zoosystema

2018 • 40 • 12

Revision of *Hesione* Savigny *in* Lamarck, 1818 (Annelida, Errantia, Hesionidae)

Sergio I. SALAZAR-VALLEJO

art. 40 (12) — Published on 19 June 2018
www.zoosystema.com

MUSÉUM
NATIONAL D'HISTOIRE NATURELLE
PUBLICATIONS SCIENTIFIQUES

Zoosystema est indexé dans / Zoosystema *is indexed in:*
– Science Citation Index Expanded (SciSearch®)
– ISI Alerting Services®
– Current Contents® / Agriculture, Biology, and Environmental Sciences®
– Scopus®

Zoosystema est distribué en version électronique par / Zoosystema *is distributed electronically by:*
– BioOne® (http://www.bioone.org)

Les articles ainsi que les nouveautés nomenclaturales publiés dans *Zoosystema* sont référencés par / *Articles and nomenclatural novelties published in* Zoosystema *are referenced by:*
– ZooBank® (http://zoobank.org)

Zoosystema est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris / **Zoosystema** *is a fast track journal published by the Museum Science Press, Paris*

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish:*
Adansonia, ***Anthropozoologica***, ***European Journal of Taxonomy***, ***Geodiversitas***, ***Naturae***.

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle
CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)
Tél. : 33 (0)1 40 79 48 05 / Fax : 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / http://sciencepress.mnhn.fr

ISSN (imprimé / *print*) : 1280-9551/ ISSN (électronique / *electronic*) : 1638-9387

Revision of *Hesione* Savigny *in* Lamarck, 1818 (Annelida, Errantia, Hesionidae)

Sergio I. SALAZAR-VALLEJO
Estructura y Función del Bentos, Depto. Sistemática y Ecología Acuática,
El Colegio de la Frontera Sur, Chetumal, Quintana Roo, 77000 (México)
savs551216@hotmail.com
ssalazar@ecosur.mx

Submitted on 13 July 2017 | Accepted on 20 February 2018 | Published on 19 June 2018

urn:lsid:zoobank.org:pub:6CBF9039-7E4D-4938-909A-2DB5113C8D35

Salazar-Vallejo S. I. — Revision of *Hesione* Savigny *in* Lamarck, 1818 (Annelida, Errantia, Hesionidae). *Zoosystema* 40 (12): 227-325. https://doi.org/10.5252/zoosystema2018v40a12. http://zoosystema.com/40/12

ABSTRACT
The species of *Hesione* Savigny *in* Lamarck, 1818 are among the most colorful marine benthic annelids, but their pigmentation often fades in ethanol, rendering it of little use as a diagnostic feature. Further, the body includes only 16 chaetigers but because parapodia are modified after preservation, several authors have lumped most species under a few names. The digestive and reproductive systems are known for a single species (*H. sicula* delle Chiaje, 1830), and its gonads are hermaphroditic. In order to improve our knowledge of the genus, available specimens in the larger collections of the world were studied under a standardised approach, parapodial/neurochaetal features were defined following previous guidelines, and pigmentation patterns were reassessed. Some observations were made on the digestive system and on some details of the gonads, including Scanning Electron Microscopy (SEM) photos of sperm. *Hesione* includes 23 species. Twelve were already known: *H. ceylonica* Grube, 1874 reinstated; *H. eugeniae* Kinberg, 1866; *H. genetta* Grube, 1867 restricted; *H. intertexta* Grube, 1878 restricted; *H. pacifica* McIntosh, 1885 reinstated; *H. panamena* Chamberlin, 1919 reinstated; *H. pantherina* Risso, 1826 restricted; *H. picta* Müller, 1858 (incl. *H. proctochona* Schmarda, 1861 and *H. vittigera* Ehlers, 1887); *H. praetexta* Ehlers, 1887 reinstated; *H. sicula* delle Chiaje, 1830 reinstated (incl. *H. steenstrupi* de Quatrefages, 1866); and *H. splendida* Savigny *in* Lamarck, 1818 (incl. *H. ehlersi* Gravier, 1900); *H. reticulata* von Marenzeller, 1879 has been recently redefined. Eleven species are newly described: *H. beneliahuae* n. sp. from La Réunion; *H. fitzhughi* n. sp. from Australia; *H. harrisae* n. sp. from Puerto Rico; *H. hartmanae* n. sp. from the Galápagos Islands; *H. helenensis* n. sp. from Saint Helena Island; *H. horsti* n. sp. from Indonesia; *H. keablei* n. sp. from Australia; *H. mooreae* n. sp. from Saudi Arabia; *H. osbornae* n. sp. from the Philippines; *H. paulayi* n. sp. from Papua New Guinea; and *H. uchidai* n. sp. from the Philippines. A key is included to identify all the species in the genus. An appendix is also included to clarify the publication dates of Stefano delle Chiaje papers on marine invertebrates.

KEY WORDS
Fallacia, *Telamone*, digestive system, gonads, chaetal blades, pigmentation, delle Chiaje, new species.

RÉSUMÉ
Révision du genre Hesione *Savigny* in *Lamarck, 1818 (Annelida, Errantia, Hesionidae).*
Les espèces de *Hesione* Savigny *in* Lamarck, 1818 sont parmi les annélides benthiques les plus colorées, mais leur pigmentation disparaît souvent dans l'éthanol, diminuant son utilité comme caractère diagnostique. De plus, le corps ne comprend que 16 sétigères mais comme les parapodes sont modifiés après conservation, plusieurs auteurs ont regroupé la plupart des espèces sous des noms distincts. Les systèmes digestifs et reproducteurs sont connus pour une seule espèce (*H. sicula* delle Chiaje, 1830) et ses gonades sont hermaphrodites. Pour améliorer notre connaissance du genre, les spécimens disponibles dans les plus grandes collections du monde ont été étudiés avec une approche standardisée, les caractères des parapodes/neurochètes ont été définis suivant des règles antérieures, et les patrons de pigmentation ont été réévalués. Des observations ont été faites sur le système digestif et sur quelques détails des gonades, y compris des photos du sperme au microscope électronique à balayage (MEB). *Hesione* inclut 23 espèces. Douze étaient déjà connues : *H. ceylonica* Grube, 1874 réhabilitée ; *H. eugeniae* Kinberg, 1866 ; *H. genetta* Grube, 1867 restreinte ; *H. intertexta* Grube, 1878 restreinte ; *H. pacifica* McIntosh, 1885 réhabilitée ; *H. panamena* Chamberlin, 1919 réhabilitée ; *H. pantherina* Risso, 1826 restreinte ; *H. picta* Müller, 1858 (incl. *H. proctochona* Schmarda, 1861 et *H. vittigera* Ehlers, 1887) ; *H. praetexta* Ehlers, 1887 réhabilitée ; *H. sicula* delle Chiaje, 1830 réhabilitée (incl. *H. steenstrupi* de Quatrefages, 1866) ; et *H. splendida* Savigny *in* Lamarck, 1818 (incl. *H. ehlersi* Gravier, 1900). *H. reticulata* von Marenzeller, 1879 a été redéfinie récemment. Onze espèces sont nouvellement décrites: *H. beneliahuae* n. sp. de La Réunion, *H. fitzhughi* n. sp. d'Australie, *H. harrisae* n. sp. de Puerto Rico, *H. hartmanae* n. sp. des îles Galápagos, *H. helenensis* n. sp. de l'île de Sainte-Hélène, *H. horsti* n. sp. d'Indonésie, *H. keablei* n. sp. d'Australie, *H. mooreae* n. sp. d'Arabie saoudite, *H. osbornae* n. sp. des Philippines, *H. paulayi* n. sp. de Papouasie-Nouvelle-Guinée, et *H. uchidai* n. sp. des Philippines. Une clef est incluse pour identifier toutes les espèces du genre. Les dates de publication des articles de Stefano delle Chiaje sur les invertébrés marins sont, d'autre part, clarifiées en annexe.

MOTS CLÉS
Fallacia,
Telamone,
appareil digestive,
gonades,
serpes des soies,
coloration,
delle Chiaje,
espèces nouvelles.

INTRODUCTION

In Greek mythology, Hesione is mostly regarded as a famous Trojan Lady, daughter of King Laomedon, who offered her life as a compensation to Poseidon after the God had sent a monster to destroy the city. However, Laomedon also asked Heracles for help and if he could save Troy, Hesione would be his wife. She was left naked on the rocks in a sea cliff out of Troy. Heracles and Telamon saved Hesione by killing the monster, but King Laomedon changed his mind and forgot his offer; this pushed Heracles to destroy Troy and later, Heracles gave Hesione to Telamon (Salazar-Vallejo & Rizzo 2009).

XIX-century scientists usually had a very good knowledge of both Greek and Latin together with Classic History. It is no surprise that the French polymath Jules-César Savigny had chosen *Hesione* to name one genus among his most spectacular polychaetes, and later Claparède proposed *Telamone* for what he regarded as a closely allied hesionid. However, because Savigny's works were circulating as preprints, Lamarck followed most of his ideas for the corresponding section in the *Histoire Naturelle des Animaux sans Vertèbres*, and this explains why the correct genus-group name, including author and date, must be written as *Hesione* Savigny *in* Lamarck, 1818.

The Hesionidae Grube, 1850 was revised by Pleijel (1998), and his conclusions have been followed in most subsequent publications. Gravier (1900: 175, footnote) indicated that the family must be regarded as Hesionidae Grube, 1880 (Grube 1880), but Ernst Ehlers made an earlier proposal for the family (Ehlers 1864: 184). Nevertheless, the proposal by Grube (1850: 303, 306) includes the type genus for the group, therein regarded as closely associated to phyllodocids, and the family full name, or tetranomen, has been followed as originally proposed.

The family members show a marked cephalisation and at least several anterior segments carry long cirri; hesionids can have large or very small bodies, live in rocky or sandy bottoms, and they are seldom abundant. They are mostly free-living and are regarded as carnivores or microphagous, especially some symbiotic forms, but there are few or no data for most species (Jumars *et al.* 2015, appendix: 135). However, *H. picta* Müller, 1858 has been shown to be associated with the brittle star *Ophionereis reticulata* (Say, 1825) in Brazil (de Assis *et al.* 2012).

Hesione includes specimens with 16 chaetigers, height pairs of long anterior cirri, and sesquiramous parapodia (with dorsal cirri but notochaetae missing). The prostomium has no palps, a unique feature in the family, although they might be fused and directed ventrally, such that only when the pharynx is fully everted, they could be noticed as a low triangular blunt lobe, but this deserves further study; tiny, lateral antennae can be present. It must be emphasised that antennae are typically simple, non-articulated, even though Saint-Joseph (1898: 331, fig. 132) regarded them as biarticulated. There are usually two pairs of eyes; anterior eyes often larger and more separated from each other than posterior eyes. *Hesione* species have spectacular pigmentation patterns; these patterns could be enough to tell species apart, but because their pigments fade off quite soon once they are preserved in ethanol, as early indicated by Grube (1880: 226), pigmentation is not used as a diagnostic feature.

Diagnostic problems

Finding out reliable diagnostic features in *Hesione* species has been problematic, especially because their bodies include long, fragile cirri, and their body wall and parapodial lobes are highly contractile, such that their general appearance can be modified because of preservation effects. *Hesione* is the type genus of the family Hesionidae, and one of the most relevant problems is that its type species, *Hesione splendida* Savigny *in* Lamarck, 1818, has not been unambiguously delineated. There are two syntypes: one from the Gulf of Suez (Red Sea), the other from the Île-de-France (Mauritius Island), and they have some differences in chaetal blades as originally indicated by Savigny (1822: 40). Further, besides the fact that dorsal cirri are fragile and usually lost, chaetal blades might be broken during collecting or handling the specimens, and this was noted since Savigny dealt with *Hesione festiva* (Savigny 1822: 40).

As indicated above, and as shown by Grube (1880) and Ehlers (1887), pigmentation might be reliable but it is useless in preserved specimens because it usually disappears soon. Dorsal pigmentation has three patterns: 1) no pigmentation, as in *H. splendida* Savigny *in* Lamarck, 1818, where the body is bright grayish, and probably in *H. eugeniae* Kinberg, 1866, although no pigmentation was given in the description; 2) transverse bands as shown in *H. picta* Müller, 1858, and *H. genetta* Grube, 1867, but in the latter there are also round spots along body; and 3) longitudinal, discontinuous lines as in *H. pantherina* Risso, 1826, *H. steenstrupi* Quatrefages, 1866, *H. intertexta* Grube, 1878, *H. reticulata* von Marenzeller, 1879, and *H. praetexta* Ehlers, 1887.

Polychaetes are among the most colorful marine invertebrates (Frédol 1866), but the study of their pigments lays behind those present in other groups, such as sponges, cnidarians and ascidians (Bandaranayake 2006). Some details regarding nereidids are relevant for hesionids, because they are closely allied (Pleijel & Gustavsson 2010). After Fauvel (1923a: 339) *Nereis zonata* Malmgren, 1867 has different pigmentation patterns throughout their distribution; northern specimens have transverse purple reddish bands on a white-yellowish background, but French specimens are brownish, pinkish or yellowish. Pettibone (1963: 182) indicated that larger Northwestern Atlantic specimens have transverse wide reddish, brownish, violet or purple red bands on each segment. An investigation about the pigments of *N. zonata* indicated that their color bands depend on the combination of several carotenoid pigments (Czeczuga 1971), such as a- and b-carotenes that give reddish or orange color, xanthins that are responsible for yellowish color, and astacenes which are responsible for the brownish color. They might be also present among hesionids. However, because pigmentation is not long-standing or reliable as a diagnostic feature, there have been five attempts to improve the taxonomy in the group.

First. Ernst Ehlers used pigmentation together with the number of chaetigers, relative size of ventral cirri (shorter vs longer than chaetal lobe), chaetal blades length (5-7 times as long as wide vs >10 times as long as wide), and type of acicular lobes (single vs double) to separate two species: *H. vittigera* and *H. praetexta* (Ehlers 1887).

Second. Charles Gravier indicated that the presence of antennae could separate *Hesione* species into two groups (Gravier 1900: 179). He listed as having antennae: *H. genetta, H. intertexta, H. pantherina* and *H. reticulata*, whereas those species listed as lacking or without antennae were *H. picta* and *H. splendida*. Nevertheless, depending on the degree of eversion of the pharynx, and especially because the pharynx outer wall is a continuation of the prostomial anterior margin, the prostomium may change its shape, and antennae might be more or less visible, as indicated by von Marenzeller (1879: 130).

Third. Ralph Chamberlin regarded chaetal blades and the development of their guards and teeth useful to separate similar species (Chamberlin 1919: 190). This was later refined by Monro (1926: 312, 1931: 10), who emphasised the relative size of the guard to blade teeth. Monro recognised three groups: 1) guard approaching subapical tooth (*H. pantherina, H. proctochona, H. margaritae*, and *H. genetta*); 2) guard approaching apical tooth (*H intertexta, H. reticulata, H. panamena*, and *H. praetexta,* being incurved in *H. ehlersi*); and 3) guard projected beyond apical tooth (*H. eugeniae*). In juveniles of what seems to be *H. picta*, Pleijel (1998: 110, fig. 5F) noted that the non-fragmented guard reaches the distal tooth such that it belongs in group 2. By the way, Ehlers (1887: pl. 41, fig. 4) illustrated a broken guard for his *H. vittigera*, a species currently regarded as a junior synonym of *H. picta*, giving the wrong impression it only reaches the subapical tooth. It must be emphasised that because chaetal guards are brittle, they should not be regarded as short if they are blunt or with tips as wide as their medial parts, and scanning for undamaged guards, several chaetae or, even better, more than one parapodia must be explored before concluding about this feature. Hartman (1940: 212) found guard development was "surprisingly uniform."

Fourth. Rutgerus Horst (1924: 193-194) indicated, by following the original observations by Ehlers (1887) and Saint-Joseph (1898), that the relative size of the distal digitate acicular projections present in neurochaetal lobes could separate similar species. Hartman (1940: 212) regarded these projections as preacicular and postacicular, but their position does not match this naming because the upper tine is usually projected from the acicular tip, whereas the lower tine, if present, is often placed slightly ahead; therefore, they are herein regarded as upper or lower in position to each other, and not as if placed ahead or after the acicular tips. In the *Siboga* material, Horst found two patterns: one having double projections of about the same length that corresponded to what he identified as *H. genetta*, and other specimens having lobes of different length corresponding to *H. intertexta*. However, it seems that smaller specimens have a single lobe and as size proceeds, another, inferior lobe is present, but it is rarely as long as the superior one. Horst also was the first to pay attention to the differences in acicular pigmentation; he indicated that some specimens of *H. intertexta* had yellow neuraciculae, but this is strange because most illustrations of *Hesione* parapodia show black neuraciculae. Regretfully, Pierre Fauvel (1911, 1923a)

rejected the use of acicular lobes to separate similar species, and he illustrated two parapodia from the same specimen; in one there was a single digitate lobe, whereas in the other two lobes were visible. Fauvel (1911: 375) also rejected, after commenting upon an illustration by Saint-Joseph (1898: fig. 135a) that the relative size of the acicular lobes could be diagnostic, but if the relative size or number of acicular lobes is widespread and consistent along the body, then it can be safely used to separate similar species, as clearly indicated by Horst (1924).

Fifth. Hiromi Uchida (2009) in a large contribution trying to make keys to identify Japanese species, used as diagnostic features for *Hesione* species several characters: pigmentation patterns, presence of antennae, length of dorsal tentacular cirri, type of acicular lobe, relative length of blades, presence of guards in blades, and relative length of blades and guards. By the way, he was the first to indicate that at least for one species, neurochaetal blades are especially long in a few anterior chaetigers (1-3 or 1-7), although size differences in the same chaetiger were noted by Augener (1933a: 182, textfig. 1). However, because Uchida's paper was issued in Japanese, its relevance has not been acknowledged outside Japan, and because of the confused state of species definition, his identifications deserve confirmation based upon specimens. However, these features deserve a further analysis based upon specimens from the same locality and its results are shown below.

These refinements of diagnostic features were overlooked or rejected; in order to improve the current taxonomy, they must be regarded under systematic and standardised approaches (see below).

Anatomy and reproduction

Septa

For *Hesione pantherina*, Clark (1962: 555) indicated that "the septum is reduced to a pair of lateral intestinal suspensory muscles, connecting the gut to the lateral body wall in the intersegmental region, at the level of the top of parapodia". And that "*Hesione* is thus reduced to an aseptate condition and there appears to be no possibility of the coelom of one segment being isolated from that of the next."

Muscle system

Storch (1968) made a detailed account about the muscle system in several polychaete families. For *Hesione pantherina*, he carefully described and illustrated the muscular packages running along the body, crossing through the coelom, and controlling parapodial movements. He pointed out that parapodial lobes can be telescoped in and out within the body, which is responsible of the variable exposure of chaetal lobes and chaetae.

Digestive system

Hessle (1925) made a detailed account of the nervous and digestive systems in Hesionidae; he concentrated his histological analyses in *Leocratides ehlersi* (Horst, 1921) mostly for the nervous system, and also on *Hesione reticulata* von Marenzeller, 1879 for other issues. Hessle (1925: 6, ff) followed Eisig (1881) and indicated there are four regions in the digestive system: the pharynx cavity, the pharynx itself, the stomach with one pair of lateral bags (*caeca ventriculares*), and the intestine driving to the anus. He noted that the pharynx has three muscular layers: longitudinal, circular and radial, with the latter making the most part of the thick pharynx wall. The lumen is covered by a soft, thin chitinous layer.

Reproduction

A series of observations about gas bubbles in the gut or caeca of *Hesione* species (de Quatrefages 1850: 299, 1866: 92; Claparède 1868: 543; Saint-Joseph 1898: 334) prompted an anatomical study by Eisig (1881) about these supposed swimming bladders. Eisig (1881: 256) concluded that the caeca were functional as air reservoirs and extended his conclusion to some syllids. His study also drove into a series of fine illustrations (his plate 12) and the branched gonads were depicted as present along chaetigers 5-16, and he referred to as hermaphroditic. Claparède (1868: 545) made an earlier observation about their purple color and arrangement, but regarded them as ovaries, although in his description he stated that as the gonad develops along blood vessel: "Tout autour de cet axe est un tissu dont la trame est semée de petites cellules larges de 5 à 6 micr. seulement, et d'ovules bien caractérisés" (Transl.: All around this axis there is a tissue which frame is seeded by small cells each about 5-6 µm long only and well characterised oocytes).

No further studies have been made and the compilation by Schroeder & Hermans (1975: 18, 48), which referred to Bergmann (1902, 1903), indicated that the only known species was *Hesione pantherina* Risso, 1826 (identified as *H. sicula* by Bergmann). The species was regarded as a protandric, sequential hermaphrodite, with eggs and sperm being developed in the same segment, and without any morphological modifications upon maturity.

Bergmann (1902: 13) indicated that gonads were visible along segments 6-16, as groups of blind tubular structures placed under parapodial bases, and branching from a common point. These gonads were growing along a blood vessel and were hermaphroditic (Bergmann 1902: 14, 15), having oocytes surrounded by spermatids closely packed into a granular mass, surrounded by depressed peritoneal epithelial cells, and that growth proceeds from the inner region towards the periphery. In the following contribution, Bergmann (1903: 416) referred to the hermaphroditic condition as protandric because although the gonad simultaneously produces sperm and oocytes, sperm is released before the oocytes; he also indicated there were no fertilised oocytes in the coelom.

Nephridia

Hessle (1925: 8) also confirmed the early description by Goodrich (1897) of nephridia and emphasised that nephridial funnels are too small, and nephridial ducts too narrow and winding, as to allow the passage of mature oocytes, en route to be released to the outside. Consequently, the release of oocytes was enigmatic and, regretfully, still is.

Distribution

The distribution of *Hesione* species is rather confusing, partly because the above diagnostic characters were not followed, partly because once these differences are disregarded as diagnostic, all described species were regarded as synonyms of one or two older names, as concluded by Fauvel (1911: 374-376), or Augener (1913: 187-189). The idea of widely distributed species is supported by some contemporary colleagues. For example, Costa *et al.* (2008) regarded *H. picta* Müller, 1858 described from Brazil and having a dark brown body with transverse pale marks, as a junior synonym of *H. splendida*, described from the Gulf of Suez with a pearly gray pigmentation. Further, Ngamniyom *et al.* (2014) found one specimen and identified it as *H.* cf. *picta* in the Gulf of Thailand, because of the presence of wide brownish bands along the body. However, there are at least two important differences regarding pigmented bands between the Thailand specimen and what we currently regard as *H. picta*: bands are divided by thin pale lines and have no marginal darkening in *H. picta*, whereas they are solid and their anterior and posterior margins are more heavily pigmented in the Thailand specimen.

In order to clarify the morphological differences and to assess the relevance of the above morphological features as specific diagnostic features, a revision is needed. Of course, more than one species might be living in the same ocean basin, and at the same time, some of the species names could be synonyms, but solving these issues must rely on the comparison of specimens from the same region as follows (in chronological sequence):

Indian Ocean (and Red Sea): *H. splendida* Savigny *in* Lamarck, 1818, *H. ceylonica* Grube, 1874*, H. ehlersi* Gravier, 1900.

Eastern Atlantic (and Mediterranean Sea): *H. pantherina* Risso, 1826, *H. sicula* delle Chiaje, 1830, *H. steenstrupi* de Quatrefages, 1866.

Western Atlantic (and Grand Caribbean): *H. picta* Müller, 1858; *H. proctochona* Schmarda, 1861; *H. margaritae* Hansen, 1882; *H. praetexta* Ehlers, 1887; *H. vittigera* Ehlers, 1887.

Western Pacific: *H. eugeniae* Kinberg, 1866; *H. genetta* Grube, 1867; *H. intertexta* Grube, 1878; *H. reticulata* von Marenzeller, 1879; *H. pacifica* McIntosh, 1885.

Eastern Pacific: *H. panamena* Chamberlin, 1919.

Hartman (1959: 185) regarded some species as widely distributed and considered that they included others as junior synonyms. In *H. splendida* she included *H. ceylonica, H. ehlersi* and perhaps *H. pacifica,* whereas *H. steenstrupi* and *H. sicula* were regarded as junior synonyms of *H. patherina;* she also regarded *H. panamena* under *H. intertexta,* and under *H. picta* she included *H. praetexta, H. proctochona* and *H. vittigera*, but she excluded *H. margaritae,* which as *H. picta* was also described from Brazil.

In this contribution after a standardised morphological evaluation, together with a careful study of published accounts, the genus *Hesione* is redefined and on the basis of all type and non-type specimens, all known species are delineated and redescribed, and 11 others are newly described. Some additional observations on digestive system and gonads are also included.

MATERIAL AND METHODS

Type and non-type materials were concentrated in several institutions: ECOSUR, the Los Angeles Natural History Museum, the Université catholique de l'Ouest, Angers, the Muséum national d'Histoire naturelle, Paris, and a research visit to the Natural History Museum, London. Field data available in labels were copied including locality, substrate, depth and collecting date and collectors name(s). Locality names were updated or translated to their English names, if any available; UPS coordinates were transformed into traditional settings (http://www.earthpoint.us/Convert.aspx), and both formats are presented; depth is given in metres.

Specimens were examined directly from the container, or after being temporarily stained by a 30-sec immersion in an oversaturated methyl-green ethanol solution. Other prostomial features such as ridges or lobes, together with the relative size and position of eyes were noted.

Parapodia are rather homogeneous along body, although their size increases progressively towards posterior region, but last chaetiger has smaller parapodia. Further, because of this homogeneity and especially because there are usually only 16 chaetigers, a single, midbody parapodium has been dissected for parapodial and chaetal features. However, because cirri and lobes are contractile, the parapodia can vary a lot in their thickness; in order to mount them semi-permanently, some further cuts were made to reduce excessive tissue. This implied slicing out some parapodial basal or lateral portions, such that the cover slip can include the ethanol-glycerol solution. Characterisation of parapodial features included the relative length and articulation of dorsal and ventral cirri, their relative size in comparison to the chaetal lobe, and chaetal features such as their number, blade-length variation (in the same parapodia and along the body), and the relative size of their accessory teeth.

For every specimen or lot, size measurements are given for the full body, excluding the pharynx if everted, and only if the specimen was not too macerated or dried-out; width was measured about chaetiger 8, excluding parapodia, and because two of the known species were proposed by using the number of chaetigers (15-17), the number of chaetigers was also counted for all specimens; however, as there are always 16, they will not be indicated, unless specimens were incomplete. Further, unless specimens were anteriorly or posteriorly incomplete, they must be regarded as complete. These observations were included for almost all specimens because they were examined and photographed before type material, or species were redefined. This resulted in a lengthy piece of information for each specimen or lot, but made it easy to incorporate them to known or undescribed species, and for future studies, it will help decide which specimens should be re-examined.

To evaluate the number of neurochaetae per chaetiger and their variation with body size, we sorted three specimens from the same lot (*Hesione panamena* Chamberlin, 1919, LACM 8555), and for each specimen one right parapodium of middle body (chaetigers 7 or 9) was removed and mounted to count chaetae. To evaluate the variation of blade length:width along

the body in specimens of different size, three right parapodia (chaetigers 3, 7, 9) were removed from Floridan specimens of *H. picta* Müller, 1858 (18-32 mm long), and of *H. praetexta* Ehlers, 1887 (22-54 mm long).

For anatomical features, one specimen of *Hesione panamena* Chamberlin, 1919 (LACM 7101) was dissected for observation of gross morphology of the digestive system. Three other specimens, one of *H. genetta* Grube, 1867 (UF 95), one of *H. paulayi* n. sp. (UF 1674), and one of *H. picta* Müller, 1858 (UF 1590) were partially dissected to remove the gonads, and from the latter also the digestive caeca; these organs were chemically dried with HMDS, then coated with gold-palladium, and later observed for fine details in a JEOL SEM in ECOSUR.

Pigmentation patterns were based upon living, relaxed specimens. Usually those specimens were also available for this study, but sometimes they were not available but their location, together with the name of the photographer, is given in figure legends. The species are presented following an alphabetical order. Material is deposited in several institutions listed below.

A short appendix was prepared to clarify the publication dates of Stefano delle Chiaje, especially because some of his plates were published separately and are relevant for nomenclatural purposes, including *H. sicula* delle Chiaje, 1830.

Abbreviations

Institutions

AM	Australian Museum, Sydney;
BMNH	Natural History Museum (NHM) (formerly, British Museum of natural History, London);
ECOSUR	El Colegio de la Frontera Sur, Chetumal;
LACM	Los Angeles County Museum of Natural History, Allan Hancock Foundation Polychaete Collection, Los Angeles;
MNHN	Muséum national d'Histoire naturelle, Paris;
MNHW	Museum of Natural History, Wroclaw University, Wroclaw;
NMW	Naturhistorisches Museum Wien, Vienna;
RBINS	Royal Belgian Institute of Natural Sciences, Brussels;
RMNH	Naturalis Biodiversity Center, National Museum of Natural History, Leiden;
SMF	Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt;
UCO	Université Catholique de l'Ouest, Angers;
UANL	Laboratorio de Biosistemática, Fac. Ciencias Biológicas, Universidad Autónoma de Nuevo León, Monterrey;
UF	University of Florida Natural History Museum, Gainesville;
USNM	Natural History Museum, Smithsonian Institution, Washington;
ZMB	Museum für Naturkunde, Berlin;
ZMH	Zoologisches Museum, Hamburg.

RESULTS

Morphology

Integument

The body wall in *Hesione* species is usually thin but provided with longitudinal and transverse muscle bundles, such that their surface might reflect the presence of these bundles. The surface rugosity can be assessed by using oblique incident light, and three different conditions can be found: smooth (often annulated), tuberculated, with tubercles arranged into longitudinal and transverse series, or with longitudinal ridges. These conditions can be extended into lateral cushions, and are regarded as diagnostic features.

Prostomial shape

The prostomium can have a rectangular shape, with more or less parallel lateral margins, or it can have a rounded shape, with lateral margins progressively expanded toward the wider posterior prostomial margin. However, because prostomial shape is frequently modified by the eversion of the pharynx, rejecting the use of prostomial shape seems to be correct. This implies that most prostomial features can be slightly or markedly modified after pharynx eversion. In the past, these features were illustrated depending upon the quality of the available equipment together with the artist capabilities for detailed observations. Nevertheless, if specimens are compared with a similar degree of pharynx eversion, then the prostomial shape can help separate similar species, if this difference is also based upon some other morphological features.

Eyes

There are two pairs of eyes; they are usually circular, paired, with the anterior eyes slightly more separated from each other than posterior ones, and they can be regarded as reaching the surface, if they are perfectly defined, or not if their margins are diffuse; this can be related to the thickness of the prostomial integument, but this requires confirmation. Anterior eyes are usually larger than posterior ones as well, and their relative size and shape is apparently stable despite the maturity of specimens, such that it can be used to separate similar species. However, because their lenses are aligned into different planes, the anterior eyes are directed anterolaterally, whereas the posterior ones are directed dorsally, this size relationship must be evaluated in dorsal view, because in lateral view anterior eyes look even larger. Futher, the relative position of the lenses can help separate similar species. Because of their perspective from a dorsal view, anterior eyes can become oval, either as long as wide, or as wide as long, and this is regarded as a diagnostic feature in the key below.

Antennae

Antennae can be short or long. Their size is distinguished in comparison to the distance between eyes of the same prostomial side, a character referred to as interocular distance (iod). Antennae will be short if their length is smaller than interocular distance, or long if they are as long as or longer than interocular distance. However, the L/W proportions of antennae will be used instead of comparing them to iod because prostomia can be distorted. In order to evaluate this feature, prostomia must be observed by adjusting the specimen such that eyes are oriented along the same focal plane in dorsal view.

Nuchal organs

They are usually regarded as fused along the posterior prostomial margin; hence, C-shaped, but there is a slight separation

between their lateral branches such that they are not really fused to each other middorsally. In most species the fusion is noted by a medial, short depression but this can vary; for example, in *H. splendida*, the fusion is anteriorly displaced along the prostomial surface, in about ¼-⅓ its length from the posterior margin.

Parapodia

The notopodia are reduced to dorsal cirri; there are 3-4 thin aciculae supporting dorsal cirrophores but no notochaetae. Dorsal cirrostyles are usually articulated, at least distally. The basal region can be smooth if no internal subdivisions are noticeable, annulated if some rings can be detected, or articulated if these rings are also defined by surface indentations. Neuropodia include a chaetal lobe, usually contractile, carrying aciculae and abundant neurochaetae, and a ventral cirrus per ramus. Ventral cirri can reach, or extend beyond chaetal lobes tip, but because they are fragile, their relative size is of little diagnostic relevance.

Acicular lobes

Over the tip of neuraciculae, there is a fleshy outgrowth or acicular lobe. This can be easily recognised since they are usually exposed, having a longer upper tine and often a shorter, round lower tine. For this revision, acicular lobes are regarded as double if both the upper tine and the lower tine are of similar size, or if the upper one is up to twice longer than the lower one. Conversely, acicular lobe will be regarded as single if only the upper tine is present, or even if there is a round lower lobe, but that it is not visibly projected from the corresponding parapodial surface, such that the upper tine looks like being 3 or more times longer than the smaller one. There can be some size variations in those species provided with double acicular lobes, but in those regarded as having a single one, the shape can vary along a pattern of tapered projections. The tip of acicular lobes can be blunt, acute, or capitate, and this feature is usually conservative along the body and among members of the same species. However, assigning specimens to each group reported as having single vs double lobe is problematic, especially if one has a single specimen which has contracted or heavily contracted neurochaetal lobes, because this contraction renders the observation of acicular lobes more difficult. This can be solved by a scan of the neuropodial lobes along the body, or in extreme conditions, by a dissection of the contracted neuropodial lobe; this involves a longitudinal dissection along the chaetal bundle to open it and find out the type of acicular lobe.

As indicated above, the type of acicular lobe has been rejected as a diagnostic attribute. However, acicular lobes are consistent throughout the body and regarding them as single or double is useful to separate similar species, although their relative size can differ along body. Acicular lobes are rarely modified by erosion, during sample processing or even by cleaning specimens, although its shape might be altered by imperfect development, regeneration, or intense contraction. Nonetheless, throughout the body its development will be either as a single or double projection, although their visibility might be altered because of the contraction of the chaetal lobe within neuropodial lobes. It must be emphasised that parapodia must be mounted to be observed from the anterior side, and that for comparing parapodia from different specimens, they must be taken from a similar region, or even from the same chaetiger.

Fauvel (1911, 1923a) was right about the variation in acicular lobes, or rather about how they look if seen in anterior or posterior view of mounted parapodia. However, he failed to note that the parapodia he illustrated were shown in different perspectives, one is seen anteriorly, the other posteriorly, and either orientation modifies how we perceive them. This different orientation can be determined by the insertion of the ventral cirri. Further, quite infrequently the larger upper lobe can be duplicated, and the resulting diverging lobes are of similar size, and this may cause some confusion because whenever an acicular lobe is double, there must be two lobes involved, one above the other. In such rare duplications of the upper tine, a single lobe could be observed if the parapodia are seen from an anterior or posterior perspective, but once they are seen from above, duplicated lobes can be seen as aligned in the same plane. This implies that in order to precise what type of acicular lobe is present, several parapodia must be observed, in anterior view, before concluding about the number and type of acicular lobes. In some species regarded as having acicular lobes single, there might be in a few parapodia a lower bump, giving the false impression of being a double acicular lobe. Defining which one is present must be based, as indicated above, on the observation of several parapodia along body.

Chaetae

Neurochaetae are abundant, their number being relatively stable despite variations in body size. For example, Western Mexico specimens of *H. panamena* Chamberlin, 1919 (LACM 8555), ranging in size 14-35 mm long, have 25-30 neurochaetae per bundle. Neurochaetae are arranged in a bundle and if the parapodium is transversely cut, neurochaetae appear before aciculae as an oval bundle; neurochaetal handles are pale to greenish, and blades are mostly transparent although in older museum specimens they can become brownish. Handles are sometimes greenish, and their tips can be cylindrical or subdistally swollen; however, the observation of this feature requires chaetae are aligned in lateral view and along the same plane. Otherwise, there might be some light diffraction leading to a wrong characterisation, and this explains why this feature has not been emphasised.

Neurochaetal blades and guards

Neurochaetal blades can be short, medium-sized or long, especially along the first few chaetigers (1-3 or 1-7) as indicated by Uchida (2009: 36); it is better to indicate this as a proportion of how many times they are as long as wide; i.e., their length/width proportions. For measuring this proportion, blade width corresponds to the widest, basal region just above the articular or hinge membrane, and this is compared to the length of the blade, which is measured from this widest

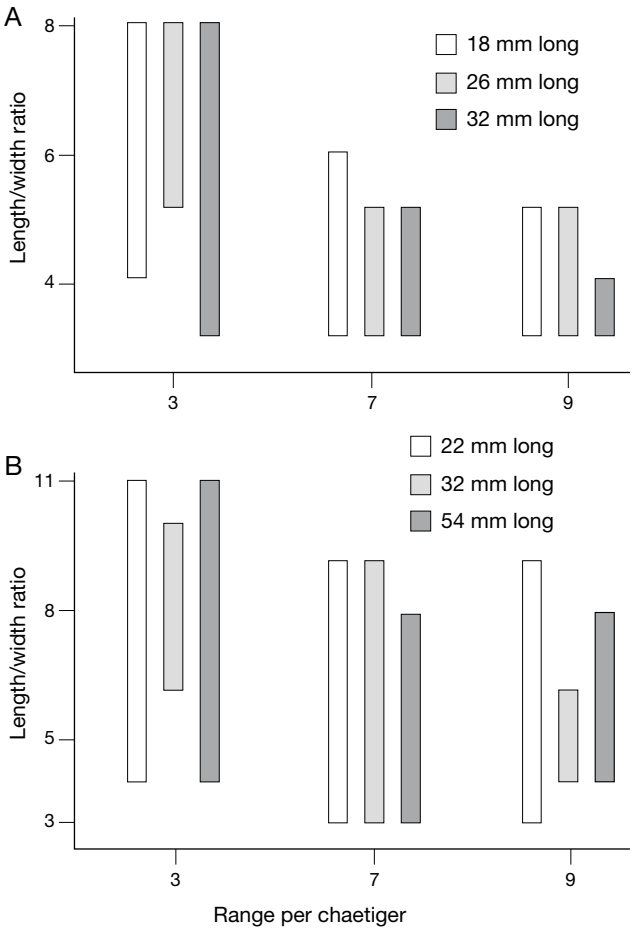

Fig. 1. — Range variation of neurochaetal blades length: width ratios in three chaetigers (3, 7, 9), observed in two different *Hesione* Savigny *in* Lamarck, 1818 species: **A**, *H. picta* Müller, 1858 from Florida (18 mm: UF 825, 26 mm: UF 826, 32 mm: UF 1593); **B**, *H. praetexta* Ehlers, 1887 from Florida (22 mm: UF 1060, 32 mm: UF 1064, 54 mm: UF 2574).

region to the tip of the apical tooth. Once this proportion is calculated, neurochaetal blades can be described depending on their relative proportions; in some species the variation would be narrow, and wider in others, and an indication of the range observed would help separating similar species. The observation of this variation in some specimens of two species and from the same region (Fig. 1) indicates that neurochaetal blades are progressively shorter along body, and that their length/width ratios are negatively size-dependent because ratios are longer in smaller specimens, and become shorter during development if similar chaetigers are compared. Consequently, in order to be reliable as a diagnostic feature, the comparison must be based on specimens of similar size, and with neurochaetae from the same chaetiger.

Blades have teeth along their cutting edge, and a medial projection, commonly regarded as guard because it lies ahead of teeth. Blades are usually bidentate, but some species have a single tooth, hence unidentate. Bidentate blades usually have their distal tooth larger than subdistal one, and in a few species subdistal teeth can be as wide as distal ones. The subdistal tooth is usually smaller and in some species it completely disappears, resulting in an unidentate blade. Blade teeth are usually directed laterally, but sometimes and especially along a few anterior chaetigers, or in the upper bundle chaetae of medial chaetigers, teeth are smaller and directed antero-laterally or even distally, instead. A few species only have this type of blade, but in some others having both types of dentition, they are usually combined in the same chaetal bundle, being those with smaller, distally directed teeth present in an upper position.

The usefulness of guards for taxonomic purposes, as indicated by Chamberlin (1919), Horst (1924) and Monro (1926, 1931), is well-supported, provided that several chaetae are examined, and whenever these delicate guards are complete because they are fragile. If undamaged, they can either approach the subdistal tooth, the distal one, surpass it, or be missing. This latter condition is rare, only known for two species; broken blade can be distinguished from other blades provided with guards, because after fracture, there is an evident marginal depression or scar where the guard used to be, whereas in those blades lacking guards, the margin is continuous. Because of its fragility, guards could be disregarded as diagnostic features, but because their relative size is fixed once the chaetae emerges from the chaetal lobe, guards are reliably diagnostic. Another means to recognize the relevance of this feature is the observation of newly exposed chaetal blades; right after being exposed, blades have a protective, ephemeral, transparent pointed hood, completely covering the blade from the handle tip, and this is progressively eroded as chaetae continue emerging from the chaetal lobe. The confirmation of the guards, as well as their relative length, can be noted after the observation of these newly emerged chaetae.

Aciculae

Dorsal cirri have 2-4 thin aciculae, sometimes half of them are darker than the others, but they are thin, barely visible by transparency of the dorsal cirrophore. Neuraciculae are thicker, longer and usually 1-2 (rarely 3) in number. In general, one neuracicula is markedly thicker and darker than the others, which are smaller and can be placed behind the largest one, such that their observation might be difficult in whole parapodial mounts. In some instances, as Horst (1924) pointed out, neuraciculae can be barely pigmented; sometimes the larger neuracicula is pale, in other cases two or all of them are pale; because aciculae consistently retain their pigmentation much longer than body wall, this feature is regarded as diagnostic.

Posterior end

The prepygidial segment has two pairs of lateral cirri, homologous to the dorsal and ventral cirri, but there are no chaetal lobes. The pygidium carries one pair of ventral cirri, often lost, and the anus is a circular opening, usually terminal, with a variable number of low, rounded to digitate papillae.

Anatomy

Digestive system

The digestive system includes four basic regions: pharynx, oesophagus, stomach, and intestine. The pharynx is short, eversible, tubular, made of three fused rings, as long as

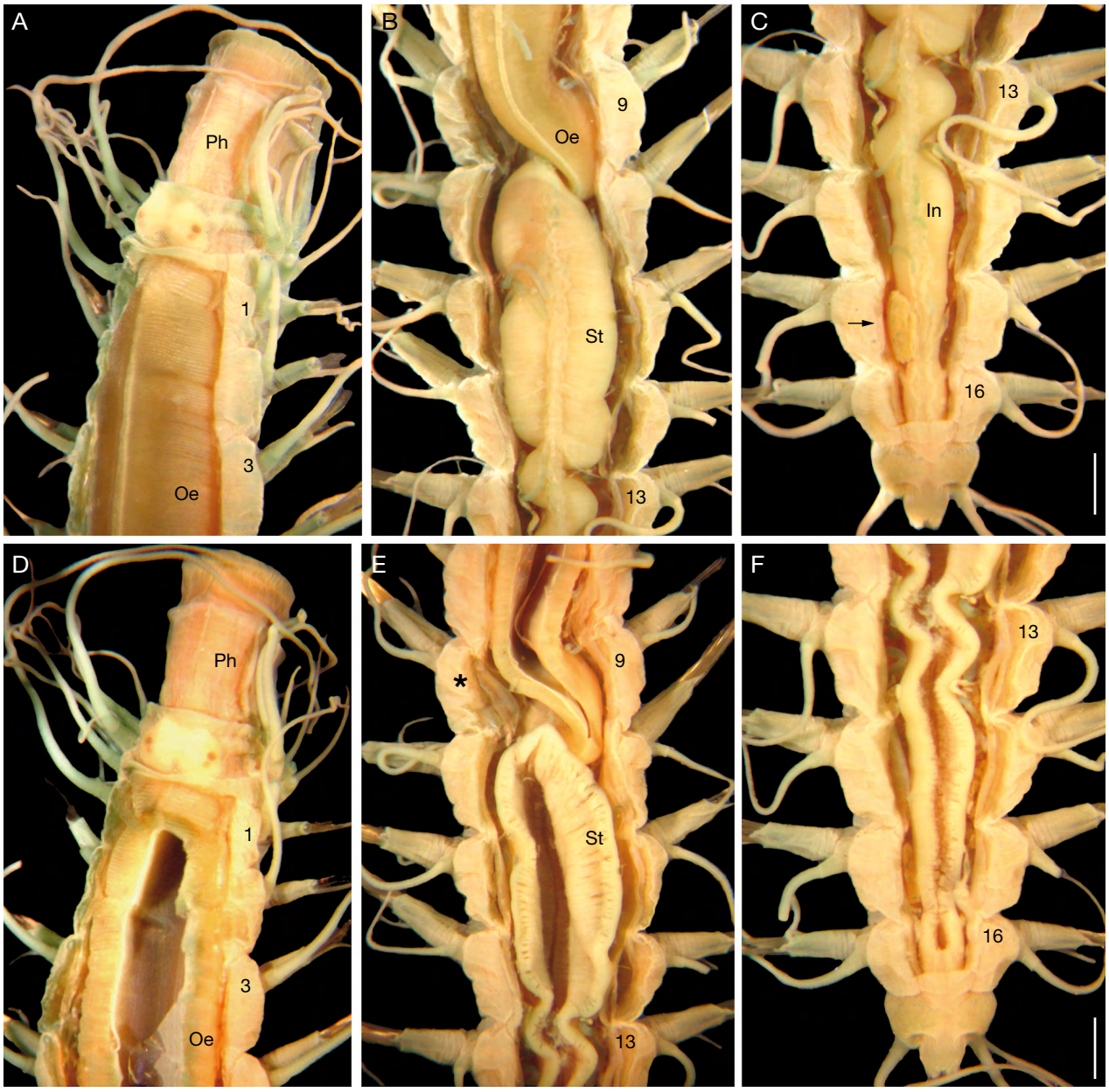

Fig. 2. — *Hesione panamena* Chamberlin, 1919, non type specimen, LACM 7101: **A**-**C**, dorsal view of anterior, medial and posterior regions; body wall removed; **D**-**F**, same body regions, digestive system organs with upper regions removed Abbreviations and symbols: arrows points to unknown gland; *, is close to enteric caecum; **numbers**, indicate chaetiger; **In**, intestine; **Oe**, oesophagus; **Ph**, pharynx; **St**, stomach). Scale bars: A-E, 0.8 mm; F, 0.7 mm.

first four chaetigers (Fig. 2A). Pharynx wall is thick, paler than following regions. A short, transitional region can be noted before the oesophagus; it has a slightly darker pigmentation, and has a clear discontinuity in the muscular rings forming the anterior enteric tube, visible at least dorsally.

The oesophagus is slightly longer than the eversible pharynx, extending along chaetigers 3 to 9; a distinct middorsal paler longitudinal band is visible along its length. Both pharynx and oesophagus have similar structure and thickness, and an inner chitinous layer (Fig. 2D). The long muscular oesophagus is displaced along the body axis by a series of long muscular fibers, stemming from the body wall, and serially attached along the middorsal and midventral oesophageal surfaces.

The stomach is roughly fusiform, paler, as long as three chaetigers; its walls are markedly more cavernous, glandular, and softer than the oesophagus (Fig. 2B, E). The oesophagus and the stomach are connected in chaetiger 10, with a progressively narrowing of the posterior oesophagal end, and slightly bent ventrally, probably because of an incomplete eversion of the pharynx; from their connection, one pair of enteric caeca extend anteriorly through 4-5 chaetigers (Fig. 2E, asterisk). The stomach has a posterior constriction and drives into a thinner, slightly sinuous intestine; the glandular walls are about as wide as those present in the stomach. The posterior

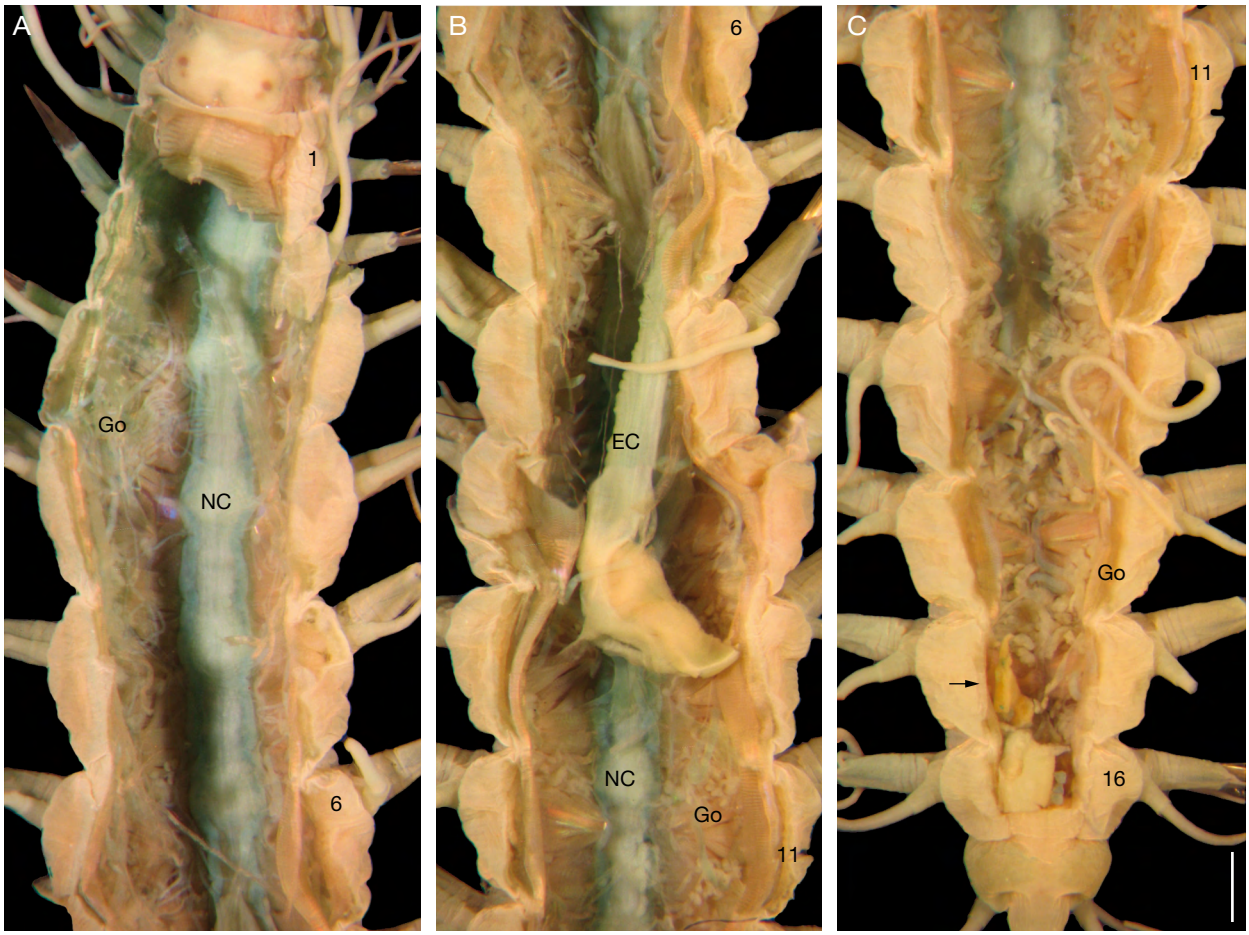

FIG. 3. — *Hesione panamena* Chamberlin, 1919, non type specimen, LACM 7101, after full removal of most parts of digestive system; numbers refer to chaetiger: **A**, anterior region, dorsal view; **B**, medial region, dorsal view; **C**, posterior region, dorsal view (arrows points to unknown gland). Abbreviations: **EC**, enteric caecum; **Go**, gonad; **NC**, nerve chord. Scale bars: A, 0.6 mm; B, C, 0.7 mm.

intestine becomes straight and drives to the anus (Fig. 2C, F). A large, apparently gland was present on the left side of the posterior intestine, in chaetiger 15 (Fig. 2C, arrow), but its function is unknown.

Pharynx and oesophagus are usually empty, but some prey items might be retained in the stomach. One specimen of *H. proctochona* from Florida (UF 1593) had its stomach slightly cut and exposed outside the body, after some parapodia were removed for molecular analysis. It had a complete, digested polynoid scale worm, but chaetae and elytra retained their original shape, such that it can be identified as *Harmothoe* sp. The thin inner cover along pharynx and oesophagus might be better developed in those species feeding upon scale worms in response to the ingestion of worms with abundant, defensive chaetae along the body.

The presence of paired caeca is shared in Nereididae and Syllidae, but in the former they are very small, whereas in the latter they are T-shaped, with an anterior and a posterior branch. In the enteric caeca of one specimen of *Hesione picta* Müller, 1858 from Florida (UF 1594), a siphonostomatoid copepod was found and it was described elsewhere (Suárez-Morales 2016).

Gonads

Gonads grow by an encirclement and lateral extension of gonadic tissue along blood vessels; gonads are more easily noticed when they are fully grown, invading most coelomic space available. In the same maturing specimens, there is a trend of increased gonadic development from the anterior region; first (Fig. 3A), the ventrolateral blood vessel ramificates into thin, whitish filaments. In median chaetigers (Fig. 3B), or in later stages, these filaments are progressively widened by the formation of oocytes, but usually retain some filament-like outlook. In the posterior region (Fig. 3C), these filaments become wider, rounded, globular to ovoid, because of the presence of abundant oocytes in the gonad.

Under low magnification, the gonad looks like an ovary because oocytes are more easily noticed (Fig. 4A, B), extended along blood vessels. Detached oocytes, released after the fracture of the gonad wall, look ovoid with irregular cover, and having a large central nucleus (Fig. 4C). Under higher magnification, the hermaphroditic gonad is shown to contain both oocytes and sperm, and oocytes look like having a central single, or double invagination and although some

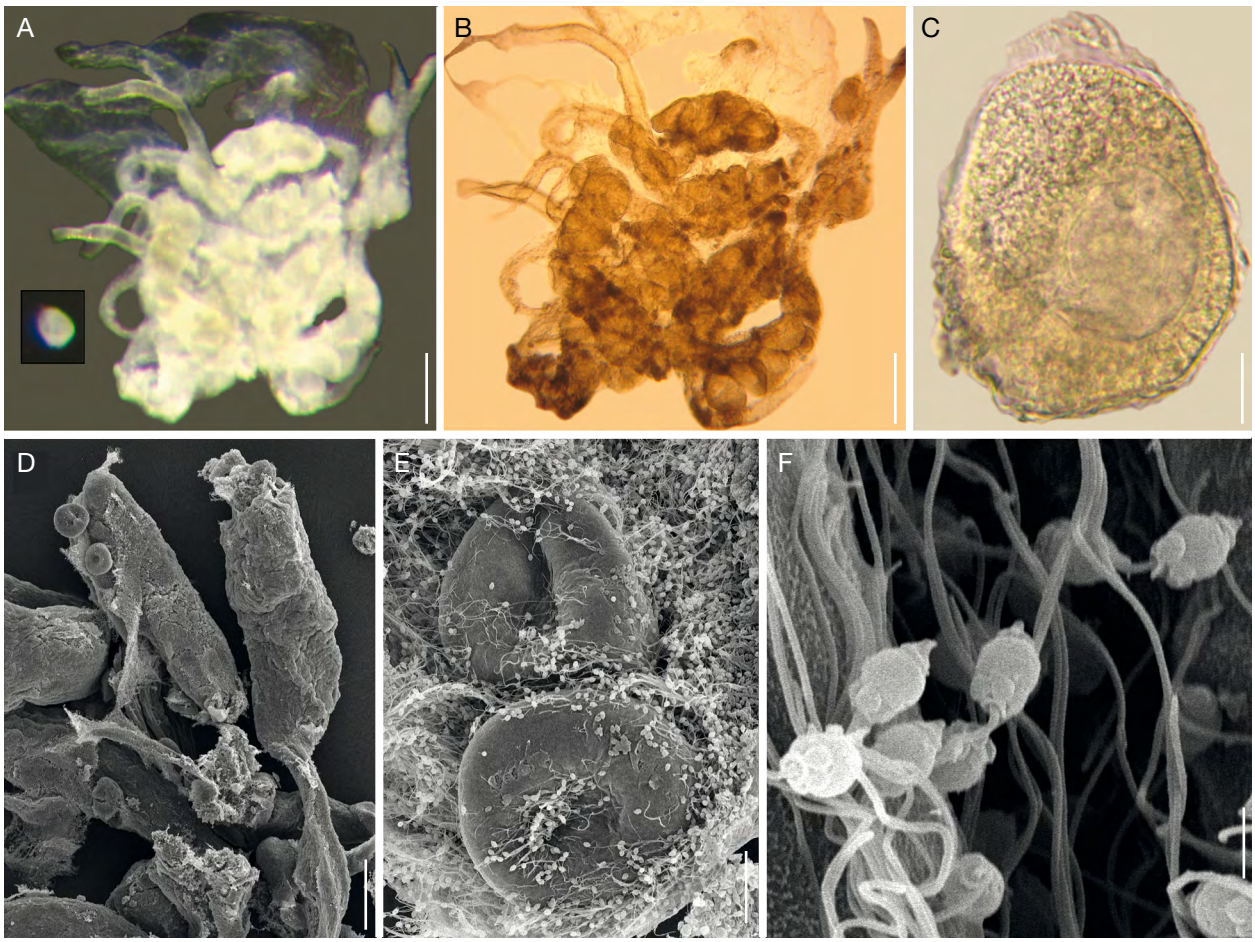

Fig. 4. — **A**-**C**, *Hesione panamena* Chamberlin, 1919, non-type specimen, LACM 7101: **A**, fragment of a gonad observed in the stereoscope (inset: isolated oocyte); **B**, same, observed in a microscope; **C**, oocyte, observed in microscope; **D**-**F**, *Hesione genetta* Grube, 1867, non-type specimen, UF 95: **D**, fragments of gonads, two oocytes shown after rupture of the gonad wall; **E**, close-up of another fragment of gonad showing two oocytes with abundant spermatozoans surrounding them; **F**, close-up of spermatozoans. Scale bars: A, B, 0.2 mm; C, E, 20 µm; D, 140 µm; F, 1.4 µm.

might be released from the gonad after fracture (Fig. 4D), the abundance of sperm in other gonad fragments confirms its hermaphroditic role (Fig. 4E). The spermatozoan is ectaquasperm (Fig. 4F). The head includes the acrosome and the nucleus; the acrosome is conical, with a well-defined tip and a basal expansion, and it is separated by a thin collar-like depression from the nucleus. The nucleus is globular, slightly as long as wide. The middle piece carries two hemispherical mitochondria, and the tail or flagellum is inserted in a well defined attachment site.

Oocytes are apparently released in the coelom, but how and when sperm is released is unknown. The gross structure of gonads shows abundant tiny, globular cells that correspond to spermatids, and once detached, they show flagella. Because this same development was found in many species, it can be concluded that *Hesione* species are simultaneous hermaphrodites. How they can manage to avoid self-fertilisation is not known, but embryos were not found in coelomic or parapodial inner spaces.

Bergmann (1902, 1903) found that the same gonad produces both oocytes and sperm in *H. sicula* and he regarded the species as hermaphrodite. His findings are confirmed for *H. genetta*, *H. paulayi* n. sp., and *H. proctochona.* Two patterns were noticed: in *H. proctochona* the gonad is a thin, almost one-oocyte thick layer along blood vessels, taking a branching arrangement with thin twigs, whereas in *H. genetta* and *H. paulayi* n. sp., the gonad is globular, about 5-10 oocytes wide, and blood vessels are not seen running through the centre of the gonad. However, these differences are rather explained by the maturity of the gonad, being more complex when fully grown. Oocytes detached from the gonads float in the coelom, and can be noticed inside parapodial lobes, but as Bergmann (1902, 1903) had indicated, despite the fact that they are being surrounded by sperm, no fertilised eggs or embryos were observed.

Nerve chord

The ventral nerve chord is thick with larger ganglia at the level of parapodia, and completely covered by a thin, transparent layer, apparently including glands or phospholipids because it stains with Methyl Green.

SYSTEMATICS

Family Hesionidae Grube, 1850
Subfamily Hesioninae Grube, 1850

Hesione Savigny *in* Lamarck, 1818

Hesione Savigny *in* Lamarck, 1818: 315. — Savigny 1822: 12. — Blainville 1828: 481-482. — Audouin & Milne Edwards 1833: 232-233. — Grube 1850: 306; 1878: 102; 1880: 220-221, 224-227. — Schmarda 1861: 79. — Ehlers 1864: 187. — Quatrefages 1866: 93, 95. — Chamberlin 1919: 185. — Horst 1921: 80, 1924: 192. — Fauvel 1923a: 233; 1932a: 60; 1934: 21; 1947a: 30; 1953b: 103. — Hartman 1940: 211-212. — Day 1967: 227. — Fauchald 1977a: 76. — Campoy 1982: 208. — Uebelacker 1984: 28-36. — Pleijel 1998: 107.

Fallacia Quatrefages, 1866: 98. Type species not designated.

Telamone Claparède, 1868: 541. Type species: *Hesione sicula* delle Chiaje, 1830, by monotypy.

Type species. — *Hesione splendida* Savigny *in* Lamarck, 1818, by subsequent designation (Quatrefages 1866: 95).

Diagnosis (modified after Pleijel 1998: 107). — Hesioninae with 8 pairs of long tentacular cirri; 21 segments, 16 chaetigers; prostomium with antennae, without palps; parapodia without notochaetae; dorsal and ventral cirri basally cylindrical, rarely swollen; acicular lobe single or double; neuraciculae usually black, at least the smaller one; neurochaetae with blades usually bidentate, rarely unidentate, usually with guards; pharynx cylindrical with a basal dorsal papilla, without marginal papillae.

Distribution. — Pantropical, reaching subtropical regions, mostly in shallow water and mixed bottoms.

Remarks

Savigny (1822: 39) indicated four anterior appendages in the diagnosis of *Hesione*, but because they were not included in the description (Savigny 1822: 40), nor in the corresponding illustration (his plate 3, figure 3), their number were regarded as a mistake. This was corrected by Grube (1867: 65), and later Chamberlin (1919: 185) followed this in his key to genera. However, by following the original diagnosis and regarding *Hesione* with 4 antennae and 8 pairs of tentacular cirri, de Quatrefages (1866) proposed *Fallacia* to include species with only 2 antennae. *Fallacia* would contain *H. pantherina* Risso, 1826 and *H. picta* Müller, 1858 (listed as *H. proctochona* Schmarda, 1861). Claparède (1868: 541) proposed *Telamone* with 2 antennae and 6 pairs of tentacular cirri, by overlooking two of the smaller, often dehiscent pairs, to include only *H. sicula* delle Chiaje, 1830, its type species. Because these two genera were proposed after an incorrect diagnosis but referred to the same body pattern, *Fallacia* and *Telamone* are junior synonyms of *Hesione,* as indicated elsewhere (Fauvel 1911: 374, Chamberlin 1919: 186, Pleijel 1998: 107).

Hesione includes 23 species. Twelve species are redescribed, restricted or reinstated: *H. ceylonica* Grube, 1874, *H. eugeniae* Kinberg, 1866, *H. genetta* Grube, 1867, *H. intertexta* Grube, 1878, *H. pacifica* McIntosh, 1885, *H. panamena* Chamberlin, 1919, *H. pantherina* Risso, 1826, *H. picta* Müller, 1858 (incl. *H. proctochona* Schmarda, 1861 and *H. vittigera* Ehlers, 1887), *H. praetexta* Ehlers, 1887, *H. sicula* delle Chiaje, 1830 (incl. *H. steenstrupi* de Quatrefages, 1866), and *H. splendida* Savigny *in* Lamarck, 1818 (incl. *H. ehlersi* Gravier, 1900); *H. reticulata* von Marenzeller, 1879 has been recently redefined (Jimi *et al.* 2017). On the other hand, 11 species are newly described: *H. beneliahuae* n. sp. from La Réunion, *H. fitzhughi* n. sp. from Australia, *H. harrisae* n. sp. from Puerto Rico, *H. hartmanae* n. sp. from the Galápagos Islands, *H. helenensis* n. sp. from Saint Helena Island, *H. horsti* n. sp. from Indonesia, *H. keablei* n. sp. from Australia, *H. mooreae* n. sp. from Saudi Arabia, *H. osbornae* n. sp. from The Philippines, *H. paulayi* n. sp. from Papua New Guinea, and *H. uchidai* n. sp. from The Philippines.

Two other species are *nomina nuda*: *H. festiva* Savigny *in* Lamarck, 1818 and *H.* de Savigny (sic) Costa, 1841. The diagnosis for the former was repeated by Audouin & Milne-Edwards (1833: 235), but it is rather incomplete. Savigny (1822: 49) indicated it referred to a species discovered by Risso, but without providing enough detail to conserve this specific combination, and this was probably the same species that was later described as *H. pantherina* by Risso himself (Risso 1826). For *H.* 'de Savigny', described by Costa (1841: 268-269, pl. 11, fig. 2), and compiled by de Quatrefages (1866: 111), Pleijel (1998: 158) correctly regarded this binomen as a *nomen nudum*. The reasons for this is that the publication by Costa (1841) did not comply with the article 11 of the *Code* (ICZN 1999: 11.3 Derivation, 11.4 Consistent use of binominal nomenclature, 11.9 Species group names). On the other hand, Marion & Bobretzky (1875: 47) regarded it as a junior synonym of *H. sicula* delle Chiaje, 1830, and because of the proximity to *H. sicula* type locality, this conclusion might be correct.

Hesione beneliahuae n. sp.
(Figs 5, 6)

urn:lsid:zoobank.org:act:1862BD5B-7FA6-49AD-9A24-05F9D55B429E

Type material. — **Western Indian Ocean. Mascarene Islands.** Holotype. UF 658, Réunion Island, Saint-Leu, Sec Jaune (-21.153333, 55.28111666; 21°09'11.9988"S, 055°16'52.0200"E), 17.VIII.2007, 6-15 m depth, H. Bruggemann, N. Hubert, F. Michonneau & G. Paulay coll.

Additional material. — **Red Sea, Saudi Arabia**. 1 specimen, UF 3658, offshore of Farasan Banks, Dolphen Lagoon (19.00533, 40.14815; 19°00'19.1880"N, 040°08'53.3400"E), reef lagoon, barrier reef flat, and fore reef wall, 4.III.2013, 1-25 m depth, A. Anker, P. Norby & G. Paulay coll. [21 mm long, 2 mm wide; no pigmentation].

Persian Gulf, Saudi Arabia. 1 specimen, UF 4222, Abu Sahim (22.65865, 38.88435; 22°39'31.1400"N, 038°53'03.6600"E), 5-9 m [without posterior end (removed for molecular analysis); 22 mm long, 3 mm wide, 13 chaetigers; longest tentacular cirri with broken tips, reach chaetiger 3; dorsal cirri longer than body width, including parapodia; acicular lobes of different size along body, subequal in some anterior and posterior chaetigers, in others upper tines twice longer or ⅓ longer than lower ones].

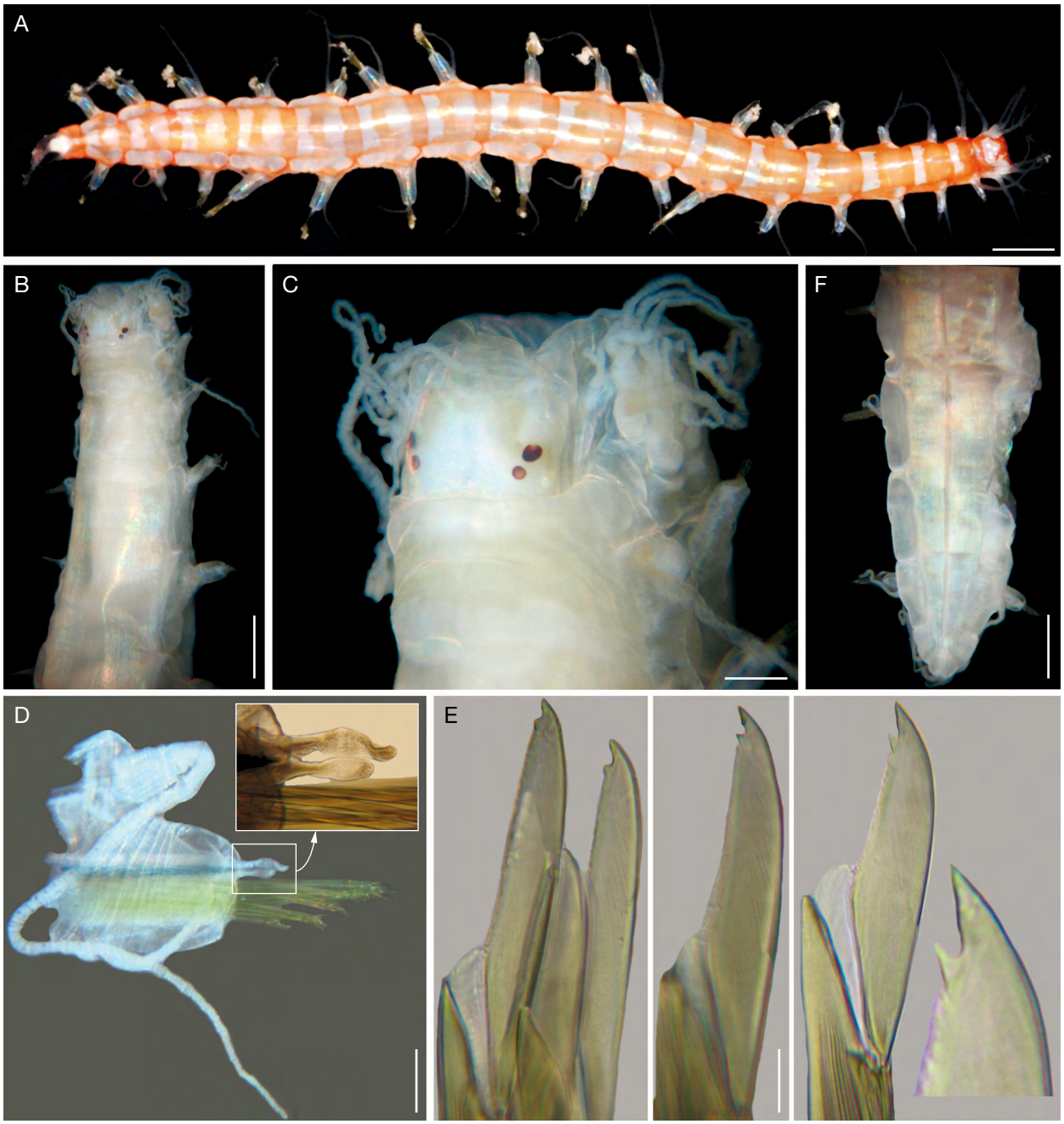

FIG. 5. — *Hesione beneliahuae* n. sp., holotype, UF 658: **A**, living specimen, dorsal view, head to the right, **B**, anterior region, dorsal view; **C**, anterior end, oblique dorsal view; **D**, chaetiger 8, left parapodium, anterior view (inset: acicular lobe); **E**, same, blades of upper, medial and lower neurochaetae (inset: lower blade tip); **F**, posterior region, dorsal view. Scale bars: A, 3.5 mm; B, 1.8 mm; C, 0.5 mm; D, 0.4 mm; E, 25 µm; F, 1.5 mm.

ETYMOLOGY. — This species is named to honor the late Dr M. Nechama Ben-Eliahu, in recognition of her many publications on taxonomy of polychaetes, and her efforts supporting scientific collections (Chipman & ten Hove 2014). The name is a noun in genitive (ICZN 1999: art. 31.1.2).

DISTRIBUTION. — Western Indian Ocean, including the Red Sea, the Persian Gulf and La Réunion Island, in shallow water (1-25 m) mixed or sandy bottoms.

DIAGNOSIS. — *Hesione* with prostomium rectangular; parapodia with dorsal cirri basally cylindrical, dorsal cirrophore as long as wide; larger neuracicula blackish; acicular lobe double, upper tine slightly longer than lower one; neurochaetal blades bidentate, subdistal tooth smaller than distal one, but without guards.

DESCRIPTION

Holotype, UF 658, complete, whitish, shiny, poorly defined pale brown bands in prostomium, and barely visible dorsally along chaetigers 1-3 (Fig. 5B) in ethanol; slightly distorted by fixation into a small container; cirri corrugated, many dorsal cirri missing; a posterolateral dissection on right side removed parapodia of chaetigers 11-15 for molecular analysis. Body subcylindical, tapered posteriorly, 34 mm long, 3.5 mm wide.

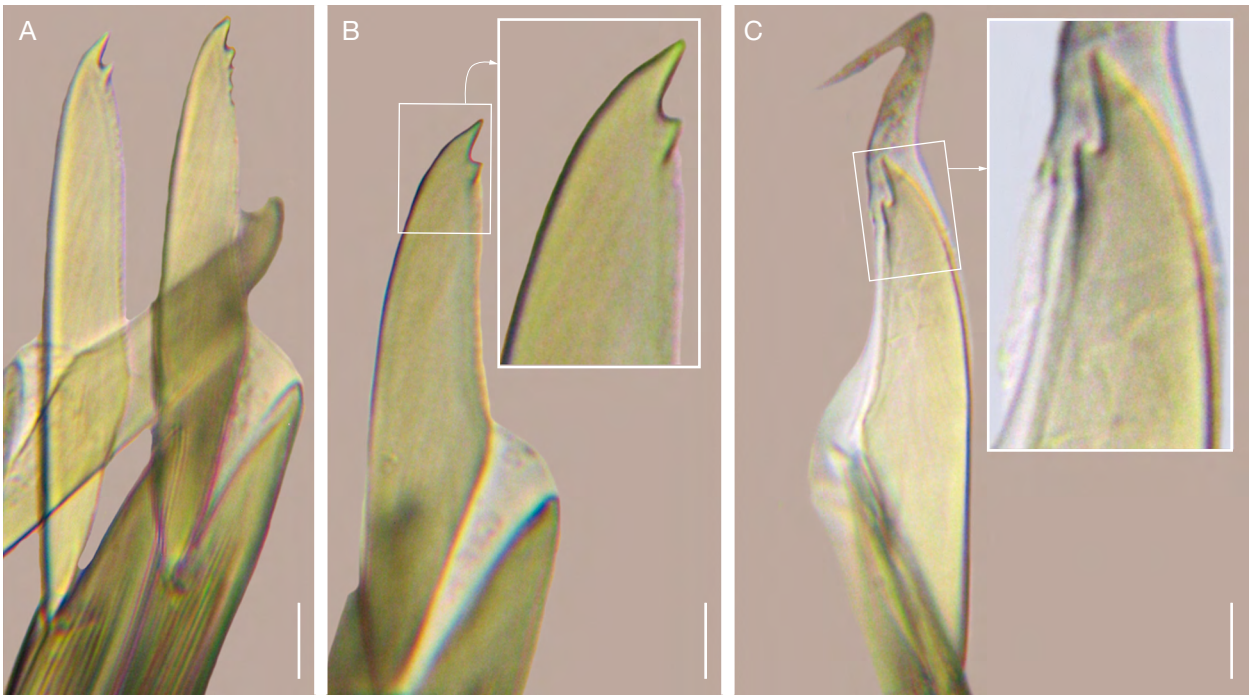

Fig. 6. — *Hesione beneliahuae* n. sp., non-type specimen, UF 3658, chaetiger 10, right parapodium, neurochaetal blades: **A**, upper chaetae, one with eroded subdistal tooth; **B**, lower chaetae, with entire teeth (inset: close-up of teeth); **C**, newly emerged blade, still covered with transparent sheet (inset: close up of teeth). Scale bars: A, 15 µm; B, C, 12 µm.

Prostomium rectangular, slightly as long as wide, anterior margin truncate, lateral margins straight, posterior margin barely exposed, longitudinal depression very shallow, restricted to prostomial posterior fourth. Antennae long, digitate, 3-4 times as long as wide. Eyes brownish, anterior ones twice larger, and slightly more separated than posterior ones (Fig. 5C).

Tentacular cirri irregularly contracted, difficult to be pulled posteriorly; relative length to anterior chaetigers unknown. Lateral cushions barely projected, some divided into anterior and posterior sections, others with three sections.

Parapodia with chaetal lobes truncate (Fig. 5D), most dorsal cirri lost; dorsal cirrophores about as long as wide, cirrostyles basally smooth, cylindrical, medially annulated, distally articulated; shorter than body width. Ventral cirri basally smooth, irregularly contracted medially and distally, surpassing chaetal lobe.

Neuraciculae blackish, two, larger one 3 times thicker than smaller one. Acicular lobes double, tines digitate; upper one tapered, slightly longer than lower one, blunt, medially wider (Fig. 5D [inset]).

Neurochaetae about 20 per bundle, handles honey-colored, blades bidentate, at a certain angle from handle, 3-5 times as long as wide, decreasing in size ventrally, each with smaller subdistal tooth, sharp to blunt, about ⅓ as wide as larger tooth, often eroded to blunt tips; guards completely absent (Fig. 5E).

Posterior region tapered into a blunt cone (Fig. 5F); pygidium smooth, anus projected with about 5 lobate papillae.

Pharynx not exposed. Oocytes not seen.

Pigmentation

Body reddish, with reddish bands dorsally over a whitish background, extended over lateral cushions (Fig. 5A), but lateral pigmentation better defined along chaetigers 1-7; reddish bands wide, with anterior margin well defined, posterior margin irregular, each band positioned along chaetal lobes, but leaving a pale, oval area over dorsal cirri; bands progressively longer along chaetigers 1-7, thereafter becoming paler medially along chaetigers 8-9, and from chaetiger 10 the central area paler such that the wide transverse bands become progressively separated into two thinner transverse bands. Prostomium reddish with a pentagonal whitish, central area. Tentacular, dorsal cirri and chaetal lobes pale.

Variation

A small specimen (UF 3658) has anterior eyes only slightly larger than posterior ones, and acicular lobes of different length along the body; in chaetigers 1-3 acicular lobes are subequal, in chaetigers 4-7 upper tines are about twice longer than lower ones, and in other chaetigers lower tines are ⅓ as long as the upper ones. Chaetal blades lack guards completely and marginal teeth are visible in upper chaetae (Fig. 6A), or barely visible at all (Fig. 6B [inset]); a newly emerged neurochaetae, still with its transparent sheet (Fig. 6C [inset]) confirms the complete absence of guards.

Remarks

Hesione beneliahuae n. sp. resembles *H. splendida* Savigny *in* Lamarck, 1818 because they both have a shiny integument, and both are present in the Western Indian Ocean.

However, they differ in two main features: acicular lobes and neurochaetal blades. In *H. beneliahuae* n. sp. acicular lobes are double, both tines blunt, of similar length, or lower tine shorter, and neurochaetal blades have no guards at all, whereas in *H. splendida* acicular lobes are single, and neurochaetal blades have guards approaching distal tooth.

On the other hand, *H. beneliahuae* n. sp. resembles *H. keablei* n. sp. (see below) because both species have blades without guards. However, they differ because in *H. beneliahuae* n. sp. dorsal cirrophores are as long as wide, and its prostomium is rectangular with well-defined eyes, whereas in *H. keablei* n. sp. the dorsal cirrophores are twice as long as wide, and its prostomium is wider posteriorly, with poorly defined eyes.

Another similar species is present in the Gulf of Manaar. A juvenile specimen (MNHN-IA-PNT90a [formerly jar 372]; 12 mm long, 2 mm wide), probably collected with other specimens reported by Fauvel (1929) from Krusadai Island, was found in a *Tubipora* mass. This species also has acicular lobe double, and neurochaetal blades without guards. It is regarded as a different species because its anterior eyes are displaced posteriorly, diffuse, and markedly as wide as long, as two brownish short, lateral transverse bands. The specimen is macerated and better material is needed to formally describe the species.

Hesione ceylonica Grube, 1874 reinstated
(Figs 7-9)

Hesione ceylonica Grube, 1874: 327. — Willey 1905: 266.

Hesione intertexta – Monro 1937: 270. — Fauvel 1953b: 105 (*non* Grube, 1878).

Hesione pantherina – Gravier 1900: 179-180, pl. 10, fig. 16. — Fauvel 1911: 374-376, fig. 6; 1919b: 370, 371; 1927: 417; 1932a: 60, 61; 1953b: 104, 105, fig. 49A-G; 1955: 105. — Aziz 1938: 23, 24, pl. 3, fig. 6, pl. 7, fig. 23, pl. 7, fig. 46. — Fishelson & Rullier 1969: 58, 59 (*non* Risso, 1826).

Hesione splendida – Augener 1926: 451, 452. — Day 1973: 343, 344. — Misra 1999: 145, 146 (*non* Savigny *in* Lamarck, 1818).

Type material. — **Indian Ocean, Sri Lanka.** Neotype, ZMH-P 9951, and one specimen labelled paraneotype, ZMUC 2432, Trincomalee (08°34'00"N, 81°14'00"E), 2.IX.1889, K. Friestedt coll. [specimen labelled paraneotype complete, 46 mm long, 5 mm wide; anterior end distorted by compression into small container, laterally bent; chaetae from left parapodium of chaetiger 10, and right parapodium of chetiger 11 previously removed; most cirri broken medially; most chaetae broken; body integument smooth along chaetigers 2-10, others with 7-9 longitudinal, continuous keels; lateral cushions with longitudinal ridges; dorsal cirri smaller than body width].

