


## *Actinopyga atypica* sp. nov. plus two new holothuroid records from the coastal waters of Pakistan (Echinodermata: Holothuroidea)


QURATULAN AHMED<sup>1\*</sup>, AHMED S. THANDAR<sup>2</sup>, QADEER MOHAMMAD ALI<sup>1</sup> & IQRA SHAIKH<sup>1</sup>


<sup>1</sup>The Marine Reference Collection and Resource Centre, University of Karachi, Karachi, 75270 Pakistan

<sup>2</sup>School of Life Sciences, University of KwaZulu-Natal, P/Bagx 54001, Durban 4000, South Africa

✉ [quratulanahmed\\_ku@yahoo.com](mailto:quratulanahmed_ku@yahoo.com);  <https://orcid.org/0000-0002-7597-2483>

✉ [thandara@ukzn.ac.za](mailto:thandara@ukzn.ac.za);  <https://orcid.org/0000-0002-7368-5560>

✉ [qmali@uok.edu.pk](mailto:qmali@uok.edu.pk);  <https://orcid.org/0000-0002-0499-0801>

✉ [iqrashahban@hotmail.com](mailto:iqrashahban@hotmail.com);  <https://orcid.org/0000-0003-2482-1631>

\*Corresponding author: ✉ [quratulanahmed\\_ku@yahoo.com](mailto:quratulanahmed_ku@yahoo.com)

### Abstract

A new species, *Actinopyga atypica* sp. nov., in the sea cucumber family Holothuriidae, plus two new holothuroid records from the Pakistan coastal waters are here described. The new species differs from all known species of *Actinopyga* in possessing a cucumariid-type of calcareous ring accompanied by slender, straight, terminally forked rods in the body wall, unlike the thick, usually well-branched rods of other species of the genus, setting it apart from all known congeners. Of the two additional records one is another holothuriid herein attributed to the Indo-West Pacific species *Holothuria* (*Selenkothuria*) *erinacea* Semper, 1868. It is suspected to be a juvenile of this species in possessing, in addition to the perforated rods and plates in the body wall, well-formed tables, suspected to be a juvenile character, as pertains in its consubgenerics *H. (S.) parva* Krauss (in Lampert, 1885) and *H. (S.) moebii* Ludwig, 1883. The third species is a thyonid, *Thyonina bijui* Thandar, 2017, belonging to the family Thyonidae (*sensu* Smirnov 2012), originally described from Kerala, India.

**Key words:** North Arabian Sea, teatfish, Holothuriida, Thyonidae, *Holothuria*, *Selenkothuria*, *Thyonina*

### Introduction

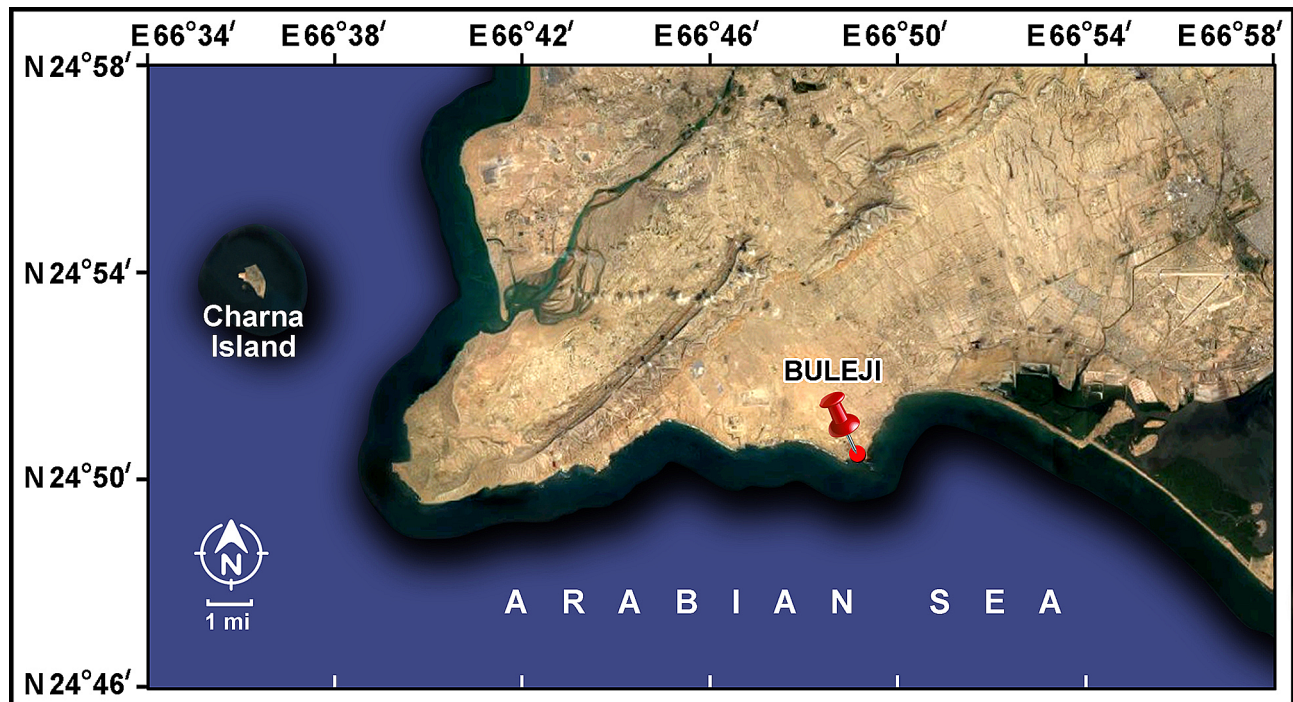
Holothuroids, also known as sea cucumbers, are dominant among the main sediment bioturbators in marine ecosystems (Mansouri & Mezali, 2018). Besides their use as food, in especially Chinese dominated markets, other interests derive from their use as models for tissue and organ regeneration, their peculiar adaptations like autotomy and self-defense mechanisms as models for tissue and organ regeneration, and their relevance in the production of bioactive compounds, such as holothurin (García Arrarás & Dolmatov, 2010; Zhang *et al.*, 2017; Eisapour *et al.*, 2021). Holothuroids are an abundant and diverse group of echinoderms, occurring in all depths of the oceans, from the intertidal zone to the deepest trenches of the world's oceans. However, despite their extensive phylogenetic analysis by Miller *et al.* (2017), based on both mitochondrial and nuclear DNA, Yang *et al.* (2020) still state that the phylogenetic and evolutionary relationships of Holothuroidea remain largely obscure and Utzeri *et al.* (2020) demand a close inspection and re-evaluation. Even the very recent work of Koch *et al.* (2023), on the phylogenomic analysis of Holothuroidea, using a highly curated dataset, only recapitulated previous results and failed to resolve interrelationships among Holothuriida clades but suggest more extensive and rigorous sampling. The classification as proposed by Miller *et al.* (2017) is accepted by WoRMS (2025).

