

A review of pygal-furrowed Synallactidae (Echinodermata: Holothuroidea), with new species from the Antarctic, Atlantic and Pacific oceans

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Abstract

O'Loughlin, P.M., and Ahearn, C. 2005. A review of pygal-furrowed Synallactidae (Echinodermata: Holothuroidea), with new species from the Antarctic, Atlantic and Pacific oceans. *Memoirs of Museum Victoria* 62(2): 147–179.

We review the genera and species of pygal-furrowed Synallactidae and describe new species from the collections of the United States National Museum of Natural History (Smithsonian Institution). *Meseres* Ludwig is reviewed and placed incertae sedis. *Molpadiodemas* Heding and *Pseudostichopus* Théel are rediagnosed. *Platystichopus* Heding is declared a junior synonym of *Molpadiodemas*. *Filithuria* Koehler and Vaney and *Peristichopus* Djakonov are declared junior synonyms of *Pseudostichopus*. Lectotypes are designated for: *Meseres involutus* Sluiter, *M. macdonaldi* Ludwig, *M. peripatus* Sluiter, *Pseudostichopus globigerinae* Hérouard, *P. mollis* Théel, *P. pustulosus* Sluiter, *P. trachus* Sluiter, *P. villosus* Théel. A neotype is designated for *Pseudostichopus nudus* Ohshima.

Except for the type species, *Meseres macdonaldi* Ludwig, and *Meseres* (?) *torvus* (Théel), all species previously referred to *Meseres* are reassigned to *Molpadiodemas* or *Pseudostichopus*. *Meseres* (?) *torvus* (Théel) is retained in its original combination. Eleven new synallactid species are described: *Molpadiodemas constrictus*, *M. crinitus*, *M. epibiotus*, *M. helios*, *M. morbillus*, *M. neovillosus*, *M. pediculus*, *M. porphyrus*, *M. translucens*, *M. ustulatus* and *Pseudostichopus tuberosus*. *Molpadiodemas constrictus* is fissiparous. *Pseudostichopus villosus* var. *violaceus* Théel is raised to species status; *Pseudostichopus alatus* Imaoka, *P. trachus* Sluiter and *P. nudus* Ohshima are junior synonyms of *Pseudostichopus mollis* Théel; *Pseudostichopus globigerinae* Hérouard and *P. dilatorbis* Imaoka are junior synonyms of *Meseres* (= *Molpadiodemas*) *involutus* Sluiter; *Pseudostichopus propinquus* Fisher and *P. lapidus* Hérouard are junior synonyms of *Meseres* (= *Pseudostichopus*) *peripatus* Sluiter; and *Pseudostichopus arenosus* Ohshima and *P. molpadioides* Ohshima are junior synonyms of *Meseres* (= *Pseudostichopus*) *hyalegerus* Sluiter.

New combinations are: *Molpadiodemas atlanticus* (Perrier), *M. depressus* (Hérouard), *M. involutus* (Sluiter), *M. pustulosus* (Sluiter), *M. villosus* (Théel), *Pseudostichopus elegans* (Koehler and Vaney), *P. hyalegerus* (Sluiter), *P. papillatus* (Djakonov), *P. peripatus* (Sluiter) and *P. spiculiferus* (O'Loughlin). Other species discussed are: *Molpadiodemas violaceus* (Théel), *Pseudostichopus aemulatus* Solís-Marín and Billett, *P. echinatus* Thandar, *P. mollis* Théel, *P. occultatus* Marenzeller, and *P. profundi* Djakonov. A key is provided for the species of *Molpadiodemas* and *Pseudostichopus*. Tables are provided of genera and subgenera with current systematic status, and species with original and current combinations.

Introduction

We report on the United States National Museum of Natural History (Smithsonian Institution) collections of synallactid holothurian species from the Atlantic, Pacific and Antarctic oceans. Only pygal-furrowed genera are dealt with. The pygal-furrowed synallactids substantially lack body wall ossicles and have a distinct pygal (posterior) vertical furrow.

Pygal-furrowed synallactids in the USNM collections comprise 345 catalogued lots (several thousand specimens) from a variety of sources. Operation Deep Freeze (USS *Edisto*) and the United States Antarctic Program (under the auspices of the

National Science Foundation, Office of Polar Programs) contributed about 47 % of the lots (research vessels USNS *Eltanin*, now the ARA *Islas Orcadas*; RV *Hero*; USCGS *Eastwind*). Between the years 1884 and 1911, the United States Fish Commission mounted expeditions to the North-west Pacific, Philippines, Hawaii, eastern Pacific, California coast, lower California and western Atlantic, and provided material (USFCS *Albatross*). When the USFC became the United States Bureau of Fisheries, cruises were conducted throughout the western Atlantic that contributed several lots from a 1970 cruise to the Gulf of Mexico (RV *Oregon II*). The Fish Commission, and later the Bureau of Fisheries, contributed about 21% of the lots.

About 12% of the lots were provided by the Ocean Minerals Company from a benthic sampling and photographic survey of the Clarion-Clipperton Fracture Zone in the eastern central Pacific during 1978-1980 (RV *Governor Ray*).

The remaining 20% of lots were donated by various institutions, universities and agencies. A significant contribution of two new species described herein (*Molpadiodemas epibiotus* and *M. constrictus*) was made by the University of Miami from cruises in 1973 and 1975 to the Puerto Rico and Cayman Trenches (RV *Gilliss*). The Southampton Oceanographic Centre (now National Oceanographic Centre) surveys of the Western European Basin in 1979 (RV *Challenger*) and Porcupine Abyssal Plain in 1999 (RV *Discovery*) added two lots which included paratypes of the recently described *Pseudostichopus aemulatus*. Thirty lots were contributed by Oregon State University from survey cruises off the coast of Oregon in the 1960s and 1970s (RV *Commando*, RV *Cobb*, RV *Yaquina*, RV *Cayuse*). The Smithsonian Oceanographic Center, supporting the International Indian Ocean Expedition and the Southeast Pacific Benthic Oceanographic Program, added 8 lots from cruises during the 1960s to Thailand and many south-eastern Pacific localities (RV *Anton Bruun*, RV *Te Vega*). Six lots were contributed by the Woods Hole Oceanographic Institute following cruises off Argentina in 1960 (RV *Atlantis II*), to the West European Basin in 1972 (RV *Chain*), and to the North American Basin in 1973 (RV *Knorr*). Several lots were added by the Virginia Institute of Marine Science cruises to the Bahamas in 1978, 1980, and 1981 (RV *Columbus Iselin*). Texas A&M University provided one lot from a 1972 cruise to the Gulf of Mexico (RV *Alaminos*). Three lots were provided by the US Bureau of Land Management surveys off South Carolina in 1985 (RV *Cape Hatteras*), and off Louisiana during the Northern Gulf of Mexico Continental Shelf project. Fourteen lots were donated by M.D. Richardson from a survey of the Venezuelan Basin in 1981 (RV *Bartlett*). One lot was donated by the Vienna Royal Imperial Natural History Museum from a survey of the eastern Mediterranean from 1890-1894 (HMS. *Pola*). Two lots were recently donated by Dr Tohru Imaoka (ex-Seto Marine Laboratory and Faculty of Science at the Kyoto University in Shirahama), one lot by Dr Ken Smith (Scripps Institution of Oceanography) and another two lots by Dr David Stein (Systematics Laboratory, National Oceanographic and Atmospheric Administration). Two lots have insufficient information as to the source of the material.

During April 2002, Mark O'Loughlin visited the Natural History Museum in London and the Zoölogisch Museum at the University of Amsterdam, and designated most of the lectotypes selected in this work. The scanning electron microscopy and most of the digital imaging were done by Cynthia Ahearn. We collaborated on systematic observations and decisions.

Because the ossicles in each pygal-furrowed synallactid species do not have a consistent form and frequently vary considerably, the SEM images selected for each species do not represent the full range of forms. They should be viewed in conjunction with the text description of forms and sizes.

In the diagnosis of *Meseres* by O'Loughlin (2002), reference was made to thin tubular appendages which are rhizomatous and sometimes branched. It is judged here that

these are epibiotas, and not holothurian appendages and not species specific.

Abbreviations for institutions are: AM, Australian Museum, Sydney; BMNH, The Natural History Museum, London; MNHN, Muséum National d'Histoire Naturelle, Paris; MOM, Musée océanographique de Monaco; NMV, Museum Victoria, Australia; OMNH, Osaka Museum of Natural History, Japan; RAS, Russian Academy of Sciences, St. Petersburg, Russia; SAM, South Africa Museum, Cape Town; SMBL, Seto Marine Biological Laboratory, Kyoto University, Japan; TM, Tasmanian Museum, Hobart; UNAM, Universidad Nacional Autonoma de Mexico; USNM, US National Museum of Natural History, Smithsonian Institution, Washington; ZMA, Zoölogisch Museum, Amsterdam; ZMUC, Zoological Museum, University of Copenhagen, Denmark.

Historically, three types of registration number have been used for USNM material, and occur in this report. Prior to 1920, museum catalogue numbers without a prefix were used. In 1920, A.H. Clark began a dedicated echinoderm numbering system with the prefix E before the registration number. Since 2001, the EMU on-line system is used, and registrations reported without an E prefix.

Throughout this paper Rowe (in Rowe and Gates, 1995) is referred to as Rowe (1995). Descriptions and measurements refer to preserved material.

History of USFCS *Albatross* 1906 material

Numerous holothurian types and other material collected in the north-west Pacific during the summer of 1906 by the USFCS *Albatross* cannot be located. Correspondence in the National Museum of Natural History's Registrar Office indicates that the final dispository of the material was to be the Smithsonian Institution. After the death of Dr Kakichi Mitsukuri (1909) the United States Bureau of Fisheries transferred the holothurians to his graduate student Mr Hiroshi Ohshima. He judged 46 of the 95 species and one subspecies to be new, and requested USNM catalog numbers for the type specimens for inclusion in his manuscript. The results of this study were published (Ohshima, 1915), but the specimens were not returned at the time (possibly due to World War I). In 1938, the Director of the Zoological Institute of the Tokyo Imperial University, Naohide Yatsu, discovered this collection stored in a cellar. Yatsu corresponded with Alexander Wetmore, then Assistant Secretary of the Smithsonian Institution, informing him of the holothurian collection and seeking advice as to the best way to ship the material. In April 1938 the holothurian collection in four wooden crates was transported on the *Kwansai Maru* via the Panama Canal to New York. In correspondence dated 10 June, 1938, Alexander Wetmore acknowledged receipt of the four crates in good condition.

The four crates should have been delivered to Dr Arthur H. Clark, curator of the Echinoderm Division in the NMNH. Some material was in fact returned and is now in the echinoderm collection. The fate of the remaining material is unknown. Archives have been searched for official memoranda, curators of other departments contacted, and the Natural History Museum basement and attic searched without success. Dr

Frederick M. Bayer, curator and research scientist of the Coelenterata collection, knew Dr Clark and recalled that he had many unpacked boxes in his office and that some were probably discarded.

Key to species of pygal-furrowed Synallactidae

(The generic assignment of *Pseudostichopus profundi* Djakonov is unresolved. The species is distinguished by the unique presence of curved mesh-like narrow plates in the tube feet.)

1. Tube feet not in prominent series on paired radii; longitudinal muscles flat, broadly attached to internal body wall; gonad tubules arising from common source at end of gonoduct, branched *Molpadiodemas* Heding 2
 - Tube feet or papillae in prominent series on paired radii; longitudinal muscles cylindrical, narrowly attached to internal body wall; gonad tubules in series along gonoduct, unbranched *Pseudostichopus* Théel 17
2. Tube feet hair-like or thin, thread-like 3
 - Tube feet cylindrical, prominent or inconspicuous 4
3. Body lacking brim; tube feet hair-like, over whole body, sometimes matted ventrally, anteriorly, pygally, frequently withdrawn ventrally; tentacle ossicles never plate-like rods with close fine spines *Molpadiodemas villosus*
 - Body with rounded lateral brim, sometimes with pustulose bulges; tube feet soft, flaccid, thread-like, sometimes matted on small specimens, readily lost with outer body layer; tentacle ossicles include wide plate-like rods with close fine spines *Molpadiodemas porphyrus*
4. Body with one, sometimes two, deep transverse constrictions; no tentacle ossicles *Molpadiodemas constrictus*
 - Body lacking deep transverse constrictions; tentacle ossicles present 5
5. Body typically with one or two concave depressions created by epibiotic attachments; body strongly posteriorly tapered; tentacle ossicles include thin, lumpy rods *Molpadiodemas epibiotus*
 - Body lacking concavities; body not strongly posteriorly tapered; tentacle ossicles not including thin lumpy rods 6
6. Ventrolateral margin with distinct raised protuberances 7
 - Ventrolateral margin lacking distinct raised protuberances 8
7. Margin serrated by transverse creasing of body; ventrolateral protuberances lacking tufts of tube feet; body wall wrinkled, with small digitate projections on low reticulate ridges; tentacle ossicles include rods; body typically encrusted with globigerines or small stones *Molpadiodemas involutus*
 - Ventrolateral margin with pustules surmounted by nipple-like protuberances; tube feet in tufts on posterior pustules; body wall not wrinkled, lacking low reticulate ridges; tentacle ossicles lace mesh only; some globigerine attachments *Molpadiodemas pustulosus*
8. Body wall thin, translucent; gonad ossicles predominantly thin lace mesh, not developed along primary rods *Molpadiodemas translucens*
 - Body wall not translucent; gonad ossicles, if present, not predominantly thin lace mesh, if mesh, developed along primary rods 9
9. Body wall thick, gelatinous; ventrolateral brim thick, rounded *Molpadiodemas depressus*
 - Body wall not thick, gelatinous; lacking thick, rounded brim 10
10. Cylindrical tube feet concentrated in conspicuous ventrolateral band; frequently contiguous, matted ventrolaterally 11
 - Tube feet not contiguous or matted ventrolaterally 13
11. Tube feet typically 2.0 mm long, 0.4 mm diameter; frequently tubercles and divided pygal lobes posteriorly *Molpadiodemas crinitus*
 - Tube feet typically less than 2.0 mm long, 0.4 mm diameter; lacking posterior tubercles and divisions of pygal lobes 12
12. Body short, diameter large (about 2:1); tube feet typically 1.6 mm long, 0.3 mm diameter; longitudinal muscles wide; gonad ossicles long, thin rods *Molpadiodemas neovillosus*
 - Body elongate, diameter small (about 5:1), long tapers distally; tube feet typically 1.0 mm long, 0.25 mm diameter; longitudinal muscles narrow; lacking gonad ossicles *Molpadiodemas pediculus*
13. Tube feet cylindrical, most evident as lateral band, not matted 14
 - Tube feet around body, not more evident as lateral band 15
14. Tube feet dark reddish brown creating a lateral spotted appearance; lacking gonad ossicles *Molpadiodemas morbillus*
 - Whole body dark brown, scorched appearance; gonad ossicles present *Molpadiodemas ustulatus*
15. Tube feet soft, scattered, lying all over body in larger specimens, sometimes erect orally and pygally; tentacles with large, conical, pointed peripheral digits *Molpadiodemas helios*
 - Tube feet not soft, scattered, lying all over body in larger specimens; tentacle digits not large, conical, pointed 16
16. Even cover of small tube feet, frequently in pits or not evident, cylindrical and firm if extended; tentacle ossicles lacking knob-like central swelling; high frequency of gonad ossicles comprising rods with extensive lateral mesh *Molpadiodemas atlanticus*
 - Even cover of small, soft, cylindrical tube feet, evident only on small specimens, never erect; many tentacle ossicles with knob-like central swelling; rare presence of gonad ossicles *Molpadiodemas violaceus*
17. Body densely encrusted with sponge spicules or globigerines or shells or small stones 18
 - Body not encrusted with attachments 22
18. Body covered predominantly with dense mat of sponge spicules 19
 - Body covered predominantly with globigerines (foraminiferans) or shells or stones 20
19. Large dense mesh ossicles in pygal lobes; lacking gonad ossicles *Pseudostichopus hyalegerus*

- Lacking mesh ossicles in pygal lobes; gonad ossicles include complex branching rods *Pseudostichopus spiculiferus*
- 20. Predominantly pointed shells with globigerines and sand cover; closely knobbed tentacle rod ossicles; lacking ossicles in gonads *Pseudostichopus echinatus*
- Predominantly globigerine or small stone cover; tentacle ossicles not closely knobbed rods; ossicles frequently in gonads 21
- 21. Ossicles in pygal lobes and respiratory trees; pygal lobe ossicles irregular perforated plates, sometimes double layered *Pseudostichopus occultatus*
- Lacking ossicles in pygal lobes and respiratory trees *Pseudostichopus peripatus*
- 22. Body with radial series of tubercles ventrolaterally or on paired radii 23
- Body lacking radial series of tubercles 24
- 23. Double series of tubercles on paired radii; ossicles present in papillae, lacking in gonads . *Pseudostichopus papillatus*
- Single series of lateroventral tubercles; ossicles in gonads, lacking in tube feet *Pseudostichopus tuberosus*
- 24. Paired radii with long tapering papillae (frequently more than 10 mm long) *Pseudostichopus elegans*
- Paired radii with short tapering papillae (up to 5.0 mm long) 25
- 25. Ossicles in tube feet, perianally, lacking in gonads *Pseudostichopus mollis*
- Ossicles in gonads, lacking perianally and in tube feet *Pseudostichopus aemulatus*

Order Aspidochirotida Grube, 1840

Synallactidae Ludwig, 1894

Table 2, Figure 1

Remarks. Although the Synallactidae (sensu lato) are characterized as deep-water forms that possess peltate tentacles, lack tentacle ampullae, have gonads in one or two tufts, and usually possess body wall ossicles (including tables and rods), this work embraces only those species of Synallactidae that substantially lack body wall ossicles, and have in addition a distinct pygal (posterior) vertical furrow. The pygal-furrowed Synallactidae are characterised by: a generally cylindrical body form; rounded anterior and posterior ends; ventral mouth and anus; presence of a pygal furrow; 18–20 peltate tentacles;

absence of tentacle ampullae; a complete cover of small and frequently inconspicuous tube feet; absence of retractor muscles; longitudinal muscles never divided; a solid calcareous ring; radial plates broader than high, anteriorly with a central notch and two central and two lateral low projections, posteriorly with a shallow smooth indentation and two pairs of "teeth" variably evident; interradial plates broad and low, anteriorly with a central spine, posteriorly with a smooth shallow indentation; madreporite sometimes evident externally on the anterior dorsal body surface; single, sac-like, elongate or short, ventral polian vesicle; gonad tubules in two groups, one on each side of the dorsal mesentery; respiratory trees comprising two long unequal branches of alveolar-like clusters along a central strap; ossicles absent from the body wall, but present in the pygal lobes in some species.

Body wall, pygal lobes, tube feet, tentacles, gonads, and respiratory trees were examined for ossicles in all species, and are reported only as found, not as absent. The colour of tentacles and internal anatomical features was noted throughout the study, and found to be not diagnostically reliable. The form of the peltate tentacles, which varies greatly with state of preservation, was found to be not diagnostically reliable. The presence or absence of "teeth" on the posterior indentation of the radial plates of the calcareous ring has been used diagnostically by some authors. This feature was found to be variable and subjective, and depended on the angle from which the plates were viewed. Descriptions of these features have been omitted.

The genera included in this paper have been shifted between the Gephyrothuriidae (now restricted after O'Loughlin, 1998) and Synallactidae (see O'Loughlin, 1998, 2002). In the *Zoological Catalogue of Australia* Rowe (1995) referred species of pygal-furrowed Synallactidae to the genera *Meseres* Ludwig, 1894 (incertae sedis below) and *Pseudostichopus* Théel, 1886 in the Gephyrothuriidae. Following the rediagnosis below of *Pseudostichopus* Théel, *Meseres peripatus* Sluiter, 1901 is reassigned to *Pseudostichopus*. Following examination of the AM collections by one of us (M.O'L), as far as the Australian fauna is concerned, Rowe (1995) correctly identified *Pseudostichopus mollis* Théel and *Pseudostichopus peripatus* (Sluiter) material, but wrongly identified some material as *Pseudostichopus pustulosus* Sluiter, 1901 (= *Molpadiodemas pustulosus* below). We judge that this material is *Pseudostichopus mollis*, and that *Molpadiodemas pustulosus* (Sluiter) is not to date represented in the Australian fauna.

Table 1. Index of genera and subgenera in paper, with current status including senior synonym.

| Genera and subgenera | Current status or senior synonym | Family |
|---|------------------------------------|----------------|
| <i>Filithuria</i> Koehler and Vaney, 1905 | <i>Pseudostichopus</i> Théel, 1886 | Synallactidae |
| <i>Meseres</i> Ludwig, 1894 | <i>Meseres</i> Ludwig, 1894 | Incertae sedis |
| <i>Molpadiodemas</i> Heding, 1935 | <i>Molpadiodemas</i> Heding, 1935 | Synallactidae |
| <i>Peristichopus</i> Djakonov, 1952 | <i>Pseudostichopus</i> Théel, 1886 | Synallactidae |
| <i>Platystichopus</i> Heding, 1940 | <i>Molpadiodemas</i> Heding, 1935 | Synallactidae |
| <i>Plicastichopus</i> Heding, 1940 | <i>Pseudostichopus</i> Théel, 1886 | Synallactidae |
| <i>Pseudostichopus</i> Théel, 1886 | <i>Pseudostichopus</i> Théel, 1886 | Synallactidae |
| <i>Trachostichopus</i> Heding, 1940 | <i>Pseudostichopus</i> Théel, 1886 | Synallactidae |

Table 2. Index of species in paper in original combination, and with current combination or senior synonym.