Additional material. — **Indian Ocean. Sri Lanka (Ceylon).** 1 specimen, BMNH 1874.10.2.10, 1874, E. W. H. Hodsworth coll. (complete, slightly macerated, longitudinal lines barely visible along last three chaetigers; left parapodia of chaetigers 5, 6, and right parapodium of chaetiger 8 previously removed; acicular lobes single; body 24 mm long, 3.5 mm wide). — 1 specimen, MNHN-IA-PNT90b [formerly jar 372], Mannar, no further data (complete, slightly macerated, longitudinal lines barely visible along last three chaetigers; left parapodia of chaetigers 5, 6, and right parapodium of chaetiger 8 previously removed; acicular lobes single; body 24 mm long, 3.5 mm wide).
India. 2 specimens, BMNH 1922.12.22.2, Madras, no further data [45-50 mm long, 6 mm wide; distorted, variably damaged, integument with longitudinal ridges in first few chaetigers, lateral cushions with longitudinal ridges in posterior chaetigers; antennae digitate, 2-3 times as long as wide; larger specimen with a longitudinal, dorsal dissection through chaetigers 1-15; right parapodia of chaetigers 7 and 10 previously removed; acicular lobe single, tapered; neurochaetae most broken or without blades]. — 2 specimens, BMNH 1926.4.30.115, Ramesvaram, Gulf of Mannar, E. Thurston coll., no further data [one macerated, with strange, destructive dissections along and across body; right parapodia of chaetigers 7 and 15 (one of each specimen) previously removed; body colorless, complete one 44 mm long, 5 mm wide; well-defined longitudinal ridges at least in posterior chaetigers; lateral cushions with longitudinal ridges; acicular lobe single, tapered].
Gulf of Aden. 7 specimens, MNHN-IA-PNT91 (formerly jar 70), Aden (12°48'N, 45°02'E), Yemen, 1893, N. Jousseaume coll. [6 specimens macerated, the other in better condition, with dorsal longitudinal bands now only visible in chaetiger 1; best preserved specimen with a longitudinal dissection ventrally].
Oman. 1 specimen, BMNH 1937.9.2.104, John Murray Expedition, Sta. 53, off Ras Al-Mabrakah, dredge, 13.5 m depth, 2.XI.1933 [35 mm long, 5 mm wide; colorless, bent ventrally, cirri slightly macerated; left parapodia of chaetigers 7 and 8 previously removed; antennae digitate, 2-3 times as long as wide; eyes brownish, anterior ones slightly larger than posterior ones; acicular lobe single, basally swollen, tapered, blunt; ventral cirri surpassing chaetal lobe]. — 1 specimen, UF 408, SSE tip of Bar Al Hikman Peninsula (20.337833, 58.387883; 20°20'16.1988"N, 058°23'16.3788"E), 4-5 m depth, V. Bonito, M Claereboudt & G. Paulay coll. [22 mm long, 3 mm wide, 15 chaetigers left; posterior end removed for molecular analysis; pigmentation barely visible; acicular lobe single, tapered, blunt].
Persian Gulf. Kuwait. 1 specimen, BMNH 1938.5.7.16, harbor, gift from the Indian Museum [partially dehydrated; 38 mm long, 5 mm wide; colorless, integument tuberculated, lateral cushions with longitudinal ridges in posterior chaetigers; acicular lobe single, tapered].
Saudi Arabia. 1 specimen, SMF 9248, Jubail Research Center, Project Marine Sanctuary for the Gulf Region 1991, leg. D. Fiege, 9.XII.1991 [27 mm long, 4 mm wide; colorless, slightly dehydrated, dorsal and tentacular cirri dehiscent, several lost; right parapodium of chaetiger 9 removed for observation (kept in vial); body slightly bent laterally, antennae ovate, twice as long as wide; eyes brownish, anterior ones slightly larger than posterior ones; acicular lobe single, basally swollen, tapered, blunt; ventral cirri surpassing chaetal lobe; neurochaetal blades bidentate, subdistal tooth smaller, guards mostly broken, if entire, approaching distal tooth].
Red Sea. 1 specimen, BMNH 1926.11.12.9, Cambridge Suez Canal Expedition, Suez, no further data [41 mm long, 9 mm wide; body slightly bent dorsally, integument smooth, pigmentation pattern as slightly discontinuous longitudinal, irregular bands throughout body; antennae digitate, 4-5 times as long as wide; right parapodium of chaetiger 13 removed for observation (kept in vial); acicular lobe single, tapered, a few with bifid tips; neurochaetae most broken, blades bidentate, subdistal tooth smaller than distal one; guards broken, approaching subdistal tooth; pharynx partially exposed, dorsal papilla slightly as long as wide]. — 1 specimen, BMNH 1926.11.12.16, Cambridge Suez Canal Expedition, Suez, Tousonu, 29.XI.1924, no further data [17 mm long, 4.5 mm wide; body distorted, bent ventrally, integument smooth, discontinuous barely-pigmented longitudinal, irregular bands throughout anterior 5-6 chaetigers; antennae broken, left one truncate, right one tapered, 3-4 times as long as wide; acicular lobe single, tapered; neurochaetae variably damaged, blades bidentate, subdistal tooth smaller than distal one; pharynx partially exposed, dorsal papilla slightly as wide as long]. — 3 specimens, BMNH 1926.11.12.19/21,

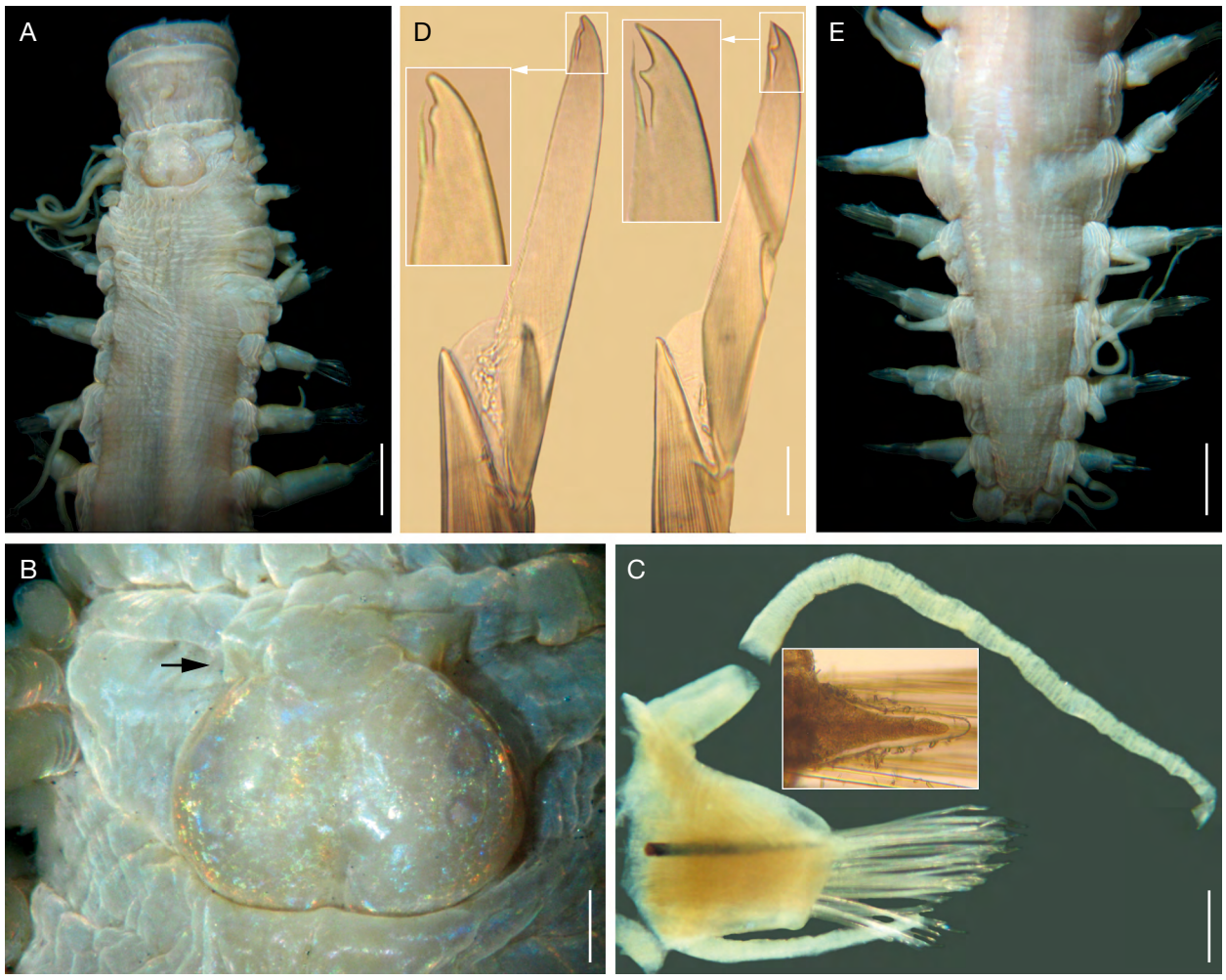

Fig. 7. — *Hesione ceylonica* Grube, 1874, neotype, ZMH-P 9951: **A**, anterior end, dorsal view; **B**, prostomium, dorsal view (arrow points to left antenna); **C**, chaetiger 7, left parapodium, anterior view (inset: close-up of acicular lobe); **D**, same, two neurochaetal blades (insets: tips of blades); **E**, posterior region, dorsal view. Scale bars: A, E, 1.4 mm; B, 0.3 mm; C, 0.4 mm; D, 25 µm.

Cambridge Suez Canal Expedition, Suez, St.K2, 17.X.1924, no further data [19-25 mm long, 4-5 mm wide; body distorted, variably damaged, bent dorsally, integument smooth, discontinuous barely-pigmented longitudinal, irregular bands, better defined along anterior chaetigers; antennae broken; acicular lobe single, tapered; neurochaetae variably damaged, parapodia not examined; pharynx variably exposed, dorsal papilla visible in 1 specimen, slightly as wide as long]. — 1 specimen, BMNH 1926.11.12.22, Cambridge Suez Canal Expedition, Suez, Sta. K1, 16.X.1924, no further data [17 mm long, 4.5 mm wide; integument smooth, discontinuous barely-pigmented longitudinal, irregular bands throughout anterior 5 chaetigers; antennae broken, tapered, 2-3 times as long as wide; acicular lobe single, tapered, if fully extended about ¼ as long as neurochaetae; neurochaetae variably damaged, not observed; pharynx partially exposed, dorsal papilla slightly as wide as long]. — 1 specimen, BMNH 1956.8.8.13, Gulf of Aqaba, Eilat, Israel, no further data [40 mm long, 8 mm wide; integument smooth, showing some longitudinal, feebly defined ridges, colorless; gonads exposed by fracture of body wall in chaetigers 6, 12 and 14; antennae digitate, 5-6 times as long as wide; left parapodium of chaetiger 6 previously removed; acicular lobe single, tapered, if fully extended about ⅙ as long as neurochaetae; neurochaetae variably damaged, not observed; oocytes about 100 µm in diameter]. — 3 specimens, SMF 2642, 1827, E. Rüppell coll., id. as *H. marmorata* [31-38 mm long, 3.0-4.5 mm wide; colorless, turgid, neurochaetal blades mostly lost, remaining blades eroded; left parapodium of chaetiger 11 removed for observation (kept in container); anterior eyes twice as large as posterior ones (colorless in larger specimen); antennae digitate, twice as long as wide; lateral cushions barely projected, entire, smaller specimen with longitudinal ridges in posterior chaetigers; acicular lobe single, tapered; neurochaetal blades and handle articulation tips severely eroded].

Saudi Arabia. 5 specimens, RMNH 282, Jeddah (21°32'36"N, 39°10'22"E), 1881, no further data [30-40 mm long, 4-5 mm wide; 2 specimens macerated, the other three in better condition including one with pharynx partially exposed, and retaining some pigmentation dorsally; eye size variable; acicular lobe single, conical to globose, depending on contraction of chaetal lobe]. — 1 specimen, UF 3486, Farasan Islands, Abu Lad (16.79772, 42.19910; 16°47'51.7920"N, 042°11'56.7600"E), fringing reef slope with abundant *Sargassum*, 1-10 m depth, 10.III.2013, A. Anker, P. Norby & G. Paulay coll. [26 mm long, 2.5 mm wide; body with 11-13 dorsal discontinuous irregular brownish longitudinal bands, separated by pale areas along chaetal lobes in chaetigers 2-9, less defined posteriorly; prostomium with brownish anterior band, and a thinner band running over eyes converging over the nuchal organs median furrow; antennae shorter than interocular distance; eyes brownish, anterior eyes darker, about twice as large as posterior ones; longest tentacular cirri reaching chaetiger 6; dorsal cirri with cirrophores twice as long as wide, cirrostyle basally cylindrical,

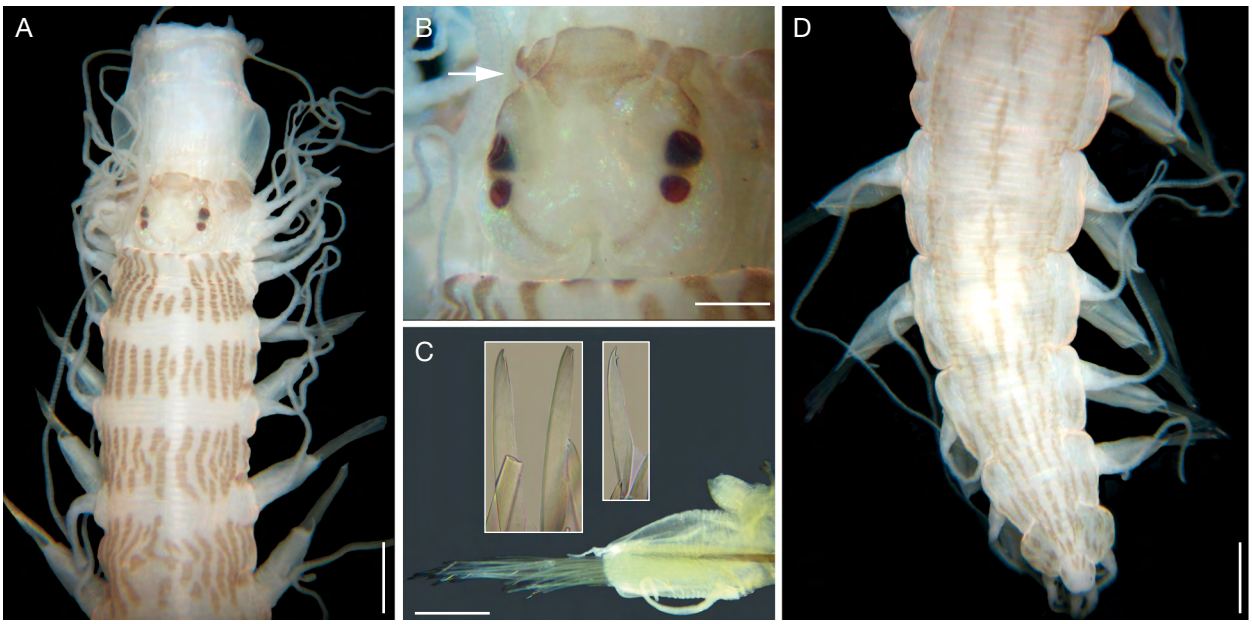

Fig. 8. — *Hesione ceylonica* Grube, 1874, UF 3486: **A**, anterior end, dorsal view; **B**, head, dorsal view (arrow points to left antenna); **C**, chaetiger 8, right parapodium, anterior view (insets, two upper and one lower neurochaetal blades); **D**, posterior region, dorsal view. Scale bars: A, 1 mm; B, 0.3 mm; C, 0.6 mm; D, 0.9 mm.

annulated, as long as body width (without parapodia); ventral cirri irregularly contracted, longer than chaetal lobe; acicular lobe single, tapered, blunt; neurochaetae about 20 per bundle; blades long, bidentate, upper ones with tiny denticles, directed subdistally, most with lateral teeth, subdistal tooth smaller, guard approaching subdistal tooth; posterior end tapered into a blunt cone; pygidium with pigmentation bands, anus projected, anal papillae not exposed].

Mozambique. 2 specimens, BMNH 1955.4.1.100/101, Capetown University Expedition to Morrumbene, 1954, Morrumbene Estuary, Sta. 155K, San José Mission, *Cymodocea* bed, 17.VII.1954, no further data [45-48 mm long, 5-6 mm wide; damaged, distorted, most cirri and chaetal blades lost; almost colorless, longitudinal lines or elongated spots visible along posterior chaetigers; eyes blackish, anterior eyes slightly larger than posterior ones; acicular lobe single; blades bidentate, guard approaching distal tooth; pharynx partially exposed, dorsal papilla as long as wide].

Distribution. — Sri Lanka throughout the Western Indian Ocean, including the Red Sea, in intertidal to shallow subtidal bottoms (10 m depth), in seaweeds (*Cymodocea*, *Sargassum*), or among pearl oysters.

Diagnosis. — *Hesione* with prostomium laterally curved; parapodia with dorsal cirri basally cylindrical, dorsal cirrophore 1.5 times as long as wide; larger acicula blackish; acicular lobe single, tapered; neurochaetal blades bidentate, 5-6 times as long as wide; subdistal tooth smaller than distal one, with guards approaching distal tooth.

Redescription

Neotype, ZMH-P 9951, complete, without pigmentation in ethanol, slightly distorted, pharynx almost fully exposed (Fig. 7A); integument with 9-11 longitudinal series of small tubercles, better defined in medial segments, reduced to 6-7 series in last three chaetigers; left parapodium of chaetiger 7 removed for observation (kept in vial). Body medially wider, tapered posteriorly, 26 mm long, 3.5 mm wide.

Prostomium ovoid, as wide as long, anterior margin projected anteriorly, lateral margins rounded, progressively expanded, posterior margin barely covered by anterior margin of tentacular segment, posterior furrow as long as ⅕ prostomial length; longitudinal depression well-defined separating prostomium into two lateral sections. Antennae minute, ovate, twice as long as wide (Figs 7B, 8B). Eyes barely pigmented, anterior ones slightly larger, and more separated from each other than posterior ones.

Tentacular cirri lost on right side, left side with curled, annulated cirri, tips eroded, longest one reaching chaetiger 4. Lateral cushions very low, most with longitudinal crests throughout their surface.

Parapodia with chaetal lobes slightly as long as wide, truncate (Fig. 7C); dorsal cirri with cirrophores smooth, about twice as long as wide; cirrostyles basally cylindrical, annulated throughout their length. Ventral cirri regularly corrugated, surpassing chaetal lobe.

Neuraciculae two, blackish, larger one thicker, tapered. Acicular lobe single, tapered, triangular to digitate, basally swollen (Fig. 7C [inset]); thinner, slightly shorter than chaetal lobe width in other specimens (Fig. 8C).

Neurochaetae about 30 per bundle, blades at a certain angle from handle, bidentate, slightly decreasing in size ventrally, 5 times as long as wide (5-6: 1 in other specimens, Fig. 8C [insets]); blades with smaller subdistal tooth, and larger distal tooth, guard approaching distal tooth (Fig. 7D).

Posterior region tapered into a truncate cone (Figs 7E, 8D); pygidium with anus terminal, anal papillae rounded, small.

Pharynx partially exposed, distal ring shorter, ciliated, medial ring three times longer, basal ring shorter than distal one; dorsal papilla round, slightly depressed, as long as wide.

Oocytes not seen.

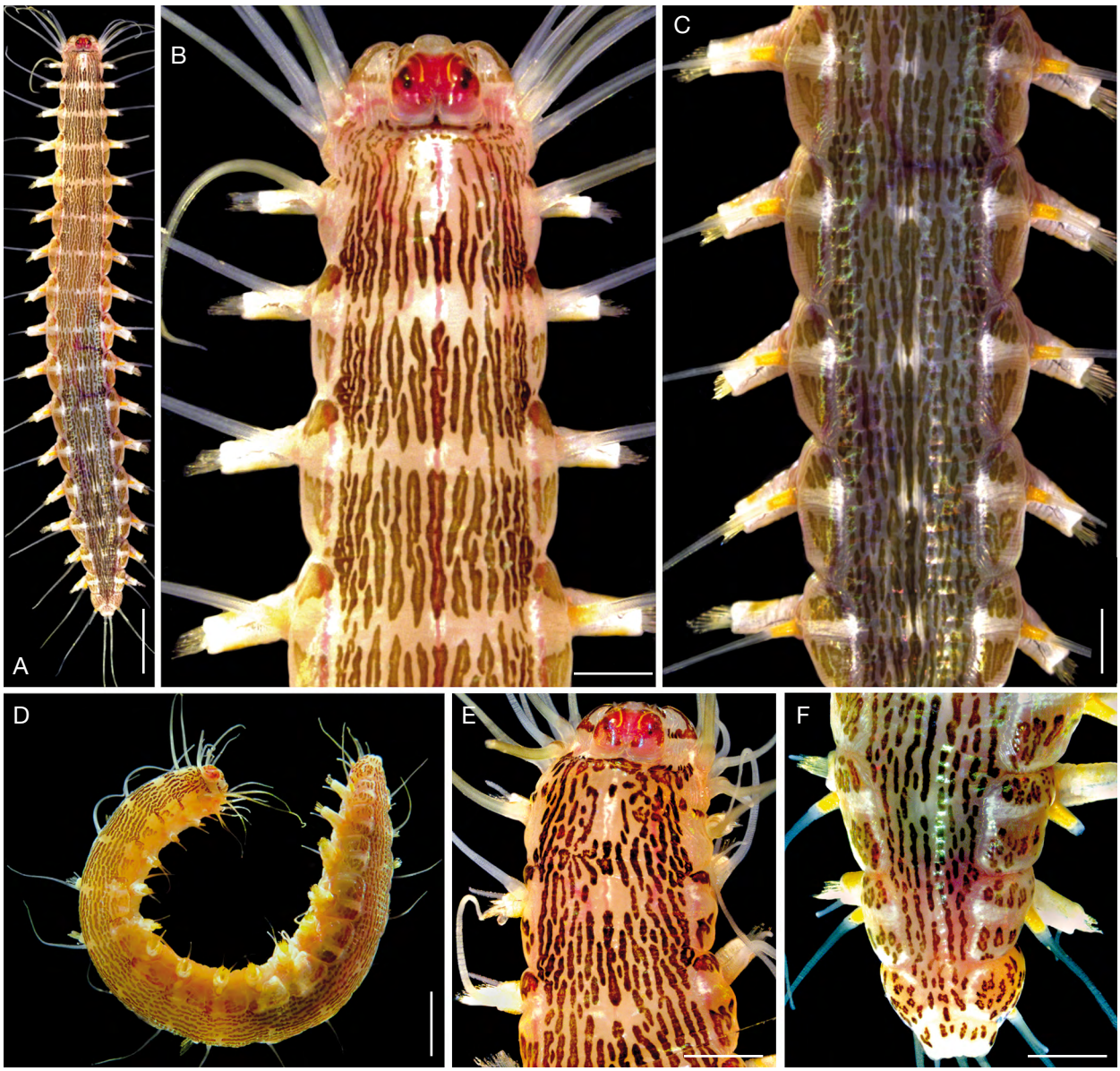

Fig. 9. — *Hesione ceylonica* Grube, 1874, living specimens, Musfat Al-Ahmadi, Kuwait: **A**, dorsal view; **B**, anterior end, dorsal view; **C**, chaetigers 10-14, dorsal view; **D**, another specimen, right lateral view; **E**, anterior end, dorsal view; **F**, posterior end, dorsal view. Scale bars: A, 4 mm; B, E, 1.3 mm; C, 1.9 mm; D, 3.8 mm; F, 1.7 mm (Photos: A-C, E, F, Anna Zhadan; D, Valery Skryabin).

Pigmentation

Body with dorsal, longitudinal, irregular, subcontinuous wide brown bands (Fig. 9A, D), over a whitish, pinkish or purplish background, especially pigmented along posterior region (Fig. 9C, F). Preserved specimens with 11-12 longitudinal bands, interrupted segmentally (Fig. 8A), discontinuities less defined posteriorly (Fig. 8D), brownish pigmentation continued into lateral cushions as large brownish spots just before chaetal lobes, and 1-3 as long as wide, lateral spots; larger spots progressively separated into three or more smaller spots in medial and posterior chaetigers. Prostomium reddish, eyes black, large (Fig. 9B) almost fused to each other, or small (Fig. 9E), distant to each other. Tentacular, dorsal cirri and chaetal lobes pale (bluish hint in figures 9E, F due to blue background); dorsal cirrophores deep yellowish, especially along medial and posterior chaetigers. Longitudinal bands solid, or with a paler central area, sometimes regularly interrupted by a pale transverse region along chaetigers 2-9 (Fig. 9A), following segments with three irregular spots, one middorsal, two lateral, or paler transverse areas poorly defined (Fig. 9E).

Remarks

Hesione ceylonica Grube, 1874, reinstated, resembles *H. uchidai* n. sp. because both have neurochaetal blades up to 6 times as long as wide. They differ, as indicated in the key below, because in *H. ceylonica* the acicular lobes are triangular or basally swollen, and neurochaetal blades are 5-6 times as long as wide, whereas in *H. uchidai* n. sp. the acicular lobes are

digitate, and the neurochaetal blades are 4-6 times as long as wide. Another difference is in the pigmentation pattern of living specimens: *H. ceylonica* has discontinuous longitudinal bands, interrupted by dorsal segmental, transverse pale, wide bands, whereas *H. uchidai* n. sp. has continuous longitudinal bands, together with discontinuous reddish brown bands, alternating with pale areas middorsally.

Gravier (1900: 179, pl. 10, fig. 16) hesitated when he identified some Red Sea specimens as *H. pantherina*. He characterised and illustrated the dorsal regular longitudinal bands, and their discontinuity in segmental limits, leaving pale areas, that can be found in fresh specimens of *H. ceylonica,* but not in *H. pantherina*, where longitudinal lines are interrupted or made as a succession of closely packed spots, and transverse pale areas are thinner. Willey (1905) studied some recently collected specimens and indicated there were dorsal longitudinal bands or streaks, but gave no further details. Augener (1926: 451) concluded that *H. ceylonica* must be included, together with *H. ehlersi* Gravier, 1900, as junior synonyms of *H. splendida*. In this conclusion he was partially correct because *H. splendida* and *H. ehlersi* are synonyms (see below), but *H. ceylonica* differs at least regarding its pigmentation pattern, as originally indicated by Grube (1874). However, for older specimens having probably no pigmentation, other differences are needed to separate the species. In *H. ceylonica,* after some photos by Anna Zhadan, the dorsum has brownish discontinuous bands over a pale reddish or yellowish background, especially because cirrophores are yellow, with small lateral darker areas just before the chaetal lobe region, and all cirri are pale; there are pale areas middorsally along most chaetigers. On the contrary, in *H. pantherina*, the dorsum has reddish discontinuous bands over a pale pink background, middorsal pale areas are much smaller without any darker spot before the chaetal lobe regions, and most cirri are dark pink or reddish, including their cirrophores.

Grube (1874: 327) detailed the pigmentation pattern: "Ex fulvescente rosea, splendens, leviter iridicolor, dorso medio e longitudinae linis fusciribus subviolaceis fere 11 contiguis, postremum versus evanesentibus striato, partibus lateralibus sepositis, e longitudine sulcatis" (Transl.: Bright pink, yellowish-brown, iridescent. Dorsum with 11 longitudinal sub-purple, subcontinuous bands, posteriorly faded off, laterally furrowed). This is surprisingly accurate despite the fact Grube did not collect the specimen, and if these observations were based upon a preserved specimen, it might be enigmatic how specimen was fixed. The answer is that the living pigmentation pattern was supplied together with the specimens by E. W. H. Holdsworth (Grube 1874: 325-326). Holdsworth was not an amateur collector; he was a fine ornithologist who made a catalogue of Sri-Lankan birds (Holdsworth 1872), and found some time to collect marine invertebrates such as polychaetes and sponges (Bowerbank 1873), providing details about their pigmentation along with specimens. Parapodial details have not been compared before. In both *H. ceylonica* and *H. pantherina,* as herein restricted, there is a single, tapered, blunt acicular lobe.

Frankfurt specimens from the Red Sea, SMF 2642, are notworthy because of several reasons. For example, they were named as "*H. marmorata*" by Eduard Rüppell, their collector, and this name indicates a pigmentation pattern which would set it apart from the other Red Sea species, *H. splendida*, which is grayish. The specimens were probably collected when Rüppell visited the Gulf of Aqaba in 1822, as indicated in his biography in Wikipedia, but deposited in the Frankfurt collections once he returned to Germany in 1827. Despite its antiquity, the body and appendages are in a remarkable preservation state, and only neurochaetal blades are lost, or severely eroded, including handles tips, which suggests an alternative, abrasive preservation method differing from the one relying only in alcohol.

On the other hand, *Hesione ceylonica* Grube, 1874 belongs in the group of species having longitudinal pigmented bands dorsally and the proposal of a neotype, its redescription and illustrations are required to clarify the taxonomic status of the species (ICZN 1999: art. 75.3.1), especially because most have been regarded as synonyms of *H. pantherina* Risso, 1828, a Mediterranean species. The above description and remarks, together with the key to species, include the differentiating features for the species and are enough to recognize the species (Art. 75.3.2-3). No type material was deposited in Berlin (Hartwich 1993) or in Wroclaw (Wiktor 1980), where most of Grube´s type specimens are; in fact, the Berlin Museum has two type lots only from the six species described from Sri Lanka in the same publication (Grube 1874): *Nereis* (*Platynereis*) *festiva* (ZMB Q 3502) and *Sabella fuscotaeniata* (ZMB Q 5222) no type specimens could be found for this species in Berlin or Wroclaw Museums (ICZN 1999: art. 75.3.4). Further, the neotype is consistent with known features of the species, as indicated in the original description and subsequent publications on it (ICZN 1999: art. 75.3.5). Both the neotype and the specimen labelled paraneotype were collected in the same locality in Trincomalee, Northeastern Sri Lanka; the original type locality was not indicated but they might have been collected in Aripo, close to Mannar, in Northwestern Sri Lanka, because some sponges were collected from there by the same person (Bowerbank 1873). Along the coast, there are about 270 km appart from these two localities, but because they are at about the same latitude, bordered by coral reefs, they are regarded as belonging to the same ecological coastal unit (ICZN 1999: art. 75.3.6; Spalding *et al.* 2007). Finally, both the neotype and the specimen labelled paraneotype are deposited in the museums of Copenhagen and Berlin respectively (ICZN 1999: art. 75.3.7); these two are long-standing, recognised institutions.

Hesione eugeniae Kinberg, 1866
(Figs 10-12)

Hesione eugeniae Kinberg, 1866: 244; 1910: 57, pl. 23, fig. 8. — Monro 1926: 312. — Hartman 1949: 46, 47, pl. 7, figs 8, 9.

Hesione intertexta – Horst 1924: 192, 193 (*partim*: *Siboga* Sta. 164, 274, *non* Grube, 1878).

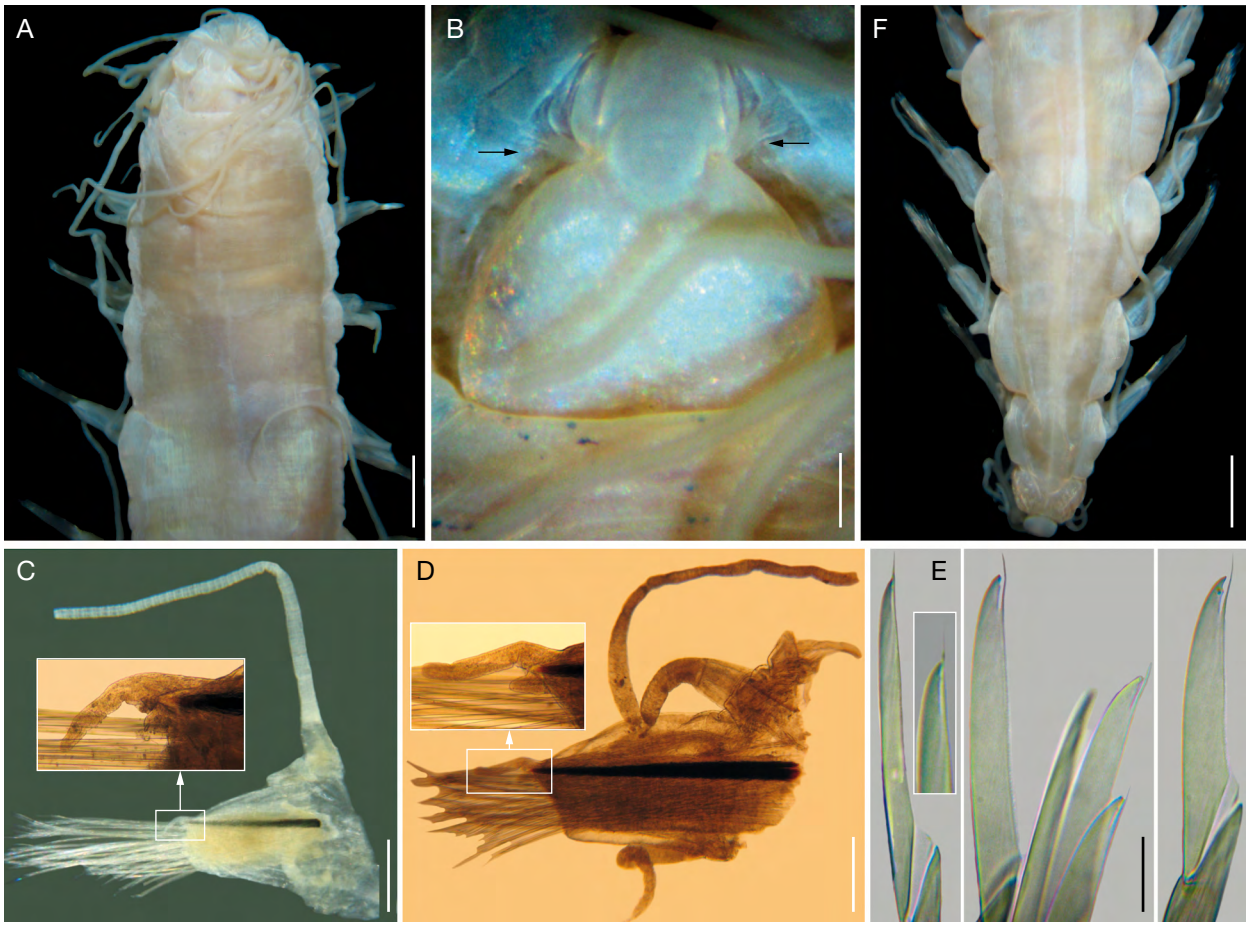

Fig. 10. — *Hesione eugeniae* Kinberg, 1866, non-type specimen, RMNH V431.6: **A**, anterior region, dorsal view; **B**, prostomium, dorsal view, illuminated from posterior region to enhance visibility of antennae (indicated by arrows); **C**, chaetiger 8, right parapodium, anterior view (inset: acicular lobe); **D**, another specimen (RMNH V431.3), chaetiger 7, right parapodium, anterior view (inset: acicular lobe); **E**, another specimen, RMNH V430, chaetiger 8, blades of upper, medial and lower neurochaetae (inset: tip of one of them); **F**, another specimen, RMNH V431.6, posterior region, dorsal view. Scale bars: A, 1.2 mm; B, 0.2 mm; C, 0.5 mm; D, 0.03 mm; E, 40 µm; F, 1 mm.

Hesione cf. *picta* – Ngamniyom *et al.* 2014: 723, 724, figs 2, 3. — Lee & Ong 2015: 201, 202, figs 1, 2.

Type material. — **Indonesia.** Holotype, RV *Eugeniae*, unnumb. Station, Bangka Strait (02°32'33"S, 105°44'36"E), between Java and Bangka Island, no further data (not seen; broken in two pieces and dried out from 1913 *fide* Hartman 1949: 46).

Additional material. — **Indonesia.** 1 specimen, RMNH V429, Nassi Besaan, Malacca Strait (04°N, 100°E), mud, 9 m depth, 23.VI.1908, P. N. van Kampen coll. [22 mm long, 4 mm wide; body fusiform, turgid, many cirri lost; prostomium fully exposed; anterior eyes about twice as large as posterior ones; antennae digitate, tips slightly eroded, 4 times as long as wide; acicular lobes without basal knob; most chaetal blades broken; gonads partially exposed by body wall fracture, with oocytes 100 µm in diameter]. — 1 specimen, RMNH V430, Malacca Strait, Gierg Exped., unnumb. Sta. (00°40'N, 99°10'E), 23.VI.1908, P.N. van Kampen coll. [30 mm long, 3 mm wide; macerated, colorless; body subcylindrical, tapered posteriorly; acicular lobe tapered, 5-7 times longer than round basal tine, visible only in a few chaetigers; gonad fragments removed through previous dissection, oocytes 100 µm in diameter]. — 1 specimen, RMNH V431.3, Irian Jaya, RV *Siboga* Exped. Stat. 164 (01°42.5'S, 130°47.5'E), 32 m depth, dredge, sand, stones, shells, 20.VIII.1899 [28 mm long, 3 mm wide; complete, resembling pigmentation pattern as in RMNH V431.6, but body thicker, right parapodium of chaetiger 7 removed for observation (kept in vial); acicular lobe with upper tine about 6 times longer than lower knob; neurochaetal blades bidentate, subdistal tooth smaller, guard markedly projected beyond distal tooth]. — 1 specimen, RMNH V431.6, Irian Jaya, RV *Siboga* Exped. Stat. 274 (05°28.2'S, 134°53.9'E), 57 m depth, dredge, sand, shells, stones, 26.XII.1899 [longest specimen, used for Redescription].

Gulf of Thailand. 1 specimen, ECOSUR 2909, Songkla, about 30 km offshore, 23 m depth, muddy sand, III.2011 [23 mm long, 2.5 mm wide; body slightly curved laterally, without pigmentation pharynx partially everted; antennae digitate, shorter than interocular distance; eyes brownish, anterior ones almost twice as large as posterior ones; acicular lobes long, tapered, ¼-⅓ as long as chaetae; dorsal cirrostyle basally annulose, cylindrical, longer than body width but not including parapodia; ventral cirri irregularly wrinkled, markedly longer than chaetal lobe; neurochaetae with blades bidentate, subdistal tooth minute, guard projected beyond distal tooth; anal cone projected, with 6 low anal papillae].

Torres Strait, Holothuria Bank. 1 specimen, BMNH 1926.4.30.106, Torres Strait [see Monro 1926] [complete, bent laterally, some parapodia previously removed; colorless, 38 mm long, 4.5 mm wide; acicular lobe single, chaetal blades long, with guard projected beyond distal tooth; pharynx exposed, dorsal papilla slightly as long as wide].

Distribution. — Gulf of Thailand, Java Sea to Torres Strait, in 3-57 m depth, in sandy or mixed bottoms.

Fig. 11. — *Hesione eugeniae* Kinberg, 1866, living specimen, Singapore: **A**, dorsal view; **B**, anterior region, dorsal view. Scale bars: A, 2.5 mm; B, 1 mm (Photos: Rene Ong).

Diagnosis. — *Hesione* with prostomium laterally curved; parapodia with dorsal cirri basally cylindrical, dorsal cirrophore twice as long as wide; larger acicula blackish; acicular lobe single, digitate; neurochaetal blades bidentate, 4-10 times as long as wide; subdistal tooth smaller than distal one, with guards surpassing distal tooth.

Redescription

Specimen RMNH V431.6, complete, with brownish diffuse dorsal pigmentation over chaetigers 1-4 (Fig. 10A), and other barely pigmented areas in medial and posterior chaetigers in ethanol; most tentacular and dorsal cirri without tips; right parapodium of chaetiger 8 removed for observation (kept in vial). Body straight, subcylindrical, tapered posteriorly, 29 mm long, 2.5 mm wide.

Prostomium semicircular, as long as wide, anterior margin projected anteriorly, lateral margins rounded, progressively expanded, posterior margin covered by tentacular segment anterior margin; without longitudinal depression. Antennae as long as anterior eye diameter, digitate, blunt, 4-5 times as long as wide (Fig. 10B). Eyes barely pigmented, anterior ones about twice as large as posterior ones.

Tentacular cirri long, irregularly twisted, longest one reaching chaetiger 5. Lateral cushions very low, most divided into three sections.

Parapodia with chaetal lobes as long as wide, tapered, truncate; dorsal cirri with cirrophores 1-2 times as long as wide; cirrostyle cylindrical basally, smooth, annulated medially, distally articulated (Fig. 10C), sometimes macerated (Fig. 10D). Ventral cirri smooth, tips eroded, if complete surpassing chaetal lobe.

Neuraciculae blackish, two, one thinner, the other thicker, tapered, tips colorless. Acicular lobe single, tapered, sometimes with a small, rounded to lobate lower tine, ⅓ as long as upper tine (Fig. 10C, D [insets]).

Neurochaetae about 40 per bundle, blades bidentate, 4-10 times as long as wide, at a certain angle from the handle, decreasing in size ventrally, each with tiny subdistal tooth, guard, if entire, markedly projected beyond distal tooth (Fig. 10E).

Posterior region tapered into a blunt cone; pygidium shiny, slightly granulate (Fig. 10F), anus with seven rounded papillae.

Pharynx not exposed. Oocytes not seen (another specimen, RMNH 430 with oocytes about 100 µm in diameter).

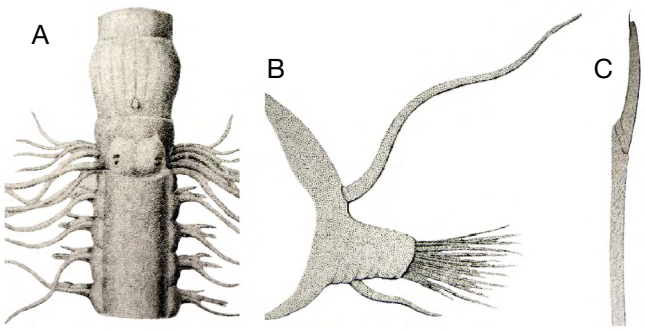

Fig. 12. — *Hesione eugeniae* Kinberg, 1866: **A**, anterior end, dorsal view; **B**, parapodium from a middle-body segment; **C**, same, close-up of neurochaetal tip; guard tip surpassing distal tooth (modif. after Kinberg 1910; original without scale bars).

Pigmentation

Body with transverse brown wide bands (Fig. 11A). Each band with darker, blackish lines along anterior and posterior margins, more irregular on anterior margins (Fig. 11B). Bands extended along body, dorsally interrupted segmentally along chaetal lobes by a narrow pale band (⅓ as long as dark band), barely visible in chaetiger 1, with unpigmented anterior and posterior rounded areas in chaetiger 16. Each band with homogeneous pigmentation, rarely with thin, irregular transverse paler lines, especially visible along chaetigers 1-2. Prostomium with a pale orange central along its anterior half, posterior half pale. Tentacular cirri, dorsal cirri, and chaetal lobes whitish. Eyes reddish brown, of similar size. Dark large pink rounded spots ventrally, at the level of chaetal lobes (Lee & Ong 2015). Pygidium with a dark thin band, and paler areas before it, and in anal region.

Remarks

Hesione eugeniae Kinberg, 1866 was briefly described (Kinberg 1866: 244) and later illustrated (Kinberg 1910: pl. 23, figs 8B, F, G) and the figures are herein reproduced (Fig. 12). Antennae were shown as long as interocular distance (Fig. 12A); the parapodium does not show an acicular lobe (Fig. 12B), probably because it is rather thin and difficult to be noticed when a single parapodium is seen in posterior view, ventral cirri extend beyond chaetal lobes but not beyond chaetal tips. The most distinctive feature, because it has been regarded as unique, is the long guard present in neurochaetal blades, which was shown as clearly projected beyond distal teeth (Fig. 12C). Further, Monro (1926: 312) indicated that in one of his specimens from Torres Strait, there was a single acicular lobe. Hartman (1948: 46, 47) corroborated this by referring that the guard "[…] extends well beyond the terminal fang", and that the subapical tooth was "small and inconspicuous". However, her figures failed to show the very long guard, but they depict a remarkable difference in neurochaetal blade length/width relationship, being 4: 1 for the short blade and 11: 1 for the long one. Because the corresponding parapodia were not detailed, these ranges would imply that probably Hartman took chaetae from the first few chaetigers and from another median chaetiger, because their proportion decreases along the body, but in our specimens this range is confirmed in the same chaetal bundle.

In his revision of the *Siboga* Expedition material, Horst (1924: 192, 193) noted three specimens with a distinct pigmentation, inserted a question mark in the labels but included them under *H. intertexta* by indicating: "Three specimens only, from Stat. 164 and 274 and from Malacca-Strait did not show any longitudinal stripes, only a pale band, bordered by a dark line, across the dorsal side of the segments, between each pair of parapodia, as in *Hes. vittata* (sic) Ehl." (synonym of *H. picta* Müller, 1858, *mihi*). Horst (1924) gave no indications for chaetal features.

Hessle (1925: 14) recorded a small specimen from Sagami, central Japan, as *H. splendida* with transverse white bands. If the brownish bands were well-defined or not was not specified, and this specimen might belong to *H. eugeniae*, or rather be a dark form of *H. reticulata* von Marenzeller, 1879, redescribed elsewhere (Jimi *et al.* 2017), as that species was described from the same area; solving this requires a study of Hessle's specimen to confirm its chaetal pattern.

The color photographs by Ngamniyom *et al.* (2014) and Lee & Ong (2015) reveal that the pigmentation pattern includes dorsal, segmental, wide, irregularly defined brownish bands, each with a darker thin line on their anterior and posterior margins, leaving the prostomium barely pigmented and the pygidium pale, although the latter has a darker bordering ring. Further, Lee & Ong (2015) also illustrated a midventral dark pink round spot per segment, including prostomium and pygidium, although in the former the spot is divided leaving a pale midventral area, and the pygidium has a smaller spot than those present in preceding segments. Chaetal features were not precised. Ngamniyom *et al.* (2014: fig. 2f) referred to unidentate falcigers although their figure could explain they confused the long guard as a single tooth, whereas Lee & Ong (2015: 201) correctly referred them as bidentate with guard (they called it accessory spine) "reaching beyond the primary (distal) tooth" but failed to illustrate them.

Hesione eugeniae Kinberg, 1866 is distinguished by having wide, transverse, solid, irregular bands along the dorsal pale surface, including the pygidium, long antennae, parapodia with acicular lobes single, and bidentate blades with tiny subdistal tooth, and guards surpassing the distal tooth. It differs from other species having transverse bands such as *H. genetta* Grube, 1864, or *H. picta* Müller, 1858 because of the relative size of antennae, parapodial features and pigmentation patterns. In *H. genetta* antennae are large (as long as interocular distance), acicular lobes are double, and in neurochaetal blades, subdistal teeth are as large as distal ones, with guards approaching subdistal teeth; for pigmentation, the first band is wider than the following ones, and there are usually round spots between bands, but intermediate spots are missing in both *H. picta* and *H. eugeniae*. The banding pattern of the two latter species is similar because they have wide dark bands throughout the body, but their pigmentation intensity is different. In *H.* eugeniae bands are solid and the marginal lines are darker, whereas in *H. picta* there are no darker marginal lines, and the band itself includes several transverse thin pale

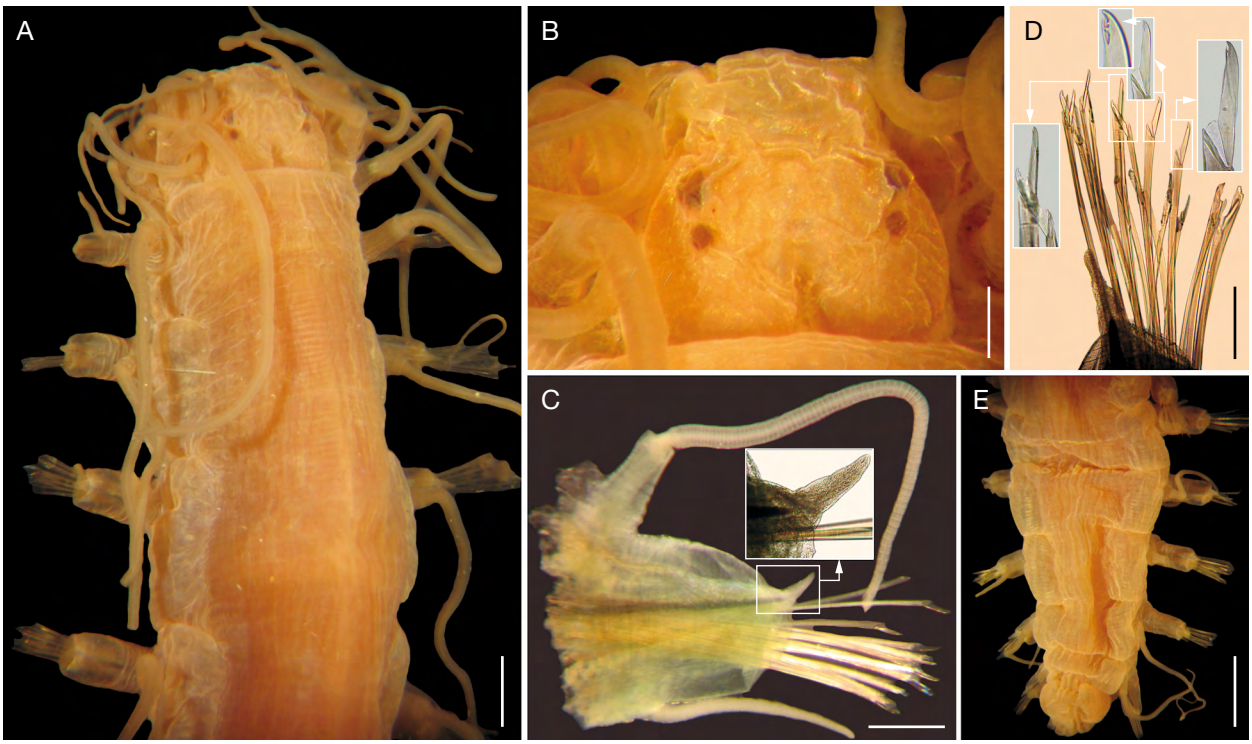

FIG. 13. — *Hesione fitzhughi* n. sp.: **A**, holotype, LACM 10152, anterior region, dorsal view; **B**, same, prostomium, dorsal view; **C**, same, chaetiger 10, left parapodium, anterior view (inset: acicular lobe); **D**, paratype, LACM 10153, chaetiger 10, left parapodium, anterior view, neurochaetae (insets: blades and their tips); **E**, holotype, posterior region, dorsal view. Scale bars: A, 0.9 mm; B, 0.3 mm; C, 0.2 mm; D, 230 µm; E, 2.3 mm.

lines. Further, unlike *H. genetta,* brownish bands in both *H. picta* and *H. eugeniae* fade off soon after specimens are preserved in ethanol, although the pygidium might retain the pigmentation for a longer time. For example, when one of the New Caledonia specimens was sorted out 16 years ago (Salazar-Vallejo 1999: 22), it had a blackish pygidium, and when it was re-examined (June, 2016) it has become reddish.

On the other hand, *H. eugeniae* resembles *H. osbornae* n. sp. because their neurochaetal blades have guards surpassing distal teeth. There are two main differences between these species. In *H. eugeniae* acicular lobes are digitate, and neurochaetal blades are 4-10 times as long as wide, whereas in *H. osbornae* n. sp. acicular lobes are tapered, and neurochaetal blades are about 15 times as long as wide.

Hesione fitzhughi n. sp.
(Figs 13, 14)

urn:lsid:zoobank.org:act:65EBF0A0-4CF8-40FD-97D2-D15EFB96CD3F

Hesione intertexta – Monro 1926: 311, 312 (*partim*, *non* Grube, 1878).

TYPE MATERIAL. — **Australia.** Holotype, LACM 10152, and paratype, LACM 10153, Brampton Island, off Mackay, Queensland, under rocks and coral boulders, 16-28.I.1949, B. Dew coll. (paratype partially dehydrated, pharynx exposed, most cirri lost; body 23 mm long, 2.5 mm wide).

ADDITIONAL MATERIAL. — **Australia.** 1 specimen, AM 4406, Little Upolo Cay, 38 km NNE off Cairns, Queensland, under coral rocks, VII.1970, P. H. Coleman & I. Loch coll., [34 mm long, 5 mm wide; splendid specimen, slightly bent laterally, integument microtuberculated, anterior eyes as long as wide; pigmentation pattern barely visible along a few anterior chaetigers, longitudinal pale brown thin bands, interrupted serially in each parapodial region, leaving middorsal large, paler areas; antennae blunt, digitate to medially wider, 3-4 times as long as wide; right parapodium of chaetiger 8 removed for observation (kept in vial); neuraciculae black, tapered; acicular lobe single, basally swollen with a shallow notch, giving the impression of a round basal tine; about 25 neurochaetae per bunde, blades bidentate, subdistal tooth smaller, guard approaching distal tooth). — 1 specimen, AM E4642, Tasmania, off Babel Island, Bass Strait (39°56'S, 148°19'E), 146 m, FIS Endeavour, 1909-1914 coll. [45 mm long, 5 mm wide; complete, body ends distorted by compression into small container; integument smooth, lateral cushions with longitudinal ridges; right parapodium of chaetiger 2 removed for observation (kept in vial), others previously removed; antennae collapsed; eyes brownish, anterior eyes slightly larger than posterior ones; acicular lobe single, tapered, blunt; neurochaetal blades bidentate, subdistal tooth smaller, directed laterally, guards broken in a single blade approaching distal tooth, others approaching subdistal tooth]. — 1 specimen, AM W.5494, Hall Bank, Fremantle, Western Australia, under rocks, 13 m depth, 25.IV.1972, N. Coleman coll. [31 mm long, 4.5 mm wide; bent laterally, pharynx exposed; antennae digitate, as long as anterior eye diameter, eyes brownish, anterior eyes slightly larger than posterior ones; acicular lobe single, mostly blunt, sometimes tapered]. — 3 specimens, BMNH 1931.7.1.18/20, Great Barrier Reef Expedition, Low Isles, Queensland, no further data [the paper indicates four specimens, but there are only three in vial; 39-53 mm long, 5-6 mm wide; one sigmoid with several parapodia previously removed, two others straight; integument tuberculated; anterior eyes as long as wide; left parapodia of chaetiger 8 (sigmoid, without dorsal cirrus), and of chaetiger 10 (largest, with dorsal cirrus), removed for observation (kept in vial); acicular lobe single,

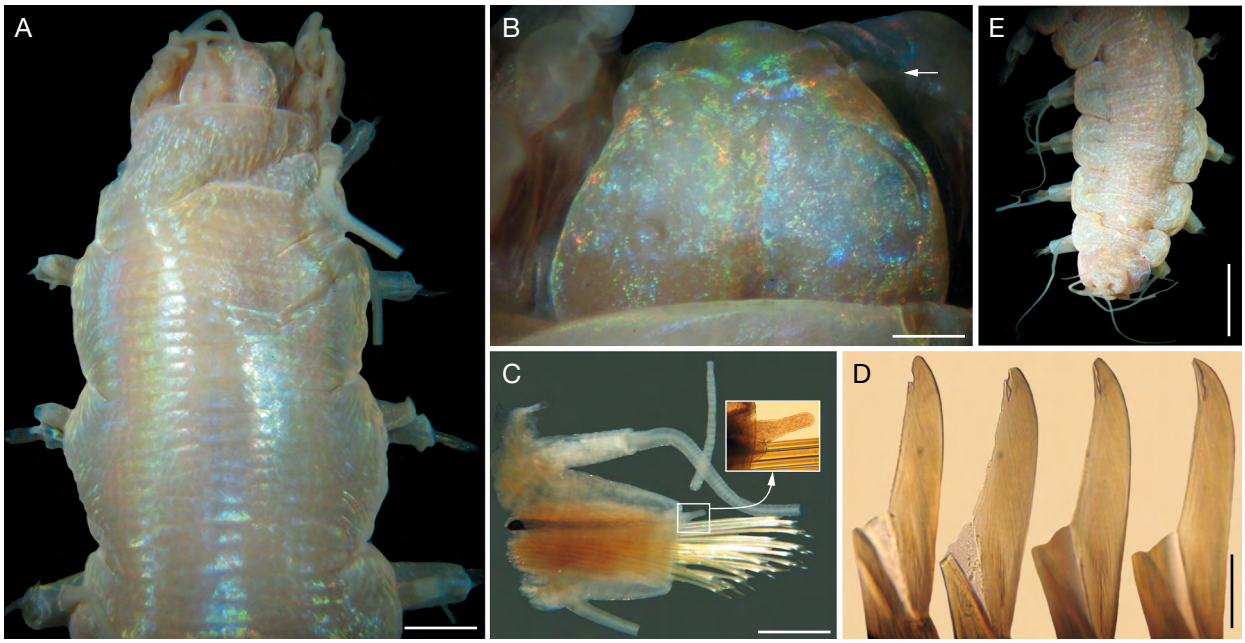

Fig. 14. — *Hesione fitzhughi* n. sp., non-type specimen, AM W.7439: **A**, anterior region, dorsal view; **B**, prostomium dorsal view (arrow points to right antenna); **C**, chaetiger 12, left parapodium, anterior view, dorsal cirrostyle broken (inset: acicular lobe); **D**, same, neurochaetal tips showing tip erosion; **E**, posterior region, dorsal view. Scale bars: A, 1.1 mm; B, 0.3 mm; C, 1 mm; D, 40 µm; E, 2.8 mm.

basally swollen, blunt in two smaller specimens; largest specimen with acicular lobe tips bifid in several chaetigers of posterior region; neurochaetal blades bidentate, subdistal tooth smaller, guards most broken, a few entire approach subdistal tooth]. — 2 specimens, UF 55, Christmas Island (10°29'S, 105°38'E, South of Java), N Coast, 4 km E of Boat Cave, just outside Thundercliff Cave, dead coral rubble field, under large limestone rocks and rubble, 10 m depth, 21.XI.1999, L. Kirkendale coll. [35-48 mm long, 5.5-6.0 mm wide; colorless; antennae minute, difficult to see; eyes brownish, anterior ones slightly larger than posterior ones, largest specimen with anterior right eye divided into two complete, smaller eyes; longest tentacular cirri reach chaetiger 4; median chaetigers with dorsal cirri as long as body width (without parapodia); acicular lobes single, tapered; smaller specimen with neurochaetal blades bidentate, subdistal tooth smaller, guard reaching distal tooth].

Indonesia. 1 specimen, MNHN-IA-PNT92 (formerly jar 890), Gorong Islands, Moluccas, in corals, 26.I.1975, Th. Monod coll. [32 mm long, 5 mm wide; partially dehydrated; anterior eyes as long as wide, right one with inner area colorless, reniform; posterior eyes round; integument smooth; acicular lobe single, blunt; neurochaetal blades bidentate, subdistal tooth smaller, guards approaching distal tooth]. — 1 specimen, UF150, Bay of Tomini, Pulau Pondang (0.45, 124.481277; 00°27'00.0000"N, 124°28'52.5972"E), Sulawesi, under rocks, 5-8 m depth, 18.IX.1999, G. Paulay coll. [30 mm long, 3.5 mm wide; bent ventrally; antennae minute; eyes of similar size, anterior ones blackish, posterior ones brownish, right posterior eyes duplicated, supernumerary one smaller; acicular lobe single, long, tapered; blades bidentate, subdistal tooth minute, guard approaching distal tooth].

Torres Strait. 2 specimens, BMNH 1926.4.30.90, RV *Alert* Expedition, Thursday Island, Torres Strait, 8-13 m depth, no further data [both complete, one pale, slightly macerated, the other grayish, stiff; anterior eyes as long as wide, slightly larger than posterior ones; integument tuberculated, lateral cushions smooth; body 35-38 mm long, 5-6 mm wide; acicular lobe single]. — 1 specimen, BMNH 1926.4.30.137, RV *Alert* Expedition, Holothuria Bank, Torres Strait [see Monro 1926] [complete, bent ventrally, right parapodia of chaetigers 7 and 8, and left one from chaetiger 10 previously removed; colorless, integument tuberculated, lateral cushions with longitudinal ridges; 40 mm long, 5 mm wide; left antenna twice as long as wide; anterior eyes as long as wide, twice larger than posterior ones; acicular lobe single, digitate; pharynx exposed, dorsal papilla blunt, twice as long as wide].

New Caledonia. 1 specimen, AM 7439, found in aquarium, Noumea, VII.1975, E. Pope coll. [complete, bent laterally, tapered posteriorly; no pigmentation pattern but with a reddish hue; integument tuberculated. Body 45 mm long, 5 mm wide; left parapodia of chaetigers 1 and 10 previously removed, left parapodium of chaetiger 12 removed for observation (kept in vial); oocytes about 100 µm in diameter.]. — 1 specimen, MNHN-IA-PNT93 (formerly jar 402), Mrs Pruvot, no further data [24 mm long, 3 mm wide (rigth parapodium of chaetiger 8 removed for observation, kept in vial); antennae digitate, 3 times as long as wide; anterior eyes as long as wide, larger than posterior ones; integument rugose, microtubercles not forming longitudinal lines; acicular lobe single, tapered; neurochaetae about 20 per bundle; blades bidentate, subdistal tooth smaller, guard approaching distal tooth].

Etymology. — This species is named after Kirk Fitzhugh, Curator of Polychaeta in the Los Angeles Museum of Natural History, Los Angeles, in recognition of his many publications on sabellid and terebellid taxonomy, as well as in philosophy of systematics, and because of his unreserved support to our research requests. The name is a noun in genitive (ICZN 1999: art. 31.1.2).

Distribution. — Indonesia to New Caledonia, including Australia, under coral rocks in 0-13 m depth.

Diagnosis. — *Hesione* with prostomium laterally curved; anterior eyes as long as wide; parapodia with dorsal cirri basally cylindrical, dorsal cirrophore twice as long as wide; larger acicula blackish; acicular lobe single, tapered; neurochaetal blades bidentate, 3-5 times as long as wide; subdistal tooth smaller than distal one, with guards approaching distal tooth.

DESCRIPTION

Holotype, LACM 10152, complete, without pigmentation pattern in ethanol (more recently collected specimens with a reddish hue), slightly dehydrated (Fig. 13A); some tentacular or dorsal cirri broken or lost; left parapodium of chaetiger 10 removed for observation (kept in vial). Body slightly distorted, partially dehydrated, becoming slightly wider posteriorly, ventrally bent, 35 mm long, 5 mm wide.

Prostomium as long as wide, anterior margin projected anteriorly, lateral margins rounded, posterior margin deeply cleft, about as long as ¼ prostomial length, reaching slightly behind posterior eyes, without longitudinal depression (Fig. 13B). Antennae minute, directed laterally, fusiform, blunt, twice as long as wide, ⅘ as long as interocular distance. Eyes brownish, anterior eyes as long as wide, larger than posterior rounded ones.

Tentacular cirri long, some twisted, tips lost, longest ones reach chaetiger 4. Lateral cushions low, most entire, some separated into two sections.

Parapodia with chaetal lobes as long as wide, truncate; dorsal cirri with cirrophores 2-3 times as long as wide; cirrostyle basally cylindrical, annulated, multiarticulated medially and distally, as long as body width (Figs 13C, 14C). Ventral cirri smooth, surpassing chaetal lobe.

Neuraciculae blackish, two, one thinner (smaller specimen with acicula less pigmented). Acicular lobe single, tapered (Figs 13C [inset]; 14C [inset]).

Neurochaetae about 20 per bundle, blades bidentate, blades at a certain angle from handle, 3-5 times as long as wide, decreasing in size ventrally, each with smaller subdistal teeth, a few blades with an additional, intermediate tooth (Fig. 13D [insets]), guard approaching distal tooth, eroded in other specimens (Fig. 14D).

Posterior region tapered into a blunt cone (Figs 13E, 14E); pygidium granulate, anus with four petaloid papillae.

Pharynx exposed in paratype, margin smooth, slightly eroded; dorsal papillae rounded, as long as wide. Oocytes not seen (in a non-type specimen, AM 7439, 100 µm in diameter).

Pigmentation

A recently collected non-type specimen (AM W.7439) shows a reddish hue but not a definite pigmentation pattern. This reddish pigmentation is visible in the anterior (Fig. 14A), and posterior regions (Fig. 14E), slightly less evident in the prostomium (Fig. 14B), and especially in the neurochaetal lobe (Fig. 14C).

REMARKS

Hesione fitzhughi n. sp. can be confused with *H. splendida* Savigny *in* Lamarck, 1818 because of its shiny integument. However, *H. splendida* has a smooth integument, whereas *H. fitzhughi* n. sp. has it tuberculated. A tuberculate integument is also present in *H. intertexta* Grube, 1878, as restricted above, but in *H. intertexta* lateral cushions are either smooth or with longitudinal ridges, whereas in *H. fitzhughi* n. sp. lateral cushions are tuberculated.

There are some photos available in internet depicting a reddish *Hesione* from the Western tropical Pacific, showing two pigmentation patterns: either with well-defined, discontinuous rectangular white areas, or with ill-defined, subcontinuous white areas. Matching this newly described species with either pigmentation pattern, or defining if there is more than a single species, requires the study of freshly collected specimens, and at least some COI-barcoding analysis. So far, *H. fitzhughi* n. sp. can be separated from other species in the *intertexta* group by having anterior eyes as long as wide and by its tuberculate integument, and in those specimens collected 40 years ago, there is a reddish hue along body.

Hesione genetta Grube, 1867
(Figs 15, 16)

Hesione genetta Grube, 1867: 65, 66; 1878: 104. — Chamberlin 1919: 186-188, pl. 22, figs 7, 8. — Treadwell 1926: 189. — Monro 1931: 10, fig. 5; 1939: 392. — Augener 1933b: 224, 225, fig. 3A-B. — Reish 1968: 212. — Wu *et al.* 1975: 75, 76. — Uchida 2011: 3, fig. 1.

Hesione pantherina – Fauvel 1953c: 174 (*non* Risso 1826).

Hesione splendida – Augener 1927a: 131. — Ehlers 1920: 25, 26. — Gibbs 1971: 139; 1972: 204 (*partim*, *non* Savigny in Lamarck, 1818).

TYPE MATERIAL. — **Samoa.** 'Syntypes' (see remarks): 1 specimen, ZMH-P 1283, identified by Grube, no further data [24 mm long, 4 mm wide; body macerated, whitish, anterior and posterior ends damaged; neuraciculae blackish, tapered; acicular lobe double, upper tine slightly longer than ventral one; neurochaetal blades with subdistal tooth as large as distal one, guard approaching subdistal tooth]. — 3 specimens, ZMH-P 1284, Upolu (13°55'S, 171°45'W), identified by Grube, no further data [17-46 mm long, 2-7 mm wide; complete, larger one macerated, with brownish round dots dorsally, smaller specimens dehydrated, with a wide brownish dorsal band in chaetiger 1, and another one with several irregular dorsal transverse bands along several anterior chaetigers, including chaetiger 1; antennae long, digitate, 6-7 times as long as wide; eyes brownish, anterior ones twice as large as posterior ones; neuraciculae blackish, tapered; acicular lobe double, blunt, digitate, upper tine slightly longer than lower one; neurochaetal blades with subdistal tooth as large as distal one; guard approaching subdistal tooth].

ADDITIONAL MATERIAL. — **Samoa.** 1 specimen, BMNH 1921.5.1.1070, W. C. McIntosh, donor, no further data [macerated, dorsal brownish dots barely visible; body 48 mm long, 6 mm wide; left paraodium of chaetiger 4, and right parapodium of chaetiger 8 previously removed; chaetal lobes invaginated; acicular lobes double, upper tine twice thicker than lower one]. — 1 specimen, MNHN-IA-PNT91b (formerly jar 70), Maru, 1887 (37), no further data [57 mm long, 7 mm wide; colorless; prostomium invaginated; acicular lobes double, long, tapered]. — 2 specimens, MCZ 46394, West Reef, 26.X.1898, no further data [17-23 mm long, 2-3 mm wide; remains of a diffuse broad band on chaetiger 1; acicular lobes double; most chaetae broken]. — 1 specimen, UF 81, used for Redescription, Tutuila Island (-14.2885, -170.68066; 14°17'18.6000"S, 170°40'50.3760"W), reef flat, under rubble, 19.X.2002, V. Bonito coll.
Palau. 1 specimen, UF 44, Malakal Sewer Outfall, under rocks, 2 m depth, 26.VII.1999, G. Paulay coll. [body complete, pigmentation with abundant small dark brown spots throughout the body, with the exception of an anterior dorsal colorless collar (wide transverse band) along chaetiger 2, and an oval, dorsal as wide as long colorless spot on the central region of chaetiger 1; pigmentation extended

ventrally in a few anterior and posterior chaetigers; pygidium with a similar pigmentation; dorsal cirri basally smooth, ventral cirri articulated, usually longer than chaetal lobe; acicular lobe double, upper tyne about twice as long as lower one; neurochaetal blades progressively shorter ventrally, subapical tooth large (as large as apical one), guard reaching subapical tooth].
Japan. 1 specimen, MCZ 84733, Ryukyu Islands, Seragaki Beach, 1.3 km ENE Maeki-zaki, Okinawa (26°30.4'N, 127°52.6'E), 3 m depth, coral rubble, 17.II.1989, R. F. Bolland coll. [32 mm long, 5 mm wide; macerated, with some dark pigment bands or spots barely visible along some anterior chaetigers; body soft depressed, pharynx fully exposed; parapodia invaginated; eyes almost colorless, antennae digitate, as long as interocular distance; dorsal cirri macerated; acicular lobe double, digitate to truncate triangular, of about the same length; parapodia not removed to avoid further damage; pygidium with anus broken].
Mariana Islands. 2 specimens, UF 34, Guam Island, Pago Bay, reef flat, under rocks, 0-0.5 m depth, 2.VII.2000, G. Paulay coll. [20.0-20.5 mm long, 2.0-2.5 mm wide; pigmentation pattern visible, smaller specimen darker, more dehydrated; pharynx not exposed; antennae as long as interocular distance]. — 1 specimen, UF 40, Guam Island, Pago Bay (13.5, 144.8; 13°30'00"N, 144°48'00"E), reef front, under rock, 1-5 m depth, 15.V.1997, G. Paulay coll. [45 mm long, 4.5 mm wide; pigmentation pattern almost completely gone, dorsal transverse bands incomplete, better defined along chaetigers 1-5; antennae longer than interocular distance; acicular lobe double, upper tine 3 times longer than lower one; neurochaetal blades bidentate, subdistal tooth as thick or thicker than distal one; guard approaching subdistal tooth; body wider posteriorly]. — 1 specimen, UF 47, Guam Island, Pago Bay (13.5, 144.8; 13°30'00"N, 144°48'00"E), dry intertidal, under rock, 9.VIII.1995, L. Ward coll. [29 mm long, 3 mm wide; body bent backwards; antennae as long as interocular distance; anterior eyes slightly larger than posterior ones; first chaetiger with a thick dark brown, irregular transverse band, missing in chaetiger 2, progressively paler, discontinuous from chaetiger 3, reduced to a half-moon middorsal spot in posterior chaetigers; acicular lobe double, upper tine larger than lower one]. — 1 specimen, UF 52, Guam Island, Orote (13.4165, 144.650166; 13°24'59.4"N, 144°39'00.5976"E), 1-9 m depth, 11.III.2000, L. Kirkendale coll. [26 mm long, 3 mm wide; slightly bent laterally; one posterior left parapodium removed; pigmentation pattern with a thick irregular transverse band on chaetiger 1, less defined on chaetigers 2-3, thereafter paler progressively loosing definition; antennae longer than interocular distance; anterior eyes twice as large as posterior ones; median chaetigers with dorsal cirri as long as body width, without parapodia]. — 1 specimen, UF 92, Guam Island, N Pago Bay (13.42453, 144.78581; 13°25'28.3080"N, 144°47'08.9160"E), 0-1 m depth, 30.IV.2003, G. Paulay coll. [24 mm long, 3 mm wide; body bent laterally, median right parapodia removed for molecular analysis; pigmentation pattern paler posteriorly, transverse bands better defined along chaetigers 1-7, thinner, less defined in following chaetigers; antennae as long as interocular distance; anterior eyes slightly larger than posterior ones; acicular lobe double, tines blunt, upper one slightly longer than lower one]. — 1 specimen, UF 95, Guam Island, N Pago Bay (13.42453, 144.78581; 13°25'28.3080"N, 144°47'08.9160"E), 0-1 m,30.IV.2003, G. Paulay coll. [34 mm long, 4 mm wide; body laterally bent, thicker posteriorly; ovaries exposed after removal of parapodia for molecular analysis; pigmentation pattern visible, darker anteriorly, paler posteriorly]. — 1 specimen, UF 100, Guam Island, Hagatna Bay (13.5, 144.8; 13°30'00"N, 144°48'00"E), E Side, outer reef flat, intertidal under rocks, 30.XI.2002, G. Paulay coll. [27 mm long, 2.5 mm wide; pigmentation pattern more intense along anterior chaetigers, a thick irregular band on chaetiger 1, tentacular cirri pale brown; pharynx exposed, dorsal papilla not seen; antennae longer than interocular distance; posterior right parapodia removed for molecular analysis; gonads thick, round, visible through dissected area; body partially dehydrated, stiff, bent dorsally]. — 1 specimen, UF 699, Guam Island, Hagatna, S of Adalupe Island (13.479906, 144.726632; 13°28'47.6616"N, 144°43'35.8752"E), fore reef, 0-1 m depth, 9.II.2008, F. Michonneau coll. [22 mm long, 3 mm wide; body bent ventrally, with some posterior left parapodia removed for molecular analysis; pigmentation pattern well defined, a thick irregular transverse band on chaetiger 1, following chaetigers with thinner, paler, irregular transverse bands; pharynx fully everted, dorsal papilla pale, as long as wide; antennae longer than interocular distance; anterior eyes twice as large as posterior ones; median chaetigers with dorsal cirri longer than body width, including parapodia; acicular lobe double, upper tine larger than lower one]. — 1 specimen, UF 1741, Guam Island, 100 m W of University of Guam Marine Lab (13.5, 144.8; 13°30'00"N, 144°48'00"E), shallow bay, backreef, algae & cyanobacteria, under big rocks among rubble/sand, 0.5-1.0 m depth, 22.VI.2010, A. Anker coll. [30 mm long, 4.5 mm wide, pigmentation pattern visible; body twisted, anterior end directed ventrally; prostomial features as those seen in other specimens].
Marshall Islands. 4 specimens, LACM 10154, Rangelap Atoll, Bokuyarito Island, shore, 28.VII.1946, J. Rachita & F. C. Fresenhinne coll. [27-36 mm long, 5-6 mm wide; macerated, pigmentation remaining along several anterior chaetigers]. — 1 specimen, LACM 10155, Bikini Atoll, V.1946, M. W. Johnson coll. [26 mm long, 2 mm wide; partially dehydrated; pigmentation mostly faded off, restricted to an irregular pale brown transverse band on chaetiger 1; gonads extended from chaetiger 8 backwards, 3-4 lobulate masses per segment, more thightly packed in chaetigers 13-16]. — 1 specimen, LACM 10157, Rangelap Atoll, Burok Island, intertidal coral, 18.VII.1946, M. W. Johnson coll. [24 mm long, 2.8 mm wide; macerated, pigmentation now restricted to a pale brown transverse band on chaetiger 1; pharynx partially everted]. — 1 specimen, USNM 23948, Ralik Chain, Enewetak Atoll, Rujoru Island, 2.VI.1946, J. Morrison coll. [24 mm long, 3.5 mm wide; splendid specimen, pigmentation still visible, irregular transverse bands on all chaetigers, darker and larger anteriorly, reducing their size and intensity posteriorly; individual spots not visible]. — 1 specimen, USNM 29890, Ralik Chain, Enewetak Atoll, Bogombogo Island, ocean side, intertidal, 2.VII.1957, D. J. Reish coll. [23.5 mm long, 3 mm wide; slightly damaged specimen; pigmentation with transverse irregular bands almost along the whole dorsum; acicular lobe double, upper one 0.5-1.0 times longer than lower one, not subequal]. — 1 specimen, USNM 118617, Bikini Atoll, Enyu Island, ocean side, Sta. E-110, 6.IX.1956, D. J. Reish coll. [43 mm long, 5 mm wide; splendid specimen, with a dark brown maculated pattern along the body, forming transverse irregular bands on chaetigers 1, 3-6, thereafter spots diminishing in size and darkness]. — 1 specimen, UF 702, Majuro Atoll, Kolalen (7.15792, 171.21438; 07°09'28.5120"N, 171°12'51.7680"E), channel (E end of the island), intertidal rocks and pools, 8.IV.2008, F. Michonneau & K. Sun coll. [37 mm long, 3 mm wide; body with irregular, discontinuous transverse dorsal bands, better defined along anterior chaetigers; body bent laterally, posterior right parapodia removed for molecular analysis; pharynx partially exposed, dorsal papilla visible].
French Polynesia. 1 specimen, BMNH 1941.4.4.683, Tahiti, Crossland Pacific Cruise 1923-1924, among corals, 10.VII.1925, C. Crossland coll. [distorted, bent laterally, abundant, dorsal brownish dots and middorsal larger spots well-defined; body 44 mm long, 4.5 mm wide; parapodia not dissected; dorsal cirri as long as body width (excluding parapodia); acicular lobes double, upper tine slightly wider and longer than lower one]. — 1 specimen, BMNH 1941.4.4.684, Tahiti, Faa, Crossland Pacific Cruise 1923-1924, barrier edge, 1.VI.1926, C. Crossland coll. [distorted, anterior end twisted laterally, posterior region bent ventrally, dorsal brownish dots and a few transverse bands barely visible; body 40 mm long, 6 mm wide; right parapodium of chaetiger 5 previously removed; chaetal lobes invaginated; acicular lobes double, tines of similar width, upper tine slightly longer than lower one]. — 3 specimens, MNHN-IA-PNT91c (formerly jar 70), Tahiti, 1952, R. Ranson

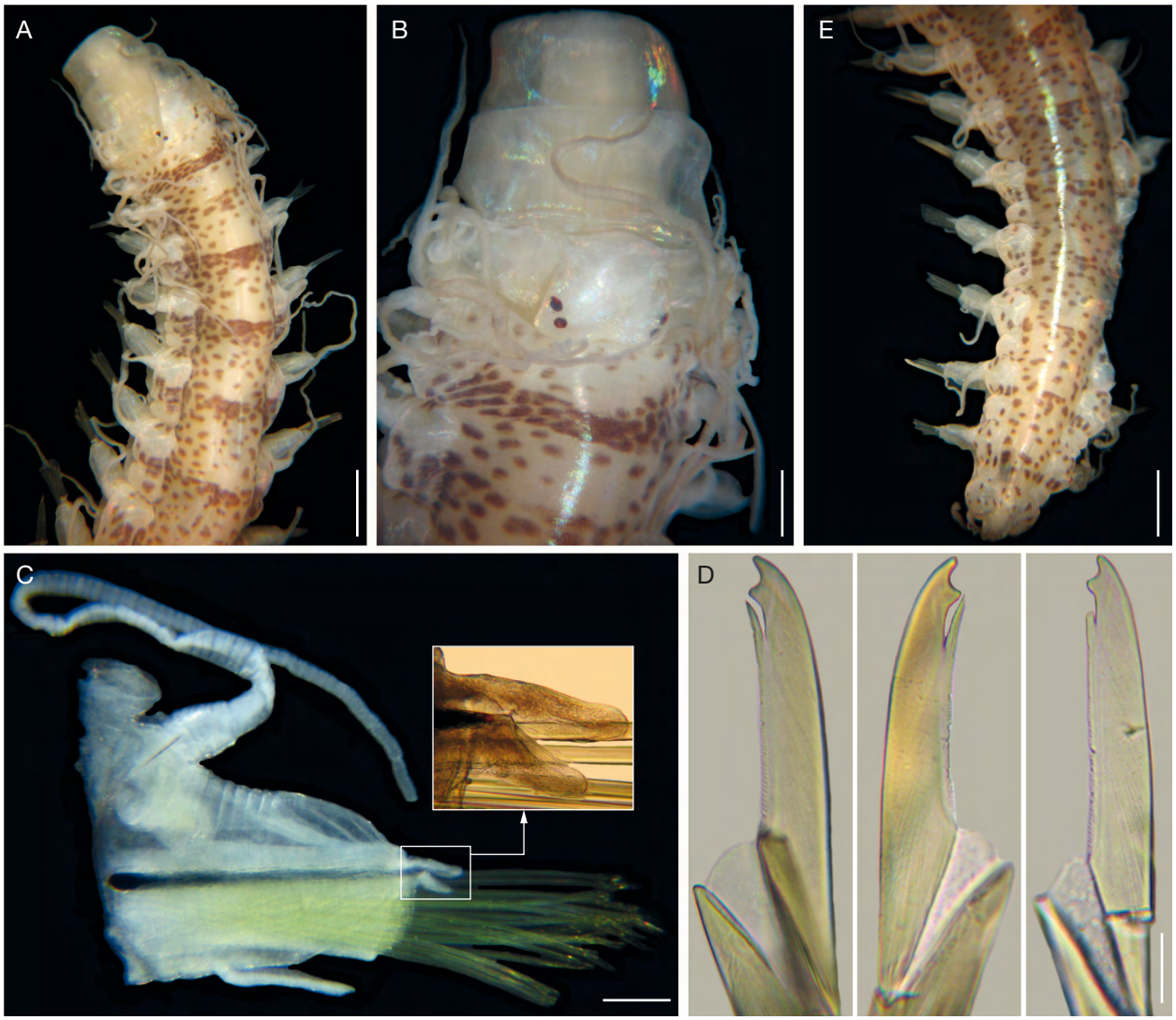

FIG. 15. — *Hesione genetta* Grube, 1867, specimen UF 81: **A**, anterior region, dorsal view; **B**, same, close up of anterior end (arrow points to left antenna); **C**, chaetiger 9, left parapodium, anterior view (inset: acicular lobes); **D**, same, neurochaetal blades; **E**, posterior region, dorsal view (right region removed for molecular studies). Scale bars: A, 1.5 mm; B, 0.6 mm; C, 0.3 mm; D, 20 µm; E, 1.8 mm.

coll. [27-28 mm long, 4 mm wide; 2 specimens with well-defined irregular transverse brownish bands and round spots throughout body; acicular lobe double]. — 1 specimen, UF 24, Tuamotu Islands, Rangiroa Atoll, Avatoru Motu, off Far W Hoa (-14.98333, -147.61666; 14°58'59.9880"S, 147°36'59.9760"W), outer reef flat, and reef crest, nestled in crevices in reef rock, 26.X.2001, G. Paulay coll. [45 mm long, 4 mm wide; complete; pigmentation pattern as typical; pharynx not everted; antennae longer than intraocular distance; acicular lobes invaginated in anterior chaetigers, clearly double in median chaetigers, but sometimes the upper one shortened or more contracted then the lower one]. — 1 specimen, UF 516, Society Islands, Moorea Island, Fringing Reef at NW side of Opunohu Bay (-17.4965, -149.8625; 17°29'47.4000"S, 149°51'45.0000"W), 0-3 m depth, 13.VII.2006, C. Lydeard, C. McKeon & C. Meyer coll. [24 mm long, 2 mm wide; pigmentation pattern with dorsal wide transverse irregular bands along chaetigers 1-9; pharynx partially exposed; ventral dissection showing a very long muscular tube extending for ⅔ body length]. — 1 specimen, UF 517, Society Islands, Moorea Island, Narrow Reef Flat Around Pt. Faupo (-17.4964, -149.7528; 17°29'47.0400"S, 149°45'10.0800"W), 0-1 m depth, 20.VI.2006, C. McKeon & G. Paulay coll. [42 mm long, 5 mm wide; body with a jaguar-like pigmentation pattern; individual spots with a paler central area, not forming dorsal wide transverse bands; dorsal cirri multiarticulated; acicular lobe double, upper one slightly longer; neurochaetal blades with guard reaching subapical tooth; posterior region with roughly verticillate ovarian tubules; oocytes compressed, each about 80-100 µm]. — 1 specimen, UF 881, Society Islands, Moorea Island, 1-2 km past CRIOBE station (-17.5145, -149.8548; 17°30'52.2000"S, 149°51'17.2800"W), 0-1 m depth, 30.X.2008, S. Fay & A. Anker coll. [30 mm long, 4 mm wide; body progressively wider posteriorly; pigmentation pattern typical but less widespread than in other specimens; acicular lobe double, invaginated in anterior chaetigers, better exposed in median ones; pharynx invaginated]. — 1 specimen, UF 934, Tuamotu Islands, Makemo Atoll, Mekemo, 31.III.2009, P. Bacchet & J. Letourneaux coll. [43 mm long, 6 mm wide; pigmentation brownish in abundant circular to transversely elliptic dots, grouped into semilunar or triangular, directed posteriorly, larger dots on the dorsal surface at the level of intersegmental areas, middorsal areas corresponding to chaetal lobes pale with a few or none dots; pigmented spots less abundant and smaller progressively towards the posterior region; pigmentation pattern

extended along prostomium and lower third of pharynx, especially dorsally, less intense ventrally; pharynx papillae not visible dorsally, hidden under prostomial lobe; eyes brownish, anterior ones twice as large as posterior ones; antennae tapered, 1.5 times longer than the distance between lateral eyes; dorsal and anal cirri pale brownish, ventral cirri pale; dorsal cirri multi-annulated; acicular lobe double, digitate, size variable and sometimes the upper lobe duplicated; neurochaetal blades short, many blades lost, guard reaching subapical tooth]. — 1 specimen, UF 935, Tuamotu Islands, Makemo Atoll, Mekemo, ethanol, 31.III.2009, P. Bacchet & J. Letourneaux coll. [29 mm long, 4.5 mm wide; pigmentation pattern typical; pharynx fully everted; body progressively wider posteriorly; acicular lobe double, better exposed in median chaetigers]. — 1 specimen, UF 936, Tuamotu Islands, Niau Atoll, Niau, 31.XII.2008, P. Bacchet & J. Letourneaux coll. [17 mm long, 2 mm wide; body bent dorsally, with thin transverse, mostly incomplete irregular lines along chaetigers 1-9; pharynx everted, dorsal papilla not seen; antennae longer than interocular distance; acicular lobes double, visible along most chaetigers]. — 1 specimen, UF 1307, Society Islands, Moorea Island, SE corner of Island, near Maatea, just off road (–17.57493, –149.79741; 17°34'29.7480"S, 149°47'50.6760"W), 0-3 m depth, 11.XI.2009, S. McPherson, T. Lotufo & N. Gravier-Bonnet coll. [17 mm long, 2 mm wide; pigmentation pattern with dorsal transverse, thin irregular lines along chaetigers 1-11, most with a median posterior rounded projection; pharynx partially everted, dorsal papilla not seen; acicular lobes double, better exposed along median and posterior chaetigers]. — 1 specimen, UF 1309, Society Islands, Moorea Island, SE corner of Island, near Maatea, just off road (–17.57493, –149.79741; 17°34'29.7480"S, 149°47'50.6760"W), 0-3 m,11.XI.2009, S. McPherson, T. Lotufo & N. Gravier-Bonnet coll. [8 + 11 mm long, 3 mm wide, 15 chaetigers (one removed for sequencing); body broken in two regions, about half-body each; pharynx tube retracted reaching about ⅔ body length, surprising because the posterior region is not hollow but has another muscular cylinder inside; posterior region of pharynx tube with a few long, ventral, transparent muscular fibers attached in a discontinuous series; pigmentation pattern resembling those present in other larger specimens, but antennae shorter, about as long as interocular distance]. — 1 specimen, UF 1364, Society Islands, Moorea Island, Temae at lighthouse (-17.48859, -149.77298; 17°29'18.9240"S, 149°46'22.7280"W), 0.5-2.0 m depth, 4.XII.2009, S. McPherson coll. [32 mm long, 4 mm wide; pigmentation, eye size and antennae features as in UF 934; pharynx papillae large, as wide as long; acicular lobe double, digitate, upper lobe slightly longer than lower one; neurochaetal blades short to long, guard reaching subapical tooth]. — 1 specimen, UF 1431, Society Islands, Moorea Island, Atiha Bay, inside barrier reef, on west side of pass (-17.59568, -149.84564; 17°35'44.4480"S, 149°50'44.3040"W), 0.5-1.0 m depth, 8.XII.2009, S. McPherson, G. Paulay & C. Meyer coll. [29 mm long, 4.5 mm wide; pigmentation, eye size and antennae features as in UF 934, but dorsal spots resembling a thick 'T' with stem directed posteriorly; pharynx papillae pale, rounded, hidden under prostomial lobe; acicular lobe double, digitate, upper lobe slightly longer than lower one; neurochaetal blades short to long, guard reaching subapical tooth]. — 1 specimen, UF 2144, Society Islands, Moorea, mouth of Cook's Bay (-17.4824, -149.824; 17°28'56.6400"S, 149°49'26.4000"W), lagoonal patch reef, in coral rubble/*Halimeda*/ green tufting algae, 1-2 m depth, 1.XI.2010, C. Watson coll. [16 mm long, 2 mm wide, 14 chaetigers left; prostomium barely pigmented; anterior eyes twice as large as posterior ones; pigmentation forming a roughly defined wide transverse band on chaetiger 1; body without posterior region]. — 1 specimen, UF 2145, Society Islands, Moorea Island, mouth of Cook's Bay (-17.4824, -149.824; 17°28'56.6400"S, 149°49'26.4000"W), lagoonal patch reef, in coral rubble/*Halimeda*/green tufting algae, 1-2 m depth, 1.XI.2010, C. Watson coll. [15 mm long, 3 mm wide; body laterally bent; prostomium without pigmentation; pharynx not exposed; body pigmentation poorly developed but progressively less intense posteriorly]. — 1 specimen, UF 2146, Society Islands, Moorea Island, mouth of Cook's Bay, lagoonal patch reef (-17.4824, -149.824; 17°28'56.6400"S, 149°49'26.4000"W), in coral rubble/*Halimeda*/ green tufting algae, 1-2 m depth, 1.XI.2010, C. Watson coll. [23 mm long, 2.5 mm wide; body laterally curved, slightly distorted, complete, pigmentation pattern typical; pharynx fully exposed; acicular lobe double, better exposed in posterior chaetigers]. — 1 specimen, UF 2229, Society Islands, Moorea Island, near Haapiti (-17.55475, -149.87899; 17°33'17.1000"S, 149°52'44.3640"W), mangroves, deep under rocks and in rubble, 0.5-1.0 m depth, 29.XI.2010. A. Anker coll. [37 mm long, 5 mm wide; body with typical pigmentation and extended ventrally to the basal pharynx region, and along chaetigers 14-16; pharynx everted]. — 1 specimen, USNM 19376, Tuamotu Islands, Mekema (Makemo) Island (16°35'S, 143°40'W), RV *Albatross*, unnumb. Sta., reef flat, ocean side, 20.X.1899 [11 mm long, 1.8 mm wide; a wide dorsal transverse band on chaetiger 1, lateral feebly defined spots on chaetigers 2-5/6; eyes circular, brownish, anterior ones almost twice as large as posterior ones; most cirri on site; pharynx partially everted; most neurochaetal blades lost; anal papilla not visible]. — 1 specimen, ZMUC 2427, Tahiti, RV *Galathea 1* Expedition 1845-1847, Sta. 145, 9.XII.1846 [52 mm long, 5 mm wide; macerated, colorless, left parapodium of chaetiger 8 removed for observation (kept in vial); acicular lobe double, blunt, upper tine slightly longer than lower one; neurochaetal blades bidentate, subdistal tooth as wide as distal one; guard approaching subdistal tooth]. — 1 specimen, ZMH-P 1282, no further data [53 mm long, 7 mm wide; prostomium collapsed by pressing body into small container; pigmentation pattern includes abundant brownish, round spots along body, becoming purple laterally, especially in the posterior sector of lateral cushions; middorsally alternating paler and slightly darker areas; antennae blunt, tapered, 7-8 times as long as wide; eyes of similar size, but difficult to observe because of distortion of anterior region; acicular lobe double, digitate, upper and lower tine of about the same length; most neurochaetal blades lost].

