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Unravelling the convoluted nomenclature of *Marphysa simplex* (Annelida, Eunicidae) with the proposal of a new name and the re-description of species

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Abstract

Marphysa simplex is a name that three species bear within the same genus, but each has a different authority and morphological characteristics. This homonymy condition leads to taxonomic confusion and the finite designation of name-bearing is imperative. The current study focuses on two species identified as *M. simplex* Crossland, 1903 and *M. simplex* Treadwell, 1922 and a third one, recently considered a secondary homonymy, *M. simplex* (Langerhans, 1884), is also assessed. The available type specimens were examined and re-described in detail using updated characters and the original descriptions. *Marphysa simplex* (Langerhans, 1884) is herein judged as an indeterminable species. *Marphysa simplex* Crossland, 1903 is confirmed as a junior synonym of *M. teretiuscula* (Schmarda, 1861a) because the differences are minimal. Moreover, *M. teretiuscula* has characteristics similar to Group B2 (Sanguinea-group; only compound spinigers), instead of the Teretiuscula-group (compound spinigers in the anterior region, subacicular limbate in all chaetigers). On the other hand, *M. simplex* Treadwell, 1922 is a junior primary homonym of Crossland's species replaced by *M. fijiensis* **nom. nov.** with the chaetal arrangement similar to Group A (limbate chaetae only). In conclusion, the name *M. simplex* is now unacceptable. The hypothesis on species group only with limbate chaetae and the redescription on *M. teretiuscula* is also given.

Key Words

Homonymy, limbate chaetae, morphological review, synonymy, type material

Introduction

Within the long story of *Marphysa* de Quatrefages, 1865, the name *M. simplex* has been referred to in several homonymy cases since three species worldwide bear this name: *Marphysa simplex* Crossland, 1903, *M. simplex* Treadwell, 1922 and *M. simplex* (Langerhans, 1884). Simultaneously, the names *M. simplex* Crossland, 1903 and Treadwell 1922 have been used as synonymies of two other *Marphysa* species (Glasby and Hutchings 2010). In this study, we provide an analysis of these taxonomic issues.

The name *M. simplex* was firstly used by Crossland (1903) for two specimens from Zanzibar (Tanzania). Although Crossland proposed a new name, he also stated that his specimens resemble *M. teretiuscula* (Schmarda, 1861a) from Sri Lanka because both species are present in the Indian Ocean. Nonetheless, he could not make an accurate comparison because Schmarda's description was short and poorly illustrated (Crossland 1903; Glasby and Hutchings 2010).

About two decades later, Treadwell (1922) described a new species, *M. simplex*, based on one specimen found together with *M. macintoshi* Crossland, 1903 in Suva

Harbour, Fiji. Even though Treadwell knew about Crossland's contributions, it is uncertain why he used an already established name for his new species.

Later, a third species with the same name appeared as a secondary homonym (ICZN 1999, Art. 57.3). Langerhans (1884) described *Amphiro simplex*, based on a single specimen from Madeira (Portugal). *Amphiro* Kinberg, 1865 was considered a junior synonym of *Marphysa* by Hartman (1949); therefore, the species described in that genus became part of *Marphysa*, including Langerhans' species.

The three species named *M. simplex* differ in morphology and can be classified into three of the informal groups proposed by Fauchald (1970). Crossland's specimens belong to *Marphysa* B2 group (with compound spinigers only), Treadwell's specimens belong to A group (without compound chaetae) and Langerhans's species to group C (with compound falcigers only).

Currently, the species *M. simplex* (Langerhans) is considered indeterminable by Molina-Acevedo and Idris (accepted, but not yet published) since the type material is lost and the original description lacks enough diagnostic characters for comparison, even if new topotypes are found. The other two species of *M. simplex* were accepted as synonyms of different *Marphysa* species. Glasby and Hutchings (2010), who commented about these homonymies, considered *M. simplex* Crossland a junior synonym of *M. teretiuscula* following Crosland's comments regarding the similarity and also because the body shape and the length of the peristomial appendages were consistent between both species. Likewise, Glasby and Hutchings (2010) synonymised *M. simplex* Treadwell with *M. mossambica* (Peters, 1854) because the only differences between both species were size-related variations.

In the present study, we confirm the synonymy of *M. simplex* Crossland and *M. teretiuscula* after a detailed evaluation of the type material. However, we propose the re-establishment of *M. simplex* Treadwell, as it is distinguished morphologically from *M. mossambica*. Since *M. simplex* Treadwell is a primary homonym of Crossland's species (ICZN 1999, Art. 53.3) and therefore no longer valid, we hereby replace Treadwell's name by erecting *Marphysa fijiensis* nom. nov. (ICZN 1999, Art. 60.3). Likewise, we provide re-descriptions of *M. teretiuscula* and *M. fijiensis* nom. nov., based on the type materials, some observations regarding group A (Fauchald 1970) and a group of *Marphysa* species with compound spinigers and subacicular limbate chaetae (Glasby and Hutchings 2010). Comparative Tables with species similar to *M. fijiensis* nom. nov. and *M. teretiuscula* are included.

Material and methods

The materials reviewed in this study were deposited in the following institutions: American Museum of Natural History, New York, USA (AMNH), Australian Museum (AM), The Natural History Museum, London (BNHM), Natural History Museum, Vienna, Austria (NHMW), National Museum of Natural History, Smithsonian Institution, Washington D.C., USA (USNM) and Museum of Natural History, Berlin, Germany (ZMB).

The re-descriptions of species were illustrated with digital photographs. A series of photos were stacked using HeliconFocus 6 (Method A) software to improve the depth of field and the final images were edited and assembled into plates using Adobe Photoshop 2020. The re-descriptions include: prostomium, body, branchiae, maxillary apparatus, parapodia, compound chaetae and simple chaetae. The terminology to describe the overall morphology of characters followed those recently provided by Molina-Acevedo and Carrera-Parra (2015, 2017), Zanol et al. (2016) and Molina-Acevedo (2018). Paired and unpaired maxillae were indicated as 'M' followed by a Roman number (e.g. MI, MII). The maxillary apparatus and the pectinate chaetae were described according to Molina-Acevedo and Carrera-Parra (2015, 2017) and Zanol et al. (2016), respectively. In addition, the definition of long and short branchial filaments, proposed by Molina-Acevedo and Idris (2020), is followed. Three or five parapodia per species were dissected to compare the different shapes of the parapodial cirri, lobes and chaetae throughout the body.

Some specimens studied were posteriorly incomplete; hence, morphological measurements for the length up to chaetiger 10 (L10) and width at chaetiger 10 (W10), excluding parapodia, were used as a size estimate of an individual worm. Additionally, the total length (TL) and the total number of chaetigers (TChae), the chaetiger number and side (R for right, L for left) from which branchiae and subacicular hooks emerged, were also recorded. Furthermore, for specimens from *M. teretiuscula*, linear regression analyses were included to evaluate the relationships between L10, W10 and several morphological features, including the starting of branchiae and subacicular chaetae and the last chaetiger with developed postchaetal lobe. The degree of predictability of variation (coefficient of determination) in the features according to the sizes is given as R^2 (e.g. $R^2 = 0.7$, $p = 0.05$, n = 8).

Results

Systematic

Order Eunicida Dales, 1962
Family Eunicidae Berthold, 1827
Genus *Marphysa* de Quatrefages, 1865

***Marphysa fijiensis* nom. nov.**

Figures 1–4, Table 1

Marphysa simplex Treadwell, 1922: 151–152, pl. 5, figs 8–12, text-figs 39 (*non* Crossland, 1903); –Hartman 1956: 254, 262, 268, 286.

Material examined. Holotype. Fiji · Suva Harbour; Apr–Jun, 1920; AMNH 1920–1530.

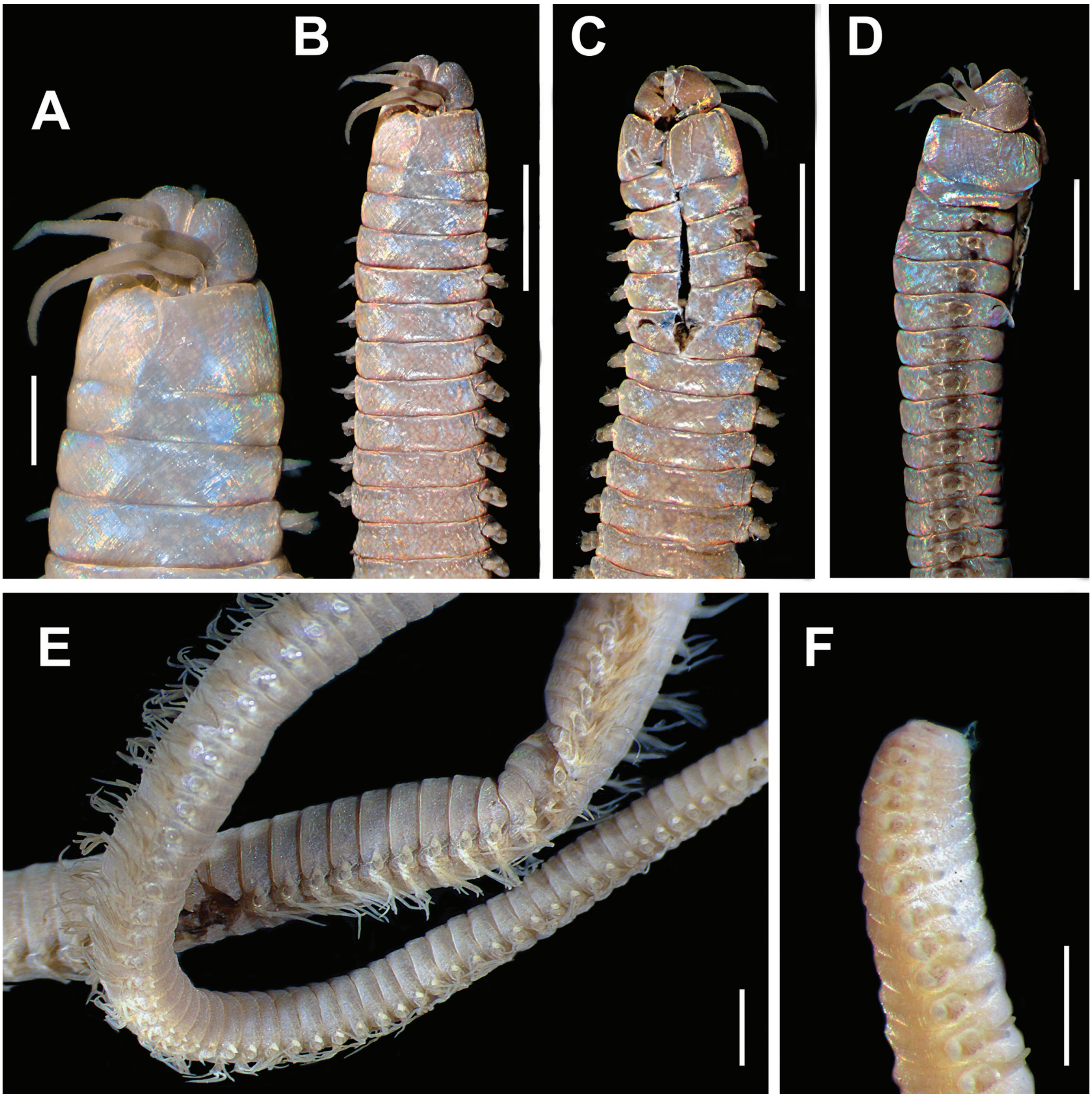

Figure 1. *Marphysa fijiensis* nom. nov., holotype (AMNH 1920–1530). **A, B.** Anterior end, dorsal view; **C.** Anterior end, ventral view; **D.** Anterior end, lateral view; **E.** Median region, lateral and ventral views; **F.** Pygidium, lateral view. Scale bars: 0.35 mm (**A**); 2 mm (**B–D**); 0.5 mm (**E, F**).