| Species in original combination | Current combination or senior synonym |
|---|--|
| <i>aemulatus</i> , <i>Pseudostichopus</i> , Sólís-Marin and Billett, 2004 | <i>Pseudostichopus aemulatus</i> , Sólís-Marin and Billett, 2004 |
| <i>acaudum</i> , <i>Molpadiodemas</i> , Heding, 1935 | <i>Molpadiodemas atlanticus</i> (Perrier, 1898) |
| <i>alatus</i> , <i>Pseudostichopus</i> , Imaoka, 1990 | <i>Pseudostichopus mollis</i> Théel, 1886 |
| <i>aleutianus</i> , <i>Pseudostichopus</i> , Ohshima, 1915 | <i>Pseudostichopus peripatus</i> (Sluiter, 1901) |
| <i>arenosus</i> , <i>Pseudostichopus</i> , Ohshima, 1915 | <i>Pseudostichopus hyalegerus</i> (Sluiter, 1901) |
| <i>atlanticus</i> , <i>Pseudostichopus</i> , Perrier, 1898 | <i>Molpadiodemas atlanticus</i> (Perrier, 1898) |
| <i>constrictus</i> , <i>Molpadiodemas</i> , sp. nov. | <i>Molpadiodemas constrictus</i> sp. nov. |
| <i>crinitus</i> , <i>Molpadiodemas</i> , sp. nov. | <i>Molpadiodemas crinitus</i> sp. nov. |
| <i>depressus</i> , <i>Pseudostichopus</i> , Hérouard, 1902 | <i>Molpadiodemas depressus</i> (Hérouard, 1902) |
| <i>dilatatorbis</i> , <i>Pseudostichopus</i> (<i>Pseudostichopus</i>), Imaoka, 1978 | <i>Molpadiodemas involutus</i> (Sluiter, 1901) |
| <i>echinatus</i> , <i>Pseudostichopus</i> , Thandar, 1992 | <i>Pseudostichopus echinatus</i> Thandar, 1992 |
| <i>elegans</i> , <i>Filithuria</i> , Koehler and Vaney, 1905 | <i>Pseudostichopus elegans</i> (Koehler and Vaney, 1905) |
| <i>epibiotus</i> , <i>Molpadiodemas</i> , sp. nov. | <i>Molpadiodemas epibiotus</i> sp. nov. |
| <i>globigerinae</i> , <i>Pseudostichopus</i> , Hérouard, 1923 | <i>Molpadiodemas involutus</i> (Sluiter, 1901) |
| <i>helios</i> , <i>Molpadiodemas</i> , sp. nov. | <i>Molpadiodemas helios</i> sp. nov. |
| <i>hyalegerus</i> , <i>Meseres</i> , Sluiter, 1901 | <i>Pseudostichopus hyalegerus</i> (Sluiter, 1901) |
| <i>ingolfi</i> , <i>Plicastichopus</i> , Heding, 1942 | <i>Pseudostichopus peripatus</i> (Sluiter, 1901) |
| <i>involutus</i> , <i>Meseres</i> , Sluiter, 1901 | <i>Molpadiodemas involutus</i> (Sluiter, 1901) |
| <i>japonensis</i> , <i>Pseudostichopus</i> , Imaoka, 1978 | <i>Pseudostichopus hyalegerus</i> (Sluiter, 1901) |
| <i>japonensis</i> , <i>Pseudostichopus</i> (<i>Trachostichopus</i>), Imoka, 1978 | <i>Pseudostichopus hyalegerus</i> (Sluiter, 1901) |
| <i>lapidus</i> , <i>Pseudostichopus</i> , Hérouard, 1923 | <i>Pseudostichopus peripatus</i> (Sluiter, 1901) |
| <i>macdonaldi</i> , <i>Meseres</i> , Ludwig, 1894 | <i>Meseres macdonaldi</i> Ludwig, 1894 |
| <i>marenzelleri</i> , <i>Pseudostichopus</i> , Hérouard, 1923 | <i>Pseudostichopus peripatus</i> (Sluiter, 1901) |
| <i>mollis</i> , <i>Pseudostichopus</i> , Théel, 1886 | <i>Pseudostichopus mollis</i> Théel, 1886 |
| <i>molpadioides</i> , <i>Pseudostichopus</i> , Ohshima, 1915 | <i>Pseudostichopus hyalegerus</i> (Sluiter, 1901) |
| <i>morbillus</i> , <i>Molpadiodemas</i> , sp. nov. | <i>Molpadiodemas morbillus</i> sp. nov. |
| <i>neovillosus</i> , <i>Molpadiodemas</i> , sp. nov. | <i>Molpadiodemas neovillosus</i> sp. nov. |
| <i>nudus</i> , <i>Pseudostichopus</i> , Ohshima, 1915 | <i>Pseudostichopus mollis</i> Théel, 1886 |
| <i>occultatus</i> , <i>Pseudostichopus</i> , Marenzeller, 1893 | <i>Pseudostichopus occultatus</i> Marenzeller, 1893 |
| <i>occultatus</i> var. <i>plicatus</i> , <i>Pseudostichopus</i> , Koehler and Vaney, 1905 | <i>Pseudostichopus peripatus</i> (Sluiter, 1901) |
| <i>papillatus</i> , <i>Peristichopus</i> , Djakonov, 1952 | <i>Pseudostichopus papillatus</i> (Djakonov, 1952) |
| <i>pediculus</i> , <i>Molpadiodemas</i> , sp. nov. | <i>Molpadiodemas pediculus</i> sp. nov. |
| <i>peripatus</i> , <i>Meseres</i> , Sluiter, 1901 | <i>Pseudostichopus peripatus</i> (Sluiter, 1901) |
| <i>porphyryus</i> , <i>Molpadiodemas</i> , sp. nov. | <i>Molpadiodemas porphyryus</i> sp. nov. |
| <i>profundi</i> , <i>Pseudostichopus</i> , Djakonov, 1952 | <i>Pseudostichopus profundus</i> Djakonov, 1952 |
| <i>propinquus</i> , <i>Pseudostichopus</i> , Fisher, 1907 | <i>Pseudostichopus peripatus</i> (Sluiter, 1901) |
| <i>pustulosus</i> , <i>Pseudostichopus</i> , Sluiter, 1901 | <i>Molpadiodemas pustulosus</i> (Sluiter, 1901) |
| <i>spiculiferus</i> , <i>Meseres</i> , O'Loughlin, 2002 | <i>Pseudostichopus spiculiferus</i> (O'Loughlin, 2002) |
| <i>tachimaruae</i> , <i>Pseudostichopus</i> (<i>Trachostichopus</i>), Imaoka, 1978 | <i>Pseudostichopus hyalegerus</i> (Sluiter, 1901) |
| <i>torvus</i> , <i>Stichopus</i> ?, Théel, 1886 | <i>Stichopus</i> ? <i>torvus</i> Théel, 1886 |
| <i>trachus</i> , <i>Pseudostichopus</i> , Sluiter, 1901 | <i>Pseudostichopus mollis</i> Théel, 1886 |
| <i>translucens</i> , <i>Molpadiodemas</i> , sp. nov. | <i>Molpadiodemas translucens</i> sp. nov. |
| <i>tuberculatus</i> , <i>Pseudostichopus</i> (<i>Trachostichopus</i>), Imaoka, 1990 | <i>Pseudostichopus peripatus</i> (Sluiter, 1901) |
| <i>tuberosus</i> , <i>Pseudostichopus</i> , sp. nov. | <i>Pseudostichopus tuberosus</i> sp. nov. |
| <i>unguiculatus</i> , <i>Pseudostichopus</i> , Ohshima, 1915 | <i>Pseudostichopus peripatus</i> (Sluiter, 1901) |
| <i>ustulatus</i> , <i>Molpadiodemas</i> , sp. nov. | <i>Molpadiodemas ustulatus</i> sp. nov. |
| <i>villosus</i> , <i>Pseudostichopus</i> , Théel, 1886 | <i>Molpadiodemas villosus</i> (Théel, 1886) |
| <i>violaceus</i> var. <i>villosus</i> , <i>Pseudostichopus</i> , Théel, 1886 | <i>Molpadiodemas violaceus</i> (Théel, 1886) |

Molpadiodemas Heding, 1935

Table 1, Figure 2

Molpadiodemas Heding, 1935: 77–78.—Heding, 1940: 356–357.—Deichmann, 1940: 209–211.—O'Loughlin, 1998: 497.—O'Loughlin, 2002: 303, 305, 315.

Platystichopus Heding, 1940: 358 (new synonym).

Type species. *Molpadiodemas acaudum* Heding, 1935 (junior synonym of *Pseudostichopus atlanticus* Perrier, 1898, by O'Loughlin, 2002).

Other included species. *Molpadiodemas atlanticus* (Perrier, 1898); *M. constrictus* sp. nov.; *M. crinitus* sp. nov.; *M. depressus* (Hérouard, 1902); *M. epibiotus* sp. nov.; *M. helios* sp. nov.; *M. involutus* (Sluiter, 1901); *M. morbillus* sp. nov.; *M. neovillosus* sp. nov.; *M. pediculus* sp. nov.; *M. porphyryus* sp. nov.; *M. pustulosus* (Sluiter, 1901); *M. translucens* sp. nov.; *M. ustulatus* sp. nov.; *M. villosus* (Théel, 1886); *M. violaceus* (Théel, 1886).

Diagnosis. Pygal-furrowed Synallactidae displaying: absence of prominent appendages (tube feet, papillae) along the paired

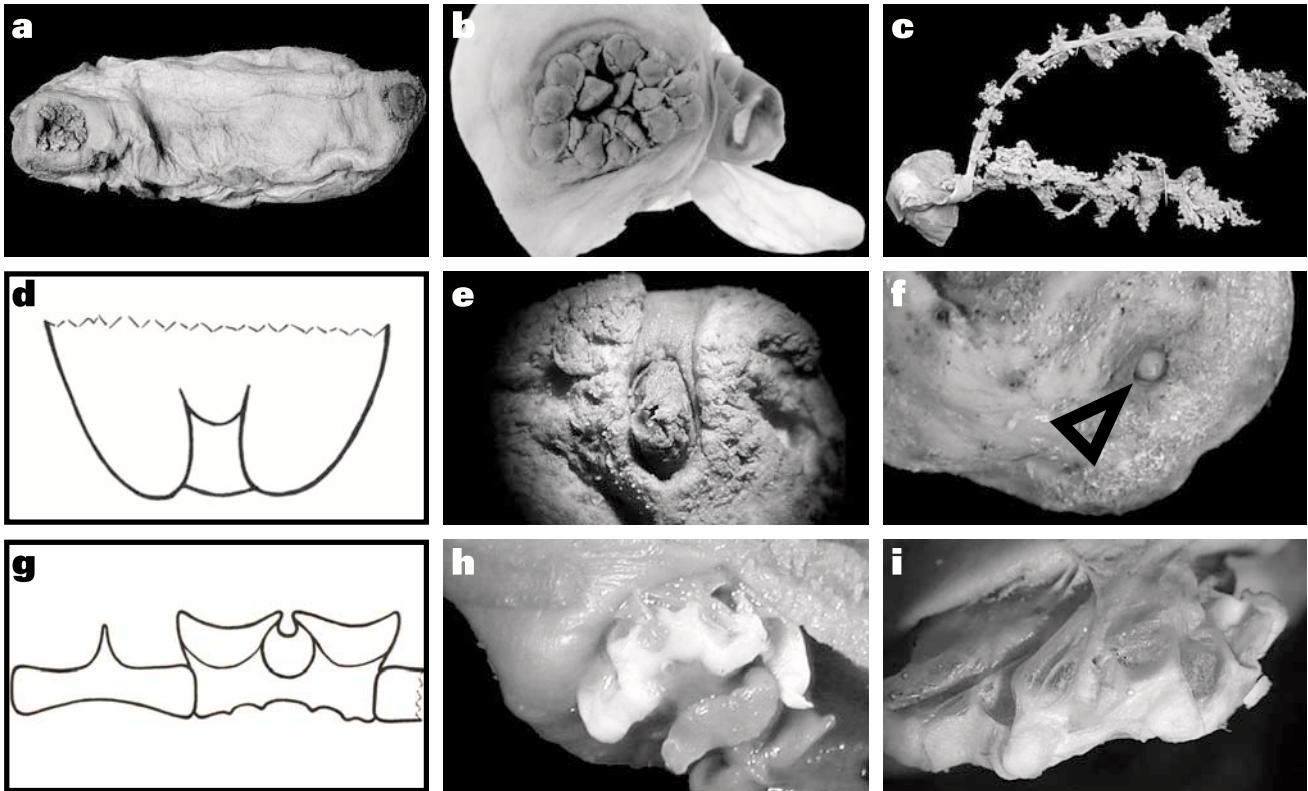


Figure 1. Characters of pygal-furrowed Synallactidae. a, ventral mouth and anus (*M. helios* sp. nov., USNM E31104, paratype, 91 mm long); b, ventral peltate tentacles, polian vesicle (*P. mollis*, TM H2004; anterior end dissected off); c, respiratory tree (*P. mollis*, TM H2004); d, drawing of dorsal posterior pygal furrow; e, posteroventral view of pygal furrow and anus (*M. violaceus*, BMNH 86.10.2.150); f, anterior dorsal madreporite (arrow) (*P. peripatus*, USNM 1008159); g, drawing of calcareous ring (radial plate right, as in *P. spiculiferus*); h, calcareous ring (*M. crinitus* sp. nov., USNM E48644, paratype); i, calcareous ring (*M. violaceus*, BMNH 86.10.2.145).

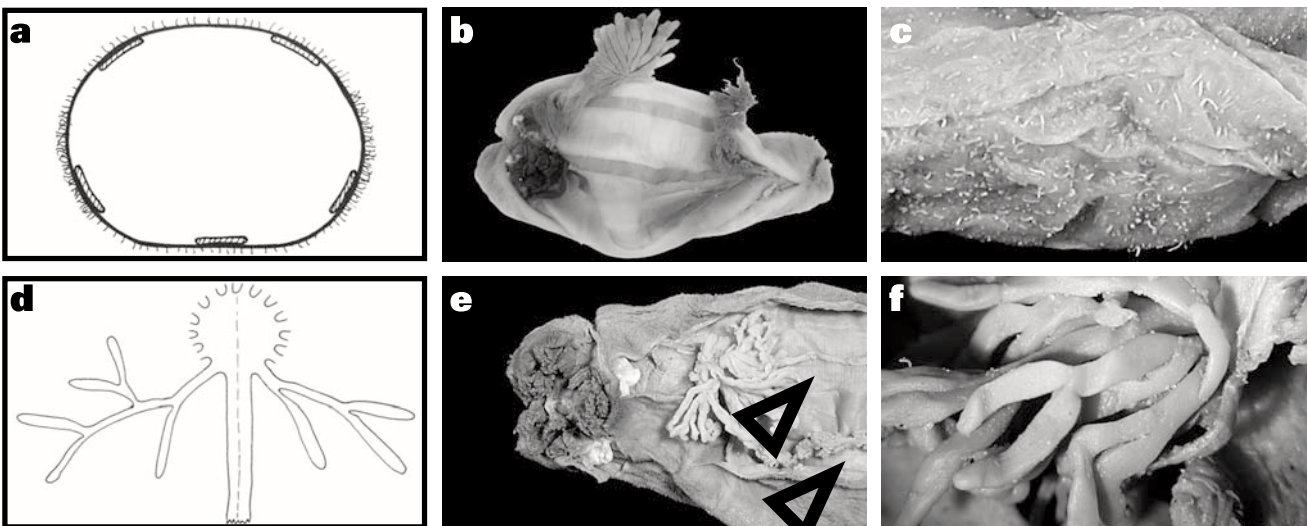


Figure 2. Characters of *Molpadiodemas*. a, drawing of transverse section of mid-body, hair-like tube foot cover, flat broadly attached longitudinal muscles (as for *M. villosus*); b, flat longitudinal muscles, gonad (upper left), respiratory tree (upper right) (*M. porphyrus* sp. nov., NMV F101871, paratype, 90 mm long); c, complete cover of tube feet (*M. translucens* sp. nov., USNM 1008072, paratype); d, drawing of part of gonad, branched tubules from common origin; e, gonad, flat longitudinal muscles (arrows) (*M. villosus*, BMNH 86.10.2.155, paralectotype); f, branched gonad tubules (*M. violaceus*, BMNH 86.10.2.145).

radii; longitudinal muscles flat, not cylindrical, broadly attached to the inner body wall; gonad tubules branched, arising from a common base on the gonoduct, not in series along the gonoduct; ossicles never present in tube feet; tentacle ossicles frequently rods with ends intertwining and side branches fused to create mesh.

Distribution. Cosmopolitan; 103–7086 m.

Remarks. Heding (1935) erected the monotypic genus *Molpadiodemas* for his new species *acaudum*, and subsequently (Heding, 1940) reassigned *Pseudostichopus atlanticus* Perrier, *P. occultatus* Marenzeller and *P. villosus* Théel to *Molpadiodemas*. O'Loughlin (1998) reassigned these four species to *Meseres* Ludwig, 1894, *Molpadiodemas* becoming a junior synonym of *Meseres*. *Molpadiodemas* is raised here out of synonymy with *Meseres* (see below under *Meseres*). O'Loughlin (2002) considered *M. acaudum* to be a junior synonym of *P. atlanticus*, and that decision is confirmed here. Heding (1940) erected the new genus *Platystichopus* for *Pseudostichopus depressus* Hérouard, 1902, which is reassigned below to *Molpadiodemas*. *Platystichopus* becomes a junior synonym of *Molpadiodemas*.

Molpadiodemas atlanticus (Perrier, 1898) comb. nov.

Figures 3a, b, 4a–d, 6a, b

Pseudostichopus atlanticus Perrier, 1898: 1665.—Perrier, 1902: 333–338, pl. 17 figs 15–20.—Mortensen, 1927: 386–387.—Deichmann, 1930: 87–88.—Deichmann, 1940: 209, 211.—Heding, 1942: 5.—O'Loughlin, 2002: 315.

Molpadiodemas acaudum Heding, 1935: 78–80, pl. 6 figs 1–2.—Heding, 1940: 354–357.—Deichmann, 1940: 209, 211.—Heding, 1942: 4–5.

Molpadiodemas atlanticus.—Heding, 1940: 353–359.

Meseres atlanticus.—O'Loughlin, 1998: 497.—Thandar, 1999: 376–379, fig. 4.

Meseres acaudum.—O'Loughlin, 1998: 497, fig. 1g–h.

Material examined. *Pseudostichopus atlanticus* Perrier, 1898. Holotype. North Atlantic, off the Azores, 42°19'N, 23°31'W, 4060 m, *Talisman* stn 134, 1883, MNHN EchH 2772. Paratype. 42°19'N, 23°36'W, 4060–4010 m, MNHN EchH 658.

Molpadiodemas acaudum Heding, 1935. Paratype. North Atlantic, 60°17'N, 54°5'W, 3230 m, *Ingolf* stn 37, 1885, ZMUC.

Other material. Pacific Ocean, New Zealand, Chatham Is, 2610–2668 m, USNM E49319 (1); Chile, 34°07'S (incorrectly recorded as N in Théel, 1886), 73°56'W (incorrectly as E), 4069 m, *Challenger* stn 298, BMNH 1886.10.2.149 (1); 33°31'S, 74°43'W, 3950 m, *Challenger* stn 299, BMNH 1886.10.2.185 (1); Peru, 3500 m, USNM 1020067 (1); California, off Point Conception, 4100 m, 1073654 (1); Oregon, 3021 m, USNM E16475 (1); 3700 m, E16488 (3); Clipperton Fracture Zone, 13°08'–13°53'N, 129°51'–129°55'W, 4801–4923M, E31100–E31102 (3); E31107, E31108 (2); E31121–E31123 (3); E31125 (1); E53278 (1); NMV F101845 (1).

Atlantic Ocean, Bahamas, 4828–4873 m, USNM 1021592 (10); NE of Bahamas, 4930–4940 m, E49466 (9); West European Basin, 4780–4795 m, E38320 (1); Caribbean Sea, Venezuelan Basin, 13°30'–14°50'N, 64°45'–67°30'W, 3411–5062 m, E38789–E38791 (20); E38798 (1); E39266 (20); 1023352 (1); NMV F101846 (2).

Description. Large, up to 210 mm long; body rounded in section, sometimes sac-like, sometimes with slight brim,

usually no detrital attachments; body wall moderately thick, soft leathery or firm gelatinous, frequently smooth surface, frequently wrinkled ventrally; uniform cover of very small tube feet, frequently not evident or in pits, most evident ventrally and pygally, from 0.1 mm long, 0.2 mm diameter up to 1.0 mm long, 0.3 mm diameter, cylindrical and firm if extended; ossicles frequently abundant in tentacles and gonads, sometimes rare or absent; tentacle ossicles frequently irregular thin rods slightly to strongly curved with ends intertwined to create small perforations, less frequently irregular straight to curved, narrow to wide, smooth to laterally spinous, variably perforated rods, ossicles variable in length, up to 500 µm long; gonad ossicles irregular rods, frequently with thin lateral branches joined to create extensive irregular lace-like mesh, non-spinous, up to 420 µm long.

Colour. Body and tube feet brown to grey-brown to off-white; frequently some residual mauve markings.

Distribution. North Atlantic, 3230–4060 m (Perrier, 1902, as *P. atlanticus*; Heding, 1935, as *M. acaudum*); south-east Atlantic, 3155–3255 m (Thandar, 1999); West European Basin, 4780–4795 m (this paper); Venezuelan Basin, 3411–5062 m (this paper); Pacific Ocean, off Chile, 3950–4069 m (Théel, 1886; see below); Pacific Ocean, 2610–4923 m (this paper).

Remarks. In agreement with the opinions of Deichmann (1940) and Heding (1942), *M. acaudum* was made a junior synonym of *P. atlanticus* by O'Loughlin (2002). That decision is confirmed here.

Théel (1886) noted that two *Challenger* specimens, taken in the Pacific Ocean off Chile at stations 298 and 299, closely resembled *Pseudostichopus villosus* but lacked tube feet. Both specimens were examined in this study, and determined as *P. atlanticus*. Théel (1886) reported sizes up to 280 mm long. The larger specimen is now only 150 mm long.

The very small dark brown attachments on the body which were noted by O'Loughlin (2002) and Théel (1886) are judged to be epibiotes. O'Loughlin (2002) judged the “mulberry” bodies in the body wall of *P. atlanticus*, illustrated by Perrier (1902) and Thandar (1999), and referred to by Théel (1886) as present in some specimens of *P. villosus*, to be detrital accretions and not holothurian ossicles. That opinion is maintained here.

The presence of *P. atlanticus* in the Pacific Ocean is confirmed by the numerous USNM specimens determined in this study. O'Loughlin (2002) summarised *P. atlanticus* distribution records as Atlantic Ocean only. This work extends the distribution to the Pacific Ocean, and to greater depths (at least 5062 m).

Amongst *Molpadiodemas* species the distinguishing characters of *M. atlanticus* are: large, sac-like form; even cover of small tube feet, frequently inconspicuous; frequent presence of large, irregular, open mesh-like gonad ossicles.

Molpadiodemas constrictus sp. nov.

Figures 3c–e

Material examined. Holotype. North Atlantic Ocean, Puerto Rico Trench, 20°08'N, 65°27'W, 7086 m, RV *Gilliss*, 20 Jan 1973, USNM 1022814.

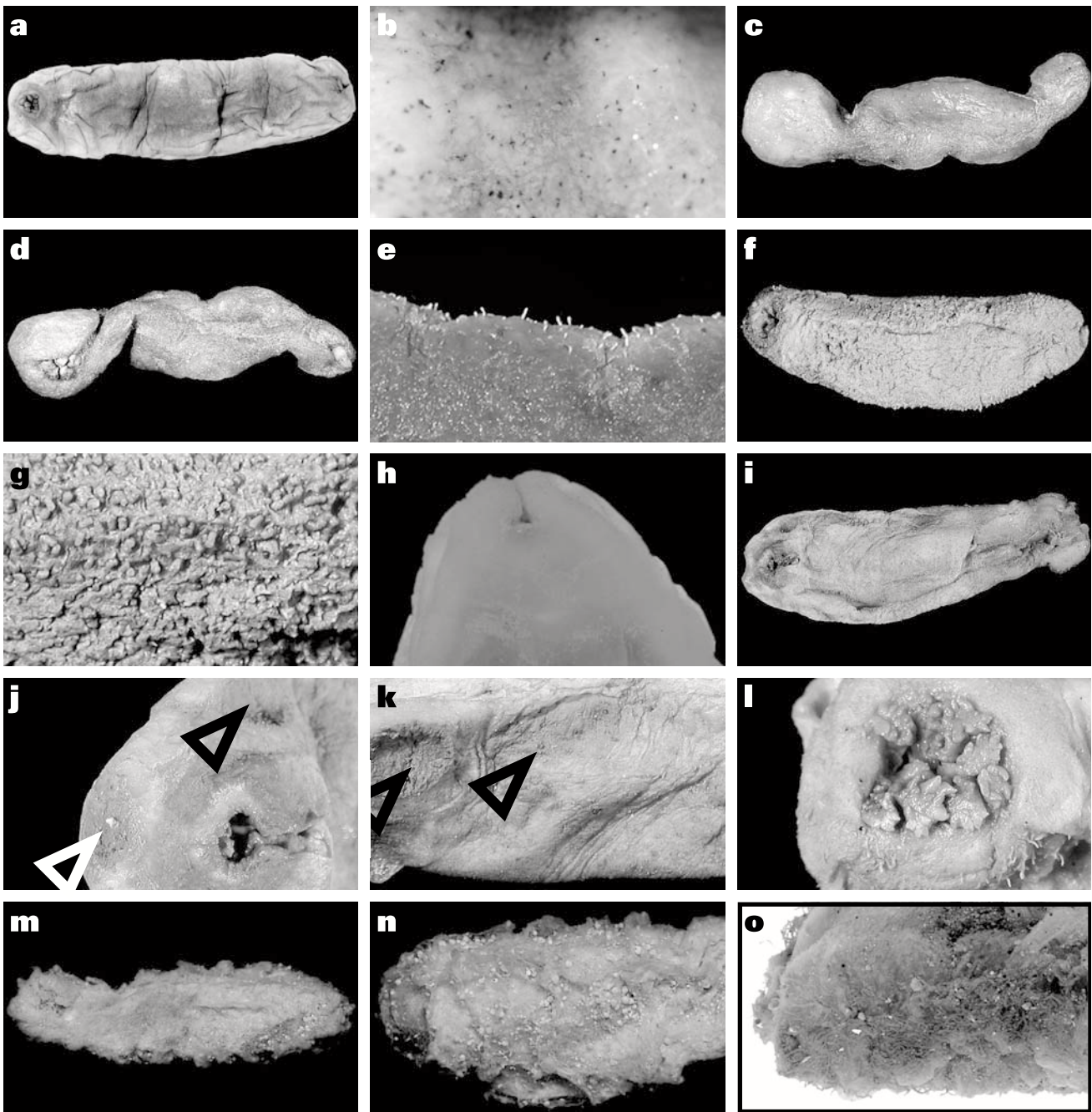


Figure 3. a–b, *M. atlanticus* (NMV F101845, 210 mm long); a, ventral view; b, small epibiotes on body wall. c–e, *M. constrictus* sp. nov. (USNM 1022815, paratypes); c, dorsal view (51 mm long); d, ventral view (51 mm long); e, tube feet. f–g, *M. crinitus* sp. nov. (USNM 1023615, holotype, 96 mm long); f, ventral view; g, ventrolateral tube feet. h, *M. depressus*, pygal furrow, gelatinous body, lateral brim (NMV F101849). i–k, *M. epibiotus* sp. nov. (USNM 1008183, holotype, 110 mm long); i, ventral view, posterior taper; j, ventral mouth, epibiote concavities (arrows); k, ventral view, epibiote concavity (left arrow), few tube feet (central arrow). l, *M. helios* sp. nov., tentacle digits, tube feet (lower right) (USNM E31104, paratype). m–o, *M. involutus* (NMV F101850, 40 mm long); m, ventral view, serrated margin; n, dorsal anterior view, globigerines attached; o, posterior ventrolateral tube feet.