Gilbert Islands. 1 specimen, MCZ 463979, Kingsmill Islands, no further data [25 mm long, 3 mm wide; partially dried out, with salt granules adsorbed throughout body; original pigmentation mostly gone and transverse bands now diffuse, a wide one over chaetiger 1 indicates it belongs in *H. genetta*; antennae blunt, directed laterally, left one broken, right one about as long as interocular distance; dorsal cirri basally articulated; ventral cirri smooth, longer than chaetal lobe; acicular lobe double, upper tine longer, digitate, lower tine wider, triangular, ⅘ as long as upper tine; neurochaetal blades mostly lost, remaining ones with guard reaching subdistal tooth]. — 1 specimen, USNM 26070, Kiribati, Onotoa Atoll, 2.VIII.1951, A. Banner coll. [22 mm long, 3 mm wide; complete; pigmentation retained; first chaetiger with a thick transverse band, anteriorly irregular, posteriorly well-defined; following chaetigers with transverse band progressively thinner and less well-defined, last 7 chaetigers with a series of unconnected dark spots and smaller, paler spots between them; eyes brownish, tiny, anterior ones slightly larger than posterior ones; antennae short, digitate, smaller than interocular distance; acicular lobe double, both tines tapered, upper one slightly longer than lower one].

Cook Islands. 1 specimen, UF 390, Rarotonga Island, W of Ava Avarua, just behind Algal Rim, low tide, under rocks, 0.15 m depth, 20.IX.1984, G. Paulay & G. McCormack coll. [31 mm long, 4 mm wide; complete specimen, reddish brown spots forming irregular transverse bands dorsally; salt masses adhered on chaetal bundles and posterior region; pharynx partially exposed; anterior eyes twice as large as posterior ones; antennae longer than interocular distance; acicular lobes double, variable eroded or damaged, upper tine slightly longer to longer than lower one].

Papua New Guinea. 1 specimen, ZMB 2964, Bismarck Archipelago, Ralum, in coral, 4.IX.1896, F. Dahl coll. [32 mm long, 3.5 mm wide; body bent ventrally, with a faint wide band on chaetiger 1, and scattered dark spots dorsally; left parapodium from chaetiger 8

Fig. 16. — *Hesione genetta* Grube, 1867, living specimens, Moorea, Society Islands, dorsal view, arranged in a progressive reduction of the continuous band in chaetiger 1: **A**, UF 516; **B**, UF 2229; **C**, UF 2146; **D**, UF 1431; **E**, UF 1309; **F**, UF 881; **G**, UF 1364; **H**, UF 517 (no scales available; photos G. Paulay).

removed for observation (kept in vial); antennae digitate, as long as interocular distance; eyes barely pigmented, anterior eyes twice as large as posterior ones; acicular lobe double, blunt, subtriangular, upper tine markedly longer than lower one; blades with subapical tooth as large as distal one, guard approaching subdistal tooth]. — 2 specimens, ZMHU 1285, Bismarck Archipelago, New Britain island (05°44'S, 150°44'E), von Gutze coll., no further data [45-50 mm long, 6-7 mm wide; macerated, smaller one colorless, the other with abundant dorsal round brownish spots along body, without transverse bands; acicular lobe double, digitate, tines of similar size or upper one slightly larger].

Solomon Islands. 4 specimens, BMNH 1970.318, Royal Society Expedition to the Solomon Islands, 1965, Graham Point, under boulders in silty sand, 21.IX.1965, MTL & LWM coll. [17-30 mm long, 2-3 mm wide; most cirri and neurochaetal blades on site, cirri without tips; pigmentation pattern variable, all with a wide transverse band in chaetiger 1, remaining body with either abundant round small brownish spots, or combined with three larger half-moon shaped spots per segment positioned over between chaetal lobes region; antennae long, 5-6 times as long as wide; eyes brownish, anterior ones slightly larger than posterior ones; acicular lobe double, neurochaetae broken, remaining blades bidentate, subdistal tooth as wide as distal one, guard approaching subdistal tooth; pharynx partially exposed in 3 specimens, dorsal papilla slightly as long as wide]. — 1 specimen, BMNH 1970.320g, Royal Society Expedition to the Solomon Islands, 1965, Graham Point, below boulders in shell gravel, 5.X.1965, LWM coll. [38 mm long, 5 mm wide; most cirri and neurochaetal blades on site; a wide transverse band in chaetiger 1, following chaetigers with abundant round small brownish spots, somehow fused into larger spots, better defined along anterior chaetigers; antennae long, 5-6 times as long as wide; eyes brownish, anterior ones slightly larger than posterior ones; acicular lobe double; pharynx partially exposed, basal ring with brownish, irregulary longitudinal lines, dorsal papilla colorless, twice as wide as long].

Indonesia. 1 specimen. RMNH 1281, Maluku, RV *Siboga* Exped. Stat. 181 (Ambon, anchorage), 36-54 m depth, dredge and trawl, reef-exploration, muddy bottom, sand + coral, 5-11.IX.1899 [32 mm long, 3 mm wide; most cirri and neurochaetal blades lost; pigmentation pattern with a wide transverse band in chaetiger 1, remaining body with abundant round brownish spots; antennae long, 7-8 times as long as wide; eyes colorless].

Timor. 1 specimen. RMNH 427, East Timor, between Timor and Nusa Besi, anchorage, RV *Siboga* Exped. Stat. 282 (08°25.2'S, 127°18.4'E), 27-54 m depth, trawl, dredge, reef expl., sand, coral, 15-17.I.1900 [28 mm long, 3.5 mm wide; body complete, partially dried-out, bent backwards a thick transverse, dorsal, dark brown band in chaetiger 1; parapodia not removed to avoid further damage].

Australia. 1 specimen, AM 2619, Low Isles, off Port Douglas, Queensland, no further data [31 mm long, 5 mm wide, 16 chaetigers; complete, many pale-brownish, irregularly rounded spots along dorsal surface, no transverse bands; pharynx partially exposed, dorsal papilla conical, twice as wide as long; antenna digitate, blunt, 4-5 times as long as wide; eyes colorless, anterior ones slightly larger than posterior ones; several parapodia previously removed; left parapodia of chaetigers 2 and 8 removed for observation (kept in vial); chaetigers with about 20 neurochaetae; anterior chaetigers with longer blades, all bidentate, subdistal tooth slightly smaller or as wide as distal one; guards mostly broken, approaching subdistal tooth]. — 2 specimens, BMNH 1931.7.1.23/24, Great Barrier Reef Expedition, Low Isles, no further data [one macerated, the other perfect; both with abundant dark dorsal spots, with a pale wide band in chaetiger 2, better defined in best-preserved specimen; body 51-53 mm long, 3.5-5.0 mm wide; right parapodia of chaetigers 8 and 9 already removed; most dorsal cirri lost, some as long as body width (excluding parapodia); acicular lobes double, upper tine slightly wider and twice longer than lower one].

DISTRIBUTION. — Western Pacific from Japan to Australia, including the Marshall Islands, and the French Polynesia, in 0-54 m depth, in coralline rocks to mixed bottoms, including silty sands.

DIAGNOSIS. — *Hesione* with prostomium rectangular; parapodia with dorsal cirri basally cylindrical, dorsal cirrophore as long as wide; larger acicula blackish; acicular lobe double, tines digitate, subequal; neurochaetal blades bidentate, 3-5 times as long as wide; subdistal tooth as large as distal one, with guards approaching subdistal tooth.

DESCRIPTION

Specimen UF 81, complete, subcylindrical, laterally bent, tapered posteriorly. Body with brownish rounded spots, variably fused middorsally forming irregular transverse bands along chaetigers 1-11, barely defined in chaetiger 2 (Fig. 15A), extended into lateral cushions, progressively less defined, posterior segments with a spotty pattern in ethanol. Tentacular cirri, dorsal cirri and neuropodial lobes whitish. Body 31 mm long, 3.5 mm wide; right parapodia of chaetigers 13 and 14 removed for molecular studies.

Prostomium slightly as wide as long (Fig. 15B), anterior margin rounded, projected anteriorly, without depression nor pigmentation, lateral margins straight, posterior margin partially covered by tentacular segment projection, longitudinal depression shallow, barely pigmented. Antennae tapered, digitate, 5-6 times as long as wide, longer than interocular distance. Eyes dark brown, circular; anterior eyes slightly larger than posterior ones.

Tentacular cirri twisted, some without tips, longest ones reaching chaetiger 5. Lateral cushions projected, most separated into a larger, anterior region, and a smaller posterior one, surface smooth.

Parapodia (Fig. 15C) with chaetal lobes wider than high, truncate; dorsal cirri with cirrophores about twice as long as wide, cirrostyle variably contracted, twisted, cylindrical, smooth basally, annulated medially, articulated distally, as long as body width (without parapodia). Ventral cirri smooth, variably damaged, if complete surpassing tip of chaetal lobe.

Neuraciculae blalckish, larger one markedly thicker than smaller one. Acicular lobe double, tines digitate, of similar size, or upper one slightly longer (Fig. 15C [inset]).

Neurochaetae about 25 per bundle, blades at a certain angle from handles, decreasing in size ventrally, 3-5 times as long as wide, each blade bidentate, subdistal tooth wider than distal one, guards, if complete, approaching subdistal tooth (Fig. 15D).

Posterior region tapered into a blunt cone (Fig. 15E); pygidium conical, anus with 8 rounded, low papillae.

Pharynx partially exposed, two smooth rings of similar length. Gonads visible through body wall in posterior region. Oocytes about 100 µm.

Pigmentation

There is a remarkable variation of dorsal pigmentation intensity in this species about a similar pattern with a whitish, yellowish or pinkish background. There is a transverse band on chaetiger 1, no transverse band in chaetiger 2, and along chaetigers 3-16 transverse bands become progressively shorter

and less defined (Fig. 16A-D), from having a straight anterior margin, with a posterior margin variably expanded caudally, to a series subcontinuous bands made up with irregular spots, sometimes as three as long as wide bands per segment, or no such distinct separation, especially in medial and posterior chaetigers (Fig. 16E-H). Lateral cushions usually pigmented; spots variably fused into larger spots or separated from each other. Tentacular cirri, dorsal cirri, and neuropodial lobes paler than dorsal background or of the same pigmentation.

Remarks

Hesione genetta Grube, 1867, restricted, is among the most colorful species in the genus, and similar specimens from the Indian Western Pacific Ocean have been regarded as conspecific. Because of the differences are consistent, the species is being restricted and other, similarly pigmented specimens are described as new species below.

Grube (1867: 64) indicated that the collector of *H. genetta* was Mr Godeffroy from Hamburg, that it was collected from Samoa (Grube 1867: 65) and that more than a single specimen was available (Grube 1867: 65). This would imply that the specimens deposited in Hamburg might be syntypes, and they were regarded as such with hesitation, because there are no more details in the labels regarding collector, or collecting dates. If this is combined with the fact that the specific locality in one of the labels was not included in the description, their status as types is doubtful. This explains why another specimen from the same area as the type was used for the redescription: this pecimen matches the body length indicated in the description. Overall, and as far as the presumptive syntypes condition allows the comparison, the specimen UF 81 matches both the original description and the morphological features, but because it was collected recently, it allowed to illustrate the remaining pigmentation pattern.

Grube (1867) did not explain the etymology for *Hesione genetta*; however, genets are small wild cats, and the southern European species (*Genetta genetta* (Linnaeus, 1758)) has its body with dark spots, more or less arranged into longitudinal lines, and a tail with a series of dark bands throughout its length. In *H. genetta* there are irregular spots along dorsal surfaces, and they can fuse into irregular transverse bands; as indicated above, these bands are missing or usually poorly defined on chaetiger 2, and better defined on most other chaetigers, and their anterior margins are sometimes straight resulting from a more complete merging of adjacent spots, whereas the posterior margin is irregular. Grube (1867: 65) indicated: "Auf dem rosigen oder blassvioleten Grunde des mit dem Rüssel 30 mm langen Thieres erscheinen an jedem Segment etwa 5 bis 6 Querreihen kleiner dunkler Rückenfleckchen, von denen die mittleren Reihen fast zu einer Querbinde verfliessen" (Transl.: The rosy or pale violet background, including the pharynx is 30 mm long, with about 5 to 6 transverse rows of small dark dorsal little spots, of which the middle rows almost merge into a transverse band, at each segment). Grube later (1878: 104) indicated: "Semiteres, elongata utrinque sensim attenuata, ex cinereo margaritacea splendens cute laevi densiore, supra violaceo fusco maculate. Segmenta 19 latitudinae 10mum versus crescentia, a 12di decrescentia, plerumque alterum tantum latiora quam longa, anteriora et posteriora breviora, omnia seriebusmacularum transversis fere 6 ornata, maculis ipsis transverse ovalibus, media cujusque segmenti majore." (Transl.: Subcylindrical, gradually tapered sides, far from bright gray pearly colored, smooth skin thicker, over violet dark spots. 19 segments, progressively thicker to segment 10, decreasing from segment 12, each usually only one time as wide as long, anterior and posterior ends thinner, all with about 6 transverse series of spots adorned with intertwined oval spots, over the middle of each segment). These pigmentation patterns are common but, as shown above, the definition of transverse bands is variable and in some specimens they are not distinct, but they are conspecific as indicated by COI-barcoding (Fig. 16D, G). Horst (1924: 193) indicated that acicular lobes were subequal, and most specimens conform to this feature.

Two other species, traditionally regarded also as *H. genetta*, have better defined transverse bands, along both anterior and posterior margins, with the first one usually wider (or longer) than following ones, but the first band is over chaetiger 2, with chaetigers 1 and 3 often without transverse bands. Irregular spots may be present and this similarity explains why they were regarded as variations of the same pigmentation pattern, but this apparently subtle difference is consistent, and long-lasting, and herein these two variants, one from the Western Indian, and the other from the Western Pacific, are regarded as distinct species and described as *H. mooreae* n. sp. and *H. paulayi* n. sp. respectively (see below).

Consequently, those records for a species having well-defined transverse bands, especially on chaetiger 2, do not belong in *H. genetta* but in *H. mooreae* n. sp., such as Willey (1905: 267) for Sri Lanka, and Fauvel (1953b: 105) for India; whereas those that might match *H. paulayi* n. sp. would be the records by Fauvel (1919b: 370; 1923b: 15-16; 1947b: 89-90) for the Gambier Islands, and Horst (1924: 193) for Indonesia. Hartman (1954: 622) recorded *H. genetta* for the Marshall Islands and indicated its distribution as ranging from Sri Lanka to Samoa, including the Philippine islands. However, she probably included some other species under the same name, as indicated above; one is newly described below as *H. paulayi* n. sp.; the record by Fauvel (1953b: 105) for India probably belongs in *H. mooreae* n. sp.

Hesione harrisae n. sp.
(Fig. 17)

urn:lsid:zoobank.org:act:E5DDED97-BF16-483F-BC1F-04FA0C33294C

Type material. — **Caribbean Sea, Puerto Rico.** Holotype, LACM 8631, Mayaguez, Cabo Rojo Light, 20.I.1946, W. G. Hewatt coll.

Etymology. — This species is named after Leslie Harris, Collection Manager of the Allan Hancock Polychaete Collection, in the Los Angeles County Museum of Natural History, in recognition of her knowledge of polychaetes in general, and because of her long-lasting and enthusiastic support to our research requests. The name is a noun in genitive (ICZN 1999: art. 31.1.2).

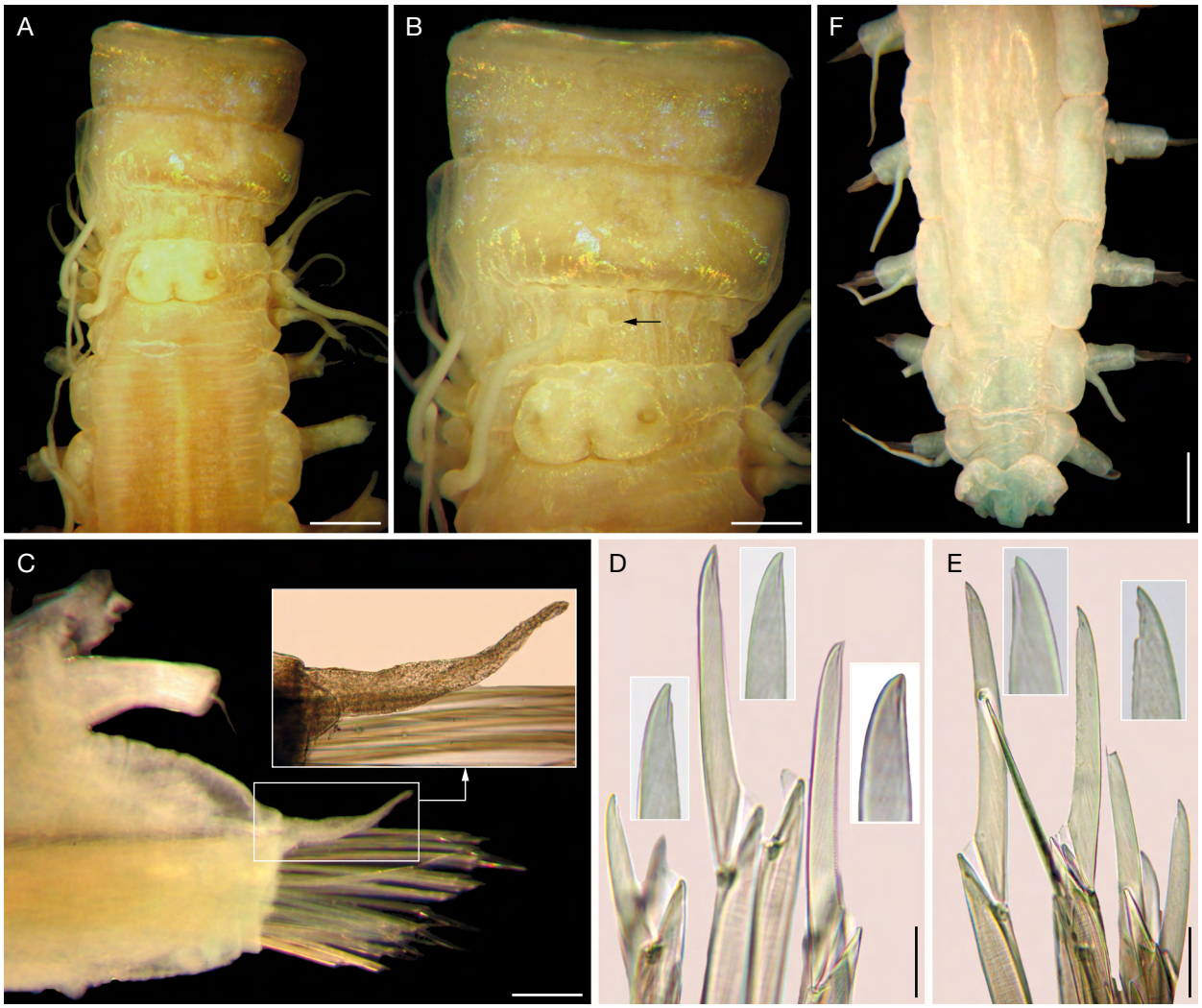

Fig. 17. — *Hesione harrisae* n. sp., holotype, LACM 8631: **A**, anterior region, dorsal view; **B**, anterior end, dorsal view, pharynx exposed (arrow points to dorsal papilla); **C**, chaetiger 11, right parapodium, anterior view (inset: acicular lobe); **D**, chaetiger 6, left parapodium, neurochaetal blades (insets: tips of blades); **E**, chaetiger 11, right parapodium, neurochaetal blades (insets: tips of blades); **F**, Posterior region, dorsal view. Scale bars: A, 1 mm; B, 0.6 mm; C, 0.3 mm; D, E, 50 µm; F, 1.4 mm.

Distribution. — Only known from the type locality in Puerto Rico, Caribbean Sea.

Diagnosis. — *Hesione* with prostomium laterally curved; parapodia with dorsal cirri basally cylindrical, dorsal cirrophore twice as long as wide; larger acicula blackish; acicular lobe single, tapered; neurochaetal blades unidentate, 6-8 times as long as wide; guards approaching distal tooth.

Description

Holotype, LACM 8631, complete, subcylindrical, tapered posteriorly, without pigmentation (Fig. 17A) in ethanol; several dorsal or ventral cirri lost, most neurochaetal blades lost; right parapodia of chaetigers 5 and 6, and left parapodium of chaetiger 11 removed (6 + 11 in vial). Body straight, 30 mm long, 3 mm wide.

Prostomium as wide as long, anterior margin truncate with a shallow depression, lateral margins rounded, slightly expanded posteriorly (Fig. 17B), posterior margin deeply cleft about as ⅓ prostomial length (reaching level of posterior eyes), longitudinal depression indistinct. Antennae minute, rounded, about as long as wide, ⅓ as long as interocular distance. Eyes feebly pigmented, anterior eyes darker, twice as large as, and more separated than posterior eyes.

Tentacular cirri damaged, twisted. Lateral cushions slightly projected, without distinctive divisions in anterior chaetigers, in posterior ones barely separated into two sections, surface smooth.

Parapodia with chaetal lobes wider than high, truncate (Fig. 17C); dorsal cirri with cirrophores twice as long as wide; cirrostyle cylindrical, smooth basally, articulated medially and distally, as long as body width (details undefined, tips eroded or broken). Ventral cirri smooth, surpassing chaetal lobe.

Neuraciculae blackish, larger one markedly thicker and darker than smaller one. Acicular lobe single, tapered, long, about 10 times longer than lower, rounded tine; upper tine as long as chaetal bundle width (Fig. 17C [inset]).

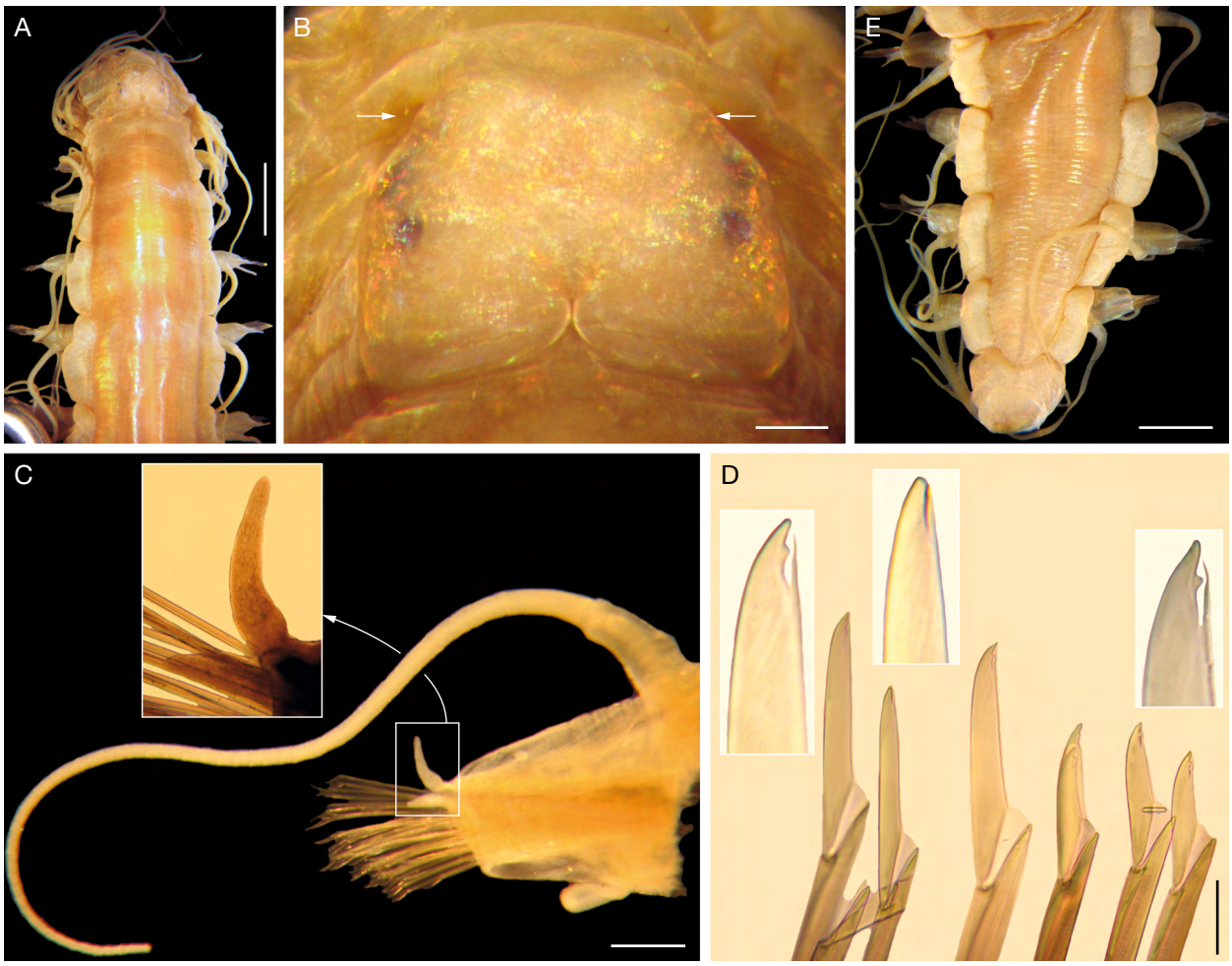

FIG. 18. — *Hesione hartmanae* n. sp., holotype, LACM 10158: **A**, anterior region, dorsal view; **B**, prostomium, dorsal view (arrows point to antennae); **C**, chaetiger 8, right parapodium, anterior view (inset: acicular lobe); **D**, same, neurochaetal blades (insets: tips of blades); **E**, posterior region, dorsal view. Scale bars: A, 2.2 mm; B, 0.3 mm; C, 0.6 mm; D, 65 µm; E, 1.5 mm.

Neurochaetae about 30 per bundle, blades unidentate (sometimes a tiny subdistal tooth present), blades at a certain angle from handles, decreasing in size ventrally, 6-8 times as long as wide, each with a distal tooth, guards often broken, if entire, approaching distal tooth (Fig. 17D, E).

Posterior region tapered into a blunt cone (Fig. 17F); pygidium swollen (now collapsed), integument slightly eroded, anus with 6 blunt papillae.

Pharynx everted, with three distinctive rings of similar length, margin smooth, slightly eroded; dorsal papillae rounded, about as long as wide. Oocytes about 100 µm in diameter.

REMARKS

Hesione harrisae n. sp. could be confused with *H. praetexta* Ehlers, 1887, reinstated (see below), another Grand Caribbean species because both have markedly different acicular lobes, and thin, long neurochaetal blades. However, in *H. harrisae* n. sp. the upper acicular lobe is at least 5 times as long as the lower one, and its neurochaetal blades are mostly unidentate, whereas in *H. praetexta* the upper acicular lobe is about 3 times longer, and the neurochaetal blades are bidentate. Further, *H. harrisae* n. sp. was identified as *H. praetexta* because both have a markedly longer acicular lobe, but in *H. praetexta* blades are bidentate, whereas in *H. harrisae* n. sp. they are unidentate.

As indicated in the key below, there is another species with unidentate neurochaetal blades: *H. osbornae* n. sp. (see below). However, there are two main differences between these two species: in *H. harrisae* n. sp. the neurochaetal blades are 6-8 times as long as wide, and their guards reach distal teeth, whereas in *H. osbornae* n. sp. neurochaetal blades are about 15 times as long as wide, and guards surpass distal teeth.

Hesione hartmanae n. sp.
(Figs 18, 19)

urn:lsid:zoobank.org:act:F50811AA-A413-4219-AAF1-0B3DD68E2E4F

Hesione splendida – Monro 1933: 26 (*non* Savigny *in* Lamarck, 1818).

Hesione intertexta – Hartman 1940: 212, pl. 33, figs 30-31 (*partim*, fig. 30).

Type material. — **Eastern Pacific. Galápagos Islands.** Holotype, LACM 10158, RV *Velero III*, Sta. 310 (00°18'20"N, 90°31'00"W), off Bindloe Island, 27 m depth, rock, tangles, 3.XII.1934. Paratypes, LACM 10159, RV *Velero III*, Sta. 167 (01°14'37"S, 90°28'08"W), Post Office Bay, Charles Island, 27 m depth, rocks, 19.I.1934 [four complete paratypes 21-40 mm long, 4-5 mm wide; some more or less macerated, most cirri and neurochaetal blades on site; chaetal lobes variably invaginated; right parapodium of chaetiger 9 in 3 specimens removed (kept in vial); even the smallest one has oocytes, each about 100 µm].

Additional material. — **Eastern Pacific. Galápagos Islands.** 1 specimen, BMNH 1932.12.24.129, RV *St-George* Pacific Expedition, 1923-1924, Galápagos Sta. 9, C. Crossland coll. [35 mm long, 5 mm wide; almost colorless, a few poorly defined transverse bands along some anterior chaetigers; antennae twice as long as wide; anterior eyes slightly larger than posterior ones; right parapodium of chaetiger 12 previously removed; right parapodium of chaetiger 10 removed for observation (kept in vial); acicular lobe double, tines digitate, blunt, upper tine slightly longer than lower one; neurochaetal blades broken or without blades; blades bidentate, subdistal tooth smaller, guards most broken, if complete surpassing subdistal tooth]. — 2 specimens, LACM 10160), RV *Velero III*, Sta. 169 (00°46'18"S, 90°19'27"W), Academy Bay, Indefatigable Island, 28-45 m depth, sand, rock, algae, 20.I.1934 [28-31 mm long, 3-4 mm wide; one macerated, the other in better condition; most cirri and neurochaetal blades on site; chaetal lobes variably invaginated; right parapodium of chaetiger 9 from both specimens removed (kept in vial); upper acicular lobe twice as long as lower one; largest specimen with oocytes, each about 100 µm].

Etymology. — This species is named after Dr Olga Hartman, eminent taxonomist of polychaetes from the Allan Hancock Foundation, University of Southern California, to honor her immense legacy including lots of publications and new taxa, and because she provided some relevant details to recognise these specimens as a different, undescribed species. The name is a noun in genitive (ICZN 1999: art. 31.1.2).

Distribution. — Galápagos Islands, Ecuador, in subtidal to 45 m depth, in mixed substrates.

Diagnosis. — *Hesione* with prostomium rectangular; parapodia with dorsal cirri basally cylindrical, dorsal cirrophore twice as long as wide; larger acicula blackish; acicular lobe double, tines long, digitate, subequal; neurochaetal blades bidentate, 3-6 times as long as wide; subdistal tooth smaller; guards approaching distal tooth.

Description

Holotype, LACM 10158, mature, complete, subcylindrical, tapered posteriorly, posterior region bent laterally, first four chaetigers with ill-defined brownish transverse bands, progressively paler (Fig. 18A) in ethanol; some cirri lost, others in regeneration, most neurochaetal blades on site; right parapodium of chaetiger 8 removed (kept in vial). Body 41 mm long, 5 mm wide.

Prostomium slightly as long as wide, anterior margin truncate with a deep depression, lateral margins straight, slightly divergent posteriorly, posterior margin deeply cleft about ¼ prostomial length (reaching level of posterior eyes), longitudinal depression indistinct (Fig. 18B). Antennae minute, digitate, twice as long as wide, about as long as free interocular distance. Eyes brownish, circular; anterior eyes slightly larger and more distant to each other than posterior ones.

Tentacular cirri undulated, longest reaching chaetiger 4. Lateral cushions projected, with 2 sections in anterior to median chaetigers, and with 3 ones in posterior segments.

Parapodia with chaetal lobes tapered, truncate, dorsal cirri with cirrophores 3 times as long as wide (Fig. 18C); cirrostyle cylindrical, smooth basally, then annulated, become articulated in distal half, as long as half body width (without parapodia). Ventral cirri smooth, tapered, surpassing chaetal lobe.

Neuraciculae blackish, 1-2 markedly thicker and 1 very thin, very close to each other, making their detection difficult. Acicular lobe double, tapered, blunt, upper lobe twice as long as lower one, half as long as chaetal fascicle width (Fig. 18C [inset]).

Neurochaetae about 30 per bundle, blades bidentate (sometimes guard and teeth eroded), subdistal tooth smaller, blades at a certain angle from the handle, 3-6 times as long as wide, decreasing in size ventrally, guard approaching distal tooth (Fig. 18D [insets]).

Posterior region tapered into a blunt cone (Fig. 18E); pygidium swollen, slightly depressed, anus with 6 digitate papillae.

Pharynx not everted in holotype (smaller paratype with pharynx almost fully everted, margin slightly eroded, made up by three rings, basal one slightly corrugated, dorsal papillae rounded, as long as wide). Oocytes about 100 µm in diameter.

Variation

A rather weak dorsal darkening in one of the smaller paratypes, even less defined in largest paratype. Prostomial shape varies depending on pharynx exposure from having a squarrish outlook, with lateral margins slightly divergent in smallest paratype (Fig. 19A, B), to one with rounded lateral margins, markedly divergent if the pharynx is not exposed (Fig. 19D, E). In smaller paratypes, acicular lobes with upper tine twice as long as lower ones (Fig. 19C), or of similar size in largest paratype (Fig. 19F).

Remarks

Hesione hartmanae n. sp. was likely recorded before under three different names. Monro (1933: 26) cited what Cyril Crossland noticed about the pigmentation of some Panamian *Hesione*: "There are five transverse brown bands of irregular outline anteriorly, the first on the anterior border of the peristomium, the others occupying the anterior third of each segment, the middle third being white, while the posterior third is a light brown but darker than the general body color behind the fifth segment." Monro referred that specimen to *H. splendida* Savigny *in* Lamarck, 1818, which had been observed alive and described with a pearly iridescent body, but without pigmentation. It must be noted that this Panamian specimen had been less than 10 years in ethanol before Monro studied it, and he indicated there was no pigmentation left on its body.

Hartman (1940: 212) preferred to use *H. intertexta* Grube, 1878, and, as indicated below in the remarks for *H. panamena* Chamberlin, 1919, her illustrations show an acicular

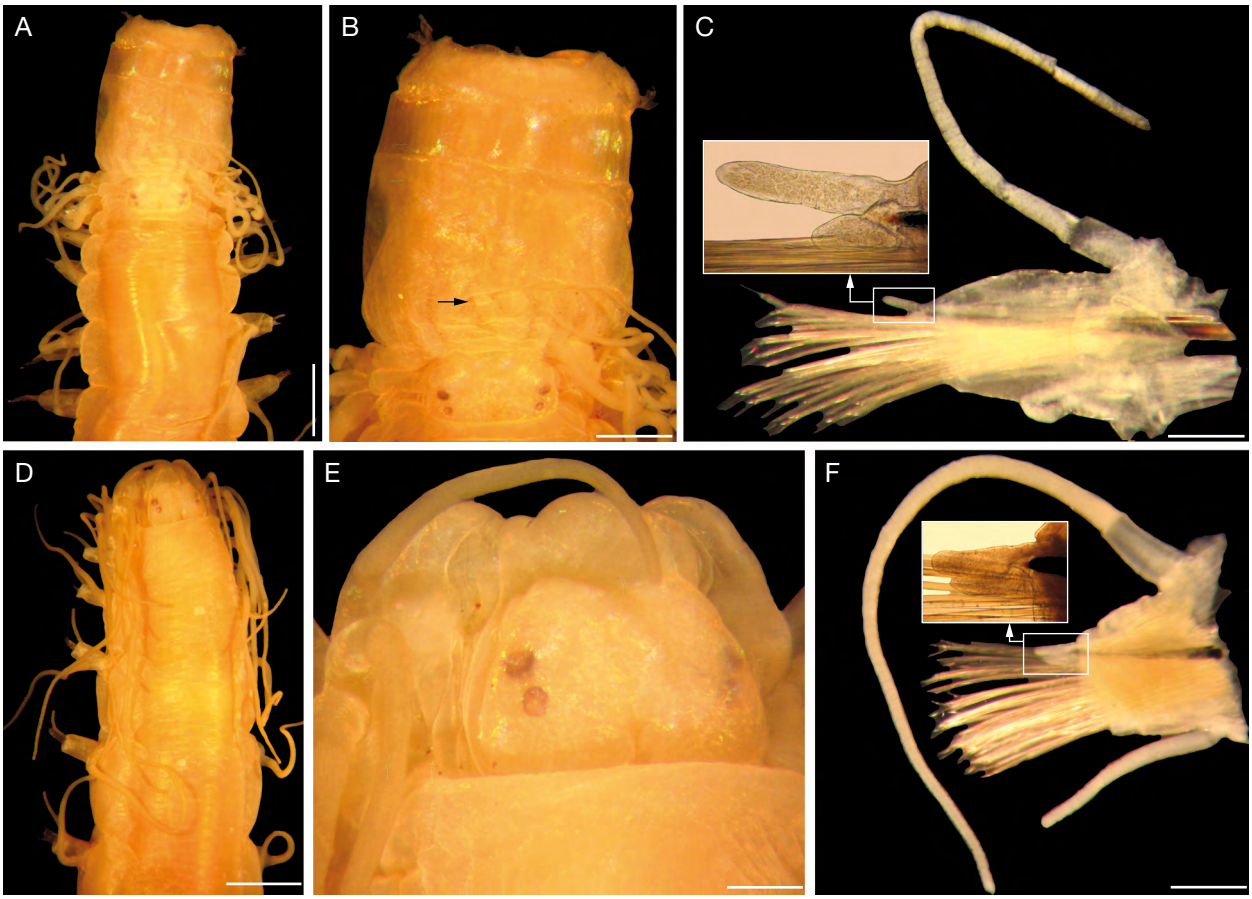

FIG. 19. — *Hesione hartmanae* n. sp., paratypes, LACM 10159: **A**, smallest paratype, anterior region, dorsal view; **B**, same, prostomium and everted pharynx (arrow points to dorsal papilla); **C**, same, chaetiger 9, right parapodium, anterior view (inset: acicular lobe); **D**, largest paratype, anterior region, slightly oblique dorsal view; **E**, same, prostomium slightly oblique dorsal view; **F**, same, chaetiger 9, right parapodium, anterior view (inset: acicular lobe). Scale bars: A, 1.3 mm; B, 0.7 mm; C, 0.4 mm; D, 1.8 mm; E, 0.3 mm; F, 0.6 mm.

lobe double with tines of similar size, which are not present in *H. intertexta*, meaning she had two species in her material. It seems she was unaware of the previous indications by Horst (1924: 193), who emphasised that acicular lobes were of very different size and shape in *H. intertexta*: a longer, digitate and the other one shorter, rounded. Different sized tines are also present in *H. panamena*, as indicated above. Hartman made no indication of transverse bands but stated that in her material: "most individuals retain the reticulated, fulvous pattern on the dorsum of the anterior segments, but in some there are almost none." This fading is typical for those species having longitudinal thin lines along the body. In some of the specimens regarded as belonging to *H. hartmanae* n. sp., there is a fine indication for darker tranverse areas in anterior segments, despite the fact they have been in ethanol for about 70 years.

As indicated in the key below, *H. hartmanae* n. sp. resembles *H. picta* Müller, 1858 and *H. reticulata* von Marenzeller, 1879. Their main difference is the length of the acicular lobe in comparison to the width of the corresponding chaetal lobe. In *H. hartmanae* n. sp. it is longer, about half as long as chaetal fascicle width, whereas it is shorter (⅓ as long) in the two other species.

Hesione helenensis n. sp.
(Fig. 20)

urn:lsid:zoobank.org:act:F44B445E-71C8-493B-B59F-2B193435A522

TYPE MATERIAL. — **South Atlantic Ocean.** Holotype, USNM 33148, and one paratype, USNM 1479052, Saint Helena Island, James Bay, IV.1964, A. Loveridge coll. [paratype 39 mm long, 4 mm wide; slightly distorted; anterior end compressed; dorsal cirrostyles swollen basally, multiarticulated; chaetal lobes markedly contracted, invaginated into neuropodia; acicular lobes barely seen, rounded, upper tine 3-4 times longer than lower one; ventral cirri basally swollen, longer than neuropodia, slightly articulated; posterior end truncate; anus with about 6 anal papillae].

ETYMOLOGY. — The species name is an adjective derived from Saint Helena island, and as in some other similar names, the last vowel in the proper name is suppressed, and the suffix *-ensis* is added to indicate its current distribution.

DISTRIBUTION. — Only known from Saint Helena island, in subtidal rocky bottoms.

DIAGNOSIS. — *Hesione* with prostomium slightly curved laterally; parapodia with dorsal cirri basally swollen, dorsal cirrophore twice as long as wide; larger acicula blackish; acicular lobe single, short, massive, blunt, upper tine 3 times longer than lower one; neurochaetal blades bidentate, 4-6 times as long as wide; subdistal tooth smaller; guards approaching distal tooth.

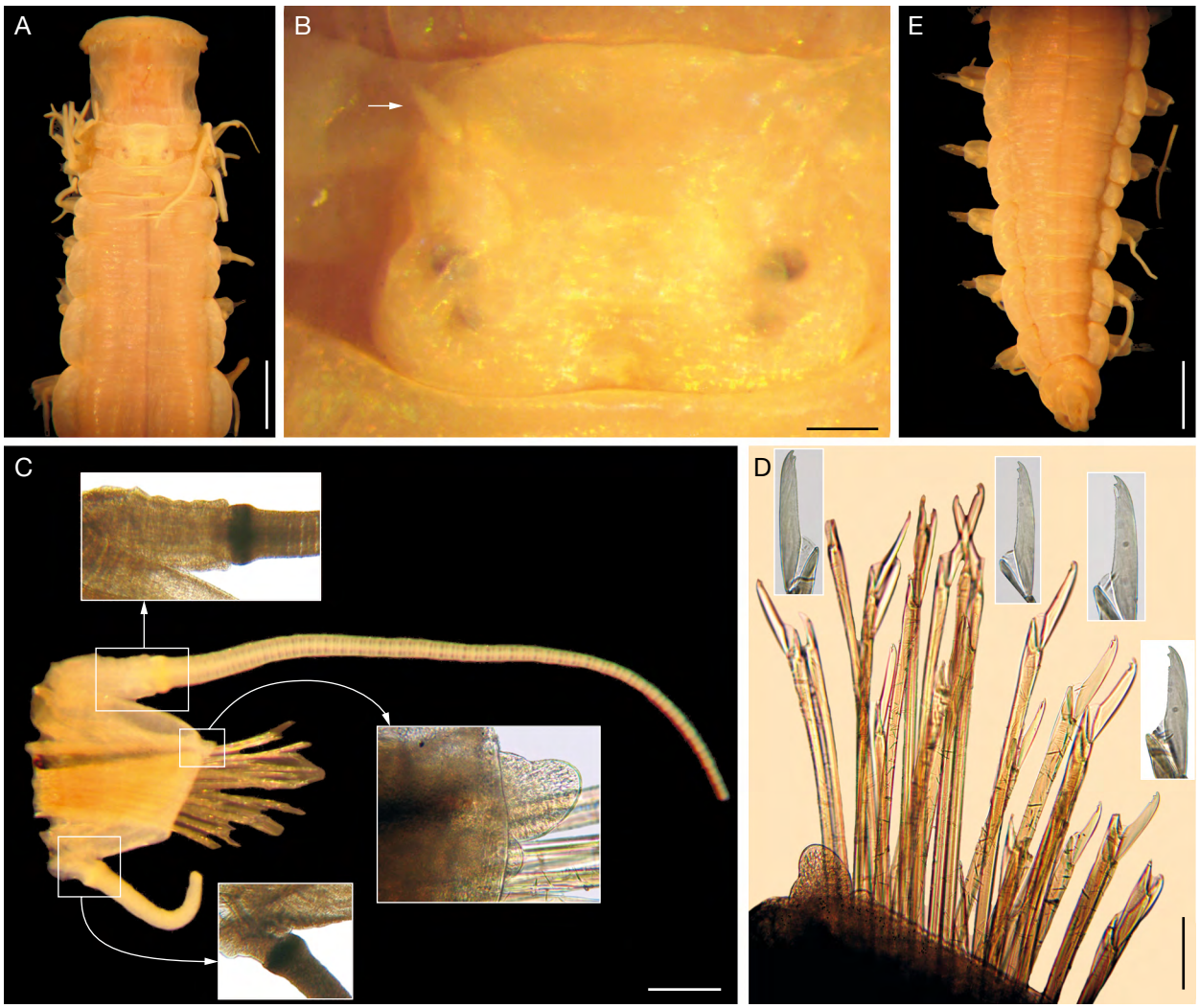

Fig. 20. — *Hesione helenensis* n. sp., holotype, USNM 33148: **A**, anterior region, dorsal view, pharynx partially exposed; **B**, prostomium, dorsal view (arrow points to left antenna); **C**, chaetiger 9, left parapodium, anterior view (insets: acicular lobe and bases of cirrostyles); **D**, same, neurochaetae (insets: blades); **E**, posterior region, dorsal view. Scale bars: A, 1.7 mm; B, 0.2 mm; C, 0.5 mm; D, 160 µm; E, 1.8 mm.

Description

Holotype, USNM 33148, complete, subcylindrical, tapered posteriorly, without pigmentation (Fig. 20A) in ethanol; most cirri and many neurochaetal blades broken; left parapodium of chaetiger 9 removed (kept in vial). Body 39 mm long, 4 mm wide.

Prostomium slightly as wide as long, anterior margin projected anteriorly, lateral margins rounded, posterior margin with a shallow cleft, about ⅕ as long as prostomial length, longitudinal depression slight (Fig. 20B). Antennae minute, left one visible, fusiform, 2-3 times as long as wide, about as long as interocular distance. Eyes brownish, anterior ones larger and more separated than posterior ones.

Tentacular cirri long, thin, broken, longest one (incomplete) reaches chaetiger 3. Lateral cushions low, smooth, barely projected, most divided into 2 or 3 regions.

Parapodia with chaetal lobes about as long as wide, truncate; dorsal cirri with cirrophores about twice as long as wide (Fig. 20C); cirrostyles basally swollen, annulated, articulated medially and distally, as long as body width (tips lost). Ventral cirri with cirrostyles basally swollen, surpassing chaetal lobe, darker than parapodia (if observed in compound microscope preparations).

Neuraciculae blackish, tapered, only one visible. Acicular lobe double, upper tine blunt, as long as wide, 4 times longer than lower tine blunt (Fig. 20C [insets]).

Neurochaetae about 20 per bundle (Fig. 20D), blades bidentate, 4-6 times as long as wide, decreasing in size ventrally, each with smaller subdistal teeth, and guards (most broken) reaching subdistal teeth (Fig. 20D [insets]).

Posterior region tapered into a blunt cone, dorsal surface rugose (Fig. 20E); pygidium smooth, anus with 7 blunt papillae.

Pharynx partially exposed, anterior margin slightly eroded, dorsal papilla not seen. Oocytes not seen.

REMARKS

Hesione helenensis n. sp. resembles Northeastern Atlantic or Mediterranean specimens of *H. pantherina* Risso, 1826, and it could be confused with it. However, as indicated in the key below, *H. helenensis* n. sp. resembles *H. praetexta* Ehlers, 1887 reinstated. The main difference is that in *H. helenensis* n. sp. dorsal and ventral cirrostyles are basally swollen, and this feature is unique for the genus, and present throughout the body, although in posterior chaetigers ventral cirrostyles are less markedly swollen. Further, these swollen areas appear darker when parapodia are mounted and observed in the compound microscope.

Hesione horsti n. sp.
(Figs 21, 22)

urn:lsid:zoobank.org:act:58221603-3923-4EA5-AFDF-3E05B2196059

Hesione intertexta – Horst 1924: 192-193 (*partim*, *non* Grube, 1878).

TYPE MATERIAL. — **Indonesia.** Holotype, RMNH 19913, East Timor, South coast, at anchorage, RV *Siboga* Exped. Stat. 285 (08°39.1'S, 127°04.4'E), 34 m depth, dredge, muddy bottom and coral, 18.I.1900.

ADDITIONAL MATERIAL. — **Indonesia.** Four specimens, RMNH 431.4, Sulawesi, RV *Siboga* Exped. Stat. 205, Buton Strait, Lohio Bay, 22 m depth, dredge, sand, muddy bottom, 20.IX.1899 [15-20 mm long, 1-2 mm wide; colorless, even aciculae being honey-colored instead of blackish; integument smooth; acicular lobe single; neurochaetal blades variable in length, upper ones longer, bidentate, teeth minute, directed upwards, smaller ones in a lower position, bidentate, subdistal tooth smaller or as large as distal one, guard approaching subdistal tooth, rarely approaching distal tooth]. — 1 specimen, RMNH 431.5, Irian Jaya, RV *Siboga* Exped. Stat. 273, Aru Islands (06°10'S, 134°30'E), Pearl Banks, anchorage off Pulu Jedan, 13 m depth, trawl, dredge and divers, sand and shells, 23-26.XII.1899 [23 mm long, 2 mm wide; macerated, many neurochaetal blades lost; integument smooth; acicular lobe single, tapered; neurochaetal blades bidentate, guard approaching distal tooth]. — 2 specimens, RMNH 1277, Sulawesi, RV *Siboga* Exped. Stat. 213, Saleyer (Selayar Island, 06°00'00"S, 120°30'00"E), anchorage, 36 m depth, coral reef expl., muddy bottom, sand, 26 Sep.1899 [27-36 mm long, 4-5 mm wide; dorsal surface rugose].
Papua New Guinea. 1 specimen, AM 48557, North side of Rasch Pass, Madang, coral substrate, 3.VII.1987, P. A. Hutchings coll. [25 mm long, 3 mm wide; complete, slightly macerated; midventral longitudinal depression reddish; anterior eyes as long as wide; pygidium granulose, reddish; acicular lobe single; blades bidentate, guard approaching distal tooth; dorsal cirrophore short; ventral cirri articulated].
Australia. 2 specimens, AM W.2938, Great Barrier Reef Expedition, Sta. 14, Queensland, 1.2 km SE off Lizard Island, 35 m, Great Barrier Reef Expedition, 9.III.1929 [29-30 mm long, 3-4 mm wide; bent laterally, integument smooth to annulated, right parapodium of chaetiger 10 removed from 1 specimen, and right parapodium of chaetiger 3 and left one from chaetiger 14 of the other, removed for observation (kept in separate vials); anterior eyes as long as wide (set at the prostomial margin), about twice larger than posterior ones; acicular lobe single, tapered; neurochaetal blades bidentate, anterior chaetigers and upper bundle chaetae with long blades, teeth small, directed distally, others with teeth larger, directed laterally, guard approaching distal tooth]. — 1 specimen, AM G.11250, Port Molle, Queensland, no further data [dried-out, stiff, dark gray, bent laterally, integument smooth, most tentacular and dorsal cirri lost, most chaetal blades lost, body 5 mm long, 1.2 mm wide; prostomium distorted; antennae tapered, 3-4 times as long as wide; anterior eyes marginal, as long as wide, twice larger than posterior ones; acicular lobe single, tapered; chaetal blades not seen, parapodia not dissected to avoid further damage]. — 1 specimen, BMNH 1931.7.1.21, Great Barrier Reef Expedition 1929, N Direction Island, no further data [body slightly bent dorsally, integument smooth, some dorsal cirri lost, most without tips; right parapodia of chaetigers 8 and 9 previously removed; body 32 mm long, 3 mm wide; prostomium as long as wide; antennae tapered, 3-4 times as long as wide; anterior eyes marginal, as long as wide, twice larger than posterior ones; acicular lobe single, tapered; chaetal blades not seen, parapodia not dissected to avoid further damage]. — 1 specimen, ZMB 5280, Hamurger SW-Australien Expedition 1905, SW Australia, Sharks Bay, 10 km S Denham, Sta. 8, 1905, Michaelsen & Hartmeyer coll. [18 mm long, 2 mm wide; slightly distorted, partially dehydrated; integument smooth, except in pygidium; antennae digitate, 4 times as long as wide, longer than interocular distance; anterior eyes as long as wide, of the same width than posterior ones; neuraciculae blackish, tapered; acicular lobe single, basally swollen, tip tapered; neurochaetae about 20 per bundle; blades bidentate, upper chaetae with smaller teeth; guard approaching distal tooth; pygidium granulose].
Japan. 1 specimen, NHMW 576, Enoshima, 1877, Drasche coll. [40 mm long, 5.5 mm wide; partially dehydrated; body pale brown without pigmentation pattern; pharynx exposed; antennae minute, smaller than posterior eyes diameter; acicular lobe single, massive, tips probably eroded; most neurochaetal blades broken; lateral cushions dehydrated, with longitudinal wrinkes resembling granular surface as seen in other specimens]. — 1 specimen, SMF 11220, Boso Peninsula, Katsuura, Yoshia, subtidal rocky shore, 4.VI.1998, E. Nishi coll. [69 mm long, 7 mm wide; colorless; slightly distorted, most tentacular and dorsal cirri lost; many chaetal blades lost, right parapodia of chaetigers 2 and 9 removed for observation (kept in vial); antennae digitate as long as interocular distance, or 3-4 times as long as wide; anterior eyes larger than posterior ones; integument smooth, lateral cushions smooth, entire; acicular lobes single, blunt, basally swollen; neurochaetal blades bidentate, distal tooth larger, guards mostly eroded, approaching subdistal tooth]. — 1 specimen, SMF 14026, Izu Peninsula, Shiduoka, Shimoda, intertidal, sandy bottom, 16.X.2002, E. Nishi coll. [32 mm long, 5.5 mm wide; colorless, most dorsal cirri and a few tentacular cirri lost; right parapodia of chaetigers 2 and 9 removed for observation (kept in vial); integument granulose; antennae digitate as long as interocular distance, or twice as long as wide; anterior eyes slightly larger than posterior ones; lateral cushions mostly smooth, entire, last three chaetigers with longitudinal ridges; acicular lobes single, blunt, basally swollen; neurochaetal blades bidentate, distal tooth larger, guards mostly eroded, approaching distal tooth].
New Caledonia. 3 specimens, MNHN-IA-PNT94 (formerly jar Musorstom 710), Lagoon Est, Sta. 710 (21°24.0'S, 166°02.5'E), 30-31 m depth, 10.VIII.1986, B. Richer coll. [20-25 mm long, 3.0-3.5 mm wide; macerated; integument smooth; body and anterior eyes unpigmented, acicular lobe single; neurochaetal blades bidentate, teeth tiny, subdistal tooth as large as distal one]. — 1 specimen, MNHN-IA-PNT94 (formerly jar Musorstom 713), Lagoon Est, Sta. 713 (22°22.6'S, 166°00.7'E), 34-35 m depth, 11.VIII.1986 [34 mm long, 5 mm wide; complete, distorted, laterally bent, with an anteroventral dissection; anterior eyes blackish, as long as wide, twice larger than posterior, round brownish eyes; integument smooth, with longitudinal furrows; acicular lobe single; most neurochaetal blades lost, bidentate, guard approaching distal tooth, most broken; dorsal cirrophore 2-3 times as long as wide; ventral cirri irregularly wrinkled].

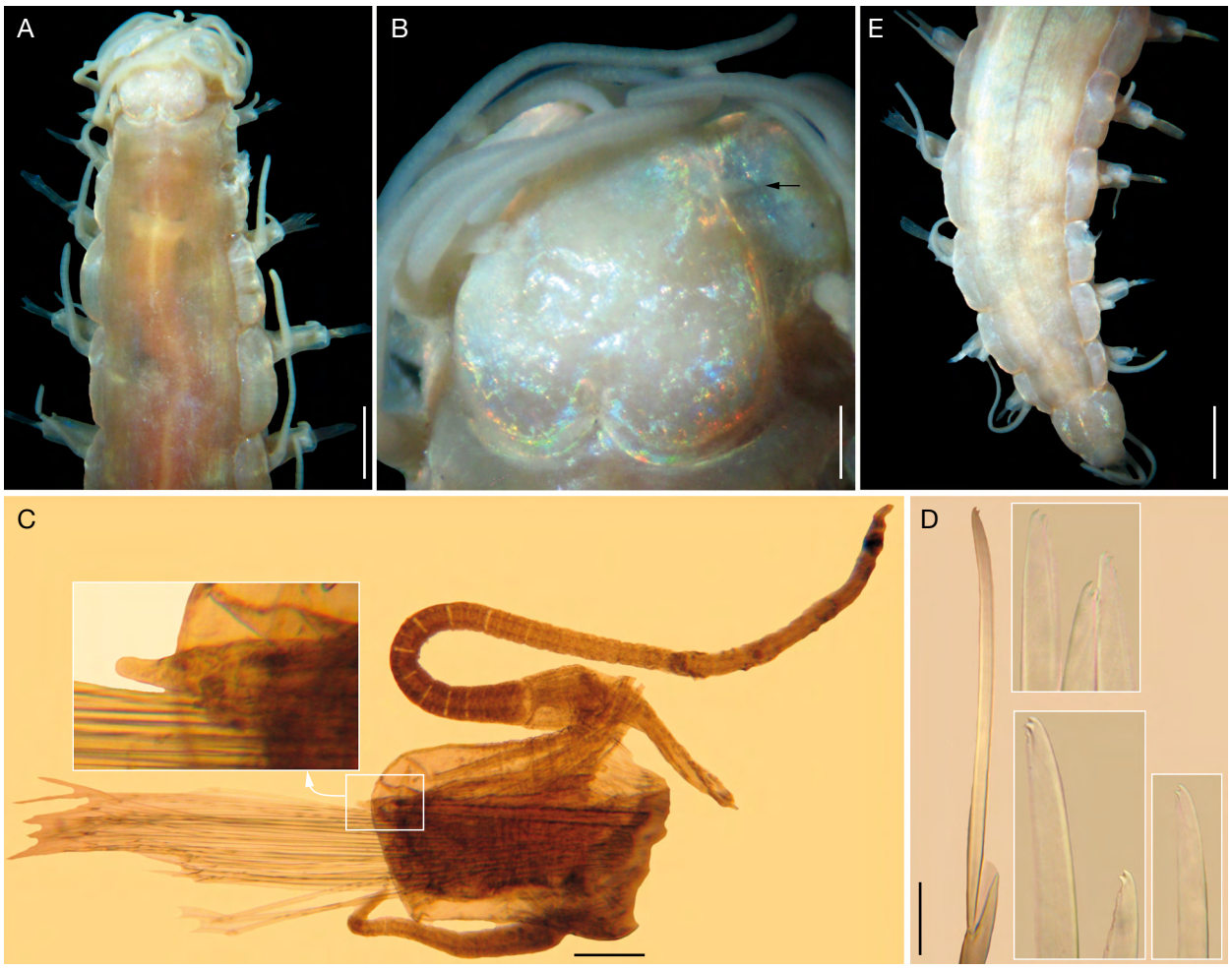

Fig. 21. — *Hesione horsti* n. sp., holotype, RMNH 19913: **A**, anterior region, dorsal view; **B**, prostomium, dorsal view (arrow points to right antenna); **C**, chaetiger 7, right parapodium, anterior view (inset: acicular lobe); **D**, same, upper neurochaetal blade (insets: tips of medial and lower neurochaetal blades); **E**, posterior region, dorsal view. Scale bars: A, 0.7 mm; B, C, 0.2 mm; D, 35 µm; E, 1 mm.

Indonesia. 2 specimens, BMNH 1910.3.10.6/7, Goram Island, Gorong Archipelago, Maluku Islands, Stalker coll., no further data [complete, colorful, bent ventrally specimens; pigmentation pattern resembles Grube's illustration for *H. intertexta*, including lateral darker spots; body 32-54 mm long, 4.5-5.5 mm wide; integument rugose, including lateral cushions, posterior ones with projected rounded tubercles along dorsal and lateral surfaces; right parapodium of chaetiger 7 removed for observation (kept in vial); acicular lobe single, with a swollen base; neurochaetal blades bidentate, subdistal tooth smaller, guards broken, remaining ones approaching subdistal tooth].

Etymology. — This species is named after the late Dr R. Horst, from the Leiden Museum, a very productive taxonomist of polychaetes, oligochaetes, sipunculans and some other invertebrate and vertebrate groups, in recognition of his many publications of Indonesian and *Siboga* Expedition polychaetes. The name is a noun in genitive (ICZN 1999: art. 31.1.2).

Distribution. — Southern Japan to Indonesia, Australia and New Caledonia, in mixed bottoms, 3-36 m water depth.

Diagnosis. — *Hesione* with prostomium laterally curved; parapodia with dorsal cirri basally cylindrical, dorsal cirrophore twice as long as wide; larger acicula pale; acicular lobe single, digitate, basally swollen, lower tine missing; neurochaetal blades bidentate, 6-12 times as long as wide; teeth subequal; guards approaching subdistal tooth.

Description

Holotype, RMNH 19913, complete, bent laterally, subcylindrical, tapered posteriorly; prostomium whithish, integument brownish, no pigmentation pattern (Fig. 21A) in ethanol; most tentacular and dorsal cirri broken; right parapodia of chaetigers 2, 7, 14 removed for observation (kept in vial). Body 20 mm long, 2 mm wide.

Prostomium as long as wide, anterior margin projected anteriorly, lateral margins slightly rounded, posterior margin exposed, deeply cleft along ⅓ prostomial surface, longitudinal depression indistinct (Fig. 21B). Antennae minute, digitate, 3-4 times as long as wide. Eyes colorless, size relationship between anterior and posterior eyes unknown.

Tentacular cirri broken. Lateral cushions barely projected, most entire but some divided into two or three sections.

Parapodia with chaetal lobes tapered, truncate; dorsal cirrophores about twice as long as wide (Fig. 21C); cirrostyle basally cylindrical, articulated, medially annulated, tips and size relationship with body width unknown. Ventral cirri smooth, barely corrugated, surpassing chaetal lobe.

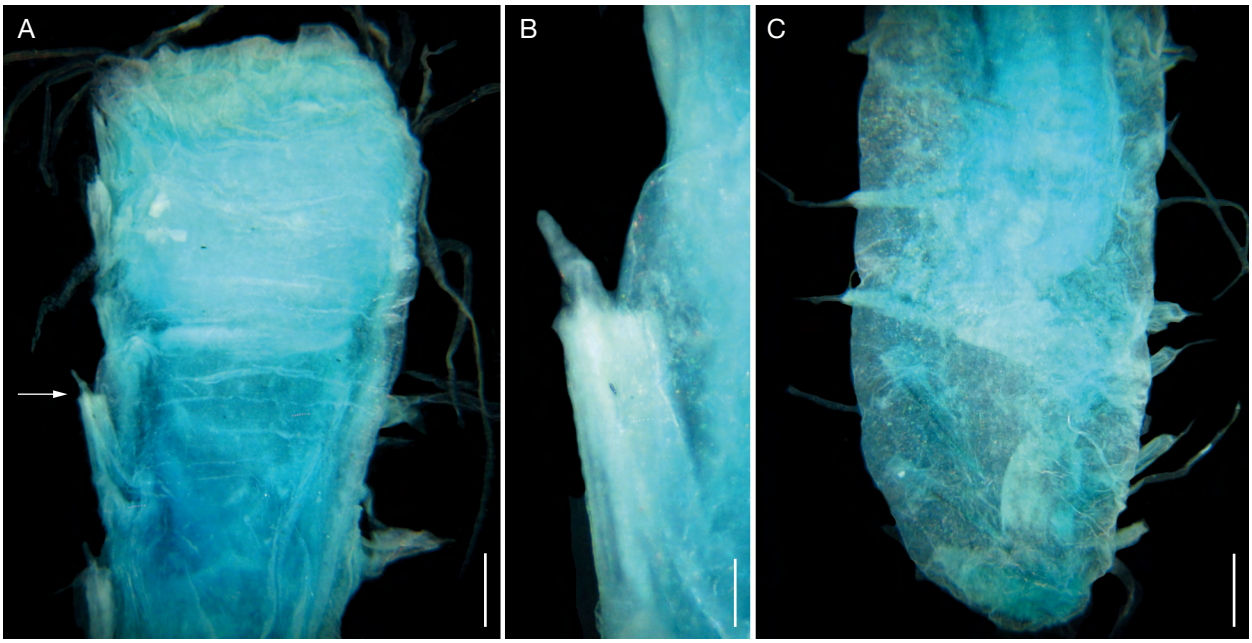

FIG. 22. — *Hesione intertexta* Grube, 1878, holotype, MNHW 293, restricted (mehtyl green pigmented): **A**, anterior region, dorsal view, pharynx everted (arrow points to left parapodium of chaetiger 4); **B**, chaetiger 4, left parapodium, upper view; **C**, posterior region, dorsal view. Scale bars: A: 0.8 mm, B: 0.3 mm, C: 1.4 mm.

Neuraciculae honey-colored, two per parapodium, thinner shorter, thicker reaching chaetal lobe margin. Acicular lobe single, digitate, swollen basally (Fig. 21C [inset]).

Neurochaetae about 30 per bundle, blades at a certain angle from handle, blades bidentate, 6-12 times as long as wide, teeth minute, similar-sized, usually directed distally, guard approaching subdistal tooth (Fig. 21D [insets]).

Posterior region tapered into a blunt cone (Fig. 21E); pygidium barely swollen, anus damaged, papillae indistinct.

Pharynx not everted in holotype. Oocytes not seen.

Pigmentation

There are no records of living specimens.

REMARKS

Hesione horsti n. sp. is unique in the genus because it has honey-colored neuraciculae, either both, or only the larger one, and its neurochaetae have guards approaching subdistal tooth, but blades are long with tiny teeth, and these blades which can be found along a few anterior chaetigers in other species, are present along all chaetigers, at least in the upper part of the chaetal bundle. The holotype was regarded as a juvenile of *H. intertexta* by Horst (1924), but despite their resemblance to the juveniles of other species, which might also have paler neuraciculae, especially along a few anterior chaetigers, larger pale neuraciculae are present along the body of the holotype of *H. horsti* n. sp., and its long neurochaetal blades are not restricted to anterior chaetigers.

Hesione intertexta Grube, 1878, restricted (Figs 22-25)

Hesione intertexta Grube, 1878: 102, 103, pl. 6, fig. 5. — Malaquin & Dehorne 1907: 336. — Ehlers 1920: 26. — Horst 1924: 192, 193. — Monro 1926: 311, 312; 1931: 9, 10. — Fauvel 1947b: 31, fig. 26B. — Wu *et al.* 1975: 76, pl. 2, figs 9, 10. — Uchida 2010: 5, fig. 3. — Lee & Ong 2015: 203, 204, figs 3, 4.

Hesione pantherina – Fauvel 1930: 511; 1947a: 30, 31, fig. 27A4, (*non* Risso, 1826).

Hesione pantherina var. *splendida* – Augener 1933b: 181, 182, fig. 1A-C (*non* Risso, 1826 *nec* Savigny *in* Lamarck, 1818).

Hesione splendida – Gibbs 1971: 139 (*non* Savigny *in* Lamarck, 1818).

TYPE MATERIAL. — **Western Pacific. Philippines.** Holotype, MNHW 293, Zamboanga, Semper coll.

ADDITIONAL MATERIAL. — **Palau**. 1 specimen, ZMB 3813, Babeldaob, Semper coll., no further data [23 mm long, 4 mm wide; complete, one parapodium previously removed and placed in permanent slide; body dried-out almost completely, anterior end features collapsed; parapodia dehydrated; acicular lobe single, shape variable, short, blunt digitate to thinner, tapered; the permanent slide has the acicular lobe bent over itself and the tip of ventral cirri is partially covering it; few neurochaetae with blades, blades bidentate, guard approaching subdistal tooth, probably eroded].

Japan. 1 specimen, UF 1772, Okinawa Prefecture, Okinawa Island, Okinawa, White Beach, campground (26.292824, 127.917392; 26°17'34.1664"N, 127°55'02.6112"E), shallow, very silty bay, 0-4 m depth, 18.VII.2010, N. Evans, F. Michonneau, G. Paulay & J. Thomas coll. (used for redescription).

Indonesia. 1 specimen, RMNH 431.1, Lesser Sunda Islands, RV *Siboga* Exped. Stat. 33 (Bay of Pidjot, Lombok), 22 m depth, trawl, muddy bottom, coral and coral sand, 24-26.III.1899 [36 mm long, 3 mm wide; colorless, bent laterally, posterior end bent dorsally; integument granulose, lateral cushions longitudinally ridged; pharynx partially everted, dorsal papilla as wide as long, surface irregular; anterior eyes twice as large as posterior ones; acicular lobe single]. — 1 specimen, RMNH 431.2, Sulawesi, RV *Siboga* Exped. Stat. 115, Kwandang Bay, E side of Pajunga Island, reef-exploration, 9-11. VII.1899 [42 mm long, 5 mm wide; colorless, integument granulose; anterior eyes twice as large as posterior ones; antennae minute 3-4 times as long as wide; longest tentacular cirri reaches chaetiger 5; dorsal cirri longer than body width, including parapodia; acicular lobe double, upper tine blunt, digitae, 3-5 times longer than lower tine, rounded to digitate]. — 1 specimen, RMNH 1278, Maluku, RV *Siboga* Exped. Stat. 144, anchorage N of Salomakiëe (Damar) Isl., reef exploration, coral, 7-9.VIII.1899 [28 mm long, 5 mm wide; macerated, fusiform, integument granulose, retaining a lateral blackish spot on intersection of lateral cushions; right parapodium from chaetiger 7 removed for observation (kept in vial); acicular lobe double, lower tine about ⅖ as long as upper tine; neurochaetal blade bidentate, guard approaching distal tooth]. — 1 specimen, RMNH 1279, East Timor, South coast, at anchorage, RV *Siboga* Exped. Stat. 285 (08°39.1'S, 127°04.4'E), 34 m depth, dredge, muddy bottom and coral, 18.I.1900 [29 mm long, 3.5 mm wide; pharynx exposed; integument granulose, especially in posterior region, lateral cushions with roughly parallel longitudinal ridges; neuraciculae blackish, paler in anterior chaetigers; acicular lobe single; neurochaetal blades bidentate, teeth laterally directed, guards mostly eroded, approaching distal tooth]. — 1 specimen, RMNH 1280, Jakarta (Batavia) Bay, Sluiter coll., no further data [50 mm long, 7 mm wide; slightly macerated, integument granulose; most chaetal blades lost, remaining ones severely eroded; acicular lobe double, lower tine very variable, rounded to digitate, ⅕-⅓ as long as upper tine]. — 1 specimen, RMNH 1962, *Siboga* Expedition, Kalimantan, Borneo Bank, 5 miles NNE from stat. 79, RV *Siboga* Exped. Stat. 79b (02°38.5'S, 117°46'E), 54 m depth, trawl, coral sand, 12.VI.1899 [17 mm long, 3 mm wide; bent dorsally, pharynx exposed; body colorless, acicular lobe single, blunt; neurochaetal blades longer and medium-sized, bidentate, guard approaching distal tooth]. — 1 specimen, ZMH-P PE 312, Ambon Island (03°42'S, 128°10'E), 1887, no further data [49 mm long, 5 mm wide; colorless, integument granulose, lateral cushions with longitudinal ridges; antennae digitate, 2-3 times as long as wide; eyes colorless, anterior lenses slightly larger than posterior ones; acicular lobe single, tapered; most neurochaetal blades lost].

Vanuatu. 1 specimen, UF 435, Sanma Province, Rotua Island off Aore Island (-15.612222, 167.1775; 15°36'43.9992"S, 167°10'39.0000"E), sea grass and soft coral beds, 0-2 m depth, 15.I.2005, C. Meyer coll. [beheaded; 34 mm long, 4 mm wide; some anterior segments with small, lateral, triangular dark spots ahead of chaetal lobes; acicular lobes single, long, tapered or blunt; neurochaetal blades bidentate, guard approaching distal tooth].

