

Revision of *Pherecardia* Horst, 1886
(Annelida, Amphinomidae)

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Pigmentation patterns: *Pherecardia striata* (Kinberg, 1857) Kwajalein, in situ, close-up of anterior ends of two specimens. Photo: S. Johnson.

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Revision of *Pherecardia* Horst, 1886 (Annelida, Amphinomidae)

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ABSTRACT

Amphinomid annelids are classified after the shape of caruncle, the presence and type of branchiae along body segments, and the type of chaetae present. *Pherecardia* Horst, 1886 was proposed to include species having a large caruncle with a heart-shaped median ridge and lateral lobes. However, generic delineation was not well understood at the time, and some species currently referred to the genus were described in *Hermodice* Kinberg, 1857 and *Amphinome* Bruguière, 1789. *Pherecardia* currently includes four shallow water species: *P. maculata* Imaijima, 2003 from Japan; *P. parva* Monroe, 1924 from the Macclesfield Bank; *P. polylamellata* de Silva, 1961 from Sri-Lanka; and *P. striata* (Kinberg, 1857) from the French Polynesia. Two other species have also been proposed as congeneric: *A. bruguieresii* de Quatrefages, 1866; and *A. formosa* de Quatrefages, 1866. The genus is best known for its type species, *Pherecardia striata* (Kinberg, 1857), a common and widespread, large and readily recognized species characterized by numerous longitudinal dorsal pigmented stripes and recorded across the Indo-Pacific from East Africa to the East Pacific. This species has been regarded as relevant for coral reef ecology since it attacks injured predatory crown-of-thorns starfish (*Acanthaster planci* (Linnaeus, 1758)). Here we review the genus based on examination of type and additional material from 10 museum collections and mitochondrial DNA comparisons of representative specimens from various localities. We recognize three species: *P. striata*, *P. distincta* (Hoagland, 1920) (new combination, including *P. polylamellata* as synonym), and *P. maculata* (retained pending the study of topotypical specimens). *Pherecardia parva* is transferred to *Pherecardites* Horst, 1912 and renamed as *Pherecardites monroi* because of homonymy with *Pherecardites parva* Horst, 1912. *Amphinome bruguieresii* is regarded as a junior synonym of *Eurythoe indica* (Schmarda, 1861); the status of *A. formosa* cannot be determined. Keys are included for species of *Pherecardia* and *Pherecardites*.

KEY WORDS

Caruncle,
dorsal pigmentation,
notopodia pigmentation,
keys,
new name,
new combination.

RÉSUMÉ

Révision de *Pherecardia* Horst, 1886 (*Annelida*, *Amphinomidae*).

Les annélides polychètes amphinomidées sont classées en fonction de la forme de leur caroncule, de la présence et du type de branchies le long des segments du corps, et des types des soies présents. *Pherecardia* Horst, 1886 a été proposé pour inclure les espèces ayant une grande caroncule avec une bordure médiane en forme de cœur et des lobes latéraux. Cependant, la définition générique n'était pas bien comprise à cette époque, et certaines espèces actuellement référencées dans ce genre ont été décrites dans *Hermodyce* Kinberg, 1857 ou dans *Amphinome* Bruguière, 1789. *Pherecardia* inclut actuellement quatre espèces d'eau peu profonde : *P. maculata* Imajima, 2003 du Japon, *P. parva* Monro, 1924 du banc Macclesfield, *P. polylamellata* de Silva, 1961 du Sri-Lanka, et *P. striata* (Kinberg, 1857) de Polynésie française. Deux autres espèces ont aussi été proposées comme congénères : *A. bruguieresii* de Quatrefages, 1866 et *A. formosa* de Quatrefages, 1866. Le genre *Pherecardia* est mieux connu pour son espèce type, *P. striata* (Kinberg, 1857), une espèce commune, largement répandue et aisément reconnaissable, caractérisée par les nombreuses rayures pigmentées dorso-longitudinales et recensée dans tout l'Indo-Pacifique, de l'Afrique de l'Est au Pacifique Est. Cette espèce a été considérée comme importante pour l'écologie des récifs de corail, car elle s'attaque aux étoiles de mer "couronne d'épines" (*Acanthaster planci* (Linnaeus, 1758), quand celles-ci sont blessées. Nous révisons ici le genre sur la base de l'examen du matériel type et de matériel supplémentaire provenant de dix collections muséales, ainsi que de comparaisons d'ADN mitochondrial de spécimens représentatifs provenant de diverses localités. Nous reconnaissons trois espèces : *P. striata*, *P. distincta* (Hoagland, 1920) (nouvelle combinaison, incluant *P. polylamellata* comme synonyme), et *P. maculata* (conservée en attendant l'étude des spécimens topotypiques). *Pherecardia parva* est transférée à *Pherecardites* Horst, 1912 et renommée *Pherecardites monroi* en raison de l'homonymie avec *Pherecardites parva* Horst, 1912. *Amphinome bruguieresii* est considéré comme un synonyme junior d'*Eurythoe indica* (Schmarda, 1861); le statut de *A. formosa* reste indéterminé. Des clefs sont incluses pour les espèces de *Pherecardia* et *Pherecardites*.

MOTS CLÉS

Caroncule,
pigmentation dorsale,
pigmentation du notopodia,
clefs,
nom nouveau,
combinaisons nouvelles.

INTRODUCTION

The taxonomy of amphinomid annelids has historically been based on the shape of the caruncle, combined with branchial and chaetal features. Horst (1886: 165) proposed *Pherecardia* Horst, 1886 with *P. lobata* Horst, 1886 as its only species, for a poorly preserved specimen of unknown provenance with distinctive caruncle with its median ridge being roughly heart-shaped, and provided the etymology in a foot note as derived from this feature after combining the Greek word *phero*, bear, carry, bring with the Latin *cardio*-, from Greek *kardia*, heart (Brown 1954: 184, 187). *Pherecardia* resembles *Hermodyce* Kinberg, 1857, another amphinomid genus that includes species with a large caruncle. Several species now placed in *Pherecardia*, including the senior synonym of the type species, were originally placed in *Hermodyce*, whereas others have been included in *Amphinome* Bruguière, 1789, another amphinomid genus that includes species of large size but with a rather short, simple caruncle.

Pherecardia currently includes four recognized species (Read & Fauchald 2025): *P. maculata* Imajima, 2003 from the Sagami Sea, Japan; *P. parva* Monro, 1924 from the Macclesfield Bank, China Sea; *P. polylamellata* de Silva, 1961 from Sri Lanka, and *P. striata* (Kinberg, 1857) from Moorea, French Polynesia. Two other species have also been assigned to this genus in the past: *Amphinome bruguieresii* de Quatrefages, 1866 and *A. formosa* de Quatrefages, 1866 (Yáñez-Rivera & Salazar-Vallejo 2011). This transfer was tentative because we did not study their type material, and their status needs to be clarified.

The most common and best-known species is *Pherecardia striata*, one of the largest amphinomids. It is commonly 10–20 cm long and reaches over 50 cm in length (Fig. 1E, Steve 2012), with large specimens common in Hawaii (Glasby & Bailey-Brock 2001). It is easily recognized by its distinctive color pattern of dorsal longitudinal stripes, interrupted in the intersegmental areas (Kinberg 1910, pl. 12, fig. 8B). It has been observed attacking injured crown-of-spines starfishes in the Eastern Pacific (Glynn 1984). The species swarms and undergoes mass spawning in the water column, and large numbers of wasted bodies have been observed washed ashore (Bailey-Brock & Magalhães 2016).

Two distinct pigmentation patterns have been observed in *Pherecardia striata*, suggesting that more than one species may be involved. The typical form has longitudinal stripes of similar length and width across each segment (Fig. 1A, B), while stripes in the second form vary substantially in their thickness and length across each segment (Fig. 1C–E). Cytochrome oxidase I (COI) sequence data comparisons indicate that these color forms represent distinct genetic lineages. A complex pattern of striping is observed in the anterior region of some specimens (Fig. 1E, F).

To assess the morphological and genetic diversity within the genus we undertook a broad study of type and non-type specimens. Based on our investigations, three species are recognized in the genus. *Pherecardia striata* (Kinberg, 1857) is redescribed and restricted; *P. distincta* (Hoagland, 1920) is transferred from *Hermodyce* to *Pherecardia* and reinstated, with *P. polylamellata* de Silva, 1961 included as a synonym; and *P. maculata* Imajima, 2003 is retained pending the study



FIG. 1. – Pigmentation patterns of *Pherecardia striata* (Kinberg, 1857) (A, B, F, G) and *P. distincta* (Hoagland, 1920) (C, D, E); A, UF 5461; B, Kwajalein, in situ; C, UF 5343; D, Kwajalein, in situ; E, Hawaiian fisherman with a large specimen (and close-up of same); F, G, Kwajalein, in situ, close-up of anterior ends of two specimens (no scales available; photos: A, C: G. Paulay; B, D, F, G: S. Johnson; E, M. Tsukamoto, reproduced with permission).

of additional specimens. *Pherecardia parva* Monro, 1924 is transferred to *Pherecardites* Horst, 1912 and is redescribed and renamed as *Pherecardites monroi* n. nom. because it becomes a junior homonym of *Pherecardites parva* Horst, 1912, the type species of *Pherecardites* Horst, 1912. Study of the syntypes of *A. bruguieresii* revealed that it is a junior synonym of *Eurythoe indica* (Schmarda, 1861), and it is herein redescribed and illustrated. *Amphinome formosa* lacks type material: its status cannot be fixed.

MATERIAL AND METHODS

Total length and width of each specimen were measured, the latter at chaetiger 10 including chaetae, and the number of chaetigers were counted.

Species are presented in chronological order of description. Species transferred to other genera are treated after *Pherecardia* and included to provide a placement for them, however the additional genera involved were not revised. Coordinates are

TABLE 1. — COI sequences used in this study.

Species	Voucher	Field Number	GenBank	BOLD Process ID	Locality	Source
<i>Pherecardia striata</i>	UF Annelida 5438	BKON-0952	MW278193	KANBI670-19	Oahu	Kaneohe Bioblitz
<i>Pherecardia striata</i>	UF Annelida 5461	BKON-1328	MW278360	KANBI894-19	Oahu	Kaneohe Bioblitz
<i>Pherecardia distincta</i>	UF Annelida 5343	BKON-0123	MW277733	KANBI074-19	Oahu	Kaneohe Bioblitz
<i>Pherecardia distincta</i>	UF Annelida 5420	BKON-0638	MW278005	KANBI427-19	Oahu	Kaneohe Bioblitz
<i>Pherecardia striata</i>	UF Annelida 2125	BMOO-14438	KC706793	GBAHO352-15	Moorea	Moorea Biocode
<i>Pherecardia striata</i>	no voucher	JF905665	GBAN5127-13	—	Moorea	Leray <i>et al.</i> 2013
<i>Pherecardia cf. striata</i>	no voucher	MZ568412	GBMNF499-22	—	Japan?	Jimi <i>et al.</i> 2022
<i>Pherecardia striata</i>	UF Annelida 545	BMOO-00384	—	MBMIE014-07	Moorea	Moorea Biocode
<i>Pherecardia striata</i>	UF Annelida 523	BMOO-00702	—	MBMIE033-07	Moorea	Moorea Biocode
<i>Pherecardia striata</i>	UF Annelida 1269	BMOO-08306	—	—	Moorea	Moorea Biocode
<i>Pherecardia striata</i>	UF Annelida 2312	BMOO-14426	—	—	Moorea	Moorea Biocode
<i>Pherecardia striata</i>	no voucher	BMOO-13917	—	—	Moorea	Moorea Biocode
<i>Pherecardia striata</i>	CAS 187536	none	—	—	Philippines	This study
<i>Pherecardia distincta</i>	CAS 185402	none	—	—	Philippines	This study
<i>Pareurythoe borealis</i>	SIO BIC A2379	JN086550	GBAN6186-14	—	Norway	Borda <i>et al.</i> 2012

included when available directly from collection labels. Photographs were made using a digital camera with an adapter for microscopes, illuminated with combinations of standard and LED microscope lamps. Specimens were temporarily stained with Methyl green or Shirlastain-A, thus some figures appear with a greenish or reddish hue in some plates. Images were stacked with HeliconFocus8 and plates were arranged with PaintShopPro9.

Gustafson (1930: 317) noted that amphinomid chaetae include abundant, thin, usually smooth capillaries, and thicker variably ornamented chaetae or aciculars. These latter chaetae can be smooth, bifurcate, denticulate, or present some of these features variably combined; when they are denticulate in a single series, they are referred to as harpoon-chaetae. Aciculae among amphinomids have exposed tips, and these tips are usually subdistally swollen and can be blunt or sharp. In *Pherecardia*, aciculars can be harpoon-chaetae or have a short series of small distal denticles, tips are bent, often with a shallow constriction (Gustafson 1930: 317, fig. 10). Acicular has been used in polychaete keys and glossaries (Fauchald 1977a: 156; Mikkelsen & Virnstein 1982: 2; Glasby *et al.* 2000: 403) for referring to thick, rod-like protruding chaetae.

In *Pherecardia*, the lateral caruncular lobes show a pattern of branching, which could match blood irrigation, along each caruncular lobe. A central vein or vessel can be pinnately branched along the lobe, and this is herein referred to as venation. Further, in some specimens these areas can be variably swollen such that the caruncular lobe is not smooth, and when this feature was noted, it was referred to as rugose. As in many morphological features, some terms were taken from botany. Botanists refer to leaf venation in general, and they recognize different patterns of venation, being parallel venation and reticulate venation the most common ones (Sack & Scoffoni 2013). Then, for simplicity, this pinnate branching pattern will be referred to as venation whenever they are present and provided as details about caruncular lobes.

There are two fleshy, longitudinal outgrowths or ridges running along the peristomium and often reaching the mouth;

they have been referred to as palps when the functional palps were regarded as antennal palp or secondary antennae, or as lips. They are not palps (Orrhage 1990), and because they do not surround the mouth they could not be lips either. However, after their shape and proximity to the mouth, they are indicated as lips, and their proximity to the mouth is sometimes included in the descriptions below, especially if not reaching the mouth.

An additional feature is the area between notopodia and parapodia, which can include some glands. When present, this feature is referred to as an interrampal belt, for emphasizing its position, and if pigmented glands are distinct, it is referred to as interrampal belt maculate, or non-maculate if there are no discrete spots in the interrampal area.

Tissues from some specimens were sequenced for mitochondrial cytochrome c oxidase I (COI) as described elsewhere (Piotrowski *et al.* 2024; Salazar-Vallejo *et al.* 2024) and combined with additional sequence data available in GenBank and BOLD (Table 1). Sequences were analyzed with MEGA (Tamura *et al.* 2021) using Maximum Likelihood with 1000 bootstrap replicates, with TN93+I as the best fit model, and *Pareurythoe borealis* (M. Sars, 1862) as outgroup (Jimi *et al.* 2022).

ABBREVIATIONS

Institutions

AM	Australian Museum, Sydney;
CAS	California Academy of Sciences, San Francisco;
LACM-AHF	Los Angeles County Museum of Natural History, Allan Hancock Polychaete collection, Los Angeles;
MAGNT	Museum and Art Gallery, Northern Territory, Darwin;
MNHN	Muséum national d'Histoire naturelle, Paris;
NHML	Natural History Museum, London;
RMNH	Rijksmuseum voor Natuurlijke Historie (now NBC: Naturalis Biodiversity Center), Leiden;
UF	University of Florida, Natural History Museum, Gainesville;
ZMA	Zoological Museum, University of Amsterdam (this collection is now housed at NBC);
ZMH	Zoological Institute, University of Hamburg, Hamburg.

KEY TO SPECIES OF *Pherecardia* HORST, 1886
(type localities after the species name)

1. Dorsum with numerous longitudinal stripes in each segment; dorsal cirri and branchiae colorful 2
— Body without patterned pigmentation; dorsal cirri and branchiae pale *P. maculata* Imajima, 2003 Japan
2. Longitudinal stripes more or less regular, of similar width and length; notopodia with anterior surface darker than posterior surface, without complete blackish ring; notochaetae very abundant and larger than dorsal cirri
..... *P. striata* (Kinberg, 1857) restricted, French Polynesia
- Longitudinal stripes irregular, of varied width and length; notopodia with distinct complete blackish ring; notochaetae moderately abundant, shorter than dorsal cirri
..... *P. distincta* (Hoagland, 1920) reinst., n. comb. Philippines (includes *P. polylamellata* de Silva, 1961 Sri Lanka).

RESULTS

Family AMPHINOMIDAE Savigny in Lamarck, 1818
Subfamily AMPHINOMINAE Savigny in Lamarck, 1818

Genus *Pherecardia* Horst, 1886

Pherecardia Horst, 1886: 165; 1909: 299 (syn.); 1911: 17-21 (syn.). — Fauchald 1977a: 102-103 (key and diagn.).

Eucarunculata Malaquin & Dehorne, 1907: 358 (type species: *E. grubei* Malaquin and Dehorne, 1907, by monotypy).

TYPE SPECIES. — *Pherecardia lobata* Horst, 1886, by monotypy; junior synonym of *Hermodice striata* Kinberg, 1857.

DIAGNOSIS (MODIF. AFTER HORST 1886). — Amphinominae with median and lateral antennae and palps. Caruncle large, median ridge heart-shaped with several lateral digitate to foliose lobes. Branchiae present in all segments, bushy. Notochaetae capillaries and aciculars, smooth or serrated (harpoon-chaetae). Neurochaetae aciculars non-furcate, often distally denticulate, hastate (tips bent).

COMPOSITION

We recognize three species in *Pherecardia* below: *P. striata*, *P. distincta*, and *P. maculata*. The last is known only from a single small specimen and additional material is necessary to evaluate and better characterize it. The first two species were previously confused and regarded as synonyms but are readily differentiated by color pattern and DNA sequence data (Fig. 8). Both range across most of the tropical Indo-Pacific to the American coasts. *Pherecardia striata* is evidently much more common. Perusing images in iNaturalist identified as *Pherecardia*, we note that only 18 pertain to *P. distincta* against 153 for *P. striata*, and one specimen from Timor-Leste was blue, probably after the presence of eggs (accessed 22.VII.2024).

REMARKS

Horst (1886: 165) diagnosed *Pherecardia* as having a caruncle with “a median, heart-shaped portion (= median ridge), which bears on each side several folded lobes” but he did not compare it against other genera. *Pherecardia* is similar to *Hermodice* but can be distinguished by caruncle shape. In *Pherecardia* the caruncle lateral lobes are separate from each other, often fused to the median ridge, whereas in *Hermodice* they are fused forming a single plate, and the median ridge is indistinct. Malaquin & Dehorne (1907: 360) differenti-

ated *Pherecardia* (under the synonym *Eucarunculata*) from *Hermodice* Kinberg, 1857 by indicating that the caruncle lobes “are aligned such that they are convergent anteriorly. This is contrary to the caruncle arrangement in *Hermodice*, where the lateral lobes are convergent posteriorly along the median ridge.” Because *Hermodice* is restricted to the Atlantic and Mediterranean, whereas *Pherecardia* is found in the Indian and Pacific Oceans, there were no comparative illustrations until Hartman (1951: 24) included anterior ends of representatives of each genus. Malaquin & Dehorne (1907) also provided a detailed description of the caruncle and dorsal pigmentation and noted that anterior eyes were larger than posterior eyes.

