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Reinstatement of species belonging *Marphysa sanguinea* complex (Annelida: Eunicidae) and description of new species from the mid-Pacific Ocean and the Adriatic Sea

ISABEL C. MOLINA-ACEVEDO[1,2*] & IZWANDY IDRIS[2,3]

[1]*Estructura y Función del Bentos, Depto. Sistemática y Ecología Acuática, El Colegio de la Frontera Sur, Chetumal, Quintana Roo, México.*

[2]*South China Sea Repository and Reference Centre, Institute of Oceanography and Environment, Universiti Malaysia Terengganu, 21030 Kuala Nerus, Terengganu, Malaysia.*

[3] *izwandy.idris@umt.edu.my, https://orcid.org/0000-0003-1516-8175*

[*]*Corresponding author. isacrismoliace@gmail.com, imolina@ecosur.edu.mx; https://orcid.org/0000-0001-5487-895X*

Abstract

Marphysa sanguinea Montagu, 1813, the type species of genus *Marphysa*, was described with few characteristics and subsequently reported in tropical and temperate waters as a cosmopolitan species. Recent comparative studies have shown that *M. sanguinea* has a limited distribution to the Northeast Atlantic. As a result, species from the tropical and subtropical zones are now being redescribed as new species. However, this issue is not completely resolved because of the taxonomic status of seven nominal species, considered as junior synonymies of *M. sanguinea*. Herein, we examined the type and additional materials from five species in synonymy *M. sanguinea* and performed a compared analysis with the neotype of *M. sanguinea.* Additionally, we reviewed specimens from two localities in the mid-Pacific Ocean and the Adriatic Sea, where *M. sanguinea* was previously reported. As a result of this study, three species were reinstated (*M. californica* Moore, 1909, *M. leidii* de Quatrefages, 1866, and *M. parishii* Baird, 1869) and two subspecies, are now raised to species level (*M. americana* n. status and *M. brevibranchiata* n. status). In addition, two new species from Hawaii and Croatia are described: *M. baileybrockae* **n. sp.** and *M. birgeri* **n. sp.**, respectively. Morphological comparisons with most species currently assigned to the *M. sanguinea* complex are presented. This work provides more support for rejecting the hypothesis that *M. sanguinea* is a cosmopolitan species and we encourage the use of novel and traditional morphological characters to differentiate species within the complex.

Key words: Branchiae, pectinate chaetae, parapodia lobes, redescription, synonymy

Introduction

In 1813, research on the genus *Marphysa* de Quatrefages, 1865, began when George Montagu described a specimen collected from the rocky coasts of Devonshire, England, and named it *Nereis sanguinea* because of the red blood color that circulated through its branchiae. A few years later, *Leodice opalina* Savigny in Lamarck (1818) was established with major characters similar to *Nereis sanguinea.* Then, de Blainville (1828) established *Nereidonta* and transferred Montagu's species to this genus and considered *L. opalina* a synonym of *N. sanguinea*. Audouin & Milne-Edwards (1834) suggested that Montagu's species should be placed in genus *Eunice* Cuvier, 1817, because of the five prostomial appendages and the pectinate branchiae along the body. Audouin & Milne-Edwards (1834) considered *L. opalina* and *N. sanguinea* as synonyms of *Eunice sanguinea*. Later, de Quatrefages (1865a, b) established the name *Marphysa* for specimens with five prostomial appendages and pectinate branchiae but lacking peristomial cirri. Given that the Montagu specimen coincided with these characters, de Quatrefages proposed a new combination, *Marphysa sanguinea*. Two years later, Malmgren (1867) designated *M. sanguinea* (=*Nereis sanguinea*) as the type species of the genus.

The original description of *Marphysa sanguinea* (Montagu, 1813) is brief and short, and in consequence several synonyms and doubtful records have been made. *Marphysa sanguinea* has been reported as a cosmopolitan species

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and found in temperate and tropical waters, e.g., France (Fauvel 1923), Spain (Parapar *et al*. 1993), Mediterranean Sea (Bellan 1964), South Africa (Day 1967), Australia (Day 1967), Japan (Miura 1977), Northern American Pacific (Hartman 1944a; Fauchald 1970), and Mexican Caribbean (Salazar-Vallejo & Carrera-Parra 1998).

The cosmopolitan status of *M. sanguinea* has been challenged by Hutchings & Karageorgopoulos (2003), who proposed a neotype of *M. sanguinea,* provided a detailed redescription and described Australian specimens previously identified as *M. sanguinea* as *M. mullawa* Hutchings & Karageorgopoulos, 2003. The authors suggested the actual distribution of *M. sanguinea* is restricted to the east of the North Atlantic as subsequently shown by Lavesque *et al.* (2019) and Martin *et al.* (2020).

This framework was replicated over time with previous misidentifications in South Africa (*M. elityeni* Lewis & Karageorgopoulos, 2008) and Australia (*M. kristiani* Zanol, da Silva & Hutchings, 2016), as well as in China (*M. tribranchiata*, *M. multipectinata*, and *M tripectinata* Liu, Hutchings & Sun, 2017; *M. bulla* and *M. maxidenticulata* Liu, Hutchings & Kupriyanova, 2018; *M. hongkongensa* Whang, Zhang & Qiu, 2018), in Gulf of Viscaya, France (*M. victori* Lavesque, Daffe, Bonifácio & Hutchings, 2017), in the Suez Canal (*M. aegypti* Elgetany, Ghobashy, Ghoneim & Struck, 2018), in Philippines (*M. iloiloensis* Glasby, Mandarino, Burghardt, Kupriyanova, Gunton & Hutchings, 2019), and Spain (*M. gaditana* Martin, Gil & Zanol in Martin *et al.* 2020 and *M. chirigota* Martin, Gil & Zanol in Martin *et al.* 2020).

Another 10 species around the world are considered junior synonyms of *M. sanguinea* but without the detailed review and comparison with the type material: *M. haemasoma* de Quatrefages, 1866 (*fide* von Marenzeller 1888), *M. leidii* de Quatrefages, 1866 (*fide* Webster 1879), *M. parishii* Baird, 1869 (*fide* Augener 1931), *M. acicularum* Webster, 1884 (*fide* Hartman 1944a), *M. iwamushi* Izuka, 1907 (*fide* Fauvel 1936), *M. californica* Moore, 1909 (*fide* Monro 1933), *M. acicularum brevibranchiata* Treadwell, 1921, *M. nobilis* Treadwell, 1917 and *M. viridis* Treadwell, 1917 (*fide* Hartman 1944a), and *M. sanguinea americana* Monro, 1933 (*fide* Monro 1933). Three of them (*M. acicularum*, *M. nobilis*, and *M. viridis*) from the Grand Caribbean were studied by Molina-Acevedo & Carrera-Parra (2015), and the type material were compared with the description of neotype *M. sanguinea*. The authors concluded that the four species were distinguished by the shape of the parapodia, the branchial distribution, and the coloration, distribution of the subacicular hook. Hence, they proposed the reinstated of the three Caribbean species and questioned the distribution of *M. sanguinea* in that region. Molina-Acevedo & Carrera-Parra (2015) also suggested that the rest of seven species in synonymy need to be re-examined.

The objectives of the present work were to continue the revision of the *M. sanguinea* species complex, focusing on five synonyms (including three species: *M. californica, M. leidii, M. parishii* and two subspecies: *M. acicularum brevibranchiata* and *M. sanguinea americana*). The type material of these species are reviewed and morphologically compared with the neotype and additional material from *M. sanguinea*. In addition, specimens from Hawaii and Adriatic Sea, previously identified as *M. sanguinea* are also described as new species.

Material and methods

The type and additional materials reviewed in this study are deposited in the following institutions: the American Museum of Natural History, New York, USA (AMNH); the Natural History Museum, London (BNHM); the California Academy of Sciences, San Francisco, USA (CAS); the Los Angeles County Museum of Natural History, Allan Hancock Foundation Polychaete Collection (LACM-AHF); the National d'Histoire Naturelle, Paris, France (MNHN); the National Museum of Natural History, Smithsonian Institution, Washington D.C., USA (USNM); and the Zoologisches Museum, Universität Humboldt, Berlin, Germany (ZMB).

All diagnostic features are based on the recent terminology following Carrera-Parra (2009), Glasby & Hutchings (2010), Carrera-Parra & Salazar-Vallejo (2011), Molina-Acevedo & Carrera-Parra (2015, 2017), and Zanol *et al.* (2014, 2016). In general, specimens were compared based on the following characters: shape of prostomium, peristomium, branchiae, maxillary apparatus, and parapodia including the form of the cirri and lobes, and simple and compound chaetae.

Morphological characters such as prostomium, branchiae, and maxillary apparatus were observed and measured under the stereomicroscope, and their variation reported. The maxillary apparatus was described according to Molina-Acevedo & Carrera-Parra (2015, 2017) and Molina-Acevedo (2019). A total of five parapodia, three in anterior region and one each median and posterior regions, were dissected for observation under the compound mi-

croscope, and details on the shape of dorsal and ventral cirri, parapodial lobes, and chaetae. We considered a long or short branchial filament when in the region of the body with the maximum number of branchial filaments, the long filaments are ≥ 4 times as long as dorsal cirri, whereas the short filaments are < 4 times as long as dorsal cirri. The classification of pectinate chaeta proposed by Molina-Acevedo & Carrera-Parra (2015) was followed. We used isodont to indicate that both external teeth are longer than internal teeth and anodont when all the internal and external teeth have the same length (Fig. 1O). We also follow the terminology of Zanol *et al.* (2016) for describing thick or thin in pectinate chaetae, when they were thicker or thinner than limbate chaetae, respectively. The pectinate blade is considered narrow if <22 μm wide and the pectinate chaetae is considered wide if ≥30 μm. Also, the internal teeth are considered long and thick if they exceed 2 μm. Moreover, we follow the methods of Steiner & Amaral (2000) and Glasby & Hutchings (2010) in describing pectinate chaetae; they are considered asymmetric when the superior edge of the blade has an inclination and symmetric when the blade is straight.

In the Material Examined section, the number of the specimens per lot is stated in parentheses. Most of the reviewed specimens are incomplete; thus, biometric data on specimen length (L10) was measured from anterior edge of prostomium to chaetiger 10; the specimen width (W10) was measured based on the chaetiger 10 excluding the parapodium; the total length (TL) and total number of chaetigers (TChae) counted for complete specimens. Additionally, the chaetiger number and side (R (right) or L (left)), of which branchiae and subacicular hooks emerged were also reported.

All descriptions were illustrated with digital photographs. A series of photos were also stacked using Helicon-Focus version 4.0.5 software to improve the depth of field.

Results

Systematic

Order EUNICIDA Dales, 1962

Family EUNICIDAE Berthold, 1827

Genus *Marphysa* de Quatrefages, 1865

Type species: *Marphysa sanguinea* (Montagu, 1813)

Diagnosis (modified after Molina-Acevedo & Carrera-Parra 2017). Single-lobe prostomium or bilobed; five prostomial appendages without articulations (Fig. 1A); eyes present or absent. Peristomium without peristomial cirri. Maxillary apparatus with four pairs of maxillae and an unpaired on left side (Fig. 1D); MI forceps-like, without attachment lamella, with falcal arch well developed, in angular shape, with the outer base of MI concave and inner base oblique (Fig. 1D); MII without attachment lamella; MIII curved, forming part of distal arc, with attachment lamella sclerotized, situated at the center of right edge of maxilla; MIV with attachment lamella sclerotized, situated in anterior edge of maxilla. Maxillae V unidentate. Branchiae distributed throughout the body. Dorsal cirri without articulation; postchaetal lobe well developed in anterior region (Fig. 1G–K); ventral cirri with swollen base, oval or circular, in more than half of parapodia of the body (Fig. 1G–K). Aciculae dark. Supracicular chaetae include limbate; pectinate chaetae thin narrow isodont in anterior region of the body (Fig. 1M), pectinate chaetae isodont wide in median-posterior region, and/or thick wide anodont pectinate chaetae in posterior region (Fig. 1N, P). Subacicular chaetae include compound falcigers, spinigers (Fig. 1L) or both. Subacicular hook, dark, or translucent, bidentate, or unidentate. Pygidium with two pairs of anal cirri, without articulation.

Remarks. The genus *Marphysa* is represented by more than 90 species that are divided into several groups: A, B1, B2, C1, C2, D1, and D2 (Fauchald 1970); Bellii group, Sanguinea group, and "Mortenseni group (Orensanz 1990); and Teretiuscula group (Glasby & Hutchings 2010). This diversity of forms and groups leads to the conclusion that the generic boundaries of *Marphysa* are in need of invetigation. Although Zanol *et al*. (2014) found that *Marphysa* formed a monophyletic grouping in a phylogenetic analysis of the Eunicidae, two new genera were erected (*Treadwellphysa* Molina-Acevedo & Carrera-Parra, 2017, and *Paucibranchia* Molina-Acevedo, 2018) based on species previously assigned to two of the *Marphysa* groups (Fauchald 1970). Morphological variability and the

description of new genera suggest that monophyly of *Marphysa*, as presently define, is doubtful. Therefore, it is still necessary to perform revisionary work on the genus, ideally based on evidence morphological, molecular, ecological data, to resolve two main issues: (1) to corroborate if questionable taxa belong to *Marphysa* or different genera and (2) to achieve a more precise delimitation of the genus *Marphysa.*

Marphysa americana Monro, 1933 n. status

Figures 1, 9A, Table 1

Marphysa sanguinea var. *americana* Monro, 1933: 68–69, Text-figs. 28.
Marphysa sanguinea americana.—Fauchald 1970: 64–66.
Marphysa sanguinea.—Fauchald 1977: 42 (*non* Montagu, 1913).

Material examined. *Type material:* Holotype BNHM 1932.12.24.554-556, Pacific Expedition 1923–1924, sta. Balboa 2, St. George, Balboa, Panama, Pacific Ocean, coll. C. Crossland.

Description. Holotype complete, laterally dissected, with 390 chaetigers, broken in three parts (anterior fragment with 183 chaetigers, median fragment with 87 chaetigers, posterior fragment with 120 chaetigers), all three parts belong to the same individual, L10 = 12 mm, W10 = 5.8 mm, TL = 278 mm. Last 53 chaetigers regenerating. Anterior region of the body with dorsum convex and flat ventrum, without groove; body depressed from chaetiger 9, widest at chaetiger 50, tapering after chaetiger 116.

Prostomium bilobed, 2.3 mm long, 4 mm wide; lobes frontally rounded; median sulcus shallow anteriorly and deep ventrally (Fig. 1A–B). Prostomial appendages in a semicircle, median antenna isolated by a gap. Palps reaching middle of first peristomial ring; lateral antennae reaching second peristomial ring; median antenna reaching first chaetiger. Palpophores and ceratophores ring-shaped, short, thick; palpostyles and ceratostyles tapering, slender. Eyes ovate, brown, between palps, and lateral antennae.

Peristomium (3.2 mm long, 7.2 mm wide) larger and wider than prostomium; first ring two times longer than second ring, separation between rings distinct only dorsal, and ventrally (Fig. 1A–B). Ventral lip with a slight central anterior depression and several shallow wrinkles (Fig. 1B).

Maxillary apparatus with MF = 1 + 1, 5 + 4, 7 + 0, 3 + 9, 1 + 1 (Fig. 1D). MI 3.2 times longer than length of maxillary carriers. MI forceps-like, MI five times longer than length of closing system (Fig. 1D); ligament between MI and MII strongly sclerotized. MII with recurved triangular teeth; MII three times longer than length of cavity opening (Fig. 1D–E); ligament between MII and MIII and right MIV, slightly sclerotized. MIII with triangular teeth; with irregular attachment lamella, situated in center of right edge of the plate, slightly sclerotized (Fig. 1D). Left MIV with three laterals teeth larger than rest; attachment lamella rectangular, wide, better developed in left side, situated 2/3 of anterior edge of maxilla, sclerotized. Right MIV with three laterals teeth larger than rest; attachment lamella rectangular, wide, better developed in central side, situated 2/3 of anterior edge of maxilla, sclerotized (Fig. 1D–E). MV rectangular, with a short triangular tooth. Mandibles dark; calcareous cutting plates broken, sclerotized cutting plates brown, with up to 25 growth rings (Fig. 1F).

Pectinate branchiae with up to 12 long filaments, present from chaetigers 45L–47R to 362L–361R (Fig. 1J). First pair with two filaments and last 18 chaetigers with one filament; reaching the maximum 11 or 12 filaments in chaetigers 93L to 121L (Fig. 9A). Branchial filaments longer than dorsal cirri except in first and last five branchiae.

First three parapodia smaller, best developed in chaetigers 6–53, following ones gradually smaller. Dorsal cirri conical, longer than ventral cirri in anterior chaetigers, similar length in median and posterior ones; best developed in chaetigers 6–57, following ones gradually smaller (Fig. 1G–K). Prechaetal lobes short, as transverse folds in all chaetigers (Fig. 1G–K). Chaetal lobes in the first 40 chaetigers rounded, shorter than postchaetal lobes, with aciculae emerging dorsal to midline; from chaetiger 41 triangular, longer than other lobes, with acicula emerging in midline (Fig. 1G–K). Postchaetal lobes well developed in first 92 chaetigers; conical in first six chaetigers, rounded in chaetigers 7–34, progressively smaller from chaetiger 34; from chaetiger 93 inconspicuous (Fig. 1G–K). Ventral cirri digitiform in first four chaetigers; in chaetigers 5 to 345 with an oval swollen base and blunt tip; conical from chaetiger 346, gradually reducing in size (Fig. 1G–K).

Aciculae blunt, reddish along most of its length, amber on the distal tip (Fig. 1K–J). First chaetiger with three aciculae; in chaetigers 2–41 with five; in chaetigers 42–51 with four; in chaetigers 52–129 with three; from chaetigers 130 with two aciculae.

Limbate chaetae of two lengths in same chaetiger: long and short, long blades are in dorsal region, short blades in ventral position; limbate chaetae reduced in number around chaetiger 27, and then maintained a similar number until the posterior end. Four types of pectinate chaetae; in anterior chaetigers, thin, isodont narrow, asymmetric, with long and slender teeth, with 3–4 pectinate, with up to 12 teeth (Fig. 1M); in median-posterior chaetigers, thick, isodont wide, symmetric, with short and slender teeth, with 3–4 pectinate with up to 16 teeth (Fig. 1N), and thick, isodont wide, asymmetric, with long and thick teeth, with 2–3 pectinate, with up to 16 teeth (Fig. 1O); in posterior chaetigers, thick, anodont wide, asymmetric, with long and thick teeth, with 1–2 pectinate, with up to 11 teeth (Fig. 1P). Compound spinigers present throughout; in anterior chaetigers with blades of two lengths: shorter bladed slightly more abundant than longer blades (Fig. 1L); in median-posterior chaetigers with blades of similar length. Subacicular hooks bidentate, reddish along most of its length, translucent on the distal tip; present only in chaetigers 117, 140, 149, and in regenerating region; blunt teeth, of similar size, distal tooth directed upward, proximal tooth directed laterally (Fig. 1Q).

Pygidium with dorsal pair of anal cirri as long as last eight chaetigers; ventral pair short, as long as last two chaetigers.

Distribution. Balboa, Panama, Pacific Ocean.

Habitat. The specimen was found in Balcoa dock, in shore-pools at low tide. The author did not specify the type of sediment.

Remarks. Monro (1933) studied the speciemens collected by Crossland in The Expedition of the S.Y. San George, specifically from the area of Balboa Docks Panama, Taboga and Perlas Islands. The material collected in this expedition was deposited in the British Museum.

Monro (1933) observed a single specimen accompanied by a long fragment of *Onuphis magna* (Andrews, 1891) placed in the same container by Crossland. Monro compared his Panama specimen with the material of *M. sanguinea* available in the collection of the British Museum and concluded that both are similar in the branchiae through the body and the compound spinigers in all chaetigers. Monro also clarified that the main difference was the number of branchial filaments (12 filaments for Panama specimen and six filaments for *M. sanguinea*); however, he attributed this to the size variation of the organisms and designated the Panamanian specimen as the *M. sanguinea americana* variety (= subspecies, see ICZN Art. 45.6.3–4). Fauchald (1970, 1977) commented that the number of branchial filaments in *M. sanguinea* could be variable (between 4 and 10 filaments); therefore, the subspecies described for Panama is not different from the original British form.

Herein, we find that the subspecies *M. sanguinea americana* (L10: 12 mm) differs from *M. sanguinea* (L10: 11.5–20.4 mm) by having branchiae from chaetiger 45; higher number of filaments (12); postchaetal lobe developed in more number of chaetiger (in 92 anterior chaetigers); and by the conical shape of the postchaetal lobe in first four chaetigers of the body. However, in *M. sanguinea* the branchiae start from chaetigers 21–25, a lower number of branchial filaments (5–6) are found, the postchaetal lobe is developed only in first 50–70 chaetigers of the body, and the postchaetal lobe is digitiform in the first four chaetigers of the body. Additionally, both taxa have differences in the number of thick and wide pectinate isodont chaetae per chaetiger. The Panama specimen has only three or four chaetae, whereas in *M. sanguinea* has between 18 and 20 pectinates. In view of these differences, the taxa are considered herein different species, and it is proposed to raise the subspecies proposed by Monro to the level of species.

