

Revision of *Iphione* Kinberg, 1856 (Annelida, Aphroditiformia, Iphionidae)

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Abstract

The only revision of *Iphione* was made by Pettibone in 1986, who recognized four species including two newly described in that work: *I. muricata* (Savigny in Lamarck, 1818) (type species), *I. ovata* Kinberg, 1856, *I. treadwelli* Pettibone, 1986, and *I. henshawi* Pettibone, 1986. She included *I. fimbriata* de Quatrefages, 1866, *I. glabra* de Quatrefages, 1866, and *I. fustis* Hoagland, 1920 within *I. muricata*, and *I. spinosa* Kinberg, 1856 and *I. hirotai* Izuka, 1912 in *I. ovata*. Three other species were later added to the genus: *I. reticulata* Amoureux, Rullier & Fishelson, 1978 from the Red Sea, *I. coriolis* Hanley & Burke, 1991 from the Coral Sea, and *I. malifera* Piotrowski, 2014 from the Philippines. A recent contribution showed that *I. ovata* ranges from the Red Sea to the Eastern Pacific and includes *I. spinosa* and *I. reticulata*. Our objectives were to revise the genus, evaluating all species and describing new ones by assessing the relevance of morphological features, assisted in part with COI sequence data. We studied the morphology of type and non-type material from 18 institutions and sequenced 52 specimens representing 11 species. We found that the size and position of eyes, the size relationships between cephalic appendages, and the number of rows of macrotubercles in elytra vary with body size. The most relevant diagnostic features for species delineation, confirmed by genetic species delineation, are the type and size relationships of macrotubercles, the presence of fimbriae, the development of the basal tubercle of dorsal cirrophores, the type of neurochaetae (falcate *versus* acicular), and their tips (uni- *vs* bidentate; or simple *vs* hooded). We clarified the type species of the genus as *I. ovata*, and recognized 17 species, nine previously described and eight new. Our main results include: 1) the restriction of *I. muricata*; 2) the reinstatement of *I. fimbriata* including *I. fustis*; 3) redescrptions of *I. coriolis*, *I. henshawi* and *I. treadwelli*; and 4) the description of eight new species: *I. ankeri* **sp. n.** from Guam, *I. corbari* **sp. n.** from the Saya de Malha Bank, *I. harrisae* **sp. n.** from French Polynesia, *I. hourdezi* **sp. n.** from New Caledonia, *I. hyndmani* **sp. n.** from Hong Kong, *I. readi* **sp. n.** from the Red Sea (including many earlier records of *I. muricata*), *I. richeri* **sp. n.** from New Caledonia, and *I. wilsoni* **sp. n.** from Australia. Descriptions the eight newly described species include only one based upon a single specimen. Keys are included for the genera in the family, and species of *Iphione*.

Keywords: morphology, COI, keys, distribution, new species.

Introduction

Jules-César Savigny participated in the French campaign in Egypt and Syria (1798–1801), and some of his results were included in the volume on annelids, communicated in 1817 and published in 1822. The manuscript was available to Lamarck who used it extensively as part of his series on invertebrates, including the description of *Polynoe muricata* Savigny in Lamarck, 1818 and included one specimen from Mauritius. This scaleworm was found under stones, living like a chiton, in shallow-water rocky bottom habitats of the Red Sea. *Iphione* Kinberg, 1856 was later proposed and included the Red Sea species as *I. muricata*, and *I. ovata* Kinberg, 1856 from Hawaii. Unlike the body fragmentation, loss of appendages, or elytra that readily occurs in many scaleworms during collection, *Iphione* is seldom broken in parts, and elytra are rarely detached from the body.

The marine scaleworm polychaetes of the family Iphionidae Kinberg, 1856 are remarkable by resembling chitons (Savigny 1822: 21; Haswell 1882b: 241). These annelids have an oval body, live under rocks, and can cling to the undersides of rocks (Storch 1967).

Another remarkable feature is that elytra are very large, overlapping adjacent elytra, and are firmly attached to the body. The anatomical features of the cuticle, epidermis, sensory structures, and subepidermal components were regarded as unique among marine annelids by Storch & Alberti (1995).

Iphione Kinberg, 1856 was the first genus proposed in the group. The name was informally introduced by Savigny as tribe “Polynoe Iphionae” (Savigny 1822: 21), contrasting with the other tribe “Polynoe Simplicies” (Savigny 1822: 22), by having an oval or elliptic body, lacking median antenna, as opposed to a rectangular body, and having a median antenna. The etymology was not explained, as was typical in those times. Jaeger (1944: 113) indicated that the Greek word *Iphis* means strong or mighty, whereas *Iphion* was the name of an herb. Similar names were used in other groups; for example, in Botany, Cassini (1817: 153) proposed *Iphiona*, and Bate (1856: 187) introduced *Iphinoe* as a replacement name for one of his diastylid cumacean genera.

An explanation for why Savigny may have chosen the tribe name “Polynoe Iphionae”, and why he contrasted it with “Polynoe Simplicies”, might relate to the features used to diagnose these tribes. For the former, he indicated (Savigny 1822: 21) “elytra of fish-scale consistency, very precisely imbricated laterally and covering the whole dorsum”, whereas for the latter he indicated (Savigny 1822: 22): “elytra coriaceous or membranaceous, rarely imbricated laterally.” Selecting a name to describe covering or hiding might stem from Ovid’s *Metamorphoses*, particularly regarding the story of Iphis (Book 9; lines 666–797). Iphis was the daughter of Ligdus and Telethusa; whose mother tried to avoid disappointing her husband by siring a girl by raising Iphis as a boy, covering or hiding her femininity until adolescence. Savigny might have applied this analogy because, as indicated above, the dorsum is completely covered by elytra in his “Polynoe Iphionae”. An alternative explanation is that elytra in *Iphione* are more strongly attached to the dorsum than in other polynoids, because the Greek word *Iphi* means stoutly or mightily (Jaeger 1944:133; Brown 1956:442).

Rouse *et al.* (2022: 46) proposed that the name is after one of Heracles lovers. However, the name for the daughter of Tinjis and Antaios, was Iphinoe (see <https://one-of-the-greatest-sources-for-greek-mythology.fandom.com/wiki/Iphinoe>), and was the basis of the name used by Bate.

Savigny (1822: 21) noted the physical resemblance of his new species, currently known as *Iphione muricata* (Savigny in Lamarck 1818), to chitons. Baird (1865: 181), de Quatrefages (1866: 268), and Gravier (1901: 227) also commented on this similarity. Potts (1910: 341) indicated it was “one of the commonest polychaetes of coral reefs” and also noted based on observations by Gardiner, that the species shows homing behavior, which is among the earliest accounts of this behavior among marine invertebrates. Davis (1885: 200) documented homing in limpets in Scotland, after an earlier account by Lukis (1831).

Kinberg (1856: 383) proposed the new family as Iphionea, currently accepted as Iphionidae, and included in its diagnosis that there was no median antenna and that elytra were reticulate. The group was used as a subfamily in the Polynoidae Malmgren, 1867, and its diagnosis was implied in the key to genera provided by Fauchald (1977: 56) as follows: lateral antennae inserted anteriorly, without median antenna. This synthetic diagnosis was expanded by Wehe (2006: 48) by indicating there were only lateral antennae attached anteriorly on short lateral extensions, and that elytra are reticulate with polygonal areas. It

is interesting that Day (1962: 628; 1967: 41, key) indicated that a median antenna was present but, in the earlier publication, he referred to it as being very small and “concealed by a fold of the second segment but if this is pushed back a small dorsal papilla is revealed.”

Iphionidae has consistently been recovered as a separate lineage from other aphroditoid families, including the Polynoidae by molecular and morphological phylogenetic analyses (Norlinder *et al.* 2012; Gonzalez *et al.* 2018; Zhang *et al.* 2018). Gonzalez *et al.* (2018: 243) concluded that Iphionidae is supported by three synapomorphies: stacked/feathered notochaetae, loss of median antennae, and areolated elytra, although also noted that the latter two are homoplastic. Feathered notochaetae are also homoplastic as they are present in *Euphione* M’Intosh, 1885 and in *Augenerilepidonotus dictyolepis* (Haswell, 1882b) (redescr. Augener 1927a: 94; Pettibone 1995: 578). The latter species also has, as its specific epithet implies, areolate elytra, a character also noted in *Harmothoe areolata* (Grube, 1860). Thus, none of the synapomorphies are unique to the family. Nevertheless, the combination of these characters, their low level of homoplasy, and robust recovery of the family by molecular and morphological phylogenetic analysis robustly support the recognition of Iphionidae at the family level. Perhaps the only unique feature for the family could be the horizontal 8-shaped elytral fixation (Duncker 1906: 226, 243).

Kinberg (1856) included two species in *Iphione*, briefly describing *I. ovata* from Hawaii, separating it from *I. muricata* by its smooth and not fimbriated elytral margins. Later, Kinberg (1858) provided an extended diagnosis for the family and genus, and descriptions and illustrations for *I. ovata*, and added *I. spinosa* from South Africa. Baird (1865: 181) regarded these three species distinct, and de Quatrefages (1866) described three additional species: *I. fimbriata* from Australia, *I. hirta* from New Guinea and *I. glabra* from Mauritius. Schmarda (1861: 157) described another species from Sri-Lanka (formerly Ceylon) as *Polynoe peronea*.

As it often was the case for polychaete species, some earlier taxonomists disregarded these different species, and most used the older name for their records. For example, while Michaelsen (1892: 95) recorded *I. spinosa* from Ceylon, Willey (1905), despite confirming the lack of elytral fimbriae which would rather indicate that this species was either *P. peronea* or *I. spinosa*, recorded it as *I. muricata*. Augener (1913: 98) followed Willey by thinking most specimens should belong in *I. muricata* and confirmed this after comparing his Australian and Eastern Africa specimens. Likewise, Horst (1917a: 286) disregarded the elytral fimbriae as a distinguishing feature and regarded *I. muricata* and *I. spinosa* as synonyms and observed that *I. muricata* was a “universally distributed worm” (Horst 1917b: 65). Later, Fauvel (1919: 334) reiterated the synonymy of *I. peronea* and *I. spinosa* with *I. muricata*, although he did not examine any type material.

Augener (1922: 5–6) made a study of an abundant collection of Australian specimens, and revised the type material of Kinberg’s *I. ovata* and *I. spinosa*. He concluded that elytral macrotubercles and fringe could be eroded, and consequently they could not be used to separate these species, and thus he regarded them conspecific with *I. muricata*. Seidler (1923: 75) expanded this idea by including all but one described species under *I. muricata*, including the recently described ones like *I. hirotai* Izuka, 1912 from Japan, and *I. fustis* Hoagland, 1920 from the Philippines, even though he did not examine

type material. Seidler retained only *I. cimex* de Quatrefages, 1866 as valid, because it was described as eyeless, and with elytra lacking macrotubercles. In her extensive study of Kinberg's type material Hartman (1949) did not include his two *Iphione* species. These were later assessed by Piotrowski *et al.* (2024).

Rullier (1972: 35) concluded "there is not a single criterium for separating species from each other and *Iphione muricata* should be the only one to be retained." Among the six specimens he studied, one had abundant marginal papillae, while the others lacked them. Dismissing marginal papillae as relevant dates back to Fauvel (1943: 2) who indicated that they were "far from being constant. The long papillae along elytral margins fall off and most specimens from India and Vietnam that I have studied lack them."

As already indicated by Day (1967: 43, key) and Barnich *et al.* (2004: 289), marginal papillae (= fimbriae) can be used to separate similar species, although these authors only recognized two *Iphione* for South Africa, or the Hainan Islands (*I. ovata* and *I. muricata*). Wu (1968: 31) provided a comparative table indicating additional differences between two common species in Taiwan, in characters including the shape of lateral antennae, relative length of ceratophores to ceratostyles in lateral antennae, and of cirrophores to cirrostyles of tentacular cirri, the presence of spines along lateral elytral tubercles, and their color in ethanol, but these have not received subsequent attention. Storch (1967) showed that the body of *I. muricata* was provided with extensive oblique muscular bundles, explaining their capacity for fixing their bodies to rock surfaces, such that muscular structures could be modified after contraction and would be of limited relevance as diagnostic features. Color is often useful in separating similar species, but Nygren *et al.* (2010) found it to be polymorphic in some polynoids.

The position, shape, and size of eyes can be useful for separating similar scaleworm species, and while these features have been generally regarded as showing little intra-specific variation, they can also be variable within some species. Variability has been scarcely addressed or illustrated. Losham (1981: 6, Figs 1A, L) showed constancy in eye size and position of his *Pettibonesia furcosetosa*. Hanley & Burke (1988: 10–11, Figs 2A, 3A, B) illustrated the eye variations in their new species of commensal polynoid, *Disconatis contubernalis*. They noted that eyes sit on the widest prostomial area, that anterior and posterior eyes were close to each other laterally, and that anterior eyes were farther apart and slightly, or up to four times larger than posterior ones. In *Paralepidonotus ampulliferus* (Grube, 1878), Hanley (1991) illustrated one syntype from the Philippines (his figure 1A) and two other Australian specimens (figure 3A, C). The syntype has eyes markedly smaller than those present in Australian worms, but the difference was not regarded as relevant. A similar condition was presented for *P. indicus* (Kinberg, 1856) with some interesting differences in eye size between type and non-type specimens collected in different localities but disregarded as relevant for separating similar species. This might be the reason why some eye-size variations were disregarded as diagnostic features in specimens of another commensal species, *Harmothoe hyalonemae* Martín, Rosell & Uriz, 1992, living in different species of hexactinellid sponges (Martin *et al.* 1992).

In *Iphione*, anterior eyes can be marginal, round, and sometimes positioned in small protuberances, whereas posterior eyes are usually marginal and round. Their position, however, might modify their appearance because if they are displaced laterally, they might look oval to reniform or even semilunar if barely visible dorsally. Estimating

eye size is easier if they are dorsally visible, and they usually are $1/9$ – $1/10$ as long as prostomial width. However, it must be kept in mind that these features can be altered, as is the case among other scaleworms, when the pharynx is fully exposed (Britayev & Fauchald 2005: 18, Fig. 2A, B). There can be interesting variations deserving some further analysis (Britayev & Martin 2005: 4085, Fig. 1B, C), and that ontogenetic modifications are little known. In a recent study on *I. ovata*, it was shown that eye size and position vary depending on the contraction of the anterior end and cannot be diagnostic (Piotrowski *et al.* 2024). It is interesting to assess this variation in other *Iphione* species.

The nuchal hood is also a useful diagnostic character. Pettibone (1986) illustrated some shape variations from semicircular, wider than long (her Figs 1A, 3A, B, 5A, 6A, B, 8A), rectangular or truncate (her figure 4A), blunt conical, to as long as wide (her figure 7A). Interestingly, she included two different shapes for *I. muricata*. These differences have not been used as diagnostic, but Reish (1974: 114) noted that three species of *Hololepida* Moore, 1905 could be separated by using the shape of nuchal hood. The differences found in *Iphione* deserve to be assessed in their connection with body size or other variations.

Pettibone (1986) illustrated some cirriferous parapodia in posterior view, including the basal tubercle associated with dorsal cirri. This was unusual, but also done by Savigny (1822, Pl. 3, Fig. 1.8), Gravier (1901: 229, Fig. 234), and incompletely by Kinberg (1858: Pl. 3, Fig. 8F), Hoagland (1920: Pl. 46, Fig. 6), and Day (1967: 46, Fig. 1.3b). Cirrophores are cylindrical with granular surface (her Figs 4D, 8F); others have a single globose protuberance (her Fig. 6D, 7C), or there can be 2–3 lobate, smooth protuberances (her Fig. 2F). Pettibone (1986) indicated that for the same species, *I. muricata*, dorsal cirrophores could have a small basal protuberance (Fiji, USNM 19192), or 2–3 large basal lobes (Northern Australia, USNM 81945). An assessment of variations along the body in the same specimen, or in specimens of different size of *I. ovata* has clarified their relevance as diagnostic features because they are consistent and not modified during growth (Piotrowski *et al.* 2024).

Two other features that Pettibone (1986) regarded as useful were the number of transverse rows of denticles in neurochaetae, and the size of fimbria filaments and the extent of the exposed margin covered in median elytra. For example, in what she regarded as belonging to *I. muricata*, she noted that specimens from Australia (USNM 81945) could have neurochaetae with 27–35 rows of denticles and fimbria 7x longer than wide running along the exposed margin, whereas those from Fiji (USNM 19192) could have 17–24 rows and fimbria 8x longer than wide running along half the exposed margin, and those from Bikini (USNM 81942) could have 17–26 rows and fimbria up to 25 times longer than wide running along the exposed margin. These features could be size-dependent, and size of specimens was not indicated, such that their variation as a size-variable feature must be assessed in order to define their potential diagnostic use.

Material and methods

Specimens were observed with stereomicroscopes and finer details of elytra and chaetae in compound microscopes. Photographs were made with a digital camera with an adapter for the microscopes. Additional LED illuminators, in combination with standard microscope lamps, were used. When some specimens had many adsorbed materials, some parapodia

or elytra were carefully brushed while immersed in a 1:1 solution of white vinegar and 70% ethanol. Some specimens were temporarily stained with Methyl Green, or Shirlastain-A, and this can be noted by the greenish or reddish color in the plates. Photos from multiple focal planes were stacked with HeliconFocus8, and plates were arranged with PaintShopPro9. One specimen was dissected for observing anatomical features. The body wall was removed with ophthalmic microscissors or mini-scalpels, the gut longitudinally cut with a mini-scalpel, and the pharynx dissected for observing papillae and jaws.

Elytral features are often obscured by the presence of adherent debris and epibionts. Because the traditional 1:1 white vinegar and 70% ethanol cleaning solution is harmful to specimens, one or two elytra from midbody segments were removed and cleaned in the solution by brushing. If this is done quickly, the tubercles are not damaged, and can be easily observed with the compound microscope.

Elytra and parapodia were mounted in ethanol-glycerol and photographed with a black background and nearly horizontal illumination. In larger specimens, parapodia were mounted in depression slides. Notochaetae were often partially or totally removed to improve visibility. Unless indicated otherwise, observations were made on the right elytron 6, and on the left parapodium of chaetiger 12. Disassociated body parts were returned to the same container with the specimen.

A median cirriferous segment was removed for assessing the number of transverse rows of denticles in neurochaetae, and the sixth elytron was removed for assessing the relative size of fimbria and their extension along their exposed margin. They all had neurochaetae with falcate, unidentate tips. After this observation, because there was no variation in specimens from the same species and locality, neurochaetal tips are regarded as a diagnostic feature for each species.

Species are presented in a chronological sequence, and if published in the same year, and the newly described ones appear in alphabetical order. The additional material starts with topotype specimens, if any available, and all others are incorporated in a West to East sequence. Coordinates are modified into the classical format (degrees, minutes, seconds, if available) from data given in the labels (see <https://www.earthpoint.us/convert.aspx>). A section on variation includes brief characterization of other specimens, often with additional illustrations, and a short paragraph compiling the available information of the additional material. Distribution and ecological data, whenever available, were also taken from the labels or from catalogue data.

Two keys to genera of Iphionidae Kinberg, 1856 are included, one to complete specimens, the other to damaged or incomplete specimens, a common problem with deep sea specimens. The key to species of *Iphione* are based on a combination of morphological characters used by Pettibone (1986) and Piotrowski (2014), with additional features added for separating the similar species described here; type localities are included for each species.

Iphione muricata (Savigny in Lamarck, 1818) is restricted and includes *I. glabra* de Quatrefages, 1866, both based on specimens from Mauritius, and one used for the original proposal of *I. muricata* and then for *I. glabra*. One species is reinstated after the study of its type material: *I. fimbriata* de Quatrefages, 1866, while one other was not clarified because of lack of type as well as topotype material (*I. hirotai* Izuka, 1912), and *Polynoe peronea* Schmarda, 1861 is regarded as belonging in *Iphione*, but indeterminable. Three other species are redescribed: *I. henshawi* Pettibone, 1986, *I. treadwelli* Pettibone, 1986,

and *I. coriolis* Hanley & Burke, 1991 *Iphione malifera* Piotrowski, 2014 was not redescribed because it was thoroughly described recently. Eight additional species are newly described.

Samples of 10 of the 17 species of *Iphione* were available as ethanol-fixed tissues and were sequenced for mitochondrial cytochrome c oxidase I (COI). Most sequences were generated as part of large-scale barcoding studies of selected regions. DNA was isolated from elytra, body wall or parapodia. Samples were processed at the Smithsonian Institution's Laboratories of Analytical Biology (LAB). Tissue portions were digested overnight in 150 µl M2 buffer and 150 µl M1 + proteinase K buffer at 56.5° C, and samples were agitated at 50 rpm on a Labnet Vortemp 56. Genomic DNA was extracted with an AutoGenprep 965 Automated DNA Isolation System using phenol-chloroform. The Folmer region of COI was amplified using the primers jgLCO_1490 (5'-TIT CIA CIA AYC AYA ARG AYA TTG G-3') and jgHCO_2198 (5'-TAI ACY TCI GGR TGI CCR AAR AAY CA-3') (Geller *et al.* 2013). PCR was performed on an ABI 2720 Thermal Cycler or MJ Research PTC-225 Peltier Cycler with an initial denaturation at 95° C for 5 min, followed by 35 cycles of denaturation at 95° C for 30 sec, annealing at 48° C for 30 sec, elongation at 72° C for 45 sec, and a terminal elongation at 72° C for 5 min. PCR products were cleaned sequenced in both directions using standard LAB protocols as described in Evans (2018). Chromatograms were cleaned, assembled, and aligned using Geneious (Kearse *et al.* 2012), and checked by eye. Cleaned sequences were checked for stop codons and indels that would be suggesting NUMTs. Sequences of *Iphione* specimens have been deposited in GenBank (PQ423922-PQ423951; see Table 1). Phylogenetic analysis was performed in MEGA (Tamura *et al.* 2021) using Maximum Likelihood, with HKY+G+I as the best fit model, and 500 bootstrap replicates.

Specimen deposition

All available material examined belongs to the following collections:

AM: Australian Museum, Sidney, Australia.

AMNH: American Museum of Natural History, New York, U.S.A.

BPBM: Bernice P. Bishop Museum, Honolulu, Hawaii, U.S.A.

CAS: California Academy of Sciences, San Francisco, California, U.S.A.

ECOSUR: El Colegio de la Frontera Sur, Unidad Chetumal, México.

LACM: Natural History Museum of Los Angeles County, Alan Hancock Foundation Polychaete Collection, California, U.S.A.

MAGNT: Museum and Art Gallery, Northern Territory, Darwin, Australia.

MNHN: Muséum National d'Histoire Naturelle, Paris, France.

NHM: Natural History Museum, London, United Kingdom.

NHMD: Natural History Museum of Denmark, Zoological Museum, University of Copenhagen, Denmark.

NMV: Museums Victoria Research Institute, Melbourne, Australia.

NMWZ: National Museum of Wales, Cardiff, United Kingdom.

RMNH: Naturalis Biodiversity Center, Leiden, The Netherlands.

SMNH: Swedish Museum of Natural History, Stockholm, Sweden.

UF: Florida Museum of Natural History, University of Florida, Gainesville, Florida, U.S.A.

USNM: National Museum of Natural History, Smithsonian Institution, Suitland, Maryland, U.S.A.

ZMA: Zoological Museum, University of Amsterdam (now in Naturalis), The Netherlands.

ZMH: Zoologisches Museum, Hamburg, Germany.

Results

Suborder Aphroditiformia Levinsen, 1883

Family Iphionidae Kinberg, 1856

Iphionea Kinberg, 1856: 383 (*Iphione* n. genus, *I. ovata* n. sp., and *I. muricata* (Savigny in Lamarck, 1818); Kinberg 1858: 7.

Iphionidae: Baird 1865: 181 (*Iphione*, *I. muricata*, *I. ovata* and *I. spinosa* Kinberg, 1858); Norlinder *et al.* 2012 (phylogeny); McCowin & Rouse 2018: 95.

Iphioninae: Horst 1917b: 64; Pettibone 1986: 2 (revision); Hanley & Burke 1991: 38; Wehe 2006: 59 (Western Indian Ocean species).

Type genus: *Iphione* Kinberg, 1856.

Diagnosis (modified after Pettibone 1986: 5). Aphroditiforms with body short, oval to elongate, depressed, dorsally arched, with up to 39 segments. Prostomium with lateral antennae as anterior prostomial extensions, sometimes very short or missing; median antenna reduced to nuchal papilla, rarely well developed. Palps stout, smooth or with longitudinal rows of two types of papillae (larger conical to aristate, and shorter truncate). Two pairs of eyes, rarely missing. Facial tubercle dorsally visible between antennae. Tentacular segment reduced dorsally, often with a few capillaries. Segment 2 often with a nuchal lappet overlapping prostomium. Pharynx usually with nine pairs of marginal papillae and two pairs of jaws. Elytra large, stiff, with polygonal areas, 13–20 pairs, overlapped, covering dorsum, present in segments 2, 4, 5, 7, alternating in successive segments. Dorsal cirrophores often with large basal bulbous tubercles, styles slender, often subdistally swollen. Parapodia biramous; notopodia reduced with abundant notochaetae, plumose or spinous. Neurochaetae stout with subdistal series of minute transverse denticulations, delicate in first two neuropodia, larger in following ones, tips falcate, unidentate or bidentate, rarely hooded. Pygidium displaced dorsally, without anal cirri.

Remarks. Pettibone (1986: 5) attributed family authorship to Baird (1865). However, Wehe (2006) noted that Kinberg (1856) erected the family, as Iphionea. Iphionea is a noun in the nominative plural formed from the stem of an available generic name, *Iphione* (ICZN 1999, Arts 11.7.1.1, 29.1). It was used as a suprageneric taxon (Art. 11.7.1.2), and even though the initial suffix differs from currently used suffixes, it must be used with the original authorship and date, but with a corrected suffix (ICZN 1999, Art. 11.7.1.3, 32.5.3.1).

Composition. Includes four genera: *Iphione* Kinberg, 1856; *Iphionella* McIntosh, 1885; *Iphionides* Hartmann-Schröder, 1977; and *Thermiphione* Hartmann-Schröder, 1992; remarkably each apparently specializing on different marine environments. *Iphione* inhabits coral reefs and adjacent shallow, rocky or mixed bottoms in the tropical Indo-West Pacific to East Pacific and includes most species in the family; *Iphionella* lives at bathyal (520–914 m) depths; the monotypic *Iphionides* was discovered in anchihaline environments in Cuba; while the four species of *Thermiphione* have all been found at Pacific hydrothermal vents. Genera are separated by the presence of eyes, development of lateral antennae, number of pairs of elytra, presence of fimbriae, and presence or number of transverse rows of spinules in neurochaetae (Hartmann-Schröder 1992).

Iphionella McIntosh, 1885 was proposed for *Iphione cimex* de Quatrefages, 1866, described from the Malacca Strait, but with a specimen collected off the Philippines. Pettibone (1986: 23–25) studied McIntosh's specimen and concluded that it was not

conspecific with *I. cimex* of de Quatrefages, but belongs to a new species, which she then named *Iphionella philippinensis* Pettybone, 1986, based on McIntosh's specimen. She also concluded that *Iphione cimex* de Quatrefages, 1866 belongs in a different genus, for which she proposed *Gaudichaudius*, and transferred it to the Harmothoinae (now Polynoinae, Polynoidae).

Key to genera of Iphionidae Kinberg, 1856

- 1** With 13–14 pairs of elytra . . . **2**
 - With about 20 pairs of elytra; elytra without fimbriae; prostomium with 2 pairs of eyes; lateral antennae minute; neurochaetae thin without annulations . . . *Iphionides* Hartmann-Schröder, 1977
- 2(1)** Prostomium with 2 pairs of eyes; palps with longitudinal series of papillae; lateral antennae on anterolateral margins; neurochaetae of a single type, with fine annulations, usually thick (13 pairs of elytra); elytra with or without fimbriae . . . *Iphione* Kinberg, 1856
 - Prostomium without eyes; palps smooth; without lateral antennae; elytra with lateral fimbriae; neurochaetae of two types (straight verticillate, and falcate subdistally denticulate) . . . **3**
- 3(2)** Falcate neurochaetae thick with series of fine annulations (13 or 14 pairs of elytra) . . . *Thermiphione* Hartmann-Schröder, 1992
 - Falcate neurochaetae thin without transverse series of annulations (13 pairs of elytra); . . . *Iphionella* M'Intosh, 1885

Alternative key to genera of Iphionidae Kinberg, 1856 (for damaged or incomplete specimens)

- 1** Neurochaetae thick, rarely thin, with subdistal rings of denticles . . . **2**
 - Neurochaetae thin, with denticles, not forming rings . . . **3**
- 2(1)** Eyes usually present; prostomium anteriorly bifid; with lateral antennae (13 pairs of elytra; margins smooth or fimbriate, fimbriae complex, never filiform) . . . *Iphione* Kinberg, 1856
 - Without eyes; prostomium completely bifid; without lateral antennae (13 or 14 pairs of elytra; lateral margins fimbriate, fimbriae filiform, often with globular bacterial masses) . . . *Thermiphione* Hartmann-Schröder, 1992
- 3(1)** With eyes; prostomium entire anteriorly; lateral antennae minute (up to 20 pairs of elytra, margins smooth) . . . *Iphionides* Hartmann-Schröder, 1977
 - Without eyes; prostomium completely bifid; without lateral antennae (13 pairs of elytra, lateral margins fimbriate, fimbriae filiform, sometimes branched) . . . *Iphionella* M'Intosh, 1885

Iphione Kinberg, 1856

Iphione Kinberg, 1856: 383, 1858: 8; Baird 1865: 181; de Quatrefages 1865: 266; Grube 1876: 50; Grube 1878: 21; Darboux 1900: 108 (syn.); Gravier 1901: 226; Izuka 1912: 63; Horst 1917b: 65; Fauvel 1932: 12; Fauvel 1953b: 32; Day 1967: 43; Fauchald 1977: 63; Pettibone 1986: 6; Hanley & Burke 1991: 38 (diagn., key); Wehe 2006: 61 (diagn., key). *Norepea* Baird, 1865: 200 (type species: *Polynoe peronea* Schmarda, 1861 by monotypy); synonymy after Chamberlin 1919: 40, Fauchald 1977: 65, and Pettibone 1986:6.

Type species. *Iphione ovata* Kinberg, 1856, by subsequent designation (Hartman 1959: 82).

Diagnosis. Iphionids with prostomium with long lateral antennae, median antenna rarely present; two pairs of eyes; palps with longitudinal rows of papillae; 13 pairs of elytra on segments 2, 4, 5, 7, alternating segments to 23, and then on 27; elytral surface with macrotubercles usually projected, spinous or smooth, elytral margins smooth or with fimbriae; most neurochaetae thick, rarely acicular, tips unidentate or bidentate, rarely hooded, with subdistal transverse rows of spinules.

Remarks. Baird (1865) was first to designate a type species for *Iphione*, stating: “The typical species is the *Polynoe muricata* of Savigny, so beautifully represented by that author in his great work on Egypt.” Further, Farber (1976: 95, footnotes 5, 6) noted that this type of phrasing was common in the 1840s, and while the Code has not been established, there were recommendations for using types and type species (Gray 1840, Strickland 1845), although the first draft of the Rules for Nomenclature was published in 1843, and adopted in 1865 (Strickland 1843, Sclater 1878). This subsequent designation was accepted by Pettibone (1986: 2). Regretfully, Article 67.5 of the Code (ICZN 1999) explicitly rules out type species designations based on the word 'typical', making Baird's designation not valid. Hartman (1959) was first to validly designate a type with *Iphione ovata* Kinberg, 1856.

While the type species of *Norepea* Baird, 1865 is clearly an *Iphione*, what species it represents has been contentious. Michaelsen (1892: 95) regarded *Polynoe peronea* Schmarda, 1861 described from Sri-Lanka, as a junior synonym of *I. spinosa* Kinberg, 1858, probably because both have elytra with smooth margins, without fimbriae. However, he noted differences: “The present specimen deviates from Kinberg's description markedly, as the antennae are not quite smooth, but with sparse (ca. 15), cylindrical papillae.” In contrast, Willey (1905: 246–247) regarded *P. peronea* as a junior synonym of *I. muricata* (Savigny in Lamarck, 1818), even though *I. spinosa* was described with smooth elytral margins and that he noted that Grube (1878: 22) “states that the outer and posterior margin of the scale is fimbriated which is not so in *I. peronea*.” Pettibone (1986: 4) regarded *P. peronea* as an unidentifiable *Iphione* species and the lack of type material implies that it will remain a *nomen dubium*.

Distribution. *Iphione* appears to be restricted to, but ranges across, the entire tropical Indo-Pacific, from the Red Sea to South Africa and east to the Hawaiian and Tuamotu Islands and Americas, mostly in shallow rocky or mixed bottoms. No specimens are known from the tropical Atlantic, except one Red Sea species has recently invaded the Mediterranean Sea (Goren *et al.* 2017). The record by Gibson (1886: 150) of *I. muricata* from the Liverpool area was shown to be erroneous (Hornell 1891: 224).

Diagnostic characters for *Iphione* species

Elytra

Variation in some morphological features of the elytra have been explored by Piotrowski *et al.* (2024). Because the elytra in *Iphione* are overlapped, portions are exposed, others are covered by adjacent elytra. Elytra are usually wider than long, the first pair oval, the second and third U-shaped, and the last roughly triangular. Elytral surface is mostly areolated, and areolation varies with size, less well-developed, but covering larger areas in small than large specimens (Piotrowski *et al.* 2024). Elytra have distinct anterior and posterior regions, and outer and inner areas. There is often a hyaline marginal band, usually along the outer elytral margins.

Elytra are ornamented by diverse projecting structures that are categorized as macrotubercles, microtubercles, and fimbriae. These can all be broken, eroded or overgrown by epibionts. Finer details are best seen in smaller specimens because their elytra are thinner and are less obscured by foreign particles.

Macrotubercles are distributed over much of the elytral surface, are fragile and often eroded, conical to digitate, ornamented by short stem spines and larger, stiff distal filaments (Fig. 1E, F), and retain a small amount of sediment. Microtubercles are similar to macrotubercles, but small and arranged in several densely packed rows, especially along the posterior elytral margin (Fig. 1D, G). Fimbriae typically occur in a marginal or submarginal band (rarely in inner elytral areas except in regenerating elytra), are flexible and easily bent, globular to cylindrical, ornamented with long, thin spines of similar size along their length and with long, flexible distal filaments, and usually covered by a thick layer of sediment particles that are difficult to remove.

Hanley & Burke (1991: 41) indicated that fimbriae might become macrotubercles depending on “the degree of chitinization of the outer edge of the elytron.” This is hardly the case; first, fimbriae and macrotubercles can be present side by side, but no intermediate forms have been documented, and their basement lies along different elytral areas (opaque *versus* hyaline), especially in larger specimens, and second, along posterior elytral margins, some small macrotubercles might proceed from a low conical stiff structure into a larger, stiff one as elytra continues growing peripherally, whereas adjacent fimbriae are shape-conservative, and do not seem to re-shape themselves into small macrotubercles.

Elytral morphology varies with growth in some species and not in others. Additional rows of macrotubercles are added with growth in *Iphione ovata* (Piotrowski *et al.* 2024), but not in *I. readi* **sp. n.** as shown in Fig. 1 A–C based on three specimens from one lot collected in the Sudanese Red Sea (NMH 1941.4.4.168–172) that were 9–25 mm long, 7.0–12.5 mm wide.

Neurochaetal rows of denticles

The number of rows of denticles on neurochaetae appears not to be a reliable diagnostic feature, because it varies substantially within species with size.

One median cirriferous parapodium was removed from seven specimens from New Caledonia, two in *I. hyndmani* **sp. nov.** (UF 5689, 15 mm long, 8 mm wide; UF 5695, 28 mm long, 13 mm wide), and five others of *I. fimbriata* de Quatrefages, 1866 (UF 5020, 5025, 5620, 5656, 5677; 20–27 mm long, 10–13 mm wide), and four specimens of *I. ankeri* **sp. nov.** from the Mariana Islands (UF 134, 217, 1691, 1704; 12–15 mm long, 6–9 mm

wide). The New Caledonia smaller specimen had 17–25 transverse rows of denticles in neurochaetae, whereas the larger specimen had 14–38 rows. Other New Caledonia specimens had 19–29 rows in the smallest specimen (UF 5656), and 28–44 in the largest one (UF 5677). Thus, some smaller specimens had 10–18 rows (UF 134, 1704), whereas the largest one (UF 217; 15x9 mm) had 20–26 rows. Consequently, the number of transverse rows of denticles is size-dependent and is discarded as diagnostic. On the other hand, even though they can be finer along first two chaetigers, most *Iphione* species have neurochaetae subdistally swollen with falcate tips, and only one species (*I. hourdezi* **sp. n.**, see below) has barely swollen neurochaetae, such that they can be regarded as acicular, with tips mostly straight.

Anatomy

The ventral surface is almost completely flat (Fig. 2A), with very shallow intersegmental borders, and a midventral longitudinal whitish band posteriorly. The digestive system is a straight tube, narrowing posteriorly (Fig. 2B); the pharynx extends $\frac{2}{5}$ body length, connects to a long, funnel-shaped stomach, the connection lies within a rather homogeneous sheath, the stomach connects to the intestine and progressively narrow towards the posterior end. The pharynx and stomach walls do not stain with Methyl Green. The pharynx wall is very thick, about 4–5 times thicker than the stomach wall (Fig. 2C), and its connection includes an elastic collar that must be fully expanded when the pharynx is exposed. Two blunt enteric caeca project near the junction of the stomach and intestine. There are additional large, globular, lateral caeca entering parapodial coelom in chaetiger 8. Histological analysis in other aphroditoideans have indicated a very narrow enteric connection, and carmine injection has shown that gut contents do not enter the metameric lateral caeca (Darboux 1900: 222); further, despite the presence of glandular epithelia, the role of lateral caeca in digestion is not completely understood.

Dissection of the pharynx revealed upper and lower jaws. Middorsal and midventral papillae at the apex of the everted pharynx are larger than the others; jaws have a roughly triangular shape, with an apical fang and two accessory denticles, the latter larger in upper (Fig. 2D) than lower jaws (Fig. 2E).

The pharynx is cylindrical with 11 pairs of marginal papillae in all specimens having pharynx exposed. In dorsal view (Fig. 3A), the marginal papillae are lobate, almost of the same size, and arranged in a row except for with two middorsal papillae that are stacked one above the other; behind the papillae there is a smooth area, followed by a rugose surface. The same smooth area is also present ventrally behind the papillae (Fig. 3B). Upper and lower jaws are both paired and very close to each other. In both frontal and lateral views (Fig. 3C, D), the main fang and accessory denticles are conspicuous because they are darker than surrounding tissues. In lateral view the pharynx aperture is semicircular with upper and lower regions projecting further anteriorly than mid-lateral areas; a semicircular ridge (also seen in dorsal view) may function as the attachment site of the lateral retractor muscles, (motor muscles of Dales, 1962: 402, Fig. 7B). Two specimens from the same locality and of different size (UF 411) had their pharynx exposed; in both cases, there are 11 pairs of marginal papillae (Fig. 3E, F) and the lateral ones are the smallest, and often difficult to be seen. Further, the smaller specimen has two accessory denticles, whereas the larger one has three, and in the larger specimen, behind the last exposed accessory denticle, there is another one still covered by integument, and it is noted

because of its paler pigmentation. The number of accessory denticles may not be a diagnostic feature because it is size-dependent.

Iphione species can be separated by features of elytra, notopodia and neurochaetae (see also Piotrowski *et al.* 2024). Elytra can have fimbriae or lack them; if present, fimbriae filaments can be minute, small or elongate. Elytral macrotubercles vary in shape, number of rows and size relationships among them: macrotubercles can be low, cushion-shaped, conical to digitate or cylindrical, and arranged in one to more than two rows in adult specimens, and although most have macrotubercles decreasing in size posteriorly, sometimes this trend is reversed, or the difference between the first and second row can be very marked. Microtubercles are usually present along posterior elytral margin; most species have them with long filaments, and only one species has short filaments. The basal tubercle of dorsal cirri of notopodia is usually projected, but in a few species it can be indistinct. Neurochaetae of most species are subdistally swollen, in one species, they are rather acicular with usually unidentate tips, a few species have bidentate tips, and one species has hooded tips. The combinations of these features were used to prepare the key to species below.

Key to species of *Iphione* Kinberg, 1856

- 1** Elytra with macrotubercles arranged in 2 or more rows, never cushion-shaped, rarely marginal . . . **2**
 - Elytra with macrotubercles arranged in a single row, cushion-shaped (falcate in juveniles), along posterior elytral half; fimbriae minute . . . **14**
- 2(1)** Elytra with margins fimbriate . . . **3**
 - Elytra with margins smooth, non-fimbriate . . . **11**
- 3(2)** Fimbriae well-developed, as long or longer than macrotubercles. . . **4**
 - Fimbriae minute, smaller than macrotubercles . . . **10**
- 4(3)** Macrotubercles distinct, arranged in up to 5 rows . . . **5**
 - Macrotubercles small, arranged in up to 10 rows; fimbriae along lateral and posterior margins . . . *I. henshawi* Pettibone, 1986 Hawaii
- 5(4)** First row of macrotubercles slightly larger than those present in other rows . . . **6**
 - First row of macrotubercles markedly larger than those present in other rows; macrotubercles in 2–three rows . . . *I. readi* **sp. n.** Red Sea
- 6(5)** Fimbriae length less than $\frac{1}{10}$ minimal elytral width . . . **7**
 - Fimbriae length about $\frac{1}{5}$ as long as minimal elytral width; macrotubercles in 1–two rows along posterior elytral margin . . . *I. richeri* **sp. n.** New Caledonia
- 7(6)** Dorsal cirrophores with distinct basal tubercle . . . **8**
 - Dorsal cirrophores with basal tubercle indistinct; elytra with 3–4(5) rows of macrotubercles . . . *I. hyndmani* **sp. n.** Hong Kong
- 8(7)** Posterior elytral margins with microtubercles with long filaments . . . **9**

- Posterior elytral margins almost smooth (microtubercles with short filaments); median elytra with 2–three rows of macrotubercles . . . *I. muricata* (Savigny in Lamarck, 1818), Mauritius
- 9(8)** Median elytra with two rows of macrotubercles . . . *I. ankeri* **sp. n.** Guam
- Median elytra with 4–5 rows of macrotubercles . . . *I. fimbriata* de Quatrefages, 1866, Northeastern Australia, Torres Strait
- 10(3)** Neurochaetae subdistally swollen, tips falcate; median elytra with macrotubercles in 2–three rows . . . *I. malifera* Piotrowski, 2014 Philippines
- Neurochaetae barely swollen subdistally, acicular, tips mostly straight; median elytra with macrotubercles in two rows . . . *I. hourdezi* **sp. n.** New Caledonia
- 11(2)** Neurochaetae unidentate . . . **12**
- Neurochaetae bidentate . . . **13**
- 12(11)** Elytra with macrotubercles conical . . . *I. ovata* Kinberg, 1856 Hawaii
- Elytra with macrotubercles subcylindrical, tapered, with distal spines, arranged in 5–6 rows . . . *I. wilsoni* **sp. n.** Coral Sea
- 13(11)** Elytral macrotubercles progressively smaller towards postero-lateral margin . . . *I. coriolis* Hanley & Burke, 1991 Chesterfield Islands
- Elytral macrotubercles progressively larger towards postero-lateral margin . . . *I. harrisae* **sp. n.** French Polynesia
- 14(1)** Neurochaetae unidentate; cirriferous parapodia with basal tubercle of dorsal cirrophore blackish distally, pale basally; ventral cirrostyles bases pale . . . *I. treadwelli* Pettibone, 1986 Hawaii
- Neurochaetae bidentate; cirriferous parapodia with basal tubercle of dorsal cirrophore blackish basally, pale distally; ventral cirrostyles bases blackish . . . *I. corbariae* **sp. n.** Saya de Malha Bank

***Iphione muricata* (Savigny in Lamarck, 1818) restricted**

Figs 1D–F, 3D–F, 4–6, 36

Polynoe muricata Savigny in Lamarck, 1818: 308–309 (diagn.).

Iphione glabra de Quatrefages, 1866: 268–269; Solís-Weiss *et al.* 2004: S14.

Iphione muricata: Potts 1910: 341; Fauvel 1919: 334; Fauvel 1932: 12–13 (*partim*); Fauvel 1935: 285–286 (*partim*); Fauvel 1939: 509 (*partim*); Monro 1939: 168 (*partim*); Day 1951: 14 (*partim*); Gibbs 1971: 123 (*partim*); Amoureux 1974: 430 (*partim*); Pettibone 1986: 9–16, Figs 1–5 (syn. *partim*); Hartmann-Schröder 1991: 19 (*partim*).

Type material. MNHN TYPE 335: Mauritius (Île de France) M. Mathieu, coll. no further data; holotype of *Polynoe muricata* and syntype of *Iphione glabra* (see Remarks) (bent ventrally, most elytra previously removed; body and elytra with a massive accumulation of precipitates, probably salts; two elytra cleaned, one median and one posterior elytra removed; body 24 mm long, 16 mm wide, 29 chaetigers). MNHN TYPE 334: Mauritius (Île de France), Péron & Lesueur, coll. no further data; syntype of *Iphione glabra* only; better preserved, used for redescription)

Additional material.

Egypt, Red Sea, Gulf of Suez. Four specimens (MNHN A274-19), Mission Jousseume, 1894 (no further data; three specimens bent ventrally; elytra brownish, oblique longitudinal band barely defined, some with calcareous epibionts; macrotubercles in two rows, progressively smaller posteriorly; body 19–28 mm long, 10–15 mm wide, 29 chaetigers). Ten specimens (MNHN A274-27), Mission Jousseume, 1894 (no further data; four specimens bent ventrally; elytra brownish, oblique longitudinal band barely defined, most with calcareous epibionts; macrotubercles in two rows, progressively smaller posteriorly; body 14–23 mm long, 7.5–14.0 mm wide, 29 chaetigers).

Sultanate of Oman. Two specimens (UF 411), Muscat Governorate, Qurm Beach (23°37'33.6" N, 58°28'51.6" E), 0–1 m, sandstone, under rocks, mid-low water intertidal, 26 Jan. 2005, V. Bonito, M. Claereboudt & G. Paulay, coll. (markedly bent ventrally; pharynx exposed; elytra golden to brownish, oblique longitudinal blackish line better defined in largest specimen; macrotubercles in two rows, progressively smaller posteriorly; cirriferous segments with basal tubercle of dorsal cirrophores projected, barely in smallest specimen; body length not measured, 0.8–1.6 mm wide, 28–29 chaetigers). One specimen (UF 9313), Muscat Governorate, Haramel Village cove (23°35'42.0" N, 58°36'03.6" E), 14 Jan. 2020, G. Paulay, S. Maslakova & M. Cherneva, coll. (markedly bent ventrally; body wall reddish; elytra brownish with an oblique, slightly darker longitudinal band; macrotubercles in three rows, progressively smaller posteriorly; basal tubercle of dorsal cirrophores projected; body not measured). One specimen (UF 9318), Muscat Governorate, Haramel Village cove (23°35'42.0" N, 58°36'03.6" E), 14 Jan. 2020, G. Paulay, S. Maslakova & M. Cherneva, coll. (complete, bent ventrally; body wall reddish; elytra brownish with an oblique, slightly darker longitudinal band; macrotubercles in two rows, progressively smaller posteriorly; basal tubercle of dorsal cirrophores projected; body 27 mm long, 16 mm wide, 29 chaetigers). One specimen (UF 9319), Muscat Governorate, Haramel Village cove (23°35'42.0" N, 58°36'03.6" E), 14 Jan. 2020, G. Paulay, S. Maslakova & M. Cherneva, coll. (complete, slightly bent ventrally; body wall reddish; elytra brownish with an oblique, slightly darker longitudinal band; macrotubercles in three rows, progressively smaller posteriorly; basal tubercle of dorsal cirrophores projected; body 27 mm long, 17 mm wide, 29 chaetigers). One specimen (UF 9320), Muscat Governorate, Haramel Village cove (23°35'42.0" N, 58°36'03.6" E), 14 Jan. 2020, G. Paulay, S. Maslakova & M. Cherneva, coll. (complete, slightly bent ventrally; body wall reddish; elytra brownish with an oblique, slightly darker longitudinal band; macrotubercles in three rows, progressively smaller posteriorly; basal tubercle of dorsal cirrophores projected; body 25 mm long, 15 mm wide, 29 chaetigers). One specimen (UF 9368), Muscat Governorate, Bandar Al Jissah (23°33'25.2" N, 58°39'03.6" E), 16 Jan. 2020, G. Paulay, M. Claereboudt, S. Maslakova & G. Kolbasova, coll. (complete, slightly bent ventrally; body wall reddish; elytra golden, without black spots; macrotubercles in two rows, progressively smaller posteriorly; basal tubercle of dorsal cirrophores projected; body 19 mm long, 13 mm wide, 29 chaetigers). One specimen (UF 9454), Muscat Governorate, West side of Fahal Island (23°40'55.2" N, 58°30'00.0" E), 19 Jan. 2020, G. Paulay, A. Bemis, G. Kolbasova & S. Brown, coll. (juvenile; right parapodia of chaetigers 13 and 14 previously removed; elytra yellowish, without black spots, macrotubercles in two rows, progressively smaller posteriorly; cirriferous segments with basal tubercle not projected; other data in variation: body 11 mm long, 6 mm wide, 28 chaetigers). One specimen (UF 10504), Dhofar Governorate, Mirbat, Chinese Wreck (16°57'57.6" N, 54°42'28.8" E), 26 Jan. 2022, G. Paulay, R. Lasley, A. Uehling & E. Claereboudt, coll. (bent ventrally; right parapodia of chaetigers 11–16 previously removed; right elytra 5 and 6

removed for observation (kept in container); elytra brownish, with an oblique longitudinal wide band, and white epibionts; macrotubercles in 2–three rows, progressively smaller posteriorly; cirriferous segments with basal tubercle projected; body mm 26 long, 15 mm wide, 29 chaetigers).