Amphinomids rarely evert their pharynx fully, as this organ does not need to be completely everted for capturing prey-items, but because of some specimens under stress evert a fairly large portion of the anterior gut, and even if the everted fraction constitutes the whole pharynx, it is rarely exposed for capturing food particles (Salazar-Vallejo 2023). In *Pherecardia*, the pharynx exhibits two morphological patterns, but the second may be a fixation artifact. Well-preserved specimens (Fig. 2A, B) exhibit a roughly spoon-shaped pharynx with granular papillae present on the dorsal depressed region. The mouth opens in the center, with a distal furrow separating lateral cushions comprised of a series of crests running ventrally, which become slightly rugose mid-ventrally. The second pattern was observed in poorly preserved specimens, where the pharynx includes three rings: 1) a short outer yellowish oval ring with a thin mid-dorsal blade (Fig. 2C, D); 2) a median pale ring with a granulose surface that is 3-4 times longer than the outer ring; and 3) an inner ring with a thinner wall that may be twice as long as the median one. There is one video showing a *P. striata* capturing a crab, but the pharynx is not shown (van Antwerp 2013). In *Hermodice*, the short cylindrical pharynx can be everted for capturing prey items offered by hand (Kosemen 2013), and in another video of a *Chloeia* Savigny in Lamarck, 1818, it eats a dying anchovy from the tail by sucking it up, and the pharynx is not exposed at all, although it can be expanded laterally for ingesting the head (MaverickDiving 2022).

As is the case in some other amphinomids with indefinite growth, the number of segments in *Pherecardia* specimens is not diagnostic. The following morphological features are not useful for separating species of *Pherecardia*. The number of lateral lobes in the caruncle, which has been applied to sepa-

rate species in the past, is problematic as it varies in number and complexity of caruncle lateral lobes due to growth and the caruncle is frequently altered by trauma (Fig. 3). The fine denticulation of neurochaetae can vary within the same parapodium, however this character must be used with caution because denticles may be damaged or corroded by fixative, resulting in the reduction or loss of subdistal denticles (de Silva 1961: 171). Consequently, these two features should be avoided to diagnose taxa.

***Pherecardia striata* (Kinberg, 1857), restricted**
(Figs 1A, B, F, G; 2A, B; 3; 4; 6-8)

Hermodice striata Kinberg, 1857: 13; 1910: 35 (diagn. repeated), pl. 12, fig. 8. — Ehlers 1920: 13-14. — Augener 1927: 122 (*partim*); 1933: 188.

Pherecardia lobata Horst, 1886: 165-166, pl. 7, figs 10-14; 1909: 300 (syn.); 1911: 17-21 (syn.); 1912: 32-33 (syn.) — Collin 1902: 741. — Fauvel 1919a: 336; 1919b: 349-350. — Day 1934: 27. — Bleeker & van der Spoel 1992: 152.

Amphinome sericata Fischli, 1903: 95-98, pl. 4, figs 1, 2, pl. 7, figs 45-49, pl. 8, figs 79-80.

Hermodice pennata Treadwell, 1906: 1165, fig. 41 (junior syn. *P. striata* *fide* Hartman 1956: 251).

Eucarunculata grubei Malaquin & Dehorne, 1907: 358-361, pl. 51, fig. 2, pl. 53, figs 12-15, 17-20. — Potts 1909: 365-366. — McIntosh 1925: 13-14, pl. 1, figs 3-4.

Eucarunculata grubei var. *gracilis* Potts, 1909: 366-367.

Eucarunculata grubei var. *minuta* Potts, 1909: 367.

Pherecardia striata — Monro 1928: 77; 1933: 7. — Fauvel 1935: 292-293 (*partim*); 1936: 257. — Okuda 1937: 265-266, fig. 5. — Monro 1939: 166-167 (epitokes). — Hartman 1948: 46; 1966: 181-182. — Day 1957: 67 (syn., *partim*); 1962: 636; 1967: 131, fig. 3.2p-t. — Fauchald 1977b: 13. — Blake 1991: 84. — Imajima 2005: 86-88, fig. 36A-G. — Cañete 2017: 199-201, Fig. 1.

DIAGNOSIS. — *Pherecardia* with dorsum bearing longitudinal stripes of similar width along body. Notopodia darker along anterior surface, posterior surface paler, not forming a complete blackish ring. Notochaetae abundant, longer than dorsal cirri along anterior chaetigers.

TYPE MATERIAL. — **Holotype of *Hermodice striata* Kinberg, 1857. French Polynesia** • 1 specimen; Moorea; KSF Eugenies Expedition; Sta. 1245; coral gravel; SMNH 6080.

Holotype of *Pherecardia lobata* Horst, 1886. Locality uncertain • 1 specimen; RMNH VER.1295 (locality given as Ambon Bay, III.1901, R. Semon leg. on label; the holotype specimen matches the original description, the label indicates that it was collected in 1901, 15 years after the original description. Horst (1886) noted that the provenance of the specimen was uncertain. Thus, the locality (Ambon Bay) on the label is a later addition and the type locality must be considered uncertain).

Holotype of *Hermodice pennata* Treadwell, 1906. Hawaiian Islands • 1 specimen; USFS Albatross; Sta. 4162; Nihoa Island; 38-44 m; 8.VIII.1902; USNM 5209.

ADDITIONAL MATERIAL. — **Kenya** • 1 specimen; Mombasa; D. MacGregor leg., no further data; NHML 1961.8.32 (complete, longitudinal stripes well defined dorsally, ventrally along anterior body half; notopodia without black rings; caruncle with eight pairs of

lateral lobes [last one tiny]; median antenna without tip, 1/3 as long as caruncle; pygidium with anus terminal, anal plate truncate, probably in regeneration; body 62 mm long, 9 mm wide, 62 chaetigers). **Madagascar** • 1 specimen; Nossy Vorona; off ENE side; 13°25'27"S, 48°21'15"E; 4 m depth; broken reef, extracted from large, dead *Porites*; 15.V.2008; A. Anker, G. Bakary, E. Boissin, H. Bruggemann, T. Horeau, F. Michonneau, G. Paulay & T. Werner leg.; UF 750 (complete; dorsal longitudinal stripes of similar width, often branching; caruncle, interramal areas and venter maculate; anterior eyes two times as large as posterior ones, not protruded; caruncle with median ridge complete, with seven pairs of lateral smooth lobes, with venation; notopodia with anterior surface darker, without distal black rings; pygidium with anus terminal, anal plate truncate, barely notched; 83 mm long, 8 mm wide, 64 chaetigers) • 1 specimen; Nosy-Be; 7-26.V.2008; G. Paulay *et al.* leg.; UF 4230 (complete; dorsal longitudinal stripes of similar width, a few branching; caruncle interramal areas and venter maculate; anterior eyes three times as large as posterior ones, not protruded; caruncle with median ridge complete, with eight pairs of lateral smooth lobes, with venation; notopodia with anterior surface darker, without distal black rings; pygidium with anus terminal, anal plate truncate, barely notched; 108 mm long, 10 mm wide, 73 chaetigers).

Mascarene Islands, La Réunion • 1 specimen; Saint Leu, Maison Verte, Cimetière; 21°11'36"S, 55°16'56"E; 8-9 m depth, fore reef, within dead digitate *Acropora*; 13.VIII.2007; H. Bruggemann, N. Hubert, F. Michonneau & G. Paulay leg.; UF 654 (anterior fragment; dorsal longitudinal stripes of similar width, a few branching; not maculate; anterior eyes two times as large as posterior ones, not protruded; caruncle with median ridge complete, with 7-8 pairs of lateral lobes, barely pinnate; notopodia with anterior surface darker, without distal black rings; 26 mm long, 7 mm wide, 26 chaetigers) • 3 specimens; Saint Leu, Sec Jaune; 21°9'11"S, 55°16'51"E; 6-15 m depth; 17.VIII.2007; H. Bruggemann, N. Hubert, F. Michonneau & G. Paulay leg.; UF 664 (two complete, one without posterior region; dorsal longitudinal stripes of similar width, a few branching; not maculate; interramal belt and venter maculate; anterior eyes two times as large as posterior ones, not protruded; caruncle with median ridge complete, twisted, with seven pairs of lateral smooth lobes; notopodia with anterior surface darker, without distal black rings; pygidium with anus terminal, anal plate truncate, margin entire; 33-34 mm long, 7-8 mm wide, 50 chaetigers).

Indonesia • 1 specimen; Lesser Sunda Islands; RV *Siboga* Expedition; Sta. 60; Timor, Samau Island, Haingsisi; 23 m depth, reef, *Lithothamnion* in 3 m and less; 27-28.IV.1899; ZMA V.POL.1070.1 (complete, slightly twisted, breaking in two from chaetiger 17; some chaetae from chaetigers 10 and 25 removed for observation; dorsum with rather regular longitudinal stripes of similar width; caruncle with 6-8 lateral lobes with venation, not rugose; branchial filaments basally darker, paler distally; pygidium with anus terminal, anal plate truncate; body 53 mm long, 7 mm wide, 48 chaetigers) • 1 specimen; Maluku; RV *Siboga* Expedition; Sta. 240; Banda anchorage; 9-45 m depth; trawl, black sand and coral; 22.XI-1.XII.1899; ZMA V.POL.1070.2 (bent ventrally; juvenile; some parapodia previously removed [lost?], breaking in two parts; dorsum with longitudinal stripes of similar width; caruncle with 5-6 lateral lobes with venation, not rugose; branchial filaments basally darker, tips paler; pygidium with anus terminal, anal plate wider than long, medially notched; body 19 mm long, 4 mm wide, 35 chaetigers) • 1 specimen; Lesser Sunda Islands, RV *Siboga* Expedition; Sta. 300; 10°48.6'S, 123°23.1'E; 918 m; trawl, muddy bottom; 30.I.1900; ZMA V.POL.1070.4 (bent laterally; juvenile; dorsum with longitudinal stripes of similar width; caruncle with 5-6 lateral lobes with venation, not rugose; branchiae basally darker, tips paler; pygidium with anus terminal, anal plate slightly longer than wide, round; body 19 mm long, 4 mm wide, 35 chaetigers) • 1 specimen; Ambon Island; 3.II.1902; V. Kamper leg.; RMNH VER.1296 (partially dried, with salt spherules over chaetae and branchiae; dorsum with rather regular longitudinal stripes; venter with paler longitudinal stripes, less regular; caruncle



FIG. 2. — Pharynx eversion in two species of *Pherecardia* Horst, 1886: **A, B**, *Pherecardia striata* (Kinberg, 1857), restricted, non-type specimen, UF 31: **A**, anterior region, right lateral view; **B**, frontal view after Shirlastain-A staining; **C, D**, *Pherecardia distincta* (Hoagland, 1920) reinstated, non-type specimen, NHML 1932.12.24.265–268, after Methyl green staining: **C**, anterior end, frontal view of pharynx; **D**, anterior region, left lateral view. Scale bars: A, C, 0.7 mm; B, D, 0.6 mm.

in regeneration; eyes black, not protruded from prostomial margin; caruncle with lateral lobes with venation, not rugose; branchiae dark with tips pale; pygidium with anus terminal, anal plate truncate; body 93 mm long, 13 mm wide, 59 chaetigers) • 25 specimens; Ambon Island; 1887; H. Brock leg.; ZMH PE29 (17 complete; most grayish with purple to blackish longitudinal rather regular stripes, other brownish with more irregular streaking; caruncle lobes foliose, slightly indented, 6–10 pairs; eyes not protruded from prostomial margins; median antenna 1/4 to 2/3 as long as caruncle; pygidium with anus terminal, anal plate lobate, often slightly notched medially; complete with body 16–70 mm long, 6–13 mm wide, 32–45 chaetigers) • 1 specimen; Ambon Island; 1887; H. Brock leg.;

ZMH PE30 (soft, complete, unpigmented [this has been retained in *P. striata* with hesitation after it was found in the type locality of *P. lobata* Horst, 1912, which is a junior synonym of *P. striata*, but the fact that this was collected in the same locality as the type does not preclude it being something else]; left parapodia of chaetigers 24 and 25 previously removed [kept in container]; caruncle with eight pairs of lateral lobes; median antenna half as long as caruncle; pygidium with anus terminal, anal plate truncate; body 50 mm long, 10 mm wide, 52 chaetigers).

East Timor • 1 specimen; Timor, between Timor and Nusa Besi; anchorage; RV *Siboga* Expedition; Sta. 282; 08°25.2'S, 127°18.4'E; 27–54 m depth, trawl, sand and coral; 15–17.I.1900; ZMA V.POL.1010.3

(complete, thinner medially, with progressively longer notochoetae from chaetiger 25 to end of body; some chaetae of chaetigers 25 and 50 removed for observation; dorsum with longitudinal stripes of similar width; caruncle with 5-6 lateral lobes with venation, not rugose; branchial filaments basally darker, paler distally; pygidium with anus terminal, anal plate with a median notch; body 60 mm long, 8 mm wide, 62 chaetigers).

South China Sea • 1 specimen; Macclesfield Bank; no further data; NHML 1925.1.128.143 (bent ventrally, without posterior end; anterior end damaged; caruncle with 5-6 pairs of lateral lobes; median antenna lost; longitudinal dorsal stripes barely visible; notopodial black rings not seen; body 39 mm long, 9 mm wide, 39 chaetigers).

Philippines • 1 specimen; Batangas Province, Tingloy, Maricaban Island, Sepok Point dive site; Hearst Philippine Biodiversity Expedition 2011; 13°41'23"N, 120°49'47"E; 6.V.2011; R. Van Syoc leg.; CASIZ 187243 (twisted dark specimen, with many longitudinal stripes, most branching laterally; notopodia with darker anterior surfaces, paler posteriorly; caruncle with median ridge complete, with 6 lateral lobes, smooth; median antenna 2/3 as long as caruncle; pygidium with anus terminal, anal plate truncate, margin incised; body 60 mm long, 10 mm wide, 59 chaetigers) • 5 specimens; Occidental Mindoro, Lubang Islands, Cabra Island, west of Cheeze Whiz Wall dive site; Verde Island Passage Expedition; Sta. LUB-12; 13°52'48"N, 120°1'11"E; 0-36 m depth; 24.V.2014; C. Piotrowski leg.; CASIZ 197440 (juveniles; two with pharynx exposed; smallest one broken in two pieces; smaller ones with paler pigmentation; all with darker areas over anterior notopodial surface; caruncle with 4-5 lateral lobes, smallest one with venation running along lobe, running across them in largest one; body 6.5-26.0 mm long, 1.5-2.5 mm wide, 20-33 chaetigers) • 1 specimen; Lubang Island "Beyond Fish" dive site; 2014 Verde Island Passage Expedition; Sta. LUB-10; 13°47'36"N, 120°5'40"E; 7-30 m depth; 23.V.2014; C. Piotrowski leg.; CASIZ 198634 (complete juvenile specimen, straight; dorsal longitudinal stripes similar width throughout; notopodia darkly pigmented anteriorly only, lacking complete distal blackish rings; anterior eyes larger than posterior, not protruded from prostomial margin; caruncle complete, smooth, 4-5 lateral lobes with violet venation; median antenna 1/3 caruncle length, branchiae dark violet basally; anus terminal; 12 mm long, 3 mm wide, 28 chaetigers) • 1 specimen; Batangas Province, Tingloy, Maricaban Island, Sepok Point dive site; Hearst Philippine Biodiversity Expedition 2011; Sta. HEP-60; 13°41'17"N, 120°49'38"E; 0-24 m depth; coral rubble; 13.V.2011; E. Jessup & C. Piotrowski leg.; CASIZ 187263 (complete juvenile specimen, proboscis everted; faint longitudinal stripes of similar width throughout, in life dorsum with white spots; notopodia with anterior dark purple inverted triangular spots reddish in life, lacking blackish ring, in life ceratophores of dorsal cirri with yellow ring; red anterior eyes twice size of posterior eyes, not protruded from margin; caruncle with smooth complete median ridge, three lobate lateral lobes with simple venation; median antenna 2/3 length of caruncle, 2/3 length of lateral antennae; branchiae unpigmented; pygidium bulbous, in life with yellow ring; 5 mm long, 1 mm wide, 16 chaetigers) • 1 specimen; Tingloy, Maricaban Island, Bethlehem dive site; Hearst Philippine Biodiversity Expedition 2011; Sta. HEP-65; 13°40'23"N, 120°49'38"E; filamentous algae; 14.V.2011; T. M. Gosliner leg.; CASIZ 187288 (straight juvenile specimen; faint purple longitudinal stripes of similar width throughout dorsum; notopodia anterior with dark purple inverted triangular spot, lacking blackish ring; notochoetae dense, longer than dorsal cirri; red anterior eyes not protruded from margin; caruncle median ridge complete, smooth, 3-4 lateral lobes with specks of pigment, minimal venation; median antenna broken; branchiae pigmented basally; pygidium bulbous, bent ventrally, yellow in life; 6 mm long, 2 mm wide, 21 chaetigers) • 1 specimen; Tingloy, Maricaban Island, Sepok Point dive site; Hearst Philippine Biodiversity Expedition 2011; Sta. HEP-115; 13°41'16"N, 120°49'37"E; 0-26 m depth; 25.V.2011; C. Piotrowski leg.; CASIZ 187536 (posterior segments twisted, damaged; longitudinal stripes of similar width throughout dorsum, faint

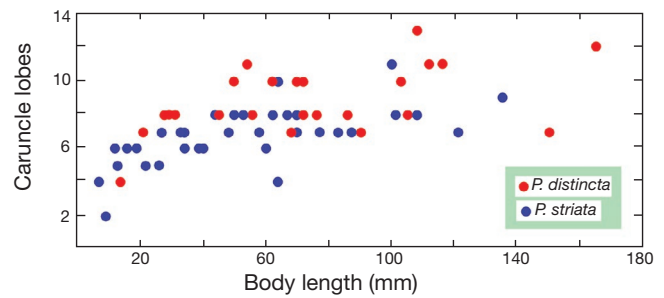


Fig. 3. — Number of caruncle lobes per body length in two *Pherecardia* species, based upon complete specimens.

ventral longitudinal stripes; notopodia pigmented anteriorly only, lacking complete dark ring, dorsal cirri nearly as long as notochoetae; anterior eyes not protruded from prostomial margin; caruncle median ridge with pigmented transverse furrows, 5-6 lateral lobes with dark venation; median antenna 2-3 as long as caruncle, at least twice length of lateral antennae; branchiae pigmented basally; anus dorsal, pygidium elongate, bulbous; 70 mm long, 5 mm wide, 58 chaetigers) • 1 specimen; Verde Island, Coral Garden dive site; 2015 Verde Island Passage Expedition; Sta. VER-21; 13°33'37"N, 121°2'38"E; 6-15 m depth; coral rubble; 9.IV.2015; G. Paulay leg.; CASIZ 214577 (specimen twisted in S curve, internal organs prolapsed through anterior body wall from tissue sampling; longitudinal stripes similar width throughout dorsum, faint longitudinal stripes ventrally; notopodia pigmented anteriorly, lacking complete dark ring, notochoetae longer than dorsal cirri; eyes not protruded from prostomial margin; caruncle median ridge with pigmented transverse furrows, 5-6 lateral lobes with dark venation; median antenna 1/3 length caruncle, 3 × length lateral antennae; branchiae pigmented basally; pygidium with terminal plate nearly twice longer than wide; 45 mm long, 6 mm wide, 51 chaetigers).

