

Description of four new species and a revision of the genus *Tripaphylus* Richiardi in Anonymous, 1878 (Copepoda: Siphonostomatoida: Sphyrriidae)

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Abstract *Tripaphylus* Richiardi in Anonymous, 1878 is one of the genera of the Sphyrriidae Wilson, 1919 and it currently accommodates ten species. Only scanty descriptions are available for the females and some males of the species. *Tripaphylus* specimens, described and illustrated in this paper, were collected from elasmobranch hosts off the South African coast or came from the private collection of the late Dr G. Benz. Collected specimens were fixed and preserved in 70% ethanol, examined by light - and scanning electron microscopy, and compared with the known species. Descriptions and illustrations are provided for the transformed adult females and males of *T. elongatus* (Wilson, 1932) and *T. versicolor* (Wilson, 1919)

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while illustrated descriptions of the transformed adult females are also provided for *T. ferox* (Wilson, 1919) and *T. vaissierei* (Delamare Deboutteville & Nuñez-Ruivo, 1954). Additionally, the material previously reported as *T. ferox* is considered to represent *T. elongatus* and that reported as *T. lobatus* (Kirtisinghe, 1964) is considered a junior synonym of *T. vaissierei*. Based on the collected material the transformed adult female and male of *T. lewisi* n. sp. are described as well as the adult transformed females of *T. benzi* n. sp., *T. hoi* n. sp., and *T. beatricae* n. sp. A summarised review of the main features is provided for each of the previously described *T. musteli* (van Beneden, 1851), *T. hemigalei* Kirtisinghe, 1964, *T. australis* (Kabata, 1993), *T. triakis* (Castro Romero, 2001) and *T. asymboli* (Turner, Kyne & Bennett, 2003). Furthermore, reasons are provided for the recommendation that *T. hemigalei* be considered a *species inquirenda*. An identification key to the transformed adult females of all species of *Tripaphylus* is provided and the host records are also updated.

Introduction

The family Sphyrriidae Wilson, 1919 (Copepoda: Siphonostomatoida) consists of eight genera, namely *Sphyrion* Cuvier, 1830; *Lophoura* Kölliker in Gegenbaur, Kölliker & Muller, 1853; *Tripaphylus* Richiardi in Anonymous, 1878; *Opimia* Wilson, 1908;

Periplexis Wilson, 1919; *Paeonocanthus* Kabata, 1965; *Norkus* Dojiri & Deets, 1988; and *Driocephalus* Raibaut, 1999 (see Walter & Boxshall, 2008; Benz & Boxshall, 2017). Kabata (1979) considered the genera infecting elasmobranchs and with simple, cylindrical posterior processes and necks devoid of holdfast outgrowths (*Opimia*, *Tripaphylus* and *Driocephalus*) as primitive. However, *Norkus*, also reported from an elasmobranch, has an expanded anterior collar on the neck (Dojiri & Deets, 1988). The remaining sphyriids, with either holdfast outgrowths on their necks or complex posterior processes or both, are considered advanced and are parasites of teleosts (Kabata, 1979; Dojiri & Deets, 1988). The elasmobranch associates are found in the olfactory and branchial chambers while species infecting teleosts penetrate the body musculature (Dojiri & Deets, 1988; Benz, 1993).

The species found on elasmobranchs were reported from hosts belonging mostly to the Carcharhiniformes but also the Rhinopristiformes. *Opimia exilis* Wilson, 1908 was reported from Carcharhiniformes (Triakidae) (see Wilson, 1908), *Driocephalus cerebrinoxius* (Diebakate, Raibaut & Kabata, 1997) from Carcharhiniformes (Leptocharidae) (see Diebakate et al., 1997), and Triakidae (Benz et al., 2006) and *Norkus cladocephalus* Dojiri & Deets, 1988 from Rhinopristiformes (Rhinobatidae) (see Dojiri & Deets, 1988).

Until recently there has been ten valid species within *Tripaphylus*. The type-species of the genus is *T. musteli* (van Beneden, 1851) and the remaining species are: *T. ferox* (Wilson, 1919); *T. versicolor* (Wilson, 1919); *T. elongatus* (Wilson, 1932); *T. vaissierei* (Delamare Deboutteville & Nuñez-Ruivo, 1954); *T. hemigalei* Kirtisinghe, 1964; *T. lobatus* (Kirtisinghe, 1964); *T. australis* (Kabata, 1993); *T. triakis* (Castro Romero, 2001), and *T. asymboli* (Turner, Kyne & Bennett, 2003). The species of *Tripaphylus* were reported mostly from hosts belonging to the orders Carcharhiniformes, i.e. *T. musteli* from species of Triakidae (see van Beneden, 1851; Scott & Scott, 1913; Benz & Boxshall, 2017), *T. ferox* from species of Carcharhinidae (see Wilson, 1919) and Sphyrnidae (see Wilson, 1935; Pearse, 1952), *T. versicolor* from species of Triakidae (see Wilson, 1919), *T. elongatus* from species of Carcharhinidae (see Wilson, 1932; Dippenaar & Jordaan, 2007), *T. vaissierei* from species of Sphyrnidae (see Delamare Deboutteville & Nuñez-Ruivo, 1954; Lewis, 1966; Dippenaar & Jordaan, 2007), *T. hemigalei* from

species of Hemigaleidae (see Kirtisinghe, 1964), *T. lobatus* from species of Hemigaleidae (see Kirtisinghe, 1964), *T. triakis* from species of Triakidae (see Castro Romero, 2001), and *T. asymboli* from species of Pentachidae (see Turner et al., 2003) and one from Rhinopristiformes i.e. *T. australis* from species of Glaucostegidae (see Kabata, 1993) and Trygonorhinidae (see Turner et al., 2003).

The literature contains reports and descriptions dealing with the general habitus of the female of each species but descriptions of the appendages and the males are very scanty which hampers attempts to compare the different species of *Tripaphylus*. This paper provides descriptions of the appendages of the female *T. elongatus* and additions to the descriptions of the males of *T. elongatus* and *T. versicolor*. It provides re-descriptions and illustrations of the habitus of the females of *T. versicolor*, *T. ferox*, and *T. vaissierei*, and a review of the main features of *T. musteli*, *T. hemigalei*, *T. australis*, *T. triakis* and *T. asymboli*. Four new species namely *T. lewisi* n. sp., *T. benzi* n. sp., *T. hoi* n. sp. and *T. beatricae* n. sp. are described based on the morphology of transformed adult females. The host reports are reviewed and a dichotomous identification key to the species of *Tripaphylus* based on the morphology of transformed adult females is provided.

Materials and methods

Copepods were collected from elasmobranchs caught in the nets set off the KwaZulu-Natal coast (east coast) by the KwaZulu-Natal Sharks Board (KZNSB); from individuals taken as bycatch in demersal trawls during surveys undertaken using the research vessel *FRS Africana* by the Department of Agriculture, Forestry and Fisheries (DAFF) (south coast), and from elasmobranchs caught by commercial fishermen off the west coast, South Africa. Collected copepods were fixed and preserved in 70% ethanol. Before selected specimens were dissected, they were cleared and stained in lactic acid with a small amount of dissolved lignin pink. Copepods were studied using stereo- and light microscopy and the wooden slide technique of Humes & Gooding (1964) and drawn with the aid of a drawing tube. Measurements were made using a stage micrometer. Some specimens were studied using

scanning electron microscopy (SEM). These specimens were dehydrated through a graded ethanol series (70, 80, 90, 100, 100%, immersed in each for 30 min), followed by immersion in a small volume of hexamethyldisilazane (30 min). Before mounting, specimens were dried by placing them under a slight vacuum to remove the hexamethyldisilazane. Specimens were sputter-coated with gold-palladium. Gross body parts nomenclature follows Huys & Boxshall (1991) while the details of appendage armament follows the system proposed by Kabata (1979) for lernaeopodid copepods. Host nomenclature follows Eschmeyer et al. (2017).

Family Sphyrriidae Wilson, 1919

Genus *Tripaphylus* Richiardi in Anonimus, 1878

Tripaphylus elongatus (Wilson, 1932)

Syns *Paeon elongatus* Wilson, 1932; *Paeon elongatus* Wilson, 1932 of Dippenaar & Jordaan (2007); *Paeon ferox* Wilson, 1919 of Delamare Deboutteville & Nuñez-Ruivo (1954)

Host: *Carcharhinus obscurus* (LeSueur) (Carcharhinidae), dusky shark.

Locality: Captured off Richards Bay (28.48'S 32.06'E), Durban (29.51'S 31.00'E), Amanzimtoti (30.03'S 30.53'E), Winklespruit (30.06'S 30.51'E), Southport (30.41'S 30.30'E) and Glenmore (30.59'S 30.16'E) along the east coast of South Africa.

Site in host: Interbranchial septa distal to free tips of the gill filaments.

Material examined: 35♀♀ (many decapitated and no cephalothoraces found) and 4♂♂ (attached to female perianal region).

Voucher material: 5♀♀ (one decapitated) and 1♂ attached (SAMC-A089330) deposited in the Iziko South African Museum, Cape Town, South Africa.

Description (Figs. 1, 2, 3, Supplementary Figure S1A)

Transformed adult female [Based on five specimens, one cephalothorax used for SEM.] Body consisting of cephalothorax, neck, trunk and small abdomen with posterior processes. Overall length in ventral view with egg-sacs 59.3–164 (59.3) mm (n = 10); body length

(without posterior processes and egg-sacs) 26.5–45.3 (36.3) mm (n = 11); neck 9.4–20.3 (20) mm (n = 11); trunk 7.5–15.3 (12.5) mm (n = 11); posterior processes 5.0–8.1 (7.0) mm (n = 11); egg-sacs 13.0–30.9 (29.0) mm (n = 10). Cephalothorax (Figs. 1A–C, 2A) subspherical, with smooth anterior and lateral margins and no swellings on dorsal surface. Ventral surface (Figs. 1A, B, 2A, Supplementary Figure S1A) with 3 sets of swellings; distally 2 separate globular antennary swellings (as) sometimes extending beyond anterior margin; posterior to them set of 3 swellings with 2 lateral globular maxillary swellings (ms) attached to larger transversely elongated central swelling (cs) consisting of 2 lateral knobs and 1 medial knob (Fig. 2A); posteriorly 2 smaller globular posterolateral swellings (ps), directly posterior to maxillary swellings, sometimes extending beyond posterior margin of cephalothorax. Neck (Fig. 1A) long, cylindrical, mostly of same diameter and almost half of body length. Trunk (Fig. 1A) gradually widening and then slightly narrowing at posterior extremity, almost third of body length with separation between neck and trunk indistinct. Abdomen (Fig. 1F) represented by small bifid tubercle ventrally with cylindrical posterior processes (Figs. 1A, F), between half and two-thirds length of trunk. Egg-sacs (Fig. 1A) cylindrical, about three and a half times length of posterior processes; eggs multiseriate.

Cephalothoracic appendages (Fig. 1D) situated posteriorly between antennary swellings with maxillipeds just anterior of central swelling. Antennule (Fig. 2B) posterolaterally to rostrum, indistinctly 3-segmented; first segment with distomedial whip; second with distoventral solus, and last segment with armature consisting of 3 short (1, 2 and 3) and 3 longer (4, 5 and 6) setae on apex (corresponding to armature of lernaeopodids of *Charopinus*-branch; see Kabata 1979). Antenna (Fig. 2C) anterolateral to antennule, biramous; sympod indistinctly segmented; endopod 2-segmented, distal segment with strongly flexed hook 1, stout seta 2, spiniform seta 3, and 4 only slightly inflated carrying spiniform seta 5; exopod 1-segmented, bulbous, slightly shorter than endopod, apex denticulated and with 2 subapical setae. Mandible not observed. Maxillule (Fig. 2D) lateral to mouth tube, biramous; palp/outer lobe with apical setae (number not discernible, probably two), endite/inner lobe with 3 long, truncated apical setae. Maxilla (Fig. 2E) small, digitiform, located anterolaterally on globular

