

MNHN	Museum Nationale D' Histoire Naturelle (Paris)
NMNH	National Museum of Natural History, United States (Smithsonian Institution)
ZMH	Zoologishes Museum Hamburg
MCZ	Museum Comparative Zoology, Harvard, USA
ZMC	Zoological Museum, Copenhagen
CAS	Academy of Sciences, San Franciso, California
FMNH	Florida Museum of Natural History
MV	Royal Museum, British Columbia, Victoria, Canada
USNM	United States National Museum, Washington
WoRMS	World Register of Marine Species
GBIF	Global Biodiversity Information Functioning
IR	Interradial plates
R	Radial plates
KZN	KwaZulu-Natal, South Africa
spec.	specimen(s)
bp	base pairs

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INTRODUCTION

Panning (1949) while revising the holothuroid family Phyllophoridae found that the classification of species using characters such as tube feet distribution posed a problem, especially in the family Cucumariidae. The separation of genera *Cucumaria* and *Thyone* using tube feet distribution could not be upheld because most juvenile of *Thyone* species, which have tube feet restricted to the ambulacra, were erroneously assigned to *Cucumaria* (Panning 1949). Panning therefore, opted to use the calcareous ring to separate genera in family-group taxa such as Phyllophoridae, Thyonidiinae, Urodeminae and Cucumariidae. He grouped the Cucumariidae into five subfamilies based on the form of calcareous ring: a) those cucumariids with the calcareous ring lacking posterior processes or only with abbreviated, undivided processes he included in the subfamilies Cucumariinae, Colochirinae and Ypsilothuriinae; b) those with the calcareous ring unfragmented but with divided or sometimes undivided processes, into the subfamily Sclerodactylinae; c) those with the calcareous ring subdivided into tiny mosaic-like fragments into the subfamily Thyoninae. Panning (1949) further, chose the form of the body wall ossicles to subdivide his subfamilies Ypsilothuriinae with table-like constructions; Colochirinae with plates and cups/baskets; and Cucumariinae with plates only, no cups nor tables, which resulted in the recognition of 39 genera of which *Heterothyone*, *Pseudothyone*, *Pseudocnus*, *Paracucumaria* and *Allothyone* were new to science. Since Panning did not re-examine most of the species, he based a large part of his revision on the often incomplete descriptions of other authors, assigning many species to wrong genera, one preoccupied. He attempted to rectify his mistakes in subsequent papers (1951, 1952, 1962, and 1964). In his first revision (1949) he designated *Cucumaria koellikeri* (Semper, 1868) as type species to his genus *Pseudocnus* in which he also included a few other species also originally described in *Cucumaria*. These species included *Cucumaria bacciliformis* Koehler & Vaney, 1908; *C. dubios*a Semper, 1868; *C. grubei* Von Marenzeller, 1874; *C. koreaensis* Östergren, 1898; *C. leonina* (Semper, 1868); *C. leonina* var. *africana* (Britten, 1910); *C. piperata* Stimpson, 1855; *C. pusillus* Ludwig, 1886; *C. rhopalodiformis* Heding, 1943; *C. sykion* Lampert, 1885; *C. echinata* Von Marenzeller, 1874; and *C. alcocki* Koehler & Vaney, 1908.

In the same paper (1949) he erroneously identified a specimen of *Cucumaria leonina* (Semper, 1868) as C. *dubiosa* (Semper, 1868), an error he rectified in 1951 by re-describing it as *C. leonina*. Panning (1949) referred *Cucumaria jaegeri* Lampert, 1885 from South

Africa to the genus *Stereoderma*. However, in 1952 he re-assigned *Cucumaria jaegeri* to *Pseudocnus* but as a subspecies of *Cucumaria dubiosa.* But, in this paper he did not mention anything about the other species he assigned to *Pseudocnus* in 1949. In his 1962 revision of *Pseudocnus*, Panning followed Deichmann (1948) by regarding *Cucumaria insolens* Théel, 1886 as a growth stage of *Cucumaria sykion* and subdivided *Pseudocnus* into two groups. Those with knobbed buttons and plates he placed in his *dubiosus* group and those without buttons but only plates in his *laevigatus* group. In the same paper (1962) he designated *Cucumaria dubiosa* (Semper, 1868) as type species of the genus with *Cucumaria koellikeri* (Semper, 1868) together with *Cucumaria leonina* (Semper, 1868), *Cucumaria leonina* var. *africana* Britten, 1910, *Cucumaria jaegeri* Lampert, 1885 as subspecies of *Cucumaria dubiosa*. Moreover, in the same (1962) paper he transferred *Pseudocnus piperata* (Stimpson, 1855) back to *Cucumaria* and regarded the South African form *C. sykion* as presumably belonging to his *dubiosus* group with *C. insolens* as a junior synonym.

Panning (1962) assigned to his *P. dubiosus* group the following 5 subspecies: *Pseudocnus dubiosus dubiosus* (Semper, 1868), *P. dubiosus leoninus* (Semper, 1868), *P. dubiosus koellikeri* (Semper, 1868), *P. dubiosus africanus* (Britten, 1910), *P. dubiosus jaegeri* (Lampert, 1885) (with *insolens* as a synonym) and 7 species to his *P. laevigatus*-group: *P. grubei* (Von Marenzeller, 1874), *P. syracusanus* (Grube, 1840), *P. laevigatus* (Verril, 1876), *P. perrieri* (Ekman, 1927), *P. cornutus* (Cherbonnier, 1941), *P. leononoides* (Mortensen, 1925) and *P. californicus* (Semper, 1868).

However, in 1962 Panning, contrary to the current rules of Zoological Nomenclature, changed the designation of the type species of his *Pseudocnus* from *C. koellikeri* to *C. dubiosa.* This change, according to O'Loughlin *et al*. (2014) and supported herein, cannot be upheld. Furthermore, *Cucumaria koellikeri* and *Cucumaria dubiosa* are morphologically distinct. *Cucumaria koellikeri* has equal tentacles and *Cucumaria dubiosa* unequal tentacles (8+2). The two species therefore cannot be classified in the same genus. Rowe (in Rowe & Gates 1995) and O'Loughlin *et al.* (2014) have correctly pointed this out. Subsequent to Panning's (1949, 1951 and 1962) papers, several other species (new and already known) were assigned to *Pseudocnus*. These include *Pseudocnus intermedia* (Théel, 1886), *P. goreensis* (Cherbonnier, 1949), *P. pawsoni* (Won & Rho, 1998), *P. sentus* O`Loughlin & Alcock, 2000, *P. thandari* Moodley, 2008 and *Pseudocnus* sp. Massin (1993).

Cherbonnier (1952) in his treatment of the South African forms considered *C. sykion* and *C. insolens* as distinct species while describing a form similar to *C. sykion* as *C. sinorbis*. Thandar (1987) also attempted to resolve the problems created by Clark (1923), Deichmann (1948), and Panning (1949, 1951, 1952, 1962) but with regard to the South African species only. He treated *Cucumaria insolens*, *C. sinorbis* and *C. sykion* as distinct species, relegating *jaegeri* to the synonymy of *sykion* and retaining, like Cherbonnier (1952), *C. leonina* var. *africana* in the synonymy of *C. insolens*. He erected the genus *Pseudocnella* to accommodate them and, with some doubt, also included in it *Cladodactyla syracusana* Grube, 1840 from the Mediterranean Sea.

According to the World Register of Marine Species (WoRMS), a total of about 30 species were previously assigned to *Pseudocnus*, but only about 23 species are now accepted and this number conforms to that recorded by the Global Biodiversity Information Facility (GBIF). The table below lists the species accepted by both WoRMS and GBIF before O'Loughlin *et al.* (2014) recent revision of the Antarctic and Subantarctic species of *Pseudocnus*.

Table 1. List of species (and their distributions) accepted in both WoRMS and GBIF before O'Loughlin *et al.* (2014) revision.

Species	**Distribution**
Pseudocnus alcocki (Koehler & Vaney, 1908)	Andaman Islands
P. californicus (Semper, 1868)	Baja, California plus other localities on West coast of Mexico; Central America (Costa Rica).
P. cornutus (Cherbonnier, 1941)	East Patagonia, Falkland Island.
P. curatus (Cowles, 1907)	Gnarled Islands, Dundas Island, British Columbia, Malpaso Creek, Monterey County, California.
P. dubiosus (Semper, 1868)	Peru (type locality) and Chile.
P. dubiosus koellikeri (Semper, 1868)	Mediterranean Sea (Sicily, Naples), Atlantic coast of Morocco and Mauritania, Senegal.
P. dubiosus leoninus (Semper, 1868)	Chile, Peru, West Tiera del Fuego, Patagonia, Falkland Islands, Argentina, Heard and McDonald Islands.
P. echinatus (Von Marenzeller, 1881)	South China, South Japan, Red Sea.
P. goreensis (Cherbonnier, 1949)	Senegal, Gambia, Sierra-Leon, Gabon, Goree Island.

P. intermedia (Théel, 1886)	Heard and Kerguelen Islands.
P. laevigatus (Verrill, 1876)	McDonald Island, Prince Edward Island, Crozet Island, Macquarie Island, Marion Island.
P. lamperti (Ohshima, 1915)	Aleutian Islands, vicinity of Commander Islands, off South Tip of Peninsula (Alaska), North Pacific Ocean, United States, Kyska harbour.
P. leoninoides (Mortensen, 1925)	New Zealand (Auckland Islands, Campbell Island, Snares Island, approximately 150 miles NNE of Macquarie Island, Masked Island, Canley Harbor.
P. lubrica (Clark, 1901)	California, Monterey Bay, Monterey county, Pacific East central, Washington State, Puget Sound (USA).
P. marionensis (Théel, 1886)	Subantarctic (Kerguelen and Marion Islands).
P. pawsoni (Won & Rho, 1998)	Korea
P. perrieri (Ekman, 1927) Panning 1963	South end of South America, off west coast of Chile, Falkland Islands, South Georgia.
P. rhopalodiformis (Heding, 1941)	Congo.
P. sentus O`Loughlin & Alcock, 2000	New Zealand, Stewart Island, Paterson inlet, Kermadec Island, Meyer Island.
P. serratus (Théel, 1886)	Kerguelen Island.
P. spinosus (Ohshima, 1915)	Off Hitaka, Hokkaido, off Oshika Peninsula, Suruga Bay, Honshu Island, Japan.
P. thandari Moodley,2008	Northern Namibia to west coast of South Africa.
P. grubei (von Marenzeller, 1874)	Adriatic and Mediterranean Sea (Naples).

This list has not yet been updated subsequent to O'Loughlin *et al*. (2014) paper.

O'Loughlin *et al.* (2014) revised the Antarctic-Subantarctic species of *Pseudocnus* and referred them to a new genus *Laevocnus* which had a very short shelf-life as it was found to

be a junior synonym of *Pentactella*, erected by Verrill with *Cucumaria laevigata* Verrill, 1876, as type species (O'Loughlin *et al.* 2015). This oversight was perhaps the result of Panning (1949) who relegated *Pentactella* to the synonymy of *Stereoderma* and is resurrected (see O' Loughlin *et al*., 2015). Species of *Pentactella* include: *L. cornuta* (Cherbonnier, 1941), *L. intermedia* (Théel, 1886), *L. katrinae* O'Loughlin in O'Loughlin *et al*., 2014, *L. leachmani* Davey and O'Loughlin in O'Loughlin *et al*., 2014, *L. leoninoides* (Mortensen, 1925), *L. leoninus* (Semper, 1867), *L. marionensis* (Théel, 1886), *L. perrieri* (Ekman, 1927), *L. serratus* (Théel, 1886). However, in WoRMS these species are still listed as belonging to *Pseudocnus*, except for the new species described by O'Loughlin (in O'Loughlin *et al*., 2014) which are listed under the genus *Pentactella*.

Following is the list of 17 species still remaining in *Pseudocnus* after O'Loughlin *et al*.'s (2014) revision of the Antarctic-Subantarctic species: *P. alcocki* (Koehler & Vaney, 1908), *P. californicus* (Semper, 1868), *P. curatus* (Cowles, 1907), *P. dubiosus* (Semper, 1868), *P. echinatus* (von Marenzeller, 1881), *P. goreensis* (Cherbonnier, 1949), *P. grubei* (von Marenzeller, 1874), *P. koellikeri* (Semper, 1868), *P. lamperti* (Ohshima, 1915), *P. lubricus* (H. L. Clark, 1901) (= *C. fisheri astigmata* Wells, 1924 (by Lambert 1998), *P. pawsoni* Won and Rho, 1998, *P. rhopalodiformis* (Heding, 1943), *P. rugosus* Cherbonnier, 1957, *P. salmini* (Ludwig, 1875), *P. sentus* O'Loughlin and Alcock, 2000, *P. spinosus* (Ohshima, 1915), and *P. thandari* Moodley, 2008.

O'Loughlin *et al.* (2014), although restricting their revision to the Antarctic-Subantarctic forms, produced an excellent revision. They restored *Cucumaria dubiosus koellikeri* and *Cucumaria dubiosus leoninus* to full species status and re-instated the former as a type species of the genus. They incorporated morphological, molecular and bio-geographic characters and erected a new genus to accommodate all the species which Panning (1949) assigned to his *laevigatus* group but also included *Cucumaria leonina*. By not considering all *Pseudocnus* species in their revision some of the problems which still exist were left unresolved. However, they re-diagnosed the genus *Pseudocnus* on the basis of its type species (*C. koellikeri*) and this diagnosis is here retained. *Pseudocnus* currently stands with species possessing both equal and unequal tentacles and species with single or multilayered plates and/or buttons in the body wall. Since freshly collected materials of species remaining in *Pseudocnus* were not available for molecular work, only morphological characters are used in this revision. Those with 10 equal tentacles and single-layered body

wall deposits are retained in *Pseudocnus* as they correspond with the characters of the type species, and the ones with unequal (8+2) tentacles and single-layered body wall deposits are re-assigned to a new genus *Panningocnus* and those also with unequal tentacles but with multilayered calcareous deposits to other new genera *Thandarocnus* and *Hemiocnus*.

Genus *Pseudocnella* Thandar, 1987

Thandar (1987) critically looked at some southern African Cucumariids previously described in *Cucumaria* and/or *Pseudocnus* and erected a new genus *Pseudocnella* to accommodate 3 species, namely, *Cucumaria insolens* Théel, 1886; *Cucumaria sykion* Lampert, 1885 and *Cucumaria sinorbis* Cherbonnier, 1952, but included in it also the Mediterranean *C. syracusana* (Grube, 1840). Thandar (1987), agreed with Cherbonnier (1952), by regarding *C. insolens* to be a species distinct from *C. sykion* and not its growth stage as determined by Clark (1923) and Deichmann (1948) and re-iterated by Panning (1951 & 1962). Panning (1952) and (1962), in addition, considered *Cucumaria jaegeri* Lampert, 1885, also from South Africa as a subspecies of *Cucumaria dubiosa* Semper, 1868. Thandar (1987) relegated this species to the synonymy of *C. sykion* in order to stabilise the latter's name. Despite Thandar's revision problems still exist since *P. insolens* has one or two tentacles reduced and also buttons as deposits in the body wall whereas *P. syracusanus* has the two ventral tentacles reduced and also buttons in the body wall. So it is obvious that both these species are not congeneric with *P. sykion* and *P. sinorbis.* In this study both morphological and molecular evidence are used to resolve the problems still existing with the South African species of *Pseudocnella*. Since no freshly collected material of *P. syracusana* was obtained only morphological characters are used for this species. A new genus *Hemiocnus* is diagnosed to accommodate *P. syracusana* and perhaps also *P. insolens.*

While examining *Pseudocnella syracusana* obtained on loan from material received from the United States National Museum (USNM) (Smithsonian Institution) a species probably belonging to *Ocnus*, perhaps new to science, was uncovered. A manuscript describing this species together with the new genus *Hemiocnus* is currently under review.

Recently molecular techniques outstripped morphological techniques in quantifying how distinct or similar species can be, and these techniques have been used repeatedly to delineate species, e.g. Arndt *et al*. (1996) for *Cucumaria curata* Cowles 1907 and *C. lubrica* Clark, 1901. These studies have shown that morphological characters alone to delineate

species is not enough as species may be similar morphologically, but appear distinct on molecular evidence. Hence in the case of the southern African species of *Pseudocnella* both molecular and morphological techniques are used to separate them.

MATERIALS AND METHODS

The following, reasonably identified, specimens of *Pseudocnus* were received on loan from the following international institutions:

ZMH: E2832 *Pseudocnus dubiosus koellikeri*, 1 spec.; E 6766 *Pseudocnus californicus,* 1 spec.; E6581 *Pseudocnus dubiosus dubiosus*, 3 spec.; E 5114 *Pseudocnus dubiosus koellikeri*, 1 spec.; E 2841 *Pseudocnus dubiosus leoninus,* 4 spec.; E 4825 *Pseudocnus leoninoides*, cotypes, 3 spec.; E 2857 *Pseudocnus perrieri*, 2 spec.

NMNH (Smithsonian Institution): E02078 *Pseudocnus lamperti*, 1 spec. NMNH: 3624 *Pseudocnus curatus* (Cowles, 1907), 1 spec.

ZMC (University of Copehagen): *Pseudocnus koellikeri*, 4 spec.; *Pseudocnus echinatus*, 5 spec.; *Pseudocnus dubiosus*, 3 spec.

MCZ: HOL- 1445 *Pseudocnus leoninoides* (paratypes), 3 spec.; HOL- 202 *Pseudocnus lubrica* (syntype), 3 fragments (dry). CAS: 35225 *Pseudocnus lubricus*, 3 spec.; 105514 *Pseudocnus californicus*, 3 spec.

MNHN (Paris): 872, 1105 *Hemioederma goreensis*, 2 spec.; 1988, *Pseudocnus grubei*, 1 spec.

FM , SA , Washington, Bell Island, 48 59 5 - 122 98 14, *Pseudocnus curatus* (Cowles, 1907), 1 spec.

M , F104820: South Atlantic Ocean, Burdwood Bank (54 12 0 -54 1 6 S, 59 48 24 - 59 51 6 W), *Pseudocnus leoninus*, 1 spec.; F106962, South Atlantic Ocean, Falkland Islands (52 21 2 S, 58 50 29 -58 5 22 W), *Pseudocnus leoninus*, 1 spec.

For *Pseudocnella*, numerous specimens of *P. sykion* were collected from KZN south coast (Park Rynie, Isipingo, and Umkomass (Green Point)) and from Eastern Cape Province (Mngazana, Port St John's) and four specimens of *P. sinorbis* were collected from south coast of KZN (Park Rynie) and Port St Johns (former Transkei). Four freshly collected specimens of *P. insolens,* collected from the Western Cape Province, were obtained by courtesy of Prof. Charles Griffiths of the University of Cape Town. All KZN and Port St Johns specimens

were narcotized by slow addition of magnesium sulphate ($MgSO_4$) to the sea water containing them, and first preserved in 95% alcohol and later transferred into 70% alcohol.

For morphological study of ossicles

Ossicles for light microscopy were prepared as follows:

1) The small piece of excised tissue/organ/structure was placed in household bleach until the soft tissue was dissolved and the ossicles separated.
2) The fluid was decanted and the remaining tissue discarded.
3) The sediment containing the ossicles was then washed in 2-3 changes of distilled water.
4) Wet preparations were made and the ossicles viewed under the compound microscope and, where necessary, illustrated by line-drawings using the camera lucida.

For scanning electron microscopy:

1) Steps 1-3 above were repeated.
2) Ossicles were rinsed in 2-3 changes of 70% and then 2 changes of absolute alcohol.
3) The ossicles were then transferred onto a clean specimen stub and allowed to dry, causing the ossicles to adhere to the stub. The stubs were coated in gold for 5-15 minutes using a Polaron SC500 Sputter Coater and viewed and photographed using the Jeol LEO SEM.

For molecular study

For each species, a piece of about 3-5 millimetres long was cut from retractor muscles and the mitochondrial ribosomal DNA was isolated using ZR Genomic DNA^{tm} –Tissue Mini Prep according to the manufacturer's instructions.

For PCR amplification, approximately 530 nucleotides were amplified using 16S primers (forward 16SARL: 5'-TGCCTGTTTATCAAAAACAT-' and reverse 16SBR: 5'-CCGGTCTGAACTCAAATCATGT-'), and a double-stranded polymerase chain reaction (PCR) was performed under the following thermal cycle: an initial denaturation of 95 C for 0 seconds followed by 40 cycles of 95 C for 1 minute, 4 .9 C for 0 seconds, and 2 C for 1 minute, then a final 4 minutes extension at 2 C. Amplified products were separated by electrophoresis using 1% Agarose gels in a 40 mM Tri-acetate, 2 mM EDTA buffer (1X

TBE) containing 0.1 µg/ml ethedium bromide. The products bands were visualized with UV translilluminator and photographed using UVP gel documentation system.
The PCR products were sent to Inqaba Biotechnical Industries for Purification using QIAquick gel extraction kit, and for sequencing using ABI 3700 DNA sequencer.

Phylogenetic Analysis

Phylogenetic Analysis

All sequences were checked by eye and compared to their respective chromatograms, and then were edited and aligned using BioEdit. The outgroups for the alignment were downloaded from GenBank for *Cucumaria miniata* (gi|37730861|gb|AY182376.1); *Cucumaria frondosa* (gi|557674370|gb|KF479389.1); *Cucumaria frondosa* (gi|301338088|gb|HM543155.1); *Cucumaria frondosa* (gi|642464|gb|U15598.1); *Pentacta pygmaea* (gi|110826358|gb|DQ777097.1); Cucumariidae sp. (gi|574961047|gb|KF713451.1); *Cucumaria* sp. (gi|568632090|gb|KF459959.1); and *Psolus phantapus* (gi|301338092|gb|HM543159.1).

The final alignment was trimmed to a length of 489 bp. Haplotypes were constructed from the sequenced genotypes using DNA SP.5. MrModeltest version 3.7 was used to search for the model of evolution which best fit the dataset. Neighbour-joining (NJ) and maximum (ML) likelihood phylogenetic trees were constructed using PAUP version 4.b10 and the Bayesian tree was constructed using MrBayes 3.1.2. NJ and ML trees were bootstrapped 1000 times, and MrBayes was run to convergence.

NB: The list of references only includes those actually cited in the text. Names included in synonymy and not cited in the text have been excluded from the list of References.

CHECK LIST OF SPECIES INCLUDED

The classification here used is the one recently proposed by Smirnov (2012).

A status of the species included in this work is dealt with in appendix A.

Class Holothuroidea de Blainville, 1834

Subclass Holothuriacea Smirnov, 2012

Order Dendrochirotida Grube, 1840

Family Cucumariidae Ludwig, 1898

Subfamily Cucumariinae Ludwig *sensu* Panning 1949

Genus *Pseudocnus* Panning, 1949

Pseudocnus koellikeri (Semper, 1868) (type species)

Pseudocnus curatus (Cowles, 1907)

Pseudocnus lubricus (Clark, 1901)

Genus *Panningocnus* n. gen

Panningocnus dubiosus (Semper, 1868) (type species) comb. new

Panningocnus echinatus (Von Marenzeller, 1881) comb. new

Panningocnus lamperti (Ohshima, 1915) comb. new

Panningocnus spinosus (Ohshima, 1915) comb. new

Panningocnus thandari (Moodley, 2008) comb. new

Panningocnus salmini (Ludwig, 1875) comb. new

Panningocnus africanus (Britten, 1910) comb. new

Panningocnus californicus (Semper, 1868) comb. new

Panningocnus sp. (Massin, 1993) comb. new

Genus *Pentactella* Verrill, 1876

Pentactella intermedia (Théel, 1886)

Pentactella laevigata (Verrill, 1876) (type species)

Pentactella leonina (Semper, 1868)

Pentactella perrieri (Ekman, 1927)

Pentactella cornuta (Cherbonnier, 1941)

Pentactella leoninoides (Mortensen, 1925)

Pentactella marionensis (Théel, 1886)

Pentactella serrata (Théel, 1886)

Genus *Thandarocnus* n. gen

Thandarocnus rhopalodiformis (Heding, 1943) comb. new

Thandarocnus rugosus (Cherbonnier, 1957) comb. new

Thandarocnus pawsoni (Won & Rho, 1998) comb. new

Thandarocnus sentus (O`Loughlin and Alcock, 2000) (type species) comb. new

Thandarocnus grubei (von Marenzeller, 1874) comb. new

Thandarocnus goreensis (Cherbonnier, 1949) comb. new

Subfamily Colochirinae Panning, 1949

Genus *Pseudocnella* Thandar, 1987

Pseudocnella sinorbis (Cherbonnier, 1952) (type species)

Pseudocnella sykion (Lampert, 1885)

Genus *Hemiocnus* n. gen

Hemiocnus syracusanus (Grube, 1840) (type species) comb. new

Hemiocnus insolens (Théel, 1886) comb. new

SYSTEMATC ACCOUNT

Class Holothuroidea de Blainville, 1834

Diagnosis (partly after Smirnov 2012)

Bilaterally symmetrical echinoderms usually with mouth and anus at opposite ends and lacking a test. Tentacles shield-shaped, dendritic, or digitate. Ambulacra with tube feet and/or papillae-like structures; anal papillae may be present. Calcareous ring calcified, well developed.

Remarks

Smirnov (2012) included four subclasses of which three are new to science: Arthrochirotacea, Elpidiacea, Holothuriacea (all new), and Synaptacea Cuenot, 1891.

Subclass Holothuriacea Smirnov, 2012

Diagnosis (partly after Smirnov 2012)

Body variously shaped.Tentacles shield-shaped, dendritic, or digitate. Radial canals present. Ambulacral processes represented by tube feet, papillae (modified tube feet), and often anal papillae. Calcareous ring usually calcified and well developed. The main types of ossicles are tables or table derivatives. Other types include plates, baskets, buttons, rods, etc., but no wheels.

Remarks

Smirnov (2012) mentioned nothing on the subclass Dendrochirotacea Grube, 1840 but included in his newly erected subclass Holothuriacea four orders: Aspidochirotida, Dendrochirotida, Molpadiida and Gephyrothuriida

Order Dendrochirotida Grube, 1840

Diagnosis (after Smirnov 2012)

Holothuroids with 10–30 dendritic tentacles. Body wall thick and dense. Body form cylindrical, U-shaped or barrel-shaped. Tube feet arranged along ambulacra or scattered throughout body. Ossicles may include tables, perforated plates, baskets, cups, rods, buttons and/or rosettes.

Remarks

Smirnov (2012) based his system of the order Dendrochirotida on the works of Panning (Panning 1949 and Heding & Panning 1954). He included in this order 14 extant and one extinct families: Cladolabidae Heding & Panning, 1954; Phyllophoridae Östergren, 1907; Rhopalodinidae Théel, 1886; Sclerothyonidae Thandar, 1989; Sclerodactylidae Panning,1949; Placothuriidae Pawson & Fell, 1965; Thyonidae Panning, 1949; Cucumariidae Ludwig, 1894; Psolidae Burmeister, 1837; Ypsilothuriidae Heding, 1942; Paracucumidae Pawson & Fell, 1965; Heterothyonidae Pawson, 1970; Thyonidiidae Panning, 1949; Cucumellidae Thandar & Arumugam, 2011; and the extinct family Monilipsolidae Smith et Gallemí, 1991 (resurrected by Smirnov 2012).

Family Cucumariidae Ludwig, 1894

Diagnosis (after Smirnov 2012)

Cucumariids with 10 tentacles. Tube feet restricted to ambulacra, sometimes also scattered, especially in dorsal interambulacra. Calcareous ring simple, without posterior processes, or at most medium high with short undivided processes. Body wall ossicles include perforated plates, sometimes baskets (complete or incomplete) but no scales.

Remarks

Panning (1949) divided this family into two subfamilies: Cucumariinae Ludwig, 1894, *sensu* Panning, 1949 with only plates in the body wall, no baskets or crosses and Colochirinae Panning, 1949 with plates and baskets or crosses. Thandar (1991) expressed the opinion that separation of the two subfamilies on the basis of a superficial layer of deposits by Panning (1949) was artificial and cannot be upheld. This is due to the fact that some species viz. *Pseudocnella sykion* (Lampert, 1885), loses baskets with age, and hence adult specimens would definitely be assigned to the Cucumariinae. Thandar (1991) further suggested that inner layer deposits should rather be used instead of the superficial layer which can change with growth or are modified due to environmental pressures. However, following Thandar (1991) and Smirnov (2012) the two subfamilies are here retained for the sake of stability of nomenclature. This division is accepted by all other current workers.

KEY TO SUBFAMILIES

1. Cucumariids with knobbed plates, and cups/baskets in the body wall..... **Colochirinae**
   Cucumariids with knobbed plates in the body wall, no cups/baskets nor tables.....**Cucumariinae**

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

Diagnosis (after Smirnov 2012)

Calcareous ring simple, lacking posterior processes; tentacles 10, equal or unequal. Body wall deposits include knobbed, perforated plates, round plates or buttons; no cups (baskets) or tables; tube feet with rods.

Remarks

Panning (1949), in his revision of the family Cucumariidae, erected several new genera to accommodate some of the species formerly described in *Cucumaria*. Some of his decisions were based on the often incomplete descriptions of other authors with the result that he made many errors and was thus criticised by many authors, including Cherbonnier (1952) who described or re-described many southern African species. Despite the criticisms, his system was slowly accepted, albeit with many changes. Panning subsequently attempted to rectify his mistakes several times (1951, 1952, 1962, and 1964. One of the genera erected by Panning (1949) is the *Pseudocnus*, one of the subjects of the current investigation. Thandar (1987) looked at the southern African species included in both *Stereoderma* and *Pseudocnus* by Panning and erected the genus *Pseudocnella* to accommodate some southern African species. ow ever, more pertinently O'Loughlin *et al*. (2014) revised the Antarctic-Subantarctic species of *Pseudocnus* and erected the genus *Laevocnus* to accommodate them. In this process they streamlined the genus *Pseudocnus* by re-diagnosing it on the basis of its type species and listed the species that still need to be revised. Hence the genus *Pseudocnus* still comprises morphologically distinct species (those with equal or unequal tentacles and those with body wall ossicles comprising knobbed, single or multi-layered plates). The current investigation attempts to revise the remaining species of the genus. Those corresponding with the type species in possessing equal tentacles and single-layered plates are left to stand in *Pseudocnus*. A new genus, *Panningocnus* is erected to accommodate all those with unequal tentacles and single-layered plates. The remaining species with unequal

tentacles and double to multilayered plates are assigned to yet another new genus *Thandarocnus*.

KEY TO GENERA OF THE SUBFAMILY CUCUMARIINAE

1. Equal tentacles..... **2**
   Unequal tentacles..... **3**

2. Buttons always present..... ***Pseudocnus*** Panning, 1949.
   Buttons absent except in the Subantarctic *Pentactella leonina* (Semper, 1868)..... ***Pentactella*** Verrill, 1876

3. Body wall plates always single layered..... ***Panningocnus*** n. gen.
   Body wall plates multilayered..... ***Thandarocnus*** n. gen.

Key to species of the genus *Pentactella* (= *Laevocnus)* will be found in O'Loughlin *et al*. (2014).

Genus *Pseudocnus* Panning, 1949 (restricted herein)

Cucumaria Panning, 1949 (partim).
Pseudocnus Panning, 1949.
Pseudocnus O'Loughlin *et al*,. 2014.

Diagnosis (after O'Loughlin *et al*. 2014, herein amended)

Body barrel-shaped, fusiform, or U-shaped. Tube feet in two rows per ambulacrum, sometimes also scattered in interambulacra, especially dorsally. Tentacles 10, all of same size. Calcareous ring simple, without posterior prolongations. Body wall ossicles include knobbed, perforated, single layered, pine-cone shaped plates, elongated, always denticulate at one end; buttons present. Tube feet ossicles always include simple, more or less curved, perforated rods; end-plates may be present. Tentacle deposits always with moderate to large, simple or curved rods, some plate-like rods; sometimes also rosettes.

Type species *Cucumaria koellikeri* Semper, 1868, designated by Panning 1949. Other species included herein: *Cucumaria curata* Cowles, 1907; *Cucumaria lubrica* Clark, 1901.

Remarks

Panning (1949) designated *Cucumaria koellikeri* Semper, 1868 as type species of the genus. Subsequently he (Panning 1951, 1952, and 1962) made several critique regarding the genus and some of the species he included in it. In 1962 he revised the genus and established two groups of species i.e., the *dubiosus* group and the *laevigatus* group characterised by the presence or absence of buttons respectively. He included several species in each group and lowered the rank of some species to subspecies of *P. dubiosus* but changed the designation of the type species from *C. koellikeri* to *C. dubiosa* perhaps influenced by Théel (1886) as to the similarity of both species. This is contrary to the rules of Zoological Nomenclature. O'Loughlin *et al*. (2014) strongly criticised this and re-instated *C. koellikeri* as type species of the genus.

It must here be noted that there are several differences between *C. koellikeri* and *C. dubiosa*. These differences include body shape, with *C. koellikeri* being U-shaped whereas *C. dubiosa* is cylindrical to barrel-shaped; *C. koellikeri* has 10 equal tentacles whereas *C. dubiosa* has the two ventral tentacles reduced. These differences were also noted by O'Loughlin *et al*., (2014). In addition the body wall ossicles in *C. koellikeri* include plates or buttons with large knobs and small holes whereas in *C. dubiosa* the holes and knobs are of almost the same size or the holes are larger in some plates; the buttons in *C. koellikeri* are usually 4-holed, rarely 5 whereas in *C. dubiosa* they are 4-8 holed ; some tube feet rods in *C. dubiosa* are knobbed but no knobs were detected in the rods of *C. koellikeri*; in *C. dubiosa* the tentacles include only rods, whereas in *C. koellikeri* rosettes are also present in addition to rods. Based on the above the two species (*C. koellikeri* and *C. dubiosa*) are so distinct that they cannot be considered congeneric.

O'Loughlin *et al*. (2014), in their revision of the Antarctic-Subantarctic species of *Pseudocnus*, raised all the subspecies of *P. dubiosus* to full specific rank and this move is here fully supported. In addition, several species were assigned to a new genus *Laevocnus,* with *C. laevigata* as type species, based on morphological, zoogeographic and molecular evidence. These species include *Pseudocnus cornutus* Cherbonnier, 1941*, Cucumaria intermedia* Théel, 1886*, Pseudocnus leoninoides* (Mortensen, 1925)*, Pseudocnus leoninus*

(Semper, 1867), *Pseudocnus perrieri* (Ekman, 1927), and *Cucumaria serrata* Théel, 1886. They, however, listed the remaining species but left them unattended to. In the current investigation of the genus O'Loughlin *et al*. (2014) restriction of *Pseudocnus* is accepted. It now accommodates only those species with equal tentacles, corresponding with the type species. Hence it now accommodates only 3 species united by 10 equal tentacles, singlelayered, knobbed, perforated, denticulate calcareous plates and buttons. All those with unequal (8+2) tentacles are re-assigned to a new genus *Panningocnus*. These include *Cucumaria dubiosa* Semper, 1868; *Cucumaria echinata* Von Marenzeller, 1881; *Cucumaria lamperti* Ohshima, 1915; *Cucumaria spinosa* Ohshima, 1915; *Pseudocnus thandari* Moodley, 2008; *Pseudocnus salmini* (Ludwig, 1875); *Cucumaria leonina* var. *africana* Britten, 1910. *Cucumaria californica* Semper, 1868; *Pseudocnus* sp. Massin, 1993; *Hemioedema goreensis* Cherbonnier, 1949.

Koehler and Vaney (1908) likened their *Cucumaria alcocki* from the Indian Ocean with *Cucumaria imbricata* Semper (included in *Leptopentacta* by WoRMS). Koehler and Vaney noted some differences such as the presence of knobbed buttons in the body wall of the latter and smooth buttons in the former. Panning (1949) transferred *C. alcocki* to *Pseudocnus* and this decision is accepted by WoRMS, GBIF and recently by O'Loughlin *et al.,* 2014. However, *C. alcocki* has the ventral tentacles reduced, multilayered plates (Panning 1949) and smooth buttons in the body wall. Hence it does not belong in *Pseudocnus* as restricted nor to the new genera *Panningocnus* and *Thandarocnus* erected herein. Since it comes close to *Leptopentacta imbricata*, it should therefore be provisionally left in *Leptopentacta* until new material emerges.

The remaining species of *Pseudocnus*, namely *Cucumaria rhopalodiformis* (Heding, 1943); *Hemioedema goreensis* Cherbonnier, 1949, *Cucumaria rugosa* Cherbonnier, 1957; *Pseudocnus sentus* O`Loughlin and Alcock, 2000; *Pseudocnus pawsoni* Won & Rho, 1998 have in their body wall ossicles as multi-layered fir-cone-shaped plates. Therefore they do not belong in *Pseudocnus*, which is characterised by having plates composed of a single layer of calcareous material. The placement of these species in *Pseudocnus* cannot be upheld and these are transferred to yet another new genus, *Thandarocnus*.

KEY TO THE SPECIES OF *PSEUDOCNUS*

1. Tube feet in double conspicuous rows, also scattered in interambulacra; body wall ossicles include knobbed, pine cone-shaped plates and buttons; tube feet with serrated rods **2**

   Tube feet in both ambulacra and interambulacra, not in distinct rows; body wall ossicles include knobbed, pine cone-shaped plates, buttons smooth or knobbed; tube feet with simple rods .....***Pseudocnus curatus*** (Cowles, 1907).

2. Pine cone-shaped plates and buttons always knobbed, oval to round plates absent; tube feet rods smooth, with serrated 3rd arm; tentacle deposits include rosettes in addition to rods..... ***Pseudocnus koellikeri*** (Semper, 1868).

   Pine cone-shaped plates and buttons always knobbed, round plates present; tube feet with knobbed rods, 3rd arm also serrated; tentacle deposits include only rods, no rosettes. ..... ***Pseudocnus lubricus*** (Clark, 1901).

Pseudocnus koellikeri (Semper, 1868) (type species)

Figure 1A-E and 2A-B

Cucumaria koellikeri Semper, 1868:237, pl. 39, fig. 17; Théel, 1886:112; Koehler, 1921:156, fig. 107; 1927:172, pl. 16, fig. 6; Hérouard, 1929:41, pl. 1, fig. 2; Tortonese, 1936:292; Panning, 1940:169, fig. 1-4; Tortonese, 1949:13;1956:231.
Semperia koellikeri Lampert, 1885:151
Pseudocnus koellikeri Panning, 1949:423, fig. 10.
Pseudocnus dubiosus-dubiosa Panning, 1951:76, fig. 2, 3.
Pseudocnus dubiosus koellikeri Panning, 1962:62, fig. 5, 6.
Pseudocnus koellikeri O'Loughlin *et al*., 2014:46, Table 2 (partim).

Diagnosis (after Panning 1949).

Body U-shaped, up to 25 mm. Tube feet in two rows per ambulacrum, also small ones in interambulacra. Tentacles 10, of equal size. Body wall ossicles include both plates and

buttons. Plates ovate, knobbed, perforated, single-layered, often denticulate at one end with denticles borne on a handle; buttons knobbed, usually with four perforations, rarely five. Tube feet deposits include 3-armed perforated rods. Tentacle deposits include rods and rosettes, rods perforated, smooth.

Material examined

ZMC, Dakar (Senegal), Cutting Coast, *Pseudocnus koellikeri,* 4 spec.; E2832, *Pseudocnus koellikeri*, Europa, Italien, Neapel, 1 spec.

Description

Body barrel to U-shaped (Figure 2A), mouth and anus turned up; length up to 22 mm, 16 mm width. Colour off white to greyish. Tube feet in two conspicuous rows in each ambulacrum, but few also scattered in interambulacra. Tentacles 10, of equal size. Calcareous ring simple, lacking posterior prolongations (Figure 2B). Respiratory trees highly branched. Gonadal tubules not branched. Retractor muscles short, arise from longitudinal muscles at about ½ body length.

Body wall deposits include knobbed, perforated plates, 90-170 µm long, 60 -90 µm wide (Figure 1A) and buttons, 60-90 µm in diameter (Figure 1B). Plates pine cone-shaped, always elongated and denticulate at one end. Buttons round, lack denticulate handle, knobs and holes about the same size (10-30 µm), with usually four (sometimes five) holes. Tube feet deposits include only 3-armed rods, third arm may be short or of medium length, serrated at margins and with up to seven holes (Figure 1C). Tentacle ossicles include simple perforated rods (Figure 1D) and rosettes (Figure 1E). No ossicles detected in introvert.

