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Redescription of *Iphione ovata* Kinberg, 1856 and confirmation of its Indian Ocean-Eastern Pacific distribution (Annelida, Aphroditiformia, Iphionidae)

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Couverture / *Cover* :
Iphione ovata Kinberg, 1856, Clipperton Island: adult specimen (ECOSUR, Sta. 17), dorsal view showing fully developed elytral pigmentation.

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Redescription of *Iphione ovata* Kinberg, 1856 and confirmation of its Indian Ocean-Eastern Pacific distribution (Annelida, Aphroditiformia, Iphionidae)

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ABSTRACT
Iphione Kinberg, 1856 includes tropical marine scaleworm species which live in rocky bottoms, often on the undersurface of coral rubble or rocks, and superficially resemble chitons. The most widely distributed species known is *Iphione ovata* Kinberg, 1856, originally described from Hawaii and recorded from the Red Sea and Indian Ocean to Western Mexico in the Eastern Pacific. A similar species, *I. spinosa* Kinberg, 1858, was described from South Africa based on a single specimen, which differed from the Hawaiian *I. ovata* by its fewer and larger elytral macrotubercles. The examination of over 100 specimens of different size and from various localities has permitted us to clarify ontogenetic variability in *I. ovata*. Certain specimens studied from the Red Sea to Hawaii and Southeastern Polynesia were sequenced for cytochrome c oxidase I and genetic variation of *I. ovata* was confined to a single genetic lineage confirming the wide range of the species and lack of cryptic lineages. Based on the available evidence, we confirm the wide distribution of *I. ovata* along the Indian and Pacific Oceans and include as junior synonyms *I. spinosa* and *I. reticulata* Amoureux, Rullier & Fishelson, 1978, originally described from the Red Sea with one small juvenile. A key for identifying all *Iphione* species from Hawaii is included.

KEY WORDS
Morphology,
elytra,
macrotubercles,
cytochrome c oxidase I,
variability.

RÉSUMÉ
*Redescription d'*Iphione ovata *Kinberg, 1856 et confirmation de sa distribution dans l'océan Indien et l'Océan pacifique (Annelida, Aphroditiformia, Iphionidae).*
Iphione Kinberg, 1856 comprend des espèces de polychètes à écailles des mers tropicales qui vivent dans les fonds rocheux, souvent sur la surface inférieure des débris coralliens ou des rochers, et qui ressemblent superficiellement à des chitons. L'espèce la plus largement distribuée est *I. ovata* Kinberg, 1856, décrite à l'origine de Hawaii et recensée depuis la mer Rouge et l'océan Indien jusqu'à l'ouest du Mexique dans le Pacifique oriental. Une espèce similaire, *I. spinosa* Kinberg, 1858, a été décrite d'Afrique du Sud sur la base d'un seul spécimen qui diffère de l'espèce Hawaiienne *I. ovata* par les macrotubercules de ses écailles, moins nombreux et plus gros. L'étude de plus de 100 spécimens de différentes tailles et provenant de diverses localités nous a permis de clarifier la variabilité ontogénétique chez *I. ovata*. Certains spécimens étudiés de la mer Rouge à Hawaii et au sud-est de la Polynésie ont été séquencés pour la cytochrome c oxydase I et la variation génétique d'*I. ovata* était confinée à une seule lignée génétique, confirmant la large aire de répartition de l'espèce et l'absence de lignées cryptiques. Sur la base des données disponibles, nous confirmons la large distribution d'*I. ovata* le long des océans Indien et Pacifique et incluons comme synonymes juniors *I. spinosa* et *I. reticulata* Amoureux, Rullier & Fishelson, 1978, décrite à l'origine de la mer Rouge sur un seul juvénile de petite taille. Une clé d'identification de toutes les espèces d'*Iphione* d'Hawaii est incluse.

MOTS CLÉS
Morphologie, écailles, macrotubercles, COI-séquences, variabilité.

INTRODUCTION

Iphione ovata Kinberg, 1856 is regarded as a cosmopolitan species after a revision by Pettibone (1986). This interesting scaleworm, originally described from Hawaii, bears a strong resemblance to chitons due to its large rigid elytra completely covering the dorsum and its habit of living on the undersurface of rocks or rubble, firmly clinging to the substrate by means of engagement of a complex set of powerful dorsoventral muscle strands (Storch 1967). Pettibone (1986) studied specimens originating from the entire Indo-Pacific, including specimens from the Indian Ocean (Red Sea to Madagascar, Maldives), Australia, and localities in the Central Pacific to the Eastern Pacific (Gulf of California, Clipperton Island). She considered *I. spinosa* Kinberg, 1858 from South Africa, and *I. hirotai* Izuka, 1912 described from Japan as junior synonyms of *I. ovata*. Pettibone (1986) studied the type specimen and illustrated its anterior end but based her redescription on a single specimen from Ifaluk Atoll, Caroline Islands, a locality quite far from Hawaii, and compiled features described in previous publications.

Augener (1922: 5-6) studied the type material of Kinberg's species, *I. ovata* and *I. spinosa*. He concluded that elytral macrotubercles and fringe may become eroded and thus they cannot be used to separate these species from *I. muricata* (Savigny *in* Lamarck, 1818); thus, he concluded that both *I. ovata* and *I. spinosa* must be junior synonyms of *I. muricata*. After his publication *I. spinosa* was not used again as a valid species name.

Hanley & Burke (1991) in their study of Coral Sea polynoids described and illustrated one specimen of *I. ovata* with red-brown elytra, yet their description includes interesting differences compared with what Pettibone observed. They noted that: 1) palps and lateral antennae were of similar length, instead of palps clearly longer than antennae; 2) dorsal cirri barely reached the neurochaetal lobe tips, instead of markedly surpassing them; 3) ventral cirri were tapered rather than medially swollen; 4) macrotubercles were sparsely arranged in three irregular rows, instead of abundantly arranged in 4-5 straight rows; and 5) bidentate neurochaetae were present instead of all unidentate chaetae.

Wehe (2006) published the most recent account of *I. ovata* based upon two Red Sea specimens. His color photograph depicts yellowish elytra with ill-defined, discontinuous longitudinal dark spots. His line drawings resemble the specimen from the Caroline Islands illustrated by Pettibone in that both illustrations depict palps as longer than lateral antennae, elytral macrotubercles abundant in several rows, long dorsal cirri, swollen ventral cirri, and all neurochaetae unidentate. The main differences between these specimens are that: 1) Red Sea specimens have neurochaetae with fewer rows of denticles, with all rows restricted to the distal region and not surpassing the well-developed swollen region, whereas there are more rows in the Caroline Islands specimen, and the swollen region is less defined; 2) the basal areas of the dorsal cirrophores are barely swollen instead of notably swollen; and 3) the paired dorsal tubercles along the first few chaetigers are larger in the Red Sea specimen than in the Caroline Islands specimen.

It is possible that all of these specimens are conspecific, and the observed differences are due to size-dependent variation; alternatively, more than one biological species could be involved across a wide geographic distribution, and these differences may be diagnostic for separating these taxa. Clarification of the characters in the type material and in topotypical specimens is necessary to permit a better understanding of the true distribution of these species. In this contribution, we redescribe *I. ovata* by studying the holotype alongside topotypical specimens. We note that some features appear to be size dependent, and we were unable to observe any consistent differences among specimens. The morphological examination, alongside a strong genetic affinity among specimens from across the Indo-Pacific, lead us to include as a junior synonym *I. spinosa* Kinberg, 1858 described from South Africa. In agreement with Wehe's (2006) assessment,

we also regard *I. reticulata* Amoureux, Rullier & Fishelson, 1978 from the Red Sea as a junior synonym. We concur with Wehe's conclusion that the holotype of this species is a juvenile *I. ovata* specimen; its morphology matches the features shown by *I. ovata* juvenile specimens. Based on the lines of evidence described herein we support conclusions reached by Pettibone regarding the taxonomic status and synonymies stated above. We include a key to identify all *Iphione* species from Hawaii in accordance with Pettibone's evaluation of *I. ovata* from the type locality, with tentative inclusion of *Iphione coriolis* Hanley & Burke, 1991.

MATERIAL AND METHODS

Morphology assessment

Morphology was assessed using a comparative approach, and the size-related changes were evaluated as follows.

Eye and nuchal hood variation

Eye size variations were studied in three *I. ovata* specimens collected in two stations in Clipperton Island. The smallest specimen (8.5 mm long, Sta. 32) has small eyes; anterior eyes are oval to circular, sit in the widest central prostomial area, but they are not on the surface, rather under it, whereas the posterior eyes are circular and lie in the posterolateral prostomial margins (Fig. 1A). The posterior eyes look slightly larger than anterior ones, probably because they are on the prostomial surface. The two other specimens were found in another locality (Sta. 17). The medium-sized specimen (16.5 mm long) had the prostomium contracted so that the posterior eyes look more marginal than in the smallest specimen (Fig. 1B), whereas the anterior eyes look oval and are within a lateral protuberance but displaced posteriorly. The largest specimen (24 mm long) has the anterior prostomial area bent ventrally, and the eyes are fully grown. The anterior eyes are not on the surface, have an oval shape, and are on the widest prostomial area, whereas the posterior eyes and close to the posterior prostomial margin (Fig. 1C). It can be concluded that anterior and posterior eyes are of similar size, that anterior eyes are directed laterally but are placed under the lateral prostomial margins, they can be projected into lateral protuberances, whereas the posterior eyes are on prostomial surface, being mostly circular to slightly oval, but their shape and position can be modified by the contraction of the anterior end, so that sometimes anterior and posterior eyes are very close to each other laterally. Once these modifications due to anterior end contractions are understood, there were no major differences regarding their relative size or position on the prostomium. However, because eye size is size-dependent, for assessing the diagnostic relevance of this feature, the size of the specimen must be taken into account. Hanley (1989, figs 4A, 5A) documented a similar trend for *Arctonoe fragilis* (Baird, 1863), with larger specimens having larger eyes. On the other hand, nuchal hoods were semicircular in all specimens, but they become better defined and larger in older specimens.

Dorsal cirrophore variation

Right parapodia of chaetigers 6, 14 and 22 were dissected from two specimens from the same locality (Sta. 32); a medium sized specimen (16 mm long), and the largest specimen (24 mm long). The dorsal cirrophore is cylindrical and there is a hypertrophied basal tubercle which is expanded along its longitudinal axis; this tubercle is regarded as projected if it is expanded laterally and obliterates the observation of the basis of dorsal cirrophores. Medium-sized specimens have a basal tubercle projected as a single lobe along body (Fig. 1D-F). Larger specimens also have a single basal tubercle to dorsal cirrophores (Fig. 1G-I). This implies that the shape of the basal tubercle of dorsal cirrophores is not modified during growth, at least when specimens are 16 mm in length, or larger. However, specimens smaller than 15 mm might not have an enlarged basal tubercle in dorsal cirrophores. An interesting difference was found regarding the development of ventral cirri; smaller specimens have them tapered, whereas in larger specimens, they are thicker, mucronate. Consequently, the type of basal tubercles in dorsal cirrophores is consistent, not modifed during growth, once a critical size has been reached (15 mm in length), and they can be used as additional diagnostic features for separating similar species. There is something that must be kept in mind; older, ethanol fixed specimens might have become relaxed, and the visibility of the basal tubercle might be more difficult to be noted than in formaline fixed specimens, because they are usually more contracted, and the basal tubercle is more easily noted.

Elytral pigmentation and ornamentation

Pigmentation of elytra was noted in gross view. Smaller specimens tend to have yellowish elytra, without black spots, although some specimens can have some irregular spots around the elytral centre. Larger specimens can have oblique longitudinal black bands, or elytra can be brownish. The number of elytral areoles and rows of macrotubercles was assessed with 87 specimens that could be measured, and one median elytron was dissected for observing and counting the rows of macrotubercles present. In general, there is a wide variation in the number of rows of macrotubercles per elytron, and their number is size-dependent (Fig. 2), although macrotubercles are progressively smaller towards posterior margins.

Because of the heterogeneous and poor condition of the type specimens, only some elytra could be observed in our attempt to understand variation across body regions. For non-type specimens, right elytra of anterior, middle and posterior regions were dissected; each was carefully cleaned with a brush (vinegar-ethanol solution was used carefully and elytra were brushed while immersed in the solution for half a minute, one elytron at a time).

Elytra were photographed to record their pigmentation; sometimes they were temporarily stained with Methyl green or Shirlastain-A for improved visibility of the elytral surface and tubercles, with finer details observed using compound microscopes.

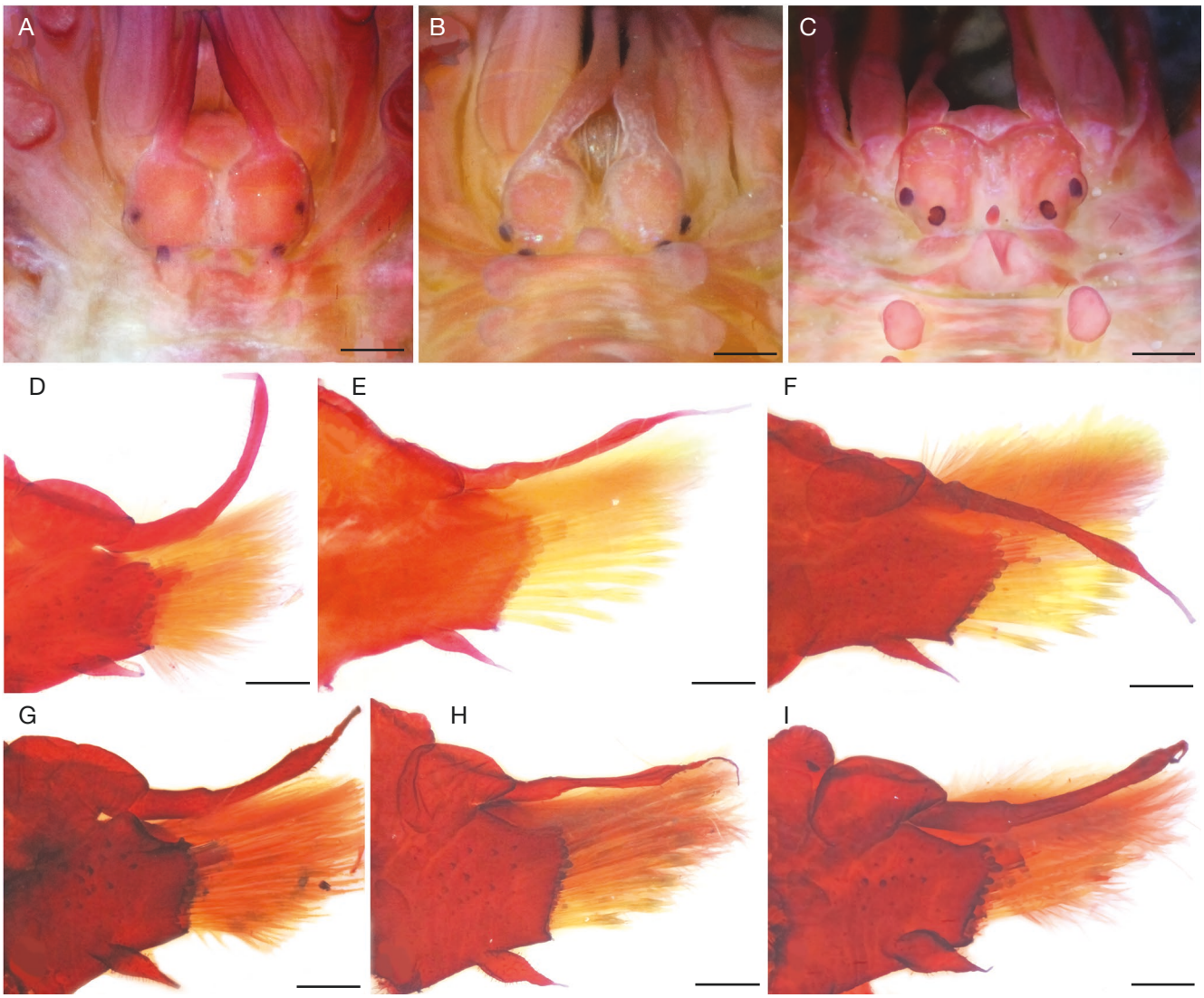

Fig. 1. — *Iphione ovata* Kinberg, 1856, non-type specimens (ECOSUR), eye and parapodial development: **A**, smallest specimen (8.5 mm long, Sta. 32); **B**, medium-sized specimen (16.5 mm long, Sta. 17); **C**, largest specimen (24 mm long, Sta. 32); right parapodia in posterior view, medium-sized specimen (16 mm long, Sta. 32); **D**, chaetiger 6; **E**, chaetiger 14; **F**, chaetiger 22; same, largest specimen (24 mm, Sta. 32); **G**, chaetiger 6; **H**, chaetiger 14; **I**, chaetiger 22. Scale bars: A, 0.23 mm; B, 0.42 mm; C, 0.50 mm; D–F, 0.33 mm; G, 0.31 mm; H, 0-45 mm; I, 0-37 mm.

