

**A CRITICAL ASSESSMENT OF THE
DENDROCHIROTID SUBFAMILIES,
SCLERODACTYLINAE AND THYONINAE, WITH
THE TAXONOMIC MANAGEMENT OF THE
“SUPERGENUS” *THYONE* (ECHINODERMATA:
HOLOTHUROIDEA)**

by

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ABSTRACT

The key character separating the dendrochirotid families Sclerodactylidae (*sensu* Pawson & Fell, 1965) and the Phyllophoridae (*sensu* Pawson & Fell, 1965), i.e. entire or undivided radial processes to the calcareous ring in the former and sub-divided processes in the latter, is unjustified since most sclerodactylid species also have sub-divided processes. It is here assumed that the basis of elevating the subfamily Sclerodactylinae Panning to family level was established on a misinterpretation or mistranslation of the original diagnosis of this subfamily or a *lapsus calumni* meaning “plates” instead of “processes”. Panning (1949) categorically states that the processes in the Sclerodactylinae are composed of 3–4 large pieces of calcite and only as an exception they are unbroken. Since Pawson & Fell gave no other distinction between the Sclerodactylidae and the Phyllophoridae, the former is here considered an invalid taxon and its three current subfamilies (Sclerodactylinae, Sclerothyoninae Thandar and Cladolabinae Heding & Panning) are re-assigned to the Phyllophoridae. This family now includes six subfamilies: Cladolabinae, Phyllophorinae Östergren, Sclerodactylinae, Sclerothyoninae, Semperiellinae Heding & Panning and Thyoninae Panning. The diagnosis of the Sclerodactylinae, restricted by Thandar (1989), is now modified to include also those forms whose radial and interradial plates may be slightly sub-divided but still form a short tube. Of the eleven genera placed within this subfamily subsequent to its erection, only ten of these remain. *Neothyone* Deichmann is a preoccupied name for which *Lisacucumis* is here proposed as a replacement. Thandar’s (1989) diagnosis of the Thyoninae is here accepted, however, the genus *Thorsonia* Heding is transferred to the Sclerodactylinae. Of the 66 nominal species which currently stand in the “supergenus” *Thyone* Jaeger, 10 are transferred to *Havelockia* Pearson within the Sclerodactylinae, while one species is regarded as a synonym of *H. herdmani* Pearson. In addition, six species are transferred to *Stolus* Selenka within the Thyoninae. Finally, three species are transferred to Sclerothyoninae, two within *Sclerothyone* Thandar and one within *Temparena* Thandar. Two species show an uncertain affinity to *Thyone* and are temporarily removed from the genus. Furthermore, two species currently classified within *Havelockia* are transferred to *Thyone*. The now remaining 46 species are separated into seven groups based on the

composition of their introvert deposits: tables only (8 spp.), rosettes only (5 spp.), tables and rosettes (21 spp.), tables and plates/?reduced tables (2 spp.), rosettes and plates/?reduced tables (3 spp.), plates only (2 spp.), or introvert deposits absent or unknown (5 spp.). Regrettably, no other character could be used in conjunction with the above to suggest at least sub-generic levels. Within the genus *Havelockia*, *Cucumaria redimita* Sluiter indicates an affinity with *Pentamera* Ayres. It is here transferred to this genus within the Thyoninae. *Havelockia*, now containing 17 species, is also revised. Keys, diagnoses and figures are provided for all nominal species now included in *Thyone* and *Havelockia*.

Key words: *Lisacucumis*; *Havelockia*; new genus; Phyllophoridae; sea cucumbers

PREFACE

The experimental work described in this dissertation was carried out in the School of Biological & Conservation Sciences, University of KwaZulu-Natal, Durban, from January 2010 to December 2011, under the supervision of Professor Ahmed. S. Thandar.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any tertiary institution. Where use has been made of the work of others it is duly acknowledged in the text.

The format and list of references of this dissertation are in accordance with the instructions to authors of the on-line journal **Zootaxa**, in which, it is anticipated, this investigation will be published.

DECLARATION - PLAGIARISM

I, Preyan Arumugam, declare that

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Signed:

To my fiancé, parents, and sister,
Thank you for being my pillar of strength and my inspiration.
I love you.

"I can do all things through Christ which strengtheneth me"

Philippians 4:13

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LIST OF ACRONYMS

ICZN:	International Code of Zoological Nomenclature.
IOAS:	Institute of Oceanology, Academia Sinica, Qingdao, Shandong, China.
IZL:	Institute of Zoology and Limnology, Innsbruck, Austria.
LACM:	Natural History Museum of Los Angeles County.
MCZ:	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.
MNHN:	Muséum National d'Histoire Naturelle, Paris.
NHMUK:	Natural History Museum, United Kingdom.
SAM:	Iziko South African Museum, Cape Town.
USNM:	United States National Museum, now National Museum of Natural History, Smithsonian Institution, Washington, DC.
ZMA:	Zoological Museum Amsterdam, University of Amsterdam Netherlands.
ZMH:	Zoologisches Museum Hamburg, Germany.
ZMUC:	Zoological Museum, University of Copenhagen, Natural History Museum of Denmark.
KZN:	KwaZulu-Natal.
WCP:	Western Cape Province.
UCT:	University of Cape Town.

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INTRODUCTION

In his revision of the then known 10-tentacled dendrochirotid family Cucumariidae Ludwig, Panning (1949) devised a new classification for these holothuroids. Panning erroneously mentioned that until then, the soft tissues such as the development and distribution of the tube feet played a large role as criteria for separating genera and species (Panning, 1949: 405). On the contrary, many prominent earlier authors such as Selenka (1867), Semper (1868) and Ludwig (1875) did use ossicle assemblages as grounds for identifying and separating species. Panning (1949) utilized the calcareous ring and calcareous deposits as taxonomic characters, thereby recognizing five subfamilies within the Cucumariidae, three of which were new. Those forms with a simple calcareous ring, i.e. those lacking posterior processes on the radial plates, were grouped within the Cucumariinae Ludwig; the Colochirinae Panning and the Ypsilothurinae Heding; while species with a complex calcareous ring with posterior processes were assembled within the Sclerodactylinae Panning and the Thyoninae Panning.

The subfamily Sclerodactylinae was characterized by undivided radial and interradial plates with the radial plates of short to medium length usually bearing posterior processes composed of about 3–4 large pieces; only as an exception were the processes unbroken. The deposits of the body wall comprised buttons only, baskets and buttons, or tables only. Panning diagnosed the Thyoninae as a group characterized by a sub-divided calcareous ring, i.e. one broken into a mosaic of small pieces and with long, also sub-divided, processes to the radial plates. Ossicle assemblage in the body wall comprised buttons only, buttons and baskets, tables and plates, or tables only.

Within the Sclerodactylinae Panning included nine genera: *Athyone* Deichmann; *Pseudothyone* Panning; *Neopentamera* Deichmann; *Neothyone* Deichmann and *Pachythyone* Deichmann (all with only buttons in the body wall); *Eupentacta* Deichmann and *Apentamera* Deichmann (with both buttons and baskets in the body wall); *Sclerodactyla* Ayres (with four-pillared tables) and *Pentathyone* H.L. Clark (with two-pillared tables in the body wall). Within the Thyoninae he included seven genera: *Stolus* Selenka (with buttons only in the body wall); *Heterothyone* Panning (with baskets and plates in the body wall); *Pentamera* Ayres and *Thorsonia* Heding (with

tables and plates in the body wall) and *Allothyone* Panning; *Havelockia* Pearson and *Thyone* Jaeger (with tables only in the body wall).

Panning characterized the genus *Havelockia* as comprising forms with two-pillared tables in the body wall and tables only in the introvert, and the genus *Thyone* comprising forms also with two-pillared tables in the body wall but only rosettes in the introvert. He, further, commented that *Pentathyone* erected by H.L. Clark (1938) for *Thyone mirabilis*, was characterized by such a diverse body form to that of a typical *Thyone* that it did deserve a new genus.

However, after receiving the original diagnosis of *Havelockia*, Panning realized that, on the basis of the calcareous ring, this genus belonged in the Sclerodactylinae and not in the Thyoninae which he originally proposed. He then, in his addendum to the same paper, transferred *Havelockia* with its type species *H. herdmani* Pearson into the Sclerodactylinae and relegated *Pentathyone* to the synonymy of *Havelockia*, with *H. herdmani* as type species. He also proposed that all those species he initially placed within *Havelockia* be transferred to *Thyone*. This resulted in there being now two groups of species within *Thyone*: those with tables only in the introvert and those with rosettes only.

It is not clear from Panning's work whether he re-examined the type material of all the species he included in *Thyone* (*s.e.*). Since many mistakes were made by him, it is here assumed that Panning relied too heavily on the works of other authors, many of whom did not examine the introvert ossicles. Panning also omitted many species, especially those placed in *Thyone* by Deichmann (1941), perhaps due to the fact that most of these species were not adequately described and/or an illustration of their calcareous ring not given. Furthermore, he included in his original assemblage of species in *Thyone* also forms with both tables and rosettes in the introvert.

Heding & Panning's (1954) revision of the polytentaculate family Phylloporidae Östergren was also on the basis of the calcareous ring. They erected five subfamilies: the Thyonidiinae Heding & Panning for those forms with a simple calcareous ring, whereas those with a complex calcareous ring, they grouped into three subfamilies: the Cladolabinae Heding & Panning (characterized by an undivided calcareous ring with short, usually undivided processes on the radials); the Phylloporinae Östergren (characterized by also an undivided calcareous ring, but with moderately long processes

made up of a few large pieces); and the Semperiellinae Heding & Panning (with long processes but in which both the processes and the plates are made up of a mosaic of small pieces of calcite). The last subfamily Rhopalodininae Perrier was assembled for those forms whose mouth and anus were situated at the same end, i.e. at the tip of a proboscis-like structure.

Fell (1965) speculated that the ambulacral plate system of the fossil edrioasteroids was perhaps reduced during holothurian evolution to what is referred to as the calcareous ring. Thus, he supposed that the more complex the calcareous ring, the more primitive the holothuroid. Therefore, in their revised classification of the dendrochirotid holothuroids, Pawson & Fell (1965) abandoned tentacle number as a criterion for separating higher taxa and presented a more natural classification based upon the form of the calcareous ring, the shape of the tentacles and the form of the calcareous deposits of the body wall. On the basis of these characters, the then known subfamilies of the Cucumariidae (*sensu* Panning, 1949) and Phyllophoridae (*sensu* Heding & Panning, 1954) became intermixed, whereby the 10-tentacled Sclerodactylinae and the polytentaculate Cladolabinae were assembled in the family-group taxon the Sclerodactylidae, and the 10-tentacled Thyoninae with the polytentaculate subfamilies Phyllophorinae and Semperiellinae assembled into the family-group taxon the Phyllophoridae. The polytentaculate Thyonidiinae was transferred to the Cucumariidae which now only encompassed forms with a simple calcareous ring. Moreover, those forms with digitate or unbranched tentacles were placed in a new order Dactylochirotida Pawson & Fell, 1965 and contained the families Ypsilothuriidae, Rhopalodinidae and their newly erected family Vaneyellidae Pawson & Fell, 1965. Although this system was not initially used by workers such as Clark & Rowe (1971) in their monograph of the shallow Indo-West Pacific echinoderms, it became widely accepted later and is utilized by Rowe in the catalogue of the Australian fauna (Rowe & Gates, 1995). Today it is the only used classification system for holothurians, albeit with some changes. Thandar (1989, 1990, 1991) also utilized the same system in his reports on the southern African Sclerodactylidae, Phyllophoridae and Cucumariidae respectively.

It is here suspected that the family Sclerodactylidae (*sensu* Pawson & Fell, 1965) was based on a mistranslation or misunderstanding of Panning's (1949) diagnosis of the Sclerodactylinae. Panning described the processes as generally broken into 3–4 large

pieces, and only as an exception are they unbroken. However, in their key to the Dendrochirotida, Pawson & Fell state that the processes in the Sclerodactylidae are entire. Pawson & Fell perhaps mistook Panning's statement that only as an exception are the processes in the Sclerodactylinae unbroken to imply that unbroken processes is a key character of this subfamily, thus elevating its status to that of family, and accommodating the Cladolabinae within it. Even if Pawson & Fell meant "*plates*" instead of "*processes*", this would also be unjustified as many sclerodactylids do possess sub-divided plates.

The genus *Thyone* within the Thyoninae has over time, become a receptacle for all 10-tentacled dendrochirotids with scattered tube feet, a complex calcareous ring, and two-pillared tables in the body wall to an extent that it has now assumed the status of a "supergen" (*sensu* Pawson & Miller, 1981). Pawson & Miller, while revising the Western Atlantic forms of this genus, attempted to re-diagnose the genus but failed to look more critically at the nature of the calcareous ring. They did, however, correctly state for the first time the presence of a third group within *Thyone*: those forms with both tables and rosettes in the introvert. However, they assumed that this group was only represented in the Western Atlantic Ocean without realizing that as early as 1940, Heding, in his Iranian Gulf report, already redescribed *T. dura* Koehler & Vaney with both tables and rosettes in the introvert.

Thandar & Rajpal (1999b) determined three types of calcareous rings among species of *Thyone*: those with the radial plates prolonged beyond the posterior border of the interradial plates before bifurcating; those with the interradials prolonged (deeply incised radials) and those where the radial plates bifurcate at the posterior border of the interradials (i.e. both radial and interradial plates are of same length). Thandar (2001) suggested a system using the type of calcareous ring as a means of dividing the genus into smaller groups. Unfortunately, he was not able to establish any correlation between the type of ring and the ossicle assemblage but noticed some correlation between the type of calcareous ring and the geographical distribution of the species, but with exceptions. He, however, declined to erect any new taxa since it was well known that the calcareous ring changes with age, as reported by Heding (1940), thus requiring adult forms for proper identification and classification or a complete series of specimens.

Thandar & Rajpal (1999b) also pointed out that the calcareous ring has thus far been used to separate only suprageneric taxa (see Concluding Remarks).

Furthermore, Thandar (1989) suggested a restriction of the Sclerodactylinae to those forms with a compact, short, tubular calcareous ring with sub-divided or undivided processes. He erected the subfamily Sclerothyoninae for those forms whose complex calcareous ring does not form a tube, as the radial and interradial plates are only united at their bases, making the ring more cucumariid-like but with long processes to the radial plates. This resulted in there now being three subfamilies within the Sclerodactylidae. Thandar further suggested that the Thyoninae should be restricted to forms with long, tubular, sub-divided calcareous rings.

Interestingly, while reporting on the phylloporid fauna of South Africa, Thandar (1990) mentioned a fourth group within *Thyone*: with plates and rods in the introvert. The presence of rods is here considered to be contamination from the tentacle deposits.

The possession of 10 dendritic tentacles, scattered tube feet and two-pillared tables has made both the genera *Thyone* and *Havelockia* receptacles to accommodate all such forms. Furthermore, since Panning's transferral of those species originally placed in *Havelockia* (*sensu* Panning, 1949) into *Thyone* and the synonymization of *Pentathyone* with *Havelockia* in the Sclerodactylinae, it would seem the characters separating these two subfamilies and these two genera are very much confused and often indistinguishable as many authors have referred their material to either *Thyone* or *Havelockia* without much criticism or forethought. Consequently, it remains without question that the both genera, and particularly *Thyone*, are in urgent need of revision.

Hence, the aims and objectives of this research were to assess the validity of the family-group taxon, the Sclerodactylidae; to critically re-define the two dendrochirotid subfamilies, the Sclerodactylinae and the Thyoninae; and to re-evaluate the two much confused genera, *Thyone* and *Havelockia*, and their included species for the effective taxonomic management of the former, providing diagnoses and keys, where necessary, for easy identifications.

MATERIALS AND METHODS

All species of *Thyone* and *Havelockia* included by Panning (1949), those omitted by him, as well as those described by subsequent authors were studied from type and/or voucher materials previously examined by Dr. Thandar and/or those obtained on loan by the writer from several museums and/or from original descriptions. Thandar examined numerous types and voucher specimens at or from seven institutions: the Zoological Museum, University of Amsterdam (ZMUA); Natural History Museum (Smithsonian Institute), U.S.A (USNM); Zoological Museum, University of Copenhagen (ZMUC); Natural History Museum, Paris (MNHN); the Natural History Museum (London) (NHMUK); the Natural History Museum of Los Angeles County (LACM) and the Museum of Comparative Zoology, Harvard (MCZ). Regrettably, most of the work has, up to now, remained unanalysed and unpublished.

The neotype of *Thyone fusus* was designated from material obtained by the writer on loan from the Natural History Museum, Oslo, Norway. Other type material was also obtained on loan from the following institutions: the ZMH; MNHN, Paris; NHMUK; LACM; MCZ and the Iziko South African Museum (SAM), Cape Town.

The morphological characters emphasized in the diagnoses of the genera and species are the form of the calcareous ring, and the body wall, tube feet, tentacle and introvert deposits. The type locality and geographical distribution of each species are also recorded.

All figures are produced from freshly prepared slides of type material or reproduced from drawings from original descriptions and/or those made by Thandar in his study of type and other materials at/from the various institutions. Figures 1–3 illustrate the calcareous ring and/or ossicles of certain species which were not previously illustrated or provide new information not hitherto described. Those species that are well described have not been re-illustrated, except species currently remaining or assigned to *Thyone* and *Havelockia*, the subject of this investigation.

SYSTEMATIC ACCOUNT

Part I

Order Dendrochirotida Grube, 1840

Family Phyllophoridae Östergren, 1907

Diagnosis (after Thandar, 1990 and Rowe & Gates, 1995, amended herein)

Dendrochirotid holothuroids without a test. Tube feet restricted to ambulacra or scattered. Tentacles 10–25, dendritic. Plates of the calcareous ring either uniting at the base only, with medium to long bifurcate, often sub-divided, processes to the radial plates; or plates compact forming a short tube with medium to long radial processes composed of a few large pieces, rarely processes unbroken; or plates elongated, tubular, composed of a mosaic of numerous pieces, with also sub-divided radial processes. Ossicles of the body wall two–four-pillared tables, plates, nodular buttons, baskets or fenestrated ellipsoids.

Remarks

Pawson & Fell (1965) separated the family Sclerodactylidae from the Phyllophoridae on the basis of unbroken or entire processes to the calcareous ring. However, Panning (1949) characterised the subfamily Sclerodactylinae as having a compact calcareous ring, in which the processes are usually broken into a few large pieces and only as an exception are they unbroken. Whether Pawson & Fell mistook the plates for processes or used, as a result of misinterpretation, the unbroken processes as a key character to separate their Sclerodactylidae (*sensu* Pawson & Fell, 1965) and Phyllophoridae is open to debate but clearly their reasoning for distinguishing both families is unjustified. Hence, the taxon Sclerodactylidae is here considered an invalid taxon and the three subfamilies (Sclerodactylinae, Sclerothyoninae and Cladolabinae) are referred to the Phyllophoridae. This thought is shared also by Thandar (1989) who emphasised the compact, short, non-tubular nature of the calcareous ring as a distinguishing character of the sclerodactylid genera.

Thandar (1989) further suggested that the Phyllophoridae, Sclerodactylidae and the Cucumariidae stem from a single lineage with a gradual reduction from a complex to a simple calcareous ring without posterior processes. He discussed that since the Sclerodactylidae contains mainly transitional forms, the simplicity of the ring in the Cucumariidae (*sensu* Panning, 1949) is perhaps derived from the reduction of the plates as in the Sclerothyoninae while the processes are completely lost in the Cucumariidae. Though, Rowe (pers. comm.) believes that the tubular nature of the ring is an adaptation to burrowing since it is more developed in such forms. Neither Thandar's nor Rowe's assumptions are without merit and can go hand in hand but the nature of calcareous ring cannot be dispensed with as a key character separating higher taxa.

Thus, it is here suggested, that the subfamilies currently classified within the Sclerodactylidae, be considered subfamilies of the Phyllophoridae (*sensu* Pawson & Fell, 1965), as suggested by Thandar (1989). There exist now six subfamilies within the Phyllophoridae: the Sclerothyoninae Thandar, Sclerodactylinae Panning, Thyoninae Panning, Semperiellinae Heding & Panning, Cladolabinae Heding & Panning and Phyllophorinae Östergren. Only the 10-tentacled subfamilies: Sclerodactylinae, Sclerothyoninae and Thyoninae are discussed in detail since the first and last are the subject of this investigation.

Key to the subfamilies of the family Phyllophoridae

1. a) Tentacles 10..... 2
 b) Tentacles more than 10..... 4

2. a) Plates of the calcareous ring not forming a tube, uniting at the base only.....
 **Sclerothyoninae** Thandar (Fig. 1A)
 b) Plates of the calcareous ring forming a tube..... 3

3. a) Plates usually compact (not sub-divided), tube short; posterior processes of the radial plates short to medium in length made up of a few large pieces of calcite, rarely undivided..... **Sclerodactylinae** Panning (Fig. 1B)

- b) Plates long, sub-divided in a mosaic, tube long; posterior processes of the radial plates medium to long in length made up of small pieces of calcite; fragmentation of plates and processes not always clearly visible..... **Thyoninae** Panning (Fig. 1C)
4. a) Plates of the calcareous ring compact (undivided)..... 5
 b) Plates of the calcareous ring made up of a mosaic of small pieces of calcite with long processes to the radial plates..... **Semperiellinae** Heding & Panning (Fig. 1F)
5. a) Radial processes short, usually entire; or sub-divided into a series of pieces.....
 **Cladolabinae** Heding & Panning (Fig. 1D)
 b) Radial processes moderately long made up of a few large pieces.....
 **Phyllophorinae** Östergren (Fig. 1E)

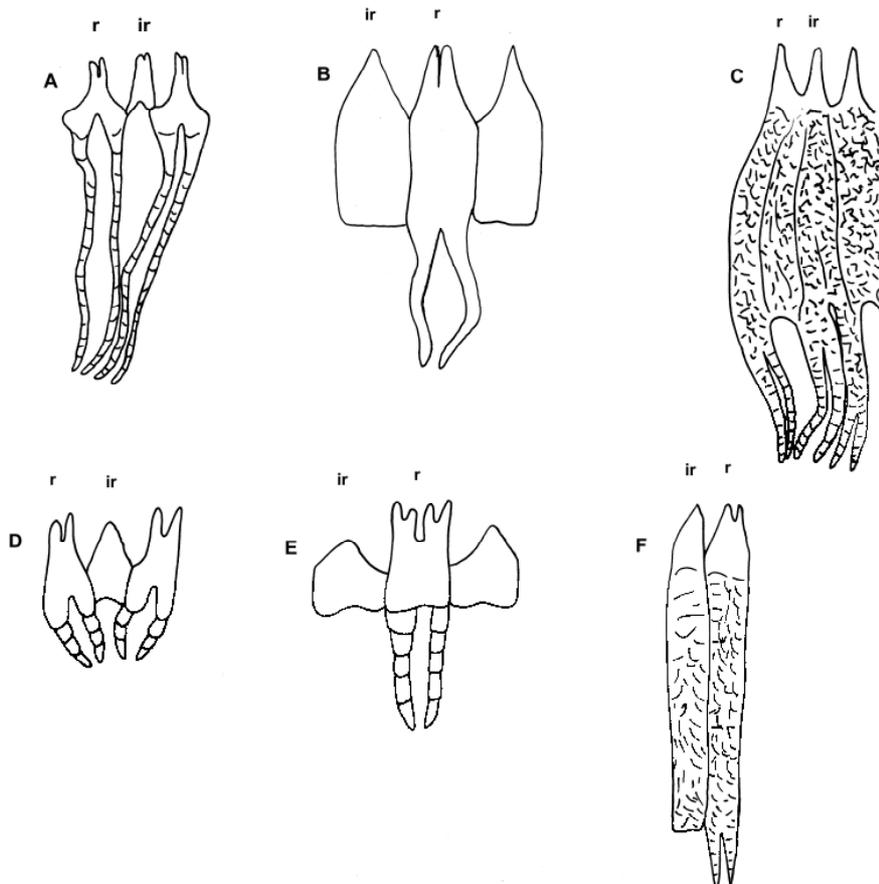


FIGURE 1. Calcareous rings of the subfamilies of the Phyllophoridae. A. Sclerothyoninae (r = radial plate; ir = interradial plate); B. Sclerodactylinae; C. Thyoninae; D. Cladolabinae; E. Phyllophorinae; F. Semperiellinae (Not drawn to scale).

Subfamily Sclerodactylinae Panning, 1949

Diagnosis (restricted by Thandar, 1989; modified herein)

Tentacles 10; calcareous ring short, radial and interradial plates usually compact, fused for most of their length forming a short tube; posterior paired processes of the radial plates of medium length, usually broken into a few large pieces of calcite; rarely processes undivided.

Type genus: *Sclerodactyla* Ayres, 1857, by original designation Panning (1949).

Other genera included: *Apentamera* Deichmann, 1941; *Athyone* Deichmann, 1941; *Deichmannia* Cherbonnier, 1958; *Engeliella* Cherbonnier, 1968; *Eupentacta* Deichmann, 1938; *Havelockia* Pearson, 1903; *Lisacucumis* nom. nov.; *Pachythyone* Deichmann, 1941; *Pseudothyone* Panning, 1949 and *Thorsonia* Heding, 1940.

Remarks

Thandar (1989) restricted the Sclerodactylinae to those forms with a “compact, short, tubular” calcareous ring. The diagnosis of the genus *Havelockia* Pearson has been here amended to now accommodate those species of *Thyone* Jaeger whose calcareous ring forms a short tube although the plates are divided in some species. Hence the diagnosis of the subfamily has been amended to also include such forms. Furthermore, the Thyoninae is restricted to include only those forms with an elongated, tubular ring.

Key to the genera of the subfamily Sclerodactylinae

1. a) Deposits of the body wall exclusively tables or in combination with plates..... 2
b) Deposits of the body wall exclusively buttons or baskets or a combination of both, plates rare or absent..... 4

2. a) Tables only..... 3
b) Tables of two types: four-pillared tables with 2–5 lobed discs, sometimes in combination with smaller, more or less symmetrical two-pillared ones and/or

- perforated plates lacking spires..... *Thorsonia* Heding
3. a) Tables two-pillared, spire well-developed or reduced or deposits absent.....
..... *Havelockia* Pearson
b) Tables with four-pillared spire..... *Sclerodactyla* Ayres
4. a) Body wall comprise buttons only or baskets only..... 5
b) Body wall comprise a combination of buttons and baskets, plates rare or
absent..... 8
5. a) Deposits buttons only..... 6
b) Deposits uniquely small, shallow to deep developing baskets.....
..... *Deichmannia* Cherbonnier
6. a) Buttons of a single type..... 7
b) Buttons of two types: a superficial layer of oval buttons with the external side
covered by a dense reticulum and an inner layer of oblong four-holed buttons,
regularly knobbed..... *Pachythyone* Deichmann
7. a) Buttons scattered, swollen, with 1–4 holes, sometimes up to six; knobs indistinct
or absent..... *Athyone* Deichmann
b) Buttons smooth to knobbed, some bearing a handle on one or both sides.....
..... *Pseudothyone* Panning
8. a) Buttons in combination with baskets, plates absent..... 9
b) Buttons in combination with baskets, plates rare..... 10
9. a) Deposits a combination of buttons and baskets, both either smooth or knobbed;
tube feet restricted to ambulacra..... *Eupentacta* Deichmann
b) Deposits a superficial layer of buttons with spinous projections on one side and a
handle on the opposite side, transformed into reticulated baskets in one species or
lost with age, and an inner layer of numerous, mostly four-holed knobbed,

sometimes smooth, buttons; tube feet scattered..... *Lisacucumis* nom. nov.

10. a) Deposits comprising a superficial layer of flattened baskets almost rosette-like and in an inner layer of regular four-holed knobbed buttons, large plates rare; introvert supported by oblong, elongated tables or plates (?reduced tables) with slightly knobbed margin..... *Apentamera* Deichmann
- b) Deposits of three types: small baskets stout, swollen mostly knobbed four-holed buttons, and large plates with lattice surface; introvert supported by numerous rosettes..... *Engeliella* Cherbonnier

Genus *Apentamera* Deichmann, 1941

Figure 2A & B

Apentamera Deichmann, 1941: 91; Panning, 1949: 459.

Diagnosis (after Deichmann, 1941 and Panning, 1949, amended herein)

Small holothuroids, measuring up to 35 mm in length; body wall rigid. Tube feet restricted to the ambulacra, becoming papilliform towards the ends forming five valves; few smaller papilliform tube feet scattered in the dorsal interambulacra. Tentacles 10, ventral pair smaller. Plates of the calcareous ring short, compact; radial plates with medium to long posterior processes broken up into few large pieces. Body wall deposits comprising a superficial layer of flattened baskets almost rosette-like and an inner layer of regular four-holed knobbed buttons; large plates rare. Tube feet with curved supporting two-pillared tables ending in a few blunt teeth; end-plates present, smaller in terminal feet. Tentacle deposits, plates and rods becoming smaller in the branches. Introvert supported by oblong, elongated tables or plates (?reduced tables) with slightly knobbed margin.

Type species: *Apentamera lepra* Deichmann, 1941, by original designation.

Other species included: none.

Remarks

Deichmann (1941) was vague when commenting on the nature of the calcareous ring of this genus which remains monotypic since its designation. She does, however, comment that the body wall and tube feet deposits of *Apentamera lepra* come close to another species described in the same paper *Neothyone gibbosa* but does not compare their calcareous rings. Panning (1949) placed both genera in the Sclerodactylinae. Fortunately, Thandar examined the type material of *A. lepra* from the LACM and determined that the calcareous ring of the holotype is definitely of the sclerodactylid type (Fig 2A). He also found some unusually large plates in the body wall (Fig 2B), not mentioned by Deichmann. Such deposits are absent in the paratype, though the other deposits are identical to those of the holotype. Hence, the diagnosis of the genus is here amended.

Genus *Athyone* Deichmann, 1941

Figure 2C

Athyone Deichmann, 1941: 118; Panning, 1949: 456.

Diagnosis (after Deichmann, 1941 and Panning, 1949, amended herein)

Medium-sized holothuroids; body wall soft. Tube feet numerous distributed over entire body, fairly stout. Tentacles 10, ventral pair smaller. Calcareous ring stout, radial plates broad with distinct posterior processes; interradial plates sometimes long, ending in a single conical point anteriorly. Deposits of body wall scattered, swollen 1–4-holed buttons, sometimes with up to six holes; knobs indistinct or absent. Tube feet with numerous two-pillared, curved, supporting tables, reduced with age or supporting rods; end-plates present. Tentacle deposits rosettes, sometimes in combination with rods. Introvert supported by tables and rosettes or deposits absent.

Type species: *Thyone glasselli* Deichmann, 1936, by original designation.

Other species included: *Athyone exila* Cherbonnier, 1988 and *Athyone maculisparsa* Cherbonnier, 1988 (*incertae sedis*).

Remarks

Deichmann's (1936) initial description of *Thyone glasselli* was rather vague and she did not illustrate the calcareous ring of her single specimen. In 1937 she re-examined the type and illustrated a fairly long, comparatively stout calcareous ring compared to species of *Thyone* with both tables and rosettes in the introvert. She consequently (1941) transferred this species to a new genus, *Athyone*, whose ossicles she claimed to be closest to the variety *T. benti* var. *zacaе* described also in 1937. Panning (1949) placed this genus within the Sclerodactylinae, which was supported by Deichmann (1955) when she re-diagnosed her *A. glasselli* following the collection of younger individuals demonstrating a "stout, short-tubular calcareous ring" with sub-divided posterior processes to the radial plates. Indeed, the holotype, re-examined by Thandar in the MCZ materials, does display a compact, stout ring with short to medium sub-divided posterior processes (Fig. 2C). Hence the species should be retained in the Sclerodactylinae.

Cherbonnier (1988) referred two species from Madagascar, one large and one rather minute, to *Athyone*, the generic position of the former the writer believes is doubtful. His *A. maculisparsa*, based on a single specimen, lacks deposits except rosettes, restricted to the anal region. Furthermore, the calcareous ring measures more than 1/10th of the body and appears tubular with the radial plates deeply incised. It is possible that the body wall ossicles of this species are lost with age and the rosettes at the anal region are persistent juvenile attributes. However, this, together with the calcareous ring, does not correspond with the generic diagnosis of *Athyone*. This species needs to be moved out of *Athyone* possibly into a new genus once new material is found.

The holotype of *A. exila*, the smaller species measuring a mere 8 mm, contains a short, compact calcareous ring with short sub-divided processes to the radial plates. Following an examination of the type material at the MNHN (EcHh no. 3599), Thandar was confident that the plates of the calcareous ring are not fragmented and the latter is typical of the sclerodactyline type. Since Cherbonnier does not mention the presence or

absence of introvert deposits it must be assumed he did not study them. No deposits were found in the introvert of the holotype or paratype by Thandar. Thus the diagnosis of the genus has been amended to accommodate this.

Genus *Deichmannia* Cherbonnier, 1958

Deichmannia Cherbonnier, 1958: 191.

Diagnosis (after Cherbonnier, 1958)

Dendrochirotid holothuroids with an almost spherical body; mouth and anus set very close to one another due to the shortening of the ventral surface. Body wall thin, smooth. Tube feet scattered dorsally; in two series per ambulacra ventrally, scattered in the interambulacra, all ending with a terminal sucker; end-plates present. Tentacles 10, ventral pair reduced. Calcareous ring short, stout with conspicuous posterior processes to the radial plates made up of a single piece. Ossicles of body wall composed uniquely of small baskets. Tentacle deposits small rods and rosettes.

Type species: *Deichmannia unica* Cherbonnier, 1958, by monotypy.

Other species included: none.

Genus *Engeliella* Cherbonnier, 1968

Engeliella Cherbonnier, 1968: 47.

Diagnosis (after Cherbonnier, 1968)

Small holothuroids; body fusiform, vaguely pentagonal in outline; body wall rigid and rough. Tube feet restricted to a single row per ambulacra, more or less retractile, small, conical or nipple-like, without terminal sucker or end-plates. Anal teeth absent. Tentacles 10, ventral pair reduced. Calcareous ring short, radial plates slightly longer made up of five or six large pieces. Deposits of body wall of three types: small stout baskets, swollen mostly knobbed four-holed buttons, and large plates with lattice

surface. Tube feet with table-like rods perforated in the centre and at the ends. Tentacle deposits as long thick rods perforated along their length. Introvert supported by numerous rosettes.

Type species: *Engeliella engeli* Cherbonnier, 1968, by monotypy.

Other species included: none.

Genus *Eupentacta* Deichmann, 1938

Figure 2D–G

Eupentacta Deichmann, 1938: 109; Panning, 1949: 458.

Diagnosis (after Deichmann, 1938 and Panning, 1949)

Medium-sized holothuroids, up to 100 mm in length; body cylindrical or barrel-shaped. Tube feet cylindrical, non-retractile, restricted to ambulacra. Tentacles 10, ventral pair reduced. Plates of calcareous ring unbroken with fairly short, broken or unbroken posterior processes to the radial plates. Deposits of body wall a combination of buttons and baskets, both either smooth or knobbed. Tube feet with large supporting tables, some with reduced spires.

Type species: *Cucumaria quinquesemita* Selenka, 1867, by original designation.

Other species included: *Cucumaria chronhjelmi* Théel, 1886; *Cucumaria exigua* Ludwig, 1875; *Cucumaria fraudatrix* Dyakonov & Baranova, 1958 and *Eupentacta pseudoquinquesemita* Deichmann, 1938.

Remarks

Deichmann (1938) included two species within her newly erected genus: *Eupentacta quinquesemita* (Selenka) and *E. pseudoquinquesemita* Deichmann. She commented that, based upon a re-examination of Selenka's (1867) material at the MCZ, she was certain that the Pacific forms from Mendocino (west coast of the United States of America) were synonymous with *Cucumaria chronhjelmi* Théel while the Atlantic

forms originating from Charleston (east coast of the United States of America) were misidentified specimens of *C. pulcherrima* = *Pentamera pulcherrima* Ayres. Panning (1949) included this genus in the Sclerodactylinae and added *C. exigua* Ludwig while ignoring Deichmann's synonymization of *C. chronhjelmi* with *E. quinquesemita*, keeping both species separate. The calcareous ring of the type of *C. chronhjelmi* (Fig 2D) housed in the NHMUK (1860.2.29.20) is definitely of the sclerodactyline type. Thandar examined the material from Mendocino from the MCZ whose tentacle deposits according to him matched those of the type of *C. chronhjelmi* (Fig 2G) but differed in the form of the introvert deposits which comprised a combination of tables, smooth to knobbed plates and rods (Fig 2E & 2F resp.). Though the differences are minor, the writer is inclined to follow Panning and leave both species as separate until a further study of the material or new material proves otherwise.

Genus *Havelockia* Pearson, 1903

Havelockia Pearson, 1903: 198; Panning, 1949: 466; Clark & Rowe, 1971: 203 (partim).

Pentathyone H.L. Clark, 1938: 458; Panning, 1949: 459.

Diagnosis (after Pearson, 1903 and Panning, 1949, amended herein)

Small to medium-sized holothuroids, up to 130 mm in length; body more or less quadrangular, almost cucumber-shaped. Tube feet scattered on dorsal surface, more numerous ventrally. Tentacles 10 (8–?13), ventral pair reduced. Calcareous ring short, stout, composed of usually compact plates; plates sometimes broken into a few large pieces but always broadly meeting each other at margins and rarely fused; posterior paired processes of radial plates of variable length, but usually short and divided into several pieces; interradial plates pointed anteriorly. Body wall ossicles tables with squarish to oval discs usually perforated by four large central and four smaller peripheral holes, the latter sometimes reduced or absent, in some species multilocular tables occur; spire of varying height made up of two pillars joined at apex, sometimes terminating in a few blunt teeth; in some species body wall deposits lacking; in one species body wall comprise plates only.

Type species: *Havelockia herdmani* Pearson, 1903, by monotypy [= synonym of *Havelockia versicolor* (Semper, 1868), according to James (1976)].

Other species included: *Cucumaria ardens* Koehler & Vaney, 1908; *Cucumaria ariana* Koehler & Vaney, 1908; *Cucumaria conciliatrix* Sluiter, 1901; *Thyone discolor* Sluiter, 1901; *Havelockia ferali* Cherbonnier, 1988; *Thyone festina* (Koehler & Vaney, 1908); *Cucumaria imbellis* Koehler & Vaney, 1910; *Pentathyone* (?) *novacorona* Cherbonnier, 1961; *Cucumaria perdita* Koehler & Vaney, 1910; *Thyone pituitosa* Sluiter, 1901; *Thyone pohaiensis* Liao, 1986; *Thyone strangeri* Deichmann, 1941; *Thyone tanyspeira* Pawson & Miller, 1988; *Cucumaria transitoria* Vaney, 1905; *Havelockia turrispinea* Cherbonnier, 1988 and *Thyone vankampeni* Sluiter, 1914.

Remarks

Rowe & Gates (1995), erroneously classified *Havelockia* under the Phyllophoridae, although citing Panning's (1949) revision of the Cucumariidae. It is here emphasized that following Panning's (1949) synonymization of *Pentathyone* with *Havelockia*, the latter genus was transferred to the Sclerodactylinae by Panning in the same paper where it currently remains.

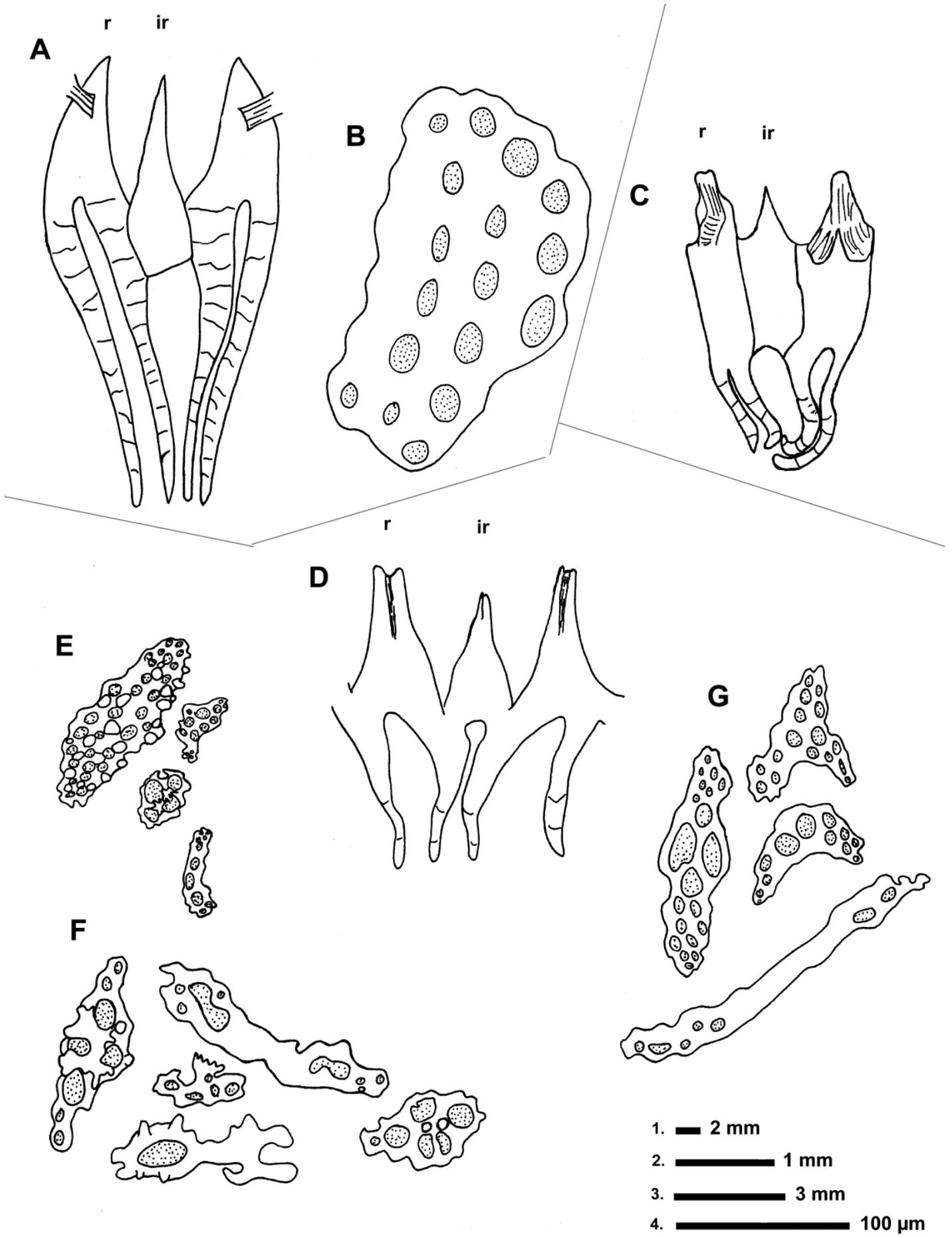
Since many species of *Thyone* have been transferred to *Havelockia*, the diagnosis of this genus has been amended to accommodate these species. *Havelockia* is dealt with in greater detail later (see page 170).

FIGURE 2

Apentamera lepra Deichmann. A. calcareous ring of holotype (r = radial plate; ir = interradial plate); B. large plate from body wall of holotype. A = Scale 2; B = Scale 4. Reproduced from Thandar's examination of the material from the LACM.

Athyone glasselli (Deichmann). C. calcareous ring of holotype. C = Scale 1. Reproduced from Thandar's examination of the material from the MCZ.

Eupentacta chronhjelmi (Théel). D. calcareous ring of holotype; E. introvert deposits of Mendocino material of *Eupentacta quinquesemita* (Selenka); F. introvert deposits of *Eupentacta chronhjelmi*; G. tentacles deposits of *E. chronhjelmi*. D = Scale 3; E, F, G = Scale 4. Reproduced from Thandar's examination of the material from the NHMUK and MCZ respectively.



Genus *Lisacucumis* nom. nov.

Neothyone Deichmann, 1941: 108; Panning, 1949: 458 [homonym = *Neothyone* Hampson, 1914: Arctiidae].

Stolus Selenka (partim) 1867: 356.

Diagnosis (after Deichmann, 1941 and Panning, 1949)

Medium-sized holothuroids with a thick body wall, packed with deposits. Tube feet numerous, distributed over entire body. Tentacles 10, ventral pair reduced. Plates of calcareous ring sub-divided with short to medium length posterior processes to the radial plates, in some species fairly short and soft, often inwardly curled, thereby escaping notice. Deposits of body wall a superficial layer of buttons with spinous projections on one side and an inner handle on the other, transformed into reticulated baskets in one species, in some cases lost with advancing age, and an inner layer of numerous, mostly four-holed knobbed, sometimes smooth, buttons. Supporting tables of tube feet numerous; spire present or reduced; end-plates present. Tentacle deposits heavy plates or rods. Introvert supported by tables or reduced buttons (plates).

Type species: *Stolus gibber* Selenka, 1867, by original designation.

Other species included: *Neothyone gibbosa* Deichmann, 1941 and *Thyone panamensis* Ludwig, 1886 (1887).

Remarks

Neothyone was erected by Deichmann (1941) for *Stolus gibber* Selenka in which she included two other species, one new. Panning (1949) placed this genus within the Sclerodactylinae, unaware that Deichmann had used a preoccupied name, a fact obviously overlooked by Deichmann herself. The name *Lisacucumis* is here proposed to replace this genus in honour of Elisabeth Deichmann for her work as a holothurian taxonomist.

Genus *Pachythyone* Deichmann, 1941

Pachythyone Deichmann, 1941: 114; Panning, 1949: 458.

Diagnosis (after Deichmann, 1941 and Panning, 1949)

Small to medium-sized holothuroids, measuring up to 50 mm in length. Tube feet stout, cylindrical in five longitudinal bands, scattered in interambulacra, becoming papilliform dorsally and toward the ends. Tentacles 10, ventral pair reduced. Plates of calcareous ring unbroken with short, broken or unbroken posterior processes to the radial plates. Deposits of body wall a superficial layer of oval buttons with the external side covered by a dense reticulum and an inner layer of oblong four-holed buttons, regularly knobbed. Tube feet with curved to straight supporting tables; spire very spinous distally; end-plates present, reduced in the papilliform feet. Tentacle deposits perforated plates. Introvert with oblong two-pillared tables; spire mostly reduced.

Type species: *Thyone rubra* H.L. Clark, 1901, by original designation.

Other species included: *Thyone lugubris* Deichmann, 1939 and *Pachythyone pseudolugubris* Deichmann, 1941.

Remarks

Deichmann (1939) hesitantly classified her new species in *Thyone* but mentioned its congeneric status with that of *Thyone rubra* described by H.L. Clark (1901) from the Pacific, differing only in the colour of their bodies and tentacles, and slightly smaller ossicles in the latter. She later (1941) placed both species in a new genus *Pachythyone* in which she included another new species *P. pseudolugubris* Deichmann. This step was accepted by Panning (1949). Thandar (in notes) examined the cotype (= syntype) of *P. rubra* from the MCZ (no. 244) and found no distinguishing characters to separate this species from *P. lugubris* (Deichmann). In time, both species may prove to be conspecific.

Genus *Pseudothyone* Panning, 1949

Pseudothyone Panning, 1949: 456.

Diagnosis (after Panning, 1949, amended herein)

Small to medium-sized holothuroids. Tentacles 10, ventral pair sometimes reduced. Plates of calcareous ring undivided; radial plates with medium length, paired posterior processes, unbroken or made up few large pieces. Deposits of body wall smooth to knobbed buttons, some bearing a handle on one or both sides.

Type species: *Thyone raphanus* Dübén & Koren, 1846, by original designation.

Other species included: *Thyone belli* Ludwig, 1886; *Pseudothyone furnestini* Cherbonnier, 1969; *Cucumaria mosaica* Koehler & Vaney, 1910; *Pseudothyone levini* Lambert & Oliver, 2001; *Pseudothyone sculponea* Cherbonnier, 1959 and *Thyone serrifera* Östergren, 1898.

Remarks

Lambert & Oliver (2001) presented a very descriptive table of the species of *Pseudothyone* Panning, but failed to include *Thyone serrifera* Östergren. They were obviously not aware that Madsen & Hansen (1994) had transferred this species to *Pseudothyone* based on the presence of plates and not two-pillared tables in the body wall, the latter are characteristic of *Thyone* species.

Genus *Sclerodactyla* Ayres, 1851

Sclerodactyla Ayres, 1851: 102; Panning, 1949: 459.

Diagnosis (after Panning, 1949)

Tube feet restricted to ambulacra or scattered. Tentacles 10, ventral pair reduced. Plates of the calcareous ring compact (unbroken) with short to medium length radial posterior processes which are undivided or consist of only a few pieces. Body wall ossicles comprise four-pillared tables.

Type species: *Holothuria briareus* Lesueur, 1824 by subsequent designation Ayres (1851).

Other species included: *Cucumaria multipes* (Théel, 1886).

Remarks

Designated as the type genus of the subfamily Sclerodactylinae by Panning (1949), this genus is characterised by possessing only four-pillared tables in the body wall.

Genus *Thorsonia* Heding, 1940

Thorsonia Heding, 1940: 131; Panning, 1949: 465; Liao & Clark, 1995: 499.

Echinocucumis Semper, 1868: 60; Sluiter 1887 (1888): 201 (partim).

Diagnosis (after Heding, 1940 and Liao & Clark, 1995)

U-shaped holothuroids. Tube feet restricted to ambulacra, more numerous ventrally. Tentacles 10, ?unequal. Calcareous ring complex, plates compact or subdivided, forming a short tube; radial plates with long paired posterior processes. Body wall deposits comprise four-pillared tables with 2–5 lobed discs only or with two-pillared rounded tables, spire high, and/or perforated plates lacking spires.

Type species: *Echinocucumis adversaria* Semper, 1868, by original designation.

Other species included: *Thorsonia fusiformis* Heding, 1940 and *Cucumaria investigatoris* Koehler & Vaney, 1908.

Remarks

Semper (1868) classified his *E. adversaria* under *Echinocucumis* Sars but unfortunately did not illustrate the calcareous ring. Sluiter recorded the species in 1888 with a more detailed description, illustrating a very short, compact calcareous ring like that of a sclerodactyline, and reported that the ten unequal tentacles are arranged in no particular order. Koehler & Vaney's (1908) *Cucumaria investigatoris* also demonstrates

a typical sclerodactyline ring, but the processes appear to be broken up into numerous small pieces of calcite. However, they did not study the arrangement of the tentacles for fear of irrevocably destroying their 20 mm specimen. Regrettably, Heding's (1940) *Thorsonia fusiformis* was described from only a fragment lacking the calcareous ring and associated structures. Despite this, Heding commented that based upon the shape of the body, arrangement of the tube feet and the presence of the large, normally four-armed plates and the tube feet deposits, his species is closely related to *Echinocucumis adversaria* and so erected a new genus to accommodate both these species. Liao & Clark (1995) in their report of *T. adversaria* from the China Sea describe a small, mosaic-like calcareous ring but failed to illustrate it. However, they report the tentacle number to be 10, with the ventral pair reduced.

This genus comes close to *Sclerodactyla* in the possession of four-pillared tables but differs in the 2–5 armed, irregular nature of the discs. It thus seems justifiable based upon the form of the calcareous ring that it be transferred to the Sclerodactylinae. Despite the mosaic-like nature of the calcareous ring of *T. adversaria* (Liao & Clark, 1995), *Thorsonia* is perhaps intermediate between the Sclerodactylinae and the Thyoninae.

Subfamily Thyoninae Panning, 1949

Diagnosis (after Panning, 1949 and Thandar, 1990)

Small to medium-sized phylloporids, rarely more than 100 mm long; body soft. Tube feet numerous, usually scattered over entire body, but often most crowded ventrally. Tentacles 10, ventral pair always reduced. Calcareous ring long, tubular, sub-divided, with long paired, sub-divided processes to radial plates. Ossicles of body wall in the form of tables or plates (buttons), or absent.

Type genus: *Thyone* Jaeger, 1833, by original designation.

Other genera included: *Allothyone* Panning, 1949; *Pentamera* Ayres, 1852; *Stolus* Selenka, 1867; and *Thyonina* Thandar, 1990.

Key to the genera of the subfamily Thyoninae

1. a) Deposits of the body wall exclusively tables or derivatives of these..... 2
b) Deposits of the body wall plates/buttons/table-like buttons or exclusively rods... 4
2. a) Spire of tables two-pillared..... 3
b) Spire of tables four-pillared..... *Allothyone* Deichmann
3. a) Tables two-pillared, spire well-developed or reduced or tables absent; tube feet scattered..... *Thyone* Jaeger
b) Tables two-pillared, or derivatives of these, spire reduced to completely absent; tube feet restricted to ambulacra..... *Pentamera* Ayres
4. a) Deposits in the form of smooth to knobbed buttons, the latter mostly regular, four-holed, with 10–12 marginal knobs, some buttons with more knobs and holes or table-like, with a ‘handle’ on one or both sides; rarely complex, multi-layered or as large, thick scales or plates, up to 1 mm in size..... *Stolus* Selenka

b) Deposits minute, slender, straight or slightly curved, smooth rods, expanded and often digitated at ends which have a single large and one or more smaller holes.....
..... *Thyonina* Thandar

Genus *Allothyone* Panning, 1949

Figure 3A & B

Allothyone Panning, 1949: 466.

Diagnosis (after Panning, 1949)

Tentacles 10. Calcareous ring tubular, sub-divided, with long posterior processes to the radial plates. Body wall deposits four-pillared tables.

Type species: *Thyone multipes* Augustin, 1908, by original designation.