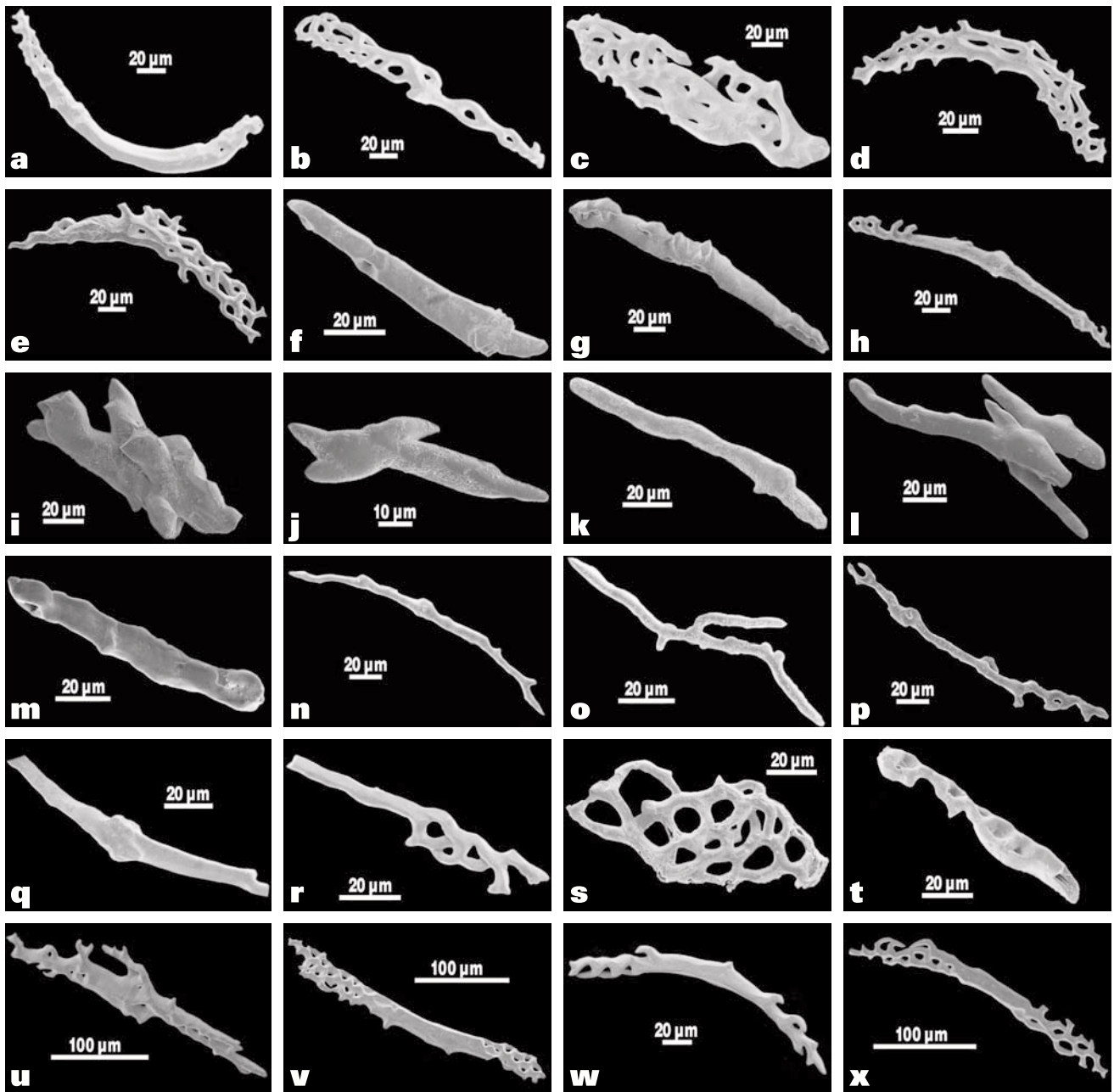


Figure 4. Tentacle ossicles (SEM). a–d, *Meseres atlanticus*, a–c (USNM E49466), d (USNM 1020067). e–h, *M. crinitus* sp. nov. (USNM E48662). i–l, *M. depressus* (USNM E53279). m–p, *M. epibiotus* sp. nov. (USNM 1008310, paratype). q–t, *M. helios* sp. nov., q–r (USNM E31104, paratype), s–t (USNM E31117, paratype). u–x, *M. involutus* (USNM E49256).

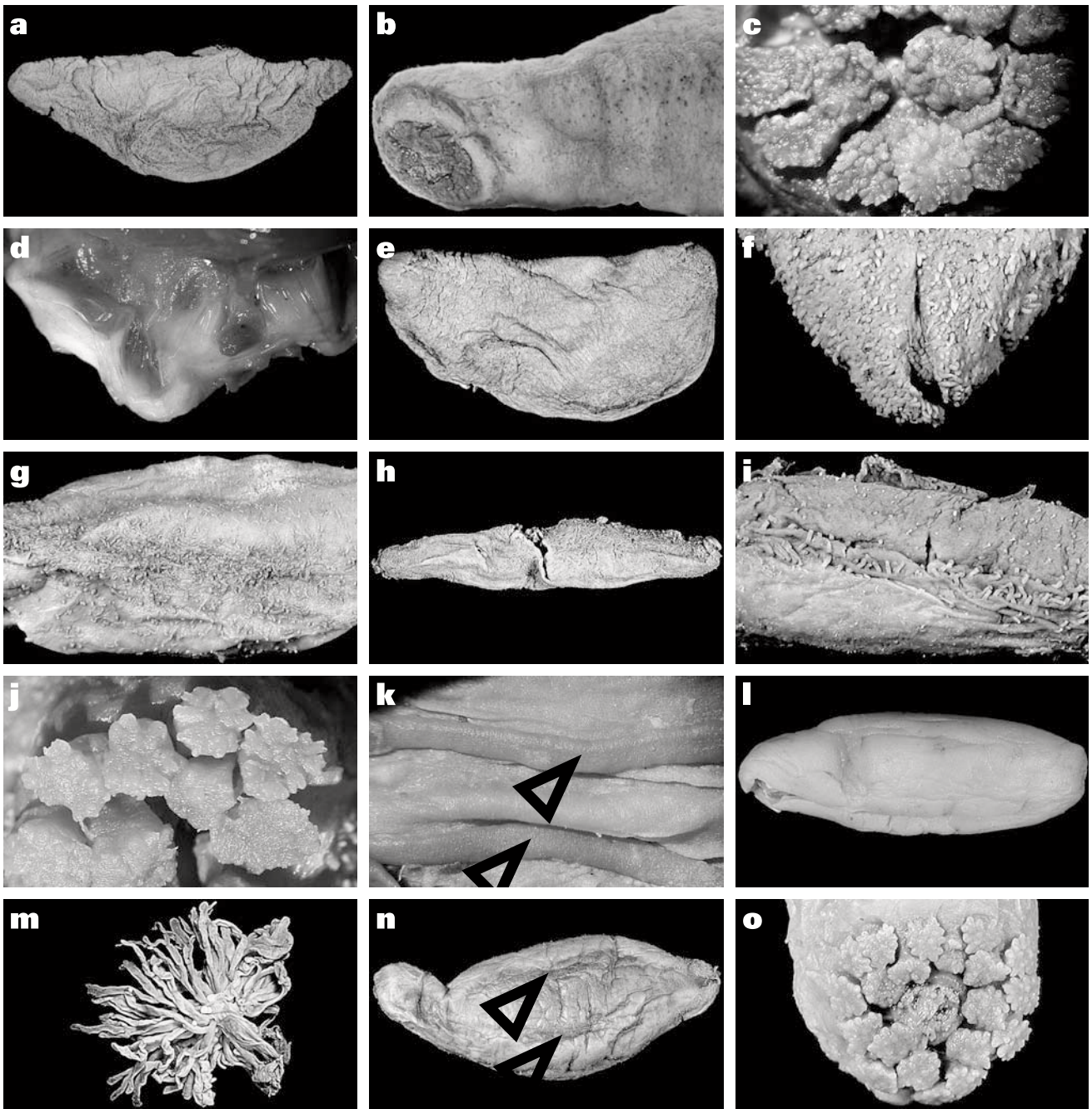


Figure 5. a–d, *Meseres morbillus* sp. nov., a, lateral view (USNM 1008093, paratype, 91 mm long); b, tentacles, ventrolateral tube feet “spotting” (NMV F101865); c, tentacles, digits (USNM E49243); d, calcareous ring (radial plate right half) (USNM 1008093, paratype). e–g, *M. neovillosus* sp. nov.; e, dorsal view (USNM 1008458, paratype, 71 mm long); f, pygal end, tube feet (USNM 1008458); g, ventrolateral tube feet (BMNH 86.10.2.151, holotype). h–k, *M. pediculus* sp. nov.; h, dorsal view, elongate form (USNM 1008318, holotype, 56 mm long); i, ventrolateral tube feet (NMV F104796, paratype); j, tentacles (holotype); k, broadly attached, relatively narrow, slightly thickened, longitudinal muscles (arrows) (paratype). l–m, *M. porphyrus* sp. nov. (USNM E38795, holotype, 114 mm long); l, dorsal view, thick rounded brim; m, gonad. n–o, *M. translucens* sp. nov. (USNM E48652, holotype, 78 mm long); n, dorsal view, longitudinal muscles visible through translucent body wall (arrows); o, tentacles.

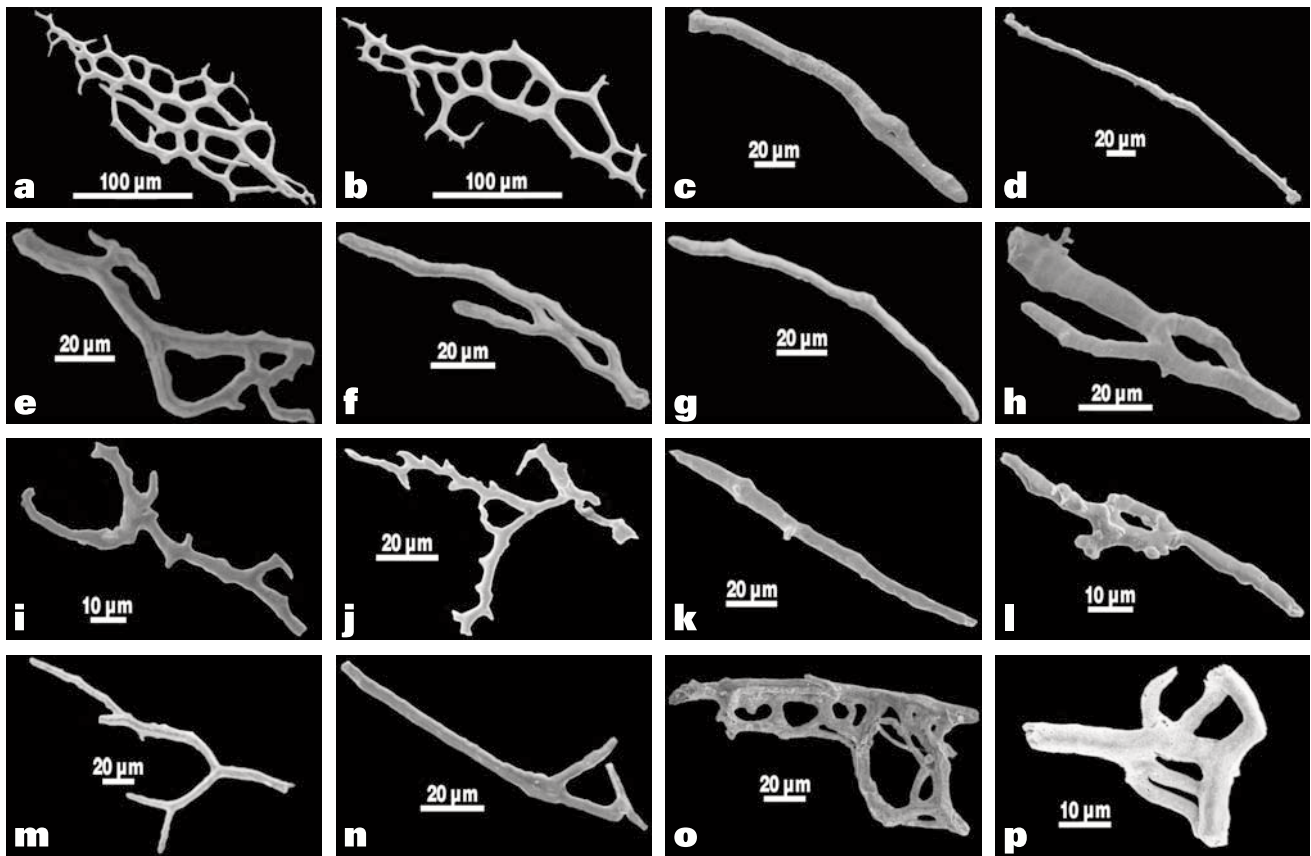


Figure 6. Gonad ossicles (SEM). a–b, *Meseres atlanticus* (USNM E53278). c–d, *M. helios* sp. nov. (USNM E31106, holotype). e–h, *M. neovillosus* sp. nov. (USNM 1008458, paratype). i–l, *M. porphyrus* sp. nov. (USNM E38795, holotype). m–p, *M. usulatus* sp. nov. (USNM 1022493, holotype).

Paratypes. Type locality and date, USNM 1022815 (20); NMV F101857 (5).

Other material. Type locality and date, USNM 1022816 (90); NMV F101856 (10).

Description. Up to 62 mm long; body rounded anteriorly, frequently strongly tapered and narrow posteriorly, dorsoventrally depressed, low convex dorsally, flat ventrally frequently with longitudinal median depression, body typically with one rarely two deep transverse constrictions most frequently posterior to calcareous ring, body rounded ventrolaterally sometimes subacute; body wall thick, firm, soft, semi-gelatinous; even cover of very small tube feet all over body, some very thin erect, about 0.2 mm long, some lying on body, cylindrical, thin, typically 0.8 mm long, 0.15 mm diameter, up to 1.5 mm long, rarely contiguous; longitudinal muscles flat, broadly attached, narrow, slightly thickened; no ossicles found.

Colour. Body dark mauve-brown (largest), pale grey-brown to translucent (smallest), largest sometimes with dark red-brown markings dorsally, sometimes with even cover of mauve to brown spots ventrally creating a mottled appearance; largest tube feet body colour, smallest off-white.

Etymology. From the Latin *constrictus* (drawn together,

contracted), referring to the characteristic deep transverse constrictions on specimens.

Distribution. North Atlantic Ocean, Puerto Rico Trench, 7086 m.

Remarks. The transverse constrictions of the body are growth constrictions. They closely resemble similar growth constrictions observed by one of us (M.O'L) in the fissiparous cucumariid species *Squamocnus aureoruber* O'Loughlin and O'Hara, 1992. Emson and Wilkie (1980) listed six fissiparous holothurian species, four of them aspidochirots. *M. constrictus* is judged to be fissiparous.

The material was at some stage preserved in formalin solution, which might account for the complete absence of ossicles. Amongst *Molpadiodemas* species the distinguishing characters of *M. constrictus* are: body form typically with a transverse constriction; distinct posterior taper; body colour frequently with dark markings dorsally and mottled ventrally; minute thin erect tube feet; absence of ossicles.

***Molpadiodemas crinitus* sp. nov.**

Figures 1h, 3f, g, 4e–h, 7h

Pseudostichopus sp. MoV 2033.—O'Loughlin et al., 1994: 253–254.

Meseres villosus.—O'Loughlin, 2002: 313, figs 3a, b, tables 1, 2 (non *Pseudostichopus villosus* Théel, 1886).

Material examined. Holotype. Eastern Antarctica, Ross Sea, 72°57'S, 171°35'E, 573–576 m, USARP, *Eltanin* stn 1878, USNM 1023615.

Paratypes. Type locality and date, USNM E48644 (8); NMV F101872 (3).

Other material. Eastern Antarctica, Prydz Bay, 66°46'–68°50'S, 72°14'–77°19'E, 333–765 m, NMV F68152 (9); F68158 (1); F68162 (5); F72534 (2); F76583 (2); F76597 (1); F76606 (1); F81816–F81817 (3); Ross Sea, 67°24'–78°23'S, 166°15'E–163°02'W, 223–923 m, USNM E48578–E48580 (8); E48597 (4); E48621, E48623 (4); E48642 (6); E48646 (9); NMV F101874 (3); USNM E48662, E48663 (32); NMV F101873 (4); E49244–E49245 (12); E49270 (1); E49283 (1); E49286 (2); E49299–E49300 (3); E49368 (1); 1005125 (1); 1005129 (2); New Zealand, Antipodes Is, Campbell Plateau, 2010–2100 m, E48655 (2); W of Antipodes Is, 103 m, E49357 (4).

Description. Up to 150 mm long; body rounded in transverse section, lacking brim and distinctive ventrolateral margin, sometimes transverse grooves, frequently tubercles and pygal sublobes posteriorly; body wall firm, thick to thin; lacking significant globigerine or sponge spicule attachments; body covered with thick, cylindrical tube feet, typically extended, longest and often matted pygally and in a conspicuous lateral to ventrolateral band, feet typically 2.0 mm long, 0.4 mm diameter, up to 3.0 mm long, smaller and more spaced dorsally and ventrally; multiple-branching gonad tubules; ossicles in tentacles only, abundant to sparse to absent, thick irregular non-spinous rods, frequently short thick rods with bluntly rounded ends, some with swelling mid-rod, some as irregular tuberous lumps, some with short branching, some with blunt spines, some ends branched, some branches intertwined to create perforations, lace-like mesh development on rods rare, rods up to 270 µm long.

Colour. Body and tube feet similar in colour, dark to pale brown, contracted tube feet rare and sometimes with dark discs.

Etymology. From the Latin *crinitus* (long-haired, fringed), referring to the lateral band of long, fringing tube feet.

Distribution. Eastern Antarctica, Prydz Bay, 333–765 m (O'Loughlin, 2002, as *Meseres villosus*); Ross Sea, 223–923 m; Antipodes Is, 103–2100 m (this paper).

Remarks. O'Loughlin (2002) considered Antarctic material to be *Pseudostichopus villosus*, and although it is similar in form it is not conspecific with any of the syntypes assigned to *P. villosus* by Théel (1886). Amongst *Molpadiodemas* species the distinguishing characters of *M. crinitus* are: wide ventrolateral band of thick, cylindrical, extended, sometimes matted tube feet, similar in colour to the body wall, typically 2.0 mm, long, 0.4 mm diameter; tentacle ossicles usually abundant, frequently short thick rods rounded distally; absence of gonad ossicles.

Molpadiodemas depressus (Hérouard, 1902) comb. nov.

Figures 3h, 4i–l

Pseudostichopus depressus Hérouard, 1902: 15–16, pl. 2 figs 15–18. *Platystichopus depressus*.—Heding, 1940: 353–358.

Holotype. North Atlantic Ocean, between Portugal and the Azores, 4360 m, Monaco stn 753, 1896, MOM (cannot be located).

Material examined. North Atlantic Ocean, West European Basin, 4426–4435 m, USNM 1005343 (2); NMV F101849 (1); NE of Bahamas, 4383–4558 m, USNM 1008242 (1); E53279 (21); NMV F101868 (4); Sargasso Sea, 5690 m, USNM E49454 (1); N of Puerto Rico, 5248–5278 m, USNM 1008241 (2).

Provisional (very damaged): Gulf of Mexico, 1353–1399 m, USNM E48661 (1).

Description. Up to 100 mm long, not tapered; body wall gelatinous, thick, firm to soft; sometimes with globigerine attachments; flat ventrally, low convex dorsally, dorsoventrally depressed; thick rounded ventrolateral brim; mouth antero-ventral; dorsally smooth to wrinkled, ventrally wrinkled, pustulose; small soft tube feet all over body, thick cylindrical not thread-like, most concentrated and largest orally and pygally, up to 1.0 mm long, 0.3 mm diameter, inconspicuous and dome-like over rest of body, 0.2 mm diameter, closer ventrally than laterally and dorsally; longitudinal muscles flat, slightly thickened, narrow; ossicles in tentacles, large, thick to thin, curved to straight rods, smooth or with few blunt to sharp spines, some with mid-rod swelling, some with branched intertwined ends creating perforations, some irregularly tuberous and rugose, some thickly bifurcate at ends, some with one or two large perforations, no lateral perforations or mesh, up to 390 µm long.

Colour. Body grey to off-white; tube feet off-white.

Distribution. North and South Atlantic Ocean, West European Basin, Sargasso Sea, off Bahamas and West Indies; 1353–5690 m.

Remarks. The holotype of *P. depressus* cannot be located (M. Bruni, MOM, pers. comm.), and has been missing for a long time. Belloc (1950) noted the absence when creating a catalogue of types, and there is no slide in Cherbonnier's comprehensive collection (F. Solis-Marin, pers. comm.).

Based on the description and figures of Hérouard (1902), the characteristics of *P. depressus* are: up to 74 mm long; off-white colour; pygal furrow; dorsoventrally depressed; thickened lateral brim extending around oral end; distinct dorsal madreporite plate; numerous inconspicuous tube feet all over body; narrow longitudinal muscles; two tufts of gonad tubules; lacking ossicles in body wall and gonads.

In this work numerous North Atlantic specimens are judged to be conspecific. Three were taken from the West European Basin at 4426–4435 m, a locality close to the type locality for *P. depressus* (between Portugal and the Azores, 4360 m). The conspecific material is characterized by an off-white colour, close cover of very small tube feet, absence of gonad ossicles, dorsoventral depression, and frequently a thick brim. No dorsal madreporite similar to that observed and illustrated by Hérouard (1902) for *P. depressus* has been seen. But the external evidence of a dorsal madreporite has been rare in this work, and not observing it is considered to be not significant diagnostically. Hérouard (1902) illustrated tufts but not series of gonad tubules (it is not possible to judge branching or not), and illustrated cylindrical longitudinal muscles. On the basis of the consistency of the diagnostic characters of *Molpadiodemas*

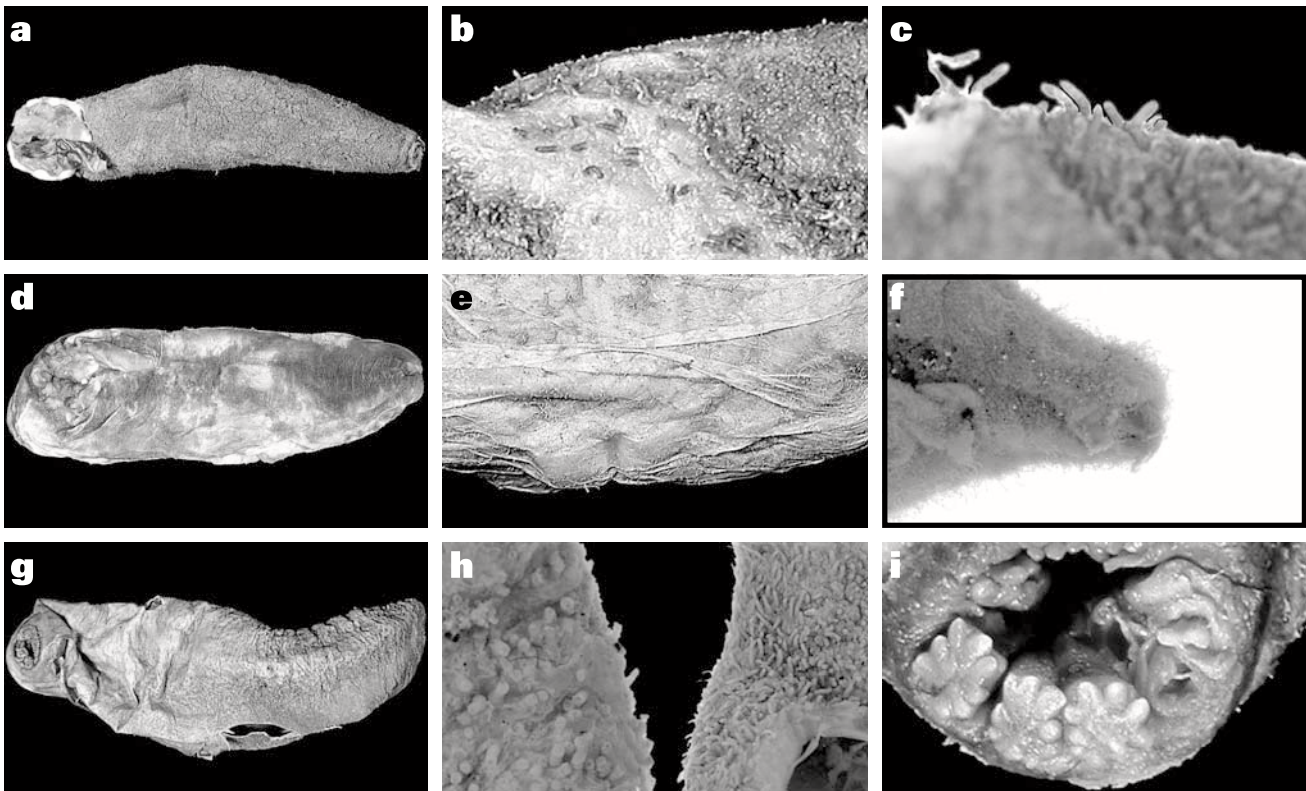


Figure 7. a–c, *Meseres ustulatus* sp. nov.; a, ventral view (USNM 1022566, paratype, 55 mm long); b, ventrolateral tube feet (USNM 1022493, holotype); c, tube feet (NMV F101858, paratype). d–f, *M. villosus*; d, ventral view (BMNH 86.10.2.147, lectotype, 90 mm long); e, ventrolateral tube feet (lectotype); f, posterior tube feet (NMV F98745). g–i, *M. violaceus* (BMNH 86.10.2.156, holotype, 142 mm long); g, ventrolateral view; h, tube feet of *M. crinitus* (left, NMV F101872, paratype) contrasted with *M. violaceus* (right, NMV F101848); i, tentacles (USNM 1022608).

