

Review of the Iphioninae  
(Polychaeta: Polynoidae) and  
Revision of *Iphione cimex* Quatrefages,  
*Gattyana deludens* Fauvel, and  
*Harmothoe iphionelloides* Johnson  
(Harmothoinae)

MARIAN H. PETTIBONE

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## ABSTRACT

Pettibone, Marian H. Review of the Iphioninae (Polychaeta: Polynoidae) and Revision of *Iphione cimex* Quatrefages, *Gattyana deludens* Fauvel, and *Harmothoe iphionelloides* Johnson (Harmothoinae). *Smithsonian Contributions to Zoology*, number 428, 43 pages, 18 figures, 1986.—The subfamily Iphioninae, including the genera *Iphione*, *Iphionella*, and *Iphionides*, is reviewed and revised, based on examination of types, other published records, and new material. Two new species of *Iphione* from Hawaiian waters are described. *Iphionella* McIntosh is revised, *I. cimex* of McIntosh is given a new name, and a new species from the hydrothermal vents in the East Pacific Rise is added. *Iphione cimex* Quatrefages is referred to the new genus *Gaudichaudius* in Harmothoinae, with *Gattyana deludens* Fauvel as a synonym. *Harmothoe iphionelloides* Johnson is referred to the same genus.

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# Contents

	<i>Page</i>
Introduction . . . . .	1
Acknowledgments . . . . .	2
Chronological Synopsis of Subfamily Iphioninae Baird and Genera <i>Iphione</i> , <i>Iphionella</i> , and <i>Iphionides</i> . . . . .	2
Family POLYNOIDAE Malmgren, 1867 . . . . .	4
Subfamily IPHIONINAE Baird, 1865 . . . . .	5
Key to the Genera of Iphioninae . . . . .	5
Genus <i>Iphione</i> Kinberg, 1856 . . . . .	6
General Characteristics of the Species of <i>Iphione</i> . . . . .	6
Key to the Species of <i>Iphione</i> . . . . .	9
<i>Iphione muricata</i> (Savigny, 1818) . . . . .	9
<i>Iphione ovata</i> Kinberg, 1856 . . . . .	16
<i>Iphione treadwelli</i> , new species . . . . .	19
<i>Iphione henshawi</i> , new species . . . . .	21
Genus <i>Iphionella</i> McIntosh, 1885 . . . . .	23
Key to the Species of <i>Iphionella</i> . . . . .	25
<i>Iphionella philippinensis</i> , new name . . . . .	25
<i>Iphionella risensis</i> , new species . . . . .	28
Genus <i>Iphionides</i> Hartmann-Schröder, 1977 . . . . .	31
<i>Iphionides glabra</i> Hartmann-Schröder, 1977 . . . . .	31
Subfamily HARMOTHOINAE Horst, 1917 . . . . .	33
<i>Gaudichaudius</i> , new genus . . . . .	33
Key to the Species of <i>Gaudichaudius</i> . . . . .	34
<i>Gaudichaudius cimex</i> (Quatrefages, 1866), new combination . . .	34
<i>Gaudichaudius iphionelloides</i> (Johnson, 1901), new combination	37
Literature Cited . . . . .	41



# Review of the Iphioninae (Polychaeta: Polynoidae) and Revision of *Iphione cimex* Quatrefages, *Gattyana deludens* Fauvel, and *Harmothoe iphionelloides* Johnson (Harmothoinae)

*Marian H. Pettibone*

## Introduction

The discovery of some scaled polychaetes that appeared to be related to the Iphioninae in the material collected during *Alvin* dives to the East Pacific Rise hydrothermal vent area at 21°N off Western Mexico prompted me to work up the collections of this group that had been accumulating in the United States National Museum collections (now deposited in the National Museum of Natural History, Smithsonian Institution), as a part of my ongoing revisionary studies on the Aphroditacea. At present, the Iphioninae includes three genera: *Iphione* Kinberg, represented by the widely distributed Indo-Pacific *Iphione muricata* (Savigny), associated with coral reefs and shallow water; *Iphionella* McIntosh, including a specimen collected in deep water off the Philippines by the *Challenger* expedition; and *Iphionides* Hartmann-Schröder, based on specimens collected in coastal ground water in Cuba.

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Fifteen species have been referred directly or indirectly to the above genera. Some have been transferred to other genera, another family, or subfamily, and some are considered to be synonyms. Types were examined where available. Cataloged specimens in the Smithsonian Institution collections (USNM), identified by A.L. Treadwell, R.A. Hoagland, R.V. Chamberlin, O. Hartman, E. and C. Berkeley, M.H. Pettibone, and D.J. Reish, were reexamined. In addition, some cataloged specimens deposited in other museums were received on loan or in exchange: from the British Museum (Natural History) (BMNH), specimens identified by W.C. McIntosh, F.A. Potts, C.C.A. Monro, P. Fauvel, J.H. Day, and P.E. Gibbs; from the Stockholm Museum (NRS), by J.G.H. Kinberg and H. Augener; from the Amsterdam Museum (ZMA), by R. Horst; from the Australian Museum, Sydney (AMS), by W.A. Haswell; and from the American Museum of Natural History, New York (AMNH), by A.L. Treadwell. Unidentified specimens from a variety of sources were studied: from the Moluccas and Australia, collected by



R.R. Miller, L.M. Joll, N. Coleman, R. and J. Brock; from Pacific Islands: Caroline, Marshall, and Gilbert Islands, Samoa, Fiji, Tahiti, collected by M.W. Johnson, J. Morrison, A.H. Banner, F.M. Bayer, and H. Rehder; from Thailand, by H.M. Smith; from the Indian Ocean off East Africa, by S.A. Earle on the *Anton Bruun* cruise; from Lower California, by G.E. Radwin; and from Pacific Panama, by M.L. Jones.

The specimens of Iphioninae, collected during *Alvin* dives of the OASIS expedition in 1982, were among the polynoid polychaetes received from I. Williams and J. Frederick Grassle of the Woods Hole Oceanographic Institution (WHOI). This publication is OASIS expedition contribution number 29.

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**Chronological Synopsis of  
Subfamily Iphioninae Baird and  
Genera *Iphione*, *Iphionella*, and *Iphionides***

1818. *Polynoe muricata* Savigny in Lamarck, 1818:308–309, from Mauritius (Île-de-France) in Indian Ocean. Preliminary listing only.

1820. *Polynoe muricata* Savigny, 1820:21–22, pl. 3: fig. 1,

under Tribe Polynoeae Iphionae. In addition to the record from Mauritius, specimens from the Gulf of Suez in the Red Sea were reported with description and excellent detailed figures.

1828. Blainville, 1829:459–501, fig. 1, placed Savigny's species under *Eumolpe muricata*. He expressed doubt that the prostomial antenna was absent, or only broken off.

1856. Kinberg, 1855 [1856]: 383, under Family Iphionea and new genus *Iphione* (*Eumolpae iphionae* Savigny), included two species, preliminary listings only:

*I. ovata* new species, from Honolulu, Oahu, Hawaiian Islands.

*I. muricata* (Polynoe) Savigny (*Eumolpe*) Blainville, from Mauritius and Red Sea.

1858. Kinberg, 1858:7–9, under Family Iphionea (Polynoeae Iphionae Savigny), included diagnoses of the family and genus *Iphione* and three species:

*I. muricata* (Savigny). Same as above.

*I. ovata* Kinberg, with description and good figures (1858:8, pl. 3: fig. 8; pl. 10: fig. 45). Holotype in Natural History Museum, Stockholm (NRS). *I. ovata* is considered to be distinct by some authors, such as Chamberlin (1919), Monro (1928a,b), Hartman (1939), and others (see synonymy of *I. ovata*, below). *I. ovata* is included as a synonym of *I. muricata* by others, such as Augener (1922:5) and Fauvel 1943:2, since the characteristic lateral fringe of the elytra of *I. muricata* drops off easily. *I. ovata* is herein considered to be distinct. Some of the records of *I. muricata*, based on reexamination of specimens, are referred to *I. ovata* (see synonymy of *I. ovata*, page 16).

*I. spinosa* new species, from Port Natal, South Africa, with short incomplete description and only the pharyngeal papillae and jaws figured. Holotype in Natural History Museum, Stockholm (NRS). Augener (1922:6) examined the type and referred the species to *I. muricata*. Based on my examination of the type, I have included it under *I. ovata*. The elytra lack the characteristic lateral fringe of *I. muricata* (see *I. muricata*, page 9).

1865. Baird, 1865:181, under the Family Iphionidae (Iphionea, Kinberg; Polynoeae Iphionae, Savigny) gave the diagnostic characters of the family as follows:

Facial tubercle small, placed between two antennae, which are produced from the surface of the face [= prostomium]; no tentacle [= median antenna]; palpi thick; tentacular and buccal cirri slender; elytra reticulated. There is only one genus as yet belonging to this family, which Kinberg, adopting the divisional denomination indicated by Savigny, has named *Iphione*. The typical species is the *Polynoe muricata* of Savigny, so beautifully represented by that author in his work on Egypt.

Thus *Polynoe muricata* Savigny was selected by Baird (1865) as the type-species for *Iphione* Kinberg. For the

additional diagnosis for *Iphione* Kinberg, Baird (1865:181) added:

Eyes four, sessile; cephalic lobe produced from between the basal joints of the antennae [= lateral antennae], which are longer than the lobe itself; elytra 13 pairs. The setae [= notosetae] of the dorsal branch [= notopodium] of feet are fine subulate hairs; bristles [= neurosetae] of ventral branch [= neuropodium] placed close to them and serrate.

- Baird then listed the three species of *Iphione*: *I. muricata*, *I. ovata*, and *I. spinosa*. In the same publication under the Family Polynoidae, Baird (1865:200) established a new genus, *Norepea*, for *Polynoe peronea* Schmarda, 1861, based on Schmarda's figures and description only. *Polynoe peronea* Schmarda (1861:157) from the south coast of Ceylon was incompletely and, in some respects, erroneously described. Types are not known to exist. The species was compared with *Polynoe muricata* and *Iphione spinosa* by Schmarda. Based on additional material from Ceylon, Michaelson (1892:95) referred Schmarda's species to *I. spinosa* Kinberg, while Willey (1905:246) referred it, with some question, to *I. muricata*. Willey corrected Schmarda's description but no mention was made of a lateral fringe of papillae on the elytra, so there is a possibility that Schmarda's species should be referred to *I. ovata* rather than to *I. muricata*. Augener (1926:442) identified some specimens from Ceylon as *I. muricata*. There is no question, however, that *Norepea* Baird, 1865, is a synonym of *Iphione* Kinberg, 1856, as indicated also by Chamberlin (1919:40).
1866. Quatrefages, 1865[1866]:266–272, under Errantes Aberrantes Aphroditiens, included 7 species of *Iphione*: *I. muricata* (Savigny) from the Red Sea near Suez; *I. ovata* Kinberg, with a new record from Australia (Nouvelle-Hollande); *I. spinosa* Kinberg (Kinberg's record); *I. glabra*, from Mauritius; *I. cimex* from Malacca Strait; *I. fimbriata* from Torres Strait; and *I. hirta* from New Guinea. (The last four were new species.) The descriptions are deficient in some respects and no figures were included. Types were not available in the Paris Museum for *I. hirta* and it is considered to be questionable. Types for the other three species were received on loan from the Paris Museum (MNHN) and were reexamined. *I. fimbriata* and *I. glabra* are referred herein to *I. muricata* (see *I. muricata*, page 9). *I. cimex* does not agree with *Iphione* and is referred herein to a new genus, *Gaudichaudius*, in Harmothoinea (see *Gaudichaudius*, page 34).
1876. Grube, 1876:51, described *Iphione magnifica* from Trinidad, West Indies. It was referred to *Chaetacanthus magnificus* (Grube) by Seidler (1924:97).
1885. McIntosh, 1885:58–61, established the new genus *Iphonella* for a specimen from off the Philippine Islands in 914 meters, to which he referred Quatrefages's species *Iphione cimex* from Malacca Strait. According to my examination of McIntosh's specimen from the Challenger

- Expedition in the British Museum BMNH, that specimen does not agree with the type of *I. cimex* Quatrefages. One wonders why McIntosh chose to refer his specimen to the species established by Quatrefages, which was poorly described and without figures. McIntosh (1885:60) also stated that *Iphione cimex* Quatrefages seemed "to be in need of reexamination." *Iphonella* is a valid genus and the specimen is given a new name, *Iphonella philippinensis*, with the Challenger specimen serving as the holotype (see *I. philippinensis*, page 25). In the same publication, in the discussion under *Iphonella*, McIntosh (1885:81, pl. 9: fig. 7) supplemented the description of *Iphione muricata* (Savigny).
1901. Gravier, 1901:226–231, figs. 232–239, pl. 9: figs. 129–135, based on numerous specimens from the Gulf of Suez and Gulf of Aden (Djibouti), supplemented the description of *Iphione muricata*. Numerous additional records for the species from tropical and subtropical waters of the Indo-Pacific have been added, some of which are indicated in the synonymy for the species (see page 9).
1912. Izuka, 1912:63–65, pl. 7: figs. 8–15, described *Iphione hirotai* from the Bonin Islands, Japan. It was well described and figured. No types are known to exist. It was included under *I. muricata* by Augener (1922:5), Okuda (1937:266), and others. Based on the description and figures, it is referred herein to *I. ovata*, as was done also by Wu (1968:30–31, fig. 1N–P) (see page 16).
1917. Horst, 1917:64–68, in the subfamily Iphoninae, based on numerous specimens from the Malay Archipelago, included brief diagnoses of the subfamily and *Iphione* Kinberg, and some additional records of *Iphione muricata* (Savigny), mostly from reefs and dredged in 13–73 meters, with one record from 894 meters. In addition, a diagnosis of *Iphonella* McIntosh and two additional records of *Iphonella cimex* (Quatrefages) from the Sulu Sea in 1270 meters and south off the isle of Roti in 420 meters were included. The description and figures of the latter specimens by Horst (1917:66–67, pl. 15: figs. 1, 2) also do not agree with the type specimen of *Iphione cimex* Quatrefages but do fit the description of *Iphonella* McIntosh. Based on examination of one of the specimens reported by Horst, deposited in the Amsterdam Museum (ZMA), it is referred herein to *Iphonella philippinensis*, new name (see page 25).
1920. Hoagland, 1920:605, pl. 46: figs. 4–8, described *Iphione fustis* from the Philippine Islands at depths of 15–55 m. It was incompletely described and figured. The types are deposited in the Smithsonian Institution (USNM). Based on an examination of the types, it is referred herein to *I. muricata* (see page 9).
1922. Augener (1922:5–6) identified some specimens from Cape Jaubert, SW Australia, collected by the Swedish Expedition, as *Iphione muricata* (Savigny) and added to the description of the species. He also examined the type specimens of *I. spinosa* Kinberg and *I. ovata* Kinberg from

- the Stockholm Museum (NRS). He indicated that the type of *I. spinosa* completely agreed with *I. muricata*. He noted some differences in the elytra of *I. ovata* but considered them to be insignificant and included *I. ovata* as a synonym of *I. muricata*. I examined at least some of the same specimens from Cape Jaubert (NRS) and agree with Augener's identification; they are listed below under *I. muricata*. Augener indicated that he examined four specimens of *I. ovata*; however, I received only the holotype of *I. ovata* from the Stockholm Museum (NRS). The elytra differ from *I. muricata* in lacking the characteristic spinous papillae on the lateral border, as indicated by Kinberg. The holotype of *I. spinosa* (NRS) agrees with *I. ovata* (see page 16).
1922. Seidler (1922:75), under *Iphione muricata* (Savigny), included in synonymy most of the above species: *I. ovata* and *I. spinosa* of Kinberg, *Polynoe peronea* Schmarda and *Norepea peronea* (Schmarda) by Baird, *I. glabra*, *I. fimbriata*, and *I. hirta* of Quatrefages, *I. hirotai* Izuka, and *I. fustis* Hoagland. Under *Iphione cimex* Quatrefages, Seidler (1922:78) included *Iphionella cimex* sensu McIntosh.
1931. Treadwell, 1931:315–317, fig. 2, described *Iphionella elongata* from off the Philippine Islands. Based on an examination of the type in the Smithsonian Institution (USNM) by Hartman (1938a:125–126, fig. 41), it was referred to *Eupolyodontes* in Polyodontidae.
1959. Hartman, 1959:82, 95, 105, in her catalog, listed under Iphioninae the genus *Iphione* Kinberg, 1856 with two synonyms: *Norepea* Baird, 1865, and *Iphionella* McIntosh, 1885. Under *Iphione* Kinberg, she listed three species:
- I. cimex* Quatrefages, 1866. As noted above, this species does not agree with *Iphione* and is referred to a new genus (see Harmothoinae, page 33).
  - I. ovata* Kinberg, 1856, with the comment "Resembles *Iphione muricata*" (see below under *I. ovata*).
  - I. muricata* (Savigny, 1818), with seven synonyms:
    - I. spinosa* Kinberg, 1858
    - Polynoe peronea* Schmarda, 1861
    - I. fimbriata* Quatrefages, 1866
    - I. glabra* Quatrefages, 1866
    - I. hirta* Quatrefages, 1866
    - I. hirotai* Izuka, 1912
    - I. fustis* Hoagland, 1920.
- As noted above, *P. peronea* Schmarda and *I. hirta* Quatrefages are considered to be questionable species of *Iphione*. *I. spinosa* Kinberg and *I. hirotai* Izuka are referred to *I. ovata*. *Iphionella* McIntosh, 1885 was earlier referred to *Iphione* Kinberg, 1856 by Chamberlin (1919:64) and Seidler (1922:78). It is considered to be distinct, based on the *Challenger* specimen described by McIntosh (see *Iphionella*, page 23).
1967. Storch, 1967:148–155, figs. 1–5, based on living specimens of *Iphione muricata* collected in the Red Sea, made important contributions regarding the mode of life of this unusual form. He included a detailed study of their musculature and structure of the elytra, including the polygonal areas and specialized border papillae, and a redescription of the species. Some of his observations on the living animals are included below under biology in the section on "General Characteristics of Species of *Iphione*."
1977. Hartmann-Schröder, 1977:51–54, figs. 1–12, described a new genus and species, *Iphionides glabra* in the Iphioninae from coastal ground water in Cuba. The types are deposited in Hamburg (ZMH) and the Smithsonian Institution (USNM) and were reexamined for this paper. The diagnosis of Iphioninae is emended to include the genus (see *Iphionides*, page 31).
1978. Amoureux, Rullier, and Fishelson, 1978:68–69, fig. 2, added a new species of *Iphione* from Sinai in the Red Sea, *I. reticulata*. The species was incompletely described and figured (elytron only). The unique type is deposited in the Laboratoire de Zoologie d'Angers but was not available on loan. It is not included in the present study.
1982. Uschakov (1982:75–78, pl. 6), under Iphioninae, included a brief diagnosis of the subfamily, with a key to the three genera: *Iphione* Kinberg, *Iphionella* McIntosh, and *Iphionides* Hartmann-Schröder, with new records of *Iphione muricata* from Haunan Island at low tide and *Iphionella cimex* from the east coast of Honshu Island in 700 meters. The latter specimen was compared with McIntosh's *Challenger* specimen in the British Museum by V.G. Averincev, according to Uschakov. It is referred herein to *Iphionella philippinensis*, new name (see page 25).

### Family POLYNOIDAE Malmgren, 1867

There has been widespread and longstanding disagreement regarding the placement of *Iphione* among the Polychaeta. It is placed in the family Aphroditidae Savigny and the subfamily Polynoinae Malmgren by some authorities, such as Fauvel (1953:32) and Day (1967:43). Day (1962:628) noted the following

The genus *Iphione* is stated to have two antennae. The posterior part of the prostomium is concealed by a fold of the second segment but if this is pushed back a small dorsal papilla is revealed; it is the third antenna so that *Iphione* like all other genera of the subfamily Polynoinae has three antennae.

In addition to the absence of a median antenna or only a remnant of one, however, there are other characters that separate *Iphione* into a separate subfamily.



A more widely accepted arrangement, and the one endorsed here, is to consider the Polynoidae as a separate family with several subfamilies, including *Iphioninae* Baird, 1865 (sometimes attributed to Horst, 1917); precedent can be found in Horst (1917:64), Hartman (1959:82), Fauchald (1977b:63), Uschakov (1977:29, 1982:61, 78), and Muir (1982:174).

#### Subfamily IPHIONINAE Baird, 1865

DIAGNOSIS.—Body short, elongate-oval, flattened ventrally, arched dorsally, consisting of less than 40 segments (29 in *Iphione* and *Iphionella*, up to 39 in *Iphionides*). Prostomium squarish to oval, with lateral antennae inserted terminally on elongate anterior extensions of prostomium (*Iphione*), or with short rudimentary anterolateral extensions only (*Iphionides*, *Iphionella*); median antenna lacking or represented by small occipital papilla (rarely with distal style in *Iphione*); pair of stout palps; 2 pairs of eyes or eyes lacking (*Iphionella*). Facial tubercle visible between bases of prostomial extensions. Mouth anterior (not ventral). First or tentacular segment not visible dorsally; tentaculophores lateral to prostomium, elongate, each with aciculum, few capillary setae and pair of tentacular cirri. Second

segment with nuchal fold overlapping prostomium (lacking in *Iphionides*), biramous parapodia extending anteriorly and enclosing prostomium and tentaculophores; elongate ventral buccal cirri lateral to mouth. Eversible pharynx with papillae and 2 pairs of jaws. Elytral pairs 13 (*Iphione*, *Iphionella*) or up to 20 pairs (*Iphionides*). Elytra large, overlapping, covering dorsum, stiff, reticulated with hexagonal or polygonal honeycomb-like areas with small areolae or lattice-like areas (*Iphionides*); elytriphores large. Dorsal cirri on non-elytrigerous segments; cirrophores with bulbous glandular bases; styles slender. Dorsal tubercles on cirriferous segments, corresponding in position to elytriphores, bulbous, thin-walled. Ventral cirri short. Parapodia biramous; small notopodia on anterodorsal side of larger neuropodia. Notosetae numerous, forming thick bundles, slender, feathery, and capillary, or moderate in number, spinous (*Iphionides*). Neurosetae numerous, stout, with close-set series of transverse spinous rows and slightly hooked bare tips or moderate in number, slender, of 2 types, including pinnate, tufted. Pygidium inconspicuous, without anal cirri, dorsal anal ridge wedged between parapodia of posterior segments; anus dorsal, between elytriphores of posterior segment.

