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An annotated checklist of brittle stars (Echinodermata: Ophiuroidea) from artificially reclaimed beaches in Sentosa Island, Singapore

Zongjing **Deng**[1,2*], Nicholas Wei Liang **Yap**[3] & Toshihiko **Fujita**[1,2]

Abstract. A total of 454 ophiuroid specimens were collected from beaches surrounding the public lagoons at Sentosa Island, Singapore, during a marine biodiversity survey in May 2023. They belong to seven species and three genera in two families, Ophiactidae and Ophiotrichidae. The most abundant species were *Ophiactis savignyi* found in sponges, and *Ophiothela mirabilis* observed amongst sponges, sea grass, and algae. *Ophiothrix* (*Ophiothrix*) *plana* is transferred to *Macrophiothrix* based on molecular evidence, with SEM observations of isolated dorsal arm plates providing morphological support for this reassignment. All seven species were previously reported from deeper waters around Singapore; this is the first time they have been documented from artificial structures in shallow-waters of reclaimed beaches. Findings from this study provide a baseline that will be useful for further biodiversity monitoring along modified coastal shores.

Key words. echinoderm, ophiuroid, Ophiactidae, Ophiotrichidae, new combination, artificial environment, Singapore

INTRODUCTION

Situated at the tip of the Malayan Peninsula, Singapore is an island city-state where much of its coastline has been artificially modified through land reclamation to support its growing urban population (Hilton & Manning, 1995; Todd & Chou, 2005; Tay et al., 2018). Coastal reclamation in Singapore began as early as the 1800s during its time as a British colony and intensified following independence in 1965 (Corlett, 2000; Tay et al., 2018). While these efforts have led to the loss of many native marine habitats (Hilton & Manning, 1995; Todd & Chou, 2005; Jaafar et al., 2018), the reclaimed areas have served a variety of residential and recreational purposes (Hilton & Manning, 1995; Todd & Chou, 2005; Tay et al., 2018). Notably, most of Singapore's public beaches are now located on reclaimed shorelines (Tay et al., 2018). To mitigate erosion and stabilise sediments, artificial structures such as seawalls and breakwaters were installed (Chew et al., 1986; Wong, 1988). In response to increasing flood risks driven by sea-level rise and climate change, Singapore—like many other low-lying nations—continues to expand the construction of such coastal defences (Oppenheimer et al., 2019; Nguyen et al., 2022).

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[1]Department of Biological Sciences, Graduate School of Science, The University of Tokyo, Japan; Email: dzj@kahaku.go.jp (*corresponding author)

[2]National Museum of Nature and Science, Japan

[3]Tropical Marine Science Institute, National University of Singapore

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In recent years, artificial coastal structures like seawalls and breakwaters have gained attention for their potential role in enhancing native biodiversity. Several studies have documented the re-establishment of marine species on and around these man-made habitats (Loke et al., 2015; Strain et al., 2017; Firth et al., 2024). However, the overall ecological impact and consistency of these benefits remain uncertain (Chapman, 2003; Strain et al., 2017). Establishing robust biodiversity baselines and conducting systematic ecological assessments are therefore critical, especially as such structures become increasingly common in response to climate-related coastal threats.

This study aims to document the diversity of brittle stars (Echinodermata: Ophiuroidea) found on artificial structures along the public beaches of Sentosa, a southern island in the Singapore Strait known for its tourism (https://www.sentosa.com.sg/en/things-to-do/attractions/siloso-beach/). Brittle stars are ecologically important marine invertebrates, contributing to nutrient cycling and serving as prey in marine food webs (Migné et al., 2012; Murat et al., 2016). Moreover, their dense aggregations have been reported to enhance habitat complexity, potentially promoting the settlement of other marine organisms (Geraldi et al., 2017)—a factor relevant to understanding the ecological value of artificial coastal habitats.

Despite their ecological significance, brittle stars in Singapore remain poorly studied. Previous studies were largely limited to species checklists (e.g., Lim & Chou, 1988; Wee & Ng, 1994), general photographic guides (e.g., Lane & Vandenspiegel, 2003), or ecological studies of echinoderm communities not mentioning exact species (Zhou & Goh, 2025) or providing any taxonomic details. However, more

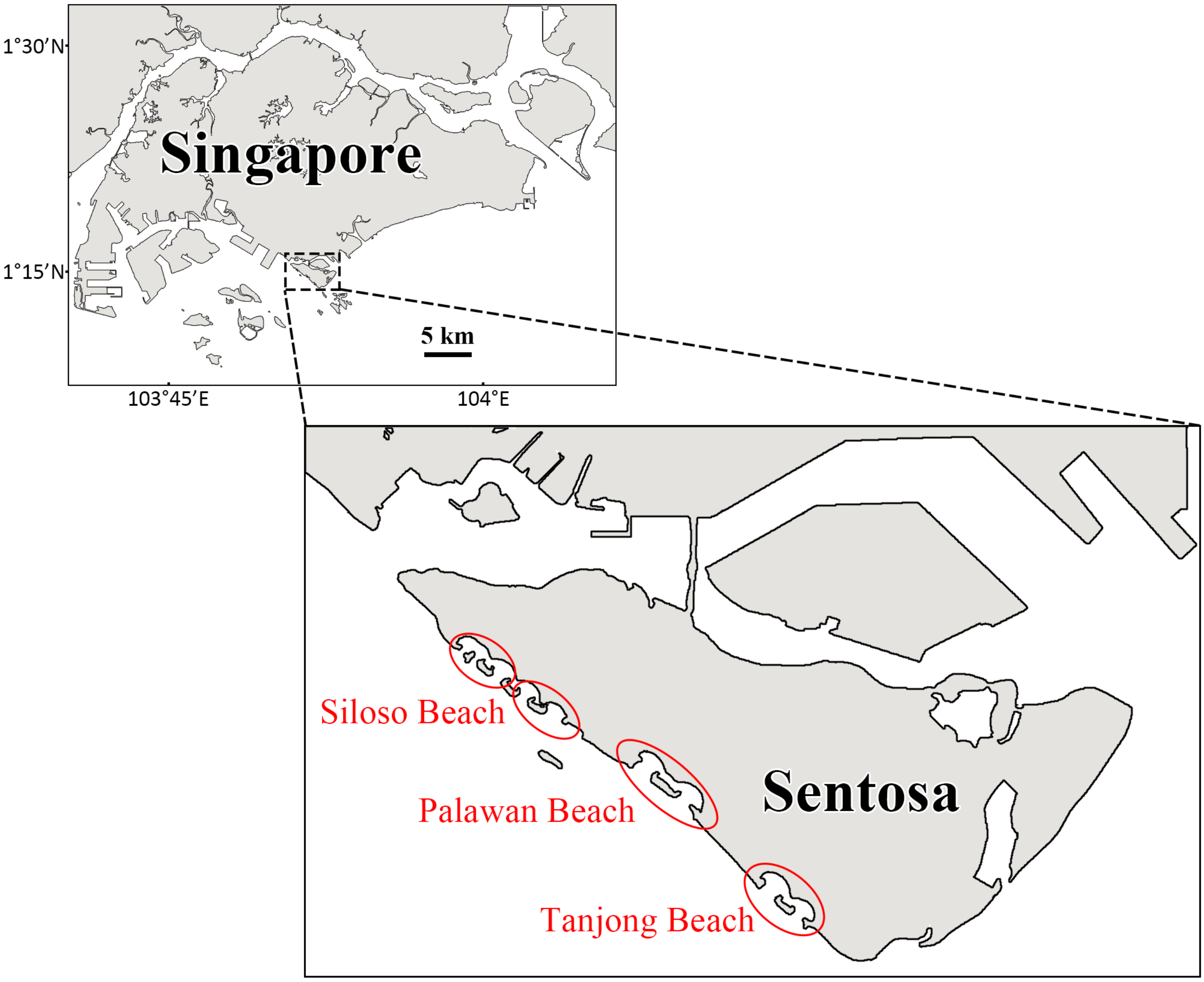

Fig. 1. Map of sampling sites at Sentosa Island located at south of Singapore. Brittle stars were collected from three artificial beaches, Siloso Beach, Palawan Beach, and Tanjong Beach.

rigorous taxonomic works have recently been undertaken. For example, Fujita & Irimura (2015) documented 22 brittle star species from the Johor Straits, north of Singapore, while Fujita (2016) recorded five additional species from the Singapore Strait, all belonging to families not previously recorded in the area. However, most of the specimens in these studies were collected from deeper waters or from natural habitats. Brittle stars were collected from a man-made structure (a floating fish farm pontoon) only in one instance (see Fujita & Irimura, 2015: Table 2).

As such, there remains a taxonomic knowledge gap concerning the diversity of brittle stars in particular, associated with shallow-water, artificial coastal structures in Singapore. This study seeks to address this gap, thus priming the way for future ecological research on these animals or the artificial structures that they are associated with.