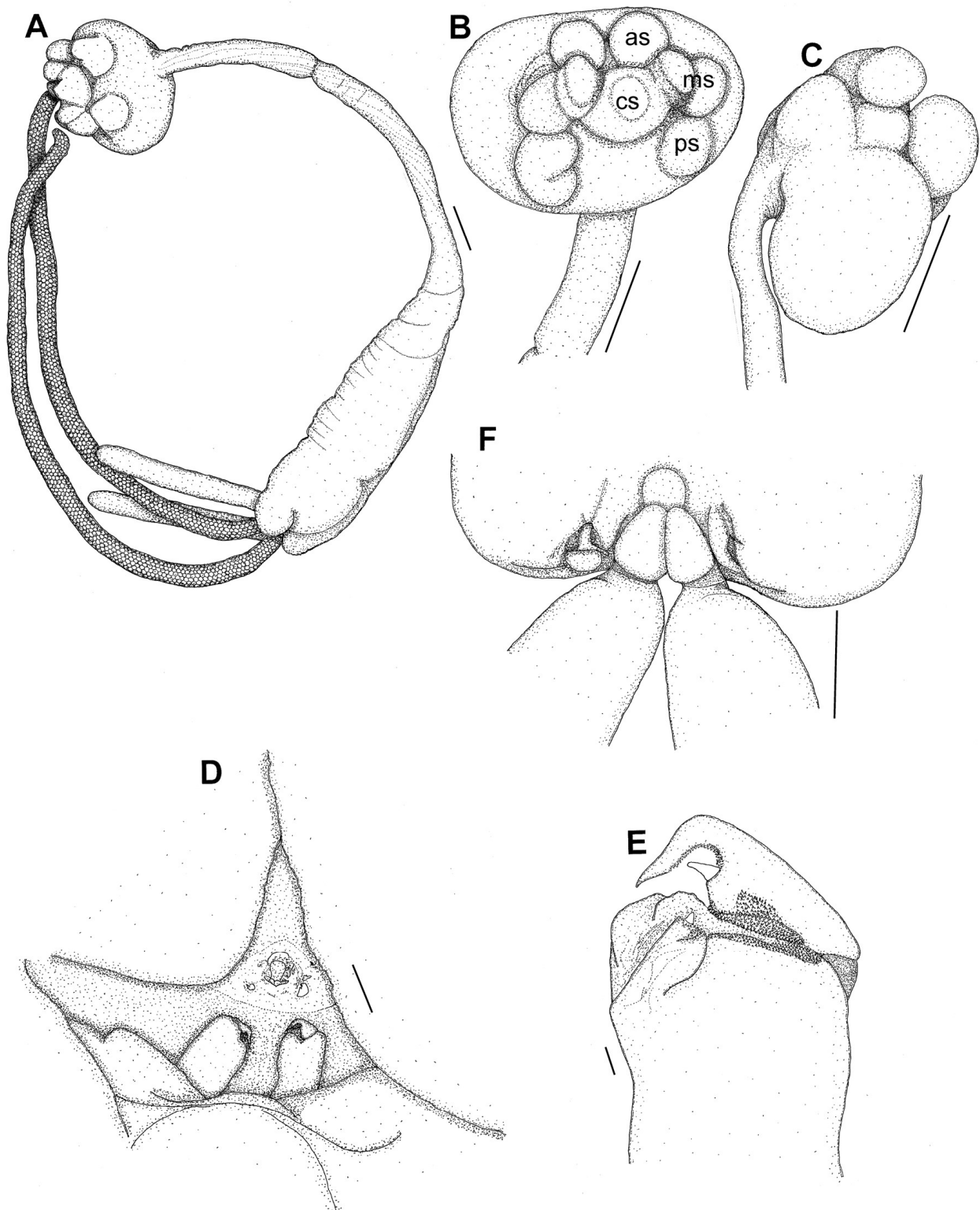


Fig. 1 *Tripaphylus elongatus* (Wilson, 1932), adult female. A, General habitus, ventral view; B, Cephalothorax, ventral view; C, Cephalothorax, lateral view; D, Appendages on cephalothorax; E, Maxilliped; F, Perianal region, ventral view. Abbreviations: as, antennary swelling; ms, maxillary swelling; cs, central swelling; ps, posterolateral swelling. Scale-bars: A–C, 2 mm; F, 1 mm; D, 100 μ m; E, 10 μ m

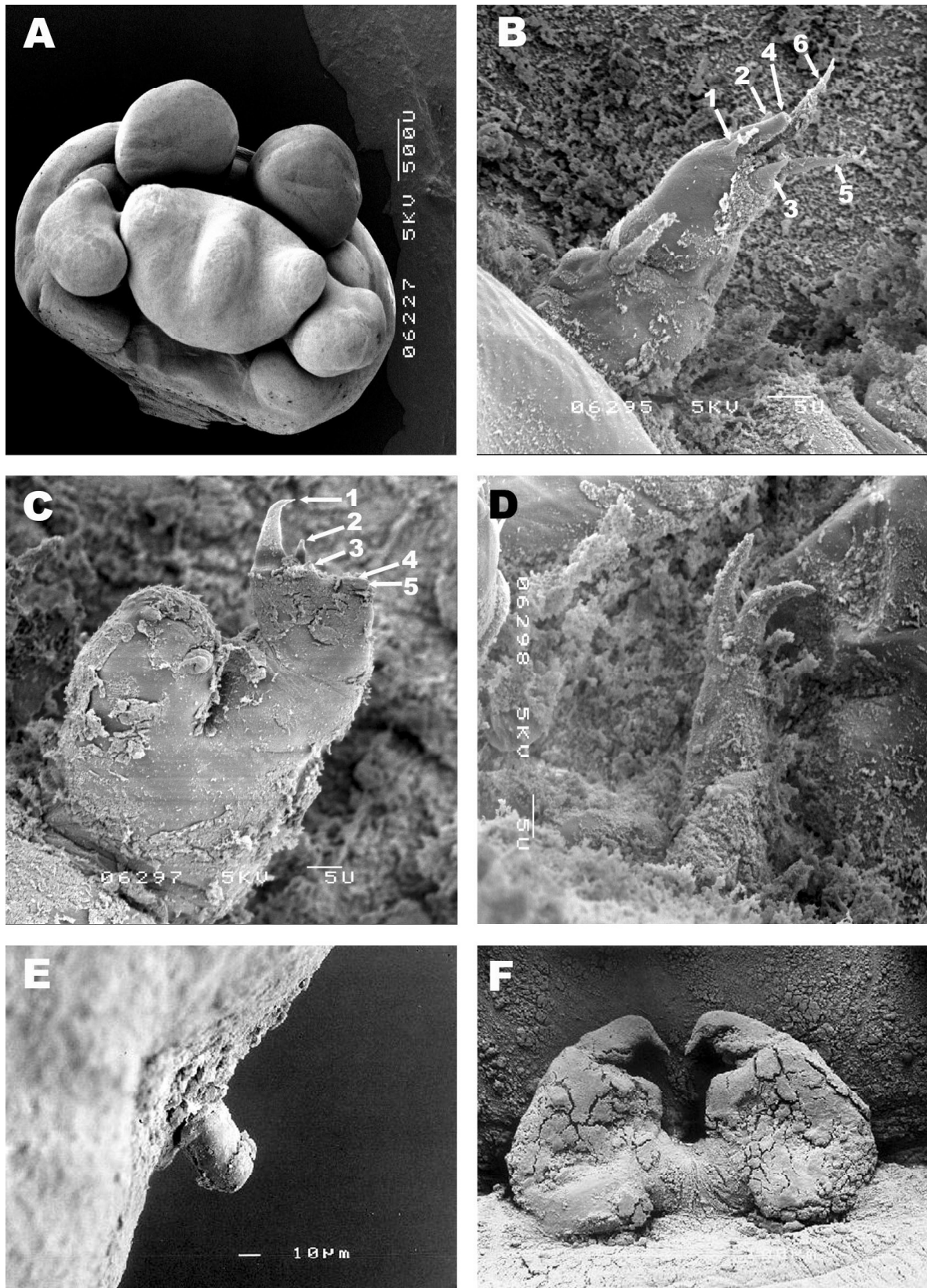


Fig. 2 Scanning electron micrographs of *Tripaphylus elongatus* (Wilson, 1932), adult female. A, Cephalothorax, ventral view; B, Antennule; C, Antenna; D, Maxillule; E, Maxilla; F, Maxillipeds. Scale-bars: A, 500 µm; B–D, 5 µm; E, 10 µm; F, 50 µm

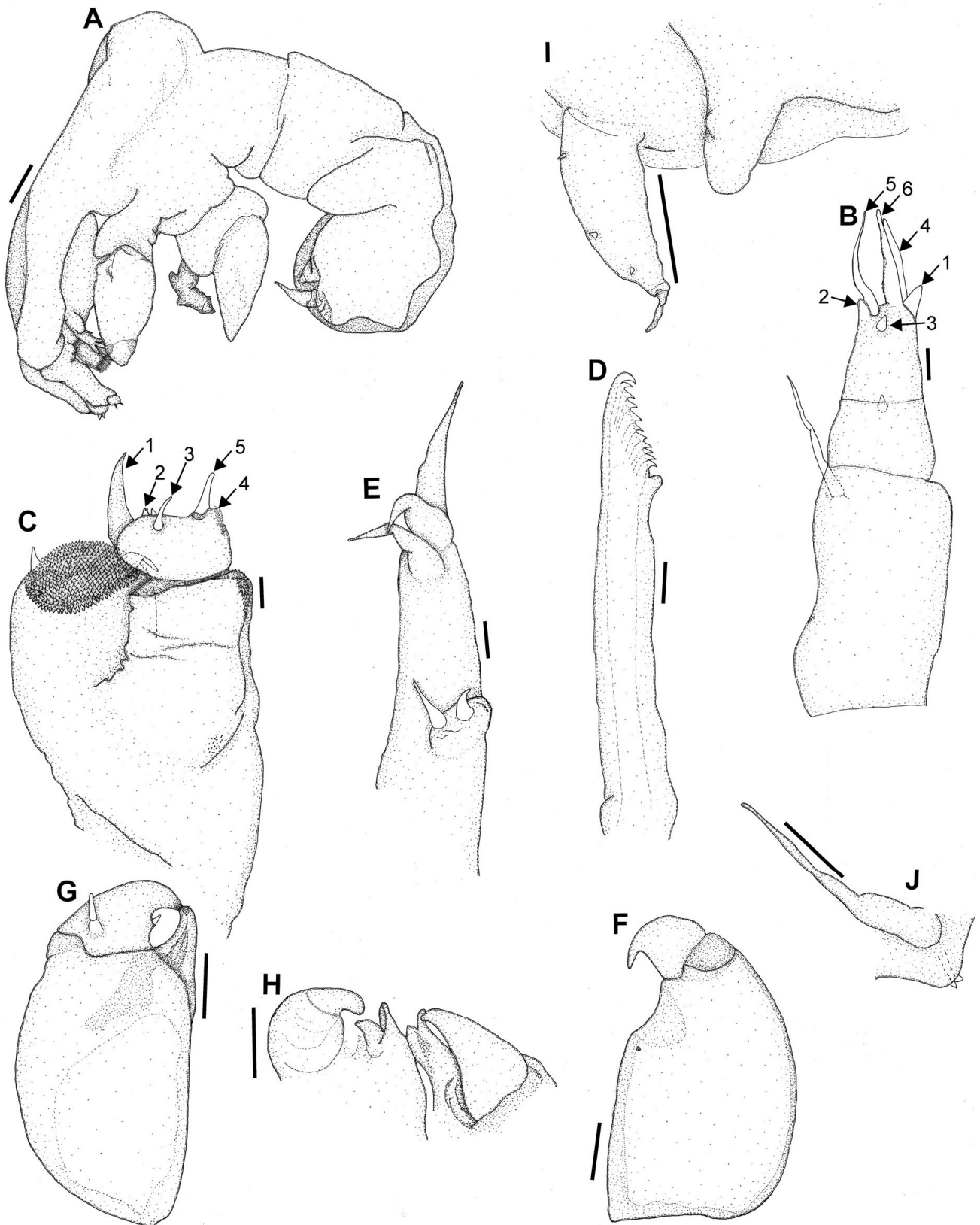


Fig. 3 *Tripaphylus elongatus* (Wilson, 1932), adult male. A, General habitus, lateral view; B, Antennule; C, Antenna; D, Mandible; E, Maxillule; F, Maxilla; G, Maxilliped; H, Myxa and subchela/claw tips of maxillipeds; I, Caudal ramus and anal process; J, Vestigial leg. Scale-bars: A, 100 μ m; B–E, J, 10 μ m; F–I, 50 μ m

maxillary swellings. Maxilliped (Figs. 1E, 2F) posterior to mouth tube, fused at base, with broad corpus, tapering subchela and elongated, flexed hook; corpus denticulated along distal margin; myxa protruding, denticulated, and armed with small tubercle-like seta; subchela with proximal patch of denticles and stout distomedial barb; hook with denticles along flexure.

Male [Based on one specimen.] Cephalothorax (Fig. 3A) about half of total length, inflated, forming arch toward ventral surface. Trunk with indistinct segmentation, ending with caudal rami posteriorly. Antennule (Fig. 3B) similar to female. Antenna (Fig. 3C) similar to female, sympod 2-segmented, first unarmed, second with medial patch of tiny denticles; endopod 2-segmented; first segment with patch of denticles near proximal medial margin, distal segment with flexed hook 1, slender seta 2 more conical, spine-like seta 3, 4 only slightly inflated, denticulated and long, stouter seta 5. Mandible (Fig. 3D) with first tooth largest followed by 10 roughly equal teeth. Maxillule (Fig. 3E) biramous; palp with 2 naked apical setae; endite armed with 3 long truncated apical setae. Maxillae (Fig. 3F) broad and stout, approximating size of maxillipeds, linked by tympanum (not illustrated); subchelate, corpus unarmed but with maxillary gland pore on inner margin, subchela indistinctly separated from claw, tip tapering and sharply curved. Maxillipeds (Fig. 3G) robust, on mediative process, fused at base; myxa unarmed, extensively elongated, with V-shaped tip; subchela short and broad with stout, elevated seta ventrolaterally and short spiniform seta mediodistally; tip of subchela broad, tapering into claw, opposing V-shaped tip of myxa (Fig. 3H). Vestigial leg (Fig. 3J), single naked seta, posterolaterally of maxillipeds. Caudal ramus (Fig. 3I) setiform, on posterior margin of body with 1 long digitiform seta on apex and 3 short spiniform setae along lateral margin. Tubercle-like anal process (Fig. 3I) anterolaterally of caudal ramus.

Remarks

Tripaphylus elongatus is easily distinguished from the other species by the structure of the cephalothoracic swellings. There is little variation in the structure of the swellings among different specimens with some specimens having antennary swellings (as) sometimes

meeting medially and/or extending beyond the anterior margin of the cephalothorax and others having posterolateral swellings (ps) sometimes extending beyond the posterior margin of cephalothorax. Although different specimens vary in size and the distinction between the neck and the trunk is often not clear, the neck is always longer than the trunk which is always longer than the posterior processes while the egg-sacs are always longer than the trunk.