#### Key to the Genera of Iphioninae

1. Segments 29. Elytral pairs 13; polygonal areas of elytra with numerous secondary areolae [Figures 1F, 10H]. Dorsal tubercles large, foliaceous [Figures 1C, 10C]. Notosetae slender, bipinnate, capillary [Figures 2G, 10F]. Without upper tufted pinnate neurosetae . . . . . 2
- Segments up to 39. Elytral pairs up to 20, on segments 2, 4, 5, 7, on alternate segments to end of body; polygonal areas of elytra with secondary lattice structure [Figure 15H]. Dorsal tubercles small. Prostomium with rudimentary triangular anterolateral extensions but without distinct lateral antennae, with 2 pairs of deeply buried eyes on brain [Figure 15A]. Notosetae slender, capillary, spinous [Figure 15E]. Few upper neurosetae tufted pinnate [Figure 15F] . . . . . *Iphionides* Hartmann-Schröder
2. Prostomium bilobed, with lateral antennae inserted terminally on anterolateral extensions of prostomium, with 2 pairs of eyes [Figure 1A,B].

- Elytra on segments 2, 4, 5, 7, on alternate segments to 23, and on 27  
 ..... *Iphione* Kinberg  
 Prostomium deeply bilobed, forming separate lobes, with anterolateral  
 extensions but without distinct lateral antennae, without eyes [Figures  
 10A, 12A]. Elytra on segments 2, 4, 5, 7, on alternate segments to 23,  
 and on 26 ..... *Iphionella* McIntosh

### Genus *Iphione* Kinberg, 1856

*Iphione* Kinberg, 1855[1856]:383. [Type-species: *Polynoe muricata* Savigny, 1818, designated by Baird, 1865:181; = *Iphione muricata* (Savigny). Gender: feminine.]  
*Norepea* Baird, 1865:181. [Type-species: *Polynoe peronea* Schmarda, 1861, by monotypy. Gender: feminine.]

**DIAGNOSIS.**—Body elongate-oval, dorsum convex, segments 29. Elytral pairs and prominent elytriphores 13, on segments 2, 4, 5, 7, on alternate segments to 23, and on 27. Elytra imbricated, covering dorsum. Elytral surface divided into polygonal or hexagonal areas with numerous secondary areolae, with or without spinous tubercles and lateral fringe of spiny papillae. Dorsal cirri with cylindrical cirrophores and distal styles, and large foliaceous dorsal tubercles on non-elytra-bearing segments. Prostomium and first or tentacular segment partially fused and withdrawn in anterior segments. Prostomium deeply bilobed, with facial tubercle visible between lobes; lateral antennae inserted terminally on elongated lateral extensions of prostomium, with distal styles; pair of stout palps and 2 pairs of eyes, with or without occipital papilla (rarely with style). Tentacular segment with elongated tentaculophores lateral and ventral to palps, each with aciculum, few capillary setae and pair of tentacular cirri. Second or buccal segment with nuchal fold covering posterior part of prostomium, with first pair of elytra on elongated elytriphores extending anterolateral to prostomium, biramous parapodia and long ventral buccal cirri inserted basally lateral to mouth. Third segment not visible dorsally, parapodia wedged between parapodia of segments 2 and 4. Parapodia biramous; notopodia on anterodorsal sides of larger neuropodia, rounded, with projecting acicular process; neu-

ropodia conical with projecting presetal acicular process. Notosetae very numerous, forming bushy bundles, slender, bipinnate, with capillary tips. Neurosetae numerous, stout, with spinous rows and slightly hooked smooth entire tips. Ventral cirri short, tapered. Dorsal anal ridge on segments 23–29, with anus bordered by last pair of elytriphores; without anal cirri. Pharynx with 9 or 11 pairs of papillae and 2 pairs of jaws, each with 3–4 teeth on inner side.

Two species are retained in *Iphione* and two new species are added:

*Iphione muricata* (Savigny, 1818, as *Polynoe muricata*), with three synonyms: *I. fimbriata* Quatrefages, 1866; *I. glabra* Quatrefages, 1866; *I. fustis* Hoagland, 1920.

*Iphione ovata* Kinberg, 1856, with two synonyms: *I. spinosa* Kinberg, 1856; *I. hirotai* Izuka, 1912.

*Iphione treadwelli*, new species.

*Iphione henshawi*, new species.

### General Characteristics of the Species of *Iphione*

**MORPHOLOGY.**—The worms are short-bodied, with 29 segments. They are elongate-oval, about twice as long as broad, arched dorsally, and flattened ventrally. Tough, sturdy, tightly imbricated elytra completely cover the dorsum except for narrow white lateral fringes of capillary notosetae. Ventrally, the segmentation and the rather short, closely approximated parapodia emerging on the same level as the flattened ventral surface, with stout copper-colored neurosetae and short ventral cirri, are visible. (For external views of complete worms, see Savigny, 1820, pl. 3: figs. 1.1, 1.2; Kinberg, 1858, pl. 3: fig. 8A; Gravier, 1901, pl. 9: fig. 129; and Day, 1967, fig. 1.3a.)

Thirteen pairs of yellow-brown elytra are firmly attached on large bulbous elytriphores on

segments 2, 4, 5, 7, on alternate segments to 23, and on 27. The first pair of elytra are small, oval; the second and third pairs are larger, with a deep anterior notch; the following pairs, increasing in size toward the middle of the body, are reniform with a distinct to slight anterior notch; the last pair are small, with a slight notch on the inner side, together forming a small opening over the underlying anal opening (Figures 1E, 4H,I, 5C). The anterior and lateral margins may be thin and membranous; most of the surface of the elytra forms a mosaic of hexagonal or polygonal areas of variable sizes, diminishing in size on the lateral and posterior areas (Figures 1F, 6F). Within the polygonal areas are numerous secondary areoles. Some spinous tubercles may be present on the posterior and lateral regions of the elytra and along the margins. The lateral margins may have an unusual type of spinous papillae loosely attached (Figure 1F). The bulbous elytriphores are transversely elongate and thin-walled, their thickened elytral scars of attachment are large and wide, with a medial posterior extension and a thick rectangular appendage on the posterolateral side (Figures 1C,D, 2E, 6C).

The dorsal cirri, with cylindrical cirrophores and distal papillate styles, and dorsal tubercles, corresponding in position to the elytriphores, are found on segments 3, 6, 8, alternate segments to 24, 25, 26, 28, and 29. The dorsal tubercles are transversely elongated, inflated, and thin-walled, with oval bubble-like extensions on the posterolateral sides (Figures 1C,D, 2F, 4D).

The prostomium and first or tentacular segment are partially fused and withdrawn into the anterior segments (2–4) and covered by the anterior three pairs of elytra (Figures 1A, 3A,B). The prostomium is oval or rectangular, with a deep anterior notch; lateral prostomial extensions, fused basally to the medial facial tubercle, exposed by the anterior notch, project anteriorly and form long basal ceratophores for the lateral antennae; the antennae are papillate, with subterminal enlargements and filamentous tips. Stout, long, tapering palps are located on the lateral sides of the prostomium; they are

equipped with longitudinal rows of papillae on the distal two-thirds (Figure 2A). Two pairs of eyes are located on the posterior half of the prostomium; they may protrude slightly on small ocular peduncles; the posterodorsal ones are often hidden from view. A typical median antenna is usually lacking (present on a specimen from Fiji, Figure 4A). It may be represented by an occipital papilla between the posterior pair of eyes, usually hidden from view (Figures 1B, 3A,B). The tentacular segment is indistinct dorsally. Long cylindrical tentaculophores, lateral to the palps, are extended anteriorly, each with a single aciculum, small acicular lobe, and few capillary setae on the inner side and distally with a pair of dorsal and ventral tentacular cirri, similar to but longer than the lateral antennae (Figures 1A, 2B).

The second or buccal segment has a rectangular or oval nuchal lobe that may cover the posterior part of the prostomium (Figures 1A, 3A,B). The first pair of elytra are borne on greatly elongated elytriphores that are directed anteriorly and medially enclose the tentaculophores and prostomium. The biramous parapodia are similar to the following ones except that the neurosetae are slender, with long spinous regions, tapering to slender tips (Figure 2C,D). Ventral buccal cirri are located basally on the neuropodia, with distinct cirrophores and styles that are similar to the tentacular cirri and longer than the following ventral cirri. The third segment is not visible dorsally; laterally the dorsal cirri and parapodia are wedged between the elytriphores and parapodia of segments 2 and 4 (Figures 1A, 4A); the lower neurosetae are similar to the slender neurosetae of segment 2. Segments 4, 5, and 7 have additional paired dorsal nodules and segments 6 and 8 have delicate dorsal folds or crests extending between the dorsal tubercles (Figures 3A,B, 4A, 6B).

Due to the withdrawal of the prostomium and tentacular segment in the more posterior segments, the mouth is anterior in position, rather than in the more usual ventral position in the Polynoidae. The mouth is enclosed in upper (continuous with the more dorsal facial tubercle),



lateral, and posterior lips of the first two segments (Figure 6A). The eversible muscular pharynx has 11 pairs of dorsal and ventral papillae around the opening, the lateral pairs smaller, and a pair of dorsal and ventral subdistal diagonal lateral ridges (Figures 2I, 3C). The two pairs of strong jaws are denticulate, having three low rounded teeth on the inner margin (Figure 3C). When not extended, the large muscular pharynx occupies the anterior two-thirds of the body.

The posterior six segments (24–29) gradually decrease in size, resulting in a rounded posterior end (Figure 1D). Middorsal oval nodules are present on segments 17–22, followed by a raised median anal ridge on segments 23–29. The elyptrophores of segment 27, bearing the last pair of elytra, are closely approximated, enclosing the dorsal anus and parapodia of the two small posterior cirriferous segments. The small parapodia of segment 29 are in contact medially. There is no distinct pygidium, and anal cirri are lacking. The ventral surface appears smooth but has a stout compressed vesicular cuticle (Storch, 1967:150, fig. 3). Nephridial papillae are usually not visible. When distinct, they are bulbous basally, then narrowed and extend dorsally between the neuropodia.

The rami of the biramous parapodia are closely approximated, such that early descriptions indicated that they were uniramous (Figure 2E,F). The smaller notopodia are situated on the anterodorsal faces of the larger neuropodia. They are rounded with a projecting acicular process but hidden by numerous notosetae forming conspicuous white bushy bundles, also hiding the neuropodia and neurosetae anteriorly. The capillary feathered notosetae are of an unusual type in the Polynoidae. They have a slender axis, tapering to capillary tips, with opposite lateral curved spines or pinnae having the shape of fringed cups; more basally the cups are separated and more distally they are more compressed and interlock (Figure 2C). The numerous notosetae form a close-meshed filter in the space between the parapodia. On the cirriferous segments, the dorsal cirri are located on the posterior sides of

the notopodia; their cylindrical cirrophores have a bulbous base; their styles are slender, papillate, with subterminal enlargements and filamentous tips; they extend slightly beyond the notosetae (Figure 2F). The neuropodia have conical pre-setal lobes with a projecting acicular process; the postsetal lobes are shorter and broadly rounded; their distal borders have short papillae (Figure 2E,F). The neurosetae are very numerous, copper-colored, arranged in about eight horizontal rows of decreasing lengths from the upper to the lower position. They are stout, with low spinous rows or cross striations and slightly hooked bare tips. The upper neurosetae are more slender and have more numerous spinous rows (Figure 2H). The ventral cirri are short, tapered, and papillate, attached on the middle of the neuropodia (Figure 2E,F).

**BIOLOGY.**—The species of *Iphione* show a superficial resemblance to chitons, in their general shape, sturdy bodies, close-fitting elytra, their tendency to recurve ventrally when collected, and their ability to cling tightly to the substratum. Their dull yellow amber-color is often masked by foreign particles, including mud, sand, and calcareous particles.

In his study of *Iphione muricata* from the Red Sea, Storch (1967:148–155, figs. 1–5) reported that specimens were found clinging to the under surface of stones in shallow water and to dead parts of the porous coral reef flat. At night, they crawled for some hours, but moved only a few inches. They were not active in the daytime. Their yellow-brown color, sometimes reddish, matched the color of the substrate. When touched, they did not attempt to escape but attached more tightly to the bottom and were removed with difficulty.

Storch described specimens of *Iphione* showing respiratory movements: except for the first three or four pairs, the elytra were elevated simultaneously; water passed between the neuropodia of the parapodia, through the feathery capillary notosetae, which acted as a filter holding back any suspended particles, and then into the subelytral area. When the elytra were lowered, a pow-

erful stream of water passed posteriorly and out of the opening between the last pair of elytra. (This would also remove faeces from the anus, located in this region.) Storch observed 30 liftings per minute on one occasion.

Storch also noted some peculiarities in the locomotion of *Iphione*. Not only did *Iphione* show superficial resemblance to chitons, it showed similar adaptations in its way of life. It lacked the sinuous, swimming body-type of locomotion found in many errant polychaetes. The sturdy flattened animal, almost half as wide as long, was confined to parapodial locomotion by pulling in and throwing out the relatively short parapodia. When removed from the substrate, the worm rotated, bent ventrally, retracting the head re-

gion and parapodia under the protection of the elytra. It was able to adapt to curved or flat substrates by extension or contraction of well-developed diagonal and dorso-ventral muscle bundles. On flat surfaces, the contraction of the muscles created a suction, and *Iphione* was attached firmly to the substrate. With the head, dorsal cirri, and parapodia retracted, it was able to survive dry periods in the tidal region.

On living animals, according to Storch, the ventral surface of *Iphione* is strongly flattened, showing no segmental grooves on its very thick cuticle. The parapodia are closely approximated and form with the ventral side of the body almost a continuous line.

#### Key to the Species of *Iphione*

1. Elytra without lateral fringe of papillae [Figure 6F] . . . . *I. ovata* Kinberg  
Elytra with lateral fringe of rounded bead-like scaled papillae and with up to 6 oval thickened areas on surface [Figure 7F] . . . . .  
..... *I. treadwelli*, new species  
Elytra with lateral fringe of long cylindrical spinous papillae with flexible bases [Figures 1F, 4H,I, 5C, 8J, 9E] . . . . . 2
2. Surface of elytra with several rows of larger conical spinous tubercles [Figures 1F, 4H,I, 5C] . . . . . *I. muricata* (Savigny)  
Surface of elytra with numerous conical tubercles with spinous base and few distal papillae [Figures 8J, 9E] . . . . . *I. henshawi*, new species

#### *Iphione muricata* (Savigny, 1818)

FIGURES 1-5

*Polynoe muricata* Savigny in Lamarck, 1818:308 [type-locality: Mauritius (Ile de France)].—Savigny, 1820:22, pl. 3: fig. 1.

*Eumolope muricata*.—Blainville, 1828:459.

*Iphione muricata*.—Kinberg, 1855[1856]:383; 1858:8.—McIntosh, 1885:61, pl. 9: fig. 7.—Gravier, 1901:226, text-figs. 232-239, pl. 9: figs. 129-135.—Treadwell, 1906:1154 [in part]; 1926a:183.—Potts, 1910:341 [in part].—Horst, 1917:65.—Augener, 1922:5.—Fauvel, 1932:12.—Monro, 1939:168 [in part].—Day, 1951:14; 1962:628 [in part]; 1967:43, fig. 1.3a-f.—Storch, 1967:148, pls. 1-4.—Gibbs, 1971:123 [in part].

*Iphione fimbriata* Quatrefages, 1865[1866]:271 [type-locality: Torres Strait].

*Iphione glabra* Quatrefages, 1865[1866]:268 [type-locality: Mauritius].

*Iphione ovata*.—Haswell, 1883:276 [in part].—Treadwell, 1926b:5. [Not Kinberg, 1856.]

*Iphione fustis* Hoagland, 1920:605, pl. 46: figs. 4-8 [type-locality: Philippine Islands].—Hartman, 1938a:107, fig. 35a; 1959:82 [“see *I. muricata*”].

*Iphione cimex*.—Treadwell, 1920:591. [Not Quatrefages, 1866.]

**MATERIAL EXAMINED.**—SOUTH AFRICA. Delagoos Bay, near Johaca Island, Jul 1935, C. van der Horst, collector, 4 specimens (ZMA 2528; USNM 81940: identified by Horst, 1917).

MOZAMBIQUE. Inhaca Island, St. IN.4, 1 specimen (BMNH 1963.1.6.; id. Day, 1951).

MADAGASCAR. Diego Suarez and Nossi-Bé, under stones, D. McGregor, collector, 1 specimen (BMNH 1961.8.3; id. Day, 1962).

MAURITIUS. Ile de France, M. Mathieu, collec-

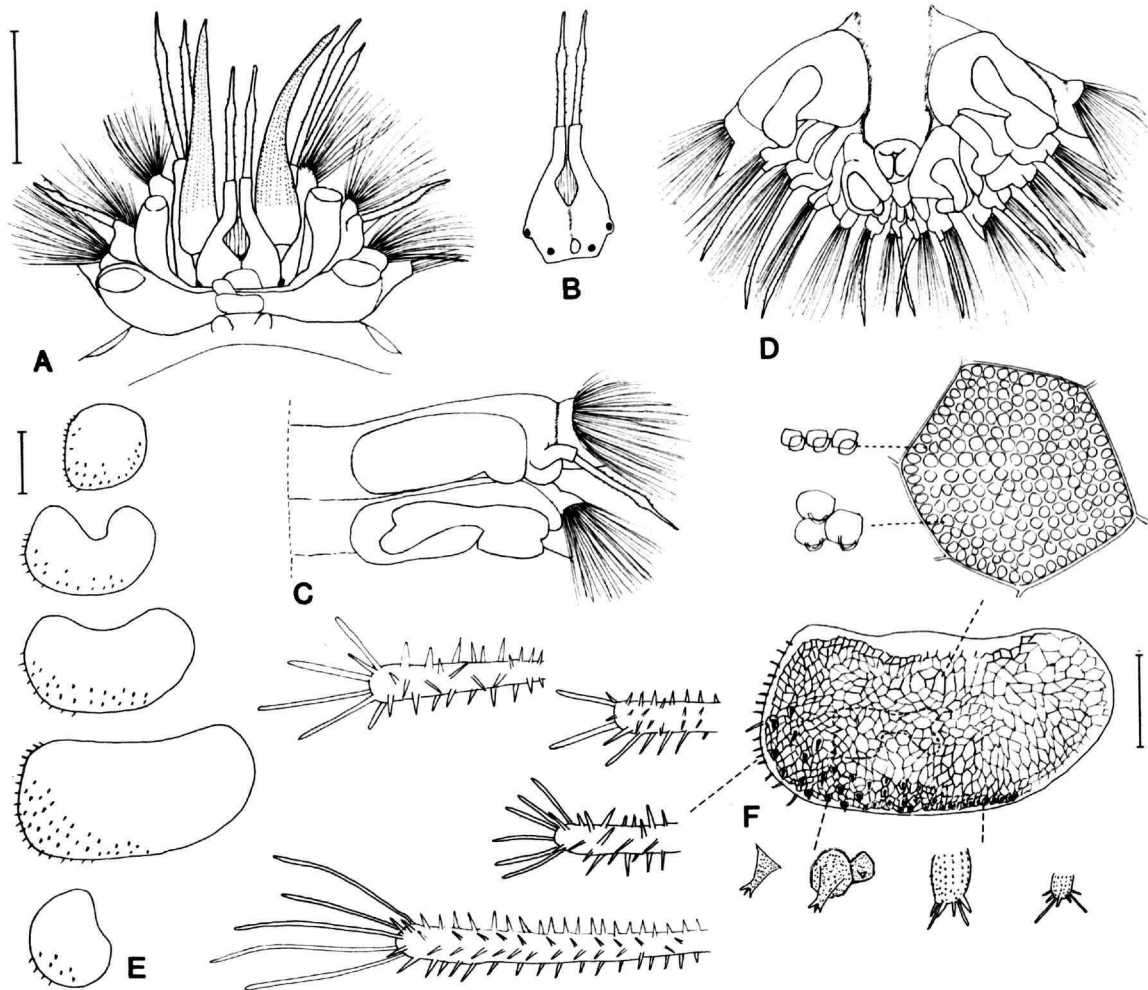


FIGURE 1.—*Iphione muricata* (USNM 81945, from Yirrkala, Australia, 21 × 11 mm): A, dorsal view of anterior end, including segments 1–4 and part of 5; B, prostomium showing lateral antennae, facial tubercle, occipital papilla and 2 pairs of eyes; C, dorsal view of right side of segments 10 (cirrigerous) and 11 (elytrigerous); D, dorsal view of posterior end including segments 23–29; E, outline of left elytra (1st, 2nd, 5th, 10th, and 13th), showing general shapes and position of larger spinous tubercles and lateral spinous papillae; F, left middle elytron, with detail of polygonal area with secondary areolae, lateral spinous papillae and spinous tubercles (not to scale); scar of attachment to elythrophere dotted. (Scales = 2.0 mm for A–D; 2.0 mm for E; 2.0 mm for F.)

tor, holotype of *Iphione glabra* (MNHNP).

ZANZIBAR. Sand Banks, Pemba Island, 18 Nov 1901, C. Crossland, collector, 3 specimens (BMNH 1941.4.4.165–167; id. Potts, 1910; Monro, 1939).

MOMBASA. From F.A. Potts, 9 specimens (BMNH 1924.6.18.187–191; USNM 97380). Nyali, beneath loose coral boulders, D. McGregor, collector, 1 specimen (BMNH 1961.8.1; id. Day, 1962).