Comparative material examined.

Eunice mossambica Peters, 1854

MOZAMBIQUE · one specimen and vial with six parapodia; **lectotype** ZMB 4005 · 3 adult specimens, same data as for the lectotype; **paralectotypes** ZMB 47 · one specimen; same data as for the lectotype; ZMB F2046 · seven adult specimens; same data as for the lectotype; ZMB 4005.

Marphysa moribidii Idris, Hutchings & Arshad, 2014

MALAYSIA · two adult specimens; Pantai Kelanang, Morib, Selangor; 2°45'39.85"N, 101°26'08"E; in mangrove vegetation; 19 Jul 2011; I. Idris leg.; **paratype** AM W.38690.

Nauphanta novaehollandiae Kinberg, 1865

AUSTRALIA · one specimen divided into four vials, one of them with maxillary apparatus; Sydney Port Jackson; 33°54'S, 151°11'E; Eugenie Epx. 1851–53; **holotype** SMNH-type-432.

Etymology. The new name denotes the geographic region where the specimen was collected.

Description. Holotype complete (Fig. 1A–F), ventrally dissected (Fig. 1C), with 198 chaetigers, L10 = 8.2 mm, W10 = 2.5 mm, TL = 93 mm. Anterior region with dorsum convex, flat ventre, body depressed from

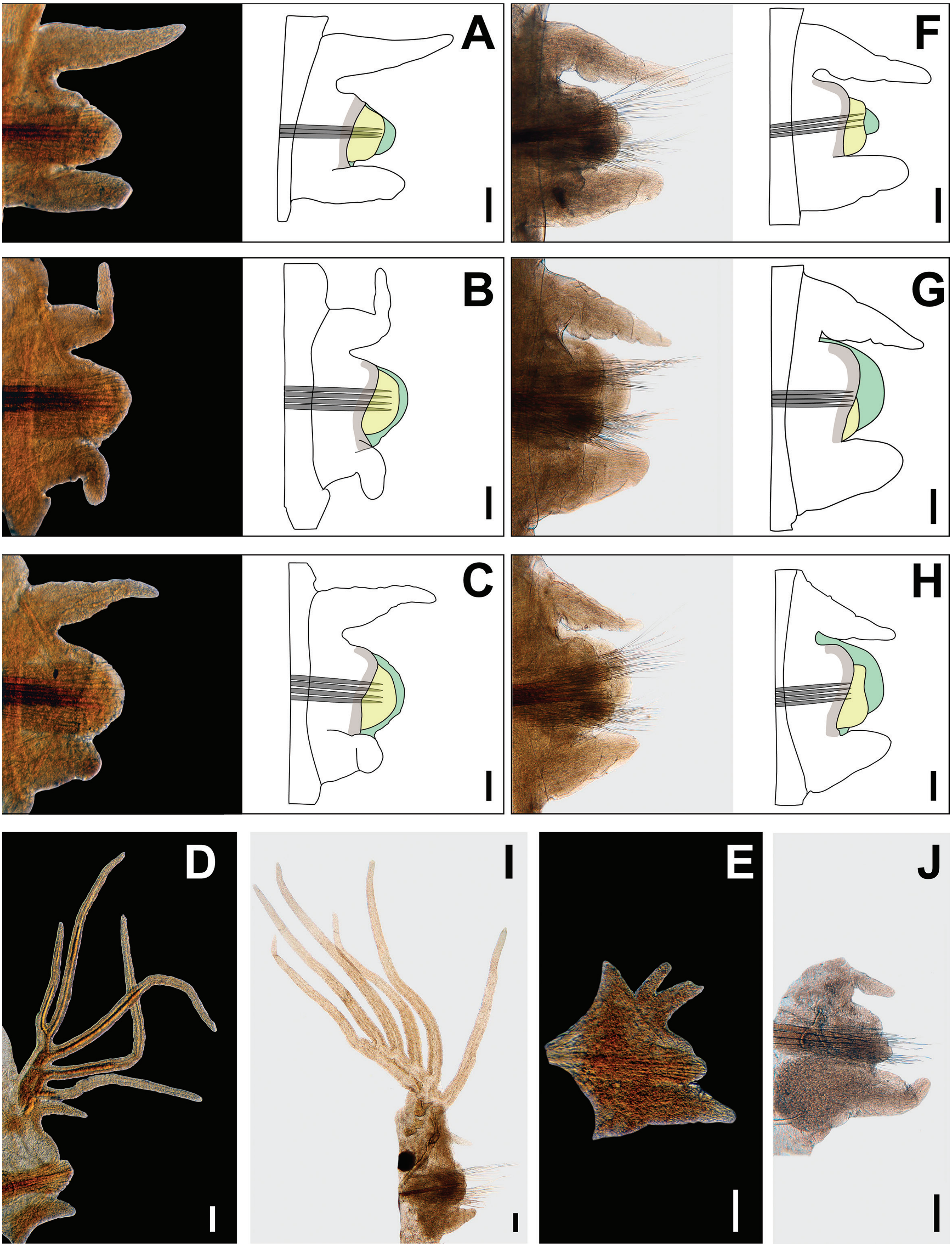

Figure 2. *Marphysa fijiensis* nom. nov., holotype (AMNH 1920–1530). **A.** Chaetiger 3; **B.** Chaetiger 8; **C.** Chaetiger 14; **D.** Chaetiger 123; **E.** Chaetiger 188. *Marphysa mossambica* (Peters, 1854), lectotype (ZMB 4005a). **F.** Chaetiger 3; **G.** Chaetiger 8; **H.** Chaetiger 15; **I.** Chaetiger 293; **J.** Chaetiger 398. All chaetigers in anterior view. The colours in drawings indicate the prechaetal (light brown), chaetal (light yellow) and postchaetal (light green) lobes. Scale bars: 0.1 mm (**A–E**); 0.2 mm (**F–J**).

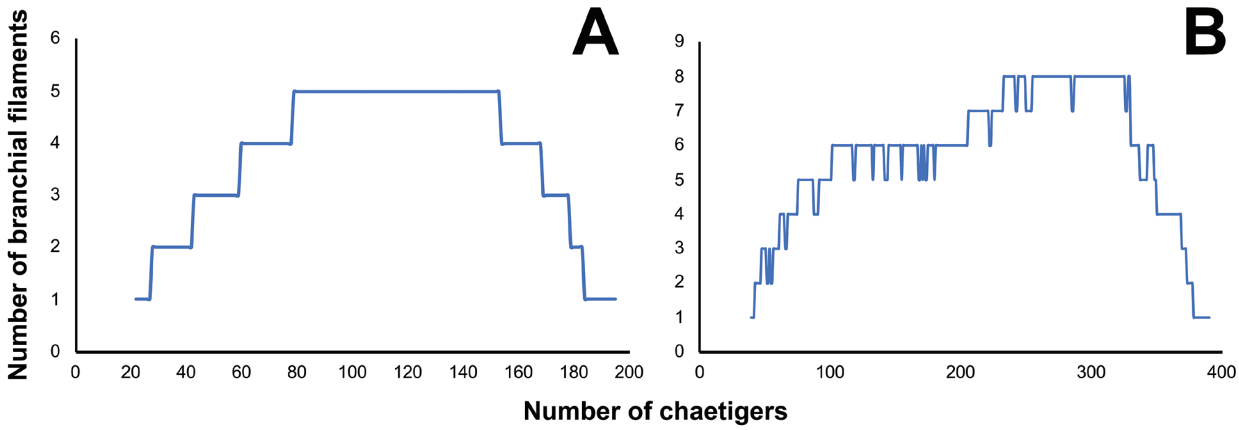

Figure 3. Distribution of branchial filaments throughout the body. **A.** Holotype of *Marphysa fijiensis* nom. nov. (AMNH 1920–1530) with L10: 8.2 mm, TL: 93 mm and 198 chaetigers; **B.** Paralectotype of *Marphysa mossambica* (Peters, 1854) (ZMB 47) with L10: 10.3 mm, TL: 290 mm and 429 chaetigers.

chaetiger 6 (Fig. 1D), widest at chaetiger 17, tapering after chaetiger 41.

Prostomium bilobed, 1.3 mm long, 1.6 mm wide; lobes frontally rounded; median sulcus shallow and deep ventrally (Fig. 1A, B). Prostomial appendages in semicircle, median antenna isolated by a gap. Palps reaching second peristomial ring; lateral antennae reaching first chaetiger; median antenna reaching second chaetiger. Palpophores and ceratophores ring-shaped, short, slender; palpostyles and ceratostyles tapering, thick. Eyes absent.

Peristomium (1.7 mm long, 2.3 mm wide) larger than prostomium, first ring twice as long as second ring, separation between rings distinct on all sides (Fig. 1A–C). Ventral lip dissected, with several shallow wrinkles (Fig. 1C).

Maxillary apparatus lost, according to Treadwell with MF = 1+1, 5+5–6, 9+0 2+8, 1+1.

Branchiae pectinate with up to five long filaments, from chaetigers 22 to 184L–195R (Figs 1E, 2D, E). Six first branchiae with one filament; reaching maximum five filaments in chaetigers 79L–178L; last 12 branchiae with one filament (Fig. 3A). Branchial filaments longer than dorsal cirri, except in first six and last 10 branchiae.

First two parapodia smaller; best developed in chaetigers 4–21, following parapodia gradually decreasing in size. Dorsal cirri conical in all chaetigers; longer than ventral cirri in anterior and posterior chaetigers, of similar size in median chaetigers; best developed in chaetigers 3–30, gradually decreasing posteriorly (Fig. 2A–E). Prechaetal lobes short, as transverse folds in first three chaetigers, following lobes with upper edge longer than lower; transverse folds in most posterior chaetigers (Fig. 2A–E). Chaetal lobes rounded in most chaetigers, shorter than postchaetal lobe, with aciculae emerging dorsal to mid-line; from chaetiger 33, longer than other lobes, aciculae emerging in mid-line (Fig. 2A–E). Postchaetal lobes slightly developed in first 55 chaetigers; ovoid in first two chaetigers, rounded in the following ones, progressively smaller from chaetiger 14; from chaetiger 56 inconspicuous (Fig. 2A–E). Ventral cirri digitiform in first 13 chaetigers; in chaetigers 14 to 126 with rounded, poorly developed swollen base and digitiform tip; conical from chaetiger 127, gradually decreasing in size posteriorly (Fig. 2A–E).

Aciculae blunt, basally reddish and translucent distally; colourless in posterior chaetigers (Fig. 2A–E). First two chaetigers with two aciculae; in chaetigers 3–10 with three or four aciculae; in chaetigers 11–24 with four aciculae; in chaetigers 25–43 with three aciculae; in chaetigers 44–85 with two aciculae; from 86 with only one acicula. In median-posterior region, aciculae twice as wide as subacicular hook (Fig. 4F, G).