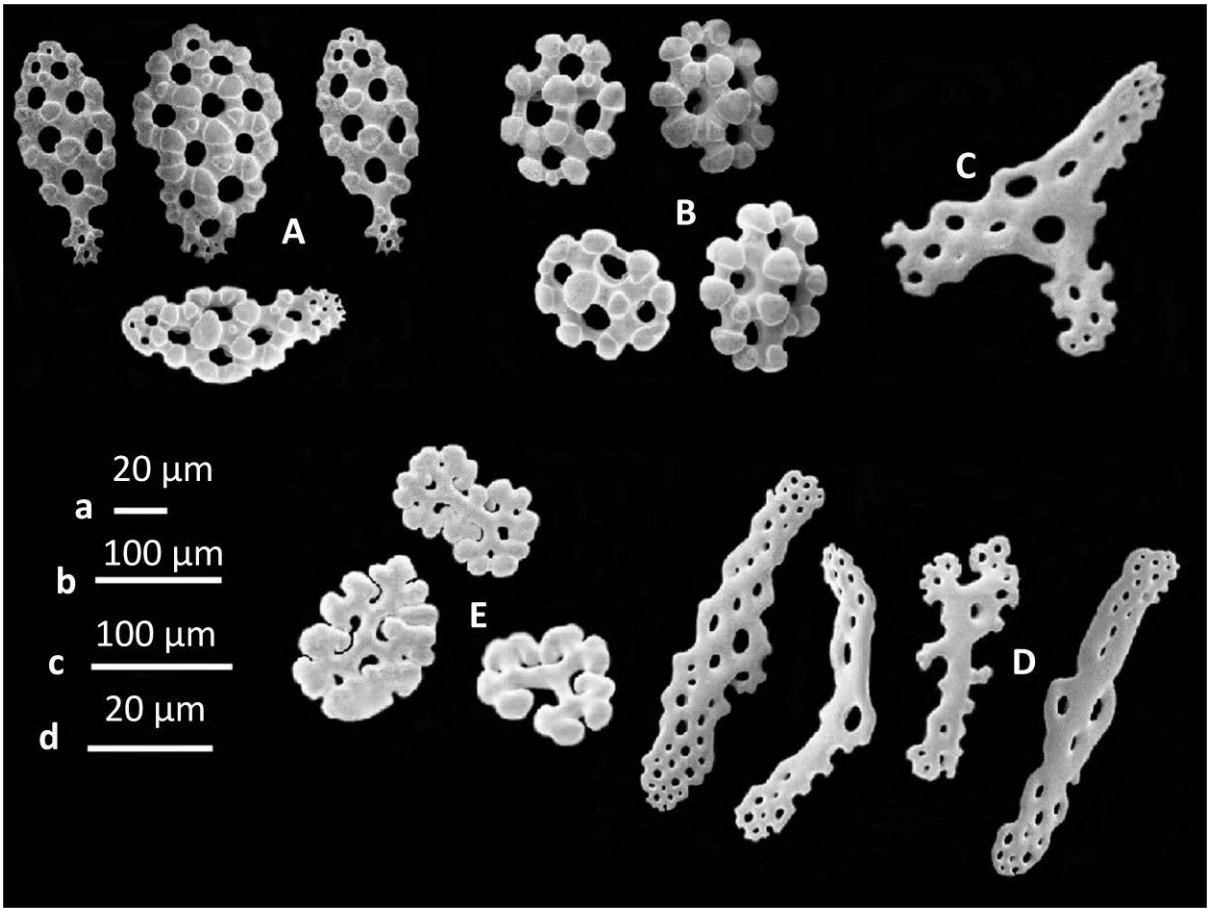


Figure 1. *Pseudocnus koellikeri* (Semper, 1868). ZMC, Dakar (Senegal). Ossicles. A. Pine cone-shaped plates from body wall; B. Buttons from body wall; C. Rod from tube feet; D. Rods from tentacles; E. Rosettes from tentacles. A and B = scale a; C = scale b; D = scale c; E = scale d.

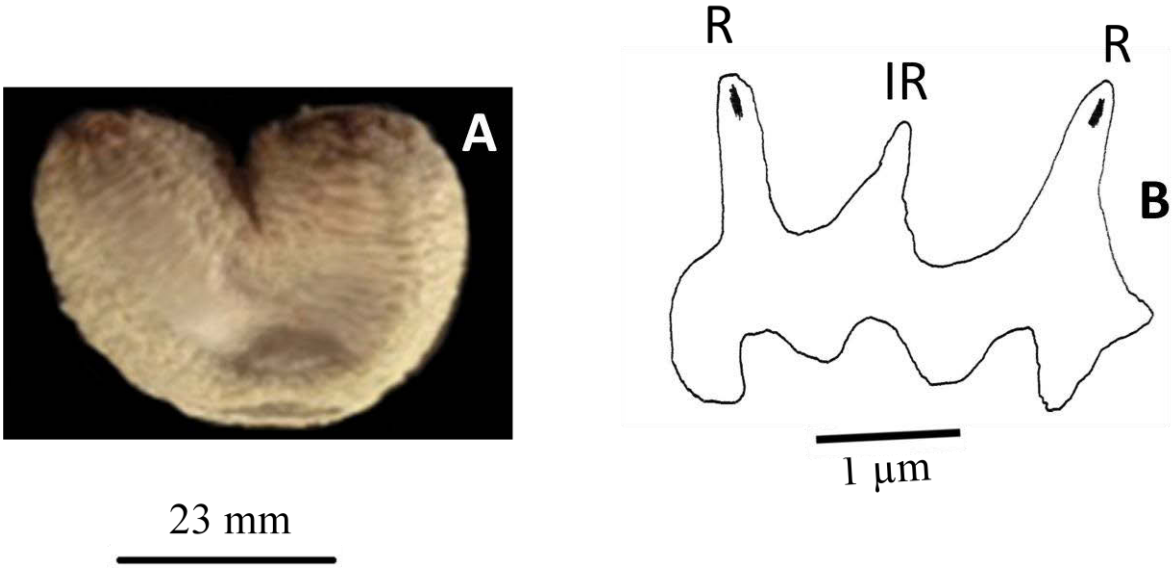


Figure 2. *Pseudocnus koellikeri* (Semper, 1868). ZMC, Dakar (Senegal). A. Entire; B. Part of calcareous ring**.**

Distribution

Mediterranean Sea (Sea of Marmara, Aegean Sea) (Ozaydin *et al*., 1995), Napels (Italy) (Panning, 1949; 1962), Senegal (this study), 50-685 meters (Ozaydin *et al*., 1995).

Remarks

Cucumaria koellikeri was described by Semper (1868) from the Mediterranean Sea. Lampert (1885) transferred it to the preoccupied genus *Semperia*. Théel (1886) and subsequent authors, including Koehler (1921) and Hérouard (1929), described it as *Cucumaria koellikeri* from the Mediterranean Sea. As stated above Panning transferred *C. koellikeri* to *Pseudocnus* and this decision prevails (see WoRMS, GBIF). However, his decision in 1962 to replace it as type species with *Cucumaria dubiosa* was criticised by O'Loughlin *et al*. (2014) and herein (see Remarks above). While working with *P. koellikeri*, a specimen labelled "*Pseudocnus dubiosus koellikeri* E5114, ZMH, South America, Brasilien, Kap St. Thome bei Rio de Janeiro, 25- 0 m, 1 specimen" received from ZMH was examined. This is a misidentification or mislabel as there is no record of this species from Brazil. Looking at the geographic distribution of *Pentactella leonina* (Semper, 1868), it is suspected that this specimen represents *P. leonina*.

Pseudocnus curatus (Cowles, 1907)

Figure 3A-C, 4A-B

Cucumaria curata Cowles, 1907:8, pl. 2, figs. 2-6, Pl. 6, fig. 7; Clark, 1901:165; Panning, 1949:416; Lampert, 1985:438, fig. 1; Bergen, 1996:21, fig. 6.13; Arndt *et al.* 1996:434-435.
Pseudocnus curatus Lambert, 1997:74-77, fig. 37; Mooi & Telford, 1998:473-477, fig. 2a, b.
Pseudocnus curatus O'Loughlin *et al*., 2014:46, Table 2 (partim).

Diagnosis (after Lambert 1997)

Body cylindrical, mouth and anus terminal. Skin hard. Colour ventral off white to cream-white, dorsally light brown. Tube feet on both ambulacra and interambulacra, numerous ventrally. Tentacles 10, of equal size. Calcareous ring simple, without prolongations. Body wall ossicles knobbed, pine-cone-shaped plates, made up of one layer of calcareous material, and knobbed round buttons. Tube feet deposits include simple rods. Tentacle deposits include straight or curved rods. No rosettes.

Material examined

FM , SA , Washington, Bell Island, 48 59 5 - 122 98 14, 1 spec., 12-18 meters.

Description

Body cylindrical, skin tough, colour cream-white ventrally and brownish dorsally. Length 30 mm, width 12 mm. Tube feet in both ambulacra and interambulacra, numerous ventrally. Tentacles extended, 10, all of the same size. Calcareous ring simple, radials anteriorly bifurcated, radials and interradials notched posteriorly. Retractor muscles attached at about ½ body length. Respiratory trees branched.

Body wall ossicles include pine-cone-shaped and knobbed, denticulate plates observed only around the anal region (Figure 3B), round, 4-holed, knobbed, perforated buttons (Figure 3A), ventral body wall ossicles include elongate plates with one end denticulate; pine cone-shaped plates, 110-190 µm, buttons 60-70 µm. Tube feet deposits include 3-armed rods, with all arms distally perforated, but not serrated. Tentacle deposits include 3-4 kind of rods; some curved, 3-armed, some straight, small to moderate, some without perforations (Figure 3C).

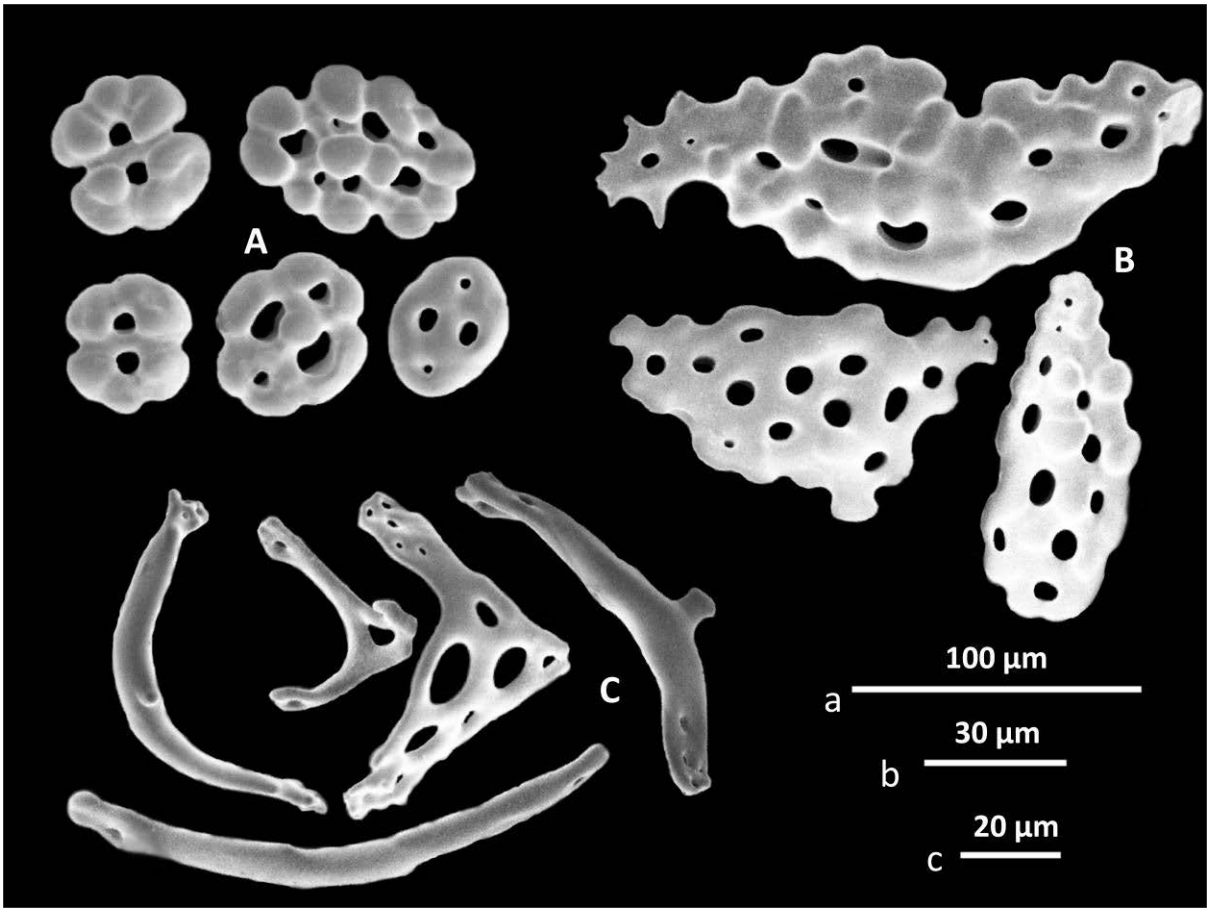


Figure 3. *Pseudocnus curatus* (Cowles, 1907). FMNH, USA, Washington. Ossicles. A. Buttons from body wall; B. Plates from anal region; C. Curved rods from tentacles. Note: A, B, C = scale a, b, c respectively.

Figure 4. *Pseudocnus curatus* (Cowles, 1907). FMNH, USA, Washington. A. Calcareous ring; B. Entire (dorsal view).

Distribution

Gnarled Islands, Dundas Island, British Columbia (; Malpaso Creek, Monterey County, California, Washington, 0-20 meters (Lambert, 1997).

Remarks

This species has been confused with *Cucumaria lubrica* Clark, 1901 by many authors including Panning (1949). Cowles (1907) recorded it from California (Cypress Point), Arndt *et al.* (1996) also examined its (*Cucumaria curata*) molecular biology and separated it from *C. lubrica.* This clearly showed that the two species are distinct both morphologically and genetically. They, however, left Cowles's *curata* in *Cucumaria*. Subsequently, Lambert (1997) transferred *C. curata* Cowles, 1907 to *Pseudocnus* since it share some characteristic features with *Pseudocnus koellikeri* (type species). Lambert strongly agreed with Arndt *et al.* (1996) that the two species *C. curata* and *C. lubrica* are distinct, and postulated that the differences lie in the colour of the species, with *C. curata* being black and *C. lubrica* white-brown with black specks on the dorsum. The two species also differ in their ventral ossicles with *C. curata* possessing the very characteristic elongated denticulate plates with few pine cone-shaped plates, and *C. lubrica* numerous pine cone-shaped plates. *Cucumaria curata* and *C. lubrica* also differ in their tentacles deposits with *C. curata* having three types of rods (small, curved, straight, some 3-armed and perforated) and *Cucumaria lubrica* having only 3-armed rods.

All previous authors failed to demonstrate pine cone-shaped ossicles in *C. curata.* From the material at hand a few were found in the dorsal body wall and numerous in the anal region. Elongated plates were also found in the ventral body wall. *C curata* has been described as having smooth, 4-holed buttons and brood pouches, but in the material at hand numerous knobbed buttons were observed but no brood pouches.

Pseudocnus lubricus (Clark, 1901)

Figure 5A-C, 6A-B and 7A-B

Cucumaria lubrica Clark, 1901:55.
Cucumaria fisheri astigmata Wells, 1924:114.
Stereoderma fisheri Panning, 1949:423; Cherbonnier, 1951:41.
Pseudocnus astigmatus Lambert, 1990:914.
Pseudocnus lubricus Lambert, 1997:78.
Pseudocnus lubricus O'Loughlin *et al*., 2014:46, Table 2 (partim).

Diagnosis (after Lambert 1997)

Body cylindrical. Tube feet in both ambulacra and interambulacra. Ten equal tentacles. Calcareous ring simple, without posterior processes. Body wall ossicles include knobbed, denticulate pine cone-shaped plates, round plates and knobbed buttons. Tube feet deposits as knobbed rods. Tentacle deposits as perforated simple rods. No rosettes.

Material examined

MCZ HOL-202, *Cucumaria lubrica* H.L Clark 1901, Pacific Ocean: Pacific East central, Washington, Puget Sound (USA), dry fragments. CAS Invertebrate Zoology, cat. 53225, *Pseudocnus lubricus*; Monterey Bay, Monterey county (California) 3 spec.

Description

Of the 3 CAS specimens, smallest is 18 mm long, 7 mm wide; largest about 23 mm long, 7 mm wide. Body sub-cylindrical. Skin soft, colour in alcohol off-white. Mouth and anus terminal. Tube feet retractile, in two rows in ventral ambulacra, few also scattered in interambulacra, dorsal tube feet scattered. Tentacles 10, bushy, of equal size. Calcareous ring simple, lacking posterior processes (Figure 7B). Retractor muscles attached to longitudinal muscles at about half of body length. Gonad of numerous, unbranched, tubules. Respiratory trees highly branched.

Body wall ossicles include thick, knobbed, perforated, denticulate pine cone-shaped plates (Figure 5A), round to oval knobbed plate (Figure 5B), and knobbed buttons (Figure 5C). Tube feet deposits include only knobbed, 3-armed rods, 3rd arm serrated (Figure 6A). Tentacle deposits consist of simple perforated rods (Figure 6B).

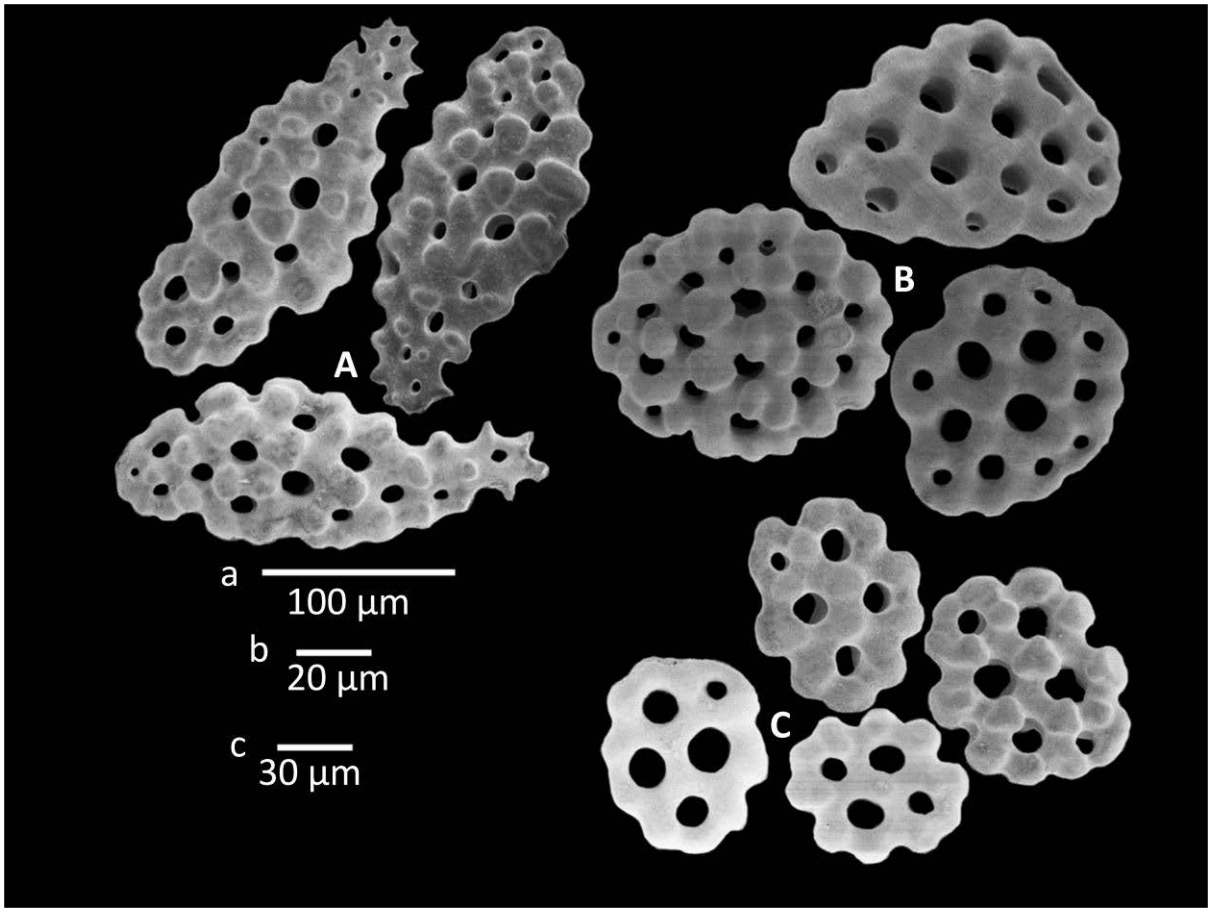


Figure 5. *Pseudocnus lubricus* (Clark, 1901). MCZ HOL-202. Ossicles. A. Pine-cone-shaped plates from body wall; B. Round to oval plates from body wall; C. Buttons from body wall. Note: A, B, and C = scale a, b, and c respectively.

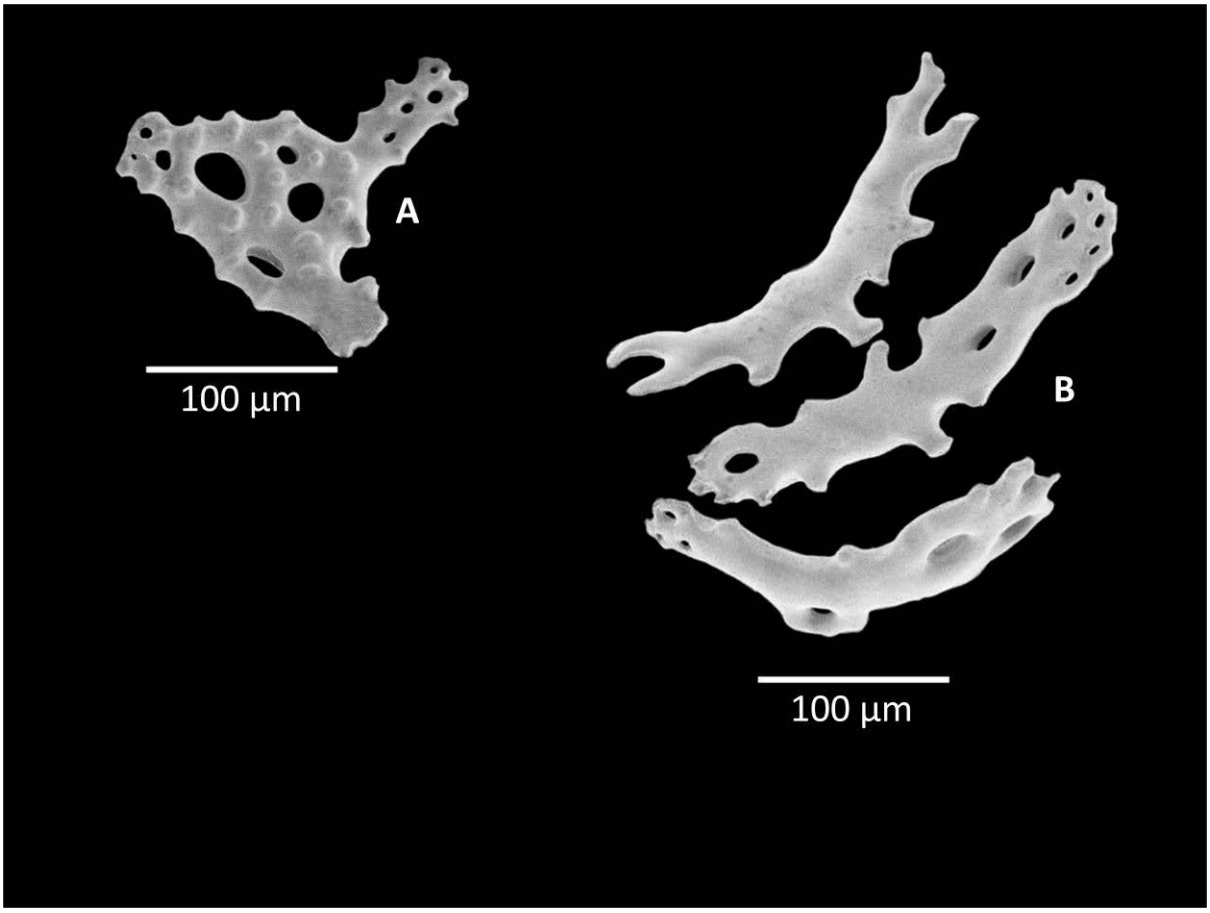


Figure 6. *Pseudocnus lubricus* (Clark, 1901). MCZ HOL-202. Ossicles. A. Knobbed rod from tube feet; B. Simple rods from tentacles.

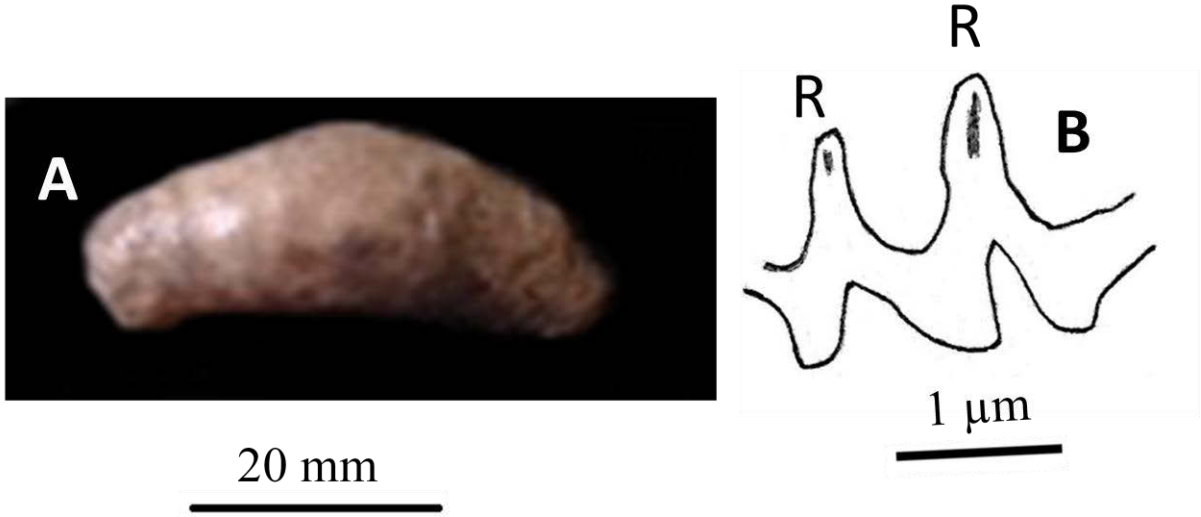


Figure 7. *Pseudocnus lubricus* (Clark, 1901). MCZ HOL-202A. Entire (dorsal view); B. Calcareous ring.

Distribution

British Colombia to California, intertidal to 82 metres (Lambert, 1990).

Remarks

Pseudocnus astigmatus was described by Wells (1924) as *Cucumaria fisheri astigmata*. Panning (1949) transferred the species to *Stereoderma*. Subsequent to this, Cherbonnier (1951) listed it as a junior synonym of *Stereoderma fisheri.* Lambert (1990) transferred the species to *Pseudocnus* based on the ossicles. This was accepted by Arndt *et al*. (1996) and Bergen (1996). Lambert (1990) further noted that *astigmatus* is similar to *Cucumaria curata* Cowles, 1907 and *Cucumaria lubrica* Clark, 1901 in many characters such as tentacle size, tube feet distribution, body shape, and the form of the ossicles. Bergen (1996), Arndt *et al*. (1996) and Lambert (1997) noted that *Pseudocnus astigmatus* and *P. lubricus* are identical on morphological and, according to Arndt *et al*. (1996), also on molecular evidence and hence they treated both as conspecific, with *P. lubricus* considered as a senior synonym.

Pseudocnus lubricus (Clark, 1901) is very close to *P. koellikeri* with which it shares similar characters such as tube feet distribution, equal tentacles in addition to knobbed single layer of calcareous material. Both *P. lubricus* and *P. koellikeri* have tube feet deposits made up of 3-armed rods, with serrated 3rd arm. However, in *P. lubricus* the tube feet rods are knobbed compared to those of *P. koellikeri* which lack knobs. *P. koellikeri* and *P. lubricus* also differ in that the former species has tentacle deposits which include rosettes in addition to rods whereas the latter species lack such characters.

Panningocnus **n. gen.**

Pseudocnus Panning, 1949 (partim); O'Loughlin *et al*., 2014 (partim).

Diagnosis

Body more or less cylindrical. Mouth and anus terminal. Tube feet in ambulacra, sometimes scattered dorsally. Tentacles 10, ventral-most two reduced. Calcareous ring simple, lacking posterior processes.

Body wall ossicles include single-layered, knobbed, perforated, oblong, pine-cone shaped plates; pine-cone shaped plates always denticulate at one end or provided with a prolonged spine(s) which sometimes branch into more short spines; small round knobbed plates or

buttons present or absent. Tentacles, tube feet, and introvert deposits comprise rods or plate-like rods; rosettes sometimes present in introvert.

Type species: *Cucumaria dubiosa* Semper, 1886, herein designated.

Other species included: *Cucumaria echinata* Von Marenzeller, 1881; *Cucumaria lamperti* Ohshima, 1915; *Cucumaria spinosa* Ohshima, 1915; *Pseudocnus thandari* Moodley, 2008; *Pseudocnus salmini* (Ludwig, 1875); *Cucumaria leonina* var. *africana* Britten, 1910. *Cucumaria californica* Semper, 1868; *Pseudocnus* sp. Massin, 1993.

Etymology

This genus takes its name from Panning A in recognition of his invaluable contribution to the taxonomy of the Class Holothuroidea.

Remarks

The new genus, diagnosed in the cucumariid subfamily Cucumariinae, resembles *Pseudocnus* but differs from it in tentacle size, with *Pseudocnus* having ten equal tentacles and the new genus has the ventral-most two reduced. The tentacle size appears to be the principal character that separates these genera, except for the plates with elongated spine(s) in some species of the new genus. All species here assigned to *Panningocnus* were previously classified in *Pseudocnus*. *Panningocnus* n. gen. can be further subdivided into two genera or subgenera with one having restricted tube feet and plates with one or two prolonged spines at one end and buttons present or absent (Table 2:Group A) and the other with restricted or scattered tube feet, buttons usually present and single-layered plates, denticulate at one end (Table 2:Group B). This step is not taken here in order to restrict further splitting. One can also subdivide this genus into those possessing buttons and those in which buttons are absent. Morphological cladistic analysis may help resolve this issue.

Table 2. Comparative characters of species of *Panningocnus* n. gen.

Group A with restricted tube feet and plates with one or two prolonged spines at one end, buttons present or absent.

	Tube feet	Buttons	Spines at end	Rosettes	Distribution
P. echinatus	Restricted	Absent	Yes	yes	South China, South Japan, Red Sea
P. lamperti	Restricted	Present	Yes	no	Aleutian Islands, vicinity of Commander Islands, off South Tip of Peninsula (Alaska)
P. spinosus	Restricted	Present	Yes	no	Off Hitaka, Hokkaido, off Oshika Peninsula, Suruga Bay, Honshu Island, Japan
P. thandari	Restricted	absent	Yes	plate-like	Northern Namibia to west coast of South Africa

Group B with restricted or scattered tube feet, buttons usually present and single layered plates denticulate at one end.

	Tube feet	Buttons	Spines at end	Rosettes	Distribution
P. dubiosus	Scattered	Present	Yes	yes	Peru, Chile
P. californicus	restricted	Absent	Yes	no	West coast of Mexico, Central America (Costa Rica) to possibly Peru
P. salmini	scattered	Present	Yes	yes	Indonesia
P. africanus	scattered	Present	Yes	no	Luderitz Bay, Namibia
P. sp.	restricted	present	Yes	Not recorded	Mauritania

KEY TO SPECIES OF *PANNINGOCNUS* n. gen.

1. buttons always present, tube feet scattered..... **2**
   buttons present or absent, tube feet restricted..... **4**

2. Knobbed plates always denticulate at one end..... **3**

Knobbed plates with smooth margins..... ***Panningocnus africanus*** (Britten, 1910).

Knobbed plates smooth or denticulate at one end ..... ***Panningocnus*** sp. (Massin, 1993).

3. Tentacle deposits as thick perforated rods..... ***Panningocnus dubiosus*** (Semper, 1868).

   Tentacle deposits as simple, thin perforated rods..... ***Panningocnus salmini*** (Ludwig, 1875).

4. Buttons present, tentacle deposits include perforated and/or plate-like rods..... **5**

   Buttons absent, tentacle deposits include rods and/or rosettes.....**6**

5. Tentacle deposits include irregular perforated rods..... ***Panningocnus spinosus*** (Ohshima, 1915).

   Tentacle deposits include plate-like rods..... ***Panningocnus lamperti*** (Ohshima, 1915).

6. Tentacle deposits include rods and/or rosettes..... ***Panningocnus echinatus*** (Von Marenzeller, 1881).

   Tentacle deposits include simple perforated rods or plate-like rods, no rosettes.....**7**

7. Tube feet deposits as simple perforated rods..... ***Panningocnus californicus*** (Semper, 1868)

   Tube feet deposits as plate-like rods, smooth to sparsely knobbed..... ***Panningocnus thandari*** (Moodley, 2008).

Panningocnus dubiosus (Semper, 1868) comb. new (type species)

Figure 8A-C, 9A-B, and 10A-B

Cucumaria dubiosa Semper, 1868:238, pl. 39, fig. 19 ; Théel, 1886:111 ; Deichmann, 1941:81, pl. 11, fig. 1,2.

Pseudocnus dubiosus-dubiosa Panning, 1951:73.

Non *Pseudocnus dubiosus* Panning, 1949:424, fig. 11 (= *P. leoninus*).

Pseudocnus dubiosus dubiosus Panning, 1962:59, fig. 1, 2.

Pseudocnus dubiosus Pawson, 1964:457-459, fig. 4-8.

Pseudocnus dubiosus O'Loughlin *et al*., 2014:46, Table 2 (partim).

Diagnosis (after Panning 1962)

Body shape cylindrical. Tube feet in two rows per ambulacrum, also scattered dorsally. Tentacles 10, mid-ventral two reduced. Calcareous ring simple, without posterior prolongations. Body wall ossicles include plates and buttons. Plates pine cone-shaped, knobbed, perforated, and often denticulate at one end. Buttons round, knobbed, non-denticulate, with four or more perforations. Tube feet deposits include 3-armed, perforated rods. Tentacle ossicles include more or less curved, perforated rods, some knobbed, no rosettes.

Material examined

ZMH E6581, S. America, Peru, Bucht von Chimbota, Sandstrand, Angespult. 3 spec.

Description

All three specimens poorly preserved. Skin leathery. Colour yellowish brown to light brown; size 22 x 9 mm, 20 x 9 mm and 24 x 10 mm. Tube feet distribution inconspicuous. Calcareous ring typical of Cucumariidae. Tentacles clumped together and cannot be counted.

Body wall ossicles comprise pine cone-shaped, knobbed, perforated plates with one end denticulate (Figure 8A), some without denticles at one end (Figure 8B), plates about 170-480 µm long and 90-140 µm wide, with up to 18 holes (up to 30 µm diameter), knobs also up to 30 µm in diameter; round, knobbed, perforated buttons also present (Figure 9A), 90-140 µm in diameter, with up to 14 holes (about 20 µm diameter), knobs about 20 µm in diameter. Tube feet deposits include perforated table-like rods (Figure 8C). Tentacle deposits comprise simple, thick rods (Figure 9B).

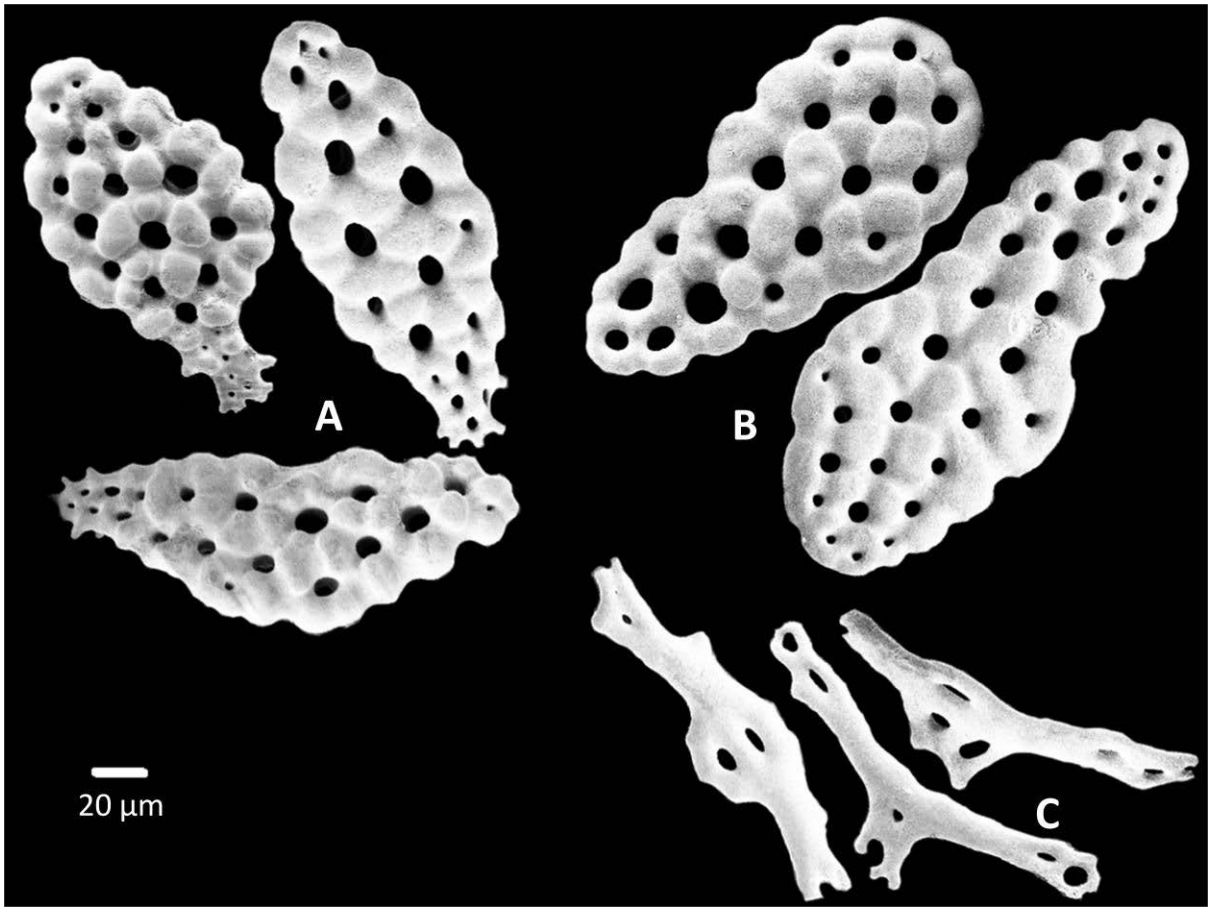


Figure 8. *Panningocnus dubiosus* (Semper, 1868). ZMH E6581. A. Pine-cone-shaped plates from body wall; B. Plates from anal region; C. Rods from tube feet. NB. all to same scale.

