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Phylogenetic revision of *Echinolaophonte* Nicholls (Copepoda, Harpacticoida, Laophontidae T. Scott) including the establishment of two new genera and two new species

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Abstract

The record of a new species of *Echinolaophonte* Nicholls, 1941 (Copepoda, Harpacticoida, Laophontidae) from Jeju Island (Korea) formed the basis for a detailed and exhaustive phylogenetic revision of the genus. Comparison of all 15 species currently assigned to *Echinolaophonte* (including the new Korean species) revealed that its current composition cannot be maintained. The phylogenetic relationships within *Echinolaophonte* were elucidated through the analysis of 135 morphological characters and the inclusion of four outgroups. As a result, four species were removed from *Echinolaophonte* and placed in two new genera: *Parechinolaophonte* **gen. nov.** for *E. tropica* Ummerkutty, 1970 and *Pseudechinolaophonte* **gen. nov.** for *E. minuta* Cottarelli & Forniz, 1991, *E. mordoganensis* Kuru, Sönmez & Karaytug, 2019 and *E. veniliae* Cottarelli, Forniz & Bascherini, 1992. *Echinolaophonte longantennata* Apostolov, 1990 had to be excluded from the analysis, due to the fragmentary and imprecise description. Accordingly, the phylogenetic relationships of the ten species remaining in *Echinolaophonte* are clarified. The new Korean species is described as *Echinolaophonte musa* **sp. nov.** Furthermore, the subspecies *E. armiger* f. *briani* Lang, 1965 is elevated to species rank as *E. briani* Lang, 1965. A detailed phylogenetic discussion is provided and a key to the species of *Echinolaophonte* is given.

Key Words

Introduction

Nicholls (1941) proposed the laophontid genus *Echinolaophonte* Nicholls, 1941, for *Laophonte horrida* (Norman, 1876) as the type species, collected from the Davis Strait (western Greenland) (Norman 1876). He also transferred *L. brevispinosa* Sars, 1908 (Norwegian Sea), *L. armiger* Gurney, 1927 and *L. mirabilis* Gurney, 1927 (Suez Canal, Egypt) to *Echinolaophonte*. In that context, Nicholls (1941) regarded *L. hystrix* Brian, 1928 and *L. steueri* van Douwe, 1929 (both from the Mediterranean Sea) as junior synonyms of *E. armiger*.

When describing *E. armiger* f. *typica* Lang, 1965 from the Mediterranean Sea and *E. armiger* f. *briani* Lang, 1965 from the Californian coast (U.S.A.), Lang (1965) was the first to discuss the possible phylogenetic relationships within *Echinolaophonte*. He meant to recognise two evolutionary lineages. The first is characterised by 3:3:2 outer spines on the P2–P4 exp-3, respectively and by a sexually dimorphic male P3 endopod. In the second lineage, the P2–P4 exp-3 bear 2:3:2 outer spines, respectively and the sexual dimorphism in the male P3 endopod is lost. Lang's (1965) hypothesis was subsequently questioned by Mielke (1981) who noted

that *E. tetracheir* Mielke, 1981 combines the P2–P4 setation (3:3:2) observed for the first lineage and the loss of sexual dimorphism observed for the second lineage. Furthermore, Mielke (1981) noted that *E. gladiator* Vervoort, 1964 cannot be assigned to either of the two lineages, because its P2–P4 exp-3 present 2:2:2 outer spines. Therefore, Mielke (1981) rejected the setation of the swimming legs as phylogenetically relevant for the establishment of the two lineages. This was subsequently adopted by Cottarelli and Forniz (1991) and Cottarelli et al. (1992), because both *E. minuta* Cottarelli & Forniz, 1991 and *E. veniliae* Cottarelli, Forniz & Bascherini, 1992 combine the sexual dimorphism observed for the first lineage with the setation pattern 2:3:2 of P2–P4 exp-3 observed for the second lineage. Like Mielke (1981), Cottarelli and Forniz (1991) and Cottarelli et al. (1992) considered the loss of sexual dimorphism in the male P3 endopod as a valuable phylogenetic character. Cottarelli et al. (1992) proposed two groups, viz. the "*horrida*" group with and the "*armiger*" group without sexual dimorphism in the male P3 endopod. According to Cottarelli et al. (1992), the "*horrida*" group encloses *E. horrida*, *E. brevispinosa*, *E. oshoroensis* Itô, 1969, *E. tropica* Ummerkutty, 1970, *E. minuta* and *E. veniliae* and the "*armiger*" group includes *E. armiger* f. *typica*, *E. armiger* f. *briani* and *E. tetracheir*. The "*horrida*" group was recently updated by Kuru et al. (2019) in the framework of their description of *E. mordoganensis* Kuru, Sönmez & Karaytug, 2019. They included *E. mordoganensis* into the "*horrida*" group, but excluded *E. tropica*, since "*E. tropica* Ummerkutty, 1970 cannot be included in any of the lineages" (Kuru et al. 2019: 183), due to confusing information with respect to the male's P3 endopod provided by Ummerkutty (1970), Wells and Rao (1987) and Wells (2007). Furthermore, Kuru et al. (2019) pointed to the pending assignment of *E. mirabilis*, *E. longantennata* Apostolov, 1990 and *E. gladiator* to any of the groups, since no males of these species have been described so far.

Lee et al. (2006) fully re-described *E. armiger* (Gurney, 1927), based on specimens collected from the Texan coast (U.S.A.) and compared them with the type specimens deposited in the Natural History Museum (London, U.K.). To clarify the taxonomy of *E. armiger*, Lee et al. (2006) carefully re-examined all records of *E. armiger* since the original publication by Gurney (1927) (namely Willey 1930; Nicholls 1945; de Paiva Carvalho 1952; Krishnaswamy 1957; Pesta 1959 (as *Onychocamptus armiger*); Vervoort 1964 (also as *O. armiger*); Lang 1965). They noted that Nicholls' (1945) and Vervoort's (1964) records of *E. armiger* from western Australia and the Caroline Islands, respectively, show a remarkable resemblance, but in fact do belong to a distinct, new species. However, Lee et al. (2006) desisted from describing that species, due to the availability of only few damaged specimens. They concluded that the "true" *E. armiger* reported from the Suez Canal by Gurney (1927) had subsequently been recorded only two times, i.e. from Bermuda (Willey 1930) and from Brazil (de Paiva Carvalho 1952). Instead, the specimens of (the supposed) *E. armiger* reported from Madras (India) (Krishnaswamy 1957), from the Cape of Sorrento (Italy) (Pesta 1959) and from the Californian Pacific coast (U.S.A.) (Lang 1965), presumably are more closely related to *E. hystrix*, which, motivated by Lang's (1965) description of *E. armiger* f. *typica*, was re-instated by Lee et al. (2006) as a valid species.

Wells (2007) recognised 11 species in *Echinolaophonte* and regarded *E. armiger sensu* Nicholls (1945), *E. armiger* f. *briani*, *Onychocamptus armiger sensu* Pesta (1959) and *O. armiger sensu* Vervoort (1964) as *species inquirendae*.

Fuentes-Reinés and Suárez-Morales (2017) investigated specimens of *E. armiger* obtained from Rodadero Bay (Colombia). A detailed comparison showed that, besides findings of *E. armiger sensu* Gurney (1927), the Colombian specimens represent a new species, but were "almost identical" with Nicholls' (1945) and Vervoort's (1964) material (Fuentes-Reinés and Suárez-Morales 2017: 28), thus confirming the assumption of Lee et al. (2006) about the Pacific specimens constituting a new species. They described the new species as *E. villabonae* Fuentes-Reinés and Suárez-Morales, 2017 and provided a key to the species of *Echinolaophonte*.

While examining collections of laophontid species deposited at the School of Biological Sciences, Seoul National University, we found a new species of *Echinolaophonte* obtained from the subtidal soft bottoms of Jeju Island, Korea. Here, we fully describe and illustrate it as *E. musa* sp. nov. Our attempt to clear the systematic relationship of the new species within *Echinolaophonte* required a fundamental, exhaustive phylogenetic analysis of the genus that is presented herein. Moreover, we provide an amended identification key to the species of the genus.

Methods

The specimens were collected by SCUBA diving from subtidal sandy bottoms at a depth range of 20–30 m at Munseom islet, Jeju Island.

The material was sieved with a 38 mm mesh and fixed in 95% ethanol. Benthic harpacticoid copepods were sorted in the laboratory using a Leica M165C (Germany) stereomicroscope. Specimens were then embedded in glycerol and dissected. The slide preparations were sealed with transparent nail varnish. Species identification and drawings were prepared using a drawing tube on an Olympus BX53 (Tokyo, Japan) differential interference contrast microscope, equipped with Nomarski optics.

Confocal Laser Scanning Microscopy (CLSM) was used at the DZMB (Senckenberg am Meer Wilhelmshaven, Germany) to examine the individuals, applying the methods shown, for example, in George et al. (2020). The phylogenetic analysis strictly follows the concept of a "consequent phylogenetics" as developed

by Hennig (1982) and substantiated by Ax (1984, 1988, 1995). It consists of a detailed and comparative character discussion that enables the formulation of an intersubjective hypothesis (Ax 1984). Computer programmes were used neither for the phylogenetic analysis nor for the generation of the presented cladogram (Fig. 10): it was not the aim of the contribution at hand to provide a methodological comparison of (hand-made and computer-based) phylogenetic analyses, but to present a first hypothesis of the systematics of and within the family under investigation; future phylogenetic analyses can use the matrix presented herein as a detailed morphological dataset. Fig. 10 represents the condensed result from the formerly undertaken detailed and complex phylogenetic analysis. Concerning the number of segments and setae/spines, the generally accepted principle of oligomerisation (Huys and Boxshall 1991; Seifried 2003), which postulates that a reduction of segments/ elements constitutes the relatively more derived state, was adopted here.

The underlying morphological comparison of the used characters was made, based on the respective original species (re-)descriptions.

The terminology used follows Huys and Boxshall (1991) and Huys et al. (1996). The term "telson" is adopted from Schminke (1976). Phylogenetic terminology is adopted and translated from Ax (1984).

Abbreviations used in the text

A1, antennule; **A2**, antenna; **ae**, aesthetasc; **cphth**, cephalothorax; **CR**, caudal ramus/rami; **GDS**, genital double somite; **md**, mandible; **mx**, maxilla; **mxl**, maxillula; **mxp**, maxilliped; **P1–P6**, first to sixth thoracopod; **exp** (enp)-1 (2, 3) to denote the proximal (middle, distal) segment of a ramus.

Scale bars are in micrometres (µm). The type specimens are deposited in the collection of The Natural Institute of Biological Resources (**NIBR**), Incheon, Korea and The National Marine Biodiversity Institute of Korea (**MABIK**), Seochun, Korea.

Results

Subclass Copepoda Milne Edwards, 1840
Order Harpacticoida Sars, 1903
Family Laophontidae T. Scott, 1905

Genus *Echinolaophonte* Nicholls, 1941

Generic diagnosis (modified from Nicholls 1941).
Laophontidae T. Scott, 1905. Body elongate, cylindrical, podoplean boundary between pro- and urosome inconspicuous. Sexual dimorphism in A1, P3 (in the *brevispinosa—oshoroensis* clade only; not yet confirmed for *E. gladiator*), P4 (part.), P5, P6 and

urosome segmentation (female with GDS due to fusion of last (P6-bearing, genital) thoracic somite with first abdominal somite). Cphth about 1/3 of total body length, with some sensilla laterally and dorsally; with strong, acute dorsal spur on posterior margin. Rostrum fused to cphth, laterally constricted, of different shape (dome, truncate, notch etc). Body somites, except preanal and telson, dorsally with cuticular processes of variable lengths. Preanal somite with highly variable pseudoperculum consisting of several, often digitate or squarrose processes (sometimes partly fused together). CR longer than broad, varying in length between species, with 7 setae. Female A1 slender, 6-segmented; male A1 sexually dimorphic, 8-segmented, subchirocer. A2 with 1-segmented exopod bearing 4 setae; allobasis with 1 or lacking abexopodal seta; endopod 1-segmented, subdistally with 2 spines and 1 slender additional seta, apically with 6 setae (2–3 geniculate)/spines. Mxp with elongated syncoxa and basis, prehensile, apical claw as long as basis. P1 prehensile, with extremely elongated coxa and basis, the latter reaching the length of enp-1. Exopod small, 2-segmented; endopod 2-segmented, enp-1 extremely elongated, enp-2 very small, with 1 strong claw and 1 tiny seta apically; P2–P4 with 3-segmented exopods, female with 2-segmented endopods; if sexually dimorphic, male P3 endopod 3-segmented, with strong apophysis on outer apical edge; those males lacking sexual dimorphism on P3 with 2-segmented endopod, resembling that of the female. Exopods of male P3 and P4 with or without sexual dimorphism. P5 of female with baseoendopod bearing 4 setae and with small distinct exopod carrying 3 setae. Male P5 smaller than in female, baseoendopod completely reduced; exopod distinct and small, with 3 setae.

Type species. *Echinolaophonte horrida* (Norman, 1876) (= *Cleta horrida* Norman, 1876; *Laophonte horrida* (Brady, 1880); *Onychocamptus horridus* (Lang, 1948)).

Additional species.

E. armiger (Gurney, 1927) (= *Laophonte armiger* Gurney, 1927; *Onychocamptus armiger* (Lang, 1948); *Echinolaophonte armiger* f. *typica* (Lang, 1965));

E. brevispinosa (Sars, 1908) (= *Laophonte brevispinosa* Sars, 1908; *Onychocamptus brevispinosus* (Lang, 1948));

E. briani Lang, 1965 (= *E. armiger* f. *briani* Lang, 1965);

E. gladiator (Vervoort, 1962) (= *Onychocamptus gladiator* Vervoort, 1964);

E. hystrix (Brian, 1928) (= *Laophonte hystrix* Brian, 1928; *L. steueri* van Douwe, 1929; *E. armiger* (Norman, 1941); *O. armiger* (Lang, 1948, Vervoort, 1964); *E. armiger* f. *typica* (Lang, 1965; Lee et al. 2006));

E. longantennata Apostolov, 1990;

E. mirabilis (Gurney, 1927) (= *Laophonte mirabilis* Gurney, 1927; *Onychocamptus mirabilis* (Lang, 1948));

E. musa sp. nov. (present contribution);

E. oshoroensis Itô, 1969;

E. tetracheir Mielke, 1981;

E. villabonae Fuentes-Reinés and Suárez-Morales, 2017.

Echinolaophonte musa sp. nov.

https://zoobank.org/1550C93D-4255-4830-9B5C-6952A27BA0BB

Figs 2–8

Korean name: Mu-Sa-Chim-Ga-Hok-No-Beol-Re

Locus typicus. Munseom Islet, Jeju Island, Korea, 33°13'42"N, 126°34'02"E, subtidal sandy bottom (20–30 m in depth) (Fig. 1).

Type material. Adult female holotype (NI-BRIV0000888158) dissected on 12 slides (Rostrum and A1; A2; mandible; maxillule; maxilla; maxilliped; P1; P2; P3; P4; P5; urosome), Munseom Islet, Jeju Island, Korea, coll. H.S. Rho, 01 Oct. 2002. Male allotype (NI-BRIV0000888157) dissected on 12 slides (Rostrum; A1; A2; maxilla; maxilliped; P1; P2; P3; P4; P5; cphth; urosome). Paratypes: two females and five males, undissected, ethanol-preserved in vial (NIBRIV0000888156) and two females and four males, as above (MABIK-CR00248285-CR00248290).

Additional studied material. 1 female and 1 male, ethanol-preserved, Munseom Islet, Jeju Island, Korea, coll. H.S. Rho, 06 Oct. 2002; 1 male, undissected, ethanol-preserved, Sagyeri, Jeju Island, 4 Sep 2008; 2 females and 1 male, undissected, ethanol-preserved, Sungsanpo, Jeju Island, 12 May, 2013, coll. S.H. Kim, deposited at the National Marine Biodiversity Institute of Korea (reg. no. MADBK 721114-001).

Description of the female. Habitus (Figs 2, 3A) slender, demarcation between pro- and urosome not clearly discernible, body somites virtually cylindrical. Total body length 660.6 μm (660.6–736.4 μm, mean = 713.1, n = 6), measured from the anterior margin of the rostrum to the posterior margin of the caudal rami. Urosome (Fig. 6A) gradually tapering posteriorly. All body somites with paired horn-like spiniform processes bearing long sensilla, except for last two abdominal somites. Paired dorsal processes from first pedigerous somite to first abdominal somite (5 segments, GDS with two pairs of processes) with bifid tip.

Cephalothorax (Figs 2, 3A) with two small and one long spiniform processes bearing numerous fine, hair-like elements at the mid-line of dorsal surface and a pair of strong and curved lateral processes; with a few scattered spinules and long sensilla. Rostrum very long and stout, with bifurcated tip as shown.

Urosome (Figs 3A, 6A) 5-segmented, comprising P5-bearing somite, genital-double somite, 2 free abdominal somites and telson. Genital double-somite (Fig. 6A) slightly wider than long, with long spinules along outer margins. P6 (Fig. 6B) represented by 2 long bare setae on a bilobed single plate covering gonopores. Third urosomite widened distally, with long spinules along the outer and distal margins and with 4 long sensilla on the distal corners. Fourth urosomite with fine spinules along the distal margin. Pseudoperculum represented by 3 squarrose lobes (Fig. 3B). Caudal ramus (Fig. 3C) long and narrow, about 5.3 times as long as greatest width, with a few spinules around setae I and III; with seven bare setae; seta I shortest, setae IV–VI situated distally, seta VII tri-articulate at base, inserted subapically on dorsal surface.

Antennule (Figs 4A, B) 6-segmented, all setae bare; segment 1 longest, with long spinular row on inner and outer margins, with 1 seta distally; segment 2 with short inner and long outer spinular row, with 3 short and 4 long bare setae; segment 3 slightly shorter than segment 2, with 5 long setae; segment 4 small, distally with aesthetasc and 2 setae, arising from pedestal; segment 5 shortest, with 1 seta; segment 6 (Fig. 4B) with 8 single setae and an acrothek formed by 2 setae and 1 aesthetasc. Setal formula: 1-[1], 2-[7], 3-[5], 4-[2 + ae], 5-[1], 6-[8 + acrothek (2 + ae)].

Antenna (Fig. 4C) comprising coxa, allobasis, free endopodal segment and 1-segmented exopod. Coxa small, without ornamentation. Allobasis as long as endopod, with spinular row along inner margin and with 1 small bare abexopodal seta (arrowed in Fig. 4C). Exopod long and 1-segmented, bearing spinules on outer margin, with
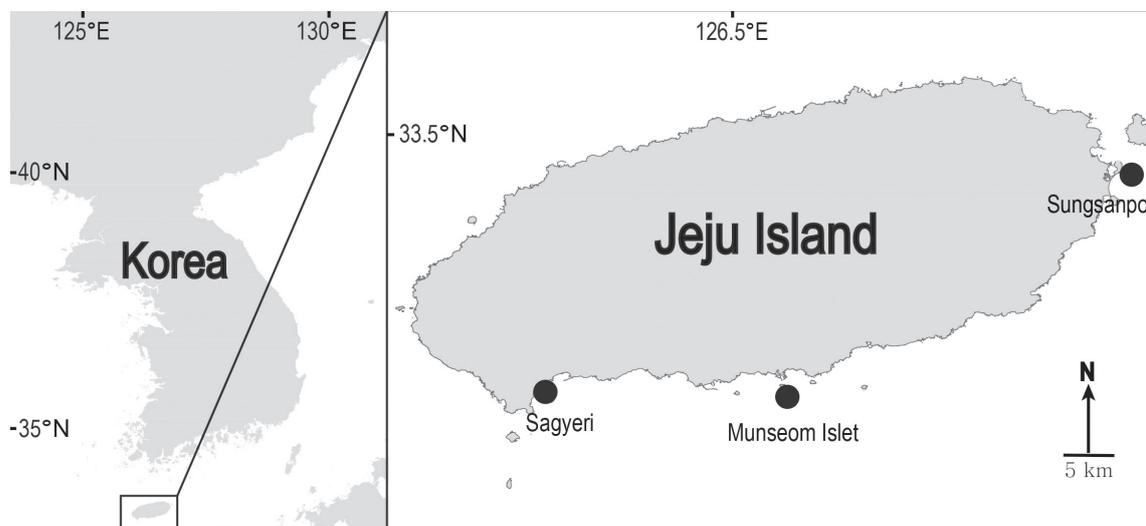
Figure 1. Map of the locus typicus (Munseom Islet) of *Echinolaophonte musa* sp. nov. and additional sampling localities of the species.

1 inner and 3 distal setae. Endopod with spinular row along inner margin. Subdistal armature consisting of 1 seta (I in Fig. 4C) and 2 spines (II and III in Fig. 4C); distal armature consisting of 2 setae (1 and 2 in Fig. 4C), 2 spines (3 and 6 in Fig. 4C) and 2 geniculate setae (4 and 5 in Fig. 4C).

Mandible (Fig. 4D). Gnathobase with 4 teeth (1 bi-, 1 tri-cuspidate and 2 with distal spinules) and 1 long unipinnate seta in dorsal corner as depicted; surface without ornamentation. Palp 1-segmented, carrying 1 lateral and 2 distal setae.

Maxillule (Fig. 4E). Praecoxa without ornamentation. Arthrite well-developed, with 7 distal spines/setae and 2 anterior surface setae. Coxa with few setules on inner margin, with 1 unipinnate and 1 bare seta distally. Basis with several spinules along inner and outer margin, with 1 unipinnate and 2 bare setae distally. Exopod 1-segmented, elongated, with 2 bare setae distally. Endopod represented by 2 plumose setae.