Limbate chaetae in supra- and subacicular positions. Limbate supracicular chaetae reduced in number around chaetiger 16, chaetae of two lengths in same chaetiger, with longer blades in dorsal position and with short blades in ventral position. Limbate subacicular of two lengths, with short blades in dorsal position and with longer blades in ventral position (Fig. 4A, B). Two types of pectinate chaetae; in all chaetigers, 2–3 thick isodont narrow chaetae, with up to 16–18 teeth short and slender teeth (Fig. 4C); in median-posterior chaetigers, 4–5 thick isodont wide chaetae, with up to 38–42 teeth short and slender teeth (Fig. 4D, E); anodont pectinate chaetae not observed. Compound chaetae absent. Subacicular hooks starting from chaetigers 38R–39L, one per chaetiger, with discontinuous distribution, in last 25 chaetigers, the hooks are absent; unidentate in median region with one hood (possibly with second hood broken) (Fig. 4F); bidentate in median-posterior region, translucent, with blunt teeth, distal tooth directed upwards, proximal tooth larger, directed laterally (Fig. 4G).

Pygidium with two pairs of anal cirri broken (Fig. 1F).

Distribution. Known only from the type locality.

Habitat. Uncertain. Possibly coral reefs or mudflats (Treadwell 1922).

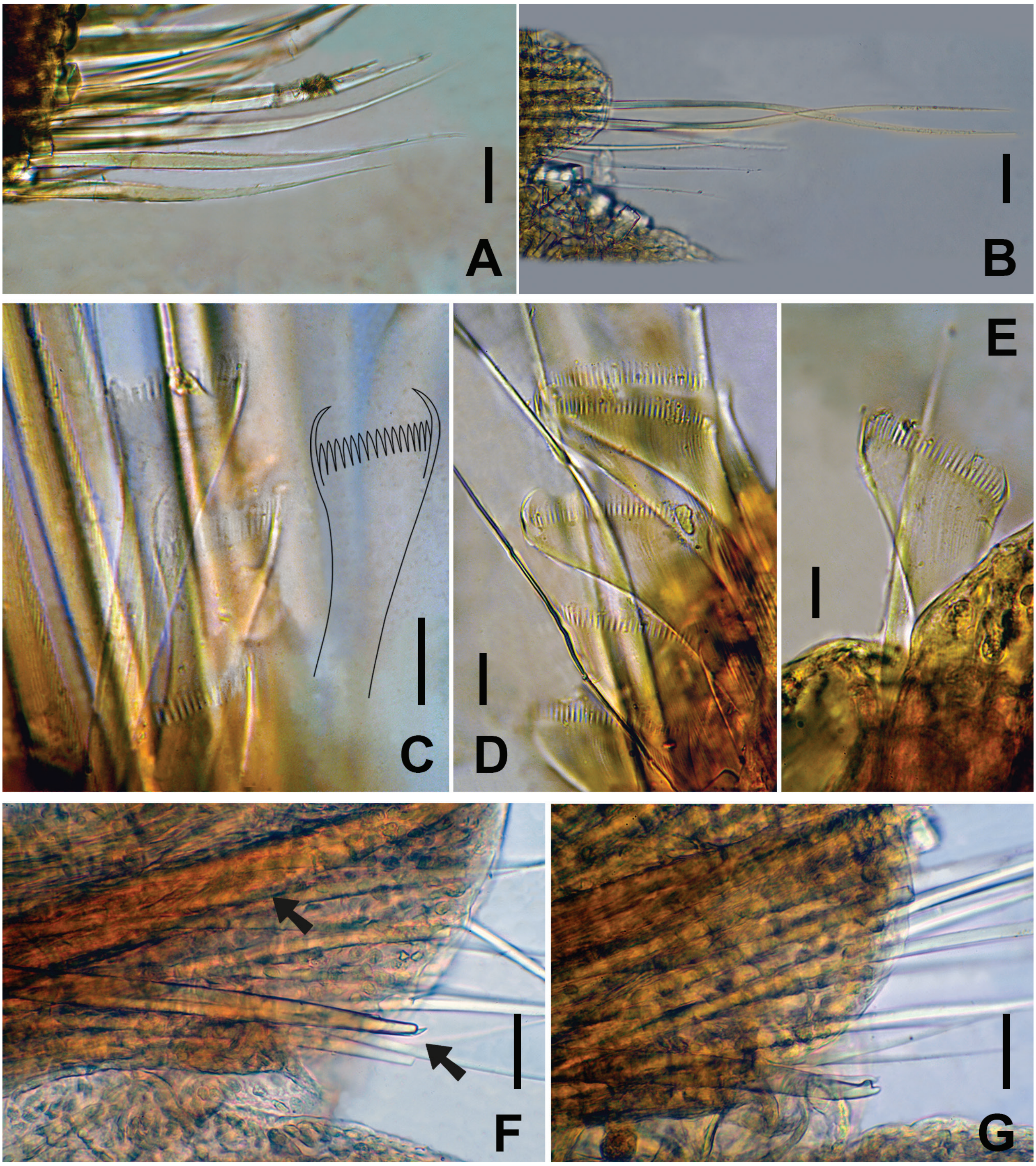

Figure 4. *Marphysa fijiensis* nom. nov.**,** holotype (AMNH 1920–1530). **A.** Limbate chaetae, chaetiger 8; **B.** Limbate chaetae, chaetiger 188; **C.** Thick isodont narrow, with short and slender teeth, chaetiger 3; **D.** Thick isodont wide with short and slender teeth, chaetiger 152; **E.** Thick isodont wide with short and slender teeth, chaetiger 188; **F.** Unidentate subacicular hook, chaetiger 123; Bidentate subacicular hook, chaetiger 152. Arrows in F: upper one indicates the acicula; lower one indicates the hood of the subacicular hook. Scale bars: 40 µm (**A, B, F, G**); 12.5 µm (**C–E**).

Remarks. The first comment on the synonymy of *Marphysa fijiensis* nom. nov. (as *M. simplex* Treadwell, 1922) and *M. mossambica* was made by Hartman (1956). Subsequently, Glasby and Hutchings (2010) supported this idea, stating that the morphology described by Treadwell was very similar to the smaller-sized specimens of *M. mossambica*. However, after a detailed morphological comparison of both species' type material, we found marked differences. *Marphysa fijiensis* nom. nov. lacks eyes, whereas they are present in *M. mossambica*. Additionally, *M. fijiensis* nom. nov. (L10: 8.2 mm) has a maximum number of five branchial filaments in the median region (Fig. 3), whereas *M. mossambica* (L10:8.5–11.5 mm), has a maximum number of eight branchial filaments in the mid-posterior region (Fig. 3). In *M. fijiensis* nom. nov., the chaetal lobe is rounded in the anterior region and the postchaetal lobe is oval in the first three

Table 1. Morphological features of *Marphysa* group A sensu Fauchald (1970). 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; IWSS: Isodont wide with short and slender teeth; IWLS: Isodont wide with long and slender teeth; AWLT: Anodont wide with long and thick teeth.

Morphological feature	*M. moribidii* Idris et al., 2014	*M. mossambica* (Peters, 1854)	*M. novaehollandiae* (Kinberg, 1865)	*M. fijiensis* nom. nov.
Source of information	paratypes AM W. 38690; additional material	lectotype ZMB 4005a; paralectotypes ZMB 47; ZMB F2046, ZMB 4005	holotype SMNH-type-432; AM W.33021	holotype AMNH 1920–1530
Size (mm): L10, W10	12.2–20, 6.3–8.2	8–11.5, 3.6–8.1	6.6–9.6, 4–4.2	8.2, 2.5
Prostomium: shape	bilobed	bilobed	bilobed	bilobed
Palps: reaching	PR–II	PR–II or Chaet 1	PR–II	PR–II
Lateral antennae: reaching	PR–II or Chaet 1	middle Chaet 1 or 2	middle Chaet 1	Chaet 1
Median antennae: reaching	Chaet 1 or 2	Chaet 2 or 3	middle Chaet 2	Chaet 2
Peduncle in prostomial appendages	present	absent	absent	absent
Eyes	absent	present	present	absent
MF: MII, MIII, MIV	5–6+4–6, 7–8, 6+8–10	5+5–6, 6–7, 3–4+8–9	4–5+6, 7, 5+8–9	5+5–6, 9, 2+8
MI vs. MxC: proportion	2.4–2.8× longer than MxC	2–3× longer than MxC	2.4–3.2× longer than MxC	?
MI vs. CIS: proportion	4.3–5.7× longer than CIS	5–7× longer than CIS	4.4–8× longer than CIS	?
MII vs. COp: proportion	4.3–4.7× longer than COp	3.2–4× longer than COp	4.5–5.3× longer than COp	?
Branchiae: shaped	pectinate	pectinate	pectinate	pectinate
Branchiae: start chaetiger; last chaetiger before pygidium	27–39; 15–37	23–48; 29–126	21–25; 15	22; 3
Branchial filaments: numbers; length of the filaments	7–10; long	7–8; long	6–7; long	5; long
Dorsal cirri: shaped	conical	conical with wide base	conical	conical
Prechaetal lobe: shaped	transverse fold	AR: upper edge longer than lower, MR, PR: transverse fold	AR, MR: upper edge longer than lower, PR: transverse fold	AR, MR: upper edge longer than lower, PR: transverse fold
Chaetal lobe: shaped	rounded	AR: rectangular MR, PR: rounded	AR, MR: rectangular, PR: rounded	rounded
Developed postchaetal lobe: end chaetiger	50–96	27–70	32–38	55
Postchaetal lobe: shape in body regions	Chaet 4: digitiform short, Chaet 4–10, 10: rounded	Chaet 4: digitiform short, Chaet 4–10, 10: rounded	Chaet 4: ovoid, Chaet 4–10, 10: rounded	Chaet 4: ovoid, Chaet 4–10, 10: rounded
Ventral cirri in first chaetigers: shape	digitiform	digitiform	digitiform	digitiform
Ventral cirri with swollen base: start chaetiger; last chaetiger before pygidium	6; 62–96	7–9; 96–208	8; 41	14; 72
Ventral cirri in most posterior chaetigers: shape	conical	conical	conical	conical
Aciculae: shape; colour	blunt, dark	blunt, dark	blunt, dark	blunt, dark
Subacicular limbate chaetae: (p/a); distribution	present; all chaet	present; all chaet	present; all chaet	present; all chaet
Pectinate chaetae: type in AR; MR, PR	INLS; IWSS, IWLS, AWLT	INLS; IWSS, IWLS, AWLT	INLS; IWSS, IWLS, ?	INSS; IWSS
Pectinate chaetae: number per type	1–2; 3–4, 1–2, 1–2	1–2; 2–3, 2–3, 1–2	1–2; 1–2, 3–4; ?	2–3; 4–5
Pectinate chaetae teeth: number per type	18; 52, 26, 7	18–19; 56, 27, 9–10	25; 50–51, 35; ?	16–18; 38–42
Subacicular hook: start chaetiger	56–65	35–65	39–42	38
Subacicular hook: shape; colour	bidentate, translucent	bidentate, translucent	bidentate, translucent	MR: unidentate, PR: bidentate, translucent
Width acicula vs. SH in MR-PR: proportion	similar width	Acicula 2× wider than SH	Acicula 2× wider than SH	Acicula 2× wider than SH
Subacicular hook: distribution	discontinuous	discontinuous	discontinuous	discontinuous

chaetigers. In contrast, in *M. mossambica*, the chaetal lobe is rectangular in the anterior region and the postchaetal lobe is digitiform in the first three chaetigers. Likewise, *M. fijiensis* nom. nov. has the subacicular hook present from chaetiger 25, contrasting to chaetigers 35–65 in *M. mossambica*.