New Caledonia. 1 specimen, MNHN-IA-PNT91d (formerly jar 70a), Collection François, 1894 [29 mm long, 3.5 mm wide; prostomium damaged; integument with small tubercles dorsally, especially in median and posterior regions; parapodial lobes projected, with single acicular lobes]. — 1 specimen, MNHN-IA-PNT91e (formerly jar 70b), Collection François, no further data [40 mm long, 8 mm wide; macerated, bent laterally, parapodial lobes mostly invaginated, some show single acicular lobes]. — 1 specimen, MNHN-IA-PNT91f (formerly jar 70c), 1880, no further data, M. Reveillere coll. [distorted, dried out, some exposed parapodia with single acicular lobes; neuraciculae tapered]. — 2 specimens, MNHNIA-PNT91g (formerly jar 70d, separate containers), Mrs Pruvot, no further data [24-33 mm long, 3-4 mm wide; without pigmentation, bent ventrally; pharynx fully everted; acicular lobes single]. — 4 specimens, MNHNIA-PNT91h (formerly jar 70e), 41, Mrs Pruvot, no further data [dried out, too brittle as to measure them; some parapodia exposing single, tapered acicular lobes]. — 1 specimen, MNHN-IA-PNT96 (formerly jar Musorstom 645), Lagoon Est, Sta. 645 (21°50.3'S, 166°39.5'E), 51 m depth, 7.VIII.1986, B. Richer coll. [18 mm long, 2.5 mm wide; colorless; integument smooth; acicular lobe single; neurochaetal blades bidentate, subdistal tooth smaller than distal one].

Marquesas Islands. 1 specimen, MNHN-IA-PNT97 (formerly jar Musorstom 1264), Ua Pou Island, Sta. 1264 CP (09°21.2'S, 140°07.7'W), 53-57 m depth, 3.IX.1997 [80 mm long, 10 mm wide; splendid, giant, without pigmentation; right parapodium from chaetiger 8 removed (kept in same container); antennae minute, twice as long as wide; anterior eyes twice larger than posterior ones; acicular lobes single, tapered; neurochaetal blades about 30 per bundle, most with guards and subdistal teeth eroded; subdistal tooth smaller, guard basally denticulated, approaching distal tooth; oocytes oval, centrally depressed, about 100 µm in diameter].

Papua New Guinea. 1 specimen, UF 3974, Madang Province, Sair Island (-5.18395, 145.802183; 05°11'02.2200"S, 145°48'07.8588"E), fringing reef inside lagoon, 8.XI.2012, J. Moore coll. [40 mm long, 5 mm wide; slightly macerated, with longitudinal, brownish irregular lines along first 6 chaetigers, chaetigers 6-10 with triangular brownish spots before chaetal lobes; antennae minute, digitate, shorter than interocular distance; anterior eyes twice as large as posterior ones; posterior prostomial margin notched, extended almost to the level of posterior eyes; acicular lobe single, variable contracted or eroded; neurochaetal blades bidentate, teeth lateral (only one with distally directed teeth in chaetiger 2), guard reaching distal tooth].

Solomon Islands. 1 specimen, BMNH 1970.316, Royal Society Expedition to the Solomon Islands, 1965, Haniara, below Hotel Mendana, Acropora rubble, 6.VII.1965, MTL coll. [30 mm long, 5 mm wide; slightly bent laterally; antennae 2-3 times as long as wide; with some pigmented longitudinal lines remaining, abundant tubercles forming longitudinal series along dorsum, including lateral cushions; anterior eyes slightly larger than posterior ones; acicular lobe single, basaly swollen, tapered, blunt]. — 1 specimen, BMNH 1970.317, Royal Society Expedition to the Solomon Islands, 1965, Komimbo Bay, in coral boulders on reef platform, 18.VIII.1965, LMW coll. [40 mm long, 8 mm wide; slightly bent dorsally; antennae twice as long as wide; with oblique pigmented lines, somehow parallel but diverging from the middorsum, abundant tubercles forming longitudinal series along dorsum, including lateral cushions, better developed anteriorly; anterior eyes slightly larger than posterior ones, left posterior eye divided into 5 or 6 complete eyes; acicular lobe single, basaly swollen, tapered, blunt; pharynx fully exposed (5 mm long), dorsal papilla as wide as long]. — 4 specimens, BMNH 1970.318, Royal Society Expedition to the Solomon Islands, 1965, Graham Point, under boulders in silty sand, 21.IX.1965, MTL & LWM coll. [35-45 mm long, 5-7 mm wide; antennae twice as long as wide; colorless; tubercles in longitudinal series along dorsum, including lateral cushions, better defined in posterior chaetigers; anterior eyes slightly larger than posterior ones; acicular lobe single, basaly swollen, tapered, blunt]. — 2 specimens, BMNH 1970.320, Royal Society Expedition to the Solomon Islands, 1965, Graham Point, below boulders in shell gravel, 5.X.1965, LWM coll. [37-40 mm long, 5 mm wide; antennae twice as long as wide; longitudinal brownish lines and intersegmental lateral spots still visible; tubercles in longitudinal series along dorsum, including lateral cushions, better defined in posterior chaetigers; anterior eyes slightly larger than posterior ones; acicular lobe single, basaly swollen, tapered, blunt; pharynx partially exposed, dorsal papilla as wide as long in one specimen, the contrary in the other; oocyte strands, probably gonad fragments, over lateral surfaces; oocytes 100 µm in diameter].

Australia. 2 specimens, AM W.2593, Low Isles, off Port Douglas, Queensland, VIII-IX.1928, G. P. Whitley & W. Boardman coll. [33-35 mm long, 6-7 mm wide; one turgid with prostomium intact

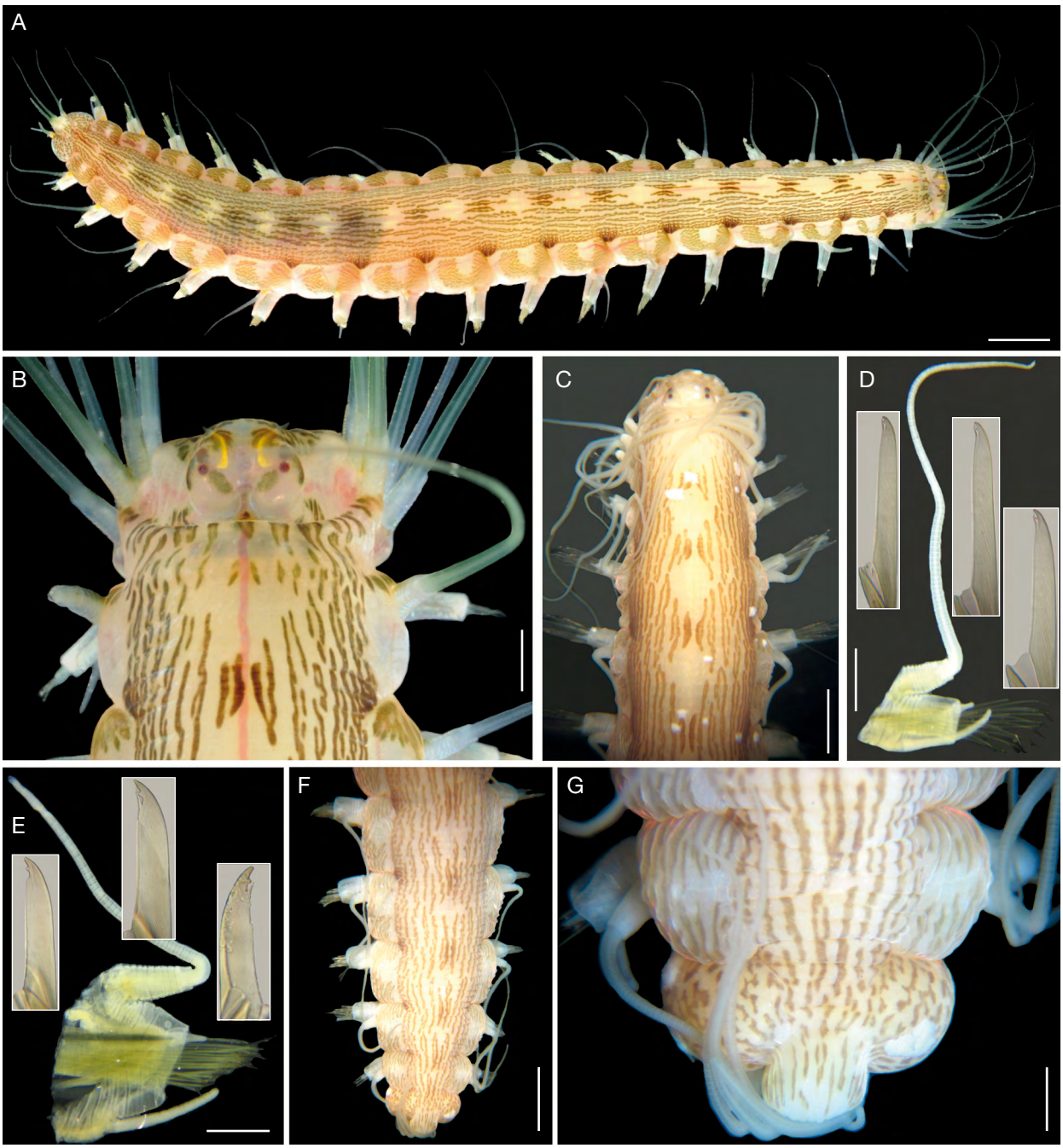

FIG. 23. — *Hesione intertexta* Grube, 1878, restricted, non-type specimen, UF 1772, alive: **A**, dorsal view; **B**, same, anterior end, dorsal view; preserved; **C**, anterior region, dorsal view; **D**, chaetiger 2, left parapodium, anterior view (insets: upper to lower chaetal blades); **E**, chaetiger 8, left parapodium, anterior view (insets: upper to lower chaetal blades); **F**, posterior region, dorsal view; **G**, posterior end, close up, dorsal view. Scale bars: A, 3.1 mm; B, D, 0.8 mm, C, 1.8 mm; E, 0.7 mm; F, 2.5 mm, G, 0.6 mm.

and parapodia macerated, the other laterally bent, prostomium collapsed by pressure, better preserved; integument tuberculated; right parapodia of chaetigers 2 and 12 removed for observation (kept in vial); many chaetal blades lost; antennae minute, twice as long as wide; eyes blackish, anterior eyes marginal, looking as long as wide, twice larger than posterior rounded ones; acicular lobe single, basally swollen, tapered, blunt; about 22 chaetae per bundle]. — 1 specimen, AM W.3674, Port Curtis, Queensland, no further data [25 mm long, 5 mm wide; cemented ventrally over an acrylic plate, integument tuberculated, most chaetae broken, pharynx exposed; antennae minute, twice as long as wide; eyes colorless; acicular lobe single, blunt]. — 1 specimen, UF 1549, Queensland, Heron Island, Harry's canyon (-23.474366, 151.950466; 23°28'27.7176"S, 151°57'01.6776"E), 12-16 m depth, 21.XI.2009, S. McKeon coll. [39 mm long, 4 mm wide; brownish longitudinal, irregular thin bands throughout body, leaving middorsal polygonal or irregular, as wide as long pale areas over chaetal lobes region, in median and posterior regions with a middorsal darker band; body bent backwards, left posterior parapodia removed for molecular analysis, pharynx exposed, dorsal papillae twice as long as wide, tapered; antennae digitate, smaller than interocular distance; eyes brownish, anterior ones slightly larger than posterior ones; acicular lobe

single, tapered; neurochaetal blades bidentate, upper ones very long, teeth minute, other ones with larger teeth, guard approaching distal tooth]. — 1 specimen, UF 1170, Western Australia, Ningaloo Reef, S Green Hole Bommies (-22.40793, 113.7073; 22°24'28.5480"S, 113°42'26.2800"E), 7-8 m depth, 30.IV.2009, F. Michonneau coll. [26 mm long, 3 mm wide; almost without pigmentation, pale brownish longitudinal, irregular thin bands along a few anterior chaetigers; one right posterior parapodium removed for molecular analysis; integument rugose; antennae smaller than interocular distance; eyes dark brown, anterior ones slightly larger than posterior ones; acicular lobes single, long, tapered; neurochaetal blades with a few longer ones with small teeth, and shorter ones with lateral teeth, guard approaching distal tooth].

DISTRIBUTION. — Southern Japan to Australia including the Philippines, Indonesia, the Solomon Islands, and French Polynesia, in mixed bottoms from the intertidal to 53 m depth.

DIAGNOSIS. — *Hesione* with prostomium laterally curved; parapodia with dorsal cirri basally cylindrical, dorsal cirrophore 2-3 times as long as wide; larger acicula blackish; acicular lobe single, tapered; neurochaetal blades bidentate, 3-4 times as long as wide; subdistal tooth smaller than distal one, with guards approaching distal tooth.

DESCRIPTION

Holotype, MNHW 293, macerated, damaged, 32 mm long, 6 mm wide. Body depressed, probably after fixation between glass slides; pharynx partially exposed, distorted (Fig. 22A); cirri macerated, chaetae without blades; neuraciculae thick, blackish, tapered; acicular lobes single, visible in several parapodia (Fig. 22B); posterior region transparent, macerated, tapered into a blunt cone (Fig. 22C); pygidial details not visible. Redescription based upon a sequenced specimen, UF 1772. Body complete, slightly bent ventrally, subcylindrical, slightly tapered posteriorly. Pigmentation: longitudinal sub-continuous brownish bands dorsolaterally, and discontinuous middorsally with an oval, as long as wide, pale area and shorter bands slightly darker (Fig. 23C); pigmentation extended into lateral cushions with paler areas coincident with lateral round areas, and darker intersegmental regions in ethanol. Integument granulose with adsorbed salt particles dorsally and ventrally, surface multituberculate, better defined along posterior region. Right parapodia of chaetigers 8-9 removed for molecular studies. Body 43 mm long, 6 mm wide.

Prostomium as long as wide, anterior margin projected anteriorly, lateral margins rounded, posterior margin exposed, deeply cleft along ¼ prostomial surface, longitudinal depression indistinct. Antennae digitate, 3-4 times as long as wide. Anterior eyes black, posterior ones brownish; anterior eyes slightly larger than posterior ones.

Tentacular cirri complete, variably contracted, longest ones reaching chaetiger 5. Lateral cushions barely projected; anterior ones divided into three sections, median and posterior segments with two sections or entire.

Parapodia with chaetal lobes digitate in anterior chaetigers (Fig. 23D), tapered in median ones (Fig. 23E); cirrostyle basally cylindrical, articulated entirely; dorsal cirri with tips lost, shorter than body width. Ventral cirri basally smooth, medially and distally regularly corrugated, surpassing chaetal lobes.

Neuraciculae pale in anterior chaetigers, blackish in median and posterior ones, two per neuropodium. Acicular lobe single, digitate to tapered.

Neurochaetae about 20 per bundle, blades at a certain angle from handle, blades bidentate, anterior parapodia with longer chaetal blades, 5-6 times as long as wide, median chaetigers with blades 3-4 times as long as wide; upper neurochaetae in anterior chaetigers with tiny denticles directed subdistally, other ones with lateral teeth, subdistal one smaller, guard approaching distal tooth.

Posterior region contracted, tapered into a blunt tube (Fig. 23F); pygidium swollen, anus terminal, with 12 thin, anal papillae.

Pigmentation

Living specimens brownish to reddish-brown (Fig. 23A). Pigmentation pattern including subcontinuous long, lateral bands, and shorter slightly darker middorsal bands, the latter interrupted by irregularly oval, as long as wide pale areas. Pigmentation extending into lateral cushions with coincident darker intersegmental areas with middorsal darker bands, and paler subcircular areas aligned with paler dorsal areas. Tentacular, dorsal cirri and neurochaetal lobes pale. Prostomium (Fig. 23B) with two short dark spots along anterior margins, and two smaller oblique central areas; anterior margin with transverse brownish bands, and two yellowish C-shaped bands arranged back to back ending in antennal bases.

Grube (1878: 102) indicated that the body was: "semitermes elongate, margaritacea, dorso transverse striato, per longitudinem virgis cinnaomemeis interruptis utrinque fer 7 ornato, confiniis segmentorum utrinque macula fusca inter dorsum medium et partes laterals sita distinctis." [Transl. Subcylindrical, long, pearly-shiny, dorsum transversely striated, interrupted with about 7 cinnamon longitudinal discontinuous lines per side, distinct middorsal and latero-dorsal black spots positioned intersegmentally]. In the following page, he indicated that neuraciculae were black (Grube 1878: 103). The original illustration is given here (Fig. 24) and the anterior region has been enlarged for detecting finer details. The dorsal surface has large oval to fusiform, as long as wide, whitish or pearl-white areas, larger and better defined along anterior region (Fig. 24A) than in posterior region (Fig. 24C); antennae are tiny and anterior eyes are slightly larger than posterior ones (Fig. 24B). Also, neuraciculae are black, and were indicated as visible by transparency of the body wall. These features are visible in living specimens (Fig. 25D) but fade out quite soon after preservation.

This pigmentation pattern is seldom retained in aged specimens, as shown by one specimen collected in 1965. The anterior region has discontinuous dorsal longitudinal bands, somehow divergent in each segment, and a large oval middorsal area, and the blackish lateral intersegmental spots have almost completely faded out (Fig. 25A). As in the original illustration, the middorsal pale spots are less defined in the posterior region (Fig. 25D). This specimen has a rare anomaly on its left eyes because right eyes are typical for the species (Fig. 25B), but left eyes are not, especially the posterior eye which is replaced by 6-7 smaller eyes arranged into a curve

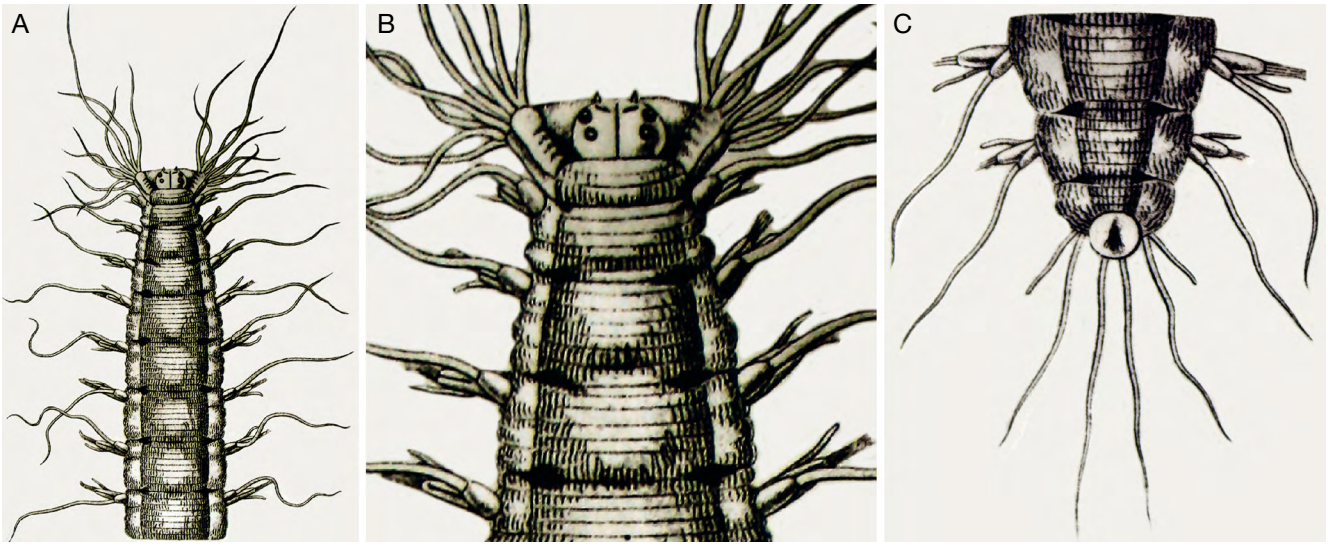

FIG. 25. — *Hesione intertexta* Grube, 1878: **A**, anterior half of body, dorsal view; **B**, anterior end, dorsal view; **C**, posterior end, dorsal view (modif. after Grube, 1878; original without scale bars).

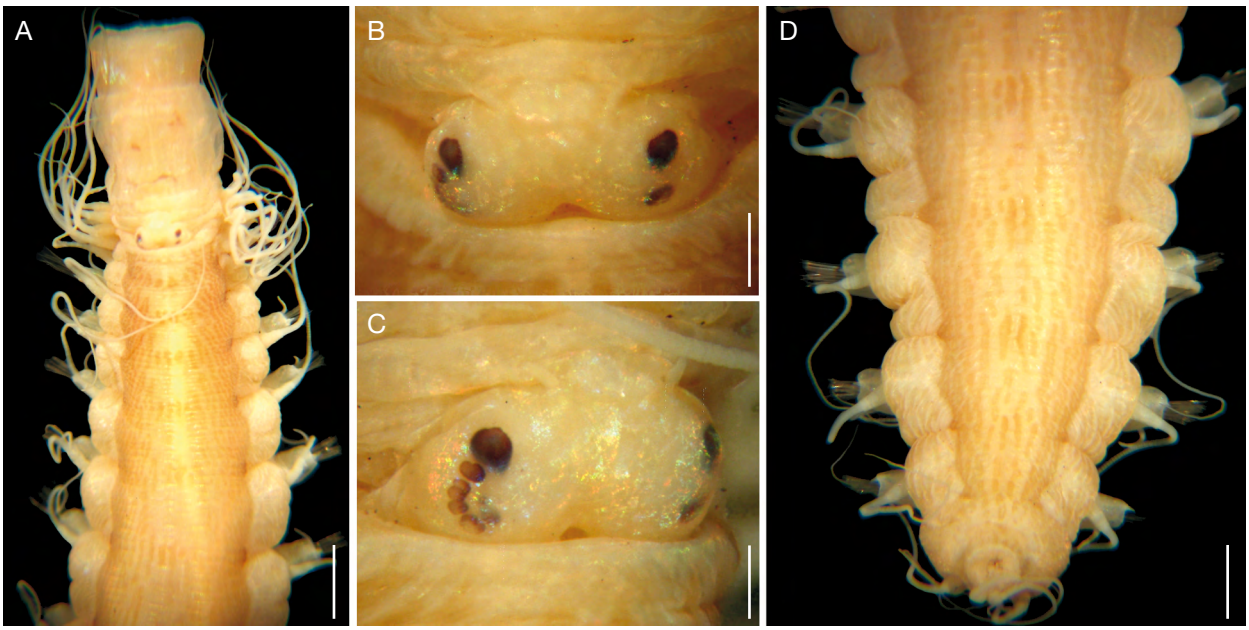

FIG. 24. — *Hesione intertexta* Grube, 1878, non-type specimen, BMNH 1970.317: **A**, anterior region, dorsal view; **B**, prostomium, dorsal view; **C**, same, oblique dorsal view from the left side; **D**, posterior region, dorsal view. Scale bars: A, 2.8 mm; B, 0.3 mm; C, 0.4 mm; D, 1.5 mm.

line towards the lateral prostomial margin, and with some of them coalescent to the adjacent ones (Fig. 25C).

REMARKS

Hesione intertexta Grube, 1878, restricted, resembles *Hesione ceylonica* Grube, 1874, reinstated, after the key below. Their main difference is that in *H. intertexta* neurochaetal blades are 5-6 times as long as wide, whereas in *H. ceylonica* they are shorter, 3-4 times as long as wide. Dorsal pigmentation of living specimens also differs because in *H. intertexta* there are segmental transverse pale wide bands, whereas in *H. ceylonica* there are middorsal oval to foliose, and as long as wide pale areas.

In the original description, Grube (1878: 103) gave measurements for a single specimen, hence the holotype, and indicated it was collected in Zamboanga (06°55'N, 122°05'E), Mindanao, in the southern region of the Philippines. This single specimen is housed in the Natural History Museum of the Wroclaw University, Poland. Another specimen, also collected by Semper in Palau, was deposited in the Zoologischen Museum, Berlin, and it is therein regarded as a syntype (ZMB 3813). This is incorrect after the *Code* (ICZN 1999: art. 73.1.2), and it is herein regarded as a non-type specimen.

Hesione intertexta Grube, 1878 was characterised and illustrated by Wu *et al.* (1975: 76) for the Xisha Islands, and recently

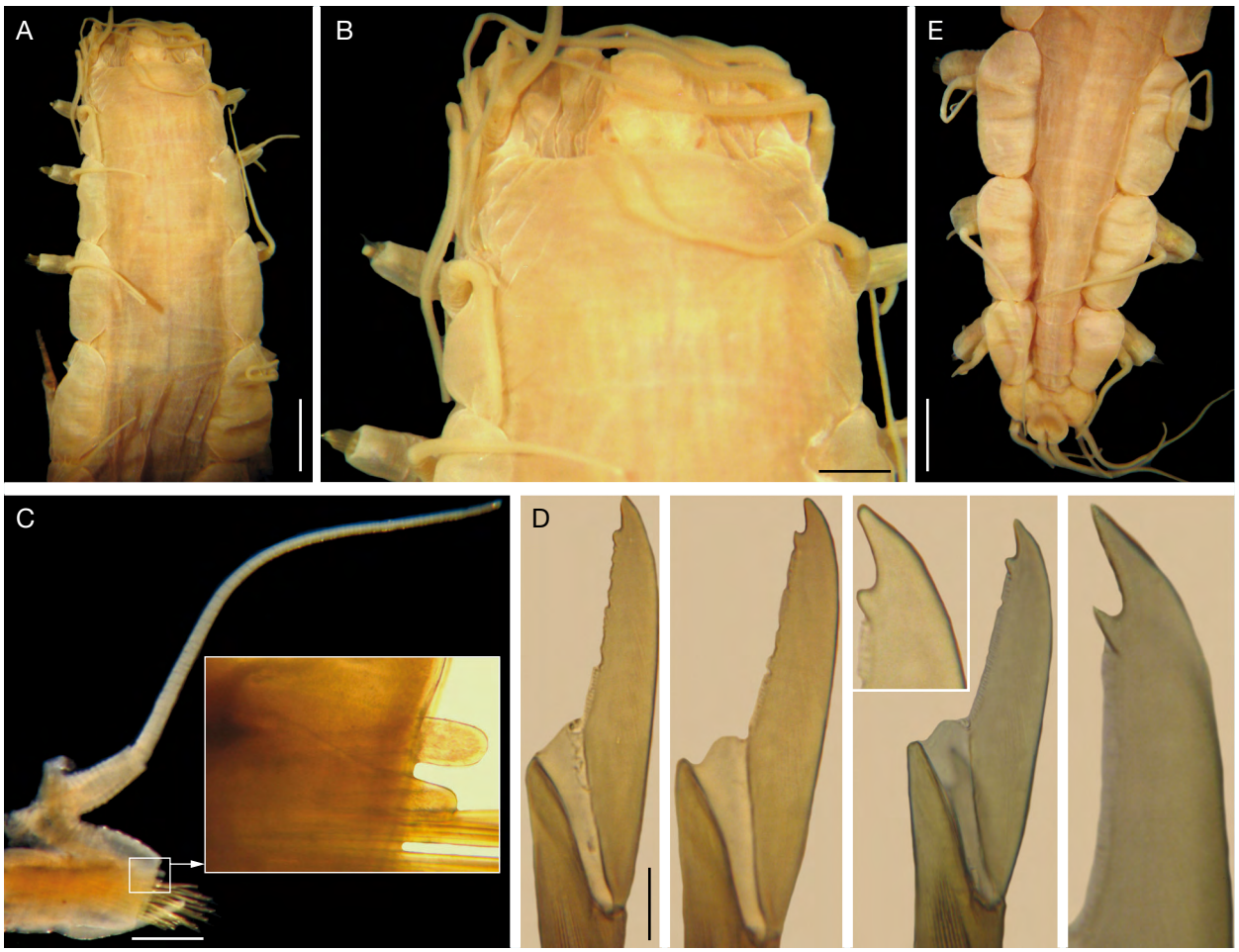

Fig. 26. — *Hesione keablei* n. sp., holotype, AM W.2939: **A**, anterior region, dorsal view; **B**, anterior end, dorsal view; **C**, chaetiger 4, left parapodium, anterior view; **D**, neurochaetal blades from the upper, medial and lower part (inset: close up of tip), and from a shorter chaetae showing acute teeth; **E**, posterior region, dorsal view. Scale bars: A, 2 mm; B, C, 0.7 mm; D, 20 µm; E, 1.8 mm.

by Lee & Ong (2015: 204) for Singapore. These reports also indicated that acicular lobes are single, and their findings are herein corroborated based upon specimens originating from area close to the type locality. However, these authors did not indicate any variation on chaetal blade length or their dentition. As restricted herein, specimens belonging to *H. intertexta* have median chaetigers (6-8) with bidentate blades, with teeth well-defined, directed laterally. Those specimens provided with bidentate blades but with tiny teeth, directed distally or subdistally, present along median chaetigers, do not belong here.

In the original description and illustrations, Grube (1878) emphasised the combination of longitudinal pigment lines and transverse annulations or striae. These features are usually associated on dorsal surfaces but not extended into lateral cushions; however, for *H. intertexta* as originally described, even lateral cushions are shown as granulose, not smooth. A recent illustration by Lee & Ong (2015: 203) confirmed all these features. Consequently, the definition for *H. intertexta* must also include this integument feature.

The record by Pruvot (1930: 27-29) is questionable because he found acicular lobes double, and hence not really *H. splendida* nor *H. intertexta*, both having single acicular lobes.

Hesione keablei n. sp.
(Figs 26, 27)

urn:lsid:zoobank.org:act:B5ECB11E-9705-4301-A130-8A2D99D19BB3

Hesione splendida? – Monro 1931: 11-12, Textfig. 6.

Type material. — **Australia.** Holotype, AM W.2939, Queensland, June Reef, outer barrier reef (14°17'S, 143°46'E), 1928, British Great Barrier Expedition 1928-1929.

Additional material. — **Australia**. 1 specimen, AM 4409, Little Upolo Cay, 38 km NNE off Cairns, Queensland, Australia; under coral rocks, 19.VII.1970, I. Loch coll. [complete, distorted by compression into small container; colorless, integument shiny; body 43 mm long, 5 mm wide; left parapodia of chaetigers 9 and 11 removed for observation (kept in vial); anterior eyes twice larger than posterior ones; right antennae remaining, digitate, tip eroded, 3-4 times as long as wide, left one lost; tentacular and parapodial cirri on site; dorsal cirrophore 4 times as long as wide, cirrostyles basally cylindrical, smooth, medially annulated, distally articulated; neuraciculae thick, black; acicular lobe double, tines digitate, of similar size; ventral cirri smooth to irregularly contracted, surpassing chaetal lobe; about 25 neurochaetae per bundle, each honey-colored, most without blades; blades bidentate, subdistal tooth smaller, margin denticulated; no guards; oocytes 70-80 µm in diameter].

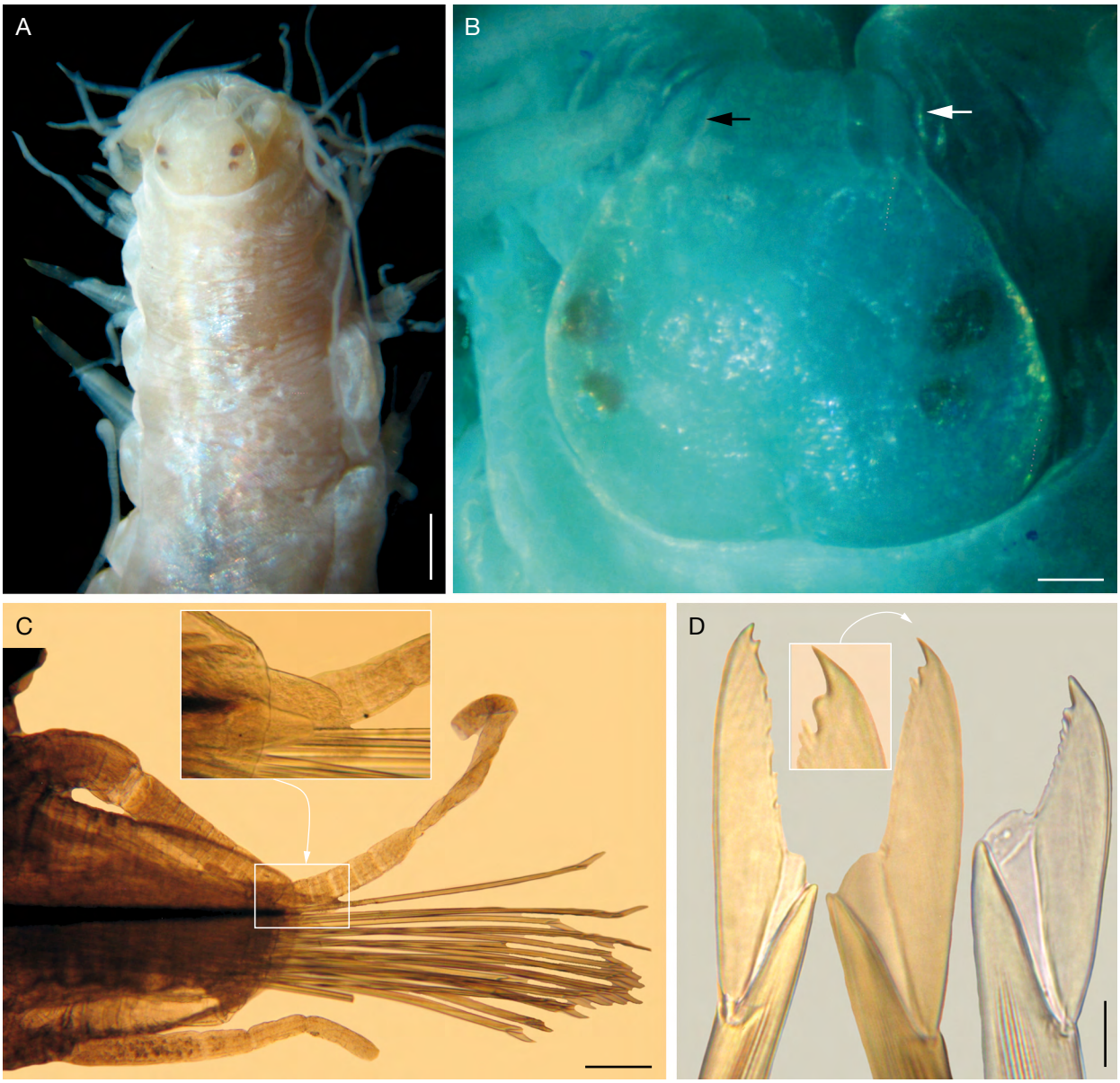

FIG. 27. — *Hesione keablei* n. sp., non type specimen, MNHN-IA-PNT98b (formerly jar Musorstom 100DW): **A**, anterior region, dorsal view; **B**, prostomium, after Methyl green staining, dorsal view (arrows point to antennae); **C**, chaetiger 9, left parapodium, anterior view (inset: acicular lobe); **D**, same, neurochaetal blades (inset: close-up showing longer teeth along cutting edge). Scale bars: A, 0.8 mm; B, C, 0.2 mm; D, 15 µm.

Indonesia, Sulawesi. 1 specimen, UF 38, Southern Outer Barrier Reef (-0.491111, 122.0725; 00°29'27.9996"S, 122°04'21.0000"E), barrier reef, 1-3 m depth, 22.IX.1999, G. Paulay coll. [44 mm long, 6 mm wide; body with anterior region markedly contracted, prostomium hidden under tentacular segment; longest tentacular cirri reach chaetiger 3; dorsal cirri shorter than body width (excluding parapodia); acicular lobe double, both tines long, sometimes about of the same length, blunt; neuraciculae black, one very thick, the other very thin; neurochaetae about 20 per bundle, with guards and teeth eroded, subdistal tooth minute, guard approaching distal tooth, but mostly broken; probably easily eroded in older specimens]. **New Caledonia.** 1 specimen, MNHN MUSORSTOM 100DW, SMIB 5 Expedition, Ride de Norfolk, 200 km SE off Nouméa, Sta. 100DW (23°22.9'S, 168°05.2'E), 80-120 m depth, 14.IX.1989, B. Richer coll. [29 mm long, 3 mm wide; slightly macerated, laterally bent; body without pigmentation, anterior eyes twice as large as posterior ones, acicular lobe double, tines blunt, of similar size; neurochaetal blades bidentate, eroded, a few blades with tiny guards]. **French Polynesia.** 1 specimen, UF 23, Tuamotu Islands, Rangiroa Atoll, circa 1 km S of NW Point of Atoll, off Motu Maeherehonae (-14.928666, -147.857833; 14°55'43.1976"S, 147°51'28.1988"W), outer reef slope, under rocks, 6-12 m depth, 10.XI.2001, G. Paulay coll. (body partially dehydrated without pigmentation; eyes and antennae minute; dorsal cirri multiarticulate, ventral cirri smooth; acicular lobe double, each tine very long, slightly capitate; neurochaetal blades short, subapical tooth minute, all guards broken).

ETYMOLOGY. — This species is being named after Stephen Keable, Curator of Marine Annelids, Australian Museum, Sydney, in recognition of his unrestricted support to our research activities in Mexico and elsewhere. The name is a noun in genitive (ICZN 1999: art. 31.1.2).

DISTRIBUTION. — Indonesia to the French Polynesia, in coral to mixed substrates, mostly in shallow water but one specimen found in 80-120 m depth.

DIAGNOSIS. — *Hesione* with prostomium wider posteriorly; parapodia with dorsal cirri basally cylindrical, dorsal cirrophore twice as long as wide; larger acicula blackish; acicular lobe double; neurochaetal blades bidentate, subdistal tooth smaller than distal one, but without guards.

DESCRIPTION

Holotype, AM W.2939, complete, bent ventrally, colorless in ethanol; integument smooth, shiny (Fig. 26A); a midventral dissection up to chaetiger 10 previously made; several parapodia already removed. Body subcylindrical, tapered posteriorly, 58 mm long, 5 mm wide; left parapodium of chaetiger 4 removed for observation (kept in vial).

Prostomium trapezoidal, about twice as long as wide, anterior margin truncate, lateral margins progressively expanded (Fig. 26B), posterior margin covered by anterior margin of tentacular segment, longitudinal depression shallow, extended along posterior prostomial half. Antennae long, medially widened, 5-6 times as long as wide. Eyes pale brown, anterior ones twice as large and more distant to each other than posterior eyes.

Tentacular cirri smooth, longest ones (without tips) reaching chaetiger 3. Lateral cushions projected, smooth, entire along anterior body half, barely separated into two sections along posterior body half.

Parapodia with chaetal lobes truncate (Fig. 26C), most dorsal cirri without tips; dorsal cirrophores twice as long as wide, cirrostyles basally cylindrical, annulated, medially annulated, distally articulated; shorter than body width. Ventral cirri smooth, surpassing chaetal lobe.

Aciculae blackish, thick, probably two. Acicular lobes double, tines digitate, blunt, of similar size (Fig. 26C [inset]).

Neurochaetae about 25 neurochaetae per bundle, honey-colored, most without blades, blades bidentate, 3-4 times as long as wide, subdistal tooth smaller, margin denticulated; no guards.

Pharynx not exposed. Oocytes not seen.

Variation

One small specimen, MNHN-IA-PNT98b (formerly jar Musorstom 100DW), herein regarded as conspecific is shown in figure 28. This identification takes into account a posteriorly expanded prostomium and well-developed lateral cushions (Fig. 27A), poorly defined eyes (Fig. 27B), dorsal cirrophores twice as long as wide and acicular lobes blunt, of similar size (Fig. 27C). However, there are two small differences. A few chaetal blades show a slightly longer tooth along its cutting edge (Fig. 27D [inset]), and because they are in the same position where guards typically are, they could be regarded as tiny guards or as elongated teeth. Another difference refers to the depth where this specimen was found because it was collected in deeper water (80-120 m). To better define its status as the same or as an independent species requires more and better specimens, but it is herein regarded as conspecific.

REMARKS

Hesione keablei n. sp., together with *H. beneliahuae* n. sp., differ from all other species in the genus because their neurochaetal blades have no guards at all. These two species differ, however, because *H. keablei* n. sp. has dorsal cirrophores twice as long as wide, its prostomium is wider posteriorly, and the eyes are poorly defined, whereas in *H. beneliahuae* n. sp. the dorsal cirrophores are as long as wide, the prostomium is rectangular, and the eyes are well-defined.

Monro (1931: 11-12) recorded a similar species after a single specimen collected during the Great Barrier Reef Expedition, in Jukes Reef. He indicated it was a "well-preserved specimen measuring" 54 mm long, 5 mm wide, that it had "a square dorsal mark paler in color than the rest of the body", and "two finger-shaped retractile processes" as acicular lobe. For chaetal blades he emphasised: "I cannot find any trace of a chaetal guard on the blades." Regretfully, this specimen was not found during a visit to the Natural History Museum, London. Monro (1931: 12) also referred to an earlier record by Pruvot (1930: 29). Pruvot found another large specimen (46 mm long) of an unidentified species whose chaetal blades did not have guards. This specimen differs from *H. keablei* n. sp., however, by having acicular lobes single, and long neurochaetal blades. So it may belong to another species, probably close to *H. intertexta*; such a large specimen was not found in Paris, but other specimens from the same study were regarded as belonging to *H. intertexta*. The record by Fauvel (1922: 493) as *H. pantherina* of two colorless specimens collected in the Wallaby Archipelago (13°22'6.57"S, 141°41'40.83"E) could not be confirmed.

Hesione mooreae n. sp.
(Fig. 28)

urn:lsid:zoobank.org:act:1862BD5B-7FA6-49AD-9A24-05F9D55B429E

Hesione genetta – Willey 1905: 267. — Fauvel 1919a: 337; 1953b: 105 (*non* Grube, 1867).

TYPE MATERIAL. — **Indian Ocean.** Red Sea. Holotype, UF 3485, Saudi Arabia, Farasan Islands, Mahama Island (16.4892, 41.94432; 16°29'21.1200"N, 041°56'39.5520"E), sand, reef, rubble fringing slope, 4-17 m depth, 9.III.2013, A. Anker, P. Norby & G. Paulay coll.

ADDITIONAL MATERIAL. — **Indian Ocean. Red Sea.** 1 specimen, UF 3624, Saudi Arabia, Al Lith (20.116983, 40.214939; 20°07'01.1388"N, 040°12'53.7804"E), Whale Shark Reef, 10 m depth, 22.III.2013, A. Anker, P. Norby & J. Moore coll. [body twisted, distorted by torsion, a small posterior region fragment removed for molecular analysis; pigmentation pattern including brownish transverse bands and spots along dorsum, with a wider band on chaetiger 2, but no bands on chaetigers 1 and 3; pharynx exposed, distorted, dorsal papilla not seen; acicular lobe double, upper tine twice longer than lower one].
Madagascar. 1 specimen, MNHN-IA-PNT91e (formerly jar 70), Nosy-Bé reefs, 27.V.1898, F. Geay coll. [31 mm long, 3.5 mm wide; complete, bent backwards; pigmentation brownish, including round dots and dorsal, irregular transverse bands, wider, better defined in chaetiger 1, missing in chaetiger 2, thinner, poorly defined in following chaetigers; acicular lobes double, tines of similar size].

FIG. 28. — *Hesione mooreae* n. sp., holotype, UF 3485, alive: **A**, dorsal view; **B**, anterior region, dorsal view; preserved; **C**, right lateral view; **D**, anterior end, dorsal view, pressed by glass slide, close-up of head, pharynx and first three chaetigers; **E**, chaetiger 8, right parapodium, anterior view (inset: acicular lobe); **F**, same, neurochaetal blades; **G**, posterior region, pressed by glass slide fragment. Scale bars: A, 2 mm, B, 1.3 mm, C, 0.9 mm; D, 1.4 mm; E, 0.3 mm; F, 20 µm; G, 1.5 mm (photos A, B, G. Paulay).

ETYMOLOGY. — This species is being named after Jenna Moore, from the University of Florida, Museum of Natural History, Gainesville, in recognition of her many sampling efforts on polychaetes, especially on hesionids, and for her kind support and help for molecular analysis of many hesionid samples. The name is a noun in genitive (ICZN 1999: art. 31.1.2).

DISTRIBUTION. — Western Indian Ocean, Red Sea to India (previous records), and Madagascar, 4-17 m depth, sand or mixed bottoms.

DIAGNOSIS. — *Hesione* with prostomium rectangular; parapodia with dorsal cirri basally cylindrical, dorsal cirrophore 1-2 times as long as wide; larger acicula blackish; acicular lobe double, tines digitate, upper one twice longer than lower one; neurochaetal blades bidentate, 2-5 times as long as wide; subdistal tooth as large as distal one, with guards approaching subdistal tooth.

DESCRIPTION

Holotype, UF 3485, complete, strongly bent dorsally. Pigmentation pattern including brownish, dorsal transverse bands and irregular spots (Fig. 28A); transverse bands better defined along most chaetigers, but none in chaetigers 2 and 16; chaetiger 1 with a wide band perfectly defined along anterior and posterior margins, 3-4 times longer than band in chaetiger 3 (Fig. 28B-D); following chaetigers with slightly less defined bands. Pigmentation extended into prostomium and pharyngeal basal ring, lateral cushions; tentacular cirri, dorsal cirri and neuropodial lobes whitish in ethanol. Body subcylindrical, 26 mm long, 4 mm wide.

Prostomium slightly as wide as long, anterior margin expanded anteriorly, lateral margins rounded, posterior margin with a shallow notch, ⅕ as long as prostomium, with irregular

brownish spots. Antennae digitate, 4-5 times as long as wide, or longer than interocular distance. Eyes brownish, anterior ones slightly larger and more separated from each other than posterior ones (Fig. 28C, D).

Tentacular cirri thin, most twisted, longest ones reach chaetiger 8. Lateral cushions low, some divided into 2 sections.

Parapodia with chaetal lobes tapered, truncate (Fig. 28E); dorsal cirri with cirrophores 1-2 times as long as wide, cirrostyles basally cylindrical, smooth medially, annulated distally, as long as body width (excluding parapodia); ventral cirri irregularly contracted, surpassing chaetal tips.

Neuraciculae blackish, three of different width, thinner one paler. Acicular lobe double, digitate, upper tine twice longer than lower one (Fig. 28D [inset]).

Neurochaetae about 20 per bundle, blades bidentate, 2-5 times as long as wide; blades aligned at a certain angle from handle, teeth of similar length, subdistal tooth usually wider, guard thick, approaching subdistal tooth (Fig. 28F).

Posterior region tapered into a blunt cone (Fig. 28G); pygidium smooth, anus with seven low, blunt papillae.

Pharynx partially exposed; dorsal papillae not seen. Oocytes not seen.

Pigmentation

Living specimens with transverse, irregular bands throughout body over a variable background, being whitish anteriorly, becoming pinkisk medially, and pale pink posteriorly (Fig. 28A). Transverse bands reddish-brown in living specimens becoming brownish once preserved; bands postioned slightly behind neuropodial region, extended into lateral cushions but no band in chaetiger 1 and rather poorly defined in chaetiger 3, following chaetigers with bands irregularly defined, poorly defined in chaetiger 15, indistinct in chaetiger 16. Prostomium mottled and a few round spots in tentacular segments. Eyes reddish-brown alive, becoming brownish once preserved. Tentacular cirri and dorsal cirri pale brown; neuropodial lobes whitish.

Remarks

Hesione mooreae n. sp. groups with *H. genetta* Grube, 1867 and *H. paulayi* n. sp. by having long-lasting pigmentation, including transverse brownish bands. As indicated in the key below, *H. genetta* has its largest transverse band in chaetiger 2, whereas both *H. mooreae* n. sp. and *H. paulayi* n. sp. have them on chaetiger 1. There are two main differences between the latter two species; in *H. mooreae* n. sp. the posterior margin of the largest band is as well defined as its anterior margin, and its longest tentacular cirri reach chaetiger 8, whereas in *H. paulayi* n. sp. the posterior margin of its largest band is not well-defined, and the longest tentacular cirri reach chaetiger 6.

Hesione osbornae n. sp.
(Fig. 29)

urn:lsid:zoobank.org:act:BE675CE0-2448-45D4-9195-6AA629DA8F59

Hesione intertexta – Hoagland 1920: 604 (*non* Grube, 1878).

Type material. — **Western tropical Pacific.** Holotype, USNM 18965, RV *Albatross*, Sta. D5355, Philippines, Palawan, North Balabac Strait, Bugsuk Island, coral and sand bottom, 2 m depth (in label; Hoagland 1920: 604 indicates 80 m depth; confirmed with the vessel database, this latter figure must be the correct depth), 5.I.1909.

Additional material. — **Gulf of Thailand.** 1 specimen, ECOSUR 291, 17 km offshore (10°30'11.985"N, 100°29'45.857"E), 16-17 m depth, muddy-shell sand, IV.2011 [11 mm long, 1 mm wide; antennae minute; eyes brownish, almost fused laterally; pharynx partially exposed; dorsal cirrosytle basally cylindrical, annulose; acicular lobe single, ⅓-¼ as long as chaetae; ventral cirri tapered, markedly longer than chaetal lobe; chaetal blades long, unidentate, guard projected beyond distal tooth].

New Caledonia. 1 specimen, MNHN-IA-PNT99 (formerly jar Musorstom 649), Lagoon Est, Sta. 649 (21°51.1'S, 166°36.6'E), 64-65 m depth, 7.VIII.1986, B. Richer coll. [28 mm long, 4 mm wide; slightly macerated, bent laterally; body without pigmentation, acicular lobe single; neurochaetal blades unidentate, guard projected beyond distal tooth].

Etymology. — This species is named after Karen Osborn, Curator of Crustacea and Polychaeta in the National Museum of Natural History, Smithsonian Institution, Washington, in recognition of her spectacular publications on bathypelagic polychaetes, and because of her enthusiastic support to our research requests. The name is a noun in genitive (ICZN 1999: art. 31.1.2).

Distribution. — From the Gulf of Thailand to New Caledonia, in mixed bottoms, in 2-80 m depth.

Diagnosis. — *Hesione* with prostomium rectangular; parapodia with dorsal cirri basally cylindrical, dorsal cirrophore twice as long as wide; larger acicula blackish; acicular lobe single, tapered; neurochaetal blades unidentate, 15 times as long as wide; guards surpassing distal tooth.

Description

Holotype, USNM 18965, complete, tapered posteriorly, without pigmentation in ethanol; some tentacular or dorsal cirri broken or lost (Fig. 29A); right parapodia of chaetigers 8 and 13 removed (kept in vial). Body bent dorsally, 31 mm long, 5 mm wide.

Prostomium as wide as long, anterior margin truncate, lateral margins barely rounded, posterior margin deeply cleft (Fig. 29B), about as long as ¼ prostomial length, longitudinally slightly depressed. Antennae minute, only left one remaining, oval, slightly as long as wide, ⅓ as long as interocular distance. Eyes brownish, anterior ones twice as large as, and darker than posterior ones.

Tentacular cirri long, thin, some broken, others twisted, longest ones reaching chaetigers 6-7. Lateral cushions low, divided into 2-3 sections.

Parapodia with chaetal lobes tapered, truncate (Fig. 29C, D); dorsal cirri with cirrophores twice as long as wide, cirrostyle basally cylindrical, annulated, multiarticulated along medial and distal regions, ½-⅔ as long as body width; ventral cirri smooth, surpassing chaetal lobes.

Neuracicula blackish, single. Acicular lobe single, thin, tapered (Fig. 29C, D [insets]).

Neurochaetae about 40 per bundle (Fig. 29E), blade unidentate, blades aligned along handle, longer ones distally curved, shorter ones straight, blade size decreasing ventrally, many lost,

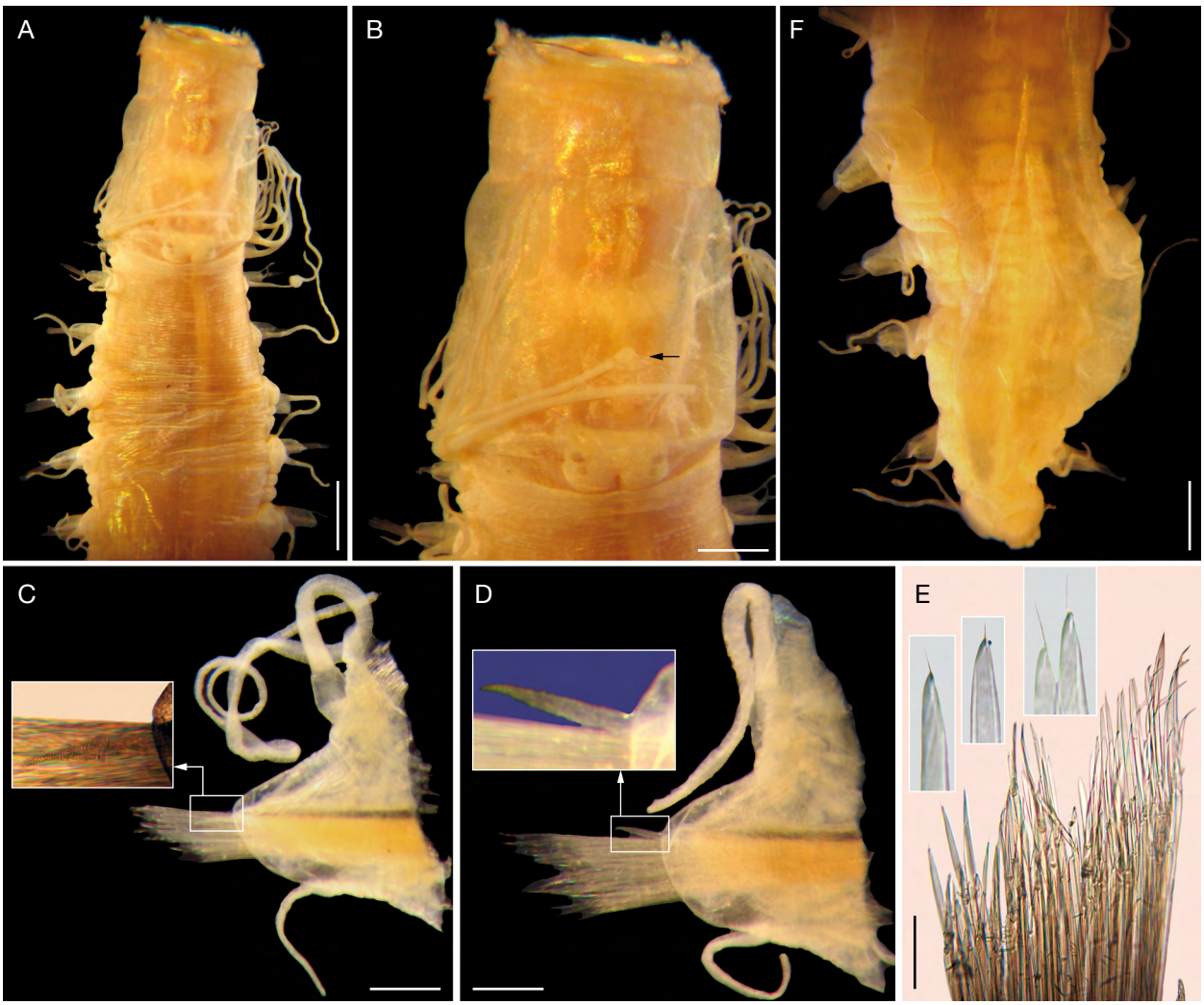

FIG. 29. — *Hesione osbornae* n. sp., holotype, USNM 18965: **A**, anterior region, dorsal view; **B**, anterior end, dorsal view, pharynx exposed (arrow points to dorsal papilla); **C**, chaetiger 8, right parapodium, anterior view (inset: acicular lobe); **D**, chaetiger 13, right parapodium, anterior view (inset: acicular lobe); **E**, same, neurochaetae (insets: tips of straight blades); **F**, posterior region, dorsal view. Scale bars: A, 1.7 mm; B, 0.8 mm; C, 0.6 mm; D, 0.4 mm; E, 0.2 mm; F, 1.4 mm.

remaining ones about 15 times as long as wide, upper chaetae with blades probably longer but twisted, each with a distal tooth and a very long guard, surpassing tooth (Fig. 29E [insets]).

Posterior region tapered into a blunt cone (Fig. 29F); pygidium smooth, anus with six low, cushion-like, thick papillae.

Pharynx fully exposed, rings poorly defined, 5 mm long, 3 mm wide, margin smooth, slightly eroded; dorsal papilla rounded, about as long as wide (Fig. 29B, arrow). Oocytes not seen.

REMARKS

Hesione osbornae n. sp. resembles *H. harrisae* n. sp. because both have unidentate neurochaetal blades. However, they differ because in *H. osbornae* n. sp. the neurochaetal blades are about 15 times as long as wide, and guards surpass distal teeth, whereas in *H. harrisae* n. sp. neurochaetal blades are 6-8 times as long as wide, and guards reach the distal teeth.

On the other hand, *H. osbornae* n. sp. resembles *H. eugeniae* Kinberg, 1866 because their neurochaetal blades have guards surpassing distal teeth. They differ, however, because in *H. osbornae* n. sp. acicular lobes are tapered, and neurochaetal blades are about 15 times as long as wide, whereas in *H. eugeniae* acicular lobes are digitate, and neurochaetal blades are 4-10 times as long as wide. *Hesione osbornae* n. sp. also resembles *H. intertexta* Grube, 1878 because both have tiny antennae and long neurochaetal blades, and it was previously identified as this species. However, in *H. intertexta* the longest blades have reduced denticles but always two are present, although the subdistal one is smaller, and the guard never extends markedly beyond the distal tooth.

Hesione pacifica McIntosh, 1885 reinstated (Figs 30-32)

Hesione pacifica McIntosh, 1885: 184, 185, pl. 29, fig. 2, pl. 32, fig. 14.

Hesione intertexta – Monro 1926: 311, 312 (*partim*, *non* Grube, 1878).

Hesione splendida – Augener 1913a: 187; 1922: 21, figs 4, 4a. — Hartman 1966: 191 (*non* Savigny *in* Lamarck, 1818).

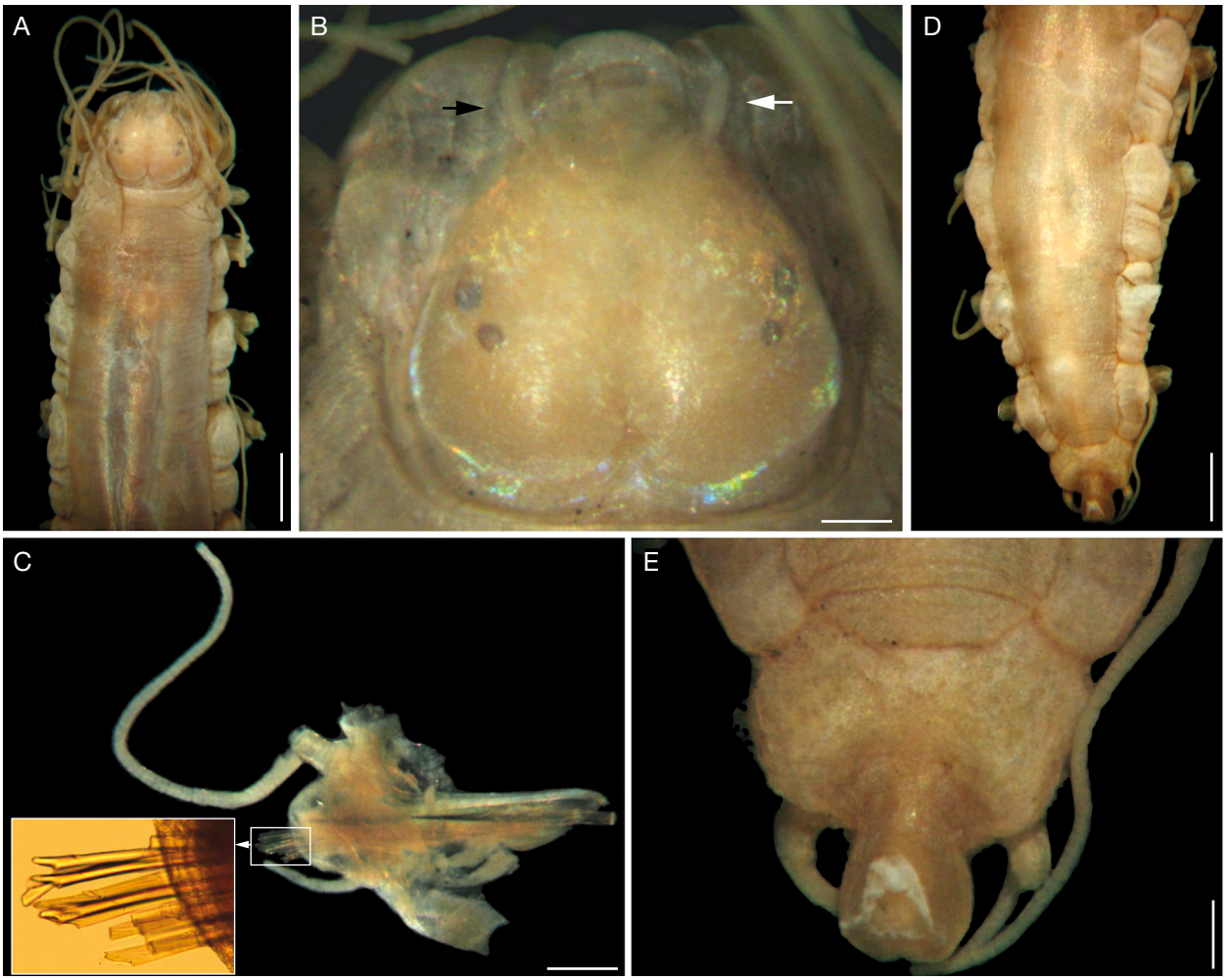

Fig. 30. — *Hesione pacifica* McIntosh, 1885, holotype, BMNH 85.12.1.136: **A**, anterior region, dorsal view; **B**, prostomium, dorsal view (arrows point to antennae); **C**, chaetiger 15, right parapodium, anterior view (inset: neurochaetal remains); **D**, posterior region, dorsal view; **E**, same, close-up of pygidium. Scale bars: A, 1 mm; B, 0.2 mm; C, E, 0.3 mm; D, 0.9 mm.

Type material. — **Tonga.** Holotype, BMNH 85.12.1.136, RV *Challenger* Expedition, Sta. 172 (20°58'S, 175°09'W), 200 km N off Tonga Island, 32 m depth, coral mud, 22.VII.1874.

Additional material. — **French Polynesia.** 1 specimen, USNM 19378, RV *Albatross*, Sta. unnumb., Society Islands, Bora Bora, between shore and fringing reef, 17.XI.1899 [21 mm long, 3.5 mm wide; body incurved; most cirri lost, all chaetae broken; pharynx exposed, short, margin smooth; prostomial anterior margin truncate, with a shallow furrow; lateral margins expanded posteriorly; posterior margin with a short longitudinal furrow; antennae tapered, ⅔ as long as prostomium; dorsal cirri basally multiarticulated; acicular lobes double, of similar size; posterior region tapered into a blunt cone; anus with thick anal cirri].
Northern Mariana Islands. 1 specimen, USNM 26069, Lagoon N of Matuis Beach, NW Saipan Island, in dead *Lithophyllum*, base of brown *Acropora*, 12.XII.1948, P. E. Cloud Burke coll. [26 mm long, 4 mm wide; body incurved; slightly dehydrated; most cirri retained on body; many chaetal blades lost; prostomium directed ventrally, antennae tapered; eyes unpigmented; dorsal cirri multiarticulated; acicular lobe double, upper tine digitate, twice as long as lower one, blunt triangular; neurochaetal blades short, bidentate, guard approaching subdistal tooth, rarely surpassing it; posterior end tapered into a blunt cone; anus terminal, no anal papillae visible].
South China Sea. 1 specimen, BMNH 1926.4.30.136, RV *Alert* Expedition, Macclesfield Bank, no further data [21 mm long, 2 mm wide; body bent laterally, integument rugose along a few anterior chaetigers, smooth in others; eyes barely pigmented; antennae tapered, 3-4 times as long as wide; anterior eyes twice larger than posterior ones; pharynx almost fully exposed, dorsal papilla covered by prostomium, slightly as long as wide, blunt; acicular lobe double, tines of similar length and width; all chaetae broken].
Australia. 1 specimen, ZMH-P 7925, Sharks Bay, SW Australien Expedition 1905, no further data [24 mm long, 3 mm wide; strongly contracted, integument smooth, prostomium invaginated; colorless, acicular lobes single; neurochaetal blades bidentate, guard approaching distal tooth]. — 1 specimen, ZMH-P 9338, Cape Jaubert, NW Australia, E. Mjöberg coll. [30 mm long, 4 mm wide; colorless, partially dehydrated; integument smooth; antennae digitate, twice as long as wide; eyes brownish, anterior ones as long as wide, twice larger than posterior ones, interocular distance barely visible, eyes almost fused laterally; aciculae blackish, thin, tapered; acicular lobe single, basally swollen, blunt; neurochaetal blades bidentate, subdistal tooth smaller, teeth and guards eroded].

Distribution. — This subtidal species is rarely found in sediments, up to 32 m water depth, from the Northern Mariana Islands to the French Polynesia and New Caledonia. The record for Hawaii by Treadwell (1906: 1149) rather matches *H. genetta* by sharing a dark brown transverse band on chaetiger 2 (see above).

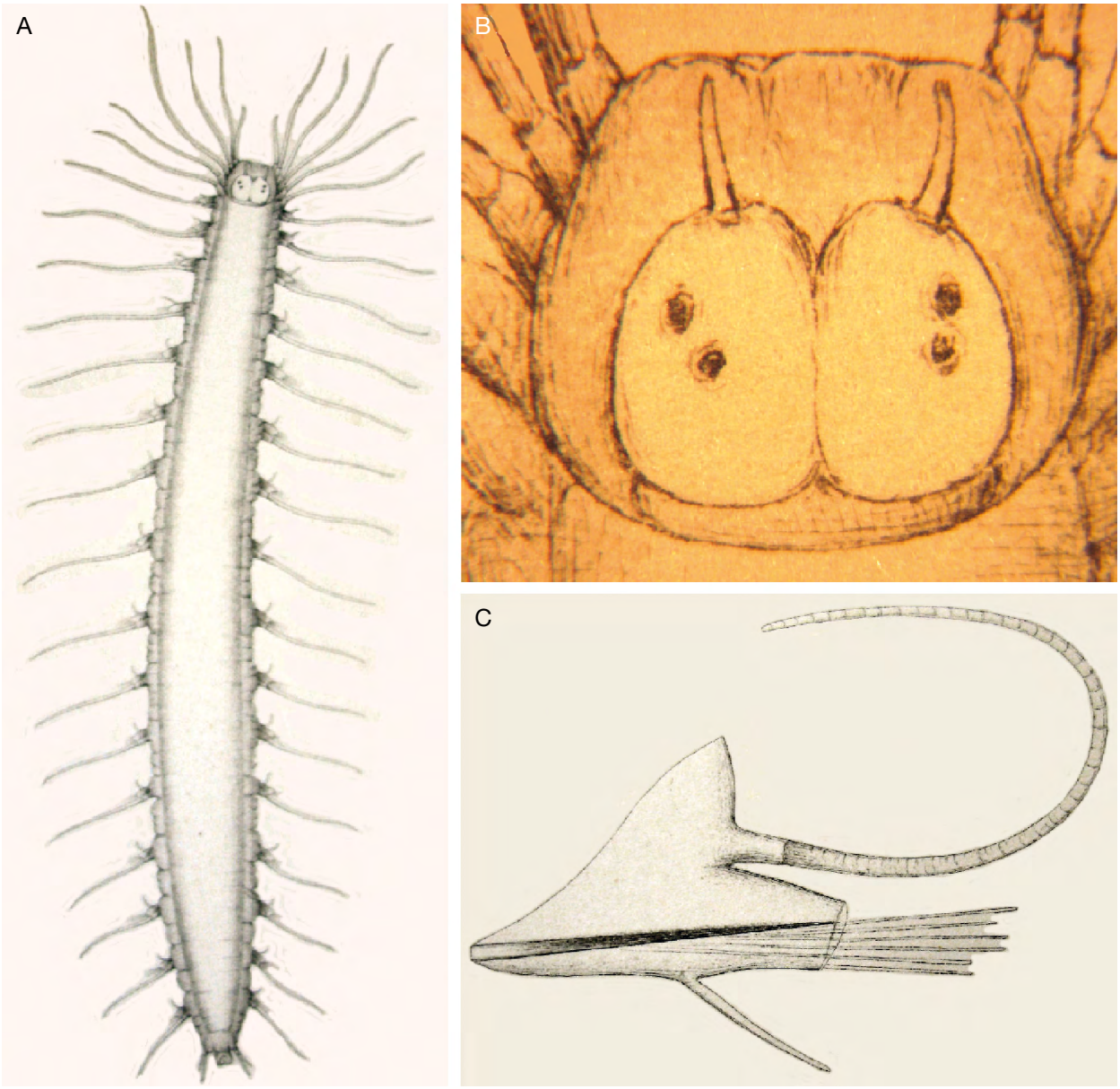

Fig. 31. — *Hesione pacifica* McIntosh, 1885: **A**, dorsal view; **B**, head, dorsal view; **C**, parapodium from a midbody segment (modif. after McIntosh 1885; original without scale bars).

Diagnosis. — *Hesione* with prostomium curved laterally; parapodia with dorsal cirri basally cylindrical, dorsal cirrophore twice as long as wide; larger acicula blackish; acicular lobe double, tines digitate, upper one twice longer than lower one; neurochaetal blades bidentate, 2-3 times as long as wide; subdistal tooth as large as distal one, with guards approaching subdistal tooth.

Description

Holotype, BMNH 85.12.1.136, complete, tapered posteriorly; integument smooth, brownish, some small middorsal dots in most segments (Fig. 30A) in ethanol; a ventral dissection running throughout first 14 chaetigers; right parapodium of chaetiger 7 and left parapodium of chaetiger 6 previously removed, right parapodium of chaetiger 15 removed for observation (kept in vial). Body straight, bent dorsally, 23 mm long, 3 mm wide.

Prostomium as long as wide, anterior margin projected anteriorly, lateral margins rounded, widest behind posterior eyes, posterior margin with a shallow notch, ⅕ as long as prostomium (Fig. 30B). Antennae digitate, longer than interocular distance, 4-5 times as long as wide. Eyes brownish, anterior ones slightly larger and farther apart than posterior ones.

Tentacular cirri thin, tips broken, longest ones reaching chaetiger 5. Lateral cushions low, surface smooth, divided into 2-3 (rarely 4) sections.

Parapodia with chaetal lobes eroded, most remaining ones invaginated; dorsal cirri most lost, with cirrophores twice as long as wide, cirrostyle basally cylindrical, smooth, medially and distally articulated, smaller than body width (Fig. 30C); ventral cirri regularly contracted, surpassing chaetal lobes.

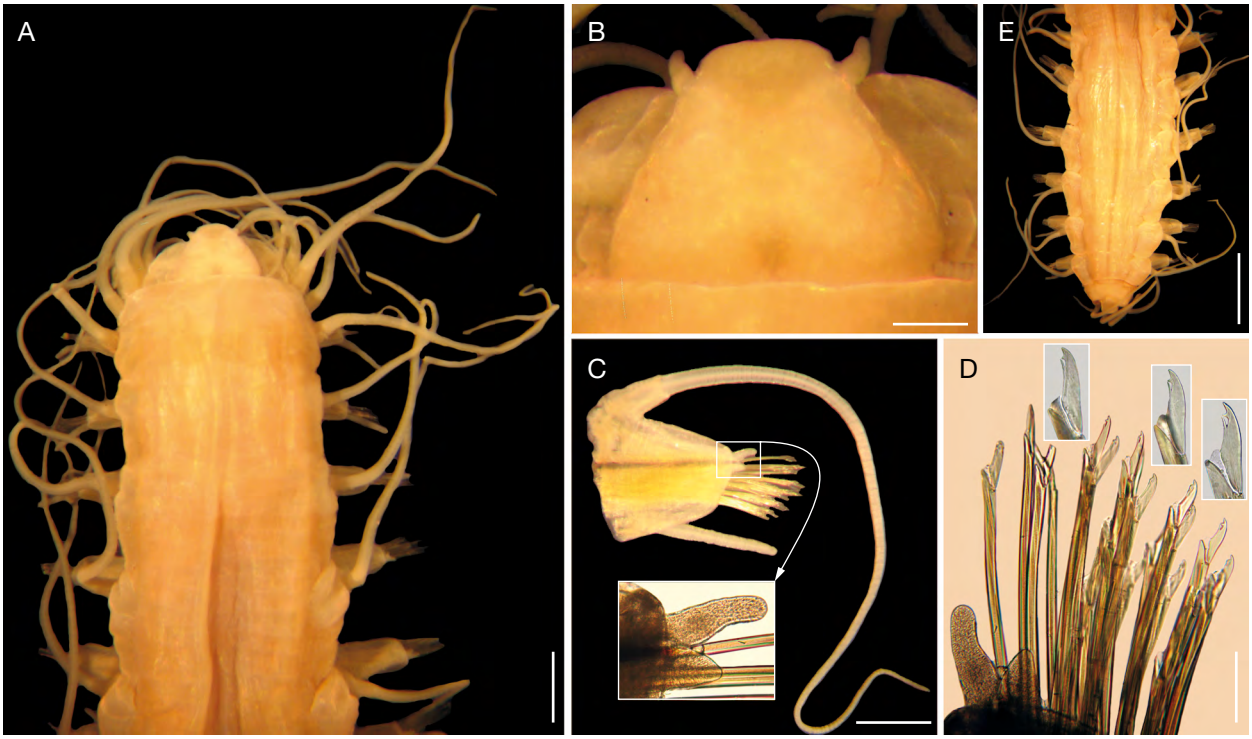

Fig. 32. — *Hesione pacifica* McIntosh, 1885, non-type specimen, USNM 26069: **A**, anterior region, dorsal view; **B**, prostomium, dorsal view, antennae directed ventrally; **C**, chaetiger 9, left parapodium, anterior view (inset: acicular lobe); **D**, same, neurochaetae (inset: tips of three blades); **E**, posterior region, dorsal view. Scale bars: A, 1.1 mm; B, 0.4 mm; C, 0.7 mm; D, 150 µm; E, 2.9 mm.

Neuraciculae blackish, tapered. Acicular lobe double, short, tines blunt of similar size (Fig. 30C, D).

Neurochaetae about 20 per bundle, most trimmed, probably during ventral dissection, some with neurochaetal blades fragments, or blades lost (Fig. 30C [inset]).

Posterior region tapered into a blunt cone (Fig. 30D); pygidium rugose, anus projected, dorsal margin and anal papillae eroded (Fig. 30E).

Pharynx not exposed. Oocytes about 100 µm in diameter.

Remarks

Hesione pacifica McIntosh, 1885, reinstated, was described with a single specimen (holotype). It was in good condition, without pigmentation pattern, but all neurochaetal blades were lost, probably as an indirect consequence of his dissection to observe the pharynx. McIntosh made two illustrations for the species (reproduced herein as Figure 31), one was a dorsal view of the whole specimen, showing all tentacular and dorsal cirri (Fig. 31A), probably before dissection, and the other was an anterior parapodium (Fig. 31C). The original prostomium was enlarged because it was too small in the original (Fig. 31B); the prostomial posterior margin has a shallow furrow and the antennae were illustrated as long, tapered filaments, 5 times as long as wide and longer than the distance between lateral eyes, but these features can only be noticed by using a hand lens over the original plates, or by observing it with a stereomicroscope. Further, the parapodium was illustrated but no acicular lobes were indicated, although the details for cirri are adequate. Once the relative size of antennae is observed, his remarks are easier to understand. He indicated that *H. pacifica* approaches *H. intertexta* but that they differ by the size of antennae, being longer in the former and shorter in the latter, and in their neurochaetal blades, because the subdistal tooth is larger in *H. pacifica* than in *H. intertexta*.

As indicated in the key below, the presence of subdistal teeth as wide as distal ones, groups *H. pacifica* with three other colorful species: *H. genetta* Grube, 1864 restricted, *H. mooreae* n. sp., and *H. paulayi* n. sp. Because the pigmentation pattern is long lasting in the latter three species (up to 100 years), and no pigmentation has been reported in *H. pacifica*, this is the main difference to sort them out. McIntosh and Chamberlin, studied their specimens 10-20 years after they were collected, and the latter also found *H. genetta* within the RV *Albatross* material.

Further, one specimen from the Mariana Islands (USNM 26069) was collected by the end of 1948, and Olga Hartman saw it 5 years after sampling, while preparing her paper on that archipelago (Hartman 1954); no pigmentation was evident then, and none is visible now (Fig. 32A), but this would be the shortest time span between collection and identification, such that its pigmentation, if any present, must fade rather soon in comparison to the long-lasting pigmentation in specimens of both *H. genetta* and *H. paulayi* n. sp.

After the study of the best preserved specimen (USNM 26069, 26 mm long), some additional observations include: 1) antennae can appear shorter and even biarticulate if they are directed ventrally (Fig. 32B); 2) dorsal cirri can be longer than body width including parapodia, and that ventral cirri

often projects beyond neurochaetal tips (Fig. 32C); 3) acicular lobes are double with the upper tines twice longer than lower ones (Fig. 32C [inset]); and 4) there are about 20 neurochaetae per bundle, blades are 2-3 times as long as wide, bidentate with subdistal tooth slightly smaller than distal one, with guards approaching subdistal tooth (Fig. 32D [inset]). Neurochaetal blade size was in a smaller range in *H. pacifica* (2-3 times as long as wide) than in *H. genetta* or *H. paulayi* n. sp. (3-5 times as long as wide).

Hesione panamena Chamberlin, 1919 reinstated (Figs 33, 34)

Hesione panamena Chamberlin, 1919: 188-190, pl. 22, figs 9, 10. — Treadwell 1937: 149.

Hesione intertexta – Hartman 1940: 212, pl. 33, figs 30, 31 (*partim*, *non* fig. 30). — Monro 1928: 79; 1933: 26. — Kudenov 1975: 78 (*non* Grube, 1878).

Hesione genetta – Fauvel 1941: 9 (*non* Grube, 1867).

Hesione pantherina – Fauvel 1941: 9 (*non* Risso, 1826).

TYPE MATERIAL. — **Eastern Tropical Pacific, Panama.** Holotype, USNM 19379, RV *Albatross*, unnumb. Sta., Perico Island (08°55'00"N, 79°31'00"W), shore, 12.III.1891.

