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Bicorniphontodes (Copepoda: Harpacticoida: Laophontodinae Lang, 1944): a new genus with description of a new species from the Napoleon Reef, Gulf of Aqaba, Red Sea, Egypt

KAI HORST GEORGE[1,3], THOMAS GLATZEL[2] & KATHARINA SCHRÖDER[2]
[1]*Senckenberg am Meer Wilhelmshaven, Abt. Deutsches Zentrum für Marine Biodiversitätsforschung, DZMB, Südstrand 44, 26382 Wilhelmshaven, Germany*
[2]*Carl von Ossietzky Universität, AG Biodiversität und Evolution der Tiere, Institut für Biologie und Umweltwissenschaften, 26111 Oldenburg, Germany*
[3]*Corresponding author: phone: +49 4421 9475-110, fax: +49 4421 9475-111. E-mail: Kai.George@senckenberg.de*

Abstract

Findings of a new representative of the Laophontodinae Lang, 1944 (Copepoda, Harpacticoida) from the Napoleon Reef (Gulf of Aqaba, Red Sea, Egypt) provided new insights into the systematics of the type genus *Laophontodes* T. Scott, 1894. *Bicorniphontodes clarae* **gen. et sp. nov.**, which is described in the present contribution, shares exclusively six derived characters with *Laophontodes bicornis* A. Scott, 1896, *L. horstgeorgei* George & Gheerardyn, 2015, and partly with *L. hamatus* (Thomson, 1883), and *L. ornatus* Krishnaswamy, 1957: (1) cephalothorax medio-laterally with triangular extensions and (2) postero-laterally with paired cuticular processes, (3) free body somites except telson dorsally with hyaline frills ending in rounded lappets, (4) furcal setae I and II displaced subapically, (5) antennar allobasis lacking abexopodal seta on endopodal half, (6) outer spines of the last segment of swimming legs 2 and 3 unipinnate and comb-like, with the pinnae being extremely long and set widely apart. Thus, the named species are excluded from *Laophontodes* and united together with *B. clarae* **gen. et sp. nov.** in *Bicorniphontodes* **gen. nov.** as *Bicorniphontodes bicornis* comb. nov., *B. hamatus* comb. nov., *B. horstgeorgei* comb. nov., and *B. ornatus* comb. nov.. Beside the description of *B. clarae* **gen. et sp. nov.**, a detailed phylogenetic discussion regarding the systematic relationships of the named species and the justification of the erection of *Bicorniphontodes* **gen. nov.** is given, including its distribution in the world's oceans. A key to species is also provided.

Key words: Crustacea, Ancorabolidae, systematics, meiofauna, littoral, coral reefs

Introduction

Enclosing about 75 species (cf. George & Müller 2013), Ancorabolidae is a comparatively small group of benthic living Harpacticoida (Crustacea, Copepoda), several of which showing a set of peculiar morphological features like e.g. cuticular processes on the dorsal and/or lateral margin of the cephalothorax and/or the body somites, laterally elongated bases of the swimming legs 1 to 4, and an atrophied or even lost exopod on the antenna (e.g. Lang 1948; Boxshall & Halsey 2004; George & Müller 2013). Lang (1944, 1948) split the family into two subfamilies, namely the Ancorabolinae Sars, 1909 and Laophontodinae. Formerly seen as monophylum, in the past decade the monophyly of Ancorabolidae and at least of one subfamily (Laophontodinae) was increasingly doubted (Conroy-Dalton 2003, 2004; George 2006; Gheerardyn & George 2010), and finally George & Müller (2013) rejected the assumption of a monophylum "Ancorabolidae".