Other species included: *Cucumaria longicauda* Östergren, 1898; *Thyone mexicana* Deichmann, 1946; *Cucumaria mucronata* Sluiter, 1901 and *Thyone spadix* Sluiter, 1901.

Remarks

This genus is separated from *Sclerodactyla* within the Sclerodactylinae by the tubular nature of its calcareous ring. Thandar examined some specimens of *Allothyone longicauda* (Östergren) at the ZMUC which contained a very tubular calcareous ring (Fig. 3A), which although not mosaic-like some incipient fragmentation was evident. He noted that the entire ring reaches half the length of the body of a 120 mm specimen. Östergren (1898) did not illustrate any aspect of the morphology of this species.

The plates of the calcareous ring of the holotype (ZMA H1084) of *A. spadix* (Sluiter) appear to be short and stout with very long, fragmented processes to the radial plates (Fig. 3B), not typical of the Thyoninae which is characterized by species with a tubular ring. Perhaps, this species represents a transitional form with reduced plates of the calcareous ring, serving as a link between the Thyoninae and Sclerothyoninae. This species is provisionally left in *Allothyone* but may later deserve a place in the Sclerothyoninae.

Genus *Pentamera* Ayres, 1852

Figure 3C

Pentamera Ayres, 1852: 207; Deichmann, 1938: 105; 1941: 84; Panning, 1949: 465.

Diagnosis (after Deichmann, 1941, amended herein)

Small to medium-sized holothuroids. Non-retractile tube feet in five series, restricted to ambulacra. Tentacles 10, ventral pair smaller. Plates of the calcareous ring unite mostly at the base but a distinct tube is formed; radial plates with long bifurcated, sub-divided processes. Deposits of body wall two-pillared tables or derivatives of these

with the spire reduced or absent. Tube feet with curved supporting tables; spire varying in height; large end-plates present. Tentacles usually with rods, plates or both.

Type species: *Pentamera pulcherrima* Ayres, 1852 by original designation.

Other species included: *Pentamera beebei* Deichmann, 1938; *Pentacta calcigera* Stimpson, 1851; *Pentamera charlottae* Deichmann, 1938; *Cucumaria chierchia* Ludwig, 1886; *Cucumaria chiloensis* Ludwig, 1886; *Cucumaria constricta* Ohshima, 1915; *Cucumaria lissoplaca* Clark, 1924; *Pentamera montereyensis* Deichmann, 1938; *Pentamera pediparva* Lambert, 1998; *Cucumaria populifera* Stimpson, 1864; *Pentamera pseudocalcigera* Deichmann, 1938; *Pentamera pseudopopulifera* Deichmann, 1938; *Cucumaria redimita* Sluiter, 1901; *Pentamera rigida* Lambert, 1998; *Cucumaria trachyplaca* Clark, 1924 and *Pentamera zaca* Deichmann, 1938.

Remarks

Pentamera Ayres is characterized by a calcareous ring in which the plates appear to unite at the bases only. Hence, the diagnosis of the genus is here amended to include this. Though, this may not be a typical Thyoninae ring in which the plates are fused, the tubular nature of the ring is evident, a feature lacking in the Sclerothyoninae. However, the fusion of the plates of the ring is not consistent within all species of the genus whereby the ring of some species appears more tubular than others. Perhaps not all species belong within *Pentamera*, some of which, in time, may be transferred to the Sclerothyoninae.

Cucumaria redimita Sluiter, erroneously attributed to Semper by Panning (1949), was transferred by him to his original *Pentathyone* H.L. Clark. In his addendum, this species became classified within *Havelockia*, but still remaining within the Sclerodactylinae. Thandar examined one of the two syntypes present at the ZMA and his illustration of the calcareous ring shows a more tubular form (Fig. 3C), typical of the Thyoninae, when compared to the figure presented by Sluiter (1901). The radial plates are not as deeply incised as figured by Sluiter and bifurcate as the posterior border of the interradial plates. The radial and interradial plates terminate in a conical point anteriorly and both the ring and processes are fragmented, the ring is mosaic-like. Further, Sluiter mentioned that the tube feet were restricted to the ambulacra. Though

the plates of the calcareous ring of the type species of the genus, *P. pulcherrima* Ayres, only fuse basally, there are other species within the genus whose plates fuse for the greater part of their length such as *P. zacaе* Deichmann. Therefore, with its tubular calcareous ring, tube feet distribution and the presence of two-pillared tables in combination with plates, although rare, in the body wall *C. redimita* agrees well with the diagnosis of *Pentamera* given by Deichmann (1941).

Genus *Stolus* Selenka, 1867

Figure 3D–G

Stolus Selenka, 1867: 355; Heding, 1940: 126; Panning, 1949: 462; Clark & Rowe, 1971: 204; Thandar, 1990: 209; Liao & Clark, 1995: 494; Rajpal & Thandar, 1999: 131; Thandar, 2005: 116.

Pseudothyone (partim) Panning, 1949: 456.

Diagnosis (after Thandar, 2005, amended herein)

Tube feet distributed over entire body. Tentacles 10, ventral pair much reduced. Calcareous ring conspicuously tubular with the radials carrying long paired, processes, both ring and processes finely broken up into a mosaic of numerous pieces. Ossicles of body wall only in the form of smooth or knobbed buttons/table-like buttons, often quite regular with 10–12 marginal knobs and four holes, or irregular with more knobs and holes; some table-like buttons with a ‘handle’ or half ring on one or both sides, with mostly four perforations (sometimes up to 10); rarely complex, multi-layered or as large, thick scales or plates, up to 1 mm in size.

Type species: *Stolus sacellus* Selenka, 1867, by subsequent designation Heding (1940) [= *Thyone buccalis* Stimpson, 1855 according to H.L. Clark (1938)].

Other species here included: *Stolus albescens* Liao & Clark, 1995; *Thyone axiologa* H.L. Clark, 1938; *Cucumaria canescens* Semper, 1868; *Semperia cognata* Lampert, 1885; *Cucumaria conjungens* Semper, 1868; *Thyone crassidisca* Pawson & Miller, 1981; *Stolus crassus* Liao & Pawson, 2001; *Stolus dentatus* Thandar, 2005; *Stolus kilberti* Rajpal & Thandar, 1999; *Stolus micronodosus* Liao & Pawson, 2001; *Thyone papillata* Sluiter, 1887 (1888); *Thyone parafusus* Deichmann, 1941; *Thyone pawsoni*

Tommasi, 1972; *Stolus pseudoalbescens* Thandar, 2005; *Thyone pseudofusus* Deichmann, 1930; *Thyone punctata* Ohshima, 1915; *Cucumaria rapax* Koehler & Vaney, 1908 and *Thyone uniannulata* Sluiter, 1914.

Remarks

Heding (1940) designated *S. sacellus* as the type species of *Stolus* without realising that H.L. Clark (1938) had synonymized this species with *Thyone buccalis* Stimpson. Since the latter species is a senior synonym, it should replace *S. sacellus* as the type species of the genus.

The tubular calcareous ring, often broken up into a mosaic of small pieces, is a character shared by *Stolus* and *Thyone*. It is here therefore recommended that those *Thyone* species, like *T. crassidisca* Pawson & Miller, with half-rings to their body wall tables, characteristic of some *Stolus* species (e.g. *S. buccalis* and *S. crassus*), be transferred into *Stolus*, a view also expressed independently by Thandar and Rowe (pers. comm). The other species are *T. axiologa* H.L. Clark, *T. parafusus* Deichmann, *T. pawsoni* Tommasi, and *T. pseudofusus* Deichmann.

The calcareous ring of *T. pseudofusus* (Fig. 3G) appears to be typical of *Pentamera* however the distribution of the tube feet over the entire body and the presence of handles to the tables restricts this species from being assigned to this genus and is subsequently transferred to *Stolus*.

Another species that is here critically looked at is *T. uniannulata* Sluiter, which Panning (1949) transferred to his original *Havelockia* Pearson thus moving it back to *Thyone* in his addendum. According to Thandar (pers. comm.), *T. uniannulata* also bears a close resemblance to species of *Stolus*. Sluiter compares the calcareous ring of his species to that of *T. sacellus* (= *Stolus buccalis*), which interestingly Thandar (in notes), upon examination of the holotype (H 2194), described the single white, rigid specimen to feel almost like *S. buccalis*. In addition, he found regular four-holed knobbed buttons/plates of the *Stolus* type, including some with up to 8 holes in the body wall. The calcareous ring (Fig. 3D) is mosaic-like, typical of *Stolus* and *Thyone*. Thandar also examined the introvert and found elongated smooth to spinous plates (Fig. 3E), perforated throughout their length, and some rosettes (Fig. 3F). Panning (1949) illustrates some large buttons, more perforated than those of the body wall, from the

introvert of his *S. sacellus* and what appears to be a rosette (Fig. 57 h), although he describes the tentacle deposits as rosettes. James (1966) described the introvert deposits of *S. buccalis* as thin, smooth buttons, while Cherbonnier (1988) illustrated rods and rosettes from the tentacles without examining the introvert of his Madagascan material. It is for this reason that *T. uniannulata* cannot be relegated to the synonymy of *S. buccalis* but is here transferred to *Stolus* as a distinct species differing from the type species on the basis of its introvert deposits.

Genus *Thyone* Jaeger, 1833

Thyone Oken, 1815: 351; Jaeger, 1833: 8; Pawson & Miller, 1981: 394; Thandar, 1990: 211.

Anaperus Troschel, 1846: 60 (partim).

Diagnosis (after Panning, 1949 and Thandar, 1990, amended herein)

Small to medium-sized dendrochirotid holothuroids, up to 200 mm in length. Tube feet numerous, distributed throughout the body, more numerous in ambulacra, scattered in the interambulacra, often more crowded ventrally; restricted to ambulacra in younger individuals. Tentacles 10, ventral pair reduced. Calcareous ring tubular, radial and interradial pieces sub-divided; radials with long posterior processes; ring and processes broken up into a mosaic of small pieces. Body wall ossicles comprise only two-pillared tables or their derivatives, often reduced with age or completely absent. Introvert supported by tables only, rosettes only, tables and rosettes, tables and plates/?reduced tables, rosettes and plates/?reduced tables, plates only, or introvert deposits absent or unknown.

Type species: *Holothuria fusus* Müller, 1776, by subsequent designation Jaeger (1833).

Other species included: *Thyone anomala* Östergren, 1898; *Holothuria aurea* Quoy & Gaimard, 1834; *Thyone avenusta* Cherbonnier, 1970; *Thyone bacescoi* Cherbonnier, 1972; *Thyone benti* Deichmann, 1937; *Thyone bicornis* Ohshima, 1915; *Thyone bidentata* Deichmann, 1941; *Thyone carens* Cherbonnier, 1988; *Thyone cherbonnieri* Reys, 1959; *Thyone comata* Cherbonnier, 1988; *Thyone crebrapodia* Cherbonnier,

1988; *Thyone deichmannae* Madsen, 1941; *Thyone dura* Koehler & Vaney, 1908; *Havelockia exigua* Cherbonnier, 1958; *Cucumaria falcata* Sluiter, 1901 (*incertae sedis*); *Cucumaria fastigata* Sluiter, 1901; *Thyone gadeana* Perrier, 1902; *Thyone grisea* H.L. Clark, 1938; *Thyone guillei* Cherbonnier, 1988; *Havelockia guttata* Cherbonnier, 1958; *Thyone herberti* Thandar & Rajpal, 1999; *Thyone hirta* Cherbonnier, 1970; *Cucumaria imperfecta* Cherbonnier, 1970; *Thyone inermis* Heller, 1868; *Thyone infusca* Cherbonnier, 1954; *Thyone longicornis* Cherbonnier, 1988; *Thyone micra* H.L. Clark, 1938; *Thyone nigra* Joshua & Creed, 1915; *Thyone okeni* Bell, 1884; *Thyone papuensis* Théel, 1886; *Thyone pedata* Semper, 1868; *Thyone profusus* Cherbonnier & Féral, 1981; *Thyone propinqua* Cherbonnier, 1970; *Thyone purpureopunctata* Liao & Pawson, 2001; *Thyone roscovita* Hérouard, 1889; *Thyone scabra* Verrill, 1873; *Thyone sinensis* Liao & Pawson, 2001; *Thyone sineturra* Cherbonnier, 1988; *Thyone spinifera* Liao, 1995; *Thyone theeli* Rowe, 1995; *Thyone vadosa* Cherbonnier, 1988; *Thyone venusta* Selenka, 1868; *Thyone venustella* Ludwig & Heding, 1935; *Cucumaria vilis* Sluiter, 1901 and *Thyone villosa* Semper, 1868.

Remarks

Pawson & Miller (1981) correctly acknowledged that Oken's work (1815–1816) was listed under the Official Index of Rejected Works by the International Commission on Zoological Nomenclature (opinion 417, 1956). They then suggested that the genus *Thyone* must therefore be attributed to Jaeger (1833) who was the first to validate the genus in accordance with the requirements stipulated by the International Code of Zoological Nomenclature (ICZN). This step was followed by Thandar (1990) and also here. Despite this, many workers, even after Pawson & Miller's work, continue to attribute this genus to Oken (1815).

Thyone Jaeger has over time become a “supergen” (Pawson & Miller, 1981). Currently 66 nominal species remain within the genus. However, based upon the nature of the calcareous ring and/or ossicle assemblage several species have been here transferred to other genera. Ten species are transferred to *Havelockia* Pearson within the Sclerodactylinae, while one species, *T. fusca* Pearson, is regarded as a synonym of *H. herdmani* Pearson (= *H. versicolor* Semper). In addition, six species are transferred to *Stolus* Selenka within the Thyoninae. Finally, three species are transferred to

Sclerothyoninae, two within *Sclerothyone* Thandar and one within *Temparena* Thandar. Two species show an uncertain affinity to *Thyone* and are temporally removed from the genus. Furthermore, two species currently classified within *Havelockia* are transferred to *Thyone*. Thus, only 46 species remain. The diagnosis of the genus has been amended based upon the composition of the introvert deposits which is here used for the taxonomic management of the genus and is discussed later in more detail (see page 45).

When reporting on the holothuroids of the Norwegian Sea and adjacent waters, Madsen & Hansen (1994) erroneously described *T. fusus* and *T. gadeana* under the family Cucumariidae despite having Pawson & Fell's (1965) revision at hand.

Genus *Thyonina* Thandar, 1990

Thyone Vaney, 1908 (non *Thyone* Jaeger, 1833).

Thyone (partim) H.L. Clark, 1923: 415; Deichmann, 1948: 354; Cherbonnier, 1952a: 491.

Thyonina Thandar, 1990: 217.

Diagnosis (after Thandar, 1990)

Small holothuroids, up to 55 mm in length; body cylindrical. Tube feet numerous, scattered. Tentacles 10, ventral pair reduced. Calcareous ring short, tubular, radials with long paired posterior processes, both ring and processes broken into a few large pieces. Body wall ossicles minute, slender, straight or slightly curved, smooth rods, expanded and often digitated at ends which have a single large and one or more smaller holes. Tube feet with end-plate (up to 135 μm in diameter) with numerous small central holes and a single series of large marginal holes, both types sharply demarcated. Tentacle deposits simple plates and rods, often provided with spiny margins. Introvert supported by rosettes.

Type species: *Thyone articulata* Vaney, 1908, by original designation.

Other species included: none.

FIGURE 3

Allothyone longicauda (Östergren). A. calcareous ring; = Scale 4. Reproduced from Thandar's examination of the material from the ZMUC.

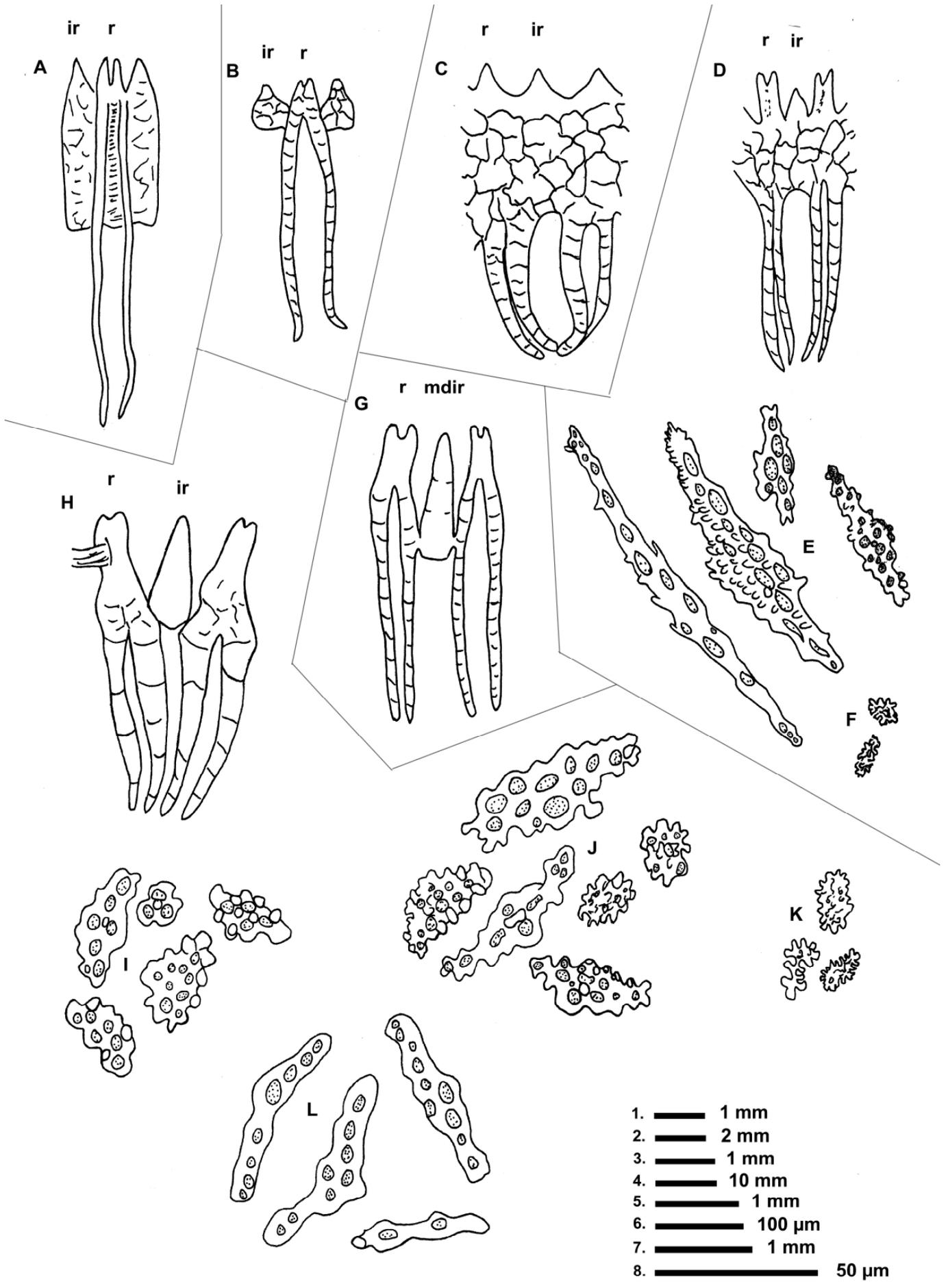
Allothyone spadix (Sluiter). B. calcareous ring of holotype; = Scale 2. Reproduced from Thandar's examination of the material from the ZMA.

Pentamera redimita (Sluiter) comb. nov. C. calcareous ring of syntype; = Scale 3. Reproduced from Thandar's examination of the material from the ZMA.

Stolus uniannulata (Sluiter) comb. nov. D. calcareous ring of holotype; E. plates of introvert; F. rosettes of introvert. D = Scale 1; E, F = Scale 6. Reproduced from Thandar's examination of the material from the ZMA.

Stolus pseudofusus (Deichmann) comb. nov. G. calcareous ring of syntype (r = radial plate; mdir = mid-dorsal interradial plate); = Scale 5. Reproduced from Thandar's examination of the material from the USNM.

Neopentamera anxigua Deichmann. H. calcareous ring of holotype (r = radial plate; ir = interradial plate); I. buttons of body wall; J. plates and rosettes of introvert; K. rosettes of tentacles; L. rods (reduced supporting tables) of tube feet. H = Scale 7; I–K = Scale 8. Reproduced from Thandar's examination of the material from the LACM.



Subfamily Sclerothyoninae Thandar, 1989

Diagnosis (after Thandar, 1989)

Tentacles 10, ventral pair much reduced. Calcareous ring not tubular, radial and interradial plates united at base only; posterior paired processes of radial plates, long, reaching 3–8 times the height of ring, either entire or broken into several pieces.

Type genus: *Sclerothyone* Thandar, 1989, by original designation.

Other genera included: *Neopentamera* Deichmann, 1941 and *Temparena* Thandar, 1989.

Key to the genera of the subfamily Sclerothyoninae

- 1. a) Body wall deposits irregular knobbed buttons; tables absent.... *Neopentamera* Deichmann
- b) Body wall deposits tables only or in combination with plates..... 2

- 2. a) Body wall deposits tables only, of two types: regular, oval, four-holed tables, with or without a half-ring on one side, and large, irregular multilocular tables; spire arched or of two separate or fused pillars..... *Sclerothyone* Thandar
- b) Body wall deposits combination of two-pillared tables and plates: tables with usually a four-holed, oval disc or lozenge-shaped and with many peripheral holes; spire short or imperfect, with or without teeth; plates thick, smooth, elongate, multilocular..... *Temparena* Thandar

Genus *Neopentamera* Deichmann, 1941

Figure 3H–L

Neopentamera Deichmann, 1941: 90; Panning, 1949: 457.

Diagnosis (after Deichmann, 1941)

External features as in *Pentamera* Ayres. Tube feet in double rows, restricted to ambulacra. Calcareous ring with well-developed posterior processes (Fig. 3H). Deposits of the body wall irregular knobbed buttons with 3–6 holes (Fig. 3I). Tube feet with narrow rods, perhaps reduced supporting tables (Fig. 3L); reduced end-plates present. Tentacle deposits rosettes (Fig. 3K). Introvert supported by plates and rosettes (Fig. 3J).

Type species: *Neopentamera anexigua* Deichmann, 1941, by original designation.

Other species included: none.

Remarks

The holotype of *Neopentamera anexigua* Deichmann housed at the LACM (no. 359.1) was studied by Thandar. He illustrated the calcareous ring and it is evident that the plates unite at the base only, not forming a tube, with the processes measuring approximately two times the length of the ring (Fig. 3H). Deichmann (1941) commented that the present species appeared almost identical to *Cucumaria exigua* Ludwig which Panning (1949) transferred to *Eupentacta*, within the Sclerodactylinae, but differed in the longer processes to the calcareous ring. The type material measured about 20 mm in length and according to Deichmann the gonadal tubules were large, perhaps representing a young-mature adult male therefore the presumption that the processes may lengthen with age is doubtful since the animal is already on its way to maturity. As the plates of the calcareous ring only unite at their base prevents this genus from being classified within the Sclerodactylinae in which the plates are fused for most of their length and is thus here assigned to the Sclerothyoninae. In addition, Thandar observed that the buttons of the body wall were perforated by usually more than four holes.

Genus *Sclerothyone* Thandar, 1989

Figure 4A–I

Sclerothyone Thandar, 1989: 294; 2008: 14.

Diagnosis (after Thandar, 2008, amended herein)

Tube feet in double rows, restricted to ambulacra or sometimes scattered. Tentacles 10, ventral pair much reduced. Calcareous ring compact, non-tubular, posterior processes of radial plates very long, entire or sub-divided. Body wall tables with regular, oval, four-holed discs, with or without a half-ring on one side, and large, irregular multilocular discs, spire arched or of two separate or fused pillars.

Type species: *Cucumaria? velligera* Ludwig & Heding, 1935, by original designation.

Other species included: *Thyone adinopoda* Pawson & Miller, 1981; *Thyone neofusus* Deichmann, 1941; *Cucumaria obunca* Lampert, 1885 and *Sclerothyone unicumulus* Thandar, 2008.

Remarks

Thandar (2008) suggested that Pawson & Miller's (1981) *Thyone adinopoda* was so similar to *Sclerothyone velligera* that it could be transferred into this genus if the generic diagnosis was amended to include those species with scattered tube feet. This step has been taken here as an examination of the illustration of the calcareous ring made by Pawson & Miller indicate a typical Sclerothyoninae ring in which the radial and interradial plates meet at their bases only.

Panning (1949) did not mention Deichmann's (1941) *Thyone neofusus* in his revision, perhaps an oversight, and hence this species remained within *Thyone*. The holotype received from the MCZ (AHF no. 30) was completely decalcified and lacked the calcareous ring or any deposits. Thandar, however, examined a paratype and illustrated a well preserved calcareous ring (Fig. 4A) which resembles a typical Sclerothyoninae ring. The tube feet deposits were unfortunately corroded (Fig. 4C), and he failed to find any introvert deposits. However the body wall contained delicate two-pillared tables (Fig. 4B). The tentacles comprised rods (Fig. 4D) and rosettes (Fig. 4E). Deichmann mentioned only rosettes in the introvert, but her figure illustrates a "disc of table from introvert". Since this species is known only from its original description, more specimens are required to be collected to confirm the introvert deposits. The shape of the calcareous ring bears close resemblance to that of *Sclerothyone velligera* and *S.*

unicolumnus but *T. neofusus* differs in the presence of only supporting plates. Hence, it is here transferred to *Sclerothyone*.

Lampert (1885) provides a rather vague description of his *C. obunca* without mentioning the number of specimens he had in his material. However, he does mention the size of his holotype (30 mm), the length of the calcareous ring (3 mm) but illustrates only a single ossicle, presumably from the body wall. Mitsukuri (1912) described two specimens from Asamushi which he claimed belonged to *Cucumaria obunca* but neither describes nor illustrates the calcareous ring or any deposits of his specimens. Östergren's (in Östergren et al., 1938) illustration of the calcareous ring, taken from presumably the type material since there are only two records of the species to date, shows the radial and interradial plates uniting at the base only, with relatively short radial processes compared to species of Sclerothyoninae (Fig. 4F). Panning (1949) transferred this species to *Pentathyone*, and after the synonymization of the latter with *Havelockia*, this species currently remains within the latter genus despite the fact that the tube feet are restricted to the ambulacra. According to the curator of the Copenhagen museum, the holotype appears to be lost, and attempts to locate the type at other museums have been unsuccessful. However, based upon the nature of the calcareous ring, the presence of two-pillared tables in the body wall (Fig. 4G) and introvert (Fig. 4I), and the restriction of tube feet to the ambulacra, this species is transferred to *Sclerothyone*. *C. obunca* differs from the other species within *Sclerothyone* in possessing well developed tables in the tentacles (Fig. 4H).

A specimen collected from the type locality in 1896 identified as *Pentathyone obunca* (Lampert) amongst the USNM collections (no. 30629), appears to have dried up prior to preservation, with the internal anatomy difficult to discern and the deposits of the body wall and tube feet corroded. However, the tube feet are not restricted to the ambulacra; hence, whether this specimen belongs to *H. obunca* or is another species is unclear.

Genus *Temparena* Thandar, 1989

Temparena Thandar, 1989: 296.

Diagnosis (after Thandar, 1989, restricted herein)

Small holothuroids, up to 25 mm long; body barrel to U-shaped, body wall thin, rigid. Tentacles 10, ventral pair reduced to stubs. Calcareous ring small, plates compact not forming a tube, with radials carrying long, undivided, paired processes, up to eight times the height of ring. In one species gonad hermaphroditic, posterior tubes developed as testis, anterior as ovary, the latter may contain embryos. Body wall ossicles two-pillared tables and plates: tables with usually a four-holed, oval disc or lozenge-shaped and with many peripheral holes; spire short or imperfect, with or without teeth; plates thick, smooth, elongate, multilocular.

Type species: *Cucumaria? chuni* Ludwig & Heding, 1935, by original designation.

Other species included: *Cucumaria nozawai* Mitsukuri, 1912.

Remarks

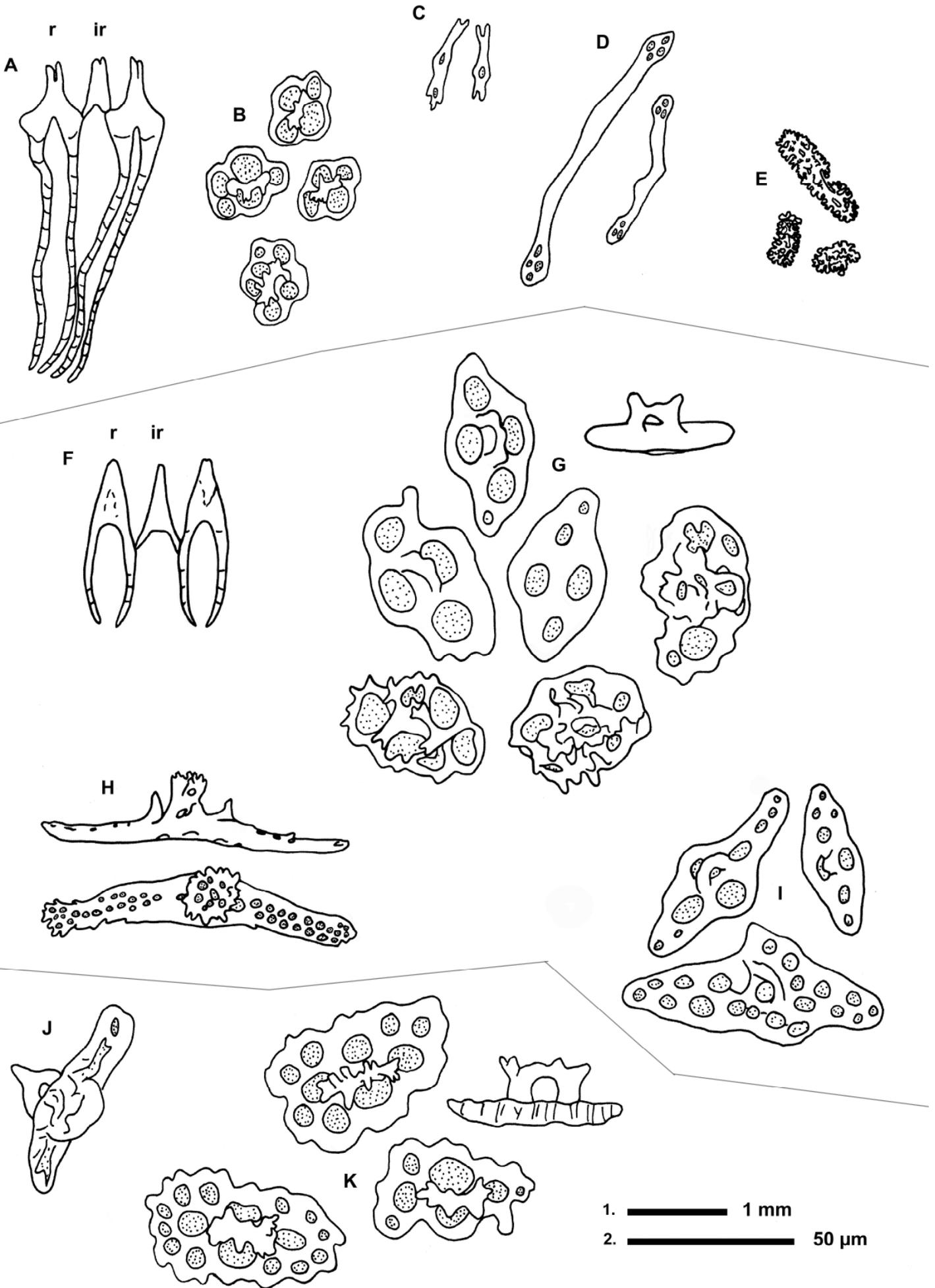
Cucumaria nozawai Mitsukuri was placed in Panning's (1949) original *Havelockia* group and later transferred to *Thyone*. This species, based upon a single specimen, has not been recorded since its original description and Mitsukuri (1912) fails to give the dimensions of his specimen though the drawing of the calcareous ring is reminiscent of the Sclerothyoninae. The presence of two-pillared tables and plates in the body wall relates this species to *Temparena*, which was initially monotypic. The introvert of *T. nozawai* comprises tables, similar to those of the body wall though larger with serrated margins while *T. chuni* (Ludwig & Heding) contains perforated plates in the introvert and tentacles, and hence this character has been removed from the generic diagnosis of the genus.

FIGURE 4

Sclerothyone neofusus (Deichmann). A. calcareous ring of paratype; B. tables of body wall; C. corroded rods of tube feet; D. rods of tentacles; E. rosettes of tentacles. A = Scale 1; B–E = Scale 2. Reproduced from Thandar's examination of the material from the MCZ.

Sclerothyone obunca (Lampert). F. calcareous ring (r = radial plate; ir = interradial plate) (x 6); G. tables of body wall (x 550); H. tables of tentacles (x 170); I. tables of introvert (x 550). Reproduced from Östergren (in Östergren et al., 1938).

? *Thyone quadruperforata* Cherbonnier. J. table of tube feet; K. tables of introvert. J & K = Scale 2. Reproduced from Thandar's examination of the material from the NHMUK.



Part II

Subfamily Thyoninae Panning, 1949

Genus *Thyone* Jaeger, 1833

Figure 4J & K

Thyone Oken, 1815: 351; Jaeger, 1833: 8; Pawson & Miller, 1981: 394; Thandar, 1990: 211.

Anaperus Troschel, 1846: 60 (partim).

Remarks

Since the designation of its type species, there have been some 148 species classified within *Thyone*. Subsequent to Panning's (1949) revision of the Cucumariidae, including the amendments made in his addendum, several species have been referred to other genera and many new ones described. There, therefore currently remain 66 species within this genus (see Appendix 1).

As mentioned previously, 19 of the remaining 66 species have been transferred to other genera within the Sclerodactylinae, Thyoninae and Sclerothyoninae (see pages ii and 38–40) while one species is regarded as a synonym of *H. herdmani* Pearson (= *H. versicolor* Semper). Two species, listed below, show an uncertain affinity to *Thyone* and are temporarily removed from the genus. Furthermore, two species currently classified within *Havelockia* are transferred to *Thyone*.

The two species that show an uncertain affinity to *Thyone* are *T. quadruperforata* Cherbonnier and *T. secunda* Vaney. Cherbonnier (1954b) doubtfully described his new species from Djibouti as *Thyone quadruperforata* commenting that regardless of its peculiar calcareous ring (which he illustrates as a simple ring, i.e. without processes to the radial plates) and the 10 equally-sized tentacles, the two-pillared tables of the body wall are reminiscent of *Thyone* species. Thandar was unable to locate the calcareous ring in the type specimen housed at the MNHN and he found no deposits in the body wall. He did, however come across some material identified as *T. cf. quadruperforata* by C. Ahearn at the NHMUK whose deposits match those described by Cherbonnier. The supporting tables of the tube feet, however, bear a handle (Fig. 4J), while the introvert comprises multilocular tables (Fig. 4K) and no rosettes. *T. secunda* Vaney possesses only perforated plates in the body wall. Both these species were originally

moved to *Havelockia* by Panning (1949) which he later transferred to *Thyone*. Here, both species are removed from *Thyone* and temporarily unassigned, possibly belonging to new genera.

Hence, the “supergen” now contains 46 species, with one species temporarily remaining as an *incertae sedis*. The calcareous ring, ossicle assemblages from the body wall, tube feet, tentacles and introvert, together with the geographical distributions of all species were critically examined to determine any correlations, but none were evident.

Thandar (2001) assessed the calcareous ring and geographical distributions of most of these species and reports on some correlations, albeit with exceptions. However, he did not advocate any subgeneric ranking to his sub-divisions since Heding (1940) reported that the interradial plates lengthen with age (Heding, 1940). Thandar & Rajpal (1999b) also pointed out that the calcareous ring has thus far only been used to separate suprageneric taxa (see Concluding Remarks). No other workers have attempted a sub-division of this genus.

Judging from Panning’s (1949) and Pawson & Miller’s (1981) works, it would seem that *Thyone* can only be sub-divided into groups based upon the composition of the introvert deposits. Regrettably, all efforts to sub-divide the genus into subgeneric taxa based on these and body wall and/or tube feet deposits in combination, failed to indicate any correlations. However, on the basis of introvert deposits, seven arbitrary groups are here assembled in only to render this genus more manageable, and the diagnosis of the genus amended accordingly.

Groups of species of *Thyone* divided upon the composition of their introvert deposits:

1. **Tables only:** *benti*; *bidentata*; *comata*; *crebrapodia*; *hirta*; *nigra*; *scabra* and *villosa*.
2. **Rosettes only:** *bicornis*; *deichmannae*; *guillei*, *longicornis* and *sineturra*.
3. **Tables and rosettes:** *avenusta*; *bacescoi*; *carens*; *cherbonnieri*; *dura*; *exigua*; *fuscus*; *gadeana*; *guttata*; *inermis*; *infusca*; *micra*; *okeni*; *papuensis*; *pedata*; *purpureopunctata*; *roscovita*; *sinensis*; *spinifera*; *vadosa* and *vilis*.
4. **Tables and plates/?reduced tables:** *aurea* and *herberti*.
5. **Rosettes and plates/?reduced tables:** *anomala*; *grisea* and *imperfecta*.
6. **Plates only:** *propinqua* and *venustella*.

7. Deposits absent/unknown: *falcata*; *fastigata*; *profusus*; *theeli* and *venusta*.

Key to the species of the genus *Thyone* Jaeger, 1833

1. a) Body wall deposits present..... 2
b) Body wall devoid of deposits except sometimes at anal end..... 43

2. a) Deposits of body wall two-pillared tables only..... 4
b) Deposits of body wall two-pillared tables with plates or plates only..... 3

3. a) Deposits of body wall more or less oval-shaped tables with four central holes and 1–4 peripheral ones; spire high, ending in 2–3 teeth and plates with 3–7 perforations..... *T. anomala* Östergren, p. 143
b) Deposits of body wall smooth, elongated plates with usually four central holes and 1–2 minute holes at each end..... *T. infusca* Cherbonnier, p. 114

4. a) Body wall with full complement of tables..... 5
b) Body wall deposits restricted to base of each tube foot or at posterior end..... 6

5. a) Body wall tables retained through to adult stage..... 7
b) Body wall tables reduced with age to slightly nodular plates with few holes or to spectacle-shaped rods or plates..... *T. aurea* (Quoy & Gaimard) juvenile, p. 138

6. a) Body wall deposits restricted to heaps of tables at base of each tube foot.....
..... *T. spinifera* Liao, p. 131
b) Body wall deposits restricted to small, regular, circular-shaped tables at posterior end..... *T. inermis* Heller, p. 110

7. a) Introvert deposits present..... 8
b) Introvert devoid of deposits or deposits unknown..... 40

8. a) Introvert comprise tables only, rosettes only or both in combination..... 9

b) Introvert comprise plates only (no tables or true rosettes), tables and plates/?reduced tables, or a combination of true rosettes and plates/?reduced tables.....	35
9. a) Tables only or rosettes only.....	10
b) Combination of tables and rosettes.....	23
10. a) Tables only.....	11
b) Rosettes only.....	18
11. a) Anal teeth present.....	12
b) Anal teeth absent.....	17
12. a) Tentacle deposits: rosettes only or in combination with rods.....	13
b) Tentacle deposits: rods and plates.....	15
13. a) Rosettes only.....	<i>T. bidentata</i> Deichmann, p. 54
b) Rosettes in combination with rods.....	14
14. a) Colour uniformly pink; deposits of body wall tables with an irregular disc with few central holes and a variable number of marginal holes of more/less equal size to central holes; spire of moderate height ending in 2–4 (up to six) teeth.....	<i>T. comata</i> Cherbonnier, p. 58
b) Colour yellow; deposits of body wall numerous tables with usually eight-holed discs (four large + four smaller marginal holes), rarely with more perforations; spires short or moderately high, ending in four apical teeth.....	<i>T. crebrapodia</i> Cherbonnier, p. 62
15. a) Tube feet supported by curved, two-pillared tables only.....	16
b) Tube feet supported by curved, supporting tables; spire two-pillared, rarely four-pillared and ?minute plates.....	<i>T. hirta</i> Cherbonnier, p. 63

16. a) Small species, holotype measuring 20 mm in length; deposits of body wall usually tables with rounded or irregular-shaped discs with four central holes and few to numerous peripheral ones; spire fused distally, ending in 2–4 teeth.....
..... *T. villosa* Semper, p. 70
- b) Medium-sized species, reaching 100 mm in length; deposits of body wall irregular tables with 7–10 or more perforations; spire ending in indistinct teeth.....
..... *T. scabra* Verrill, p. 66
17. a) Small species, up to 30 mm in length; deposits of body wall tables with irregular, oblong-shaped, flat discs with four large, central holes and few peripheral ones; spire short, ending in several teeth..... *T. nigra* Joshua & Creed, p. 65
- b) Medium-sized species, up to 110 mm in length; deposits of body wall four-holed, round or oval to diamond-shaped tables, often becoming reduced to button-like plates and rods..... *T. bentii* Deichmann, p. 52
18. a) Tentacle deposits of one type..... 19
- b) Tentacle deposits of more than one type..... 20
19. a) Tentacle deposits only complicated rosettes..... *T. deichmannae* Madsen, p. 76
- b) Tentacle deposits rods only, of three kinds: long, smooth rods perforated at the ends, some crinkly rods with scalloped edges and some rosette-like rods at the base of the tentacles..... *T. longicornis* Cherbonnier, p. 79
20. a) Tentacle deposits of two types in different combination..... 21
- b) Tentacle deposits of three types: long rods with slightly expanded ends and shorter, thicker rods with crinkly margins, both usually perforated once at ends, rosettes and nodular buttons..... *T. guillei* Cherbonnier, p. 78
21. a) Anal region with tables only..... 22
- b) Anal region with tables and rosettes, the latter rare or two forms: some crinkly and others with a more reticulated surface..... *T. sineturra* Cherbonnier, p. 81

22. a) Small species, up to 47 mm in length; tentacle deposits curved, elongated, slender rods, usually perforated at ends, rosette-like rods, minute slender rods and rosettes..... *T. avenusta* Cherbonnier, adult p. 87
- b) Small species, up to 37 mm in length; tentacle deposits: branches and tips with slender, smooth rods, perforated at each extremity; stalk deposits rod-like or derived from complicated rosettes..... *T. bicornis* Cherbonnier, p. 72
23. a) Anal teeth present..... 24
- b) Anal teeth absent or unknown..... 29
24. a) Tentacle deposits rods only..... 25
- b) Tentacle deposits rods and plates or rods and rosettes..... 27
25. a) Deposits of body wall sparsely scattered, small tables with oblong disc perforated by four large and four small holes; spire low, with 2–4 apical teeth... *T. papuensis* Théel, p. 118
- b) Deposits of body wall tables with multilocular disc (> eight holes)..... 26
26. a) Calcareous ring stout in juveniles, becoming tubular in adults with radial plates bifurcating near posterior border of interradial plates, both ring and processes mosaic-like..... *T. dura* Koehler & Vaney, p. 97
- b) Radial plates of calcareous ring prolonged posteriorly to terminate in short, bifurcate processes, both ring and processes sub-divided..... *T. avenusta* Cherbonnier juvenile, p. 87
27. a) Rods and plates..... 28
- b) Rods and rosettes in tentacles; deposits of body wall scarce tables with discs of four large central holes and four peripheral ones; spire ending in up to eight teeth; anal tables larger, discs more perforated; spires ending in numerous teeth.....
..... *T. guttata* (Cherbonnier) comb. nov., p. 108

28. a) Deposits of body wall tables with mainly 4–8-holed discs, sometimes with only four primary holes and 1–3 peripheral ones; spire of moderate height, ending in inconspicuous teeth..... *T. fusus* (Müller), p. 102
 b) Deposits of body wall tables with rounded to slightly scalloped edges pierced by usually eight but up to 20 holes; spire low, ending in a variable number of spiny teeth..... *T. gadeana* Perrier, p. 107
29. a) Tentacle deposits of one type..... 30
 b) Tentacle deposits of two types..... 31
30. a) Tentacle deposits numerous stout rods..... *T. pedata* Semper, p. 121
 b) Tentacle deposits supporting, perforated plates of varying size.....
 *T. sinensis* Liao & Pawson, p. 128
31. a) Tentacle deposits rods and rosettes..... 32
 b) Tentacle deposits quadrilocular tables in stalk and rods at tip..... *T. vilis* (Sluiter), p. 133
32. a) Deposits of the body wall exclusively tables with quadrilocular discs.....
 *T. micra* H.L. Clark, p. 115
 b) Deposits of body wall tables with multilocular discs..... 33
33. a) Tables of two kinds..... 34
 b) Tables of three kinds: eight-holed (four primary + four peripheral) table discs with scalloped edge; spire low, ending in 2–3 teeth; some tables with only 4–5 large holes or conversely with 12–16 perforations of unequal size.....
 *T. exigua* (Cherbonnier) comb. nov., p. 98
34. a) Tables mostly four central-holed tables discs with 8–10 slightly smaller marginal holes; some eight-holed table discs also present, although less common; spire with general one crossbar, sometimes two..... *T. cherbonnieri* Reys, p. 93

- b) Tables with irregularly elongated discs with up to 19 holes of more/less equal size; some four-holed table discs also present; spires low, arched, ending in a single conical point..... *T. purpureopunctata* Liao & Pawson, p. 123
35. a) Plates only, no true tables or true rosettes..... 36
 b) Tables and plates/?reduced tables or a combination of true rosettes and plates/?reduced tables..... 38
36. a) Introvert supported by plates only..... 37
 b) Introvert supported by perforated plates with some evidence of a reduced spire....
 *T. aurea* (Quoy & Gaimard) young adult, p. 138
37. Introvert supported by elongated, small knobbed, multilocular plates with irregular margin..... *T. venustella* Ludwig & Heding, p. 154
 b) Introvert supported by perforated plates and crinkly rosette-like deposits, but not true rosettes..... *T. propinqua* Cherbonnier, p. 150
38. a) Introvert supported by tables and plates/?reduced tables.....
 *T. herberti* Thandar & Rajpal, p. 142
 b) Introvert supported by plates/?reduced tables in combination with true rosettes...
 39
39. a) Small, stout species, up to 55 mm in length; anal teeth absent; deposits of body wall numerous stout tables with oval to elliptical discs pierced by four or more perforations, larger tables with 12–15 holes; spire low, converging at tip, some smaller tables without spires also present..... *T. grisea* H.L. Clark, p. 145
 b) Medium-sized, synaptid-like species, up to 110 mm in length; anal teeth present; deposits of body wall exclusively tables with two large and usually two smaller central holes and 6–16 marginal holes of more or less the same size; spire short, often distorted or reduced to two central knobs on surface of disc; anal tables larger with more perforations..... *T. imperfecta* (Cherbonnier), p. 149

40. a) Tentacle deposits present: branches with straight or curved rods with/without perforations; stalks with perforated plates..... *T. profusus*
Cherbonnier & Féral, p. 159
- b) Tentacle deposits absent or unknown..... 41
41. a) Supporting tables of tube feet with curved discs..... 42
- b) Supporting tables of tube feet with straight discs..... *T. falcata* (Sluiter), p. 157
42. a) Deposits of body wall crowded tables with an irregularly perforated, round to angular disc and uneven margins; spire short, often terminating in several teeth.....
..... *T. theeli* Rowe, p. 161
- b) Deposits of body wall tables with eight-holed discs (four large and four smaller peripheral); spire short, united by a cross-bar terminating in finely, serrated teeth....
..... *T. fastigata* Sluiter, p. 158
43. a) Anal region of body wall with/without deposits; tube feet end-plates present... 44
- b) Deposits completely absent from body wall or restricted to tube feet end-plates..... 48
44. a) Anal region comprise perforated, branched rods and large, perforated plates.....
..... *T. roscovita* Hérourard, p. 125
- b) Anal region devoid of deposits..... 45
45. a) Tentacle deposits rods only..... *T. bacescoi* Cherbonnier, p. 88
- b) Tentacle deposits rods and rosettes only or in combination with rosette-like rods..... 46
46. a) Tentacle deposits rods and rosettes only; anal teeth absent..... 47
- b) Tentacle deposits rods, rosettes and rosette-like rods; anal teeth present.....
..... *T. okeni* Bell, p. 116

47. a) Small species, up to 35 mm in length; introvert supported by few tables, of two types: small with rounded disc pierced by 8–15 holes; spire ending in a single, bifid tooth or disc large, circular to triangular; spire ending in an irregular crown of teeth; rosettes also present, concentrated at base of tentacles..... *T. carens* Cherbonnier, p. 92
- b) Medium-sized species, up to 80 mm in length; introvert supported by tables with multilocular disc; spire branching distally, ending in two clusters of small teeth; rosettes also present..... *T. vadosa* Cherbonnier, p. 132
48. a) Deposits absent from body wall..... *T. aurea* (Quoy & Gaimard) mature adult, p. 138
- b) Deposits restricted to tube-feet end-plates..... *T. venusta* Selenka, p. 165

GROUP 1. INTROVERT DEPOSITS: TABLES ONLY

Thyone benti Deichmann, 1937

Figure 5A–G; H–N

Thyone benti Deichmann, 1937: 170, text-fig. 2; Lambert, 1997: 106, text-figs. 56, 57.

Thyone benti. var. *zacae* Deichmann, 1938: 376.

Havelockia benti Panning, 1949: 466; Bergen, 1996: 233, text-fig. 9.21 A–C.

Havelockia benti. var. *zacae* Panning, 1949: 466; Bergen, 1996: 233, text-fig. 9.21 D–E.

Diagnosis (after Deichmann, 1937)

Medium-sized species, up to 110 mm in length. Colour in alcohol pale brown, some with scattered pigments. Tube feet numerous, comparatively slender, scattered over the body, often indistinctly arranged in bands along the ambulacra. Anal teeth not mentioned. Tentacles 10, small, ventral pair smaller. Calcareous ring long, narrow, with long processes to the deeply incised radial plates; interradials narrow (Fig. 5A). Deposits of the body wall four-holed, round or oval to diamond-shaped, two-pillared tables (Fig. 5B), often becoming reduced to button-like plates and rods (Fig. 5C). Tube

feet with curved supporting tables (Fig. 5E); end-plates well-developed. Tentacle deposits oblong, thick rods with small holes (Fig. 5F) and delicate reticulated plates (Fig. 5G). Introvert supported by multilocular tables (Fig. 5D).

Name-bearing type

MCZ, no. 1810.

Type locality

Puget Sound, United States of America.

Habitat

Firm mud, sand or gravel.

Distribution

Puget Sound, to west coast of Lower California, 73–110 m.

Remarks

Deichmann (1937) described this species from three considerably large specimens, ranging from 50–110 mm in length. A year later (1938), she came across a single 30 mm individual, an apparent juvenile, which she classified as *T. benti* var. *zacaе* (MCZ no. 1954), differing from the type in the absence of the large rods from the tentacles which possesses only rosettes (Fig. 5N) and it displayed an advanced reduction of the body wall (Fig. 5H) and tube feet deposits (Fig. 5M). At first thought, the rosettes in the tentacles could indeed reflect a juvenile feature which is resorbed or lost during growth and replaced by the large rods and perforated plates as illustrated by Deichmann (1937) for the type. However, Deichmann (1937) stresses the reduction of the ossicles with age. Therefore, if the *zacaе* specimen represents a juvenile of the type, the table discs would show at least some evidence of a former spire, but it does not. Furthermore, Thandar's study of the introvert of the juvenile revealed the presence of two-pillared tables (Fig. 5I), smooth (Fig. 5L) and complex reticulated plates (Fig. 5J) and rosettes (Fig. 5K). *T. benti*, however, possesses only tables in the introvert. Thandar (pers. comm.) speculates that perhaps this variety may deserve a new genus or be elevated to

full species rank. In fact, the latter opinion is here supported but more adult material needs to be collected.

Bergen (1996) discussed the Holothuroidea of the Santa Maria Basin and claimed to have identified many specimens of this species and the variety. She mentions that in *T. benti* the introvert comprises tables and delicate plates resembling rosettes, while the tentacles contain delicate rods, plates and tables. She states that the tables in the introvert and tentacles of the variety are rare. A re-examination of this material is necessary and may support the opinion given above.

Thyone bidentata Deichmann, 1941

Figure 6A & B

Thyone bidentata Deichmann, 1941: 105, pl. 18, fig. 13–16; text-fig. 4.

Diagnosis (after Deichmann, 1941)

Small species, about 20 mm in length; body barrel-shaped. Colour in alcohol, pale brown. Tube feet delicate to fairly stout, often in distinct bands but also scattered in the interambulacra. Larger paratype with anal teeth. Calcareous ring typical of *Thyone*. Ossicles in body wall tables with oval to lozenge-shaped discs with four central holes and a few marginal ones in elongated/rectangular discs, spire tapering to a cone with few teeth (Fig. 6A). Supporting tables of the tube feet strongly curved, spire composed of two rods united distally ending in two diverging teeth (Fig. 6B). Tentacle deposits rosettes, few. Introvert supported by tables with numerous holes; spire low, with diverging teeth.

Type Material

Holotype perhaps lost, MCZ, Allan Hancock Foundation (AHF), no. 31; LACM, 1934-149.20 (2 *paratypes*).

Type locality

Tenacatita Bay, Mexico.

Habitat

Unknown.

Distribution

Gulf of California to Colombia, 22–55 m.