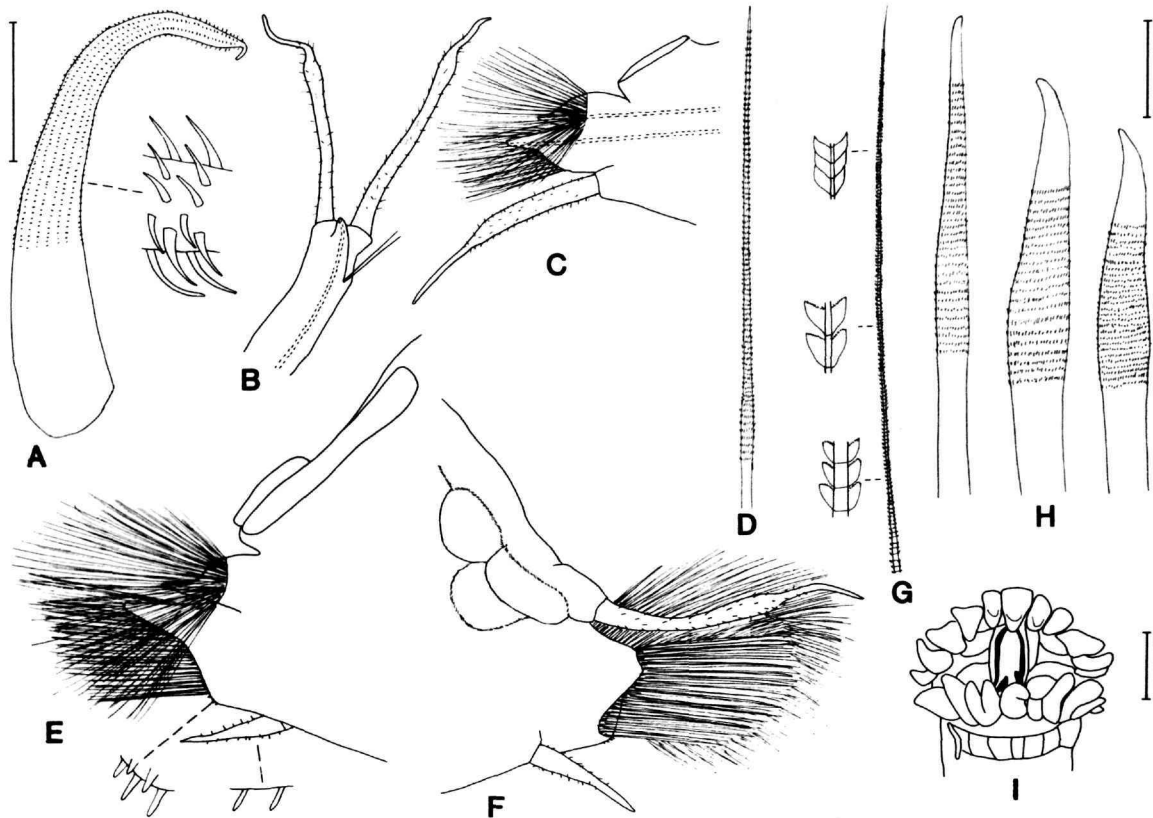


FIGURE 2.—*Iphione muricata* (A–H, USNM 81945, from Yirrkala, Australia; I, USNM 81972, from Samoa, 28 × 15 mm): A, isolated palp, with detail of papillae; B, right tentaculophore, inner view, aciculum dotted; C, right parapodium from segment 2, anterior view, acicula dotted; D, neuroseta from same; E, right middle elytrigerous parapodium, anterior view, with detail of papillae on neuropodium and on ventral cirrus; F, right middle cirriferous parapodium, posterior view; G, notoseta, with detail of part; H, upper, middle, and lower neurosetae; I, ventral view of distal end of extended pharynx, tipped slightly to right, showing marginal papillae, jaws, and left subdistal lateral ridge. (Scales = 1.0 mm, for A–C, E, F; 0.1 mm for D, G, H; 2.0 mm for I.)

RED SEA. C. Crossland, collector, 7 specimens (BMNH 1941.4.4.168–172; USNM 97381; id. Monro, 1939).

SOUTH INDIA. Kottaymam, 2 Feb and 18 Mar 1971, Mrs. K. Srivastave and D.K. Massey, collectors, 2 specimens (USNM 81949). Gulf of Manaar, 2 specimens (BMNH 1928.4.26.889–890; id. P. Fauvel, 1932).

BAY OF BENGAL. Andamans, South Point, Outram Island, shore, *Investigator* sta. 665, 1 speci-

men (BMNH 1938.5.7.3; id. Fauvel, 1932).

THAILAND (SIAM). Koh Pipidon, 3 Sep 1925, H.M. Smith, collector, 2 specimens (USNM 81938). Koh Tao, in coral, shoal water, 24 Sep 1928, H.M. Smith, collector, 1 specimen (USNM 81939).

NETHERLAND INDIES. Batavia Bay, West Java Province, C.P. Sluiter, collector, 3 specimens (ZMA 473, 475). S coast of Nias, off W coast of Sumatra, 1 specimen (ZMA 476). Moluccas

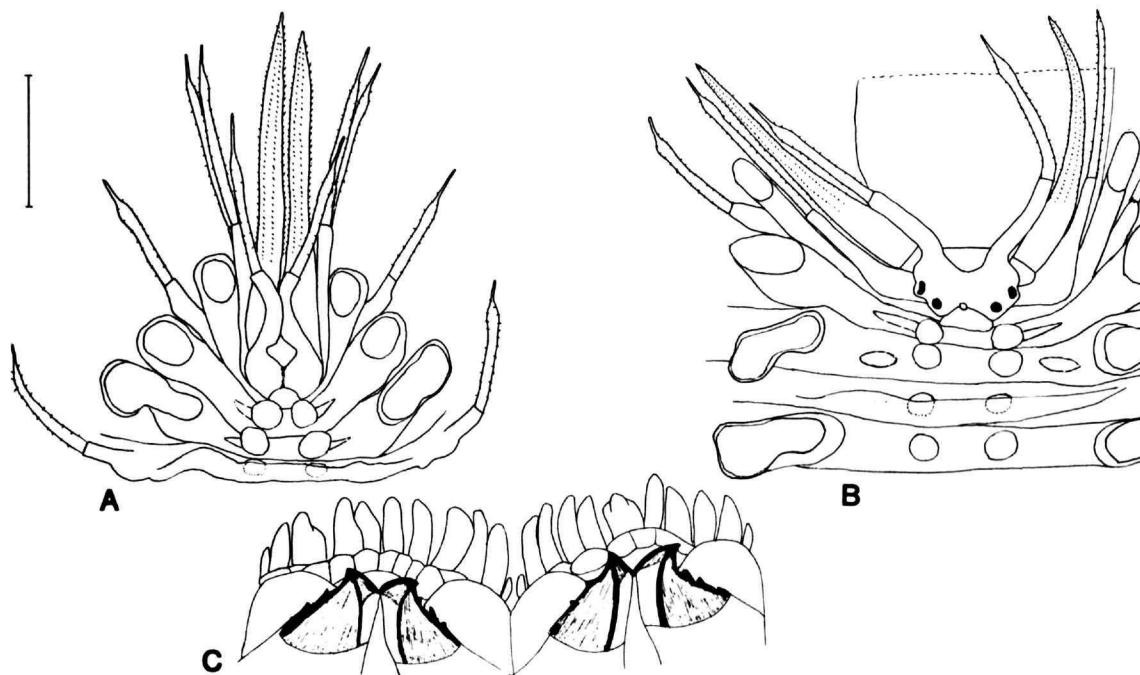


FIGURE 3.—*Iphione muricata* (A, ZMA 2528, from South Africa, 23 × 14 mm; B,C, USNM 81940, from South Africa, 26 × 15 mm): A, dorsal view of anterior end, including segments 1–6, parapodia not completely shown; eyes hidden; B, dorsal view of anterior end, including segments 1–7, pharynx completely extended, only basal part indicated; parapodia not completely shown; C, pharynx cut open, showing inner view of marginal papillae and jaws spread apart. (Scale = 2.0 mm.)

(Spice Islands), NW of Kampong, Namatabung, Laguan Olendir, Seipry, Tanimbar, 08°07'S, 130°66'E, 0–3 m, 25 Jun 1970, L.M. Joll, collector, 1 specimen (WAM). Dutch New Guinea, Mios Woendi, Padaido Island, 2 Oct 1944, A.G. Humes, collector, 1 specimen (USNM 96001). Torres Strait, Hombron and Jacquinet, collectors, holotype of *Iphione fimbriata* (MNHNP).

**AUSTRALIA.** *Northern Territory:* Yirrkala, N.W. of Cape Arnhem, coral reef, Jul 12 and Aug 20, 1948, R.R. Miller and natives, collectors, 2 specimens (USNM 81945, 81946). Mandora, Darwin, low tide under rocks, 22 Nov 1977, N. Coleman, collector, 2 specimens (AMS W5432; USNM 81947).

*Queensland:* Eagle Cay, Palfrey Island off Lizard Island, 2–3 m, among dead coral, 17 Nov

1977, R. and M. Brock, collectors, 1 specimen (USNM 81948).

*New South Wales:* Albury Passage, Haswell, collector, 1 specimen (AMS 11282, as *I. ovata* Haswell, 1883). *Southwest Australia:* WSW Cape Jaubert, 15–22 m, Swedish Expedition, Jun, Jul 1911, E. Mjöberg, collector, 5 specimens (NRS 1832–1835; id. Augener, 1922). *Western Australia:* Kendrew Island: Dampier, under rocks, low tide, 14 Oct 1972, N. Coleman, collector, 1 specimen (AMS 5437); Blow Holes (Quobba), Carnarvon, 2 m, under rocks, 22 Jun 1972, N. Coleman, collector, 1 specimen (AMS 5452).

**PHILIPPINES.** Naw Wawa, Taiwan, *Albatross* Philippine Exp., 27 Jun 1910, 1 specimen (USNM 19308; id. Treadwell, 1926a). Jolo Island, 06°09'N, 120°58'E, 53 m, *Albatross* sta

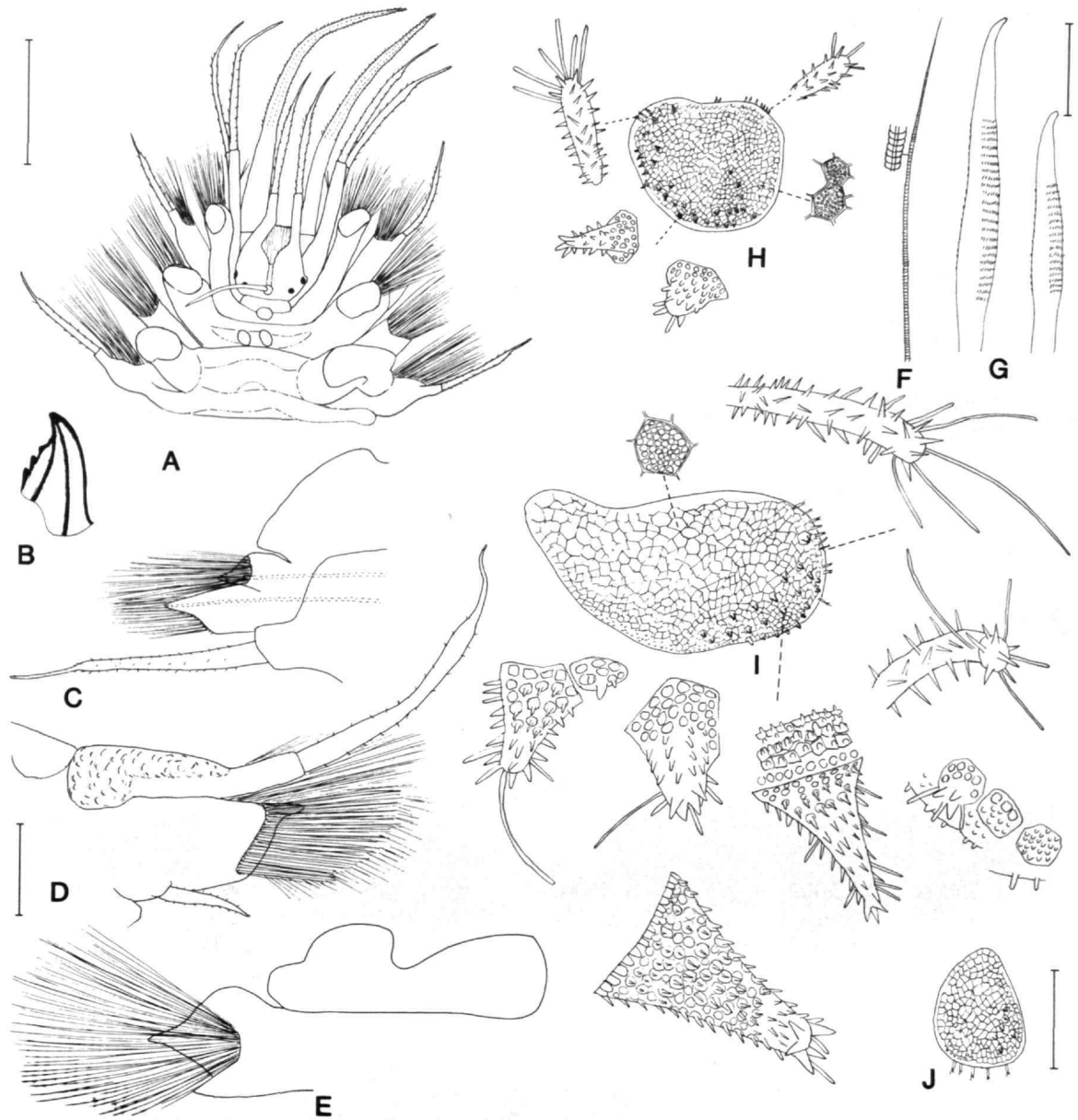


FIGURE 4.—*Iphione muricata* (USNM 19192, from Fiji, 20 × 9 mm): A, dorsal view of anterior end, including segments 1–6; B, isolated jaw; C, right elytrigerous parapodium from segment 2, anterior view, acicula dotted; D, right middle cirriferous parapodium, posterior view; E, right middle elytrigerous parapodium, anterodorsal view; F, notoseta, with detail of part; G, middle and lower neurosetae; H, left 1st elytron, with details of polygonal areas with secondary areolae, spinous papillae, and spinous tubercles (not to scale); I, right 6th elytron, with details of same; J, left 13th elytron. (Scales = 2.0 mm for A,B; 0.5 mm for C–E; 0.1 mm for F,G; 2.0 mm for H–J.)

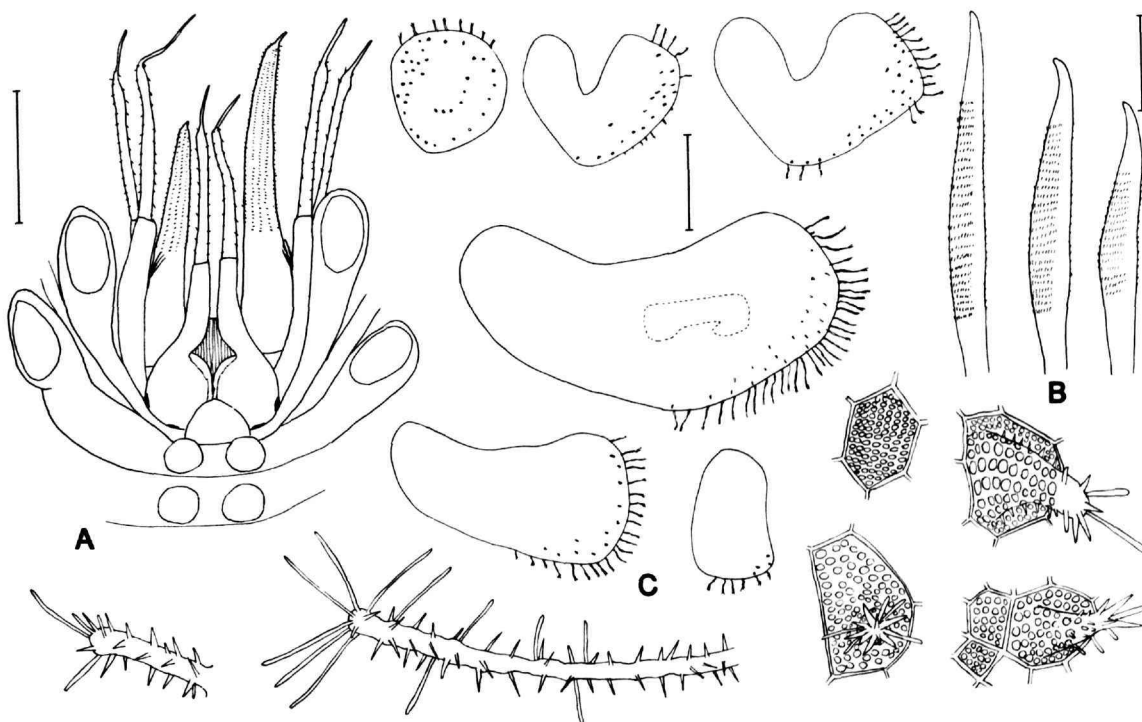


FIGURE 5.—*Iphione muricata* (USNM 81942, from Bikini, 17 × 10 mm): A, dorsal view of anterior end, including segments 1–5, parapodia not shown; B, upper middle and lower neurosetae; C, outlines of right elytra (1st, 2nd, 3rd, 7th, 12th, and 13th) showing general shapes, position of larger spinous tubercles and lateral spinous papillae, with details of polygonal area with secondary areolae, spinous tubercles, and spinous papillae (not to scale). (Scales = 1.0 mm for A; 0.1 mm for B; 2.0 mm for C.)

D5141, 15 Feb 1908, holotype of *I. fustis* (USNM 18941). Caguayan Point off east coast Leyte Island, 11°19'N, 124°58'E, 15 m, *Albatross* sta D5205, 13 Apr 1908, paratype of *I. fustis* (USNM 18969). Tanguingui Island north of Cebu, 11°24'N, 124°06'E, 55 m, fine sandy bottom, *Albatross* sta D5401, 16 Mar 1909, paratype of *I. fustis* (USNM 18968). Caguayan Point north of Cebu, *Albatross* sta, 16 Mar 1909, paratype of *I. fustis* (USNM 18970).

SULU ARCHIPELAGO. Tataan, Simaluc, Tawi Tawi group, shore, *Albatross*, 19 Feb 1908, 1 specimen (USNM 17589; as *I. cimex* by Treadwell, 1920). Linao Point, Gulf of Davao, 42 m, coral and sandy bottom, *Albatross* sta 5250, 18 May 1908, 1 specimen (USNM 17484, as *I. cimex* by Treadwell, 1920).

SAMOA. C.N. Eliot, collector, 4 specimens (USNM 81972; BMNH). D.S. Jordan, collector, U.S. Fish Commission, 1 specimen (USNM 81936). Pago, Pago, 2 specimens (USNM 81937).

FIJI. Suva, A.L. Treadwell, collector, 2 specimens (AMNH 1615; USNM 19192, as *I. ovata* by Treadwell, 1926b). SW side of Ovatova shallows, N coast of Vanna Levu, 18 Jul 1966, H.A. Rehder, collector, 1 specimen (USNM 81944).

WESTERN CAROLINES. Palau Island, Ngaremdin Reef, E side of Uruk Chapel, 07°13'09"N, 134°26'40"E, exposed boulder tract, 19 Aug 1955, F.M. Bayer, collector, 1 specimen (USNM 81943).

MARSHALL ISLANDS. Bikini Atoll, dredged in lagoon, 55–60 m, 29 Mar 1946, L.P. Schultz,

collector, 1 specimen (USNM 81941). Bikini Atoll, 4 miles S of W end of Bikini, dredged in 51 m, 25 Apr 1946, J.P.E. Morrison, collector, 1 specimen (USNM 81942).

SOLOMON ISLANDS. Graham Point, Guadalcanal, under boulders in silty sand, 21 Sept 1965, P.E. Gibbs, collector, 19 specimens (BMNH 1970.113; USNM 97382).

MEASUREMENTS.—Species moderate in size, with 29 segments, ranging from 8 to 32 mm in length and from 6 to 16 mm in greatest width. Length  $\times$  greatest width in mm of specimens examined measured as follows: from South Africa and Mozambique, 23–26  $\times$  14–15; from Madagascar, 19  $\times$  10; from Mauritius (holotype of *Iphione glabra*), 24  $\times$  16; from Zanzibar, 25  $\times$  14; from Mombasa, 14–25  $\times$  10–15; from Red Sea, 10–24  $\times$  7–14; from South India, 26–32  $\times$  13–15; from Thailand, 12–23  $\times$  7–15; from Netherland Indies, 12–23  $\times$  8–13; from Torres Strait (holotype of *Iphione fimbriata*), 31  $\times$  15; from Northern Territory, Australia, 16–21  $\times$  9–11; from Queensland, Australia, 9  $\times$  6; from New South Wales, 29  $\times$  16; from SW Australia, 12–21  $\times$  9–13; from Western Australia, 24–26  $\times$  13–16; from Taiwan, 20  $\times$  13; from Philippines (paratypes of *Iphione fustis*), 12–21  $\times$  8–12; [holotype of *I. fustis* a young specimen, 6  $\times$  5 mm with 26 (?) segments]; from Sulu Archipelago, 10–11  $\times$  8–10; from Samoa, 28  $\times$  15; from Fiji, 20–26  $\times$  9–12; from Palau, 20  $\times$  12; from Bikini, 11–17  $\times$  8–10; from Solomon Islands, 8–24  $\times$  6–13.