Djibouti.

Two specimens (MNHN A274-7), Djibouti, 1897, No. 29, M. Coutière, coll. (largest specimens with all left elytra previously removed; elytra brownish without black spots; macrotubercles in two rows, progressively smaller posteriorly; body 19–27 mm long, 11–13 mm wide, 29 chaetigers). One specimen (MNHN A274-12), Mission Gravier Djibouti, Île Moucha, Gulf of Tadjourah, coral, 23 Jan. 1904, C. Gravier, coll. (bent ventrally; elytra brownish; macrotubercles in two rows, decreasing in size posteriorly; body 17.5 mm long, 9.5 mm wide, 29 chaetigers).

Seven specimens (MNHN A274-23), Obock, Obock, Mission Jousseume, 1895, M. Jousseume, coll. (body damaged; two with most elytra detached, some in container; elytra brownish without black spots; macrotubercles in two rows progressively smaller posteriorly; body 14–27 mm long, 9–15 mm wide, 29 chaetigers). One specimen (MNHN A274-32), Mission Gravier Djibouti, Îlot Residence, in mixed bottoms (sand and rock), 1904, C. Gravier, coll. (markedly bent ventrally; elytra brownish without black spots; macrotubercles in two rows progressively smaller posteriorly; not measured).

Kenya. Seven specimens (NHM 1924.6.18.187–191), F.A. Potts, coll. (no further data; elytra yellowish to brownish, most with a barely pigmented longitudinal blackish band, macrotubercles in two rows, first row with macrotubercles slightly larger than those in second row; body 10–21 mm long, 9.0–9.5 mm wide, 29 chaetigers).

Mozambique. One specimen (NHM 1963.1.6), Delagoa Bay, Inhaca Island (25°50' S, 32°50' E), J.H. Day, coll. (elytra brownish, blackish band barely visible, macrotubercles slightly smaller posteriorly, in 2 irregular rows; body 23 mm long, 14 mm wide, 29 chaetigers).

Tanzania. One specimen (CAS 227559), complete, Zanzibar Expedition 2018, Zanzibar, Mangapwani (05°59'24.0" S, 39°11'24.0" S), 0.2–3.0 m, T.M. Gosliner, coll. (data used for variation). Three specimens (NHM 1941.4.4.165–167), Pemba Island, sandbanks, 18 Nov. 1901, C. Crossland, coll. (one completely bent, another one almost without elytra; elytra brownish with a longitudinal blackish band barely visible, macrotubercles in two rows of similar size; body 17–25 mm long, 11–14 mm wide, 29 chaetigers). One specimen (ZMH PE 187b), Bawe, Zanzibar, 15 Jul. 1989, Votzkow, coll. (no further data; slightly dehydrated; first few pairs of anterior and posterior elytra, and left parapodium of chaetiger 16 previously removed (parapodium lost); elytra brownish with two rows of macrotubercles progressively smaller posteriorly; cirriferous segments with basal tubercle of dorsal cirrophores projected; body 28.5 mm long, 11 mm wide, 29 chaetigers). One specimen (ZMH V4575), Bani Island, Zanzibar, Stuhlmann, coll. (no further data; markedly bent ventrally, partially dehydrated; elytra brownish, without black bands, with two rows of macrotubercles decreasing in size posteriorly; not measured). One specimen (ZMH V4577), Kokotoni, Zanzibar, Stuhlmann, coll. (no further data; bent ventrally; elytra brownish with high amount of sediment particles mostly on fimbriae; darker middorsal bands indistinct; elytra with two rows of macrotubercles heavily eroded, progressively smaller posteriorly; body 20.5 mm long, 14 mm wide, 29 chaetigers).

Mayotte. One specimen (MNHN A274-9), 1883, A. Vinnout, coll. (no further data; markedly bent ventrally; left elytron 10 removed for observation (kept in container); elytra

with an oblique, longitudinal black band, expanded anteriorly; macrotubercles in two rows, progressively smaller posteriorly; not measured).

Madagascar. One specimen (MNHN A274-10), Baie St. Augustin, No. 23, 1909, M. Bastard, coll. (no further data; some elytra previously removed; elytra brownish without black spots; macrotubercles in two rows, progressively smaller posteriorly; cirriferous segments with basal tubercle of dorsal cirrophores barely projected; body 20 mm long, 12 mm wide, 29 chaetigers). Four specimens (MNHN A274-29), Mission F. Geay, Tuléar, reefs, No. 4978 (no further data; partially dehydrated, one markedly bent ventrally with pharynx fully exposed, jaws with one additional denticle; elytra brownish without black spots, outer elytral surface darker than inner one; macrotubercles in two rows, progressively smaller posteriorly; body 14.0–19.5 mm long, 8.0–10.5 mm wide, 29 chaetigers). Five specimens (MNHN A274-35), 1919, M. Decary, coll. (no further data; very soft specimens, elytra detaching or in situ; elytra with an oblique longitudinal blackish band in two specimens, the others with elytra brownish; macrotubercles in two rows, progressively smaller posteriorly; not measured). One specimen (NHM 1961.8.3), Diego Suarez & Nossy-Bé (no further data; elytra covered with fine particles, with a wide oblique blackish band, two rows of macrotubercles, first one with tubercles slightly larger than those in second row, probably after the sedimentary environment; body 18 mm long, 11 mm wide, 28 chaetigers).

Mascarene Islands. One specimen (ZMH V499), Mauritius. Robillard, coll. (no further data; markedly bent ventrally; no other dissections to avoid further damage; elytra brownish with two rows of macrotubercles progressively smaller posteriorly; not measured). One specimen (UF 635), Réunion Island, La Saline, Trou d'eau (21°06'03.6" S, 55°14'38.4" E) 0–2 m, 27 Jul. 2007, N. Hubert & F. Michonneau, coll. (markedly bent ventrally, pharynx exposed; left parapodia of chaetigers 15–20 previously removed; elytra brownish, oblique longitudinal black band barely defined, with three rows of macrotubercles progressively smaller towards margins; pharynx exposed, jaws with 2 mostly eroded accessory denticles; body length not measured, 13 mm wide, 29 chaetigers). One specimen (UF 636), Réunion Island, Saint-Leu, Sec Jaune (21°09'19.8" S, 55°16'52.02" E), 0–2 m, 17 Aug. 2007, H. Bruggemann, N. Hubert & F. Michonneau, coll. (bent laterally after removal of left parapodia of chaetigers 12–17; elytra with wide blackish band, with three rows of macrotubercles progressively smaller towards margins; pharynx exposed, jaws with 3 accessory denticles; body 17 mm long, 8 mm wide, 29 chaetigers). One specimen (UF 638), Réunion Island, La Saline, Trou d'eau (21°06'03.6" S, 55°14'38.4" E), 0–2 m, 30 Jul. 2007, N. Hubert & F. Michonneau, coll. (bent laterally after removal of right parapodia of chaetigers 15–19; elytra with three rows of macrotubercles progressively smaller towards margins; pharynx exposed, upper jaws with 3 accessory denticles, lower ones with 4; body 25 mm long, 13 mm wide, 29 chaetigers). One specimen (UF 662), Réunion Island, La Posses, Banc des Lataniers (20°55'21.0" S, 55°20'29.04" E), boulder and cobble beach, under rocks, 0–2 m, 7 Aug. 2007, H. Bruggemann, N. Hubert, F. Michonneau & G. Paulay, coll. (slightly bent ventrally; elytra with three rows of macrotubercles progressively smaller towards margins; body 31 mm long, 16 mm wide, 29 chaetigers).

Seychelles. One specimen (ZMH 5758), Brauer, coll. (no further data; bent ventrally, pharynx fully exposed; elytra brownish with an oblique, longitudinal darker band barely distinct; elytra with two rows of macrotubercles progressively smaller posteriorly; body 20 mm long, 12 mm wide, 29 chaetigers).

Nicobar Islands. One specimen (NHMD 1184777), RV Galathea Expedition, Unspecified locality and date (fixed in ethanol, bent ventrally; elytra with a barely pigmented dark band; 3–4 rows of macrotubercles, progressively smaller towards margins; basal tubercle of dorsal cirrophores bilobed; neurochaetae unidentate; body 27 mm long, 13 mm wide, 29 chaetigers).

Vietnam. Two specimens (MNHN A274-1), Tonkin, Mar. 1897, M. Lichtenfelder, coll. (no further data; one bent ventrally; some elytra previously removed; elytra brownish with an oblique longitudinal blackish band; macrotubercles in two rows, decreasing in size posteriorly; basal tubercle to dorsal cirrophore bilobed; body 19–22 mm long, 11.5–12 mm wide, 29 chaetigers). One specimen (MNHN A274-2), Cap St. Jacques, Capt. Modest, Sep. 1908 (no further data; bent ventrally, some elytra previously removed; elytra brownish with an oblique, longitudinal black band; macrotubercles in two rows, decreasing in size posteriorly; cirrigerous segments with basal tubercle of dorsal cirrophore projected; neurochaetae slightly falcate, unidentate; body 22 mm long, 10 mm wide, 29 chaetigers). Two specimens (MNHN A274-5), Cap St. Jacques, Capt. Modest, No. 37, Sep. 1908 (poorly preserved; elytra brownish with an oblique, longitudinal black band, better defined in a few elytra; macrotubercles in two rows, decreasing in size posteriorly; most fimbriae detached; body 20–28 mm long, 12.0–13.5 mm wide, 29 chaetigers).

Indonesia. One specimen (ZMA V471.7), Sulawesi, RV Siboga Exped., Stat. 127 (Great Sangir Island, Taruna Bay), 45 m, trawl and reef-exploration, fine sand, 20–21 Jul. 1899 (markedly bent; elytra yellowish, without black spots, with fine sediment particles; macrotubercles in two rows, progressively smaller posteriorly; not measured). One specimen (ZMA V471.9), Maluku, RV Siboga Exped., Sta. 142 (Obi Major, anchorage off Laiwui), 23 m, dredge + reef exploration, muddy bottom, 5–7 Aug. 1899 (markedly bent ventrally; elytra yellowish, oblique longitudinal darker band barely visible; macrotubercles in two rows, progressively smaller posteriorly; not measured). One specimen (ZMA V471.12), Irian Jaya, RV Siboga Exped., Stat. 164 (01°42.5' S, 130°47.5' E), 32 m, dredge, sand, stones, shells, 20 Aug. 1899 (bent ventrally; right elytra 6 and 7 removed for observation (kept in container); elytra yellowish, without black spots, with some areas in regeneration, with different epibionts, without fine sediment particles; macrotubercles in two rows, progressively smaller posteriorly; body 17 mm long, 11 mm wide, 29 chaetigers). One specimen (ZMA V471.13), Maluku, RV Siboga Exped., Sta. 174 (Ceram (Seram), N coast, Waru Bay), 18 m, dredge, reef exploration, muddy bottom, 28–29 Aug. 1899 (elytra yellowish, without black spots; macrotubercles in two rows, progressively smaller posteriorly; body 9.5 mm long, 6 mm wide, 29 chaetigers). One specimen (ZMA V471.24), Lesser Sunda Islands, Rotti (or Rodti) Island, E coast, Pepela Bay, RV Siboga Exped., Sta. 301 (10°38' S, 123°25.2' E), 22 m, dredge, muddy bottom, coral, 30 Jan. 1900 (markedly bent; elytra brownish with white epibionts towards posterior margins, without black spots; macrotubercles in two rows, progressively smaller posteriorly; not measured). One specimen (ZMA V471.30), Maluku, RV Siboga Exped., Sta. 250 (Kur Island, anchorage off Kilsuin), 20–45 m, coral, 6–7 Dec. 1899 (bent ventrally; elytra yellowish, without black spots, macrotubercles in two rows, progressively smaller posteriorly; body 8 mm long, 6 mm wide, 28 chaetigers). One specimen (ZMA V476), Sumatra, Nias Island, southern coast, Telok Dalam (Teluk Dalam), de Zwaan, coll. (no further data; complete, right elytra 6 and 7 previously removed; elytra with oblique longitudinal black band, and darker posterior margins, with white and filamentous epibionts; macrotubercles in two rows, progressively smaller posteriorly; body 23 mm long, 13 mm wide, 29 chaetigers).

Philippines. Two specimens (ZMH V500), Mactan Island, Cebu, Ringe, coll. (no further data; bent ventrally, one without elytra; the other with elytra brownish; elytra with oblique

longitudinal blackish band, and darker posterior elytral area, with two rows of macrotubercles progressively smaller posteriorly; cirriferous segments with basal tubercle of dorsal cirrophore projected; body 19 mm long, 11 mm wide, 29 chaetigers).

Hong Kong. One specimen (AM 20043), Chek Chau, W side of Hong Kong, 5 m, 14 Apr. 1986, P.A. Hutchings, coll. (bent ventrally; elytra brownish with an oblique longitudinal black band; macrotubercles in two rows, progressively smaller posteriorly; cirriferous segments with basal tubercle of dorsal cirrophore projected; body 22 mm long, 10 mm wide, 29 chaetigers).

Australia. One specimen (AM 2650), Lindeman Island, Whitsunday Pass, Queensland, 16 m, Jan. 1929, M. Ward, coll. (elytra brownish, oblique longitudinal black band better defined in posterior chaetigers; macrotubercles in two rows, progressively smaller posteriorly; basal tubercle of dorsal cirrophore projected); body 22.5 mm long, 14.5 mm wide, 29 chaetigers). One specimen (AM 2737), Northwest Island, Capricorn Group, Queensland, 1929, Ward & Boardman, coll. (no further data; elytra dark brown; elytra with a few sediment particles and epibionts; macrotubercles in two rows, decreasing in size posteriorly; basal tubercle of dorsal cirrophore projected; body 21 mm long, 12.5 mm wide, 29 chaetigers). Three specimens (AM 2750), Rat Island, Port Curtis, Queensland, Jul. 1929, Ward & Boardman, coll. (no further data; elytra brownish with an oblique longitudinal black band; macrotubercles in 2–three rows, progressively smaller posteriorly; cirriferous segments with basal tubercle of dorsal cirrophore projected; body 28–29 mm long, 14.0–14.5 mm wide, 29 chaetigers). One specimen (AM 2845), Ninety Mile Beach, between Broome and Wallal, 13 m, 1931, R. Bourne, coll. (markedly bent ventrally; elytra yellowish with an oblique longitudinal black band; macrotubercles in two rows, progressively smaller posteriorly; basal tubercle of dorsal cirrophore projected; not measured). One specimen (AM 2934), Great Barrier Expedition, Queensland, N of North Direction Island, Great Barrier Reef, Sta. 17 (14°43'48.0" S, 145°30'00.0" E), 35 m, 9 Mar. 1929 (bent ventrally; elytra yellowish with an oblique longitudinal ill-defined band; macrotubercles in two rows, progressively smaller posteriorly; basal tubercle of dorsal cirrophore projected; body 20 mm long, 10.5 mm wide, 29 chaetigers). One specimen (AM 5432), Mandorah, Darwin, NT, under rock, low tide, 22 Nov. 1972, N. Coleman, coll. (slightly bent ventrally; elytra with an oblique black longitudinal band and several black spots; macrotubercles in two rows, progressively smaller posteriorly; body 15.5 mm long, 10 mm wide, 29 chaetigers). One specimen (AM 5437), Kendrew Island, Dampier, WA, under rocks, low tide, 14 Oct. 1972, N. Coleman, coll. (slightly bent ventrally, some elytra previously removed (kept in container); elytra yellowish with an oblique longitudinal black band; macrotubercles in two rows, decreasing in size posteriorly; body 22 mm long, 15 mm wide, 29 chaetigers). One specimen (AM 5452), Blow Holes, Quobba, WA, 2 m, 22 Jun 1972, N. Coleman, coll. (markedly bent ventrally; elytra brownish with an oblique longitudinal black band; macrotubercles in two rows, progressively smaller posteriorly; not measured). One specimen (AM 38418), Dampier Archipelago, Georgeff Reef, intertidal, 28 Aug. 1999, R.A. Peart, coll. (bent ventrally; some elytra previously removed; elytra yellowish with an oblique longitudinal black band and some calcareous epibionts; macrotubercles in two rows, progressively smaller posteriorly; body 16 mm long, 11 mm wide, 29 chaetigers). One specimen (AM 38419), Dampier Archipelago, W side Malus Island, 2.6 m, sand and algae bottom, 27 Aug. 1999, R.A. Peart, coll. (juvenile, posterior end bent ventrally; all elytra previously removed; elytra yellowish without black spots; macrotubercles in two rows, second row with a few macrotubercles, progressively smaller posteriorly; body 14 mm long, 6 mm wide, 28 chaetigers). One specimen (MAGNT W252), Oxley Island, NT, Sta. OX2, Acropora, low subtidal, 26 Oct. 1982, J.R. Hanley, coll. (markedly bent ventrally; elytra with abundant sediment particles, and a tapered, oblique

longitudinal dark band; macrotubercles in two rows, anterior row with macrotubercles slightly larger than those of second, more irregular row; not measured). One specimen (MAGNT W4894), Lee Point, Darwin, NT, Sta. RH 87-48, coral rubble, subtidal, 23 Oct. 1987, J.R. Hanley, coll. (juvenile, slightly bent ventrally, posterior end damaged; elytra yellowish with spread black spots, 2–3 submarginal fimbriae, macrotubercles in two rows, decreasing in size posteriorly; cirriferous segments with basal tubercle of dorsal cirrophore projected; neurochaetae unidentate; body 6 mm long, 4 mm wide, 28 chaetigers). One specimen (MAGNT W4897), Lee Point, Darwin, NT, Sta. RH 87-48, coral rubble, subtidal, 23 Oct. 1987, J.R. Hanley, coll. (bent ventrally; elytra yellowish with oblique longitudinal black band, some fimbriae between macrotubercles, macrotubercles in two rows, decreasing in size posteriorly; body 14 mm long, 9.5 mm wide, 29 chaetigers). One specimen (MAGNT W4939), Lee Point, Darwin, NT, Sta. RH 87-48, exposed rocky reef, subtidal, 25 Sep. 1987, J.R. Hanley, coll. (bent ventrally, some elytra previously detached; elytra yellowish with oblique longitudinal wide black band, macrotubercles in two rows, decreasing in size posteriorly; body 11 mm long, 7.5 mm wide, 28 chaetigers). One specimen (MAGNT W5139), Point Samson, near Roebourne, WA, Sta. RH 88-35, coral rubble, low tide, 9 Feb. 1988, J.R. Hanley, coll. (bent ventrally; many elytra and left parapodium of chaetiger 12 previously removed (all kept in container); elytra covered with orange silt; prostomium paler than adjacent body wall regions; elytra yellowish with an irregular median black spot; macrotubercles in two rows, gradually smaller posteriorly; cirriferous segments with basal tubercle of dorsal cirrophore projected; body 10 mm long, 7 mm wide, 28 chaetigers). One specimen (MAGNT W5140), Point Samson, near Roebourne, WA, Sta. RH 88-35, coral rubble, low tide, 9 Feb. 1988, J.R. Hanley, coll. (some elytra previously removed (kept in container), left parapodium of chaetiger 10 previously removed (lost); elytra covered with orange silt; prostomium white, contrasting with body wall pigmentation; pharynx partially exposed, slightly damaged by compression, partially dissected for observing jaws and its 2 accessory denticles, elytra yellowish with an oblique longitudinal black band; macrotubercles in two rows, gradually smaller posteriorly; body 15 mm long, 10 mm wide, 29 chaetigers). One specimen (MAGNT W5141), Point Samson, near Roebourne, WA, Sta. RH 88-35, coral rubble, low tide, 9 Feb. 1988, J.R. Hanley, coll. (markedly bent ventrally; many elytra, and right parapodium of chaetiger 10 previously removed (all kept in container); elytra covered with orange silt; prostomium white; elytra yellowish, median black spots barely visible; macrotubercles in two rows, gradually smaller posteriorly; cirriferous segments with basal tubercle of dorsal cirrophore projected; not measured). One specimen (MAGNT W6882), Scorpion Island, WA, Sta. RH 91-54, fringing shore reef, low tide, 14 Aug. 1991, J.R. Hanley, coll. (bent ventrally; elytra yellowish with a wide irregular dark band; macrotubercles in two rows, decreasing in size posteriorly; body 14 mm long, 7 mm wide, 29 chaetigers). One specimen (MAGNT W5142), Point Samson, near Roebourne, WA, Sta. RH 88-35, coral rubble, low tide, 9 Feb. 1988, J.R. Hanley, coll. (markedly bent ventrally; many elytra previously removed, left parapodium of chaetiger 13 previously removed (all kept in container); elytra covered with orange silt; prostomium white, contrasting with body wall pigmentation; pharynx partially exposed, slightly damaged by compression; elytra yellowish with an irregular medial spot; macrotubercles in two rows, gradually smaller posteriorly; not measured). One specimen (MAGNT W28949), East Point, NT, Sta. EP 11, rocks imbedded in mud, low tide, 18 May 1985, J.R. Hanley, coll. (bent ventrally; pharynx fully exposed, jaws with 2 accessory denticles; right elytra 5 and 7 removed for observation; elytra with a wide, ill-defined black band; macrotubercles in two rows decreasing in size posteriorly; body 11.5 mm long, 7.5 mm wide, 28 chaetigers). Eleven specimens (NHM 1970.113a), Grahams Point (no further data; elytra yellowish in smaller specimens, progressively darker in larger ones; many elytra eroded, with white epibionts; two rows of macrotubercles, first one with macrotubercles slightly larger than those present in second

row; body 10–28 mm long, 6.0–13.5 mm wide, 29 chaetigers). Two specimens (ZMH P 20976), Heron Island, coral reef, under rocks, intertidal, 3 Feb. 1976, G. Hartmann-Schröder, coll. (smallest specimen broken by compression, largest one bent ventrally, with elytra yellowish, without black spots, two rows of macrotubercles progressively smaller posteriorly; body 25 mm long, 14 mm wide, 29 chaetigers).

One specimen (ZMH V7883), Turtle Island, Western Australia, Gale, coll. (no further data; elytra brownish with an oblique longitudinal black band; two rows of macrotubercles, progressively smaller posteriorly; basal tubercle of dorsal cirrophore projected as a single lobe; body 25 mm long, 14 mm wide, 29 chaetigers). One specimen (ZMH V9333), Cape Jaubert, Western Australia (no further data; body brownish, slightly bent ventrally; elytra with two rows of macrotubercles, progressively smaller posteriorly; basal tubercle of dorsal cirrophore with a projected lobe; body 21 mm long, 12 mm wide, 29 chaetigers).

Papua New Guinea. One specimen (MNHN IA 0000-000), Papua Niugini Expedition, Sta. PR 149 (5°09.4' S, 145°48' E), 19 m, 1 Dec. 2012, S. Hourdez *et al.*, coll. (markedly bent ventrally; elytra brownish, with oblique longitudinal black band, macrotubercles in two rows, progressively smaller posteriorly; cirriferous segments with basal tubercle of dorsal cirrophore projected; body 9 mm wide).

Solomon Islands. Two specimens (NHM 1970.11), Komimbo Bay, Guadalcanal (no further data; smaller specimen with tiny black dots on elytra, larger specimen with brownish elytra, each with 2–three rows of macrotubercles; basal tubercle of dorsal cirrophores projected; neurochaetae unidentate, slightly falcate; body 7–16 mm long, 4.5–10 mm wide, 28–29 chaetigers). One specimen (NHM 1970.107), Tetel Island, 8 Jul. 1975, P.E. Gibbs, coll. (elytra yellowish with a darker band over an area larger than external elytral half, macrotubercles in two rows; left elytra 1–3 previously removed (not in container); body 13.5 mm long, 7 mm wide, chaetigers).

New Caledonia. One specimen (MNHN A274-11), Grand Terre, Kuto Bay, Île des Pins (no further data; bent ventrally, partially dehydrated; pharynx fully exposed, jaws with 3 accessory denticles, elytra brownish with a small black spot; macrotubercles arranged in two rows, progressively smaller posteriorly; body 22 mm long, 9.5 mm wide, 29 chaetigers).

Samoa. One specimen (MNHN A274-22), Moris, Sta. 56, 1889 (no further data; bent ventrally; right elytron 6 removed for observation (kept in container); elytra brownish, without black spots; macrotubercles in two rows, progressively smaller posteriorly; body 20 mm long, 13 mm wide, 29 chaetigers). One specimen (NHM 1921.5.1.533), Upolu, W.C. McIntosh, coll. (no further data; bent ventrally; elytra brownish, darker along posterior margins; macrotubercles in two rows, first row with macrotubercles slightly larger; two elytra previously removed (kept in container); body 25 mm long, 15 mm wide, chaetigers).

Diagnosis. *Iphione* with median antenna reduced to nuchal papilla; elytra fimbriate; macrotubercles spine-like, barely longer than wide, with distal spines, in 2–three rows, first row with macrotubercles slightly larger than those in other rows; cirriferous segments with dorsal cirrophores with basal tubercle projected; neurochaetae unidentate.

Description. Syntype of *Iphione glabra* de Quatrefages, 1866 (MNHN TYPE 334) bent ventrally, first eight pairs of elytra previously removed (Fig. 4A), some left in container; right parapodia of chaetigers 15 and 16 previously removed (lost), left parapodium of chaetiger 14 removed for observation (kept in container); body 17 mm long, 9 mm wide, 29

chaetigers). Elytra brownish, with sediment particles and an oblique dark band visible in most elytra; notochaetae whitish, neurochaetae golden. Body wall pale, venter pale.

Elytra with fimbriae, eroded from most detached elytra (Fig. 4B, C), better preserved in the other syntype (MNHN TYPE 335) (Fig. 4F–H), with variable amounts of sediment particles, especially along posterior segments. Fimbriae 6–10 times longer than wide, with a few spines along stem in syntype 334 (Fig. 4B, inset), or markedly spinous, probably after contraction in syntype 335 (Fig. 11I); macrotubercles conical, most eroded, about twice longer than wide, arranged in two rows, decreasing in size posteriorly and laterally.

Prostomium roughly hexagonal, wider than long, with anterior incision running along anterior prostomial third. Anterior lobes projected into ceratophores, longer than prostomium, shorter than ceratostyles, subdistally swollen, tips tapered. Eyes colorless, indistinct. Palps thick, bent, left one bent to the right, right one bent dorsally, slightly longer than antennae, with longitudinal rows of papillae, tips mucronate. Nuchal papillae not visible dorsally, covered by nuchal flap.

Tentacular segment dorsally reduced, with chaetae; tentacular cirri slightly shorter than palps. Facial tubercle not visible dorsally, pale.

Segments 2–4 directed anteriorly. Second segment visible dorsally, with a semicircular nuchal lappet, wider than long, covering nuchal papilla. Ventral buccal cirri inserted ventrally, almost three times longer than following cirri, left lost, right one not projected beyond chaetal tips. Dorsal nodules barely projected, more elevated in segment 2, progressively shorter.

Median cirriferous segments with dorsal cirri markedly projected beyond chaetal tips, cirrophore smooth, with a projected, single barely projected lobe (Fig. 4D). Cirrostyle subdistally swollen, surface papillate. Notochaetae very abundant, dirty white, with series of transverse funnel-shaped spinose rows, tips bare. Neuropodia with neuracicular lobe blunt, with globular papillae. Neurochaetal lobe with marginal papillae, neurochaetae abundant, basally smooth, subdistally swollen with many rows of fine denticulations along swollen region, tips slightly falcate, unidentate, sharp (Fig. 11E).

The other syntype (MNHN 335) brownish, with large amounts of adsorbed materials on body and elytra (Fig. 4F), and a few elytra attached; body 24 mm long, 16 mm wide, 29 chaetigers. After cleaning, both median (Fig. 4G) and posterior elytra (Fig. 4H) with two irregular rows of macrotubercles, mostly eroded to their base; oblique darker longitudinal band barely visible; fimbria subcylindrical, with abundant large spines along stem, and with long blunt spines distally (Fig. 4I). Left parapodium of chaetiger 12 removed for observation (kept in container); cirriferous parapodia with a barely developed basal tubercle to dorsal cirrophore, cirrostyles slightly swollen subdistally (Fig. 4J).

Variation. Some features of the exposed pharynx (Fig. 3D–F) were referred to above. One specimen (CAS 227559) complete, brownish, slightly bent dorsally, pharynx fully exposed, jaws with three accessory denticles; body 27 mm long, 13 mm wide, 29 chaetigers (Fig. 5A); left elytron 7 removed for observation, and left parapodium of chaetiger 12 removed for observation (kept in container); elytra brownish, larger macrotubercles arranged in two rows, macrotubercles about 2–3 times longer than wide (Fig. 5B); fimbriae arranged along lateral and posterior margins, longer in lateral (Fig. 5C) than in posterior region (Fig. 5D); macrotubercles blunt conical, each with 2–3 distal spines (Fig. 5E). Median cirriferous

segments with dorsal cirri reaching neurochaetal tips, basal tubercle of dorsal cirri swollen, bilobed, not projected as a cone (Fig. 5F); ventral cirri blackish basally. Neurochaetae bronze to brownish, smooth basally, denticulate along swollen subdistal region, tips slightly falcate, unidentate, smooth (Fig. 5G).

A juvenile 11 mm long specimen (UF 9454) has elytra without black spots (Fig. 6A). The elytra have two rows of macrotubercles and their size decreases posteriorly (Fig. 6B, insets 1, 2), whereas the posterior microtubercles have short filaments (Fig. 6B, inset 3). The cirriferous parapodia have long cirrophores and tapered cirrostyles (Fig. 6C), and its neurochaetae are unidentate.

Additional specimens were 6–29 mm long, 4–16 mm wide. There are two rows of macrotubercles, the first row has slightly larger ones than those present in the second row, and this does not change with body size, although the second row can be more irregular and have additional tubercles.

Remarks. Nomenclatural problems regarding the type material of *Polynoe muricata* have confounded identification of this species. Savigny in Lamarck (1818: 308–309) provided a short diagnosis for the species and recorded it only from Mauritius (Île-de-France), based on one specimen collected by M. Mathieu (MNHN TYPE 335). Later, Savigny (1822: 21–22, Pl. 3, Fig. 1) described and illustrated a different specimen, from the Gulf of Suez, as *P. muricata* that actually belonged to a different species (here described as *I. readi* **sp. n.**). Most subsequent authors followed Savigny's (1822) text and illustration to identify *I. muricata*, which together with a poor understanding of species limits led to substantial confusion about the identity of *I. muricata*.

De Quatrefages (1866: 268) recognized Savigny's specimen from Suez and Lamarck's specimen from Mauritius as different species, incorrectly applied *I. muricata* to the former, and redescribed the latter specimen (including the holotype of *P. muricata*), as *I. glabra*, together with a second syntype (MNHN TYPE 334), collected from the same locality (Mauritius) by Péron & Lesueur. His selection of Lamarck's type for his *I. glabra*, makes *P. muricata* and *I. glabra* objective synonyms. De Quatrefages provided some additional measurements and details for the illustrated specimen from Suez and noted differences between the two species. The main differences noted for *I. glabra* were that antennae, tentacular and dorsal cirri were tapered, not subdistally swollen, antennae were tiny, elytral margins were barely fimbriate, posteriorly smooth (hence the name), dorsal cirri were short, not surpassing notochaetae, and ventral cirri were minute. The slight difference in size of macrotubercles in rows 1 and 2 was indicated as “not resembling the spines illustrated by the naturalist (Savigny)” (de Quatrefages 1866: 269).

We are thus restricting *I. muricata* (Savigny in Lamarck, 1818) to specimens with elytra having fimbriae and macrotubercles progressively smaller posteriorly. Day (1951: 14) noted that “there is great variation in the tubercles of the elytra.” However, elytra have mostly two rows of macrotubercles, and even though they can be eroded in older specimens, the striking size difference between those of the first row against the second one in *I. readi* **sp. n.** (= *I. muricata sensu* Savigny 1822) separates it from those being gradually smaller posteriorly as in *I. muricata*. After the study of juvenile specimens of both species, we conclude this difference is present once they have two rows of macrotubercles; in *I. muricata* they are progressively smaller posteriorly, whereas in *I. readi* the first row has markedly larger macrotubercles.

Pettibone (1986: 3, 9–10) studied the syntype of *I. glabra*, MNHN 335 that was also the holotype of *I. muricata*. She did not illustrate it and correctly regarded it as a junior synonym of *I. muricata* (Savigny in Lamarck, 1818).

Iphione muricata resembles *I. ankeri* **sp. n.** from Guam because both have two or up to three rows of macrotubercles; they differ because in *I. muricata* the posterior elytral margin is almost smooth, whereas in *I. ankeri* the microtubercles have long filaments. Omani specimens of *I. muricata* appears to be closely related to *I. fimbriata* based on COI sequence data (Fig. 36).

Distribution. Red Sea to Mozambique, east to Samoa, on coral reefs and in rocky or mixed bottoms in shallow water (0–45 m).

***Iphione ovata* Kinberg, 1856**

Figs 2, 36

Iphione ovata Kinberg, 1856: 383; Kinberg 1858: 8, Pl. 3, Fig. 8; Pl. 10, Fig. 45; Baird 1865: 181; de Quatrefages 1866: 269–270; Chamberlin 1919: 64; Pettibone 1986: 16–19, Fig. 6 (*partim*, holotype); Piotrowski *et al.* 2024: 4–19, Figs 1–9 (redescr., syn.).

Diagnosis. *Iphione* with median antenna reduced to nuchal papilla; elytra with smooth margins; macrotubercles spine-like, in 2–5 rows, slightly larger in first than subsequent rows; cirriferous segments with dorsal cirrophores with basal tubercle projected; neurochaetae unidentate.

Remarks. *Iphione ovata* Kinberg, 1856 has been recently redescrbed (Piotrowski *et al.* 2024). *I. ovata* resembles *I. hirotai* Izuka, 1913 from Japan. No specimens of the latter species were studied, but its original description indicates that it differs from *I. ovata* in that its nuchal lappet is wide, round, macrotubercles, 2–5 times longer than wide, arranged in 3–5 rows, whereas in *I. hirotai* the nuchal lappet is thin, round, and macrotubercles up to twice longer than wide.

Distribution. Red Sea to South Africa and across entire Indo-West Pacific to the Eastern Pacific, on reefs and in shallow rocky or mixed bottoms.

Iphione peronea* (Schmarda, 1861) **n. comb., indeterminate*

Polynoe peronea Schmarda, 1861: 157, Textfigs 315, 316, Pl. 36, Figs 315, 315a; Chamberlin 1919: 40 (syn.).

?*Iphione spinosa*: Michaelsen 1892: 95 (record from Sri-Lanka).

?*Iphione muricata*: Willey 1905: 246–248, Pl. 1, Fig. 6; Augener 1926: 442 (*partim*) (*non* Savigny in Lamarck, 1818) record from Sri Lanka.

Remarks. *Iphione peronea* (Schmarda, 1861) was described from Sri Lanka, having elytra without oblique blackish lines. Schmarda also noted a long median antenna, that elytral margins were fimbriate, and illustrated neurochaetae as subdistally swollen with unidentate, slightly falcate tips. Other features were not clarified, so it could not be incorporated in the key above. Willey (1905: 247) attributed his specimen to *I. imbricata*, found in his specimens that elytra were fimbriate, and he indicated they were smooth in *I.*

peronea, but this is not the case. Chamberlin (1919: 40) indicated *I. peronea* was ‘the same as *Iphione muricata*.’

The original Sri-Lankan specimens are not in Vienna, they are presumed lost (F. Pedro, e-mail, 21 Feb. 2023). Because of the confusing original description, the fact that some records regarded it as a junior synonym of *I. spinosa* that has smooth elytral margins (Michaelsen 1892), or of *I. muricata* that has fimbriate margins (Willey 1905, Augener 1926), and the lack of type material, *Polynoe peronea* is herein regarded as belonging in *Iphione*, hence the new combination, but its status is indeterminable. Two additional species have been recorded from Sri Lanka whose identity is poorly understood: *I. spinosa* (Michaelsen, 1892) and *I. muricata* (Willey, 1905). Whether these represent the same species as Schmarda’s is unknown.

Distribution. Originally described from Sri Lanka

***Iphione fimbriata* de Quatrefages, 1866 reinstated**

Figs 7–9, 36

Iphione fimbriata de Quatrefages, 1866: 271–272; Haswell 1882b: 277 (after de Quatrefages 1866); Solís-Weiss *et al.* 2004: S14.

Iphione fustis Hoagland, 1920: 605, Pl. 46, Figs 4–8; Hartman 1938: 107; Suárez-Morales & Salazar-Vallejo 2022:502–503, Fig. 4 (parasites).

Iphione muricata: Monro 1924: 46 (*partim*); Pettibone 1986: 9–16, Figs 1, 2 (*partim, non* (Savigny in Lamarck, 1818)).

Holotype. Northeastern Australia, Torres Strait. Holotype of *I. fimbriata* de Quatrefages, 1866 (MNHN POLY TYPE 325), 1 Jan. 1841, Hombron & Jacquinot, coll.

Other type material examined. Philippine Islands. Paratype of *I. fustis* Hoagland, 1920 (USNM 18968), USFCS Albatross, Sta. 5401, off Tanguingui Island Light, North of Cebu, fine sand, 54 m, 16 Mar. 1909 (bent ventrally, partially dried out, five elytra previously removed (kept in container); body 22 mm long, 10 mm wide, 28 chaetigers). Paratype of *I. fustis* Hoagland, 1920 (USNM 18969), USFCS Albatross, Sta. 5202, off East coast of Leyte Island, Caguyan Point, 14 m, 13 Apr. 1908 (used for redescription).

Additional material.

Australia. Seven specimens (AM 2612), Low Isles, Queensland, Feb. 1929, Whitley & Boardman, coll. (no further data; soft, probably ethanol-fixed, 4 bent ventrally, smallest one broken; elytra brownish with an oblique longitudinal black band in a few specimens only, with abundant sediment particles; macrotubercles in 3–5 rows (size-dependent), progressively smaller posteriorly; cirriferous segments with basal tubercle of dorsal cirrophore projected (barely visible in softer specimens; body 19–23 mm long, 8–13 mm wide, 29 chaetigers). Two specimens (AM 2814), East Point, near Darwin NT, 22 Jun. 1929, A.A. Livingstone, coll. (one markedly bent, not measured; elytra with abundant sediment particles; macrotubercles in 3–4(5) rows, decreasing in size posteriorly; basal tubercle of dorsal cirrophore distinct, not projected over cirrophore base; body 28.5 mm long, 14 mm wide, 29 chaetigers). Two specimens (AM 5720), Brampton Island, Queensland, Jan. 1949, Zoology Department, University of Sydney, coll. (no further data; bent ventrally; elytra brownish with an oblique longitudinal black band; macrotubercles in 4–5 rows; basal tubercle of dorsal cirrophore projected; body 20–26 mm long, 15.5–17.0 mm wide, 29 chaetigers). Two specimens (MAGNT W270), Oxley Island, NT, coral rubble,

reef edge, low tidal, 20 Oct. 1982, R. Hanley, coll. (bent ventrally, one too bent to be measured; right elytra 7 removed for observation; elytra with oblique longitudinal blackish band, 3–5 rows of macrotubercles, progressively smaller posteriorly; cirriferous segments with basal tubercle of dorsal cirrophores projected; body 30 mm long, 14 mm wide, 29 chaetigers).

Australia. Two specimens (MAGNT W6780), Scorpion Island, WA, Sta. RH 91-55, fringing shore reef, low subtidal, 14 Aug. 1991, J.R. Hanley, coll. (bent ventrally; elytra with oblique longitudinal black band, and darker posterior margins; macrotubercles in 3–4 rows, progressively smaller posteriorly; ventral cirri base blackish; body 20–32 mm long, 12–15 mm wide, 29 chaetigers). One specimen (NMH 1925.1.28.17), H.M.S. Alert, Port Denison (no further data; bent ventrally, some parapodia and elytra previously removed (lost); elytra brownish, with a wide oblique longitudinal darker band, macrotubercles in 4 rows; neurochaetae unidentate, slightly falcate; body 28 mm long, 17 mm wide, 29 chaetigers). Three specimens (NHM 1925.1.28.18–20), H.M.S. Alert, Claremont and Bird Islands (no further data; one markedly bent, elytra brownish, each with 3–4 rows of macrotubercles; basal tubercle of dorsal cirrophore projected; body 12–25 mm long, 11.5–13.0 mm wide, 29 chaetigers). Three specimens (NHM 1925.1.28.21–23), H.M.S. Alert, Torres Strait Islands, Thursday Island, sand, 7–13 m (no further data; smallest one damaged, some elytra previously removed; elytra yellowish to brownish, oblique longitudinal darker band visible; each elytron with 3–4 rows of macrotubercles (2–3 in smallest specimen) progressively smaller towards posterior margin; basal tubercle of dorsal cirrophores projected; neurochaetae unidentate, slightly falcate; body 11–34 mm long, 6–15 mm wide, 29 chaetigers). Seven specimens (NHM 1925.1.28.26–34), H.M.S. Alert, Port Molle, beach and coral reef (no further data; three markedly bent, one dried-out; elytra yellowish to brownish, often with a wide oblique longitudinal band, or darker posterior elytral margins, with 3–5 rows of macrotubercles (size-dependent); body 15–25 mm long, 8–15 mm wide, 29 chaetigers). Three specimens (NHM 1970.113b), Grahams Point (no further data; one bent ventrally; elytra brownish, darker in posterior regions, oblique longitudinal wide darker bands, with 4–5 rows of macrotubercles; body 22–26 mm long, 12.0–12.5 mm wide, 29 chaetigers). One specimen (ZMH V497), Bowen, Queensland (no further data; body incurved, anterior parapodia bent ventrally; elytra brownish, with fimbriae short (shrunk), with oblique darker band, and 4–5 rows of macrotubercles progressively smaller posteriorly; body 23 mm long, 14 mm wide, 29 chaetigers).

Thailand. One specimen (NHM 1925.1.28), Gulf of Siam (Thailand) (no further data; bent ventrally; elytra brownish with an oblique wide darker band; macrotubercles in 4 rows; basal tubercle of dorsal cirrophore projected; neurochaetae unidentate, slightly falcate; body 36 mm long, 14.5 mm wide, 29 chaetigers).

Indonesia. One specimen (RMNH unnumb.), Indonesian Snellius II Exped., Sta. 4.232 (06°32.1' S, 121°09' E), NE Taka Bone Rate, Tiger Islands, south of Pulau Tarupa Kecil, 59 m, calcareous nodules, sponges, 16 Oct. 1984 (markedly bent ventrally; elytra with oblique longitudinal black band poorly defined; macrotubercles in 5 rows, decreasing in size posteriorly; cirriferous segments with basal tubercle of dorsal cirrophore projected; not measured). One specimen (ZMA V471.1), Lesser Sunda Islands, RV Siboga Exped., Stat. 34 (Lombok, anchorage off Labuan Pandan), 18 m, coral reef, shore-expl., 27 Mar. 1899 (slightly bent ventrally; elytra with silt and abundant epibionts, oblique longitudinal line barely visible; macrotubercles in three rows, progressively smaller posteriorly; basal tubercle of dorsal cirrophore projected; body 20 mm long, 11 mm wide, 29 chaetigers). One specimen (ZMA V471.4), Sulawesi, RV Siboga Exped., Sta. 115 (Kwandang Bay, E side of Pajunga Island), reef-exploration, 9–11 Jul. 1899 (markedly bent ventrally; elytra with

oblique longitudinal band barely visible, posterior margins darker; macrotubercles in 3–4 rows, progressively smaller posteriorly; not measured). One specimen (ZMA V471.5), Sulawesi, RV Siboga Exped., Sta. 125 (Siau Island, anchorage off Sawan), 27 m, dredge, townet, Monaco trap, reef-exploration, stones, 18–19 Jul. 1899 (markedly bent; elytra brownish without black spots; macrotubercles in three rows; not measured). Two specimens (ZMA V471.8), Sulawesi, RV Siboga Exped., Stat. 131 (Karakelang Island, anchorage off Beo), 13 m, muddy bottom, sand, 24–25 Jul. 1899 (largest markedly bent ventrally; elytra brownish, oblique longitudinal band barely visible, with abundant sediment particles and epibionts; macrotubercles in 3–4 rows, decreasing in size posteriorly; smaller one with body 15 mm long, 9 mm wide, 29 chaetigers). One specimen (ZMA V471.10), Maluku, RV Siboga Exped., Stat. 144 (anchorage N of Salomakië (Damar) Island), 45 m, dredge, townet + reef exploration, coral, 7–9 Aug. 1899 (bent ventrally; elytra brownish with abundant white epibionts; macrotubercles in three rows, progressively smaller posteriorly; body 17.5 mm long, 10 mm wide, 29 chaetigers). Three specimens (ZMA V471.15), Sulawesi, RV Siboga Exped., Stat. 213 (Saleyer anchorage), 36 m, coral reef expl., muddy bottom + sand, 26 Sep. 1899 (markedly bent ventrally; elytra yellowish in smaller specimens, largest one with oblique longitudinal black band; macrotubercles in 1–two rows; smaller ones not measured, largest 15 mm long, 9 mm wide, 29 chaetigers). One specimen (ZMA V471.15b), Sulawesi, RV Siboga Exped., Stat. 213 (Saleyer anchorage), 36 m, coral reef expl., muddy bottom + sand, 26 Sep. 1899 (bent ventrally; elytra brownish with oblique longitudinal black band, and darker posterior margins; macrotubercles in 4–5 rows, progressively smaller posteriorly; body 30 mm long, 12 mm wide, 29 chaetigers). One specimen (ZMA V471.17), Sulawesi, RV Siboga Exped., Sta. 225 (Lucipara Island, S point), reef (in label), coral + shells, 8 Nov. 1899 (slightly bent ventrally; several elytra previously removed (kept in container); elytra brownish, with oblique longitudinal black band, posterior margins darker, some with white epibionts; macrotubercles in 4 rows, progressively smaller posteriorly; body 26 mm long, 15 mm wide, 29 chaetigers). Five specimens (ZMA V471.18), Maluku, RV Siboga Exped., Sta. 231 (Ambon, at anchorage), 40 m, reef exploration, coral sand, 14–18 Nov. 1899 (markedly bent ventrally; several elytra removed from each specimen; elytra yellowish in smaller specimens, with oblique longitudinal black band and darker posterior margins in largest specimen; macrotubercles in 3–5 rows (size dependent), decreasing in size posteriorly; not measured). One specimen (ZMA V471.19), Maluku, RV Siboga Exped., Stat. 234 (Nusa Laut Isl., Nalahia Bay), 46 m, reef exploration, stones, 19–20 Nov. 1899 (slightly bent ventrally; elytra brownish with abundant epibionts; macrotubercles in three rows, progressively smaller posteriorly); body 25 mm long, 11 mm wide, 29 chaetigers). Two specimens (ZMA V473), Java, Jakarta Bay (Batavia Bay), Sluiter, coll. (no further data; markedly bent specimens; some elytra previously removed; elytra with oblique longitudinal dark wide band; macrotubercles in 2–4 rows; basal tubercle of dorsal cirrophores projected; not measured).

Philippines. One specimen (LACM 6916), Palawan, North Verde Island, mangroves along shore (10°07'44.4" S, 119°14'27.6" E), 0.46 m, underside of coralline rock, 23 Apr. 1995, J.K. Fitzhugh, coll. (bent ventrally; pharynx exposed; elytra yellowish, oblique longitudinal band wide, diffuse; macrotubercles in 2–three rows, progressively smaller posteriorly; cirriferous segments with basal tubercle of dorsal cirrophore projected; body 14 mm long, 9 mm wide, 29 chaetigers). One specimen (LACM 6917), Tubatatha (08°55'26.4" S, 119°59'56.4" E), 24–38 m, sand, 20 Apr. 1995, C. Arneson, coll. (bent ventrally; elytra yellowish, oblique blackish bands barely visible, posterior elytral region darker; macrotubercles in 3–4 rows, decreasing in size posteriorly; cirriferous segments with basal tubercle of dorsal cirrophore projected; body 24 mm long, 16 mm wide, 29 chaetigers). Two specimens (LACM 6918), East side of Palawan Island, off Fondeado Island, Hondo

Bay, 100 m from shore (09°55'51.6" N, 118°55'01.2" E), 0.6 m, beneath coral rubble, 24 Apr. 1995, J.K. Fitzhugh, coll. (one with pharynx slightly exposed; elytra yellowish, oblique black bands well-defined in one specimen, paler in the other; with 2–3 of macrotubercles, decreasing in size posteriorly; cirriferous segments with basal tubercle projected; body 19.0–19.5 mm long, 11 mm wide, 29 chaetigers).