Remarks

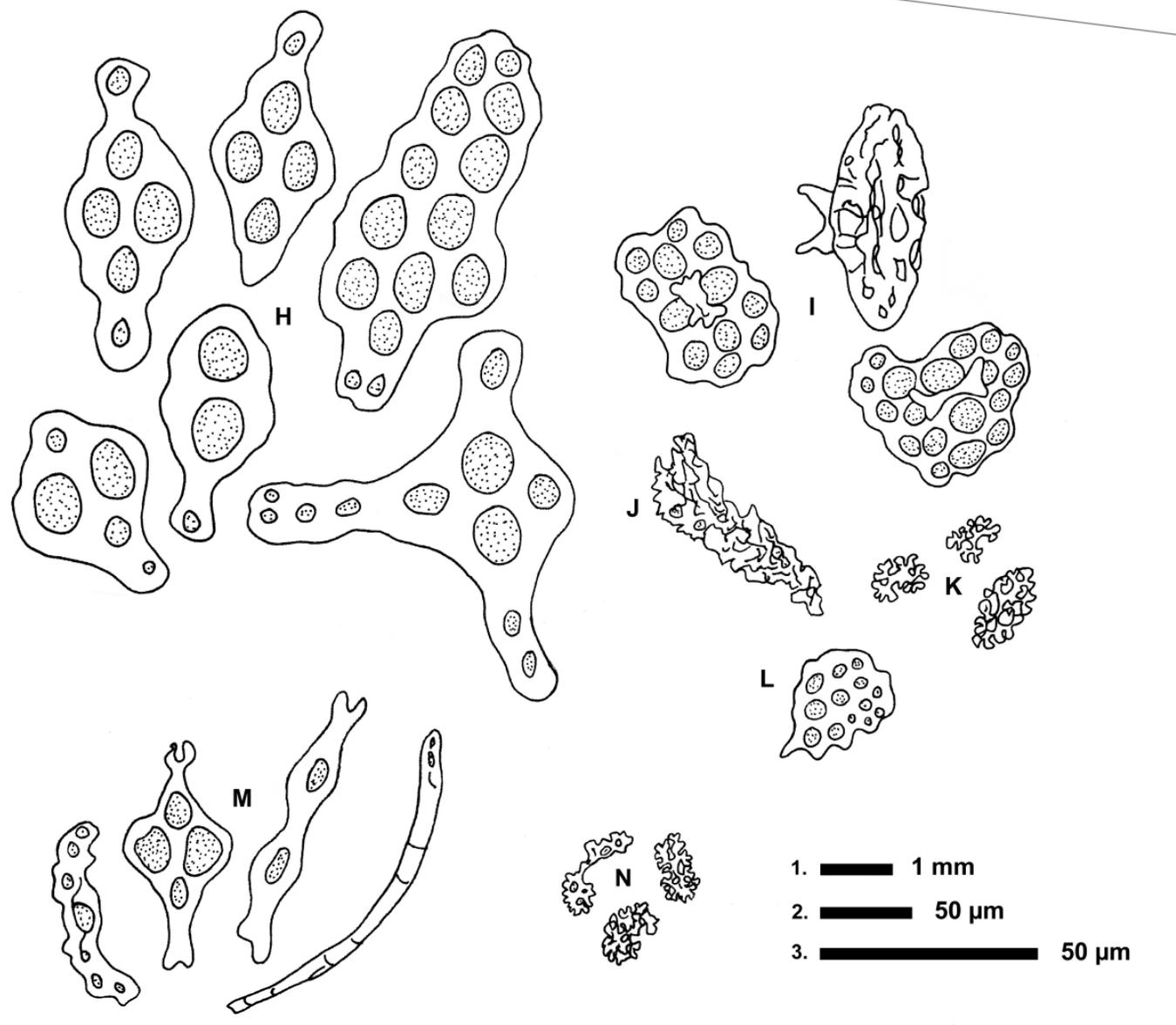
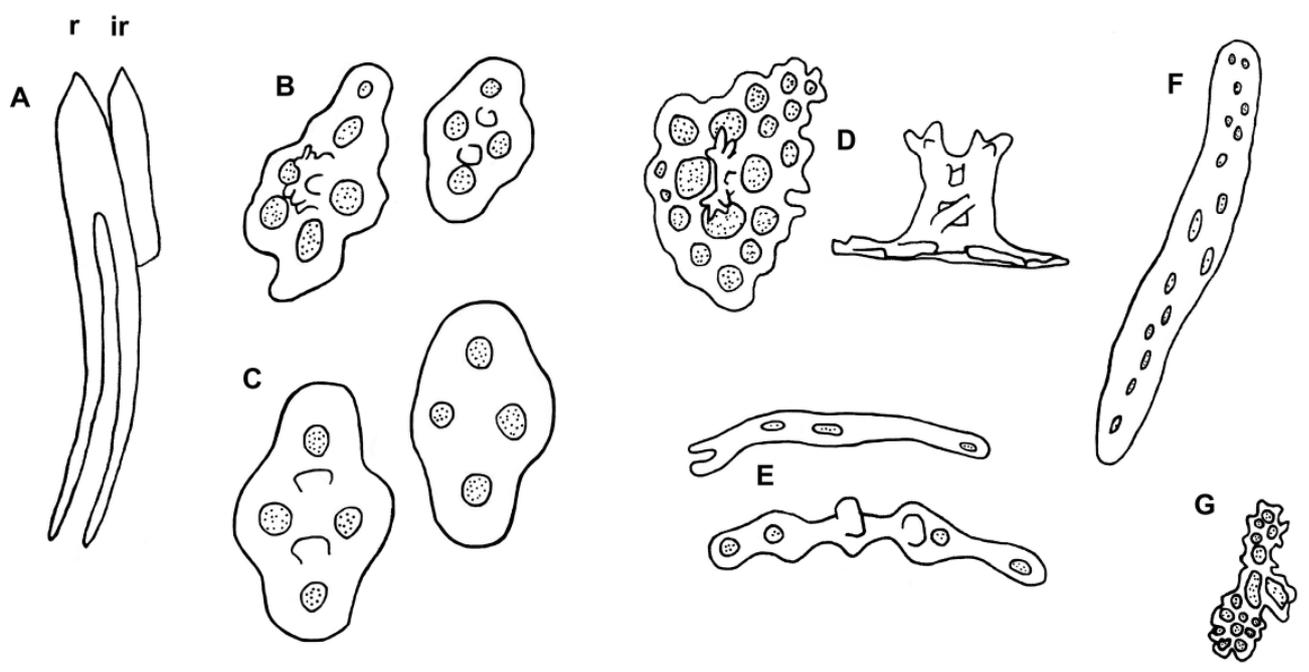
Deichmann (1941) described this species from a range of specimens: the type material consisting of three specimens, two of approximately 20 mm in length, the smallest being 5 mm. Unfortunately, Deichmann's description of the calcareous ring is poor possibly resulting in Panning (1949) omitting this species from his revision.

According to Gordon Hendler of the Natural History Museum of Los Angeles County (LACM), the holotype of *Thyone bidentata* was missing when the Allan Hancock Foundation Collection was transferred from the MCZ to the LACM, and has subsequently not been located. However, the two paratypes originating from the type locality were obtained and studied. Disappointingly, the larger specimen, as reported by Deichmann to be a similar size as the holotype, lacked all internal structures. The calcareous ring of the smaller specimen was irrevocably damaged, probably during examination by Deichmann herself or subsequent workers. The tube feet deposits comprise strongly curved supporting tables, with a two-pillared spire ending in a single conical point. This is perhaps a juvenile feature since Deichmann illustrates a spire ending in two diverging teeth. However, the tube feet deposits of the larger paratype show similar deposits and it is uncertain if Deichmann's material was entirely juvenile as she does not confirm the state of maturity of the gonad.

FIGURE 5

Thyone bentii Deichmann. A. calcareous ring (r = radial plate; ir = interradial plate); B. tables of body wall; C. buttons (reduced tables) of body wall; D. tables of introvert; E. supporting tables of tube feet; F. rods of tentacles; G. reticulated plates of tentacles. A = Scale 1; B–G = Scale 2. Reproduced from Deichmann (1937).

Thyone bentii var. *zacaë* Deichmann. H. plates of body wall; I. tables of introvert; J. complex reticulated plates of introvert; K. rosettes of introvert; L. smooth plates of introvert; M. supporting rods and plates of tube feet; N. rosettes of tentacles. H–N = Scale 3. Reproduced from Thandar's examination of the material from the MCZ.



- 1. 1 mm
- 2. 50 μ m
- 3. 50 μ m

Three lots of material, comprising four specimens were also obtained on loan from the USNM, identified as *T. bidentata* by Pawson. The label E17365 states two specimens present, collected from the South Pacific, near Ecuador, however only one was detected, indicating that five specimens should have been present in total. The remaining specimen from lot E17635 lacked any deposits from the body wall and tube feet, as did a single specimen from lot E21422 collected from the Gulf of California, possibly dissolved. Interestingly, the other specimen from lot E21422 contained some knobbed buttons with 5–7 holes and large fenestrated spheres or multilayered plates. Some smooth four-holed plates were also detected. This specimen, undeniably, does not belong to *T. bidentata* and possibly represents a species of *Stolus* but the form of the calcareous ring is of the sclerodactyline type. The body wall of specimen from lot E21452 also collected from the Gulf of California contains corroding ossicles but with some evidence for four-holed plates (without spires) and corroding rosettes in the tentacles.

It would seem imperative at this stage to establish a neotype for this species, but this step was not taken given that both paratypes lack internal structures. Hence, a collection of more material from the type locality is imperative.

Thyone comata Cherbonnier, 1988

Figure 6C–J

Thyone comata Cherbonnier, 1988: 188, text-fig 80 A–K; Thandar, 2006: 7, text-fig. 2.

Diagnosis (from Thandar, 2006)

Small species, up to 35 mm in length; body cucumber-shaped, narrowing posteriorly. Colour uniformly pink. Tube feet with suckers, elongated, evenly scattered over entire body, more numerous ventrally giving the body a villose appearance. Anal teeth present. Tentacles 10, ventral pair reduced. Calcareous ring tubular with long processes to radial plates; radial plates anteriorly notched and deeply incised posteriorly i.e. bifurcating before posterior border of interradial plates; interradial plates triangular, pointed anteriorly; ring and processes fragmented, the latter in a single series (Fig. 6D).

Deposits of the body wall irregular, two-pillared table discs with four central holes and a variable number of marginal holes of more or less equal size to central holes; spire of moderate height ending in 2–4 (up to six) teeth (Fig. 6F); numerous smaller tables at anal end (Fig. 6C). Supporting tables of tube feet curved, two-pillared, spire ending in a single conical point, rarely in two teeth (Fig. 6E); end-plates well-developed. Anal papillae with smaller supporting tables, spire ending in two teeth (Fig. 6I). Tentacle deposits delicate, perforated rods in stalk (Fig. 6G) and rosettes at tips (Fig. 6H). Introvert supported by smaller two-pillared, tables with multilocular discs of varying shapes, spire low (Fig. 6J).

Name-bearing type

MNHN, EcHh no. 3592.

Type locality

Tuléar, Madagascar.

Habitat

Sand, fine sand, coral sand, algae.

Distribution

Southwest Indian Ocean, 8–50 m.

Remarks

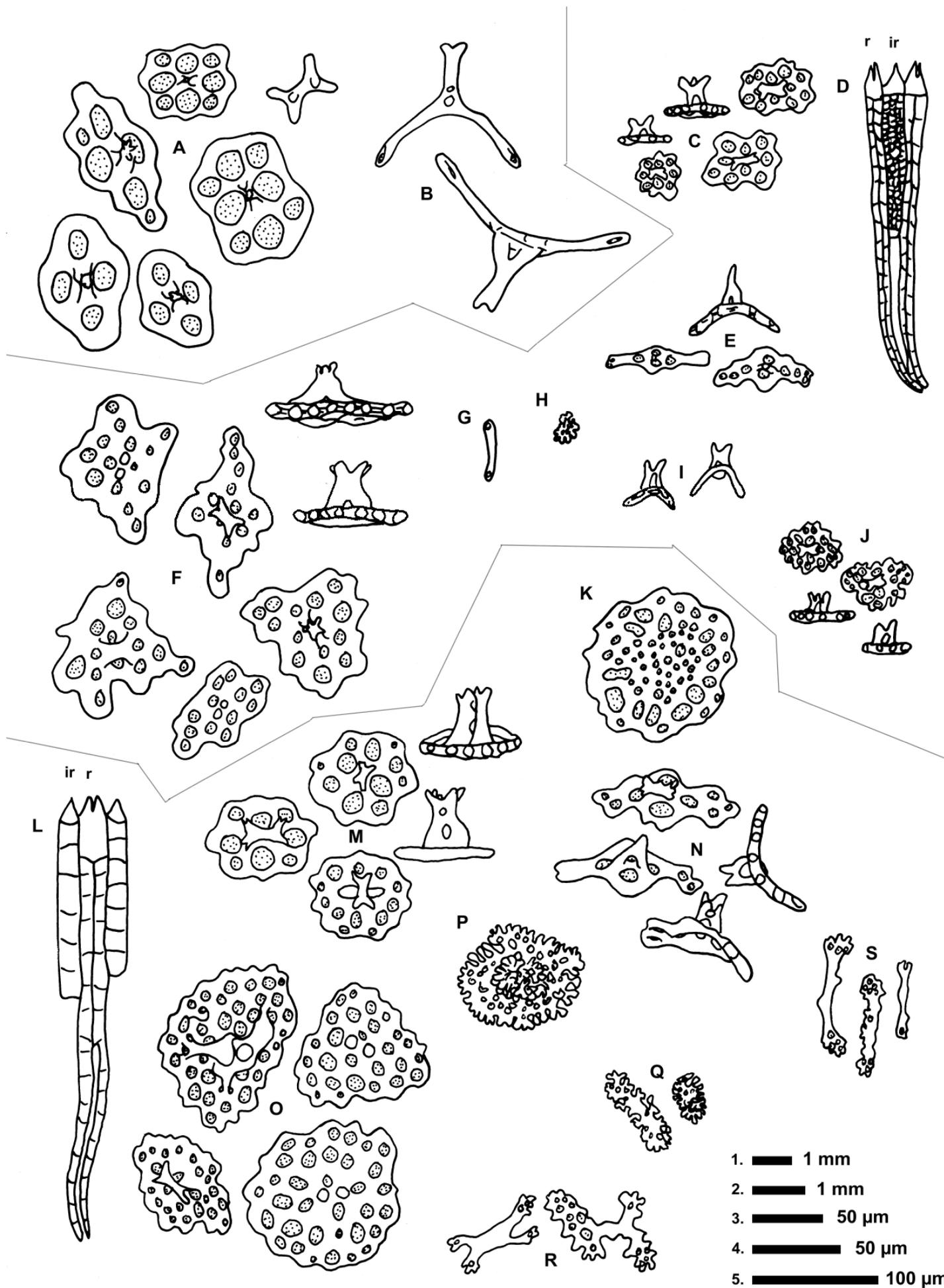
Cherbonnier (1988) described the introvert deposits as comprising both rosettes and multilocular tables. Conversely, after studying some specimens from the east coast of South Africa, Thandar (2006) observed only tables in the introvert and rosettes present only in the tentacle tips. Hence, the rosettes cited by Cherbonnier were possible contamination with tentacle deposits.

FIGURE 6

Thyone bidentata Deichmann. A. tables of body wall; B. supporting table of tube feet of holotype; H. supporting table of tube feet of paratype. A, B = Scale 3. Reproduced from Deichmann (1941).

Thyone comata Cherbonnier. C. small tables of anal region; D. calcareous ring (r = radial plate; ir = interradial plate); E. supporting tables of tube feet; F. tables of body wall; G. rod of tentacles; H. rosette of introvert; I. tables of anal papillae; J. tables of introvert. D = Scale 2; C, E–J = Scale 5. Reproduced from Cherbonnier (1988).

Thyone crebrapodia Cherbonnier. K. end-plate; L. calcareous ring; M. tables of body wall; N. supporting tables of tube feet; O. tables of introvert; P. large rosette with superstructure of tentacles; Q. rosettes of tentacles; S. rods of tentacles; R. branched rods of tentacles. L = Scale 1; K, M–R = Scale 4. Reproduced from Cherbonnier (1988).



Thyone crebrapodia Cherbonnier, 1988

Figure 6K–R

Thyone crebrapodia Cherbonnier, 1988: 197, text-fig. 84 A–I; Liao & Pawson, 2001: 76, text-fig. 15 A–E, 20 K.

Thyone cf. villosa Liao, 1997: 206.

Non *Thyone villosa* Semper, 1868.

Diagnosis (after Cherbonnier, 1988)

Small species, up to 24 mm in length. Colour yellow. Tube feet large, numerous, distributed all over body. Anal teeth present. Tentacles 10, ventral pair reduced. Calcareous ring long, tubular; radial plates prolonged before bifurcating into two long processes; both ring and processes fragmented (Fig. 6L). Deposits of body wall numerous tables with usually eight-holed discs (four large + four smaller marginal holes), rarely with more perforations; spire two-pillared, short or moderately high, ending in four apical teeth (Fig. 6M). Wall of tube feet supported by tables with curved disc, spire ending in 2–4 teeth (Fig. 6N); small end-plate present (Fig. 6K). Tentacle deposits simple (Fig. 6S) or branched rods (Fig. 6R) accompanied by rosettes (Fig. 6Q), those near the introvert with large superstructure in the centre (Fig. 6P). Introvert supported by tables with ovoid, triangular or circular, multilocular discs, reduced spires with rarely a sort of irregular bridge (Fig. 6O).

Name-bearing type

MNHN, EcHh no. 3557.

Type locality

Tuléar, Madagascar.

Habitat

At the great reef of Tuléar, found among the tropical seagrass species (*Thalassodendron ciliatum*, *Syringodium* sp. and *Cymodocea serrulata*) and at Sarodrano reef amongst the many microatolls, on reduced coarse sediment (Cherbonnier, 1988).

Distribution

Madagascar to East and South China Sea; 47–73 m

Remarks

Cherbonnier (1988) merely stated that his new species shared affinities with *Thyone villosa* Semper and *T. dura* Koehler & Vaney, but did not elaborate further. Indeed, this species is very similar to *T. villosa*, so much so, that Liao (1997) misidentified a specimen as *T. villosa* which he later corrected as *T. crebrapodia*, after examination of the holotype of *T. villosa* (Liao & Pawson, 2001). This extended the distribution of the species to the East China Sea. Thandar (2006) listed the diagnostic features of *T. villosa* after studying the holotype at the ZMA and other related species, and commented that *T. crebrapodia* differs from *T. villosa* in its smaller body wall and tube feet tables and the presence of rosettes and not plates in the tentacles.

Thyone hirta Cherbonnier, 1970

Figure 7A–G

Thyone hirta Cherbonnier, 1970: 288, fig. 4 N–S, 5 A–B; Thandar, 1990: 214; 2008: 6, fig. 2 A–F.

Diagnosis (after Cherbonnier, 1970 and Thandar, 2008)

Small species, up to 27 mm ventrally; body U-shaped. Colour orange. Tube feet long, thin, numerous, giving the body a hairy appearance. Anal teeth present, flanked by terminal tube feet. Tentacles 10, ventral pair reduced. Calcareous ring high, poorly calcified, radial plates slightly notched anteriorly, deeply incised posteriorly with long posterior processes, elements of radials in two series, separated by a non-calcified membrane; interradial plates ending in a single conical point anteriorly, elements in a single series (Fig. 7A). Deposits of body wall numerous tables with multilocular ovoid discs, 73–93 µm long; spire short (30–38 µm), two-pillared, terminating in one or two clusters of teeth (Fig. 7B). Tube feet with minute plates (Fig. 7G) and tables, the latter with elongate curved discs (90–105 µm) with usually four central holes and one at each

extremity; spire two-pillared, rarely four-pillared (33–45 μm high) (Fig. 7C). Tentacle deposits perforated plates and rods (Fig. 7D). Introvert supported by tables, similar but smaller than those of the body wall (Fig. 7F), and ? perforated rod-like plates (Fig. 7E).

Name-bearing type

MNHN, EcHh no. 1488.

Type locality

False Bay, WCP, South Africa.

Habitat

Sand, gravel, shelly sand, *Phyllochaetopterus* debris.

Distribution

Known only from False Bay, WCP, 40–53 m.

Remarks

Thandar (2008) upon subsequent re-examination of the type material relegated three out of the six specimens to *Thyonina articulata* (Vaney, 1908).

Thandar (2008) further reported on the composition of the introvert deposits which Cherbonnier (1970) failed to study. The introvert comprises two-pillared tables similar but smaller than those of the body wall, and relatively large but rare rod-like plates. These plates are very similar to those illustrated by Cherbonnier for the tentacles, giving rise to the suspicion that again there may have been contamination with ossicles of the tentacles. Hence, this species is provisionally placed in the ‘*tables only*’ group until the presence of these plates is confirmed in both the tentacles and introvert.

This species comes closest to *T. dura* in terms of its body wall deposits but differs in the arrangement of the tube feet, the longer spires to the tube feet tables, an absence of rosettes from the introvert and the form of the calcareous ring.

***Thyone nigra* Joshua & Creed, 1915**

Figure 7H–K

Thyone nigra Joshua & Creed, 1915: 20, pl. III, fig. 3–4; Rowe, 1982: 462, text-fig. 10.29a; Rowe & Gates, 1995: 316 (partim).

Diagnosis (after Joshua & Creed, 1915 and Rowe, 1982)

Small species, up to 30 mm long; body fusiform. Colour deep purplish-black, feet white. Tube feet with no particular arrangement, distributed over entire body. Anal teeth absent. Tentacles 10, ventral pair reduced. Calcareous ring tubular; radial plates slightly notched anteriorly, with long posterior processes arising at more or less the level of the interradial plates; interradials shorter, with an anterior conical point (Fig. 7K). Body wall tables with oblong-shaped, flat discs (96 x 60 µm long) with four large central holes and a few peripheral ones; spire short, ending in several spinous teeth (Fig. 7H). Tube feet with curved supporting tables with spire similar to that of body wall tables (Fig. 7I). Introvert supported by multilocular tables with numerous teeth (Fig. 7J), no rosettes. No deposits detected in tentacles.

Name-bearing type

South Australian Museum K1376.

Type locality

33–37° S, 132–140° E, off South Australia.

Habitat

Unknown.

Distribution

South and West Australia, up to 20 m.

Remarks

Joshua & Creed (1915) omitted the dimensions of their single specimen in their description, nor did they study the tentacles and introvert for deposits. Panning (1949)

did not include this species in his revision, possibly due to these reasons or due to oversight. Rowe (1982) merely reported *T. nigra* to reach 30 mm in length while Rowe & Gates (1995) confirm this species to be endemic to the south and west coasts of Australia.

Thandar examined some specimens at the NHMUK (1963.8.15.86–90 & 91) collected at Corio Bay, Port Phillip and Point Wilson respectively, which contained body wall and tube feet deposits similar to those illustrated by Joshua & Creed, and was able to determine the introvert deposits which comprise tables only, similar in size to those of the body wall but with smaller, more numerous perforations and a more spinous spire top. The calcareous ring of one of the NHMUK specimens however, is more sub-divided, showing two series of divisions when compared to that indicated by Joshua & Creed. Regrettably, no deposits were detected in the tentacle tips and it is unclear if this was due to decalcification or just an absence thereof.

***Thyone scabra* Verrill, 1873**

Figure 7L–P

Thyone scabra Verrill, 1873: 100; Deichmann, 1930: 166, pl. 13, fig. 3, 4 (synonymy before 1930).

Havelockia scabra Panning, 1949: 466; Pawson, 1977: 12, text-fig. 14; Pawson et al., 2010: 25, text-fig.

17.

Diagnosis (after Verrill, 1873 and Pawson et al., 2010, modified herein)

Medium-sized species, reaching 100 mm in length; body fusiform, strongly curved. Colour in alcohol yellowish-brown, some whitish, often with a brownish tinge. Tube feet hair-like, uniformly distributed. Anal teeth present. Tentacles 10, ventral pair reduced. Calcareous ring tubular with some “incipient” fragmentation; radial plates deeply incised posteriorly, bifurcating into two long processes made up of 8–10 pieces of calcite; interradials triangular with an anterior conical point (Fig. 7L). Deposits of body wall irregular tables (up to 130 µm in diameter) with 7–10 or more holes; spire two-pillared, ending in indistinct teeth (Fig. 7M). Tube feet with elongated, curved supporting tables (Fig. 7O). Tentacle deposits perforated rods and plates (Fig. 7P).

Introvert supported by tables with larger, more delicate, more circular disc; spire low (Fig. 7N).

Name-bearing type

Unknown.

Type locality

St. George's Bank (Verrill, 1873), Coast of New England, Western Atlantic.

Habitat

Sand or mud.

Distribution

Gulf of Mexico, 10–1170 m.

Remarks

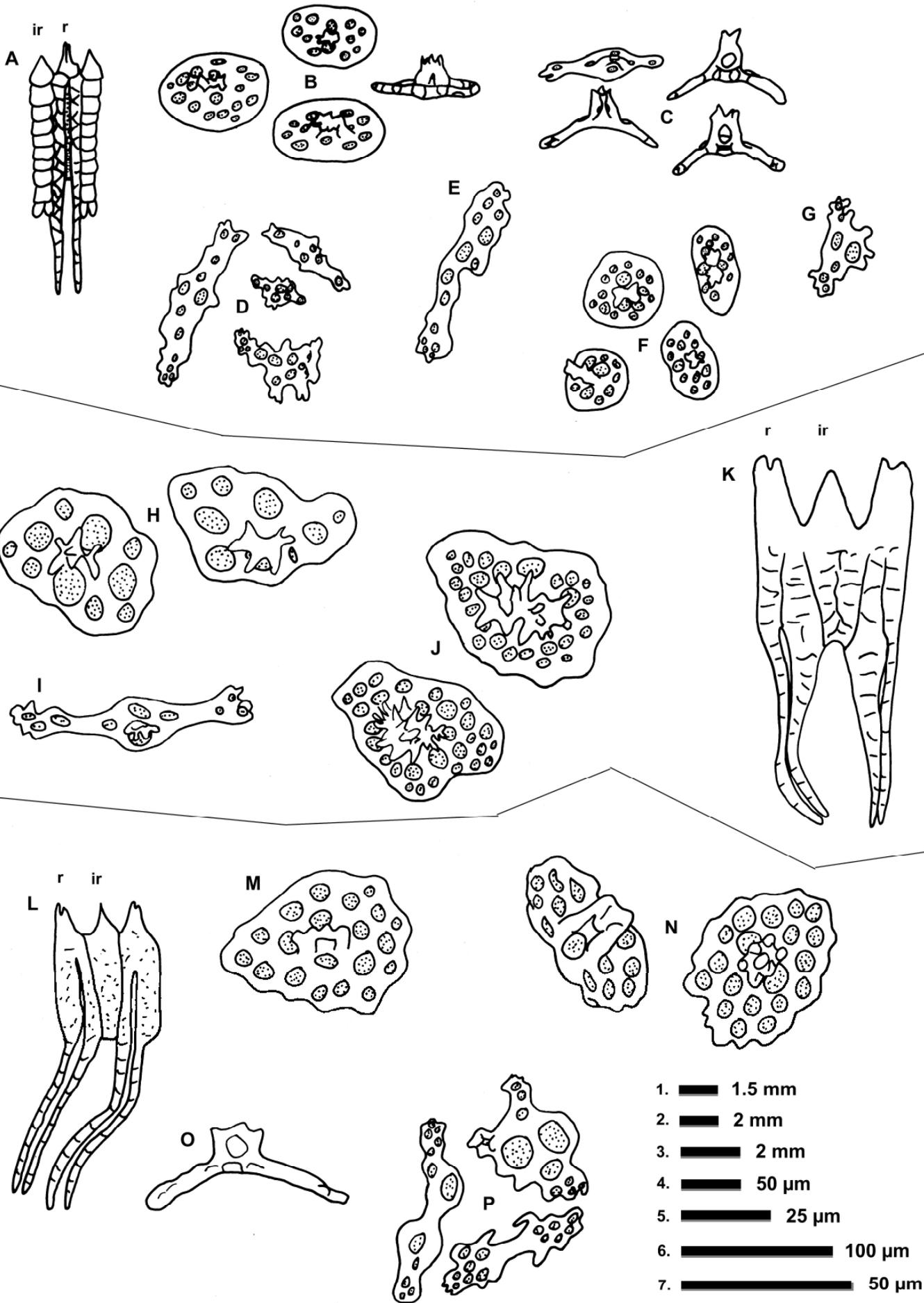
Pawson & Miller (1981), obviously unaware of Panning's (1949) addendum, list this species under *Havelockia* where Panning had originally placed this species in his revision, later moving this species back into *Thyone*. This error was repeated in Pawson et al.'s (2010) recent list of the Holothuroidea of the South Atlantic Bight. Verrill (1873) did not describe the nature of the calcareous ring but from Thandar's examination of a large specimen identified by Verrill present amongst the USNM collections (no. 21414), the ring is typically of the *Thyone* type being tubular, radially symmetrical with deeply incised radial plates posteriorly and long posterior processes made up of 8–10 pieces. Thandar recorded the plates as whole but suspected some incipient fragmentation. He also studied the introvert and tentacles for deposits which agree with Deichmann's (1930) description of the species.

FIGURE 7

Thyone hirta Cherbonnier. A. calcareous ring (ir = interradial plate; r = radial plate); B. tables of body wall; C. supporting tables of tube feet; D. plates and rods of tentacles; E. ?plate of introvert; F. tables of introvert; G. plate of tube feet. A = Scale 2; B–D, G = Scale 4; E, F = Scale 5. E, F reproduced from Thandar's examination of the material at the MNHN; other figures reproduced from Cherbonnier (1970).

Thyone nigra Joshua & Creed. H. tables of body wall; I. supporting table of tube feet; J. tables of introvert; K. calcareous ring. H–J = Scale 5; K = Scale 1. Reproduced from Thandar's examination of the material at the NHMUK.

Thyone scabra Verrill. L. calcareous ring; M. table of body wall; N. tables of introvert; O. supporting table of tube feet; P. plate and rods of tentacles. L = Scale 3; M, O = Scale 6; N, P = Scale 7. M, O reproduced from Deichmann (1930); L, N, P reproduced from Thandar's examination of the material at the USNM.



Thyone villosa Semper, 1868

Figure 8A–E

Thyone villosa Semper, 1868: 65, pl. XI, fig. 3, pl. XIII, fig. 24, pl. XV, fig. 6, pl. XXXVI, pl. 12; Théel, 1886: 135; Thandar, 2006: 11, text-fig. 3.
Havelockia villosa Panning, 1949: 466, text-fig. 61.

Diagnosis (after Semper, 1868 and Thandar, 2006)

Small species, holotype measuring 20 mm in length; body curved tapering at both extremities. Tube feet distributed equally over entire body. Anal teeth present. Tentacles 10, ventral pair reduced. Calcareous ring tubular, long, almost half the length of the body with long posterior processes to the radial plates; radials anteriorly bifurcate. Deposits of body wall tables with usually rounded to irregular-shaped discs with four central holes and few to numerous peripheral ones; spire two-pillared, fused distally ending in 2–4 teeth (Fig. 8A). Tube feet with elongated, curved, two-pillared supporting tables, pillars proximally fused and elongated, ending in an undivided or bifid tip; end-plates present (Fig. 8C). Tentacle deposits slender to branched rods (Fig. 8D) and larger perforated plates (Fig. 8E). Introvert supported by multilocular tables slightly smaller than those of body wall (Fig. 8B).

Name-bearing type

ZMH, 2909.

Type locality

Cebu, Philippines.

Habitat

Unknown.

Distribution

Known from the type locality only, 26 m.

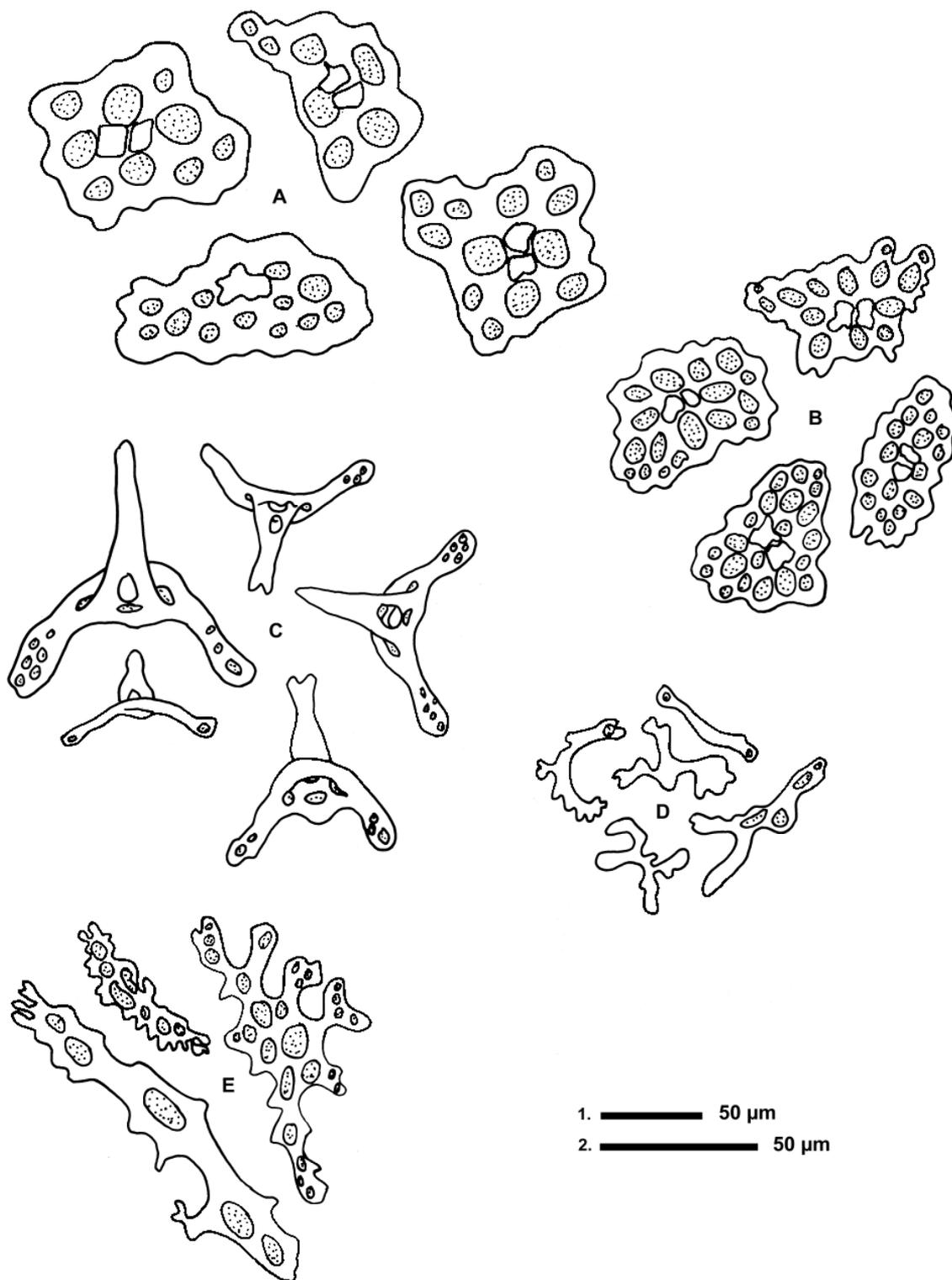


FIGURE 8. *Thyone villosa* Semper. A. tables of body wall; B. tables of introvert; C. supporting tables of tubefeet; D. branched rods of tentacles; E. perforated plates of tentacles. A–C = Scale 1; D, E = Scale 2. Reproduced from Thandar (2008).

Remarks

The holotype, the only record of this species to date, was re-described by Panning (1949) and transferred into his *Havelockia* due to the presence of tables in the introvert. This species was then moved to *Thyone* together with the other *Havelockia* species by Panning in his addendum. Thandar (2006) described some material from off the east coast of South Africa as *T. comata* and discussed the close resemblance of this species to Semper's (1868) *T. villosa* and *T. pedata*, both poorly described and distinguished by the absence of anal teeth in the latter. Thandar (2008) also studied the holotype from the ZMH and provides a table highlighting the similarities and differences among the three species above and *T. crebrapodia*, while illustrating the ossicle assemblage of *T. villosa*. From this, it is clear that *T. villosa* is a valid species of *Thyone*.

GROUP 2. INTROVERT DEPOSITS: ROSETTES ONLY

Thyone bicornis Ohshima, 1915

Figure 9A–E

Thyone bicornis Ohshima, 1915: 270, pl. 10, fig. 24 a–d; Panning, 1949: 467; Chang & Liao, 1964: 26; Liao & Clark, 1995: 503, text-fig. 305 a–e; Liao, 1997: 198, fig. 117 a–e; Won & Rho, 1998: 9, fig. 2 A–H; Lane et al., 2000: 491; Massin, 2005: 69, text-fig. 7 A–E.

Non *Thyone bicornis*; Yang, 1937: 6, fig. 3 a–g (?possibly *Thorsonia* sp. according to Liao & Clark, 1995).

Diagnosis (after Liao & Clark, 1995 and Massin, 2005)

Small species, length up to 37 mm; body fusiform, tapering equally towards both ends. Colour in alcohol greyish-brown, yellowish in smaller individuals. Tube feet numerous, distributed all over the body, with some indication of double rows in each ambulacrum. Anal teeth not mentioned. Tentacles 10, small, ventral pair smaller. Calcareous ring long, tubular, mosaic-like; radial plates anteriorly bifurcate with posterior processes made up of 6–7 pieces (Fig. 9A). Deposits of body wall sparsely scattered tables, with four large primary holes and generally four peripheral ones; spire two-pillared, ending in two diverging spines, sometimes bifurcating distally (Fig. 9B).

Tube feet with elongated, curved, supporting tables; spire ending in two diverging teeth or in a single conical point (tack-like) (Fig. 9C); end-plates small, rudimentary, some star-shaped (Fig. 9D). Tentacle branches and tips with slender, smooth rods perforated at each extremity; stalk with rod-like deposits. Rosettes in introvert, complicated (Fig. 9E).

Name-bearing type

USNM, no. 34173.

Type locality

Suruga Bay, south Japan.

Habitat

Sandy-muddy bottom.

Distribution

S. China to Japan; Gulf of Tonkin to eastern Guangdong to Papua New Guinea, 23–61 m.

Remarks

The tentacle deposits are not illustrated by any of the authors who recorded this species. However, since Liao & Clark (1995) provide a good description of the ossicle assemblage of *T. bicornis*, there was no need to examine the type or voucher specimens.

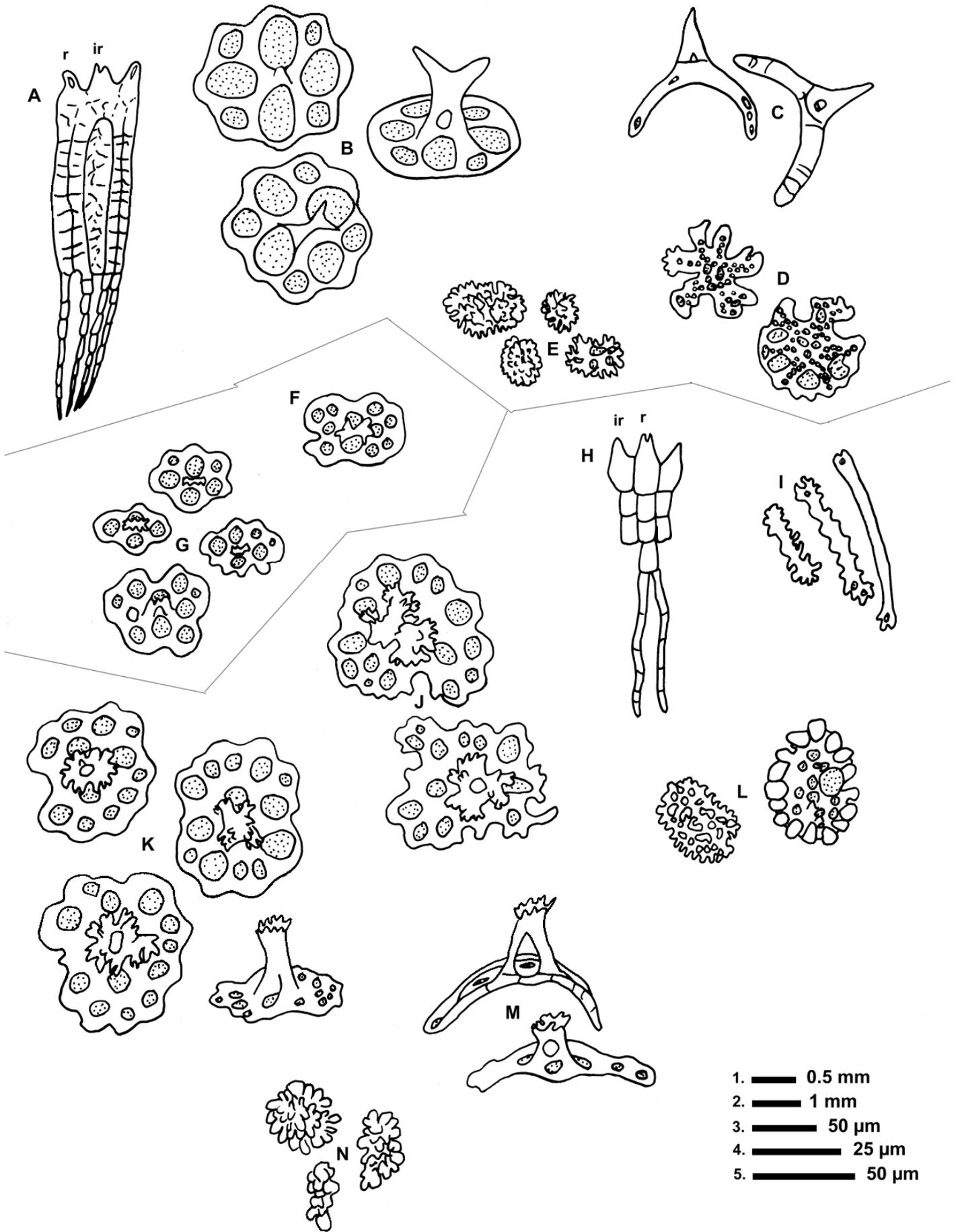
According to Massin (2005), the two diverging spines of the spires of the tables bear some resemblance to those of *T. crebrapodia* Cherbonnier and *T. longicornis* Cherbonnier, both described from Madagascar in 1988. *T. crebrapodia* however, possesses multilocular tables in the introvert, while the introvert deposits of *T. bicornis* comprise rosettes only. *T. longicornis*, on the other hand, is a smaller species and the perforations of the end-plates are much larger and fewer in number than those of *T. bicornis*.

FIGURE 9

Thyone bicornis Ohshima. A. calcareous ring (r = radial plate; ir = interradial plate); B. tables of body wall; C. supporting tables from tube feet; D. end-plates; E. rosettes of introvert. A = Scale 2. B–E = Scale 5. Reproduced from Massin (2005).

Thyone deichmannae Madsen. F. table of body wall; G. tables of body wall. F, G = Scale 3. Reproduced from Deichmann (1930).

Thyone guillei Cherbonnier. H. calcareous ring; I. rods of tentacles; J. tables of anal region; K. tables of body wall; L. rosette and nodular button of tentacles; M. supporting tables of tube feet; N. rosettes and rosette-shaped bodies of introvert. H = Scale 1; I–N = Scale 4. H–M reproduced from Cherbonnier (1988); N from paratype EcHh 22064 from MNHN.



1. ——— 0.5 mm
2. ——— 1 mm
3. ——— 50 μ m
4. ——— 25 μ m
5. ——— 50 μ m

***Thyone deichmannae* Madsen, 1941**

Figure 9F & G

Thyone fusus Deichmann, 1930: 167, pl. 14, figs. 1–5.

Thyone deichmannae Madsen, 1941: 26; Panning, 1949: 467; Hendler et al., 1995: 276, figs. 153, 182 H–J; Pawson et al., 2010: 28, fig. 21 A–D.

Thyone inermis. Pawson & Miller, 1981: 394; Miller & Pawson, 1984: 40, figs. 32, 33.

Non *Thyone inermis* Heller, 1868.

Diagnosis (after Deichmann, 1930 and Pawson et al., 2010)

Medium-sized species, up to 120 mm in length; body cylindrical. Colour greyish-brown. Tube feet numerous, hair-like, arranged in indistinct double rows along ambulacra, scattered in interambulacra. Anal teeth not mentioned. Tentacles 10, ventral pair smaller. Calcareous ring tubular, with long posterior processes on radial plates; radials deeply incised, bifurcating almost at middle of interradial plates. Deposits of body wall comprise tables with mostly 4–8-holed discs, sometimes with up to 10 marginal holes; spire two-pillared, ending in a few teeth (Fig. 9G, ?F). Tube feet with elongate supporting tables with spire gently tapering; small end-plate present. Tentacles and introvert supported only with complicated rosettes.

Name-bearing type

Probably at MCZ.

Type locality

Tobago, Republic of Trinidad.

Habitat

Soft sediment such as crushed shell, quartz sand, and calcareous silt.

Distribution

North Carolina to Florida, Gulf of Mexico, 6–366 m.

Remarks

Deichmann (1930) reluctantly identified some West Indian forms as *Thyone fusus* (Müller) citing that the calcareous ring bears a close resemblance to the Mediterranean *Cucumaria aurantiaca* Costa (= *T. inermis* Heller), differing in the absence of supporting tables in the tube feet. She illustrated a single table from the introvert (pl. 14, fig. 5; Fig. 9F), but, in her description, she mentions no other deposits but rosettes from the tentacles and introvert. Neither Deichmann nor subsequent authors illustrate the calcareous ring but Deichmann's description is consistent with that of a typical *Thyone* ring.

Madsen (1941) considered her specimens as a distinct species and so named it *T. deichmannae*. In 1947, Deichmann, obviously ignoring Madsen's decision, argued that the West Indian forms could not be separated from the Mediterranean forms (*T. inermis*) which differ slightly from the typical Northern European *T. fusus* in its deeply cleft radials and the tendency to reduce its ossicles faster with age. Deichmann claimed that it was possible that larvae of *T. inermis* might have been transported via the Atlantic to the western hemisphere, however, not reaching maturity in these waters, thus explaining the lack of large, mature individuals in her collection. McKenzie (1991) pointed out that such an occurrence is not totally absurd; however, the likelihood that the West Indian forms are endemic to the West Indies appears more reasonable as are most dendrochirotidids because of their direct development (Thandar, pers. comm.), as assumed by Madsen (1941).

Pawson and Miller (1981) hesitantly agreed with Madsen's (1941) opinion but accepted Deichmann's decision and recorded the West Indian forms as *Thyone inermis*. McKenzie (1991) further argued that in all but one specimen, the species contained a full complement of deposits throughout the body and hence is not referable to *T. inermis* which lack deposits in the body wall except at the posterior end. It was not until the publication of Hendler et al. (1995), in which Pawson and Miller were co-authors, that the West-Indian forms were regarded as *T. deichmannae*.

Pawson et al. (2010) confirm the presence of only rosettes in the introvert and the table (Fig. 9F) illustrated by Deichmann perhaps came from the body wall.

Thyone guillei Cherbonnier, 1988

Figure 9H–N

Thyone guillei Cherbonnier, 1988: 198, text-fig. 86.

Diagnosis (after Cherbonnier, 1988)

Minute, sub-cylindrical species, up to 7 mm in length. Colour pinkish. Body covered by long tube feet relative to the size of the specimen. Tentacles 10, ventral pair reduced. Anal teeth present, crowned by a circle of five large conical papillae. Calcareous ring tubular, composed of several large pieces; radial plates slightly notched anteriorly, with long posterior processes, roughly the same length as the ring (Fig. 8H). Body wall ossicles comprise only two-pillared tables with irregular margins and variable number of holes; spire low, thick terminating in either a perforated crown of teeth or pillars fused, ending in variable number of spiny teeth; some spires slender (Fig. 9K); anal table discs more irregular in shape, also multilocular (Fig. 9J). Tube feet tubes with curved discs with 6–7 perforations, also perforated at ends; spire two-pillared, ending in small teeth (Fig. 9M). Tentacle deposits of three types: long rods with slightly expanded ends; shorter, thicker rods with crinkly margins, both usually perforated once at ends (Fig. 9I); and rosettes and nodular buttons (Fig. 9L). Introvert supported by rosettes and rosette-shaped bodies (Fig. 9N).

Name-bearing type

MNHN, EcHh no. 3558.

Type locality

Tuléar, Madagascar.

Habitat

Muddy sand, some associated with Madreporaria and Foraminifera.

Distribution

Madagascar, 6–33 m.

Remarks

Cherbonnier (1988), despite providing a detailed description of this species, did not study the introvert ossicles and unfortunately, nor did Thandar as the type could not be located during his visit. An examination of a few paratypes on loan from the MNHN revealed that the introvert comprises numerous rosettes and rosette-shaped bodies.

T. guillei shares a close resemblance to *T. dura* in terms of its body wall and tentacle deposits, but differs in the more irregular margin of the tables and the crown at the top of the spire which bears numerous spiny teeth.

***Thyone longicornis* Cherbonnier, 1988**

Figure 10A–G

Thyone longicornis Cherbonnier, 1988: 200, text-fig. 87 A–L.

Diagnosis (after Cherbonnier, 1988)

Small species, up to 18 mm in length. Colour pink. Tube feet long, distributed throughout the body, more crowded in ambulacra. Anal teeth absent. Tentacles 10, 8 rather long and finely branched, ventral pair tiny. Calcareous ring tubular, long, with incipient fragmentation; radial plates slightly notched anteriorly and much prolonged before bifurcating posteriorly into two narrow processes; interradials pointed anteriorly (Fig. 10A). Body wall tables with sub-circular discs with eight holes, four of which are interposed between four smaller triangular holes; spire low, both pillars joined by a single cross-bar forming a very obtuse angle between them, and ending in two diverging teeth (Fig. 10D). Tube feet with smaller, curved, supporting tables (Fig. 10B); large end-plates present (Fig. 10C). Tentacle deposits rods of three kinds: long, smooth rods perforated at the ends (Fig. 10E), some crinkly rods with scalloped edges (Fig. 10F) and some rosette-like rods at the base of the tentacles and introvert (Fig. 10G).

Name-bearing type

MNHN, EcHh no. 2771.

Type locality

Tuléar, Madagascar.

Habitat

Among highly oxidized sand and coarse sediment in the micro atoll reef, Beloza.

Distribution

Known only from type locality, 10 m.

Remarks

The holotype, measuring only 12 mm in length, is in a poor state, which Thandar assumes to be attributed to the specimen drying up before preservation. The minute holotype did not appear to have been dissected for study of the tentacle and introvert deposits; hence, Thandar assumes that those illustrated by Cherbonnier (1988) are from the paratypes. Furthermore, he comments that although Cherbonnier describes the calcareous ring as not being mosaic-like, the incipient divisions illustrated by him are present.

Interestingly, an examination of one of the paratypes by Thandar, in which the calcareous ring is preserved, demonstrated a different form of body wall ossicles and it is doubtful whether this specimen belongs to *T. longicornis*. Unfortunately, the other paratypes all lack calcareous rings, probably destroyed during Cherbonnier's examination. Thandar did not confirm the composition of their body wall ossicles.

Cherbonnier describes the rosette-like rods at the base of the tentacles and introvert, implying that the introvert may comprise rosettes or rosette-like deposits. Thandar did not study the introvert of the holotype for fear of irrevocably damaging the minute specimen. However, Thandar & Dunlevey (2004) discussed the variations in the form of ossicles along the length of the introvert in several dendrochirotid species and showed transitional deposits along the entire length in some species. From this, it can be concluded that the introvert-tentacle area may bear transitional deposits, while the part closest to the body wall has ossicles resembling body wall deposits (Thandar, pers. comm.). Hence, *T. longicornis* is provisionally listed in the “*rosettes only*” group.

Thyone sineturra Cherbonnier, 1988

Figure 10H–J, 11A–F

Thyone sineturra Cherbonnier, 1988: 194, text-fig. 83 A–K.

Diagnosis (after Cherbonnier, 1988)

Minute species, holotype measuring 7 mm in length; body cucumber-shaped. Colour uniformly creamish-white. Tube feet large, distributed over the entire body. Anus surrounded by five anal teeth. Tentacles 10, ventral pair reduced. Calcareous ring coarsely mosaic, broken up into large pieces of calcite; radial plates pointed anteriorly and two posterior processes arising at posterior border of interradial plate, each made up of four large pieces; interradials also triangular, more or less the same length as the radial plates (Fig. 10H). Tables of body wall comprising disc with a sharply serrate margin, often perforated by 4–6 holes and with two central nodules more or less triangular in shape; some discs more elongated with more holes (Fig. 10I). Some other supporting tables also present with disc bearing an abbreviated two-pillared spire with a rather unusual nature. Table discs of anal region also with two central nodules (Fig. 11A) and rosettes, although rare, of two forms: some crinkly and others with a more reticulated surface (Fig. 11B). Tube feet with rods of various forms, mostly perforated along the length (Fig. 11C); end-plates small. Tentacle deposits as rods, larger and often with enlarged multi-perforated ends (Fig. 10J, 11E) and numerous rosettes (Fig. 11D). Introvert supported by numerous rosettes (Fig. 11F).

Name-bearing type

MNHN, EcHh no. 3566.

Type locality

Tuléar, Madagascar.

Habitat

Unknown.

Distribution

Known only from type locality.

