

## Revision of the genus *Phyrella* (Holothuroidea: Dendrochirotida) with the description of a new species from Guam

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### Abstract

Recently collected material from Australia, Japan and Guam allowed us to revise *Phyrella* and describe *Phyrella mookiei* sp. nov. We redefine the genus based on combined morphological and molecular analyses. *Phyrella* unlike most dendrochirotids eviscerate posteriorly. The number of tentacles is variable (14–20), as is the degree of fragmentation of the calcareous ring, calling into question the separation of Phyllophorinae and Semperiellinae, and suggest that *Semperiella* and *Thyonidiella* are synonymous with *Phyrella*. We recognize five species in *Phyrella* (*Phyllophorus trapezus* Clark, 1932, *Phyllophorus fragilis* Mitsukuri & Ohshima, 1912 (synonymized with *Thyonidiella oceana* Heding & Panning, 1954), *Phyllophorus thyonoides* Clark, 1938, *Semperiella drozdovi* Levin & Stepanov, 1999, and *Phyrella mookiei*), assign three others provisionally (*Lipotrapeza ambigua* Cherbonnier, 1988 (synonymized with *Phyllophorus contractura* Cherbonnier, 1988 and *Thyonidiella cherbonnieri* Rowe & Richmond, 2004), *Phyllophorus bedoti* Koehler, 1895, and *Orcula tenera* Ludwig, 1875), considering the last two species *inquirenda*. *Phyrella aculeatus* (Ludwig, 1894), is transferred to *Euthyonidiella*. *Orcula* (*Phyllophorus?*) *dubia* Bedford, 1899, *Thyonidiella exigua* Cherbonnier, 1988 and *Thyonidiella kungi* O'Loughlin, 2012 are provisionally transferred to *Phyllophorus sensu lato*, the first is considered *species inquirenda*. Molecular phylogenetic analysis recovers a well-supported *Phyrella*, but suggests that some genera and subfamilies of Phyllophoridae are not monophyletic.

**Key words:** Sea cucumbers, Phyllophoridae, Indo-Pacific, Australia, Micronesia, Japan, *Phyllophorus*, *Lipotrapeza*, *Thyonidiella*, *Orcula*, Evisceration, Cytochrome oxidase sub-unit 1 (COI)

## Introduction

The Phyllophoridae as defined by Pawson & Fell (1965; Pawson, 1970) encompass dendrochirotid holothuroids with a complex, tubular calcareous ring, and is divided into three subfamilies: the Thyoninae for species with 10 tentacles, and the Phyllophorinae and Semperiellinae for species with more than 10. Prior to Pawson & Fell's (1965) redefinition of dendrochirotid families, the Phyllophoridae was separated from the Cucumariidae by the possession of more than 10 tentacles, thus thyonines were considered to be cucumariids. The distinction between the Phyllophorinae and Semperiellinae is more subtle, and was based mostly on the fragmented nature of inter-radial elements in the calcareous ring of the latter. Heding & Panning (1954) erected the latter for *Semperiella*, *Cladolella*, *Neopentadactyla*, *Neothyridium*, *Pentadactyla*, and *Phyrella*, to accommodate Phyllophoridae with elongated and fragmented inter-radial (in addition to the radial) elements of the calcareous ring. These five genera are distinguished from each other by the number of tentacles (15 vs. 20), presence vs. absence of tables, and geographical distribution (Atlantic vs. Indo-West Pacific). Samyn & Thandar (2003) added *Massinium* by subdividing *Neothyridium*. *Semperiella* was synonymized with *Thyonidiella* (Phyllophorinae in Heding & Panning, 1954) by Rowe & Richmond (2004), calling into question the separation of these subfamilies (see below). Other phyllophorine genera: *Anthochirus*, *Lipotrapeza*, *Phyllophorus*, *Phyllophorella*, *Phyllostauros*, and *Selenkiella* can be distinguished from typical semperiellines by their simple or only slightly fragmented (as in some *Lipotrapeza*) inter-radial elements. The phylogenetic relationships of phyllophorid genera and species, as that of other dendrochirotids remains poorly explored. Recently Smirnov (2012) separated the Thyoninae and Semperiellinae into a separate family, the Thyonidae, restricting the Phyllophoridae to the nominotypical subfamily.

The discovery of a new species of *Phyrella* in Micronesia, together with fresh material of related species led to this revision. Prior to this study, *Phyrella* included 4 species: *Phyrella fragilis* (Mitsukuri & Ohshima, 1912) from Okinawa, Japan, *P. thyonoides* (Clark, 1938) from Western Australia, *P. trapeza* (Clark, 1932) from Queensland, Australia, and *P. aculeata* (Ludwig, 1894) from the Pacific coast of Panama. While *Phyrella fragilis* was described in substantial detail (Ohshima, 1912), the original descriptions of *P. thyonoides* and *P. trapeza* are succinct, with only a few ossicles illustrated. The type specimens of the latter two are also not in good condition; in particular *P. thyonoides* was described based on animals collected in beach drift. Recent biodiversity surveys in Australia, Japan and Guam brought fresh material that allows us to revise, and complete the descriptions of these species with information regarding their ecology and live appearance, as well as to explore their relationship based on DNA sequence data.

It became quickly apparent that not all species assigned to *Phyrella* belong there and conversely that species in related genera may need to be transferred to *Phyrella*. Consideration of all genera of polytentaculate phyllophorids currently recognized (Table 1) shows that *Phyrella* is particularly close to *Thyonidiella/Semperiella*. In addition the large genus *Phyllophorus* remains heterogeneous and includes species that are close to and may belong in *Phyrella*. *Phyrella* was erected for phyllophorids with fragmented inter-radials (a defining character of the Semperiellinae), 20 tentacles, and body wall tables with four pillars. However we found that the number of tentacles in *Phyrella* is more variable than previously recognized, as hinted by Clark (1938), ranging at least between 14–20. We also found that juveniles may have inter-radials composed of a single element, and that the amount of fragmentation observed in the calcareous ring (in particular in the inter-radials) increases through ontogeny. Thus the principal character that distinguishes the Semperiellinae (fragmented inter-radials) and Phyllophorinae (inter-radials entire) is ontogenetically variable, calling into question both subfamily and family (as in Smirnov 2012) level separation. A phylogenetic assessment of the family is beyond the scope of this paper, so we follow the conservative approach of recognizing a broad Phyllophoridae.

Genetic data was particularly informative in guiding us to recognize *Phyrella* as a valid, monophyletic genus, and to confirm intra-specific and intra-generic variability in number of tentacles and shape of the calcareous ring.

The results of our revision highlight the importance of indicating the size of specimens in descriptions. It also suggests that other phyllophorid species may also be misassigned. To cover all potential *Phyrella* species, we

considered all phyllophorid species that have been described with calcareous rings characterized by fragmented inter-radial elements, anal teeth, table ossicles with four pillars (when tables present) and/or perforated plates.

**TABLE 1.** Comparison of recognized genera of Phyllophorinae prior to this study. EA: East Atlantic; EP: East Pacific; IWP: Indo-West Pacific; NEA: North East Atlantic; NZ: New Zealand; WA: West Atlantic.

Genus	Number of valid species	Region	Inter-radials fragmented	Calcareous ring forming a tube	Tentacle number	Tables in body wall	Number of pillars to tables
<i>Lipotrapeza</i>	7	EA, IWP, temperate Australia	no (limited in some)	no	20	no	NA
<i>Selenkiella</i>	3	IWP	no	no	25	yes	4
<i>Phyllophorus</i>	21	NEA, WA, IWP, Japan, temperate Australia	no	no	15–20	yes	4
<i>Phyllophorella</i>	13	IWP, South Africa, temperate Australia, NEA	no	no	20	yes	4
<i>Phyllostauros</i>	1	temperate Australia	no	no	20	no	NA
<i>Anthochirus</i>	1	IWP	no	no	30	yes	4
<i>Cladolella</i>	1	IWP	yes	no	20	no	NA
<i>Neopentadactyla</i>	1	NEA	yes	no	20	yes	4
<i>Thyonidiella</i> (= <i>Semperiella</i> )	5	IWP	yes	no	15	yes	4
<i>Phyrella</i>	4	IWP, temperate Australia, “EP”	yes (no in some juveniles)	no	“20” (14–20)	yes	4
<i>Pentadactyla</i>	2	Japan, NZ	yes	no	20	yes (apomorphic)	2
<i>Massinium</i>	9	IWP, South Africa, temperate Australia	yes	yes	20	yes/no	2
<i>Neothyonidium</i>	10	IWP, Japan, NZ, Brazil	yes	yes	20	yes	2

## Material and methods

Specimens obtained during recent field expeditions in Micronesia, Japan and Australia are deposited at the Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA (UF). Additional material was studied from the Western Australian Museum, Perth, Western Australia (WAM); the Museum Victoria, Melbourne, Victoria, Australia (NMV); US National Museum of Natural History, Washington, DC, USA (USNM); Zoologisk Museum Universitets Copenhagen, Copenhagen (ZMUC); Muséum National d'Histoire Naturelle, Paris (MNHN); and Muséum d'Histoire Naturelle de la ville de Genève, Switzerland (MHNG). Photographs of the syntypes of *Phyrella fragilis*, at the University Museum, University of Tokyo, Japan (UMUTZ), were provided by Junko Inoue and Rei Ueshima. Ossicles were extracted by dissolving tissues in household bleach, rinsed at least 5 times in distilled water, mounted on slides using Euparal as a mounting medium, and illustrated with camera lucida. We examined ossicles found in body wall and podia from mid-dorsum, mid-venter, cloacal region, introvert, and tentacles.

Five types of ossicles were encountered in *Phyrella*: table and rosettes (in body wall), rods (in tentacles), end plates and perforated plates (in pedicels). Three of these are standard, well established terms, but two require definition. The plates in podia that lie near the end plate are termed perforated plates (cf. Ohshima, 1912 and Levin & Stepanov, 1999); the same have also been referred to as “end plate support ossicles” (O'Loughlin *et al.*, 2012),

“perforated supporting plates” (Clark, 1932; Clark, 1938), “Gitterplatte” (Heding & Panning, 1954), “plaques” (Cherbonnier, 1988). We refer to the finely branched ossicles in the body wall as “rosettes” (Ohshima, 1912 and O’Loughlin *et al.*, 2012), the same have also been referred to as “miliary granular plates” (Clark, 1932), “miliary granules or rosettes” (Clark, 1938), “Rosetten” (Heding & Panning, 1954), “corpuscules crépus” (Cherbonnier, 1988), and “dichotomously branched plates” (Levin & Stepanov, 1999).

A portion of the mitochondrial gene cytochrome oxidase subunit 1 (COI) was sequenced for available specimens (see Table 2 for voucher information). DNA was extracted from ethanol-fixed tissues using the Omega Bio-Tek E.Z.N.A. Mollusc DNA kit. Approximately 655 bp of the COI gene was amplified using the echinoderm barcoding primers COIceF (5'-ACTGCCACGCCCTAGTAATGATATTATGGTNATGCC-3') and COIceR (5'-TCGTGTCTACGTCCATTCCACTGTRAACATRTG-3') (Hoareau & Boissin, 2010). PCR conditions were an initial denaturation cycle at 95°C for 90 seconds, followed by 40 cycles of denaturation at 94°C for 1 minute, annealing at 42°C for 40 seconds, elongation at 72°C for 1:00, and a final elongation step at 72°C for 4 minutes. The PCR products were sequenced at the Interdisciplinary Center for Biotechnological Research at the University of Florida. The chromatograms were edited in Geneious 5.5 (Drummond *et al.*, 2011), the sequences aligned with Muscle (Edgar, 2004), and the alignment checked by eye using SeaView (Gouy *et al.*, 2010). The sequences were translated to check for evidence of non-sense or stop codons but none were detected. The sequences have been deposited in Genbank (accession numbers: JX544956-JX544968, KF142162-KF142189, Table 2). We analyzed the sequence data with RAxML 8.0.1 (Stamakis, 2006) using the GTRGAMMA model of molecular evolution on each codon position separately. This model and partition scheme was favored by PartitionFinder 1.1.1 (Lanfear *et al.*, 2012) using the Bayesian Information Criterion. We used the RAxML algorithm allowing to conduct simultaneously the rapid bootstrap analysis (500 replicates) and the search for the best-scoring maximum likelihood tree. We used *Holothuria impatiens* as an outgroup. The tree was deposited in TreeBASE: <http://purl.org/phylo/treebase/phylows/study/TB2:S15218>

## Systematic account

### **Phyllophoridae Östergren, 1907**

#### ***Phyrella* Heding & Panning, 1954**

- *Phyrella* Heding & Panning, 1954: 181, type species: *Phyllophorus trapezus* Clark, 1932, by original designation
- = *Thyonidiella* Heding & Panning, 1954: 171, type species: *Thyonidiella oceana* Heding & Panning, 1954, by original designation; new synonymy
- = ?*Semperiella* Heding & Panning, 1954: 179, type species: *Orcula tenera* Ludwig, 1875, by original designation; synonymy with *Thyonidiella* by Rowe & Richmond, 2004; but see discussion under *Phyrella?* *tenera*.

**Diagnosis.** Small to medium-sized Phyllophoridae with 14–20 tentacles of varying size, typically arranged in an outer and inner circle; the tentacles can be paired or single, and are usually larger in the outer circle. Podia dispersed across body surface, numerous, cylindrical, 100–300 µm in diameter, 1–3 mm in length, all with terminal suckers. Posterior end conical, gradually narrowing to a small cloaca, surrounded by 5 lightly-calcified podia developed as anal teeth. Calcareous ring with both radials and inter-radials with posterior prolongations, composed of multiple plates, closely associated along most of their lengths; anterior margins of radials unequally divided by well-formed notch serving for attachment of retractor muscles; anterior margins of inter-radials arrow-head shaped. Body wall ossicles of (1) tables with a circular/subrectangular disc, usually with 8 regular holes, with a smooth, sometimes slightly serrated rim, and spire with 4 pillars, connected by a single-cross beam, ending in a small, often incomplete crown; (2) rosettes, typically restricted to the introvert and cloacal regions, but sometimes more widespread. Tube feet with perforated plates developed as elongated perforated plates in addition to typical end plates; rosettes also present in podia of the cloacal region. Tentacles with rods. No ossicles detected in cloacal gut tract, cloacal retractor muscles, longitudinal muscles, respiratory trees, intestine. Single Polian vesicle. Single stone canal at least partially embedded in dorsal mesentery or membrane surrounding calcareous ring, ending in small, single madreporite. Gonads in two tufts, one on each side of dorsal mesentery. Respiratory trees extend entire length of animal. Evisceration through cloaca, not involving the pharyngeal complex, respiratory trees, gonads, but only the gut. Known only from shallow-waters (< 10 m) of the Indo-West Pacific.

**TABLE 2.** Information for the specimens included in the phylogenetic analysis with their Catalog numbers and the GenBank accession numbers for the portion of COI. Museum abbreviations: UF: Florida Museum of Natural History; WAM: Western Australian Museum; NMV: Museum Victoria, Australia.

Catalog Number	Genus	species	Locality	GenBank accession
UF 9414	<i>Phyrella</i>	cf. <i>thyonoides</i>	Ningaloo, WA	JX544966
UF 9598	<i>Phyrella</i>	cf. <i>thyonoides</i>	Ningaloo, WA	JX544958
UF 9601	<i>Phyrella</i>	cf. <i>thyonoides</i>	Ningaloo, WA	JX544967
UF 4770	<i>Phyrella</i>	<i>mookiei</i>	Guam	JX544960
UF 10336	<i>Phyrella</i>	<i>mookiei</i>	Guam	JX544957
UF 11013	<i>Phyrella</i>	<i>fragilis</i>	Okinawa, Japan	JX544968
UF 11016	<i>Phyrella</i>	<i>fragilis</i>	Okinawa, Japan	KF142172
UF 11011	<i>Phyrella</i>	<i>fragilis</i>	Okinawa, Japan	JX544965
UF 4096	<i>Phyrella</i>	<i>fragilis</i>	Taiwan	JX544962
WAM Z26012	<i>Phyrella</i>	<i>fragilis</i>	Kimberley, WA	JX544962
WAM Z26013	<i>Phyrella</i>	<i>fragilis</i>	Kimberley, WA	JX544959
WAM Z21215	<i>Phyrella</i>	<i>fragilis</i>	Barrow I, WA	JX544956
NMV F165728	<i>Lipotrapeza</i>	<i>vestiens</i>	Victoria, Australia	JX544961
NMV F151822	<i>Stolus</i>	sp. 1	NW Australia	KF142177
UF 7885	<i>Pentamera</i>	<i>calcigera</i>	Georgia, USA	KF142181
UF 6011	<i>Pentamera</i>	<i>rigida</i>	Washington, USA	KF142166
UF 9494	<i>Stolus</i>	sp. 2	Ningaloo, WA	KF142173
UF 7486	<i>Hemithyone</i>	<i>semperi</i>	Nosy Bé, Madagascar	KF142175
UF 7487	<i>Hemithyone</i>	<i>semperi</i>	Nosy Bé, Madagascar	KF142185
NMV F151830	<i>Havelockia</i>	sp. 1	NW Australia	KF142180
NMV F151829	<i>Havelockia</i>	sp. 2	NW Australia	KF142167
NMV F151855	<i>Thyone</i>	<i>nigra</i>	Victoria, Australia	KF142163
NMV F151847	<i>Thyone</i>	<i>flindersi</i>	Victoria, Australia	KF142164
NMV F150806	<i>Neothyonidium</i>	sp. 1	NW Australia	KF142176
UF 10191	<i>Massinium</i>	<i>magnum</i>	Heron I, Australia	KF142162
NMV F151827	<i>Neothyonidium</i>	sp. 2	NW Australia	KF142179
NMV F150801	<i>Phyllophorus</i>	<i>kohkutiensis</i>	NW Australia	KF142184
NMV F125359	<i>Lipotrapeza</i>	<i>eichleri</i>	SE Australia	KF142182
NMV F127403	<i>Lipotrapeza</i>	<i>eichleri</i>	SE Australia	KF142168
NMV F173274	<i>Phyllophorus</i>	<i>brocki</i>	N Australia	KF142188
UF 9620	<i>Phyllophorus</i>	sp. 1	Ningaloo, WA	KF142170
UF 9621	<i>Phyllophorus</i>	sp. 1	Ningaloo, WA	KF142178
UF 9622	<i>Phyllophorus</i>	sp. 1	Ningaloo, WA	KF142171
UF 9624	<i>Phyllophorus</i>	sp. 1	Ningaloo, WA	KF142174
WAM Z31837	<i>Phyllophorus</i>	sp. 1	Perth, WA	KF142187
WAM Z11501	<i>Phyllophorus</i>	sp. 1	Ningaloo, WA	KF142169
WAM Z21137	<i>Phyllophorus</i>	sp. 2	Perth, WA	KF142189
WAM Z29789	<i>Phyllophorus</i>	sp. 2	Perth, WA	KF142186
NMV F151845	<i>Lipotrapeza</i>	<i>vestiens</i>	Victoria, Australia	JX544963
NMV F173267	<i>Thyone</i>	<i>pedata</i>	Western Australia	KF142165
UF 10955	<i>Holothuria</i>	<i>impatiens</i>	Okinawa, Japan	KF142183

**Remarks.** Since the original recognition of *Phyrella* by Heding & Panning (1954), no species have been added to or removed from the genus. Heding & Panning (1954) erected *Thyonidiella*, *Semperiella*, and *Phyrella* in the same paper, differentiating them by the structure of the calcareous ring, number of tentacles, and presence/absence of body wall ossicles. They assigned *Thyonidiella* to their restricted Phyllophorinae, and the other genera to the newly erected Semperiellinae. The Semperiellinae were distinguished from the Phyllophorinae in having inter-radials fragmented into numerous pieces, although genera that include species with modest fragmentation of inter-radials (i.e., *Lipotrapeza* and *Thyonidiella*) were retained in the latter. Such variability brings into question the taxonomic usefulness of this character. We also found variation in the degree of fragmentation of the inter-radials in *Phyrella fragilis*, with some smaller specimens (e.g., WAM Z26012) having unfragmented inter-radials.