Marshall Islands. One specimen (UF 719), Majuro Atoll, Eneko, channel, Western side of the island (07°08'57.552" N, 171°16'58.512" E), intertidal, tide pools, under rocks, 6 Apr. 2008, F. Michonneau & S. Kim, coll. (posterior end removed for molecular analysis; right elytron 8 and one of the last pair, and right parapodium of chaetiger 12 removed for observation; elytra brownish with an oblique black band, expanding laterally along posterior elytral margins; macrotubercles in four rows, decreasing in size towards posterior margins; ventral cirrophores blackish; body 22 mm long, 12.5 mm wide, 23 chaetigers). One specimen (USNM 81942), Bikini Atoll, 6.4 km from west end of island, 51 m, 25 Apr. 1946, J.P.E. Morrison, coll. (most elytra and some parapodia previously removed (kept in container); elytra brownish without black banding, macrotubercles in four rows, decreasing in size towards posterior margins; fimbriae ventral cirrophores barely darker than adjacent tissues, especially along posterior region; body 18 mm long, 10.5 mm wide, 29 chaetigers).

Papua New Guinea. One specimen (CAS 190471), Papua New Guinea Biodiversity Expedition 2012, Madang Province, Rempi, depth undefined, 20 Nov. 2012, V. Knutson, coll. (bent ventrally; elytra yellowish, with four rows of large spine-like macrotubercles; body 11 mm long, 6 mm wide, 28 chaetigers; two copepod parasites on dorsum, visible between elytra, they might be responsible of the lack of typical pigmentation).

Solomon Islands. Three specimens (USNM 97382), Guadalcanal, Raham Point, 21 Sep. 1965, P.E. Gibbs, coll. (two slightly bent ventrally, some elytra previously removed (kept in container); anterior and posterior eyes close to each other laterally; elytra with one row of large spine-like macrotubercles in smallest specimen, largest with 3–4 rows, slightly decreasing in size towards posterior margins; body 11–23 mm long, 6–12 mm wide, 28–29 chaetigers).

New Caledonia. Two specimens (UF 5020), Province Sud, Nouméa, Baie des Citrons, South end (22°18'13.536" S, 166°26'03.66" E), 0–2 m, shore and fringing reef, 5 Dec. 2016, G. Paulay & L. Moroz, coll. (one bent ventrally, pharynx fully exposed; right parapodia of chaetigers 15–18 removed for molecular analysis; elytra brownish, without black band, some with white epibionts, with three rows of macrotubercles; dorsal cirrophore with a low projected basal tubercle; body 21.5–25.0 mm long, 10.5–12.0 mm wide, 29 chaetigers). Two specimens (UF 5025), Province Sud, Nouméa Lagoon, Îlot N'Do (22°18'48.528" S, 166°28'12.9" E), 1–8 m, lagoon fringing reef, 7 Dec. 2016, G. Paulay & L. Moroz, coll. (one bent ventrally; some elytra removed; elytra brownish, without black band, some with white epibionts; with 3–4 rows of macrotubercles; dorsal cirrophore with a globular basal tubercle; body 25–26 mm long, 12–13 mm wide, 29 chaetigers). One specimen (UF 5620), Province Sud, Nouméa Commune, Baie des Citrons, South part (22°18'13.536" S, 166°26'03.66" E), 0–2 m, shore and fringing rocks, 31 Oct. 2017, G. Paulay & M. Hoban, coll. (slightly bent laterally; pharynx fully exposed, jaws with 3–4 additional denticles; right parapodia of chaetigers 17–25 removed for molecular studies; elytra brownish, some with white epibionts; macrotubercles in 3–4 rows; fimbriae along lateral margins, extended along posterior margins in last two elytral pairs; dorsal cirrophore with a globular basal tubercle; body 24.5 mm long, 11 mm wide, 29 chaetigers). One specimen (UF 5656), Province Sud, Banc Ouest (22°26'40.704" S, 166°28'54.336" E), 0–1 m, patch

reef, flat top, 13 Nov. 2017, G. Paulay, D. Uyeno & L. Moroz, coll. (slightly bent ventrally; right parapodia of chaetigers 16–20 removed for molecular studies; left elytra 1–3, and right elytra 1–4, 6 removed for observation; prostomium pale, eyes black, similar-sized, anterior ones lateral, posterior ones dorsal; lateral antennae ceratophores blackish, ceratostyles pale; palps slightly longer than antennae; median antenna minute, blackish; nuchal lappet slightly longer than wide, not covering median antenna; elytra brownish, with a wide ill-defined oblique darker band, with macrotubercles in 2–3; dorsal cirrophore with projected basal tubercle; anus visible between last pair of elytra; body 21 mm long, 11 mm wide, 29 chaetigers). One specimen (UF 5677), Province Sud, Nouméa Commune, East side of Nouméa (22°17'28.248" S, 166°27'34.236" E), 0–2 m, sand flat and reef, under rocks, 2 Nov. 2017, G. Paulay & M. Hoban, coll. (right elytra 1–3, 7 removed; elytra brownish, most with double oblique longitudinal black lines, with white epibionts; macrotubercles in 3–4 rows; fimbria mostly lateral; dorsal cirrophore with basal tubercle barely projected; anus visible between last elytral pair; body 26 mm long, 13 mm wide, 29 chaetigers).

Vanuatu. Two specimens (MNHN 0000), Efate, Port Vila Bay, 28 Aug. 2011, S. Hourdez, coll. (markedly bent ventrally; one median elytron removed for observation; elytra yellowish to brownish, with oblique longitudinal band ill defined, or without it; macrotubercles in 3–4 rows, progressively smaller posteriorly; cirriferous segments with basal tubercle of dorsal cirrophore projected; not measured).

Samoa. Two specimens (USNM 81972), from Samoa Investigations, 1902 (One with body 30 mm long, 14 mm wide, 29 chaetigers; pharynx exposed, it was dissected open previously (notes in variation); three parapodia previously dissected. Another specimen middorsally dissected and all elytra removed shows anterior eyes in lateral projections, very close to posterior ones).

Diagnosis. *Iphione* with median antenna reduced to nuchal papilla; elytra fimbriate, filaments markedly longer than wide; macrotubercles spine-like, up to twice longer than wide, with distal spines, in 3–5 rows, first row with macrotubercles slightly larger than those in other rows; cirriferous segments with dorsal cirrophores with basal tubercle projected; neurochaetae unidentate.

Description. Holotype of *Iphione fimbriata* de Quatrefages, 1866 (MNHN TYPE 325) complete, slightly bent ventrally, some elytra detaching from body (Fig. 7A), right elytron 7 and left parapodium of chaetiger 16 previously removed; two punctations along anterior body third; body 31 mm long, 15 mm wide, 29 chaetigers. Elytra brownish, with abundant fine sediment particles; notochaetae whitish, neurochaetae golden. Body wall pale, venter pale.

Elytra with fimbriae (Fig. 7B), better developed along lateral margins throughout body; fimbriae incorporate abundant sediment particles, rarely without them (Fig. 7B, inset), fimbriae 3–12 times longer than wide; abundant polygonal areas throughout most elytral surface, many with a projecting tip pointing posteriorly; macrotubercles conical, partially buried by sediment, visible after brushing off foreign particles, about 2–3 times longer than wide, arranged in 4–5 rows, decreasing in size posteriorly and laterally.

Prostomium roughly hexagonal, longer than wide, with anterior incision running along anterior prostomial third. Anterior lobes projected into ceratophores, as long as prostomium, shorter than ceratostyles, subdistally swollen, tips tapered. Eyes colorless, indistinct. Palps thick, bent ventrally, about twice longer than antennae, with longitudinal

rows of papillae, tips mucronate (it seems de Quatrefages confused the palps with the antennae). Nuchal papilla visible under nuchal flap.

Tentacular segment dorsally reduced, without chaetae; tentacular cirri about half as long as palps. Facial tubercle visible dorsally, colorless.

Segments 2–4 directed anteriorly. Second segment visible dorsally, with a semicircular nuchal lappet, wider than long, covering nuchal papilla. Ventral buccal cirri inserted ventrally, almost three times longer than following cirri, projected beyond chaetal tips. Dorsal nodules not observed to avoid further damage to the specimen.

Median cirriferous segments (Fig. 7C, D) with dorsal cirri markedly surpassing chaetal tips, subdistally swollen, cirrophore smooth, with a basal single tubercle. Cirrostyle subdistally swollen, surface papillate. Notochaetae very abundant, dirty white, with series of transverse funnel-shaped spinose rows, tips bare. Neuropodia with neuracicular lobe blunt, with globular papillae. Neurochaetal lobe with marginal papillae, neurochaetae abundant, basally smooth, subdistally swollen with many rows of fine denticulations along swollen region, tips barely falcate, unidentate, sharp (Fig. 7E, F).

Anus not seen.

Paratype of *I. fustis* Hoagland, 1919 (USNM 18969) complete, mature female, bent ventrally; 8 anterior elytra previously removed, left parapodium of chaetiger 14 dissected (kept in container); body 18 mm long, 13 mm wide, 29 chaetigers. Elytra brownish, often with calcareous epibionts; notochaetae whitish, neurochaetae golden. Body wall pale, transparent, parapodia with large coelomic spaces; venter pale.

Elytra with fimbriae, better developed along median and posterior segments but variably eroded; better developed in the other paratype (USNM 18968, 6–7 times longer than wide, extended along almost all exposed elytral margin); macrotubercles conical, largest ones 3–4 times longer than wide, longer towards central elytral areas, progressively shorter towards margins (Fig. 8C, inset, Fig. 9D, E).

First elytra lost, second pair with large conical macrotubercles each with 3–4 distal spines in 2–3 rows (Fig. 8B, upper; Fig. 9A, B). Following elytra with macrotubercles in 3–4 rows (Fig. 8B, lower, C; Fig. 9D, E), larger macrotubercles towards central elytral areas, progressively smaller towards margins. Fimbriae delicate, submarginal, along posterolateral margins, each with a thin spinous stem, and distal soft tubules, each about 3 times as long as fimbria stem (Fig. 8C, inset).

Prostomium wider than long, with anterior incision running along $\frac{1}{3}$ prostomial surface (Fig. 8A). Anterior lobes projected into pale ceratophores, as long as prostomium, shorter than ceratostyles (right one broken), ceratostyles markedly thinner than ceratophores, tapered. Palps thick, bent ventrally, longer than lateral antennae, with longitudinal rows of papillae, tips mucronate. Eyes black, anterior ones placed behind the median prostomial region, barely visible dorsally, posterior ones in posterior prostomial margins. Nuchal papillae not visible dorsally, broken.

Tentacular segment dorsally reduced, without chaetae; tentacular cirri slightly longer than palps, resembling lateral antennae. Facial tubercle not visible dorsally, pale.

Segments 2–4 directed anteriorly. Second segment visible dorsally, with a nuchal lappet, semicircular, wider than long (slightly broken), covering nuchal papilla. Ventral buccal cirri inserted ventrally, twice longer than following ventral cirri, projected beyond chaetal tips. From segment 3 one pair of globular dorsal nodules per segment, first pair connected by a transverse ridge, separated from each other. Segments 2–3 with fine neurochaetae, barely swollen distally, with a longer region covered by series of transverse denticulations.

Median cirriferous segments (Fig. 8D) with dorsal cirri reaching chaetal tips, subdistally swollen; dorsal cirrophore smooth, with a basal single tubercle. Cirrostyle subdistally swollen, with papillae along its surface. Notochaetae very abundant, pale to transparent, with series of transverse funnel-shaped spinose rows, tips bare. Neuropodia with neurochaetal lobe posterior margin with small papillae. Neurochaetae abundant, basally smooth, subdistally swollen, sometimes with a pale or dark core, with many rows of fine denticulations along swollen region, tips barely falcate, sharp (Fig. 8E, F).

Anus not seen. Oocytes in irregular masses in coelom, each oocyte about 80 μm in diameter.

Variation. One specimen from Samoa (USNM 81972), middorsally dissected and all elytra removed; the anterior eyes are in lateral projections, very close to posterior ones (Fig 9F), although the prostomium has to be depressed to note the blackish eyes; another specimen had its pharynx exposed and it was dissected open previously; papillae digitate, middorsal one more opaque, jaws similar, apparently eroded, without accessory denticles (Fig. 9G); three parapodia previously dissected; neurochaetae all unidentate. Ventral cirrophore blackish in some specimens.

The additional specimens were 11–36 mm long, 6–16 mm wide. The number of rows of macrotubercles is size dependent. Smaller specimens (11–15 mm long) usually have 2–3 rows, whereas larger ones (20–36 mm long) have 4–5 rows.

Remarks. *Iphione fimbriata* de Quatrefages, 1866 was described with very long antennae, elytral margins fimbriate (hence the name), barely overlapping mid-dorsally, and without elytral macrotubercles. The holotype, however, has macrotubercles arranged in 4–5 rows as indicated above, but there are some sediment particles partially blocking their visibility. Haswell (1892: 277) indicated the “upper antennae very long”, but he was following the original description because no specimens were indicated. Pettibone (1986: 9) studied the holotype and regarded it as a junior synonym of *I. muricata* (Savigny in Lamarck, 1818). However, as noted above, the delineation by Pettibone of *I. muricata* was very wide, encompassing multiple species.

Iphione fustis Hoagland, 1920 was described from the Philippines, and a juvenile was selected as the holotype. Hartman (1938: 107) revised the holotype, not the paratypes, and noted and illustrated that neuracicular lobes are more projected than the indication in the original illustration, where it was shown truncate, with ventral cirri reaching the tip of neuracicular lobe.

Iphione fimbriata (de Quatrefages, 1866) resembles *I. ankeri* **sp. n.**, from Guam because both species have dorsal cirrophores with distinct basal tubercle, and posterior elytral margins with long filaments. They differ because in *I. fimbriata* there are 4–5 rows of macrotubercles (2–3 in specimens 11–15 mm long; 4–5 in larger than 20 mm), whereas in *I. ankeri* there are only two rows (body 11.5–17.0 mm long). An additional difference is in

the neurochaetae; in *I. fimbriata* they are brownish, and markedly falcate, whereas in *I. ankeri* they are golden, barely falcate.

Iphione fimbriata also resembles *I. hyndmani* **sp. n.** from Hong Kong in its fimbriate elytra, macrotubercles conical arranged in 3–5 rows, and unidentate neurochaetae. The main difference between these two species lies in the development of the basal tubercle of dorsal cirrophores. In *I. fimbriata* the basal tubercle is distinct, whereas in *I. hyndmani* **sp. n.** it is not projected (holotype 32 mm long).

Iphione fimbriata appears to be closely related to *I. muricata* based on COI sequence data (Fig. 36).

Distribution. Thailand to Australia, east to the Marshall Islands and Samoa, on reefs and rocky or mixed bottoms in shallow water (0–48 m).

***Iphione hirta* de Quatrefages, 1866 indeterminate**

Iphione hirta de Quatrefages, 1866: 272.

Remarks. De Quatrefages (1866: 272) based this species on a damaged specimen from New Guinea, with some elytra lost; he thought there were 11 pairs of elytra, and thus that the species would be easily separated from all others in the genus, which have 13 pairs. He indicated that elytral margins were smooth, barely fimbriated. Pettibone (1986: 3) indicated that the type was lost and because it was inadequately described, it was regarded as indeterminate. We agree with her conclusion.

***Iphione hirotai* Izuka, 1912**

Iphione hirotai Izuka, 1912: 63–65, Pl. 7, Figs 8–15.

Iphione muricata: Fauvel 1936: 51; Imajima & Hartman 1964: 17 (*non* Savigny in Lamarck, 1818).

Remarks. *Iphione hirotai* Izuka, 1913 resembles *I. ovata* Kinberg, 1856, described from Hawaii and widely distributed from the Red Sea to the Eastern Pacific (Piotrowski *et al.* 2024). We did not have any specimens of the former species but, after the original description, and as indicated in the key above, the main differences are in the shape of nuchal lappets, and in the size and number of macrotubercles in elytra. Thus, *I. hirotai* has a truncate nuchal lappet, and its macrotubercles are digitate, up to twice longer than wide, arranged in 5–6 rows (body 14 mm long), whereas *I. ovata* has round nuchal lappet, and its macrotubercles are conical, 2–5 times longer than wide, and arranged in 3–5 rows (size-dependent).

Izuka (1912) illustrated the elytra with smooth margins and with macrotubercles arranged in 5–6 rows. Because the presence of fimbriae was regarded as irrelevant, it was regarded as a junior synonym of *I. muricata* (Augener 1922: 5–6; Okuda 1937: 266). Imajima & Hartman (1964: 17) indicated neurochaetae were unidentate, with 11–12 rows of serrations, but Izuka (1912: 65, Pl. 7, Fig. 15) indicated 2–3 rows. Pettibone (1986: 16) noted there was no type material, and regarded it as a junior synonym of *I. ovata* Kinberg, 1856. Against this synonymy, it should be noted the lack of basal tubercle in dorsal cirrophores, as indicated by Izuka (1912, Pl. 7, Fig. 12), whereas it is present in *I. ovata*.

Distribution. Originally described with a single specimen from one locality in Japan (Peel Island, Bonin Islands).

***Iphione henshawi* Pettibone, 1986**

Figs 3A–C, 10, 11, 36

Iphione henshawi Pettibone, 1986: 21–23, Figs. 8, 9; Wehe 2006: 62, Fig. 7a–h.

Type material. Hawaii. Holotype (USNM 81936), Hilo, low water, May 1904, H. Henshaw, coll. (holotype in worse condition than paratype; body pale, without elytra; right parapodia of chaetigers 2, 9, 12–15 previously removed (kept in container); prostomium with eyes black, anterior eyes in lateral projections, very close to posterior eyes; elytra with epibionts, variably eroded, dark yellow, with one to a few thin blackish oblique lines, some without lines; macrotubercles small, in median elytra about 10 rows; cirriferous segments with dorsal cirrophores without projected basal tubercle; body 29 mm long, 16 mm wide, 29 chaetigers). Paratype (USNM 5439), USFCS Albatross, Sta. 3999 (21°56'20" N, 159°42'45" W), Kaulakahi Channel, between Kauai and Nihau Islands, 13–271 m, 16 Jun. 1902 (used for redescription).

Additional material. Hawaii. One specimen (BPBM R481), Oahu, Makapuu Point, 1 Jul. 1955, depth not given, C.E. Cutress, coll. (body 35 mm long, 17 mm wide, 28 chaetigers; data used for variation). One specimen (CASIZ 10057), Hawaii, Hilo, July 1915, E.M. Erhorn, coll. (dark brown elytra, moderately covered in debris, with narrow oblique dark band submedially, lighter pigment at lateral margin, 10 diffuse rows of small macrotubercles, progressively smaller posteriorly, prostomium damaged and retracted into anterior segments; body 29 mm long, 19 mm wide, 29 chaetigers). One specimen (CAS 10075) Honolulu, Portlock (Portlock), 9 m, from Steinhart Aquarium, 26 Nov. 1971 (first four elytral pairs removed; right parapodium of chaetiger 13 dissected, basal lobe of cirrophore brownish (kept in container); elytra dark brown with a thin, oblique blackish line towards inner region; basal tubercle of dorsal cirri enlarged, elongate, blackish dorsally; prostomium distorted by eversion of pharynx; jaws with 3 denticles, a fourth barely visible; neurochaetal rows of denticles partially eroded; body 37 mm long, 23 mm wide, 28 chaetigers). One specimen (LACM 7461), Maui, Lahaina District, Kapalua, Kapalua Bay (20°59.98' N, 156°40.06' W), 3.6–4.5 m, under large pieces of coral rubble, 18 Jun. 2013, G. Hendler, coll. (elytra brownish, with epibionts, oblique longitudinal line blackish, macrotubercles small, in 10 rows, progressively smaller posteriorly; cirriferous segments with basal tubercle of dorsal cirrophore projected; body 37 mm long, 22 mm wide, 29 chaetigers). One specimen (LACM 0000), Maui, 1967, J. & D. Soulé, coll. (bent ventrally; some elytra previously removed; elytra dirty yellowish, with epibionts, oblique longitudinal lines better defined in posterior elytra, with 6–7 rows of macrotubercles; cirriferous segments with basal tubercle of dorsal cirrophore projected; body 21 mm long, 14 mm wide, 29 chaetigers). One specimen (UF 152), off Cook Point (19°28'36.9001" N, 155°56'23.5" W), 5–10 m, under rocks, 4 Nov. 1997, G. Paulay, coll. (right elytron 7 removed, with a marginal bryozoan with a darker core and transparent cortex resembling a subdistal round dark spots in some elytra; with 12 rows of macrotubercles; basal tubercle of dorsal cirrophore pale; neurochaetae with 36–54 transverse rows of denticles; body 42 mm long, 21 mm wide, 29 chaetigers).

Red Sea. One specimen (UF 3666), Saudi Arabia, off Thuwai, Shark Reef (22°25'37.2" N, 38°59'45.6" E), 0–20 m, offshore reef, A. Anker, P. Norby, J. Moore & J. Bouwmeester, coll. (complete, left elytron 7 previously removed; elytra yellowish with 1–2 oblique

longitudinal black bands; macrotubercles small in 8–9 rows; cirriferous segments with basal tubercle of dorsal cirrophore not projected; body 23 mm long, 12 mm wide, 29 chaetigers).

South Africa. Three specimens (ZMA V2580), Delagoa Bay, near Johaca Island, Jul. 1935, C.J. van der Horst, coll. (one specimen with most elytra and three median right parapodia previously removed (in separate vial); two other ones markedly bent ventrally; elytra fimbriae long, including some posterior margins parts, especially in regenerating areas; macrotubercles small, in two rows; basal tubercle of dorsal cirrophores projected; neurochaetae unidentate, slightly tapered; non-bent specimen 29 mm long, 14.5 mm wide, 29 chaetigers).

Madagascar. One specimen (MNHN A 274-33), 1901–1911, M. Ferlus, coll. (no further data; fixed in ethanol, bent ventrally, regenerating posterior region; most elytra detaching from body; elytra yellowish with 7–8 rows of microtubercles; body 22 mm long, 13 mm wide, 29 chaetigers). One specimen (MNHN IA 2015-162), Cruise Madagascar 2010, RV Miriky, Sta. DW 3238 (14°29' S, 47°27' E), 139–48 m, 6 Jul. 2009, L. Albenga *et al.*, coll. (bent ventrally; elytra yellowish, with few epibionts, macrotubercles small, conical, in 10 rows; cirriferous segments with basal tubercle of dorsal cirrophore projected; body 30 mm long, 19 mm wide, 29 chaetigers).

Mascarene Islands, La Réunion. One specimen (UF 647), Saint-Paul, Trou d'eau, Passe de l'hermitage (-21°06'06.0012" S, 55°14'36.9996" E), 9–12 m, fore reef, under rock, 8 Aug. 2007, H. Bruggemann, N. Hubert, F. Michonneau & G. Paulay, coll. (right parapodia of chaetigers 15–17 removed for molecular analysis; elytra golden with about 10 rows of macrotubercles, elytra pairs 1–6 with indistinct black spots, elytra pairs 7–10 with 1–2 oblique thin blackish lines, elytra pairs 11–13 with a single line; neurochaetae with 20–28 transverse rows of denticles; body 33 mm long, 12 mm wide, 28 chaetigers). One specimen (UF 657), Saint-Leu, Sec Jaune (21°09'19.8" S, 55°16'52.0201" E), 10–19 m, rocky slope, basalt blocks, 17 Aug. 2017, H. Bruggemann, N. Hubert & F. Michonneau, coll. (right parapodia of chaetigers 13, 14 removed for molecular analysis; basal tubercle of dorsal cirrophore brownish, a discontinuous spot extended dorsally, base of cirrostyle with a short, slightly longer than wide brownish band; neurochaetae with 40–50 transverse rows of denticles; elytra dark golden, with an oblique black line along elytra pairs 5–13, double in elytra pairs 8–12, right elytron 6 removed, with 12 transverse rows of macrotubercles; ceratophores of lateral antenna and facial tubercle blackish; body 46 mm long, 23 mm wide, 28 chaetigers).

Sultanate of Oman. One specimen (UF 10473), Dhofar Governate, Mirbat, Tinawelli, ARMS site 1 (16°56'02.4" N, 54°47'06.0" E), 24 m, rocky and sandy bottom, 24 Jan. 2022, G. Paulay, C. Meyer, S. Maslakova, M. Casterelli & F. Berzoni, coll. (slightly bent ventrally; right parapodia of chaetigers 13–20 previously removed; elytra yellowish, with an oblique longitudinal black band, and a few other ill-defined bands; 9–10 rows of tiny macrotubercles, slightly smaller towards posterior margin; cirriferous segments with basal tubercle of dorsal cirrophores projected; body 26 mm long, 16 mm wide, 29 chaetigers).

Maldives. One specimen (UF 4069), Blue Cove, 1.5 km NNE of Magoodhoo Island (03°05'37.788" N, 72°57'59.4" E), 10–28 m, high coral cover, slope, 6 May 2014, J Moore, coll. (juvenile; left elytron 7 and left parapodium of chaetiger 11 removed for molecular analysis; right elytron 7 and left parapodium of chaetiger 13 removed for observation (kept in container); elytra golden with a series of blackish spots forming two longitudinal discontinuous bands along body; elytron with 3–4 rows of short conical macrotubercles,

each with margins rough, with one median spine and 2–3 distal curved spines; basal tubercle of dorsal cirrophore pale; neurochaetae with 14–32 transverse rows of denticles; body 12 mm long, 6 mm wide, 28 chaetigers).

Japan. One specimen (UF 383), Okinawa, Ie Island, NE end of Island, area around Crevice and Daidokutsu Cave (26°43'28.4401" N, 127°49'53.94" E), 15–18 m, outer reef slope, under rocks, 7 Jul. 2004, G. Paulay & Kinjo, coll. (slightly bent ventrally; first left and sixth right elytra; anterior appendages blackish; elytra brownish, anterior pairs 1–5 almost without spots, following ones with 1–3 oblique blackish bands, thinner and discontinuous or wider and solid; elytra with 12–14 rows of macrotubercles; neurochaetae with 30–42 transverse rows of denticles; body 31 mm long, 18 mm wide, 28 chaetigers). Three specimens (USNM 100444), Okinawa, Horseshoe Cliffs, 1 km WNW off Omna Village (26°30'00" N, 127°50'54" E), 54.9 m, 23 May, 25 Sep. 1981, R.F. Bolland, coll. (anterior appendages blackish; eyes black, anterior and posterior eyes very close to each other laterally; one specimen straight, others bent ventrally; several elytra and parapodia previously removed (kept in container), one with a anteroventral previously made dissection for observing jaws; macrotubercles abundant, in elytra with fewer rows, slightly larger than in Hawaiian specimens; basal pharynx area blackish; jaws with tips brownish, and 3 accessory denticles; body 25–32 mm long, 13–16 mm wide, 28–29 chaetigers).

Mariana Islands, Guam. One specimen (UF 21), Sella Bay (13°30'00" N, 144°48'00" E), 5–10 m, patch reef, under hanging *Leptoseris* coral, 22 Aug. 1984, G. Paulay, coll. (bent ventrally; right elytra 6 and 7 previously removed (only one left in container), left parapodium of chaetiger 14 previously removed (not in container); left parapodium of chaetiger 11 removed for observation (kept in container), basal tubercle of dorsal cirrophore without dark pigmentation; neurochaetae with 42–50 transverse rows of denticles; lateral antennae and facial tubercle pale; body 50 mm long, 22 mm wide, 28 chaetigers).

Australia. One specimen (AM W37302), Woodside Kimberley Survey 2010, Sta. 34, 12 m, 16 Oct. 2010, A. Hosie, coll. (bent ventrally, elytra yellowish with a blackish oblique band, some with white epibionts (bryozoans, ascidians, algae); some posterior elytra previously removed; elytra with two rows of low conical macrotubercles; basal tubercle of dorsal cirrophores projected; neurochaetae unidentate; body 12 mm long, 6.5 mm wide, 28 chaetigers).

Papua New Guinea. One specimen (UF 3989), Madang Province, Madang, University Road (05°13'46.4412" S, 145°47'58.0344" E), 15 m, 12 Nov. 2012, B. Faure, R. Ibik, P.-H. Kuo, coll. (non-distorted specimen; first left elytron lost, right one detaching; macrotubercles arranged in 9 rows, many tubercles broken; left parapodium of chaetiger 11 removed for observation (both kept in container); basal tubercle of dorsal cirrophore tapered, not projected; 29 mm long, 14 mm wide, 28 chaetigers).

Kiribati, Line Islands. One specimen (UF 592), Kiritmati Atoll, under rocks, 21 Aug. 2005, G. Paulay, coll. (elytra yellowish with a thin oblique, longitudinal blackish band; basal tubercle without dark pigmentation; neurochaetae with 40–50 transverse rows of denticles, mostly eroded; body 45 mm long, 21 mm wide, 29 chaetigers).

French Polynesia, Society Islands. One specimen (UF 918), Tahiti Island, Motu-Uta (17°36'00" S, 149°24'00" W), 21 m, 1 Nov. 2008, P. Bacchet, coll. (juvenile, bent ventrally, right elytron 8 removed for observation (kept in container) with 4–5 rows of low macrotubercles; parapodia not removed; 14 mm long, 6.5 mm wide, 28 chaetigers).

Diagnosis. *Iphione* with median antenna reduced to nuchal papilla; elytra fimbriate; macrotubercles conical, slightly longer than wide, in 2–11 rows, first row with macrotubercles slightly larger than those in other rows; cirriferous segments with dorsal cirrophores with basal tubercle indistinct; neurochaetae unidentate.

Description. Paratype (USNM 5439) bent ventrally, 41 mm long, 29 mm wide, 29 chaetigers; several elytra previously removed, remaining ones with long fimbriae and abundant epibionts (hydroids, sponges, three median parapodia previously dissected (in container); mature male, testes occupying most of coelom space. Body wall pale dorsally and ventrally, elytra brownish.

Elytra brownish to bronze, with fimbriae (Fig. 10B, inset), 1–2 thin blackish bands in some posterior elytra; macrotubercles short, round, slightly projected into single spine, of similar size, with long blunt fragile spines (Fig. 10D, inset), arranged in 5–18 rows, occupying $1/5$ – $1/3$ elytral surface, more widespread in smaller elytra.

Prostomium wider than long, with a shallow longitudinal depression restricted to anterior prostomial margin. Anterior lobes projected into ceratophores, longer than prostomium, ceratostyles lost. Palps previously removed, size proportion to antennae unknown. Eyes black, positioned in posterior prostomial half (Fig. 10A), anterior eyes projected laterally, as large as posterior eyes; anterior and posterior eyes along the same side very close to each other, $1/3$ as far as distance between posterior eyes. Nuchal papilla not visible dorsally, covered by nuchal hood, slightly longer than wide.

Tentacular segment dorsally reduced, cirri and chaetae not seen. Facial tubercle visible dorsally, pale.

Segments 2–4 directed anteriorly. Second segment visible dorsally, with a projected nuchal lappet, lobate, longer than wide, completely covering nuchal papilla. Ventral buccal cirri inserted ventrally, slightly longer than following ventral cirri, extended beyond chaetal tips. From segment 3, one pair of globular, separate dorsal nodules per segment, barely visible after compression. Segments 2–3 with finer neurochaetae, barely swollen subdistally, with a longer region covered by series of transverse denticulations.

Median cirriferous segments with dorsal cirri surpassing chaetal tips (Fig. 10E), shape resembling lateral antennae; dorsal cirrophore smooth, without basal tubercle. Notochaetae brownish, very abundant, delicate capillaries with series of transverse funnel-shaped spinose rows, tips bare. Neuropodia with neuracicular lobe 3 times longer than wide, blunt; neurochaetal lobe with small globular papillae. Neurochaetae thick, abundant, basally smooth, subdistally swollen, with series of fine denticulations along swollen region, tips falcate, sharp (Fig. 10F, G).

Anus dorsal, positioned between elytral pairs 12 and 13.

Variation. Pharynx features (Fig. 3A–C) were indicated above. A non-type specimen (BPBM R481) is a mature female, slightly bent ventrally, pharynx fully exposed (Fig. 3, explained above in anatomy); prostomium oval, pale, lateral antennae ceratophores brownish (Fig. 15A); palps almost twice longer than antennae, darker from medial region to tips; eyes blackish, of similar size, anterior eyes in small protuberances at the widest prostomial surface, about the middle of prostomium; median antenna reduced to small lobe; nuchal lappet semicircular; first four pairs of elytra removed, two left parapodia of

median chaetigers dissected (retained in container); elytra dark brown with fimbriae elongate, with spinous lobe and long, blunt spines (Fig. 11C); macrotubercles conical to irregular, arranged in 15–20 rows, each often with a main short, straight spine and 1–4 lateral curved, blunt long spines (Fig. 11D); dorsal cirrophore lobe conical, tapered, without ventral projections (Fig. 11E); oocytes of about 100 μm in diameter.

The additional specimens were 12–50 mm long, 6–23 mm wide. The number of rows of macrotubercles is roughly size-dependent, but it can be modified if the tubercles are small, there can be more rows even in specimens of similar size.

Remarks. *Iphione henshawi* Pettibone, 1986 was described with two specimens being indicated as 29–41 mm in length. The holotype was the largest specimen (described as 41 mm long, it is 29 mm long) and was collected in the low intertidal; its median elytra were illustrated as having rows of small macrotubercles, whereas the paratype was smaller (29 mm long; actually of the same size) and was sampled in a haul along 13–271 m, and its median elytra have about 10 rows of small macrotubercles. The confusion of the size and the number of rows of macrotubercles were misleading, because it implied that at least regarding the number of rows of macrotubercles, they are not size-dependent after these two specimens. However, they are of the same length and have a similar number of rows of macrotubercles. In both specimens, the anterior eyes are in small lateral projections, very close to posterior eyes laterally, and dorsal cirrophores have barely projected basal tubercles. Two different non-type specimens were COI-sequenced: one from Papua New Guinea (UF 3989) is 29 mm long and has about 10 rows of macrotubercles, the other one is from the Maldives (UF 4069) being 12 mm long and has 4–5 rows of macrotubercles; both have barely developed basal tubercles in dorsal cirrophores. They fall very close to each other in the dendrogram (Fig. 36); consequently, the number of rows of macrotubercles is size dependent, and not a diagnostic feature for *I. henshawi*.

The specimen recorded by Wehe (2006) from the Red Sea was 12 mm long, and it has anterior and posterior eyes very close in lateral view. The Red Sea specimen shows some differences from the larger Hawaiian specimens. For example, the Red Sea specimen has no nuchal flap or lappet, and its first dorsal tubercles are poorly defined, elytra have 2–3 rows of macrotubercles whereas there are 3–10 in Hawaiian specimens, and neurochaetae have fewer rows of spines (11 were illustrated) whereas there are 18–33 in Hawaiian specimens. The difference in notochaetal pigmentation and the number of rows of macrotubercles are size-dependent, and consequently, Red Sea specimens are herein regarded as conspecific.

Iphione henshawi Pettibone, 1986 belongs in the group of species having fimbriate elytra. As indicated in the key above, it differs from all other species in the group by having small macrotubercles, arranged in 2–10 or more rows, and fimbriae well defined.

Iphione henshawi is sister to *I. malifera* in the COI phylogeny (Fig. 36).

Distribution. Red Sea to South Africa, east to the Hawaiian, Line, and Society Islands, on reefs and rocky or mixed bottoms in shallow water to shelf depths (0–271 m).

***Iphione treadwelli* Pettibone, 1986**

Figs 12–14

Iphione treadwelli Pettibone, 1986: 19–21, Fig. 7; Hanley & Burke 1991: 43–45, Fig. 13A–F; Imaijima 2005: 55–59, Figs 15–17; Imaijima 2011: 153.

Type material. Hawaii. Holotype (USNM 5435), Auau Channel, Maui Island, Lahaina, RV Albatross, unnumb. Sta. (20°51'35" N, 156°42'35" W), 51–79 m, 14 Apr. 1902. Paratype (USNM 81934), off Laysan Island, USFCS Albatross, Sta. 3936, 142–234 m, 16 May 1902 (body 9 mm long, 5 mm wide, probably 28 chaetigers, not manipulated to avoid further damage).

Additional material.

Philippines. One specimen (ECOSUR 3-117), Musorstom 3, Sta. DR 117 (12°31' N, 120°39' E), 92 m, 3 Jun. 1985 (markedly bent ventrally; elytra with macrotubercles short, digitate, in a single row; not measured to avoid further damage). Two specimens (ECOSUR 3-131), Musorstom 3, Sta. CP 131 (11°36.6' N, 121°43.0' E), 111–113 m, 5 Jun. 1985 (bent ventrally, some elytra detached and one specimen distorted by compression; elytra yellow with abundant brownish spots; macrotubercles arranged in a single row, as fragile blunt spines, eroded to low, cushion-shaped tubercles; median cirriferous segments with a projected basal tubercle to dorsal cirrophores; neurochaetae unidentate; undamaged specimen 13 mm long, 7 mm wide, 29 chaetigers). One specimen (ECOSUR 3-137), Musorstom 3, Sta. DR 137 (12°03' N, 111°06' E), 56 m, 6 Jun. 1985 (markedly bent ventrally; right elytron 6 removed for observation (kept in container); macrotubercles cushion-shaped, in a single row; not measured to avoid further damage).

Mariana Islands. One specimen (UF 133), Guam, Hagatna Bay, East side (13°30'00" N, 144°48'00" E), 115 m, reef talus, 14 Jul. 1997, G. Paulay & B. Smith, coll. (markedly bent ventrally, dried-out; not measured to avoid further damage; left parapodium of chaetiger 14 removed for observation, kept in container; elytra yellowish, with sessile to pedunculate fimbriae, and macrotubercles along a single row, darker than other areas with oblique illumination).

Australia. One specimen (NMV F185639), Western Australia, RV Southern Surveyor, L30 Transect (12°25'57" S, 123°35'47" E to 12°26'04" S, 123°35'52" E), 111 m, Sherman sled, 7 Jul. 2007, D. J. Bray, coll. (bent ventrally; most elytra previously removed; elytra yellowish with 4–7 short macrotubercles in a single row; body 8 mm long, 5.5 mm wide, 29 chaetigers).

Taupo Seamount. Two specimens (AM 21762), 500 km ENE off Sydney (33°06'11.9999" S, 156°09'18.00" E), 164 m, 7 Oct. 1982, R.T. Springthorpe & W.F. Ponder, coll. (bent ventrally, several elytra previously removed; elytra yellowish, with a small central black spot, better defined in smallest specimen; macrotubercles in a row, with up to five macrotubercles per row, progressively smaller middorsally; cirriferous segments with basal tubercle slightly projected, glandular area not pigmented, if present; body 5–7 mm long, 3.5–5.0 mm wide, 27–29 chaetigers).

Coral Sea. One specimen (MAGNT 5456), RV Corail, Sta. 94DW (19°86' S, 158°58' E), 36–53 m, 27 Aug. 1988, J.R. Hanley, coll. (all right elytra and left anterior ones previously removed, two parapodia previously removed (all kept in container); elytra yellowish with spread black dots medially, 6–7 macrotubercles in a row; cirriferous segments with basal tubercle of dorsal cirrophores projected; neurochaetae unidentate, barely falcate, some with distal keel; body 8.5 mm long, 5 mm wide, 29 chaetigers). One specimen (MAGNT W5457), RV Corail, Sta. 26DW (20°21.98' S, 161°04.87' E), 62 m (after cruise data; 88 m on label), 22 Jul. 1988, J.R. Hanley, coll. (markedly bent ventrally; some elytra previously

detached (kept in container) and 3 parapodia (lost); elytra yellowish, with spread black spots medially, macrotubercles in a single row with 6–7 macrotubercles, each one blunt conical, directed or bent middorsally; fimbriae minute, restricted to outer margin; cirriferous segments with basal tubercle of dorsal cirrophores bilobed; cirrostyles tapered, not subdistally swollen; neurochaetae unidentate, slightly falcate, some with a distal keel reaching tip; not measured to avoid further damage).

Papua New Guinea. One specimen (NMV F227776), Gulf of Papua, Stat. unnumbered (08°36'08" S, 144°54'32" E), trawl, 96 m, 7 Nov. 2015, M. Wright, coll. (slightly bent ventrally; elytra yellowish, with sessile to pedunculate fimbriae, macrotubercles in a single row; basal tubercle of dorsal cirrophores projected; neurochaetae subdistally expanded, unidentate; body 12 mm long, 7.5 mm wide, 29 chaetigers).

New Caledonia. One specimen (ECOSUR 6-458), Îles Loyauté, Musorstom 6, Sta. DW 458 (21°00.93' S, 167°28.96' E), 415 m, 20 Feb. 1989 (complete; data used for variation; body 10 mm long, 6 mm wide, 29 chaetigers). One specimen (MNHN IA 2015-73), Mission KANACONO, Sta. DW 4732 (22°34' S, 167°36' E), 194–168 m, 22 Aug. 2016, S. Hourdez *et al.*, coll. (juvenile; markedly bent ventrally; a few elytra previously removed, kept in container; elytra yellowish, with one row of falcate macrotubercles; body width 5 mm). One specimen (MNHN IA 2015-74), Mission KANACONO, Sta. DW 4763 (23°17' S, 168°15' E), 192–260 m, 27 Aug. 2016, S. Hourdez *et al.*, coll. (juvenile; markedly bent ventrally; elytra mottled, middorsal longitudinal band brownish, ill defined, with some brownish spots along posterior region; macrotubercles in one row, low digitate; cirriferous segments with basal tubercle of dorsal cirrophore projected; not measured).

French Polynesia. One specimen (MNHN IA 2013-154), Palliser Islands, Mission TARASOC, SW off Raitahti, Sta. CP 3386 (15°42' S, 146°54' W), 400–440 m, 5 Oct. 2009, S. Hourdez, *et al.*, coll. (slightly bent ventrally; elytra brownish, macrotubercles cushion-shaped, in a single row, slightly raised along the inner side; cirriferous segments with basal tubercle of dorsal cirrophore projected, with abundant black globular glands; body 18 mm long, 13 mm wide, 29 chaetigers). Two specimens (MNHN IA 2013-163), Palliser Islands, Mission TARASOC, NNW off Niau Atoll, Sta. DW 3362 (16°07' S, 146°23' W), 198–280 m, 5 Oct. 2009, S. Hourdez *et al.*, coll. (bent ventrally; elytra blackish along chaetigers 1–7, posterior ones yellowish, without black spots; macrotubercles in a single row, cushion shaped, falcate in smallest specimen; cirriferous segments with basal tubercle of dorsal cirrophore projected, with black globular glands, less defined in smallest specimen; body 13–15 mm long, 6–9 mm wide, 29 chaetigers). Two specimens (MNHN IA 2013-166), Palliser Islands, Mission TARASOC, among Apataki, Aratika and Toau atolls, Sta. DW 3372 (15°39' S, 145°55' W), 326–540 m, 3 Oct. 2009, S. Hourdez *et al.*, coll. (smaller markedly bent ventrally; elytra brownish, macrotubercles cushion-shaped in a single row; body 12 mm long, 9 mm wide, 29 chaetigers).

Diagnosis. *Iphione* with median antenna reduced to nuchal papilla; elytra fimbriate, fimbriae short, globose; macrotubercles cushion-shaped without distal spines, in a single row; cirriferous segments with dorsal cirrophores with basal tubercle projected, tip blackish; neurochaetae unidentate; ventral cirrostyles bases pale.

Description. Holotype (USNM 5435) markedly bent ventrally (Fig. 12A); most elytra and right parapodia of chaetigers 13–15 previously detached, left parapodium of chaetiger 12 removed for observation (kept in container). Elytra yellowish, with macrotubercles arranged in a single row, without black spots; notochaetae whitish, neurochaetae golden;

midventrally paler than lateral areas; ventral cirrophores pale. Body length not measured, body width 5.5 mm; chaetigers not counted.

Elytra with fimbriae small (Fig. 12C), each fimbria globular, reduced, present along external lateral margins; macrotubercles conical, distal spines present in many macrotubercles, directed middorsally, slightly decreasing in size middorsally.

Prostomium oval, wider than long (Fig. 12B), with a deep longitudinal depression along anterior prostomial fourth. Anterior lobes projected into ceratophores, slightly longer than prostomium, pale, ceratostyles pale, directed ventrally, slightly longer than ceratophores, tips tapered, thread-like. Palps pale, twice longer than lateral antennae. Eyes black, positioned in posterior prostomial half; anterior eyes directed laterally, slightly larger than posterior eyes, directed dorsolaterally; anterior and posterior eyes not close to each other along same side. Nuchal papilla not visible dorsally.

Tentacular segment reduced dorsally, tentacular cirrophores and cirrostyles pale, without chaetae. Facial tubercle visible dorsally, pale.

Segments 2–4 directed anteriorly. Second segment visible dorsally, with a projected semicircular nuchal lappet, about as wide as long, completely covering nuchal papilla. Ventral buccal cirri inserted ventrally, almost twice longer than following ones. Dorsal nodules indistinct. Segments 2–3 with finer neurochaetae, barely swollen subdistally, with a longer region with transverse denticulations.

Median cirriferous segments with dorsal cirri broken (Fig. 12D); dorsal cirrophore smooth, with projected basal tubercle. Notochaetae whitish, very abundant, delicate capillaries with series or transverse funnel-shaped spinose rows, tips bare. Neuropodia with neuracicular lobe about twice longer than wide, truncate; neurochaetal lobe with short papillae. Neurochaetae thick, abundant, basally smooth, subdistally swollen, with series of fine denticulations along swollen region, tips falcate, unidentate.

Anus not seen.

Variation. The paratype (USNM 81934) is dried out, bent ventrally (Fig. 13A, B), nine elytra were previously removed (kept in container); median elytra with a single row of tubercles, dark brown, bent, tips broken, without large spines (Fig. 13C); fimbriae globose, short, mostly sessile or with very short peduncles (Fig. 13D, E), a single long one in one of the 9 elytra. The paratype has a transverse anteroventral dissection.

A non-type specimen (ECOSUR 6-458) has the first five pairs of elytra darker than following ones, and elytra pairs 4–5 forming a wide transverse black band, and darker inner margins forming a longitudinal wide band (Fig. 14A). Elytra are brittle (Fig. 14B), with large cushion-shaped macrotubercles (Fig. 14C), each longer than wide, arranged in a single row, lateral margins with deciduous tiny fimbriae (Fig. 14D). Cirriferous segments with basal tubercle to dorsal cirrophore projected, with brownish glands (Fig. 14E, inset); neurochaetae unidentate, tips slightly falcate (Fig. 14F).

The additional specimens were 5–18 mm long, 3.5–13.0 mm wide. Macrotubercles are arranged in a single row, and this does not change with body size; each macrotubercle is cushion-shaped with a distal tip, and this is better seen in smaller specimens. Older ones have macrotubercles variably eroded.

Remarks. *Iphione treadwelli* Pettibone, 1986 resembles *I. corbariae* **sp. n.** from the Indian Ocean (see below), because they are the only species having elytra with cushion-shaped macrotubercles (once the distal spine is broken) arranged in a single row, and minute fimbriae. The main differences can be noted in the type of neurochaetae, and in the pigmentation pattern of some parapodial features. In *I. treadwelli* neurochaetae are unidentate, and the basal tubercles of dorsal cirrophores have blackish tips and pale bases, whereas in *I. corbariae* neurochaetae are bidentate, and the basal tubercle is basally blackish and distally pale. Further, the ventral cirrostyles of *I. treadwelli* are pale, whereas they are blackish in *I. corbariae*. An additional difference is in elytral pigmentation. In *I. treadwelli* elytra are rather homogeneously pigmented, either yellowish or blackish, without spots, whereas in *I. corbariae* median elytra have 2–3 darker spots each.

Iphione treadwelli Pettibone, 1986 and *I. henshawi* were described from Hawaii, and they include the *Iphione* specimens provided with elytral fimbriae, previously often recorded from the Hawaiian Archipelago as *I. muricata* (Savigny in Lamarck, 1818).

Besides pigmentation, which can be lost after long time preservation in ethanol, there are several differences between the type specimen described from Hawaii, and the specimens from New Caledonia. As indicated in the key above, the type has distinct nuchal lappets, whereas they are not well-developed in the New Caledonia specimens, but these features are often modified after preservation. In the elytra, the macrotubercles are blackish in the Hawaiian type specimens, but pale in the New Caledonian ones, and lateral fringe papillae also differ, being mostly sessile in the type, and with short stems in the other specimens. Further, neurochaetae from median chaetigers are straighter, and less swollen subdistally in the New Caledonia specimens than in those from Hawaii. The only difference found in Japanese specimens, as illustrated by Imajima (2005: 55–59, Figs 15–17) is that the series of rows of denticles do not completely cover chaetae but apparently leave the dorsal surface smooth. However, this might be an artifact because tips of the series of spines are visible along the dorsal surface in his figures.

Distribution. From western Australia and Philippines, east to Hawaii and the Tuamotu Islands, on deep reefs and in rocky or mixed bottoms at moderate depths (36–540 m).

***Iphione coriolis* Hanley & Burke, 1991**

Figs 15–17, 36

Iphione coriolis Hanley & Burke, 1991: 45, Fig. 14A–E; Solís-Weiss *et al.* 2004: S14.

Type material. Coral Sea, Chesterfield Islands. Holotype (MNHN POLY TYPE 574), RV Coriolis, Cruise Corail 2, Sta. RH 88-65 (19°06' S, 158°53.26' E), 32–60 m, coral, coral rubble and coral sand with some *Halimeda*, 27 Jul. 1988, R. Hanley, coll.

Additional material.

Philippines. One specimen (CASIZ 214326), Batangas Province, Verde Island Pinnacles dive site, sea mount with coral rubble, on red sponge, 2015 Verde Island Passage Expedition, sta. VER-02 (15°31'59.088" N, 121°01'14.52" E), 6–20 m, 30 Mar. 2015, J. Comendador coll. (markedly bent, elytra yellowish, 4 rows of low curved falcate macrotubercles directed mid-dorsally and decreasing in size posteriorly; body approximately 10 mm long, 5 mm wide, chaetigers not counted).