Remarks

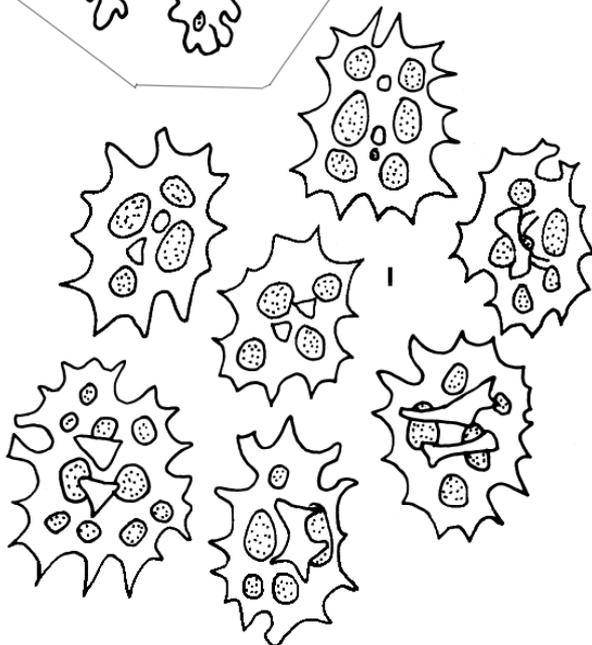
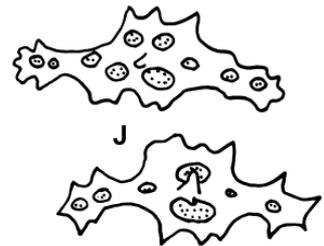
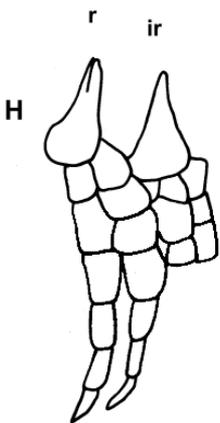
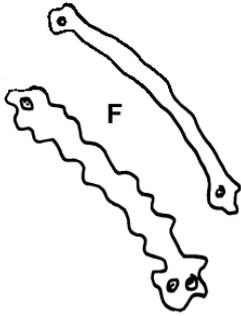
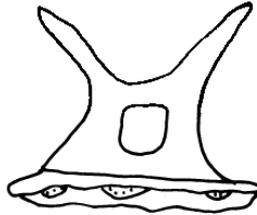
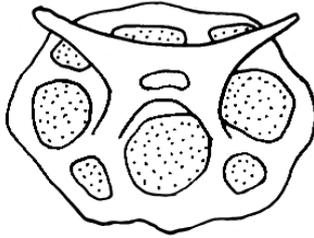
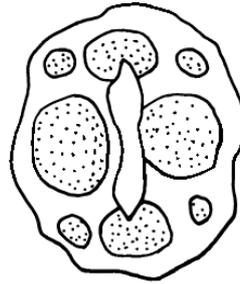
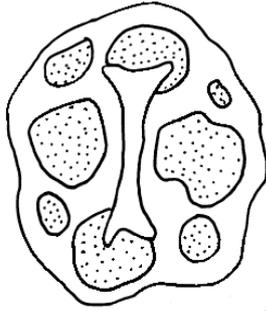
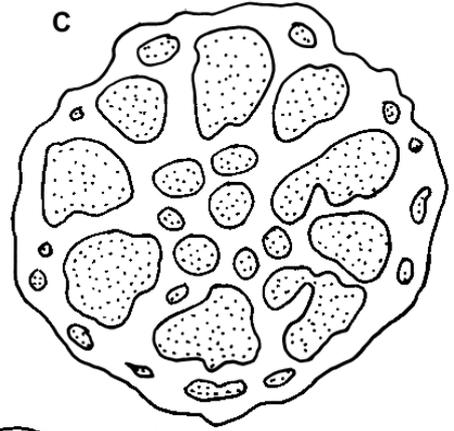
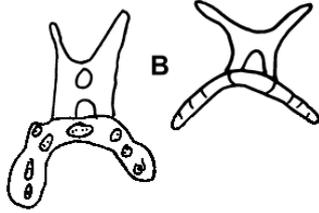
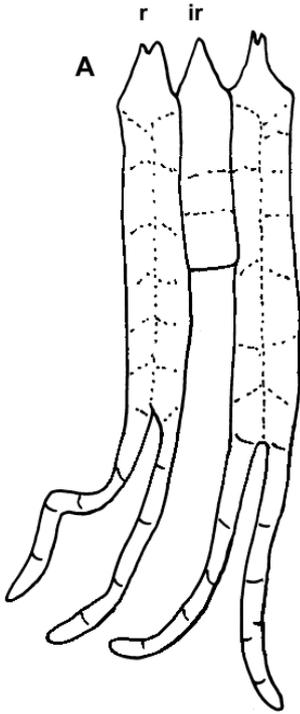
It appears that Cherbonnier (1988) failed to examine the introvert while Thandar recorded an abundance of rosettes in combination with a few very large rods, similar to those illustrated by Cherbonnier for the tentacles. Bearing in mind that the holotype only measures 7 mm in length, it is expected that the deposits of the tentacles and introvert would be immensely difficult to distinguish in such a minute specimen. It is assumed that the introvert of this species comprises only rosettes as the writer is of the opinion that no other species of *Thyone* possess rods in the introvert and is therefore assigned to the “*rosettes only*” group, until more material is collected to confirm the presence of these very large rods.

This species may deserve a new genus based upon the unusual body wall deposits. However, this is discouraged since it will add to the number of monotypic genera within the dendrochirotidids. Furthermore, it is because of the tubular nature of its calcareous ring and some evidence of a former or abbreviated two-pillared spire of the tables that *T. sineturra* is here retained in *Thyone*.

FIGURE 10

Thyone longicornis Cherbonnier. A. calcareous ring (r = radial plate; ir = interradial plate); B. supporting tables of tube feet; C. end-plate; D. tables of body wall; E. long rod of tentacles; F. crinkly rods of tentacles; G. transitional rosette deposit of tentacles. A = Scale 2; B = Scale 1; C–G = Scale 4. Reproduced from Cherbonnier (1988).

Thyone sineturra Cherbonnier. H. calcareous ring; I. tables of body wall; J. perforated rods of tentacles. H = Scale 1; I, J = Scale 3. Reproduced from Cherbonnier (1988).

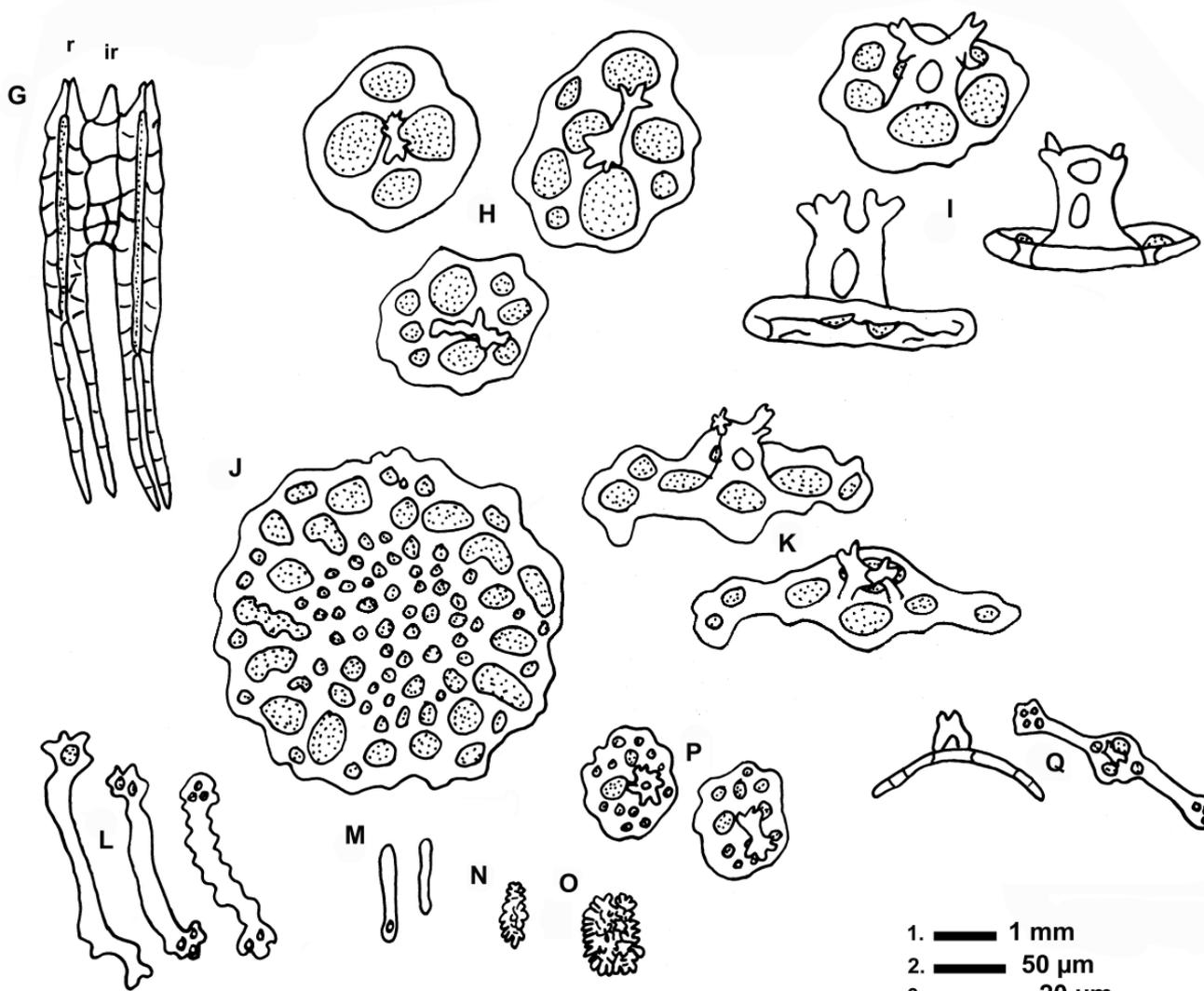
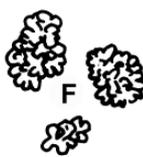
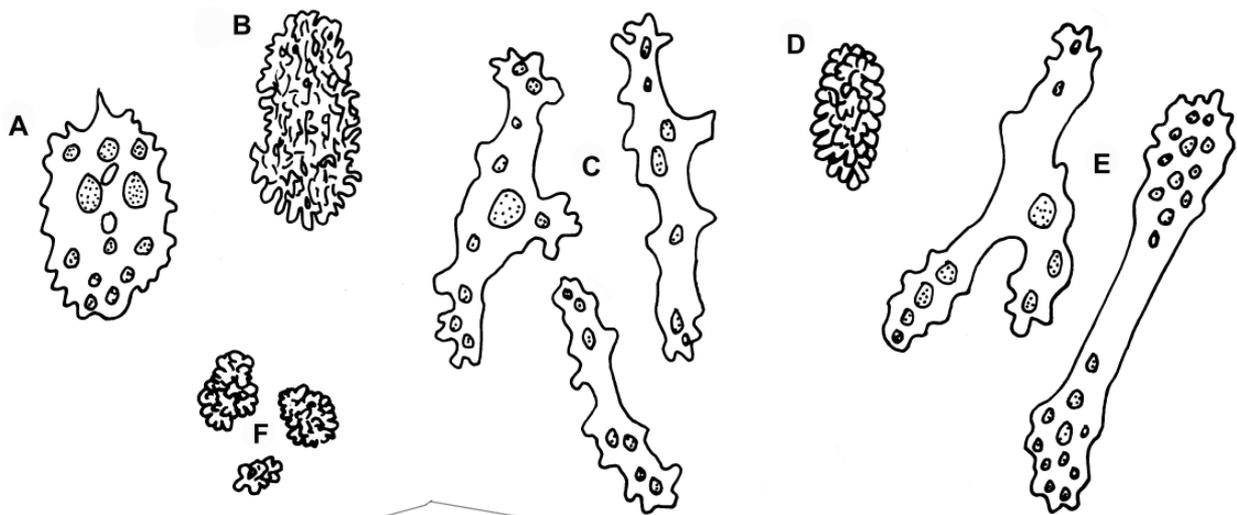


- 1.  25 μ m
- 2.  1 mm
- 3.  50 μ m
- 4.  20 μ m

FIGURE 11

Thyone sineturra Cherbonnier. A. table of anal region; B. rosette of anal region; C. rods of tube feet; D. rosette of tentacles; E. rods of tentacles; F. rosettes of introvert. A, C–E = Scale 4; B, F = Scale 3. A–E reproduced from Cherbonnier (1988); F from Thandar's examination of the material at MNHN.

Thyone avenusta Cherbonnier. G. calcareous ring (r = radial plate; ir = interradial plate); H. tables of body wall; I. tables of anal region; J. end-plate; K. tables of tube feet; L. slender and rosette-like rods of tentacles; M. minute slender rods of tentacles in juveniles; N. rosette of tentacles; O. rosette of introvert; P. tables of introvert in juveniles; Q. tables of tube feet. G = Scale 1; H–Q = Scale 2. G–J, L reproduced from Cherbonnier (1970); M–Q reproduced from Cherbonnier (1988) from specimens of 10–12 mm in length.



- 1. ——— 1 mm
- 2. ——— 50 μ m
- 3. ——— 20 μ m
- 4. ——— 50 μ m

GROUP 3. INTROVERT DEPOSITS: TABLES AND ROSETTES

Thyone avenusta Cherbonnier, 1970

Figure 11G–Q

Thyone avenusta Cherbonnier, 1970: 286, fig. A–M; Cherbonnier 1988: 197, fig 85 A–M; Thandar, 1990: 214, fig. 5 a–g; Thandar, 2006: 5, fig. 1.

Diagnosis (after Thandar, 1990)

Small species, up to 47 mm in length. Colour in alcohol, brown. Tube feet scattered, sometimes more numerous in ambulacra. Anal teeth present. Tentacles 10, ventral pair reduced. Radial plates of calcareous ring prolonged posteriorly to terminate in short bifurcate processes (Fig. 11G). Body wall comprise two-pillared tables with circular to sub-circular discs, 50–90 μm , pierced with up to 16 holes, spire low, 20–50 μm ; terminating usually in two clusters of teeth (Fig. 11H). Spires of anal tables more developed (Fig. 11I). Tube feet with oblong tables (Fig. 11K, Q); end-plates present (Fig. 11J). Tentacle deposits curved, elongated, slender rods, usually perforated at ends, rosette-like rods (Fig. 11L), minute slender rods (Fig. 11M) in juveniles, and rosettes (Fig. 11N). Introvert supported by rosettes only (Fig. 11O), but found in combination with small multilocular tables (Fig. 11P) in juveniles.

Name-bearing type

MNHN, EcHh no. 1487.

Type locality

Morrumbene, Mozambique.

Habitat

Mangrove, sand.

Distribution

Madagascar, Mozambique and east coast of South Africa, up to 70 m.

Remarks

Thandar (1990) examined a 47 mm specimen from the UCT material, which was already established to be collected with the 30 mm holotype, commenting on some slight differences in both specimens, which he attributed to age. Thandar found that the tube feet are uniformly distributed and anal teeth were present in the larger specimen, whereas Cherbonnier (1970) recorded more tube feet ventrally and the absence of anal teeth. Thandar (1990) was obviously unaware that Cherbonnier (1988) also recorded this species from Madagascar on the basis of smaller individuals (10–12 mm in length) and found tiny anal teeth. This was confirmed when Thandar (2006) recorded the same in an 11 mm specimen from the KwaZulu-Natal coast. In addition, this specimen also had large curved rods in the tube feet, perhaps a juvenile character. It can be safely concluded that the absence of anal teeth in the holotype was perhaps an abnormality or the teeth were overlooked.

Moreover, Cherbonnier (1970) describes the composition of the introvert deposits as rosettes only, a view supported by Thandar. However, in Cherbonnier's Madagascan material the rosettes are found in combination with small multilocular tables, unlike those of the body wall. This could perhaps represent another juvenile feature, but since present, this species is here placed within the '*tables and rosettes*' group.

Thandar (2006) commented that *T. avenusta* comes very close to *T. propinqua* in terms of its body wall ossicles but differs in the presence of the three types of tentacles deposits. The tentacles deposits of the latter species comprise only plates which are also present in the introvert.

Thyone bacescoi Cherbonnier 1972

Figure 12A–H

Thyone bacescoi Cherbonnier, 1972: 291, fig. 1 A–L; Massin, 1993: 425 (zoogeography).

Diagnosis (after Cherbonnier, 1972)

Small species, holotype 45 mm in length; body cucumber-shaped. Colour pinkish white ventrally, greyish-white dorsally. Tube feet numerous, uniformly distributed with no radial seriation. Anal teeth present. Tentacles 10, ventral pair reduced. Calcareous

ring high, tubular; radial processes equal to length of tube, broken into 5–6 pieces; interradials triangular, blunt (Fig. 12D). Deposits in body wall lacking. Tube feet with large end-plates (Fig. 12B) except at anal region which contain straight rods perforated at ends (Fig. 12E) and irregular, more or less branched plates with unequal holes (Fig. 12A). Tentacle deposits numerous slender rods at base of tentacles (Fig. 12H), and multilocular rods with scalloped edges (Fig. 12G). Introvert supported by multilocular tables (Fig. 12C) and rosettes (Fig. 12F).

Name-bearing type

MNHN, EcHh no. 3398.

Type locality

Coast of Mauritania.

Habitat

Sand.

Distribution

Known only from type locality, 25 m.

Remarks

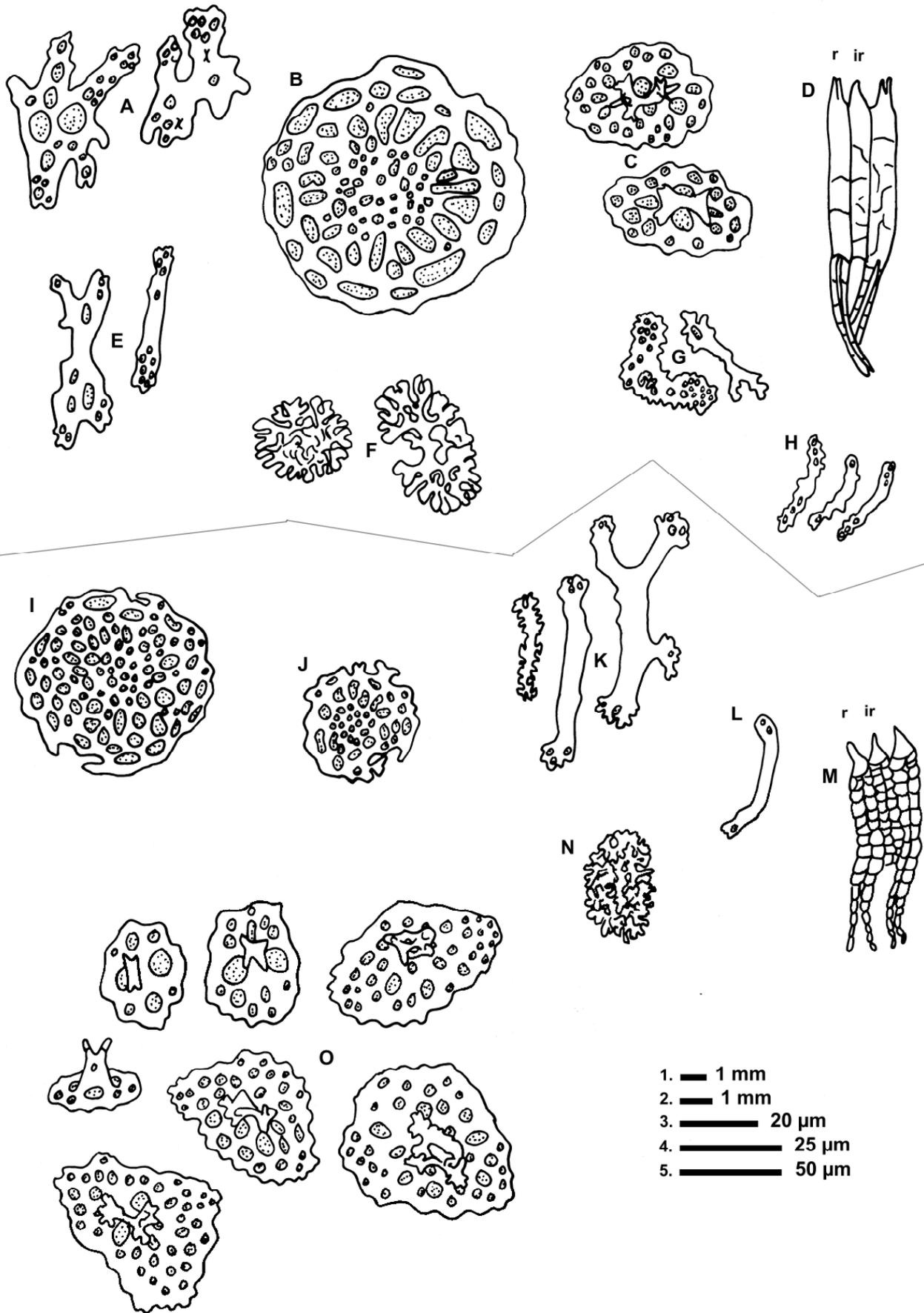
Cherbonnier (1972) compared his single specimen to two European species *T. roscovita* Hérouard and *T. inermis* Heller whose deposits are restricted to the terminal end-plates of the tube feet, tentacles, introvert and anal region. However, the table discs of the introvert of *T. roscovita* are larger and have an irregular margin, while the anal end of *T. inermis* contains circular tables, absent in the other two species. Furthermore, *T. bacescoi* is well characterized by its peculiar tube feet deposits.

The holotype was re-examined by Thandar but he found no deposits even in the anal region except for end-plates in the tube feet.

FIGURE 12

Thyone bacescoi Cherbonnier. A. plates of anal region; B. end-plate; C. tables of introvert; D. calcareous ring (r = radial plate; ir = interradial plate); E. rods of anal region; F. rosettes of introvert; G, H. rods of tentacles. A–C, E, G, H = Scale 5; D = Scale 1; F = Scale 4. Reproduced from Cherbonnier (1972).

Thyone carens Cherbonnier. I. end-plate; J. end-plate of anal papillae; K. elongated rosette and rods of tentacles; L. rod of anal papillae; M. calcareous ring; N. rosette of introvert; O. tables of introvert. I–L, O = Scale 5; M = Scale 2; N = Scale 3. Reproduced from Cherbonnier (1988).



Thyone carens Cherbonnier, 1988

Figure 12I–O

Thyone carens Cherbonnier, 1988: 190, text-fig. 81 A–O.

Diagnosis (after Cherbonnier, 1988)

Small species, up to 35 mm in length; body cucumber-shaped tapering at ends. Colour pinkish-white to pink, sometimes brown, slightly darker dorsally. Tube feet distributed throughout the body, more numerous on the dorsal radius where they are aligned in two alternating rows, short, thick with a large sucker. Anal teeth present. Tentacles 10, ventral pair reduced. Anterior part of radial and interradial plates of calcareous ring slightly curved; radials made up of a mosaic of small pieces, posterior processes split beyond posterior border of interradial plates, each sub-divided into 7 or 8 pieces of calcite; interradials also mosaic-like (Fig. 12M). Body wall and tube feet without ossicles, the latter occurring in only the tentacles, introvert and anal papillae. Anal papillae with simple rods (Fig. 12L). Tube feet supported by large end-plates (Fig. 12I), smaller in anal papillae (Fig. 12J). Tentacle deposits a few elongated rosettes and numerous unbranched or X-shaped rods, perforated at ends (Fig. 12K). Deposits of introvert few two-pillared tables with either a small rounded disc with 8–15 perforations, spire ending in a single-bifid tooth or disc larger, circular to triangular-shaped, spire ending in an irregular crown of teeth (Fig. 12O); rosettes also present (Fig. 12N), mainly concentrated at base of tentacles.

Name-bearing type

MNHN, EcHh no. 3555.

Type locality

Nosy Be to Tuléar, Madagascar.

Habitat

Unknown (in detritus).

Distribution

Known only from type locality, shallow.

Remarks

Cherbonnier (1988) compared his species to *T. okeni* Bell citing an absence of ossicles from the body wall in both species; however *T. okeni* lacks anal teeth or any deposits in the anal papillae except for end-plates and is a larger species. Furthermore, the tentacle rods of *T. okeni* are large and expanded at the ends with many perforations while its calcareous ring appears to be more fragmented than *T. carens*.

Thyone cherbonnieri Reys, 1959

Figure 13A–G

Thyone cherbonnieri Reys, 1959: 173, fig. 1–6; Tortonese, 1965: 88; Zavodnik, 1979: 122, text-fig. 1; 1980: 444; Koukouras & Sinis, 1981: 277.

Diagnosis (after Reys, 1959)

Small species, up to 47 mm in length; body lemon-shaped in preserved specimen, ventral surface slightly convex, dorsal surface slightly concave. Colour in life greyish-brown. Tube feet scattered, more numerous on ventral surface; two rows of feet dorsally. Anal teeth not mentioned. Tentacles 10, ventral pair reduced. Calcareous ring long, tubular, broken up into a mosaic, splitting beyond posterior border of interradial plates dorsally, processes long; radial plates deeply cleft anteriorly; anterior end of interradials ending in a conical point (Fig. 13A). Ossicles of body wall mostly four central-holed table discs with 8–10 slightly smaller, marginal perforations; some eight-holed table discs also present, although less common, spires two-pillared with generally one crossbar, sometimes two (Fig. 13B). Supporting tables of the tube feet curved, spires ending in 2–3 teeth (Fig. 13C); end-plates present (Fig. 13E). Tentacle deposits small, relatively thin rods, sometimes branched, perforated at each end and some along surface (Fig. 13G); rosettes present, rare. Introvert supported by tables with multilocular discs (Fig. 13D) and rosettes, the latter rare (Fig. 13F).

Type material

MNHN, EcHh no. 4075 (*syntype*).

Type locality

Gulf of Lion, off the south coast of France.

Habitat

Substrata of silt, sand silt, pebbles, or in *Zostera* and *Posidonia* meadows.

Distribution

South coast of France, north Aegean Sea, Adriatic Sea to East Mediterranean, 3–63 m.

Remarks

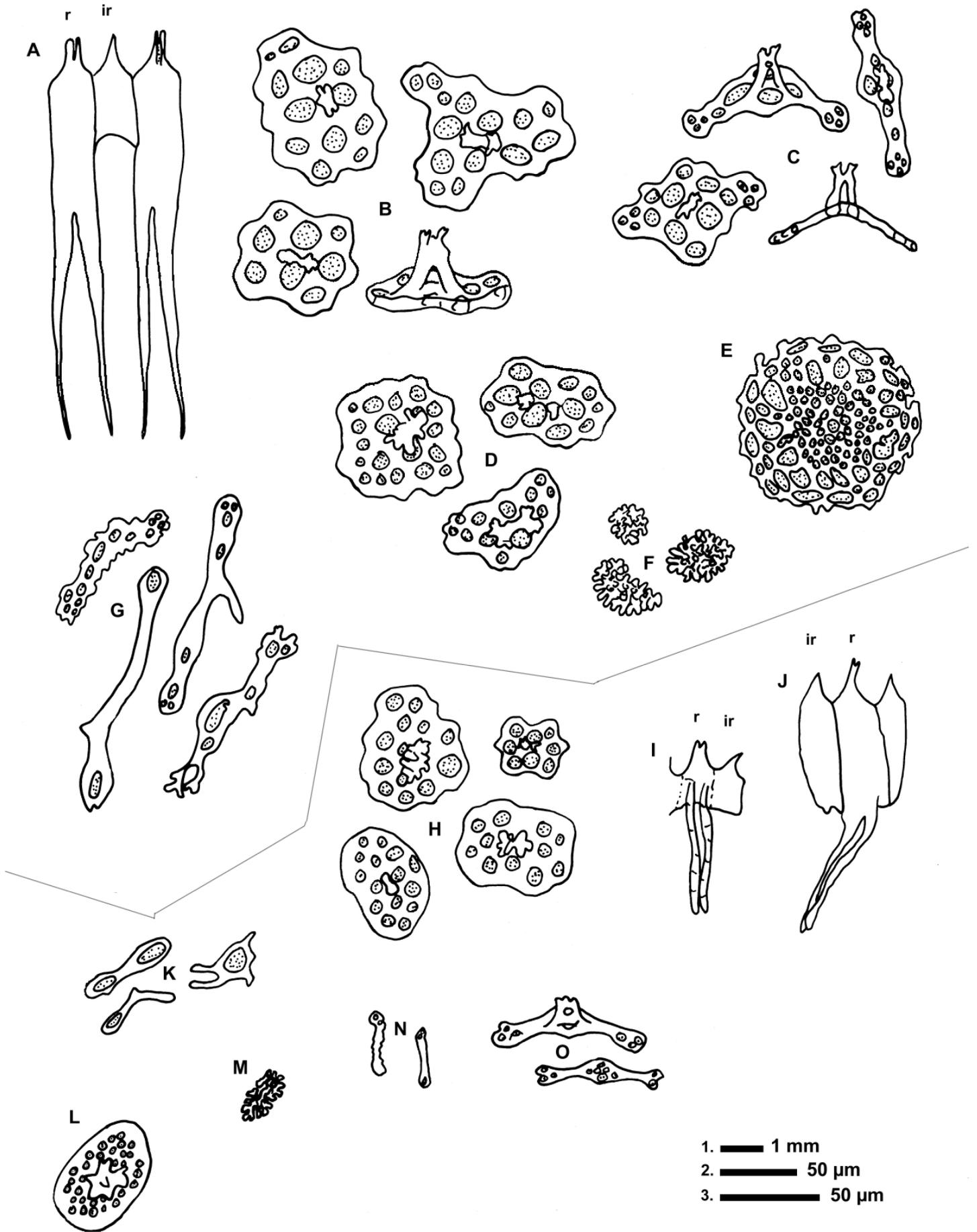
Reys (1959) discussed his species as forming a natural group of closely related species with *T. fusus* and *T. gadeana*, but provides a detailed table highlighting the differences in the diagnostic features of all three species. *T. cherbonnieri* differs from *T. fusus* and *T. gadeana* in the longer processes of its radial plates making up almost 2/3 of the entire ring.

In his description, however, he mentions rosettes in the tentacles, although few in number but his illustration figures only rosettes from the introvert. Thandar's examination of a syntype at the MNHN (EcHh no. 4075) showed tables and rosettes, although few, from the introvert. No deposits were detected in the tentacles, probably dissolved. Reys does mention that most branches of the tentacles are without deposits, which are mostly gathered at the base of the trunk.

FIGURE 13

Thyone cherbonnieri Reys. A. calcareous ring (r= radial plate; ir = interradial plate); B. tables of body wall; C. supporting tables of tube feet; D. tables of introvert; E. end-plate; F. rosettes of introvert; G. rods of tentacles. A = Scale 1; B–F = Scale 2; G = Scale 3. A–C, E, G reproduced from Reys (1959); D, F reproduced from Thandar's examination of a syntype at MNHN.

Thyone dura Koehler & Vaney. H. tables of body wall; I. calcareous ring of small specimen; J. calcareous ring of large specimen; K. spectacle-shaped rods of gonad; L. table of introvert; M. rosette of introvert; N. rods of tentacles; O. supporting tables of tube feet. H, K–O = x 300; I = x 20, J = x 6. Reproduced from Heding (1940).



Thyone dura Koehler & Vaney, 1908

Figure 13H–O

Thyone dura Koehler & Vaney, 1908: 40, pl. III, figs. 9–12; Heding, 1940: 126, text-fig. 38; Panning, 1949: 467; Clark & Rowe, 1971: 182 (dist.); Rowe & Gates, 1995: 315.

Thyone alba H.L. Clark, 1938: 464, fig. 38; 1946: 400; Panning, 1949: 467.

Diagnosis (after Koehler & Vaney, 1908 and Heding, 1940)

Small species, up to 32 mm in length; body attenuating at ends, slightly curved dorsally. Colour white. Tube feet distributed in more or less alternating rows all over the body, more numerous ventrally. Anal teeth present. Tentacles 10, ventral pair reduced. Calcareous ring stout in juveniles (Fig. 13I) becoming tubular in adults with radials bifurcating near posterior border of interradial plates (Fig. 13J); both ring and processes mosaic-like. Body wall ossicles comprise tables with a multilocular, oval to squarish disc; spire two-pillared, ending in a cluster of teeth (Fig. 13H). Tube feet with curved supporting tables; spire low (Fig. 13O). Tentacle deposits slender rods, perforated at the ends, some with a crinkly margin (Fig. 13N). Introvert supported by regular tables with oval discs with rounded, smooth margins and many small perforations (Fig. 13L) and heaps of rosettes (Fig. 13M). Gonads with some irregular spectacle-shaped rods (Fig. 13K).

Type material

Unknown; *T. alba* (*holotype*), MCZ no. 1610.

Type locality

Strait of Hormuz, Persian Gulf (*T. dura*); Broome, Western Australia (*T. alba*).

Habitat

Unknown.

Distribution

Persian Gulf, W India, Pakistan and north Australia (Clark & Rowe, 1971); Australia (Rowe & Gates, 1995), up to 80 m.

Remarks

After examining some material from the Iranian Gulf, Heding (1940) had no doubt that his specimens represented *T. dura* Koehler and Vaney, from the Indian Ocean. With a wider range of specimens, he was able to support H.L. Clark's (1938) assumption that *T. alba* might represent a mature specimen of *T. dura*. Although Heding did note some similarities between the two species, he admitted that the calcareous deposits of both species were so different that they should be left separate. Despite this, he synonymized both species, albeit with some hesitation, perhaps following H. L. Clark.

Panning (1949), retained both species as distinct, apparently overlooking both Heding's and H.L. Clark's descriptions, and hence diagnosing *Thyone* with "rosettes only" in the introvert.

Pawson and Miller (1981) were the first to report a third group of *Thyone* species with both tables and rosettes in the introvert, under the supposition that this group was restricted to the Western Atlantic Ocean, thus they also overlooked the descriptions of *T. dura* and *T. alba* from the Indo-West Pacific.

Thyone exigua (Cherbonnier, 1958) comb. nov.

Figure 14A–K

Havelockia exigua Cherbonnier, 1958: 196: text-fig. 9 a–q; 1965: 658, text-fig. 8 o.

Diagnosis (from Cherbonnier, 1958, amended herein)

Small species, up to 21 mm in length; body cucumber-shaped, anterior end truncated, anal region slightly attenuated. Colour yellowish-white. Body covered with relatively small tube feet, with no radial seriation. Anal teeth not mentioned. Tentacles 10, ventral pair reduced. Calcareous ring high, reaches almost half the body length; radial plates notched anteriorly, bifurcating beyond posterior border of interradial plates, processes long (Fig. 14A). Deposits of body wall eight-holed tables (four primary + four peripheral holes), discs with a scalloped edge; spire two-pillared, ending in 2–3 teeth

(Fig. 14B). Some tables with only 4–5 large holes (Fig. 14F) or conversely with 12–16 perforations of unequal size (Fig. 14E). Discs of the supporting tables of tube feet expanded in the middle, with four central holes and a single perforation at each end (Fig. 14D); end-plates present (Fig. 14C). Tentacle deposits composed of thin rods (Fig. 14J), some crinkly (Fig. 14K), and rosettes (Fig. 14I). Introvert supported by large, irregular, multilocular tables (Fig. 14H) and rosettes (Fig. 14G).

Name-bearing type

MNHN, EcHh no. 1499.

Type locality

Sierra Leone River, Western Sierra Leone.

Habitat

Sticky grey mud.

Distribution

Sierra Leone to the coasts of Dahomey (now Republic of Benin), 25–48 m.

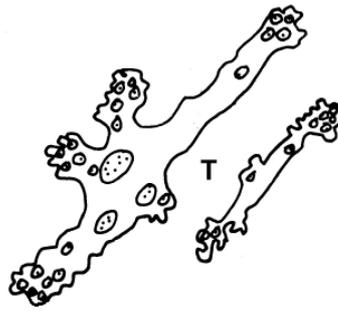
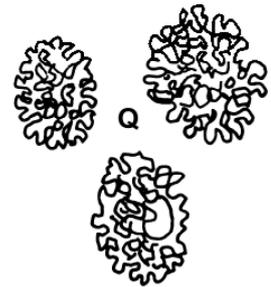
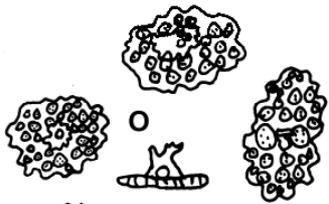
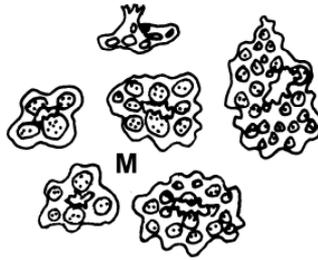
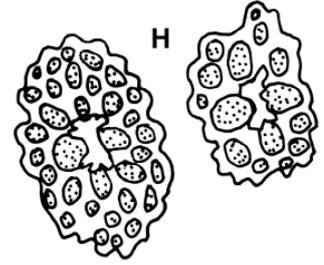
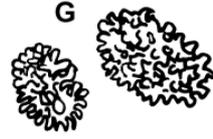
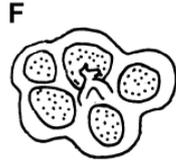
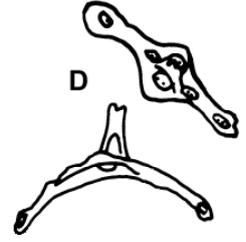
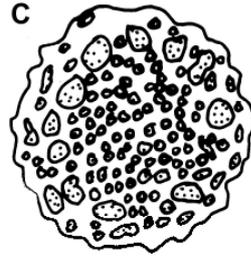
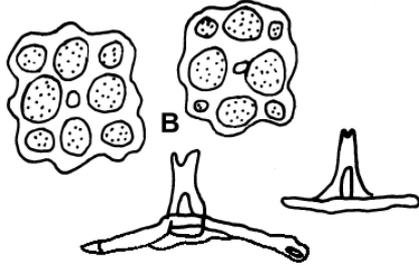
Remarks

Cherbonnier (1958) did not critically examine the nature of the calcareous ring of his new species which he assigned to *Havelockia* probably due to the similarity of the body wall ossicles figured by Ludwig & Heding (1935) for *Thyone venustella*, cited by him as *Havelockia venustella*, clearly not taking note of Panning's (1949) addendum. It differs from the latter species which possesses only plates in the tentacles and introvert. The introvert deposits are here recorded for the first time for this species following an examination of the holotype at the MNHN by Thandar. The ring is tubular, typically of the Thyoninae type, and hence, this species has been here re-assigned to *Thyone*.

FIGURE 14

Thyone exigua (Cherbonnier). A. calcareous ring (x 6) (r= radial plate; ir = interradial plate); B, E, F. tables of body wall; C. end-plate; D. supporting tables of tube feet; G. rosettes of introvert; H. tables of introvert; I. rosettes of tentacles; J. thin rods of tentacles; K. crinkly rods of tentacles. B–F, I–K = Scale 4; G, H = Scale 1. B–F, I–K reproduced from Cherbonnier (1958); G, H reproduced from Thandar's examination of the material at the MNHN.

Thyone gadeana Perrier. L. calcareous ring (x 6); M. tables of body wall; N. supporting tables of tube feet; O. tables of introvert; P. end-plate; Q. rosettes of introvert; R. plates of tentacle branches; S, T. irregular rods of tentacle stalks. M–O, Q–S = Scale 3; P, T = Scale 2. L reproduced from Perrier (1902); M–T reproduced from Madsen & Hansen (1994).



- 1. ————— 25 μm
- 2. ————— 50 μm
- 3. ————— 100 μm
- 4. ————— 100 μm

Thyone fusus (Müller, 1776)

Figure 15A–F

Holothuria fusus O.F. Müller, 1776: 232, pl. 10, figs. 5–6.

Thyone fusus Madsen, 1941: 17, text-figs. 12–16; Madsen & Hansen, 1994: 40, figs. 5, 23–24, map. 10; McKenzie, 1991: 136 (synonymy).

? *Thyone flexus* Hodge, 1867: 44, pl. 10, fig. 2–11.

Diagnosis (amended from Madsen & Hansen, 1994)

Medium-sized species, reaching up to 70 mm in length; body fusiform to spindle-shaped, tapering posteriorly. Colour greyish-white to light brown. Tube feet distributed over entire body, numerous ventrally, scattered dorsally. Anal teeth present. Tentacles 10, ventral pair smaller. Calcareous ring long, tubular, both ring and processes subdivided; radial plates deeply notched anteriorly, extended posteriorly before bifurcating, posterior processes long; interradials prolonged, the two ventral ones slightly longer (Fig. 15A). Deposits of body wall tables with mainly 4–8-holed discs, sometimes with only four primary and 1–3 peripheral ones; spire two-pillared, of moderate height, ending in inconspicuous teeth (Fig. 15B). Supporting tables of tube feet curved (Fig. 15D); end-plates present, delicate in smaller individuals. Tentacle deposits perforated rods and plates (Fig. 15E). Introvert supported by multilocular tables, spires with or without cross-bar (Fig. 15F), and rosettes (Fig. 15C).

Material Examined

Neotype E1279, N.V. for Stormeberget, Drøbak, Oslo Fjord, 25.x.1952, M.E. Hammerstad, det. B. Christiansen (designated herein).

Description of neotype

Specimen young male, spindle-shaped, tapering posteriorly. Length 34 mm, breadth in mid-body 9 mm. Colour in alcohol greyish-white, true colour masked by debris on tube feet. Tube feet non-retractile, distributed over entire body, more numerous ventrally, in two rows per ambulacrum, continuing posteriorly; interambulacra at posterior end naked. Mouth and anus terminal; anus surrounded by five calcareous teeth. Tentacles retracted, dendritic, 10, ventral pair reduced.

Calcareous ring long, tubular, sub-divided, almost two-thirds the length of body. Radial plates anteriorly notched for attachment of retractor muscles; prolonged posteriorly before bifurcation into two processes. Interradials differing slightly in length, prolonged, slightly notched anteriorly and pointed; posterior margin concave. Both ring and processes fragmented (Fig. 15A). Polian vesicle single, large; single stone canal, madreporite rounded, almost bean-shaped. Gonad on its way to maturation, as unbranched tubules, situated on the left mid-portion of body. Retractor muscles thick, branched at point of origin, arising from thick, unpaired longitudinal muscles; the two dorsal retractors originate more anteriorly. Respiratory trees well-branched, left one much longer, reaching anterior tip of body, right one reaching half length of body.

Ossicles of body wall regular 4–8-holed discs, peripheral holes vary from 1–5 (59–83 μm , mean = 68.4 μm , \pm 7.1, n = 20); spire two-pillared, unfused, meeting distally, terminating in a few inconspicuous teeth (Fig. 14B). Tube feet with curved, supporting, two-pillared tables with four large central holes and 1–3 holes at each extremity (88–113 μm , mean = 97.3 μm , \pm 11.1, n = 20) (Fig. 15D); end-plates present, delicate, often broken. Tentacles with slender rods (81–104 μm , mean = 91.7 μm , \pm 9.5, n = 20) sometimes expanded at the ends and perforated, and perforated plate-like rods, some elongated (51–117 μm , mean = 73.1 μm , \pm 23.9, n = 20) (Fig. 15E). Introvert supported with multilocular tables, slightly larger than those of body wall (99.5–119 μm , mean = 107.8 μm , \pm 8.2, n = 20); spire two pillared with a cross-bar, ending in two diverging teeth (Fig. 15F); and rosettes, either elongated or oval to circular (Fig. 15C).

Type material

Lost; *neotype* here designated; will be deposited in the Natural History Museum, Norway.

Type locality

Drøbak, Oslo Fjord.

Habitat

Mud and shell debris.

Distribution

Western Norway from Trondheim Fjord and southwards to coast of Skagerrak and northern Kattegat, North Sea, Faroes, 10–200 (400) m (Madsen & Hansen, 1994) and the British Isles (McKenzie, 1991).

Remarks

Disappointingly, the type specimen of *T. fusus* is in all probability lost. Even Madsen & Hansen (1994) record the holotype as lost. Hence, the establishment of a neotype is imperative since this species is the type species of *Thyone*, a genus here revised.

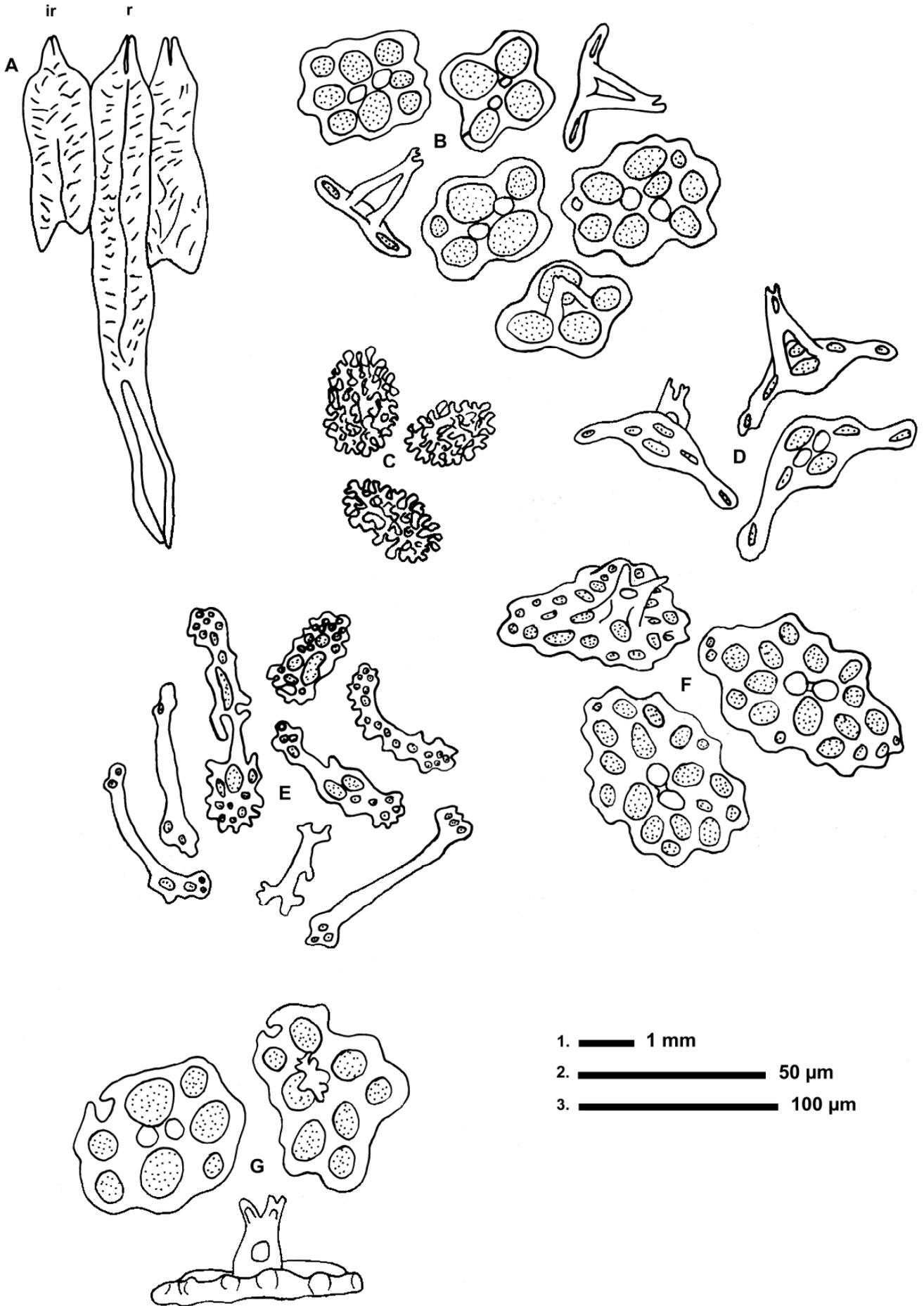
Only four specimens, identified as *T. fusus* and originating from the type locality were received from the Natural History Museum, Oslo, Norway. The largest specimen of the lot was designated as the neotype and was dissected, while the other three specimens were studied only for their body wall ossicles and found to correspond to those of the neotype. Despite the neotype being a young adult, its maturity is not of grave concern, considering the species is well known and is well described by many workers.

Madsen (1941) presented a good argument on the validity of *T. flexus* Hodge citing its affinities to his *T. wahrbergi*, *T. gadeana* and *T. fusus* but was rather indecisive in his conclusion, keeping all four species separate. Madsen & Hansen (1994) mention that the former species has tables and end-plates similar to that of *T. gadeana* but its tentacle deposits were not described. McKenzie (1991) dubiously added *T. flexus* to the synonymy of *T. fusus* but suspected that *T. flexus* may represent the link in distribution between *T. gadeana* and *T. wahrbergi*, the latter of which is now a junior synonym of *T. gadeana*. Though, this remains a speculation since *T. flexus* is known only from the holotype which is also claimed to be lost (McKenzie, 1991 and Madsen & Hansen, 1994). Thandar found some slides of the body wall ossicles of the type of *T. flexus* at the NHMUK, and his illustration of these correspond well with those illustrations for the neotype (Fig. 15G). Thus, *T. flexus* is here also provisionally relegated to the synonymy of *T. fusus*, in view of Madsen's (1941) comment of it representing an abnormal form of *T. fusus*.

FIGURE 15

Thyone fusus (Müller). Neotype (designated herein). A. calcareous ring (ir = interradial plate; r = radial plate); B. tables of body wall; C. rosettes of introvert; D. supporting tables of tube feet; E. rods and plates of tentacles; F. tables of introvert. A = Scale 1; B–F = Scale 3.

Thyone flexus Hodge. G. tables of body wall = Scale 2. Reproduced from Thandar's examination of some slides at the NHMUK.



Thyone gadeana Perrier, 1902

Figure 14L–T

Thyone gadeana Perrier, 1902: 510, pl. 21, figs. 29–31; Panning, 1949: 467; Madsen & Hansen, 1994: 44, text-figs. 25–26, map 11.

Non *T. gadeana* Madsen, 1941: 26, text-fig. 17 (= *T. cherbonnieri* Reys, 1959)

Thyone wahrbergi Madsen, 1941: 5, text-figs. 1–11; Panning, 1949: 467.

Diagnosis (after Perrier, 1902 and Madsen & Hansen, 1994)

Small species, up to 55 mm in length; body fusiform. Colour whitish or very light brownish. Tube feet slender, numerous, scattered all over the body, giving the body a rather villose or hairy appearance when extended. Anal teeth present. Tentacles 10, ventral pair reduced. Calcareous ring long, tubular; both radial and interradial plates anteriorly notched; radials deeply cleft posteriorly or only slightly incised with long paired processes arising almost at the posterior border of the interradial plates; ventral interradial plates longer than the mid-dorsal and dorso-lateral ones (Fig. 14L). Body wall tables with rounded to slightly scalloped edges with usually eight but up to 20 holes; spire two-pillared, low, ending in a variable number of spiny teeth (Fig. 14M). Tube feet with elongated, curved tables with four (2–5) central holes and some distal ones, some perforated along entire length of disc (Fig. 14N); end-plates present (Fig. 14P). Tentacle deposits as slender rods in smaller specimens, much larger, irregular rods in larger individuals (Fig. 14S, T) transforming to irregular perforated plates in distal branches (Fig. 14R). Introvert supported by tables with multilocular discs (Fig. 14O), more elongated at the base of tentacles, and elaborate rosettes (Fig. 14Q).

Name-bearing type

Probably at MNHN.

Type locality

Gulf of Cadiz, Atlantic coast of southern Spain, 106 m.

Habitat

Infaunal, in fine sand with mud, often intermixed with gravel.

Distribution

Western Norway from Trondheim Fjord southwards to Swedish coast of Skagerrak to Bay of Biscay, Gulf of Cadiz, western Mediterranean, 20–1045 m (Madsen & Hansen, 1994).

Remarks

Perrier (1902) separated his species from the type species with which it shares many characters, deviating from it in its longer calcareous ring, rather fine, more numerous tube feet and the slightly different body wall table discs which are more perforated and bear shorter spires than those of *T. fusus*.

Madsen (1941) erroneously referred some material to *T. gadeana* which Reys (1959) correctly assigned to a new species, *T. cherbonnieri*. In the same paper, Madsen described a new species, from Skagerrak, which he named *T. wahrbergi*. He then claimed that *T. gadeana* was an intermediate form between *T. fusus* and the newly erected *T. wahrbergi*, whose introvert deposits are similar to those of *T. fusus* while those of the body wall match those of *T. wahrbergi*. Reys (1959) rightfully relegated *T. wahrbergi* to the synonymy of *T. gadeana* following Cherbonnier's (unpubl.) notes based on the presence of large rods at the base of the tentacles in the type of *T. gadeana* similar to those figured by Madsen for *T. wahrbergi*. McKenzie (1991) with only slight hesitation concluded that both species may be synonymous, erroneously listing *T. gadeana* as a possible synonym of *T. wahrbergi* and not vice versa. Madsen & Hansen (1994) agreed with Reys's conclusion and listed *T. wahrbergi* under the synonymy of *T. gadeana*, which is here adopted.

Thyone guttata (Cherbonnier, 1958) comb. nov.

Figure 16A–K

Havelockia guttata Cherbonnier, 1958: 193, text-fig. 8 a–q.