MATERIAL AND METHODS

Field surveys were conducted during morning low tides on three public beaches of Sentosa Island: Siloso Beach, Palawan Beach, and Tanjong Beach, located at the south of Singapore, in the Singapore Strait, on 8–13 May 2023 (Fig. 1). These beaches were artificially constructed from land reclamation efforts between 1975 until the early 2000s (Historical Maps of Singapore: https://libmaps.nus.edu.sg/about/). The beaches have small man-made islets, and the environment of the beaches and islets is composed of both sandy and rocky habitats (Fig. 2). Rocky habitats are typically provided by seawalls. The main beach and islets are interconnected by bridges with underlying floating pontoons.

Ophiuroid specimens were collected by hand during low tide and snorkelling in intertidal and subtidal habitats at depths of no more than 3 metres. The collected specimens were anesthetised by immersion in $MgCl_2$ solution (34.2 g/L), photographed, then fixed by 80% ethanol and later preserved in 99% ethanol. For the new combination species, *Macrophiothrix plana*, an arm fragment from the first to sixth

Fig. 2. Siloso Beach at Sentosa, Singapore. This artificial beach has a small man-made islet which is connected by a bridge with underlying pontoon. The islet has both sandy beach and rocky seawalls. Palawan and Tanjong beaches also consist of similar structures and habitats.

segments was dissected, and arm ossicles were isolated using household bleach for examination under a scanning electron microscope (JSM-IT200 InTouchScope™). The examined specimens are deposited at the Lee Kong Chian Natural History Museum, National University of Singapore (ZRC).

Morphological terms follow Stöhr et al. (2012), Thuy & Stöhr (2016), and Goharimanesh et al. (2022). For molecular analyses, DNA was extracted from dissected arm tips using the Qiagen DNAeasy Tissue Kit following manufacturer protocols. Extracted DNA was preserved in Qiagen Buffer EB for later processes. To confirm species identities, we obtained partial sequences (549 bp and 363 bp) of mitochondrial cytochrome c oxidase subunit I (COI) and 16S ribosomal RNA genes of *Macrophiothrix longipeda* (ZRC ECH 2165) and *Macrophiothrix plana*, new combination. (ZRC ECH 2166, 2167, 2417). Polymerase chain reaction (PCR) was carried out using Ex Taq (Takara Bio) with the primers COIceF/COIceR (Hoareau & Boissin, 2010) and 16Sofi_F/16Sofi_R (Pérez-Portela et al., 2013) following the cycle conditions they provided. Amplified DNA was purified by ExoSAP-IT (Affymetrix) and sequenced using BigDye Terminator v3.1 Cycle Sequencing Kit and 3500xL genetic analyzer (Applied Biosystems). Forward and reverse sequences were assembled and edited using GeneStudio version 2.2.0.0 (GeneStudio, Inc., available from https://genestudio-pro.software.informer.com). The sequences were queried using the Basic Local Alignment Search Tool (BLAST; Camacho et al., 2009) online at the NCBI website (https://blast.ncbi.nlm.nih.gov/Blast.cgi) using default parameters. The sequences were aligned using MUSCLE (Multiple Sequence Comparison by Log-Expectation) implemented in MEGA11 (https://www.megasoftware.net/), with default settings (Edgar, 2004; Tamura et al., 2021). Uncorrected pairwise distance (p-distance) was calculated in MEGA 11, with all three codon positions included.

To confirm the generic status of *Macrophiothrix plana*, new combination, we sequenced fresh exons of a specimen (ZRC ECH 2417) and the sequence was compared with those of 40 ophiotrichid species and 2 outgroup species using the dataset of O'Hara et al. (2017). We used 14 exons longer than 600 bp (cdk9_ex4, fbxl14b_ex1, fzd9_ex2, kbtbd8_ex3, LOC100891299_ex1, LOC580672_ex1, mab21l1_ex1, ran_ex1, RBBP4_ex2, sdcbp_ex3, SoxB1_ex1, spna2_ex34, syne1_ex14, and tcp1_ex1). DNA library was prepared using the Collibri™ ES DNA Library Prep Kit for Illumina® (Thermo Fisher Scientific), following the manufacturer's instructions for next generation sequencing (NGS) on platform NovaSeq. Paired-end raw reads were imported into CLC Genomics Workbench (QIAGEN) and mapped to the reference sequence (Ophiothrix caespitosa_MVF214044 and Ophiothrix lepidus_IE.2007.39 in O'Hara et al., 2017) using default parameters. Consensus sequences were extracted from the mapped reads for each exon. Sequences were aligned using the MUSCLE (Edgar, 2004) in MEGA11 (Tamura et al., 2021) with default settings as well.

Initial model selection was conducted using MrModeltest 2.4 (Nylander, 2004), and all partitions (exons) converged on the same best-fit model (GTR+G+I). Thus, an unpartitioned ML tree was constructed using IQ-TREE 2 (Minh et al., 2020), employing 1,000 ultrafast bootstrap replicates. Baysian analysis was performed using MrBayes v3.2.7 (Ronquist et al., 2012). The analysis was conducted with a single run comprising four Markov chains for 1,000,000 generations, sampling every 1,000 generations and first 25% of trees were discarded as burn-in.

RESULTS

A total of 454 ophiuroid specimens were collected from three artificial beaches of Sentosa Island. They belong to seven species and four genera of Ophiactidae and Ophiotrichidae. The most abundant species were *Ophiactis savignyi* and *Ophiothela mirabilis*, especially from sponges.

TAXONOMIC SECTION

Order Amphilepidida O'Hara, Hugall, Thuy, Stöhr & Martynov 2017

Family Ophiactidae Matsumoto, 1915

Genus *Ophiactis* Lütken, 1856

Ophiactis savignyi (Müller & Troschel, 1842)
(Fig. 3A)

Ophiolepis savignyi Müller & Troschel, 1842: 95.
Ophiactis krebsii Lütken, 1856: 12.
Ophiactis virescens Lütken, 1856: 24.
Ophiolepis sexradia Grube, 1857: 343.
Ophiactis sexradia – Lütken, 1859: 126; Lyman, 1865: 115; Koehler, 1898: 72.
Ophiactis reinhardtii Lütken, 1859: 263, pl. 3, fig. 7.