The armament of the appendages is slightly different from that described for *T. musteli* (see Benz & Boxshall, 2017) with the antennule of *T. elongatus* indistinctly 3-segmented; first segment with distomedial whip; second with distoventral solus, and last segment with armature consisting of six setae on apex (see Fig. 2B) while the antennule of *T. musteli* is 2-segmented and the apex armed with four elements (see figure 3B in Benz & Boxshall (2017)). The antennae (see Fig. 2C and figure 3C in Benz & Boxshall (2017)) and maxillules (see Fig. 2D and figure 3F in Benz & Boxshall (2017)) of the two species are mostly similar. The maxillae of both species are small and digitiform while the maxillipeds (Figs. 1E, 2F and figure 3H in Benz & Boxshall (2017)) differ slightly in detail and the presence of a small seta on the myxal area and a barb on the subchela of *T. elongatus*.

Tripaphylus versicolor (Wilson, 1919)

Syn. *Paeon versicolor* Wilson, 1919

Host: *Mustelus canis* (Mitchill) (Triakidae), dusky smooth-hound.

Locality: Captured off Beaufort (34.37°N 76.41°W), North Carolina, USA.

Site in host: Interbranchial septa distal to free tips of gill filaments.

Material examined: 1♀ and 1♂ (attached to female perianal region) from the personal collection of the late Dr G. W. Benz.

Description (Figs. 4, 5)

Transformed adult female [Based on one specimen.] Body consisting of cephalothorax, neck, trunk, and small abdomen with posterior processes. Overall length in ventral view with egg-sacs 28.9 mm; body length (without posterior processes and egg-sacs) 20.4 mm; neck 12.8 mm; trunk 4.5 mm; posterior processes 5.6

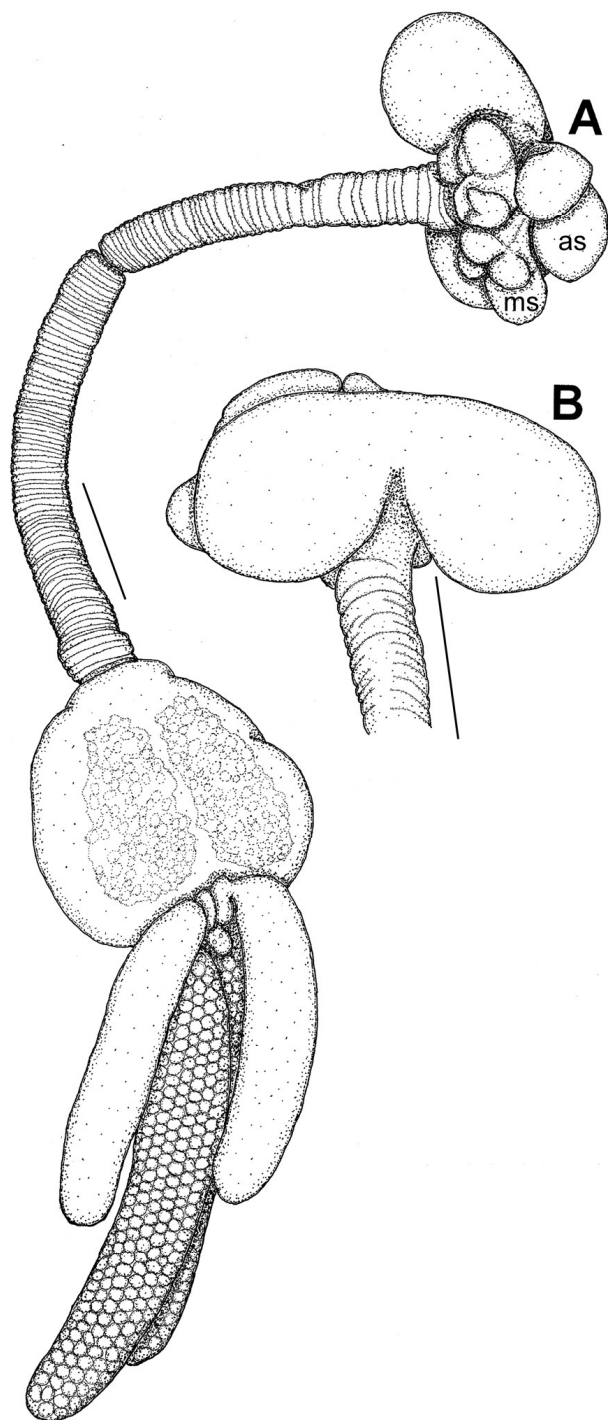


Fig. 4 *Tripaphylus versicolor* (Wilson, 1919), adult female. A, General habitus, ventral view; B, cephalothorax, dorsal view. Abbreviations: as, antennary swelling; ms, maxillary swelling. Scale-bars: 2 mm

mm; egg-sacs 8.9 mm. Cephalothorax (Figs. 4A, B) transversely elongate with smooth anterior and lateral margins, posterodorsal surface divided into 2 swellings separated posteromedially (Fig. 4B). Ventral surface

(Fig. 4A) with 2 sets of swellings; anteriorly with 2 separate globular antennary swellings (as) which may extend beyond anterior margin of cephalothorax; posteriorly with paired touching maxillary swellings (ms) consisting of 3 knobs each, 2 anterior closely related knobs, central one with finger-like projection and one posterior smaller globular knob. Neck (Fig. 4A) cylindrical, mostly of same diameter, transversally wrinkled, about half of body length. Trunk (Fig. 4A) compact, abruptly expanding from distinct junction with neck, about as wide as long, wider posterior than anterior, slightly more than fifth of body length. Abdomen (Fig. 4A) small bifid tubercle, ventrally with 2 cylindrical posterior processes, slightly longer than trunk. Egg-sacs, cylindrical, slightly less than twice length of posterior processes; eggs multiseriate.

Appendages not examined.

Male [Based on one specimen.] Cephalothorax (Fig. 5A), trunk and antennule (Fig. 5B) similar to *T. elongatus*. Antenna (Fig. 5C) similar to that of *T. elongatus* with notable differences as follows: exopod with apex less denticulated; endopod first segment with larger patch of denticles on medial margin; distal segment with flexed hook 1, slender seta 2, (more conical than slender), stout seta 3, inflated denticulated process 4, and seta 5 with inflated base. Mandible (Fig. 5D) with dental formula P1, S1, P1, S1, P1, S1, B5. Maxillule (Fig. 5E) similar to *T. elongatus*. Maxilla (Fig. 5F) robust, larger than maxilliped, subchelate, linked to its opposite by tympanum; corpus broad, myxal area with prominent tubercle, distally with 3 denticulated knobs (Fig. 5G); base of subchela broad, tapering into strongly curved, blunt claw. Maxillipeds (Fig. 5H) robust, situated on mediative process (Fig. 5I), fused at base; myxa unarmed, elevated to receive tip of claw; subchela short and broad with seta arising from small swelling near base and spiniform seta distomedially; claw tapered and curved. Caudal ramus (Fig. 5J) setiform on posterior margin of body with 1 long stout digitiform seta on apical tubercle and 3 short spiniform setae along lateral margin.

Remarks

Tripaphylus versicolor can easily be distinguished from most species by the compact trunk with the neck, posterior processes and egg-sacs longer than the trunk.

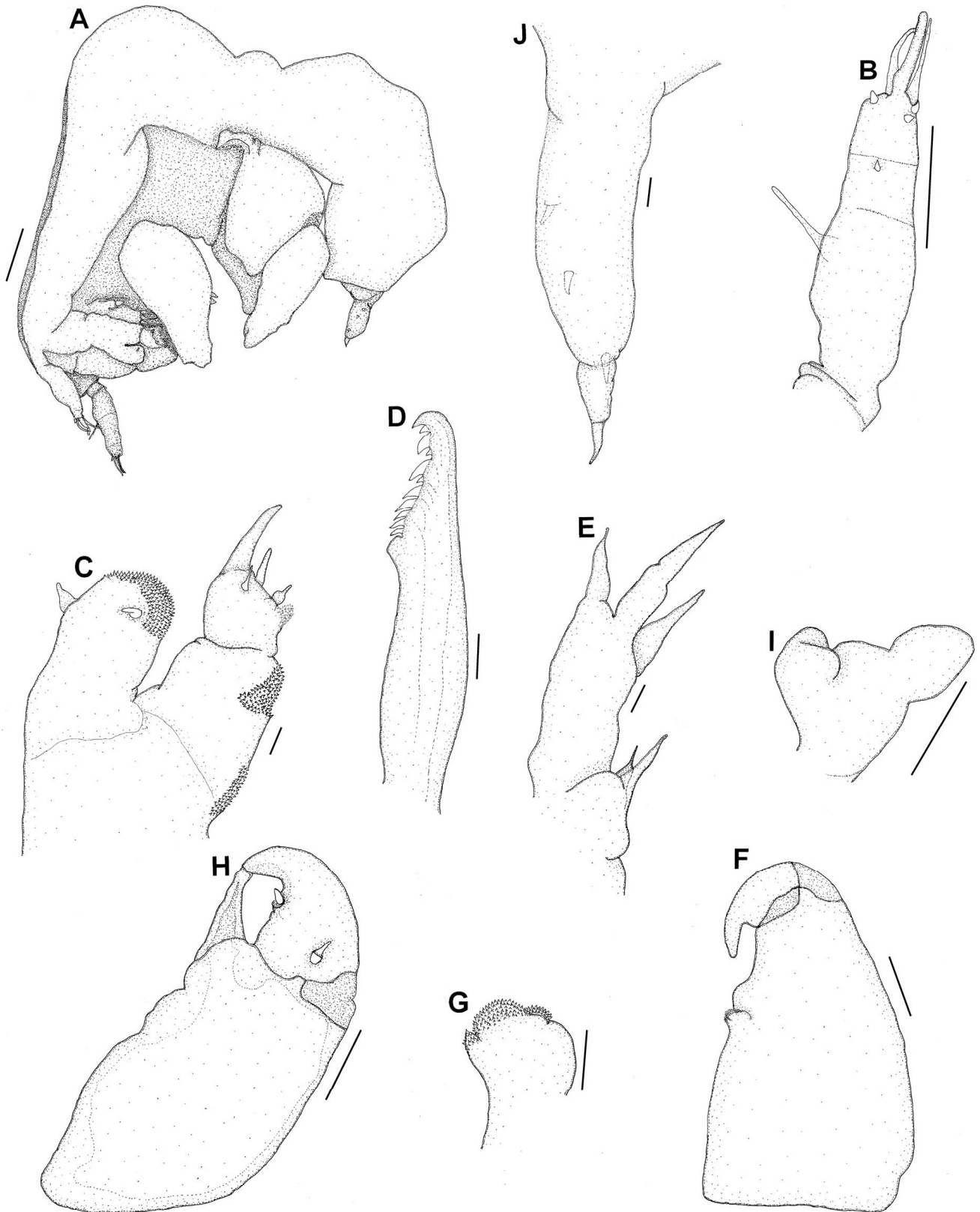


Fig. 5 *Tripaphylus versicolor* (Wilson, 1919), adult male. A, General habitus, lateral view; B, Antennule; C, Antenna; D, Mandible; E, Maxillule; F, Maxilla; G, Myxal area of maxilla; H, Maxilliped; I, Mediative process; J, Caudal ramus. *Scale-bars*: A, 100 μ m; B, H, F, 50 μ m; C–E, G, J, 10 μ m; I, 25 μ m

Additionally, this is the only species in which the posterodorsal surface of the cephalothorax is divided into two swellings separated posteromedially. The two sets of swellings ventrally on the cephalothorax are also structurally different from those of all the other species with two sets of swellings ventrally on the cephalothorax. The male of *T. versicolor* is similar to *T. elongatus* with slight differences in the armature of the antenna, mandible, maxilla, maxilliped and caudal ramus.

***Tripaphylus vaissierei* (Delamare Deboutteville & Nuñez-Ruivo, 1954)**

Syns *Paeon vaissierei* Delamare Deboutteville & Nuñez-Ruivo, 1954; *Paeon vaissierei* Delamare Deboutteville & Nuñez-Ruivo, 1954 of Dippenaar & Jordaan (2007); *Paeon lobatus* Kirtisinghe, 1964 of Kirtisinghe (1964) and Pillai (1985)

Host: *Sphyrna lewini* (Griffith & Smith) (Sphyrnidae), scalloped hammerhead shark.

Locality: Captured off Richards Bay (28.48'S 32.06'E) along the east coast of South Africa.

Site in host: Interbranchial septa distal to free tips of the gill filaments.

Material examined: 2♀♀ (one complete).

Voucher material: 1♀ (SAMC-A089331) deposited in the Iziko South African Museum, Cape Town, South Africa.

Description (Figs. 6, Supplementary Figure S1B)

Transformed adult female [Based on two specimens.] Body consisting of cephalothorax, neck, trunk, and small abdomen with posterior processes. Overall length in ventral view with egg-sacs 45.7 mm; body length (without posterior processes and egg-sacs) 24 mm; neck 10.8 mm; trunk 11.8 mm; posterior processes 12 mm; egg-sacs 23 mm. Cephalothorax (Fig. 6A–D) subquadrate, dorsoventrally compressed, with 2 large swellings anterolaterally, each with 1 small posterolateral knob (Fig. 6B). Posterodorsally cephalothorax with 3 globular swellings (Fig. 6C). Ventrally cephalothorax (Figs. 6B, Supplementary Figure S1B) comprising previously mentioned large anterolateral swellings, pair of antennary swellings

(as), and maxillary swellings (ms) that are separated by central swelling (cs). Antennary swellings each comprised of about five confluent knobs forming almost triangular protuberance, separated medially to reveal cephalothoracic appendages, extending over part of anterolateral and maxillary swellings; flanked by small globular lateral swelling (ls). Antennary swellings possibly less developed in younger female (Fig. 6D). Maxillary swellings, bi-lobed process consisting of thumb-like knob posterolaterally and smaller posteromedial knob, separated from each other by central oval swelling. Neck (Fig. 6A) slightly less than half of body length, cylindrical, gradually increasing in diameter anterior to posterior, posterior half transversally wrinkled. Delineation between neck and trunk indistinct (Fig. 6A). Trunk (Fig. 6A) slightly dorsoventrally compressed, longer than wide, gradually widening toward abdomen with slight narrowing at terminus, about half of body length. Abdomen small bifid tubercle, ventrally with 2 cylindrical posterior processes (Fig. 6A), about as long as trunk. Egg-sacs (Fig. 6A) almost twice as long as posterior processes, egg arrangement multiserial.