ADDITIONAL MATERIAL. — **Eastern Tropical Pacific, Panamá.** 2 specimens, BMNH 1928.9.13.54/55, Taboga Island (08°47'00"N, 79°33'00"W), 8-10 m depth, 8.II.1916, T. Mortensen coll. [both complete, one lateraly bent; left parapodia of chaetigers 8 and 10 (one of each specimen) previously removed; body 28-29 mm long, 3-4 mm wide; anterior eyes twice larger than posterior ones, darker in larger specimen; acicular lobe single, tapered, variably contracted; if fully extended, about ⅓ as large as neurochaetae]. — 1 specimen, BMNH 1932.12.24.130, Balboa (08°57'N, 79°34'W), St. George Pacific Expedition, 1923-1924, C. Crossland coll. [complete, splendid, body 46 mm long, 5.5 mm wide; anterior eyes slightly larger than posterior ones; acicular lobe single, tapered, if fully extended, about ⅓ as large as neurochaetae; pharynx fully exposed, dorsal papilla round]. — 2 specimens, ZMUC 2423, Taboga Island (08°47'00"N, 79°33'00"W), 8-10 m depth, 8.II.1916, T. Mortensen coll. [one complete 21 mm long, 3 mm wide; the other reduced to fragments; colorless, acicular lobe single, tapered].
Western Baja California Sur. 1 specimen, LACM 85732, RV *Velero IV*, Sta. 2024 (27°48'33"N, 114°42'30"W à 27°49'00"N, 114°42'09"W), 30 km E off Punta Eugenia, 16 m depth, rocks and sand, 18.IV.1951 [35 mm long, 4 mmm wide; upper acicular lobes tapered or digitate, 4-6 times longer than rounded lower ones]. — 1 specimen, LACM 8556, Punta Abreojos (26°42'N, 113°35'W), Knelpen shoal, 18 m depth, in kelp holdfast, 2.III.1959, D. Miller coll. [21 mm long, 5 mm wide; dehydrated, compressed, ventrally bent; pharynx exposed, prostomium collapsed; acicular lobe double, upper one tapered, very long, lower one rounded, short; two neuraciculae; neurochaetal blades bidentate, subdistal tooth small, guard approaching distal tooth].
Gulf of California. Baja California. 1 specimen, LACM 8565, RV *Velero III*, Sta. 719 (30°53'00"N, 114°28'35"W), Consag Rock, 18-45 m depth, basket stars, 24.III.1937 [48 mm long, 6 mm wide; laterally bent; antennae minute, as long as interocular distance; longest tentacular cirri reach chaetiger 5; upper acicular lobe long, tapered, lower one rounded, barely visible].
Sonora. 1 specimen, LACM 8569, Punta Cholla, Puerto Peñasco, 9.V.1941, S. A. Glassell coll. [32 mm long, 4 mm wide; prostomium not collapsed, pharynx partially exposed; several parapodia previously removed; most dorsal cirri on site; upper acicular lobe contracted, digitate, 3-4 times longer than lower one, rounded; in chaetiger 10, left parapodium, upper lobe bifid into two similar sized ones, but placed at the same plane; other parapodia with lobes as indicated before]. — 1 specimen, LACM 8567, Puerto Lobos, 16.IV.1965, P. Pickens coll. [38 mm long, 4 mm wide; partially dehydrated; upper acicular lobe tapered, 4-6 times longer than lower one rounded]. — 1 specimen, LACM 8559, Playa Miramar, Guaymas, 10.II.1948, G. W. & N. MacGinitie coll. [22 mm long, 2.5 mm wide; prostomium with a longitudinal depression throughout its length; most dorsal cirri lost; acicular lobe with upper tine tapered, 4-5 times longer than lower one, rounded]. — 4 specimens, LACM 8562, RV *Velero III*, Sta. 1042 (28°43'30"N, 112°19'05"W), Turner's Island, S of Tiburon Island, rocky shore, 24.VI.1940 [macerated, probably very long; neuropodia with a long tapered acicular lobe].
Baja California Sur. Isla Tortuga. 1 specimen, LACM 8571, RV *Velero III*, Sta. 576 (27°25'30"N, 111°53'25"W), 38 m depth, volcanic sand, 13.III.1936 [27 mm long, 2.5 mm wide; acicular lobe with upper tine tapered, 4-5 times longer than lower rounded ones].
Bahía Concepción. 2 specimens, ECOSUR 2186, Laguna Terminal, 1 m depth, rocky bottom, 8.V.1981, R. Ríos coll. [34-40 mm long, 4 mm wide; smaller one with pharynx exposed, without dorsal papilla]. — 3 specimens, LACM 8574, RV *Velero III*, Sta. 585 (26°43'25"N, 111°54'05"W), Coyote Bay, 3.6-7.2 m depth, sand and kelp, 14.III.1936 [37-38 mm long, 4.5-5.0 mm wide; macerated; pharynx exposed in 1 specimen, margin integument ciliated, partially eroded; chaetal lobe invaginated in many parapodia; acicular lobe with upper tine long tapered, lower one inconspicuous]. — 1 specimen, LACM 8570, RV *Velero III*, Sta. 688 (26°41'40"N, 111°51'05"W), 22 m depth, mud and sand, 16.III.1937 [body macerated; pharynx barely exposed; chaetal lobe invaginated in many parapodia; acicular lobe with upper tine tapered, 4-5 times longer than lower one]. — 1 specimen, LACM 8560, RV *Velero IV*, Sta. 1771 (26°42'03"N, 111°53'34"W to 26°42'17"N, 111°53'33"W), 13 m depth, rocky bottom, 27.III. — 1 specimen, UANL 641, 18.VII.1985, J. A. de León-González coll. [5.5 mm long, 1 mm wide; partially dehydrated; pigmentation lost; body cylindrical, pharynx everted, pharynx papilla covered by prostomial anterior margin; prostomium with posterior depression barely visible, eyes not seen; dorsal cirri multi-annulated basally; acicular lobe single, tapered]. — 1 specimen, UANL 642, 20.VII.1985, J. A. de León-González coll. [21 mm long, 3 mm wide; poorly preserved; most integument detached from body wall; cirri macerated; body depressed, parallel sided pharynx invaginated; prostomium with posterior depression visible, eyes visible, brownish, very close to each other, anterior ones slightly more separated and larger than posterior ones; most chaetae lost; posterior end cirri lost].
Bahía de La Paz. 1 specimen, UANL 128, 14.XI.1984, U. Garza coll. [21 mm long, 3.5 mm wide; pharynx everted, dorsal papillae digitate, twice as long as wide; prostomium with posterior depression visible, eyes visible, brownish, very close to each other; dorsal cirri basally multiarticulated; acicular lobe double, upper tine digitate, lower lobe conical, blunt, ⅕ as long as upper one; posterior end cirri lost, anus in an 8-shaped area]. — 5 specimens, LACM 8566, RV *Velero III*, Sta. 503, off Lighthouse, coralline algae, 9 m depth, 21.II.1936 [19-25 mm long, 2.0-4.5 mm wide; largest specimen mature (25 mm long, 4.5 mm wide), oocytes about 100 µm; acicular lobe double, upper tine tapered, sometimes basally contracted, 5-8 times longer than lower, rounded one; neurochaetal blades longer in smaller specimens (series of slides and photos in 3 specimens of different length and width)]. — 4 specimens, LACM 8575, RV *Velero III*, Sta. 1111 (24°21'55"N, 110°15'15"W), San Lorenzo Channel, 11 m depth, sand, shell, coralline, 14.II.1940 [29-41 mm long, 3.5-5.0 mm wide; macerated; chaetal lobes invaginated; acicular lobe with upper tine tapered, 5-8 times longer than lower, rounded one].
Espíritu Santo Island. 2 specimens, USNM 35566, 24 m depth, 30.III.1934, E. & C. Berkeley coll. [damaged, most cirri and many

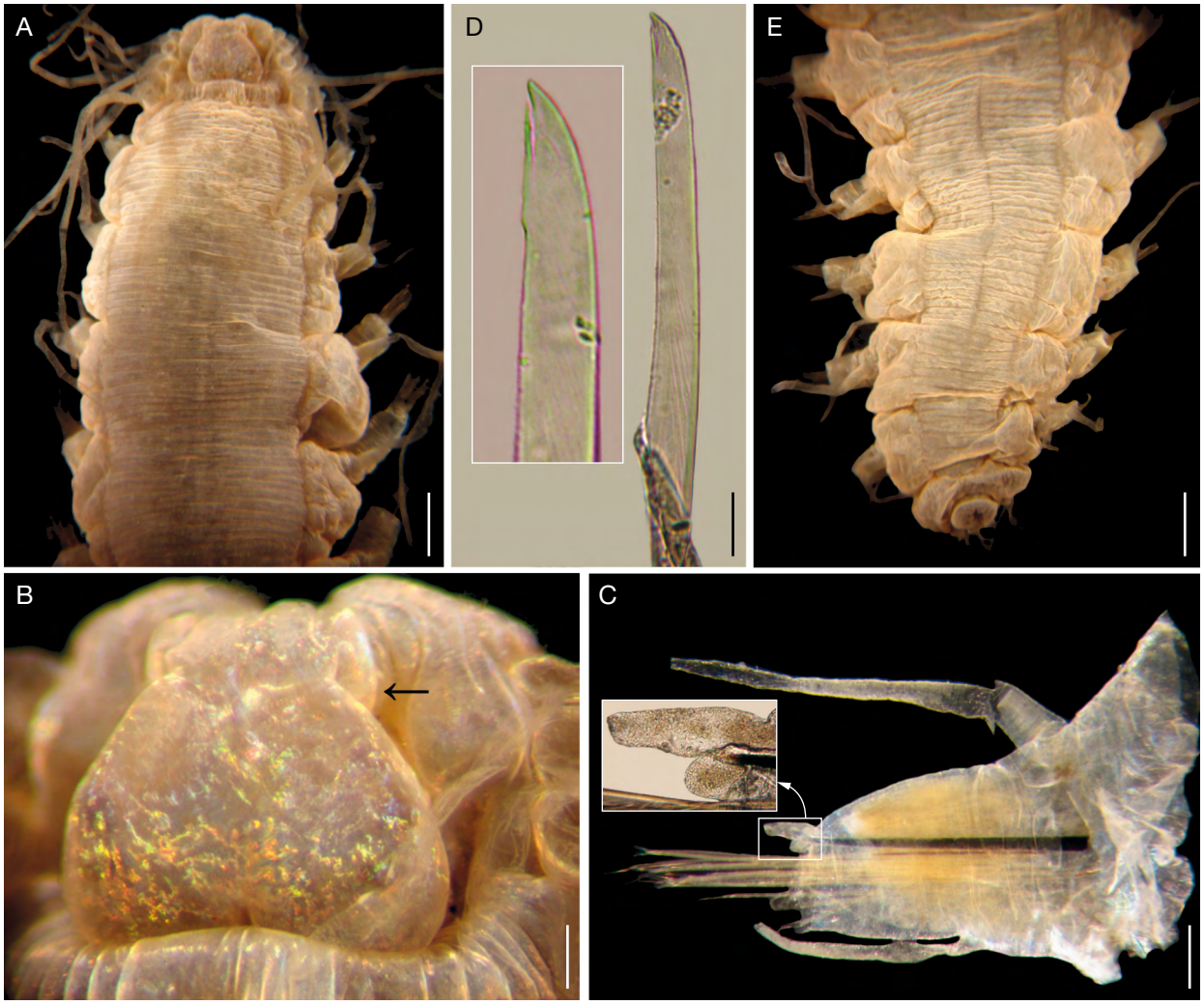

Fig. 33. — *Hesione panamena* Chamberlin, 1919, holotype, USNM 19379: **A**, anterior end, dorsal view; **B**, close-up of head (arrow points to right lateral antenna); **C**, chaetiger 8, right parapodium (inset: close-up of acicular lobe, upper tine eroded); **D**, same, blade of neurochaeta (inset: close-up of another neurochaetal blade tip); **E**, posterior region, dorsal view. Scale bars: A, 1.3 mm; B, 0.3 mm; C, 70 µm; D, 30 µm; E, 1.7 mm.

chaetal blades lost, partially dehydrated, stiff, many parapodia with longer upper acicular lobe and smaller, rounded lower lobe; not measured to avoid further damage].
San José Island. 2 specimens, MNHN-IA-PNT91f (formerly jar 70), in different containers; one from the southern lagoon, among corals; the other without precise locality, 1904, L. Diguet coll. [specimen in better condition 24 mm long, 3 mm wide; the other distorted, dried-out; acicular lobe single, can be seen in several parapodia despite their condition; acicular lobes single throughout body].
Ensenada de Muertos. 1 specimen, LACM 8564, RV *Velero III*, Sta. 627 (23°58'55"N, 109°49'25"W), 9 m depth, sand, 5.III.1937 [27 mm long, 2.5 mm wide; many cirri lost; body with circular adsorbed salts throughout the body; acicular lobe with upper tine tapered, long, sometimes digitate, lower one minute].
Gulf of California, Baja California Sur(?). 1 specimen, MNHN-IA-PNT91g (formerly jar 70), no locality, 1894, L. Diguet coll. [13 mm long, 2 mm wide; distorted, partially dehydrated, acicular lobes single, can be seen in several parapodia]. — 1 specimen, MNHN-IA-PNT91h (formerly jar 70b), no locality, II.1895, L. Diguet coll. [32 mm long, 4 mm wide; distorted by compression; body almost without pigmentation, one middorsal pale spot between chaetigers 2 and 3]. — 2 specimens, MNHN-IA-PNT91i (formerly jar 70c), no locality, II.1895, L. Diguet coll. [31-36 mm long, 5-7 mm wide; macerated; both with pharynx fully everted; acicular lobes single].
Western Mexico. Sinaloa. Sixteen specimens, LACM 7101, Topolobampo (25°36'N, 109°04'W), 26.I.1971, R. C. Brusca coll. [17-28 mm long, 2-3 mm wide; upper acicular lobe tapered, 4-5 times longer than lower rounded one; 1 specimen mature, 25 mm long, 3 mm wide, dissected for anatomical features]. — 1 specimen, UANL EMU 442, Estero de Urías, Mazatlán, intertidal, 1980, A. Rutgers coll. [11.5 mm long, 2 mm wide; bent ventrally; colorless; acicular lobe single, tapered].
Nayarit. 1 specimen, LACM 8572, RV *Velero III*, Sta. 745 (21°54'10"N, 105°53'05"W), Isabel Island, 18-32 m depth, corallines, 2.IV.1937 [37 mm long, 4 mm wide; slightly macerated; acicular lobe rounded, upper tine contracted, 3-4 times longer than lower ones].
Guerrero. 1 specimen, ECOSUR OH-374, Hornos Beach, Acapulco, on oysters (*Spondylus calcifer*), 4 m depth, 19.IV.2008, L. F. Carrera-Parra & SISV coll. [23 mm long, 3 mm wide; irregular, thin longitudinal lines still visible on tentacular segment only, rest of body colorless; pharynx not exposed; prostomial anterior margin depressed; anterior eyes twice as large as posterior ones; parapodia with acicular lobes single, tapered; posterior end smashed, integument smooth]. — 5 specimens, LACM 8555, RV *Velero*, Sta. 2596, Santa Lucía bay (16°50'33"N, 99°55'28"W), Acapulco, 2-8 m depth, sponges, algae, rock, muddy sand bottoms, 1.II.1954 [four in better

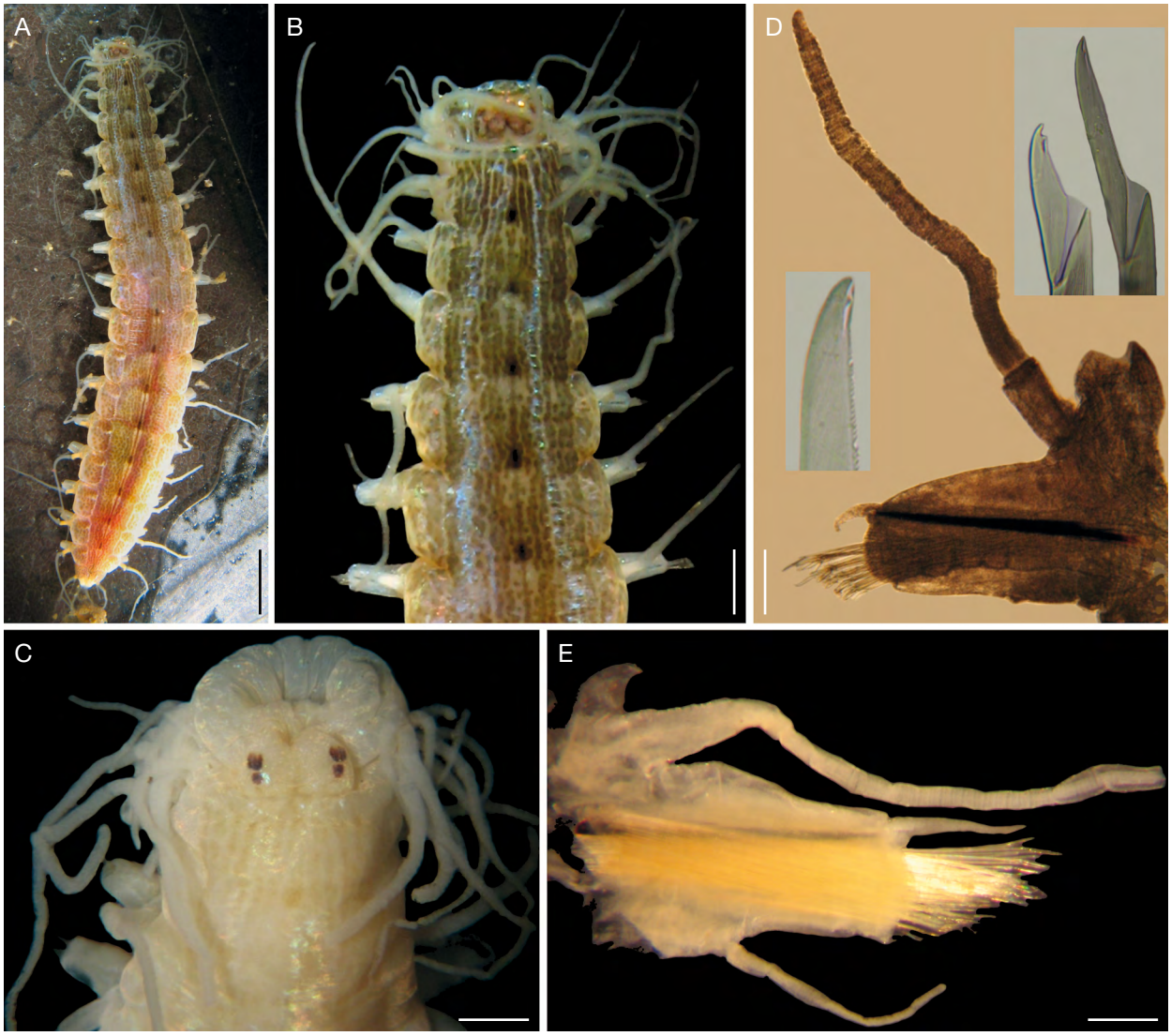

Fig. 34. — *Hesione panamena* Chamberlin, 1919, non-type specimens: **A**, dorsal view of living specimen, depressed by glass slide, ECOSUR OH 374, reddish hue due to blood vessels fracture after pressure and osmotic shock; **B**, same, anterior end, dorsal view; **C**, same, after some time in ethanol, pharynx barely exposed; **D**, chaetiger 6, right parapodium, anterior view (insets: blade tips); **E**, another specimen, LACM 8556, chaetiger 10, left parapodium, anterior view. Scale bars: A, 3 mm; B, 1 mm; C, 0.7 mm; D, 0.4 mm; E, 0.5 mm (photos: A, B, H. Bahenas).

condition, 14-35 mm long, 2.5-5.0 mm wide; dorsal cirri longer than body width, including parapodia; one right parapodium (chaetigers 7-9) removed (kept in container); oocytes 100 µm in diameter].
Revillagigedo Islands, México. 1 specimen, LACM 134 34, RV *Velero III*, Sta. 134 (18°20'35"N, 114°44'20"W), 25 m depth, rock, nullipores, 5.I.1934 [extremely distorted, body twisted over itself, posterior region compressed; 17 mm long, 2 mm wide; acicular lobe with upper tine tapered, 4-5 times longer than rounded lower one]. — 1 specimen, LACM 8563, RV *Velero III*, Sta. 289 (18°41'50"N, 110°57'20"W), 8-27 m depth, sand and nullipores, 8.VI.1934 [16 mm long, 2.5 mm wide; mature, gonads visible through body wall from chaetiger 10, as homogeneous masses; acicular lobe digitate, upper tine 5-7 times longer than rounded lower one]. — 1 specimen, LACM 8561, RV *Velero III*, Sta. 304 (18°20'25"N, 114°44'30"W), 36 m depth, nullipores, algae, 11.VI.1934 [26 mm long, 3 mm wide; mature; body distorted, gonads exposed after body wall rupture; acicular lobe digitate, upper tine 4-5 times longer than rounded lower one; sperm spherical, about 5 µm in diameter].
Ecuador. 1 specimen, LACM 8583, RV *Velero III*, Sta. 213 (01°15'25"S, 81°05'15"W), off La Plata Island, 13-18 m depth, rock, nullipores, 10.II.1934 [14 mm long, 2 mm wide; macerated, body soft, semitransparent, including cirri; acicular lobe with upper tine very long, about 10 times longer than lower, rounded one]. — 1 specimen, LACM 10150, RV *Velero III*, Sta. 59 (01°14'31"S, 90°26'30"W), off Cormoranat Bay, Charles Island, Galápagos Islands, 23 m depth, 6.II.1933 [27 mm long, 4 mm wide; macerated; chaetal lobes invaginated, acicular lobe with upper tine 4-5 times longer than lower, rounded one]. — 1 specimen, LACM 148-34, RV *Velero III*, Sta. 148 (00°16'41"S, 91°22'39"W), Tagus Cove, Albermarle Island, Galápagos Islands, 22-45 m depth, 13.I.1934 [20 mm long, 2.8 mm wide; macerated, with abundant adsorbed particles on body and chaetae; chaetal lobes invaginated, acicular lobe with upper tine 4-5 times longer than lower, rounded one]. — 5 specimens, LACM 10151, RV *Velero III*, Sta. 167 (01°14'37"S, 90°28'08"W), Post Office Bay, Charles Island, Galápagos Islands, 27 m depth, rocks, 19.I.1934 [20-32 mm long, 2-4 mm wide; macerated, most cirri and neurochaetal blades on site; chaetal lobes variably invaginated; right parapodium of chaetiger 9 in 3 specimens removed (kept in vial); acicular lobe with upper tine 3-4 times longer than lower one; largest specimen mature; oocytes about 100 µm]. —

1 specimen, LACM 10151, RV *Velero III*, Sta. 336 (00°16'30"S, 90°35'20"W), Sullivan Bay, James Island, Galápagos Islands, 36 m depth, 12.XII.1934 [25 mm long, 3 mm wide; macerated; pharynx fully everted; chaetal lobes slightly invaginated, acicular lobe with upper tine 4-5 times longer than lower, rounded one]. — 1 specimen, LACM 10161, RV *Velero III*, Sta. 811 (00°51'35"S, 90°02'00"W), Barrington Island, Galápagos Islands, shore, *Pocillopora*, 26.I.1938 [30 mm long, 4 mm wide; macerated; chaetal lobes invaginated; acicular lobe with upper tine tapered or digitate, 3-5 times longer than lower, rounded one].

Distribution. — Eastern tropical Pacific, From Punta Eugenia, Baja California Sur, México to the Galápagos Islands, from intertidal to 45 m depth, in sandy or mixed bottoms.

Diagnosis. — *Hesione* with prostomium slightly curved laterally; parapodia with dorsal cirri basally cylindrical, dorsal cirrophore twice as long as wide; larger acicula blackish; acicular lobe single, long, tapered, lower tine rounded, small; neurochaetal blades bidentate, 3-8 times as long as wide; subdistal tooth smaller than distal one, with guards approaching distal tooth.

Description

Holotype, USNM 19379, complete, tapered, colorless in ethanol, slightly macerated with several dorsal cirri and ventral cirri damaged or lost; chaetae from chaetiger 1 lost; body integument finely annulated dorsally, annulations not continued into lateral cushions, especially behind chaetal lobes (Fig. 33A). Body 39 mm long, 5 mm wide.

Prostomium as long as wide, anteriorly narrower, expanded towards posterior margin; anterior margin projected, posterior margin with a small furrow (Fig. 33B). Antennae minute, blunt, slightly as long as wide. Eyes barely pigmented, anterior ones placed by the middle of the prostomium, slightly larger and farther apart than posterior ones, displaced posteriorly.

Tentacular cirri damaged, longest ones reaching chaetiger 4. Lateral cushions projected, corrugated in anterior region, divided into two sections in posterior region.

Parapodia with dorsal cirri damaged; cirrophore annulated, about twice as long as wide; cirrostyle macerated, looking smooth. Ventral cirri with cirrophores small, indistinct; cirrostyle longer than chaetal lobe. Chaetal lobe thick, with parallel sides, slightly tapered, annulated basally (Figs 33C, 34D, E).

Neuraciculae blackish, two, one markedly thicker than the other. Acicular lobe single, tapered, rarely directed upwards, mostly projected laterally, sometimes with a round basal projection, upper tine (eroded) 3 times longer than lower one (basal tine not visible in other specimens, Fig. 34E).

Neurochaetae about 16 neurochaetae per bundle, blades bidentate, slightly shorter ventrally, 8 times as long as wide, with a small subdistal tooth, guard usually passing it (Fig. 33D) (other specimens with blades 3-7 as long as wide, Fig. 34D).

Pygidium with integument smooth; anus projected as a short, distally expanded cylinder (Fig. 33E); about 8 short, digitate anal papillae.

Pharynx not exposed. Oocytes not seen.

Pigmentation

Body with longitudinal, dorsal, irregular, discontinuous thin dark green or pale brown bands (Fig. 34A), restricted to first 2-3 anterior chaetigers, alternating with small, round spots, and completely replaced by them in medial and posterior chaetigers, expanded into lateral cushions, but not into pygidium. Tentacular and dorsal cirri colorless; cirrophores pale in anterior chaetigers, yellowish in posterior ones; chaetal lobes pale. Prostomium with thin irregular marginal lines. Longitudinal bands progressively thinner (Fig. 34B); all chaetigers with an irregular middorsal spot, irregularly ovoid, as long as wide, along chaetigers 1-6, becoming as long as wide in following chaetigers, connected by a thin, darker middorsal line continued to the last achaetous segment. This thin middorsal line bordered by paler areas, short in anterior and medial segments, becoming longer, running throughout all dorsal segmental surface in posterior segments. Pigmentation remaining visible after 8 years in ethanol (Fig. 34C).

Remarks

Hesione panamena Chamberlin, 1919, reinstated, resembles *H. pantherina* Risso, 1826 in the key below. Their main difference is the type of acicular lobe. In *H. panamena* acicular lobes are long, tapered, whereas in *H. pantherina* they can be short or long but their tips are blunt to distally swollen. Living specimens also differ because in *H. panamena* there are middorsal blackish, round spots whereas in *H. pantherina* there are middorsal pale areas.

Hesione panamena was originally spelled as such for the description (Chamberlin 1919: 188) and *H. panamica* for the legends to figures, and although both epithets are correct, the former has been followed by subsequent authors. Chamberlin (1919: 189) indicated that antennae were broken off, but they are present in the type, although because their bases are not exposed, they are difficult to observe. The details of the neurochaetal blades, as indicated in the original illustrations (his plate 22, figures 9-10) are accurate by showing long blades, with a small subdistal tooth, and its guard usually passing subapical tooth.

Hesione panamena resembles *H. intertexta* Grube, 1878 by the small size of the eyes and antennae, and they also have similar neurochaetal blades. However, in *H. panamena* the blade length/width proportions are smaller and the antennae are ovoid, whereas in *H. intertexta* there is a wider variation in blade size, and antennae are tapered. Further, although pigmentation fades quite soon in ethanol, their patterns show some differences; in *H. panamena*, segmental longitudinal lines are discontinuous whereas they are continuous in *H. intertexta,* and in *H. panamena*, there is a blackish, as long as wide middorsal spot just before a paler area, and this is not so evident in *H. intertexta*. Further, in *H. intertexta* acicular lobe is single, without any lower one, whereas in *H. panamena* there can be a smaller, rounded lower tine.

Fauvel (1941: 9) recorded two *Hesione* species for the Gulf of California: *H. pantherina* Risso, 1826 (this record is herein regarded as belonging to *H. panamena*), and *H. genetta* Grube, 1867 because of its pigmentation pattern: "à la face dorsale des traces de mouchetures brunes, ovales, alternées, qui rappellent la robe de la Genette." (Transl.: on the dorsal surface there are remains of brown oval, alternating spots, resembling the

genette skin). This specimen was found in the Paris museum, it differs from *H. hartmanae* n. sp. described above, and initially regarded as having potential affinities because acicular lobes are double in *H. genetta* and *H. hartmanae* n. sp., but the Paris specimen has acicular lobes single. Fauvel's specimen had been in ethanol for about 50 years before he saw it, and he referred to a pigmentation pattern, but after other half a century spent before I studied the specimen, this pigmentation is now completely faded out. This specimen is also regarded as conspecific with *H. panamena*.

Monro (1926: 312) made a comparison of the size of guards and separated *Hesione* species into three groups; among those having guards approaching the apical tooth he listed *H intertexta*, *H. reticulata* von Marenzeller, 1879, *H. praetexta* Ehlers, 1885 and *H. panamena* Chamberlin, 1919. Further, in the previous page, Monro rejected, following Fauvel (1923a), the use of pigmentation pattern and the development of acicular lobes. As a consequence, in two of his publications on Panamian polychaetes (Monro 1928: 79; 1933: 26) he regarded *H. panamena* as a junior synonym of *H. intertexta*, and recorded it for the Pacific coast of Panama. Hartman (1940: 212) followed this synonymy and listed specimens from Western Mexico to the Galápagos Islands, but her material includes two species: one with a very long upper acicular lobe, herein retained as *H. panamena*, and another one with two acicular lobes, which were illustrated, and were based on Galápagos specimens, which are regarded as belonging to an undescribed species and described above as *H. hartmanae* n. sp. The record of *Hesione pantherina* Risso, 1826 for the Gulf of California (Fauvel 1941: 9) is regarded as belonging to *H. panamena.* Consequently, there are two species in the Galapagos (Blake 1991: 78) but their names should be changed to *H. panamena* and *H. hartmanae* n. sp. (see above).

Hesione pantherina Risso, 1826, restricted
(Figs 35, 36)

Hesione pantherina Risso, 1826: 418, 419. — Audouin & Milne Edwards 1833: 234, 235, pl. 15, fig. 4. — Fauvel 1914: 121, 122; 1923a: 233, 234, fig. 87 (*partim*); 1932b: 20 (Toulon); 1934: 21; 1950: 349. — Fauvel & Rullier 1957: 36; 1959b: 512.

Fallacia pantherina – Quatrefages 1866: 98, 99. — Malaquin 1894: 417.

Hesione splendida – Campoy 1982: 208-210, pl. 11, figs A-D. — Kirkegaard 1983: 213. — Sordino 1990: 35. — Brito *et al.* 1996: 163, fig. 5A-C. — Parapar *et al.* 2004: 216, fig. 76 (*partim*, *non* Savigny *in* Lamarck, 1818).

TYPE MATERIAL. — **Mediterranean Sea, France.** Neotype, MNHN-IA-TYPE1850 (formerly jar 70.190b), Mer de Nice, labeled in 1868, no further data. 2 specimens labelled paraneotype: MNHN-IA-TYPE1851 (formerly jar 70.190c), Mer de Nice, no further data; MNHN-IA-TYPE1852 (formerly jar 70.190d), mer de Nice, no further data [54 mm long, 7 mm wide; body distorted by compression in small container, especially anterior end; most parapodial lobes invaginated, once exposed, all with acicular lobe single; neuraciculae black, subdistally expanded, mucronate].

ADDITIONAL MATERIAL. — **Mediterranean Sea. Argelia**. 3 specimens, MNHN-IA-PNT91j (formerly jar 70), 1900, no further data, M. Pallary coll. [25-38 mm long, 3-4 mm wide; two slightly macerated; acicular lobes single, neuraciculae blackish tapered, distally swollen, mucronate].
France. 1 specimen, SMF 15475, Gulf of Marseille, Pointe Donnelle, Sta. A4H, 2.XI.1982, A. Willsie coll. [17 mm long, 2 mm wide; colorless, bent ventrally, all dorsal and tentacular cirri lost, left parapodium of chaetiger 10 removed for observation (kept in vial); pharynx partially exposed, dorsal papilla not seen; antennae digitate, 2-3 times as long as wide; eyes barely pigmented, anterior ones twice as large as posterior ones; acicular lobe single, blunt; neurochaetal blades bidentate, subdistal tooth smaller, guards mostly broken, if entire, approaching distal tooth].
Undefined locality. 2 specimens, ZMB 3812, Grube Collection, Dr Bergmann coll., no further data [44-48 mm long, 6-8 mm wide; a few parapodia previously removed and set into permanent slides; smaller slightly macerated, larger better preserved; antennae about 4 times as long as wide; acicular lobe single, a few parapodia with a short, rounded, basal lobe but most with a tapered, blunt acicular lobe].
Northwestern Africa. 1 specimen, BMNH 1955.8.22.9, Canary Islands, Arrecife, spring 1955, C. Totton coll. [43 mm long, 5 mm wide; prostomium as long as wide; antennae digitate, 4-5 times as long as wide; anterior eyes slightly larger than posterior ones; right parapodium of chaetiger 9 removed for observation (kept in vial); acicular lobe single; neurochaetal blades bidentate, subdistal tooth as wide as distal one, guards approaching subdistal tooth; oocytes 100 µm in diameter].

DISTRIBUTION. — Despite the fact that Fauvel recorded this species for many localities worldwide, its distribution is rather restricted to the Mediterranean region, and adjacent areas in the Eastern Atlantic, in shallow water.

DIAGNOSIS. — *Hesione* with prostomium rectangular; parapodia with dorsal cirri basally cylindrical, dorsal cirrophore twice as long as wide; larger acicula blackish; acicular lobe single, short or long, digitate or slightly swollen distally, lower tine missing; neurochaetal blades bidentate, 6-7 times as long as wide; subdistal tooth smaller than distal one, with guards approaching distal tooth.

DESCRIPTION

Neotype, MNHN-IA-TYPE1850 (formerly jar 70-190b), complete, tapered, colorless (Fig. 35A) in ethanol, integument dorsally smooth, variably corrugated; posterior end smashed, bent laterally, several tentacular and dorsal cirri lost; neurochaetal lobes contracted; right parapodium from chaetiger 9 removed and dissected for acicular features (kept in container); body 37 mm long, 5 mm wide.

Prostomium rectangular, slightly as wide as long (Fig. 35B), anterior margin projected, posterior margin with a shallow, short furrow, about as long as ⅕ prostomial length; longitudinal depression very shallow. Antennae minute, digitate, tapered, directed laterally, as long as anterior eyes cornea, or 3-4 times as long as wide. Eyes without pigmentation, corneas distinct, anterior ones larger, placed about the median region, more distant to each other than posterior ones.

Tentacular cirri without tips, reaching anterior margin of pharynx, or back to chaetiger 4. Lateral cushions barely projected, separated into two sections in anterior and medial regions, three posteriorly.

Parapodia with dorsal cirri mostly without tips (Fig. 35C); cirrophore annulated, twice as long as wide; cirrostyle cylindrical,

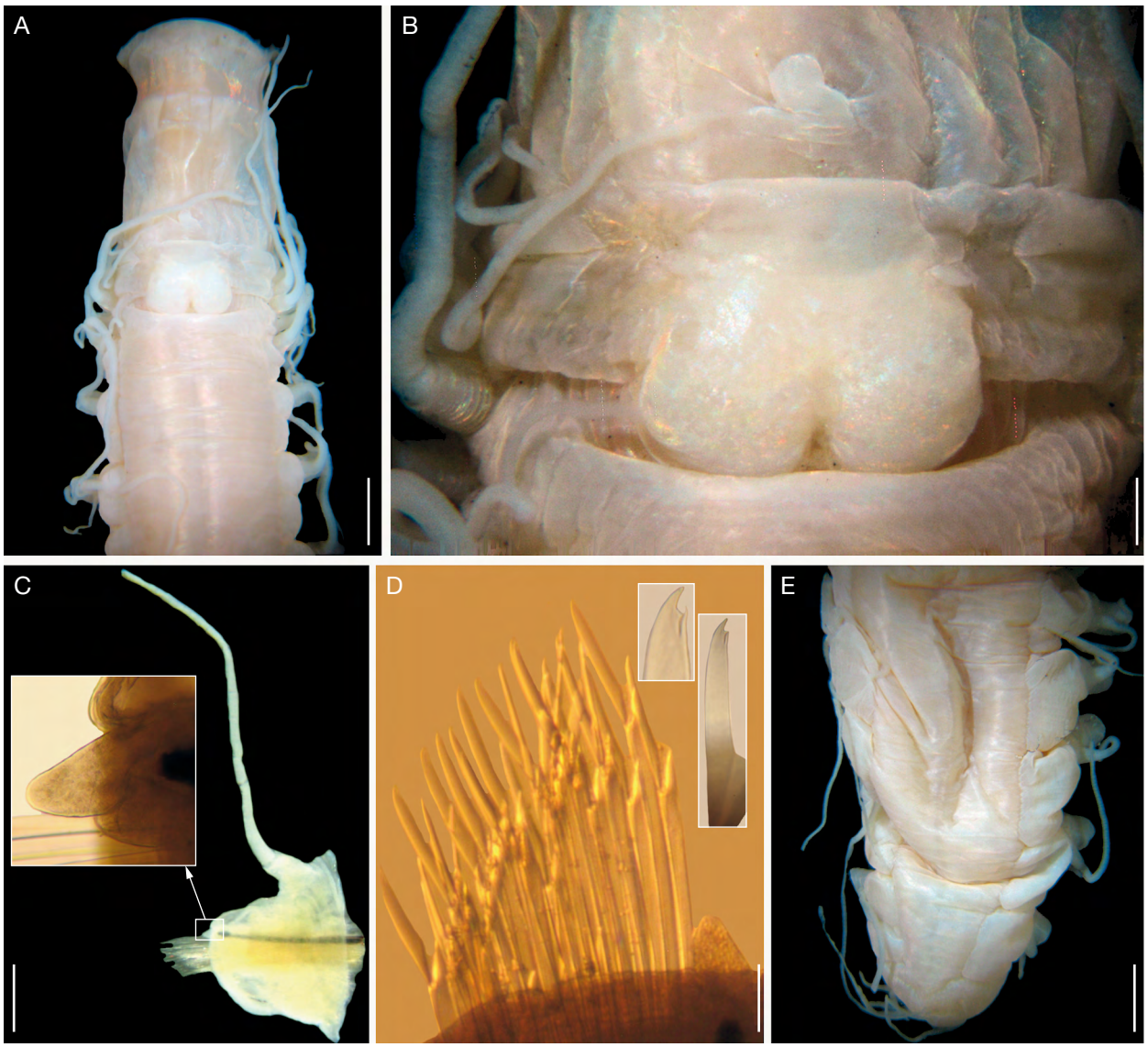

Fig. 35. — *Hesione pantherina* Risso, 1826, neotype, MNHN-IA-TYPE1850 (formerly jar 70.190b): **A**, anterior region, dorsal view; **B**, prostomium and basal ring of pharynx; **C**, chaetiger 9, right parapodium, anterior view (inset: acicular lobe); **D**, same, neurochaetae (insets: blades); **E**, posterior region, dorsal view. Scale bars: A, 1 mm; B, 0.4 mm; C, 1.7 mm; D, 75 µm; E, 1.5 mm.

smooth basally, articulated medially and distally. Neuropodia thick, tapered, blunt, annulated basally. Ventral cirri with cirrophore small, almost indistinct; cirrostyle longer than chaetal lobe.

Neuraciculae black, tapered, distally swollen, some mucronate. Acicular lobes single, digitate, blunt (Fig. 35C [inset]), markedly projected in specimen MNHN-IA-TYPE1850 (Fig. 36A, B [insets]).

Neurochaetae about 20 per bundle (Fig. 35D), blades bidentate, 6-7 times as long as wide, slightly shorter ventrally, with a smaller subdistal tooth, guard approaching or barely surpassing subdistal tooth (Fig. 35D [insets]).

Posterior end tapered into a blunt cone (Fig. 35E), directed ventrally; pygidium with all cirri on site, anus exposed with about 6 low papillae.

Pharynx fully exposed, 5 mm long, made by two rings, distal one ¼ as long as whole pharynx, basal ring longer; dorsal papilla 1.5 times as long as wide, tip rounded. Oocytes not seen.

Remarks

Hesione pantherina Risso, 1826 has been confused for several reasons (see below), and it has been regarded as a cosmopolitan species; in order to clarify its taxonomic status (ICZN 1999: art. 75.3.1), a neotype is proposed to define and restrict it. The neotype has been described above and the differences to other species are listed below (ICZN 1999: art. 75.3.2, 75.3.3). There were no type specimens deposited nor present in the Paris museum (ICZN 1999: art. 75.3.4), and the neotype and additional specimens share the same diagnostic features (ICZN 1999: art. 75.3.5). The neotype was collected in the

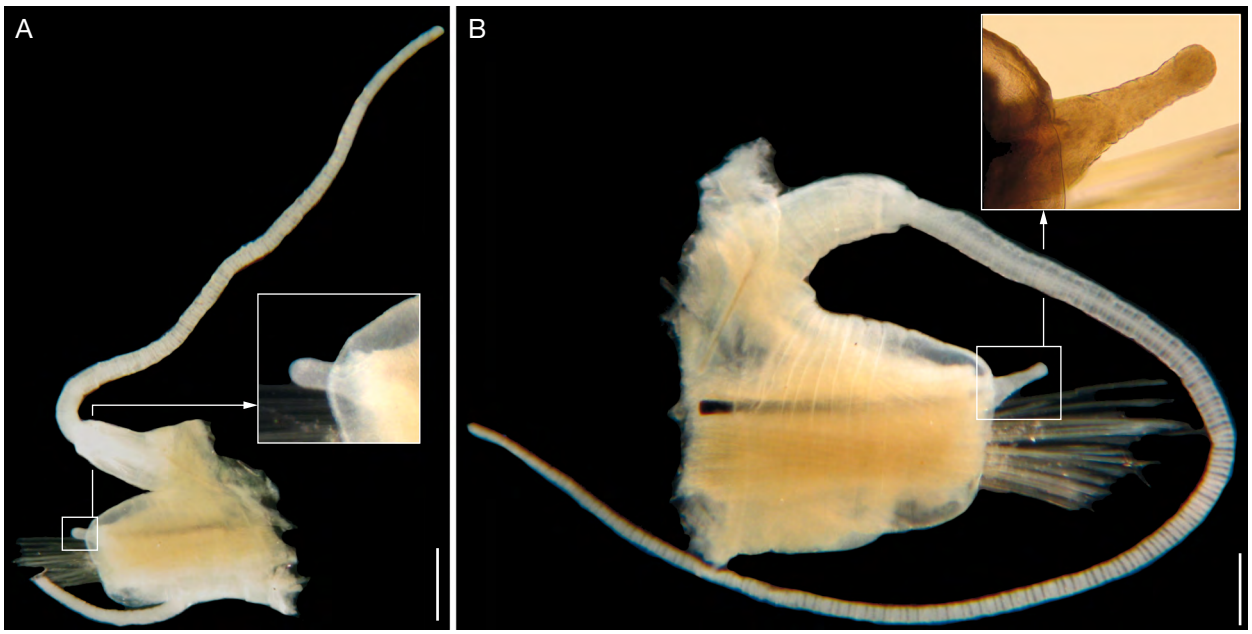

Fig. 36. — *Hesione pantherina* Risso, 1826, specimen MNHN-IA-TYPE1851 (formerly jar 70.190c): **A**, chaetiger 4, right parapodium, anterior view (inset: acicular lobe); **B**, chaetiger 7, left parapodium, anterior view. Scale bars: A, 0.6 mm; B, 0.3 mm.

same region, off Nice (ICZN 1999: art. 75.3.6), and it is now deposited in the Paris museum (ICZN 1999: art. 75.3.7).

In the original description of *Hesione pantherina*, Risso (1826) confused body ends and this explains why there is a discordance between the number of cirri indicated for each body end, against the number that are usually present. This confusion was noted by Audouin & Milne-Edwards (1833: 234, footnote 1). Further, Risso described the pigmentation pattern including transverse lemon-yellow bands, but these bands have not been confirmed, although paler transverse bands can be present in some specimens.

Perhaps the best account of *H. pantherina* was made by Fauvel (1923a: 233); however, there are some differences between his illustrations and the observed features in the Mediterranean specimens. The main differences are: 1) the anterior prostomial margin is not incurved as illustrated if specimens have their pharynx invaginated, but appears anteriorly projected; 2) antennae are as long as interocular distance, not shorter as indicated in his illustrations; and 3) ventral cirri are markedly longer than chaetal lobes, not slightly longer as depicted in the illustrations. Neurochaetal blades, however, were well illustrated with their guards reaching subdistal tooth. These discrepancies imply Fauvel grouped different species under the same name, and this is evident from the pigmentation pattern; he indicated: "coloration assez variable, moucheté de brun et réticulé de blanc, ou tigré de taches brunes allongés ou arrondies." (Transl.: pigmentation very variable, spotted with brown and reticulated white, or striped with longitudinal or round brownish spots).

As shown in the key below, *H. pantherina* resembles *H. panamena* Chamberlin, 1919, reinstated. Their main difference is the type of acicular lobe because in *H. pantherina* they can be short or long but their tips are blunt to distally swollen, whereas in *H. panamena* acicular lobes are long, tapered. Another difference is in pigmentation of living specimens: in *H. pantherina* there are middorsal pale areas, whereas in *H. panamena* there are middorsal blackish, round spots.

Besides *H. pantherina*, there are two other species described from the Northeastern Atlantic and Mediterranean: *H. sicula* delle Chiaje, 1830 and *H. steenstrupi* de Quatrefages, 1866. It must be emphasised that parapodial features, especially the type of acicular lobes, were not included for the original description of any of these three species. Saint-Joseph (1898) made a detailed illustration of parapodial and chaetal features and, quite surprisingly, he even illustrated acicular tips. Thus, his plate 19 shows that antennae are shorter than interocular distance (1898: fig. 131), acicular lobes are double and blunt (1898: fig. 135), neuraciculae are slightly capitate with distal tiny spines (1898: fig. 137), and chaetal blades are bidentate with subdistal tooth larger than distal tooth and guard approaches subdistal tooth (1898: fig. 136). As indicated below, these features match *H. steenstrupi* and his material was collected in Saint-Jean-de-Luz, close to the type locality (Guethary), in the Gulf of Vizcaya.

Saint-Joseph (1898) also compared his material against specimens from Naples, close to the type locality of *H. sicula*, and concluded that they were identical with his materials, leading him to conclude that the three species (*H. pantherina, H. sicula, H. steenstrupi*) were synonyms and the senior synonym should be *H. pantherina*. It must be emphasised that *H. sicula* and *H. steenstrupi* share the presence of acicular lobes double, and some other differences are needed to retain both specific names, but none has been found (see below).

On the other hand, as indicated above, *H. pantherina* has acicular lobes single, and this difference is enough to keep it separate from the two other species. Fauvel (1923a: 234)

followed Saint-Joseph about the synonymy, and when referring to acicular lobes, he indicated that "au-dessus des soies une ou deux petites languettes coniques, souvent rétractées" (Transl.: over the chaetae there is one or two small conical lobes, often retracted). Fauvel was actually reiterating something he had concluded before (Fauvel 1911: 375), when he recorded *H. pantherina* for the Persian Gulf, and rejected the use of acicular lobes as diagnostic features: "j'observe à cet égard une grande variabilité, non seulement d'un individu à l'autre mais encore d'un parapode à l'autre sur un même animal." (Transl.: I observe about this (acicular lobes) a large variability, not only from one specimen to the other but even from one parapodium to another one in the same specimen). This is incorrect. After a comparison of the corresponding illustrations (Fauvel 1911: 375, fig. IV), it is clear that parapodia were mounted differently, as indicated by the relative position of the ventral cirri, such that if these parapodia came from the same specimen they were probably drawn from different perspectives, or worse, they belong to different specimens.

Pleijel (1998: 159) indicated that "*H. sicula* delle Chiaje, 1822" could be a junior synonym of *Hesione pantherina* Risso, 1826. If they are really the same species, the senior synonym should be *H. sicula*; the contrary perspective rejects the principle of priority (ICZN 1999: art. 23), but as indicated below, the type of acicular lobe separates these two species. Further, the correct publication date for *H. sicula* is 1830, as part of a series of plates, as indicated below.

The record by McIntosh (1885: 185, 186, pl. 29, fig. 1, pl. 32, fig. 16, pl. 15A, fig. 10) as *Hesione* (*Fallacia*) *pantherina* for the Cape Verde islands could not be resolved because the specimen is dried out (BMNH 1885.12.1.137), and the original illustrations do not depict the acicular lobe.

Hesione paulayi n. sp.
(Figs 37, 38)

urn:lsid:zoobank.org:act:1ECD169E-717B-458F-8F82-B252A684074F

Hesione genetta – Fauvel 1919b: 370; 1923b: 15, 16; 1947b: 89, 90 (*partim*, Gambier Islands). — Horst 1924: 193 (*partim*, Indonesia). — Hartman 1954: 622 (*partim*, Marshall Islands).

Hesione pacifica – Treadwell 1906: 1149, fig. 4 (*non* McIntosh, 1885).

Hesione splendida – Bailey-Brock & Hartman 1987: 261, fig. 3.II.32 (Hawaii; *non* Savigny *in* Lamarck, 1818).

Hesione sp. TRANS. — Uchida 2011: 3-4, fig. 1.

TYPE MATERIAL. — **Papua New Guinea.** Holotype, UF 32 and two paratypes (UF 5845), Milne Bay Province, Louisiade Archipelago, Misima Island, 1.6 km NW of Pt. Ebola, along North coast (-10.612, 152.539833; 10°36'43.2000"S, 152°32'23.3988"E), 31.V.1998, G. Paulay coll. [paratypes 30-33 mm long, 2.5 mm wide; slightly dehydrated, one laterally bent; both with a well-defined brownish band along chaetiger 2, 3 times wider than following ones, but no band in chaetiger 1, and feebly defined in chaetiger 3; present along chaetigers 4-10(11); pharynx partially exposed, dorsal papilla not seen; antennae digitate, longer than interocular distance; eyes brownish, anterior ones about twice as large as posterior ones; right parapodia removed from one paratype in chaetigers 2, 8, 14; longest tentacular cirri reaching chaetiger 5; median parapodia with dorsal cirri longer than body width, including parapodia; posterior end maculate; pygidium with anus projected, with 7 blunt anal papillae].

ADDITIONAL MATERIAL. — **French Polynesia. Society Islands, Moorea Island.** 1 specimen, UF 887, mid-way between Sheraton and Gump station (-17.4801, -149.8351; 17°28'48.3600"S, 149°50'06.3600"W), lagoon, 2-4 m depth, 11.XI.2008, A. Anker, J. Moore, S. McKeon & V. Ivanenko coll. [38.5 mm long, 3 mm wide; slightly wider towards the posterior region; pigmentation includes transverse bands and circular spots, progressively less marked posteriorly; a wider, darker transverse band in chaetiger 2; body wall transparent; neuraciculae visible dorsally; parapodia with multiarticulated cirri; acicular lobe double, each capitae, upper one longer; neurochaetal blades bidentate, guard reaching subapical tooth; sometimes apical tooth with a shallow nuchal depression].
Tuamotu Islands. 1 specimen, MCZ 46413, RV *Albatross*, unnumb. Sta., Mekema (Makemo) Island (16°35'S, 143°40'W), 21.X.1899 [18.5 mm long, 4 mm wide).
Gambier Islands. 3 specimens, MNHN-IA-PNT911 (formerly jar 70, in separate containers), Vaiatekeue, Gambier Group, 13.X.1903, L. G. Seurat coll. [25-30 mm long, 2.5-4.0 mm wide; pigmentation almost completely faded out, only a wide barely-defined brownish band on chaetiger 2 ("sublimé" in label), better defined in the other specimen; smaller specimen with body wall broken, exposing oocytes now adhered on back; oocytes about 100 µm].
Philippines. 1 specimen, UF 586, Negros Oriental Prov., Dumaguete, behind Silliman University Marine Lab and Dumaguete Airport (9.33592, 123.3097; 09°20'09.3120"N, 123°18'34.9200"E), patch reef, lagoon, methylated spirits, 3-4 m depth, 22.V.2006, K. Netchy & A. Kerr coll. [27 mm long, 3 mm wide, partially dehydrated; pigmentation pattern including a wide dorsal transverse dark bands on chaetiger 2, but no transverse bands on chaetigers 1 and 3; transverse bands and dark spots progressively thinner, paler posteriorly].
Northern Marshall Islands. 1 specimen, LACM 10162, Eniwetak Atoll, 17.XII.1946, F. C. Z. coll. [26 mm long, 2.5 mm wide; pinkish, with abundant salt particles adsorbed; eyes unpigmented; antennae as long as interocular distance; prostomium as long as wide, prostomial posterior margin completely exposed, deeply furrowed, reaching ¼ prostomial surface; dorsal cirri thin, delicate; acicular lobe double, upper tine digitate, lower tine shorter, blunt; neurochaetal blades with large subdistal tooth, guard approaching it; pygidium smooth, irregular because of adsorbed materials; anal tube projected, anal papillae not visible].
Mariana Islands. 1 specimen, UF 43, Guam Island, Cocos Island, S side (13.5, 144.8; 13°30'00.0000"N, 144°48'00.0000"E), forereef, under rubble, 20 m depth, 2.XI.1999, L. Kirkendale coll. [37 mm long, 3 mm wide; body bent laterally, slightly distorted; pigmentation pattern with a thick brown transverse band on chaetiger 2, missing on chaetigers 1 and 3, thinner, paler on chaetigers 4-8; pharynx not exposed; antennae digitate, longer than interocular distance; eyes dark brown, fading out, anterior ones about twice as large as posterior ones]. — 1 specimen, UF 50, Guam Island, Apra Harbor, Gab Gab Beach (13.5, 144.8; 13°30'00.0000"N, 144°48'00.0000"E), in rubble, 3-5 m depth, 9.XII.1997, L. Kirkendale coll. [26 mm long, 3.5 mm wide, stiff, bent dorsally; pigmentation pattern as thin transverse lines on chaetigers 2, 4-7, following ones without transverse bands, first band twice as wide as others, missing on chaetigers 1 and 3; pharynx partially exposed, dorsal papilla not seen; antennae longer than interocular distance; acicular lobes capitate]. — 1 specimen, UF 700, Guam Island, Mangilao, Pago Bay (13.426695, 144.796052; 13°25'36.1020"N, 144°47'45.7872"E), fore reef, 0-1 m depth, 14.III.2008, F. Michonneau & S. Kim coll. [38 mm long, 3 mm wide, partially dehydrated, distorted, parapodia directed ventrally; one dorsal, wide, dark brown transverse band on chaetiger 2, no bands in chaetigers 1 and 3, and discontinuous bands in chaetigers

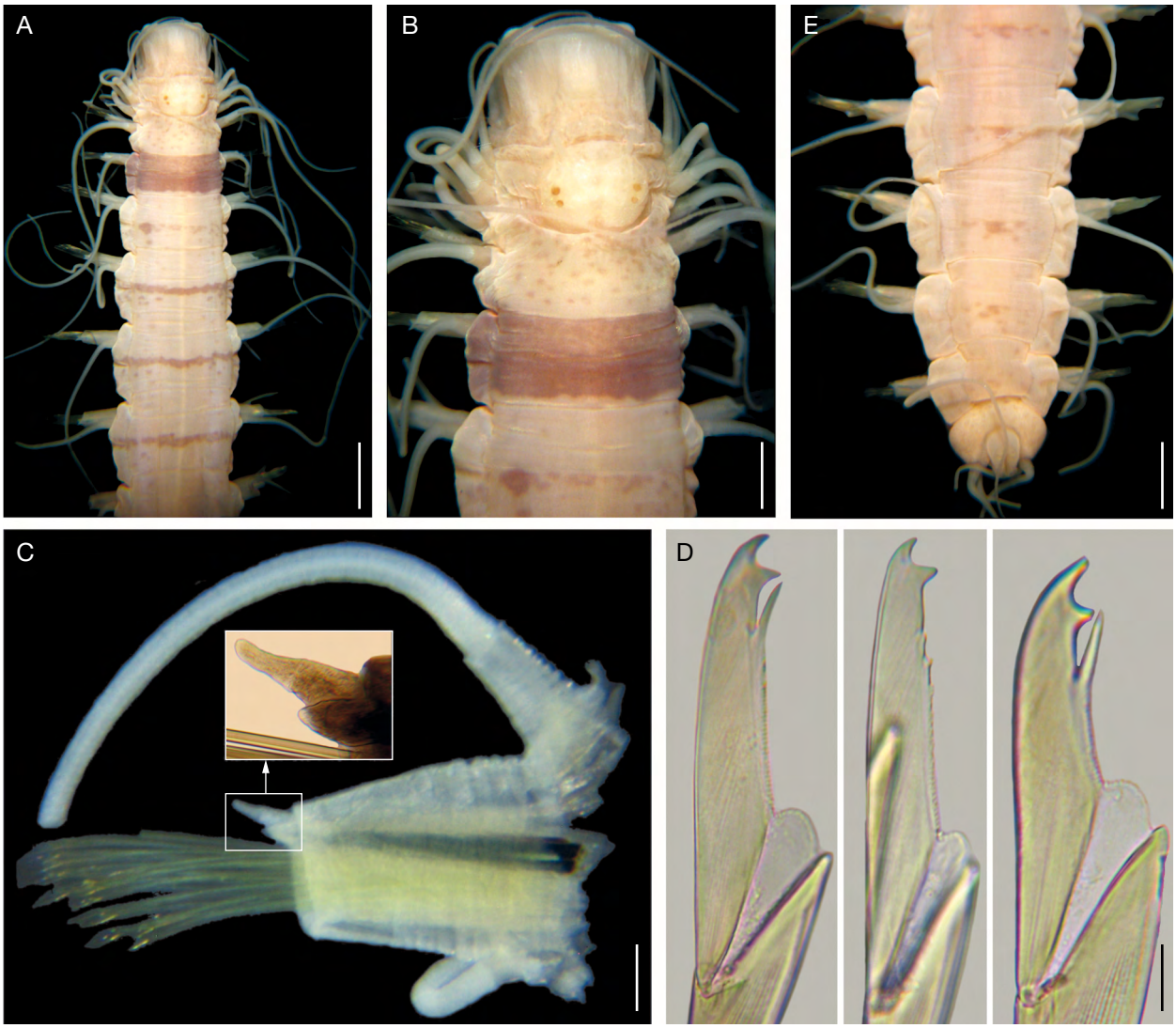

FIG. 37. — *Hesione paulayi* n. sp.: **A**, holotype, UF 32, anterior region, dorsal view; **B**, same, anterior end, dorsal view; **C**, paratype, UF 5845, chaetiger 8, right parapodium anterior view (inset: acicular lobe); **D**, same, neurochaetal blades; **E**, holotype, posterior region, dorsal view. Scale bars: A, 1.5 mm; B, 0.7 mm; C, 0.2 mm; D, 20 µm; E, 1.3 mm.

4-8, progressively thinner and less defined; pharynx everted, basal ring with small brown spots; acicular lobe double, slightly notched subdistally, upper tine slightly longer than lower one; chaetal blades bidentate, subdistal tooth thicker than distal one, guard approaching subdistal tooth]. — 1 specimen, UF 1674, Guam Island, Guam, Tepungan Channel under road (13.4649, 144.6872; 13°27'53.6400"N, 144°41'13.9200"E), inflow channel, 0-2 m depth, 12.VI.2010, N. Evans, F. Michonneau, G. Paulay, A. Anker, T. Naruse & D. Uyeno coll. [42 mm long, 3.5 pmm wide, bent laterally, median right parapodia removed for molecular studies; one gonadal tip removed; pigmentation pattern fading off, a thick dark, transverse brown band on chaetiger 2, chaetigers 1 and 3 without dark bands, barely visible along chaetigers 4-6, following segments pale; eyes almost depigmented, anterior ones twice as large as posterior ones; antennae longer than interocular distance; acicular lobe double, contracted, blunt, upper tine larger, slightly capitate, lower one rounded; neurochaetal blades medium-sized or short, bidentate, subdistal tooth wider than distal one, guard reaching subdistal tooth].

Indonesia. Banda Islands. 1 specimen, RMNH V427, May, 1921, van der Velde coll. [33 mm long, 5.5 mm wide; slightly distorted, many chaetae broken; a thick brownish transverse band on chaetiger 2, no band on chaetigers 1 and 3, other segments with thinner, barely pigmented bands; antennae tapered, 4-5 times as long as wide; eyes colorless; acicular lobe double; neurochaetal blades broken].

Australia. 1 specimen, AM 31859, Surgeons Reef, N off North West Solitary Island; 30°00'28.8"S, 153°16'12.94"E, coral rubble & coarse shelly sediment, 30.IV.2005, R. T. Springthorpe coll. [33 mm long, 3.7 mm wide, body wall broken, previously midventrally dissected along first 7 chaetigers; first band wider with irregular margins; neurochaetal blades bidentate, subdistal tooth as wide or wider than distal one; guard approaching subdistal tooth].

Coral Sea. 1 specimen, MNHN MUSORSTOM 10, Beffona Expedition, Sta. 10DE (21°24.3'S, 158°56.8'E), 52 m depth, 20.X.1985 [22 mm long, 2.5 mm wide; bent laterally, almost without pigmentation, only first band on chaetiger 2 barely visible; prostomium and most parapodial lobes invaginated; acicular lobe double, exposed in several chaetigers].

Hawaii. 2 specimens, USNM 5433, RV *Albatross*, Sta. 3876, Auau Channel, Maui Island, Lahaina, 3 m depth, 14.IV.1902 [16-21 mm long, 2 mm wide; juveniles; body slightly macerated, larger specimen regurgitated sediment, both with pharynx partially everted; antennae medium-sized, digitate, visible after methyl-green staining; chaetal lobes invaginated; pigmentation lost].

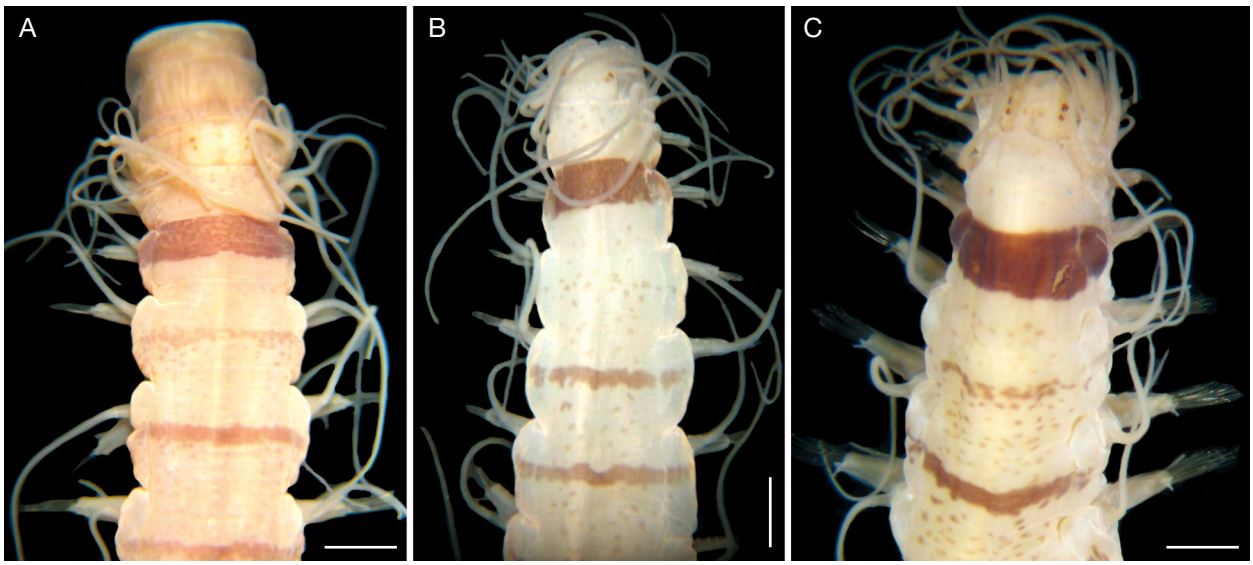

Fig. 38. — *Hesione paulayi* n. sp., anterior region of three different specimens, arranged in a progressive reduction of the discontinuous band in chaetiger 3: **A**, paratype, Papua New Guinea, UF 5845; **B**, non-type specimen, Society Islands, Moorea, UF 887; **C**, non-type specimen, Eastern Australia, AMNH 31859. Scale bars: A, 1.1 mm; B, 0.8 mm; C, 1.2 mm.

Etymology. — This species is named after Gustav Paulay, Curator of Malacology and Marine Invertebrates, Florida Museum of Natural History, University of Florida, Gainesville, in recognition of his efforts to sample and study tropical marine invertebrates all over the world, and because of his long-term sustained efforts to collect specimens of *Hesione*, including the type specimens. The name is a noun in genitive (ICZN 1999: art. 31.1.2).

Distribution. — Widely distributed along the tropical Western Pacific, including Hawaii, in shallow water, mixed bottoms; localities for the Paumotu (Tuamotu) Archipelago were adjusted after the compilation by Young (1899).

Diagnosis. — *Hesione* with prostomium laterally curved; parapodia with dorsal cirri basally cylindrical, dorsal cirrophore twice as long as wide; larger acicula blackish; acicular lobe double, tines digitate, upper one twice longer than lower one; neurochaetal blades bidentate, 3-4 times as long as wide; subdistal tooth as large as distal one, with guards approaching subdistal tooth.

Description

Holotype, UF 32, complete, tapered posteriorly. Pigmentation pattern including brownish, dorsal transverse bands and irregular spots; transverse bands better defined along anterior chaetigers but none in chaetiger 1, barely defined, discontinuous in chaetiger 3 (Fig. 37A); chaetiger 2 with a wide band, better defined, straight, along its anterior margin, posterior margin irregular, 3-4 times longer than band in chaetiger 4; following chaetigers with progressively less defined bands. Pigmentation extended into lateral cushions; tentacular cirri, dorsal cirri and neuropodial lobes whitish in ethanol. Body straight, 29 mm long, 3 mm wide.

Prostomium slightly as wide as long, anterior margin truncate, lateral margins rounded, posterior margin with a shallow notch, ⅓ as long as prostomium (Fig. 37B). Antennae digitate, 4-5 times as long as wide, or longer than interocular distance. Eyes brownish, anterior ones twice as large as posterior ones.

Tentacular cirri thin, some broken, others twisted, longest ones reaching chaetiger 5. Lateral cushions low, divided into 2-3 sections.

Parapodia (dissected from paratypes) with chaetal lobes tapered, truncate (Fig. 37C); dorsal cirri with cirrophores about twice as long as wide, cirrostyle basally cylindrical, smooth, articulated throughout most of its length, longer than body width (including parapodia); ventral cirri irregulary contracted, few complete, reaching chaetal tips.

Neuraciculae blackish, two very thick, and one additional thinner, paler. Acicular lobe double, tapered, capitate, at least upper tine, lower tine thicker, tapered, size variable, up to twice as long as lower one (Fig. 37C [inset]).

Neurochaetae about 20 per bundle, blades bidentate, 3-4 times as long as wide; blades aligned at a certain angle from handle, teeth of similar length, subdistal tooth usually wider, guard thick, approaching subdistal tooth (Fig. 37D).

Posterior region tapered into a blunt cone (Fig. 37E); pygidium rugose, anus with seven low, blunt triangular papillae.

Pharynx partially exposed, dorsal papilla not seen. Oocytes not seen.

Pigmentation

Preserved specimens with long-lasting distinct pigmentation pattern: first chaetiger pale or with scattered roundish spots. Second chaetiger with a distinct transverse, wide band. Chaetiger 3 with a subcontinuous thinner band, sometimes replaced by scattered roundish spots, or by irregular spots (Fig. 38A-C).

Remarks

As indicated above, *Hesione paulayi* n. sp. belongs to the group with long-lasting pigmentation, including transverse brownish bands, together with *H. genetta* Grube, 1867 restricted, and

H. mooreae n. sp. As indicated in the key below, *H. genetta* has its larger transverse band in chaetiger 1, whereas both *H. paulayi* n. sp. and *H. mooreae* n. sp. have them on chaetiger 2. These two latter species have three main differences; in *H. paulayi* n. sp. the upper acicular lobe is tapered, the posterior margin of its largest band is not well-defined, and the longest tentacular cirri reach chaetiger 6, whereas in *H. mooreae* n. sp. the upper acicular lobe is digitate, the posterior margin of the largest band is as well defined as its anterior margin, and its longest tentacular cirri reach chaetiger 8.

As indicated in the remarks for *H. genetta* Grube, 1867 there are at least three similar, long-lasting pigmentation patterns, both having a variable number of purple to brownish circular spots per segment, sometimes middorsally grouped into larger irregular bands. However, in *H. paulayi* n. sp. transverse bands are better defined, usually with a larger darker band over chaetiger 2, but no bands over chaetigers 1 and 3 (sometimes an irregular, discontinuous thin line can be present), whereas in *H. genetta* transverse bands are present on chaetigers 1 and 3, and sometimes an ill-defined band, or none at all on chaetiger 2. Further, in *H. paulayi* n. sp. the upper tines of acicular lobes are usually larger, digitate to capitate. These features are consistently different and specimens with these pigmentation patterns turned out separately in their COI-sequences.

Hesione picta Müller, 1858
(Figs 39-42)

Hesione picta Müller, 1858: 213, 214, pl. 6, fig. 3. — Fauvel 1953d: 7. — Hartman 1951: 35. — Jones 1962: 180. — Nonato & Luna 1970: 67, fig. 9. — Nonato & Amaral 1979: 49, fig. 100 (same fig. as in Nonato & Luna, 1970). — Fauchald 1977b: 16, 17. — Rullier & Amoureux 1979: 159. — Dueñas 1980: 86, pl. 5, figs A-D. — Ibarzábal 1988: 3, 4, fig. 2. — San Martín & Gómez Esteban 1992: 104.

Hesione proctochona Schmarda, 1861: 79, 80, pl. 28, fig. 226, plus one unnumb. textfig. — Treadwell 1902: 184; 1928: 473; 1939: 217, 218, fig. 45A-B. — Hoagland 1919: 571 — Horst 1922: 200, 201. — Augener 1927b: 49; 1933b: 224.

Fallacia proctochona – Quatrefages 1866: 99. — Webster 1884: 311, pl. 8, fig. 21.

Hesione margaritae Hansen, 1882: 6, pl. 1, figs 18-22.

Hesione vittigera Ehlers, 1887: 143-147, pl. 41, figs 1-4. — Hartman 1938: 6.

Hesione splendida – da Costa 2013: 30-41, figs 1, 3-5 (*non* Savigny *in* Lamarck, 1818).

TYPE MATERIAL. — **Brazil, Florianópolis.** Neotype, ZMB 3815, and one specimen labelled paraneotype, ZMB 3815p, Grube Collection, Desterro (*olim* Santha Catharina Island, now Florianópolis), no further data, F. Müller coll. [paraneotype 36 mm long, 5 mm wide, slightly swollen medially, tapered towards both body ends, some parapodia previously removed and preserved as permanent slides; body grayish, without pigmentation in ethanol; prostomium as long as wide, subpentagonal, projected anteriorly into a round lobe; antennae digitate, 3 times as long as wide; eyes brownish, anterior eyes slightly larger than posterior ones; dorsal cirrophore 2-3 times as long as wide; cirrostyle basally smooth, cylindrical, annulated medially, articulated distally; neuraciculae black, tapered; acicular lobe double, upper tine digitate about 4 as times long as wide, lower tine rounded, bifid, about half as long as upper tine; neurochaetae about 20 per bundle, blades bidentate, subdistal tooth variable, usually smaller than distal one, guard approaching distal tooth, usually broken; posterior end tapered, pygidium granulose; anus open with 7 rounded anal papilla, three superior, smaller, and four laterals, larger].
Brazil, Rio de Janeiro. Four syntypes of *Hesione margaritae* Hansen, 1882, RMNH 1275, 1872 (*fide* de Bont 2008), no further data, E. van Beneden coll. [18-34 mm long, 3-6 mm wide; slightly distorted by pressing them in small container; many cirri lost, many chaetal blades broken, at least one parapodium removed per specimen; acicular lobe double, blunt, upper tine twice longer than lower one, better developed in larger specimens; neurochaetal blades bidentate, guard approaching distal tooth].
Gulf of Mexico, Florida. Four syntypes of *Hesione vittigera* Ehlers, 1887, MCZ 837, RV *Blake*, Sta. unnumb., Key West, 2-4 m depth, A. Agassiz coll. [15-26 mm long, 3-4 mm wide; macerated, most chaetal blades lost; body pale, largest syntype depressed, probably for observation; pharynx barely exposed; eyes almost colorless, anterior ones slightly larger than posterior ones; acicular lobe double, digitate, upper tine about twice longer than lower one but in smaller syntypes upper one 3-4 times longer than lower one; pygidium broken with 7 marginal, short digitate anal papillae].

ADDITIONAL MATERIAL. — **Brazil.** 1 specimen, LACM 8581, juvenile, Ilha do Mel, Paranagua Bay, Parana, rocks, 30 m depth, 15.VIII.1998, G. Rouse, F. Pleijel & A. Nygren coll. [11 mm long, 2 mm wide; pigmentation lost; eyes barely pigmented; acicular lobe double, only one tine visible over chaetal lobe margin]. — 2 specimens, MNHN-IA-PNT101a (formerly jar 888a), RV *Calypso*, Sta. 17 (03°48'35"S, 33°24'50"W), 52 m depth, 18.XI.1961 [20-22 mm long, 4 mm wide; macerated, colorless; neuraciculae tapered, largest one black, smallest one brownish; acicular lobe double, blunt, upper tine digitate, four times longer than lower one; neurochaetal blades about 20 per bundle, blades bidentate, distal tooth larger, guard approaching distal tooth]. — 1 specimen, MNHN-IA-PNT101b (formerly jar 888b), RV *Calypso*, Sta. 19 (03°49.7'S, 32°26.0'W), 31 m depth, sand, 18.XI.1961 [dried out, probably under coverslip]. — 1 specimen, NHMW unnumb., Desterro (Florianópolis), F. Müller coll., no further data (39 mm long, 6 mm wide; macerated, pigmentation lost, eyes colorless, after methyl-green staining anterior ones twice as large as posterior ones; neuraciculae blackish tapered; acicular lobe double, upper tine slightly longer; about 30 neurochaetae but handles damaged, distorted by dissolution or other chemical damage, no blades left; body depressed, progressively wider up to chaetiger 14; without chaetal features it cannot be proposed as a neotype). — 1 specimen, ZMUC 2424, Rio de Janeiro, van Benyon coll., no further data [23 mm long, 3 mm wide; colorless, sligthly bent backwards, most cirri and neurochaetal blades lost; some parapodia previously removed; acicular lobe double, blunt, upper tine 2-3 times longer than lower one].
Northwestern Atlantic. Virginia. 1 specimen, LACM 10163, collected near Washington, D.C., 9.I.1938, O. Hartman coll. [35 mm long, 3.5 mm wide; splendid, perfectly relaxed specimen; eyes barely pigmented; chaetal lobes slightly invaginated; acicular lobe double, upper tine longer, tapered, lower tine blunt; neurochaetal blades medium-sized or short, bidentate, guard approaching distal tooth; Hartman indicated its pigmentation resembled the one given for *H. vittigera* Ehlers, 1887].
Gulf of Mexico. Florida, United States. 1 specimen, UF 685, Palm Beach Co., Peanut Island (26.7, -80.03; 26°42'00.0000"N, 080°01'48.0000"W), fixed dead, but on ice, 0-2 m depth, 4.III.2008, G.Paulay coll. [28 mm long, 4 mm wide; pigmentation visible as thick pale brown bands transversely separated by whitish lines into

6-8 narrow bands; posterior end regenerated, bent posteriorly; antennae minute; anterior eyes slightly larger and darker than posterior ones; most tentacular and dorsal cirri lost; dorsal cirri with cirrophores 3 times as long as wide; cirrostyle cylindrical basally, smooth (cells arranged into longitudinal lines); chaetal lobe slightly tapered; acicular lobe double, digitate, upper tine about twice longer than lower one; blades of chaetigers 3, 7, and 9 progressively smaller, teeth lateral; subdistal tooth smaller; guards mostly broken, some reaching distal tooth]. — 1 specimen, UF 825, Tampa Bay, 3 km E of Sunshine Skyway Bridge (27.631, –82.628; 27°37'51.6000"N, 082°37'40.8000"W), 8-9 m depth, 6.II.2009, G. Paulay coll. [18 mm long, 2 mm wide; acicular lobe double, blunt, upper one twice as long as lower one; pharynx not exposed; blades of chaetigers 3, 7, and 9 progressively smaller, teeth lateral; 4-8: 1 in chaetiger 3, 3-6: 1 in chaetiger 7 and 3-5: 1 in chaetiger 9]. — 1 specimen, UF 826, Tampa Bay, 3 km E of Sunshine Skyway Bridge (27.631, –82.628; 27°37'51.6000"N, 082°37'40.8000"W), 8-9 m depth, 6.II.2009, G. Paulay coll. [26 mm long, 4 mm wide; pigmentation fading out, darker along anterior chaetigers; posterior region distorted by dissection and muscular anterior enteron exposed; longest tentacular cirri reaching chaetiger 5; dorsal cirri as long as body width (excluding parapodia); blades of chaetigers 3, 7, and 9 progressively smaller, teeth lateral; 5-8: 1 in chaetiger 3, 3-5: 1 in chaetigers 7 and 9]. — 1 specimen, UF 1590, Dade County, Biscayne Bay National Park, Elliott Key (25.4517, -80.1972; 25°27'06.1200"N, 080°11'49.9200"W), bay side off jetty, 30.IV.2010, F. Michonneau, G. Paulay, S. McPherson, M. Bemis, H. Lin, J. Moore & N. Evans coll. [34 mm long, 5 mm wide; slightly distorted, body wall dissected for molecular studies; gonads partially exposed; dorsal transverse brownish bands separated into 6-8 thinner bands by whitish lines; acicular lobe double, upper tine about twice as long as lower one; body]. — 1 specimen, UF 1591, Monroe County, Florida Keys, Tennessee Reef (24.7651, -80.7542; 24°45'54.3600"N, 080°45'15.1200"W), 6 m depth, 3.V.2010, F. Michonneau, G. Paulay, S. McPherson, M. Bemis, H. Lin, J. Moore & N. Evans coll. (18 mm long, 2.5 mm wide; pharynx not exposed; pigmentation pattern still visible]. — 1 specimen, UF 1593, Dade County, Biscayne Bay National Park, Elliott Key, bay side off jetty (25.4517, -80.1972; 25°27'06.1200"N, 080°11'49.9200"W), 30.IV.2010, F. Michonneau, G. Paulay, S. McPherson, M. Bemis, H. Lin, J. Moore & N. Evans coll. (32 mm long, 4 mm wide; pigmentation pattern visible; transverse white band complete only in chaetigers 2 and 16, chaetigers 3-6 with a middorsal spot, following ones with bands extended along the whole dorsal segmental surface, 6-8 per segment; body distorted by two lateral dissections to remove parapodia for molecular studies; one complete *Harmothoe* sp. in its stomach; blades of chaetigers 3, 7, and 9 progressively smaller, teeth lateral; 3-8: 1 in chaetiger 3, 3-5: 1 in chaetiger 7 and 3-4: 1 in chaetiger 9]. — 1 specimen, UF 1594, Monroe County, Florida Keys, Long Key, LONF1 tower dive site, W of Florida Keys Marine Laboratory (24.843, -80.862; 24°50'34.8000"N, 080°51'43.2000"W), 2 m depth, 2.V.2010, F. Michonneau, G. Paulay, S. McPherson, M. Bemis, H. Lin, J. Moore & N. Evans coll. (28 mm long, 5 mm wide; body wall originally dissected for molecular studies; stomach and ovaries partially exposed (photos), now opened ventrally for study of digestive caeca (one copepod inside one of the caeca: given to E. Suárez); dorsal transverse brownish bands separated into 6-8 thinner bands by whitish lines; body; oocytes about 100 µm]. — 2 specimens, ECOSUR 2913, 800 m SSW off Alligator Reef Light, 5-7 m depth, 30.IV.1960, WA Starck, T. Starck & HA Feddern coll. [28-29 mm long, 4.0-5.5 mm wide; larger specimen fusiform, not subcylindrical; no pigmentation; pharynx papilla as long as wide; dorsal cirri smooth; acicular lobe double, digitate, most with one lobe larger than the other]. — 1 specimen, LACM 10164, Thornton Island, near Englewood, Florida, in crevices, 15.I.1938, O. Hartman coll. (22 mm long, 3 mm wide; juvenile, body posterior region laterally collapsed in vial; antennae minute].

Veracruz, México. 1 specimen, UANL 3988, Bajo La Galleguilla, 4.XI.1992, J. A. de León-González coll. [without pigmentation; antennae minute; pharynx invaginated; dorsal cirri smooth basally; acicular lobes double, of about the same length; anal cirri low, blunt; body 29 mm long, 4 mm wide]. — 1 specimen, UANL 4119, La Galleguita, 9.VIII.1999, J. A. de León-González coll. [29 mm long, 3 mm wide; prostomium posteriorly covered by tentacular segment, no pigmentation; antennae minute; pharynx invaginated nuchal organs connected middorsally, only the posterior depression visible; acicular lobe double, both truncate triangular, upper one 1.2 times longer than lower one]. — 1 specimen, UANL 4120, Isla Sacrificios, 11.VIII.1999, J. A. de León-González coll. [25 mm long, 4 mm wide; macerated, no pigmentation, probably dead before fixation; prostomium fully exposed, nuchal organs connected middorsally; antennae minute; pharynx invaginated; most cirri and chaetal blades lost; acicular lobe double, both digitate, upper one longer than lower one].

Campeche, México. 1 specimen, ECOSUR 2914, Laguna de Términos, Sta. 27A, July, 1984, E. Escobar coll. [40 mm long, 4.5 mm wide; no pigmentation; antennae minute; pharynx papilla not seen; dorsal cirri smooth basally; acicular lobes double, of about the same length; anal cirri low, blunt]. — 1 specimen, ECOSUR 2915, Champotón, 1 km S of river mouth, 4 m depth, rock, 16.II.1999, J. R. Bastida & SISV coll. [20 mm long, 3 mm wide, slightly distorted; no antennae; pharynx everted; dorsal cirri multiarticulated; acicular lobes double, upper tine digitate, longer, lower tine blunt, shorter; pygidium granulose, slightly smashed, anal cirri blunt, short, barely seen]. — 1 specimen, UANL 127, Isla Pérez, 7.VII.1977, U. Garza coll. [34 mm long, 4 mm wide; partly dehydrated, without pigmentation; dorsal cirri basally smooth; acicular lobe double, of about the same length; most cirri and chaetal blades lost; prepygidial segment granulose; anus projected with blunt cirri, 6 upper, shorter, two lower wider].

Yucatán, México. 1 specimen, ECOSUR 2916, Celestún, 1 m depth, 17.II.1991, SISV coll. [12.5 mm long, 2.5 mm wide; juvenile, pharynx invaginated; dorsal cirri basally smooth, medially and distally multiarticulated; acicular lobes double digitate, upper lobe twice as long as lower one]. — 1 specimen, ECOSUR OH-486, San Felipe, 500 m W off lagoon's mouth, 2 m depth, 10.VI.2009, L. F. Carrera-Parra & SISV coll. [36 mm long, 4 mm wide; pharynx not exposed, some pigmentation left 7 years after collection, chaetal lobes slightly invaginated]. — 1 specimen, ECOSUR 2917, Ría Lagartos, 1 km E of channel mouth, 2 m depth, rock, 18.II.1999, J. R. Bastida & SISV coll. [24 mm long, 3 mm wide, chaetigers; no antennae; dorsal cirri multiarticulated; acicular lobes double, one digitate longer, the other blunt, shorter; anal cirri not seen].

Quintana Roo, México. 1 specimen, ECOSUR 2918, Holbox, in seagrasses, 1 m depth, 4.V.2000, C. Campos coll. [17 mm long, 2.5 mm wide; pharynx everted, dorsal papilla slightly as long as wide; dorsal cirri multi-annulated; acicular lobes double, one digitate, longer, the other blunt, rounded; anal cirri not projected]. — 1 specimen, ECOSUR OH-468, Cabo Catoche, 800 m N off Lighthouse, 10.VI.2009, 4 m depth, L. F. Carrera-Parra & SISV coll. [35 mm long, 4 mm wide; pigmentation still visible].