Marphysa americana n. status resembles *M. depressa* (Schmarda, 1861) (New Zealand), *M. emiliae* Molina-Acevedo & Carrera-Parra, 2017 (Yucatan, Mexico), *M. teretiuscula* (Schmarda, 1861) (Sri Lanka), and *M. tripectinata* (Beihai, China) by having subacicular hook bidentate and reddish along most of its length. However, *M. americana* n. status has postchaetal lobes which are conical in first four chaetigers of the body; in contrast, *M. depressa* and *M. emiliae* have digitiform postchaetal lobes, and *M. teretiuscula* and *M. tripectinata*, have ovoid-shaped postchaetal lobes in the first four chaetigers of the body. Also, *M. americana* n. status has branchiae pectinate with a well-defined main axis in most segments, whereas in *M. teretiuscula* and *M. tripectinata*, in some regions of the body, the main axis are poorly developed, similar to palmate form. On the other hand, in *M. americana* n. status, there are only one type of anodont pectinate in posterior region, whereas in *M. teretiuscula* and *M. emiliae* there are two types of anodont pectinate in the same region. Moreover, *M. americana* n. status (Ll0 = 12 mm) has up 12 brachial filaments, whereas in *M. depressa* (L10 = 4.2–11.5 mm), there are only 2–4 branchial filaments. The comparison of *M. americana* n. status with the related species is provided in Table 1.

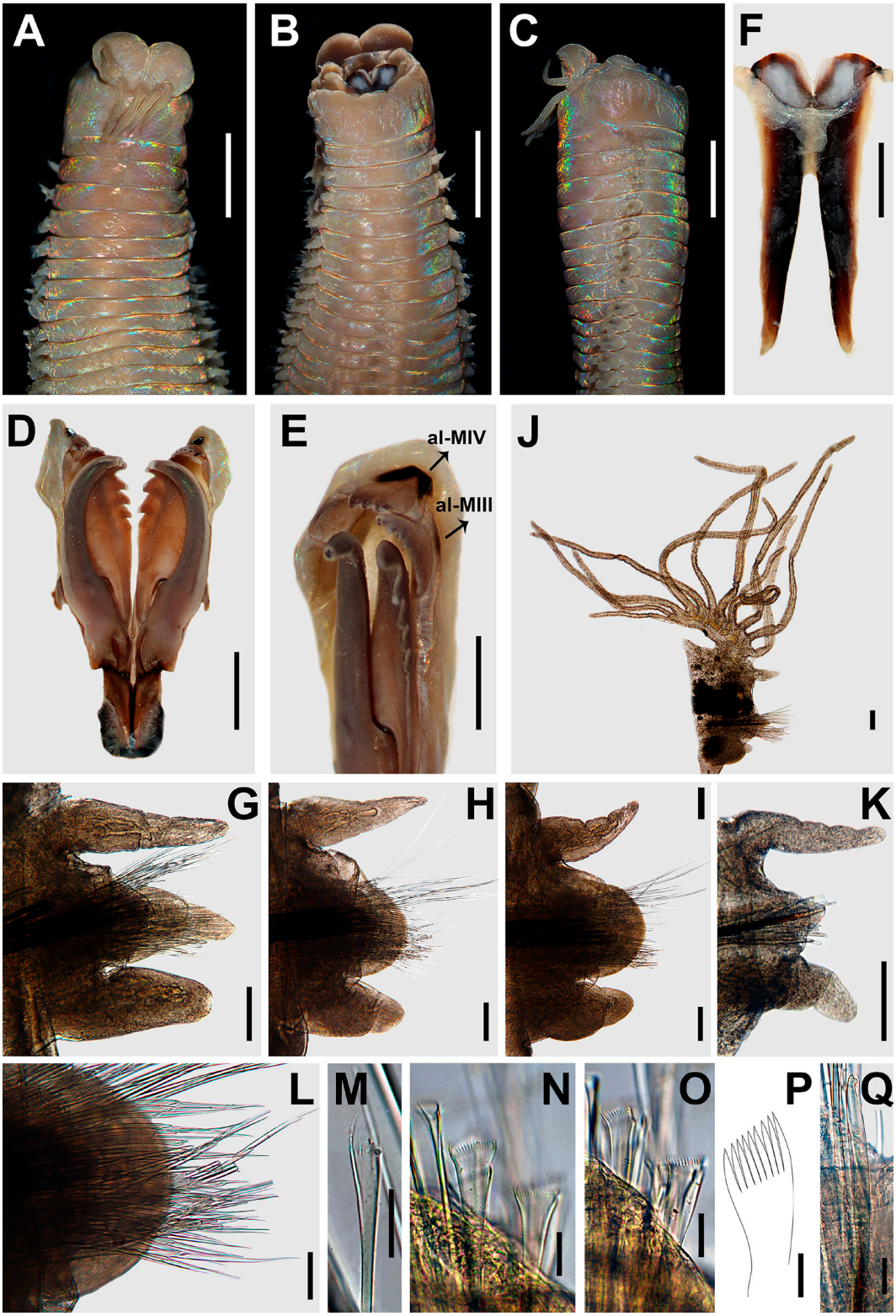

FIGURE 1. *Marphysa americana*. Holotype BNHM 1932.12.24.554-556. A. Anterior end, dorsal view; B. Anterior end, ventral view; C. Anterior view, lateral view; D. Maxillary apparatus, dorsal view; E. Left MI-II-III-IV-V, lateral view; F. Mandible; G. Parapodium 3; H. Parapodium 6; I. Parapodium 12; J. Parapodium 247; K. Parapodium 377; L. Compound spinigers, chaetiger 6; M. Thin, isodont narrow, asymmetric, with long and slender teeth, chaetiger 6; N. Thick, isodont wide, symmetric, with short and slender teeth, chaetiger 325; O. Thick, isodont wide, asymmetric, with long and thick teeth, chaetiger 325; P. Thick, anodont wide, asymmetric, with long and thick teeth, chaetiger 377; Q. Subacicular hook, chaetiger 367. All chaetigers in anterior view; al-MIII: attachment lamella MIII; al-MIV: attachment lamella MIV. Scale bars: A–C, 3 mm; D, 1.4 mm; E. 0.9 mm; F. 1.3 mm; G–K, 0.2 mm; L, 0.1 mm; M–Q, 30 μm.

***Marphysa baileybrockae* n. sp.**
Figures 2, 9B, Table 1

Marphysa teretiuscula.—Treadwell 1906: 1172 (*non* Schmarda, 1861).
Marphysa sanguinea.—Abbott, 1946: 6.—Hartmann-Schröder 1965: 137.—Hartman 1966: 218 (*non* Montagu, 1813).

Examined material. *Type material:* Holotype USNM 5444, paratype AMNH 367 (1 specimen), Honolulu Reef, Oahu Island, Hawaii, United States, North Pacific Ocean, Albatross, 1902, col. United States Fish Commission.

Description. Holotype complete, dorsally dissected, with 312 chaetigers, broken in two parts (first one with 137 chaetigers), L10 = 11.7 mm, W10 = 3.8 mm, TL = 151 mm. Last 16 chaetigers regenerating. Anterior region of the body with dorsum convex and flat ventrum; body depressed from chaetiger 11, widest at chaetiger 33, tapering after chaetiger 41.

Prostomium bilobed, 1.2 mm long, 2.5 mm wide; lobes frontally trucate; median sulcus shallow anteriorly and deep ventrally (Fig. 2A–B). Prostomial appendages in a semicircle, median antenna isolated by a gap. Palps reaching second peristomial ring; lateral antennae reaching first chaetiger; median antenna broken, reaching first chaetiger; in paratype median antenna reaching second chaetiger. Palpophores and ceratophores ring-tapering, short, slender; palpostyles and ceratostyles tapering, slender. Eyes rounded, brown, between palps, and lateral antennae.

Peristomium (1.9 mm long, 4 mm wide) larger than prostomium, first ring two times longer than second ring, separation between rings distinct on all sides (Fig. 2A–C). Ventral lip without central anterior depression (Fig. 2B).

Maxillary apparatus with MF = 1 + 1, 4 + 5, 7 + 0, 4 + 8, 1 + 1 (Fig. 2D). MI 2.4 times longer than length of maxillary carriers. MI forceps-like, MI 3.8 times longer than length of closing system (Fig. 2D–E); ligament between MI and MII sclerotized. MII with recurved triangular teeth; MII 4.8 times longer than length of cavity opening (Fig. 2D–E); ligament between MII and MIII and right MIV, sclerotized. MIII with rounded teeth; with irregular attachment lamella, situated in center of the right edge of the plate, sclerotized (Fig. 2D–E). Left MIV with three lateral teeth larger than rest; attachment lamella semicircle, slender, better developed in left side, situated 4/3 along anterior edge of the maxilla, sclerotized. Right MIV with teeth of similar size; attachment lamella semicircle, wide, better developed in left side, situated 4/3 along anterior edge of the maxilla, sclerotized (Fig. 2D–E). MV square with a short, rounded tooth. Mandibles dark; calcareous cutting plates present in left side, sclerotized cutting plates brown, with 16 growth rings (Fig. 2F).

Pectinate branchiae with up to three long filaments, present from chaetigers 30R–32L to 293 (Fig. 2K–J). First seven and last 20 chaetigers with one filament; reaching the maximum three filaments in chaetigers 54L to 215L (Fig. 9B). Branchiae with filaments longer than dorsal cirri.

First four parapodia smaller, best developed in chaetigers 5–34, following ones gradually smaller. Dorsal cirri conical in all chaetigers; longer than ventral cirri in anterior and posterior chaetigers, shorter in median chaetigers; best developed in chaetigers 1–16, following ones gradually smaller (Fig. 2G–K). Prechaetal lobes short, in the first 23 chaetiger with dorsal edge longer than ventral; following ones as a transverse fold in all chaetigers (Fig. 2G–K). Chaetal lobes rounded in first 22 chaetigers, shorter than postchaetal lobes, with aciculae emerging dorsal to midline; from chaetiger 23 triangular, longer than other lobes, with acicula emerging in midline (Fig. 2G–K)). Postchaetal lobes well developed in first 59 chaetigers; conical with distal edge directed to dorsal side in first five chaetigers, ovoid with dorsal edge longer than ventral in chaetigers 6 to 11, progressively smaller from chaetiger 13; from chaetiger 60 inconspicuous (Fig. 2G–K). Ventral cirri digitiform in first four chaetigers; from chaetigers 5 to 287 with an oval swollen base and digitiform tip; digitiform from chaetiger 288, gradually reducing in size (Fig. 2G–K).

Aciculae blunt, reddish along most of its length, and translucent on the distal tip in first 16 chaetigers; following aciculae translucent completely (Fig. 2G–K). First four chaetigers with two aciculae; in chaetigers 5–14 with three or four; in chaetigers 15–137 with four or five; in chaetigers 138–174 with four; in chaetigers 175–277 with three; in chaetigers 278–295 with two; from chaetiger 296 with two or one acicula.

Limbate chaetae of two length sizes in same chaetiger: long and short, long blades in dorsal position, short blades in ventral position; limbate chaetae reduced in number around chaetiger 19, and then maintained a similar number until the posterior end. Three types of pectinate chaetae; in most of chaetigers, thin, isodont narrow, symmetric, with short, and slender teeth, with 6–8 pectinate, with up to 20–22 teeth (Fig. 2L); in median-posterior chaetigers, thick, isodont wide, symmetric, with long, and slender teeth, with 1–2 pectinate, with up to 24 teeth

(Fig. 2N), and thick, anodont wide, symmetric, with long and thick teeth, with 1–2 pectinate, with up to six teeth (Fig. 2M). Compound spinigers present throughout, with blades of two lengths in all chaetigers: shorter blades more abundant than longer blades (Fig. 2O). Subacicular hooks unidentate, translucent (Fig. 2P); starting from chaetiger 32, one or two per chaetiger (second replacement hook), present discontinuously after chaetigers 32; in posterior chaetigers hooks bidentate, with blunt teeth, distal tooth smaller than proximal, directed upward, proximal directed laterally (Fig. 2Q).

Pygidium with dorsal pair of anal cirri as long as last four chaetiger; ventral pair short, as long as last chaetiger.

Variation. Material examined with L10 = 4.8–11.7 mm, W10 = 2.3–3.8 mm, TChae = 182–312. Palps reaching second peristomial ring; lateral antennae reaching first or second chaetiger; median antenna reaching second chaetiger. Branchiae from chaetigers 22–30 to 19–20 chaetigers before pygidium. Maximum number of branchial filaments is three. Postchaetal lobe conspicuous in first 47–59 chaetigers. Ventral cirri with a swollen base from chaetigers 5–6 to 21–25 chaetigers before of pygidium. Start of subacicular hooks in chaetigers 27–32.

Type locality. Honolulu Reef, Hawaii.

Distribution. Honolulu, Kaneohe Bay, Hawaii.

Habitat. According to Treadwell (1906), the material was collected from Honolulu reef. Hartmann-Schröder (1965) studied three specimens from Oahu, Kaneohe Bay, collected from coral sand.

Etymology. The species is named after Dr. Julie H. Bailey-Brock, in recognition of her valuable contributions to the taxonomic study of the polychaete from Hawaii.

Remarks. Treadwell (1906) identified two specimens collected from Honolulu as *M. teretiuscula,* a species described by Schmarda (1861) from Sri Lanka. Later, Abbott (1946) and Hartmann-Schröder (1965) reported specimens with similar features to Treadwell's specimens but identified them as *M. sanguinea* from Kaneohe Bay, Hawaii. Then, Hartman (1966) reviewed the species studied by Treadwell and concluded that the material previously identified as *M. teretuiscula* belongs to *M. sanguinea.*

Treadwell (1906) only indicated a small difference in the number of branchial filaments from Schmarda's original description; however, after a detailed comparison between the type material of *M. teretiuscula, M. sanguinea* and Treadwell's specimens, herein some significant differences were found. Hence, the specimens from Honolulu are considered as a new species, *Marphysa baileybrockae* **n. sp.**.

Marphysa baileybrockae **n. sp.** (type material L10 = 4.8–11.7 mm) has branchiae from chaetigers 22 to 30 with up to three branchial filaments, whereas *M. teretiuscula* (type and additional material, L10 = 5.5–12.4 mm) has branchiae from the chaetigers 18 to 32 with up to four to six branchial filaments. Furthermore, in *M. baileybrockae* **n. sp.** the postchaetal lobe is conical in anterior chaetigers, the ventral cirri with a swollen base end 21–25 chaetigers before of pygidium, and the subacicular hook is translucent, instead of *M. teretiuscula* in which the postchaetal lobe is ovoid in anterior chaetigers, the ventral cirri with a swollen base end 34–68 chaetigers before pygidium, and the subacicular hook is reddish in most of its length and translucent distally.

M. baileybrockae **n. sp.** is different from *M. sanguinea* (type and additional material L10 = 11.5–20.4 mm) by the color translucent of the subacicular hook, whereas in *M. sanguinea* the subacicular hook is reddish on the base and translucent in distal end. Furthermore, the new species only has up to three branchial filaments, and the distal edge of the postchaetal lobe is directed to dorsal side, instead of *M. sanguinea* that has up to five or six branchial filaments, and the distal edge is straight. Also, *M. baileybrockae* **n. sp.** has only one or two thick isodont wide pectinate, with long and slender teeth in median and posterior chaetigers, whereas in *M. sanguinea* there are 18–20 pectinate chaetae in the same region or the body.

Marphysa baileybrockae **n. sp.** resembles *M. acicularum* (Bermuda), *M. brasiliensis* (Hansen, 1882) (Brazil), *M. bulla* (Yellow Sea, China), *M. californica* (California), *M. maxidenticulata* (Yellow Sea, China), and *M. parishii* (Brazil) by having the pectinate branchiae with long branchial filaments, absence of subacicular limbate chaetae, subacicular hook translucent, and the dorsal cirri conical in all chaetigers. Nonetheless, *M. baileybrockae* **n. sp.** has three types of pectinate chaetae throughout the body, whereas *M. bulla* and *M. parishii* have five types, and *M. californica* and *M. maxidenticulata* have four types of pectinate chaetae. Moreover, *M. baileybrockae* **n. sp.** has the prechaetal lobe in first chaetigers with dorsal edge longer than ventral, in contrast of *M. brasiliensis*, *M. bulla*, *M. californica*, *M. maxidenticulata*, and *M. parishii* that the prechaetal lobe is as a transversal lobe. Furthermore, *M. baileybrockae* **n. sp.** has the postchaetal lobe directed to dorsal side, instaed of *M. acicularum*, *M. brasiliensis*, *M. bulla*, *M. californica*, *M. maxidenticulata*, and *M. parishii* which the postchaetal lobe is straight. The comparison of *M. baileybrockae* **n. sp.** with related species is provided in Table 1.

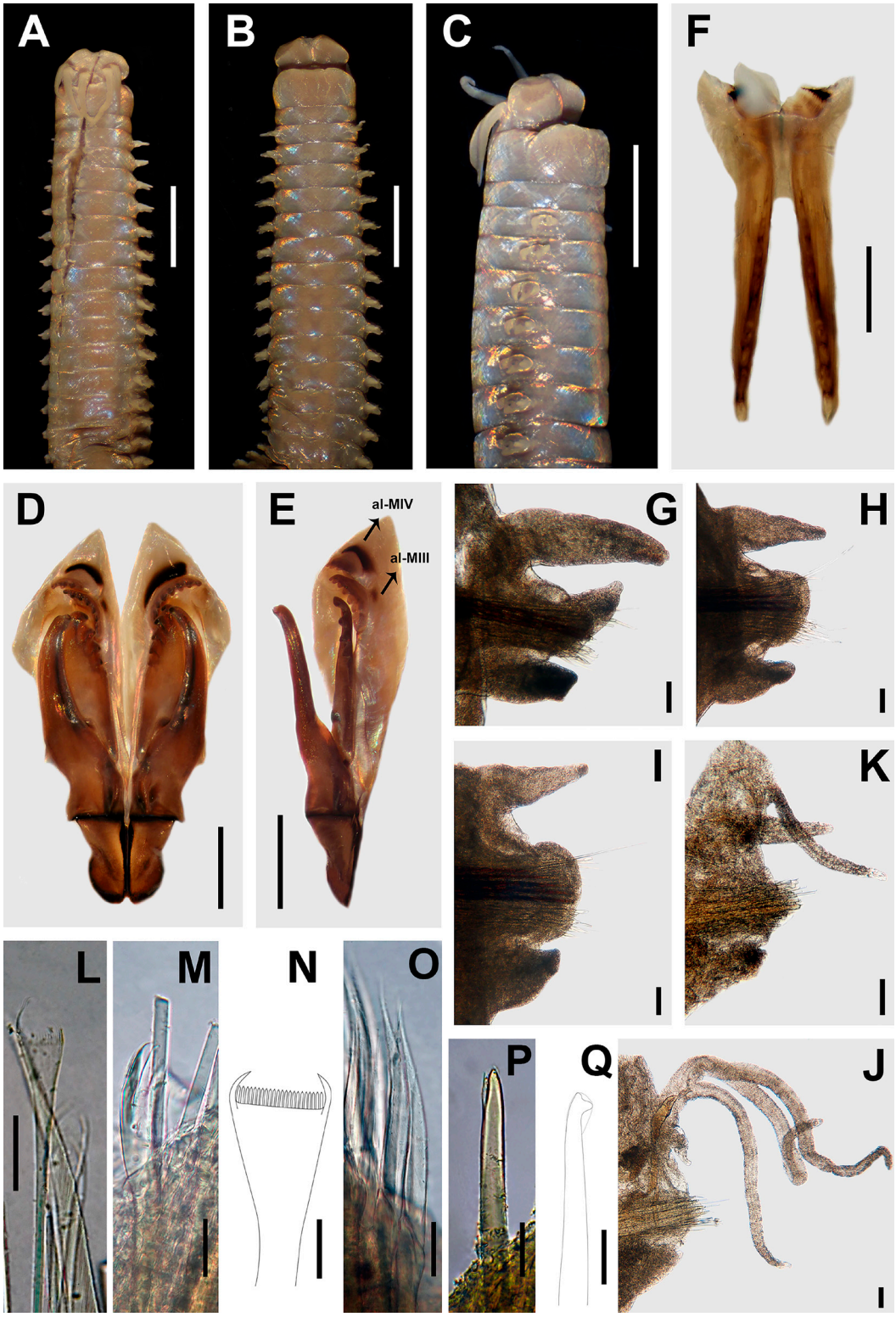

FIGURE 2. *Marphysa baileybrockae* **n. sp.** A. Anterior end, dorsal view; B. Anterior end, ventral view; C. Anterior end, lateral view; D. Maxillary apparatus, dorsal view; E. Left MI-II-III-IV-V, lateral view; F. Mandible; G. Parapodium 3; H. Parapodium 8; I. Parapodium 16; J. Parapodium 250; K. Parapodium 308; L. Thin, isodont narrow, symmetric, with short and slender teeth, chaetiger 8; M. Thick, anodont wide, symmetric, with long and thick teeth, chaetiger 295; N. Thick, isodont wide, symmetric, with long and slender teeth, chaetiger 358; O. Compound spinigers, chaetiger 8; P. Subacicular hook unidentate, chaetiger 122; Q. Subacicular hook bidentate, chaetiger 152. A–O from holotype USNM 5444, P–Q from paratype AMNH 367. All chaetigers in anterior view; al-MIII: attachment lamella MIII; al-MIV: attachment lamella MIV. Scale bars: A–C, 2.9 mm; D–E, 1 mm; F, 0.8 mm; G–K, 0.1 mm; L–Q, 30 µm.

***Marphysa birgeri* n. sp.**
Figures 3, 9C, Table 1

Eunice sanguinea.—Grube 1864: 79 (*non* Montagu, 1813)

Material examined. *Type material:* Holotype ZMB F.2021 and four Paratypes ZMB 12273, Trieste and Cres Island, Adriatic Sea, Mediterranean Sea, coll. A.E. Grube.

***Additional material*:** ZMBQ.2265 (1 specimen), Lussingrande, Croatia, Adriatic Sea, Mediterranean Sea, August, or September 1861, coll. A.E. Grube. ZMB 7596 (1 specimen), Rovinj, Croatia, Adriatic Sea, Mediterranean Sea, coll. S. Heider.