DESCRIPTION.—Mostly covered under general characteristics of *Iphione*. The 13 pairs of tightly imbricated elytra covering the dorsum are variable in coloration: yellowish, reddish, yellow with brownish streaks or dark lateral streaking, sometimes masked by foreign particles. The elytra are variable in shape along the body (Figures 1E,F, 4H–J, 5C). The polygonal or hexagonal areas, with secondary areolae, nearly cover the surface of the elytra, becoming smaller toward the lateral and posterior borders where several diagonal rows of larger conical spinous tubercles occupy some of the smaller areas. The larger conical tubercles have 1 to several distal spines, with

shorter spines or roughened surface basally. Along the posterior border, the smaller areas are occupied by smaller spiny tubercles of variable development. Along the lateral borders, spinous papillae occur. They consist of a cylindrical column with a flexible base, with radiating spines along the column and distally with a group of long papillae. The lateral spinous papillae were extra long on the specimen from Bikini (Figure 5C).

The prostomium, anterior segments and pharynx follow the usual pattern in *Iphione* (Figures 1A,B; 2A–C; 3A–C; 4A–C; 5A). The anterior lateral extensions of the prostomium, forming terminal insertions for the lateral antennae, are fused basally to the medial facial tubercle and are free distally where they may be curved medially (Figure 1A) or widely separated when the pharynx is extended (Figure 3B). The median antenna is represented by a small occipital papilla hidden by the nuchal fold of segment 2 unless the fold is pulled back. On one of the specimens from Bikini Atoll, a well-developed style was present on a small papilla-like ceratophore (Figure 4A). A distinct antenna was not observed on any of the other specimens examined. The palps and tentacular cirri are about equal in length, the lateral antennae and ventral buccal cirri somewhat shorter. The paired dorsal nodules on the anterior segments are somewhat variable in shape and distribution, always a pair on segments 4 and 5 and sometimes additional pairs on more posterior segments. Delicate transverse crests or folds, extending between the dorsal tubercles, are found on segments 6 and 8 (Figures 3A,B, 4A).

The parapodia follow the general pattern of *Iphione* (Figures 2C–H, 4C–G). The bushy white bundles of feathery capillary notosetae extend slightly beyond the neurosetae and hide the neuropodia dorsally and anteriorly. The neurosetae of segment 2 and the lower neurosetae of segments 3 and 4 differ from the following neurosetae: they are slender, tapering to sharp tips, with a long region of close-set spinous rows (Figure 2D). The numerous copper-colored stout neurosetae have close-set spinous rows and



slightly hooked bare tips (Figures 2H, 4G, 5B). The posterior end follows the general pattern in *Iphione* (Figure 1D).

**DISTRIBUTION.**—Widely distributed in tropical and subtropical regions of the Indo-Pacific, mainly intertidal and low water, associated with coral reefs.

### *Iphione ovata* Kinberg, 1856

#### FIGURE 6

*Iphione ovata* Kinberg, 1855[1856]:383 [type-locality: Honolulu, Oahu, Hawaii]; 1858:8, pl. 3: fig. 8, pl. 10: fig. 45.—Chamberlin, 1919:64.—Monro, 1928a:557; 1928b:471.—Hartman, 1939:27, pl. 3: figs. 31, 32.—Rioja, 1962[1963]:137, figs. 30–36.—Wu, 1968:30, fig. 1 N–P.—Fauchald, 1977a:5.—Buzhinskaja, Obut, and Potin, 1980:229, 246, 247, 250.

*Iphione spinosa* Kinberg, 1858:8, pl. 10: fig. 46 [type-locality: Port Natal, South Africa].

*Iphione muricata*.—Treadwell, 1906:1154 [in part].—Potts, 1910:341 [in part].—Pruvot, 1930:3, fig. 1a–d.—Monro, 1939:168 [in part].—Fauvel, 1943:2.—Cloud, 1959:422.—Day, 1962:628 [in part].—Reish, 1968:211 [in part?].—Gibbs, 1971:123 [in part]. [Not Savigny, 1818].

*Iphione hirotai* Izuka, 1912:63, pl. 7: figs. 8–15 [type-locality: Bonin Islands, Japan].

**MATERIAL EXAMINED.**—BAJA CALIFORNIA. Isla Cerralbo, Piedras Gordas, 24°09'N, 109°52'W, 26 m, 1 Jun 1969, G.E. Radwin and F.H. Wolfson, collectors, 1 specimen (USNM 81965).

GULF OF CALIFORNIA. 24°22'N, 110°19'W, 15 m, broken shells, *Albatross* sta 2824, 30 Apr 1888, 1 specimen (USNM 81964).

CLIPPERTON ISLAND. NE side, 13 m, 28 Aug. 1958, T. Chess, A. Hambly, and C. Limbaugh, collectors, 1 specimen (USNM 81966).

PANAMA (Pacific). Perlas Islands, Gonzales Island, SW shore, 08°22'N, 79°05'W, Panama Survey sta. 33–3, 30 Apr 1971, M.L. Jones, collector, 1 specimen (USNM 81962). Perico Island, SE side, tide pool at low tide, under rocks, Panama Survey sta. 82B, 12 Apr 1972, M.L. Jones, collector, 2 specimens (USNM 81963).

HAWAIIAN ISLANDS. Honolulu, Oahu, Eugenie Exp., holotype of *I. ovata* (NRS 388). South coast of Molokai Island, 42–44 m, sand and stones,

*Albatross* sta. 3847, 8 Apr 1902, 1 specimen (USNM 5434; as *I. muricata* by Treadwell, 1906). French Frigate shoal, 23°46'N, 116°18'W, 26–30 m, coarse sand and coral, *Albatross* sta 3968, 29 May 1902, 4 specimens (USNM 5438; BMNH; as *I. muricata* by Treadwell, 1906).

MARIANA ISLANDS. N.W. Saipan, lagoon N of Matus beach, picked from dead and porous *Lithophyllum* on base of head of brown *Acropora*, 12 Dec 1948, P.E. Cloud, collector, 1 specimen (USNM 26061; as *I. muricata* by Cloud, 1959).

CAROLINE ISLANDS. Ifalik Atoll, reef flat half-way between NW end of Falarik and Elangelap, beneath large rock, 21 Sep 1953, F.M. Bayer, collector, 1 specimen (USNM 81952). Ifalik Atoll, south end of Falarik, 32 Oct 1953, F.M. Bayer, collector, 1 specimen (USNM 29962). Palau, Ngadarak Reef, north of mouth of Malakae Pass, 07°16'N, 134°28'E, exposed coral rubble and residual pools with sponges, 17 Aug 1955, F.M. Bayer, collector, 1 specimen (USNM 81953). Palau, Ngaremdin Reef, east side of Urukthapel, 07°13'N, 134°26'E, exposed boulder tract, 19 Aug 1955, F.M. Bayer, collector, 2 specimens (USNM 81954).

MARSHALL ISLANDS. Rigoman Island, Rongelap Atoll, 17 Jun 1947, M.W. Johnson, collector, 1 specimen (USNM 81955).

BIKINI ATOLL. Enyu Island, ocean side, under old coral head on reef flat, 6 Sep 1956, D.J. Reish, collector, 1 specimen (USNM 29892; as *I. muricata* by Reish, 1968).

GILBERT ISLANDS. Onotoa, 1 Aug 1951, A.H. Banner, collector, 1 specimen (USNM 26062).

TUAMOTU ARCHIPELAGO. Paumotu Islands, Rangiroa Island, Mohican Reef, *Albatross* East Pacific Expedition, 23 Sep 1899, 1 specimen (USNM 19385; id. Chamberlin, 1919).

SOCIETY ISLANDS. Tahiti, Hitiaa, reef flat, from coral heads, May 1978, A.H. Banner, collector, 1 specimen (USNM 81956).

SOLOMON ISLANDS. Tetel Island, with *Porites*, 28 Jul 1965, P.E. Gibbs collector, 1 specimen (BMNH 1970.109; as *I. muricata* by Gibbs, 1971).

SOUTH AFRICA. Port Natal, J.A. Walberg, col-

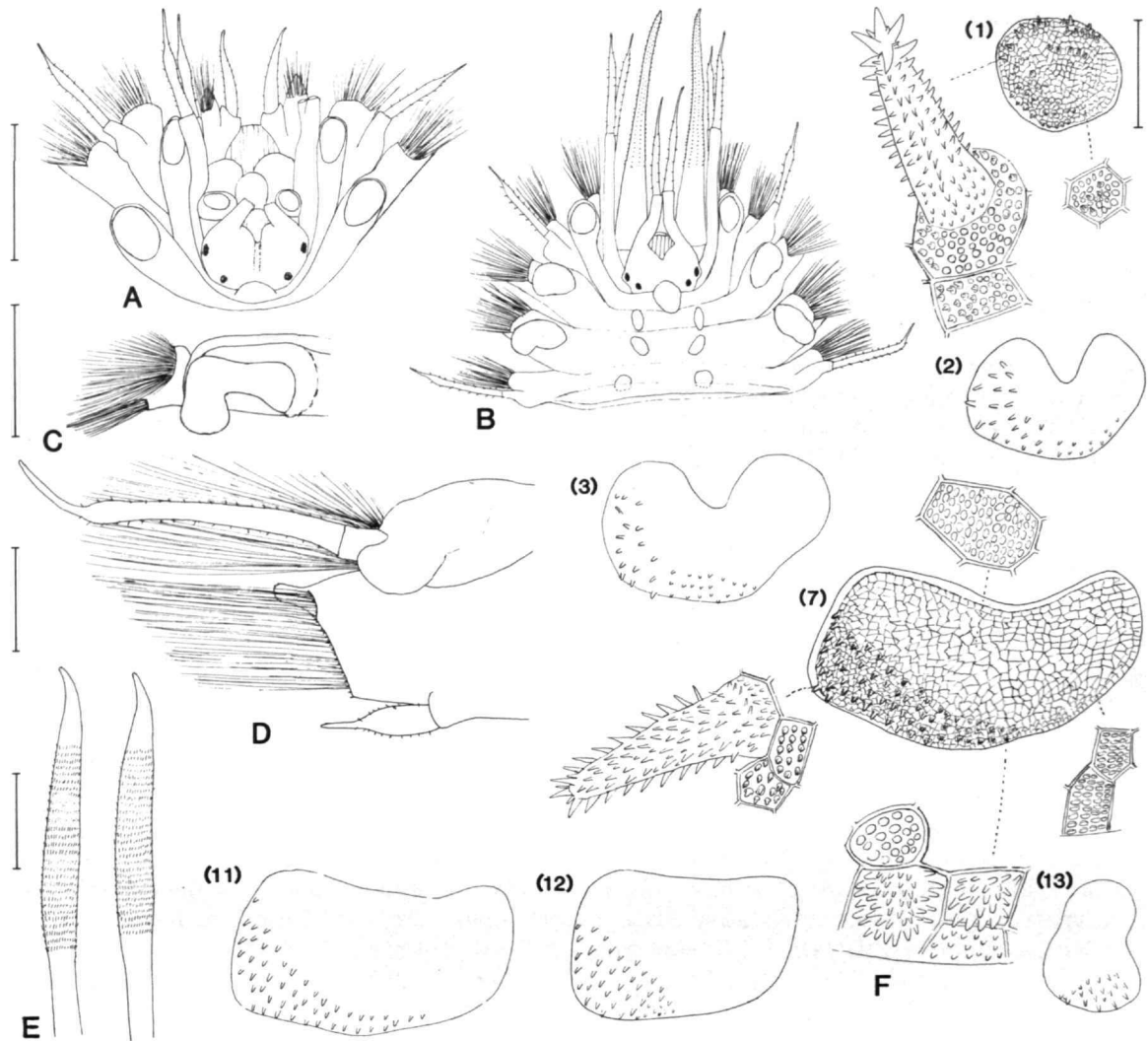


FIGURE 6.—*Iphione ovata* (A, NRS 388, holotype; B–F, USNM 81952, from Ifalik Atoll, 20 × 10 mm): A, anterior end, including segments 1–4, dorsoanterior view, palps, and right tentacular cirri missing; B, dorsal view of anterior end, including segments 1–6; C, dorsal view of left elytrigerous parapodium from segment 13; D, left middle cirriferous parapodium, posterior view; E, upper and lower neurosetae; F, left elytra (1st, 2nd, 3rd, 7th, 11th, 12th, and 13th) showing general shapes and location of larger spinous tubercles, with details of some polygonal areas and tubercles (numbers are elytral numbers, details not to scale). (Scales = 1.0 mm for A; 2.0 mm for B,C; 0.5 mm for D; 0.1 mm for E; 2.0 mm for F.)

lector, holotype of *I. spinosa* (NRS 392).

**MOMBASA.** Nyali, 1 specimen (BMNH 1961.8.2; mixed with *I. muricata* by Day, 1962). Andromach Reef, mouth of Mombasa Harbor, 04°05'S, 39°40'E, 3–10 m, calcareous algae and *Caulerpa*, *R/V Anton Bruun* cruise 9, 18 Nov 1964, S.A. Earle, collector, 2 specimens (USNM 81959).

**COMORO ISLAND.** Outer reef at south end of Pamanzi Island, 1 m, associated with coral, *R/V Anton Bruun* cruise 9, 25 Nov 1964, S.A. Earle, collector, 1 specimen (USNM 81960).

**MADAGASCAR.** Diego Suarez and Nossi-Bé, D. McGregor, collector, 2 specimens (BMNH 1961.8.4/5; mixed with *I. muricata* Day, 1962).

**SEYCHELLES.** Coetivy, Percy Slade Trust Exp. Indian Ocean 1905, 1 specimen (BMNH 1941.4.4.175; as *I. muricata* by Potts, 1910 and Monro, 1939). Aldabra Island, 3 m, associated with coral in main channel, *R/V Anton Bruun* cruise 9, 4 Dec 1964, S.A. Earle, collector, 3 specimens (USNM 81961).

**RED SEA.** Suakim Harbor, on coral, C. Crossland, collector, 1 specimen (BMNH 1941.4.4.173; as *I. muricata* by Monro, 1939).

**MALDIVES.** Reef Manadu, Addu Atoll, on "white-brown holothurian," 1899, J.S. Gardiner, collector, 1 specimen (BMNH 1941.4.4.174; as *I. muricata* by Potts, 1910 and Monro, 1939).

**AUSTRALIA.** *Queensland:* Heron Island, Great Barrier Reef, coral reef flat, 1954, J.K. Howard, collector, 1 specimen (USNM 81957). Lizard Island, Coconut Beach, limestone platform with coral rubble, 1–2 m, 20 Nov 1977, R. and J. Brock, collectors, 2 specimens (USNM 81958).

**MEASUREMENTS.**—Species moderate in size, with 29 segments, ranging from 7 to 22 mm in length and from 4.5 to 12 mm in greatest width. Length  $\times$  greatest width in mm of specimens examined measured as follows: from Baja California, 9.5  $\times$  6; from Gulf of California, 11  $\times$  7; from Clipperton Island, 15  $\times$  8; from Panama (Pacific), 11–22  $\times$  7–12; from Hawaiian Island (holotype of *Iphione ovata*), 9  $\times$  6; and 9–12  $\times$  6–8; from Mariana Islands, 9–16  $\times$  6–10; from Caroline Islands, 10–20  $\times$  6–10; from Marshall

Islands, 10  $\times$  7; from Bikini, 13  $\times$  6; from Gilbert Islands, 19  $\times$  9; from Tuamotu Archipelago, 17  $\times$  10; from Society Islands, 14  $\times$  7; from Solomon Islands, 11  $\times$  7; from South Africa (holotype of *Iphione spinosa*), 10  $\times$  8; from Mombasa, 8–11  $\times$  4.5–6; from Comoro Island, 10  $\times$  7; from Madagascar, 11–12  $\times$  7–8; from Seychelles, 10–15  $\times$  6–8; from Red Sea, 12  $\times$  7; from Maldives, 20  $\times$  12; from Queensland, Australia, 12–15  $\times$  6–9.

**DESCRIPTION.**—The thirteen pairs of tightly imbricated elytra covering the dorsum are generally uniformly red-brown in color. The elytra are variable in shape along the body (Figure 6F). The polygonal or hexagonal areas, with secondary areolae, nearly cover the surface of the elytra except for narrow anterior and lateral borders; the areas become smaller toward the lateral and posterior borders where there are several rows of large spinous tubercles. The distal spines of the conical spinous tubercles are large, with a few short papillae between the spines. The lateral spinous papillae with flexible bases, as found in *I. muricata*, are absent. Along the posterior borders the areolae of some of the smaller polygonal areas are raised into low conical spines (Figure 6F; Kinberg, 1858, pl. 3: fig. 8H; Rioja, 1963, figs. 34, 35).

The prostomium, anterior segments and pharynx follow the usual pattern in *Iphione* (Figure 6A,B; Kinberg, 1858, pl. 3: figs. 8b, 45). The palps extend slightly beyond the tentacular cirri. The lateral antennae and tentacular cirri are about equal in length. A small occipital papilla is hidden by the nuchal lobe of segment 2. Paired oval nodules occur on anterior segments 4–6, with delicate transverse folds or crests between the dorsal tubercles on segments 6 and 8 (Figure 6B). Single middorsal nodules occur on segments 17–22, followed by the dorsal anal ridge on segments 23–29, with the anal opening between the elytophores of segment 27.

The parapodia follow the general pattern of *Iphione* (Figure 6C,D). The bushy white bundles of feathery capillary notosetae extend about to the tips of the neurosetae (not quite as long as in

*I. muricata*). The neurosetae of segments 2 and 3 differ from the following neurosetae: they are slender, tapering to sharp tips, with longer regions of close-set spinous rows. The numerous copper-colored stout neurosetae have close-set spinous rows and slightly hooked bare tips (Figure 6E; Kinberg, 1858, pl. 3: fig. 8b; Rioja, 1963, figs. 30–33).

**DISTRIBUTION.**—Widely distributed in tropical and subtropical regions of the Eastern, Central and Western Pacific, Indian Ocean and Red Sea, mainly intertidal and shallow depths, associated with coral reefs.

### *Iphione treadwelli*, new species

#### FIGURE 7

*Iphione muricata*.—Treadwell, 1906:1154 [in part]. [Not *Polynoe muricata* Savigny, 1818.]

**MATERIAL EXAMINED** (Hawaiian Islands).—*Holotype*: USNM 5435 (as *I. muricata* by Treadwell), Auau Channel between Maui and Lanai Islands, 51–79 m, sand, gravel, *Albatross* sta. 3876, 14 Apr 1902.

*Paratypes*: USNM 5436 (as *I. muricata* by Treadwell), vicinity of Laysan Island, 104–145 m, white sand, broken shells, *Albatross* sta. 3935, 16 May 1902. USNM 81934, off Laysan Island, 145–238 m, small broken shells, coralline, *Albatross* sta. 3936, 16 May 1902.

**DESCRIPTION.**—Length of holotype and paratype (USNM 5435, 5436) 9 mm, width 6 and 7 mm, respectively, segments 29 (both females with eggs in body cavity). The body is oval, flattened ventrally and arched dorsally, covered with tightly imbricated rusty-brown elytra. The 13 pairs of elytra are firmly attached on large bulbous elytraphores of the usual shape and arrangement. The elytra vary in shape along the body (Figure 7F). They are nearly covered with polygonal areas of various sizes, with secondary areolae. Near the posterolateral borders, there are some raised oval thickened areas: 3 on the first pair, 4 on the 2nd, 5–6 on the middle elytra, 2 on the twelfth, none of the thirteenth. The

lateral borders have a bead-like fringe of oval scaly papillae, with a short stem, widened distally with overlapping scales and terminally with 0–3 short papillae (Figure 7F).

The prostomium and tentacular segment are partially fused and withdrawn into the anterior segments (Figure 7A). The prostomium is oval, with a deep anterior notch; the lateral borders are extended anteriorly forming terminal insertions for the lateral antennae; the styles are papillate with a filamentous tip. Stout palps are long, tapered, with longitudinal rows of minute papillae on the distal half. Two pairs of lateral eyes occupy the posterior half of the prostomium. A small occipital papilla is located between the posterior pair of eyes. The first or tentacular segment is not visible dorsally. The tentaculophores, lateral to the prostomium, are long, cylindrical, each with a few capillary setae on the inner side and a pair of dorsal and ventral tentacular cirri, similar to but longer than the lateral antennae. The facial tubercle, visible in the notch between the ceratophores of the lateral antennae, is continuous ventrally with the upper lip of the mouth.

The second segment has a rectangular nuchal lobe with a conical projection overlapping the prostomium and nearly hiding the occipital papilla; large elytraphores and biramous parapodia are directed anteriorly, enclosing the prostomium and tentaculophores; the ventral buccal cirri are inserted basally on the neuropodia lateral to the mouth; they are similar to the tentacular cirri and longer than the following ventral cirri. The third segment is not visible dorsally; the dorsal cirri and parapodia are wedged between the parapodia of segments 2 and 4 (Figure 7A). The neurosetae of segments 2 and 3 differ from the following: they are more slender, with longer spinous regions and taper to slender sharp tips. Dorsally, segments 4 and 5 have a pair of rounded nodules and segment 6 has a delicate transverse crest between the dorsal tubercles.