(above), it is anticipated that the longitudinal muscles were broadly attached to the body wall, and that the gonad tubules were branched.

Heding (1940) erected the monotypic genus *Platystichopus* for the species *depressus*, and referred *Platystichopus* with *Benthothuria* Perrier to the Benthostichopodinae (subfamily of the Gephyrothuriidae). *P. depressus* has a distinct pygal furrow, has a close cover of minute tube feet, and lacks body wall ossicles. It shares more significant diagnostic characters with *Molpadiodemas* than *Benthothuria*, and is referred here to *Molpadiodemas*. *Platystichopus* is a junior synonym of *Molpadiodemas* (see above).

On specimens of *M. depressus* there are ventral minute red to violet conical attachments similar to those found on *M. atlanticus*, and considered here to be epibioties. Amongst *Molpadiodemas* species the distinguishing characters of *M. depressus* are: thick gelatinous grey to off-white body wall; dorsoventrally depressed body form; ventrolateral brim; thick cylindrical small tube feet; absence of gonad ossicles.

Molpadiodemas epibiotus sp. nov.

Figures 3i–k, 4m–p

Material examined. Holotype. North Atlantic Ocean, Caribbean Sea, Cuba, Cayman Trench, 19°39'N, 76°17'W, 6195–6320 m, RV *Gilliss*, stn GS-121, 21 Jul 1975, USNM 1008183.

Paratypes. Type locality and date, USNM 1008310 (4); NMV F101862 (1).

Description. Up to 125 mm long; body strongly tapered posteriorly, dorsoventrally depressed, low convex dorsally, flat ventrally; thin brim anteriorly around mouth, variably developed laterally, posteriorly; all specimens with anterior large concave depression suggesting epibiotie attachment, some smaller depressions mid-body; body wall firm, thin, soft, semi-gelatinous, embedded with white granules, surface wrinkled, additionally pustulose ventrally; complete cover of small tube feet, translucent and merged into body wall dorsally; latero-ventral tube feet in widely spaced band, sparse, subglobular, up to 0.5 mm long, 0.25 mm diameter, some with dark red markings; ventral tube feet closer, smaller, some with red markings, not extended, 0.2 mm diameter as domes; ossicles in tentacles only, abundant, variable, rods, thick to thin, lumpy to smooth to bluntly spinous, with or lacking swelling in mid-rod, limited branching at ends, some branches fused to create perforations, ossicles up to 300 µm long.

Colour. Dorsally off-white to greyish-white; ventrally reddish-brown around mouth, dark red flecking on surface and on some tube feet.

Etymology. From the Greek *epi* (upon) and *bios* (life), referring to the evidence for epibiotic attachments on all specimens.

Distribution. North Atlantic Ocean, Caribbean Sea, Cayman Trench, 6195–6320 m,

Remarks. Amongst *Molpadiodemas* species, the distinguishing characters of *M. epibiotus* are: distinctly posteriorly tapered body; dorsoventral depression of the body; presence of a thin brim anteriorly; presence of anterior concavities from epibioties; fine dark red markings ventrally on the body surface and tube feet.

***Molpadiodemas helios* sp. nov.**

Figures 1a, 3l, 4q–t, 6c, d

Material examined. Holotype. Central Pacific Ocean, Clipperton Fracture Zone, 13°13'N, 129°53'W, 4877 m, RV *Governor Ray*, Ocean Minerals Co., 15 Feb 1980, USNM E31106.

Paratypes. Type locality, 13°13'N, 129°52–53'W, 4724–4892 m, 1980, USNM E31104 (1), E31117 (1), E31134 (1), E31137 (1), E31141 (1), NMV F101852 (1), F101854 (1).

Other material. Type locality, 13°13'N, 129°52–55'W, 4755–4938 m, 1980, USNM E31097 (1), E31103 (1), E31105 (1), E31110–E31114 (5), E31118 (1), E31129 (2), E31133 (1), E31138–E31140 (3), E31144 (1), E48515 (1), NMV F101853 (1).

Description. Up to 170 mm long; body wall soft-leathery to semi-gelatinous; no body attachments (encrustations); body rounded in transverse section, lacking brim; tentacles with about 10 large conical pointed digits peripherally, some digits bifid; tube feet soft, white to semi-translucent, scattered and lying all over body, most dense around oral and pygal areas, up to 2.0 mm long, 0.15 mm diameter, frequently cylindrical digitate erect orally and pygally, typically 0.8 mm long, 0.2 mm diameter; ossicles in tentacles and gonad; tentacle ossicles sparse to rare, thick to thin rods up to 150 µm long, rare branches, rare perforations at ends or branches joined to form perforations, lacking spines, sometimes swollen mid-rod; gonad tubules with abundant irregular thin rods, some irregularly branched, branches sometimes joined to create perforations, lacking spines, swellings rare, up to 280 µm long.

Colour. Body off-white to grey, frequently semi-translucent, smaller specimens sometimes with pale brown.

Etymology. From the Greek *helios* (sun), referring to the sunflower appearance of the radiating tentacle digits.

Distribution. Central Pacific Ocean, Clipperton Fracture Zone, 13°13'N, 129°53'W, 4724–4938 m.

Remarks. Amongst *Molpadiodemas* species, the distinguishing characters of *M. helios* are: relatively prominent soft tube feet scattered over the body, sometimes cylindrical and erect posteriorly and anteriorly; prominent conical tentacle digits; predominantly smooth rod ossicles in gonad.

***Molpadiodemas involutus* (Sluiter, 1901) comb. nov.**

Figures 3m–o, 4u–x

Meseres involutus Sluiter, 1901a: 11–12.—Sluiter, 1901b: 49–50, pl. 8 fig. 6.—Perrier, 1902: 359. (*Meseres convolutus*) [lapsus].—O'Loughlin, 2002: 306, fig. 2e, tables 1, 3, 4.

Pseudostichopus globigerinae Hérouard, 1923: 23–25, pl. 4 fig. 6.—Mortensen, 1927: 386–388.—Deichmann, 1930: 87, 90.

Pseudostichopus (Pseudostichopus) globigerinae.—Heding, 1940: 353–360.—Imaoka, 1978: table 1–1.—Thandar, 1992: 167.

Pseudostichopus villosus.—Hansen, 1956: 47–48 (part; non *Pseudostichopus villosus* Théel, 1886).

Pseudostichopus (Pseudostichopus) dilatorbis Imaoka, 1978: 378–380, 384, fig. 1 B–E, table 1–1 (new synonym).

Meseres globigerinae.—O'Loughlin, 2002: 305, tables 1, 3 (new synonym).

Material examined. *Meseres involutus* Sluiter. Lectotype (designated here). Indonesia, Sawu Sea, 10°49'S, 123°23'E, 918 m, *Siboga* stn 300, ZMA V.Ech.H1052. Paralectotype. Seram Sea, 3°27'S, 131°01'E, 567 m, *Siboga* stn 173, ZMA V.Ech.H1051 (1).

Pseudostichopus globigerinae Hérouard, 1923. Lectotype (larger syntype, with pygal furrow, designated here). North Atlantic, off Newfoundland, 46°18'N, 50°42'W, 4380 m, Monaco stn 2964, 20 Jul 1910, MOM (examination via pers. comm. by M. Bruni at MOM). Second syntype, type locality and date, MOM.

Pseudostichopus (Pseudostichopus) dilatorbis Imaoka, 1978. Holotype. Japan, W of Kyushu, near Shimo-Koshiki I., 400–450 m., SMBL 309.

Other material. Pacific Ocean, eastern Australia, Tasman Sea, Lord Howe Rise, 1423 m, AM J23326 (1); off Newcastle, 2984–3058 m, J16833 (1); off Nowra, 1650–1750 m, NMV F80451 (1); Japan, East China Sea, off Kagoshima, 420 m, USNM 1071585 (3), NMV F104793 (2); 300–330 m, USNM 1071802 (1); Galapagos, 3667 m, USNM E950 (1).

Atlantic Ocean, West European Basin, 4426–4435 m, USNM 1005340 (8); NMV F101850 (2); off South Carolina, 2100 m, USNM E41392 (3); NMV F101851 (1); Gulf of Mexico, 1668 m, USNM E46796 (3); off Louisiana, 2063–2085 m, USNM 1008165 (2); NMV F101869 (1); 1829 m, USNM E46798 (2); 1646 m, E46799 (1).

South Atlantic Ocean, Argentina, Buenos Aires, SE of Mar Del Plata, 5208–5223 m, USNM 1005317 (1); 1008207 (1); off Falkland Is, 5687–5801 m, E49256 (5); E49359 (1); Scotia Sea, 2250–2404 m, E49295 (2).

Description. Up to 155 mm long; typically encrusted with globigerine or small stone attachments; body usually dorsoventrally depressed; flat ventrally, low convex dorsally; margin subacute, partly serrated because of transverse creasing of body wall, sometimes narrow rounded brim; body wall thin to thick, firm, wrinkled, with small digitate projections on low reticulate ridges; raised protuberances ventrolaterally, pygally; close cover of thin cylindrical tube feet, sometimes larger and more evident and reddish-brown in ventrolateral band, sometimes matted, typically 1.0 mm long, 0.2 mm diameter, up to 3.0 mm long, 0.5 mm diameter; multiple branching gonad tubules; ossicles in tentacles only, sometimes not detected; ossicles unbranched rods with thick central swelling and branched rods, branches frequently intertwining at ends or joining laterally to create irregular perforated mesh, ossicles up to 330 µm long.

Colour. Body grey to off-white; tube feet sometimes reddish-brown ventrolaterally.

Distribution. Indonesia, Seram and Sawu Seas, 567–918 m (Sluiter, 1901a); eastern Australia, Tasman Sea, 1423–3058 m (O'Loughlin, 2002); Japan, W of Kyushu, 400–450 m (Imaoka, 1978; as *P. dilatorbis*); East China Sea, off Kagoshima, 300–420 m (this paper); Galapagos Islands, 3667 m (this paper); northern Atlantic Ocean, off Newfoundland, 4380 m (Hérouard, 1923, as *P. globigerinae*); West European Basin,

4426–4435 m; western Atlantic Ocean, off South Carolina, Gulf of Mexico, 1646–2100 m; southern Atlantic Ocean, off Argentina, 5208–5223 m; Falkland Is, 5687–5801 m; Scotia Sea, 2250–2404 m (this paper).

Remarks. Sluiter (1901a) described two syntypes, and both were examined during a visit to the University of Amsterdam (Apr 2002). One is designated above as the lectotype.

Hansen (1956) considered *P. globigerinae* to be a junior synonym of *P. villosus*. O'Loughlin (2002) rejected the synonymy on the evidence that *P. villosus* never has tufts of tube feet on tubercles along the posterior margin, or a globigerine cover, or translucent body wall. A further synonymy was not suggested. Based on the description by Hérouard (1923), on observations communicated by Michèle Bruni (MOM), and on photographs by Francisco Solis-Marin (UNAM) of a tentacle ossicles slide prepared by Gustav Cherbonnier (MNHN box 108 slide 44), the characters of the larger syntype are: up to 30 mm long; body completely covered by globigerines; body wall thin, soft, translucent; pygal furrow present; villous-like cover of unequal and unevenly distributed small tube feet, rare mid-ventrally, in tufts on posterior ventrolateral tubercles creating serrated appearance; flat longitudinal muscles; lacking gonad; and tentacle ossicles branched closed mesh fragments. O'Loughlin (2002) noted that there was inadequate descriptive information to confirm any synonymy, but in the light of further data *P. globigerinae* is considered here to be a junior synonym of *M. involutus*.

Hérouard noted that there was no pygal furrow on the 15 mm long smaller syntype of *P. globigerinae*, and M. Bruni observed a cylindrical longitudinal muscle. The smaller of the two syntypes is not conspecific with *P. globigerinae*, but cannot be identified. The larger syntype is designated above as lectotype.

The description of *P. dilatorbis* by Imaoka (1978) refers to the external characters of the large paratypes and the internal characters of the holotype. The holotype has the diagnostic characters of *Molpadiodemas*; the paratypes those of *Pseudostichopus*. Although the holotype lacks tentacles ossicles, several specimens of *Pseudostichopus dilatorbis* recently donated by Tohru Imaoka yielded abundant tentacle ossicles and possess external characters similar to those of *M. involutus*. *Pseudostichopus dilatorbis* is considered here to be a junior synonym of *Molpadiodemas involutus*. The two paratypes of *P. dilatorbis* are much larger (up to 180 mm long) than the holotype, and are very close in appearance and diagnostic characters to the types of *Pseudostichopus trachus* Sluiter, 1901, which is considered below to be a junior synonym of *Pseudostichopus mollis*. The paratypes are referred below to *P. mollis*.

Material determined here extends the distribution of *M. involutus* from the western Pacific Ocean into the eastern Pacific Ocean, northern and southern Atlantic Ocean and Scotia Sea.

Amongst *Molpadiodemas* species, the distinguishing characters of *M. involutus* are: body wall with small digitate projections on low reticulate ridges; margin partly serrated because of transverse creasing of body wall; cylindrical tube feet most

evident in ventrolateral band; tentacle ossicles rods and mesh on primary rods; typical dense cover of globigerines.

Molpadiodemas morbillus sp. nov.

Figures 5a–d, 8a–d

Material examined. Holotype. Antarctic Ocean, South Shetland Is, Bransfield Strait, Livingston I., 62°38'S, 59°37'W, 681–1409 m, RV *Eltanin*, USARP Cr 6 stn 430, 7 Jan 1963, USNM E48647.

Paratypes. Type locality and date, USNM 1008093 (31); NMV F101866 (5).

Other material. Scotia Sea, 55°01'–59°37'S, 26°00'–45°05'W, 1071–3040 m, USNM E48601 (4); E48653 (3); E49243 (10); NMV F101865 (3); USNM E49251 (1); E49253 (12); E49254 (49); NMV F101867 (5); USNM 1008094–1008096 (7); 1022457 (9); 1022461 (1); South Sandwich Trench, 5350 m, USNM 1071583 (8); South Shetland Is, 884–935 m, USNM 1005127 (2); 2119–2562 m, E48569 (1); W of Elephant I., 2672–3020 m, E48625 (1); N of Amundsen Sea, 4682 m, USNM 1022460 (1); 4866–4881 m, E48649 (2); 4709 m, E48650 (1); NW of Amundsen Sea, 4575–4813 m, E48631 (1).

Description. Up to 143 mm long; body tapered anteriorly and posteriorly, frequently rounded in transverse section, sometimes with transverse folds and ridges; ventrolateral margin commonly rounded, sometimes with distinct serrated margin created by transverse folds; body wall firm, soft, thin (small to medium specimens) to thick (largest specimens), surface wrinkled and pustulose; some specimens with grit or globigerine attachments; complete cover of scattered small tube feet, predominantly not extended, frequently evident as a broad ventrolateral band, frequently extended and close pygally, frequently lost with loss of outer body wall, cylindrical not thread-like when extended, not villous or matted, sometimes contiguous pygally, never ventrolaterally, typically 0.5 mm long, 0.2 mm diameter pygally and when extended ventrolaterally, 0.2 mm diameter when contracted; ossicles in tentacles only, abundant to sparse to absent, irregular rods, thick to thin to wide, some perforated, frequently narrow rods with large central knob and pointed ends, some long thin rods with closely intertwined branches at ends, some with short branches, some with blunt spines, up to 300 µm long.

Colour. Body reddish-brown to brown, smallest grey, largest off-white; tube feet typically dark reddish-brown to chocolate, creating a spotted appearance.

Etymology. From the Latin *morbillus* (measles), referring to the typically spotted body appearance created by the dark-coloured tube feet.

Distribution. Amundsen Sea, Scotia Sea, 681–4881 m.

Remarks. One specimen was covered by a rhizomatous epibiotte with vertical tongue-like stems, that could be mistaken as a character of the species. *M. morbillus* is similar to *M. crinitus* (above), from which it is distinguished by: smaller, usually contracted, tube feet (thick and extended in *M. crinitus*, typically 2.0 mm long, 0.3 mm diameter, up to 3.0 mm long, 0.5 mm diameter); tube feet which are scattered and never contiguous ventrolaterally (often matted ventrolaterally in *M. crinitus*); and tube feet which are darker in colour than the body wall (same colour as body wall in *M. crinitus*).

Table 3. Revised systematic status of the ten syntypes of *Pseudostichopus villosus* Théel, 1886 and variety *P. villosus* var. *violaceus* Théel, 1886.

| Challenger | BMNH Registration | Type status | Revised systematic status |
|--------------------------------|-------------------|---------------|---|
| stn 244 | 86.10.2.147 | Lectotype | <i>Molpadiodemas villosus</i> (Théel, 1886) |
| stn 157 | 86.10.2.155 | Paralectotype | <i>Molpadiodemas villosus</i> (Théel, 1886) |
| stn 156 | 86.10.2.156 | Holotype | <i>Molpadiodemas violaceus</i> (Théel, 1886) |
| stn 61 | 86.10.2.145 (2) | Syntypes | <i>Molpadiodemas violaceus</i> (Théel, 1886) |
| stn 147 | 86.10.2.154 | Syntype | <i>Molpadiodemas violaceus</i> (Théel, 1886) |
| stn 325 | 86.10.2.150 | Syntype | <i>Molpadiodemas violaceus</i> (Théel, 1886) |
| stn 216 | 86.10.2.151 | Holotype | <i>Molpadiodemas neovillosus</i> sp. nov. |
| stn 302 | 86.10.2.153 | Syntype | <i>Pseudostichopus</i> ? <i>peripatus</i> (Sluiter, 1901) |
| Unconfirmed (small specimens): | | | |
| stn 146 | 86.10.2.148 | Paralectotype | <i>Molpadiodemas villosus</i> (Théel, 1886) |
| stn 156 | 86.10.2.146 | Paralectotype | <i>Molpadiodemas villosus</i> (Théel, 1886) |
| stn 296 | 86.10.2.152 | Paralectotype | <i>Molpadiodemas villosus</i> (Théel, 1886) |

Amongst *Molpadiodemas* species, the distinguishing characters are: conspicuous ventrolateral band of small dark cylindrical tube feet which create a spotted appearance; tentacle ossicles irregularly present, frequently narrow rods, tapered at ends, with central knob; absence of gonad ossicles.

***Molpadiodemas neovillosus* sp. nov.**

Table 3, Figures 5e–g, 6e–h, 8e, f

Pseudostichopus villosus Théel, 1886: 170–171 (part; syntype from Challenger stn 216 only; non *Pseudostichopus villosus* Théel, 1886, lectotype designated below).

Material examined. Holotype. Syntype, *P. villosus* Théel, 1886. Northern Pacific Ocean, Caroline Is, 2°56'N, 134°11'E, 3658 m, Challenger stn 216, 16 Feb 1875, BMNH 86.10.2.151.

Paratypes. Galapagos Is, 2°34'N, 92°6'W, 2487 m, USNM 18275 (1); NMV F101847 (1); 4°33'S, 87°42'W, 3667 m, USNM 1008458 (1).

Other material. North Pacific Ocean, Mexico, S of Punta Maldonado, 3436 m, USNM 18276 (1).

Description. Up to 70 mm long; body rounded in transverse section, narrower anteriorly and posteriorly, lacking tubercles on pygal lobes, lacking brim; body wall thin, smooth, thicker and wrinkled if contracted, lacking globigerine or sponge spicule attachments; tube feet in conspicuous ventrolateral wide band, continuous anteriorly and pygally, feet cylindrical, frequently overlapping and matted, typically 1.6 mm long, 0.3 mm diameter; tube feet smaller, more spread, dorsally, smallest ventrally; broad, flat longitudinal muscles about 4.0 mm wide; multiple branching gonad tubules; ossicles in tentacles and gonads; tentacle ossicles abundant rods, variable form, predominantly thin, curved, smooth to rugose, not spinous, blunt to tapered, frequently intertwined at ends, rarely branched or with slight mid-rod swelling, some with lateral fused branches creating narrow mesh, rods up to 320 µm long; gonad ossicles abundant rods, predominantly thin, long, rarely branched, straight to slightly bent to irregular, rarely with slight swelling mid-rod, up to 350 µm long.

Colour. Body and tube feet pale brown to off-white.

Etymology. From the Latin *neo* (new, recent), referring to this recently recognized new species with villous ventrolateral tube feet.

Distribution. Central Pacific Ocean, Caroline and Galapagos Is, Mexico, 2487–3667 m.

Remarks. Théel (1886) commented specifically on this specimen, noting that “the individual obtained at Station 216 is remarkable in that the pedicels of the dorsal surface and the sides of the body are slightly thicker and larger than those of the ventral surface which are thread-like and very minute”. Further to this comment is the observation that the tube feet are largest and most dense and frequently matted in a wide ventrolateral band which extends around the anterior and posterior ends of the body.

Amongst *Molpadiodemas* species, the distinguishing characters are: ventrolateral band of villous cylindrical tube feet that are distinctly smaller than those of the similar *M. crinitus* (above); tentacle ossicles predominantly thin curved rods with intertwined ends, some with slight swelling centrally; gonad ossicles abundant thin, short to very long, rods.

***Molpadiodemas pediculus* sp. nov.**

Figures 5h–k, 8g–h

Material examined. Holotype. South Atlantic Ocean, NE of South Sandwich Is, 55°07'S, 25°59'W, 5435–5453 m, RV *Eltanin*, Cr 8 stn 591, 29 Apr 1963, USNM 1008318.

Paratypes. Type locality and date, NMV F104796 (1).

Other material. Scotia Sea, N of South Orkney I., 2800 m, USNM E48635 (1).

Description. Up to 60 mm long; body small, rounded in section, elongate, tapered anteriorly and posteriorly, lacking brim; body wall firm, semi-gelatinous, surface smooth, not covered with attachments; tube feet all over body, overlapping ventrolaterally, distinctly cylindrical, frequently erect, close cover, anteriorly and pygally, typically 1.0 mm long, 0.25 mm diameter, up to 1.5 mm long; tube feet typically shorter, more thread-like, dorsally and ventrally than ventrolaterally; longitudinal muscles broadly attached, relatively narrow, slightly thickened; some unbranched gonad tubules; ossicles in tentacles only, predominantly irregular, thick, rough to smooth, sometimes bluntly spinous rods, swollen mid-rod, tapering at ends, rare branches joined to create thick intertwining mesh, sometimes irregularly tuberos, up to 280 µm long.

Colour. Body, tube feet off-white to pale brown.

Etymology. From the Latin *pediculus* (little foot), referring to the prominent ventrolateral band of small tube feet.

Distribution. South Atlantic Ocean, off South Sandwich and South Orkney Is, 2800–5453 m.

Remarks. Amongst *Molpadiodemas* species, the distinguishing characters are: body tapering orally and anally; close cylindrical tube feet overlapping ventrolaterally; longitudinal muscles broadly attached, relatively narrow, slightly thickened.

***Molpadiodemas porphyrus* sp. nov.**

Figures 2b, 5l, m, 6i–l, 8i–l

Material examined. Holotype. North-west Atlantic Ocean, Caribbean Sea, Venezuelan Basin, 13°30'N, 64°45'W, 3459–3503 m, Norda Thru IRCZM, RV *Bartlett* 1301-82, 27 Nov 1981, USNM E38795.

Paratypes. Type locality, date, depth, USNM 1008206 (1); NMV F101870 (1); type locality, 3428–3476 m, USNM E38792 (1); NMV F101871 (1); type locality, 3422–3464 m, USNM E38797 (2).