Description. Holotype complete, with 113 chaetigers, L10 = 5.7 mm, W10 = 2.5 mm TL = 43 mm. Anterior region of the body with dorsum convex and flat ventrum; body depressed from chaetiger 10, widest at chaetiger 15, tapering after chaetiger 44.

Prostomium bilobed, 1 mm long, 1.6 mm wide; lobes frontally rounded; median sulcus shallow anteriorly and deep ventrally (Fig. 3A–B). Prostomial appendages in a semicircle, median antenna isolated by a gap. Palps reaching middle of second peristomial ring; lateral antennae reaching first chaetiger; median antenna reaching middle of first chaetiger. Palpophores and ceratophores ring-shaped, short, slender; palpostyles and ceratostyles tapering, slender. Eyes ovate, brown, between palps, and lateral antennae.

Peristomium (1.2 mm long, 2.3 mm wide) larger and wider than prostomium, first ring two times longer than second ring, separation between rings distinct on all sides (Fig. 3A–C). Ventral lip with a slight central anterior depression, with a pair of shallow wrinkles (Fig. 3B).

Maxillary apparatus with MF = 1 + 1, 3 + 4, 5 + 0, 4 + 7, 1 + 1 (Fig. 3D). MI 3 times longer than length of Maxillary carriers. MI forceps-like, MI 4.3 times longer than length of closing system (Fig. 3D); ligament between MI and MII, strongly sclerotized. MII with recurved triangular teeth; MII 3.6 times longer than length of cavity opening (Fig. 3D); ligament between MII and MIII and right MIV, sclerotized. MIII with triangular teeth; with irregular attachment lamella, situated in center of the right edge of the plate, slightly sclerotized (Fig. 3D). Left MIV with two lateral teeth larger than rest; attachment lamella rectangular, wide, better developed in right side, situated along anterior edge of maxilla, sclerotized. Right MIV with three lateral teeth larger than rest; attachment lamella semicircle, wide, better developed in right side, situated 2/3 along anterior edge of maxilla, sclerotized (Fig. 3D). MV square, with a short, rounded tooth. Mandibles amber; calcareous cutting plates absent, sclerotized cutting plates amber, with 14 growth rings (Fig. 3E).

Pectinate branchiae with up to two long filaments, present from chaetigers 17L–18R to 97 (Fig. 3I). One filament in chaetigers 17L to 41L; two filaments in chaetigers 42L to 75L; one filament in chaetigers 76L to 97L (Fig. 9C). Branchial filaments longer than dorsal cirri except in first three chaetigers.

First three parapodia smaller, best developed in chaetigers 4–26, following ones becoming gradually smaller. Dorsal cirri digitiform in first chaetigers, conical in median-posterior ones; longer than ventral cirri in all chaetigers; best developed in chaetigers 2–16, following ones smaller (Fig. 3F–J). Prechaetal lobes short, as transverse folds in all chaetigers (Fig. 3F–J). Chaetal lobes rounded in first 25 chaetigers, shorter than postchaetal lobe, with aciculae emerging dorsal to midline; from chaetiger 26 triangular, longer than other lobes, with acicula emerging in midline (Fig. 3F–J). Postchaetal lobes well developed in the first 32 chaetigers; digitiform in the first five chaetigers, ovoid in chaetigers 6 to 10, rounded from chaetiger 11, progressively smaller from chaetiger 10; from chaetiger 33 inconspicuous (Fig. 3F–J). Ventral cirri digitiform in the first five chaetigers; from chaetigers 6 to 68 with an oval swollen base and digitiform tip; digitiform from chaetiger 69, gradually reducing in size (Fig. 3F–J).

Aciculae blunt, reddish along most of its length, and amber on the distal tip (Fig. 3F–J). First three chaetigers with two aciculae; in chaetigers 4–17 with three aciculae; in chaetigers 18–32 with two aciculae; from chaetiger 33 with only one.

Limbate chaetae of two lengths in same chaetiger: long and short, long blades in dorsal position, short blades in ventral position; limbate chaetae reduced in number around chaetiger 20, and then maintained a similar number until the posterior end. Four types of pectinate chaetae; in anterior chaetigers, thin, isodont narrow, symmetric, with long and slender teeth, 1–2 chaetae, up to 17 teeth (Fig. 3K); in median-posterior chaetigers, thin, isodont wide, asymmetric, with short and slender teeth, 15–16 chaetae, up to 26 teeth (Fig. 3L); in posterior chaetigers, thick, anodont wide, symmetric, with short and slender teeth, 3–5 chaetae, between 17 and 18 teeth (Fig. 3M), and thick, anodont

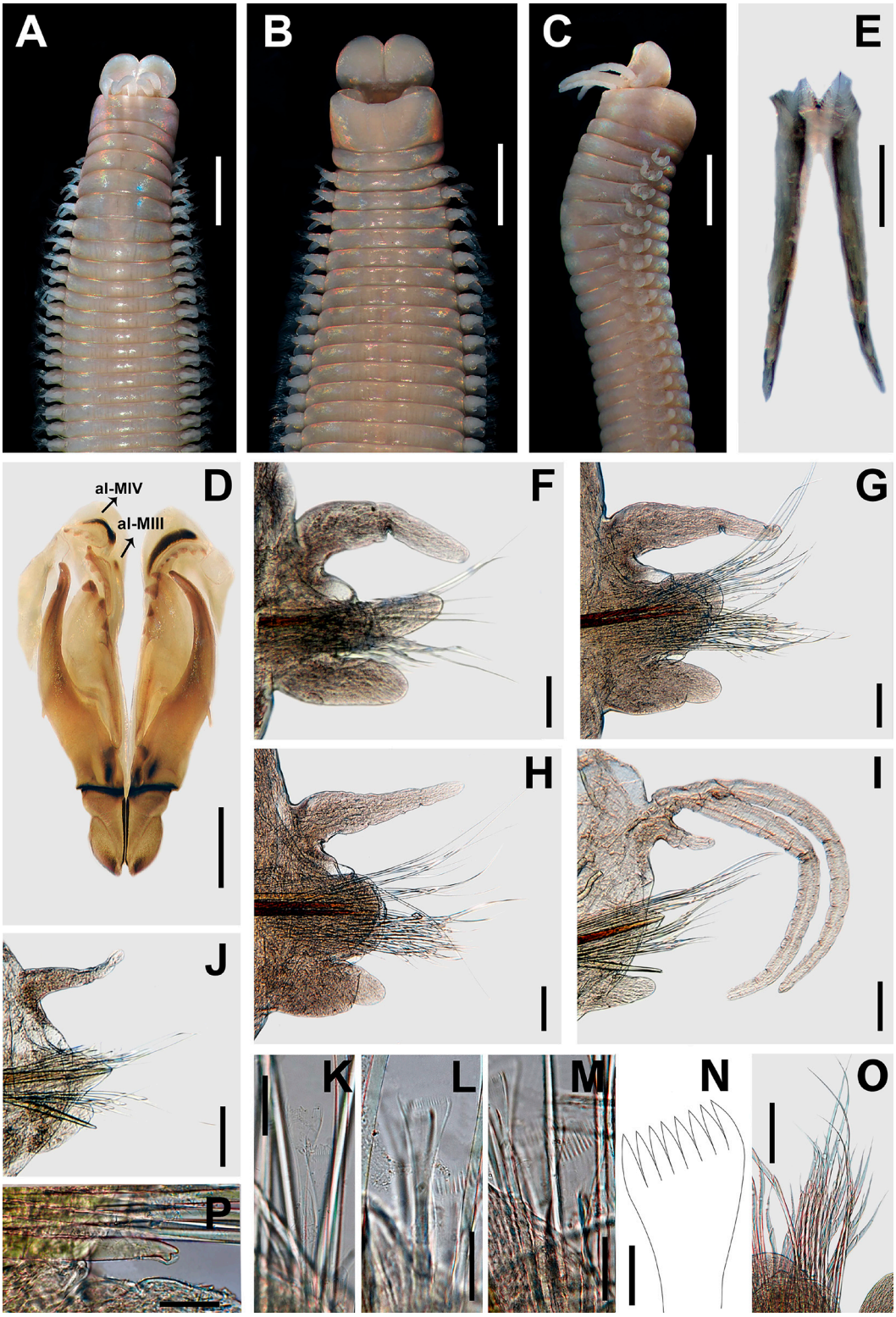

FIGURE 3. *Marphysa birgeri* **n. sp.** A. Anterior end, dorsal view; B. Anterior end, ventral view; C. Anterior end, lateral view; D. Maxillary apparatus, dorsal view; E. Mandible; F. Parapodium 3; G. Parapodium 7; H. Parapodium 14; I. Parapodium 67; J. Parapodium 103; K. Thin, isodont narrow, symmetric, with long and slender teeth, chaetiger 14; L. Thin, isodont wide, asymmetric, with short and slender teeth, chaetiger 85; M. Thick, anodont wide, symmetric, with long and slender teeth, chaetiger 85; N. Thick, anodont wide, asymmetric, with long and thick teeth, chaetiger 105; O. Compound spinigers, chaetiger 7; P. Subacicular hook, chaetiger 85. A–O from holotype F.2021, P from paratype 12273. All chaetigers in anterior view; al-MIII: attachment lamella MIII; al-MIV: attachment lamella MIV. Scale bars: A–C, 1.4 mm; D–E, 0.5 mm; F–J, 0.2 mm; K–N, 30 µm; O–P, 0.1 mm.

wide, asymmetric, with long and thick teeth, 1–2 chaetae, and up to eight teeth (Fig. 3N). Compound spinigers present throughout; with blades of three sizes in anterior chaetigers: shorter and median blades more abundant than longer blades; two lengths blades in median-posterior chaetigers: shorter blades more abundant than longer blades (Fig. 3O). Subacicular hooks bidentate, translucent; starting from chaetigers 25L–27R, one per chaetiger, present continuously in all chaetigers, with blunt teeth, distal smaller than proximal, both teeth directed upward. In some chaetigers, unidentate subacicular hook with a hood in distal end (Fig. 3P).

Pygidium with dorsal pair of anal cirri as long as the last seven chaetigers, left cirrus lost; ventral pair short, as long as the last chaetiger.

Variation. Material examined with L10 = 3.5–10.4 mm, W10 = 1.2–4.8 mm, TChae = 87–124. Palps reaching the second peristomial ring or first chaetiger; lateral antennae reaching first or second chaetiger; median antenna reaching the middle of first or second chaetiger. The maxillary formula is variable: MII 3–4 + 4, MIII 5–6, MIV 3–4 + 7. The proportions of the maxillary apparatus vary as follows: MI are 2.3–2.8 times longer than the length of maxillary carriers; MI are 4.2–6 times longer than length of closing system; MII are 3–4 times longer than length of cavity opening. Branchiae from chaetigers 15–19 to 13–17 chaetigers before pygidium. Maximum number of branchial filaments varied from two to three and postchaetal lobes were conspicuous in first 18–42 chaetigers. Ventral cirri with a swollen base from chaetiger 6 to 41–51 chaetigers before of pygidium. Start of subacicular hooks in chaetigers 20–27.

Type locality. Trieste and Cres Island, Adriatic Sea.

Distribution. Adriatic Sea, Mediterranean Sea.

Habitat. According to Grube (1864) the material from Lussingrande was possibly collected in the port area, somewhere between 31.1 and 36.6 mm. The substrate type was not recorded.

Etymology. The species is named after Dr. Birger Neuhaus, in recognition of his support and facilities while ICMA carried out the research stay in Berlin, and for allowing the review of this material and other European collections at the Museum für Naturkunder, Berlin.

Remarks. The specimens collected by Grube from the Adriatic Sea and misidentified as *Eunice sanguinea* (= *Marphysa sanguinea*) presented important differences from the neotype of *M. sanguinea* after a thorough comparison. Herein, the Adriatic Sea material was described as a new species, *Marphysa birgeri* **n. sp.**.

Marphysa birgeri **n. sp.** differ from *M. sanguinea* by the color of subacicular hook, because in former is translucent, whereas in latter species the subacicular hook is reddish on its base, and translucent in distal end. Also, *M. birgeri* **n. sp.** (type and additional material, L10 = 3.5–10.4 mm) has branchiae from chaetigers 15–19, the specimens have only two to three branchial filaments, and there are four types of pectinate chaetae present, whereas in *M. sanguinea* (neotype and additional material, L10 = 11.5–20.4 mm), the branchiae starts in chaetigers 21–25, specimens have from five to six branchial filaments, and there are only three types of pectinate chaetae.

Marphysa birgeri **n. sp.** resembles *M. acicularum* (Bermuda), *M. brasiliensis* (Brazil), *M. bulla* (Yellow Sea, China), *M. californica* (San Diego, California), *M. maxidenticulata* (Yellow Sea, China), *M. parishii* (Brazil), and *M. baileybrockae* **n. sp.** (Hawaii) by having pectinate branchiae with long filaments, the absence of limbate subacicular chaetae, and by the subacicular hook translucent. However, *M. birgeri* **n. sp.** has the dorsal cirri digitiform in anterior region, instead of *M. acicularum*, *M. brasiliensis*, *M. bulla*, *M. maxidenticulata*, *M. parishii*, and *M. baileybrockae* **n. sp.** in which the dorsal cirri are always conical. Moreover, in *M. birgeri* **n. sp.** the prechaetal lobe is as transverse fold in anterior chaetigers, whereas in *M. baileybrockae* **n. sp.** the prechaetal lobe has the dorsal edge longer than ventral in the first few chaetigers. Furthermore, *M. birgeri* **n. sp.** has four types of the pectinate chaetae, in contrast of *M. acicularum* and *M. brasiliensis*, that have only three types, and in *M. bulla* and *M. parishii*, there are five types of pectinate chaetae. Also, *M. birgeri* **n. sp.** has eyes, but in *M. maxidenticulata*, eyes are absent. Finally, in *M. birgeri* **n. sp.** the ventral cirri with swollen base start from chaetiger 6, whereas in *M. californica* the swollen base start from chaetigers 13–14. The comparison of *M. birgeri* **n. sp.** with the related species is provided in Table 1.

Marphysa brevibranchiata Treadwell, 1921 n. status

Figures 4, 9D, Table 1

Marphysa acicularum var. *brevibranchiata* Treadwell, 1921: 60–61, Pl. 5, Figs. 5–8, text-figs. 194–200.
Marphysa sanguinea.—Hartman 1944a: 128 (*non* Montagu, 1813).

Material examined. *Type material*: Lectotype AMNH 1358 designated here, Paralectotypes (3 specimens) AMNH_IZC 00361334, Bermuda, 1916, coll. A. Treadwell.

Description. Lectotype complete, dissected ventrally, with 289 chaetigers, L10 = 11.5 mm, W10 = 3.6 mm; TL: 172 mm. Last 28 chaetigers regenerating. Anterior region of the body with dorsum convex and flat ventrum; body depressed from chaetiger 7, widest at chaetiger 22, tapering after chaetiger 40.

Prostomium bilobed, 1.7 mm long, 2.6 mm wide; lobes frontally truncated; with median sulcus shallow anteriorly and deep ventrally (Fig. 4A–B). Prostomial appendages in a semicircle, median antenna isolated by a gap. Palps reaching second peristomial ring; lateral antennae reaching first chaetiger; median antenna reaching middle of the first chaetiger. Palpophores and ceratophores ring-shaped, short, thick; palpostyles and ceratostyles tapering, slender. Eyes not observed.

Peristomium (2.3 mm long, 3.8 mm wide) larger than prostomium; first ring two times longer than second ring; separation between rings distinct on all sides (Fig. 4A–B). Ventral lip dissected, in paralectotype L10 = 12.4 mm, with a slight central anterior depression and a couple of shallow wrinkles (Fig. 4B).

Maxillary apparatus with MF = 1 + 1, 6 + 6, 8 + 0, 3 + 9, 1 + 1 according to Treadwell, 1921: 61. In paralectotype with MF = 1 + 1, 6 + 5, 7 + 0, 3 + 9, 1 + 1 (Fig. 4D). MI 2.8 times longer than length of maxillary carriers. MI forceps-like, MI five times longer than length of closing system (Fig. 4D–E); ligament between MI and MII sclerotized. MII with recurved triangular teeth; MII 3.8 times longer than length of cavity opening (Fig. 4D–E); ligament between MII and MIII and right MIV, slightly sclerotized. MIII with triangular teeth; with irregular attachment lamella, situated in center of the right edge of the plate, slightly sclerotized (Fig. 4D–E). Left MIV with second lateral tooth larger than rest; attachment lamella rectangular, wide, better developed in left side, situated 2/3 of anterior edge of maxilla, sclerotized. Right MIV with teeth of similar size; attachment lamella semicircle, wide, better developed in left, situated 2/3 of anterior edge of maxilla, sclerotized (Fig. 4D–E). MV square with a short, rounded tooth. Mandibles dark; calcareous cutting plates broken, sclerotized cutting plates brown, oval, up to 25 growth rings (Fig. 4F).

Pectinate branchiae up to seven short filaments, present from chaetigers 28 to 277 (Fig. 4J). First and last 17 chaetigers with one filament; reaching the maximum seven filaments in chaetigers 123L–257L (Fig. 9D). Branchial filaments longer than dorsal cirri except in the last branchiae. In paralectotype without regeneration posterior region, branchiae ending at six chaetigers before pygidium.

First four parapodia smaller, best developed in chaetigers 6–83, following ones becoming gradually smaller. Dorsal cirri conical, longer than ventral cirri in anterior chaetigers, of similar size in the following ones; best developed in chaetigers 2–25, following ones gradually smaller (Fig. 4G–K). Prechaetal lobes short, as transverse folds in all chaetigers (Fig. 4G–K). Chaetal lobes in first 44 chaetigers rounded, shorter than postchaetal lobe, with aciculae emerging dorsal to midline; from chaetiger 45 triangular, longer than other lobes, with acicula emerging in midline (Fig. 4G–K). Postchaetal lobes well developed in the first 50 chaetigers; digitiform in the first four chaetigers, rounded from chaetiger 5, progressively smaller from chaetiger 19; chaetiger 51 inconspicuous (Fig. 4G–K). Ventral cirri digitiform in the first five chaetigers; chaetigers 6 to 260 with an oval swollen base and digitiform tip; digitiform from chaetiger 261, gradually reducing in size (Fig. 4G–K).

Aciculae blunt, reddish along most of its length, amber on the distal tip (Fig. 4G–K). First 20 chaetigers with three aciculae; in chaetigers 21–147 with two aciculae; from chaetiger 148 with only one acicula.

Limbate chaetae with two lengths in same chaetiger: long and short, long blades in dorsal position, short blades in ventral position; limbate chaetae reduced in number around chaetiger 28, and then maintained a similar number until the posterior end. Four types of pectinate chaetae; in anterior-median chaetigers, thin, isodont narrow, symmetric, with long, and slender teeth, 1–2 chaetae, with up to 14 teeth (Fig. 4N); in median-posterior chaetigers, thick, isodont wide, asymmetric, with short and slender, 1–2 chaetae with up to 40 teeth (Fig. 4L); in posterior chaetigers, thick, anodont wide, symmetric, with long and slender teeth, 1–2 chaetae, up to nine teeth (Fig. 4M), and thick, anodont wide, symmetric, with short and thick teeth, 1–2 chaetae, up to 16 teeth (Fig. 4O). Compound spinigers present throughout; in anterior chaetigers with blades of three lengths in the same chaetiger: shorter and median blades more abundant than longer blades (Fig. 4P); in median-posterior chaetigers with blades of two lengths. Subacicular hooks unidentate, translucent; starting from chaetigers 35L–36R, one or two per chaetiger (second replacement hook); present continuously in all chaetigers (Fig. 4Q).

Pygidium with dorsal pair of anal cirri as long as the last 10 chaetigers; ventral pair short, as long as the last four chaetigers (Fig. 4C).