The class comprises seven orders: Dendrochirotida, Holothuriida, Elasipodida, Apodida, Synallactida, Molpadida and Persiculida (Miller *et al.* 2017) and includes over 1819 extant species (Paulay, pers. com.). However, only four orders have this far been reported from Pakistan: Dendrochirotida with 10 species, Holothuriida with 12 species, Apodida with two species and Synallactida with a single species (see TABLE 1 in Ali *et al.*, 2024 and Ahmed *et al.*, 2025). The present study adds three more species from Buleji, Karachi Coast (North Arabian Sea): *Actinopyga*

*atypica* **sp. nov.**, *Holothuria* (*Selenkothuria*) cf. *erinacea* Semper, 1868, both in the family Holothuriidae and a dendrochiorotid, *Thyonina bijui* Thandar, 2017), in the family Thyonidae (*sensu* Smirnov, 2012).

## Materials and methods

During regular surveys of the coastal areas of Karachi, specimens of sea cucumbers were collected by hand, during spring low tide, from Buleji (24°50'20.41" N, 66°49'24.15" E) (Figure 1). Three specimens, herein described as *Actinopyga atypica* **sp. nov.**, *Holothuria* (*Selenkothuria*) cf. *erinacea* Semper (collection date 23-06-2023) and *Thyonina bijui* Thandar, (collection date 11-08-2017), were taken from intertidal waters. Morphological and taxonomic studies were conducted under dissecting and compound microscopes. Specimens were photographed immediately after capture, thereafter anesthetized in 5% magnesium chloride solution before examination, following Rowe & Doty's (1977) methodology, in order to relax the specimens and allow their tentacles, tube feet and papillae to extend. For species determination the dorsal and ventral body wall, tentacles and podia were examined for their ossicles. Ossicles were prepared for light microscopy by placing the excised structures on a slide to which were added few drops of 3.5% home or commercial bleach. The slides were then dried, rinsed in a few drops of distilled water, dehydrated using various concentrations of ethanol, and finally mounted in Canada balsam for permanent preservation. The ossicles were examined under a compound microscope and photographed using a digital camera (Fujifilm 16 MP) attached to the microscope. All specimens are deposited in the Marine Reference Collection and Resource Centre of the University of Karachi, Pakistan.



**FIGURE 1.** Map showing location of Buleji (map developed by Abrar Ali, Marine Reference Collection and Resource Centre, University of Karachi).

## Results and discussion

### Taxonomic account

**Order Holothuriida** Miller, Kerr, Paulay, Reich, Wilson, Carvajal & Rouse, 2017

**Family Holothuriidae** Burmeister, 1837

## Genus *Actinopyga* Bronn, 1860

**Diagnosis** (from Samyn *et al.* 2006, amended herein). Moderate to large species, reaching a length of 400 mm; body stout, body wall thick and firm, covered by tube feet ventrally and numerous modified, elongate tube feet or papillae dorsally. Mouth ventral, surrounded by 15–30 large peltate tentacles. Anus dorsal to terminal, guarded by five heavily calcified anal papillae or teeth. Calcareous ring firm, radial plates about twice as large as interradial plates. Ossicles of body wall rosettes and smooth to branched, often spiny rods of various form. Tentacles with rods often spiny at extremities. Tube feet and papillae with rods and rosettes similar to those of body wall, but often with more complex branched rods. Tables, buttons or other ossicle types absent. Cuvierian tubules present or absent, when present, never expelled.

### *Actinopyga atypica* sp. nov.

(Figures 2 & 3)

**Diagnosis.** A species of *Actinopyga* with an unusual cucumariid or *Labidodemas* type of calcareous ring and simple, smooth, slender, terminally forked rods in the body wall, accompanying simple rosettes, no complex branched rods in body wall and podia. Anal teeth light cream in color with multi-cusped tips.

**Etymology.** This species is so-named because of the atypical nature of the calcareous ring and the simple, slender, smooth, body wall rods compared to all species of *Actinopyga* known to date.

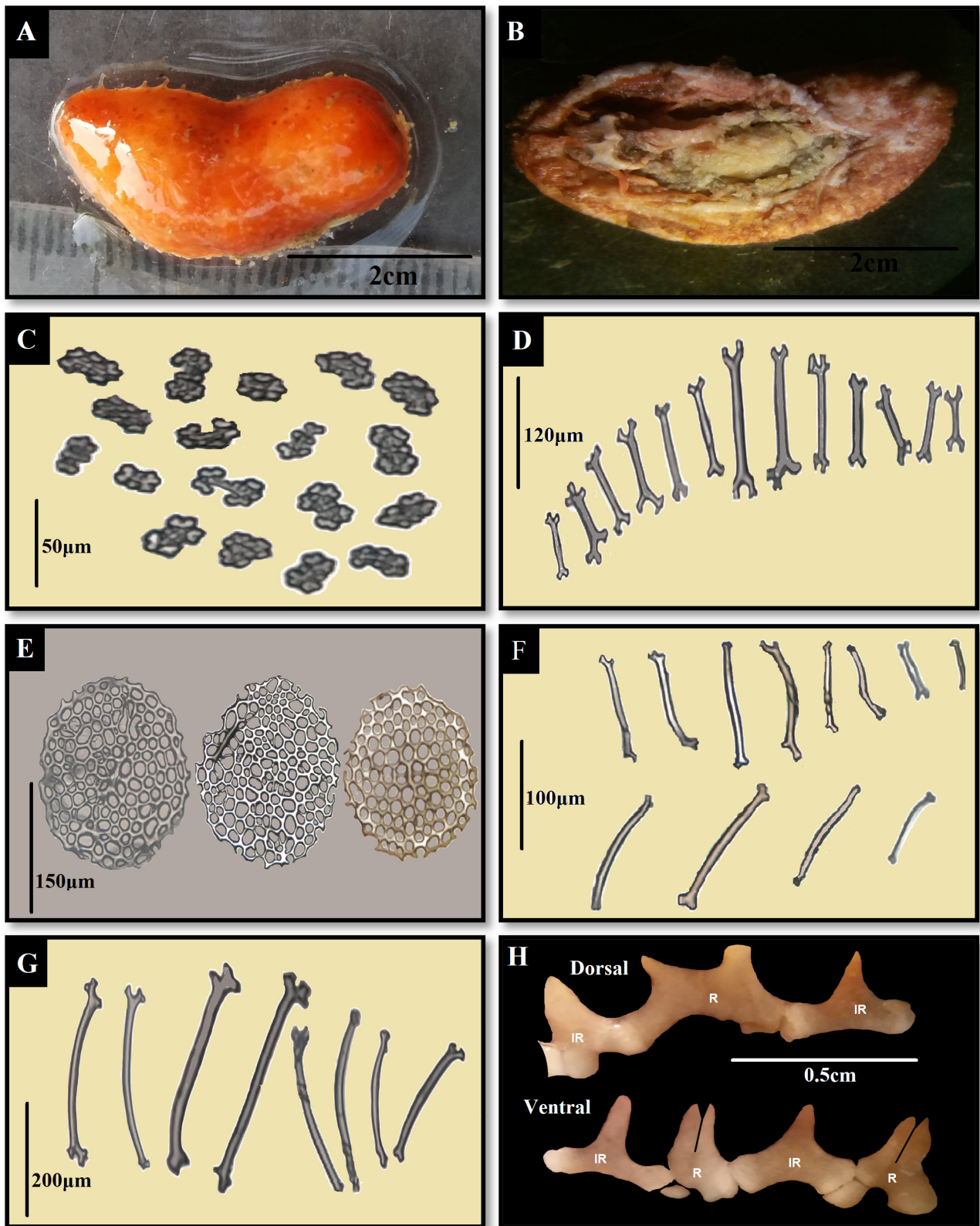
**Material examined.** Single specimen (Cat. no. MRC&RC-UOK-Holo 30), collected from the intertidal zone at Buleji, Karachi, Pakistan (24°50'20.41" N 66°49'24.15" E), at low tide (about 0.1 m depth) by Quratulan Ahmed and Qadeer Mohammad Ali, 23-06-2023.