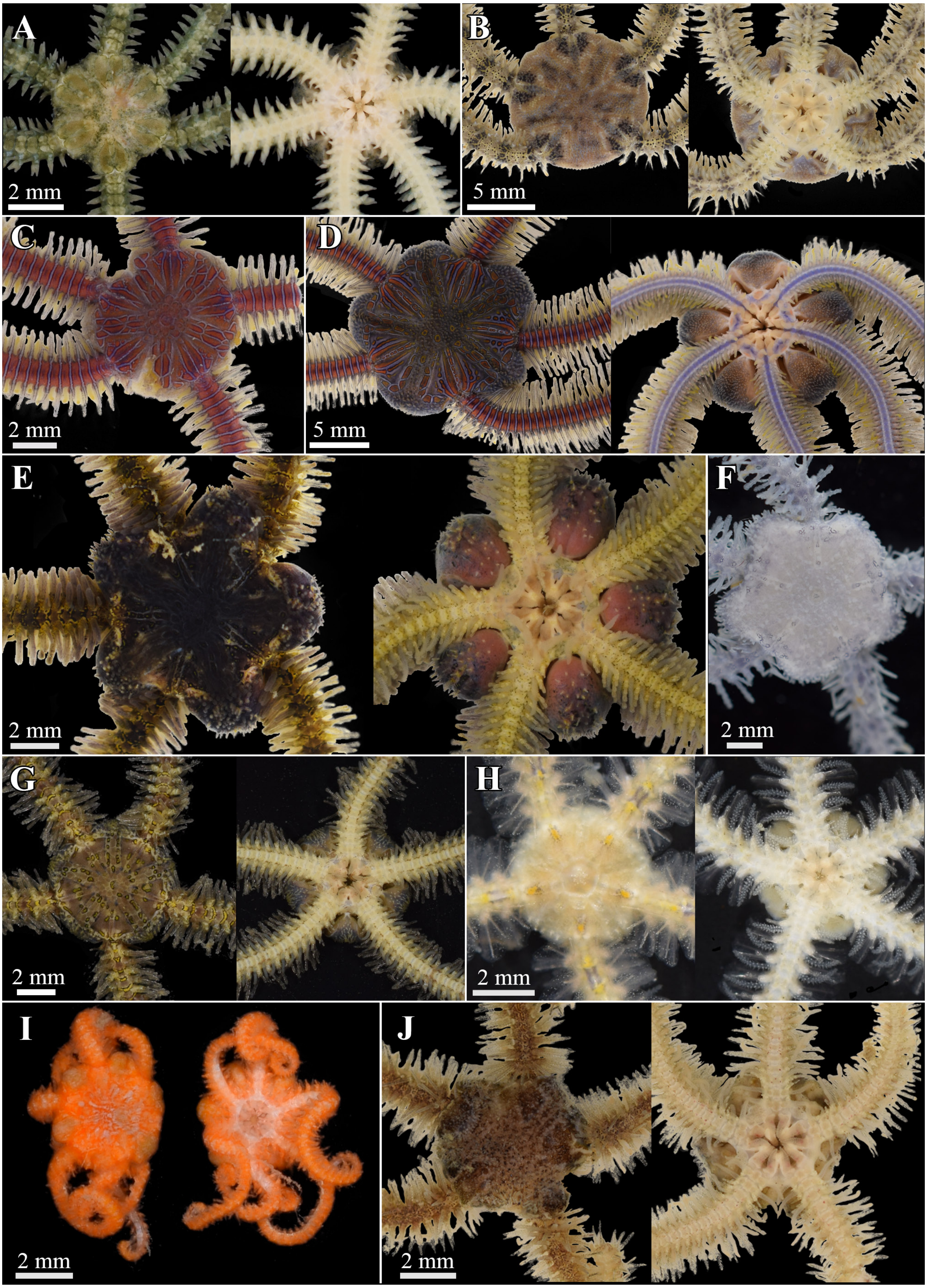

Fig. 3. Brittle stars from Sentosa Island, Singapore. Colour photographs of dorsal and ventral views of animals before fixation. A, *Ophiactis savignyi* (Müller & Troschel, 1842), ZRC ECH 2162; B, *Macrophiothrix longipeda* (Lamarck, 1816), ZRC ECH 2165; C, *Macrophiothrix nereidina* (Lamarck, 1816), ZRC ECH 2159; D, *Macrophiothrix nereidina* (Lamarck, 1816), ZRC ECH 2160; E, *Macrophiothrix plana*, new combination, ZRC ECH 2417; F, *Macrophiothrix plana*, new combination, ZRC ECH 2166, in ethanol, only dorsal view; G, *Macrophiothrix plana*, new combination, ZRC ECH 2167; H, *Macrophiothrix striolata* (Grube, 1868), ZRC ECH 2172; I, *Ophiothela mirabilis* (Verrill, 1867), ZRC ECH 2161; J, *Ophiothrix* (*Ophiothrix*) *exigua* Lyman, 1874, ZRC ECH 2168.

Ophiactis maculosa von Martens, 1870: 248.
Ophiactis incisa von Martens, 1870: 248.
Ophiactis savignyi – Lyman, 1882: 115; Koehler, 1905: 26; Matsumoto, 1917: 158, fig. 39; HL Clark, 1921: 108; Koehler, 1922: 193, pl. 64, figs. 5–6, pl. 96, fig. 2; Ely, 1942: 42, fig. 10, pl. 10, fig. B; HL Clark, 1946: 210; Chang et al., 1964: 110; Irimura, 1969: 40; AM Clark & Rowe, 1971: 82, 103, pl. 14 fig. 4; AM Clark, 1976: 112, fig. 4; Gibbs et al., 1976: 259; AM Clark & Courtman-Stock, 1976: 164; Liao, 1978: 72, fig. 2; Cherbonnier & Guille, 1978: 125, fig. 57; Irimura, 1981: 21; 1982: 28, text-fig. 17; Lim & Chou, 1988: 246, 247; Liao & AM Clark, 1995: 217, fig. 110; Rowe & Gates, 1995: 380; Shin & Rho, 1996: 411, pl. 68; Lane et al., 2000: 480; Lane & Vandenspiegel, 2003: 94; Liao, 2004: 236, fig. 140; Fujita et al., 2008: 5, fig. 3S; Fujita & Irimura, 2015: 265, 270.
Ophiactis brocki de Loriol, 1893b: 401, pl. 14, fig. 1.
Ophiactis conferta Koehler, 1905: 25, pl. 3, figs. 15–17.
Ophiactis versicolor HL Clark, 1939: 81, fig. 36.

Material examined. ZRC ECH 2158, 8 specimens, 2023/5/8, northwest Siloso Beach, pontoons; ZRC ECH 2162, 334 specimens, 2023/5/8, northwest Siloso Beach, pontoons; ZRC ECH 2163, 1 specimen, 2023/5/8, northwest Siloso Beach, pontoons; ZRC ECH 2169, 35 specimens, 2023/5/9, southeast Siloso Beach, pontoons; ZRC ECH 2171, 1 specimen, 2023/5/8, northwest Siloso Beach, seagrass on rocky shores.

Diagnosis. Disc round; diameter less than 5 mm. Six arms; length 10–30 mm. Dorsal disc bearing rounded scales with short spinelets. Radial shields droplet-shaped, separated proximally by 2–3 large elongated scales; length approximately 1/3 of disc diameter. Ventral disc covered by scales, lacking spinelets. Oral shields rounded, longer than wide. Adoral shields triangular. Teeth square, arranged in 1 row. Two oral papillae, rounded. Genital slits extending to disc edge. Dorsal arm plates oval, wider than long; distal edge slightly convex. Ventral arm plates rounded, as long as wide. 6–7 arm spines on basal segments, 5 subsequently. Arm spine as long as corresponding arm segment length. One tentacle scale, round.

Remarks. This species is distributed widely in the Indo-West Pacific Region, and often nestles among various animals and plants (Hendler et al., 1995; Fujita & Irimura, 2015; Hayashi & Okanishi, 2019), and the present specimens were all found inside mycalid sponges. Live colour is greenish dorsally and white ventrally (Fig. 3A).

Family Ophiotrichidae Ljungman, 1867

Genus *Macrophiothrix* H. L. Clark, 1938

Macrophiothrix longipeda (Lamarck, 1816)

(Fig. 3B)

Ophiura longipeda Lamarck, 1816: 544.
Ophiothrix longipeda – Müller & Troschel, 1842: 113; von Martens, 1870: 254; Lyman, 1879: 54 (part); Ljungman, 1866: 332; de Loriol, 1893a: 36; 1893b: 415; Koehler, 1905: 92; 1907a: 252; 1922: 235, pl. 31, fig. 3, pl. 33, fig. 10, pl. 100, fig. 2 [non pl. 31, fig. 4, pl. 33, fig. 9] (part); 1930: 143; HL Clark, 1911: 263; 1921: 110, pl. 15, fig. 5, pl. 33, fig. 1 (part).
Ophiothrix punctolimbata von Martens, 1870: 257. [Synonymised by AM Clark (1968)]
Ophiothrix microplax Bell, 1884: 143. [Synonymised by AM Clark & Rowe (1971)]
Ophiothrix picturatus de Loriol, 1893a: 49, pl. 25, fig. 3. [Synonymised by Jangoux (1985)]
Macrophiothrix longipeda – HL Clark, 1938: 288; 1946: 221; Balinsky, 1957: 17; Fell, 1960: 24; Chang et al., 1964: 114; AM Clark, 1967: 637, pl. 11, fig. 1; 1968: 300, figs. 3m–o, 4p–r, 5p–r, 7l–m; AM Clark & Rowe, 1971: 82, 114, pl. 16, fig. 4; Devaney, 1974: 140; AM Clark & Courtman-Stock, 1976: 139; Liao, 1978: 77, pl. 2, fig. 2, figs. 7(3), 8(2), 9(2), 10(2), 11(2); Cherbonnier & Guille, 1978: 153, fig. 61, fig. 28 (non pl. 4, figs. 3–4) (part); Kingston, 1980: 131; Irimura, 1981: 16, 33; 1982: 55, fig. 33, pl. 9, fig. 6; Marsh & Marshall, 1983: 677; Guille & Vadon, 1985: 62; Marsh, 1986: 70 (part); Lim & Chou, 1988: 246, 247; Hoggett, 1991: 1103–1108, figs. 14, 15; Liao & AM Clark, 1995: 226, figs. 112b, 113b, 114b, 115b, 116c; Rowe & Gates, 1995: 413; Lane et al., 2000: 480; Liao, 2004: 250, figs. 145B, 146C, 147B, 148B, 149B; Fujita et al., 2008: 3, fig. 3: E, F; Fujita & Irimura, 2015: 265, 267.

Material examined. ZRC ECH 2165, 1 specimen, 2023/5/9, southeast Siloso Beach, rocky shores.

Diagnosis. Disc round, diameter reaching 24 mm. Five arms, length more than 15 times of disc diameter. Short stumps evenly on dorsal disc. Radial shields covered by stumps as rest of disc. Ventral disc covered by sparser stumps than dorsal disc. Oral shields distal edges rounded, not particularly short. Adoral shields triangular and narrow, separated abradially. Minute teeth papillae on jaws. Dorsal arm plates trapeziform, wider than long; distal edge straight or slightly concave; lateral angles acute. Ventral arm plates width equal length, distal edge rounded. Arm spines not glassy; 10 on basal segments, 8 subsequently; 2nd dorsalmost one longest, exceeding corresponding segment width; ventralmost one shortest, not hook-like. One tentacle scale, small, present at proximal side of ventral arm plate.