Maxilla (Fig. 4F). Syncoxa with a long spinular row on the outer surface and lots of tiny spinules on the inner proximal surface and with 2 endites, both fused to the syncoxa; proximal endite with 2 bare and 1 multipinnate setae, the latter fused to endite; distal endite with 1 bare, 1 bipinnate and 1 unipinnate seta, the latter fused to endite. Allobasis drawn out into strong claw with 1 accessory seta; Endopod represented by 2 bare setae.

Maxilliped (Fig. 5A). Well-developed, prehensile, with elongated syncoxa and basis. Syncoxa with several spinules proximally and subdistally and with 1 short bare and 1 plumose distal seta. Basis elongated, with few spinules on middle outer margin. Endopod represented by an apically curved claw, slightly longer than basis; accessory armature consisting of 1 bare proximal seta.

P1 (Fig. 5B). Intercoxal sclerite narrow, bow-like. Praecoxa small, elongated, triangular, with few small spinules on distal corner. Coxa elongated, with long outer and short inner spinules. Basis about 2 times as long as coxa, with a small outer protuberance on the proximal quarter and setule rows on posterior surface, inner and outer margins; with 1 outer seta in proximal third and 1 tiny inner seta subdistally. Exopod 2-segmented, much shorter than enp-1; exp-1 tiny, almost square in shape, with 1 outer seta; exp-2 about 3 times longer than exp-1, with 2 long outer setules, 3 outer and 2 distal bare setae; inner distal seta geniculate. Endopod 2-segmented, prehensile; enp-1 very long, without ornamentation; enp-2 with a tiny seta and a strong claw, the latter about 2 times longer than enp-2.

P2 (Fig. 6C). Intercoxal sclerite narrow, unornamented. Praecoxa triangular, unornamented. Coxa almost square, with few spinules on outer surface. Basis smaller than coxa, with few spinules and pore on outer distal surface and with 1 biplumose outer seta. Exopod 3-segmented; exp-1 with spinules on outer margin and 1 short spinular row distally and with 1 bipinnate outer spine; exp-2 shortest, with spinules on outer and distal margin; with 1 bipinnate outer spine and 1 biplumose inner seta; exp-3 with spinules on outer margin, with 3 bipinnate outer

Figure 2. Confocal laser scanning of *Echinolaophonte musa* sp. nov. female. Habitus, dorsal view.
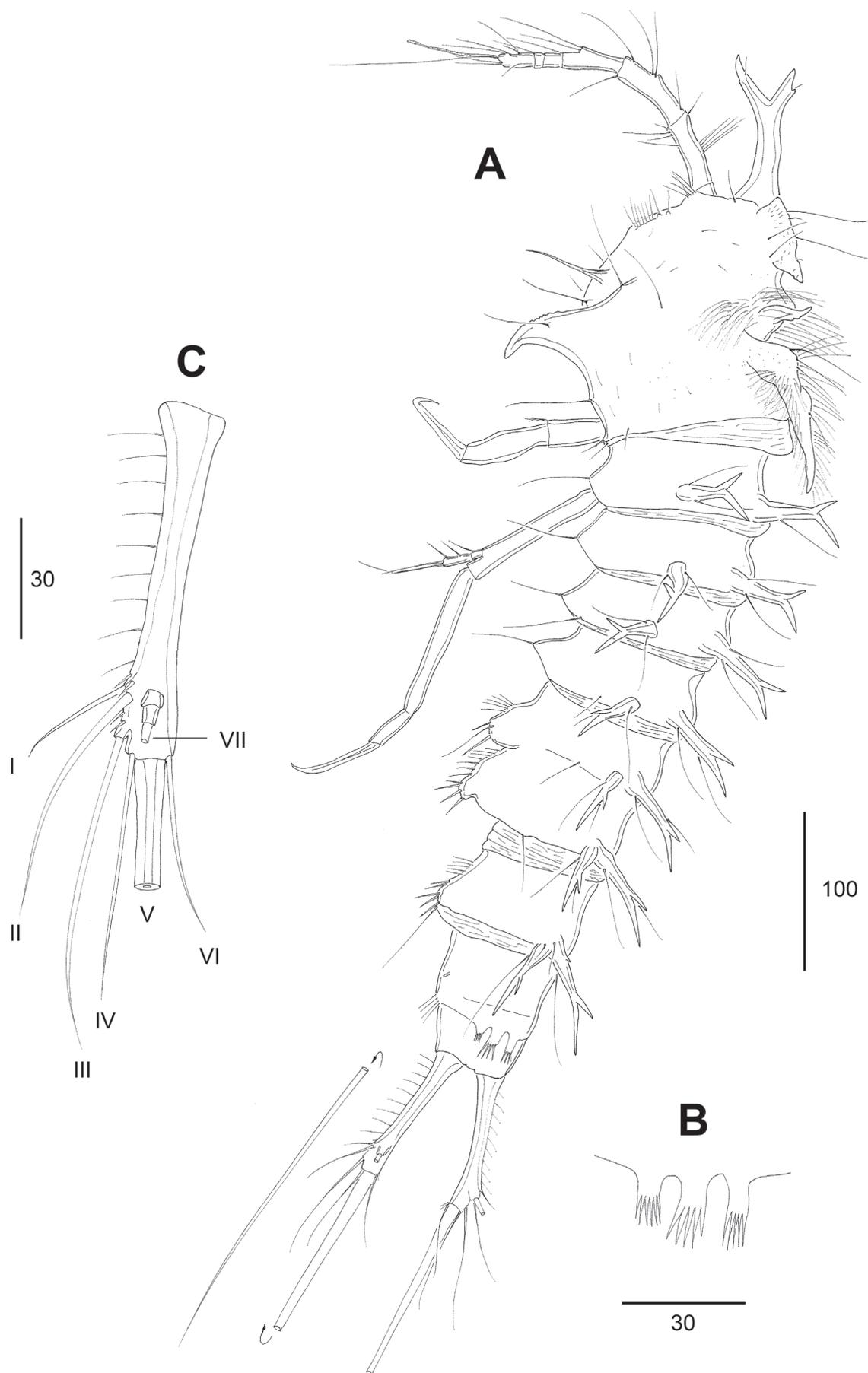
Figure 3. *Echinolaophonte musa* sp. nov. female. **A.** Habitus, lateral; **B.** Pseudoperculum; **C.** Caudal ramus, dorsal view.

spines, 2 distal and 1 inner seta, all biplumose. Endopod 2-segmented, reaching proximal third of exp-3; enp-1 with inner and distal spinules; enp-2 slightly longer than enp-1, with spinules along both margins and with 2 distal and 1 inner seta.

P3 (Fig. 6D). Intercoxal sclerite narrow, unornamented. Praecoxa triangular, with spinular row on distal margin. Coxa slightly wider than long, with few spinules on outer surface. Basis nearly as long as coxa, with spinules on outer distal surface and with 1 bare composite outer seta; articulation in the distal third. Exopod 3-segmented; exp-1 with spinules on outer margin and 1 bipinnate outer spine; exp-2 shortest, with outer and distal short spinules, with 1 bipinnate outer spine and 1 biplumose inner seta; exp-3 with spinules on outer margin and with 3 bipinnate outer spines, 2 distal and 2 inner biplumose setae. Endopod 2-segmented, almost reaching margin of exp-2; enp-1 much shorter than enp-2, with spinules along both margins; enp-2 with spinules on both margins, additionally with 2 distal and 2 inner setae.

P4 (Fig. 6E). Intercoxal sclerite narrow, unornamented. Praecoxa small and triangular, with few tiny spinules along distal margin. Coxa as long as wide, with outer spinule. Basis with outer spinules and 1 bare composite outer seta. Exopod 3-segmented; exp-1 with spinules on outer and distal margins and with 1 bipinnate outer spine; exp-2 shortest, with outer and distal spinules, with 1 bipinnate outer spine and 1 biplumose inner seta; exp-3 with spinules on outer and distal margins, with 1 bipinnate spine and 1 biplumose seta on outer margin, 2 inner and 2 distal biplumose setae. Endopod 2-segmented, shorter than exp-1; enp-1 short and with few tiny outer spinules; enp-2 with a spinule and 1 tube pore on outer margin, with 2 distal and 1 inner biplumose seta. The armature formula is given in Table 1.

Table 1. Setal formula of swimming legs of *Echinolaophonte musa* sp. nov.

Thoracopod	Exopod	Endopod
P2	0 1 123	0 120
P3	0 1 223	0 220
P4	0 1 222	0 120

P5 (Fig. 5C) with completely separated baseoendopod and exopod. Baseoendopod reaching middle of exopod, with outer seta arising from elongated setophore bearing 1 tube pore (arrowed) and some spinules at distal half; endopodal lobe reaching half the length of exopod, apically with 1 tube pore (arrowed) and 4 setae. Exopod longer than broad, with spinules on inner and outer margins and distal surface, with 3 plumose setae distally.

Description of male. Total body length 648.5 μm (642.4–721.2 μm, mean = 681.8 μm, n = 10), measured from anterior margin of rostrum to posterior margin of caudal rami (Fig. 7A). Urosome (Fig. 8E) gradually tapering posteriorly. Cephalothorax as in female, with numerous fine, hair-like elements and long sensilla on surface as shown in Fig. 7C; paired cuticular dorsal processes of

first pedigerous somite trifid, those of second pedigerous somite to fourth urosomite with bifid tip. Rostrum very similar to female (Fig. 7A).

Urosome (Figs 7C, 8E) 6-segmented, comprising P5-bearing somite, genital somite, third to fifth urosomite and telson. Genital somite and telson without, third to fifth urosomites with long spinules ventrally on distal margin; third and fourth somites with remarkably long sensilla on each distal corner. Pseudoperculum (Fig. 8F) represented by 2 pairs of lobes, inner pair with 3 respectively 4 spikes, outer lobes squarrose; the margin in between the lobes bearing fine setules.

Antennule (Fig. 8B) 8-segmented; subchirocer, with geniculation between segments 5 and 6; segment 1 longest, with numerous spinules on anterior and posterior surfaces and with 1 small seta on anterior distal corner; segment 2 with long spinules on surface and both margins and with 8 setae, two of which arising from strong pedestal; segment 3 with 3 setae; segment 4 smallest, with 4 setae; segment 5 swollen, with 9 bare setae, 1 bipinnate seta and 1 long seta and aesthetasc arising from long pedestal; segment 6 unarmed; segment 7 with 1 seta; segment 8 with 8 setae and acrothek (2 setae and 1 aesthetasc).

Setal formula: 1-[1], 2-[8], 3-[7], 4-[11 + ae], 5-[0], 6-[1], 7-[8 + acrothek (2 + ae)].

Antenna, mouthparts and P1, P2 and P4 as in female.

P3 (Fig. 8D). Both rami very similar to female, except for 2 strong outer pinnate spines (arrowed) on exp-1 and exp-2.

P5 (Fig. 7B) with separated baseoendopod and exopod. Baseoendopod with few spinules on anterior surface and distally, 1 tube pore subdistally and 1 outer bare composite seta. Exopod elongate, with 3 biplumose setae distally.

P6 (Fig. 7C) very small, bearing a few setules, 1 outer bare composite and 1 plumose inner seta.

Etymology. The epitheton originates from the Korean word 'mu-sa [무사]', which means "warrior".