Pharynx

Pharynx was fully exposed in about 20% of all specimens. Kinberg (1858) included details for the pharynx of *I. ovata* and *I. spinosa*, showing there were 9-10 pairs of lobate papillae along their margins, and that jaws have 2-4 accessory denticles. Pettibone (1986) did not include this feature in the diagnosis of *Iphione*, nor discussed it in the section on the morphology of the species. However, she illustrated the tip of pharynx of two specimens of what she regarded as *I. muricata* (her Figs 2I; 3C); these figures show the pharynx has 10 pairs of lobate papillae along its margin, and four jaws, each with 3-4 accessory denticles. We noted that the number of accessory denticles is size-dependent, whereas the shape of individual papillae varies after preservation. This is why we have not paid special attention to these features, especially because the pharynx is exposed in only about 20% of specimens.

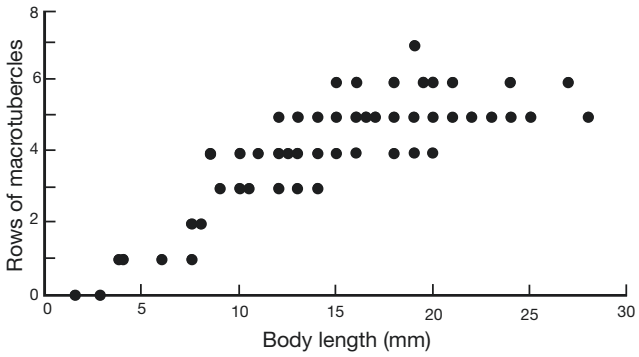

Fig. 2. — Variation in the number of rows of macrotubercles per elytron against body length of *Iphione ovata* Kinberg, 1856, non-type specimens from different localities.

Molecular affinities

Tissues from some specimens were sequenced for mitochondrial cytochrome c oxidase I (COI). Most of these sequences were generated as parts of large-scale barcoding studied of regional faunas, but some were carried out for this study. To enlarge our sampling, we include also sequences from other *Iphione* species (see Figure 11); these will be fully reported upon in a future revision of the genus. DNA was isolated from body wall or parapodia tissue. Tissue samples were processed at the Smithsonian Institution Laboratories of Analytical Biology (LAB). Tissue samples were digested overnight in 150 ul M2 buffer and 150 ul M1 + proteinase K buffer at 56.5°C while 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. PCR was performed on an ABI 2720 Thermal Cycler or MJ Research PTC-225 Peltier Cycler. The PCR profile used for amplifying COI was as follows: initial denaturation at 95°C for 5 minutes, 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 minutes. The PCR products were cleaned using ExosapIT (from USB). Sequence data were collected for the mitochondrial marker CO1 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); all samples were sequenced in both directions. Chromatograms were cleaned, assembled, and aligned using the program Geneious (Kearse *et al.* 2012), and checked by eye. Cleaned sequences were checked for stop codons and indels suggesting NUMTs. A neighbor joining tree was generated using MEGA (Tamura *et al.* 2007). Sequences for specimens identified as *I. ovata* have been deposited in GenBank (PP216738-PP216756).

Illustrations and museums

Photographs were made with a digital camera with an adapter for the microscopes. Additional LED illuminators, in combination with standard microscope lamps, were used. Specimens were temporarily stained with Methyl green, or Shirlastain-A, and this can be noted by their greenish or reddish color in the plates. Series of focus stacked photos were rendered with HeliconFocus8 and plates were arranged with PaintShopPro9. Details of the molecular analysis, together with a clarification of the species included in the tree will be provided in a forthcoming publication addressing all other *Iphione* species. Specimens are deposited n the institutions listed below.

Abbreviations

AM	Australian Museum, Sidney;
BPBM	Berenice P. Bishop Museum, Honolulu;
CASIZ	California Academy of Sciences Invertebrate Zoology Collection, San Francisco;
ECOSUR	El Colegio de la Frontera Sur, Unidad Chetumal;
LACM	Allan Hancock Polychaete Collection, Natural History Museum of Los Angeles County, Los Angeles;
MAGNT	Museum and Art Gallery, Northern Territory, Darwin;
MNHN	Muséum national d'Histoire naturelle, Paris;
NHM	Natural History Museum, London;
RMNH	Naturalis Biodiversity Center, Leiden;
SMNH	Swedish Museum of Natural History, Stockholm;
UCO	Molecules, Mer, Santé, Université catholique de l'Ouest, Angers;
UF	Museum of Natural History, University of Florida, Gainesville;
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.;
ZMA	Zoological Museum, University of Amsterdam (now in Naturalis);
ZMH	Zoologisches Museum, Hamburg.

RESULTS

Family Iphionidae Kinberg, 1856
Genus *Iphione* Kinberg, 1856

Iphione ovata Kinberg, 1856
(Figs 1-11)

Iphione ovata Kinberg, 1856: 383; 1858: 8, pl. 3, fig. 8; pl. 10, fig. 45. — Baird 1865: 181. — de Quatrefages 1866: 269-270. — Chamberlin 1919: 64. — Treadwell 1926: 5. — Monro 1928: 557-558. — Hartman 1939: 103-104, pl. 3, figs 31, 32. — Rioja 1963: 137-41, figs 30-36. — Pettibone 1986: 16-19, fig. 6 (syn.). — Wehe 2006: 67-69, fig. 9a-I, pl. 1a. — Dean 2009: 181 (photo). — Solís-Weiss & Hernández-Alcántara 2009: 257, fig. 273. — Cortés *et al.* 2017: 217, fig. 7.4c.

Iphione spinosa Kinberg, 1858: 8-9, pl. 10, fig. 46. — Baird 1865: 181. — de Quatrefages 1866: 272. — Michaelsen 1892: 95.

Iphione muricata – Willey 1905: 246-248. — Horst 1917: 286 (*non* Savigny *in* Lamarck 1818). — Augener 1926: 442 (*partim*). — Pruvot 1930: 3-5, fig. 1. — Monro 1939: 168 (*partim*). — Fauvel 1943: 2 (*non* Savigny *in* Lamarck 1818); 1953: 173. — Gibbs 1971: 123 (*partim*). — Hartmann-Schröder 1991: 19 (*partim*) (*non* Savigny *in* Lamarck 1818).

Iphione reticulata Amoureux, Rullier & Fishelson, 1978: 68-69, fig. 2. — Solís-Weiss *et al.* 2004: S14.

Type material. — **Hawaii** • 5 specimens, holotype of *I. ovata* Kinberg, 1856 and 4 paratypes; Oahu, Honolulu; 21°19'N, 157°52'W; Eugenie Expedition 1851-1853, no further data; holotype SMNH Type 388, paratypes SMNH Type 8410.
South Africa • 1 specimen, holotype of *I. spinosa* Kinberg, 1858; Port Natal; 30°S, 31°E; Eugenie Expedition 1851-1853; Wahlberg J. A. leg.; coll., no further data; SMNH Type 392.
Red Sea • 1 specimen, holotype of *Iphione reticulata* and microslide containing posterior elytra and left parapodium from same; Gulf of Eilat, Eilat, artificial lagoon; 1974; Fishelson L. or Rullier F. leg.; MNHN-POLY-TYPE-1430; microslide UCO Y97'.

Additional material. — **Hawaii** • 1 specimen; Oahu, Laie, Makua; 8.VIII. 1949; Fellows D. B. leg.; coll.; BPBM R1377 (complete, slightly bent; body 19 mm long, 9 mm wide, 28 chaetigers; first pair of chaetigers and elytra directed ventrally; midbody elytra yellowish, with short, oblique blackish band, surface with 6-7 concentric rows of macrotubercles) • 1 specimen; Kauai County, Kauai, Port Allen; 13-30 m; 12.IX.1959; no further data; BPBM R1383 (orange reddish; body 11 mm long, 6 mm wide, 28 chaetigers) • 1 specimen; Lanai, Kalaeahole; 2.III.2005; Bolick H. leg.; BPBM R3741 (minute, colorless, body transparent; elytra transparent with wide band of diffuse black spots, elytra with undulated margins, no macrotubercles observed; body 2.8 mm long, 2.8 mm wide, 18 chaetigers)

• 2 specimens; Oahu, Black Point, Khala side; VI.1939; Abbott D. P. leg.; shallow water, under rocks and inside coral rocks; CASIZ 16707 (bent ventrally; elytra orange with small oblique blackish bands, or without them, 5 diffuse rows of digitate spinulose macrotubercles; anterior elytral pairs removed for observing anterior end, right parapodium of chaetiger 14 dissected (retained in container); body 18-21 mm long, 8.5-11.0 mm wide, 29 chaetigers) • 1 specimen; Maui, Pali, Scenic Lookout; 20°37'30.0"N, 156°10'01.9"W; 2-20 m; 24.X.2005; Pittman C. leg.; UF 423 (bent ventrally; first 4 pairs or elytra removed and two parapodia dissected (retained in container); 5 rows of spinulose macrotubercles, no visible pigment but elytra with heavy debris; body 15 mm long, 6.5 mm wide, 28 chaetigers) • 1 specimen; Kaneohe Bay, outer reef north, end of bay; 21°30'14.4"N, 157°48'07.2"W; 14 m; 28.V.2017; Paulay G. *et al.* leg.; outer reef slope; UF 5492 (juvenile, elytra undulated due to dehydration; elytra maculate, with a single series of short macrotubercles at edge of polygonal area internal to wide margin rim; body 3.8 mm long, 2.6 mm wide, 22 chaetigers) • 2 specimens; *USFSS Albatross*, Sta. 3968; 23°46'00"N, 166°18'55"W; French Frigate Shoals; 26-30 m; 29.V.1902; USNM 5438 (slightly bent ventrally, dark gray, largest specimen with several elytra previously removed (retained in container); elytra with 3-4 rows of short spine-like tubercles; body 12-16 mm long, 6.0-7.5 mm wide, 28-29 chaetigers).

Red Sea. Israel • 1 specimen; Elat, Gulf of Akaba, Sta. 22; no further data; NHM 1956.8.8.14 (most anterior elytra previously removed, some in container; elytra yellowish with an irregular central dark spot; each with 3 rows of macrotubercles; body 10.5 mm long, 5.5 mm wide, 29 chaetigers).

Saudi Arabia • 1 specimen; Red Sea Biodiversity Cruise, Ablo Island reef; 18°39.57'N, 40°49.62'E; 0-40 m; 5.III. 2013; Gosliner T. M. leg.; CASIZ 192037 (bent ventrally, left parapodium from chaetiger 14 and one elytron removed for observation (kept in container; body 20 mm long, 9 mm wide, 28 chaetigers; elytra orange with short, oblique black bands; macrotubercles conical, arranged in 5-6 irregular concentric rows, each macrotubercle with stem spiny, tip with 2-3 long spines) • 1 specimen; Farassan Banks, Shi'b Ammar; 19°34'15"N, 40°0'32"E; 2-20 m; 3.III.2013; Anker A., Norby P. & Paulay G. leg.; reef lagoon and fore reef wall; UF 3661 (juvenile, markedly bent ventrally; elytra yellowish with abundant dark spots; body 5.1 mm long, 4 mm wide, chaetigers not counted) • 1 specimen; Island near Jaz'air Sila; 27°39'03.5"N, 35°16'59.7"E; 10-30 m; 27.IX.2013; Paulay G., McKeon S., Uyeno D., Moore J. & Zakroff C. leg.; fore reef, under rocks; UF 3828 (slightly bent dorsally, light yellow elytra with diffuse black spots forming two dorsal bands, spinulose macrotubercles in 4-5 rows; body 14 mm long, 6.5 mm wide, 29 chaetigers • 1 specimen; Gulf of Aquaba, Magna Coast Guard; 28°24'14"N, 34°44'27"E; 0-1 m; 29.IX.2013; Paulay G. leg.; reef flat, under rock; UF 3838 (elytra orange with a few dark spots; right elytron 6 and left parapodium of chaetiger 12 removed for observation; 3.4 rows of macrotubercles; basal tubercle of dorsal cirrophore projected; body 12.5 mm long, 6.5 mm wide, 29 chaetigers) • 1 specimen; An-Numan; 27°8'20"N, 35°45'3"E; 0-1 m; 2.X.2013; Moore J. leg.; silty fringing reef; UF 3875 (markedly bent juvenile, right elytron 6 removed for observation, 3 rows of macrotubercles; body 9 mm long, 4.5 mm wide, chaetigers not counted for avoiding further damage) • 1 specimen; Gulf of Aqaba, Magna Coast Guard; 28°24'13.9"N, 34°44'26.4"E; 0-60 m; 29-30.IX.2013; Paulay G., McKeon C., Uyeno D., Moore J., Zakroff C. & Hobbs J.-P. leg.; UF 3898 (slightly bent ventrally; elytra black spots barely visible; right elytron 6 and left parapodium of chaetiger 12 removed for observation (kept in container); macrotubercles in 4 rows; body 10 mm long, 6.5 mm wide, 28 chaetigers) • 1 specimen; Yanbu, Racon, Marker 2R; 23°34'51"N, 38°27'17"E; 1-20 m; 4.III.2014; Paulay G. leg.; steep reef slope; UF 4207 (right median parapodia and elytral fractions removed for molecular studies; elytra yellow, with black central spots; left elytron 6 and parapodium of chaetiger 12 removed for observation; 4-5 rows of macrotubercles; basal tubercle of dorsal cirrophore well-defined; body 13 mm long, 7 mm wide, 29 chaetigers) • 1 specimen; Gulf of Aqaba, Magna Coast Guard; 28°24'13.9"N, 34°44'26.4"E; 0-1 m; 29.IX.2013; Paulay G. leg.; reef flat; UF 4281 (markedly bent ventrally; elytra with black spots forming dorsal bands, larger along anterior chaetigers, macrotubercles in 3-4 rows, pharynx exposed, jaws with 2 denticles; body 12 mm long, 5 mm wide, chaetigers not counted).