Other material. Type locality, date, 3476–3518 m, USNM E38793 (2); 3967–4009 m, USNM E38799 (1); Caribbean Sea, off Cuba, 2997 m, E2589 (1); South-west Atlantic Ocean, off Brazil, 1227 m, E2584 (14).

Description. Up to 115 mm long; body wall thick, firmly gelatinous; some globigerines attached, no overall cover; to varying degrees flattened dorsoventrally, distinct rounded brim laterally, sometimes with slightly pustulose bulges; body covered with small soft flaccid thread-like tube feet, usually spread, sometimes matted in smaller specimens, readily lost with loss of outer body layer, typically 0.7 mm long, 0.15 mm diameter, pygally up to 1.0 mm long, 0.2 mm diameter; ossicles in tentacles and gonad; tentacle ossicles numerous, variable, curved thin spinous rods (predominant in small specimens), closely finely spinous and smooth unbranched thick to broad plate-like rods, sometimes perforated, sometimes branched and intertwined at ends, spinous or smooth mesh, up to 270 µm long; gonad ossicles abundant to sparse, small thin rods, bluntly spinous or smooth or knobbed, branched or unbranched, some branching creating narrow mesh, up to 140 µm long.

Colour. Very soft outer body layer brown, thick semi-gelatinous layer grey with distinct overall violet mauve hue, some sparse violet mauve colour spots; tube feet off-white.

Etymology. From the Greek *porphyro* (purple), referring to the violet mauve colour hue and colour spots.

Distribution. North-west and South-west Atlantic Ocean, Caribbean Sea, and off Brazil; 1227–4009 m.

Remarks. Amongst *Molpadiodemas* species, the distinguishing characters are: firm thick gelatinous body wall; lateral brim; grey-mauve colouration; thread-like flaccid tube feet; tentacle ossicles frequently closely bluntly spinous.

***Molpadiodemas pustulosus* (Sluiter, 1901) comb. nov.**

Pseudostichopus pustulosus Sluiter, 1901a: 16–17.—Sluiter, 1901b: 53–55, pl. 4 fig. 6, pl. 9 fig. 1.

Material examined. Lectotype (designated here). Indonesia, Halmahera Sea, 0°45'S, 128°40'E, 827 m, *Siboga*, stn 145, ZMA V.Ech.H1012. Paralectotypes. Lectotype locality and date, ZMA V.Ech.H1011 (1); Ceram Sea, 3°38'S, 131°26'E, 924 m, *Siboga* stn 170, ZMA V.Ech.H1006 (1).

Description. Up to 115 mm long; some globigerines attached; distinct ventrolateral margin with series of nipple-like pustules, most conspicuous posteriorly and around anus on lobes of pygal furrow, some pustules lobed; body covered with elongate tube feet, present but not extended mid-ventrally; tube feet clustered in tufts on posterior pustules; gonad tubules short, fat, multiple-branching; ossicles in tentacles only; tentacle ossicles non-spinous lace mesh, comprising thin branched joined rods, not perforated plates.

Distribution. Indonesia, Halmahera and Ceram Seas, 827–924 m.

Remarks. During an examination (Apr 2002) of the holothurian types in the University of Amsterdam, four specimens were found to be registered as syntypes of *P. pustulosus*. This was in accord with the catalogue published by Jangoux (1991). But only three syntypes were recorded by Sluiter (1901a). One of the four, registered and recorded by Jangoux (1991) as ZMA 1303 from Station 170, was not conspecific with the other syntypes. Sluiter (1901) reported, and Jangoux (1991) listed, two syntypes of *P. trachus*, but the syntype registered as ZMA E2496/2 was missing from the collection. The extraneous syntype of *P. pustulosus* (ZMA 1303) was conspecific with the syntype of *P. trachus*, and is now registered as a *P. trachus* type (ZMA V.Ech.H2496/2, following the catalogue registration number of Jangoux, 1991). A lectotype of *P. pustulosus* is designated above.

The designated lectotype is the specimen figured by Sluiter (1901b), and does not show all of the characters referred to here in the description. The syntype showing the diagnostic characters most completely, such as the tube feet, is the smallest (ZMA V.Ech.H1006; 63 mm long).

Rowe (1995) judged that *Pseudostichopus propinquus* Fisher, 1907 and *Pseudostichopus nudus* Ohshima, 1915 were junior synonyms of *P. pustulosus*. *M. pustulosus* has the diagnostic characters of *Molpadiodemas* (above), not *Pseudostichopus* (below). Both synonymies are rejected on the grounds of the relevant generic diagnostic characters. *P. propinquus* and *P. nudus* are discussed below. Rowe (1995) identified material from off Newcastle on the eastern Australian slope as *Pseudostichopus pustulosus*. All Australian slope material has been examined and none determined as *P. pustulosus*. Material from off Newcastle (AM J16749) was determined as *P. mollis* (below).

Amongst *Molpadiodemas* species, the distinguishing characters of *M. pustulosus* are: conspicuous nipple-like pustules on the ventrolateral margin; tufts of tube feet on the pustules posteriorly; lace-mesh tentacle ossicles.

***Molpadiodemas translucens* sp. nov.**

Figures 2c, 5n, o, 8m–p, 12e, f

Material examined. Holotype. Weddell Sea, Antarctic Peninsula, 64°07'S, 40°48'W, 4465–4557 m, RV *Eltanin*, USARP Cr 12 stn 1018, 21 Mar 1964, USNM E48652.

Paratypes. Type locality and date, USNM 1008072 (5); NMV F101863 (2).

Other material. South-east Pacific Basin, 4575–4813 m, E49487 (2).

Description. Up to 79 mm long; body wall thin, soft, translucent; no body attachments; body typically rounded in transverse section, not elongate, tapered anteriorly and posteriorly, lateroventral margin sometimes subacute or slightly bulbous; complete body cover of small, cylindrical, soft, scattered tube feet, erect or lying on body, typically 0.3 mm long, 0.1 mm diameter, rarely contiguous over most of body, slightly more concentrated ventrolaterally, most concentrated and frequently contiguous pygally, typically 0.6 mm long, 0.2 mm diameter; longitudinal muscles flat, slightly narrow; ossicles in tentacles and gonads; tentacle ossicles abundant, variable in form, thin to thick tapered smooth distally bluntly pointed rods sometimes with central rounded thickening, rods with intertwined branched ends creating small perforations, rods with fused side branches creating small lateral perforations, fused branches sometimes creating large perforated irregular mesh, ossicles up to at least 520 μm long; gonad ossicles abundant, predominantly thin lace mesh with irregular large perforations, not developed on primary thick rod, some irregular finely spinous thin rods with irregular branching closing to create perforations, ossicles up to 320 μm long.

Colour. Pale greyish brown, with traces of mauve colouration; tube feet off-white to semi-translucent.

Etymology. From the Latin *lux* (light) and *trans* (through), referring to the translucent body wall.

Distribution. South-east Pacific Basin, Weddell Sea, Antarctic Peninsula, 4465–4813 m.

Remarks. Amongst *Molpadiodemus* species, the distinguishing characters are: translucent body wall; lace mesh gonad ossicles.

***Molpadiodemus ustulatus* sp. nov.**

Figures 6m–p, 7a–c, 12q–t

Material examined. Holotype. South-east Pacific Ocean, Peru, Peru-Chile Trench, 8°48'S, 80°40'W, 5069–5173 m, RV *Anton Bruun*, Cr 11 stn 178, 3 Nov 1965, USNM 1022493.

Paratypes. Type locality and date, USNM 1022566 (3); NMV F101858 (1).

Description. Up to 73 mm long; form cylindrical, narrowly elongate, slightly dorsoventrally depressed (possible artefact), lacking brim; outer body wall soft, pustulose, wrinkled; inner body wall soft, thin, semi-gelatinous; close cover of small cylindrical tube feet all over body, extended but not erect, longest and most evident in lateral band, not matted, up to 1.0 mm long, typically 0.6 mm long, 0.2 mm diameter; ossicles in tentacles and gonad; tentacle ossicles abundant smooth rods, thick to thin, straight to curved, some with central swellings, some with short branches, some with intertwined joined ends creating large and small perforations, some irregularly tuberos, up to at least 270 μm long; gonad ossicles numerous thick to thin smooth rods, some lateral branches fused to form mesh with large perforations, fragments up to 280 μm long.

Colour. Body and tube feet very dark brown.

Etymology. From the Latin *ustulatus* (scorched), referring to the dark brown blistered appearance of the specimens.

Distribution. South-east Pacific Ocean, Peru-Chile Trench, 5069–5173 m.

Remarks. The specimens are in poor condition, but adequate for establishing morphological diagnostic characters. Amongst *Molpadiodemus* species the distinguishing characters of *M. ustulatus* are: very dark brown colour; narrowly elongate body; tube feet most evident in lateral band; gonad rod ossicles with open lateral mesh.

***Molpadiodemus villosus* (Théel, 1886) comb. nov.**

Table 3, Figures 2a, e, 7d–f, 8q–t, 12a–d

Pseudostichopus villosus Théel, 1886: 170–171 (part; syntypes from *Challenger* stns 157, 244 only; not *Pseudostichopus villosus* var. *violaceus* Théel, 1886).

Material examined. Lectotype (designated here). North-west Pacific Ocean, off Japan, 35°22'N, 169°53'E, 5304 m, *Challenger* stn 244, BMNH 86.10.2.147.

Other material. Paralectotype, Southern Indian Ocean, 53°55'S, 108°35'E, 3566 m, *Challenger* stn 157, BMNH 86.10.2.155 (1).

Northern Pacific Ocean, Clarion-Clipperton Fracture Zone, no depth, USNM E48492 (1); Galapagos Is, 3667 m, E9929 (1); South-east Pacific Basin, N of Amundsen Sea, 5042–5045 m, USNM 48659 (3); 4709 m, E49280 (1); 4676 m, E48584 (1); 4740–4742 m, E49333 (5); N of Marie Byrd Land, 4682 m, E48658 (1); Ross Sea, 3495–3514 m, E48583 (4); 2005–2010 m, E48620 (7); NMV F101859 (2).

North Atlantic Ocean, North American Basin, 3264–3356 m, USNM 1006292 (1).

Scotia Sea, S of South Georgia I., 3413–3446 m, USNM E48634 (1); E48633 (8); NMV F98745 (2); 2742–2758 m, USNM E48640 (2); NMV F101860 (2); 2384–2416 m, USNM E49257 (1, with commensal gastropods); South Georgia I., 3166–3255 m, USNM E48609 (1); South Shetland Is, 681–1409 m, E48571 (2); N of Bellingshausen Sea, 4941 m, E48589 (1).

Description. Up to 110 mm long; body variably elongate and tapered anteriorly and posteriorly; subcylindrical, lacking brim, sometimes sac-like; lacking globigerine or sponge spicule or grit attachments; body wall thick semi-gelatinous to thin firm, surface smooth to wrinkled and pustulose; tube feet small, soft, hair-like, never erect, close to sparse cover over whole body, dorsally typically 1.5 to 2.0 mm long, up to 3.0 mm long, 0.05 mm diameter; tube feet sometimes matted ventrolaterally, anteriorly and pygally, typically 1.0 to 1.3 mm long, 0.2 mm diameter; ventral tube feet frequently withdrawn, if extended typically 0.5 mm long, 0.2 mm diameter; gonad tubules unbranched and multibranched; ossicles in tentacles and gonad; tentacle ossicles abundant, variable form, large, up to 530 μm long, frequently rods perforated entire length, rods variably with mid-rod swelling, thick rods with branches at ends intertwined to create mesh, thick rods with lateral joined branches creating mesh, large mesh ossicles (intertwined, joined rods, not perforated plates), club-shaped rods with minute perforations, smooth thick to thin rods tapered at ends, sometimes blunt spines, some knots of thick irregularly branching rods; gonad ossicles abundant, long thin branched and unbranched

irregular rods, many with lateral mesh with large perforations, many thick smooth rods with central knobbed swelling, many central knobs elongating into short thick branches which fuse to create perforations, up to 270 μm long.

Colour. Greyish-white, sometimes with reddish-brown hue; tube feet off-white, sometimes pale brown ventrolaterally.

Distribution. Atlantic, Indian, Pacific and Southern Oceans, Ross Sea, N of Amundsen Sea, N of Bellingshausen Sea, Scotia Sea; 681–5304 m.

Remarks. Théel (1886) listed ten syntypes of *P. villosus* (nominal subspecies *villosus*), plus a type of his variety *P. villosus* var. *violaceus*. All have been examined in this study. Théel noted the “villous” appearance of the specimen from stn 244 and it is this one we have chosen as lectotype. One other, from stn 157, is a paralectotype. Of the others, the one from stn 216 is not conspecific and is described above as the new species, *M. neovillosus*.

Four of the remaining types are also not *P. villosus*. The type of the variety and three of the syntypes are referred below to the species *Molpadiodemas violaceus* (Théel, 1886). The seventh syntype (Southern Pacific Ocean, off Chile, 42°43'S, 82°11'W, 2652 m, *Challenger* stn 302, BMNH 86.10.2.153) is not *P. villosus*. It was 80 mm long, and had a close cover of globigerines, strong transverse ridges ventrally, an acute serrated ventrolateral margin, and cylindrical longitudinal muscles. No gonad was present. It is probably *Pseudostichopus peripatus* (Sluiter), but there is insufficient evidence to confirm a determination. The three remaining syntypes are small, and remain unconfirmed paralectotypes: stn 146, BMNH 86.10.2.148 (1); stn 156 (of two lots from this Station the lot with the *P. villosus* syntype), BMNH 86.10.2.146 (1); stn 296, BMNH 86.10.1.152 (1).

Dr Frank Rowe (pers. comm.) observed eggs or embryos amongst the tentacles of the paralectotype (stn 157), and considered the possibility of brood-protection. The observation was confirmed during this study.

The distribution of *P. villosus* given by O'Loughlin (2002) is not valid, since only one of the syntypes is conspecific with the designated lectotype, and most previous determinations of *P. villosus* are in doubt.

Amongst *Molpadiodemas* species, the distinguishing characters are: close to sparse body cover of small, hair-like, off-white tube feet, sometimes matted ventrolaterally and pygally; gonad ossicles.

Molpadiodemas violaceus (Théel, 1886) comb. nov.

Table 3, Figures 1e, i, 2f, 7g–i, 8u–x

Pseudostichopus villosus var. *violaceus* Théel, 1886: 172, pl. 10 fig 6b (raised to species status here).

Pseudostichopus villosus Théel, 1886: 170–171 (part; syntypes from *Challenger* stns 61, 147, 325; non *Pseudostichopus villosus* Théel, 1886).

Material examined. Holotype. *Pseudostichopus villosus* var. *violaceus* Théel, 1886. Southern Ocean, off Shackleton Ice Shelf, 62°26'S, 95°44'E, 3612 m, *Challenger* stn 156, BMNH 86.10.2.156.

Other material. *Pseudostichopus villosus* Théel, 1886. Syntypes. North-western Atlantic Ocean, 34°54'N, 56°38'W, 5212 m, *Challenger* stn 61, BMNH 86.10.2.145 (2); southern Indian Ocean, off Crozet I., 46°16'S, 48°27'E, 2926 m, *Challenger* stn 147, BMNH 86.10.2.154 (1); south Atlantic Ocean, off Argentina, 36°44'S, 46°16'W, 4846 m, *Challenger* stn 325, BMNH 86.10.2.150 (1).

Weddell Sea, S of South Orkney Is, 3587–3660 m, USNM E48600 (1); 1008106 (4); NMV F101844 (2).

South Atlantic Ocean, Scotia Sea, South Orkney Is, 2196 m, USNM E49337 (2); 3250–3285 m, E48651 (11); NMV F101843 (2); Burdwood Bank, 3514–3642 m, USNM E48627 (1); 4026–4063 m, E48654 (2); South Sandwich Is, 5435–5453 m, E48637 (6); NMV F101842 (2); 4758 m, E48626 (1); 1190–1469 m, 1022456 (3); Drake Passage, 3788–3944 m, USNM 1008117 (1); 2324–3020 m, E48591 (1).

South Pacific Ocean, Chile, depth unknown, USNM E48636 (1); Peru-Chile Trench, 6006 m, E48611 (1); 6146–6354 m, 1022608 (2); NMV F101848 (1); 5069–5173 m, USNM 1022609 (1); SE Pacific Basin, 4731 m, E48630 (3); 4773 m, E49334 (1); 3859 m, E48657 (3); 4572–4848 m, E49366 (1); 3694 m, E48605 (2); 4682 m, 1022455 (1).

Description. Up to 220 mm long; body wall leathery, pliable, surface folded and wrinkled, sometimes mucilaginous; sparse small grit and globigerine attachments; body rounded in transverse section, tapered anteriorly, posteriorly, frequently sac-like; ventrolateral margin rounded, not distinctive, lacking brim, mouth terminal ventral; even cover of small soft cylindrical tube feet all over body, never erect, evident in small specimens only, slightly larger anteriorly and pygally, may be matted, typically 1.0 mm, long, 0.3 mm diameter, frequently withdrawn in small pits, not evident on smooth leathery body wall of largest specimens; ossicles in tentacles abundant, rare in gonad; tentacle ossicles variable, predominantly bluntly tapered rarely curved unbranched smooth thick rods with distinct knob-like central swelling, some rods lacking central swelling, some rods with bifurcate or intertwined ends, some with lateral and terminal perforations, rare blunt spines and knobs, rods frequently 250 μm long, up to 350 μm long; gonad ossicles rarely present, straight and irregular sometimes bluntly spinous short thin rods, some with central swelling, some branching creating perforations, never mesh ossicles, up to 150 μm long.

Colour. Brown to grey-brown to off-white; tube feet brown to pale brown to off-white.

Distribution. Atlantic, southern Indian and Pacific, and Southern Oceans, Weddell Sea, Scotia Sea, SE Pacific Basin, 2196–6354m.

Remarks. Théel (1886) established ten syntypes for *Pseudostichopus villosus*, and a holotype for *P. villosus* var. *violaceus*. Three of the ten syntypes of *P. villosus* are conspecific with the type of *P. villosus* var. *violaceus*.

Amongst *Molpadiodemas* species, the distinguishing characters are: leathery body wall; tube feet inconspicuous in large specimens, when small even cover of soft cylindrical tube feet with some anterior and pygal matting; tentacle ossicles frequently thick smooth bluntly-tapered rods, many with large knob-like central swelling; rare presence in gonad of short, thin rod ossicles.

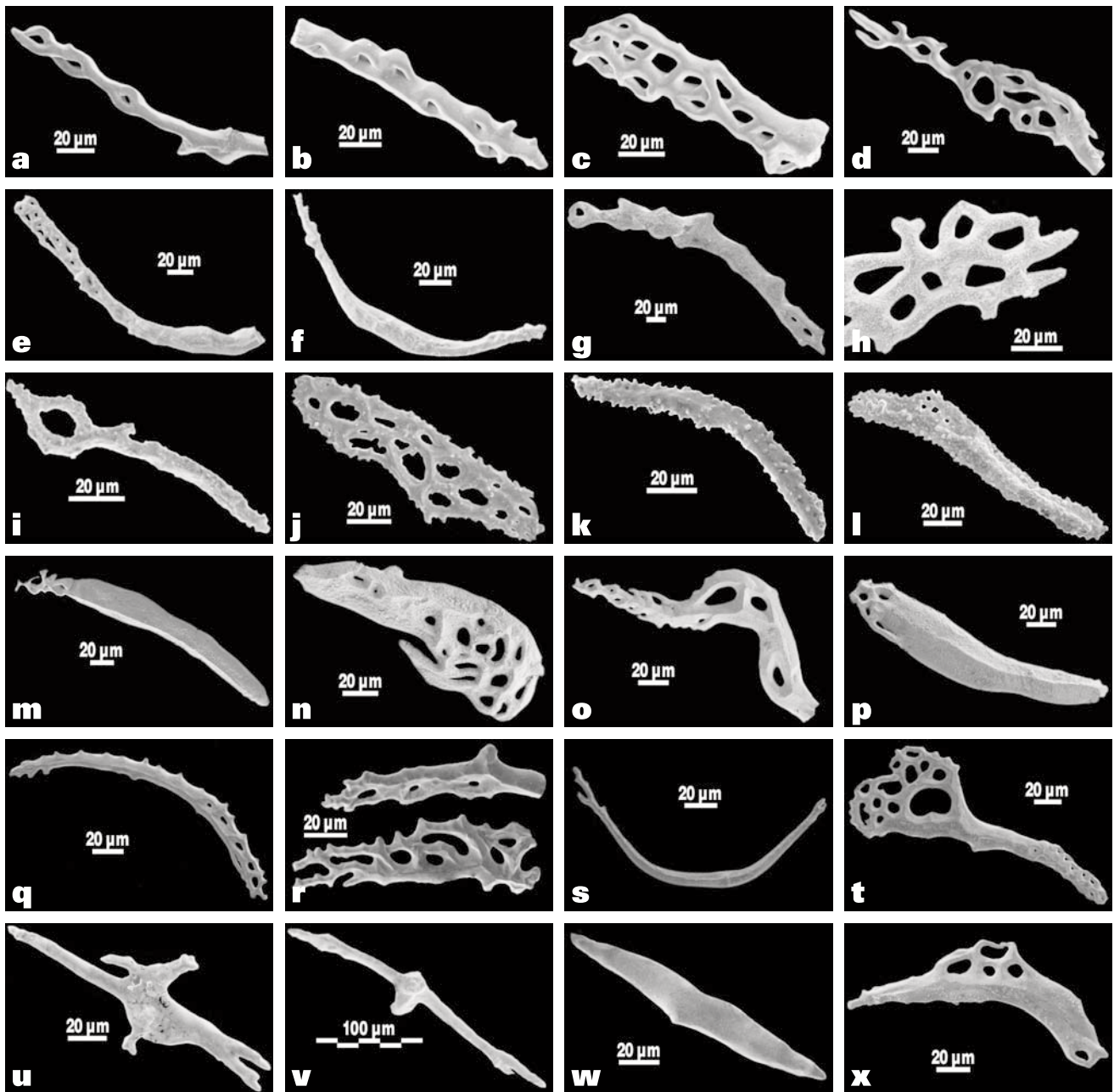


Figure 8. Tentacle ossicles (SEM). a–d, *Meseres morbillus* sp. nov. (USNM E49251). e–f, *M. neovillosus* sp. nov. (USNM 1008458, paratype). g–h, *M. pediculus* sp. nov. (USNM 1008318, holotype). i–l, *M. porphyrus* sp. nov. (USNM E38795, holotype). m–p, *M. translucens* sp. nov. (USNM E48652, holotype). q–t, *M. villosus*, q–r (USNM E48640), s–t (USNM E9929). u–x, *M. violaceus*, u–v (USNM 1022608), w–x (USNM E49366).

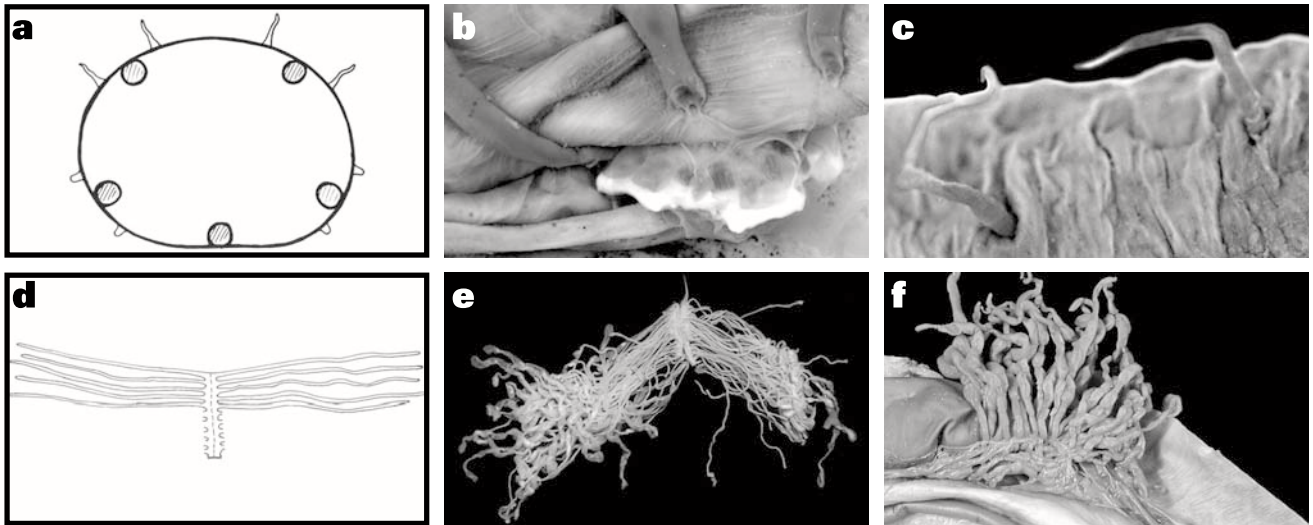


Figure 9. Characters of *Pseudostichopus*. a, drawing of transverse section of mid-body (as in *P. mollis*); b, cylindrical longitudinal muscles detached from calcareous ring (*P. tuberosus* sp. nov., NMV F101864, paratype); c, dorsolateral radial papillae (*P. elegans*, NMV F97447, papillae up to 8 mm long); d, drawing of part of gonad, unbranched tubules, arising separately along gonoduct; e, two series of unbranched gonad tubules along gonoduct (*P. mollis*, TM H2004); f, gonad (*P. tuberosus* sp. nov., paratype, USNM 1008333).