Appendages not examined and male not found.

Remarks

Tripaphylus vaissierei was collected and described from *Sphyrna couardi* Cadenat (Sphyrnidae) (Delamare Deboutteville & Nuñez-Ruivo, 1954). Thereafter Kirtisinghe (1964) described *T. lobatus* from *Hemipristis elongata* (Klunzinger) (Hemigaleidae) and named it in reference to the possession of a pair of genital lobes (see figure 183 in Kirtisinghe (1964)) and stated that it is clearly different from the five already known species (including *T. vaissierei*). However, comparing the swellings of the cephalothorax of the two species (see figure 182 in Kirtisinghe (1964) and figure 15b in Delamare Deboutteville & Nuñez-Ruivo (1954)) they seem to be very similar in structure. Additionally, *T. vaissierei* also seems to have slightly elevated posterolateral corners of the trunk (see figure 15a in Delamare Deboutteville & Nuñez-Ruivo (1954)) which were not observed in the current examined specimens. The presence of swollen posterolateral corners maybe a variable condition possibly associated with age or reproductive status of

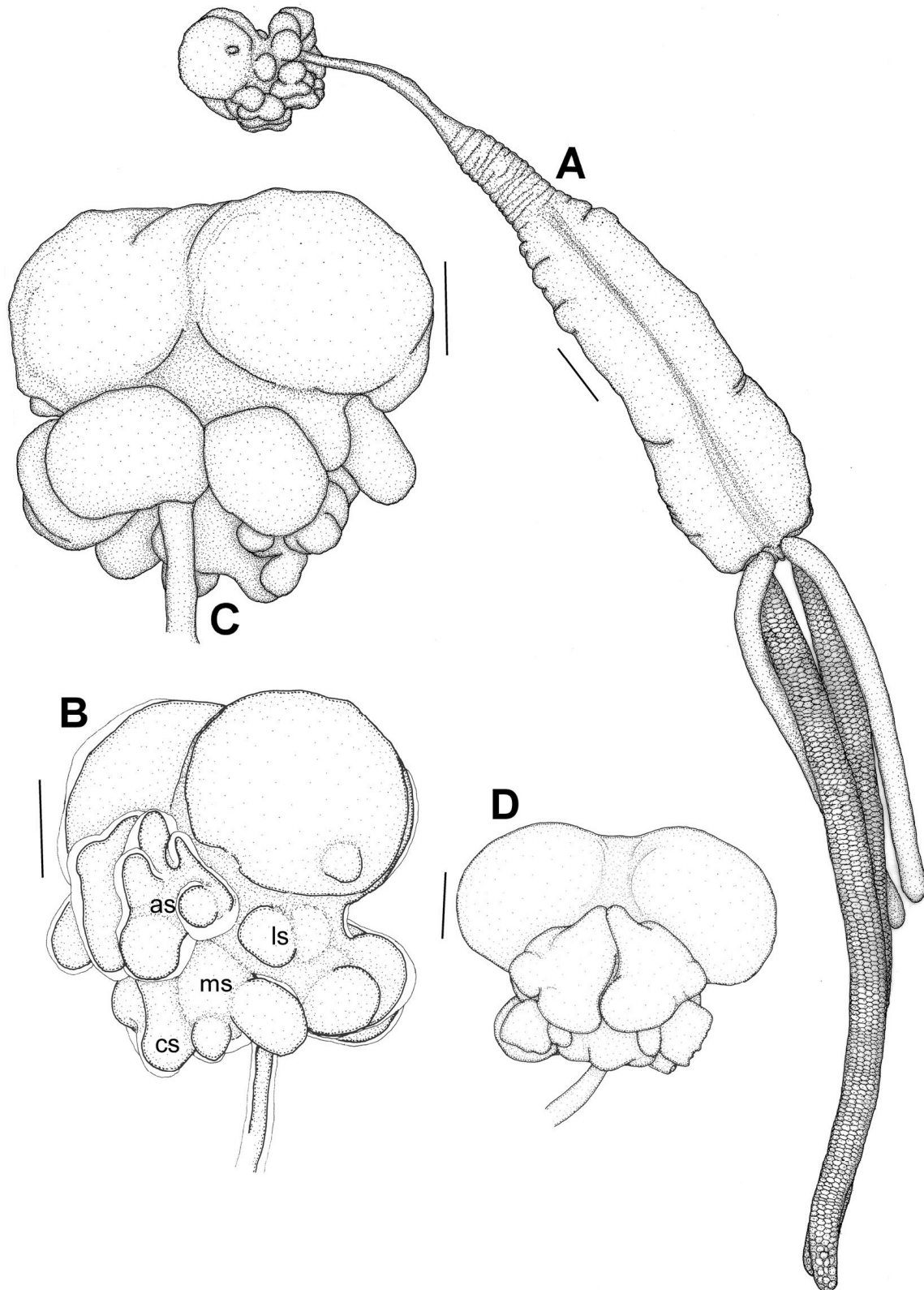


Fig. 6 *Tripaphylus vaissierei* (Delamare Debutteville & Nuñez-Ruivo, 1954), adult female. A, General habitus, ventral view, with posterolateral view of cephalothorax; B, Cephalothorax, ventrolateral view; C, cephalothorax, posterodorsal view; D, cephalothorax (young female?) ventral view. *Abbreviations:* as, antennary swelling; ms, maxillary swelling; cs, central swelling; ls, lateral swelling. *Scale-bars:* A, 2 mm; B–D, 1 mm

the female (i.e. older specimens possessing more pronounced swellings). The similarities between the two species (*T. vaissierei* and *T. lobatus*) were also noticed by Pillai (1985) who mentioned that the cephalothoraces are identical. It is therefore suggested herewith that *T. lobatus* (Kirtisinghe, 1964) be regarded as a junior synonym of *T. vaissierei* (Delamare Deboutteville & Nuñez-Ruivo, 1954). This then extends the host records of *T. vaissierei* to include representatives of Hemigaleidae from the Indian Ocean. Kabata (1993) synonymised *T. vaissierei* from *S. lewini* reported by Lewis (1966) with *T. lobatus* described by Kirtisinghe (1964). However, the specimens described by Lewis (1966) have some obvious differences from those described by Kirtisinghe (1964). First, the dorsal surface of the cephalothorax in the specimens as described by Kirtisinghe (1964) have “posterior corners produced into a pair of more oval lobes” mostly consistent with *T. vaissierei* (Fig. 6C) while that of Lewis (1966) have “a single flap-like lobe arising from the posteromedial dorsal surface of knobs and projecting posteriorly over anterior end of neck”. The ventral surface of the cephalothorax as described by Kirtisinghe (1964) has three sets of swellings mostly consistent with the current description (Fig. 6B) while that described by Lewis (1966) has six pairs of knobs. According to Kirtisinghe (1964) the neck and trunk are almost equal in length [similar to current description, different from original illustration (Delamare Deboutteville & Nuñez-Ruivo, 1954)] while the posterior processes are slightly shorter [almost equal to trunk length in current description and original illustration (Delamare Deboutteville & Nuñez-Ruivo, 1954)] while according to Lewis (1966) the neck is slightly shorter than the trunk while the posterior processes and the trunk are almost equal in length. Based mostly on the arrangement and shape of the cephalothorax swellings the specimens described by Lewis (1966) should not be synonymised with those of Kirtisinghe (1964) (here treated as conspecific with *T. vaissierei*).

***Tripaphylus ferox* (Wilson, 1919)**

Syn. *Paeon ferox* Wilson, 1919

Host: *Rhizoprionodon terraenovae* (Richardson) (Carcharhinidae), Atlantic sharpnose shark.

Locality: Captured off Beaufort (34.37°N 76.41°W), North Carolina, USA.

Site in host: Interbranchial septa distal to free tips of the gill filaments.

Material examined: 1♀ (decapitated) from the personal collection of the late Dr G. W. Benz.

Description (Fig. 7)

Transformed adult female [Based on one specimen.] Body consisting of cephalothorax, neck, trunk, and small abdomen with posterior processes. Length of neck at least 13.3 mm; trunk 14.9 mm; posterior processes 17 mm; egg-sacs broken. Cephalothorax missing. Neck (Fig. 7), cylindrical and gradually slightly increasing in diameter, diagonally striped, about same length as trunk. Trunk (Fig. 7) gradually widening with signs of transverse wrinkling, separation between neck and trunk indistinct. Posterolateral corners of trunk inflated lobes with abdomen forming bifid tubercle between lobes. Posterior processes cylindrical, longer than trunk. Egg-sacs cylindrical; eggs multiseriate.

Appendages not examined and male not found.

Remarks

Tripaphylus ferox was originally described from *Rhizoprionodon terraenovae* (Richardson) (see Wilson, 1919) where after it was reported from *Sphyrna tiburo* (Linnaeus) (see Wilson, 1935; Pearse, 1952) and again from *R. terraenovae* (see Delamare Deboutteville & Nuñez-Ruivo, 1954). However, when comparing the illustrations and description of the cephalothorax swellings of *T. ferox* in Wilson (1919) (see his figures 54, 55) with the illustrations of Delamare Deboutteville & Nuñez-Ruivo (1954) (their figures 14a, c), the report by Delamare Deboutteville & Nuñez-Ruivo (1954) does not seem to pertain to *T. ferox*. First, the proportions of the body, posterior processes and egg-sacs are quite different (also see current illustration, Fig. 7), with the original description having a trunk of almost similar length to the neck and longish posterior processes (about as long as trunk) while the egg-sacs are only slightly longer than the posterior processes whereas the trunk of the specimen illustrated by Delamare Deboutteville & Nuñez-Ruivo (1954) is slightly more than half the

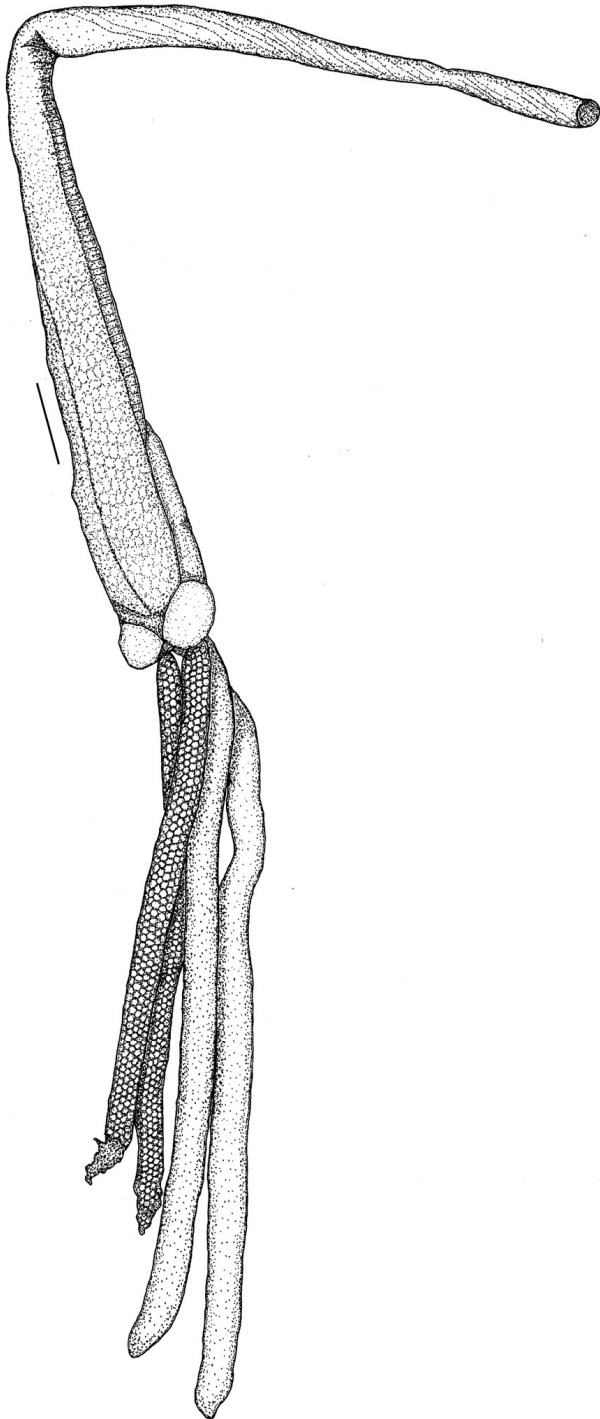


Fig. 7 *Tripaphylus ferox* (Wilson, 1919), adult female, general habitus without cephalothorax, ventral view. Scale-bar: 2 mm

length of the neck while the posterior processes are shorter than the trunk with the egg-sacs almost twice as long as the posterior processes (Delamare Deboutteville & Nuñez-Ruivo, 1954). Secondly, the arrangement of the swellings on the cephalothorax is also different. Wilson (1919) indicated the second pair of

processes, i.e. maxillary swellings as “diagonally elliptical” with “concave posterior margins”, while the second row of processes of the specimen illustrated by Delamare Deboutteville & Nuñez-Ruivo (1954) consists of three independent swellings with the central one divided into three knobs while the outside ones, i.e. maxillary swellings are globular with convex margins. The swellings of the cephalothorax illustrated by Delamare Deboutteville & Nuñez-Ruivo (1954) seem to be more similar to those of *T. elongatus* (see Figs. 1B, 2A and plate 40, figures a, c in Wilson, 1932). Therefore, it is suggested herewith, the *T. ferox* reported from *R. terraenovae* by Delamare Deboutteville & Nuñez-Ruivo (1954) be synonymised with *T. elongatus* Wilson, 1932.