Diagnosis (Cherbonnier, 1958, amended herein)

Small species, up to 20 mm in length; body cylindrical, with attenuated anal end. Colour yellowish to greyish-white mottled with many dark brown spots. Tube feet distributed throughout the whole body with no radial seriation. Anal teeth present. Tentacles 10, ventral pair reduced. Calcareous ring tubular, mosaic-like; radial plates anteriorly bifid, with long paired posterior processes arising at posterior border of interradial plates; interradials of unequal length with triangular anterior projections (Fig. 16A). Deposits of body wall scarce, mainly tables with discs of four large central holes, and four peripheral ones; spire two-pillared, ending in up to eight teeth (Fig. 16B). Anal tables larger, discs more perforated; spires ending in numerous teeth (Fig. 16C). Tube feet deposits also few, comprising rods; those of anal region tables with curved discs, spire also two-pillared, with denticulate tip (Fig. 16D); small end-plates present (Fig. 16E). Tentacle deposits as slender rods (Fig. 16H), crinkly rods (Fig. 16G) and rosettes (Fig. 16I); rod-like plates rare (Fig. 16F). Introvert supported by tables similar to those of body wall (Fig. 16J) and rosettes (Fig. 16K).

Name-bearing type

MNHN, EcHh no. 4087

Type locality

Sierra-Leone.

Habitat

Unknown.

Distribution

Known only from type locality, 25–56 m.

Remarks

Cherbonnier (1958) commented that this species belongs within the group of species that have very few deposits in the body wall, namely *Havelockia inermis* (Heller) and *Havelockia villosa* (Semper), not realising that Panning (1949) had re-

assigned both these species back into *Thyone*. The illustration of the calcareous ring of the species indicates a very long, tubular ring, which was confirmed by Thandar upon examination of the holotype, and judging from this and the long paired processes to the radial plates this species fits well within *Thyone*, and is thus here re-assigned to this genus.

The composition of the introvert deposits is here recorded for the first time and hence the diagnosis of the species is amended to accommodate this.

***Thyone inermis* Heller, 1868**

Figure 16L–N

Thyone inermis Heller, 1868: 78, pl. III, fig. 12; Koehler, 1921: 167, text-fig. 123; Mortensen, 1927: 408; McKenzie, 1991: 141, text-fig. 5 a–h; Bohn, 2004: 517.

? *T. elegans* Norman, 1869: 317.

Uroxia aurantiaca Costa, 1869: 58.

T. aurantiaca Hérouard, 1889: 684.

Non *T. inermis* Deichmann, 1947: 86; Pawson & Miller, 1981: 394.

Havelockia inermis Panning, 1949: 466.

Diagnosis (after Heller, 1868 and McKenzie, 1991)

Small species, holotype 25 mm in length; body spindle-shaped, narrowed at each extremity. Colour of holotype yellowish grey, other specimens pinkish, rather transparent. Tube feet numerous, scattered over the entire body. Tentacles 10, ventral pair reduced. Deposits of body wall lacking except for tube feet end-plates and small, regular, circular two-pillared tables at the posterior end (Fig. 16N). Tentacles and introvert with larger tables than those of body wall (Fig. 16L), some small without spires, rosettes (Fig. 16O), numerous rods and flat perforated plates (Fig. 16M).

Type material

IZL 9384 (*syntype*).

Type locality

Lesina, Italy, 18–37 m.

Habitat

Unknown.

Distribution

British Isles, Mediterranean and the Atlantic coasts of France, 0–30 m (according to McKenzie, 1991).

Remarks

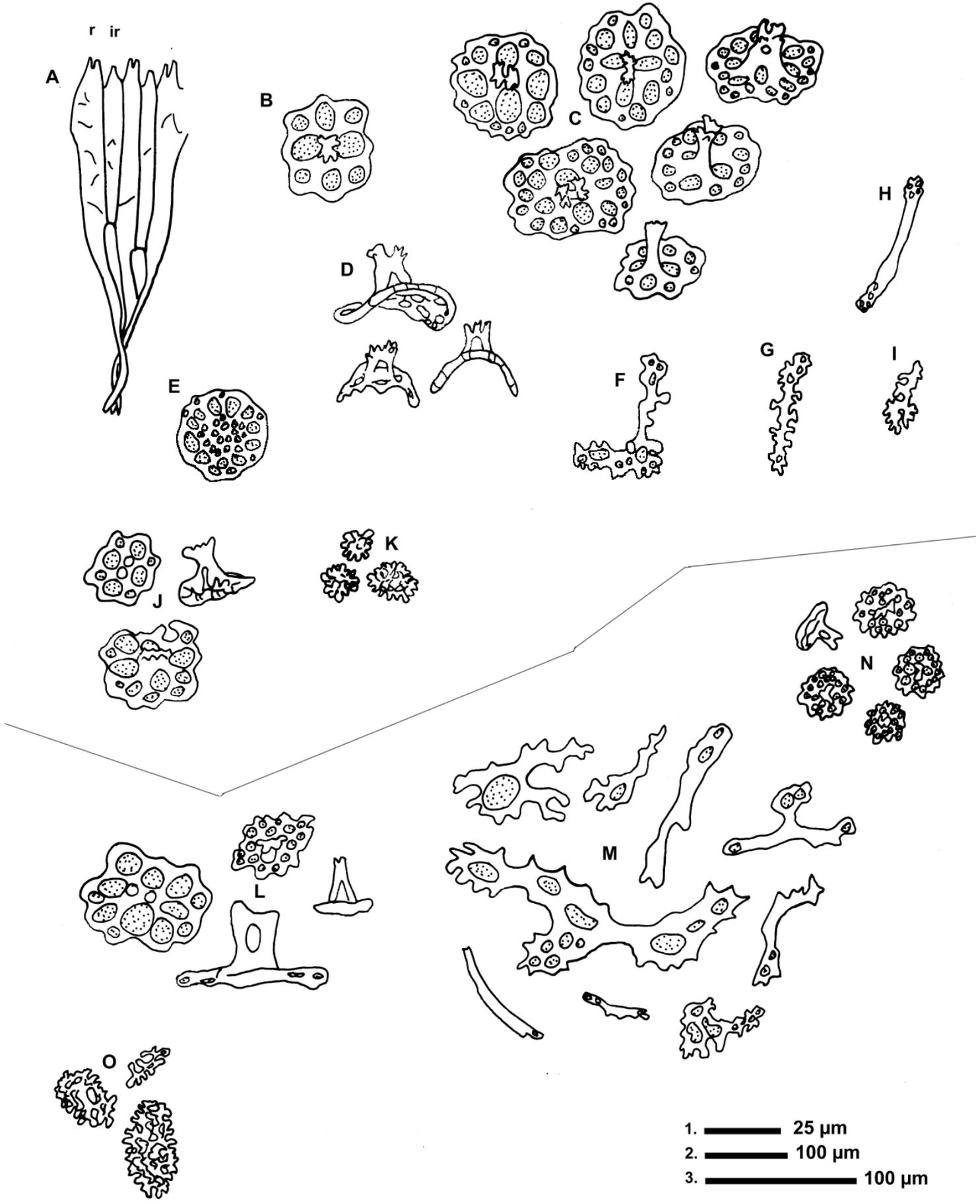
Heller's (1868) description of *T. inermis* is rather brief, not mentioning the number and size of the tentacles or the form of the calcareous ring, but he correctly classified the species within *Thyone*. Deichmann (1930) dubiously recorded a *fuscus*-like *Thyone* from the West Indies which she classified as *Thyone fuscus*, but in 1947 referred these forms to *T. inermis*, ignoring Madsen's (1941) decision to regard them as a new species (see remarks for *T. deichmannae*). In this paper she also synonymized *T. roscovita* Hérouard with *T. inermis* and attempted to separate the latter species from the typical northern European *fuscus* by the possession of deeply cleft radial plates and the greater tendency to reduce its ossicles with age. McKenzie (1991), the most recent reviser of the north European dendrochirotes, critically disregarded the synonymization of *T. roscovita* with *T. inermis* citing that the former species lacks deeply cleft radials in its calcareous ring. Furthermore, both species differ in the presence of small tables at the posterior end of *T. inermis*. The anal region of *T. roscovita* comprises perforated branched rods and large perforated plates, and anal teeth are present. The presence of anal teeth in *T. inermis* is unknown as neither Heller nor McKenzie report on them.

Examination of a syntype of *T. inermis* by Bohn (2004) indicated a completely decalcified, fragmented specimen. However, a second specimen labelled as "*Thyone*" thought to represent *T. inermis* by Bohn, has the ossicle assemblage of *T. inermis* as described by McKenzie (1991)

FIGURE 16

Thyone guttata (Cherbonnier). A. calcareous ring (r = radial plate; ir = interradial plate) (x 4); B. table of body wall; C. tables of anal region; D. supporting tables of tube feet; E. end-plate; F. rod-like plate of tentacles; G. crinkly rod of tentacles; H. slender rod of tentacles; I. rosette of tentacles; J. tables of introvert; K. rosettes of introvert. B–I = Scale 3; J, K = Scale 1. A–I reproduced from Cherbonnier (1958); J, K reproduced from Thandar's examination of the material at the MNHN.

Thyone inermis Heller. L. large and small tables of tentacles and introvert; M. large rods and plates of tentacles; N. tables of posterior region; O. rosettes of tentacles and introvert. L–O = Scale 2. Reproduced from McKenzie (1991).



Thyone infusca Cherbonnier, 1954

Figure 17A–I

Thyone infusca Cherbonnier, 1954: 119, fig. 2 (1–13); Day, et al. 1970: 83; Thandar 1990: 215, fig. 7 a–c.

Diagnosis (after Thandar, 1990, amended herein)

Small species, holotype 25 mm in length; body cucumber-shaped. Colour, in alcohol, chocolate brown. Tube feet numerous, distributed over entire body. Anal teeth present. Tentacles 10, ventral pair smaller. Calcareous ring tubular; radial plates broken into two series of large pieces, interradials in a single series of three large pieces; posterior processes of radials almost as long as height of ring and arise at posterior level of the interradial plates (Fig. 17A). Deposits of body wall smooth, elongate (40–90 μm) plates with usually four central holes and 1–2 minute holes at each end (Fig. 17B). Supporting tables of tube feet tables slightly curved, elongate (80–100 μm), bearing four central holes and usually an additional hole at each end; spire short (10–30 μm), two-pillared, with 4–8 blunt teeth, or spire reduced to knobs on surface of discs (Fig. 17E); end-plates present (120–165 μm) (Fig. 17H). Tentacle deposits small perforated rods (Fig. 17C) and rosettes (Fig. 17D). Introvert supported by well developed two-pillared tables with 4–10 perforations (Fig. 17G) and few rosettes or rosette-like rods (Fig. 17F).

Name-bearing type

MNHN, EcHh no. 1482.

Type locality

False Bay, WCP, South Africa.

Habitat

Rock.

Distribution

Known only from False Bay, 8–9 m.

Remarks

Thandar examined the well preserved holotype of *T. infusca* and concluded that although the specimen was still immature, the gonads are in the process to maturation. Cherbonnier (1954a) separated his species from the then known southern African species of *Thyone* on the presence of the reduced body wall plates, which although lacking any remains of a spire, may be regarded as such since well-developed curved tables are present in the anal region, tube feet and introvert, supporting its status in *Thyone*. Unfortunately, these deposits in the type are on their way to corrosion. Thandar (1990) suspected that, based upon the apparent reduction of the body wall ossicles, this species may be conspecific with the South African, *T. aurea*, which is known to lose its ossicles with age. Since similar sized specimens of *T. aurea* contain well developed tables in the body wall, he left both species separate. Furthermore, the introvert deposits of *T. aurea* show a reduction of table-like deposits with age and lack any rosettes or derivatives of these. The holotype remains the only record of *T. infusca*; hence more material is required to determine its relationship with other species.

Thyone micra H.L. Clark, 1938

Figure 17J–N

Thyone micra H.L. Clark, 1938: 468, text-fig. 41; Panning, 1949: 467; Rowe & Gates, 1995: 315.

Diagnosis (after H.L. Clark, 1938, amended herein)

Small species, holotype measuring 17 mm in length; body elongated, cylindrical. Colour in alcohol white, tentacles white; colour in life light brown. Tube feet small, numerous, more or less in regular rows near extremities. Anal teeth absent. Tentacles 10, ventral pair reduced. Calcareous ring tubular, sub-divided; radial plates slightly notched anteriorly, slightly incised posteriorly, processes also sub-divided (Fig. 17J). Body wall ossicles comprise tables with stout elongated disc, with four perforations; spire two-pillared, ending in two clusters, each with 2–3 teeth (Fig. 17K). Tube feet with curved, supporting rods and tables (Fig. 17L); end-plates rather large. Stalk of

tentacles with numerous rosettes, branches with few, scattered, slender, supporting rods. Introvert supported by multilocular tables (Fig. 17N) often becoming merely perforated plates, and rosettes (Fig. 17M).

Name-bearing type

MCZ, no. 1616.

Type locality

Pearl Shoal, Broome, Western Australia.

Habitat

Sandy mud bottom.

Distribution

NW coast, Western Australia; Dampier Archipelago to Broome, 0–15 m.

Remarks

H.L. Clark (1938) neither illustrated the calcareous ring of his new species nor examined the tentacle and introvert deposits. Thandar studied the holotype which contains a very mosaic-like tubular ring typical of *Thyone*, as described by H.L. Clark. Unfortunately, the deposits from the tube feet, tentacles and a large part of the introvert are dissolved. Nevertheless, Thandar was able to identify some introvert ossicles which comprised large, perforated table discs and rosettes. Moreover, the tentacles contained rosettes similar to those of the introvert and some rods.

Thyone okeni Bell, 1884

Figure 17O–T

Thyone okeni Bell, 1884: 149, pl. IX, fig. D; H.L. Clark, 1921: 167; 1946: 402; Clark & Rowe, 1971: 182 (dist.); Rowe & Doty, 1977: 226, fig. 8 a; Rowe, 1982: 462; Rowe & Gates, 1995: 316.

Thyone venusta (non Selenka, 1868); Thandar, 1990: 214 (partim).

Diagnosis (after Bell, 1884, amended herein)

Medium-sized species, reaching up to 85 mm in length; body elongated. Colour in alcohol dark brown. Tube feet closely packed and distributed over the whole body. Anal teeth absent. Tentacles 10, ventral pair reduced. Calcareous ring tubular and sub-divided into large mosaic-like pieces; radial plates prolonged before bifurcation, processes broken into several large pieces (Fig. 17O). Calcareous deposits in body wall lacking, except for tube feet end-plates (Fig. 17S). Tentacle deposits characteristically large rods, expanded at the ends with many perforations (Fig. 17P), rosette-like rods and rosettes (Fig. 17T). Introvert supported by tables with large multilocular discs and short spire (Fig. 17Q) and rosettes (Fig. 17R).

Type material

NHMUK 1881.10.26.203 (*syntypes*, 2 spec.)

Type locality

Port Jackson, New South Wales, Australia.

Habitat

Cryptic, found under rock fragments.

Distribution

Port Jackson (see Rowe and Gates, 1995), 0–30 m.

Remarks

Bell (1884) did not comment on the nature of the tentacles of his new species, nor did Thandar upon his examination of the type material at the NHMUK. However, since Bell classified the species within *Thyone*, the tentacle number is assumed to be ten with the ventral pair reduced.

Because of the absence of deposits except for tube feet end-plates, Thandar (1990) erroneously synonymized *T. okeni* with *T. venusta* Selenka. However, subsequent examination of the tentacle and introvert deposits of *T. okeni* (here reported for the first

time) he now regards both species as distinct (Thandar pers. comm.), as listed by Rowe & Gates (1995).

***Thyone papuensis* Théel, 1886**

Figure 18A–H

Holothuria dietrichii Ludwig, 1875: 105, fig. 31 [not listed as accepted name to avoid resurrection of an unused name (Rowe & Gates, 1995)].

Thyone fusus var. *papuensis* Théel, 1886: 92, pl. 17, fig. 1.

Thyone castanea Lampert, 1889: 836, fig 8.

Thyone papuensis H.L. Clark, 1921: 167; 1932: 221; Clark & Rowe, 1971: 182 (dist.); A.M. Clark, 1982: 489, 495, fig. 2; Cannon & Silver, 1987: 32, fig. 9 g; Rowe & Gates, 1995: 316; Liao & Clark, 1995: 504, text-fig. 306; Liao, 1997: 203, fig. 119; Liao & Pawson, 2001: 79, text-fig. 79.

Diagnosis (after Théel, 1886 and Liao & Pawson, 2001)

Small species, up to 50 mm in length; body spindle-shaped. Tube feet numerous, scattered all over body. Anal teeth present. Tentacles 10, ventral pair reduced. Calcareous ring long, tubular, both radial and interradial plates composed of mosaic of small pieces; radials prolonged before bifurcation, processes short to medium in length, also sub-divided, (Fig. 18A, D). Ossicles in body wall sparsely scattered small, two-pillared tables with oblong disc with four large and four small perforations; spire low, with 2–4 apical teeth (Fig. 18B, C). Tube feet with curved, supporting tables (Fig. 18E); end-plate present, large. Tentacle deposits thin, slender rods (Fig. 18H). Introvert supported by mulberry-like, oval rosettes (Fig. 18F) and two-pillared tables with numerous holes (Fig. 18G).

Name-bearing type

NHMUK, 1886.10.2.107 (*holotype* of *T. fusus* var. *papuensis*).

Type locality

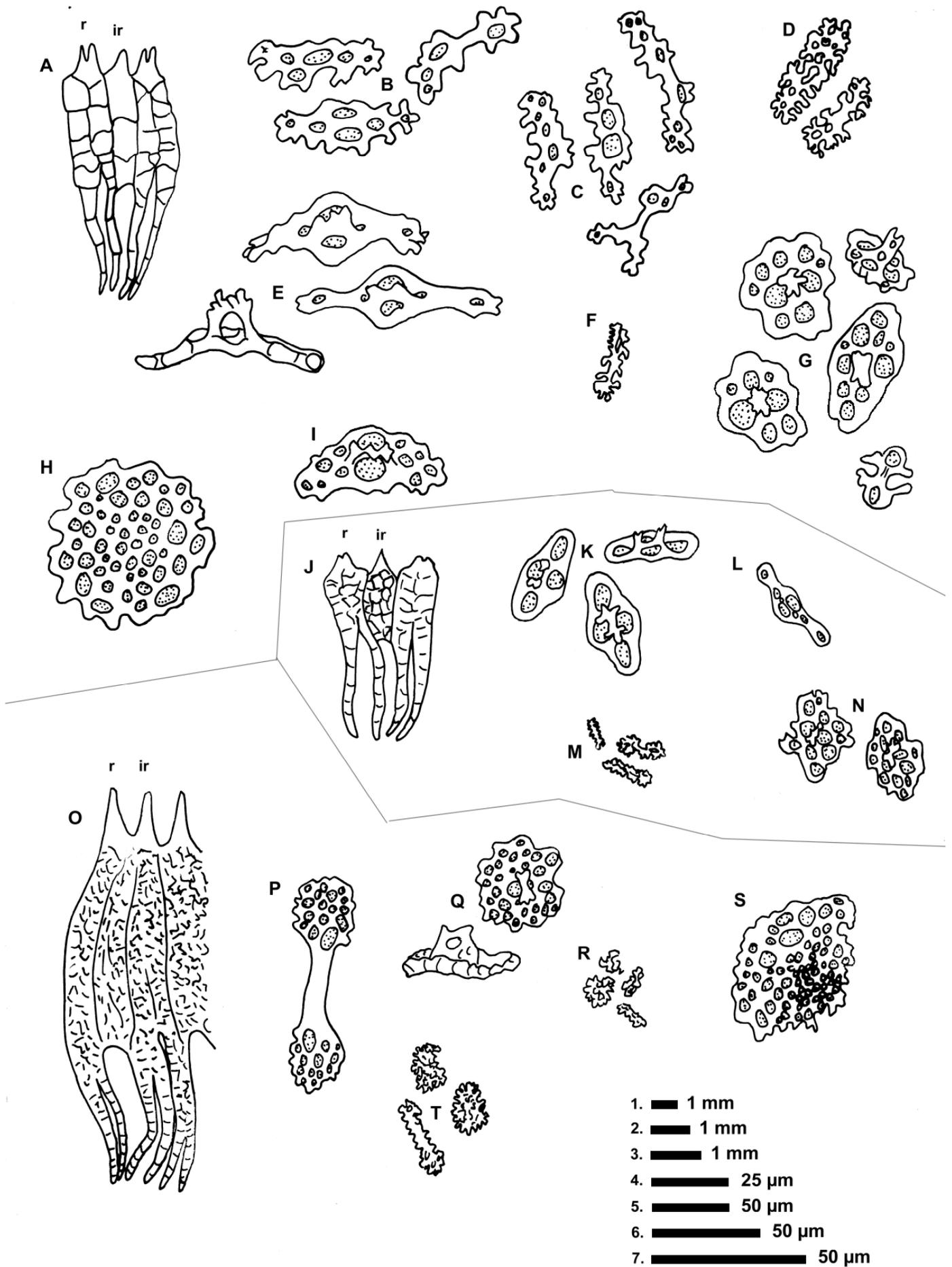
Torres Strait, between Australia and Papua New Guinea.

FIGURE 17

Thyone infusca Cherbonnier. A. calcareous ring (r = radial plate; ir = interradial plate); B. plates of body wall; C. rods of tentacles; D. rosettes of tentacles; E. supporting tables of tube feet; F. rosette/rosette-like rod of introvert; G. tables of introvert; H. end-plate; I. table of anal feet. A = Scale 1; B–E, I = Scale 6; H = Scale 5; F, G = Scale 7. A–E, H, I reproduced from Cherbonnier (1954a); F, G reproduced from Thandar's examination of the material at the MNHN.

Thyone micra H.L. Clark. Holotype. J. calcareous ring (r = radial plate; ir = interradial plate); K. tables of body wall; L. supporting table of tube feet; M. rosettes of introvert; N. tables of introvert. J = Scale 3; K–N = Scale 4. Reproduced from Thandar's examination of the material from the MCZ.

Thyone okeni Bell. Type. O. calcareous ring; P. rod of tentacles; Q. tables of introvert; R. rosettes of introvert; S. part of end-plate; T. rosettes of tentacles. O = Scale 2; P–T = Scale 5. Reproduced from Thandar's examination of the material at the NHMUK.



Habitat

Unknown.

Distribution

Western Australia to the Gulf of Tonkin and Yellow Sea, China; Indo-West Pacific Ocean, 0–60 m.

Remarks

Théel (1886) commented that the specimen from Torres Strait resembled so much the northern European *fuscus* that he considered this Indo-West Pacific form as a variety of the type species, noting the superior length of the calcareous ring, longer in the *papuensis* variety, and the predominantly eight-holed tables in the body wall. This specimen, present at the NHMUK, contains a note stating that the specimen is completely decalcified and according to Thandar, also lacks a calcareous ring.

Another specimen from the NHMUK studied by Thandar and identified by A. M. Clark as *T. papuensis*, lacked deposits from the body wall except for the supporting tables and end-plates in the tube feet. In addition, the introvert contained only tables and no rosettes. However, Liao & Clark (1995) and Liao & Pawson (2001) both mention rosettes in the introvert. The calcareous ring is similar to that illustrated by Théel and the fragmentation is obvious (Fig. 18D).

Liao & Pawson's (2001) material from China had deposits similar to those described by Théel, however, the radial plates of the calcareous ring illustrated by Théel appears to be deeply cleft when compared to that illustrated by Liao & Pawson (2001).

***Thyone pedata* Semper, 1868**

Figure 18I & J

Thyone pedata Semper, 1868: 67; Clark & Rowe, 1971: pl. 29, fig. 17; Liao & Clark, 1995: 505, text-fig. 307; Lane et al., 2000: 491 (dist).

Diagnosis (after Semper, 1868 and Liao & Clark, 1995)

Small species, up to 22 mm in length; body fusiform, more or less elongated, tapering at each extremity. Ventral tube feet longer, more crowded than dorsal feet. Anal teeth absent. Tentacles 10, ventral pair reduced. Calcareous ring mosaic-like; radial plates with long bifurcate posterior processes. Body wall tables with an irregular disc (Fig. 18I) with numerous holes; spire high, two-pillared, ending in 2–4 teeth. Tube feet with curved, supporting tables (Fig. 18J). Tentacle deposits numerous stout rods. Introvert supported by tables similar to those of body wall and small heaps of rosettes.

Name-bearing type

Unknown.

Type locality

China Sea.

Habitat

Unknown.

Distribution

Gulf of Tonkin, South China Sea, 55 m.

Remarks

Semper's (1868) brief description of the single holotype collected from the China Sea does not mention the nature of the body wall deposits nor does he illustrate them or any other characteristic features of this species. Clark & Rowe (1971) omitted this species from their distribution list of the Indo-West Pacific fauna but included a light micrograph of a slide prepared by Semper (1868) and assumed to be taken from the type material. Liao & Clark's (1995) specimens from the Gulf of Tonkin are the only subsequent record of the species since the holotype. Judging from Semper's slide and the tables illustrated by the latter authors and the type locality, it is with little doubt that the Gulf of Tonkin specimens represent *T. pedata*. Liao & Clark provide a rather descriptive account in terms of the morphology and ossicle assemblage of the species

but draw only a few ossicles from the body wall and tube feet and fail to illustrate the calcareous ring.

Thyone purpureopunctata Liao & Pawson, 2001

Figure 19A–F

Thyone purpureopunctata Liao & Pawson, 2001: 79, text-fig. 17, 20 L.

Diagnosis (after Liao & Pawson, 2001)

Medium-sized species, up to 60 m in length; body spindle-shaped, more tapered posteriorly than anteriorly. Colour in alcohol greyish-white with numerous scattered purple spots. Tube feet delicate, numerous, scattered all over the body. Anal teeth absent. Tentacles 10, ventral pair smaller. Calcareous ring tubular, composed of a mosaic of small pieces; radial plates prolonged before bifurcation into short posterior processes (Fig. 19B). Ossicles in body wall two-pillared tables with irregularly elongated, multilocular discs; spire low, arched, terminating in a conical solid point (Fig. 19A). Tube feet with curved, elongated supporting tables; spire of fused high pillars, ending in a conical point (Fig. 19C); end-plates present. Tentacle deposits rosettes and slender, supporting rods of various sizes (Fig. 19D). Introvert supported by rosettes (Fig. 19E) and two-pillared tables with multilocular discs (Fig. 19F).

Name-bearing type

IOAS, E1059.

Type locality

Off Sanya, Hainan Island, China.

Habitat

Muddy bottom.

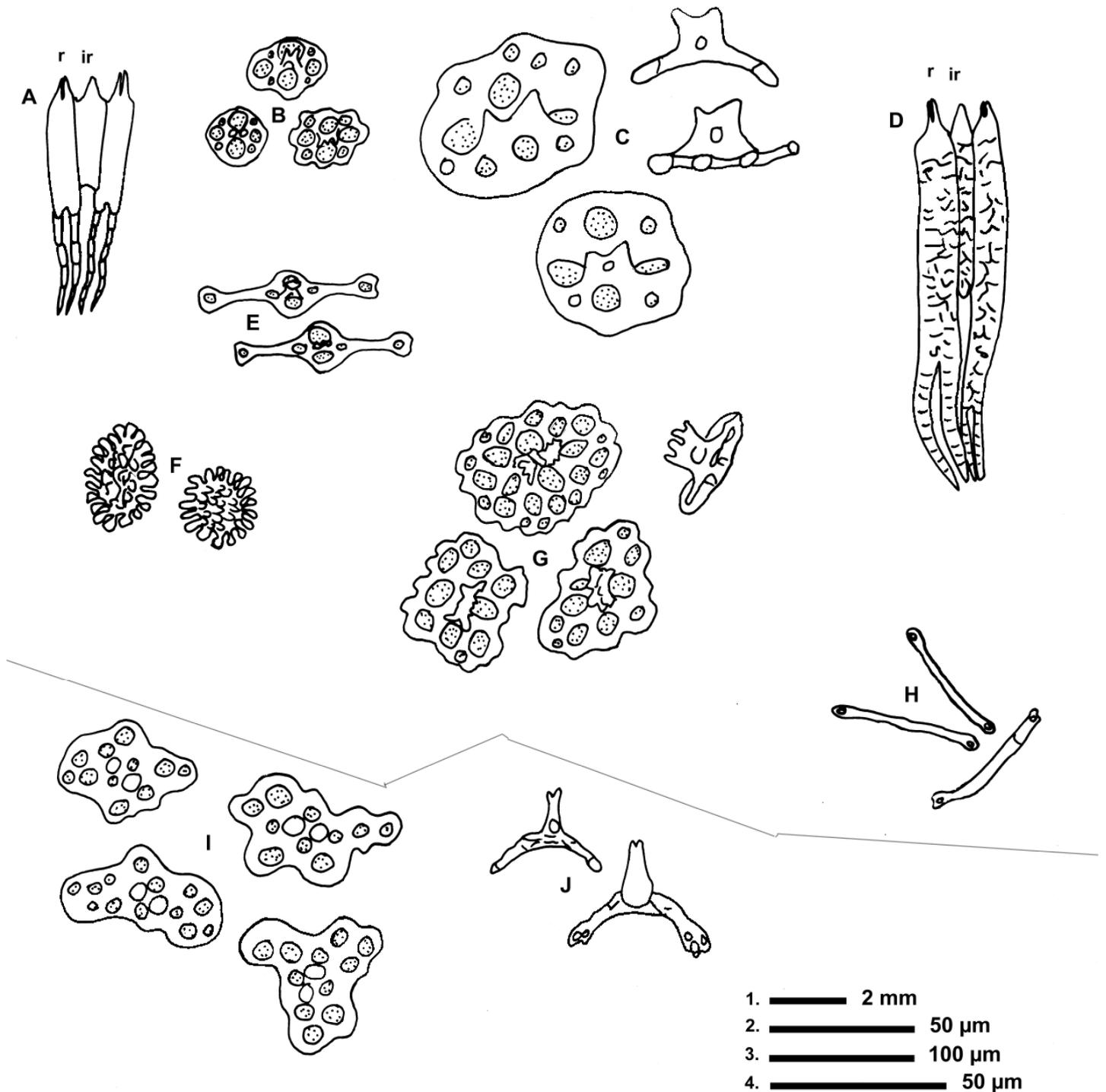


FIGURE 18. *Thyone papuensis* Théel. A. calcareous ring (r = radial plate; ir = interradial plate) (x 5); B, C. tables of body wall; D. calcareous ring of voucher specimen; E. supporting tables of tube feet; F. rosettes of introvert; G. tables of introvert; H. rods of tentacles. B, D (no scale given by Théel); C, F = Scale 2; D = Scale 1; G, H = Scale 4. A, B, D reproduced from Théel (1886); C, F reproduced from Liao & Pawson (2001); G, H reproduced from Thandar's examination of the NHMUK material. *Thyone pedata* Semper. I. tables of body wall; J. supporting tables of tube feet. I, J = scale 3. Reproduced from Liao & Clark (1995).

Distribution

Off Sanya, Hainan Island to Gulf of Tonkin, China, 30.5–60 m.

Remarks

This species was established on its distinctive greyish-white colour with numerous scattered purple spots and its rather thick body wall tables with low spires resembling an arch. Liao & Pawson (2001) compared their species to *T. villosa* Semper with which it shares a slight resemblance in terms of its body wall tables. However, *T. villosa* lacks simple, slender rods in the tentacles and its table discs are much larger as seen in those illustrated from the holotype by Thandar (2006).

Thyone roscovita Hérrouard, 1889

Figure 19G–J

Thyone roscovita Hérrouard, 1889: 682; Koehler, 1921: 166, text-figs. 121 & 122; McKenzie, 1991: 139, text-fig. 4 a–f.

? *T. elegans* Norman, 1869: 317.

Diagnosis (after McKenzie, 1991)

Large species, reaching up to 200 mm in length; body broader centrally, tapering at each extremity. Colour variable, ranging from dirty white to rosy grey, with dense or scattered purplish brown pigments. Tube feet scattered over the whole body; confined to ambulacra in very small specimens. Anal teeth present. Tentacles 10, ventral pair reduced. Deposits from body wall lacking except for tube feet end-plates (Fig. 19I). Anal region comprise perforated, branched rods and large, flat perforated plates (Fig. 19J). Tentacles lack supporting rods. Introvert often without deposits, when present introvert and tentacles comprise rosettes (Fig. 19H), small rods and two-pillared tables with a perforated spire top (Fig. 19G).

Name-bearing type

Unknown.

Type locality

Roscoff, France.

Habitat

Found commonly in rock crevices and under stones with *Aslia* and *Pawsonia*, along clumps of *Modiolus* or raft-cultured *Mytilus* (McKenzie, 1991).

Distribution

Atlantic coast of France, Strangford Lough, west and north coasts of Ireland, from near Oban, Loch Nevis and the Inner Hebrides, 0–40 m (McKenzie, 1991).

Remarks

McKenzie (1991) provides a rather detailed discussion on the comparison of *T. roscovita* and *T. inermis* which, according to him, appear so similar that they are often misidentified with each other. He believes that *T. inermis* is distributed mainly on the southern coast of England and therefore questioned the synonymization of *T. elegans* Norman (Koehler, 1921; Mortensen, 1927) with that of *T. inermis* suggesting that *T. elegans* is perhaps a synonym of *T. roscovita* based upon its distribution. Alternatively, McKenzie presents a good argument highlighting *T. elegans* to be a distinct species based upon its colouration and complete lack of ossicles, but with the lack of more material he is inclined to dubiously add the former species to the synonymy of both *T. inermis* as well as *T. roscovita*. McKenzie, following Koehler (1921), separates both *T. roscovita* and *T. inermis* by the presence of tables at the posterior end in the latter species.

Regrettably, no illustration of the calcareous ring of this species is given by Hérouard (1889) nor subsequent workers. This species is well known and distinct from other species of *Thyone* which lack deposits. It is characterized by possessing perforated, branched rods and large, flat perforated plates in the anal region.

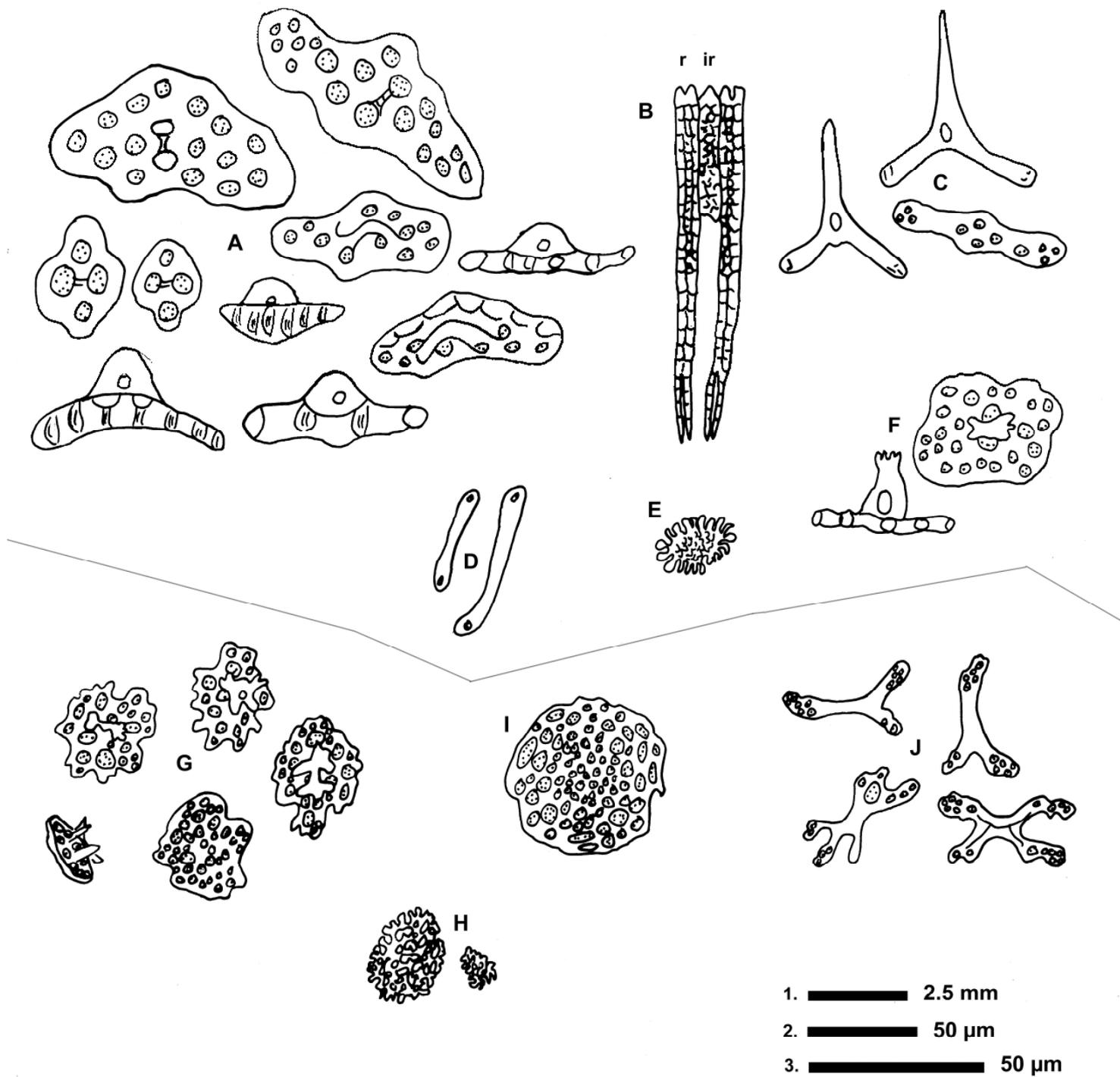


FIGURE 19. *Thyone purpureopunctata* Liao & Pawson. A. tables of body wall; B. calcareous ring (r = radial plate; ir = interradial plate); C. supporting tables of tube feet; D. rods of tentacles; E. rosette of introvert; F. tables of introvert. A, C–F = Scale 3; B = Scale 1. Reproduced from Liao & Pawson (2001).

Thyone roscovita Hérouard. G. tables of tentacles and introvert; H. rosettes of tentacles and introvert; I. end-plate; J. rods of posterior end. G–J = Scale 2. Reproduced from McKenzie (1991).

Thyone sinensis Liao & Pawson, 2001

Figure 20A–G

Thyone sinensis Liao & Pawson, 2001: 83, text-figs. 18, 20 M.

Diagnosis (after Liao & Pawson, 2001)

Small species, reaching up to 50 mm in length; body U-shaped. Colour in alcohol white with yellowish tinge, especially ventrally; tube feet orange, numerous, apparently non-retractile, delicate, more numerous ventrally, with tendency to be arranged in bands on ambulacra. Anal teeth absent. Tentacles 10, ventral pair smaller. Calcareous ring tubular, composed of relatively large pieces; radial plates prolonged posteriorly before bifurcation (Fig. 20A). Ossicles in body wall two-pillared tables with irregular, multilocular discs; spire low, ending in four teeth (Fig. 20B). Tube feet with elongate, curved supporting tables; spire high with 3–4 cross-bars ending in six teeth (Fig. 20C); well-developed end-plates present (Fig. 20D). Tentacle deposits supporting perforated plates of varying size (Fig. 20G). Introvert supported by tables with multilocular discs (Fig. 20E) and rosettes (Fig. 20F).

Name-bearing type

IOAS, E1065.

Type locality

Dongshan, Fujian Province, China.

Habitat

Muddy bottom.

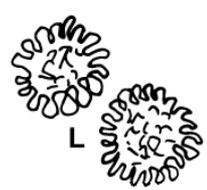
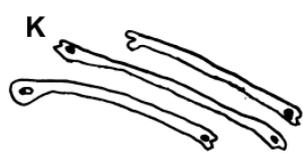
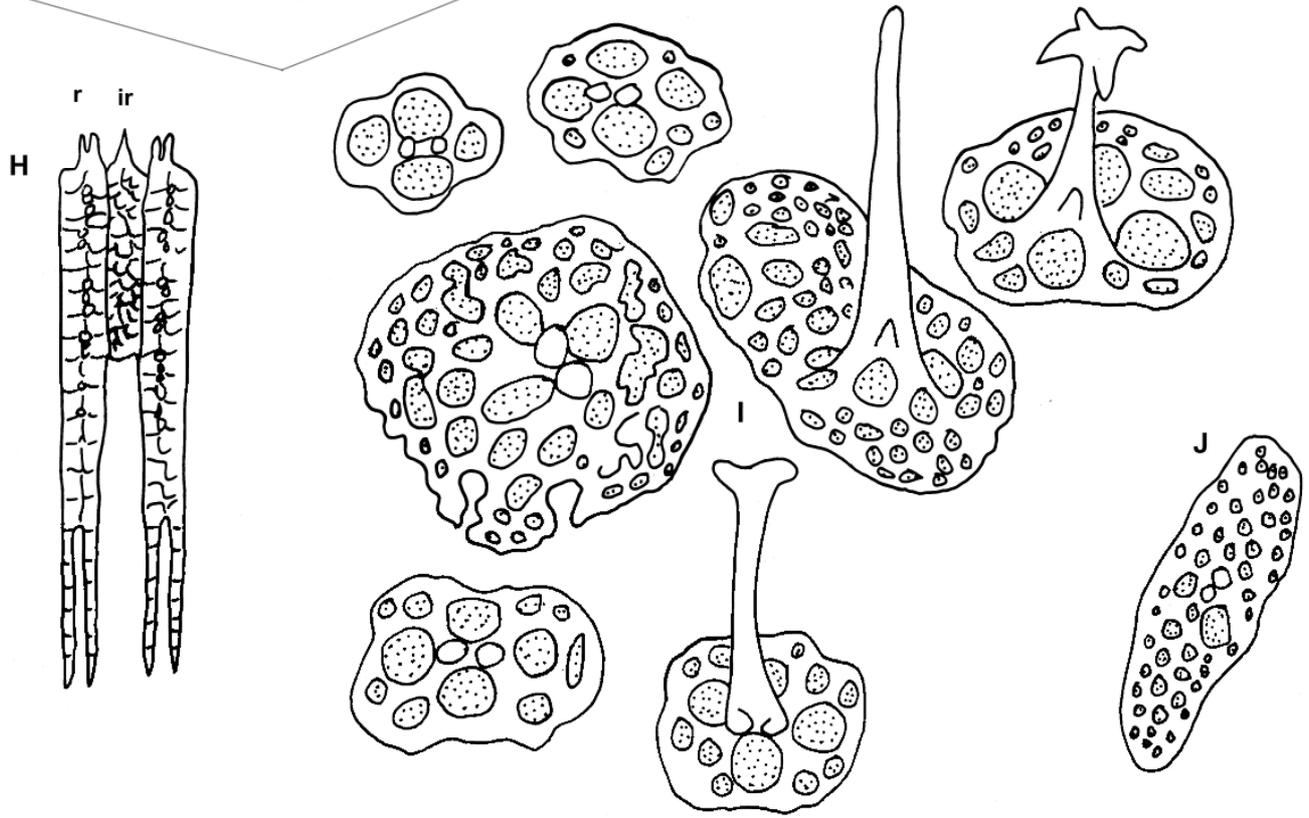
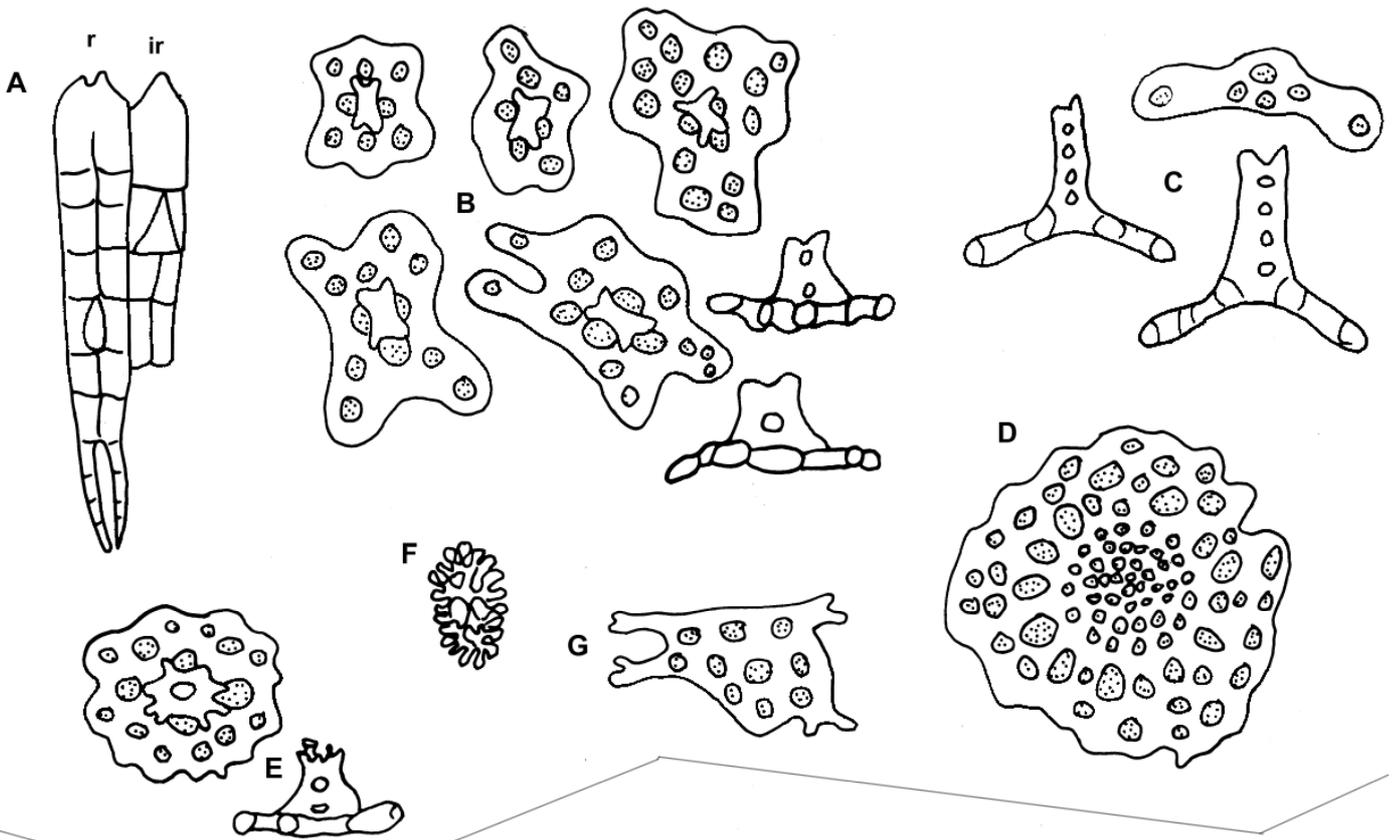
Distribution

Dongshan to Guangdong Province, southern China, 4 m.

FIGURE 20

Thyone sinensis Liao & Pawson. A. calcareous ring (r = radial plate; ir = interradial plate); B. tables of body wall; C. supporting tables of tube feet; D. end-plate; E. tables of introvert; F. rosette of introvert; G. perforated plate of tentacles. A = Scale 2; B, C, E–G = Scale 3; D = Scale 4. Reproduced from Liao & Pawson (2001).

Thyone spinifera Liao. H. calcareous ring; I. tables at base of tube feet; J. table of introvert; K. rods of tentacles; L. rosettes of introvert. H = Scale 1; I–L = Scale 4. Reproduced from Liao & Clark (1995).



- 1. 3.5 mm
- 2. 2 mm
- 3. 50 μ m
- 4. 100 μ m

Remarks

Liao & Pawson (2001) compared their species to *T. pedata* Semper noting the similarity in the irregular margin of the table discs and its multilocular nature, differing in the presence of lower spires to the tables and 3–4 cross-bars in the spires of the tube feet deposits. The spires of the tube feet deposits resemble those seen in *Havelockia tanyspeira* (Pawson & Miller), but in this species they are characteristically twisted.

Thyone spinifera Liao, 1995

Figure 20H–L

Thyone spinifera Liao, 1995: 506, pl. 23, fig. 3, text-fig. 308.

Diagnosis [after Liao (in Liao & Clark, 1995)]

Small species, up to 55 mm in length; body more or less fusiform, cylindrical near the middle but tapering a little anteriorly and more so posteriorly; each end is slightly upturned. Colour, in alcohol, whitish but more or less grey-brown at each end. Tube feet numerous, small, delicate, irregularly scattered over the body. Anal teeth absent; anal papillae present. Tentacles 10, ventral pair reduced. Calcareous ring tubular, mosaic-like; radial plates posteriorly prolonged before bifurcation, processes short, sub-divided (Fig. 20H). Deposits generally lacking from body wall but heap of tables with multilocular discs found near the base of each tube foot, each with a disc of four large primary holes only or a variable number of small peripheral ones; spire high, of two fused pillars, tapering to a pointed apex, or ending in 2–4 spines with an anchor-like formation (Fig. 20I). Tube feet deposits comprise only rudimentary end-plates. Tentacle deposits as supporting rods, delicate with a small perforation at each end (Fig. 20K). Introvert supported by numerous multilocular tables with an elliptical disc (Fig. 20J) and small heaps of rosettes (Fig. 20L).

Name-bearing type

IOAS-E1003.

Type locality

Gulf of Tonkin, China, 42 m.

Habitat

Sandy mud.

Distribution

Gulf of Tonkin to eastern Guangdong, China, 15–115 m.

Remarks

This species appears common in southern China. Its unique anchor-like spire top gives the ossicles of this species a characteristic feature and so separating it from other species of *Thyone* is presents no difficulty.

Thyone vadosa Cherbonnier, 1988

Figure 21A–E

Thyone vadosa Cherbonnier, 1988: 193, text-fig. 82 A–G.

Diagnosis (after Cherbonnier, 1988)

Medium-sized species, reaching 80 mm in length; body cucumber-shaped. Colour uniformly brown, anus rimmed with black. Tube feet short, cylindrical, distributed tightly throughout body. Anal teeth present. Tentacles 10, ventral pair smaller. Calcareous ring tubular, mosaic-like, radial plates apparently prolonged before bifurcating into two posterior processes, each made up of a variable number of sclerites; both radials and interradials pointed anteriorly (Fig. 21B). Deposits of body wall lacking, except for tube feet end-plates (Fig. 21E). Tentacles with perforated rods (Fig. 21D) and ? rosettes (Fig. 21C). Introvert supported with rosettes (Fig. 21C) and tables with multilocular discs; spire two-pillared, branching distally and ending in two clusters of small teeth (Fig. 21A).

Name-bearing type

MNHN, EcHh no. 3594.

Type locality

Tuléar, Madagascar.

Habitat

Mud.

Distribution

Known from type locality and the lagoon of Ifaty, Madagascar.

Remarks

Cherbonnier (1988) described this species from the Madagascan fauna and provides a rather detailed description except for the tentacle and introvert deposits which need clarification. He mentions the presence of rods in the branches of the tentacles, and the presence of rosettes in the peristome and introvert. Yet, in the diagram of these deposits, he labels the rosettes as coming from the tentacles. This is perhaps an error and hence the presence of rosettes in the tentacles is here questioned. However, Cherbonnier does illustrate some crinkly rods from the tentacles which can transform into the type of rosettes he drew. Thandar unfortunately did not study this species during his visits to the MNHN. Attempts to borrow the material have thus far been unsuccessful but at this point not imperative since *T. vadosa* is well described.

Thyone vilis (Sluiter, 1901)

Figure 21F–K

Cucumaria vilis Sluiter, 1901: 86, pl. VII, fig. 5 a–e.

Thyone villis Panning, 1949: 467 (*lapsus calami*).

Diagnosis (after Sluiter, 1901, amended herein)

Small species, up to 9 mm in length. Tube feet distributed all over body, in double rows on each ambulacrum, more numerous in the ventral interambulacra. Anal teeth absent. Tentacles 10, ventral pair reduced. Calcareous ring tubular, short, fragmented into a few large pieces; radial plates with long posterior processes arising slightly beyond posterior border of interradial plates, curled distally; interradial plates shorter anteriorly (Fig. 21F). Deposits of body wall comprise tables with quadrilocular (Fig. 21G) to multilocular discs and a two-pillared spire ending in a few teeth. Tube feet with elongated, supporting tables (Fig. 21H); end-plates present. Tentacle deposits quadrilocular tables in the stalk and rods at the tips, similar to those of the tube feet. Introvert supported by small multilocular tables (Fig. 21I) and rosettes (Fig. 21J).

Name-bearing type

ZMA, H1114.

Type locality

Banda, Indonesia, 10–40 m.

Habitat

Sand and coral.

Distribution

Known from type locality only.