Sudan • 1 specimen; Suakin Harbor; 1904-1905; Crossland C. leg.; coral; NHM 1941.4.4.173 (markedly bent; elytra yellowish, two already removed, and left parapodium of a median chaetiger; elytra with 4-5 rows of macrotubercles; neurochaetae unidentate, slightly falcate; not measured to avoid further damage).

Kenya • 1 specimen; Diani Beach, in front of Two Fishes hotel, lagoon near high tide; 04°18'S, 39°38'E; 1.3-2.7 m; 26.III.1981; Ferreira A. J. leg.; CASIZ 204323 (complete, some elytra dislodged, contracted, exposing chaetae; anterior elytra removed for observing anterior end; right elytron 7 removed for observing details, left parapodium of chaetiger 14 and pharynx dissected (kept in container); elytra golden with some epizoans; body 20 mm long, 11 mm wide, 29 chaetigers; other details indicated in Variation section) • 1 specimen; Nyal, Mombassa; low water mark; McGregor D. leg.; under coral boulders; NHM 1961.8.2 (juvenile, markedly bent ventrally, some elytra previously removed (kept in container), elytra yellowish with spread central dark spots, with macrotubercles arranged in 2-3 rows; not measured) • 2 specimens; Andromache Reef, 800-1200 m offshore, mouth Mombasa Harbor; 04°05'S, 39°40'E; 3-10 m; 18.XI.1964; Earle S. A. leg.; USNM 81959 (soft, likely preserved in ethanol; body 10.5-11.0 mm long, 5.0-5.5 mm wide, 28 chaetigers).

Tanzania • 1 specimen; Bani Island, Zanzibar; Struhlmann leg.; no further data; ZMH V4576 (bent ventrally; elytra yellowish with abundant calcareous epibionts; elytra with 5-6 rows of macrotubercles; body 19.5 mm long, 10 mm wide, 29 chaetigers).

Seychelles, Aldabra Island • 3 specimens; main channel; 3 m; 4.XII.1964; Earle S. A. leg.; coral rocks; USNM 81961 (elytra previously removed, kept in container; two specimens bent ventrally; body 10-14 mm long, 5-7 mm wide, 29 chaetigers) • 2 specimens; 25.IV.1895; Voltzkow leg.; no further data; ZMH PE 187a (one markedly bent ventrally, the other slightly bent; right elytron 6 and left parapodium of chaetiger 12 removed for observation (kept in container); elytra yellowish with an irregular central dark spot, and 3-4 rows of macrotubercles; basal tubercle of dorsal cirrophore barely projected; neurochaetae unidentate; body 19 mm long, 10 mm wide, 29 chaetigers).

Seychelles • 1 specimen; Sea Lark Expedition, Coetiay (sic, probably Coëtivy Island); 07°08'S, 56°16'E; Seychelles after Gardiner 1907: 137; 1905; Gardiner J. S. leg.; no further data; NHM 1941.4.175; (slightly bent ventrally; elytra yellowish with oblique longitudinal bands barely visible, some previously removed (kept in container), each with 5 rows of macrotubercles; body 13 mm long, 7 mm wide, 29 chaetigers).

Madagascar • 2 specimens; Diego Suarez and Nosy-Bé; no further data; NHM 1961.8.4-5 (one markedly bent, some elytra previously removed; left parapodium of chaetiger 12 removed for observation (kept in container); elytra with oblique longitudinal dark band, and 4-5 rows of macrotubercles; neurochaetae unidentate, slightly falcate; body 12-15 mm long, 7.0-7.5 mm wide, 29 chaetigers).

Réunion Island • 1 specimen; Saint-Paul, Trou d'eau; 21°06'06.0"S, 55°14'37.0"E; 0-1.5 m; 8.VIII.2007; Bruggemann H., Nicolas H., Michonneau F. & Paulay G. leg.; fringing reef moat and reef; UF 644 (bent ventrally, elytra with oblique black band, macrotubercles in 4-5 rows; body 15 mm long, 8.5 mm wide, 28 chaetigers).

Sri-Lanka • 1 specimen; Trincomali; Sarasin leg.; no further data; ZMH V9843 (bent ventrally; right elytron 6 removed for observation; elytra yellowish, with a central black spot, and darker posterior region; 4-5 rows of macrotubercles, progressively smaller posteriorly; not measured for avoiding further damage).

Indonesia • 1 specimen; Maluku, RV *Siboga* Exped., Stat. 144; anchorage N of Salomakiëe (Damar) Island; 45 m; 7-9.VIII.1899;

dredge, townet + reef exploration, coral; ZMA V471.10b (juvenile, markedly bent ventrally; elytra yellowish with black spots; macrotubercles in 2 rows, progressively smaller posteriorly; not measured) • 3 specimens; Maluku, RV *Siboga* Exped., Sta. 193; Sula Besi Island, E coast, Sanana Bay; 22 m; 13-14.IX.1899; reef exploration, muddy bottom; ZMA V471.14 (juveniles, markedly bent; elytra yellowish with black central spots, or without them; macrotubercles in 2-3 rows; not measured) • 1 specimen; Sulawesi, RV *Siboga* Exped., Stat. 213; Saleyer anchorage; 36 m; 26.IX.1899; coral reef expl., muddy bottom; ZMA V471.15 (markedly bent ventrally; elytra yellowish, oblique longitudinal band barely visible; macrotubercles in 3-4 rows; not measured) • 2 specimens; Sulawesi, RV *Siboga* Exped., Sta. 220; Binongka, W coast, anchorage off Pasir Pandjang; 278 m; 1-3.XI.1899; dredge, coral sand; ZMA V471.16 (smallest markedly bent; right elytra 6 removed from both specimens (kept in container); elytra yellowish without black spots, with white epibionts; macrotubercles in 4-5 rows, progressively smaller posteriorly; largest one 19 mm long, 12 mm wide, 29 chaetigers) • 1 specimen; Maluku, RV *Siboga* Exped., Stat. 234; Nusa Laut Island, Nalahia Bay; 46 m; 19-20.XI.1899; reef exploration, stones; ZMA V471.19b (juvenile, markedly bent ventrally; elytra yellowish with some black central spots; macrotubercles in 3 rows; not measured) • 1 specimen; Banda Anchorage; 9-45 m; 22.XI.1899; ZMA V471.20 (markedly bent ventrally; elytra yellowish with black spots; macrotubercles in 3 rows, progressively smaller posteriorly; not measured) • 1 specimen; Lesser Sunda Islands, RV *Siboga* Exped., Sta. 310; 08°30'S, 119°07.5'E; 73 m; 12.II.1900; dredge, sand/coral; ZMA V471.25 (juvenile; some anterior elytra previously removed (kept in container); elytra yellowish with black spots; macrotubercles in 2 rows, decreasing in size posteriorly; body 8 mm long, 5 mm wide, 28 chaetigers) • 1 specimen; Lesser Sunda Islands, RV *Siboga* Exped., Sta. 315; Paternoster Island, anchorage E of Sailus Besar; 36 m; 17-18.II.1900; dredge, coral; ZMA V471.26 (markedly bent; right elytra 5 and 6 removed for observation (kept in container); elytra yellowish with a few black spots; macrotubercles in 4-5 rows, progressively smaller posteriorly; not measured) • 2 specimens; Java; no further data; ZMH PE187 (yellowish, elytra with abundant sediment and epibionts; 3-4 rows of macrotubercles; body 13.0-18.5 mm long, 7-10 mm wide, 29 chaetigers).

East Timor • 2 specimens; Timor, between Timor and Nusa Besi, anchorage; RV *Siboga* Exped., Sta. 282; 08°25.2'S, 127°18.4'E; 27-54 m; 15-17.I.1900; trawl; ZMA V471.23 (juveniles, markedly bent; anterior elytra with black spots, posterior elytra yellowish; macrotubercles in 2-3 rows; not measured).

Philippine Islands • 3 specimens; Luzon, Batangas Province, Mabini (Calumpan Peninsula), Balayan Bay, Eagle Point; 13°43'12"N, 120°52'12"E; 0-10 m; 2.V.2014; Principe A. leg.; CASIZ 197936 (bent ventrally, all with large spine-like macrotubercles; elytra of smallest specimen reddish with polygonal darker areas and three rows of macrotubercles, medium-sized specimen with blackish polygonal areas concentrated towards elytral center, four rows of macrotubercles; largest specimen with diffuse pigmentation, 5 rows of macrotubercles; body 10-17 mm long, 4.3-7.5 mm wide, 28 chaetigers) • 6 specimens; Luzon, Batangas Province, Mabini (Calumpan Peninsula), Balayan Bay, between Koala and Cathedral dive sites; 13°43'12"N, 120°52'12"E; depth not indicated; 29.IV.2014; Principe A. leg.; CASIZ 197947 (bent ventrally; five complete and one smallest specimen without anterior region, cannibalized in sampling bag; elytra orange reddish, venter pink; complete with body 16-22 mm long, 7-10 mm wide, 29 chaetigers).

Coral Sea, Chesterfield Reefs • 1 specimen; Cruise Corail 2, RV *Coriolis*, Chesterfield Reefs, Sta. RH 88-62; 19°12'S, 158°56'E; 16-26 m; 25.VII.1988; Hanley J. R. leg.; coral; MAGNT W5445 (some elytra and right parapodium of chaetiger 10 previously removed (parapodium lost), left parapodium of chaetiger 12 removed for observation; elytra yellowish with some calcareous epibionts; with 2-3 rows of macrotubercles; cirrigerous segments with basal tubercle of dorsal cirrophore projected, single-lobed; body 8.5 mm long, 5.5 mm wide, 28 chaetigers) • 1 specimen; Cruise Corail 2, RV *Coriolis*, Chesterfield Reefs, Sta. RH 88-73; 19°44'S, 158°21'E; 23-56 m; 2.VIII.1988; Hanley J. R. leg.; coral rubble and sand, MAGNT W5446 (many elytra and 3 parapodia previously removed (kept in container, only one parapodium); elytra yellowish with abundant epibionts; with 4-5 rows of macrotubercles, tips broken; cirrigerous segments with basal tubercle of dorsal cirrophore projected, bilobed; body 16.5 mm long, 10 mm wide, 29 chaetigers).

Australia • 1 specimen; Woodside Kimberley Survey 2010, Sta. 30; 12 m; 15.X.2010; Hosie A. & Betteridge L. leg.; AM 37296 (bent ventrally, pharynx fully exposed; elytra yellowish, darker along posterior margin, without black bands or spots; right elytron 6 and left parapodium of chaetiger 12 removed for observation (kept in container); elytra with 5-6 rows of macrotubercles; basal tubercle of dorsal cirrophores projected; neurochaetae unidentate; body 18 mm long, 10 mm wide, 29 chaetigers) • 1 specimen; Christmas Island, Flying Fish cove; no further data; NHM 1933.10.11.23 (juvenile, markedly bent ventrally; some elytra previously removed (lost), elytra yellowish without black spot, macrotubercles in 3 rows, not measured for avoiding further damage) • 1 specimen; Christmas Island, Flying Fish cove; no further data; NHM 1933.10.11.29 (juvenile; some elytra previously removed (lost), elytra yellowish with dispersed darker spots, areolation includes larger areas; macrotubercles in 2 rows; body 7.5 mm long, 4 mm wide, 29 chaetigers) • 5 specimens; Grahams Point; no further data; NHM 1970.114 (3 small specimens markedly bent ventrally; elytra yellowish, smaller specimens with black spots; elytra with 4-5 rows of macrotubercles; body 10-15 mm long, 4-9 mm wide, 28-29 chaetigers) • 1 specimen; Cocos (Keeling) Islands, West Island; 12°11'13"S, 96°49'42"E:, Q Station Bay; 10-20 m; 6.XII.1999; Kirkendale L. leg.; outer fore reef, under dead coral; UF 57 (elytra yellowish, without dark bands or spots; right elytron 6 and left parapodia of chaetigers 13 and 14 removed for observation (kept in container); 4-5 rows of macrotubercles; basal tubercle of dorsal cirrophores projected; body 24 mm long, 9 mm wide, 29 chaetigers) • 2 specimens; Queensland, Lizard Island, Coconut Beach; 1-2 m; 20.XI.1977; Brock R. & Bailey-Brock J. leg.; limestone platform with coral rubble; USNM 81958 (largest slightly bent ventrally, without elytra [retained in container], with anteroventral dissection previously made; body 12.5-15.0 mm long, 5.5-9.0 mm wide, 29 chaetigers; smallest with a wide, diffuse, oblique black band; largest with jaws with 2-3 accessory denticles) • 2 specimens; Heron Island; intertidal; 3.II.1976; Hartmann-Schröder G. leg.; coral reef, under rocks; ZMH P 20976 (smallest one breaking in pieces; largest specimen medially distorted by compression, with elytra yellowish, without black spots, 6 rows of macrotubercles progressively smaller posteriorly; body 20 mm long, 12 mm wide, 29 chaetigers).

Papua New Guinea • 1 specimen; Papua New Guinea Biodiversity Expedition 2012, Madang Province, Rasch Passage; 10 m; 6.XII.2012; Knutson V. leg.; CASIZ 190468 (bent ventrally; elytra orange-brownish, with 4-5 concentric rows of large spine-like macrotubercles; body 21 mm long, 8 mm wide, 28 chaetigers) • 1 specimen; Papua New Guinea Biodiversity Expedition 2012, Madang Province, Planet Rock dive site; depth undefined; 16.XI.2012; Gosliner T. & Knutson V. leg.; CASIZ 190469 (slightly bent ventrally; elytra orange-brownish, with 4-5 concentric rows of large spine-like macrotubercles; body 20 mm long, 8.5 mm wide, 28 chaetigers).

New Caledonia • 1 specimen; Dubatche; 1880; Heutel M. leg.; no further data; MNHN A274-14 (bent ventrally; soft; elytra yellowish with a black spot; macrotubercles in 5-6 rows, progressively smaller posteriorly; body 15 mm long, 9 mm wide, 29 chaetigers) • 1 specimen; Province Sud, Noumea, baie des Citrons, South end; 22°18'13.54"S, 166°26'03.7"E; 0-2 m; 5.XII.2016; . Paulay G & Moroz L. leg.; shore and fringing reef; UF 5016 (bent ventrally, elytra with thin oblique black band, macrotubercles in 3-4 rows; pharynx fully exposed, jaws with 2 denticles; body 15 mm long, 6.5 mm wide, 28 chaetigers) • 2 specimens; Province Sud, Noumea, baie des Citrons, South end; 22°18'13.54"S, 166°26'03.7"E; 0-2 m;

5.XII.2016; Paulay G. & Moroz L. leg.; shore and fringing reef; UF 5019 (elytra with blackish oblique bands better defined in larger specimen, macrotubercles in 4-5 rows; body 12-15 mm long, 6.0-7.5 mm wide, 29 chaetigers) • 2 specimens; Province Sud, Noumea Commune, baie des Citrons, South part; 22°18'14.4"S, 166°26'02.4"E; 0-2 m; 31.X.2017; Paulay G. & Hoban M. leg.; UF 5621 (posterior fragments removed for molecular studies; elytra brownish homogeneously scaly medial to macrotubercles, with 4-5 rows of digitate macrotubercles, some posterior ones broken, regenerated; ceratophores and base of ventral cirri blackish; nuchal lappet truncate; median antenna twice longer than wide; body 19.5 mm long, 9 mm wide, 29 chaetigers) [elytra with diffuse black spots, with 2 rows of macrotubercles; lateral ceratophores and ventral cirri pale; body 8 mm long, 4 mm wide, 28 chaetigers].