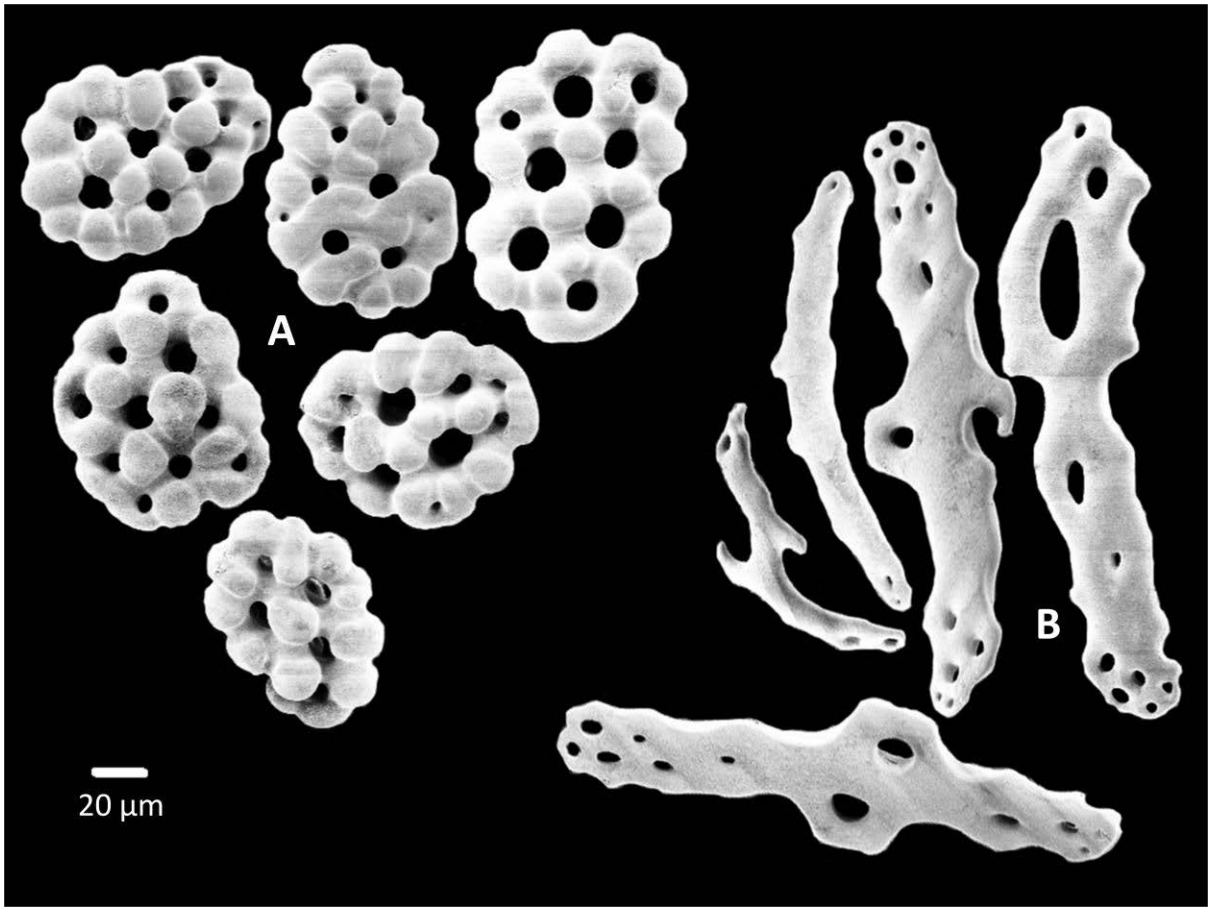


Figure 9. *Panningocnus dubiosus* (Semper, 1868). ZMH E6581. A. Buttons from body wall; B. Rods from tentacles. NB. All to same scale.

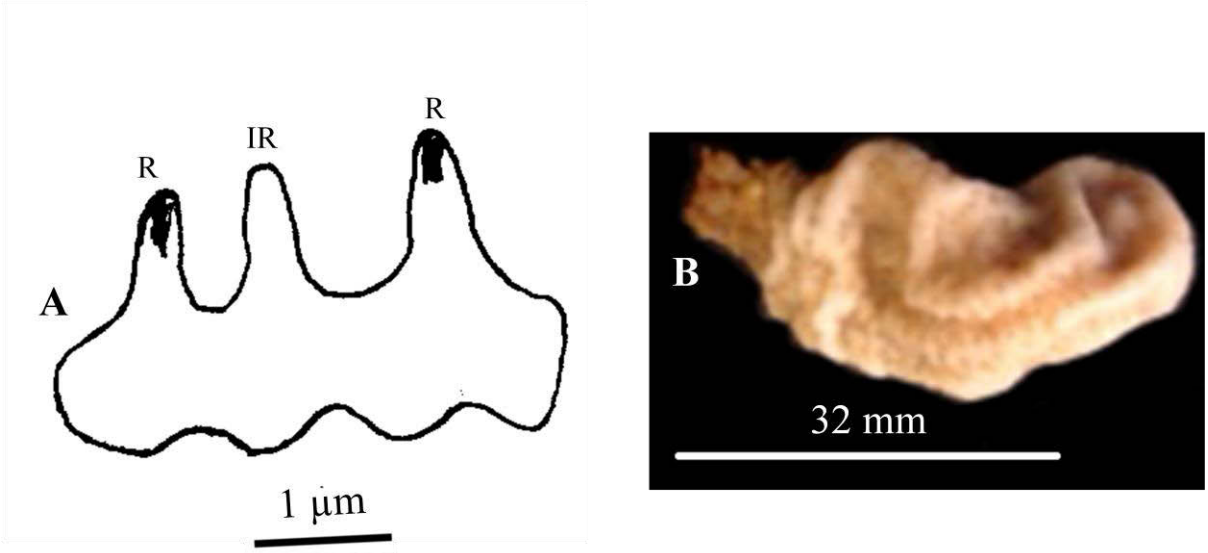


Figure 10. *Panningocnus dubiosus* (Semper, 1868). ZMH E6581. A. Calcareous ring; B. Entire.

Distribution: Peru, Chile (Pawson, 1964).

Remarks

This species was described by Semper (1868), based on a specimen from Peru. It was also recorded by Théel (1886) from Peru. Deichmann (1941) also recorded it as *Cucumaria dubiosa* Semper, 1868. Subsequently, Panning (1949) transferred the species to his newly erected genus *Pseudocnus* but later (in 1962), erroneously designated it as a type species of this genus since he now regarded *Cucumaria koellikeri* as a subspecies of *C. dubiosa*, but this was recently rectified by O'Loughlin *et al*., 2014, who reinstated *Cucumaria koellikeri* (Semper, 1868) as type species of the genus. A short history of the two species is given under remarks for *Pseudocnus*.

Panningocnus californicus (Semper, 1868) comb. new

Figure 11A-C, and 12A-B

Cucumaria californica Semper, 1868:235, pl. 39 Fig. 16, pl. 40 fig. 10; Lampert, 1885:147, pl. 34, fig. 16, pl. 40; Théel, 1886:109;1886:8; Deichmann, 1938:372; 1941:79, pl. 10, figs. 6-8; Caso, 1957:309, pls. 1, 2; 1961: 359, pl. 17, 18.
Pseudocnus californicus Panning, 1962:75, fig. 18, 19.
Pseudocnus californicus O'Loughlin *et al*., 2014:46, Table 2 (partim).

Diagnosis (after Semper 1868)

Body oviform. Skin soft, slippery, colour black to greyish or even white. Tube feet only on ambulacra, interambulacra completely naked. Tentacles 10, ventral-most two reduced. Calcareous ring simple, lacking posterior prolongations. One or two Polian vesicles, single stone canal. Body wall ossicles include knobbed pine cone-shaped plates, prolonged and denticulate at one end. Buttons absent. Tube feet deposits include perforated rods, end-plates present. Tentacle and introvert deposits include perforated rods, plate-like rods may be present. No rosettes.

Material examined

CAS. Cat. No. 105514, Mexico, Baja California, 3 spec. ZMH E6766 *Pseudocnus californicus,* 1 spec.

Description

Specimens strongly contracted, body cylindrical, largest specimen about 30 mm long, 15 mm wide. Smallest about 15 mm long and 5 mm wide. Colour light brown in alcohol. Tube feet retracted, two rows along ambulacra, interambulacra naked. Tentacles 10, ventral-most two slightly reduced. Calcareous ring simple, without posterior processes, both radial and interradial plates anteriorly prolonged, radials deeply notched posteriorly.

Body wall ossicles include pine cone-shaped, knobbed, perforated plates with denticulate, perforated handle (Figure 11A) at one end. Plates about 190 - 270 µm long and 80-140 µm wide, with 6-14 holes, about 10-30 µm in diameter; handle with up to 3 spines. No buttons. Tube feet deposits include simple perforated rods, end-plate multilayered and multilocular. Tentacle deposits include simple rods, plate-like rods, some 3-armed (Figure 11B). Introvert deposits include plate-like rods (Figure 11C). Rosettes absent.

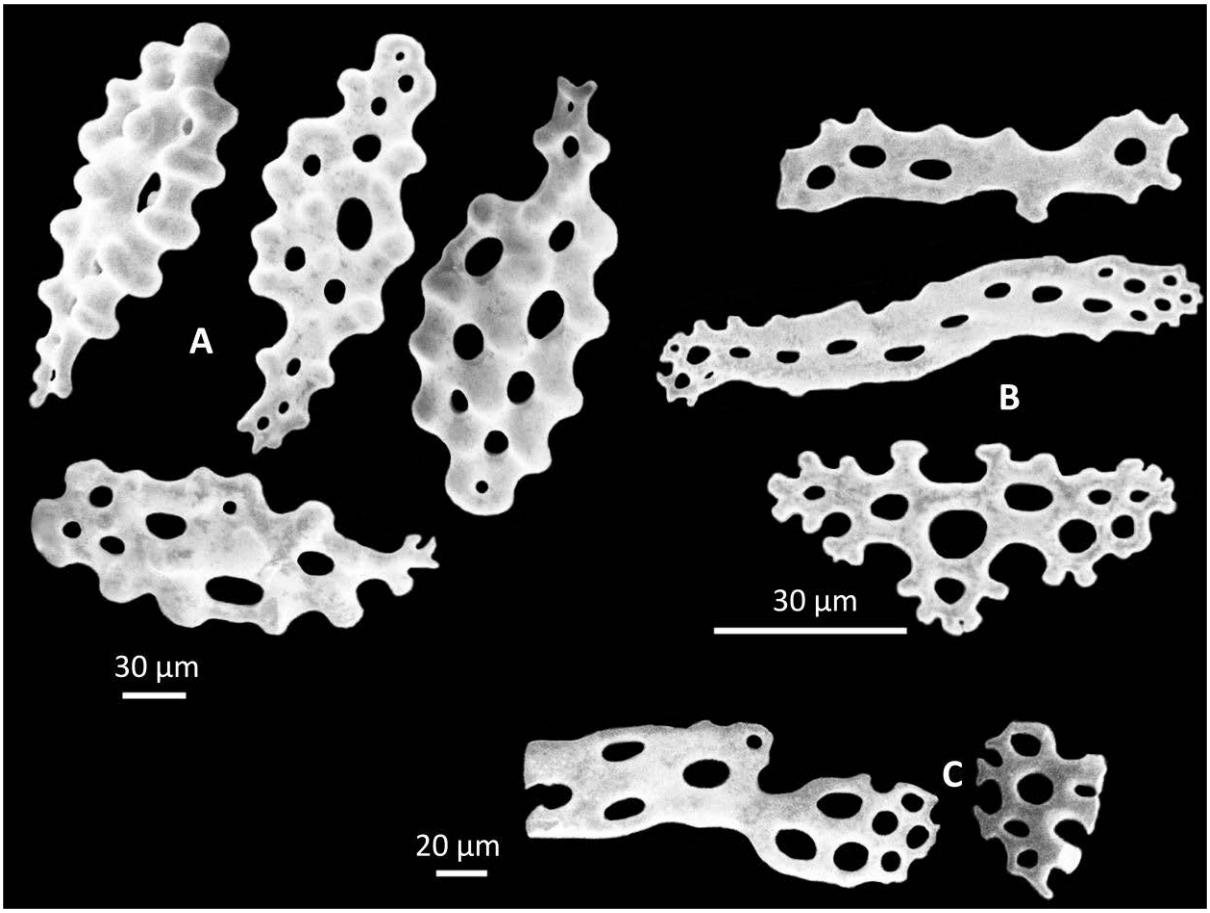


Figure 11. *Panningocnus californicus* (Semper, 1868). CAS 105514. A. Pine-cone-shaped plates from body wall; B. Rods from tentacles; C. Ossicles from introvert.

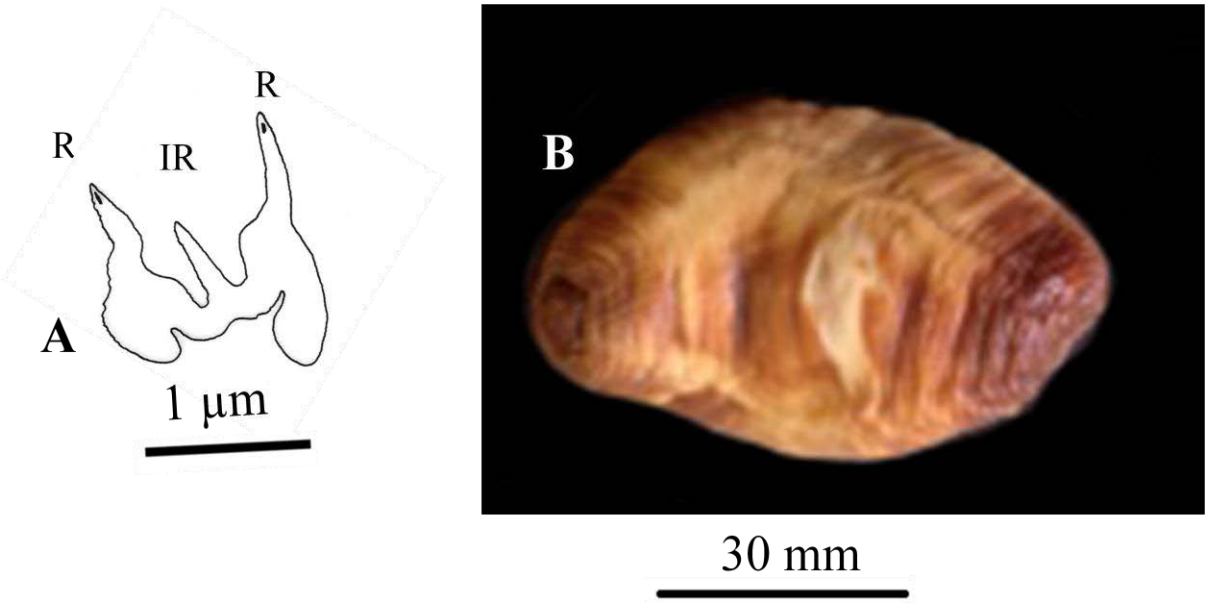


Figure 12. *Panningocnus californicus* (Semper, 1868). CAS 105514. A. Calcareous ring, B. Entire (dorsal view).

Distribution

West coast of Mexico, Central America (Costa Rica) to possibly Peru, 183 meters (Deichmann, 1941). Hooker *et al*. (2005) found a specimen of *P. californicus* from Peru (Isla Lobos) at approximately 7 m depth.

Remarks

This species has been well studied by many authors including Théel (1886), Deichmann (1938 and 1941) and others (cited in the synonymy). Semper (1868) did not find end-plates in his specimens but later Deichmann (1941) reported rudiments of these. In the current material some broken end-plates were observed. Panning (1962) postulated that *Pseudocnus californicus* can reach Peru, however, there are still no records of the species from this region. Since the species lacks buttons *Panning* (1962) assigned it to his *laevigatus* group. Recently, O'Loughlin *et al*. (2014) revised most of the species previously assigned to the *Laevigatus* group from the Subantarctic region and erected a new genus *Laevocnus* (=*Pentactella*) to accommodate them, but did not include *P. californicus* in that genus instead left it in *Pseudocnus*. Since *californicus* has unequal tentacles and close to other species of *Panningocnus*, it is now re-assigned to *Panningocnus*.

Panningocnus echinatus (Von Marenzeller, 1881) comb. new

Figure 13A-D, and 14A-B

Cucumaria echinata Marenzeller, 1881:127, pl. 5, fig. 9; Koehler & Vaney, 1908:29; Mitsukuri, 1912:239, fig. 47, pl. 8, fig. 70; Liao *et al*., 1964:24.
Pseudocnus echinatus Panning, 1949:422; Cherbonnier, 1963:10, fig. 2; Clark & Rowe, 1971:183; Liao & Clark, 1995:478, fig. 288; Moodley, 2000 (passim); O'Loughlin *et al*., 2014:46, Table 2 (partim).

Diagnosis (after Koehler & Vaney 1908; Mitsukuri 1912)

Body barrel-shaped, up to 60 mm long and 20 mm wide. Colour white in alcohol, pinkish in life. Tube feet only on ambulacra, in two conspicuous rows, interambulacra naked. Tentacles 10, ventral two reduced. Calcareous ring simple, typically cucumariid. Body wall deposits include knobbed plates, with an elongated spine at one end, rarely plates smooth, with numerous holes. Tube feet deposits include knobbed rods, some rods slender, some simple without knobs or tri-radiate with one end enlarged and perforated, end-plate present. Tentacles and introvert with rods and rosettes.

Material examined

ZMC (Copenhagen Museum); labelled as *Pseudocnus echinata*: South Africa (apparent donation to Mortensen during his Java South Africa Exp 1929-1930, Gilchrist, Cape Town, #P. 1236, det. Heding 1943, 5 spec.

Description

Specimens, barrel-shaped to cylindrical, largest 31 mm long, 9 mm wide; smallest 16 mm long, 7 mm width. Skin thin, rough to the touch. Colour off white to light brown. Tube feet only on ambulacra, in two conspicuous rows, interambulacra naked. Calcareous ring simple, devoid of posterior processes. Tentacles 10, ventral two slightly reduced. Polian vesicle single, large. Retractor muscles attached to longitudinal muscles at about ½ body length. Gonad mature, in two tufts of numerous unbranched tubules. Respiratory trees highly branched.

Body wall ossicles comprise oblong or ovate, knobbed (knobs 10-20 μm), perforated plates with up to 15 holes (10-30 μm diameter), with a single long spine at one end, plates

measure about 120-170 µm long, and 50-90 µm wide, spine sometimes with one or two perforations at base (Figure 13A); very few plates without spine. Large, oblong, knobbed plates without spines occur in anal region (Figure 14A). Tube feet deposits include 3-armed rods with a large central hole, and 1-4 terminal perforations; some rods knobbed (Figure 13B). End-plates present (Figure 14B). Tentacle deposits include rods (Figure 13C) and rosettes (Figure 13D); rods straight or curved, sometimes with small perforated 3rd arm. Some rods very small, slightly curved, some knobbed. Introvert deposits include slender rods and rosettes, a few knobbed large rods also present.

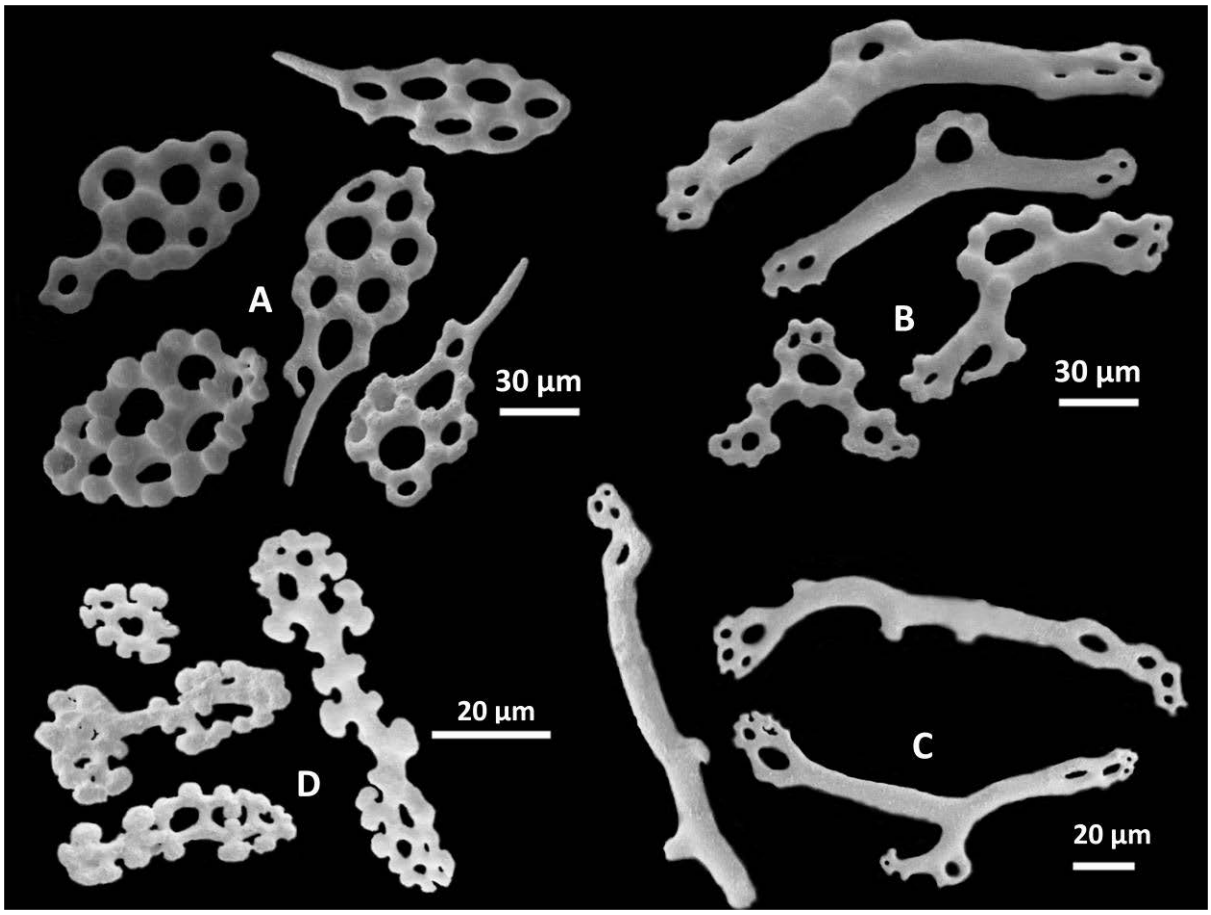


Figure 13. *Panningocnus echinatus* (Von Marenzeller, 1881). ZMC (Copenhagen Museum). A. Oblong /ovate plates from body wall; B. Knobbed rods from tube feet; C. Rods from tentacles; D. Rosettes from tentacles.

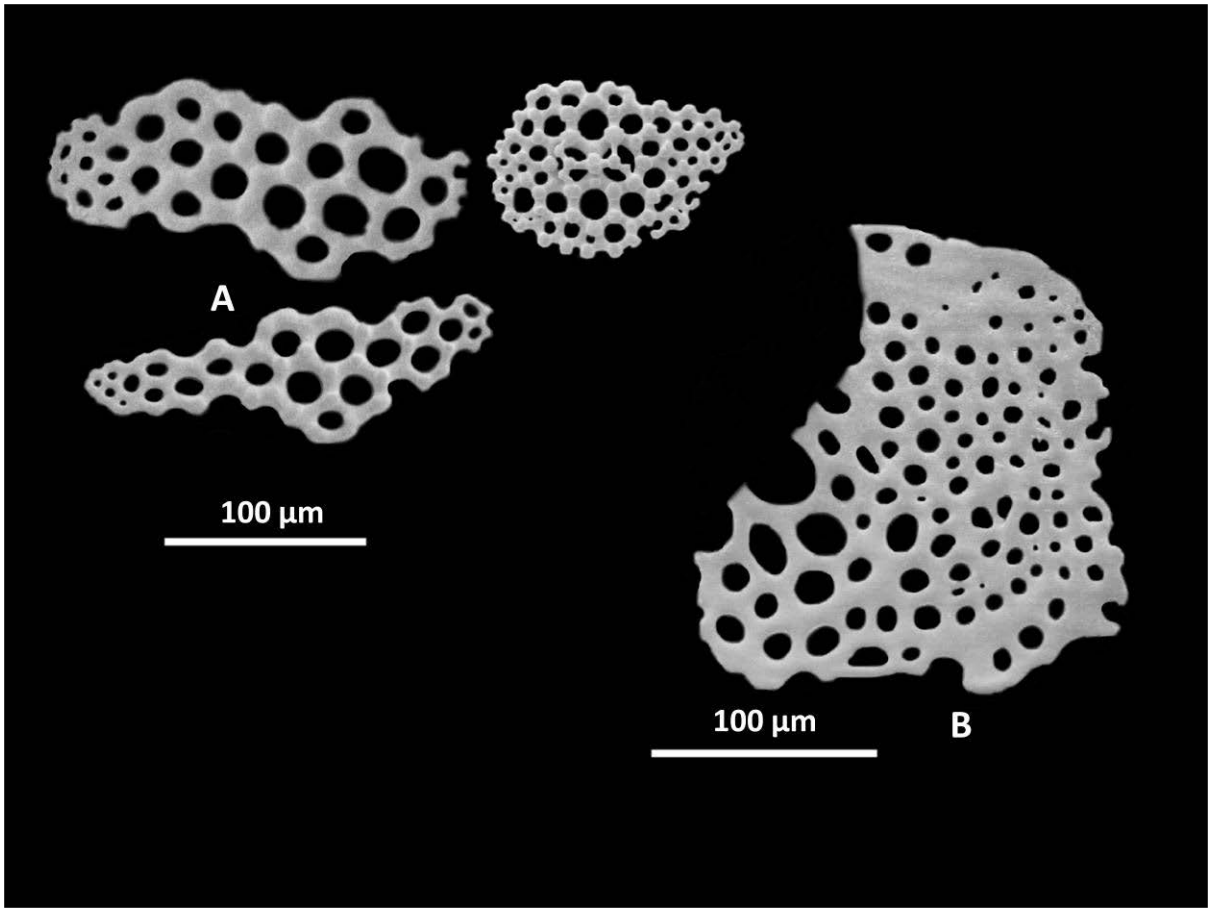


Figure 14. *Panningocnus echinatus* (Von Marenzeller, 1881). ZMC (Copenhagen Museum). A. Plates from anal region; B. Broken end-plate from tube foot.

Distribution

South China, South Japan, Red Sea (generally Indo-West Pacific), 0-50 metres (Liao & Clark, 1995).

Remarks

This species has been described by many authors (see synonymy). Panning (1949) transferred this species to his newly erected genus *Pseudocnus*. In this he was supported by Cherbonnier (1963). However, Liao *et al*. (1964) ignored or overlooked Panning's and Cherbonnier's papers by re-describing the species as *Cucumaria echinatua* Von Marenzeller, 1881. Clark and Rowe (1971) and Liao and Clark (1995) followed Panning (1949) and Cherbonnier (1963) by re-describing it as *Pseudocnus echinatus*. Since *Pseudocnus* is now restricted to species with 10 equal tentacles, the species is now transferred to *Panningocnus*. It was first recorded by Von Marenzeller (1881) from Japan. Clark and Rowe (1971) recorded its distribution as South China, South Japan and Red sea.

The material examined here is labelled "*Pseudocnus echinata*: South Africa (apparent donation to Mortensen during his Java-South Africa Exp 1929-1930, Gilchrist, Cape Town, #P. 1236. Det. Heding 1943). There is no record of this species from South Africa despite the fact that the fauna of South Africa is so well known. Therefore, the occurrence of *P. echinatus* (Marenzeller, 1881) in South Africa is doubtful unless *P. thandari* described by Moodley (2000) from St. Helena Bay is its synonym. However, *P. echinatus* differs from *P. thandari* in the presence of rosettes in the tentacles and introvert. In *P. echinatus* slender curved rods also occur in the tentacles whereas in *P. thandari* there are thick rods. Moreover, in *P. echinatus* the spine on the plates is elongated, slender, whereas in *P. echinatus* it is thick. These differences suggest possible mislabelling. *P. echinatus* is found only in the Indo-West Pacific Region.

Panningocnus lamperti (Ohshima, 1915) comb. new

Figure 15

Cucumaria lamperti Ohshima, 1915:260, pl. 10, figs.19a-b.

Stereoderma lamperti Panning, 1949:422 (passim).

Pseudocnus lamperti O'Loughlin *et al*., 2014:46, Table 2 (partim).

Diagnosis (after Ohshima 1915)

Body ovoid, up to 34 mm long and 14 mm wide, mouth and anus turned up. Colour whitish, skin tough. Brood pouches present. Tube feet only in ambulacra, in single-double rows, interambulacra naked. Tentacles 10, mid-ventral two greatly reduced. Calcareous ring simple, without posterior prolongations. Calcareous deposits include thick, knobbed plates, spinous at one end. Smooth buttons also present, with one end spinous. Pedicels with delicate, smooth plates, end-plates present. Tentacles include rod-like or plate-like supporting structures, knobbed or smooth. Introvert ossicles include oblong, knobbed, denticulate plates.

Material examined

NMNH: E02078 - *Pseudocnus lamperti* (Ohshima), North Pacific Ocean, United States, Alaska, Kyska harbour, 14-19 fm, 07 July 1893, 1 spec.

Description

Specimen very small, about 6 mm long and 2 mm wide. Colour light brown. Tube feet only in ambulacra, in single zigzag rows, interambulacra naked. Tentacles retracted, could not be counted as specimen very small and brittle.

Ossicles could not be observed, much corroded and fragmented.

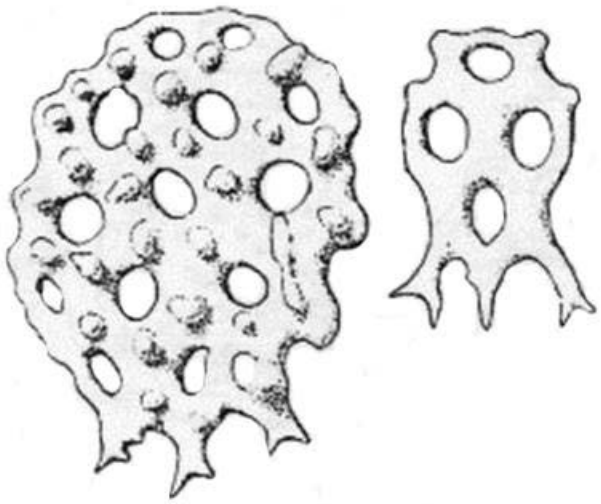


Figure 15. *Panningocnus lamperti* (Ohshima, 1915). Ossicles from body wall. Scale 150X (figure copied from Ohshima, 1915).

Distribution

Aleutian Islands, vicinity of Commander Islands (Ohshima, 1915), off South Tip of Peninsula (Alaska), (this study).

Remarks

There is nothing to conclude as the specimen could not be critically examined without damaging it irrevocably. Based on available description the species does share some characters with the type species of *Panningocnus* and this indicates that it is perhaps referable to this genus.

Panningocnus spinosus (Ohshima, 1915) comb. new

Figure 16

Cucumaria spinosa Ohshima, 1915:262, pl. 10 fig. 20a-c.

Stereoderma spinosa Panning, 1949:422 (passim).

Pseudocnus spinosus O'Loughlin *et al*., 2014:46, Table 2 (partim).

Diagnosis (after Ohshima 1915)

Body fusiform, strongly curved, tapering posteriorly. Colour white in alcohol. Skin thin, rough to the touch, leathery. Tube feet nipple-like in single zigzag row per ambulacrum, interambulacra naked. Anal papillae present. Tentacles 10, ventral two reduced. Calcareous ring simple, radials deeply notched posteriorly. Retractor muscles slender, originate from longitudinal muscles at about one third of body length from anterior end. Polian vesicle and stone canal single.

Body wall ossicles include elongated plates, thick in the middle, prolonged spinous end and with small holes (Figure 16). Tube feet deposits include irregular, rod-like plates, end-plates present. Tentacle deposits include irregular, perforated rods; introvert with thin scattered plates.

Material examined

None.

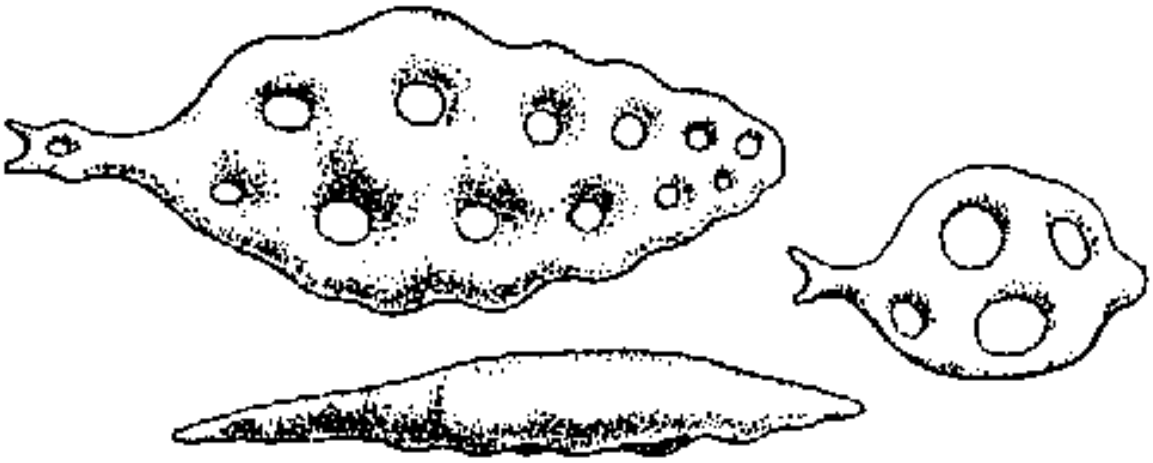


Figure 16. *Panningocnus spinosus* (Ohshima, 1915), Body wall ossicles (figure extracted from Ohshima 1915).

Distribution

Off Hitaka, Hokkaido, off Oshika Peninsula, Suruga Bay, (Ohshima, 1915).

Remarks

The species, described by Ohshima (1915) under the genus *Cucumaria,* has been only documented by few workers (see synonymy). Panning (1949) transferred it to *Stereoderma*. The species is currently listed in WoRMS and by O'Loughlin *et al*., (2014) as *Pseudocnus spinosus* (Ohshima, 1915). *Panningocnus spinosus* (Ohshima, 1915) is close to *P. echinatus* (Von Marenzeller, 1881), *P. thandari* (Moodley, 2008) and *P. lamperti* (Ohshima, 1915) with which it shares similar characters such as restricted tube feet distribution, spinous pine-cone shaped plates in addition to unequal tentacles. Amongst all *Panningocnus* species, *P. spinosus* is very close to *P. lamperti* but the two species differ slightly in that the former possesses irregular perforated rods as tentacle deposits whereas in the latter plate-like rods are observed in the tentacles. Based on its diagnosis Ohshima's species is now assigned to *Panningocnus.*

Panningocnus thandari (Moodley, 2008) comb. new

Figure 17A-B, 18A-B, and 19A-C

Pseudocnus thandari Moodley, 2008:61-64, 2 text figures.
Pseudocnus thandari: Thandar *et al*., 2010:18.
Pseudocnus thandari O'Loughlin *et al*., 2014:46, Table 2 (partim).

Diagnosis (after Moodley 2008)

Barrel to slightly U-shaped body. Mouth and anus terminal. Colour greyish-white to pinkish-brown. Anal teeth absent. Anus dorsally directed. Tube feet only in ambulacra, in double rows. Tentacles 10, ventral two reduced. Calcareous ring simple, typically cucumariid.

Body wall ossicles consist of knobbed, single-layered plates, of two types: one type elongated with a short, smooth process/spine; the other type rounded without spine. Tube feet with rods, sometimes plate-like, curved, smooth to sparsely knobbed. Tentacles with curved rods; introvert with large, round to oval plates, rosettes present.

Material examined

South-west of Walvis Bay, Namibia, 200 meters, June 2014, 4 spec., collected by Tim McClurg.

Description

Largest specimen about 30 mm long and 10 mm wide, smallest about 21 mm long and 11 mm in width. Body shape cucumber-like or sub-cylindrical, mouth terminal, anus slightly curved up. Skin thin, of rough texture; colour greyish to off white. No anal papillae or teeth detected. Tube feet non-retractile, in double conspicuous rows, interambulacra naked. Tentacles 10, retracted, bushy, ventral two considerably reduced. Calcareous ring simple, without processes (Figure 19B). Polian vesicle single, large stone canal of medium-size, madreporite bean-shaped (Figure 19A). Retractor muscles very thin, attached to longitudinal muscles at about ½ body length. Respiratory trees highly branched. Gonad in two tufts of undivided tubules, mature.

Body wall ossicles comprise ovate/oblong, knobbed and perforated plates prolonged at one end which terminates in one or two short spines (Figure 17A), sometimes perforated by a single hole; some pine cone-shaped plates lack spinous end. Plates about 130-190 µm long and 50-90 µm wide with about 4-12 holes, holes about 10-30 µm diameter. Tube feet deposits comprise curved and straight, knobbed, perforated rods, sometimes smooth rods, and some table-like rods (Figure 17B). Tentacle deposits as rosette-like rods (Figure 18A). Introvert with smooth plate-like rosettes (Figure 18B).

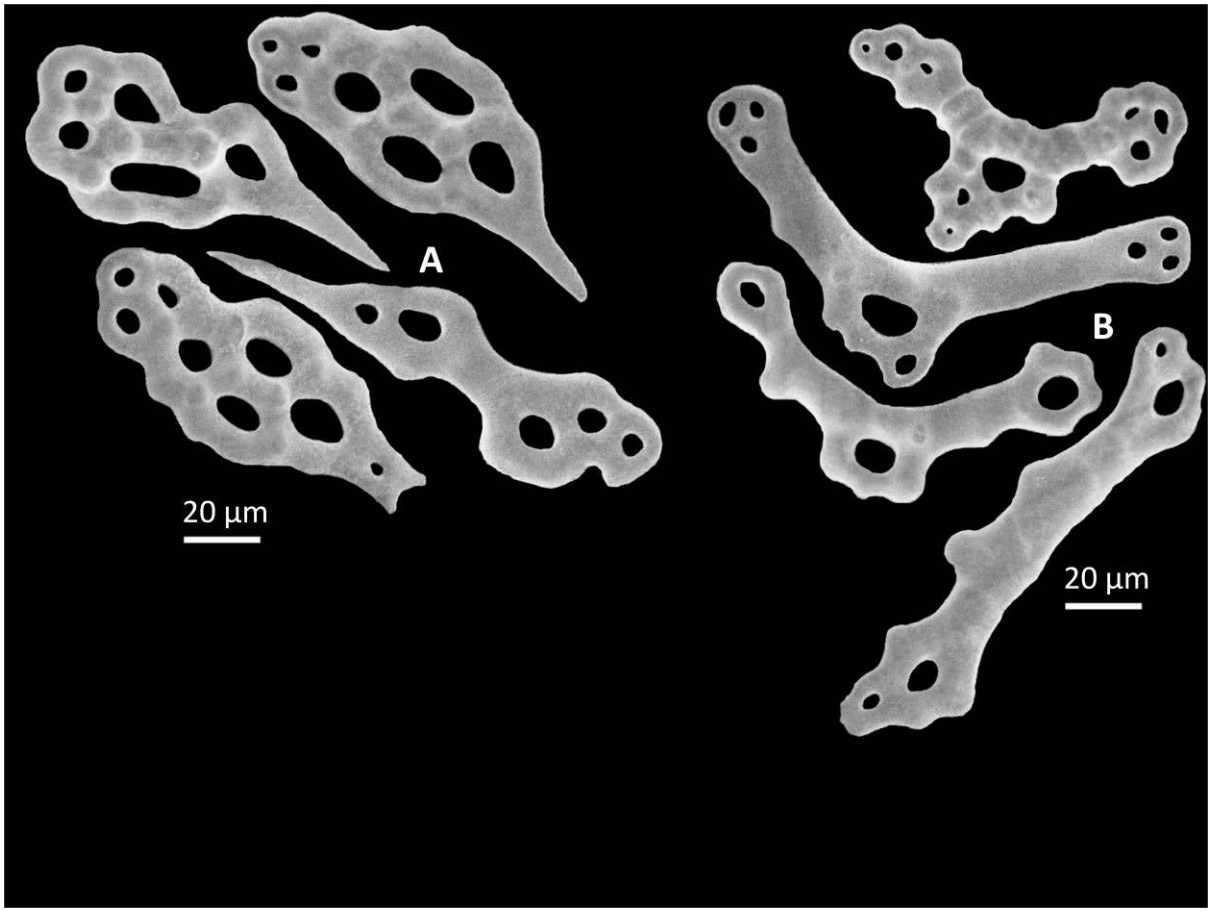


Figure 17. *Panningocnus thandari* (Moodley, 2008). South-west of Walvis Bay, Namibia. A. Ossicles from body wall; B. Ossicles from tube feet.