**Description.** Color uniform orange-brown. Tentacles dark brown, tube feet creamy white. Mouth ventral, anus sub-dorsal. Length and weight of live specimen as follows: length 40 mm, weight 6.7 gm. Body elongate, cylindrical, papillae of bivium long, slender. Mouth ventral, surrounded by 20 stout, peltate tentacles. Anus surrounded by five, creamy white, triangular teeth with multi-cusped ends, 0.1 mm long. Gonad mature, in a single tuft of branched tubules, pale yellow in color, full of gametes. Calcareous ring 10 mm wide, 5 mm high, thick, more cucumariid or *Labidodemas*-like, with wide anteriorly bifurcate radial plates and narrow interradial plates (Figure 2H and 3F). Polian vesicle single, clavate; stone canal and madreporite not observed. Cuvierian tubules present.

Ossicles of both dorsal and ventral body wall similar, scattered, in the form of straight, smooth, slender, terminally forked or spanner-like rods, dorsally about 132 µm long (Figure 2D and 3B), and rosettes (Figure 2C and 3A). No complex, branched rods in the body wall. Podial rods about 120 µm long (Figure 2F and 3D), also smooth but slightly thinner and curved compared to those of body wall, but also with simple forked ends. End plates present, multilocular, flat, about 190 µm in diameter (Figure 2E and 3C). Tentacle ossicles comprise elongated, straight or slightly arched rods, 280 µm long (Figure 2G and 3E), branched at ends.

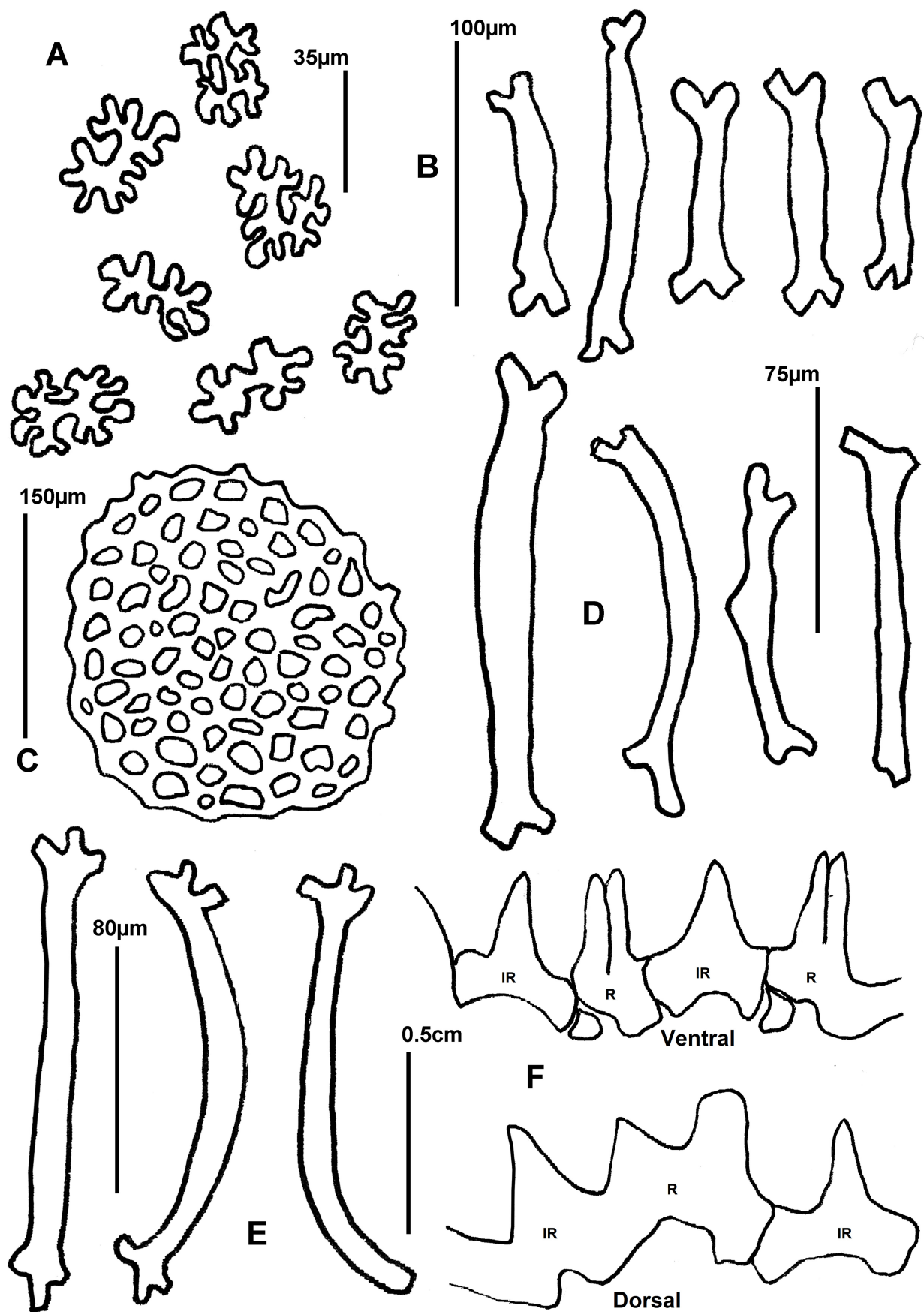
**Remarks.** The calcareous ring of our specimen is very different from those described for other species of *Actinopyga*, since it has a “cucumariid” or *Labidodemas* ring morphology. Since the tentacles are not borne on an introvert and retractor muscles are absent, we ruled out Cucumariidae and as there are no table-like deposits in the body wall, we also ruled out *Labidodemas*. The presence of rosettes in the body wall in combination with rods and the five conspicuous anal teeth confirm the specimen’s genus. A comparison of our specimen with all species of *Actinopyga* described to date, that its peculiar calcareous ring, despite the specimen’s maturity, the very simple rosettes of the body wall and podia, and the very simple, slender, spanner-like rods with usually a single or double dichotomous branchings at each end convinced us that the specimen in question belongs to a new species of *Actinopyga*. In the simplicity of its rods and the presence of multi-cusped anal teeth the new species comes quite close to *A. agassizi* Selenka, 1867 and *A. serratidens* Pearson, 1903. However, *A. agassizi* is a south-west Atlantic species with about 25 or more tentacles. A study by one of us (AST) of some reliably identified specimens of the former species at the Natural History Museum, UK, showed that this species, in addition to mostly simple rods in the body wall, also possesses other rods which are more complex when compared to those of our specimen. *Actinopyga serratidens*, on the other hand, like the new species, also also with 20-tentacles and an Indo-West Pacific distribution, but it is a large, darkly-colored species which has, in addition to simple forked rods, other rods which are slightly more complex and still others which are dumbbell or skittle-shaped, absent in our species. We therefore describe our specimen as a new species of *Actinopyga*.