Japan • 1 specimen; Okinawa Island, White Beach, Navy Pier; 26°17'44"N, 127°54'22"E; semi-exposed, shaded artificial substrate; 0-1 m depth; 3.VII.2010; N. Evans, F. Michonneau, T. Schils & A. Devilliers leg.; UF 1723 (complete, twisted; dorsal longitudinal stripes of similar width, a few branched, integument maculate; notopodia without black distal rings; anterior end smashed, eyes of similar size, collapsed; caruncle with median ridge complete, 7-8 pairs of lateral lobes, barely pinnate; median antenna broken; pygidium with anus terminal, anal plate truncate, margin entire; body 101 mm long, 11 mm wide, 66 chaetigers).

Mariana Islands • 1 specimen; Guam, West Cocos Barrier Reef; 13°14'00"N, 144°38'28"E; 10-15 m depth; fore reef, rubble; 19.V.1997; J. Starmer & G. Paulay leg.; UF 19 (regenerating posterior end; dorsal longitudinal stripes of different width, about four wider dorsal and three on each side; integument without maculae; notopodia without distal blackish rings; anterior eyes two times as large as posterior ones, not protruded from prostomial margins; caruncle pale, with median ridge complete, with 8-9 pairs of lateral smooth lobes; median antenna without tip, 2/3 as long as caruncle; pygidium with anus terminal, anal plate truncate; 135 mm long, 12 mm wide, 75 chaetigers) • 1 specimen; Guam, Pago Bay; 13°25'11"N, 144°47'36"E; 7 m depth; fore reef, under rocks; 20.II.1996; G. Paulay leg.; UF 49 (complete; dorsal longitudinal stripes of similar width, some branching; integument without maculae; notopodia without distal blackish rings; anterior eyes two times as large as posterior ones, not protruded from prostomial margins; caruncle pale, with median ridge complete, with 10 pairs of lateral pinnate lobes; median antenna entire, half as long as caruncle; pygidium with anus terminal, prolapsed, anal plate truncate; 64 mm long, 10 mm wide, 60 chaetigers) • 1 specimen; Guam, Orote Peninsula; 13°26'19"N, 144°37'39"E; 20-25 m depth; under rocks; 6.II.1998; G. Paulay leg.; UF 173 (complete; dorsal longitudinal stripes of similar width,

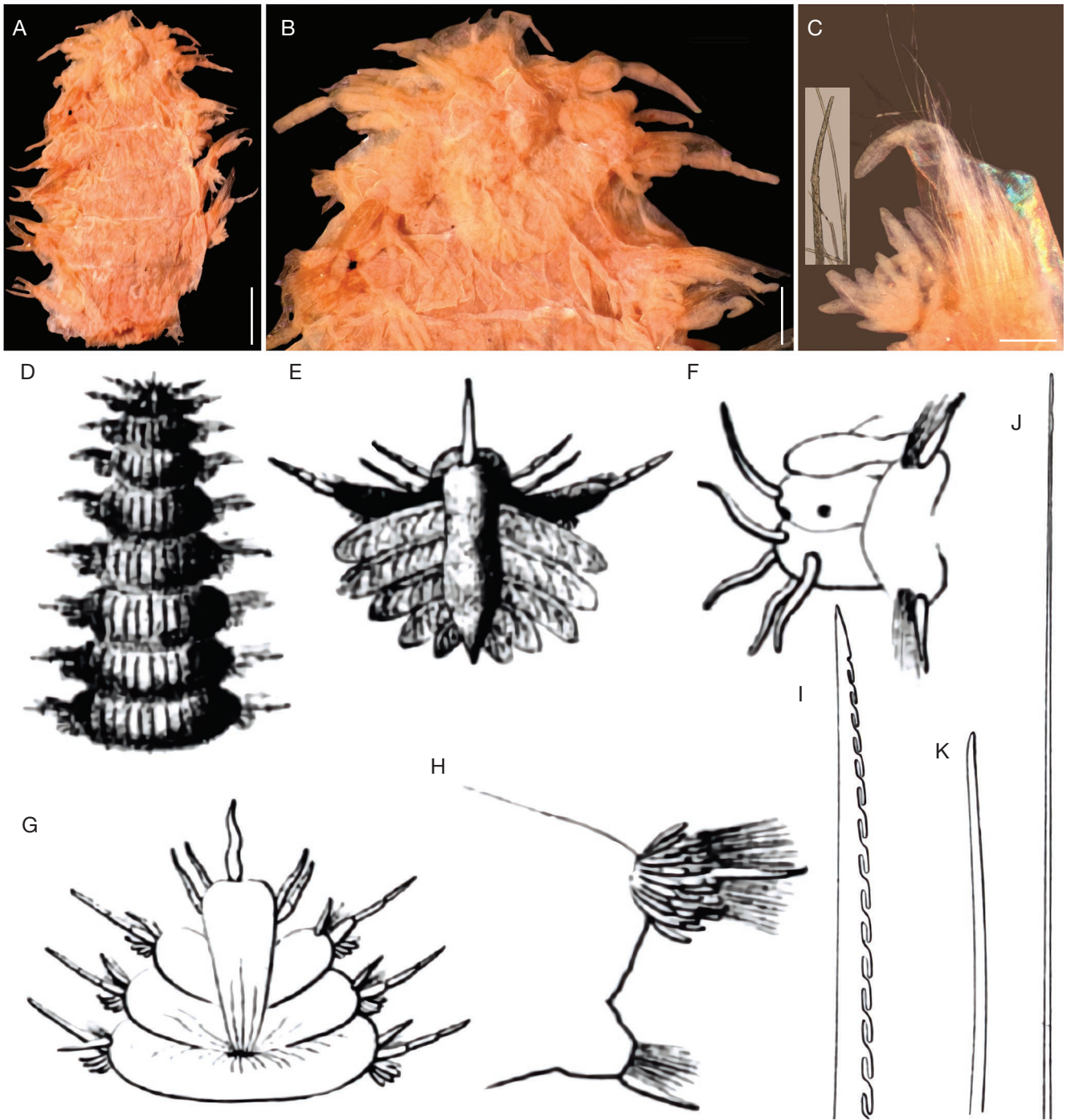


FIG. 4. — *Pherecardia striata* (Kinberg, 1857), holotype, SMNH 6080: **A**, dorsal view after Shirlastain-A; **B**, anterior end; **C**, notopodia of one of the last median chaetigers of the anterior fragment (inset: notochaetal tips, harpoon-chaetae in frontal view). Original drawings after Kinberg, 1910: **D**, dorsal view; **E**, anterior end, dorsal view; **F**, anterior end, left lateral view; **G**, anterior end, ventral view; **H**, chaetiger 7, right parapodium, posterior view; **I**, same, harpoon-notochaetae; **J**, same, capillary notochaetae; **K**, same, neurochaeta. Scale bars: A, 1.2 mm; B, 0.5 mm; C, 0.3 mm.

some branching; integument without maculae; notopodia without distal rings; anterior eyes two times as large as posterior ones, not protruded from prostomial margins; caruncle pale, with median ridge complete, with seven pairs of lateral smooth lobes; median antenna without tip, 1/3 as long as caruncle; pygidium with anus terminal, anal plate notched; 58 mm long, 10 mm wide, 61 chaetigers) • 1 specimen; Asuncion Island, NE of island; 19°41'59"N, 145°25'0"E; 10-16 m depth; 5.IX.2003; M. Malay leg.; UF 2876 (pharynx partially exposed; without pygidium; dorsal longitudinal

stripes of similar width, a few branching; integument without maculae; notopodia without distal rings; anterior eyes two times as large as posterior ones, not protruded from prostomial margins; caruncle pale, with median ridge complete, with 6-7 pairs of lateral smooth lobes; median antenna without tip, half as long as caruncle; 33 mm long, 10 mm wide, 51 chaetigers) • 1 specimen; Maug Islands; 20°02'N, 145°13'E; 12 m depth; reef slope, in holes along crevices; 2.VI.1992; P. Schupp leg.; UF 163 (complete; dorsal longitudinal stripes of similar width, a few branching; integument

without maculae; notopodia without distal blackish rings; anterior eyes slightly larger than posterior ones, not protruded from prostomial margins; caruncle pale, with median ridge complete, with eight pairs of lateral smooth lobes; median antenna broken, 1/5 as long as caruncle; pygidium with anus terminal, anal plate truncate, margin entire; 44 mm long, 7 mm wide, 47 chaetigers).

Line Islands • 1 specimen; Kiritimati Atoll, West side of atoll, north of passage, outer reef slope; 2°0'30"N, 157°29'22"E; 10–14 m depth; from dead *Pocillopora* head; 4.VIII.2005; G. Paulay & N. Knowlton leg.; UF 572 (without posterior region, anterior region with gut exposed in chaetiger 9; dorsal longitudinal stripes of similar width, rarely branching; notopodia with an anterior darker area, without distal black rings; caruncle with median ridge complete, five pairs of lateral lobes with venation, not pinnate, distal pair smooth; median antenna without tip, half as long as caruncle; 22 mm long, 8 mm wide, 31 chaetigers) • 1 specimen; Palmyra Atoll, southern outer reef at North-South Causeway intersection; CAS Palmyra Expedition 2006; Sta. CP-18; 5°52.069'N, 162°4.156'W; 9–18 m depth; 11.IX.2006; M. Roth & T. Konotchick leg.; CASIZ 174407 (complete, twisted, small specimen; dorsal longitudinal stripes of similar width; notopodia dark basally, distally unpigmented, lacking distal blackish rings; anterior eyes slightly protruded from prostomial margin; caruncle median ridge complete, smooth, 5–6 lateral lobes with purple venation; median antenna 2/3 as long as caruncle; branchiae basally dark, distally unpigmented; pygidium with anus terminal, ringed in purple distally; 17–20 mm long, 3 mm wide, 35 chaetigers).

Hawaii • 1 specimen; Hawaii Island, Kona coast, in front of Hotel Kona Surf; 3–10 m depth; VI.1973; A. J. Ferreira leg.; CASIZ 4899 (complete; regular longitudinal stripes distinct; anterior surfaces of notopodia darker than adjacent areas, without black ring; body 29 mm long, 4 mm wide, 45 chaetigers) • 4 specimens; Oahu Island, Honakalu Harbor, near Kailua; 7–8 m depth; no date; J. Bailey leg.; LACM-AHF 14775 (complete; regular longitudinal stripes distinct, anterior surfaces of notopodia darker than adjacent areas, without black rings; body 30–57 mm long, 5–10 mm wide, 47–54 chaetigers) • 1 specimen; Oahu Island, off Kewalo; 21°17'20"N, 157°51'54"W; 9–12 m depth; outer reef slope, settling plates, ARMS 1; 1.XII.2008; R. Moffitt leg.; UF 822 (without pygidium, bent laterally; dorsal longitudinal stripes of similar width, a few branching; notopodia without distal rings; anterior eyes two times as large as posterior ones, not protruded from prostomial margins; caruncle brownish, median ridge complete, with seven pairs of lateral lobes; median antenna half as long as caruncle; 34 mm long, 6 mm wide, 41 chaetigers) • 1 specimen; Oahu Island, Kaneohe Bay, N of Kekepa Island; 21°28'37"N, 157°46'33"W; 15–18 m; 26.V.2017; IZ team leg.; UF 5438 (anterior fragment, markedly contracted, bent ventrally; dorsal longitudinal stripes of similar width, some branching; notopodia without distal rings; anterior eyes larger than posterior ones; caruncle whitish with median ridge distinct, and seven pairs of lateral lobes, mostly smooth; median antenna without tip, 1/3 as long as caruncle; 21 mm long, 8 mm wide, 25 chaetigers) • 1 specimen; Oahu Island, Kaneohe Bay, N of Kapapa Island; 21°29'23"N, 157°47'20"W; 16–19 m depth; 27.V.2017; IZ team leg.; UF 5461 (without pygidium, twisted; dorsal longitudinal stripes of similar width, some branching; notopodia without distal rings; abundant white spots along notopodial bases, continued ventrally, abundant ventrally; anterior eyes slightly larger than posterior ones; caruncle brownish, maculate, with median ridge distinct, and seven pairs of lateral pinnate lobes; median antenna without tip, 4/5 as long as caruncle; 121 mm long, 12 mm wide, 70 chaetigers) • 1 specimen; Oahu Island, Kaneohe Bay, outside main reef pass; 21°28'37"N, 157°46'15"W; 14–17 m depth; 28.V.2017; IZ team leg.; UF 5499 (complete, twisted, some anterior left parapodia removed for molecular studies; dorsal longitudinal stripes of similar width, a few branching; notopodia without distal rings; anterior eyes two times as large as posterior ones, not protruded from prostomial margins; caruncle pinkish with median ridge distinct, 7–8 pairs of lateral

lobes, mostly smooth; median antenna almost complete, 1/2 as long as caruncle; pygidium terminal, anal plate truncate; 70 mm long, 6 mm wide, 62 chaetigers).

Papua New Guinea • 1 specimen; Louisiades Archipelago, Misima Island, 1.6 km North of Point Ebola; 10°36'43"N, 152°32'23"E; north coast; 31.V.1998; G. Paulay leg.; UF 31 (complete; dorsal longitudinal stripes of similar width; eyes of similar size, not protruded, caruncle with median ridge complete, with six pairs of lateral lobes, smooth; median antenna 1/3 as long as caruncle; notopodia without distal black rings; pygidium with anus terminal, anal plate truncate cleft; 34 mm long, 9 mm wide, 54 chaetigers) • 1 specimen; East New Britain, Ralum; dead coral; 4.X.1896; H. Dahl leg.; ZMH V10312 (complete, regenerating posterior end; anterior end compressed; longitudinal stripes of different width, reaching intersegmental spaces, well-defined dorsally and ventrally, distinct laterally; notopodia with black rings; caruncle asymmetric, with 11 left lobes and six right lobes; median antenna without tip, surpassing anterior caruncle half; right parapodium of chaetiger 25 removed for observation (kept in container); dorsal cirrophore 2–3 times wider and about three times longer than cirrostyle; pygidium with anus terminal, anal plate small, truncate; body 100 mm long, 18 mm wide, 58 chaetigers).

Australia • 1 specimen; Harry's Canyon, Heron Island, Queensland; 15 m depth; 18.XI.2009; Creefs Heron 2009 team leg.; MAGNT 28828 (twisted, without posterior end, broken in two pieces, dorsal longitudinal stripes of similar width along body; eyes not protruded from prostomial margin; fragment 15 + 36 mm long, 11 mm wide, 17 + 35 chaetigers) • 1 specimen; fore reef north of Tantabiddi, Ningaloo Reef, WA; 23 m depth; 14.VI.2008; G. M. Dally leg.; MAGNT 29300 (juvenile, bent laterally; longitudinal stripes of similar width along body; notopodia with black band anteriorly; branchiae blackish with tips pale; caruncle with 6 lateral foliose lobes, all with blackish venation; median antenna bent posteriorly; 1/4 as long as caruncle, as long as palps; lateral antenna slightly shorter than palps; eyes not protruded from prostomial margin, anterior eyes almost 2× as large as posterior ones; pygidium with anus terminal, anal plate slightly notched; body 11.5 mm long, 5 mm wide, 32 chaetigers).

New Caledonia region: Matthew Island • 1 specimen; Northwest side; 22°20'29"S, 171°21'1"E; 10 m depth; 1.VIII.2017; S. Hannam, A. Reid, C. Bedford & I. Middleton leg.; AM 51660 (body twisted, broken in two fragments; longitudinal anastomosing stripes blackish dorsally and ventrally, paler ventrally, present throughout body; caruncle with pale ridges, darker blades, with eight lateral lobes foliose, rugose; median antenna 1/3 as long as caruncle; a few noto- and neurochaetae removed from chaetigers 9 and 25; harpoon notochoetae present, with more denticles in median chaetigers; neurochaetae with denticles better defined in anterior chaetigers, some with sharp tips and over 20 subdistal denticles; anus dorsal between last two chaetigers, anal plate round, blunt; body 23 + 44 mm long, 11 mm wide, 21 + 40 chaetigers) • 1 specimen; Northwest side; 22°20'29"S, 171°21'1"E; 10 m depth; 1.VIII.2017; S. Hannam, A. Reid, C. Bedford & I. Middleton leg.; AM 51662 (anterior fragment, bent dorsally; longitudinal anastomosing stripes blackish dorsally and ventrally, paler ventrally, present throughout fragment; caruncle with thin blackish anastomosing stripes, 1/2 as wide as anterior end; with eight lateral foliose lobes; median antenna 1/4 as long as caruncle; chaetae no removed; fragment 19 mm long, 8 mm wide, 27 chaetigers).

Samoa • 1 specimen; Upolu; from Museum Godeffroy; no further data; ZMH V694 (colorless; caruncle asymmetrical with four left and six right lobes, median ridge base smooth; median antenna lost; pygidium with anus terminal, anal plate barely bifid; body 40 mm long, 7 mm wide, 46 chaetigers).

Cook Islands • 1 specimen; Aitutaki, Rapae Canyon; 18°50.868'S, 159°48.041'W; 20 m depth; coral rubble; 30.VI.2001; R. Wetzer & N. D. Pentcheff leg.; LACM-AHF 14777 (complete; regular longitudinal stripes, anterior surface of notopodial lobes darker, without black ring; body 61 mm long, 10 mm wide, 59 chaetigers).