In the frame of trying to prove or to discard the phylogenetic status of Laophontodinae, several recent papers focused in particular on its type genus *Laophontodes* T. Scott, 1894 (Gheerardyn & George 2010; Gheerardyn & Lee 2012; George & Gheerardyn 2015; George 2017, 2018). In that context, George & Gheerardyn (2015) already noted a strong similarity of *Laophontodes bicornis* A. Scott, 1896, *L. hamatus* (Thomson, 1883), *L. horstgeorgei* George & Gheerardyn, 2015, and *L. ornatus* Krishnaswamy, 1957. They assumed that the named species may form a monophyletic group within *Laophontodes*, as they share some derived characters, especially a pair of lateral cuticular processes on the cephalothorax. Nonetheless, George & Gheerardyn (2015) foresaw from uniting the named species in a newly established genus. This is done in the present contribution. The finding of the here newly described *Bicorniphontodes clarae* sp. nov., collected during a marine biology field excursion to the Red Sea Napoleon Reef (south-eastern part of the Sinai Peninsula, Egypt) and yielding some derived characters feasible for a detailed comparison with the above mentioned species, enabled us to provide a phylogenetic analysis basing on morphology that resulted in the erection of a monophyletic taxon *Bicorniphontodes* **gen. nov.** and the allocation of *L. bicornis*, *L. hamatus*, *L. horstgeorgei*, *L. ornatus*, and *Bicorniphontodes clarae* **gen. et sp. nov.** into that genus.

Material and methods

The Napoleon Reef (eastern edge of the Dahab lagoon in the south-eastern part of the Sinai Peninsula (Egypt)) is a shallow fringing reef (Fig. 1). It is partly separated from the beach by a reef channel with a longitudinal flow into the lagoon during low tide, and influenced by moderate waves. The top of the reef is permanently covered by seawater (depth: approximately 1m) and encloses many single (patchy) blocks of stone corals, e.g. *Acropora* spp., *Porites* spp., and *Pocillipora* spp. (Scleractinia). These blocks are surrounded by coral sediment and fragments, which generate a diversity of macro- and micro-habitats with many heterogeneous biocenoses (El-Serehy *et al.* 2015), like for instance the interstitial copepod fauna that encompasses e.g. *Mircocanuella* spp. (Canuelloida Khodami, McArthur, Blanco-Bercial & Martínez Arbizu, 2017: Canuellidae Lang, 1944), and the harpacticoid taxa *Laophontodes* spp. (Laophontodinae Lang, 1944), *Leptocaris* spp. (Darcythompsoniidae Lang, 1936), *Delavalia* sp. (Miraciidae Dana, 1846), *Stenhelia* sp. (Miraciidae Dana, 1846), *Apodopsyllus* sp. (Paramesochridae Lang, 1944) (Kühne unpubl.).

The sampling site is situated in the inner reef flat next to the reef channel of the Napoleon Reef, nearby the city of Dahab, Sinai, Egypt (Fig.1). The sampling took place on the 5th of September 2015. Five sediment cores, 5cm long, were taken between small coral blocks with a single core, with a diameter of 4.1cm at a depth of 0.7m. All samples were placed in small PVC jars with a volume of 200ml, fixed with 37% formaldehyde and seawater (ratio 1:9) and transported to the laboratory.

The samples were centrifuged three times with 4,000rpm for 6min, using Levasil® as floating medium and Kaolin to separate the sediment from the organisms. The centrifuged material was subsequently stained with Rose Bengal and then sorted under a Leica MZ 125 stereo microscope. Specimens of *Bicorniphontodes clarae* **gen. et sp. nov.** were separated and embedded into glycerine for further processing. Sample centrifugation was realized at the German Centre for Marine Biodiversity Research (DZMB) at Senckenberg am Meer, Wilhelmshaven (Germany). Sorting and drawings were made at the Animal Biodiversity and Evolution group of the Carl von Ossietzky University, Oldenburg, Germany, using a camera lucida on a Leica DMLB compound microscope equipped with differential interference contrast. The complete type material is kept in the collection of the Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt (Germany).

General terminology is adopted from Huys & Boxshall (1991). Phylogenetic terminology follows Ax (1984), whilst the technical terms "telson" and "furca" are adopted from Schminke (1976).