**FIGURE 2.** *Actinopyga atypica* sp. nov. A. live specimen, B. preserved specimen (Cat no.MRCC-Holo 30), C. body wall rosettes, D. body wall rods, E. tube feet plates, F. tube feet rods, G. tentacle rods, H. calcareous ring.





**FIGURE 3.** *Actinopyga atypica* sp. nov. A. body wall rosettes, B. body wall rods, C. tube feet plates, D. tube feet rods, E. tentacle rods, F. calcareous ring.

## Genus *Holothuria* Linnaeus, 1767

**Diagnosis** (partly after Rowe, 1969). A large genus of Holothuriidae, up to 450 (600?) mm in length, with usually 20–30 tentacles; body cylindrical or subcylindrical, vermiform. Podia either as tube feet only, or papillae only, or both. Calcareous ring with radial plates 2–3x the height of interradial plates, rarely with scalloped anterior margin. Tables usually present, except in a few species where they are secondarily reduced or absent; buttons, pseudobuttons, rosettes, small branched rods and perforated plates usually accompany well-developed tables.

## Subgenus *Selenkothuria* Deichmann, 1958

**Diagnosis** (partly after Rowe, 1969). A subgenus of *Holothuria* comprising medium-sized to large, cylindrical species up to 150–200 mm long. Tentacles 20. Tube feet crowded ventrally, forming a sole; papillae small, scattered dorsally. Ossicles in the form of perforated and/or rugose (spinose) plates or rods; tables rare or more often absent, when present (in juveniles of 3 species), nearly always rudimentary and/or sparsely distributed.

## *Holothuria* (*Selenkothuria*) *cf. erinacea* Semper, 1868

(Figures 4 & 5)

*Holothuria erinaceus* Semper, 1868:91k, 250, 279, pl.30: fig.24, p1.34:fig.9, p1.35: fig.14, p1.36: fig.11, p1.38, figs. 1 & 2.

*Holothuria erinaceus* var. *pygmaea* Semper, 1868:91, pl 30, figs. 23,24.

*Holothuria* (*Selenkothuria*) *erinaceus* Cherbonnier, 1988: 60 (synonymy before 1988), fig. 22.

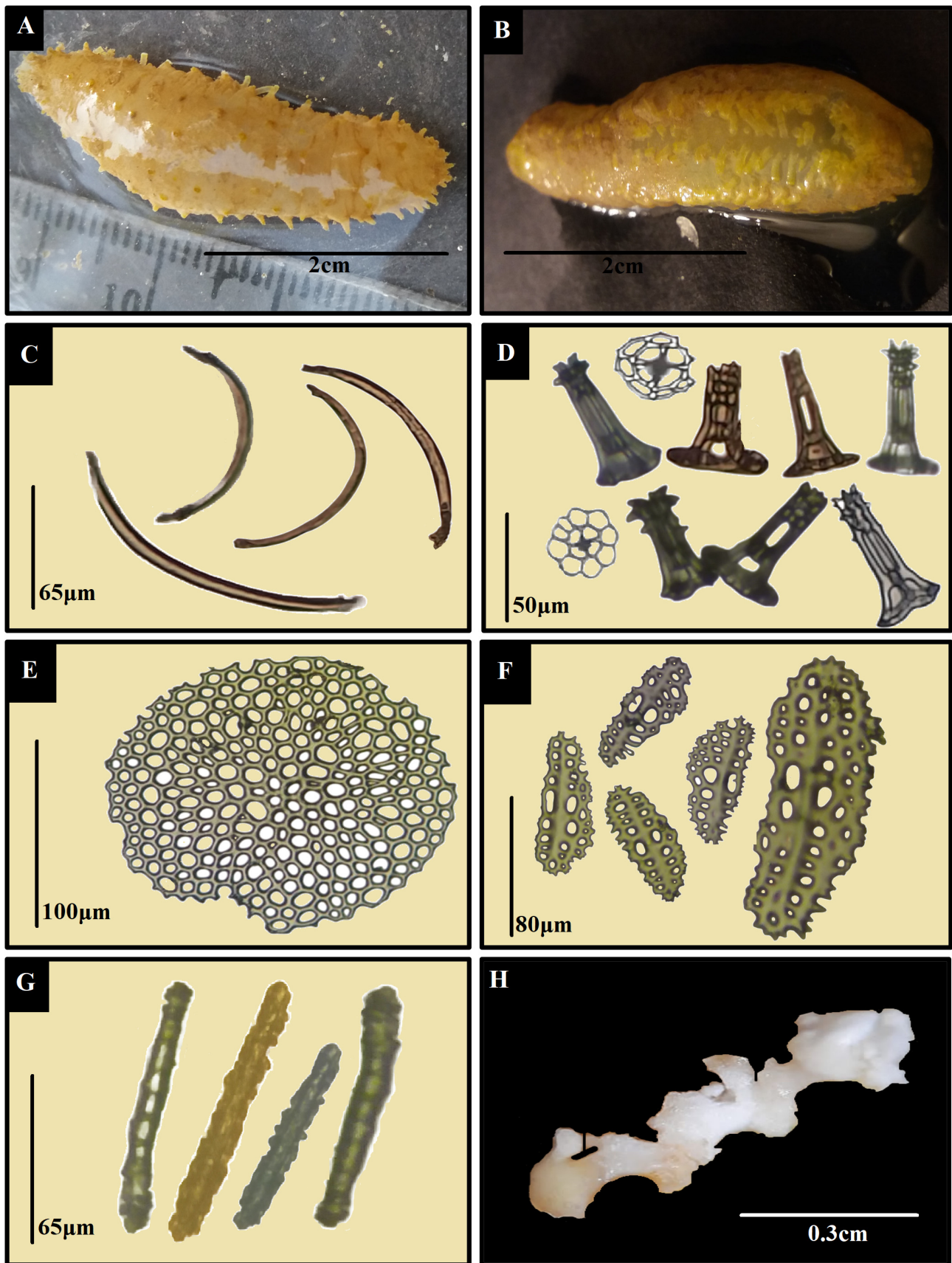
*Holothuria* (*Selenkothuria*) *erinacea* Samyn 2003: 68 (records after 1988), figs. 27 A–E, 54B; Thandar (2007): 29–32 (with text-fig.); Kawaida *et al.*, 2023: 61–70 (with figs.).

**Diagnosis** (after Semper, 1868, amended herein). A medium-sized, cylindrical species, sometimes with a double series or poorly defined blotches on dorsum, tube feet green; Cuvierian tubules present. Ossicles short or elongate (50–140 µm long), curved or somewhat straight, flat rods or bars, usually spinulate and often dichotomously branched at ends and pierced by few lateral or terminal holes, or with a festoon of holes along the sides, then forming elaborate fenestrated plates. Rudimentary or well-developed tables present in juveniles, absent in adults. Tube feet and tentacles with elongate rods usually multilocular at ends.