French Polynesia • 1 specimen; Austral Islands, Rurutu, near the village; 22°28'48"S, 151°21'17"W; 5 m depth; sandy bottom next to reef, hard bottom outside lagoon; 10.VIII.1991; J. K. Lowry & J. M. Poupin leg.; AM 35512 (body twisted, without posterior end; longitudinal stripes visible, some anastomosing, better retained along a few anterior segments; caruncle pale, 1/6–1/5 as wide as anterior end, with 8 lateral foliose lobes; a few noto- and neurochaetae removed from chaetigers 9 and 25; harpoon notochaetae present; neurochaetae with tip blunt, slightly falcate, emerging from a short basal hood; margin denticulate with about 10 subdistal denticles; body 135 mm long, 17 mm wide, 83 chaetigers) • 1 specimen; Society Islands; Moorea, Vai'are Pass, north side; Sta. BIZ 713; 17°31.338'S, 149°45.7308'W; 20 m depth; 10.XII.2010; J. Moore leg.; MAGNT 29885 (juvenile, twisted; longitudinal stripes of similar width along body; notopodia without black ring; branchiae blackish with tips pale; caruncle with five lateral foliose lobes, all with brownish venation; median antenna bent laterally, 1/4 as long as caruncle, slightly longer than palps and lateral antennae; eyes not protruded from prostomial margin, anterior eyes almost 2 × as large as posterior ones; pygidium with anus terminal, anal plate slightly notched; body 12 mm long, 3 mm wide, 32 chaetigers) • 1 specimen; Society Islands, Moorea; barrier reef between Cook's and Opunohu Bays; 17°28'37"N, 149°49'50"W; 0–2 m depth; fore reef, under rocks; VII.2006, K. McKeon & G. Paulay leg.; UF 523 (complete, some parapodia removed for molecular studies; dorsal longitudinal stripes of similar width, some branching; notopodia with anterior surfaces dark, without distal rings; anterior eyes two times as large as posterior ones, not protruded; caruncle with median ridge complete, with 6–7 pairs of lateral smooth lobes, with venation; median antenna 1/2 as long as caruncle; pygidium with anus terminal, anal plate truncate, margin entire; 77 mm long, 8 mm wide, 60 chaetigers) • 1 specimen; Society Islands, Moorea; Price's settling plates, CTD1; 17°28'28"S, 149°48'46"W; ex Nicole, no depth or date data; N. Price leg.; UF 545 (without posterior end, removed for molecular studies; dorsal longitudinal stripes of similar width, a few branching; notopodia with anterior surfaces darker, without distal rings; anterior eyes three times as large as posterior ones, not protruded; caruncle with median ridge complete, with 6–7 pairs of lateral crenulate lobes, with venation; median antenna erect, as long as caruncle; 48 mm long, 4 mm wide, 46 chaetigers) • 1 specimen; Society Islands, Moorea; lagoon pinnacle, south of Afareaitu; 17°33'50"S, 149°47'21"W; 15–18 m depth; silty patch reef with overhangs; 12.XI.2009; S. McPherson leg.; UF 1330 (juvenile, complete; without longitudinal stripes; anterior stomach greenish; notopodia with anterior surfaces black, without distal rings; anterior and posterior eyes of similar size, not protruded; caruncle with median ridge complete, with two pairs of lateral smooth lobes, without venation; lateral antennae and palps biarticulate, ceratophores and ceratostyles, and palpo-phores and palpostyles of similar size; median antenna directed forward, 1/2 as long as caruncle; branchiae single filaments along chaetigers 1–2, other segments without branchiae; pygidium with anus terminal, anal plate truncate, notched; 9.4 mm long, 0.8 mm wide, 9 chaetigers, last segment achaetous) • 1 specimen; Society Islands, Moorea; in front of Hilton; 17°28'37"S, 149°50'41"W; 13–24 m depth; fore reef, rubble; 8.XII.2009; K. White, W. El-Tourky & J. Thomas leg.; UF 1434 (juvenile, complete, some parapodia removed for molecular studies; dorsal longitudinal stripes of similar width, not branching; notopodia with anterior surfaces darker, without distal rings; anterior and posterior eyes of similar size, not protruded; caruncle with median ridge complete, with 4–5 pairs of lateral smooth lobes, with venation; median antenna 1/4 as long as caruncle; pygidium with anus terminal, anal plate truncate, notched; 13 mm long, 3 mm wide, 27 chaetigers) • 1 specimen; Society Islands, Moorea, off NW Motus; 17°29'2"S, 149°54'59"W; 19–20 m depth; outer reef, under rocks; 3.XI.2009; G. Paulay, S. McKeon & T. Lotufo leg.; UF 1269 (small juvenile, cut in two fragments, a few segments removed for molecular stud-

ies; dorsal longitudinal stripes of similar width, none branched; integument not maculate; notopodia with anterior surfaces blackish, without distal rings; anterior eyes slightly larger than posterior ones, not protruded; caruncle with median ridge complete, 3–4 pairs of smooth lobes, with minimal venation; branchiae few, single filaments throughout body; pygidium fleshy, tubular, anus terminal, anal plate barely developed; 3 + 2 mm long, 2 mm wide, 9 + 7 chaetigers) • 1 specimen; Society Islands, Moorea; between Opunohu Bay and Motus; 17°28'56"S, 149°53'27"W; 18–22 m depth; outer reef, rubble; 3.XI.2010; J. Moore leg.; UF 2125 (without posterior region; bent in three; dorsal longitudinal stripes of similar width, a few branched; caruncle, dorsum, interramal belt and venter maculate; notopodia without distal black rings; anterior eyes three times as large as posterior ones, not protruded; caruncle with median ridge complete, 6–7 pairs of smooth lobes; 27 mm long, 7 mm wide, 37 chaetigers) • 1 specimen; Society Islands, Moorea; between Opunohu Bay and Motus; 17°28'56"S, 149°53'27"W; 18–22 m; outer reef, rubble; 3.XI.2010; J. Moore leg.; UF 2312 (without posterior region; soft, colorless, dorsum and venter maculate; notopodia without distal black rings; prostomium broken, eyes indistinct; caruncle distorted, median ridge indistinct, four pairs of smooth lobes; 64 mm long, 7 mm wide, 58 chaetigers) • 1 specimen; Marquesas Islands; Nuku Hiva, Les 4 Grottes; 8°56'13"S, 140°7'14"W; 20–23 m depth; I.2012; J. Starmer leg.; UF 3804 (markedly contracted, anterior and posterior fragments; dorsal longitudinal stripes of similar width; notopodia with darker anterior surfaces, without distal black rings; anterior eyes barely visible, posterior eyes hidden after body contraction; caruncle with median ridge complete, 6–7 pairs of lateral smooth lobes, with venation; pygidium with anus terminal, anal plate truncate; 37 + 33 mm long, 10 mm wide, 36 + 30 chaetigers).

Pacific Panama • 1 specimen; Gulf of Chiriqui, Coiba National Park; off Isla Uva; 7°48'57"N, 81°45'36"E; coral reef; 13.III.2006; P. W. Glynn leg.; LACM-AHF 14778 (complete, regenerating posterior body half; regular longitudinal stripes, anterior surface of notopodia darker, without black ring; body 43 mm long, 8 mm wide, 48 chaetigers) • 4 specimens; Taboga; S. Y. St. George Expedition, 1923–1924; from colony of *Pocillopora*; C. Crossland leg.; NHML 1932.12.24.271–275 (none complete, two with posterior end in regeneration; longitudinal stripes better retained in largest specimen; all with notopodia with black rings; two with duplicate parapodia between chaetigers 10/11; median antenna 2/3–4/5 as long as caruncle; caruncle with 7–8 pairs of lateral lobes; body 40–53 mm long, 5–10 mm wide, 39–42 chaetigers).

DISTRIBUTION. — East Africa to West America, in shallow water, coral or rocky bottoms.

DESCRIPTION OF TYPE SPECIMENS

Holotype of *Hermodice striata* (SMNH 6080) consisting of an anterior fragment and two dissected chaetigers, both compressed by labels and partially dehydrated; anterior fragment 8 mm long, 5.5 mm wide, six chaetigers (Fig. 4A). Anterior end damaged, median antenna without tip, lateral antennae complete, left palp complete, right palp broken; caruncle eroded or removed (Fig. 4B); first two chaetigers with notochaetae longer than dorsal cirri. Dissected segments depressed, one notopodium separate from remains, with dorsal cirrophore about as long as cirrostyle, notochaetae abundant, longer than dorsal cirrus, mostly capillaries and shorter harpoon-chaetae (Fig. 4C, inset); branchiae with approximately 10 filaments. Following details after original illustration: Dorsum with homogeneous longitudinal stripes (Fig. 4D). Median antenna slightly longer than laterals or palps, 1/3 as long as caruncle; caruncle with five pairs of lateral lobes (Fig. 4E). Eyes black,



FIG. 5. – *Pherecardia striata* (Kinberg, 1857), restricted, holotype of *P. lobata* Horst, 1886, RMNH VER.1295: **A**, anterior region, dorsal view; **B**, same, anterior end, dorsal view; **C**, chaetiger 8, neurochaetae. Scale bars: A, 1.5 mm; B, 0.5 mm; C, 30 µm.

of similar size (Fig. 4F). Mouth between chaetigers 2 and 3 (Fig. 4G). Dorsal cirri longer than ventral cirri (Fig. 4H), branchiae arborescent, shorter than dorsal cirri. Notochaetae including harpoon chaetae (Fig. 4I); neurochaetae including smooth capillaries (Fig. 4J), and acicular neurochaetae, tips entire, slightly bent (Fig. 4K).

Holotype of *Pherecardia lobata* (RMNH VER.1295) complete, anterior end damaged from compression in container, dissections, and pinning for illustrations; posterior region bent ventrally, last six chaetigers partially detached. Dorsum brownish, longitudinal stripes faded, with regular, longitudinal thin furrows along each segment (Fig. 5A); venter brownish with a longitudinal midventral blackish thin line. Dorsal and ventral cirri and branchiae markedly contracted. Many notochaetae broken. Body 87 mm long, 9 mm wide, 66 chaetigers.

Prostomium bent dorsally, ovoid, approximately as long as wide, anterior margin and longitudinal lip broken, mouth ventrally restricted to first chaetiger. Lateral antennae short, right one without tip, palps lost (Fig. 5B). Median antenna with ceratophore partially surrounded by base of caruncle median ridge, ceratostyle lost. Eyes black, of similar size, not protruded from prostomial margins. Mouth opens between chaetigers 2 to 4.

Caruncle pale, reaching chaetiger 3, 1/4 as wide as anterior end; median ridge transversely sliced previously, cut extended throughout caruncle length, with 6–7 lateral foliose lobes, some cut off, blades pinnate.

Parapodia not dissected to avoid further damage, all segments with arborescent branchiae with many filaments as long as dorsal cirrophores. Notopodia cylindrical with dorsal cirrophores twice as wide and 2/3 as long as cirrostyles; notochaetae surrounding dorsal cirrophores, abundant, soft. Neuropodial lobes subcylindrical, neurochaetae arise from middle. Ventral cirri with cirrophore short, subcylindrical,

as long as wide, cirrostyle 3–4 times longer than cirrophores. Neurochaetae with distinct distal tooth, subdistal denticles eroded, barely visible in smaller neurochaetae (Fig. 5C).

Posterior region tapered; anus terminal, broken; anal plate indistinct.

Holotype of *Hermodice pennata* Treadwell, 1906 (USNM 5209) including two fragments, without pigmentation pattern; anterior fragment 11 mm long, 6 mm wide, 15 chaetigers, and median fragment 9 mm long, 9 mm wide, 10 chaetigers.

VARIATION

Other specimens of *P. striata* exhibit interesting modifications in ocular and caruncle development. Eyes are protruded from the prostomial surface in most specimens, but not in all of them and this is not a size-related modification (Fig. 6A–D). The caruncle may be modified due to the loss of the median ridge such that the lateral lobes become distorted, and symmetry is difficult to assess (Fig. 6E, F), yet pinnate development remains visible.

The caruncle lobes are smooth with venation barely protruded [28 mm specimen, Fig. 6A, B], but caruncle lobes are rugose due to venation from transverse low projections on each lobe, resulting in a pinnate appearance, especially in larger specimens (Fig. 6C, D).

The number of longitudinal stripes decreases with size in preserved specimens, being more abundant and thinner in smaller specimens (Fig. 7A). They remain of similar width and length in each segment in larger specimens (Fig. 7D), although the branching of each stripe tends to be reduced in larger individuals. The prostomium is difficult to observe due to contraction of the anterior end, especially in the smaller specimen. The caruncle has a distinct median ridge with an expanded, roughly heart-shaped anterior region, but the lateral foliose lobes become more developed with maturity; small

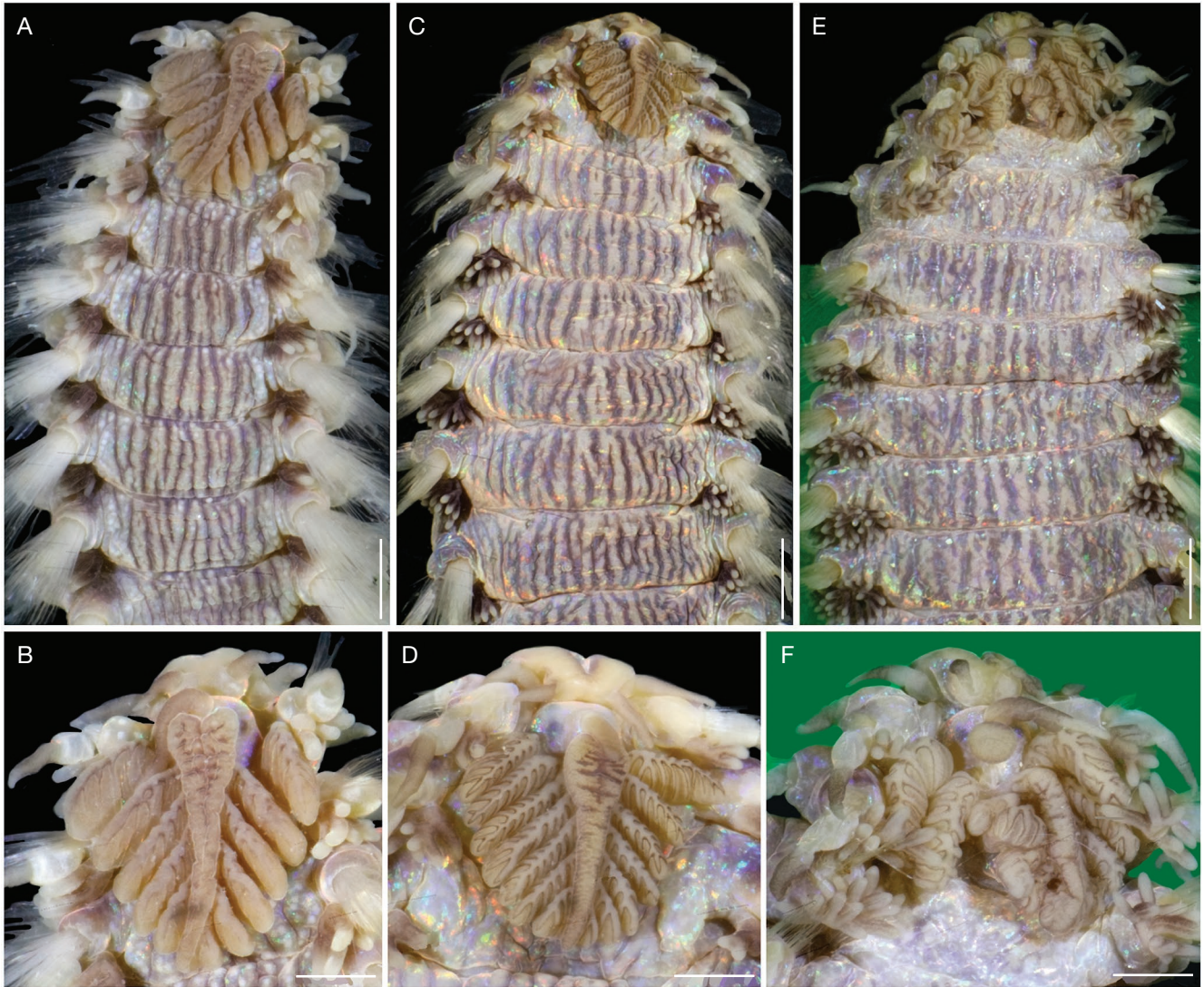


FIG. 6. — *Pherecardia striata* (Kinberg, 1857), restricted, non-type specimens, ZMH PE29: **A**, smaller specimen (28 mm long), anterior region, dorsal view; **B**, same, caruncle, dorsal view; **C**, larger specimen (75 mm long), anterior region, dorsal view; **D**, same, caruncle; **E**, large, anomalous specimen (71 mm long), anterior region, dorsal view; **F**, same, caruncle. Scale bars: A, 0.6 mm; B, 0.4 mm; C, E, 1.2 mm; D, 0.5 mm; F, 0.9 mm.

specimens have fewer and almost smooth lobes (Fig. 7C), whereas larger specimens have more lobes and each is pinnate (Fig. 7F). Along the body, there is a lateral longitudinal rugose belt, usually paler than in adjacent parapodial areas (Fig. 7B, E), which becomes mottled in larger specimens. Branchiae are abundant with reddish filaments and pale tips; in larger specimens the paler area is relatively smaller than observed in small specimens. Notopodia are protruded muscular cylinders, slightly darker in their anterior aspects than in adjacent areas (Fig. 7G), and notochaetae are very abundant and surround the dorsal cirri, with dorsal cirri having cirrophores about as long as, or up to twice longer than cirrostyles; whereas the neuropodia are lobate with chaetae emerging above the ventral cirri (Fig. 7G). Staining with Methyl green pigment failed to reveal a glandular role for the maculate interrampal belt (Fig. 7H). A cross section of this area reveals a thick furrowed integument and mel-

anophores concentrated mostly in furrows, with the paler spots corresponding to non-acidic glands (Fig. 7I). Neurochaetae include denticulate capillaries and aciculars with a small distal tooth, and often a series of subdistal denticles which are better defined in upper than in lower chaetae of the same chaetiger (Fig. 7J).

REMARKS

Hartman (1948: 46) indicated the holotype of *Hermodice striata* Kinberg, 1857 was an anterior fragment 8 mm long with seven segments, with branchiae from chaetiger 1, each with five filaments, and mouth in chaetiger 3. We observed some minor differences between her description and the type, but its condition is rather precarious, such that manipulation was kept as minimal as possible.

De Quatrefages (1866) introduced *Amphinome formosa* for a specimen collected in Hawaii (Sandwich Islands) that was



FIG. 7. — *Pherecardia striata* (Kinberg, 1857) restricted, COI-sequenced non-type specimens: **A**, 6 mm wide specimen, UF 5438, anterior region, dorsal view; **B**, same, left lateral view; **C**, same, anterior end, dorsal view; **D**, 8 mm wide specimen, UF 5461, anterior region, dorsal view; **E**, same, right lateral view; **F**, same, anterior end, dorsal view; **G**, same, chaetiger 8, left parapodium, anterior view (IB: interramal belt); **H**, same, after Methyl green staining (asterisks indicate dissected section); **I**, cross section of interramal band, pigment concentrated in furrows; **J**, same, upper and lower neurochaetae. Scale bars: A, 1.5 mm; B, 1 mm; C, 0.6 mm; D, 2 mm; E, 0.9 mm; F, 0.7 mm; G, 0.5 mm; H, 0.4 mm; I, 0.1 mm; J, 30 μ m.