The rami of the biramous parapodia are closely allied, the small conical notopodia located on the anterodorsal sides of the large neuropodia (Figure 7B,C). Numerous white feathered capil-

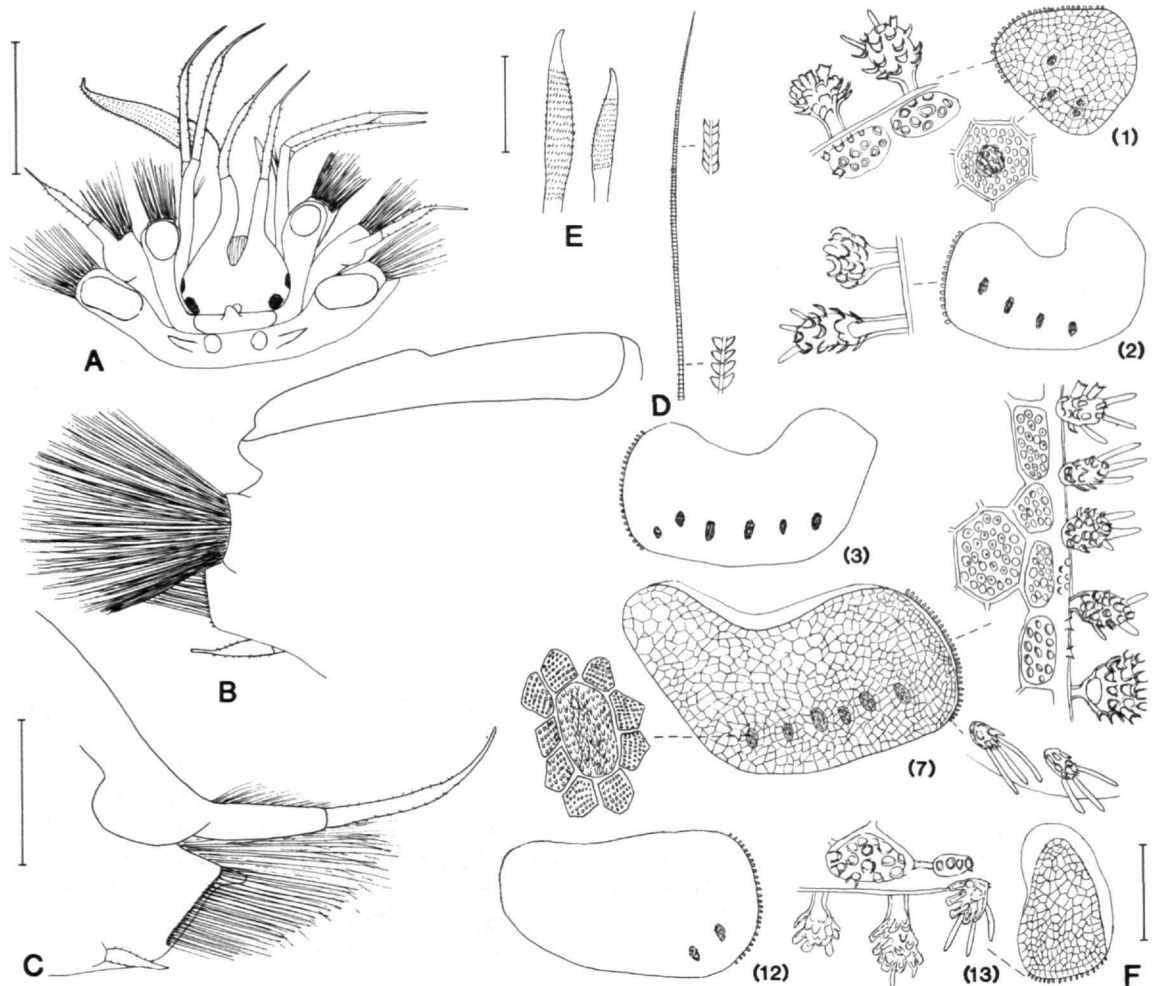


FIGURE 7.—*Iphione treadwelli* (USNM 5435, holotype): A, dorsal view of anterior end, including segments 1–4, right palp shorter, regenerating; B, right elytrigerous parapodium, anterior view; C, right cirriferous parapodium, posterior view; D, notoseta, with detail of part; E, upper and lower neurosetae; F, left (1st, 2nd, 3rd) and right (7th, 12th, 13th) elytra, showing general shapes, position of lateral fringe of scaled papillae and larger tubercles on surface, with detail of some parts (numbers are elytral numbers, details not to scale). (Scales = 1.0 mm for A; 0.5 mm for B,C; 0.1 mm for D,E; 1.0 mm for F.)

lary notosetae form bushy bundles extending slightly beyond the tips of the neurosetae, nearly hiding the neuropodia anteriorly and dorsally. The notosetae are of the usual type for *Iphione* (Figure 7D). The cirrophores of the dorsal cirri are long, cylindrical, with a bulbous base, continuing medially with the large thin-walled bulbous

dorsal tubercles; the styles are papillate, with filamentous tips and extend beyond the notosetae (Figure 7C). The stout neuropodia are conical, with a projecting acicular process on the anterior side; their distal borders have short papillae. Numerous copper-colored neurosetae are arranged in about 8 horizontal rows of decreas-



ing lengths from the upper to the lower position. The neurosetae are stout, with close-set spinous rows and slightly hooked bare tips; the upper ones have longer spinous regions (Figure 7E). The ventral cirri are short, papillate, and tapered (Figure 7B,C).

The pharynx was not examined. The anal ridge is located middorsally on segments 23–29, with the anus between the elythrochlores on segment 27, under the slight slit formed by the posterior pair of elytra.

**DISTRIBUTION.**—Hawaiian Islands, in 51–238 meters.

**ETYMOLOGY.**—The species is named for the late Aaron L. Treadwell, a well-known polychaete specialist.

**REMARKS.**—*I. treadwelli* can be separated from other species of the genus as indicated in the “Key to the Species of *Iphione*.”

### *Iphione henschawi*, new species

FIGURES 8, 9

*Iphione muricata*.—Treadwell, 1906:1154 [in part]. [Not Savigny, 1818.]

**MATERIAL EXAMINED** (Hawaiian Islands).—*Holotype*: USNM 81935, Hilo, Hawaii, low water, May 1904, H.W. Henshaw, collector.

*Paratype*: USNM 5439 (as *I. muricata* by Treadwell, 1906), Vicinity of Kauai, 13–271 m, coral sand and shell, *Albatross* sta. 3999, 16 Jun 1902.

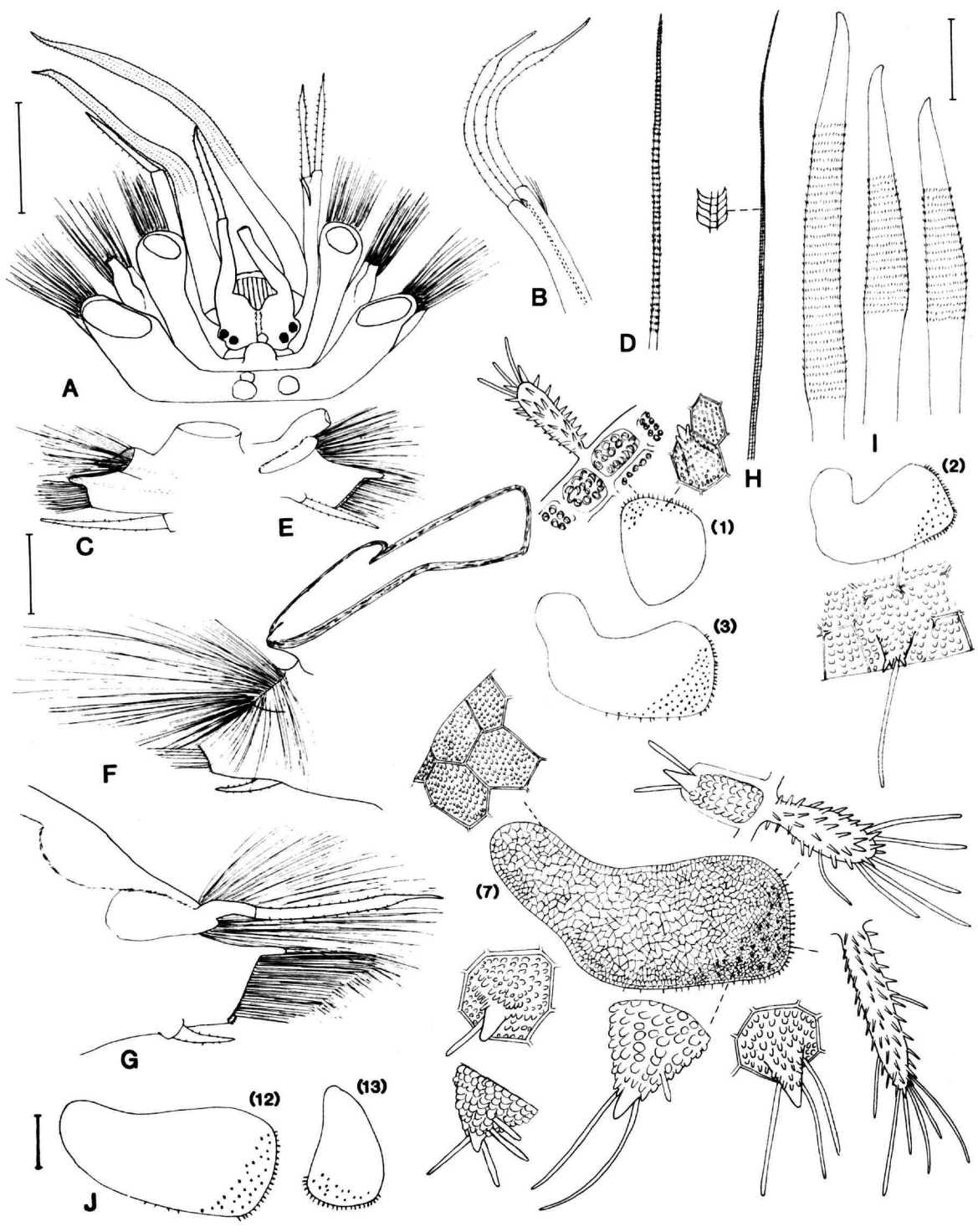
**DESCRIPTION.**—Length of holotype (female with eggs) 29 mm, width 17 mm, segments 29. Length of paratype (male with sperm) 41 mm, width 29 mm, segments 29. The body is elongate-oval, arched dorsally and flattened ventrally. Thirteen pairs of reddish-brown imbricated elytra completely cover the dorsum. The elytra vary in shape along the body (Figures 8J, 9E). The polygonal areas, with areolae, are larger on the medial and anterior parts, becoming smaller posteriorly and laterally. The lateral borders have numerous spinous papillae with flexible bases, similar to that in *I. muricata*. Several rows of conical tubercles occupy some of the

small polygonal areas near the posterolateral borders. They are variable in form, the central cone surrounded by more or less raised and overlapping areolae, forming a spinous base, with a few long distal papillae. They are more numerous and much smaller than the large tubercles of *I. muricata* and differ in type (Figures 8J, 9E).

The anterior end, large bulbous elythrochlores and dorsal tubercles follow the general pattern in *Iphione* (Figures 8A–C,E, 9A). The palps are extra long and tapering, extending far beyond the tentacular cirri and lateral antennae. The two pairs of eyes project from small ocular peduncles. The nuchal lobe of segment 2 overlaps the posterior part of the prostomium and hides the occipital papilla. The parapodia of segment 2, with long ventral buccal cirri, and segment 3 are smaller than the following (Figure 8C,E). The neurosetae of segment 2 and the lower neurosetae of segment 3 differ from the following: they are more slender, with long spinous regions, tapering to pointed tips (Figure 8D). Paired dorsal nodules are found on segments 4, 5, and 7, with delicate transverse crests between the dorsal tubercles on segments 6 and 8 (Figures 8A, 9A).

The biramous parapodia, dorsal and ventral cirri are also typical for *Iphione* (Figures 8F,G, 9B,C). The very numerous white feathery capillary notosetae (Figure 8H) form very large bundles and extend beyond the neurosetae. The dorsal cirri extend beyond the notosetae. The conical neuropodia have a projecting acicular process on the anterior side. The numerous stout copper-colored neurosetae are arranged in about 10 horizontal rows, decreasing in length from the upper to the lower position. They have rather long, bare, slightly hooked tips, with close-set spinous rows, the upper ones with longer spinous regions (Figures 8I, 9D).

Oval middorsal nodules are present on posterior segments 17–22, with a slightly raised anal ridge on segments 23–29 and the anus on segment 27 between the last pair of elythrochlores. Nephridial papillae are present from segment 6 and continue posteriorly. They are bulbous basally, then narrowed and directed dorsally be-



tween the neuropodia. The pharynx was not examined.

DISTRIBUTION.—Hawaiian Islands, in 13–271 meters (?).

ETYMOLOGY.—The species is named for H.W. Henshaw, the collector of the holotype.

REMARKS.—*I. henshawi* can be separated from other species of the genus by the numerous conical tubercles on the surface of the elytra (see “Key to the Species of *Iphione*”).

### Genus *Iphonella* McIntosh, 1885

*Iphonella* McIntosh, 1885:58–61. [Type-species: *Iphonella cimex*; not *Iphione cimex* Quatrefages, 1866 (= *Iphonella philippinensis*, new name). Gender: feminine.]

DISCUSSION.—As already indicated above in the “Chronological Synopsis” for the subfamily Iphoninae, McIntosh (1885) established the new genus *Iphonella* based on a *Challenger* specimen from off the Philippines in 914 meters under the name *I. cimex* (Quatrefages), deposited in the British Museum and examined by me. *Iphione cimex* Quatrefages, 1866, from Malacca Strait, was poorly described and without figures. McIntosh himself indicated that it was in need of reexamination. It is difficult to understand why he chose to use Quatrefages’s name. My examination of the holotype of *Iphione cimex* in the Paris Museum showed that it does not agree with

*Iphione*, *Iphonella*, or Iphoninae; it is referred herein to a new genus in Harmothoinae. Since the diagnosis of *Iphonella* is based on the *Challenger* specimen from the Philippines as described by McIntosh, I have designated it as the holotype and given it the new name *I. philippinensis*. Following the description by McIntosh, *Iphonella cimex* was used subsequently by Horst (1917) for two specimens: one from the Sulu Sea in 1270 meters, and one from off Rotti in 520 meters; and by Uschakov (1982) for a specimen from off the east coast of Honshu Island in 700 meters. Uschakov compared the specimen with the *Challenger* specimen in the British Museum; it was also figured by V. Averincev (Uschakov (1982, pl. 16: figs. 1–8).

In addition to *I. philippinensis*, a new species from the hydrothermal vents in the East Pacific Rise at 21°N, *I. risensis*, is added to *Iphonella*.

DIAGNOSIS.—Body ovate, flattened, segments 29. Elytra and prominent elytriphores 13 pairs, on segments 2, 4, 5, 7, on alternate segments to 23, and on 27. Elytra imbricated, covering dorsum. Elytral surface divided into polygonal or hexagonal areas with numerous secondary areolae, with lateral fringe of papillae. Dorsal cirri, with cylindrical cirrophores and distal styles, and large dorsal tubercles on non-elytra-bearing segments. Prostomium and first or tentacular segment partially fused and withdrawn in anterior segments. Prostomium deeply bilobed, forming separate rounded lobes, with anterolateral extensions but without lateral antennae, with paired palps, without eyes. Tentacular segment with long tentaculophores lateral to prostomium, each with aciculum, few capillary setae and pair of tentacular cirri; large facial tubercle, continuous with upper lip of mouth, anterior to prostomium. Second or buccal segment with small medial nuchal nodule, first pair of elytra on elongated elytriphores extending anterolateral to prostomium, biramous parapodia and long ventral buccal cirri inserted basally lateral to mouth. Third segment not visible dorsally, parapodia wedged between parapodia of segments 2 and 4. Parapodia biramous; notopodia on anter-

FIGURE 8.—*Iphione henshawi* (holotype, USNM 81935): A, dorsal view of anterior end, including segments 1–4, styles of right lateral antenna and dorsal cirri of segment 3 missing; B, right tentaculophore, inner view, aciculum dotted; C, right elytrigerous parapodium of segment 2, anterior view, acicula dotted; D, Neuroseta from same; E, right cirriferous parapodium of segment 3, posterior view, style of dorsal cirrus missing; F, right middle elytrigerous parapodium, anterior view; G, right middle cirriferous parapodium, posterior view; H, notoseta, with detail of part; I, upper, middle and lower neurosetae; J, right elytra (1st, 2nd, 3rd, 7th, 12th, 13th) showing general shapes and location of larger spinous tubercles, lateral and posterior borders of spinous papillae, with details of parts (numbers are elytral numbers, details not to scale). (Scales = 2.0 mm for A; 1.0 mm for B,C,E–G; 0.1 mm for D,H,I; 2.0 mm for J.)

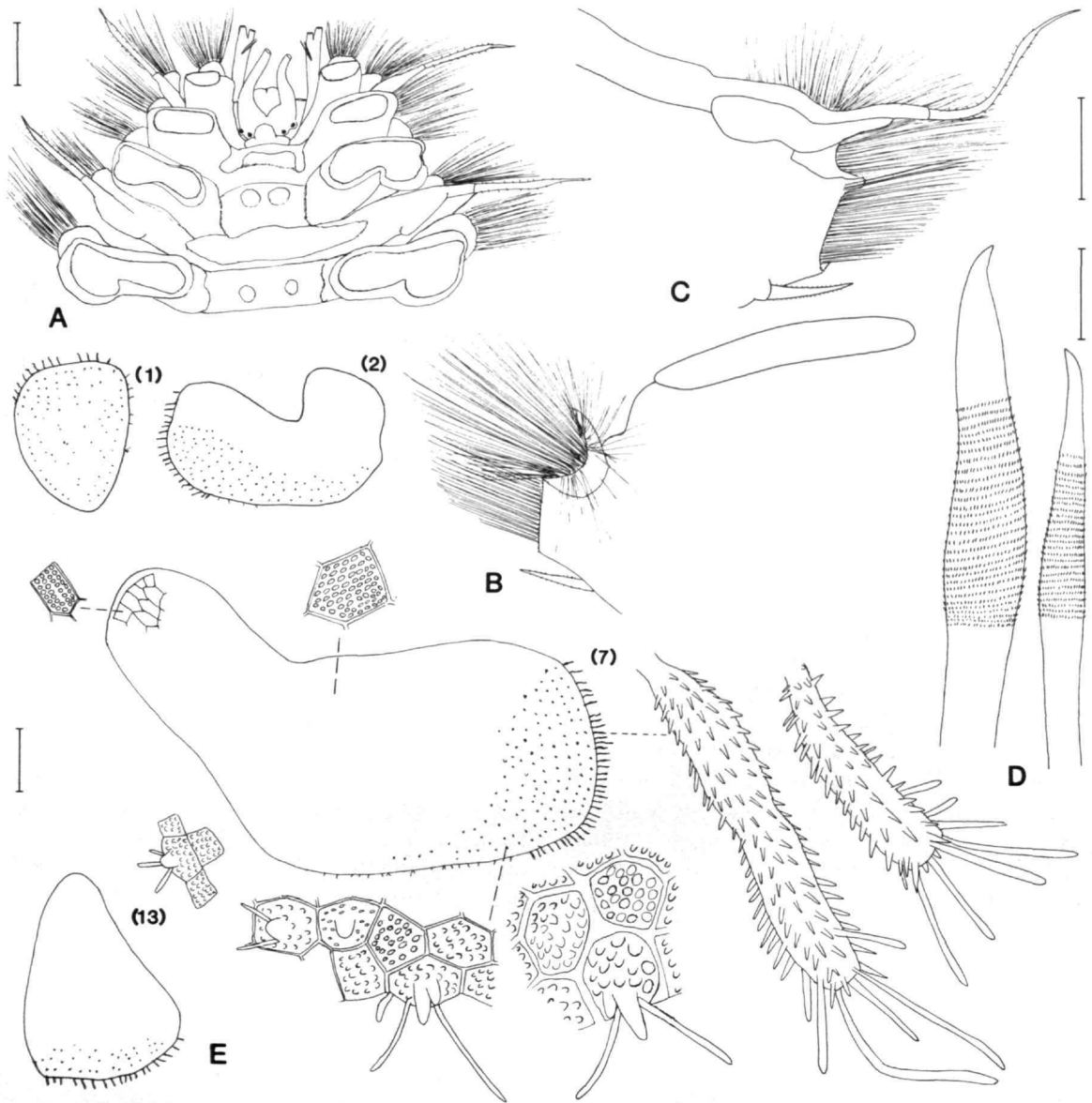


FIGURE 9.—*Iphione henshawi* (USNM 5439, paratype): A, dorsal view of anterior end, palps, styles of lateral antennae, and tentacular cirri missing; B, right elytrigerous parapodium, anterior view; C, right cirriferous parapodium, posterior view; D, middle and lower neurosetae; E, left (1st, 2nd, 13th) and right (7th) elytra, showing general shapes, location of larger spinous tubercles and spinous border papillae, with details of some parts (numbers are elytral numbers, details not to scale). (Scales = 2.0 mm for A; 2.0 mm for B,C; 0.1 mm for D; 2.0 mm for E.)

odorsal sides of larger neuropodia, rounded, with projecting acicular process; neuropodia conical with projecting presetal acicular process. Notosetae numerous, slender, bipinnate, with capillary tips. Neurosetae numerous, stout, with spi-

nous rows and slightly hooked smooth entire tips; upper ones slender, with pointed tips. Ventral cirri short, tapered. Dorsal anal ridge on segments 26–29, without anal cirri. Pharynx with 9 pairs of papillae and 2 pairs of jaws.

### Key to the Species of *Iphonella*

- Middle segments with 2 transverse ciliated bands and 2 pairs of dorsal nodules; places of attachment of elytophores transversely elongated, with lateroposterior extension [Figure 10C]. Upper group of neurosetae slender, with spinous rows [Figure 11D] . . . . . *I. philippinensis*, new name
- Middle segments with 2 transverse dorsal ridges, without dorsal nodules; place of attachment of elytophores oval, with thin-walled medioposterior extension [Figure 12C]. Upper group of neurosetae slender, bipinnate [Figure 13G] . . . . . *I. risensis*, new species

### *Iphonella philippinensis*, new name

FIGURES 10, 11

*Iphonella cimex*—McIntosh, 1885:58, pl. 9: figs. 4–6. pl. 17: fig. 3, pl. 8A: figs. 7, 8.—Horst, 1917:66, pl. 15: figs. 1, 2.—Uschakov, 1982:77, pl. 16: figs. 1–8. [Not *Iphonella cimex* Quatrefages, 1866].

*Iphonella cimex*.—Seidler, 1922:78 [in part]. [Not Quatrefages, 1865 [1866]].

**MATERIAL EXAMINED.**—PHILIPPINES. S of Mindanao, 04°33'N, 127°06' E, 914 m, blue mud, *Challenger* sta 214, 10 Feb 1875, holotype (BMNH 1885.12.1.43; as *Iphonella cimex* by McIntosh, 1885). INDONESIA. S of Rotti, 10°39'S, 123°40'E, 520 m, soft grey mud with brown upper layer, *Siboga* sta 297, 27 Jan 1900. (ZMA 477, as *Iphonella cimex* by Horst, 1917).