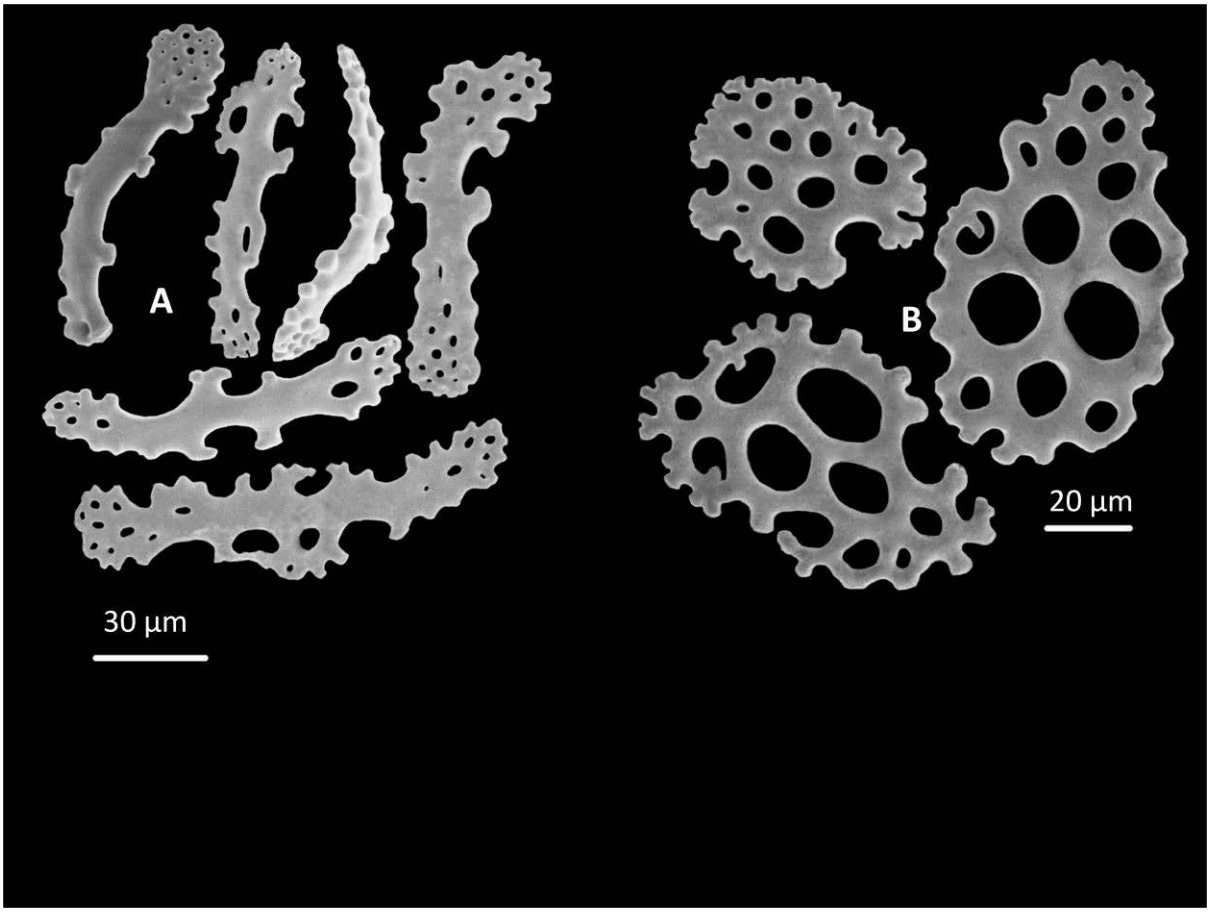


Figure 18. *Panningocnus thandari* (Moodley, 2008). South-west of Walvis Bay, Namibia. A. Ossicles from tentacles; B. Ossicles from introvert.

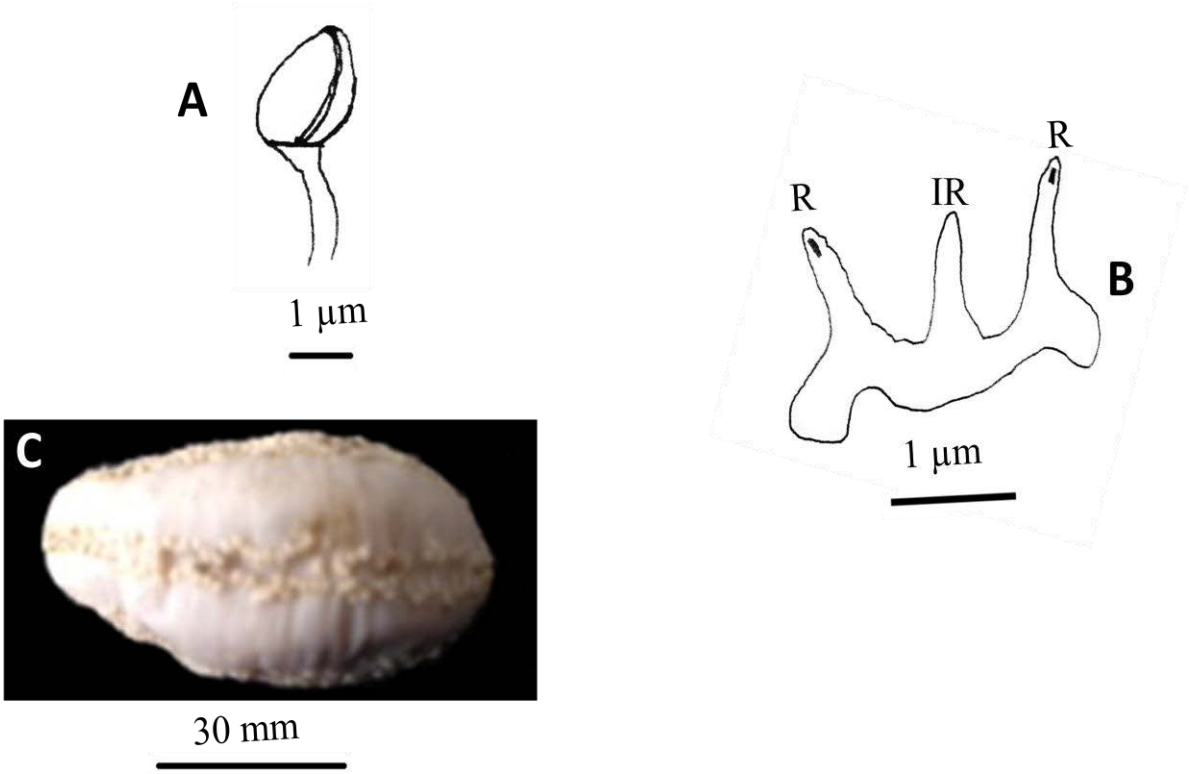


Figure 19. *Panningocnus thandari* (Moodley, 2008). South-west of Walvis Bay, Namibia. A. Bean-shaped madreporite; B. Calcareous ring; C. Entire.

Distribution

Northern Namibia to west coast of South Africa (Moodley, 2008; Thandar *el al*., (2010)), 18-200 meters (this study).

Remarks

The species is well described by Moodley (2008). From the specimen at hand, plate-like rosettes were found in the introvert, but Moodley could not find such structures.

Moodley recorded *P. thandari* from the south-west coast of Western Cape Province at about 32 meters, but Thandar *el al*., (2010) extended its horizontal distribution northwards into Namibia and the vertical distribution to 117 meters. The latter figure is now extended to 200 meters.

Panningocnus salmini (Ludwig, 1875) comb. new

Cucumaria salmini Ludwig, 1875 :86.

Cucumaria salmini Théel, 1886:113.

Pseudocnus salmini O'Loughlin *et al*. 2014:46, table 2 (passim).

Diagnosis (after Ludwig 1875; Théel 1886)

Body tapering posteriorly, anus dentate. Tube feet in two rows per ambulacrum, numerous also in interambulacra. Tube feet more numerous dorsally. Tentacles unequal, ventral two reduced. Deposits like those in *Panningocnus dubiosus* (Semper, 1868).

Material examined

None.

Distribution

Indonesia (O'Loughlin *et al*., 2014).

Remarks

Théel (1886) noted that *Cucumaria salmini* and *C. koellikeri* share similar ossicles but differ in that in *C. salmini* the two ventral tentacles are reduced whereas in *C. koellikeri* the tentacles are of equal size. Théel further suspected that both are probably conspecific. However, based on tentacle size this opinion cannot be accepted. Ludwig (1875) likened the ossicles of *C. salmini* to those of *Cucumaria dubiosa* Semper, 1868. Diechmann (1941) relegated *C. salmini* to the synonymy of *Cucumaria leonina* because of identical ossicles, however, O'Loughlin *et al*. (2014) considered it unlikely that a tropical Pacific species would be conspecific with a sub-Antarctic South American species and therefore raised *C. salmini* out of synonymy (by Deichmann, 1941). A full history of *Panningocnus salmini* is given by O'Loughlin *et al*. (2014) and there is no need to repeat it here. O'Loughlin *et al*. (2014) re-assigned it to *Pseudocnus.* However, it is here re-assigned to *Panningocnus* because of its unequal tentacles and due to the fact that its ossicles are similar to *Panningocnus dubiosus* as alluded to by Ludwig 1875 but differs in the thickness of tentacle rods.

P. salmini is also very close to *P. africanus* with which it shares scattered tube feet distribution in addition to unequal tentacles and plates consisting of a single layer of calcareous material.

Panningocnus africanus (Britten, 1910) comb. new

Figure 20 A-K, 21 A-E

Cucumaria leonina var. *africana* Britten, 1910:40.

Cucumaria insolens Clark, 1923:411; Deichmann, 1948:346 (partim)(not *insolens* Théel).

Diagnosis (after Britten 1910)

Tube feet in ambulacra in double rows, large on introvert. Tentacles 10, unequal. Body wall ossicles as knobbed, ovate plates (Figure 20 A-E) and buttons (Figure 20 F-K), no baskets. Plates single-layered. Buttons with 5-14 holes. Rods present in tube feet (Figure 21 A-D), end-plates present.

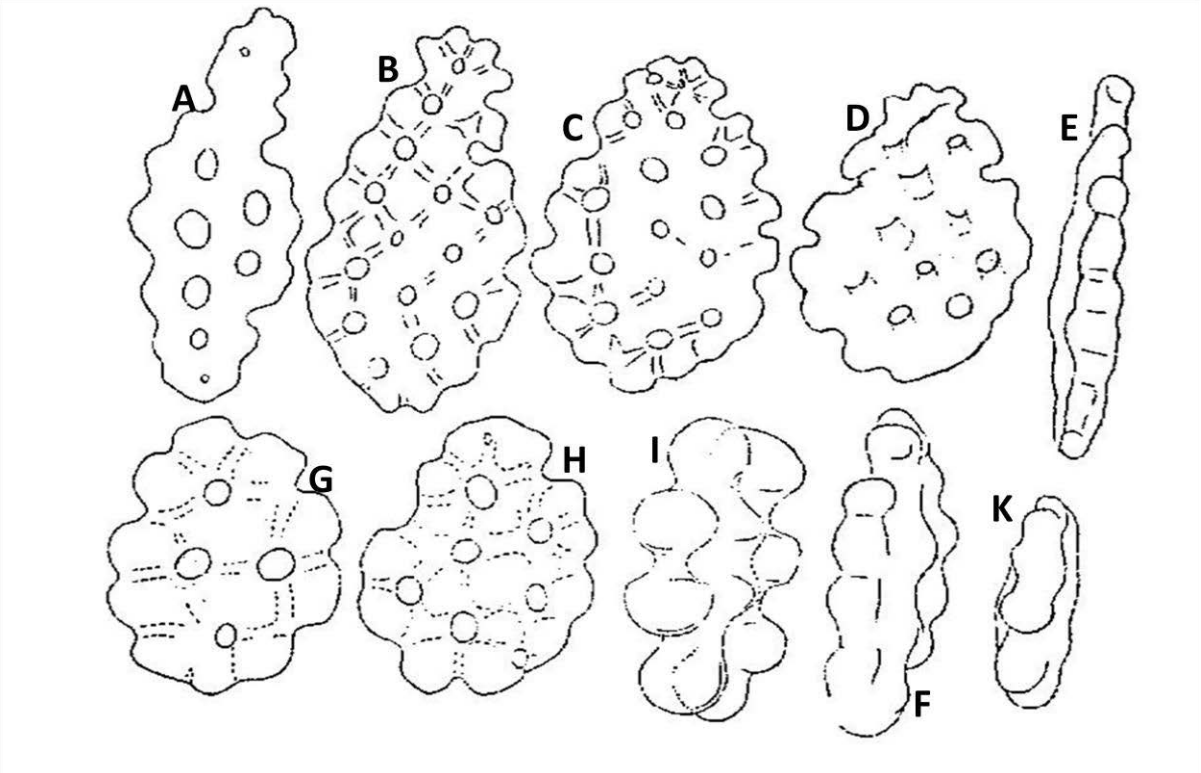


Figure 20. *Panningocnus africanus* (Britten, 1910). A-E. Fircone-shaped plates from body wall; F-K. Round plates/buttons from body wall (Figure extracted from Panning 1962:64).

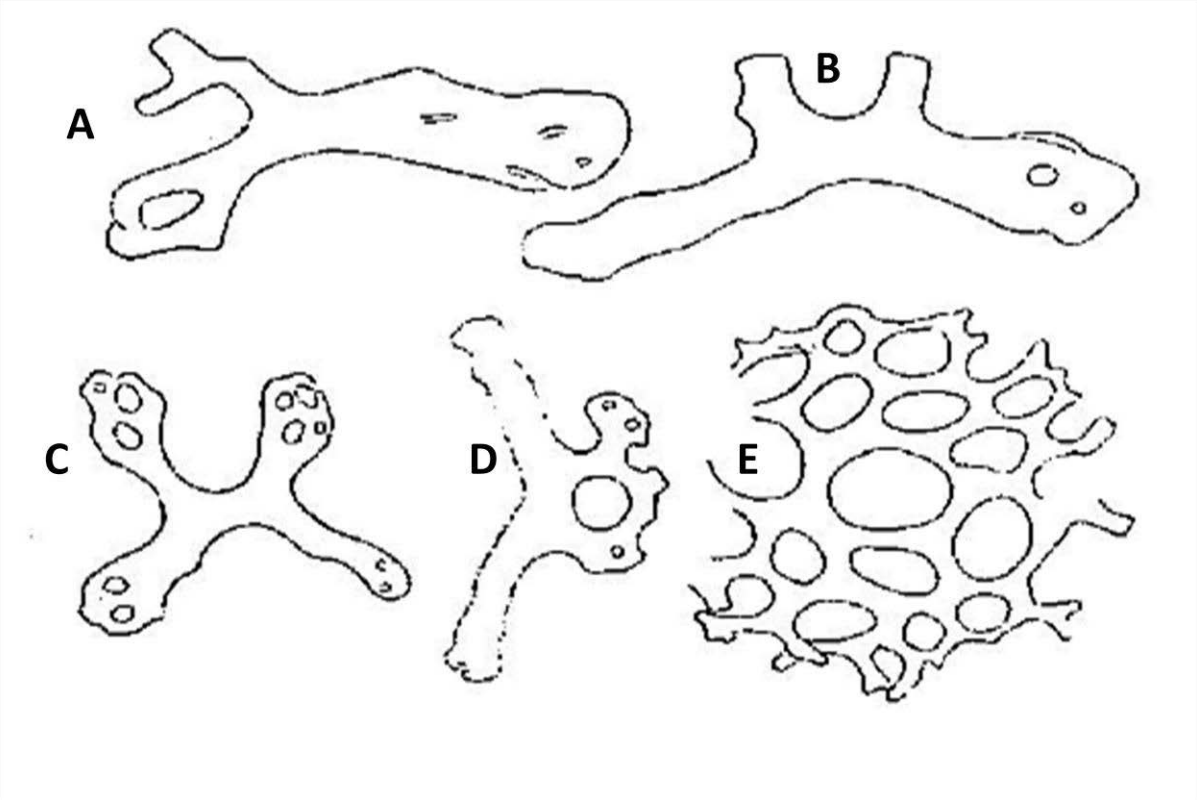


Figure 21. *Panningocnus africanus* (Britten, 1910). A, B. Rods from tube feet; C,D. rods from ventral tube feet; E. Endplate (Figure extracted from Panning 1962:65).

Material examined

None.

Distribution

Luderitz Bay (former Angra Penquena Bay), Namibia (Britten, 1910).

Remarks

Britten (1910) described a form from the Luderitz (Namibia)) as a variety of *Cucumaria leonina* since it shared most of its characters with this species. However, Clark (1923) criticized Britten's (1910) decision of describeing it as a new species and, therefore, relegated it to the synonymy of *Cucumaria insolens*. Deichmann (1948), Cherbonnier (1952) and Thandar (198) reiterated Clark's (192) decision. Panning (1962) re-described *Cucumaria leonina* var. *africana*, presumably from the type, as a subspecies of *Pseudocnus dubiosus*. It is for this reason that Thandar and Rambaran (2015) recently suggested that Britten's species should be retained. This viewpoint is here accepted because Britten's form, as illustrated by Panning (1962), perhaps has plates made up of a single layer of calcareous material whereas *Pseudocnella insolens* has multilayered plates with one end prolonged into a denticulate handle and in addition incomplete baskets. e nce Britten's species is raised out of synonymy

with *C. insolens* and reassigned to *Panningocnus* since it shares similar characters with the type species and its congeners.

***Panningocnus* sp.** (Massin, 1993) comb. new

Figure 22 A-C and 23

?*Pseudocnus* sp. indet. Massin, 1993:412-413, figs. 11-12.

Diagnosis (after Massin 1993)

Small specimen (41 mm long). Tube feet only in ambulacra, in two conspicuous rows, but four rows in mid-ventral ambulacrum. Body wall ossicles of two types. Large, thick, knobbed multilocular plates anteriorly; knobbed round buttons also present (Figure 22A); posteriorly, large smooth, thick multilocular plates, slightly knobbed and denticulate at one end (Figure 22B). Tube feet ossicles comprise more or less straight (Figure 22C), v-shaped rods (Figure 23) and knobbed irregular plates (Figure 23).

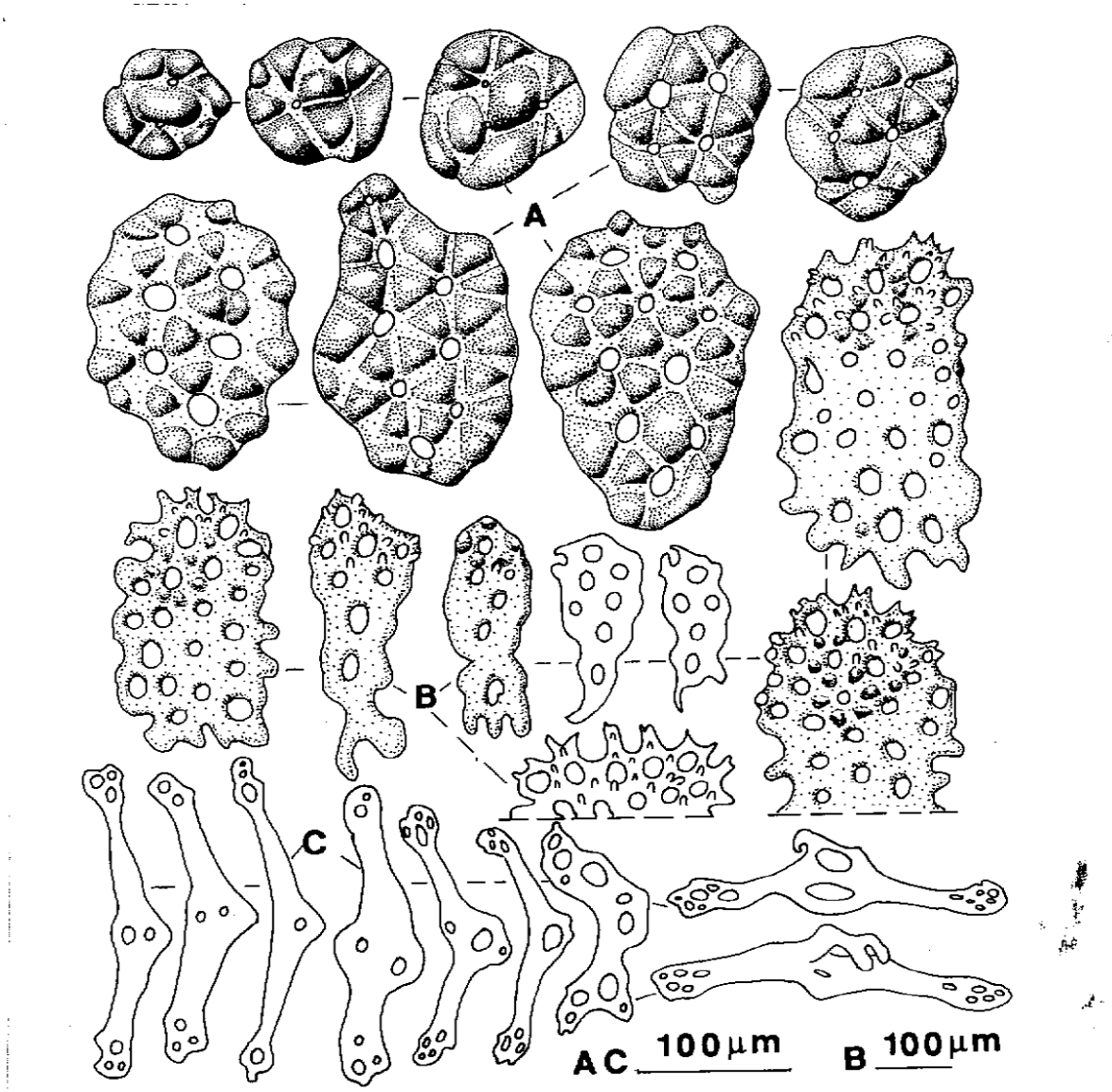


Figure 22. *Panningocnus* sp. (Massin, 1993). Ossicles from anterior body wall; B. Ossicles from posterior body wall; C. rods from anterior body wall. Extracted from Massin 1993: 413.

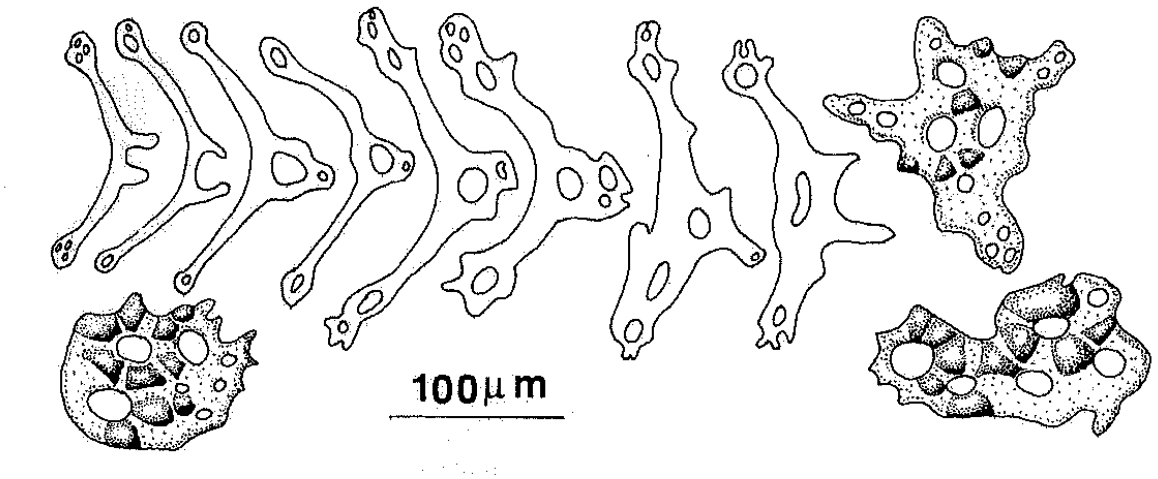


Figure 23. *Panningocnus* sp. (Massin, 1993). Ossicles of posterior tube feet. Figure extracted from Massin 1993:412.

Material examined

None.

Distribution

Mauritania (Massin, 1993).

Remarks

Since the specimen lacked tentacles, calcareous ring and introvert, Massin (1993) did not name the species. Massin, however, classified the species in *Pseudocnus*, and postulated that the species resembles *Panningocnus africanus* (Britten, 1910). Based on the fact that the ossicles illustrated by Massin, resemble those of *P. africanus* it is tentatively assigned to the same genus. It differs in the restricted distribution of the tube feet (perhaps a juvenile character) and the posterior ossicles. However, more specimens need to be discovered.

Pentactella Verrill, 1876

Pentactella Verrill, 1876.

Cucumaria Théel, 1886 (passim).

Cucumaria Ekman, 1925 (partim).

Stereoderma Panning 1949 (partim).

Pseudocnus Panning, 1962 (partim).

Laevocnus O'Loughlin *et al*., 2014.

Pentactella O'Loughlin *et al*., 2015.

Type species : *Petactella laevigata* Verrill, 1876 (by original designation) .

Other species included : *Pseudocnus cornutus* (Cherbonnier, 1941)*, Cucumaria intermedia* Thèel, 1886*, Pseudocnus leoninoides* (Mortensen, 1925)*, Pseudocnus leoninus* (Semper, 1867)*, Pseudocnus perrieri* (Ekman, 1927)*,* and *Cucumaria serrata* Théel, 1886; *Laevocnus katrinae* O'Loughlin, 2014; *Laevocnus leachmani* Dave & O'Loughlin, 2014.

Diagnosis (as for *Laevocnus* O'Loughlin *et al*. 2014)

Tentacles 10, of equal size. Tube feet in ambulacra only, crossing introvert to base of tentacles. Calcareous ring lacking posterior prolongations, sometimes not calcified. Gonad tubules not branched. Body wall ossicles single-layered, perforated, knobbed plates with one end tapered and distally spinous, no buttons. Tentacle ossicles include perforated plates, rarely rods, and no rosettes.

Remarks

O'Loughlin *et al*. (2014) erected a new genus *Laevocnus,* with *Petactella laevigata* Verrill, 1876 as type species, to accommodate all the species Panning (1949) assigned to his *laevigatus* group but also *Cucumaria leonina* and two new species. This genus was based on morphological, molecular and biogeographic data. It was soon discovered by the moderator of WoRMS (Gustav Paulay) that *Laevocnus* is synonymous with *Pentactella,* a genus that was erected by Verrill 1876 with his *Petactella laevigata* as type species. O'Loughlin *et al*. (2014) overlooked this perhaps because Panning (1949), without any comments, relegated the genus to the synonymy of *Stereoderma* Ayres, 1851. Panning's lack of comments was perhaps due to the fact that Ekman (1925) considered *P. laevigata* to be *Cucumaria leonina* since it shares some characteristics with this species. According to O'Loughlin *et al*. (2015) *Pentactella* is now resurrected to replace *Laevocnus.* The two new species viz. *Laevocnus katrinae* O'Loughlin, 2014 (in O'Loughlin *et al*., 2014) and *Laevocnus leachmani* Dave & O'Loughlin, 2014 (in O'Loughlin *et al*., 2014) are well illustrated by O'Loughlin *et al*. (2014) and there is no need to re-illustrate them here, only those species previously assigned to *Pseudocnus* are here dealt with.

Pentactella intermedia (Théel, 1886)

Cucumaria serrata var *intermedia* Théel, 1886:74, pl. 3 fig. 6, pl. 4 fig. 2.

Cucumaria laevigata Ekman, 1927:396-403, fig. 15 (partim) (non *Pseudocnus laevigatus* (Verrill, 1876)).

Pseudocnus intermedia O`Loughlin, 2009:7-8, fig. 2d.

Laevocnus intermedius O'Loughlin et al., 2014:4 .

Pentactella intermedia O'Loughlin et al., 2015:80.

Diagnosis (after Théel 1886)

Body fusiform, elongate, thin, up to 80 mm long and 12 mm wide. Tube feet in single to double zigzag rows in each ambulacrum, sometimes scattered dorsally, dense in ventral ambulacra. Anal teeth present. Ten equal Tentacles. Calcareous ring uncalcified. Polian vesicles 3-4. Body wall ossicles comprise pine cone-shaped, knobbed, perforated plates with one end denticulate.

Material examined

None.

Distribution

Heard and Kerguelen Islands, 2-275 meters (O'Loughlin, 2009).

Remarks

Théel (1886), in his description of this subspecies, noted that it differs from its consubspecific *Cucumaria serrata* in ossicle size, with the latter having large ossicles with long and narrower handle. Théel found four Polian vesicles in his form from Heard Island but O`Loughlin (2009) mentioned only three in his description of the specimen from Kerguelen Island. *Cucumaria serrata* has only two Polian vesicles. Ekman (1927) concluded that Théel`s *Cucumaria serrata, Cucumaria marionensis* and *Cucumaria serrata* var. *intermedia* were junior synonyms of *Cucumaria laevigata* (Verrill, 1876). However, O`Loughlin (2009), who re-examined the materials from Heard and Kerguelen Islands, supported Théel's recognition of the three forms, O`Loughlin (2009) therefore raised *Cucumaria serrata* var. *intermedia* out of synonymy of *laevigata* to full specific rank and assigned it to *Pseudocnus*. Subsequently, O`Loughlin (2009) noted that *P. intermedia* and *P. leoninus* share similar ossicles , but differ in tube feet distribution with *P. leoninus* having a complete cover of tube feet while *P. intermedia* has tube feet restricted to the ambulacra. Recently, O'Loughlin *et al*., 2014 transferred both species to the new genus *Laevocnus*.now the synonym of *Pentactella*.

Pentactella laevigata Verrill, 1876

Figure 24

Pentactella laevigata Verrill, 1876:68 ; Studer, 1876 :453.
Cucumaria laevigata Théel, 1886 :109.
Stereoderma laevigata Panning, 1949 :422 (passim).
Cucumaria laevigata Ekman, 1927:396, fig. 15.
Pseudocnus laevigatus Panning, 1962:71; Pawson, 1968: 145, fig. 2-11; 1969:134 (partim); O`Hara, 1998: 210-211, pl. 4g, 5p-q.
Laevocnus laevigatus O'Loughlin *et al*., 2014:47.
Pentactella laevocnus O'Loughlin *et al*., 2015:80.

Diagnosis (mostly after Pawson 1968; and Verrill 1876)

Body fusiform, more or less elongated. Tube feet only in ambulacra in double rows, interambulacra naked. Tentacles 10, equal. Calcareous ring simple, typically cucumariid. Polian vesicles 3-5. Retractor muscles attached at approximately ½ body length. Brood pouches present. Body wall ossicles comprise ovate to elongate, knobbed, perforated plates, single-layered, with one end denticulate (Figure 24A). Tube feet deposits as small plates, like those of body wall (Figure 24C-D), end-plates large. Tentacle deposits as knobbed, perforated plates, in addition to rods (Figure 24 E, F, and H). Introvert ossicles include round or oblong, knobbed plates, with one end denticulate (Figure 24B).

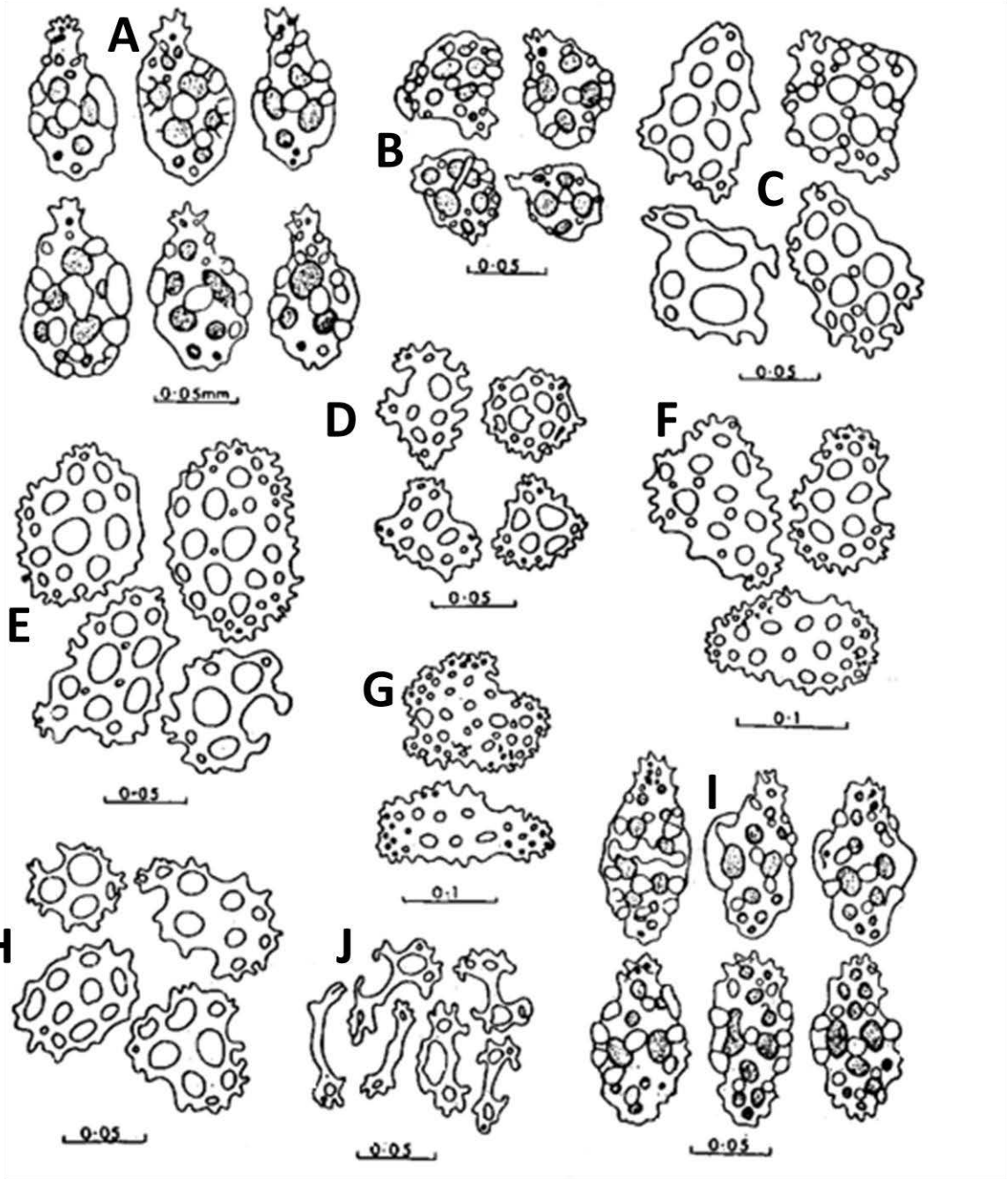


Figure 24. *Pentactella laevigata* Verrill, 1876. A, I knobbed plates from body wall; C,D deposits from tube feet; B knobbed plates from introvert; E, H smaller plates from tentacles; F, G large plates from tentacles; J perforated plates from tentacles, (plates extracted from Pawson 1968).

Material examined

None.

Distribution

McDonald Island, Prince Edward Island, Crozet Island, Macquarie Island, Marion Island, littoral to 1000 metres (Pawson, 1969; O' a ra, 1998; O'Loughlin *et al*., 2014).

Remarks

Deichmann (1947) postulated that the type material of *Pentactella laevigata* is lost. However, Pawson (1968) found a specimen in the collections of United States National Museum, labelled "Co-type *Pentactella laevigata*", and thought that he had the only existing specimen of the original series as the measurements of specimens harmonized well with those of the type described by Verrill (1876). According to Pawson (1968), Verrill did not mention anything about brood pouches, but in the specimen he (Pawson) studied brood pouches are present. Pawson (1968) also noted the presence of a calcareous ring which Verrill mentioned as lacking in this species, hence assigning it to his new genus *Pentactella*. Pawson (1968) and Deichmann (1947) concurred that the specimens do not exactly conform with Verrill`s description, but since there were only a few differences they amended Verrill's diagnosis by adding more characters. *Pentactella laevigata* has been studied by many subsequent authors including Ekman (1925, 1927) who in the latter paper split the South American form from the sub-Antarctic form, naming the former as *Cucumaria perrieri*. This was supported by Panning (1962) and Pawson (1969). According to Pawson, *Pentactella laevigata* is now restricted to Sub-antarctic Islands, including Prince Edward Islands, Crozet Islands and Macquarie Island. Recently O`Hara (1998) added Marion Island. Since there were no material/specimens of this species to work on, the diagnosis of the species is extracted from the literature.

Pentactella leonina (Semper, 1868)

Figure 25A-B, 26A-F

Cucumaria leonina Semper, 1868:53, p. 15 fig. 9; Ludwig, 1898:39; Perrier, 1905:25, pl. 1 fig. 6-8; Hérouard, 1906:3, pl. 2 fig. 7-9; Dendy, 1909:146-149, pl. 5, figs. 1a-c; Ekman, 1925:52, fig. 10.

Cucumaria dubiosa Théel, 1886:111; Ludwig, 1887:14, pl. 1 fig. 1 (non *dubiosus* Semper, 1868).

Cucumaria mendax Théel, 1886:65, pl. 5 fig. 3, pl. 16 fig. 3.

Pseudocnus dubiosus Panning, 1949:424, fig. 11 (non *dubiosus* Semper, 1868).

Pseudocnus dubiosus leonina Panning, 1951:73.

Pseudocnus dubiosus leoninus Panning, 1962:60-62, fig. 3, 4.

Laevocnus leoninus O'Loughlin *et al*., 2014:47.

Pentactella leonina O'Loughlin et al., 2015:80.

Diagnosis (mostly after Semper 1868)

Tube feet in both ambulacra and interambulacra. Anal teeth present. Tentacles 10, all of same size. Calcareous ring simple, typically cucumariid. Body wall ossicles consist of knobbed, perforated, single-layered, denticulate plates, small round plates or buttons present with 3-4 holes. Tube feet deposits as perforated rods, with a large central hole and small distal perforations. Tentacle deposits comprise only rods, straight or curved with 1-4 large central holes. Introvert ossicles as knobbed, perforated, oblong or round plates in addition to rods.

Material examined

ZMC: Pisco, Peru, 3 spec. E2841**,** ZMH; South America, Falkland Island, Port Stanley, Fd., Tangwurzeln, Hbg. 4 spec. M , F104820: South Atlantic Ocean, Burdwood Bank (54 12 0 -54 1 6 S, 59 48 24 - 59 51 6 W), 1 spec.; F106962, South Atlantic Ocean, Falkland Islands (52 21 2 S, 58 50 29 -58 5 22 W), 1 spec.

Description

Body sub-cylindrical, up to 20 mm long and 11 mm wide. Colour white-grey. Tube feet in two conspicuous rows per ambulacrum, also scattered in dorsal interambulacra. Tentacles 10, all of same size. Calcareous ring simple, radial plates notched posteriorly. Respiratory trees highly branched. Gonad mature, in two tufts. Retractor muscles very short, attached to longitudinal muscle at about ¼ body length

Body wall ossicles comprise knobbed, perforated, oblong or irregular, single-layered plates (Figure 25A). Round, knobbed, perforated buttons are also present (Figure 25B). Oblong plates denticulate at one end, 140-150 µm long, 70-80 µm wide, denticles (3-5), borne on short, perforated handle. Irregular plates lack handle. Small buttons are often 4-holed, sometimes 3-holed but always with 1-2 large central knob(s); buttons measure about 80-100 µm. Tube feet deposits as rods, with a reduced 3rd arm, a large central hole and minute distal perforations, scarce knobbed rods (Figure 26A) and some plate-like rods (Figure 26C). Tentacle deposits as only curved rods, some as in tube feet (Figure 26B). Introvert ossicles include oblong to round plates in addition to rods, plates with large holes and small knobs; rods elongate, some rosette-like, some knobbed with large central holes and small distal perforations (Figure 26D).