65 mm long, 7 mm wide, and 90 segments. The caruncle was described as ‘very developed, reaching segment 4. Its shape is oval, with 7–8 foliose lobes fused medially by a ridge with a free margin.’ These features match *Pherecardia*; however, because there is no type specimen the status of the species cannot be determined (see below).

Horst (1886) proposed *Pherecardia*, with *P. lobata* as its type species, based on a damaged specimen with most of its pigmentation faded away, but he noted that it was ‘marked on its dorsal side with faint longitudinal folds’ which may have corresponded with longitudinal stripes. Details of the prostomium were not provided because it was damaged.

Fischli (1903) described *Amphinome sericata* in detail with several illustrations, and although prostomial details were not given, the color plates portray the dorsum with rather regular longitudinal stripes of similar width, and this explains why Horst (1911) may have synonymized it with *P. striata*. Fischli lived in Linthal, Switzerland, but whether his type specimens are extant and if so where they are located, could not be clarified. Inquiries to nearby natural history museums about potential types were not answered.

Treadwell (1906) proposed *Hermodice pennata* based on a 15-segment anterior fragment collected in Hawaii. He indicated that pigmentation included numerous longitudinal stripes extending across segments, and that the eyes were 'prominent on dorsal view', and his illustration shows them not protruded from the prostomial margin. The caruncle was described and illustrated as having seven smooth lobes per side. The holotype is in two fragments. The caruncle is as illustrated and while the pigmentation is now gone it is indicated in the original description. Based on examination of the type and Treadwell's description we confirm that this species is a synonym of *P. striata*, as proposed by Augener (1927).

Malaquin & Dehorne (1907) proposed *Eucarunculata* with *E. grubei* as its type species without citing any of the previous literature on the above species. They indicated that anterior eyes were slightly larger than posterior ones, and that the animal had 10-15 'dark longitudinal stripes running from segment to segment along the whole body.' Their illustrations show the anterior end with longitudinal stripes of similar width. Horst (1909) indicated that *E. grubei* was a junior synonym of his *P. lobata*. We did not locate the type of *E. grubei*. Based on the description and illustration we agree with Horst that *E. grubei* is a synonym of *P. striata*.

Potts (1909) proposed two varieties for *E. grubei* based on two smaller specimens: *E. g.* var. *gracilis* and *E. g.* var. *minuta*, both with regular longitudinal stripes, but no type specimens were deposited. He noted in a footnote (page 365) that 'the differences in form of caruncle and chaetae are probably due to varying age.' His specimens have not been located, and it is likely that they were not deposited in a museum. The typical form in his treatment included a specimen 104 mm long, 7 mm wide, and with 73 segments; its caruncle had 6-7 lateral lobes, notochaetae included smooth capillaries and non-spurred harpoon chaetae, neurochaetae were distally falcate, either with subdistal denticles or smooth. His variety *gracilis* included one specimen 24 mm long, and 4 mm wide with 41 segments, with 5-6 lateral lobes in the caruncle, and the neurochaetae had 'more distinct and numerous serrations' than in the typical form. His variety *minuta* was based on a specimen 16 mm long, 2 mm wide, and with 34 segments. He noted that neurochaetae had distinct, variable serrations. Hartman (1959: 133) regarded both as junior synonyms of *Pherecardia lobata*. We agree with her conclusions.

Differences between *Pherecardia striata* and *P. distincta*, are mostly in pigmentation pattern, as indicated in the key

above. In *P. striata* the longitudinal stripes are more or less regular, having similar width and length, and the notopodia have a darker pigmentation along anterior surface than on posterior one, whereas in *P. distincta* the longitudinal stripes are irregular, of different width and length, and the notopodia have a blackish ring. Further, these two species are separated by 22.4-23.5 % K2P distance in COI (Fig. 8). Intraspecific variation between the two sequenced species is 0.3-2% in *P. striata*, and 1.2% in *P. distincta*. The records by Amoureux (1977: 1095) and Rajasekaran & Fernando (2012: 3) could not be confirmed.

Pherecardia distincta (Hoagland, 1920) reinst., n. comb.
(Figs 1C-E; 2C, D; 8-14)

Hermodice distincta Hoagland, 1920: 612, pl. 48, figs 13-15.

Hermodice pennata var. *tutuilensis* Treadwell, 1926: 2.

Pherecardia striata – Fauvel 1935: 292 (*partim*). — Hartman 1940: 207 (*partim*). — Pillai 1965: 121, fig. 4F-H (*non* (Kinberg, 1857)).

Pherecardia polylamellata de Silva, 1961: 170, fig. 4.

DIAGNOSIS. — *Pherecardia* with longitudinal stripes of variable width and length along dorsal surfaces of body. Notopodia with a black distal ring. Notochaetae moderately abundant, shorter than dorsal cirri along anterior chaetigers.

TYPE MATERIAL. — **Holotype of *Hermodice distincta* Hoagland, 1920. Philippines** • 1 specimen; Mindanao Island, Misamis Oriental, Macajalar Bay, Suluan Point, Opol; USFS Albatross; unnumbered station; 2-4 m depth; after dynamite explosion (original label indicates "EL", and identification label indicates "Electric Light"), 4.VIII.1909; USNM 18953.

Paratype of *Pherecardia polylamellata* de Silva, 1961. Sri Lanka, Gulf of Manaar • 1 specimen; ; Ceylon Pearl Banks; no further data; NHML 1962.14.1.

ADDITIONAL MATERIAL. — **Madagascar** • 1 specimen; Nossy Vorona, off ENE side; 13°25'27"S, 48°21'15"E; 4 m depth; broken reef, extracted from large, dead *Porites*; 15.V.2008; A. Anker, G. Bakary, E. Boissin, H. Bruggemann, T. Horeau, F. Michonneau, G. Paulay & T. Werner leg.; UF 749 (complete; dorsal longitudinal stripes irregular, often branching, thinner towards notopodia; some parapodial areas and branchiae maculate; anterior and posterior eyes of similar size, not protruded; caruncle with median ridge complete, with 6-7 pairs of lateral smooth lobes, with venation; notopodia with distal black rings; pygidium with anus prolapsed, anal plate semicircular, slightly notched; 150 mm long, 20 mm wide, 74 chaetigers) • 1 specimen; Nossy Vorona, off ENE side; 13°25'27"S, 48°21'15"E; 4 m depth; broken reef, extracted from large, dead *Porites*; 15.V.2008; A. Anker, G. Bakary, E. Boissin, H. Bruggemann, T. Horeau, F. Michonneau, G. Paulay & T. Werner leg.; UF 751 (complete; dorsal longitudinal stripes irregular, often branching, thinner towards notopodia; some parapodial areas and branchiae maculate; anterior and posterior eyes of similar size, not protruded; caruncle with median ridge complete, with seven pairs of lateral smooth lobes, with venation; notopodia with distal black rings; pygidium slightly damaged, anus prolapsed, anal plate globose, margin entire; 90 mm long, 14 mm wide, 55 chaetigers). **Mascarene Islands, La Réunion** • 1 specimen; Saint Leu, Maison Verte, Cimetière; 21°11'36"S, 55°16'56"E; 8-9 m depth; fore reef,

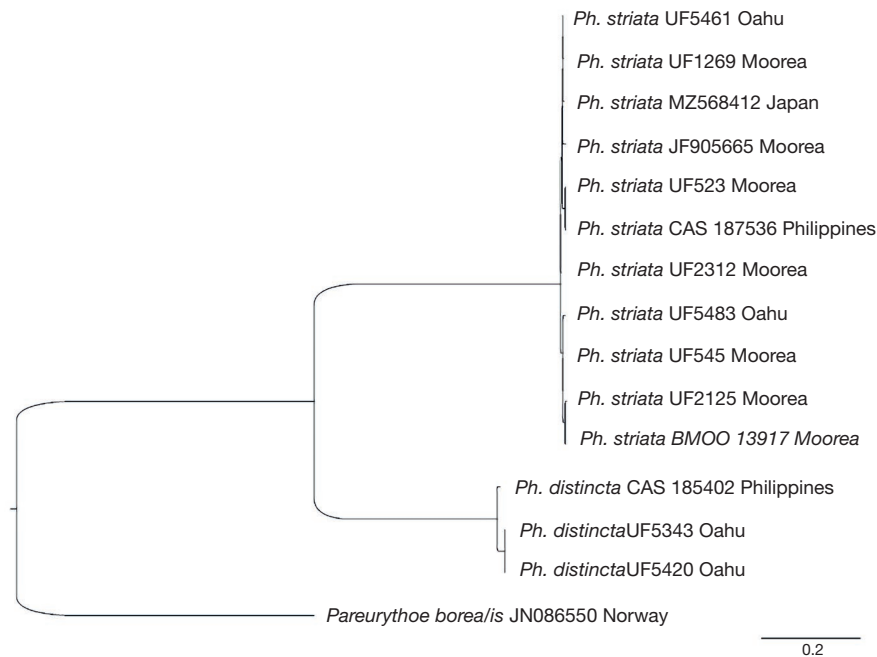


Fig. 8. — Maximum likelihood tree of *Pherecardia* Horst, 1886 based on COI sequence data; both species have 100% bootstrap support.

within dead digitate *Acropora*; 13.VIII.2007; H. Bruggemann, N. Hubert, F. Michonneau & G. Paulay leg.; UF 655 (anterior fragment; dorsal longitudinal stripes irregular, dorsal ones wider, thinner towards notopodia; not maculate; anterior eyes three times as large as posterior ones, slightly protruded; caruncle with median ridge complete, with seven pairs of lateral pinnate lobes; notopodia with distal black rings; 21 mm long, 5 mm wide, 28 chaetigers).

Gulf of Thailand • 1 specimen; Thailand, Chantabun; no further data; MNHN A431 (complete; dorsal longitudinal stripes irregular, especially from chaetiger 12 where some stripes become wider than others; venter with midventral thin bluish line; caruncle with 10 pairs of crenulated lobes; median antenna 1/3 as long as caruncle, slightly larger than lateral antennae and palps; eyes large, protruded from prostomial margin; anus terminal, anal plate medially notched; body 103 mm long, 15 mm wide, 82 chaetigers).

Vietnam • 1 specimen; Nha-trang; no further data; MNHN A398 (body twisted, anterior end heavily contracted; dorsal stripes fading, especially thinnest ones; midventral line faded; caruncle with 10 pairs of lateral crenulate lobes; median antenna lost, upper lips separate lateral antennae; eyes protruded from prostomial margins; anus terminal, anal plate rounded, not notched; body 62 mm long, 15 mm wide, 74 chaetigers).

Indonesia • 1 specimen; Java; “Outer Islands Archipelago”; no further data; ZMA V.POL. 1071 (epitoke, progressively wider medially and posteriorly; dorsal stripes irregular; eyes protruded from prostomial margins; caruncle with 10-11 lateral rugose (pinnate) lobes; median antenna 4/5 as long as caruncle; some median and posterior intersegmental areas broken, exposing inner organs; venter with a blackish, discontinuous midventral line; posterior region in regeneration, pygidium damaged; body 116 mm long, 13 mm wide, 70 chaetigers) • 4 specimens; Java Bay, near Batavia, Eil Edam; 19.IX.1930; Museum Buitenzorg, J. Versvey leg.; ZMH V12095 (soft, apparently spent epitokes based on the amount of foreign material accumulated on chaetae; longitudinal stripes irregular, with variable width and length, wider mid-dorsally, thinner marginally; stripes visible ventrally along a few chaetigers; eyes protruded from prostomial margins; caruncle with 8-10 pairs of lateral foliose, pinnate lobes; caruncle

median ridge base and ridge areolated; median antenna 1/2-2/3 as long as caruncle, slightly longer to twice longer than lateral antennae and palps, both of similar shape and length; body 28-50 mm long, 8-12 mm wide, 45-46 chaetigers • 3 specimens; Poeloe (Pulau) Weh; 1902; G.A.Y. van den Samde leg.; no further data; RMNH VER.1297 (twisted, two without posterior region; two females, ovigerous, one male epitoke; dorsum with purple to blackish longitudinal, rather regular stripes; eyes large, very close to each other on each side, not protruded from prostomial margins; notopodia with distal black rings; male epitoke with caruncle median ridge rugose, with 12-13 lateral foliose lobes; base of median ridge and supraocular areas between posterior eyes with low lobes; females with caruncle median ridge smooth, without additional lobes between posterior eyes; parapodia with many chaetae, capillaries not abundant; female epitoke without pygidium, with egg-sac extruded from last chaetiger; 75 mm long, 17 mm wide, 77 chaetigers; male epitoke; pygidium tapered, anus terminal, anal plate rounded; 108 mm long, 13 mm wide, 96 chaetigers).

Philippines • 1 specimen; Lubang Islands, Bahura Reef, N of Lubang Island; Sta. LB-003; 13.0°51.0'53.3"N, 120.0°11.0'31.6"E; 0-5 m depth; 6.IX.2011; B. Moore leg.; CASIZ 185402 (complete; dorsal longitudinal stripes irregular, often branching; notopodia with distal black ring; anterior eyes two times as large as posterior ones, not protruded; caruncle with median ridge complete, with 7-8 lateral pinnate lobes; pygidium with anus prolapsed, anal plate truncate, entire; 86 mm long, 9 mm wide, 71 chaetigers).

Mariana Islands • 1 specimen; Guam; right side of Cocos Island; no depth data; rubble; 23.IV.1999; G. Paulay leg.; UF 22 (complete, regenerating posterior segments; pharynx fully exposed; dorsal longitudinal stripes of differing width along segments, lateral stripes thinner; integument without maculae; notopodia with distal blackish rings, better defined along anterior segments; anterior eyes slightly larger than posterior eyes, barely protruded from prostomial margins; caruncle pale, with median ridge complete, with 11 pairs of lateral pinnate lobes; median antenna without tip, half as long as caruncle; pygidium with anus terminal, anal plate indistinct; 112 mm long, 20 mm wide, 74 chaetigers).

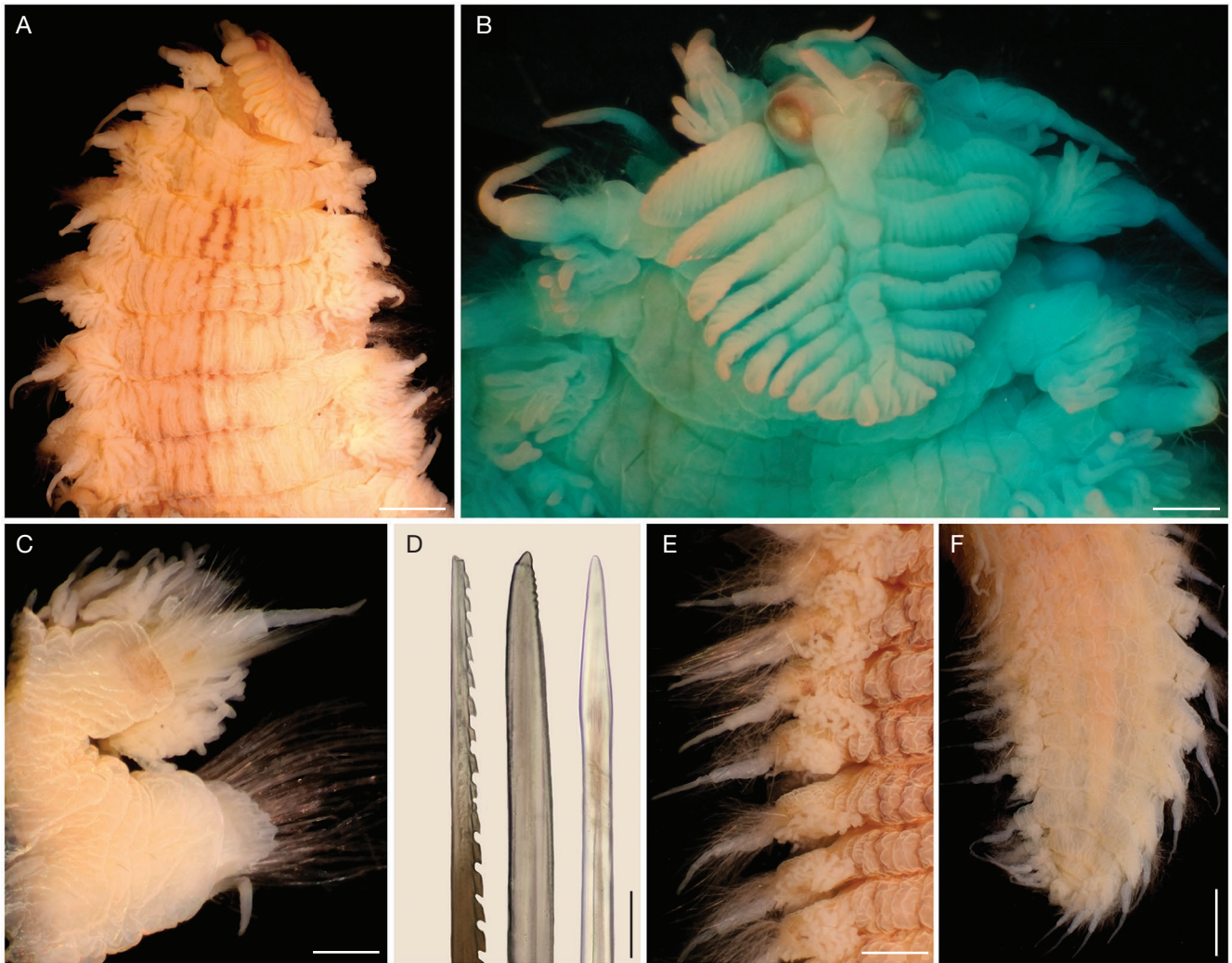


FIG. 9. — *Pherecardia distincta* (Hoagland, 1919) n. comb., holotype, USNM 18953: **A**, anterior region, dorsal view (anterior end bent ventrally); **B**, anterior end, dorsal view, after Methyl green staining; **C**, chaetiger 20, left parapodium, anterior view; **D**, same, harpoon-notochaetae, neurochaetae, neuracacula; **E**, chaetigers 68–74, dorsum and left parapodia, seen from above, showing remaining pigmentation; **F**, posterior region, dorsal view. Scale bars: A, 1.8 mm; B, 0.5 mm; C, 0.6 mm; D, 80 μ m; E, 1.9 mm.