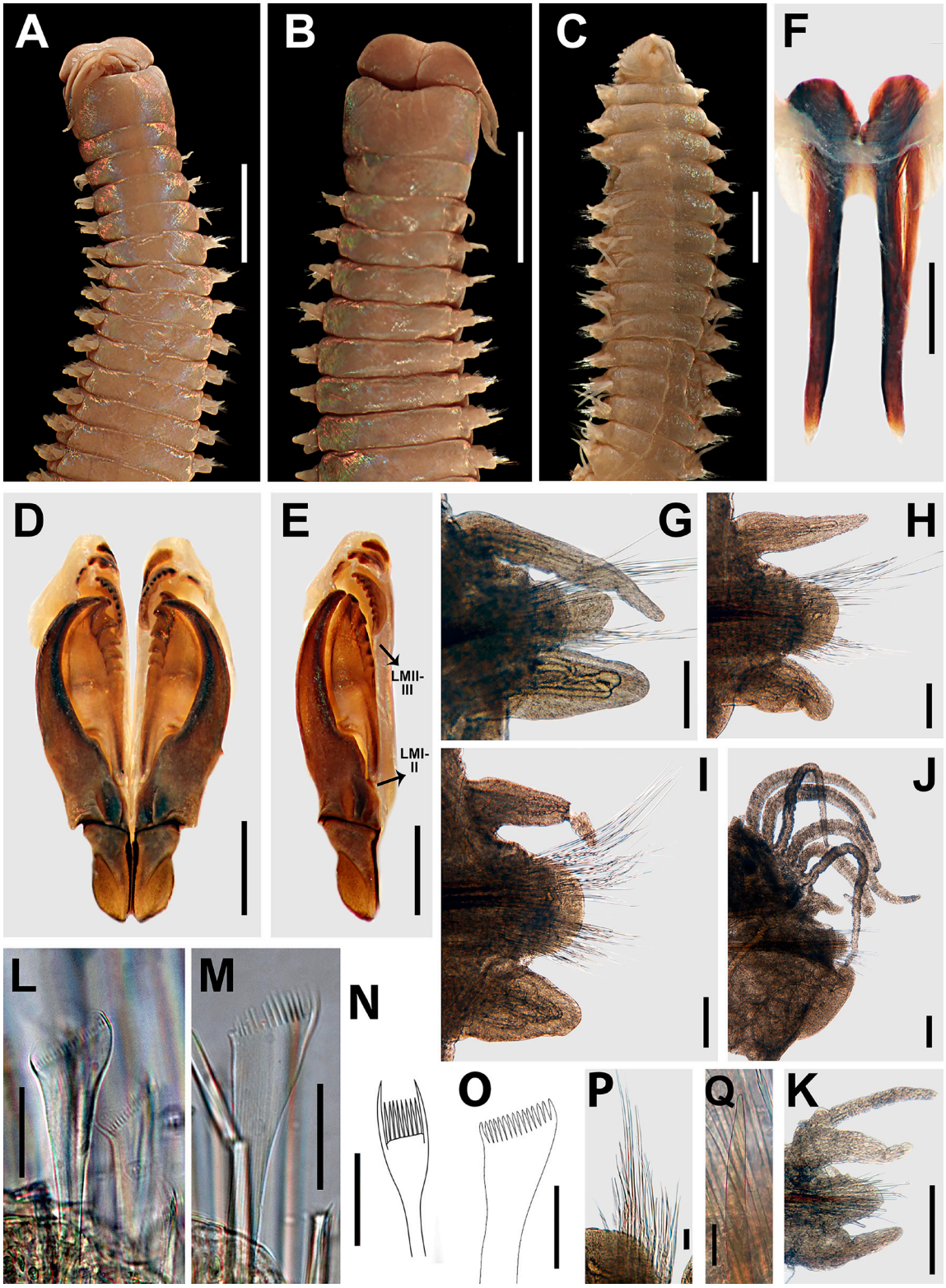

FIGURE 4. *Marphysa brevibranchiata* Treadwell, 1921 n. status. A. Anterior end, dorsal view; B. Anterior end, ventral view; C. Posterior view, dorsal view; D. Maxillary apparatus, dorsal view; E. Left MI-II-III-IV-V, lateral view; F. Mandible; G. Parapodium 3; H. Parapodium 8; I. Parapodium 25; J. Parapodium 125; K. Parapodium 266; L. Thick, isodont wide, asymmetric, with short and slender teeth, chaetiger 258; M. Thick, anodont wide, symmetric, with long and slender teeth, chaetiger 266; N. Thin, isodont narrow, asymmetric, with long and slender teeth, chaetiger 15; O. Thick, anodont wide, symmetric, with short and thick teeth, chaetiger 266; P. Compound spinigers, chaetiger 8; Q. Subacicular hook, chaetiger 258. A–C, GA–C, G–Q from lectotype AMNH 1358, D–F from paralectotype AMNH_IZC 00361334. All chaetigers in anterior view; LMI-II: Ligament between MI and MII; LMII-III: Ligament between MII and MIII. Scale bars: A–B, 2.9 mm; C, 2.4 mm; D–E, 0.9 mm; F, 1.3 mm; G–K, 0.2 mm; L–N, O, Q, 30 µm; P, 0.1 mm.

Variation. Material examined with L10 = 11.5–14.2 mm, W10 = 3.4–4 mm, TChae = 289–310. Median antenna reaching middle of first or second chaetiger. The maxillary formula is variable: MII 6 + 5–6, MIII 7, MIV 3–4 + 9. The proportions of the maxillary apparatus vary as follows: MI are 2.7–2.8 times longer than the length of the maxillary carriers; MI are 4.5–5 times longer than the length of the closing system; MII are 3.3–3.8 times longer than the length of the cavity opening. Branchiae start from chaetigers 28–36 and end 6–12 chaetigers before pygidium. Maximum number of branchial filaments varied from seven to eight and postchaetal lobes were conspicuous in first 50–75 chaetigers. Ventral cirri with a swollen base start from chaetigers 5–6 to 128–168 chaetigers before the pygidium. Subacicular hooks start from chaetigers 36–46.

Distribution. Bermuda, Atlantic Ocean.

Habitat. According to Treadwell (1921), *M. brevibranchiata* co-occurred with *M. acicularum* in Flatts Inlet, Ely's Harbor, and Fairyland Creek, Bermuda, in the intertidal region of muddy flats.

Remarks. Treadwell (1921) studied some specimens that were morphologically close to *M. acicularum* collected by himself, from several locality of Bermuda. According to his description, the specimens presented minor differences from *M. acicularum* in the branchiae and maxillary apparatus shape, which he attributed to a variation on these characters. For this reason, Treadwell assigned his Bermuda specimens as the variety *M. acicularum brevibranchiata*. Several years later, Hartman (1944a) suggested this subspecies, like other three species from the Grand Caribbean (*M. acicularum, M. nobilis* and *M.* viridis), were junior synonyms of *M. sanguinea* (England). Nonetheless, Molina-Acevedo & Carrera-Parra (2015) reinstated the three *Marphysa* species; but not *M. a. brevibranchiata* because the type material was not found at the USNM, as reported by Hartman (1956). Herein, the syntypes were finally found in the general collection at the AMNH, where most of the Treadwell's species were deposited. The specimen used for the description of *M. a. brevibranchiata* was identified and proposing as lectotype, the rest of the material is considering as paralectotypes (ICZN 1999, Art. 74F).

Treadwell correctly highlighted the differences between *M. acicularum* and the subspecies *M. a. brevibranchiata.* The first species has a low number of teeth in MIV (6–7), and the branchial filaments are long, whereas *M. a. brevibranchiata* has more teeth on the right MIV (9), and the branchial filaments are short. On the other hand, in *M. acicularum* (L10 = 4–15.8 mm), the branchiae start from chaetigers 22–27, there are 2–5 branchial filaments, the postchaetal lobe is developed in anterior chaetigers (first 28–56 chaetigers), and the ventral cirri with swollen base end 13 chaetigers before pygidium or in the last chaetiger; in constrat of *M. a. brevibranchiata* (L10 = 11.5–14.2 mm) that the branchiae start from chaetigers 28–36, with up to 7–8 branchial filaments, the postchaetal lobe is developed in more chaetigers (first 50–75 chaetigers), and the ventral cirri with swollen base end 128–168 chaetigers before of pygidium. Hence, both are considered unique species, the subspecies *M. acicularum brevibranchiata* is raised to species status.

Marphysa brevibranchiata n. status (L10 = 4–15.8 mm) differs from *M. sanguinea* (neotype and additional material, L10 = 11.5–20.4 mm) because in the former the branchiae start from chaetigers 22–27, branchial filaments are short, there are two types of anodont pectinate, and the subacicular hook is translucent. In contrast, in *M. sanguinea* the branchiae start from chaetigers 21–25, only one type of anodont pectinate are present, the branchial filaments are longer, and the subacicular hook is reddish basally and translucent distally. Based on these visual differences, we conclude that *M. brevibranchiata* n. status is a valid species and different from *M. sanguinea*.

Marphysa brevibranchiata n. status resembles *M. aransensis* Treadwell, 1939, *M. kristiani*, and *M. sebastiana* Steiner & Amaral, 2000 by having short branchial filaments, the absence of limbate subacicular chaetae, and the translucent subacicular hook. However, *M. brevibranchiata* n. status has only pectinate branchiae, in contrast to *M. kristiani* that has pectinate and palmate branchiae in some regions of the body, and *M. sebastiana* only has palmate branchiae. Moreover, *M. brevitentaculata* has the postchaetal lobe digitiform in the first four chaetigers, whereas in *M. aransensis*, the postchaetal lobe is rounded in the first chaetigers. The comparison of *M. brevibranchiata* n. status with the related species is provided in Table 1.

Marphysa californica Moore, 1909

Figures 5, 9E, Table 1

Marphysa californica Moore, 1909: 251–253, Pls. 7–8, Figs. 13–20.—Carrera-Parra 2009: 179.—Zanol *et al.* 2010: Fig. 1–3, 5 (phylogenetic trees).—Zanol *et al*. 2014: 93.

Marphysa sanguinea.—Monro 1933: 69.—Hartman 1944a: 127–128, Pl. 8, Figs. 179–183.—1961: 84–85 (*non* Montagu, 1813).

Material examined. *Type material:* Holotype CAS 020357, San Diego County, California, USA, 1902, coll. E.C. Starks. *Additional material:* LACM-AHF POLY 52710 (1 specimen), Point Fermin, California, 10 Apr 1911. LACM-AHF POLY 0000 (1 specimen), Bluff Cove, Redondo Beach, California, 26 Oct 1935.

Description. Holotype incomplete, ventrally dissected, with 92 chaetigers, L10 = 15.6 mm, W10 = 8.3 mm TL = 86 mm. Anterior region of the body with dorsum convex and flat ventrum; body depressed from chaetiger 11, widest at chaetiger 30, tapering after chaetiger 43.

Prostomium bilobed, 3.1 mm long, 5 mm wide; lobes frontally rounded; median sulcus shallow anteriorly and deep ventrally (Fig. 5A–B). Prostomial appendages in a semicircle, median antenna isolated by a gap. Palps reaching first chaetiger; lateral antennae reaching middle of first chaetiger; median antenna reaching second chaetiger. Palpophores and ceratophores ring-shaped, short, thick; palpostyles and ceratostyles tapering, slender. Eyes ovate, brown, between palps, and lateral antennae.

Peristomium (3.8 mm long, 9 mm wide) larger and wider than prostomium; first ring two times longer than second ring, separation between rings distinct on all sides (Fig. 5A–C). Ventral lip with a slight central anterior depression and several shallow wrinkles (Fig. 5B).

Maxillary apparatus with MF = 1 + 1, 4 + 4, 5 + 0, 4 + 8, 1 + 1 (Fig. 5D). MI three times longer than length of maxillary carriers. MI forceps-like, MI 4.4 times longer than length of closing system; ligament between MI and MII, strongly sclerotized. MII with recurved triangular teeth; MII 4.5 times longer than length of cavity opening (Fig. 5D–E); ligament between MII and MIII and right MIV sclerotized. MIII with triangular teeth; with irregular attachment lamella, situated only in center of right edge of the plate, sclerotized (Fig. 5D–E). Left MIV with three lateral teeth smaller than rest; attachment lamella semicircle, slender, better developed on right side, situated 2/3 of anterior edge of maxilla. Right MIV with three lateral teeth larger than rest; attachment lamella semicircle, wide, better developed in central side, situated 3/4 of anterior edge of maxilla, sclerotized (Fig. 5D–E). MV square, with a short, rounded tooth. Mandibles dark, becoming light amber toward the outer edge; with calcareous cutting plates present and sclerotized cutting plates brown (Fig. 5F). Number of growth rings not observed.

Pectinate branchiae with up to six long filaments, present from chaetigers 31L–34R to last chaetiger of the fragment (Fig. 5J–K). Two filaments in first chaetiger; reaching the maximum five or six filaments from chaetigers 58L to the last chaetiger of the fragment (Fig. 9E). Branchial filaments longer than dorsal cirri except in the first three branchiae.

First two parapodia smaller, best developed in chaetigers 5–32, following ones becoming gradually smaller. Dorsal cirri conical; longer than ventral cirri in anterior region, following ones of similar size; best developed in chaetigers 4–25, following ones gradually smaller (Fig. 5G–K). Prechaetal lobes short, as transverse folds in all chaetigers (Fig. 5G–K). Chaetal lobes in the first 46 chaetigers rectangular, shorter than postchaetal lobe, with aciculae emerging dorsal to midline; from chaetiger 47 triangular, longer than other lobes (Fig. 5G–K), with acicula emerging in midline. Postchaetal lobes well developed in the first 92 chaetigers; digitiform in the first three chaetigers, ovoid in chaetigers 4–10, rounded from chaetiger 11, progressively smaller from chaetiger 22; from chaetiger 93 inconspicuous (Fig. 5G–K). Ventral cirri digitiform in first 12 chaetigers; in chaetigers 13 to last part of the fragment with an oval swollen base and digitiform tip (Fig. 5G–K).

Aciculae blunt, reddish along most of its length, amber on the distal tip (Fig. 5G–K). First 2 chaetigers with six aciculae; in chaetigers 3–9 with five; in chaetigers 10–54 with four; in chaetigers 55–61 with three; from chaetiger 62 with two aciculae.

Limbate chaetae of two lengths in same chaetiger: long and short, long blades are in dorsal position, short blades in ventral position; limbate chaetae reduced in number around chaetiger 28, and then maintained a similar number until the posterior end. Four types of pectinate chaetae; in anterior chaetigers, thin, isodont narrow, symmetric, with short, and slender teeth, 2–3 chaetae, up to 15 teeth (Fig. 5L). In median-posterior chaetigers, thin, isodont wide, symmetric, with short, and slender teeth, 8–9 chaetae, up to 26 teeth (Fig. 5M), and thick, isodont wide, symmetric, with long and thick teeth, 1–2 pectinate, and up to 18 teeth. In posterior chaetigers, thick, pectinate anodont, symmetric, wide with long and thick teeth, 1–2 chaetae, up to 18 teeth (Fig. 5N). Compound spinigers present throughout, in anterior chaetiger with blades of two lengths: shorter blades slightly more abundant than longer blades (Fig. 5O). Subacicular hook absent; in additional material LACM-AHF POLY 52710 (L10 = 13.5 mm) subacicular hook unidentate, translucent; starting from chaetiger 204, present discontinuously in all chaetigers (Fig. 5P).

Variation. Material examined with L10 = 13.5–19 mm, W10 = 6.5–10.3 mm. All specimens incomplete. Palps reaching second peristomial ring or first chaetiger; lateral antennae reaching middle of first chaetiger; median

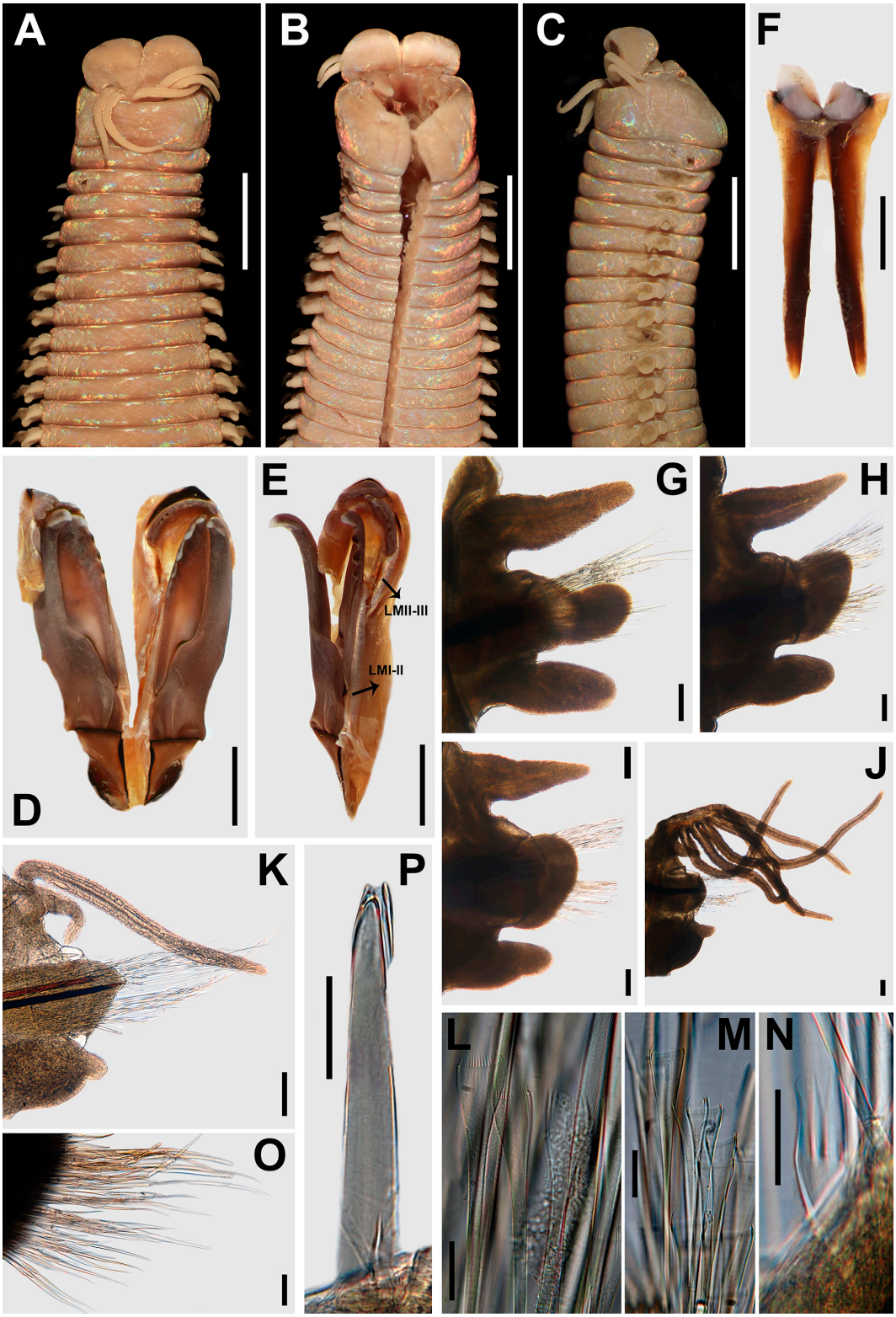

FIGURE 5. *Marphysa californica* Moore, 1909. A. Anterior end, dorsal view; B. Anterior end, ventral view; C. Anterior view, lateral view; D. Maxillary apparatus, dorsal view; E. Left MI-II-III-IV-V, lateral view; F. Mandible; G. Parapodium 3; H. Parapodium 6; I. Parapodium 12; J. Parapodium 86; K. Parapodium 212; L. Thin, isodont narrow, symmetric, with long and slender teeth, chaetiger 17; M. Thin, isodont wide, symmetric, with short and slender teeth, chaetiger 86; N. Thick, anodont wide, symmetric, with long and thick teeth, chaetiger 212; O. Compound spinigers, chaetiger 12; P. Subacicular hook, chaetiger 212. A–J, O from holotype CAS 020357; K, M–N, P from LACM-AHF POLY 52710. All chaetigers in anterior view; LMI-II: Ligament between MI and MII; LMII-III: Ligament between MII and MIII. Scale bars: A–C, 3.9 mm; D–E, 1.6 mm; F, 1.5 mm; G–K, 0.2 mm; L–M, N, P, 30 μm; O, 0.1 mm.

antenna reaching second chaetiger. Maxillary formula is variable: MII 3–4 + 5, MIII 5, MIV 4 + 7–8. Branchiae from chaetigers 28–40. Maximum number of branchial filaments varied from four to eight and postchaetal lobes were conspicuous in first 41–92 chaetigers. Ventral cirri with a swollen base from chaetigers 13–14. Subacicular hook from chaetigers 204 or absent.

Distribution. California, USA.

Habitat. According to Moore (1909) the holotype was collected by Profesor E.C. Starks from San Diego Bays, in the sand-bar, within the intertidal zone.

Remarks. *Marphysa californica*, described by Moore (1909) from San Diego (California), it was later consider as a junior synonym of *M. sanguinea* by Monro (1933). Based on the distance between the type localities of *M. sanguinea* and *M. californica*, Carrera-Parra (2009) suggested a review on *M. californica* to solve the validity of the species. Later, according to molecular evidence taken from the type locality, Zanol *et al*. (2010) recognized *M. californica* as valid species and different from *M. sanguinea*, although they did not clarify its taxonomic status. Herein, after a morphological comparison between both type and additional materials, the following differences were found. In *M. californica* (L10 = 13.5–19 mm) the branchiae start from chaetigers 28–40, the chaetal lobe is rectangular in anterior region, the ventral cirri with swollen base start from chaetigers 13–14, there are two types of isodont pectinate chaetae in median-posterior region, and the subacicular hook is translucent. In *M. sanguinea* (L10 = 11.5–20.4 mm) the branchiae start from chaetigers 21–25, the chaetal lobe is rounded in anterior region, the ventral cirri with swollen base start from chaetigers 5–8, there is only one type of isodont pectinate chaetae in posterior region, and the subacicular hook is reddish. Because of the above and the molecular evidence presented by Zanol *et al*. (2010), *M. californica* should be considered as a valid species.

Marphysa californica resembles *M. acicularum* (Bermuda), *M. baileybrockae* **n. sp.** (Hawaii), *M. brasiliensis* (Brazil), *M. bulla* (Yellow Sea, China), *M. maxidenticulata* (Yellow Sea, China), and *M. parishii* (Brazil) by having branchiae pectinate with long branchial filaments, the absence of the subacicular limbate chaetae, and the subacicular hook translucent. However, *M. californica* has eyes, in contrast of *M. bulla* and *M. maxidenticulata* in which lack eyes. Moreover, *M. californica* has conical dorsal cirri in all chaetigers, whereas in *M. acicularum*, the dorsal cirri are conical with a broad base. *Marphysa californica* has the prechaetal lobe as a transversal fold in anterior region, instaed of *M. acicularum* and *M. baileybrockae* **n. sp.** in which the prechaetal lobe has dorsal edge longer than ventral in the same region. In addition, *M. californica* has the chaetal lobe rectangular in first chaetigers, whereas in *M. acicularum*, *M. baileybrockae* **n. sp.**, *M. brasiliensis*, *M. bulla*, *M. maxidenticulata*, and *M. parishii*, the chaetal lobe is rounded in first chaetigers. Also, *M. californica* (type and additional material, L10 = 13.5–19 mm) has the postchaetal lobe developed up to chaetigers 41–92, different from *M. brasiliensis* (L10 = 17 mm) and *M. parishii* (L10 = 12.2 mm), in which the postchaetal lobe is developed in more than 200 chaetigers. Finally, in *M. californica* the ventral cirri with swollen base start from chaetigers 13–14, whereas in *M. acicularum* and *M. brasiliensis*, start from chaetigers 3–5. The comparison of *M. californica* with related species is provided in Table 1.