The monotypic *Thyonidiella* was further differentiated from *Semperiella* by a perceived lack of body wall ossicles. However Heding & Panning (1954) apparently only examined the ventral body wall and Cherbonnier (1988) found tables in the dorsal body wall of the holotype of *Thyonidiella oceana*. Adding to the confusion was that Heding & Panning's (1954) material on which they erected *Thyonidiella oceana* inadvertently included two species: the type from Ambon and two specimens (later referred to the newly erected *T. cherbonnieri* Rowe & Richmond, 2004) from Mauritius. Cherbonnier (1988), who did not realize that the Ambon specimen represented the holotype, considered the Mauritius species typical and referred the Ambon one to *Semperiella tenera* (Ludwig, 1875) (Rowe & Richmond, 2004). Thus Cherbonnier's (1988) subjective synonymy of *Semperiella tenera* with the holotype of *Thyonidiella oceana* renders *Semperiella* a synonym of *Thyonidiella*, as designated by Rowe & Richmond (2004) as first revisers. However none of these authors (Heding & Panning, 1954, Cherbonnier, 1988, Rowe & Richmond, 2004) have examined the type of *S. tenera*; our attempts to locate that type have also been unsuccessful.

The distinction between *Semperiella* and *Phyrella* was based on the number of tentacles: 15 in *Semperiella* and 20 in *Phyrella*. The number of tentacles in *Phyrella* is variable however, ranging between at least 15-20, rendering the distinction moot. Furthermore, examination of the holotype of *Thyonidiella oceana* revealed that it is a synonym of *Phyrella fragilis*, further supporting the synonymy of *Semperiella* and *Phyrella*. As first revisers, we select *Phyrella* as the senior synonym.

*Phyrella* is distinguished from the polytentaculate phyllophorid genera *Lipotrapeza*, *Selenkiella*, *Phyllophorus* and *Anthochirus* by its fragmented inter-radials elements, at least in adult stages. It is distinguished from the “semperielline” genera *Cladolella*, *Pentadactyla*, *Neothytonidium*, *Neopentadactyla*, *Massinium* by the presence of well-formed table ossicles in the body wall, with regular disc with typically 8 peripheral holes, a four-pillared spire united by a single cross-beam ending in an often incomplete crown.

**Included species:** After reviewing described species in relevant phyllophorid genera we consider 12 nominal species to be attributable to *Phyrella* or to have been assigned to *Phyrella* or to one of its synonyms in the past. *Phyllophorus aculeata* Ludwig, 1894, *Phyllophorus fragilis* Mitsukuri & Ohshima, 1912, *Phyllophorus thyonoides* Clark, 1938, and *Phyllophorus trapeza* Clark, 1932 are currently assigned to *Phyrella*. *Orcula tenera* Ludwig, 1875, *Thyonidiella oceana* Heding & Panning, 1954, *Thyonidiella exigua* Cherbonnier, 1988, *Thyonidiella cherbonnieri* Rowe & Richmond, 2004, and *Semperiella drozdovi* Levin & Stepanov, 1999 are currently assigned to *Thyonidiella*. Finally, *Phyllophorus bedoti* Koehler, 1895, *Phyllophorus contractura* Cherbonnier, 1988, currently assigned to *Phyllophorus*; and *Lipotrapeza ambigua* Cherbonnier, 1988, currently assigned to *Lipotrapeza*, belong to this complex.

Based on the amended diagnosis for the genus, and after examining relevant type material, we propose that *Phyrella* includes the following species:

- *Phyrella trapeza* (Clark, 1932);
- *Phyrella drozdovi* (Levin & Stepanov, 1999);
- *Phyrella fragilis* (Mitsukuri & Ohshima in Ohshima, 1912) of which *Thyonidiella oceana* Heding & Panning, 1954 is a junior synonym;
- *Phyrella mookiei* sp. nov.;
- *Phyrella thyonoides* (Clark, 1938).

Because original descriptions are not detailed enough, genetic material is lacking, or the type material is not located, we putatively assign these species to *Phyrella*, but additional data are needed to confirm this generic assignment:

TABLE 3. Summary of distinguishing characters for *Phyrella* species.

	Number of tentacles	Color	Disc diameter of tables in body wall ( $\mu\text{m}$ )	Length/Width of perforated plates ( $\mu\text{m}$ )	Diameter of rosettes in introvert and cloacal region ( $\mu\text{m}$ )	Geographical Range
<i>Phyrella trapeza</i>	16	Light brown	80–105	140–155/40–80	80–125	Queensland, Australia
<i>Phyrella drozdovi</i>	14–15	Dingy-white or yellowish	60–75	100–200/50–60	10–60	Vietnam
<i>Phyrella fragilis</i>	15–17	Beige to gray to orange, some with deep purple patches and/or small brown spots all over the body	100–125	160–250/65–100	20–30	Western Australia, through Indonesia and Philippines, to Taiwan and Okinawa
<i>Phyrella mookei</i>	17?–18	Beige to off-white with well-defined burgundy to dark brown spots	70–125	135–185/70–100	20–70	Guam
<i>Phyrella thyonioides</i>	16–20	Dark brown with yellow tube feet, red ring around sucker margin	Lacking (in our specimens)	120–220/20–65	20–50	Western Australia
<i>Phyrella? ambigua</i>	15	Light to dark brown	Lacking	100–150/30–60	40	Madagascar, Rodrigues?, Mauritius?
<i>Phyrella? tenera</i>	15	Light yellow	Undetermined	Undetermined	Undetermined	Samoa
<i>Phyrella? bedoti</i>	17	Gray/light brown with irregular dark brown spots all over the body	Undetermined	Apparently lacking	Apparently lacking	Ambon, Indonesia

- *Phyrella? ambigua* (Cherbonnier, 1988) of which *Thyonidiella cherbonnieri* Rowe & Richmond, 2004 and *Phyllophorus contractura* Cherbonnier, 1988 are synonyms;
- *Phyrella? bedoti* (Koehler, 1895);
- *Phyrella? tenera* (Ludwig, 1875).

*Phyrella? bedoti* and *Phyrella? tenera* are poorly known species with incomplete descriptions, their types are not located, and these names are currently not in use. We therefore suggest that they be treated as *species inquirenda* until they are re-described.

Finally, the following species have been attributed to *Phyrella* or to a genus we now consider a synonym of *Phyrella*, but do not belong there:

- *Orcula (Phyllophorus?) dubia* Bedford, 1899;
- *Phyllophorus aculeatus* Ludwig, 1894;
- *Thyonidiella exigua* Cherbonnier, 1988;
- *Thyonidiella kungi* O'Loughlin, 2012.

*Phyllophorus aculeatus* is here transferred to the sclerodactylid genus *Euthyonidiella*. Generic assignment of the other remains unresolved, we provisionally place them in *Phyllophorus sensu lato*. *Orcula (Phyllophorus?) dubia* Bedford, 1899 is poorly known, the type appears to be lost, and the name is currently not in use. We suggest that it is treated as *species inquirenda* until it is re-described.

The characters that can be used to distinguish among the species attributable to *Phyrella* are listed in Table 3.

### ***Phyrella trapeza* (Clark, 1932)**

Figures 1–3; 27 d,e

*Phyllophorus trapezus* Clark, 1932: 224–226, text-fig. 4–9. Holotype: BMNH 1932.4.28.177; type locality: Low Isles, Queensland, Australia

*Phyrella trapeza*: Heding & Panning, 1954: 182–183, fig. 87

**Material examined:** MCZ HOL1488 (2 paratypes), Australia, Queensland, 1/4 mile South of Cape Kimberley, 4 fathoms, 2 December 1928, coll. H.L. Clark.

**Description based on the paratypes. External morphology.** Paratype A with thin, transparent, very relaxed body wall (Fig. 1, bottom); B with thick leathery, contracted body wall (Fig. 1, top). Tube feet dispersed across entire body, denser toward anterior and posterior, less dense than in other *Phyrella*; generally same color as body wall, except some tube feet darker on venter. Body wall uniformly light brown (paratype A) to dark brown with some lighter areas (paratype B). Body arched, both specimens 35 mm along the dorsum, 45 mm along venter, and 13 mm (B) vs. 15 mm (A) wide. Introvert lighter color than rest of body, 6 mm (A) and 8 mm (B) in length, retracted and partially dissected in both specimens. With 16 tentacles varying in size, 10 on the outer circle and 6 on the inner circle (A) vs. 9 on the outer circle large and 7 on the inner circle (B); larger tentacles ~5 mm, shorter tentacles ~2 mm long in paratype A (poorly preserved in B). Cloacal area missing in both specimens, probably removed for ossicle preparation by previous workers.

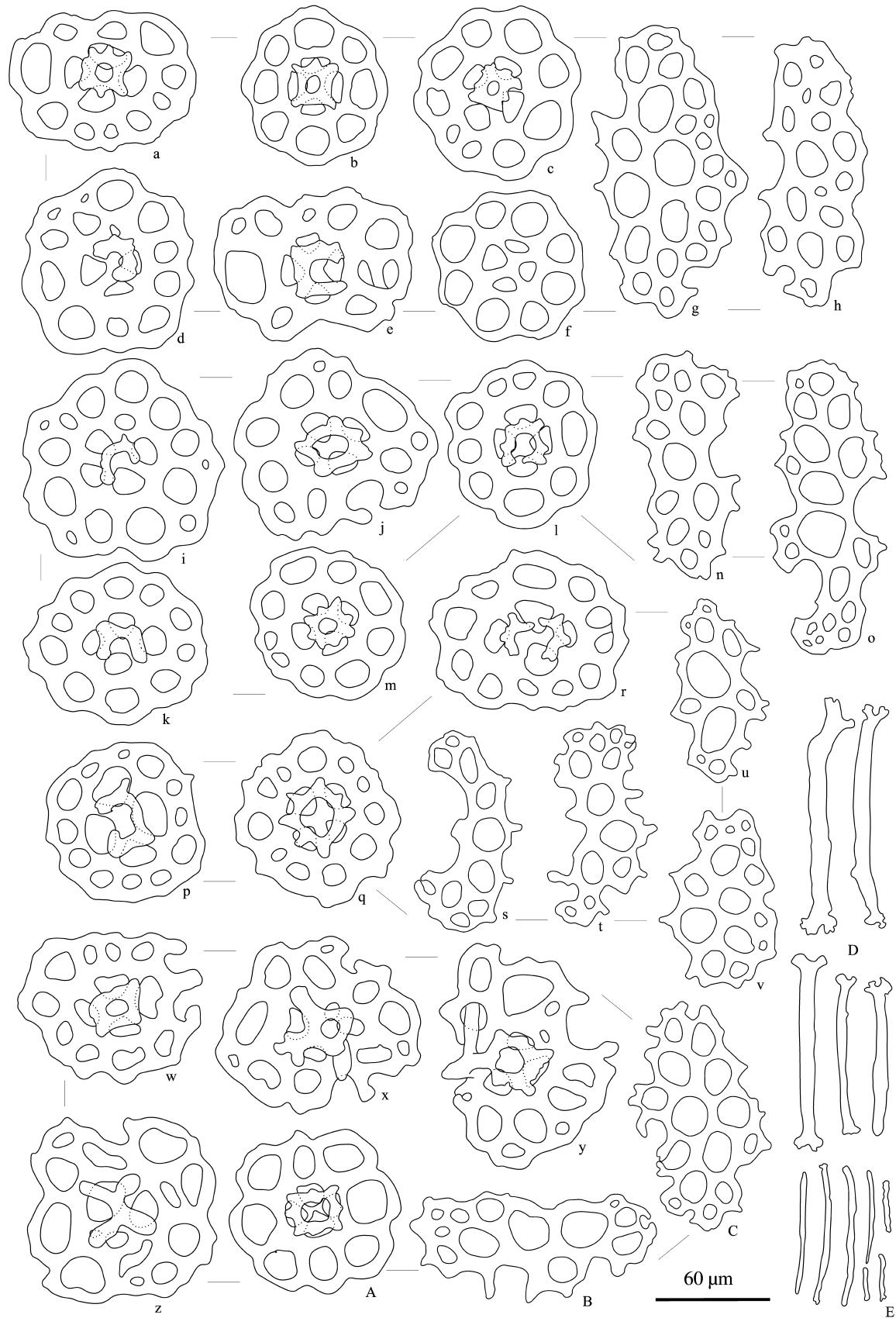
**Internal anatomy.** Polian vesicle, single, contracted, 6–7 mm long, 1 mm wide, tube-shaped. Stone canal short (< 2 mm), with a slight orange coloration, embedded in dorsal mesentery; madreporite small (< 1 mm), partially attached to membrane surrounding the calcareous ring (paratype A), missing in paratype B. Gonads in two 8–10 mm long tufts, composed of simple, unbranched, 3–4 mm long tubes. Both specimens eviscerated. Respiratory trees extending almost entire length of animals, bunches more developed in specimens with thick body wall.

**Calcareous ring.** Calcareous ring 8 mm (A), 10 mm (B) long, 6 (A) 8 (B) mm wide (Fig. 27d, e), embedded in thin and transparent membrane. Radials with 5–8, and inter-radials with 10–12 elements. Anterior margins of radial plates unequally divided by well-formed notches. Anterior margins of inter-radial plates arrow-head shaped. Radials and inter-radials closely associated along most of their lengths. Radials project posteriorly forming tails that curve to point anteriorly.

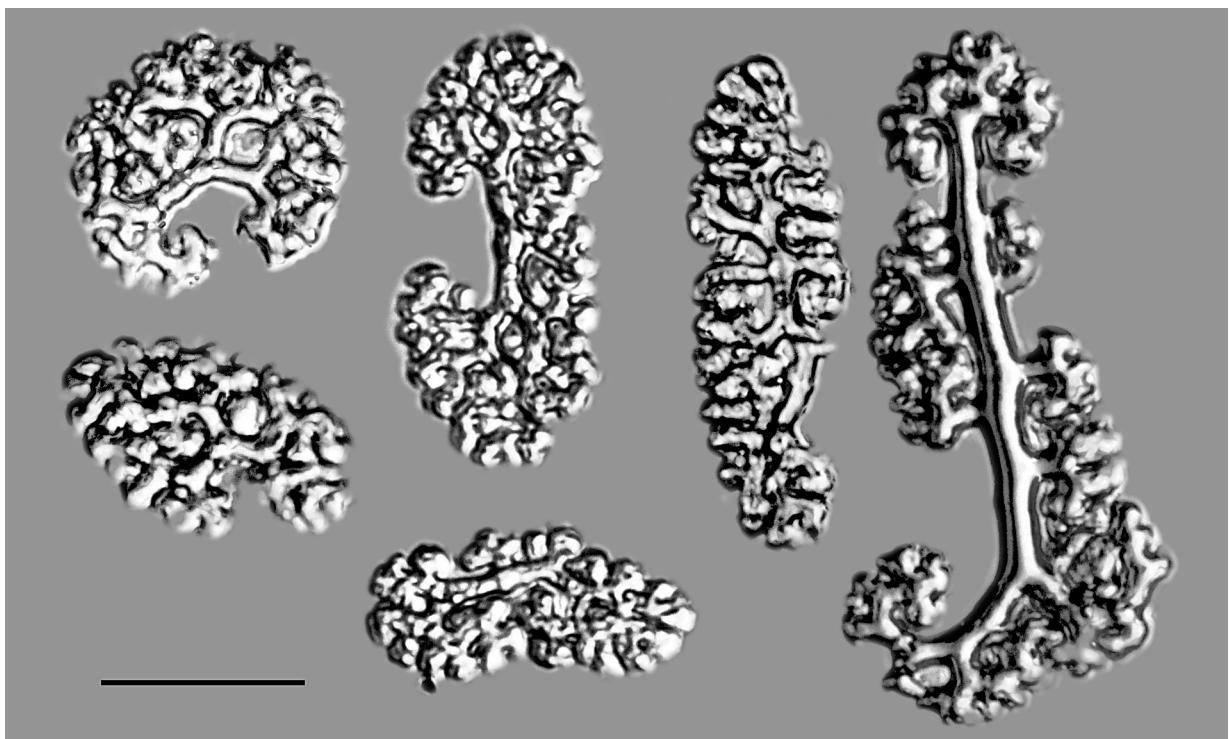


**FIGURE 1.** Paratypes of *Phyrella trapeza* MCZ HOL1488. Lateral view. Scale bar, 1 cm.

**Ossicle assemblage. Dorsal and ventral body wall** with tables only. Tables variable; disc 80–500  $\mu\text{m}$  in diameter, most with complete rim, with smooth, circular to slightly rectangular outline contoured around marginal perforations, with 8–10 holes in a marginal ring (Fig 2b, f, l, m); irregular tables with 1–3 additional holes peripheral to these (Fig 2d, i, j, k); spire variably developed, often absent in tables from paratype A, but usually developed in B, with four (rarely five) pillars connected by a single cross-beam, giving rise to a relatively narrow, thin, slightly spiny crown; crown usually forming a complete ring, with a 6–15  $\mu\text{m}$  central opening. Podia with elongate, perforated plates, 140–155  $\mu\text{m}$  long, 40–80  $\mu\text{m}$  wide, with holes smaller toward periphery or of relatively constant size throughout (Fig 2g, h, n, o); well-developed end plate. **Cloacal region body wall** (paratype B) with tables and abundant rosettes (Fig. 12B). Tables variable; disc 80–125  $\mu\text{m}$  in diameter; regular tables similar to those of dorsal and



**FIGURE 2.** Ossicle assemblage of *Phyrella trapeza* (MCZ HOL1488, thick body wall). a–h: tables (a–f) and perforated plates (g–h) from mid-dorsal body wall; i–o: tables (i–m) and perforated plates (n–o) from mid-ventral body wall; p–v: tables (q–r) and perforated plates (s–v) from introvert; w–z; A–C: tables (w–z, A) and perforated plates (B–C) from cloacal region; D–E: rods from tentacles.



**FIGURE 3.** Rosettes from introvert of *Phyrella trapeza* MCZ HOL1488. Scale bar, 20  $\mu\text{m}$ .

ventral body wall (Fig 2A); irregular tables with incomplete rims and additional holes (Fig 2w–z), some with spiny lateral projections that connect to the spire (Fig 2x, y). Rosettes abundant, 20–30  $\mu\text{m}$  long. Podia with few reduced perforated plates, 100–130  $\mu\text{m}$  long, 60–70  $\mu\text{m}$  wide (Fig 2B, C). **Introvert** (paratype B) with tables and rosettes. Table discs 85–105  $\mu\text{m}$  in diameter, with 11–13 peripheral holes (Fig 2p–r) and smooth margins; crown often incomplete (Fig 2p, r), typically wider and larger than in body wall tables. Rosettes 30–55  $\mu\text{m}$  long (Fig 3). Podia with few perforated plates (Fig 2s–v). **Tentacles** (paratype B) with large (80–125  $\mu\text{m}$ ) rods with slightly branching ends, (Fig 2D), and small (15–65  $\mu\text{m}$ ) simple rods with simple ends (Fig 2E).

**Remarks.** Clark (1932) noted the similarity between *P. trapeza* and *P. fragilis*. It can be distinguished from *P. fragilis* and other *Phyrella* species by less abundant and smaller podia, relatively large holes in the disc of the tables, perforated plates with barely serrated margins. *P. trapeza* is the type species of *Phyrella*.

**Ecology and distribution.** This species is currently only known from the type material, collected in Queensland, Australia, from Low Isles (holotype) and Cape Kimberley (paratypes). Paratypes were collected by dredging, on a bottom of shells and gravels 4 fathoms ( $\sim 7.5$  m) deep.

#### *Phyrella drozdovi* (Levin & Stepanov, 1999)

*Semperiella drozdovi* Levin & Stepanov, 1999: 71–74, figs. 1–8. Holotype: Kamchat-NIRO, catalog number: KNIRO-V-001; Paratypes: KNIRO-V-002, KNIRO-V-003; types transferred to Zoological Institute Russian Academy of Sciences, Saint Petersburg, Russia (Alexey Smirnov, pers. comm.); type locality: Vietnam, Gulf of Nhatrang, Tam Island, intertidal zone

**Remarks.** This species is known from three specimens from Tam Island, Vietnam: the 5.2 cm long holotype, and 4.6 and 3.4 cm long paratypes. The general appearance (coloration, shape, arrangement of the tube feet, presence of anal teeth), shape of calcareous ring, ossicle assemblage, and number of tentacles (14–15) are all characteristic of *Phyrella*. This species was originally assigned to *Semperiella* because of its 15 tentacles, previously thought to be of generic significance. The ecology of *P. drozdovi* is also similar to *P. fragilis* (abundant, intertidal, under rocks, densely coated with adhering sediment). However, there are also some differences, in particular in the ossicles: most if not all tables have a poorly developed spire, there are perforated plates in the tentacles, and elongated perforated plates in the introvert. This species appears to belong to *Phyrella*. We have not been able to study the

type series, which will be necessary to evaluate the species' distinctiveness from *P. fragilis*, the congener most similar in morphology, distribution, and ecology.