Mariana Islands, Guam • 1 specimen; Double Reef; 13°30'00.0"N, 144°48'00.0"E; 3-10 m; 3.II.1998; Paulay G. & Starmer J. leg.; under rocks; UF 168 (slightly bent ventrally, elytra with oblique blackish band, macrotubercles in 4-5 rows; body 14 mm long, 7 mm wide, 28 chaetigers) • 3 specimens; Pago Bay, in front of Marine Lab; 13°30'00.0"N, 144°48'00.0"E; 5 m; 4.XII.1998; Kirkendale L. leg.; basin hole, under rubble; UF 169 (slightly bent ventrally, elytra with wide black spot in smaller specimens, becoming an oblique black band in larger specimen, macrotubercles in 2-4 rows; body 8.0-12.5 mm long, 5-7 mm wide, 28-29 chaetigers) • 1 specimen; NCS Beach, Dededo; 13°32'26.9"N, 144°48'16.9"E; 18.XI.1966; among dead and living corals; no further data; UF 185 (preserved in ethanol, with abundant adsorbed salt particles on chaetae, elytra without black spots, macrotubercles in 3-4 rows; body 10 mm long, 5 mm wide, 28 chaetigers) • 1 specimen; Haputo, South Side; 13°30'00.0"N, 144°48'00.0"E; 6-9 m; 2.VIII.2000; Paulay G. leg.; fore reef, under rubble, UF 197 (slightly bent laterally, elytra with wide black oblique band, macrotubercles in 4-5 rows; body 16 mm long, 7.5 mm wide, 28 chaetigers).

Western Caroline Islands • 2 specimens; Palau Islands, Ngaremdin Reef, East side of Urukthapel; 07°13'09"N, 134°26'40"E; 19.VIII.1955; Bayer F. M. *et al.* leg.; USNM 81954 (extremely bent ventrally; body about 11-13 mm long, 5.5-7.0 mm wide; chaetigers not counted).

Cook Islands • 2 specimens; Rarotonga Island, just west of Ava Avarua, behind algal rim; 15 cm, low tide; 20.IX.1984: Paulay G. & McCormack G. leg.; under rocks; UF 391 (bent ventrally; with abundant salt deposits between parapodia; right elytron 6 removed from one specimen (kept in container); elytra yellowish, black bands barely visible; elytra with 3-4 rows of macrotubercles; body 12-20 mm long, 7-8 mm wide, 28-29 chaetigers).

Solomon Islands • 1 specimen; Tetel Island; low water mark; 28.VII.1965; Gibbs P. E. leg.; Porites; NHM 1970.109 (bent ventrally; elytra golden with 5-6 rows of macrotubercles; not measured).

Republic of Kiribati, Phoenix Islands • 1 specimen; Enderbury Atoll; 03°08.855'S, 171°04.761'W; 12-20 m; 27.VI.2002, MJA leg.; under coral rubble; LACM 12812 (anterior and posterior ends depressed, a few elytra removed; elytra without black spots or bands, 4-5 rows of macrotubercles; lateral ceratophores purplish; body 13 mm long, 6.5 mm wide, 28 chaetigers).

Line Islands, Territory of Palmyra Islands • 1 specimen; Palmyra Atoll, southern outer reef at North-South causeway intersection; 05°52.07'N, 162°04.14'W; 13-16 m; 12.IX.2006; Piotrowski C. leg.; coral rubble; CASIZ 174438 (bent ventrally; elytra orange-yellowish with small, diffuse blackish spots; body 23 mm long, 9 mm wide, 30 chaetigers).

French Polynesia, Society Islands, Moorea • 1 specimen; North Shore of Moorea, Osenberg Coral Transplant Site; 17°31'59.9"S, 149°49'59.9"W; 3-5 m; 13.IV.2006; Malay M. C. leg.; lagoon, under rocks; UF 468 (juvenile, slightly bent ventrally, elytra with a diffuse large dark spot, macrotubercles in 3-4 rows; body 8.5 mm long, 4.5 mm wide, 29 chaetigers) • 2 specimens; Aroa, Northeast Corner of Moorea; 17°31'59.9"S, 149°49'59.9"W; 1.4-3.0 m; 4.V.2006; Malay M. C. & Emmanuelli E. leg.; lagoon, rubble; UF 474 (bent ventrally, elytra with oblique black band in larger specimen, macrotubercles in 3-5 rows; body 18-20 mm long, 8.0-9.5 mm wide, 28 chaetigers) • 1 specimen; fore reef between Cook's and Opunohu Bays; 17°28'35"S, 149°50'41"W; 11-13 m; 20.VII.2006; McKeon C., Meyer C. & Paulay G. leg.; outer reef slope, under rubble; UF 513 (bent ventraly, elytra with oblique black bands reduced to irregular spots, with macrotubercles in 4-5 rows; body 20 mm long, 10 mm wide, 29 chaetigers) • 1 specimen; fore reef between Cook's and Opunohu Bays; 17°28'35.0"S, 149°50'42.0"W; 11-13 m; 20.VII.2006; McKeon C., Meyer C. & Paulay G. leg.; outer reef slope, under rubble; UF 514 (barely bent ventrally, elytra without black spots, with macrotubercles in 4-5 rows; body 15.5 mm long, 8 mm wide, 29 chaetigers) • 1 specimen; barrier reef between Cook's and Opunohu Bays (Vaipahu); 17°28'37.9"S, 149°49'50.2"W; 0-2 m; 30.VI.2006; McKeon C. & Paulay G. leg.; outer part of barrier reef; UF 524 (slightly bent ventrally, elytra with a short black oblique band, 4-5 rows of macrotubercles, pharynx exposed, jaws with 2-3 denticles; body 28 mm long, 8.5 mm wide, 28 chaetigers) • 1 specimen; barrier reef between Cook's and Opunohu Bays (Vaipahu); 17°28'37.9"S, 149°49'50.2"W; 0-2 m; 30.VI.2006; McKeon C. & Paulay G. leg.; outer part of barrier reef; UF 525 (barely bent ventrally, elytra with a short black spot, 4-5 rows of macrotubercles; body 16 mm long, 8.5 mm wide, 29 chaetigers) • 1 specimen; Northwestern side of Cook's Bay; 17°29'15"S, 149°49'35"W; 0-2 m; 12.VI.2006; Paulay G. leg.; fringing reef flat, under rocks; UF 537 (bent ventrally, elytra dirty yellowish, 4-5 rows of macrotubercles; body 19.5 mm long, 9 mm wide, 29 chaetigers) • 1 specimen; NW Motus, in channel between islands and beach; 17°29'18.2"S, 149°54'48.2"W; 0.5-1.0 m; 10.XI.2009; Anker A. & Liao V. leg.; UF 1296 (bent ventrally, elytra with a black oblique band, 4-5 rows of macrotubercles; body 23 mm long, 10 mm wide, 29 chaetigers) • 1 specimen; Moorea; 17°30'00.0"S, 149°48'00.0"W; 31.X.2009; no further data; UF 1341 (bent ventrally, elytra nearly lacking black spots, barely visible along anterior elytra, macrotubercles in 4-5 rows, pharynx exposed, jaws with 3 denticles; body 22 mm long, 11.5 mm wide, 28 chaetigers) • 1 specimen; Temae at lighthouse; 17°29'18.9"S, 149°46'22.7"W; 0.5-2.0 m; 4.XII.2009; McPherson S. leg.; reef crest and lagoon; UF 1363 (slightly bent ventrally, elytra with oblique black bands and additional spots along a few anterior elytra, macrotubercles in 4 rows; body 18 mm long, 10 mm wide, 29 chaetigers) • 1 specimen; SW of Motus; 17°29'38.4"S, 149°55'15.6"W; 1.5 m; 30.X.2010; Watson C. leg.; lagoon, sand and coral fragments; UF 1980 (juvenile, markedly bent ventrally, elytra with many large dark spots, 1 row of macrotubercles; pharynx exposed, jaws with 1-2 denticles; body 6 mm long, 3 mm wide, chaetigers not counted) • 1 specimen; off channel, MPA marker; 17°28'33"S, 149°49'51"W); 10-11 m; 7.XI.2010; McKeon S. leg.; fore-reef, in rubble; UF 2060 (markedly bent ventrally; elytra yellowish with central brownish spots; right elytron 6 and a median cirrigerous segment removed for observation (kept in container); 2-3 rows of macrotubercles; basal tubercle of dorsal cirrophore projected; body not measured for avoiding further damage) • 2 specimens; between Opunohu Bay and Motus; 17°28'56.6"S, 149°53'27.6"W;, 18-22 m; 3.XI.2010; Moore J. leg.; outer reef slope, in rubble; UF 2097 (juveniles, markedly bent ventrally, elytra with extended black spots, reduced in larger juvenile, macrotubercles in 1 row, indistinct in smaller juvenile; body 1.5-3.9 mm long, 1.2-2.5 mm wide, 15-25 chaetigers) • 1 specimen; between Opunohu Bay and Motus; 17°28'56.6"S, 149°53'27.6"W; 18-22 m; 3.XI.2010; Moore J. leg.; outer reef slope, rubble; UF 2107 (juvenile, bent ventrally, elytra with many blackish spots, especially along anterior ones, macrotubercles in 1 row; body 4 mm long, 2 mm wide, 26 chaetigers).

French Polynesia, Society Islands, Tahiti • 5 specimens; Mission Ranson, Sta. 3; 1952; no further data; MNHN A274-3 (some elytra previously removed; no further dissected for avoiding more damage; smallest one with pharynx partially exposed; elytra yellowish to brownish, without black spots; body 9.5-18.0 mm long,

6.0-9.5 mm wide, 29 chaetigers) • 1 specimen; no further data; NHM 1928.1.11.4 (juvenile; elytra yellowish with black spots; each elytron with 1 row of macrobubercles; body 7.5 mm long, 4 mm wide, 23 chaetigers, without posterior end) • 1 specimen; no further data; NHM 1928.1.11.29 (slightly bent ventrally, some elytra previously removed; right elytron 6 removed for observation (kept in container), elytra with 4 rows of macrotubercles; body 19 mm long, 10.5 mm wide, 29 chaetigers) • 1 specimen; Motu-Uta; 17°36'00.0"S, 149°24'00.0"W; 21 m; 1.XI.2008; Bacchet P. leg.; UF 918 (bent ventrally, elytra without black spots, macrotubercles in 4-5 rows; body 24 mm long, 10 mm wide, 28 chaetigers).

French Polynesia, Tuamotu Archipelago • 1 specimen; Tikehau Atoll, Hoa at East end of Tuaherahera Motu and adjacent outer reef flat, Southeast of Hoa, just off Ohotu Motu; 15°07'15.2"S, 148°13'22.8"W; 10.VII.2001; Paulay G. leg.; outer reef flat, under rocks; UF 53 (bent ventrally, elytra without black spots, macrotubercles in 4-5 rows; body 25 mm long, 11.5 mm wide, 27 chaetigers).

French Polynesia, Marquesas Islands • 1 specimen; Taiohae, entrie 2; 15.XII.1925; Nelmas S. leg.; MNHN A274-4 (bent ventrally; elytra brownish without black spots; not measured for avoiding further damage) • 1 specimen; Nuku Hiva Island, Ohotea Point, W side of Taiohae Bay; 08°55'51.2"S, 140°05'52.1"W; 36 m; 28.XI.2011; Evans N., Andrefouet S., Benzoni F., Menou J.-L., Olivirio M. & Payri C. leg.; cliffs with narrow steps; UF 2352 (bent ventrally, elytra with tiny black spots, 3 rows of macrotubercles; body 14 mm long, 7 mm wide, 28 chaetigers) • 1 specimen; Ua Huka Island, SW side of islet between Teuaua and Hemeni islets; 08°57'17.6"S, 139°35'40.9"W; 20 m; 30.XI.2011; Evans N., Andrefouet S., Benzoni F., Menou J.-L., Olivirio M. & Payri C. leg.; coarse sand plain with *Halimeda*; UF 2355 (markedly bent ventrally, elytra with oblique black band, macrotubercles in 4-5 rows; body 18 mm long, 9 mm wide, chaetigers not counted) • 1 specimen; Hiva Oa Island, South of Kiukiu, West side of island; 09°47'26.6"S, 139°09'27.7"W; 30 m; 8.XII.2011; Evans N., Andrefouet S., Benzoni F., Menou J.-L., Olivirio M. & Payri C. leg.; large blocks of madreporarians; UF 2362 (markedly bent ventrally, elytra with black oblique bands, macrotubercles in 4-5 rows; body 16 mm long, 8 mm wide, chaetigers not counted).

Clipperton Island • 3 specimens; St. 30; 10°18.72'N, 109°12.01'W; 15 m; 24.VI.2005; Hourdez S., Kaiser K.-L. & Bompar J.-M. leg.; coral rubble and red algae; 1 MNHN, 2 ECOSUR (elytra yellowish to brownish, without black bands; macrotubercles in 4-5 rows and sometimes with calcareous epibionts; body 14-21 mm long, 8.5-11.5 mm wide, 29 chaetigers) • 2 specimens; St. 17; 10°19.22'N, 109°13.39'W; 23 m; 20.I.2005; Bouchard J.-M., Albenga L. & Dugrais L. leg.; sponge and epifauna, hand collecting; ECOSUR (largest specimen elytra with more pigmented melanophores forming oblique blackish bands, macrotubercles partially covered by calcareous crust; body 17.0-18.5 mm long, 9.5-9.9 mm wide; palps longer or shorter than lateral antennae depending on preservation) • 1 specimen; St. 20; Anchoring point of *Rara Avis*; 10°17.50'N, 109°13.55'W; 20 m; 22.I.2005; Bouchard J.-M., Albenga L. & Dugrais L. leg.; coral rubble; MNHN (brushed in vinegar-ethanol for removing foreign particles; most elytra fixed on specimen, dark oblique bands barely visible; body 14 mm long, 6.5 mm wide, 28 segments, 13 pairs of elytra; palps and lateral antennae of similar size) • 2 specimens; St. 24; 10°17.93'N, 109°14.00'W; 23 m; 22.I.2005; Bouchard J.-M. Albenga L. & Dugrais L. leg.; coral rubble, night dive; MNHN (elytra with abundant melanophores; elytrophore inner and posterior margins dark body 6.5-12.0 mm long, 4.0-7.5 mm wide: palps as long as lateral antennae; lateral antennae ceratophores shorter than prostomium in smallest specimen, longer in largest specimen; nuchal lappet partially concealed by following segment) • 4 specimens; St. 32; 10°18.81'N, 109°12.27'W; 18 m; 25.I.2005; Hourdez S., Kaiser K.-L. & Bompar J.-M. leg.; coral mound; ECOSUR (9-23 mm long, 5-11 mm wide; elytra with oblique narrow bands, larger, more diffuse in smallest specimen, largest specimens with calcareous deposits; all with palps about three times longer than lateral antennae).