Marphysa fijiensis nom. nov. resembles *M. moribidii* Idris, Hutchings & Arshad, 2014 and *M. novaehollandiae* (Kinberg, 1865) in lacking compound chaetae. However, *M. fijiensis* nom. nov. lacks the peduncle in prostomial appendages, with swollen base in ventral cirri starting from chaetiger 14 and the acicula is twice as wide as the subacicular hook in the median-posterior region. In contrast, *M. moribidii* (L10: 12.2–20 mm) has a peduncle at the base of the palpo- and ceratostyles, bears ventral cirri with a swollen base starting from chaetiger 6 and has a subacicular hook similar in width to the acicula throughout the body. Furthermore, *M. fijiensis* nom. nov. has the prechaetal lobe as a transverse fold throughout the body, the chaetal lobe rounded throughout the body, the ventral cirri with a swollen base starting from chaetiger 14 and the subacicular hook starting from chaetiger 25; while *M. novaehollandiae* (L10: 6.6–9.6 mm) has the prechaetal lobe with dorsal edge longer than the ventral side in the first chaetigers, the chaetal lobe rectangular in the anterior region, the ventral cirri with a swollen base starting from chaetiger 8 and the subacicular hook starting from chaetigers 39–42. The comparison of *M. fijiensis* nom. nov. with related species is provided in Table 1.

Marphysa teretiuscula **(Schmarda, 1861a)**

Figures 5–9, Table 2

Eunice teretiuscula Schmarda, 1861a: 129, pl. 32, fig. 59, text-figs a–d, f, OK, UK; Grube 1878: 59.

Marphysa teretiuscula – de Quatrefages 1866: 337; Ehlers 1868: 359; Crossland 1903: 136; – Hartman 1959: 332; – Glasby and Hutchings 2010: 32, 40–41, table 2; Liu et al. 2017: 244–247, table 3; – Liu et al. 2018: 210–211, table 1.

Marphysa simplex Crossland, 1903: 140–141, pl. 15, figs. 11–12, text-fig. 13.

Material examined.

Eunice teretiuscula Schmarda, 1861a

Sri Lanka · two specimens, one of them missing anterior end; Trincomalee, east of Sri Lanka; May 1853 to Jan 1854; L.K. Schmarda leg.; **syntypes** NHMW type 1092.

Marphysa simplex Crossland, 1903

Zanzibar · two adult specimens; 11 Jan 1934; Murray Exped. St. 104, Petersen Grab, V.310, 207 m; **syntypes** BNHM type 1937.9.2.325.

Other material.

Marphysa teretiuscula (Schmarda, 1861a)

Mozambique · two specimens; Morrumbene Estuary; 16 Jan 1954; BNHM 1955.4.1.21-25.

India · one specimen; Ratnagiri Creek, Shirgaon, Maharashtra; 17°17'13.78"N, 73°17'13.87"E; 18 Apr 1994; USNM 1128572 · one specimen; same data as for preceding; USNM 1128570.

Comparative material examined.

Marphysa furcellata Crossland, 1903

Zanzibar · two specimens; 1901; between tidemarks, 27.4 m; C. Crossland leg.; **syntypes** BNHM 1924.3.1.139.

Marphysa macintoshi Crossland, 1903

Zanzibar · three specimens; 1901–1902; collected by digging in sand between tidemarks on both east and west coast of Zanzibar; **syntypes** BNHM 1924.3.1.22-3, slide BNHM.1924.3.1.22A.

Description. Syntype NHM type 1092 incomplete, gravid female, with 210 chaetigers, L10 = 9.3 mm, W10 = 5 mm TL = 860 mm (Fig. 5A–C). Anterior region with dorsum convex, flat ventre (Fig. 5C, E); body depressed from chaetiger 13 (Fig. 5C, E), widest at chaetiger 51, tapering after chaetiger 173.

Prostomium bilobed, 4 mm long, 2.5 mm wide; lobes frontally rounded; median sulcus (Fig. 5A, B, D) shallow and deep ventrally. Prostomial appendages in semicircle, median antenna isolated by a gap. Palps reaching second chaetiger; lateral antennae reaching middle of third chaetiger; median antennae reaching fourth chaetiger. Palpophores and ceratophores ring-shaped, short, thick; palpostyles and ceratostyles tapering, slender. On right side with two palpostyle in the same palpophore (Fig. 5C). Eyes oval, brown, between palps and lateral antennae.

Peristomium (2 mm long, 5.2 mm wide) wider than prostomium, first ring twice as long as second ring, separation between rings distinct on all sides (Fig. 5A–E). Ventral lip with slight central depression, with several shallow wrinkles (Fig. 5B).

Maxillary apparatus with MF = 1+1, 4+4, 5+0, 5+7, 1+1 (Fig. 5H). MI three times longer than length of maxillary carriers. MI forceps-like, MI four times longer than closing system (Fig. 5H, I); sclerotised ligament between MI and MII. MII wider than rest of maxillae, with triangular teeth; MII 3.2 times longer than cavity opening (Fig. 5H); ligament between left MII–MIII and right MII–MIV, slightly sclerotised. MIII with triangular teeth; with irregular attachment lamella, situated in centre of ventral edge of maxilla, slightly sclerotised (Fig. 5I). Left MIV with two teeth larger than rest of teeth; attachment lamella semicircle, wide, better developed in right portion, situated 2/3 along anterior edge of maxilla (Fig. 5J). Right MIV with four teeth larger than rest of teeth; attachment lamella semicircle, wide, better developed in central portion, situated 2/3 along anterior edge of maxilla (Fig. 5K). MV square, with a short triangular tooth. Mandibles dark; with calcareous cutting plates; sclerotised cutting plates brown, with nine growth rings (Fig. 5L).

Branchiae from chaetiger 32, with up to five long filaments; with two forms: palmate with short button-shaped branchial stem in anterior chaetigers (Fig. 6F, H), pectinate in median chaetigers (Fig. 6G). In second syntype, branchiae ending 25 chaetigers before pygidium. One filament in chaetigers 32L–34L; 2 in chaetigers 35L–39L; 3 in chaetigers 40L–48L; 3, 4 or 5 from chaetiger 49L to last chaetiger of the fragment. In second syntype, last 18 branchiae with one filament. Branchial filaments longer than dorsal cirri.

First pair of parapodia small; best developed in chaetigers 11–56, following parapodia gradually decreasing in size. Dorsal cirri conical in all chaetigers; longer than ventral cirri in anterior and posterior chaetigers, shorter in median chaetigers; best developed in chaetigers 3–37, following gradually decreasing in size (Fig. 6A–K). Prechaetal lobes short, in anterior chaetigers dorsal edge longer than ventral, in median-posterior chaetigers, as transverse

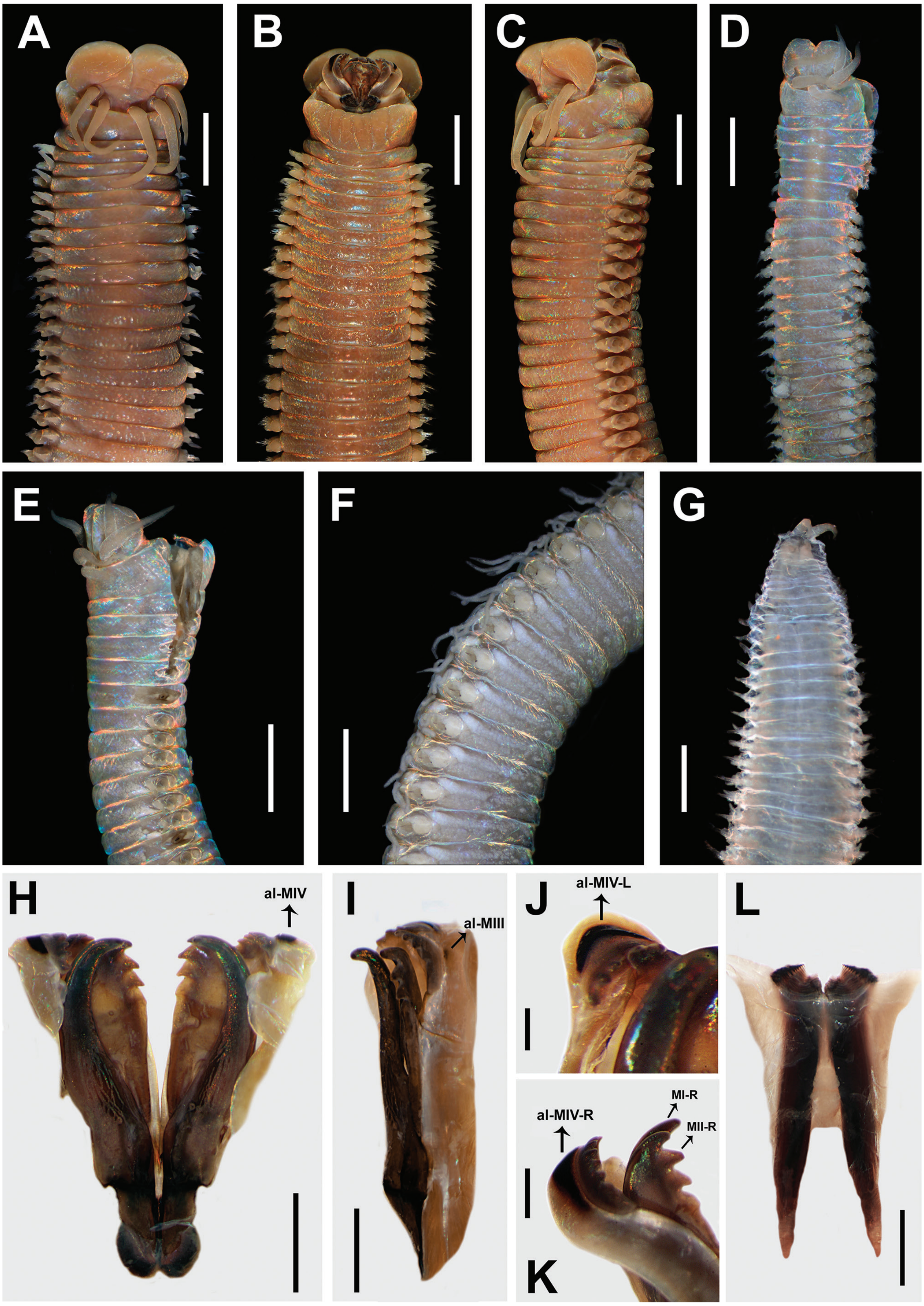

Figure 5. *Marphysa teretiuscula* (Schmarda, 1861a). **A.** Anterior end, dorsal view; **B.** Anterior end, ventral view; **C.** Anterior end, lateral view; **D.** Anterior end, dorsal view; **E.** Anterior end, lateral view; **F.** Median region, ventral view; **G.** Pygidium, dorsal view; **H.** Maxillary apparatus, dorsal view; **I.** Left MI-II-III-IV-V, lateral view; **J.** Attachment lamella in left side, dorsal view; **K.** Attachment lamella in right side, lateral view; **L.** Mandible, ventral view. **A–C, H–L.** from *M. teretiuscula* (Schmarda, 1861) syntype 1 (NHMW type 1092); **D–G.** from *Marphysa simplex* Crossland, 1903 syntype 1 (BNHM 1955.4.1.21-25). al-MIII: attachment lamella MIII; al-MIV: attachment lamella MIV; al-MIV-L: attachment lamella MIV on left side; al-MIV-R: attachment lamella MIV on right side; MI-R: Maxilla I on right side; MII-R: Maxilla II on right side. Scale bars: 2.3 mm (**A–C**); 3.1 mm (**D–F**); 1.16 mm (**G**); 3.0 mm (**H, I, L**); 1.13 mm (**J**); 0.9 mm (**K**).