Marphysa leidii de Quatrefages, 1866

Figures 6, 9F, Table 1

Eunice sanguinea.—Leidy 1855: 147.
Marphysa leidii de Quatrefages, 1866: 22.
Marphysa leidyi.—Verrill 1873: 319, Pt. II, Fig. 64.
Marphysa sanguinea.—Webster 1879: 36–40.—Fauvel 1911: 18.—Hartman 1944b: 339.—Hartman 1945: 23–24.—Pettibone 1963: 236–238, Fig. 62 (*non* Montagu, 1813).

Material examined. *Type material:* Neotype USNM 71609, EVG 73 123 Little Sheepshead creek by Big stake, Heading North, New Jersey, United State, 3 Oct 1973, coll. Garlo, E.V. *Additional material:* USMN 4469 (2 specimens), USNM 6194 (1 specimen) Vineyard Sound, Massachusetts, United States, in mud. USNM 3860 (5 specimens) Woods Hole, Massachusetts, United States (4131.1987'N, 7040.9677'W), 5 Sep 2017, 1 m. USNM 61734 (2 specimens), Cape Lookout, North Carolina, United States, 16 Apr 1976. USNM 61736 (4 specimens) Wrightsville Beach, Banks Channel, North Carolina, United States, 17 Apr 1976.

Description. Neotype complete, with 175 chaetigers, broken in three parts (first one with 59 chaetigers, second with 31 and third one with 69 chaetigers), with last 24 chaetigers regenerating, L10 = 6.4 mm, W10 = 3.5 mm; LT:

48 mm. Anterior region of the body with dorsum convex and flat ventrum; body depressed from chaetiger 11, widest at chaetiger 33, tapering after chaetiger 81.

Prostomium bilobed, 1.3 mm long, 2 mm wide; lobes frontally rounded; median sulcus shallow anteriorly and deep ventrally (Fig. 6A–B). Prostomial appendages in a semicircle, median antenna isolated by a gap. Palps reaching second peristomial ring; lateral antennae reaching first chaetiger; median antenna reaching the middle of first chaetiger. Palpophores and ceratophores ring-shaped, short, thick; palpostyles and ceratostyles tapering, slender. Eyes brown, reniform, between palps and lateral antennae.

Peristomium (1.5 mm long, 3.5 mm wide) wider than prostomium, first ring two times longer than second ring, separation between rings distinct on all sides (Fig. 6A–C). Ventral lip with a shallow central anterior depression with a couple of shallow wrinkles (Fig. 6B).

Maxillary apparatus with MF = 1 + 1, 5 + 5, 6 + 0, 3 + 7, 1 + 1 (Fig. 6D). MI three times longer than length of maxillary carriers. MI forceps-like, MI 4.8 times longer than length of closing system (Fig. 6D–E); ligament between MI and MII, sclerotized. MII with recurved triangular teeth; MII three times longer than length of cavity opening (Fig. 6D–E); ligament between MII and MIII and right MIV slightly sclerotized. MIII with triangular teeth; with irregular attachment lamella, situated in central of the right edge of the plate, sclerotized (Fig. 6D–E). Left MIV with two lateral teeth larger than rest; attachment lamella semicircle, wide, better developed in left side, situated 2/3 of anterior edge of maxilla, sclerotized. Right MIV with four lateral teeth larger than rest; attachment lamella semicircle, wide, better developed in left side, situated along posterior edge of maxilla, sclerotized (Fig. 6D–E). MV rectangular, wider than longer, with a short, rounded tooth. Mandibles dark; calcareous cutting plates broken, sclerotized cutting plates brown, with up to 12 growth rings (Fig. 6F).

Pectinate branchiae with up to three long filaments, present from chaetigers 20L–21R to 131L–134R (Fig. 6J–K). First two and last 21 chaetigers with one filament; reaching the maximum three filaments in chaetigers 33L to 99L (Fig. 9F). Branchiae with filaments longer than dorsal cirri except in first and last four branchiae.

First four parapodia smaller, best developed in chaetigers 5–40, following ones becoming gradually smaller. Dorsal cirri conical in all chaetigers; longer than ventral cirri in anterior chaetigers, shorter in median, become similar size in posterior chaetigers; best developed in chaetigers 2–25, following ones gradually smaller (Fig. 6G–K). Prechaetal lobes short, as transverse folds in all chaetigers (Fig. 6G–K). Chaetal lobes in first 39 chaetigers rounded, shorter than postchaetal lobe, aciculae emerging dorsal to midline; from chaetiger 40 triangular, longer than other lobes, with acicula emerging dorsal to midline (Fig. 6G–K). Postchaetal lobes well developed in the first 57 chaetigers; conical in the first six chaetigers, ovoid in chaetigers 7–10, rounded and progressively smaller from chaetiger 11; from chaetigers 58 inconspicuous (Fig. 6G–K). Ventral cirri ovoid in the first five chaetigers; in chaetigers 6 to 107 with an oval swollen base and digitiform tip; conical from chaetiger 108 with digital end, gradually reducing in size (Fig. 6G–K).

Aciculae blunt, reddish along most of its length, and amber on the distal tip (Fig. 6G–K). First four chaetigers with three aciculae; in chaetigers 5–19 with four aciculae; in chaetigers 20–42 with three aciculae; in chaetigers 43–94 with two aciculae; from chaetigers 95 with only one acicula.

Limbate chaetae of two lengths in same chaetiger: long and short, long blade in dorsal position, short blades in ventral position; limbate chaetae reduced in number around chaetiger 18, and then maintained until a similar number until the posterior end. Five types of pectinate chaetae; in anterior chaetigers, thin, isodont narrow, symmetric, with long and slender teeth, 1–2 chaetae with up to 11–12 teeth (Fig. 6L); in median chaetigers, thick, isodont wide, symmetric, with short and slender teeth, 1–2 chaetae, up to 17 teeth (Fig. 6M3); in posterior chaetigers, and thick, isodont wide, symmetric, with long and slender teeth, three chaetae, up to 17 teeth (Fig. 6N1), thick, anodont wide, symmetric, with long and thick, 3–4 chaetae, up to seven teeth (Fig. 6O), and thick, anodont wide with long and slender, 3–4 chaetae, up to 14 teeth (Fig. 6N2). Compound spinigers present throughout; with blades of two lengths: shorter blades more abundant than longer blades (Fig. 6P). Subacicular hook bidentate, translucent; starting from chaetiger 35, one or two per chaetiger, second completely internal within the parapodia and probably a replacement hook, present in all chaetigers subsequently; with blunt teeth, distal tooth smaller than proximal, directed upward, proximal triangular, directed laterally (Fig. 6Q).

Pygidium with dorsal pair of anal cirri as long as the last 13 chaetiger; ventral pair short, as long as the last two chaetigers.

Variation. Material examined with L10 = 6.4–17 mm, W10 = 3.5–5.3 mm, TChae = 175–231. Palps reaching middle of first peristomial ring or middle of the second peristomial ring; lateral antennae reaching second

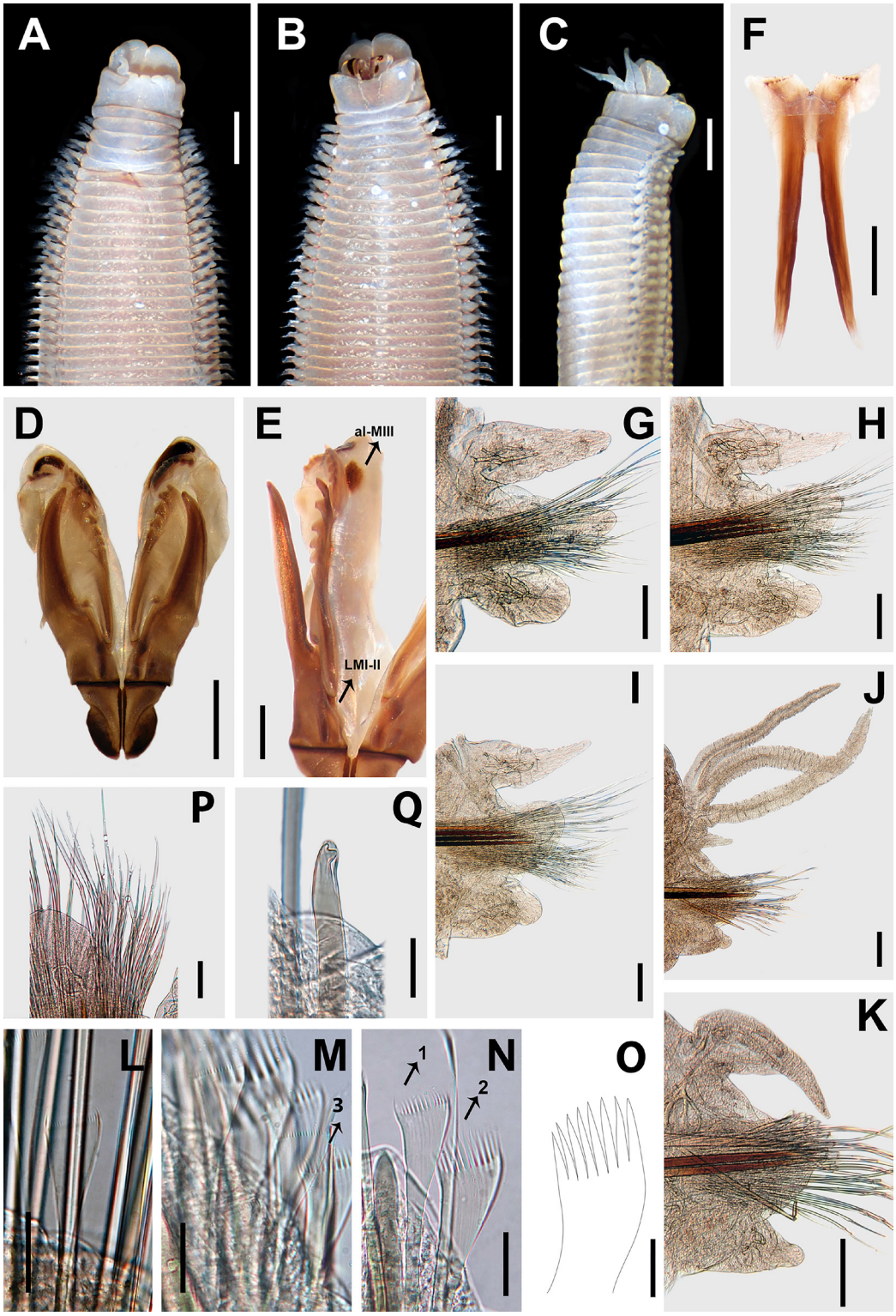

FIGURE 6. *Marphysa leidii* de Quatrefages, 1866. Neotype USNM 71609. A. Anterior end, dorsal view; B. Anterior end, ventral view; C. Anterior end, lateral view; D. Maxillary apparatus, dorsal view; E. Left MI-II-III-IV-V, lateral view; F. Mandible; G. Parapodium 3; H. Parapodium 8; I. Parapodium 13; J. Parapodium 99; K. Parapodium 161; L. Thin, isodont narrow, symmetric, with long and slender teeth, chaetiger 8; M. Thick, isodont wide, symmetric, with short and slender teeth, chaetiger 37; N. Thick, pectinate chaetae, chaetiger 162; O. Thick, anodont wide, symmetric, with long and slender, chaetiger 134; P. Compound spinigers, chaetiger 8; Q. Subacicular hook, chaetiger 37. All chaetigers in anterior view; al-MIII: attachment lamella MIII; LMI-II: ligament between MI and MII; 1: Isodont wide with long and slender teeth; 2: Anodont wide with short and slender teeth; 3: Anodont wide with long and slender teeth. Scale bars: A–C, 1.6 mm; D, 0.7 mm; E, 0.4 mm; F, 1.3 mm; G–K, 0.2 mm; L–N, O, Q, 30 µm; P, 0.1 mm.

peristomial ring or middle of first chaetiger; median antenna reaching first or second chaetiger. The maxillary formula is variable: MII 4–5 + 4–5, MIII 6, MIV 3–4 + 7–9. The proportions of the maxillary apparatus vary as follows: MI are 2.6–3.1 times longer than length of maxillary carriers; MI are 4.5–4.9 times longer than length of closing system; MII are 4.5–5.8 times longer than length of cavity opening. Branchiae from chaetigers 20–27 to 31–41 chaetigers before pygidium. Maximum number of branchial filaments varied from three to five and postchaetal lobes were conspicuous in first 48–70 chaetigers. Ventral cirri with a swollen base from chaetigers 5–7 to 54–68 chaetigers before of pygidium. Start of subacicular hooks in chaetigers 35–75.

Distribution. New Jersey, Rhode Island, Massachusetts, North Carolina, USA.

Habitat. According to Leidy (1855), the specimens were found co-occurring with *Lumbrinereis splendida* de Blainville, 1828(b) (= *Lumbrineris lumbricalis* (de Blainville, 1825)) in an oyster bed. Verrill (1873) commented that *M. leidii* lives under stones at low-water mark, but is more common on shelly bottoms in shallow water offshore. In North Carolina, the specimens lives in stiff clay, or in exposed muddy banks at moderately low water, also under boards or large stones (Hartman 1945). Some specimens studied here were found in mud (USMN 4469, USNM 6194).

Reproduction. According to Pettibone (1963), the eggs are released in firm gelatinous masses between June and July in the Woods Hole region. Hartman (1945) reported that juvenile stages could be found around June in North Carolina.

Remarks. The name *Marphysa leidii* was assigned by de Quatrefages (1866) to the specimen identified and described by Leidy (1855) as *Eunice sanguinea* from Great Egg Harbor, New Jersey. de Quatrefages explained the main difference between the species is the beginning of branchiae, starting from chaetiger 60 in *M. leidii*, whereas in *M. sanguinea* the branchiae have an earlier beginning. However, Webster (1879) clarified that de Quatrefages misinterpreted the beginning of the branchiae (Leidy described it from chaetiger 16 and not in chaetiger 60). Hence, Webster (1879) considered *M. leidii* as a small specimen of *M. sanguinea* with branchiae emerging earlier.

Specimens studied by Leidy are lost; apparently, these materials were not formally deposited in the Academy of Natural Sciences of Philadelphia (Salazar-Vallejo 2014). However, enough material deposited at the Smithsonian was found; one of the specimens was collected near to the type locality (about 35 km north). Herein, that specimen was assigned as neotype, according to Art. 75 (ICZN 1999), which suggests assigning a neotype to clarify the taxonomic position of a species.

Marphysa leidii is different from *M. sanguinea* because the former has translucent subacicular hooks and the postchaetal lobe is conical in the first three chaetigers, whereas in latter, the subacicular hook is reddish at the base and translucent distally, and the postchaetal lobe is digitiform in first chaetiger. Moreover, *M. leidii* has two types of the pectinate anodont, whereas *M. sanguinea* only has one type of pectinate anodont.

Marphysa leidii resemble *M. brasiliensis* (Brazil), *M. bulla* (Yellow Sea, China), *M. californica* (San Diego, California), *M. formosa* Steiner & Amaral, 2000 (Sao Paulo, Brazil), *M. haemasoma* (South Africa), *M. maxidenticulata* (Yellow Sea, China), *M. parishii* (Brazil), and *M. baileybrockae* **n. sp.** (Hawaii) by having pectinate branchiae with long filaments, the limbate chaetae subacicular absent, the subacicular hook translucent, and the dorsal cirri conical in all chaetigers. However, *M. leidii* has conical postchaetal lobe in first four chaetigers, whereas in *M. brasiliensis*, *M. bulla*, *M. californica*, *M. maxidenticulata*, *M. parishii*, and *M. baileybrockae* **n. sp.** the postchaetal lobe is conical with distal edge directed to dorsal side, and in *M. formosa* and *M. haemasoma*, the postchaetal is ovoid in the first four chaetigers. Furthermore, *M. parishii* has five types of pectinate chaetae as in *M. leidii*, whereas in *M. californica*, *M. haemasoma*, and *M. maxidenticulata*, there are only four types, and in *M. brasiliensis*, *M. formosa*, and *M. baileybrockae* **n. sp.**, there are only three types of pectinate chaetae. Also, *M. leidii* has eyes, but *M. bulla* lacks eyes. Finally, *M. leidii* (type and additional material, L10 = 10.7–17 mm) has the postchaetal lobe well developed in first 48–70 chaetigers, yet in *M. parishii* (type material, L10 = 17.2 mm) the postchaetal is developed in first 292 chaetigers. The comparison of *M. leidii* with related species is provided in Table 1.

Marphysa parishii Baird, 1869

Figures 7, 9G, Table 1

Marphysa parishii Baird, 1869:352–353.
Marphysa sanguinea.—Augener 1931: 291–292 (*non* Montagu, 1813).
Marphysa januarii Grube, 1881: 111–112.

Material examined. *Type material:* Holotype *Marphysa parishii* BNHM 1972.75A, paratype (1 specimen) BNHM 1972.75B, Brazil, coll. Cap. J. Parish, R.N. (is a posterior region of the body). Holotype *Marphysa januarii* ZMB 861, Rio de Janeiro, Brazil, coll. V. Martens S.

Description. Holotype complete, gravid female, with 478 chaetigers, broken in two parts (anterior fragment with 250 chaetigers), L10 = 17.2 mm, W10 = 9.5 mm TL = 814 mm. Anterior region of the body with dorsum convex and flat ventrum; body depressed from chaetiger 8, widest at chaetiger 24, tapering after chaetiger 63.

Prostomium bilobed, 2.7 mm long, 5 mm wide; lobes frontally rounded; median sulcus shallow anteriorly and deep ventrally (Fig. 7A–B). Prostomial appendages in a semicircle, median antenna isolated by a gap. Palps reaching middle of first peristomial ring; lateral antennae reaching second peristomial ring; median antenna reaching first peristomial ring. Palpophores and ceratophores ring-shaped, short, slender; palpostyles and ceratostyles tapering, slender. Eyes ovate, brown, between palps, and lateral antennae.

Peristomium (4.3 mm long, 8.2 mm wide) larger than prostomium, first ring two times longer than second ring, separation between rings distinct on all sides (Fig. 7A–C). Ventral lip with a slight central anterior depression and several shallow wrinkles (Fig. 7C).

Maxillary apparatus with MF = 1 + 1, 3 + 3, 4 + 0, 3 + 7, 1 + 1 (Fig. 7D). MI 2.6 times longer than length of maxillary carriers. MI forceps-like, MI 4.9 times longer than length of closing system (Fig. 7D–E); ligament between MI and MII, strongly sclerotized. MII with recurved triangular teeth; MII 3.6 times longer than length of cavity opening (Fig. 7D–E); ligament between MII and MIII and right MIV, sclerotized. MIII with triangular teeth; with rectangular attachment lamella, situated in center of right edge of the plate, sclerotized (Fig. 7D–E). Left MIV with lateral tooth larger than rest; attachment lamella semicircle, wide, better developed in right side, situated 1/3 of anterior edge of maxilla. Right MIV with two lateral teeth larger than rest; attachment lamella semicircle, wide, better developed in central side, situated along anterior edge of the maxilla, sclerotized (Fig. 7D–E). MV square, with a short triangular tooth. Mandibles dark; calcareous cutting plates broken, sclerotized cutting plates brown, with 10 growth rings (Fig. 7F).

Pectinate branchiae with up to six long filaments, present from chaetigers 25 to 453 (Fig. 7J). First nine chaetigers with two filaments; reaching the maximum five or six filaments in chaetigers 151L to 215L (Fig. 9G). Branchial filaments longer than dorsal cirri except in first two branchiae.

First four parapodia smaller, best developed in chaetigers 5–64, following ones becoming gradually smaller. Dorsal cirri conical in all chaetigers; longer than ventral cirri in anterior and posterior chaetigers, similar size in median chaetigers; best developed in chaetigers 5–43, following ones gradually smaller (Fig. 7G–K). Prechaetal lobes short, as transverse folds in all chaetigers (Fig. 7G–K). Chaetal lobes in all chaetiger rounded, from chaetiger 140 longer than other lobes, with aciculae emerging dorsal to midline (Fig. 7G–K). Postchaetal lobes well developed in first 292 chaetigers; digitiform in first four chaetigers, ovoid in chaetigers 5–8, rounded from chaetiger 9; progressively smaller from chaetiger 31; from 292 inconspicuous (Fig. 7G–K). Ventral cirri digitiform in first seven chaetigers; in chaetigers eight to 478 with an oval swollen base and digitiform tip; conical from chaetiger 479, gradually reducing in size (Fig. 7G–K).

Aciculae blunt, reddish along most of its length, translucent on the distal tip (Fig. 7G–K). First four chaetigers with two aciculae; in chaetigers 5–10 with three aciculae; in chaetigers 11–87 with four or five aciculae; in chaetigers 88–147 with four aciculae; in chaetigers 148–271 with three aciculae; from chaetiger 272 with only one acicula.