Western Mexico • 1 specimen; Baja California Sur, La Paz, Punta Calerita; intertidal; 12.II.1987; Salazar-Vallejo S. I. leg.; rocky shore; ECOSUR P2407 (elytra brownish, with small blackish central spots; macrotubercles in 4-5 rows, tips slightly eroded, with 2-3 distal spines, longer than tip width; oocytes in ovaries, 60-80 µm in diameter; body 19 mm long, 11 mm wide, 29 segments) • 1 specimen; Baja California Sur, Cabo Pulmo; intertidal; 25.IX.1988; Bastida-Zavalla J. R. leg.; rocky shore; ECOSUR P2417 (elytra yellowish; macrotubercles in 2-3 rows, tips slightly eroded, with 2-3 distal spines, longer than tip width; body 9 mm long, 5 mm wide, 29 segments) • 1 specimen; Nayarit, Bahía Banderas, Punta Mita; intertidal; I.1995; Cadien D. leg.; LACM (slightly bent ventrally, some elytra and one parapodium previously removed, elytra with a wide oblique black band, 3-4 rows of macrotubercles; body 18 mm long, 10 mm wide, 28 chaetigers) • 3 specimens; Gulf of California; 1904; Diguet L. leg.; no further data; MNHN A274-17 (slightly bent; elytra brownish without black spots; macrotubercles in 3-4 rows, decrasing in size posteriorly; body 10.0-10.5 mm long, 6.0-7.5 mm wide, 29 chaetigers) • 1 specimen; Gulf of California, Sta. 47; 1898; Diguet L. leg.; no further data; MNHN A274-25 (slightly bent; elytra brownish without black spots; macrotubercles in 5-6 rows, decrasing in size posteriorly; body 27 mm long, 13.5 mm wide, 29 chaetigers) • 1 specimen; Baja California Sur, Los Frailes; 23°22'57"N, 109°25'31"E; 0-1 m; 28.I.1972; Ebert T. A. & Dexter D. M. leg.; rocky bottom; UF 4178 (slightly distorted, elytra with oblique black band barely defined, macrotubercles in 4-5 rows; body 20 mm long, 12 mm wide, 28 chaetigers).

Pacific Panama, Gulf of Chiriqui, Coiba National Park • 1 specimen; off Isla Uva, reef; 7°49'1"N, 81°46'1"E; 9.III.2005; Glynn P. leg.; coral rubble; LACM 12808 (slightly bent ventrally, pharynx exposed, jaws with 2 denticles, elytra with diffuse black spots; body 13.5 mm long, 5 mm wide, 28 chaetigers) • 3 specimens; off Isla Uva, reef; 7°49'1"N, 81°46'1"E; 9.III.2005; Glynn P. leg.; coral rubble; LACM 12815 (slightly bent ventrally, elytra with diffuse black oblique bands; body 11.0-16.5 mm long, 5-7 mm wide, 27-29 chaetigers) • 6 specimens; off Isla Uva, reef; 7°48'57"N, 81°45'36"E; 13.III.2006; Glynn P. leg.; coral, scuba; LACM 12816 (variably bent ventrally, elytra with diffuse black oblique bands, narrower in larger specimens; body 10-16 mm long, 5.0-7.5 mm wide, 28-29 chaetigers) • 3 specimens; off Isla Uva, reef; 7°49'1"N, 81°46'1"E; 10.III.2005; Glynn P. leg.; artificial PVC tube habitat, scuba; LACM 12817 (bent ventrally, pharynx exposed, jaws with 3 denticles, elytra with diffuse black spots; body 12 mm long, 6 mm wide, 29 chaetigers) • 3 specimens; off Isla Uva, reef; 7°49'1"N, 81°46'1"E; 9.III.2005; Glynn P. leg.; coral rubble, scuba; LACM 12818 (variably bent ventrally, pharynx exposed in one specimen, jaws with 1-3 denticles, elytra with diffuse black oblique bands; body 9-14 mm long, 4.0-6.5 mm wide, 28-29 chaetigers) • 3 specimens; off Isla Uva, reef; 7°49'1"N, 81°46'1"E; 15.III.2006; Glynn P. leg.; coral rubble, scuba; LACM 12819 (straight, elytra with diffuse black spots, 3-4 rows of macrotubercles; body 13.3 mm long, 6 mm wide, 28 chaetigers) • 1 specimen; off Isla Uva, reef; 7°49'1"N, 81°46'1"E; 10.III.2005; Glynn P. leg.; artificial PVC tube habitat, scuba; LACM 12820 (juvenile, bent ventrally, elytra with diffuse black spots, 2 rows of macrotubercles towards margin, lateral most tubercles transparent, medial most with darker tips; body 8 mm long, 1.8 mm wide, 27 chaetigers) • 1 specimen; Coibita (Isla Ranchería), southeast of Smithsonian beach house; 7°39'18"N, 81°44'38"E; 12.III.2005; Harris L. & Wehrtmann I. leg.; rock pools; LACM 12821 (bent ventrally, elytra with diffuse black oblique bands; body 12 mm long, 5.5 mm wide, 28 chaetigers) • 1 specimen; Coibita (Isla Ranchería), southeast of Smithsonian beach house; 7°39'18"N, 81°44'38"E; 13.III.2005; Harris L. & Wehrtmann I. leg.; rock pools; LACM 12822 (bent ventrally, pharynx exposed, jaws with 2 denticles, elytra with diffuse black oblique bands; body 21 mm long, 8.5 mm wide, 28 chaetigers) • 1 specimen; Coibita (Isla Ranchería), southeast of Smithsonian beach house; 7°39'18"N, 81°44'38"E; 13.III.2005; Harris L. & Wehrtmann I. leg.; rock pools; LACM 12823 (bent

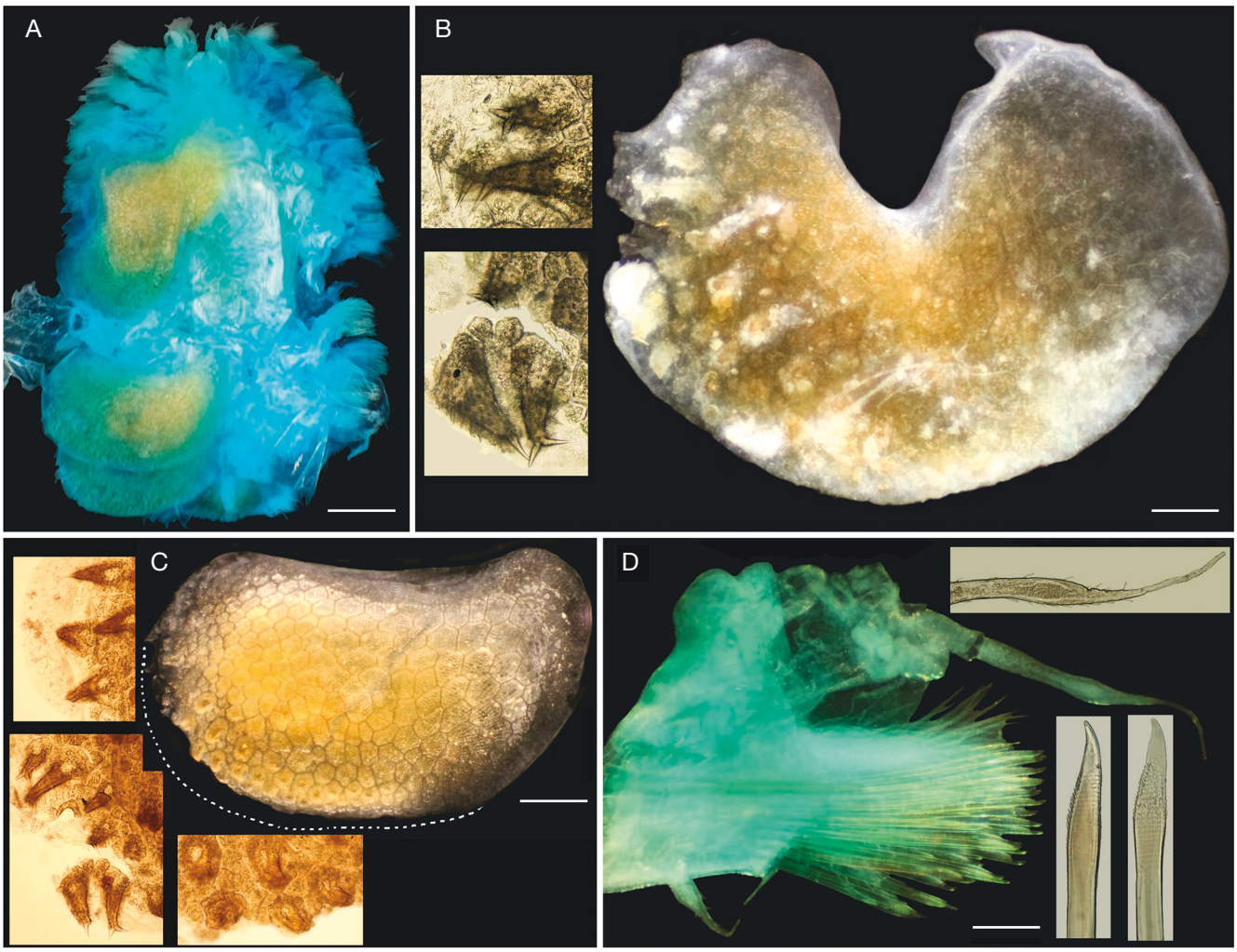

Fig. 3. — *Iphione ovata* Kinberg, 1856, holotype, SMNH Type 388, Hawaii: **A**, dorsal view, posterior segments bent ventrally; **B**, second left elytron (insets: macrotubercles); **C**, posterior elytron (insets: macrotubercles); **D**, median chaetiger, right parapodium, posterior view, dorsal cirrus breaking off (insets: close-up of dorsal cirrostyle and tips of two neurochaetae). Scale bars: A, 1.2 mm; B, 0.2 mm; C, 0.5 mm; D, 30 µm.

ventrally, elytra with diffuse black spots, 3-4 rows of macrotubercles; body 16 mm long, 8 mm wide, 28 chaetigers) • 2 specimens; S. Y. St. George Expedition; 3.IX.1924; no further data; NHM 1928.9.14.53/54 (one specimen with pharynx fully exposed; elytra brownish, each with 5-6 rows of macrotubercles; body 15-16 mm long, 9.0-9.5 mm wide, 29 chaetigers).

Description

Holotype of *I. ovata* (SMNH Type 388), mature female, bent ventrally, fragmenting into two parts, last chaetigers bent ventrally (Fig. 3A); right parapodia of chaetigers 12-15 previously removed, left parapodium of chaetiger 11 dissected (retained in container), 14 elytra previously removed. Body oval, depressed, arched dorsally, flattened ventrally, 11.5 mm long, 6 mm wide, 27 chaetigers. Body wall pale, broken in several regions; elytra dirty or pale orange, venter pale.

Elytra with smooth margins; elytra retained on holotype dark orange, detached elytra brownish, macrotubercle tips not surpassing elytral borders (Fig. 3B) (slightly surpassing borders in some paratypes), shorter in posterior elytra (Fig. 3C); with eroded posterolateral margin; macrotubercles in the few attached elytra shorter, blunt, tips not surpassing elytral margins, macrotubercle stem with spines, tip with 1-2 long spines (Fig. 3B, insets, C, insets). A few elytra remaining on body, not removed to avoid further damage. Macrotubercles in 2-3 rows along elytral posterior and lateral regions (5-6 rows in paratypes), each tubercle with spinulose surface, tips with 1-3 spines, often broken.

Prostomium slightly wider than long, longitudinal incision not visible. Anterior lobes projected into converging ceratophores, part of ceratophores and ceratostyles lost, size proportions unknown (in one paratype ceratophores as long as prostomium and ceratostyles). Palps previously removed, not in container (markedly longer than antennae in one paratype). Eyes minute, brownish, anterior eyes positioned near widest prostomial area, posterior eyes not visible dorsally, covered by second segment. Nuchal papillae not visible (visible in one paratype due to transparency of nuchal lappet).

Tentacular segment dorsally reduced, without chaetae; left tentacular cirri complete, only inferior right tentacular cirrus intact; cirrophore thick, cirrostyle very thin. Facial tubercle pale, visible dorsally between lateral ceratophores.

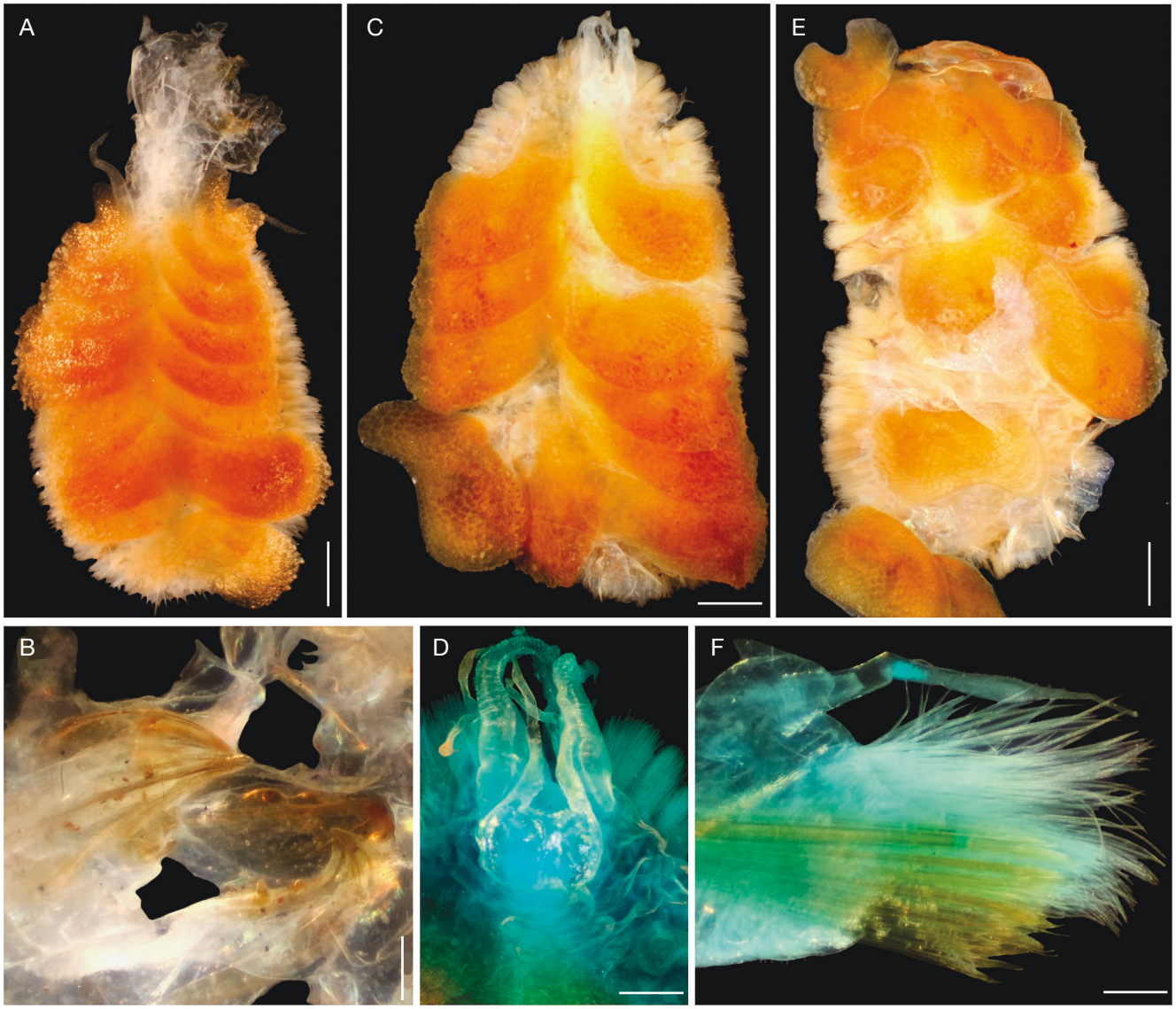

FIG. 4. — *Iphione ovata* Kinberg, 1856, paratypes, SMNH Type 8410, Hawaii: **A**, small paratype (8 mm long), dorsal view, pharynx exposed; **B**, same, pharynx jaws, oblique lateral view; **C**, medium-sized paratype (11 mm long), dorsal view; **D**, same, close-up of anterior end, dorsal view; **E**, largest paratype (12 mm long), dorsal view; **F**, same, chaetiger 11, right parapodium, posterior view. Scale bars: A, 1.5 mm; B, F, 0.2 mm; C, 1.2 mm; D, 0.5 mm; E, 1.3 mm.