**Ecology & distribution.** Known only from the type locality, Tam Island, Vietnam, where it is common in an intertidal pebble-cobble beach.

### ***Phyrella fragilis* (Mitsukuri & Ohshima in Ohshima, 1912)**

Figures 4–9; 27 a–c

*Phyllophorus fragilis* Mitsukuri & Ohshima in Ohshima, 1912: 81–87. Pl. I, Fig. 3; textfig 6. Syntypes UMUTZ-Ecn-H-Den-144 (was 1658 in Mitsukuri & Ohshima, 9 specimens), Nishino-omote, Tanegashima, Stasuma; Satsukawa, Amami-Oshima (1 specimen); Sakibaru, near Naha, Okinawa island (12 specimens)

*Phyrella fragilis*: Heding & Panning, 1954: 185–186. Fig. 90

*Thyonidiella oceana* Heding & Panning, 1954: 172–173, Fig. 82. Holotype: ZMUC HOL-253; type locality: Ambon, Moluccas, Indonesia

*Thyonidiella oceana*: Cherbonnier, 1988: 229–232, Fig. 102 A–H

**Material examined:** ZMUC HOL-253 (Holotype of *Thyonidiella oceana*), Ambon, February 1922, coll. Th. Mortensen; UF 4096, Taiwan, Wanlitung, W of Kenting National Park, 0 m, 14 May 2005, coll. Kris Netchy & Robert Lasley; UF 11011, UF 11013, UF 11014, UF 11016, Japan, Okinawa Island, Sunabe (adjacent to the type locality), 19 May 2011, coll. Yoshida Ryuta. WAM Z26012, Western Australia, Kimberley, Coulomb Point, -17.3975, 122.148500, Tide pool, 8 October 2009, coll. A. Sampey; WAM Z26013 Western Australia, Kimberley, James Price Point, -17.501667, 122.143167, 7 October 2009, coll. G. Young.

**Description. External morphology.** Body wall soft, fairly thin and covered with tube feet. Color in preservative, beige (UF 11011, UF 11013, UF 11014, UF 11016, ZMUC HOL-253, Fig. 5B) to gray (UF 4096) to orange (WAM Z26012, WAM Z26013), some with deep purple patches usually in the middle of the body and/or with small brown spots that can be fairly abundant all over body (Fig. 5A); some specimens with darker coloration on both ends (e.g., UF 11011, Fig. 5A). Body arched, slightly U-shaped, generally cylindrical with a tapering posterior end. Largest animal (UF 4096) 65 mm along dorsum, 92 mm along venter, and 30 mm wide across mid-body; most 40–55 mm along dorsum, 55–75 mm along venter, and 20+/- mm wide. Introvert retracted in all specimens examined, short (7 mm long, 4 mm wide for UF 4096), variable in color from almost white to dark brown. Tube feet same color as body wall and purple when originating in patches of this color; very abundant, evenly spread across radial and inter-radial areas, more abundant on venter and toward extremities; fairly large (~2 mm long, ~1 mm wide relaxed). 15–17 tentacles of varying size [UF 4096: 17 tentacles (10 in outer circle, 7 in inner circle), WAM Z26012: 16 tentacles (10 in outer circle, 6 in inner circle), WAM Z26013: 15 tentacles (9 in outer circle, 6 in inner circle), ZMUC HOL-253: 15 tentacles (disposition too difficult to discern)]. Cloacal membrane white. Cloaca surrounded by 5 small, lightly calcified anal teeth.

**Internal anatomy.** Polian vesicle single, white with sparse small brown spots; variable in size and with no clear relation to size of animal (4 mm in UF 4096, > 10 mm in all other dissected specimens). Stone canal inconspicuous, lightly calcified, at least proximally embedded in either the membrane surrounding the calcareous ring or the dorsal mesentery. Madreporite single, white, inconspicuous, small (< 1 mm in diameter), spherical, either embedded in membrane surrounding calcareous ring, dorsal mesentery or free in the body cavity. Gonads well developed in mature individuals, in two tufts; composed of simple, up to 8 mm long, white or yellow tubes branching dichotomously up to a few times. Four of six dissected specimens examined were eviscerated, these retaining gonads, both respiratory trees, and a small anterior portion of the esophagus. Intestine long, distended when packed with fine, muddy sand. Respiratory trees white, extending almost entire body length.

**Calcareous ring.** Calcareous ring embedded in a relatively thick membrane; radials and inter-radials typically highly fragmented elements; radial and inter-radial elements closely associated along most of their length (Fig. 27a,b,c). Anterior margin of radial plates unequally divided by a well formed notch. Anterior margin of the inter-radial plates arrow-head shaped. Fragmentation of radial and inter-radial elements appears to increase with size; with inter-radials entire in one of the smallest specimens studied (WAM Z26012, Fig. 27b), to fragmented to 15–20 elements each, in largest (UF 4096, Fig. 27a). Radials extend posteriorly as long tails that tend to recurve at their tip.

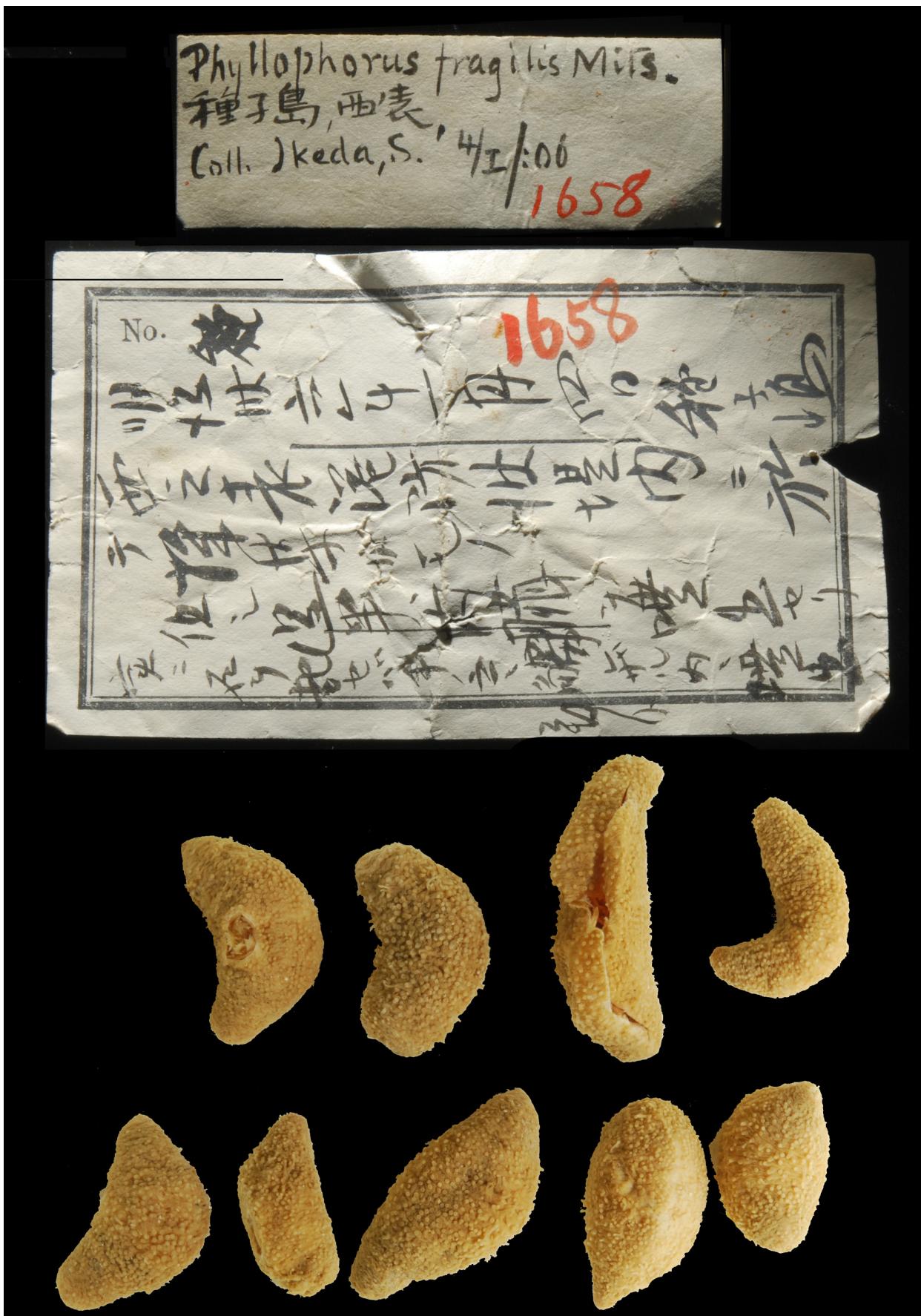


FIGURE 4. Syntypes of *Phyrella fragilis* UMTZ-Ecn-H-Den-144.

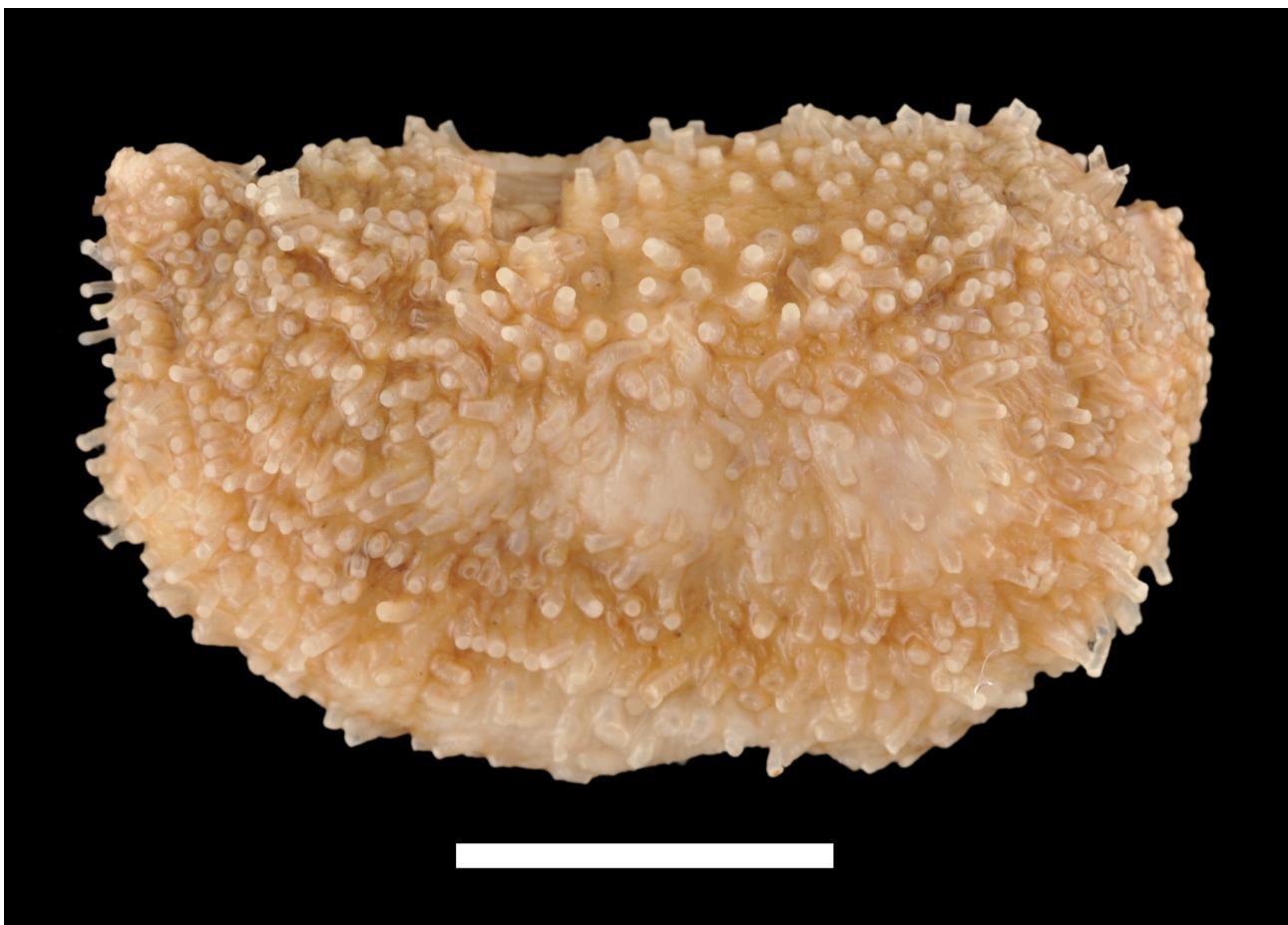


A



B

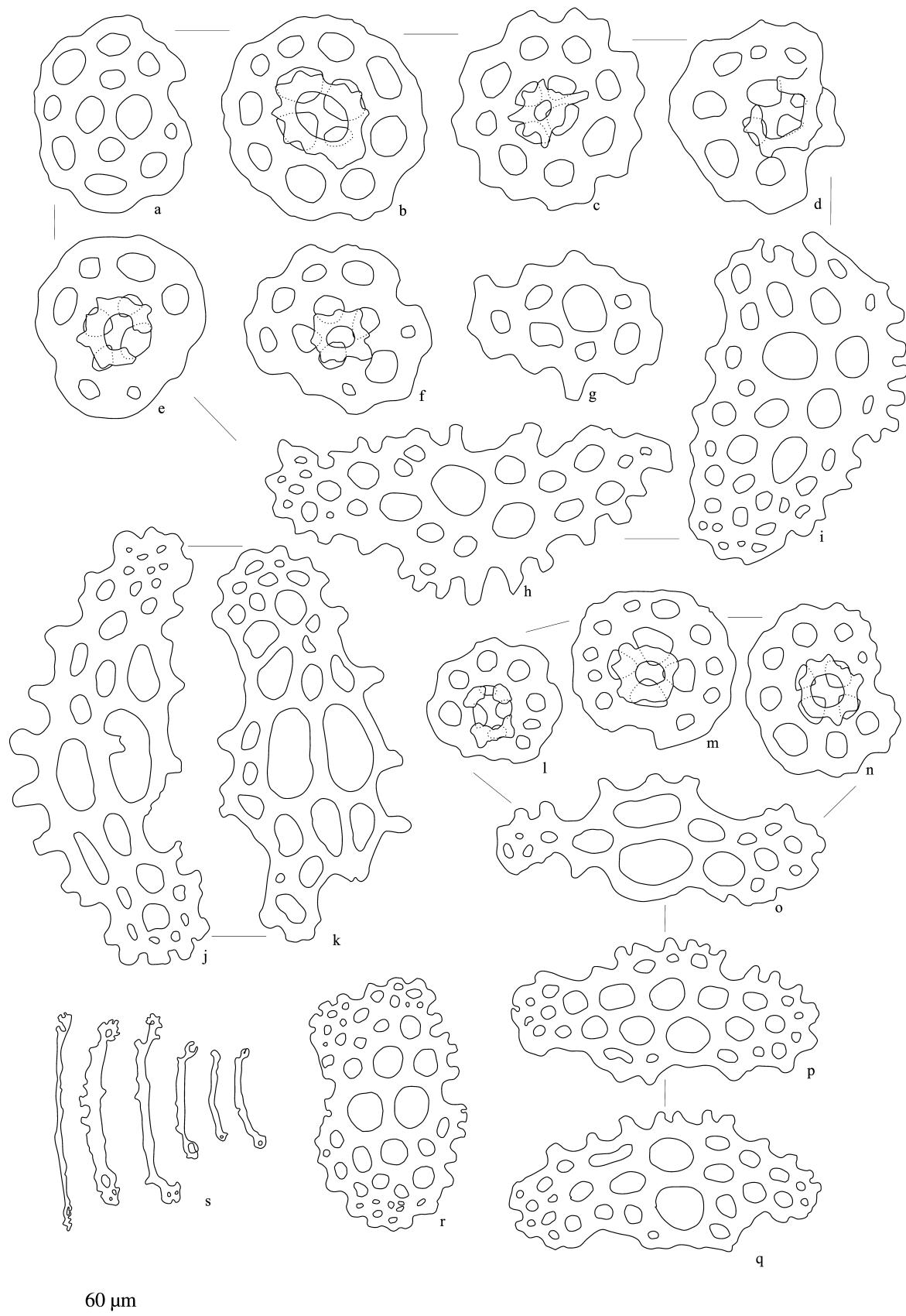
**FIGURE 5.** Live appearance of *Phryrella fragilis* from Okinawa, Japan. A: UF 11011, about 50 mm long; B: UF 11013; about 55 mm long.



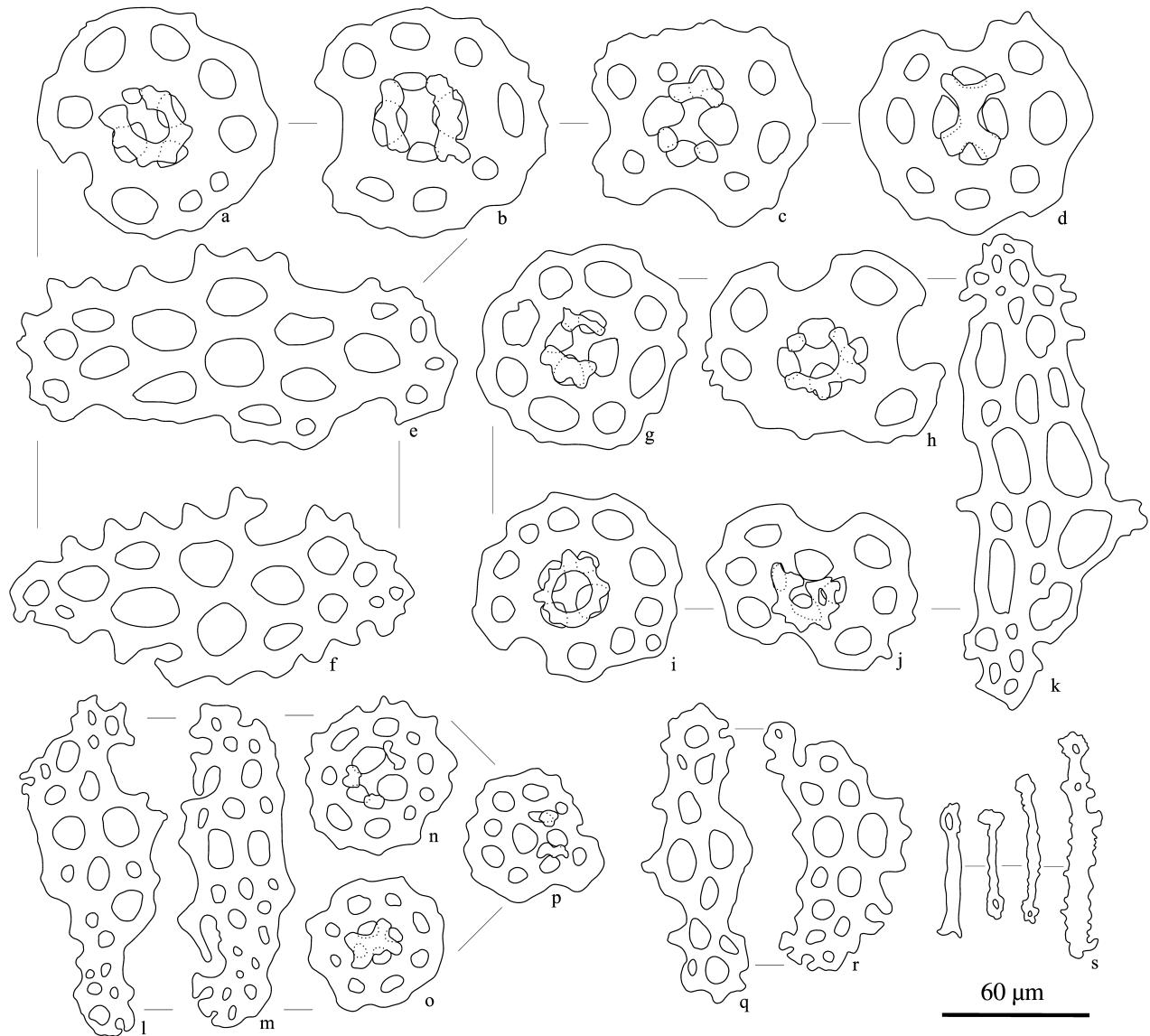
**FIGURE 6.** Holotype of *Thyoniella oceana* ZMUC HOL-253. Scale bar, 1 cm.