Northern Mariana Islands. One specimen (UF 77), Mariana Islands, Guam Island. Orote Northern Tip, Harry's Rubble Field (13°30'00.0" N, 144°48'00.0" E), 25 m, under coral rubble, 20 Jun. 2002, L. Kirkendale, coll. (complete, markedly bent ventrally; elytra yellow, with 9–10 rows of macrotubercles darker, decreasing in size towards margins; largest tubercle towards middorsal line; left parapodium of chaetiger 12 removed for observation, kept in container; basal tubercle of dorsal cirrophore projected with minute globular black glands; body length not measured, 9 mm wide, chaetigers not counted). One specimen (UF 162), Mariana Islands, Pagan Island (18°07' N, 145°46' E), Southwestern side, rock wall, 23 m, 22 May 1992, P. Schupp, coll. (complete, slightly bent ventrally; elytra yellow, with largest macrotubercles darker, arranged along first row, decreasing in size towards margins; largest tubercle towards middorsal line; body 15 mm long, 7.5 mm wide, 29 chaetigers). One specimen (UF 168), Guam Island, Double Reef (13°30'00.0" N, 144°48'00.0" E), 3–10 m, under rocks, 3 Feb. 1998, G. Paulay & J. Starmer, coll. (complete; elytra yellow, first row of macrotubercles slightly larger than those present along following rows, largest middorsal tubercle barely projected; left parapodium of chaetiger 14 removed for observation; body 22 mm long, 12 mm wide, 29 chaetigers;).

Papua New Guinea. One specimen (MNHN IA 2014-218/2021-685), Papua Niugini Expedition, Sta. PB 29 (05°18' S, 145°46.1' E), 17 m, 27 Nov. 2012. S. Hourdez *et al.*, coll. (markedly bent ventrally; elytra yellowish, with one series of macrotubercles, without fimbriae; cirriferous segments with basal tubercle of dorsal cirrophore projected; body 9 mm wide, 29 chaetigers).

French Polynesia, Society Islands, Moorea. One specimen (UF 1429), Atiha Bay, inside barrier reef, on West side of pass (17°35'44.448" S, 149°50'44.304" W), near pass channel, 0.5–1.0 m, 8 Dec. 2009, S. McPherson, G. Paulay, C. Meyer, coll. (bent ventrally; left elytra 6 and 10 removed for observation (kept in container), each with 5–6 rows of macrotubercles, largest ones in first row; body 14 mm long, 7 mm wide, chaetigers not counted to avoid damaging the specimen).

Hawaii. One specimen (LACM 12809), Northwestern Hawaiian Islands, French Frigate Shoals, lagoon patch reef (23°49'01.2" N, 166°17'20.4" W), 10.7 m, 25 Oct. 2006, S. Godwin, R. Most, J. Starmer, J. Maragos, G. Paulay & S. McKeon, coll. (bent ventrally; some elytra previously removed (kept in container); elytra yellowish, macrotubercles in 5 rows, progressively smaller posteriorly; cirriferous segments with basal tubercle of dorsal cirrophore not projected; body 13.5 mm long, 9 mm wide, 29 chaetigers). Two specimens (LACM 12810), Northwestern Hawaiian Islands, French Frigate Shoals, fore reef (23°51'46.8" N, 166°11'02.4" W), 25.9 m, 12 Oct. 2006, G. Paulay, S. McKeon, B. Zglicinski, R. Brainard, J. Maragos & J. Starmer, coll. (bent ventrally; some elytra previously removed (kept in container), elytra yellowish with 3–4 rows of macrotubercles, progressively smaller posteriorly; cirriferous segments with basal tubercle of dorsal cirrophore not projected; body 8–11 mm long, 6–8 mm wide, 29 chaetigers). One specimen (LACM 12811), Northwestern Hawaiian Islands, French Frigate Shoals, La Perouse Pinnacle (23°46'12.0" N, 166°15'39.6" W), 9.8 m, 21 Oct. 2006, G. Paulay, S. McKeon, T. Lotufo, S. Godwin, J. Starmer, J. Maragos, A. Collins & E. Soto, coll. (left elytra of chaetigers 1, 2, and left parapodia of chaetiger 11 removed for observation; elytra yellowish with 4 rows of macrotubercles decreasing in size posteriorly; cirriferous segments with basal tubercle of dorsal cirrophore not projected; body 14 mm long, 6 mm wide, 28 chaetigers). One specimen (UF 5449), Honolulu, Kaneohe Bay, North of Kapapa Island (21°30'05.652" N, 157°47'47.148" W), 15–18 m, outer reef slope, 27 May 2017, Invertebrate Zoology team, coll. (data in variation). One specimen (UF 5450), Honolulu, Kaneohe Bay, North of Kapapa Island (21°30'05.652" N, 157°47'47.148" W), 15–18 m,

outer reef slope, 27 May 2017, Invertebrate Zoology team, coll. (complete, breaking in two; right parapodia of chaetigers 11–19 removed for molecular analysis; body 14 mm long, 6.5 mm wide, 29 chaetigers).

Diagnosis. *Iphione* with median antenna reduced to nuchal papilla; elytra with margins smooth, non-fimbriate; macrotubercles blunt conical with distal spines, often eroded, in 3–4 rows, first row with macrotubercles markedly larger than those in other rows; cirriferous segments with dorsal cirrophores with basal tubercle indistinct; neurochaetae bidentate.

Description. Holotype (MNHN POLY TYPE 574) bent ventrally, first few right parapodia slightly distorted by compression, all elytra and right parapodium of chaetiger 10 previously removed (25 elytra and parapodium kept in container). Elytra yellowish, with macrotubercles arranged in 5–6 rows, without dark spots; notochaetae whitish, neurochaetae golden; midventrally paler than surrounding darker bands; ventral cirrophores pale. Body 10.5 mm long, 6 mm wide, 29 chaetigers.

Elytra without fimbriae; macrotubercles conical, slightly falcate, smaller ones with single distal spine (eroded in larger ones), directed middorsally; macrotubercles largest in first rows, slightly decreasing in size towards margins (Fig. 15B, C).

Prostomium roughly hexagonal, as long as wide, with a deep longitudinal depression along anterior prostomial third (Fig. 15A). Anterior lobes projected into ceratophores, about as long as prostomium, blackish, ceratostyles pale, directed ventrally, subdistally swollen, tips tapered. Palps paler than ceratophores, barely longer than lateral antennae. Eyes black positioned in posterior prostomial half; anterior eyes displaced laterally, slightly larger than posterior round, dorsal eyes; anterior and posterior eyes very close to each other in lateral view. Nuchal papilla not seen dorsally, covered by nuchal hood, slightly wider than long.

Tentacular segment dorsally reduced, tentacular cirrophores blackish, cirrostyles pale, without chaetae. Facial tubercle visible dorsally, blackish.

Segments 2–4 directed anteriorly. Second segment visible dorsally, with a projected, semicircular nuchal lappet, lobate, wider than long, completely covering nuchal papilla. Ventral buccal cirri inserted ventrally, twice larger than following ventral cirri, extending beyond chaetal tips. Dorsal nodules indistinct (probably after ventral contraction). Segments 2–3 with finer neurochaetae, barely swollen subdistally, with a longer region covered by series of transverse denticulations.

Median cirriferous segments with dorsal cirri markedly surpassing chaetal tips (Fig. 15D), shape resembling lateral antennae; dorsal cirrophore smooth, with projected basal tubercle. Notochaetae whitish, very abundant, delicate capillaries with series of transverse funnel-shaped spinose rows, tips bare. Neuropodia with neuracicular lobe about three times longer than wide, truncate; neurochaetal lobe with very long papillae. Neurochaetae thick, abundant, basally smooth, subdistally swollen, with series of fine denticulations along swollen region, tips falcate, bidentate.

Anus dorsal, positioned between elytral pairs 12 and 13.

Variation. Large specimen (UF 5450) breaking into two parts (Fig. 16A). Elytra yellowish, with macrotubercles slightly darker, arranged in 5–6 rows, with first row with larger

macrotubercles (Fig. 16B), becoming larger in more posterior chaetigers (Fig. 16C), but progressively smaller towards posterior margin. Notochaetae whitish, neurochaetae golden; venter pale, ventral cirrophores pale.

Elytrae without fimbriae; macrotubercles conical, falcate, with a single distal spine (mostly eroded), directed middorsally; pairs of elytra 10–11 with largest macrotubercles in the first row, largest ones approaching middorsal elytral edge (Fig. 16C).

Median cirriferous segments (Fig. 16D) with dorsal cirri markedly surpassing neurochaetal tips, subdistally swollen; dorsal cirrophore smooth, cirrostyle subdistally swollen, papillate. Notochaetae very abundant, opaque, with a series of transverse funnel-shaped spinose rows, tips bare. Neuropodia with neurochaetal lobe blunt, neuracicular lobe with long papillae, longest ones 5–6 times longer than tip width. Neurochaetae abundant, basally smooth, subdistally swollen, especially the lower ones, with many rows of fine denticulations along swollen region, tips falcate, bidentate (Fig. 16E). Anus not seen.

Small, mature female (UF 5449), anterior and posterior ends bent ventrally (Fig. 17A, B); right parapodia of segments 7–20 previously removed for molecular studies; left parapodia of segments 11 and 13 removed for observing parapodial features (kept in container): body 12 mm long, 6 mm wide, 28 chaetigers. Elytra yellowish, with macrotubercles slightly darker, arranged in 2–3 rows of larger ones, and 1–2 others with fewer, smaller tubercles, with scattered brownish spots forming irregular areas; notochaetae whitish, neurochaetae golden, parapodia with densely packed, irregular oocytes; venter pale, ventral cirrophores barely brownish.

Elytra without fimbriae; macrotubercles conical, falcate, with a single distal spine, directed middorsally (Fig. 17C), pairs of elytra 10–11 with largest macrotubercles approaching middorsal elytral edge (Fig 17D).

Median cirriferous segments (Fig. 17E) with dorsal cirri surpassing neurochaetal tips, subdistally swollen; dorsal cirrophore smooth, cirrostyle subdistally swollen, papillate. Notochaetae very abundant, dirty white to opaque, with series of transverse funnel-shaped spinose rows, tips bare. Neuropodia with neurochaetal lobe blunt, neuracicular lobe with long papillae, longest ones 3–4 times longer than tip width (Fig. 17F). Neurochaetae abundant, basally smooth, subdistally swollen, especially the lower ones, with many rows of fine denticulations along swollen region, tips falcate, bidentate (Fig. 17G). Anus not seen. Oocytes in densely packed masses in coelom, each oocyte about 80–90 μm in diameter.

The small female (UF 5449) differs from the holotype of *I. coriolis* because it has 2–3 rows of larger macrotubercles against 5–6 rows in the holotype. However, there are other, smaller macrotubercles, but it is regarded as belonging to the same species because the size of macrotubercles decreases towards posterior margin, as is the case in the holotype.

The additional specimens were 8–22 mm long, 6–12 mm wide. Macrotubercles are arranged in rows, and their number is size dependent. The size of macrotubercles show a consistent trend; the first row has the largest macrotubercles, and the other rows have tubercles progressively smaller posteriorly.

Remarks. *Iphione coriolis* Hanley & Burke, 1991 was described with a 10.5 mm long specimen from the Coral Sea, and its accompanying illustrations include the anterior end, the right cirriferous parapodium of chaetiger 12 in anterior view, and a midbody elytron with 5–6 rows of macrotubercles, with the first row having larger macrotubercles. It has been unique among *Iphione* by having bidentate neurochaetae (but see *I. harrisae* **sp. n.** and *I. corbari* **sp. n.** described below); besides, its elytra have smooth margins, with low, blunt macrotubercles, and neuracicular lobes have papillae 3–4 times longer than neuracicular tip width.

Iphione coriolis and *I. harrisae* **sp. n.** are very similar by having elytra without fimbriae and bidentate neurochaetae, but they are different species, and their main difference lies in the size of macrotubercles. In *I. coriolis* elytra have a single row of macrotubercles progressively larger posteriorly, but the other rows have macrotubercles decreasing in size posteriorly, whereas in *I. harrisae* **sp. n.** the size of macrotubercles is progressively larger towards posterior margin.

Distribution. From the Philippines and Coral Sea to Hawaii and French Polynesia, in reef habitats (0.5–60.0 m).

***Iphione malifera* Piotrowski, 2014**

Figs 18, 36

Iphione malifera Piotrowski, 2014: 156–162, Figs 1–3.

Type material. Philippines. Holotype (CAS 187234), Hearst Philippine Biodiversity Expedition 2011, Luzon Island, Batangas Province, Tingloy, Maricaban Island, Sea Pen dive site (13°41'24.0" N, 120°49'48.0" W), coral reef rubble, 33 m, 7 May 2011, A. Hermosillo, coll.

Additional material. Philippines. One specimen (CASIZ 197953), Manbini, Balayan Bay, Cathedral dive site, under *Fungia* rubble near sponge, 2014 Verde Island Passage Expedition, sta. MAB-14 (13°43'12.0" N, 120°52'48.0" E), 40 ft, 28 Apr. 2014, C.N. Piotrowski coll. (intact specimen with few calcareous encrustations, long dark palps and tentacular cirri, elytra beige with mottled dark brown fanned striations across median elytra, progressively more pigment in posterior elytra, cylindrical inflated macrotubercles in 2 uniform rows; body 15 mm long, 7 mm wide, 29 chaetigers).

Diagnosis. *Iphione* with median antenna reduced to nuchal papilla; elytra fimbriate; macrotubercles digitate or blunt conical, rarely with distal spines, in 3–4 rows, first row with macrotubercles slightly larger than those in other rows; cirriferous segments with dorsal cirrophores with basal tubercle projected; neurochaetae unidentate.

Comments. The species was described recently. The holotype retains most elytra on site (Fig. 18A), but parapodial features were not detailed, especially the presence of tubercles in bases of dorsal cirrophores (Fig. 18B); they are conical, without basal projections. Neurochaetae are unidentate, with tips falcate (Fig. 18C).

Remarks. *Iphione malifera* Piotrowski, 2014 resembles *I. hourdezi* **sp. n.** from New Caledonia because both have elytra with fimbriae tiny and digitate macrotubercles. Their main differences are in the number of rows of macrotubercles, and in the shape of neurochaetae. In *I. malifera*, macrotubercles are in 2–3 rows, and neurochaetae are

subdistally swollen with falcate tips, whereas *I. hourdezi* has macrotubercles in two rows, and neurochaetae are acicular (barely swollen subdistally) with tips mostly straight.

Iphone malifera is sister species to *I. henshawi* in the COI tree (Fig. 36).

Distribution. Only known from the Philippines, in subtidal mixed bottoms (12–33 m).

***Iphone ankeri* sp. n.**

urn:lsid:zoobank.org:act:0000

Figs 19, 20, 36

Type material. Mariana Islands, Guam. Holotype (UF 1691), Apra Harbor, East side of Middle Shoals (13°26'42.0" N, 144°39'32.4" E), 1–15 m, lagoon patch reef, 17 Jun. 2010, N. Evans & F. Michonneau, coll. COI barcode: GenBank PQ423922 Paratype (UF 1704), Apra Harbor, near Machinist dry dock (13°26'37.1688" N, 144°39'34.0416" E, 22 Jun. 2010, no depth or substrate data, N. Evans, F. Michonneau, G. Paulay & A. Anker, coll. (body 11.5 mm long, 6.5 mm wide, 29 chaetigers; other data in variation).

Additional material. Mariana Islands, Guam. Four specimens (UF 129), Apra Harbor, Sumay Cove (13°30'00.0" N, 144°48'00.0" E), 3–5 m, patch reef, under rubble, 24 Oct. 1999, L. Kirkendale, coll. (bent ventrally; one with pharynx fully exposed; elytra yellowish with an oblique brownish band, expanded laterally along posterior elytral margin; macrotubercles in two rows, sometimes the second row more irregular; cirriferous segments with dorsal cirrophore with a projected globular basal tubercle; body 12–17 mm long, 7.0–10.5 mm wide, 29 chaetigers). Two specimens (UF 131), Apra Harbor, across Sumay Cove (13°30'00.0" N, 144°48'00.0" E), 5 m, patch reef, under rubble, 10 Dec. 1999, L. Kirkendale, coll. (bent ventrally; elytra 1 and 6 removed for observation; elytra yellowish with a black oblique band and macrotubercles in two rows; dorsal cirrophore with basal tubercle projected; body 15–16 mm long, 7.0–8.5 mm wide, 29 chaetigers). One specimen (UF 134) Apra Harbor, Western Shoals (13°30'00.0" N, 144°48'00.0" E), 16 m, rubble, 1 Apr. 1998, G. Paulay & B. Smith, coll. (slightly bent ventrally, many elytra and two parapodia previously removed (kept in container); eyes displaced towards posterior prostomial half; elytra yellowish, without black banding; macrotubercles in two rows, second row barely developed; dorsal cirrophores with basal tubercle barely projected; body 11.5 mm long, 6.5 mm wide, 28 chaetigers). One specimen (UF 217), Apra Harbor, Western Shoals, Southern Face (13°30'00.0" N, 144°48'00.0" E), 9 m, under coral, 15 Apr. 1997, J. Starmer, coll. (slightly bent ventrally; right elytra 6 and 7 removed for observation; elytra yellowish with an ill-defined oblique brownish band; macrotubercles in two rows, first row with larger ones; dorsal cirrophores with basal tubercle globular, well-defined; body 15.5 mm long, 9 mm wide, 29 chaetigers).

Australia. One specimen (UF 1754), Western Australia, Ningaloo Reef, North Black Rock (22°43'38.136" S, 113°38'45.816" E), 27 m, in rubble crevices, 30 May 2010, C. Bagnato & A. Anker, coll. (juvenile; elytra golden, oblique longitudinal bands barely defined; macrotubercles in two rows, larger along first row; dorsal cirrophores with basal tubercle globular; body 12 mm long, 6.5 mm wide, 29 chaetigers).

Diagnosis. *Iphone* with median antenna reduced to nuchal papilla; elytra fimbriate, filaments barely developed, often as long as wide; macrotubercles spine-like up to twice longer than wide, with distal spines, in two rows, first row with macrotubercles slightly

larger than those in other rows; cirriferous segments with dorsal cirrophores with basal tubercle distinct; neurochaetae unidentate.

Description. Holotype (UF 1691), complete, bent ventrally (Fig. 19A); right elytra 1–4 and 6, left elytron 1, and both parapodia of chaetiger 12 removed, left parapodia of chaetigers 17–19 removed for molecular studies; body 16 mm long, 8.5 mm wide, 29 chaetigers. Elytra yellow with brownish oblique wide band, and diffuse pigmentation along posterior elytral region, some elytra with whitish epibionts; notochaetae whitish, neurochaetae golden. Body wall pale, parapodia with large coelomic spaces; venter pale, with adsorbed salts in spread granules, ventral cirrophores pale.

Elytra with fimbriae, variably eroded, restricted to a thin submarginal band along lateral margins in median elytra, continued along posterior margins in posterior elytra. Macrotubercles conical, about twice longer than wide, tips with a single spine; first row with macrotubercles barely longer than those present in second row.

First and second elytra with macrotubercles in one row (Fig. 19B), following elytra with macrotubercles in two rows; larger macrotubercles towards lateral margins, progressively smaller along series (Fig. 19C). Fimbriae delicate, with fine sediment particles, submarginal along lateral in median elytra, continued to posterior region in posterior elytra, fimbriae with a spinous stem, and distal soft tubules, each about as long as fimbria stem, some larger than stems also present.

Prostomium as long as wide, with anterior incision running along half prostomial surface. Anterior lobes projected into ceratophores, blackish, about as long as prostomium and as long as ceratostyles, ceratostyles markedly thinner than ceratophores, tapered. Palps thick, slightly longer than lateral antennae, pale, with longitudinal rows of papillae, right palp with tip tapered, left one mucronate. Eyes black, anterior and posterior eyes displaced posteriorly, almost fused laterally, barely visible dorsally, posterior eyes in posterior prostomial corners. Nuchal papilla pale, rounded, not visible dorsally.

Tentacular segment dorsally reduced, with a few chaetae present; tentacular cirri about as long as palps (observed ventrally). Facial tubercle pale, visible dorsally.

Segments 2–4 directed anteriorly. Second segment visible dorsally, nuchal lappet semicircular, wider than long, completely covering nuchal papilla. Ventral buccal cirri inserted ventrally, three times longer than following ventral cirri, barely projected beyond chaetal tips. From segment 3 one pair of globular dorsal nodules per segment, barely projected dorsally; first pair not connected by transverse ridges. Segments 2–3 with fine neurochaetae, barely swollen subdistally, with a longer region covered by series of transverse denticulations.

Median cirriferous segments (Fig. 19D) with dorsal cirri surpassing chaetal tips, subdistally swollen; dorsal cirrophore smooth, contracted, basal tubercle globose, projected. Cirrostyle subdistally swollen, with papillae along its surface. Notochaetae very abundant, pale to transparent, with series of transverse funnel-shaped spinose rows, tips bare. Neuropodia with neurochaetal lobe posterior margin with papillae. Neurochaetae thin, abundant, basally smooth, subdistally swollen, sometimes with darker core, with many rows of fine denticulations along swollen region, tips falcate, sharp (Fig. 19D, insets).

Anus visible in middorsal areas of last two pairs of elytra.

Variation. The paratype (UF 1704) is a juvenile, complete. Right elytra 1, 6, 7, left elytra 1 and 4, and parapodia of chaetigers 12 (both) and 13 (left) removed, and left parapodia of chaetigers 19, 20 removed for molecular analysis. The pharynx is fully exposed (Fig. 20A); it is conical, with a transparent barely rugose outer layer, and a muscular inner tube (Fig. 20B, C). The pharynx opening has two sets of papillae each with 10 papillae, dorsal and ventral, and a middorsal fleshy tubercle above the middorsal papilla. Jaws are brownish with red tips, each jaw has two accessory denticles, and the dorsal pair is more exposed (Fig. 20D) than the ventral one. Elytra have an oblique, ill-defined black band, and macrotubercles arranged in two rows, with macrotubercles slightly larger in first row (Fig. 24E); fimbriae well developed along lateral and posterior margins, with variable amounts of sediment particles covering the short spines along the stems and distal filaments longer than fimbriae stems (Fig. 20E, insets).

The additional specimens were 11.5–17.0 mm long, 6.5–10.5 mm wide. Elytra have only two rows of macrotubercles and they are progressively smaller posteriorly.

Etymology. The specific name is derived after Dr. Arthur (Art) Anker, in recognition of his long-term involvement in the Marine Biodiversity Expeditions of the University of Florida, Gainesville, through his collecting efforts, including the collection of some specimens used for describing this species. The specific name is a noun in the genitive case (ICZN 1999, Art. 31.1.2).

Remarks. *Iphione ankeri* **sp. n.** resembles *I. fimbriata* de Quatrefages, 1866, and *I. hyndmani* **sp. n.** from Hong Kong because they have fimbriae short (less than 1/10 elytral width) and first row of macrotubercles slightly larger than those present in following rows. However, *I. ankeri* differs from the two other species by having fimbriae barely developed (against well-developed in the others), two rows of macrotubercles (against 3–5 in the others), and dorsal cirrophore with basal tubercle distinct (present in *I. fimbriata*, indistinct in *I. hyndmani*). Further, neurochaetae can separate *I. ankeri* from *I. fimbriata*; in *I. ankeri* they are golden, barely falcate, whereas in *I. fimbriata* neurochaetae are brownish, markedly falcate.

Iphione ankeri is sister to *I. hyndmani* **sp. n.** (see below) in the COI tree (Fig. 36).

Distribution. Known from West Australia and Guam, in shallow reef habitats (1–27 m).

***Iphione corbariae* sp. n.**
urn:lsid:zoobank.org:act:0000
Fig. 21

Type material. **Saya de Malha Bank (Indian Ocean, N off Mauritius).** Holotype (MNHN IA 2021-682), Mission SAYA, RV Agulhas II, Sta. DW 5424 (11°28' S, 62°01' E), 171–150 m, 12 Nov. 2022, S. Hourdez *et al.*, coll.

Diagnosis. *Iphione* with median antenna reduced to nuchal papilla; elytra fimbriate, fimbriae short, globose; macrotubercles cushion-shaped without distal spines, in a single row; cirriferous segments with dorsal cirrophores with basal tubercle projected, tip pale; neurochaetae bidentate; ventral cirrostyles bases blackish.

Description. Holotype (MNHN IA 2021-682) bent ventrally (Fig. 21A), 15 mm long, 10 mm wide, 29 chaetigers; first three right and two left elytra previously removed; right

elytron 6 and left parapodium of chaetiger 12 removed for observation. Elytra exposed areas brownish, protected areas yellowish, notochaetae whitish, neurochaetae yellowish; right palp pale purple, lateral ceratophores brownish, left tentaculophore with black spots (Fig. 21B); venter pale, ventral cirri with cirrostyles base blackish.

Elytra yellowish with 2–3 dark spots, fimbriae minute along lateral margins (Fig. 21C, insets). Macrotubercles in a single row, cushion-shaped (Fig. 21, inset left); a few microtubercles in lateral margins.

Prostomium bent ventrally, oval, twice wider than long, with deep longitudinal depression along anterior prostomial half (Fig. 21B). Anterior lobes projected into ceratophores, brownish, slightly longer than prostomium, ceratostyles lost. Right palp pale purple, bent ventrally, slightly shorter than tentacular cirri. Eyes black, positioned along prostomial margin, anterior and posterior eyes of similar size, separate, with a smaller black spot between them. Nuchal papilla visible dorsally, pale.

Tentacular segment dorsally reduced, with black spots, lower cirrus left, slightly longer than palps, base blackish, chaetae not seen. Facial tubercle blackish, barely visible dorsally.

Segments 2–4 directed anteriorly. Second segment not visible dorsally; nuchal lappet small, semicircular, as long as wide. Ventral buccal cirri inserted ventrally, twice longer than those present in following segments. From segment 3, one pair of small, separate, dorsal nodules per segment, only first pair visible, others covered by elytra. Segments 2–3 with neurochaetae thin, resembling those present in following chaetigers.

Median cirriferous segments (Fig. 21D) with dorsal cirri barely surpassing chaetal tips, slightly swollen subdistally; dorsal cirrophores smooth, basal tubercle of dorsal cirrophore projected, basally blackish, distally pale. Notochaetae abundant, whitish, delicate capillaries with series of transverse funnel-shaped spinose rows, tips bare. Neuropodia with supracicular lobe 2–3 times longer than wide, with small papillae. Neurochaetae abundant, yellowish, basally smooth, subdistally with series of denticles, tips bidentate, many with accessory denticle broken (Fig. 21E). Ventral cirri pale, base of cirrostyle blackish.

Anus not seen.

Etymology. The specific epithet is after Dr. Laure Corbari, a French carcinologist of the Muséum National d'Histoire Naturelle, Paris, in recognition of her achievements in organizing several sampling expeditions, and after her activities as an editor of the series Tropical Deep Sea Benthos. The specific epithet is a noun in the genitive case (ICZN 1999, Art. 31.1.2).

Remarks. *Iphione corbariae* **sp. n.** resembles *I. treadwelli* Pettibone, 1986 described from Hawaii because they are the only species having elytra provided with cushion-shaped macrotubercles, arranged in a single row, and minute fimbriae. The main differences lie in the type of neurochaetae, and pigmentation pattern of some parapodial features. In *I. corbariae* neurochaetae are bidentate, and the basal tubercle of dorsal cirrophores is basally blackish, distally pale, whereas *I. treadwelli* has unidentate neurochaetae, and basal tubercles with blackish tips and pale bases. Further, in *I. corbariae*, the bases of ventral cirrostyles are blackish, whereas they are pale in *I. treadwelli*. Another difference relies in the pigmentation pattern of elytra. In *I. corbariae* median elytra have 2–3 darker

spots each, whereas in *I. treadwelli* no such spots are present, with elytra being rather homogeneously pigmented, either yellowish or blackish.

Distribution. Only known from the type locality, in mixed bottoms at moderate depths (150–171 m).

***Iphione harrisae* sp. n.**
urn:lsid:zoobank.org:act:0000
Figs 22, 36

Type material. French Polynesia, Society Islands, Moorea. Holotype (UF 2170), Afareitu, South of Ferry Pass (17°31'45.732" S, 149°45'42.66" W), 18 m, *Halimeda* sand, 15 Nov. 2010, N. Wilson, coll. COI barcode: **GenBank** PQ423924. One paratype (UF 870), between Temae and Afareaitu (17°30'52.128" S, 149°45'41.76" W), 6–14 m, outer reef slope, under rocks, 23 Oct. 2008, C. Meyer, S. McKeon, J. Moore, S. Fay, & G. Paulay, coll. (juvenile, left parapodia of chaetigers 11–20 removed for molecular analysis; elytra detaching, yellowish, without blackish spots, each with 5–6 rows of macrotubercles; body 5 mm long, 3.5 mm wide, 28 chaetigers).

Diagnosis. *Iphione* with median antenna reduced to nuchal papilla; elytra with margins smooth, non-fimbriate; macrotubercles blunt conical with distal spines, often eroded, in 3–4 rows, progressively larger posteriorly; cirriferous segments with dorsal cirrophores with basal tubercle projected; neurochaetae bidentate.

Description. Holotype (UF 2170), mature male, without some anterior elytra and posterior region (Fig. 22A); left parapodium of chaetiger 12 removed for observing parapodial features, body 12 mm long, 7 mm wide, 21 chaetigers. Elytra yellowish, with macrotubercles arranged in 5–6 rows, without additional dark spots; notochaetae whitish, neurochaetae golden, parapodia with densely packed spermatid masses; midventrally paler than surrounding longitudinal darker bands (Fig. 22B), ventral cirrophores pale.

Elytra without fimbriae; macrotubercles conical, falcate, with a single distal spine, directed middorsally (Fig. 22C), pairs of elytra 10–11 with largest macrotubercles along posterior margin (Fig. 22D). Not dissected to avoid further damage; prostomial and anterior end features unknown.

Median cirriferous segments (Fig. 22E, F) with dorsal cirri surpassing neurochaetal tips, subdistally swollen; dorsal cirrophore smooth, cirrostyle subdistally swollen, papillate; basal tubercle of dorsal cirrophore projected. Notochaetae very abundant, opaque, with series of transverse funnel-shaped spinose rows, tips bare. Neuropodia with neurochaetal lobe blunt, neuracicular lobe with long papillae, longest ones 5–6 times longer than tip width. Neurochaetae abundant, basally smooth, subdistally swollen, especially the lower ones, with many rows of fine denticulations along swollen region, tips falcate, bidentate (Fig. 22G).

Posterior region missing. Spermatids in irregular, densely packed masses in coelom.

Variation. The additional specimen is about half the size of the holotype (5 mm long, 3.5 mm wide), and has the same number of rows of macrotubercles and the same trend in their size, with the largest ones in the posterior row, close to the posterior elytral margin.

Etymology. The specific epithet is derived from Leslie Harris, collection manager of the Allan Hancock Polychaete Collection in the Museum of Natural History of Los Angeles County, California, in recognition of her long-term support of our research activities. The specific name is a noun in the genitive case (ICZN 1999, Art. 31.1.2).

Remarks. *Iphione harrisae* **sp. n.** differs from *I. coriolis* Hanley & Burke, 1991 from the Coral Sea because although both have 5–6 rows of macrotubercles, in *I. harrisae* the larger ones are along the posterior margin, whereas they are progressively smaller in *I. coriolis*. This is a small subtle difference, but they have deeply divergent COI sequences (Fig. 36).

Distribution. French Polynesia, Moorea, from reef and inter-reef sandy bottoms (6–18 m).

***Iphione hourdezi* sp. n.**
urn:lsid:zoobank.org:act:0000
Fig. 23

Type material. New Caledonia. Holotype (MNHN TYPE 000), Cruise SPANBIOS (<http://dx.doi.org/10.17600/18000701>), RV Alis, Sta. CP5289 (21°27' S, 166°12' E), 171–193 m, 29 Jul. 2021, S. Hourdez, coll.

Additional material. Fiji. One specimen (MNHN IA 2023-55), Cruise MUSORSTOM 10, RV Alis, Sta. CP1363 (18°12'23.3964" S, 178°33'0.6156" E), 144–150 m, 15 Aug. 1998 (complete, brownish; right elytra 1–3, 5 and left parapodia of chaetigers 14, 16 removed for observation (kept in container); elytra brownish, with two rows of blunt macrotubercles; cirriferous segments with dorsal cirrophore with basal tubercle projected; neurochaetae almost straight; body 29 mm long, 15 mm wide, 28 chaetigers).

Diagnosis. *Iphione* with median antenna reduced to nuchal papilla; elytra with margins fimbriate, fimbriae minute; macrotubercles blunt conical with distal spines, often eroded, in two rows, first row with macrotubercles markedly larger than those in other rows; cirriferous segments with dorsal cirrophores with basal tubercle projected; neurochaetae acicular, unidentate.

Description. Holotype (MNHN TYPE 000) slightly bent ventrally (Fig. 23A), 26 mm long, 19 mm wide, 29 chaetigers; first 4 pairs of elytra, right elytron 6, and left parapodium of chaetiger 12 removed for observation. Elytra grayish, notochaetae whitish, neurochaetae golden; palps, lateral antennae, and tentacular cirri black; venter pale, ventral cirri pale.

Elytra grayish without black spots, fimbriae short, bent over elytra (Fig. 23C), outer fimbriae short, apparently sessile (Fig. 23C, inset 1), posterior fimbriae pedunculate (Fig. 23C, inset 2). Macrotubercles arranged in two rows, digitate, first row with macrotubercles slightly larger than those present in second row, tips blunt. Microtubercles in two marginal rows, decreasing in size middorsally.

Prostomium bent ventrally, oval, twice wider than long, with deep longitudinal depression along anterior prostomial half (Fig. 23B). Anterior lobes projected into ceratophores, blackish, about twice longer than prostomium, ceratostyles bent ventrally. Palps black, left one longer than antennae and tentacular cirri, right palp in regeneration, short, pale. Eyes black, positioned in posterior prostomial half, anterior and posterior eyes

of similar size, very close to each other laterally. Nuchal papilla not visible dorsally, blackish.

Tentacular segment dorsally reduced, cirri slightly shorter than palps, chaetae not seen. Facial tubercle blackish, visible dorsally.

Segments 2–4 directed anteriorly. Second segment not visible dorsally; nuchal lappet distinct, semicircular, wider than long. Ventral buccal cirri inserted ventrally, about twice longer than those present in following segments. From segment 3, one pair of depressed, separate dorsal nodules per segment, only first pair visible, others covered by elytra. Segments 2–3 with neurochaetae thin, similar to those present in following chaetiers.

Median cirriferous segments (Fig. 23D) with dorsal cirri slightly surpassing chaetal tips, barely swollen subdistally; dorsal cirrophores smooth, basal tubercle projected. Notochaetae abundant, whitish, delicate capillaries with series of transverse funnel-shaped spinose rows, tips bare. Neuropodia with neuracicular lobe 4–5 times longer than wide with a large, globular, subdistal papilla. Neurochaetae acicular, thin, golden, abundant, basally smooth, slightly swollen subdistally, with series of denticulations, tips straight, sharp (Fig. 23E). Ventral cirri pale.

Anus dorsal, positioned between elytral pairs 12 and 13.

Etymology. The specific name is after Dr. Stéphane Hourdez, a deep-sea French ecologist, in recognition of his studies on benthic fauna, and because he collected the holotype of this species. The name is a noun in the genitive case (ICZN 1999, Art. 31.1.2).

Remarks. *Iphione hourdezi* **sp. n.** resembles *I. malifera* Piotrowski, 2014 from the Philippines by having digitate macrotubercles, although elytra in *I. hourdezi* have homogeneous pigmentation, whereas *I. malifera* has elytra with oblique longitudinal black bands. However, *I. hourdezi* differs from this and from any other species in the genus by having thin neurochaetae with straight tips, whereas in all other species neurochaetae are thick, with falcate tips, mostly unidentate, with a few species having bidentate neurochaetae.

Distribution. New Caledonia to Fiji, in mixed bottoms in platform depths (144–193 m).

***Iphione hyndmani* sp. n.**

urn:lsid:zoobank.org:act:0000

Figs 24–26, 36

Iphione muricata: Pettibone 1986: 13, Fig. 4 (*partim*, only USNM 19192; *non* (Savigny in Lamarck, 1818)).

Type material. Hong Kong. Holotype (UF 5695), Port Island (22°30'03.744" N, 114°21'23.22" E), 1 m, patchy coral, rocks, sand, 27 Oct. 2017, G. Paulay & J. Moore, coll. COI barcode: GenBank PQ423938 Paratype (UF 5689), Tung Ping Chau (22°32'33.504" N, 114°26'18.816" E), 1 m, patchy coral, rocks, sand, 25 Oct. 2017, G. Paulay & J. Moore, coll.

Additional material.

Hong Kong. One specimen (AM 19902), Peng Chau, Mirs Bay, southern tip of Hong Kong, 10 m, rocks, 15 Apr. 1986, P.A. Hutchings, coll. (bent ventrally, some elytra previously removed; elytra brownish, oblique longitudinal band barely visible; macrotubercles in two rows, progressively smaller posteriorly; basal tubercle of dorsal cirrophores not projected; body 26 mm long, 14 mm wide, 29 chaetigers). One specimen (AM 19977), Cox Head Rock, 19 Apr. 1986 (bent ventrally; some elytra previously detached; elytra yellowish with oblique longitudinal band barely visible; macrotubercles in two rows, progressively smaller posteriorly; basal tubercle of dorsal cirrophore not projected; body 18 mm long, 11 mm wide, 29 chaetigers). One specimen (AM 20023), Sui Mun (deep pass), off Double Haven, 15 m, rocks, 7 Apr. 1986, P. Hutchings, coll. (bent ventrally; elytra brownish with an oblique longitudinal black band; macrotubercles in two rows, decreasing in size posteriorly; basal tubercle of dorsal cirrophore not projected; body 24 mm long, 10 mm wide, 29 chaetigers). One specimen (AM 20050), Chik Chau, Dragons Head, 15 m, 6 Apr. 1986, P. Hutchings, coll. (bent ventrally; pharynx exposed, jaws with two accessory denticles; elytra brownish with an oblique longitudinal black band; macrotubercles mostly broken, in 3–4 rows progressively smaller posteriorly; basal tubercle of dorsal cirrophore not projected; body 22 mm long, 14 mm wide, 29 chaetigers). One specimen (UF 5839), Shelter Island, patchy coral (22°19'51.6" N, 114°17'34.8" E), 2–5 m, sand bottom with large rocks, 2 Nov. 2017, J. Moore, coll. (bent ventrally; elytra brownish with an oblique longitudinal black band and some dispersed black spots, some epibionts present; macrotubercles in 5–6 rows, progressively smaller posteriorly; cirriferous segments with basal tubercle of dorsal cirrophores not projected; neurochaetae unidentate with masses of filamentous bacteria on their tips; body 23 mm long, 14 mm wide, 29 chaetigers).

Mascarene Islands. One specimen (NMWZ 2001.060.0001), Rodrigues Expedition 2001, Sta. 3RIO, Île aux Fous, 0.5 m, under rocks, no date, P.G. Oliver, coll. (complete; left elytron 3 previously removed, left parapodium of chaetiger 12 removed for observation (kept in container); elytra with abundant epibionts, an ill-defined oblique black band; fimbriae short, present along external margins; macrotubercles in 3–4 rows, progressively smaller posteriorly; cirriferous segments with basal tubercle not projected; body 33 mm long, 16 mm wide, 29 chaetigers).

Australia. Two specimens (AM 199666), Queensland, Kewarra Beach, 23 Sep. 1980, D. Hoese, coll. (smaller specimen bent ventrally, anterior end smashed, larger one markedly bent; some elytra previously detached; elytra yellowish with an oblique longitudinal black band; macrotubercles in 3–4 rows, progressively smaller posteriorly; cirriferous segments with basal tubercle not projected; smaller specimen 10.5 mm long, 6.5 mm wide, 29 chaetigers). Four specimens (NMV F224150), Queensland, Dingo Beach, north of Proserpine (20°05' S, 148°30' E), intertidal, in old shell attached to underside of rocks, 3 Aug. 2009, T.J. Hales, coll. (slightly bent ventrally; elytra dirty yellow to brownish, with oblique dark band in larger specimens; some elytra previously removed; elytra with 3–4 rows of low conical macrotubercles; dorsal cirrophores with basal tubercle not projected; neurochaetae unidentate; body 17–28 mm long, 10.5–16.5 mm wide, 29 chaetigers).

Federated States of Micronesia, Caroline Islands. Two specimens (UF 204), Pohnpei Island, Sokehs Island, Dock at Pier (06°58'58.8" N, 158°10'33.6" E), 1–5 m, reef adjacent to mangrove forest, no date (fixed in 75% ethanol), J. Starmer, coll. (elytra with abundant fine sediment particles and whitish epibionts; dark oblique bands better defined in small specimen (although most elytra detached; prostomium distorted, anterior and posterior eyes in a single row, anterior eyes dorsal); larger specimen with eyes displaced posteriorly, anterior eyes lateral; macrotubercles in three rows; cirriferous segments with

dorsal cirrophore with basal tubercle not projected; body 15–28 mm long, 8–14 mm wide, 29 chaetigers). One specimen (UF 205), Pohnpei Island, Lenger Island, next to Japanese Dock at Clam Hatchery (06°59'24.0" N, 158°13'48.0" E), 2–3 m, reef flat, under rock, 13 Mar. 2003 (fixed in 75% ethanol), J. Starmer, coll. (elytra detaching from body, with fine sediment particles and whitish epibionts; dark oblique bands not visible; eyes unpigmented; macrotubercles in 3–4 rows; cirriferous segments with dorsal cirrophore with basal tubercle not projected; body 26 mm long, 14 mm wide, 29 chaetigers).

Fiji. One specimen (AMNH 1615), Suva, 1920, A.L. Treadwell, coll. (no further data; left parapodia of chaetigers 9, 12, 13, and 7 anterior elytra previously removed (some kept in container); elytra with macrotubercles in three rows, microtubercles approaching elytral margin, not surpassing it; dorsal cirrophore with basal tubercle not projected, smooth; body 28 mm long, 13 mm wide, 29 chaetigers). One specimen (UF 73), Viti Levu Island, Man Friday Resort, 80 km West of Suva, 0–2 m, fringing reef, freely moving on rocks, 2 Feb. 1989, B. Holthuis & G. Paulay, coll. (elytra yellowish with some whitish epibionts, without black marks; macrotubercles in three rows; cirriferous segments with dorsal cirrophore with basal tubercle barely projected; body 12 mm long, 5.5 mm wide, 29 chaetigers). One specimen (USNM 19192), Suva, 1920, A.L. Treadwell, coll. (no further data; dried out, bent ventrally; some elytra examined, macrotubercles in three rows, microtubercles surpassing eroded elytral margin giving a denticulate outlook; dorsal cirrophore with basal tubercle not projected; not measured).

Diagnosis. *Iphione* with median antenna reduced to nuchal papilla (rarely with a full antenna); elytra fimbriate, filaments markedly longer than wide; macrotubercles spine-like up to twice longer than wide, with distal spines, in 3–5 rows, first row with macrotubercles slightly larger than those in other rows; cirriferous segments with dorsal cirrophores with basal tubercle indistinct; neurochaetae unidentate.

Description. Holotype (UF 5695) complete; first three and sixth right elytra, left first four and sixth and seventh elytra removed; left parapodia of chaetigers 13 and 14, and right parapodia of chaetiger 12 removed; body 32 mm long, 14 mm wide, 29 chaetigers. Elytra brownish with an oblique blackish band, and darker posterior margins, some elytra with whitish epibionts (Fig. 24A); notochaetae whitish, neurochaetae golden. Body wall pale, parapodia with large coelomic spaces; venter pale, ventral cirrophores blackish.

Elytra with fimbriae, better developed along median and posterior segments, variably eroded, extended along almost all exposed elytral margin but submarginal along lateral margins, marginal along posterior margins. Macrotubercles conical, largest ones 3–4 times longer than wide, arranged in 3–4 rows, longer towards external lateral elytral areas (Fig. 24C, D).

Second pair of elytra with macrotubercles in 2–3 rows, following elytra with macrotubercles in 3–4 rows, posterior rows irregular; larger macrotubercles towards lateral marginal areas, progressively smaller towards posterior margins, if eroded, making elytral margin denticulate. Fimbriae delicate, short, along lateral and posterior margins, fimbriae with thin spinous stem, and distal soft tubules, each about twice as long as fimbria stem.

Prostomium as long as wide (Fig. 24B), with anterior incision running along all prostomial surface. Anterior lobes projected into ceratophores, blackish, longer than prostomium, and about twice longer than ceratostyles, ceratostyles markedly thinner than ceratophores, tapered. Palps thick, twice longer than lateral antennae, brownish, with

longitudinal rows of papillae, tips mucronate. Eyes black, anterior ones placed behind the medial prostomial region, projected laterally, visible dorsally, posterior eyes in posterior prostomial corners. Nuchal papilla blackish, rounded.

Tentacular segment dorsally reduced, with a few chaetae present; tentacular cirri $2/3$ as long as palps, resembling lateral antennae. Facial tubercle blackish, visible dorsally.

Segments 2–4 directed anteriorly. Second segment visible dorsally, nuchal lappet semicircular, wider than long, not covering nuchal papilla. Ventral buccal cirri inserted ventrally, three times longer than following ventral cirri, projected beyond chaetal tips. From segment 3 one pair of globular dorsal nodules per segment, barely projected dorsally; first pair not connected by transverse ridges. Segments 2–3 with fine neurochaetae, barely swollen subdistally, with a longer region covered by series of transverse denticulations.

Median cirriferous segments (Fig. 24E) with dorsal cirri surpassing chaetal tips, subdistally swollen; dorsal cirrophore smooth, basal tubercle not projected. Cirrostyle subdistally swollen, with papillae along its surface. Notochaetae very abundant, pale to transparent, with series of transverse funnel-shaped spinose rows, tips bare. Neuropodia with neurochaetal lobe posterior margin with small papillae. Neurochaetae thin, abundant, basally smooth, subdistally swollen, sometimes with a pale or dark core, with many rows of fine denticulations along swollen region, tips falcate, sharp (Fig. 24E, insets).

Anus visible in middorsal areas of last two pairs of elytra.

Variation. The paratype (UF 5689) is bent ventrally (Fig. 25A); elytra yellowish with oblique black band and middorsal posterior elytral areas darker; macrotubercles conical, larger laterally, decreasing in size dorsally and posteriorly (Fig. 25B), arranged in 3–4 rows, last row irregular. Cirriferous segments with dorsal cirrophore contracted, not surpassing neurochaetal lobe, ceratostyle papillose, subdistally swollen, surpassing neurochaetal tips (Fig. 25C). Pharynx with smooth surface, with small glandular areas; pharynx opening with two series of globose papillae, 12 on the upper part, 12 in the lower one, and a middorsal muscular lobe behind middorsal papilla (Fig. 25D). Jaws brownish, sharp, each with two accessory denticles. In lateral view, the subdistal reinforcement for adductor muscles is roughly semicircular (Fig. 25E), glandular areas not projected, arranged in roughly parallel series along pharynx.

The additional specimens were 10.5–28.0 mm long, 6.5–16.5 mm wide. The number of rows of macrotubercles is size dependent, with smaller specimens having only two rows.

Etymology. The specific name is derived after Philip Hyndman, husband of Chrissy Piotrowski, in recognition of her long-term love and support of her research activities.

Remarks. *Iphione hyndmani* **sp. n.** resembles *I. fimbriata* de Quatrefages, 1866, reinstated, from the Torres Strait (incl. *I. fustis* Hoagland, 1920 from the Philippines), as redescribed above, by having elytra with macrotubercles progressively smaller posteriorly and arranged in 3–4(5) rows. However, the main difference is in the development of the basal tubercle of the dorsal cirrophore, because in *I. hyndmani* it is barely visible whereas in *I. fimbriata* it is a large projected lobe. Pettibone (1986: 13, Fig. 4A) illustrated one specimen with a very long, thin median antenna, about as long as reaching tips of lateral ceratophores, and that the dorsal cirrophore was granulose or maculate. However, in this

specimen (USNM 19192) a filiform median antenna is present, about as long as to reach the anterior prostomial depression, it has a distinctive ceratophore, $\frac{1}{4}$ as long as ceratostyle (Fig. 26), or about half as long as Pettibone illustrated it, whereas it is missing in all other specimens identified as *I. hyndmani*, where only a small papilla is visible, as usual among all other members of the genus. The apparent granular or pigmented base of dorsal cirrophores (see Pettibone 1986, Fig. 4D), we think it was an interpretation of the inner contents of a dried-out specimen, because the surface is smooth, not granular nor pigmented. Consequently, that specimen (USNM 19192) is herein regarded as belonging to *I. hyndmani*, and we also think that median antennae are extremely rare among *Iphione* species, and this can be regarded as an atavism. Another indication for this is that the other specimen from the same locality (AMNH 1615) does not have the median antenna and completely matches *I. hyndmani*. Nevertheless, it could be that the median antenna is present among *Iphione* species, but being extremely fragile, it becomes detached during manipulation or fixation, and what remains in almost all specimens is the basal knob, and no traces of the median ceratophore have been found after the study of many specimens. This would also imply that there is an abscission zone in the borderline between the basal knob and the bottom of the median ceratophore, such that when it becomes detached, there would be no tissue fragments over the rather smooth, clean basal knob. This happens in lateral antennae but there it is the ceratostyle what becomes lost, and the tips of ceratophores look clean, without tissue fragments. This could be clarified during the study of living specimens, and about their capabilities of regeneration.