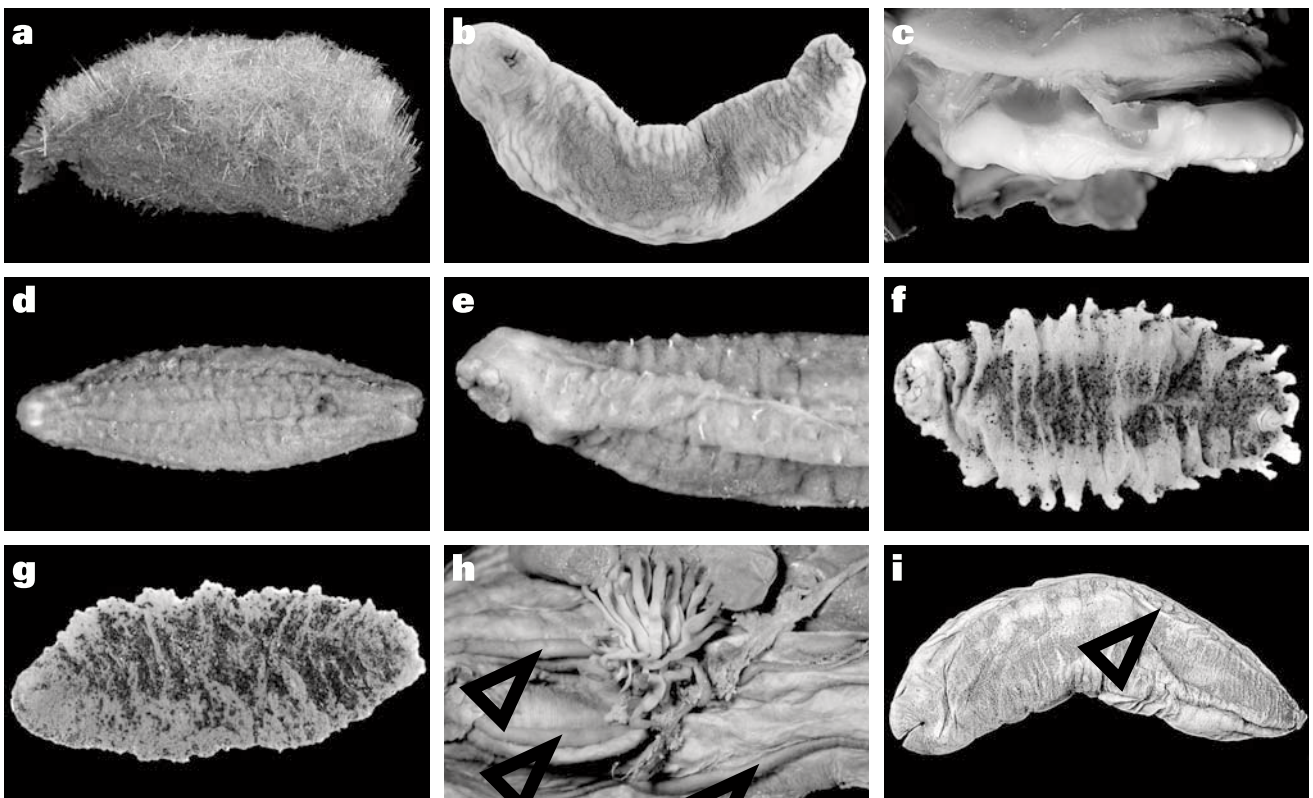


Figure 10. a, *Pseudostichopus hyalegerus*, sponge spicule cover (*P. japonensis*, paratype, SMBL 314, junior synonym, 29 mm long). b–c, *P. mollis*; b, rugose ventrum (TM H3111, 145 mm long); c, calcareous ring (TM H2004). d–e, *P. papillatus* (RAS, syntype, 27 mm long); d, dorsal view of paired radial tubercles; e, ventrolateral view, tube feet. f–h, *P. peripatus*; f, ventral view, marginal tubercles, grit attachment, transverse creases (NMV F101840, 60 mm long); g, ventral view, marginal tubercles, grit attachment, transverse creases (NMV F101839, 45 mm long); h, cylindrical muscles (arrows), gonad tubules (*P. tuberculatus*, holotype, OMNH Iv1190, junior synonym). i, *P. tuberosus* sp. nov. (USNM E16721, holotype, 115 mm long), ventral view, lateroventral tubercles (arrow).

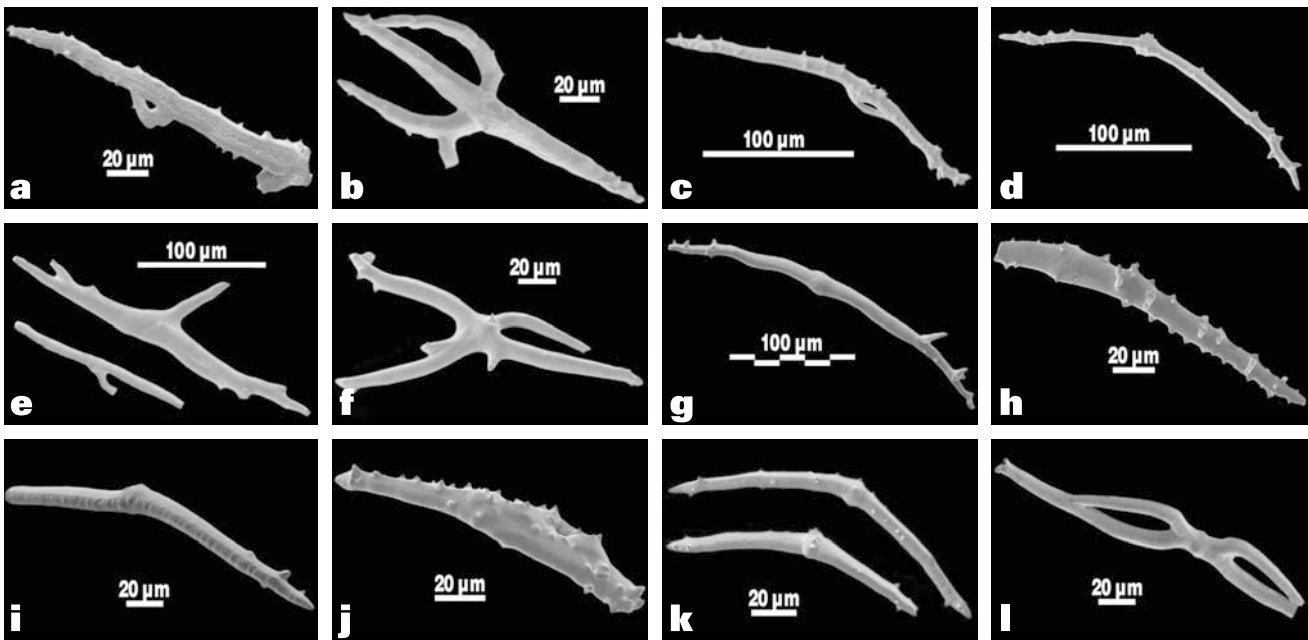


Figure 11. Tentacle ossicles (SEM). a–b, *Pseudostichopus aemulatus* (USNM 1025525, paratype). c–d, *P. elegans* (USNM E16505). e–f, *P. mollis* (USNM E48656). g–h, *P. tuberosus* sp. nov. (USNM E16721, holotype). i–l, *P. peripatus*, i (USNM 12198), j (USNM E38794), k (USNM E38796), l (USNM E49349).

Pseudostichopus Théel, 1886

Table 1, Figure 9

Pseudostichopus Théel, 1886: 169.—Ludwig, 1894: 38.—Perrier, 1902: 337–338.—Hérouard, 1902: 11.—Fisher, 1907: 691.—Mitsukuri, 1912: 3.—Hérouard, 1923: 21–23.—Ekman, 1925: 32–36.—Ekman, 1926: 451–470, fig. I.—Mortensen, 1927: 386–388.—Deichmann, 1930: 86–87.—Heding, 1940: 356, 358–360.—Djakonov, 1952: 125.—Imaoka, 1978: 377–378.—Thandar, 1992: 163–164.—Rowe, 1995: 285.—O'Loughlin, 1998: 497.—O'Loughlin, 2002: 304.

Filithuria Koehler and Vaney, 1905: 81–81.—Heding, 1940: 356–357 (new synonym).

Pseudostichopus (*Pseudostichopus*).—Heding, 1940: 357, 360.—Imaoka, 1978: 378.—Thandar, 1992: 164.

Pseudostichopus (*Trachostichopus*) Heding, 1940: 357, 361.—Imaoka, 1978: 380 (new synonym).

Plicastichopus Heding, 1940: 357 (nomen nudum).—Heding, 1942: 5–6 (new synonym).

Peristichopus Djakonov, 1952: 125 (new synonym).

Type species. *Pseudostichopus mollis* Théel, 1886 (subsequent designation by Fisher, 1907).

Other included species. *Pseudostichopus aemulatus* Solís-Marín and Billett, 2004; *P. echinatus* Thandar, 1992; *P. elegans* (Koehler and Vaney, 1905); *P. hyalegerus* (Sluiter, 1901); *P. mollis* Théel, 1886; *P. occultatus* Marenzeller, 1893; *P. papillatus* (Djakonov, 1952); *P. peripatus* (Sluiter, 1901); *P. profundus* Djakonov, 1952; *P. spiculiferus* (O'Loughlin, 2002); *P. tuberosus* sp. nov..

Diagnosis. Characters of pygal-furrowed Synallactidae (above); prominent appendages (tube feet, papillae) along the paired radii only; longitudinal muscles cylindrical, not flat,

narrowly attached to the body wall; gonad tubules not branched, arising in series along the gonoduct, not from a common base; ossicles sometimes present in tube feet and papillae; tentacle ossicles predominantly unbranched rods, rarely rods with ends intertwining and side branches fused to create mesh.

Distribution. Cosmopolitan; 91–5453 m.

Remarks. The larger radial appendages of the species of *Pseudostichopus* are frequently tapered and variably elongate, extremely so in *P. elegans* (below), and when distinctly tapered are described in this work as papillae rather than tube feet.

The monotypic genus *Filithuria* Koehler and Vaney, 1905 was established for *F. elegans* Koehler and Vaney, 1905 which is assigned here to *Pseudostichopus* and described in detail below. *F. elegans* has the diagnostic characters of *Pseudostichopus* (above), and the dorsolateral radial papillae are distinctively elongate. The dorsolateral appendages in the type species for *Pseudostichopus*, *P. mollis*, are moderately elongate and distinctly tapered, and have the appearance of papillae more than tube feet. The length of the dorsolateral papillae is an inadequate single character on which to maintain the monotypic genus *Filithuria*, which becomes a junior synonym of *Pseudostichopus*.

Heding (1940) erected the genus *Plicastichopus* citing as type species the manuscript name *Plicastichopus ingolfi*. Until he formalised the name in 1942, the genus remained a nomen nudum. O'Loughlin (2002) synonymised *P. ingolfi* Heding, 1942 with *Meseres peripatus* (Sluiter), *Plicastichopus* Heding, 1942 becoming a junior synonym of *Meseres*. *Meseres peripatus* is reassigned below to *Pseudostichopus*, *Plicastichopus* now becoming a junior synonym of *Pseudostichopus*.

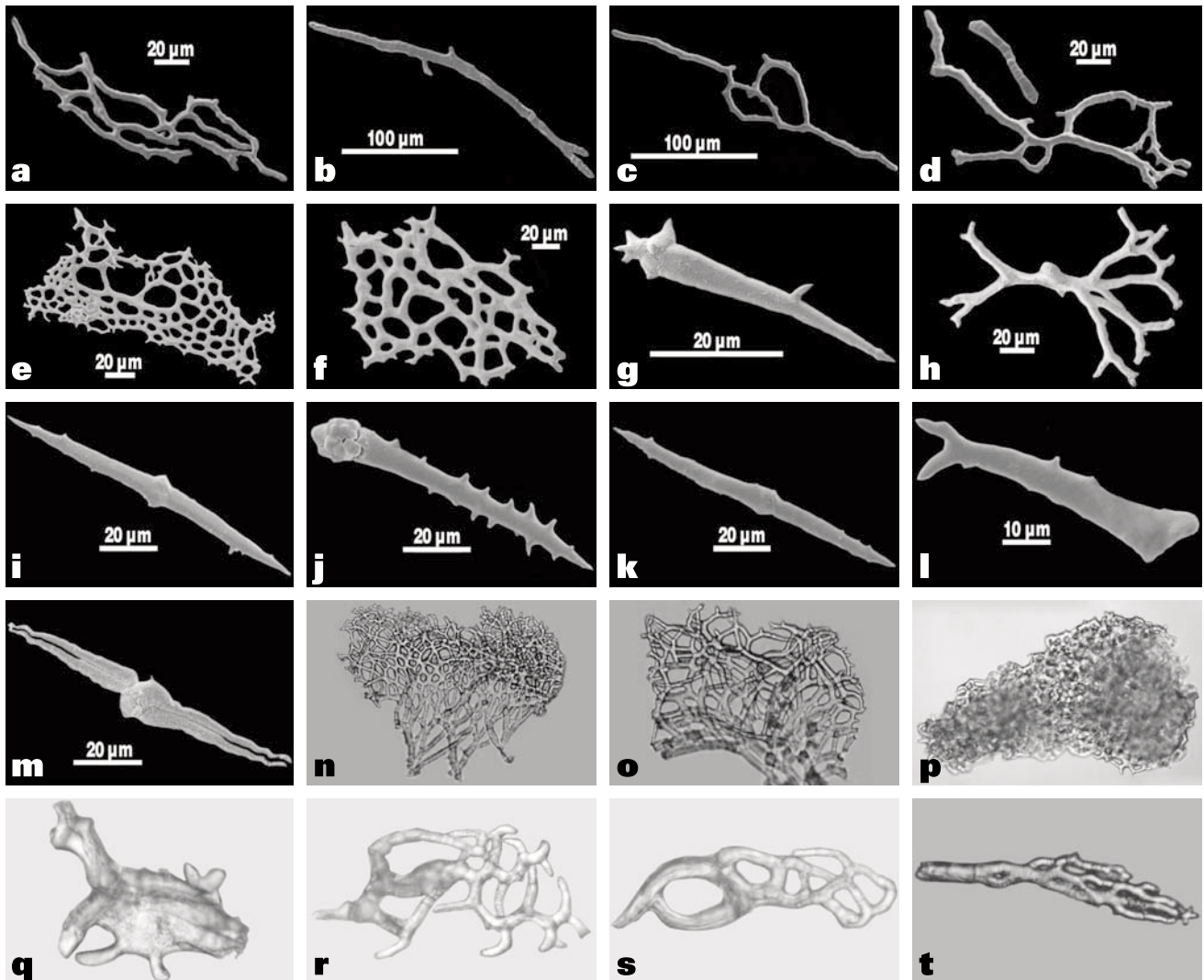


Figure 12. Gonad ossicles (SEM). a–d, *Meseres villosus* (USNM E9929). e–f, *M. translucens* sp. nov. (USNM E48652, holotype). g–h, *Pseudostichopus peripatus*, g (USNM 12198), h (USNM E48638). i–l, *P. tuberosus* sp. nov. (USNM E16721, holotype). m, *P. aemulatus* (USNM 1025525, paratype).

Posterior lobe ossicles (compound microscope). n–p, *P. hyalegerus*, n–o (NMV F80181), p (NMV F80178).

Tentacle ossicles (compound microscope). q–t, *M. ustulatus* sp. nov. (NMV F101858, paratype).

Heding (1940) erected the subgenus *Trachostichopus* (of *Pseudostichopus*), with type species *Pseudostichopus trachus* Sluiter. Rowe (1995) referred *trachus* to *Meseres* Ludwig, *Pseudostichopus* (*Trachostichopus*) becoming a junior synonym of *Meseres*. *P. trachus* is considered below to be a junior synonym of *Pseudostichopus mollis*, *Trachostichopus* now becoming a junior synonym of *Pseudostichopus*.

The monotypic genus *Peristichopus* was established for *Peristichopus papillatus* Djakonov, 1952. Djakonov (1952) characterised the genus by: cylindrical body; ventral mouth, anus; pygal furrow; small tube feet on paired radii; cylindrical longitudinal muscles; unbranched gonad tubules in two bundles; tentacles with rod ossicles, some rod ossicles perianally and in tube feet; and body wall, genital tubules, respiratory

trees lacking ossicles. Djakonov (1952) noted that *Peristichopus* was close to *Pseudostichopus*, but gave no diagnostic distinctions. *Peristichopus papillatus* is very close to *Pseudostichopus mollis*, and no justification is found here for maintaining *Peristichopus* Djakonov which is a junior synonym of *Pseudostichopus* Théel.

Pseudostichopus aemulatus Solís-Marín and Billett, 2004

Figures 11a, b, 12m

Pseudostichopus sp.—Billett, 1988: 196–197.—Billet et al., 2001: 325–348.

Pseudostichopus aemulatus Solís-Marín and Billett (in Solís-Marín et al.), 2004: 1079–1084, figs 1, 2, tables 5, 6.

Material examined. Paratypes. Northeast Atlantic Ocean, Porcupine Abyssal Plain, 48°45'–48°48'N, 16°36'–16°41'W, 4835–4838 m, RRS *Discovery*, stn 54901#5, 28 Apr 1999, USNM 1025525 (3).

Description. Up to 146 mm long; body wall thick, gelatinous, opaque, sometimes encrusted with foraminiferans and sand; distinct brim, flat ventrally, convex dorsally; body surface smooth, lacking close wrinkling with ridges and digitate projections; tapering papillae in double irregular series on dorso-lateral radii, series not widely separated, papillae typically up to 1.5 mm long, 1.0 mm diameter at base; papillae in widely separated double series ventrolaterally, dorsal to or ventral to or on brim; ossicles in tentacles and gonad; tentacle ossicles abundant, tapering rods, thick to thin, finely to bluntly spinous or smooth, with or lacking mid-rod swelling, rarely with short branches, up to 260 µm long; gonad ossicles predominantly small, thin, pointed, unbranched rods with mid-rod swelling, some with sparse blunt spines, rods up to 140 µm long.

Colour. Body off-white.

Distribution. NE Atlantic Ocean, Porcupine Abyssal Plain, 4350–4850 m (Solís-Marín et al., 2004).

Remarks. *P. aemulatus* is similar to *P. peripatus* (below), but is distinguished by: body wall off-white (not greyish), opaque (not semi-translucent), smooth (lacking ridges with digitate projections); dorsolateral double series of papillae not widely separated; ventrolateral double series of papillae widely separated; papillae lack ossicles; gonad ossicles predominantly unbranched pointed rods with mid-rod swelling. These characters also distinguish *P. aemulatus* from other *Pseudostichopus* species.

***Pseudostichopus echinatus* Thandar, 1992**

Pseudostichopus (Pseudostichopus) sp.—Heding, 1940: 360–361, fig. 16.

Pseudostichopus (Pseudostichopus) echinatus Thandar, 1992: 164–167, fig. 2.

Description (based on the descriptions by Heding, 1940, as *P. (Pseudostichopus) sp.*, and Thandar, 1992, and on additional observations by A. Thandar, pers. comm.). Up to 65 mm long; dense dorsal and lateral encrustation of shells, globigerines, sand; subcylindrical body; 19 tentacles; scattered cover of very small tube feet, some more prominent dorsolateral tube feet evident amongst encrustations, series of ventrolateral tube feet in prominent series; longitudinal muscles cylindrical; unbranched gonad tubules in 2 series along gonoduct; ossicles in tentacles and tube feet only; tentacle ossicles irregular closely knobbed rods with some branching and perforations created by joined branches, not mesh-like, up to 300 µm long.

Distribution. Indian Ocean, off eastern Africa, 1°41'–28°22'S, 32°35'–41°47'E, 200–825 m.

Remarks. *P. echinatus* is known from the holotype (SAM A23435), a specimen discussed by Heding (1940), and a recent specimen from KwaZulu-Natal, 200 m (A. Thandar, pers. comm.). It has the diagnostic characters of *Pseudostichopus* above. Amongst *Pseudostichopus* species the distinguishing characters of *P. echinatus* are: encrusting cover of shells,

globigerines and sand; very irregular closely knobbed tentacle rod ossicles; absence of gonad ossicles.

***Pseudostichopus elegans* (Koehler and Vaney, 1905) comb. nov.**

Figures 9c, 11c, d

Filithuria elegans Koehler and Vaney, 1905: 81, pl. 6 figs 1, 2, pl. 12 figs 29–31.—Heding, 1940: 357, 362–363, fig. 18.

Material examined. NE Pacific Ocean, off Oregon, 3021 m, USNM E16815 (1); 1008097 (3); 2510 m, USNM E16505 (3); NMV F97447 (1); 2884 m, USNM E16497 (1); 2710 m, E16490 (4); NMV F97446 (1).

Description. Up to 145 mm long; elongate, subcylindrical, tapering anteriorly and posteriorly, flat ventrally, high convex dorsally, sometimes brim weakly developed; body wall thick, leathery, firm thin outer layer, soft thin semi-gelatinous inner layer; surface smooth dorsally and laterally, rugose ventrally; paired radii with double series of long tapering papillae, very thin distally, longest in upper dorsolateral series, up to 22 mm long, smaller in lower dorsolateral and double ventrolateral series; small tube feet all over body, up to 0.5 mm long, 0.3 mm diameter; ossicles in tentacles, papillae, tube feet; tentacle ossicles abundant tapering rods, long to short, thick to thin, with or lacking central thickening, rare short branching, spinous or smooth, up to 490 µm long; large dorsal papillae with rods similar to tentacles, some more sharply and abundantly spinous, shorter, up to 260 µm long; small papillae and tube feet with thick to thin rods, many with central swelling, bluntly spinous or smooth, short, up to 160 µm long.

Colour. Body violet-brown to reddish-brown to off-white; gonad tubules and respiratory trees pale brown; longitudinal muscles chocolate to reddish-brown.

Distribution. Bay of Bengal, off Andaman Is., 741 m (Koehler and Vaney, 1905); Indian Ocean, off Sumatra, 750 m (Heding, 1940); North-east Pacific Ocean, off Oregon, 2510–3021 m (this paper).

Remarks. Koehler and Vaney (1905) and Heding (1940) reported single specimens of *Filithuria elegans*. *Filithuria* Koehler and Vaney is considered above to be a junior synonym of *Pseudostichopus* Théel. The distribution of *P. elegans* is extended here from the Indian Ocean to the NE Pacific Ocean, to greater depths. Amongst *Pseudostichopus* species the distinguishing characters of *P. elegans* are: distinctly long papillae on the paired radii; numerous tapered rod ossicles in the papillae.

***Pseudostichopus hyalegerus* (Sluiter, 1901) comb. nov.**

Figures 10a, 12n–p

Meseres hyalegerus Sluiter, 1901a: 12.—Sluiter, 1901b: 50–51, pl. 5 figs 2–4.—Perrier, 1902: 359.

Pseudostichopus trachus.—Mitsukuri, 1912: 3–9, pl. 1 figs 1–5.—Ohshima, 1915: 227–228.—Mortensen, 1918: 80–81, fig. 16 (non *Pseudostichopus trachus* Sluiter, 1901).

Pseudostichopus (Trachostichopus) tachimaruae Imaoka, 1978: 380–382, fig. 2A–E, table 1–2 (synonymy by O'Loughlin, 2002).

Pseudostichopus (Trachostichopus) japonensis Imaoka, 1978: 382–384, fig. 3A–D, table 1–2.—Imaoka, 1990: 148 (synonymy by O'Loughlin, 2002).

Pseudostichopus molpadioides Ohshima, 1915: 228–229, pl. 8 figs 6a–c.—Heding, 1940: 353–359.—Imaoka, 1978: 384, tables 1, 2.—Imaoka, 1990: 152.—O’Loughlin, 2002: 304–305 (new synonym).

Pseudostichopus arenosus Ohshima, 1915: 229.—Heding, 1940: 353–359.—Imaoka, 1978: table 1–2.—O’Loughlin, 2002: 304–305 (new synonym).