Remarks. The present specimen is relatively small with a disc diameter of 10 mm. Some morphological characters were slightly different from typical *Macrophiothrix longipeda*. The dorsal arm plates are narrower in shape compared to larger individuals with convex distal edge rather than flat or concave. In addition to black line or spots along the proximal margin (Hoggett, 1991; Liao, 2004), this specimen also bears a couple of spots in the central part of plate (Fig. 3B). However, we confirmed the identity of this specimen by COI and 16S sequences (PX578058, PX637840). The BLAST results indicated of the sequence of the present specimen showed highest homology to those (Acc. No. PP652101.1, LC749647.1 and OM994402.1) of three specimens of *Macrophiothrix longipeda* (Florida Museum of Natural History, BHKG-1553, National Museum of Nature and Science, NSMT E-13948 and The First Institute of Oceanography, Ministry of Natural Resources, China, WZD-2021, respectively), and p-distances between the present specimens and the latter *M. longipeda* specimens (16S: 0.003–0.032, COI: 0.014–0.045) were sufficiently small to suggest all specimens are intraspecific (see Remarks under *Macrophiothrix plana*).

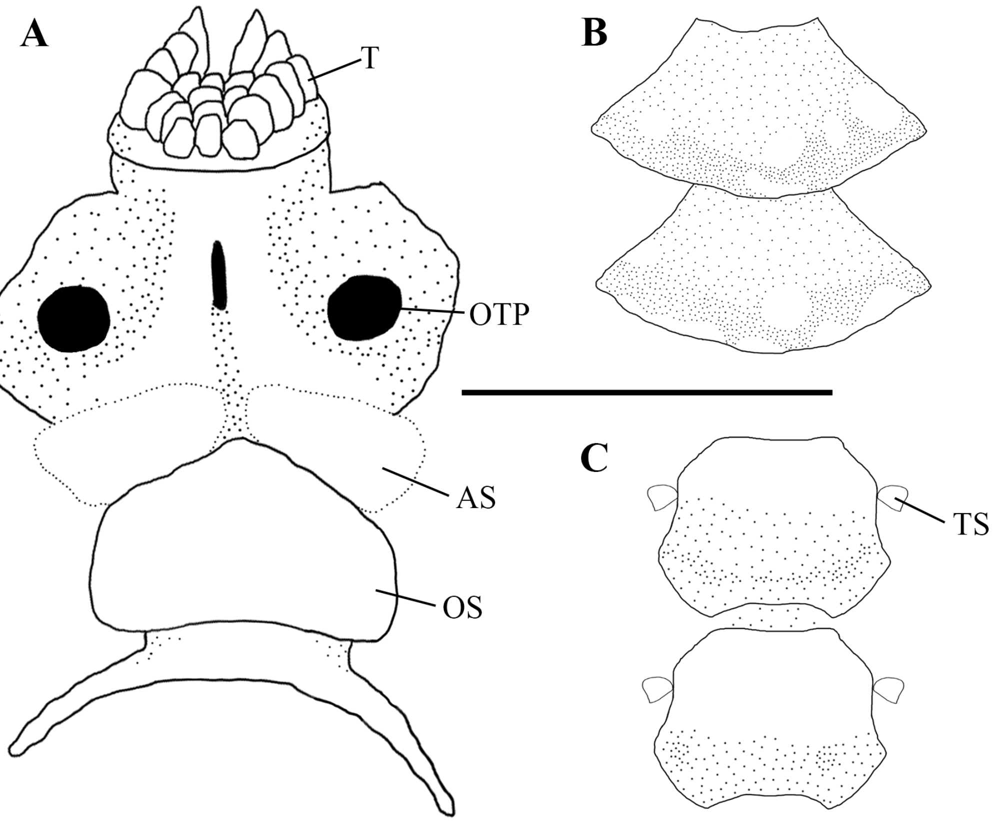

Fig. 4. *Macrophiothrix plana*, new combination, ZRC ECH 2417. A, Dorsal arm plates (6th and 7th from disc); B, Ventral arm plates (6th and 7th from mouth) and tentacle scales. Abbreviations: A, jaw; AS, adoral shield; OS, oral shield; OTP, oral tentacle pore; T, tooth papillae; TS, tentacle scale. Scale bar: 1 mm.

The specimen was collected from ulvacean algae attached to seawalls.

Macrophiothrix nereidina (Lamarck, 1816)
(Fig. 3C, D)

Ophiura nereidina Lamarck, 1816: 544.
Ophiothrix nereidina – Müller & Troschel, 1842: 115; Lyman, 1882: 221; Studer, 1882: 26; Marktanner-Turneretscher, 1887: 309; Döderlein, 1888: 832, pl. 32, figs. 5a–c; 1896: 293, pl. 16, fig. 16a; Koehler, 1898: 97; 1907b: 334; 1922: 252, pl. 101, fig. 1; Matsumoto, 1917: 224, fig. 61; HL Clark, 1921: 112, pl. 15, figs. 2, 8, 9.
Ophiothrix cataphracta von Martens, 1870: 259.
Ophiothrix andersoni Duncan, 1887: 95, pl. 9, figs. 12, 13, pl. 11, figs. 28–30.
Ophiotrichoides nereidina – HL Clark, 1938: 306; 1946: 232; Murakami, 1963: 176.
Ophiothrix (*Keystonea*) *nereidina* – AM Clark, 1967: 648; AM Clark & Rowe, 1971: 84, 107, fig. 34b; Liao, 1978: 75; Irimura, 1982: 54, fig. 32, pl. 12, figs. 3, 4; Liao & AM Clark, 1995: 244, fig. 128a; Rowe & Gates, 1995: 426; Liao, 2004: 279, fig. 164; Fujita et al., 2008: 4, fig. 3L.
Macrophiothrix nereidina – Hoggett, 1991: 1082; Fujita & Irimura, 2015: 265.

Material examined. ZRC ECH 2159, 1 specimen, 2023/5/8, northwest Siloso Beach, rocky shores; ZRC ECH 2160, 3 specimens, 2023/5/8, northwest Siloso Beach, pontoons.

Diagnosis. Disc rounded or inflated interradially, diameter more than 10 mm. Five arms, length more than ten times disc diameter. Dorsal disc naked or bearing few spinelets on central area in large individual; underlying fine scales indistinct; spinelets at interradial disc edge taller and denser. Radial shields length approximately 2/3-disc radius, naked. Ventral disc covered by spinelets. Oral shield width twice its length; distal edge slightly convex; proximal edge sharply convex. Adoral shields short, oval, contiguous abradially. Dorsal arm plates broad, width twice its length; distal edge slightly concave at center. Ventral arm plates wider than long; distal edge concave. 8–9 arm spines on basal segments, 5–6 subsequently; second dorsal-most one longest, exceeding corresponding segment width; ventral-most one hook-like, with three curved thorns. One tentacle scale.

Remarks. AM Clark (1967) included this species in the subgenus *Ophiothrix* (*Keystonea*) due to its naked dorsal disc, as seen in one of the present specimens (ZRC ECH 2159, Fig. 3C), whereas the other three specimens (ZRC ECH 2160, Fig. 3D) have spinelets at the central part of their dorsal disc. This intraspecific variation of disc armament has been mentioned by Duncan (1887) and Liao (2004), in particular for larger specimens. Similar variation was also found in the species *Macrophiothrix plana*, new combination, collected in this study (see below).

The dorsal disc shows reticulate pattern and the dorsal arm displays transverse white bands, both formed by the whitish edge of scales (Fig. 3C, D). A purple line is present on each of the ventral arms.

Macrophiothrix plana **(Lyman, 1874), new combination**
(Fig. 3E–G)

Ophiothrix plana Lyman, 1874: 238, pl. 4, figs. 1–8; Koehler, 1905: 75, pl. 8, fig. 3; 1922: 255, pl. 38, figs. 3–5, pl. 101, fig. 2.
Placophiothrix plana – HL Clark, 1938: 313; 1946: 227; Chang et al., 1964: 115.
Ophiothrix (*Ophiothrix*) *plana* – AM Clark, 1967: 647; AM Clark & Rowe, 1971: 110; AM Clark, 1982: 492, 493; Liao & AM Clark, 1995: 250, fig. 133; Rowe & Gates, 1995: 423; Lane et al., 2000: 481; Liao, 2004: 286, fig. 169; Fujita et al., 2008: 4, fig. 3N–O.

Material examined. ZRC ECH 2166, 1 specimen, 2023/5/9, southeast Siloso Beach, rocky shores; ZRC ECH 2167, 1 specimen, 2023/5/9, southeast Siloso Beach, rocky shores, pontoons; ZRC ECH 2417, 1 specimen, 2023/5/9, southeast Siloso Beach, rocky shores, pontoons.

Diagnosis. Disc diameter 5–9 mm, round. Arm length 4 times disc diameter. Disc naked or with few spinelets. Radial shields triangular, naked. Oral shields lozenged with round distal edge, or straight in large individual. Dorsal arm plates fan shaped, wider than long in large individual. Ventral arm plates square, with concave proximal and distal edges. Eight arm spines on basal segments; in adult individual, dorsalmost one tapering, and the lower ones swelled on tip; ventralmost spine hook-shaped, with 3 thorns. One tentacle scale.