Iphione hyndmani is sister to *I. ankeri* **sp. n. (see below)** in the COI tree (Fig. 36).

Distribution. Recorded from the Mascarene Islands east to Micronesia and Fiji, on reefs and in rocky or mixed bottoms in shallow water (0–15 m).

***Iphione readi* sp. n.**

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Figs 1A–C, 27–30, 36

Polynoe muricata: Savigny 1822: 21–22, Pl. 3, Fig. 1 (descr., *partim*).

Eumolpe muricata: de Blainville 1828: 459, Pl. Chétopodes, Homocriciens Aphrodités, Fig. 1 (same figure from Savigny).

Iphione muricata: Kinberg 1856: 383; Kinberg 1858: 8; Baird 1865: 181; de Quatrefages 1866: 266–268; Gravier 1901: 226–231, Textfigs 232–239, Pl. 9, Figs 129–135 (redescr.); Potts 1910: 341; Fauvel 1932: 12–13; Fauvel 1933: 40–41; Fauvel 1935: 285–286; Day 1951: 14; Fauvel 1957: 3; Storch 1967: 148, Pls 1–4; Gibbs 1971: 123 (*partim*); Amoureux 1974: 430; Amoureux *et al.* 1978: 68; Pettibone 1986: 9–16, Figs 1–5 (syn. *partim*, no figures made after Red Sea specimens); Wehe 2006: 62–67, Fig. 8 (*partim*); Goren *et al.* 2017: 134–136, Fig. 2 (*non* Savigny in Lamarck, 1818).

Type material. Red Sea, Saudi Arabia. Holotype (UF 6343), Farasan Islands, Shuma Island (16°39'24.48" N, 41°33'16.92" E), 025 m, 25 Oct. 2014, R. Lasley, J. Moore & D. Uyeno, coll. One paratype (UF 6340), Farasan Islands, Sarad Sarso (16°50'06.00" N, 41°36'48.24" E), 0.25 m, 25 Oct. 2014, D. Uyeno, R. Lasley & J. Moore, coll. (bent ventrally, elytra yellowish, with darker posterior margins and macrotubercles, some with white epibionts; macrotubercles in two rows, first one with largest tubercles; not measured nor dissected to avoid further damage). COI barcode: **GenBank** PQ423939. One paratype (UF 6360), Farasan Islands, Dumsuq Island (16°33'50.76" N, 42°03'30.6" E), 0–25 m, 26

Oct. 2014, R. Lasley, J. Moore & D. Uyeno, coll. (slightly bent ventrally, elytra with barely defined oblique dark bands, and darker areas along middorsal marginal portions, some with calcareous epibionts; elytra with two rows of macrotubercles, first row with largest tubercles; fimbriae often as long as macrotubercles along lateral margins; cirriferous segments with basal tubercle of dorsal cirrophore projected; body 14 mm long, 9.5 mm wide, 29 chaetigers). COI barcode: [GenBank](#) PQ423940.

Additional material.

Red Sea, Gulf of Suez. Four specimens (MNHN A-274 18), Mission Jousseume, 1894 (no further data) (one straight, three specimens bent ventrally; elytra brownish, oblique longitudinal band well-defined, some with calcareous epibionts; macrotubercles in two rows, first row with markedly larger ones; body 15–29 mm long, 10–12 mm wide, 29 chaetigers). One specimen (MNHN A274-16), Mission Dolfuss Egypte, Gulf of Suez, Sta. 17bis (28°14' N, 33°22' E), muddy sand and corals, 22 m, 25 Dec. 1928 (field data after Billard 1933), R.P. Dolfuss, coll. (slightly bent ventrally; elytra brownish without black spots; macrotubercles in two rows, first one with largest macrotubercles; body 19 mm long, 12.5 mm wide, 29 chaetigers). Eleven specimens (MNHN A274-28), Mission Jousseume, Suez, 1894 (no further data; eight specimens bent ventrally; elytra brownish, oblique longitudinal band well-defined in most specimens, some with calcareous epibionts; macrotubercles in two rows, first row with largest ones; body 13.5–23 mm long, 8.0–13.5 mm wide, 29 chaetigers). One specimen (MNHN A894), Mission A. Gruvel-P.G. Moazzo, Suez Bay, Jan. –Feb. 1934, entrance of canal (no further data; bent ventrally, some elytra detached, right parapodia of chaetiger 16 previously removed; elytra brownish, longitudinal bands barely visible; macrotubercles in two rows, first one with largest ones; body 31.5 mm long, 14 mm wide, 29 chaetigers). One specimen (ZMH PE 186), Gulf of Suez, 1914, F. Banarate, coll. (elytra yellowish, with an oblique darker band barely visible, with abundant sediment and epibionts; elytra with two rows of macrotubercles, first row with largest ones; cirriferous segments with basal tubercle of dorsal cirrophore projected; body 25 mm long, 15 mm wide, 29 chaetigers). One specimen (ZMH V8365), Gulf of Suez, Bawmwarth, coll. (no further data; markedly bent ventrally; elytra yellowish without black bands, macrotubercles in two rows, first one with largest macrotubercles; not measured).

Red Sea. Egypt. One specimen (ZMH V6120), Khalij al Jimshan, Hartmeyer, coll. (no further data; elytra brownish with abundant white epibionts; elytra with two rows of macrotubercles, first row with largest ones, sometimes duplicate; body 21 mm long, 13 mm wide, 29 chaetigers).

Red Sea. Saudi Arabia. One specimen (CAS 192038), Red Sea Biodiversity Cruise 2013, Makkah Province, Thuwal, Kaust Beach, intertidal, 15 Mar. 2013, T.M. Gosliner, coll. (complete; two right parapodia dissected for observation, one midbody elytron removed for observing details; body 12.5 mm long, 8 mm wide, 28 chaetigers). One specimen (UF 2847), Thuwal (22°16'26.4" N, 39°03'03.6" E), 2–20 m, seaward reef slope and front of shelf reef, 10 Oct. 2012, M. Berumen & G. Paulay, coll. (bent ventrally; right parapodial and elytral fragments removed for molecular studies; 1 row of macrotubercles; basal tubercle of dorsal cirrophore projected; body 11 mm long, 6.5 mm wide, 29 chaetigers). One specimen (UF 3498), Farasan Islands, Naf Shuma (16°45'10.8" N, 41°36'18.0" E), 1–5 m, silty reef flat to slope, 9 Mar. 2013, A. Anker, P. Norby & G. Paulay, coll. (slightly bent ventrally; oblique brownish longitudinal bands, and posterior elytral margins barely pigmented; left parapodia of chaetigers 13 and 14 removed for observation; body 23 mm long, 12 mm wide, 29 chaetigers). One specimen (UF 3500), Farasan Islands, Mahama Island (16°29'20.4" N, 41°56'38.4" E), 4–17 m, reef rubble, fringing slope, 9 Mar. 2013, A. Anker, P. Norby & G.

Paulay, coll. (elytra brownish with wide oblique blackish bands, and darker posterior elytral margins in posterior segments, many elytra with white epibionts; two rows of macrotubercles; basal tubercle of dorsal cirri clearly projected; body 15 mm long, 8.5 mm wide, 29 chaetigers). One specimen (UF 3505), Farasan Islands, Naf Shuma (16°45'10.8" N, 41°36'18.0" E), 1–5 m, silty reef flat to slope, 9 Mar. 2013, A. Anker, P. Norby & G. Paulay, coll. (slightly bent ventrally; elytra brownish with wide oblique blackish band and darker posterior elytral margins in median and posterior elytra; basal tubercle of dorsal cirrophore barely projected; body 18 mm long, 9 mm wide, 29 chaetigers). One specimen (UF 3514), Farasan Islands, Zahrat Durakah (16°50'09.6" N, 42°18'21.6" E), 4 m, fringing reef slope around sand canal, in rubble, 11 Mar. 2013, A. Anker, P. Norby & G. Paulay, coll. (bent ventrally; elytra brownish with wide oblique longitudinal band; body 17 mm long, 9 mm wide, 29 chaetigers). One specimen (UF 3583), off Thuwal, Abu Shosha Reef (22°12'10.8" N, 39°02'52.8" E), 5 m, sheltered side, 24 Mar. 2013, J. Moore & J. Bouwmeester, coll. (slightly bent ventrally; elytra yellowish with a barely continuous, longitudinal black band; two rows of macrotubercles; basal tubercle of dorsal cirri barely projected; body 11.5 mm long, 7.5 mm wide, 29 chaetigers). One specimen (UF 4488), Amr's Dropoff (25°39'24.5916" N, 36°42'43.4592" E), 3–12 m, silty fringing reef, 1 Feb. 2016, J. Moore, coll. (juvenile; brownish longitudinal bands discontinuous in same elytron, made by darker areas; middorsal elytral margins darker than other areas; some elytra removed for observation; macrotubercles in two rows, first one with largest tubercles; body 17 mm long, 8.5 mm wide, 29 chaetigers). One specimen (UF 4489), Amr's Dropoff (25°39'24.5916" N, 36°42'43.4592" E), 3–12 m, silty fringing reef, 1 Feb. 2016, J. Moore, coll. (juvenile; right elytron 4 and parapodium previously removed, left parapodium of chaetiger 10 removed for observation (kept in container); macrotubercles in two rows, each with a few tubercles, first row with largest tubercles; body 5.5 mm long, 2.5 mm wide, 23 chaetigers; 11 elytral pairs). One specimen (UF 6287), Wasaliyat Island (17°46'58.08" N, 41°26'08.88" E), 0–25 m, patch reef, 17 Oct. 2014, D. Uyeno, R. Lasley & J. Moore, coll. (markedly bent ventrally, not measured to avoid any damage; elytra with discontinuous oblique dark bands, posterior elytral margins darker in posterior elytra; macrotubercles in two rows, first row with tubercles markedly larger than the others). One specimen (UF 6320), Farasan Islands, North Ghorab Island (17°06'30.96" N, 42°04'07.68" E), 5–7 m, fringing reef, silty bottom, 22 Oct. 2014, D. Uyeno, R. Lasley & J. Moore, coll. (elytra yellowish with brown spots forming irregular longitudinal band, some with white epibionts; macrotubercles darker, in two rows, size markedly different; median cirriferous segments with dorsal cirrophore with basal tubercle barely bilobate; body 10.5 mm long, 6 mm wide, 29 chaetigers). One specimen (UF 6338), Farasan Islands, Dhi Dahaya (16°52'22.44" N, 41°26'27.6" E), 0.25 m, 24 Oct. 2014, D. Uyeno, R. Lasley, & J. Moore, coll. (juvenile; left parapodium of chaetiger 14 removed for observation; elytra maculate, dark areas small, spread apart, not forming distinct longitudinal bands; macrotubercles in two rows; basal tubercle indistinct; body 13 mm long, 7.5 mm wide, 29 chaetigers).

Sudan. Six specimens (NHM 1941.4.4.168-172), Sudan Pearl Fisheries Investigations, Dongonab, 1905, C. Crossland, coll. (variably bent; most elytra on site, smaller ones yellowish, larger ones with brownish elytra, oblique longitudinal black band indistinct; left elytra 7 removed from 3 specimens for observation (kept in container), macrotubercles of first row very large; body 9–23 mm long, 6.5–14 mm wide, 29 chaetigers).

Djibouti. Two specimens (MNHN A274-8), Djibouti, 1897, No. 29, M. Coutière, coll. (bent ventrally; elytra brownish, smallest one with a black spot, largest one with an oblique, longitudinal black band; macrotubercles in two rows, first row with largest macrotubercles; body 15–24 mm long, 8–11 mm wide, 29 chaetigers). Four specimens (MNHN A274-11), Mission Gravier, Pingodiu & Météor reefs, 18–20 m, 17 Jan. 1906, C.

Gravier, coll. (dehydrated, one bent ventrally; elytra brownish with a black spot to an oblique longitudinal black band; macrotubercles in two rows, first one with markedly larger macrotubercles; no further dissected; body 10–16 mm long, 4.5–9.0 mm wide, 29 chaetigers). One specimen (MNHN A274-12), Mission Gravier, Île Moucha, Gulf of Tadjourah, coral, 23 Jan. 1904, C. Gravier, coll. (slightly bent ventrally; elytra brownish without black spot; macrotubercles in two rows, first row with markedly larger ones; body 10.5 mm long, 7.5 mm wide, 29 chaetigers). One specimen (MNHN A274-24), Obock, Obock, Mission Jousseume, 1895, M. Jousseume, coll. (body damaged; most elytra detached, some in container; elytra brownish with a darker area over outer elytral half; macrotubercles in two rows, first row with largest macrotubercles; body 19 mm long, 11.5 mm wide, 29 chaetigers). One specimen (MNHN A274-30), Mission Gravier Djibouti, Djibouti Bay, in base of coral, 13 Jan. 1904, C. Gravier, coll. (elytra brownish, outer elytral area darker; macrotubercles in two rows, first row with largest ones; body 17 mm long, 9.5 mm wide, 29 chaetigers). One specimen (MNHN A274-31), Mission Gravier Djibouti, Île Moucha, Gulf of Tadjourah, in rocky shore, 23 Jan. 1904, C. Gravier, coll. (juvenile, markedly bent ventrally; elytra brownish with dispersed black spots; macrotubercles in 1 row, very large and bent dorsally, at least the largest ones; not measured).

Kenya. One specimen (NHM unnumb.), Nyal, Mombasa, under coral boulders, D. McGregor, coll. (no further data; bent ventrally, some elytra detached; elytra yellowish, with two rows of macrotubercles, first row with largest ones; body 16 mm long, 8 mm wide, 29 chaetigers). Two specimens (USNM 97380) Mombasa, off South coast, removed from NHM 1924.6.18.187–191 (Elytra without blackish bands, with two rows of macrotubercles; body 16–33 mm long, 9–14 mm wide, 29 chaetigers; smallest specimen with longer macrotubercles; neurochaetae unidentate).

Tanzania. One specimen (NHM 1937.9.2.44–45), John Murray Expedition, Sta. 111 (05°04'18" S, 39°14'12" E), Agassiz trawl, 73–165 m, 14 Jan. 1934 (juvenile; partially dissected, 9 pairs of elytra, some elytra previously removed; elytra yellowish, with 1–2 fimbriae, and two large macrotubercles, each representing one row, largest macrotubercle towards external margin, additional one close to posterior margin; no further dissections to avoid further damage; body 4 mm long, 2.5 mm wide, 23 chaetigers).

South Africa. One specimen (USNM 81940), Delagoa Bay, near Johaca Island, Jul. 1935, C.J. van der Horst, coll. (all elytra previously removed, and two right parapodia dissected from chaetigers 14 and 15, all kept in container; body 25 mm long, 15 mm wide, 29 chaetigers).

Sri Lanka. Two specimens (NHM 1928.4.26.889/890), Gulf of Manaar (no further data; one markedly bent ventrally; elytra brownish, with 2–3 rows of macrotubercles, first row with the largest ones; less bent specimen 19.5 mm long, 11.5 mm wide, 29 chaetigers).

Andaman Islands. Four specimens (MNHN A399), RV Investigator, Sta. 665, 5 Feb. 1924 (no further data; slightly bent ventrally; elytra golden to brownish, with a wide longitudinal blackish band, most with 2–3 rows of macrotubercles, largest ones lateral in first row; cirriferous parapodia with large basal tubercle to dorsal cirrophore; body 14.5–34 mm long, 8.5–14.0 mm wide, 29 chaetigers). One specimen (NHM 1938.5.7.3), Sta. 665, South Point, Outram Island, no further data (slightly bent ventrally; some elytra previously removed (kept in container), each with two rows of macrotubercles, the first row with largest ones; body 27.5 mm long, 17 mm wide, 29 chaetigers).

Indonesia. One specimen (ZMA V475) Yakarta Bay, Java, C.P.H. Sluiter, coll. (no further data; markedly bent ventrally; elytra brownish, darker along external elytral half; macrotubercles in two rows, first row with macrotubercles markedly larger than those present in second row; cirriferous segments with basal tubercle of dorsal cirrophore projected; not measured). One specimen (ZMH PE 187), Java (no further data; markedly bent ventrally; brownish, elytra without dark bands, and with abundant sediment and epibionts; elytra with two rows of macrotubercles, first row with largest ones, some broken; not measured to avoid further damage).

Hong Kong. One specimen (AM 19943), Breaker Reef, 6 Apr. 1986, P. Hutchings, coll. (juvenile, markedly bent ventrally; elytra yellowish with an oblique longitudinal black band; macrotubercles in two rows, first one with largest ones; not measured). One specimen (AM 20044), Chek Chau, W side of Hong Kong, 5 m, 14 Apr. 1986, P.A. Hutchings, coll. (bent ventrally; elytra with an oblique longitudinal, ill-defined black band; macrotubercles in two rows, first row with largest ones; cirriferous segments with basal tubercle of dorsal cirrophore projected; body 12 mm long, 8 mm wide, 29 chaetigers).

Vietnam. Four specimens (MNHN A398), Bay of Nhatrang. 1931, C. Dawydoff, coll. (no further data; three markedly bent specimens, elytra yellowish to brownish, with a wide, longitudinal black band, and darker posterior margins; each elytron with 1–3 rows of macrotubercles, smallest specimen with a single row; body 9–29 mm long, 4–15 mm wide, 28–29 chaetigers).

Australia. One specimen (AM 17861), Christmas Island, 1980, R. Hicks, coll. (no further data; juvenile, markedly bent ventrally; elytra yellowish, without black spots; macrotubercles in two rows, first one with largest macrotubercles; not measured). One specimen (MAGNT W17), Burford Island, NT, Sta. CP 14, reef flat, under rocks, low subtidal, 13 Oct. 1981, J.R. Hanley, coll. (markedly bent ventrally; all elytra previously detached; elytra brownish with an oblique longitudinal black band; macrotubercles in two rows, some broken, first row with macrotubercles markedly larger than those present in second row; not measured). One specimen (MAGNT W18), Burford Island, NT, Sta. CP 14, reef flat, under rocks, low subtidal, 13 Oct. 1981, J.R. Hanley, coll. (markedly bent ventrally; many elytra previously detached; elytra brownish with an oblique longitudinal black band, and two rows of macrotubercles, many broken, first row with macrotubercles markedly larger than those present in second row; not measured). One specimen (MAGNT W2816), East Point, NT, Sta. EP 11, rock embedded in mud, subtidal, 18 May 1985, J.R. Hanley, coll. (juvenile; elytra brownish, with two rows of macrotubercles, first row with largest ones; body 10 mm long, 7 mm wide, 28 chaetigers). One specimen (MAGNT W2817), East Point, NT, Sta. EP 11, rock embedded in mud, subtidal, 18 May 1985, J.R. Hanley, coll. (juvenile; elytra brownish, with two rows of macrotubercles, first row with largest ones; body 11.5 mm long, 7 mm wide, 29 chaetigers). One specimen (MAGNT W6883), Scorpion Island, WA, Sta. RH 91-55, fringing shore reef, low subtidal, 15 Aug 1991, J.R. Hanley, coll. (bent ventrally; first right elytron detached; elytra with a oblique longitudinal black band, macrotubercles in two rows, many broken, first row with largest macrotubercles; body 12 mm long, 8 mm wide, 29 chaetigers). Five specimens (NHM 1925.1.28.36–40), Christmas Island, no date or depth data, C.W. Andrews, coll. (elytra yellowish to brownish, at least external elytral half, with abundant sediment particles and some epibionts; some elytra previously removed, each with two rows of macrotubercles, first one with macrotubercles markedly larger than those in second row; body 10–23 mm long, 6.5–11.0 mm wide, 29 chaetigers).

Papua New Guinea. One specimen (MNHN IA 2021-686), Papua Niugini Expedition, Sta. PS 31 (5°08.2' S, 145°49.4' E), 10–37 m, 27 Nov. 2012, S. Hourdez *et al.*, coll. (markedly bent ventrally; elytra dirty yellowish, oblique longitudinal black band present; macrotubercles in two rows, first row with tubercles markedly larger than those present in following row; cirriferous segments with basal tubercle of dorsal cirrophore projected; not measured).

Vanuatu. Two specimens (MNHN A274-6), Malekula (Mallicolo), Malampa, Nov. 1894, M. Francois, coll. (tied up, poorly preserved; elytra brownish with a median oval black spot (smaller specimen), or an oblique longitudinal black band; not further dissected; body 17–19 mm long, 9–11 mm wide, 29 chaetigers).

American Samoa. Two specimens (USNM 81937), Tutuila Island, Pago Pago, without further data (body 28–30 mm long, 13–14 mm wide, 29 chaetigers).

Diagnosis. *Iphione* with median antenna reduced to nuchal papilla; elytra fimbriate; macrotubercles spine-like to digitate with distal spines, in 2–3 rows, first row with macrotubercles markedly larger than those in other rows; cirriferous segments with dorsal cirrophores with basal tubercle projected; neurochaetae unidentate.

Description. Holotype (UF 6343) complete, slightly bent ventrally, a few elytra previously detached (in container); body 19.5 mm long, 11 mm wide, 29 chaetigers. Elytra brownish, with oblique longitudinal black bands, darker areas along inner posterior margins, fimbriae with abundant fine calcareous particles, and calcareous epibionts (Fig. 27A); notochaetae whitish, neurochaetae golden. Body wall pale, venter pale.

Elytra with fimbriae (Fig. 27C, inset 2), better developed along lateral margins throughout body, peduncle thin, fimbriae incorporate abundant sediment particles, fimbriae about 5 times longer than wide; macrotubercles digitate, about 3 times longer than wide, arranged in two rows, first one with largest macrotubercles, the largest one usually in the borderline between hyaline and opaque elytral surfaces, bent middorsally (Fig. 27C, inset 1), macrotubercles in irregular second row markedly smaller, digitate; microtubercles along posterior margin, some with long filaments (Fig. 27C, 3).

Prostomium roughly hexagonal (Fig. 27B), wider than long, with anterior incision running along anterior prostomial third. Anterior lobes projected into ceratophores, slightly darker, longer than prostomium, as long as ceratostyles, subdistally swollen, tips tapered. Eyes black, positioned in posterior prostomial half, anterior eyes slightly larger than posterior ones, placed in lateral protuberances, posterior eyes dorsal, in prostomial posterior margins. Palps thick, bent ventrally, twice longer than antennae, with longitudinal rows of papillae, tips tapered, elongate. Nuchal papillae distinct, pear-shaped, under nuchal flap.

Tentacular segment dorsally reduced, without chaetae, tentacular cirri about as long as palps. Facial tubercle visible dorsally, pale.

Segments 2–4 directed anteriorly. Second segment visible dorsally, with a semicircular nuchal lappet, expanded laterally, slightly wider than long, covering nuchal papilla. Ventral buccal segment inserted ventrally, almost three times longer than following cirri, directed ventrally, projected beyond chaetal tips. Dorsal nodules well-developed in segment 3, markedly smaller in segments 4–5.

Median cirriferous segments with dorsal cirri projected beyond chaetal tips; basal tubercle of dorsal cirrophore projected as a single lobe (Fig. 27D). Notochaetae very abundant, dirty white, with series of transverse funnel-shaped spinose rows, tips bare. Neuropodia with neuracicular lobe truncate, with small globular papillae. Neurochaetal lobe with marginal papillae, neurochaetae abundant, basally smooth, subdistally swollen, with many rows of fine denticulations along swollen region, tips barely falcate, unidentate, sharp (Fig. 4D, inset).

Anus dorsal, visible between elytral pairs 12 and 13.

Etymology. The specific epithet is after Dr. Geoffrey Read, editor of *Annelida* in the World Register of Marine Species (WoRMS), in recognition for his long-term editorial efforts for updating the website. The specific epithet is a noun in the genitive case (ICZN 1999, Art. 31.1.2).

Variation. Examined specimens were 4–34 mm long, 2.5–15.0 mm wide. The first row of macrotubercles includes the largest ones, however, their size depends on the number of macrotubercles such that when there are only 3–4, they can be markedly larger than when there are 6–7 (Fig. 1A–C), but even then, they are markedly larger than those present in the following row.

Some specimens (MNHN A 274 18) are bent ventrally, and elytral features were observed in their right elytron 6. The elytra have an oblique longitudinal black band, macrotubercles in two rows but first one had the largest macrotubercles, and the largest macrotubercle is the outermost, usually rising from the borderline between the hyaline and opaque elytral surfaces; the second row is more irregular and its macrotubercles are markedly smaller than those present in first row, although the outermost can be slightly smaller than the largest one, the others are markedly smaller. The filaments of the marginal microtubercles are delicate and are not as long as those present in the neotype.

One Red Sea specimen (CAS 192038) has a longitudinal wide rust-red band along the elytra (Fig. 28A); elytra with fimbriae and a row of very large conical macrotubercles (Fig. 28B), and 1–2 additional ones, size decrement exponential, not gradual, with smaller tubercles along margin (Fig. 28B, insets); cirriferous segments with dorsal cirri markedly surpassing chaetae (Fig. 28C), cirrophore with basal tubercle conical; neurochaetae unidentate, tips falcate.

A juvenile (5.5 mm long) (UF 4489) has cephalic appendages and dorsal cirri tapered, not subdistally swollen, as is the case in larger specimens; elytra transparent with irregular brownish spots (Fig. 29A, B). The elytra have a single row with 2–3 large conical macrotubercles, and fimbriae are very short, 8-shaped structures bordering elytra along their posterior margin (Fig. 29C). The cirriferous segments have dorsal tubercles without basal tubercle (Fig. 29D); neurochaetae falcate, sharp.

Remarks. *Iphione readi* **sp. n.** corresponds to *I. muricata* *sensu* Savigny (1822). *Iphione readi* resembles *I. muricata* (Savigny in Lamarck, 1818) (see above) by having elytra with fimbriae well-developed, and neurochaetae unidentate. These two species differ in the relative size of macrotubercles and in the presence of fimbriae along posterior elytral margins. In *I. readi*, the macrotubercles of the first row are markedly larger than those present in the following row, and the posterior margin has microtubercles with distal spines, whereas *I. muricata* has macrotubercles progressively smaller posteriorly, and the microtubercles along the posterior margin have very few or no spines.

Savigny (1822: 21) indicated that the plate for his *I. muricata* was made after a specimen from the Gulf of Suez. The original figure by Savigny has been simplified (Fig. 30) to illustrate the main diagnostic features. The body is oval, almost completely covered by elytra (Fig. 30A), and cephalic appendages and dorsal cirri are exposed beyond the elytral margins, they are all subdistally swollen. The anterior end was observed from an oblique frontal perspective; palps have distinct rows of papillae, there is no median antenna and only one pair of eyes is visible after the first elytra were removed, leaving the basal elytral plate fixed on elytophores (Fig. 30B). Elytra are areolate and have a thin longitudinal dark band along body, and each elytron has two rows of macrotubercles, those present along the first row are markedly larger than the others, but their arrangement was unclear because it looks like a row with alternating long and short, instead of being shown as arranged in two rows, and lateral margins are fimbriate (Fig. 30C). The pharynx was dissected, as indicated by the collapsed marginal papillae (Fig. 30D), and the jaws have two accessory denticles (Fig. 30E). The cirriferous segments show a dorsal cirrophore with a round, projected basal tubercle (Fig. 30F).

The dissection damaged the specimen that Savigny illustrated, and it appears to have been lost soon after his publication. However, de Quatrefages (1866: 266–268) provided additional information of the specimen, but it was based upon the illustrations, not on the specimen that Savigny had studied and illustrated, though de Quatrefages did not include any illustration. An earlier repetition of the original Savigny's illustration was made by de Blainville (1828: 459), who made slight modifications to the original illustration, because he indicated a wider longitudinal black band. Grube (1870: 281) noted that Savigny's collection was not transferred to the Paris Museum. The specimen that Savigny had illustrated was not found in the Paris collections.

Gravier (1901: 226) studied and illustrated several Red Sea specimens of *I. muricata sensu* Savigny (1822). His close-up of the marginal portion of the elytra (his Pl. 9, Fig. 133) shows the large, finger-shaped, slightly bent macrotubercles and fimbriae. The macrotubercles in the first row are 3–5 times larger than those present in the second row.

Pettibone (1986) did not illustrate specimens from the Red Sea, but used specimens from other localities including type specimens of other species she regarded as junior synonyms. None of her figures show the striking size difference in macrotubercles characterizing *I. readi* **sp. n.** and none may represent this species. Wehe (2008) redescribed the species with Red Sea specimens; he illustrated the larger macrotubercles in the first row.

Although many records for *I. muricata* followed Savigny illustrations, once the presence of fimbriae or the size of macrotubercles were disregarded as diagnostic features, several records of *I. muricata* do not match *I. muricata* (Savigny in Lamarck, 1818), or *I. readi*. For example, Gibson (1886: 150) recorded it from Liverpool, but he noted all scales were lost, which is rarely the case in *Iphione*; it was later shown by Hornell (1891: 224) that this record belonged to *Gattyana cirrhosa* (Pallas, 1766). Potts (1910: 341) noted one of his many specimens was found on a white-brown holothurian in the Addu Atoll, Maldives. Horst (1917b: 65) reported 50 specimens from Indonesia. Pruvot (1930: 3) recorded *I. muricata* from New Caledonia and described and illustrated the elytra as marginally smooth, which is not the case for true *I. muricata*. Monro (1931: 7) recorded the same species from several Southeastern Australian reefs. Fauvel (1932: 12) recorded it from several localities in the Indian Ocean. Day (1934: 25; 1962: 628) recorded *I. muricata* for South Africa and Madagascar, but no diagnosis or illustration were given. Fauvel (1937:

51) recorded *I. muricata* as a senior synonym of *I. hirotai* Izuka, 1912 from Japan, even though the latter has smooth elytral margins. Okuda (1937: 267) reached the same conclusion and recorded it from Koror (or Kororu), Palau Islands. Monro (1939: 168) also disregarded the difference in elytral margins and recorded smooth and papillose specimens under the same name. For his paper on New Caledonian polychaetes, Fauvel (1947: 13) used Schmarda (1861) illustration for his *I. peronea*. Fauvel (1953a: 173) recorded this species for Tahiti without diagnosis or description. Hartman (1966: 175) recorded it from subtidal substrates in Hawaii. The record by Amoureux (1974: 430) from 15 m off Tanikely, Madagascar is challenging to interpret because it was based upon a 4 mm long specimen with 20 pairs of elytra. He indicated he was following Rullier (1972: 34), but the latter indicated there were only 13 pairs of elytra, although the latter recorded one specimen with marginal papillae and five others without them, just as recorded by Pruvot (1930: 4) for New Caledonia. Bailey-Brock & Hartman (1987: 235, Fig. 3.2.4) used Gravier (1901) illustrations, made after Red Sea specimens, for their report on Hawaiian polychaetes. The record by Hanley (1992: 364) for Hong Kong did not include diagnosis or illustrations. This series of records emphasizes the historical confusion regarding the delineation of *I. muricata* (Savigny in Lamarck, 1818).

Distribution. Red Sea, South Africa and east to Samoa, on reefs and rocky or mixed bottoms (0–165 m).

***Iphione richeri* sp. n.**

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Figs 31–33

Iphione muricata: Pettibone 1986: 14–15, Fig. 5 (Bikini Atoll) only Fig. 5, *non* (Savigny in Lamarck, 1818).

Type material. New Caledonia. Holotype (MNHN TYPE POL 0000), Lagons de Nouvelle Calédonie, Campagne 10, Lagon Est, Sta. 724 (21°19.7' S, 165°57.9' E), 36–38 m, medium sand with foraminiferans and *Halimeda*, 12 Aug. 1986, B. Richer de Forges, coll.

Additional material.

Indonesia. One specimen (ZMA V471.11), Irian Jaya, RV Siboga Exped., Stat. 162 (between Loslos and Broken Islands, Salawatti, W coast), 18 m, dredge, sand, shells, 18 Aug. 1899 (data in variation; body 14 mm long, 9.5 mm wide, 29 chaetigers). One specimen (ZMA V471.2), Lesser Sunda Islands, Sapeh Strait, RV Siboga Exped., Sta. 49a (08°23.5' S, 119°04.6' E), 69 m, dredge, coral + shells, 14 Apr. 1899 (juvenile; some elytra and one anterior parapodium previously removed; elytra yellowish with oblique longitudinal brownish band; fimbriae long, discontinuous, in lateral and posterior margins; macrotubercles in two rows, decreasing in size posteriorly; cirriferous segments with basal tubercle of dorsal cirrophores projected; neurochaetae unidentate, upper neurochaetae more straight, median and lower ones slightly falcate; prostomium oval, wider than long, lateral antennae as long as palps, lateral ceratophores twice longer than prostomium, ceratostyles slightly longer than ceratophores; palps with very long papillae, shorter basally, becoming 1/3 as long as palp width in distal third; tentacular cirri slightly longer than palps; eyes not seen; body 13 mm long, 8 mm wide, 29 chaetigers). One specimen (ZMA V471.22), Irian Jaya, RV Siboga Exped., Sta. 273 (Aru Island, Pearl Banks, anchorage off Pulu Jedan), 13 m, trawl, dredge and divers, sand and shells, 23–26 Dec. 1899 (markedly bent ventrally; elytra yellowish with a wide oblique, longitudinal band and

some central spots; macrotubercles in two rows; fimbriae lateral, very long, longest about 1/3 as long as minimal elytral width; not measured).

Australia. One specimen (AM 2935), Great Barrier Reef Expedition 1928–1929, Sta. 14 (14°40'12.0" S, 145°27'00.0" E), off Lizard Island, Queensland (no further data; slightly bent ventrally, some elytra and parapodia previously removed; elytra brownish with long fimbriae, without black spots, variably eroded; macrotubercles small, eroded, in a single row, close to posterior elytral margin; cirriferous segments with basal tubercle of dorsal cirrophores projected; body 15.5 mm long, 9.5 mm wide, 29 chaetigers).

Republic of Palau. One specimen (UF 202), Koror State (07°20'20" N, 134°28'43" E), Lighthouse Basin, 48 m, lagoon bottom, silty sand, 4 Aug. 1995 (fixed in 75% ethanol), J. Starmer, coll.

Diagnosis. *Iphione* with median antenna reduced to nuchal papilla; elytra fimbriate, filaments markedly longer than wide; macrotubercles low conical with distal spines, in 1–2 rows along elytral margins; cirriferous segments with dorsal cirrophores with basal tubercle indistinct; neurochaetae unidentate.

Description. Holotype (MNHN TYPE POL 0000) fixed in ethanol, slightly bent ventrally (Fig. 31A), 14 mm long, 7.5 mm wide, 29 chaetigers; first four pairs of elytra removed for observing anterior end, left elytron 6 and left parapodium of chaetiger 12 removed for observation.

Elytra yellowish with an oblique longitudinal wide blackish band, laterally expanded along posterior elytral region, with a few smaller, irregular black spots, with white epibionts, with very long fimbriae (Fig. 31C). Macrotubercles small, conical, arranged in a single marginal row, conical, projected as small denticles.

Prostomium retracted, oval, wider than long, with a deep longitudinal depression along anterior prostomial half. Anterior lobes projected into ceratophores (Fig. 31B), bent ventrally, wider medially, transparent, slightly longer than prostomium, ceratostyles tapered, slightly shorter than palps. Palps pale, about three times longer than ceratophores. Eyes blackish, positioned in posterior prostomial half, anterior eyes lateral, slightly larger than posterior, marginal eyes. Nuchal papilla visible under nuchal lappet.

Tentacular segment dorsally reduced, cirri slightly shorter than palps, chaetae not seen, probably lost. Facial tubercle pale, visible dorsally.

Segments 2–4 directed anteriorly. Second segment not visible dorsally; nuchal lappet semicircular, as wide as long. Ventral buccal cirri inserted ventrally, 2–3 times longer than following ventral cirri, surpassing chaetal tips. From segment 3, one pair of separate dorsal nodules per segment, markedly larger in segment 3, smaller in segment 4, not visible in segment 5. Segments 2–3 with finer neurochaetae, barely swollen subdistally, with a longer region provided with series of transverse denticulations.

Median cirriferous segments (Fig. 31D) with dorsal cirri not surpassing chaetal tips, cirrostyle tapered, not subdistally swollen; dorsal cirrophores smooth, basal tubercle indistinct (due to rotting of body wall, indicated by transparency). Notochaetae whitish, very abundant, delicate capillaries with series of transverse funnel-shaped spinose rows, tips bare. Neuropodia with neuracicular lobe twice longer than wide, blunt; neurochaetal lobe with small digitate papillae. Neurochaetae golden, thick, abundant, basally smooth,

subdistally swollen, with series of denticulations along swollen region, tips falcate, sharp (Fig. 31E).

Posterior end bent ventrally; anus not seen.

Etymology. The specific epithet is after Dr. Bertrand Richer de Forges, now retired, as a recognition for his long-term collecting efforts in New Caledonia, during one of the cruises he collected the holotype of this species. The specific epithet is a noun in the genitive case (ICZN 1999, Art. 31.1.2).

Variation. A 14 mm long specimen (ZMA V471.11) had elytra brownish without black spots (Fig. 32A). The fimbriae extend along lateral and posterior margins (Fig. 32B), longest filaments are $\frac{1}{4}$ as long as minimal elytral width along body, up to 20 times longer than wide (Fig. 32B, inset); macrotubercles conical, small, in two rows displaced towards posterior margin, first row with macrotubercles slightly longer than those present in second row; microtubercles barely developed. Cirriferous segments with basal tubercle of dorsal cirrophore projected as a single lobe (Fig. 32C). Neuropodia with acicular lobe blunt, with small papillae. Neurochaetal lobe with marginal papillae; neurochaetae abundant, basally smooth, subdistally swollen, with many rows of fine denticulations along swollen region, tips barely falcate, unidentate, sharp (Fig. 32C, inset).

A juvenile specimen (UF 202), fixed in ethanol, is 10 mm long, 6 mm wide, 29 chaetigers, has most elytra detached; left parapodium of chaetiger 12 removed for observation (kept in container). Eyes displaced towards posterior prostomial half, fading off. Elytra yellowish with an oblique brownish band (Fig. 33A). Macrotubercles in 2–3 rows, fimbriae very long, especially along posterior margins, longest ones about half to one-third as long as elytral width (Fig. 33B, C). Parapodia soft; cirriferous segments with dorsal cirrophore with a low, barely defined basal tubercle (Fig. 33D). Notochaetae abundant, white to transparent; neurochaetae golden, unidentate, tips falcate, with 20–30 transverse rows of denticles.

The additional specimens were 13.0–15.5 mm long, 8.0–9.5 mm wide. The macrotubercles are arranged in two rows, and these rows are displaced towards the posterior elytral margin.

Remarks. Some specimens resembling *Iphione richeri* **sp. n.** were included in *I. muricata* (Savigny in Lamarck 1818) by Pettibone (1986). These two species have macrotubercles arranged in 2–3 rows, progressively smaller posteriorly. However, these two species differ on the position of the macrotubercular rows; in *I. richeri* they are displaced towards the posterior margin, whereas in *I. muricata* they extend along the posterior elytral half. Further, *I. richeri* differs from other species provided with short macrotubercles by having very long, thin fimbriae, with longest filaments about $\frac{1}{7}$ as long as elytral minimal width ($\frac{1}{2}$ – $\frac{1}{3}$ as long as elytron width in juveniles) or 25 times longer than wide.

Distribution. From Indonesia and Australia, east to Palau and New Caledonia and Marshall Islands (Pettibone, 1986), in subtidal sandy bottoms (13–69 m).

***Iphione wilsoni* sp. n.**

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Figs 34, 35

Iphione muricata: Hanley & Burke 1991: 39–41, Fig. 11 (*non* (Savigny in Lamarck, 1818)).

Type material. Australia. Holotype (NMV F164310), Western Australia, Ashmore L30 Transect, SS05/2007 Sta. 188 (12°26'42.0" S, 123°36'03.6" E), 95 m, beam trawl, 6 Jul. 2007.

Additional material.

Coral Sea. One specimen (MAGNT W5511), Cruise Corail 2, RV Coriolis, Fairway Atoll (Reef), Sta. RH 88.46 (20°53' S, 161°41' E), 60 m, 20 Aug. 1988, J.R. Hanley, coll.

Indonesia. One specimen (ZMA V471.5), Sulawesi, RV Siboga Exped., Sta. 125 (Siau Island, anchorage off Sawan), 27 m, dredge, townet, Monaco trap, reef-exploration, stones, 18–19 Jul. 1899 (markedly bent ventrally; juvenile; right elytra 3, 6 and 9 removed for observation; elytra yellowish without black spots; macrotubercles in two rows, towards posterior margin, each erect, subcylindrical, brittle, with many spines along stem; no further dissected nor measured to avoid further damage).

Diagnosis. *Iphione* with median antenna reduced to nuchal papilla; elytra with margins smooth, non-fimbriate; macrotubercles cylindrical or tapered, with distal spines, in six or more rows, first row with macrotubercles markedly larger than those in other rows; cirriferous segments with dorsal cirrophores with basal tubercle projected; neurochaetae unidentate.

Description. Holotype (NMV F164310) bent ventrally (Fig. 34A), 22 mm long, 12 mm wide, 29 chaetigers; first four pairs of elytra previously removed; right elytron 6 and left parapodium of chaetiger 12 removed for observation.

Elytra yellowish with an oblique, irregular black band, and darker along posterior margins, almost without calcareous epibionts, without fimbriae (Fig. 34B). Macrotubercles arranged in 5–6 rows, subcylindrical, largest along external margins, markedly larger and bent middorsally, other erect or bent anteriorly, with spiny stems and stellate tips, each with 4–5 spines (Fig. 34C). Macrotubercles with spines more abundant along posterior margins (Fig. 34D).

Prostomium retracted, roughly hexagonal, as long as wide, with a deep longitudinal depression along anterior prostomial half. Anterior lobes projected into ceratophores, blackish, longer than prostomium, ceratostyles lost. Palps pale, three times longer than ceratophores. Eyes blackish, positioned in posterior prostomial half, anterior eyes lateral, $\frac{1}{3}$ – $\frac{1}{2}$ as large as posterior, dorsal eyes. Nuchal papilla not visible.

Tentacular segment dorsally reduced, cirri as long as palps, chaetae not seen, probably lost. Facial tubercle blackish, visible dorsally.

Segments 2–4 directed anteriorly. Second segment not visible dorsally; nuchal lappet hidden below anterior margin of segment 2, semicircular. Ventral buccal cirri inserted ventrally, longer than following ventral cirri, right one lost, left one not surpassing chaetal tips. From segment 3, one pair of depressed, separate dorsal nodules per segment, only first pair visible, the others distorted by body contraction. Segments 2–3 with finer neurochaetae, barely swollen subdistally, with a longer region covered by series of transverse denticulations.

Median cirriferous segments (Fig. 34E) with dorsal cirri slightly surpassing chaetal tips (many cirrostyles lost), resembling tips of tentacular cirri; dorsal cirrophores smooth, basal tubercle projected. Notochaetae whitish, very abundant, delicate capillaries with series of transverse funnel-shaped spinose rows, tips bare. Neuropodia with neuracicular lobe 2–3 times longer than wide, blunt; neurochaetal lobe with small globular papillae. Neurochaetae golden, thick abundant, basally smooth, subdistally swollen, with series of denticulations along swollen region, tips falcate, sharp (Fig. 34F).

Anus dorsal, positioned between elytral pairs 12 and 13.

Etymology. This species is being named after Robin Wilson, a well-known polychaete specialist working in the Museums Victoria Research Institute, Australia, in recognition of his many publications on taxonomy of marine annelids, and by his support for our studies on scaleworms. The specific epithet is a noun in the genitive case (ICZN 1999, Art. 31.1.2).

Variation. A large specimen (MAGNT W5511) has a body rather truncate, instead of being oval, 30 mm long, 18 mm wide, 29 chaetigers. The anterior 7 pairs of elytra, and two left and one right parapodia previously removed (most elytra in container, parapodia lost), right parapodium of chaetiger 12 removed for observation. Elytra yellowish with an oblique longitudinal black band (Fig. 35A, B); macrotubercles subcylindrical, tapered, bent middorsally or anteriorly, smaller ones erect, tips stellate, arranged in 6 rows, progressively smaller posteriorly. Cirriferous segments with basal tubercle of dorsal cirrophores projected (Fig. 35C); dorsal cirrostyles tapered, ventral cirrostyles mucronate; neurochaetal lobe with one long cirriform papillae, if seen in anterior view (Fig. 35D, inset), other papillae globular; neurochaetae unidentate.

Remarks. *Iphione wilsoni* **sp. n.** separates from other species of *Iphione* lacking elytral fimbriae by the type and shape of macrotubercles, and by the type of neurochaetae. In *I. wilsoni* macrotubercles are subcylindrical with tips stellate, whereas they are blunt in the other species, and it has unidentate neurochaetae, whereas they can be bidentate in some other species.

Hanley & Burke (1991: 39) illustrated what they regarded as *I. muricata* (Savigny in Lamarck, 1818). However, the elytra lack fimbriae and are different from *I. muricata* by having thinner, mostly erect macrotubercles, and the additional smaller ones have stellate tips. These specimens were not available but they seem conspecific with *I. wilsoni*.

Distribution. Western Australia through Indonesia to the Coral Sea, in deeper subtidal mixed bottoms (27–95 m).

Concluding remarks

The most useful morphological characters for differentiating *Iphione* species include the eyes (size and position), relative length of palps and lateral antennae, and some elytral and parapodial features.

The highly developed oblique muscles of *Iphione* (Storch 1967) that are responsible for these worms' ability to attach themselves to hard bottoms, together with the intrinsic musculature of cephalic appendages, can impact the shape and length of cephalic appendages as well as the position of eyes. Consequently, size relationships of palps and

antennae and size and position of eyes are too variable to be reliable for separating species. Other scaleworm groups have a stiffer prostomium and their bodies have less developed oblique muscles system, such that the relative shape of prostomium and size and position of eyes can be diagnostic.

The main features of elytra are the fimbriae and macrotubercles. Because fimbriae filaments are elastic, they were regarded as fragile and of little diagnostic relevance. We conclude otherwise; fimbriae are distinctive, even if the filaments are very short, and provide a reliable diagnostic feature. Macrotubercles show two different trends regarding the number of rows per elytron. There are some species where the number of rows is size-dependent, with larger specimens having more rows than smaller ones, as it was shown elsewhere (Piotrowski *et al.* 2024) for *I. ovata* Kinberg, 1856, or as indicated above for *I. fimbriata* de Quatrefages, 1866, and there are other species where the number of rows does not change with body size, such that there can be a single row, like in *I. treadwelli* Pettibone, 1986 or *I. corbariae* **sp. n.**, or two rows as in *I. muricata* (Savigny in Lamarck, 1818), or *I. hourdezi* **sp. n.**

Shapes of macrotubercles are also useful, especially if the impact of erosion that can damage tips and more exposed surfaces, is taken into consideration. Macrotubercles can be conical, digitate, subcylindrical, or cushion-shaped, and useful to separate species. Most species have conical macrotubercles, a few have them digitate (e.g., *I. muricata*), cushion-shaped (*I. treadwelli*), or subcylindrical (*I. wilsoni* **sp. n.**).

The most useful parapodial features are the degree of development of the basal tubercle of dorsal cirrophores, and the shape and type of neurochaetae. The basal tubercle is often projected laterally as a low blunt cone; rarely it is not developed and indistinct. In a few species, pigmented globular glands can be seen in the basal tubercle, distally or basally, and can be diagnostic, although their persistence in preserved specimens deserves to be assessed. When specimens are fixed in ethanol, or placed in the fixative after they are dead, deterioration of body wall muscles can lead them to become transparent, and the basal tubercle can be completely reduced. A comparison with better-preserved specimens from the same locality, can help clarify if the basal tubercle is really indistinct or reduced due to inadequate fixation.

Neurochaetae include diagnostic as well as size-dependent features. Among the latter is the number of transverse rows of denticles along the subdistally swollen region; we have confirmed that these changes depending on the position of chaetae in the chaetal bundle and noted their dependence on body size. Neurochaetae are typically subdistally swollen, but in one species (*I. hourdezi*) they are barely swollen and, although thin, can be regarded as acicular. Neurochaetal tips are also diagnostic; most species have unidentate tips, and a few species have them bidentate.

These characters allowed us to better understand the taxonomy of *Iphione* species, further tested with COI sequence data (Fig. 36). We now recognize 8 described and 9 new species in the genus, and regard *I. peronea* (Schmarda, 1861) as indeterminable, whereas *I. hirotai* Izuka, 1912 from Japan, could not be clarified, and this requires the study of topotype material, which were not available.

The species of *Iphione* can be grouped after some morphological features as follows:

- 1) Elytra fimbriate.
- 1A) Neurochaetae unidentate.

- 1A.1) Macrotubercles arranged in 1(–2) rows: *I. treadwelli* Pettibone, 1986, *I. hourdezi* sp. n.; *I. richeri* sp. n.
- 1A.2) Macrotubercles arranged in 2–3 rows: *I. muricata* (Savigny in Lamarck, 1818); *I. malifera* Piotrowski, 2014; *I. ankeri* sp. n., *I. readi* sp. n.
- 1A.3) Macrotubercles arranged in 3–5 rows: *I. fimbriata* de Quatrefages, 1866, *I. hyndmani* sp. n.
- 1A.4) Macrotubercles arranged in about 10 rows: *I. henshawi* Pettibone, 1986
- 1B) Neurochaetae bidentate: *I. corbariae* sp. n.
- 2) Elytra with smooth margins.
 - 2A) Tips unidentate: *I. ovata* Kinberg, 1856, *I. wilsoni* sp. n.
 - 2B) Tips bidentate: *I. coriolis* Hanley & Burke, 1991; *I. harrisae* sp. n.