Segments 2-4 directed anterolaterally. Second segment visible dorsally, with semicircular nuchal lappet, wider than long. Ventral buccal cirri inserted ventrally, projecting beyond chaetal tips. Dorsal nodules indistinct due to damaged body wall (in one paratype three pairs visible, each nodule small, circular). Segments 2-3 with finer neurochaetae, slightly swollen subdistally, with a longer denticulate region than neurochaetae in following chaetigers.

Median cirrigerous segment with dorsal cirri reaching chaetal tips; dorsal cirrophore smooth, basal tubercle small (Fig. 3D) (not developed in median chaetiger of one paratype); cirrostyle long, papillate (Fig. 3D, inset). Notochaetae very abundant, transparent, delicate capillaries with series of transverse funnel-shaped spinose rows, tips bare. Neuropodia with neurochaetal lobe with small, globular papillae. Neurochaetae thick, basally smooth, subdistally swollen, with series of 16-24 rows of fine transverse denticulations not surpassing swollen region of chaeta, tips falcate, sharp (Fig. 3D, insets).

Anus position not detected due to body wall damage.

Pharynx exposed in one paratype; jaws brownish, sharp, each with two accessory denticles.

Other type materials

The paratypes of *I. ovata* (SMNH Type 8410) soft, variably damaged, elytra yellowish to orange, several elytra removed previously (16 in container), others almost detached (Fig. 4A, C, E); in two paratypes elytra with small dark spots arranged in an irregular, diffuse spot, resembling oblique longitudinal band per elytron, without marginal fimbriae; abundant polygonal areas throughout most elytral surface; macrotubercles from detached elytra conical to digitate, 2-3 times longer than wide along exposed posterolateral margins, longer to-

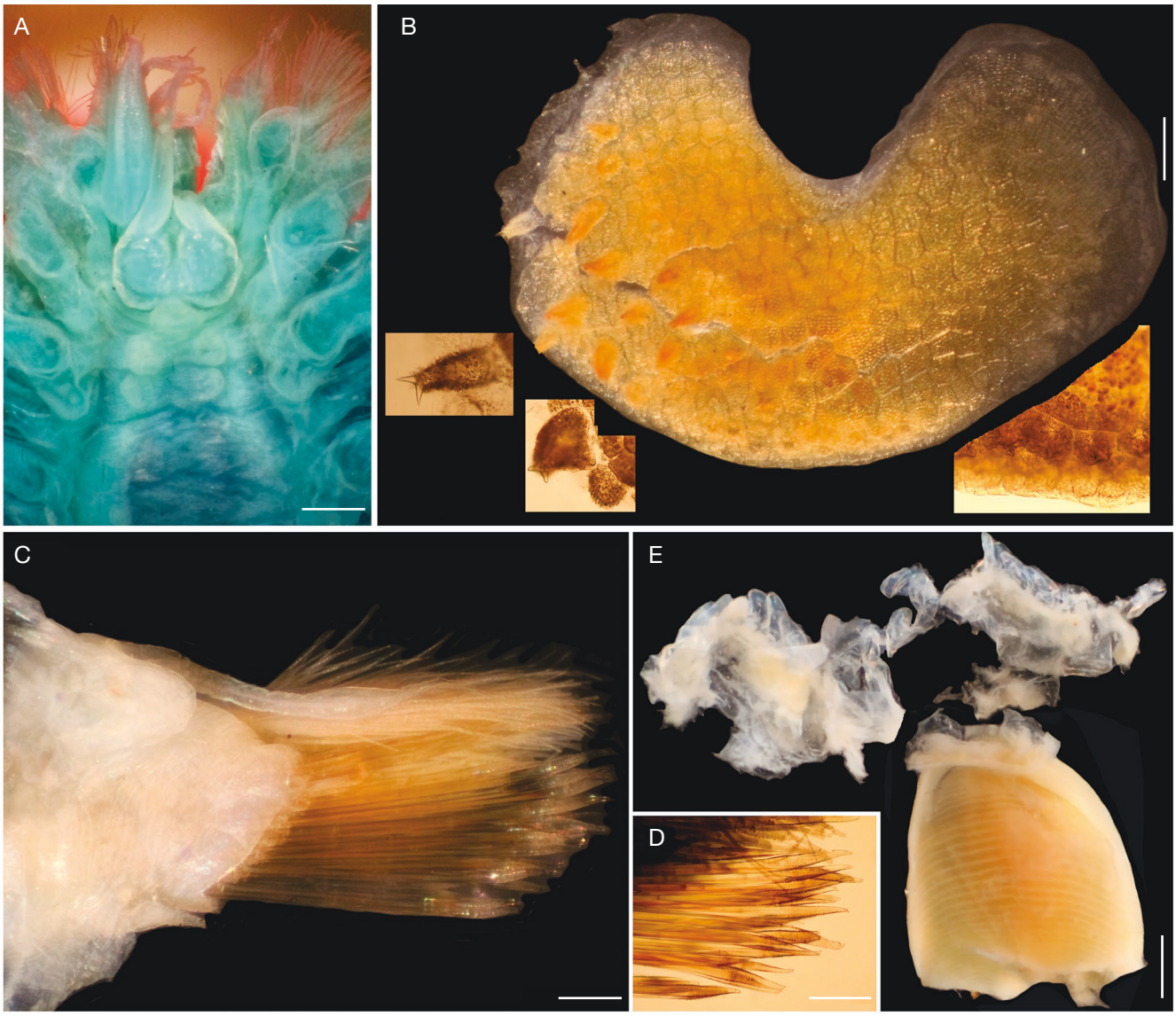

Fig. 5. — *Iphione ovata* Kinberg, 1856, holotype of *I. spinosa* Kinberg, 1858, SMNH Type 392, South Africa: **A**, anterior region, dorsal view; **B**, same, second elytron (insets: macrotubercles along elytral margin); **C**, chaetiger 11, right parapodium, posterior view; **D**, same, tips of neurochaetae; **E**, pharynx marginal papillae, jaws removed, and fragment of pharynx tube. Scale bars: A, 0.5 mm; B, 0.3 mm; C, D, 0.2 mm; E, 0.8 mm.

wards elytral margin (slightly larger in elytra 1-3); pharynx exposed in one paratype (Fig. 4A, B), dissected previously, jaws with two accessory denticles; another with several median parapodia (Fig. 4F) previously removed (two dissected, kept in container), basal tubercle of dorsal cirrophore rounded, cirrophore smooth, cirrostyle subdistally swollen, papillate; smallest paratype without elytra, distorted by compression, twisted, anterior end transparent (Fig. 4D), body 2.5 mm long, 2.3 mm wide; larger paratypes with body 8-12 mm long, 5-6 mm wide, 26-29 chaetigers.

Holotype of *I. spinosa* (SMNH Type 392) bent ventrally, all elytra previously removed (14 kept in container), a longitudinal dissection running along ⅘ body length, and another one between right parapodia of chaetigers 7⁄8 to body axis; some median parapodia previously dissected (two left in container); body colorless, 14 mm long, 8 mm wide, about 29 chaetigers. Prostomium wider than long, anterior lobes projected into converging ceratophores, ceratophores longer than prostomium, ceratostyles tapered; palps thick, mucronate, as long as lateral antennae. Eyes indistinct; nuchal papilla covered by nuchal hood (Fig. 5A). Elytra brownish, without dorsal spots; macrotubercles conical, 3-4 times longer than wide along exposed posterolateral margins, longer towards elytral margin (slightly larger in anteriormost elytra, first pair lost), macrotubercle tips surpassing elytral borders. Macrotubercles in 3-4 rows along posterior and lateral regions, each with spinulose surface, tips with 1-2 distal spines, often broken (Fig. 5B). Median cirrigerous segments with dorsal cirri reaching chaetal tips; dorsal cirrophore smooth, basal tubercle globose, cirrostyle long, barely papillate (Fig. 5C). Notochaetae transparent; neurochaetae thick, basally smooth, subdistally swollen, with rows of fine transverse denticulations,

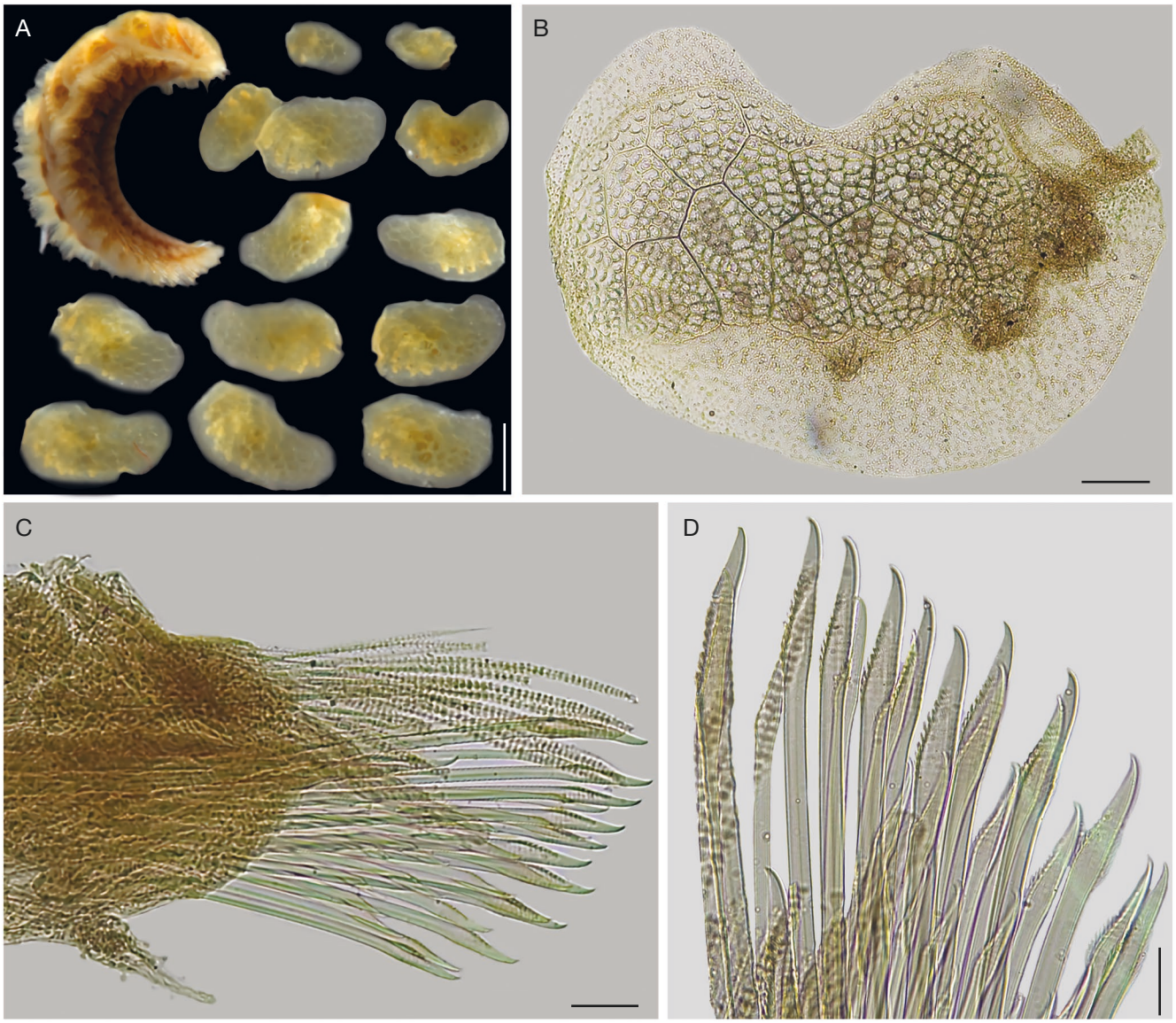

FIG. 6. — *Iphione ovata* Kinberg, 1856, holotype of *I. reticulata* Amoureux, Rullier & Fishelson, 1978, MNHN-POLY-TYPE-1430, Red Sea: **A**, holotype, right lateral view, bent ventrally, and elytra; **B**, same, right elytron from microslide UCO Y97'; **C**, undetermined left parapodium from same slide, anterior view, dorsal cirrus damaged; **D**, neurochaetae from chaetiger 5. Scale bars: A, 1.3 mm; B, 100 µm; C, 60 µm; D, 30 µm.

mostly eroded, difficult to count (about 20 rows, Fig. 5D), tips falcate, many with tips broken or eroded, sharp. Pharynx previously removed, jaws lost (Fig. 5E).

Type material of *I. reticulata* including the holotype (MNHN-POLY-TYPE-1430) and 13 detached elytra, and one microscope slide (UCO Y97') with one parapodium and several posterior elytra. Holotype bent ventrally (Fig. 6A), about 8 mm long, 3 mm wide, 28 chaetigers. One elytron in the slide mounted upside down (Fig. 6B) so that the macrotubercles are not visible, but elytron showing 10 large areoles and large smooth areas in the anterior and posterior regions. Anterior elytra intact; elytra with wide smooth rims free of polygonal areas, posterior rims approximately ⅓ to ⅕ elytron width, elytral surface with 20 to 50 polygonal areas varying by body region, 2-10 macrotubercles arranged in 1 or 2 diagonal rows across posterolateral corner, tubercle development varying by body region with first row developing at edge of polygonal area, posterior elytra bearing 2-3 undeveloped short tubercles with pair of divergent distal spines and several vertical rows of shorter surface spines. Median elytra with 1-2 rows of up to ten digitate macrotubercles bearing similar spines and up to 50 polygons. Parapodium included in the slide with some notochaetae with funnel-shaped spines, and unidentate, falcate neurochaetae with transverse rows of denticles (Fig. 6C), better defined in a closer look of another neuropodium (Fig. 6D).