Phylogenetic analysis. Currently, the taxon *Echinolaophonte* encloses 16 species: *E. armiger*, *E. brevispinosa*, *E. briani*, *E. gladiator*, *E. horrida*, *E. hystrix*, *E. longantennata*, *E. minuta*, *E. mirabilis*, *E. mordoganensis*, *E. musa* sp. nov., *E. oshoroensis*, *E. tetracheir*, *E. tropica*, *E. veniliae* and *E. villabonae*. These are in the following referred to as "*Echinolaophonte*–CS" ("current status") to distinguish them from both Nicholls' (1941) and the new combination proposed herein (see Discussion). Based on 135 morphological characters (Table 2), an exhaustive phylogenetic analysis was undertaken. It included the comparison of 15 *Echinolaophonte*–CS species; *E. longantennata* was excluded from the phylogenetic analysis (see below). Furthermore, with *Coullia* Hamond, 1973 (mostly exemplified by *C. tongariki* (Gómez & Boyko, 2006)), *Hemilaophonte janinae* (Jakubisiak, 1933) and *Xanthilaophonte* Fiers, 1991, three potential close relatives were selected as outgroups. This is considered here as necessary, because they share features that were seen as characteristic for *Echinolaophonte* by Nicholls (1941). Moreover, *Heterolaophonte minuta* (Boeck, 1872) was added as a fourth outgroup to include a comparatively distant representative of Laophontidae.
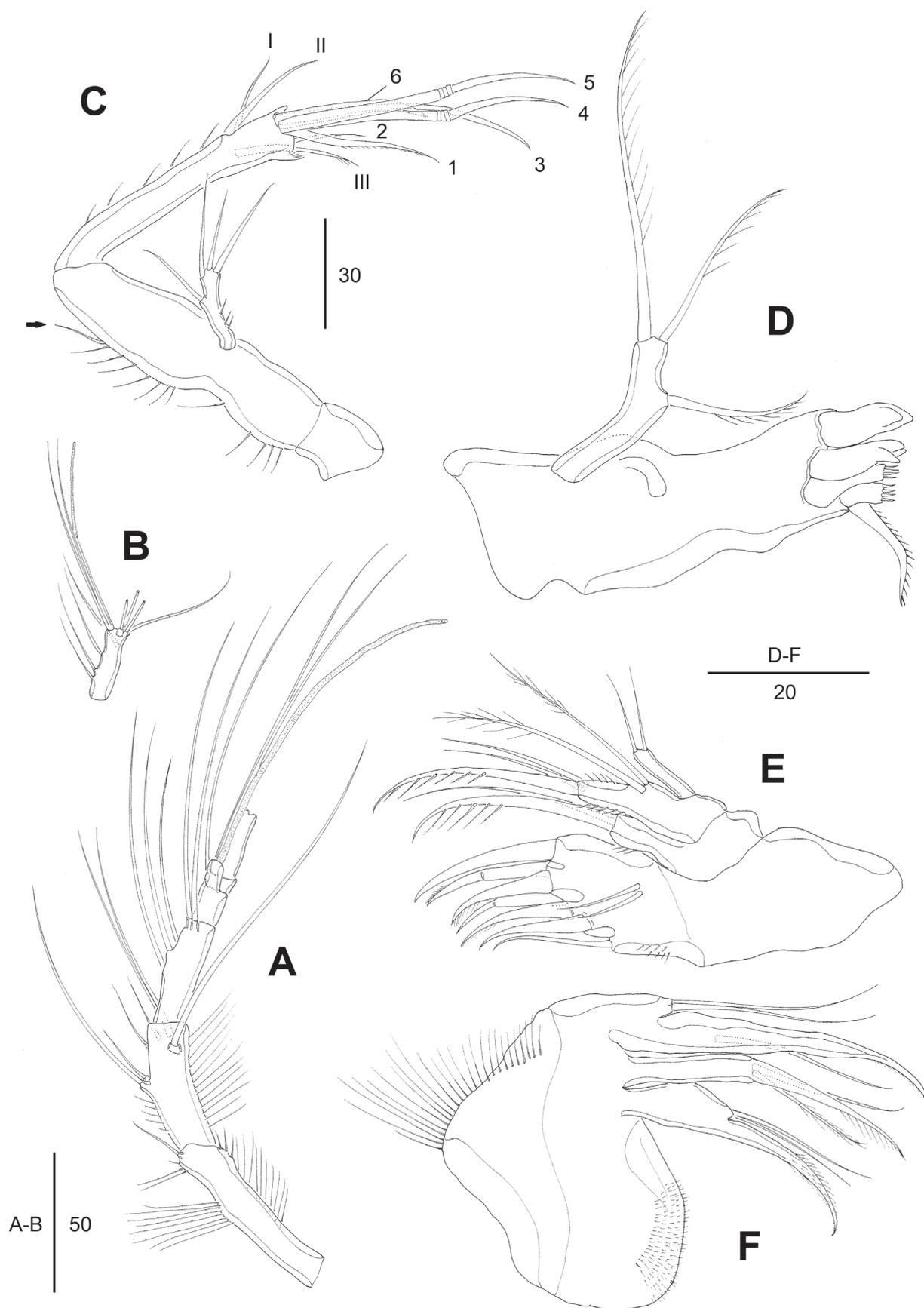
Figure 4. *Echinolaophonte musa* sp. nov. female. **A.** Antennule; **B.** Distal segment of antennule; **C.** Antenna; arrow pointing to abexopodal seta; Roman numerals labelling subapical, Arabian numerals labelling apical elements; **D.** Mandible; **E.** Maxillule; **F.** Maxilla.
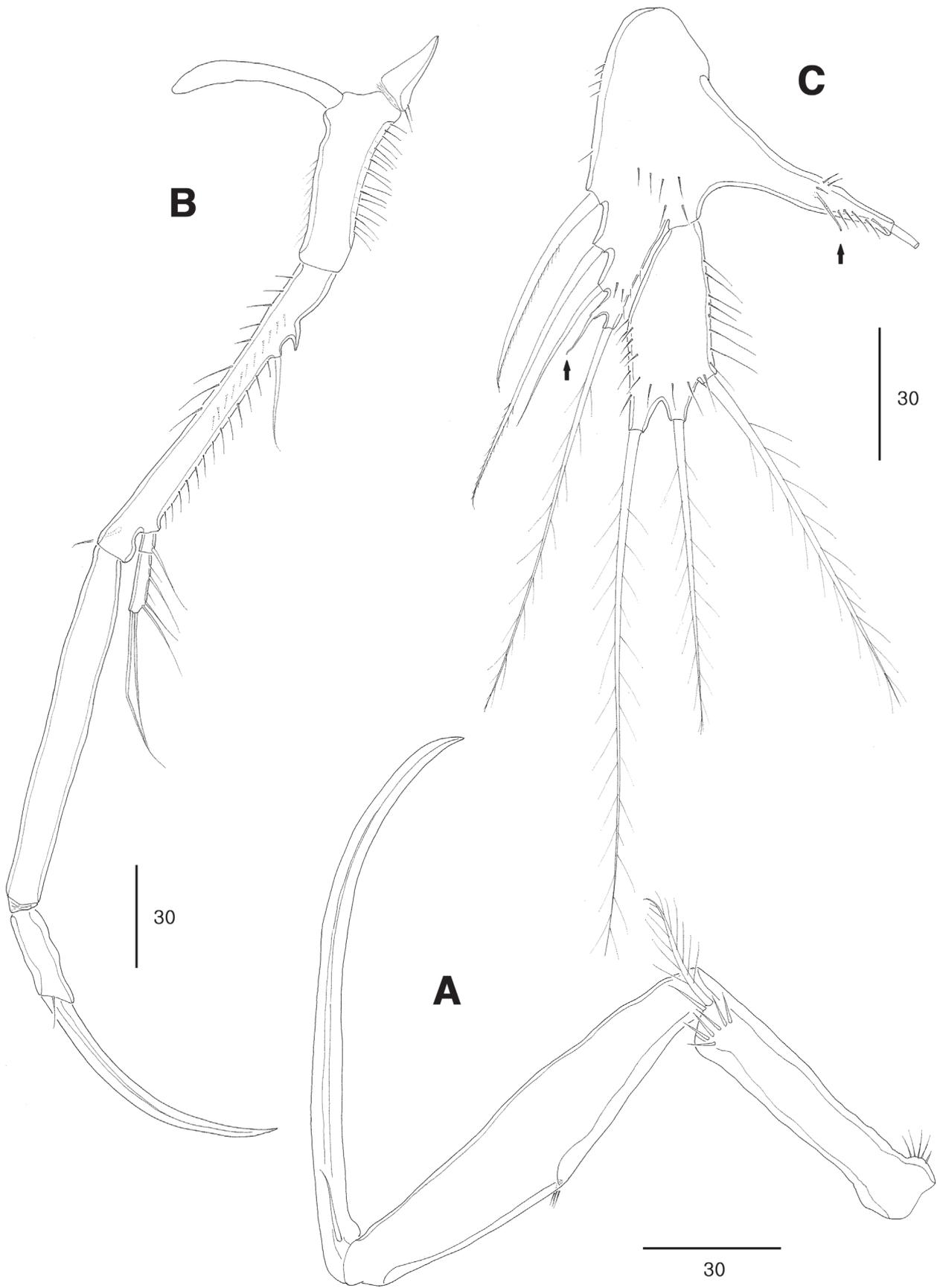
Figure 5. *Echinolaophonte musa* sp. nov. female. **A.** Maxilliped; **B.** P1; **C.** P5; arrows point to tube pores.
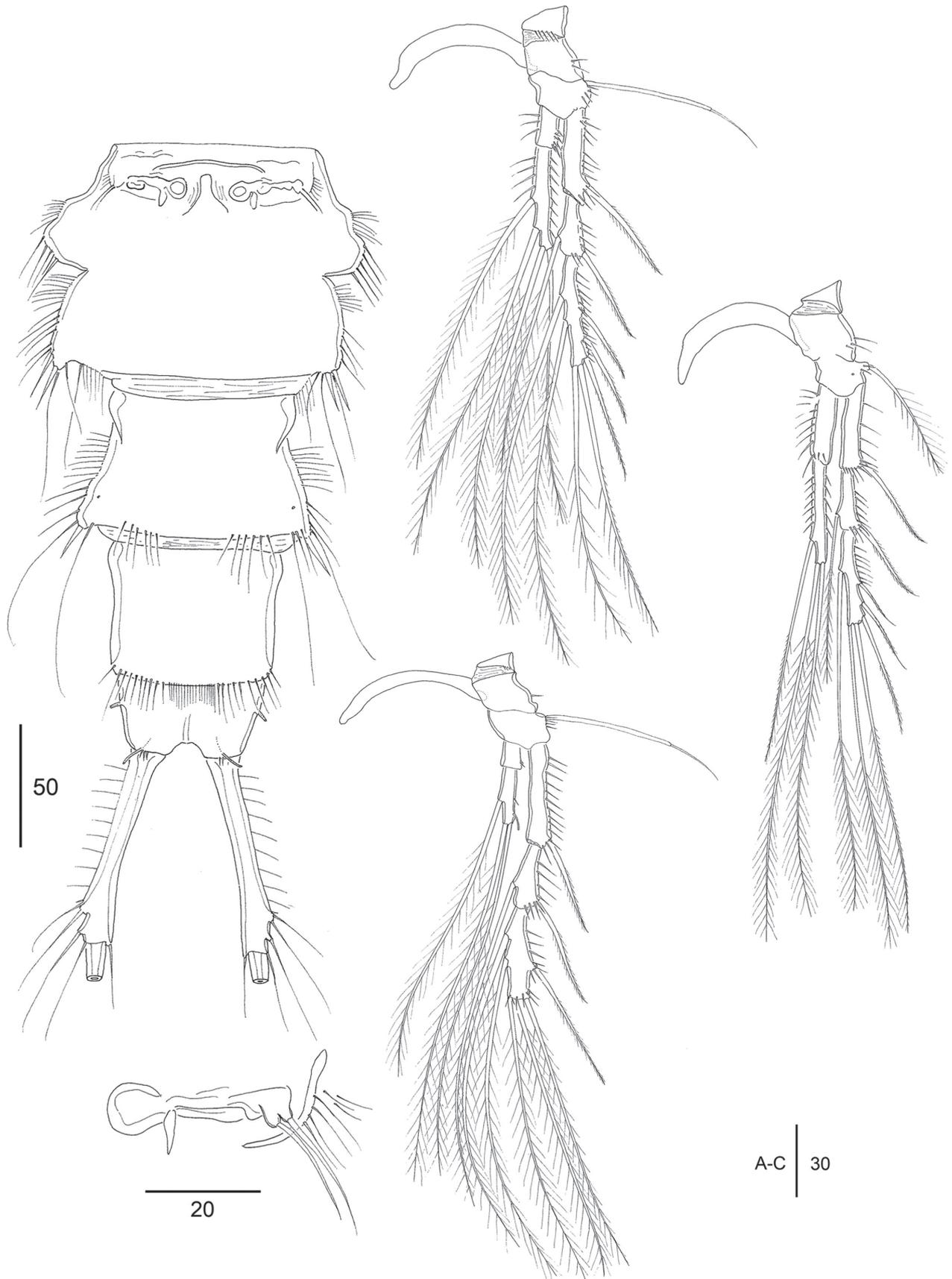
Figure 6. *Echinolaophonte musa* sp. nov. female. **A.** P2; **B.** P3; **C.** P4.
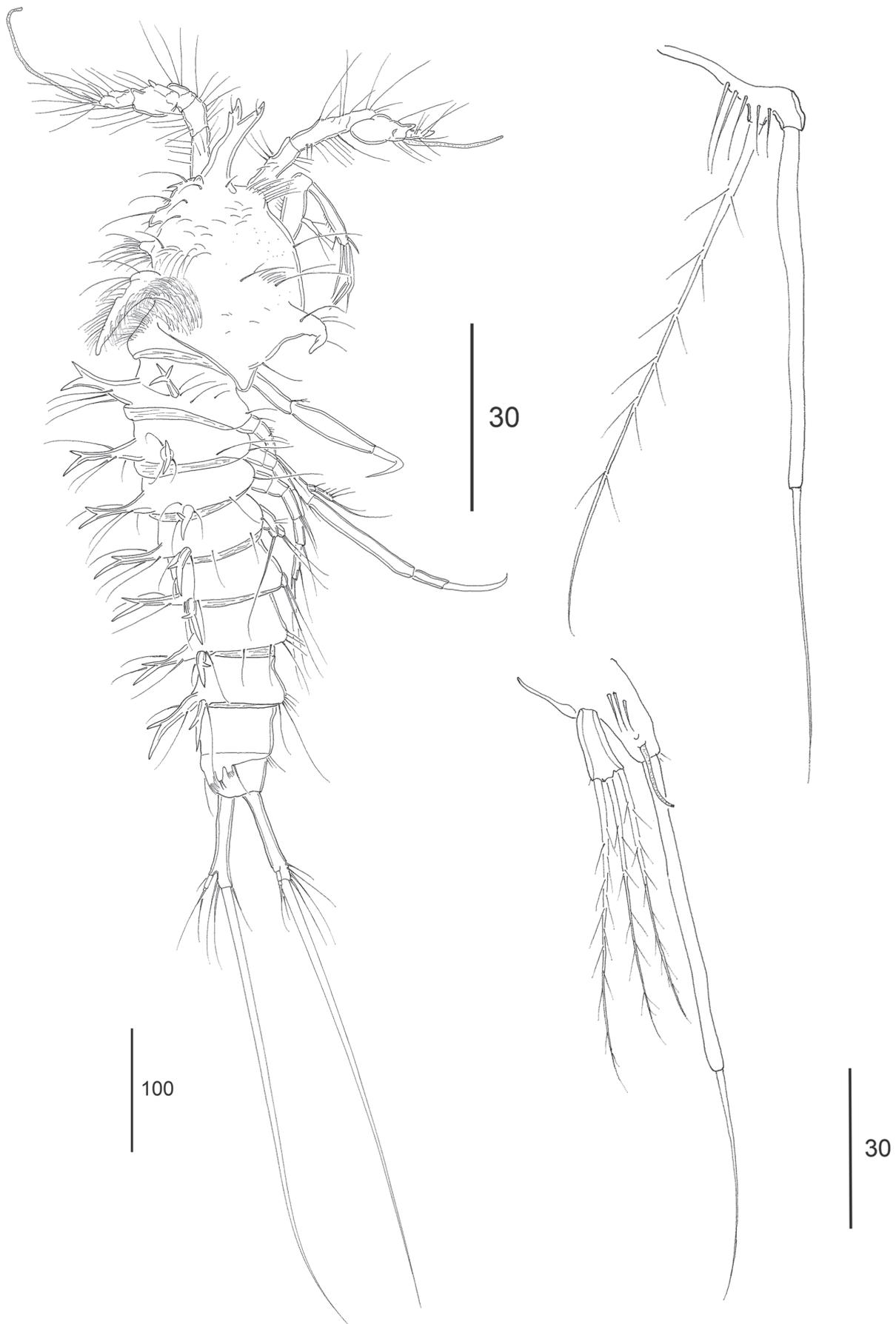
Figure 7. *Echinolaophonte musa* sp. nov. **A.** Female urosome, ventral view; **B.** female P6; **C.** Male habitus, lateral view; **D.** Male P5; **E.** Male P6.
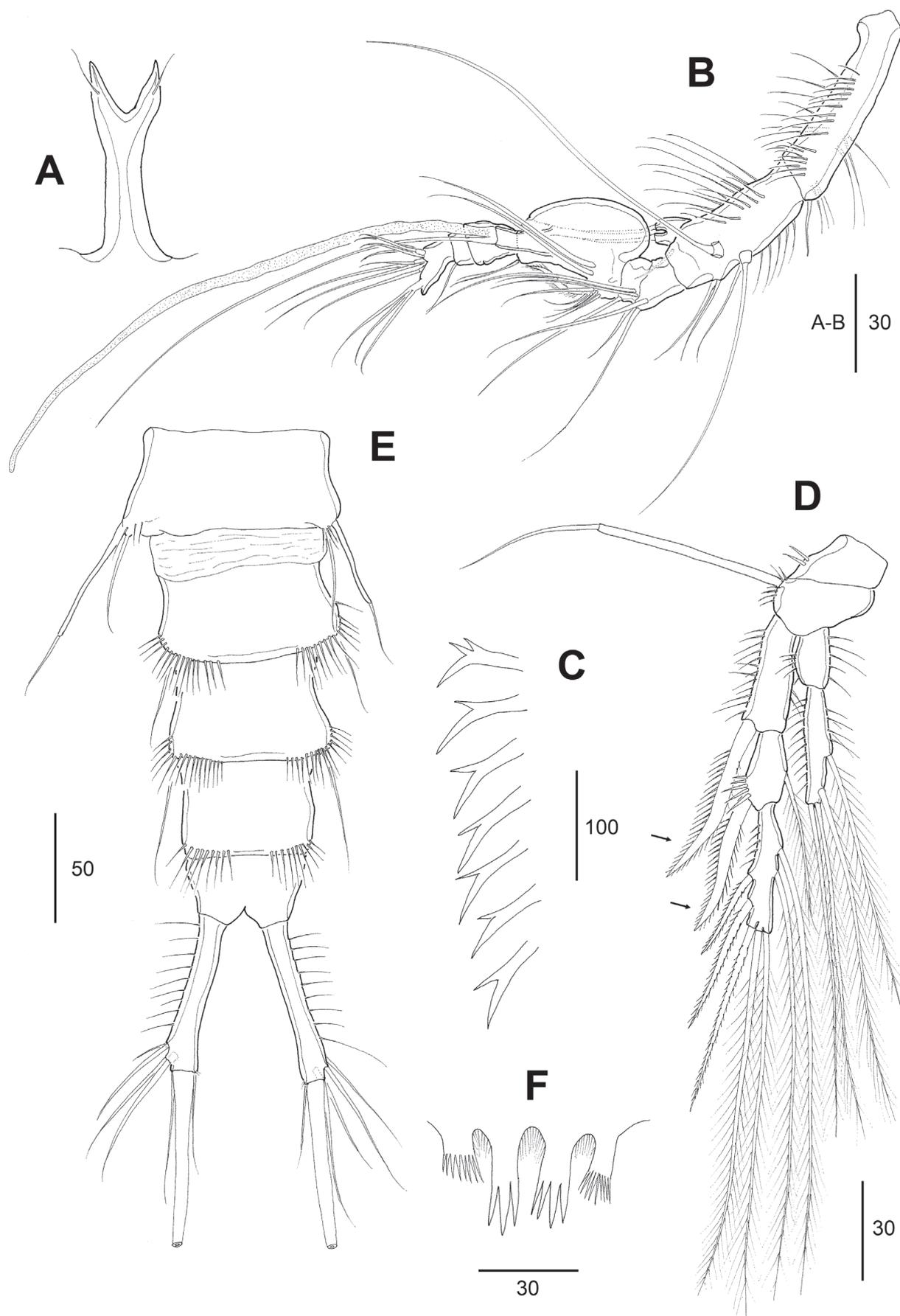
Figure 8. *Echinolaophonte musa* sp. nov. male. **A.** Rostrum; **B.** Antennule; **C.** Dorsal processes on first pedigerous somite to fourth urosomite; **D.** P3; **E.** Urosome, ventral view; **F.** Pseudoperculum.

Eightteen out of 135 characters (= 13.3%) emerged as convergent deviations. They mostly distribute heterogeneously over the species and are set in underlined bold italics in Table 2. Vertical arrows in characters 31 and 32 (Table 2) point towards a further deviation in *E. oshoroensis* (see Discussion).

The results of the phylogenetic analysis are discussed in detail below. The resulting phylogenetic relationships are presented in Fig. 10. The cladogram shows the 135 apomorphies spread over the respective nodes (Figs 10, A–EE). For a better orientation, the different nodes, as well as their assigned clades and characters, are summarised in Table 3, with the hypothesised convergences set in underlined bold italics.

The results suggest that *Echinolaophonte*–CS consists of several subordinated clades that complicate an unambiguous characterisation of the genus (Fig. 10). *Echinolaophonte longantennata* had to be excluded from the phylogenetic analysis due to the imprecise and only fragmental description provided by Apostolov (1990), combined with the lack of material for re-examination and comparison. Two synapomorphies were detected for the remaining 15 species, namely a narrowed rostrum (Table 2, character 13) and the syncoxa of the mxp being almost as long as the basis (Table 2, character 14). Nonetheless, a further careful comparison resulted in the division of *Echinolaophonte*–CS: *E. tropica* was placed into *Parechinolaophonte* gen. nov. as *Pa. tropica* (Ummerkutty, 1970), gen. et comb. nov., based on six autapomorphies (Table 2, characters 15–20; cf. Fig. 10, node F) and *E. minuta*, *E. mordoganensis* and *E. veniliae* were transferred into *Pseudechinolaophonte* gen. nov. as *Ps. minuta* (Cottarelli & Forniz, 1991), gen. et comb. nov., *Ps. mordoganensis* (Kuru, Sönmez & Karaytug, 2019), gen. et comb. nov. and *Ps. veniliae* (Cottarelli, Forniz & Bascherini, 1992), gen. et comb. nov., based on 14 synapomorphies (Table 2, characters 23–36; cf. Fig. 10, node H). The 11 species remaining in *Echinolaophonte* can be characterised by means of one synapomorphy (Table 2, character 54, cphth with single spur dorsally on posterior margin; cf. Fig. 10, node H). In the following, the generic diagnoses of the two new genera are given.

Parechinolaophonte gen. nov.

https://zoobank.org/EE6E91A6-34BC-4765-B667-892B66C88117

Diagnosis. Laophontidae T. Scott, 1905. Body elongate, cylindrical, podoplean boundary between pro- and urosome inconspicuous. Whole body minutely punctate. Sexual dimorphism in A1, P5 and P6; female with GDS. Cphth reaching about 1/3 of total body length; lateral margins of cphth extended outwardly, triangular; distal outer edges of cphth with paired backwardly directed protrusions, dorsally with longitudinal cuticular ridge crossed by 2 furrows. Rostrum fused to cphth, laterally constricted, almost square. Body somites without pronounced dorsal cuticular processes; abdominal somites, except telson, with weakly developed cuticular spinulose structures on

posterior margins. Pseudoperculum weakly developed, consisting of 4 small protrusions bearing several fine spinules apically. CR about twice as long as broad, with 7 setae (cf. Wells and Rao (1987), fig. 143i). Female A1 slender, 6-segmented; male A1 subchirocer, number of segments unknown. A2 with 1-segmented exopod bearing 4 setae, allobasis with 1 abexopodal seta; endopod 1-segmented, with 2 lateral spines and 5 apical setae/spines (cf. Wells and Rao (1987), fig. 143j). Mxp prehensile, syncoxa and basis of approximately the same length; syncoxa with 1 pinnate seta on apical margin, basis with spinulose field on anterior margin; claw massive, accompanied by minute seta. P1 prehensile, with extremely elongated coxa and basis, the former massive and larger than the latter, nearly reaching the length of enp-1. Exopod 2-segmented, more than half the length of enp-1; exp-1 half as long as exp-2, with 1 outer spine, exp-2 with 3 outer and 2 apical spines/setae. Endopod 2-segmented, enp-1 extremely elongated, massive, enp-2 small, apically with 1 strong curved claw and 1 tiny seta. P2–P4 with 3-segmented exopods and 2-segmented endopods. Female P5 with baseoendopod bearing 4 setae; exopod fused with baseoendopod, with 3 setae. Male P5 with completely reduced baseoendopod, exopod small and distinct, with 3 setae. Female "genital field simple, without trace of P6" (Wells and Rao 1987: 177); male P6 small, with 1 seta and 1 strong spine.

Etymology. The generic name is composed of the Greek prefix *pará-*, meaning similar and the generic name *Echinolaophonte*. Gender: feminine.

Type and only species. *Parechinolaophonte tropica* (Ummerkutty, 1970), gen. et comb. nov., by original designation.

Pseudechinolaophonte gen. nov.

https://zoobank.org/03B316FE-329E-476B-B1BB-F51289DAA8A0

Diagnosis. Laophontidae T. Scott, 1905. Body elongate, cylindrical, podoplean boundary between pro- and urosome inconspicuous. Sexual dimorphism in the A1, P3, P5 and P6; female with GDS. Cphth almost squarish, reaching about 1/3 of total body length; dorsally with spinulose, broad cuticular projection bearing 2–4 apical spikes on posterior margin (cf. Fig. 9A). Rostrum small, laterally constricted, square, fused to cphth. Thoracic body somites with paired strong spikes centrally on the posterior margin (cf. Fig. 9A); abdominal somites, except telson, dorsally with sclerotised clasp-like area bearing 2 spikes on posterior margins (cf. Fig. 9A). First abdominal somite (posterior half of female GDS) and second abdominal somite laterally with well-developed, wing-like epimeres (cf. Fig. 9A). Pre-anal somite with well-developed pseudoperculum, with 2 strong tridentate spikes (cf. Fig. 9A), but with some variability. CR at the most twice as long as broad, with 7 setae. Female A1 slender, 6-segmented; male A1 7–8-segmented, subchirocer. A2 with 1-segmented exopod bearing 4 setae, allobasis with or without abexopodal seta; endopod 1-segmented, with
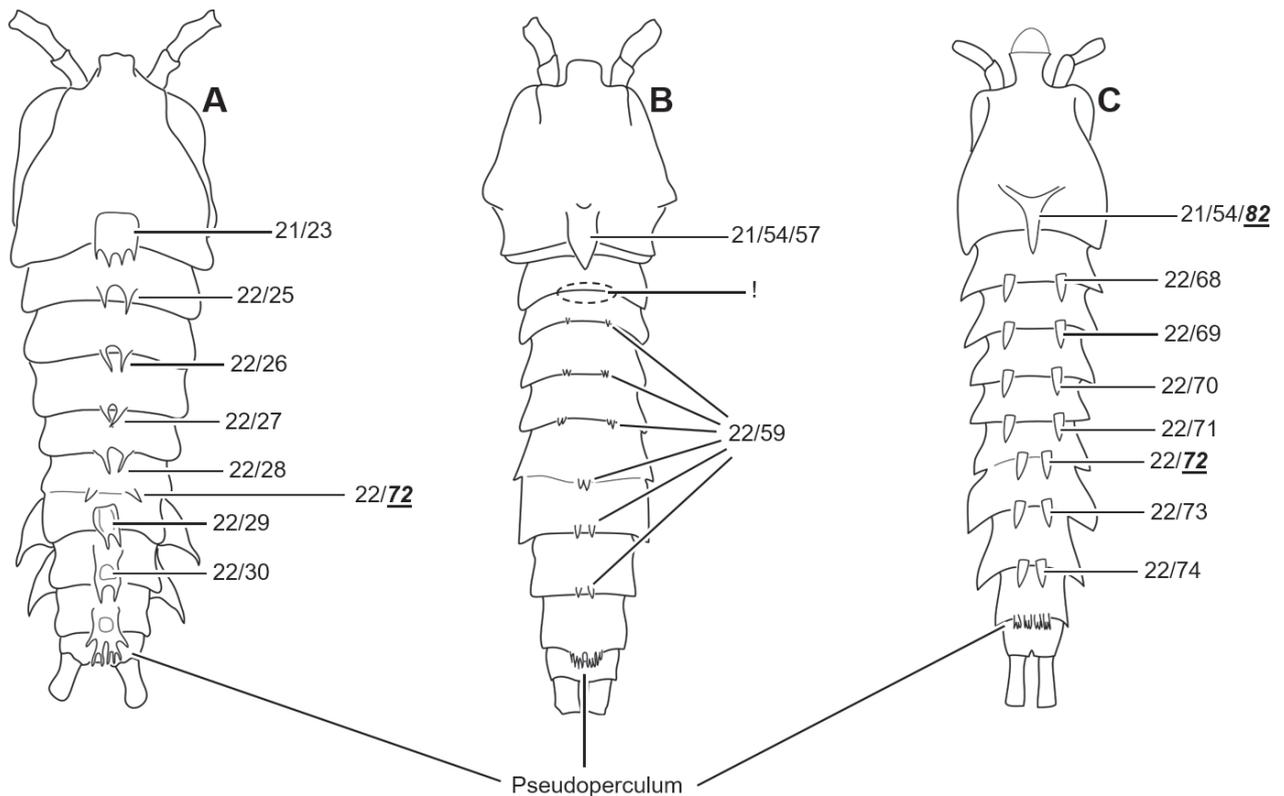
Figure 9. Schematic depiction of **A.** *Pseudechinolaophonte minuta* gen. et comb. nov.; **B.** *Echinolaophonte armiger* and **C.** *Echinolaophonte horrida*, illustrating and exemplifying the general shape of the cuticular structures located dorsally on the cephalothorax and free body somites of the closely-related taxa treated in the present contribution. The assigned numbers reflect the corresponding morphological characters as listed in Table 2. Explanations are given in the text.

2 lateral spines and 1 seta; 1 spine modified with a rounded tip that differs between the species; apically with 5–6 setae/spines, 2–3 of which geniculate. Mxp prehensile, with elongated syncoxa and basis; syncoxa with 1–2 setae on its apical edge. Endopod produced into long claw that surpasses the length of the basis. P1 prehensile, with elongated coxa and basis, but none reaching the length of enp-1. Exopod 2-segmented, not reaching half the length of the enp-1. Exp-1 about twice as long as exp-2, with 1 outer spine; exp-2 with 3 outer spines and 2 apical setae. Endopod 2-segmented, enp-1 long, without any ornamentation; enp-2 small, apically with strong serrated claw and 1 tiny seta. P2–P4 with 3-segmented exopods, P2 and P4, as well as female P3 endopods 2-segmented; outer basal seta of P2 biplumose, with extremely long pinnae. Male P3 and P4 sexually dimorphic; male P3 exopod more compact than in female, endopod 3-segmented, second segment with pronounced apophysis. Male P4 exopod also stronger than in female, somewhat bent inwards. P4 endopods particularly small in both sexes, not reaching the distal margin of exp-1. Female P5 with baseoendopod bearing 2 setae; exopod distinct, with 3 setae. Male P5 with completely reduced baseoendopod, exopod with 3 setae. Female P6 very small, knob-like, with 2 tiny setae. Male P6 small, consisting of simple lobe carrying 1 small bare and 1 long biplumose seta.