**Ossicle assemblage.** **Dorsal and ventral body wall** with tables only. Tables variable, disc with complete (Fig. 7b) or incomplete rim (Fig. 7f,d; Fig. 8a,d), 100–125  $\mu\text{m}$  in diameter; central perforation 10–35  $\mu\text{m}$  in diameter, surrounded by a ring of 8 perforations (Fig. 7b,c; Fig. 8g), rarely with additional holes peripheral to these; margins slightly raised; spire formed by four pillars connected by a single cross-beam half way up, terminating in a narrow, often incomplete crown; irregular and incomplete tables also present, spire completely (Fig. 7a,g) or partially wanting (Fig. 8d, h), often with larger central perforation than regular tables. Podia with perforated plates 160–250  $\mu\text{m}$  long and 65–100  $\mu\text{m}$  wide, with holes decreasing in size toward periphery; margins serrated; serrations most developed along the more convex margin (Fig. 7h–k; Fig. 8e,f,k). **Cloacal body wall** with tables and rosettes. Tables similar to those found elsewhere in body wall. Rosettes abundant, 20–30  $\mu\text{m}$  long (Fig. 9A). Podia with shorter perforated plates, up to 150  $\mu\text{m}$  long (Fig. 7r, Fig. 8q,r). Podia that flank anal teeth with rods, 40–65  $\mu\text{m}$  long (Fig. 8s), and some rosettes. **Introvert body wall** with tables and rosettes (20–30  $\mu\text{m}$  in length) (Fig. 9B); tables drop out toward tentacles. Tables similar to, but typically smaller (60–90  $\mu\text{m}$ ) (Fig. 7l–n; Fig. 8n–p) than those elsewhere in the body wall. Podia with perforated plates variable and mostly similar to those of body wall near cloaca (Fig. 7o–q; Fig. 8l,m); and with rosettes, mostly toward the base of podia. **Tentacles** with rods, 40–95  $\mu\text{m}$  long, with no, one or a few perforations toward ends, some with serrations along margin (Fig. 7s). No ossicles were observed in the cloacal, longitudinal and retractor muscles; intestine; cloacal wall; gonads; and respiratory tree.

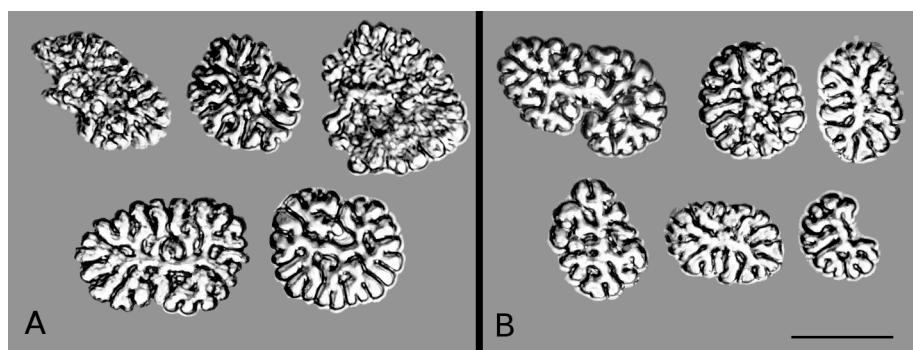
**Remarks.** Mitsukuri noted in his original description (quoted in Ohshima, 1912) that the species has 15 tentacles (10 large and 5 small); however Ohshima adding to this description in the same paper notes that this species has “invariably” 20 tentacles. Heding & Panning (1954) followed Ohshima to assign this species to *Phyrella* based on having 20 tentacles. Specimens examined had 15–17 tentacles. This species can be distinguished from other *Phyrella* by the abundant, large tube feet, the regular tables in the body wall and the large serrations on the more convex margins of the perforated plates.



**FIGURE 7.** Ossicle assemblage of *Phyrella fragilis* (UF 4096). a–i: tables (a–g) and perforated plates (h–i) from mid-dorsal body wall; j–k: perforated plates from mid-ventral body wall; l–q: tables (l–n) and perforated plates (o–q) from introvert; r: perforated plate from cloacal region; s: rods from tentacles.



**FIGURE 8.** Ossicle assemblage of *Phyrella fragilis*. a–f: tables (a–d) and perforated plates (e,f) from mid-dorsal body wall of WAM Z26012; g–k: tables (g–j) and perforated plate (k) from mid-dorsal body wall of WAM Z26013; l–p: perforated plates (l–m) and tables (n–p) from introvert of WAM Z26012; q–r: perforated plates from podia of cloacal region of WAM Z26012; s: rods from podia that flank anal teeth of WAM Z26012.



**FIGURE 9.** Rosettes from cloacal region (A) and introvert (B) of *Phyrella fragilis* UF 4096. Scale bar, 20  $\mu\text{m}$ .

**Synonymy of *Thyonidiella oceana*.** Heding & Panning (1954) studied three specimens that they attributed to their *Thyonidiella oceana*, one from Ambon and two from Mauritius, designating the first as the holotype. The Mauritius specimens pertain to *Phyrella? ambigua* (see below). Heding & Panning noted that the holotype is 25 mm long, appears contracted so that the body wall is thick, both mouth and anus are dorsal, and possesses 10 large and 5 small tentacles. They illustrated the calcareous ring showing that both radials and inter-radials are fragmented, and the inter-radials have posterior projections. They also noted that the body wall lacks ossicles, as they were able to recover only tube feet end plates. The absence of signs of corrosion on the latter suggested to the authors that the absence of ossicles was not an artifact. They end their description by providing notes from Mortensen who collected the Ambon specimen and indicated that it lives buried in the sand under rocks (presumably in the intertidal), and eviscerates readily.

Cherbonnier (1988) redescribed and illustrated the holotype. He noted that the specimens from Mauritius are devoid of ossicles except for tube feet end plates and rosettes in the cloacal region. This may explain why Heding & Panning did not find ossicles if they only examined the Mauritius specimens for ossicles. In his description, Cherbonnier confirmed Heding & Panning's description, and in particular the absence of ossicles in the ventral body wall of the holotype. However, he found and illustrated ossicles in the dorsal body wall. These include tables with a four pillar spire, and a crown which can be incomplete; perforated plates; and rosettes in the introvert and cloacal region. He concluded by noting that the original description is incomplete due to the lack of illustration of the dorsal body wall ossicles, and that the Ambon specimen appears to be *Semperiella tenera* (Ludwig, 1875). His concept of *S. tenera* was based on Heding & Panning account for this species, which in turn was not based on type material.

The ossicles and calcareous ring of the holotype of *T. oceana*, as illustrated by Cherbonnier (1988: Fig 102) are indistinguishable from *Phyrella fragilis*. Examination of the holotype of *T. oceana* (Fig. 6), confirms Cherbonnier's observations (absence of ossicles in the ventral body wall, tables and perforated plates in the dorsal body wall and tube feet, fragmented inter-radial elements in the calcareous ring), and we found no difference between it and specimens of *P. fragilis* taken near the type locality of the latter species.

**Ecology & distribution.** *Phyrella fragilis* is an intertidal species found under rocks in calcareous sand; the animal usually covers itself with large sand grains and pieces of shells. It is common in intertidal areas of Ilocos Norte province, Philippines (-17.501667, 122.143167), where it is commercially harvested and eaten by the local population who call it *sorsorbot* (R. Olavides, pers.comm.). Ohshima & Mitsukuri (1912) named the species for its propensity to eviscerate, noting: "As soon as the stone under which these animals live are lifted up, they throw off the viscera, even before they are touched in any way." This species has the widest known distribution of any *Phyrella*, extending from Western Australia, through Indonesia and the Philippines, to Taiwan and Okinawa.

### *Phyrella mookiei* sp. nov.

Figures 10–16; 27 h

<http://zoobank.org/D3E02B0E-308A-4C67-A143-05DB64692E75>

**Material examined.** Holotype: UF 10336, Guam, North end of Tumon Bay, Gun Beach, reef flat 0–1 m, 12 June 2010, coll. Nathaniel Evans, François Michonneau, Gustav Paulay, Arthur Anker. Paratypes: UF 4770, Guam, Pago Bay outer reef flat, 0–1 m, May 2003, coll. Gustav Paulay; UF 11539, Guam, Piti Power plant intake tunnel under road, 2 m, 17 September 2011, coll. David Burdick.

**Description. External morphology.** Body wall soft, fairly thin, densely covered with tube feet. Beige (UF 4770, UF 11539) to off-white (UF 10336), with well-defined burgundy (UF 4770, UF 10336) to dark brown (UF 11539) spots either restricted to venter (UF 4770) or across entire body (UF 10336, UF 11539); area around introvert and cloaca with diffuse burgundy coloration in UF 10336 (Fig. 11A). Coloration in preservative similar to live after 3 years. Oral disc marbled with burgundy and white (Fig. 10, Fig. 11B). Tentacles dendritic with long-stalk, with small dark spots at their extremities (Fig. 10, Fig. 11B). Body relatively straight when fully relaxed, contracting to U-shaped. Holotype 60 mm long along dorsum, 64 mm along venter and 18 mm wide; UF 4770, more contracted, 40 mm long along dorsum, 57 mm long along venter, and 23 mm wide; UF 11539 very contracted, 37 mm long along dorsum, 45 mm long along venter, and 16 mm wide. Introvert retracted in all

specimens, 4 mm (UF 10336), 6 mm (UF 4770), and 12 mm (UF 11539) long. Tube feet abundant, evenly dispersed across radial and inter-radial areas, slightly denser ventrally, generally same color as body wall near base, lightening distally. Eighteen tentacles (10 on outer circle, 8 on inner circle) in UF 4770, ~17 tentacles in holotype based on live pictures (introvert retracted and not dissected). Cloacal membrane white; surrounded by 5 calcified anal teeth.



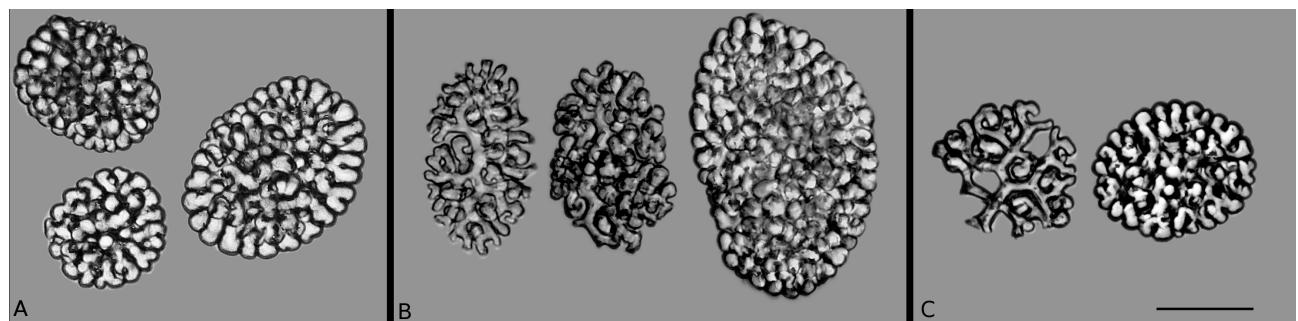
**FIGURE 10.** *Phryrella mookiei* in situ, Guam. The animal is buried in sediment; the oral disc with extended tentacles is visible. Oral disc diameter approximately 1 cm in diameter. Photograph by David Burdick.

**Internal anatomy (UF 4770, UF 11539).** Polian vesicle single, white, 5–7 mm long. Stone canal short (2 mm), partially embedded in membrane surrounding calcareous ring. Madreporite free, small (< 1 mm), spherical. Gonads well developed in both dissected specimens, both tufts extending almost entire length of animal; gonadal tubules unbranched to dichotomously branched 1–3 times; white with minute burgundy spots (similar color to body wall), with spots more common proximally and distally (UF 4770); in UF 10336, oocytes are clearly discernible, white, aligned in a row, encased in the thin, translucent gonadal tube wall, with abundant, minute, burgundy spots. Both dissected specimens have eviscerated, retaining gonads, anterior fragment of esophagus, cloaca and both respiratory trees. Intestine (retained separately for UF 4770) distended where filled with fine sand and other debris. Respiratory trees white with minute burgundy spots that are much less abundant in UF 4770 than in UF 11549, both branches extending almost entire length of animal.

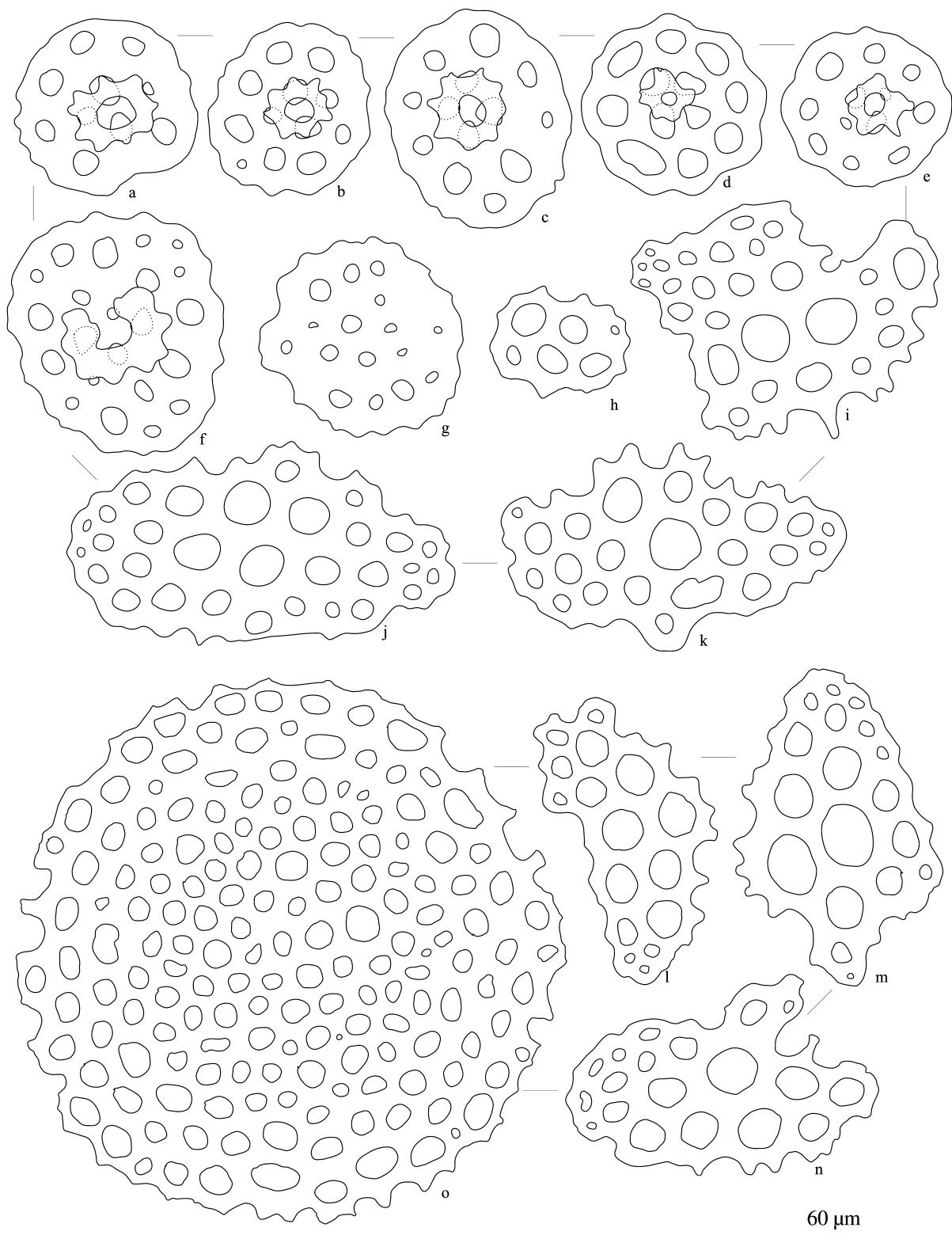
**Calcareous ring.** Calcareous ring embedded in a fairly thin membrane, with highly fragmented radial and inter-radial elements (Fig. 27h). Anterior margins of radial plates unequally divided by well-formed notches. Anterior margins of inter-radial plates arrow-head shaped, more pointed and elongated in UF 4770 than UF 10336. Radial and inter-radial elements closely associated along most of their length. Inter-radials each composed of 5–12 elements. Radials each composed of 14–16 elements. Radials form posteriorly tails that curve to point anteriorly.



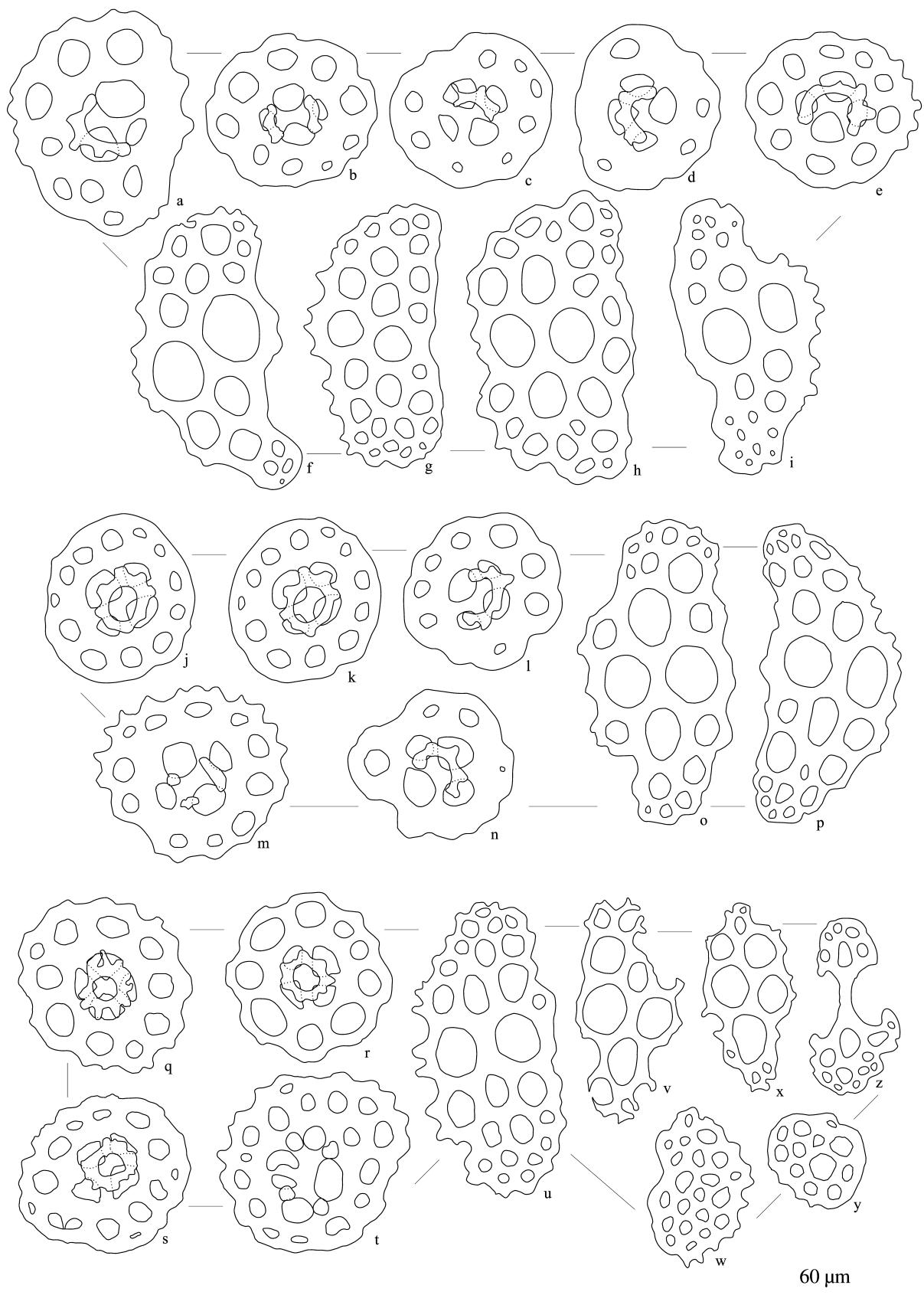
**FIGURE 11.** Live appearance of *Phyrella mookiei* UF 10336 (Holotype). A: Dorsal view, about 65 mm long; B: close-up view of oral region.