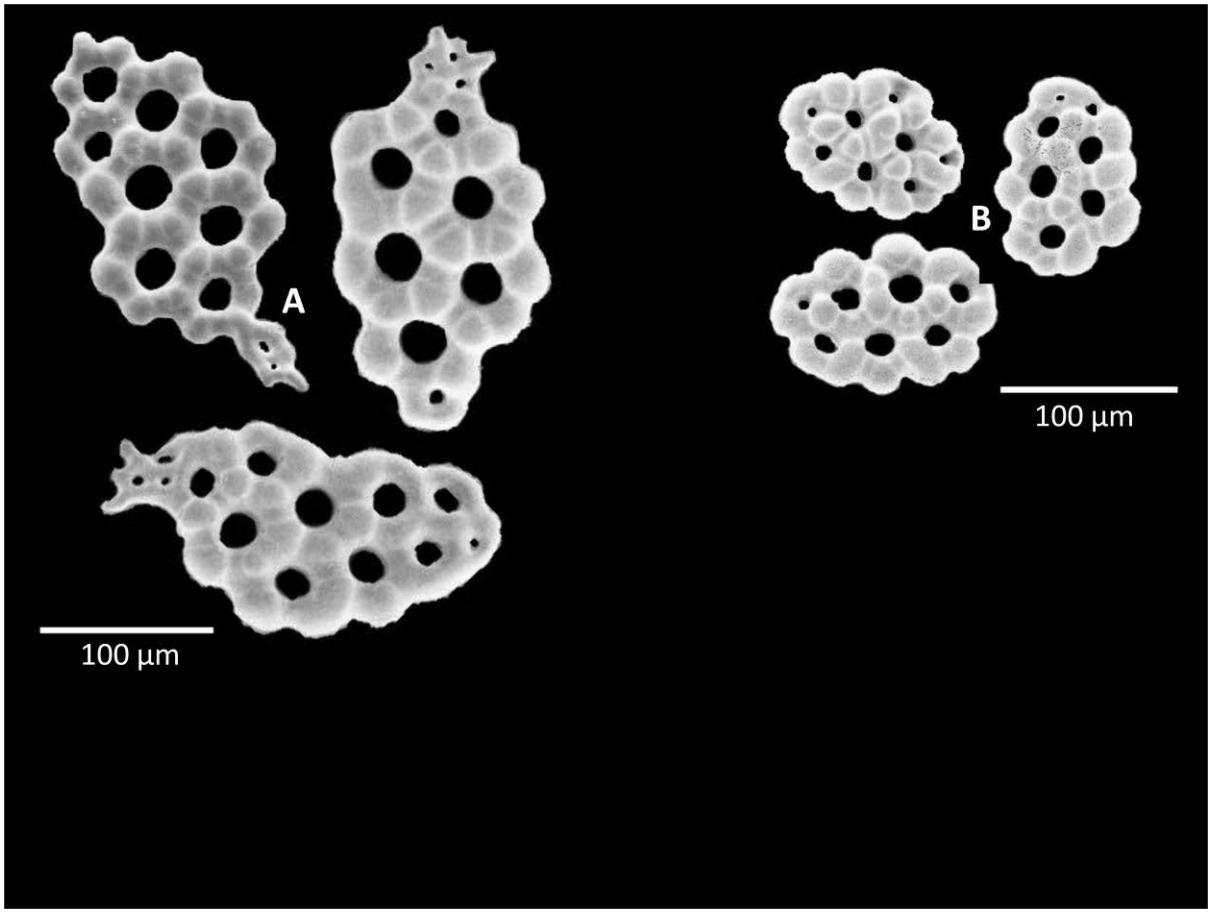


Figure 25. *Pentactella leonina* (Semper, 1867). ZMC E2841. A. Pine-cone-shaped plates from body wall; B. Buttons from body wall.

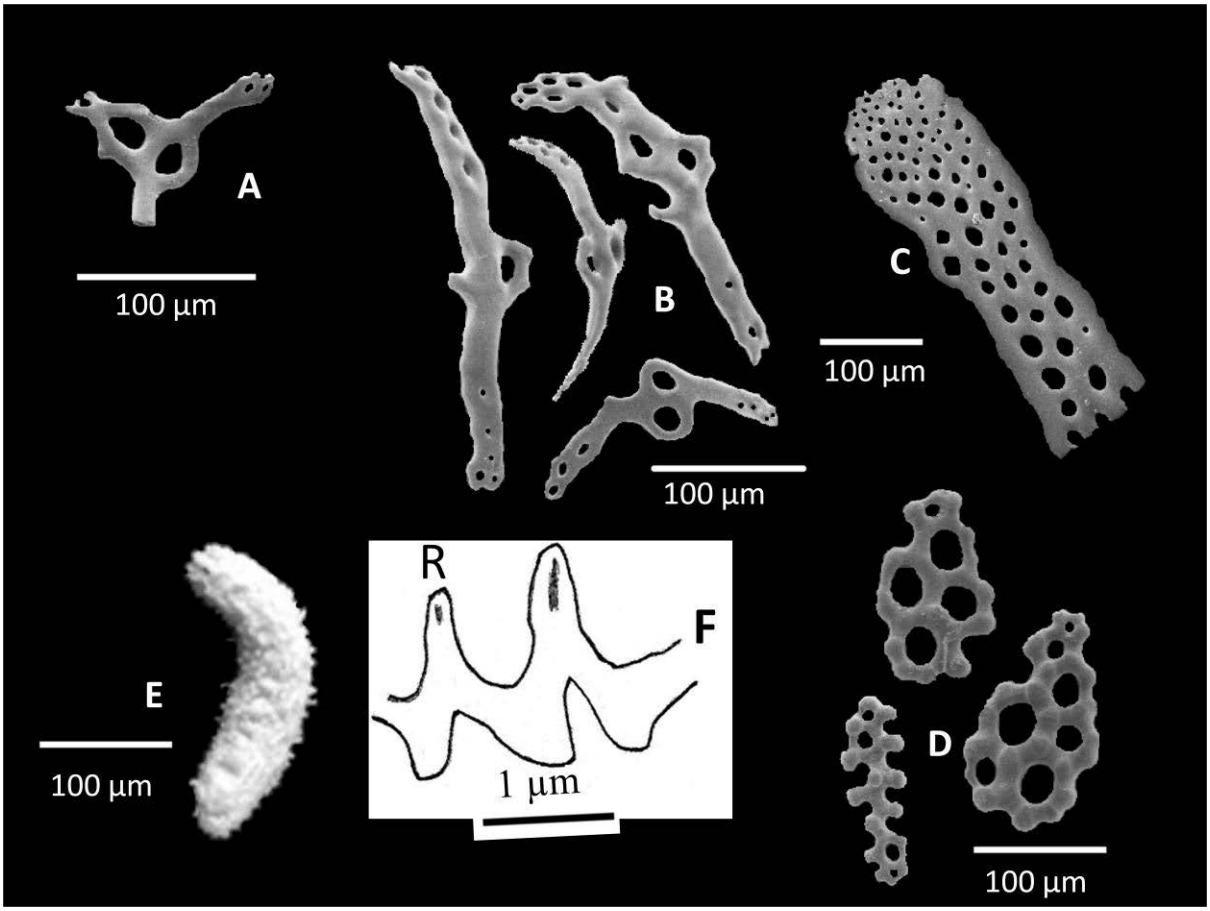


Figure 26. *Pentactella leonina* (Semper, 1867). ZMC E2841. A. Rod from tube feet; B. Rods from tentacles; C. Plate-like rod from tube feet; D. ossicles from introvert; E. Entire; F. Calcareous ring.

Distribution

Chile, Peru, West Tierra de Fuego, Patagonia (Panning, 1962), Falkland Islands (O'Loughlin *et al*., 2014; Pawson, 1969).

Remarks

Panning (1962) believed that his description of *Pseudocnus dubiosus* in 1949 was a specimen of *Cucumaria leonina* Semper, 1868. This was rectified in his synonymy of *C. leonina* in 1962. Ludwig (1898), Panning (1962) and Pawson (1969) believed that *Cucumaria leonina* and *Cucumaria dubiosa* are identical. Panning (1962) regarded *Cucumaria leonina* as a subspecies of *Cucumaria dubiosa*, naming it *Pseudocnus dubiosa leoninus.* The two species differ in that *Cucumaria leonina* has 10 equal tentacles while *Cucumaria dubiosa* Semper, 1868 has the two ventral reduced. The two species also differ in body wall ossicles composition with *Cucumaria leonina* having oblong knobbed plates with a denticulate

handle, absent *in C. dubiosa.* Based on the above the two species are distinct and should be treated as such. Ludwig (1898) and Ekman (1925) also noted that *Cucumaria leonina* and *Cucumaria mendax* Théel, 1886 are identical, and suggested that Théel`s *C. mendax* be treated as a junior synonym of *Cucumaria leonina*. Panning's 1962 decisions are still accepted in WoRMS and GBIF. o wever, recently O'Loughlin *et al.,* 2014 transferred *C. leonina* Semper, 1868 to *Laevocnus* (currently replaced by *Pentactella*). The horizontal distribution of *leonina* is now extended to Peru.

This species, based on form and complement of ossicles alone, is clearly referable to *Pseudocnus* herein restricted but O'Loughlin *et al*. (2014) assigned it to their *Laevocnus* as an exception because of the distribution and gene sequencing. Hence it is here retained in *Pentactella.*

Pentactella perrieri (Ekman, 1927)

Figure 27A-D, 28A-B

Cucumaria laevigata Ludwig, 1898:32, pl. 2 fig. 25; Perrier, 1905:22; Hérouard, 1906:12, pl. 1 fig. 6, pl. 6 figs. 5, 6; Vaney, 1909:430; Ekman, 1925:56; Deichmann, 1947:333 (non *laevigata* Verrill).
Cucumaria perrieri Ekman, 1927:403.
Stereoderma perrieri Panning, 1949:457.
Stereoderma laevigata Pawson, 1964:457.
Pseudocnus perrieri Panning, 1962:71, figs. 15, 16; Pawson, 1969:133-134.
Laevocnus perrieri O'Loughlin *et al*., 2014:47.
Pentactella perrieri O'Loughlin et al., 2015:80.

Diagnosis (after Panning 1962)

Body elongate, cylindrical, slightly tapered at rear end. Tube feet restricted to ambulacra, interambulacra naked. Calcareous ring simple, weakly calcified. Tentacles 10, of equal size. Body wall ossicles comprise oblong, knobbed, perforated plates with one end denticulate. Buttons absent. Tube feet deposits include perforated, knobbed, 3-armed rods, knobs few and inconspicuous. Tentacle deposits include perforated rods, sometimes sparingly knobbed, straight or with a third arm. Introvert with 4-holed buttons, sometimes with a denticulate end.

Material examined

M : F106964, South Atlantic Ocean, Burdwood Bank (54 12 0 - 54 1 6 S, 59 48 24 - 59 51 6 W), 1 spec.; F106968, South Atlantic Ocean, Falkland Islands (52 0 04 - 52 09 00 S, 58 04 22-58 06 04 W), 1 spec.

Description

Specimens small , body cylindrical, slender, up to 14 mm long and 5 mm wide. Colour off-white. Tube feet highly retractile, only in ambulacra in double rows, interambulacra naked. Ten equal tentacles. Calcareous ring simple, poorly calcified, covered with tissue, damaged when clearing, Radial plates elongate. Retractor muscles attached at about half body length. Body wall ossicles as only oblong, knobbed, single-layered, perforated plates, with one end extended into a short to moderate denticulate arm (Figure 27A); plates 160-200 µm long and 60-70 µm wide; knobs as well as holes 10-20 µm, but holes mostly about 10 µm. Tube feet deposits include only 3-armed rods, with few inconspicuous knobs and small to moderate holes, 3rd arm medial, spinous at distal end (Figure 27B). Tentacle deposits include only elongate, sometimes knobbed rods, some with a medial 3rd arm (Figure 27D). Introvert ossicles include small, smooth, plate-like rods (Figure 27C).

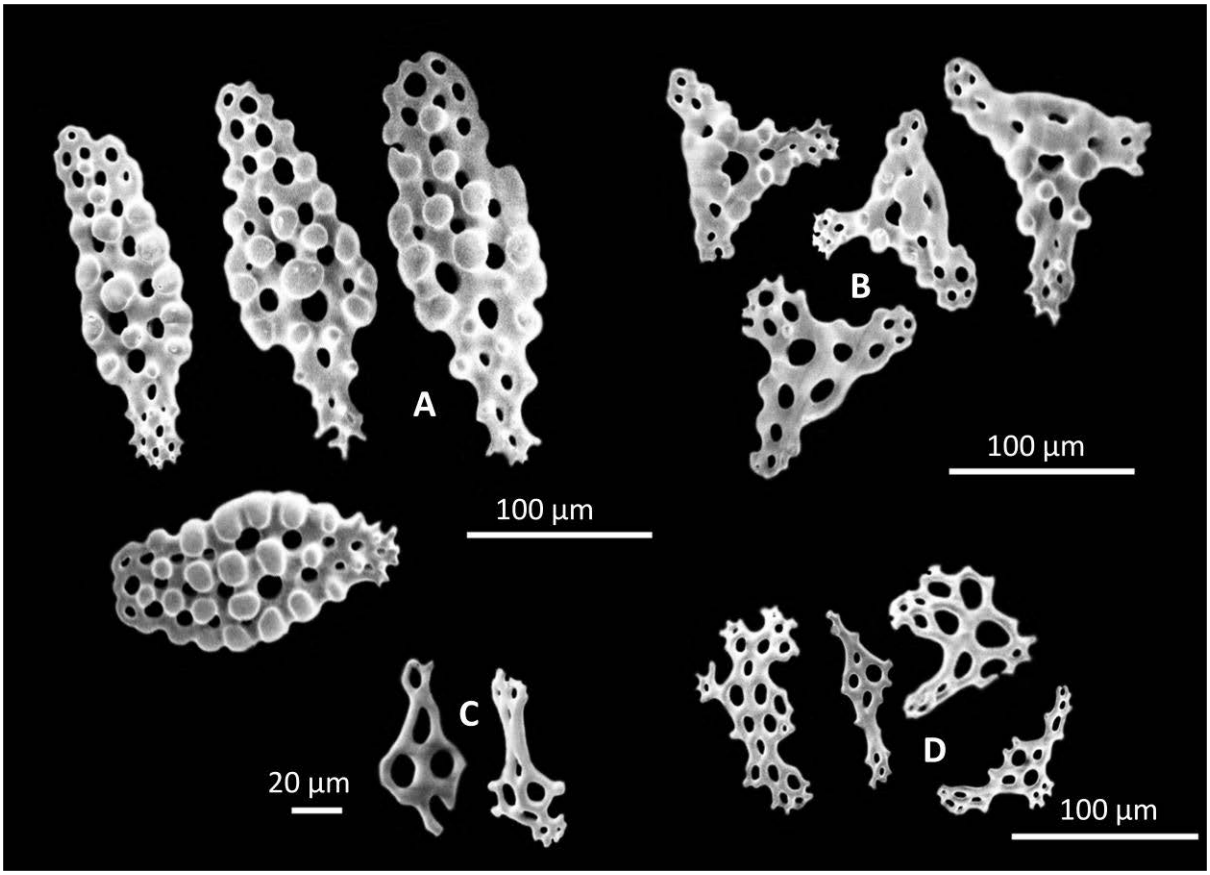


Figure 27. *Pentactella perrieri* (Ekman, 1927). Falkland Islands F106968. A. Pine-cone-shaped plates from body wall; B. Knobbed, 3-armed rods from tube feet; C. Rods from introvert; D. rosettes-like deposits from tentacles.

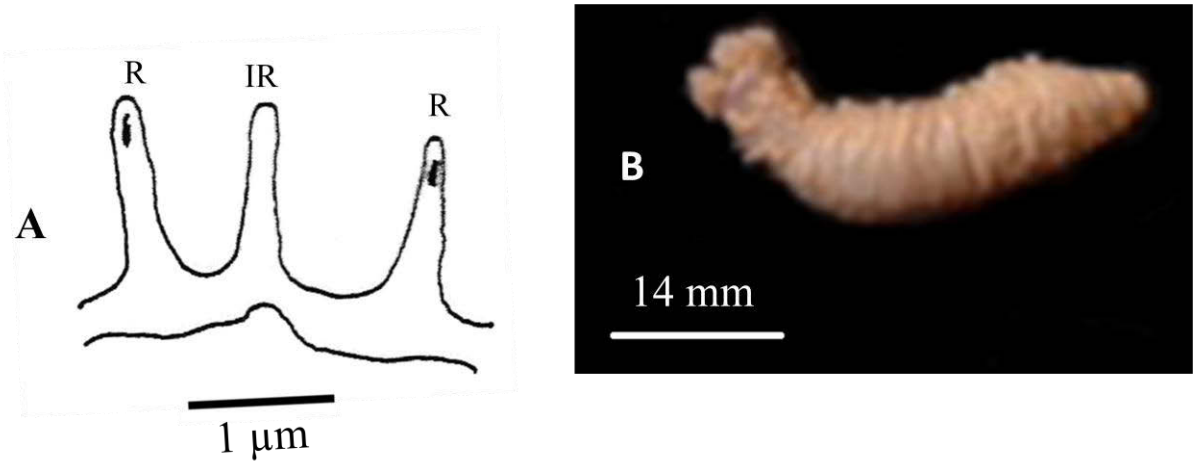


Figure 28. *Pentactella perrieri* (Ekman, 1927). Falkland Islands F106968. A. Calcareous ring; B. Entire specimen.

Distribution

South end of South America, off west coast of Chile, Falkland Islands, South Georgia, 0 - 272 meters (Deichmann, 1947).

Remarks

Ludwig (1898) studied a specimen from South America (Falkland Islands) and thought that he was examining Verrill's (18 6) *Pentactella laevigata*. He was followed by Perrier (1905) who studied specimens from Cape Horn (south of South America). Subsequent to Ludwig (1898) and Perrier (1905), other workers including Hérouard (1906), Ekman (1925), Deichmann (194), and Pawson (1964) also assigned the South American forms to e rril's species. According to Pawson (1969), Ekman (1927) studied Verrill's species critically and showed that those South American cucumariids previously referred to *Cucumaria laevigata* belonged to a new species which he named *Cucumaria perrieri*. This was supported by many authors including Panning (1962) and Pawson (1969). *Cucumaria perrieri* is known to be endemic to South America and its surrounding southern Islands. *Cucumaria perrieri* defers from *Cucumaria laevigata* in that the former has tube feet deposits comprising of 3-armed rods whereas the latter has irregular plates as tube feet deposits. Moreover, tentacle deposits include rosettes in *Cucumaria perrieri* whereas in *Cucumaria laevigata* large plates are observed as tentacle deposits.

Pentactella cornuta (Cherbonnier, 1941)

Figure 29

Cucumaria cornuta Cherbonnier, 1941:271 fig. A, B.
Pseudocnus cornutus Panning, 1962:73.
Laevocnus cornutus O'Loughlin *et al*., 2014:47.
Pentactella cornuta O'Loughlin *et al*., 2015:80.

Diagnosis (after Panning 1962 and Cherbonnier 1941)

Body sub-cylindrical, slightly curved, skin thin and soft. Colour pale yellow. Tube feet in double rows, numerous ventrally, interambulacra naked. Tentacles 10, unequal. Calcareous ring small and delicate, radial and interradial plates not fused. Body wall ossicles numerous plates, with up to 20 or more holes, knobs present. Plates end in two horn-shaped spines, simple or branched (Figure 29: a, b, c, n, and e). Tube feet ossicles consist of 3-armed rod-

like plates (Figure 29: d, f, g, and m). Tentacles ossicles as 3-armed rods, sometimes straight, long, and simple plates with one end serrated (Figure 29 h, j, k, and i).

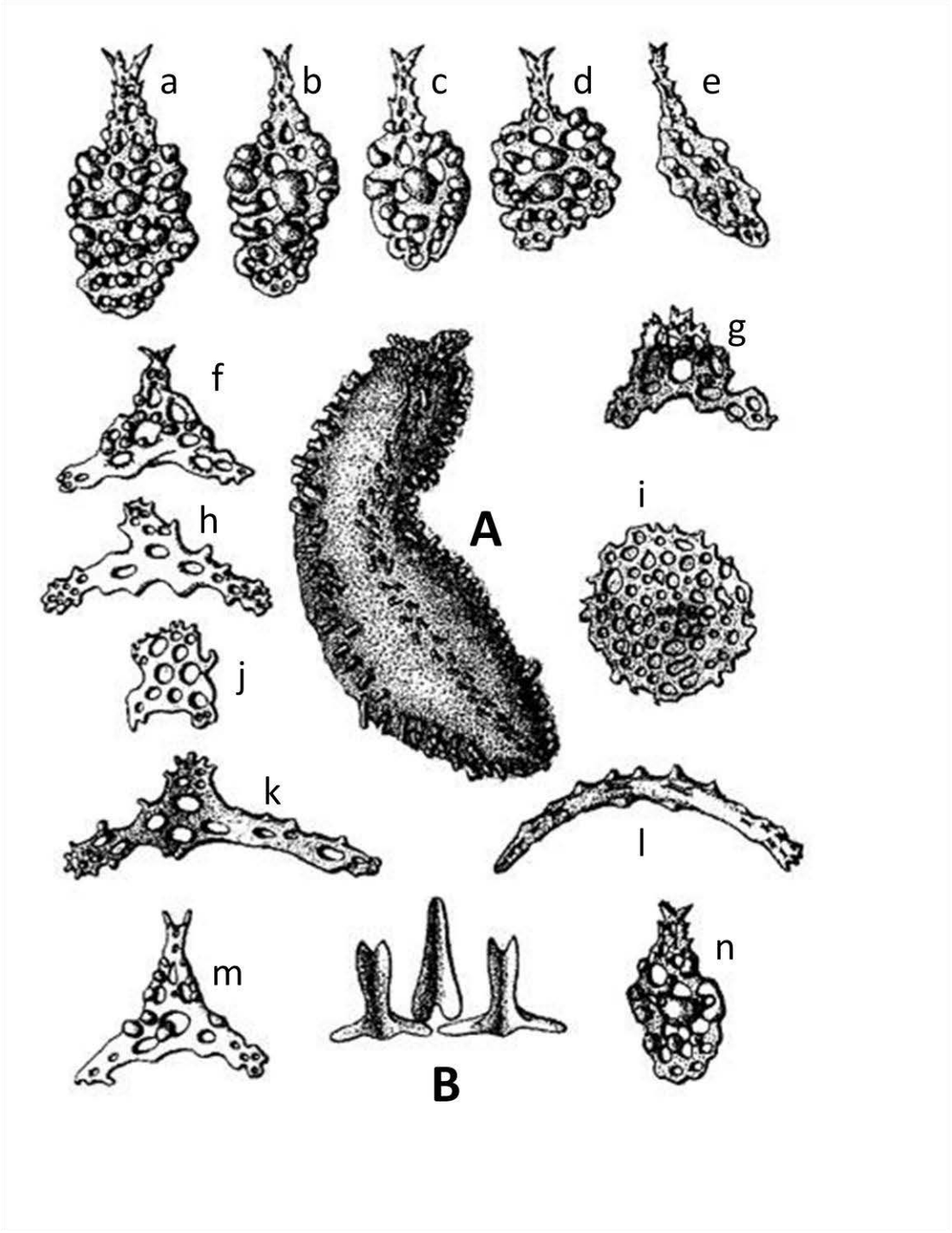


Figure 29. *Pentactella cornuta* (Cherbonnier, 1941). a, b, c, n, and e. Ossicles from body wall; d, f, g, and m. Ossicles from tube feet; h, j, k, and i. Ossicles from tentacles: A. Entire; B. Calcareous ring. Scale for all figures 3/4X. Figure copied from Cherbonnier 1941.

Material examined

None.

Distribution

East Pantagonia, Falkland Island (Panning, 1962).

Remarks

O'Loughlin *et al*. (2014), despite the fact that this species has unequal tentacles, included it in their *Laevocnus* (=*Pentactella*) group. However, *Pseudocnus californicus* Semper, 1868, a species which Panning (1962) also assigned to his *laevigatus*-group, was retained in *Pseudocnus* although it also has unequal tentacle and lacks buttons. However, they included *cornutus* with some hesitation because of its subantarctic distribution and tube feet arrangement but without any molecular evidence. Since *P. cornutus* is very similar to *P. californicus* it is suggested that *P. cornutus* be re-assigned to *Panningocnus* until some molecular work surfaces, since it shares some characteristic features with *P. californicus* Semper, 1868 and some other species assigned to this genus.

Pentactella leoninoides (Mortensen, 1925)

Figure 30

Cucumaria leonina Dendy, 1909:146, pl. 6 fig. 1a-c.
Cucumaria leoninoides Mortensen, 1925:338, fig. 27a-b; Dawbin, 1950:38.
Stereoderma leoninoides: Panning, 1949:422; Pawson, 1961:16; 1965:258.
Pseudocnus leoninoides Panning, 1962:74, fig. 12; Pawson, 1968:22; 1970:34, fig. 6a-d.
Laevocnus leoninoides O'Loughlin *et al*., 2014:47.
Pentactella leoninoides O'Loughlin et al., 2015:80.

Diagnosis (after Pawson 1970)

Body fusiform, slightly curved. Colour in alcohol greyish to white. Tube feet only in ambulacra, in two irregular rows. Tentacles 10, equal or two slightly reduced. Calcareous ring absent. Body wall deposits as knobbed perforated plates, one end denticulate, each plate with large central holes and numerous small holes, buttons may be present. Tube feet with smooth reticulate end plate. Tentacles with smooth irregular plates or rods.

Material examined

MCZ: HOL-1445, paratypes, Pacific Ocean, south west of Auckland Islands, Masked Kland, Canley Harbor. 3 spec.

Description

Body elongate, mouth and anus slightly turned up. Colour in alcohol greyish to off white. Length 27 mm, width 2-3 mm. Tube feet only on ambulacra, in double zigzag rows, some present in introvert as a single row per ambulacrum. Tentacles 10, equal or two slightly reduced, attached to a transparent introvert. Calcareous ring absent. Retractor muscles arise from longitudinal muscles near posterior end.

Body wall deposits comprise only oblong, knobbed plates with one end denticulate; holes large, central (Figure 30A); plates 90-140 μm long and 40-70 μm wide. Tube feet deposits as knobbed buttons or plates, knobs fewer than holes (Figure 30B); end-plate present. Tentacles and introvert without deposits.

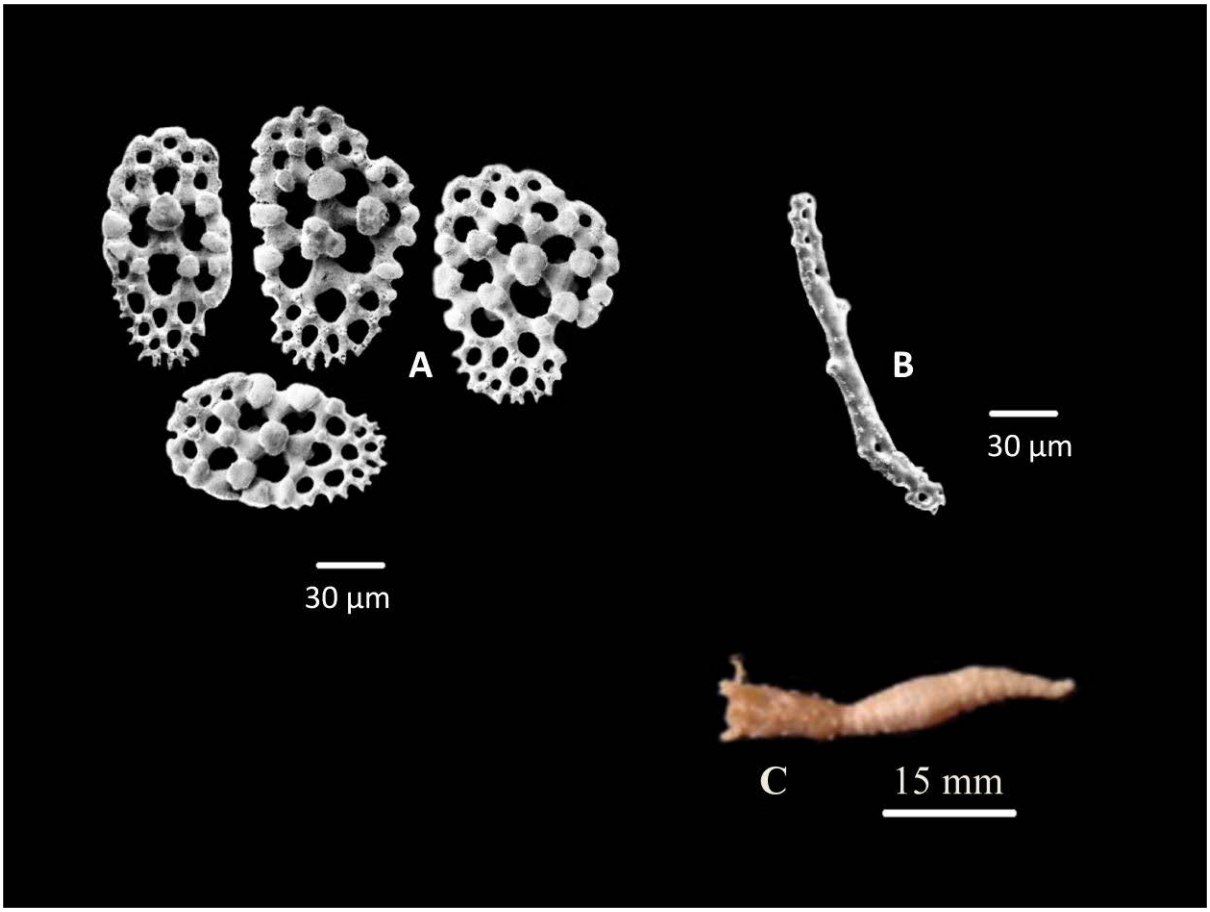


Figure 30. *Pentactella leoninoides* (Mortensen, 1925). MCZ HOL-1445. A. Plates from body wall; B. Rod from tube foot; C. Entire specimen.

Distribution

Auckland Islands, Campbell Island, Snares Island, approximately 150 miles NNE of Macquarie Island, 0-112 metres (Pawson, 1970).

Remarks

From the specimens at hand, the largest measures 27 mm long and 3 mm wide; Dendy's (1909) largest specimen measured 15 mm in length and 5 mm wide. The three specimens are well preserved with the tentacles fully extended. Out of the three specimens, two had two slightly reduced tentacles while the smallest one had 10 equal tentacles; this perhaps implies that some tentacles may be reduced in size with age. In the dissected specimen (the largest), no calcareous ring was observed. Panning (1962) and Dendy (1909) also failed to find the calcareous ring, but Dendy (1909) recorded five rudimentary radial plates, and expressed the opinion that the interradial plates are either absent or represented by granules. Hence, the calcareous ring is either absent or very rudimentary. Panning (1962) illustrated table-like deposit from the introvert. No ossicles were detected in the tentacles, but there were some remnants of previous ossicles but their form could not be determined. Ossicles were also not detected in the introvert. This perhaps suggests that the ossicles might have dissolved in alcohol.

Pentactella marionensis (Théel, 1886)

Cucumaria serrata var. *marionensis* Théel, 1886:74-75, pl. 4 fig.3.
Cucumaria laevigata; Ekman, 1927:396-403, fig. 15 (partim, non *Pseudocnus laevigatus*).
Pseudocnus laevigatus Pawson, 1971: 288-289; Rowe & Clark, 1975:187-188 (non *P. laevigatus* Verrill).
Pseudocnus marionensis O`Loughlin, 2009:9.
Laevocnus marionensis O'Loughlin *et al*., 2014:47.
Pentactella marionensis O'Loughlin et al., 2015:80.

Diagnosis (after Théel 1886)

Body cucumber-like. Colour white to light pink. Tube feet in ambulacra, in double rows. Tentacles 10, more or less equal. Polian vesicles 2-4. Body wall ossicles include oblong denticulate, knobbed, perforated plates. Brood pouches present. No buttons.

Distribution

Marion Island (O'Loughlin, 2009).

Material examined

None.

Remarks

This species was treated by Ekman (1927), Rowe & Clark (1975) and Pawson (1971) as a junior synonym of *Cucumaria laevigatus* (Verrill, 1876) (O`Loughlin, 2009). Rowe and Clark (1975) did not find brood pouches from the materials of *C. laevigata* examined except from the largest syntype of *Cucumaria serrata* var. *marionensis*. According to O`Loughlin (2009), Pawson (1970) found brood-pouches on one Marion specimen. O`Loughlin 2009 raised Théel's variety to species level and reassigned it to *Pseudocnus* and then O'Loughlin *et al*. (2014) reassigned the species to *Laevocnus* (= *Pentactella*).

Pentactella serrata (Théel, 1886)

Cucumaria serrata Théel, 1886:73, pl. IV fig. 1.
Laevocnus serratus O'Loughlin *et al*., 2014:47.
Pentactella serrata O'Loughlin *et al*., 2015:80.

Diagnosis (after Théel 1886)

Body elongate, fusiform, tapered posteriorly. Tube feet in a single zigzag row per ambulacrum, but in two rows near introvert, interambulacra naked. Tentacles 10, equal or unequal. Calcareous ring simple, with radials deeply notched. Calcareous deposits include knobbed, perforated, cone-shaped plates, with one end drawn out into a bent or straight spinous projection. Tube feet deposits include plates similar to those of body wall; end plate present. Tentacles ossicles large, perforated, smooth plates and minute fenestrated plates.

Distribution

e rguelen (52 4 S, 1 22 E), coarse gravel, 274 meters (Théel, 1886).

Material examined

None.

Remarks

This species is well described by various authors. WoRMS and GBIF record it as *Pseudocnus serrata* (Théel, 1886). O'Loughlin *et al*., 2014) reassigned the species to *Laevocnus* (= *Pentactella*).

***Thandarocnus* n. gen.**

Pseudocnus Panning, 1949 (partim).

Diagnosis

Body sub-cylindrical. Tube feet in zigzag to double rows per ambulacrum sometimes scattered in interambulacra. Tentacles ten, two ventral reduced. Calcareous ring simple, lacking posterior prolongations. Body wall deposits include multilayered, knobbed fir corne-shaped plates with one end denticulate. Knobbed single layered buttons present or absent altogether. Tube feet deposits include irregular, curved rods. End-plate may be present. Tentacles and introvert deposits include perforated rods. Rosettes may be present or absent.

Type species: *Pseudocnus sentus* O'Loughlin & Alcock, 2000 (herein designated).

Other species included: *Cucumaria rhopalodiformis* Heding, 1943; *Pseudocnus rugosus* Cherbonnier, 1957; *Pseudocnus pawsoni* Won & Rho, 1998; *Cucumaria grubei* von Marenzeller, 1874.

Etymology

This genus is named after my chief supervisor (A.S. Thandar) in recognition of his contributions to the taxonomy of holothuroids.

Remarks

Since *Pseudocnus* is now restricted to include species with equal tentacles and single-layered multilocular plates and buttons and *Panningocnus* to species with unequal tentacles and also single-layered plates, those species with unequal tentacles and multilayered plates are now referred to yet another new genus, *Thandarocnus*. The new genus resembles *Pseudocnella* Thandar, 1987 and *Hemiocnus* Mjobo & Thandar (MS under review, see below) in that it has multilayered fircone-shaped plates in the body wall. However, it differs from these genera in that it lacks a layer of incomplete baskets.

Of the species here assigned to *Thandarocnus*, *Pseudocnus lamperti* (Ohshima, 1915) is closest to the type species *Pseudocnus sentus* O'Loughlin & Alcock, 2000. *Cucumaria grubei* Von Marenzeller, 1874 may not belong to this genus because it lacks knobbed buttons possessed by other species of the genus. It is very close to some of the species currently assigned to *Panningocnus,* for example *Panningocnus californicus* with which it shares some characteristic features such as restricted tube feet distribution, lack of knobbed buttons in the body wall and unequal tentacles. However, it differs slightly in the presence of fir cone shaped plates of a different type. But since it comes close to *P. rhopalodiformis* and *P. rugosus*, and has unequal tentacles in addition to multilayered fir cone plates, it is provisionally assigned to *Thandarocnus* until molecular studies emerge.

KEY TO SPECIES OF *THANDAROCNUS* n. gen.

1. Tube feet restricted, in double conspicuous rows per ambulacrum, interambulacra naked..... **2**
   Tube feet in a zigzag to double rows in ambulacra, also present in interambulacra, sometimes without distinct rows..... **4**

2. Knobbed buttons present..... **3**
   Buttons absent..... ***Thandarocnus grubei*** (von Marenzeller, 1874).

3. Tube feet deposits include curved rods, tentacle deposits as straight perforated rods ..... ***Thandarocnus rhopalodiformis*** (Heding, 1943).
   Tube feet with straight and/or branched rods, tentacles with 3-armed rods..... ***Thandarocnus rugosus*** (Cherbonnier, 1957).

4. Fircone shaped plates, spines never borne on "handle" .....***Thandarocnus goreensis*** (Cherbonnier, 1949)
   Fircone shaped plates with spinous "handle".....**5**
5. Buttons irregular, heavily knobbed; tube feet with irregular curved support plates; tentacles with irregular plates and rosettes..... .....***Thandarocnus sentus*** (O'Loughlin & Alcock, 2000).

Round-oval scarcely knobbed buttons; tube feet with simple perforated rods; tentacles with plate-like rods and rosettes..... ***Thandarocnus pawsoni*** (Won & Rho, 1998).

Thandarocnus rhopalodiformis (Heding, 1943) comb. new

Figure 31

Cucumaria rhopalodiformis Heding 1943:1-4, fig. 1, 2 and 3.
Pseudocnus rhopalodiformis O'Loughlin *et al*. 2014: 46, table 2 (passim).

Diagnosis (after Heding 1943)

Body more or less U-shaped. Mouth and anus terminal. Tube feet in double rows per ambulacrum. Tentacles 10, ventral two reduced. Calcareous ring simple but radial plates with posterior bifurcations, radial and interradial plates very thin.

Body wall deposits include multi-layered, knobbed, pine-cone-shaped plates with one end denticulate (Figure 31A, F, and J); round knobbed buttons with four central holes (Figure 31B-E). Baskets absent but minute perforated plates also present. Tube feet deposits include curved rods (Figure 31L-M). Tentacles with simple perforated rods (Figure 31N-O).

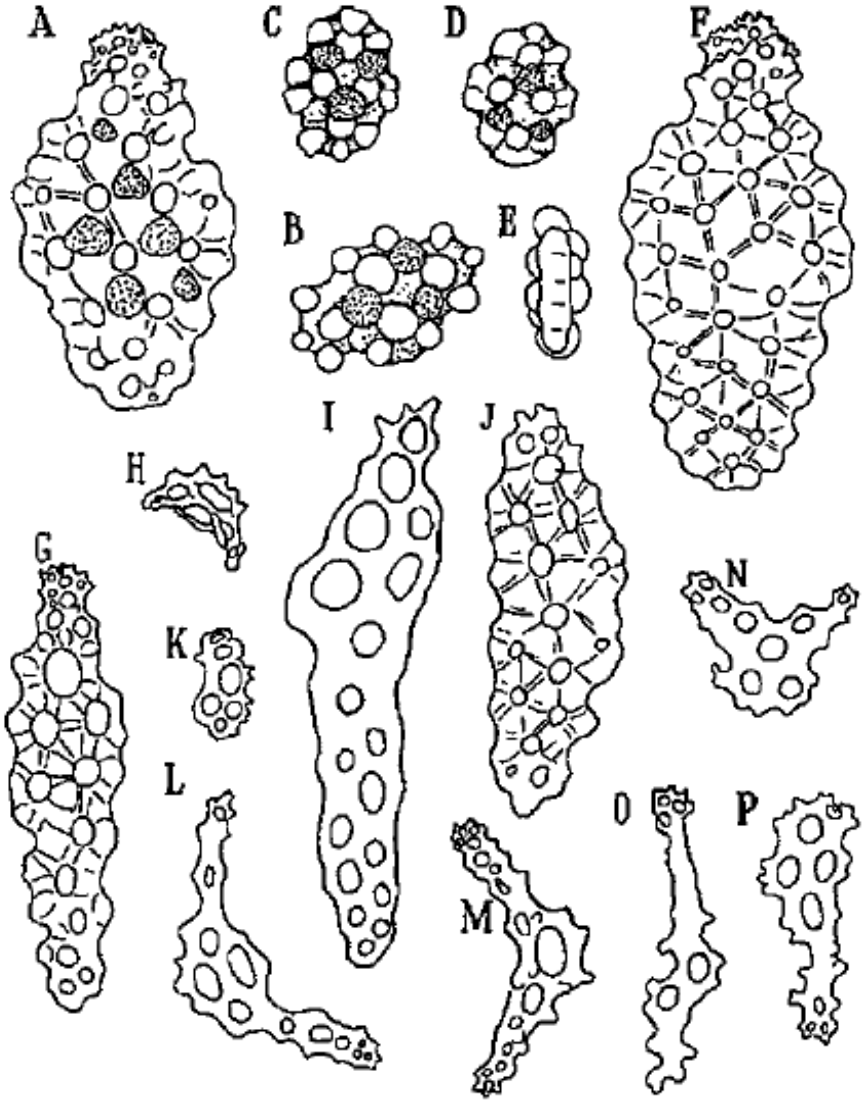


Figure 31. *Thandarocnus rhopalodiformis* (Heding, 1943) Ossicles. A-B. Plates from ventral body wall; C-F. buttons from dorsal body wall; G-H. plates from anterior body wall; I-K. plates from posterior body wall; L-M. rods from tube feet; N-O. rods from tentacles. (Figure extracted from Heding 1943:3).