***Tripaphylus lewisi* n. sp.**

Syn. *Paeon vaissierei* Delamare Deboutteville & Nuñez-Ruivo, 1954 of Lewis (1966)

Type-host: *Hemipristis elongata* (Klunzinger) (Hemigaleidae), snaggletooth shark.

Type-locality: Captured off Durban (29.51'S 31.00'E) along the east coast of South Africa.

Type-material: One complete female (holotype) and two decapitated females (one cephalothorax included), one with male (allotype) attached to perianal region, deposited in the collection of the Iziko South African Museum (SAMC-A089332). One decapitated cephalothorax used in SEM.

ZooBank registration: To comply with the regulations set out in article 8.5 of the amended 2012 version of the *International Code of Zoological Nomenclature* (ICZN, 2012), details of the new species have been submitted to ZooBank. The Life Science Identifier (LSID) for *Tripaphylus lewisi* n. sp. is urn:lsid:zoobank.org:act:3A7D1A3A-AF3A-47D5-BA28-60D68F1B1450.

Site in host: Interbranchial septa distal to free tips of the gill filaments.

Etymology: The species is named for Dr Alan G. Lewis for describing this species the first time in 1966.

Description (Figs. 8, 9, 10, Supplementary Figure S1C)

Transformed adult female [Based on three specimens, one decapitated cephalothorax used for SEM.] Body

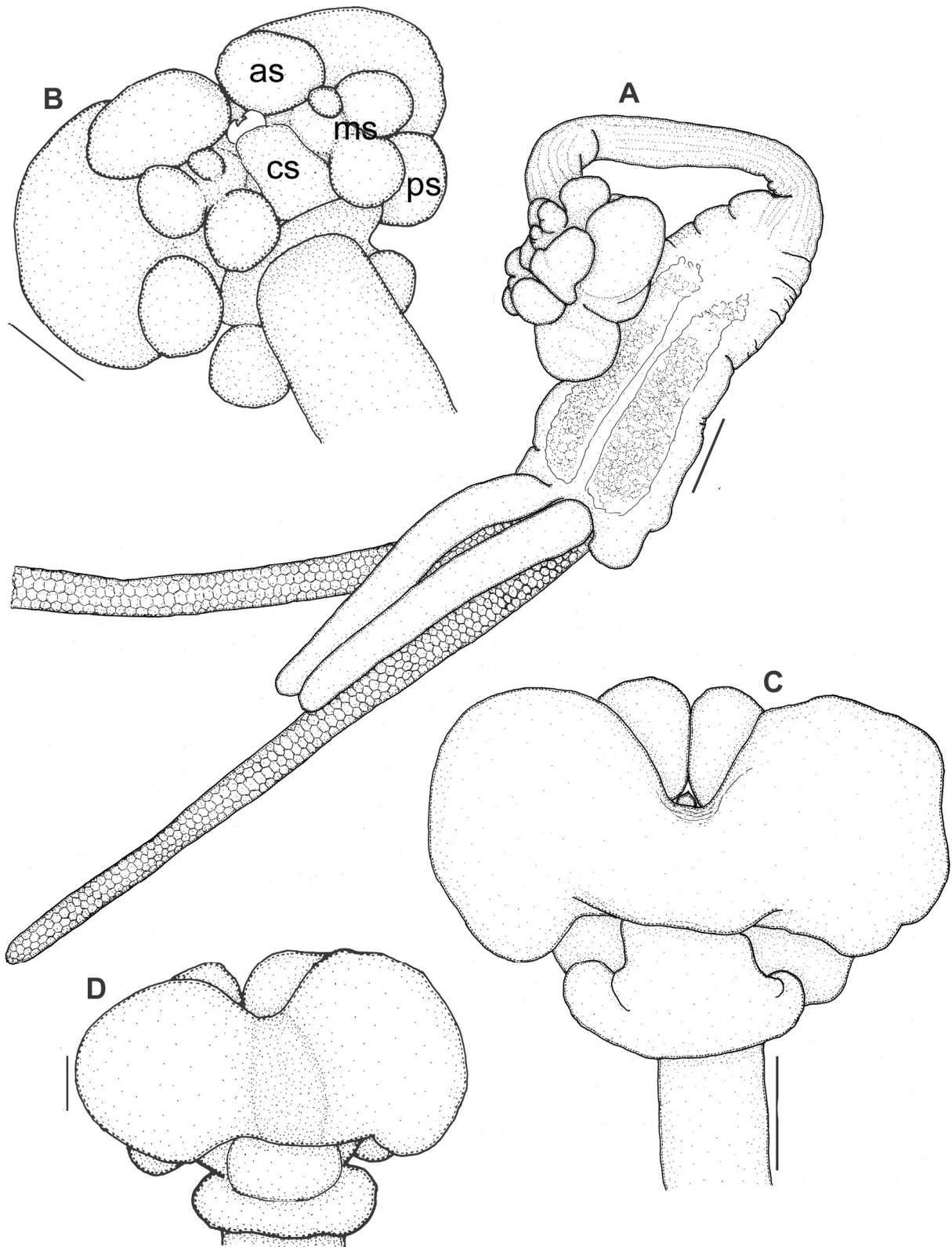


Fig. 8 *Tripaphylus lewisi* n. sp., adult female. A, General habitus, ventral view, with anteroventral view of cephalothorax; B, Cephalothorax, posteroventral view; C, D, Cephalothorax, dorsal view (2 specimens). Abbreviations: as, antennary swelling; ms, maxillary swelling; cs, central swelling; ps, posterolateral swelling. Scale-bars: A, 2 mm; B–D, 1 mm



Fig. 9 Scanning electron micrographs of *Tripaphylus lewisi* n. sp., adult female. A, Cephalothorax, ventral view; B, Maxillipeds, posteroventral view; C, Maxillipeds, ventral view. Scale-bars: A, 1 mm; B, C, 100 μ m

consisting of cephalothorax, neck, trunk and small abdomen with posterior processes. Overall length in

ventral view with egg-sacs 41.4 mm; body length (without posterior processes and egg-sacs) 23.6 mm; neck 8.75 mm; trunk 8.8 mm; posterior processes 12 mm; egg-sacs 21 mm. Cephalothorax (Figs. 8A–D, 9A) transversely elongated and dorsoventrally flattened, with 2 large swellings forming anterior part of both dorsal and ventral surfaces; posterodorsal surface with transversely elongated swelling extending into another wider and more protruded swelling appearing like collar around anterodorsal part of neck (Fig. 8C, D). Ventral surface (Figs. 8B, Supplementary Figure S1C) with 3 sets of swellings; 2 central anterior elongated globular antennary swellings (as) separated medially where cephalothoracic appendages situated posteriorly; middle set of swellings consisting of 1 central elongated swelling, laterally with maxillary swellings consisting of 3 knobs (2 large and 1 smaller); posterolaterally with 2 globular posterolateral swellings, extending beyond posterior margin of cephalothorax. Neck (Fig. 8A) cylindrical, slightly less than third of body length. Trunk (Fig. 8A) gradually widening and then slightly narrowing toward posterior extremity, with separation between neck and trunk relatively distinct, slightly more than third of body length. Abdomen small bifid tubercle ventrally with 2 cylindrical posterior processes, longer than trunk. Egg-sacs (Fig. 8A), cylindrical, almost twice length of posterior processes; eggs multiseriate. Maxilla (Fig. 9A) small thumb-like process on maxillary swelling. Maxilliped (Fig. 9B, C) less distinctly fused at base, with broad corpus, tapering subchela and elongated, flexed hook; corpus with no armature observed; myxa palp-like, elevated to meet tip of claw; subchela with proximal seta and stout distomedial barb; hook strongly curved to meet raised myxa.

Male [Based on one specimen.] Cephalothorax (Fig. 10A), slightly less than half of total length, inflated, forming arch with ventral surface. Trunk with indistinct segmentation ending posteriorly with caudal rami. Antennule (Fig. 10B) indistinctly 3-segmented; first segment with distomedial whip; second with distoventral solus, and last segment with armature consisting of 3 short (1, 2 and 3) and 3 longer (4, 5 and 6) setae on apex. Antenna (Fig. 10C) sympod indistinctly 2-segmented; endopod 2-segmented; first segment with patch of denticles near proximal medial

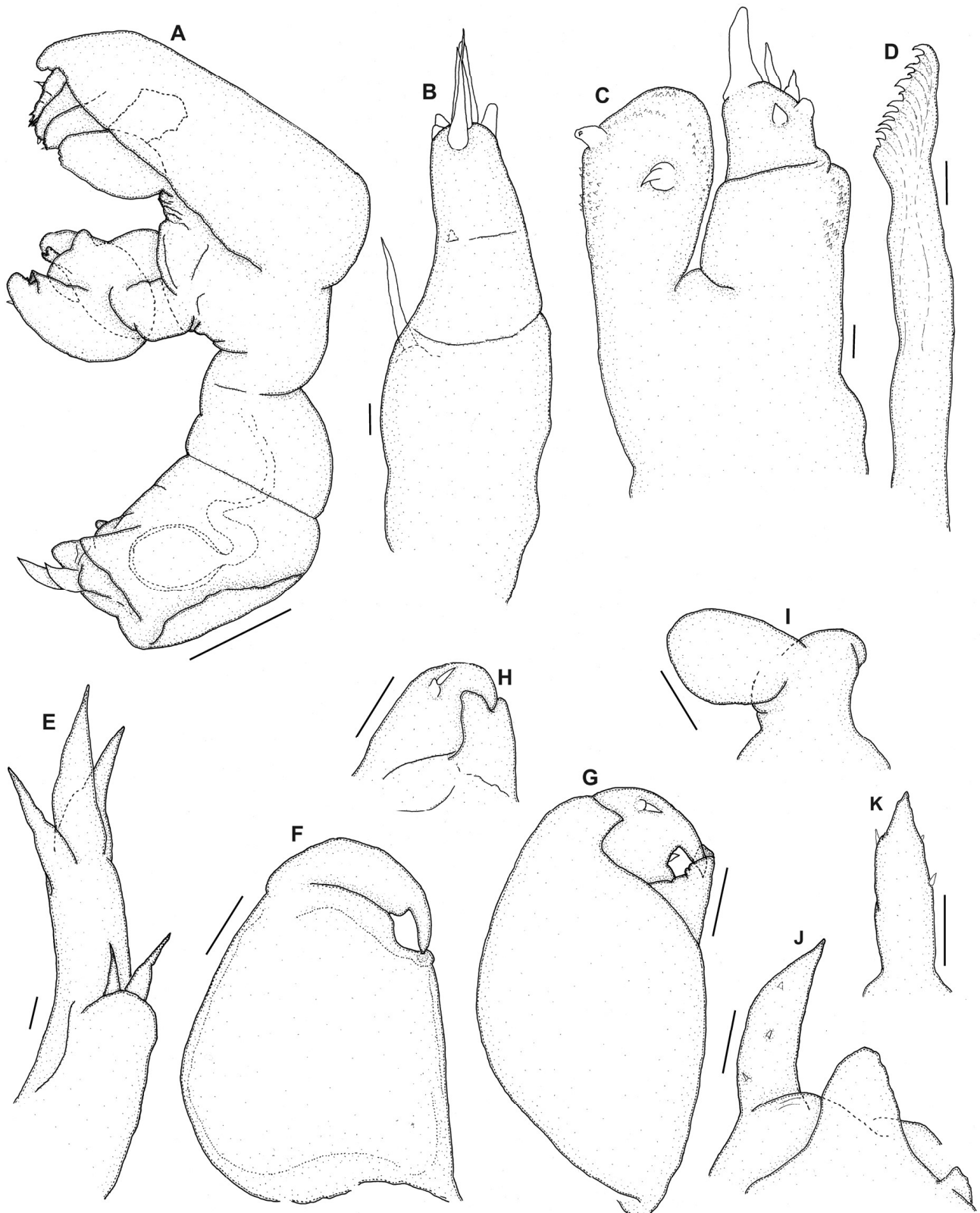


Fig. 10 *Tripaphylus lewisi* n. sp., adult male. A, General habitus, lateral view; B, Antennule; C, Antenna; D, Mandible; E, Maxillule; F, Maxilla; G, Maxilliped; H, Myxa and subchela/claw tips of maxillipeds; I, Mediative process; J, Caudal ramus and anal process; K, Caudal ramus. Scale-bars: A, 250 μ m; B–E, 10 μ m; F–K, 50 μ m

margin, distal segment with flexed hook 1, slender seta 2 more conical, spine-like seta 3, 4 only slightly inflated and stouter seta 5 with inflated base; exopod 1-segmented, bulbous, sparsely denticulated and with 2 subapical setae with inflated bases. Mandible (Fig. 10D) with dental formula P1, S1, P1, S1, P1, S1, B5. Maxillule (Fig. 10E) biramous, palp with 2 naked apical setae; endite with 3 long truncated apical setae. Maxilla (Fig. 10F) robust, larger than maxilliped, linked to its opposite member by tympanum; corpus broad, myxal area raised; base of subchela broad, tapering into strongly curved, blunt claw opposing raised myxa. Maxillipeds (Fig. 10G) robust, situated on mediative process (Fig. 10I), claw opposing raised myxa (Fig. 10H). Caudal ramus (Figs. 10J, K) setiform on posterior margin of body next to tubercle with 3 short spiniform setae along lateral margin.