**Material examined.** Single specimen (cat. no. MRC&RC-UOK-Holo 31), collected from the intertidal zone at Buleji, Karachi Coast (24°50'20.41" N 66°49'24.15" E), at low tide (about 0.1 m depth) by Qadeer Mohammad Ali and Quratulan Ahmed, 23-06-2023.

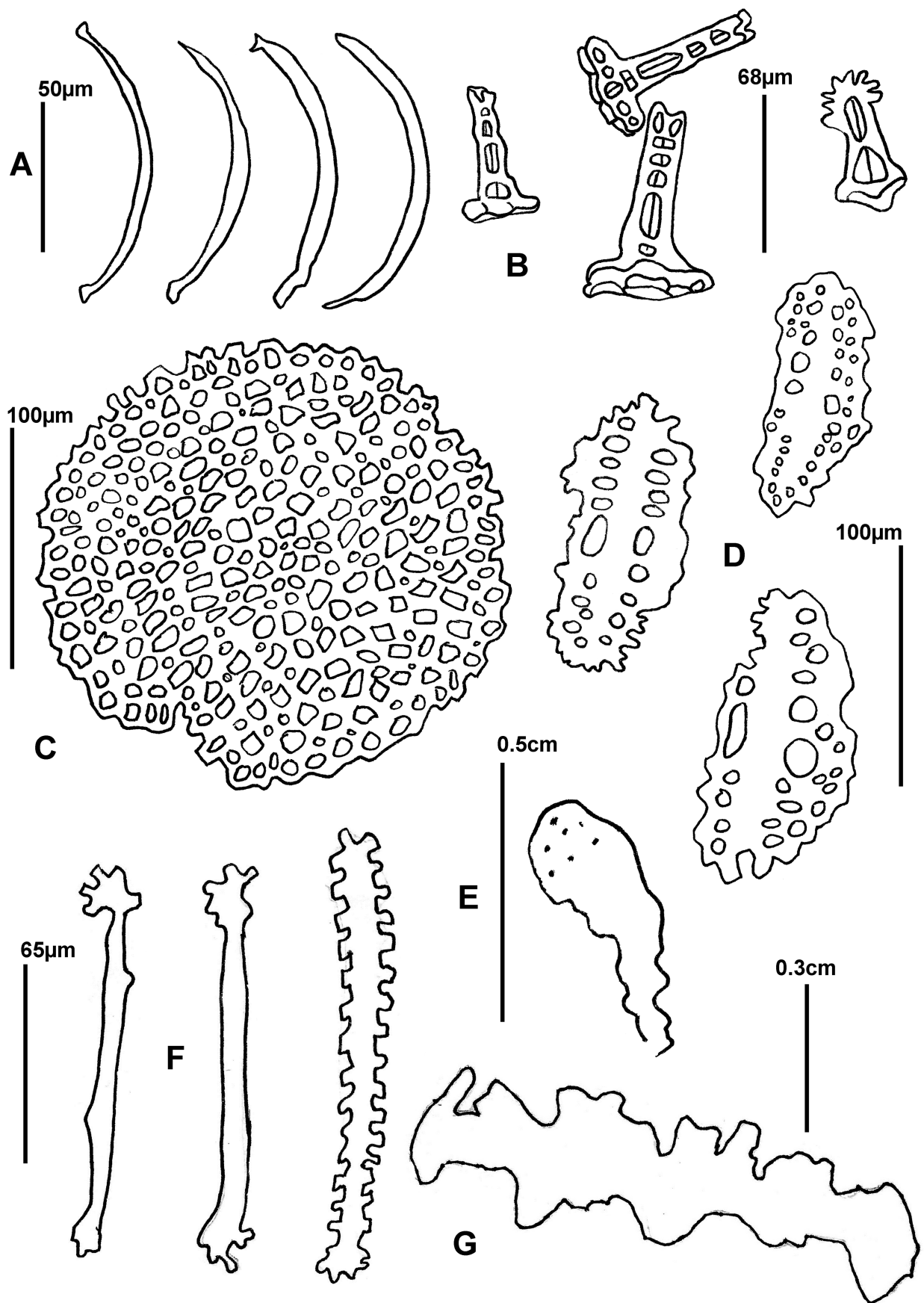
**Description.** Body subcylindrical, elongate, ventrally flattened, dorsally arched, 43 mm in length, breadth in mid-body 11 mm (Figure 4A, B). Color uniform light yellow to creamy white, tentacles pastel yellow. Tegument smooth, not very thick, about 1 mm. Tube feet small, dispersed in rows on the dorsal surface and in three bands on the ventral surface. Calcareous ring simple, radial plates more robust, rectangular, with recesses in the central region. Interradial plates also robust, smaller than radial plates, triangular in shape (Figure 4H, 5G). Anal teeth absent. Polian vesicle single; stone canal single, short, madreporite clavate. Gonad as a tuft of numerous, thread-like, white, unbranched tubules; gametes not detected. Cuvierian tubules absent. Respiratory trees well ramified.

Body wall deposits include tables, curved rods, other rods and plate-like deposits. Tables tall, disc flat with smooth to spinous to irregular margin, spire of four parallel pillars joined by 1–4 cross bars and often with spines at tips of pillars. Spire-top adorned by a crown of thorns/teeth, arranged to resemble a flat 'Maltese' cross formed by eight spines and sometimes few accessory ones; table height 50–75 µm; disc diameter 35–45 µm (Figure 4D and 5B). Rods, slender, smooth, curved, 65–80 µm long (Figure 4C and 5A). Multilocular, plate-like deposits or pseudoplates (Figure 4F, 5D), developed from simple branching rods, usually straight or curved, 65–80 µm long; podial end plates 100–200 µm in diameter (Figure 4E, 5C). Tentacle deposits as non-perforated, straight rods with roughened margins (Figure 4G, 5F). Ossicles of cloaca in the form of tables similar to those of body wall but more slender.



**FIGURE 4.** *Holothuria* (*Selenkothuria*) cf. *erinacea* Semper, 1868. A. live specimen, B. preserved specimen (Cat no. MRCC-Holo 31), C. body wall C-shaped rods, D. body wall tables, E. tube feet end plate, F. body wall pseudoplates, G. tentacle rods, H. calcareous ring.





**FIGURE 5.** *Holothuria (Selenothuria) cf. erinacea* Semper, 1868. A. body wall C-shaped rods, B. body wall tables, C. tube feet endplates, D. Body wall pseudoplates, E. madreporite, F. tentacle rods, G. calcareous ring.