Description of large individual. [ZRC ECH 2417, disc diameter 9.1 mm] Longest arm length 43 mm. Disc inflated interradially with mature gonads (Fig. 3E). Dorsal disc scales small, circular and imbricated, lacking any armament. Radial shield triangular, naked, length 2.1 mm. Ventral interradii covered by sparse scales with spinelets. Oral shields pentagonal, 1.6× wider than long, distal edge straight or slightly concave (Fig. 4A). Madreporite oval, longer than other oral shields. Adoral shields triangular (Fig. 4A). Lateral edges of adoral dental plate with a single row of conspicuously broader (adoral) or taller (aboral) and more pointed teeth, enclosing a group of short papillary teeth (Fig. 4A). Oral papillae absent. Oral tentacle pore rounded, visible from outside (Fig. 4A). In basal arm, dorsal arm plates trapezoidal, 1.5–2.1× wider than long, maximum width close to distal edge (Fig. 4B); distal edge convex. Ventral arm plates square, lateral and distal edges concave (Fig. 4C). Eight arm spines on basal segments, six subsequently, non-glassy, coarse; dorsalmost one straight, tapering; 2nd dorsalmost one longest, somewhat longer than corresponding arm segment width; ventralmost one hook-shaped with 3 thorns; the others' tips thorny, mildly swollen. One tentacle scale (Fig. 4B).

Comparison of arm ossicles. [ZRC ECH 2166, disc diameter 5.8 mm] Vertebrae width 0.9 mm, height 0.8 mm (Fig. 5A–E). Dorsal depression reversed trapeziform from proximal view (Fig. 5A). Keel present (Fig. 5C). Articulation well-developed, zygosphene with 2 separated articulating facets (Fig. 5B). Interlayer of proximal/distal dorsal muscle attachment area thin, 1/12 of vertebra length at the thinnest (Fig. 5E). Distal part of dorsal arm plate slightly trilobed (Fig. 5F, G). Ventral arm plate concave distally (Fig. 5H, I). Lateral arm plates arched, sickle-shaped; six spine articulations oblique, each consisting of two bent ridges, dorsal second biggest (Fig. 5J); two oval knobs on internal lateral arm plate well defined; single perforation near the lower knob; dorsal ridge oval (Fig. 5K). arm spine flat; dorsal first and second arm spines tapering with few thorns (Fig. 7A); dorsal second one longest; ventralmost spine hood-like with three long thorns (Fig. 7B); the rest spine truncated in tip, never swollen.

[ZRC ECH 2417, disc diameter 9.1 mm] Vertebrae width 1.2 mm, height 1.0 mm, length 0.7 mm (Fig. 6A–E). Dorsal depression U-shaped from proximal view (Fig. 6A), shallow with maximum width inside from dorsal view (Fig. 6C). Dorso-distal keel present (Fig. 6C). Articulation well-developed, zygosphene broad, with 2 separated articulating facets; dorsal muscle attachment area with nodules on distal side (Fig. 6B). Interlayer of proximal/distal dorsal muscle attachment area thin, 1/10 of vertebra length at the thinnest (Fig. 6E). Dorsal arm plate slightly arched; pair of oval protrusions on proximal internal plate (Fig. 6F, G). Ventral arm plate concave laterally and distally; proximal part coarse, margin jagged (Fig. 6H, I). Lateral arm plates strongly arched, sickle-shaped; ventral-mid lobe on proximal margin; 6 spine articulations oblique, each consisting of two bent ridges, dorsal second biggest (Fig. 6J); 2 knobs on internal lateral arm plate well defined; single perforation under the lower knob; dorsal ridge short, distant from upper knob (Fig. 6K). Dorsalmost arm spine tapering with few thorns (Fig. 7C); ventralmost spine hood-like with three long thorns (Fig. 7D); thorns abundant on the rest arm spine's tip, not single-layered.

Remarks. The sequence data of 16S (363 bp) and COI (512 bp) indicated these three specimens are conspecific. The highest p-distance of 16S among ZRC ECH 2166 (Acc. No. PX446560, PX570224), 2167 (PX446559, PX570223), 2417 (PV670008, PV669895) was 0.006, lower than the minimum interspecific p-distance of 16S (0.030) and maximum intraspecific p-distance of 16S (0.042) reported by Hart & Podolsky (2005) for *Macrophiothrix* species. Moreover, the phylogenetic tree of Ophiotrichidae using 14 exons showed the specimen ZRC ECH 2417 was nested within *Macrophiothrix* (Fig. 8). Consequently, *Ophiothrix* (*Ophiothrix*) *plana* was transferred to *Macrophiothrix* in this study. Compared to the body size of this species so far reported (disc diameter up to 7 mm; Lyman, 1874; HL Clark, 1938; Liao, 2004), the specimen ZRC ECH 2417 is larger (disc diameter 9.1 mm). This large specimen shows some features that differ from previous descriptions reported for *Ophiothrix* (*Ophiothrix*) *plana*. The oral shield has a concave distal border (Fig. 4A) rather than oval-shaped (Lyman, 1874) or lozenged in smaller specimens (Chang et al., 1964; Liao, 2004). The dorsal arm plates of the basal segments are more than twice as wide as long (Fig. 4B), whereas in smaller specimens the length approaches the width (Lyman, 1874). On the other hand, the ventral arm plates (Fig. 4C) are similar in shape to previous descriptions (Lyman, 1874; Chang et al., 1964; Liao, 2004).

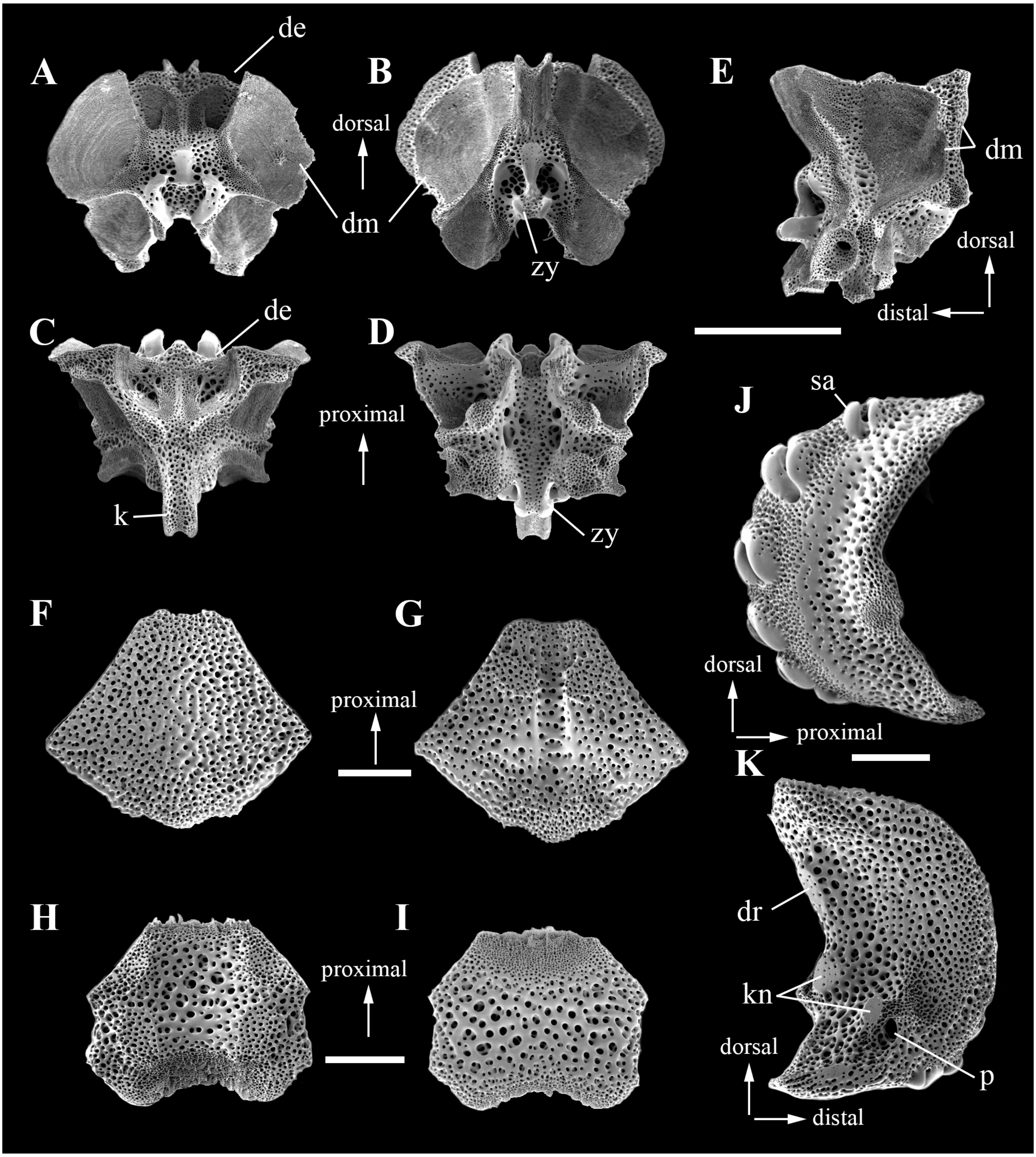

Fig. 5. *Macrophiothrix plana*, new combination, ZRC ECH 2166 (disc diameter 5.8 mm). SEM photographs of isolated arm ossicles from basal arm (1st to 6th segments from disc). A–E, Vertebrae (A: proximal view; B: distal view; C: dorsal view; D: ventral view; E: lateral view); F, G, Dorsal arm plates (F: external view; G: internal view); H, I, Ventral arm plates (H: external view; I: internal view); J, K, Lateral arm plates (J: external view; K: internal view). Orientation is shown by arrow heads. Abbreviations: de, dorsal depression; dm, dorsal muscle attachment area; dr, dorsal vertebral articular ridge; k, keel; kn, vertebral articular knob; p, perforation; sa, spine articulation; zy, zygosphene. Scale bars: 500 µm (A–E); 200 µm (F–K); 100 µm (M).