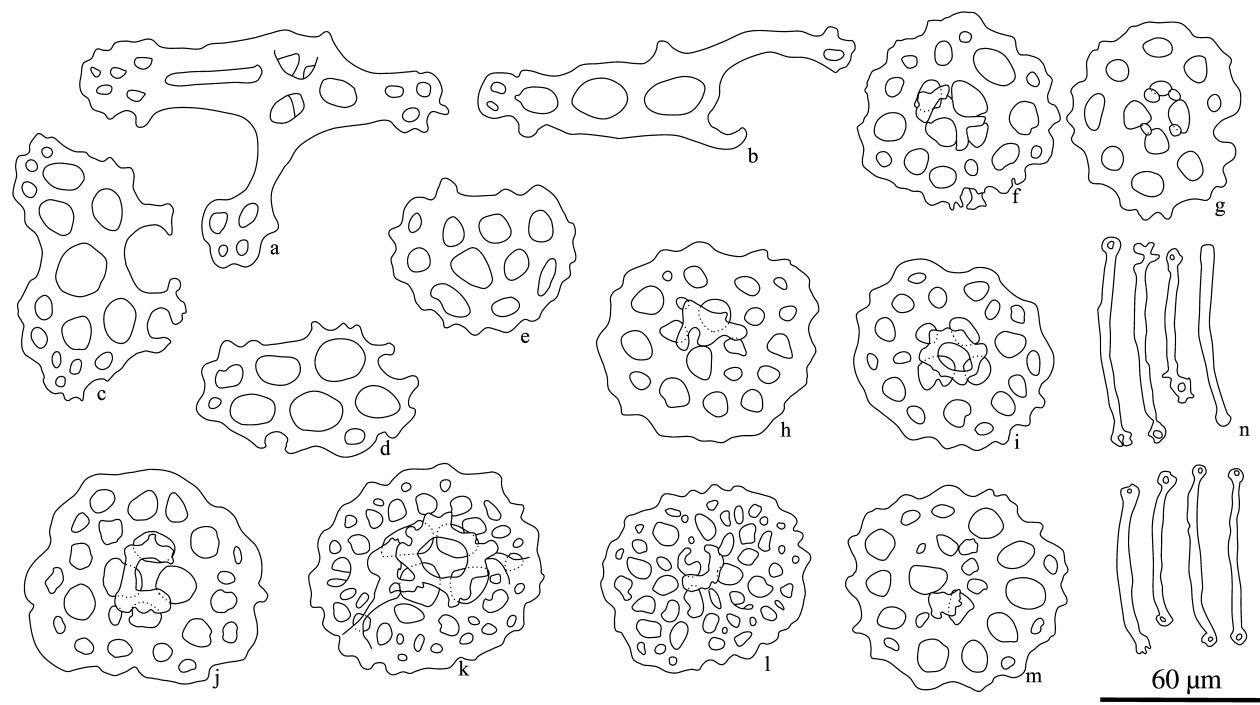
**FIGURE 12.** Rosettes of *Phyrella mookiei*. A: UF 10336 (Holotype), mid-dorsal body wall; B: UF 4770 (Paratype), introvert; C: UF 4770 (Paratype), cloacal region. Scale bar, 20  $\mu$ m.



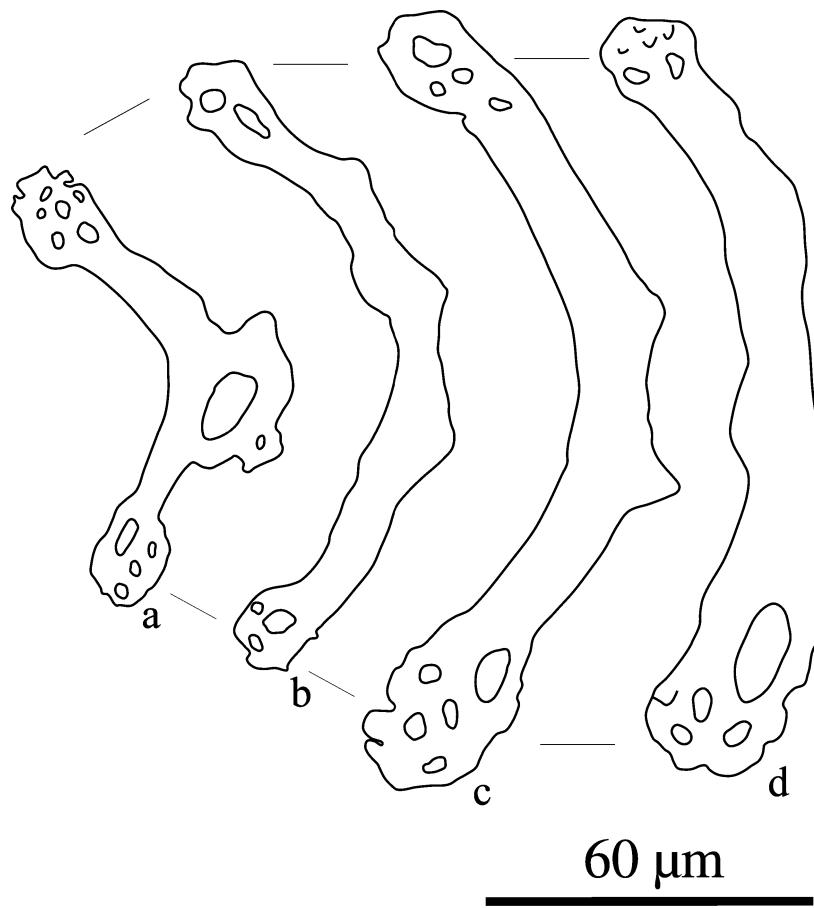
**FIGURE 13.** Ossicle assemblage of *Phyrella mookiei* UF 10336 (Holotype). a–k: tables (a–h) and perforated plates (i–k) from mid-dorsal body wall; l–o: perforated plates (l–n) and tube foot end plate (o) from ventral body wall.



**FIGURE 14.** Ossicle assemblage of *Phyrella mookei* UF 4770 (Paratype). a–i: tables (a–e) and perforated plates (f–i) from mid-dorsal body wall; j–p: tables (j–n) and perforated plates (o–p) from mid-ventral body wall; q–z: tables (q–t) and perforated plates (u–z) from introvert.



**FIGURE 15.** Ossicle assemblage of *Phyrella mookiei* UF 4770 (Paratype). a–m: perforated plates (a–e) and tables (f–m) from cloacal region; n: rods from tentacles.



**FIGURE 16.** Ossicle assemblage of *Phyrella mookiei* UF 11359 (Paratype). a–d: rods in podia that flank anal teeth.

**Ossicle assemblage.** **Dorsal and ventral body wall** with similar ossicle complements of tables and rosettes (Fig. 12A), latter more abundant dorsally than ventrally. Tables of variable forms; disc 70–125  $\mu\text{m}$  in diameter, with 10–25  $\mu\text{m}$  diameter central perforation, and 4–15 (8 in the most symmetrical tables) holes arranged in a ring (Fig. 13d) or dispersed more irregularly in more highly perforated discs (Fig. 13f), disc margin smooth (Fig. 13e) to undulating (Fig. 13f), to partially (Fig. 13a, Fig. 14m) or completely serrated, barely raised; spire absent (Fig. 13g–h), to partially (Fig. 14a–e) or well developed (Fig. 13a), when complete, formed by four pillars connected by a single cross-beam half way along spire; crown variable in diameter when present, forming a spiny ring when well developed (Fig. 13a,c). Podia with perforated plates, 130–185  $\mu\text{m}$  long, 70–100  $\mu\text{m}$  wide; wider and not as elongated as in *P. fragilis* or *P. thyonoides*; with large holes in center and smaller toward periphery; with large well-defined serrations, along at least part of the more convex margin (Fig. 13l–o; Fig. 14f–i, o–p). **Cloacal body wall** with tables and abundant rosettes. Tables of variable form ranging from similar to body wall tables (Fig. 15g), to others that show a much greater number of disc perforations (Fig. 15k); disc 75–85  $\mu\text{m}$  in diameter, rim typically more serrated in tables of cloacal region than elsewhere in body wall; spire absent (Fig. 15e), incomplete (Fig. 15m), or complete, ending in a crown with teeth or lateral projections (Fig. 15k). Podia near cloaca with abundant rosettes (Fig. 12C) and perforated plates; latter smaller (80–100  $\mu\text{m}$  long) and often narrower (40–60  $\mu\text{m}$  wide) than those elsewhere in body wall (Fig. 15c,d), some with unusual lateral extensions (Fig. 15a). Podia that flank anal teeth with rods and abundant rosettes; rods often with marked curvature; ends with 2–6 holes and sometimes small spines (Fig. 16a–d). **Introvert** with similar ossicle assemblage to cloacal region; with tables and abundant rosettes. Tables 95–105  $\mu\text{m}$  in diameter. Podia with abundant rosettes, and perforated plates. Perforated plates variable, ranging from similar to those from the body wall (Fig. 14u–v, x), to much smaller (80  $\mu\text{m}$  long), almost circular, with small perforations (Fig. 14w,y). **Tentacles** with rods, 50–65  $\mu\text{m}$  long, with one or no perforation at ends (Fig. 15n). No ossicles observed in cloacal, longitudinal and retractor muscles; cloaca; intestine; gonads; and respiratory tree.

**Etymology.** Named after Mookie, the dog of our collection assistant Ms. Mandy Bemis, because the “woolly” appearance and color of this species is similar to the soft coat of wheaten terriers, the breed to which Mookie belongs.

**Remarks.** *Phyrella mookiei* resembles *P. fragilis* externally, but the ossicle assemblage and color pattern distinguish the two. In *P. mookiei*, holes in the disc of the tables are smaller, the margins of the disc are often at least partially serrated, the crowns are often more complete and wider; the perforated plates of the podia are shorter and wider; and the irregular tables in cloacal region have many holes in their rim. Rosettes occur throughout the body wall in *P. mookiei* but are restricted to introvert and near-cloacal body wall in other *Phyrella*. While both species have a beige-tan base color, the well-defined dark spotting distinguishes *P. mookiei*.

**Ecology & distribution.** The specimens were found in shallow waters (< 2 m), under rocks, in coarse coralline sediments in areas of high flow. *Phyrella mookiei* is currently only known from Guam, where it is fairly rare.

### *Phyrella thyonoides* (Clark, 1938)

Figures 17–22; 27 f,g

*Phyllophorus thyonoides*, Clark, 1938:492–494. fig. 48. Holotype, MCZ HOL1654; type locality: Western Australia, Cottesloe Beach (Perth)

*Phyrella thyonoides*: Heding & Panning, 1954:183–184, fig. 88

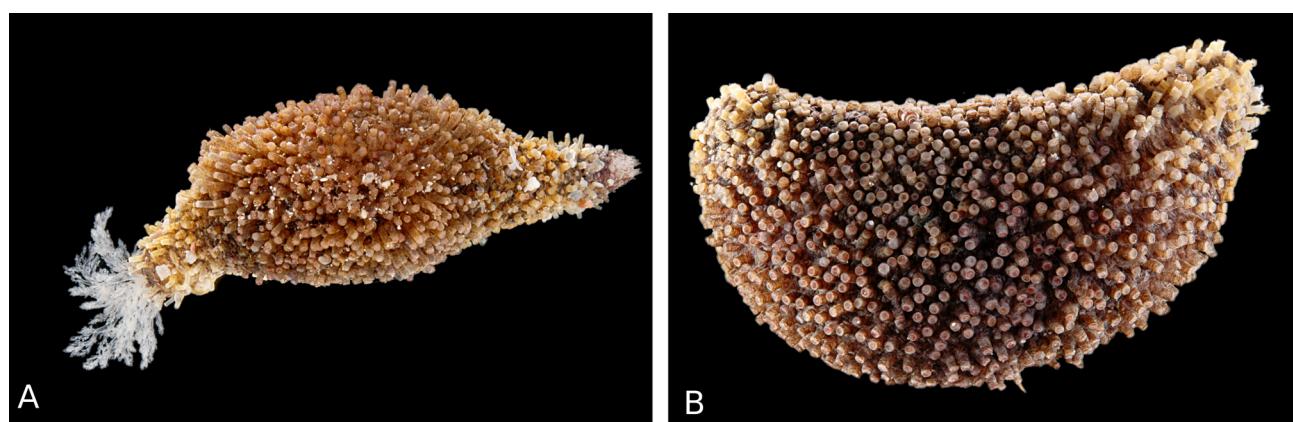
**Material examined.** MCZ HOL1654, (Holotype), Western Australia, Cottesloe Beach, from beach drift, July 1926, coll. L. Glauert. *Phyrella cf. thyonoides*: UF 9414, UF 9598, UF 9601, Western Australia, Ningaloo Reef, Ningaloo station, -22.6753 113.684, 1–3 m, under rocks on sand, May 2009. coll. François Michonneau.

**Description of holotype.** Specimen in poor condition; 33 mm along dorsum, about 45 mm along venter, 13 mm wide at mid-body (Fig. 17). Body wall dried out, very stiff, leathery. Body wall and most organs uniformly dark brown. Introvert retracted; only a small piece remains; 12 mm long. With 16 tentacles of varying sizes, longest about 13 mm, shortest about 1 mm; arrangement difficult to discern because of the state of contraction and preservation of specimen. Cloacal region dissected out, missing. Calcareous ring 17 mm long, 8 mm wide, embedded in a fairly thin and transparent membrane (Fig. 27f). Anterior margins of radials divided slightly unequally by deep notch. Anterior margins of the inter-radials arrow-head shaped. Inter-radials each composed of

11–13 elements. Radials each composed of 14–18 elements, forming long posterior tails. Radials and inter-radials closely associated along most of their lengths. Single Polian vesicle, 4 mm long, brown and pear-shaped. Stone canal and madreporite embedded in membrane surrounding the calcareous ring. Stone canal 2 mm long, madreporite about 1 mm in diameter, spherical with convolutions. After multiple attempts in different parts of specimen, no ossicles were found in the body wall or in the tentacles, likely because of corrosion. Clark illustrated and described body wall tables and tentacle supporting rods.



**FIGURE 17.** Holotype of *Phyrella thyonoides* MCZ HOL1654. Lateral view. Scale bar, 1 cm.



**FIGURE 18.** Live appearance of *Phyrella* cf. *thyonoides* A: UF 9598, dorsal view, about 35 mm long; B: UF 9601, lateral view, about 30 mm.

**Description of *Phyrella* cf. *thyonoides* from Ningaloo. External morphology.** Body wall slightly firmer and more leathery than in other *Phyrella*. Living animal dark brown, densely covered with tube feet with yellow base color overlain with dark brown transverse lines and with red ring around sucker margin (Fig. 18). Preserved specimens relatively straight 30–35 mm (excluding introvert and tentacles when extended) and 13 mm wide. Introvert short (4 mm). Introvert and tentacles white, peppered with small, dark brown flecks; base of tentacles also have small light brown blotches. With 15 tentacles in outer circle (about 3 mm) and 5 tentacles in inner circle

(< 1 mm), latter aligned with ambulacra (UF 9414 and UF 9601). Oral disc with light brown line around mouth. Cloacal membrane white, with 5 lightly calcified anal teeth, each associated with a few tube feet with minute brown spots.

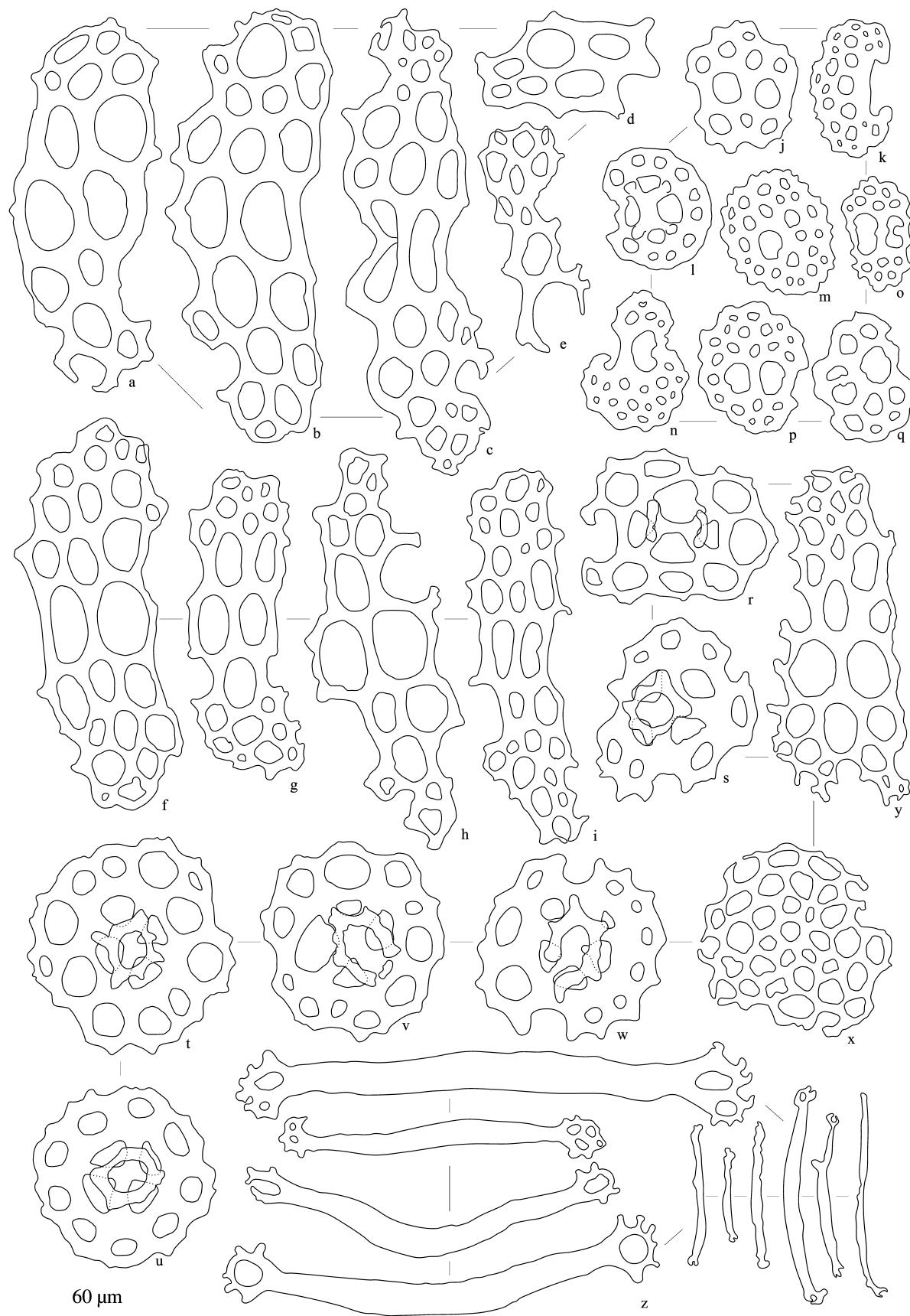
**Internal anatomy** (based on UF 9601). Polian vesicle single, light brown with very sparse minute dark spots, 5 mm long. Madreporite and stone canal inconspicuous, embedded in the membrane surrounding the calcareous ring. Stone canal short (< 2 mm) and narrow (< 1 mm) embedded in the membrane surrounding the pharyngeal complex. Gonads with two well-developed tufts of unbranched, semi-transparent tubes, with small dark purple spots, up to 5 mm long. Respiratory trees light gray with minute dark purple spots, both extending almost entire length of animal. Specimen eviscerated, but retaining pharyngeal complex, gonads, respiratory trees and proximal end of esophagus.

**Calcareous ring** (based on UF 9601). Calcareous ring embedded in a relatively thin membrane (Fig. 27g). Anterior margins of radials divided unequally by a well-formed notch. Anterior margins of inter-radials arrow-head shaped. Radial and inter-radial elements are closely associated along most of their respective lengths. Inter-radials each composed of 5–8 elements. Radials each composed of 14–18 elements. Radials project posteriorly forming long tails that curve anteriorly at their tips.