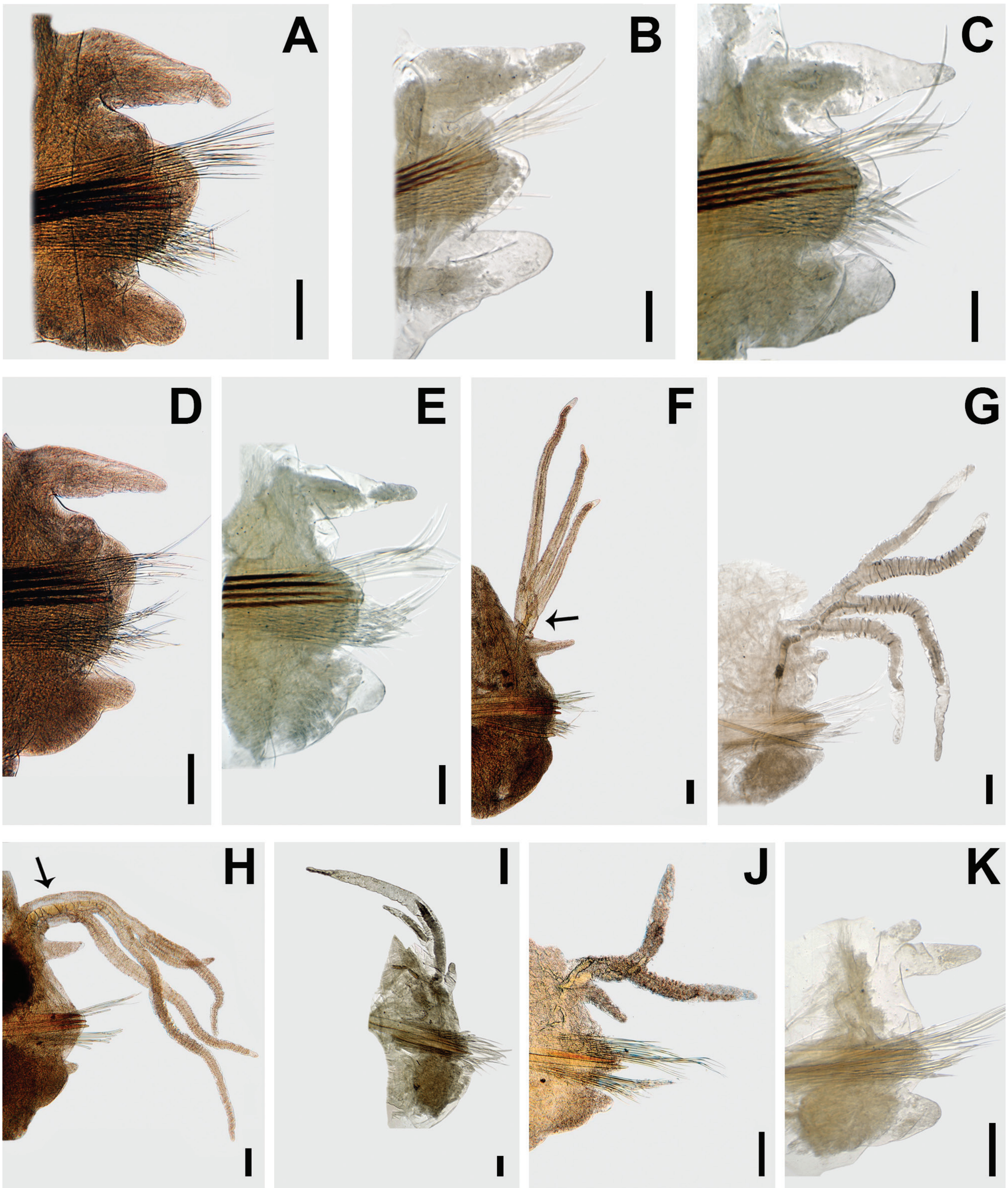

Figure 6. *Marphysa teretiuscula* (Schmarda, 1861a). **A, B.** Chaetiger 3; **C.** Chaetiger 7; **D.** Chaetiger 12; **E.** Chaetiger 14; **F.** Chaetiger 47; **G.** Chaetiger 97; **H.** Chaetiger 143; **I.** Chaetiger 162; **J.** Chaetiger 44 before pygidium; **K.** Chaetiger 256. All chaetigers in anterior view. **A, D, F, H.** from *M. teretiuscula* (Schmarda, 1861a) syntype 1 (NHMW type 1092); **J.** from *M. teretiuscula* (Schmarda, 1861a) syntype 2 (NHMW type 1092); **B, C, E, G, I, K.** from *Marphysa simplex* Crossland, 1903 syntype 1 (BNHM 1955.4.1.21-25). Arrows in **F, H.** indicate the button-shaped branchial stem. Scale bars: 0.2 mm (**A, D, F, H, J**); 0.1 mm (**B, C, E, G, I, K**).

fold (Fig. 6A–K). Chaetal lobes rounded in first 35 chaetigers, shorter than other lobes, with aciculae emerging dorsal to mid-line; triangular from chaetiger 36, longer than other lobes, with aciculae emerging in mid-line (Fig. 6A–K). Postchaetal lobes well developed in first 56 chaetigers; ovoid with dorsal edge longer than ventral edge in following chaetigers; progressively smaller from chaetiger 19; from chaetiger 57, inconspicuous (Fig. 6A–K). Ventral cirri conical in first five chaetigers; from chaetiger 6 to last chaetiger of fragment with short oval swollen base and digitiform tip (Fig. 6A–K). Second syntype with ventral cirri with short oval swollen base and digitiform tip up to 27 chaetigers before pygidium; digitiform in following ones, gradually decreasing in size posteriorly.

Aciculae blunt, basally reddish and translucent distally (Fig. 6A–K). First two chaetigers with two aciculae; in chaetigers 3–5 with three or four; in chaetigers 6–47 with four or five; in chaetigers 48–139 with three; from chaetiger 140, with two. In second syntype, last 20 chaetigers with one acicula.

Limbate chaetae of two lengths in same chaetiger, dorsalmost chaetae longer; reduced in number around chaetiger 13. Three types of pectinate chaetae; from chaetiger 11 thin, isodont narrow chaetae, with short and slender teeth; in anterior chaetigers with 1–2 pectinate and with up to 21–22 teeth; in median-posterior chaetigers, with 20–25 pectinate and 30–32 teeth (Fig. 7A, B). In median-posterior chaetigers, 3–4 thick, isodont wide chaetae, with up to 16–18 long and wide teeth (Fig. 7C). In posterior chaetigers, 2–3 thick, anodont wide chaetae, with up to 6–7 long and thick teeth (Fig. 7D). Compound spinigers present in all chaetigers, with blades of two lengths in the same chaetiger, shorter ones more abundant (Fig. 7E, F, G). Subacicular hooks present from chaetiger 33 to 140, with continuous distribution, one or two per chaetiger (second one replacement); unidentate in anterior chaetigers (Fig. 7H), bidentate in median chaetigers, basally reddish translucent distally; with blunt teeth, distal and proximal teeth of similar sizes, booth teeth directed upwards (Fig. 7I).

In second syntype, pygidium with dorsal pairs of anal cirri, as long as last 12 chaetigers; ventral pair of anal cirri short, as long as last three chaetigers (Fig. 5G).

Variation. Material examined varied in the following features: L10 = 3.1–12.4 mm, W10 = 0.8–5 mm, TChae = 88–265. Palps reaching middle of first peristomial ring or first chaetiger; lateral antennae reaching first or middle of first chaetiger; median antenna reaching middle of first or second chaetiger. Maxillary formula: MII 4–6+4–7, MIII 5–8, MIV 4–5+7–9. MI is 3–3.1× longer than maxillary carriers; MI is 4.4–5.5× longer than closing system; MII is 2.7–3.4× longer than cavity opening. Branchiae starting from chaetigers 15–32 and disappearing 7–12 chaetigers before pygidium. The maximum number of branchial filaments varies from two to six. Postchaetal lobes well developed in first 20–56 chaetigers. Ventral cirri with swollen base starting from chaetigers 4–8 and disappearing 34–68 chaetigers before pygidium. Start of subacicular hooks from chaetigers 23–38.

Regression analyses showed a correlation between L10/W10 and the first branchiate chaetiger ($R^2 = 0.7328$, $p = 1.65708E\text{-}05$, n = 7, Fig. 8A), the last chaetiger with developed postchaetal lobe ($R^2 = 0.7976$, $p = 0.00028646$, n = 7, Fig. 8B) and the first chaetiger with subacicular hook ($R^2 = 0.6291$, $p = 2.02774E\text{-}07$, n = 7, Fig. 8C). Most of the specimens were incomplete and regression analysis regarding the maximum number of branchial filaments in the body could not be performed.

Distribution. Sri Lanka, Maharashtra (India), Zanzibar.

Habitat. Unknown. Schmarda (1861a) did not indicate the habitat of the species.

Remarks. Schmarda (1861a) collected *M. teretiuscula* (firstly in the genus *Eunice*) in the east of Ceylon (now Sri Lanka) during a series of expeditions around the world to collect fauna and flora (Schmarda 1859; Villalobos-Guerrero 2019). The syntypes label only states 'Trincomalie' (Trincomalee) as the collecting site, but no collecting date is given. However, the expedition notes (Schmarda 1861b) state that he visited Ceylon from May 1853 to January 1854, whereby, based on this information, the syntypes of *M. teretiuscula* were most likely collected during this time.

Crossland (1903) described *M. macintoshi*, *M. simplex* and *M. furcellata* from Zanzibar. These species were differentiated, based on the shape of the prostomium and the pectinate chaetae. However, some authors considered these features irrelevant over time and proposed several synonyms between them or other species from distant regions. For instance, Fauvel (1919) considered *M. furcellata* to be a junior synonym of *M. sanguinea* Montagu, 1813. On the contrary, Day (1957) indicated that *M. sanguinea* differed from *M. furcellata* by having bidentate subacicular hooks, whereas, in the latter species, they are unidentate. However, Day regarded *M. furcellata* as a junior synonym of *M. simplex* (Crossland). Later, Day (1962) pointed out that *M. furcellata* and *M. simplex* (Crossland) were synonyms of *M. macintoshi*, considering that the prostomium's shape was insufficient to differentiate them. More recently, Glasby and Hutchings (2010) recognised that an entire prostomium is useful to distinguish *M. macintoshi* from *M. furcellata* and *M. simplex* (Crossland). Simultaneously, Glasby and Hutchings (2010) compared *M. simplex* (Crossland) and *M. teretiuscula*, but they also did not detect morphological differences between them. After examining the type materials, we confirm the validity of Crossland's species *M. macintoshi* and *M. furcellata* and the synonymy of *M. simplex* (Crossland) with *M. teretiuscula* (see Figs 5–7).

Marphysa teretiuscula resembles *M. borradailei* Pillai, 1958 from Sri Lanka and the Indian Ocean, *M. furcellata* from Zanzibar, *M. gravelyi* Southern, 1921 from Chilka Lake, India, *M. macintoshi* from Zanzibar and *M. madrasi* Hutchings, Lavesque, Priscilla, Daffe, Malathi & Glasby, 2020 from Ennore Creek, India by having compound spinigers and inhabiting the same geographical area.