**MEASUREMENTS.**—Length of holotype 14 mm, width with setae 8 mm, segments 29. Length of specimen from *Siboga* station 297, 14 mm, width 9 mm, segments 29. Length of specimen from off Japan by Uschakov, 15 mm, width 5.5 mm, segments 29.

**DESCRIPTION.**—The body is ovate, arched dorsally, and flattened ventrally. Thirteen pairs of strongly imbricated, light yellow elytra completely cover the dorsum, except for the tips of the parapodia (McIntosh, 1885, pl. 9: fig. 4). The elytra are firmly attached on prominent elytophores on segments 2, 4, 5, 7, alternate segments to 23 and 26 (Figure 10A,C,D). Dorsal cirri and prominent dorsal tubercles are present on segments 3, 6, alternate segments to 24, 25, 27, 28, and 29 (Figure 10A,C,E). The elytra are oval and elongate reniform, narrower medially and wider laterally, with fringes of short papillae all around on first pair, on lateral borders of others; some papillae are bifid and quadrifid (Figure 10H; McIntosh, 1885, pl. 9: figs. 4–6, pl. 17: fig. 3; Uschakov, 1982, pl. 16: figs. 6–8). The elytral surface is covered with hexagonal or polygonal areas with secondary areolae. The areolae of some of the polygonal areas near the external borders are more or less raised, forming thickened tubercles or conical spines.

The prostomium and the first or tentacular segment are partially fused and withdrawn in the anterior segments (Figures 10A,B; 11A; Horst, 1917, pl. 15: fig. 1; Uschakov, 1982, pl. 16: fig. 1). The prostomium is bilobed, forming two separate rounded lobes, and with lateral anterior extensions enclosing a wide facial tubercle, continuous with the upper lip of the anterior mouth. Lateral antennae are lacking. Horst (1917:66) suggested that the anterior lateral extensions might be considered to be reduced lateral antennae. Eyes and median antenna or occipital papilla are lacking. Stout smooth tapered palps emerge



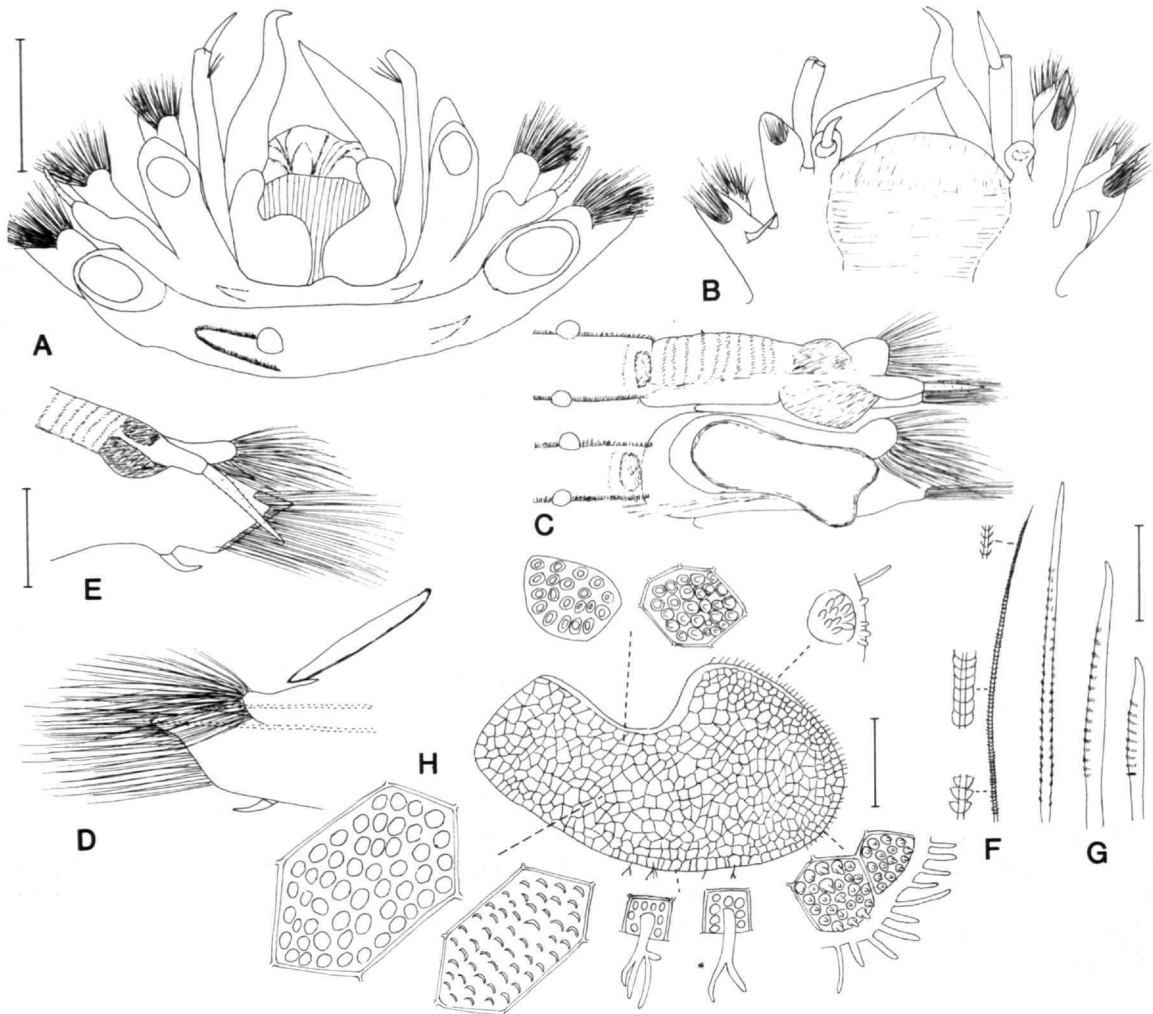


FIGURE 10.—*Iphionella philippinensis* (BMNH 1885.12.1.43, holotype): A, dorsal view of anterior end, styles of left dorsal, right dorsal, and ventral tentacular cirri missing; right side of segment 4 somewhat damaged; B, ventral view of same, style of left ventral buccal cirrus missing; C, dorsal view of right half of segments 12 (cirriferous) and 13 (elytrigerous); D, right elytrigerous parapodium, anterior view, acicula dotted; E, right cirriferous parapodium, posterior view; F, notoseta, with details of parts; G, upper, middle, and lower neurosetae; H, right elytron, with details of parts (not to scale). (Scales = 1.0 mm for A–C; 0.5 mm for D,E; 0.1 mm for F,G; 1.0 mm for H.)

ventral to the lateral prostomial extensions. Long cylindrical tentaculophores are directed anteriorly, enclosing the prostomium and palps, each with a single aciculum and few capillary setae on the inner side and distally with a pair of short tentacular cirri (Figures 10A,B,11A).

Segment 2 bears a small rounded nuchal lobe, elongated elytriphores and biramous parapodia directed anteriorly and enclosing the tentaculophores and prostomium, and ventrally with buccal cirri similar to the tentacular cirri, and lateral and wide lower lips of the mouth (Figures 10A,

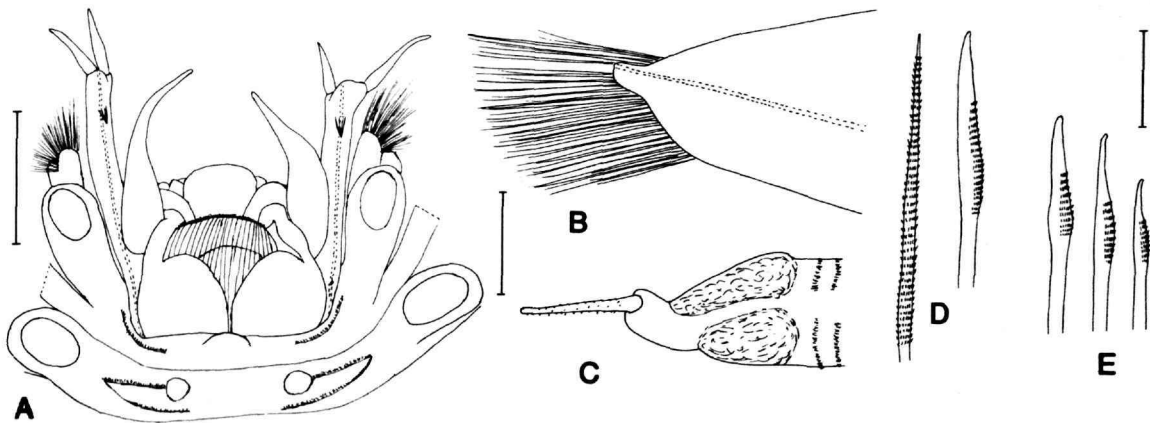


FIGURE 11.—*Iphionella philippinensis* (ZMA, from Siboga station 297): A, dorsal view of anterior end, parapodia of segments 3 and 4 not shown; acicula of tentaculophores of segment 1 dotted; B, right neuropodium, anterior view, aciculum dotted; C, dorsal view of dorsal cirrus and part of dorsal tubercle; D, shorter and longer supraacicular neurosetae; E, upper, middle, and lower subacicular neurosetae. (Scales = 1.0 mm for A; 0.5 mm for B,C; 0.1 mm for D,E.)

B, 11A). Segment 3 is not visible dorsally: the dorsal cirri and parapodia are wedged between the elytriphores of segments 2 and 4. Segment 4 has a pair of rounded dorsal nodules and 2 transverse ciliated ridges, incomplete middorsally (Figures 10A, 11A). Beginning with segment 5 through the middle of the body, there are 2 ciliated ridges and 2 pairs of rounded dorsal nodules, with oval depressed areas medial to the elytriphores and dorsal tubercles (Figure 10C). The elytriphores are bulbous, transversely elongated, their place of attachment having a latero-posterior extension (Figure 10C). The dorsal tubercles on the cirrigerous segments are also bulbous and transversely elongated, with vertical ciliated ridges and distally with bulbous glandular areas on the anterior and posterior sides of the bases of the cylindrical cirrophores of the dorsal cirri; the styles of the dorsal cirri are rather short, with short clavate papillae (Figures 10C,E, 11C).

The parapodia are biramous (Figures 10C–E, 11B,C; Uschakov, 1982, pl. 16: fig. 2). The notopodia are short, rounded, on the anterodorsal sides of the larger neuropodia, with a projecting acicular process. The notosetae are numerous, light-colored, forming dense tufts and project on the anterodorsal sides of the neuropodia and are

shorter than the neurosetae. The feathered notosetae (Figure 10F; McIntosh, 1885, pl. 8A: fig. 7; Uschakov, 1982, pl. 16: fig. 4) are slender, tapering to capillary tips, with a slender axis and opposite lateral curved pinnae (similar to *Iphione*). The stout neuropodia have conical pre-setal lobes with a projecting acicular process, the postsetal lobes are shorter, conical, together enclosing very thick bundles of numerous neurosetae. The neurosetae (Figures 10G, 11D,E; McIntosh, 1885, pl. 8A: fig. 8; Uschakov, 1982, pl. 16: fig. 5) are light amber-colored, stout, with close-set spinous rows. The upper few are more slender, with longer spinous regions and tapered tips. The rest have shorter spinous regions and slightly hooked bare tips. The neurosetae of segments 2–4 differ in that they are slender, tapering to sharp tips, with spinous regions continuing up to the tips (Uschakov, 1982, pl. 16: fig. 3). The ventral cirri are short and tapered (Figure 10D,E).

The dorsal anal ridge extends between segments 26 and 29, including the very small three posterior segments, with the dorsal anus between the posterior large elytriphores of segment 26. The pharynx was not extended on the specimens examined. According to Uschakov (1982), there

are two pairs of large jaws and border papillae (number?). The ventral nephridial areas are thin-walled and inflated, with a small papilla on the posterolateral side.

**DISTRIBUTION.**—Philippines, Indonesia, and Japan. In 520–1270 meters.

**ETYMOLOGY.**—The species is named *philippinensis* for the locality of the holotype.

***Iphionella risensis*, new species**

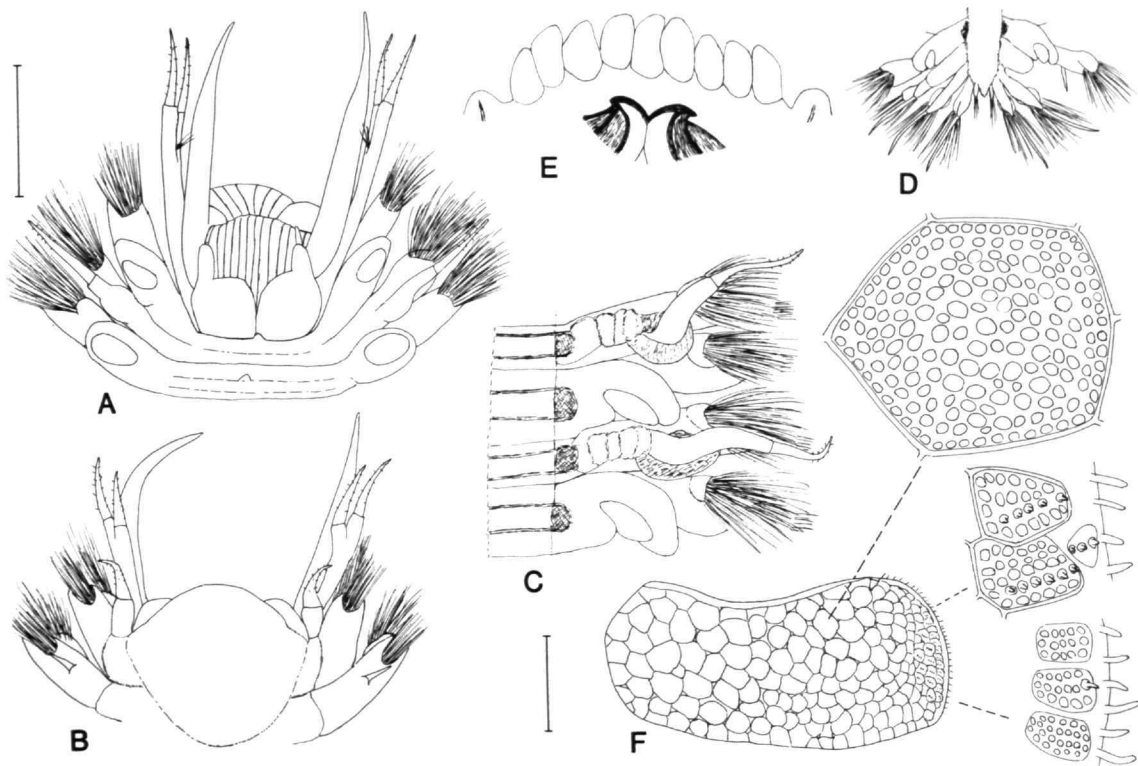
FIGURES 12–14

**MATERIAL EXAMINED (East Pacific Rise).**—*Holotype*: USNM 81967, 20°50'N, 109°06'W,

*Alvin* dive 1226-7, 10 May 1982, 2616 m, *Riftia*, *Calyptogena*, and *Alvinella* wash, coarse fraction.

*Paratypes*: USNM 81969, 20°50'N, 109°06'W, *Alvin* dive 1222-5b, 6 May 1982, 2614 m, rubble sample from *Calyptogena* residue, young of 11 segments. USNM 81970, 20°50'N, 109°06'W, dive 1223-17, 7 May 1982, 2616 m, rubble, 1 paratype. USNM 81971, same coordinates and dive, 2 paratypes, young of 24 and 18 segments. USNM 81968, 97401, same coordinates, *Alvin* dive 1226-7, 10 May 1982, *Riftia*, *Calyptogena*, and *Alvinella* wash, coarse fraction, 2 paratypes, young of 11 segments.

**DESCRIPTION.**—Length of holotype 10 mm, width 6 mm with setae, segments 28 (incom-



**FIGURE 12.**—*Iphionella risensis* (A–C, F USNM 81967, holotype; D USNM 81968, paratype; E USNM 81970, paratype): A, dorsal view of anterior end, including segments 1–4; B, ventral view of anterior end, including segments 1–3; C, dorsal view of right half of segments 8–11; D, dorsal view of posterior end, including segments 26–29 and remnant of a 30th lateral to conical pygidium; right parapodium of segment 27 missing; E, distal end of pharynx showing jaws; F, right elytron, with details of parts (not to scale). (Scales = 1.0 mm for A–E; 1.0 mm for F.)

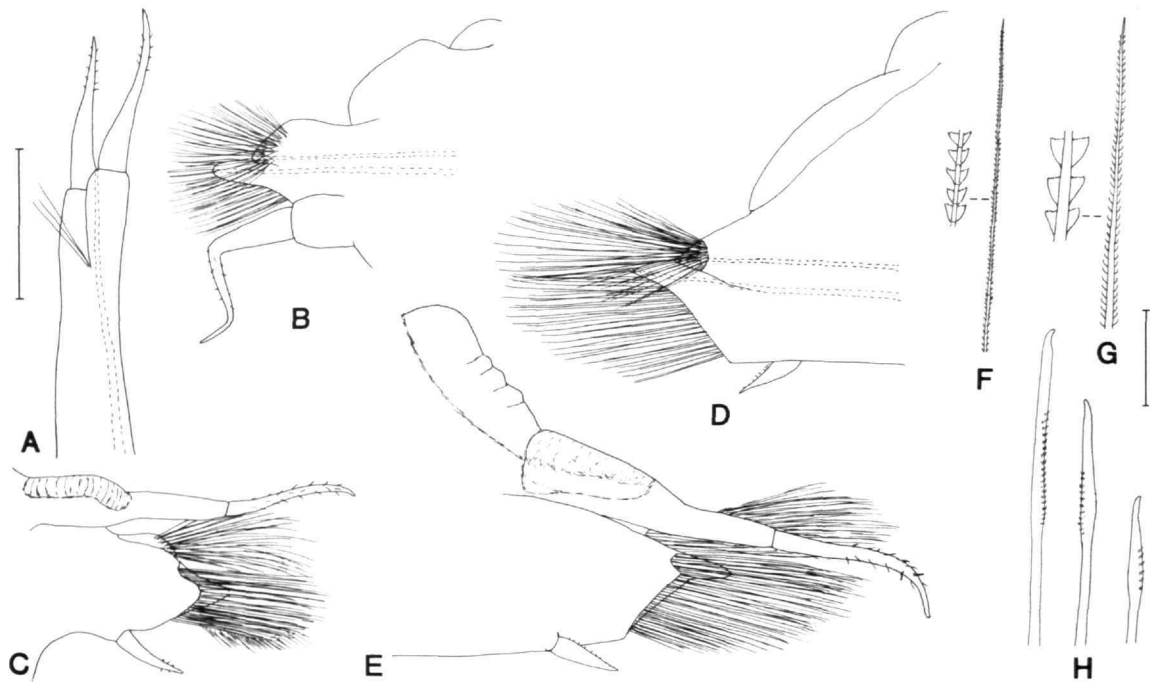


FIGURE 13.—*Iphionella risensis* (USNM 81967, holotype): A, right tentaculophore, inner view, aciculum dotted; B, right elytrigerous parapodium from segment 2, anterior view, acicula dotted; C, right cirriferous parapodium from segment 3, posterior view; D, right middle elytrigerous parapodium, anterior view, acicula dotted; E, right middle cirriferous parapodium, posterior view; F, notoseta, with detail of part; G, upper feathered neuroseta, with detail of part; H, upper middle, and lower neurosetae. (Scales = 0.5 mm for A–E; 0.1 mm for F–H.)

plete); lengths of two complete paratypes 9 and 11 mm, widths 5 and 8 mm, segments 29. Young of 24 segments,  $4.5 \times 3$  mm; young of 18 segments,  $3 \times 2$  mm; two young of 11 segments, 1.2 and  $1.0 \times 1.0$  mm.

The body is ovate, greatly flattened, tapered slightly anteriorly and more so posteriorly, with the parapodia very close and crowded. Thirteen pairs of reddish elytra (mostly missing) and large elyptrophores are found on segments 2, 4, 5, 7, on alternate segments to 23, and on 26, with dorsal cirri and large dorsal tubercles on segments 3, 6, 8, alternate segments to 24, and on 25, 27, 28, and 29 (Figure 12A,C,D). The elytra are oval and reniform (Figures 12F, 14A,B,E,F). The elytral surface is nearly covered with hexagonal or polygonal areas enclosing small areo-

lae, with scattered lateral papillae. Along the lateral borders some of the areolae are raised, forming conical microtubercles.

The elyptrophores are large and bulbous, their place of attachment oval with a thin-walled medioposterior extension (Figures 12A,C,D; 13B,D). The dorsal tubercles are thin-walled and somewhat ruffled, continuing laterally with a large curved glandular area on the posterior basal part of the long cirrophores of the dorsal cirri; the styles are papillate, tapered and extend beyond the tips of the setae (Figures 12C; 13C,E).