Limbate chaetae of two lengths in same chaetiger: long and short, long blades in dorsal position, short blades in ventral position; limbate chaetae reduced in number around chaetiger 54, and then maintained a similar number until the posterior end. Five types of pectinate chaetae; in anterior chaetigers, thin, isodont narrow, symmetric, with long and slender teeth, with 1–2 pectinate, up to 12 teeth (Fig. 7L); in median-posterior chaetigers, thick, isodont wide, asymmetric, with short and slender teeth, 4–5 chaetae with up to 28 teeth (Fig. 7M1), and thick, isodont wide, asymmetric, with long and thick teeth, 3–4 chaetae, up to 15 teeth (Fig. 7O); in posterior chaetigers, thick, anodont wide, symmetric, with short and slender teeth, 3–4 chaetae with up to 15 teeth (Fig. 7M2), and thick, anodont wide, symmetric, with long and thick teeth, 1–2 chaetae, with up to 4–6 teeth (Fig. 7N). Compound spinigers present throughout, with blades of two lengths in the same chaetiger: shorter blades slightly more abundant than longer blades. Subacicular hook unidentate, translucent; starting from chaetiger 124, one per chaetiger, present discontinuously after chaetigers 124 (Fig. 7P).

Pygidium with broken dorsal pair of anal cirri; ventral pair short, as long as the last chaetiger.

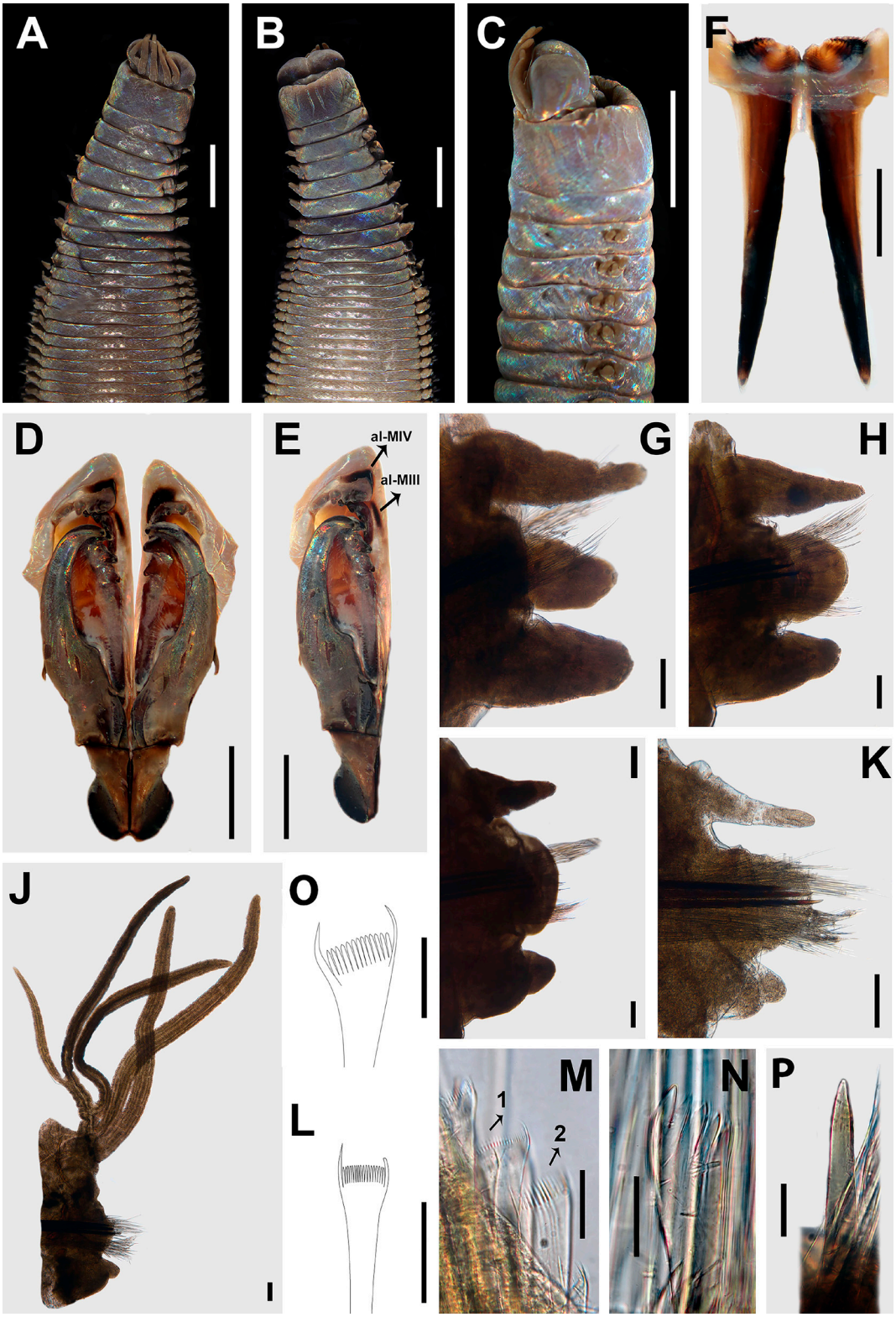

FIGURE 7. *Marphysa parishii* Baird, 1869. Holotype BNHM 1972.75A. A. Anterior end, dorsal view; B. Anterior end, ventral view; C. Anterior end, lateral view; D. Maxillary apparatus, dorsal view; E. Left MI-II-III-IV-V, lateral view; F. Mandible; G. Parapodium 3; H. Parapodium 7; I. Parapodium 12; J. Parapodium 211; K. Parapodium 457; L. Thin, isodont narrow, symmetric, with long and slender teeth, chaetiger 21; M. Thcik, pectinate chaetae posterior, chaetiger 457; N. Thick, anodont wide, symmetric, with long and thick teeth, chaetiger 457; O. Thick, isodont wide, asymmetric, with long and thick teeth, chaetiger 457. P. Subacicular hook, chaetiger 211. All chaetigers in anterior view; al-MIII: attachment lamella MIII; al-MIV: attachment lamella MIV; 1. Isodont wide, asymmetric, with short and slender teeth; 2. Anodont wide, symmetric, short and slender teeth. Scale bars: A–C, 4.3 mm; D–E, 1.8 mm; F, 1.2 mm; G–K, 0.2 mm; L–P, 30 µm.

Variation. Branchiae end in chaetigers 25–34 chaetigers before pygidium. The maximum number of branchial filaments varied from four to six. Ventral cirri with a swollen base from chaetigers 8 to 9–18 chaetigers before of pygidium.

Distribution. Brazil.

Habitat. Baird (1869) commented the specimens were collected by Captain John Parish, but he did not report on the specific locality or the substrate type.

Remarks. The type series of *Marphysa parishii* consists of the holotype (BNHM 1972.75A) and two paratypes (BNHM 1972.75B). One of the paratypes is a posterior end which coincides with holotype morphology; however, the second paratype presented some marked differences. The holotype (L10 = 17.2 mm) has branchiae from chaetiger 25 with up to six filaments, dorsal cirri are conical in all chaetigers, the postchaetal lobe is digitiform in first four chaetigers, the last chaetiger with developed postchaetal lobe is in chaetiger 292, and the subacicular hooks are translucent. While in the second paratype (L10 = 14.2 mm) the branchiae start from chaetiger 19, with up to eight filaments, the dorsal cirri have a swollen base near its base in anterior-median parapodia, postchaetal lobe is ovoid in first four chaetigers, the last chaetiger with developed postchaetal lobe is in chaetiger 96, and the subacicular hook is reddish in most of its length. These differences provide evidence that second paratype (BNHM 1972.75B) belongs to a different or a possible new species that is living in the same region. However, it is necessary to obtain more specimens to corroborate this hypothesis.

Marphysa parishii was considered to resemble *M. sanguinea* by Augener (1931), since both species have similarity in branchiae form and the presence of compound spinigers (see Augener (1931) remarks on *M. hentscheli* (= *Nicidion hentscheli*)). Herein, a morphological comparison of the type materials showed some important differences between the species, allowing for the re-establishment of *M. parishii*. *Marphysa parishii* is different from *M. sanguinea* because in the former (holotype, L10 = 17.2 mm) the branchiae end 25–34 chaetigers before pygidium, the postchaetal lobe is developed in first chaetiger 292, and the subacicular hook is translucent, instead of *M. sanguinea* (L10 = 11.5–20.4 mm), in which the branchiae end 9–18 chaetigers before pygidium, the postchaetal lobe is developed to chaetigers 50–70, and the subacicular hook is reddish basally and translucent distally.

Nevertheless, *Marphysa januarii* described by Grube (1881) from Rio de Janeiro have similarity with *M. parishii* in the branchiae distribution, the number of filaments, the shape of parapodia, the coloration and form of subacicular hook, and the chaetae consists only compound spinigers. Although the preservation status of the *M. januarii* (dry specimen) is problematic, no differences were found; thus, this species is considered as junior synonym of *M. parishii*.

Marphysa parishii resembles *M. acicularum* (Bermuda), *M. brasiliensis* (Brazil), *M. bulla* (Yellow Sea, China), *M. californica*, *M. maxidenticulata* (Yellow Sea, China), and *M. baileybrockae* **n. sp.** (Hawaii) by having pectinate branchiae with long filaments, the limbate chaetae subacicular absent, and the subacicular hook translucent. However, *M. parishii* has prechaetal lobe as transversal fold in anterior region, whereas in *M. acicularum* and *M. baileybrockae* **n. sp.**, the prechaetal lobe has dorsal side longer than ventral side in anterior body region. Furthermore, in *M. parishii* (L10 = 17.2 mm), the postchaetal lobe is developed in the first 292 chaetigers, but in *M. acicularum* (type and additional material, L10 = 4–15.8 mm), *M. baileybrockae* **n. sp.** (type material, L10 = 4.8–11.7 mm), and *M. californica* (type and additional material, L10 = 13.5–19 mm), the postchaetal lobe is developed in the first 92 chaetigers. On the other hand, in *M. parishii* the ventral cirri with swollen base start from chaetiger 8, in contrast, *M. californica* has the swollen base from chaetigers 13–14. Also, in *M. parishii* the branchiae start from chaetiger 25, whereas in *M. brasiliensis* (additional material, L10 = 17 mm), the branchiae start from chaetiger 33 and in *M. bulla* (L10 = 6.3–7.9 mm), from chaetiger 36. Furthermore, in *M. parishii* there are five types of pectinate chaetae, but in *M. brasiliensis*, there are only three types of pectinate chaetae. Finally, *M. parishii* has eyes, instead of *M. bulla* in which lacks eyes. The comparison of *M. parishii* with related species is provided in Table 1.

Marphysa sanguinea (Montagu 1813)

Figures 8, 9H, Table 1

Nereis sanguinea Montagu, 1813: 20–21, Plate 3, Figs. 1–3.
Leodice opalina.—Savigny in Lamarck, 1818: 323.
Nereidonta sanguinea.—de Blainville 1828a: 477.
Eunice sanguinea.—Audouin & Milne-Edwards 1834: 147–148 (*partim*).—Grube 1878: 51–52.

Marphysa sanguinea.—de Quatrefages 1866: 332–333.—Baird 1869: 352.—McIntosh 1910: 442–448.—Fauvel,1923: 408–410, Fig. 161.—Hutchings & Karageorpolous 2003: 88–90, Figs. 1A–F, 2A, C, 4A, C.—Wijnhoven & Dekker 2010: 431–435, Figs. 2, Table 1–2.—Hutchings, Glasby & Wijnhoven 2012: 278–281, Fig. 2–3.—Lavesque *et al.* 2019: 4–10, Fig.1–3.—Martin *et al.* 2020: 27–28 (Distribution range).

Material examined. *Type material:* Neotype BNHM 1867.1.7.24, Polperro, Cornwall, in mud and gravel at low water mark, coll. R. Laughrin, P. Hutchings (two specimens from this lot), Desig. P. Hutchings, 5019.6667'N 430.75'W. *Additional material:* LACM-AHF-P0000, Mount Edgecombe Plymouth, UK, 5021.1667'N 049.5'W, 25 Oct 1999–28 Sep 2000, in burrows in rock crevices, low intertidal, coll. P. Karageorgopoulos. BNHM 1 ex 1867.1.24, 2002.844-845, NHM 2 ex 1867.1.24, Polperro, Cornwall, 2002, in mud and gravel at low water mark, coll. R. Laughrin, P. Hutchings.

Description. Neotype complete, gravid female, with 286 chaetigers, L10= 16.7 mm, W10= 10 mm TL= 300 mm, last four chaetigers regenerating. Anterior region of the body with dorsum convex and flat ventrum; body depressed from chaetiger 12, widest at chaetiger 33, tapering after chaetiger 99.

Prostomium bilobed, 5 mm long, 3.2 mm wide; lobes frontally rounded; median sulcus shallow anteriorly and deep ventrally (Fig. 8A–B). Prostomial appendages in a semicircle, median antenna isolated by a gap. Palps reaching second peristomial ring; lateral antennae reaching first chaetiger; median antenna broken, reaching first chaetiger, (in BNHM ex 1867.1.24. reaching middle of first chaetiger). Palpophores and ceratophores ring-shaped, short, thick; palpostyles and ceratostyles tapering, slender. Eyes oval, brown, between palps, and lateral antennae.

Peristomium (4 mm long, 9.5 mm wide) wider than prostomium, first ring two times longer than second ring, separation between rings distinct only dorsal and ventrally (Fig. 8A–C). Ventral lip dissected, in BNHM ex 1867.1.24 with a slight central anterior depression and several shallow wrinkles (Fig. 8B).

Maxillary apparatus with MF= 1 + 1, 4 + 4, 5 + 0, 3 + 6, 1 + 1 (Fig. 8D). MI 2.9 times longer than length of maxillary carriers. MI forceps-like, MI 4 times longer than length of closing system (Fig. 8D–E); ligament between MI and MII, sclerotized. MII wide, with recurved triangular teeth; MII 3.7 times longer than length of cavity opening (Fig. 8D–E); ligament between MII and MIII and right MIV, slightly sclerotized. MIII with triangular teeth; with irregular attachment lamella, situated in center of right edge of the plate, slightly sclerotized (Fig. 8D–E). Left MIV with two lateral teeth larger than rest; attachment lamella semicircle, slender, better developed in right side, situated 2/3 along of anterior edge of maxilla. Right MIV with three lateral teeth larger than rest; attachment lamella semicircle, wide, better developed in central side, situated 2/3 along anterior edge of maxilla, sclerotized (Fig. 8D–E). MV square, with a short triangular tooth. Mandibles lost, in BNHM ex 1867.1.24 dark; ; calcareous cutting plates presents, sclerotized cutting plates brown, with 17 growth rings (Fig. 8F).

Pectinate branchiae with up to five long filaments, present from chaetigers 23L–25R to 273L–277R (Fig. 38J). First three chaetigers with one filament; reaching the maximum five in chaetigers 75L–152L (Fig. 9H). Branchial filaments longer than dorsal cirri except in first four branchiae.

First three parapodia smaller, best developed in chaetigers 5–65, following ones becoming gradually smaller. Dorsal cirri conical in all chaetiger; longer than central cirri in anterior and posterior chaetigers, shorter in median chaetigers; best developed in chaetigers 4–33, following ones gradually smaller (Fig. 8G–K). Prechaetal lobes short, as transverse folds in all chaetigers (Fig. 8G–K). Chaetal lobes rounded in first 48 chaetigers, shorter than postchaetal lobe, aciculae emerging dorsal to midline; triangular from chaetiger 49, longer than other lobes, acicula emerging in midline (Fig. 8G–K). Postchaetal lobes well developed in first 50 chaetigers; digitiform in first four chaetigers, ovoid in chaetigers 5–9, rounded from chaetiger 10; progressively smaller from chaetiger 22; from chaetiger 51 inconspicuous (Fig. 8G–K). Ventral cirri digitiform in first four chaetigers; in chaetiger five to 252 with a short oval swollen base and digitiform tip; conical from chaetiger 253, gradually reducing in size (Fig. 8G–K).

Aciculae blunt, reddish basally amber distally (Fig. 8G–K). First chaetiger with three aciculae; in chaetigers 2–4 with four aciculae; in chaetigers 5–15 with five aciculae; in chaetigers 16–21 with six aciculae; in chaetigers 22–38 with eight aciculae; in chaetigers 39–51 with six aciculae; in chaetigers 52–77 with five aciculae; in chaetigers 78–100 with four aciculae; in chaetigers 101–128 with four or three aciculae; from chaetigers 165 with two aciculae.

Limbate chaetae of two lengths in same chaetiger; long and short, long blades in dorsal position, short blades in ventral position; limbate chaetae reduced in number around chaetiger 29, and then maintained a similar number until the posterior end. Three types of pectinate chaetae; in anterior chaetigers, thin, isodont narrow, asymmetric, with long and slender teeth, with 1–2 pectinate, up to 10 teeth (Fig. 8L); in median-posterior chaetigers, thick, isodont

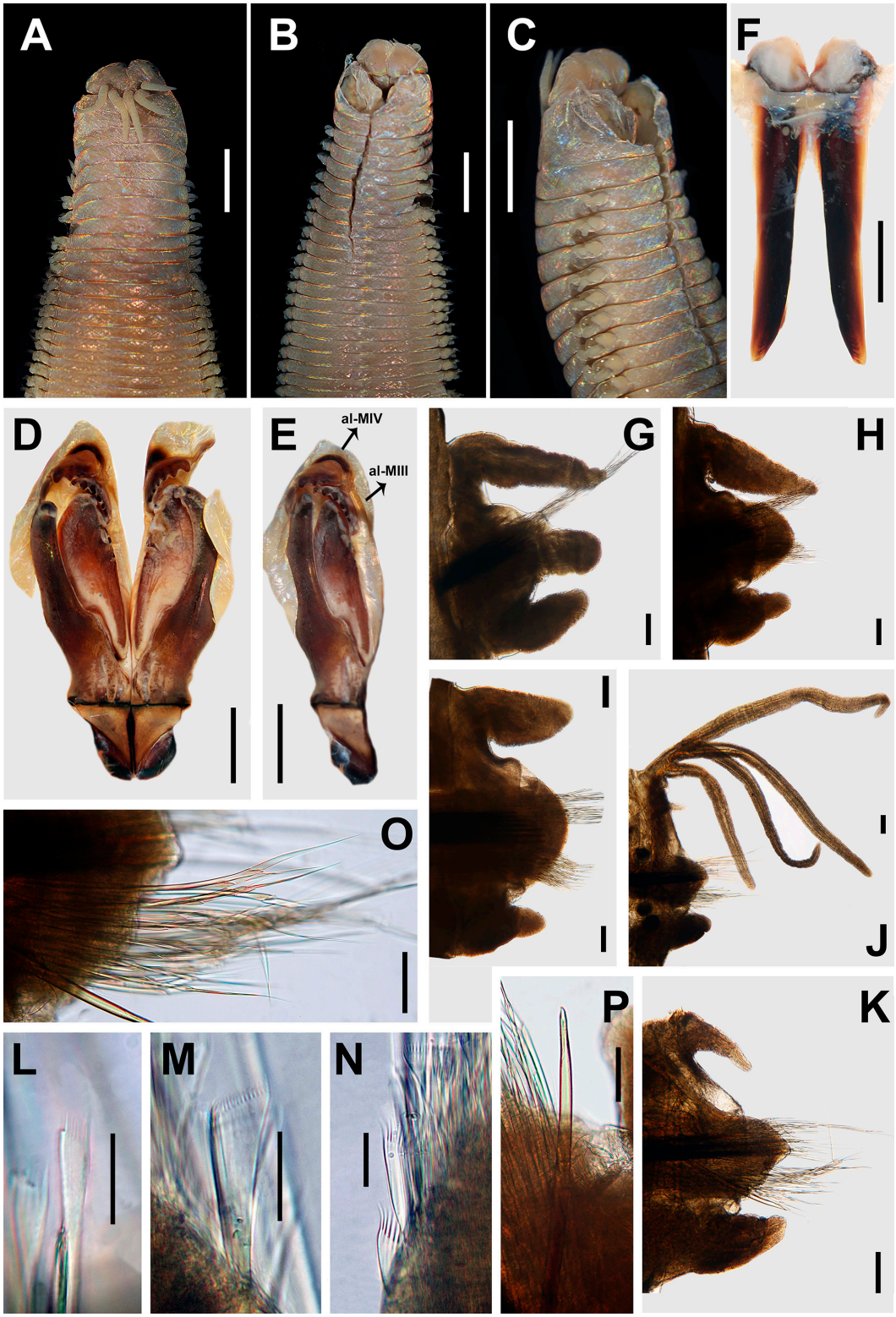

FIGURE 8. *Marphysa sanguinea* (Montagu, 1813). A. Anterior end, dorsal view; B. Anterior end, ventral view; C. Anterior end, ventro-lateral view; D. Maxillary apparatus, dorsal view; E. Left MI-II-III-IV-V, lateral view; F. Mandible; G. Parapodium 3; H. Parapodium 5; I. Parapodium 12; J. Parapodium 174; K. Parapodium 275; L. Thin, isodont narrow, asymmetric, with long and slender teeth, chaetiger 30; M. Thick, isodont wide, asymmetric, with short and slender teeth, chaetiger 174; N. Thick, anodont wide, symmetric, with long and slender teeth, chaetiger 275; O. Compound spiniger, chaetiger 193; P. Subacicular hook, chaetiger 193. A–E, G–P from BNHM 1867.1.7.24; F from BNHM 1 ex 1867.1.24, 2002.844-845. All chaetigers in anterior view; al-MIII: attachment lamella MIII; al-MIV: attachment lamella MIV. Scale bars: A–C, 4.2 mm; D–E, 1.8 mm; F, 1.2 mm; G–K, 0.2 mm; L–O, 30 µm; P, 0.1 mm.