Caribbean Sea. México. 1 specimen, ECOSUR OH-371, under coral rock, 2 m depth, 30.VIII.2004, L. F. Carrera-Parra coll. (21.5 mm long, 3 mm wide; no pigmentation; body incurved; eyes dark brown, anterior ones slightly larger than posterior ones; acicular lobes double, upper tine digitate, longer, lower one shorter, rounded to digitate].

West Indies. Undefined locality. 1 specimen, ZMUC 2430, 1860, Marboc coll., no further data [38 mm long, 6 mm wide; body macerated, pharynx partially exposed; chaetal lobes invaginated; acicular lobe double, blunt, upper tine larger, 2-3 times larger than lower one].

Puerto Rico. 5 specimens, MCZ 46504, La Parguera, 25.I.1971, L. S. Roberts coll. (25-36 mm long, 3 mm wide; slightly dehydrated; prostomium projected anteriorly into a blunt, tapered lobe; eyes of similar size, anterior ones slightly more separated; pharynx not exposed; dorsal cirri basally smooth; acicular lobe

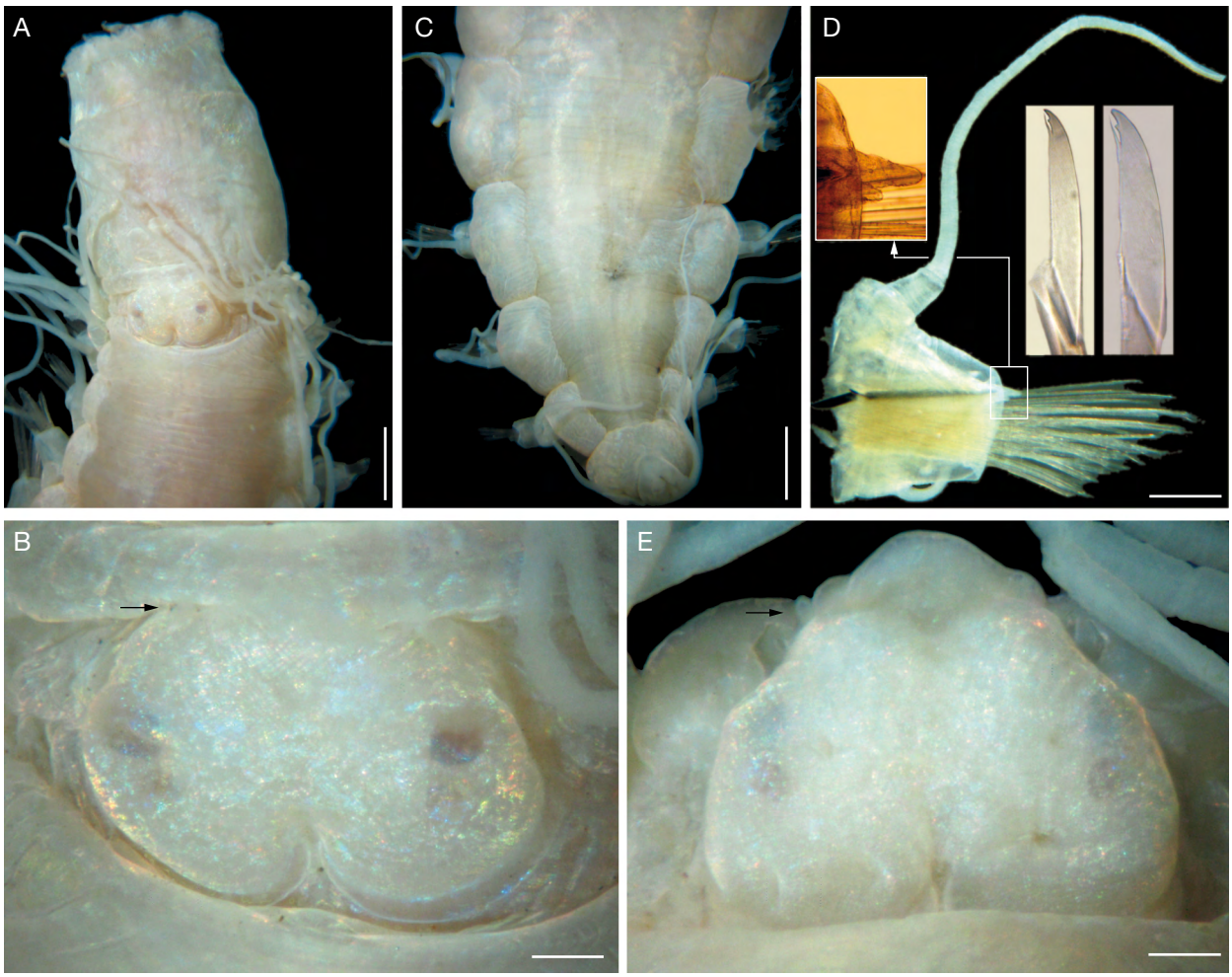

FIG. 39. — *Hesione picta* Müller, 1858, neotype, ZMB 3815: **A**, anterior end, dorsal view; **B**, head, close up (arrow points to left antenna); **C**, posterior end, dorsal view; **D**, chaetiger 10, left parapodium, anterior view (insets: acicular lobe, and long and short neurochaetal blades); **E**, specimen ZMB 3815b, head, close-up (arrow points to left antenna). Scale bars: A, 1.5 mm; B, 0.3 mm; C, 1.7 mm; D, 0.7 mm; E, 0.2 mm.

double, upper tine digitate, lower tine rounded to triangular, ¼ to ⅔ as long as upper one; neurochaetal blades long and short, guard reaching distal tooth; pygidium granulose, with 4-7 short, thick digitate anal cirri]. — 6 specimens, USNM 15972, RV *Fish Hawk*, Sta. unnumb., Port Real, 1898 [juveniles, 8-17 mm long, 1.5-2.0 mm wide; one with pharynx exposed; partly dehydrated, most chaetae broken]. — 1 specimen, ZMH-P 1295, Ponce, Dr Bock coll., no further data [18 mm long, 3 mm wide; dorsum darker but without transverse dark bands; antennae digitate, tiny, twice as long as wide; eyes brownish, anterior ones slightly larger than posterior ones; acicular lobes double but chaetigers 14-16 with lower tine barely visible, blunt, digitate, upper tine often twice longer then lower one].

Haiti. 1 specimen, ZMH-P 1292b, Port au Prince, Kepperschmidt coll. No further data (42 mm long, 5 mm wide; bent laterally, without pigmentation; acicular lobe double, digitate, of similar size]. — 5 specimens, ZMH-P 2887, Port au Prince, A. Gagzo coll., no further data [18-21 mm long, 2.5-4.0 mm wide; colorless, two bent ventrally, two others with pharynx exposed, dorsal papilla rounded, as long as wide; body anterior eyes slightly larger or up to twice larger than posterior eyes; antennae minute, digitate, 3-4 times as long as wide, or about as long as posterior eyes diameter; longest tentacular cirri reaching chaetiger 7; dorsal cirri as long as body width (excluding parapodia); acicular lobe double, digitate, upper tine twice as long as lower one].

Jamaica. 5 specimens, BMNH 1912.2.2.18/22, Duerden coll., no further data [23-58 mm long, 4-8 mm wide; colorless, variably distorted; two large specimens with a ventral dissection through chaetigers 1-14 (or 16); antennae 3-4 times as long as wide; eyes almost colorless, anterior ones slightly larger than posterior ones; acicular lobe double; most chaetae without blades; pharynx exposed in one specimen, dorsal papilla slightly as long as wide]. — 1 specimen, ZMB 6313, Kingston, Kükenthal & Hartmeyer [23 mm long, 4 mm wide; partially dehydrated, some cirri lost; pharynx slightly exposed; prostomium projected anteriorly; antennae minute, slightly as long as wide; eyes brownish, anterior ones slightly larger than posterior ones; dorsal cirri partially dehydrated; dorsal cirrophore twice as long as wide; neuraciculae blackish, tapered; acicular lobe double, blunt, upper tine slightly longer than lower one; about 20 neurochaetae per bundle; blades bidentate, guard approaching distal tooth]. — 1 specimen, ZMH-P 6752, Kingston, 4.VI.1905, O. Gagzo coll. [32 mm long, 3.5 mm wide; complete, bent dorsally, eyes colorless, anterior lenses twice as large as posterior ones; antennae minute, about twice as long as wide; acicular lobe double, digitate, blunt, lower tine slightly smaller than upper tine; most neurochaetal blades lost]. — 1 specimen, ZMH-P 9043, Kingston, Hartmeyer & Kükenthal coll., identified by Augener, no further data [complete, bent dorsally; dorsum brownish, lateral cushions pale; eyes brownish, of similar size; antennae minute, digitate, about twice as long as wide; acicular lobe double; many chaetae broken, many neurochaetal blades lost].

Virgin Islands. 1 specimen, LACM LHarrisJul2000, Beef Island, Trellis Bay, coral rubble, 1-2 m depth, 12.VII.2000, G. Hendler, J. Martin, K. Fitzhugh & R. Ware coll. [36 mm long, 3 mm wide, splendid specimen; some neurochaetae without blades; body pale, laterally contracted; antennae not visible; anterior eyes slightly larger than posterior ones; anterior margin slightly projected, lateral margins rounded, posterior margins with a deep furrow, running close to the posterior eyes; dorsal cirri smooth basally, annulated medially, multiarticulated distally; chaetal lobe truncate; acicular lobe double, upper tine slightly longer than inferior one; ventral cirri surpassing chaetal lobe; neurochaetal blades medium-sized to short, bidentate, guards broken; pygidium granulose, anus projected, with six anal papillae, short, rounded]. — 1 specimen, UF 670, St John Island, T-kai (18.339097, -64.676144; 18°20'20.7492"N, -064°40'34.1184"W), 0.5-6.0 m depth, 30.XI.2002, V. Bonito coll. [18 mm long, 3 mm wide; a dark brown spot in posterior surfaces of parapodial bases from chaetiger 9, not visible in anterior chaetigers; acicular lobes double, blunt, upper tine twice as long as lower one].
Saint-Thomas. 2 specimens, ZMUC 2428, 1860, Krebs coll., no further data [15-34 mm long, 3.0-4.5 mm wide; body damaged, colorless, most cirri and chaetal blades lost, larger specimen distorted, acicular lobe double, blunt, upper tine larger than lower one]. — 2 specimens, ZMUC 2429, 1860, Krebs coll., no further data [26-31 mm long, 3-6 mm wide; larger one in better condition, smaller one macerated; colorless, without most cirri and chaetal blades, larger one distorted, acicular lobe double, blunt, upper tine 1-2 times longer than lower one]. — 5 specimens, ZMUC 2431, coral, no further data [32-34 mm long, 3.5-4.0 mm wide; macerated, chaetal lobes invaginated, cirri and neurochaetal blades variably lost; acicular lobe double, upper tine 2-3 times longer than lower one]. — 3 specimens, ZMH-P 5457, C. Calwood coll., no further data [26-29 mm long, 3.0-3.5 mm wide; partially dehydrated, colorless, one bent dorsally, another one laterally; acicular lobe double, upper tine and lower tine of similar size, or upper tine larger, up to twice as large as lower one].
Saint-Martin. 1 specimen, UF 2679, Creole Rock (18.118, -63.056; 18°07'04.8000"N, 063°03'21.6000"W), 3-10 m depth, 18.IV.2012, G. Paulay, J. Slapcinsky, M. Bernis, F. Michonneau, A. Anker, J.-P. Marechal coll. [36 mm long, 4 mm wide; pigmentation pattern clearly defined; mature female, oocytes released through body wall cut, about 100 µm in diameter each].
Panama. 1 specimen, UF 1176, Bocas del Toro, Isla Bastimentos, Salt Creek, 1-2 m depth, A. Anker coll. [35 mm long, 4 mm wide, 16 chaetigers; mature, bent ventrally, pigmentation pattern fading off, visible only along anterior 9 chaetigers; a dark brown spot in the basis of all parapodia; oocytes about 100 µm in diameter]. — 1 specimen, USNM 61643, Galeta Reef, Colón, *Acanthophora* zone, 8.VIII.1972, A. Reimer coll. [24 mm long, 2 mm wide; body without pigmentation; distorted, laterally contracted, anterior prostomial margin truncate; anterior eyes slightly larger than posterior ones; acicular lobe double, blunt, upper tine longer; neurochaetal blades bidentate, guard approaching distal tooth].
Colombia. 1 specimen, USNM 58277, Caño de Loro, Cartagena, rocky bottom, subtidal, X.1977, P. R. Dueñas coll. [24 mm long, 4 mm wide; most cirri on site; several neurochaetal blades lost; no pigmentation; prostomium barely projected forward; antennae minute, ovoid; eyes almost without pigmentation, anterior ones larger than posterior ones; neurochaetal blades bidenate, guard approaching distal tooth; pygidium granulose; anal tube collapsed, only ventral papillae visible, rounded, slightly as long as wide].
Venezuela. 1 specimen, ECOSUR 2919, E Margarita Island, Pilsbury Sta. 712 (11°09'N, 63°18'W), 26 m depth, 19.VII.1968 [32 mm long, 4 mm wide; no pigmentation; antennae tiny; pharynx papilla not visible; dorsal cirri multi-annulated; acicular lobes double, upper tine digitate, longer, lower tine blunt, shorter; anal cirri short, blunt, 5-6].
Curaçao. 1 specimen, RMNH 1276, 1920, van der Horst coll., no further data [35 mm long, 5 mm wide; complete, slightly distorted by pressing it in small container; colorless, eyes barely pigmented, anterior eyes larger than posterior ones; antennae minute, smashed over prostomial surface; acicular lobe double, digitate]. — 3 specimens, ZMH-P 10343, Spaansch Water, in *Porites fucata*, 7.IV.1920 (18.V.1920), van der Horst coll. [27-34 mm long, 4-5 mm wide; smaller one bent laterally, smaller and largest with pharynx exposed; acicular lobe double, digitate, upper tine up to twice as long as lower one; most neurochaetal blades lost].

Distribution. — Western Atlantic, from Virginia, United States to southern Brazil (Florianópolis), including the Gulf of Mexico and Caribbean Sea, in mixed bottoms, sea grasses, macroalgae, or rocks from the intertidal to 52 m depth; sometimes with other invertebrates as bryozoans, brittle-stars, and mussels (da Costa 2013: 41).

Diagnosis. — *Hesione* with prostomium laterally curved; parapodia with dorsal cirri basally cylindrical, dorsal cirrophore twice as long as wide; larger acicula blackish; acicular lobe double, tines long, digitate, upper tine twice longer than lower one; neurochaetal blades bidentate, 4-5 times as long as wide; subdistal tooth smaller; guards approaching distal tooth.

Description

Neotype, ZMB 3815, complete, pharynx fully exposed, without pigmentation pattern (Fig. 39A) in ethanol; most tentacular or dorsal cirri on site; left parapodium of chaetiger 10 removed for observation (kept in vial), right parapodia of chaetigers 10 and 13 previously removed, preserved in separate permanent slide. Body bent laterally, becoming wider posteriorly (widest about chaetigers 12-13), 36mm long, 5 mm wide.

Prostomium as wide as long, anterior margin truncate, lateral margins rounded, posterior margin deeply cleft, about as long as ¼ prostomial length, reaching about posterior eyes, without longitudinal depression (Fig. 39B; specimen labelled paraneotype with pharynx invaginated, prostomium anteriorly projected, antennae positioned slightly ventrolaterally, appearing smaller than diameter of posterior eyes, Fig. 39E). Antennae minute, digitate, directed laterally, twice as long as wide, as along as diameter of posterior eyes. Eyes brownish, anterior ones darker, twice larger than posterior ones.

Tentacular cirri long, variably twisted, longest ones reaching chaetiger 4 (right) or 6 (left) (reaching chaetiger 5 in syntypes of *H. margaritae*). Lateral cushions slightly projected, surface entire in first three and last three chaetigers, other ones divided into anterior and posterior sections.

Parapodia with chaetal lobes as long as wide, truncate; dorsal cirri with cirrophores about twice as long as wide; cirrostyle smooth, cylindrical basally, annulated medially, articulated distally, as long as body width (without parapodia). Ventral cirri smooth, surpassing chaetal lobes. Ventral cirri smooth, surpassing chaetal lobe tip, as long as chaetal lobe width (Figs 39D, 42F).

Neuraciculae blackish, single, tapered. Acicular lobe double, digitate, upper tine twice longer than ventral one.

Neurochaetae about 30 per bundle, blades bidentate, blades at a certain angle from handle, decreasing in size ventrally, 4-5 times as long as wide, each with usually smaller subdistal tooth, guard approaching distal tooth.

Posterior region tapered into a blunt cone; pygidium subspherical, surface granulate, anus projected (Fig. 39C), with

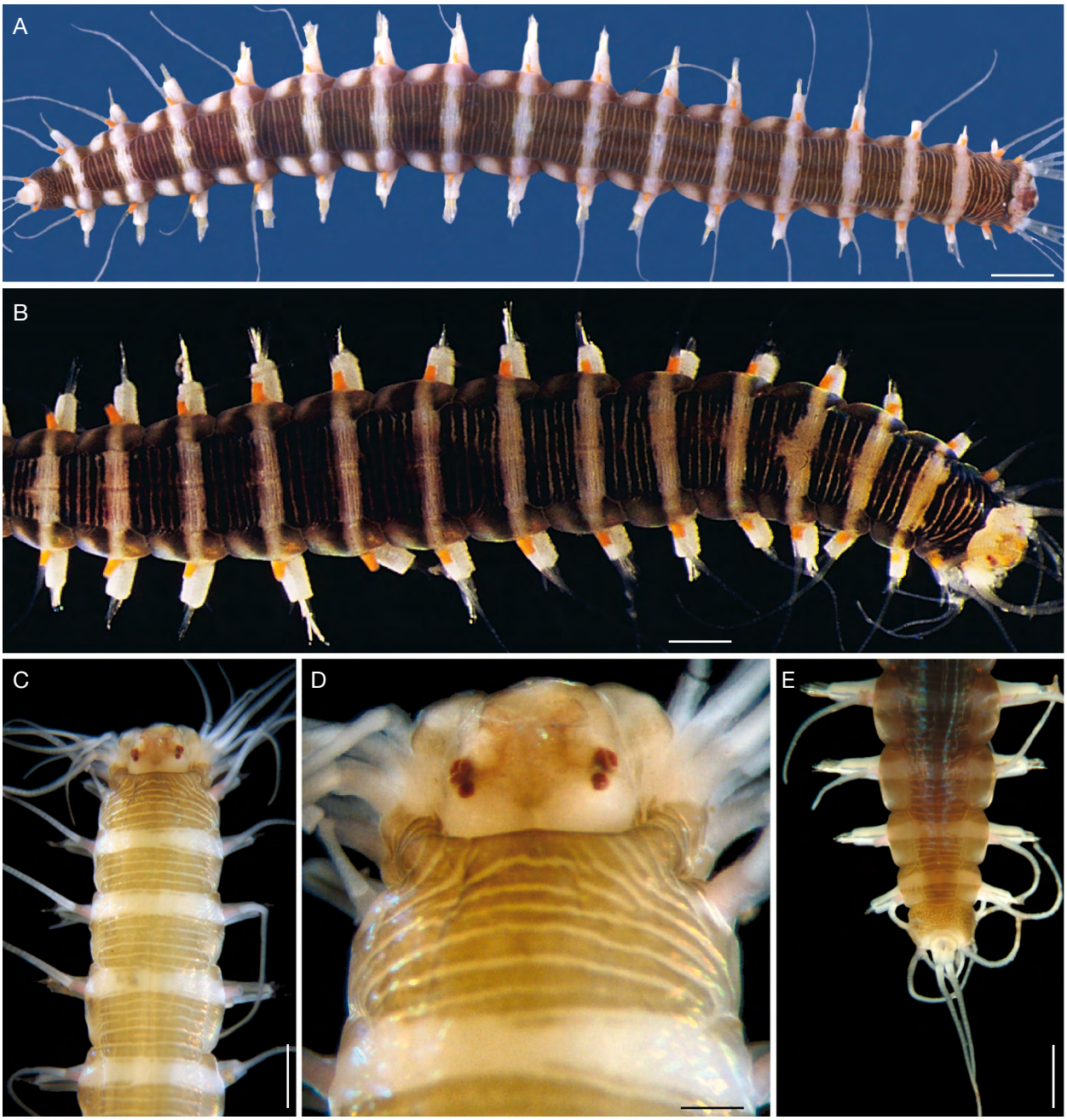

FIG. 40. — *Hesione picta* Müller, 1858, living specimens: **A**, Virgin Islands, LACM 10165, dorsal view; Brazil; **B**, Juvenile, LACM 8581, dorsal view, posterior region omitted; **C**, anterior end, dorsal view; **D**, head, dorsal view; **E**, posterior end, dorsal view. Scale bars: A, E, 1.3 mm; B, 0.8 mm; C, 2.4 mm; D, 1.7 mm (Photos: A, B, Leslie Harris; C-E, Vinicius da Rocha Miranda).

7 round, blunt papillae, four lateral, three dorsal (5-7 in syntypes of *H. margaritae*).

Pharynx fully exposed, with two muscular rings, anterior ring ⅓ as long as posterior one, with granulose margin; dorsal papilla rounded, twice as wide as long. Some oocytes within parapodia, about 100 µm in diameter.

Pigmentation

Body with transverse brown wide bands (Figs 40A-C, 41A). Each band with similar intensity throughout body, sometimes slightly darker along a wide middorsal region, especially along posterior segments (Figs 40C, 41B). Dark bands present along body, interrupted dorsally along chaetal lobes by a wide pale band (½-⅓ as long as dark bands, sometimes poorly defined as in Fig. 40B), missing in chaetiger 1, and in pygidium. Each band interrupted by 6-8 thin, pale transverse lines along a wide middorsal region, sometimes incomplete or fused to others, but dark bands continued over lateral cushions without being interrupted by pale transverse lines. This pigmentation pattern modified over anterior region as follow: prostomium with an inverted irregular pentagonal dark area, projected posteriorly beyond the level of posterior eyes, with

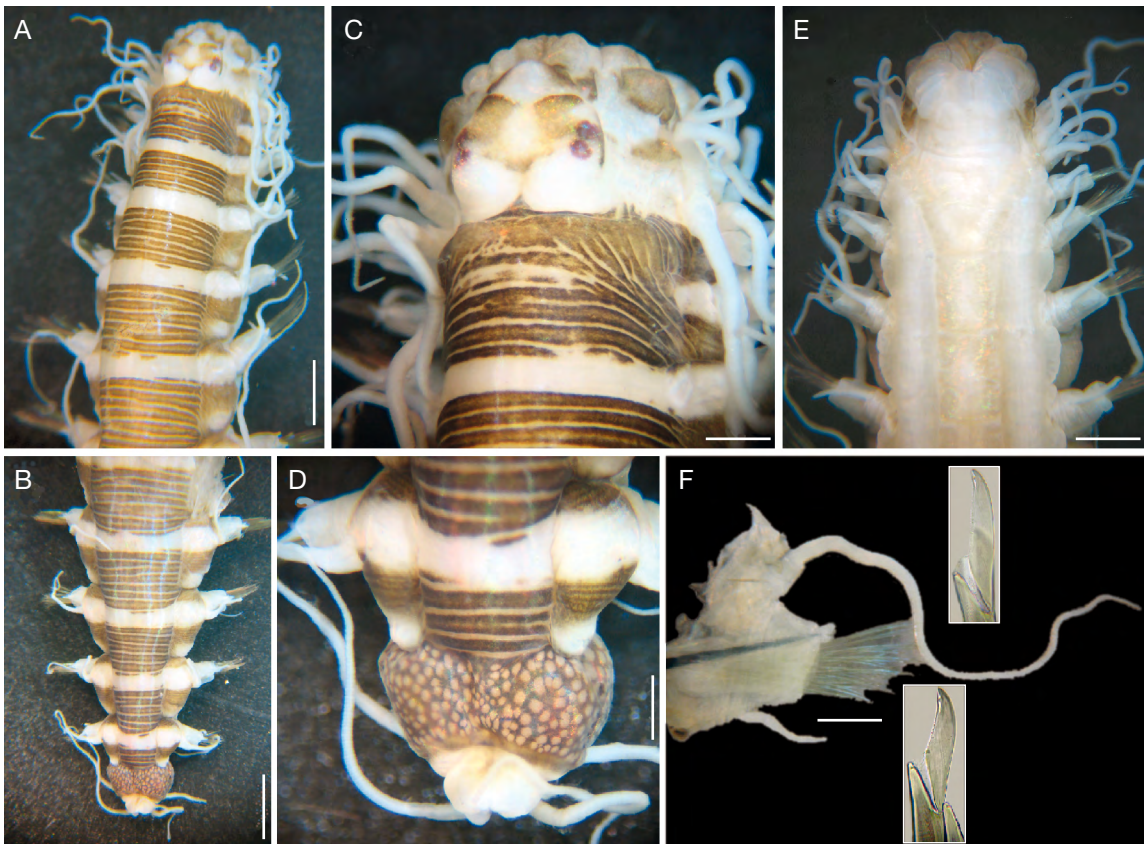

Fig. 41. — *Hesione picta* Müller, 1858, non-type specimen, ECOSUR OH 468: **A**, anterior region, dorsal view; **B**, posterior region, dorsal view; **C**, head, close-up, dorsal view; **D**, pygidium, close-up, dorsal view; **E**, anterior region, ventral view; **F**, chaetiger 8, left parapodium, anterior view (insets upper and lower neurochaetal blades). Scale bars: A, 1.5 mm; B, 2 mm; C, D, 0.6 mm; E, 1.1 mm; F, 0.7 mm.

paler areas ahead of anterior eyes, and over anterior middorsal prostomial surface, and projected laterally along peristomial dorsolateral surfaces (Fig. 41E). Tentacular segment and first chaetiger with several thin transverse pale lines but towards its anterior margin, lines becoming directed anteriorly, not middorsally connected. Eyes dark-brown to reddish, usually anterior eyes larger than posterior ones (Fig. 40C, D), but subequal also commonly found (Fig. 41C). In less than 10% of living specimens, pale transverse bands sometimes reduced to rounded middorsal spots (da Costa 2013: 39, fig. 5), or even disappearing completely. Pygidium with a wide band leaving a paler anal region (Fig. 40A, E, 41D).

Remarks

Hesione picta Müller, 1858, as indicated in the key below, is very similar to *H. reticulata* von Marenzeller, 1879. There are two main differences between them regarding their integument and pigmentation. In *H. picta* the dorsum is smooth, annulated without longitudinal striae, and living specimens have transverse dark brown bands, whereas in *H. reticulata* the back is rugose because there are longitudinal striae, and living specimens have a complex, reticulate pigmentation pattern.

Müller (1858) described *H. picta* from Santa Catharina Island (now Florianópolis), Brazil, but no specimens were deposited and no type specimen is listed in the museums where Grube used to deposit his material: Wroclaw, Poland (Viktor 1980), or Berlin, Germany (Hartwich 1993). Hartman (1951: 35) regarded *H. picta* as a valid species and included two other species as junior synonyms: *H. proctochona* Schmarda, 1861, and *H. vittigera* Ehlers, 1887 (she misspelled it as *vittata*). Later, Hartman (1959: 185) expanded the list of synonyms by including *H. praetexta* Ehlers, 1887, which was followed by Pleijel (1998: 159) who regarded it as a "possibly junior synonym of *H. picta* Müller, 1858". This latter species is regarded below as distinct, but the two other names are confirmed as junior synonyms.

The original description by Müller (1858) included a figure for the prostomium, and the description is very short but contains enough detail including the distinctive pigmentation pattern. In contrast, the description by Schmarda (1861) for *H. proctochona* is much more detailed and richly illustrated.

It must be taken into account that there are several differences regarding the shape of prostomium, presence of antennae and about the position and size of the eyes in the species currently regarded as synonyms. Müller (1858) described *H. picta* from Southern Brazil; the single illustration shows a prostomium slightly as wide as long, depressions along the anterior and posterior prostomial margins, no antennae, and four large eyes, all of similar size, placed towards the anterior prostomial surface. As indicated above,

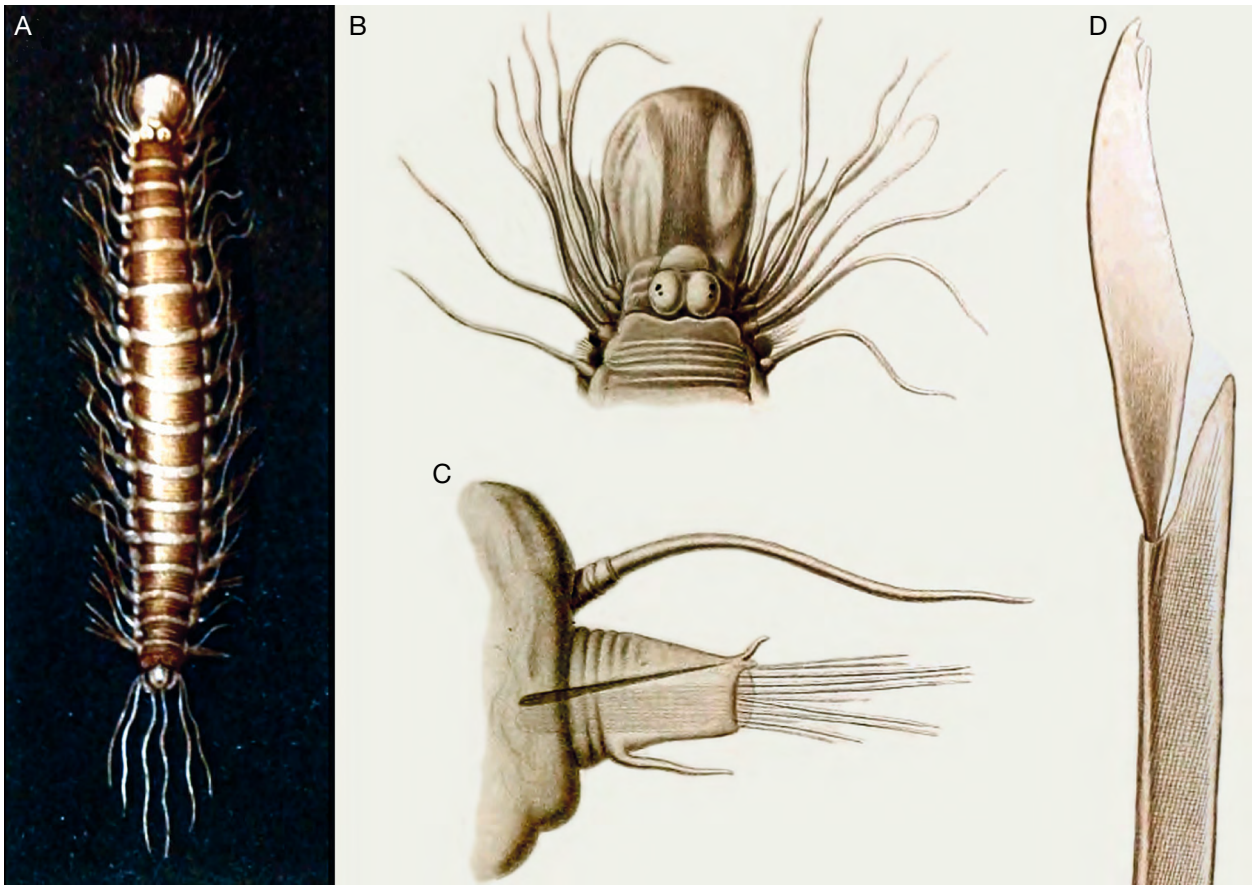

FIG. 42. — *Hesione picta* Müller, 1858: **A**, dorsal view; **B**, anterior end, dorsal view; **C**, parapodium from a middle-body segment, anterior view; **D**, same, close-up of neurochaetal tip; guard tip broken (modif. after Ehlers 1887, scale bars missing in original).

H. margaritae Hansen, 1882, has a transversely banded dorsum, and was described from Southern Brazil too, and Horst (1921: 80) regarded it as a junior synonym of *H. picta*; however, the original illustration indicates a prostomium as long as wide, its posterior margin is entire, antennae are shown as tiny projections, and the four large eyes are placed over the central prostomial region. These differences in prostomial shape might be explained by variations in pharynx eversion, whereas the size of eyes is not as constant and specimens from the same locality and date (see characteristics of materials) have eyes of similar or different size. Further, because pigmentation pattern and eye pigments fade off quite soon once specimens are preserved in alcohol, although eye pigments last longer, and because the prostomium can be modified depending on the contraction state of the specimen, or the degree of pharyngeal eversion, prostomial shape and eye size are informative but barely relevant as diagnostic features. The most detailed illustration for *H. picta* was made by Nonato & Luna (1970: fig. 9), with specimens from Northern Brazil, and their specimen shows several differences: the prostomium is slightly as long as wide, and there are furrows over its anterior and posterior margins, there are two minute antennae, and the anterior eyes are twice as large as posterior ones, being placed towards posterior prostomial surface. Other Brazilian specimens, resembling *H. picta*, were recorded as *H. splendida* by Costa *et al.* (2008), and their illustration shows a as wide as long prostomium with anterior and posterior furrows, antennae minute, and anterior eyes larger than posterior ones, placed over the medial prostomial surface. These differences do not warrant specific status and consequently *H. margaritae* is herein confirmed as another junior synonym of *H. picta*.

On the other hand, *H. vittigera* was separated from other similarly pigmented species such as *H. picta* Müller, 1858, *H. proctochona* Schmarda, 1861, and *H. margaritae* Hansen, 1882 because it was regarded as having only 15 chaetigers. However, the largest syntype (and the three other ones), which was probably used for the description since it lacks the right parapodium of chaetiger 1, has 16 chaetigers as any other member of the genus. In the first chaetiger the left parapodium has no chaetae remaining, and on the right side only one chaeta remains (now the body wall is transparent and neuraciculae are visible). All other illustrated features (herein reproduced as Figure 42), match the features shown in *H. picta* and the other species described from the Eastern Atlantic, such as overall pigmentation pattern (Fig. 42A) prostomial features (Fig. 42B), parapodia including the acicular lobe (Fig. 42C), and the size and dentition of blades. Another difference that Ehlers (1887: 147) regarded as diagnostic was the presence and number of anal cirri, and he stated none was visible in

his material; however, at least in the largest syntype, they are visible despite the poor state of the pygidial integument.

Augener (1934: 123) studied the type collection of Hansen. Augener could not find the type specimen for one species each from the families Amphinomidae, Aphroditidae, Chaetopteridae, Terebellidae and Hesionidae, including the type of *H. margaritae.* At least for the last species, it seems that it was overlooked because it was reidentified by Horst as *H. proctochona* (Horst 1922: 200), who also corrected the relative size, originally stated as up to 75 mm long, by indicating that it "likely is a mistake, for the largest specimen found by myself in the collection of van Beneden only has a length of 36 mm." Consequently, the Leiden specimens must be the syntypes that Augener could not find, and have been regarded as such above.

The original description of *H. vittigera* completely matches the description of *H. proctochona*, including the intense lead-oxyde (reddish orange) color of dorsal cirrophores that both Schmarda and Ehlers observed in freshly collected or living specimens. On the contrary, the specimens Hansen (1882: 6) saw had been about 10 years in ethanol before he studied them, such that he did not see the dark brown transverse bands and instead found that: "la surface dorsale des anneaux transversalement striée avec un éclat brunâtre" (Transl.: the dorsal surface of the segments transversely streaked by a brownish burst).

Because of the prevalining confusion, the neotype and specimen labelled paraneotype have been designated for *H. picta*. In full agreement with the *Code* (ICZN 1999: art. 75), this designation will clarify the taxonomic status of the species (art. 75.3.1), and the above description and remarks provide its diagnostic features together with a comparison with its junior synonyms (art. 75.3.2-3). A formal request for searching its type material was submitted to the curatorial staff in the museums of Berlin and Wroclaw, where most of Grube specimens were deposited, and none was found (art. 75.3.4). The neotype and pareneotype specimens were collected by Fritz Müller from the type locality (art. 75.3.5-6), and for selecting the neotype, the specimen with a round prostomial shape was preferred because it resembles what Müller illustrated (1858: pl. 6, fig. 3); these specimens might be the type material, but they were not designated as such.

Hesione praetexta Ehlers, 1887 reinstated
(Figs 43-46)

Hesione praetexta Ehlers, 1887: 147, pl. 41, figs 5, 6. — Hartman 1938: 6.

Hesione proctochona – Horst 1921: 80 (*non* Schmarda, 1861).

Hesione picta? – Uebelacker 1984: 28.36-28.38, fig. 28.34 (*non* Müller, 1858).

TYPE MATERIAL. — **Gulf of Mexico, Florida.** Two syntypes, MCZ 762, Dry Tortugas, RV *Albatross*, Sta. 11 (24°43'N, 83°25'W), 67 m depth, 14.XII.1877 [syntypes 18-19 mm long, 3.0-3.3 mm wide; in poor condition, dried-out, most chaetae broken or without blades].

ADDITIONAL MATERIAL. — **Northwestern Atlantic Ocean.** Gulf of Mexico. Florida. — 2 specimens, ECOSUR 2920, Florida Keys, 800 m SSW off Alligator Reef Light, 5-7 m depth, 30.IV.1960, WA Starck, T. Starck & HA Feddern coll. [16-20 mm long, 3 mm wide; no pigmentation; tiny antennae; pharynx papilla as long as wide; dorsal cirri multi-annulated; acicular lobes single, tapered]. — 1 specimen, UF 1060, Monroe County, N of Florida Keys, Florida Bay (24.8899, -81.442816; 24°53'23.6400"N, -081°26'34.1376"W), 12 m depth, 7.VI.2009, A. Anker, A. Bernis, C. Ewers, G. Hecht, M. Krisberg, S. McPherson, J. Zil coll. [22 mm long, 2.5 mm wide, 14 chaetigers, posterior region bent dorsally, some portions removed for molecular analysis; pigmentation pattern visible dorsally, lateral lobes almost without pigmentation; pharynx fully exposed; blades of chaetigers 3, 7 and 9 progressively smaller, teeth antero-lateral initially, progressively lateral; 4-11: 1 in chaetiger 3, 3-9: 1 in chaetiger 7 and 3-9: 1 in chaetiger 9]. — 1 specimen, UF 1063, Monroe County, N of Florida Keys, Florida Bay (24.892683, -81.866116; 24°53'33.6588"N, 081°51'58.0176"W), 16 m depth, 7.VI.2009, A. Anker, A. Bernis, C. Ewers, G. Hecht, M. Krisberg, S. McPherson, J. Zil [15 mm long, 2.8 mm wide, body bent dorsally, pigmentation still visible as longitudinal irregular lines; two posterior left parapodia removed for molecular analysis; antennae tiny; pharynx not exposed; longest tentacular cirri reaching chaetiger 6; dorsal cirri basally straight; acicular lobe single, thin, tapered]. — 1 specimen, UF 1064, Monroe County, N of Florida Keys, Florida Bay (24.892683, -81.866116; 24°53'33.6588"N, 081°51'58.0176"W), 16 m depth, 7.VI.2009, A. Anker, A. Bernis, C. Ewers, G. Hecht, M. Krisberg, S. McPherson, J. Zil [32 mm long, 3.5 mm wide, pigmentation pattern barely visible; no parapodia removed; blades of chaetigers 3, 7 and 9 progressively smaller, teeth antero-lateral, progressively lateral; 6-10: 1 in chaetiger 3, 3-9: 1 in chaetiger 7 and 4-6: 1 in chaetiger 9]. — 1 specimen, UF 1077, W of St. Petersburg (27.441, -82.992333; 27°26'27.6000"N, 082°59'32.3988"W), 18-19 m depth, 11.XI.2007, G. Paulay coll. [35 mm long, 3.5 mm wide, unpigmented; acicular lobe with an upper tine tapered, thin, 3-4 times longer than lower rounded one]. — 1 specimen, UF 1874, N of St. Petersburg, fossil patch reefs (29.028, -83.588666; 29°01'40.8000"N, 083°35'19.1976"W), 19-21 m depth, 12.III.2011, G. Paulay, M. Bernis, N. Evans, F. Michonneau, C. Thacker, R. Wiliams, A. Baeza coll. [14 mm long, 2 mm wide, 13-14 chaetigers (on each side); pigmentation faded off, visible along chaetigers 1-3; body without posterior region, pharynx not exposed; antennae tiny, conical; tentacular cirri without tips; acicular lobe single, thin, tapered]. — 1 specimen, UF 2569, NNW of St. Petersburg, S of Big Bend area (28.68105, -84.3928; 28°40'51.7800"N, 084°23'34.0800"W), 27-32 m depth, 25.V.2012, J. Slapcinsky coll. [28 mm long, 4.5 mm wide; body distorted because of a lateral dissection to remove parapodia for molecular analysis; muscular anterior enteron exposed with long muscular fibers (photos); pigmentation pattern extended into lateral lobes, now faded out; acicular lobe single, long, tapered]. — 1 specimen, UF 2574, NNW of St. Petersburg, S of Big Bend area (28.68105, -84.3928; 28°40'51.7800"N, 084°23'34.0800"W), 35-40 m depth, 25.V.2012, J. Slapcinsky coll. [54 mm long, 5 mm wide, pigmentation pattern visible along body, including anterior prostomial region; body wall broken by muscular enteric region; longest tentacular cirri reaching chaetiger 4; midbody chaetigers with dorsal cirri longer than body width, including parapodia; acicular lobe long, tapered, thin; blades of chaetigers 3, 7 and 9 progressively smaller, teeth antero-lateral progressively lateral; 4-11: 1 in chaetiger 3, 3-8: 1 in chaetiger 7 and 4-8: 1 in chaetiger 9]. — 1 specimen, UF 3173, Palm Beach County, Peanut Island, western shore, rock jetty on sand (26.77488, -80.04844; 26°46'29.5680"N, 080°02'54.3840"W), 12.II.2013, J. Slapcinsky coll. [body 21 mm long, 3 mm wide; right parapodia of chaetigers 12-13 removed for molecular studies; pigmentation pattern visible, restricted to dorsal surface, not extended into lateral lobes; pharynx fully everted, dorsal papillae as long as wide; acicular lobe single, long, tapered].

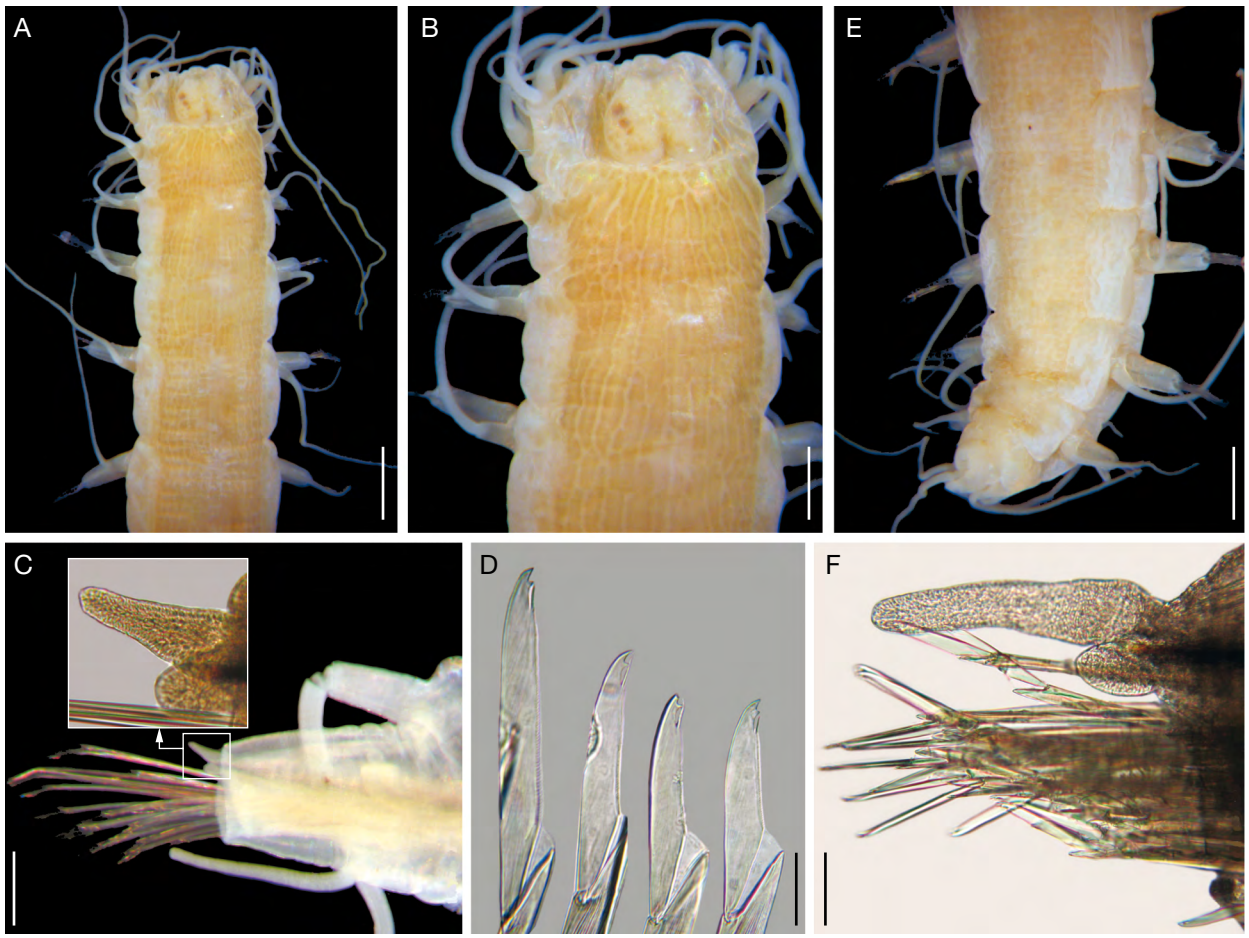

FIG. 43. — *Hesione praetexta* Ehlers, 1887, non-type specimen, LACM 10166: **A**, anterior region, dorsal view; **B**, same, close-up; **C**, chaetiger 8, right parapodium, anterior view (inset: acicular lobe); **D**, same, neurochaetal blades; **E**, posterior region, dorsal view; **F**, another non-type specimen, MCZ 46395, chaetiger 6, right parapodium, anterior view. Scale bars: A, 1.6 mm; B, 1 mm; C, 0.4 mm; D, 40 µm; E, 1.2 mm; F, 0.1 mm.

Bermuda. 1 specimen, MCZ 70247, Bermuda Sta. 501, 24.VIII.1903, Bermuda Institute of Ocean Sciences coll. [46 mm long, 5 mm wide; splendid specimen; prostomium anteriorly truncate, with a longitudinal furrow; antennae minute, blunt fusiform, slightly as long as wide; eyes almost colorless; pharynx not exposed; dorsal cirri basally smooth; acicular lobe with upper tine medially swollen, blunt, three times longer than smaller one, rounded; neurochaetal blades long and medium-sized, guards mostly eroded, some remaining approaching distal tooth; pygidium smooth, reddish, six blunt anal cirri]. — 1 specimen, USNM 32494, no further data, T. Kincaid coll. [30 mm long, 4 mm wide; mature, some gonadic tubules protrudring throughout body wall in posterior segments; most cirri and chaetal blades lost; with an irregular anteroventral dissection, and left parapodium of chaetiger 10 previously removed; acicular lobe single, tapered].

Bahamas. 1 specimen, MCZ 46395, off Matthew Town, Great Inagua Island, 1.VIII.1938, McLean & Shreve coll. [35 mm long, 4 mm wide; mature, pharynx invaginated; prostomium with a deep longitudinal furrow; eyes of similar size, anterior ones slightly more separated, posterior ones duplicated; antennae minute, not visible dorsally; acicular lobe single, long tapered with a rounded shorter base; neurochaetae with long blades, guard approaching distal tooth; oocytes about 100 µm].

Gulf of Mexico. Yucatán, México. 1 specimen, ECOSUR 2921, 1 km W off San Felipe lagoon mouth, 2 m depth, 18.II.1999, J. R. Bastida-Zavala & SISV coll. [23.5 mm long, 3 mm wide; pharynx not exposed, prostomium projected anteriorly; dorsal cirri multi-articulated; parapodia with chaetal lobes invaginated; acicular lobe single]. — 1 specimen, ECOSUR OH-592, Ría Lagartos, 1 km W off lagoon mouth, 3 m, 14.VI.2009, L. F. Carrera-Parra & SISV coll. [10 mm long, 1.5 mm wide; pharynx everted, margin smooth; no pigmentation].

Caribbean Sea. México. Quintana Roo. Isla Contoy. 1 specimen, ECOSUR 2922, Playa Camping, rocky shore, 0.5 m depth, 13.II.1999, SISV coll. [36 mm long, 4 mm wide; with an anterior dissection; no pigmentation; antennae not seen; pharynx papilla not visible, dissected; dorsal cirri multi-annulated; acicular lobes single, tapered]. **Punta Nizuc**. 1 specimen, ECOSUR 2292, outer reef, 4 m depth, under rock, 10.II.2001, L. F. Carrera-Parra & SISV coll. [26 mm long, 3 mm wide; right parapodia of chaetigers 4, 9 and 15 removed; no pigmentation; antennae not seen; pharynx papilla rounded, as long as wide; dorsal cirri multi-annulated basally and throughout it; acicular lobes single, tapered; neurochaetal blades bidentate]. — 1 specimen, UMML351, RV *Gerda*, Arrowsmith Bank, Sta. 951 (21°06'N, 86°28'W), 249 m depth, 28.I.1968 [30 mm long, 5 mm wide; body laterally bent, distorted, prostomium with tiny antennae; pygidium with anal cone, anal cirri minute; parapodial lobes deeply invaginated; dorsal cirri smooth; chaetae lost; acicular lobes single, contracted].

Cuba. 1 specimen, ZMUC 2426, Yversen coll., no further data [macerated, enigmatic fixation resulting in pale soft body and whitish, brittle cirri; body 27 mm long, 4.5 mm wide; acicular lobe single, tapered].

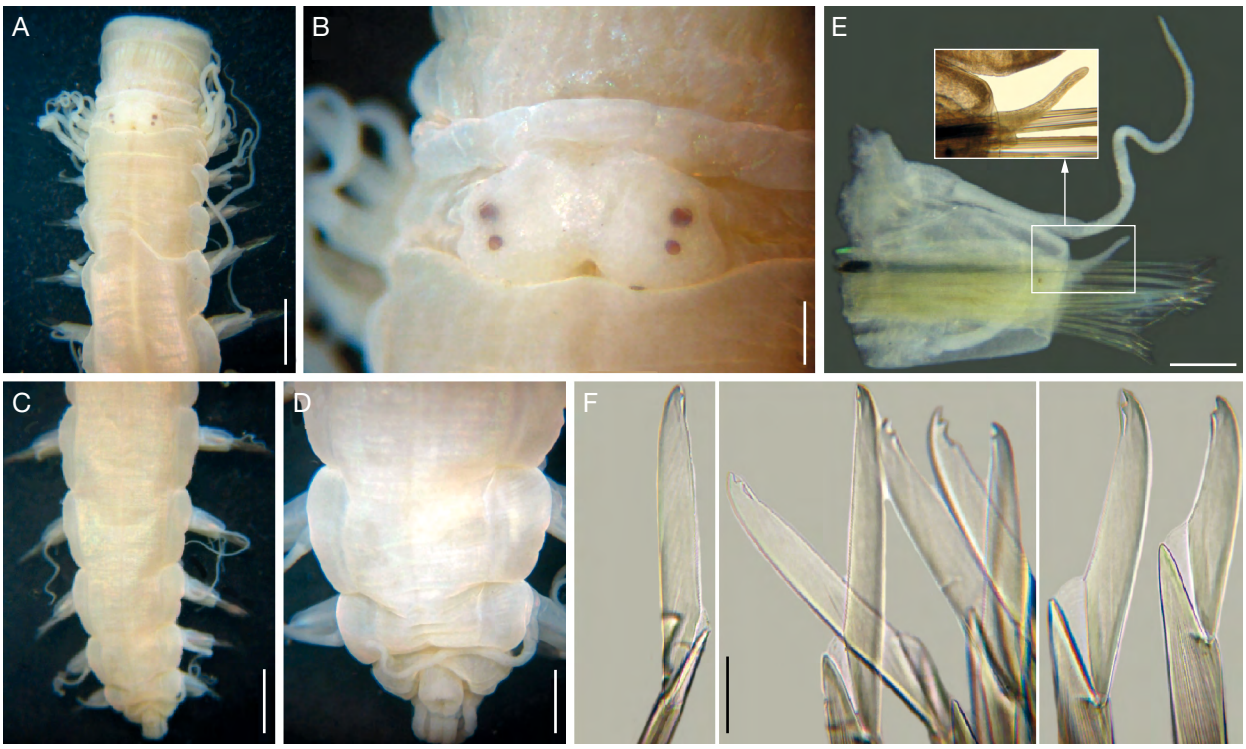

Fig. 44. — *Hesione praetexta* Ehlers, 1887, non-type specimen, ECOSUR 2292: **A**, anterior end, dorsal view; **B**, head, dorsal view; **C**, posterior end, dorsal view; **D**, pydidium, dorsal view; **E**, chaetiger 9, right parapodium, posterior view (inset: acicular lobe); **F**, same, upper, medial and lower neurochaetal blades. Scale bars: A, 1.7 mm; B, E, 0.4 mm; C, 1.8 mm; D, 0.8 mm; F, 40 µm.

Puerto Rico. 1 specimen, MCZ 46415, La Parguera, 19.I.1969, L. S. Roberts coll. [11.5 mm long, 2 mm wide; slightly distorted; most chaetae broken; prostomium anteriorly cleft, with a longitudinal furrow; eyes dark brown, anterior ones twice as large as posteriors; dorsal cirri basally smooth; acicular lobes with an upper tine large, medially swollen, 3 times longer than lower one; few chaetal blades remaining, mostly long; pygidium smooth, with 5-6 blunt anal papillae].
Haiti. 1 specimen, ZMH-P 1292a, Port-au-Prince, Kepperschmidt coll., no further data [15 mm long, 2 mm wide, colorless; acicular lobe single, basally swollen, digitate].
Jamaica. 1 specimen, LACM 10166, Saint Ann Parish, St. Ann's Bay, Hofstra University Marine Laboratory Cove, in *Acetabularia*, 0-10 m depth, 25.V-3.VI.2006, K. Rawlinson, M. Bolanod, A. DuPont, A. Allan, J. Dunn & L. Harris coll. [splendid specimen, used for Redescription]. — 1 specimen, ZMH-P 6787, Kingston, 24.IX.1905, A. Gagzo coll. [25 mm long, 4 mm wide; slightly bent backwards; colorless; right chaetal lobe of chaetiger 7 previously removed; most cirri on site, most neurochaetal blades lost; antennae blunt, minute about twice as long as wide; eyes brownish, anterior ones twice as large as posterior ones; acicular lobe single, long, tapered].
Saint-Thomas. 1 specimen, ZMUC 2429b, 1860, Krebs coll., no further data [28 mm long, 3 mm wide, macerated, colorless; left parapodium of chaetiger 8 removed for observation (kept in container); acicular lobe single, thick, blunt; neurochaetal blades bidentate, guard approaching distal tooth].
Guadeloupe. 1 specimen, MNHN-IA-PNT102 (formerly jar 914), Sta. 4B 600, no further data [22 mm long, 3 mm wide; dark pinkish because of Bengal Rose stain; macerated, most dorsal cirri and neurochaetal blades lost, distorted posteriorly; several parapodia previously removed; acicular lobe single, thin, very long; about 20 neurochaetae per bundle; not listed by Amoureux (1985) but probably based upon the same study].
Colombia. 1 specimen, ECOSUR 2294, RV *Pilsbury*, Sta. 772 (12°20'N, 71°55'W), 11 m depth, 29.VII.1968 (21 mm long, 3 mm wide; pharynx not exposed; eyes depigmented; dorsal cirri multiannulated; acicular lobes single, long, tapered].
Trinidad and Tobago. 1 specimen, MCZ 46401, E. Deichmann coll. [19 mm long, 2 mm wide, partially dehydrated; prostomium slightly projected anteriorly; pharynx not exposed; eyes almost colorless; dorsal cirri annulated basally; acicular lobe long tapered, some parapodia with a smaller round to triangular smaller lower lobe; neurochaetal blades long to medium-sized; pygidium barely rugose].
Venezuela. 1 specimen, ECOSUR 2925, mature female, ENE off Margarita Island, RV *Pilsbury* Sta. 712 (11°09'N, 63°18'W), 26 m depth, 19.VII.1968 [36 mm long, 4.5 mm wide; antennae minute; eyes dark brown, anterior ones larger, slightly more separated than posterior eyes; dorsal cirri multi-articulated; acicular lobe double, upper lobe longer, taperer, ventral lobe, blunt; oocytes 90-100 µm].
Brazil. 1 specimen, MNHN-IA-PNT103 (formerly jar 879), RV *Calypso*, off Pernambuco coast, Sta. 23 (08°19'S, 34°39'W), 75 m depth, 21.XI.1961 [27 mm long, 4 mm wide; slightly macerated, integument shiny with pale brown longitudinal, irregular lines; antennae minute, slightly as long as wide; eyes difussely pigmented, anterior and posterior lateral eyes close to each other; acicular lobe double, blunt, upper tine digitate, 5 times longer than lower, round one; neurochaetae about 20 per bundle, blades bidentate, distal tooth larger, guard approaching distal tooth]. — 5 specimens, MNHN-IA-PNT101b (formerly jar 888a), RV *Calypso*, Sta. 19 (03°49.7'S, 32°26'W), 31 m depth, 18.XI.1961 [17-26 mm long, 2.5-4.0 mm wide; macerated, integument shiny with pale brown longitudinal, irregular lines, especially visible along chaetigers 1-3, and in posterior chaetigers of 1 specimen; antennae minute, slightly as long as wide; eyes almost colorless, anterior eyes twice larger than posterior ones; acicular lobe double, blunt, upper tine digitate, 5 times longer than lower, round one; neurochaetae about 20 per bundle, blades bidentate, distal tooth larger, guard approaching distal tooth]. — 1 speci-

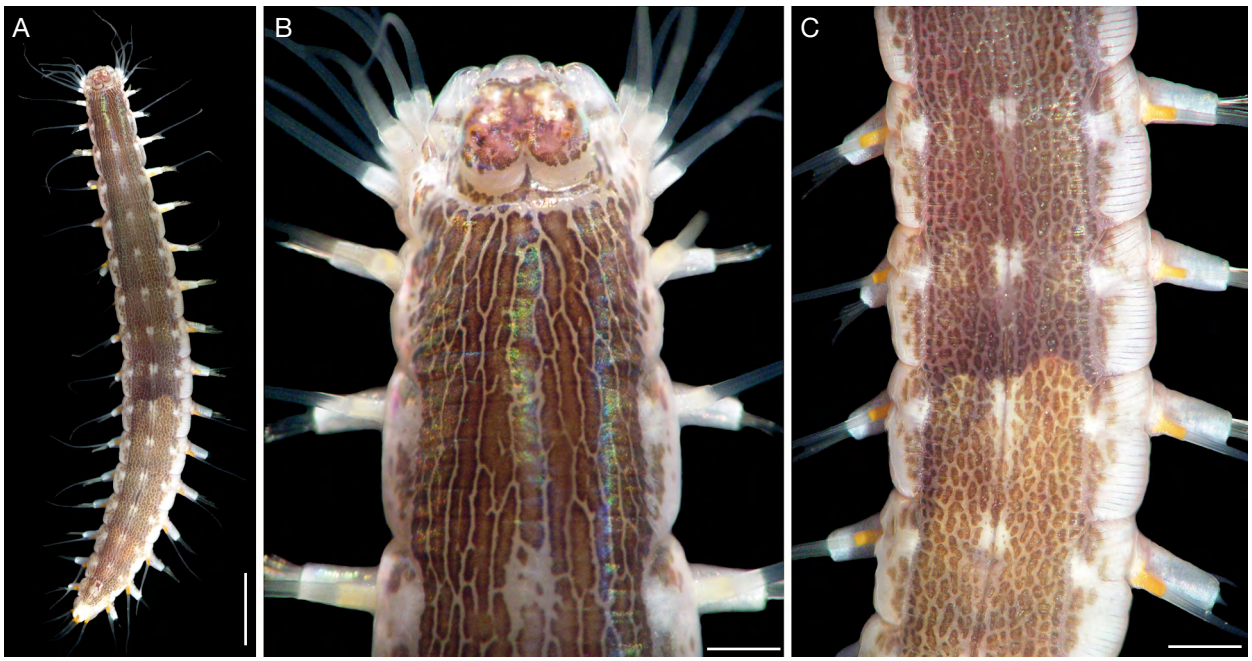

FIG. 45. — *Hesione praetexta* Ehlers, 1887, non-type specimen, LACM 10166: **A**, dorsal view; **B**, anterior end, dorsal view; **C**, chaetigers 8–11, dorsal view. Scale bars: A, 3 mm; B, 0.7 mm; C, 0.8 mm. Photos: Leslie Harris, LACM.

men, MNHN-IA-PNT101c (formerly jar 888b), RV *Calypso*, Sta. 7 (03°50'S, 33°54'W), 54-47 m depth, 17.XI.1961 [16 mm long, 2 mm wide; colorless juvenile, dried-out but not brittle, with salt particles adsorbed forming flat, squarish spots throughout body; acicular lobe projected in some chaetigers with upper tine very long; not dissected to avoid further damage].

DISTRIBUTION. — Western Atlantic, from Bermuda to Northern Brazil, in mixed or rocky bottoms in 0-249 m water depth.

DIAGNOSIS. — *Hesione* with prostomium rectangular, or slightly curved laterally; parapodia with dorsal cirri basally cylindrical, dorsal cirrophore twice as long as wide; larger acicula blackish; acicular lobe single, long, tapered or blunt, lower tine rounded, small; neurochaetal blades bidentate, 4-7 times as long as wide; subdistal tooth smaller than distal one, with guards approaching distal tooth.

REDESCRIPTION

Best preserved specimen, LACM 10166, mature, complete, subcylindrical, tapered posteriorly, with some traces of original pigmentation: longitudinal, irregular lines throughout body (Fig. 43A, B) in ethanol; most cirri and neurochaetal blades on site; right parapodium of chaetiger 8 removed (kept in vial). Body 33 mm long, 3 mm wide.

Prostomium slightly as long as wide, anterior margin slightly projected anteriorly, lateral margins rounded, posterior margin deeply cleft, about ¼ as long as prostomial length, longitudinal depression barely detected (Fig. 43B). Antennae minute, left one visible, ovoid, barely as long as wide, about ⅓ as long as interocular distance. Eyes brownish, anterior ones slightly larger than posterior ones.

Tentacular cirri long, thin, twisted, longest ones reaching chaetiger 4. Lateral cushions low, barely projected (specimen relaxed before preservation), surface smooth.

Parapodia with chaetal lobes slightly as long as wide, truncate; dorsal cirri with cirrophores about twice as long as wide (Fig. 43C); cirrostyle basally cylindrical, annulated, articulated medially and distally, as long as body width, including parapodia. Ventral cirri smooth, surpassing chaetal lobe.

Neuraciculae blackish, tapered, larger one markedly thicker and darker than smaller one. Acicular lobe double, upper tine digitate, 3 times longer than lower, round one (Fig. 44C [inset]).

Neurochaetae about 20 per bundle, blades bidentate, 4-7 times as long as wide (Fig. 43D), blades at a certain angle from handle, decreasing in size ventrally, each with smaller subdistal teeth, guard approaching distal tooth.

Posterior region tapered into a blunt cone, dorsal surface rugose (Fig. 43E); pygidium smooth, anus with 5 low, blunt papillae.

Pharynx not exposed. Oocytes about 100 µm in diameter.

Variation

Lateral cushions can be more projected if the body was more contracted (Fig. 44A, C, D). The prostomium can become markedly as wide as long (Fig. 43B), but the size proportions of eyes are less variable. In some specimens, the upper tine of acicular lobe can be digitate, 4 times longer than the lower one (Fig. 43F), or it can be tapered and longer in other specimens (Fig. 44E). Neurochaetal blades are 4-11 times as long as wide in anterior chaetigers, and reduce their proportions to 3(4)-8(9) median chaetigers (Fig. 44F).

Pigmentation

Body with dorsal, longitudinal, irregular, discontinuous wide brown bands (Fig. 45A), barely expanded into lateral cushions, but not into pygidium. Tentacular, dorsal cirri

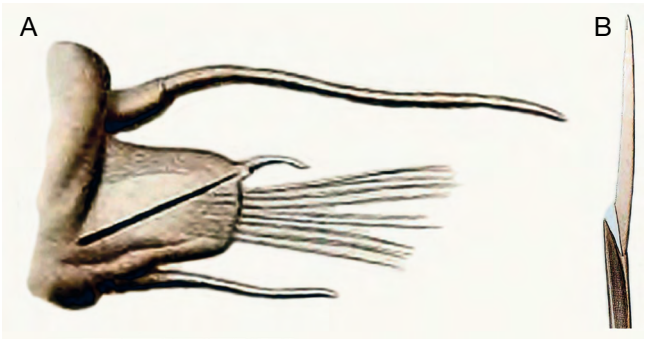

Fig. 46. — *Hesione praetexta* Ehlers, 1887: **A**, parapodium from a middle-body segment; **B**, same, tip of neurochaetal tip (modif. after Ehlers, 1887, scale bars missing in original).

and chaetal lobes pale, cirrophores yellowish. Prostomium (Fig. 45B) with brownish marginal bands, continuous along anterior margin, interrupted along posterior one, over a red-brownish background. Longitudinal bands longer along a few anterior chaetigers, each as long as segmental length, often with irregular, slightly darker limits, leaving a middorsal spot unpigmented, except in chaetiger 1, and in last chaetiger where the spot is larger; in median and posterior chaetigers with two additional lateral spots. Middorsal pale spots connected by a thin, middorsal brownish line, better defined along medial and posterior chaetigers. Longitudinal bands progressively smaller in median (Fig. 45C) and posterior chaetigers, becoming 1/6-1/10 as long as segmental length, as rounded, irregular spots

Remarks

Hesione praetexta Ehlers, 1887 reinstated, has been regarded as a potential junior synonym of *H. picta* Müller, 1858 by Hartman (1938: 6), or of *H. proctochona* Schmarda, 1861 by Horst (1921: 80), and even Ehlers doubted about its independent status. In his original description, he thought pigmentation differences could be related to sexual dimorphism (Ehlers 1887: 147). At the same time, however, Ehlers indicated and illustrated some other differences besides pigmentation patterns in the diagnosis, his drawings reproduced herein as Figure 46, such as the presence of single acicular lobe (Fig. 46A), against double in *H. vittigera* (syn. *H. picta*), and longer, thinner chaetal blades (Fig. 46B), instead of shorter, thicker in *H. vittigera*. These differences have been found consistent and not modified during ontogeny (Fig. 1), such that they are herein regarded as sufficient to separate *H. praetexta* from the other common Grand Caribbean species, *H. picta* Müller, 1858.

In the key below, *H. praetexta* resembles *H. helenensis* n. sp. because both have digitate acicular lobes. They differ in cirrostyles bases and on the size of neurochaetal blades and guards. In *H. praetexta* cirrostyles are basally cylindrical, blades are 4-6 times as long as wide, and guards approach distal tooth, whereas in *H. helenensis* n. sp. cirrostyles are basally swollen, blades are 4-5 times as long as wide, and guards approach subdistal tooth.

Hesione reticulata von Marenzeller, 1879
(Fig. 47)

Hesione reticulata von Marenzeller, 1879: 129-131, pl. 3, fig. 4. — Izuka 1912: 192-194, pl. 2, fig. 7. — Imajima & Hartman 1964: 80. — Jimi *et al.* 2017: 32-37, figs 1-3.

Hesione pantherina – Fauvel 1937: 59, 60. — Wu *et al.* 1975: 75, pl. 2, figs 7, 8 (*non* Risso, 1826).

Hesione splendida – Hessle 1925: 13, 15. — Imajima 2003: 132, 134, fig. 78 (*non* Savigny *in* Lamarck, 1818).

Non-Type material. — **New Caledonia.** 1 specimen, UF 151, Noumea, Île Nou, Anse Kuendo, sand and reef slope, fringing rock, under rocks, 0-3 m depth, 27.I.1999, G. Paulay coll.

Distribution. — Japan to New Caledonia, in shallow water mixed bottoms.

Diagnosis. — (Modif. after Jimi *et al.* 2017) *Hesione* with rectangular prostomium; parapodia with dorsal cirri basally cylindrical, dorsal cirrophore twice as long as wide; larger acicula blackish; acicular lobe double, tines short, massive, blunt, upper tine slightly longer than lower one; neurochaetal blades bidentate, 3-5 times as long as wide; subdistal tooth smaller; guards approaching distal tooth.

Description

Specimen macerated, UF 151, body wall broken along a posterior right section (removed for molecular analysis); body colorless in ethanol, progressively wider, tapered posteriorly, 52 mm long, 7 mm wide.

Prostomium as wide as long, anterior margin truncate, lateral margins rounded, medially expanded, posterior margin exposed, posterior depression as long as ¼ prostomial length. Antennae not visible. Eyes colorless.

Tentacular cirri macerated, transparent, tips broken, reaching chaetiger 3. Lateral cushions projected, smooth, probably by maceration.

Parapodia with chaetal lobes projected, truncate, twice as long as wide (Fig. 47B, D); dorsal cirri with cirrophores too relaxed, four times as long as wide, cirrostyles basally cylindrical, annulated medially and distally, as long as body width (excluding parapodia). Ventral cirri smooth, surpassing chaetal lobe.

Neuraciculae blackish. Acicular lobe double (Fig. 47B, C [insets], B, D), tines digitate, upper tine slightly longer than, or up to ⅓ longer than lower tine; in one median parapodium lower tine larger, probably a maceration artifact.

Neurochaetae about 15 per bundle in anterior chaetigers (Fig. 47C), about 20 in median chaetigers (Fig. 47E), handles honey-colored, blades bidentate, at a certain angle from handle, most eroded or with adsorbed particles, decreasing in size ventrally, 5-8 times as long as wide in anterior chaetigers (Fig. 47D), 4-5 times in posterior chaetigers (Fig. 47C); subdistal teeth smaller, guards, if complete, approaching distal tooth.

Posterior region tapered into a blunt cone; pygidium macerated, relaxed, with 7 blunt papillae.

Pharynx exposed; dorsal papilla rounded, as long as wide. Oocytes not seen.

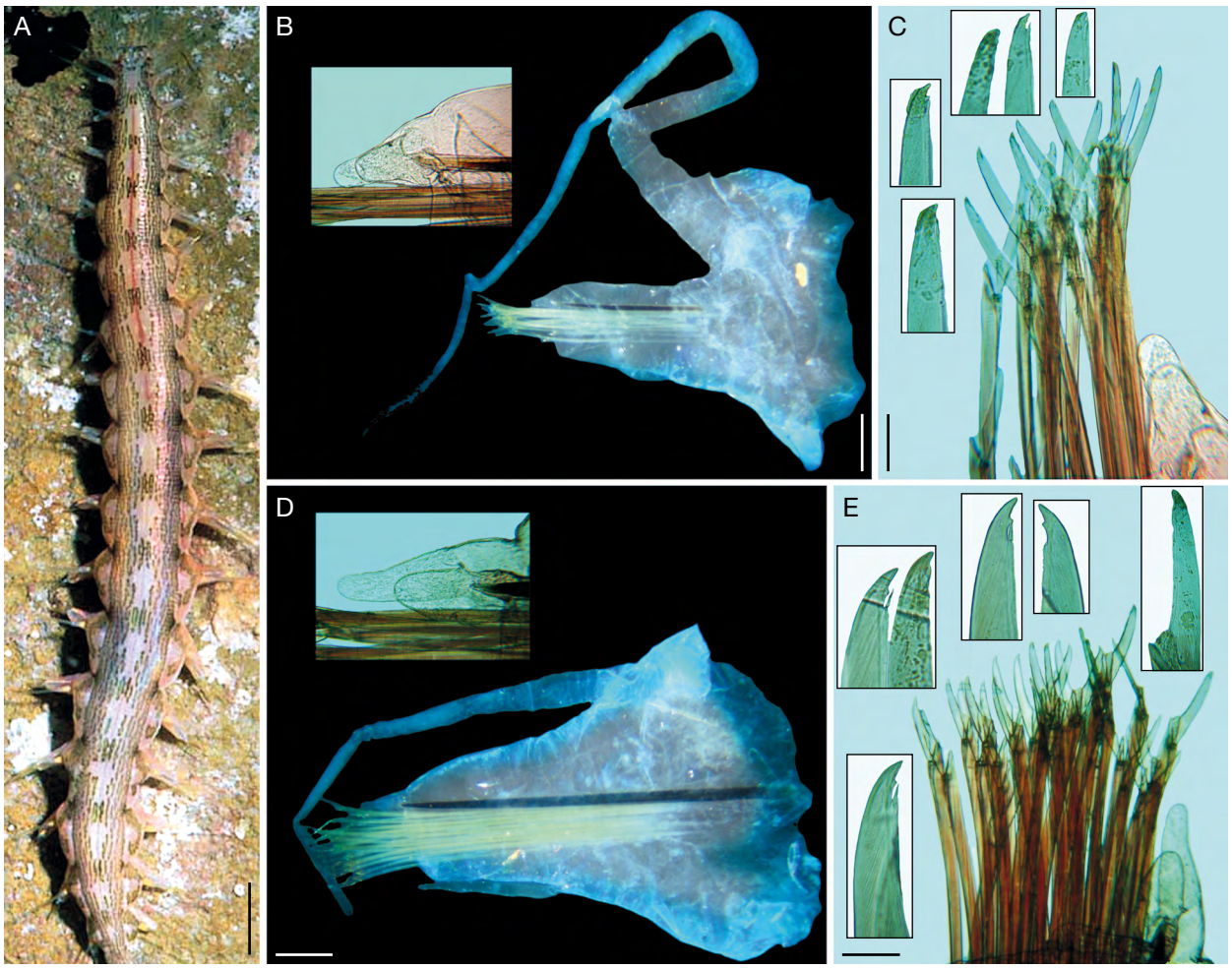

FIG. 47. — *Hesione reticulata* von Marenzeller, 1879, non-type specimen, UF 151, alive: **A**, dorsal view; parapodia after a brief immersion in methyl-green: **B**, chaetiger 2, right parapodium, anterior view (inset: acicular lobe); **C**, same, neurochaetae (insets: blade tips); **D**, chaetiger 8, right parapodium, anterior view (inset: acicular lobe); **E**, same, neurochaetae (insets: blade tips). Scale bars: A, 0.5 mm; B, 80 µm; C, 0.6 mm; D, 140 µm; E, 35 µm (photo A: G. Paulay).

Pigmentation

Living specimen (Fig. 47A) with longitudinal, irregular brownish bands, with oval pale areas in each chaetiger and over central areas of lateral cushions; bands extending towards lateral cushions. Tentacular, dorsal cirri and neuropodial lobes pale. A middorsal reddish line showing the dorsal blood vessel; middorsal lines slightly darker than the others.

REMARKS

Hesione reticulata von Marenzeller, 1879 resembles, as indicated in the key below, *H. picta* Müller, 1858. These two species differ in two main features related to their integument and pigmentation. In *H. reticulata* integument is rugose because there are transverse and longitudinal striae, and living specimens have a complex, reticulate pigmentation pattern, whereas in *H. picta* the dorsum is rather smooth, annulated, but without longitudinal striae, and living specimens have transverse dark brown bands. On the other hand, by their pigmentation pattern, *H. reticulata* resembles *H. intertexta* Grube, 1878 by having longitudinal lines throughout the body, and short antennae. However, because *H. reticulata* has an acicular lobe double, it differs from *H. intertexta* that has a single acicular lobe. The species has been recently redescribed, a neotype was proposed (Jimi *et al.* 2017), and the acicular lobe was confirmed as double. The specimens recorded by Imajima (2003: 132), albeit partially, might belong to this species; in one of his illustrations, a thick acicular lobe can be noted, which can be confused with a single tine, but as shown elsewhere (Jimi *et al.* 2017), the shorter tine is difficult to be observed.

Hesione sicula delle Chiaje, 1830, reinstated (Figs 48-51)

Hesione sicula delle Chiaje, 1830: pl. 82, fig. 24; 1841a: 3: 95; 1841b, 5: 102; 1841c, 7: pl. 103, fig. 2; pl. 155, fig. 24 (same as 1830: pl. 82, fig. 24).

Telamone sicula – Claparède 1868: 541-545, pl. 18, fig. 4 (plate indicated, never published).

Fallacia sicula – Marion & Bobretzky 1875: 46-48, pl. 12, fig. 28.

Hesione steenstrupii Quatrefages, 1866: 96-98, pl. 9, fig. 17. — Solís-Weiss *et al.* 2004: S5.

Hesione pantherina – Grube 1864: 83. — Saint-Joseph 1898: 329-337, pl. 19, figs 131-144. — Rioja 1918: 36; 1925: 18. — Fauvel 1913: 56 (*partim*, Sta. 2096); 1953a: 18 (*partim*). — Fauvel & Rullier 1959a: 512; 1959b: 158 (*non* Risso, 1826).

Hesione picta – Rullier 1964: 155 (*non* Müller, 1858).

Hesione splendida – Hartmann-Schröder 1982: 8. — Kirkegaard 1983: 213. — Parapar *et al.* 2004: 216, fig. 76 (*partim*) (all *non* Savigny *in* Lamarck, 1818).

TYPE MATERIAL. — **Mediterranean Sea, Italy.** *Hesione sicula* delle Chiaje, 1830: Neotype, ZMB 7529, and five specimens labelled paraneotypes, ZMB 11597, Naples, X.1924, G. H. Heider coll. [paraneotypes complete, body cylindrical, variably dissected for observation of inner organs; body 45-76 mm long, 5 mm wide, 16 chatigers; antennae digitate 4-5 times as long as wide; eyes brownish, anterior ones slightly larger than posterior ones; posterior eyes with lenses directed posteriorly, better observed when pharynx is fully exposed; acicular lobe double, rounded; upper tine slightly longer than lower one; neuraciculae blackish, subdistally swollen, aristate; neurochaetal blades bidentate, guard approaching subdistal tooth]. **Northeastern Atlantic, France**. Holotype of *Hesione steenstrupi* Quatrefages, 1866, MNHN-IA-TYPE0479, Guettary (43°25'36"N, 01°36'28"W), no further data, A. de Quatrefages coll.