Material examined

None.

Distribution

Known only from its type locality Congo (Heding, 1943).

Remarks

The species is well described by Heding (1943). *T. rhopalodiformis* is very close to *Hemiocnus syracusan*us differing in having two distinct rows of tube feet per radius instead

of scattered tube feet as in the latter species, and also in the absence of incomplete baskets which are present in *Hemiocnus* species. *T. rhopalodiformis* is very close to *T. rugosus* but differ in that the former possesses curved rods in the tube feet and simple, straight perforated rods in the tentacles, whereas the latter species possess straight rods in the tube feet and 3-armed rods in the tentacles. Based on e ding's (194) description (fig.3), *T. rhopalodiformis* does not belong in *Pseudocnus* since it has multi-layered plates coming close to some of the species here assigned to *Thandarocnus*, it is also assigned to this genus.

Thandarocnus rugosus (Cherbonnier, 1957) comb. new

Figure 32

Pseudocnus rugosus Cherbonnier, 1957: 490-492, fig. 2.
Pseudocnus rugosus O'Loughlin *et al.* 2014: 46, table 2 (passim).

Diagnosis (after Cherbonnier 1957)

Body cylindrical. Skin thin, rough. Tube feet in double rows per ambulacrum, interambulacra naked. Tentacles 10, ventral two reduced. Calcareous ring with undulating posterior end and triangular interradials. Polian vesicle large, stone canal short, madreporite well developed.

Body wall deposits comprise short, thick, thorny, pine cone-shaped multilayered plates (Figure 32A) with one end denticulate, some plates oval or rounded (Figure 32B). Buttons knobbed (Figure 32C), with 4-20 holes. Baskets absent. Tube feet deposits include straight or branched rods (Figure 32D). Tentacle deposits include large thin rods (Figure 32E).

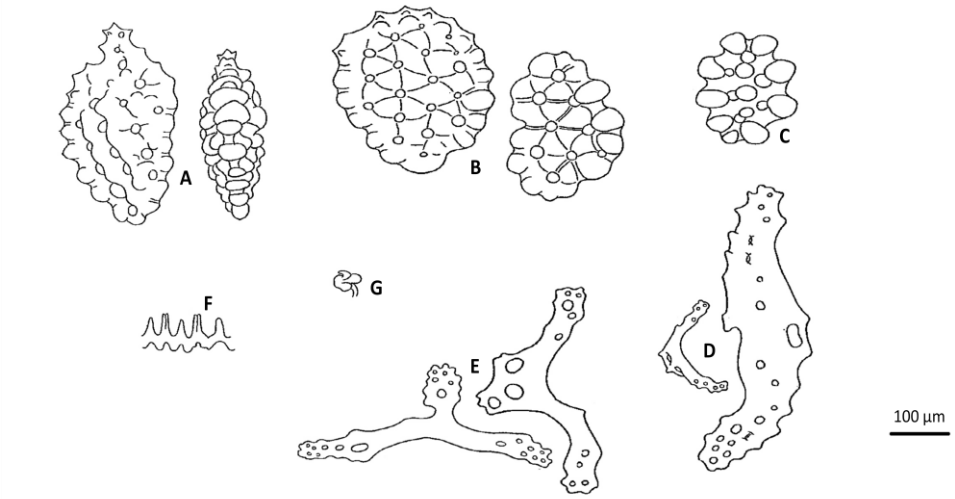


Figure 32. *Thandarocnus rugosus* (Cherbonnier, 1957) ossicles. A. Pine cone-shaped plates from body wall; B. Round, oval plates from body wall; C. Button from body wall; D.

Ossicles from tube feet; E. Ossicles from tentacles; F. Calcareous ring; G. Madreporite, (All on same scale, extracted from Cherbonnier, 1957).

Material examined

None.

Distribution:

Sierra-Leone (Cherbonnier, 1957).

Remarks

Thandarocnus rugosus was described from Sierra-Leone by Cherbonnier (1957) as *Pseudocnus rugosus* and recorded as such by O'Loughlin *et al*., 2014. However, based on the unequal size of tentacles (8+2) and ossicle type (multilayered pine cone-shaped plates) which resemble the type species of this genus it is also re-assigned to *Thandarocnus.*

Thandarocnus sentus (O`Loughlin and Alcock, 2000) comb. new (type species)

Figure 33

Pseudocnus sentus O'Loughlin and Alcock, 2000:4-5, fig. 1a-j.

Pseudocnus sentus O'Loughlin and andenspiegel, 2012:6 -65, fig. 4.

Pseudocnus sentus O'Loughlin *et al*. 2014:46, table 2 (passim).

Diagnosis (after O'Loughlin and Alcock 2000)

Body rounded to pentagonal. Skin thin, firm, rough. Anal teeth microscopic. Tube feet in zigzag to double rows ventrally, less regular double to zigzag rows dorsally, rare in interambulacra. Tentacles 10, unequal (8+2). Calcareous ring simple, with parallel anterior projections, and deep posterior notches on the interradials. Polian vesicles 1-2; madreporite small, free.

Body wall ossicles include multilayered, denticulate plates (Figure 33); irregular to thick knobbed buttons (Figure 34). Tube feet with thin, irregular, perforated, oval, curved support plates; end-plate present. Tentacles with denticulate perforated irregular plates, oval convex plates, rosettes present, irregular, elongated, with central hole. Introvert deposits include non-denticulate plates with four central holes, plates smooth or knobbed; densely branched and knobbed rosettes.

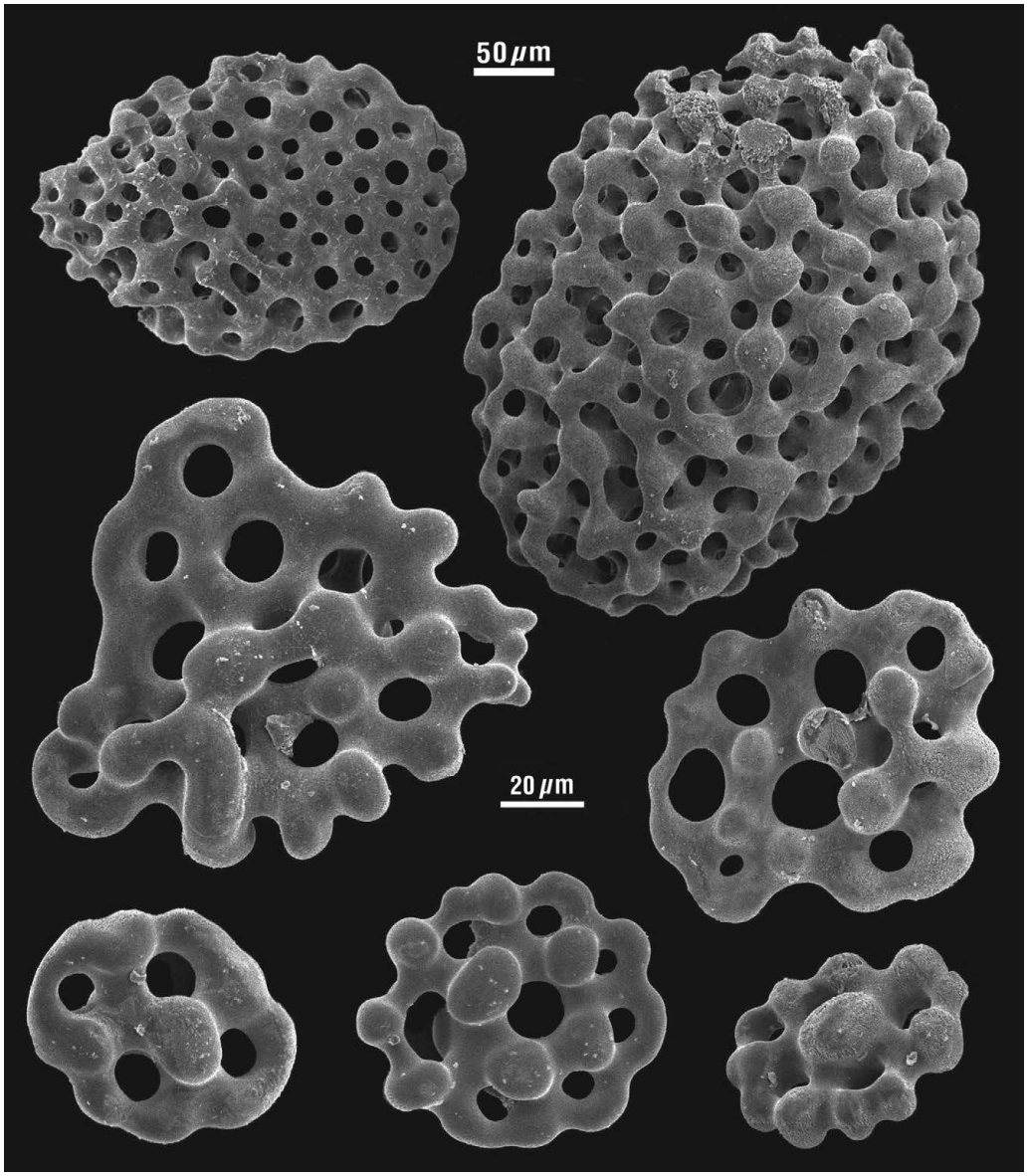


Figure 33. *Thandarocnus sentus* (O'Loughlin and Alcock, 2000). Ossicles from body wall, (copied from O'Loughlin & a ndenspiegel, 2012).

Distribution

New Zealand, Stewart Island, Paterson inlet, Kermadec Island, Meyer Island, 0-15m (O'Loughlin & a ndenspiegel, 2012).

Remarks

This species was recorded from e w Zealand by O'Loughlin and Alcock (2000), O'Loughlin and a ndenspiegel (2012) and O'Loughlin *et al*. (2014) as *Pseudocnus sentus*, Based on the size of tentacles (8+2) and ossicle type (multilayered plates), this species is also

here transferred to *Thandarocnus* since it has all the characters possessed by other species of this genus, and due to the fact that it is well described compared to other species.

Thandarocnus pawsoni (Won & Rho, 1998) comb. new

Pseudocnus pawsoni Won & Rho, 1998:16, fig. 6A-H.
Pseudocnus pawsoni O'Loughlin et al. 2014:46, table 2 (passim).

Diagnosis (after Won & Rho 1998)

Body fusiform, turned up. Tube feet in both ambulacra in double conspicuous rows and also in interambulacra. Anal teeth and anal papillae present. Calcareous ring simple, radials notched posteriorly and anteriorly. Tentacles 10, ventral two reduced. Body wall ossicles include multi-layered fircone-shaped plates with one end denticulate; small round plates or buttons also present (scarcely knobbed). Baskets absent. Tube feet with rods, end-plate present. Tentacles with rosettes and plate-like rods.

Material examined

None.

Distribution

Only from its type locality, Korea (Won & Rho, 1998).

Remarks

This species is also now transferred to *Thandarocnus* based on tentacle size (8+2) and the presence of multi-layered fir-cone-shaped plates. *Thandarocnus pawsoni* (Won & Rho, 1998) is very close to the type species *Thandarocnus sentus* (O'Loughlin & Alcock, 2000) with which it shares similar characters such as tube feet distribution, multilayered calcareous material in addition to unequal tentacles. *T. pawsoni* and *T. sentus* differ in that the latter species possesses irregular knobbed buttons in the body wall and irregular curved support plates in the tube feet whereas the former has round to oval scarcely knobbed buttons in the body wall and simple perforated rods in the tentacles.

Thandarocnus grubei (Marenzeller, 1874) comb. new

Figure 34 A-C and 35 A-B

Cucumaria grubei Marenzeller,1874:3031; Lampert, 1885:138; Théel, 1886:100; Koehler, 1921:154 fig. 105.

Pseudocnus grubei Panning, 1949:423 fig. 9; 1962:67 fig. 12.

Pseudocnus grubei O'Loughlin *et al*., 2014:46, Table 2 (passim).

Diagnosis (after Panning 1949)

Body cylindrical to barrel-shaped. Tube feet restricted to ambulacra, interambulacra naked. Tentacles 10, ventral two reduced. Calcareous ring simple, lacking posterior prolongations. Body wall ossicles consist of knobbed, multilayered, pine-cone-shaped plates, with one end denticulate. Buttons absent. Tube feet deposits as perforated, curved rods. Tentacles and introvert deposits comprise only simple rods.

Material examined

MNHN (Paris) cat. # 1988, G. Cherbonnier, det. 1966, 12 specimens.

Description

All specimens more or less barrel-shaped, largest 16 mm long, 12 mm wide; smallest 6 mm long and 3 mm wide. Colour off-white in alcohol. Mouth and anus turned up. Tube feet restricted to ambulacra, in two or more zigzag rows, interambulacra naked. Tentacles 10, ventral two reduced. Calcareous ring simple, without posterior processes (Figure 35A). Stone canal very short, madreporite bean-shaped. Retractor muscles arise from longitudinal muscles at about ½ body length. Respiratory trees highly branched. Gonad mature, unbranched.

Body wall ossicles include knobbed, perforated, multilayered, fir cone-shaped plates with one end spinous (Figure 34A), plates 270 -350 μm; holes minute, round plates may be present; buttons absent. Tube feet deposits as perforated, curved rods. Tentacle deposits as simple perforated rods (Figure 34B). Introvert deposits comprise small to moderate rods (Figure 34C), some similar to those in tentacles.

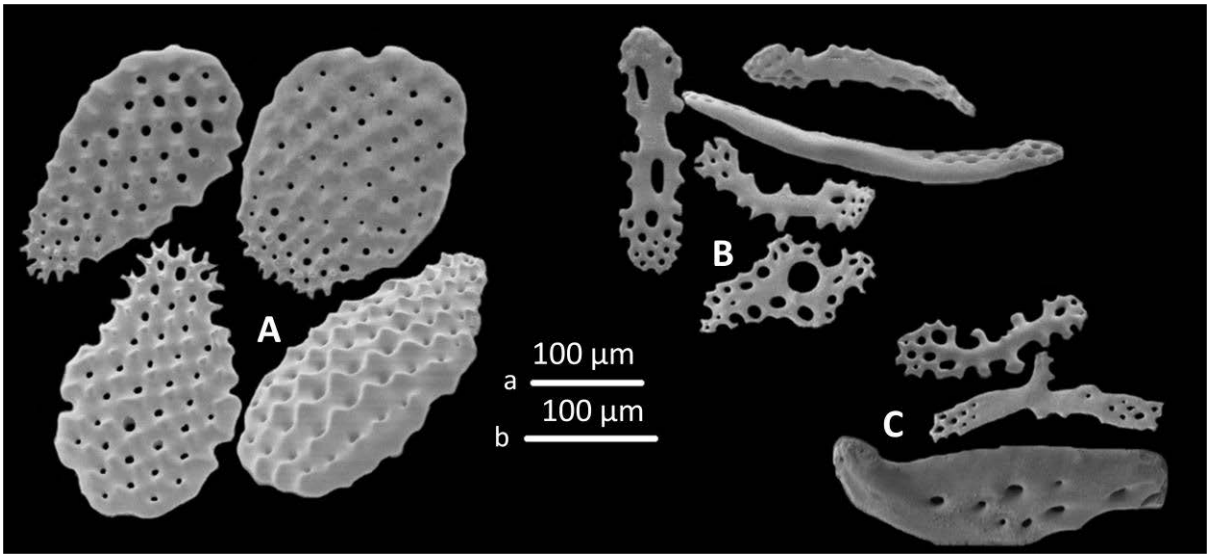


Figure 34. *Thandarocnus grubei* (Marenzeller, 1874) ossicles. MNHN (Paris) cat. # 1988. A. Pine-cone-shaped plates from body wall; B. Rods from tentacles; C. Rods from introvert. Note: figure A = scale a, figure B & C =scale b.

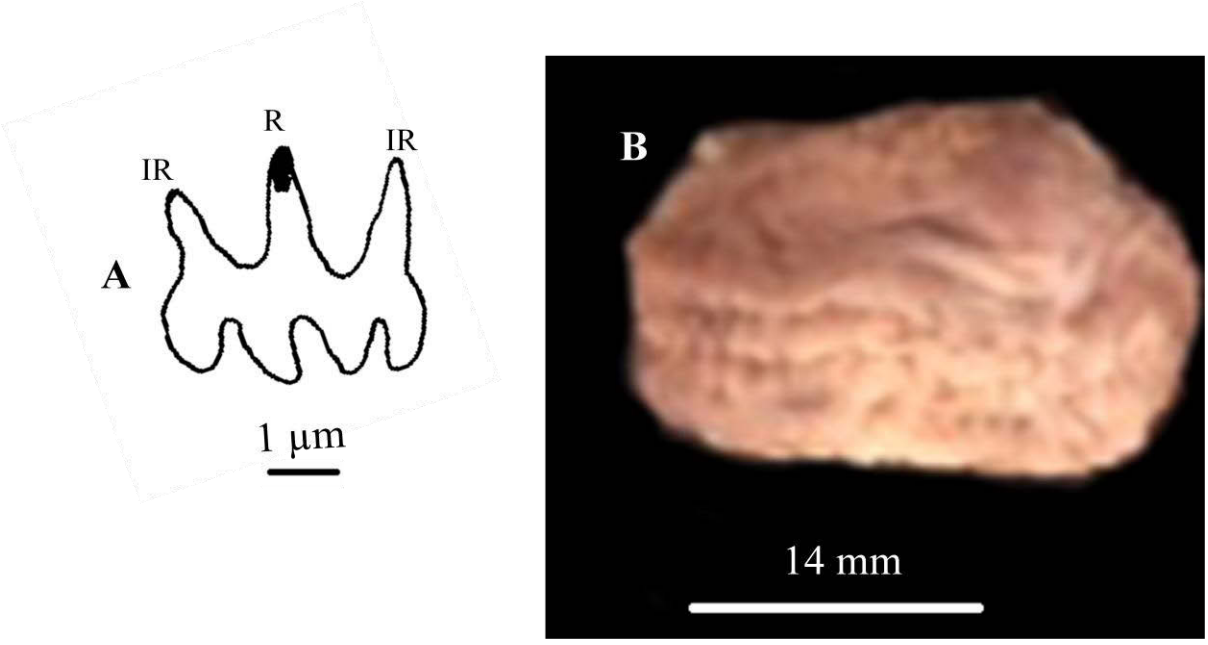


Figure 35. *Thandarocnus grubei* (Marenzeller, 1874). MNHN (Paris) cat. # 1988. A. Calcareous ring; B. Entire.

Distribution

Adriatic Sea, Mediterranean Sea (Théel, 1886; Koehler, 1921).

Remarks

This species is well described. Koehler (1921) found rosettes in the tentacles and buttons in the body wall, but these are absent in the current specimens. Panning (1949 and 1962) did not describe any tentacle deposits. Lampert (1885) reported two Polian vesicles, but these were not identifiable in the disseted specimen. *Thandarocnus grubei* (Von Marenzeller,

1874) is close to *T. rhopalodiformis* (Heding, 1943) and *T. rugosus* (Cherbonnier, 1957) with which it shares similar characters such as restricted tube feet distribution, naked interambulacra and multilayered plates in addition to unequal tentacles. However, *T. grubei* differs from its congeners in that it lacks buttons in the body wall.

Thandarocnus goreensis (Cherbonnier, 1949) comb. new

Figure 36 A-D, 37 A-B

Hemiodema goreensis Cherbonnier, 1949:585-589, fig. 1-2; 1950:378; 1957:487; 1958:325; 1965:5-6.
Pseudocnus goreensis O'Loughlin *et al*. 2014:46, table 2 (partim).

Diagnosis (after Cherbonnier 1949 modified herein)

Body ovoid, cylindrical. Skin thick, tough. No anal teeth/papillae. Tube feet distributed in both ambulacra and interambulacra. Tentacles 10, unequal (8+2). Calcareous ring simple, without posterior processes. Body wall deposits comprise single to multilayered plates and buttons; plates knobbed, fircone-shaped, often denticulate at one end but denticles not borne on handle. Buttons small, knobbed, single-layered. Tube feet deposits include straight or curved rods. Tentacle deposits include large curved rods, some knobbed, others with a prolonged central projection, rosette-like deposits present. Introvert deposits include small perforated rods.

Material examined

MNHN (Paris), *Hemiodema goreensis*, cat. # 872 (Cherbonnier, Port Ofentil; Gabon), M. Roux, G. Cherbonnier, det. 1958, 1 spec.; *Hemiodema goreensis* Cherbonnier, Siera-Leone cat.# 1105. Le 9.11.1954. Station opp Lumery frigasi, profondem, 7 meters, G. Cherbonnier det. 1957, 1 spec.

Description

Specimen (cat no. 1105) 30 mm long and 23 mm wide previously dissected, specimen (cat no. 872) 39 mm long and 21 mm wide. Body cylindrical, skin tough/leathery; colour light brown in alcohol, one specimen with hardened skin, dark brown colouration, lighter

tube feet and nipple-shaped papullae-like structures. Tube feet numerous, distributed throughout body, no distinct rows discernible. In dissected specimen (cat. No. 1105) tentacles 10, bushy, retracted, ventral two reduced. Calcareous ring simple, without posterior prolongations, radials and interradials meet at base, radials posteriorly notched (Figure 37B). Retractor muscles attached at about half body length. Polian vesicle single. Stone canal very short. Gonad not detected, perhaps lost in previous dissection remaining specimen with hardened skin. Respiratory trees highly branched.

Body wall deposits comprise thick, knobbed, perforated fir or pine-cone-shaped plates with single to multilayered (Figure 36A). multilayered plates from anal region 180 -250 µm long, 130-210 µm wide, and single-layered plates from dorsal and ventral region 130-200 µm long, 90-110 µm width. Knobbed, perforated round plates or buttons also present (Figure 36B) baskets not observed. No deposits in tube feet. Tentacles deposits include more or less curved rods, with central hole and distal perforations (Figure 36C). Introvert deposits include curved perforated minute rods (Figure 36D).

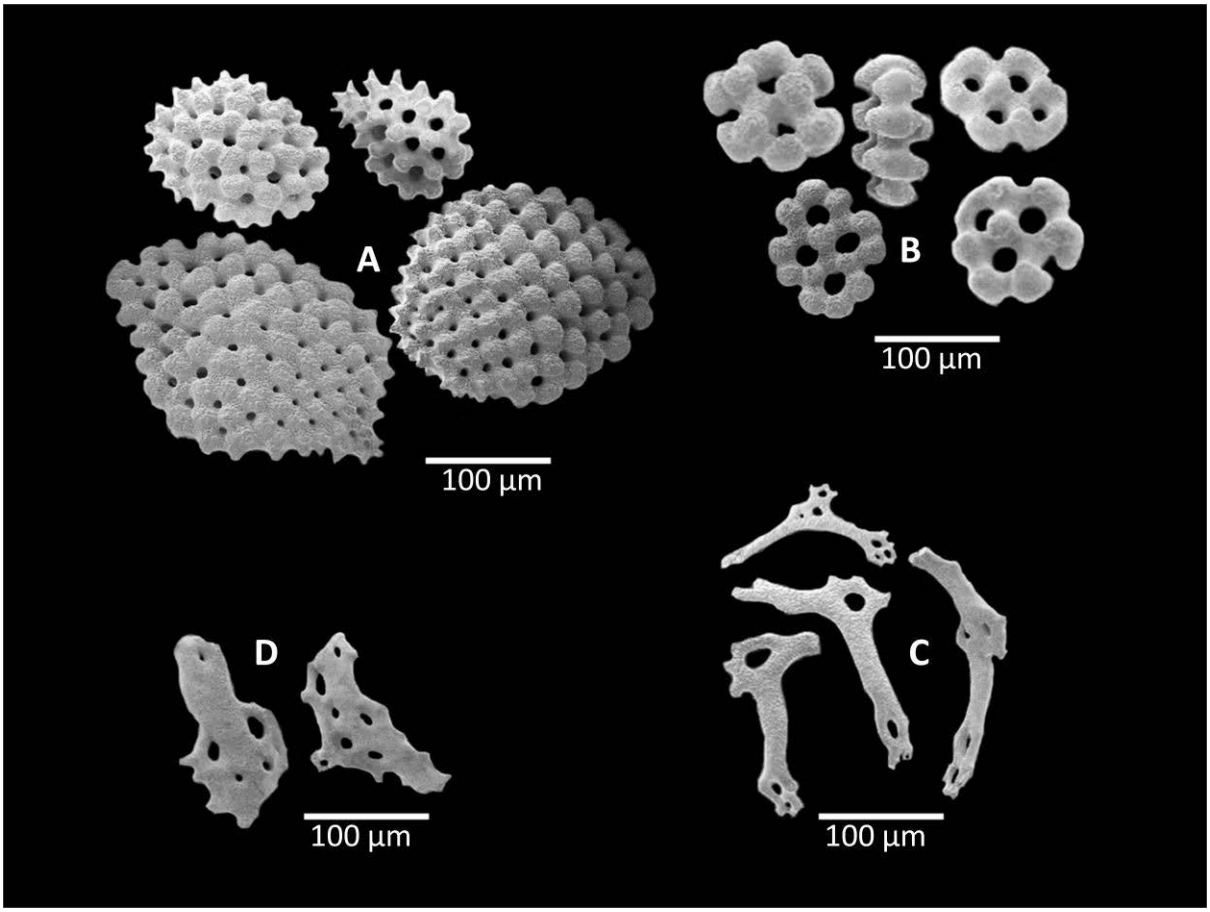


Figure 36. *Thandarocnus goreensis* (Cherbonnier, 1949) ossicles. MNHN (Paris) cat. # 1105. A. Multilayered plates from body wall; B. Buttons from body wall; C. Rods from tentacles; D. Ossicles from introvert.

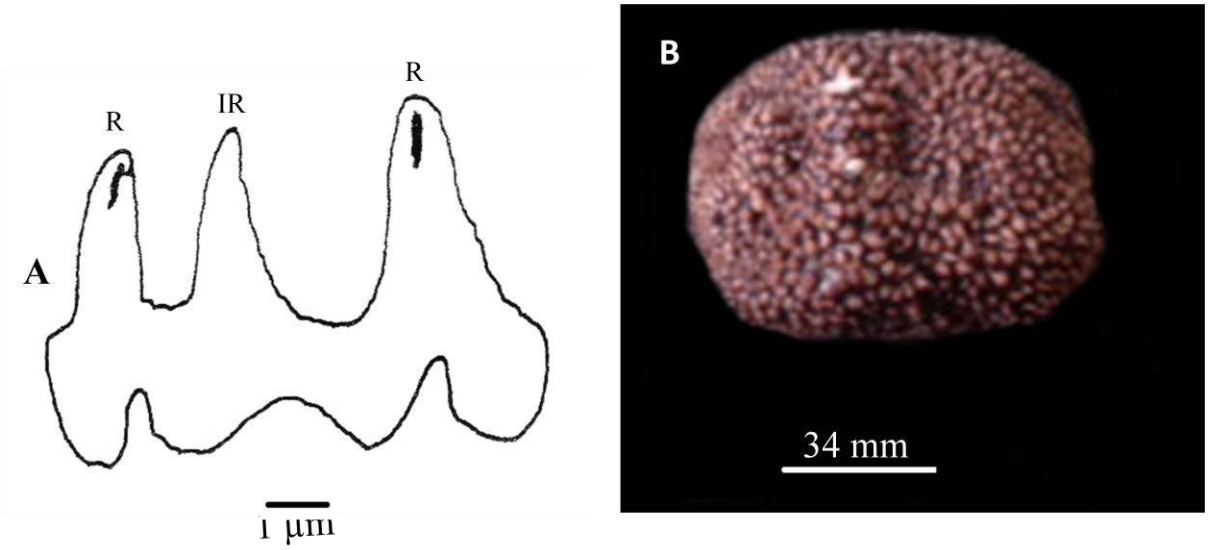


Figure 37. *Thandarocnus goreensis* (Cherbonnier, 1949). MNHN (Paris) cat. # 872. A. Calcareous ring; B. Specimen entire.

Distribution

Senegal, Gambia, Siera-Leon, Gabon, Goree Island (Cherbonnier, 1949; 1957).

Remarks

From the specimens at hand, it appears that the tube feet are evenly distributed throughout body, but Cherbonnier found these to be more numerous ventrally. Multilayered plates are numerous in the anal region compared to other regions. Based on the presence of such plates, the species is now removed from *Pseudocnus* as *Pseudocnus* is herein restricted to include only species with a single layer of calcareous material. Although O'Loughlin *et al*., 2014 did not specify the reason for removing *T. goreensis* from *Hemioederma*, their decision was correct, but here since the species share some characteristic features with the type species and other species assigned to *Thandarocnus*, it is here provisionally re-assigned to *Thandarocnus*.

Subfamily Colochirinae Panning, 1949

Diagnosis (after Pawson 1963)

Calcareous ring simple, lacking posterior prolongations. Radials and interradials undivided. In the skin plates and baskets; no tables.

KEY TO GENERA OF THE SUBFAMILY COLOCHIRINAE

4. Tentacles of equal size; body wall with multilayered fir cone-shaped plates with one end sometimes denticulate; round to oval plates also present; buttons absent; a superficial layer of incomplete basket present, at least in juvenile..... ***Pseudocnella*** Thandar, 1987.

   Tentacles of unequal size; body wall with multilayered fircone-shaped plates with one end sometimes denticulate; buttons present; a superficial layer of complete/incomplete basket present..... ***Hemiocnus*** n. gen.

A key to *Pseudocnella* species have been given by Thandar 1987, and there is no need to repeat it here.

Pseudocnella Thandar, 1987

Semperia Lampert, 1885: 250 (preoccupied).
Cucumaria (partim) H.L. Clark 1923: 409; Deichmann, 1948: 342; Cherbonnier 1952: 477.
Pseudocnus Panning, 1949: 422; 1962: 58 (partim).
Stereoderma Panning, 1949: 422 (partim).
Ocnus Panning, 1949: 437 (partim).
Pseudocnella Thandar, 1987: 288.

Diagnosis (after Thandar 1987, restricted herein)

Body barrel-shaped. Tube feet in both ambulacra and interambulacra. anal teeth/papillae present. Calcareous ring simple, lacking posterior processes. Tentacles 10, equal. Body wall ossicles include a superficial layer of dichotomously branched, cross-shaped, incomplete baskets, lost with age in one species, and knobbed, fir cone-shaped, multilayered plates, often with one end denticulate; multilayered round to oval plates also present. No buttons. Tube feet, tentacles and introvert ossicles include only rods.

Type specie: *Cucumaria sinorbis* Cherbonnier, 1952 (by original designation)

Other species included: *Pseudocnella sykion* (Lampert, 1885).

Remarks

This genus was erected by Thandar (1987) to accommodate three southern African nominal species: *Cucumaria sinorbis* Cherbonnier, 1952; *C. sykion* Lampert, 1885; *C. insolens* Théel, 1886; and, with reservation, the Mediterranean form *Cladodactyla syracusana* Grube, 1840. A full history of the genus is given in the introduction under the genus. Both morphological and molecular techniques have been used here to determine if the three southern African species assigned to this genus are really congeneric. Since fresh material of *P. syracusanus* was not obtained this species was only examined morphologically. Morphological study of the three southern African nominal species shows that, although all three species have multi-layered plates which may be denticulate at one end, in *C. insolens* one or two tentacles may be reduced whereas in its congeners there are equal tentacles , the calcareous ring has deeply notched radial plates, the madreporite is bean-shaped and not spherical, the crosss-haped incomplete baskets are spinous, ossicles also include regular to irregular single-layered buttons, and the spines of the plates are borne on a projecting handle. From these morphological differences it becomes apparent that *P. insolens* is not congeneric with the other two southern African species of *Pseudocnella* and therefore requires to be re-assigned (see molecular evidence that follows). As far as *P. syraracusanus* is concerned, although very similar to *P. sykion* and *P. sinorbis,* it has unequal tentacles as well as buttons and hence it is herein assigned to a new genus *Hemiocnus* (Mjobo & Thandar, under review).

Molecular evidence

Of 489 nucleotides of mitochondrial DNA in the analysed alignment, 261 characters were invariant, 210 characters were parsimony-uninformative, leaving 51 informative characters. The three species (i.e. *P. sykion*, *P. insolens*, and *P. sinorbis*) studied here are currently classified in *Pseudocnella*.

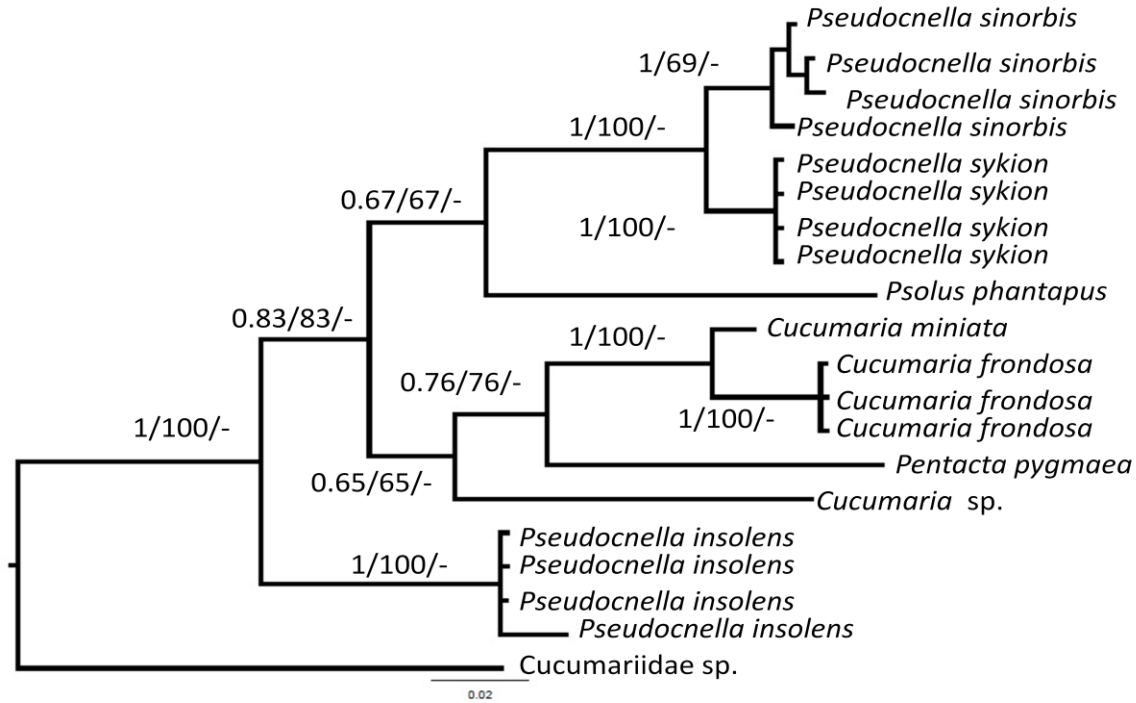


Figure 38. Bayesian tree of obtained mitochondrial 16S ribosomal DNA (mt 16S rDNA) for the genus Pseudocnella from Southern Africa. Values at branches represent Bayesian probabilities, Maximum likelihood and Neighbour-joining bootstrap values. Sequences labelled with other species than those of *Pseudocnella* represents outgroups and were obtained from GenBank (accession numbers in Materials and Methods).

All *Pseudocnella* specimens formed a well supported paraphyletic clade (B=1, ML=100). Within this clade *Pseudocnella insolens* formed a well supported subclade (B=1, ML=100). The other clade of *Pseudocnella* was also well supported (B=1, ML=100), but not supported by neighbour-joining bootstrap values. Within this clade *P. sinorbis* formed a small subclade which was supported by (B=1, ML=69) and not supported by NJ. Specimens of *P. sykion* sequences formed a well supported subclade (B=1, ML= 100). *Pseudocnella insolens* was paraphyletic with the other *Pseudocnella sp*. included in this study and indicates that *P. insolens* may be misplaced in terms of its taxonomy.

Both Bayesian and Maximum likelihood phylogenetic trees show that the three species do not form a monophyletic group, placing *P. insolens* in a paraphyletic clade. This confirms the suspicions by Thandar (1987) that all the species assigned to *Pseudocnella* may not be conspecific. This is also confirmed by molecular diversity measures (see Table 3) when *P. insolens* was compared to other species of *Pseudocnella*.

The present results showed that morphologically and genetically, two (*P. sykion* and *P. sinorbis*) of the observed samples belong to *Pseudocnella* whereas *P. insolens* appears to belong to another genus entirely. Bayesian and maximum likelihood trees showed that *P.*

insolens is well differentiated from *P. sykion* and *P. sinorbis*. Both morphological and molecular evidence place *P. insolens* separately from *Pseudocnella* and for this reason *P. insolens* is now placed in *Hemiocnus* since it shares some characteristic features with the type species of this genus. It appears that *Pseudocnella* is now strictly a South African genus with only 2 nominal species united by 10 equal tentacles, cross-shaped incomplete baskets at least in juvenile, and knobbed multilayered calcareous plates and the absence of buttons.

Table 3. Molecular diversity statistics for the mt 16S rDNA sequences for *P. insolens*, *P. sykion*, and *P. sinorbis*. S, number of variable sites; H, number of haplotypes; h, haplotype (genetic) diversity; π, nucleotide diversity; k, mean pairwise differences.

species	**n**	**S**	**GC content**	**H**	***h***	**π**	***k***	**Tajima's D**	***P***	**Fu and Li's D**	***P***
P. insolens	4	6	0.393	2	0.5000	0.006	3.000	- 0.8061	$P > 0.10$	-0.8061	$P > 0.10$
P. sinorbis	4	7	0.400	4	1.000	0.00784	3.8333	0.03892	$P > 0.10$	0.03892	$P > 0.10$
P. sykion	4	1	0.393	2	0.500	0.00102	0.5000	-0.61237	$P > 0.10$	-0.61237	$P > 0.10$
P. sykion vs *P. sinorbis*	8	15	0.393	6	0.893	0.00102	7.57143	1.16634	$P > 0.10$	0.89912	$P > 0.10$
P. sykion vs *P. insolens*	8	58	0.390	4	0.786	0.06318	30.89286	2.05656	$*P < 0.05$	1.19889	$P > 0.10$
P. sinorbis vs *P. insolens*	8	64	0.393	6	0.893	0.06931	33.89286	1.90376	$0.10 > P < 0.05$	1.19272	$P > 0.10$
All sequences	12	66	0.393	8	0.909	0.6141	30.03030	1.45483	$P > 0.10$	1.19008	$P > 0.10$

Pseudocnella sinorbis (Cherbonnier, 1952) type species

Figure 39 A-D, 40 A-D, and 41 A-C.

Cucumaria sykion Deichmann, 1948: 346 (partim), pl. 19, figs. 3 & 4; pl. 326.
Cucumaria sykion (*insolens* stage) Deichmann, 1948: 372 (partim).
Cucumaria sinorbis Cherbonnier, 1952: 482, pl. 38, figs. 1-13, pl. 39, figs. 24-31.
Pseudocnella sinorbis Thandar, 1987: 91, figs. 1d, 3, 5e and 5f); 1991:130.

Diagnosis (after Cherbonnier 1952)

Body shape sub-cylindrical, skin leathery, colour light brown. Mouth terminal, anus subdorsal. Anal papillae present. Tube feet in 2-4 rows per ambulacrum; interambulacra papillae present. Ten equal tentacles. Calcareous ring simple. Body wall ossicles include fir-cone-shaped multilayered round to oval plates, knobbed, perforated small round plates and a superficial layer of incomplete baskets, X-shaped. Tube feet deposits include 3-armed rods, some small and curved. Tentacle deposits include large rods, triangular plate-like rods and small curved rods. Introvert deposits include only rods.

Material examined

Eastern Cape, Port St Johns, Umngazana, 12-07-2013, 2 spec.; KZN, south coast, Park Rynie, 13-09-2013, 2 spec.

Description

Specimens sub-cylindrical, largest 28 mm long and 12 mm wide, smallest about 17 mm long and 5 mm wide. Colour greyish to light brown, skin leathery. Tube feet in more than two rows ventrally, dorsally in two distinct rows, also scattered in interambulacra. Tentacles 10, dendritic, all of the same size; colour dark brown. Calcareous ring simple, without posterior prolongations, radials notched posteriorly (Figure 41B). Polian vesicle single; stone canal short, madreporite spherical (Figure 41C). Retractor muscles attached to longitudinal muscles at about ½ body length. Gonadal tubules unbranched. Respiratory trees highly branched.