**Remarks.** From the literature studied no species has yet been described in *Holothuria*, with this combination of ossicles (tall tables with 1–4 cross bars, perforated plates/pseudoplates, and curved C-shaped rods in the body wall). However, both reviewers suspected that the species may belong to Deichmann's (1958) and Rowe's *Selenkothuria* group. We then critically looked at all species within this subgenus and are now convinced that the perforated plate-like deposits, come quite close to those of Semper's *H. erinacea*, closely resembling those described for this species by Cherbonnier (1988), Samyn (1993), Thandar (2007) and more recently Kawaida *et al.* (2023). However, Semper (1868) described reduced table-like deposits in his *H. erinaceus* var. *pygmaea* (unaccepted by WoRMS, accessed 25/10/2025), which we think was a juvenile of his *erinaceus*. The single table disc illustrated by him comes quite close to the table discs of our specimen. Semper's specimens of his variety *pygmaea* measured up to 60 mm while our specimen is only 43 mm in length and perhaps smaller—hence the presence of well-developed tables. We, therefore, opine that our specimen is perhaps a juvenile of *H. erinacea*, which like its consubgenera, *H. parva* Krauss (in Lampert, 1885) and *H. moebii* Ludwig, 1883 may lose the table deposits later in development. In fact, the single table disc illustrated by Semper for his *pygmaea* variety, appears to be degenerated, while those of our specimen are well developed, without any sign of degeneration. In fact they come quite close to those of juveniles of the southern African stichopodid, *Neostichopus grammatus* (H.L. Clark, 1923), described by Thandar (1987), which also rapidly disappear in specimens over 30 mm in length, to be replaced by peculiar bodies of various form. Therefore we argue that our specimen is a juvenile of *H. erinacea*, identical to Semper's (1868) var. *pygmaea*, which must now be resurrected as a synonym of *H. erinacea*. To our knowledge, none of the other authors, who have described this species, mentions any table-like deposits, perhaps all of them worked with adult specimens as did Cherbonnier (1988), Samyn (2003), Thandar (2007) and Kawaida *et al.* (2023). Hence, the diagnosis of the species is here amended.

## Order Dendrochirotida Grube, 1840

### Family Thyonidae Panning, 1949 (*sensu* Smirnov, 2012)

#### Genus *Thyonina* Thandar, 1990

**Diagnosis** (after Thandar 1990, amended herein). A genus of the family Thyonidae with 9–10 tentacles, ventral-most two reduced; tube feet scattered. Calcareous ring short, tubular, radial plates with short paired posterior prolongations, both ring and prolongations broken into a few large pieces of calcite. Body wall ossicles as minute, smooth, slender, straight or slightly curved rods, expanded and often digitated at ends which are perforated by a single large and one or more smaller holes. Tube feet with regular or irregular end-plate.

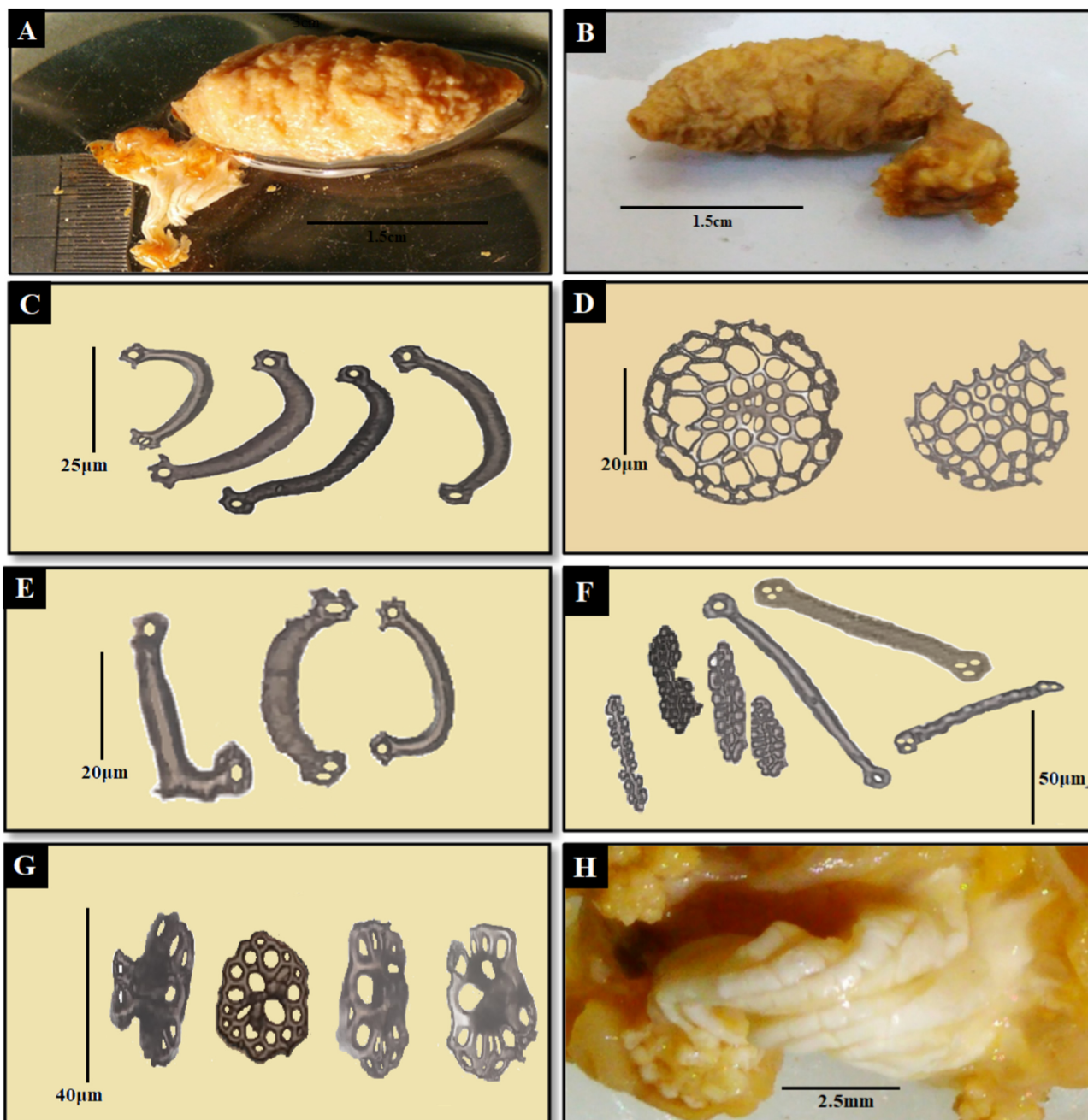
#### *Thyonina bijui* Thandar, 2017

(Figures 6 & 7)

*Thyonina bijui* Thandar, 2017: 414–416, fig. 2.

**Diagnosis** (from Thandar 2017, amended herein). A small, barrel-shaped species, about 20 mm in length. Color in alcohol greyish-black to greyish white or yellowish brown; live coloration reddish or orange-brown with dark streak. Anal teeth absent, anal papillae present. Tube feet scattered, dorsally papilliform. Tentacles about 10 (9 in holotype), mid-ventral two reduced, blackish/yellowish in color. Calcareous ring tubular, subdivided, posterior processes of radial plates longer than height of ring, all arising from more or less the same level. Polian vesicle and stone canal single. Ossicles of body wall as slender, curved, smooth rods, expanded and digitated at ends with one or more holes. Ossicles of tube feet similar; end plates typical of type species [*Thyonina articulata* (Vaney, 1908)]. Tentacle ossicles comprise slender rods, rosette-like rods and minute mulberry-like rosettes. Introvert with tables and rosettes, similar to those of tentacles.