ADDITIONAL MATERIAL. — **Mediterranean Sea. Italy.** 3 specimens, MNHW unnumb., Broni (probably Genoa since it is the closest port), Kükhental coll. no further data [grayish, one with darker spots along body; acicular lobe double; neurochaetal handles colorless; 45-64 mm long, 5-6 mm wide]. Four specimens, MNHW unnumb., Naples, no further data [47-52 mm long, 5-6 mm wide, 3 specimens with transverse cuts along body, probably to improve preservation; two with pygidial gland ring reddish; acicular lobe double; neurochaetal handles brownish]. — 2 specimens, RMNH 281, Naples, probably purchased, 1888, no further data (50-72 mm long, 5-8 mm wide; larger specimen grayish, with pharynx everted, wider in posterior third of body, smaller specimen pale brownish, slightly wider in posterior third of body; posterior eyes with lenses centrally positioned; chaetal lobes invaginated; acicular lobe double). — 2 specimens, SMF 8530, Sherki Bank, off Sicily, RV *Urania*, Sta. 297, 45 m depth, 7.I.1997, H. Zibrowius coll. [31-43 mm long, 3-4 mm wide; partially dehydrated, with abundant salt particles adsorbed on body, both with pharynx partially exposed, larger one bent ventrally, right parapodia of chaetiger 9 removed for observation; anterior eyes twice larger than posterior ones, posterior eyes with lenses directed posteriorly; acicular lobe double, upper tine 3-4 times longer than lower one; about 25 neurochaetae per bundle, blades bidentate, guard approaching subdistal tooth]. — 2 specimens, USNM 5111, purchased from the Zoological Station, Naples, 1893 [45-66 mm long, 5-8 mm wide; without pigmentation, well preserved; parapodial cirri macerated in 1 specimen, in the other dorsal cirri basally articulated, articles as wide as long, ventral cirri articulated, articles as long as wide; acicular lobe double, globose, upper tine slightly longer than lower one; blades with guard reaching subdistal tooth; posterior end tapered into a blunt cone; pygidium with six low, thick papillae]. — 1 specimen, ZMB 811, Naples, A. Dohrn coll., plus 3 slides made by Dr Bergmann (44 mm long, 5 mm wide; body slightly bent ventrally, swollen, probably injected; left parapodium from chaetiger 8 removed for observation (kept in vial); antennae digitate, 4-5 times as long as wide; eyes colorless; neuraciculae blackish, capitate, mucronate; acicular lobe double; upper neurochaetae with blades unidentate, probably eroded; other chaetae with blades bidentate, guard approaching subdistal tooth]. — 1 specimen, ZMB 3800, and one slide with gonad fragments (made by Dr Bergmann), Zoological Station, Naples, received 21.I.1903, W. Bergmann coll. [50 mm long, 6 mm wide; body with a longitudinal middorsal dissection throughout most of body, for observation of inner organs; antennae digitate, 4-5 times as long as wide; eyes brownish, anterior ones twice as large as posterior ones; chaetal lobes variably invaginated; neuraciculae blackish, subdistally swollen, capitate; acicular lobe double, digitate, upper one slightly longer than lower one; neurochaetal blades bidentate, guard approaching subdistal tooth]. — 1 specimen, ZMB 3804, Bay of Naples, probably purchased from the Zoological Station, Dr Bergmann (author of the slides; 60 mm long, 6 mm wide; left parapodia of chaetigers 13-14 previously removed for permanent slides; antennae digitate, 4-5 times as long as wide; eyes brownish, anterior ones slightly larger than posterior ones; acicular lobe double, neuraciculae blackish, subdistally swollen, tapered; blades bidentate, guard approaching subdistal tooth]. — 1 specimen, ZMUC 2425, plus anterior and posterior fragments, probably purchased from the Stazione Zoologica Napoli, 1882, no further data (50 mm long, 5 mm wide; slightly dehydrated, distorted, most cirri broken, many chaetae without blades; several parapodia previously removed, left parapodium of chaetiger 9 removed for observation (kept in vial); acicular lobe double, blunt, upper tine 3 times longer than lower tine]. — 2 specimens, ZMH-P PE 314, Neapel Zoological Station, 1885 [53-58 mm long, 5 mm wide; complete, smaller one with pharynx slightly exposed, dorsal papilla blunt, as wide as long; eyes colorless; antennae digitate, 3-4 times as long as wide; acicular lobe double, upper tine slightly longer than lower one]. — 1 specimen, ZMH-P 1289, Naples, no further data [48 mm long, 6 mm wide; complete, colorless, dorsum darker than other body parts; eyes colorless; antennae about 3-4 times as long as wide; parapodia with chaetal lobes invaginated; acicular lobe double, upper tine slightly longer than lower one].
Croatia. 1 specimen, UCO HES 4, Rovinj, no further data [25 mm long, 3 mm wide; no pigmentation; acicula blackish, subdistally swollen, mucronate; acicular lobe double]. — 2 specimens, ZMB 3809, Collection Grube, Crivizza (Krivica), Dr Bergmann and Lussin Piccolo, Dr Bergmann made slide, no further data [15-26 mm long, 2.0-2.5 mm wide; no pigmentation, eyes barely visible; parapodial features seen in permanent slide: acicular lobe double, blunt, upper one slightly longer than lower one; neuraciculae blackish tapered, not swollen subdistally; probably size-dependent]. — 3 specimens, ZMB 3811, Collection Grube, Lesina (Hvar Island), Dr Bergmann coll. no further data [28-40 mm long, 3.5-5.0 mm wide; one without dorsal prostomial surface (in permanent slide), smaller one with pharynx exposed; antennae 2-3 times as long as wide, blunt; anterior eyes twice larger than posterior ones; dorsal cirrophore 2-3 times as long as wide; neuraciculae blackish, subdistally swollen, smooth (in permanent slides); neurochaetae with blades bidentate, guard approaching subdistal tooth]. — 3 specimens, ZMB 7567, Saint Girolamo (Jerolim) island, SW Brijuni, Fažana Canal, 1933, G. K. Heider coll. [45-65 mm long, 6-8 mm wide; splendid specimens; two with pharynx exposed, dorsal papillae rounded, as long as wide; antennae longer than anterior eyes diameter; dorsal cirrophores 2-3 times as long as wide, cirrostyles basally cylindrical, reddish, smooth, medially annulated, distally articulated; neuraciculae blackish, subdistally swollen, mucronate; neurochaetal blades bidentate, anterior chaetigers with longer blades, with smaller teeth, shorter with larger teeth in median and posterior chaetigers; guard approaching subdistal tooth].
Monaco. 1 specimen, MNHN-IA-PNT105 (formerly jar 404), Collection Prince de Monaco, Sta. 2029, off Monaco, III.1913, no further data [51 mm long, 7 mm wide (right parapodium of chaetiger 7 removed for observation, kept in vial); antennae digitate 3-4 times as long as wide; anterior eyes darker, slightly larger than posterior ones; pharynx exposed, dorsal papillae slightly as long as wide; acicular lobe double, blunt, upper tine 2-3 times longer than lower one; neurochaetae about 30 per bundle, blades bidentate, subdistal tooth smaller, guard approaching subdistal tooth].

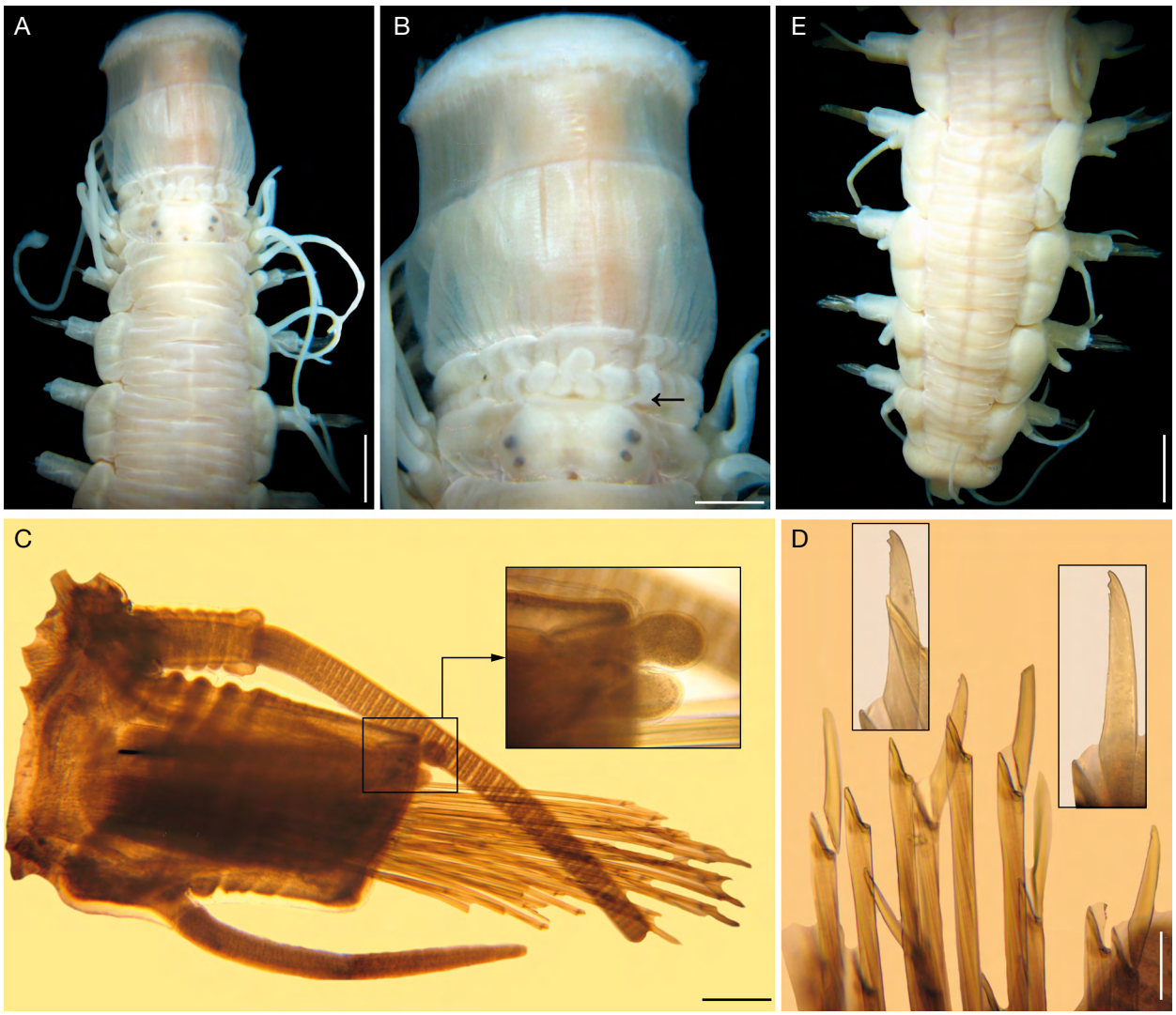

FIG. 48. — *Hesione sicula* delle Chiaje, 1830, reinst., neotype, ZMB 7529: **A**, anterior region, dorsal view; **B**, prostomium and everted pharynx, dorsal view (arrow points to right lateral antenna); **C**, chaetiger 9, left parapodium, anterior view (inset: acicular lobe); **D**, same, lower half of neurochaetal bundle (insets: blades); **E**, posterior region, dorsal view. Scale bars: A, E, 1.8 mm; B, 0.9 mm; C, 0.5 mm; D, 80 µm.

France. 1 specimen, MNHN-IA-PNT91m (formerly jar 70-190a),Marseille, no further data, labelled in 1868, M. Barban coll. [32 mm long, 5 mm wide; damaged, anterior muscular digestive system fully exposed, as long as whole body; larger neuraciculae tapered, tip granulose, mucronate; acicular lobe double, upper tine twice as long as lower one. — 1 specimen, SMF 16084, Rade Sud de Marseille, Sta. A2HC1(I), 20.X.1982, A. Willsie coll. [juvenile, 10 mm long, 2 mm wide; colorless, distorted, parapodia displaced ventrally, all dorsal and some tentacular cirri lost, right parapodium of chaetiger 9 removed for observation (kept in vial); antennae digitate, 2-3 times as long as wide; eyes colorless; acicular lobe double, upper tine twice longer than lower one; neurochaetal blades bidentate, teeth smaller in upper bundle chaete, larger medially and ventrally, subdistal tooth smaller, guards mostly broken, if entire, approaching distal tooth].
Spain. 1 specimen, MCZ 126440, Es Caials, Cadaqués (42.28919, 3.2757), Girona, 12.VIII.1997, C. Palacín & G. Giribet coll. [44 mm long, 4 mm wide; body bent ventrally, pharynx not exposed; eyes dark brown, anterior ones slightly larger than posterior ones (in lateral view look twice as large); antennae tapered, as long as interocular distance on the same prostomial side; acicular lobe digitate, double, mostly with an upper tine twice larger than lower one; chaetal blades long or short, with guard reaching subdistal tooth]. — 3 specimens, MCZ 134169, Catalunya, Blanes (41.676°N, 2.793°E), 31.VII.1997, C. Palacín & G. Giribet coll. [juveniles, 13-14 mm long, 1.5 mm wide; two complete; one without anterior region; body straight, stiff, with some pale red irregular bands dorsally, better retained over first few chaetigers; most cirri lost; pharynx completely invaginated; eyes reddish, anterior ones slightly larger than posterior ones (in lateral view look twice as large); antennae tapered, as long as interocular distance; acicular lobe double, mostly with upper tine digitate, twice larger than lower, round one; chaetal blades long or short, guards reaching subdistal tooth, most broken]. — 1 specimen, UF 4180, Girona Province, Tossa de Mar, fixed dead, 2-4 m depth, 23.VI.2014, G. Paulay coll. [juvenile, 22 mm long, 4 mm wide, two left ones removed for molecular analysis; twisted specimen, with brownish longitudinal lines throughout body, especially dorsally, laterally lines shorter, becoming long spots in posterior segments, continued to anal tube; body pharynx exposed, basally constricted (distorted) with some pigmentation, margin ciliated band eroded, dorsal papilla low, as long as wide; prostomium slightly as wide as long, with a shallow anterior depression, lateral margins rounded, posterior margin deeply cleft, extended for about ⅓ prostomial length; eyes brownish, anterior ones slightly larger than posterior ones; antennae pale, tapered, longer than

interocular distance; parapodia with cirrophores 3 times as long as wide; cirrostyles basally straight, annulated; chaetal lobe slightly tapered, blunt; acicular lobe double, digitate, upper tine slightly longer than ventral one; neurochaetal blades bidentate, teeth of similar size, guard usually reaching subdistal tooth, rarely passing it]. — 2 specimens, UF 4181, Girona Province, Tossa de Mar (41.7226, 2.9396; 41°43'21.3600"N, 002°56'22.5600"E), 2-4 m depth, 23.VI.2014, G. Paulay coll. [43.0-43.5 mm long, 4.0-4.5 mm wide (1 specimen with two left parapodia removed for molecular analysis); excellent specimens; pigmentation less intense than in UF 4180; pharynx not exposed; prostomium fully relaxed, slightly as long as wide, with a shallow anterior depression, lateral margins slightly rounded, posterior margin deeply cleft, extended for about ⅛ prostomial length; nuchal organs exposed throughout their length; eyes brownish, anterior ones slightly larger than posterior ones; antennae pale, tapered, longer than interocular distance; parapodia with cirrophores three times as long as wide; cirrostyles basally straight, annulated; chaetal lobe slightly tapered, blunt; acicular lobe double, digitate, upper tine twice longer than ventral one; neurochaetal blades bidentate, teeth of similar size, guard reaching subdistal tooth]. — 1 specimen, MCZ 1158, Adriatic Sea, Heller coll., no further data [24 mm long, 4 mm wide; colorless, laterally bent; eyes dark brown, anterior ones slightly larger than posterior ones (in lateral view twice as large); antennae smaller than interocular distance; dorsal cirri very long, markedly articulated throughout its length; ventral cirri smooth, markedly longer than chaetal lobe; acicular lobe double; neurochaetal blades long, guard mostly eroded, reaching subdistal tooth].

Mediterranean, locality not precised. 4 specimens, RMNH 280, no further field data [32-75 mm long, 4-8 mm wide; colorless, two with glass bubbles for exhibition; body antennae broken in 3 specimens, smallest with antennae digitate, 4-5 times as long as wide; eyes visible in 2 specimens, anterior eyes twice as large as posterior ones, posterior eyes with lens centrally positioned; chaetal lobes invaginated, all with acicular lobe double, blunt, upper tine markedly longer than lower tine].

Northeastern Atlantic, France. 7 specimens, MNHNIA-PNT91n (formerly jar 70x), Saint-Jean-de-Luz, 1.II.1891 and 21.III.1892, A. Saint-Joseph coll. [47-62 mm long, 5-6 mm wide; splendid specimens, three with pharynx fully everted, several with eyes with pigmentation, one with a longitudinal dissection passing the body completely and used for details of pharynx muscles; body tapered, all with acicular lobe double, if small of the same size, if larger, upper tine longer]. — 3 specimens, MNHN-IA-PNT106 (formerly jar Coll. de Saint-Joseph, 20), Saint-Jean-de-Luz, 27.III.1892 [58-63 mm long, 4.0-5.5 mm wide; all with pharynx exposed and eyes pigmented]. — 5 specimens, MNHN-IA-PNT91o (formerly jar 70y), Saint-Jean-de-Luz, 1.VIII.1903, A. Saint-Joseph coll. (47-68 mm long, 6-8 mm wide; splendid specimens, three with pharynx fully everted, body fusiform, one with anteroventral dissection already made; parapodium of the smallest and largest specimens removed for acicular features (kept in same container); all with acicular lobe double, neuraciculae capitate]. — 4 specimens, MNHN-IA-PNT91p (formerly jar 70z), Saint-Jean-de-Luz, 1.VIII.1903, A. Saint-Joseph coll. [16-22 mm long, 2-3 mm wide; acicular lobes double; largest specimen dissected middorsally, coelomic contents removed, stained with Carmin Red, anterior and posterior fragments from the same specimen, and two small complete specimens, laterally contracted]. — 8 specimens, MNHN-IA-PNT91q (formerly jar 70x), Saint-Jean-de-Luz, data unreadable in ancient label, A. Saint-Joseph coll. [54-63 mm long, 5-6 mm wide; colorless; 4 with pharynx variable everted; acicular lobes double; acicular tips capitate; 1 specimen with right antenna basally bifurcated]. — 3 specimens, MNHN-IA-PNT91r (formerly jar 70), Concarneau (47°52'31"N, 03°55'08"W), no further data [40-48 mm long, 5-7 mm wide; acicular tips become more spinulose in larger specimens].

Northwestern Africa. Cape Verde Islands. 5 specimens, ZMUC 2433, off São Pedro Bay, São Vicente Island, RV *Atlantide* Expedition, Sta. 40, 32 m (in publication) or 100 m (label), 11.XII.1945, J. B. Kirkegaard coll. [20-32 mm long, 3 mm wide; complete, two with prostomia invaginated, bent ventrally, two others ventrally bent with prostomia exposed, the last one with pharynx exposed; colorless, dorsal cirrostyle cylindrical, smooth; acicular lobe double, digitate, upper tine about twice longer than lower one; neurochaetal blades bidentate, upper chaetae with smaller teeth, lower ones with larger teeth; guard fragile, in a few chaetae approaching distal tooth]. — 1 specimen, MNHN-IA-PNT90d (formerly jar 372c), RV *Calypso*, Campagne aux îles du Cap Vert 1959, Sta. 34, 0.5 km SW off Santa Encarnação, 20-25 m depth, 20.XI.1959 [20 mm long, 3 mm wide; colorless, anteroventrally dissected, including a longitudinal cut throughout pharynx; several parapodia previously removed; antennae 3-4 times as long as wide; eyes brownish, anterior ones twice larger than posterior ones; acicular lobe double, upper tine slightly longer than lower one; neurochaetae about 20 per bundle, blades bidentate, many lost, distal tooth larger, guard mostly eroded, if complete, approaching distal tooth].

Western Sahara (Morocco). 1 specimen, ZMH-P 17727, RV *Meteor*, Cruise 36, Sta. 115 (21°17.1'N, 17°10.2'W), 50 m depth, 3.III.1975 [49 mm long, 5 mm wide; partially dried-out, pharynx exposed, integument annulated; most cirri and chaetal blades on site; antennae and eyes not visible due to integument foldings; right parapodia of chaetigers 2 and 9 removed for observation (kept in vial); parapodial lobes variably contracted; neuraciculae blackish, thick, tapered; acicular lobes double, massive, blunt, neurochaetal blades bidentate, guards mostly broken, a few blades with guards approaching distal tooth]. — 3 specimens, ZMH-P 17728, RV *Meteor*, Cruise 36, Sta. 118(?), 3.III.1975 [26-32 mm long, 3.0-3.5 mm wide; partially dried-out, integument annulated; most cirri and chaetal blades on site; one with pharynx exposed, another one with most cirri and chaetae broken; antennae digitate 2-3 times as long as wide; eyes colorless, anterior ones twice larger than posterior ones; parapodial lobes variably contracted; neuraciculae blackish, thick; acicular lobes double, massive, blunt, upper tine twice as long as lower, rounded one; neurochaetal blades bidentate, guards mostly broken, a few blades with guards approaching distal tooth].

Gulf of Guinea. 12 specimens, MNHN-IA-PNT90f (formerly jar 372b), (plus one syllid ant. fragm.), RV *Calypso*, Campagne Golfe de Guinée, Sta. 1 (21°05'N, 17°14'W), off Cap Blanc Peninsula, sand, 43-45 m depth, 10.V.1956 [20-41 mm long, 3-4 mm wide; variably distorted by compression, most with pharynx exposed; colorless; antennae 3-4 times as long as wide; eyes rounded, brownish, anterior ones slightly larger to twice as large as posterior ones; dorsal pharynx papilla rounded, slightly as wide as long; dorsal cirrophore 2-3 times as long as wide; cirrostyle basally cylindrical, smooth, medially annulated, distally articulated; acicular lobe double, blunt, upper tine slightly longer than lower one; neurochaetae about 30 per bundle, blades bidentate, subdistal tooth smaller, guard usually eroded, if complete, approaching distal tooth]. — 2 specimens, MNHN 372b, RV *Calypso*, Campagne Golfe de Guinée, Sta. 1 (21°05'N, 17°14'W), off Cap Blanc Peninsula, sand, 43-45 m depth, 10.V.1956 [33-46 mm long, 4-5 mm wide; macerated, damaged, distorted by compression, most cirri and chaetae lost; one with pharynx exposed; colorless; anterior end features damaged; dorsal pharynx papilla rounded, as wide as long; neurochaetae about 25 per bundle, blades bidentate, subdistal tooth smaller, guard usually eroded, if complete, approaching distal tooth].

Southwestern Africa. Angola. 1 specimen, RBINS unnumb., Expédition océanographique belge dans les eaux côtières africaines de l'Atlantique Sud 1948-1949, Sta. 116 (after label; Fauvel indicated it was from station 106; 09°20'S, 13°04'E), 13 km W Rio Cuanza, 17 m depth, 31.I.1949 [macerated, apparently fixed in ethanol; body pale, soft, cirri transparent; pharynx exposed, dorsal papilla as wide as long; antennae small, barely visible, right one lost, left one with tip eroded; eyes unpigmented, after methyl green staining, anterior eyes twice as large as posterior ones; dorsal cirrophores about twice as long as wide; parapodial lobes contracted; chaetal bundles barely visible; neuraciculae blackish, tapered; acicular lobe double; neurochaetal blades bidentate, guard approaching distal tooth].

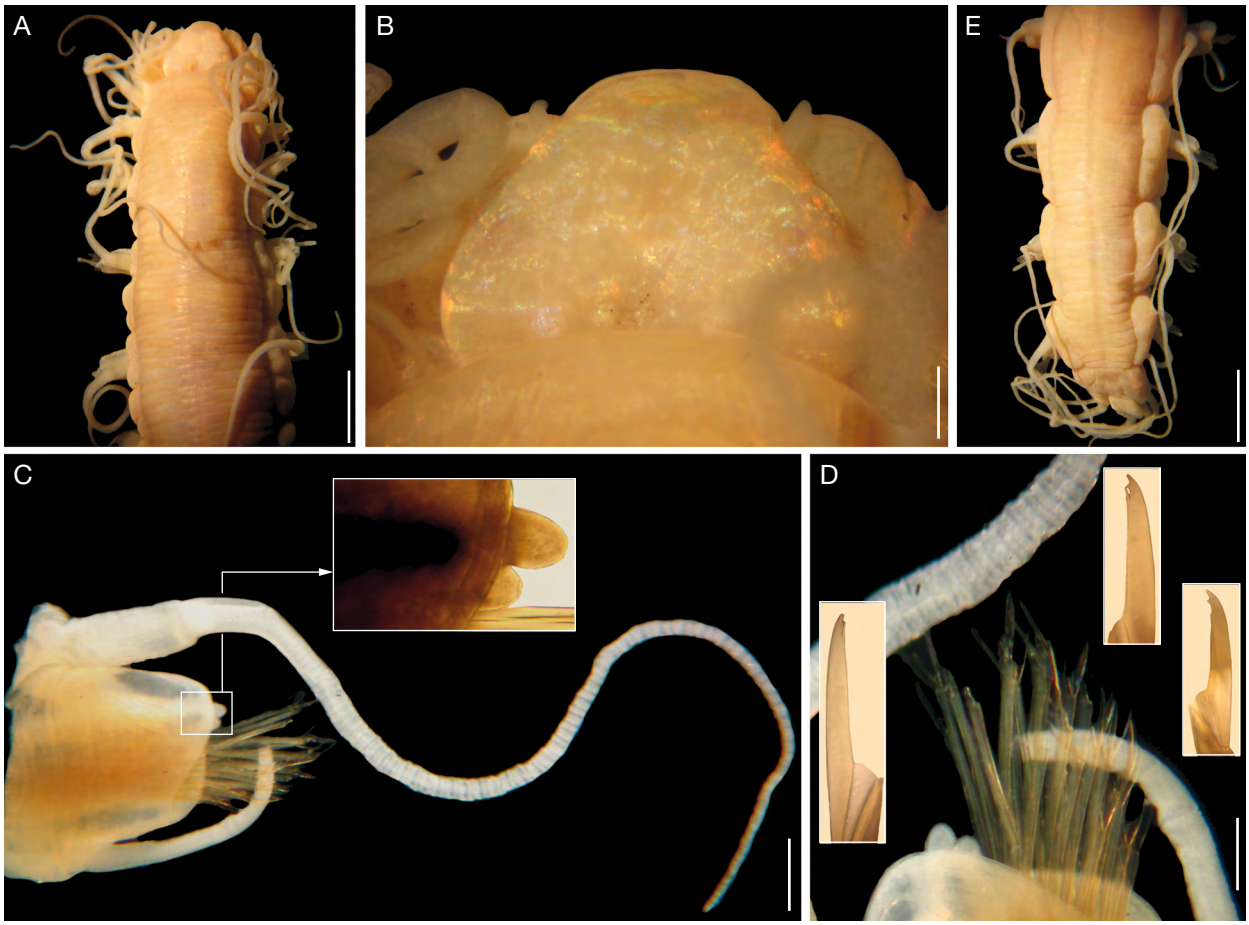

Fig. 49. — *Hesione sicula* delle Chiaje, 1830, reinst., holotype of *H. steenstrupi* Quatrefages, 1866, MNHN-IA-TYPE0479: **A**, anterior region, dorsal view; **B**, prostomium; **C**, chaetiger 10, left parapodium, anterior view (inset: acicular lobe); **D**, same, neurochaetae (insets: blades); **E**, posterior region, dorsal view. Scale bars: A, 1.5 mm; B, D, 0.3 mm; C, 0.5 mm; E, 1.9 mm.

Distribution. — From the Gulf of Vizcaya to the Northwestern African region, including the Mediterranean Sea. Records for more tropical localities like the Gulf of Guinea are dubious and the specimens might belong to another species. In mixed bottoms, from the intertidal to 50 m depth.

Diagnosis. — *Hesione* with prostomium curved laterally; parapodia with dorsal cirri basally cylindrical, dorsal cirrophore three times as long as wide; larger acicula blackish; acicular lobe double, tines short, blunt, upper tine slightly longer than lower one; neurochaetal blades bidentate, 4-6 times as long as wide; subdistal tooth smaller than distal one, with guards approaching distal tooth.

Description

Neotype of *H. sicula,* ZMB 7529, complete, subcylindrical (Fig. 48A), tapered posteriorly, slightly bent ventrally, with a longitudinal dissection over lateral cushions along chaetigers 4-13. Body 45 mm long, 5 mm wide (left parapodium of chaetiger 9 removed for observation, kept in smaller container in same vial).

Holotype of *H. steenstrupi,* MNHN-IA-TYPE0479 (indicated as holotype below) without pigmentation (Fig. 49A) in ethanol; body 43 mm long, 4 mm wide (left parapodia of chatigers 6 and 10 removed for observation, now kept in plastic vial with the holotype).

Prostomium as wide as long, anterior margin barely projected, covered by basal pharynx ring corrugations, lateral margins rounded, widest in anterior eyes region, posterior margin with a shallow depression, partially covered by anterior margin of tentacular segment, reaching slightly behind posterior eyes (Fig. 48B). Antennae digitate, three times as long as wide, as long as interocular distance. Eyes brownish, anterior ones twice larger than posterior ones, posterior eyes with lenses directed posteriorly (holotype with antennae fusiform, 3 times as long as wide; eyes colorless [Fig. 49B]).

Tentacular cirri long, with tips eroded, longest ones reaching chaetiger 5. Lateral cushions low, slightly projected, smooth, separated into three (anteriorly) or two sections.

Parapodia with chaetal lobes truncated, as long as wide; dorsal cirri with cirrophores 3 times as long as wide; cirrostyles basally cylindrical, annulated, articulated medially and distally, tips lost (Fig. 48C), probably longer than body width including parapodia (length confirmed in holotype Fig. 49C). Ventral cirri smooth, slightly rugose medially and distally, surpassing chaetal lobes.

Neuraciculae blackish, cylindrical, tapered, larger one often subdistally swollen, mucronate; thinner one tapered. Acicular lobe double, tines blunt, short, upper one slightly longer

than lower one (Fig. 48C [inset]) (confirmed in holotype Fig. 49C [inset]).

Neurochaetae about 30 per bundle (about 20 in holotype), handles honey-colored, blades bidentate (many lost), blades at a certain angle from handle, 4-5 times as long as wide, slightly decreasing in size ventrally, each with smaller to equal-sized subdistal tooth, guards delicate, most broken (Fig. 48D [insets]), approaching subdistal tooth, if complete, approaching subdistal one (confirmed in holotype Fig. 49D [insets], or Fig. 51C [insets]).

Posterior end tapered into a blunt cone; pygydium smooth (Fig. 48E; slightly depressed in holotype, Fig. 49E), anus with seven low, rounded anal papillae.

Pharynx exposed, divided into three rings; basal ring corrugated, shortest; medial and distal rings of similar length, distal ring with a thick glandular margin, cilia mostly eroded; dorsal papilla rounded, distorted by ring foldings (Fig 48A, B). Whitish, anastomosing gonadal tubules visible through previously made dissection; a small fragment removed from chaetiger 14, without mature oocytes.

Pigmentation

Pigmentation pattern observed in a recently collected specimen, UF 4180: dorsal surface with irregular, thin, solid longitudinal bands, barely interrupted intersegmentally (Fig. 50A), better defined along anterior region, more irregular in posterior region (Fig. 50D), extended into lateral cushions. Middorsal surface with irregular pale spots, rounded, less defined in posterior region. Prostomium with anterior marginal brownish band, projected posteriorly medially and to anterior eyes, with some pale spots just ahead of anterior eyes (Fig. 50B); posterior prostomial half pale. Brownish pigmentation extended into basal pharynx half, progressively paler, dorsal papillae pale, rounded. Tentacular segment, tentacular and dorsal cirri pale. Neuropodia extended, blunt, about twice as wide as long (Fig. 50C).

Among the Saint-Joseph collection in the Paris museum, one specimen preserved over 100 years ago, surprisingly retained its pigmentation pattern (Fig. 51A): dorsal surface markedly annulated, with brownish longitudinal bands interrupted by integument foldings into spots, round to polygonal, usually with a central paler thin band, more or less arranged into longitudinal, discontinuous series (Fig. 51B), continued to the end of body (Fig. 51E); these longitudinal irregular bands are extended into lateral cushions, but segmentally interrupted by irregular, as wide as long pale middorsal spots, on parapodial lobes level, sometimes another pale area basal to parapodial lobes. Prostomium (Fig. 51C), tentacular segment, tentacular and dorsal cirri without pigmentation.

Variation

Among the same splendid specimens referred to above, MNHN IA-PNT 106 (formerly de Saint-Joseph 20), three variations must be indicated. First, the left antenna diverges into two tines (Fig. 51C), and this separation is from a common base. Second, in another specimen, the right posterior eye is duplicated, but coalescent, such that it looks twice as large as the left posterior eye (Fig. 51D). Third, the dorsal papillae can be low, as wide as long (Fig. 51C, asterisk) or markedly projected as a blunt, twice as long as wide lobe (Fig. 51D [asterisk]). On the other hand, a small specimen, MNHN-IA-PNT91s (formerly 70-190a), 32 mm long, 5 mm wide has acicular lobe double, upper tine twice as long as lower one.

Remarks

Hesione sicula delle Chiaje, 1830 has a complex, confusing taxonomic perspective (see below); together with *H. pantherina*, they live in the Mediterranean and adjacent regions, and despite being regarded as synonyms, they are different. As indicated above, a neotype was proposed for *H. pantherina*, and it was restricted; a similar approach is needed for *H. sicula* in order to clarify its taxonomic status (ICZN 1999: art. 75.3.1). The neotype of *H. sicula* was described above and the differences to other species are listed below (ICZN 1999: art. 75.3.2, 75.3.3). There were no type specimens deposited by delle Chiaje (ICZN 1999: art. 75.3.4), and the neotype and additional specimens have the same set of diagnostic features (ICZN 1999: art. 75.3.5). Further, the neotype was collected in the same region in the Gulf of Naples (ICZN 1999: art. 75.3.6), and it is now deposited in the Berlin museum (ICZN 1999: art. 75.3.7).

Hesione pantherina, and *H. sicula* together with *H. steenstrupi* Quatrefages, 1866 were all described from the Northeastern Atlantic and Mediterranean region having a colorful, reddish-brown pattern on their bodies. As indicated above, parapodial features, especially the type of acicular lobes, were not included in the original description of any of these three species. The observations on a small specimen of *H. sicula* (MNHN-IA-PNT91s, formerly 70-190a, 32 mm long, 5 mm wide) confirm that acicular lobes are double, with upper tine twice longer than lower one. Consequently, the development of acicular lobe is not size-dependent; further, in *H. pantherina* acicular lobes are single and its specimens do not reach the same large size as those of *H. sicula* (incl. *H. steenstrupi*).

Saint-Joseph (1898) provided a detailed illustration of parapodia for what he regarded as *H. pantherina* and illustrated acicular tips. The main diagnostic features in his plate 19 were that antennae are shorter than interocular distance (Fig. 131), acicular lobes are double and blunt (Fig. 135), neuraciculae are slightly capitate with tiny spines on its tip (Fig. 137), chaetal blades are bidentate with subdistal tooth larger than distal tooth, and guard approaches subdistal tooth (Fig. 136). As indicated below, these features match *H. steenstrupi* and his material was collected in Saint-Jean-de-Luz, close to the type locality (Guethary), in the Gulf of Vizcaya. Further, Saint-Joseph (1898) compared specimens from Naples and concluded that they were identical with his materials from the Atlantic French coast, leading him to conclude that the three species were synonyms. It is true that *H. sicula* and *H. steenstrupi* have acicular lobes double, and there are subtle differences in the color of neurochaetal handles, being honey-color in *H. steenstrupi* and chocolate-color in *H. sicula*, besides the pigmentation differences in body and neurochaetal handles. Consequently, it is difficult to regard them as distinct species,

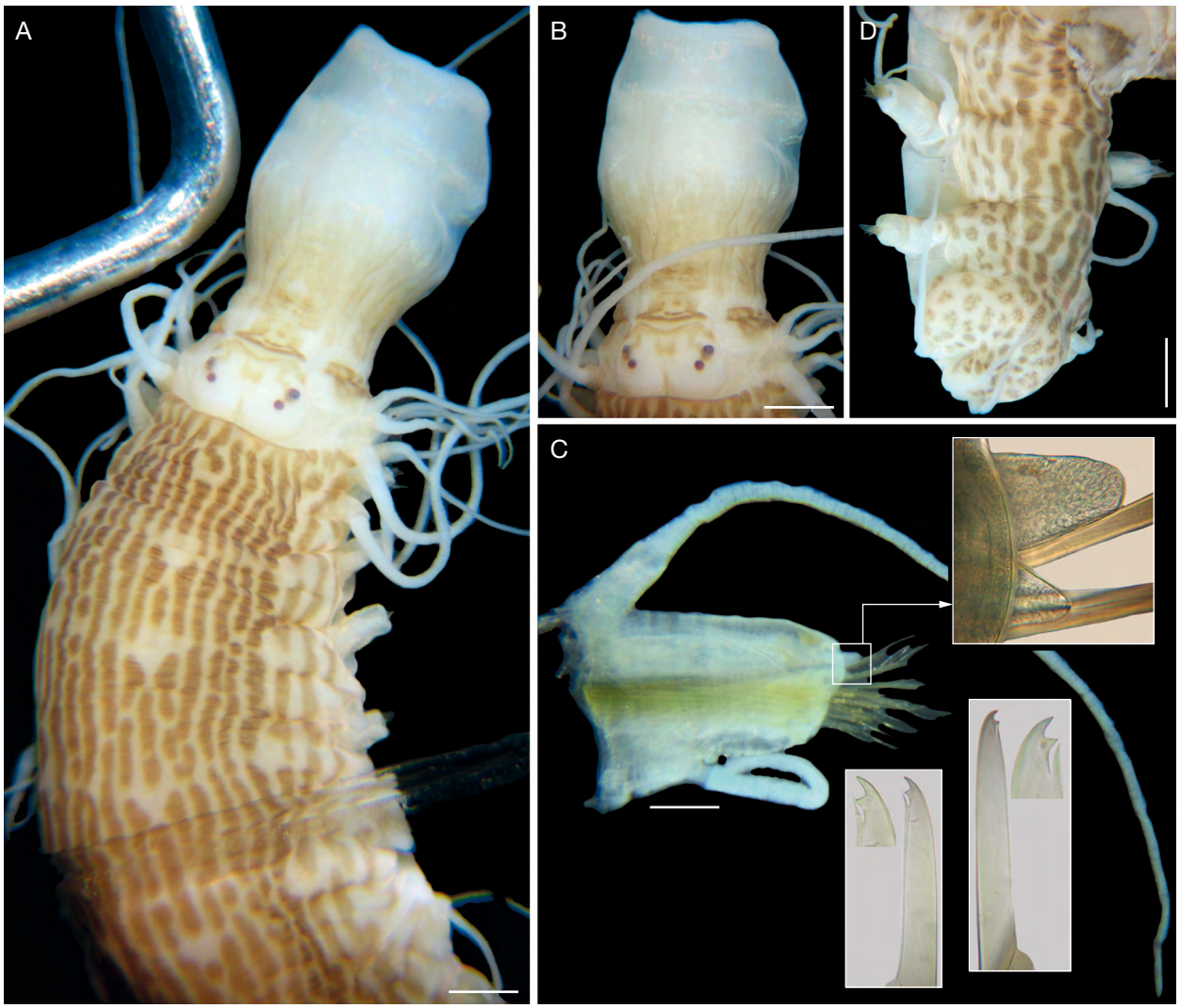

Fig. 50. — *Hesione sicula* delle Chiaje, 1830, reinst., non-type specimen, UF 4180: **A**, anterior region, dorsal view; **B**, prostomium and everted pharynx, dorsal view; **C**, chaetiger 9, left parapodium, anterior view (insets: acicular lobe, upper and lower chaetal blades); **D**, posterior region, oblique dorsal view. Scale bars: A, 0.7 mm; B, 0.8 mm; C, 0.4 mm; D, 0.9 mm.

and *H. sicula* has priority over *H. steenstrupi*. On the other hand, as indicated above, *H. pantherina* has acicular lobes single, and this difference is enough to separate it from the two other ones. Pleijel (1998: 159) indicated that *H. sicula* could be a junior synonym of *H. pantherina*; after the comparision of specimen originating from area close to the type locality and additional material of both species, it is herein concluded they are different species.

As indicated above, Fauvel (1923a: 234) followed the Saint-Joseph conclusion on synonymy and regarding acicular lobes, he indicated that "au-dessus des soies une ou deux petites languettes coniques, souvent rétractées" (Transl.: over the chaetae there is one or two small conical lobes, often retracted). Fauvel was actually reiterating something he had concluded before (Fauvel 1911: 375) when he recorded *H. pantherina* for the Persian Gulf, rejected the use of the acicular lobe as a diagnostic feature, and indicated that "j'observe à cet égard une grande variabilité, non seulement d'un individu à l'autre mais encore d'un parapode à l'autre sur un même animal". (Transl.: I observe about this a large variability, not only from one specimen to the other but even from one parapodium to another in the same specimen). This is incorrect and by taking a look at the corresponding illustrations (Fauvel 1911: 375; fig. IV), it is clear that the parapodia were mounted differently by the relative position of the ventral cirri, such that if these parapodia came from the same specimen they were probably drawn from different perspectives, or worse, they belong to different specimens.

Regarding pigmentation, delle Chiaje (1841a: 95) indicated: "Corpo […] roseo tigrato di ovali macchiette rosso-fosche, giù cerulescente con duplice filiera mediana di macchie rossastre; testa rosso-iridea[…]" [Transl.: Body banded as a tiger with oval reddish spots, pale grayish with double medial reddish series, head iridescent red…]. Some additional details were given by de Quatrefages (1866: 96, 97, as *H. steenstrupi*): "bruneo longitudinaliter striatum" [Transl.: brownish striated longitudinal

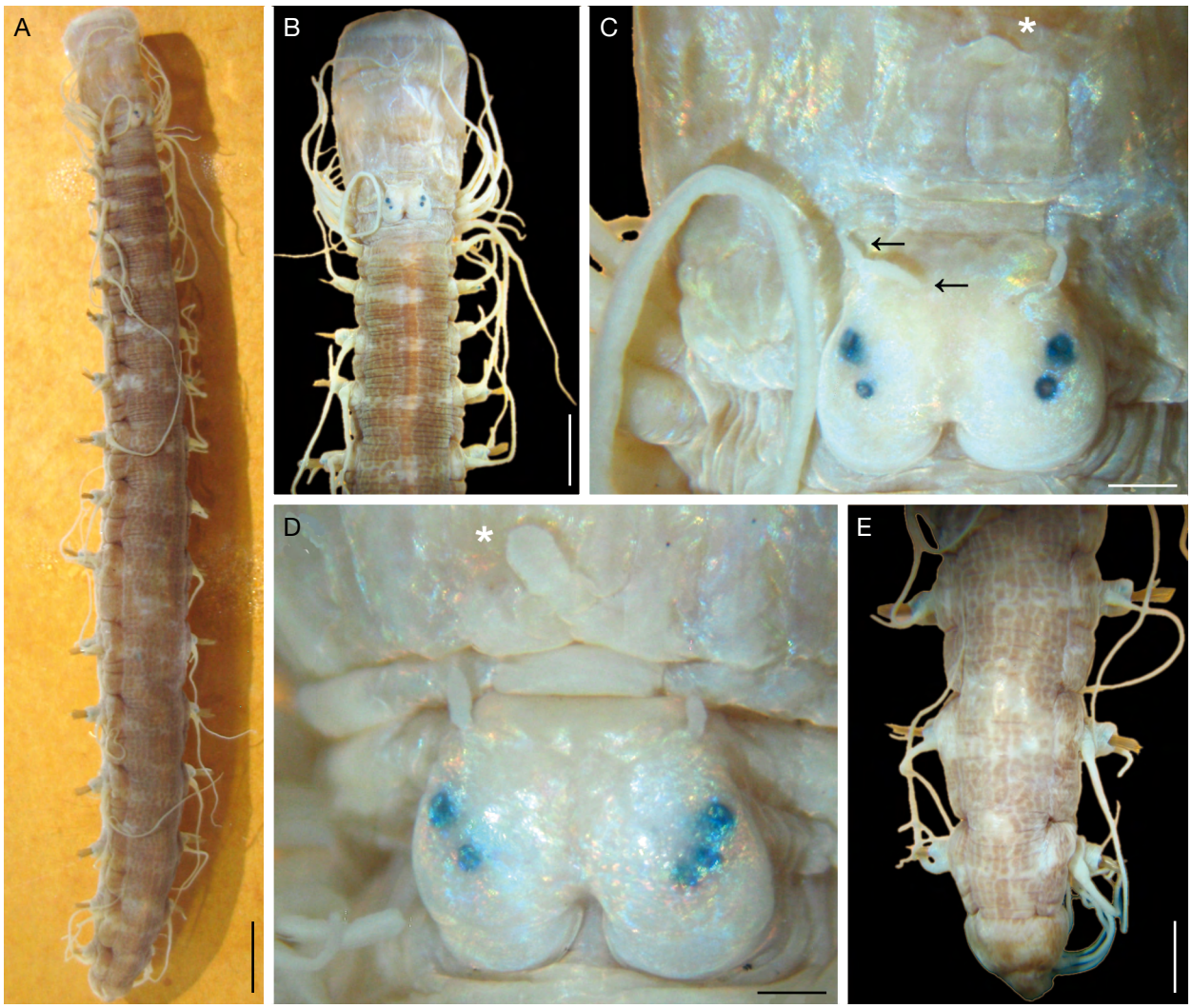

Fig. 51. — *Hesione sicula* delle Chiaje, 1830, reinst., non-type specimens, MNHN IA-PNT-106 (formerly jar de Saint-Joseph 20): **A**, complete, oblique dorsal view; **B**, anterior region, pharynx exposed, dorsal view; **C**, prostomium and base of pharynx, dorsal view (arrows point to left lateral antennae, asterisk indicates dorsal papilla); **D**, another specimen, prostomium and base of pharynx, dorsal view (asterisk indicates dorsal papilla); **E**, another specimen, posterior region, dorsal view. Scale bars: A, 4 mm; B, 2.4 mm; C, 0.5 mm; D, 0.4 mm; E, 1.8 mm.

lines], or "Le dessus du corps est strié de blanc jaunatre et de brun. La separation des 7-8 premiers anneaux est nettement indiquée par une bande transversale tirant sur le jaune. Vers le 7e anneau, une ligne blanche nait sur le côté, se pronounce de plus en plus en arrière, et s'élargit en un point blanc diffus à chaque séparation." [Transl.: The back of the body is streaked by yellowish white and brown. The separation of the first 7-8 rings is clearly indicated by a transverse yellowish band. Over the 7th ring, a white line starts over the side, is progressively more defined posteriorly, and enlarges into a diffuse white point on each separation]. Saint-Joseph (1898: 330) confirmed this pattern: "Le côté dorsal d'un brun rougeâtre est parcouru par 8 à 10 raies longitudinales blanches qui sont coupées à angle droit par de nombreuses raies blanches transversales, de sorte que le corps paraît moucheté de brun et réticulé de blanc… Quatre bandes blanches transversales assez larges relient l'un à l'autre les pieds des segments 2 à 5, et quelquefois ceux de presque tous les autres… Enfin, quelques exemplaires ont une grosse tache blanche au milieu du dos de chaque segment." [Transl.: The brown reddish dorsal side is browsed by 8-10 longitudinal stripes that are cut in right angles by numerous transverse stripes, such that the body appears with brownish spots and reticulated by white […] Four large transverse white bands connect the parapodia in segments 2-5, and sometimes those of nearly all others […] Finally, some specimens have a large white spot middorsally in every segment]. The record by Fauvel (1953a: 18, Sta. 122) indicated the body had dark brown transverse bands, subdivided by thin white lines, approaching *H. picta*. However, this specimen is a *Leocrates* cf. *diplognathus*; it differs from the China Sea specimens by having longer palpophores, and double J-shaped nuchal organs, which rather corresponds with an undescribed species. Further, the record of *H. picta* for the Cape Verde islands by Rullier (1964: 155) cannot be confirmed because his specimen was without pigmentation when he studied it, and its neurochaetal blades do not match the *H. picta* pattern as illustrated above, and it is

being regarded as belonging to *H. sicula*. The records for the Gulf of Guinea by Fauvel & Rullier (1959a: 512; b: 158) are included here with hesitation because they indicated there were transverse bands ("quelques rayures transversales"), instead of the typical longitudinal, discontinuous lines. Further, the specimen was somehow distorted preventing separating them into another species. Better specimens are needed to clarify this point. Likewise, the specimen from Angola (Fauvel 1953a) is very poorly preserved as to be confidently included with this species, and is listed above with hesitation.

Hesione splendida Savigny *in* Lamarck, 1818 (Figs 52-54)

Hesione splendida Savigny *in* Lamarck, 1818: 316. — Savigny 1822: 40, pl. 3, fig 3.1-3.7. — de Blainville 1825: 443; 1828: 482; 1830, pl. 17, fig. 1 (copied from Savigny). — Audouin & Milne-Edwards 1833: pl. 15, figs 1-3. — de Quatrefages 1866: 95-96. — Day 1967: 228, fig. 11.2A-C. — Solís-Weiss *et al.* 2004: S5.

Hesione ehlersi Gravier, 1900: 175-179, figs 42-45, pl. 9, figs 14, 15. — Wehe & Fiege 2002: 57 (**n. syn.**). — Solís-Weiss *et al.* 2004: S5.

Hesione pantherina – Fauvel 1918: 332, 333; 1927: 417. — McIntosh 1924: 15, 16; 1925: 40-41, pl. 5, fig. 4 (upside down). — Day 1951: 21 (*non* Risso 1826).

Hesione reticulata – Stagl *et al.* 1996: 34, table 2 (*non* von Marenzeller, 1879).

TYPE MATERIAL. — **Western Indian Ocean, Red Sea.** Lectotype of *Hesione splendida,* MNHN-IA-TYPE0140, designated herein, originally collected in the Suez Gulf, M. Botta coll., no further data. Paralectotype of *H. splendida,* MNHN-IA-TYPE0139, smashed down (probably by labels), partially dehydrated, Île-de-France (Mauritius), M. Mathieu coll. [55 mm long, 6 mm wide, 15 chaetigers; pharynx exposed, posterior end lost; no other morphological feature can be noticed (right parapodium of chaetiger 8 removed) acicula black, thick, single; acicular lobe single, blunt; neurochaetae about 40 per bundle, neurochaetal blades mostly lost, remaining ones bidentate, subdistal tooth minute, guard approaching subdistal tooth]. Syntypes of *Hesione ehlersi*, MNHN 287, Djibouti, 1897, H. Coutière, coll. [used for Redescription].

ADDITIONAL MATERIAL. — **Red Sea.** 1 specimen, BMNH 1926.11.12.10, Cambridge Suez Canal Expedition, Suez, Sta. T8, 9.XII.1924, no further data [21 mm long, 4 mm wide; body straight, medially wider, integument smooth, colorless; antennae digitate, 2-3 times as long as wide; right parapodium of chaetiger 8 removed for observation (kept in vial); acicular lobe single, tapered; neurochaetae most broken, blades bidentate, subdistal tooth smaller than distal one; guards broken, approaching subdistal tooth]. — 2 specimens, BMNH 1926.11.12.11/12, Cambridge Suez Canal Expedition, Suez, Sta. T8, 4.XII.1924, no further data [one distorted by compression, the other straight; straight one 30 mm long, 6 mm wide; both medially wider, integument smooth, colorless; antennae digitate, 2-3 times as long as wide; acicular lobe single, tapered; neurochaetae with blades bidentate, subdistal tooth smaller than distal one; guards, if entire, approaching distal tooth]. — 1 specimen, BMNH 1926.11.12.14, Cambridge Suez Canal Expedition, Suez, Sta. K9, 25.X.1924, no further data [29 mm long, 4.5 mm wide; bent dorsally, medially wider, integument smooth, colorless; antennae digitate, 2-3 times as long as wide; acicular lobe single, tapered; neurochaetae most without blades; pharynx exposed, dorsal papilla minute, slightly as wide as long]. — 1 specimen, BMNH 1926.11.12.15, Cambridge Suez Canal Expedition, Suez, Sta. El Ferdane, 27.X.1924, no further data [22 mm long, 5 mm wide; medially wider, integument smooth, colorless; antennae digitate, 2-3 times as long as wide; right posterior eye duplicated, almost fused to anterior right eye; several chaetal lobes invaginated; acicular lobe single, tapered; neurochaetae complete, blades bidentate]. — 1 specimen, BMNH 1926.11.12.17, Cambridge Suez Canal Expedition, Suez, Sta. P1, 13.XII.1924, no further data [21 mm long, 4 mm wide; body depressed, medially wider, integument smooth, colorless; antennae digitate, 2-3 times as long as wide; all chaetal lobes exposed; acicular lobe single, tapered, if fully extended, about as 1/10 as long as neurochaetae]. — 1 specimen, BMNH 1926.11.12.18, Cambridge Suez Canal Expedition, Suez, Sta. T9, dredge, 6.XII.1924, no further data [20 mm long, 2.5 mm wide; body slightly bent dorsally, integument smooth, annulated, colorless; antennae digitate, 2 times as long as wide; anterior eyes obliquely as long as wide; chaetal lobes variably invaginated; acicular lobe single, tapered; pharynx exposed, apillae small, as long as wide]. — 2 specimens, MNHN-IA-PNT91t (formerly jar 70), Djibouti Bay, in *Ircinia* cavities, with amphinomids, eunicids and nereidids, 13.I.1904, C. Gravier coll. [27-31 mm long, 3-4 mm wide; body pearly gray, with tiny black spots irregularly distributed along body; body slightly distorted, one with pharynx fully exposed, dorsal papilla round, as long as wide; neuraciculae tapered; acicular lobe single, tapered or blunt]. — 1 specimen, MNHN-IA-PNT107 (formerly jar 419), Ayna Massa, Gulf of Suez, no further data [52 mm long, 6.5 mm wide (right parapodia of chaetigers 7 and 16 removed for observation, kept in vial); integument rugose, shiny; antennae tapered, 2-3 times as long as wide; eyes rounded, anterior ones darker, slightly larger than posterior ones; pharynx exposed, dorsal papilla slightly as wide as long; acicular lobe single, digitate; neurochaetae about 30 per bundle, neurochaetal blades bidentate, subdistal tooth smaller, guard approaching distal tooth]. — 1 specimen, MNHW unnumb., Ehrenberg coll. [28 mm long, 4 mm wide; macerated but integument still shiny, smooth; pharynx fully everted with three muscular rings; eyes colorless, visible after short-term staining with methyl-green; antennae short, only right one left, digitate, 2.0-2.5 times as long as wide, tip broken; neuraciculae black, tapered; acicular lobe single; neurochaetal blades transparent, body]. — 2 specimens, NHMW 575, *Pola* Red Sea Expedition 1895-1898, no further data [20-30 mm long, 2-3 mm wide; partially dried out; one pale brown, the other grayish, both with pharynx exposed; integument shiny; antennae shorter than posterior eyes diameter; antennae minute, digitate, about twice as long as wide, difficult to be seen because of pharyngeal folds; parapodia with neuraciculae blackish, tapered, single; acicular lobe single; most neurochatal blades lost]. — 7 specimens, ZMB 534, and one slide, Egypt, Gulf of Suez, Janub Sina', El Tor, Ehrenberg coll. [27-33 mm long, 4.0-5.5 mm wide; specimens probably collected in different dates because they differ in their condition; one is too macerated, whereas two others are in much better condition; four paler, two other darker; body antennae digitate, often eroded, as long as interocular distance; anterior eyes about twice as large as posterior ones; neuraciculae thick, blackish, tapered; acicular lobe single; neurochaetal blades bidentate, most broken, guards, if complete, approaching distal tooth]. — 5 specimens, ZMB 535, and one slide (535a), Egypt, Gulf of Suez, Janub Sina', El Tor, Ehrenberg coll. [30-46 mm long, 4-7 mm wide; variably macerated, one whitish, three grayish, one brownish with scattered white spots like bacteria or fungi growing on it; parapodial lobes invaginated, neuraciculae blackish, thick, tapered; acicular lobes single, tapered; neurochaetal blades bidentate, guards, if complete, approaching distal tooth]. — 1 specimen, ZMB 3805, and one slide made by Dr Bergmann, no further data [57 mm long, 6 mm wide; dissected throughout the body to study inner organs; prostomium removed; acicular lobe double, short, rounded, upper tine about twice as long as lower one; neurochaetal blades bidentate, anterior ones with teeth smaller, guard approaching subdistal tooth]. — 1 specimen, ZMB 3806, and one slide, Grube Collection, Ehrenberg coll. [25 mm long, 5 mm wide; macerated; some left parapodia previously removed; integument

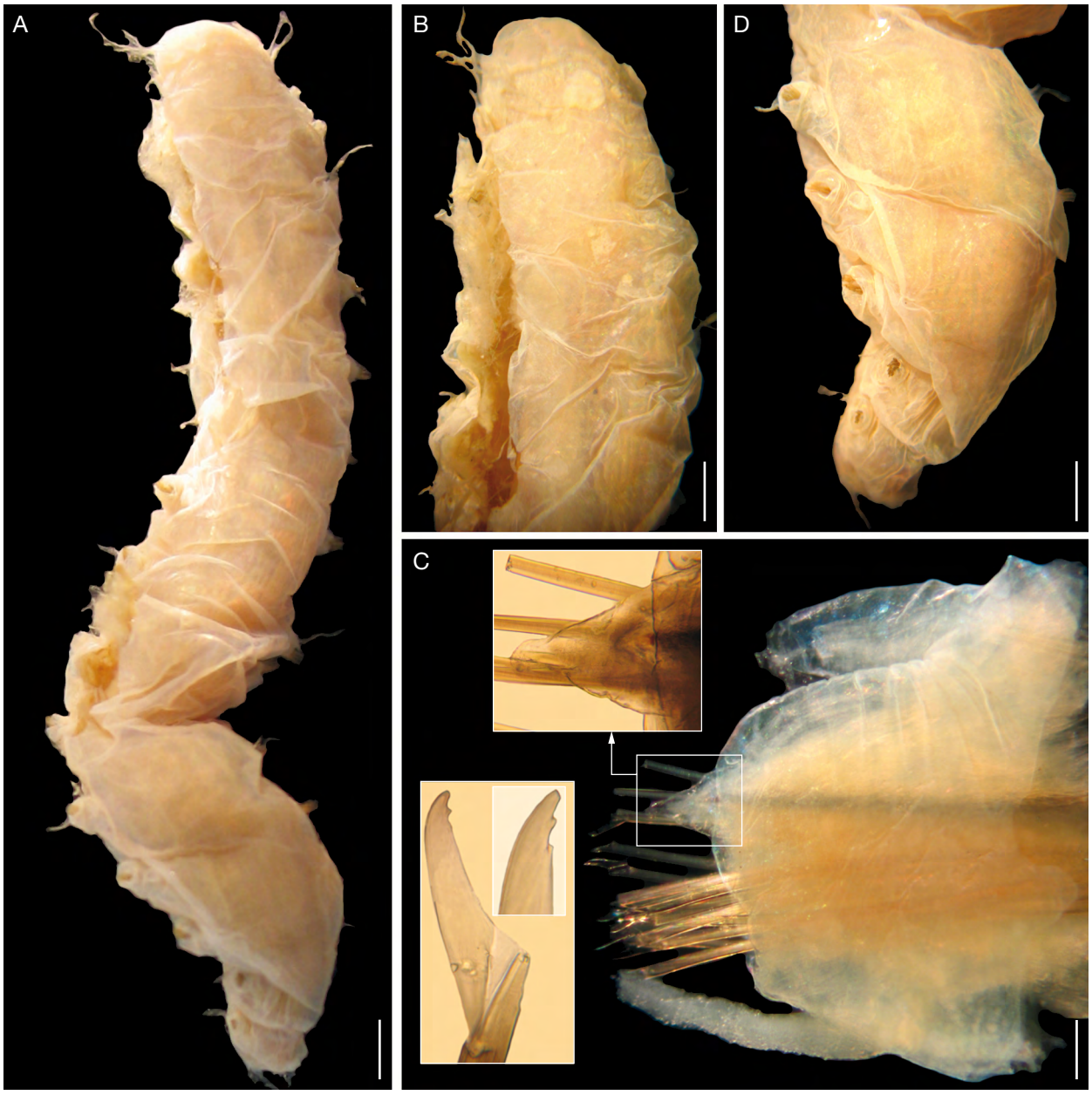

Fig. 52. — *Hesione splendida* Savigny *in* Lamarck, 1818, lectotype, MNHN-IA-TYPE-140: **A**, dorsal view, note the longitudinal eccentric dissection; **B**, anterior region, dorsal view; **C**, chaetiger 8, right parapodium, anterior view (insets: close-ups of acicular lobe and tips of blades); **D**, posterior region, oblique dorsal view. Scale bars: A, 2.3 mm; B, 1.7 mm; C, 0.2 mm; D, 1 mm.

shiny, grayish; pharynx exposed, dorsal papillae rounded, slightly as wide as long; antennae digitate, 4-5 times as long as wide; eyes colorless; acicular lobe single, long, tapered; neurochaetal blades bidentate, guard approaching subdistal tooth].

Western Indian Ocean. Oman. 1 specimen, UF 46, Masirah Island, 2 to 4 km S of SE tip of Island, coarse sand and rocks, 20-22 m depth, 8.XI.1999, G. Paulay coll. [35 mm long, 7 mm wide; colorless, integument areolated, not tuberculated as in *H. intertexta*; antennae minute, smaller than interocular distance; eyes brownish, anterior eyes slightly larger than posterior ones; dorsal cirrophore 3-4 times as long as wide, cirrostyle cylindrical basally, annulated; ventral cirri articulated, longer than chaetal lobe; acicular lobe single, wide basally, digitate, tapered distally; neurochaetal blades bidentate, guard approaching distal tooth in anterior chaetigers as well]. — 1 specimen, UF 48, Masirah Island, South-southwest tip of Masirah, 100 m from shore, rocks and reef, under rocks, 1-7 m depth, 6.XI.1999, G. Paulay coll. [46 mm long, 5.5 mm wide; body stiff, bent ventrally, without pigmentation; acicular lobe single, wide basally, digitate, tapered distally]. — 1 specimen, UF 410, Qurm Beach, near Muscat (23.626, 58.481; 23°37'33.6000"N, 058°28'51.6000"E), 0-1 m depth, 26.I.2005, V. Bonito, M. Claereboudt & G. Paulay coll. [32 mm long, 4 mm wide; body laterally bent, without pigmentation; acicular lobe single, wide basally, digitate, tapered distally]. — 2 specimens, MNHN-IA-PNT91 (formerly jar 70), Mission Bouvier-Perez, Sta. 50, Banc Rák-as-Zakoum, 6.4 km off Oman, 8-12 m depth, 19.III.1901 [38-48 mm long, 4-8 mm wide; slightly damaged, many chaetae broken; body grayish, integument markedly shiny, areolated in anterior and posterior regions; acicular lobes single, tapered]. — 2 specimens, MNHN-IA-PNT91 (formerly jar 70), Mission Bouvier-Perez, Sta. 53, probably near to

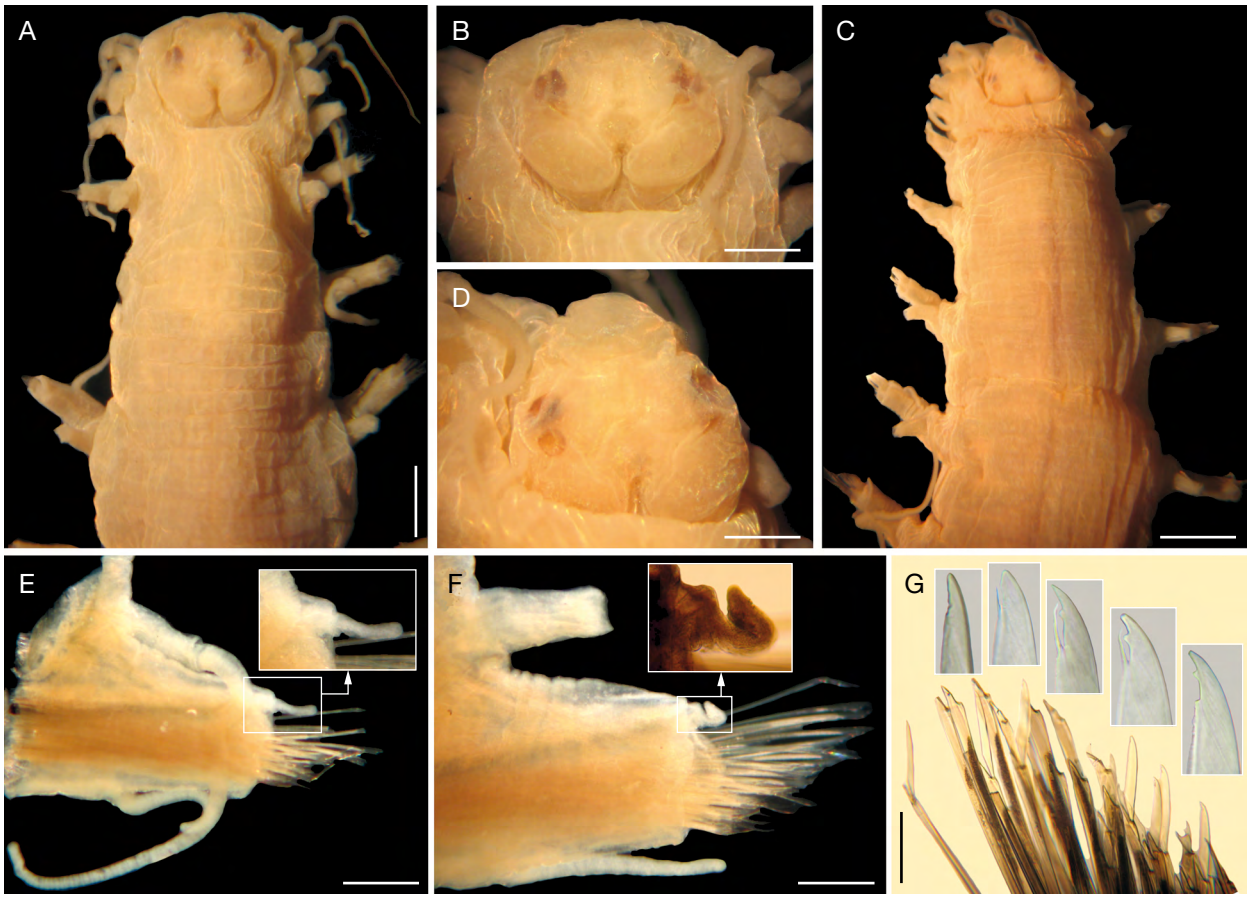

FIG. 53. — *Hesione splendida* Savigny *in* Lamarck, 1818, syntypes of *H. ehlersi* Gravier, 1900, MNHN-IA-TYPE0287: **A**, largest syntype, anterior region, dorsal view; **B**, same, anterior end, dorsal view; **C**, second largest syntype, anterior region, dorsal view; **D**, same, anterior end, dorsal view; **E**, largest syntype, chaetiger 9, left parapodium, anterior view (inset: acicular lobe); **F**, same, chaetiger 10, left parapodium, anterior view (inset: acicular lobe, folded); **G**, same, neurochaetae (insets: blade tips). Scale bars: A, 1 mm; B, D, E, 0.5 mm; C, 1.4 mm; F, 0.3 mm; G, 0.2 mm.

station 50, but without further data [dried-out; too brittle to be measured; acicular lobes single and tentatively regarding in this species]. **Zanzibar.** 1 specimen, MCZ 1215, 25.III.1862, C. Cooke coll. [59 mm long, 8 mm wide; body distorted by pressure in container, with many amphinomid chaetae; integument opaque; prostomium distorted; antennae ovoid, smaller than interocular distance; eyes dark brown, anterior ones twice as large as posterior ones; cirrophores 4 times as long as wide; dorsal cirri basally articulated; acicular lobe single, digitate; neurochaetae brownish, very abundant, most with long or medium-sized blades, subdistal tooth smaller; most guards broken, those entire approach distal tooth; pygidium rugose, anus projected, without anal cirri]. — 2 specimens, MCZ 46506, 25.III.1863, C. Cooke coll. [49-57 mm long, 6-8 mm wide; body macerated, integument transparent; most chaetal lobes invaginated; chaetae dark brown; one chaetal lobe from the larger specimen was removed for observation (kept in vial); one thick black acicula; most with long or very long blades, subdistal tooth smaller, guard approaching distal tooth]. **Madagascar.** 4 specimens, UCO HES 11, Expedition MD/08, Sta. 6, Banc Walters, no further data [23-39 mm long, 3-4 mm wide; damaged, most cirri and chaetal blades lost; colorless, eyes without pigmentation; acicular lobe single; blades bidentate, guard approaching subdistal tooth]. — 1 specimen, UF 737, Nosy Iranja, off N side, 3-4 m depth, 24.V.2008, G. Bakary, F. Michonneau, G. Paulay & T. Werner coll. [34 mm long, 4 mm wide; body almost colorless, pigmentation resembling *H. intertexta* by having granulose or regularly rugose dorsal integument along posterior body half, and weak longitudinal lines and some triangular spots between lateral cushions, but anterior neurochaetal blades without tiny denticles, pointing distally; acicular lobe single, blunt, about 20 neurochaetae per bundle; blades bidentate, guard straight approaching distal tooth]. **Persian Gulf.** 1 specimen, SMF 19491, near PTL 9, MSGR 1993, 7.II.1993, M. Apel coll. [32 mm long, 4 mm wide; colorless, bent laterally; antennae globose, 1.5 times as long as wide; eyes barely pigmented, anterior ones twice as large as posterior ones; most cirri and neurochaetal blades broken; right parapodium of chaetiger 9 removed for observation (kept in vial); acicular lobe single, tapered; neurochaetal blades bidentate, subdistal tooth smaller; guards mostly broken, a few left approaching distal tooth].

DISTRIBUTION. — Western Indian Ocean, from the Persian Gulf to Madagascar, in 0-22 m depth, in mixed bottoms.

DIAGNOSIS. — *Hesione* with prostomium curved laterally; parapodia with dorsal cirri basally cylindrical, dorsal cirrophore twice as long as wide; larger acicula blackish; acicular lobe single, long, blunt or slightly swollen distally, lower tine missing; neurochaetal blades bidentate, 5-9 times as long as wide; subdistal tooth smaller than distal one, with guards approaching distal tooth.

DESCRIPTION

Lectotype of *Hesione splendida*, MNHN-IA-TYPE0140, 41 mm long, 6 mm wide; slightly macerated, longitudinally dissected anteriorly over the left side above parapodia (Fig. 52A), and another lateral dissection in the posterior third of body; ante-

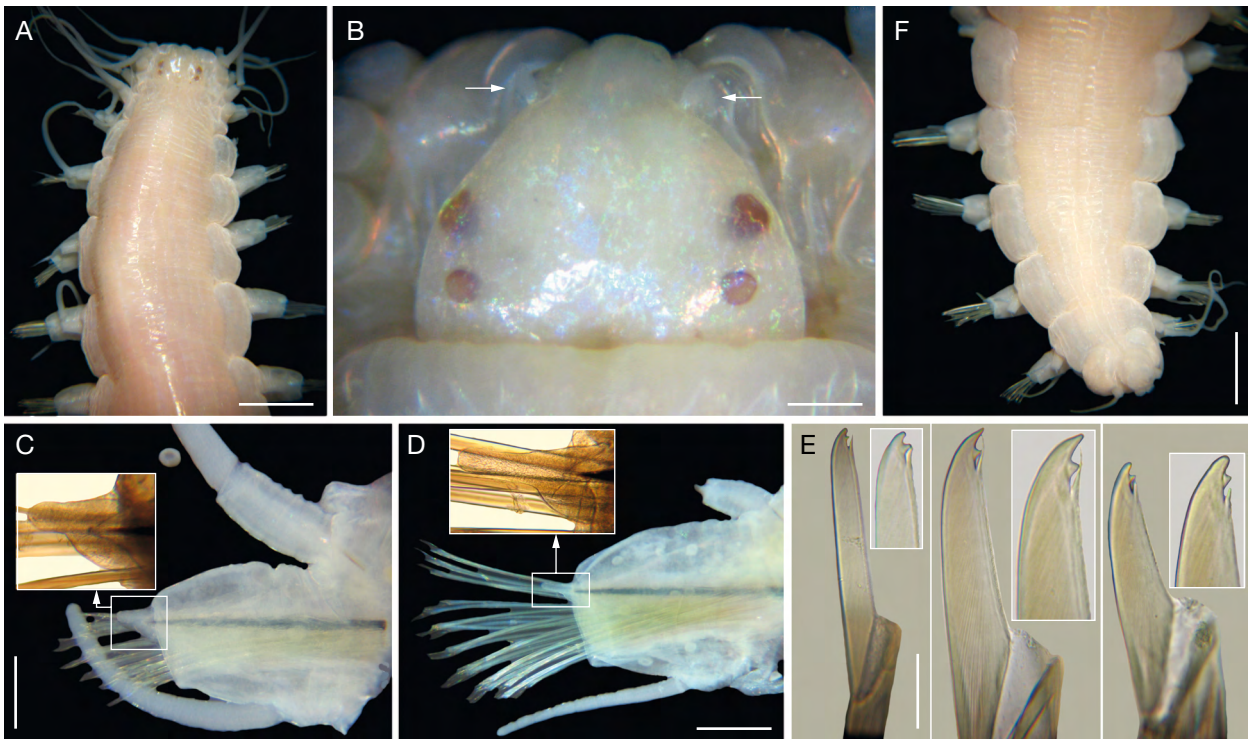

Fig. 54. — *Hesione splendida* Savigny *in* Lamarck, 1818, non-type specimen, UF 46: **A**, anterior region, dorsal view; **B**, prostomium, dorsal view (arrows point to antennae); **C**, chaetiger 2, right parapodium, anterior view, an oocyte released (inset: acicular lobe); **D**, chaetiger 6, right parapodium, anterior view, oocytes inside parapodial coelom (inset: acicular lobe); **E**, neurochaetal blades, left one from chaetiger 2, others from chaetiger 6 (insets: close-up of tips); **F**, posterior region, dorsal view. Scale bars: A, 2 mm; B, 0.3 mm; C, 0.4 mm; D, 0.7 mm; E, 60 µm; F, 0.5 mm.

rior and posterior ends collapsed; anterior region macerated, prostomial features unclear (Fig. 52B); right parapodium of chaetiger 8 removed for observation; dorsal cirrophore macerated, about three times longer than wide (Fig. 52C), ventral cirri eroded, surpassing chaetal lobe; parapodial lobe contracted; neuraciculae black, one very thick, another one markedly thinner, only visible after dissecting parapodia; acicular lobe single, tapered (Fig. 52C [inset]); most neurochaetal blades lost, those remaining eroded, blades bidentate, guards broken bases visible in a few blades (Fig. 52C [inset]); posterior region tapered into a conical pygidium (Fig. 52D), anal papillae not seen; mature, larger oocytes about 100 µm in diameter.

Syntypes of *H. ehlersi*, MNHN-IA-TYPE0287, complete, some laterally bent, integument areolated (Fig. 53A, C), partially dehydrated, colorless in ethanol; most without dorsal cirri, chaetal blades broken, longest one with a longitudinal mid-ventral dissection, running through 14-15 chaetigers. Body subcylindrical, tapered posteriorly, 31-44 mm long, 3-4 mm wide.

Prostomium as long as wide, anterior margin truncate (Fig. 53B) to slightly projected anteriorly (Fig. 53D), lateral margins rounded, progressively wider, posterior margin exposed, with a deep depression, as long as ⅓ prostomial length, longitudinal depression very shallow, barely detected. Antennae minute, digitate, as long as interocular distance, or 1-2 times as long as wide. Several syntypes with eyes retaining brownish pigmentation; anterior eyes larger, sometimes twice larger than posterior ones.

Tentacular cirri and development unknown (originally illustrated as reaching chaetiger 5). Lateral cushions low, barely projected, most divided into anterior and posterior sections.

Parapodia with chaetal lobes truncate, as long as wide (Fig. 53E); dorsal cirri with cirrophores 2-3 times as long as wide (Fig. 53F), cirrostyles basally cylindrical, annulated, medially annulated, distally articulated (originally illustrated as completely annulated or articulated). Ventral cirri smooth throughout its length, surpassing chaetal lobe.

Neuraciculae blackish, larger one visible by transparency. Acicular lobes single, long (5-6 times as long as wide), blunt, slightly capitate in some parapodia (Fig. 54E [inset]), to tapered in the same specimen (Fig. 53F [inset]).

Neurochaetae about 25 per bundle, handles honey-colored, blades bidentate, at a certain angle from handle, many lost, remaining ones decreasing in size ventrally, 5-9 times as long as wide, each with smaller subdistal tooth, guards, if complete, approaching or slightly surpassing subdistal tooth (Fig. 53G [insets]).

Posterior region tapered into a blunt cone; pygidium smooth, anus projected with 7 low, blunt papillae.

Pharynx not exposed. Oocytes not seen.

Variation

In syntypes of *H. ehlersi* (MNHN-IA-TYPE0287), anterior eyes can be slightly larger to twice larger than posterior ones. Antennae are difficult to see, partially because they are small, partially because bodies are partially dehydrated.

Dorsal cirri shorter than body width (excluding parapodia). Acicular lobes are almost always single; rarely, especially when the upper tine is very short, a lower shorter tine can be noted. Anterior chaetigers with longest blades, teeth tiny, distal one larger, laterally directed; guards mostly broken, those remaining approaching distal tooth. In better preserved specimens, the integument is areolated (Fig. 54A, F), eyes brownish, anterior ones larger and antennae are wider medially, 2-3 times as long as wide, although the posterior furrow is not visible (Fig. 54B); dorsal cirrophores are twice as long as wide, and acicular lobes are single and become narrower in the first body third (Fig. 54C, D), whereas neurochaetal blades are thinner and have smaller teeth in anterior chaetigers in comparison to those present in following chaetigers (Fig. 54E).

Remarks

Hesione splendida Savigny *in* Lamarck, 1818 was described with two specimens (syntypes); they belong to the same species despite their distant localities: Mauritius Island, MNHN-IA-TYPE0139, and Red Sea, MNHN-IA-TYPE0140). Both have a very thick black acicula and another one, markedly thinner, and their acicular lobes are single. Because one of the syntypes, MNHN-IA-TYPE0139, is in poor condition, being smashed and partially dehydrated, the other one is herein designated as the lectotype for *H. splendida* Savigny *in* Lamarck, 1818. Because Savigny (1822: 40) indicated a slight difference in the length of neurochaetal blades, and because they tend to be shorter in posterior chaetigers or, in the same chaetal bundle, if they are in lower portion. This proposal complies with the *Code* (ICZN 1999: art. 74.7, recomm. 74B).

For the corresponding remarks of *H. ehlersi*, Gravier (1900: 179) preferred to compare it to other species instead of contrasting it against *H. splendida,* which had been also described fom the Red Sea. Gravier indicated it had no pigmentation pattern, a feature which is usually non-diagnostic, especially if it fades off soon in ethanol. Because the only other species described from the same region was *H. splendida* Savigny *in* Lamarck, 1818, it is enigmatic why these two species were not compared to each other, especially because the syntypes of the latter were in Paris, where Gravier used to work. Gravier thought his new species resembled *H. pantherina* Risso, 1826, described from the Mediterranean Sea, at least regarding prostomial features (Gravier 1900: 179). However, Gravier noted that regarding parapodial features *H. ehlersi* differs from *H. pantherina* (probably referable to *H. sicula*) because it has a single acicular lobe, whereas in the latter a double lobe is present. However, this feature is also present in *H. splendida* and these two species are herein shown to be synonyms, something other authors have anticipated. Gravier also indicated that his *H. ehlersi* resembled *H. praetexta* Ehlers, 1887, and *H. vittigera* Ehlers, 1887 because all were supposed to have single acicular lobes. This is incorrect. A single acicular lobe is present only in *H. praetexta*, not in *H. vittigera* (junior synonym of *H. picta*, see above).

Other species provided with single, tapered acicular lobes are *H. eugeniae* and *H. intertexta*, and the type of neurochaetal blades could easily separate them. In *H. eugeniae* the guard extends beyond distal tooth, which is a rather unique feature present only in another species (described above as *H. osbornae* n. sp.). Then, the most similar species to *H. splendida* is *H. intertexta* by having similar prostomial and chaetal features with blades bidentate, with subdistal tooth minute and guard approaching distal tooth, but they differ because in the latter blade teeth can be directed distally in upper bundle chaetae (especially common in smaller specimens), but usually teeth are laterally directed and in either case, the guard approaches the distal tooth.

The specimens from Zanzibar (MCZ 46506) have a single, thick black acicula, despite the fact their bodies and parapodia are very large; this could be a useful difference among similar species but parapodial slides must be thoroughly compared. Further, in these specimens the guards, if entire, approach the distal tooth, and not just the subdistal tooth as illustrated by Day (1967). Because guards are very brittle, this is not regarded as a diagnostic difference, pending the study of specimens from Mozambique and Madagascar, which were apparently used by Day for his illustrations and description; it must be noted that he indicated a single conical acicular lobe (Day 1967: 228). Further, guards can be broken in a few chaetal blades per bundle; they cannot be confused with those chaetae deprived of guards because there is an evident marginal depression where the guard used to be.

The affinities between *H. ehlersi* and *H. intertexta* Grube, 1878 deserve clarification. Wehe & Fiege (2002: 57) indicated that *H. ehlersi* has been regarded as a junior synonym of *H. pantherina* Risso, 1826 by Fauvel (1953b: 104), or of *H. splendida* Savigny *in* Lamarck, 1818 by Pleijel (1998: 158). Dimitri Costa reached the same conclusion as Pleijel after studying the type series, as indicated by the labels left with the specimen. It can be concluded that *H. ehlersi* is a junior synonym of *H. splendida,* but as indicated above, *H. pantherina* is a distinct species.

The record for Western Australia by Hartmann-Schröder (1979: 84, ZMH-P 16538) is a posterior fragment of another hesionid, or from a syllid; it has pale, thin, tapered neuraciculae, and the neurochaetal blades are thin, unidentate; these features do not match with the nominal form.

Hesione uchidai n. sp.
(Figs 55, 56)

urn:lsid:zoobank.org:act:C805FD51-1E9F-499C-ACA6-A7704D6D77FC

Hesione cf. *ehlersi* – Uchida 2010: 4-5, figs 1, 2 (*partim*).

Type material. — **Western Pacific. Philippines.** Holotype, UF 4384, Batangas Province, Verde Island Channel, Mabini, W side Bonito Island, Sta. VIP15-GP-0911 (13.6297, 120.9478; 13°37'46.9200"N, 120°56'52.0800"E), 1 m depth, 18.IV.2015, G. Paulay coll.