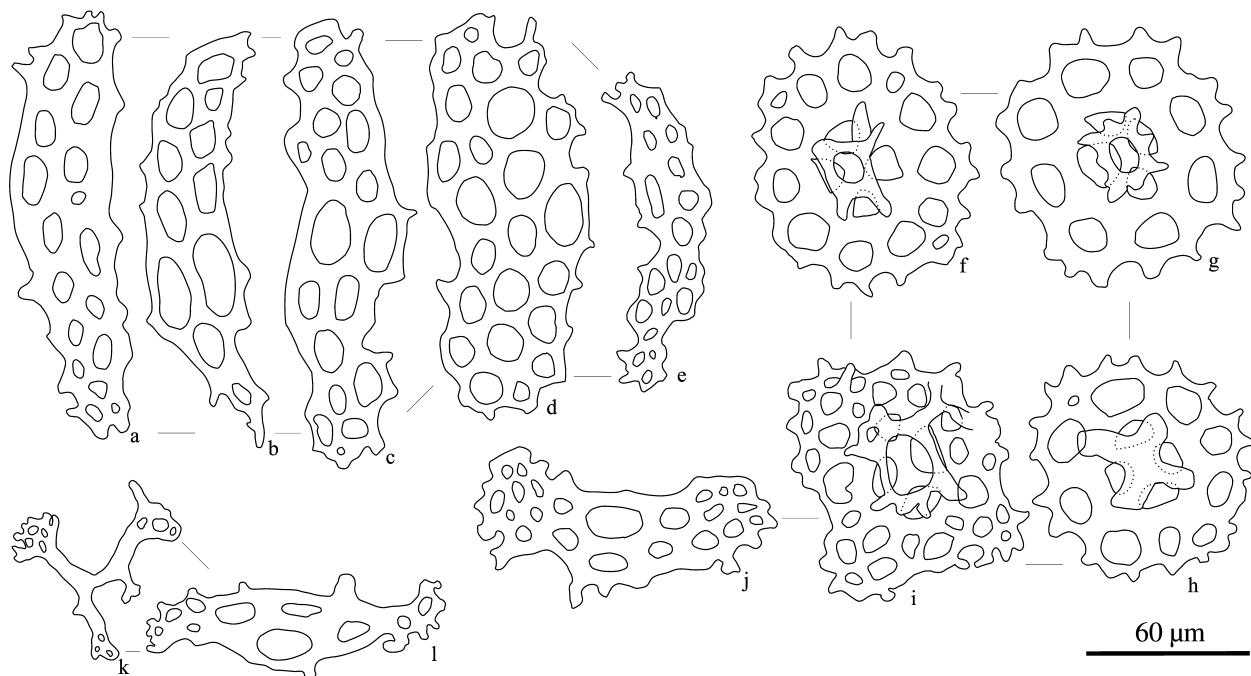
**Ossicles. Dorsal and ventral body wall** lacking ossicles except in podia. Podia with perforated plates (120–220  $\mu\text{m}$  long, 20–65  $\mu\text{m}$  wide), more elongated and with typically larger holes, in particular towards the ends of the plates than in the other species (Fig. 19a–i; Fig. 20a–e). **Cloacal body wall** with tables and rosettes (20–40  $\mu\text{m}$  long, Fig. 22B). Tables variables; disc 90–115  $\mu\text{m}$  in diameter, with either a single circle of 8–11 holes (Fig. 19u,v), sometimes with a few extra holes at the periphery (Fig. 19t), or with very numerous holes that are not arranged in any particular order (Fig. 20i), with a highly serrated rim; spire (sometimes wanting, Fig. 19x) formed by four (rarely five) pillars united by a single cross-beam, surmounted with a crown; crown often incomplete (Fig. 19r), when complete sometimes with spines (Fig. 19w), which in some tables that have numerous holes in their disc, extend and connect to the disc margin (Fig. 20i). Podia with perforated plates; less abundant and generally smaller than in mid body wall, 110–165  $\mu\text{m}$  long, 40–60  $\mu\text{m}$  wide (Fig. 20j). Podia that flank anal teeth with rosettes and perforated plates (Fig. 20l, Fig. 21a–c), some of the latter with unusual lateral extensions (Fig. 20k), many plates incomplete with no or few large perforations and only a few small perforations at the extremities (Fig. 21d). **Introvert** body wall with variable tables, disc 60–80  $\mu\text{m}$  in diameter, with smooth rim margins, complete and regular with 10–12 holes in the rim, to irregular either with incomplete rim or with additional scattered holes; spire poorly developed or missing for most (Fig. 19l). Podia with abundant rosettes, 30–50  $\mu\text{m}$  long (Fig. 22A); perforated plates that range from typical to small, more or less circular (60–80  $\mu\text{m}$  in diameter), with a few large holes in the center and smaller holes toward the periphery (Fig. 19m–q). **Tentacles** with two sizes of rods. Large rods (110–270  $\mu\text{m}$ ) with one or a few holes at the ends. Small rods (50–100  $\mu\text{m}$ ) generally with no holes at the ends (Fig. 19z). No ossicles observed in cloacal, longitudinal and retractor muscles; cloacal wall; gonads; or respiratory tree.

**Remarks.** In the original description of *Phyrella thyonoides*, Clark only illustrates one table from the body wall and three rods from the tentacles. Overall, the description he provides and the holotype fit reasonably well with our new material from Ningaloo, but there are some differences. Thus, in Clark's description, the ends of the large rods in the tentacles have numerous perforations and are spiny; in our specimens, the large rods have only a few holes at their ends and are not spiny. In our specimens, we did not observe any tables in the mid-dorsal or mid-ventral body wall, whereas Clark noted that the tables were "rather scattered, but by no means rare" but did not indicate in which part of the animal he observed them. The table he illustrates is relatively similar to the ones we observed in the anal region of our specimens. Unfortunately, the poor condition of the holotype and the complete corrosion of the ossicles do not allow for an adequate comparison with the Ningaloo material. A full evaluation of *P. thyonoides* and its relation to the Ningaloo population must await collection of new topotypical material. Surprisingly, none of the specimens loaned to us by the Western Australian Museum identified as *P. thyonoides*, turned out to belong to this species or to *Phyrella*. *P. thyonoides* can be distinguished from other *Phyrella* by its thick, leathery, dark brown body wall; the elongated perforated plates with large perforations, and the circular perforated plates in the introvert.

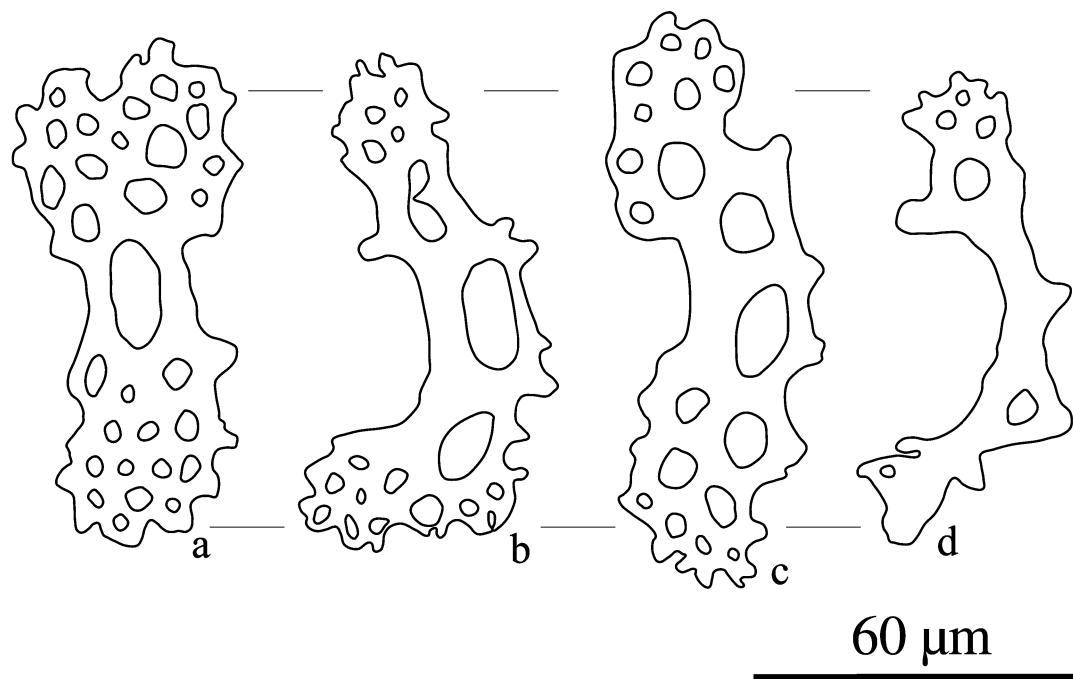
Recently, O'Loughlin *et al.* (2012) proposed to transfer *Phyrella thyonoides* to *Phyllophorella* based on the number of tentacles and the shape of the calcareous ring for the specimens they examined, however most of the specimens they report upon do not appear to pertain to *P. thyonoides*, but to an undescribed species of *Phyllophorella*. The tables illustrated (O'Loughlin *et al.*, 2012:Fig. 10) with marginal teeth are unlike those found



**FIGURE 19.** Ossicle assemblage of *Phyrella* cf. *thyonoides* UF 9601. a–e: perforated plates from mid-dorsal body wall; f–i: perforated plates from mid-ventral body wall; j–q: incomplete tables (l) and perforated plates (j,k,m–q) from introvert; r–y: tables (r–w) and perforated plates (x–y) from cloacal region; z: rods from tentacles.

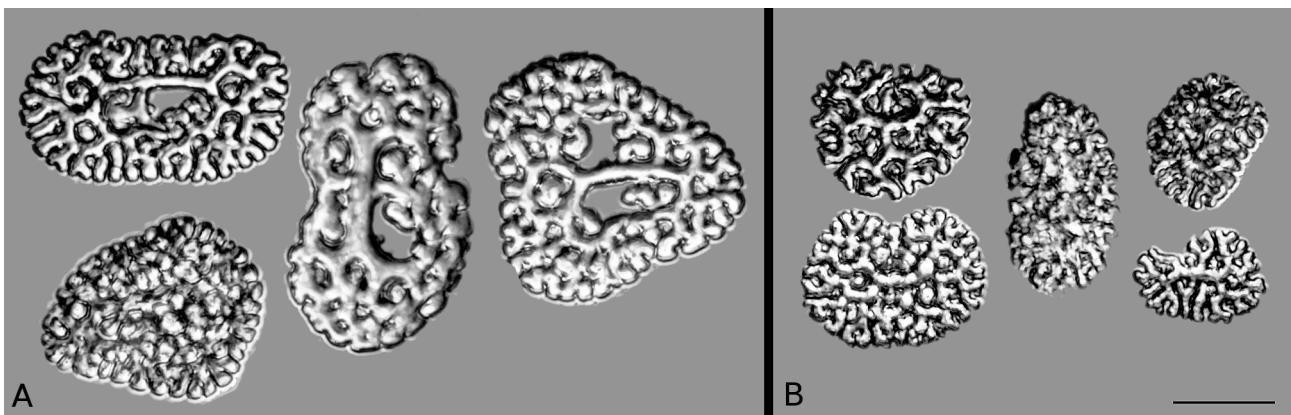


**FIGURE 20.** Ossicle assemblage of *Phyrella* cf. *thyonoides* UF 9598. a–e: perforated plates from mid-ventral body wall; f–j: tables (f–i) and perforated plate (j) from cloacal region; k–l: perforated plates from podia that anal teeth.



**FIGURE 21.** Ossicle assemblage of *Phyrella* cf. *thyonoides* UF 9414. a–d: perforated plates from podia that flank anal teeth.

in any *Phyrella*. The general appearance of the animal and shape of the calcareous ring illustrated (O'Loughlin *et al.*, 2012:Fig. 9) also do not match *Phyrella*. O'Loughlin *et al.* (2012) note that there are single posterior extensions on the calcareous ring in this species (and other *Phyllophorella*) arising either from radial or jointly from radial and inter-radial elements; this contrasts with the clearly separate series of plates that arise from the fragmentation of both inter-radial and radial elements of all *Phyrella* species. One of the specimens examined by the authors (WAM Z31837) was sequenced and matches a *Phyllophorus* species we collected along with *P. thyonoides*, in Ningaloo, Western Australia (*Phyllophorus* sp. 1 in Fig. 28).



**FIGURE 22.** Rosettes of *Phyrella* cf. *thyonoides* A: UF 9601, introvert; B: UF 9598, cloacal region. Scale bar, 20  $\mu\text{m}$ .

**Ecology & distribution.** In Ningaloo, animals were adhering to dead shells or rocks that were buried in sand and on which algae was growing, close to shore at 1–3 m depth. They co-occurred with *Holothuria michaelensi*. The types were cast up on the beach, suggesting shallow habits. Known from Perth and Ningaloo, Western Australia.

#### Other species that may belong to *Phyrella*

##### *Phyrella? ambigua* (Cherbonnier, 1988)

Fig. 23

*Lipotrapeza ambigua* Cherbonnier, 1988: 236–237, fig. 104 A–H; Type series: MNHN EcHh 2767; type locality: Madagascar, Tuléar

= *Phyllophorus* (*Phyllophorella*) *contractura* Cherbonnier, 1988: 226–228, fig. A–L; Holotype: MNHN EcHh 3601; type locality: Madagascar, Tuléar

= *Thyonidiella oceana* Heding & Panning, 1954: 172–173 (in part)

*Thyonidiella oceana*: Cherbonnier, 1988: 229–232, fig. 101 A–G

= *Thyonidiella cherbonnieri* Rowe & Richmond, 2004: 3306–3307

**Material examined.** Madagascar, Tuléar (all): MNHN EcHh 2767, (syntypes of *Lipotrapeza ambigua*). MNHN EcHh 3601 (Holotype of *Phyllophorus contractura*). MNHN EcHh 2918 (Paratype of *Phyllophorus contractura*), September 12<sup>th</sup> 1972, coll. Thomassin, 1 specimen. MNHN EcHh 2969, August 17<sup>th</sup>, 1969, coll. Thomassin. Paratypes: MNHN EcHh 3863, June 10<sup>th</sup>, 1972, coll. Thomassin, 9 specimens. MNHN EcHh 2223, 1972, coll. Galénon, 7 specimens. MNHN EcHh 2913, May 16<sup>th</sup>, 1972, coll. Thomassin, 8 specimens. MNHN EcHh 2921, June 11<sup>th</sup>, 1972, coll. Thomassin, 1 specimen. MNHN EcHh 3794, 1975, coll. Galénon, 4 specimens. MNHN EcHh 2905, June 12<sup>th</sup>, 1972, 1 specimen. MNHN EcHh 2920, May 29<sup>th</sup>, 1972, coll. Thomassin, 1 specimen.

**Description based on type series of *P. ambigua*.** Two specimens partially dried up. One specimen is intact with introvert retracted; the other is dissected, with pharyngeal complex removed and in the jar. Body wall stiff, leathery, brown, covered with tube feet without any particular arrangement. Specimens about 1 cm long and 5 mm wide, light brown with relatively large, tubular podia covering the entire body wall; anal teeth present. Cherbonnier indicates that this species has 20 tentacles in 3 circles. The examination of the tentacles associated with the calcareous ring found in the jar reveals at least 16 tentacles (exact number difficult to assess given the state of preservation) in 2 circles. Cherbonnier indicates that radials and inter-radials are not fragmented, however his drawing (Fig. 104, H), which matches closely the calcareous ring found in the jar, shows that they are. Internal anatomy shows absence of intestine, respiratory trees shorter than in other *Phyrella*, gonads in two tufts formed by long, thin tubes, madreporite and stone canal apparently missing (Cherbonnier indicates that the stone canal is long and thin ending in a spherical madreporite), one globular Polian attached to the pharyngeal complex. Mid-dorsal body wall devoid of ossicles; podia with end plates and perforated plates. Cloacal region body wall with rosettes

(Fig. 104, D in Cherbonnier, 1988) and irregular tables (Fig. 104, A, B in Cherbonnier, 1988), podia have end plates and perforated plates (Fig. 104, E in Cherbonnier, 1988).

**Remarks.** We consider *Lipotrapeza ambigua* Cherbonnier, 1988, *Phyllophorus contractura* Cherbonnier, 1988, and *Thyonidiella cherbonnieri* Rowe & Richmond, 2004 to all represent the same species. As first revisers, we select *ambigua* as the valid name for this species, appropriate given the confusion surrounding this assemblage and the poor state of preservation of the specimens. It is notable that the type series of all three species were collected at the same locality.

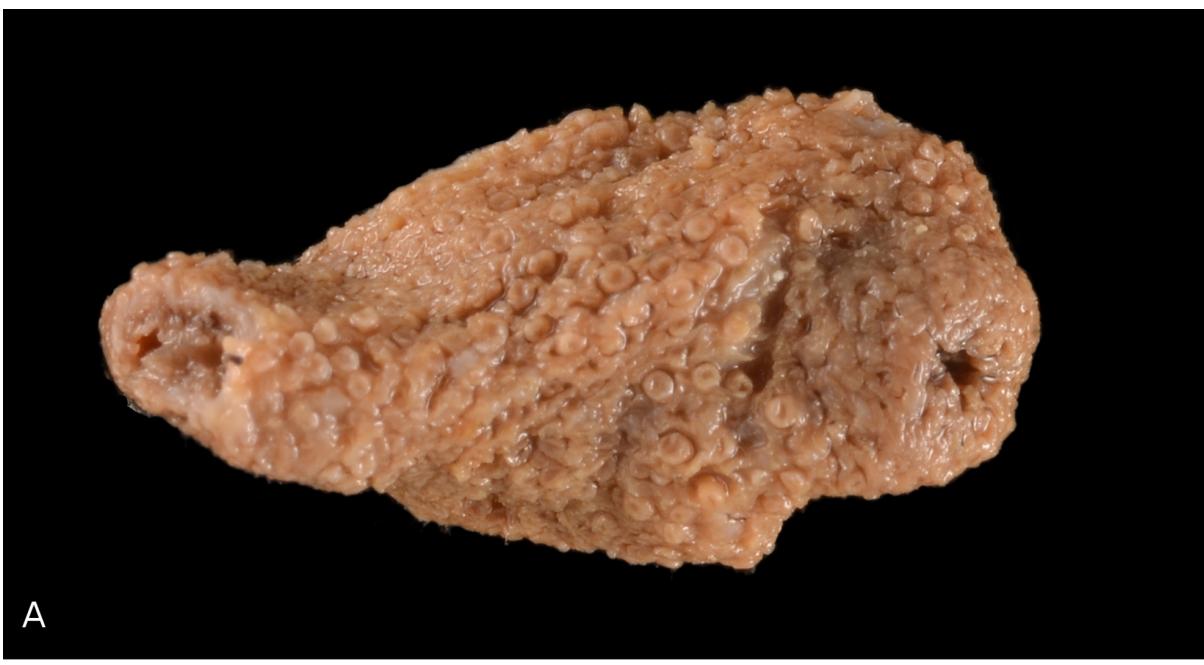
In the description of *Lipotrapeza ambigua*, Cherbonnier noted that the lot 2767 includes 12 specimens (holotype and paratypes). However, this lot only includes 2 specimens, and the holotype was not identified within the lot.

**Synonymy and description of *Phyllophorus (Phyllophorella) contractura*.** The holotype (MNHN Hol 3601) is in poor condition. As indicated by Cherbonnier, it is about 9 mm long, 4 mm wide, light brown with relatively large, tubular podia covering the entire body. The body wall shows evidence of decomposition. All internal organs and the cloacal region are missing. The small calcareous ring has been opened, and some of its elements are not in their natural position, however one of the inter-radials is clearly fragmented and does not match Cherbonnier's drawing (Fig. 99, I). Furthermore, the body wall does not contain ossicles, and the podia have end plates and perforated plates. The general appearance of the holotype, in conjunction with the fragmented inter-radials, the ossicle assemblage, the presence of anal teeth (as reported by Cherbonnier), and the collection locality indicate that this specimen is indistinguishable from *Lipotrapeza ambigua*. Examination of the paratype indicates that it was used for illustrations, and is a different species, assignable to *Phyllophorus sensu lato*.

**Synonymy and description of *Thyonidiella cherbonnieri*.** This species was erected as a new name for Malagasy specimens incorrectly attributed to *Thyonidiella oceana* by Cherbonnier (1988) (see Remarks under *Phyrella* above). As noted by Rowe & Richmond (2004) this species resembles *T. oceana* except for the lack of tables and presence of plates in the body wall. Most of the specimens identified by Cherbonnier as *T. oceana* are fairly similar. Body wall soft, fairly thin and covered with tube feet (Fig. 23, MNHN EcHh 2969). Color light to dark brown in preservative; some specimens darker at the extremities. Small (11–21 mm long, 5–8 mm wide), mostly cylindrical, with tapering posterior end and blunt anterior end when the introvert is retracted. Introvert retracted in all specimens examined, 1–2 mm long, light gray to almost black. Tube feet relatively long (~1 mm), of the same color as the rest of the body, abundant, covering both radial and inter-radial area without particular arrangement. Fifteen small, dark brown tentacles (number of tentacles on each circle difficult to discern). Cloaca dark brown, surrounded by 5 small anal teeth. Polian vesicle single, light brown, with sparse small dark spots, about 1 mm long. Stone canal lightly-calcified, embedded in membrane surrounding calcareous ring; madreporite single, small (<1 mm in diameter), spherical, partially embedded in membrane surrounding calcareous ring. When present, gonads in two tufts, composed of single, unbranched, 2–4 mm tubes. Digestive tract relatively short, most specimens eviscerated. Mid-dorsal body wall without ossicles. Podia with end plate and perforated plates. Cloacal region body wall with rosettes and tables in some specimens (not reported by Cherbonnier), podia with end plate and perforated plates. Cherbonnier notes he examined 25 specimens collected by Galéon, Thomassin in Tuléar Madagascar in 1975. MNHN holds 32 specimens in 8 lots of this species, all collected by Galéon or Thomassin in Tuléar Madagascar, between 1969 and 1975; four specimens date from 1975. We consider these discrepancies to be likely *lapsus calami*, and consider all material listed above to correspond to the syntype series designated by Rowe & Richmond (2004).