Etymology. The generic name is composed of the Greek prefix *pseudo-*, meaning false or fake and the generic name *Echinolaophonte*. Gender: feminine.

Type species. *Pseudechinolaophonte minuta* (Cottarelly & Forniz, 1991), gen. et comb. nov., by original designation.

Additional species. *Ps. mordoganensis* (Kuru, Sönmez & Karaytug, 2019) gen. et comb. nov., *Ps. veniliae* (Cottarelly, Forniz & Bascherini, 1992), gen. et comb. nov.

Restructuring *Echinolaophonte* Nicholls, 1941

After the exclusion of *Parechinolaophonte tropica* gen. et comb. nov., *Pseudechinolaophonte minuta* gen. et comb. nov., *Ps. mordoganensis* gen. et comb. nov. and *Ps. veniliae* gen. et comb. nov. from *Echinolaophonte*–CS, the genus *Echinolaophonte* retains 11 species (Fig. 10, node M). They can be characterised by the synapomorphic dorsal spur on the posterior margin of the cphth (Table 2, character 54). This dorsal cuticular spur on the posterior margin of the cphth is quite rare in Harpacticoida, had been recognised as a characteristic feature for *Echinolaophonte* by Nicholls (1941) and is hypothesised here as a strong synapomorphic character for all 11 species.

Table 2. Matrix listing the 135 morphological characters used in the here presented phylogenetic analysis. 1 = supposed apomorphies; 0 = supposed plesiomorphies; *1* = supposed convergent apomorphies. Vertical arrows in characters 31 and 32 point towards a further deviation in *E. oshoroensis*. For character state justification, see character discussion.

No.	No. Conv.	Character/species (1 = apomorphy; 0 = plesiomorphy; *1* = supposed convergence; ? = no data available)	Heterolaophonte minuta	Coullia	Hemilaophonte janinae	Xanthilaophonte	Parechinolaophonte tropica	Pseudechinolaophonte minuta	Pseudechinolaophonte veniliae	Pseudechinolaophonte mordoganensis	Echinolaophonte armiger	Echinolaophonte gladiator	Echinolaophonte brevispinosa	Echinolaophonte horrida	Echinolaophonte oshoroensis	Echinolaophonte villabonae	Echinolaophonte briani	Echinolaophonte hystrix	Echinolaophonte tetracheir	Echinolaophonte musa sp. nov.	Echinolaophonte mirabilis
1		P1 of characteristic laophontid shape (cf. Huys 1990)	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
2		P2 female enp(-2) with at most 1 inner seta	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
3		P3 female enp(-2) with at most 2 inner setae	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
4		P1 exopod at most 2-segmented	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
5		P1 coxa slender, elongate	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
6		P1 basis slender, elongate	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
7		P3 female enp(-2) without outer spine	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
8		A1 female 6-segmented	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
9		P5 female benp with at most 4 setae	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
10		P4 female enp(-2) without outer spine	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
11		P5 female exopod with at most 3 setae	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
12		Preanal somite dorsally with pseudoperculum formed by cuticular spikes	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
13		Rostrum narrowed	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
14		Mxp syncoxa as long as or slightly shorter than basis	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
15		Cphth with dorsal cuticular ridge crossed by two furrows	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16	1(?)	**Cphth laterally extended**	0	0	0	0	1	0	0	0	*1?*	*1?*	0	0	0	0	0	0	0	*1?*	*1?*
17		Cphth on lateral posterior corners with backwardly directed projections	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18		1st abdominal somite with small spinulose cuticular structure	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19		2nd abdominal somite with small spinulose cuticular structure	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20		P5 female baseoendopod and exopod fused	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21		Cphth dorsally with strong cuticular structure centrally on posterior margin	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
22		Free body somites except preanal somite and telson with cuticular structures on posterior margin	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
23		Cphth dorsally with spinulose, broad projection bearing 2-4 apical spikes	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
24		Cphth rectangular, almost square	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
25		P2-bearing somite dorsally with pair of strong spikes standing close together	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
26		P3-bearing somite dorsally with pair of strong spikes standing close together	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
27		P4-bearing somite dorsally with pair of strong spikes standing close together	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
28		P5-bearing somite dorsally with pair of strong spikes standing close together	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
29		1st abdominal somite (= posterior GDS) with dorsal sclerotized clasp-like area bearing 2 spikes	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
30		2nd abdominal somite with dorsal sclerotized clasp-like area bearing 2 spikes	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
31	2	**1st abdominal somite (= posterior GDS) with epimeres extended laterally**	0	0	0	0	0	1	1	1	0	0	*1*	*1*	*1*↑	0	0	0	0	0	*1*
32	3	**2nd abdominal somite with epimeres extended laterally**	0	0	0	0	0	1	1	1	0	0	*1*	*1*	*1*↑	0	0	0	0	0	*1*
33		Pseudoperculum developed as sclerotized clasp-like area bearing spikes	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
34		A2 endopodal surface seta with strongly derived tip	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0

No.	No. Conv.	Character/species (1 = apomorphy; 0 = plesiomorphy; *1* = supposed convergence; ? = no data available)	*Heterolaophonte minuta*	*Coullia*	*Hemilaophonte janinae*	*Xanthilaophonte*	*Parechinolaophonte tropica*	*Pseudechinolaophonte minuta*	*Pseudechinolaophonte veniliae*	*Pseudechinolaophonte mordoganensis*	*Echinolaophonte armiger*	*Echinolaophonte gladiator*	*Echinolaophonte brevispinosa*	*Echinolaophonte horrida*	*Echinolaophonte oshoroensis*	*Echinolaophonte villabonae*	*Echinolaophonte briani*	*Echinolaophonte hystrix*	*Echinolaophonte tetracheir*	*Echinolaophonte musa* sp. nov.	*Echinolaophonte mirabilis*
35		P2 outer basal seta longer than exp-1 and exp-2, biplumose	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
36		P5 baseoendopod female with 2 setae	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
37		Cphth dorsal process square, spinulose, with 2 strong spikes, each outwardly accompanied by 2 small ones	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
38		A1 female 2nd segment 1 subapical outer seta remarkably elongated, longer that remaining segments together	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
39		A2 endopod: surface seta comb-like at distal half; not tapering gradually	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
40		P5 female baseoendopodal setae not reaching apical margin of exopod	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
41		Posterior half of GDS lateral wing-like epimeres strongly pronounced	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
42		2nd abdominal somite lateral wing-like epimeres strongly pronounced	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
43		Pseudoperculum consisting of paired y-shaped spikes accompanied each by single spike	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
44	**4**	**A2 allobasis without abexopodal seta**	0	0	0	0	0	1	1	0	0	*1*	0	0	0	0	*1*	0	0	0	0
45		Md palpus lost exopodal seta (= with 4 setae)	0	0	0	0	0	1	1	0	0	?	0	0	0	0	0	0	0	0	0
46	**5**	**Mxp syncoxa with 1 apical seta**	0	0	0	0	0	1	1	0	0	0	0	0	0	0	*1*	0	0	0	0
47		Cphth dorsal process square, spinulose, with 4 strong spikes	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
48		A2 endopod seta with club-shaped, apically pinnate tip	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
49	**6**	**Mxl coxa with 1 apical seta**	0	0	0	*1*	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
50	**7**	**Mxl basis with 1 apical seta**	0	0	0	*1*	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
51		Cphth dorsal process spinulose, elongate, with rounded apex carrying 4 spikes	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
52		A2 endopod seta with square-cut, fork-like tip	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
53		P3 male endopodal apophysis with indentation near its tip	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
54		Cphth with single spur dorsally on posterior margin	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1
55		Whole body surface densely covered with fine cuticular structures	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
56	**8**	**Cphth laterally protruded**	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	*1*	*1*
57		Cphth dorsal spur broad, rather short	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
58	**9**	**Female GDS laterally of slightly inflated aspect**	0	0	0	*1*	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
59		Pedigerous and first 2 abdominal somites dorsally with small spiny processes on posterior margin	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
60		Dense body coverage developed into tiny denticles	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
61		P4-bearing somite dorsally with 4 spiny processes standing pairwise together	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
62		Anterior half of female GDS with pair of spiny processes fused at their bases	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
63		Posterior half of GDS and second abdominal somite dorsally with spiny processes standing close together	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
64		Dense body coverage developed into short setules	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
65		Cphth lateral protrusions produced into pair of narrow, backwardly directed cuticular jags	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
66		Mxp strong, allobasis swollen on inner margin, claw massive, curved about 90°	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
67	**10**	**P3 female exp-3 with 2 outer spines**	0	0	0	*1*	*1*	0	0	0	0	*1*	0	0	0	*1*	0	0	0	0	0
68		P2-bearing somite with paired dorsal processes	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1
69		P3-bearing somite with paired dorsal processes	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1
70		P4-bearing somite with paired dorsal processes	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1
71		P5-bearing somite with paired dorsal processes	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1
72	**11**	**P6-bearing somites with paired dorsal processes**	0	0	0	0	0	*1*	*1*	*1*	0	0	1	1	1	1	1	1	1	1	1
73		1st abdominal somite with paired dorsal processes	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1

Header spanning columns *Parechinolaophonte tropica* through *Echinolaophonte mirabilis*: **Echinolaophonte-CS**

Character matrix (continued). Columns under the spanning header **Echinolaophonte-CS** cover *Parechinolaophonte tropica* through *Echinolaophonte mirabilis*.

No.	No. Convergences	Character/species (1 = apomorphy; 0 = plesiomorphy; *1* = supposed convergence; ? = no data available)	*Heterolaophonte minuta*	*Coullia*	*Hemilaophonte janinae*	*Xanthilaophonte*	*Parechinolaophonte tropica*	*Pseudechinolaophonte minuta*	*Pseudechinolaophonte veniliae*	*Pseudechinolaophonte mordoganensis*	*Echinolaophonte armiger*	*Echinolaophonte gladiator*	*Echinolaophonte brevispinosa*	*Echinolaophonte horrida*	*Echinolaophonte oshoroensis*	*Echinolaophonte villabonae*	*Echinolaophonte briani*	*Echinolaophonte hystrix*	*Echinolaophonte tetracheir*	*Echinolaophonte musa* sp. nov.	*Echinolaophonte mirabilis*
74		2nd abdominal somite with paired dorsal processes	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1
75		Cphth laterodistally extended cheek-like	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0
76		Rostrum elongate, with rounded tip	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0
77		P3 male exopod powerfully developed	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0
78		P3 male exp-2 outer spine massive, s-shaped	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0
79		Tip of rostrum minutely emarginated	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
80		Cphth: lateral "cheeks" bulging considerably	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
81		Rostrum basally remarkably constricted	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
82	**12**	**Cphth spur strongly tapering apically, apical half quite narrow**	0	0	0	0	0	0	0	0	0	0	1	1	0	*1*	0	0	0	0	0
83		Pseudoperculum consisting of 4 tridenticulated processes	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
84	**13**	**P1 exopod reduced in length, not even reaching half the length of enp-1**	0	0	0	*1*	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
85		P3 male enp-2 apophysis with acute jag basally on inner margin	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
86		P2-bearing somite dorsal processes denticulated	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
87		P3-bearing somite dorsal processes denticulated	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
88		P4-bearing somite dorsal processes denticulated	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
89		P5-bearing somite dorsal processes denticulated	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
90		Dorsal cuticular processes of P6-bearing somite (= female anterior half of GDS) denticulated	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
91		Dorsal cuticular processes of 1st abdominal somite (= female posterior half of GDS) denticulated	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
92		Dorsal cuticular processes of 2nd abdominal somite denticulated	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
93		1st abdominal somite (= posterior GDS) lateral wing-like epimeres extended completely reduced	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
94		2nd abdominal somite lateral wing-like epimeres extended completely reduced	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
95	**14**	**Cphth spur laterally with tufts of long and fine setules**	0	0	0	0	0	0	0	0	0	0	0	0	1	0	*1*	0	*1*	*1*	*1*
96		P2-bearing somite with lateral cuticular processes	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
97		P3-bearing somite with lateral cuticular processes	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
98		P4-bearing somite with lateral cuticular processes	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
99		P5-bearing somite with lateral cuticular processes	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
100		1st abdominal somite (= posterior half of female GDS) with lateral cuticular processes	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
101		2nd abdominal somite with lateral cuticular processes	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
102		P3 exopod male remakably strengthened	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
103	**15**	**P3 endopod male 2-segmented**	0	0	0	*1*	*1*	0	0	0	*1*	?	0	0	0	1	1	1	1	1	1
104	**16**	**P3 male endopod lost sexual dimorphism**	0	0	0	*1*	*1*	0	0	0	*1*	?	0	0	0	1	1	1	1	1	1
105		Rostrum slightly trapezoid, constricted basally and broadening apically, rather flat/concave apical margin	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0
106		Cphth laterally with intricate cuticular ornamentation	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0
107		Female GDS dorsally with cuticular "ring"	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0
108		1st abdominal somite (= posterior half of female GDS) dorsally with strengthened, spinules-bearing cuticular area	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0
109		2nd abdominal somite dorsally with strengthened, spinules-bearing cuticular area	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0
110		Female pseudoperculum consisting of 2 bi- or tri-denticulate processes, laterally accompanied each by 2 spikes	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0
111		Cphth dorsal spur robust, short, with 2 dorsal notches	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	?	0	0	0
112		Cphth: lateral cuticular ornamentation considerably pronounced	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	?	0	0	0
113		Rostrum granular on anterior half	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	?	0	0	0
114		Preanal somite with 2 spinulose rows in front of pseudoperculum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	?	0	0	0

No.	No. Conv.	Character/species (1 = apomorphy; 0 = plesiomorphy; *1* = supposed convergence; ? = no data available)	*Heterolaophonte minuta*	*Coullia*	*Hemilaophonte janinae*	*Xanthilaophonte*	*Parechinolaophonte tropica*	*Pseudechinolaophonte minuta*	*Pseudechinolaophonte veniliae*	*Pseudechinolaophonte mordoganensis*	*Echinolaophonte armiger*	*Echinolaophonte gladiator*	*Echinolaophonte brevispinosa*	*Echinolaophonte horrida*	*Echinolaophonte oshoroensis*	*Echinolaophonte villabonae*	*Echinolaophonte briani*	*Echinolaophonte hystrix*	*Echinolaophonte tetracheir*	*Echinolaophonte musa* sp. nov.	*Echinolaophonte mirabilis*
115		Rostrum elongate, with bifurcated tip	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
116		CR at least 3,5 times longer than broad	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
117	**17**	**P3 outer basal seta of composite shape**	0	0	0	0	0	0	0	0	0	0	0	0	*1*	0	*1*	0	1	1	1
118	**18**	**P4 outer basal seta of composite shape**	0	0	0	0	0	0	0	0	0	0	0	0	*1*	0	0	0	1	1	1
119		1st abdominal somite (= posterior half of female GDS): processes arising from H-like fortification	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
120		2nd abdominal somite: processes arising from H-like fortification	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
121		Pseudoperculum consisting of 4 palmate processes carrying each 5-6 "fingers"	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
122		Cphth lateral processes elongated, slender	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
123		Cphth anteriorly with moderate dorsal process	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
124		Cphth centrally with moderate dorsal process	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
125		CR at least 5,5 times longer than broad	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
126		Cphth lateral processes backwardly curved	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
127		P2-bearing somite of female: processes strongly elongate and bifurcate	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
128		P3-bearing somite: processes strongly elongate and bifurcate	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
129		P4-bearing somite: processes strongly elongate and bifurcate	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
130		P5-bearing somite: processes strongly elongate and bifurcate	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
131		P6-bearing somite: processes strongly elongate and bifurcate	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
132		1st abdominal somite: processes strongly elongate and bifurcate	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
133		2nd abdominal somite: processes strongly elongate and bifurcate	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
134		P2-bearing somite dorsal processes long, bearing 3 long setules basally	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
135		2nd abdominal somite dorsal processes fused basally, with 2 denticles basally and centrally, and with 2 long setules	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

Phylogenetic relationships within *Echinolaophonte*

Echinolaophonte splits into two main subordinated clades, namely the *armiger–gladiator* clade enclosing *E. armiger* and *E. gladiator* (Fig. 10, node N) and the *brevispinosa–mirabilis* clade that includes the remaining eight species (Fig. 10, node Q). The monophyly of the *armiger–gladiator* clade is supported by five autapomorphies (Table 2, characters 55–59) and each species is also characterised by four autapomorphies (Table 2, characters 60–67).

The *brevispinosa–mirabilis* clade is characterised by seven unambiguous autapomorphies (Table 2, characters 68–74). It splits again into two subordinated clades, i.e. the *brevispinosa–oshoroensis* clade (Fig. 10, node R) and the *villabonae–mirabilis* clade (Fig. 10, node W). Both clades are supported by four and two autapomorphies, respectively (Table 2, characters 75–78 and 103, 104, respectively) and also, the relationships within the subclades can be supported by some apomorphic characters (Table 2). Within the *villabonae–mirabilis* clade, a further splitting took

place: the *villabonae–briani* clade encompasses *E. villabonae* and *E. briani* (and tentatively *E. hystrix*) (Fig. 10, node X), whose status as sister species is supported by six synapomorphies (Table 2, characters 105–110). Together they constitute the sister taxon of the *tetracheir–mirabilis* clade (Fig. 10, node AA), whose monophyly is supported by four autapomorphies (Table 2, characters 115–118). Within the *tetracheir–mirabilis* clade, the first branch-off is *E. tetracheir* (Fig. 10, node BB), forming the sister species of the *musa–mirabilis* clade (Fig. 10, node CC). All named species can be characterised by distinct autapomorphies that are discussed in detail below.

Establishment of *Echinolaophonte briani* Lang, 1965

Lang (1965) reported and described a new presumed subspecies from Dillon Beach, California (U.S.A.), which he named *E. armiger* f. *briani* Lang, 1965. He assumed a close relationship with *E. armiger* f. *typica sensu* Gurney (1927), but at the same time, noted some

morphological differences that justified, in his opinion, the establishment of a new form (subspecies) *briani*. Based on the detailed re-description of *E. armiger* by Lee et al. (2006), as well as on the here presented detailed phylogenetic analysis, it became clear that Lang's (1965) *E. armiger* f. *briani* in fact represents a distinct species that is closely related to *E. villabonae*. Thus, it is here elevated to species rank as *Echinolaophonte briani* Lang, 1965.

The status of *Echinolaophonte hystrix* and *Laophonte steueri* van Douwe, 1929

Echinolaophonte hystrix had been synonymised with *E. armiger* by Nicholls (1941) and later by Lang (1948) as *Onychocamptus armiger*. Lee et al. (2006) provided a well-justified re-instatement of *E. hystrix* and, at the same time, recognised that Lang's (1965) description of *E. armiger* f. *typica* (Gurney, 1927) most probably was a re-description of Brian's (1928) *E. hystrix*, whose underlying Mediterranean material had been donated to K. Lang by A. Brian (Lang 1965: 5). The argumentation given by Lee et al. (2006) is adopted here and the identity of *E. hystrix* is confirmed.

Van Douwe (1929) described another species from the French, Italian and Croatian Mediterranean coast, *Laophonte steueri*. That author provided a quite detailed textual description that lacks, however, a similarly detailed set of illustrations. He pointed towards the strong similarity of *L. steueri* with *L. horrida* and *L. brevispinosa*, apparently unaware of Brian's (1928) description of *L. hystrix*. Like the latter, also *L. steueri* was subsequently synonymised with *E. armiger* by Nicholls (1941) and Lang (1948). The WoRMS database synonymises *L. steueri* with *Echinolaophonte hystrix* (Walter and Boxshall 2022), albeit without mentioning the corresponding literature that might justify that synonymisation.

The here presented phylogenetic analysis aimed at elucidating the systematic relationship of both *E. hystrix* and *L. steueri*. However, the available information is scarce and the descriptions of both species are rather imprecise and incomplete. Though, the synonymisation of *L. steueri* with *E. hystrix* is tentatively confirmed here (see Discussion); however and despite some indications for an allocation of *E. hystrix* into the *villabonae–briani* clade, due to the gap of detailed information, the systematic position of *E. hystrix* within *Echinolaophonte* remains unclear (Fig. 10, node X).

Diagnostic key to the genera and species of *Echinolaophonte* and the here established new genera (note: *E. longantennata* was excluded from the analysis due to lack of data)

1   Cphth without strong, cuticular dorsal structure centrally; free body somites, except pre-anal somite and telson without well-developed cuticular structures 2

–   Cphth with strong cuticular dorsal structure centrally; free body somites, except pre-anal somite and telson with well-developed cuticular structures 3

2   P2 exp-2 with inner seta; P1 exp reaching over middle of enp· ....*Parechinolaophonte tropica* gen. et. comb. nov.

3   Cphth rectangular, almost square; P2–P6-bearing somites dorsally with pair of with spikes that are basally connected to each other; A2 enp with 1 spine bearing strongly derived tip 4 ....*Pseudechinolaophonte* gen. nov.

–   Cphth not square; P2–P6-bearing somites dorsally with pair of basally separated processes instead of pair of connected spikes; A2 enp without blunt-tip-bearing spine 6 .... *Echinolaophonte*

4   P4 exp-3 with 4 setae/spines 5

–   A2 enp derived seta comb-like at distal half; P4 exp-3 with 5 setae/spines .... *Ps. mordoganensis* comb. nov.