Remarks

Sluiter (1901) established this species on the basis of two specimens, one from Banda, and one from Molo Strait, Indonesia (H1109) collected at 69–91 m in sand, shells and stones. Sluiter only briefly comments on the nature of the calcareous ring, presumably from the Banda specimen, since the Molo Strait one lacks a calcareous ring and tentacles (noted by Thandar during his examination of both specimens). According to him, the ring is short, tubular, but based upon the fragmentation of the ring and the long posterior processes of the radial plates, he is convinced that this species belongs in

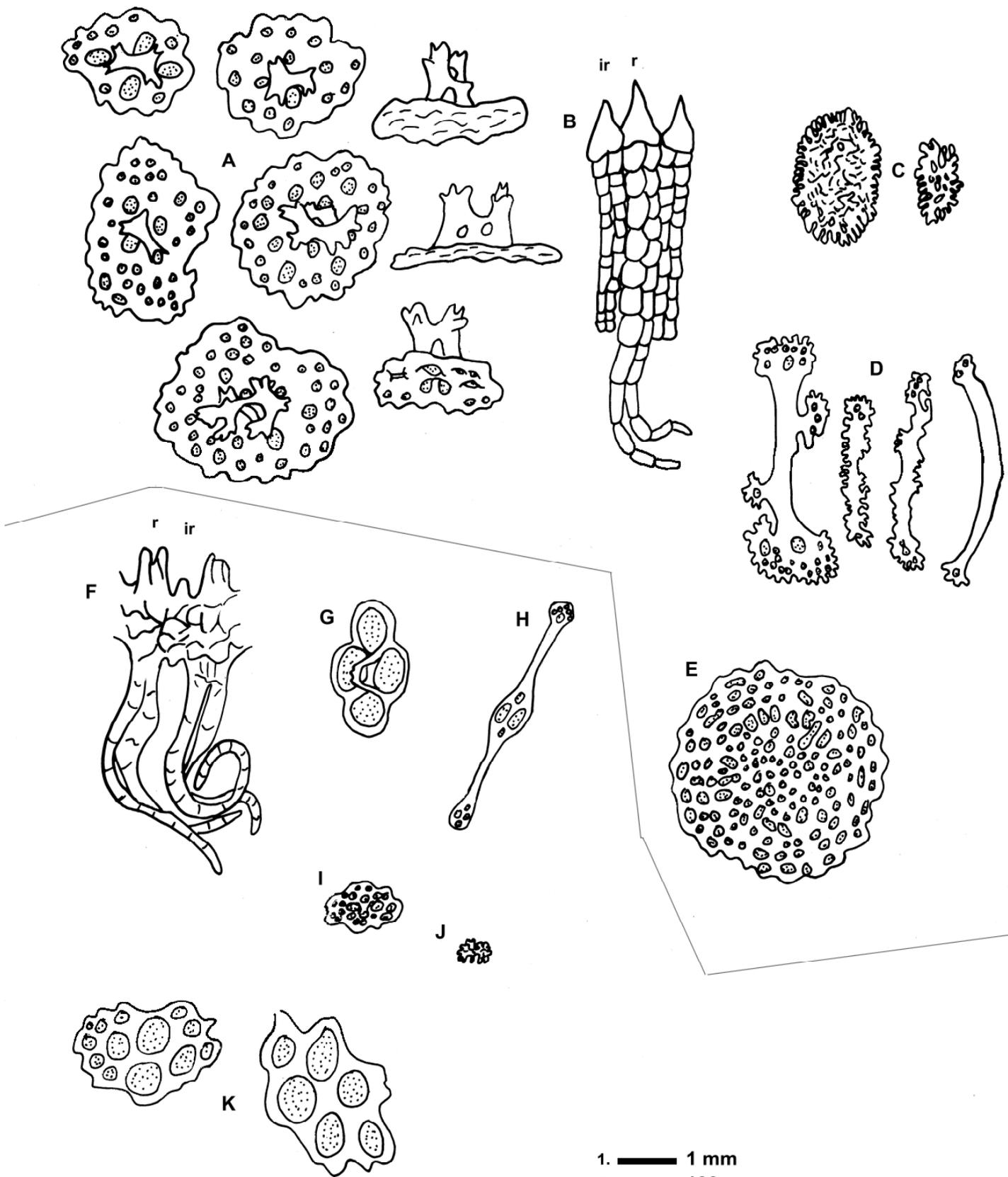
the Thyoninae. Thandar observes that the quadrilocular plate illustrated by Sluiter (pl. VII, fig. 5b) originates from the Molo Strait specimen which contains very large, often broken plates (Fig. 21K) accompanied by rosettes and lacks any tables in the body wall. Conversely, the other deposits illustrated by Sluiter match those found in the Banda specimen which has only quadrilocular to multilocular tables that are on their way to corrosion. It is for this reason that Thandar is certain that both syntypes are not conspecific and that the Banda specimen should be regarded as the holotype and establishing the identity of the other syntype must await the collection of more material. This step has here been taken.

Interestingly, Thandar mentions the presence of quadrilocular tables in the stalk of the tentacles of the Banda specimen though he does not illustrate them. This is indeed peculiar as no other species within *Thyone* possess tables in the tentacles. However, since all tentacles in the type were fully extended, and Thandar (pers. comm.) was careful not to contaminate the tentacle and introvert deposits, his viewpoint is here upheld awaiting re-examination of the type. Furthermore, the table discs of the introvert are multilocular.

FIGURE 21

Thyone vadosa Cherbonnier. A. tables of introvert; B. calcareous ring (ir = interradial plate; r = radial plate); C. rosettes of tentacles and ?introvert; D. rods of tentacles; E. end-plate. A, C, D = Scale 3; B = Scale 1; E = Scale 2. Reproduced from Cherbonnier (1988).

Thyone vilis (Sluiter). F. calcareous ring of Banda specimen; G. table of body wall; H. supporting table of tube feet; I. table of introvert; J. rosette of introvert; K. large plates of body wall of Molo Strait specimen. F = Scale 5; K = Scale 4; G–J see diagnosis given by Sluiter (1901) for dimensions. F, K reproduced from Thandar's examination of the material at the ZMA; G–J reproduced from Sluiter (1901).



- 1. ——— 1 mm
- 2. ——— 100 μ m
- 3. ——— 50 μ m
- 4. ——— 100 μ m
- 5. ——— 1 mm

**GROUP 4. INTROVERT DEPOSITS: TABLES AND PLATES/?REDUCED
TABLES**

Thyone aurea (Quoy & Gaimard, 1834)

Figure 22A–H

Holothuria aurea Quoy & Gaimard, 1834: 120, pl. 7, figs. 15–17.

Cladolabes aureus Brandt, 1835: 74.

Thyone aurea Semper, 1868: 66; Lampert, 1885: 163; Théel, 1886: 141; H.L. Clark, 1923: 415 (partim); Deichmann, 1948: 354 (partim), text-figs. 1–5, pl. 19, figs. 13–18; Cherbonnier, 1952a: 493, pl. 45, figs. 1–28, pl. 46, figs. 1–2, 6–7; 1952b: 12; Branch & Branch, 1981: 247, 1 text-fig.; Thandar, 1990: 211, figs. 1 b–c, 3–4, 10 b–c.

Thyone serratus Britten, 1910: 242.

Thyone serrata H.L. Clark, 1923: 415.

Thyone proceracorona Cherbonnier, 1952a: 492, pl. 44, figs. 1–16.

Thyone turrisolidi Cherbonnier, 1954a: 117, fig. 1 (1–24), fig. 2 (14); Day et al., 1970: 83.

Diagnosis (after Thandar, 1990, amended herein)

Medium-sized species, up to 130 mm in length. Colour in life orange to pink. Tube feet in 2–3 zigzag rows in each ventral ambulacrum, few in interambulacra; scattered dorsally. Anal teeth present. Tentacles 10, ventral pair reduced. Calcareous ring tubular, broken into a mosaic of tiny pieces; posterior bifurcate processes of radial plates shorter than height of ring, also compound (Fig. 22B). Deposits of body wall two-pillared tables with characteristically knobbed to spinose discs, well developed in juveniles (Fig. 22E), severely reduced in adults to slightly nodular plates with few holes or to spectacle-shaped rods or plates (Fig. 22A), or altogether absent. Tube feet with curved, supporting tables (Fig. 22H), reduced or lost with age; end-plates well developed (Fig. 22F). Tentacle deposits rods and perforated plates (Fig. 22C). Introvert supported by reduced tables (Fig. 22G), often completely transformed to perforated plates (Fig. 22D) in larger individuals.

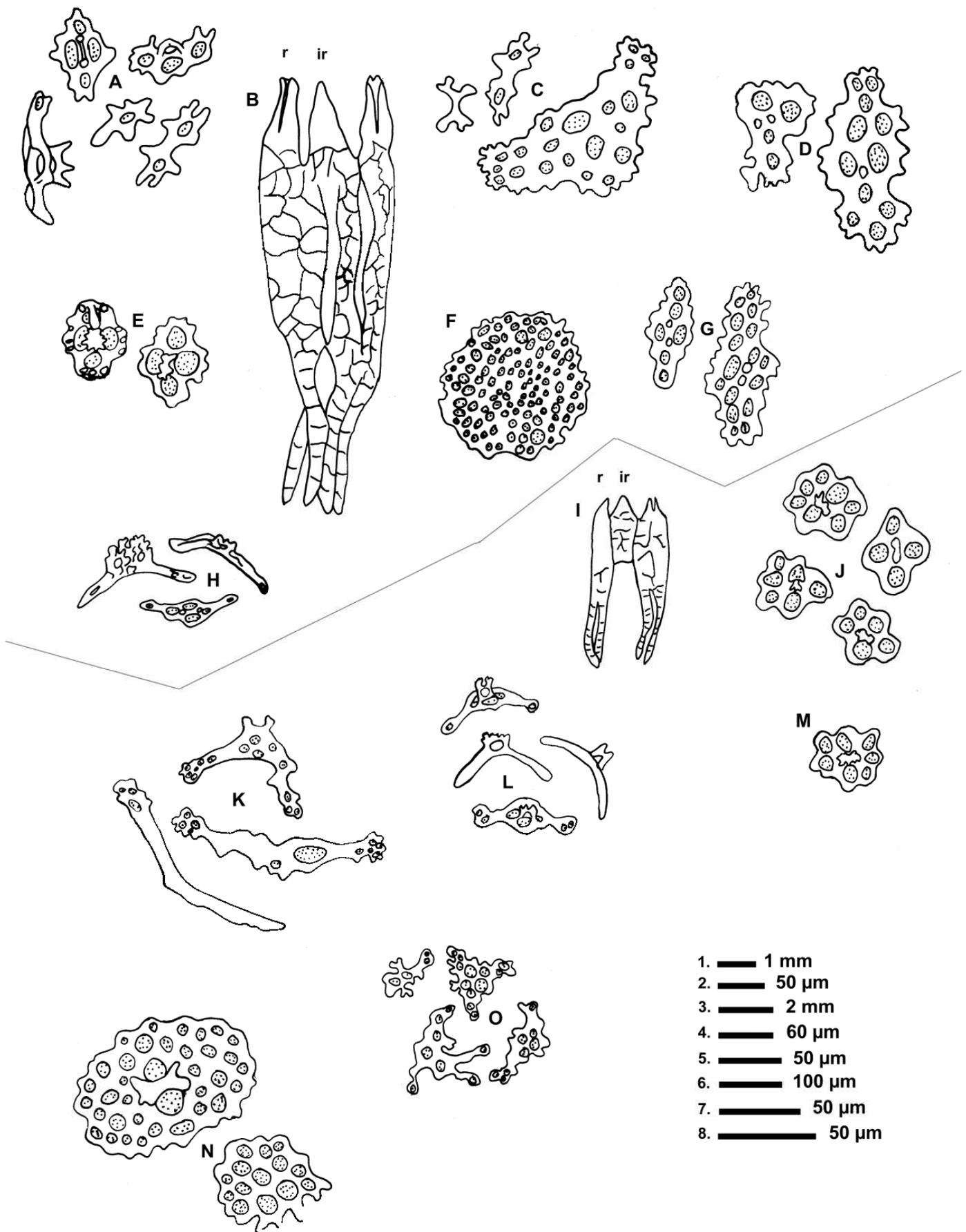
Name-bearing type

Unknown.

FIGURE 22

Thyone aurea (Quoy & Gaimard). A. tables, reduced tables and spectacle-shaped rods of body wall; B. calcareous ring of 36 mm specimen (r = radial plate; ir = interradial plate); C. rods and plates of tentacles; D. reduced tables/plates of introvert (36 mm specimen); E. small tables of body wall from 8 mm juvenile; F. end-plate; G. reduced tables of introvert from juvenile; H. tables from tube feet from juvenile. B = Scale 3; H = Scale 5; F = Scale 6; A, C, D, E, G = Scale 7. Reproduced from Thandar (1990).

Thyone herberti Thandar & Rajpal. I. calcareous ring; J. tables of dorsal body wall; K. rods of tentacles; L. supporting tables of tube feet; M. table of ventral body wall; N. tables and plates (reduced tables) of introvert; O. plates of anal papillae. I = Scale 1; J, L, M = Scale 4; K, O = Scale 2; N = Scale 8. Reproduced from Thandar & Rajpal (1999).



Type locality

Cape of Good Hope, South Africa.

Habitat

Sand, white sand, fine sand, rock. Species often cryptofaunic or amongst *Pyura*, sometimes washed up on shore amongst *Laminaria* roots. Juveniles found in association with *Ciona* under stones at low tide (Thandar, 1990).

Distribution

Luderitz (Namibia) to False Bay, 0–70 m.

Remarks

T. aurea has been demonstrated to undergo an immense reduction in its calcareous deposits, to be virtually absent in adults (Thandar, 1990). This feature resulted in the description of two new species, *Thyone proceracorona* Cherbonnier and *Thyone turrissolida* Cherbonnier; the former was described from only the calcareous ring and fragment of its body wall.

Cherbonnier (1952a) separated his *T. proceracorona* from *T. aurea* arguing a stronger development of the calcareous ring and the presence of peculiar tube feet deposits in his species. Thandar's (1990) examination of the holotype, though lacking any deposits, showed no significant difference in the calcareous rings of both species. He further commented that those tube feet deposits mentioned by Cherbonnier are indeed present in some growth stages of *T. aurea* thus justifying the relegation of *T. proceracorona* to the synonymy of *T. aurea*.

Cherbonnier (1954a), failed to compare his *T. turrissolida* to any other nominal species of *Thyone*. His material consisted of just two specimens up to 12 mm in length with the gonad of the larger specimen consisting of twenty large, unbranched, short tubes. Thandar (1990) found identical ossicles in some smaller immature specimens of *T. aurea*, thus declared *T. turrissolida* a growth stage of *T. aurea*.

Thandar (1990) described the introvert deposits of *T. aurea* as comprising rods and perforated plates similar to those of the tentacles. However, an examination of the introvert in three juveniles ranging from 15–20 mm in length, indicated a clear

reduction of the deposits from tables to plates. Therefore, this species has been placed into the “tables and plates/?reduced tables” group. No rods were present in any of the preparations of the introvert deposits mentioned above and hence the rods described by Thandar (1990) may have been contamination with tentacle deposits.

This species differs from *T. fusus* in lacking the presence of elongate tables in the body wall and rosettes from the introvert.

Thyone herberti Thandar & Rajpal, 1999

Figure 22I–O

Thyone herberti Thandar & Rajpal, 1999a: 190, fig. 1 a–e, 2 a–j.

Diagnosis (after Thandar & Rajpal, 1999a, amended herein)

Small species, up to 27 mm along the ventral surface; body somewhat U-shaped. Colour in alcohol uniformly white. Anal teeth present. Tentacles 10, ventral pair reduced. Calcareous ring tubular, sub-divided, radial plates prolonged posteriorly and then divided into paired bifurcate processes, each made up of several pieces of calcite (Fig. 22I). Ossicles of body wall two-pillared tables with smooth, 4–12-holed discs (Fig. 22J, M). Supporting tables of tube feet with curved discs, spire two-pillared (Fig. 22L); end-plates present. Anal papillae with irregular plates (Fig. 22O). Tentacle deposits rods only (Fig. 22K). Introvert supported by tables and plates (?reduced tables) (Fig. 22N).

Name-bearing type

SAM-A27724.

Type locality

Off Matigulu Bluff, KZN, South Africa.

Habitat

Soft mud and clay lumps.

Distribution

KwaZulu-Natal, South Africa, 300–520 m.

Remarks

Thandar & Rajpal (1999a) described the introvert deposits of this fairly deep-sea species as a composition of tables, plates and rods. The presence of the latter seems highly doubtful. A re-examination of the type shows that rods are more evident in the anal region, tube feet and tentacles. Indeed, the introvert of the holotype comprises only multilocular, oval to elongate or irregularly shaped tables and multilocular plates, possibly representing reduced tables as the shape and size of the plate are similar to those of the table discs. However, there is no evidence of a reduced spire. It is suspected that the rods illustrated by Thandar & Rajpal in fact originate from the tentacles as they are similar in size and form to those illustrated for the tentacles.

The colour of the holotype in alcohol is yellowish brown, perhaps as a result of preservation, however, the paratype (SAM-A27725) remains uniformly white as described by Thandar & Rajpal (1999a).

GROUP 5. INTROVERT DEPOSITS: ROSETTES AND PLATES/?REDUCED TABLES

Thyone anomala Östergren, 1898

Figure 23A–E

Thyone anomala Östergren, 1898: 110; Massin, 1987: 97, text-fig. 1; Liao & Clark, 1995: 501, text-fig. 304, pl. 23, fig. 1.

Cucumaria citrea Yang, 1937: 2, text-fig. 1, pl. 1, fig. 4.

Non *C. citrea* Semper, 1868.

Diagnosis (after Massin, 1987 and Liao & Clark, 1995, amended herein)

Medium-sized species, up to 90 mm in length; body more or less fusiform. Colour in alcohol, dark brown with occasional light brown spots. Tube feet large, numerous, in

five faint bands along ambulacra, scattered in interambulacra but limited to 2–3 rows on each ambulacrum at the ends. Anal teeth present. Tentacles 10, ventral pair reduced. Calcareous ring tubular, radials deeply incised with long posterior processes; both ring and processes broken up into a mosaic of small pieces of calcite (Fig. 23A). Deposits of body wall comprise more or less oval-shaped, two-pillared tables with four central holes and 1–4 peripheral ones, spires high, ending in 2–3 teeth (Fig. 23B), and plates with 3–7 perforations (Fig. 23D). Tube feet with curved, supporting two-pillared tables; end-plates present. Tentacle deposits delicate rods and rosettes. Introvert supported by reduced tables, perforated plates (Fig. 23E) and rosettes (Fig. 23C).

Name-bearing type

MNHN, according to Massin (1987).

Type locality

Strait of Formosa, Taiwan Strait.

Habitat

Unknown.

Distribution

Taiwan Strait to Southern China and east Indonesia, 0–103 m.

Remarks

Östergren (1898) distinguished his species from the type, *T. fusus* (Müller), on the basis of its much thicker deposits with larger table discs. Moreover, the presence of the characteristic perforated plates (Fig. 23D) in the body wall of *T. anomala* further separates both species.

This is one of the many species that Panning (1949) failed to cite in his revision, perhaps an oversight, or because Östergren's description did not include an illustration of the calcareous ring. Liao & Clark (1995) identified a few specimens which they classified as the rare *T. anomala* but overlooked Massin's (1987) record of the species from East Indonesia. Massin's material contained much younger individuals (13–33 mm

in length) while Liao & Clark's material consisted of much older specimens (60–90 mm in length). Massin illustrates some tables of the body wall which appear to have reduced spires and a plate which appears to be a reduced table (Fig. 23E). Perhaps, the perforated plates mentioned in both records are reduced tables, showing the reduction of tables with age. However, since these plates are found in combination with tables with well-developed spires (Fig. 23B), the above conclusion is doubtful. Nonetheless, the species is typically a *Thyone* due to the form of the calcareous ring and the distribution of the tube feet.

It is also assumed that the rods mentioned by Liao & Clark in the introvert may be the result of contamination with the tentacle deposits, as Massin illustrates only what appear to be reduced tables, perforated plates and rosettes from the introvert of his material. Thus, the diagnosis of the species given by Liao & Clark has been amended.

Thyone grisea H.L. Clark, 1938

Figure 23F–N

Thyone grisea H.L. Clark, 1938: 467, text-fig. 40 a–c; Panning, 1949: 467.

Diagnosis (after Clark, 1938, amended herein)

Small, stout species, measuring 50–55 mm in length. Colour in preservation, off-white. Tube feet numerous, distributed over entire body, but less so mid-dorsally. Anal teeth absent. Tentacles 10, ventral pair reduced. Calcareous ring mosaic-like in younger individuals becoming more compact in adults; both plates of similar length; radial plates anteriorly bifid with paired posterior processes which apparently become shorter with maturity (Fig. 23F). Deposits of body wall numerous stout tables with oval to elliptical discs with four or more perforations, larger tables with 12–15 holes; spire two-pillared, low, converging at the tip; some smaller tables without a spire also present (Fig. 23L). Tube feet with curved, supporting tables (Fig. 23M), some also without a spire; large end-plates present. Branches of tentacles with minute, somewhat crinkly rods (Fig. 23N) and numerous rosettes (Fig. 23K), rods becoming larger and more perforated (Fig. 23I) with fewer rosettes (Fig. 23H) in tentacle stalks. Introvert supported by numerous

larger mulberry-like rosettes (Fig. 23G) and fewer multilocular, circular to slightly elongated plates (Fig. 23J).

Name-bearing type

MCZ, no. 1612.

Type locality

False Cape Boosut, Western Australia.

Habitat

Found near the jetty-flat.

Distribution

False Cape Bossut to Roebuck Bay, Western Australia, littoral waters.

Remarks

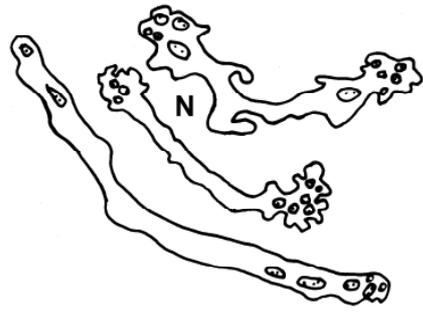
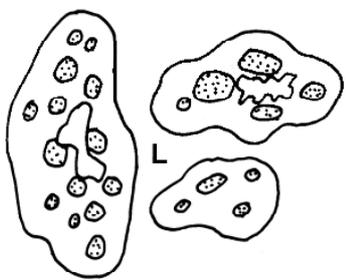
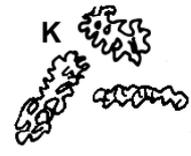
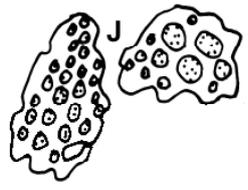
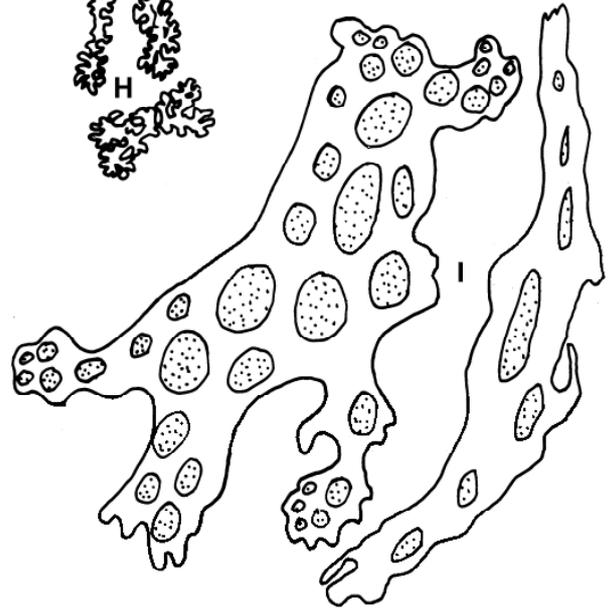
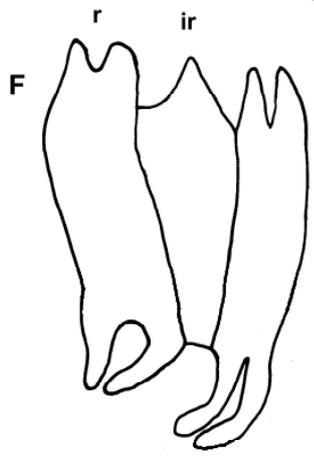
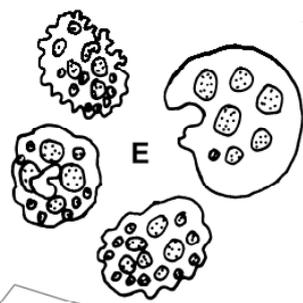
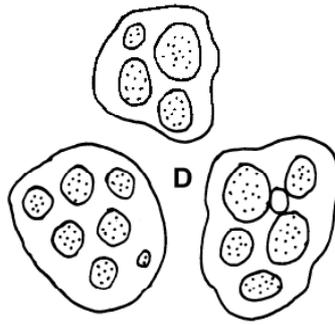
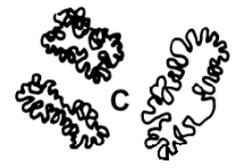
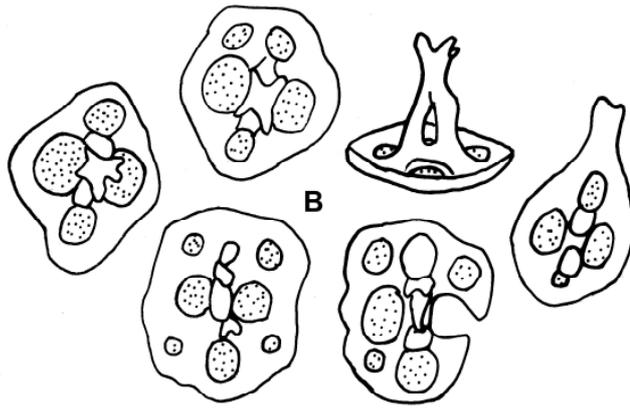
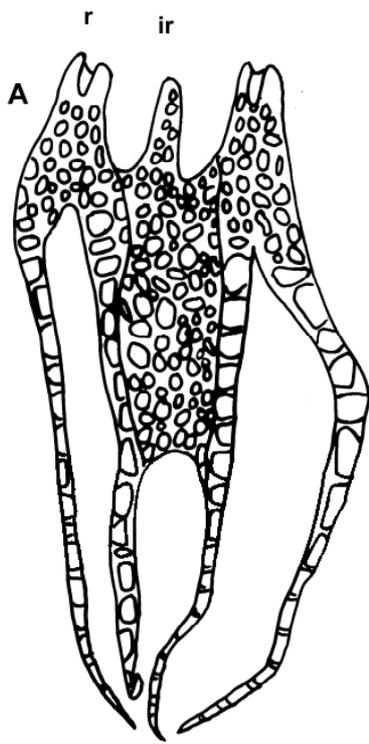
H.L. Clark (1938) did not illustrate the calcareous ring of his species, but his description of the ring appears accurate and is here illustrated from the holotype. Further, he describes the composition of the introvert deposits to be the same as that of the stalk of the tentacles. For fear of damaging the ring of the holotype, a dissected paratype was examined for introvert deposits. This revealed larger, mulberry-like rosettes, more rounded than those of the tentacles and small, circular to slightly elongated, perforated plates.

T. grisea comes close to the Indo-West Pacific *T. anomala* in possessing small plates and rosettes in the introvert. However, the rosettes in the latter species are more elongated.

FIGURE 23

Thyone anomala Östergren. A. calcareous ring (r = radial plate; ir = interradiial plate); B. tables of body wall; C. rosettes of introvert; D. plates of body wall; E. reduced tables/plates of introvert. A = Scale 2; B–E = Scale 3. Reproduced from Massin (1987).

Thyone grisea H.L. Clark. F. calcareous ring of holotype; G. rosettes of introvert; H. rosettes of tentacle stalk; I. rods of tentacle stalk; J. plates of introvert; K. rosettes of tentacle branches; L. tables of body wall; M. supporting table of tube feet; N. rods of tentacle branches. F = Scale 1; G–K, N = Scale 4; L, M = x 425. L, M reproduced from H.L. Clark (1938).



- 1. ——— 1 mm
- 2. ——— 5 mm
- 3. ——— 50 μm
- 4. ——— 50 μm

Thyone imperfecta (Cherbonnier, 1970)

Figure 24A–J

Havelockia imperfecta Cherbonnier, 1970: 284, fig. 3 A–T.

Thyone imperfecta Thandar, 1990: 215, fig. 6; 2008: 7, fig. 3 A–D.

Diagnosis (after Cherbonnier, 1970 and Thandar, 2008)

Medium-sized, synaptid-like species, holotype 110 mm long. Colour violet dorsally, maroon ventrally. Body covered with small cylindrical tube feet. Anal teeth present, flanked by tube feet. Tentacles 10, ventral pair reduced. Calcareous ring high, tubular, poorly calcified; posterior processes of radial plates longer than height of ring, arising at posterior level of the interradial plates (Fig. 24A). Body wall ossicles exclusively tables with circular to sub-rectangular discs (80–100 μm) with two large and usually two smaller central holes and 6–16 small marginal holes; spire short (20–40 μm), two-pillared, often distorted or reduced to two central knobs on surface of disc (Fig. 24B). Anal tables with larger discs and more perforations (Fig. 24C). Tube feet with elongate (80–120 μm), curved, perforated supporting tables with an arched spire terminating in one or two blunt teeth, some tables with 3–4 arms (Fig. 24G); end-plates absent. Tentacle deposits numerous perforated rods (Fig. 24D), often branched (Fig. 24E), crinkled rosette-shaped bodies (Fig. 24H) and scarce rosettes (Fig. 24I). Introvert supported by large plates (Fig. 24J), rosette-like plates and true rosettes (Fig. 24F).

Name-bearing type

MNHN, EcHh no. 1486.

Type locality

False Bay, WCP, South Africa.

Habitat

Shell, sand.

Distribution

False Bay, WCP, South Africa, 60–67 m.

Remarks

Thandar (1990) correctly re-assigned Cherbonnier's species to *Thyone* based upon the nature of the calcareous ring which is clearly tubular, sub-divided, with long radial processes unlike the short, stout ring as seen in species of *Havelockia*. Thandar related the body wall ossicles to those found in *T. hirta* Cherbonnier, differing in the larger table discs, distorted to reduced table spires, the absence of end-plates and the presence of rosette-like bodies in the tentacles. The latter deposits were reported to be found in combination with true rosettes in the introvert by Thandar (2008).

GROUP 6. INTROVERT DEPOSITS: PLATES ONLY

Thyone propinqua Cherbonnier, 1970

Figure 24K–S

Thyone propinqua Cherbonnier, 1970: 289, fig. 5 c–k; Day et al. 1970: 83; Thandar, 1990: 216; 2008: 8, fig. 4 A–D.

Diagnosis (after Cherbonnier, 1970; modified by Thandar, 2008)

Small species, up to 23 mm in length; body tapering at ends. Colour pink. Tube feet large, long, distributed over entire body. Anal teeth present, each flanked by a single papilla. Calcareous ring tubular with anteriorly notched radial plates, deeply incised posteriorly; processes long, both broken into two series of elements; interradials spear-shaped with a single, larger series of elements (Fig. 24L). Body wall tables with lobed discs (40–50 μm), usually perforated by four large holes (Fig. 24K), rarely more (up to eight) (Fig. 24M); spire low (*ca.* 13 μm), two-pillared, often arched, terminating in a few blunt teeth or conical projections. Tube feet supported by large (100–120 μm), curved tables with four central holes and one at each extremity, and an arched spire (*ca.* 18 μm) with several conical teeth (Fig. 24Q); end-plates 120–130 μm in diameter. Tentacle deposits large (up to 260 μm), curved, perforated plates (Fig. 24O, R) and small (70 μm), rosette-shaped bodies (Fig. 24S). Introvert supported by perforated

plates (Fig. 24P) and crinkly rosette-like deposits (Fig. 24N) but no tables and true rosettes.

Name-bearing type

MNHN, EcHh no. 1492.

Type locality

Mossel Bay, WCP, South Africa.

Habitat

Sand and shell.

Distribution

False Bay to Mossel Bay, WCP, South Africa, 19–51 m.

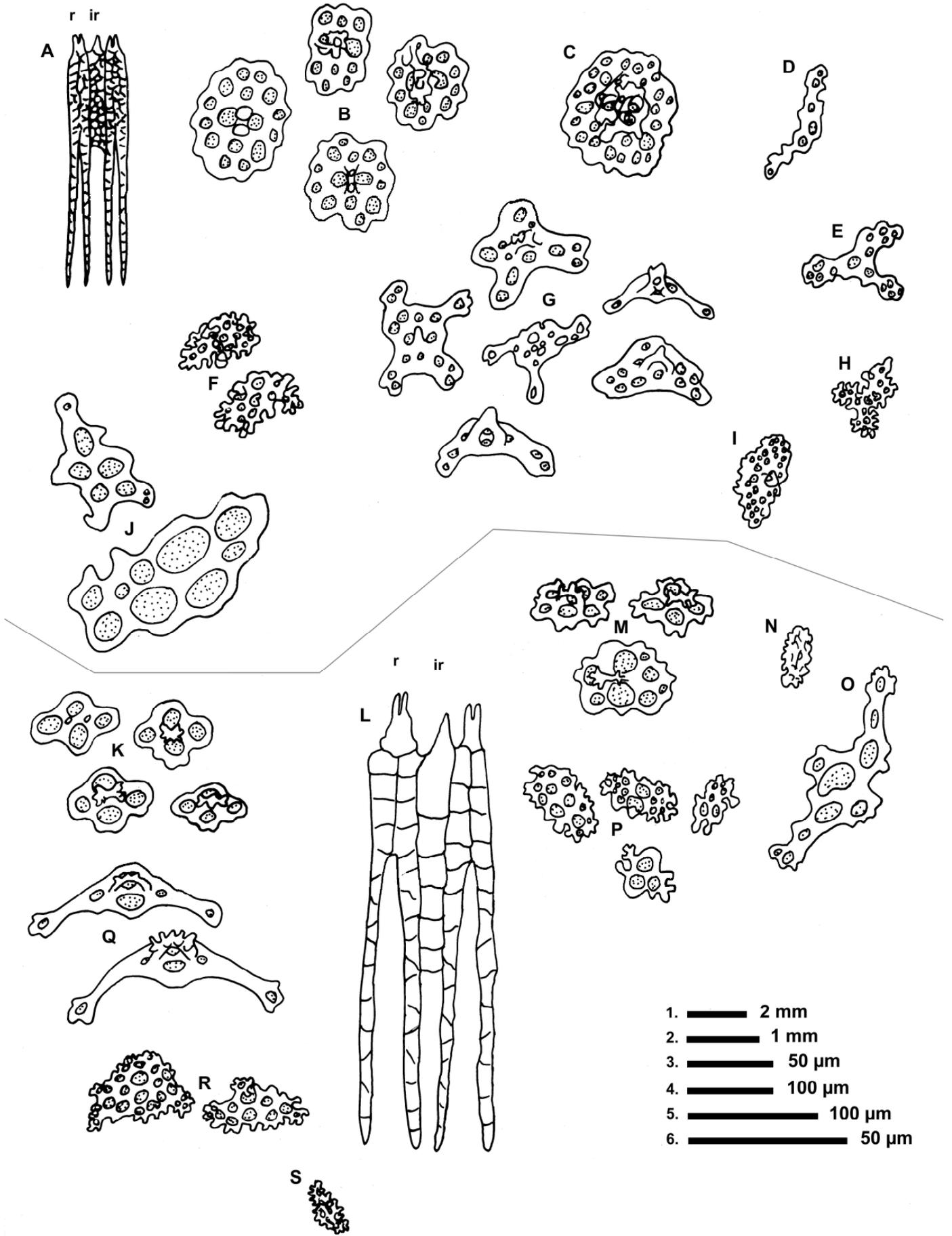
Remarks

Cherbonnier's (1970) detailed description of *T. propinqua* did not include a study of introvert deposits which were subsequently examined and recorded by Thandar (2008). This species comes close to *T. venustella* with regard to the form of its body wall ossicles and the presence of plates in the introvert. However, these plates are smooth whereas they are finely knobbed in *T. venustella*. Moreover, the tube feet deposits of *T. propinqua* comprise well developed supporting tables, lacking in *T. venustella*.

FIGURE 24

Thyone imperfecta (Cherbonnier). A. calcareous ring (r = radial plate; ir = interradial plate); B. tables of body wall; C. table of anal region; D. rod of tentacles; E. plate of tentacles; F. rosettes of introvert; G. tables of tube feet; H. crinkled rosette-shaped body of tentacle; I. rosette of tentacle; J. plates of introvert. A = Scale 1; B–E, G–I = Scale 5; F, J = Scale 6. F, J reproduced from Thandar's examination of the material at the MNHN; A–E, G–I reproduced from Cherbonnier (1970).

Thyone propinqua Cherbonnier. K, M. tables of body wall; L. calcareous ring; N. rosette-like deposit of introvert; O, R. plates of tentacles; P. plates on introvert; Q. supporting tables of tube feet; S. rosette-shaped body of tentacles. K, M, Q = Scale 3; L = Scale 2; O, R, S = Scale 4; N, P = Scale 6. K–M, O, Q–S reproduced from Cherbonnier (1970); N, P reproduced from Thandar's examination of type material at the MNHN.



Thyone venustella Ludwig & Heding, 1935

Figure 25A–H

Thyone venusta Schmidt, 1926: 125, fig. b.

Thyone venustella Ludwig and Heding, 1935: 203, pl. 2, figs. 15–20; Panning, 1949: 466; Thandar 2008: 9, fig. 4 E–K, 5.

Havelockia venustella Thandar, 1989: 292, figs. 2, 9 a (syn. & records).

Diagnosis (after Thandar, 2008)

Small species, up to 55 mm in length; body slender. Tube feet numerous, minute, scattered. Anal teeth present. Tentacles 10, ventral pair reduced. Calcareous ring elongated, tubular, mosaic-like (Fig. 25A). Body wall tables with oval, lobed discs pierced by four large central holes in juveniles (Fig. 25C) and often as equal number of alternating marginal ones (1–4 or more) or marginal holes incomplete or absent in adults (Fig. 25B); spire short, of two pillars uniting at apex by a horizontal bar bearing a cluster of teeth at each end; table discs at anal region of adults smaller, with more perforations (Fig. 25H). Anal region with huge perforated plates. Tube feet with end-plates only (Fig. 25D), smaller in juveniles (Fig. 25E). In juvenile, tentacle deposits as developing perforated plates (Fig. 25G). Introvert supported by elongated, small-knobbed, multilocular plates with irregular margins (Fig. 25F).

Name-bearing type

Perhaps in Bonn, Germany (Thandar, 2008).

Type locality

Agulhas Bank, South Africa.

Habitat

Green mud, khaki and black sand, gravel and nodules.

Distribution

Lambert's Bay to just east of Cape St. Francis, WCP, South Africa, 155–400 m.

Remarks

Ludwig (in MS) had originally identified the three specimens in his material as *T. venusta* since the two larger specimens (47 and 27 mm in length) lacked body wall deposits which Heding (in Ludwig & Heding, 1935) suspected might have dissolved, despite the fact that both specimens also lacked their calcareous ring and its associated structures. However, the smaller individual measuring only 9 mm contained a full complement of tables in the body wall including its calcareous ring. Heding, correctly, assigned this material to a new species citing the presence of tables in the body wall and the smaller end-plates of the tube feet as characteristic features separating this species from *T. venusta*. Unfortunately, the two larger specimens lacked their calcareous ring and its associated structures. Thandar (2008) was the first author to illustrate the calcareous ring of this southern African species, the nature of which conforms to that of a typical *Thyone*: tubular and mosaic-like.

In the form of the body wall ossicles and in lacking any tables or true rosettes but perforated plates in the introvert, this species approaches another southern African form, *T. propinqua*. Thandar (1990) suspected that both species could be conspecific, with *T. propinqua* representing a juvenile of *T. venustella*. This view, he later (2008) retracted, after examining more specimens of both species. Also, *T. venustella* has thin-margined tables and lacks any supporting tables in the tube feet except for end-plates, whereas these are present in *T. propinqua*.

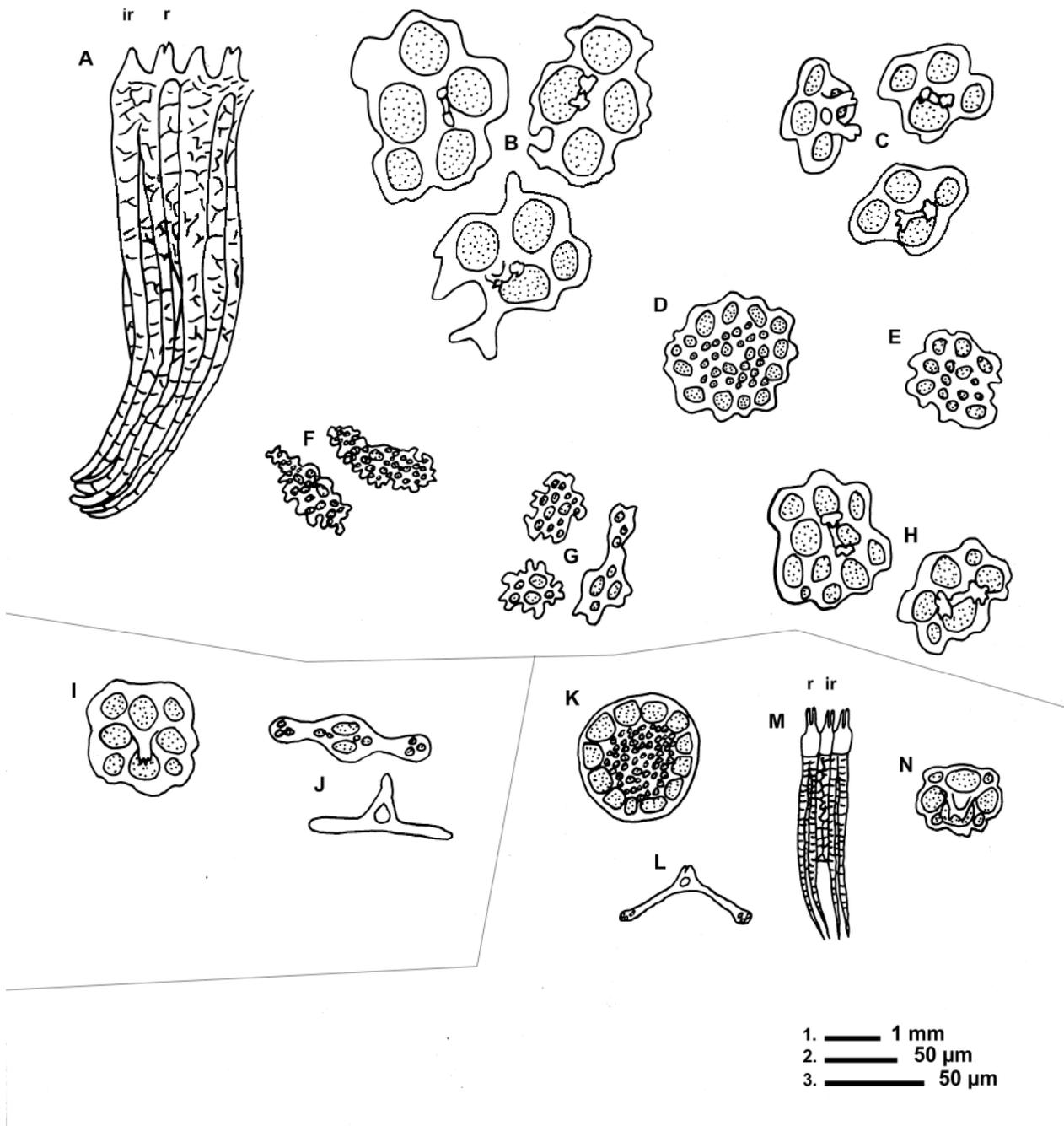


FIGURE 25. *Thyone venustella* Ludwig & Heding. A. calcareous ring (ir = interradial plate; r = radial plate); B. tables of body wall of 1 mm juvenile; C. tables of body wall of 28 mm adult; D. end-plate of anal tube feet of adult; E. end-plate of 1 mm juvenile; F. plates of introvert of 6 mm specimen; G. plates of tentacles of 6 mm specimen; H. tables of anal body wall of 28 mm adult. A = Scale 1; B–E, H = Scale 3; F, G = Scale 2. Reproduced from Thandar (2008).

Thyone falcata (Sluiter). I. tables of body wall; J. supporting tables of tube feet. I, J = Scale 3. Reproduced from Sluiter (1901).

Thyone fastigata (Sluiter). K. end-plate; L. supporting table of tube feet; M. calcareous ring; N. table of body wall. See diagnosis for dimensions. Reproduced from Sluiter (1901).

GROUP 7. INTROVERT DEPOSITS: DEPOSITS ABSENT/UNKNOWN

Thyone falcata (Sluiter, 1901)

Figure 25I & J

Cucumaria falcata Sluiter, 1901: 91.

Havelockia falcata Panning, 1949: 466.

Diagnosis (after Sluiter, 1901)

Small species, up to 13 mm in length; body tapering, more so posteriorly, broader in the middle. Tube feet in a single row in each ambulacrum. Anal teeth not mentioned. Tentacles 10, ventral pair reduced. Calcareous ring with posterior processes to the radial plates. Body wall table discs thick but delicate, some with four central holes and four peripheral ones, often consisting of more than eight holes or fewer; spire short to moderate in height, ending in 1–2 points (Fig. 25I). Supporting tables of tube feet with straight discs measuring almost 75 μm in length; spire two-pillared, ending in a single conical point (Fig. 25J); end-plates well-developed.

Name-bearing type

ZMA, H1119.

Type locality

Molo Strait, Indonesia.

Habitat

Sand with rocks and shells.

Distribution

Known only from type locality, 69–91 m.

Remarks

This rare species, known only from the holotype was adequately described by Sluiter (1901), although he failed to comment on the presence or absence of anal teeth

or study the tentacles and introvert for deposits. Thandar's examination of the holotype, although well preserved, provided no new information as the calcareous ring was missing and the deposits were on their way to corrosion. He also failed to find any evidence of ossicles in either the tentacles or the introvert which were still intact.

Panning (1949) initially assigned this species to his original *Havelockia* group which he later moved to *Thyone* in which genus this species currently stands. Since the exact nature of the calcareous ring cannot be determined, this species remains provisionally within *Thyone* since the body wall comprises two-pillared tables and the tentacles number ten, of which the ventral pair is reduced. The ambulacral restriction of the tube feet may be attributed to the juvenility of the specimen as Sluiter merely described the gonad as two small tufts, without commenting on its state of maturity. More material is required to confirm the generic status of *T. falcata*, possibly within *Havelockia*.

Thyone fastigata (Sluiter, 1901)

Figure 25K–N

Cucumaria fastigata Sluiter, 1901: 86, pl. 7, fig. 9 a–d.

Havelockia fastigata Panning, 1949: 466.

Diagnosis (after Sluiter, 1901)

Small-sized species, up to 16 mm in length; body circular, tapering posteriorly. Tube feet arranged in double rows in each ambulacrum, also numerous in interambulacra. Anal teeth not mentioned. Tentacles 10, ventral pair reduced. Calcareous ring long, tubular, sub-divided, both radial and interradial plates notched anteriorly; radials slightly broader, bifurcating beyond posterior border of interradial plates, each with long posterior processes measuring about a third of ring (Fig. 25M). Deposits of body wall exclusively tables (50 μm in length) with four large perforations and four smaller peripheral ones; spire consist of two short pillars, united by a cross-bar, terminating in fine teeth (Fig. 25N). Tube feet with elongated, curved supporting tables (45 μm in length) (Fig. 25L); end-plates present, with larger holes around the margin and smaller ones in the middle (Fig. 25K). Introvert and tentacle deposits unknown.

Name-bearing type

?ZMA.

Type locality

6° 36′.5 S, 114° 55′.5 E and Molo Strait, Indonesia.

Habitat

Mud, sand, shells and stones.

Distribution

Known only from type locality, 89–91 m.

Remarks

This is another species that Sluiter (1901) described from the Siboga Expedition that has not been taken since. Sluiter classified his new species in *Cucumaria* citing a similarity of the deposits with that of *C. citrea* (Semper). Panning (1949) referred this species to his *Havelockia*. Hence, it now stands in *Thyone*. Sluiter did not record any deposits from the tentacles or introvert and Thandar unfortunately did not examine the type during his visit to the ZMA. Hence, this species is temporarily placed with the “*deposits absent/unknown*” group until more material is collected that provides new information.

However, based upon the illustration of the end-plate by Sluiter, this species does not resemble any of the known species of *Thyone*.

Thyone profusus Cherbonnier & Féral, 1981

Figure 26A–G

Thyone profusus Cherbonnier & Féral, 1981: 391, fig. 21 A–K; Lane et al., 2000: 491 (dist.).

Diagnosis (after Cherbonnier & Féral, 1981)

Small species, up to 45 mm in length; body fusiform. Colour grey, spotted with black dots. Tube feet small, wiry, in two rows in the ventral ambulacra, scattered in the interambulacra, evenly distributed dorsally, with no radial seriation. Anal teeth present, each flanked by a large conical tube foot. Tentacles 10, ventral pair reduced. Calcareous ring tubular, mosaic-like; radial plates slightly notched anteriorly, with long processes arising at posterior border of interradial plates, made up of ten pieces (Fig. 26C). Discs of body wall tables usually perforated by four large more/less equal holes; spire short, two-pillared, terminating in 2–4 branches with many teeth; some discs irregular with 5–6 holes (Fig. 26A). Anal region comprise slightly larger, more perforated table discs (5–10 holes), with a better developed spire (Fig. 26B) and other elongated discs with a reduced spire (Fig. 26D), sometimes appearing as an arch. Wall of tube feet with curved, supporting tables, centre of disc expanded (Fig. 26E); end-plates small. Anal papillae with large, multilocular, smooth plates (Fig. 26G). Branches of tentacles with straight or curved rods, with/without perforations; stalks with perforated plates (Fig. 26F). Introvert lacking deposits.

Name-bearing type

MNHN, EcHh no. 3006.

Type locality

Philippines (13° 46.9' N, 120° 29.5' E).

Habitat

Unknown.

Distribution

South China Sea, 592–610 m.

Remarks

Cherbonnier & Feral (1981) erected this species on two specimens. Thandar was able to study these specimens at the MNHN and found that the calcareous ring of the

holotype is asymmetrical, in that the interradial plates are of unequal length; the radials, however, are all posteriorly prolonged before bifurcation. This does not correspond with the drawing made by Cherbonnier & Feral, which Thandar suspects is incorrect or that the ring he examined does not belong to the holotype as it was preserved in a separate vial. Unfortunately, the specimen appeared to be decalcified, with no ossicles in the body wall. Furthermore, a large portion of the introvert dissected out by him lacked any deposits. Cherbonnier & Feral mention the absence of rosettes from the introvert but not the lack of deposits in it. If indeed the introvert lacks deposits, *T. profusus* is provisionally listed in the “*deposits absent/unknown*” group.

The paratype also studied by Thandar lacked the calcareous ring and associated structures but the body wall contained the characteristic four-holed tables. Thandar, however, was unable to detect any of the other body wall deposits illustrated by Cherbonnier & Feral.

Thyone theeli Rowe in Rowe & Gates, 1995

Figure 26H–J

Cucumaria mirabilis Théel, 1886: 61, pl. IX, fig. 5.

Thyone theeli Rowe & Gates, 1995: 316.

Diagnosis (after Théel, 1886, amended herein)

Small-sized species, up to 13 mm in length; body curved, tapering towards each extremity. Colour in alcohol light yellowish-grey. Tube feet in two or three rows in each ambulacrum, a few scattered in interambulacra. Tentacles 10, ventral pair reduced. Calcareous ring tubular, sub-divided, radial plates bifurcating at posterior border of interradial plates; processes sub-divided (Fig. 26H). Deposits of body wall crowded, comprising tables with an irregularly perforated, round to angular disc with uneven margins (40–50 μm in diameter) and a short (~ 28 μm) two-pillared spire, the tip of which terminating in several teeth (Fig. 26J). Supporting tables of tube feet with curved discs (Fig. 26I); end-plates present. Tentacle and introvert deposits unknown.

Type material

NHMUK, 1886.10.2.50 (2 *syntypes*).

Type locality

Cebu, Philippines.

Habitat

Unknown.

Distribution

Cebu to Port Jackson, Australia, 11–183 m.

Remarks

Théel (1886) classified this species within *Cucumaria* Blainville. Rowe (in Rowe & Gates, 1995), noting its tubular calcareous ring, tentacle number and ossicles similar to that of *Thyone fusus*, transferred this species to *Thyone* re-naming it after its original authority providing a replacement name for the junior secondary homonym: *Thyone mirabilis* Ludwig = *Havelockia versicolor* (Semper).

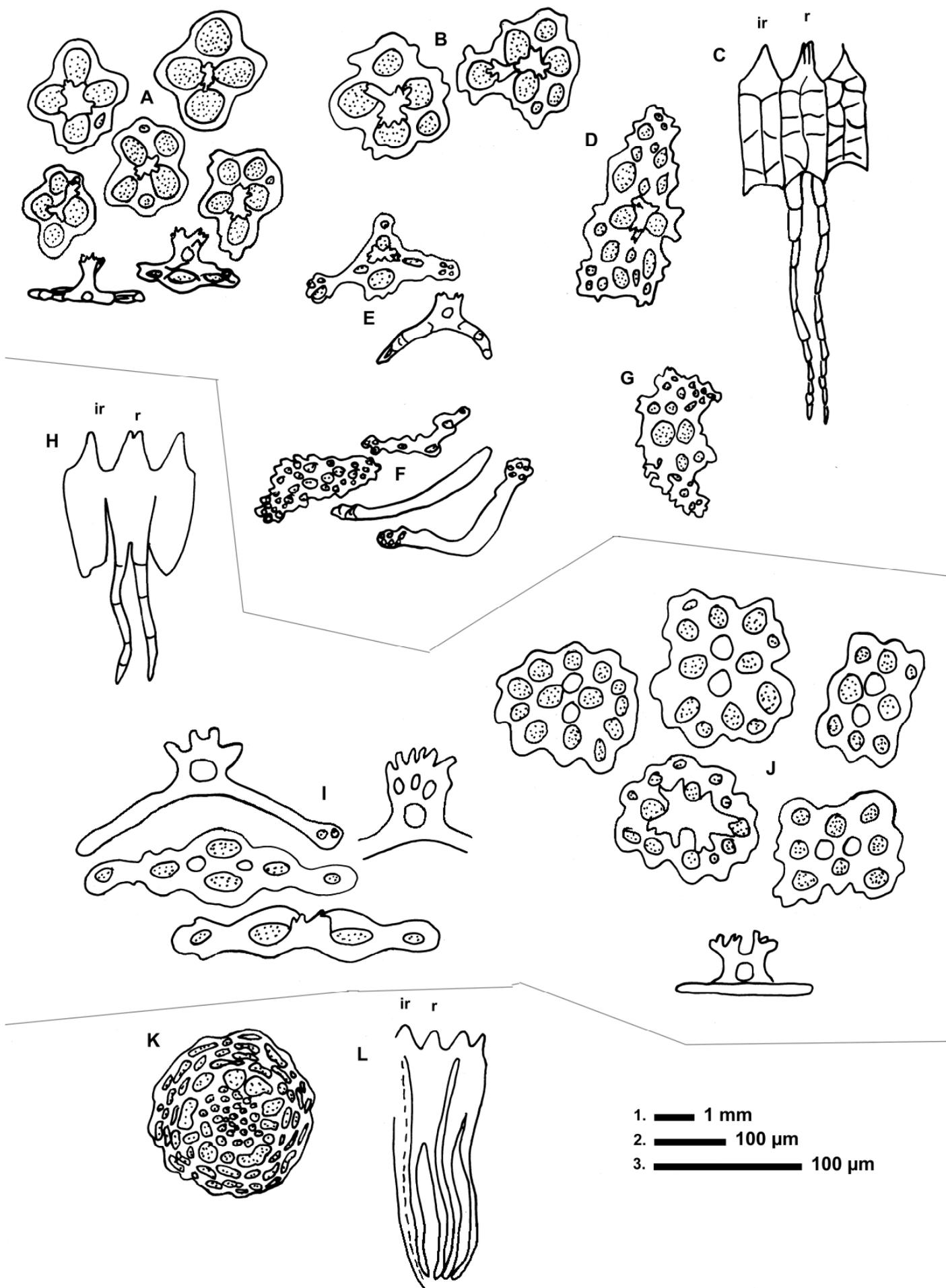
Thandar's examination of the syntypes yielded no new information as the calcareous ring and its associated structures were missing from both. Hence, the introvert deposits of *T. theeli* remains unknown placing this species in the “*deposits absent/unknown*” group. He did, however, note the presence of numerous corroded “crosses” in the body wall, perhaps representing the corroded tables.