**Remarks.** The diagnosis is here modified from Thandar (2017) to accommodate color variations and tentacle number.

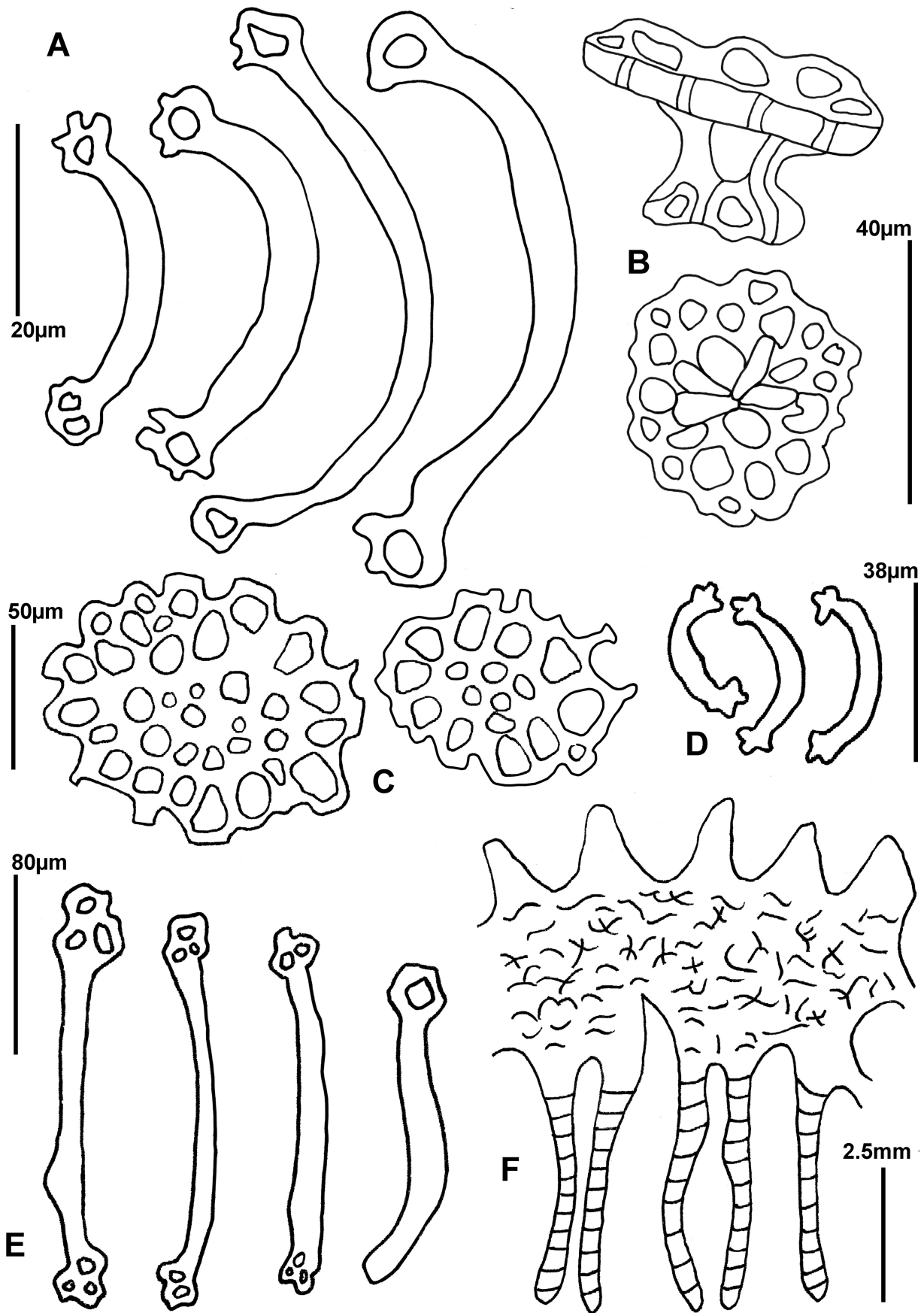


**FIGURE 6.** *Thyonina bijui* Thandar, 2017. A. live specimen, B. preserved specimen (Cat no.MRCC-Holo 22), C. body wall rods, D. tube feet plates, E. tube feet rods, F. simple and rosette-shaped tentacle rods, G. introvert tables, H. calcareous ring.

**Material examined.** Single specimen (Cat. no. MRC&RC-UOK-Holo 22), collected from the intertidal zone at Buleji (24°50'20.41" N 66°49'24.15" E), at low tide (about-0.14m depth) by Qadeer Mohammad Ali and Quratulan Ahmed, 11-08-2017.

**Description.** Length and weight of live specimen 30 mm x 5.95 g respectively. Live coloration dark orange with brownish tinge, podia and tentacles yellowish, preserved specimen turned yellowish-brown within 24 hrs. Body wall thin, rough to the touch. Mouth and anus terminal. Podia scattered but some arranged in rows. Tentacles 10 (eight large and two mid-ventral small), typically dendrochirotid, well-branched. Calcareous ring complex (Figure 6H and 7F), radial and interradial plates fused; anterior tips of both radial and inter-radial plates triangular; posterior processes slightly longer than height of ring. Gonad mature, female, with unbranched tubules. Polian vesicle single, elongated; stone canal short and straight; madreporite small, dicotyledonous.





**FIGURE 7.** *Thyonina bijui* Thandar, 2017. A. body wall rods, B. introvert tables, C. tube feet plates, D. tube feet rods, E. tentacle rods, F. calcareous ring.

Body wall ossicles cylindrical, curved rods with digitated ends provided with one or more terminal holes, 25–50 µm long (Figure 6C and 7A). Podial ossicles similar to those of body wall, 20–40 µm long (Figure 6E and 7D), end plates multilocular, flat, with small central holes and large marginal ones, 80 µm in diameter (Figure 6D and 7C). Tentacle ossicles cylindrical smooth rods and mulberry-like rosettes, rods 80–100 µm (Figure 6F and 7D). Introvert ossicles as tables with a short, 2-pillared spire, and smooth, multilocular disc, 40 µm in diameter (Figure 6G and 7B).

**Distribution.** Recorded once from type locality Vizhinjam Bay, Kerala, India, and now from Pakistan.

**Habitat.** Specimen was taken from the intertidal zone, attached to rock.

**Remarks.** We compared our specimen with those originally diagnosed and described by Thandar (2017). This is the second record of this species. It is the smallest dendrochirotid sea cucumber in the Indian waters around Kerala. Our specimen resembles the holotype described by Thandar (2017), except for color and ossicle size. Thandar (2017) described the body wall rods as 30–60 µm long, the podial rods 50–60 µm long, the end plates 100 µm in diameter, tentacle rods 80 µm long and introvert table discs 60 µm in diameter. In our specimen the body wall rods are 25–50 µm long, podial rods 20–40 µm long, end plates 80 µm in diameter, tentacle rods 100 µm, and introvert table discs 40 µm in diameter. Thandar (2017) described his specimen's live coloration as reddish-brown and preserved coloration as greyish-black dorsally, greyish-white ventrally. Tentacles nine (seven large + two small), blackish. No special ossicles in anal region except for some rods. These differences perhaps indicate intraspecific, geographic or age variations, perhaps of no taxonomic significance.