5   A2 enp derived seta club-shaped; P2 exp-3 twice as long as exp-3; CR 2.0 times longer than wide *Ps. minuta* comb. nov.

–   A2 enp derived seta with a trifid tip; P2 exp-3 only slightly longer than exp-3; CR 1.5 times longer than wide ....
.... *Ps. veniliae* comb. nov.

6   Paired dorsal processes tiny; cphth dorsal spur with broad base 7

–   Paired dorsal processes strongly developed; cphth dorsal spur with narrow base 8

7   P3 exp-3 with 7 setae/spines ....*E. armiger*

–   P3 exp-3 with 6 setae/spines .... *E. gladiator*

8   Cphth laterodistally exended cheek-like; Ro elongate, with rounded tip 9

–   These characters not combined 11

9   P2 exp-3 with inner seta; CR at least 2 times as long as wide 10

–   P2 exp-3 without inner seta; CR at most 2 times as long as wide .... *E. oshoroensis*

10   Rostrum with rounded tip; P1 exp not reaching middle of enp-1 .... *E. horrida*

–   Rostrum with bilobed tip; P1 exp reaching middle of enp-1 .... *E. brevispinosa*

11   Rostrum slightly trapezoid, broadening apically; Cphth with lateral cuticular ornamentation................................... 12

–   Rostrum narrow and elongate; Cphth without lateral cuticular ornamentation 14

12   P3 exp-3 with 7 setae/spines 13

–   P3 exp-3 with 6 setae/spines .... *E. villabonae*

Discussion

Echinolaophonte: a systematic tangle

The statement of Boxshall and Halsey (2004: 316), that the taxon Laophontidae "is a large and heterogeneous family, much in need of comprehensive revision" remains valid and is reflected even at the genus level. Therefore, the aimed phylogenetic revision of the here treated genus *Echinolaophonte*, which hitherto encloses 16 species (including the here described *E. musa* sp. nov., *E. longantennata* that is excluded from our analysis and the re-instated *E. briani*), turned out to be a complex, sometimes confusing and ambitious challenge.

The topic began at the end of the 18th century: Müller (1792) described a new and rare marine species from Danish and Norwegian waters: *Cyclops minuticornis* Müller, 1792. He provided a very brief textual description and just one illustration of the habitus that lacks any detailed characteristics (Müller 1792: plate XIX). Subsequently, Baird (1850) synonymised *Cy. minuticornis* with *Canthocamptus minuticornis* (Müller, 1792), reported from Berwick Bay, Dover (U.K.). He also provided only a short and imprecise textual description, mentioning, however, that the thoracic somites bear "a sharp spine" dorsally (Baird 1850: 211). His description was complemented by a single illustration of a lateral habitus (Baird 1850: plate XXV, fig. 3).

Claus (1863) rejected Baird's (1850) assignment of *Ca. minuticornis* to *Canthocamptus*, substantiating it by the quite different shape of the P1: *Ca. minuticornis* bears a peculiar, prehensile P1 endopod consisting of a very long enp-1 and a small enp-2, apically equipped with a strong curved claw. Such prehensile P1 is not found in *Canthocamptus*. Claus (1863) established the genus *Cleta* Claus, 1863, however, without placing *Ca. minuticornis* into that taxon. This was undertaken by Buchholz (1874) as "*Cleta minuticornis* Müller", who, at the same time, provided the first detailed illustrations of the lateral habitus, the cphth and first pedigerous somite, the antenna, mxp, P1 and P5 of that species (Buchholz 1874: plate XV, fig. 3).

Norman (1876: 206) reported a "beautifully spinose Copepod" from a tow-net in Davis Strait (North Atlantic Ocean), assigning it to Buchholz' (1874) specimen. Though, Norman (1876) doubted that this species might be the same as that which had been previously described by Müller (1792) and Baird (1850). Therefore, he proposed the name *Cleta horrida* for Buchholz' (1874) and the Davis Street specimens.

Nowadays, *Cleta* is synonymised with *Laophontopsis* Sars, 1908 and, thus, assigned to the Laophontopsidae Huys & Willems, 1989 (cf. Huys and Willems (1989); Walter and Boxshall (2022)). In that context, it is noteworthy that, according to the WoRMS database (Walter and Boxshall 2022), *Laophontopsis* encloses nine species, amongst them also "*L. minuticornis* (Buchholz, 1874)". However, other corresponding literature (Huys and Willems 1989; Bodin 1997; Boxshall and Halsey 2004; Wells 2007) lists only three species allocated to *Laophontopsis*, namely *L. lamellifera* (Claus, 1863) (type species), *L. borealis* Huys & Willems, 1989 and *L. monardi* Huys & Willems, 1989. To the knowledge of the authors, in the meantime, no re-evaluation of *Laophontopsis* has been realised. Future investigation may resolve the systematics of *Laophontopsis* as well as the affiliation of the six additional species listed in the WoRMS database.

It was Brady (1880) who removed *C. horrida* Norman, 1876 into *Laophonte* Philippi, 1840, providing an almost complete species description of *Laophonte horrida* (Norman, 1876). That species was later on (partly) re-described by Sars (1908; Norway), Chislenko (1967, 1977; Franz Joseph Land, White Sea) and Kornev and Chertoprud (2008; White Sea).

Sars (1908) described a second Norwegian species that strongly resembles *L. horrida*: *Laophonte brevispinosa* Sars, 1908. So far, it is the only report of that species. Lang (1948) added the record of *L. brevispinosa* from the Mediterranean by Brian (1917); nevertheless, comparison of the descriptions by Sars (1908) and Brian (1917) clearly reveals that the Mediterranean species does not belong to *L. brevispinosa*. The main difference between the latter and Brian's (1917) specimen is the presence of paired dorsal processes on all free body somites, except the two last ones in *L. brevispinosa* (Sars 1908: pl. 168); instead, Brian's (1917) specimen lacks dorsal processes on the pedigerous somites and bears only single processes on the remaining body somites (Brian 1917: figs 1, 2).

Nineteen years after Sars (1908), Gurney (1927) described two new species from the Suez Canal (Egypt): *Laophonte armiger* Gurney, 1927 and *L. mirabilis* Gurney, 1927. Subsequent re-descriptions of both species, particularly of *L. armiger*, reflect the increasing confusion that finally lead to the current tangle within *Echinolaophonte*. Besides nomenclatoric confusion—*L. armiger*, for instance, has been alternately allocated to *Laophonte*, *Echinolaophonte* and *Onychocamptus* (e.g. Gurney (1927); Nicholls (1941, 1945); Lang (1948, 1965); Pesta (1959); Vervoort (1964)) — the main impediment to allow

an unambiguous determination of the concerned specimens resulted from imprecise and incomplete (re-)descriptions and the unavailability of original material for direct comparison. In that context, especially the extraordinary and highly valuable contribution of Lee et al. (2006) has to be mentioned; these authors undertook an enormous effort to clear up the systematic status of *E. armiger sensu* Gurney, 1927 and, thus, started to disentangle the phylogenetic confusion within *Echinolaophonte*.

A further obstacle is that, since the establishment of *Echinolaophonte* by Nicholls (1941) and despite the increase of species from four to 14 until 2019, no amendment of Nicholls' (1941) generic diagnosis has been provided. This is particularly surprising, as several of the subsequently assigned species do not fit Nicholls' (1941) diagnosis of the genus. As a result, *Echinolaophonte* became a heterogeneous conglomerate of species, lacking an unambiguous characterisation of the genus.

Echinolaophonte was proposed by Nicholls (1941) to allocate *Laophonte horrida*, *L. brevispinosa*, *L. armiger* and *L. mirabilis*. In that context, Nicholls (1941) considered two further species, *L. hystrix*, and *L. steueri* as synonyms of *L. armiger* (but see below). He provided a key to the four assigned *Echinolaophonte* species and a generic diagnosis (setation of P2–P4 omitted here): (I) cphth with single large spur on posterior dorsal margin; (II) all free body somites, except penultimate somite and telson dorsolaterally with paired processes; (III) rostrum large and expanded; (IV) female A1 6-segmented, ae on fourth segment; (V) P1 with long and slender coxa, basis and enp-1; exopod 2-segmented, short, almost reaching half the length of enp-1; (VI) female P5 with narrow baseoendopod that carries four or five setae; exopod elongate, with three setae. As mentioned above, no amendment of the generic diagnosis has been made since then. Therefore, it is the aim of the following evaluation to provide an unambiguous phylogenetic characterisation of *Echinolaophonte*, with Nicholls' (1941) generic diagnosis as the starting basis.

Phylogenetic analysis

Validity of the generic diagnosis from Nicholls (1941)

In a first step, the 15 species (*E. longantennata* was excluded from the analysis) were examined in relation to Nicholl's (1941) generic diagnosis, i.e. the above listed characters I–VI. These constitute remarkable morphological deviations and, thus, are seen here as phylogenetically highly relevant.

Character I, presence of a single, well-developed spur on the posterior margin of the cphth (cf. Figs 9B, C): The development of a single acute spur on the posterior margin of the cphth is observable in some Harpacticoida, like in the *Mesocletodes abyssicola* group (Argestidae Por, 1986) (e.g. Sars (1921); Lang (1948); Menzel and George (2009)). However, in the Laophontidae, that feature is

absolutely rare; actually, only 11 *Echinolaophonte*–CS species share that peculiar deviation: *E. armiger*, *E. brevispinosa*, *E. briani*, *E. gladiator*, *E. horrida*, *E. hystrix*, *E. mirabilis*, *E. musa* sp. nov., *E. oshoroensis*, *E. tetracheir* and *E. villabonae*. The remaining four species assigned to *Echinolaophonte*–CS do not fit with character I. Although three species, namely *E. minuta*, *E. mordoganensis* and *E. veniliae* also present, a cuticular structure on the posterior cephalothoracic margin – which is seen here as homologous to the spur of the above listed 11 species (cf. Table 2, character 21), it is of a quite different shape, consisting of

"*...a chitinous process nearly quadrangular, the posterior margin of which is provided with strong spines and many thin setae lined on dorsal surface and along margins.*" (Cottarelli and Forniz (1991: 666) (cf. Fig. 9A).

That structure is interpreted here as having undergone a different further development than the single acute spur in *Echinolaophonte*. It is, therefore, listed as distinct apomorphy (Table 2, character 23, see below).

Finally, the last of the four species, *E. tropica*, presents neither a single acute spur nor a squarish spinulose and setulose structure; instead, it presents two dorsal furrows crossing a longitudinal cuticular ridge on its cphth (cf. Wells and Rao (1987); Ummerkutty (1970) did not provide any detailed description of the cphth).

Character II, presence of dorsolateral pairs of processes on all free body somites, except penultimate somite and telson (cf. Fig. 9B, C): That character actually constitutes a character complex, as it unites all body somites, which is not applicable for all involved species. For instance, *E. armiger*, *E. gladiator* and *E. tropica* lack well-developed dorsolateral processes on pedigerous somites P2 and P3 (cf. Fig. 9B) (*E. armiger*, however, presents at least very small paired socles that might be homologised with the processes found in the remaining 12 species). Moreover, *E. tropica* lacks dorsolateral processes on the pedigerous somites P4–P6 (anterior half of female GDS), as well as on the first (posterior half of female GDS) and second abdominal somites.

Character III, a large and expanded rostrum (cf. Fig. 9C): this character is actually restricted to *E. brevispinosa*, *E. horrida* and *E. oshoroensis*; the remaining *Echinolaophonte*–CS species bear a long, bifurcate rostrum (*E. mirabilis*, *E. musa* sp. nov., *E. tetracheir*), a narrowed, rather square (*E. armiger*, *E. briani*, *E. minuta*, *E. tropica*) or trapezoid rostrum whose anterior margin is broader than its base (*E. gladiator*, *E. hystrix*, *E. villabonae*) or a small rectangular rostrum (*E. mordoganensis*, *E. veniliae*).

Characters IV (female A1 6-segmented), V (P1 with long and slender coxa, basis and enp-1; exopod 2-segmented, short, almost reaching half the length of enp-1) and VI (female P5 with narrow baseoendopod that carries four setae; exopod elongate, with three setae) are confirmed for all species. It has to be objected, however, that at least characters IV and V are not exclusively found in *Echinolaophonte*–CS; for instance, a 6-segmented female A1 (character IV) is also found in the laophontids

Carraroenia McCormack, 2006, *Hemilaophonte janinae* Jakubisiak, 1933, *Psammoplatypus* Lee & Huys, 1999, *Xanthilaophonte*, and *Coullia* (part.), a P1 as described in character V is also present at least in *Hemilaophonte janinae*, *Xanthilaophonte* and *Coullia* and a female P5 baseoendopod bearing four setae is also present in *Hemilaophonte janinae* and *Xanthilaophonte* (e.g. Jakubisiak (1933); Noodt (1958); Por and Marcus (1972); Hamond (1973); Fiers (1991, 1992); Lee and Huys (1999); Gómez and Boyko (2006); McCormack (2006); Huys (2009)).

Therefore, it is concluded here that, based on Nicholl's (1941) generic diagnosis, characters I–VI are not shared by all *Echinolaophonte*–CS species or they are present also in other laophontid genera.

Relationship of *Echinolaophonte*–CS with other laophontid genera

In the following, a detailed character comparison is presented. For that purpose, 135 morphological characters were selected (Table 2).

Discussion of the membership of all here treated taxa in a monophylum Laophontidae is not an objective of the contribution at hand. Therefore, it is simply underlined by just one unambiguous apomorphy, the characteristic laophontid shape of the P1 (Table 2, character 1; Fig. 10/ Table 3: node A). For detailed discussion of laophontid systematics, see, for example, Huys (1990), Huys and Lee (1998/1999) and Lee and Huys (1999).

Compared with the first outgroup *Heterolaophonte minuta*, a set of five apomorphies characterise *Coullia*, *Hemilaophonte janinae*, *Xanthilaophonte* and *Echinolaophonte*–CS (Table 2, characters 2–6; Fig. 10/Table 3: node B) [plesiomorphic states in square brackets]:

Character 2, female P2 endopod with at most 1 inner seta [with 2 setae]: whilst *H. minuta* retains 2 inner setae on the female P2 endopod, *Echinolaophonte*–CS and *Xanthilaophonte* lost 1 and *Coullia* and *Hemilaophonte janinae* lost both inner setae.

Character 3, female P3 endopod with at most 2 inner setae [with 3 setae]: as for character 2, *H. minuta* retains the ancestral state of 3 inner setae, whilst *Echinolaophonte*–CS and *Xanthilaophonte* lost 1 seta, *Coullia* lost 2 and *Hemilaophonte janinae* lost all three setae.

Character 4, P1 exopod at most 2-segmented [3-segmented]: in *H. minuta* the P1 presents the ancestral 3-segmented exopod; the exopod is (at most) 2-segmented in *Coullia*, *Hemilaophonte janinae*, *Xanthilaophonte* and *Echinolaophonte*–CS.

Characters 5 and 6, P1 coxa and basis elongate and slender [coxa short, squarish or broader than long]: *H. minuta* presents the rather ancestral state of a short coxa and basis. In contrast, in *Coullia*, *Hemilaophonte janinae*, *Xanthilaophonte* and *Echinolaophonte*–CS, both the coxa and the basis are remarkably elongated.

Characters 2–6 clearly separate the *Coullia*–*Echinolaophonte*–CS clade from *Heterolaophonte minuta*. It

remains, however, unclear, to what extent that clade constitutes a monophyletic unity. Other taxa like, for example, *Carraroenia* and *Psammoplatypus*, also share at least single deviations with the *Coullia*–*Echinolaophonte*–CS clade. Nonetheless, as the here presented study explicitly focuses on the systematic status of *Echinolaophonte*–CS, the expansion of the phylogenetic analysis by adding further supraspecific taxa is beyond the scope of the present analysis.

The first branch-off from the *Coullia*–*Echinolaophonte*–CS clade is *Coullia*. It differs from the *Hemilaophonte*–*Echinolaophonte*–CS clade (Fig. 10/Table 3: node C) in the lack of the following three apomorphies (Table 2, characters 7–9):

Character 7, female P3 enp-2 without outer spine [outer spine still present]: *Hemilaophonte janinae*, *Xanthilaophonte* and *Echinolaophonte*–CS have lost the outer spine on the female P3 enp-2, which is still present in *Coullia*.

Character 8, female A1 6-segmented [at least 7-segmented]: *Hemilaophonte janinae*, *Xanthilaophonte* and *Echinolaophonte*–CS show a 6-segmented female antennule; the ae-bearing fourth segment is followed by 2 segments only. In *Coullia*, all except one species also present a 6-segmented female A1 (including the here exemplified *C. tongariki*). Nonetheless, as *C. platychelipusoides* (Noodt, 1958) still retains 7 segments in the female A1 (Noodt, 1958) — the ae-bearing fourth segment followed by 3 segments, the reduction of one antennular segment in the remaining *Coullia* species must be regarded as further deviation within *Coullia* and is, therefore, interpreted here as independent and convergent development.

Character 9, female P5 baseoendopod with at most 4 setae [with at least 5 setae]: At least *C. tongariki* and *C. platychelipusoides* bear five setae on the female P5 baseoendopod, whilst in *Hemilaophonte janinae*, *Xanthilaophonte* and *Echinolaophonte*–CS, only four setae are retained.

The monophyletic characterisation of *Coullia* is not pursued here. Contrariwise, the exclusive presence of the derived characters 7–9 in *Hemilaophonte janinae*, *Xanthilaophonte* and *Echinolaophonte*–CS support the hypothesis of these taxa being sister groups, with characters 7–9 constituting unambiguous synapomorphies.

Without aiming to provide an extensive characterisation of *Hemilaophonte janinae*, its distinct phylogenetic status may probably be supported by the shape, size and ornamentation of the rather short and blunt P2–P4; especially the (female) endopods stick out because of their small size that scarcely reaches the length of the respective exp-1. These derived features are missing in *Xanthilaophonte* and *Echinolaophonte*–CS and may probably build important hints for a future phylogenetic characterisation of *Hemilaophonte janinae*. It is, however, relevant in the present context, that *H. janinae* lacks the supposed apomorphies 10–12 (Table 2), which are hypothesised here as synapomorphic for *Xanthilaophonte* and *Echinolaophonte*–CS (Fig. 10/Table 3: node D):
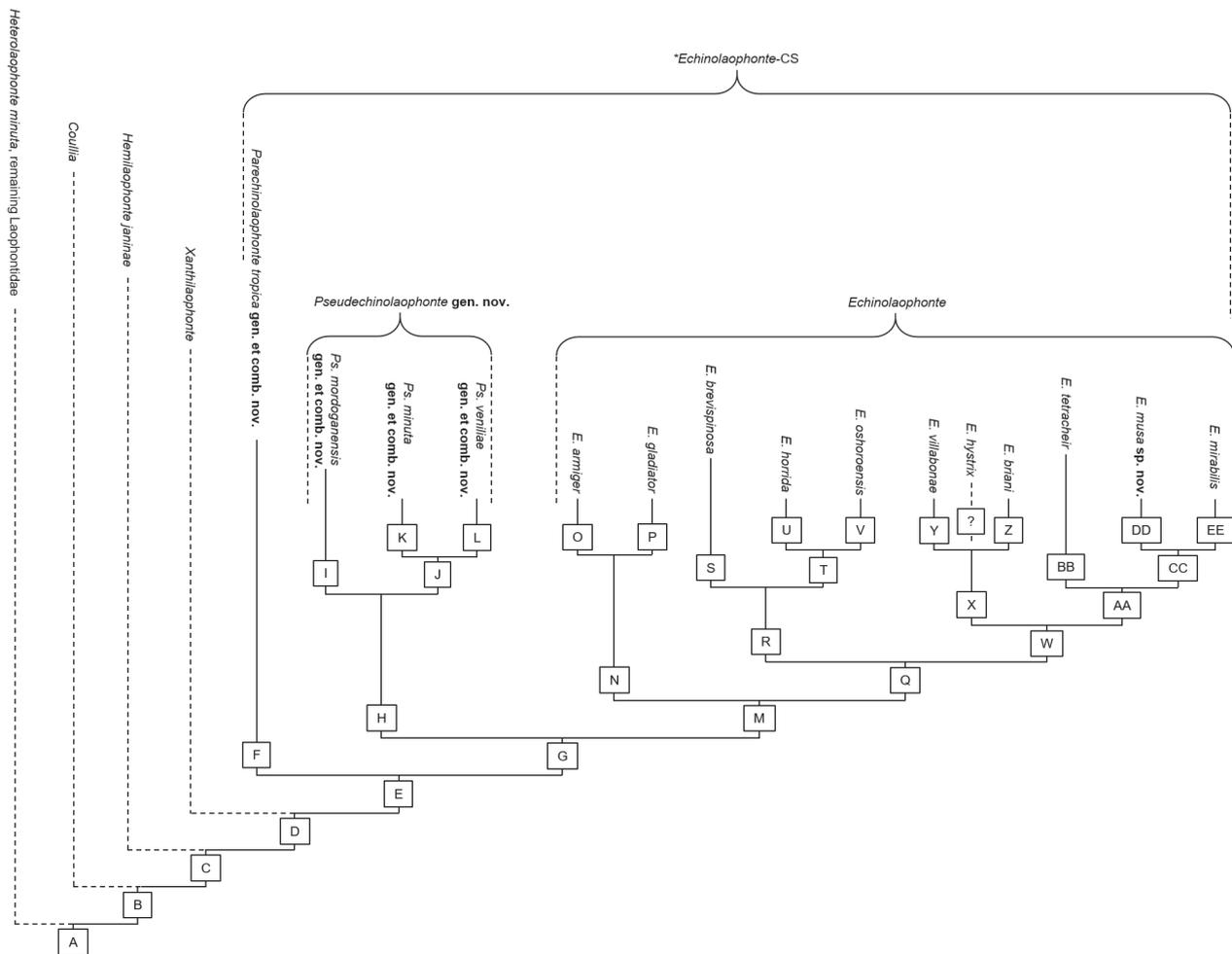
Figure 10. Cladogram presenting the result of the phylogenetic analysis, showing the hypothesised relationships of the investigated species. The apomorphies of the nodes (**A–FF**) are provided in Table 3. *Echinolaophonte*–CS = group of species united hitherto in the genus *Echinolaophonte*.