All specimens examined here are substantially smaller than other *Phyrella* species. This species fits *Phyrella* except for the absence of tables in the body wall, that it is smaller, and the presence of “bâtonnets des podia” (which we did not observe in our preparations). The shape of the body; the propensity to eviscerate; the size, shape and distribution of tube feet on the body; the shape of the perforated plates; the fragmentation of the calcareous ring and the presence of posterior prolongations; the presence of anal teeth; the presence of rosettes in cloaca and introvert make this species closer to *Phyrella* than to any other phyllophorid genus with fragmented inter-radials.

**Ecology & distribution.** Known from Madagascar, with specimens from Mauritius & Rodriguez, Mascarene Islands (not seen by us) also attributed to this species by Rowe & Richmond (2004). Malagasy specimens were collected at low tide level under rocks set in sand on the Tuléar barrier reef. In Rodriguez, the species was found in a fore reef habitat under coral rock in 13–15m, as well as in a coastal bay. The Mauritius specimens were collected at Cannoniers Point.



**FIGURE 23.** A: One of the syntypes of *Phyrella? ambigua*, MNHN EcHh 2767 (dissected specimen); B: one of the syntypes of *Thyonidiella cherbonnieri* MNHN EcHh 2969. Scale bar, 1 cm.

***Phyrella? bedoti* (Koehler, 1895)**

Figure 24

*Phyllophorus bedoti* Koehler, 1895: 278–279, fig. 1–2. Holotype: MHNG INVE82061; type locality: Baie d’Amboine

**Material examined:** MNHG INVE82061 (Holotype), Indonesia, Maluku Islands, Ambon Island, Ambon Bay, 1890.

**Description. External morphology.** Body wall soft, slightly contracted, covered with tube feet. Gray/light brown with irregular dark brown spots all over the body wall, tips of podia lighter (Fig. 24). 40 mm along dorsum, 55 mm along venter, and 23 mm wide. Apparently, the specimen was preserved with its introvert retracted which has been removed and is missing. Tube feet abundant, covering entire body, spread across radial and inter-radial areas without clear arrangement except towards oral end they converge in rows corresponding to the ambulacra. Described to have 17 tentacles, now missing.

**Internal anatomy.** Polian vesicle, madreporite, stone canal are missing along with introvert and calcareous ring. Gonads in two tufts composed of thin, simple, unbranched tubes. Intestine fairly long, with fairly coarse sand. Both respiratory trees extend almost entire length of animal.

**Calcareous ring.** Dissected out and missing, described as elongated, with both radials and inter-radials fragmented.

**Ossicle assemblage.** Ossicles very corroded; only rare, small and indistinguishable fragments remain. Description notes rare, typical (4-pillared united by a single cross-beam, 8-holes, smooth-rimmed), with incomplete spire, tables.

**Remarks.** This species, known only from the type, appears not to have been studied since its description. The reported fragmented inter-radials, regular tables, and 17 tentacles indicate it is a species of *Phyrella* rather than *Phyllophorus*. The loss of the type's introvert, calcareous ring, and the corrosion of its ossicles prevent effective comparison with species of *Phyrella*, and we regard it as *species inquirenda*. The type locality is the same as *Thyonidiella oceana*, and no character currently contradicts the synonymy of these two species. Fresh material from the type locality would be necessary to evaluate the status of this species.

**Ecology & Distribution.** Only recorded from the type locality, Ambon, Indonesia.



**FIGURE 24.** Holotype of *Phyllophorus bedoti* MHNG INVE82061. Lateral view. Scale bar, 1 cm.

## *Phyrella? tenera* (Ludwig, 1875)

*Orcula tenera* Ludwig, 1875:95, fig. 21. Holotype, Museum Godeffroy (no longer extant as an institution; type not located); type locality: Samoa, Upolu Island, 20 fathoms  
*Orcula tenera*: Lampert, 1885: 167–168; Théel, 1886: 149; Ludwig, 1888: 812–813 (fig. 18–20 pertain to Indonesian specimen that may not pertain to species)  
*Semperiella tenera*: Heding & Panning, 1954:180–181, fig. 86

**Remarks.** Described from a small specimen (2.5 cm long, 6 mm wide) without gonads suggesting to Ludwig that it is a juvenile. The specimen was described as light yellow, with not very numerous tube feet scattered all over the body, and 10 large and 5 small tentacles. The ossicle assemblage is composed of very few tables and some rosettes. The calcareous ring (Ludwig fig. 21c) has fragmented radials and inter-radials, former extended in long posterior prolongations.

This species is only unambiguously known from the type and has not been studied since its original description, and its whereabouts is unknown. It was not found during recent searches of the ZMH (Zoologisches Museum zu Universität Hamburg), ZMB (Museum für Naturkunde, Berlin), ZMUC, MCZ. The description is insufficiently detailed and the specimen is a juvenile making species level identification and even generic assignment impossible. Therefore, we consider this to be *species inquirenda*. Based on the limited information on hand, this species fits best in *Phyrella*; based on the number of tentacles, structure of calcareous ring, the presence of tables and rosettes. It was considered a likely synonym of *Thyonidiella oceana* by Cherbonnier (1988, see also Rowe & Richmond, 2004) a species we consider a synonym of *Phyrella fragilis*. The specimen was taken much deeper than any other species of *Phyrella*, and from further out in the Pacific.

This species has also been recorded in the literature from the Red Sea (Lampert, 1885 and Heding & Panning, 1954 based on different specimens) and Java (Pulo Edam - Ludwig, 1888 and Bay of Batavia - Sluiter, 1887 and Engel, 1933). Heding & Panning (1954) considered the two specimens from Bay of Batavia reported on by Sluiter and Engel to pertain to *Phyrella fragilis*, because they were described with 20 rather than 15 tentacles. However as noted above, tentacle number is not a reliable distinguishing feature of these species, and 15–17 tentacles are known from reliably identified and studied *P. fragilis*. The descriptions provided by all these papers are too limited to allow reliable species attribution without reexamining the specimens, although all could pertain to *Phyrella*.

**Ecology & Distribution.** Recorded with certainty only from the type locality, Samoa from fairly deep water (20 fathoms, ~ 37 m) relative to other *Phyrella*.

## Species removed from *Phyrella* or synonyms

### *Euthyonidiella aculeata* (Ludwig, 1894)

Figures 25–26, 27 i

*Phyllophorus aculeatus* Ludwig, 1893a: 111 1893b: 183: *nomen nudum*

*Phyllophorus aculeatus* Ludwig, 1894: 128–129, pl. XIII, fig 6–11. Holotype: USNM 18171; type locality: Gulf of Panama, shore

*Phyllophorus aculeatus*: Deichmann, 1941: 133–134, pl. 25; fig. 1–3

*Phyrella aculeata*: Heding & Panning, 1954: 184–185, fig. 89

**Material examined:** USNM 18171 (Holotype), Gulf of Panama, 12 March 1891.

**Description. External morphology.** Body wall rough like sand paper, fairly contracted, uniformly light gray (Fig. 25). Body cylindrical with ends tapering bluntly; 60 mm along dorsum, 65 mm along venter, and 25 mm wide at mid-body. Tube feet same color as body wall, most are retracted, very abundant, cover both radial and inter-radial areas without any clear arrangement. Introvert retracted, short (7 mm long, 3 mm wide), light gray. Tentacles vary in size between 2 and 22 mm long; exact number and arrangement cannot be discerned given the state of preservation of the specimen. No anal teeth.

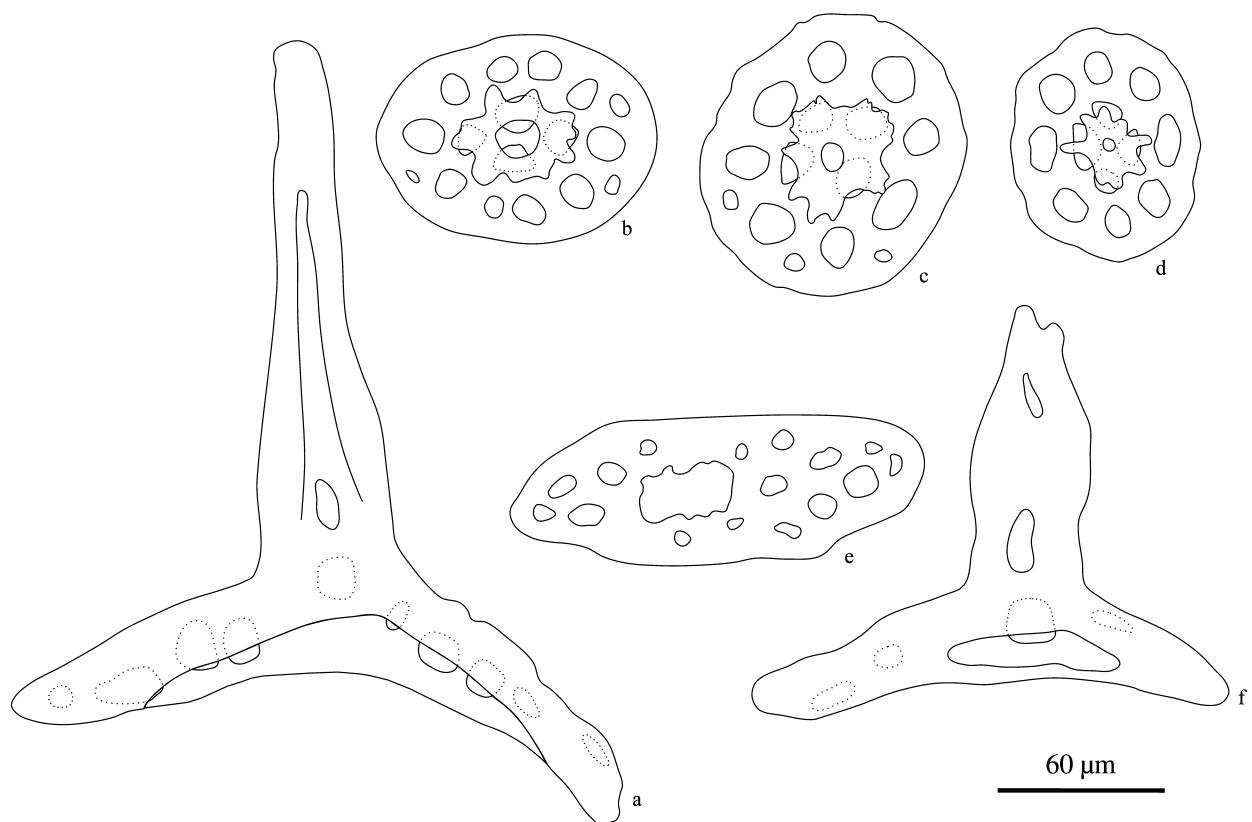
**Internal anatomy.** Three Polian vesicles (4–16 mm), thin, light brown. Stone canal and madreporite not observed. Most of the intestine and sections of the dorsal mesentery have been removed from the animal and are in the jar. Gonads in two tufts, formed by brown tubes that branch a few times, mostly near origin, up to 25 mm in

length. Intestine fairly long, empty. Respiratory tree, only left side remaining, dense, extending almost entire length of animal.

**Calcareous ring.** Calcareous ring with narrow radials and inter-radials, formed by barely fragmented elements, embedded in a fairly thick membrane (Fig. 27i). Anterior margins of radials straight, lightly notched at center. Anterior margins of inter-radials acutely pointed, arrow-head shaped. Inter-radials lie on top of radials, due to contraction of the structure. Radials project posteriorly forming short tails. Inter-radials lack posterior projections.



**FIGURE 25.** Dorsal view of holotype of *Phyllophorus aculeatus* USNM 1871. Scale bar, 1 cm.



**FIGURE 26.** Ossicle assemblage from holotype of *Phyllophorus aculeatus* USNM 1871 (mid-dorsal body wall). a,e,f: tack-like tables; b-d: regular tables. b-d, e: top view; a, f: lateral view.

**Ossicle assemblage.** **Dorsal body wall** with two types of tables. Regular tables (Fig. 26b–d) with disc nearly circular or ellipsoidal, 90–105 µm in diameter, 8–12 holes arranged in one circle with sometimes 2–4 smaller holes at the periphery, with complete rim; spire formed by four pillars united by a single cross-beam, with continued projections usually forming well-developed, spiny crown with a central hole. Podia with large tack-like tables (Fig. 26a,f), with a convex, elongated, elliptical disc that is perforated by a large central hole, up to 250 µm in diameter, and 10–15 smaller, scattered holes; spire 120–230 µm high, with four pillars that are fused along much of their length, but leave occasional perforations, usually ending bluntly, compressed in same plane as disc.

**Remarks.** This species is known only from the holotype, reexamined and further reported on by Deichmann (1941), who confirmed its uniqueness. The calcareous ring has not been previously illustrated. In the original description Ludwig notes that the anterior end of the radials are pointy, monocuspid, slender and are not typical of other *Orcula* and *Phyllophorus*. Indeed, the calcareous ring has the structure of a sclerodactylid, rather than a phyllophorid. The regular tables in the body wall are somewhat similar to *Phyrella* and other genera including *Phyllophorus*, but are more regular and ellipsoidal than in other *Phyrella*. Furthermore, no species of *Phyrella* have the large, tack-like tables that occur in the tube feet of *E. aculeata*, or have three Polian vesicles, and all have anal teeth unlike this species. *Euthyonidiella aculeata* lacks perforated plates, and rosettes in the introvert and cloacal body wall, contrary to *Phyrella*. These characters, together with the distant occurrence (in the East Pacific, rather than Indo-West Pacific) indicate that this species is not attributable to *Phyrella* and differs from other genera as well.

The calcareous ring, regular tables, and tack-like tables are all similar to species of the sclerodactylid genus *Euthyonidiella* Heding & Panning, 1954, and we transfer *P. aculeatus* to that genus. The only other polytentaculate phyllophorid known from the East Pacific, *Phyllophorus zacae* Deichmann, 1938, was also transferred to *Euthyonidiella* by Heding & Panning (1954).

### *Phyllophorus dubia* (Bedford, 1899)

*Orcula* (?*Phyllophorus*) *dubia* Bedford, 1899:144, pl. XVII, fig. 4. Holotype not located; type locality: Loyalty Islands, Lifu

**Remarks.** This species was only known from the type, 10.5 cm long with ca. 15 tentacles; it was described as lacking tables, with only rosettes and needles (latter likely contaminating sponge spicules) as ossicles, and with the calcareous ring with fragmented radials and inter-radials. The species was collected in the intertidal. The species was compared with *Phyllophorus bedoti* and *Orcula tenera* by Bedford. The species is closest to *Phyrella*, but differs in lacking tables. It has not been studied since the original description. The holotype has not been located, it is not at the BMNH. *Orcula* Troschel, 1846 (*non* Held, 1837, renamed *Ekmania* Hansen & McKenzie, 1991) is a cucumariid genus, so we tentatively assign this species to *Phyllophorus sensu lato* for nomenclatural purposes. Specific-level comparisons and generic assignment is not possible without restudy; we consider this to be *species inquirenda*.

### *Phyllophorus exigua* (Cherbonnier, 1980)

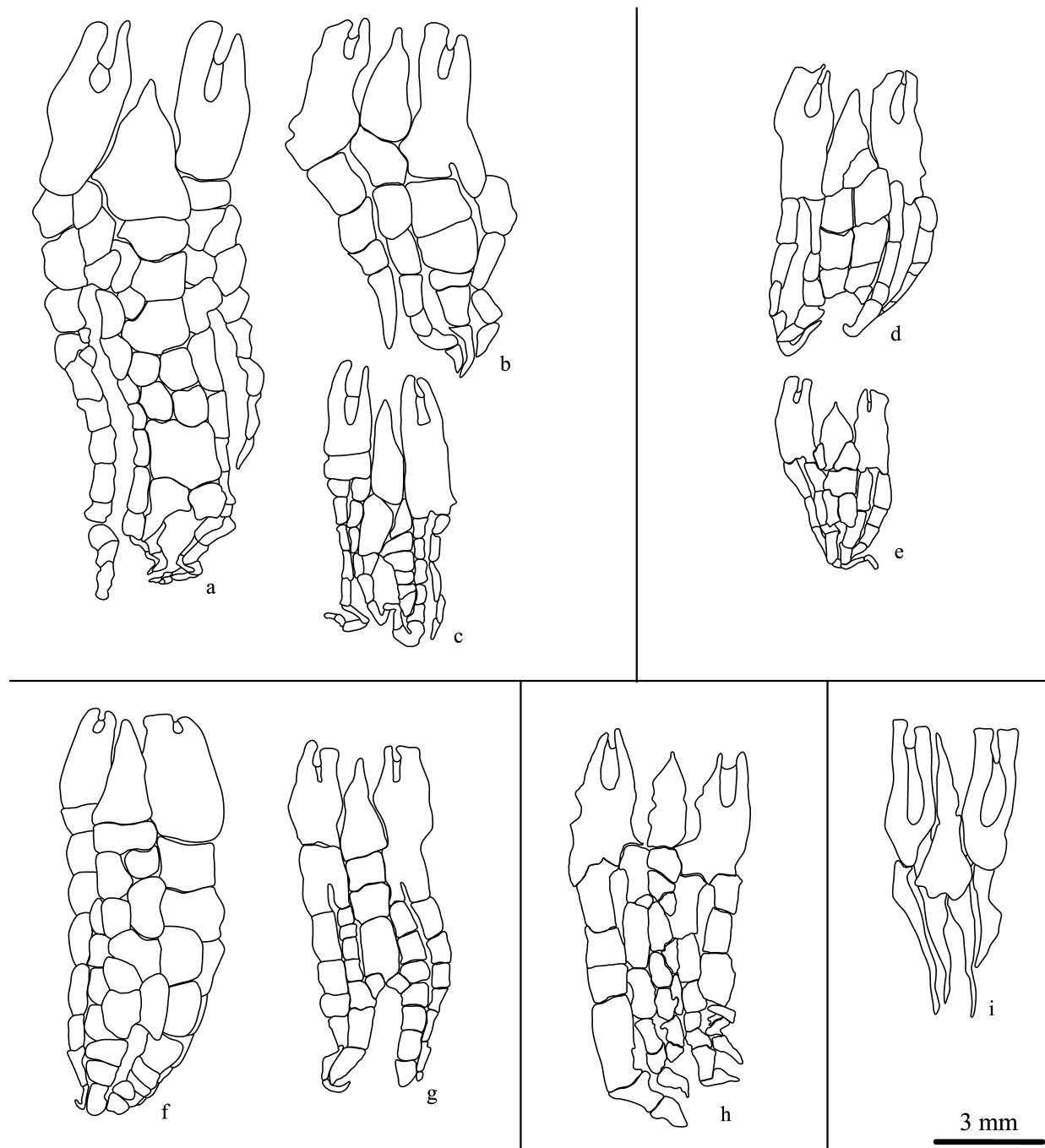
- *Thyonidiella exigua* Cherbonnier, 1980: 228–231, fig 100 A–Q. Holotype: not MNHN 1499, Madagascar, Tuléar  
- *Thyonidiella exigua*: Rowe & Richmond, 2004: 3307

**Remarks.** This species is known only from the holotype, a small juvenile (< 9 mm) specimen with 15 tentacles and a calcareous ring with short, unfragmented inter-radials. The structure of the calcareous ring thus suggests that it does not belong in *Phyrella*. Furthermore, the elongated plates in the body wall and the modified plates found in the podia illustrated by Cherbonnier do not coincide with the type of ossicles observed in *Phyrella*. Rowe & Richmond (2004) note that except for the number of tentacles (which could increase with age), it is close to *Selenkiella paradoxa* and could represent a juvenile of that species, also recorded from Tuléar. The holotype listed by Cherbonnier is MNHN HOL1499; however this catalog number corresponds to the type of *Havelockia exigua* Cherbonnier, 1958 from Sierra Leone. The holotype has not been located. Generic assignment of this species awaits additional material from the type locality; we provisionally assign it to *Phyllophorus sensu lato* for nomenclatural purposes.