Hawaii • 1 specimen; Oahu, Kaneohe Bay, NW end of Ahu'olaki Island; the Sand Bar; 21°28'26"N, 157°49'11"W; 0–2 m depth; 22.V.2017; Bioblitz team leg.; UF 5343 (without pygidium, regenerating posterior end, cut into two sections, left parapodium of chaetiger 8 removed for study; longitudinal brown stripes irregular, some wide, others narrow; notopodia with distal brown ring; anterior eyes larger than posterior eyes, protruded from prostomial margin; caruncle whitish, venation barely darker, with 12–14 pinnate lateral lobes, median ridge discontinuous; median antennae 2/3 as long as caruncle; anterior fragment 20 mm long, 16 mm wide, 13–14 chaetigers; posterior fragment 41 mm long, 15 mm wide, 28 chaetigers) • 1 specimen; Oahu, Kaneohe Bay; 21°30'0"N, 157°48'0"W; 0–20 m depth; 21.V.2017; Bioblitz team leg.; UF 5420 (anterior fragment, markedly contracted, bent ventrally; dorsal longitudinal stripes irregular, alternating wide and narrow, thinner stripes towards parapodia; notopodia with distal brown rings; anterior eyes larger, with lenses, not protruded from prostomial margin; caruncle whitish, without median ridge, with 7–8 lateral lobes per side; median antennae without tip, half as long as caruncle; fragment 32 mm long, 12 mm wide, 39 chaetigers).

New Caledonia • 1 specimen; Mathew Island, Northwest side; 22°20'29"S, 171°21'1"E; boulders and large rocks on black sand; 5 m; 1.VIII.2017; S. Hannam, A. Reid, C. Bedford, & I. Middleton leg.; AM 51661 (juvenile, distorted due to label compression; longitudinal anastomosing stripes dorsally, ventrally visible along a few anterior chaetigers; caruncle grayish, with thin anastomosing stripes, 2/3 as wide as anterior end, with four lateral foliose, rugose lobes; median antenna 1/5 as long as caruncle; chaetae not removed to avoid further damage; body 13.5 mm long, 1.5 mm wide, 31 chaetigers).

French Polynesia • 3 specimens; Society Islands, Tahiti, Papeete Harbour; swimming at night; Crossland Pacific Expedition 1923–24; V.1923; B. Grey leg.; NHML 1941.4.4.146–152 (epitokes, twisted, without posterior region, gametes and debris adhered, stained pink the formalin solution (“formol in which they were preserved pink; under lens this seen to be eggs and sperm” as indicated by Monro 1939: 167); dark purple longitudinal stripes, becoming more irregular medially and posteriorly, visible ventrally; eyes not protruded from prostomial margin; caruncle grayish (pale green after Crossland), contracted, with 11–12 lateral foliose lobes; caruncle median ridge with base smooth; median antennae 1/4

as long as caruncle; eyes larger than in non-epitokous specimens, of similar size; one parapodium of each specimen removed for comparing cirri development; notopodial lobes blackish, dorsal cirrophores 3 times wider and about as long as cirrostyles; body 54–165 mm long, 13–20 mm wide, 52–73 chaetigers) • 5 specimens; Society Islands, Tahiti, Crossland Pacific Expedition, 1923–24; C. Crossland leg.; no further data; NHML 1941.4.4.153–157 (3 complete, 2 without posterior end; longitudinal brownish stripes along dorsum, less regular posteriorly or ventrally; notopodial lobes blackish; caruncle with fine stripes along ridges of lateral lobes, with 8 lateral foliose lobes; median antenna 3/4 to 4/5 as long as caruncle; posterior end tapered, anus terminal, anal plate short; body 56–76 mm long, 3.5–6.0 mm wide, 53–54 chaetigers). **Panama** • 8 specimens; Coiba National Park, Isla Coibita, North of Smithsonian beach house, small islet connected by causeway; 07°38.036'N, 81°41.847'W; subtidal, dead *Pocillopora*; 16.III.2005; L. Harris & I. Wehrmann leg.; LACM-AHF 14779 (complete specimens, some regenerating anterior or posterior ends; irregular longitudinal stripes dorsally and black rings in notopodia; median antenna as long as caruncle in smallest and largest specimens; body 22–78 mm long, 4–9 mm wide, 34–61 chaetigers) • 2 specimens; Taboga Island, Taboga Channel; with an associated polycladid flatworm, 19.II.2007; A. Anker leg.; LACM-AHF 14780 (irregular longitudinal stripes dorsally and black rings in notopodia; largest one regenerating posterior region; body 30–57 mm long, 7–12 mm wide, 40–45 chaetigers) • 2 specimens; Secas Islands; RV *Velero III*; Sta. 454; 07°57'10"N, 82°00'45"W; shore, tide flats, coral; 6.II.1935; LACM-AHF 14781 (complete specimens; irregular longitudinal stripes and black rings in notopodia; median antenna 1/2–3/4 as long as caruncle; caruncle with eight pairs of lateral lobes; body 45–72 mm long, 7–10 mm wide, 47–52 chaetigers) • 1 specimen; Gulf of Chiriqui, Coiba National Park, Isla Coibita, SE of Smithsonian beach house; causeway connecting third island; 7°41'38"N, 81°48'28"E; in dead *Pocillopora*; 16.III.2005; L. Harris & I. Wehrmann leg.; LACM-AHF 14782 (fragmented in two pieces, anterior end in regeneration; irregular longitudinal stripes, notopodia with black ring; not measured) • 7 specimens; Secas Islands; Panamá; RV *Velero III*; Sta. 447; 07°57'10"N, 82°00'45"W; shallow water, coral; 4.II.1935; LACM-AHF 14783 (complete, some regeneration anterior or posterior regions, with little or no pigmentation, some specimens with asymmetrical caruncles; irregular longitudinal stripes dorsally and black rings around notopodia; body 26–92 mm long, 5–11 mm wide, 30–66 chaetigers) • 2 specimens; Gulf of Chiriqui; Uva Island; Canteras Islands; 3 m depth; feeding on *Acanthaster*; 22.VI.1978; P. W. Glynn leg.; LACM-AHF 14784 (complete, heavily contracted, bent ventrally; irregular longitudinal stripes, and black ring around notopodia; body 45–54 mm long, 10–12 mm wide, 42–48 chaetigers) • 3 specimens; Taboga; Dr Th. Mortensen's Pacific Expedition 1914–1916; shore at low tide; T. Mortensen leg.; NHM 1928.9.13.15–17 (complete specimens, regenerating posterior region; smallest one smashed medially; median antenna 1/4 to 1/3 as long as caruncle (tips lost); caruncle with 6–7 to 7–8 pairs of lateral lobes; pygidium with anus terminal, anal plate round or truncate (barely bifid); body 68–105 mm long, 8–10 mm wide, 51–61 chaetigers) • 2 specimens; Taboga; from colony of *Pocillopora*; S. Y. St. George Expedition 1923–1924; C. Crossland leg.; NHML 1932.12.24.269–270 (complete specimens; largest bent laterally; longitudinal stripes best preserved in largest specimen; median antenna 4/5 as long as caruncle; caruncle with 7–8 or 9–10 pairs of lateral lobes; pygidium with anus terminal, anal plate round; body 29–72 mm long, 5–9 mm wide, 37–55 chaetigers). **Colombia** • 4 specimens; Gorgona; S. Y. St. George Expedition 1923–1924; from coral; C. Crossland leg.; NHML 1932.12.24.265–268 (soft, without posterior end, two with duplicate parapodia at chaetigers 10/11, one with pharynx exposed; dorsal longitudinal stripes better preserved in largest specimen; median antenna nearly as long as caruncle; caruncle with 7–8 or 9–10 pairs of lateral lobes; body 31–70 mm long, 5–12 mm wide, 35–43 chaetigers).

OTHER MATERIAL. — **Maldives** • <https://www.inaturalist.org/observations/150011379> southern Maldives (approximately 2°1'52"N, 73°31'13"E), (longitudinal stripes brownish, irregular, vary in width and shape along dorsal segments; blackish ring in notopodia distinct).

DESCRIPTION OF TYPE SPECIMENS

Holotype of *Hermodice distincta* (USNM 18953) complete, anterior end damaged, with an anteroventral dissection, folded over in two posterior sections; right parapodia of chaetigers 6 and 14 previously removed (lost), left parapodium of chaetiger 20 removed for observation (retained in container). Dorsum with longitudinal stripes faded almost completely, wider stripes medially, thinner stripes lateral (Fig. 9A). Dorsal and ventral cirri exposed, tapered, pale. Many chaetae broken. Venter with one thin, almost complete black line. Body 132 mm long, 12 mm wide, 87 chaetigers.

Prostomium bent ventrally, ovoid, wider than long, anterior margin and longitudinal lips entire, ventrally restricted to chaetiger 1 (ventral dissection reaching its anterior margin). Lateral antennae and palps of similar length. Median antenna directed anteriorly, tip broken (Fig. 9B). Eyes black, of similar size, protruded from prostomial margins. Mouth opening between chaetigers 2–3(4), damaged after ventral dissection.

Caruncle pale, reaching chaetiger 3, 2/3 as wide as anterior end; median ridge cut along caruncle length, with 10 pairs of lateral foliose lobes, blades pinnate.

Parapodia biramous; notopodia cylindrical with distal black ring, including chaetae and dorsal cirri (Fig. 9C), barely visible dorsally (Fig. 9E) in markedly bent portions along posterior regions. Dorsal cirrophores about as long as cirrostyles throughout body. Branchiae arborescent, each with 3–4 short main stems, with abundant filaments, progressively reduced in number posteriorly. Notochaetae including harpoon-chaetae (Fig. 9D, left), and abundant smooth capillaries. Neuropodial lobes subcylindrical, neurochaetae arising directly from neurochaetal lobe. Ventral cirri with cirrophore 1/3 as long as cirrostyle in anterior and median chaetigers, 1/4 as long in posterior ones. Abundant capillary neurochaetae, acicular spines with slightly bent tips, some with tiny subdistal denticles (Fig. 9D, center); neuracillae subdistally swollen, tapered (Fig. 9D, right).

Posterior region tapered (Fig. 9F); anus terminal, anal plate minute, rounded.

Paratype of *P. polylamellata* (NHML 1962.14.1) complete, regenerating posterior region; body brownish with irregular, longitudinal stripes barely visible along anterior chaetigers (Fig. 10C); palps and dorsal cirrostyles blackish; thin darker line midventrally along body; first right parapodium, notopodia of chaetiger 13 and 28, and neuropodia of chaetiger 15 and 28 previously removed; right parapodium of chaetiger 25 removed for observation; body 195 mm long, 15 mm wide, 91 chaetigers.

Prostomium ovoid, wider than long; lateral antennae positioned on round projections, ceratostyles lost, ceratophores separated by dorsal longitudinal 'lip' projection reaching about half prostomial length (Fig. 10B, restricted to chaetiger 1 ven-

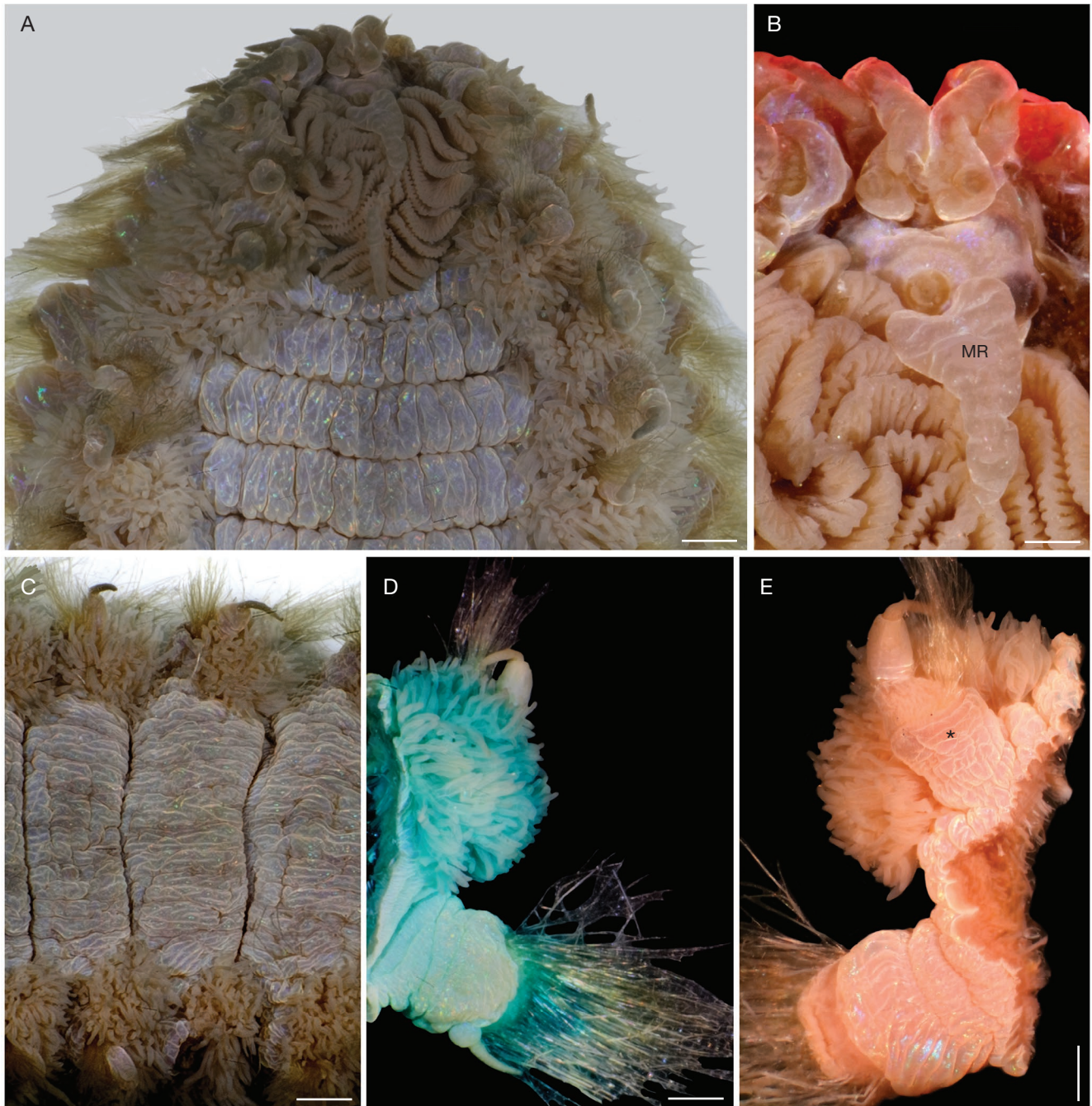


FIG. 10. — *Pherecardia distincta* (Hoagland, 1920) n. comb., paratype of *P. polylamellata* de Silva, 1961, NHML 1962.14.1: **A**, anterior region, dorsal view; **B**, anterior end, after Shirlastain-A staining (MR: median ridge); **C**, chaetigers 13–15, dorsal view; **D**, chaetiger 25, right parapodium, posterior view, after Methyl green staining; **E**, same, after Shirlastain-A, enlarged (*: slightly darker distal ring in dorsal base of cirrophore). Scale bars: A, 1 mm; B, 0.4 mm; C, 1.4 mm; D, 1.1 mm; E, 0.9 mm.

trally. Palps biarticulate, positioned in a constriction between the projection of dorsal lips. Median antenna lost. Eyes black, globular, anterior eyes slightly smaller than posterior ones, both protruded from prostomial margins. Mouth opening between chaetigers 2 and 4.

Caruncle pale, nearly reaching chaetiger 5, 1/3 as wide as anterior end; median ridge slightly damaged, extending throughout caruncle length (Fig. 10A), with 10–11 lateral foliose lobes, corrugated (pinnate).

Parapodia bearing arborescent branchiae with abundant filaments from chaetiger 1 to posterior segments, as long as dorsal cirrophores (Fig. 10C). Notopodia cylindrical with dorsal cirrophores 4–5 times wider and slightly shorter than cirrostyles, notochaetae rise from a protruded cone, surrounding dorsal cirrophores with dorsal cirri at apex of the cone (Fig. 10D); notopodia with a barely visible distal black ring (Fig. 10E). Neuropodial lobes subcylindrical, neurochaetae arising from between these lobes. Ventral cirri with

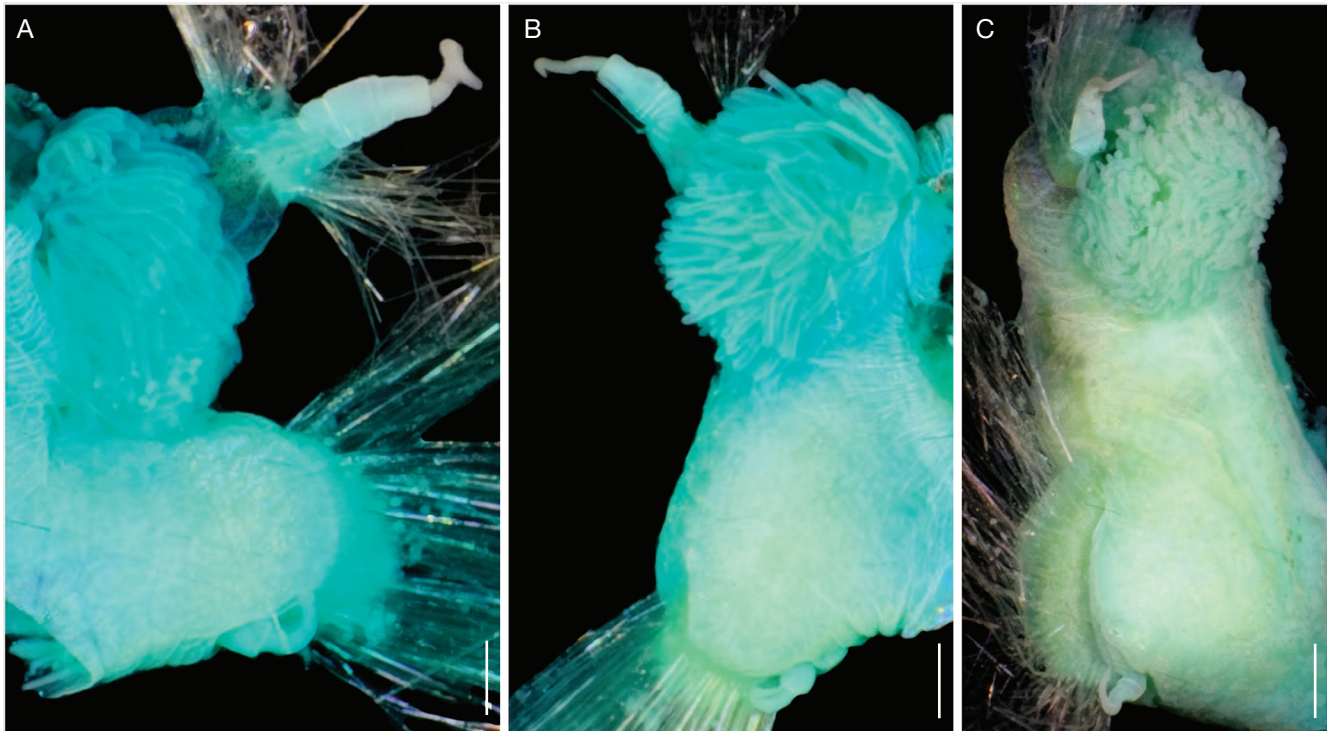


FIG. 11. — *Pherecardia distincta* (Hoagland, 1920), reinstated, non-type, epitokes, NHML 1941.4.4.146–152: **A**, epitoke 54 mm long, 13 mm wide, chaetiger 25, right parapodium, posterior view; **B**, epitoke 130 mm long, 18 mm wide, chaetiger 32, left parapodium, posterior view; **C**, epitoke 165 mm long, 20 mm wide, chaetiger 27, left parapodium, posterior view. Scale bars: A, 0.5 mm; B, 0.8 mm; C, 1 mm.

cirrophores globose, about twice wider than and 1/4–1/5 as long as cirrostyle.