The prostomium and first or tentacular segment are partially fused and withdrawn in segments 2 and 3 (Figure 12A,B). The prostomium is bilobed, forming two separate rounded lobes, with anterolateral bulbous extensions fused to

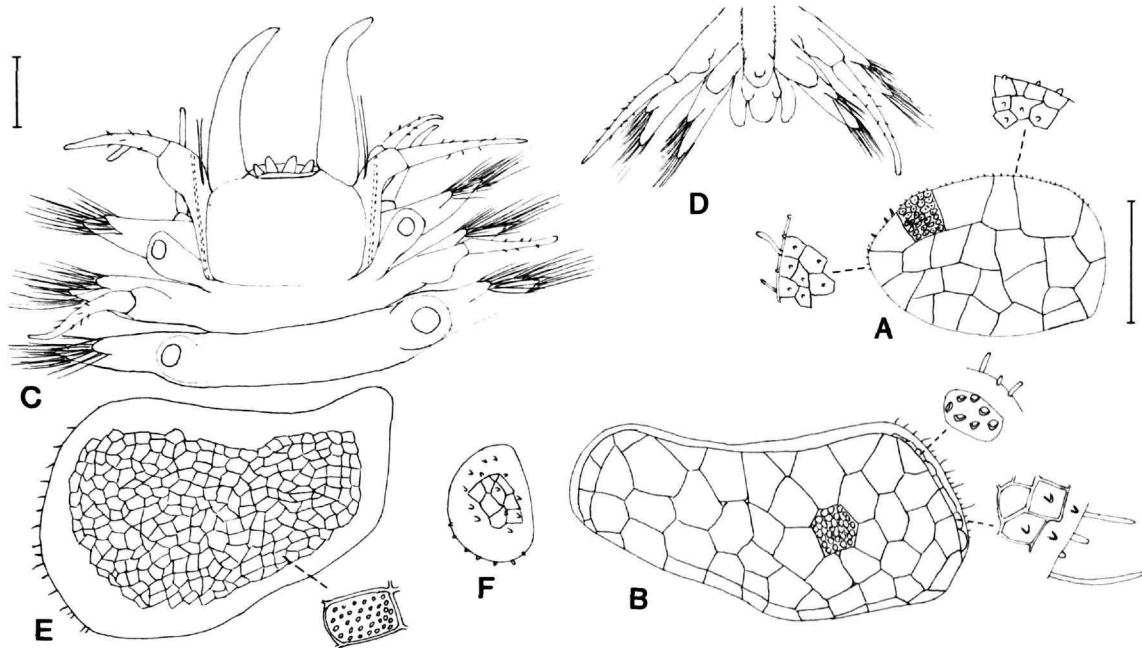


FIGURE 14.—*Iphonella risensis* (A,B, USNM 81971, small paratype of 18 segments,  $3 \times 2$  mm; C-F, USNM 97401, young paratype of 11 segments,  $1 \times 1$  mm): A, first left elytron, with details of parts; B, right middle elytron; C, dorsal view of anterior end; tip of pharynx with papillae extended from mouth; D, dorsal view of posterior end, including segments 10, 11, developing segment 12, and pygidium with dorsal anus; E, left 3rd elytron from segment 5; F, right 6th elytron from segment 11. (Scales = 0.5 mm for A,B; 0.1 mm for C-F.)

the medial facial tubercle, which is continuous with the upper lip of the anterior mouth, and enclosed by the stout, smooth, tapered palps. Antennae and eyes are lacking. The first segment is not visible dorsally; long cylindrical tentaculophores emerge lateral to the prostomium and palps, each with a stout aciculum, a few capillary setae on the inner side and distally with a pair of short, papillate dorsal and ventral tentacular cirri (Figures 12A,B, 13A).

The second segment has a small medial nodule overlapping the prostomium, large elytriphores bearing the first pair of elytra and biramous parapodia directed anteriorly and enclosing the prostomium and tentaculophores, and ventrally, with stout buccal cirri similar to the tentacular cirri (Figures 12A,B, 13B). The large ventral lip is enclosed in the biramous parapodia of seg-

ments 2 and 3. Due to the anterior position of the mouth, the anterior, lateral and posterior lips of the mouth are visible dorsally, anterior to the prostomium.

The distal rim of the eversible stout muscular pharynx has 9 pairs of soft, transparent dorsal and ventral papillae and 2 pairs of stout hooked jaws (Figure 12E).

Segment 3 is indistinct dorsally, the dorsal cirri and parapodia are wedged between the large elytriphores and parapodia of segments 2 and 4. Small oval medial nodules are found on segments 4 and 5 (Figure 12A). Most of the segments have slightly raised transverse dorsal ridges, 2 per segment, with deep rounded depressed areas medial to the dorsal tubercles and elytriphores (Figure 12C,D). The small conical pygidium and dorsal anus are enclosed in the small posterior



segments (28, 29, plus remnants of additional minute parapodia on one of the paratypes; Figure 12D).

The rami of the biramous parapodia are closely allied, with conical notopodia on the anterodorsal sides of the neuropodia (Figure 13B-E). The very numerous notosetae are straw-colored, delicate, capillary, and bipinnate feathered, with a slender axis and close-set lateral spines emerging on the same level (similar to the notosetae of *Iphione*; Figure 13F). The presetal lobes of the larger neuropodia are conical with a projecting acicular process, the postsetal lobes are shorter and rounded, together enclosing very numerous amber-colored neurosetae. The upper group of neurosetae are feathered, similar to the notosetae except that they are stouter, with shorter bare pointed tips (Figure 13G). The rest of the neurosetae are stouter, longer (upper ones) to shorter (lower), with close-set spinous rows on the basal enlarged part and with rather long bare slightly hooked tips (Figure 13H). The neurosetae of segments 2 and 3 are of the slender feathered type, similar to the upper neurosetae of the following segments. The ventral cirri are short, tapering and papillate (Figure 13C-E). The ventral nephridial papillae are small, beginning about segment 8.

A minute young paratype, 1 mm in length, possessed 11 segments, with indication of developing twelfth parapodia (Figure 14C-F). The prostomium is squarish, showing slight indications of developing anterolateral extensions; some pharyngeal papillae protrude from the mouth. Two elytra remained: a large reddish one on segment 5 and a small transparent developing one on segment 11 (Figure 14E,F).

**BIOLOGY.**—*I. risensis* was collected in rubble, residue, and washes associated with vestimentiferans, *Riftia pachytila* Jones, giant clams, *Calyptogenia magnifica* Boss and Turner, and ampharetid polychaetes, *Alvinella pompejana* Desbruyères and Laubier.

**DISTRIBUTION.**—Off western Mexico, in 2614–2616 meters.

**ETYMOLOGY.**—The species is named *risensis*

based on its association with the hydrothermal rift-area on the East Pacific Rise.

**REMARKS.**—*I. risensis* can be separated from *I. philippinensis* as indicated in the “Key to the Species of Genus *Iphionella*” (page 25).

### Genus *Iphionides* Hartmann-Schröder, 1977

*Iphionides* Hartmann-Schröder, 1977:51–54. [Type-species: *I. glabra* Hartmann-Schröder, 1977, by original designation and monotypy. Gender: feminine.]

**DIAGNOSIS.**—Body elongate, rectangular, segments up to 39. Elytra imbricated, covering dorsum, up to 20 pairs on bulbous elytophores, on segments 2, 4, 5, 7, alternate segments to end of body. Elytra with honeycomb-like lattice pattern. Small dorsal tubercles and dorsal cirri, with bulbous cirrophores and distal styles, on segments 3, 6, 8, alternate segments to end of body. Prostomium and first or tentacular segment partially fused and withdrawn in anterior segments. Prostomium with small triangular anterolateral extensions, without distinct lateral antennae, with long paired palps and 2 pairs of deeply buried eyes on brain. Tentaculophores lateral to palps, each with aciculum, few setae and pair of tentacular cirri. Second or buccal segment covering posterior part of prostomium, with first pair of elytra, biramous parapodia, and ventral buccal cirri lateral to mouth, similar to tentacular cirri. Parapodia biramous, notopodia smaller than neuropodia, both with projecting acicular processes. Notoetae slender, capillary, spinous. Neurosetae slender, of 2 kinds: tufted pinnate and spinous, with slightly hooked tips. Ventral cirri short, tapered. Pharynx with 2 pairs of jaws; papillae (?).

### *Iphionides glabra* Hartmann-Schröder, 1977

FIGURE 15

*Iphionides glabra* Hartmann-Schröder, 1977:51, figs. 1–12.

**MATERIAL EXAMINED.**—CUBA. Playa Siboney, Provincia Oriente, coastal ground water, lower eulittoral, coarse sand with coral debris and de-

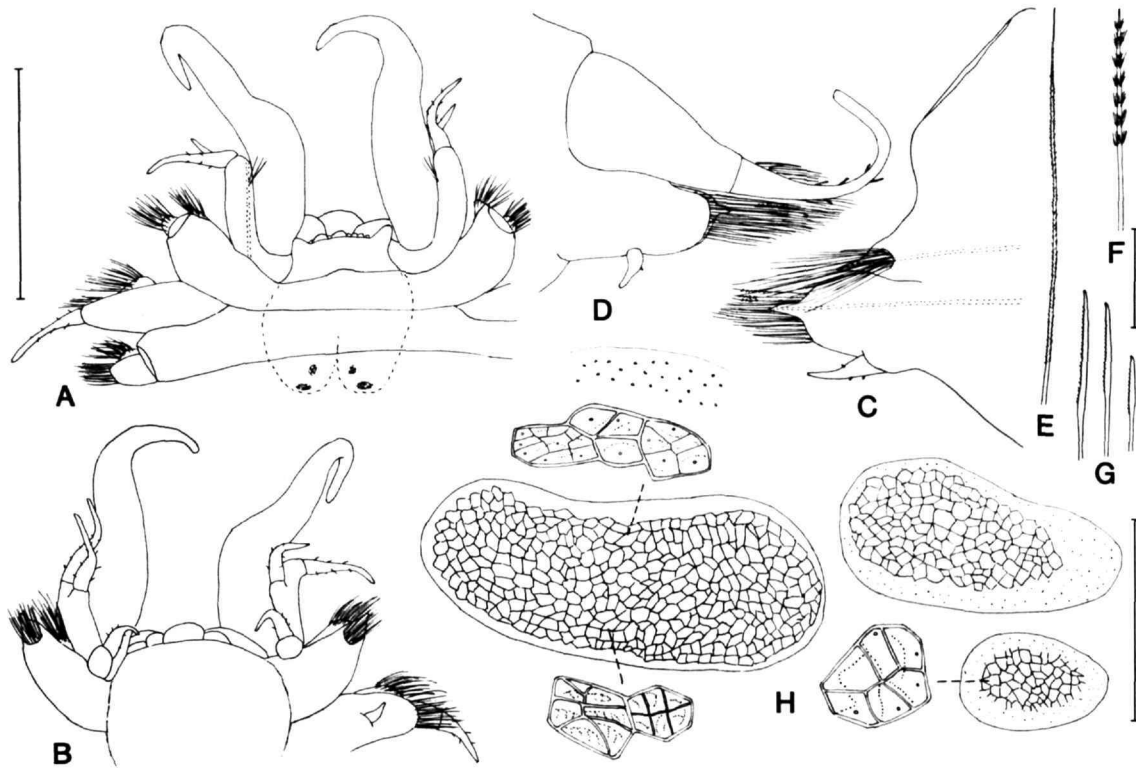


FIGURE 15.—*Iphionides glabra* (USNM 60005, paratype): A, anterior end, dorsal view, posterior part of prostomium and aciculum of tentaculophore dotted; B, ventral view of same; C, right elytrigerous parapodium, anterior view, acicula dotted; D, right cirriferous parapodium, posterior view; E, notoseta; F, pinnate tufted neuroseta; G, upper, middle and lower neurosetae; H, large middle and 2 smaller posterior elytra, with detail of some areas (not to scale). (Scales = 0.5 mm for A,B; 0.1 mm for C-G; 0.5 mm for H.)

tritus, 1973, L. Botosaneanu, collector, holotype (ZMH P-13634) and 2 paratypes (USNM 60005, exchange from ZMH P-13635).

**DESCRIPTION.**—Length of male holotype 5 mm, width with setae 2 mm, segments 39. Length of 2 male paratypes (USNM 60005) 4–4.5 mm, width 1.5 mm, segments 30–33. The body is elongate, rectangular, flattened ventrally and arched dorsally, colorless except for some scattered brown spots. The elytra, attached on bulbous elytriphores, are imbricated, cover the dorsum and continue to the end of the body (Figure 15A,C; Hartmann-Schröder, 1977, figs. 1, 2, 4). The surface of the elytra is nearly covered with hexagonal or polygonal areas, en-

closing a secondary lattice pattern, differing from the numerous areolae, as found in *Iphione* (Figure 15H; Hartmann-Schröder, 1977, figs. 10, 11). Additional faint lines and scattered vesicles appear within the lattice structure. Near the elytral borders lacking the honeycomb lattice structure, there are more numerous scattered vesicles. Dorsal tubercles, corresponding in position to the elytriphores on the non-elytra-bearing segments, are slightly inflated medial to the large cirriferous of the dorsal cirri, wider basally, and with distal cirriform styles with scattered papillae (Figure 15A,D; Hartmann-Schröder, 1977, figs. 1, 2, 5).

The prostomium and first or tentacular seg-

ment are partially fused and withdrawn in the anterior segments (Figure 15A,B; Hartmann-Schröder, 1977, figs. 1-3). The prostomium is oval; the anterior exposed part, not covered by segment 2, is slightly curved, with the anterolateral borders projecting anteriorly into triangular extensions (referred to as rudimentary lateral antennae by Hartmann-Schröder). The posterior part of the prostomium, covered by segments 2-4, is deeply incised with 2 pairs of eyes deeply buried on the brain and visible through the transparent integument; the anterior pair are smaller and closer together than the larger posterior pair. Stout tapered smooth palps emerge lateral and ventral to the prostomium. The facial tubercle, anterior to the prostomium and medial to the anterior extensions, appears somewhat papillose and continuous with the anterior lip of the mouth. The tentaculophores are cylindrical, extending anterolateral to the palps, each with an aciculum, few capillary setae, and pair of cirri-form papillate tentacular cirri, the dorsal ones longer than the ventral. Segment 2 has large elyptrophores bearing the first pair of elytra and extend anterolateral to the tentaculophores, with biramous parapodia and ventral buccal cirri, similar to the tentacular cirri, lateral to the lateral and posterior lips of the mouth (Figure 15A,B; Hartmann-Schröder, 1977, figs. 1-3). Segment 3 is not visible dorsally, the dorsal cirri and parapodia are wedged between the large elyptrophores of segments 2 and 4.

The notopodia of the biramous parapodia are smaller than the larger neuropodia, rounded, with a projecting acicular process; the presetal lobes of the neuropodia are conical, with a projecting acicular process, the postsetal lobes being slightly shorter and rounded (Figure 15C,D; Hartmann-Schröder, 1977, figs. 4, 5). The notosetae are moderate in number, slender, spinous, tapering to capillary tips (Figure 15E; Hartmann-Schröder, 1977, fig. 6). The neurosetae are moderate in number, rather slender, of two types: upper few are tufted pinnate (similar to the upper neurosetae found in many sigalionids; Figure 15F; Hartmann-Schröder, 1977, figs. 7, 8), middle and lower ones with enlarged spinous

regions and slightly hooked bare tips (Figure 15G; Hartmann-Schröder, 1977, fig. 9). The ventral cirri are short, tapered, with few papillae.

The pharynx has 2 pairs of yellow clasping jaws (Hartmann-Schröder, 1977, fig. 12). Nephridial papillae are indistinct. The posterior pygidium lacks anal cirri.

### Subfamily HARMOTHOINAE Horst, 1917

#### *Gaudichaudius*, new genus

TYPE-SPECIES.—*Iphione cimex* Quatrefages, 1866. Gender: masculine.

COMPOSITION.—*G. cimex* (Quatrefages, 1866), which includes *Gattyana deludens* Fauvel, 1932; *G. iphionelloides* (Johnson, 1901, as *Harmothoe iphionelloides*).

DISCUSSION.—The type specimen of *Iphione cimex* from the Strait of Malacca in the Paris Museum (MNHN) was examined. It was incomplete posteriorly, consisting of an anterior fragment of 30 segments, 13 mm long, 6 mm wide including setae, with 14 pairs of elyptrophores and most of the elytra still attached. The anterior 15 segments were in fair shape but the remaining ones were extremely flattened and hardened. The specimen was insufficiently and erroneously described by Quatrefages, and was not figured. It does not agree with *Iphione*, as indicated by the description and figures below. The prostomium is harmothoid and should be placed in Harmothoinae, rather than Iphioninae. It agrees with *Gattyana deludens* Fauvel from the Bay of Bengal, well described and figured by Fauvel (1932:18). Both species are here referred to a new genus, with Fauvel's species as a junior synonym of *cimex*.

*Harmothoe iphionelloides* Johnson, 1901, from Puget Sound, Washington, was referred to *Gattyana* by Berkeley and Berkeley (1945:321), based chiefly on the character of the setae. Pettibone (1953:39) emended *Gattyana* to include *G. iphionelloides* but pointed out that the several differences might prove sufficient to establish a new genus. This species is now added to the new genus established for *I. cimex*. Fauvel (1953:41)

indicated that Johnson's species of *G. iphionelloides* was a closely allied species to his *G. deludens*.

**DIAGNOSIS.**—Body short, less than 40 segments. Elytral pairs 15, completely covering dorsum, attached on prominent elytriphores on segments 2, 4, 5, 7, on alternate segments to 23, and on 26, 29, and 32. Elytra covered with honey-combed polygonal areas and with lateral fringes of papillae. Dorsal cirri with prominent cirrophores and long distal styles on non-elytra-bearing segments. Dorsal tubercles on cirriferous segments transversely elongate or forming digitiform branchial extensions (*G. cimex*). Prostomium withdrawn into anterior 2 segments, bilobed, without distinct cephalic peaks, with 3 antennae, paired palps and 2 pairs of eyes; lateral antennae inserted ventrally (*G. cimex*) or terminoventrally (*G. iphionelloides*). Tentaculophores of first segment lateral to prostomium, each with aciculum, few setae and pair of tentacular cirri. Second or buccal segment with nuchal fold, first

pair of elytra, biramous parapodia and long ventral buccal cirri lateral to ventral mouth. Parapodia biramous; notopodia on anterodorsal side of larger neuropodia; neuropodia diagonally truncate with projecting acicular process on anterior side. Notosetae numerous, with spinous rows, of 2 types: short with blunt tips and long, slender, tapering to fine tips. Neurosetae numerous, stouter than notosetae, with spinous regions and entire, bare, slightly hooked tips. Ventral cirri short, tapered. Pygidium with pair of anal cirri. Pharynx with 9 pairs of papillae and 2 pairs of entire hooked jaws.

**ETYMOLOGY.**—The genus is named for M. Gaudichaud, the collector of the type specimen of *Iphione cimex*.

**REMARKS.**—*Gaudichaudius* differs from *Gattiyana* McIntosh, in Harmothoinae, chiefly on the character of the elytra. It differs from *Iphione* Kinberg and *Iphionides* McIntosh, in Iphioninae, in the type of prostomium and other features.

#### Key to the Species of *Gaudichaudius*

- Honey-comb compartments of elytra close-fitting, with surface somewhat roughened but without tubercles [Figure 16G,H]. Dorsal tubercles on cirriferous segments extend laterally and forming digitiform branchial structures [Figures 16C, 17B,C]. Lateral antennae of prostomium inserted ventrally, nearly hidden by bulbous ceratophore of median antenna [Figures 16A,B, 17A]. Only relatively few shorter notosetae with blunt tips, mostly with long capillary tips [Figures 16E, 17E]. Body greatly flattened, commensal with hermit-crabs in snail shells. . . . . *G. cimex* (Quatrefages)
- Honey-comb compartments of elytra loose-fitting, some very small, some with microtubercles [Figure 18I-L]. Dorsal tubercles on cirriferous segments inflated, transversely elongated, not extended laterally [Figure 18B,D]. Lateral antennae of prostomium inserted termino-ventrally, lateral to cylindrical ceratophore of median antenna [Figure 18A]. Notosetae with blunt tips very numerous, in several rows, longest ones with slender tips [Figure 18E-G]. Body not greatly flattened, free-living . . . . .  
 . . . . . *G. iphionelloides* (Johnson)

#### *Gaudichaudius cimex* (Quatrefages, 1866), new combination

FIGURES 16, 17

*Iphione cimex* Quatrefages, 1865 [1866]: 270. [Not sensu Treadwell, 1920:591 (= *Iphione muricata*).]

Not *Iphionella cimex*.—McIntosh, 1885:58.—Horst, 1917:66.—Uschakov, 1982: 77 (= *Iphionella philippinensis*, new name).]

*Gattiyana deludens* Fauvel, 1932:18, figs. 1, 2; 1939:259; 1953:39, figs. 15, 16.—Uschakov and Wu, 1959: 33, pl. 5: figs. D-G, pl. 6: figs. A,B; 1965:166, fig. 7A-F [1979 (translation):25, fig. 7A-F].—Srikrishnadhas and Rama-

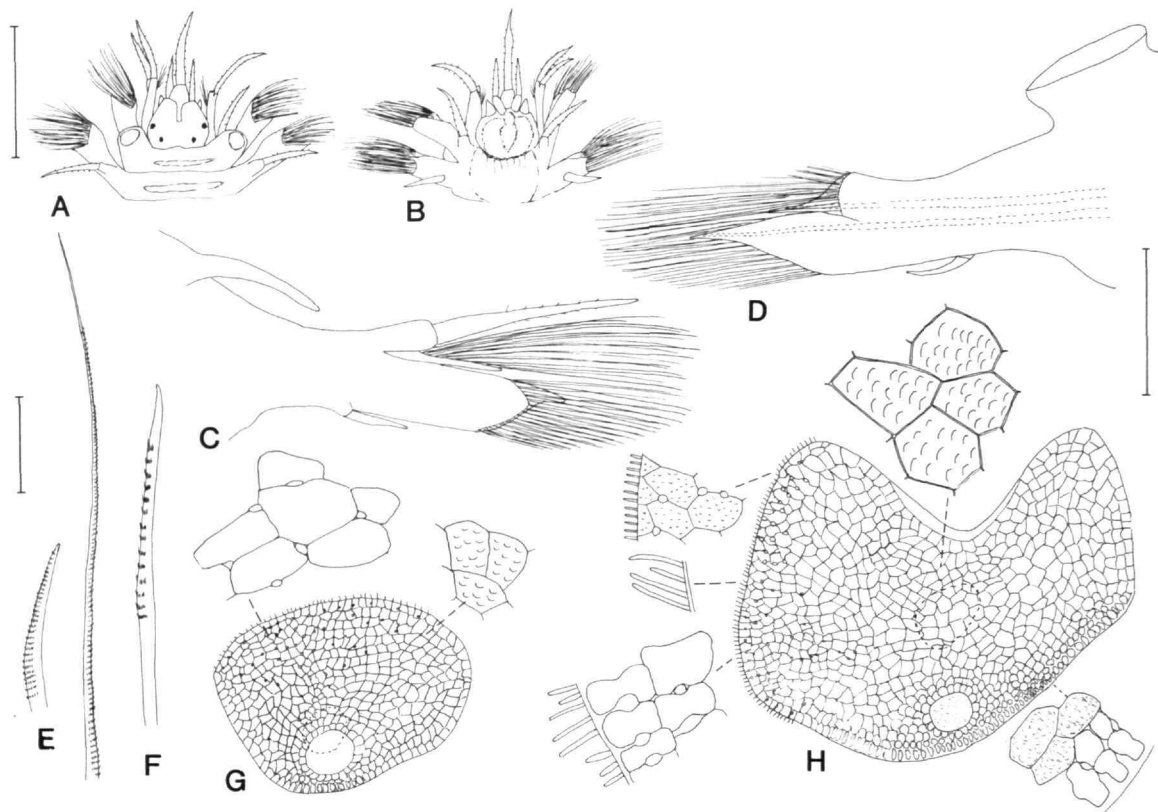


FIGURE 16.—*Gaudichaudius cimex* (holotype, MNHNP): A, anterior end, dorsal view; palps very short, regenerating; right dorsal tentacular cirrus missing; B, ventral view of same; C, right cirrigerous parapodium from segment 10, posterior view; D, right elytrigerous parapodium from segment 11, anterior view, acicula dotted; E, short and long notosetae; F, middle neuroseta; G, first left elytron from segment 2, with detail of some areas (not to scale); scar of attachment to elytrephore dotted; H, same, of left middle elytron. (Scales = 1.0 mm for A,B; 0.5 mm for C,D; 0.1 mm for E,F; 1.0 mm for G,H.)

moorthi, 1975: 734, fig. 1.—Soota and Rao, 1977: 327.—Kumaraswamy Achari, 1974 [1977]: 839, fig. 1.—Uschakov, 1982:156, pl. 55: figs. 1–6.