FIGURE 26

Thyone profusus Cherbonnier & Féral. A. tables of body wall; B, D. tables of anal region; C. calcareous ring (ir = interradial plate; r = radial plate); E. supporting tables of tube feet; F. rods of tentacles branches and plate of tentacle stalk; G. plate of anal papillae. A, B, D, E, G = Scale 3; C = Scale 1; F = Scale 2. Reproduced from Cherbonnier & Féral (1981).

Thyone theeli Rowe. H. calcareous ring. I. supporting tables of tube feet; J. tables of body wall. H–J x 2 as that illustrated by Théel (1886).

Thyone venusta Selenka. K. end-plate; L. calcareous ring. K, L x 2 as that illustrated by Selenka (1868).



Thyone venusta Selenka, 1868

Figure 26K & L

Thyone venusta Selenka, 1868: 115, fig. 11, 12; Thandar, 1990: 216.

Diagnosis (after Selenka, 1868 and Thandar, 1990)

Small species, up to 85 mm in length; body cucumber-shaped, tapering posteriorly. Colourless, probably transparent. Tube feet appear to be in two series per ambulacrum, scattered in interambulacra. Anal teeth present. Tentacles 10, ventral pair reduced. Calcareous ring long, tubular with long posterior processes to the radials plates (Fig. 26L). Deposits absent except for tube feet end-plates (Fig. 26K).

Name-bearing type

Berlin Museum (according to Selenka).

Type locality

Red Sea.

Habitat

Unknown.

Distribution

Red Sea and ?KwaZulu Natal, South Africa.

Remarks

Selenka (1868) described just a single specimen lacking deposits except for tube feet end-plates. Thandar (1990) found a mature female, from KwaZulu-Natal (KZN), off the east coast of South Africa, lacking the calcareous ring and its associated structures and any deposits, not even end-plates, which he identified as *T. venusta*, despite the fact that the specimen also lacked anal teeth. He justified this by commenting that the Red Sea species might extend south to the KZN and that the absence of end-plates might be a local variation. However, Selenka describes his

specimen as colourless (possibly a preserved specimen) while Thandar mentions a brown to dark purple colouration anteriorly and posteriorly. It is believed that the South African specimen may represent another species or does perhaps show local variation.

Thandar further synonymized Bell's *T. okeni* with *T. venusta* since both species only possess tube feet end-plates. This again was done in error which Thandar later realised (pers. comm.) as the type specimen of *T. okeni* differs in being much larger, more colourful, and contains a full complement of ossicles in the tentacles and introvert (see remarks for *T. okeni*). Moreover, Rowe and Gates (1995) list both species as separate.

Subfamily Sclerodactylinae Panning, 1949

Genus *Havelockia* Pearson, 1903

Havelockia Pearson, 1903: 198; Panning, 1949: 466; Clark & Rowe, 1971: 203

Pentathyone H.L. Clark, 1938: 458; Panning, 1949: 459.

Remarks

Pearson (1903) described a single quadrangular holothurian from Ceylon with deposits comprising only two-pillared tables and a complex calcareous ring with posterior processes to the radial plates that were broken up into a number of smaller pieces which he correctly placed into a new genus, *Havelockia* with his species, *H. herdmani*, as type species. He, however, did not distinguish his species from *Cucumaria versicolor* Semper and *Thyone mirabilis* Ludwig reported earlier from the Philippines and Queensland respectively.

Pentathyone was erected by H.L. Clark (1938) for *Thyone mirabilis*, which he commented as having such a diverse body form to that of a typical *Thyone* and so deserved a new genus. He also appeared to have overlooked the description of *C. versicolor*. Panning (1949), in his revision of the Cucumariidae, included several species in *Pentathyone* including *C. versicolor* and placed this genus within his newly erected subfamily Sclerodactylinae. It is not certain whether Panning examined the type specimens of *C. versicolor* or *T. mirabilis*. He further, assigned *Havelockia* to his newly erected subfamily Thyoninae, separating it from *Thyone* on the basis of introvert ossicles which, according to him, comprised only tables when compared to only rosettes in his *Thyone*.

However, when he received the original description of *Havelockia*, he realized that, on the basis of the calcareous ring, this genus belonged in the Sclerodactylinae rather than in the Thyoninae. As a result, Panning transferred *Havelockia* with its type species *H. herdmani* into the Sclerodactylinae relegating *Pentathyone* to the synonymy of *Havelockia*. Because of this, he stated that those species he initially placed within *Havelockia* should be moved into *Thyone*.

Following a critical analysis of the descriptions of the type specimens of *C. versicolor* and *T. mirabilis*, James (1976) synonymized both species. This view has been supported here by examination of the type specimens of each. James further

examined a specimen identified as *H. herdmani* by Koehler & Vaney (1908) in the Indian Museum which prompted him to conclude that *H. herdmani* should also be relegated to the synonymy of *C. versicolor* together with *T. mirabilis* (for full synonymy see James 1976). However, in his synonymy James incorrectly listed *C. versicolor* as *Thyone versicolor* Semper, 1868.

Interestingly, in their Australian catalogue of echinoderms, Rowe & Gates (1995), although citing Panning's 1949 revision and recognising Panning's decision to synonymize *Pentathyone* with *Havelockia*, still listed *Havelockia* under the Phylloporidae, perhaps in error or assumed that the genus remained within the subfamily Thyoninae which Pawson & Fell (1965) placed in the Phylloporidae. Rowe & Gates do cite the latter authors' revision in which they elevated the subfamily Sclerodactylinae to the rank of family together with the subfamily Cladolabinae. It must be here emphasised that the genus *Havelockia* is typically a sclerodactyline genus due to the nature of its calcareous ring and must be classified in the Sclerodactylinae.

After Panning's 1949 revision, there remained 10 species in *Havelockia* of which three species were relegated to the synonymy of *C. versicolor* as discussed above. Moreover, two species, *Thyone trita* Sluiter and *T. constituta* Sluiter, have long been assigned to other genera, whereas Clark and Rowe (1971) transferred another two species into *Havelockia*. Cherbonnier (1958, 1988) described four new species in *Havelockia*, two of which have been here transferred to *Thyone* based upon the nature of the calcareous ring, while *Cucumaria redimita* Sluiter is here moved into *Pentamera* Ayres (see remarks for *Pentamera*). In addition to this, ten species currently classified in *Thyone* are here transferred to *Havelockia* for the same reason stated above. Hence, *Havelockia* now contains 17 species.

Key to the species of the genus *Havelockia* Pearson, 1903

- 1. a) Body wall devoid of deposits..... 2
- b) Body wall deposits present..... 3

2. a) Tube feet deposits also lacking except for small terminal end-plates.....
..... ***H. discolor*** (Sluiter), p. 175
b) Papillae comprise numerous elongated, supporting, straight, two-pillared tables;
spire arched, fused distally ending in two diverging teeth or spire absent and leaving
only a perforated disc; wall of tube feet with small four-holed tables.....
..... ***H. conciliatrix*** (Sluiter), p. 174
3. a) Body wall deposits comprise only tables only..... 4
b) Body wall deposits comprise uniquely four-holed plates with rounded, irregular
margins..... ***H. imbellis*** (Koehler & Vaney), p. 182
4. a) Tentacle deposits present..... 5
b) Tentacle deposits absent or unknown..... 14
5. a) Tentacles comprise rods only, or in combination with rosettes..... 6
b) Tentacles comprise rosette-shaped bodies and larger derivatives of these.....
..... ***H. ferali*** Cherbonnier, p. 177
6. a) Rods only..... 7
b) Rods and rosettes..... 10
7. a) Introvert supported by rosettes only..... 8
b) Introvert supported by elongated tables with well-developed or reduced spire and
large plates of variable size, some appearing spinous, others rosette-like, large rods
also present..... ***H. pituitosa*** (Sluiter), p. 188
8. a) Tube feet deposits curved, two-pillared tables with/without spire, the latter
appearing as rods..... 9
b) Tube feet deposits curved, oblong, supporting two-pillared tables; disc perforat-
ed; spire high, often twisted and perforated throughout its length or solid.....
..... ***H. tanyspeira*** (Pawson & Miller, 1988), p. 197

9. a) Tentacles 10; body wall deposits two-pillared tables with circular, quadrangular to elongated discs; some tables larger with up to 20 perforations; spire cross-shaped, each branch terminating into 2–4 denticules..... *H. novacorona* (Cherbonnier), p. 183
- b) Tentacles 8–13; body wall deposits massive two-pillared tables with squarish disc with usually two large central holes and six peripheral ones, sometimes with up to two additional holes; spire ending in a finely branched spinous tip; other tables rare with irregular discs; spire same as above or ending in a crown of numerous teeth..... *H. turrispinea* Cherbonnier, p. 202
10. a) Introvert supported by tables only, rosettes only or a combination of both..... 11
- b) Introvert deposits unknown; body wall deposits numerous small oval tables with 2–4 central holes and a variable number of peripheral ones; spire short, two-pillared, ending in a crown of a large number of teeth; tube feet with reticulated plates.....
..... *H. transitoria* (Vaney), p. 198
11. a) Introvert supported by oblong tables with knobbed edge; spire low.....
..... *H. strangeri* (Deichmann), p. 193
- b) Introvert supported by rosettes only or in combination with tables..... 12
12. a) Introvert with rosettes only; body wall deposits scarce, dorsal body wall tables with eight-holed discs (four large + four smaller marginal ones), ventral tables with mostly four-holed discs; spire two-pillared, of moderate height, taller in ventral tables, connected by a cross-bar, ending in 1–2 teeth..... *H. vankampeni* (Sluiter), p. 203
- b) Introvert with both tables and rosettes..... 13
13. a) Body wall deposits numerous tables with oblong to roundish, eight-holed discs, some with 5–13 holes; spire two-pillared, cross-shaped distally, each branch ending in 3–4 teeth; tube feet with supporting tables only..... *H. pohaiensis* (Liao), p. 192

- b) Body wall deposits sparse minute tables with four central holes, often with four or more smaller ones; spire two-pillared, tall ending in 2–4 teeth or often reduced to knobs on surface or absent; tube feet with irregular plates and tables.....
..... *H. versicolor* (Semper), p. 206
14. a) Tube feet with flattened rods, slightly curved, perforated in the middle and at each extremity..... *H. ariana* (Koehler & Vaney), p. 173
b) Tube feet with curved supporting tables.....15
15. a) Body wall deposits irregular, unbranched tables..... 16
b) Body wall with irregular, multilocular tables with more or less quadrangular disc branching into 3–4 arms; spire low, made up of two converging pillars.....
..... *H. festina* (Koehler & Vaney), p. 180
16. a) Tables elongated, multilocular; plates of calcareous ring compact (undivided).....
..... *H. ardens* (Koehler & Vaney), p. 171
b) Tables more or less rounded, with four central and few to many peripheral ones; plates of calcareous ring broken up into many pieces of calcite.....
..... *H. perditia* (Koehler & Vaney), p. 185

Havelockia ardens (Koehler & Vaney, 1908)

Figure 27A–C

Cucumaria ardens Koehler & Vaney, 1908: 31, pl. II, fig 24–35, pl. III, fig 1–3.

Havelockia ardens Panning, 1949: 466.

Diagnosis (after Koehler & Vaney, 1908)

Small species, up to 20 mm in length when tentacles extended; body V-shaped. Tube feet in two rows dorsally, more or less alternating, restricted to ambulacra, ventrally scattered, more abundant in ambulacra; restricted to ambulacra at posterior end. Anal teeth and tentacles not mentioned. Calcareous ring ‘non-tubular’, plates short, unfused, compact; radial plates anteriorly bifid, deeply cleft posteriorly, posterior

processes made up of about two dozen pieces; interradials broad, anterior end ending in a conical point (Fig. 27A). Deposits of body wall numerous tables with irregular, multilocular discs; spire two-pillared, ending in a crown of small teeth (Fig. 27B). Tube feet with smaller, curved, supporting tables with elongated discs; spire sometimes well developed, ending in a conical point (Fig. 27C); end-plates not mentioned.

Name-bearing type

?Calcutta (= Kolkatta) Museum.

Type locality

Coast of Orissa, east coast of India.

Habitat

Unknown.

Distribution

Known only from type locality, 45.7 m.

Remarks

Koehler & Vaney (1908) do not comment on the colour or the tentacle number of their single specimen, nor the presence/absence of anal teeth and tube feet end-plates. It is doubtful whether the tentacles and the introvert were studied for deposits as this information is also not given. They do, however, admit that their new species comes close to *Thyone*, especially *Thyone pituitosa* Sluiter (= *Havelockia pituitosa*) but decided to classify it within *Cucumaria* Blainville due to the ambulacral restriction of the tube feet. However, the ambulacral restriction of the tube feet is only at the posterior end, perhaps a juvenile feature.

It differs from *H. pituitosa* by its larger, more multilocular table discs. Panning (1949) placed *C. ardens* and *T. pituitosa* in his original *Havelockia* group, but after transferring *Havelockia* into the Sclerodactylinae, re-assigned this group of species to *Thyone* within the Thyoninae, where it currently stands. The calcareous ring of *C.*

ardens and *T. pituitosa* are both short and compact and so belong within the Sclerodactylinae.

Havelockia ariana (Koehler & Vaney, 1908)

Figure 27D–F

Cucumaria ariana Koehler & Vaney, 1908: 33, pl. II, fig. 20–23.

Havelockia ariana Panning, 1949: 466.

Diagnosis (after Koehler & Vaney, 1908)

Small species, holotype reaching 30 mm in length; body more or less U-shaped, with both ends slightly folded. Colour white, tube feet reddish-yellow. Tube feet in two rows radially, more/less alternating; few in interambulacra. Anal teeth not mentioned. Tentacles eight. Calcareous ring about a third of the body length; radial plates bifurcated anteriorly with paired posterior processes consisting of a series of 10 pieces; interradials large, quadrangular, anterior part ending in a conical point (Fig. 27E). Deposits of body wall large, tables with oval (four-holed) to quadrangular (eight-holed) discs with undulating margins (Fig. 27D); spire two-pillared, sometimes reduced. Tube feet with flattened rods, slightly curved, perforated in the middle and at each extremity (Fig. 27F); end-plates not mentioned.

Name-bearing type

?Calcutta (= Kolkatta) Museum.

Type locality

Indian Ocean, 124–270 m.

Habitat

Unknown.

Distribution

Known only from type locality.

Remarks

The record of this species is confined to the holotype. Koehler & Vaney (1908) record the tentacle number of their single specimen to be eight. Perhaps the ventral pair was absent or much reduced and escape detection. However, this may only be confirmed with the collection of new material as attempts to contact the Calcutta (= Kolkatta) Museum have yet to be rewarding.

The body wall tables are very similar to those illustrated for *H. herdmani* Pearson (= *H. versicolor*) but differ by possessing curved, perforated rods in the tube feet and shorter interradial plates in the calcareous ring.

Havelockia conciliatrix (Sluiter, 1901)

Figure 27G–J

Cucumaria conciliatrix Sluiter, 1901: 89, pl. VII, fig. 12.

Pentathyone conciliatrix Panning, 1949: 459.

Havelockia conciliatrix Clark & Rowe, 1971: 180 (dist.).

Diagnosis (after Sluiter, 1901)

Small species, up to 22 mm in length. Colour in alcohol grey-violet, mottled darker in the interambulacra. Tube feet arranged in irregular double rows in the ventral ambulacra, also distributed in interambulacra; a zigzag series of thick, conical papillae in ventro-lateral and dorsal ambulacra; dorsal interambulacra naked. Anal teeth not mentioned. Tentacles 10, ventral pair reduced. Calcareous ring stout, plates not fused; radial plates anteriorly bifurcated with slender, narrow, posterior processes about the same length as the plate; interradial plates pointed anteriorly, broader proximally; both ring and processes entire (Fig. 27G). Body wall ossicles lacking, present only in papillae and wall of tube feet. Papillae comprise numerous, elongated supporting tables with a straight disc (200–300 µm long); spire two-pillared, arched, fused distally, ending in two diverging points (Fig. 27I); some lacking a spire and perforated throughout length of disc (Fig. 27J). Wall and base of tube feet supported by scarce

tables with small (60 µm long), straight discs with four large central holes; spire two-pillared, arched, ending in two diverging points (Fig. 27H); end-plates not mentioned.

Type material

ZMA, E.1104 (3 *syntypes*).

Type locality

Jedan Island, Indonesia, 13 m.

Habitat

Sand and shells.

Distribution

Known only from type locality.

Remarks

Sluiter (1901), with only slight hesitation, classified his new species in *Cucumaria*, mentioning an affinity with *Colochirus* Troschel with regard to the distribution of the papillae and tube feet. However, he believed that based upon the nature of the radial processes of the calcareous ring and the ossicle composition of the papillae and tube feet, this species belongs in *Cucumaria*.

Panning (1949) initially transferred this species into *Pentathyone*, but since its synonymization with *Havelockia*, this species became assigned to the latter genus, as noted by Clark & Rowe (1971), where it currently stands.

Havelockia discolor (Sluiter, 1901) comb. nov.

Figure 27K–N

Thyone discolor Sluiter, 1901: 96.

Diagnosis (after Sluiter, 1901, amended herein)

Small species, up to 35 mm in length; body tapering slightly posteriorly. Colour in preservation fairly bright yellowish-grey with irregular purple spots. Tube feet thin, long, distributed all over the body with some radial seriation. Anal teeth not mentioned. Tentacles 10, ventral pair reduced. Calcareous ring delicate; radial and interradial plates broad, unfused, short; radial processes of medium length, fragmented with slight fragmentation of the plates as well (Fig. 27K). Body wall and tube feet deposits lacking, except for small end-plates (Fig. 27N). Tentacles ?and/or introvert supported by very slender rods, delicate stouter rods (Fig. 27L), and rosettes (Fig. 27M) .

Type material

ZMA, E1083 (1 *syntype*), E1088 (1 *syntype*).

Type locality

Jedan Island, 13 m; Molo Strait, Indonesia, 69–91 m.

Habitat

Sand with shells and rocks.

Distribution

Known only from type locality.

Remarks

Regrettably, Sluiter (1901) did not illustrate the calcareous ring or any ossicles from his new species, which he assigned to *Thyone*, comparing his species to *Thyone meridionalis* Bell (= *Hemioedema spectabilis* (Ludwig)), *T. okeni* Bell and *T. venusta* Selenka as they all lacked ossicles from the body wall except for tube feet end-plates. Panning (1949) also failed to cite this species in his revision, perhaps another over sight, or because Sluiter failed to illustrate the calcareous ring.

The Jedan specimen (E.1083) studied by Thandar lacked a calcareous ring, perhaps damaged or destroyed during Sluiter's examination, as well as deposits in the body wall, tube feet and tentacles. On the other hand, the Molo Strait specimen (E.1088) confirmed the presence of only end-plates as described by Sluiter. The

calcareous ring of this specimen, although slightly damaged, resembles a ring typical of *Havelockia* to which genus it is here transferred.

Unfortunately, Thandar was not able to confirm the introvert deposits with any degree of certainty due to the minuteness of the specimen (10 mm) and so was unsure if the tentacle deposits he found were indeed from the tentacles only, the introvert or both, although Sluiter did mention the presence of rosettes in the tentacles. In the diagnosis it is therefore stated that the rods and rosettes originate from the tentacles and/or introvert. It is also questionable whether both syntypes are conspecific.

Havelockia ferali Cherbonnier, 1988

Figure 28A–I

Havelockia ferali Cherbonnier, 1988: 183, text-fig. 78 A–M.

Diagnosis (after Cherbonnier, 1988)

Small species, body straight to slightly curved, up to 17 mm in length. Colour yellowish. Tube feet long, thin, tightly distributed throughout the whole body without any radial seriation. Anal teeth absent. Tentacles 10, ventral pair reduced. Radial and interradial plates of the calcareous ring unbroken, unfused; radials notched anteriorly with fairly long posterior processes made up of few pieces of calcite (Fig. 28A). Deposits of body wall tables with elongated to irregular shaped discs, perforated by four central holes and a few peripheral ones (Fig. 28B); spire two-pillared, low; some rare, squarish-shaped perforated discs (plates) devoid of any spires also present (Fig. 28C). Discs of tables towards the anus much circular to oval; spires ending in a perforated crown of teeth (Fig. 28D). Tube feet with narrow, elongated, curved, supporting tables with short spires (Fig. 28E, F); end-plates present. Tentacle deposits rosette-shaped bodies (Fig. 28H) and larger derivatives of these (Fig. 28I). Introvert supported by large, slightly elongated multilocular tables (Fig. 28G).

Name-bearing type

MNHN, EcHh no. 3544.

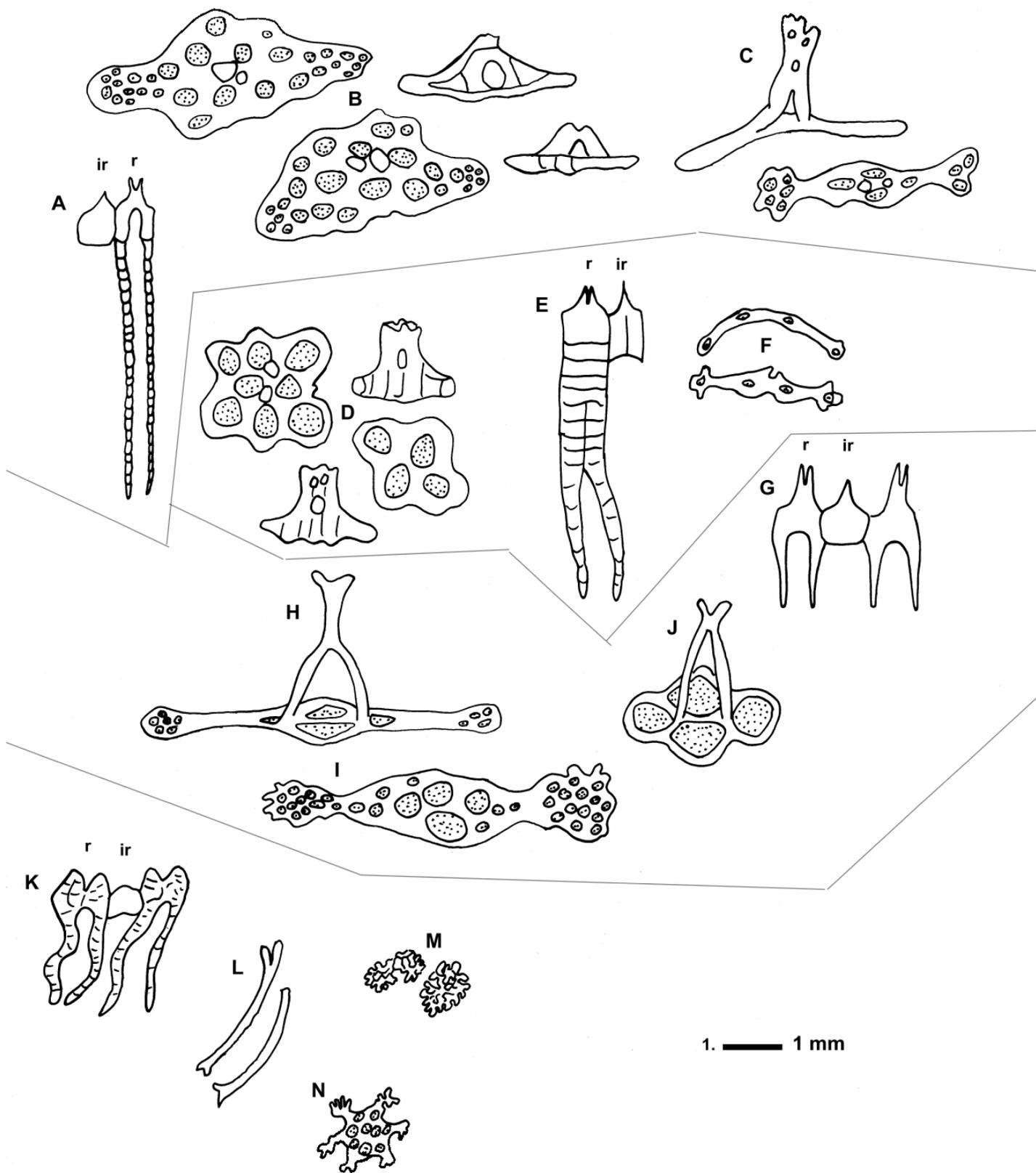
FIGURE 27

Havelockia ardens (Koehler & Vaney). A. calcareous ring (x 10) (ir = interradial plate; r = radial plate); B. tables of body wall (x 370); C. supporting tables of tube feet (x 740). Reproduced from Koehler & Vaney (1908).

Havelockia ariana (Koehler & Vaney). D. tables from body wall (x 370); E. calcareous ring (x 8); F. rods of tube feet (x 370). Reproduced from Koehler & Vaney (1908).

Havelockia conciliatrix (Sluiter). G. calcareous ring; H. table at base and wall of tube feet; I. supporting table of papillae; J. supporting table of papillae lacking spire. Reproduced from Sluiter (1901) (Scales not given by Sluiter).

Havelockia discolor (Sluiter). K. calcareous ring; L. rods from tentacles and ? introvert; M. rosettes from tentacles and ? introvert; N. small end-plate. K = Scale 1; L–N (not drawn to scale). Reproduced from Thandar's examination of the material at the ZMA.



Type locality

Tuléar, Madagascar.

Habitat

Among *Cymodocea serrulata* and dead coral.

Distribution

Tuléar to Nosy Be, Madagascar, 0–10 m.

Remarks

The type material comprised only two specimens (no. 3544 and no. 3591). Thandar examined a dissected specimen (EcHh 7077) which he records as type, perhaps in error, and notes the calcareous ring as “tubular” with both radial and interradial plates fragmented into large pieces, which is not illustrated in Cherbonnier’s (1988) drawing. He concluded that the fragmentation could not have happened after preservation since the interradial plates are fragmented into a single series and the radial into two, seen also in the calcareous ring of the paratype (no. 3591). The latter also showed some incipient division in the interradials and deeply cleft radials. The body wall and introvert deposits of the dissected specimen are identical to those illustrated by Cherbonnier. Thandar (in notes) does admit that despite the fragmentation of the ring, the ring is of the sclerodactyline type, and hence correctly placed in *Havelockia* by Cherbonnier.

Havelockia festina (Koehler & Vaney, 1908)

Figure 28J–M

Thyone festina Koehler & Vaney, 1908: 41, pl. III, fig. 4–8.

Havelockia festina Panning, 1949: 466.

Diagnosis (after Koehler & Vaney, 1908)

Medium-sized species, holotype measuring 95 mm in length; body curved, fusiform, swollen in the middle. Colour whitish, dotted at intervals with grey spots often

clustered in the bulbous region and widely scattered at ends. Tube feet scattered without any seriation in the middle of the body but in longitudinal rows terminally; more numerous ventrally. Anal teeth not mentioned. Calcareous ring short with both radial and interradial plates united along entire length but not fused; radial plates bifurcated anteriorly, deeply cleft posteriorly into two long processes made up of a dozen elongated pieces of calcite; interradial plates quadrangular with a pointed tip (Fig. 28J). Body wall ossicles tables with irregular, more or less quadrangular discs, with 3–4 arms, often perforated by numerous holes with the central four being the largest (Fig. 28K); spire low, made up of two converging pillars. Base of tube feet with elongated plates, broader centrally and perforated throughout length (Fig. 28L). Walls of tube feet with curved, supporting tables; spire two-pillared, fused, high, ending in a conical point or low and bifid terminally (Fig. 28M); end-plates not mentioned.

Name-bearing type

?Calcutta (= Kolkatta) Museum.

Type locality

Arabian Sea, Western Indian Ocean (27° 5' 12'' N, 50° 55' 20'' E), 71 m.

Habitat

Unknown.

Distribution

Known only from type locality.

Remarks

Koehler & Vaney's (1908) description of the single holotype is somewhat superficial as they do not mention the tentacle number. However, since they included this species in *Thyone* it is assumed that there are 8 + 2 tentacles. Further, they neither mention the tentacle nor introvert deposits or absence thereof, nor the presence or absence of anal teeth and tube feet end-plates. It is unknown if the '*Investigator*' material is deposited at the MNHN or at the Calcutta (= Kolkatta) Museum. Thandar

was unable to locate the type specimen at the MNHN, and attempts to contact the Calcutta (= Kolkatta) Museum have been unsuccessful.

Panning (1949) initially, and correctly, transferred this species to his original *Havelockia* group, which he later moved back to *Thyone*, despite that it clearly has a sclerodactyline ring.

The body wall ossicles, as noted by Koehler & Vaney, do approach those illustrated by Pearson (1903) for *Thyone* (?) *calcareo* which James (1976) synonymized with *H. versicolor* but the calcareous rings are different (see Pearson, 1903: pl. I, fig. 17.). The plates of the body wall also come close to that of *H. tanyspeira* but both forms differ in their tube feet deposits, which in the latter species, possesses a rather characteristic elongated and twisted spire.

Based upon the nature of the calcareous ring and ossicles, this species may represent an adult of *H. ardens*, also in the *Investigator* material. However, until more material is collected, *H. festina* should remain a separate species.

Havelockia imbellis (Koehler & Vaney, 1910)

Figure 28N–O

Cucumaria imbellis Koehler & Vaney, 1910: 97, pl. iii, fig. 2–5.

Havelockia imbellis Panning, 1949: 466.

Diagnosis (after Koehler & Vaney, 1910)

Small, barrel-shaped species, up to 12 mm in length. Ventral tube feet arranged in double rows per ambulacrum; dorsally, feet scattered, more numerous in interambulacra. Anal teeth present. Calcareous ring complex, appearing compact, radial and interrational plates fused forming a short tube; radial processes bifurcating at the posterior margin of interrational plates (Fig. 28P). Body wall ossicles comprise mainly four-holed plates with rounded, irregular margins (Fig. 28N). Tube feet with elongated to more rhomboid-shaped plates with 2–4 large holes (Fig. 28O).

Name-bearing type

?Calcutta (= Kolkatta) Museum.

Type locality

21° 49' 50' N, 59° 48' E.

Habitat

Unknown.

Distribution

Known only from type locality, 899.8 m.

Remarks

Cucumaria imbellis Koehler & Vaney was placed in Panning's (1949) original *Havelockia* group, and thereafter together with the other *Havelockia* species transferred to *Thyone*, where it currently stands. Since Koehler & Vaney's (1910) illustration of the calcareous ring (Fig. 28P) shows the formation of a short tube, this species is here included in the Sclerodactylinae. Since the single holotype measures only 12 mm in length, the possibility exists that the ring is not fully formed.

Although the plates of the body wall (Fig. 28N) and tube feet (Fig. 28O) do not compare with those of any of the nominal genera of the Sclerodactylinae, the erection of another monotypic genus based upon a single specimen is here discouraged. Therefore *C. imbellis*, is provisionally transferred back into *Havelockia* until the collection of more specimens.

Havelockia novacorona (Cherbonnier, 1961)

Figure 29A–G

Pentathyone (?) *novacorona* Cherbonnier, 1961: 429, text-figs. 2, c–h, 3, 4 a.

Havelockia novacorona Clark & Rowe, 1971: 180 (dist.).

Diagnosis (after Cherbonnier, 1961)

Minute, cucumber-shaped species (holotype 5 mm in length). Colour greyish-white. Body covered with long feet, more numerous in the ambulacra, especially

ventrally where two series of feet are evident per ambulacrum. Anal teeth absent. Tentacles 10. Calcareous ring compact; radial plates entire, anteriorly bifid, each bearing two long slender posterior processes, each made up of 7–8 pieces of calcite; apex of interradial plates triangular, the latter with a concave posterior margin (Fig. 29G). Deposits of body wall exclusively tables with circular, quadrangular or elongated discs; some tables larger, with up to 20 perforations; spire two-pillared, top cross-shaped, each branch terminating into 2–4 teeth (Fig. 29B). Tube feet comprise curved, supporting tables with undulating margin; spire ending in 4–6 teeth (Fig. 29C); some tables lack spire and appear as rods (Fig. 29D); end-plates present (Fig. 29G). Branches of tentacles with short, slender, crinkly rods becoming larger towards the stalk and with smoother margins (Fig. 29E). Introvert supported by numerous heaps of rosettes (Fig. 29F).

Name-bearing type

MNHN.

Type locality

Nha Trang, South Vietnam (12° 8' N, 109° 13' 30'' E).

Habitat

Unknown.

Distribution

Known only from type locality, 14 m.

Remarks

Cherbonnier (1961) dubiously placed his new species in *Pentathyone* within the Sclerodactylinae although noting that the species also shared some affinities with *Havelockia*, then within the Thyoninae, which possesses similar two-pillared tables in the body wall. He perhaps overlooked Panning's (1949) decision to synonymize *Pentathyone* with *Havelockia*, which resulted in *Havelockia* now moving into the

Sclerodactylinae. Clark & Rowe (1971) realising Cherbonnier's error listed this species as *Havelockia novacorona*.

This species comes quite close to *H. pohaiensis* Liao (see remarks for *H. pohaiensis*) differing in the nature of the interradial plates of the calcareous ring and the composition of the introvert deposits.

Havelockia perdit (Koehler & Vaney, 1910)

Figure 29H–M

Cucumaria perdit Koehler & Vaney, 1910: 99, pl. iii, fig. 6–9.

Havelockia perdit Panning, 1949: 466.

Diagnosis (after Koehler & Vaney, 1910)

Small species, up to 22 mm in length; body slightly curved. Colour whitish. Tube feet arranged in two rows per ambulacrum, more numerous ventrally, few also scattered in interambulacra, more so dorsally; at extremities restricted to ambulacra. Anal teeth not mentioned. Tentacles 10, ventral pair reduced. Plates of calcareous ring short, fused, mosaic-like; radial processes longer than length of ring, also sub-divided (Fig. 29H). Deposits of body wall tables with irregular shaped disc with four central holes and few to many peripheral holes of variable size; spire short, two-pillared, ending in a crown of few teeth (Fig. 29L). Dorsal tube feet with slightly curved, supporting tables, disc with four central holes and 1–2 at each extremity; spire short, ending in a few teeth (Fig. 29I, K). Deposits of ventral tube feet similar but discs rod-like, with expanded middle; spire absent (Fig. 29J); end-plates not mentioned.

Name-bearing type

?Calcutta (= Kolkatta) Museum.

Type locality

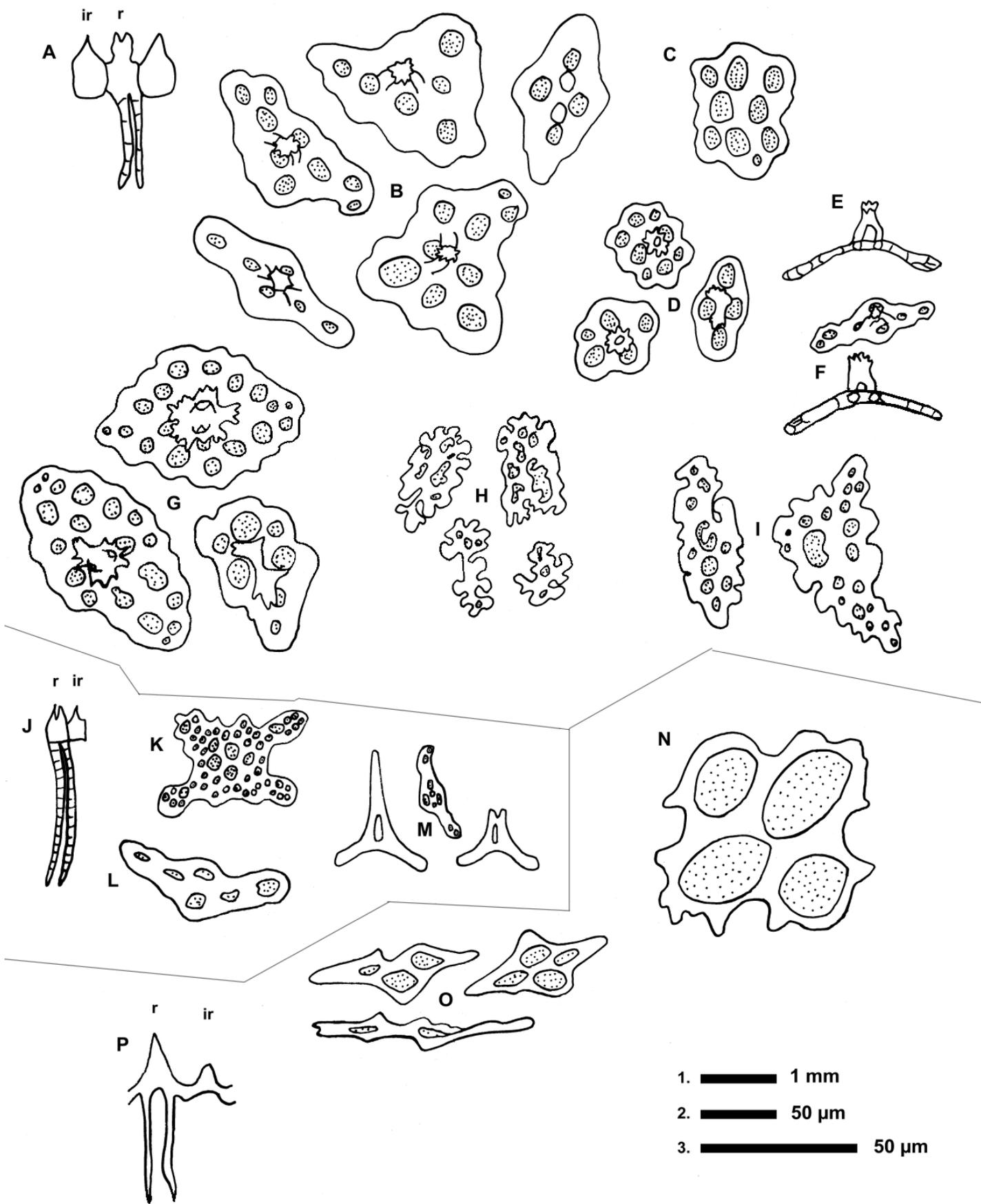
17° 59' N, 57° 22' 30'' E.

FIGURE 28

Havelockia ferali Cherbonnier. A. calcareous ring (r = radial plate; ir = interradial plate); B. tables of body wall; C. plate of body wall; D. tables of anal region; E, F. supporting tables of tube feet; G. tables of introvert; H. rosette-shaped bodies of tentacles; I. larger derivatives of these. A = Scale 1; G = Scale 2; B–F, H–I = Scale 3. Reproduced from Cherbonnier (1988).

Havelockia festina (Koehler & Vaney). J. calcareous ring (x 3); K. table of body wall; L. plate at base of tube feet; M. supporting tables of tube feet;. K–M = (x 370). Reproduced from Koehler & Vaney (1908).

Havelockia imbellis (Koehler & Vaney). N. plate of body wall (x 660); O. plates and rod of tube feet (x 660); O. calcareous ring (x 48). Reproduced from Koehler & Vaney (1910).



Habitat

Unknown.

Distribution

Known only from type locality, 285–366 m.

Remarks

This species has not been recorded since its description. Panning (1949) included it in *Havelockia* whose species he later moved to *Thyone*. Although fragmented, this species lacks the long, tubular calcareous ring of *Thyone*. The curved, supporting tables from the body wall (Fig. 29M) figured by Koehler & Vaney are perhaps due to contamination with tube feet deposits. Regrettably, the tentacle and introvert deposits were not examined. The whereabouts of the type material is uncertain but assumed to be in the Calcutta (= Kolkatta) Museum.

Havelockia pituitosa (Sluiter, 1901)

Figure 29N–O

Thyone pituitosa Sluiter, 1901: 94, pl. IV, fig. 7.

Pentathyone pituitosa Panning, 1949: 459.

Diagnosis (after Sluiter, 1901, amended herein)

Small species, holotype measuring 50 mm in length. Tube feet thin, long, crowded medially but distributed evenly over the ambulacra and interambulacra. Anal teeth absent. Tentacles 10, about the same length, poorly branched. Calcareous ring short, narrow; radial and interradial plates of calcareous ring entire, unfused, both deeply bifurcated anteriorly; radials with thin, long posterior processes, apparently also entire (Fig. 29N). Body wall ossicles large (up to 150 μm), well developed, overlapping tables with usually four large central holes and four accessory ones; spire two-pillared, of moderate height (up to 75 μm), terminally trifid, with each branch ending with a few teeth (Fig. 29O). Tables of tube feet with curved discs (Fig. 29P); end-plates not

mentioned. Tentacle deposits rods of variable form and size, trilobed, often with a side branch, appearing almost table-like. Introvert supported by tables with elongated disc, spire either reduced or well developed, and large plates of variable size, some spinous and some appearing rosette-like plus large tentacle-like rods.

Name-bearing type

ZMA, H1093.

Type locality

5° 40' S, 132° 26' E, 310 m.

Habitat

Fine grey mud.

Distribution

Known only from type locality.

Remarks

Despite being described from only a single specimen, Sluiter (1901) gives a very detailed description of his species, which remains well preserved at the ZMA. The tentacle and introvert deposits are here described from Thandar's examination of the type which he unfortunately did not illustrate.

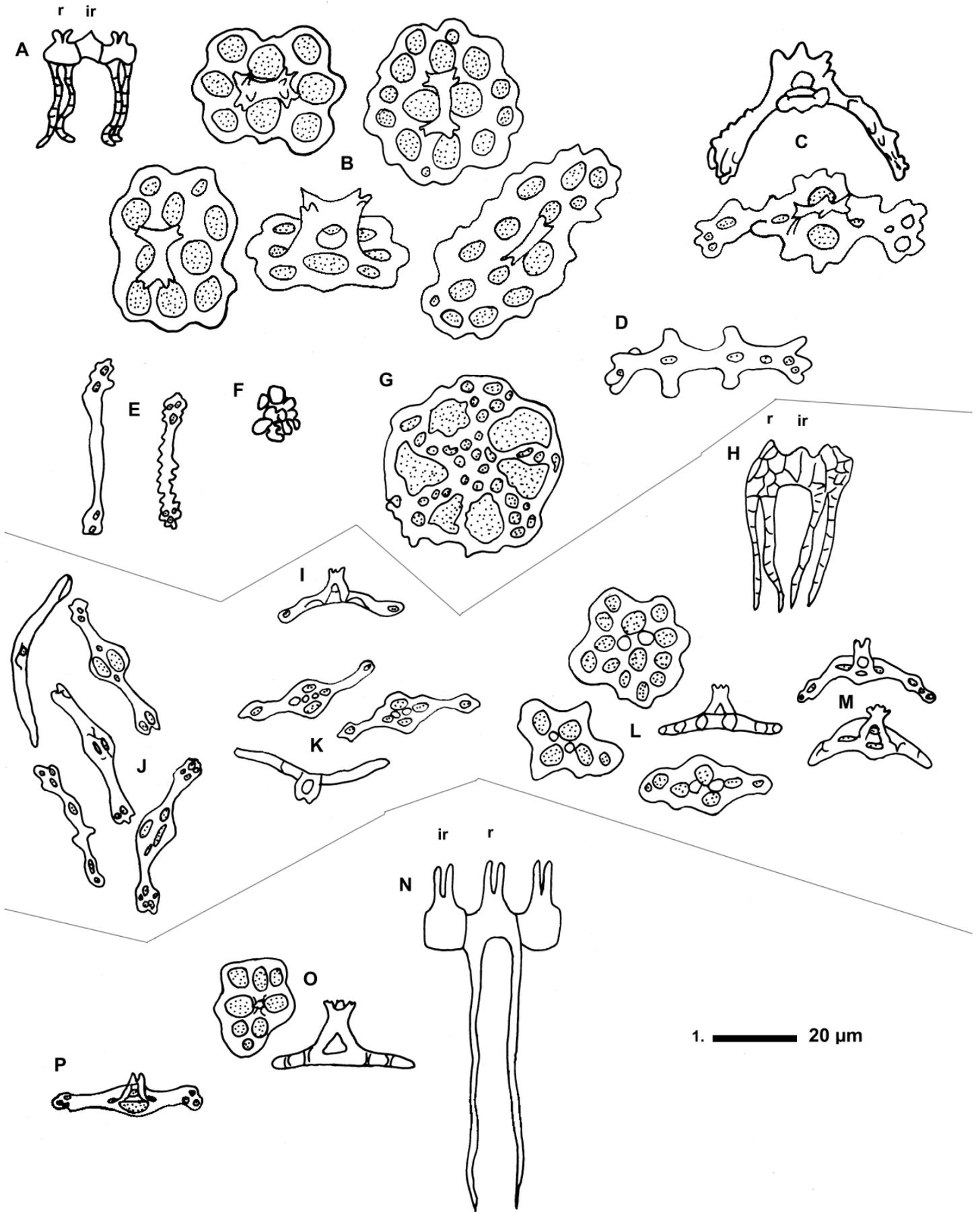
The nature of the calcareous ring is typically of the sclerodactyline type and hence Panning (1949) assigned this species to *Pentathyone* = *Havelockia* where it correctly stands.

FIGURE 29

Havelockia novacorona (Cherbonnier). A. calcareous ring (r = radial plate; ir = interradial plate) (x 18); B. tables of body wall; C. supporting tables of tube feet; D. rod of tube feet; E. rods of tentacles; F. rosette of introvert. B–F = Scale 1. Reproduced from Cherbonnier (1961).

Havelockia perditia (Koehler & Vaney). H. calcareous ring (x 10); I, K. supporting tables of dorsal tube feet (x 250 & 350 resp.); J. supporting tables of ventral tube feet (x 350); L. tables of dorsal body wall (x 350); M. ?tables of tube feet (x 350). Reproduced from Koehler & Vaney (1908).

Havelockia pituitosa (Sluiter). N. calcareous ring (x 4 as illustrated by Sluiter); O. tables of body wall; P. supporting table of tube feet. O, P drawn to scale as illustrated by Sluiter (1901).



Havelockia pohaiensis (Liao, 1986) comb. nov.

Figure 30A–G

Thyone pohaiensis Liao, 1986: 313, text-fig. 2

Diagnosis (after Liao, 1986)

Small species, up to 18 mm in length; body elongated to fusiform. Tube feet delicate, not crowded, in five bands radially, scattered in interambulacra; longer and more numerous ventrally. Anal teeth absent. Tentacles 10, ventral pair reduced. Calcareous ring compact, radial and interradial plates unfused; radials bifurcated anteriorly, with long posterior processes made up of several pieces of calcite (Fig. 30B). Body wall deposits numerous tables with oblong to roundish disc with normally eight perforations, sometimes 5–13; spire two-pillared, terminating in cross-shaped crown with 3–4 teeth on each arm (Fig. 30A). Tube feet with supporting tables with curved disc (Fig. 30C); end-plates well developed (Fig. 30F). Tentacle deposits numerous elongated rosettes and supporting rods which are forked and/or perforated at ends (Fig. 30G). Introvert and base of tentacles supported by numerous multilocular tables (Fig. 30E) and fewer minute rosettes (Fig. 30D).

Name-bearing type

IOAS-E00982.

Type locality

Cangshan, Yexian, Shandong Province, China.

Habitat

Sand.

Distribution

Gulf of Bohai, Bohai Sea, China, 5–10 m.

Remarks

Interestingly, Liao (1986) commented on the close affinity of this species with *Havelockia novacorona* Cherbonnier described from Vietnam but, despite this, still described his species in *Thyone*.

Indeed both species bear close resemblance with respect to the form of the calcareous ring, the cross-shaped nature of the crowns of the tables and similarity in the end-plates of the tube feet which, as mentioned by Cherbonnier (1961), are reminiscence of the genus *Havelockia*. However, the anterior end of the interradial plates in *H. pohaiensis* is slightly notched and much longer than in *H. novacorona* in which they are pointed and stout. Further, the spires of the body wall tables in *H. novacorona* are shorter and stout, and the discs with more numerous perforations (8–20), including some elongated discs. Furthermore, *H. pohaiensis* contains both multilocular tables and rosettes in the introvert, while *H. novacorona* has only rosettes.

Havelockia strangeri (Deichmann, 1941) comb. nov.

Figure 30H–L

Thyone strangeri Deichmann, 1941: 107, pl. 19, fig. 1–11.

Diagnosis (from Deichmann, 1941, amended herein)

Small species, up to 40 mm in length. Tube feet numerous, scattered all over the body, often with conical or wart-like base. Anal teeth not mentioned. Tentacles 10, ventral pair reduced. Calcareous ring with some incipient fragmentation, radial and interradial plates forming a short tube; radials slightly bifurcated anteriorly, with long posterior processes broken into four large pieces; interradials broad, united by sutures to the radials for more than half their length (Fig. 30H). Body wall deposits oblong, multilocular tables with thickened edge and varying number of knobs; spire, two-pillared, arch-like, short, becoming reduced (Fig. 30K). Tube feet with numerous supporting, tack-like tables with strongly curved disc; spire two-pillared, pillars mostly fused, ending in a single point (Fig. 30J); end-plate large. Tentacle deposits rosettes

(Fig. 30L) and delicate rods. Introvert supported by oblong tables with knobbed edge and low, toothed spire (Fig. 30I).

Name-bearing type

MCZ, no. 2142.

Type locality

Isle Grande, west Coast of Mexico.

Habitat

Unknown.

Distribution

Known only from type locality, > 13 m.