Chaetae broken, damaged because of prolonged exposure to formalin (de Silva 1961: 171).

Posterior end tapered; anus dorsal, extended along last three chaetigers; anal plate round.

DESCRIPTION OF EPITOKES

Three epitokes (NHML 1941.4.4.146–152), showing little modifications for swimming along median chaetigers (Fig. 11); notopodia and neuropodia massive, with dorsal cirri slightly longer than ventral cirri, ceratophores and ceratostyles cylindrical; notopodia with black distal rings, visible once branchiae contract and expose the tips of notopodia (Fig. 11A) or if branchiae are displaced (Fig. 11B, C).

VARIATION

Specimens with well-preserved color pattern have wider longitudinal stripes along mid-dorsal region and thinner stripes laterally, together with distinctive black rings in the notopodia. This pattern is not size-dependent; the same characters are observed in small (Fig. 12A), medium (Fig. 12C), and large (Fig. 12E) specimens, and occur along the body, although longitudinal stripes become progressively thinner posteriorly, where they become of similar width along each segment; this pattern is shown in small (Fig. 12B), medium (Fig. 12D), and large specimens (Fig. 12F).

The caruncle has 8–10 foliose lobes, and small specimens exhibit distinctive venation along each lobe (Fig. 13B), with pigmented areas transitioning into furrows such that the regular rugosity results in a pinnate appearance to each lobe (Fig. 13B, E). Another variations are found in eye and caruncular development.

A small 28 mm long specimen (Fig. 13A) has dorsal longitudinal stripes of differing length and width along anterior segments. The prostomium has black eyes protruded from the prostomial surface (Fig. 13B), and despite its size the caruncle has nine pairs of lateral lobes. A larger, 50 mm long specimen has the same pattern of irregular dorsal longitudinal stripes (Fig. 13D), eyes more clearly protruded from the prostomial surface (Fig. 13E), and the caruncle has 11–12 pairs of lateral lobes. The posterior region in both specimens (Fig. 13C, F) share similar pigmentation patterns, with discontinuous longitudinal striping and thinner stripes near the parapodia, as shown in other specimens referred to above.

The number of longitudinal dorsal stripes decreases with body size, and stripes are thinner in smaller specimens (Fig. 14A), becoming wider and more irregular, and often stripes are narrower adjacent to parapodia (Fig. 14D); however, the unpigmented spaces between stripes are obviously narrower near parapodia in all cases figured (Figs 13D; 14D). The prostomium is more easily observed in the larger specimen with anterior eyes protruded from the prostomial surface. The caruncle has lateral pinnate lobes, but in the

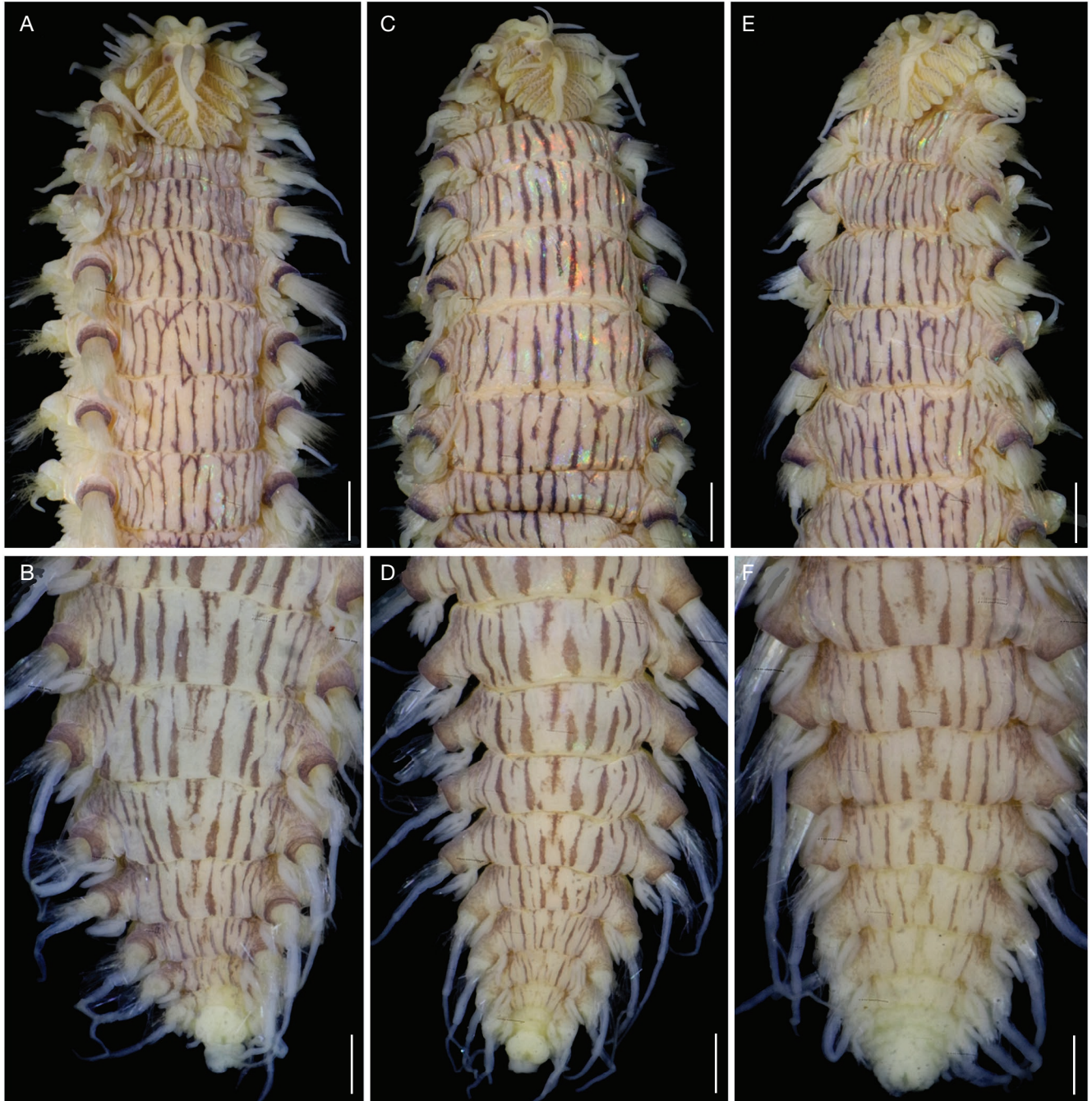


FIG. 12. — *Pherecardia distincta* (Hoagland, 1920), reinstated, non-type complete specimens, NHML 1941.4.4.153–157: **A**, specimen 56 mm long, 3.5 mm wide, anterior region, dorsal view; **B**, same, posterior region; **C**, specimen 62 mm long, 7 mm wide, posterior region, dorsal view; **D**, same, posterior region, dorsal view; **E**, specimen 76 mm long, 6 mm wide, anterior region, dorsal view; **F**, same, posterior region, dorsal view. Scale bars: A, 0.9 mm; B, F, 0.5 mm; C, 1 mm; D, 0.7 mm; E, 1.2 mm.

two specimens figured in Figure 14 the median ridge is not fully developed and is even missing in the smaller specimen, such that counting the lobes is problematic; there are about eight lobes in the smaller specimen (Fig. 14C), and about 14 in the larger one (Fig. 14F), in which the posterior median ridge is visible but the middle section is missing. The interrampal belt is indistinct (Fig. 14B, E), with this area smoother than in *P. striata*. Branchiae are abundant

and although they have paler tips, they are not as dark as in *P. striata*. Notopodia are protruded muscular cylinders, each with a distinct blackish distal ring (Fig. 14B, E). Notochaetae are abundant but shorter and less numerous than in *P. striata*, surrounding the dorsal cirri upon notopodial contraction, with dorsal cirri having dorsal cirrophores as long as the cirrostyles or up to twice longer. The interrampal belt is less plicate with no maculae (Fig. 14H, I) as indi-



FIG. 13. — *Pherecardia distincta* (Hoagland, 1920), non-type specimens, ZMH V12095: **A**, smallest specimen (28 mm long), anterior region, dorsal view; **B**, same, close-up of prostomium and caruncle; **C**, same, posterior region, dorsal view; **D**, largest specimen (50 mm long), anterior region, dorsal view; **E**, same, close-up of prostomium and caruncle; **F**, same, posterior region. Scale bars: A, 1.3 mm; B, 0.3 mm; C, 1.2 mm; D, 1.5 mm; E, 0.4 mm, F, 1.1 mm.

cated above, no large glands are visible in the corresponding body wall. Neurochaetae include denticulate capillaries and aciculars with a small distal tooth. Subdistal denticles are barely visible, even in the upper chaetae (Fig. 14J).

REMARKS

Pherecardia distincta can be distinguished from *P. striata* as indicated above. The main differences rely in the pigmentation pattern; in *P. distincta* the longitudinal stripes are irregular, varying in width and length, and notopodia have a blackish ring, whereas in *P. striata* the longitudinal stripes are rather regular, having similar width and length, and notopodia have a darker pigmentation along their anterior surfaces than along posterior ones. In addition, these two species are separated by 22.4–23.5% K2P dis-

tance in COI (Fig. 8). Intraspecific variation between the two sequenced *P. distincta* is 1.2%, while it ranges between 0.3–2% in *P. striata*.

Pherecardia distincta (Hoagland, 1920) was described as having irregular blue-gray streaks and a dorsal chaetal “bundle borne on stout darkly pigmented lobe, also bearing dorsal cirrus.” Hoagland’s illustration of the anterior end shows eyes protruded from the prostomial margins, median antenna slightly longer than the laterals or palps, and the caruncle with 10 pairs of lateral, pinnate lamellae. Two of the labels with the holotype indicate the specimens were caught with electric light, suggesting that it was a swimming epitoke.

Soon after its description, Augener (1927: 123) regarded *P. distincta* as a junior synonym of *P. striata*, because he found

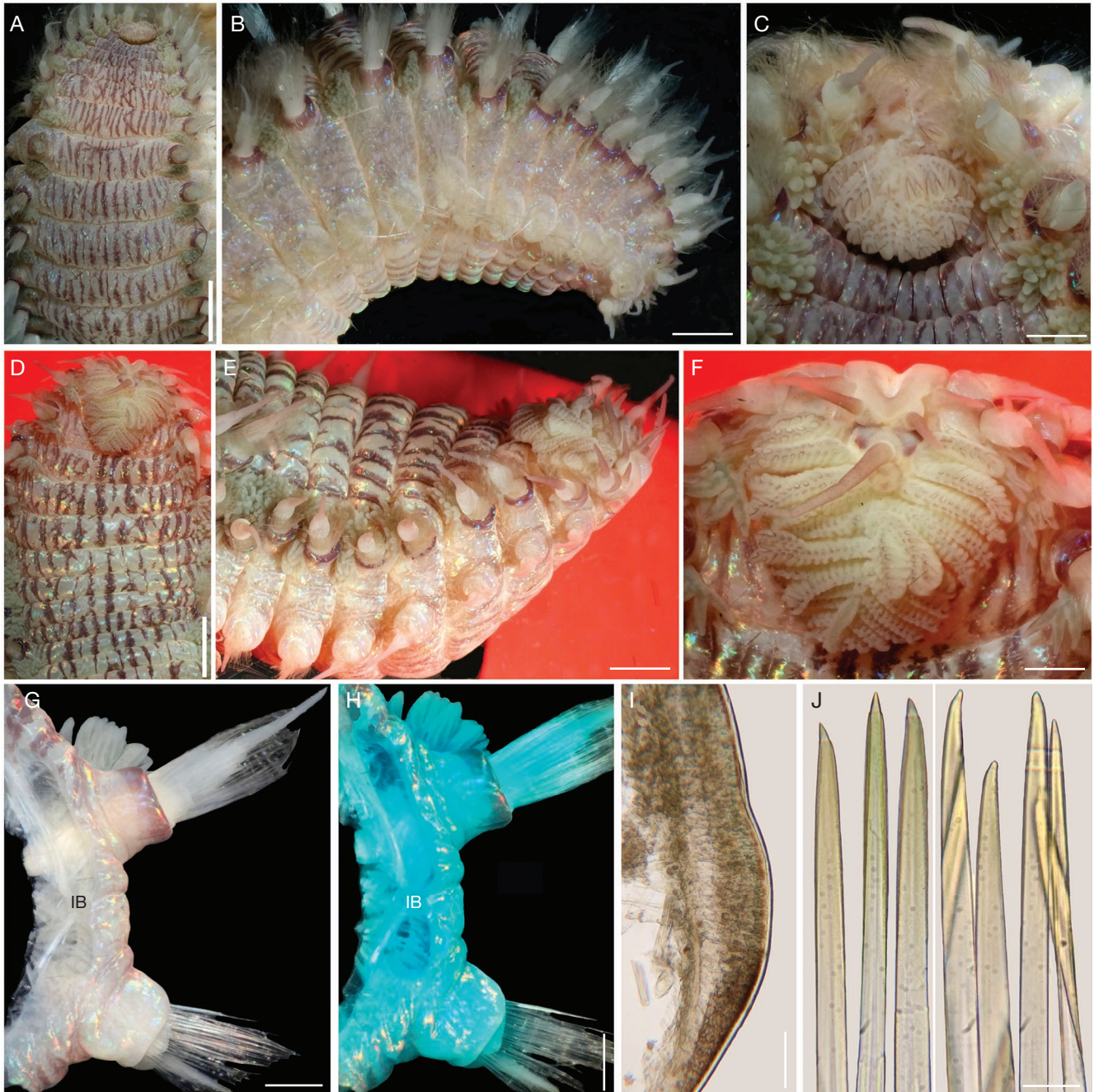


FIG. 14. — *Pherecardia distincta* (Hoagland, 1920) reinstated, n. comb., COI-sequenced non-type specimens: **A**, 8 mm wide specimen, UF 5420, anterior region, dorsal view; **B**, same, right lateral view; **C**, anterior end, dorsal view; **D**, 12 mm wide specimen, UF 5343, anterior region, dorsal view; **E**, same, right lateral view; **F**, anterior end, dorsal view; **G**, chaetiger 8, left parapodium, anterior view (IB: interramal belt); **H**, same, after Methyl green staining (IB: interramal belt); **I**, same, cross section of interramal area; **J**, same, tips of upper and lower neurochaetae. Scale bars: A, 2.1 mm; B, 1.2 mm; C, 0.6 mm; D, 2.2 mm; E, 1.6 mm; F, 0.9 mm; G, H, 0.8 mm; I, 0.3 mm; J, 30 μ m.

no differences in chaetae and regarded pigmentation pattern and stripes to be variable; Augener was following and expanding on Ehlers' (1920: 13) synonymy. Hartman (1959: 134) regarded *P. distincta* as 'questionably *P. striata*.'

Pherecardia polylamellata de Silva, 1961 was described (with specimen size not specified), as lacking pigmentation and having dorsal cirri with thicker cirrophores, and with dorsal cirri and branchiae having blackish tips. However, as

indicated above, the type specimens exhibit remaining dorsal pigmentation as diffuse irregular longitudinal stripes, and notopodia have barely pigmented black distal rings.

DISTRIBUTION

From the Western Indian Ocean to the Eastern Pacific, including Hawaii and French Polynesia, in shallow water, coral or rocky bottoms.

Pherecardia maculata Imajima, 2003
(Fig. 15)

Pherecardia maculata Imajima, 2003: 191–194, figs 96a–f, 97a–l.

DIAGNOSIS. — *Pherecardia* with anterior dorsal surface bearing abundant small white spots, but otherwise lacking pigmented pattern. Anterior chaetigers, dorsum, and caruncle with small white spots. Median antenna slightly shorter than caruncle. Anterior eyes twice as large as posterior ones. Neurochaetae aciculars distally denticulate.

TYPE MATERIAL. — **Japan, Sagami Sea. Holotype** • Okinoyama; 85 m depth; 26.III.1967; NSMT Pol.R 1020 (specimen not studied).

REMARKS

The species was described from a single 22 mm long, 4 mm wide specimen with 49 segments. The integument was described as smooth, with abundant small white spots along the anterior dorsum, a feature not previously recorded in the genus. Whether these white spots are due to pigmentation, to salt particles embedded in the integument, or to the presence of acidophilic glands is unknown. The presence of adsorbed particles and the lack of pigmentation may reflect past practices, as the specimen was collected in 1967 when samples were not as carefully washed of excess salts and formalin, as was common practice later (de Silva 1961).

The photograph of the holotype (kindly provided by Dr H. Komatsu, NSMT), shows no whitish dots remaining. Further, the integument appears furrowed, which might be due to dehydration because it was described by Imajima as smooth (Fig. 15).

Preserved specimens of *P. striata* (e.g., UF 2312) can lose their pigment pattern and have maculae, thus the color pattern of *P. maculata* is difficult to interpret. However, older *P. striata* specimens still present the typical longitudinal furrows where melanocytes are usually present, even where pigments have completely faded. On the contrary, in *P. maculata* dorsal and ventral surfaces were described as smooth. This is an interesting difference; however, the affinities of *P. maculata* with other species could be clarified after collection of additional specimens from the type locality (Sagami Sea, Japan).

Eyes are not included in the *Pherecardia* key, nor in the diagnoses for the other species. This is because eye size was found to vary with specimen size, and during maturity and epitoky. Because *P. maculata* was described with a single specimen, there is no information available about this feature and it was included in the diagnosis, despite the heterogeneity this introduces across the *Pherecardia* diagnoses herein.

DISTRIBUTION

Only known from the type locality, Okinoyama, Sagami Sea, 85 m water depth.

OTHER SPECIES PREVIOUSLY ASSIGNED TO *Pherecardia*

Pherecardites Horst, 1912

Pherecardites Horst, 1912: 33. — Bleeker *et al.* 2023: 437.



FIG. 15. — *Pherecardia maculata* Imajima, 2003, holotype, NSMT Pol.R 1020, anterior region, dorsal view (no scale provided; photo courtesy of Dr Hironori Komatsu).