Material examined. *Meseres hyalegerus* Sluiter. Syntypes. Indonesia, Banda Sea, 5°28’S, 132°00’E, 204 m, Siboga stn 251, ZMA V.Ech.H9499 (1); ZMA V.Ech.H2177/1 (6); ZMA V.Ech.H21772/2 (1, mounted on glass in alcohol).

Pseudostichopus (Trachostichopus) tachimaruae Imaoka. Holotype. Japan, W of Kyushu, near Shimo-Koshiki I., 400–450 m, T. Imaoka, 27 Oct 1976, SMBL 311. Paratypes. Type locality, date, SMBL 312 (2).

Pseudostichopus (Trachostichopus) japonensis Imaoka. Holotype. Japan Sea, off the Akita Prefecture, 200–300 m, S. Nishimura, 1972–1973, SMBL 313. Paratypes. Type locality and date, SMBL 314 (3).

Other material. North-west Pacific Ocean, Japan, 350–400 m, USNM 1025085 (3); 300–450 m, 1025086 (17); NMV F101861 (5); 420 m, 1071801 (1); Sagami Bay, 128–553 m, Northwest Pacific Expedition, *Albatross* stn 5092, USNM E17147 (42); NMV F101855 (5); stn 4968, USNM 1001645 (1); stn 5069, 1001646 (1); stn 5093, 1001647 (1); stn 5055, 1001648 (5); stn 5094, 1001649 (7).

Eastern Australian continental slope, Tasman Sea and Bass Strait, 293–1100 m, NMV F80171–F80175 (21), F80178 (3), F80181 (19), F80448 (1); 3300–3350 m, AM J23009 (1).

Description. Up to 120 mm long; typically encrusted with dense mat of predominantly sponge spicules, with shells and globigerines; frequently densely covered with tubular, thin, branched, tangled, epibiotite; body dorsoventrally depressed, subacute margin; body wall semi-gelatinous, firm, translucent to opaque, wrinkled with pits and raised protuberances all over body; short papillae on paired radii, sparse irregular double series dorsolaterally, more numerous in band ventrolaterally; papillae cylindrical at base, tapering distally, typically 2.0 mm long, 0.3 mm diameter (at base); gonad tubules predominantly unbranched, rarely singly branched, rarely bifid distally; ossicles in tentacles, papillae, pygal lobes; tentacle ossicles irregular, frequently spinous, elongate rods, branching rare, up to 340 µm long; papillae with rare irregular rods up to 100 µm long; papillae sometimes with “endplates”, very irregular perforated plates or irregular mesh of branched rods, up to 70 µm wide; pygal lobe ossicles single, large, elongate, up to 800 µm long, comprising dense perforated mesh of branched rods connected with open mesh, bluntly spinous marginally.

Colour. Body grey to off-white; papillae pale brown to off-white.

Distribution. West Pacific, Indonesia, Banda Sea, 204 m (Sluiter, 1901a); Japan, Sagami Sea, 141–564 m (Mitsukuri, 1912, as *P. trachus*); Japan Sea, south of Honshu, 128–553 m (Ohshima, 1915, as *P. trachus*); 200–300 m (Imaoka, 1978, as *P. japonensis*); Hokkaido, Shiribeshi, 714 m (Ohshima, 1915, as *P. molpadioides*), Kyushu, Koshiki Is, 781 m (Ohshima, 1915, as *P. arenosus*); 400–450 m (Imaoka, 1978, as *P. tachimaruae*); eastern Australia, Tasman Sea and Bass Strait, 293–1100 m (this work).

Remarks. Eight of the eleven syntypes were present (Apr 2002) in the ZMA and examined. All were taken from the same locality, and the establishment of a lectotype is not necessary.

The characters of *Meseres hyalegerus* are consistent with the diagnosis of *Pseudostichopus*, and *M. hyalegerus* is reassigned to *Pseudostichopus*.

The types of *Pseudostichopus molpadioides* Ohshima, 1915 and *P. arenosus* Ohshima, 1915 cannot be located (see Introduction). The principal characters of *Pseudostichopus molpadioides* given by Ohshima (1915) are: up to 52 mm long; cylindrical form; pygal furrow; covered by sand, foraminiferans, some sponge spicules; 20 tentacles; tube feet in double rows on paired radii, most numerous ventrolaterally, up to 2.0 mm long; unbranched gonad tubules; irregular spiny ossicles perianally, up to 200 µm long; tube feet support rods up to 120 µm long, endplates up to 140 µm wide; lacking gonad ossicles. Ohshima (1915) considered that *Pseudostichopus arenosus* closely resembled *P. molpadioides*, the two species differing only in minor differences in the form of tentacle ossicles and absence of tube feet support rods in *P. arenosus*. In this study the detection of tube foot support rods in *P. hyalegerus* was not consistent, and the differing details of tentacle ossicle form in *P. hyalegerus* fell within the variations reported by Ohshima (1915). *P. arenosus* is considered here to be a junior synonym of *P. molpadioides*. The only characters distinguishing *P. molpadioides* from *P. hyalegerus* are the typical cover of predominantly sponge spicules in the latter, and possible differing form of perianal ossicles. The drawing of a perianal ossicle for *P. molpadioides* by Ohshima (1915) is identical with a fragment of the large perianal ossicles found in *M. hyalegerus*. A variation in body cover from predominantly to only some sponge spicules is considered here to be not diagnostically adequate for distinguishing the species. *P. molpadioides* and *P. arenosus* are thus junior synonyms of *P. hyalegerus*.

O’Loughlin (2002) considered *P. tachimaruae* and *P. japonensis* to be junior synonyms of *M. hyalegerus*, based on the descriptions by Imaoka (1978). The types were examined in this work, and the pygal lobe mesh ossicles unique to *P. hyalegerus* were found in paratypes of both *P. tachimaruae* and *P. japonensis*. The synonymies are confirmed here.

Amongst *Pseudostichopus* species, the distinguishing characters of *P. hyalegerus* are: encrusting mat of sponge spicules and other attachments; ossicles in the papillae and pygal lobes.

Pseudostichopus mollis Théel, 1886

Figures 1b, c, 9a, e, 10b, c, 11e, f

Pseudostichopus mollis Théel, 1886: 169–170, pl. 10 figs 5, 6.—Ludwig, 1898: 7.—Perrier, 1902: 337–338.—Fisher, 1907: 691.—Ekman, 1925: 5, 28–36, figs 4, 5.—Ekman, 1926: 451–470, fig. Id.—Heding, 1940: 353–360.—Imaoka, 1978: table 1–1.—Imaoka, 1990: 148.—Gutt, 1991a: 147, 152, figs 3, 6, table 2.—Gutt, 1991b: 321, 324.—Thandar, 1992: 167.—Rowe, 1995: 285.—O’Loughlin, 2002: 304.

Pseudostichopus trachus Sluiter, 1901a: 15–16.—Sluiter, 1901b: 52–53, pl. 5 fig. 1, pl. 8 fig. 8.—Perrier, 1902: 337–338.—Fisher, 1907: 693.—Ekman, 1925: 32–36.—Savel’eva, 1941: 74.—Djakonov, 1952: 127, 129.—Baranova, 1957: 239.—Djakonov et al., 1958:

366.—Imaoka, 1978: 384.—Cherbonnier and Féral, 1981: 383, 385, fig. 16.

Pseudostichopus nudus Ohshima, 1915: 230.—Ekman, 1925: 32–36.—Heding, 1940: 353–359.—Djakonov et al., 1958: 367.—Rowe, 1995: 285 (as junior synonym of *Pseudostichopus pustulosus*; non *Pseudostichopus pustulosus* Sluiter, 1901; new synonym).

Pseudostichopus (Trachostichopus) trachus.—Heding, 1940: 353–362, fig. 17.—Imaoka, 1978: table 1–2.—Thandar, 1992: 166.

Pseudostichopus (Pseudostichopus) dilatorbis Imaoka, 1978: 378–380, 384, fig. 1 A–E, table 1–1 (part; paratypes non *P. dilatorbis*; new synonym).

Pseudostichopus (Pseudostichopus) alatus Imaoka, 1990: 146–148, fig. 1A–E (new synonym).

Meseres trachus.—Rowe, 1995: 285.—O'Loughlin, 1998: 497.—O'Loughlin, 2002: 300, 312, table 3 (new synonym).

Pseudostichopus pustulosus.—Rowe, 1995: 285 (non *Pseudostichopus pustulosus* Sluiter, 1901).

Material examined. *Pseudostichopus mollis* Théel, 1886. Lectotype (designated here). Southern Pacific Ocean, off Chile, 52°45'S, 73°46'W, 448 m, *Challenger* stn 311, BMNH 2002.293. Paralectotypes, type locality and date, 86.10.2.143 (3), 1956.10.3.6 (2); off Chile, 50°56'S, 74°14'W, 256 m, *Challenger* stn 309A, 86.10.2.142 (3); Southern Indian Ocean, off Marion I., 46°48'S, 37°49'E, 91–137 m, *Challenger* stn 144A, 86.10.2.144 (2).

Pseudostichopus trachus Sluiter, 1901. Lectotype (designated here). Indonesia, Ceram Sea, 1°11'S, 130°09'E, 798 m, *Siboga* stn 161, ZMA V.Ech.H2496.2 (1). Paralectotype, Timor Sea, 8°50'S, 127°02'E, 883 m, *Siboga* stn 286, V.Ech.H2496.1 (1).

Pseudostichopus nudus Ohshima, 1915. Neotype (designated here). North Pacific Ocean, Bering Sea, USA, Alaska, Aleutian Is, Bowers Bank, 54°33'N, 178°45'E, 1019–1068 m, RV *Albatross*, North-west Pacific Expedition, stn 4774, 4 Jun 1906, USNM E10787. Same locality and date, 1008140 (4).

Pseudostichopus (Pseudostichopus) alatus Imaoka, 1990. Holotype. Japan, Tosa Bay, 350 m, H. Horikawa, 30 Jan 1989, OMNH Iv1188. Paratype. Tosa Bay, 390–410 m, Iv1189 (1).

Other material. North Pacific Ocean, Bering Sea, Alaska, Bowers Bank, 1068 m, USNM E10697 (1); off southern California, W of San Nicolas I., 825 m, 32416 (19); off Oregon, 44°36'–46°01'N, 124°40'–124°45'W, 320–466 m, USNM E16503 (13); E16734–E16742 (20); E16745, E167446 (6); E16749–E16752 (9); E16886 (3); E16888 (16); E53270 (2); off San Diego, 572 m, E2042 (2); 762 m, E02035 (4); 379–636 m, E17014 (1); 914–969 m, E17016 (1); 1587 m, 32410 (3); Costa Rica, 245 m, 18269 (2).

South Pacific Ocean, south-eastern Australian continental slope, 460–1200 m, AM J16749 (1); J16836 (1); J20028 (2); J22248 (1); J22938, J22939 (3); J22943 (2); J22955 (5); J22957 (1); J22960 (7); J22964 (1); J22967–J22969 (9); J22972 (1); J22974, J22975 (6); J23218 (1); J23220 (1); J23268 (1); NMV F80176, F80177 (2), F80179, F80180 (5); TM H3111 (1); H3114 (2); W of Cape Sorrell, 972 m, H2004 (2); Tasman Sea, Lord Howe Rise, 1920 m, NMV F97692–F97694 (4); New Zealand, Campbell I., 589–594 m, USNM E48604 (2); Chatham Is, 964–1067 m, E48641 (1); Antipodes Is, 384–397 m, E48665 (7); off Chile, 960 m, 1002911 (2); Macquarie I., NMV F89907 (1); F85036 (4); 900 m, F89908 (1); Strait of Magellan, 485 m, USNM E48639 (3); 256–320 m, E48666 (25); 769–869 m, E48656 (7).

Antarctica, Palmer Archipelago, 460–500 m, USNM 1005855 (1); 460–500 m, 1008441 (2); Antarctic Peninsula, 500–670 m, 1005856 (1); 630–650 m, 1022611 (2).

Description. Up to 225 mm long; body rounded in transverse section, frequently flat ventrally, high convex dorsally; some-

times thick to thin, rounded, ventrolateral brim, especially anteriorly; pygal furrow sometimes barely evident in largest specimens; body wall leathery, firm, thick to thin; anterior mid-dorsal soft inconspicuous madreporite; ventrally frequently rugose, wrinkled with pockets and fine transverse ridges, folds and protuberances sometimes evident along ventrolateral margin, sometimes with raised multilobed tubercles pygally or midventrally or in lateroventral series, tubercles sometimes surmounted by tube feet, ventrum frequently encrusted with globigerines; papillae most evident dorsolaterally in sparse radial band, frequently 2 up to 4 wide, strongly tapered, somewhat whip-like, up to 5 mm long (170 mm long specimen), frequently withdrawn or lost leaving pits; double series of ventrolateral tube feet rarely externally evident; minute tube feet ventrally, rarely evident; ossicles in tentacles, tube feet, perianally; tentacle ossicles numerous to sparse, irregular rods, typically 120–240 µm long, frequently swollen mid-rod, some thin branches, rare blunt spines, branches rarely connecting to create perforations, lacking mesh ossicles, rare large irregular tuber-like ossicles, up to 380 µm long; tube feet ossicles predominantly irregular, smooth, rarely branched rods, frequently with swelling mid-rod, typically 100–130 µm long; pygal lobes with small globular mesh ossicles, difficult to detect.

Colour. Body, tube feet pale brown to off-white; tentacles, longitudinal muscles dark brown to brown; gonad tubules, respiratory trees pale brown.

Distribution. Western Antarctica, Weddell Sea, 65°19'S, 56°48'W, 400 m (Ekman, 1925); Weddell Sea, 340–470 m (Gutt, 1991); North and South Pacific Ocean, southern Indian Ocean, eastern Australian continental slope, Antarctic Ocean in Palmer Archipelago and off Antarctic Peninsula, 91–1587 m (this work).

Remarks. Théel (1886) listed “numerous” syntypes from *Challenger* stn 311. Six of these specimens (in three lots) were examined in the BMNH (Apr 2002), and one disintegrated specimen examined (Apr 2002) in ZMU (ZMA V.Ech.H2999). One of these specimens is designated as lectotype above. Théel (1886) also listed six specimens from stn 309A of which three were examined in the BMNH. Théel (1886) further listed two specimens from stn 144A, and both were present in the BMNH.

During an examination (Apr 2002) of holothurian types in the University of Amsterdam, a type specimen of *Pseudostichopus trachus* Sluiter was found to be registered as *Pseudostichopus pustulosus* (discussed above under *M. pustulosus*). This specimen is designated the lectotype for *P. trachus*. O'Loughlin (2002) judged material referred to *P. trachus* by Mitsukuri (1912) and Ohshima (1915) to be *M. hyalegerus*, and raised doubts about determination of material as *P. trachus* by Heding (1940), Savel'eva (1941), Baranova (1957), Djakonov et al. (1958), and Cherbonnier and Féral (1981).

Significant features of the types of *P. trachus* are: large size, up to 180 mm long (Sluiter, 1901b); slightly dorsoventrally depressed, flat ventrally, convex dorsally, pygal furrow, leathery wrinkled body wall, subacute pustulose margin with distinct small irregular protuberances; densely covered with globigerine attachments; tube feet all withdrawn, paired radial

series ventrolaterally, small ones ventrally (Sluiter 1901b), dorsal tube feet sparsely evident dorsally (Sluiter, 1901b); cylindrical longitudinal muscles ("not round in cross section" according to Sluiter, 1901b), but seen here to be round but sometimes slightly flattened); long thin unbranched gonad tubules; "teeth" on posterior margin of radial plates of ring; tentacle ossicles irregular thick rods, sometimes branched, branches sometimes fused to create perforations, smooth or with large thorny spines, sometimes with central swellings, up to 200 μm long; tube foot ossicles short smooth tapered rods, frequently with central swelling; body wall, gonads, respiratory trees lacking ossicles. The types were taken in Indonesia at 798–883 m. In all respects, except the dorsal cover of globigerines and uncertain distribution of dorsolateral tube feet, *P. trachus* is indistinguishable from *P. mollis*. Many specimens of *P. mollis* have a dense ventral encrustation of globigerines, and quite wrinkled and pitted and ridged and pustulose ventrum and lateroventral edge. The presence of encrusting globigerines dorsally is considered to be not grounds for separating the species diagnostically. The various forms and sizes of the tentacle ossicles are noticeably similar for the *P. mollis* and *P. trachus* types, as are the teeth on the radial plates of the ring. The longitudinal muscles are cylindrical, and sometimes slightly flattened, in both species. The gonad tubules are uniquely long and thin and unbranched in both species. *P. mollis* is found on the Australian continental slope at depths similar to those of the *P. trachus* types. This study has shown that the degree to which the ventrolateral margin develops protuberances and serrations varies from strongly developed to non-existent within the same species such as in *Pseudostichopus peripatus* below. Similarly the ventrum may be relatively smooth or strongly pustulose with raised protuberances as observed here for *P. mollis*. *P. trachus* is thus judged here to be a junior synonym of *P. mollis*.

The "Type" for *P. nudus* nominated by Ohshima (1915), and given USNM Cat. No. 34150, cannot be traced (see Introduction). A neotype, selected from Ohshima's original material, is designated above. *P. nudus* has all but one of the distinguishing characters of *P. mollis*: firm, leathery body wall; potentially large sac-like form; small tapered tube feet on the paired radii; cylindrical longitudinal muscles; very long unbranched gonad tubules, in series along gonoduct; tentacles with irregular rod ossicles; tube feet with small rod ossicles with central swellings; absence of gonad, respiratory tree, posterior lobe ossicles. Ohshima (1915) distinguished *P. nudus* by a midventral band of tube feet which were each surrounded by pustular protuberances. A prominent midventral band of tube feet arising from protuberances was seen in a number of specimens in this study, but other specimens showed a range of ventral conditions intergrading with *P. mollis*. Small tube feet are present ventrally in *P. mollis*, and in some specimens become evident and in some arise from irregular swollen protuberances. *P. nudus* is also considered here to be a junior synonym of *P. mollis*.

Rowe (1995) considered *P. nudus* to be a junior synonym of *P. pustulosus*. This synonymy is rejected above (see *M. pustulosus*). Rowe (1995) identified material from off Newcastle on

the eastern Australian slope as *Pseudostichopus pustulosus*. All Australian slope material has been examined and none determined as *P. pustulosus*. Material from off Newcastle (AM J16749) was determined as *P. mollis*. Ludwig (1894) referred material to *P. mollis*, but illustrated (Ludwig, 1894, pl. 9 figs 5–9) ossicles from the genital tubules that are similar to those in the gonads of *P. peripatus* (see below). At least some of the material was not *P. mollis*, which consistently lacks gonad ossicles.

The two paratypes of *P. dilatorbis* have all the diagnostic characters of *P. mollis*, and are so assigned (see above).

The distinctive features of the two type specimens of *P. alatus* are: up to 115 mm long; pale brown to white, opaque body encrusted with sponge spicules, foraminiferans, shell, sand; 19 pale brown tentacles; tube feet on paired radii, more numerous ventrolaterally; very small tube feet ventrally; long thin unbranched gonad tubules in series along gonoduct; ossicles in tentacles only, not in gonads or tube feet; tentacle ossicles irregular rods about 150–400 μm long, frequently with fairly large spines, rare branching. The types of *P. alatus* exhibit all of the characteristics of *P. mollis* and *P. trachus*, and these observations are confirmed by the description of Imaoka (1990). *P. alatus* is considered here to be a junior synonym of *P. mollis*.

Amongst *Pseudostichopus* species, the distinguishing characters of *P. mollis* are: leathery brown body wall; typical absence of a dense cover of globigerines or sponge spicules; distinct papillae on the paired radii; absence of gonad ossicles.

Pseudostichopus occultatus Marenzeller, 1893

Pseudostichopus occultatus Marenzeller, 1893a: 15–17, pl. 4 fig. 9.—Marenzeller, 1893b: 10, pl. 2 fig. 3a–c.—Perrier, 1902: 337–338.—Mortensen, 1918: 81.—Mortensen, 1927: 387–388.—Deichmann, 1930: 89–90.

Molpadiodemas occultatus.—Heding, 1940: 353–359.

Meseres occultatus.—O'Loughlin, 1998: 497.—O'Loughlin, 2002: 307, tables 1, 3.

Material examined. Syntypes. Mediterranean Sea, Crete, 35°4'N, 24°17'E, 1445 m, 31 Aug 1891, MNHN EcHh 3658 (2); USNM 18294 (2).

Description. Up to 40 mm long; encrusted with shell, sand, sponge spicule attachments; body dorsoventrally depressed, flat ventrally, low convex dorsally, acute ventrolateral margin or thin brim; body wall parchment-like, wrinkled with low reticulate ridges; appendages most evident as papillae dorsolaterally and in ventrolateral band, typically 1 mm long; ossicles in tentacles, pygal lobes, tube feet, respiratory trees; tentacle ossicles thick to thin irregular rods, some with central swellings, rare short branches, rare blunt spines, lacking mesh developments, up to 280 μm long; pygal lobe ossicles irregular perforated plates, partly double-layered, up to 400 μm long; tube foot ossicles smooth tapered rods with central swelling, typically 80 μm long, "endplates" clusters of very irregular twisted branched rods or irregular perforated plates, typically 80 μm wide; respiratory tree ossicles abundant thin, smooth, symmetrically branched, pointed rods, typically 80 μm long.

Colour. Body surface appearance brown, body wall texture grey.

Distribution. Mediterranean Sea, 415–1445 m (Marenzeller, 1893a); North Atlantic, Spain, off Cape Finisterre, 363–510 m (Marenzeller, 1893b).

Remarks. *P. occultatus* has the diagnostic characters of *Pseudostichopus*, and is returned to its original combination. O'Loughlin (2002) described thin, tubular appendages covering the whole body. These are considered here to be epibiotes. Amongst *Pseudostichopus* species, the distinguishing characters of *P. occultatus* are: short, thin, smooth, distally pointed, symmetrically branched, respiratory tree ossicles; "endplate" ossicles; irregular, partly double-layered, perforated plate ossicles in the pygal lobes.

Pseudostichopus papillatus (Djakonov, 1952) comb. nov.

Figures 10d, e

Peristichopus papillatus Djakonov, 1952: 125–127, figs 11–14.

Material examined. Syntypes. Russia, SE of Kamtchatka, 52°45'N, 161°41'E, 4100–4200 m, 25 Jul 1946, RAS (6).

Description. Up to 65 mm long; torpedo-shaped body, some gravel attachments; translucent body wall; prominent small tapered papillae, arising singly on wart-like tubercles in double rows on paired radii, typically 1.5 mm long; ossicles in tentacles, papillae; tentacle ossicles unbranched thick to thin, irregular rods, some swollen centrally, rugose at ends, some bluntly spinous, up to 280 µm long; papillae ossicles irregular branching rosette-like endplates, irregular rods, some swollen centrally, some spinous, up to 260 µm long.

Distribution. Russia, SE of Kamtchatka, 4100–4200 m.

Remarks. Djakonov (1952) referred this species to his new genus *Peristichopus*, which is considered above to be a junior synonym of *Pseudostichopus*. Amongst *Pseudostichopus* species, the distinguishing characters of *P. papillatus* are: the regular paired series of low tubercles and papillae on each of the paired radii; rosette-like "endplate" ossicles in papillae.

Pseudostichopus peripatus (Sluiter, 1901) comb. nov.

Figures 1f, 10f–h, 11i–l, 12g, h

Meseres peripatus Sluiter, 1901a: 10–11.—Sluiter, 1901b: 48–49, pl. 5 fig. 5, pl. 8 fig. 7.—Perrier, 1902: 359.—Rowe, 1995: 285.

Pseudostichopus occultatus.—Hérouard, 1902: 14–15, pl. 2 figs 4–14 (part, illustrated; non *Pseudostichopus occultatus* Marenzeller, 1893).

Pseudostichopus occultatus var. *plicatus* Koehler and Vaney, 1905: 9–10, pl. 3 fig. 8, pl. 9 figs 1–3.—Heding, 1940: 353 (non *Pseudostichopus occultatus* Marenzeller, 1893).

Pseudostichopus propinquus Fisher, 1907: 691–693, pl. 71 fig. 3, pl. 72 fig. 2, pl. 73 fig. 3, pl. 74 fig. 1, pl. 76 fig. 3.—Imaoka, 1978: 382 (new synonym).

Pseudostichopus aleutianus Ohshima, 1915: 228, pl. 8 figs 5a–c.—Imaoka, 1978: 380.

Pseudostichopus unguiculatus Ohshima, 1915: 230–231, pl. 8 figs 7a–c.—Imaoka, 1978: 384.—Rowe, 1995: 285.

Pseudostichopus marenzelleri Hérouard, 1923: 25.—Mortensen, 1927: 287–288.—Deichmann, 1930: 90.

Pseudostichopus lapidus Hérouard, 1923: 26–28, pl. 4 fig. 5.