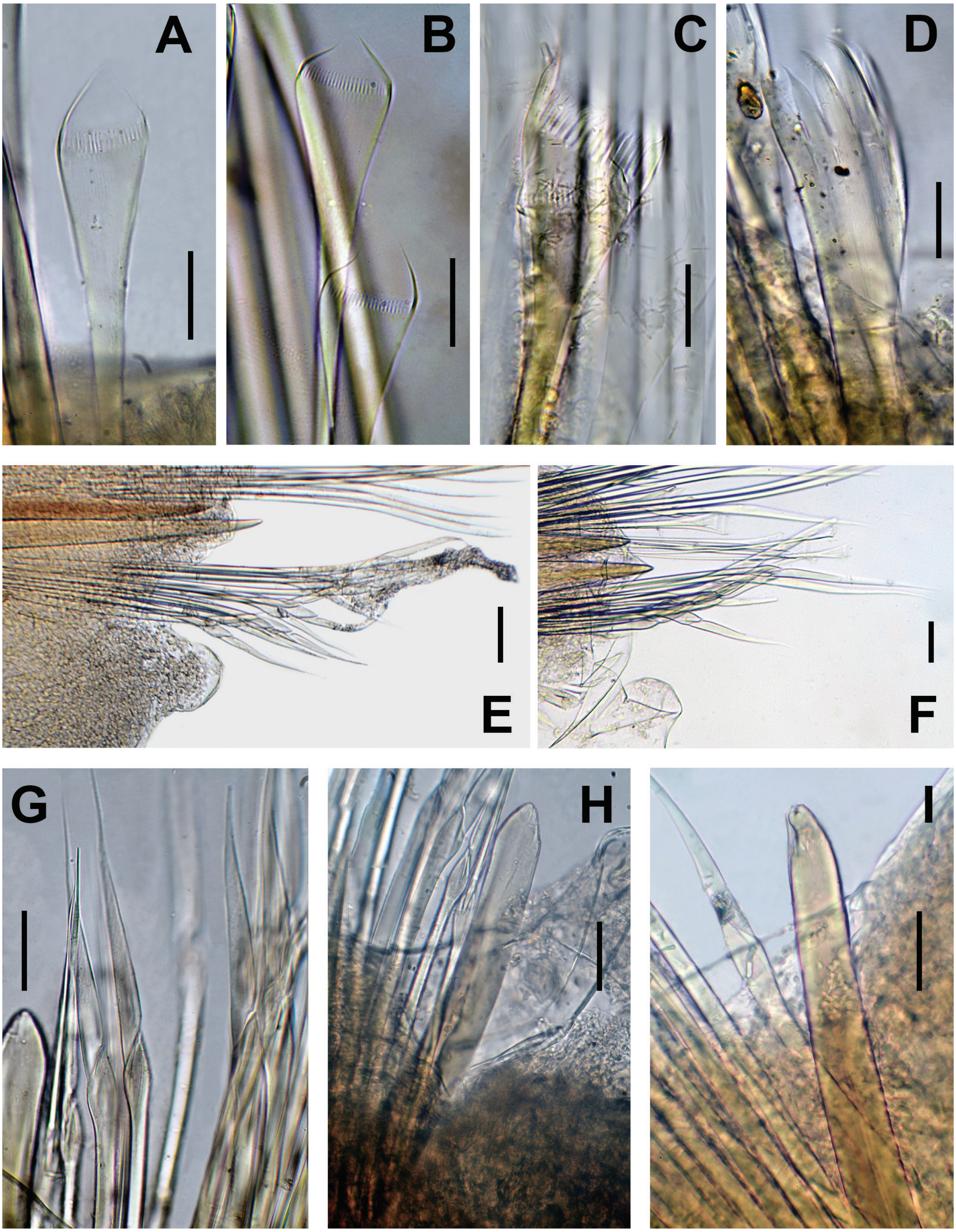

Figure 7. *Marphysa teretiuscula* (Schmarda, 1861a). **A.** Thin, isodont narrow pectinate, with short and slender teeth, chaetiger 47; **B.** Thin, isodont narrow pectinate, with short and slender teeth, chaetiger 189; **C.** Thick, isodont wide, with long and wide teeth, chaetiger 44 before pygidium; **D.** Thick, anodont wide, with long and wide teeth, chaetiger 256; **E.** Compound spinigers, chaetiger 44 before pygidium; **F.** Compound spiniger, chaetiger 211; **G.** Compound spinigers, chaetiger 47; **H.** Unidentate subacicular hook, chaetiger 47; **I.** Bidentate subacicular hook, chaetiger 73 before pygidium. **A, B.** from *M. teretiuscula* (Schmarda, 1861a) syntype 1 (NHMW type 1092); **C, E, I.** from *M. teretiuscula* (Schmarda, 1861a) syntype 2 (NHMW type 1092); **D, F.** from *Marphysa simplex* Crossland, 1903 syntype 1 (BNHM 1955.4.1.21-25); **G, H.** from *M. simplex* Crossland, 1903 syntype 2 (BNHM 1955.4.1.21-25). Scale bars: 20 µm (**A–D, G**); 60 µm (**E**); 50 µm (**F, H, I**).

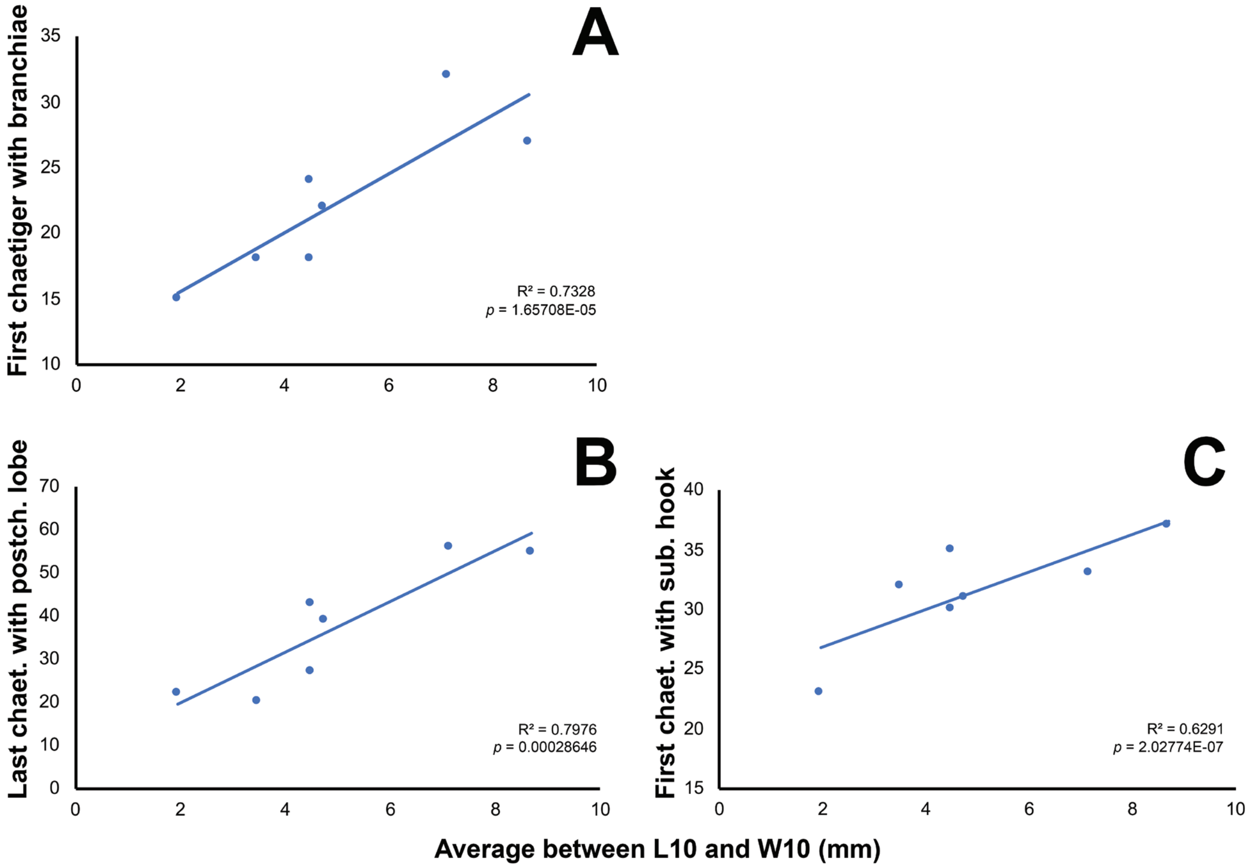

Figure 8. Large chaetiger 10 (L10)/Wide chaetiger 10 (W10)-dependent variation of some morphological features in *Marphysa teretiuscula* (Schmarda, 1861a). **A.** First chaetiger where the branchiae start ($R^2 = 0.7328$, $p = 1.65708E-05$, n = 7); **B.** Last chaetiger where the postchaetal lobe is developed ($R^2 = 0.7976$, $p = 0.00028646$, n = 7); **C.** Chaetiger where the subacicular hook starts ($R^2 = 0.6291$, $p = 2.02774E-07$, n = 7).

However, *M. teretiuscula* bears only subacicular chaetae compound spinigers, while *M. borradailei*, *M. gravelyi* and *M. madrasi* have both subacicular spinigers and limbate chaetae. Furthermore, *M. teretiuscula* has distinct bilobed prostomium, in contrast to an entire prostomium in *M. macintoshi*. Moreover, *M. teretiuscula* has palmate branchiae with a short button-shaped branchial stem in the anterior region, the postchaetal lobe is rounded in the first three chaetigers and the subacicular hooks are reddish basally and translucent distally. In contrast, *M. furcellata* has pectinate branchiae in the anterior region, digitiform postchaetal lobes in the first chaetigers and translucent subacicular hooks. In addition, *M. teretiuscula*, *M. furcellata* and *M. macintoshi* differ by distributing the branchial filaments throughout the body. In *M. teretiuscula*, the maximum number of five branchial filaments is present only in a small/low number of chaetigers (between chaetiger 86 and 106), while in *M. furcellata* and *M. macintoshi*, the maximum number of five branchial filaments (in each species) is found in a larger number of chaetigers (in *M. furcellata* from chaetiger 80 to 120+ and in *M. macintoshi* from chaetiger 105 to 236; Fig. 9).

Marphysa teretiuscula resembles *M. americana* Monro, 1933, *M. angelensis* Fauchald, 1970, *M. depressa* (Schmarda, 1861a), *M. emiliae* Molina-Acevedo and Carrera-Parra, 2017, *M. nobilis* Treadwell, 1917, *M. sanguinea* (Montagu, 1913) and *M. tripectinata* Liu, Hutchings & Sun, 2017 in having reddish subacicular hooks, the presence of compound spinigers and the absence of subacicular limbate chaetae. However, *M. teretiuscula* has palmate branchiae with a short bottom-stem in the anterior region, contrary to *M. americana*, *M. angelensis*, *M. depressa*, *M. emiliae*, *M. nobilis* and *M. sanguinea* which have pectinate branchiae throughout the body. Furthermore, *M. teretiuscula* has compound spinigers in all chaetigers, while in *M. depressa*, the spinigers are restricted to the anterior region. In addition, *M. teretiuscula* has the postchaetal lobe rounded in the first three chaetigers, while it is conical in the first three parapodia of *M. americana* and digitiform in *M. angelensis*, *M. depressa*, *M. emiliae* and *M. sanguinea*. Moreover, *M. teretiuscula* has distinctly longer branchial filaments than in *M. angelensis*. Additionally, *M. teretiuscula* has the subacicular hook as wide as the acicula, in contrast to that half as wide as acicula in *M. nobilis* and *M. tripectinata*. The comparison of *M. teretiuscula* with similar species is provided in Table 2.