TYPE SPECIES. — *Pherecardites parva* Horst, 1912, by monotypy.

REMARKS

As indicated elsewhere (Bleeker *et al.* 2023: 438, key), *Pherecardites* Horst, 1912 resembles *Eurythoe* Kinberg, 1857 by having branchiae from chaetiger 1. These genera differ in that in *Pherecardites* the caruncle has a median ridge with up to four digitate lobes and spurred neurochaetae with denticles along the inner side, whereas *Eurythoe* has a caruncle with a median ridge concealing lateral plates but without lateral digitate lobes, and its spurred neurochaetae lack denticles. Horst (1912: 33) regarded *Pherecardites* as “intermediate between *Hermodice* and *Pherecardia*, its ventral bristles resembling those of *Hermodice*, the dorsal ones those of *Pherecardia*.”; however, the caruncle of the members of these two genera differ. In *Pherecardites* the lateral lobes are digitate and smooth, whereas in *Pherecardia* the lateral lobes are foliose and pinnate.

Pherecardites monroi n. nom.
(Fig. 16)

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Pherecardia parva Monro, 1924: 73 (*non Pherecardites parva* Horst, 1912).

DIAGNOSIS. — *Pherecardites* without patterned pigmentation. Median antenna almost as long as caruncle. Anterior eyes 2–3 times as large as posterior ones. Neurochaetae aciculars, subdistally denticulate, tips bent.

TYPE MATERIAL. — **Holotype. China Sea, Macclesfield Bank** • 1 specimen; no further data; NHML 1925.1.28.144.

ETYMOLOGY. — The specific epithet is derived after the late Dr C. C. A. Monro, a taxonomist of polychaetes in the then British Museum of Natural History, London (Baylis 1942), in recognition of his many

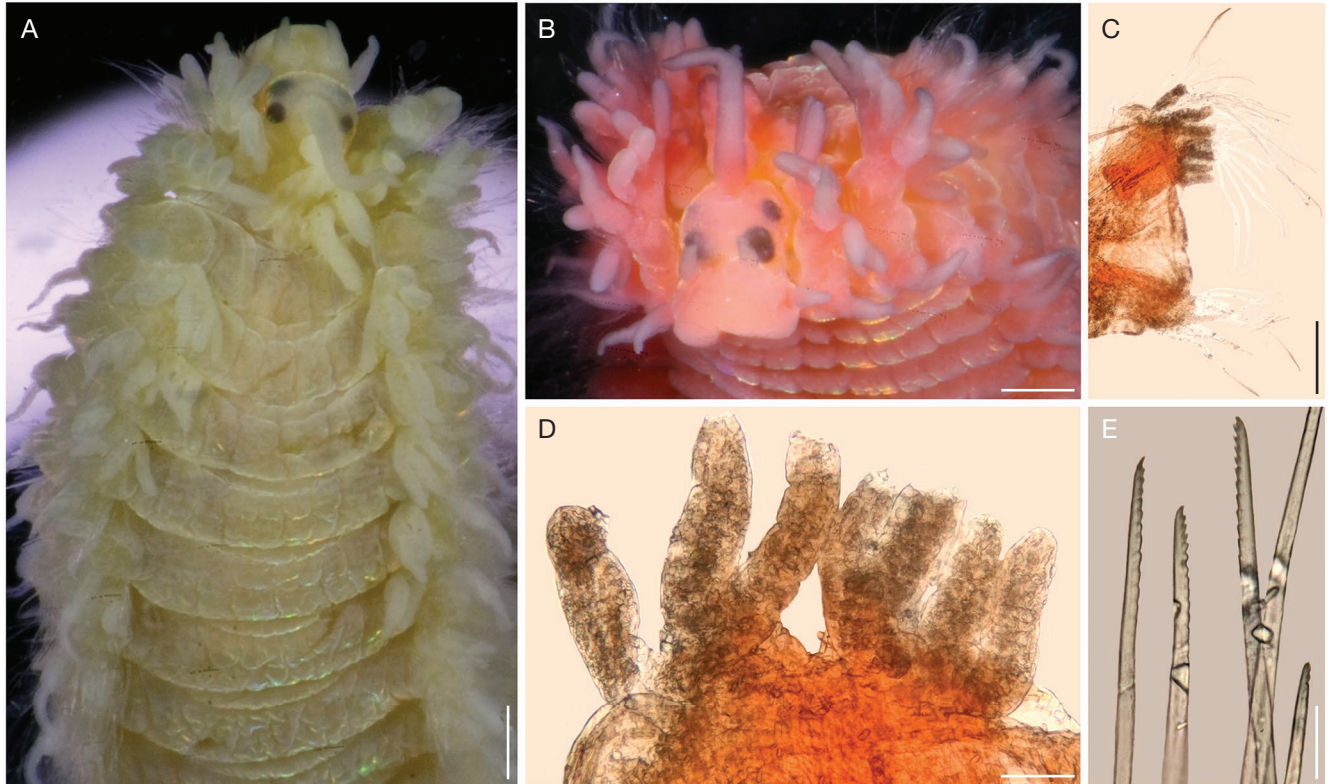


FIG. 16. — *Pherecardites monroi* n. nom., holotype, NHML 1925.1.28.144: **A**, anterior region, dorsal view; **B**, anterior end, frontal view, after Shirlastain-A staining; **C**, chaetiger 13, right parapodium, posterior view; **D**, same, close-up of branchial filaments (tips damaged); **E**, same, close-up of neurochaetal tips. Scale bars: A, C, 0.3 mm; B, 0.2 mm; D, 70 μ m; E, 40 μ m.

faunistic publications and because he described the holotype used for the new combination.

DISTRIBUTION. — Only known from the Macclesfield Bank, China Sea, at unspecified depth or substrate (see Salazar-Vallejo 2020: 89 for notes on the HMS *Alert* Expedition and its specimens).

DESCRIPTION OF TYPE SPECIMEN

Holotype (NHML 1925.1.28.144) complete, delicate, almost broken into two parts; body roughly rectangular, tapered posteriorly, bent ventrally, pale. Right parapodia of chaetiger 20, notopodia of chaetigers 14–16, left parapodia of chaetigers 15, 20, 25–27, and notopodia of chaetigers 19 and 28 previously removed (lost), right parapodium of chaetiger 13 removed for observation. Body about 15 mm long, 3 mm wide, 41 chaetigers.

Prostomium oval, barely longer than wide (Fig. 16A). Eyes black, oval and posterior eyes laterally separated, anterior eyes 2–3 times as large as posterior ones (Fig. 16B). Lateral antennae tapered, 1/4 as long as median antenna, palps as long as antennae, tapered. Median antenna cirri-form, about as long as caruncle. Caruncle with six radiating smooth lobes, left ones removed. Mouth opening between chaetigers 2 and 3.

Parapodia with divergent notopodial and neuropodial lobes (Fig. 16C). Dorsal and ventral cirri biarticulate; dorsal cirrophore and cirrostyles of similar length, both longer posteriorly; ventral cirrophore 1/4 to 1/5 as long as cirrostyle.

Branchiae arborescent from chaetiger 1 to posterior-most chaetiger; each with a single stem diverging into two branches, which are usually transversely aligned behind notopodia, and with about eight filaments in median chaetigers (Fig. 16D); largest branchiae in chaetiger 2, progressively smaller posteriorly.

Chaetae damaged, presumably due to long preservation in formalin. Notochaetae including harpoon chaetae and thin smooth capillaries; neurochaetae including aciculars with multidentate tips (Fig. 16E) and smooth capillaries.

Posterior end tapered; pygidium with anus terminal; anal plate fleshy, truncate.

REMARKS

Pherecardia parva Monroe, 1924 was based on a single small specimen without pigment pattern. Chaetae were found to be similar to those present in *P. striata*. Monroe (1924: 73) indicated that his new species differed from typical *P. striata* by lacking pigmentation, the position of the caruncle, the longer median antenna, and the larger size of branchial filaments. However, the specimen had been in preservative for some 40 years before he studied it, potentially impacting its pigmentation. The primary difference between these species regarding the caruncle is its general shape.

As indicated above, the lateral lobes of the caruncle in *Pherecardites* Horst, 1912 are roughly digitate and smooth, whereas in *Pherecardia* they are foliose, and rugose (pinnate)

KEY TO SPECIES OF *Pherecardites* HORST, 1912
(modified after bleeker *et al.* 2023, references therein, type localities after the species name)

1. Prostomium with well-defined, with margins distinct; first branchiae with 3 or more filaments 2
- Prostomium with ill-defined eyes, margins indistinct; first branchiae with 1-2 filaments
..... *P. parva* Horst, 1912 Indonesia
2. Branchiae of median segments with 15-20 filaments; dorsum without pigmented pattern
..... *P. antarctica* (Hartman, 1967) Antarctic seas
- Branchiae of median segments with 4-12 filaments; dorsum pigmentation variable 3
3. Dorsum pale 4
- Body dorsally pigmented; eyes separate, not coalescent 5
4. Eyes separate, anterior eyes 2-3 times as large as posterior ones
..... *P. monroi* nom. n. Macclesfield Bank, China Sea
- Eyes nearly coalescent, 8-shaped *P. islandica* (Detinova, 1968) NE Atlantic
5. Branchiae in median segments with 4-8 filaments 6
- Branchiae in median segments with about 12 filaments; dorsal pigmentation includes 5 dark elongate spots,
three dorsal and two interramal *P. quinquemaculata* Augener, 1927 New Zealand
6. Venter of first four chaetigers pigmented, following segments pale
..... *P. kohtsukai* (Jimi in Jimi *et al.*, 2021) Japan
- Venter with similar pigmentation throughout body
..... *P. tropicalis* (Barroso, Ranauro & Kudenov, 2017) SW Atlantic

when fully developed. This structural difference is evident even in small (11.5 mm long) *Pherecardia* specimens (MAGNT 29300; see above). Because the caruncle of the type of *P. parva* has digitate instead of foliose rugose (pinnate) lobes, it falls in *Pherecardites*. The neurochaetae of *Pherecardia*, but not in *Pherecardites*, have falcate tips.

Transfer of *Pherecardia parva* to *Pherecardites* makes it a homonym of *Pherecardites parva* Horst, 1912, the type species of *Pherecardites*, thus we provide the replacement name *Pherecardites monroi* n. nom. This species can be separated from other *Pherecardites* with the key below.

Genus *Eurythoe* Kinberg, 1857

Eurythoe indica (Schmarda, 1861)
(Fig. 17)

Amphinome indica Schmarda, 1861: 142, pl. 35, fig. 294, 3 text figs.

Amphinome bruguieres de Quatrefages, 1866: 398-399. — Baird 1868: 229 (n. syn.).

Eurythoe indica – Baird 1868: 224 (n. comb.). — Bindra 1927: 5-9, Textfigs 1-18, pl. 1, figs 1-4 (syn.).

Eurythoe complanata – Fauvel 1932: 45-46 (*non* (Pallas, 1776)).

TYPE MATERIAL. — Indian Ocean, Seychelles. Syntypes • 2 specimens; no further data; MNHN TYPE 152 (used for description); MNHN TYPE 153.

DISTRIBUTION. — Widely distributed in the Indian Ocean.

DESCRIPTION OF TYPE SPECIMENS

Syntype (MNHN TYPE 153) pale, anterior end compressed, without posterior end; caruncle depressed, twice longer than wide; first branchiae with 9-10 filaments; body 110 mm long, 9 mm wide, 94 chaetigers.

Syntype (MNHN TYPE 152) complete, slightly tapered posteriorly. Body wall grayish, with longitudinal or irregular stripes; branchiae and chaetae brownish (Fig. 17A); some chaetae removed from chaetigers 9 and 25; body 84 mm long, 10 mm wide, 69 chaetigers.

Prostomium transparent, reduced, oval, wider than long. Median antenna slightly shorter than lateral antennae; lateral antennae and palps of similar length. No eyes observed. Caruncle cushion-shaped, smooth, about twice as long as wide, reaching anterior margin of chaetiger 4 (Fig. 17B). Mouth opens between chaetigers 2-4; superior lips reaching mouth.

Parapodia massive, biramous. Notopodia with dorsal cirri larger than branchiae, with cirrophore half as long as cirrostyle. Neuropodia with ventral cirri short, ventral cirrophore 1/3 as long as cirrostyle.

Branchiae from chaetiger 2, with 2-4 main stems; first branchiae with 5-7 filaments, rapidly increasing in number to about 50-100 filaments in following segments.

Notochaetae of three types (Fig. 17C): thin spurred or simple capillaries, aciculars, and harpoon chaetae. Neurochaetae mostly furcate, of two different sizes (Fig. 17D), some simple capillaries or spurred capillaries present especially in anterior chaetigers.

Posterior end slightly damaged (Fig. 17E); pygidium with anus terminal; anal plate or cirri not observed.

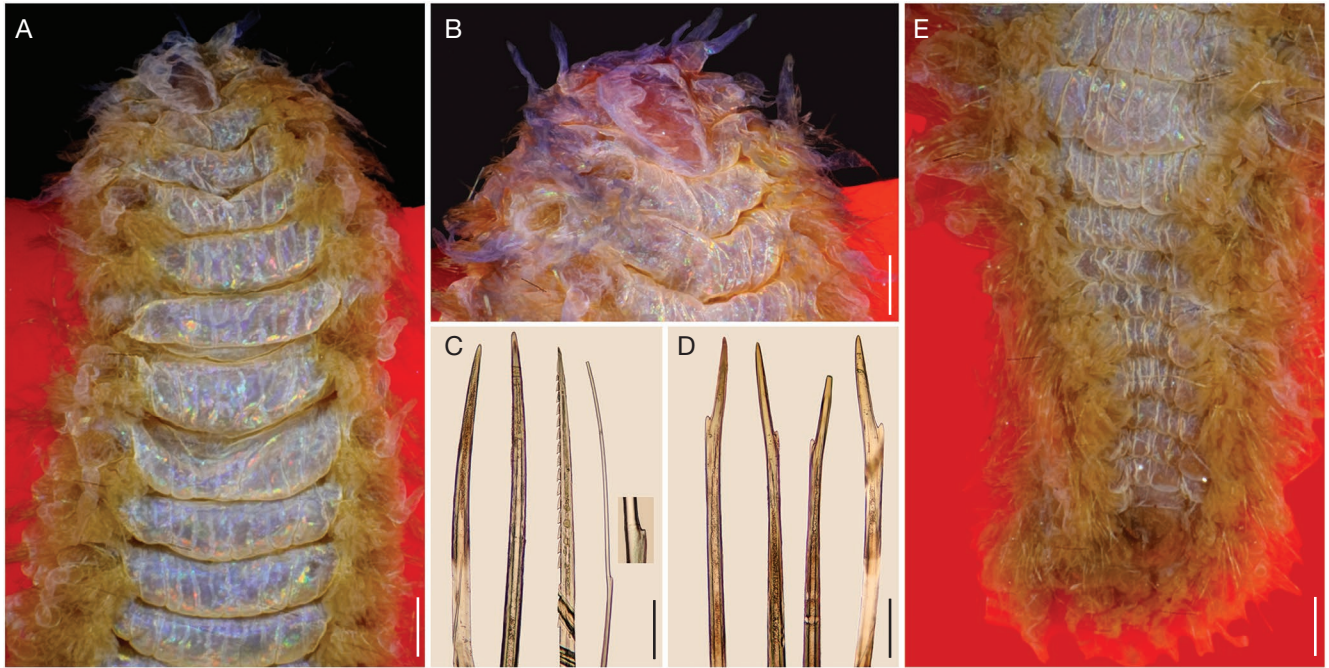


FIG. 17. — *Eurythoe indica* (Schmarda, 1861), syntype of *Amphinome bruguieresii* de Quatrefages, 1866, MNHN TYPE 152: **A**, anterior region, dorsal view; **B**, anterior end, dorsal view, after Shirlastain-A staining; **C**, chaetiger 25, notochaetal tips; **D**, same, neurochaetal tips; **E**, posterior region, dorsal view. Scale bars: A, 1.5 mm; B, 1 mm; C, 150 μ m; D, 100 μ m; E, 1.2 mm.

REMARKS

Baird (1868: 229) indicated that *Amphinome bruguieresii* de Quatrefages, 1866 does not belong in *Amphinome* Bruguère, 1789. Yáñez-Rivera & Salazar-Vallejo (2011: 252, Table 1) regarded this species as belonging in *Pherecardia*, which is the reason for its inclusion and re-assignment herein. The diagnosis indicated the caruncle was elongate and trilobed, which is not the case for typical *Amphinome*, in which the caruncle is heart-shaped, not trilobed, and made of a single fleshy cushion (de Quatrefages 1866: 398). The caruncle was described as oval, elongate, and apparently having three lobes on one side, with the other side damaged in the specimen examined. The MNHN types were recently studied, and they have a globular, rather smooth caruncle cover or roof. This species does not belong to *Pherecardia*, as previously assessed; it rather belongs in *Eurythoe* Kinberg, 1857.

Bindra (1927) revised *Eurythoe* Kinberg, 1857, and included a key to the then known species. He regarded the genus with a rather wide definition, and consequently numerous species were included in it. Bindra also included a complete characterization and several illustrations of *E. indica* (Schmarda, 1861). *Amphinome indica* Schmarda, 1861 falls within *Eurythoe* because its caruncle has a cover or roof which partially obscures the lateral lobes. Additionally, branchial and chaetal patterns resemble *Eurythoe* Kinberg, 1857 and these character states explain the transfer of *A. bruguieresii* into *Eurythoe*. Consequently, *E. indica* (Schmarda, 1861) includes *A. bruguieresii* de Quatrefages, 1866. The affinities of this species were discussed by Bindra (1927: 5, key).

Amphinome formosa

de Quatrefages, 1866

Amphinome formosa de Quatrefages, 1866: 399. — Baird 1868: 229.

TYPE MATERIAL. — Not located by Solís-Weiss *et al.* (2004); it must be regarded as lost.

TYPE LOCALITY. — Hawaii.

DISTRIBUTION. — Only known from the original description.

REMARKS

Baird (1868: 229) indicated that *A. formosa* de Quatrefages, 1866 does not belong in *Amphinome*. Yáñez-Rivera & Salazar-Vallejo (2011: 252, table 1) regarded this species as belonging in *Pherecardia* based on the caruncle features. The caruncle was originally described as foliose and very large, reaching segment 4, oval with 7-8 lobes connected mid-dorsally to a median ridge. De Quatrefages (1866: 400) also indicated that neurochaetae were smooth, lacking denticles or a fang. As the pigmentation was not described and the type material is lost, it is not possible to assign this species within *Pherecardia*. Because there is no type material, and because the original description is incomplete, and no illustrations were provided, its status cannot be determined. Further, there were no details about dorsal pigmentation nor any color indicated for notopodia, and this explains why we are unsure about which species it might be conspecific with.

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