Some *Iphione* species have very large distributions. For example, *I. ovata* can be found from the Red Sea to the Eastern Pacific (Piotrowski *et al.* 2024), *I. muricata* and *I. readi* range from the Red Sea to Samoa, and *I. henshawi* thrives from the Red Sea to Hawaii. On the contrary, some other species are only known from a single locality such as *I. hirotai* from Japan, *I. malifera* from the Philippines, and *I. peronea* from Sri Lanka. However, because we ignore the reproductive biology and larval dispersal for all *Iphione* species, we have no means to explain the larger distributional ranges and, likewise, we have no idea about any ecological segregation for those species living in the same area. We wish to encourage our fellow colleagues to undertake some studies on the ecology and reproduction of *Iphione* species.

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Legends for figures

FIGURE 1. *Iphione readi* sp. n. (incl. *I. muricata* sensu Savigny (1822)), non-type specimens, left elytra 7 of non-type specimens (NHM 1941.4.4.168–172), arranged vertically. A. 9 mm long specimen. B. 16 mm long specimen. C. 23 mm long specimen. D. *Iphione muricata* (Savigny in Lamarck, 1818) non-type small specimen (11.5 mm long, MAGNT W2894), elytron 6 (E, F indicate areas enlarged in E and F, and asterisk indicates the enlarged area in G). E. Close-up of macrotubercle (Mt) and fimbriae. F. Same. G. Close-up of microtubercles along posterior margin. Scale bars: A, 0.4 mm; B, D, 0.5 mm; C, 0.8 mm; E, F, 100 μ m; G, 70 μ m.

FIGURE 2. *Iphione ovata* Kinberg, 1856, non-type specimens (2 ECOSUR 0000, Sta. 30, 13 mm long). A) Ventral view. B. Ventral body wall and most muscle bundles removed, oval masses are ovaries. C. Pharynx and gut ventral wall removed (*: enteric caeca). D. Pharynx, upper jaws separated medially. E. Pharynx, lower jaws separated medially (Pa: papilla, Ph: pharynx, St: stomach). Scale bars: A, 1.38 mm; B, 1.43 mm; C, 1.48 mm; D, 0.32 mm; E, 0.27 mm.

FIGURE 3. Pharynx features. A. *Iphione henshawi* Pettibone, 1986, non-type specimen (BPBM R481), anterior end, pharynx exposed, dorsal view. B. Same, ventral view. C. Same, frontal view of pharynx (numbers indicate papillae). D. Same, left lateral view. E. *Iphione muricata* (Savigny in Lamarck, 1818), restricted, non-type specimens (UF 411), smaller specimen (9 mm wide), pharynx, frontal view (numbers indicate upper papillae). F. Another, larger specimen (16 mm wide), pharynx, frontal view (numbers indicate upper papillae). Scale bars: A, B, 1.3 mm; C, 0.9 mm; D, 0.7 mm; E, 0.3 mm; F, 0.6 mm.

FIGURE 4. *Iphione muricata* (Savigny in Lamarck, 1818), restricted. A. Syntype MNHN 334, dorsal view. B. Same, anterior elytron (inset: fimbriae from another elytron). C. Same, median elytron. D. Chaetiger 14, left parapodium, posterior view after removal of notochaetae. E. Same, median neurochaetal tips. F. Syntype MNHN 335, two detached elytra before cleaning. G. Same, median elytron. H. Same, posterior elytron. I. Fimbriae of posterior elytron. J. Chaetiger 12, left parapodium, posterior view, after removal of notochaetae. Scale bars: A, 2 mm; B, 0.7 mm; C, 1 mm; D, 0.4 mm; E, 30 μ m; F, 1.3 mm; G, 1.2 mm; H, 1.6 mm; I, 30 μ m; J, 0.6 mm.

FIGURE 5. *Iphione muricata* (Savigny in Lamarck, 1818), restricted, non-type specimen (CAS 227559). A. Dorsal view, depressed by glass slide. B. Left elytron 7, dorsal view (C–E: sections enlarged in following pictures). C. Close-up of fimbriae. D. Close-up of smaller, marginal spines. E. Close-up of larger, inner spines. F. Chaetiger 12, left parapodium, posterior view, notochaetae partially trimmed off (after Methyl green staining). G. Same, basal neurochaetal tips. Scale bars: A, 2.5 mm; B, 1.5 mm; F, 0.9 mm; G, 0.3 mm.

FIGURE 6. *Iphione muricata* (Savigny in Lamarck, 1818), restricted, non-type specimen (UF 9454), juvenile. A. Dorsal view, after Methyl green staining. B. Right elytron 6, dorsal view (insets: enlarged areas indicated by numbers). C. Chaetiger 12, left parapodium, posterior view after removal of notochaetae. Scale bars: A, 0.8 mm; B, 0.4 mm; C, 0.2 mm.

FIGURE 7. *Iphione fimbriata* de Quatrefages, 1866, reinstated, holotype (MNHN POLY TYPE 325). A. Anterior region, dorsal view. B. Left elytron 7, after brushing off sediment, dorsal view (inset: close up of dirty to clean fimbriae). C. Chaetiger 16, left parapodium, posterior view. D. Chaetiger 12, left parapodium, after removal of notochaetae and Methyl

green stain. E. Same, upper notochaetae. F. Same, lower neurochaetae. Scale bars: A, 1.7 mm; B, 1 mm; C, 0.6 mm; D, 0.5 mm; E, 170 μ m; F, 200 μ m.

FIGURE 8. *Iphione fimbriata* de Quatrefages, 1866, reinstated, paratype of *I. fustis* Hoagland, 1920 (USNM 18969). A. Anterior end, dorsal view, after Methyl green staining. B. Anterior elytra, above: right elytron from chaetiger 2; below: left elytron from chaetiger 4. C. Left elytron from median chaetiger, dorsal view (insets: fimbriae, and smaller marginal spines). D. Chaetiger 14, left parapodium, posterior view after Methyl green staining. E. Same, upper and medial neurochaetae. F. Same, medial and lower neurochaetae. Scale bars: A, 1.1 mm, B, 1 mm; C, 2 mm; D, 0.6 mm; E, 100 μ m; F, 80 μ m.

FIGURE 9. *Iphione fimbriata* de Quatrefages, 1866, reinstated, paratype of *I. fustis* Hoagland, 1920 paratype (USNM 18968), elytra previously removed, seen from above. A. Second right elytron. B. Third right elytron. C. Fourth right elytron. D. Fifth left elytron. E. Sixth left elytron. F. Non-type specimen (USNM 81972), anterior end, dorsal view. G. Another specimen from same lot, pharynx previously dissected, seen from inside, depressed by glass slide. Scale bars: A, 0.7 mm; B, G, 0.8 mm; C, 1.1 mm; D, E, 0.6 mm, F, 1.3 mm.

FIGURE 10. *Iphione henshawi* Pettibone, 1986, paratype (USNM 5439). A. Anterior end, dorsal view. B. First elytron, dorsal view (inset: close-up of fimbriae). C. Right anterior elytron, with some calcareous epibionts. D. Left posterior elytron (inset: close-up of macrotubercles and spines). E. Cirriferous right parapodium, posterior view. F. Same, neurochaetae of mid-bundle. G. Same, neurochaetae of lower bundle. Scale bars: A, 1.8 mm; B, C, 1.4 mm; D, 2.6 mm; E, 1.1 mm; F, G, 0.7 mm.

FIGURE 11. *Iphione henshawi* Pettibone, 1986, non-type specimen (BPBM R481). A. Anterior end, dorsal view (elytra 1–3 removed). B. Left elytra 1–3, dorsal view. C. Elytron 3, close-up of fimbriae, some macrotubercles in the lower area. D. Same, close-up of macrotubercles. E. Cirriferous left parapodium of median segment, posterior view. Scale bars: A, 0.8 mm; B, 1.4 mm; C, D, 0.3 mm; E, 0.5 mm.

FIGURE 12. *Iphione treadwelli* Pettibone, 1986, holotype (USNM 5435). A. Right lateral view (head points to the right). B. Same, anterior region, after Methyl green staining. C. Previously detached median left chaetiger. D. Chaetiger 12, left parapodium, posterior view, after Shirlastain-A staining (inset: upper neurochaetae tips). Scale bars: A, 0.8 mm; B, C, 0.4 mm; D, 150 μ m.

FIGURE 13. *Iphione treadwelli* Pettibone, 1986, paratype (USNM 81934). A. Dorsal view. B. Anterior end, dorsal view. C. Left median elytron, dorsal view. D. Same, marginal macrotubercle and fimbriae. E. Same, fimbriae. Scale bars: A, 0.7 mm; B, 0.4 mm; C, 0.2 mm; D, 0.1 mm; E, 50 μ m.

FIGURE 14. *Iphione treadwelli* Pettibone, 1986, non-type specimen (ECOSUR). A. Dorsal view. B. Right elytron 6, dorsal view (asterisks indicate enlarged areas). C. Same, one macrotubercle. D. Same, outer fimbriae. E. Left parapodium of chaetiger 12, posterior view (inset: close-up of basal tubercle showing darker glandular area). F. Same, upper neurochaetae. Scale bars: A, 0.9 mm; B, 0.6 mm; C, 140 μ m; D, 30 μ m; E, 0.2 mm; F, 50 μ m.

FIGURE 15. *Iphione coriolis* Hanley & Burke, 1991, holotype (MNHN TYPE 574). A. Anterior end, dorsal view. B. Right elytron from median chaetiger. C. Left elytron from postmedian chaetiger. D. Chaetiger 12, right parapodium, posterior view. Scale bars: A, B, 0.4 mm; C, 0.5 mm; D, 0.2 mm.

FIGURE 16. *Iphione coriolis* Hanley & Burke, 1991, non-type specimen (UF 5450). A. Dorsal view. B. Left, elytron 6, dorsal view. C. Left, elytron 10, dorsal view. D. Chaetiger 12, left parapodium, posterior view (notochaetae removed). E. Same, tips of upper neurochaetae. Scale bars: A, 1.4 mm; B, 0.8 mm; C, 0.6 mm; D, 0.3 mm; E, 50 μ m.

FIGURE 17. *Iphione coriolis* Hanley & Burke, 1991, non-type specimen (UF 5449). A. Dorsal view (asterisks indicate largest macrotubercles in posterior elytra). B. Ventral view (asterisks indicate same as above). C. Left elytron 9, posterior and external margins. D. Left elytron 10 (previously detached), posterior and external margins. E. Chaetiger 12, left parapodium, posterior view. F. Same, anterior view after removing most notochaetae, neuracicular lobe showing long papillae (Ne: neurochaetae, Pa: papilla). G. Upper and lower neurochaetae showing bidentate tips. Scale bars: A, B, 1 mm; C, 0.6 mm; D, 0.5 mm; E, 0.3 mm, F, 40 μ m, G, 100 μ m (left), 40 μ m (right).

FIGURE 18. *Iphione malifera* Piotrowski, 2014, holotype (CAS 187234). A. Dorsal view. B. Chaetiger 14, left parapodium, posterior view (after Methyl green staining). C. Same, lower and middle neurochaetae. Scale bars: A, 2 mm; B, 0.4 mm; C, 110 μ m.

FIGURE 19. *Iphione ankeri* **sp. n.**, holotype (UF 1691). A. Dorsal view. B. Right elytra 1 and 2, dorsal view. C. Right elytron 6, dorsal view. D. Chaetiger 12, left parapodium, posterior view (insets: upper and lower neurochaetae). Scale bars: A, B, 1 mm; C, 0.5 mm; D, 0.2 mm.

FIGURE 20. *Iphione ankeri* **sp. n.**, paratype (UF 1704). A. Dorsal view. B. Pharynx, dorsal view. C. Pharynx, ventral view. D. Pharynx, oblique frontal view. E. Right elytron 7, seen from above (asterisks indicate enlarged areas inserted). Scale bars: A, 1.4 mm; B, C, 0.6 mm; D, 0.4 mm; E, 0.5 mm.

FIGURE 21. *Iphione corbariae* **sp. n.**, holotype (MNHN IA 2021-682). A. Dorsal view. B. Anterior end, dorsal view. C. Right elytron 6, dorsal view (insets: macrotubercle indicated by an asterisk, and lateral fimbriae). D. Chaetiger 12, left parapodium, posterior view. E. Same, tips of median and upper neurochaetae. Scale bars: A, 1.4 mm; B, 0.6 mm; C, 1 mm; D, 0.3 mm; E, 40 μ m.

FIGURE 22. *Iphione harrisae* **sp. n.**, holotype (UF 2170). A. Dorsal view. B. Ventral view. C. Left elytron 6. D. Left elytron 10. E. Chaetiger 14, left parapodium, posterior view. F. Same, notochaetal bundle removed. G. Same, tips of neurochaetae. Scale bars: A, B, 1.3 mm; C, 0.6 mm; D, 0.5 mm; E, F, 0.3 mm; G, 60 μ m.

FIGURE 23. *Iphione hourdezi* **sp. n.**, holotype (MNHN TYPE 000). A. Dorsal view. B. Anterior end, dorsal view after removal of elytral pairs 1–4. C. Right elytron 6, dorsal view (insets: 1, lateral fimbria; 2, posterior fimbria). D. Chaetiger 12, left parapodium, posterior view after removal of notochaetae (inset: ventral cirri and basal papillae). E. Same, upper, middle and lower neurochaetal tips. Scale bars: A, 2.9 mm; B, 0.9 mm; C, 1.4 mm; D, 1.2 mm; E, 170 μ m.

FIGURE 24. *Iphione hyndmani* **sp. n.**, holotype (UF 5695). A. Anterior end, dorsal view after removal of some elytra. B. Same, close-up of prostomium and appendages. C. Right elytron 2 (above), and left elytron 4, dorsal view. D. Left elytron 6, dorsal view. E. Chaetiger 14, left parapodium, posterior view after removal of notochaetae and Methyl green staining (insets: above, upper neurochaetae; below, lower neurochaetae). Scale bars: A, 2 mm; B, 1.1 mm; C, 1 mm; D, 0.9 mm; E, 0.6 mm.

FIGURE 25. *Iphione hyndmani* **sp. n.**, paratype (UF 5689). A. Dorsal view. B. Sixth right elytron, dorsal view. C. Chaetiger 12, right parapodium, posterior view (notochaetae removed) after Methyl green staining (AMGS). D. Pharynx, frontal view (AMGS). E. Same, right lateral view (AMGS). Scale bars: A, 1.2 mm; B, D, 0.5 mm; C, 0.2 mm; E, 0.6 mm.

FIGURE 26. *Iphione hyndmani* **sp. n.**, non-type specimen (USNM 19192). A. Anterior region, dorsal view, after Shirlastain-A. B. Close-up of prostomium. Scale bars: A, 0.8 mm; B, 0.2 mm.

FIGURE 27. *Iphione readi* **sp. n.** (incl. *I. muricata sensu* Savigny (1822)) holotype (UF 6343). A. Dorsal view. B. Anterior end, dorsal view, after Shirlastain-A. C. Left elytron 6, insets indicated by number (1, macrotubercle; 2, smallest fimbria; 3, microtubercle). D. Chaetiger 12, left parapodium, posterior view after removal of notochaetae (inset: close up of upper neurochaetal tips). Scale bars: A, 2 mm; B, D, 0.5 mm; C, 1.2 mm.

FIGURE 28. *Iphione readi* **sp. n.** (incl. *I. muricata sensu* Savigny (1822)), non-type specimen (CAS 192038). A. Dorsal view. B. Left elytron 6, seen from above (insets, from left to right: fimbriae, large macrotubercle, marginal tubercles). C. Chaetiger 12, left parapodium, posterior view, after Methyl green staining (inset: median neurochaetae). Scale bars: A, 1 mm; B, 0.7 mm; C, 0.3 mm.

FIGURE 29. *Iphione readi* **sp. n.** (Incl. *I. muricata sensu* Savigny (1822)), non-type juvenile specimen (UF 4489). A. Dorsal view. B. Same, after Methyl green staining. C. Right elytron 4, inner margin slightly bent. D. Chaetiger 10, left parapodium, posterior view. Scale bars: A, B, 0.6 mm; C, 0.4 mm; D, 0.1 mm.

FIGURE 30. *Iphione readi* **sp. n.** (Incl. *I. muricata sensu* Savigny (1822)), original illustrations after explanation by Audouin (1825: 66). A. Dorsal view. B. Anterior end, oblique frontal view. C. Median elytron, schematic. D. Pharynx with jaws and papillae, lateral view. E. Jaws in lateral, frontal and posterior views. F. Median cirriferous chaetiger, right parapodium, posterior view (Abbreviations: LA, lateral antennae; Pa, palp; TC, tentacular cirri; VC2, ventral cirrus segment 2; 3, segment 3).

FIGURE 31. *Iphione richeri* **sp. n.**, holotype (MNHN TYPE 000). A. Dorsal view, last segments bent ventrally. B. Anterior end, after Shirlastain-A staining. C. Left elytron 6, dorsal view. D. Chaetiger 12, left parapodium, posterior view. E. Same, upper and middle neurochaetal tips. Scale bars: A, 1.3 mm; B, 0.5 mm; C, 0.7 mm; D, 0.3 mm; E, 100 μ m.

FIGURE 32. *Iphione richeri* **sp. n.**, non-type specimen (ZMA V471.11). A. Bent ventrally, dorsal view, left elytron 6 and right elytra 6 and 7 removed. B. Right elytron 6, frontal view (inset: largest fimbriae). C. Chaetiger 12, left parapodium, posterior view (inset: upper neurochaetal tips). Scale bars: A, 1.1 mm; B, 0.7 mm, C, 0.3 mm.

FIGURE 33. *Iphione richeri* **sp. n.**, non-type specimen (UF 202). A. Dorsal view after Methyl green staining. B. Right elytron 6, dorsal view. C. Right elytron 7, dorsal view. D. Chaetiger 12, left parapodium, anterior view, notochaetae removed. Scale bars: A, 0.6 mm; B, C, 0.7 mm; D, 0.2 mm.

FIGURE 34. *Iphione wilsoni* **sp. n.**, holotype (NMV F164319). A. Dorsal view. B. Right elytron 6, dorsal view. C. Same, close-up of external margin after Shirlastain-A. D. Another elytron, transverse section across central macrotubercles region. E. Chaetiger 12, left parapodium, posterior view after removal of notochaetae. F. Same, neurochaetal tips. Scale bars: A, 2.7 mm; B, 0.8 mm; C, E, 0.4 mm; D, 150 μ m; F, 130 μ m.

FIGURE 35. *Iphione wilsoni* **sp. n.**, non-type specimen (MAGNT w5511). A. Anterior left elytron. B. Median left elytron. C. Chaetiger 12, right parapodium, posterior view (after Methyl green staining). D. Same, anterior view (inset: tip of neuracicular lobe). Scale bars: A, 1.1 mm; B, 1.2 mm; C, 0.7 mm; D, 0.5 mm.

FIGURE 36. Maximum Likelihood phylogeny of *Iphione* species with localities and catalog numbers. Numbers above branches are bootstrap support (>70 only) (PNG: Papua New Guinea) (modified after Piotrowski *et al.* 2024).

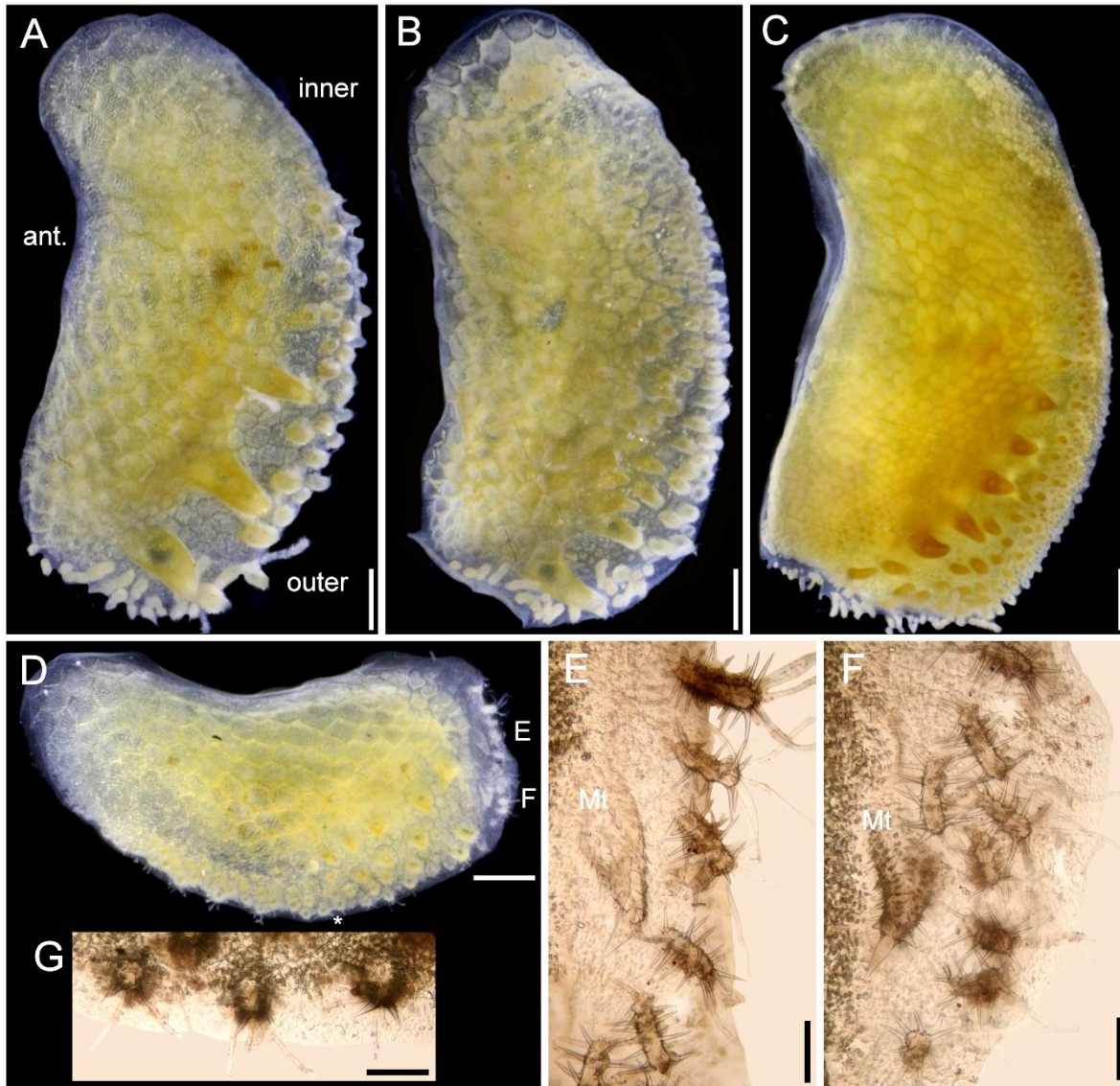


FIGURE 1. *Iphione readi* **sp. n.** (incl. *I. muricata* *sensu* Savigny (1822)), non-type specimens, left elytra 7 of non-type specimens (NHM 1941.4.4.168–172), arranged vertically. A. 9 mm long specimen. B. 16 mm long specimen. C. 23 mm long specimen. D. *Iphione muricata* (Savigny in Lamarck, 1818) non-type small specimen (11.5 mm long, MAGNT W2894), elytron 6 (E, F indicate areas enlarged in E and F, and asterisk indicates the enlarged area in G). E. Close-up of macrotubercle (Mt) and fimbriae. F. Same. G. Close-up of microtubercles along posterior margin. Scale bars: A, 0.4 mm; B, D, 0.5 mm; C, 0.8 mm; E, F, 100 μ m; G, 70 μ m.

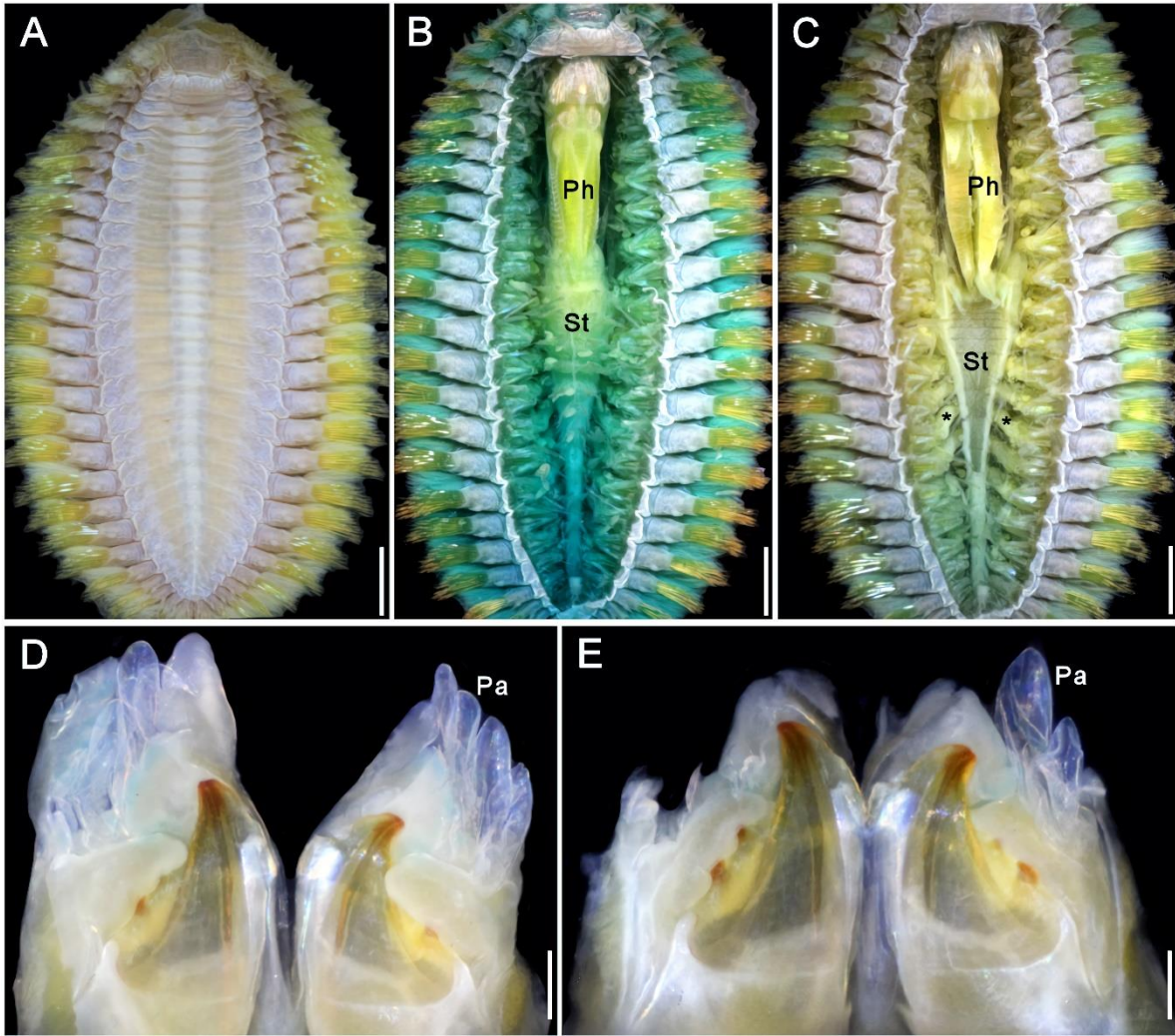


FIGURE 2. *Iphione ovata* Kinberg, 1856, non-type specimens (2 ECOSUR 0000, Sta. 30, 13 mm long). A) Ventral view. B. Ventral body wall and most muscle bundles removed, oval masses are ovaries. C. Pharynx and gut ventral wall removed (*: enteric caeca). D. Pharynx, upper jaws separated medially. E. Pharynx, lower jaws separated medially (Pa: papilla, Ph: pharynx, St: stomach). Scale bars: A, 1.38 mm; B, 1.43 mm; C, 1.48 mm; D, 0.32 mm; E, 0.27 mm.

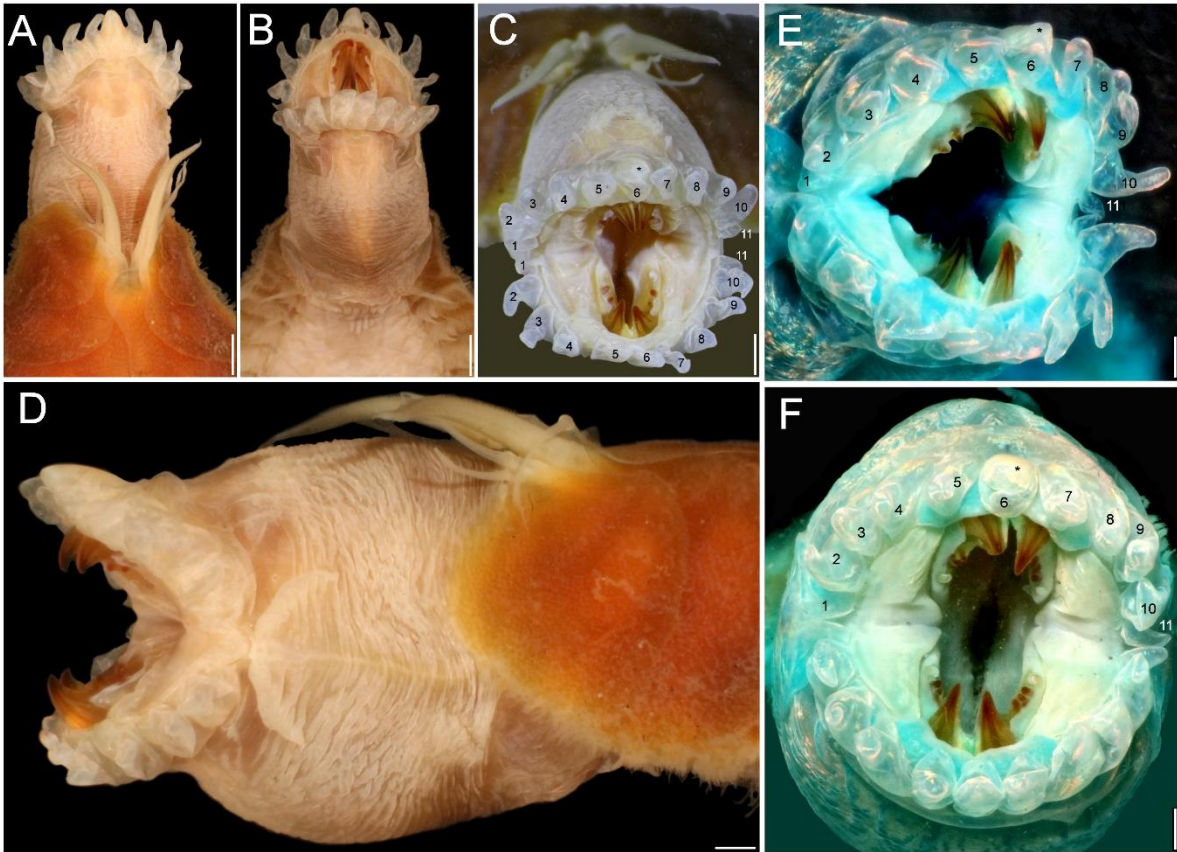


FIGURE 3. Pharynx features. A. *Iphione henshawi* Pettibone, 1986, non-type specimen (BPBM R481), anterior end, pharynx exposed, dorsal view. B. Same, ventral view. C. Same, frontal view of pharynx (numbers indicate papillae). D. Same, left lateral view. E. *Iphione muricata* (Savigny in Lamarck, 1818), restricted, non-type specimens (UF 411), smaller specimen (9 mm wide), pharynx, frontal view (numbers indicate upper papillae). F. Another, larger specimen (16 mm wide), pharynx, frontal view (numbers indicate upper papillae). Scale bars: A, B, 1.3 mm; C, 0.9 mm; D, 0.7 mm; E, 0.3 mm; F, 0.6 mm.

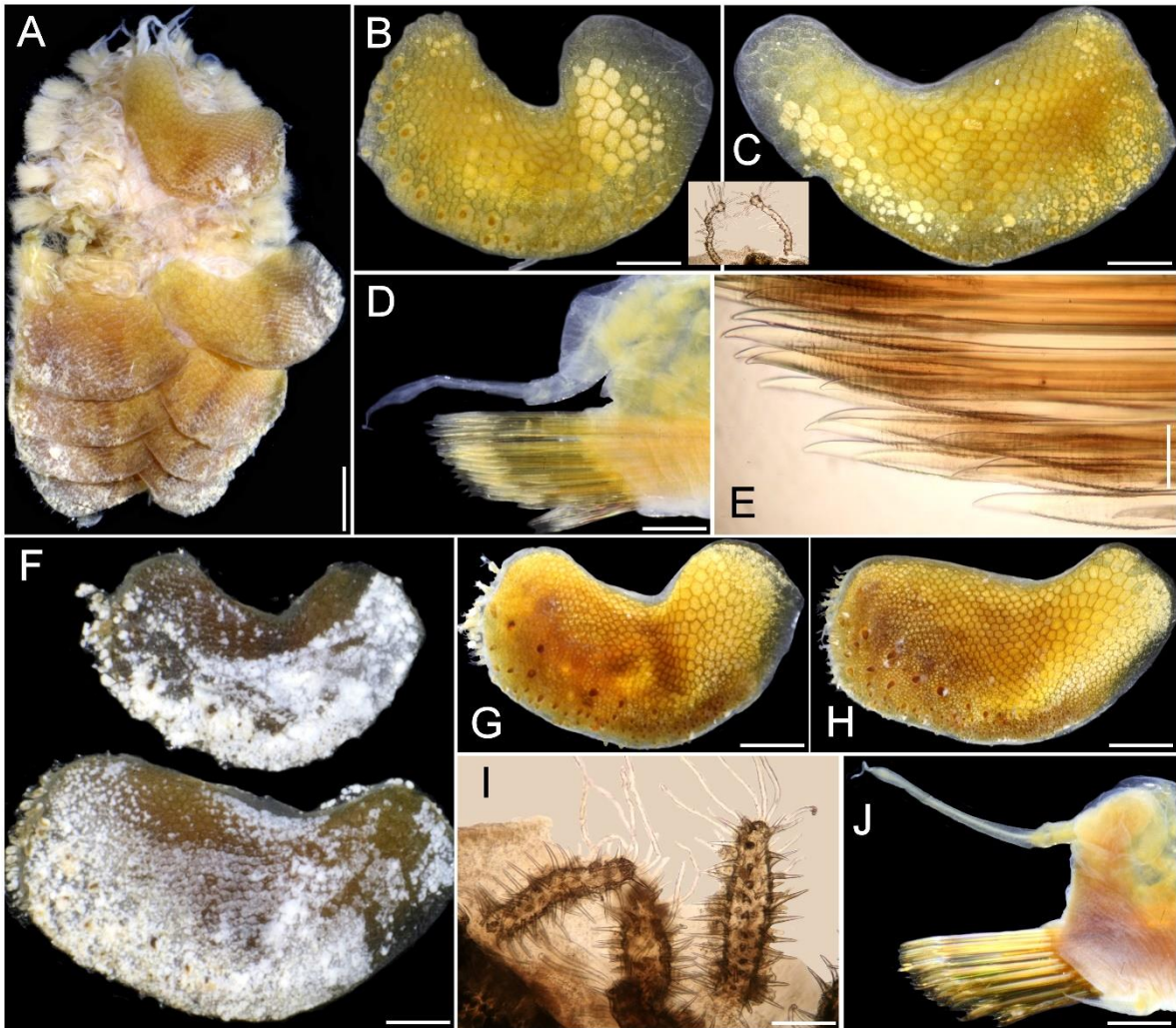


FIGURE 4. *Iphione muricata* (Savigny in Lamarck, 1818), restricted. A. Syntype MNHN 334, dorsal view. B. Same, anterior elytron (inset: fimbriae from another elytron). C. Same, median elytron. D. Chaetiger 14, left parapodium, posterior view after removal of notochaetae. E. Same, median neurochaetal tips. F. Syntype MNHN 335, two detached elytra before cleaning. G. Same, median elytron. H. Same, posterior elytron. I. Fimbriae of posterior elytron. J. Chaetiger 12, left parapodium, posterior view, after removal of notochaetae. Scale bars: A, 2 mm; B, 0.7 mm; C, 1 mm; D, 0.4 mm; E, 30 µm; F, 1.3 mm; G, 1.2 mm; H, 1.6 mm; I, 30 µm; J, 0.6 mm.

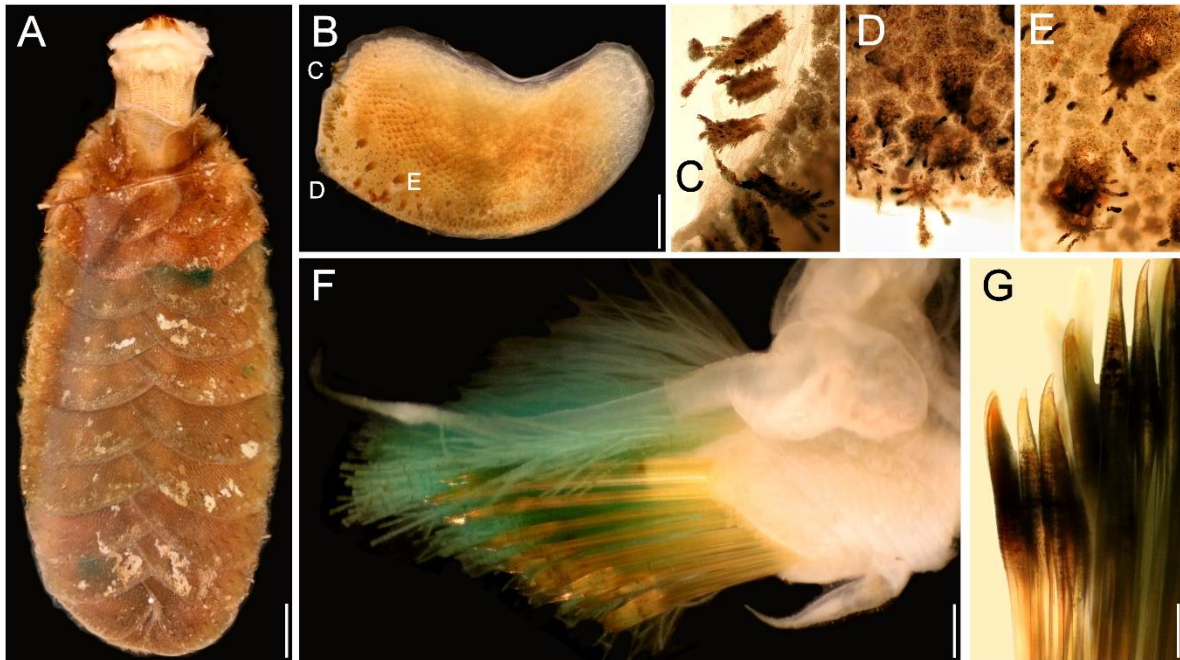


FIGURE 5. *Iphione muricata* (Savigny in Lamarck, 1818), restricted, non-type specimen (CAS 227559). A. Dorsal view, depressed by glass slide. B. Left elytron 7, dorsal view (C–E: sections enlarged in following pictures). C. Close-up of fimbriae. D. Close-up of smaller, marginal spines. E. Close-up of larger, inner spines. F. Chaetiger 12, left parapodium, posterior view, notochaetae partially trimmed off (after Methyl green staining). G. Same, basal neurochaetal tips. Scale bars: A, 2.5 mm; B, 1.5 mm; F, 0.9 mm; G, 0.3 mm.

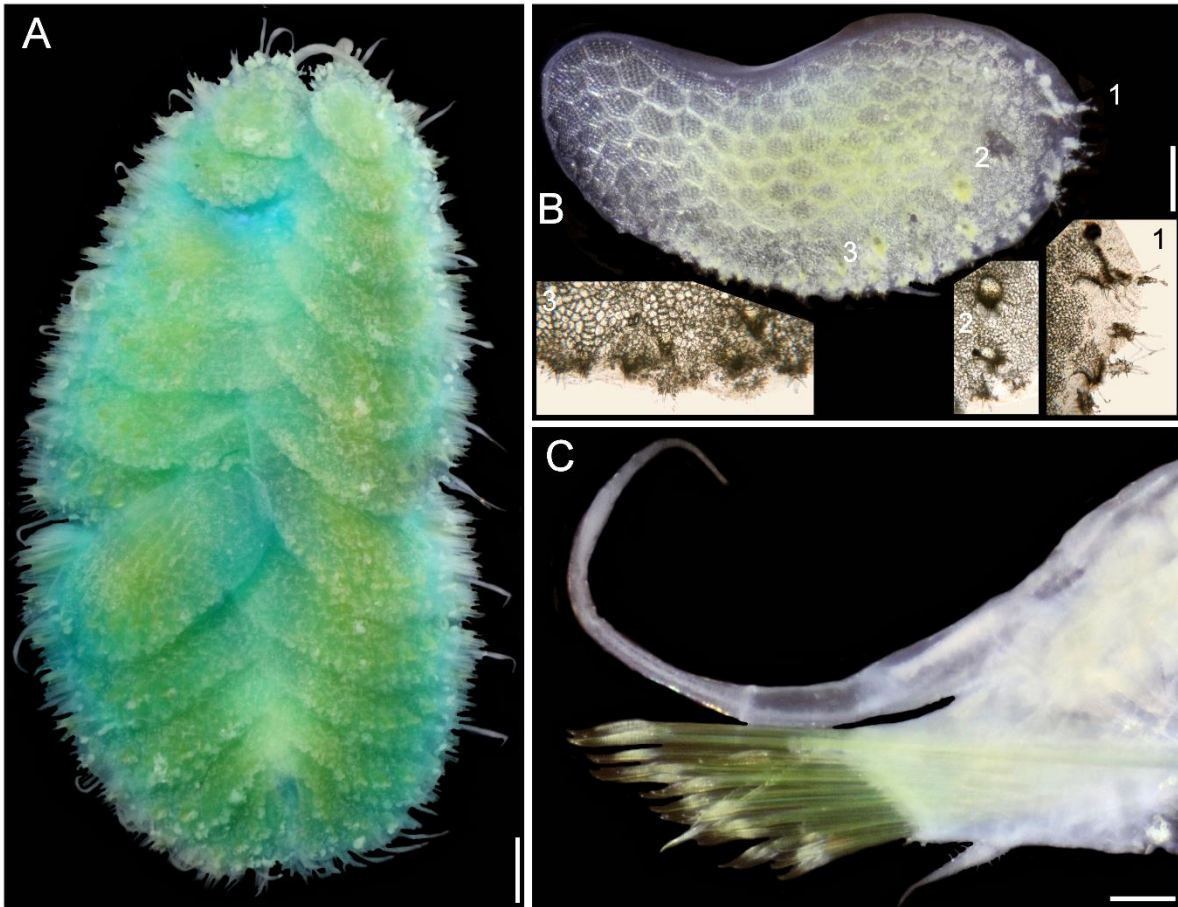


FIGURE 6. *Iphione muricata* (Savigny in Lamarck, 1818), restricted, non-type specimen (UF 9454), juvenile. A. Dorsal view, after Methyl green staining. B. Right elytron 6, dorsal view (insets: enlarged areas indicated by numbers). C. Chaetiger 12, left parapodium, posterior view after removal of notochaetae. Scale bars: A, 0.8 mm; B, 0.4 mm; C, 0.2 mm.

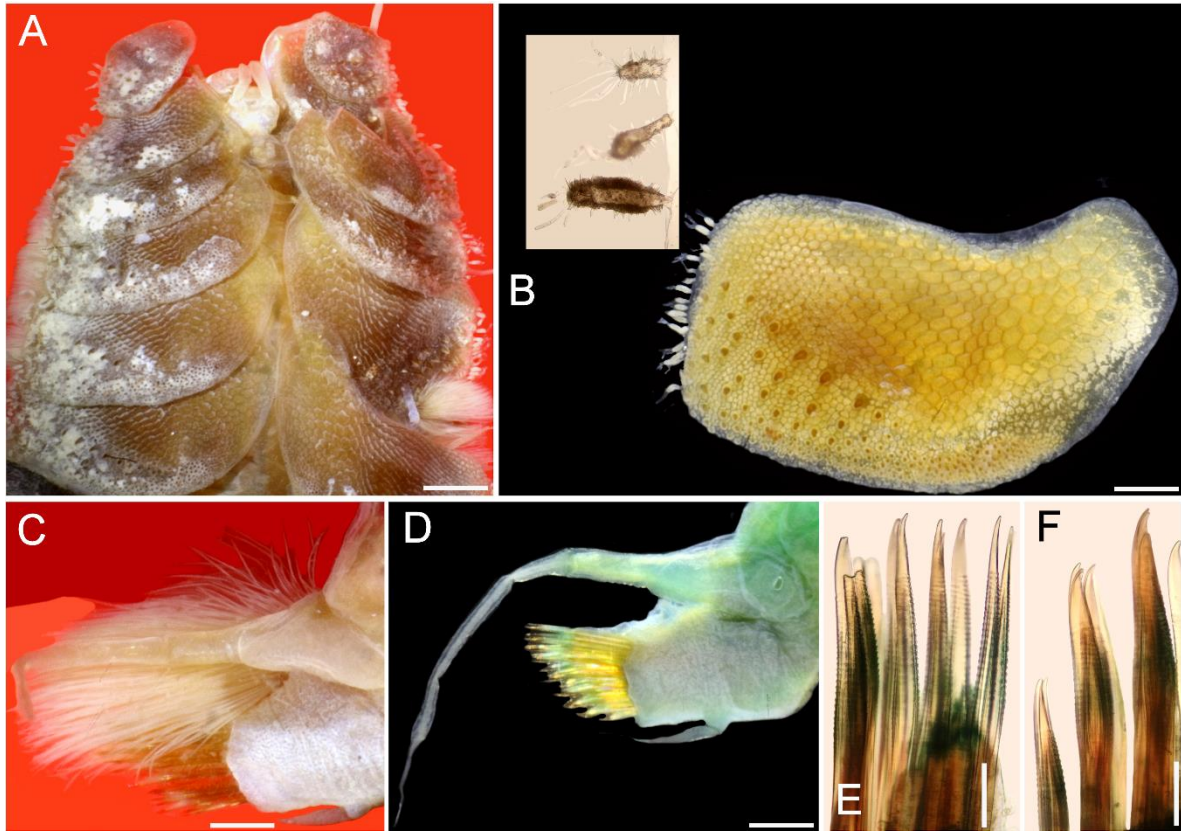


FIGURE 7. *Iphione fimbriata* de Quatrefages, 1866, reinstated, holotype (MNHN POLY TYPE 325). A. Anterior region, dorsal view. B. Left elytron 7, after brushing off sediment, dorsal view (inset: close up of dirty to clean fimbriae). C. Chaetiger 16, left parapodium, posterior view. D. Chaetiger 12, left parapodium, after removal of notochaetae and Methyl green stain. E. Same, upper notochaetae. F. Same, lower neurochaetae. Scale bars: A, 1.7 mm; B, 1 mm; C, 0.6 mm; D, 0.5 mm; E, 170 µm; F, 200 µm.

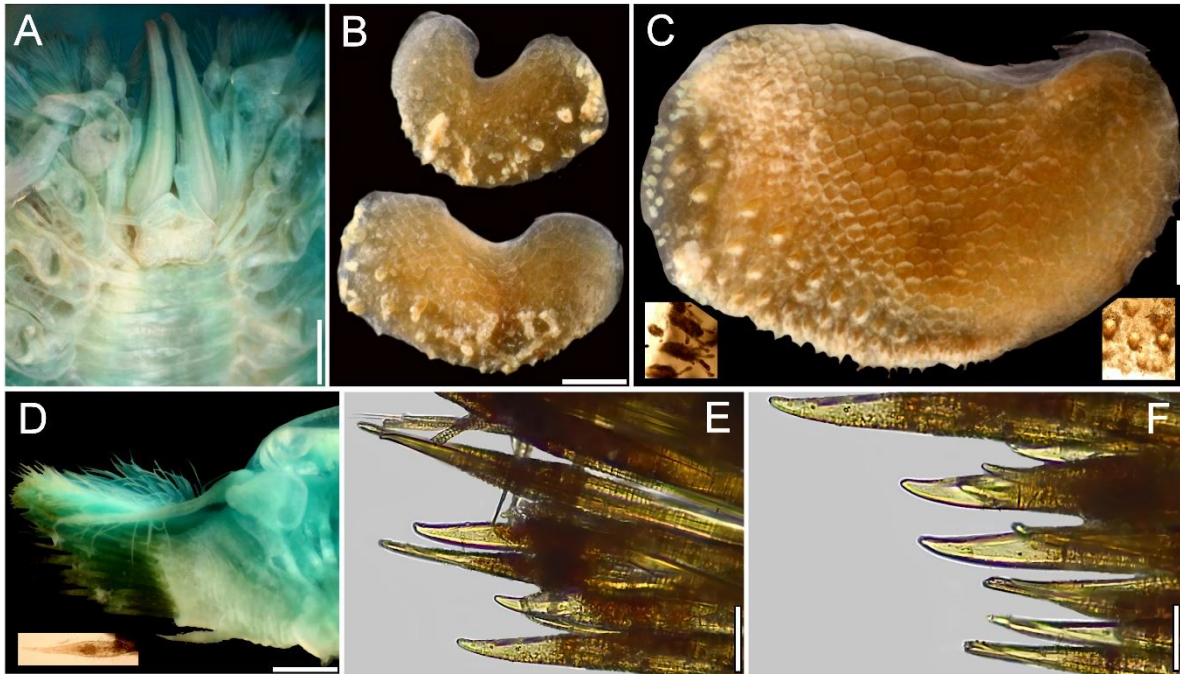


FIGURE 8. *Iphione fimbriata* de Quatrefages, 1866, reinstated, paratype of *I. fustis* Hoagland, 1920 (USNM 18969). A. Anterior end, dorsal view, after Methyl green staining. B. Anterior elytra, above: right elytron from chaetiger 2; below: left elytron from chaetiger 4. C. Left elytron from median chaetiger, dorsal view (insets: fimbriae, and smaller marginal spines). D. Chaetiger 14, left parapodium, posterior view after Methyl green staining. E. Same, upper and medial neurochaetae. F. Same, medial and lower neurochaetae. Scale bars: A, 1.1 mm, B, 1 mm; C, 2 mm; D, 0.6 mm; E, 100 μm ; F, 80 μm .