VARIATION

A total of 103 non-type specimens were studied. Body length range was 1.5-28.0 mm long, their elytra were transparent in smallest specimens, maculate in slightly larger ones, and in larger specimens mostly yellow to orange, often with a black oblique band, and had 0-8 rows of macrotubercles.

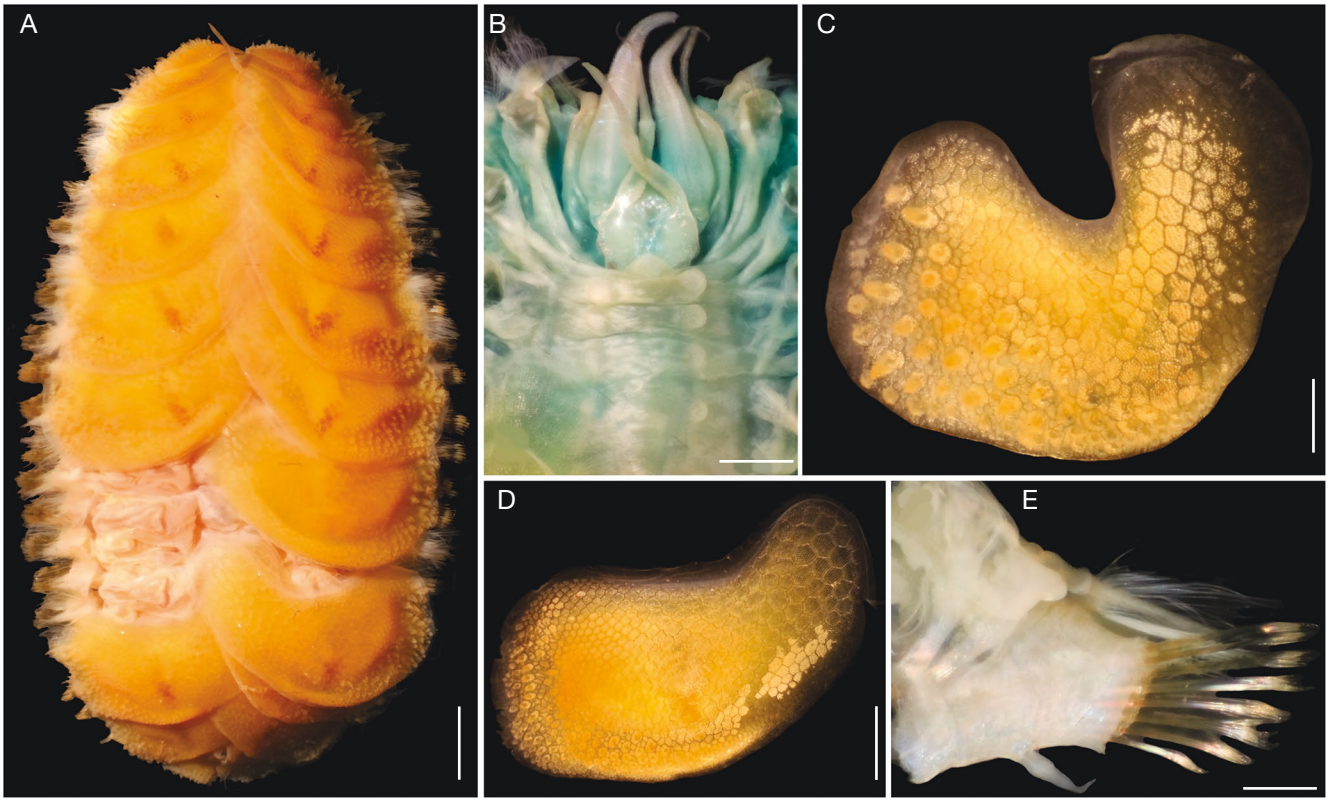

Fig. 7. — *Iphione ovata* Kinberg, 1856, CASIZ 16707, Hawaii: **A**, dorsal view; **B**, anterior end, dorsal view; **C**, second left elytron, dorsal view; **D**, sixth left elytron, dorsal view; **E**, chaetiger 14, right parapodium, posterior view, some notochaetae removed. Scale bars: A, 1.8 mm; B, 0.7 mm; C, 0.5 mm; D, 1.2 mm; E, 0.4 mm.

Nine Hawaiian specimens exhibit interesting details for clarifying the size-dependent variation in the number of chaetigers, elytra, and rows of elytral macrotubercles. The body was 2.8-21 mm long. Smaller specimens (2.8-3.8 mm long) had transparent elytra with black spots, and without macrotubercles or with a single row of macrotubercles. Medium sized specimens (12-16 mm long) had elytra yellowish or orange, often with a narrow oblique black band (Fig. 7A). The prostomium is wider than long; lateral ceratophores longer than prostomium, ceratostyles slightly thinner, tips flagellate (Fig. 7B). Palps slightly longer than antennae. Eyes blackish, anterior eyes lateral, barely visible dorsally, posterior eyes partially blocked by segment 3 anterior margin. Nuchal papilla not seen; nuchal hood semicircular; dorsal nodules well defined, separated from each other, broken. First elytra with larger macrotubercles in up to 5-6 concentric rows (Fig. 7C); median elytra with smaller macrotubercles in up to 7-8 concentric rows, tubercles progressively smaller toward lateral margins (Fig. 7D). Dorsal cirri with large, globular basal tubercles (Fig. 7E).

One medium-sized Hawaiian specimen (UF 423), slightly larger than holotype (SMNH Type 388), elytra with large conical macrotubercles close to posterior margins (Fig. 8A, C, D), only one row of barely projecting macrotubercles in smallest specimens. Increasing to 4-5 diagonal rows as specimen size increases, and in larger specimens up to 7-8 rows; some elytra with foreign particles, rarely eroded. Ceratophores orange, longer than prostomium (Fig. 8B). Lateral antennae and tentacular cirri flagellate, distal ceratostyles and cirrostyles very thin, about ⅓ as long as palps. Facial tubercle grayish. Anterior eyes marginal, barely visible dorsally, posterior eyes visible dorsally. Nuchal papilla digitate, about twice longer than wide or as long as wide. Dorsal nodules round, separate from each other. Neurochaetae with rows of spines continued beyond the swollen subdistal area, spines short, apparently eroded. Parapodia with basal tubercle to dorsal cirrophore barely visible (Fig. 8E).

Eastern Pacific specimens match the body pattern of Hawaiian *I. ovata*. Best preserved specimen (MNHN) 21 mm long, 11.5 mm wide (Fig. 9A), anterior end partially visible through anterior elytra (Fig. 9B). Prostomium as long as wide (Fig. 9C), with deep longitudinal incision; ceratophores slightly pigmented, as long as ceratostyles, longer than prostomium. Palps thick, as long as lateral antennae. Eyes black, positioned over posterior half of prostomium, anterior eyes projected beyond lateral margins; nuchal papilla as long as wide. Median cirrigerous segments with dorsal cirri reaching chaetal tips (Fig. 9D), dorsal cirrophore smooth, with basal blunt, conical, tubercle. Notochaetae pale to transparent (Fig. 9E). Neurochaetae subdistally swollen, sometimes with a darker core, with 26-28 rows of fine denticulations along swollen region, tips falcate, sharp (Fig. 9F).

One eastern Pacific juvenile (ECOSUR) slightly bent ventrally, 4.5 mm long, 3 mm wide, 12 pairs of elytra, 24 segments

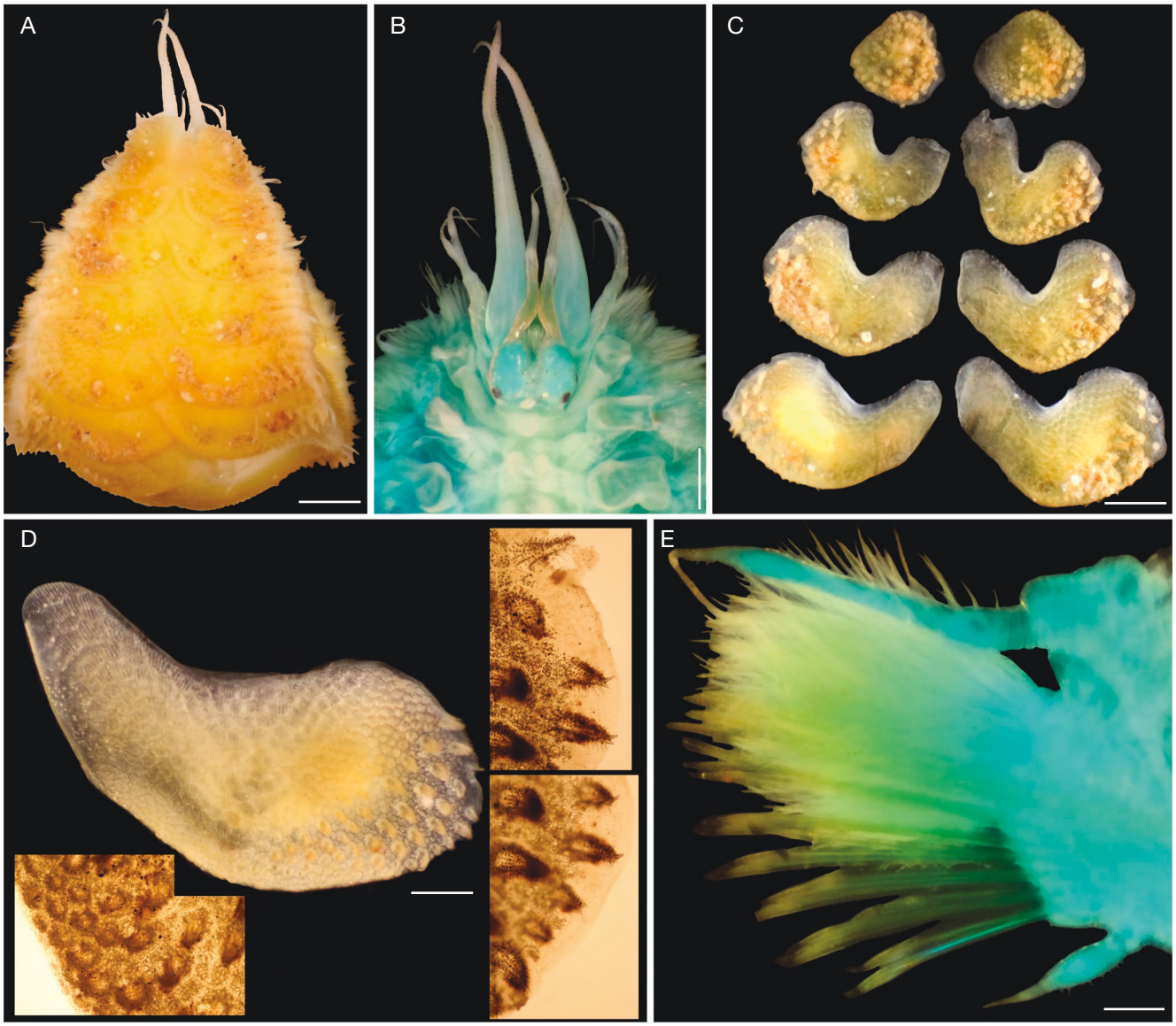

FIG. 8. — *Iphione ovata* Kinberg, 1856, UF 423, Hawaii: **A**, anterior region, dorsal view; **B**, anterior end, dorsal view; **C**, first four pairs of elytra with large macrotubercles in a few rows, seen from above; **D**, right elytron 8, seen from above (insets: close-up of macrotubercles in different areas); **E**, chaetiger 14, left parapodium, posterior view. Scale bars: A, 1.1 mm; B, D, 0.6 mm; C, 1 mm; E, 0.2 mm.

(Fig. 10A). Prostomium as long as wide, with black spots (Fig. 10B). Anterior lobes projected into lateral ceratophores, shorter than prostomium or ceratostyles. Palps thick, mucronate, slightly longer than lateral antennae, longitudinal rows of papillae barely visible. Eyes blackish, positioned on posterior prostomial half, anterior eyes not visible dorsally. Two blackish spots slightly ahead of posterior eyes. Nuchal papillae not visible. Elytrae with less than 50 polygonal areas, with large conical macrotubercles, first pair of elytra with macrotubercles along its surface (Fig. 10C), in following elytrae restricted to 2 rows along posterior submarginal areas, often positioned over posteriorly projected areolae, smooth marginal area wide (Fig. 10E, G), without calcareous particles, pigmented areolae barely visible towards the central elytral portions. Largest macrotubercles 2-3 times longer than wide, surface spinulose, distal spines 2-3 times longer than macrotubercle tip width (Fig. 10D, F, H). Another specimen (ECOSUR Sta. 17) with palps markedly longer than lateral antennae, and blackish convergent dorsally diffuse wide bands (Fig. 6J). Median cirrigerous segments with short cirrophores, cirrostyles reaching chaetal tips (trimmed in figure), sparsely papillate (Fig. 10I). Notochaetae pale to transparent; neurochaetae golden, upper ones thinner, tips falcate, sharp (Fig. 10I, insets).

Three specimens from the same station in the Clipperton Island (ECOSUR) were studied for the relationship between body size and number of transverse rows of denticulation in neurochaetae: left parapodium of chaetiger 12 were dissected, notochaetae were removed, and they were mounted in anterior view for countint the series in upper, median and lower neurochaetae. The smallest specimen (9 mm long) had

FIG. 9. — *Iphione ovata* Kinberg, 1856, MNHN, Clipperton Island: **A**, dorsal view; **B**, same, anterior end, dorsal view; **C**, same, anterior end, dorsal view after removing right elytra of segments 2, 4, 5, 7, left elytra of segments 2, 4, 5; **D**, another specimen (ECOSUR), segment 14, right parapodium, posterior view; **E**, same, some notochaetae (inset: enlargement of notochaetal tip); **F**, same, tips of two neurochaetae. Scale bars: A, 1.3 mm; B, 0.5 mm; C, 0.4 mm; D, 0.3 mm; E, 110 µm; F, 70 µm.

18-24 rows, the medium sized specimen (14.5 mm long) had 18-30, whereas the largest one (23 mm long) had 28-40 transverse rows of denticles per chaetae. Consequently, this is a size dependent feature without diagnostic relevance.

Photographs of living specimens show that cephalic appendages such as palps, antennae and tentacular cirri, are usually extended beyond elytral margins, and dorsal cirri are often extended beyond neurochaetal tips (Kwajalein Underwater 2019). The body and appendages are very elastic and contractile and include a highly developed system of oblique muscular fibers (Storch 1967), such that the size proportions of these appendages to one another depends on the contraction of the specimen, and consequently are not useful as diagnostic features.

Regarding pigmentation, smallest specimens have transparent to maculate elytra, sometimes with several diffuse polygonal black spots extended along elytral surface. During growth these spots tend to either disappear or fuse to each other, such that a single, oblique black band might be seen in some specimens, whereas in others, the spots are not present.