***Phyllophorus kungi* (O'Loughlin, 2012)**

- *Thyonidiella kungi* O'Loughlin, 2012 in O'Loughlin et al., 2012:289, fig. 1d, 8. Holotype: NMV F76637; type locality: Australia, Victoria, Bass Strait

**Remarks.** This recently described species is small (up to 16 mm), lacks anal teeth, has 15 tentacles, posterior extensions on the radial plates only, tables with 3 cross-beams, highly branched rosettes in the tentacles, and was found deeper (57–58 m) than *Phyrella* species. The species does not appear to be attributable to *Phyrella* (=*Thyonidiella*) and awaits phylogenetic study; we provisionally assign it to *Phyllophorus* *sensu lato* for nomenclatural purposes.



**FIGURE 27.** Calcareous rings. a–c: *Phyrella fragilis* (a: UF 4096, b: WAM Z26012, c: WAM Z26013); d–e: *Phyrella trapeza*, syntypes (d: MCZ HOL1488, thick body wall; e: MCZ HOL1488, thin body wall); f: *Phyrella thyonoides*, holotype (MCZ HOL1654); g: *Phyrella cf. thyonoides* (UF 9601); h: *Phyrella mookei*, paratype (UF 4770); i: *Phyllophorus aculeatus*, holotype (USNM 1871).

## Discussion

*Phyrella* is a well-defined genus in the relatively murky world of dendrochirotids, by its apomorphic calcareous ring morphology, conserved anatomy and ossicle complements/morphology. To test the monophyly of *Phyrella* and have a quick assessment of the relationships of phyllophorid genera, we constructed a phylogeny from partial COI sequences assembled as part of a large holothuroid DNA barcoding project (Fig. 28). The genus as here redefined is robustly recovered (bootstrap 96) with COI sequences, nestled among other phyllophorids. Within *Phyrella*, *P. fragilis* and *P. mookiei* are recovered as sisters; their affinity is supported by their similar general appearance and shape of ossicles. The three species we have sequences for form a relatively shallow branch, nestled within a branch with several *Phyllophorus* species. Some species of the large and heterogeneous genus *Phyllophorus* are very similar to *Phyrella* in anatomy and ossicles, but distinguishable by their undivided inter-radials.

While COI sequences are short and rapidly evolving, and thus limited in their utility for resolving relationships at the genus level in holothuroids, the phylogeny obtained from available phyllophorid sequences makes morphological sense, and provides the first phylogenetic evidence on the debate about suprageneric relationships in the family, so we briefly discuss it here. More rigorous phylogenetic studies will follow. At the family level, the phylogenetic tree recovered three clades among sequenced Phyllophoridae: (1) *Stolus*, *Pentamera*, *Hemithyone*, *Thyone*, *Havelockia*; (2) *Neothyonidium* and *Massinium*; (3) *Lipotrapeza*, *Phyllophorus*, *Phyrella*. Even though the bootstrap values for these clades is overall relatively low (65, 99 and 64, respectively), the tree is only based on partial COI sequence data, and several phyllophorid genera are not included, it lends some support to the division of Phyllophoridae into sub-families, with some modifications. Thus the first clade corresponds to the Thyoninae, i.e. dendrochirotids with elongated calcareous rings and ten tentacles. *Hemithyone* falls well within this clade. Smirnov (2012) raised questions about the inclusion of this genus in the Thyoninae. This clade was transferred from cucumariids to phyllophorids by Pawson & Fell (1965) who considered calcareous ring morphology more important than tentacle number for defining families. Evaluating the relationship of this clade to cucumariids and polytentaculate phyllophorids is beyond this paper. The other two clades represent polytentaculate phyllophorid genera and show some relationship to the Phyllophorinae and Semperiellinae of Heding & Panning (1954). Thus clade 2 comprises genera with exceptionally complex calcareous rings, included highly divided inter-radials, which were included in the Semperiellinae, and may indeed form a distinct branch of the family, although the name Semperiellinae cannot be applied to them. In contrast the *Phyrella* (= *Semperiella*–*Thyonidiella*) is nested within the Phyllophorinae, a position that makes morphological sense, as discussed above.

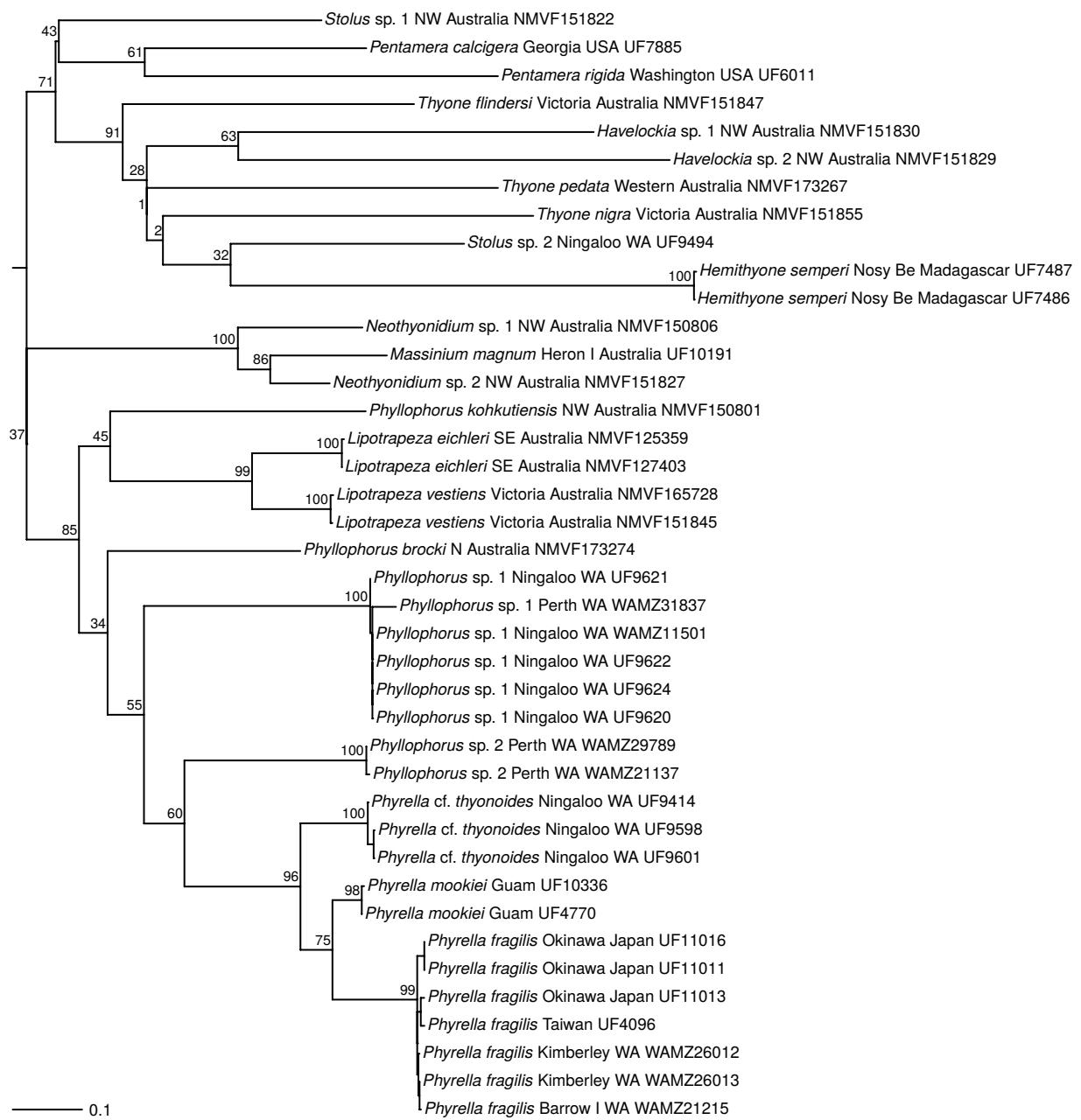
Even with the limited markers and species diversity, the phylogeny suggests that several genera as currently defined are not monophyletic. Together with the phylogenetic reassessments suggested at suprageneric level, these results indicate that the taxonomy of the Dendrochirotida needs to be re-evaluated. Genera and families of dendrochirotids have often been delineated typologically, based on single characters (tentacle number, calcareous ring fragmentation, disposition of podia, ossicle types) favored by different authors, and need a thorough reevaluation under phylogenetic scrutiny.

Thus we found that tentacle number and degree of fragmentation of the calcareous rings, characters deemed to be of generic or sub-familial significance, were variable within species of *Phyrella*. Overall, it appears that the characters used by various authors to establish the classification within Dendrochirotida might evolve more rapidly than previously thought, and also show some level of convergent evolution, hindering our understanding of the evolution of this diverse order of sea cucumbers.

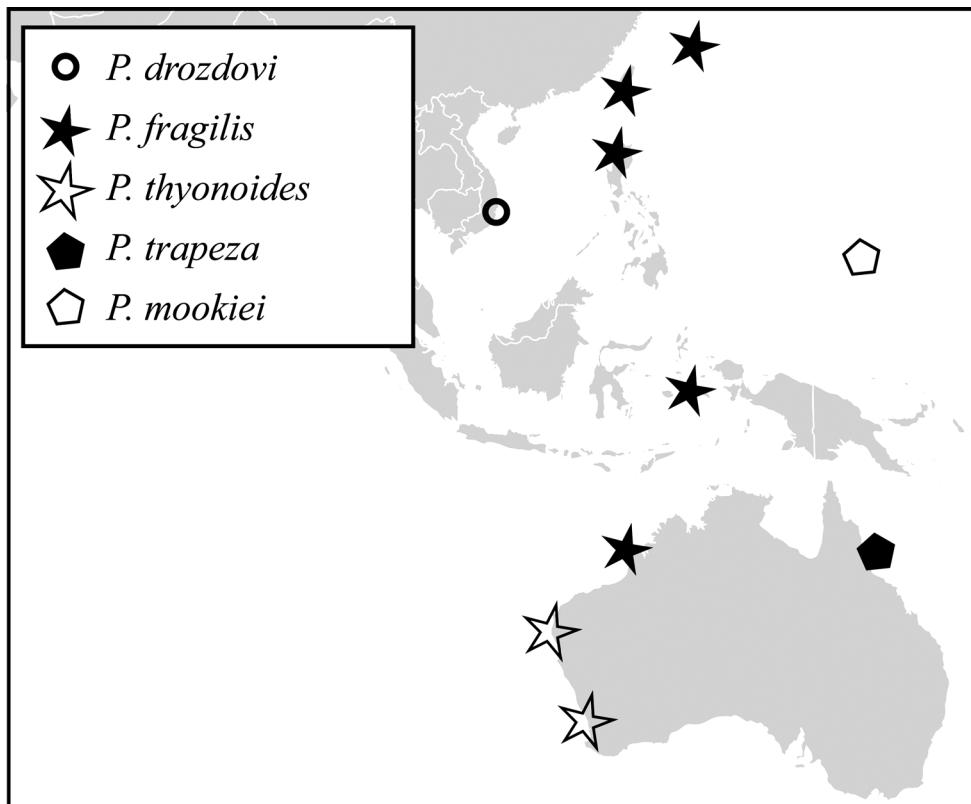
*Phyrella* is a tropical Indo-West Pacific genus which extends into the sub-tropical waters in Western Australia and Japan (Fig. 29). It appears that *Phyrella* species have restricted geographical ranges with three of the five recognized species known only from their type localities. *Phyrella fragilis* is the most widespread extending from the Ryukyu archipelago to the northern parts of Western Australia. Comparative studies on their reproductive biology may explain why this species has a broader geographical range than congeners. Confirmation of the generic assignment of *Phyrella?* *ambigua* and *Phyrella?* *tenera* would potentially extend the range of the genus considerably to the Western Indian Ocean and to the Central Pacific.

Evisceration has generally been considered to occur through the anterior in dendrochirotids (Byrne, 1985), although posterior evisceration has also been documented in *Pseudocolochirus violaceus* under highly stressful conditions (Dolmatov *et al.*, 2012). Contrary to many dendrochirotids, evisceration in *Phyrella* occurs posteriorly. Furthermore, the calcareous ring, gonads, respiratory trees, water ring and associated structures are retained by the

animal and only the intestine is ejected. Dissection of eviscerated specimens reveals that the intestine is autotomized anteriorly in the region of the esophagus, below the calcareous ring, and posteriorly near the opening of the cloaca. Evisceration is easily induced in *Phyrella* and the retention of most of the anatomy may be an adaptation to make it a less costly process.



**FIGURE 28.** Maximum-likelihood phylogram of some of the species of the genus *Phyrella* (estimated using RAxML 8.0.1). Bootstrap values based on 500 rapid replicates are reported above the edges. Bootstrap values within species have been removed for clarity. Tree rooted using *Holothuria impatiens* (not shown). Tree deposited in TreeBASE <http://purl.org/phylo/treebase/phylows/study/TB2:S15218>.



**FIGURE 29.** Distribution map of *Phyrella* species.

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### References

- Bedford, F.P. (1899) Holothurians. In: Willey, A. (Ed.), *Zoological results based on material from New Britain, New Guinea, Loyalty Islands and elsewhere collected during the years 1895, 1896, and 1897. Parts I–VI*. The University Press, Cambridge. pp. 141–150.
- Byrne, M. (1985) Evisceration behaviour and the seasonal incidence of evisceration in the holothurian *Eupentacta quinquesemita* (Selenka). *Ophelia*, 24 (2), 75–90.  
<http://dx.doi.org/10.1080/00785236.1985.10426621>
- Cherbonnier, G. (1988) *Echinodermes: Holothurides. Faune de Madagascar; 70. Faune de Madagascar. Vol. 70*. ORSTOM, Paris, 292 pp.

- Clark, H.L. (1932) Echinodermata (other than Asteroidea) of the Great Barrier Reef Expedition 1928–29. *Scientific Reports of the Great Barrier Reef Expedition*, 4 (7), 197–239.
- Clark, H.L. (1938) *Memoirs of Comparative Zoology at Harvard College. Vol. LV. Echinoderms from Australia an account of collections made in 1929 and 1938*. Museum of Comparative Zoology, Cambridge, MA, USA, 596 pp. + 28 plates.
- Deichmann, E. (1941) The Holothurioidea collected by the Velero III during the years 1932 to 1938. Part I, Dendrochirota, Allan Hancock Pacific Expeditions. Los Angeles, 8, 61–153.
- Dolmatov, I.Y., Khang, N.A. & Kamenev, Y.O. (2012) Asexual reproduction, evisceration, and regeneration in holothurians (Holothuroidea) from Nha Trang Bay of the South China Sea. *Russian Journal of Marine Biology*, 38 (3), 243–252.  
<http://dx.doi.org/10.1134/s1063074012030042>
- Drummond, A.J., Ashton, B., Buxton, S., Cheung, M., Cooper, A., Duran, M., Field, M., Heled, J., Kearse, M., Markowitz, S., Moir, R., Stones-Havas, S., Sturrock, S., Thierer, T. & Wilson A. (2011) Geneious v5.5. Available from: <http://www.geneious.com> (accessed 3 January 2014)
- Edgar, R.C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, 32 (5), 1792–1797.  
<http://dx.doi.org/10.1093/nar/gkh340>
- Engel, H. (1933) Resultats scientifiques du voyage aux Indes Orientates Néerlandaises Vol. III Fasc. 13. Holothuries. *Mémoires du Musée Royal d'Histoire naturelle de Belgique. Hors Serie*, III (1), 1–42.
- Gouy, M., Guindon, S. & Gascuel, O. (2010) SeaView version 4: A multiplatform graphical user interface for sequence alignment and phylogenetic tree building. *Molecular biology and evolution*, 27 (2), 221–224.  
<http://dx.doi.org/10.1093/molbev/msp259>
- Heding, S.G. & Panning, A. (1954) Phyllophoridae. Eine bearbeitung der polytentaculaten dendrochiroten holothurien des zoologischen museums. in Kopenhagen. *Spolia Zoologica Musei Hauniensis*, 13, 1–209.
- Hoareau, T.B. & Boissin, E. (2010) Design of phylum-specific hybrid primers for DNA barcoding: addressing the need for efficient COI amplification in the Echinodermata. *Molecular Ecology Resources*, 10 (6), 960–7.  
<http://dx.doi.org/10.1111/j.1755-0998.2010.02848.x>
- Koehler, R. (1895) Echinodermes de la Baie d'Amboine (Holothuries et Crinoïdes). In: Bedot, M. (Ed.), *Annales du Musée d'Histoire Naturelle de la ville de Genève*, III, 275–293.
- Lampert, K. (1885) Die Seewalzen (Holothurioidea). In: Semper, C. (Ed.), *Reisen im Archipel der Philippinen*. Wiesbaden (2) 4 (3), 1–312, 1 pl.
- Lanfear R., Calcott B., Ho S.Y.M. & Guindon S. (2012). PartitionFinder: Combined Selection of Partitioning Schemes and Substitution Models for Phylogenetic Analyses. *Molecular Biology and Evolution*. 29(6):1695–1701.  
<http://dx.doi.org/10.1093/molbev/mss020>
- Levin, V.S. & Stepanov, V.G. (1999) *Semperiella drozdovi* sp. n. (Dendrochirota, Phyllophoridae, Semperiellinae), a New Holothurian from the Gulf of Nhatrang (Vietnam). *Russian Journal of Marine Biology*, 25 (1), 71–74.
- Ludwig, H.L. (1875) Beiträge zur Kenntniss der Holothurien. *Arbeiten aus dem Zoologisch-Zootomischen Institut in Würzburg*, 2, 77–118.
- Ludwig, H. (1888) Die von Dr. J. Brock im Indischen Archipel gesammelten Holothurien. *Zoologische Jahrbücher*, 3, 805–820.
- Ludwig, H.L. (1893) Vorläufigen Bericht über die auf den Tiefsee-Fahrten des ALBATROSS (Fruhling, 1891) im östlichen Stillen Ocean erbeuteten Holothurien. *Zoologischer Anzeiger*, 16, 177–186.
- Ludwig, H.L. (1894) Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands, in charge of Alexander Agassiz, by the U. S. Fish Commission Steamer "Albatross", during 1891, Lieut. Commander Z. L. Tanner, U. S. N., comm. *Memoirs of the Museum of Comparative Zoology. Harvard*, XVI(3), 183.
- O'Loughlin, P.M., Barmos, S. & VandenSpiegel, D. (2012) The phyllophorid sea cucumbers of southern Australia (Echinodermata: Holothuroidea: Dendrochirotida: Phyllophoridae). *Memoirs of Museum Victoria*, 308, 269–308.
- Ohshima, H. (1912) On the system of Phyllophorinae with descriptions of the species found in Japan. *Annotationes zoologicae Japonenses*, 8, 53–96.
- Pawson, D.L. (1970) The marine fauna of New Zealand: sea cucumbers (Echinodermata: Holothuroidea). *New Zealand Department of Scientific and Industrial Research Bulletin*, 201, 1–70.
- Pawson, D.L. & Fell, H.B. (1965) A revised classification of the dendrochirote holothurians. *Breviora*, 214, 1–7.
- Rowe, F. & Richmond, M. (2004) A preliminary account of the shallow-water echinoderms of Rodrigues, Mauritius, western Indian Ocean. *Journal of Natural History*, 38 (23–24), 3273–3314.  
<http://dx.doi.org/10.1080/002229301695105>
- Samyn, Y. & Thandar, A.S. (2003) *Massinium*, a new genus in the family Phyllophoridae (Echinodermata: Holothuroidea: Dendrochirotida) with description of a new south-west Indian Ocean species *M. maculosum*. *Belgian Journal of Zoology*, 133 (July), 135–142.
- Sluiter, C.P. (1887) Die Evertebraten aus der Sammlung des Königlichen Naturwissenschaftlicher Vereins in Niederländisch Indien in Batavia. Die Echinodermen. 1. Holothuroidea. *Naturkundig Tijdschrift voor Nederlandsch Indië*, 47, 8e Serie, 8, 18–220, 2 pls.
- Smirnov, A.V. (2012) System of the class Holothuroidea. *Paleontological Journal*, 46 (8), 793–832.  
<http://dx.doi.org/10.1134/s0031030112080126>
- Stamatakis, A. (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics (Oxford, England)*, 22 (21), 2688–90.  
<http://dx.doi.org/10.1093/bioinformatics/btl446>
- Théel, H. (1886) Report on the Holothurioidea dredged by H.M.S. 'Challenger' during the years 1873–76. *Report on the Scientific Results of the Voyage of H.M.S. Challenger, 1873–1876, Zoology*, 14 (39), 1–290, 16 pls.