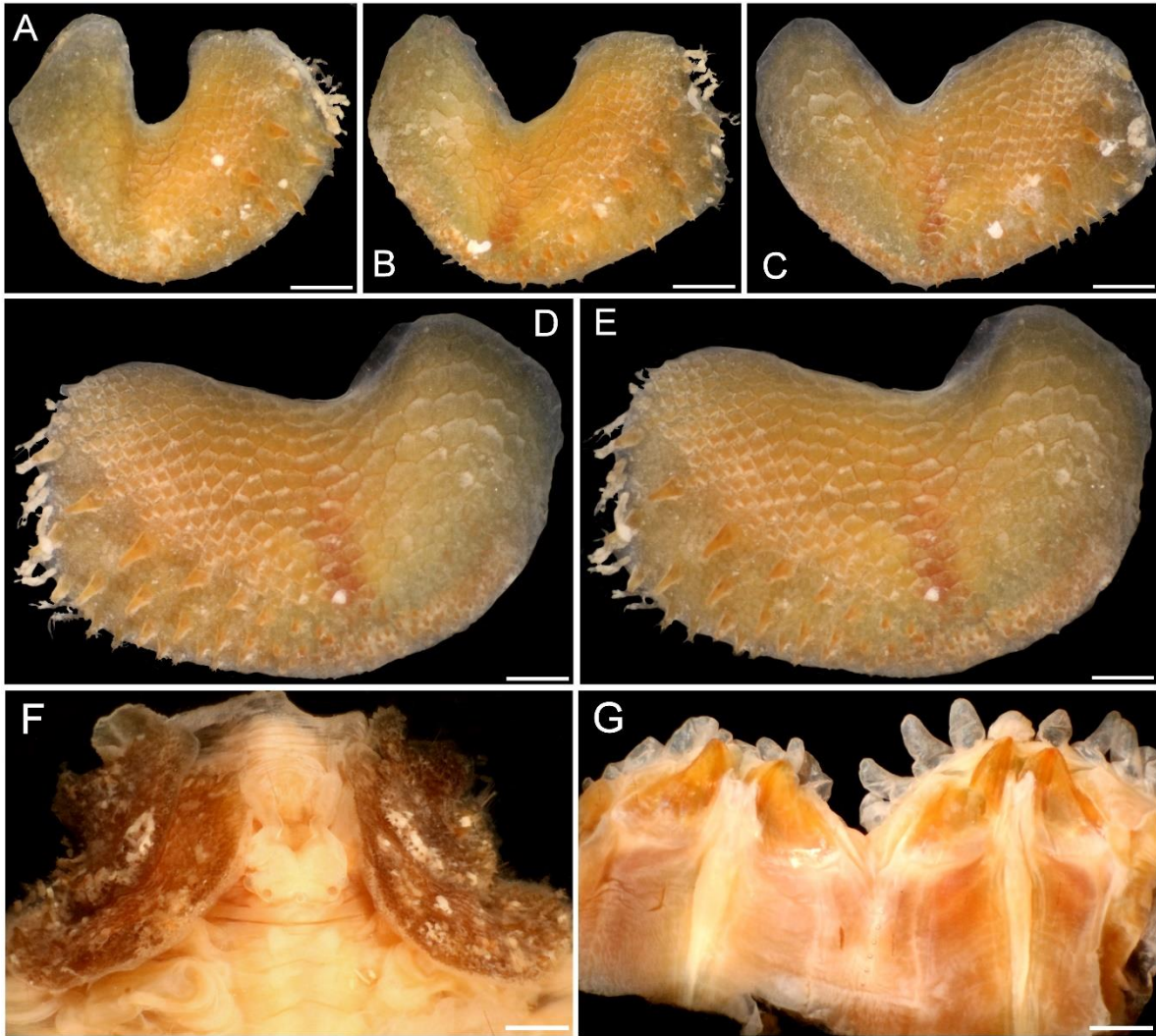


FIGURE 9. *Iphione fimbriata* de Quatrefages, 1866, reinstated, paratype of *I. fustis* Hoagland, 1920 paratype (USNM 18968), elytra previously removed, seen from above. A. Second right elytron. B. Third right elytron. C. Fourth right elytron. D. Fifth left elytron. E. Sixth left elytron. F. Non-type specimen (USNM 81972), anterior end, dorsal view. G. Another specimen from same lot, pharynx previously dissected, seen from inside, depressed by glass slide. Scale bars: A, 0.7 mm; B, G, 0.8 mm; C, 1.1 mm; D, E, 0.6 mm, F, 1.3 mm.

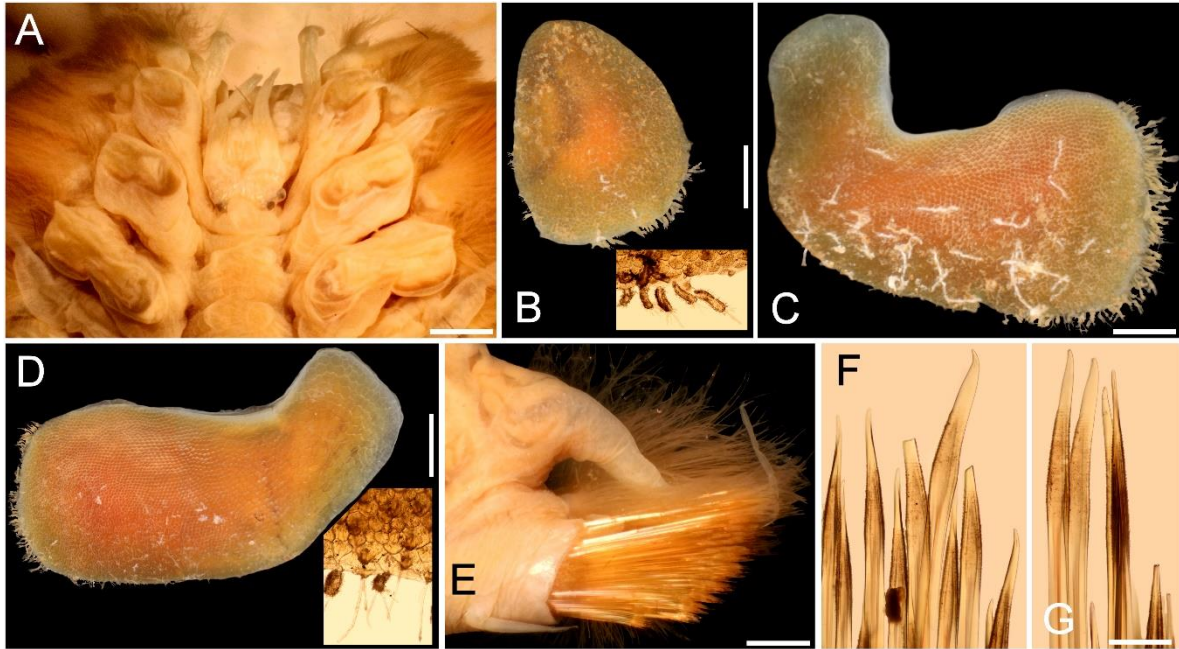


FIGURE 10. *Iphione henshawi* Pettibone, 1986, paratype (USNM 5439). A. Anterior end, dorsal view. B. First elytron, dorsal view (inset: close-up of fimbriae). C. Right anterior elytron, with some calcareous epibionts. D. Left posterior elytron (inset: close-up of macrotubercles and spines). E. Cirriferous right parapodium, posterior view. F. Same, neurochaetae of mid-bundle. G. Same, neurochaetae of lower bundle. Scale bars: A, 1.8 mm; B, C, 1.4 mm; D, 2.6 mm; E, 1.1 mm; F, G, 0.7 mm.

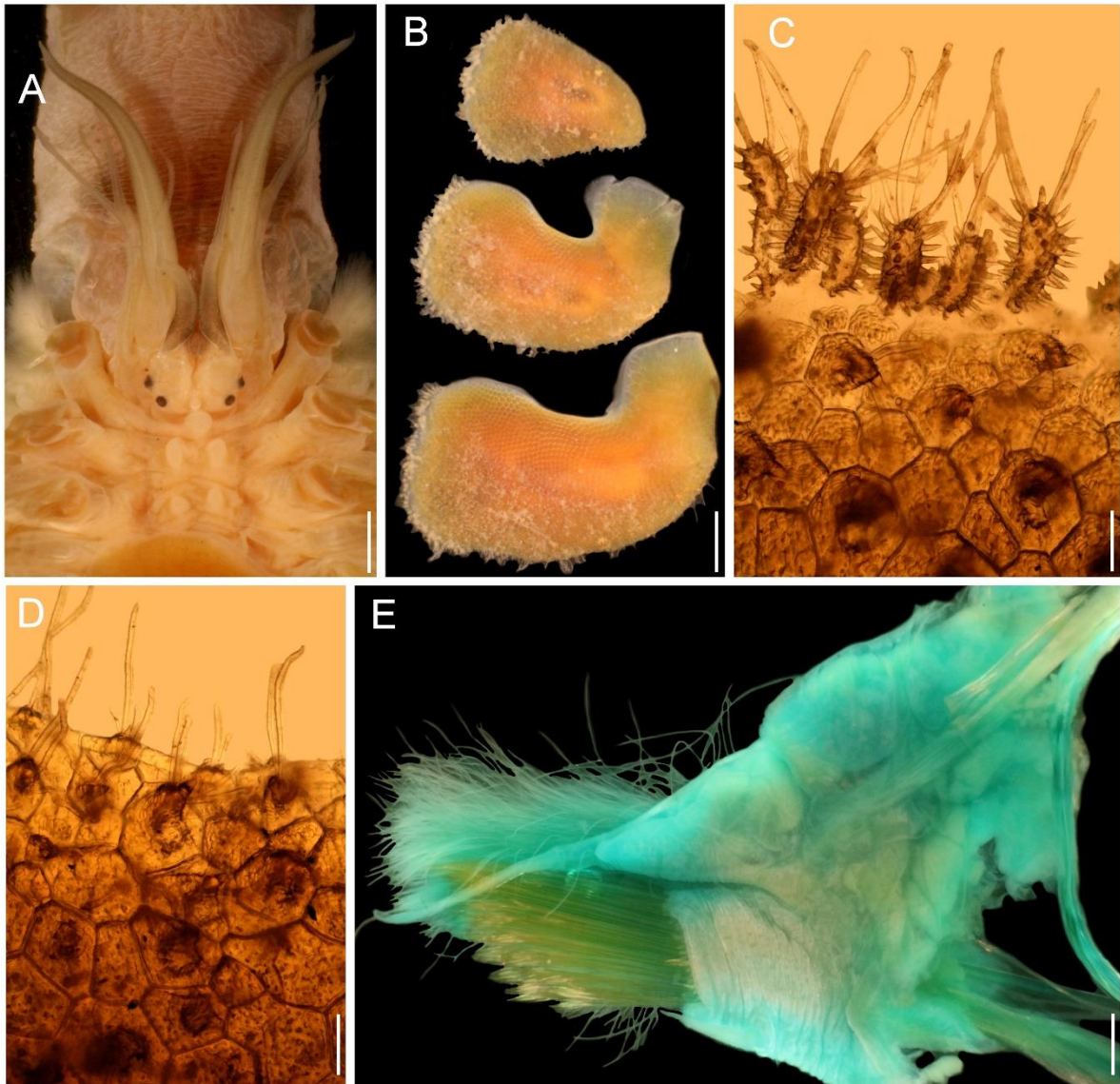


FIGURE 11. *Iphione henshawi* Pettibone, 1986, non-type specimen (BPBM R481). A. Anterior end, dorsal view (elytra 1–3 removed). B. Left elytra 1–3, dorsal view. C. Elytron 3, close-up of fimbriae, some macro tubercles in the lower area. D. Same, close-up of macro tubercles. E. Cirriferous left parapodium of median segment, posterior view. Scale bars: A, 0.8 mm; B, 1.4 mm; C, D, 0.3 mm; E, 0.5 mm.

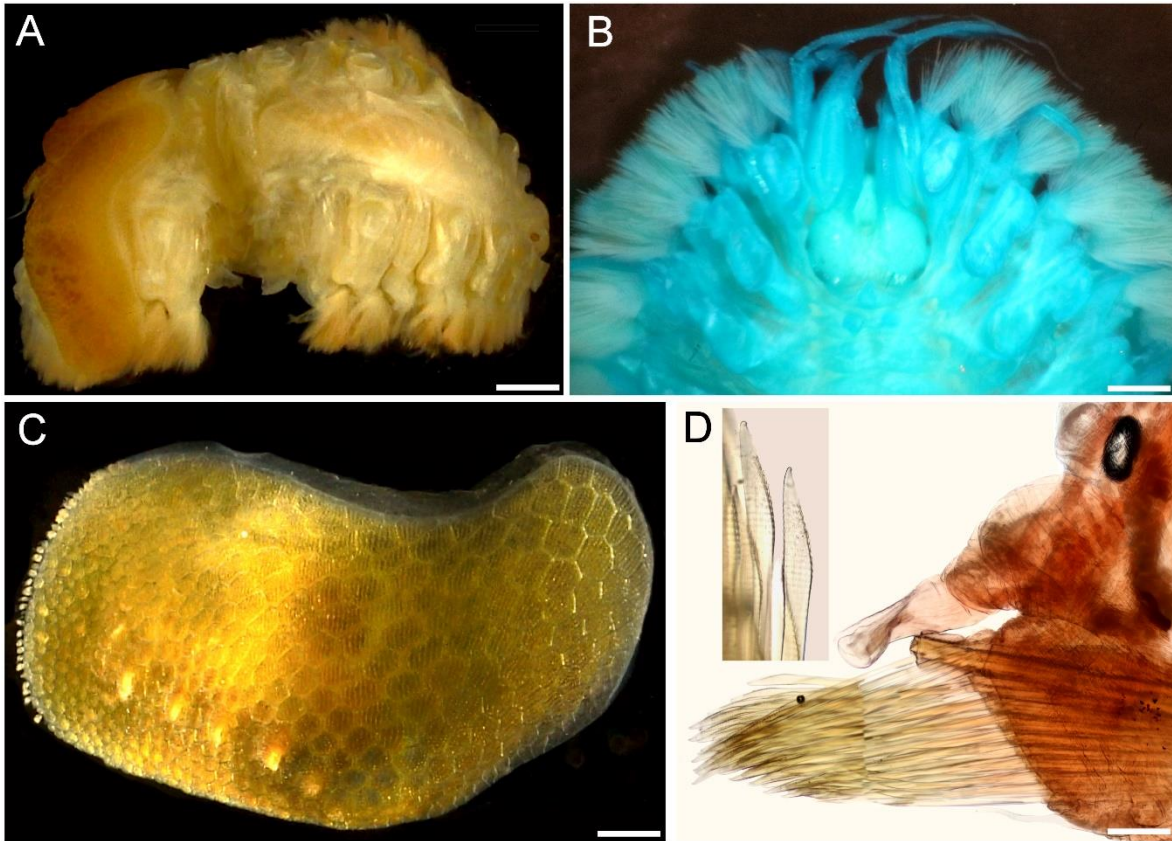


FIGURE 12. *Iphione treadwelli* Pettibone, 1986, holotype (USNM 5435). A. Right lateral view (head points to the right). B. Same, anterior region, after Methyl green staining. C. Previously detached median left chaetiger. D. Chaetiger 12, left parapodium, posterior view, after Shirlastain-A staining (inset: upper neurochaetae tips). Scale bars: A, 0.8 mm; B, C, 0.4 mm; D, 150 μ m.

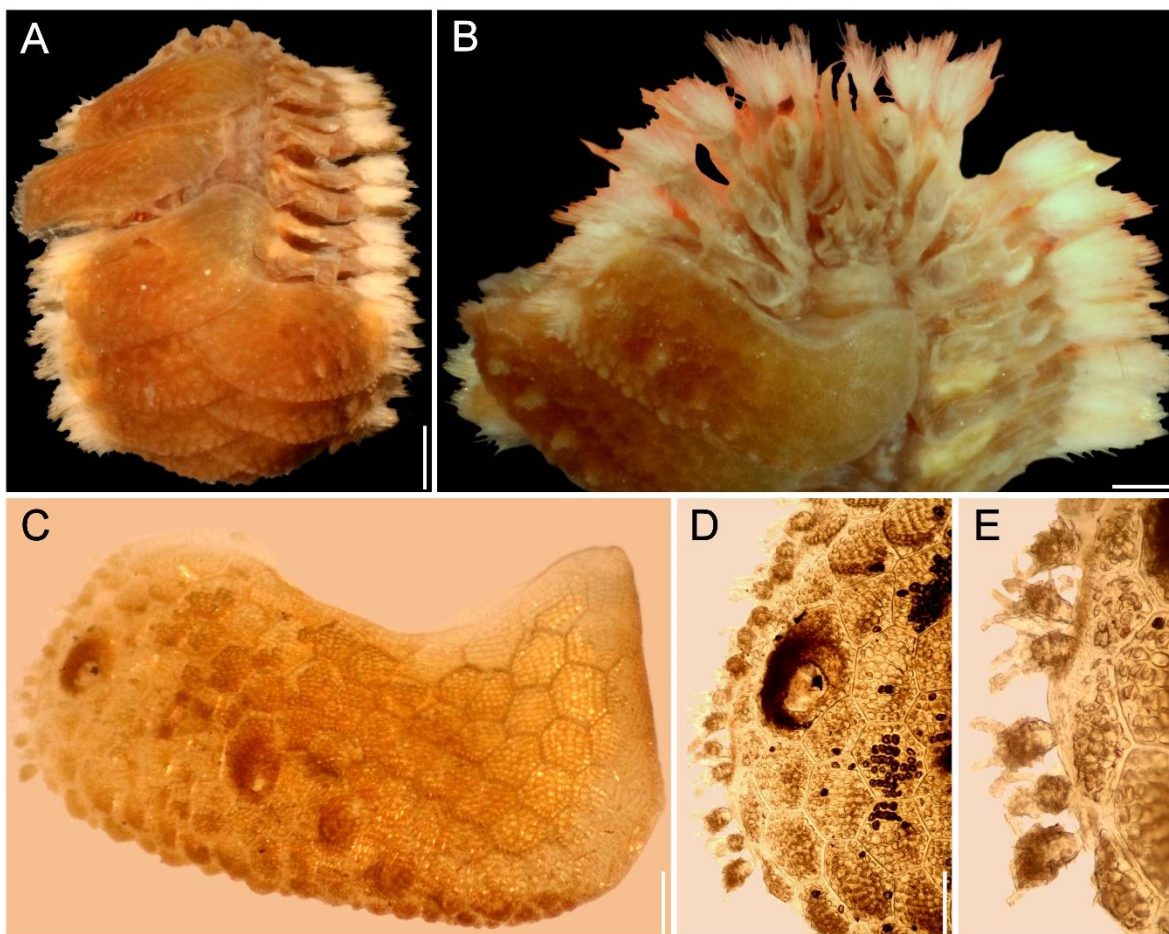


FIGURE 13. *Iphione treadwelli* Pettibone, 1986, paratype (USNM 81934). A. Dorsal view. B. Anterior end, dorsal view. C. Left median elytron, dorsal view. D. Same, marginal macrotubercle and fimbriae. E. Same, fimbriae. Scale bars: A, 0.7 mm; B, 0.4 mm; C, 0.2 mm; D, 0.1 mm; E, 50 μ m.

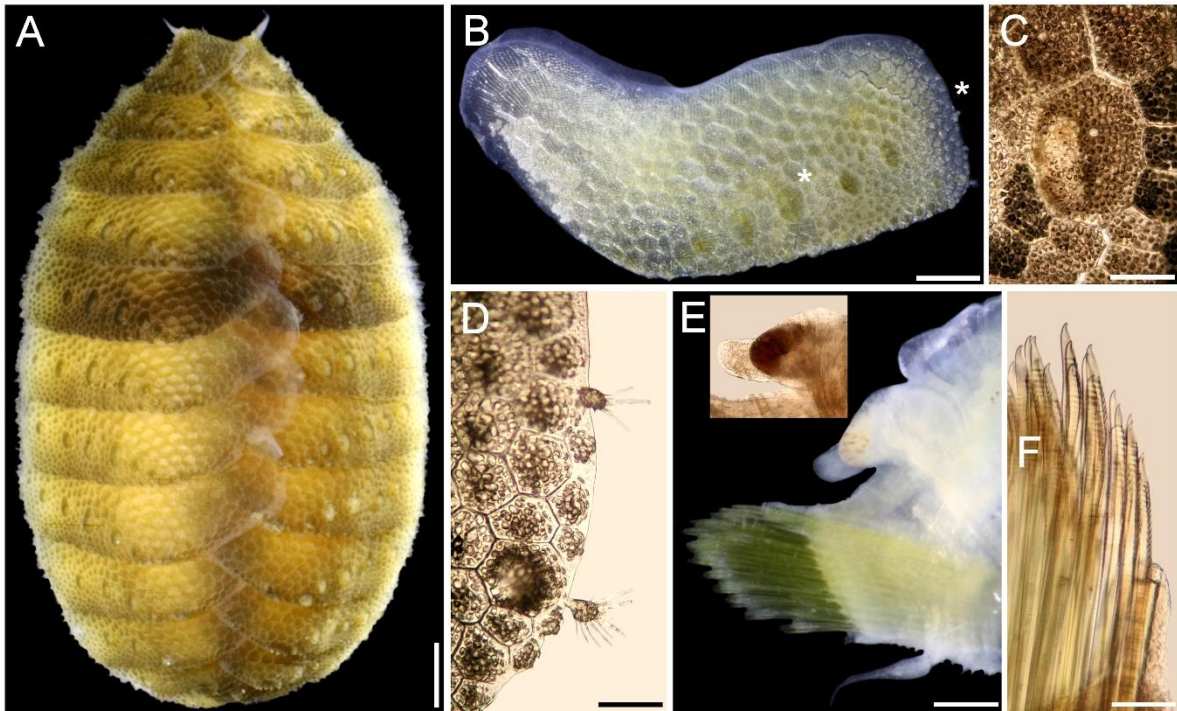


FIGURE 14. *Iphione treadwelli* Pettibone, 1986, non-type specimen (ECOSUR). A. Dorsal view. B. Right elytron 6, dorsal view (asterisks indicate enlarged areas). C. Same, one macrotubercle. D. Same, outer fimbriae. E. Left parapodium of chaetiger 12, posterior view (inset: close-up of basal tubercle showing darker glandular area). F. Same, upper neurochaetae. Scale bars: A, 0.9 mm; B, 0.6 mm; C, 140 µm; D, 30 µm; E, 0.2 mm; F, 50 µm.

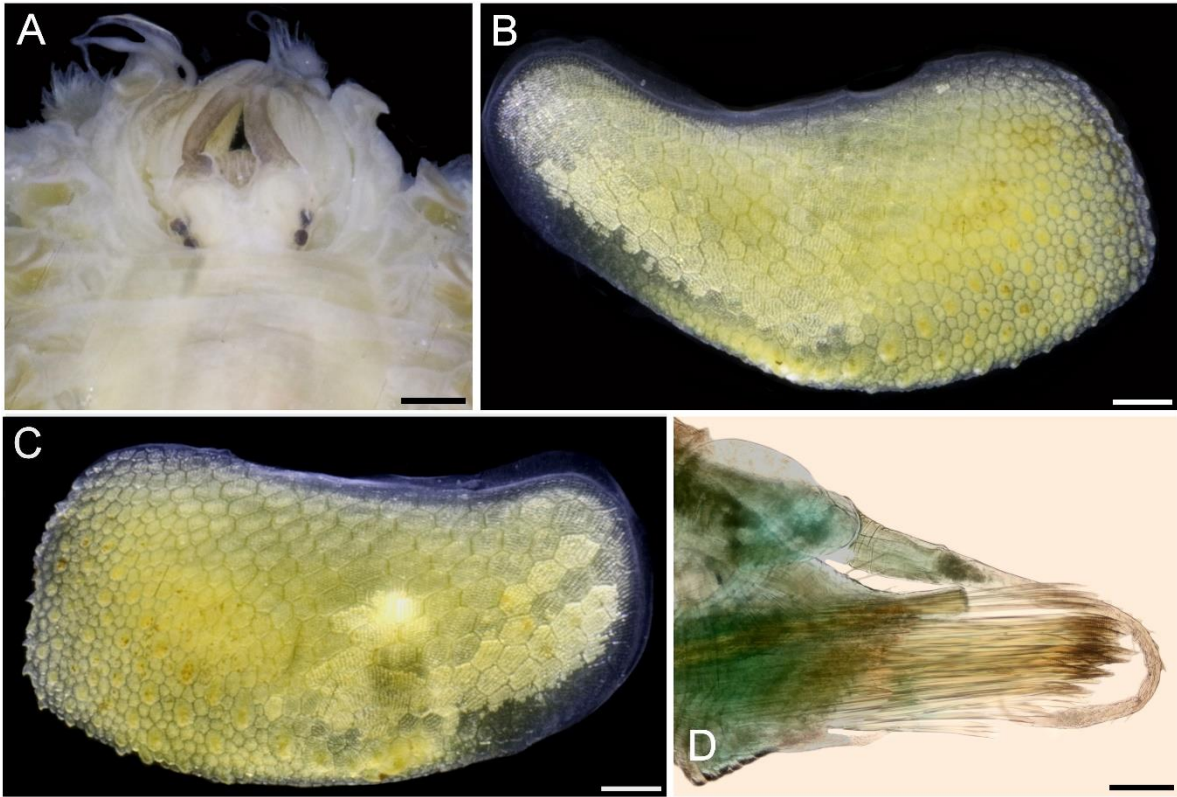


FIGURE 15. *Iphione coriolis* Hanley & Burke, 1991, holotype (MNHN TYPE 574). A. Anterior end, dorsal view. B. Right elytron from median chaetiger. C. Left elytron from postmedian chaetiger. D. Chaetiger 12, right parapodium, posterior view. Scale bars: A, B, 0.4 mm; C, 0.5 mm; D, 0.2 mm.

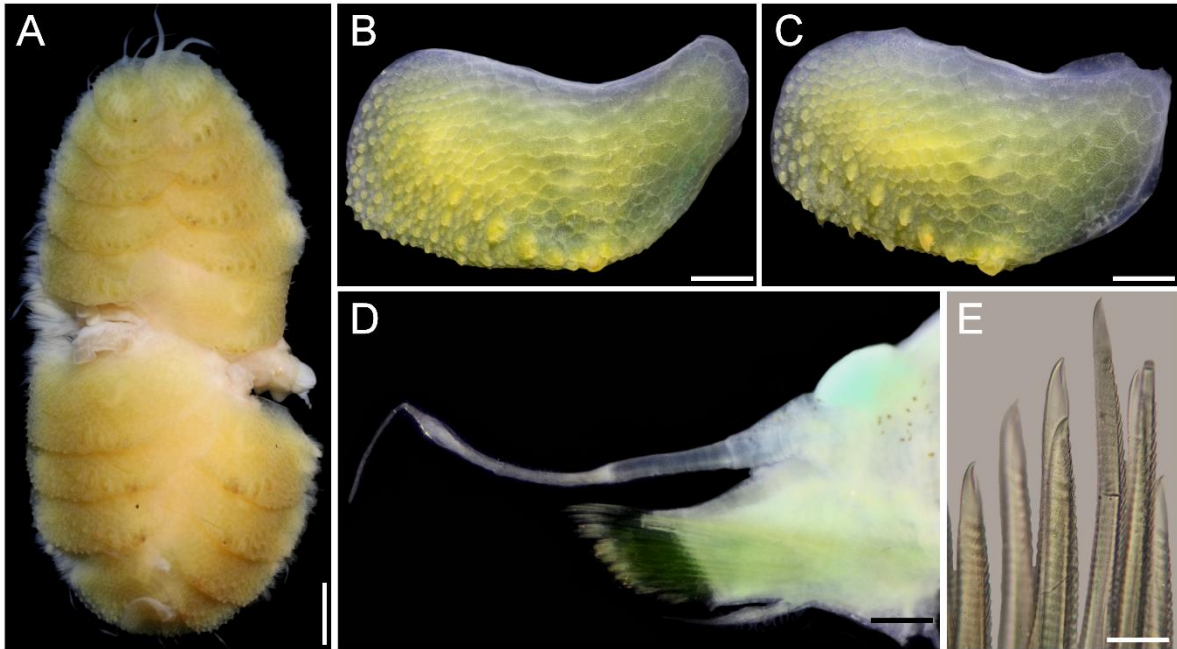


FIGURE 16. *Iphione coriolis* Hanley & Burke, 1991, non-type specimen (UF 5450). A. Dorsal view. B. Left, elytron 6, dorsal view. C. Left, elytron 10, dorsal view. D. Chaetiger 12, left parapodium, posterior view (notochaetae removed). E. Same, tips of upper neutochaetae. Scale bars: A, 1.4 mm; B, 0.8 mm; C, 0.6 mm; D, 0.3 mm; E, 50 μ m.

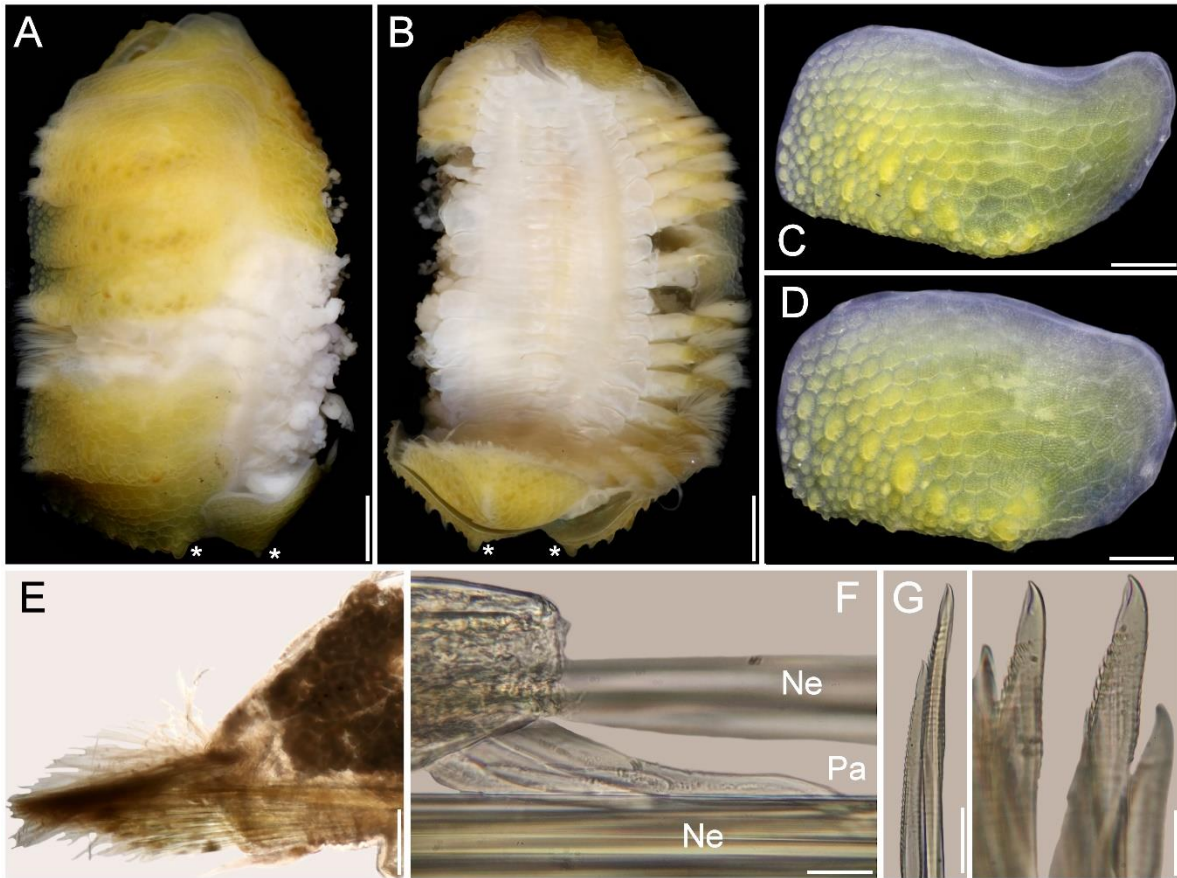


FIGURE 17. *Iphione coriolis* Hanley & Burke, 1991, non-type specimen (UF 5449). A. Dorsal view (asterisks indicate largest macrotubercles in posterior elytra). B. Ventral view (asterisks indicate same as above). C. Left elytron 9, posterior and external margins. D. Left elytron 10 (previously detached), posterior and external margins. E. Chaetiger 12, left parapodium, posterior view. F. Same, anterior view after removing most notochaetae, neuracicular lobe showing long papillae (Ne: neurochaetae, Pa: papilla). G. Upper and lower neurochaetae showing bidentate tips. Scale bars: A, B, 1 mm; C, 0.6 mm; D, 0.5 mm; E, 0.3 mm, F, 40 μ m, G, 100 μ m (left), 40 μ m (right).

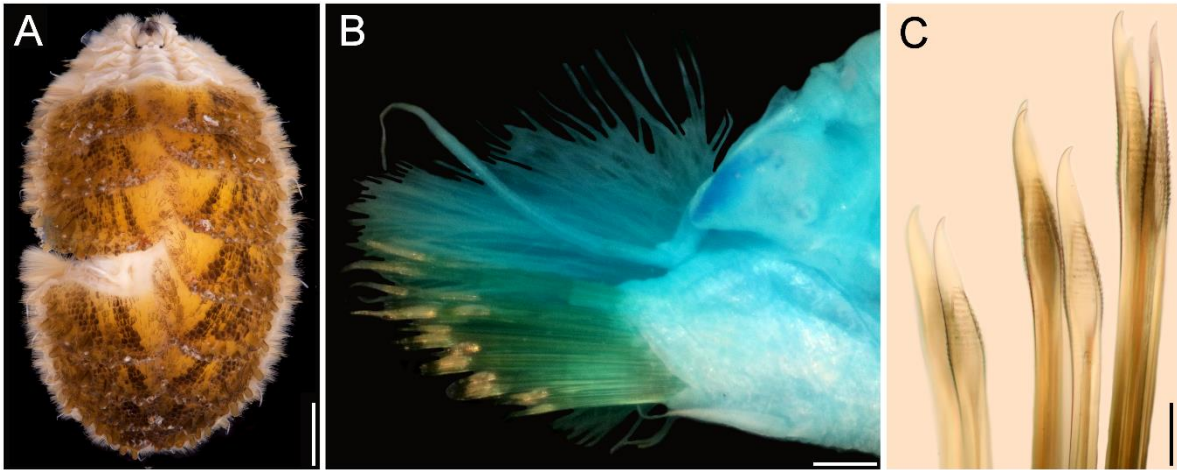


FIGURE 18. *Iphione malifera* Piotrowski, 2014, holotype (CAS 187234). A. Dorsal view. B. Chaetiger 14, left parapodium, posterior view (after Methyl green staining). C. Same, lower and middle neurochaetae. Scale bars: A, 2 mm; B, 0.4 mm; C, 110 μ m.

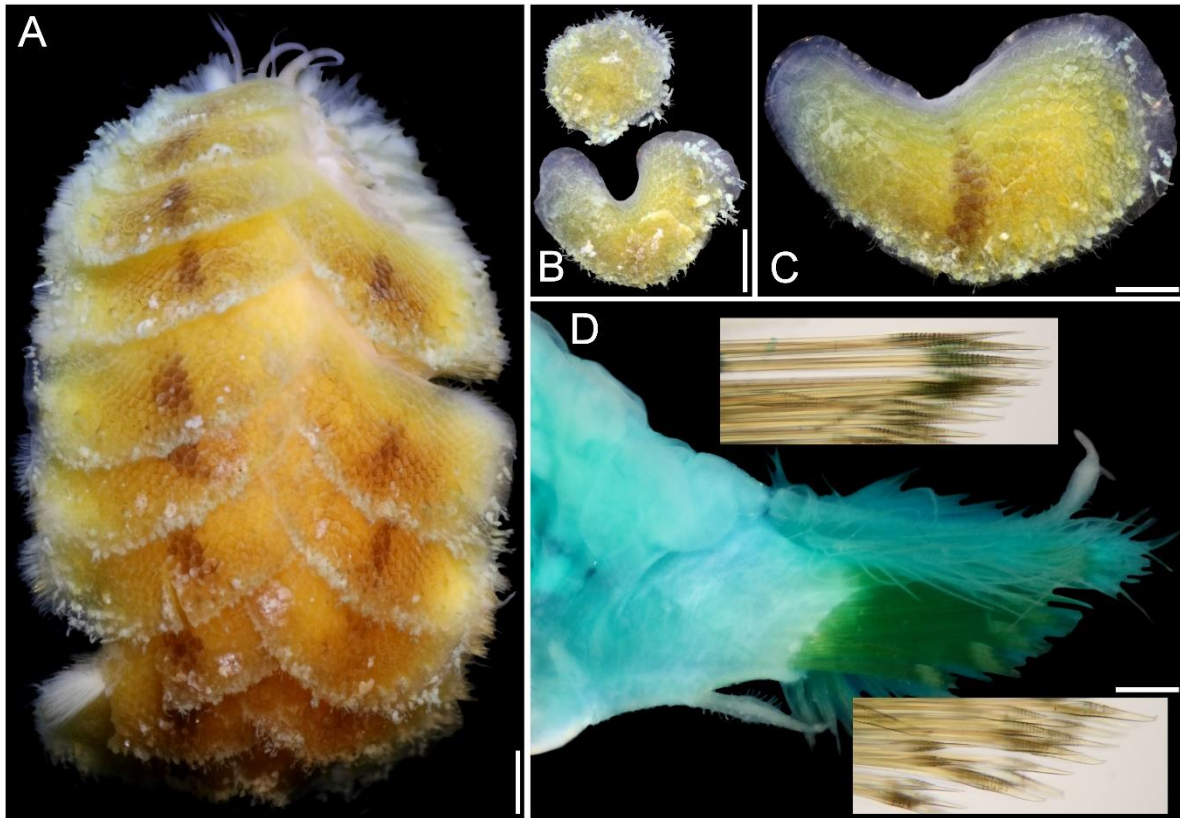


FIGURE 19. *Iphione ankeri* **sp. n.**, holotype (UF 1691). A. Dorsal view. B. Right elytra 1 and 2, dorsal view. C. Right elytron 6, dorsal view. D. Chaetiger 12, left parapodium, posterior view (insets: upper and lower neurochaetae). Scale bars: A, B, 1 mm; C, 0.5 mm; D, 0.2 mm.

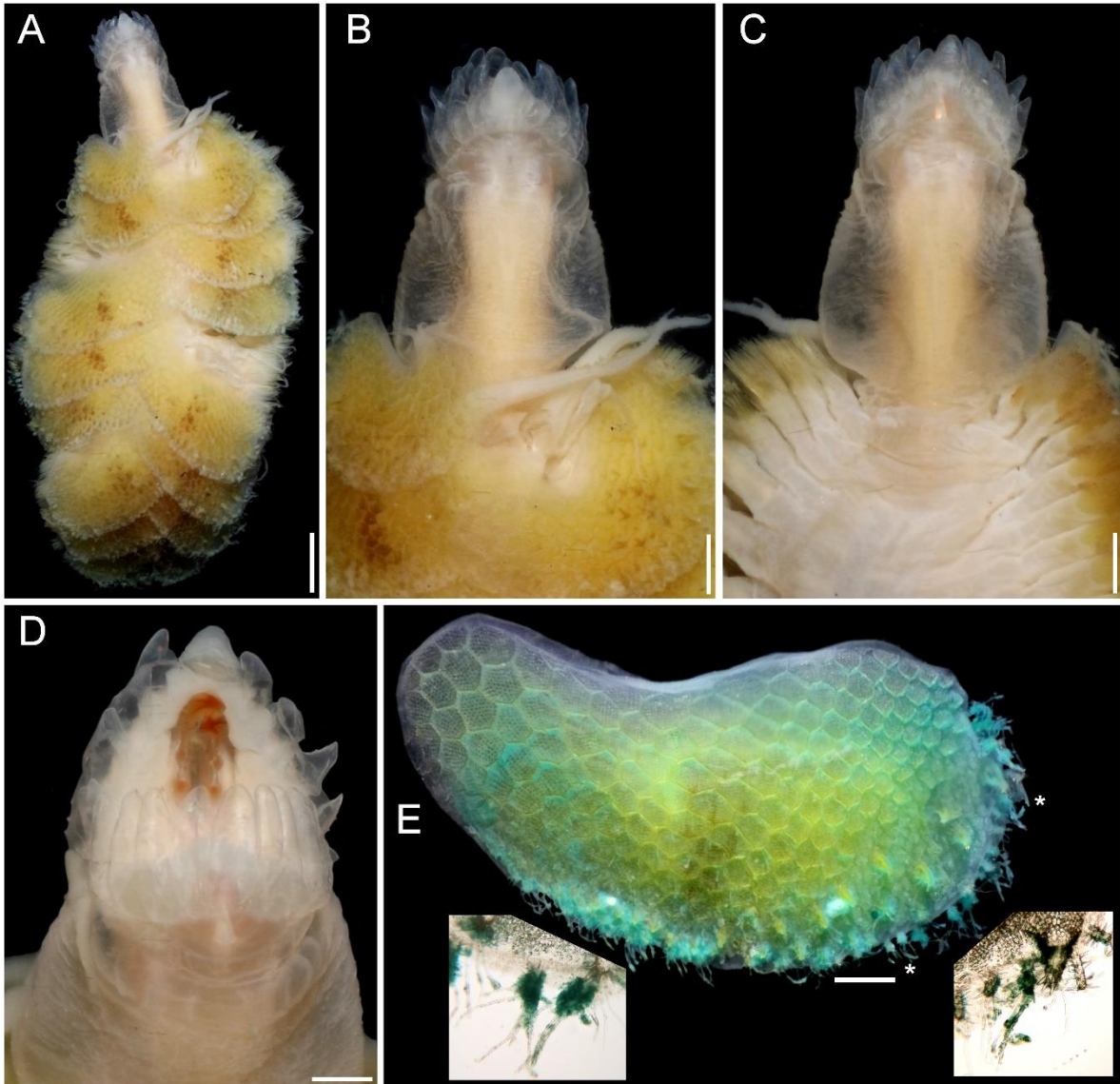


FIGURE 20. *Iphione ankeri* **sp. n.**, paratype (UF 1704). A. Dorsal view. B. Pharynx, dorsal view. C. Pharynx, ventral view. D. Pharynx, oblique frontal view. E. Right elytron 7, seen from above (asterisks indicate enlarged areas inserted). Scale bars: A, 1.4 mm; B, C, 0.6 mm; D, 0.4 mm; E, 0.5 mm.

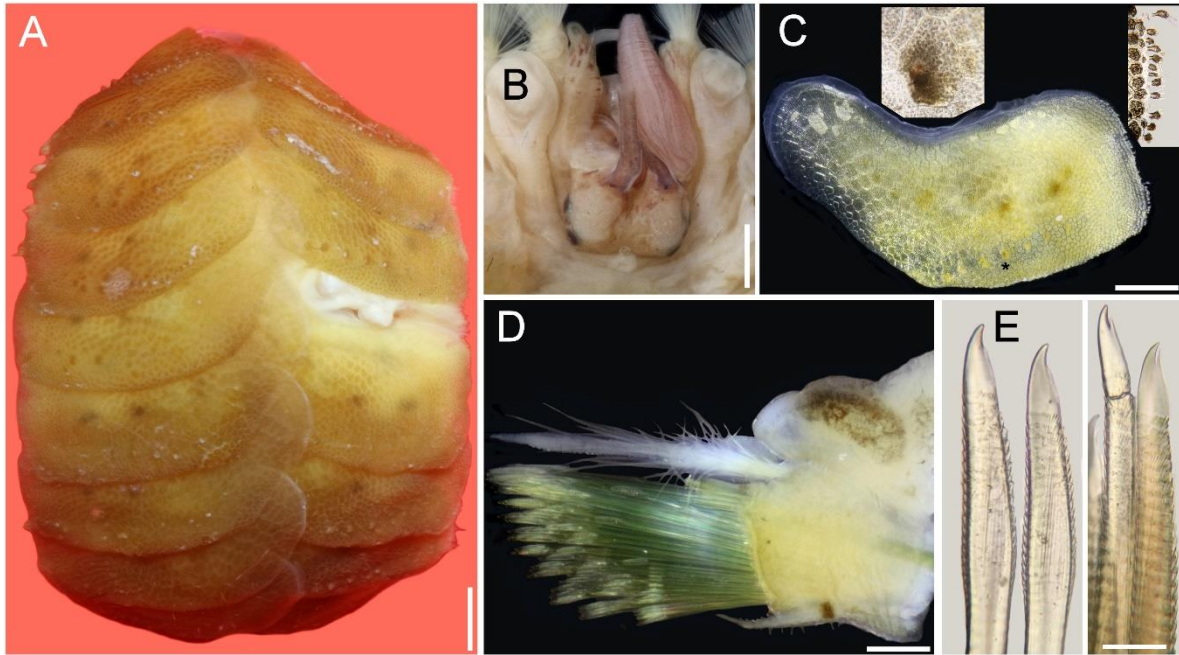


FIGURE 21. *Iphione corbariae* **sp. n.**, holotype (MNHN IA 2021-682). A. Dorsal view. B. Anterior end, dorsal view. C. Right elytron 6, dorsal view (insets: macrotubercle indicated by an asterisk, and lateral fimbriae). D. Chaetiger 12, left parapodium, posterior view. E. Same, tips of median and upper neurochaetae. Scale bars: A, 1.4 mm; B, 0.6 mm; C, 1 mm; D, 0.3 mm; E, 40 μ m.

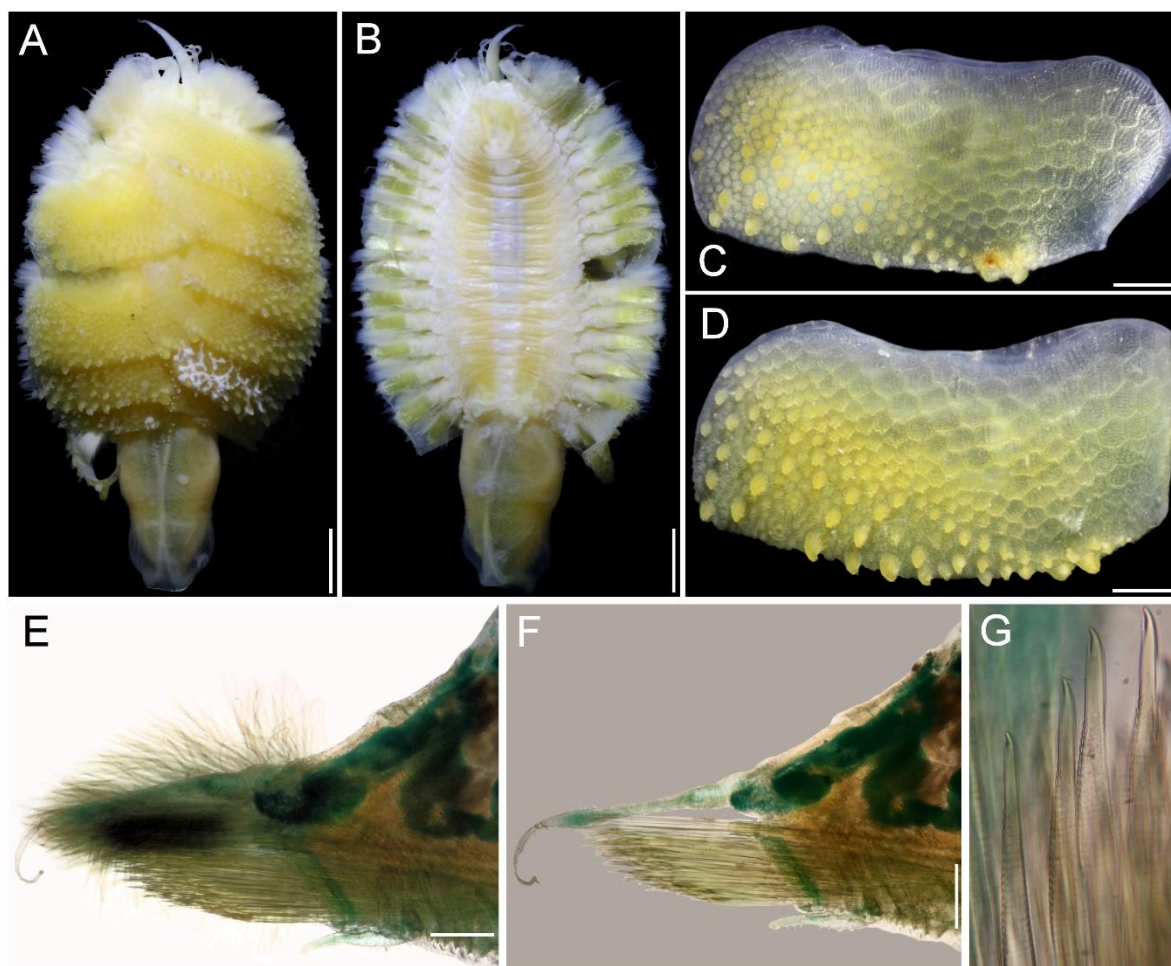


FIGURE 22. *Iphione harrisae* **sp. n.**, holotype (UF 2170). A. Dorsal view. B. Ventral view. C. Left elytron 6. D. Left elytron 10. E. Chaetiger 14, left parapodium, posterior view. F. Same, notochaetal bundle removed. G. Same, tips of neurochaetae. Scale bars: A, B, 1.3 mm; C, 0.6 mm; D, 0.5 mm; E, F, 0.3 mm; G, 60 μ m.