To observe such size-dependent difference of ossicles in detail, we compared isolated arm ossicles between a smaller specimen (ZRC ECH 2166) and the large specimen (ZRC ECH 2417) (Figs. 5–7). For vertebrae, the dorsal depression has a flat bottom in the smaller specimen (Fig. 5A), whereas it is curved in the large specimen. The stereom of the dorsal muscle attachment areas is finer in the smaller specimens (Figs. 5B, 6B). The dorsal arm plates vary in length-to-width ratio, but a slightly trilobed distal edge is evident in both specimens (Figs. 5F–G, 6F–G). All arm spines except the dorsalmost and ventralmost ones have swollen tips in the larger specimen (Fig. 7C), whereas the arm spines of the

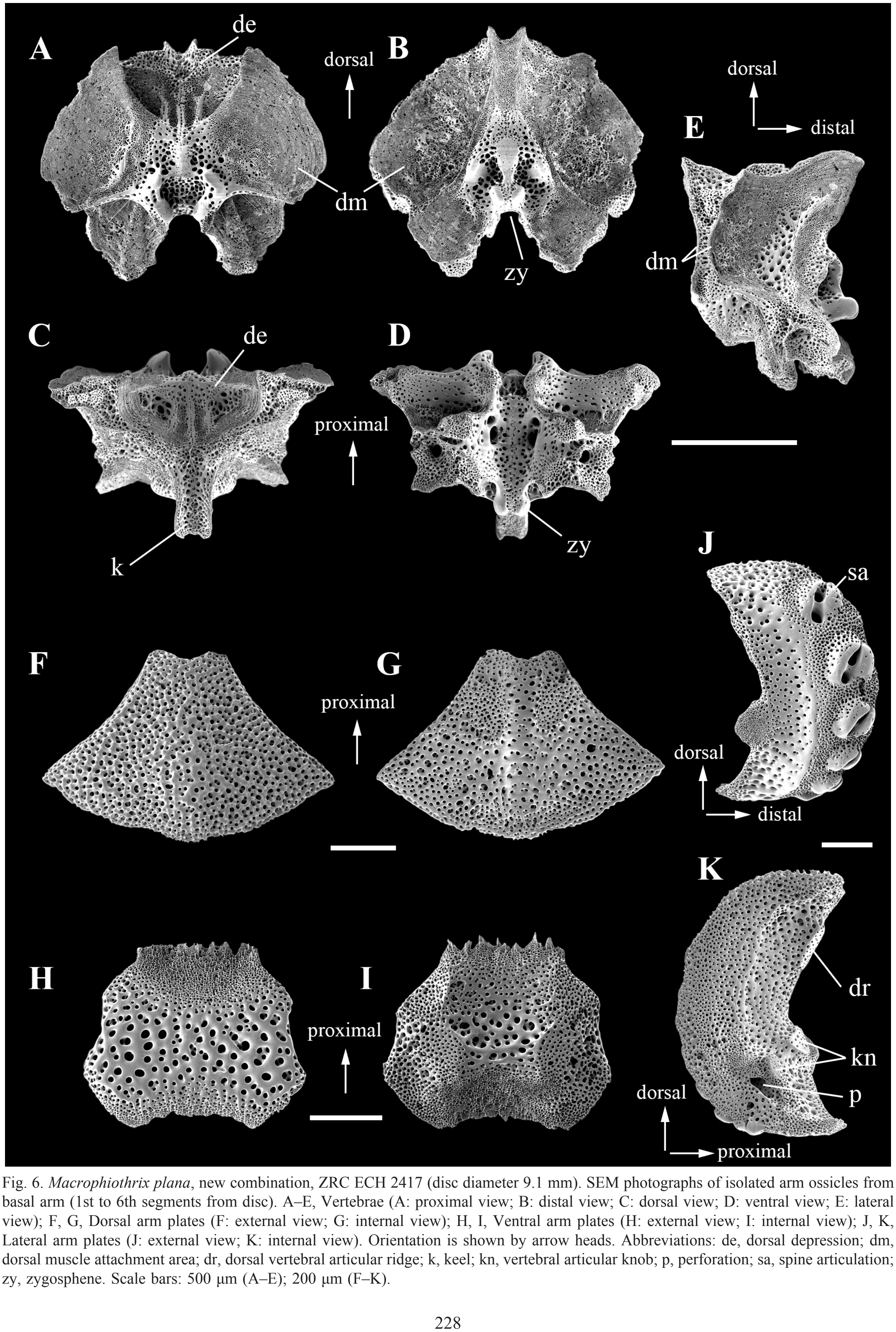

Fig. 6. *Macrophiothrix plana*, new combination, ZRC ECH 2417 (disc diameter 9.1 mm). SEM photographs of isolated arm ossicles from basal arm (1st to 6th segments from disc). A–E, Vertebrae (A: proximal view; B: distal view; C: dorsal view; D: ventral view; E: lateral view); F, G, Dorsal arm plates (F: external view; G: internal view); H, I, Ventral arm plates (H: external view; I: internal view); J, K, Lateral arm plates (J: external view; K: internal view). Orientation is shown by arrow heads. Abbreviations: de, dorsal depression; dm, dorsal muscle attachment area; dr, dorsal vertebral articular ridge; k, keel; kn, vertebral articular knob; p, perforation; sa, spine articulation; zy, zygosphene. Scale bars: 500 µm (A–E); 200 µm (F–K).