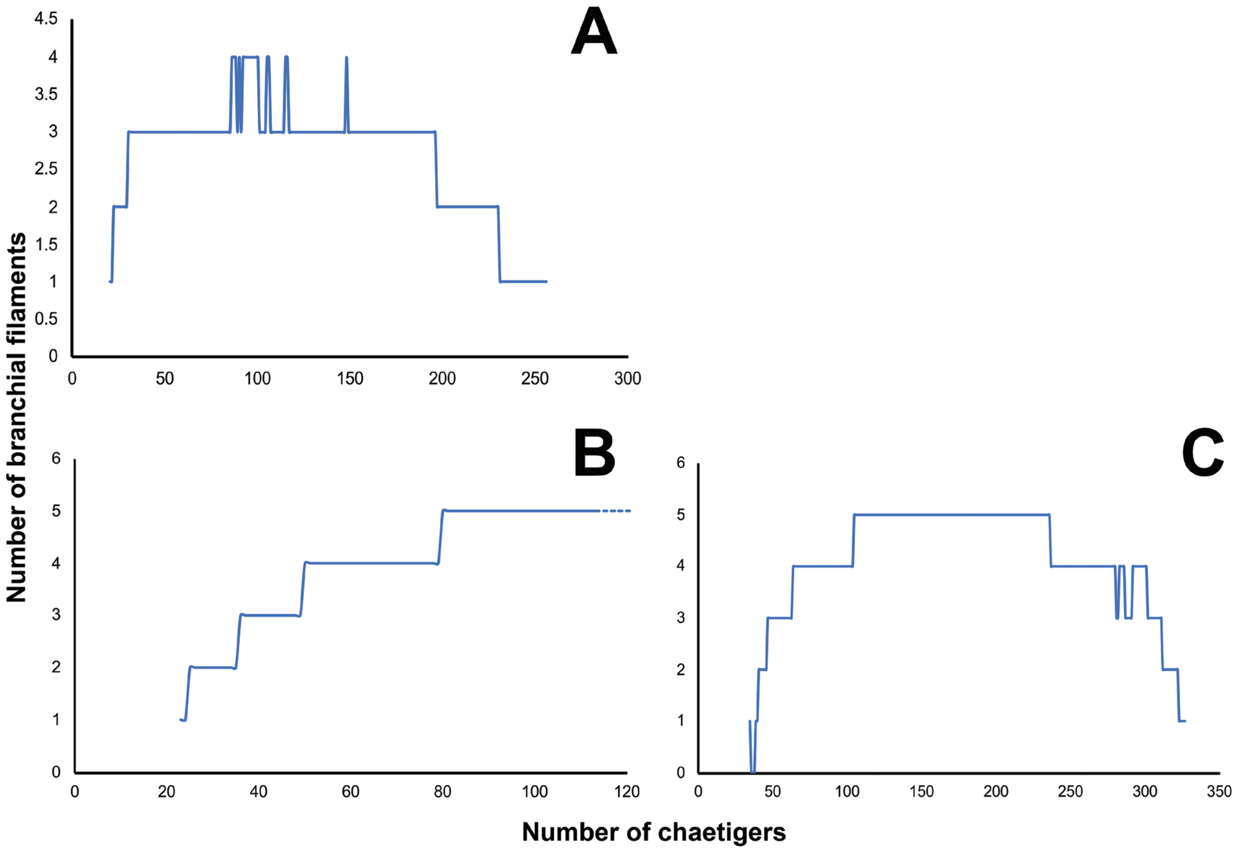

Figure 9. Distribution of branchial filaments throughout the body. **A.** Syntype 1 of *Marphysa simplex* Crossland, 1903 (BNHM 1924.3.1.1-2) with L10: 8.6 mm, TL: 137 mm and 273 chaetigers; **B.** Syntype 1 of *Marphysa furcellata* Crossland, 1903 (BNHM 1924.3.1.139) with L10: 6.3 mm, TL: 40 mm and 114 chaetigers; **C.** Syntype 1 of *Marphysa macintoshi* Crossland, 1903 (BNHM 1924.3.1.22-3) with L10: 8.1 mm, TL: 18.8 mm and 262 chaetigers. Dotted blue line in B indicates the organism is incomplete.

Discussion

Marphysa group without compound chaetae

At present, the small *Marphysa* group A proposed by Fauchald (1970) consists of four species characterised by the absence of compound chaetae: *Marphysa mossambica* from Mozambique, *M. novaehollandiae* from Sydney, *M. moribidii* from Malaysia and *M. fijiensis* nom. nov. from Fiji. All these species are represented by large organisms with a high number of segments (more than 200) in the adult stage. However, the ontogenetic development of these species and the presence of compound chaetae in the early stages, a common condition in other *Marphysa* species (Southern 1921; Aiyar 1931; Pillai 1958), are unknown.

The absence of compound chaetae was an important character to consider the species in the *Marphysa* group A as an independent genus, *Nauphanta* Kinberg, 1865 (Fauchald 1987). However, Glasby and Hutchings (2010) regarded *Nauphanta* as a junior synonym of *Marphysa*, based on the variation in that feature in ontogeny. In addition, Zanol et al. (2014) supported this synonymy in a phylogenetic analysis of Eunicidae, based on morphological and molecular evidence, confirming this uncommon condition is developed in some *Marphysa* species.

The emergence of compound chaetae in the early stages has been well documented in some *Marphysa* species from India: *Marphysa borradailei* (Borradaile 1902; Pillai 1958), *M. gravelyi* (Malathi et al. 2011) and *Marphysa* sp. (Aiyar 1931). During the development of the first chaetiger in the metatrochophore larvae of these species, the first compound chaeta is characterised by having convex and straight edges as they emerge (Borradaile 1902; Southern 1921; Aiyar 1931; Pillai 1958) just after the appearance of two unjointed (simple) chaetae (Borradaile 1902; Aiyar 1931; Malathi et al. 2011). This compound chaeta resembles the blade of the compound falciger, although it lacks the typical distal teeth. When the third chaetiger is developed, only the same compound chaeta emerges in chaetigers 2 and 3 (Borradaile 1902; Southern 1921; Aiyar 1931; Pillai 1958). At the time of development of chaetigers 12–13, two types of compound chaetae can be observed (Aiyar 1931; Pillai 1958): (1) a hooked chaeta, herein judged as the compound falciger; and (2) a sickle-shaped chaeta, also called falcigerous by Aiyar (1931) and Pillai (1958), herein interpreted as the typical compound spiniger.

Aiyar (1931) also described the shift and loss of chaetae in larger specimens of *Marphysa* sp. The specimens have limbate chaetae throughout the body regardless of size, in

Table 2. Morphological features of *Marphysa* species with reddish subacicular hook and three types of pectinate chaetae. 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; INLT: Isodont narrow with long and thick teeth; IWSS: Isodont wide with short and slender teeth; IWLS: Isodont wide with long and slender teeth; IWLT: Isodont wide with long and thick teeth; AWLT: Anodont wide with long and thick teeth; AWLS: Anodont wide with long and slender teeth.

Morphological feature	*M. americana* Monro, 1933	*M. angelensis* Fauchald, 1970	*M. depressa* (Schmarda, 1861a)	*M. emiliae* Molina-Acevedo & Carrera-Parra, 2017	*M. nobilis* Treadwell, 1917	*M. sanguinea* (Montagu, 1913)	*M. teretiuscula* (Schmarda, 1861a)	*M. tripectinata* Liu, Hutchings & Sun, 2017
Source of information	holotype BNHM 1932.12.24.554-556	holotype LACM-AHF POLY 285; and additional material	syntypes NHM 1044	holotype ECOSUR0180; paratype ECOSUR0181	holotype AMNH VI–1915–1350, additional material	neotype BNHM 1867.1.7.24; additional material	syntypes NHM 1092, *M. simplex* Crossland, 1903 syntypes BNHM 1937.9.2.325	paratypes AM W.49071, AM W.49072
Size (mm): L10, W10	12, 5.8	2.1–5.4, 17	4.2–11.5, 1.9–4.8	3.5, 1.6	6 –13.6, 6.5	11.5–20.4, 7.2–11	5.5–12.4; 0.8–5	11–12.3, 4–5
Prostomium: shape	bilobed	bilobed	bilobed	bilobed	bilobed	bilobed	bilobed	bilobed
Palps: reaching	PR–I	PR–II, Chaet 1	PR–I, Chaet 1	PR–II	PR–I, PR–II	PR–I, PR–II	PR–I, Chaet 1	PR–II
Lateral antennae: reaching	PR–II	PR–II, Chaet 2	Chaet 1, 2	Chaet 1	PR–II, Chaet 2	PR–II, Chaet 1	Chaet 1	Chaet 1
Median antennae: reaching	Chaet 1	Chaet 1, 3	Chaet 1, 3	Chaet 1	Chaet 1, 3	PR–II, Chaet 2	Chaet 1, 2	Chaet 1, 2
Peduncle in prostomial appendages	absent	absent	absent	absent	absent	absent	absent	absent
Eyes	present	present	present	present	present	present	present	present
MF: MII, MIII, MIV	5+4, 7+0, 3+9	3–5+4–5, 4–6, 3–4+6–8	3–4+4, 4–5, 3–5+6–8	4+4, 5+0, 3+8	3–4+3–4, 5–6, 3–4+7–8	4+4–5, 5–6, 3–4+6–8	4–6+4–7, 5–8, 4–5+7–9	5+5–6, 7, 4–5+8
MI vs. MxC: proportion	3.2× longer than MxC	2.1–3.4× longer than MxC	2–2.8× longer than MxC	2.5× longer than MxC	3.8× longer than MxC	2.9–3.2× longer than MxC	3–3.1× longer than MxC	2.6–2.8× longer than MxC
MI vs. CIS: proportion	5× longer than CIS	3–4.5× longer than CIS	3.5–4× longer than CIS	4.8× longer than CIS	5× longer than CIS	3.8–5.6× longer than CIS	4.4–5.5× longer than CIS	4–4.5× longer than CIS
MII vs COp: proportion	3× longer than COp	4.3–6× longer than COp	3.1–5× longer than COp	3.5× longer than COp	3.2× longer than COp	3.7–4.4× longer than COp	2.7–3.4× longer than COp	3.6–3.8× longer than COp
Branchiae: shaped	pectinate	pectinate	pectinate	pectinate	pectinate	pectinate	palmate/pectinate	palmate/pectinate
Branchiae: start chaetiger; last chaetiger before pygidium	45; 28	9–14; 3–31	26–44; 20–39	8–12; 10–13	17–27; 34–37	21–25; 9–18	18–32; 7–12	13–20; 16
Branchial filaments: numbers, length of the filaments	12, long	2–6, short	2–4, long	2–5, long	4–6; long	5–6; long	4–6; long	5–6; long
Dorsal cirri: shape	conical	conical	conical	AR, MR: conical, PR: digitiform	AR: digitiform, MR: digitiform with swollen base, PR: conical	conical	conical	AR: digitiform, MR, PR: conical
Prechaetal lobe: shape	transverse fold	transverse fold	transverse fold	transverse fold	AR, MR, PR: transverse fold	AR, MR, PR: transverse fold	AR: dorsal edge longer, MR, PR: transverse fold	AR: dorsal edge longer, MR, PR: transverse fold
Chaetal lobe: shape	AR: rounded, MR, PR: triangular	AR: rounded, MR, PR: triangular	AR: rounded, MR, PR: triangular	AR: rounded, MR, PR: triangular	AR: rounded, MR, PR: triangular	AR: rounded, MR, PR: triangular	AR: rounded, MR, PR: triangular	AR: rounded, MR, PR: triangular
Developed postchaetal lobe: end chaetiger	92	18–61	27–60	42	39–71	50–70	20–56	50–131
Poschaetal lobe: shape in body regions	Chaet 1–4: conical; from Chaet 5: rounded	Chaet 1–4: digitiform, from Chaet 5: rounded	Chaet 1–4: digitiform, from Chaet 5: auricular	Chaet 1–4: digitiform, from Chaet 5: rounded	rounded	Chaet 1–4: digitiform, from Chaet 5: ovoid	ovoid dorsal edge longer	rounded with dorsal edge longer
Ventral cirri in first chaetigers: shape	digitiform	digitiform	rounded	digitiform	conical	digitiform	conical	conical
Ventral cirri with swollen base: start chaetiger; last chaetiger before pygidium	5; 45	4–7; 28–58	5–6; 22–28	4–7; 39–44	10–11; 44	5–8; 8–18	4–8; 34–68	6–8; 151
Ventral cirri in most posterior chaetigers: shape	conical	digitiform	conical	digitiform	conical	conical	digitiform	conical
Aciculae: shape; colour	blunt, dark	blunt, dark	blunt, dark	blunt, dark	blunt, dark	blunt, dark	blunt, dark	blunt, dark

Table 2. Continued.