MORPHOLOGY OF SEQUENCED SPECIMENS

Mitochondrial DNA was extracted, and cytochrome oxidase I fragment was amplified from 52 specimens of *Iphione*

Fig. 10. — *Iphione ovata* Kinberg, 1856, Clipperton Island: **A**, juvenile (ECOSUR), dorsal view, right elytra and two parapodia removed; **B**, same, anterior end, dorsal view; **C**, right elytron from segment 2, dorsal view (asterisk indicates larger macrotubercle); **D**, same, larger macrotubercle in lateral view; **E**, right elytron from segment 4, dorsal view (asterisk indicates largest macrotubercle); **F**, same, large macrotubercle seen from above; **G**, right elytron from segment 7, dorsal view (asterisk indicates large macrotubercle); **H**, same, large macrotubercle seen from above; **I**, segment 10, right cirrigerous parapodium, posterior view (insets: upper, middle and lower neurochaetae); **J**, adult specimen (ECOSUR, Sta. 17), dorsal view showing fully developed elytral pigmentation. Scale bars: A, 0.5 mm; B, C, E, F, H, I, 0.2 mm; D, G, 0.3 mm; J, 2.0 mm.

collected from the Red Sea to Hawaii and Southeastern Polynesia for an initial exploration of COI gene tree topology. Nineteen specimens belonging to *I. ovata* and 33 specimens of five congeneric taxa were compared to assess genetic affinities (Fig. 11). The size-dependency in elytral morphology noted above for *I. ovata* found in Hawaii was supported by the genetic affinities. Barcoded specimens of various body sizes (listed above) were between 3.8 mm (UF 5492) and 23 mm long (CAS 174438), and their elytra varied from 1 to 4-5 macrotubercle rows on each median

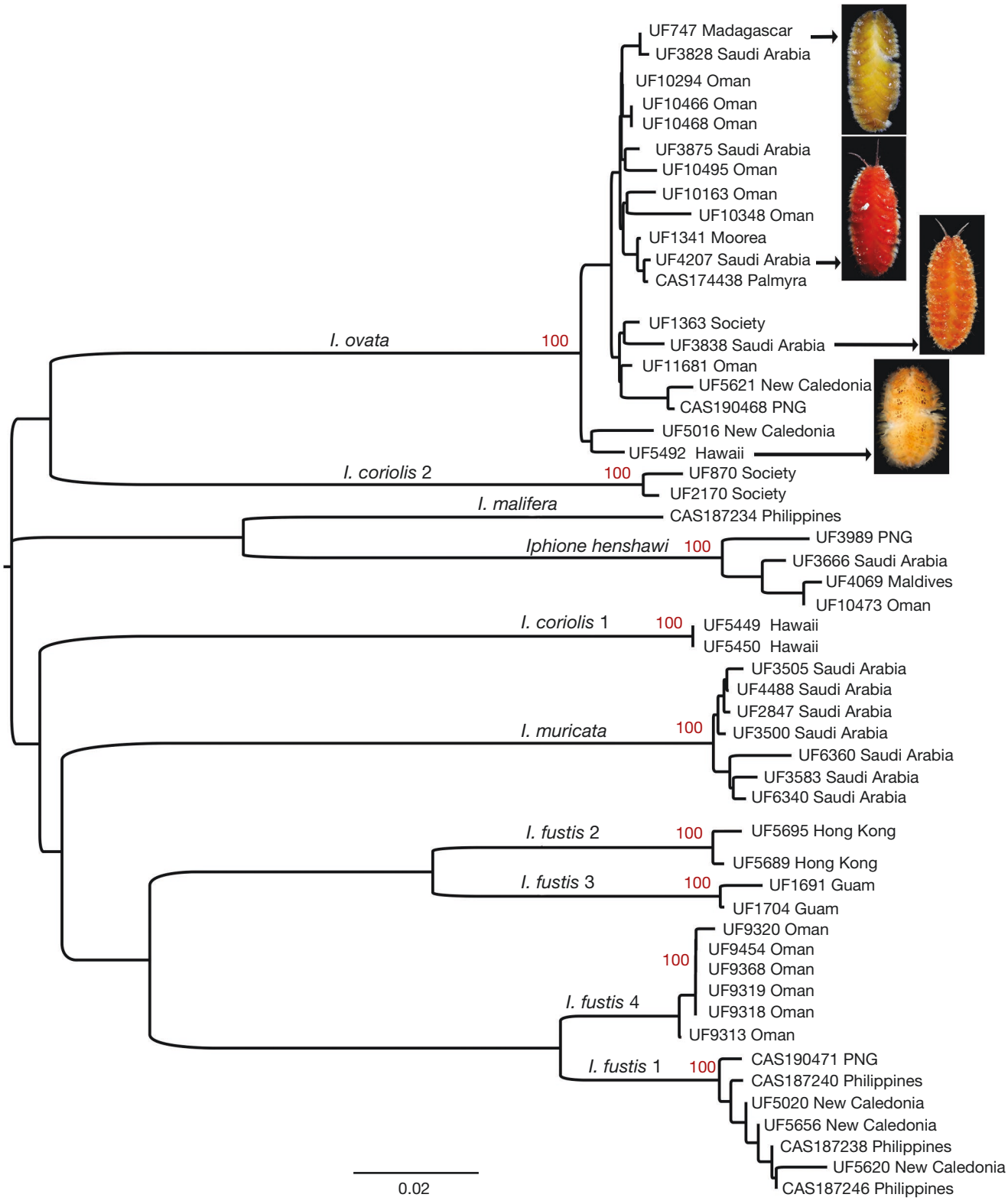

Fig. 11. — Affinities of several species of *Iphione* Kinberg, 1856 after their COI sequences, some names are tentative pending the study of their type specimens; most specimens from the University of Florida, Natural History Museum (PNG: Papua New Guinea). Bootstrap support data in red.

elytron. These specimens cluster as a strong COI sequence group when compared with all other specimens belonging to *I. ovata* collected across the tropical Indo-Pacific region. Future inclusion of additional taxa and other genetic markers may more clearly elucidate evolutionary distinct lineages within this group.

On the contrary, two of the congeneric taxa included in the analysis, *I. coriolis* and *I. fustis* Hoagland, 1920, gathered in different groups reflecting different intraspecific genetic affinities indicating the presence of cryptic or pseudocryptic species, some with distribution restricted to a few regions of the Indo-Pacific (Fig. 11). A detailed morphological revision is needed to clarify these taxonomic problems; however, it is beyond the scope of this study to provide a complete revision of all species in this contribution, and we are moving in that direction.

It can be concluded that some morphological features are not diagnostic, such as the shape and position of eyes, or the number of rows of macrotubercles on elytra. The first, because the prostomium can be distorted after preservation; the second, because it is a size-dependent feature. Neurochaetal features such as the number of rows of denticles vary in the same parapodium depending of the position (upper, medial, lower) of chaetae, and tips are invariable. Here, the number of rows per neurochaeta depends on size and position, whereas the tip is rather fixed in most species in the genus. On the contrary, the type of development of the basal tubercle of dorsal cirrophores is distinctive and diagnostic, because it is modified during growth.

DISCUSSION

Kinberg (1856: 383) diagnosis for his *I. ovata* emphasized that, unlike in *I. muricata* (Savigny *in* Lamarck, 1818), elytra are smooth whereas in the latter they are fimbriate (*laevia* vs *ciliate*). Another difference included in his diagnosis was that in *I. ovata* the antennae and palps were tapered, not clavate, whereas in *I. muricata* they were clavate. Later, Kinberg provided a more detailed description for his *I. ovata* and for another new species, *I. spinosa*, and included several illustrations (Kinberg 1858). These descriptions included a comparison of elytral surfaces in these two species. For *I. ovata*, he indicated (Kinberg 1858: 8) minute tubercles (‘*minute tuberculosa*’), whereas for *I. spinosa* he noted (Kinberg 1858: 9) conspicuous tubercles, densely spinulose (‘*tuberculis eminentibus, dense spinulosis*’). The main difference regarding elytral surface was that in *I. ovata* tubercles are shorter and lower than those present in *I. spinosa*, however this character could become modified by erosion or overgrowth by epizoans. However, as indicated above, the number of rows of elytral macrotubercles (and their size) is dependent on body size. The holotype of *I. spinosa* is larger than the holotype of *I. ovata*.

A second difference was described and illustrated between these two species (Kinberg 1858: 9, pl. 10, figs 45, 46) regarding the pharynx papillae and jaws. In *I. ovata* he described that papillae are about twice longer than wide, and that the jaws have two accessory denticles, whereas in *I. spinosa* papillae are about as long as wide, and jaws have 3-4 accessory denticles. These differences are size-dependent, regarding the number of denticles, whereas the shape of the papillae might be a preservation artifact.

There are three problems exacerbated by the condition of the type material for these two species. First, there are only a few elytra still attached to the holotype of *I. ovata*, and they have short, round macrotubercles as indicated above. Second, the holotype of *I. spinosa* is without elytra, but several elytra are present in the same container. Third, as indicated below, the pharynx has been cut open and jaws are lost, so that examination of the fine details of the jaws must rely on topotypic specimens; further, in its present condition, the number of pharynx terminal papillae in *I. spinosa* type material is not determinable.

In a Western Indian Ocean specimen (CASIZ 204323) the upper jaws have 3-4 denticles, suggesting that the presence of long spine-like macrotubercles in a few rows might be the only distinguishing feature between *I. spinosa* and *I. ovata*, the latter of which has several rows of smaller spines. However, one specimen from Papua New Guinea (CASIZ 190468) with a genetic sequence very similar to other specimens identified as *I. ovata* has 4-5 concentric rows of larger spine-like macrotubercles, thus most closely resembling descriptions for *I. spinosa*. Consequently, we herein regard *I. spinosa* as a junior synonym of *I. ovata* because the number of macrotubercles rows and macrotubercle size are size-dependent and thus are not diagnostic characters.

There is some confusion regarding the validity of *Polynoe peronea* Schmarda, 1861 described from Sri-Lanka with fimbriate elytral margins. Willey (1905: 246) noted some specimens whose elytra had smooth margins, but he regarded the species as a junior synonym of *I. muricata* (Savigny *in* Lamarck, 1818), originally described from the Red Sea and Mauritius. Pettibone (1986: 4) regarded *P. peronea* as a questionable species name and regarded *I. spinosa* Kinberg, 1858 as a junior synonym of *I. ovata*, but was unable to address *I. reticulata*. We have not studied specimens from Sri Lanka, and the assessment of the affinities between *P. peronea* and *I. ovata* must be postponed until topotype specimens are available because there is no type material (F. Pedro 2023 in litt.). However, topotypic specimens from Sri Lanka may not resolve this unless Schmarda’s description is sufficiently detailed to recognize the species. Willey’s specimen, if it exists, needs to be examined to confirm which species it is.

Seidler (1923: 75) regarded most species described in *Iphione* as junior synonyms of *I. muricata* Savigny *in* Lamarck, 1818, including *I. ovata*. Pettibone (1986: 16) modified this synonymy and regarded *I. spinosa* as a junior synonym of *I. ovata* Kinberg, 1856, described from Hawaii. Wehe (2006) was probably following the same conclusion by reporting this Hawaiian species for the Red Sea. Specimens from the Red Sea differ from others illustrated by Pettibone (1986) by a few details. For example, Pettibone (1986: 17, fig. 6 (7)) illustrated that macrotubercles extend along half the length of elytra, whereas in Red Sea specimens they are restricted to the posterior fifth or sixth of elytral surface. Further, Pettibone illustrated that the dorsal cirrophore basal lobe is markedly globose, and the ventral cirrostyle is basally widened (Pettibone 1986: 17, fig. 6D), whereas in Red Sea specimens the basal cirrophore lobes is slightly developed or projected, and the ventral cirrostyle is thinner. The third difference is that

KEY TO *IPHIONE* SPECIES KINBERG, 1856 RECORDED IN HAWAII
(MODIFIED AFTER PETTIBONE 1986)

1 Elytra with lateral fringe of papillae 2
— Elytra without lateral fringe of papillae; elytral macrotubercles spine-like, arranged in 3-8 concentric rows, neurochaetae unidentate ..... *I. ovata* Kinberg, 1856

2(1) Elytral macrotubercles spine-like, arranged in 4-5 concentric rows; neurochaetae unidentate .... *I. muricata* (Savigny *in* Lamarck, 1818)
— Elytral macrotubercles projected as blunt lobes, or low conical or cushion-like lobes 3

3(2) Neurochaetae unidentate 4
— Neurochaetae bidentate; macrotubercles low ridges, arranged in 3-4 concentric rows .... *I. coriolis*? Hanley & Burke, 1991

4(3) Macrotubercles projected as blunt lobes, arranged in a single series, without long spines; marginal fringe with papillae short (up to twice longer than wide) ..... *I. treadwelli* Pettibone, 1986
— Macrotubercle low ridges with 2-4 long blunt spines, arranged in up to 10 concentric rows; marginal fringe with papillae long (3-5 times longer than wide) ..... *I. henshawi* Pettibone, 1986

Pettibone illustrated the rows of denticles in neurochaetae extending basally beyond the swollen region (Pettibone 1986: 17, fig. 6E), whereas in the Red Sea specimens they do not reach the swollen region basally. These differences, however, are size-dependent as indicated above, and soft tissue characters might be altered depending on the contraction of the complex body muscle system, so that they are not diagnostic. Nevertheless, we agree with Pettibone regarding the synonymy of *I. ovata*.

Iphione reticulata Amoureux, Rullier & Fishelson, 1978 was described from one specimen collected in the Gulf of Eilat, Israel. Elytra were described with smooth margins, their surfaces with large polygons filled with fewer areolae, wide smooth margin rims, and lacking macrotubercles. Wehe (2006: 69) noted the holotype (and only) specimen was a 7 mm long juvenile. He observed rudimentary macrotubercles and, upon comparisons with similarly small specimens of *I. muricata* and *I. ovata*, regarded it as a junior synonym of *I. ovata* Kinberg, 1856, described from Hawaii. Piotrowski (2014) studied the holotype of *I. reticulata* and regarded it as a valid species based on what seemed the unique morphology of its elytra. It is interesting that Willey (1905: 247-248) noted in a 5 mm long juvenile a 'wide membranous fringe around the outer and posterior border, not yet areolated; there are no fimbriae; about 17 primary meshes across the scale'. Consequently, *I. reticulata* may in fact be a juvenile of another species described with smooth margins as concluded by Wehe (2006: 69). Wehe regarded *I. reticulata* as a junior synonym of *I. ovata*, and based on further comparisons with morphologically and genetically confirmed juvenile *I. ovata* (see Fig. 8), we concur.

Iphione ovata is distinguished from other species recorded from Hawaii as indicated in the key above.

DISTRIBUTION

Originally described from Hawaii, *Iphione ovata* distribution is herein confirmed across the entire Indian and Pacific tropics from the Red Sea, and from the Western Pacific to Western Mexico, and other nearby localities in the Eastern Pacific, in shallow mixed coral rubble or rocky substrates.

REMARK

Iphione muricata was recorded in Hawaii by Hartman (1966: 175), and by Bailey-Brock & Hartman (1987: 235). Some specimens with yellow elytra have been identified as *I. Coriolis*, described from the Coral Sea, however the type must be studied before concluding that this species is also present in the Hawaiian Archipelago. The key above has been assembled for adult specimens, since juvenile specimens may vary in the characters included herein.

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