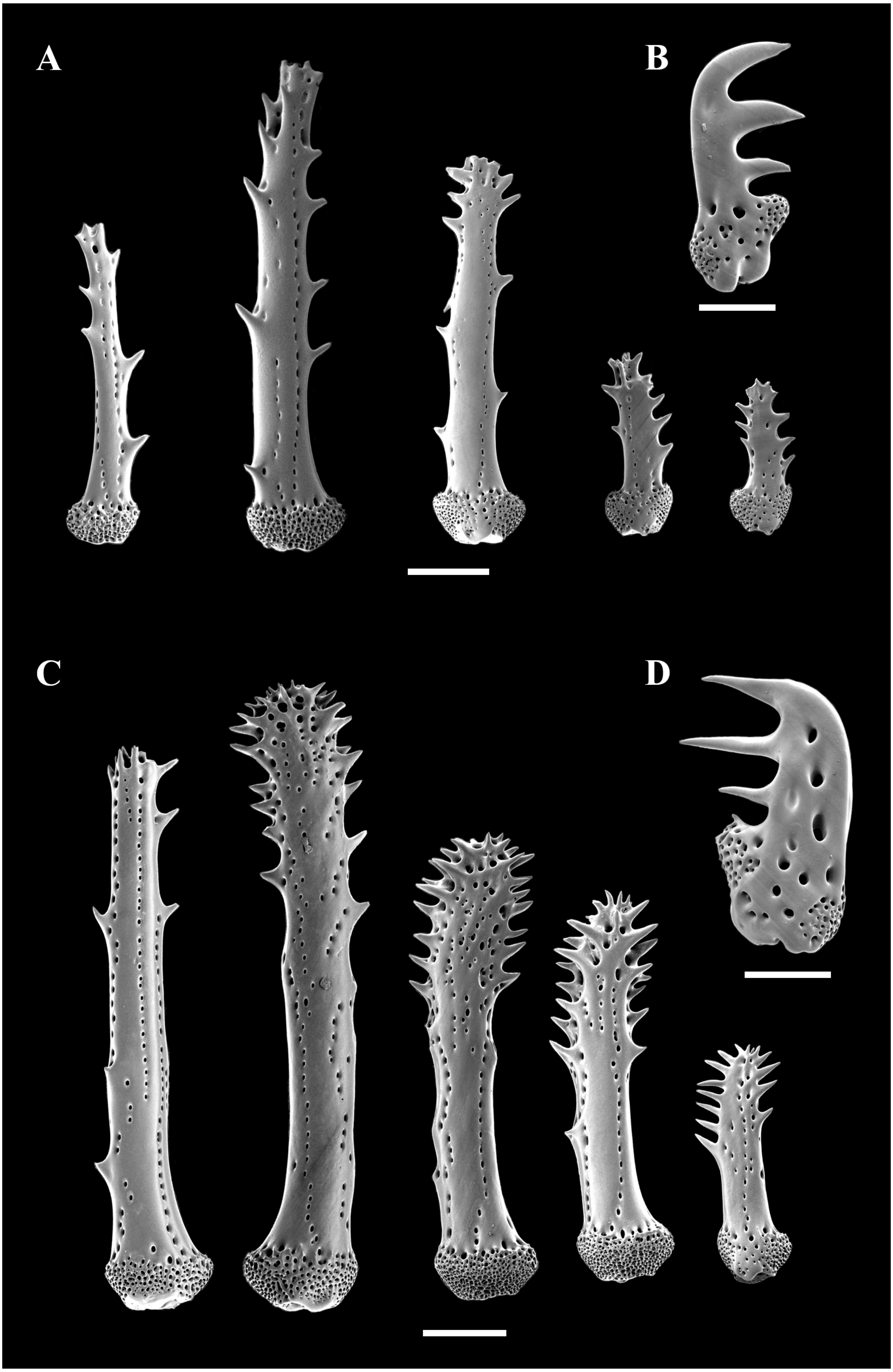

Fig. 7. *Macrophiothrix plana*, new combination, ZRC ECH 2166 (A, B), ZRC ECH 2417 (C, D). SEM photographs of isolated arm spines (1st to 6th segments from disc). A, C, First to fifth dorsal-most arm spines (left to right); B, D, Ventral-most arm spine. Scale bars: 200 µm (A, C); 100 µm (B, D).

smaller individual (Fig. 7A) resemble the dorsalmost spine of the larger specimen. The dorsal arm plates of the smaller specimen, with their back-set lateral corners, resemble those of *Macrophiothrix* juveniles (Hoggett, 1991), suggesting a possible affinity with the genus, which is further supported by the broad dorsal arm plates of the larger specimen. The broad dorsal arm plates of larger specimen with their back-set lateral corners of both specimens may indicate an affinity with the genus *Macrophiothrix*.

As for colouration, the large specimen has a darker dorsal disc, with yellow dots on radial shields and a row of scales between them. The distal halves of dorsal arm plates are variegated (Fig. 3E). Smaller specimens have a shallower disc, and as a result, the yellow dots with outline are more obvious. The bands on distal edge of distal dorsal arm plates are continuous (Fig. 3G), unlike in the large specimen.

Macrophiothrix striolata (Grube, 1868)
(Fig. 3H)

Ophiothrix striolata Grube, 1868: 45; Lyman, 1882: 222; Döderlein, 1896: 295, pl. 14, fig. 2, pl. 17, fig. 22, 22a; HL Clark, 1921: 114, pl. 15, fig. 1; Koehler, 1922: 277, pl. 33, figs. 1–2, pl. 34, fig. 5, pl. 102, fig. 1; 1930: 151; Mortensen, 1932: 13.
Ophiopteron punctocaeruleum Koehler, 1905: 114, pl. 12, figs. 5–7, pl. 15, fig. 6; 1922: 305, pl. 58, figs. 5–7, pl. 103, fig. 3. (synonymised by Mortensen, 1932).
Placophiothrix striolata – HL Clark, 1938: 314; 1946: 225; Chang et al., 1964: 116.
Ophiothrix (*Placophiothrix*) *striolata* – AM Clark, 1967: 648; AM Clark & Rowe, 1971: 86, 113; Liao & AM Clark, 1995: 253, fig. 135; Rowe & Gates, 1995: 428; Liao, 2004: 291, fig. 171.
Macrophiothrix striolata – Lane et al., 2000: 481.

Material examined. ZRC ECH 2172, 1 specimen, 2023/5/11, Palawan Beach, rocky shores.

Diagnosis. Disc round, diameter 10–13 mm. disc covered by scales with long spinelets. Large radial shields triangular, separated by 3 narrow scales. Oral shields diamond shaped, wider than long. Dorsal arm plates fan shaped, with round distal edge, wider than long. Ventral arm plates hexagonal, small in basal segments. 6–7 arm spines.

Remarks. Beside the yellow patterns on radial shields and dorsal arm plates as possessed by the adults, the examined specimen with disc diameter of 2.3 mm has prominent fin-like arm spines united with a membrane like *Ophiopteron* (Fig. 3H). Koehler (1905) described *Ophiopteron punctocaeruleum* on account of its fin-like arm spines but HL Clark (1921) suggested that it is a juvenile of this species and Mortensen (1932) synonymised them formally. Mortensen (1932) reported that the fin-like arm spines disappear with growth (Mortensen, 1932). This specimen was found in the foramen of a vertebral bone belonging to a dead anguid lizard.

Genus *Ophiothela* Verrill, 1867

Ophiothela mirabilis (Verrill, 1867)
(Fig. 3I)

Ophiothrix (*Ophiothela*) *mirabilis* Verrill, 1867: 268.
Ophiothela isidicola Lütken, 1872: 92; de Loriol, 1893a: 52; Koehler, 1905: 117; HL Clark, 1915: 285; Matsumoto, 1917: 230.
Ophiothela dividua von Martens, 1879: 127; HL Clark, 1923: 343; Balinsky, 1957: 22; AM Clark, 1974: 470.
Ophiothela verrilli Duncan, 1879: 477.
Ophiothela danae var. *involuta* Koehler, 1898: 88, pl. 1 & 2, fig. 4.
Ophiothela danae Koehler, 1905: 117; Matsumoto, 1917: 230–232, fig. 67; AM Clark, 1974: 470; 1976: 111, fig. 3; Lane et al., 2000: 481; Lane & Vandenspiegel, 2003: 98; Liao, 2004: 271, fig. 159; Fujita et al., 2008: 4, figs. 2A, 3J, K; Fujita & Irimura, 2015: 267; Goh & Chou, 1994: 216. (Synonymised by Alitto et al., 2020)
Ophiothela caerulea HL Clark, 1915: 283; AM Clark & Rowe, 1971: 116, 130.
Ophiothela hadra HL Clark, 1915: 284, pl. 14, fig. 4; Goh & Chou, 1994: 216.
Ophiothela mirabilis – Alitto et al., 2020: 419, figs 9–11.

Material examined. ZRC ECH 2161, 47 specimens, 2023/5/8, northwest Siloso Beach, pontoons; ZRC ECH 2170, 10 specimens, 2023/5/9, southeast Siloso Beach, pontoons; ZRC ECH 2173, 8 specimens, 2023/5/11, Palawan Beach, snorkelling.

Diagnosis. Disc almost occupied by huge radial shields, diameter about 2 mm. 6 arms, longest arm about 3 times disc diameter. Disc covered by skin; scales invisible. Oral papillae absent; teeth on apical jaw; the other oral parts covered by skin. Dorsal arm covered by skin; dorsal arm plate obscured; rows of granules on dorsal arm plate; 3 arm spines restricted to ventral side; 2 ventral-most arm spines hook-shaped. Ventral arm plates distal edge deeply concave, clearly separated. One tentacle scale, small.

Remarks. *Ophiothela mirabilis* is the second most abundant species in this study. They were found inhabiting sponges, seagrass, and algae. This species is 6-armed and asexually reproducing by fission (Clark, 1976), similar to the most abundant species *Ophiactis savignyi* (see remarks for *Ophiactis savignyi*). The present specimens' dorsal disc and arms are orange, while ventral disc and arms pale yellow (Fig. 3I). Body colour variegated with rosy, brown and purple in some individuals, with bands on arms (Liao, 2004).

Genus *Ophiothrix* Müller & Troschel, 1840

Ophiothrix (*Ophiothrix*) *exigua* Lyman, 1874
(Fig. 3J)

Ophiothrix exigua Lyman, 1874: 236, pl. 4, figs. 24–26; 1882: 217, 220; Koehler, 1905: 86, pl. 9, figs. 15–16; 1922: 228, pl. 40, figs. 1–4, pl. 98, fig. 4; 1930: 139; Mortensen, 1934: 10; HL Clark, 1938: 273; AH Clark, 1952: 293; Chang et al., 1964: 113; Irimura, 1981: 28; Shin & Rho, 1996: 440, pl. 88.
Ophiothrix marenzelleri Koehler, 1904: 103, figs. 77–78; Matsumoto, 1917: 220; Koehler, 1922: 248, pl. 39, figs. 3–5, pl. 100, fig. 4; Matsumoto, 1941: 342, fig. 8; Murakami, 1943: 233; 1944: 267; 1963: 176; Chang et al., 1964: 113; Lane & Vandenspiegel, 2003: 90.
Ophiothrix hylodes HL Clark, 1911: 263, fig. 130 [Synonymised as *Ophiothrix marenzelleri* by Matsumoto (1917)].