Body wall ossicles as fir-cone shaped plates, often with one end denticulate, the denticles may or may not be borne on a short handle (Figure 38A); non-denticulate plates mostly multilayered, round to oval (Figure 39B). Small, multi-layered, knobbed, perforated

small round plates (Figure 39C); incomplete X-shaped baskets as superficial layer, often terminally bifurcating (Figure 39D) also present. Tube feet deposits include rods, some elongate, some small, often with a medial 3rd arm, some with 4 arms, and distal perforations, others with 2-3 large central holes and minute distal perforations (Figure 40A). Tentacle deposits include small curved rods (Figure 40C) and thick elongated rods (Figure 40D). Introvert ossicles consist of minute to moderate-sized rods (Figure 40B).

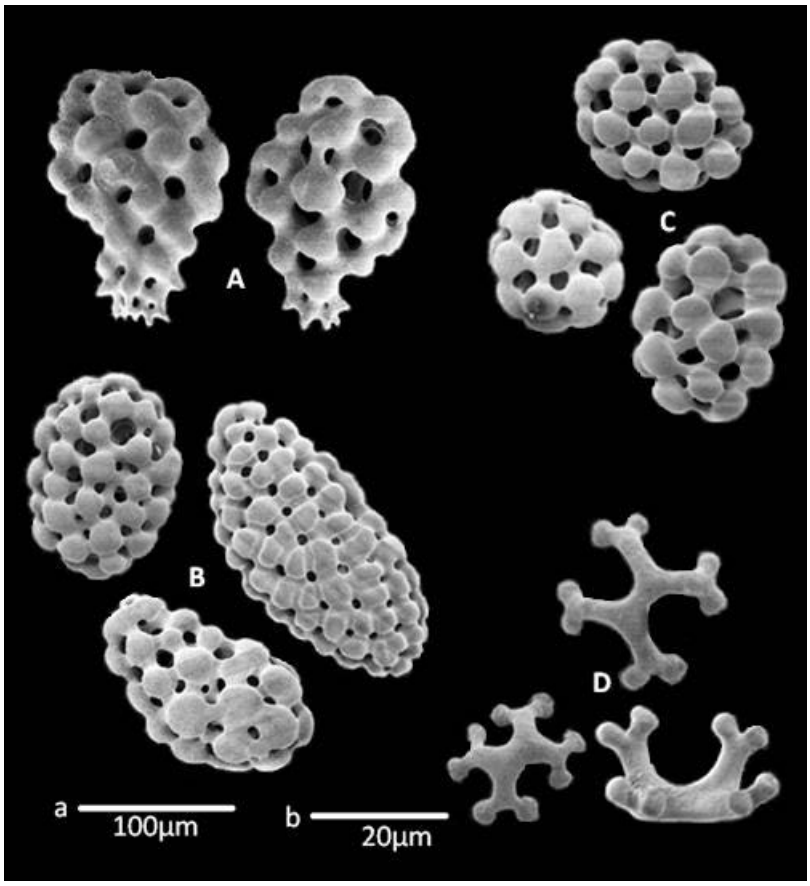


Figure 39. *Pseudocnella sinorbis* (Cherbonnier, 1952) KZN, Park Rynie. A. Fir-cone plates from body wall; B. Round to oval plates from body wall; C. Small round plates from body wall; D Cross- shaped baskets from body wall.

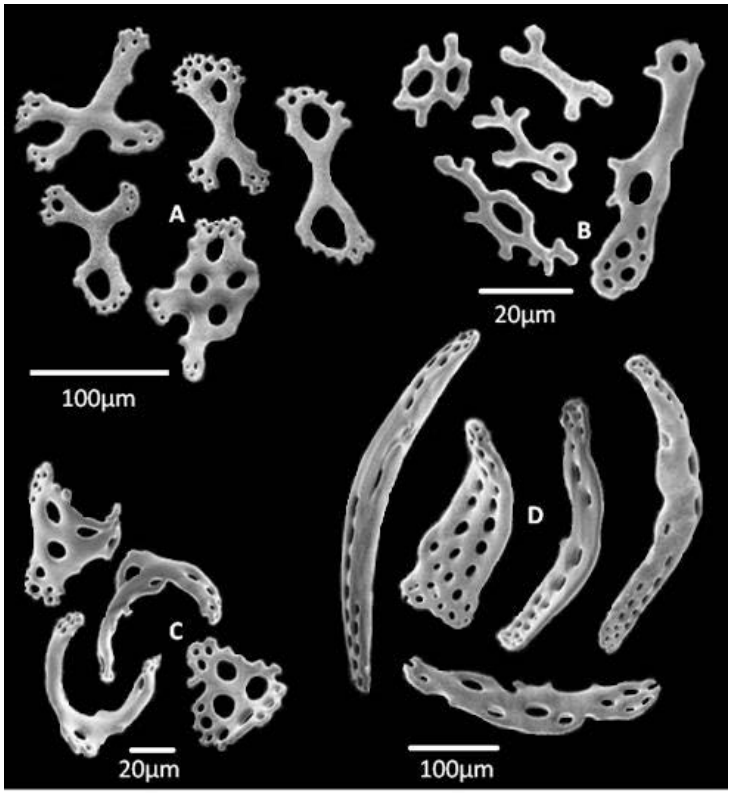


Figure 40. *Pseudocnella sinorbis* (Cherbonnier, 1952). KZN, Park Rynie. A. rods from tube feet; B. rods from introvert; C. small curved ossicles from tentacles; D. large rods from tentacles.

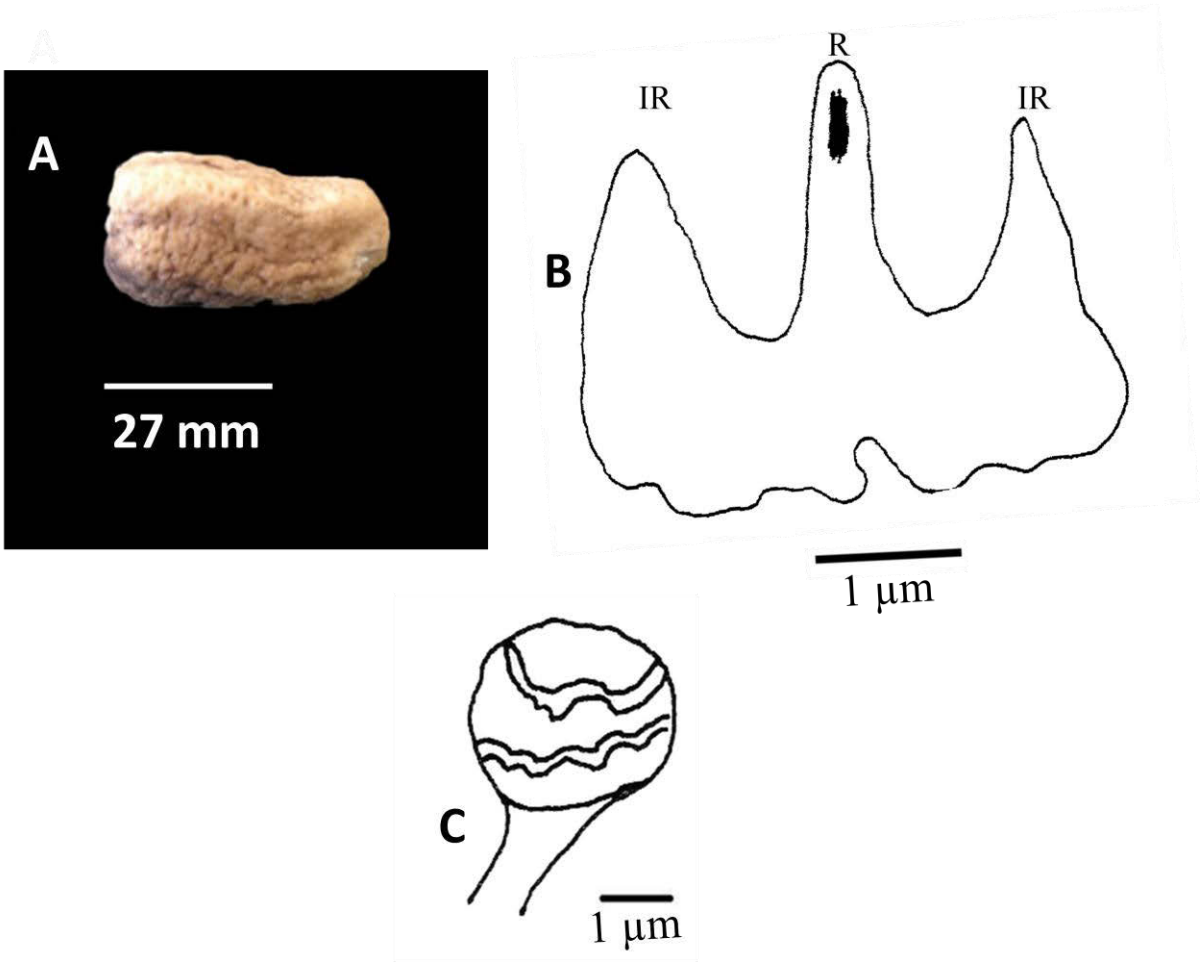


Figure 41. *Pseudocnella sinorbis* (Cherbonnier, 1952). KZN, Park Rynie. A. Entire specimen; B. Calcareous ring. C. Madreporite.

Distribution

Table Bay to Jangamo, south of Inhambane (Mozambique); intertidal (Thandar, 1987).

Remarks

The species is well described by Cherbonnier (1952). *Pseudocnella sinorbis* has been confused with the dark *sykion* by Deichmann (1948), but Cherbonnier (1952) and later and moreso Thandar (1987) clearly resolved the confusion. *P. sinorbis* differs from *P. sykion* by its lighter colouration, longer interradial papillae and the presence of incomplete baskets throughout life. In *P. sinorbis* some of the plates may have denticles borne on a projecting handle. Such a handle was not reported by either Cherbonnier (1952) or Thandar (1987) and hence the identity of the current specimens may be doubted. Both these authors illustrate spinous plates similar to those of *P. sykion*.

Pseudocnella sykion (Lampert, 1885)

Figure 42 A-D, 43 A-B, and 44 A-D

Semperia sykion Lampert, 1885: 250.
Cucumaria sykion Théel, 1886: 266; Clark, 1923 (partim): 412; Deichmann, 1948: 346 (partim); Cherbonnier, 1952: 483. Pl. 40, figs. 1-18.
Cucumaria jaegeri Lampert, 1885: 249.
Cucumaria dubiosus jaegeri Panning, 1952: 126, figs. 6-9; 1962: 66, figs. 10 & 11.
Pseudocnella sykion Thandar, 1987:292, figs 1b-c, 4 & 5d; Branch *et al.,* 1994: 204, fig. 96.3.

Diagnosis: (After Moodley 2000, unpublished MSc thesis)

Body barrel-shaped, up to 60 mm long. Colour dark olive to black. Tube feet in 4-7 rows. Interambulacral papillae minut, often retractile. Anal teeth present. Ossicles consist of a superficial layer of incomplete baskets, present only in young individuals under 25 mm, adults with densely packed round to oval multilayered knobbed plates, few (often 20%) with one end denticulate, but the denticles are never borne on a "handle"; smallround plates also present. Tube feet with straight or curved rods, some 3-armed. Tentacle rods curved or straight. Introvert with simple rods, some plate-like.

Material examined

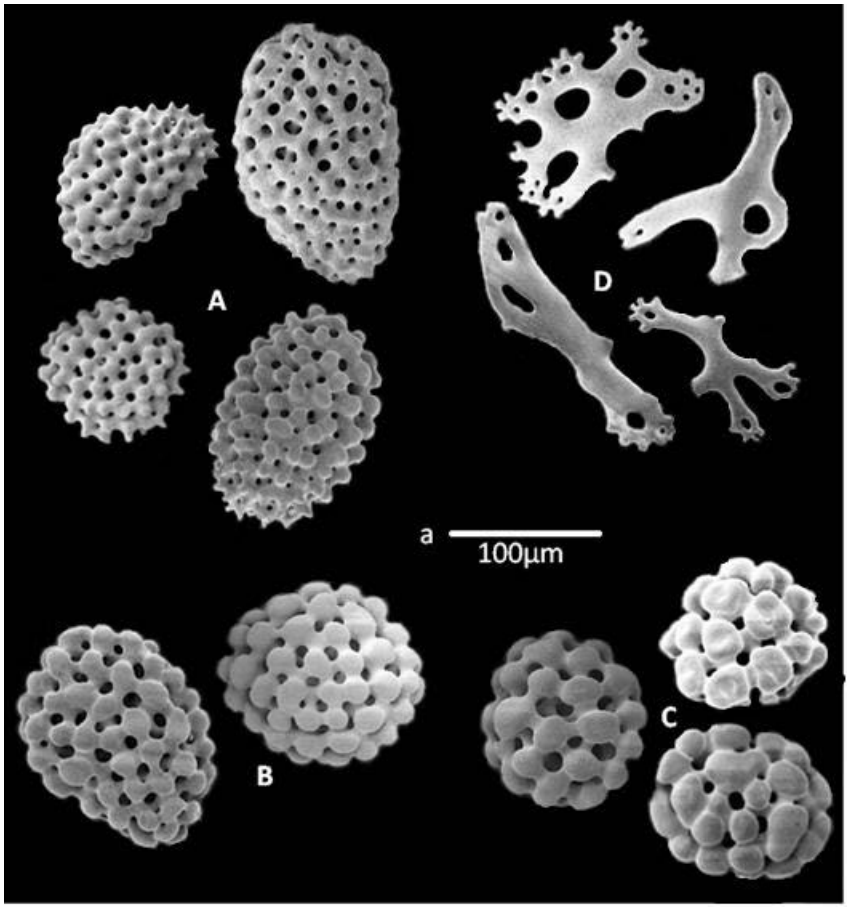
KwaZulu-Natal, south coast, Umkomasi, Green Point, 23/06/2013, 34 spec., rocky shore Park Rynie, 08/05/2013, 9 spec; Eastern Cape coast, Port St Johns, 12/09/2013, 18 spec.

Description

Body cylindrical, more or less barrel-shaped. Largest specimen 56 mm long and 24 mm wide, smallest 11 mm long and 6 mm wide. Mouth terminal, anus more or less dorsally directed. Skin very tough and leathery. Colour in life dark brown to black. Tube feet 4-7 rows ventrally, 2 rows dorsally. Interambulacral papillae present, retracted. Anal teeth present. Tentacles 10, all of same size. Calcareous ring simple, without posterior prolongations (Figure 44C). Polian vesicle single; stone canal single, madreporite spherical (Figure 44B).

Retractor muscles attached to longitudinal muscles at about ½ body length. Gonad tubules unbranched, in two tufts. Respiratory trees highly branched.

Body wall deposits include knobbed, multilayered fir-cone shaped plates, often with one end denticulate (Figure 42A), plates 210 – 450 µm long and 140 – 250 µm wide; knobbed and perforated round plates (Figure 42B), 170 – 220 µm wide; multilayered knobbed and perforated buttons (Figure 42C) 130 – 150 µm wide; a superficial layer of incomplete baskets present only in juvenile. Tube feet deposits include straight, sometimes 3-armed, perforated rods, some plate-like rods also present (Figure 42D). Tentacle deposits include thick rods, some straight, others curved, few with a 3rd arm, sometimes elongated (Figure 43B). Introvert deposits consist of straight, elongated rods, some plate-like rods also present (Figure 43A).



Figur 42. *Pseudocnella sykion* (Lampert, 1885). KZN, Park Rynie. A. fir-cone plates from body wall; B. round to oval plates from body wall; C. round plates from body wall; D. ossicles from tube feet.

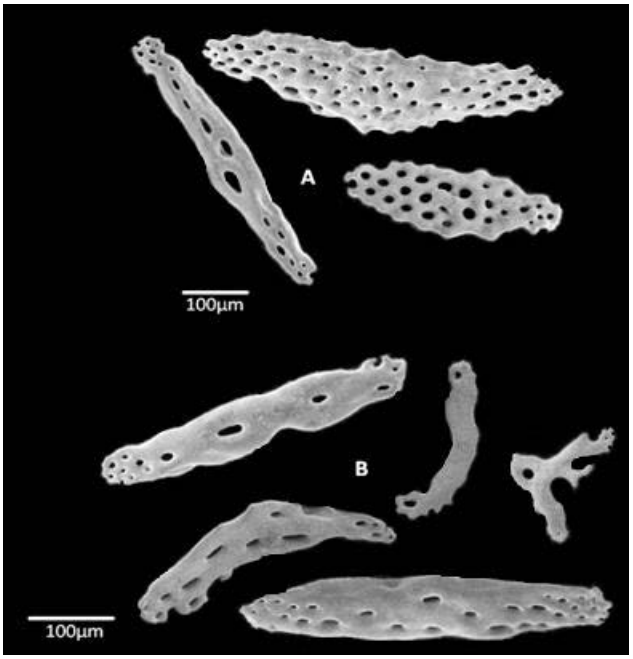


Figure 43. *Pseudocnella sykion* (Lampert, 1885). KZN, Park Rynie. A. ossicles from introvert; B. ossicles from tentacles.

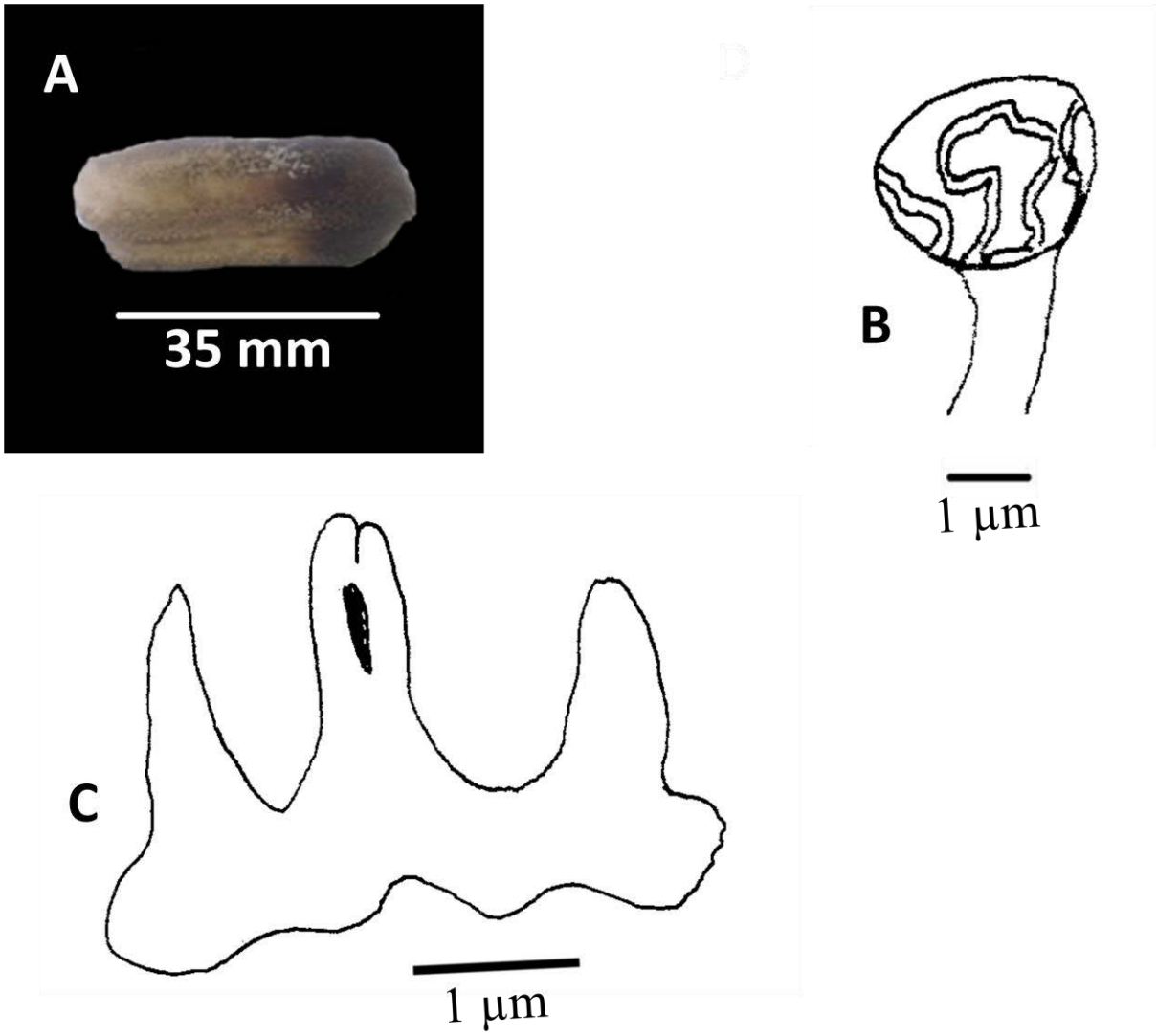


Figure 44. *Pseudocnella sykion* (Lampert, 1885). KZN, Park Rynie. A. Whole animal; B. Madreporite; C. Calcareous ring.

Distribution

Cape Agulhas to Jangamo, south of Inhambane, Mozambique, intertidal (Thandar, 1987).

Remarks

Lampert (1885) described two species from South Africa: *Semperia sykion* and *Cucumaria jaegeri*. A full history with all relevant arguments concerning these species and *P. insolens* is given by Thandar (1987) and it is unnecessary to repeat it here. *Pseudocnella sykion* is well diagnosed by Thandar (1987) and recently described by Moodley (2000) but the latter still awaits publication. In the present study there are no significant findings except that the spinous plates measure 210-445 µm compared to 100 -250 µm recorded by Thandar (1987) and 180 -270 µm recorded by Moodley (2000). The larger plates were observed from around the anal region which has numerous fir-cone shaped plates but few oval plates

measuring 170-220 µm. No buttons were observed. On the ventral side more round plates were observed compared to fir-cone-shaped plates.

Genus *Hemiocnus* n. gen.

Cladodactyla Grube, 1940:40 (*partim*).
Cucumaria Sars,1857:123, Pl. 1 figs. 24-29. Théel, 1886a:113; Koehler, 1921:155, fig. 106; Cherbonnier, 1956:20 (*partim*).
Ocnus Panning, 1949:438, fig. 33, 34 (*partim*).
Pseudocnus Panning, 1962:68, fig. 13, 14 (partim); Tortonese, 1984:12 (*partim*).
Pseudocnella Thandar, 1987:288, 289 (*partim*).

Diagnosis

A genus of Cucumariidae with tube feet on both ambulacra and interambulacra, sometimes also with minute 'papulae-like' structures dorsally. Tentacles 10, ventral-most two reduced. Calcareous ring simple, without posterior prolongations. Body wall deposits include multilayered fir-cone-shaped plates, often with one end denticulate, and rounded, knobbed plates/buttons; an external layer of cross-shaped, incomplete baskets present. Tube feet with rods or plate-like rods. Tentacle and introvert ossicles usually include rosettes in addition to rods.

Type species: *Cladodactyla syracusana* Grube, 1840 (designated by Mjobo and Thandar [MS under review]).
Other species included: *Pseudocnella insolens* (Théel, 1886) with one or two tentacles reduced but not necessarily the ventral-most two. DNA sequencing of this species throws it out of the *Pseudocnella* group.

Etymology

Since this genus is close to *Ocnus* it takes its name from it.

Remarks

The new genus is diagnosed in the cucumariid subfamily Colochirinae because of presence of baskets of some form in the body wall of all genera in this subfamily. The new genus resembles *Pseudocnella* Thandar, 1987 and *Ocnus* Forbes & Goodsir, 1841. However, Thandar (1987) transferred *Pseudocnus syracusanus* and *Cucumaria insolens* to *Pseudocnella* with some doubt because it shares some characters with each of the *Pseudocnella* species. It now appears that *Pseudocnella* is strictly a southern African genus in which the tentacles are of equal size. Further, the presence of rosettes in the tentacles separates the new genus from *Pseudocnella*. *Hemiocnus* resembles *Ocnus* in the 8+2 tentacle arrangement and the presence of rosettes in the tentacles. However, the two genera are distinct in that *Hemiocnus,* like *Pseudocnella* and *Pseudocnus,* has in its body wall fir-cone-shaped plates often with one end denticulate while *Ocnus* lack plates of this form.

KEY TO SPECIES OF HEMIOCNUS n. gen

1. Fir cone-shaped plates prolonged at one end to form denticulate handle, incomplete basket with branched thorny ends..... ***Hemiocnus insolens*** (Théel, 1886).

   Fir cone-shaped, plates denticulate but denticles not borne on a handle; incomplete baskets with smooth ends lacking knobs..... ***Hemiocnus syracusanus*** (Grube, 1840).

Hemiocnus syracusanus (Grube, 1840)

Figures 45 & 46

Cladodactyla syracusana Grube, 1940:40.

Cucumaria syracusana Sars, 1857:123, Pl. 1 fig. 24-29; Théel, 1886:113; Koehler, 1921:155, fig. 106; Cherbonnier, 1956:20.

Ocnus syracusanus Panning, 1949:438, fig. 33, 34.

Pseudocnus syracusanus Panning, 1962:68, fig. 13, 14 (?*partim*); Tortonese, 1984:12.

Pseudocnella syracusana Thandar, 1987:288, 289 (partim).

Diagnosis (after Sars 1857, amended herein)

Body sub-cylindrical, colour light-brown in alcohol. Dorsal tube feet in both ambulacra and interambulacra. Tentacles 10, ventral-most two reduced. Calcareous ring simple, without posterior processes. Ossicles of body wall comprise fir-cone-shaped plates, often denticulate at one end, and round, knobbed, often 4-holed buttons. Incomplete baskets may also occur as dichotomously branched rods, usually in association with bases of tube feet. Tube feet with rods; tentacles with rods and rosettes.

Material examined

Zoologisches Museum Hamburg, E2877, Zool. Stat. Europa, Italien, Neapel, 1 spec. ; NHMUK, 1982.6.1.6-8, *P. syracusanus* (Grube), Shigmona, South of Haifa, Dr. Lewinsohn, 4 spec.

Description

This species is well known and hence only a brief description of the Hamburg specimen from Naples follows. Body curved, mouth and anus turned up; colour light brown in alcohol; length 56 mm, width in mid-body 19 mm. Tube feet in two rows ventrally, but scattered dorsally. Anal papillae present. Tentacles 10, ventral two reduced. Calcareous ring simple, without posterior prolongations, radials slightly notched posteriorly. Retractor muscles arise from longitudinal muscles at about ½ body length. Polian vesicle and stone canal not detected. Gonad of numerous, unbranched tubules. Respiratory trees highly branched.

Body wall ossicles comprise large multi-layered fir-cone-shaped knobbed plates denticulate at one end; large knobbed non-denticulate round plates; smaller rounded knobbed buttons/plates; and occasionally incomplete cross-shaped baskets appearing as dichotomously branched rods (Figure 45A). Denticulate fir-cone-shaped plates (290-340 µm) (Figure 46 A); large knobbed round non-denticulate plates (150-210µm) (Figure 46 B); small knobbed buttons/plates up to 120 µm, with 4-8 holes (Figure 46 C), holes up to 10 µm, knobs up to 30 µm; incomplete baskets (Figure 45 A), typically like those of *Pseudocnella sinorbis* (Cherbonnier, 1952). Tube feet deposits include perforated rods (Figure 45 B) and often also incomplete baskets; end-plates present. Tentacle deposits include rods (Figure 46 D, E) and rosettes (Figure 45 C), but latter not as numerous as in *Ocnus rubrobrunneus.*

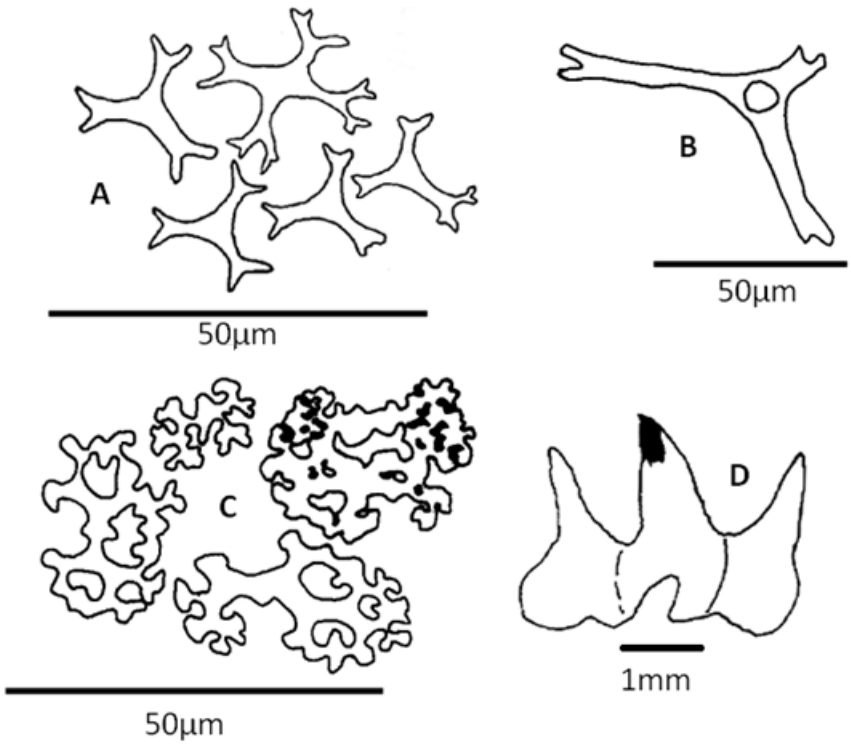


Figure 45. *Hemiocnus syracusanus* (Grube, 1840). ZMH E2877A. Incomplete baskets from body wall; B. Rod from tube foot; C. Rosettes from tentacles; D. Calcareous ring.

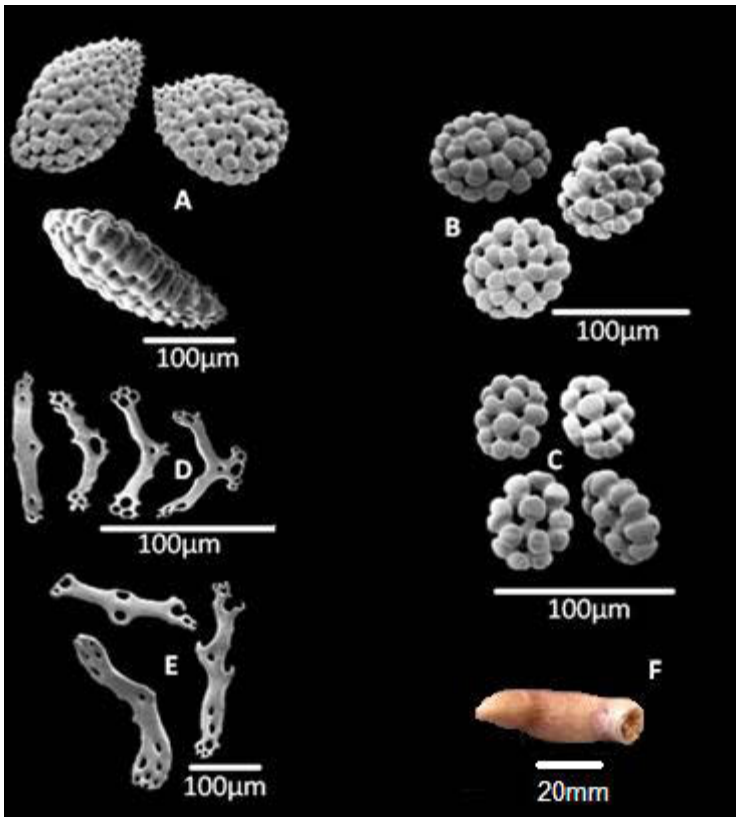


Figure 46. *Hemiocnus syracusanus* (Grube, 1840). ZMH E2877A .A. Fir-cone-shaped plates from body wall; B. Large round plates from body wall; C. Buttons from body wall; D. Small rods from tentacles; E. Large rods from tentacles; F. Entire.

Distribution

Mediterranean Sea, off west coast of Africa (Théel 1886).

Remarks

This species was described from the Mediterranean Sea by Grube (1840) as *Cladodactyla syracusana* but transferred to *Cucumaria* by Sars (1857). Théel (1886) followed Sars and accepted the species as *Cucumaria syracusana*, recording its distribution as the Mediterranean Sea and off west coast of Africa. Panning (1949) transferred the species to *Ocnus*. Grube (1840), Sars (1857) and Théel (1886) did not describe the calcareous ring, but this was done by Panning (1949). Later Panning (1962) transferred the species to *Pseudocnus*. Subsequent to this, Thandar (1987), in his revision of some southern African Cucumariids erected a new genus *Pseudocnella* to accommodate three common southern African species and hesitantly included in it *P. syracusanus*. Panning's (1962) supposed mis-identification of part of his material, overlooked by Thandar (1987), has been commented on above. The specimen from Hamburg Museum and those in the NHMUK, represent the true *syracusanus* as their characters match those recorded for this species by various authors. Any re-assignation of part of Panning's (1962) material will require its re-examination. According to Thandar (1987) the genus *Pseudocnella* is characterized by 10 more or less equal tentacles with only one species *(P. insolens)* having one or more reduced, but not necessarily the ventral-most two. In addition, all species possess, at least at some stage of their development, an external layer of incomplete baskets. Since *syracusanus* has an 8+2 arrangement of tentacles and rarely incomplete baskets it cannot be classified in *Pseudocnella*. It also not referable to *Ocnus* because of the presence of large knobbed, multi-layered, often denticulate plates and 'papulae-like' extensions dorsally. The new genus is closer to *Pseudocnella* than it is to *Ocnus*.

Hemiocnus insolens (Théel, 1886) comb. new

Figure 47 A-D, 48 A-D and 49 A-C

Cucumaria insolens Théel, 1886: 70, pl. 4, fig. 5; Vaney, 1908: 431; 1910: 431; 1912: 27; Clark, 1923: 411; Cherbonnier, 1952: 40, pl. 39, figs. 1-23;.

Semperia insolens Ludwig, 1887: 1231, 1236.

Cucumaria sykion Deichmann, 1948: 346 (partim), pl. 19, figs. 1 and ?2.

Pseudocnella insolens Thandar, 1987b: 289, figs. 1a, 2, 5a-c; 1991:121-122, fig. 14f; 2008:22-24, fig. 9A-M.

Diagnosis (After Moodley, 2000, unpublished MSc thesis)

Body sub-cylindrical to barrel-shaped. Colour off-while in alcohol. Mouth and anus terminal; anus slightly turned up. Tentacles 10, one or two reduced. Ventral tube feet 2-3 rows, dorsal in 2 rows, often present in interambulacra; "papulae" like structures present dorsally. Body wall ossicles consist of knobbed, perforated fir-cone shaped plates with one end drawn-out and denticulate; some plates round to oval, lacking denticulate handle. Single-layered, knobbed, perforated buttons and a superficial layer of dichotomously branched X-shaped baskets also present. Tube feet deposits include 3-armed rods. Tentacle deposits include straight or curved rods. Introvert ossicles exclusively rods and rosettes.

Material examined

Millers Point, Cape Town, donated by Two Oceans Aquarium, 18m, June 2013, 4 spec.

Description

Specimens, barrel-shaped, largest 32 mm long and 9 mm wide, smallest 20 mm long and 5 mm wide. Colour, in alcohol, off white-to cream white. Mouth and anus terminal. Anal teeth absent. Tube feet in two distinct rows per ambulacrum, also scattered in interambulacra; interradial "papullae"-like structures present. Tentacles 10, ventral two reduced, very bushy. Calcareous ring simple without posterior prolongations, radials posteriorly notched (Figure 49B). Stone canal short, Polian vesicle single. Madreporite bean-shaped (Figure 49C). Retractor muscles attached to longitudinal muscles at about ½ body length. Gonad unbranched, two tufts. Respiratory trees highly branched.

Body wall ossicles include fir-cone shaped, knobbed and perforated plates, usually with one end drawn-out and denticulate (Figure 47A); knobs usually larger than holes; some plates round to oval, without denticulate handle (Figure 47B); fir-cone plates 190-300 µm long and 100-130 µm wide. Small round buttons also present with 3-5 holes (Figure 47C), 80-110 µm wide. A superficial layer of, dichotomously branched (Figure 47D), spiny incomplete baskets also present. Tube feet deposits as 3-armed rods, some table -like (Figure 48A); end plate present. Tentacle deposits include only small to large perforated, straight and curved rods (Figure 48B). Introvert deposits include small rods (Figure 48D) and rosettes (Figure 48C).

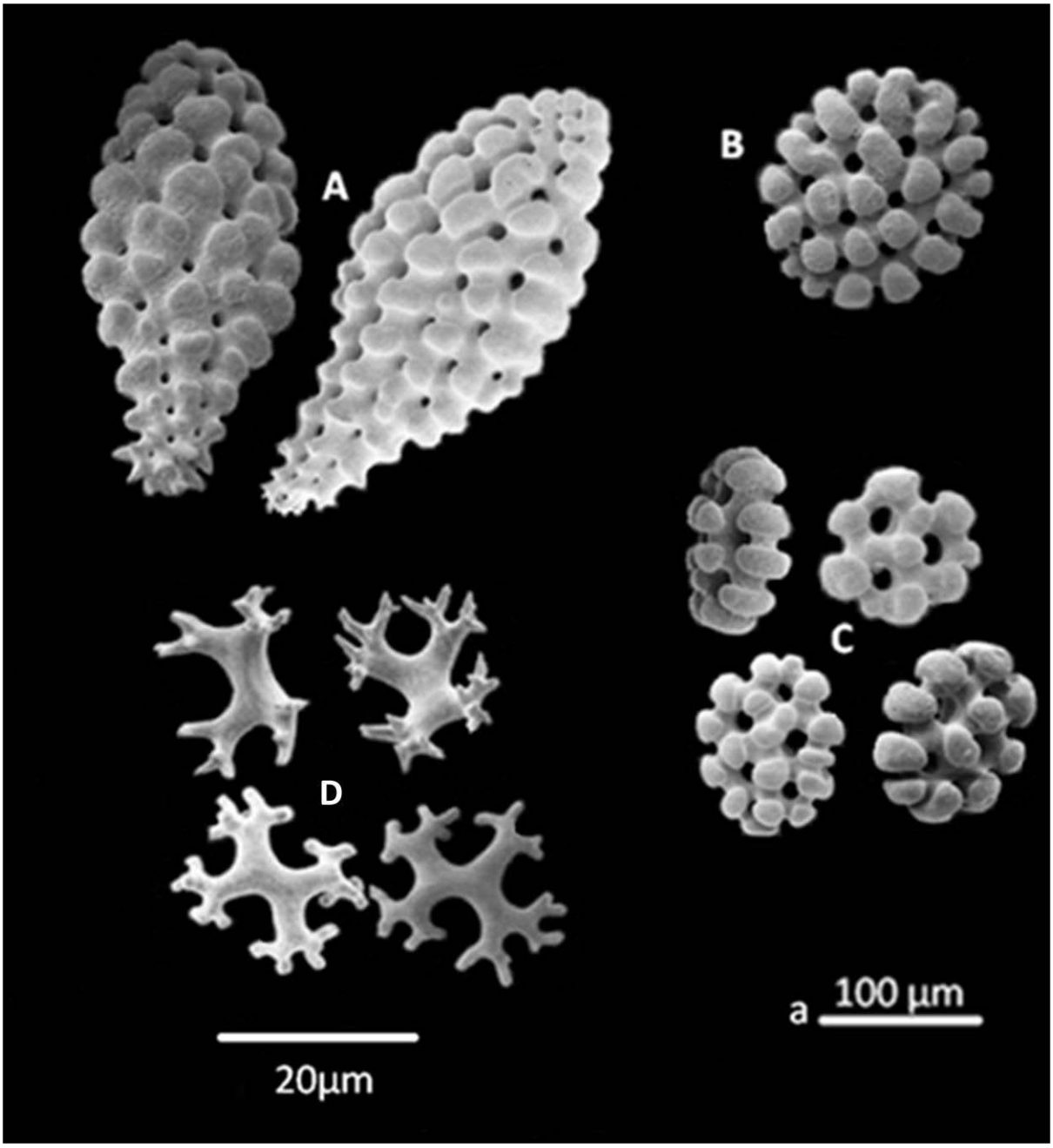


Figure 47. *Hemiocnus insolens* (Théel, 1886). Millers Point, Cape Town. A. fir-cone plates from body wall; B. round plate from body wall; C. buttons from body wall; D. incomplete baskets from body wall. Note: A-C from the same scale.