Character 10, female P4 enp-2 without outer spine [outer spine still present]: *Hemilaophonte janinae* still retains an outer spine on the distal endopodal segment of the P4, whereas such outer spine became lost in *Xanthilaophonte* and in the *Echinolaophonte*–CS species.

Character 11, female P5 exopod with three setae [with at least four setae]: *Xanthilaophonte* and *Echinolaophonte*–CS are characterised by a strongly reduced setation of the female P5 exopod; only three setae are present. In contrast, *Hemilaophonte janinae* still retains six setae on the female P5 exopod.

Character 12, the presence of a peculiar pseudoperculum dorsally on the posterior margin of the pre-anal somite [no pseudoperculum]: *Hemilaophonte janinae*, *Coullia* and *Heterolaophonte minuta* share a pseudoperculum on the posterior margin of the pre-anal somite. In contrast, *Xanthilaophonte* and *Echinolaophonte*–CS developed a quite peculiar pseudoperculum. It carries several digitate, cuspidate processes of high inter- and even intraspecific variability (e.g. Lang (1965); Wells and Rao (1987); Kuru et al. (2019)) and is seen here as a synapomorphy for the respective species.

From the above given comparative argumentation it is concluded that characters 10–12 unite *Xanthilaophonte* and the 15 species currently assigned to *Echinolaophonte*–CS. Although not providing the complex quality of, for example, Nicholl's (1941) characters I–VI, they are exclusive deviations of them and may, therefore, support their state as monophylum.

As for *Coullia* and *Hemilaophonte*, it is neither the intention here to discuss the phylogenetic status of *Xanthilaophonte*. In the present context, it is, however, important to assert that, apart from single supposed convergences at lower taxonomic level (cf. Table 2), *Xanthilaophonte* does not share the autapomorphies of the *Echinolaophonte*–CS clade, as demonstrated and discussed below.

The *Echinolaophonte*–CS clade (Fig. 10/Table 3: node E)

As shown in Table 2, the 15 species remaining in the *Echinolaophonte*–CS group — named from now on *Parechinolaophonte–Echinolaophonte* clade — share just two exclusive deviations (Table 2, characters 13, 14):

Table 3. List of nodes and assigned clades/taxa and apomorphies shown in Fig. 9. Presumed convergences are set in bold italics.

Node	Clade/taxon	Included studied taxa	No. apomorphies
A	Laophontidae	all studied taxa	1
B	*Coullia–Echinolaophonte* clade	*Coullia, Hemilaophonte, Parechinolaophonte* gen. nov., *Pseudechinolaophonte* gen. nov., *Echinolaophonte*	2, 3, 4, 5, 6
C	*Hemilaophonte–Echinolaophonte* clade	*Hemilaophonte, Parechinolaophonte* gen. nov., *Pseudechinolaophonte* gen. nov., *Echinolaophonte*	7, 8, 9
D	*Xanthilaophonte–Echinolao-phonte* clade	*Parechinolaophonte* gen. nov., *Pseudechinolaophonte* gen. nov., *Echinolaophonte*	10, 11, 12
E	*Parechinolaophonte* gen. nov.–*Echinolaophonte* clade	*Parechinolaophonte* gen. nov., *Pseudechinolaophonte* gen. nov., *Echinolaophonte*	13, 14
F	*Parechinolaophonte* gen. nov.	*Parechinolaophonte tropica* gen. et comb. nov.	15, ***16?***, 17, 18, 19, 20, ***67***, ***103***, ***104***
G	*Pseudechinolaophonte* gen. nov.–*Echinolaophonte* clade	*Pseudechinolaophonte* gen. nov., *Echinolaophonte*	21, 22
H	*Pseudechinolaophonte* gen. nov.	*Pseudechinolaophonte minuta* gen. et comb. nov., *Ps. mordoganensis* gen. et comb. nov., *Ps. veniliae* gen. et comb. nov.	23, 24, 25, 26, 27, 28, 29, 30, ***31***, ***32***, 33, 34, 35, 36, ***72***
I	*Pseudechinolaophonte mordoganensis* gen. et comb. nov.	*Pseudechinolaophonte mordoganensis* gen. et comb. nov.	37, 38, 39, 40
J	*Pseudechinolaophonte minuta–veniliai* clade	*Pseudechinolaophonte minuta* gen. et comb. nov., *Ps. veniliae* gen. et comb. nov.	41, 42, 43, ***44***, 45, ***46***
K	*Pseudoechinolaophonte minuta* gen. et comb. nov.	*Pseudechinolaophonte minuta* gen. et comb. nov.	47, 48, ***49***, ***50***
L	*Pseudoechinolaophonte veniliae* gen. et comb. nov.	*Pseudechinolaophonte veniliae* gen. et comb. nov.	51, 52, 53
M	*Echinolaophonte*	*E. armiger, E. gladiator, E. brevispinosa, E. horrida, E. oshoroensis, E. villabonae, E. briani, E. tetracheir, E. musa* sp. nov., *E. mirabilis*	54
N	*Echinolaophonte armiger–gladiator* clade	*Echinocletodes armiger, E. gladiator*	***16?***, 55, ***56***, 57, ***58***, 59
O	*Echinolaophonte armiger*	*Echinolaophonte armiger*	60, 61, 62, 63, ***103***, ***104***
P	*Echinolaophonte gladiator*	*Echinolaophonte gladiator*	***44***, 64, 65, 66, ***67***
Q	*Echinolaophonte brevispinosa–mirabilis* clade	*Echinolaophonte brevispinosa, E. horrida, E. oshoroensis, E. villabonae, E. briani, E. tetracheir, E. musa* sp. nov., *E. mirabilis*	68, 69, 70, 71, 72, 73, 74
R	*Echinolaophonte brevispinosa–oshoroensis* clade	*Echinolaophonte brevispinosa, E. horrida, E. oshoroensis*	***31***, ***32***, 75, 76, 77, 78
S	*Echinolaophonte brevispinosa*	*Echinolaophonte brevispinosa*	79, 80
T	*Echinolaophonte horrida–oshoroensis* clade	*Echinolaophonte horrida, E. oshoroensis*	81, ***82***, 83, ***84***, 85
U	*Echinolaophonte horrida*	*Echinolaophonte horrida*	86, 87, 88, 89, 90, 91, 92
V	*Echinolaophonte oshoroensis*	*Echinolaophonte oshoroensis*	93, 94, ***95***, 96, 97, 98, 99, 100, 101, 102, ***117***, ***118***
W	*Echinolaophonte villabonae–mirabilis* clade	*Echinolaophonte villabonae, E. briani, E. tetracheir, E. musa* sp. nov., *E. mirabilis*	***103***, ***104***
X	*Echinolaophonte villabonae–briani* clade	*Echinolaophonte villabonae, E. briani*	105, 106, 107, 108, 109, 110
Y	*Echinolaophonte villabonae*	*Echinolaophonte villabonae*	***67***, 111, 112, 113
Z	*Echinolaophonte briani*	*Echinolaophonte briani*	***44***, ***46***, ***82***, ***95***, 114, ***117***
AA	*E. tetracheir–mirabilis* clade	*Echinolaophonte tetracheir, E. musa* sp. nov., *E. mirabilis*	***95***, 115, 116, ***117***, ***118***
BB	*Echinolaophonte tetracheir*	*Echinolaophonte tetracheir*	119, 120, 121
CC	*Echinolaophonte musa* sp. nov.–*mirabilis* clade	*Echinolaophonte musa* sp. nov., *E. mirabilis*	***16?***, ***56***, 122, 123, 124, 125
DD	*Echinolaophonte musa* sp. nov.	*Echinolaophonte musa* sp. nov.	126, 127, 128, 129, 130, 131, 132, 133
EE	*Echinolaophonte mirabilis*	*Echinolaophonte mirabilis*	***31*** , ***32***, 134, 135

Character 13, rostrum narrowed, not tapering apically [rostrum with broad base, triangular]: *Hemilaophonte janinae* and *Coullia* retain the ancestral shape of the rostrum, which consists of a broad base tapering apically, giving the rostrum a triangular shape. Therefore, the narrowed rostrum as present in the *Parechinolaophonte—Echinolaophonte* clade (cf. Fig. 9) is regarded as a deviation. A similar rostral shape, as shown for *Xanthilaophonte trispinosa* (Sewell, 1940) by Fiers (1991), is interpreted here as a convergence, because its congener, *X. carcinicola* Fiers, 1991, retains the ancestral triangular shape (Fiers 1991).

Character 14, syncoxa of the mxp as long as or only slightly shorter than the basis [syncoxa reaching only

nearly half the length of the basis]: the species of the *Parechinolaophonte–Echinolaophonte* clade share the remarkable derived elongation of the maxilliped. It bears a syncoxa, a basis and an endopod produced into a long, curved claw. The syncoxa and basis are equally long and slender and the claw reaches or even surpasses the length of the basis. Instead, the maxillipedal syncoxa in *Hemilaophonte janinae* and *Xanthilaophonte* is short (Fiers 1991, 1992).

The first branch-off in the *Parechinolaophonte–Echinolaophonte* clade is *Echinolaophonte tropica* (Fig. 10/ Table 3: node F). That species lacks the supposed synapomorphies of the remaining species (*Pseudechinolaophonte–Echinolaophonte* clade; see below), but can be

characterised by six autapomorphies (Table 2, characters 15–20):

Character 15, cphth dorsally with cuticular ridge crossed by two furrows [without dorsal ridge and furrows]: Whilst the *Pseudechinolaophonte–Echinolaophonte* clade bears characteristic cuticular processes on the cphth, *E. tropica* does not. Instead, its cphth is dorsally characterised by a kind of cuticular longitudinal ridge that is crossed by two furrows (Wells and Rao 1987). That exclusive deviation is hypothesised as an apomorphy for *E. tropica*.

Character 16, cphth laterally extended [not extended]: As indicated by Ummerkutty (1970) and further described by Wells and Rao (1987), *E. tropica* has a cphth that shows some exclusive deviations. Besides the dorsal cuticular ridge with furrows (character 15), the lateral margins of the cphth are remarkably extended and of triangular shape. Although lateral outgrowths are also present in *E. mirabilis* (Gurney 1927; Wells and Rao 1987) and *E. musa* sp. nov. (present contribution, Figs 2, 3A, 7C) and at least indicated in *E. armiger* (Gurney 1927; Lee et al. 2006) and *E. gladiator* (Vervoort 1964), their shape differs remarkably from that in *E. tropica*. Moreover, the latter does not share further deviations with the named species and, finally, the development of lateral processes occurs independently several times within the Harpacticoida (e.g. Cletodinae T. Scott, 1904 (part.), Laophontodinae Lang, 1944 (part.), Idyanthidae Lang, 1944 (part.) (cf. George (2020, 2021)). Thus, their development in *E. tropica* is regarded here as convergent apomorphy. The possible convergent development of character 16 in the above-mentioned species is indicated by a question mark in Table 2.

Character 17, cphth laterally on posterior corners with backwardly directed projections [no projections]: *E. tropica* is the only species assigned to the *Parechinolaophonte—Echinolaophonte* clade that presents peculiar backwardly directed projections laterally on the posterior corners of the cphth—an unambiguous specific apomorphy.

Characters 18 and 19, the presence of small spinulose cuticular structures on the posterior margins of the first and second abdominal somites [no such structures present]: *E. tropica* lacks the presence of paired processes on the body somites, except for the penultimate somite and the telson. Nonetheless, *E. tropica* indeed has small spinulose structures on the posterior margins of the first abdominal somite (posterior half of the female GDS), as well as on the second one. However, these structures differ remarkably from the paired cuspidate processes of *Echinolaophonte sensu* Nicholls (1941) and are, therefore, considered as having independently evolved in *E. tropica*.

Character 20, baseoendopod and exopod of the female P5 fused: *E. tropica* is the only species in the *Parechinolaophonte—Echinolaophonte* clade, whose female P5 presents a fusion of the exopod and the baseoendopod. In all remaining 14 species, the P5 exopod and the baseoendopod are separated. The fusion is hypothesised here as clear autapomorphy for *E. tropica*.

The clear-cut characterisation of *E. tropica* by six autapomorphies, combined with the absence of the apomorphies of the *Pseudechinolaophonte–Echinolaophonte* clade (see below) lead to the exclusion of that species from *Echinolaophonte*. Instead, *E. tropica* is transferred into a new genus *Parechinolaophonte* gen. nov. as *Pa. tropica* (Ummerkutty, 1970), gen. et comb. nov. (Fig. 10/Table 3: node F).

The *Pseudechinolaophonte—Echinolaophonte* clade (Fig. 10/Table 3: node G)

The remaining 14 species of the *Parechinolaophonte—Echinolaophonte* clade, here named *Pseudechinolaophonte—Echinolaophonte* clade, share two unambiguous synapomorphies:

Character 21, cphth dorsally with strong cuticular structure centrally on posterior margin [no cuticular structure developed] (cf. Fig. 9): All 14 species bear a strongly-developed cuticular structure posteriorly on their cphth; although the shape of that structure differs within the *Pseudechinolaophonte–Echinolaophonte* clade (see below), its general development is hypothesised here as synapomorphic for all 14 species. Fiers (1991) noted a strong morphological similarity of the cephalic plate in *Xanthilaophonte* and the juvenile cephalic ornamentation in certain *Echinolaophonte* species, which, during the ontogenesis, develop into the characteristic single spur present in the adults. He, therefore, postulated a close relationship between both genera. Future studies will have to shed light on the relationships of *Xanthilaophonte* and *Echinolaophonte*.

Character 22, free body somites, except the pre-anal one and the telson with well-developed cuticular structures on posterior margin [no cuticular structures present]: as for the cephalothoracic dorsal structure (character 21), all 14 species of the *Pseudechinolaophonte–Echinolaophonte* clade bear well-developed cuticular structures on the posterior margins of all, except two, free body somites. Such processes are (like the dorsal process on the cphth) absent in the above treated outgroups *Heterolaophonte minuta*, *Coullia*, *Hemilaophonte janinae*, *Xanthilaophonte* and *Pa. tropica* gen. et comb. nov. Therefore, they are seen as an unambiguous autapomorphic character complex of the *Pseudechinolaophonte–Echinolaophonte* clade.

Establishment of *Pseudechinolaophonte* gen. nov. (Fig. 10/Table 3: node H)

The *Pseudechinolaophonte–Echinolaophonte* clade itself splits into two lineages. One lineage, enclosing *Echinolaophonte minuta*, *E. mordoganensis* and *E. veniliae*, can be characterised by 14 autapomorphies (Table 2, characters 23–36). Twelve of them (characters 23–30, 33–36) are unique deviations of the three species, whilst characters 31 and 32 also arise as supposed convergences in *E. brevispinosa*, *E. horrida* and *E. mirabilis*.

Character 23, cphth dorsally with spinulose, broad projection bearing 2–4 apical teeth [no such projection] (cf. Fig. 9A): As described above for Nicholls' (1941) character I, the peculiar structure arising on the dorsal posterior margin of the cphth of *E. minuta*, *E. mordoganensis* and *E. veniliae* is quite different from the single acute spur present in the remaining 11 species of the *Pseudechinolaophonte–Echinolaophonte* clade. It is, moreover, unique within Laophontidae and, thus, considered here as synapomorphic for the three species.

Character 24, cphth rectangular, almost squarish [cphth somewhat ovoid, tapering anteriorly, lateral margins convex]: the outgroups *Coullia*, *Hemilaophonte* and *Xanthilaophonte* possess a cphth with rounded, convex lateral margins, with the posterior part being broader than the anterior one. In the *Parechinolaophonte–Echinolaophonte* clade, however, the cphth underwent different morphological modifications. *Echinolaophonte minuta*, *E. mordoganensis* and *E. veniliae* present a clearly rectangular cphth that is even almost squarish in shape and differs remarkably from the cphth of the remaining 11 species of the *Pseudechinolaophonte–Echinolaophonte* clade. This clearly different cphth is hypothesised here as a synapomorphic character of the three species.

Characters 25–28, P2–P6-bearing somites dorsally with pair of strong spikes standing closely together [no paired spikes developed] (cf. Fig. 9A): *E. minuta*, *E. mordoganensis* and *E. veniliae* bear strong, but narrow spikes on their free thoracic somites that differ clearly from the processes on several species of the remaining *Pseudechinolaophonte–Echinolaophonte* clade. These are seen as synapomorphic for the three species.

Characters 29, 30, first and second abdominal somite with dorsal sclerotised clasp-like area bearing 2 spikes [these structures not developed] (cf. Fig. 9A): The development of such structures is unique within Laophontidae and, thus, regarded as clear synapomorphy for *E. minuta*, *E. mordoganensis* and *E. veniliae*.

Characters 31, 32, first two abdominal somites with laterally extended epimeres [abdominal somites not extended laterally] (cf. Fig. 9A): in *E. minuta*, *E. mordoganensis* and *E. veniliae*, the first (= posterior half of female GDS) and the second abdominal somites are laterally extended into flat wing-like structures. Such structures are absent in the compared outgroups, as well as in most remnants of the *Pseudechinolaophonte–Echinolaophonte* clade. Similar extensions are, however, also observable in *E. brevispinosa*, *E. horrida* and *E. mirabilis* (cf. Fig. 9C), see Discussion below). As the latter do not share further synapomorphies with *E. minuta*, *E. mordoganensis* and *E. veniliae*, but present derived features that are missing in *E. minuta*, *E. mordoganensis* and *E. veniliae*, their development of similar wing-like structures is hypothesised here as a convergent evolution.

Character 33, pseudoperculum developed as sclerotised clasp-like area bearing spikes [no clasp-like area developed] (cf. Fig. 9A): all three *Pseudechinolaophonte* species are characterised by a pseudoperculum that forms a clasp-like, square area that bears several spikes. Instead, in the remaining species of *Echinocletodes*–CS, the pseudoperculum consists of paired to several well-developed digitate processes arising from the distal margin. The pseudoperculum of the *Pseudechinolaophonte* species is regarded here as derived state, i.e. as synapomorphic for the three assigned species.

Character 34, A2 endopod surface seta with strongly derived tip [element of regular bipinnate shape]: in *E. minuta*, *E. mordoganensis* and *E. veniliae*, one of the elements arising on the lateral margin in the distal half of the A2 endopod is remarkably transformed and presents a remarkably derived tip that even differs amongst the three species. Nonetheless, whilst all outgroup taxa, as well as *Parechinolaophonte tropica* gen. et comb. nov. and the remaining species of the *Pseudechinolaophonte–Echinolaophonte* clade, retain the ancestral bipinnate spine, the development of a strongly deviated element is considered as synapomorphic for the three species.

Character 35, P2 outer basal seta longer than exp-1 and exp-2, biplumose [seta bipinnate, not reaching the distal margin of exp-2]: in *E. minuta*, *E. mordoganensis* and *E. veniliae*, the P2 carries an outer basal seta that is stronger and much more elongated than in all remaining here compared species. Moreover, it is biplumose, with the setules being considerably long. This is regarded as an unambiguous synapomorphy for the three species.

Character 36, female P5 baseoendopod with 2 setae [baseoendopod with at least 3 setae]: in Laophontidae, the female P5 baseoendopod consists of a large, ovoid lobe representing the former endopod with five setae (e.g. *Heterolaophonte minuta*, cf. Willen (1992)). The endopodal lobe becomes continuously reduced in size from *Coullia* via *Hemilaophonte janinae* and *Xanthilaophonte* towards the *Parechinolaophonte–Echinolaophonte* clade and also the number of setae decreases (*Coullia*: five setae, *Hemilaophonte janinae*, *Xanthilaophonte* and the *Parechinolaophonte–Echinolaophonte* clade: four setae). Within the latter, however, *E. minuta*, *E. mordoganensis* and *E. veniliae* stick out by the presence of only two setae. This is seen here as a clear synapomorphy for the three species.

From the argumentation given above and based on the derived characters 23–36, of which the majority is exclusive to *E. minuta*, *E. mordoganensis* and *E. veniliae*, it is here concluded that the three species form a monophyletic taxon within the genus *Echinolaophonte* as currently composed. Nevertheless, the detected deviations shared by the three species and the recognised remarkable differences between them and the remaining 11 species of the *Pseudechinolaophonte–Echinolaophonte* clade led to the decision to transfer *E. minuta*, *E. mordoganensis* and *E. veniliae* from the *Echinolaophonte*–CS group into a distinct, new taxon *Pseudechinolaophonte* gen. nov. (Fig. 10/Table 3: node H) instead of placing them into a new subgenus. The synapomorphies of the three species, therefore, turn into autapomorphies of the new genus that encloses *Ps. minuta* (Cottarelli & Forniz, 1991)

gen. et comb. nov. (here designated as type species), *Ps. mordoganensis* (Kuru, Sönmez & Karaytug, 2019) ,gen. et comb. nov. and *Ps. veniliae* (Cottarelli, Forniz & Bascherini, 1992), gen. et comb. nov.