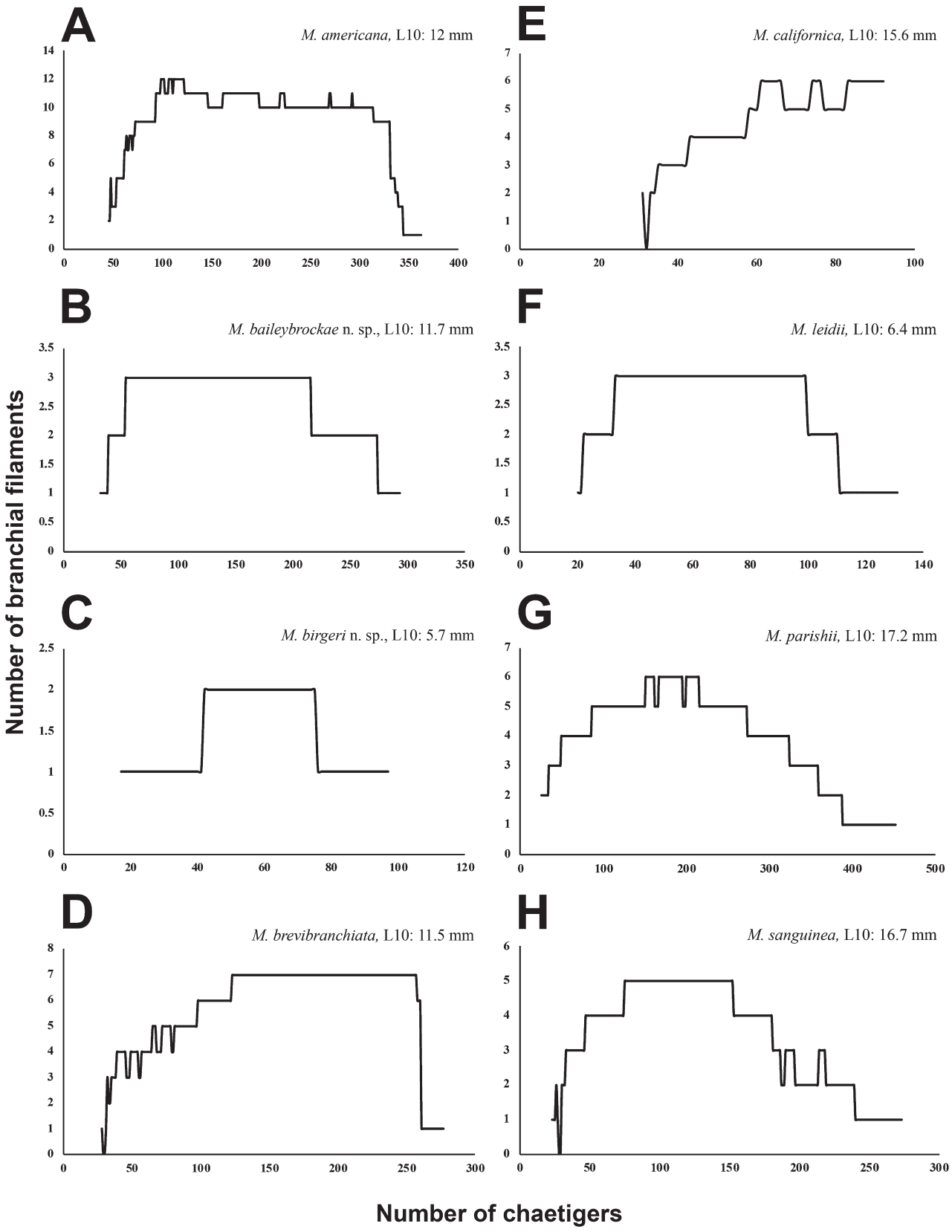

FIGURE 9. Distribution of branchial filaments throughout the body in A. *Marphysa americana* Monro, 1933 n. status.; B. *Marphysa baileybrockae* **n. sp.**; C. *Marphysa birgeri* **n. sp.**; D. *Marphysa brevibranchiata* Treadwell, 1921 n. status.; E. *Marphysa californica* (Moore, 1909); F. *Marphysa leidii* de Quatrefages, 1866; G. *Marphysa parishii* Baird, 1869; H. *Marphysa sanguinea* (Montagu, 1813).

wide, asymmetric, with short and slender teeth, 18–20 chaetae with up to 18 teeth (Fig. 8M); in posterior chaetigers, thick, anodont wide, symmetric, with long and slender teeth, 4–5 chaetae with up to 10–12 teeth (Fig. 8N). Compound spinigers present throughout, with blades of two lengths in the same chaetiger: shorter blades slightly more abundant than longer blades (Fig. 8O). Subacicular hooks unidentate, reddish basally translucent distally; starting from chaetiger 109, one per chaetiger, present discontinuously after chaetigers 109 (Fig. 8P). In LACM-AHF 0000 subacicular hook bidentate, amber at the base, translucent distally; with blunt teeth, of similar size, distal teeth directed upward, proximal directed laterally.

Pygidium with dorsal pair of anal cirri as long as last five chaetigers; ventral pair short, as long as last chaetiger.

Variation. Material examined with L10 = 11.5–20.4 mm, W10 = 7.2–11 mm, TChae = 239–320. Palps reaching middle of first or second peristomial ring; lateral antennae reaching second peristomial ring or first chaetiger; median antenna reaching middle second peristomial ring or second chaetiger. The maxillary formula is variable: MII 4 + 4–5, MIII 5–6, MIV 3–4 + 6–8. The proportions of the maxillary apparatus vary as follows: MI are 2.9–3.2 times longer than length of maxillary carriers; MI are 3.8–5.6 times longer than length of closing system varies; MII are 3.7–4.4 times longer than length of cavity opening. Branchiae from chaetigers 21–25 to 9–18 chaetigers before pygidium. Maximum number of branchial filaments varied from five to six and postchaetal lobes were conspicuous in first 50–70 chaetigers. Ventral cirri with a swollen base from chaetigers 5–8 to 8–18 chaetigers before of pygidium. Start of subacicular hooks in chaetigers 74–286. In LACM-AHF 0000 the subacicular hook bidentate, amber at the base, translucent distally.

Distribution. Northeast Atlantic states (south England, France, and Netherland). See Martin *et al.* (2020) for more information.

Habitat. According to Hutchings & Karageorgopoulos (2003) the specimens live in a deep burrows, in crevices inside the rocks at low watermark.

Remarks. The species was recently characterized by Lavesque *et al.* (2019), and this authors disclosed its COI sequences from material from the type locality. Herein, based on the neotype, the descriptions of the maxillary apparatus, the branchiae, parapodia, simple and compound chaetae were expanded. The materials studied in Lavesque *et al.* (2019) presented a swollen triangular postchaetal lobe in anterior region; however, we find more than a single shape in the neotype. In the first four chaetigers the postchaetal is digitiform, from chaetigers 5–9 it is ovoid, and that from chaetiger 10 it is rounded and reduced in size. Possibly the triangular swollen shape matches the ovoid shape found in the neotype. Furthermore, Lavesque *et al.* (2019) described the specimens with subacicular hook bidentate; however we found unidentate subacicular hooks in the neotype. This pattern, where the two types of hooks are present, was already found in *M. acicularum* (Molina-Acevedo & Carrera-Parra 2015) and herein in *M. baileybrockae* **n. sp.**. The presence of unidentate hook was explained probably due to wear on the proximal tooth. Likewise, smallest organism in *Paucibranchia disjuncta* (Hartman, 1961) presented bidentate hooks, but in the larger ones the hook was unidentate (Molina-Acevedo 2018).

Discussion

After a detailed morphological analysis, three species and two subspecies synonymized with *M. sanguinea* are now elevated to species status: *M. americana* n. status, *M. brevibranchiata* n. status, *M. californica, M. leidii* and *M. parishii*. Also, two species in mid-east Pacific (Hawaii) and Adriatic Sea (Croatia) previously identified as *M. sanguinea* are now given new names, *M. baileybrockae* **n. sp.** and *M. birgeri* **n. sp.**.

The cosmopolitan status applied to *M. sanguinea* has been challenged for many years, starting from a study by Hutchings & Karageorgopoulos (2003). *Marphysa sanguinea* is now known restricted only to the Northeast Atlantic including English Channel (Lavesque *et al.* 2019; Martin *et al.* 2020). Hence, any local *M. sanguinea* species described or identified outside of *M. sanguinea* known distribution area is likely a different species. This last statement must be taken carefully since Wijnhoven & Dekker (2010) reported to *M. sanguinea* as introduced species in Netherland; however, this introduction was questioned by Martin *et al.* 2020 since they clarified that Netherland is possibly the Northest distribution limit of the species.

This study managed to examined the species in synonymized inside *M. sanguinea* complex; many species within this complex either have been redescribed, reinstated, or given a new name (Zanol *et al*. 2016; Liu *et al*.

2017; Lavesque *et al*. 2017; Liu *et al*. 2018; Elgetany *et al*. 2018; Whang *et al*. 2018; Glasby *et al.* 2019; Martin *et al.* 2020). The exception applies to *M. iwamushi* and *M. haemasoma.* The first one was described by Izuka (1907) from several localities in Japan where it is commonly used as bait for fishing. Fauvel (1936) suggested that *M. iwamushi* was similar in morphology to *M. sanguinea* from England and thus proposed its synonymy. Unfortunately, the type material that is deposited at the University Museum of the University of Tokyo (Nishi & Tanaka 2011) was not available for this study. Therefore, *M. iwamushi*'s taxonomic issue could not be solved. Nevertheless, because the distribution of *M. sanguinea* does not include Japan, we suspect that *M. iwamushi* is a valid species. Moreover, a recent molecular study by Abe *et al*. (2019) has found five cryptic species from Japan, previously identified as *M. iwamushi*. Hence, it is imperative to compare with the type material to differentiate the species morphologically and determine the status of *M. iwamushi*. Currently, *M. haemasoma* is being covered in studies on the *Marphysa* species from South Africa (Kara *et al.* in review).

In view of the proposed new species and the restoration of species in synonymy within *M. sanguinea* complex, it is possible to conclude that *Marphysa sanguinea* complex consists of at least 24 species. Although morphological differences seem subtle, they can be distinguished by stable characters such as the form of branchiae and parapodia lobe, subacicular hook color, and pectinate chaetae presence. In addition, size dependent characters such as the beginning of branchiae and subacicular hook, and number of branchial filaments and its distribution pattern throught the body could also be informative (Miura 1986; Fauchald 1991; Molina-Acevedo & Carrera-Parra 2015; 2017). The use of morphology characters to describe a species in great detail is still capable of distinguishing species within this complex. Although molecular analysis offers a good support, conventional taxonomy work is still imperative, especially when working with specimens collected in the pre-molecular taxonomy period or with vague data on localities hampering resampling attempts.

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TABLE 1. Morphological features of the 24 currently recognized species from the species from *Marphysa sanguinea* complex. Abbreviations: MF: Maxillary formula, roman numerals refer to number of maxilla; MxC: maxillary carriers; CIS: closing system; COp: cavity opening; PR-I: first peristomial ring; PR-II: second peristomial ring; Chaet: chaetiger; p/a: present/absent; AR: anterior region; MR: median region; PR: posterior region; SH: subacicular hook. INSS: Isodont narrow with short and slender teeth; INLS: Isodont narrow with long and slender teeth; INST: Isodont narrow short and thick teeth; IWSS: Isodont wide with short and slender teeth; IWST: Isodont wide with short and thick teeth; IWLS: Isodont wide with long and slender teeth; IWLT: Isodont wide with long and thick teeth; AWSS: Anodont wide with short and slender teeth; AWST: Anodont wide short and thick teeth; AWLS: Anodont wide with long and slender teeth; AWLT: Anodont wide with long and slender teeth; sym: symmetric; asym: asymmetric.

Morphological features	*M. acicularum* Webster, 1884	*M. aegypti* Elgetany, Ghobashy, Ghoneim & Struck, 2018	*M. americana* Monro, 1933	*M. baileybrockae* **n. sp.**	*M. birgeri* **n. sp.**
Reference	Type and additional material	Original description, and redescription Martin *et al.* (2020)	Type material	Type material	Type material
Size (mm): L10, W10	L10: 4–15.8, W10:4–5.2	6 mm wide	12, 5.8	4.8–11.7, 2.3–3.8	3.5–10.4, 1.2–4.8
Prostomium: shaped	bilobed	bilobed	bilobed	bilobed	bilobed
Palps: length to	PR–I, PR–II	PR–I	PR–I	PR–II	PR–II, Chaet 1
Lateral antennae: length to	Chaet 1, 2	Chaet 1	PR–II	Chaet 1, 2	Chaet 1, 2
Median antennae: length to	Chaet 2, 3	Chaet 4	Chaet 1	Chaet 2	Chaet 1, 2
Peduncle in prostomial appendages (p/a)	absent	absent	absent	absent	absent
Eyes (p/a)	present	present	present	present	present
MF: MII, MIII, MIV	4–5+4–5, 5–6, 3–4+6–7	4+4, 5+0, 4+6	5+4, 7+0, 3+9	4+5, 7+0, 4+8	3–4+4, 5–6, 3–4+7
Maxillary carriers vs MI: proportion	MI 2.4–3.2 times longer than MxC	MI 3.1 times longer than MxC	MI 3.2 times longer than MxC	MI 2.4 times longer than MxC	MI 2.3–2.8 times longer than MxC
Closings system vs MI: proportion	MI 3.7–5 times longer than CIS	MI 5.1 times longer than CIS	MI 5 times longer than CIS	MI 3.8 times longer than CIS	MI 4.2–6 times longer than CIS
Cavity opening vs MII: proportion	MII 3–44 times longer than COp	MII 3.3 times longer COp	MII 3 times longer than COp	MII 4.8 times longer than COp	MII 4.2–6 times longer than COp
Branchiae: shape	pectinate	pectinate	pectinate	pectinate	pectinate
Branchiae: initial chaetiger	22–27	28	45	22–30	15–19
Branchiae: end chaetiger before pygidium	5–17	48	28	19–20	13–17

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TABLE 1. (Continued)

Morphological features	*M. acicularum* Webster, 1884	*M. aegypti* Elgetany, Ghobashy, Ghoneim & Struck, 2018	*M. americana* Monro, 1933	*M. baileybrockae* **n. sp.**	*M. birgeri* **n. sp.**
Branchial filaments: number	2–5	6	12	3	2–3
Branchiae: size of filaments	long	long	long	long	long
Dorsal cirri: shape	AR: conical with wide base, MR, PR: conical	AR, MR, PR: conical	AR, MR, PR: conical	AR, MR, PR: conical	AR: digitiform, MR, PR: conical
Prechaetal: shape	AR: dorsal edge longer, MR, PR: transversal fold	AR, MR, PR: transversal fold	AR, MR, PR: transversal fold	AR: dorsal edge longer, MR, PR: transversal fold	AR, MR, PR: transversal fold
Chaetal: shape	AR: rounded, MR, PR: triangular	AR: rounded	AR: rounded, MR, PR: triangular	AR: rounded, MR, PR: triangular	AR: rounded, MR, PR: triangular
Developed postchaetal lobe: end chaetiger	28–56	?	92	47–59	18–42
Postchaetal lobe: shape in body regions	Chaet 4: digitiform, Chaet 4–10: rounded, Chaet 10: auricular	Chaet 4: ovoid Chaet 4–10, 10: rounded	Chaet 4: conical Chaet 4–10, 10: rounded	Chaet 4: conical directe dorsally, Chaet 4–10, 10: ovoid directed dorsally	Chaet 4: digi, Chaet 4–10: ovoid, Chaet 10: rounded
Ventral cirri in first chaetigers: shape	digitiform	conical	digitiform	digiform	digitiform
Ventral cirri with swollen base: initial chaetiger	3–4	?	5	5–6	6
Ventral cirri with swollen base: end chaetiger before pygidium	13–last chaetiger	?	45	21–25	41–51
Ventral cirri in most posterior chaetigers: shape	?	?	conical	digitiform	digitiform
Aciculae: shape, color	blunt, dark	blunt, dark, one translucent	blunt, dark	blunt, dark	blunt, dark
Subacicular limbadate chaetae: (p/a)	absent	present	absent	absent	absent
Subacicular limbadate chaetae: distribution	-	all chaet	-	-	-
Pectinate chaetae: types	INSS; IWLS; AWLT	INLS; IWSS; IWLS; AWLT	INLS; IWLT; IWSS; AWLT	INSS; IWLS; AWLT	INLS; IWSS; AWSS; AWLT

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TABLE 1. (Continued)

Morphological features	*M. acicularum* Webster, 1884	*M. aegypti* Elgetany, Ghobashy, Ghoneim & Struck, 2018	*M. americana* Monro, 1933	*M. baileybrockae* **n. sp.**	*M. birgeri* **n. sp.**
Pectinate chaetae: shalf	thin; thick; thick	thin; thick; thick; thick	thin; thick; thick; thick	thin; thick; thick	thin; thin; thick; thick
Isodont pectinate chaetae blade	sym; asym; sym	sym; asym; asym; asym	asym; asym, sym; asym	sym; sym; sym	sym; asym; sym; asym
Pectinate chaetae: number per type pectinate	2–3; 8; 3	?	3–4; 3–4; 1–2	6–8; 1–2; 1–2	1–2; 15–16; 3–5; 1–2
Pectinate chaetae teeth: number per type pectinate	15; 23; 10	19; 9; 6	12; 16; 11	20–22; 24; 6	17; 26; 17–18; 1–2
Spiniger blade: length in anterior region	2 lengths	?	2 lengths	2 lengths	3 lengths
Spiniger blade: length in median–posterior region	2 lengths	?	similar lengths	2 lengths	2 lengths
Subacicular hook: initial chaetiger	27–47	?	117	27–32	20–27
Subacicular hook: shape, color	bidentate, translucent	unidentate, translucent	bidentate, reddish basally and translucent distally	bidentate, translucent	bidentate, translucent
Aciculae vs Subacicular hook: proportion	SH 2 times shorter	similar size	similar size	SH 2 times shorter	similar size
Subacicular hook: distribution	discontinuous	discontinuous	discontinuous	continuous	continuous

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TABLE 1. (Continued)

Morphological features	*M. brevibranchiata* Treadwell, 1921	*M. bulla* Liu, Hutchings & Kupriyanova, 2018	*M. californica* Moore, 1909	*M. chirigota* Martin, Gil & Zanol in Martin et al. 2020	*M. elityeni* Lewis & Karageorpolous, 2008
Reference	Type material	Original description	Type and additional material	Original description	Type material
Size (mm): L10, W10	11.5–14.2, 3.4–4	6.3–7.9, 7.9–14	13.5–19, 6.5–10.3	26.5 mm total long, 79 mm total wide	9.3–18.5, 3.6–4
Prostomium: shaped	bilobed	bilobed	bilobed	bilobed	bilobed
Palps: length to	PR–II	PR–II	PR–II, Chaet 1	Chaet 1.5, 3.5	PR–II, Chaet 1
Lateral antennae: length to	Chaet 1	Chaet 2	Chaet 1	Chaet 1, 3	Chaet 1, 2
Median antennae: length to	Chaet 1, 2	Chaet 2	Chaet 2	Chaet 1, 3	Chaet 1, 2
Peduncle in prostomial appendages (p/a)	absent	absent	absent	absent	absent
Eyes (p/a)	?	absent	present	present	present
MF: MII, MIII, MIV	6+5–6, 7, 3–4+9	4+4, 6+0, 3+9	4+4, 5+0, 4+8	4–5+5, 6+0, 4–5+7	4+4, 4–5, 3+6–7
Maxillary carriers vs MI: proportion	MI 2.7–2.8 times longer than MxC	MI 2.5 times longer than MxC	MI 3 times longer than MxC	MI 2.5 times longer than MxC	MI 2.6–3 times longer than MxC
Closings system vs MI: proportion	MI 4.5–5 times longer than CIS	MI 5 times longer than CIS	MI 4.4 times longer than CIS	?	MI 4.1–4.6 times longer than CIS
Cavity opening vs MII: proportion	MII 3.3–3.8 times longer than COp	MII 4.1 times shorter than Cop	MII 4.5 times longer than COp	?	MII 4–4.3 times longer than COp
Branchiae: shape	pectinate	pectinate	pectinate	pectinate	pectinate
Branchiae: initial chaetiger	28–36	36	28–40	25–30	26–37
Branchiae: end chaetiger before pygidium	6–12	35	?	40	10
Branchial filaments: number	7–8	5	4–8	6	6–10
Branchiae: size of filaments	short	long	long	long	long
Dorsal cirri: shape	AR, MR, PR: conical	AR, MR, PR: conical	AR, MR, PR: conical	AR, MR, PR: conical	AR, MR, PR: conical
Prechaetal: shape	AR, MR, PR: transversal fold	AR, MR, PR: transversal fold	AR, MR, PR: transversal fold	AR: dorsal edge longer, MR, PR: transversal fold	AR, MR, PR: transversal fold

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TABLE 1. (Continued)