Pseudostichopus (Pseudostichopus) lapidus.—Heding, 1940: 353–360 (new synonym).

Pseudostichopus (Pseudostichopus) marenzelleri.—Heding, 1940: 353–359.—Imaoka, 1978: table 1–1.—Thandar, 1992: 167 (synonymy by O'Loughlin, 2002).

Pseudostichopus (Pseudostichopus) unguiculatus.—Heding, 1940: 353–360.—Imaoka, 1978: table 1–1.—Imaoka, 1990: 152.—Thandar, 1992: 167 (synonymy by Rowe, 1995).

Pseudostichopus (Trachostichopus) aleutianus.—Heding, 1940: 353–359.—Imaoka, 1978, table 1–2 (synonymy by O'Loughlin 2002).

Plicastichopus plicatus.—Heding, 1940: 354–359.—Heding, 1942: 6. (synonymy by O'Loughlin, 2002).

Pseudostichopus (Trachostichopus) propinquus.—Heding, 1940: 357.—Imaoka, 1978: table 1–1.—Imaoka, 1990: 148, 152.

Plicastichopus ingolfi Heding, 1942: 5–6, figs 4–5, pl. 1 figs 4–5.

Pseudostichopus (Trachostichopus) tuberculatus Imaoka, 1990: 149–152, pl. p. 149, fig. P. 15. (synonymy by O'Loughlin, 2002).

Meseres ingolfi.—Rowe, 1995: 285 (synonymy by O'Loughlin, 2002).

Meseres propinquus.—O'Loughlin, 2002: 309.

Material examined. *Meseres peripatus* Sluiter, 1901. Lectotype (designated here). Indonesia, Flores Sea, 7°24'S, 118°15'E, 794 m, *Siboga* stn 45, ZMA V.Ech.H9500. Paralectotypes. Type locality and date, ZMA V.Ech.H1048 (2); Maluka Sea, 1°59'N, 125°01'E, 1200 m, *Siboga* stn 122, ZMA V.Ech.H1049 (1); Banda Sea, 5°41'S, 120°46'E, 1158 m, *Siboga* stn 211, ZMA V.Ech.H1050 (2).

Pseudostichopus propinquus Fisher, 1907. Holotype. Hawaiian Is, 21°11'N, 156°35'W, 518–519 m, USNM 21217.

Pseudostichopus lapidus Hérouard, 1923. Syntypes. North Atlantic Ocean, off the Azores, 4020 m, Monaco stn 527, 1895, MOM (3) (examination by M. Bruni, pers. comm., MOM).

Pseudostichopus (Trachostichopus) tuberculatus Imaoka, 1990. Holotype. Japan, Tosa Bay, 660–700 m, H. Horikawa, 23 May 1989, OMNH Iv1190.

Pseudostichopus unguiculatus Ohshima, 1915. Syntypes. North Pacific Ocean, off Japan, 1058–1680 m, *Albatross* stns 4960, 5083, 5084, USNM 34151 (2), E24543 (1), E24544 (1).

Other material. Pacific Ocean, Tasman Sea, eastern Australia continental slope, 823–1750 m, AM J20026, J20027 (3); J23219 (1); J23267 (2); J22980 (9); NMV F80449, F80450 (3); F90070 (2); Philippines, 878 m, USNM E48764 (2); est. 1300 m, E48770 (2); off Thailand, 370 m, I017465 (7); off Oregon, 1646 m, E48586 (3); 411 m, E17035 (2); 1946 m, E1972 (29); Mexico, 1608 m, 32389 (1); 2014 m, 32391 (2); Costa Rica, 1789 m, 18267 (1); Peru–Chile Trench, 3500 m, E53272 (1); NMV F101841 (1); Galapagos Is, 2418 m, USNM 18272 (4); 1158 m, E949 (1); 3667 m, 1008450 (1); 1008457 (2); South-west Pacific Basin, 3386–3422 m, E49306 (1); South-east Pacific Basin, N of Amundsen Sea, 4978–5043 m, E48660 (5); 4709 m, E48590 (1); 4682 m, 1022459 (1); 4575–4813 m, E48629 (1); W Balleny Is, 2836–2864 m, E48632 (2); off Victoria Land, 3459–3492 m, E48624 (2); 566–569 m, 1022604 (2); Ross Sea, 3495–3514 m, 1008176 (1).

North Atlantic Ocean, off Florida, 931m, USNM E1990 (1); off Massachusetts, 3235 m, 12198 (1); 3682 m, E53743 (1); off South Carolina, 1337 m, E2581 (2); Bahamas, 4763–4803, 1021900 (1); 4578–4778 m, 1021902 (1); 4783–4823 m, 1021901 (1); Caribbean Sea, Venezuelan Basin, 3428–3476 m, E38794 (2); 3411–3459 m, E38796 (1).

Weddell Sea, 1025–1153 m, USNM E48573 (1).

South Atlantic Ocean, Scotia Sea, 52°00'–62°30'S, 14°54'–60°40'W, 267–5453 m, USNM E48572 (1); E48574–E48577 (15); E48581 (1); E48585 (9); E48587, E48588 (2); E48592 (1); E48596 (6); E48599 (2); E48602, E48603 (5); E48607, E48608 (5); E48628 (2); NMV

F101840 (1); USNM E48638 (45); E48648 (23); NMV F101839 (5); USNM E49241 (5); E49255 (10); E49325, E49326 (7); E49348, E49349 (2); E49351 (1); E49444, E49445 (3); 1008141 (6); NMV F101838 (3); USNM 1008159, 1008160 (7); 1008166 (5); 1008297 (4); 1022445 (2); 1022463 (3).

Antarctic Ocean, South Orkney Is, 3250–3285 m, USNM 1008177 (3); 1228–1400 m, E49393 (1); South Shetland Is, 662–1120 m, E48570 (1); 884–935 m, E48610 (7); 213–311 m, E49350 (1); South Sandwich Trench, 5350 m, USNM 1071584 (2); Palmer Peninsula, 134 m, E49259 (1).

Description. Up to 140 mm long; form of body variable, typically with encrusting globigerine or grit attachments; body elongate, slightly tapered anteriorly and posteriorly, depressed to varying degrees dorsoventrally, flat ventrally, typically low convex dorsally; body wall firm, leathery, thick to thin, semi-gelatinous, frequently with deep transverse grooves and ridges, frequently wrinkled with low reticulate ridges surmounted by small digitate projections, frequently pitted with withdrawn very small interradial tube feet; ventrolateral margin acute to subacute, rounded, variably serrated by the transverse body folds and irregular transverse creases; ventrolateral margin variable from rounded, to mammiform, to rounded protuberances surmounted by elongate to multiple-knobbed extensions, to knobbed domes further surmounted by smaller knobs or small tube feet or larger radial tube feet; larger tube feet surmount double radial series of mammiform bases, not present midventrally, mammiform base and papilla typically 2.0 mm long; ossicles in tentacles and gonad, larger papillae; tentacle ossicles abundant large irregular rods, thick to thin, terminally tapered, frequently with central swelling, sometimes swollen distally, sometimes with small terminal knobs, sometimes bluntly spinous, sometimes branched along rod with branches closed to create perforations, rods up to 360 μm long; papillae with spinous to smooth rods, frequently with central swelling, up to 160 μm long; “endplates” sometimes detected in papillae as perforated plates with mesh collar or tangled mesh of joined irregular rods, up to 340 μm diameter; gonad ossicles frequently present, abundant, typically small predominantly slender tapering rods with small central hub, spinous to smooth, unbranched or Y- or X-shaped, sometimes irregular thick variably spinous branched rods, up to 200 μm long.

Colour. Body grey to off-white, to residual pale reddish-brown on some small specimens, sometimes semi-translucent; radial tube feet brown, smaller tube feet off-white.

Distribution. Indo-Pacific Region, North and South Pacific Ocean, North and South Atlantic Ocean, Scotia Sea, Antarctic Ocean, Ross Sea, Weddell Sea; 134–5453 m.

Remarks. Seven syntypes of *Meseres peripatus* Sluiter, 1901 are listed (ZMA E1050) by Jangoux (1991). Only two were present when the syntypes were examined (April 2002). *M. peripatus* has the diagnostic characters of *Pseudostichopus* detailed above, and is reassigned.

The description of *P. propinquus* Fisher, 1907 referred to: thin translucent body wall, with some foraminiferan attachment; distinct thickened lateroventral margin, with mammi-

form tubercles surmounted by tube feet; paired radii with tube feet; round longitudinal muscles; unbranched gonad tubules; gonad with fine branched sometimes spinous rod ossicles, up to about 200 μm long; respiratory tree ossicles similar to gonad. All of these characters accord with the diagnosis of *Pseudostichopus* above, and *propinquus* is returned to its original combination. All of the features of *P. propinquus*, except the presence of respiratory tree ossicles, are diagnostic features of *Pseudostichopus peripatus*. Fisher (1907) referred to two specimens. The holotype is in very poor condition, and respiratory tree ossicles could not be confirmed. The second specimen was not located. If gonad-type ossicles were found in the respiratory trees of material otherwise conspecific with *P. peripatus*, this would be judged to be an individual variation rather than a basis for a separate species. *P. propinquus* is considered here to be a junior synonym of *P. peripatus*. Rowe (1995) made *P. propinquus* a junior synonym of *P. pustulosus* Sluiter, 1901. This synonymy is rejected. *P. propinquus* has the diagnostic characters of *Pseudostichopus*, and *P. pustulosus* those of *Molpadiodemas* (above).

Based on the description by Hérouard (1923), on observations communicated by M. Bruni (MOM), and on photographs by Francisco Solis-Marin (UNAM) of a tentacle ossicles slide prepared by Gustav Cherbonnier (MNH box 108 slide 45), the characters of *P. lapidus* are: up to 15 mm long; pygal furrow; encrusting cover of foraminiferans, sand, stones; tube feet on paired radii, small to absent on midventral radius; longitudinal muscles narrow; gonad tubules unbranched; ossicles in tentacles only, lacking in body wall and internal organs; tentacle ossicles predominantly rods without branches and associated mesh. Although gonad ossicles have not been detected, *P. lapidus* has the distinctive characters of *Pseudostichopus peripatus* and it is judged here to be a junior synonym.

O’Loughlin (2002) considered *P. marenzelleri* to be a junior synonym of *P. peripatus*, based on the description and figures by Hérouard (1923). Based on the additional description by M. Bruni (MOM, pers. comm.) of cylindrical longitudinal muscles and unbranched gonad tubules, the synonymy is confirmed here. O’Loughlin (2002) considered *P. tuberculatus* to be a junior synonym of *P. peripatus*, based on the photograph and description in Imaoka (1990). Following an examination of the holotype the synonymy is confirmed.

The considerable variety in ossicle and body form, and cosmopolitan distribution and depth range, suggested to us that there are probably more than one species involved. We were unable to recognize discrete diagnostic characters on which to distinguish further species.

The distribution summary by O’Loughlin (2002) indicated an Indo-Pacific and North Atlantic distribution for *P. peripatus*. Data above extend the distribution to the eastern Pacific, western and southern Atlantic, and Antarctic Oceans, and to significantly shallower and greater depths.

Amongst *Pseudostichopus* species, the distinguishing characters of *P. peripatus* are: dorsoventrally depressed body, with strong wrinkling and transverse creases creating a serrated ventrolateral margin; typical encrusting cover of globigerines or rounded grit attachments, not sponge spicules; rods of various forms in gonads, no mesh ossicles.

Pseudostichopus profundus Djakonov, 1952

Pseudostichopus profundus Djakonov, 1952: 127–129, figs 15–18.

Material examined. Syntype (RAS). Russia, SE of Kamtchatka, 52°45'N, 161°41'E, 4100–4200 m, 25 Jul 1946.

Description. Up to 56 mm long; body cylindrical; body wall thick, opaque, soft; few sand grain attachments; very small tube feet unevenly distributed all over body, lengths variable, largest anteriorly and posteriorly, fewest mid-dorsally and mid-ventrally; 20 tentacles; radial plates of calcareous ring lacking "teeth"; longitudinal muscles cylindrical; gonad tubules unbranched; tentacle ossicles thick, broad, bent, irregular, variably perforated, somewhat mesh-like, typically 200 µm long; tube feet ossicles variable from irregular rods, to knots, to irregular curved mesh-like narrow plates, up to 180 µm long; posterior lobes with rare unbranched rods, irregular ends, up to 0.17 mm long; gonad and respiratory trees with small, smooth, sparse rod fragments.

Colour. Body and tube feet brown to grey.

Distribution. Russia, SE of Kamtchatka, 4100–4200 m.

Remarks. The description above is based on Djakonov (1952). The syntype that was examined here was 27 mm long, and very soft. The longitudinal muscles were rounded laterally, but broadly attached to the body wall and not cylindrical, and are considered here to be flat. No gonad was found. The pygal tube feet were soft, cylindrical, and typically 0.3 mm long, 0.15 mm diameter. No ossicles were found in the tube feet. The absence of ossicles in the tube feet, and flat longitudinal muscles, suggest that the syntype examined here is not conspecific with *P. profundus* as described. Djakonov (1952) described very small, smooth rods in genital tubules and respiratory trees. We judge these to be probably artefacts and not ossicles, since such very small fragmentary rods are frequently present in gonad and respiratory tree preparations.

Reference by Djakonov (1952) to cylindrical longitudinal muscles and unbranched gonad tubules indicate an appropriate assignment of the species to *Pseudostichopus*. But the flat longitudinal muscles, and absence of prominent tube feet on the paired radii, indicate that the syntype examined here belongs in *Molpadiodemas*. The characters of the species, and generic assignment, remain unresolved.

Amongst *Pseudostichopus* species the unique character of *P. profundus* (as described by Djakonov) is the presence of curved mesh-like narrow plates in the tube feet.

Pseudostichopus spiculiferus (O'Loughlin, 2002) comb. nov.

Figure 1g

Pseudostichopus sp. MoV 2068.—O'Loughlin et al., 1994: 253–255.

Meseres spiculiferus O'Loughlin, 2002: 309–312, figs 1a–f, 2a–d, tables 1–3.

Material examined. (See O'Loughlin, 2002). Antarctic Ocean, Weddell Sea, 1554 m, USNM 49279 (1); Antarctic Peninsula, 370–375 m, E48582 (1); 246–270 m, E49242 (2); 326 m, 49258 (2); 460–500 m, E49472 (4); Ross Sea, 73°58'–78°23'S, 168°50'E–161°57'W, 364–728 m, E48598 (2); E48643 (2); E49268, E49269 (7);

1005124 (1); E49287 (2); E49354 (1); E49358 (2); 485–490 m, 1005121 (4); 1005123 (3); New Zealand, Antipodes Is, 2010–2100 m, 1005113 (1).

Description. Up to 105 mm long; body typically encrusted with sponge spicules, sometimes globigerines; body flat ventrally, convex dorsally; lateroventral margin subacute, some reticulate ridges with small digitate projections, lacking prominent ventrolateral projections; irregular double rows of tube feet dorsolaterally, larger along ventrolateral margin in band up to 5 irregular rows wide and continuous around anterior body, sometimes contiguous, up to 3.0 mm long, 0.8 mm diameter; ossicles in tentacles, tube feet and gonad; tentacle ossicles thick to thin, curved to straight irregular rods, frequently swollen mid-rod, rarely swollen terminally, rarely branched, rarely bluntly spinous, up to 320 µm long; tube feet with rods distally, same form as tentacle rods, up to 200 µm long; "end-plates" of close cluster of irregular rods, up to 130 µm wide; gonad ossicles abundant smooth rods, tapered to points at ends, variable shape, frequently with central swelling, X- or Y-shaped or complex multiple branching, branches sometimes joined to create large perforations, ossicles frequently 120 µm long, up to 300 µm long.

Colour. Body off-white or grey or grey-brown; tube feet off-white to reddish-brown.

Distribution. Eastern Antarctica, off Wilkes, MacRobertson, Enderby Lands, 177–695 m (O'Loughlin, 2002); Ross Sea, 364–728 m; Antarctic Peninsula, 246–500 m; Weddell Sea, 1554 m; New Zealand, Antipodes Is, 2100 m.

Remarks. *Meseres spiculiferus* has the diagnostic characters of *Pseudostichopus* above, and is reassigned. The above data extend the distribution of O'Loughlin (2002) from eastern Antarctica to the Weddell Sea and New Zealand Antipodes Is, and depth to 2100 m. Amongst *Pseudostichopus* species, the distinguishing characteristics of *P. spiculiferus* are: dense cover of sponge spicules; absence of large pygal lobe ossicles; lateral band of tube feet; complex branching gonad ossicles.

Pseudostichopus tuberosus sp. nov.

Figures 9b, f, 10i, 11g, h, 12i–l

Material examined. Holotype. North Pacific Ocean, off Oregon, 45°43'N, 125°13'W, 1920 m, *Commando*, 28 May 1964, USNM E16721.

Paratypes. Holotype locality and date, USNM 1008333 (1); NMV F101864 (1).

Other material. North Pacific Ocean, off southern California, 32°33'N, 118°04'W, 1937 m, USNM E17015 (1).

Description. Up to 140 mm long; body wall leathery, thin, firm; body flat ventrally, convex dorsally; prominent single series of ventrolateral protuberances ("warts"), irregularly rounded, typically 2.0 mm wide, domed, soft and thin-walled, or firm and flat, not surmounted by papillae, ventral to series of ventrolateral papillae; body transversely creased and wrinkled ventrally, sometimes dorsally, abundant grit attachments, ventrolateral margin with indentations and lobes created by transverse

creases; irregular double rows of tapering papillae on both paired radii, up to 2.0 mm long; minute tube feet all over body, up to 0.2 mm long; ossicles in tentacles and gonad; tentacle ossicles abundant, predominantly small thick to thin curved rods, bluntly to finely spinous or smooth, swelling mid-rod sometimes, rare short branches, rods up to 340 μm long; gonad ossicles abundant, small unbranched rods, tapering to pointed ends, slightly spinous to smooth, typically with central swelling, up to 140 μm long.

Colour. Body, tube feet and protuberances off-white.

Etymology. From the Latin *tuberosus* ("full of lumps or protuberances"), referring to the distinct large protuberances along each ventrolateral margin.

Distribution. North-eastern Pacific Ocean, off Oregon and southern California, 1920–1937 m.

Remarks. The ventrolateral protuberances are wart-like ("fungiform papillae"), and resemble similar features in *Bathyploetes moseleyi*. Amongst *Pseudostichopus* species the distinguishing characters of *P. tuberosus* are: ventrolateral series of wart-like protuberances; presence of small unbranched tapered rods in the gonad.

Incertae Sedis

Meseres Ludwig, 1894

Meseres Ludwig, 1894: 34, 36, 38.—Perrier, 1902: 359.—Rowe, 1995: 284–285.—O'Loughlin, 1998: 497.—O'Loughlin, 2002: 303–305.

Type species. *Meseres macdonaldi* Ludwig, 1894 (monotypy).

Diagnosis (emended from O'Loughlin, 2002). Up to 30 mm long; completely lacking ossicles; thin translucent body wall; body rounded anteriorly, posteriorly; mouth, anus ventral; lacking pygal furrow; ventrolateral margin with series of pyramidal protuberances surmounted by typically 3 digitate projections / (? tube feet); close body cover of small papillae / (? tube feet) and thin tubular appendages (probably epibiotic); 15 small shield-shaped tentacles; lacking tentacle ampullae; five small radial and five interradial plates in ring; longitudinal muscles undivided; unbranched gonad tubules on each side of dorsal mesentery; respiratory tree comprising two thin-walled tubes with sacs.

Material examined. *Meseres macdonaldi* Ludwig, 1894. Lectotype (designated here). Pacific Ocean, off Costa Rica, Cocos I., 5°56'N, 85°10'W, 2149 m, RV *Albatross* stn 3362, 26 Feb 1891, USNM 30501 (1). Paralectotypes. Pacific Ocean, off Colombia, Malpelo I., 4°3'N, 81°31'W, 1644 m, RV *Albatross* stn 3380, 5 Mar 1891, USNM 18190 (5 now unrecognisable specimens).

Remarks. The diagnosis of *Meseres* by O'Loughlin (2002) was based on the species assigned at that time to *Meseres*, and not exclusively on the type species *M. macdonaldi*. The emended diagnosis is based solely on the description of the type material by Ludwig (1894), and some observations on the remaining type material. The syntypes of *M. macdonaldi* were taken off Costa Rica at 2149 m (USNM 30501 (1)), and off Colombia at

1644 m (USNM 18190 (5)). All are in very poor condition, but a single syntype (USNM 30501) retains some recognisable tissue and body parts. For the purpose of having a precise type locality for this type species of *Meseres*, and some specific tissue for possible molecular analysis, the syntype registered alone is designated here as lectotype.

The characters of *M. macdonaldi* were not illustrated by Ludwig (1894), and all of the type material is in an advanced state of decomposition. Whether the body was covered with tube feet or papillae remains subjective. The upper limit of 15 tentacles (in this study Synallactidae species 30 mm long have more than 15 tentacles), and complete absence of ossicles, indicate that *Meseres* does not belong in the Synallactidae. *Meseres* has most of the characters of the Gephyrothuriidae as re-diagnosed by O'Loughlin (1998), with the exception of digitate tentacles. Ludwig (1894) described small shield-shaped tentacles, but there is no evidence as to what precise form they took. It is relevant to note that one of the two species of the Gephyrothuriidae reviewed by O'Loughlin (1998), *Hadalothuria wolfii* Hansen, had ventrolateral protuberances surmounted by rudimentary (?) tube feet. This feature appears to be shared with *M. macdonaldi*. The description of shield-shaped tentacles is an obstacle to referring the genus to the Gephyrothuriidae and *Meseres*, as exemplified by its type species, is treated here as incertae sedis.

Sluiter (1901) and O'Loughlin (1998, 2002) referred species to *Meseres* principally on the basis of a distinctive ventrolateral margin, and Rowe (1995) on the basis of "gonads in two discrete bunches of divided or undivided tubules, one on each side of the dorsal mesentery". All of these species referred to *Meseres* had 18–20 tentacles, a distinct pygal furrow, and tentacle ossicles, and are hence not congeneric with *M. macdonaldi*. Except for the type species *M. macdonaldi*, and *Meseres* (?) *torvus* (Théel, 1886), all species previously referred to *Meseres* are reassigned above to *Molpadiodemas* Heding or *Pseudostichopus* Théel. O'Loughlin (2002) listed *Molpadiodemas* Heding, 1935, *Trachostichopus* Heding, 1940 and *Plicastichopus* Heding 1940 as junior synonyms of *Meseres* Ludwig, 1894. These three genera are removed from the synonymy, and are discussed under *Molpadiodemas* and *Pseudostichopus* above.

O'Loughlin (2002) referred *Stichopus* (?) *torvus* Théel, 1886 to *Meseres*, based on the original description and the comparison with *Meseres macdonaldi* by Ludwig (1894). The single type specimen was collected in the South Pacific Ocean off Chile at 2516 m. A subsequent examination (Apr 2002) of the type revealed the following: strongly contracted, 160 mm long (210 mm in Théel 1886); cylindrical; irregular double rows of large tube feet on paired radii; dorsal and lateral surfaces covered with long conical papillae of varying sizes, largest ventrolaterally, rare branching; small pygal furrow present as a split above anus (possible artefact); longitudinal muscles round, deeply split (probable artefact); gonad tubules short, sac-like, branched; ossicles not detected in body wall, tentacles, papillae, tube feet, gonad, or respiratory trees. The calcareous ring was not *Pseudostichopus*-like. These characters have little affinity with *Molpadiodemas* Heding or *Pseudostichopus* Théel, and *torvus* is referred back to the original combination *Stichopus* (?) *torvus*.

Acknowledgments

We are grateful for the commitment of resources by successive United States Administrations, which has resulted in the invaluable collections now held by the Smithsonian Institution and which were the principal subjects of this work. We are appreciative of the assistance with materials, resources and advice given by: Nadia Améziane (MNHN); Joke Bleeker (ZMA); Ben Boonen (manipulation of images and format of figures); Susann Braden, Scott Whittaker (USNM; assistance with SEM); Michèle Bruni (MOM); Andrew Cabrinovic, Sheila Halsey, Miranda Lowe (BMNH); Tohru Imaoka (OMNH); David Pawson (USNM); Gary Poore (NMV); Frank Rowe (AM); Alexei Smirnov (RAS); Francisco Solis-Marin (UNAM; recognised additional pygal-furrowed synallactid material in the unidentified collections of the USNM which yielded two of the new species); Ahmed Thandar (University of KwaZulu-Natal); Linda Ward (USNM; assistance with EMU); and Shigeyuki Yamato (SMBL). We are particularly grateful for corrections and suggestions proposed by the editor, Gary Poore, and three reviewers David Pawson, Frank Rowe and Ahmed Thandar.

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