The first branch-off within *Pseudechinolaophonte* gen. nov. is *Ps. mordoganensis* gen. et comb. nov. (Fig. 10/Table 3: node I). That species forms the sister taxon of a *minuta–venilia* clade (Fig. 10/Table 3: node J) and can be characterised by four autapomorphies (Table 2, characters 37–40):

Character 37, cphth dorsal process square, spinulose, with two strong spikes, each outwardly accompanied by two small ones [dorsal process absent or of different shape]: the cephalothoracic dorsal process is different in all three species that are so far assigned to *Pseudechinolaophonte* gen. nov. *Pseudechinolaophonte mordoganensis* gen. et comb. nov. presents a squarish sclerotised structure, covered with fine setules and bearing a pair of comparatively stronger spikes that are accompanied on their respective outer sides by two smaller spinules. This is considered as an autapomorphy for the species.

Character 38, A1 female second segment with one sub-apical outer seta being remarkably elongated, longer that remaining segments together [corresponding seta short]: only *Ps. mordoganansis* gen. et comb. nov. shows a sub-apical seta on the second segment of the female A1. It surpasses the apical edge of the last antennular segment; this is regarded as autapomorphic for the species.

Character 39, A2 endopodal surface surface seta comb-like at distal half; not tapering gradually [setal tip of different shape]: as discussed for character 34, the new genus is characterised by a particular lateral spine that ends in a blunt tip; in *Ps. mordoganansis* gen. et comb. nov. that spine is rounded and finely serrated in its distal half, presenting a somewhat comb-like shape. This is seen here as autapomorphic for *Ps. mordoganensis* gen. et comb. nov.

Character 40, P5 female baseoendopodal setae not reaching apical margin of exopod [setae at least reaching end of exopod]: whilst in *Ps. minuta* gen. et comb. nov. and in *Ps. veniliae* gen. et comb. nov., the setae of the female baseoendopod reach or even surpass the apical edge of the exopod (Cottarelli and Forniz 1991; Cottarelli et al. 1992), these setae are considerably reduced in size in *Ps. mordoganansis* gen. et comb. nov. (Kuru et al. 2019). That reduction is interpreted here as derived, i.e. as autapomorphic for *Ps. mordoganensis* gen. et comb. nov.

The *minuta–veniliae* clade (Fig. 10/Table 3: node J)

The *minuta–veniliae* clade, on its part, provides six autapomorphies confirming its monophyletic status (Table 2, characters 41–46). Such deviations refer to a strong pronunciation of the wing-like epimeres of the first two abdominal somites (characters 41, 42), which are only moderately developed in *Ps. mordoganensis* gen. et comb.

nov. Further shared deviations concern the shape of the pseudoperculum (character 43), which, in the *minuta–veniliae* clade, consists of a pair of Y-shaped spikes that are accompanied each by an outer single spike; in contrast, *Ps. mordoganensis* gen. et comb. nov. presents a rather crown-like pseudoperculum that may vary considerably in shape and in the number of spikes (cf. Kuru et al. (2019)). Nonetheless, it is admitted here, that also the pseudoperculum of *Ps. mordoganensis* gen. et comb. nov. may constitute a deviation. However, because of the high intraspecific variability documented by Kuru et al. (2019), that feature is not considered in the present analysis.

Moreover, both species share the loss of the abexopodal seta in the A2 allobasis (Table 2, character 44) and of the exopodal seta on the mandibular palp (Table 2, character 45), which are retained, not only in *Ps. mordoganensis* gen. et comb. nov., but in most of the here compared species. The loss of the abexopodal seta in the A2 allobasis has, however, also been documented for *E. gladiator* and *E. briani* (Vervoort 1964; Lang 1965). Though, as the loss of single setal elements occurs quite often and independently in Harpacticoida and because the here presented clear phylogenetic characterisation of the *minuta–venilia* clade, it is assumed here that the simultaneous deviation considering character 44 took place independently in both *E. gladiator* and *E. briani* and is, therefore, regarded as convergent development. Finally, the syncoxa of the mxp is equipped with only one instead of two setae (Table 2, character 46). The loss of one maxillipedal seta is also documented for *Echinolaophonte briani*; it is seen here as convergent reduction, as the latter is embedded in a group of *Echinolaophonte* species that does not share the autapomorphies of *Pseudechinolaophonte* gen. nov., but is characterised by its own autapomorphies (see below).

Pseudechinolaophonte minuta gen. et comb. nov. (Fig. 10/Table 3: node K) and *Ps. veniliae* gen. et comb. nov. (Fig. 10/Table 3: node L) can be characterised by a set of unequivocal autapomorphies (Table 2, characters 47–50 and 51–53, respectively). These refer to the specific shape and ornamentation of the cephalothoracic posterior dorsal structure (Table 2, characters 47, 51; both species show considerable and quite unequal transformations), the shape of the antennal derived endopodal surface seta (characters 48, 52; that seta is differently transformed in both species, cf. Table 2), the loss of one seta in the maxillular coxa and basis (characters 49, 50; only *Ps. minuta* gen. et comb. nov., but presumably convergent in *Xanthilaophonte*) and the exclusive shape of the male apophysis that presents an indentation at its tip (character 53; only *Ps. veniliae* gen. et comb. nov.).

Revised compilation of *Echinolaophonte*

After the above-discussed and phylogenetically justified exclusion of *E. tropica*, *E. minuta*, *E. mordoganensis* and *E. veniliae* in combination with their transfer to

Parechinolaophonte gen. nov. and *Pseudechinolaophonte* gen. nov., respectively, 11 species remain in *Echinolaophonte* (Fig. 10/Table 3: node M). Coming back to Nicholls' (1941) original generic diagnoses, just these 11 species share a main feature:

Character 54, cphth with single spur dorsally on posterior margin [no spur developed] (cf. Figs 9B, C): the well-developed cuticular "single large recurved spur" (Nicholls 1941: 95), one main attribute of *Echinolaophonte* sensu Nicholls (1941), is present exclusively in these ten species. It is regarded here as of high phylogenetic relevance, because it is not found in any other Laophontidae (see above, discussion of Nicholls' (1941) character I). Thus, the development of such a spur is hypothesised as an unambiguous autapomorphy for the monophylum *Echinolaophonte* Nicholls, 1941, comprising *E. armiger*, *E. brevispinosa*, *E. briani*, *E. gladiator*, *E. horrida*, *E. hystrix*, *E. mirabilis*, *E. musa* sp. nov., *E. oshoroensis*, *E. tetracheir* and *E. villabonae*.

The *armiger–gladiator* clade (Fig. 10/Table 3: node N)

Within that genus, two main clades are discernible. A first clade is composed of *E. armiger* and *E. gladiator* (*armiger–gladiator* clade). They share five synapomorphies (Table 2, characters 55–59):

Character 55, whole body surface densely covered with fine cuticular structures [body surface smooth]: for two species, their (re-)descriptors explicitly mentioned a coverage of the whole body with "minute denticles" (Lee et al. 2006: 55, for *E. armiger*) or short "hairs" (Vervoort 1964: 366, for *E. gladiator*); such fine body ornamentation has not been documented for any other *Echinolaophonte* species. Although admitting that the coverage with minute cuticular elements may have been overlooked in other species, it is hypothesised here that the ornamentation observed in *E. armiger* and *E. gladiator* constitutes a synapomorphy for both species. That assumption is substantiated by the presence of characters 56–59, which also are regarded as synapomorphic for *E. armiger* and *E. gladiator*.

Character 56, cphth laterally protruded [no protrusions developed]: In *Echinolaophonte*, the cphth, particularly its lateral margins, present a remarkable variability (see below, characters 75, 80, 106, 112, 122, 126). *Echinolaophonte armiger* and *E. gladiator* share the development of small lateral protrusions (cf. Vervoort (1964); Lee et al. (2006)), that are absent in most remaining species of the taxon. Two further species also developed lateral protrusions, i.e. *E. mirabilis* and *E. musa* sp. nov. (cf. Gurney (1927); Wells and Rao (1987); present contribution: Figs 2, 3A, 7A). These are, however, much more developed than in *E. armiger* and *E. gladiator*, reaching their maximal size in *E. musa* sp. nov. Moreover, *E. mirabilis* and *E. musa* sp. nov. share well-developed dorsal cuticular processes on the free body somites, except for the pre-anal

one and the telson with all remaining *Echinolaophonte* species, except *E. armiger* and *E. gladiator* (Table 2, characters 68–74, see below). Therefore, the development of lateral processes on the cphth is hypothesised here as synapomorphic for *E. armiger* and *E. gladiator*, but convergent in comparison with *E. mirabilis*/*E. musa* sp. nov.

Character 57, cphth dorsal spur broad, rather short [spur long, slender] (cf. Fig. 9B): *E. armiger* and *E. gladiator* are characterised by a cephalothoracic spur that is compact and rather short, with a broad base, whilst the remaining *Echinolaophonte* species share a long and comparatively narrow process (cf. Fig. 9C). The development of a compact spur is considered here as shared deviation and, thus, as synapomorphic for *E. armiger* and *E. gladiator*.

Character 58, a slight lateral inflation of the female GDS [female GDS laterally not inflated]: the female GDS of *E. armiger* and *E. gladiator* presents a somewhat inflated and confluent aspect, blurring the former frontier between the original urosomites and showing its broadest extension in the area of the fusion. In contrast, in the remaining *Echinolaophonte* species, the previous distinction between the now fused somites remains clearly discernible by a remarkable lateral constriction in the area of fusion. The lateral inflation, combined with the confluent lateral borders, is seen here as synapomorphic for *E. armiger* and *E. gladiator*. A similar shape documented for *E. oshoroensis*, *Xanthilaophonte trispinosa* by Fiers (1991) (but not for *X. carcinicola*) is regarded here as convergence.

Character 59, the development of small spiny processes on the dorsal posterior margin of the pedigerous and first 2 abdominal somites [no cuticular processes developed] (cf. Fig. 9B): As discussed above, *Pa. tropica* gen. et comb. nov. does not bear any cuticular projections on the dorsal posterior margin of the body somites. Otherwise, *Pseudechinolaophonte* gen. nov. and *Echinolaophonte* are characterised by (different) cuticular structures on the respective body parts. In *E. armiger* and *E. gladiator*, these structures are developed as small spiny processes, which are hypothesised here as synapomorphic for both species.

Each species can be characterised by four autapomorphies (Table 2, characters 60–63 and 64–67, respectively). In *Echinolaophonte armiger* (Fig. 10/Table 3: node O), the deviations refer to:

Character 60, the coverage of the body with small cuticular denticles (cf. Lee et al. (2006));

Character 61, the presence of 4 spiny processes standing pairwise together dorsally on the P4-bearing somite;

Character 62, the development of a pair of spiny processes that are fused at their bases on the anterior half of the female GDS, respectively the last thoracic somite of the male (cf. Lee et al. (2006): figs 1A, 6A);

Character 63, the posterior half of GDS/last thoracic somite of the male and second abdominal somite dorsally with spiny processes standing close together (cf. Lee et al. (2006): figs 1A, 6A).

Characters 60–63 are exclusively present in *E. armiger* and, thus, regarded here as unambiguously autapomorphic for that species.

As indicated in Fig. 9B (exclamation mark), cuticular processes on the P2-bearing somite are apparently absent in *E. armiger* (cf. Lee et al. 2006). However, it is not possible to determine at this point whether they are primarily absent or secondarily regressed. Therefore, this feature is not considered in the analysis.

On the other hand, *E. gladiator* (Fig. 10/Table 3: node P) is characterised by:

Character 64, the coverage of the body with fine setules ("hairs") instead of small denticles;

Character 65, the cephalothoracic lateral protrusions produced into pair of narrow, backwardly directed cuticular jags;

Character 66, the remarkable transformation of the mxp into a strong appendage whose allobasis is swollen on its inner margin and the endopodal claw being massive and curved about 90°;

Character 67, the (female) P3 exp-3 with only two outer spines (cf. Vervoort (1964)).

Character 67 is also observable in *Xanthilaophonte*, *Parechinolaophonte tropica* gen. et comb. nov. (cf. Fiers (1991); Ummerkutty (1970); Wells and Rao (1987)) and in *Echinolapohonte villabonae* (cf. Fuentes-Reinés and Suárez-Morales (2017)). Nevertheless, as discussed above, the former branched off much earlier and *Pa. tropica* gen. et comb. nov. is characterised by six autapomorphies (Table 2, characters 15–20), whilst *E. villabonae* belongs to a well-supported monophylum with the remaining *Echinolaphonte* species (see below). The loss of one outer spine in both species is, therefore, seen as convergence.

The *brevispinosa–mirabilis* clade (Fig. 10/Table 3: node Q)

The remaining clade, here named *brevispinosa–mirabilis* clade, encloses nine species. It is unambiguously supported by seven autapomorphies (Table 2, characters 68–74). The deviations apply to the development of dorsal processes on all free body somites, except the pre-anal one and the telson (cf. Fig. 9C). The processes show a considerable variability in the different species. Nonetheless, particularly those of the thoracic somites differ remarkably from the spikes observable in *Pseudechinolaophonte* gen. nov., being stronger, often spinulose and basally accompanied by two sensilla (e.g. Sars (1908); Lang (1965); Itô (1969); Mielke (1981); Fuentes-Reinés and Suárez-Morales (2017); present contribution: Figs 2, 3A, 7C, 8C). The development of such cuticular structures is hypothesised here as synapomorphic for all remaining nine *Echinolaophonte* species, supporting so their monophyletic character.

The *brevispinosa–mirabilis* clade divides again into two clades, namely the *brevispinosa–oshoroensis* clade (three species) and the *villabonae–mirabilis* clade (six species). These clades are characterised by four and two autapomorphies, respectively.

The *brevispinosa–oshoroensis* clade (Fig. 10/Table 3: node R)

The species united in the *brevispinosa–oshoroensis* clade share – besides the supposed convergently developed characters 31 and 32 – four unique characters (Table 2, characters 75–78) that enable the confirmation of a monophyletic group:

Character 75, the lateral cheek-like extension of the cphth [lateral margins of cphth different]; whilst the species pooled here to *Pseudechinolaophonte* gen. nov. present an almost squarish cphth and that of *Parechinolaophonte tropica* gen. et comb. nov. displays unique deviations, the cphth of the *Echinolaophonte* species presents three main variations: (a) the development of lateral protrusions like in *E. armiger* and *E. gladiator* and presumably convergent in *E. mirabilis* and *E. musa* sp. nov. (Table 2, character 56; cf. discussion above), (b) The formation of a bulbous, so-called "intricate cuticular ornamentation" (Fuentes-Reinés and Suárez-Morales 2017: 22) on the distal half of the cphth (Table 2, character 106, see Discussion below) and (c) the cphth being cheek-like extended laterally on its distal half (character 75). Such kind of extension is shared by the species assigned here to the *brevispinosa–oshoroensis* clade. It gives the respective species a kind of "chubby cheek"-like aspect in the dorsal view and is clearly noticeable in *E. brevispinosa* and *E. horrida* (cf. Sars 1908, plates 166–168), as well as in *E. oshoroensis* (cf. Itô (1969), fig. 6.1). This lateral convexity is regarded here as synapomorphy for the named three species.

Character 76, rostrum elongate, with rounded tip: All three species present a rostrum of a peculiar shape (Sars 1908, plates 166–168; Itô 1969, fig. 7.1). It is remarkably elongated and divided into a proximal half that is sclerotised, laterally constricted, but broadening distally. The pair of sensilla arises laterally at the broadest area. The distant half is rather soft, reaching almost the length of the proximal half and ending in a rounded tip. The shape of the rostrum is unique within *Echinolaophonte* and is hypothesised as synapomorphic for *E. brevispinosa*, *E. horrida* and *E. oshoroensis*. (see Discussion of character 13 for *Xanthilaophonte*).

Characters 77, 78, the male P3 exopod is powerfully developed (character 77) and bears on its exp-2 a massive, s-shaped outer spine (character 78): the strengthening of the P3 and P4 exopods seem to form part of a sexual dimorphism in *Echinolaophonte*. In *E. brevispinosa*, *E. horrida* and *E. oshoroensis*, particularly the P3 exopod suffers a remarkable strengthening as compared to the female (Sars (1908) plates 166–168; Itô (1969), fig. 9.3). Moreover, the outer spine of the P3 exp-2 is robust, comparatively short and curved outwards, reminding weakly

of an "s". Both characters are seen here as clearly synapomorphic for the three species.

Echinolaophonte brevispinosa (Fig. 10/Table 3: node S) is the first branch-off in the *brevispinosa–oshoroensis* clade and is considered the sister taxon of a *horrida–oshoroensis* clade. Its distinct phylogenetic state is supported by 2 supposed autapomorphies (Table 2, characters 79, 80):

Character 79, the emargination of the rostral tip: the rostral tip is rounded regularly in *E. horrida* and *E. oshoroensis*, but presents a narrow, but distinct emargination in *E. brevispinosa*, which is considered as a deviated feature and, thus, as autapomorphic for the latter.

Character 80, the considerable bulging of the cephalothoracic lateral "chubby cheeks": the lateral "cheeks" present their strongest expression in *E. brevispinosa* (Sars (1908), plate 168) and is considered as autapomorphic for the species.

The *horrida–oshoroensis* clade (Fig. 10/Table 3: node T)

The monophyly of the *horrida–oshoroensis* clade is supported by five autapomorphies (Table 2, characters 81–85):

Character 81, lateral constriction of the rostral proximal half considerably pronounced;

Character 82, cephalothoracic spur elongated, surpassing posterior margin of cphth;

Character 83, pseudoperculum consisting of 4 tri-denticulated processes (cf. Fig. 9C);

Character 84, P1 exopod diminished in length, not reaching half the length of enp-1;

Character 85, male P3 enp-2 apophysis with acute jag basally on inner margin.

In *E. brevispinosa*, the lateral margins of the rostrum are constricted, but much less than in *E. horrida* and *E. oshoroensis* (character 81); the spur on its cphth is small and does not surpass the posterior margin (Sars 1908: plate 168), whilst the spur of *E. horrida* and *E. oshoroensis* clearly surpasses the posterior margin of the cphth; moreover, it tapers remarkably, presenting a quite narrow distal half (character 82) (Sars (1908): plate 166; Itô (1969): figs 6.1, 6.2); the pseudoperculum of *E. brevispinosa* consists of only two tri-denticulated processes that are accompanied by three single spikes on their outer sides (character 83) (Sars (1908): plate 168). Admittedly, this character remains somewhat vague, because also the peculiar pseudoperculum of *E. brevispinosa* may constitute an apomorphic feature. Here it is, however, assumed that the single outer spikes found in the pseudoperculum of *E. brevispinosa* may have fused together in the last common ancestor of *E. horrida* and *E. oshoroensis*, forming the outer tri-denticulate processes as found in these species. In *E. brevispinosa*, the P1 exopod – in particular the exp-2 – is long and still surpasses the length of the P1 enp-1 (character 84). In contrast, the diminution of the P1 exopod has progressed, resulting in an exopod whose length barely reaches 1/3 of the length of the enp-1; as

shown by Sars (1908: plates 166, 167) and Itô (1969: fig. 9.3), both species bear an acute jag basally on the inner margin of the apophysis in the male P3 enp-2 (character 85). That jag is absent in *E. brevispinosa* (Sars (1908): plate 168).

Basing on the description of Sars (1908) and the re-description of Kornev and Chertoprud (2008), *E. horrida* (Fig. 10/Table 3: node U) can be characterised by seven autapomorphies: the dorsal cuticular body processes are equipped with several fine spinules (Table 2, characters 86–92). In contrast, both *E. brevispinosa* and *E. oshoroensis* lack such spinulose coverage, retaining the original bare setae. Therefore, the development of fine spinules on the cuticular body processes is hypothesised here as autapomorphic for *E. horrida*.

In contrast, *E. oshoroensis* (Fig. 10/Table 3: node V) presents ten morphological deviations, here hypothesised as specific autapomorphies (Table 2, characters 93–102):

Characters 93, 94, secondary loss of the wing-like lateral epimers: As explained in the discussion of features 31 and 32, lateral wing-like epimeres are considered to have arisen convergently on the first two abdominal segments on three occasions: once in *Pseudechinolaophonte*, once in *E. mirabilis* and once in the *brevispinosa–oshoroensis* clade. While *E. brevispinosa* and *E. horrida* retained the epimeres, they were secondarily reduced again in *E. oshoroensis*. This hypothesis is based on the fact that *E. horrida* and *E. oshoroensis* are well justifiable as sister-groups on the basis of synapomorphies 81 to 85, whereas neither species shares exclusive derived characters with *E. brevispinosa*. Only the presence of lateral epimers could be an indication of a closer relationship between *E. brevispinosa* and *E. horrida*, which, however, led to the not very plausible assumption that the common derived characters of *E. horrida* and *E. oshoroensis* would have to be interpreted as convergences in return. A secondary reduction of the wing-like epimeres in *E. oshoroensis*, therefore, seems the most plausible and parsimonious explanation.

Character 95, Cphth spur laterally with tufts of long and fine setules: A very similar kind of process has also been observed in *Echinolaophonte briani*, *E. tetracheir* (only textual description by Mielke (1981): 53), *E. mirabilis* and *E. musa* sp. nov. (cf. Lang (1965): fig. 280a, c; described as *E. armiger* f. *typica*; Mielke 1981; Mielke (1981); Wells and Rao (1987); present contribution; see below). However, *E. briani* lacks apomorphic characters 75–78 of the *brevispinosa–oshoroensis* clade, but shares characters 103 and 104 with *E. villabonae*, *E. tetracheir*, *E. mirabilis* and *E. musa* sp. nov. (see below). Nonetheless, as the close relationship between *E. oshoroensis* and *E. horrida* seems to be well-founded by shared apomorphies 81–85, likewise, the support of a close relationship of both species with E. *brevispinosa* (characters 75–78), the expression of a similar cephalothoracic spur in *E. briani* is interpreted here as convergent evolution.