Morphological feature	*M. americana* Monro, 1933	*M. angelensis* Fauchald, 1970	*M. depressa* (Schmarda, 1861a)	*M. emiliae* Molina-Acevedo & Carrera-Parra, 2017	*M. nobilis* Treadwell, 1917	*M. sanguinea* (Montagu, 1913)	*M. teretiuscula* (Schmarda, 1861a)	*M. tripectinata* Liu, Hutchings & Sun, 2017
Subacicular limbate chaetae	absent	absent	absent	absent	absent	absent	absent	absent
Pectinate chaetae: type in AR; MR, PR	INLS; IWSS, IWLT, AWLT	INST; IWSS, AWLS	INSS; IWLT, AWLT	IWSS; AWLT	INLS; IWSS, AWLS	INLS; IWSS, AWLS	INLS; INLS, IWLT, AWLT	INLS; IWLS, AWLS
Pectinate chaetae: number per type	3–4; 3–4, 2–3, 1–2	1–2; 3–4, 2–3	2–3; 3–4, 3–4	6–8; 3–4	2–3; 10–12, 6–7	1–2; 18–20, 4–5	1–2; 20–25, 3–4, 2–3	1–2; 16–17, 4–5
Pectinate chaetae teeth: number per type	12; 16, 16, 11	15; 18, 8–9	8–9; 14, 13–14	20–22; 13	16–17; 17, 16	10; 18, 10–12	21–22; 30–32, 16–18, 6–7	18; 25, 15–17
Spiniger blade: length in AR	2 lengths	2 lengths	similar length	2 lengths	2 lengths	2 lengths	2 lengths	2 lengths
Spiniger blade: length in MR-PR	similar length	2 lengths	-	2 lengths	2 lengths	2 lengths	2 lengths	2 lengths
Spiniger: distribution	all chaet	all chaet	AR only	all chaet	all chaet	all chaet	all chaet	all chaet
Falciger: (p/a); distribution	a; NA	p; all chaet or AR	p; all chaet	p; AR	absent	absent	absent	absent
Subacicular hook: start chaetiger	117	14–29	33–68	21–28	31–94	74–286	30–38	62–115
Subacicular hook: shape; colour	bidentate, reddish basally and translucent distally	bidentate, reddish basally and translucent distally	bidentate, reddish basally and translucent distally	bidentate, reddish basally and translucent distally	unidentate, reddish basally and translucent distally	bidentate, reddish basally and translucent distally	bidentate, reddish basally and translucent distally	bidentate, reddish basally and translucent distally
Width acicula vs. SH in MR-PR: proportion	similar width	similar width	similar width	similar width	Acicula 2× wider than SH	Acicula 2× wider than SH	similar width	Acicula 2× wider than SH
Subacicular hook: distribution	discontinuous	continue	continue	continue	discontinuous	discontinuous	discontinuous	continuous

contrast to the compound chaetae lost to different extents. The compound spinigers are present in all chaetigers in specimens with up to 150 chaetigers, but they disappear in the most-posterior chaetigers in larger specimens; on the contrary, the compound falcigers appear only in the posterior region of specimens with 70–80 chaetigers and entirely disappear in specimens with 150 or more chaetigers.

Glasby and Hutchings (2010) indicated that the lack of compound falcigers in *Marphysa* is due to their loss during the transition from juvenile to young adults, as occurs in *M. angelensis* Fauchald, 1970 (Molina-Acevedo and Villalobos-Guerrero, in prep.), *M. borradailei* (Southern 1921; Pillai 1958), *M. brevitentaculata* Treadwell, 1921 (Salazar-Vallejo and Carrera-Parra 1998; Molina-Acevedo and Carrera-Parra 2017), *M. gravelyi* (Southern 1921; Pillai 1958) and *M. sherlockae* Kara et al. 2020 (Kara et al. 2020). Likewise, Glasby and Hutchings (2010) stated that the absence of compound spinigers is a paedomorphic condition in *Marphysa* group A since they are supposedly lacking in the juveniles. However, it contradicts the evidence demonstrated by Aiyar (1931) and Pillai (1958) for juveniles of *Marphysa* sp. and *M. borradailei* having compound spinigers.

The absence of both compound spinigers and falcigers in species of *Marphysa* group A is more likely due to their gradual loss as the body of the specimens increases in size. The small juveniles have both compound spinigers and falcigers, but the latter chaetae begin to disappear as the animal grows. In juveniles or young adults, the falcigers may be lost entirely, with the compound spinigers being replaced by limbate chaetae. Finally, in adults, both compound spinigers and falcigers may be lacking. Several suitable examples allude to this chaetal transition. For instance, in the group with limbate subacicular chaetae sensu Glasby and Hutchings (2010, see below), the adults have compound spinigers in the anterior-median region, which are replaced by limbate chaetae in the median-posterior. Likewise, in *M. brevitentaculata*, *M. digitibranchia* Hoagland, 1920 and *M. mangeri* Augener, 1918, the compound falcigers are present solely in the anterior region, the compound spinigers only in the anterior-median region and limbate subacicular chaetae only in median-posterior region (Augener 1918; Hoagland 1920; Molina-Acevedo and Carrera-Parra 2017). To confirm this hypothesis, a thorough ontogenetic study on the chaetal shift is needed to understand the absence of compound chaetae in Group A.

Marphysa teretiuscula, a misinterpreted species

Marphysa teretiuscula has received little attention since Schmarda (1861a) described it initially from the east coast of Sri Lanka (formerly Ceylon). Although de Quatrefages (1866), Ehlers (1868) and Crossland (1903) recognised the species as valid in *Marphysa*, it was overlooked by some authors who extensively studied the polychaetous annelids from India, such as Gravely (1927) and Fauvel

(1930, 1932, 1940, 1953). *Marphysa teretiuscula* was briefly mentioned in the early 1900s when Borradaile (1902) described the larval development of specimens from the north of Sri Lanka that release the embryos in jelly cocoons attached to the bottom by a stem. One of these worms was identified by Arthur Willey as allied to, or identical with, *M. teretiuscula* (see Borradaile 1902), the only species known at that time from the area. Later, Southern (1921) and Aiyar (1931) found a specimen with similar reproductive patterns to those described by Borradaile, which were identified as *M. gravelyi* (Southern) from the Chilka Lake and *Marphysa* sp. from Madras. Pillai (1958) studied the specimens from the Negombo Lagoon, Sri Lanka, which also fitted in terms of ontogeny to *M. teretiuscula sensu* Borradaile (1902), but differed from Schmarda's original description in several morphological respects. In this regard, Pillai (1958) described these specimens as a new species, *M. borradailei*. Regrettably, the reproduction and development of *M. teretiuscula* are still unknown.

Marphysa teretiuscula was chosen by Glasby and Hutchings (2010) to create the informal 'Teretiuscula-group' within *Marphysa*, which is featured by having species with compound spinigers restricted to anterior chaetigers and subacicular limbate chaetae present throughout the body, in addition to the formation of jelly cocoons as part of a reproductive strategy. The species included in the 'Teretiuscula-group' are *M. fauchaldi*, *M. borradailei*, *M. gravelyi*, *M. teretiuscula* (Glasby and Hutchings 2010) and the recently described species, *M. madrasi* (Hutchings et al. 2020). However, the stem species *M. teretiuscula*, in fact, lacks those relevant features encompassing the 'Teretiuscula-group'. As demonstrated in the present study's re-description, *M. teretiuscula* bears compound spinigers only and lacks subacicular limbate chaetae in all parapodia (Fig. 7E, F). Furthermore, the reproduction of *M. teretiuscula* is unknown compared with those species from the same region, *M. borradailei* and *M. gravelyi*. Herein, we judge *M. teretiuscula* as belonging to the group B2 sensu Fauchald (1970), whereas the 'Teretiuscula-group' sensu Glasby and Hutchings (2010) is renamed with the earliest species described within, 'Gravelyi-group'.

Two other species have also been described from near the type locality of *M. teretiuscula*: *Paramarphysa orientalis* Willey, 1905 and *M. chevalensis* Willey, 1905, both from the Gulf of Manaar (India). The first species is recently considered indeterminable by Molina-Acevedo and Idris (accepted, but not yet published), while the second species is here treated in the same manner. *Marphysa chevalensis* was described, based on two specimens: the smaller has both compound falcigers and spinigers in all chaetigers, whereas the larger has a similar chaetal pattern; however, the falcigers are restricted to the anterior-median region (Willey 1905). The larger specimen could have undergone a loss of falcigers as demonstrated in the young adults of *M. gravelyi*, *M. brevitentaculata* and *M. sherlockae* (Southern 1921; Pillai 1958; Salazar-Vallejo and Carrera-Parra 1998; Kara et al. 2020). *Marphysa chevalensis* may be the young adult of one of the species described from Sri Lanka or India (*M. gravelyi*, *M. borradailei* and *M. teretiuscula*) that has not yet developed its adult complement of chaetae. On the other hand, the type material of *M. chevalensis* is lost and relevant diagnostic characters, such as the shape of parapodia, the maxillary formula, the presence of subacicular limbate chaetae, the colour of the subacicular hook, among others, were not included in the original description. This lack of information hinders the differentiation between similar species, even when fresh topotype material is available. Therefore, we also consider *M. chevalensis* as an indeterminable species.

Conclusion

In the present work, we clarified the taxonomic status of five *Marphysa* species. The synonymy of *M. teretiuscula* over *M. simplex* Crossland was confirmed and the re-description of the species was provided using the type material. *Marphysa simplex* Treadwell was re-established, re-described and a new name for this homonym species was proposed, *M. fijiensis* nom. nov. Likewise, *M. simplex* (Langerhans), *M. chevalensis* and *Paramarphysa orientalis* were considered indeterminable.

On the other hand, the informal groups (B2, C and D) into which *Marphysa* has been split, have not yet been monophyletically tested. These divisions are used here to highlight the diversity of forms within the genus and help differentiate the species morphologically. However, it is imperative to carry out a species revision and a phylogenetic analysis to help reveal these artificial groups' status.

Historically, many synonyms have been subjectively proposed for *Marphysa* species causing a simultaneous decline in the species richness and an increase in either cosmopolitan species or species complexes. We strongly recommend that, before establishing a new synonymy, researchers should rely on the review of the type material of the species in question to describe it in detail, including the overlooked characters and to compare the species for distinguishing them accurately and ideally collecting fresh material from the type locality for molecular work and morphological variation.

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Supplementary material 1

Template for primary biodiversity data of *Marphysa* species

Authors: Isabel Cristina Molina-Acevedo, Izwandy Idris
Data type: template

Link: https://doi.org/10.3897/zse.97.59559.suppl1