Morphological features	*M. brevibranchiata* Treadwell, 1921	*M. bulla* Liu, Hutchings & Kupriyanova, 2018	*M. californica* Moore, 1909	*M. chirigota* Martin, Gil & Zanol in Martin et al. 2020	*M. elityeni* Lewis & Karageorpolous, 2008
Chaetal: shape	AR: rounded, MR, PR: triangular	AR: rounded	AR: rectangular MR, PR: triangular	AR, MR, PR: rounded	AR, MR, PR: rounded
Developed postchaetal lobe: end chaetiger	50–75	?	41–92	?	33–82
Postchaetal lobe: shape in body regions	Chaet 4: digitiform, Chaet 4–10, 10: rounded	Chaet 4: digitiform, Chaet 4–10, 10: ovoid	Chaet 4: digitiform, Chaet 4–10: ovoid, Chaet 10: auricular	chaet 4: ovoid, Chaet 4–10: ? Chaet 10: rounded	Chaet 4: ovoid, Chaet 4–10, 10: auricular
Ventral cirri in first chaetigers: shape	digitiform	digitiform	digitiform	conical	digitiform
Ventral cirri with swollen base: initial chaetiger	5–6	?	13–14	5	4
Ventral cirri with swollen base: end chaetiger before pygidium	128–168	?	?	20	last chatetiger
Ventral cirri in most posterior chaetigers: shape	digitiform	?	?	conical	?
Aciculae: shape, color	blunt, dark	blunt, dark	blunt, dark	blunt, dark	blunt, dark
Subacicular limbadate chaetae: (p/a)	absent	absent	absent	absent	absent
Subacicular limbadate chaetae: distribution	-	-	-	-	-
Pectinate chaetae: types	INLS; IWSS; AWLS; AWST	INSS; IWLS; IWSS; IWLT; AWLT	INSS; IWSS; IWLT; AWLT	INLS; IWSS; IWLT; AWLT	INLS; IWSS; AWSS; AWLT
Pectinate chaetae: shalf	thin; thick; thick; thick	thin; tick; thin; thick; thick	thin; thin; thick; thick	thin; thin; thick; thick	thin; thick; thick; thick
Isodont pectinate chaetae blade	sym; asym; sym; sym	sym; sym, asym; ?; sym	sym; sym; sym; sym	asym; asym; asym; asym	sym; asym; asym; asym
Pectinate chaetae: number per type pectinate	1–2; 1–2; 1–2; 1–2	?; 13–17; ?; ?; ?	2–3; 8–9; 1–2; 1–2	2–10; 2–10; 5–6; 2–5	2–3; 6–7; 6–7; 1–2

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TABLE 1. (Continued)

Morphological features	*M. brevibranchiata* Treadwell, 1921	*M. bulla* Liu, Hutchings & Kupriyanova, 2018	*M. californica* Moore, 1909	*M. chirigota* Martin, Gil & Zanol in Martin et al. 2020	*M. elityeni* Lewis & Karageorpolous, 2008
Pectinate chaetae teeth: number per type pectinate	14; 40; 9; 16	13–17; 13–17; 14; 3–4; ?	15; 26; 18; 18	20–30; 20–30; 13–16; 4–7	17; 17; 13–14; 10
Spiniger blade: length in anterior region	3 lengths	2 lengths	2 lengths	?	2 lengths
Spiniger blade: length in median–posterior region	2 lengths	2 lengths	2 lengths	?	2 lengths
Subacicular hook: initial chaetiger	36–46	71	204	30–45	absent
Subacicular hook: shape, color	unidentate, translucent	unidentate, translucent	?	unidentate, translucent	bidentate, translucent
Aciculae vs Subacicular hook: proportion	similar size	?	?	?	similar size
Subacicular hook: distribution	continuous	discontinuous	discontinuous	continuous	discontinuous

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TABLE 1. (Continued)

Morphological features	*M. gaditana* Martin, Gil & Zanol in Martin *et al.* 2020	*M. hongkongensa* Whang, Zhang & Qiu, 2018	*M. iloiloensis* Glasby, Mandario, Burghardt, Kupriyanova, Gunton & Hutchings, 2019	*M. kristiani* Zanol, Silva & Hutchings, 2016	*M. leidii* de Quatrefages, 1866
Reference	Original description	Original description	Original description	Type material	Type material
Size (mm): L10, W10	121.7 mm total long, 6.5 mm total wide	3.2–11, 2.2–5.3	9–165+ total long, 2.6 – 3.7	11.6–13	10.7–17
Prostomium: shaped	bilobed	bilobed	bilobed	bilobed	bilobed
Palps: length to	Chaet 2,	PR–II	PR–II	PR–II	PR–I, PR–II
Lateral antennae: length to	Chaet 2, 3	Chaet 2	Chaet 1	PR–II, Chaet 1	PR–II, Chaet 1
Median antennae: length to	Chaet 2, 3	Chaet 2	Chaet 1	Chaet 1	Chaet 1, 2
Peduncle in prostomial appendages (p/a)	absent	absent	absent	present	absent
Eyes (p/a)	present	?	present	absent	present
MF: MII, MIII, MIV	5+6, 5+0, 3+5	5–6+5–6, 7, 4+8	4+5, 4–5, 3–4+5–6	6–7+6, 8–10, 6+9–11	4–5+4–5, 6, 3–4+7–9
Maxillary carriers vs MI: proportion	MI 2.8 times longer than MxC	MI 2.4 times longer than MxC	MI 2.5–2.7 times longer than MxC	MI 2.1–2.4 times longer than MxC	MI 2.6–3.1 times longer than MxC
Closings system vs MI: proportion	?	?	MI 6 times longer than CIS	MI 3.5–3.8 times longer than CIS	MI 4.5–4.9 times longer than CIS
Cavity opening vs MII: proportion	?	?	?	MII 3.8–5.7 times longer COp	MII 4.5–5.8 times longer COp
Branchiae: shape	pectinate	pectinate/palmate	pectinate	palmate/pectinate	pectinate
Branchiae: initial chaetiger	20–25	15–35	16–20	57	21–27
Branchiae: end chaetiger before pygidium	35	?	?	?	31–40
Branchial filaments: number	5	5–10	6–7	3	4–5
Branchiae: size of filaments	long	short	short	short	long
Dorsal cirri: shape	AR, MR, PR: conical	AR, MR, PR: conical	AR, MR, PR: conical	AR, MR, PR: conical	AR, MR, PR: conical
Prechaetal: shape	AR: dorsal edge longer, MR, PR: transversal fold	AR, MR, PR: transversal fold	AR, MR, PR: transversal fold	AR, MR, PR: transversal fold	AR, MR, PR: transversal fold

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TABLE 1. (Continued)

Morphological features	*M. gaditana* Martin, Gil & Zanol in Martin *et al.* 2020	*M. hongkongensa* Whang, Zhang & Qiu, 2018	*M. iloiloensis* Glasby, Mandario, Burghardt, Kupriyanova, Gunton & Hutchings, 2019	*M. kristiani* Zanol, Silva & Hutchings, 2016	*M. leidii* de Quatrefages, 1866
Chaetal: shape	AR, MR: bilobed, PR: ?	AR: rounded, MR, PR: triangular	AR, MR, PR: rounded	AR: rounded, MR, PR: triangular	AR: rounded, MR, PR: triangular
Developed postchaetal lobe: end chaetiger	more than 120 chaetigers	?	?	70	48–70
Postchaetal lobe: shape in body regions	Cheat 4: conical, Chaet 4–10: ?, Chaet 10: rounded	Chaet 4: digitiform, Chaet 4–10, 10:?	Chaet 4: ?, Chaet 4–10: ?, Chaet 10: auricular	Chaet 4: digitiform, Chaet 4–10; rounded, Chaet 10: auricular	Chaet 4: conical, Chaet 4–10: ovoid, Chaet 10: rounded
Ventral cirri in first chaetigers: shape	conical	digitiform	conical	digitiform	ovoid
Ventral cirri with swollen base: initial chaetiger	6	?	?	9–10	5–7
Ventral cirri with swollen base: end chaetiger before pygidium	185	?	?	?	54–60
Ventral cirri in most posterior chaetigers: shape	conical	?	?	?	conical
Aciculae: shape, color	blunt, dark, one pale	?	blunt, dark	blunt, dark	blunt, dark
Subacicular limbadate chaetae: (p/a)	absent	absent	absent	absent	absent
Subacicular limbadate chaetae: distribution	-	-	-	-	-
Pectinate chaetae: types	INLS; IWLT; AWLT	NLSS; IWSS; IWLS; AWLT; AWLS	INLS; IWSS, ANLT	INLS; IWLS, AWLT	INLS; IWSS; IWLS; AWLT; AWSS
Pectinate chaetae: shalf	thin; thick; thick	thin; thick; thick; thick; thick	thin; thick; thick	thin; thick; thick	thin; thick; thick; thick; thick
Isodont pectinate chaetae blade	asym; asym; asym	sym; asym; asym; asym; asym	sym; asym; asym	sym; asym	sym; sym; sym; sym

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TABLE 1. (Continued)

Morphological features	*M. gaditana* Martin, Gil & Zanol in Martin *et al.* 2020	*M. hongkongensa* Whang, Zhang & Qiu, 2018	*M. iloiloensis* Glasby, Mandario, Burghardt, Kupriyanova, Gunton & Hutchings, 2019	*M. kristiani* Zanol, Silva & Hutchings, 2016	*M. leidii* de Quatrefages, 1866
Pectinate chaetae: number per type pectinate	8–10; 4–6; 3–6	1–3; 1–7; 1–3; 1–2; 1–2	?	1; 3–4	1–2; 1–2; 3–4; 3–4; 3
Pectinate chaetae teeth: number per type pectinate	17–22; 10–14; 5–10	8–15; 15–23; 15; 7; 13	8–19; 22–28; 5–10	8–10; 25	11–12; 17; 10; 14; 17
Spiniger blade: length in anterior region	2 lengths	?	?	2 lengths	2 lengths
Spiniger blade: length in median–posterior region	?	?	?	2 lengths	2 lengths
Subacicular hook: initial chaetiger	40–45	?	30–38	48	41–75
Subacicular hook: shape, color	bi/unidentate, translucent	bidentate, amber	unidentate, reddish	bidentate, translucent	bidentate, translucent
Aciculae vs Subacicular hook: proportion	?	SH 2 times shorter	similar size	similar size	similar size
Subacicular hook: distribution	discontinuous	continuous	continuous	continuous	continuous

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TABLE 1. (Continued)

Morphological features	*M. maxidenticulata* Liu, Hutchings & Kupriyanova, 2018	*M. mullawa* Hutchings & Karageorgopoulos, 2003	*M. multipectinata* Liu, Hutchings & Sun, 2017	*M. nobilis* Treadwell, 1917	*M. parishii* Baird, 1869
Reference	Original description	Type material	Type material	Type and additional material	Type material
Size (mm): L10, W10	8.7, 7	7–13.5	9–17	6 –13.6	17.2, 9.5
Prostomium: shaped	bilobed	bilobed	bilobed	bilobed	bilobed
Palps: length to	PR–II	PR–II	PR–I, PR–II	PR–I, PR–II	PR–I
Lateral antennae: length to	Chaet 1	PR–II, Chaet 1	PR–II, Chaet 2	PR–II, Chaet 2	PR–II
Median antennae: length to	Chaet 1	Chaet 1, 2	Chaet 1, 2	Chaet 1, 3	Chaet 1
Peduncle in prostomial appendages (p/a)	absent	absent	absent	absent	absent
Eyes (p/a)	absent	present	present	present	present
MF: MII, MIII, MIV	4+6, 5+0, 4+7	3–5+4–5, 4–6, 3–4+6	3–4+4–5, 5–6, 3–4+6–9	3–4+3–4, 5–6, 3–4+7–8	3+3, 4+0, 3+7,
Maxillary carriers vs MI: proportion	MI 3 times longer than MxC	?	MI 2.7–3.2 times longer than MxC	MI 3.8 times longer than MxC	MI 2.6 times longer than MxC
Closings system vs MI: proportion	MI 6 times longer than CIS	?	MI 3.5–4.8 times longer than CIS	MI 5 times longer than CIS	MI 4.9 times longer than CIS
Cavity opening vs MII: proportion	MII 3.1 times longer than COp	?	MII 3.5–4 times longer than COp	MII 3.2 times longer than COp	MII 3.6 times longer than COp
Branchiae: shape	pectinate	palmate/pectinate	pectinate	pectinate	pectinate
Branchiae: initial chaetiger	28	14–31	19–36	17–27	25
Branchiae: end chaetiger before pygidium	20	?	10–15	34–37	25–34
Branchial filaments: number	3	5–6	3–6	4–6	4–6
Branchiae: size of filaments	long	long	long	long	long
Dorsal cirri: shape	AR, MR, PR: conical	AR, MR, PR: conical	AR: digitiform, MR, PR: conical	AR: digitiform, MR: with swollen base, PR: conical	AR, MR, PR: conical
Prechaetal: shape	AR, MR, PR: transversal fold	AR, MR, PR: transversal fold	AR: dorsal edge longer, MR, PR: transversal fold	AR, MR, PR: transversal fold	AR, MR, PR: transversal fold

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TABLE 1. (Continued)

Morphological features	*M. maxidenticulata* Liu, Hutchings & Kupriyanova, 2018	*M. mullawa* Hutchings & Karageorgopoulos, 2003	*M. multipectinata* Liu, Hutchings & Sun, 2017	*M. nobilis* Treadwell, 1917	*M. parishii* Baird, 1869
Chaetal: shape	AR: rounded, MR, PR: rectangular	AR: rounded, MR, PR: triangular	AR, MR, PR: rounded	AR: rounded, MR, PR: triangular	AR, MR, PR: rounded
Developed postchaetal lobe: end chaetiger	?	29–41	55–67	39–71	292
Postchaetal lobe: shape in body regions	Chaet 4: digitiform, Chaet 4–10. 10: ?	Chaet 4: conical, Chaet 4–10: ovoid, Chaet 10: rounded	Chaet 4: digitiform, ovoid directed dorsally, Chaet auricud	Chaet 4: ovoid, Chaet 4–10, 10: rounded	Chaet 4: digitiform, Chaet 4–10: ovoid, Chaet 10: auricular
Ventral cirri in first chaetigers: shape	?	conical	conical	conical	digitiform
Ventral cirri with swollen base: initial chaetiger	?	16–25	4–7	10–11	8
Ventral cirri with swollen base: end chaetiger before pygidium	?	66	18–39	44	9–18
Ventral cirri in most posterior chaetigers: shape	?	conical	conical	conical	conical
Aciculae: shape, color	blunt, dark	blunt, dark	blunt, dark	blunt, dark	blunt, dark
Subacicular limbadate chaetae: (p/a)	absent	absent	absent	absent	absent
Subacicular limbadate chaetae: distribution	-	-	-	-	-
Pectinate chaetae: types	INLS; IWSS; AWSS; AWLT	INLS; IWSS; AWLS	INLS; IWSS; AWSS; AWLT	INLS; IWSS; AWLS	INLS; IWSS; IWLT; AWSS, AWLT
Pectinate chaetae: shalf	thin; thick; thick; thick	thin; thick; thick	thin; thick; thick; thick	thin; thick; thick	thin; thick; thick; thick; thick
Isodont pectinate chaetae blade	sym; sym; asym; asym	sym; sym; sym	sym; ?; ?; asym	sym; asym; asym	sym; asym; asym; sym; sym
Pectinate chaetae: number per type pectinate	1–2; 10–11; 1–2; 1–2	1–2; 3–4; 2–3	1–2; 26; 3–4; 1–2	2–3; 10–12; 6–7	1–2; 4–5; 3–4; 3–4; 1–2

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TABLE 1. (Continued)

Morphological features	*M. maxidenticulata* Liu, Hutchings & Kupriyanova, 2018	*M. mullawa* Hutchings & Karageorgopoulos, 2003	*M. multipectinata* Liu, Hutchings & Sun, 2017	*M. nobilis* Treadwell, 1917	*M. parishii* Baird, 1869
Pectinate chaetae teeth: number per type pectinate	18–19; 16–17; 15–16; 3–6	8; 34; 12–13	18; 18; 20; 4	16–17; 17; 16	12; 28; 15; 15; 4–6
Spiniger blade: length in anterior region	2 lengths	2 lengths	2 lengths	2 lengths	2 lengths
Spiniger blade: length in median–posterior region	2 lengths	2 lengths	2 lengths	2 lengths	2 lengths
Subacicular hook: initial chaetiger	25	33–76	27–33	31–94	124
Subacicular hook: shape, color	unidentate, translucent	bidentate, translucent	bidentate, amber	unidentate, reddish	unidentate, translucent
Aciculae vs Subacicular hook: proportion	?	similar size	SH 2 times shorter	SH 2 times shorter	SH 2 times shorterP43:U43
Subacicular hook: distribution	continuous	discontinuous	discontinuous	discontinuous	discontinuous

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TABLE 1. (Continued)

Morphological features	*M. tripectinata* Liu, Hutchings & Sun, 2017	*M. sanguinea* (Montagu, 181	*M. victori* Lavesque, Daffe, Bonifácio & Hutchings, 2017	*M. viridis* Treadwell, 1917
Reference	Type material	Type material	Original description	Type and additional material
Size (mm): L10, W10	11–12.3	11.5–20.4	12, 11	2–10.2
Prostomium: shaped	bilobed	bilobed	bilobed	bilobed
Palps: length to	PR–II	PR–I, PR–II	PR–II	PR–I, Chaet 1
Lateral antennae: length to	Chaet 1	PR–II, Chaet 1	Chaet 2	Chaet 1, 3
Median antennae: length to	Chaet 1, 2	PR–II, Chaet 2	Chaet 3	Chaet 2, 4
Peduncle in prostomial appendages (p/a)	absent	absent	absent	absent
Eyes (p/a)	present	present	present	present
MF: MII, MIII, MIV	5+5–6, 7, 4–5+8	4+4–5, 5–6, 3–4+6–8	5+5, 5–6+0, 3–4+6–7	4–5+4–5, 5–8, 3–5+7–10
Maxillary carriers vs MI: proportion	MI 2.6–2.8 times longer than MxC	MI 2.9–3.2 times longer than MxC	MI 2.4 times longer than MxC	MI 3 times longer than MxC
Closings system vs MI: proportion	MI 4–4.5 times longer than CIS	MI 3.8–5.6 times longer than CIS	MI 5.2 times longer than CIS	MI 6 times longer than CIS
Cavity opening vs MII: proportion	MII 3.6–3.8 times longer than COp	MII 3.7–4.4 times longer than COp	MII 3.6 times longer than COp	MII 4.1 times longer than COp
Branchiae: shape	palmate/pectinate	pectinate	pectinate	pectinate
Branchiae: initial chaetiger	13–20	21–25	32	17–25
Branchiae: end chaetiger before pygidium	16	9–18	?	23–50
Branchial filaments: number	5–6	5–6	6	2–6
Branchiae: size of filaments	long	long	long	long
Dorsal cirri: shape	AR: digitiform, MR, PR: conical	AR, MR, PR: conical	AR, MR conical, PR: digitiform	AR, MR, PR: conical
Prechaetal: shape	AR: dorsal edge longer, MR, PR: transversal fold	AR, MR, PR: transversal fold	AR, MR, PR: transversal fold	AR, MR, PR: transversal fold
Chaetal: shape	AR: rounded, MR, PR: triangular	AR: rounded, MR, PR: triangular	AR: rounded	AR: rectangular MR, PR: rounded

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TABLE 1. (Continued)

Morphological features	*M. tripectinata* Liu, Hutchings & Sun, 2017	*M. sanguinea* (Montagu, 181	*M. victori* Lavesque, Daffe, Bonifácio & Hutchings, 2017	*M. viridis* Treadwell, 1917
Developed postchaetal lobe: end chaetiger	50–131	50–70	?	27–52
Postchaetal lobe: shape in body regions	Chaet 4: ovoid dorsal edge longer, Chaet 4–10, 10: rounded dorsal edge longer	Chaet 4: digitiform, Chaet 4–10: ovoid, Chaet 10: auricular	Chaet 4: conical, Chaet 4–10: ovoid, Chaet 10: rounded	Chaet 4: digitiform, Chaet 4–10, 10: rounded
Ventral cirri in first chaetigers: shape	conical	digitiform	?	conical
Ventral cirri with swollen base: initial chaetiger	6–8	5–8	5–6	9
Ventral cirri with swollen base: end chaetiger before pygidium	151	8–18	?	23–54
Ventral cirri in most posterior chaetigers: shape	conical	conical	?	conical
Aciculae: shape, color	blunt, dark	blunt, dark	blunt, dark	blunt, dark
Subacicular limbadate chaetae: (p/a)	absent	absent	absent	absent
Subacicular limbadate chaetae: distribution	-	-	-	-
Pectinate chaetae: types	INLS; IWLS; AWLS	INLS; IWSS; AWLS	INSS; IWLS; IWSS; IWLT; AWLT	INLS; IWSS; AWSS; AWLS
Pectinate chaetae: shalf	thin; thick; thick	thin; thick; thick	thin; tick; thin; thick; thick	thin; thick; thick
Isodont pectinate chaetae blade	sym; asym; asym	asym; asym; sym	sym; sym, asym; ?; sym	asym; sym; sym; asym
Pectinate chaetae: number per type pectinate	1–2; 16–17; 4–5	1–2; 18–20; 4–5	?	1–3; 2–3; 4–5; 3–4
Pectinate chaetae teeth: number per type pectinate	18; 25; 15–17	10; 18; 10–12	12–16; 16; 14; 4–6	12–14; 20; 20–26; 11
Spiniger blade: length in anterior region	2 lengths	2 lengths	?+S36:X36	2 lengths

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TABLE 1. (Continued)

Morphological features	*M. tripectinata* Liu, Hutchings & Sun, 2017	*M. sanguinea* (Montagu, 181	*M. victori* Lavesque, Daffe, Bonifácio & Hutchings, 2017	*M. viridis* Treadwell, 1917
Spiniger blade: length in median–posterior region	2 lengths	2 lengths	?	2 lengths
Subacicular hook: initial chaetiger	62–115	74–286	absent	21 – 42
Subacicular hook: shape, color	bidentate, reddish basally and translucent distally	bidentate, reddish basally and translucent distally	?	bidentate, amber
Aciculae vs Subacicular hook: proportion	SH 2 times shorter	SH 2 times shorter	?	SH 2 times shorter
Subacicular hook: distribution	discontinuous	discontinuous	?	discontinuous

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