Characters 96–101, presence of lateral cuticular processes from the P2-bearing somite to the second abdominal

somite: *Echinolaophonte oshoroensis* is the only species bearing additional lateral cuticular processes on the body somites, except the pre-anal one and the telson (Itô 1969). This derived condition is regarded as autapomorphic for *E. oshoroensis*.

Character 102, the male P3 exopod remarkably strengthened: The powerful development of the male P3 exopod (character 78, see above) is further strengthened in *E. oshoroensis*, having been developed into a massive and broad appendage (Itô 1969: fig. 9.3), which is unique within *Echinolaophonte*.

The *villabonae–mirabilis* clade (Fig. 10/Table 3: node W)

The supposed sister group of the *brevispinosa–oshoroensis* clade is composed of six species, namely *E. villabonae*, *E. briani*, *E. hystrix*, *E. tetracheir*, *E. musa* sp. nov. and *E. mirabilis*. These are united into the *villabonae–mirabilis* clade and share the following two apomorphic characters related to the shape of the male P3 (Table 2, characters 103, 104):

Character 103, male P3 endopod 2-segmented [endopod 3-segmented]: The Laophontoidea present a 3-segmented male P3 endopod that is sexually dimorphic, with the enp-2 bearing a well-developed apophysis on its apical outer margin; this is considered as autapomorphy for the Laophontoidea (e.g. Huys (1990), Huys and Lee (1998/1999)) and retained in almost all laophontid species, so is the ground-pattern of *Echinolaophonte*. However, the six species pooled into the *villabonae–mirabilis* clade share the derived state of the reduction of 1 endopodal segment.

Character 104, male P3 endopod lost sexual dimorphism [male P3 endopod sexually dimorphic]: The loss of a pronounced sexual dimorphism in the male P3 endopod is presumably linked with the reduction of 1 segment. Like character 103, it is a clear deviation as compared with the remaining *Echinolaophonte* species.

Remarks: It is assumed here that, during the ontogenetic development, the formation of the second segment, which carries the apophysis in the adult male, has been suppressed. However, compared with Huys' (1990) hypothesis regarding the development of the male P3 endopod, the conditions observed in the *villabonae–mirabilis* clade are not yet fully understood. Here, a detailed description of juvenile stages is necessary. As mentioned in the Introduction, the loss of the sexual dimorphism has been regarded as an important phylogenetic feature by several authors (e.g. Lang (1965); Mielke (1981); Cottarelli and Forniz (1991); Kuru et al. (2019)). Nevertheless, the character matrix (Table 2) reveals that characters 103 and 104 distribute somewhat heterogeneously over the different taxa that are otherwise well-justified by other supposed apomorphies. Therefore, although it is on the one hand observable that the reduction of one endopodal segment in the male P3 seems to be linked

unquestionably to the loss of the sexual dimorphism, one may, on the other hand, see that such loss occurs in quite different taxa like *Xanthilaophonte*, *Parechinolaophonte* gen. nov., *E. armiger* and the *villabonae–mirabilis* clade. Uniting all these different taxa because of their collective loss of the sexual dimorphism in the male P3 would result in incongruencies with respect to many other derived characters that clearly separate them. Consequently, it is hypothesised here that the simultaneous loss of the sexual dimorphism on the male P3, combined with the loss of one endopodal segment in the above-named taxa, is due to convergent development.

The *villabonae–mirabilis* clade divides into two monophyletic taxa, each characterisable by distinct autapomorphies: the *villabonae–briani* clade (Table 2, characters 105–110) and the *tetracheir–mirabilis* clade (Table 2, characters 115–118).

The *villabonae–briani* clade (Fig. 10/Table 3: node X)

The *villabonae–briani* clade is characterised by the following derived features provided by *E. villabonae*, *E. briani* and *E. hystrix*:

Character 105, rostrum slightly trapezoid, constricted basally and broadening apically, with rather flat/concave apical margin, distal half smooth: with a basal constriction and a soft distal part, the shape of the rostrum in *E. briani* (Lang (1965): fig. 280b), *E. hystrix* (Brian (1928): fig. 131) and *E. villabonae* (Fuentes-Reinés and Suárez-Morales (2017): figs 1D, 2B) reminds us on the rostrum of the *brevispinosa–oshoroensis* clade; however, without the rounded extension of the distal half. Compared with earlier branch-offs like, for example, *Pseudechinolaophonte* gen. nov., *Echinolaophonte armiger* and *E. gladiator*, the rostrum observed in the *villabonae–briani* clade is seen here as a shared deviation of the enclosed species.

Character 106, cphth laterally with intricate cuticular ornamentation: *E. villabonae*, *E. briani* and *E. hystrix* share the peculiar cuticular ornamentation along the extended laterodistal margin of the cphth (Lang (1965): fig. 280c; Fuentes-Reinés and Suárez-Morales (2017): fig. 1D). This feature is unique within *Echinolaophonte*.

Character 107, the female GDS dorsally with cuticular "ring": Both Lang ((1965): figs 280e, 284c) and Fuentes-Reinés and Suárez-Morales ((2017): fig. 1E) documented what Lang (1965: 509) described as "conical elevation, in dorsal aspect giving impression of a ring". That structure is located dorsally on the border between the anterior and the posterior halves of the female GDS. It is exclusively present in the *villabonae–briani* clade.

Characters 108, 109, posterior half of female GDS and second abdominal somite dorsally with strengthened, spike-bearing cuticular process: such structure is only present in the *villabonae–briani* clade. Superficially, in dorsal view, it may resemble the respective cuticular structures described for *Pseudechinolaophonte* gen. nov.

(Table 2, characters 29, 30), but, whilst these represent squarish, clasp-like spinulose areas bearing two strong spikes, the processes in the *villabonae–briani* clade present several strong spinules on their posterior margins (cf. Lang (1965); Fuentes-Reinés and Suárez-Morales (2017)).

Character 110, the female pseudoperculum consisting of two bi- (or tri-)denticulate processes, laterally accompanied each by two spikes: As already mentioned (cf. discussion of characters 43, 83), the shape of the pseudoperculum is, either intra- and interspecific, highly variable. Otherwise, as discussed above for *Pseudechinolaophonte minuta* gen. et comb. nov. and *Ps. veniliae* gen. et comb. nov. (character 43), respectively for *Echinolaophonte horrida* and *E. oshoroensis* (character 83), supposed closely-related species can be characterised by an almost identical shape of the pseudoperculum, supporting that close relationship. This applies also to *E. villabonae*, *E. briani* and *E. hystrix*, whose pseudoperculum is almost identical in shape, but differs from that of all remaining species under consideration. Thus, it is seen here as a common deviation.

Echinolaophonte villabonae (Fig. 10/Table 3: node Y) can be characterised by three autapomorphies (Table 2, characters 111–113). It presents its cephalothoracic dorsal spur robust, short, with two dorsal notches (character 111); the lateral cuticular ornamentation is considerably pronounced (character 112); its rostrum is granular on apical half (character 113) (cf. Fuentes-Reinés and Suárez-Morales (2017)). The supposed sister taxon *E. briani* lacks all these features; as mentioned above (characters 82, 95), that species bears a dorsal spur on the cphth that reminds us on that of *E. oshoroensis*, which is also seen as specific (and convergent) autapomorphy; the ornamentation along the lateral margins of the cphth are clearly discernible, but much less pronounced than in *E. villabonae*; the rostrum of *E. briani* lacks the granular shape on its apical half.

Echinolaophonte briani (Fig. 10/Table 3: node Z) is characterisable by one autapomorphy (Table 2, character 114). It is the only representative of *Echinolaophonte* that bears two rows of spinules running parallel and longitudinally in front of the pseudoperculum on the pre-anal somite. Furthermore, the A2 allobasis lacks an abexopodal seta (character 44) and the syncoxa of the mxp bears only one apical seta (character 46). The latter two deviations are, however, hypothesised as convergent developments, as they are also present in *Pseudechinolaophonte minuta* and *Ps. veniliae* (see above).

Remarks: from the descriptions by Brian (1928) and van Douwe (1929), it can be concluded that *L. hystrix* and *L. steueri*, in fact, stand in close relationship with *E. villabonae* and *E briani*. They share synapomorphies 105–110. Character 107, i.e. the cuticular "ring" on the female GDS, was described for *E. hystrix* by Lang (1965) as *E. armiger* f. *typica*, but was neither textually described nor illustrated by Brian (1928) and van Douwe (1929) and the textual description of the shape of the pseudoperculum of *L. steueri* (character 110) given by van Douwe (1929) is too imprecise for comparison. However, the pseudoper-

culum shown in van Douwe's (1929) fig. 18 indicates the similarity with the corresponding structure present in *E. villabonae* and *E. briani*. However, as documented by Lang ((1965): figs 284c–e), the inter- and even intraspecific variability seems not to be insignificant. Therefore, character 110 should be interpreted with caution.

Direct comparison of the species reveals that, in *L. steueri*, the posterolateral cuticular ornamentation on the cphth is as strongly pronounced as in *E. villabonae*. Otherwise, *L. steueri* shares an almost identical cephalothoracic dorsal spur with *E. briani*, although van Douwe (1929) did not mention any setular tufts. Moreover, as discernible from van Douwe's (1929) fig. 18, the preanal somite seems to bear spinules – perhaps in 2 rows – in front of the pseudoperculum. Due to these similarities and because both Brian (1928) and van Douwe (1929) found their species in the same location (Rovigno, Croatia) or close geographical surroundings (the coast between Italy and France), *L. steueri* is synonymised here with *E. hystrix*. Nevertheless, as both species are imprecisely and/or incompletely (re-)described (Brian 1928; van Douwe 1929; Lang 1965) and, thus, inhibit a detailed comparison, the systematic position of *E. hystrix* within the *villabonae–briani* clade can be only tentative (cf. Fig. 10, dotted line).

The *tetracheir–mirabilis* clade (Fig. 10/Table 3: node AA)

That clade encloses the species *Echinolaophonte tetracheir*, *E. musa* sp. nov. and *E. mirabilis*. Within *Echinolaophonte*, they share the following four synapomorphies:

Character 115, an elongated rostrum with a bifurcated tip: although the development of an elongated, bifurcated rostrum is also present in other Harpacticoida (e.g. *Ancorabolus* Norman, 1903 (Ancorabolidae Sars, 1909), *Pseudechinopsyllus* George, 2006, *Pseudopolyascophorus* George, 2021 (Cletodinae T. Scott, 1904)), in Laophontidae, only the representatives of the *tetracheir–mirabilis* clade show that derived development. It is hypothesised here as synapomorphic for the enclosed species.

Character 116, CR at least 3.5 times longer than broad: the caudal rami of the here treated outgroups, as well as of the other here treated taxa are short, reaching mostly twice the length of their broadest width. Instead, the *tetracheir–mirabilis* clade displays caudal rami that are clearly elongated and slender. This is regarded as autapomorphic for that clade.

Characters 117, 118, outer basal seta of P3 and P4 of composite shape: The development of composite setae in the bases of the P3 and P4 is not common within Laophontidae, as observable, for example, in the here treated outgroups *Heterolaophonte minuta*, *Coullia*, *Xanthilaophonte* and *Hemilaophonte janinae*. (Fiers 1991, 1992; Willen 1992; Gómez and Boyko 2006). A composite seta is also missing in *Pseudechinolaophonte* gen. nov. (e.g. Cottarelli and Forniz (1991); Kuru et al. (2019)). For *Parechinola-*

ophonte tropica gen. et comb. nov., however, Wells and Rao (1987: fig. 144d–f) illustrated bi-articulated outer basal setae in P2–P4. Due to the relatively large phylogenetic distance between *Pa. tropica* and the *tetracheir-mirabilis* clade evidenced in the present work, a convergent evolution of the composite setae can, however, be assumed. After all, the first articulation is very small in *Pa. tropica*, whilst it is particularly long in the *tetracheir–mirabilis* clade, occupying half of the total setal length. In *Echinolaophonte*, an elongated composite seta is also present in the P3 basis of *E. oshoroensis* and *E. briani*; the former bears a composite seta also on the basis of the P4. This sporadic development is a clear indication for the convergent formation of composite setae; nonetheless, as characters 117 and 118 are present in all three species of the *tetracheir–mirabilis* clade, it is assumed here that a composite seta may have evolved in the P3 and P4 of the last common ancestor, thus constituting a synapomorphy for the three species.

The first branch-off within the *tetracheir–mirabilis* clade is *Echinolaophonte tetracheir* (Fig. 10/Table 3: node BB). It has three morphological deviations, here considered as autapomorphies (Table 2, characters 119–121): in the first abdominal somite (posterior half of female GDS) and the second abdominal somite, the cuticular processes arise from cuticular fortifications that are of a H-like shape (characters 119, 120), i.e. they do neither form a clasp-like area as in *Pseudechinolaophonte* gen. nov. (cf. characters 29, 30) nor strengthened squarish spinulose areas like in the *villabonae–briani* clade (cf. characters 108, 109). Furthermore, the pseudoperculum of *E. tertacheir* consists of four palmate processes carrying four to seven finger-like spinules with slightly rounded tips (character 121); it was that special shape of the pseudoperculum that prompted Mielke (1981: 59) to give the specific epitheton *tetracheir*. It differs remarkably from the pseudopercula of *E. musa* sp. nov. (two central processes with three to four acute spinules, accompanied each at its outside by a smaller process with several fine spinules apically; cf. Fig. 8F) and *E. mirabilis* (four processes ending each in two to three acute spinules; cf. Wells and Rao (1987: fig. 140g); not documented by Gurney (1927)).

The *musa–mirabilis* clade (Fig. 10/Table 3: node CC)

The remaining *musa–mirabilis* clade presents four derived characters (Table 2, characters 122–125) that are seen here as synapomorphies of *E. musa* sp. nov. and *E. mirabilis*:

Character 122, cphth laterally with long and slender processes: both species present remarkably long and slender lateral processes on the cphth. Their development is unique not only within *Echinolaophonte*, but also in Laophontidae and, therefore, considered as synapomorphic for *E. musa* sp. nov. and *E. mirabilis*.

Characters 123, 124, cphth equipped with a further anterior and central cuticular process: Besides the dorsal spur that is characteristic for *Echinolaophonte*, *E. musa*

sp. nov. and *E. mirabilis* bear two further structures dorsally on the cphth. Behind the rostral area and in the centre of the cphth, two moderate spurs arise (Gurney (1927): figs 162C, D; present contribution, Figs 2, 7A). Their exclusive development in these species leads to the assumption of their synapomorphic characteristic.

Character 125, CR at least 5.5 times longer than broad: *Echinolaophonte musa* sp. nov. and *E. mirabilis* are the only species within *Echinolaophonte*, whose caudal rami are remarkably elongated, reaching a length/width ratio of > 5:1. This is regarded as synapomorphic for both species.

The here described *Echinolaophonte musa* sp. nov. (Fig. 10/Table 3: node DD) presents a rich set of morphological deviations, ranging from a general somewhat "haggard" body shape, the extreme elongation of the rostrum and CR, to the special shape of the dorsal body processes (cf. Figs 2, 3A, 7C). For the here presented phylogenetic analysis, eight clear deviations were selected (Table 2, characters 126–133); they unambiguously support the characterisation of *E. musa* sp. nov. as a distinct taxon. Character 126 refers to the lateral processes on the cphth; these are remarkably elongated and curved backwardly. Such lateral processes are unique in *Echinolaophonte*. The same applies to the following characters 127–133. These consider the shape and size of the particular free body somites, which are remarkably elongated in comparison with all remaining *Echinolaophonte* species. Moreover, the processes end in bifurcated tips, which is also an exclusive characteristic within *Echinolaophonte*. Thus, by means of characters 126–133, the establishment of a new species *Echinolaophonte musa* sp. nov. is well-supported and doubtless.

In contrast, a clear-cut characterisation of *E. mirabilis* (Fig. 10/Table 3: node EE) is difficult. This is due to the fragmentary description provided by Gurney (1927), as well as to the somewhat imprecise and confusing re-description given by Wells and Rao (1987). The latter disposed of the type material plus a single male and female specimen collected from the Andaman Islands (Wells and Rao 1987). Whilst being convinced that the Andaman male belongs to *E. mirabilis*, Wells and Rao (1987) were sceptical with respect to the Andaman female that showed several differences compared to the female holotype. Unfortunately, the authors desisted from re-describing *E. mirabilis*, based on the female holotype. As a result, no detailed description of *E. mirabilis* is available, whilst the (also incomplete) description of the Andaman female tended to increase confusion rather that resolving it.

However, based on particular re-described body parts provided by Wells and Rao (1987), two potential autapomorphies were detected to characterise *E. mirabilis*:

Character 134, the dorsal processes on the P2-bearing somite dorsal processes being long, bearing three long setules basally: no other *Echinolaophonte* presents such dorsal processes (cf. Wells and Rao (1987): fig. 140a), which are, therefore, regarded as exclusive deviation in *E. mirabilis*.

Character 135, the dorsal processes on the second abdominal somite are fused basally, with two denticles

basally and centrally and with two long setules: As for the previous character, also these processes are unique in *Echinolaophonte*.

Remarks on previous findings of *E. mirabilis* in Asia

Amongst the congeners of the *Echinolaophonte* complex, two *Echinolaophonte* species were reported from Asia: *E. oshoroensis* from Japan (Itô 1969) and *E. mirabilis* from China (Zhang and Li 1976) and Korea (Kim 2013). Zhang and Li (1976) recorded 20 harpacticoid copepods belonging to 11 families, including the then new species *Eupelte acutispinis* Zhang & Li, 1976 (Peltidiidae Claus, 1860) from Xisha Island, China. They listed the species name *Onychocamptus mirabilis* (= *E. mirabilis*) without any information (e.g. sex, number of specimens, figures, short descriptions etc.). Recently, Kim (2013) reported *E. mirabilis* from Jeju Island (Korea) amongst 40 harpacticoid species belonging to 13 families. He found the *Echinolaophonte* specimens at Sungsanpo, a locality that is situated close to the type locality of *E. musa* sp. nov. Nevertheless, Kim's (2013) information on the reported species is quite rudimentary, providing only short diagnoses and few photographic images. To clarify the identity of the Korean *Echinolaophonte* species, we re-examined the specimens deposited by Kim (2013) at the National Marine Biodiversity Institute of Korea (reg. no. MADBK 721114-001). After careful re-examination we confirmed that the specimens, in fact, represent the new species *E. musa* sp. nov., not *E. mirabilis*.

Conclusions

The description of a new laophontid species from Jeju Island (Korea) and the subsequent attempt to allocate it to *Echinolaophonte* Nicholls, 1941 (Copepoda, Harpacticoida, Laophontidae T. Scott, 1904) revealed that this genus actually constitutes a heterogeneous conglomerate of species that cannot be united by means of clear-cut synapomorphies. Therefore, an exhaustive phylogenetic analysis of *Echinolaophonte* was undertaken, based on 135 morphological characters. Until the here presented phylogenetic re-evaluation, the genus enclosed 14 species. The phylogenetic analysis resulted, however, in the exclusion of four species from *Echinolaophonte*: *E. tropica* Ummerkutty, 1970, was assigned to *Parechinolaophonte* gen. nov. as *Pa. tropica* (Ummerkutty, 1970) gen. et comb. nov.; the three Mediterranean species *E. minuta* Cottarelli & Forniz, 1991, *E. mordoganensis* Kuru, Sönmez & Karaytug, 2019 and *E. venilia* Cottarelli, Forniz & Bascherini, 1992 were allocated to *Pseudechinolaophonte* gen. nov. as *Ps. minuta* (Cottarelli & Forniz, 1991), gen. et comb. nov., *Ps. mordoganensis* (Kuru, Sönmez & Karaytug, 2019), gen. et comb. nov. and *Ps. venilia* (Cottarelli, Forniz & Bascherini, 1992), gen. et comb. nov. Both new genera are characterised by exclusive autapomorphies. *Echinolaophonte longantennata* Apostolov, 1990 had to be excluded from the phylogenetic revision, due to imprecise and fragmentary description; its systematic position is pending until further material is available for re-examination and re-description, so within the Laophontidae, it is regarded here as species *incertae sedis*. The remaining nine species are retained in *Echinolaophonte*, which is now characterised as a monophylum by means of one autapomorphy, i.e. the presence of a dorsal single spur on the posterior margin of the cephalothorax. Moreover, with the description of *E. musa* sp. nov. from Jeju Island and the elevation of *E. armiger* f. *briani* Lang, 1965 to the species level (*E. briani* Lang, 1965), the number of species assigned to *Echinolaophonte* increases to 11.

Together with findings of *E. oshoroensis* in Japan (Itô 1969) and *E. mirabilis* Gurney, 1927 in China (Zhang and Li 1976), *E. musa* sp. nov. is the third representative of *Echinolaophonte* reported from Asian waters. The report of *E. mirabilis* from Jeju Island (Korea) by Kim (2013) is, however, erroneous. Re-exmination of that material revealed that it actually belongs to *E. musa* sp. nov.

The here presented phylogenetic re-evaluation of *Echinolaophonte* elucidates its former ambiguous phylogenetic status and, thus, might be a helpful step towards the solution of the phylogenetic unclarities within the Laophontidae.

Acknowledgements

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