Remarks

The transformed adult female *T. lewisi* n. sp. is most similar to that of *T. vaissierei* and therefore it has not been considered a new species distinct from *T. vaissierei* (see Lewis, 1966). However, there are distinct differences in the detail of the cephalothorax swellings between the two species, most notably the posterodorsal swellings which form a single, collar-like swelling in *T. lewisi* n. sp. (Fig. 8C, D) [also see Lewis (1966) “single flap-like lobe arising from posteromedian dorsal surface of knobs and projecting posteriorly over anterior end of neck”] and a row of three swellings in *T. vaissierei* (Fig. 6C). Additionally, *T. lewisi* n. sp. has three rows of ventral swellings (as, ms, ps), excluding the large rounded anterolateral swellings (seen dorsally and ventrally) (Figs. 8B, 9A) while *T. vaissierei* has only two rows of ventral swellings (as, ms), excluding the large rounded anterolateral swellings (more distinctly seen ventrally) (Fig. 6B). The shape of antennary swellings of *T. lewisi* n. sp. was variable between collected specimens (see Figs. 8B, 9A) possibly due to the age of the specimen with the various knobs representing the antennary swelling not completely developed in young females. The neck of *T. vaissierei* is comparatively much thinner and increases in diameter posteriorly with a more indistinct connection with the trunk (Fig. 6A)

while that of *T. lewisi* n. sp. is wider in diameter and does not obviously increase posteriorly, joining the trunk somewhat more distinctly (Fig. 8A). Both species have posterior processes of about the same length as the trunk and egg-sacs about twice as long as the posterior processes. The cephalothorax of the male of *T. lewisi* n. sp. is less inclined towards the trunk than those of *T. elongatus* and *T. versicolor* (see Fig. 10A and figure 40a in Lewis (1966) as well as Figs. 3A, 5A) while the trunk, antennule, maxillule and maxilliped of *T. lewisi* n. sp. are similar to those of *T. elongatus* and *T. versicolor*. The antenna of *T. lewisi* n. sp. is similar to that of *T. elongatus* and *T. versicolor* with following notable differences: exopod with apex less denticulated; endopod first segment with scattered patch of denticles on medial margin; distal segment with flexed hook 1, slender seta 2 (more conical than slender), stout seta 3, slightly inflated process 4 (without denticles), and seta 5 with inflated base similar to that of *T. versicolor*. Mandible of *T. lewisi* n. sp. similar to that of *T. versicolor*, but different from *T. elongatus* with one large and 10 almost equal-sized teeth. Minor differences exist between the current description of the male and that of Lewis (1966). However, these can be mostly attributed to lack of detail in the description and illustrations of Lewis (1966).

Tripaphylus benzi n. sp.

Type-host: *Mustelus palumbes* Smith (Triakidae), whitespotted smooth-hound.

Type-locality: Captured off the south coast (35.45'S 21.47'E) of South Africa.

Infection site: Interbranchial septa distal to free tips of the gill filaments.

Type-material: The holotype (one female with decapitated cephalothorax included) is deposited in the collection of the Iziko South African Museum (SAMC-A089333).

ZooBank registration: To comply with the regulations set out in article 8.5 of the amended 2012 version of the *International Code of Zoological Nomenclature* (ICZN, 2012), details of the new species have been submitted to ZooBank. The Life Science Identifier (LSID) for *Tripaphylus benzi* n. sp. is

urn:lsid:zoobank.org:act:89E317CA-17F6-4EB5-9253-9CCE62E33752.

Etymology: The species is named for the late Dr George W. Benz for his assistance with *Paeon* species in 1999 and his overall influence in my interest in symbiotic copepods.

Description (Fig. 11, Supplementary Figure S1D)

Transformed adult female [Based on one specimen.] Body consisting of cephalothorax, neck, trunk and small abdomen with posterior processes. Overall length in ventral view with egg-sacs 42 mm; body length (without posterior processes and egg-sacs) 29.1 mm; neck 16.7 mm; trunk 9.6 mm; posterior processes 7.3 mm; egg-sacs 13 mm. Cephalothorax (Fig. 11A–C) dorsoventrally flattened with smooth, extended dorsal surface and ventrally with extended swellings in two rows (Supplementary Figure S1D). Antennary swellings (as) consisting of 2 globular processes slightly separated medially to reveal maxillipeds posteriorly; posterior row consisting of 2 large maxillary swellings (ms) each resembling bifid knob with oval swelling (cs) separating them medially. Neck (Fig. 11A) cylindrical, slightly widening posteriorly, more than half of body length. Trunk (Fig. 11A) gradually widening toward posterior extremity, with separation between neck and trunk indistinct, about third of body length. Abdomen small bifid tubercle ventrally with 2 cylindrical posterior processes, slightly longer than two-thirds length of trunk. Egg-sacs (Fig. 11A), cylindrical, slightly less than twice length of posterior processes; eggs multiseriate. Maxilla (Fig. 11B) thumb-like tubercle posteroventral on maxillary swelling. Maxilliped (Fig. 11B) less distinctly fused to opposite member, with broad corpus, tapering subchela and elongated, flexed hook.

Appendages not examined and male not found.

Remarks

The transformed adult female *T. benzi* n. sp. is most similar to that of *T. elongatus* in terms of the elongate neck (longer than the trunk) that joins the trunk indistinctly and the short (shorter than the trunk) posterior processes. However, the shape of the cephalothorax and the number and shape of ventral swellings are different, with the swellings of *T. benzi* n. sp. consisting of two rows of mostly rounded knobs

while those of *T. elongatus* consist of three rows. The paired globular antennary swellings of *T. elongatus* may extend beyond anterior margin of cephalothorax while it is only the maxillary swellings of *T. benzi* n. sp. that extend beyond the lateral margin of the cephalothorax. The shape of the cephalothorax and the swellings of *T. musteli* (see Benz & Boxshall, 2017) seem to be similar to those of *T. benzi* n. sp. but those of *T. benzi* n. sp. essentially forms two sets with the maxillary swellings being separated by an oval swelling medially, which is absent in *T. musteli*, and bifid maxillary swellings in *T. benzi* n. sp. while those of *T. musteli* are simple and round (see figures 1, 2B in Benz & Boxshall, 2017). *Tripaphylus musteli* also have an additional pair of lateral swellings which are absent in *T. benzi* n. sp. Additionally the body proportions of the two species are also different with the neck distinctly separated from the trunk in *T. musteli* while the neck gradually leads into the trunk in *T. benzi* n. sp. The posterior processes are slightly shorter than the trunk in both species but quite a bit shorter than the egg-sacs in *T. benzi* n. sp. than in *T. musteli*.

Tripaphylus hoi n. sp.

Type-host: *Mustelus palumbes* Smith (Triakidae), whitespotted smooth-hound.

Type-locality: Captured off the south coast (34.17°S 25.58°E) of South Africa.

Type-material: The holotype (one complete female with male attached to perianal region, is deposited in the collection of the Iziko South African Museum (SAMC-A089334).

Site in host: Interbranchial septa distal to free tips of the gill filaments.

ZooBank registration: To comply with the regulations set out in article 8.5 of the amended 2012 version of the *International Code of Zoological Nomenclature* (ICZN, 2012), details of the new species have been submitted to ZooBank. The Life Science Identifier (LSID) for *Tripaphylus hoi* n. sp. is urn:lsid:zoobank.org:act:60A477A2-B58B-42D7-9768-893259F887FB.

Etymology: The species is named after Dr Ju-shey Ho for his non-tiring assistance with questions and literature about symbiotic copepods over the last 10+ years.

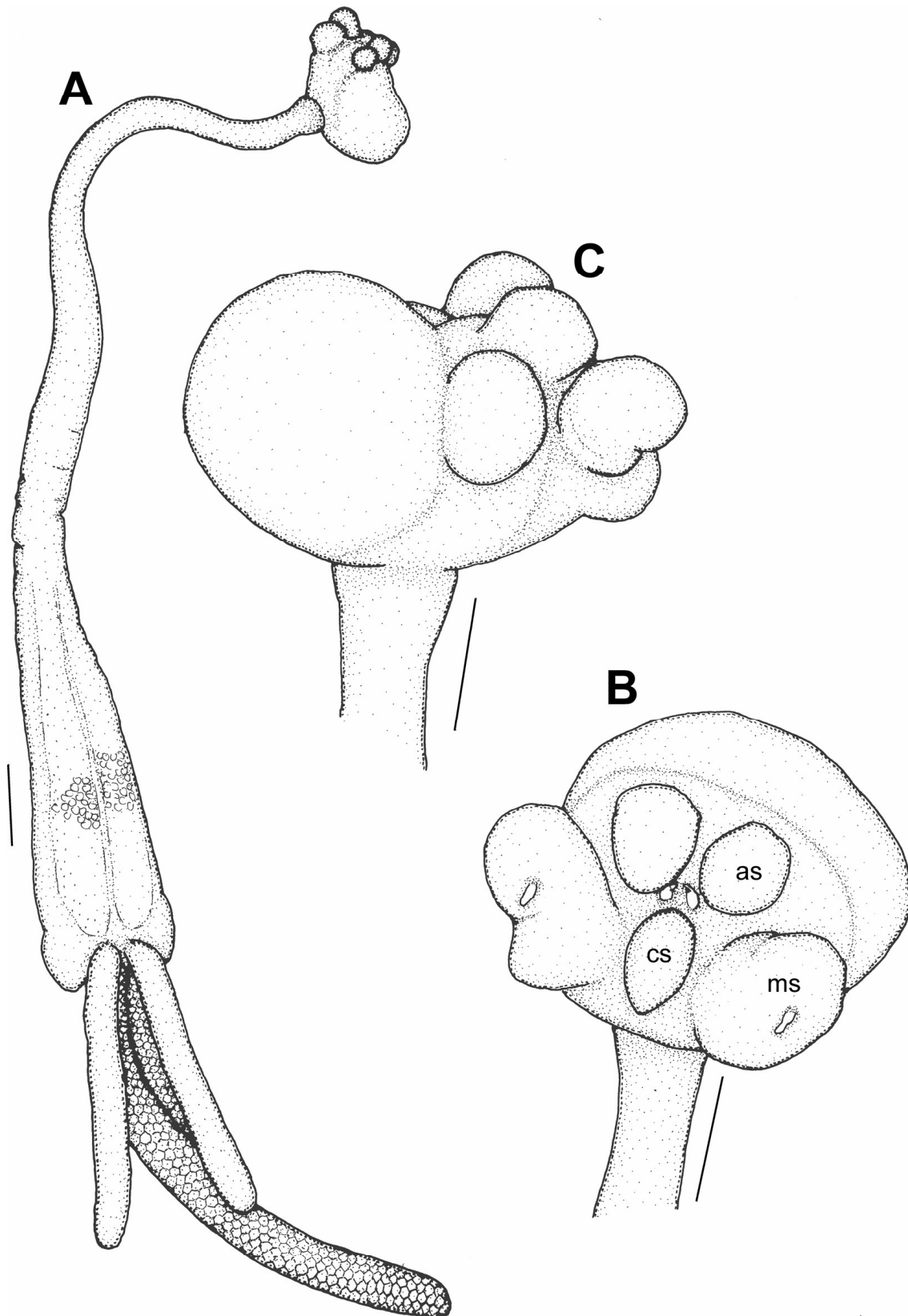


Fig. 11 *Tripaphylus benzi* n. sp., adult female. A, General habitus, ventral view, with ventrolateral view of cephalothorax; B, Cephalothorax, ventral view; C, Cephalothorax, lateral view. *Abbreviations:* as, antennary swelling; ms, maxillary swelling; cs, central swelling. *Scale-bars:* A, 2 mm; B, C, 1 mm

Description (Fig. 12, Supplementary Figure S1E)

Transformed adult female [Based on one specimen.] Body consisting of cephalothorax, neck, trunk, and small abdomen with posterior processes. Overall length in ventral view with egg-sacs 32.2 mm; body length (without posterior processes and egg-sacs) 23.9 mm; neck 13.2 mm; trunk 8.1 mm; posterior processes 7.7 mm; egg-sacs 8 mm. Cephalothorax (Fig. 12A–C) suborbicular with smooth, globular anterior and dorsal surfaces; posteroventrally with 1 pair of globular antennary swellings (as) each extending from lateral arm-like swelling and touching posteromedially with another posterior pair of laterally directed thumb-like maxillary swellings (ms) separated by slight round medial swelling (cs) (Supplementary Figure S1E). Neck (Fig. 12A) cylindrical, slightly widening posteriorly, just more than half of body length. Trunk (Fig. 12A) gradually widening toward posterior extremity, with separation between neck and trunk indistinct, slightly more than third of total body length. Abdomen bifid small tubercle ventrally with two cylindrical posterior processes (Fig. 12A) slightly shorter than trunk length. Egg-sacs (Fig. 12A), cylindrical, slightly longer than posterior processes; eggs multiseriate. Maxilla (Fig. 12C) small thumb-like tubercle posterior on maxillary swelling. Maxillipeds obscured posteriorly between antennary swellings.

Appendages not examined and male not found.

Remarks

Even though *T. benzi* n. sp. and *T. hoi* n. sp. are both collected from *M. palumbes* (different specimens) the difference in the structure of the cephalothoracic swellings and the body proportions of the two individuals justify the description of two new species since such variation among different specimens was not encountered in specimens of *T. elongatus* (see above). Furthermore, other species (e.g. *T. vaissierei* and *T. lewisi* n. sp.) both occur on *S. lewini* and *H. elongata* indicating that different species do infect the same host species. The transformed adult female *T. hoi* n. sp. is most similar to that of *T. benzi* n. sp. However, the shape of the cephalothorax and the ventral swellings are different, with the swellings of *T. hoi* n. sp. located mostly posteroventrally on the cephalothorax (Fig. 12A, B) rather than medio- and posteroventrally as those of *T. benzi* n. sp. (Fig. 11A–

C). Additionally, the swellings of *T. hoi* are essentially two sets with the antennary swellings touching posteromedially and the maxillary swellings projecting laterally while those of *T. benzi* n. sp. have separated antennary swellings and the maxillary swellings project anterolaterally. The body proportions also differ with *T. hoi* n. sp. having a trunk of similar length to the egg-sacs and the posterior processes are only slightly shorter while the posterior processes of *T. benzi* n. sp. are shorter than the trunk which is shorter than the egg-sacs. Thus the posterior processes of *T. benzi* n. sp. are distinctly shorter than the egg-sacs while those of *T. hoi* n. sp. are almost the same length as the egg-sacs.