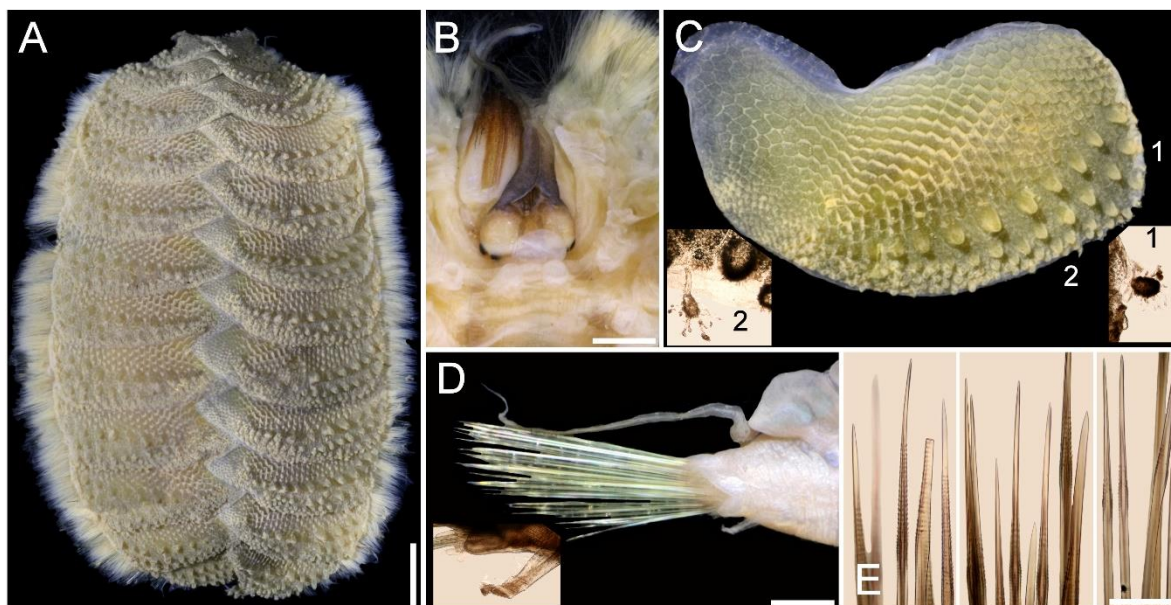


FIGURE 23. *Iphione hourdezi* **sp. n.**, holotype (MNHN TYPE 000). A. Dorsal view. B. Anterior end, dorsal view after removal of elytral pairs 1–4. C. Right elytron 6, dorsal view (insets: 1, lateral fimbria; 2, posterior fimbria). D. Chaetiger 12, left parapodium, posterior view after removal of notochaetae (inset: ventral cirri and basal papillae). E. Same, upper, middle and lower neurochaetal tips. Scale bars: A, 2.9 mm; B, 0.9 mm; C, 1.4 mm; D, 1.2 mm; E, 170 μ m.

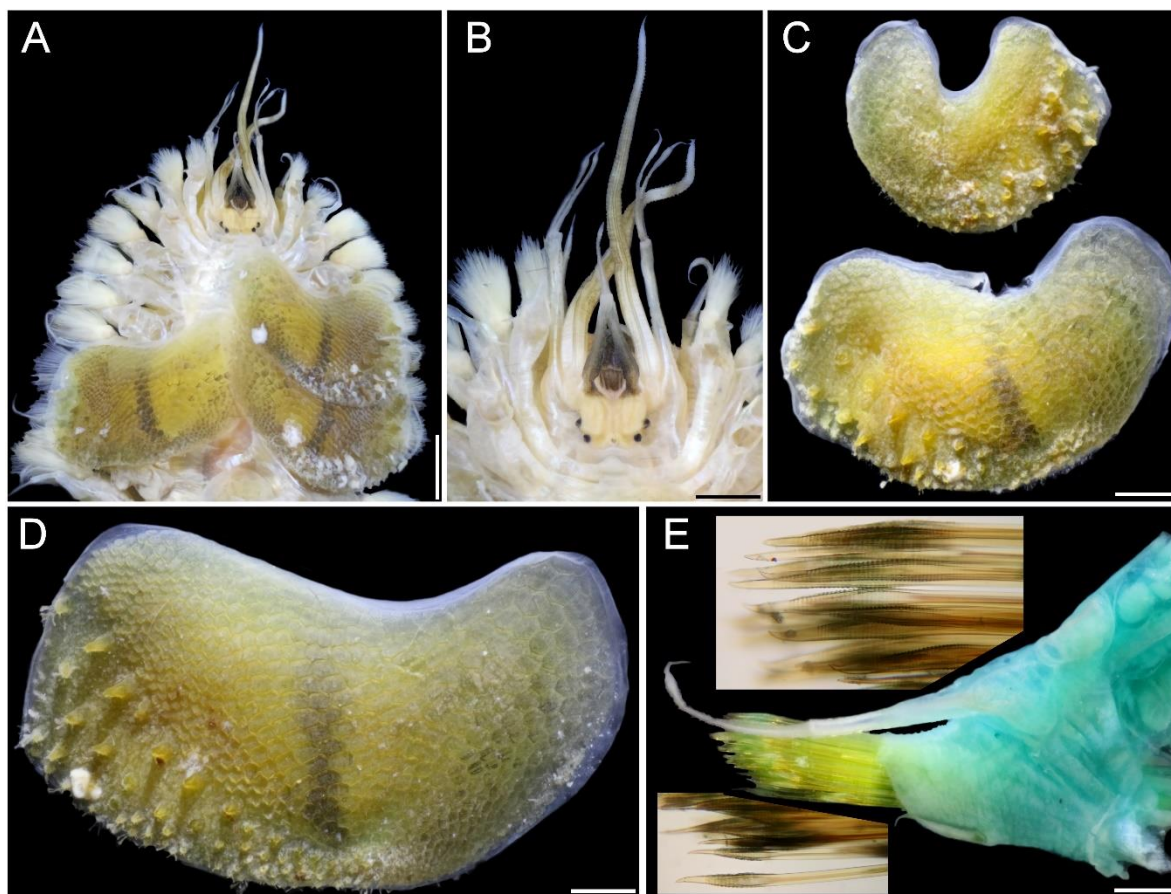


FIGURE 24. *Iphione hyndmani* **sp. n.**, holotype (UF 5695). A. Anterior end, dorsal view after removal of some elytra. B. Same, close-up of prostomium and appendages. C. Right elytron 2 (above), and left elytron 4, dorsal view. D. Left elytron 6, dorsal view. E. Chaetiger 14, left parapodium, posterior view after removal of notochaetae and Methyl green staining (insets: above, upper neurochaetae; below, lower neurochaetae). Scale bars: A, 2 mm; B, 1.1 mm; C, 1 mm; D, 0.9 mm; E, 0.6 mm.

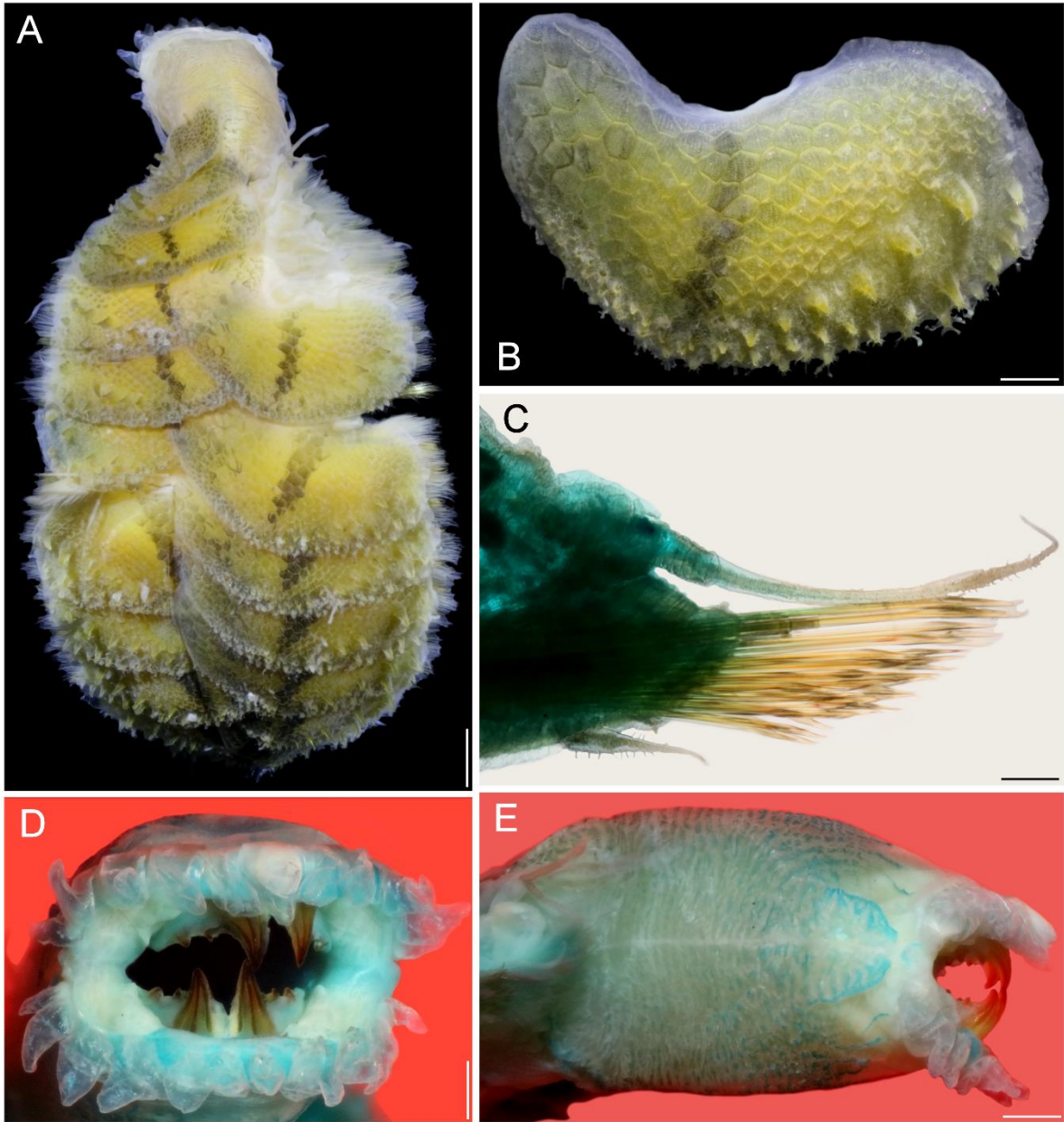


FIGURE 25. *Iphione hyndmani* **sp. n.**, paratype (UF 5689). A. Dorsal view. B. Sixth right elytron, dorsal view. C. Chaetiger 12, right parapodium, posterior view (notochaetae removed) after Methyl green staining (AMGS). D. Pharynx, frontal view (AMGS). E. Same, right lateral view (AMGS). Scale bars: A, 1.2 mm; B, D, 0.5 mm; C, 0.2 mm; E, 0.6 mm.

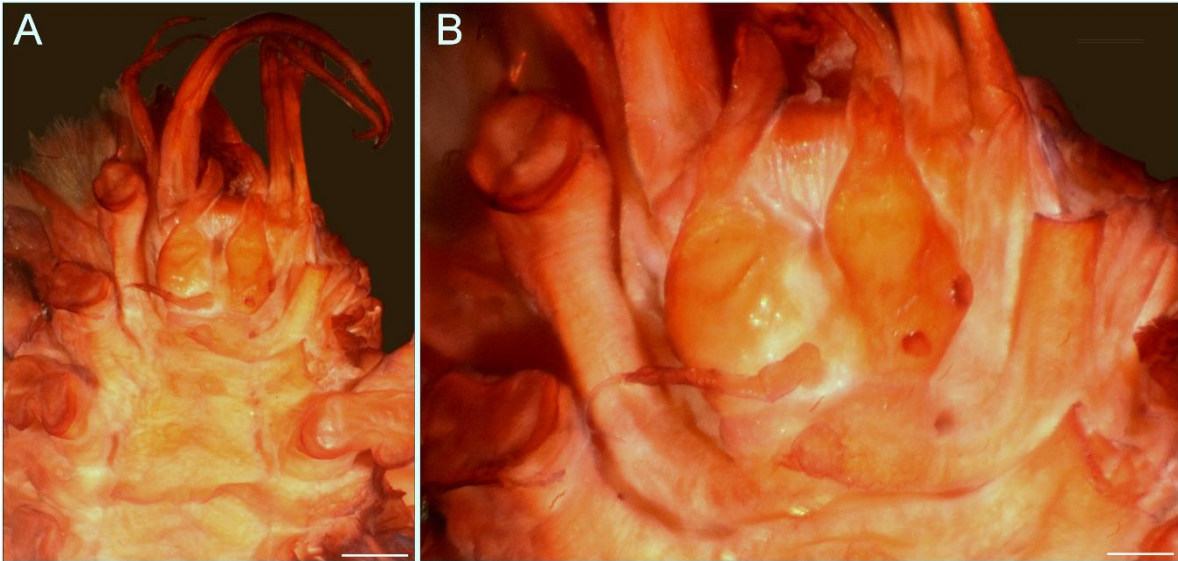


FIGURE 26. *Iphione hyndmani* **sp. n.**, non-type specimen (USNM 19192). A. Anterior region, dorsal view, after Shirlastain-A. B. Close-up of prostomium. Scale bars: A, 0.8 mm; B, 0.2 mm.

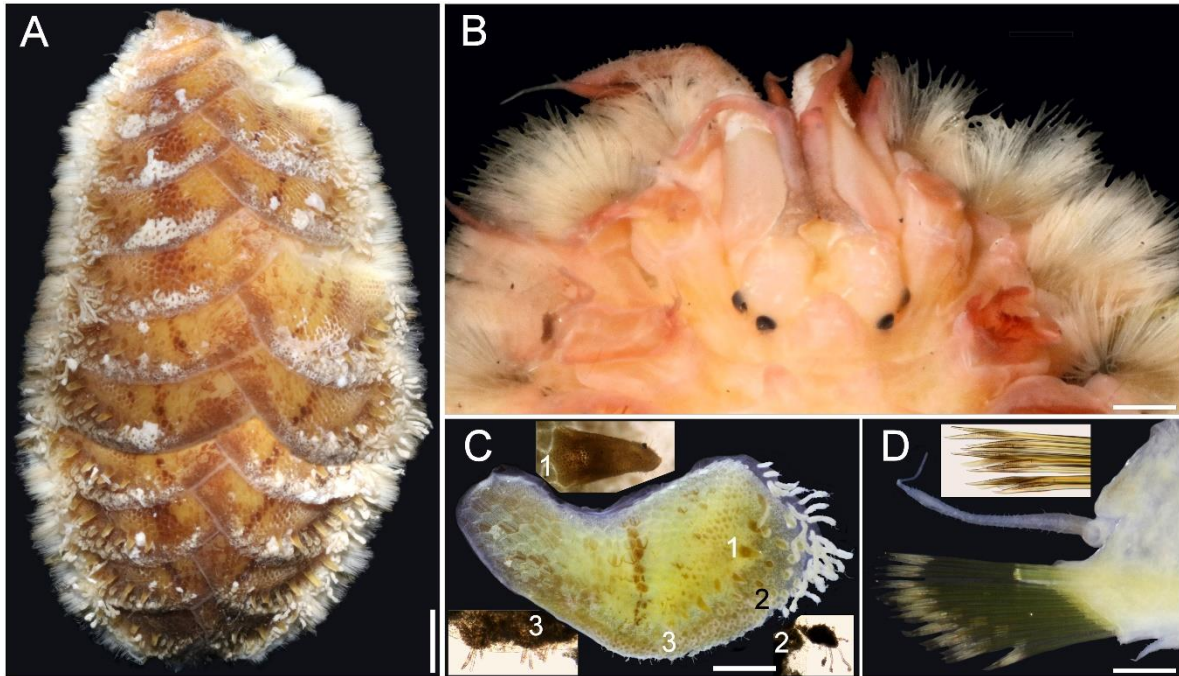


FIGURE 27. *Iphione readi* **sp. n.** (incl. *I. muricata* *sensu* Savigny (1822)) holotype (UF 6343). A. Dorsal view. B. Anterior end, dorsal view, after Shirlastain-A. C. Left elytron 6, insets indicated by number (1, macrotubercle; 2, smallest fimbria; 3, microtubercle). D. Chaetiger 12, left parapodium, posterior view after removal of notochaetae (inset: close up of upper neurochaetal tips). Scale bars: A, 2 mm; B, D, 0.5 mm; C, 1.2 mm.

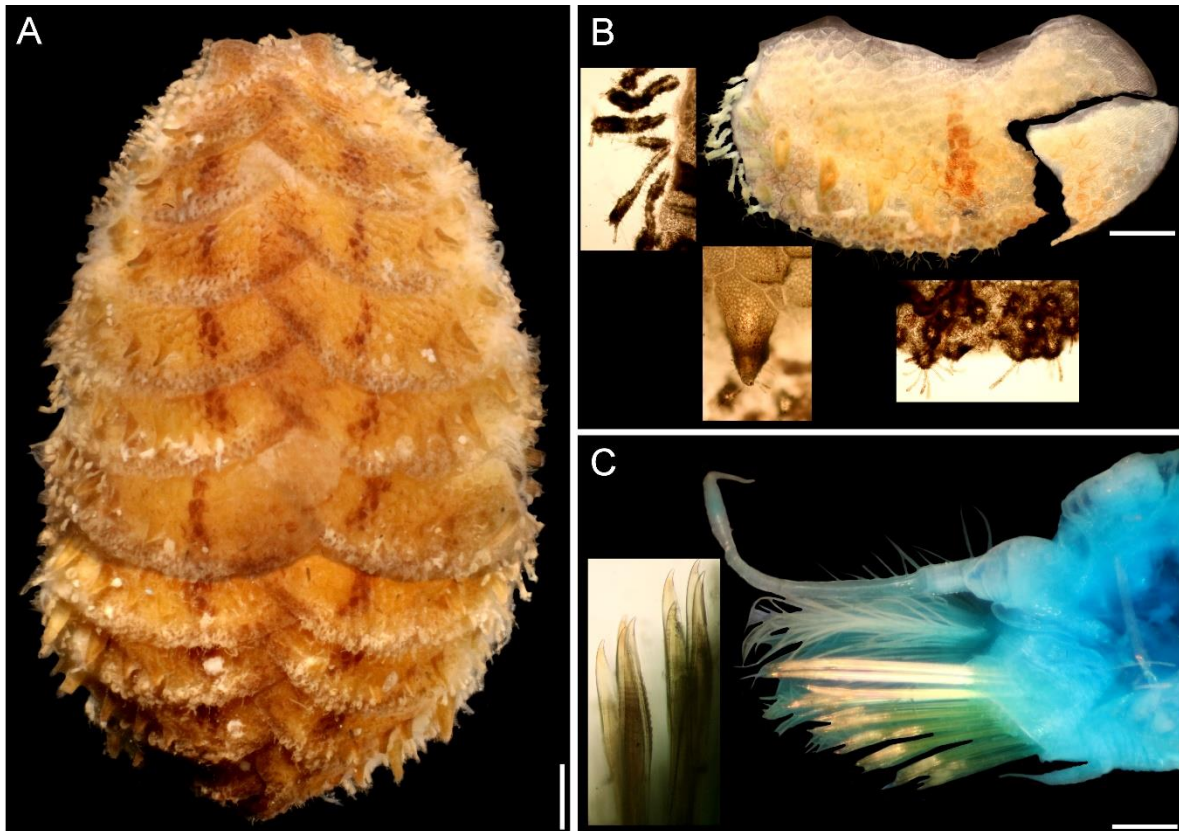


FIGURE 28. *Iphione readi* **sp. n.** (incl. *I. muricata* *sensu* Savigny (1822)), non-type specimen (CAS 192038). A. Dorsal view. B. Left elytron 6, seen from above (insets, from left to right: fimbriae, large macrotubercle, marginal tubercles). C. Chaetiger 12, left parapodium, posterior view, after Methyl green staining (inset: median neurochaetae). Scale bars: A, 1 mm; b, 0.7 mm; C, 0.3 mm.

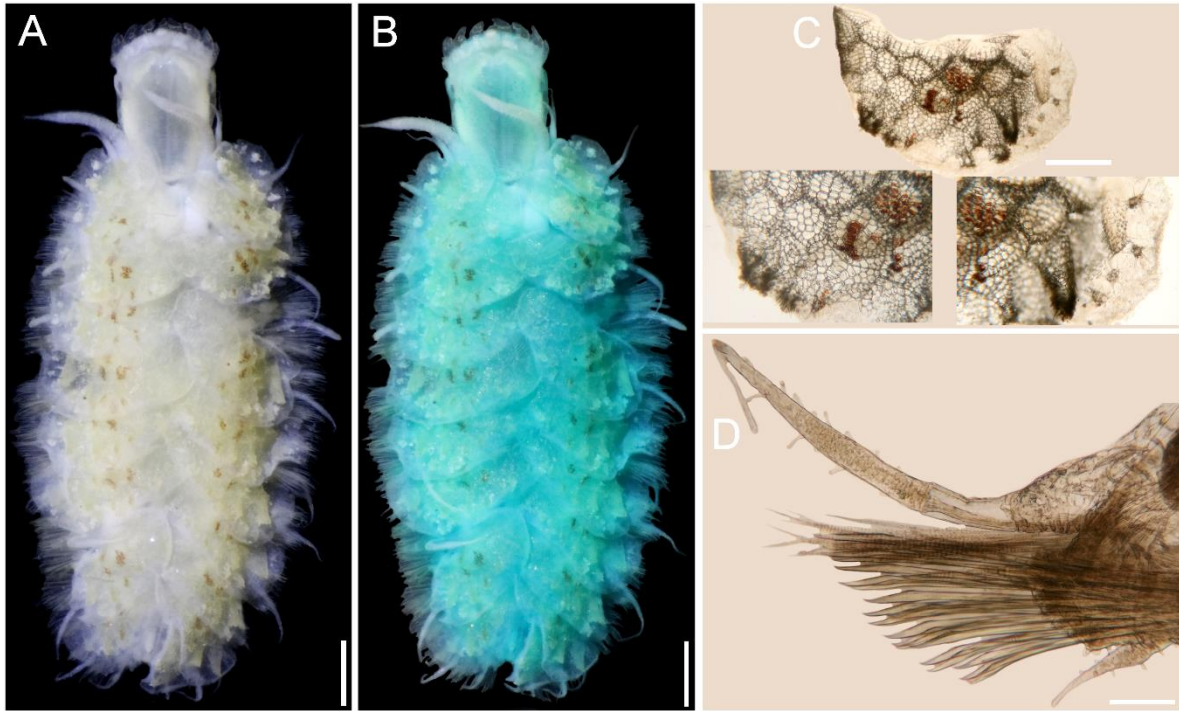


FIGURE 29. *Iphione readi* **sp. n.** (Incl. *I. muricata* sensu Savigny (1822)), non-type juvenile specimen (UF 4489). A. Dorsal view. B. Same, after Methyl green staining. C. Right elytron 4, inner margin slightly bent. D. Chaetiger 10, left parapodium, posterior view. Scale bars: A, B, 0.6 mm; C, 0.4 mm; D, 0.1 mm.

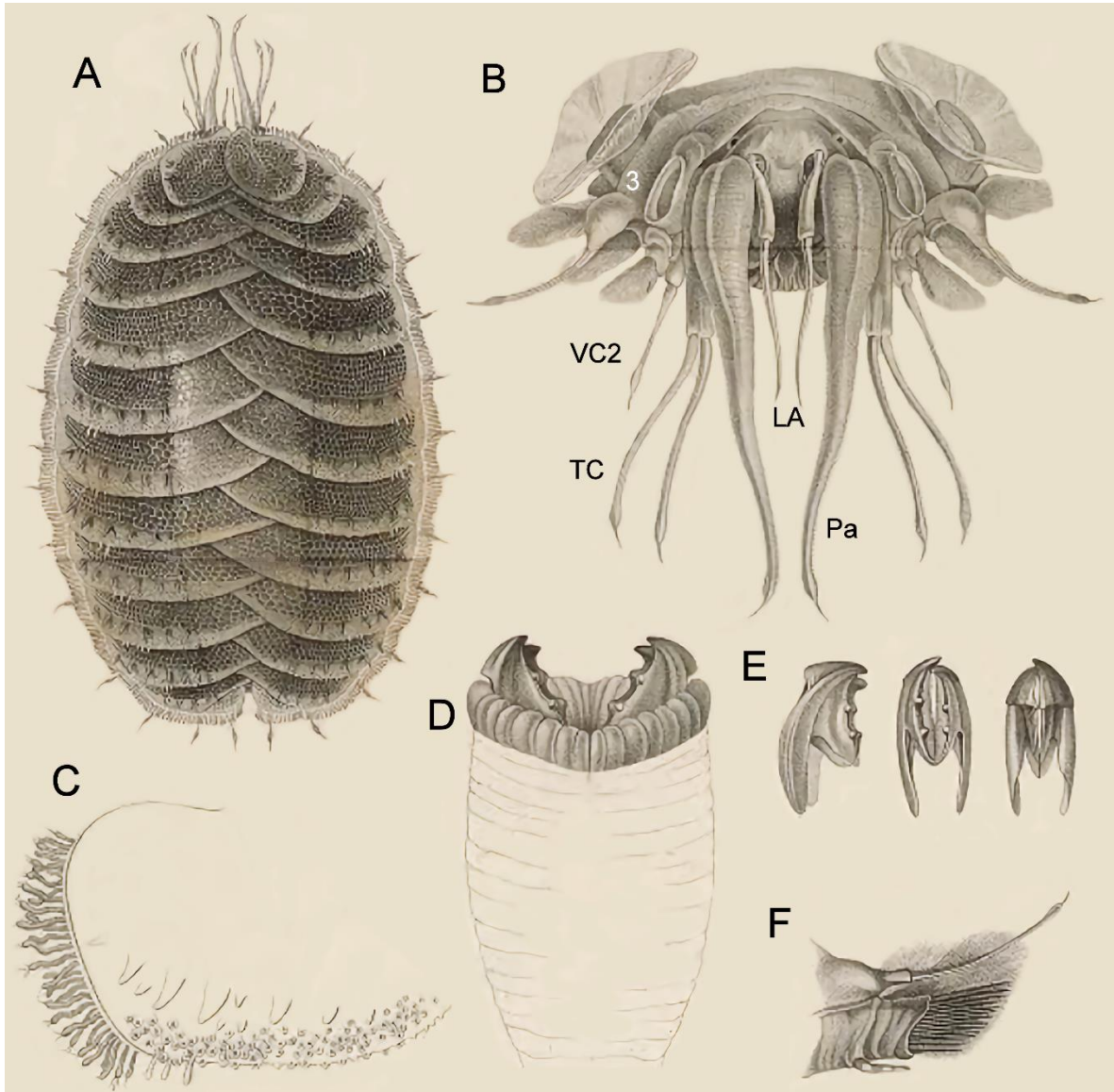


FIGURE 30. *Iphione readi* **sp. n.** (Incl. *I. muricata* *sensu* Savigny (1822)), original illustrations after explanation by Audouin (1825: 66). A. Dorsal view. B. Anterior end, oblique frontal view. C. Median elytron, schematic. D. Pharynx with jaws and papillae, lateral view. E. Jaws in lateral, frontal and posterior views. F. Median cirriferous chaetiger, right parapodium, posterior view (Abbreviations: LA, lateral antennae; Pa, palp; TC, tentacular cirri; VC2, ventral cirrus segment 2; 3, segment 3).

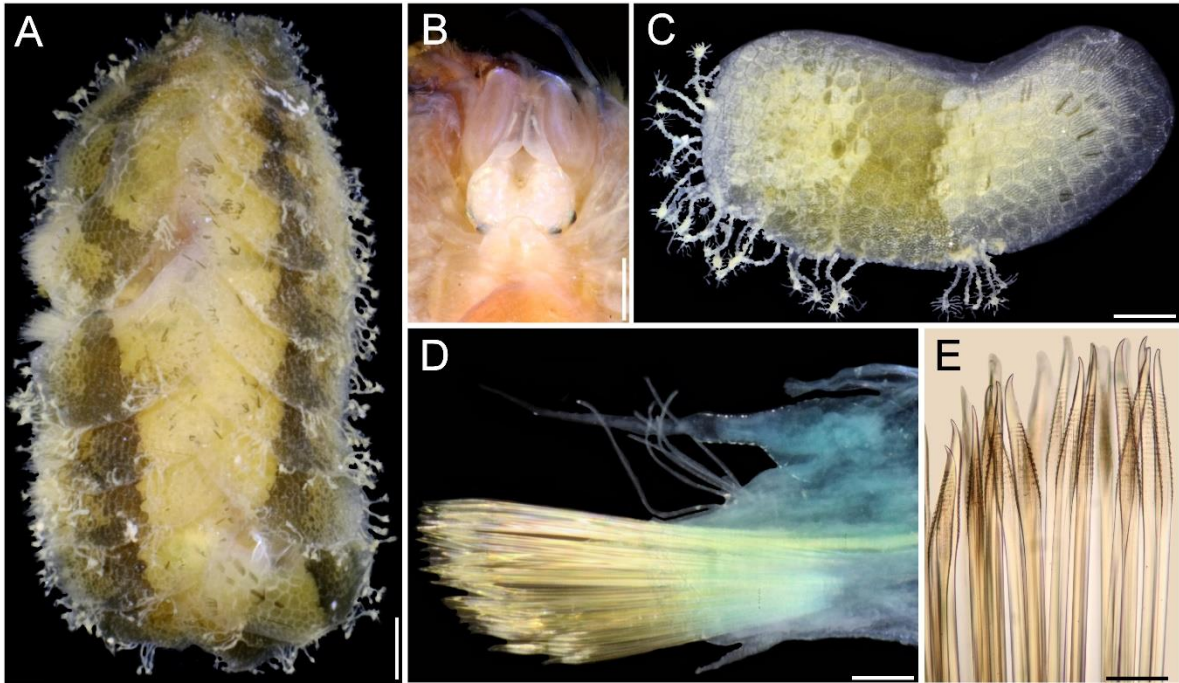


FIGURE 31. *Iphione richeri* **sp. n.**, holotype (MNHN TYPE 000). A. Dorsal view, last segments bent ventrally. B. Anterior end, after Shirlastain-A staining. C. Left elytron 6, dorsal view. D. Chaetiger 12, left parapodium, posterior view. E. Same, upper and middle neurochaetal tips. Scale bars: A, 1.3 mm; B, 0.5 mm; C, 0.7 mm; D, 0.3 mm; E, 100 μ m.

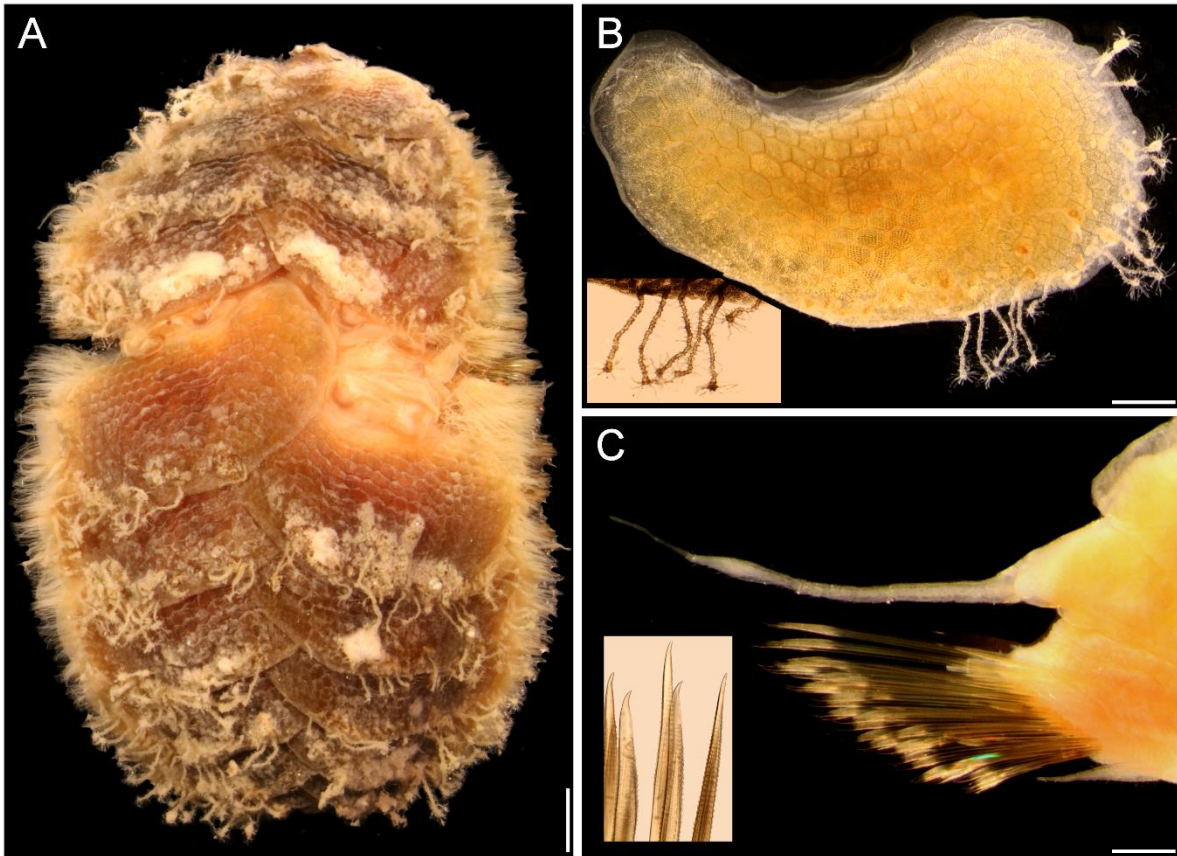


FIGURE 32. *Iphione richeri* **sp. n.**, non-type specimen (ZMA V471.11). A. Bent ventrally, dorsal view, left elytron 6 and right elytra 6 and 7 removed. B. Right elytron 6, frontal view (inset: largest fimbriae). C. Chaetiger 12, left parapodium, posterior view (inset: upper neurochaetal tips). Scale bars: A, 1.1 mm; B, 0.7 mm, C, 0.3 mm.

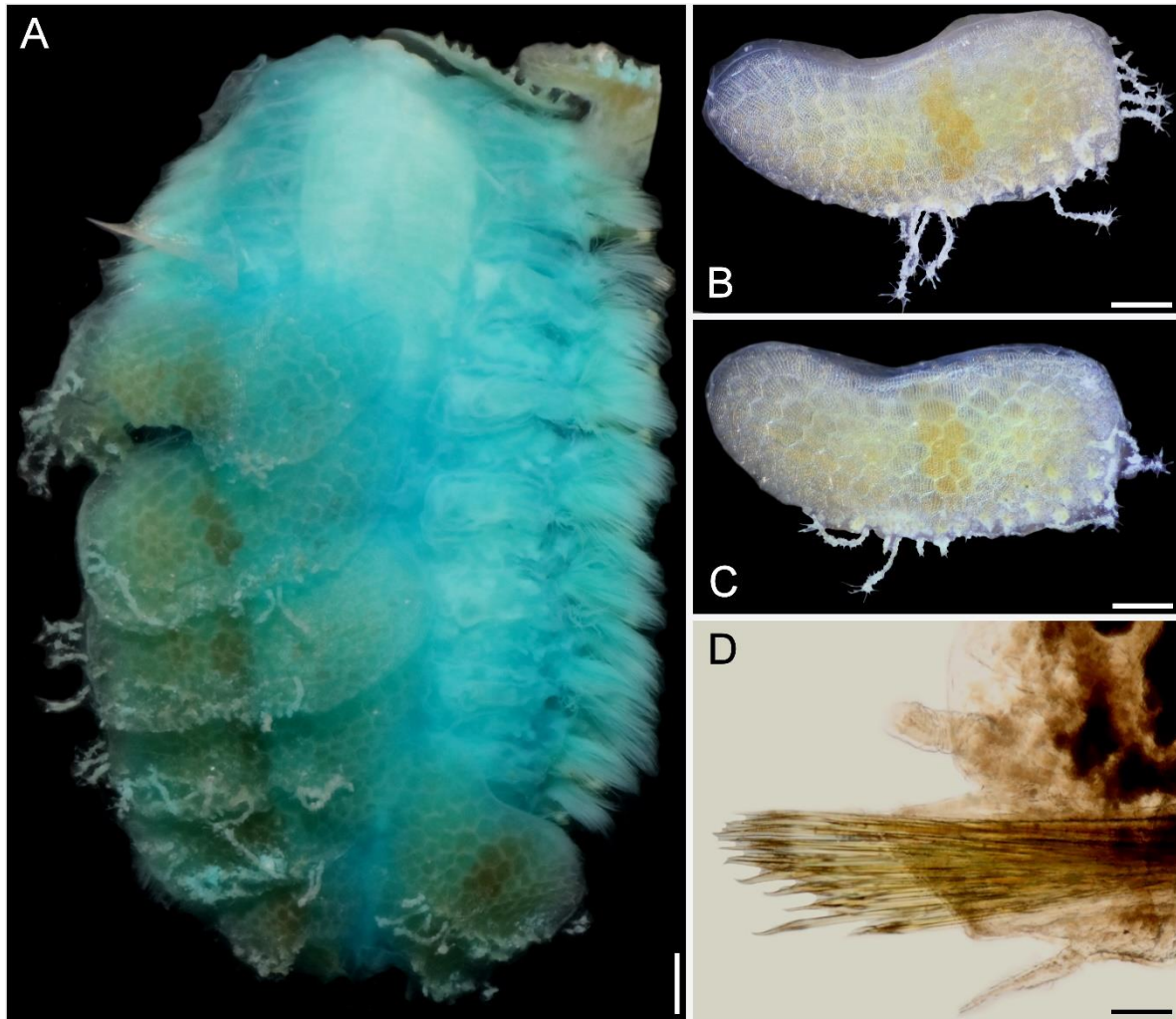


FIGURE 33. *Iphione richeri* **sp. n.**, non-type specimen (UF 202). A. Dorsal view after Methyl green staining. B. Right elytron 6, dorsal view. C. Right elytron 7, dorsal view. D. Chaetiger 12, left parapodium, anterior view, notochaetae removed. Scale bars: A, 0.6 mm; B, C, 0.7 mm; D, 0.2 mm.

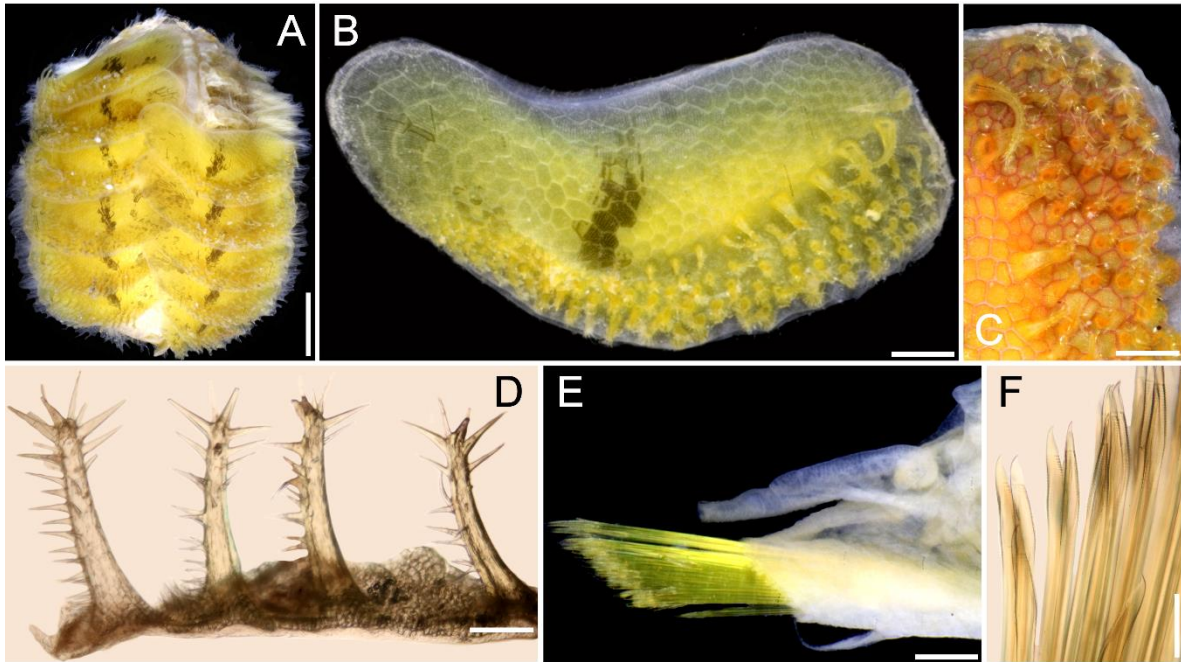


FIGURE 34. *Iphione wilsoni* **sp. n.**, holotype (NMV F164319). A. Dorsal view. B. Right elytron 6, dorsal view. C. Same, close-up of external margin after Shirlastain-A. D. Another elytron, transverse section across central macrotubercles region. E. Chaetiger 12, left parapodium, posterior view after removal of notochaetae. F. Same, neurochaetal tips. Scale bars: A, 2.7 mm; B, 0.8 mm; C, E, 0.4 mm; D, 150 μ m; F, 130 μ m.

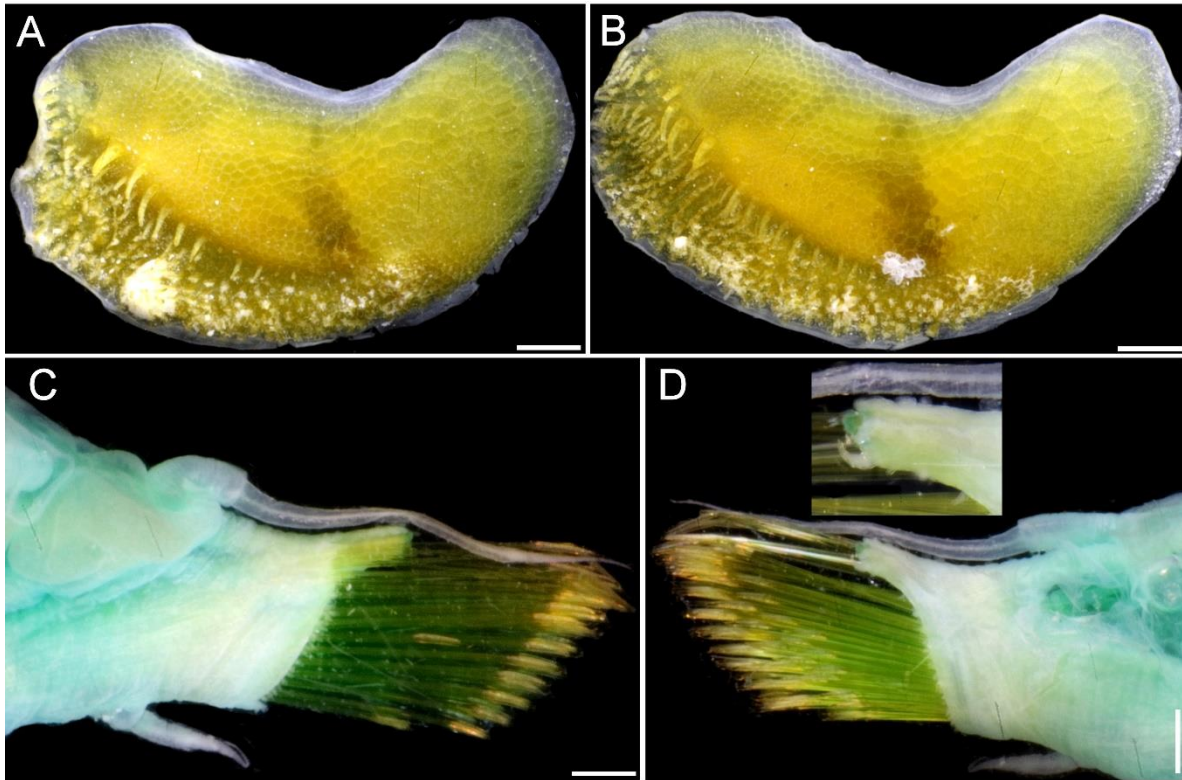


FIGURE 35. *Iphione wilsoni* **sp. n.**, non-type specimen (MAGNT w5511). A. Anterior left elytron. B. Median left elytron. C. Chaetiger 12, right parapodium, posterior view (after Methyl green staining). D. Same, anterior view (inset: tip of neuracicular lobe). Scale bars: A, 1.1 mm; B, 1.2 mm; C, 0.7 mm; D, 0.5 mm.

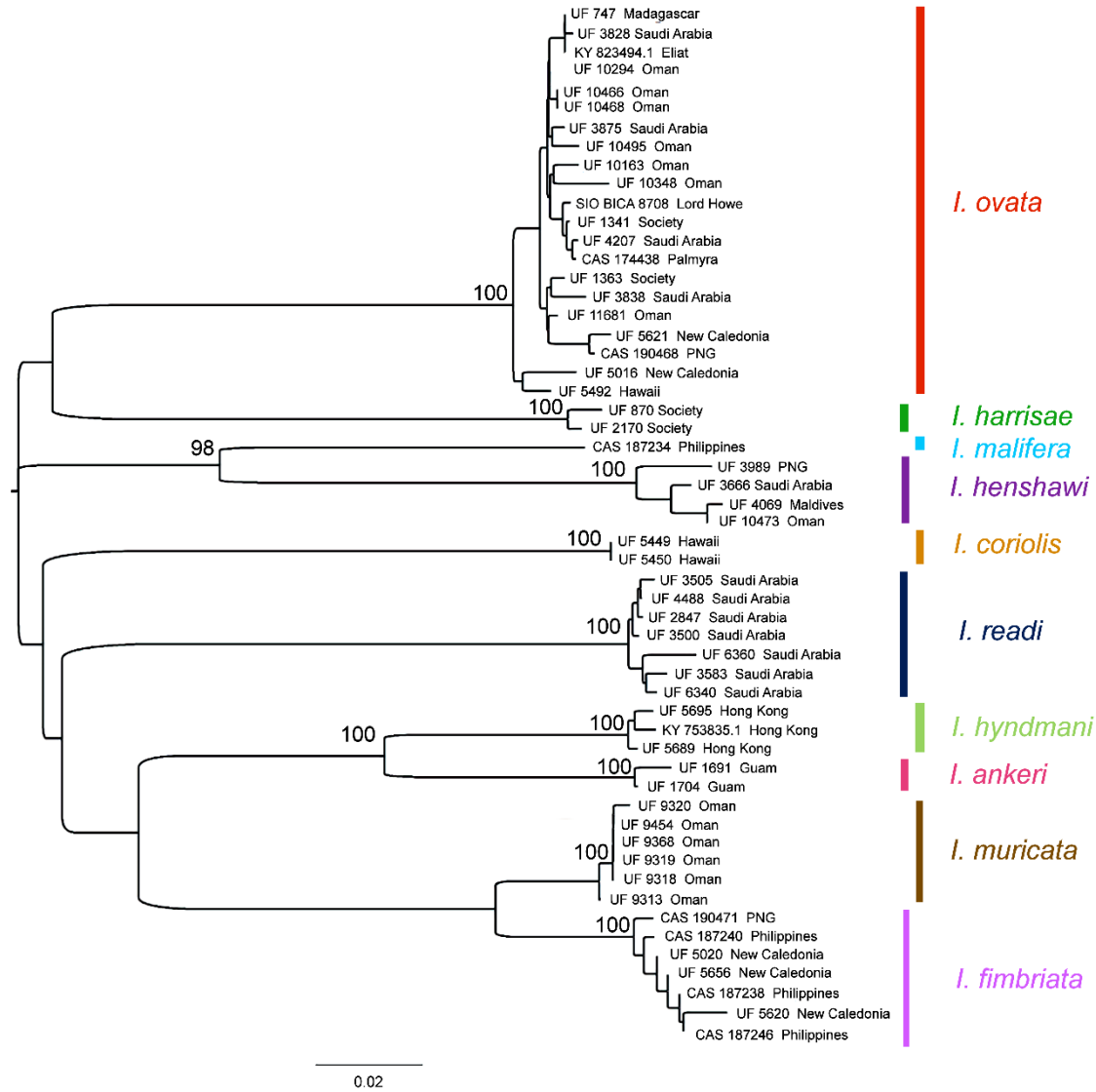


FIGURE 36. Maximum Likelihood phylogeny of *Iphione* species with localities and catalog numbers. Numbers above branches are bootstrap support (>70 only) (PNG: Papua New Guinea) (modified after Piotrowski et al. 2024).