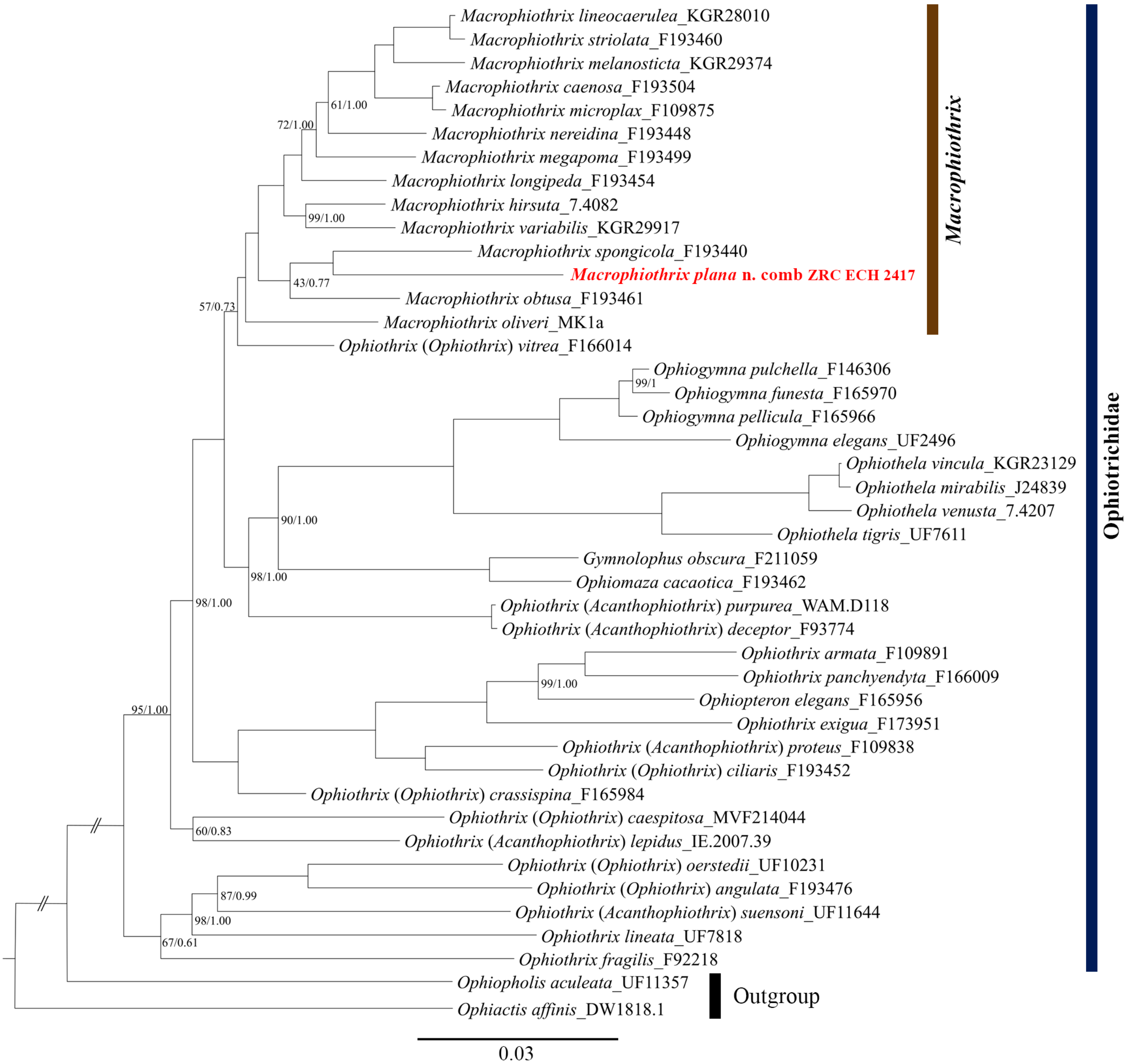

Fig. 8. Maximum likelihood tree of Ophiotrichidae inferred from 14 exons (14,343 bp). Bayesian tree showed the same topology. Bootstrap values and posterior probabilities are indicated on the nodes; values equal to 100/1.00 are not shown. All sequences were based on O'Hara et al. (2017) except *Macrophiothrix plana*, new combination, (ZRC.ECH.2417) which was obtained from this study.

Ophiothrix (*Ophiothrix*) *exigua* AM Clark, 1967: 647; AM Clark & Rowe, 1971: 84, 110; Cherbonnier & Guille, 1978: 140, pl. 5, figs. 5–6, figs. 61: 3–4; Guille & Jangoux, 1978: 61; AM Clark, 1982: 492, 493; Irimura, 1982: 43, fig. 28, pl. 8, figs. 2–6, pl. 10, figs. 1–3, 5, 6; Liao & AM Clark, 1995: 247, fig. 131; Rowe & Gates, 1995: 422; Lane et al., 2000: 481; Liao, 2004: 282, fig. 166; Fujita & Irimura, 2015: 265.

Ophiothrix (*Ophiothrix*) *marenzelleri* – AM Clark, 1967: 647; 1982; 492, 493; Liao & AM Clark, 1995: 248, fig. 132; Lane et al., 2000: 481; Liao, 2004: 285, fig. 168.

Material examined. ZRC ECH 2168, 1 specimen, 2023/5/9, southeast Siloso Beach, pontoons.

Diagnosis. Disc diameter 5–10 mm, arm length 4–5 times disc diameter. Dorsal disc fully covered by trifid spinelets. Radial shields also covered by spinelets. Ventral interradial disc naked proximally; spinelets present on lateral areas of ventral interradial disc. Oral shields rhombic with rounded lateral edges, wider than long; adoral plates separated abradially. Dorsal arm plates rhombic, longer than wide, proximal edge short, lateral angles acute. Ventral arm plates wide, distal edge concave and adjacent plates separated. Seven arm spines on basal segments, five subsequently; longest one exceeds corresponding segment width; ventral-most one hook-shaped. One tentacle scale.

Remarks. This species exhibits high morphological diversity, in particular, in the arrangement of spinelets on dorsal disc. Disc and arms are coloured variously gray, yellow or green (Liao, 2004). Dorsal disc of the present specimen is darker, and dorsal arm is variegated (Fig. 3J).

DISCUSSION

In this study, we report the presence over 450 individuals of brittle stars, representing seven species, encountered from artificial structures of shallow-water reclaimed public beaches. Broadly, for six of the seven species reported here (i.e., *Ophiactis savignyi*, *Macrophiothrix longipeda*, *Macrophiothrix nereidina*, *Macrophiothrix striolata*, *Ophiothela mirabilis*, and *Ophiothrix (Ophiothrix) exigua*), they do not have any unresolved taxonomic nor nomenclatural issues as of writing. Pertaining to our placement of *Ophiothrix (Ophiothrix) plana* in the genus *Macrophiothrix*, evidence marshalled from both molecular and morphological data supported this placement. Thus, we propose here the new combination of *Macrophiothrix plana*.

While all seven species documented in this study have been reported from the Central Indo-Pacific realm (e.g., Lane et al., 2000; Fujita, 2016; see Spalding et al., 2007 for definitions of marine realms), two species, *M. striolata* and *M. plana* have thus far have only been exclusively documented from this marine realm. The global distribution of the remaining five species exhibit broader global distributions. Three species, *M. longipeda*, *M. nereidina*, and *O. exigua* have been reported to occur at the westernmost extent of the Indo-Pacific (i.e., the Western Indo-Pacific), along the eastern coastline of continental Africa (WoRMs Editorial Board, 2026). In contrast, both *O. savignyi* and *Ophio. mirabilis* appear to be cosmopolitan and opportunistic species, as they are reported to also occur in the Atlantic (WoRMs Editorial Board, 2026).

None of the brittle star species documented here represent new records for Singapore. However, all seven reported here were encountered and collected from artificial structures present in shallow-water public beaches for the first time; all previous reports of them were from deeper waters surrounding the Republic (e.g., Lane et al., 2000; Fujita & Irimura, 2015). Although the ecological benefits of these structures are unclear (Chapman, 2003), the presence and abundance of these brittle stars (total >400 individuals) observed and collected here suggest that these structures were suitable for their establishment. During our sampling efforts, we observed that these structures were encrusted with fouling invertebrates such as sponges and gorgonians; both *O. savignyi* and *Ophio. mirabilis* are well-reported to be associated with these foulers (e.g., Lane & Vandenspigel, 2003; Fujita, 2016). Additionally, the crevices and interstices present in these artificial structures likely provide refuge and protective spaces for the brittle stars (Baroliya et al., 2023), in an otherwise exposed environment.

The public beaches surveyed in this study are entirely artificial (Fig. 2). Despite their proximity to the heavy ship traffic in the Singapore Strait and the status of these beaches being a popular recreational area (Lee, 2003; Ng et al., 2011), these modified environments support a diversity of brittle stars. While the focus of the present study is one of an assessment of ecological impacts of coastal modification, it demonstrates that the presence of artificial coastal structures provide suitable habitats for a range of ophiuroid species—including generalists (e.g., *O. savignyi*) as well as others more restricted in their biographic distribution (e.g., *M. plana).* Long-term and broad-scale monitoring will be necessary to assess changes in species composition and to better understand the role of artificial habitats in sustaining marine biodiversity within heavily urbanised coastal systems.

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