Additional material. — **Japan.** 13 specimens, MCZ 84730, Ryukyu Islands, Seragaki Tombs, 1.3 km ENE Maeki-zaki, Okinawa (26°30.4'N, 127°52.6'E), 6 m depth, silty-sand and coral rubble,

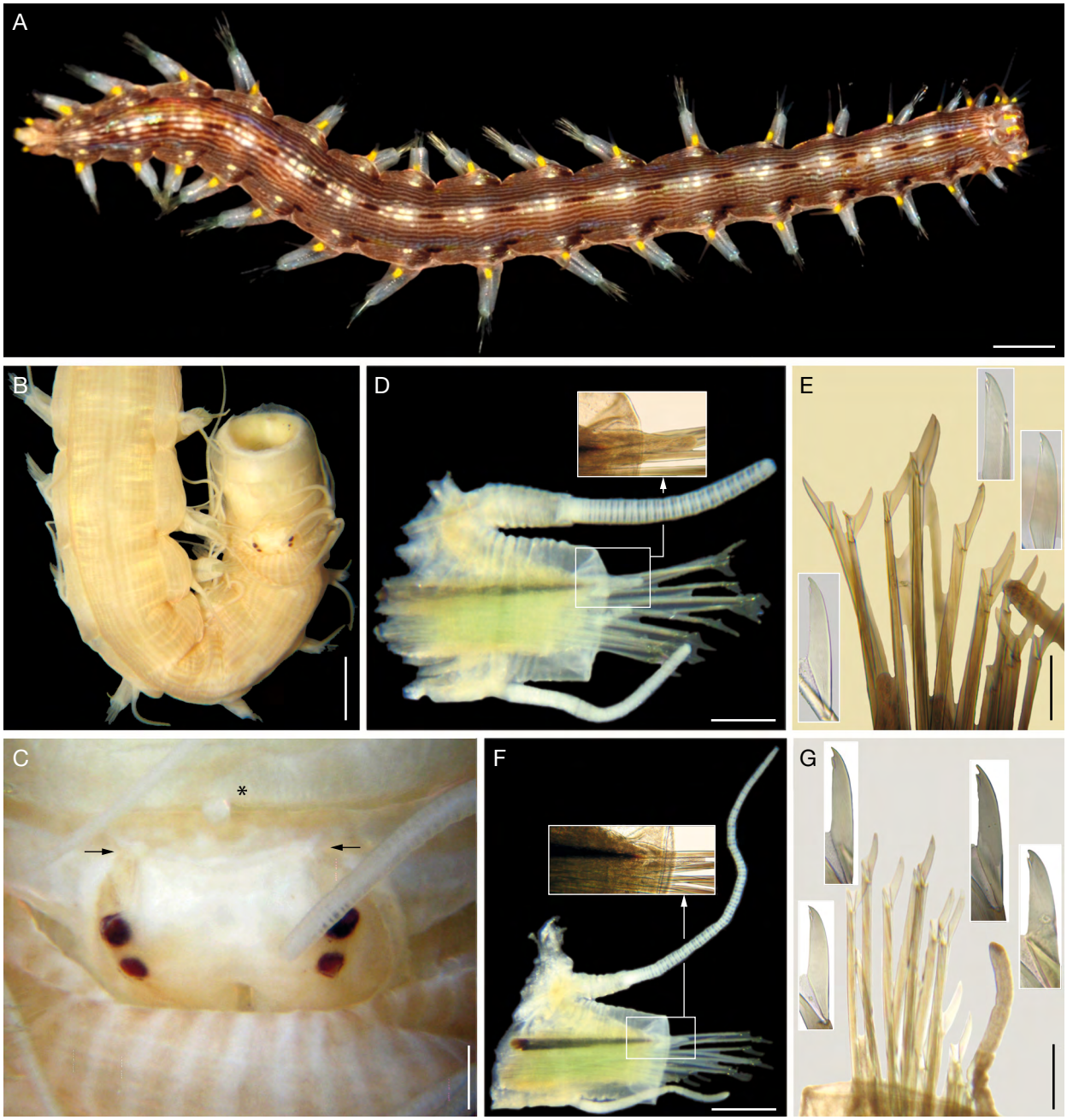

Fig. 55. — *Hesione uchidai* n. sp., holotype, UF 4384: **A**, alive, dorsal view; **B**, anterior body half, dorsal view, pharynx exposed; **C**, prostomium and basal pharynx ring, prostomium slightly oblique, bent dorsally (arrows point to antennae, asterisk indicates dorsal papilla); **D**, chaetiger 7, left parapodium, anterior view (inset: acicular lobe); **E**, same, neurochaetae (insets: blades); **F**, chaetiger 12, left parapodium, anterior view; **G**, same, neurochaetae (insets: blades). Scale bars: A, 2.2 mm, B, 2 mm; C, D, 0.3 mm; E, 150 µm; F, 0.5 mm; G, 230 µm.

26.V.1995, R. F. Bolland coll. [8-14 mm long, 1-2 mm wide; most cirri lost; antennae minute; acicular lobe single, tapered; neurochaetal blades very long with tiny denticles, or long with better defined teeth]. — 1 specimen, MCZ 84732, Ryukyu Islands, Seragaki Beach, 1.3 km ENE Maeki-zaki, Okinawa (26°30.4'N, 127°52.6'E), 3 m depth, mixed sand and coral rubble, 21.III.1990, R. F. Bolland coll. [34 mm long, 3 mm wide; bent laterally; most dorsal cirri lost; pharynx fully exposed, divided into three rings, medial one longer, dorsal papilla slightly as long as wide; antennae tapered, directed anterolaterally, shorter than interocular distance; anterior prostomial margin with a shallow depression, longitudinal furrow shallow, becoming deeper towards postectal margin; eyes dark brown, anterior ones twice as large as posterior ones; dorsal cirri basally smooth; acicular lobe single, tapered; neurochaetal blades very long and long, with guard passing subdistal tooth; pygidium smooth, slightly darker than surrounding integument; anus with anal cirri invaginated].

Philippines. 1 specimen, UF 4354, Oriental Mindoro Province, Mindoro, Puerto Galera, Batangas Channel, "School Beach" (13.51688, 120.95983; 13°31'00.7680"N, 120°57'35.3880"E), VIP15-GP-0017, 7-14 m depth, 8.IV.2015, G. Paulay coll. [body pale, with a dissection towards posterior region; eyes dark brown, anterior ones slightly larger than posterior ones; antennae minute, pale, difficult to see; pharynx exposed, dorsal papilla not seen; acicular lobe single, tapered; neurochaetae with pale handles, blades of about the same

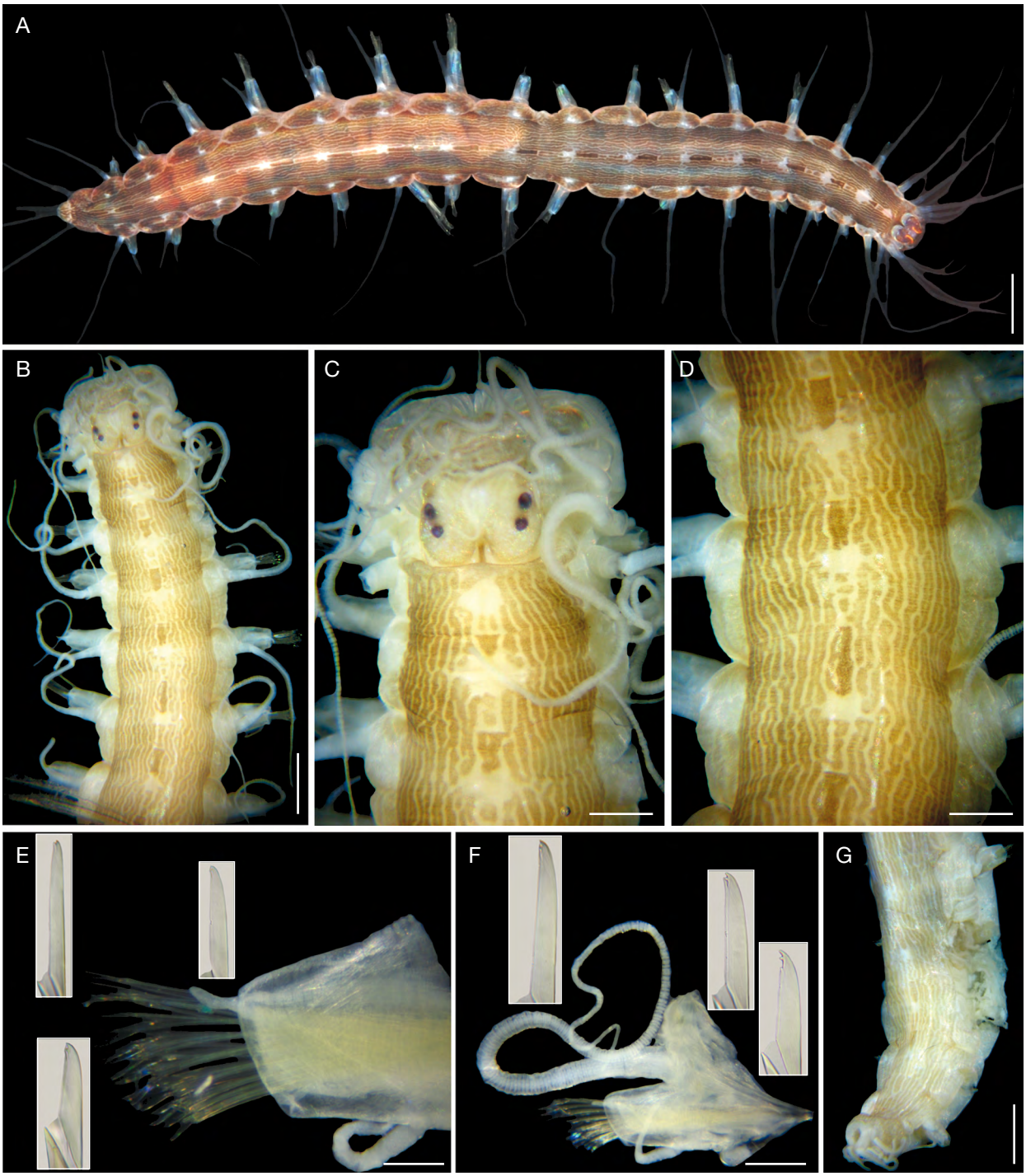

Fig. 56. — *Hesione uchidai* n. sp., non-type specimen, UF 1761: **A**, complete, dorsal view; **B**, anterior region, dorsal view, depressed by a glass slide fragment; **C**, anterior end, dorsal view; **D**, chaetigers 4–6, dorsal view; **E**, chaetiger 3, right parapodium, anterior view (insets: neurochaetal blades); **F**, chaetiger 7, right parapodium, anterior view (insets: neurochaetal blades); **G**, posterior end, oblique dorsal view. Scale bars: A, 1.5 mm; B, C, 0.6 mm; D, 0.7 mm; E, 130 µm; F, 0.8 mm; G, 1.1 mm (photo A, G. Paulay).

length in median chaetigers, decreasing in size ventrally in posterior chaetigers, with subapical tooth smaller, guard overpassing subapical tooth; however, in chaetiger 2 most very long with tips simplified, sometimes with teeth minute, or probably eroded].

Australia. 1 specimen, UF 1761, Western Australia, Ningaloo Reef, ARMS site (-22.76912, 113.70458; 22°46'08.8320"S, 113°42'16.4880"E), 12 m depth, 1 Jun. 2010, team, coll. [28 mm long, 3 mm wide; antennae digitate, shorter than interocular distance; eyes dark brown, anterior ones slightly larger than posterior ones; acicular lobe single, tapered; neurochaetal blades include longer ones with smaller teeth and shorter ones with larger teeth].

Etymology. — This species is named after Dr Hiro'omi Uchida, in recognition of his publications on hesionid polychaetes, and because he illustrated the pigmentation pattern shown by living specimens of this species.

Distribution. — From Japan to the Philippines to Western Australia, in mixed bottoms in areas up to 12 m water depth.

Diagnosis. — *Hesione* with prostomium laterally curved; parapodia with dorsal cirri basally cylindrical, dorsal cirrophore twice as long as wide; aciculae blackish; acicular lobe single, digitate, basally swollen, lower tine missing; neurochaetal blades bidentate, 3-6 times as long as wide; teeth subequal; guards approaching subdistal tooth.

Description

Holotype (UF 4384) pale, without posterior region, with a series of longitudinal pale brown lines (Fig. 55A), middorsal one slightl wider, and some darker areas between lateral cushions in ethanol. Body 24 mm long, 4 mm wide, 14 chaetigers.

Prostomium subrectangular, as wide as long, anterior margin truncate, lateral margins slightly rounded, wider towards posterior margin, posterior margin covered by tentacular segment, posterior furrow deep, reaching close to posterior eyes level, ¼ as long as prostomial length; longitudinal depression barely defined. Antennae minute, blunt, almost transparent, twice as long as wide (Fig. 55B). Eyes dark brown, anterior ones slightly larger and more separated than posterior ones.

Tentacular cirri without tips, articulated throughout its length, longest one reaching chaetiger 5. Lateral cushions projected, most with surface smooth.

Anterior parapodia contracted, chaetal lobes slightly as long as wide (Fig. 55C); posterior parapodial lobes as long as wide (Fig. 55E), all truncate; dorsal cirri with cirrophores corrugated, 3 times as long as wide; cirrostyles basally cylindrical, smooth, annulated medially, distally articulated. Ventral cirri articulated, surpassing chaetal lobe.

Neuraciculae two, blackish, larger one thicker, tapered. Acicular lobe single, tapered, blunt (Fig. 55C, E [insets]), shorter than chaetal lobe distal width.

Neurochaetae about 20 per bundle, blades at a certain angle from handle, bidentate, slightly decreasing in size ventrally, 3-4 times as long as wide (Fig. 55D, F [insets]).

Posterior region lost; another specimen with posterior region tapered (Fig. 56G), pygidum with pale brown spots throughout its surface, anus colorless, projected, anal papillae not visible.

Pharynx partially exposed, distal ring longer than basal, median ring larger than others; anterior margin slightly eroded; dorsal papilla round, as long as wide (seen from above in Fig. 55B). Oocytes not seen.

Pigmentation

Living specimens brownish (Fig. 55A) to pale brown (Fig. 56A) with longitudinal, irregular, continuous bands dorsally, and alternating reddish-brown thin bands and wider whitish areas middorsally; pigmentation pattern extended into lateral cushions with darker or paler pigmentations aligned transversally, dorsal deep yellow to whitish, probably fading out quickly in stressed specimens. Tentacular, dorsal cirri and neuropodial lobes pale. Prostomium with two lateral brownish bands, fused posteriorly; nuchal organs colorless.

Preserved specimens with dorsal, brownish longitudinal, irregular, thin bands, middorsal areas include a colorless squarish to as wide as long spot in chaetal lobes section, and a darker as long as wide spot immediately ahead of the colorless spots (Fig. 56A-D), smaller in chaetiger 1, progressively longer towards posterior end. The area having the middorsal darker spot, is slightly darker along a transverse band half as wide as each segment, better defined along anterior segments. In other specimens (UF 1170), having pigmentation less intense, these pigmentation bands are retained, especially along the anterior tip of lateral cushions. Pigmentation present in prostomium as small round spots ahead of eyes, or diffuse along the basal pharyngeal ring (Fig. 56B); anterior and posterior eyes dark brown, of similar size. Brownish pigmentation extended into lateral cushions leaving a paler area at the same level as the middorsal paler spot (Fig. 56C), giving the impression of two bands per segment.

Remarks

In specimens from the Philippines, UF 4354 (22-24 mm long), medial chaetigers have upper bundle chaetae with longer blades, their teeth are smaller, point more distally, and guards are barely seen, whereas most other chaetae from the same bundle have shorter blades, their teeth are laterally directed, and guards approach distal tooth. This pattern is modified in anterior chaetigers because chaetae with longer blades and smaller, distally pointing teeth are more abundant. Smaller specimens from Japan, MCZ 84730 (8-14 mm long), have more chaetae with longer blades, and smaller teeth pointing distally, and in some chaetae teeth are not developed at all.

Uchida (2010: 4) provided two photos for what he regarded as *H.* cf. *ehlersi*. One is a dorsal view of the whole specimen; the other shows a few median body segments. In both, the discontinuous narrow darker, middorsal band is shown along with other paler longitudinal bands. Further, he also keyed out this species, as indicated elsewhere (Jimi *et al.* 2017: 38), by emphasising the pigmentation pattern. Uchida (2010) regarded his material as resembling *H. ehlersi* Gravier, 1900, but this latter species is colorless. Uchida might have confused the illustration for what Gravier recorded as *H. pantherina* Risso, 1828 (his figure 16 in plate 10). The illustration is a dorsal view of four midbody segments with longitudinal, discontinuous lines; this record, however, has been indicated above as belonging to *H. ceylonica* Grube, 1874.

Hesione uchidai n. sp. resembles *H. ceylonica* Grube, 1874, reinstated, because they have neurochaetal blades up to 6 times as long as wide. As indicated in the key below, they differ in the shape of the acicular lobes and size of neurochaetal blades. In *H. uchidai* n. sp. lobes are digitate, and blades are 4-6 times as long as wide, whereas in *H. ceylonica* the lobes are triangular or basally swollen, and blades are 5-6 times as long as wide. The pigmentation pattern of living specimens clearly separates these two species because in *H. uchidai* n. sp. the longitudinal bands are continuous, and there are discontinuous reddish brown bands, alternating with pale areas middorsally, whereas in *H. ceylonica* the longitudinal bands are discontinuous, interrupted by dorsal transverse pale, wide bands.

Key to species of *Hesione* Savigny *in* Lamarck, 1818

1. Neuraciculae blackish 2
— Neuraciculae both pale, colorless; acicular lobes single, tapered; neurochaetal blades very long (6-12 times as long as wide) ..... *H. horsti* n. sp.

2. Parapodia with acicular lobe single (lower tine, if present, reduced to a small round lobe; upper tine three or more than four times longer than lower one; see figs 7C, 8C, 10D) 3
— Parapodia with acicular lobe double (of similar length, or upper tine 2-3 times longer than lower one; see Figs 5D, 15C, 18C); neurochaetal blades bidentate 13

3. Neurochaetal blades bidentate 4
— Neurochaetal blades unidentate (subdistal tooth missing) 12

4. Neurochaetal blades guards approaching distal tooth 5
— Neurochaetal blades guards surpassing distal tooth; dorsal cirrophore twice as long as wide (living specimens with dorsal wide homogeneous brownish transverse bands) ..... *H. eugeniae* Kinberg, 1866 (incl. *H.* cf. *picta ex auct.*)

5. Dorsal surface usually shiny, often areolated; dorsal cirrophore 2-3 times as long as wide (living specimens grayish) ..... *H. splendida* Savigny *in* Lamarck, 1818
— Dorsal surface opaque; dorsal cirrophore variable (living specimens often with dorsal longitudinal brownish discontinuous bands) 6

6. Anterior eyes circular 7
— Anterior eyes as wide as long 11
— Anterior eyes as long as wide; dorsal surface smooth or with tubercles arranged into longitudinal series, at least along posterior chaetigers ..... *H. fitzhughi* n. sp.

7. Acicular lobes tapered, without basal tine; dorsum rugose to microtuberculated, at least along posterior chaetigers 8
– Acicular lobes digitate, blunt, with a small basal round tine; dorsum smooth to slightly rugose, at least along posterior chaetigers 10

8. Neurochaetal blades 3-4 times as long as wide (living specimens with middorsal oval to foliose, as long as wide pale areas)..... *H. intertexta* Grube, 1878 restricted
— Neurochaetal blades up to 6 times as long as wide..... 9

9. Acicular lobe triangular or basally swollen; neurochaetal blades 5-6 times as long as wide (living specimens with discontinuous longitudinal bands, and dorsal segmental, transverse pale, wide bands) ..... *H. ceylonica* Grube, 1874 reinstated
— Acicular lobe digitate; neurochaetal blades 4-6 times as long as wide (living specimens with continuous longitudinal bands, and discontinuous reddish brown bands alternating with pale areas middorsally)..... *H. uchidai* n. sp.

10. Parapodial cirri with cirrostyles basally smooth; neurochaetal blades 4-6 times as long as wide..... *H. praetexta* Ehlers, 1887 reinstated
— Parapodial cirri with cirrostyles basally swollen; neurochaetal blades 4-5 times as long as wide ..... *H. helenensis* n. sp.

11. Acicular lobes blunt; subdistal tooth as wide as distal one, guard surpassing subdistal tooth (living specimens with middorsal pale areas) ..... *H. pantherina* Risso, 1826
— Acicular lobes tapered; subdistal tooth thinner than distal one, guard approaching distal tooth (living specimens with middorsal blackish round spots) ..... *H. panamena* Chamberlin, 1919 reinstated

12. Neurochaetal blades guards approaching distal tooth; neurochaetal blades 6-8 times as long as wide ..... *H. harrisae* n. sp.
— Neurochaetal blades guards surpassing distal tooth; neurochaetal blades about 15 times as long as wide ..... *H. osbornae* n. sp.

13. Subdistal tooth thinner or smaller than distal tooth 14
— Subdistal tooth as wide as distal tooth 19

14. Antennae long, 4-6 times as long as wide; neurochaetal blades with guards approaching subdistal tooth (living specimens with dorsal longitudinal brownish bands) ..... *H. sicula* delle Chiaje, 1830 reinstated (incl. *H. steenstrupi* de Quatrefages, 1866)
— Antennae short, smaller than interocular distance, about 3 times as long as wide 15

15. Neurochaetal blades with guards approaching distal tooth 16
— Neurochaetal blades without guards 18

16. Acicular lobe as long as half chaetal fascicle width (living specimens with irregular transverse brown bands along tentacular segment and chaetigers 1-4 only) ..... *H. hartmanae* n. sp.
— Acicular lobe as long as 1/3 chaetal fascicle width 17

17. Dorsum annulated, without longitudinal striae, smooth (living specimens with transverse dark brown bands along the whole body) ..... *H. picta* Müller, 1858 (incl. *H. proctochona* Schmarda, 1861 and *H. margaritae* Hansen, 1882)
— Dorsum annulated and with longitudinal striae, rugose (living specimens with a complex, reticulate pigmentation pattern) ..... *H. reticulata* von Marenzeller, 1879

18. Dorsal cirrophore as long as wide; prostomium rectangular; eyes well-defined (integument thin; living specimens with wide transverse red bands along chaetigers 1-6(7), progressively separated into two bands in following segments) ..... *H. beneliahuae* n. sp.
— Dorsal cirrophore twice as long as wide; prostomium wider posteriorly; eyes poorly defined (integument thick; pigmentation unknown) ..... *H. keablei* n. sp.

19. Dorsum of preserved specimens with transverse dark brown bands 20
— Dorsum of preserved specimens colorless; acicular lobe with tines of different length ..... *H. pacifica* McIntosh, 1885 reinstated

20. Wide dark brown transverse band on chaetiger 2; chaetiger 1 mottled or pale; acicular lobe with tines of different length 21
— Wide dark brown transverse band on chaetiger 1; chaetiger 2 mottled or pale; acicular lobe with tines of similar length ..... *H. genetta* Grube, 1864 restricted

21. Longest tentacular cirri reach chaetigers 5-6; dorsal transverse band better defined along anterior margin ..... *H. paulayi* n. sp.
— Longest tentacular cirri reach chaetigers 8-9; dorsal transverse band well defined along anterior and posterior margins ..... *H. mooreae* n. sp.

CONCLUDING REMARKS

Anatomy

The gross morphology of the digestive system is quite uniform. Most features have been studied before, and the most remarkable difference along the gut relates to the thickness of the enteric wall. This is thinner and stiff, including an inner reinforced layer along the pharynx lumen and oesophagus, and becomes thicker, softer, and more glandular in the stomach and intestine. The enteric caeca, however, were regarded as gas bladders. They are not. Further, with the exception of the finding of a strange copepod inside it, the cavity is empty. As is the case in other predatory polychaetes, there is rarely a prey item inside the gut, but at least a partially digested specimen of a scale worm was found in a single specimen. More studies on freshly collected specimens, together with some field or aquaria experiments, are needed to clarify their ecological role in the marine environment. Likewise, the posterior gland has not been recorded before, and defining its role needs some histological studies to clarify its contents and connections to the intestine or to the coelom.

The study of gonads confirmed the earlier observations as hermaphrodites. However, they are simultaneously functional. Both oocytes and sperm are found to be mature, but the means to avoid self fertilisation, as well as the means to find mates and release their oocytes or sperm remain enigmatic. Because they are frequently found by divers making photographs, but there are no details about their reproduction, this implies they are probably nocturnal, despite their striking coloration. Again, some aquaria experiments might reveal how they spawn, and these efforts could also clarify the early development and larvae, which are also poorly known.

Morphology

Most prostomial features, antennae and tentacular cirri have a scarce diagnostic use. Especially because they are fragile, such as antennae and tentacular cirri, or because they change during ontogeny, like the size of eyes, especially the posterior ones. The anterior eyes, however, being larger and directed anterolaterally provide diagnostic features regarding their relative shape as being circular, or ovoid, either as long as wide, or as wide as long. The latter condition is rather rare among the species in the genus.

Parapodia provide useful diagnostic features, especially regarding the base of dorsal cirrostyles, but dorsal cirrophores are promising at much. The length/wide proportion can be useful, but the number of rings may change depending on the contraction state, and some experiments about the effect of different fixation and preservation methods would clarify its utility. Ventral cirri have been referred as reaching or surpassing neurochaetal lobes, but because they are fragile and

neurochaetal lobes are retractable, its utility is scarce. Acicular lobes are, by far, the best diagnostic parapodial feature, once their development is scanned throughout the body, such that their type, shape and size are defined. Another useful feature is the pigmentation of neuraciculae; the larger one is usually black, but in only one species it was found to be pale. The smaller aciculae can be dark, together with a pale larger acicula, but because this difference was not linked to other morphological feature, they were not used to separate similar species, but this needs confirmation.

Neurochaetae are very useful. Handles are usually subdistally swollen, but this was not evaluated as a diagnostic tool, because handles must remain in the same plane, in full lateral view, because sometimes the swollen area is not too long. Blades are extremely important as diagnostic features. Their size along body, together with the fine details regarding size proportions among teeth and guards, has the largest relevance as diagnostic tools.

Pigmentation

Four patterns of dorsal pigmentation are confirmed: 1) transverse bands; 2) longitudinal lines; 3) mixed, with transverse variable bands and spots; and 4) no pigmentation. Between the three colorful patterns, only the mixed one is long standing in ethanol. Because the colors are similar to those found in the other patterns, these pigments might be arranged or combined in a different way, such that they can resist the fading effect of ethanol. Likewise, the ecological role for this pigmentation patterns remain unknown, but at least this latter issue could be evaluated in some aquaria experiments.

Species richness

The number of undescribed species was unexpected, especially because most specimens were found in places that have been sampled before. This increased number, as much as the reinstatement or restriction for several species, is rather explained because the morphology was assessed after a standardisation of their terms and variations, such that their differences, probably disregarded in the past, could be reinterpreted and concluded they are enough as to warrant independent specific status. Nevertheless, this scenario cannot be regarded as a final point. Rather, several regions in the world remain poorly studied, even regarding tropical, coralline fauna, such as Western Africa, and in other better-known regions, subtidal and nocturnal sampling might result in other undescribed species.

Acknowledgements

The now classical revision by Fredrik Pleijel of Hesionidae was essential for this contribution. Leslie Harris and Dave Ocker, as part of their generous tradition, provided a home to share with them during my second sabbatical leave. Karen Osborn and Geoff Keel (USNM) kindly arranged a loan, and Linda Ward (USNM) kindly provided several difficult to find references. Ángel de León-González (UANL) allowed me to study his collections. Gustav Paulay and Jenna Moore (UFNMM) kindly supported my request for specimens and helped a lot by extracting DNA and sequencing COI. Jokke Bleker and Harry ten Hove supported my request for specimens from Naturalis, containing the former Amsterdam collections and the Leiden collection. Jose Santos-Gómez (ECOSUR) helped finding out and getting some other difficult to find publications. Kirk Fitzhugh (LACM) kindly supported my frequent and usually untimely requests for help. Patrick Gillet (UCO) helped by providing some lab space, and supported my request for a University dormitory room to facilitate my work in Angers. Hanane Perrein was also very helpful by sharing some motivational morning talks. Tarik Meziane (MNHN) supported my request for funding and provided some space lab and access to their collections. Gerald Islebe (ECOSUR) kindly reviewed and improved my translations from German. Naoto Jimi and Hiroshi Kajihara (Univ. Hokkaido) shared their observations for a note in Japanese on *Hesione reticulata*. Several collection managers were very kind by sending specimens to be included in this study: Birger Neuhaus (ZMB), Emma Sherlock (BMNH), Helmut Sattmann (NHMW), Joke Bleeker and Harry ten Hove (RMNH), Jolanta Jurkowska (MNHW), Kathrin Philipps and Petra Wagner (ZMH-P), Marie-Louise Tritz and Dieter Fiege (SMF), Stephen Keable (AM), and Yves Samyn (RBINS). Jintana Klaklong Plathong, Prince of Songkla University, Thailand, donated some specimens to our collection. Anna Zhadan, Gustav Paulay, Humberto Bahena, Leslie Harris, Rene Ong, and Vinicius da Rocha Miranda shared some photographs of living specimens. Emilia González helped cataloguing ECOSUR specimens. Jenna Moore and Luis F. Carrera-Parra provided some COI data and trees. Geoff Read helped to clarify some classical citations and references. And last but not least, Emilia González allowed me to travel away from home in order to complete some parts of this revision. Luis F. Carrera-Parra supported my request for permits to leave, and helped in our combined teaching duties. Funding for this research was provided by ECOSUR, MNHN-Paris through Tarik Meziane, and UCO-Angers through Patrick Gillet. Lena Gustavsson, Swedish Museum of Natural History, kindly shared a pdf of an original figure. The very careful reading of earlier drafts by Alexandra Rizzo, Laure Desutter-Grandcolas, and Naoto Jimi resulted in a much improved final contribution. Anne Mabille carefully set the draft into this final format.

REFERENCES

Amoureux L. 1985. — Annélides polychètes récoltées à l'entrée de la lagune de la Manche-à-Eau, Guadeloupe (Antilles). *Bulletin du Muséum national d'Histoire naturelle, Paris, 4e série, section A 7*: 93-107.

Audouin J. V. & Milne-Edwards H. 1833. — Classification des Annélides, et description de celles qui habitent les côtes de la France (Suite (1)). *Annales des Sciences naturelles* 29: 195-269, pls 15-18. http://www.biodiversitylibrary.org/item/29342#page/199/mode/1up

Augener H. 1913. — Polychaeta I, Errantia. *Die Fauna Südwest-Australiens* 4 (5): 63-304, pls 2-3. https://biodiversitylibrary.org/page/7160887

Augener H. 1922. — Results of Dr E. Mjöbergs Swedish Scientific Expeditions to Australia 1910-13, 32. Polychaeten. *Svenska*

Vetenskapsakademiens handlingar 63 (6): 1-49. https://biodiversitylibrary.org/page/41849959
Augener H. 1926. — Ceylon-Polychäten (Fauna et Anatomia ceylanica 4, 2). *Jenaische Zeitschrift fur Naturwissenschaft* 62: 435-472.
Augener H. 1927a. — Polychaeten von Neu-Pommern. *Gesellschaft naturforschender Freude zu Berlin* 1926: 119-152.
Augener H. 1927b. — Polychaeten von Curaçao. *Zoologisk Genootschop Natura artis Magistra, Amsterdam, Bijdragen tot de Kennis der Fauna von Curaçao* 25: 39-82.
Augener H. 1933a. — Polychaeten und Hirudineen aus dem Zoologischen Museum in Buitenzorg. *Treubia* 14: 173-206.
Augener H. 1933b. — Polychaeten aus den Zoologischen Museum von Leiden und Amsterdam, 1. *Zoologische Mededeelingen* 15: 177-260. http://www.repository.naturalis.nl/document/149941
Augener H. 1934. — Polychaeten aus den Zoologischen Museum von Leiden und Amsterdam, 4 (Schluss) [*plus* Polychaeten-Typen von Arm. Hansen 1881, aus dem Naturhistorischen Reichmuseum Leiden]. *Zoologische Mededeelingen* 17: 67-160. http://www.repository.naturalis.nl/document/149757
Aziz N. D. 1938. — Fauna of Karachi, 2. Polychaetes. *Memoirs of the Department of Zoology, Panjab University* 1: 18-52, pls 3-8.
Bailey-Brock J. H. & Hartman O. 1987. — Polychaeta, *in* Devaney D. M. & Eldredge L. G. (eds). Reef Shore Fauna of Hawaii, section 2: Platyhelminthes through Phoronida; section 3: Sipuncula through Annelida. *Bishop Museum Special Publication* 64 (2-3): 216-454.
Bandaranayake W. M. 2006. — The nature and role of pigments of marine invertebrates. *Natural Products Reports* 23: 223-255. https://doi.org/10.1039/b307612c
Bergmann W. 1902. — Untersuchungen über die Eibildung bei Anneliden und Cephalopoden. Dissertation, Universität Marburg, 26 pp, 3 pls [Publ. 1902 in *Zeitschrift für wissenschaftliche Zoologie* 73: 278-301, pls 17-19]. https://biodiversitylibrary.org/page/43239588
Bergmann W. 1903. — Über das spätere Schicksal der Zwitterdrüssen von *Hesione sicula*. *Zoologischer Anzeiger* 26: 415-417. https://biodiversitylibrary.org/page/30125385
Blainville H. de 1825. — Néréide, *Nereis* (Chétopodes). *Dictionnaire des Sciences naturelles* 34: 408-455. https://biodiversitylibrary.org/page/25303363
Blainville H. de 1828. — Vers à sang rouge. *Dictionnaire des Sciences naturelles* 57: 368-501. https://biodiversitylibrary.org/page/25316890
Blainville H. de 1830. — Vers et Zoophytes. *Dictionnaire des Sciences Naturelles, Planches, 2e Partie: Régne Organisé. Zoologie*. https://biodiversitylibrary.org/page/24394694
Blake J. A. 1991. — The polychaete fauna of the Galápagos Islands, *in* James M. J. (ed). *Galápagos Marine Invertebrates: Taxonomy, Biogeography, and Evolution in Darwin's Islands.* Topics in Geobiology, volume 8, Plenum Press, New York: 75-96.
Brito M. C., Núñez J., Bacallado J. J. & Ocaña O. 1996. — Anélidos poliquetos de Canarias: Orden Phyllodocida (Chrysopetalidae, Pisionidae, Glyceridae, Sphaerodoridae, Hesionidae y Pilargidae), *in Oceanografía y Recursos Marinos en el Atlántico Centro-Oriental*. Instituto Canario de Ciencias Marinas, Tenerife: 155-179. http://www.museodelmarceuta.com/papers/Orden%20Phyllodicida.pdf
Bowerbank J. S. 1873. — Report on a collection of sponges found at Ceylon by E. W. H. Holdsworth. *Proceedings of the Zoological Society of London* 1873: 25-32, pls 5-7. https://biodiversitylibrary.org/page/28504208
Campoy A. 1982. — Fauna de anélidos poliquetos de la península Ibérica. *Publicaciones de Biología, Universidad de Navarra, Serie Zoológica* 7: 1-781.
Chamberlin R. V. 1919. — The Annelida Polychaeta of the Albatross Tropical Pacific Expedition, 1891-1905. *Memoirs of the Museum of Comparative Zoology of Harvard College* 31: 1-514. https://doi.org/10.5962/bhl.title.49195
Chipman A. D. & ten Hove H. 2014. — M. Nechama Ben-Eliahu, 4 January 1935 – 23 March 2014: Obituary and some personal reminiscences. *Memoirs of Museum Victoria* 71: 347-351. https://museumvictoria.com.au/pages/58047/347-352_mmv71_chipman_obituary_2p_web.pdf
Claparède E. 1868. — Les annélides chétopodes du Golfe de Naples. *Mémoires de la Société de Physique et d'Histoire naturelle de Genève* 19 (2): 313-584. https://biodiversitylibrary.org/page/14309905
Clark R. B. 1962. — On the structure and functions of polychaete septa. *Proceedings of the Zoological Society, London* 138: 543-578. http://onlinelibrary.wiley.com/doi/10.1111/j.1469-7998.1962.tb05332.x/pdf
Costa D. A., de Assis J. E. &. Christoffersen M. L. 2008. — New synonym of *Hesione splendida* (Hesionidae, Polychaeta, Annelida). *Biociéncias* 16: 131-133. http://revistaseletronicas.pucrs.br/fabio/ojs/index.php/fabio/article/view/6503/4716
Costa G. 1841. — Description de quelques annélides nouvelles du golfe de Naples. *Annales des Sciences Naturelles, seconde série* 16: 267-280. https://biodiversitylibrary.org/page/35730724
Costa J. F. da. 2013. — *Taxonomia da família Hesionidae Grube, 1850 (Annelida: Polychaeta) da costa da Paraíba*. Monografia Bacharel em Ciencias Biológicas, Universidade Federal da Paraíba, 84 p. http://www.ccen.ufpb.br/cccb/contents/monografias/2013.1/taxonomia-da-familia-hesionidae-grube-1850-annelida-polychaeta-da-costa-da-paraiba.pdf/view
Czeczuga B. 1971. — The coloration of specimens of *Nereis zonata* Mal. (Annelides (sic), Polychaeta) from the Black Sea. *Hydrobiologia* 37: 301-307. https://doi.org/10.1007/BF00015577
Day J. H. 1951. — The polychaete fauna of South Africa, 1. The intertidal and estuarine Polychaeta of Natal and Mosambique [sic]. *Annals of the Natal Museum* 12: 1-67. http://bionames.org/references/a2e899e3a9d9f52ce63764e044ff14b0
Day J. H. 1967. — A Monograph on the Polychaeta of South Africa, 1. Errantia. London: *British Museum (Natural History) Publications* 656: 1-458. https://biodiversitylibrary.org/page/8725653
Day J. H. 1973. — Polychaeta collected by U. D. Gaikwad at Ratnagiri, south of Bombay. *Zoological Journal of the Linnean Society* 52: 337-361. http://onlinelibrary.wiley.com/doi/10.1111/j.1096-3642.1973.tb01888.x/pdf
De Assis J. E., Bezerra E. A. S., de Brito R. J., Gondim A. I. & Christoffersen M. L. 2012. — An association between *Hesione picta* (Polychaeta: Hesionidae) and *Ophionereis reticulata* (Ophiuroidea: Ophionereididae) from the Brazilian coast. *Zoological Studies* 51: 762-767.
de Bont R. A. F. 2008. — Evolutionary morphology in Belgium: The fortunes of the "van Beneden School", 1870-1900. *Journal of the History of Biology* 41: 81-118. https://doi.org/10.1007/s10739-007-9129-5
Delle Chiaje S. 1830(1822). — *Memorie sulla Storia e Notomia degli Animali senza Vertebre del Regno di Napoli*, pls 70-109. Societá Tipografica, Napoli. [Publication date after Oken, 1836: 290-293] https://biodiversitylibrary.org/page/10662978
Delle Chiaje S. 1841a. — *Descrizione e Notomia degli Animali Invertebrati della Sicilia Citeriore Osservati Vivi negli Anni 1822-1830, 3. Molluschi Acefali, Bracciopedi, Cirropedi, Crostacei, Annellosi*. Batelli e Comp., Napoli. https://biodiversitylibrary.org/page/10599408
Delle Chiaje S. 1841b. — *Descrizione e Notomia degli Animali Invertebrati della Sicilia Citeriore Osservati Vivi negli Anni 1822-1830, 5. Polipi, Amorfi, Descrizione Tecnique*. Batelli e Comp., Napoli. https://biodiversitylibrary.org/page/10689723
Delle Chiaje S. 1841c. — *Descrizione e Notomia degli Animali Invertebrati della Sicilia Citeriore Osservati Vivi negli Anni 1822-1830, 7. Figures (Tav. 87-173)*. Batelli e Comp., Napoli. https://biodiversitylibrary.org/page/10695041
Dueñas P. R. 1980. — Inventario preliminar de los poliquetos (Annelida) de aguas someras de la Bahía de Cartagena y áreas adyacentes. *Boletín del Museo del Mar, Punta de Betín* 10: 82-138.

EHLERS E. 1864. — *Die Borstenwürmer (Annelida Chaetopoda), nach Systematischen und Anatomischen Untersuchungen Dargestellt, Erste Abtheilung*. Leipzig: Wilhelm Engelmann, 265 p, pls 1-11. https://doi.org/10.5962/bhl.title.2081

EHLERS E. 1887. — Reports on the results of dredging under th direction of L. P. Pourtalès, during the years 1868-1870, and of Alexander Agassiz in the Gulf of Mexico (1877-78), and in the Caribbean Sea (1878-79) in the U.S. Coast Survey Steamer 'Blake', 31. Reports on the annelids. *Memoirs of the Museum of Comparative Zoology, Harvard College* 15: 1-335, pls 1-60. https://biodiversitylibrary.org/page/30734338

EHLERS E. 1920. — Polychaeten von Java und Amboina: Ein Beitrag zur Kenntnis der malaiischen Strandfauna. *Abhandlungen der Königlichen Gesellschaft der Wissenschaften zu Göttingen, Mathematischen-Physikalische Klasse, neue folge* 10 7: 1-73, 3 pls.

EISIG H. 1881. — Über das Vorkommen eines schwimmblasenähnlichen Organs bei Anneliden. *Mittheilungen aus der Zoologischen Station zu Neapel zugleich ein Repertorium für Mittelmeerkunde* 2: 255-304, pls 12-14. https://biodiversitylibrary.org/page/9678100

FAUCHALD K. 1977a. — The polychaete worms. Definitions and keys to the orders, families and genera. *Natural History Museum of Los Angeles County, Science Series* 28: 1-188. www.vliz.be/imisdocs/publications/123110.pdf

FAUCHALD K. 1977b. — Polychaetes from intertidal areas in Panama, with a review of previous shallow-water records. *Smithsonian Contributions to Zoology* 221: 1-81. https://repository.si.edu/handle/10088/5511

FAUVEL P. 1911. — Annélides polychètes du Golfe Persique recueillies par M. N. Bogoyawlensky. *Archives de Zoologie expérimentale et générale, 5e série* 6: 353-439, pls 19-21. https://biodiversitylibrary.org/page/6200721

FAUVEL P. 1913. — Quatrième note préliminaire sur les polychètes provenant des campagnes de l'*Hirondelle* et de la *Princesse-Alice,* ou déposées dans le Musée océanographique de Monaco. *Bulletin de l'Institut océanographique, Monaco* 270: 1-80. https://biodiversitylibrary.org/page/46001401

FAUVEL P. 1914. — Annélides polychètes non pélagiques provenant des campagnes de l'*Hirondelle* et de la *Princesse-Alice* (1885-1910). *Résultats des Campagnes scientifiques accomplies sur son yacht par Albert 1er, Prince Souverain de Monaco* 46: 1-432, pls 1-31. https://biodiversitylibrary.org/page/2117722

FAUVEL P. 1918. — Annélides polychètes des côtes d'Arabie récoltées par M. Ch. Pérez. *Bulletin du Muséum national d'Histoire naturelle* 24: 329-344. https://biodiversitylibrary.org/page/5037658

FAUVEL P. 1919a. — Annélides polychètes des Îles Gambier et Touamotou. *Bulletin du Muséum national d'Histoire naturelle* 25: 336-343. https://biodiversitylibrary.org/page/5027005

FAUVEL P. 1919b. — Annélides polychètes de Madagascar, de Djibouti et du Golfe Persique. *Archives de Zoologie expérimentale et générale* 58: 315-473. https://doi.org/10.5962/bhl.part.8154

FAUVEL P. 1922. — Annélides polychètes de l'Archipel Houtman Abrolhos (Australie Occidentale) recueillies par M. le Prof. W. J. Dakin, F. L. S. *Journal of the Linnean Society, Zoology* 34: 487-500. https://doi.org/10.1111/j.1096-3642.1922.tb01843.x

FAUVEL P. 1923a. — Polychètes Errantes. *Faune de France* 5: 1-488. http://www.faunedefrance.org/bibliotheque/docs/P.FAUVEL(FdeFr05)Polychetes-errantes.pdf

FAUVEL P. 1923b. — Annélides polychètes des Îles Gambier et de la Guyane. *Memorie della Pontificia Accademia Romana dei Nuovi Lincei, Serie 2* 6: 1-59.

FAUVEL P. 1927. — Cambridge Expedition to the Suez Canal, 1924, 29. Rapport sur les annélides polychètes errantes. *Transactions of the Zoological Society, London* 22: 411-439. https://doi.org/10.1111/j.1096-3642.1927.tb00203.x

FAUVEL P. 1929. — Polychètes nouvelles du Golfe de Manaar (Inde). *Bulletin de la Societé zoologique de France* 54: 180-186. http://gallica.bnf.fr/ark:/12148/bpt6k5442558m/f241.item.r=Fauvel

FAUVEL P. 1930. — Annélides polychètes de Nouvelle-Calédonie recueillies par Mme A. Pruvot-Fol en 1928. *Archives de Zoologie expérimentale et générale* 69: 501-562.

FAUVEL P. 1932a. — Annelida Polychaeta of the Indian Museum, Calcutta. *Memoirs of the Indian Museum* 12: 1-262. http://faunaofindia.nic.in/PDFVolumes/memoirs/012/01/0001-0262.pdf

FAUVEL P. 1932b. — Annélides polychètes provenant des campagnes de l'Hirondelle II (1911-1915). *Résultats des Campagnes scientifiques accomplies sur son yacht par Albert 1er, Prince Souverain de Monaco* 85: 1-50, pl. 1.

FAUVEL P. 1934. — Annélides polychètes de Rovigno d'Istria. *Thalassia* 1: 1-78.

FAUVEL P. 1937(1936). — Annélides polychètes du Japon. *Memoirs of the College of Science, Kyoto Imperial University, Series B* 12: 41-92.

FAUVEL P. 1941. — *Annélides Polychètes de Californie recueillies par L. Diguet*. Muséum national d'Histoire naturelle, Paris, 32 p. (Mémoires du Muséum national d'Histoire naturelle 18 (1).

FAUVEL P. 1947a. — Annélides polychètes de Nouvelle-Calédonie et des Îles Gambier, 1. Annélides polychètes de Nouvelle-Calédonie. *Faune de l'Empire français* 8: 1-87.

FAUVEL P. 1947b. — Annélides polychètes de Nouvelle-Calédonie et des Îles Gambier, 2. Annélides polychètes des Îles Gambier. *Faune de l'Empire français* 8: 88-108.

FAUVEL P. 1950. — Contribution a la faune des annélides polychètes du Sénégal. *Bulletin de l'Institut français d'Afrique noire* 12: 335-394.

FAUVEL P. 1953a. — Annélides polychètes non pélagiques. *Expédition océanographique belge dans les eaux côtières africaines de l'Atlantique Sud* 4: 1-56.

FAUVEL P. 1953b. — *The Fauna of India including Pakistan, Ceylon, Burma and Malaya: Annelida Polychaeta*. Allahabad, Indian Press, 507 p. https://archive.org/details/FBIPolychaeta

FAUVEL P. 1953c. — Sur quelques annélides polychètes d'Océanie. *Bulletin du Muséum national d'Histoire naturelle, 2e série* 25: 173-175.

FAUVEL P. 1953d. — Annélides polychètes de la croisière du *'President Théodore Tissier'* aux Antilles (1951). *Bulletin de l'Institut océanographique, Monaco* 50: 1-23.

FAUVEL P. 1955. — Campagne en Mer Rouge (1951-1952), 3. Annélides polychètes de la croisière de la 'Calypso' en Mer Rouge en 1952. *Résultats scientifiques des Campagnes de la 'Calypso'* 1: 101-120.

FAUVEL P. & RULLIER F. 1957. — Nouvelle contribution à la faune des annélides polychètes du Sénégal. *Bulletin de l'Institut français d'Afrique noire* 19: 24-96.

FAUVEL P. & RULLIER F. 1959a. — Contribution a la faune des annélides polychètes du Sénégal et de Mauritanie. *Bulletin de l'Institut Français d'Afrique noire* 21: 477-533.

FAUVEL P. & RULLIER F. 1959b. — Campagne de la 'Calypso': Golfe de Guinée, 6. Annélides polychètes. *Résultats scientifiques des Campagnes de la 'Calypso', Annales de l'Institute océanographique* 37: 143-205.

FISHELSON L. & RULLIER F. 1969. — Quelques annélides polychètes de la mer Rouge. *Israel Journal of Zoology* 18: 49-117. http://www.tandfonline.com/doi/pdf/10.1080/00212210.1969.10688275?needAccess=true

FRÉDOL A. 1866. — Le Monde de la Mer. 2nd Éd., Hachette, Paris, 693 p, 22 pls. https://biodiversitylibrary.org/page/2073099

GIBBS P. E. 1971. — The polychaete fauna of the Solomon Islands. *Bulletin of the British Museum (Natural History)* 21: 101-211. https://doi.org/10.5962/bhl.part.10154

GIBBS P. E. 1972. — Polychaete annelids from the Cook Islands. *Journal of Zoology, London* 168: 199-220. https://doi.org/10.1111/j.1469-7998.1972.tb01347.x

GOODRICH E. S. 1897. — On the nephridia of the Polychaeta, 1. On *Hesione, Tyrrhena*, and *Nephthys*. *Quarterly Journal of Microscopical Science* 40: 185-196, pls 6-9. https://biodiversitylibrary.org/page/13827399

GRAVIER C. 1900. — Contribution à l'étude des annélides polychètes de la Mer Rouge. *Nouvelle Archives du Muséum d'Histoire naturelle, 4e série*, 2 (2): 137-282. https://biodiversitylibrary.org/page/36872698

GRUBE A. E. 1850. — Die Familien der Anneliden. *Archiv für Naturgeschichte* 16 (1): 249-364. https://biodiversitylibrary.org/page/14713278

GRUBE A. E. 1864. — *Die Insel Lussin und ihre Meeresfauna*. Ferdinand Hirt, Breslau, 116 p., 2 pls. https://biodiversitylibrary.org/page/3148838

GRUBE A. E. 1867(1866). — Neue Anneliden aus den Gattungen *Eunice, Hesione, Lamprophaës* und *Travisia*. Jahres-*Bericht der Schlesischen Gesellschaft für vaterländische Cultur* 44: 64-66. https://biodiversitylibrary.org/page/46548206

GRUBE A. E. 1874. — Descriptiones Annulatorum novorum mare Ceylonicum habitantium ab honoratissimo Holdsworth collectorum. *Proceedings of the Scientific Meetings of the Zoological Society of London* 1874: 325-329. https://biodiversitylibrary.org/page/28502469

GRUBE A. E. 1878. — Annulata Semperiana. Beiträge zur Kenntnis der Annelidenfauna der Philippinen nach den von Herrn Prof. Semper mitgebrachten Sammlungen. *Mémoires de l'Académie Impériale des Sciences de St-Pétersbourg (série 7)* 25 (8): 1-300, pls 1-15.

GRUBE A. E. 1880. — Mittheilungen über die Famile der Phyllodoceen und Hesioneen. *Jahresbericht der Schlesischen Gesellschaft für vaterländische Cultur* 57: 204-228. https://biodiversitylibrary.org/page/46547075

HANSEN A. 1882. — Recherches sur les annélides recueillies par M. le professeur Édouard van Beneden pendant son voyage au Brésil et a La Plata. *Mémoires Couronnés et Mémoires des Savants étrangers publiés par l'Académie royale des Sciences, des Lettres et Beaux-Arts de Belgique, Bruxelles* 44 (3): 1-29, pls 1-7. https://biodiversitylibrary.org/page/5943290

HARTMAN O. 1938. — Annotated list of the types of polychaetous annelids in the Museum of Comparative Zoölogy. *Bullletin of the Museum of Comparative Zoology, Harvard* 85: 1-31, pls 1-3. https://biodiversitylibrary.org/page/4537955

HARTMAN O. 1940. — Polychaetous annelids, 2. Chrysopetalidae to Goniadidae. *Allan Hancock Pacific Expeditions* 7: 173-287, pls 31-34. http://cdm15799.contentdm.oclc.org/cdm/ref/collection/p15799coll82/id/5767

HARTMAN O. 1949(1948). — The marine annelids erected by Kinberg, with notes on some other types in the Swedish State Museum. *Arkiv för Zoologi* 42A: 1-137.

HARTMAN O. 1951. — The littoral marine annelids of the Gulf of Mexico. *Publications of the Institute of Marine Science, University of Texas* 2: 7-124. https://repositories.lib.utexas.edu/handle/2152/22162

HARTMAN O. 1954. — Marine annelids from the Northern Marshall Islands: Bikini and nearby atolls, Marshall Islands. *United States Geological Survey Professional Paper* 260Q: 617-644. https://pubs.er.usgs.gov/publication/pp260Q

HARTMAN O. 1959. — Catalogue of the Polychaetous Annelids of the World. *Allan Hancock Foundation Publications, Occasional Paper* 23: 1-628.

HARTMAN O. 1966. — Polychaetous annelids of the Hawaiian Islands. *Occasional Papers of the Bernice P. Bishop Museum* 23: 163-252.

HARTMANN-SCHRÖDER G. 1979. — Die Polychaeten der tropischen Nordwestküste Australiens (zwischen Derby in Norden und Port Hedland im Süden). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 76: 77-219.

HARTMANN-SCHRÖDER G. 1982. — Die Polychaeten der Fahrt 36 (1975) on F. S. "Meteor" in das Auftriebsgebiet vor Nordwest-Afrika. *"Meteor" Forschungs-Ergbnisse, D* 35: 1-20.

HARTWICH G. 1993. — Die Polychaeten-Typen des Zoologischen Museums in Berlin. *Mitteilungen aus dem Zoologischen Museum in Berlin* 69: 73-154.

HESSLE C. 1925. — Einiges über die Hesioniden und die Stellung der Gattung *Ancistrosyllis*. *Arkiv för Zoologi* 17: 1-36.

HOAGLAND R. A. 1919. — Polychaetous annelids from Porto Rico, the Florida Keys and Bermuda. *Bulletin of the American Museum of Natural History* 41: 517-591. http://digitallibrary.amnh.org/handle/2246/1161

HOAGLAND R. A. 1920. — Polychaetous annelis collected by the United States Fisheries Steamer 'Albatross' during the Philippine Expedition of 1907-1909. *Bulletin of the United States National Museum* 100 (1) (9): 603-635. https://biodiversitylibrary.org/page/7628628

HOLDSWORTH E. W. H. 1872. — Catalogue of the birds found in Ceylon; with some remarks on their habits and local distribution, and descriptions of two new species peculiar to the island. *Proceedings of the Zoological Society, London* 1872: 404-483, Pl. 20. https://doi.org/10.5962/bhl.title.49537

HORST R. 1921. — A review of the family of Hesionidae with a description of two new species. *Zoologische Mededeelingen* 6, 73-83. http://www.repository.naturalis.nl/document/149445

HORST R. 1922. — On some polychaetous annelids from Curaçao. *Bijdragen tot de Dierkunde* 22: 193-201. http://www.repository.naturalis.nl/document/547967

HORST R. 1924. — Polychaeta Errantia of the *Siboga*-Expedition, 3. Nereidae and Hesionidae. *Siboga-Expeditie Monographs* 24 (1c): 145-198.

IBARZÁBAL D. R. 1988. — Poliquetos de Punta del Este, Isla de la Juventud, 2. Familias Phyllodocidae, Hesionidae y Syllidae. *Poeyana, Instituto de Zoología, Academia de Ciencias de Cuba* 6 (359): 1-10.

IMAJIMA M. 2003. — Polychaetous annelids from Sagami Bay and Sagami Sea collected by the Emperor Showa of Japan and deposited at the Showa Memorial Institute, National Science Museum, Tokyo, 2. Orders included within the Phyllodocida, Amphinomida, Spintherida and Eunicida. *National Science Museum Monographs* 23: 1-221. http://ci.nii.ac.jp/naid/110004708004/en

IMAJIMA M. & HARTMAN O. 1964. — The polychaetous annelids of Japan, 1. *Allan Hancock Foundation Publications, Occasional Paper* 26: 1-166.

ICZN (INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE). 1999. — *International Code of Zoological Nomenclature*, Fourth Edition. International Trust for Zoological Nomenclature in association with the British Museum (Natural History), London, 306 p. http://www.iczn.org/iczn/index.jsp

IZUKA A. 1912. — The errantiate Polychaeta of Japan. *Journal of the College of Science, Tokyo* 30: 1-262. http://repository.dl.itc.u-tokyo.ac.jp/dspace/handle/2261/32884?mode=full

JIMI N., SALAZAR-VALLEJO S. I. & KAJIHARA H. 2017. — Designation of a neotype and Redescription of *Hesione reticulata* von Marenzeller, 1879 from Japan (Annelida, Hesionidae). *ZooKeys* 657: 29-41. https://doi.org/10.3897/zookeys.657.11064

JONES M. L. 1962. — On some polychaetous annelids from Jamaica, the West Indies. *Bulletin of the American Museum of Natural History* 124: 173-212. http://digitallibrary.amnh.org/handle/2246/1213

JUMARS P. A., DORGAN K. M. & LINDSAY S. M. 2015. — Diet of worms emended: An update of polychaete feeding guilds. *Annual Review of Marine Science* 7: 497-520 (+ Appendix A. Family per family updates: A1-350). https://doi.org/10.1146/annurev-marine-010814-020007

KINBERG J. G. H. 1866(1865). — Annulata nova (Nephtydea, Phyllodocea, Alciopea, Hesionida, Glycerea, Goniadea, Syllidea, Ariciea, Spiodea, Aonidea, Cirratulida, Opheliacea). *Öfversigt af Kongelige Vetenskaps-Akademiens Förhandlingar* 22: 239-258. https://biodiversitylibrary.org/page/32339515

KINBERG J. G. H. 1910. — Zoologi. Annulater. Kongliga Svenska Fregatten *Eugenies* Resa omkring jorden under befäl af C. A. Virgin Anen 1851-1853. *Vetenskapliga Iakttagelser på Konung Oscar den Förstes befallning utgifna af Kongliga Svenska Vetenskapsakadeinien, Zoologi* 3 (Annulaten): 33-78, pls 9-29 [first part: 1-32, pls 1-8 published 1853].

KIRKEGAARD J. B. 1983. — The Polychaeta of West Africa, 2. Errant species, 1. Aphroditidae to Nereididae. *Atlantide Reports* 13: 181-240.

KUDENOV J. D. 1975. — Errant polychaetes from the Gulf of California, Mexico. *Journal of Natural History* 9: 65-91. https://doi.org/10.1080/00222937500770061

LAMARCK J. B. 1818. — *Histoire Naturelle des Animaux sans Vertèbres, présentant les Caractères Généraux et Particuliers de ces Animaux, leur Distribution, leurs Classes, leurs Familles, leurs Genres, et la Citation des principales Espèces qui s'y rapportent; Précédés d'une Introduction offrant la Détermination des Caractères Essentiels de l'Animal, sa distinction du Végétal et des autres Corps Naturels, en fin, l'Exposition des Principes fondamentaux de la Zoologie*, Deterville & Verdiere, Paris, volume 5, 612 p. http://gallica.bnf.fr/ark:/12148/bpt6k64280058

LEE Y. & ONG R. 2015. — New records of two hesionid polychaetes from the Singapore Strait. *Singapore Biodiversity Records* 2015: 201-204. https://lkcnhm.nus.edu.sg/nus/images/pdfs/sbr/2015/sbr2015-201-204.pdf

MALAQUIN A. 1894. — Voyage de la Goëlette *Melita* sur les côtes occidentales de l'Océan Atlantique: Annélides polychètes. *Revue biologique du Nord de la France* 6: 411-418. https://biodiversitylibrary.org/page/10877655

MALAQUIN A. & DEHORNE A. 1907. — Voyage de MM. M. Bedot et C. Pictet dans l'Archipel Malais: Les annélides polychètes de la Baie d'Amboine, 1. Faune; 2. L'encéphale et la caroncule (organe nucal) de *Notopygos labiatus* Gr. *Revue Suisse de Zoologie, Annales de la Société Zoologique Suisse* 15: 335-400, pls 51-58. https://doi.org/10.5962/bhl.part.82525

MALMGREN A. J. 1867. — Annulata Polychaeta: Spetsbergiae, Groenlandiae, Islandiae et Scandinaviae. Hactenus Cognita. *Kongl. Vetenskaps-Akademiens Förhandlingar* 1867 (4): 127-235, pls 2-15. https://biodiversitylibrary.org/page/32326667

MARION A.-F. & BOBRETZKY N. 1875. — Étude des annélides du Golfe de Marseille. *Annales des Sciences naturelles, 6e série* 2: 1-106, pls 1-12. https://biodiversitylibrary.org/page/33155516

MCINTOSH W. C. 1885. — Report on the Annelida Polychaeta collected by H.M.S. Challenger during the years 1873-76. *Report on the Scientific Results of the H.M.S. Challenger 1873-76, Zoology* 12: 1-554, pls 1-55 + 1A-39A. https://biodiversitylibrary.org/page/50688432

MCINTOSH W. C. 1924. — Notes from the Gatty Marine Laboratory, St. Andrews, 46.2: Preliminary notice of a second contribution to the marine Polychaeta of South Africa. *Annals and Magazine of Natural History* 14: 2-52.

MCINTOSH W. C. 1925. — A second contribution to the marine polychaetes of South Africa. *Union South African Fisheries Marine Biological Survey* 4: 1-93.

MISRA A. 1999(1998). — Polychaete (sic); *in State Fauna Series 3, Fauna of West Bengal, Part 10*. Zoological Survey of India, Calcutta, 489 p.: 125-225.

MONRO C. C. A. 1926. — Polychaeta of the H.M.S. Alert Expedition, 1881-1882. Families Hesionidae and Nereidae. *Journal of the Linnaean Society* 36: 311-323. https://doi.org/10.1111/j.1096-3642.1926.tb02172.x

MONRO C. C. A. 1928. — Papers from Dr Th. Mortensen's Pacific Expedition 1914-16, 45. On the Polychaeta collected by Dr Th. Mortensen off the coast of Panama. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening* 85: 75-103.

MONRO C. C. A. 1931. — Polychaeta, Oligochaeta, Echiuroidea, and Sipunculoidea. *Great Barrier Reef Expedition 1928-29, Scientific Reports* 4: 1-37. https://biodiversitylibrary.org/page/49516539

MONRO C. C. A. 1933. — The Polychaeta Errantia collected by Dr C. Crossland at Colón, in the Panama Region, and the Galapagos Islands during the Expedition of the S.Y. "St. George". *Proceedings of the Zoological Society, London* 1933 (1): 1-96. http://onlinelibrary.wiley.com/doi/10.1111/j.1096-3642.1933.tb01578.x/full

MONRO C. C. A. 1937. — Polychaeta. *Scientific Reports, John Murray Expedition 1933-34* 4: 243-321. https://biodiversitylibrary.org/page/49518759

MONRO C. C. A. 1939. — On some tropical Polychaeta in the British Museum, mostly collected by Dr C. Crossland at Zanzibar, Tahiti, and the Marquesas, 2. Families Syllidae and Hesionidae. *Novitates Zoologicae* 41: 383-393. https://biodiversitylibrary.org/page/34053626

MÜLLER F. 1858. — Einiges über die Annelidenfauna der Insel Santa Catharina an der brasilianischen Küste. *Archiv für Naturgeschichte* 24: 211-220, pls 6-7. https://biodiversitylibrary.org/page/7460059

NGAMNIYOM A., SILPRASIT K. & SRIYAPAI T. 2014. — Morphological and molecular evidence for a new record of *Hesione* cf. *picta* (Polychaeta: Hesionidae) from the Western coast of the Gulf of Thailand. *Kasetsart Journal, Natural Sciences* 48: 719-728. http://www.thaiscience.info/journals/Article/TKJN/10961404.pdf

NONATO E. F. & AMARAL A. C. Z. 1979. — *Anelídos Poliquetas*. Sáo Paulo, 78 pp.

NONATO E. F. & LUNA J. A. C. 1970. — Anelídeos poliquetas do nordeste do Brasil, 1. Poliquetas bentónicos da costa de Alagoas e Sergipe. *Boletim do Instituto Oceanografico de São Paulo* 19: 57-130. https://doi.org/10.1590/S0373-55241970000100004

OKEN L. 1836. — Memorie(sic) sulla Storia e Notomia delli Animali senza Vertebre, 1823-1829, Vol. IV et 72. *Isis, Encyclopädische Zeitschrift* 29: 290-293. https://biodiversitylibrary.org/page/13245579

PARAPAR J., BESTEIRO C. & MOREIRA J. 2004. — Familia Hesionidae Grube, 1850. *Fauna Ibérica* 25: 210-267.

PETTIBONE M. H. 1963. — Marine polychaete worms of the New England Region, 1: Aphroditidae through Trochochaetidae. Bulletin of the United States National Museum 227: 1-356. https://repository.si.edu/handle/10088/3416

PLEIJEL F. 1998. — Phylogeny and classification of Hesionidae (Polychaeta). *Zoologica Scripta* 27: 89-163. https://doi.org/10.1111/j.1463-6409.1998.tb00433.x

PLEIJEL F. & GUSTAVSSON L. 2010. — Chambered chaetae in nereidiform polychaetes (Annelida). *Zoomorphology* 129: 93-98. https://doi.org/10.1007/s00435-010-0102-z

PRUVOT G. 1930. — Annélides polychètes de Nouvelle-Calédonie recueillies para M. François (edited and issued by Pierre Fauvel). *Archives de Zoologie expérimentale et générale, Paris* 70: 1-94. http://gallica.bnf.fr/ark:/12148/bpt6k5455977j/f8.image

QUATREFAGES A. DE 1850. — Études sur les types inférieurs de l'embranchement des annelés: Sur la circulation des annélides; sur la respiration des annélides. *Annales des Sciences naturelles, troisième série* 14: 290-301, pl. 5. https://biodiversitylibrary.org/page/13433737

QUATREFAGES A. DE 1866. — *Histoire naturelle des Annelés marins et d'eau douce. Annélides et Gephyriens*. Librarie Encyclopèdique de Roret, Paris, volumen 1, 588 p.

REISH D. J. 1968. — The polychaetous annelids of the Marshall Islands. *Pacific Science* 22: 208-231. https://scholarspace.manoa.hawaii.edu/handle/10125/6824

RIOJA E. 1918. — Datos para el conocimiento de la fauna de anélidos poliquetos del Cantábrico (2a parte). *Trabajos del Museo Nacional de Ciencias Naturales, serie Zoológica* 37: 1-99. https://biodiversitylibrary.org/page/13722697

RIOJA E. 1925. — Anélidos poliquetos de San Vicente de la Barquera (Cantábrico). *Trabajos del Museo Nacional de Ciencias Naturales, serie Zoológica* 53: 1-62.

RISSO A. 1826. — *Histoire naturelle des principales productions de l'Europe Méridionale et particulièrement de celles des environs de Nice et des Alpes Maritimes*. Volume 4, Paris: Livrault Libraire, 439 p. https://biodiversitylibrary.org/page/50455192

RULLIER F. 1964. — Résultats scientifiques des campagnes de la 'Calypso'. Campagne aux îles du Cap Vert 1959. Annélides polychètes. *Annales de l'Institut océanographique* 41: 113-218.

Rullier F. & Amoureux L. 1979. — Campagne de la *Calypso* au large des côtes Atlantiques de l'Amerique du sud (1961-1962), 1 Annélides polychètes. *Annales de l'Institut océanographique* 55: 145-206.
Saint-Joseph A. de 1898. — Les annélides polychètes des côtes de France (Manche et Ocean). *Annales des Sciences naturelles, Zoologie, série 8* 5: 209-464, pls 13-23. https://biodiversitylibrary.org/page/35661652
Salazar-Vallejo S. I. 1999. — *Polychaetes (Polychaeta) in the Muséum national d'Histoire naturelle collected mainly during ORSTOM cruises*. Mimeo, 40 p.
Salazar-Vallejo S. I. & Rizzo A. E. 2009. — Hesionidae Grube, 1850 y hesionoideos, *in* de León-González J. A., Bastida-Zavala J. R., Carrera-Parra L. F., García-Garza M. E., Peña-Rivera A., Salazar-Vallejo S. I. y Solís-Weiss V. (eds), *Poliquetos (Annelida: Polychaeta) de México y América Tropical*. Universidad Autónoma de Nuevo León, Monterrey, México: 227-243.
San Martín G. & Gomez Esteban C. 1992. — Anélidos poliquetos procedentes de la I expedición Cubano-Española a la Isla de la Juventud y archipieélago de los Canarreos. IV. Familias Hesionidae, Pilargidae, Glyceridae y Phyllodocidae. *Revista de Investigaciones Marinas* 13: 103-109.
Savigny J.-C. 1822. — Système des Annelides, principalemente de celles des Côtes de l'Égypte et de la Syrie, offrant les Caractères tant distintifs que naturels des Ordres, Familles et Genres, avec la Description des espèces. *Description de l'Égypte. Histoire naturelle, Paris* 21: 325-472 (publication date fixed after Sherborn, 1897, and after ICZN 1987, Op. 1461; reprint pages 1-128). https://www.deutsche-digitale-bibliothek.de/item/A2H7RCHYNZ-2BLOBAZBXMYYI5FJ5LVR4N
Schmarda L. K. 1861. — *Neue wirbellose Thiere beobachtet und gesammelt auf einer Reise um die Erde 1853 bis 1857, Erster Band: Turbellarien. Rotatorien und Anneliden*, Zweite Hälfte. Leipzig: Wilhelm Engelmann, 164 pp, pls 16-37. https://biodiversitylibrary.org/page/50385225
Schroeder P. C. & Hermans C. O. 1975. — Annelida: Polychaeta, *in* Giese A. C. & Pearse J. S. (eds), *Reproduction of Marine Invertebrates.* Academic Press, New York, volume 3. Annelids and Echiurans: 1-213.
Solís-Weiss V., Bertrand Y., Helléouet M.-N. & Pleijel F. 2004. — Types of polychaetous annelids at the Muséum national d'Histoire naturelle, Paris. *Zoosystema* 26: 377-384. http://sciencepress.mnhn.fr/sites/default/files/articles/pdf/z2004n3a2.pdf
Sordino P. 1990(1989). — Censimento dei policheti (Annelida) dei mari Italiani: Hesionidae Sars, 1862. *Atti della Società Toscana di Scienze Naturali, Memoria, Serie B,* 96: 31-52.
Spalding M. D., Fox H. E., Allen G. R., Davidson N., Ferdaña Z. A., Finlayson M., Halpern B. S., Jorge M. A., Lomana A., Lourie S. A., Martin K. D., McManus E., Molnar J., Recchia C. A. & Roberston J. 2007. — Marine ecoregions of the World: A bioregionalization of coastal and shelf areas. *BioScience* 57: 573-583. https://doi.org/10.1641/B570707
Stagl V., Sattmann H. & Dworschak P. C. 1996. — The material of the *Pola* Red sea expeditions (1895-1898) in the collections of the Natural History Museum in Vienna. *Biosystematics and Ecology Series* 11: 29-41. http://www.nhm-wien.ac.at/jart/prj3/nhm/data/uploads/mitarbeiter_dokumente/dworschak/Stagl_et_al1996_Pola.pdf
Storch V. 1968. — Zur vergleichenden Anatomie der segmentalen Muskelsysteme und zur Verwandtschaft der Polychaeten-Familien. *Zeitschrift für Morphologie der Tiere* 63: 251-342. https://doi.org/10.1007/BF00292073
Suárez-Morales E. 2016. — A new species of *Monocheres* Stock (Copepoda, Siphonostomatoidea, Asterocheridae) from shallow waters off Florida, USA: an unexpected discovery. *ZooKeys* 607: 93-102. https://doi.org/10.3897/zookeys.607.9137
Treadwell A. L. 1902(1900). — Investigations of the Aquatic Resources and Fisheries of Porto Rico by the United States Fish Commission Steamer Fish Hawk in 1899. The polychaetous annelids of Porto Rico. *Bulletin of the United States Fish Commission, 20, second part*: 181-210. http://docs.lib.noaa.gov/rescue/Fish_Commission_Bulletins/BFC1900-v20-pt2.pdf
Treadwell A. L. 1906(1903). — Polychaetous annelids of the Hawaiian Islands collected by the steamer *Albatross* in 1902. *Bulletin of the United States Fish Commission* 23 (3): 1145-1181. http://docs.lib.noaa.gov/rescue/Fish_Commission_Bulletins/BFC1903-v23.pt3.pdf
Treadwell A. L. 1926. — Additions to the polychaetous annelids collected by the United States Fisheries Steamer 'Albatross', 1907-1910, including one new genus and three new species. *Bulletin of the United States National Museum* 100 (6) (2): 183-193. https://biodiversitylibrary.org/page/7691900
Treadwell A. L. 1928. — Polychaetous annelids from the *Arcturus* Oceanographic Expedition. *Zoologica, Scientific Contributions of the New York Zoological Society* 8: 449-485. https://biodiversitylibrary.org/page/51020854p
Treadwell A. L. 1937. — The Templeton Crocker Expedition: Polychaetous annelids from the west coast of Lower California, the Gulf of California and Clarion Island. *Zoologica, New York* 22: 139-159, pls 1-2. https://biodiversitylibrary.org/page/50969597
Treadwell A. L. 1939. — Polychaetous annelids of Porto Rico and vicinity. *Scientific Survey of Porto Rico and the Virgin Islands* 16 (2): 149-319.
Uchida H. 2009. — [Polychaetologica 55. Key to genus and description of species (40), Hesionidae 4]. *Marine Pavilion, Kushimoto Marine Park* 38: 36-37. (In Japanese).
Uchida H. 2010. — [Polychaetologica 56. *Hesione* cf. *ehlersi* and *H. intertexta*]. *Marine Pavilion, Kushimoto Marine Park* 39: 4-5.
Uchida H. 2011. — [Polychaetologica 57. *Hesione genetta* to *Hesione* sp]. *Marine Pavilion, Kushimoto Marine Park* 40: 2-5.
Uebelacker J. M. 1984. — Family Hesionidae Sars, 1862, *in* Uebelacker J. M. & Johnson P. G. (eds), *Taxonomic Guide to the Polychaetes of the Northern Gulf of Mexico*. Barry A. Vittor & Associates, Inc. Mobile, Volume 4: 28.1-28.39. https://biodiversitylibrary.org/page/3249029
von Marenzeller E. 1879. — Sudjapanische Anneliden, 1. Amphinomea, Aphroditea, Lycoridea, Phyllodocea, Hesionea, Syllidea, Eunicea, Glycerea, Sternaspidea, Chaetopterea, Cirratulea, Amphictenea. *Denskschriften der Mathematisch-Naturwissenschaftlichen classe der Kaiserlichen Akademie der Wissenschaften* 41 (2): 109-154. https://biodiversitylibrary.org/page/7215498
Webster H. E. 1884. — Annelida from Bermuda collected by G. Brown Goode. *Bulletin of the United States National Museum* 25: 305-327. https://biodiversitylibrary.org/page/7725366
Wehe T. & Fiege D. 2002. — Annotate checklist of the polychaete species of the seas surrounding the Arabian Peninsula: Red Sea, Gulf of Aden, Arabian Sea, Gulf of Oman, Arabian Gulf. *Fauna of Arabia* 19: 7-238. http://www.senckenberg.de/files/content/forschung/abteilung/aquazool/mev2/wehe_%26_fiege.pdf
Wiktor J. 1980. — Type-specimens of Annelida Polychaeta in the Museum of Natural History of the Wroclaw University. *Annales Zoologici* 35 (20): 267-283.
Willey A. 1905. — Report on the Polychaeta collected by Professor Herdman at Ceylon, in 1902. *Report to the Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manaar* 4 (30): 243-324, pls 1-8. https://biodiversitylibrary.org/page/1936112
Wu B., Shen S. & Chen M. 1975. — [Preliminary report of polychaetous annelids from Xisha Islands, Guangdong Province, China]. *Studia Marina Sinica* 10: 65-104.
Young J. L. 1899. — Names of the Paumotu Islands, with the old names so far as they are known. *Journal of the Polynesian Society* 8: 264-268. https://www.jstor.org/stable/pdf/20701552.pdf

Submitted on 13 July 2017;
accepted on 20 February 2018;
published on 19 June 2018.

Appendix 1. — Revised publication dates of Stefano delle Chiaje.

AUTHOR'S OFFICIAL NAME

The original name is Stefano delle Chiaje after Torino & Maio (2013: 158, footnote), despite the fact he signed some of his letters or publications by using delle Chiaie. Stefano delle Chiaie is an Italian terrorist and we should avoid confusing these two very different persons.

PLATES

Because there are compilations of the plates dated 1822, and because they have species group names as their legends, clarifying their publication dates is relevant for nomenclatural purposes. The date 1822 has been indicated in several authoritative compilations, but this is a mistake, as indicated by Alós *et al.* (2004: 519), because they were published along with the text with a single exception, appearing as a much delayed publication.

PUBLICATIONS

The following list is modified after Sherborn (1922) and Alós *et al.* (2004). An internal sequence was inserted to indicate pages per section, although most were not indicated as *memoria* by delle Chiaje).

DELLE CHIAJE S. 1823. — *Memoria sulla Storia e Notomia degli Animali senza Vertebre del Regno di Napoli*: volumen 1. Societá Tipographica, Napoli. Memoria I (Hirudinea): 1-52; Memoria II (Clio, Planarias, Vorticella, others): 53-74; Memoria IIIa (Cassiopea): 75-84, pls 1-4.

DELLE CHIAJE S. 1824a. — *Sunto del fascicolo III e IV delle Memorie su la Storia e Notomia degli Animali senza Vertebre del Regno di Napoli*, Part 1 (Sipunculus: 1-4, Aplysia: 5-12, Holothurians: 13-22, Doridio *et al.*: 23-28); Part 2 (Nautilius: 1-24). Societá Tipografica, Napoli.

DELLE CHIAJE S. 1824b. — *Memoria sulla Storia e Notomia degli Animali senza Vertebre del Regno di Napoli*: Volume 1. Prefazione, Societá Tipographica, Napoli. Memoria IIIb (Sipunculus): 1-24, pl. 1; Memoria IIIc (Aplysia): 25-76, pls 2-5; Memoria IIId (Holothurians): 77-116, pls 6-9; Memoria IIIe (Doridio, Sipunculus, Pleurophyllidia): 117-138, Pl. 10; Memoria IIIf (Taenia): 139-181, pls 11-12; additional explanations for plates 1-7, p. 181-184.

DELLE CHIAJE S. 1825. — *Memoria sulla Storia e Notomia degli Animali senza Vertebre del Regno di Napoli*, Volume 2, Part 1. Societá Tipographica, Napoli. Memoria IIIe (Doridio, cont.): 185-192, Pl. 13; Memoria IIIg (Pterotrachea): 193-218, Pl. 14-15; Memoria IIIh (Argonauta): 219-225; Memoria IIIi (Tricocephalus): 225-227.

DELLE CHIAJE S. 1827. — *Memoria sulla Storia e Notomia degli Animali senza Vertebre del Regno di Napoli*, Volume 2, Part 2. Societá Tipographica, Napoli. Memoria IIIj (Actinia): 228-245, pls 16; Memoria IIIk (Helix): 246-258; Memoria IIIl (Internal water channels): 259-278; Memoria IIIm (Alcyonum): 279-285, pl. 18; Memoria IIIn (Echinoderms): 286–, pls 18-26; Memoria IIIo (Poisonous molluscs): 384-388; Memoria IIIp (Annelids): 389-438, pls 27-29, Index to volumes 1-2: 439-444 (Note that there is no indication for a predated plates' volume).

DELLE CHIAJE S. 1828. — *Memoria sulla Storia e Notomia degli Animali senza Vertebre del Regno di Napoli*, Volume 3. Societá Tipographica, Napoli. Prefazione: i–xx; Memoria 1 (Pennatula, Lobolaria, corals and gorgonians): 1-28, pl. 31; Memoria II (Cellepora, Millepora, Cellaria, Codonita): 29-52. pls 32-34; Memoria III (Pirosoma, Beroe, Salpa. Gleba, Holothuria, Actinia, Asteria): 53-81, pls 34-35; Memoria IV (Compound ascideans, sponges): 82-117, pls 35-37, Memoria V (Planaria, Doris, Tethys, Pleurobranchia): 118-162, pls 38-41; Memoria VI (Annelids): 163-182, pls. 42-44; Memoria VII (simple ascideans): 183-204, pls 45-47; Memoria VIII (Gastropods (+ serpulids, sabellids), supplement): 205-228, pls 48-49; Index to volume 3: 229-232.

DELLE CHIAJE S. 1830 (1822). — *Memoria sulla Storia e Notomia degli Animali senza Vertebre del Regno di Napoli*, Plates 70-109. Societá Tipographica, Napoli [Publication date after Oken, 1836: 290-293].

DELLE CHIAJE S. 1830 (1829). — *Memoria sulla Storia e Notomia degli Animali senza Vertebre del Regno di Napoli*, Volume 4, Part 1. Societá Tipographica, Napoli. Prefazione: i–viii; Memoria I (Fissophora, Rhyzophysa, Racemida, Sefanomia, Ippopo, Alcynoe, Beroe, Cestum, Aplisiottero, Comatula, Teredini): 1-37, pls 50-53; Memoria II (Cephalopoda): 38-116, Pl. 54.

DELLE CHIAJE S. 1831 (1829). — *Memoria sulla Storia e Notomia degli Animali senza Vertebre del Regno di Napoli*, Volume 4, Part 2. Societá Tipographica, Napoli. Memoria III (Balanoglossum, Sertularia, Corallina, sponges, Alcyona): 117-160, pls 55-60; Memoria IV (appendix to Cephalopoda, Salpa, annelids, asterias, Pterotrachia, Gorgonia, Reyepora): 161-210, pls 61-68; Index: 211-213 (up to Plate 69). Erratum: 214.

DELLE CHIAJE S. 1841. — *Animali senza Vertebre del Regno di Napoli. Descrizione e notomia degli animali invertebrati della Sicilia citeriore osservati vivi negli anni 1822-1830*: 1. Molluschi Cefalopedi e Pteropedi; 2. Molluschi Gasteropedi; 3. Molluschi Acefali, Bracciopedi, Cirropedi, Crostacei, Anellosi. Batelli e Comp., Napoli, 1: 19+98, 2: 1-146; 3: 1-142, 6: pls 1-180.

REFERENCES

ALÓS C., LABORDA J., NÚÑEZ J., PARAPAR J., BESTEIRO C., MOREIRA J., SAN MARTÍN G. & ALONSO-ZARAZAGA M.A. 2004. — Apéndice 1. Nomenclatura: lista de sinónimos y combinaciones. *Fauna Ibérica* 25: 495-521.

OKEN L. 1836. — Memorie(sic) sulla Storia e Notomia delli Animali senza Vertebre, 1823-1829, Vol. IV et 72. *Isis, Encyclopädische Zeitschrift* 29: 290-293.

TORINO M. & MAIO N. 2013. — La collezione cetologica di Stefano delle Chiaje presso il Gabinetto di Anatomia Generale e Patologica dell'Università di Napoli. *Atti Societá italiana de Sciences Naturales, Museo Civico di Storia Naturale de Milano* 154: 157-171.