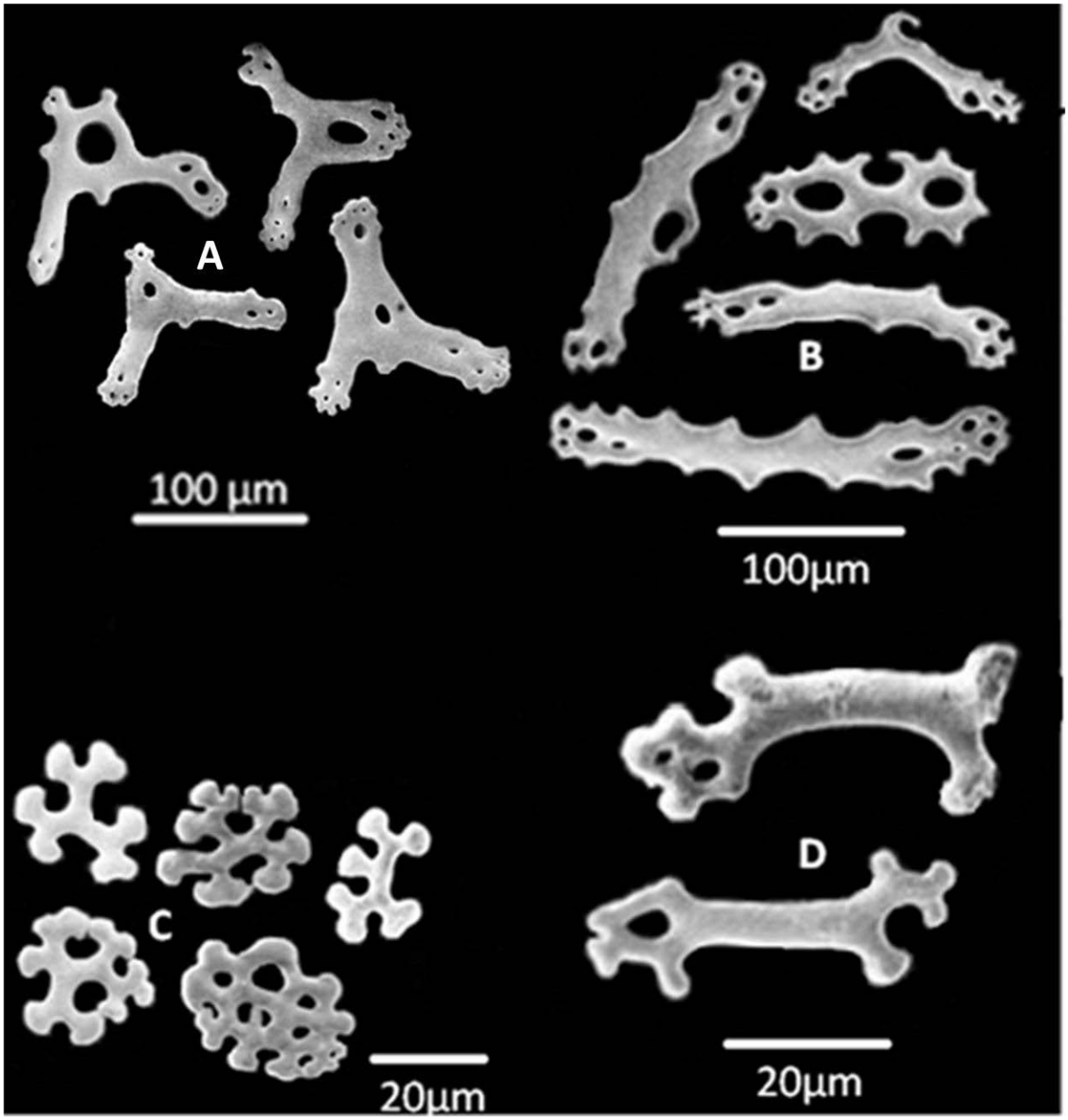


Figure 48. *Hemiocnus insolens* (Théel, 1886) Miller's Point, Cape Town. A. -armed rods from tube feet; B. rods from tentacles; C. rosettes from the introvert; D. rods from the introvert.

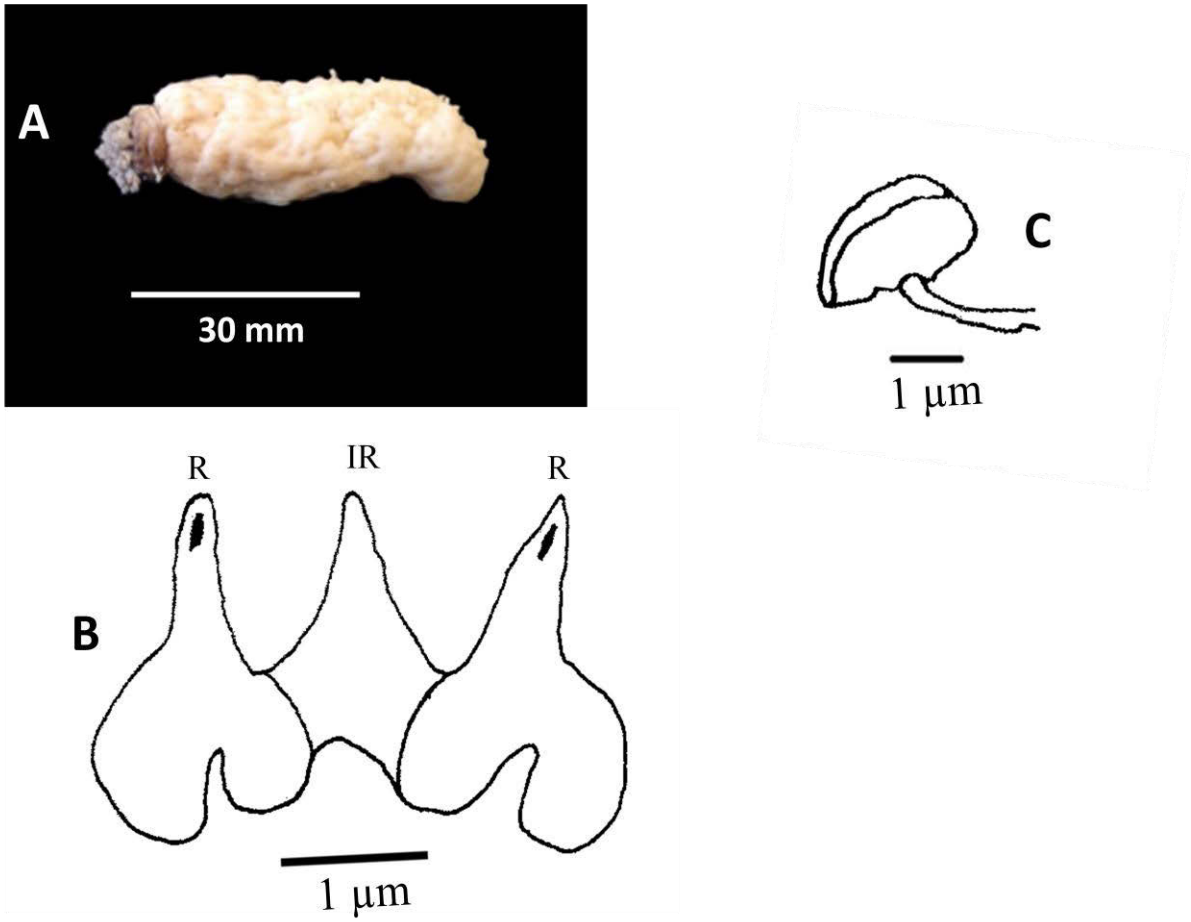


Figure 49. *Hemiocnus insolens* (Théel, 1886) Millers Point, Cape Town. A. Entire; B. Calcareous ring; C. Madreporite.

Distribution

Luderitz **(**Namibia) to Port Elizabeth (South Africa), 0-110 meters (Thandar 2008).

Remarks

This species has been described by many workers including Théel (1886), Cherbonnier (1952), Thandar (1987; 1991 and Clark (1923). Clark (1923) and Diechmann (1948) synonymised it with *sykion* because they believed that *insolens* is a growth stage of *sykion*. Cherbonnier (1952) corrected the error made by Diechmann (1948), and concluded that *insolens* and *sykion* are two distinct species. Regrettably, Panning (1962) ignored Cherbonnier's decisions by following Diechmann (1948). Thandar (1987) cleared the confusion made by Diechmann when he critically examined the southern African Cucumariids. Thandar (1987) followed Cherbonnier (1952) but erected a new genus *Pseudocnella* to accommodate *insolens*, *sykion*, *sinorbis* and the Mediterranean form *C.*

syracusana. He further expressed the opinion that the three southern African nominal species may not be congeneric.

Similarities and differences between species previously assigned to *Pseudocnella* have been given under the remarks for this genus. Morphological differences (unequal tentacles, spinous incomplete baskets and buttons in addition to plates) do not support the placement of *insolens* in *Pseudocnella*. Molecular evidence also supports this contention. *H. insolens* shares some characteristic features with *syracusanus* is here assigned to a new genus *Hemiocnus* (Mjobo & Thandar, MS under review). These features include unequal tentacles, presence of large multilayered plates with one end denticulate, incomplete baskets and knobbed buttons in the body wall and rosettes in the introvert. For these reasons *insolens* is here re-assigned to *Hemiocnus*.

Cherbonnier (1952) and Thandar (1987) mentioned the presence of brood pouches in this species but from the material at hand such structures were not observed. In this material no complete baskets were found, mentioned by Thandar (1987) in his descriptions of *insolens*. Théel (1886) and subsequent authors did not report rosettes in the introvert which are plentiful in the current specimens. *P. insolens* differs from its congener in the presence of knobs at the end of the branches of the baskets.

DISCUSSION

Despite several revisions of the genus *Pseudocnus* Panning, 1949 by Panning himself (1951, 1952, and 1962), and after the erection of the genus *Pseudocnella* by Thandar (1987) to accommodate three southern African Cucumariids and a Mediterranean form, formerly in *Pseudocnus* many problems still remained. Some of these were resolved by O'Loughlin *et al*. (2014) after their recent revision of the Antarctic-Subantarctic species of *Pseudocnus*. *Pseudocnus,* as was characterised by Panning (1949 & 1962), included species with both equal or unequal tentacles; plates of the body wall composed of a single and/or double layer of calcareous material; smooth plates in *Pseudocnus alcocki* (Koehler & Vaney, 1908) knobbed plates in others and the presence or absence of buttons..

O'Loughlin *et al*., (2014) attempt to streamline the genus by re-assigning the Antarctic-Subantarctic forms previously assigned by Panning (1962) to his *laevigatus*- group on the bases of morphology, molecular biology and zoogeography to a new genus *Laevocnus* with *Cucumaria laevigata* Verrill, 1876 as type species is commendable. Regrettably, this genus had a very short shelf-life as it was soon realized that the designated type species of *Pentactella* was previously designated by Verrill (1876) to his new genus *Pentactella*, a genus sunk by Panning (1949), who considered it a synonym of *Stereoderma*. According to O'Loughlin (pers. com.) and O'Loughlin *et al*. (2015) *Pentactella* must be resurrected to replace *Laevocnus*. O'Loughlin *et al*. (2014) included in this group also *Cucumaria leonina* Semper, 1868, based on molecular evidence, and *Cucumaria cornuta* Cherbonnier, 1941 based on similar geographic distribution. However, *Pentactella* Verrill, 1876 is diagnosed as a genus with equal tentacles, *C. cornuta* unlike the other species of *Pentactella* has two ventral tentacles reduced whereas *C. leonina* has buttons in addition to plates, In the current revision, it is suggested that *C. cornuta* be re-assigned together with some other species to a new genus *Panningocnus* because it shares features of the species assigned to this genus.

Another excellent contribution by O'Loughlin *et al*. (2014) was their restriction of the genus *Pseudocnus* to species corresponding with the type species *Cucumaria koellikeri* Semper, 1868. Thus they re-diagnosed *Pseudocnus* without assigning the remaining species to other genera but only listing them. The current research is intended to clarify this situation and on this basis *Pseudocnus* now comprises only three species and the remaining species transferred to two new genera based only on morphological evidence of tentacle size and structure of the body wall plates, based on materials obtained on loan from various

international institutions (see Materials & Methods section) and available literature. It is regretted that no fresh materials were available for molecular work.

Since *Pseudocnus* was restricted on the bases of equal tentacles and single-layered plates, these characters are here used to separate genera.Two new genera *Panningocnus* (with *Cucumaria dubiosa* Semper, 1868, as type species) and *Thandarocnus* (with *Pseudocnus sentus* O'Loughlin & Alcock, 2000, as type species) have been erected to accommodate respectively those species with plates made up of a single or multiple layers of calcareous material and unequal tentacles. Time also did not permit any morphometric studies of ossicles nor cladisitc relationships based on morphological characters. This is intended for future analysis to prove the validity of the new taxa erected.

Even after Thandar's (1987) revision of some southern African Cucumariids and their referral to the genus *Pseudocnella*, few problems remained, eg. the inclusion of the southern African *C. insolens* Théel and the Mediterranean *Cladodactyla syracusana* Grube in this genus, the former because of the presence of buttons in addition to plates and the latter because of unequal tentacles. In this study both morphological and molecular techniques have been used to separate the southern African species. On this basis only two South African species remain in *Pseudocnella* with *P. insolens* and *P. syracusana* now referred to yet another genus *Hemiocnus*, the latter only on morphological evidence. Morphological evidence showed that *C. insolens* is quite different from its congeners in most characters including the form of calcareous ring, some reduced tentacles, the form of madreporite, spiny baskets, rosettes in introvert and buttons in the body wall. These differences were confirmed by molecular study. It is apparent that *Pseudocnella* now accommodates species with only ten equal tentacles, no buttons and rosettes.

ZOOGEOGRAPHY

It is widely held that species belonging to the Dendrochrotida undergo direct development whereby the gastrula develops directly into the doliolaria larva, thus lacking the auricularia stage (Smiley *et al*. 1991; Sewell & McEuen 2002; Samyn & Tallon 2005). Species of *Pseudocnus* (s.l.) are all dendrochirotids and because of the lack of a free-swimming larval stage each species is not widely distributed. Dendrochirotids mostly inhabit temperate rather than tropical waters (Bakus 1973). This has been attributed to their feeding habits, preferring, as suspension feeders, cooler richer waters. Hence, due to their lack of a free-swimming larva and their feeding habits we notice that they are mostly highly endemic, with high latitudinal distribution patterns. High levels of endemicity amongst dendrochirotids have been reported by various authors working on the fauna of their particular regions (see Thandar 1989). Those dendrochirotids which do have a wide distribution may have been transported by flotsam, drift-wood, bottom of boats, etc with ocean currents playing an insignificant role. Those species occurring in the tropics must have migrated here during shallower or cooler times and have now become adapted to these conditions. Samyn & Tallon (2005) demonstrated that, in South Africa, the faunistic similarity between the subtropical Natal Province and the warm temperate Agulhas Province is so small that the action of the Agulhas counter-current appears to be negligible in transporting the temperate Agulhas species into the subtropical Natal province. The distributions of all species of *Pseudocnus* (s.l.), except for those dealt with by O'Loughlin *et al.* (2014), are mapped and discussed below (see Figures 50-52).

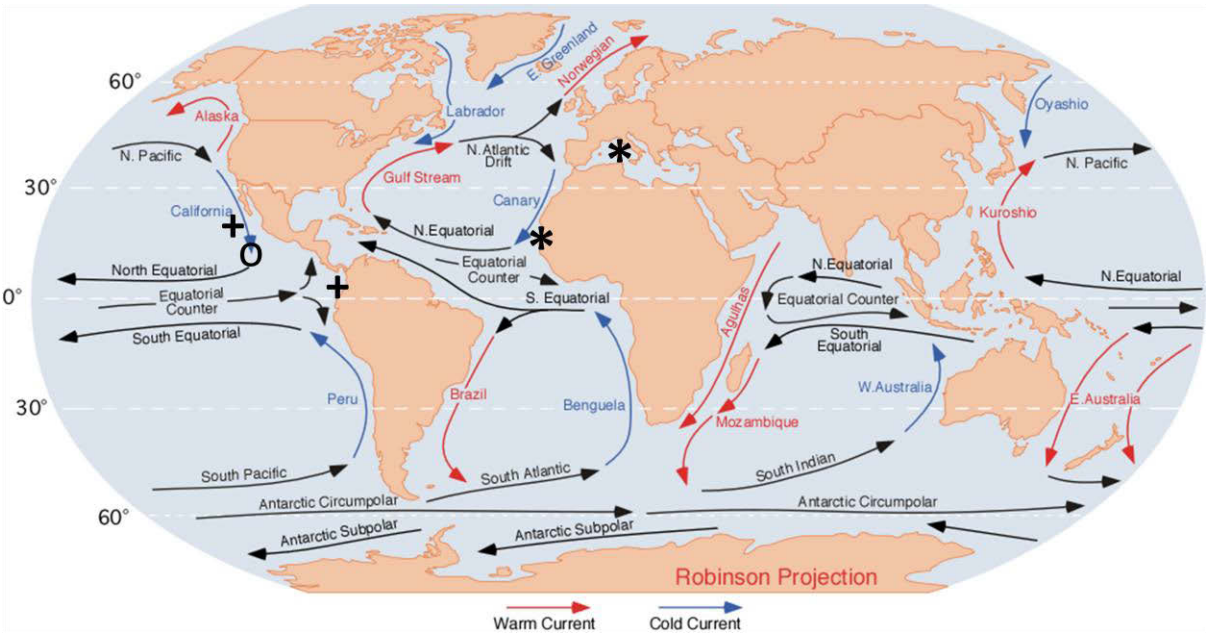


Figure 50. Distribution pattern of *Pseudocnus* species. (Map extracted from http://www.physicalgeography.net/fundamentals/images/oceancurrents.gifaccessed 02/02/2015). **Key**: **Pseudocnus koellikeri* (Semper, 1868), + *Pseudocnus curatus* (Cowles, 1907), O *Pseudocnus lubricus* (Clark, 1901).

Pseudocnus was formerly known to be a cosmopolitan genus but now appears to be restricted to the northern hemisphere, particularly the North-East (NE) Pacific and the North-East (NE) Atlantic, including the west Mediterranean region of Briggs (1974) (Figure 50). Of the three species currently remaining in *Pseudocnus*, one (the type species) occurs in the Mediterranean Sea and the NE Atlantic Ocean, whereas the other two on the west coast of Central America (Figure 50). This suggests the restriction of the genus to warm temperate and Mediterranean regions. The occurrence of *Pseudocnus curatus* (Cowles, 1907) in Columbia may be due to the California Current flowing southwards from California to Costa Rica. This current can transport flotsam, sea weeds, etc. on which the species may become attached and be transported southwards or individuals can become attached to bottom of boats and transported in this manner. *Pseudocnus koellikeri* has been recorded from the Mediterranean Sea by Semper (1868) and Théel (1886). Koehler (1921) recorded it from Naples and Sicily. Hérouard (1929) recorded the species from the Atlantic coast of Morocco and from Mauritania. Its horizontal distribution is now extended to Senegal (see Figure 50). The occurrence of *P. koellikeri* on the north-west African coast may be the result of the Canary Current that flows southwards parallel to the northern coast of Africa carrying the weeds, flotsam, etc.

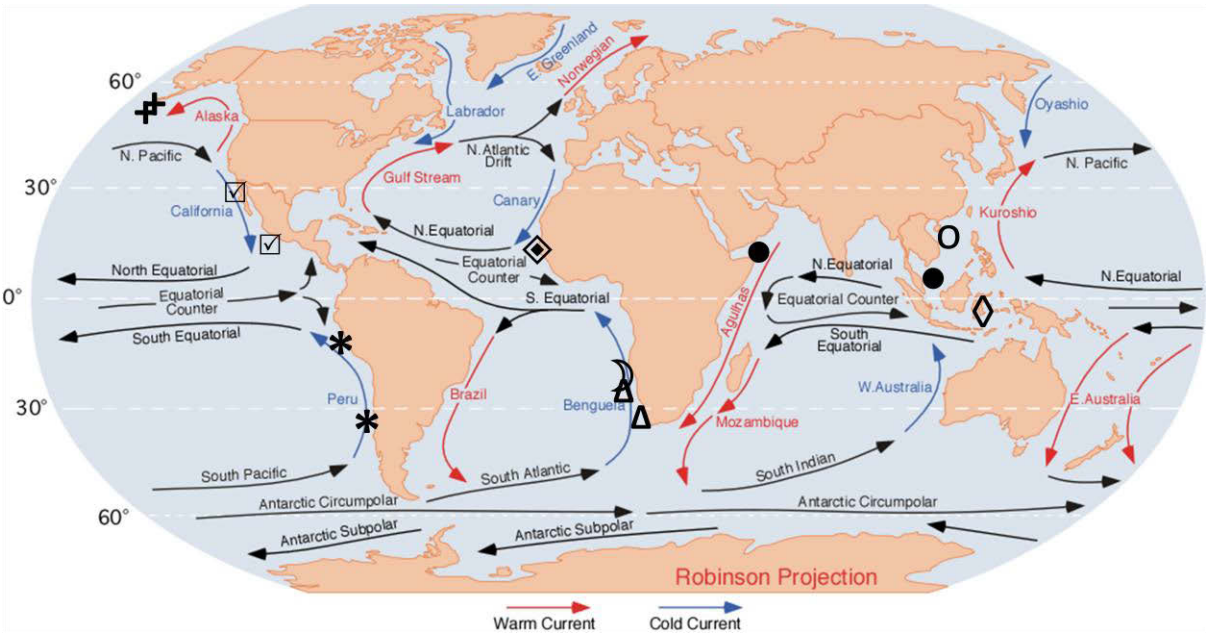


Figure 51. Distribution pattern of *Panningocnus* n. gen. species. (Map extracted from http://www.physicalgeography.net/fundamentals/images/oceancurrents.gif - access date 02/02/2015). **Key**:**Panningocnus dubiosus* (Semper, 1868);● *P. echinatus* (Von Marenzeller,1881); + *P. lamperti* (Ohshima, 1915); O *P. spinosus* (Ohshima, 1915) ; Δ *P. thandari* (Moodley, 2008); ◊ *P. salmini* (Ludwig, 1875) ; ◈ *Panningocnus* sp. nov.; ☽ *P. africanus* (Britten, 1910); ☑ *P. californicus* (Semper, 1868).

Panningocnus species are distributed in various regions of the world *viz*. the Indo-West Pacific Region of Clark & Rowe (1971), East Pacific Region, including the California Region, and the Eastern Pacific Boreal region, and the West Atlantic Region of Briggs (1974) (see Figure 51).

Panningocnus dubiosus has been recorded by many authors from Peru (type locality) and Chile. The occurrence of *P. dubiosus* in Peru might be due to its transportation by flotsam or the bottom of boats, ships, etc, or by way of the South Pacific Currrent flowing northwards along the Chilean coast. Equatorial Counter Current which flows from the west to the east of northern South America and which then deflects southwards will be affected in its southwards flow by the South Pacific current and may not have been responsible for transporting the species southwards from Peru to Chile. *P. dubiosus* appears endemic to the west South American region, i.e. the Peru-Chilean Province of Briggs (1974).

Panningocnus echinatus is found in the Indo-West Pacific region, in Korea, Japan and Red Sea, but its South African record is questionable (see Remarks under this species). The species hence appears to be restricted to the Indo-West Pacific region of Briggs (1974), Clark & Rowe (1971) and Ekman (1967). *P. lamperti* is endemic to the Aleutian province of the Eastern Pacific Boreal region. Its occurrence here on the Alaskan Peninsula and not

elsewhere is probably due to its adaptations to living in extremely cold water conditions. *P. thandari* is found in the south West Atlantic province of the Western Atlantic region of Briggs (1974), it is possible that this cold water (cold temperate) species originated on the west coast of South Africa and was perhaps transported by the Benguela Current or other means eg. flotsam, etc. as far northwards as Northern Namibia but not beyond into the subtropical waters of Angola. *P. spinosus* appears endemic to the Japan province of Briggs (1974). *P. salmini* has only been recorded from Indonesia in the Indo-West Pacific region. *P. africanus*, recorded once only, like *P. thandari* is found in the South West Atlantic province of the Western Atlantic region whereas *Panningocnus* sp is found further north in the North-East Atlantic region of (Briggs 1974). Both species are perhaps synonymous but require further records. *Panningocnus californicus* was first recorded by Semper (1868) from California and subsequently from other areas such as Mexico, Central America (Costa Rica), Mazatlan, Sinaloa, Gulf of California (Deichmann 1941). It appears to be a subtropical species endemic to the California Region in the Cortez province of Briggs (1974).

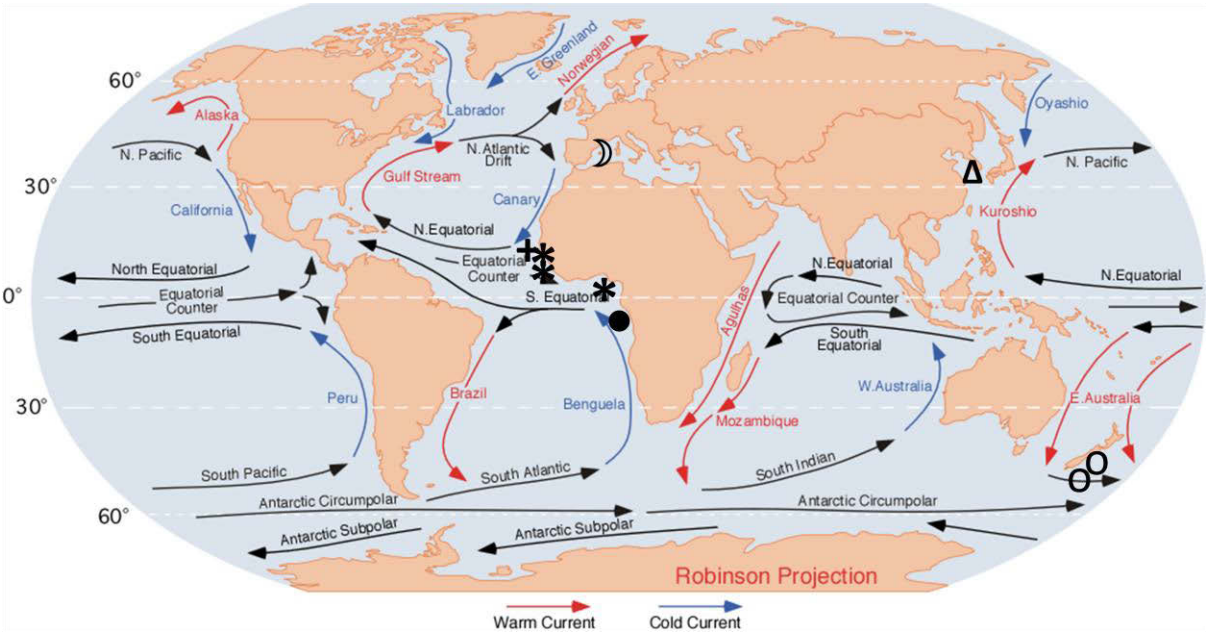


Figure 52. *Thandarocnus* n. gen. species distribution (Map extracted from http://www.physicalgeography.net/fundamentals/images/oceancurrents.gif - access date 02/02/2015) **Key**:● *Thandarocnus. rhopalodiformis* (Heding, 1943); + *T. rugosus* (Cherbonnier, 1957); O *T. sentus* (O'Loughlin & Alcock, 2000); Δ *T. pawsoni* (Won & Rho, 1998); ☽ *T. Grubei* (Marenzeller, 1874); * *T. goreensis* (Cherbonnier, 1949).

Thandarocnus species are distributed in two separate regions, i.e, North and South Atlantic; and North and South Pacific. *T. pawsoni* has only been recorded from Korea in the

Indo-Western Pacific Region of Ekman (1967) and Clark & Rowe (1971) (see Figure 52). *T. rugosus* (Cherbonnier, 1957) has only been recorded from the Western African province in the Eastern Atlantic Region of Briggs (1974). *T. grubei* (von Marenzeller, 1874) was recorded by Marenzeller (1974) from Adriatic Sea. Hence WoRMS records its distribution as the Mediterranean Sea. The species appears to be restricted to the warm temperate region of the Northern Hemisphere (in the Mediterranean Atlantic Region of Briggs 1976) in the Lusitania province, and has not been recorded elsewhere. O'Loughlin (2012) listed the horizontal distribution of *T. sentus* as New Zealand, Steward Island, Paterson inlet, and New Zealand Bay. The species is endemic to the Southern New Zealand Region in Cookian Province of Briggs 1974. *T. rhopalodiformis*, on the other hand, is endemic to the West Atlantic province of the Western Atlantic region of Congo (type locality). *T. goreensis* was described by Cherbonnier (1949) from Senegal (Type locality). It is now known to be distributed only as far south as Sierra-Leon.

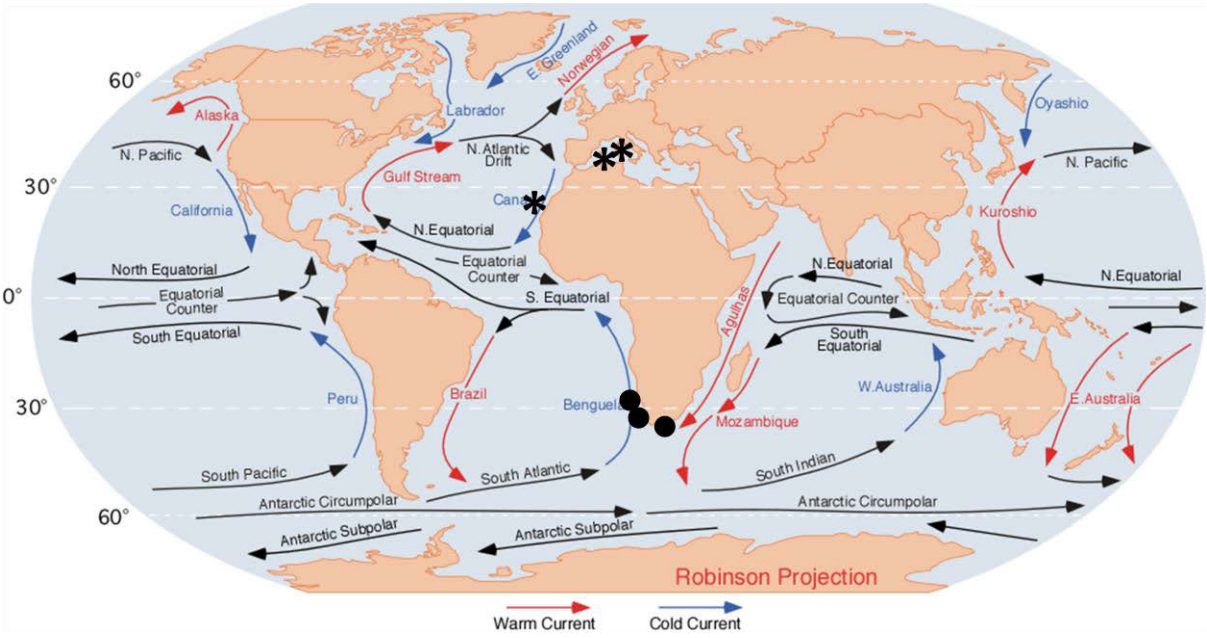


Figure 53. *Hemiocnus* n. gen. species distribution map (extracted from http://www.physicalgeography.net/fundamentals/images/oceancurrents.gif - access date 02/02/2015). **Key:** **Hemiocnus syracusanus* (Grube, 1840); ● *H. insolens* (Théel, 1886).

Hemiocnus syracusanus is endemic to the Warm Temperate region of the Northern Hemisphere (the Mediterranean-Atlantic Region of Briggs 1974), extending to off west coast

of North-West Africa. This extension in horizontal distribution might be due to the Canary Current which flows southwards parallel to the west coast of Africa (Figure 53). This current may carry some young or adult individuals attached flotsam (Thandar 1989; Ekman 1967) or they may be transported on the bottom of boats to which they attach themselves. *H. insolens* is endemic to the South East Atlantic and South West Indian Ocean waters of southern Africa Namibian and Namaquan Provinces (Cold Temperate) and the Agulhas (Warm Temperate) Province of southern Africa) and has not yet been recorded outside these.

CONCLUSION AND RECOMMENDATIONS

A critical revision of those species still remaining in *Pseudocnus* after O'Loughlin *et al*.'s (2014) revision of the Antarctic-Subantarctic species has been attempted. The genus, as diagnosed by O'Loughlin *et al*. (2014), is now restricted to species with only 10 equal tentacles and knobbed, single-layered, plates as calcareous deposits in the body wall, accompanied by knobbed buttons. Following O'Loughlin *et al*. (2014) *Cucumaria koellikeri* Semper, 1868 is reinstated as type species of the genus despite Panning's re-designation of *Cucumaria dubiosa* as the type species in 1962.

A new genus *Panningocnus* is erected with *Cucumaria dubiosa* Semper, 1868 as type species, to accommodate those species with unequal (8+2) tentacles and also pine-cone-shaped plates made up of a single layer of calcareous material in the body wall. *Cucumaria leonina* var. *africana* Britten, 1910 is raised out of synonymy with *Pseudocnella insolens* as was done by Panning (1962) who described it as a valid subspecies *viz*. *Pseudocnus dubiosus africanus*. It is here re-assigned to *Panningocnus*. In the latter genus buttons may be present or absent and because of this, the presence of plates with elongated spine(s) and the restriction or scattering of tube feet this genus can be further split but this is avoided here in order to restrict the number of new taxa.

Another new genus *Thandarocnus* with *Pseudocnus sentus* O'Loughlin & Alcock 2000 as type species is also erected to accommodate those species also with unequal tentacles (8+2), but with multilayered plates in the body wall in addition to those that are single-layered. Following O'Loughlin (pers. comm. & O'Loughlin *et al*. 2015.) *Laevocnus* O'Loughlin 2014 is now replaced by *Pentactella* Verrill, 1876, a genus resurrected out of synonymy of *Stereoderma,* by O'Loughlin himself, together with its type species *Cucumaria laevigata* (see Panning 1949). It is hoped that molecular characters will in future support the new classification here proposed.

Both molecular and morphological examinations were performed to test the assignment of species to *Pseudocnella* by Thandar (1987) and it was found that *C. insolens* does not strictly belong in *Pseudocnella* and on morphological evidence not even *P. sinorbis*. Both these species are herein re-assigned to the new genus *Hemiocnus,* with *Cladodactyla syracusana* as type species (Mjobo & Thandar, under review) since they share many characteristic features. Both morphological and molecular techniques appeared to be useful tools in quantifying the classification and assignment of *Pseudocnella* species.

It is regretted that due to time constraints morphometry of the body wall ossicles and cladistic analyses of morphological characters to determine phylogeny were not performed to test the validity of the new taxa, nor any molecular examination of species of all the species of *Pseudocnus* due to the unavailability of fresh materials as only two species are southern African with one not found again since its description in 1910.

A brief section on zoogeography is included explaining why dendrochirotids show restricted distributional patterns due to the lack of a free-swimming larval stage and specialised feeding habits, with preference for cold nutrient-rich waters. The distributions of all species dealt with in this thesis are mapped and discussed.

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Appendix A. Status of the species included in this work.

Nominal species	**Current status**	**Disposition (changes) herein**
*Cucumaria dubios*a Semper, 1868	*Pseudocnus dubiosus* (Semper, 1868) by Panning 1949	*Panningocnus dubiosus* (Semper, 1868)
Cucumaria grubei Von Marenzeller, 1874	*Pseudocnus grubei* (Von Marenzeller, 1874) by Panning 1949	*Panningocnus grubei* (Von Marenzeller, 1874)
Cucumaria leonina Semper, 1867	*Laevocnus leoninus* (Semper, 1868) by O'Loughlin *et al*. (2014)	*Pentactella leonina* (Semper, 1868)
Cucumaria. leonina var. *africana* Britten, 1910	*Pseudocnus leoninus* var. *africanus* (Britten, 1910) by Panning 1962 and in Thandar & Rambaran 2015 (passim)	*Panningocnus africanus* (Britten, 1910)
Cucumaria rhopalodiformis Heding, 1943	*Pseudocnus rhopalodiformis* (Heding, 1943) in WoRMS and O'Loughlin *et al*. (2014)	*Thandarocnus rhopalodiformis* (Heding, 1943)
Cucumaria sykion Lampert, 1885	*Pseudocnella sykion* (Lampert, 1885) by Thandar, 1987	No changes
Cucumaria echinata Von Marenzeller, 1881	*Pseudocnus echinatus* (Von Marenzeller, 1881) by Panning, 1949	*Panningocnus echinatus* (Von Marenzeller, 1881)
Cucumaria grubei Von Marenzeller, 1874	*Pseudocnus grubei* (Von Marenzeller, 1874) by Panning, 1949	*Thandarocnus grubei* (Von Marenzeller, 1874)
Pentactella laevigata Verril, 1876	*Laevocnus laevigatus* (Verril, 18 6) by O'Loughlin *et al*. (2014)	*Pentactella laevigata* Verril, 1876
Cucumaria cornuta (Cherbonnier, 1941),	*Laevocnus cornutus* (Cherbonnier, 1941)	*Pentactella cornuta* (Cherbonnier, 1941)

	O'Loughlin *et al*. (2014)	
Cucumaria leoninoides (Mortensen, 1925)	*Laevocnus leoninoides* (Mortensen, 1925) by O'Loughlin *et al*. (2014)	*Pentactella leoninoides* (Mortensen, 1925)
Cucumaria californica (Semper, 1868)	*Pseudocnus californicus* (Semper, 1868) by Panning, 1949	*Panningocnus californicus* (Semper, 1868)
Cucumaria lamperti Ohshima, 1915	*Pseudocnus lamperti* (Ohshima, 1915) in WoRMS and by O'Loughlin *et al*. (2015)	*Panningocnus lamperti* (Ohshima, 1915)
Cucumaria curata Cowles, 1907	*Pseudocnus curatus* (Cowles, 1907) by Lambert 1997	No changes
Cucumaria koellikeri (Semper, 1868)	*Pseudocnus koellikeri* (Semper, 1868) by Panning 1949	No changes
Cucumaria lubrica Clark, 1901	*Pseudocnus lubricus* (Clark, 1901) in WoRMS and O'Loughlin *et al*. (2014)	No changes
Pseudocnus thandari Moodley, 2008	*Pseudocnus thandari* Moodley, 2008	*Panningocnus thandari* (Moodley, 2008)
Cucumaria salmini Ludwig, 1875	*Pseudocnus salmini* (Ludwig, 18 5) by O'Loughlin *et al*. (2014)	*Panningocnus salmini* (Ludwig, 1875)
Pseudocnus sp. indet. Massin, 1993	*Pseudocnus* sp. indet. Massin, 1993	*Panningocnus* sp. indet. (Massin, 1993)
Cucumaria intermedia Théel, 1886	*Laevocnus intermedius* Théel, 1886 (O'Loughlin *et al*. (2014)	*Pentactella intermedia* (Théel, 1886)
Cucumaria marionensis Théel, 1886	*Laevocnus marionensis* (Théel, 1886) by O'Loughlin *et al*. (2014)	*Pentactella marionensis* (Théel, 1886)

Cucumaria serrata Theél, 1886	*Laevocnus serratus* ((Theél, 1886) by O'Loughlin *et al*. (2014)	*Pentactella serrata* (Théel, 1886)
Cucumaria rugosa Cherbonnier, 1957	*Pseudocnus rugosus* (Cherbonnier, 1957) by Panning, 1949	*Thandarocnus rugosus* (Cherbonnier, 1957)
Pseudocnus pawsoni Won & Rho, 1998	*Pseudocnus pawsoni* (Won & Rho, 1998)	*Thandarocnus pawsoni* (Won & Rho, 1998)
Pseudocnus sentus O`Loughlin and Alcock, 2000	*Pseudocnus sentus* O`Loughlin and Alcock, 2000	*Thandarocnus sentus* (O'Loughlin & Alcock, 2000) type specie (this paper)
Cucumaria sinorbis Cherbonnier, 1952	*Pseudocnella sinorbis* (Cherbonnier, 1952) by Thandar 1987	No changes
Cladodactyla syracusana Grube, 1840	*Pseudocnella syracusana* (Grube, 1840) by Thandar, 1987	*Hemiocnus syracusanus* (Grube, 1840)
Hemioedema goreensis Cherbonnier, 1949	*Pseudocnus goreensis* (Cherbonnier, 1949) by Panning, 1949	*Thandarocnus goreensis* (Cherbonnier, 1949)
Cucumaria insolens Théel, 1886	*Pseudocnella insolens* (Théel, 1886) by Thandar 1987	*Hemiocnus insolens* (Théel, 1886)