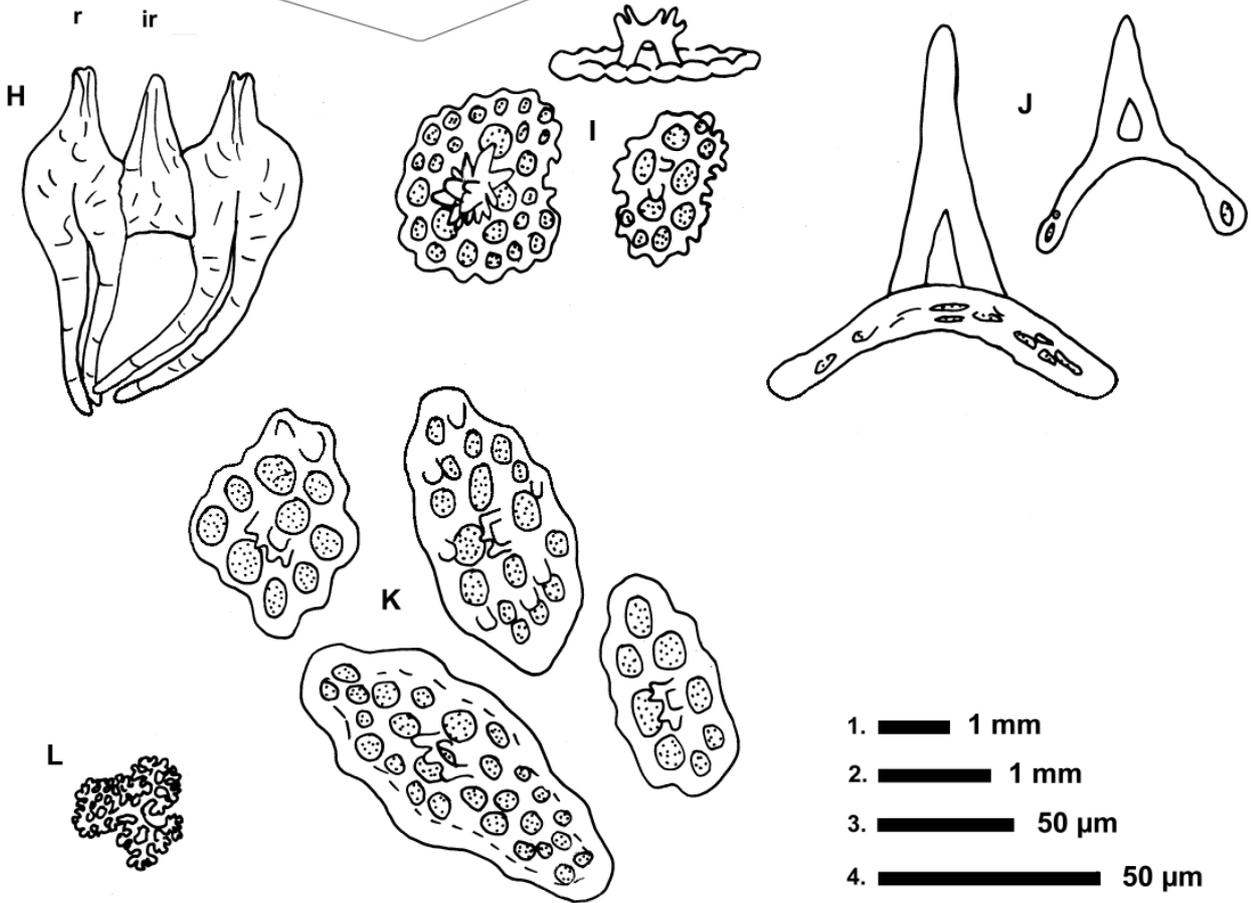
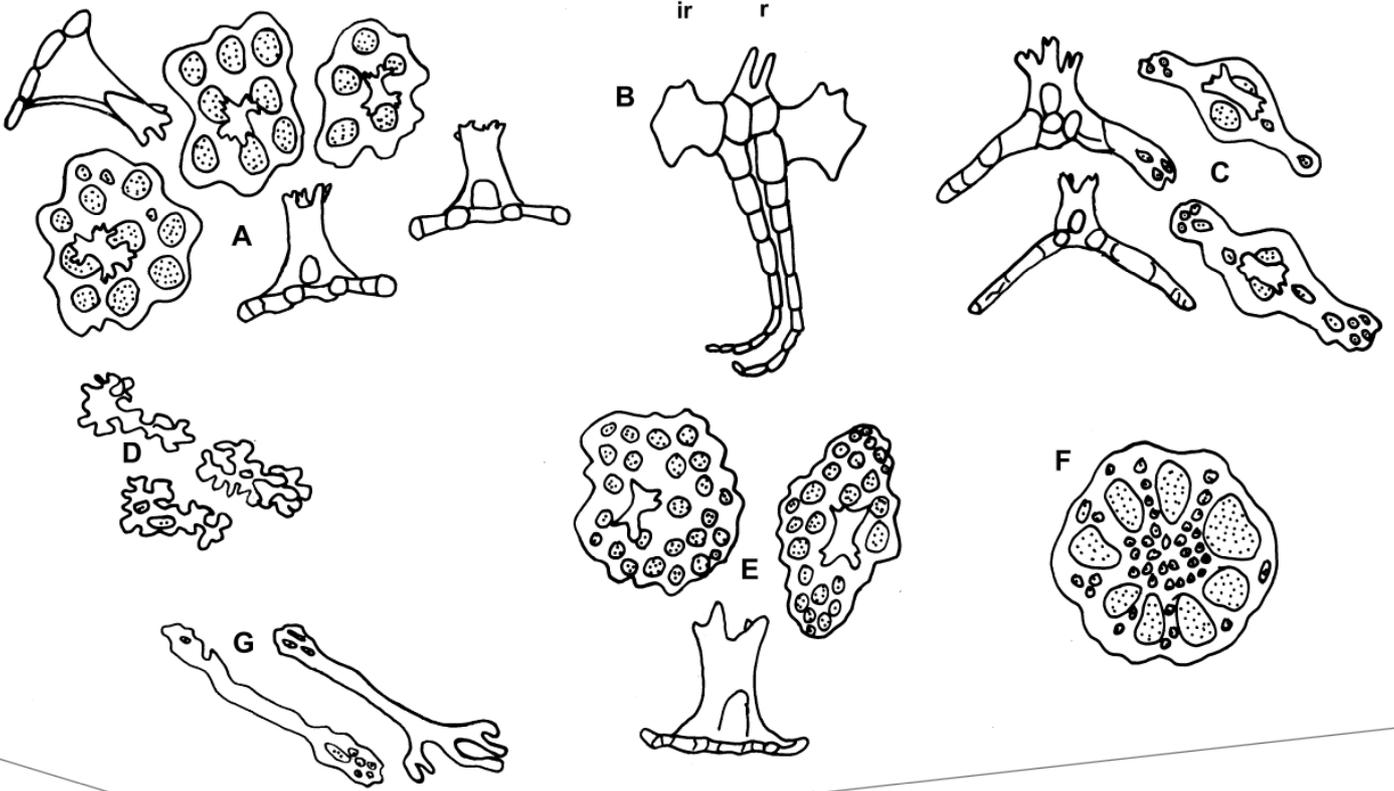
Remarks

This species was described from a single 40 mm holotype and has not been recorded since. Interestingly, Panning in his revision of the Cucumariidae, failed to mention this species or any of those *Thyone* species described by Deichmann (1941). Thandar's examination of the holotype noted a short calcareous ring with moderately long radial processes broken up into about four pieces. It is for this reason that this species is here moved out of *Thyone* and referred to *Havelockia*.

FIGURE 30

Havelockia pohaiensis Liao. A. tables of body wall; B. calcareous ring (ir = interradial plate; r = radial plate); C. supporting tables of tube feet; D. rosettes of introvert; E. tables of introvert; F. end-plate; G. rods of tentacles. A, C, E–F = Scale 3; B = Scale 2; D, G = Scale 5; H, J = Scale 5. Reproduced from Liao (1986).

Havelockia strangeri (Deichmann). H. calcareous ring; I. tables of introvert; J. supporting tables on tube feet; K. tables of body wall; L. rosette of tentacles. H = Scale 1; I–L = Scale 4. H reproduced from Thandar's examination of the material from the MCZ; other figures reproduced from Deichmann (1941).



- 1. 1 mm
- 2. 1 mm
- 3. 50 μ m
- 4. 50 μ m
- 5. 100 μ m

Havelockia tanyspeira (Pawson & Miller, 1988) comb. nov.

Figure 31A–P

Thyone tanyspeira Pawson & Miller, 1988: 311, text-figs. 1–4.

Diagnosis (after Pawson & Miller, 1988)

Small species, up to 26 mm in length; body crescent- or U-shaped. Colour in preservation tan to brown, feet white. Tube feet long, hair-like, numerous; restricted to ambulacra in juvenile and only at anterior and posterior ends of larger individuals. Anal teeth not mentioned. Tentacles 10, ventral pair reduced. Calcareous ring compact; radials bifurcate anteriorly with long, fragmented, posterior processes; interradials pointed anteriorly with concave posterior margin (Fig. 31F). Deposits of body wall oblong tables with undulating margin and 4–45 perforations, posterior tables smaller; spire two-pillared, reduced, lacking teeth, few spires more prominent ending in a single conical point; cross-shaped table discs also occur (Fig. 31A–G). Tube feet with numerous curved, oblong, supporting tables, discs perforated; spire two-pillared, high, frequently twisted, perforated or solid (Fig. 31H–L, N); end-plates well-developed (Fig. 31M). Tentacle deposits straight to C-shaped rods with enlarged perforated ends (Fig. 31O), more numerous in central stalk of tentacles. Introvert supported by circular to oblong rosettes (Fig. 31P).

Name-bearing type

USNM E34405.

Type locality

South east of Trinidad (10° 0.98' N, 60° 34.3' W to 10° 10.3' N, 60° 33.2' W, 55m).

Habitat

Smooth sand.

Distribution

Trinidad, Colombia and Honduras, 51–170 m.

Remarks

Pawson & Miller (1988) classified their new species in *Thyone* based upon the presence of two-pillared tables in the body wall and the nature of the calcareous ring. However, judging from their illustration, the ring appears to be very short, compact with long posterior processes, typical of many sclerodactylines. The holotype was studied by Thandar and lacks a calcareous ring explaining why the illustration made by Pawson & Miller was from a paratype.

This species is very distinct in the elongated, twisted spires of the tube feet tables unlike any of the other species of *Havelockia*.

Havelockia transitoria (Vaney, 1905)

Figure 31Q–T

Cucumaria transitoria Vaney, 1905: 187.

Thyone transitoria Panning, 1949: 467.

Athyone transitoria Cherbonnier, 1955: 164, pl. 44, fig. o–t.

Havelockia transitoria Clark & Rowe, 1971: 194.

Diagnosis (after Vaney, 1905 and Cherbonnier, 1955)

Small species, up to 16 mm in length; body more or less pentagonal in shape. Colour light brown interspersed with some brownish mottling. Tube feet in two rows in each ambulacrum, more visible ventrally, scattered irregularly in dorsal interambulacra. Anal teeth not mentioned. Tentacles 10, ventral pair reduced. Radial plates of calcareous ring notched anteriorly, with paired posterior processes made up of a series of pieces; anterior end of interradials ending in a conical point (Fig. 31Q). Body wall ossicles numerous small tables with oval, serrated and/or spinous disc 2–4 central holes and a few peripheral ones (Fig. 31R); spire short, two-pillared. Tube feet with reticulated plates; end-plates not mentioned. Tentacle deposits as rods, perforated at the ends (Fig. 31T), and some rosettes (Fig. 31S).

Name-bearing type

MNHN, EcHh no. 7109.

Type locality

Iles Musha (aka Iles Moucha), Grand Reef, Djibouti.

Habitat

Unknown.

Distribution

Northeast Africa, southern entrance to the Red Sea, 20 m.

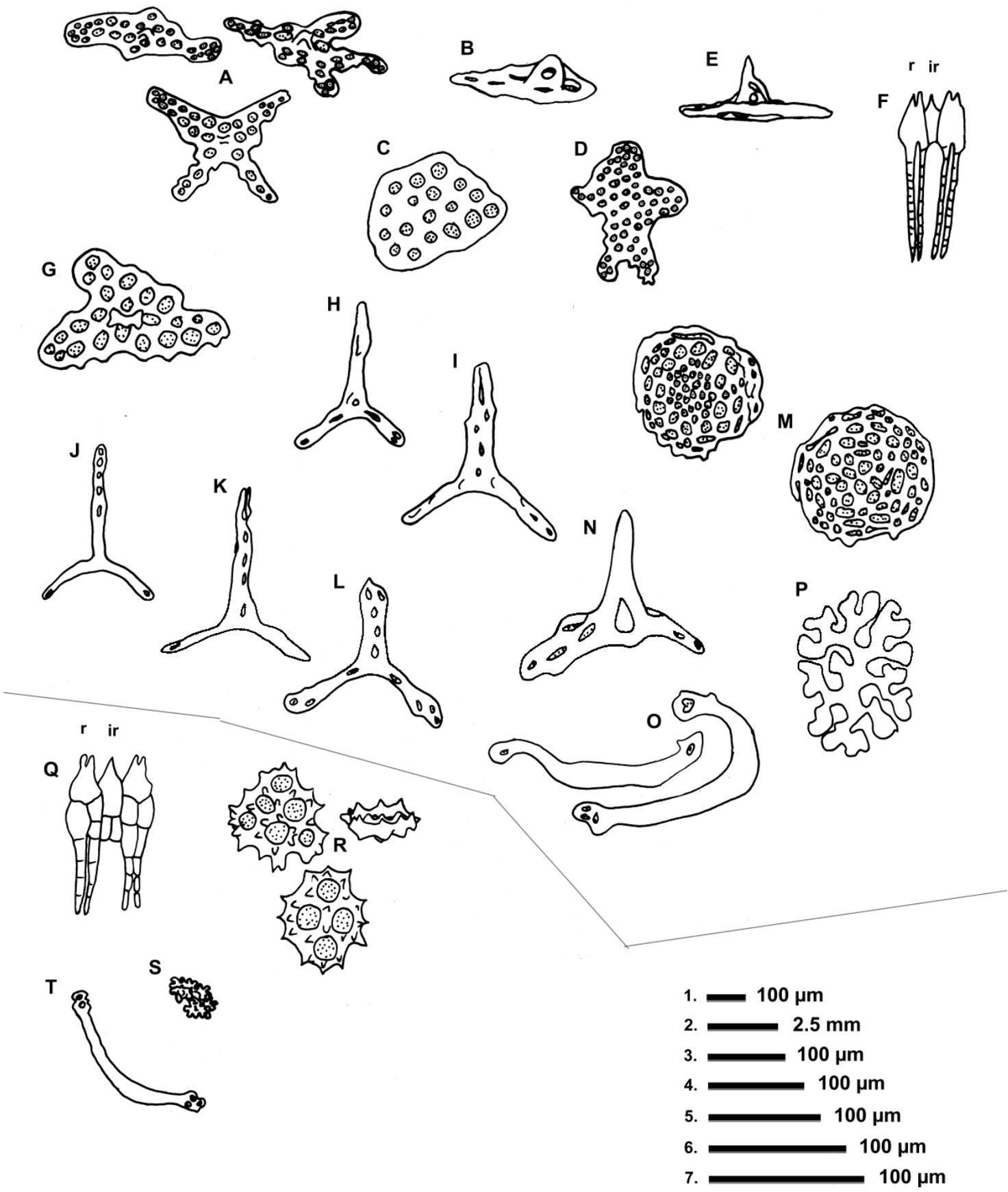
Remarks

Vaney (1905) did not illustrate the calcareous ring or ossicles of his new species which he assigned to *Cucumaria*. *C. transitoria* was re-assigned to *Thyone* by Panning (1949) after initially placing it in his *Havelockia* group. Cherbonnier (1955), after examining the type material, transferred the species to *Athyone*. Cherbonnier mentions that he failed to find any small tables mentioned by Vaney but only small plates with deeply indented margins and denticulate surfaces, which may be due to corrosion as he found only a few ossicles. Clark & Rowe (1971), after studying Vaney's description, re-assigned it to *Havelockia*, citing a congeneric status with that of Pearson's *herdmani*. This designation is here accepted.

FIGURE 31

Havelockia tanyspeira (Pawson & Miller). A, B. tables of dorsal body wall; C, D. tables of lateral body wall (inner surface); E. tables of anterior body wall; F. calcareous ring (r = radial plate; ir = interradial plate); G. table of ventral body wall; H. supporting table of dorsal tube feet; I. supporting table of ventral body wall; J, K, L. supporting tables of lateral tube feet; M. end-plates on ventral tube feet; N. supporting table of anterior tube feet; O. rods of tentacles; P. rosette of introvert. A = Scale 1; B–D, G = Scale 3; E = Scale 4; F = Scale 2; H–L = Scale 7; M = Scale 5; N–P = Scale 6. Reproduced from Pawson & Miller (1988).

Havelockia transitoria (Vaney). Q. calcareous ring (x 40); R. ?corroded tables of body wall; S. rosette of tentacles; T. rod of tentacles. R–T = Scale 3. Reproduced from Cherbonnier (1955).



Havelockia turrispinea Cherbonnier, 1988

Figure 32A–G

Havelockia turrispinea Cherbonnier, 1988: 184, text-fig. 79.

Diagnosis (modified from Cherbonnier, 1988)

Small species, up to 12 mm in length; body barrel-shaped. Tube feet long, distributed over entire body. Anal teeth not mentioned. Tentacles 8–13, ventral pair reduced in latter case. Both radial and interradial plates of the calcareous ring compact, anteriorly pointed; radials with long posterior processes broken up into several pieces of calcite, although not mosaic-like (Fig. 32C). Deposits of body wall large tables with squarish disc with usually four central holes and up to six peripheral ones, sometimes more; spire two-pillared, ending in a circular, tripartite or quadripartite crown, densely toothed, crown sometimes perforate (Fig. 32B); other tables less common with more irregular disc, with similar spires or spire top ending in a crown (Fig. 32A). Tube feet supported by simple curved rods perforated throughout surface (Fig. 32F) and curved supporting tables (Fig. 32G); end-plates not mentioned. Tentacle deposits numerous long, thin rods perforated at each end (Fig. 32D). Introvert supported by rosettes only (Fig. 32E).

Name-bearing type

MNHN, EcHh no. 2953.

Type locality

Mayotte Island, northern Dzaoudzi, Madagascar.

Habitat

Muddy to sandy bottom among *Heteropsammia* and a number of antipatharians, pennatulids and *Acropora*.

Distribution

Mayotte Island to Tuléar, Madagascar, 20 m.

Remarks

Thandar noted that the calcareous ring of the holotype is as illustrated by Cherbonnier (1988) except that the posterior processes are much thinner and of the same length as the radial plates. The ring itself is not fragmented and is short, typical of the sclerodactyline type.

Havelockia vankampeni (Sluiter, 1901)

Figure 32H–J

Thyone vankampeni Sluiter 1914: 8, fig 2 a–c.

Havelockia vankampeni Panning, 1949: 466.

Diagnosis (after Sluiter, 1901, amended herein)

Medium-sized species, up to 110 mm in length; body cucumber-like. Colour in alcohol dirty chestnut brown. Tube feet irregularly scattered over the whole body, more numerous in the ventral ambulacra. Anal teeth absent. Tentacles 10, ventral pair reduced. Calcareous ring high, short, with shorter processes on the radials (Fig. 32H). Deposits of body wall scarce four-holed tables with almost always an additional four smaller marginal holes; spire two-pillared, connected by a cross-bar almost at apex, of moderate size, taller in ventral tables, terminating in 1–2 teeth (Fig. 32I). Supporting tables of tube feet with elongated, curved discs, some similar to those of body wall (Fig. 32J); end-plates present. Tentacle deposits as slender rods, some rosette-like rods, and rosettes. Introvert supported by rosettes only.

Type material

ZMA, H2192 (1 *syntype*).

Type locality

Malay Archipelago.

Habitat

Unknown.

Distribution

Known only from type locality, 20–35 m.

Remarks

Sluiter (1901) noted great similarity of this species with *Thyone castanea* Lampert relegated to the synonymy of *T. papuensis* by Rowe and Gates (1995). However, Sluiter pointed out the differences in the form of the calcareous ring, calcareous deposits and the presence of only a single stone canal in his new species.

Panning (1949) placed this species within his *Havelockia* group which he characterised as having only tables in the introvert. Interestingly, when Thandar examined the type specimen housed in the ZMA, he noted only rosettes in the introvert; hence it is not clear if Panning examined the type or assigned it to *Havelockia* in error. Since Panning moved all his *Havelockia* species to *Thyone*, this species currently stands in *Thyone*. However, on the nature of the calcareous ring, it is clear that it belongs within *Havelockia*. *H. vankampeni* differs from the type species *H. versicolor* in possessing a shorter calcareous ring with even shorter processes compared to the length of the animal.

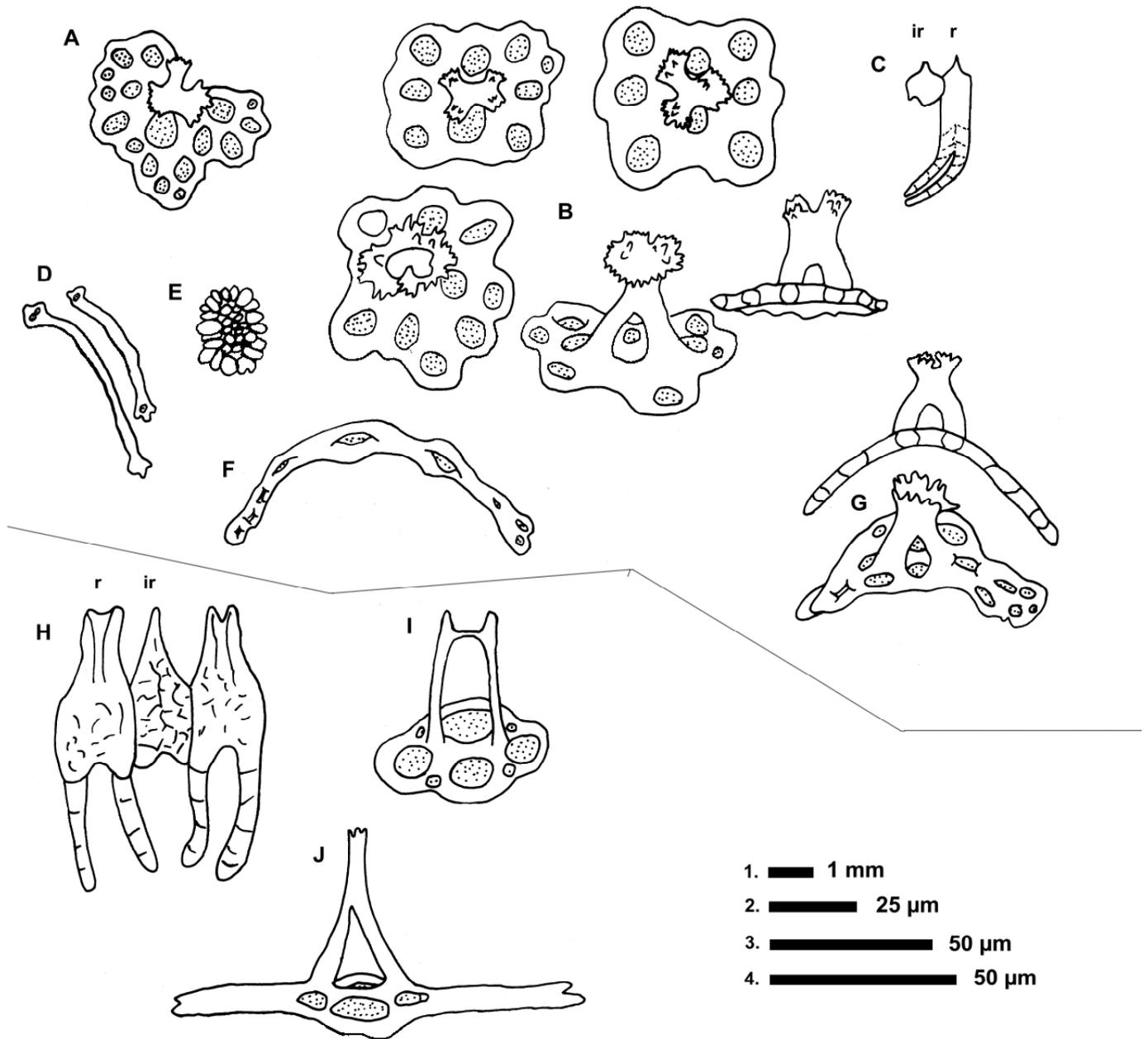


FIGURE 32. *Havelockia turrispinea* Cherbonnier. A, B. tables of body wall; C. calcareous ring (r = radial plate; ir = interradial plate); D. rods of tentacles; E. rosette of introvert; F. rod of tube feet; G. supporting tables of tube feet. A–B, D–G = Scale 7; C = Scale 2. Reproduced from Cherbonnier (1988).

Havelockia vankampeni (Sluiter). H. calcareous ring (x 4); I. table of body wall; J. supporting table of tube feet. I = Scale 3; J = Scale 6. E reproduced from Thandar's examination of the material at ZMA; I, J reproduced from Sluiter (1901).

***Havelockia versicolor* (Semper, 1868)**

Figure 33A–I

Cucumaria versicolor Semper, 1868: 49, pl. XII, fig. 4, pl. XIII, fig. 11, pl. XIV, fig. 8.

Thyone mirabilis Ludwig, 1875: 93, pl. 6, fig. 18; Lampert, 1885: 162; Théel, 1886: 138; Sluiter, 1901: 93; Kalk, 1958: 216.

Thyone mirabilis? Bell, 1884: 149.

Thyone (?) *calcarea* Pearson, 1903: 194

Havelockia herdmani Pearson, 1903: 197; Koehler & Vaney, 1908: 25; Panning, 1949: 466; Clark & Rowe, 1971: 180.

Cucumaria areolata Ekman, 1918: 35.

Pentathyone mirabilis H. L. Clark, 1938: 459, pl. 16, fig. 3; 1946: 396; Panning, 1949: 459, text-fig. 55.

Pentathyone versicolor Panning, 1949: 460

Thyone herdmani James, 1969: 60

Havelockia mirabilis Clark & Rowe, 1971: 180

Havelockia versicolor Clark & Rowe, 1971: 180, text-fig. 91b, 92h, pl. 29, fig. 13; James, 1976: 55, text-fig. 1a–f; Thandar: 1989: 294; Liao & Clark: 1995: 484, text-fig. 292.

Diagnosis (after James, 1976)

Medium-sized species, up to 130 mm in length; body more or less quadrangular in cross section, Colour in alcohol white to brownish. Tube feet scattered on dorsal surface, more numerous ventrally, in three rows; anal papillae present. Anal teeth absent. Tentacles 10, ventral pair reduced. Calcareous ring compact, short, tubular with posterior processes to the radial plates; interradials pointed anteriorly; ring and processes compact, more or less same length (Fig. 33A). Deposits of body wall sparse, comprising minute table discs with four central perforations, often with four or more smaller ones; spire tall, two-pillared, ending in 2–4 teeth, pillars often reduced to knobs on surface of disc or absent (Fig. 33B). Tube feet with irregular plates (Fig. 33C) and tables (Fig. 33E); end-plates present (Fig. 33D). Tentacle deposits as slender rods (Fig. 33F) and rosette/rosette-like rods (Fig. 33G). Introvert supported by tables with multilocular disc and tall spire ending in several teeth, arranged in two clusters (Fig. 33I), and rosettes (Fig. 33H).

Type material

NHMUK 1884.3.8.32 (*lectotype*); ZMH, E 2873 (*paralectotype*).

Type locality

Philippines.

Habitat

Coral.

Distribution

Indo-West Pacific extending to Inhaca Island, Mozambique, 0–59 m.

Remarks

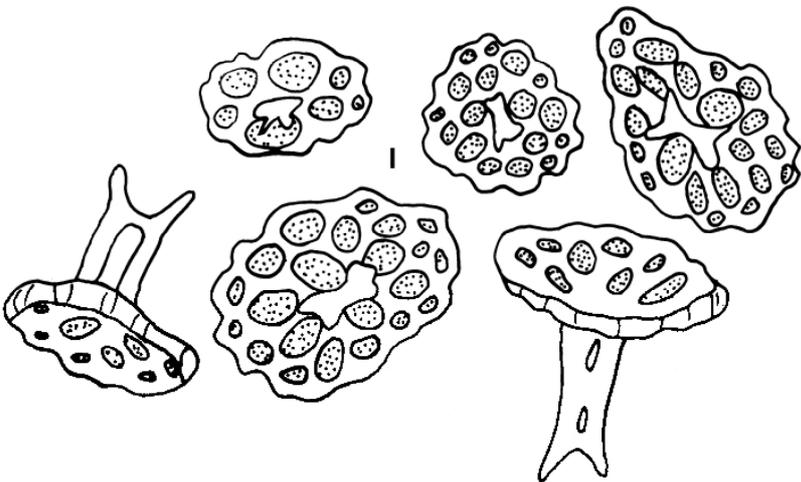
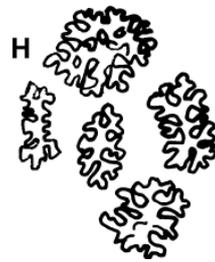
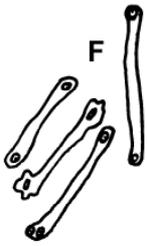
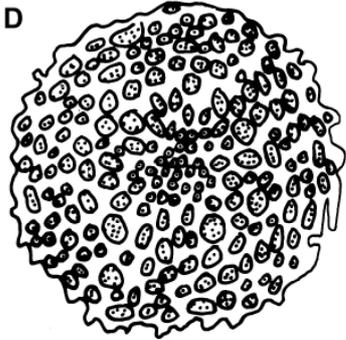
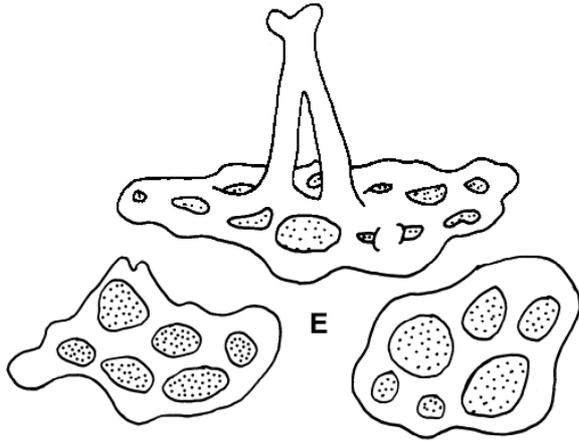
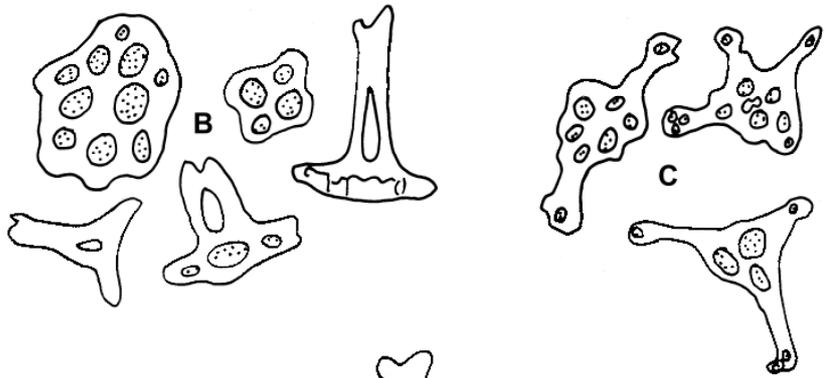
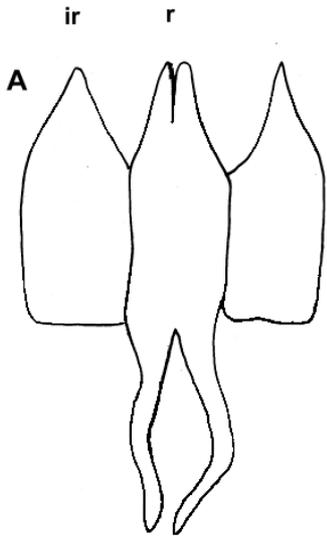
This species was first recorded from the Philippines as *Cucumaria versicolor* by Semper (1868). As discussed above, James (1976) synonymized *H. herdmani* Pearson and *T. mirabilis* Ludwig with *Cucumaria versicolor* Semper as a senior synonym.

It is unclear precisely how many specimens were present within Semper's material. However, he did record the length of his material to be 6–7 cm, implying the presence of more than one specimen. Hence, the ZMH and NHMUK specimens are probably from the same type material.

Examination of the type specimens of *C. versicolor* (E 2873 - ZMH), (1884.3.8.32 - NHMUK) and *T. mirabilis* (E 2891 - ZMH) agrees well with James's conclusions. Semper's type from the ZMH collections lacks all internal structures, probably lost or damaged during examination. The colour, however, appears whitish and slightly narrower when compared with Ludwig's type which appears more brownish, though there are tinges of white in-between the body wall. The NHMUK type is yellowish-brown and slightly larger than the ZMH one, still retaining most of its internal anatomy. The calcareous ring matches that of *T. mirabilis*. The variability in colour has been discussed by James (1976). All attempts, however, to locate Pearson's material were unsuccessful, even by Dr. Rowe (pers. comm.) at the Manchester and Liverpool Museum. Since the NHMUK specimen appears to be well preserved, it is here designated as a lectotype, with the other two ZMH specimens as paralectotypes, to stabilise the species.

FIGURE 33

Havelockia versicolor (Semper). A. calcareous ring of type of *Thyone mirabilis* Ludwig (E2891) (ir = interradial plate; r = radial plate); B. tables of body wall; C. plates of tube feet; D. end-plate; E. tables of tube feet; F. rods of tentacles; G. rosettes/rosette-like rods of tentacles; H. rosettes of introvert; I. tables of introvert. A = Scale 1; B, F–H = Scale 2; E = Scale 3; D = Scale 4; I = Scale 5. B, D, E, I reproduced from NHMUK specimen (1884.3.8.32), C, F–H from James (1976).



- 1. — 1 mm
- 2. — 50 μm
- 3. — 100 μm
- 4. — 100 μm
- 5. — 50 μm

CONCLUDING REMARKS

It is here argued that the basis of the erection of the family Sclerodactylidae (*sensu* Pawson & Fell, 1965) was erroneous, perhaps due to a mistranslation or misinterpretation of Panning's (1949) diagnosis of the Sclerodactylinae or a *lapsus calumni*. Pawson & Fell characterized the family Sclerodactylidae as having unbroken or entire processes to the radial plates of the calcareous ring, thus separating this family from the Phyllophoridae which they characterized as possessing divided processes. It must be here noted that Panning diagnosed the subfamily Sclerodactylinae as possessing an undivided calcareous ring in which the processes of the radial plates are broken into a few large pieces and only as an exception are they unbroken. Despite this, Pawson & Fell regarded the exception as a key character to separate their Sclerodactylidae from their Phyllophoridae. Thus, on this basis alone, the elevation of the Sclerodactylinae to family rank is clearly unjustified even if the Cladolabinae is included within the Sclerodactylidae. Even if Pawson & Fell implied unbroken plates instead of unbroken processes, this would constitute a *lapsus calumni* and would be the only character uniting the subfamilies within the Sclerodactylidae. However, there are some sclerodactylids in which the plates are broken and many phyllophorids in which the plates are unbroken.

This observation is in agreement with Thandar (1989) who commented that the Sclerodactylidae (*sensu* Pawson & Fell) contains seemingly unrelated forms, although some would appear to be transitional between the Phyllophoridae and the Cucumariidae. The latter family is characterized by a simple calcareous ring but contain some forms with rudimentary/reduced processes. Thandar further speculated that these families perhaps originated from the same lineage where there was a gradual reduction in the plates and processes of the calcareous ring on the basis of Fell's (1965) supposition that there was a reduction of the ambulacral plate system in fossil edrioasteroids during holothuroid evolution thus producing the calcareous ring. This implies that the Cucumariidae with their simple ring would be the most recently derived family, arising from the Phyllophoridae with a complex calcareous ring through the Sclerodactylidae. Rowe (pers. comm.), alternatively, believes that the complex, tubular calcareous ring of the phyllophorids is perhaps an adaptation to aid in burrowing since it

is best developed in such forms. This speculation may be true implying that the complex calcareous ring is a new development in the dendrochirotids, hence contradicting or negating Fell's viewpoint of the reduction of the ambulacral plate system of fossil edrioasteroids. Whatever the case may be, the writer is in agreement with Thandar (1989) that the Sclerodactylidae (*sensu* Pawson & Fell) does bridge the gap between the Phyllophoridae and the Cucumariidae. Even if the family-group taxon Sclerodactylidae is dispensed with as proposed here, one can still see a continuum of the reduction of the calcareous ring within the 10-tentacled dendrochirotids from the Thyoninae through the Sclerodactylinae, through the Sclerothyoninae to the Cucumariidae. Alternatively, if Rowe's viewpoint is true then one must argue for the advancement of the calcareous ring from the Cucumariidae to the Phyllophoridae. Similarly, amongst the polytentaculate forms there also appears to be such a reduction of the ring from the very complex Semperiellinae through the Phyllophorinae and Cladolabinae to the Thyonidiinae (or an elaboration from the Cladolabinae through to the Semperiellinae).

This theory is supported by Arndt et al. (1996) who suggested that, based on mitochondrial DNA sequence analysis, the Sclerodactylidae and Phyllophoridae lineage separated earlier from the Cucumariidae. Furthermore, their analysis of IrRNA gene sequence data support a close relationship between the Sclerodactylidae and the Phyllophoridae, commenting that the only character separating both families is the form of the calcareous ring. However, their analysis was based upon a few representatives of each family and more species should be examined to support their conclusions.

Based on the arguments presented above, the Sclerodactylidae as a family-group taxon is abandoned in this work and its three subfamilies are considered as subfamilies of the Phyllophoridae which now contains six subfamilies. The latter family is now characterized by forms with complex calcareous rings made up of divided or undivided radial and interradial plates and long to short, usually divided, paired radial processes. Whether the calcareous ring is tubular or not should not form the key diagnostic feature of this family, which has been done here. The other polytentaculate phyllophorids, i.e. the Phyllophorinae and Semperiellinae, must be retained as subfamilies within the Phyllophoridae but do not constitute the subject of this investigation.

Of the eleven genera previously described within the Sclerodactylinae, *Neopentamera* Deichmann is here transferred to the Sclerothyoninae. *Lisacucumis* is

proposed for *Neothyone* Deichmann which is preoccupied. Of the six genera within the Thyoninae, *Thorsonia* Heding is transferred to the Sclerodactylinae, and hence only five genera remain, some of which are re-diagnosed because of the inclusion of more species within them, and now includes 88 species. The Sclerodactylinae still contains eleven genera with 47 species while the Sclerothyoninae now includes three genera with eight species.

It is repeatedly emphasized that *Thyone* Jaeger has, over time, become a “supergen­us” (*sensu* Pawson & Miller, 1981) since all 10-tentacled (8 + 2) species with scattered tube feet, a complex calcareous ring and two-pillared tables in the body wall were lumped together and described in *Thyone*, a genus which became a receptacle for all such forms. Panning (1949) separated his original *Havelockia* group from *Thyone* by the presence of tables only in the introvert in the former and rosettes only in the latter, but included both genera within the Thyoninae. However, in the addendum of the same paper he transferred *Havelockia*, with its type species *H. herdmani*, into the Sclerodactylinae, with *Pentathyone* as a junior synonym, and stated that the other species he placed within his original *Havelockia* group be transferred to *Thyone*. This implied that there now existed two groups of species within *Thyone* based upon the composition of their introvert deposits. Pawson & Miller (1981) attempted to re-diagnose the genus when they identified a third group of species within *Thyone* from the Western Atlantic with tables and rosettes in the introvert. Panning as well as Pawson & Miller were obviously unaware that as early as 1940 Heding redescribed *T. dura* and Madsen (1941) the type species, *T. fusus*, with both tables and rosettes in the introvert. Thandar (1990) suggested a fourth group with rods and plates in the introvert, however the rods are here believed to be contamination with tentacle deposits.

Thandar & Rajpal (1999b) mentioned three types of calcareous rings within *Thyone*: those with the radial plates prolonged beyond the posterior border of the interradial plates before bifurcating (Fig. 34A); those with the interradials prolonged (deeply incised radials) (Fig. 34B) and those where the radial plates bifurcate at the posterior border of the interradials (i.e. both radial and interradial plates are of same length) (Fig. 34C). Thandar (2001) experimented with using the type of ring in an attempt to divide the “supergen­us” into smaller, more manageable groups. He found some correlation, albeit with exceptions, with the type of ring and the geographical

distribution of the various species, except for the Indo-West Pacific forms which were represented by all three types of rings. This, Thandar (pers. comm.) suggest was not extraordinary as most of our marine fauna originated from the central Indo-West Pacific region (Indo-Malayan Archipelago). Thus, as species evolved and moved away, a standard form of calcareous ring with one or two exceptions became dominant in a particular geographical region. Thandar (2001), however, refrained from proposing any new subgeneric taxa or groups because of the lack of any other correlation and the fact that the calcareous ring has thus far only been used to separate suprageneric taxa and that the interradial plates do lengthen with age (Heding, 1940; Deichmann, 1947) as suggested by Thandar & Rajpal (1999b). Furthermore, the length of the plates of a ring may vary even within a single specimen (Madsen, 1941) (Fig. 34D).

After critical assessment of *Thyone* herein, there now remain within the genus only 46 species out of 66. Based on Panning's (1949) use of introvert deposits, seven groups of species have been formulated within the genus: tables only (8 spp.), rosettes only (5 spp.), tables and rosettes (21 spp.), tables and plates/?reduced tables (2 spp.), rosettes and plates/?reduced tables (3 spp.), plates only (2 spp.), or introvert deposits absent or unknown (5 spp.). Such an approach simplifies the handling of the genus. It is rather unfortunate that no other character was found in correlation with the introvert deposits to enable the elevation of each group to the level of a subgenus. Hence, these groups should be regarded as purely artificial units.

Though the extent of Panning's (1949) work is remarkable, it included many errors since he relied too heavily on the original descriptions of species without referring to the works of some re-describers who did provide new information prior to his revision. Furthermore, he excluded from his revision many species whose calcareous rings were not illustrated in their original description, particularly those of Deichmann (1941).

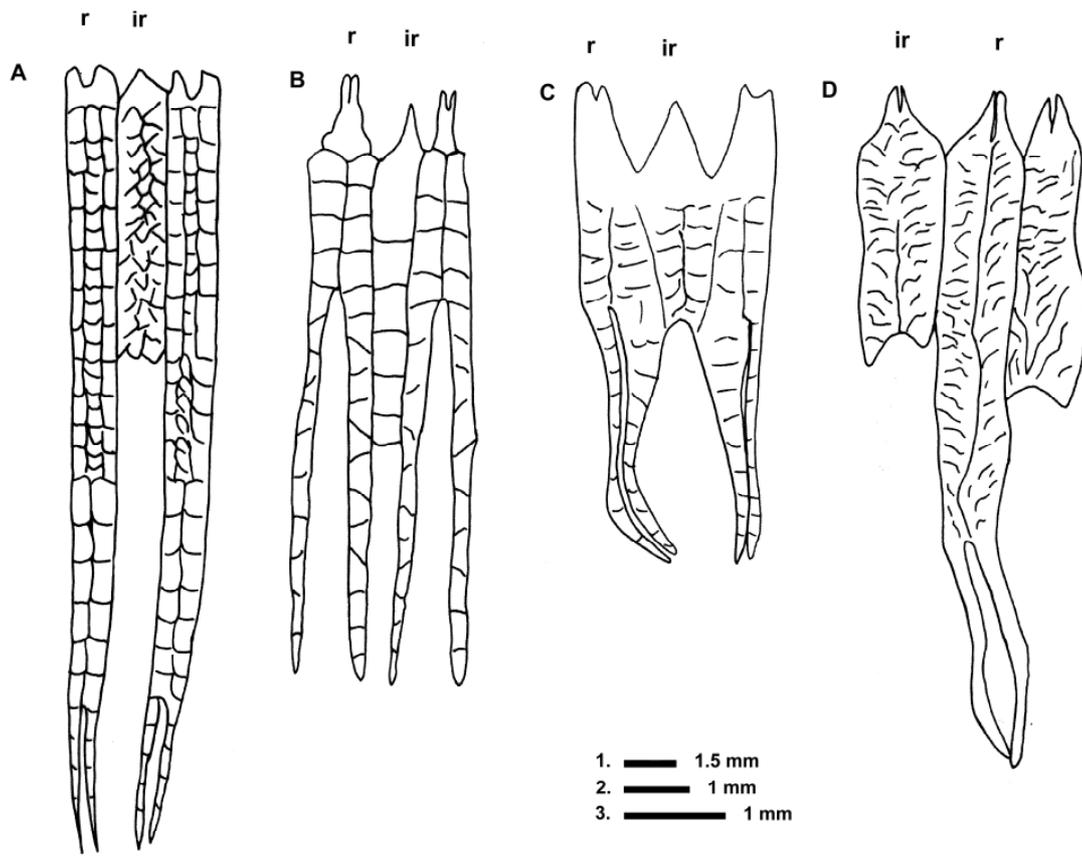


FIGURE 34. Types of calcareous ring in *Thyone*. A. *Thyone purpureopunctata* Liao & Pawson - radial plates prolonged beyond the posterior border of the interradial plates before bifurcating (r= radial plates; ir = interradial plate), Scale 3, reproduced from Liao & Pawson (2001); B. *T. propinqua* Cherbonnier - interradials prolonged (deeply incised radials), Scale 3, reproduced from Cherbonnier (1970); C. *T. nigra* Joshua & Creed - radial plates bifurcate at the posterior border of the interradials (same length), Scale 1, reproduced from Thandar's examination of the material from the NHMUK. D. *Thyone fusus* (Müller) - variability in length of interradial plates in same specimen Neotype, Scale 2.

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Appendix 1: Nominal list of *Thyone* Jaeger species listed by Panning (1949), those excluded by him and those subsequently described and their disposition herein.

Nominal Species	Current Status	Disposition herein
<i>adinopoda</i> Pawson & Miller, 1981	transferred to the Sclerothyoninae (this work)	<i>Sclerothyone adinopoda</i>
<i>alba</i> H.L. Clark, 1938	synonym of <i>T. dura</i> by Heding 1940	
<i>anomala</i> Östergren, 1898	unchanged	<i>Thyone anomala</i>
<i>ardens</i> (Koehler & Vaney, 1908)	moved to <i>Havelockia</i> (this work)	<i>Havelockia ardens</i>
<i>ariana</i> (Koehler & Vaney, 1908)	moved to <i>Havelockia</i> (this work)	<i>Havelockia ariana</i>
<i>articulata</i> Vaney, 1908	type species of <i>Thyonina</i> Thandar 1990	<i>Thyonina articulata</i>
<i>aurea</i> (Quoy & Gaimard, 1834)	unchanged	<i>Thyone aurea</i>
<i>avenusta</i> Cherbonnier, 1970	unchanged	<i>Thyone avenusta</i>
<i>axiologa</i> H.L. Clark, 1938	moved to <i>Stolus</i> (this work)	<i>Stolus axiologa</i>
<i>bacescoi</i> Cherbonnier, 1972	unchanged	<i>Thyone bacescoi</i>
<i>benti</i> Deichmann, 1937	unchanged	<i>Thyone benti</i>
<i>bicornis</i> Ohshima, 1915	unchanged	<i>Thyone bicornis</i>
<i>bidentata</i> Deichmann, 1941	unchanged	<i>Thyone bidentata</i>
<i>calcarea</i> Pearson, 1903	synonym of <i>Havelockia versicolor</i> by James 1976	<i>Havelockia versicolor</i>
<i>carens</i> Cherbonnier, 1988	unchanged	<i>Thyone carens</i>
<i>castanea</i> Lampert, 1889	synonym of <i>Thyone papuensis</i> by Rowe & Gates 1995	
<i>charlottae</i> (Deichmann, 1938)	transferred back to <i>Pentamera</i> by Lambert (1998)	<i>Pentamera charlottae</i>
<i>cherbonnieri</i> Reys, 1959	unchanged	<i>Thyone cherbonnieri</i>
<i>comata</i> Cherbonnier, 1988	unchanged	<i>Thyone comata</i>
<i>conjungens</i> (Semper, 1868)	transferred to <i>Stolus</i> by Clark & Rowe 1971	<i>Stolus conjungens</i>
<i>crassidisca</i> Pawson & Miller, 1981	moved to <i>Stolus</i> (this work)	<i>Stolus crassidiscus</i>
<i>crebrapodia</i> Cherbonnier, 1988	unchanged	<i>Thyone crebrapodia</i>
<i>deichmannae</i> Madsen, 1941	unchanged	<i>Thyone deichmannae</i>
<i>discolor</i> (Sluiter, 1901)	moved to <i>Havelockia</i> (this work)	<i>Havelockia discolor</i>
<i>dura</i> Koehler & Vaney, 1908	unchanged	<i>Thyone dura</i>
<i>falcata</i> (Sluiter, 1901)	unchanged	<i>Thyone falcata</i>
<i>fastigata</i> (Sluiter, 1901)	unchanged	<i>Thyone fastigata</i>
<i>festina</i> Koehler & Vaney, 1908	moved to <i>Havelockia</i> (this work)	<i>Havelockia festina</i>

<i>flexus</i> Hodge, 1867	possible senior synonym of <i>T. gadeana</i> relegated to the synonymy of <i>T. fusus</i> with doubt (this work)	
<i>fusca</i> Pearson, 1903	suspected by Rowe (pers comm.) to be a synonym of <i>H. herdmani</i> = <i>H. versicolor</i>	
<i>fuscus</i> (Müller, 1776)	unchanged	<i>Thyone fusus</i>
<i>fuscus chinensis</i> Yang, 1937	Liao & Clack 1995 suspect Yang's slide might have been contaminated with sponge spicules	
<i>fuscus mediterranea</i> Madsen 1941	???	
<i>fuscus papuensis</i> Théel, 1886	synonym of <i>Thyone papuensis</i> by Rowe and Gates 1995	
<i>gadeana</i> Perrier, 1902	unchanged	<i>Thyone gadeana</i>
<i>grisea</i> H.L. Clark, 1938	unchanged	<i>Thyone grisea</i>
<i>guillei</i> Cherbonnier, 1988	unchanged	<i>Thyone guillei</i>
<i>herberti</i> Thandar & Rajpal, 1999	unchanged	<i>Thyone herberti</i>
<i>hirta</i> Cherbonnier, 1970	unchanged	<i>Thyone hirta</i>
<i>hornelli</i> Pearson, 1903	synonym of <i>Phyllophorus (Urodemella) brocki</i> according to Heding & Panning, 1954	<i>Phyllophorus (Urodemella) brocki</i>
<i>imbellis</i> Koehler & Vaney, 1908	transferred to <i>Havelockia</i> (this work)	<i>Havelockia imbellis</i>
<i>imperfecta</i> Cherbonnier, 1970	unchanged	<i>Thyone imperfecta</i>
<i>inermis</i> (Heller, 1868)	unchanged	<i>Thyone inermis</i>
<i>infusca</i> Cherbonnier, 1954	unchanged	<i>Thyone infusca</i>
<i>longicornis</i> Cherbonnier, 1988	unchanged	<i>Thyone longicornis</i>
<i>longidentis</i> Hutton, 1872	moved to <i>Pentadactyla</i> by Pawson 1963	<i>Pentadactyla longidentis</i>
<i>micra</i> H.L. Clark, 1938	unchanged	<i>Thyone micra</i>
<i>montereyensis</i> (Deichmann, 1938)	transferred back into <i>Pentamera</i> by Lambert, 1998	<i>Pentamera montereyensis</i>
<i>neofusus</i> Deichmann, 1941	transferred to the Sclerothyoninae (this work)	<i>Sclerothyone neofusus</i>
<i>nigra</i> Joshua & Creed, 1915	unchanged	<i>Thyone nigra</i>
<i>nozowai</i> Mitsukuri, 1912	transferred to the Sclerothyoninae (this work)	<i>Temparena nozawai</i>
<i>okeni</i> Bell, 1884	unchanged	<i>Thyone okeni</i>
<i>papuensis</i> Théel, 1886	unchanged	<i>Thyone papuensis</i>
<i>parafusus</i> Deichmann, 1941	moved to <i>Stolus</i> (this work)	<i>Stolus parafusus</i>
<i>pawsoni</i> Tommasi, 1972	moved to <i>Stolus</i> (this work)	<i>Stolus pawsoni</i>
<i>pedata</i> Semper, 1868	unchanged	<i>Thyone pedata</i>
<i>perdita</i> Koehler & Vaney, 1908	transferred to <i>Havelockia</i> (this work)	<i>Havelockia perdita</i>

<i>pituitosa</i> Sluiter, 1901	moved to <i>Pentathyone</i> = <i>Havelockia</i> by Panning 1949	<i>Havelockia pituitosa</i>
<i>pohaiensis</i> Liao, 1986	transferred to <i>Havelockia</i> (this work)	<i>Havelockia pohaiensis</i>
<i>proceracorona</i> Cherbonnier, 1952	declared growth stage of <i>T. aurea</i> & synonym by Thandar 1990	
<i>profusus</i> Cherbonnier & Féral, 1981	unchanged	<i>Thyone profusus</i>
<i>propinqua</i> Cherbonnier, 1970	unchanged	<i>Thyone propinqua</i>
<i>pseudofusus</i> Deichmann, 1930	moved to <i>Stolus</i> (this work)	<i>Stolus pseudofusus</i>
<i>purpureopunctata</i> Liao & Pawson, 2001	unchanged	<i>Thyone purpureopunctata</i>
<i>quadruperforata</i> Cherbonnier, 1954	uncertain affinity to <i>Thyone</i>	unassigned
<i>roscovita</i> Hérouard, 1889	unchanged	<i>Thyone roscovita</i>
<i>scabra</i> Verrill, 1873	unchanged	<i>Thyone scabra</i>
<i>secunda</i> Vaney, 1908	uncertain affinity to <i>Thyone</i>	unassigned
<i>sinensis</i> Liao & Pawson, 2001	unchanged	<i>Thyone sinensis</i>
<i>sineturra</i> Cherbonnier, 1988	unchanged	<i>Thyone sineturra</i>
<i>spinifera</i> Liao, 1995	unchanged	<i>Thyone spinifera</i>
<i>strangeri</i> Deichmann, 1941	transferred to <i>Havelockia</i> (this work)	<i>Havelockia strangeri</i>
<i>striata</i> (Joshua & Creed, 1915)	synonym of <i>Mensamaria intercedens</i> (Lampert, 1885)	
<i>tanyspeira</i> Pawson & Miller, 1988	transferred to <i>Havelockia</i> (this work)	<i>Havelockia tanyspeira</i>
<i>theeli</i> Rowe, 1995	unchanged	<i>Thyone theeli</i>
<i>turissolida</i> Cherbonnier, 1954	declared growth stage of <i>T. aurea</i> by Thandar 1990	
<i>uniannulata</i> Sluiter, 1901	moved to <i>Stolus</i> (this work)	<i>Stolus uniannulata</i>
<i>vadosa</i> Cherbonnier, 1988	unchanged	<i>Thyone vadosa</i>
<i>vankampeni</i> Sluiter, 1914	transferred to <i>Havelockia</i> (this work)	<i>Havelockia vankampeni</i>
<i>venusta</i> Selenka, 1867	unchanged	<i>Thyone venusta</i>
<i>venustella</i> Ludwig & Heding, 1935	unchanged	<i>Thyone venustella</i>
<i>vilis</i> (Sluiter, 1901)	unchanged	<i>Thyone vilis</i>
<i>villosa</i> Semper, 1868	unchanged	<i>Thyone villosa</i>
<i>wahrbergi</i> Madsen, 1941	synonym of <i>T. gadeana</i> by Reys 1959	