Tripaphylus beatricae n. sp.

Type-host: *Mustelus mustelus* (Linnaeus) (Triakidae), smooth-hound.

Type-locality: Captured off Gansbaai (34.35'S 19.20'E) of the west coast of South Africa.

Type-material: One complete female (holotype) and one decapitated female (damaged cephalothorax included) deposited in the collection of the Iziko South African Museum (SAMC-A089335).

Site in host: Interbranchial septa distal to free tips of the gill filaments.

ZooBank registration: To comply with the regulations set out in article 8.5 of the amended 2012 version of the *International Code of Zoological Nomenclature* (ICZN, 2012), details of the new species have been submitted to ZooBank. The Life Science Identifier (LSID) for *Tripaphylus beatricae* n. sp. is urn:lsid:zoobank.org:act:507CE880-2C2F-499B-8735-FC72509E2B54.

Etymology: The species is named for Ms Beatrice P. Jordaan for her endless assistance in the collection of symbiotic Siphonostomatoidea during the past 20 years.

Description (Fig. 13, Supplementary Figure S1F)

Transformed adult female [Based on two specimens.] Body consisting of cephalothorax, neck, trunk, and small abdomen with posterior processes. Overall length in ventral view with egg-sacs 57.1 mm; body length (without posterior processes and egg-sacs) 28 mm; neck 21.6 mm; trunk 9.9 mm; posterior processes 13.4 mm; egg-sacs 22 mm. Cephalothorax (Fig. 13A–

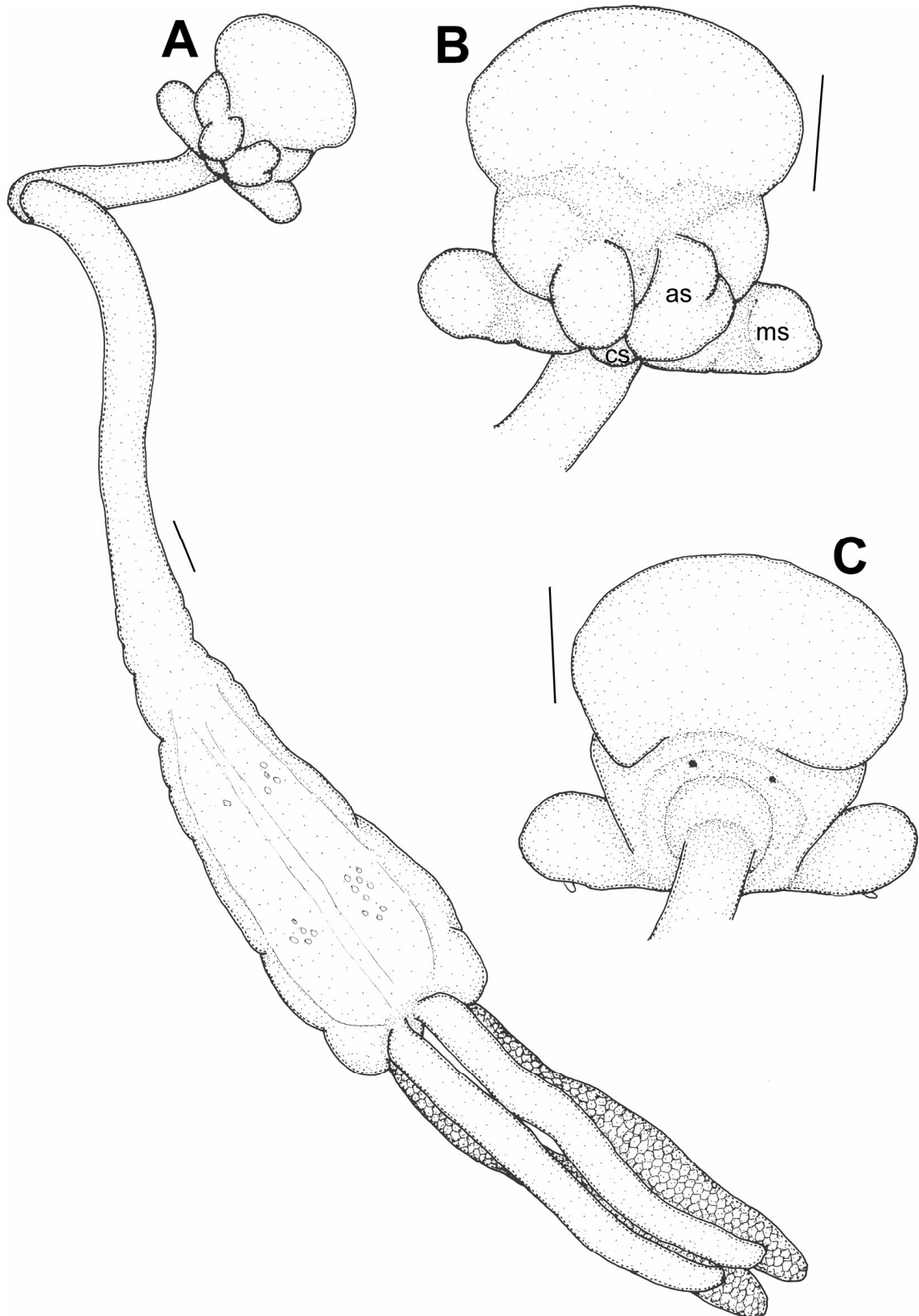


Fig. 12 *Tripaphylus hoi* n. sp., adult female. A, General habitus, ventral view, with cephalothorax; B, Cephalothorax, ventral view; C, cephalothorax, posterodorsal view. Abbreviations: as, antennary swelling; ms, maxillary swelling; cs, central swelling. Scale-bars: 1 mm

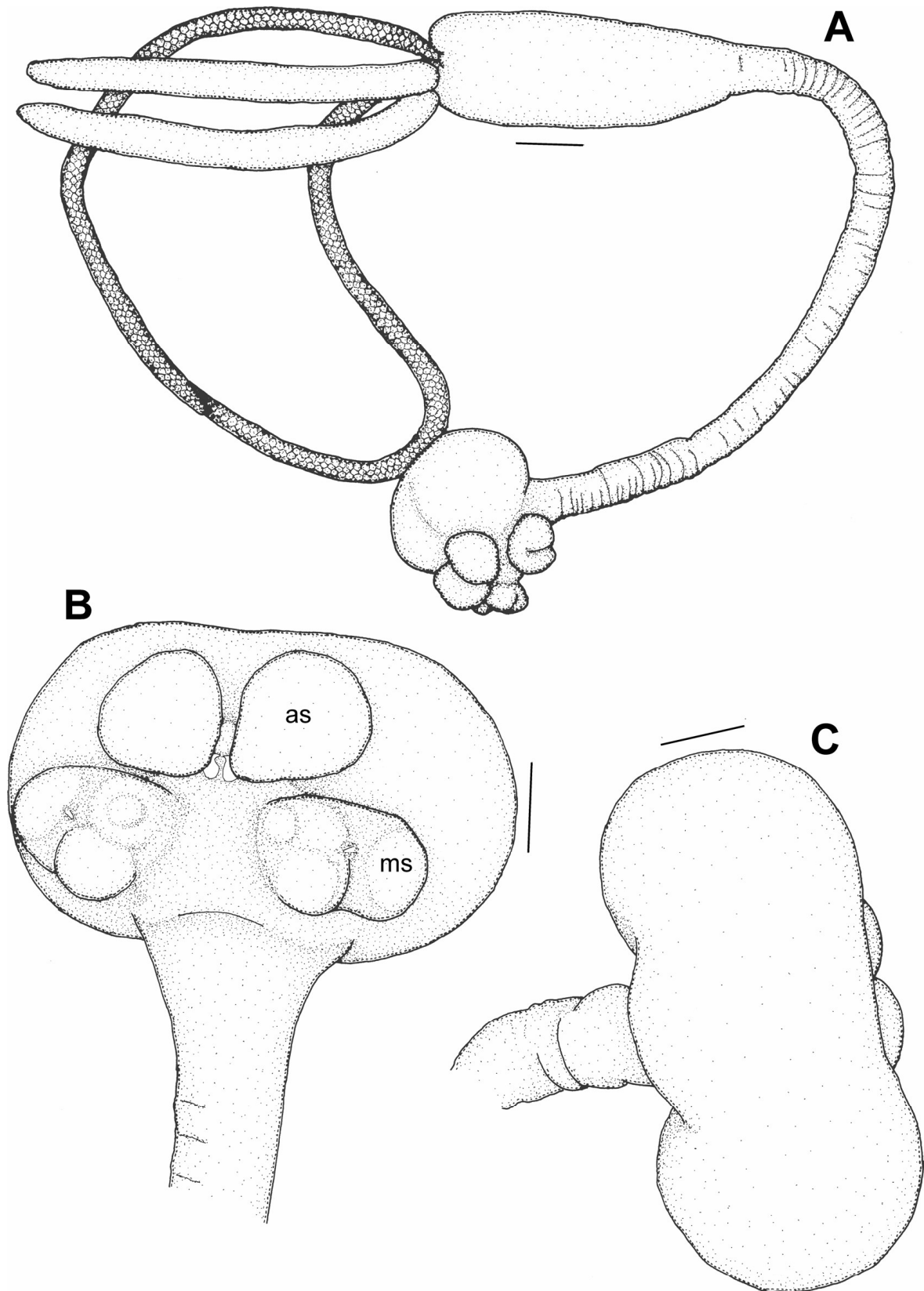


Fig. 13 *Tripaphylus beatricae* n. sp., adult female. A, General habitus, ventral view, with ventrolateral view of cephalothorax; B, Cephalothorax, ventral view; C, Cephalothorax, anterodorsal view. *Abbreviations:* as, antennary swelling; ms, maxillary swelling. *Scale-bars:* A, 2 mm; B, C, 1 mm

C) dorsoventrally flattened with smooth dorsal surface posteriorly indistinctly divided into 3 parts (Fig. 13C), ventrally with 2 rows of swellings (Figs. 13A, B, Supplementary Figure S1F). Antennary swellings (as) consisting of 2 globular processes slightly apart medially (or meeting); posterior row consisting of 2 large maxillary swellings (ms) each divided into 2 knobs (1 medial knob comprising of 2 swellings), separated medially by flat extension of raised swelling carrying maxillary swellings (maxillary swellings meeting medially in one specimen). Neck (Fig. 13A) cylindrical, only slightly widening posteriorly, almost three-quarters of body length. Trunk (Fig. 13A) gradually widening toward posterior extremity, with separation between neck and trunk indistinct, slightly more than third of body length. Abdomen small bifid tubercle ventrally with 2 cylindrical posterior processes (Fig. 13A), almost one and a third length of trunk. Egg-sacs (Fig. 13A) cylindrical, slightly less than twice length of posterior processes; eggs multi-seriate. Maxilla (Fig. 13B) thumb-like tubercle on inner margin of lateralmost maxillary swelling. Maxilliped (Fig. 13B) obscured by posterior parts of antennary swellings, seemingly fused to opposite member, with broad corpus, tapering subchela and elongated, flexed hook.

Appendages not examined and male not found.

Remarks

The transformed adult female *T. beatricae* n. sp. is most similar to that of *T. musteli* and *T. benzi* n. sp. However, the shapes of the maxillary swellings are different. In *T. beatricae* n. sp. the maxillary swellings are each divided into two knobs (Fig. 13B) similar to those of *T. benzi* n. sp. (Fig. 11B) while the maxillary swellings of *T. musteli* are simple and undivided. The knobs of the maxillary swelling of *T. beatricae* n. sp. consist of a lateral and medial knob while those of *T. benzi* consist of an anterior and posterior knob. Additionally, the maxillary swellings of *T. beatricae* n. sp. occur on a raised swelling and are separated from each other by a flat continuation of this swelling while those of *T. benzi* n. sp. are not situated on a raised swelling and are separated by an additional oval swelling. The body proportions of the three species are also different with the neck relatively longer in *T. beatricae* n. sp. (Fig. 13A) than in the other two while the posterior processes are shorter than the trunk

in *T. benzi* n. sp. (Fig. 11A) and *T. musteli* but longer than the trunk in *T. beatricae* n. sp. The egg-sacs of *T. musteli* are just longer than the posterior processes while those of *T. benzi* n. sp. (Fig. 11A) and *T. beatricae* n. sp. (Fig. 13A) are slightly less than twice the length of the posterior processes.

Revised species

Tripaphylus musteli (van Beneden, 1851)

Syns *Lerneonema musteli* van Beneden, 1851; *Tripaphylum musteli* (van Beneden, 1851) of Anonymous (1878), Wilson (1919), van Oorde-de-Lint & Schuurmans Stekhoven (1936), Kirtisinghe (1964) and Pillai (1985); *Lernaenicus musteli* (van Beneden 1851) of Bassett-Smith (1899) and Scott (1904)

Remark

A species with relatively elongated trunk distinctly separated from neck. Neck longer than trunk, posterior processes and egg-sacs slightly shorter than trunk, but egg-sacs longer than posterior processes. Cephalothorax ventrally with three sets of swellings: antennary swellings meeting medially, paired maxillary swellings separated medially and paired less defined lateral swellings (Benz & Boxshall, 2017).