## Acknowledgements

We like to acknowledge the Marine Reference collection and Resource Centre, University of Karachi, for providing facilities for sample collection and laboratory examinations. We also thank Mr. Abrar Ali, for his assistance and guidance in drawings and micro-photography of the ossicles. Finally, we gratefully acknowledge the two reviewers (Dr Samyn and anonymous) and the editor (Dr Chris Mah) for valuable suggestions. The Natural History Museum (UK) is thanked for working space and logistic support offered to AST.

## References

- Ahmed, Q., Ali, Q.M., Shaikh, I. & Thandar, A. (2025) *Holothuria (Selenkothuria) parva* Krauss (in Lampert, 1885) (Holothuroidea: Holothuriida: Holothuriidae), new addition to the holothuroid fauna of Pakistan. *Zootaxa*, 5569 (2), 393–399.  
<https://doi.org/10.11646/zootaxa.5569.2.10>
- Ali, Q.M., Shaikh, I., Thandar, A. & Ahmed, Q. (2024) *Actinopyga spinea* Cherbonnier, (1980) (Holothuroidea: Holothuriida: Holothuriidae), new addition to the holothuroid fauna of Pakistan. *Zootaxa*, 5432 (2), 151–159.  
<https://doi.org/10.11646/zootaxa.5432.2.1>
- Bronn, H.G. (1860) Die Klassen und Ordnungen der Strahlenthiere (Actinozoa) wissenschaftlich dargestellt. In: *Die Klassen und Ordnungen des Thier-Reichs, wissenschaftlich dargestellt in Wort und Bild. Zweiter Band. Aktinozoen*. C.F. Winter, Leipzig & Heidelberg, pp. 1–434, pls. 1–48.  
<https://doi.org/10.5962/bhl.title.11639>
- Burmeister, H. (1837) Handbuch der Naturgeschichte. Zum Gebrauch bei Vorlesungen. Zweite Abtheilung, Zoologie. T.C.F. Enslin, Berlin, 489 pp. [pp. 369–858]  
<https://doi.org/10.5962/bhl.title.100177>
- Deichmann, E. (1958) The Holothuroidea collected by the Velero III and IV during the years 1932 to 1954. Part II. Aspidochirota. *Allan Hancock Pacific Expeditions*, 11 (2), 249–349.
- Grube, A.E. (1840) *Actinien, Echinodermen und Würmer des Adriatischen- und Mittelmeer snacheigenen Sammlungenbeschrieben*. J.H. Bon, Königsberg, 92 pp., 12 figs.  
<https://doi.org/10.5962/bhl.title.10133>
- Kawaida, S., Yamana, Y., Tanita, I. & Nanjo, K. (2023) First record of the sea cucumber *Holothuria (Selenkothuria) erinaceus* Semper, 1868 (Holothuroidea: Holothuriida: Holothuriidae) from a Japanese mangrove forest. *Laguna*, 30, 61–70.
- Miller, A.K., Kerr, A.M., Paulay, G., Reich, M., Wilson, N.G., Carvajal, J.I. & Rouse, G.W. (2017) Molecular phylogeny of extant Holothuroidea (Echinodermata). *Molecular Phylogenetics and Evolution*, 111, 110–131.  
<https://doi.org/10.1016/j.ympev.2017.02.014>
- Mongiardino Koch N, Tilic E, Miller AK, Stiller J, Rouse GW (2023) Confusion will be my epitaph: genome-scale discordance

- stifles phylogenetic resolution of Holothuroidea. *Proceedings of the Royal Society B: Biological Sciences*, 290, 20230988. <https://doi.org/10.1098/rspb.2023.0988>.
- Panning, A. (1949) Versucheiner Neuordnung der Familie Cucumariidae (Holothuroidea, Dendrochirota). *Zoologische jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere*, 78 (4), 404–470.
- Pearson, J. (1903) Report on the Holothuroidea collected by Prof. Herdman, at Ceylon, in 1902. *Report to the Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manaar*, Supplement 5 (1), 181–208, pls. 1–3. [only mentioned as authority of *H. serratidens*]
- Rowe, F.W.E. (1969) A review of the family Holothuriidae (Holothuroidea: Aspidochirotida). *Bulletin British Museum natural History, Zoology*, 18, 119–170. <https://doi.org/10.5962/bhl.part.18419>
- Rowe, F.W.E. & Doty, J.E. (1977) The shallow-water holothurians of Guam. *Micronesica*, 13, 217–250.
- Selenka, E. (1867) Beiträge zur anatomie und systematik der holothurien. *Zeitschrift für wissenschaftliche Zoologie*, 17, 291–374.
- Semper, C. (1868) *Holothurien Reisen in Archipel der Philippinen. 2. Wissenschaftliche Resultate*. W. Engelmann, Leipzig. [unknown pagination] <https://doi.org/10.5962/bhl.title.11687>
- Smirnov, A.V. (2012) System of the Class Holothuroidea. *Paleontological Journal*, 46, 793–832. <https://doi.org/10.1134/S0031030112080126>
- Thandar, A.S. (1987) The southern African stichopodid holothurians, with notes on the changes in spicule composition with age in the endemic *Neostichopus grammatus* (H.L. Clark). *South African Journal of Zoology*, 22, 278–286. <https://doi.org/10.1080/02541858.1987.11448058>
- Thandar, A.S. (1990) The phylloporid holothurians of southern Africa with the erection of a new genus. *South African Journal of Zoology*, 25 (4), 207–223. <https://doi.org/10.1080/02541858.1990.11448215>
- Thandar, A.S. (2007) Additions to the aspidochirotid, molpadid and apodid holothuroids (Echinodermata: Holothuroidea) from the east coast of southern Africa, with descriptions of new species. *Zootaxa*, 1414 (1), 1–62. <https://doi.org/10.11646/zootaxa.1414.1.1>
- Thandar, A.S. (2017) Two new subfamilies, three new species and a new subspecies of dendrochirotid sea cucumbers (Echinodermata: Holothuroidea). *Zootaxa*, 4365 (4), 410–420. <https://doi.org/10.11646/zootaxa.4365.4.2>
- Utzeri, V.J., Ribani, A., Bovo, S., Taurisano, V., Calassanzio, M., Baldo, D. & Fontanesi, L. (2020) Microscopic ossicle analyses and the complete mitochondrial genome sequence of *Holothuria (Roweothuria) polii* (Echinodermata; Holothuroidea) provide new information to support the phylogenetic positioning of this sea cucumber species. *Marine Genomics*, 51, 100735. <https://doi.org/10.1016/j.margen.2019.100735>
- Yang, F., Zhou, C., Tran, N.T., Sun, Z., Wu, J., Ge, H., Lu, Z., Zhong, C., Zhu, Z., Yang, Q. & Lin, Q. (2020) Comparison of the complete mitochondrial genome of *Phyllophorus liuwutiensis* (Echinodermata: Holothuroidea: Phyllophoridae) to that of other sea cucumbers. *FEBS Open Bio*, 10 (8), 1587–1600. <https://doi.org/10.1002/2211-5463.12914>