**MATERIAL EXAMINED.**—Malacca Strait, M. Gaudichaud, collector, Holotype of *Iphione cimex* (MNHNP 1868.38a). Maungmagaun, Burma, G.E. Gates, collector, 1937, 1 specimen (BMNH 1937.1.4.3, as *Gattyana deludens*).

**DESCRIPTION.**—The body is elongate, uniform in width, much flattened, with the length up to 23 mm, width up to 7 mm with setae, and segments up to 38. The 15 pairs of elytra are firmly attached on bulbous elytrephores, deeply imbricated and cover the dorsum. The elytra are tough, yellow amber-colored, orbicular (first pair) and irregularly reniform with a deep or shallow anterior notch and with a short lateral fringe of cylindrical papillae (Figure 16G,H; Fauvel, 1932, fig. 1a–e). The elytra are nearly covered with conspicuous close-fitting honey-combed polygonal areoles (without secondary areoles, as in *Iphione*), with some stomata-like rounded spots between some of the areoles and a large bare oval spot near the posterior border (erroneously referred to as the scar of attachment by Fauvel). The surfaces of some of the areoles

cated and cover the dorsum. The elytra are tough, yellow amber-colored, orbicular (first pair) and irregularly reniform with a deep or shallow anterior notch and with a short lateral fringe of cylindrical papillae (Figure 16G,H; Fauvel, 1932, fig. 1a–e). The elytra are nearly covered with conspicuous close-fitting honey-combed polygonal areoles (without secondary areoles, as in *Iphione*), with some stomata-like rounded spots between some of the areoles and a large bare oval spot near the posterior border (erroneously referred to as the scar of attachment by Fauvel). The surfaces of some of the areoles



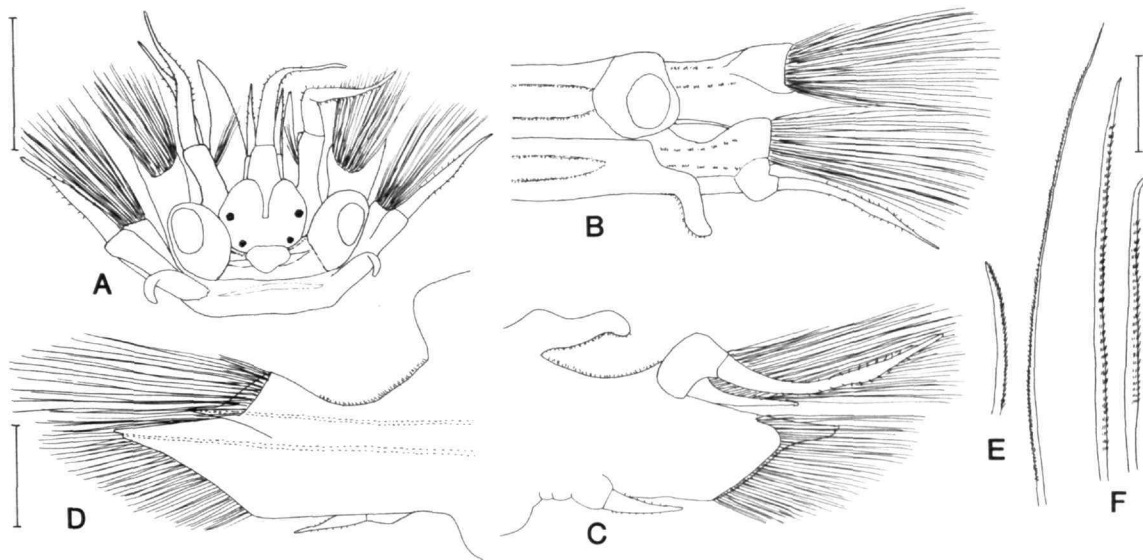


FIGURE 17.—*Gaudichaudius cimex* (BMNH 1937.1.4.3, from Burma): A, dorsal view of anterior end, right palp smaller, regenerating, right ventral tentacular cirrus missing; dashed line = slight depression; B, dorsal view of right side of segments 15 and 16; C, right cirriferous parapodium of segment 12, posterior view; D, right elytrigerous parapodium of segment 13, anterior view, acicula dotted; E, short and long notosetae; F, upper and middle neurosetae. (Scales = 1.0 mm for A,B; 0.5 mm for C,D; 0.1 for E,F.)

are smooth, others are roughened due to broad depressions and swellings of the cuticle but without definite tubercles.

The prostomium is oval, bilobed, without distinct cephalic peaks, with 2 pairs of rather small eyes (Figure 16A,B, 17A; Fauvel, 1932, fig. 1a). The ceratophore of the median antenna is large, bulbous, inserted in the anterior notch of the prostomium, with a papillate style. The ceratophores of the lateral antennae are inserted ventrally, nearly hidden by the ceratophore of the median antenna and nearly meet midventrally, with short, tapered papillate styles. The palps are stout, tapered, and smooth. The tentaculophores of the first segment are lateral to the prostomium, each with a few (4–6) setae on the inner side and a pair of dorsal and ventral tentacular cirri, similar to the median antenna. The second or buccal segment has an inflated nuchal fold, large bulbous elytriphores of the first pair of elytra, biramous parapodia and long ventral buc-

cal cirri, similar to the tentacular cirri and attached basally on the neuropodia lateral to the ventral mouth (Figure 16B).

The dorsal cirri with bulbous cirrophores are attached on the dorsoposterior bases of the notopodia, with long papillate styles extending to near the tips of the setae; the dorsal tubercles on the cirriferous segments, in line with the elytriphores, are inflated and extend laterally as digitiform ciliated branchial extensions (Figures 16C, 17A–C; Fauvel, 1932, fig. 1G). The dorsum has two transverse ciliated bands extending between the elytriphores and the dorsal tubercles and two bands on the bases of the notopodia (Figure 17B).

The biramous parapodia have smaller conical notopodia with a projecting acicular process on the lower side, located on the anterodorsal sides of larger neuropodia; the latter have a conical presetal lobe extending into an acicular process with a small supraacicular digitiform extension

and a shorter rounded postsetal lobe (Figures 16C,D, 17C,D; Fauvel, 1932, fig. 1g). The notosetae are numerous, white, with spinous rows; the upper few are shorter, slightly curved, with blunt entire tips; the remaining notosetae are slender, tapering to long capillary tips and extending to the tips of the neurosetae or beyond (Figures 16E, 17E; Fauvel, 1932, fig. 2a, b). The neurosetae are numerous, yellowish, with slightly enlarged spinous regions and curved or straight smooth entire tips; the upper neurosetae have longer and the lower ones have shorter spinous regions (Figures 16F, 17F; Fauvel, 1932, fig. 2c-h). The ventral cirri are short, tapering, papillate, attached on small cirrophores on the middle of the neuropodia (Figure 17C,D). The pygidium has a pair of long papillate anal cirri.

DISCUSSION.—Fauvel (1932) compared his specimens of *Gattyana deludens* (collected in the Bay of Bengal at low tide and in 6 meters) with *Iphionella cimex*. The comparison was based in large part on the description of the specimen from off the Philippines in 914 meters identified as *Iphionella cimex* by McIntosh (1885) and not that of *Iphione cimex* from Malacca Strait by Quatrefages (1866). As McIntosh (1885:60) indicated, *Iphione cimex* Quatrefages was in need of reexamination. He did not do so, but proceeded to describe his specimen from deep water off the Philippines under the name *Iphionella cimex* (Quatrefages). Based on examination of both specimens (MNHN, BMNH), it is evident that they are very different and belong to different subfamilies. It is apparent that Quatrefages (1866) placed his specimen from Malacca Strait in *Iphione* based on the elytra, which superficially resemble those of species of that genus. He could not have examined the prostomium and parapodia. The 13 pairs of elytra attributed to *I. cimex* by Quatrefages can be explained by his incomplete specimen.

BIOLOGY.—*Gaudichaudius cimex* (as *Gattyana deludens*) has been reported to be commensal with hermit-crabs. Fauvel (1932:21) indicated that his specimens probably were from a shell with a hermit-crab, and collected at low tide.

Kumaraswamy Achari (1977) described these polynoids as commensal with hermit-crabs, chiefly *Diogenes diogenes* Herbst and *D. custos* Fabricius from the east and west coasts of India. The polynoids were only found with hermit-crabs, never free-living. Their highly flattened bodies enabled them to move freely in the narrow space available between the body of the hermit-crab and the shell. They were able to collect food particles that escaped when the crabs were feeding on other animals. Two to three worms were collected from a single shell. This association of the polynoids and hermit-crabs appeared to be mutual. Larvae with 10 segments and 5 pairs of elytra were collected in the plankton in Porto Nova waters in August by Srikrishnadhas and Ramamoorthi (1975). Adaptations of this polynoid to its particular commensal habitat are the extremely flattened body, the slick tough elytra without tubercles, and the ciliated branchial extensions of the dorsal tubercles, an unusual condition in the Polynoidae.

Some specimens had numerous epizoic loxosomatid entoprocts attached on the dorsum and parapodia, as noted by Fauvel (1932:20) and on the specimen examined from Burma (BMNH).

DISTRIBUTION.—Arabian Sea, west and east coasts of India, Bay of Bengal, Burma, Malacca Strait, Indochina, and Yellow Sea. In low water to 50 meters.

***Gaudichaudius iphionelloides* (Johnson, 1901),  
new combination**

FIGURE 18

*Harmothoe iphionelloides* Johnson, 1901:391, pl. 1: figs. 2-7.—Hartman, 1938b:4.

*Gattyana iphionelloides*.—Berkeley and Berkeley, 1945:321; 1948:12, fig. 12.—Hartman, 1948:14.—Pettibone, 1949:2; 1953:44, pl. 22: figs. 194-200.—Reish, 1965:136.—Uschakov, 1982:155, pl. 54: figs. 7-12.

MATERIAL EXAMINED.—WASHINGTON. Off Foulweather Bluff, Puget Sound, 60-64 m, 2 Aug 1938, M. Pettibone, collector, 1 specimen (USNM 25182). West Sound, Orcas Island, San Juan Archipelago, dredged in mud, 16 Jul 1940,

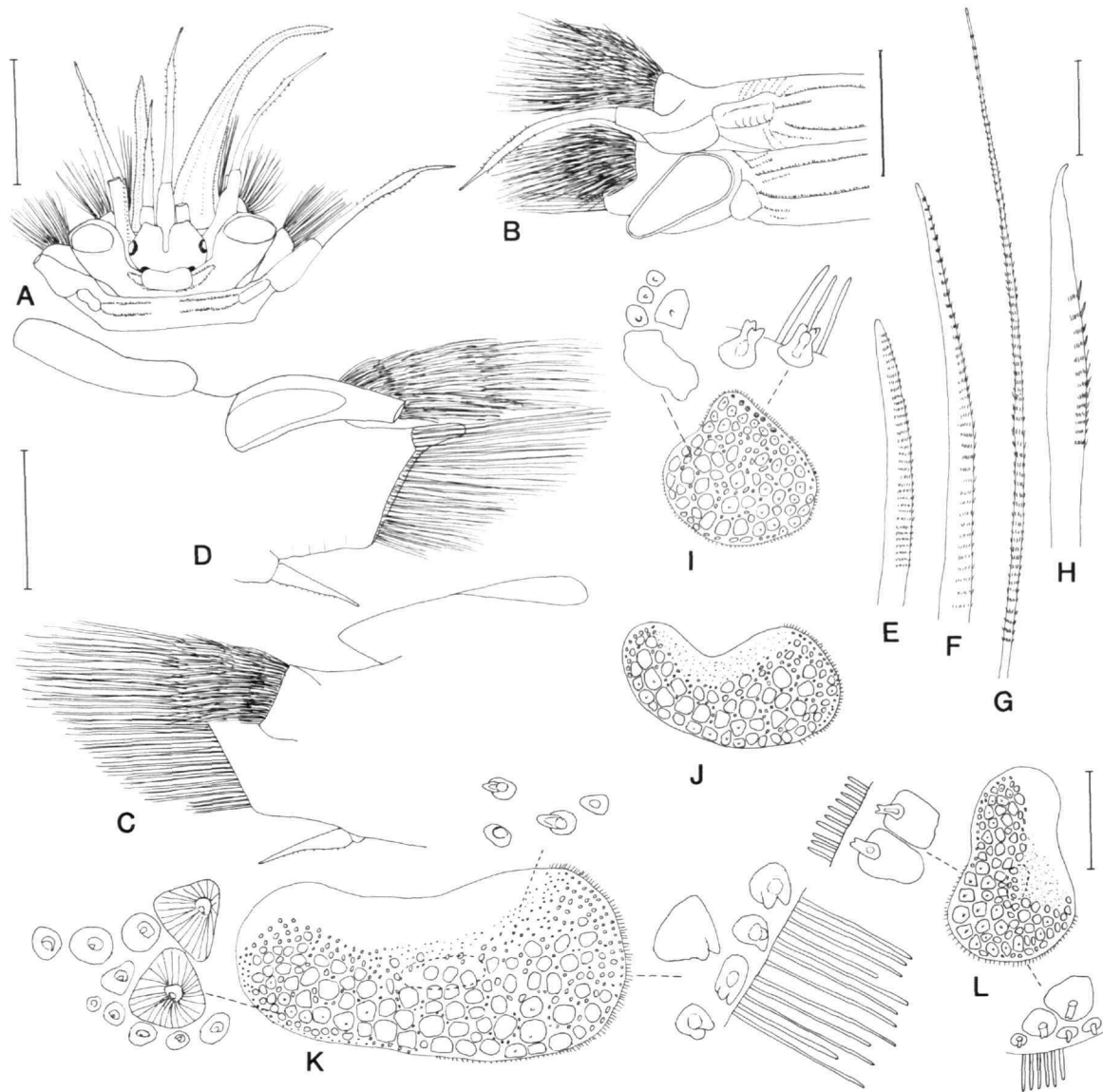


FIGURE 18.—*Gaudichaudius iphionelloides* (A, C–L USNM 21120, B USNM 32249): A, Dorsal view of anterior end, styles of right lateral antenna, right ventral and left dorsal tentacular cirri, and left dorsal cirrus of segment 3 missing; left palp smaller than right palp, regenerating; B, dorsal view of left side of segments 16 and 17; C, Right elytrigerous parapodium, anterior view; D, right cirriferous parapodium, posterior view, style of dorsal cirrus broken off; E, short notoseta from first row; F, longer notoseta from third row; G, longest notoseta from fourth row; H, middle neuroseta; I, right first elytron from segment 2, with details of some areas (not to scale); J, right 2nd elytron from segment 4; K, right 8th elytron from segment 15, with details of some areas (not to scale), scar of attachment to elytriphore dotted; L, same, of right 15th elytron from segment 32. (Scales = 2.0 mm for A; 1.0 mm for B; 1.0 mm for C,D; 0.1 mm for E–H; 2.0 mm for I–L.)

M. Pettibone, collector, 1 specimen (USNM 32249). SE Lawrence Point, Orcas Island, 82 m, shelly, 7 Aug 1940, M. Pettibone, collector, 1 specimen (USNM 21120). Between Dinner Island and Griffin Bay, San Juan Island, dredged in eel grass, Aug 1934, M. Pettibone, collector, 1 specimen (USNM 25181). Off Neah Bay, Strait of Juan de Fuca, 27 m, 7 Jul 1940, M. Pettibone, collector, 2 specimens (USNM 25183).

**BRITISH COLUMBIA.** Cardale Point, Valdez Island, 19 May 1921, E. Berkeley, collector, 1 specimen (USNM 41653). Reef at False Narrows and near Dodds Narrows, Nanaimo, 17 Jul 1940, E. and C. Berkeley, collectors, 2 specimens (USNM 41651, 41652).

**ALASKA.** Alitak Bay, 27–55 m, Alaska King Crab Invest. sta. 106-40, 2 Nov 1940, 1 specimen (USNM 21385).

**BERING SEA.** Little Diomed Island, 65°36.7'N, 168°45'W, 0–30 m, Hugh Smith sta. 54, 30 Jul 1960, J. Tibbs, collector, 1 specimen (USNM 31416).

**DESCRIPTION.**—The body is oval, tapering anteriorly and posteriorly, flattened dorsoventrally, with lengths up to 35 mm, widths up to 12 mm, and up to segments 36. The 15 pairs of elytra are deeply imbricated and cover the dorsum. The elytra are thick, light amber-colored to dark brown, orbicular (first pair) and irregularly reniform with a deep or shallow anterior notch, and with lateral and posterior fringes of long and short papillae (Figure 18I–L; Johnson, 1901, pl. 1: fig. 3; Pettibone, 1953, pl. 22: fig. 195). The elytra are covered in large part with areoles, variable in size, very small and numerous on the anterior part of the elytra. The surface of the areoles are smooth or roughened, some with raised microtubercles. The elytriphores are prominent, extending posteriorly and with an extra lobe on the base of the posterior side (Figure 18B).

The prostomium is oval, bilobed, without or with only a slight indication of cephalic peaks, and with 2 pairs of rather large eyes (Figure 18A; Johnson, 1901, pl. 1: fig. 2; Pettibone, 1953, pl. 22: fig. 194). The ceratophore of the median

antenna is long, slender, inserted in the anterior notch of the prostomium, with a long papillate style. The ceratophores of the lateral antennae are inserted terminoventrally, lateral to the ceratophore of the median antenna, with short, tapered papillate styles. The palps are stout, tapered, and minutely papillate. The tentaculophores of the first segment are lateral to the prostomium, each with a few (3–4) setae on the inner side and a pair of dorsal and ventral tentacular cirri similar to the median antenna. The second or buccal segment has a raised nuchal fold covering the posterior part of the prostomium, large bulbous elytriphores of the first pair of elytra, biramous parapodia and long ventral buccal cirri similar to the tentacular cirri and attached basally on the neuropodia lateral to the ventral mouth.

The dorsal cirri have elongate cirrophores, bulbous basally, attached on the dorsoposterior bases of the notopodia; the long papillate styles extend beyond the tips of the setae. The dorsal tubercles on the cirriferous segments, in line with the elytriphores, are delicate, transparent, forming raised subrectangular areas (Figure 18A,B,D; Johnson, 1901, pl. 1: fig. 4). The dorsum has transverse ciliated bands extending between the elytriphores and dorsal tubercles, 2 per segment (Figure 18A,B).

The biramous parapodia have small rounded notopodia with a projecting acicular process on the lower side, located on the anterodorsal side of the large neuropodia; the neuropodia are diagonally truncate with a projecting acicular process on the anterior side (Figure 18C,D; Johnson, 1901, pl. 1: fig. 4; Pettibone, 1953, pl. 22: figs. 196, 197). The notosetae are very numerous, white, spreading fanlike anteriorly and dorsally, all with spinous rows; they are of 4 lengths: those of the first and second rows are stout, short and longer, curved, with blunt tips (Figure 18E; Johnson, 1901, pl. 1: fig. 6); those of the third row are stout, longer, slightly curved, with more slender blunt tips (Figure 18F); and those of the fourth row are slender, longest, tapering to long slender, almost capillary tips (Figure 18G; John-

son, 1901, pl. 1: fig. 7*a,b*). The neurosetae are numerous, straw-colored, stout, with spinous rows and rather long, slightly hooked bare tips (Figure 18H; Johnson, 1901, pl. 1: fig. 5; Pettibone, 1953, pl. 22: fig. 200); the upper neurosetae are longer, with longer spinous regions, and the lower ones are shorter, with shorter spinous regions. The ventral cirri are short, tapering, papillate, attached on small cirrophores on the middle of the neuropodia (Figure 18C,D).

The pygidium has a pair of rather short papillate anal cirri.

**BIOLOGY.**—*G. iphionelloides* is found intertidally under rocks and dredged in eel grass and on muddy, shelly and rocky bottoms in 4–82 meters.

**DISTRIBUTION.**—Northeastern Pacific from the Arctic (near Bering Strait), Kurile Islands to Washington (Puget Sound), in low water to 82 meters.

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