Tripaphylus hemigalei Kirtisinghe, 1964

Remark

A species with elongated trunk distinct from neck. Posterior processes little shorter than trunk with egg-sacs about twice length of posterior processes. Cephalothorax anteriorly with median and two lateral lobes, laterally with “short, unbranched horns” projecting backwards. Maxillipeds “occupy considerable area of ventral surface” (Kirtisinghe, 1964).

Tripaphylus australis (Kabata, 1993)

Syn. *Paeon australis* Kabata, 1993

Remark

A species with a compact trunk with clear distinction from neck. Posterior processes slightly longer than trunk while egg-sacs are longer than trunk and posterior processes. Cephalothorax ventrally with

three sets of swellings: separated paired antennary swellings, medially fused maxillary swellings (“shelf-like”) and pair of lateral swellings between antennary and maxillary swellings (Kabata, 1993).

***Tripaphylus triakis* (Castro Romero, 2001)**

Syn. *Paeon triakis* Castro Romero, 2001

Remark

A species with a compact trunk longer than wide, fairly distinct from neck. Posterior processes longer than trunk while egg-sacs are longer than both trunk and posterior processes. Cephalothorax with three sets of swellings: paired lobular swellings anterolaterally as well as posterolaterally, paired antennary swellings between pair of anterolateral swellings. Unclear which pair of lobular processes represent maxillary swellings, maybe anterolateral pair (Castro Romero, 2001).

***Tripaphylus asymboli* (Turner, Kyne & Bennett, 2003)**

Syn. *Paeon asymboli* Turner, Kyne & Bennett, 2003

Remark

A species with a compact trunk, slightly elongated with fairly clear distinction from neck. Posterior processes almost same length as trunk while egg-sacs are longer than trunk. Ventrally on cephalothorax two sets of swellings: paired antennary swellings separated by midline swelling and complex paired maxillary swellings consisting of various knobs (Turner et al., 2003).

Discussion

Thorough illustrated descriptions of the appendage of the female of the genus *Tripaphylus* exist only for *T. musteli* (see Benz & Boxshall, 2017) while scanty descriptions exist only for *T. ferox*, *T. versicolor* and *T. elongatus* (see Wilson 1919, 1932) and *T. lewisi* n. sp. (as *Paeon vaissierei*; see Lewis, 1966). The appendages described for *T. elongatus* are antennae similar to those found in this study with additional information on the armature (see Fig. 2C) and with similar maxillipeds (see Figs. 1E, 2F and plate 40 of Wilson, 1932). In this study detailed descriptions are also

provided for the antennules, maxillules and the maxillae (see Figs. 2B, D, E). Additional descriptions and illustrations of the adult transformed female habitus of *T. versicolor* (including the swellings of the cephalothorax) (Fig. 4) and *T. ferox* (excluding the cephalothorax) (Fig. 7) are provided. A description and illustrations are also done of the habitus with cephalothorax of the adult transformed female *T. vaissierei* (which is considered to be conspecific to *P. lobatus* as described by Kirtisinghe, 1964) (Fig. 6). Unfortunately, the appendages were not examined and thus there is still no description of the appendages of *T. vaissierei*. A new species *T. lewisi* n. sp. (Figs. 8, 9) is described which includes in its synonymy *P. vaissierei* as reported by Lewis (1966). Unfortunately, the appendages were not examined in the present study but were vaguely described by Lewis (1966) and seem to correspond to the general structure of those of the other species but cannot be used for detailed comparisons. Three additional new species *T. benzi* n. sp. (Fig. 11), *T. hoi* n. sp. (Fig. 12) and *T. beatricae* n. sp. (Fig. 13) are described based on the different structures of the cephalothoraces and different body proportions. For all of these there are currently no descriptions of the appendages other than the maxillipeds. Comparing all the illustrations of the transformed adult females of the accepted species and the newly described species, *T. musteli*, *T. ferox*, *T. versicolor*, *T. elongatus*, *T. vaissierei*, *T. hemigalei*, *T. australis*, *T. triakis*, *T. asymboli*, *T. lewisi* n. sp., *T. benzi* n. sp., *T. hoi* n. sp., and *T. beatricae* n. sp., it is clear that they all have a cephalothorax with swellings that mostly obscure the majority of the appendages (except maybe *T. hemigalei*), a neck, trunk and paired posterior processes, and egg-sacs of variable lengths. However, it is impossible to understand and explain why Kirtisinghe (1964) provided a description and illustration of the transformed adult female of *T. vaissierei* (as *Paeon lobatus*) clearly indicating the swellings on the cephalothorax, but then provided only a very rudimentary illustration of the cephalothorax of *T. hemigalei* with no indication of any cephalothoracic swellings apart from the “short, unbranched horn on each side” (Kirtisinghe 1964). It is unclear what is indicated as the median and lateral lobes on the anterior margin of the cephalothorax since most species have no swellings anteriorly. In all species, the maxillipeds are small and often obscured by the antennary swellings, while Kirtisinghe (1964)

indicated that the maxillipeds of *T. hemigalei* occupy most of the ventral surface of the cephalothorax but did not illustrate them on the cephalothorax. Due to these inconsistencies it is therefore recommended that *T. hemigalei* be considered as a *species inquirenda* within the genus *Tripaphylus* until more information becomes available.

Descriptions, although lacking finer detail of some of the armature, are available for the antennules, antennae, maxillules, maxillae and maxillipeds of the males of *T. musteli* (see Scott & Scott, 1913), *T. ferox* and *T. versicolor* (see Wilson, 1919). This study provides a more detailed description and illustrations of the appendages of the male of *T. versicolor* (Fig. 5). As in the female, the descriptions of the appendages of the male *T. elongatus* (see Wilson, 1932) are similar to those in this study with additional detail provided on the armature (Fig. 3). A detailed description and illustrations of the male of *T. lewisi* n. sp. (Fig. 10) are provided with more detail and some minor differences from the description and illustrations done by Lewis (1966). When comparing the present findings on the males of *T. elongatus*, *T. versicolor* and *T. lewisi*, it seems that differences exist mainly in the detail of the armature of the antennae, the mandibles and the myxal area of the maxillae with other features showing a lot of similarity among the different species.

Tripaphylus musteli was reported from *Mustelus asterias* Cloquet in the Northern Atlantic (van Beneden, 1851; Scott & Scott, 1913; Benz & Boxshall, 2017). *Tripaphylus ferox* specimens were collected and described from the gill cavity of *R. terraenovae* from the Atlantic Ocean (Wilson, 1919). Since then the same species has been reported by Wilson (1935) and Pearse (1952) from the gills of *Sphyrna tiburo* (Linnaeus) from the Gulf of Mexico and the Atlantic Ocean, respectively. This report of *T. ferox* is also from *R. terraenovae* from the Atlantic Ocean. *Tripaphylus versicolor* was reported from *Mustelus canis* (Mitchill) from the Atlantic Ocean (Wilson, 1919) and again from the same host and locality in this report. *Tripaphylus elongatus* was found on *Carcharhinus plumbeus* (Nardo) and *C. obscurus* from the Atlantic Ocean (Wilson, 1932). Thereafter it was reported from *R. terraenovae* from the Atlantic Ocean (reported as *P. ferox*, but synonymised in this report) (Delamare Deboutteville & Nuñez-Ruivo, 1954) and also from *C. obscurus* from the Indian Ocean off South Africa (Dippenaar & Jordaan, 2007). *Tripaphylus vaissierei*

was described from the gill cavity of *Sphyrna couardi* and another unknown species reported from *S. lewini* both from the Atlantic Ocean (Delamare Deboutteville & Nuñez-Ruivo, 1954). Kirtisinghe (1964) reported *T. vaissierei* (described as *P. lobatus*, but synonymised in this report) from *Hemipristis elongata* from the Indian Ocean while it was also reported from *S. lewini* from the Indian Ocean off South Africa (Dippenaar & Jordaan, 2007). A new species, *T. lewisi* n. sp., is reported from *H. elongata* from the Indian Ocean off South Africa. This species is conspecific to the one reported by Lewis (1966) from *S. lewini* captured in the Pacific Ocean (reported as *P. vaissierei* but synonymised with *T. lewisi* n. sp.). Two other new species, *T. benzi* n. sp. and *T. hoi* n. sp., are reported from *M. palumbes* off the south coast of South Africa (Indian Ocean) while *T. beatricae* n. sp. from *M. mustelus* is reported off the west coast of South Africa (Atlantic Ocean). *Tripaphylus australis* was reported from the gills of *Glaucostegus typus* (Anonymous [Bennett]) (see Kabata, 1993) and *Aptychotrema rostrata* (Shaw) (see Turner et al., 2003) from the Pacific Ocean. Castro Romero (2001) described *T. triakis* from *Triakis maculata* Kner & Steindachner and *Mustelus mento* Cope, also from the Pacific Ocean with *T. asymboli* being described from *Asymbolus analis* (Ogilby) and *A. rubiginosus* Last, Gomon & Gledhill also from the Pacific Ocean (Turner et al., 2003). Considering all the reports, *Tripaphylus* spp. have mostly been reported from Carcharhiniformes (Carcharhinidae: *T. ferox*, *T. elongatus*; Sphyrnidae: *T. ferox*, *T. vaissierei*, *T. lewisi* n. sp.; Triakidae: *T. musteli*, *T. versicolor*, *T. triakis*, *T. benzi* n. sp., *T. hoi* n. sp., *T. beatricae* n. sp.; Hemigaleidae: *T. vaissierei*, *T. lewisi* n. sp.; and Pentachidae: *T. asymboli*) but also from Rhinopristiformes (Glaucostegidae: *T. australis*; and Trygonorrhinidae: *T. australis*).

Kabata (1993) suggested the use of: (i) the size and shape of cephalothorax; (ii) length and width of neck; and (iii) size and shape of the trunk, as features to use when attempting to identify *Tripaphylus* species. However, more specifically the use of: (i) the number, size and position of the cephalothoracic swellings; and (ii) the proportions between the cephalothorax and trunk lengths and widths were recommended by Turner et al. (2003). From the current study, the following characteristics seem to be most important:

(i) the shape of the trunk and its size in relation to that of the neck, posterior processes and egg-sacs; and (ii) the number, size, shape and position of cephalothoracic swellings.

A key to the species of *Tripaphylus* based on the morphology of transformed adult females

- 1a Trunk compact, less than 45% of the length of neck 2
- 1b Trunk elongated, 45% or more length of neck 5
- 2a Posterior processes about twice as long as length of trunk; cephalothorax with 4 prominent protuberances, i.e. one pair anterolateral, other pair posterolateral; and one pair smaller anteromedial antennary swellings *T. triakis*
- 2b Posterior processes about as long or slightly longer than trunk 3
- 3a Transition from neck to trunk gradual, cephalothorax ventrally with mainly 2 sets of swellings (antennary swellings simple globular swellings, separated by midline papilla medially, attached to laterally projecting complex pair of maxillary swellings consisting various smaller knobs) *T. asymboli*
- 3b Transition from neck to trunk abrupt 4
- 4a Cephalothorax dorsally smooth without any swellings; ventrally with central row of 4 swellings (antennary and lateral swellings and a posterior shelf-like swelling) *T. australis*
- 4b Cephalothorax posterodorsally divided into 2 swellings that are separated ventromedially; ventrally with 2 globular antennary swellings which may extend beyond anterior margin of cephalothorax, posteriorly with a pair of 2 touching maxillary swellings consisting of 3 knobs each (anterior knob, central one with fingerlike projection and one posterior smaller globular knob) *T. versicolor*
- 5a Cephalothorax dorsally smooth without swellings 6
- 5b Cephalothorax dorsally with distinct posterolateral swellings 10
- 6a Posterior processes slightly shorter or equal to trunk length 7
- 6b Posterior processes longer than trunk 11
- 7a Cephalothorax with ventral swellings in one or two rows 8
- 7b Cephalothorax ventrally with 3 rows of swellings; distally 2 separate globular antennary swellings which may extend beyond anterior margin; posterior to them a set of 3 swellings (2 lateral globular-like maxillary swellings attached to a larger transversely elongated central swelling with 2 lateral knobs and 1 medial knob); posteriorly 2 smaller globular swellings, which may extend beyond posterior margin of cephalothorax *T. elongatus*
- 8a Cephalothorax with swellings covering most of ventral surface 9
- 8b Cephalothorax with swellings occurring posteroventrally, anteroventral surface smooth and globose *T. hoi*
- 9a Cephalothorax with antennary swellings apart and maxillary swellings separated by oval medial swelling *T. benzi*
- 9b Cephalothorax with antennary swellings meeting at midline and oval medial swelling between maxillary swellings absent, trunk width mostly constant along length *T. musteli*
- 10a Cephalothorax posterodorsally with 3 globular swellings; ventrally with 2 sets of swellings (excluding the large rounded anterolateral knobs); neck width less than a third of trunk width, increasing in diameter posteriorly as it indistinctly joins trunk *T. vaissierei*
- 10b Cephalothorax posterodorsally with a transversely elongated swelling extending into another wider and more protruded process appearing like a collar around dorsal part of neck; ventrally with three sets of swellings (excluding the large rounded anterolateral knobs); neck width at least a third of trunk width, joins trunk more distinctly *T. lewisi*
- 11a Cephalothorax with 3 sets of swellings: antennary, maxillary (“diagonally elliptical” with “concave posterior margins” and posterolateral swellings) *T. feroxi*
- 11b Cephalothorax with 2 sets of swellings: antennary, maxillary (consisting of 2 knobs each on raised swelling), posterodorsal surface indistinctly divided into 3 *T. beatricae*

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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