Abbreviations used in the text: A1: antennule, A2: antenna, aes: aesthetasc, benp: basoendopod, cphth: cephalothorax, enp: endopod, enp-1/enp-2/enp-3: endopodal segments 1–3, exp: exopod, exp-1/exp-2/exp-3: exopodal segments 1–3, FR: furcal ramus/rami, GDS: genital double somite, GF: genital field, md: mandible, mxl: maxillule, mx: maxilla, mxp: maxilliped, P1–P6: swimming legs 1–6.

Results

Systematics

Subclass: Copepoda Milne-Edwards, 1840

Order Harpacticoida Sars, 1903

Family: "Ancorabolidae" Sars, 1909

Subfamily: Laophontodinae Lang, 1944

Genus: *Bicorniphontodes* gen. nov.

Type species: *Bicorniphontodes bicornis* (A. Scott, 1896) **comb. nov.** Additional species: *B. hamatus* (Thomson, 1883) **comb. nov.**, *B. horstgeorgei* (George & Gheerardyn, 2015) **comb. nov.**, *B. ornatus* (Krishnaswamy, 1957) **comb. nov.**, *B. clarae* **gen. et sp. nov.** (present contribution).

Etymology: The generic name refers to the paired posterolateral "horns" on the cphth of the assigned species.

Remark: two of the assigned species, *B. hamatus* **comb. nov.** and *B. ornatus* **comb. nov.**, were described only fragmentary and in an unsatisfying quality (Thomson 1883; Monard 1935; Lang 1936; Krishnaswamy 1957), and the respective type material is not available for direct comparison. Thus, many characters cannot be confirmed for these species. Nonetheless, they fit the main generic diagnostic and phylogenetic characters (see discussion), in particular the shape of the cphth with its lateral triangular extensions and the paired cuticular laterodistal processes. Therefore, both species are placed into the new genus. Features that cannot be confirmed are marked with an asterisk * in the generic diagnosis.

Generic diagnosis. Harpacticoida Sars, 1903, Laophontodinae Lang, 1944. Body slender and cylindrical; inconspicuous podoplean boundary between pro- and urosoma. Cphth anteriorly laterally stretched, forming triangular lateral extensions; moreover, latero-distally with pair of backwardly directed strong cuticular processes; in some representatives, the cephalothoracic cuticula is distinctively structured at its dorsal side*. Free thoracic and abdominal somites clearly distinct. Cphth and free thoracic somites carrying P2–P4 (in some species, even P5-bearing somite) dorsally with sensilla on apical margin, which arise from small socles*. Females with fused last thoracic (P6-bearing) and first abdominal somite, forming a genital double somite. All body somites except cphth and telson dorsally on apical margin with hyaline frills that end in round lappets*. FR long and slender, reaching almost the length of penultimate abdominal somite and telson together; with 7 setae, all of which located subapically. A1 5-segmented in female, fourth segment very small, aes on third segment; 6-segmented (chirocer) or 7-segmented (subchirocer) in male*, aes on fifth segment. A2 with allobasis lacking an abexopodal seta*; exp represented by 1 small seta*. Md* slender, gnathobase with some multicuspidate teeth; md palp a single lobe, with 4–6 setae. Mxl* with prominent precoxal gnathobase bearing apically several strong spines and setae; coxa elongated, with 2 apical setae; basis, exp, and enp fused to single lobe carrying several lateral and apical setae. Mx* with 2 endites, each carrying 3 setae; enp small, knob-like, with 2 setae, or completely reduced and represented by 2 setae. Mxp* prehensile, syncoxa with or without apical seta, enp apically with 1 long slender claw that is accompanied by minute seta. P1 of typical laophontodin shape: coxa* and basis elongated, basis with 1 inner* and 1 outer seta; enp prehensile, 2-segmented, apically with 1 claw, 1 (sometimes geniculate) seta and 1 minute seta*; exp 3-segmented, exopodal segments without inner setae, exp-1 with 1 outer spine, exp-2* with 1 geniculate outer seta, exp-3 with 4 geniculate* apical setae. P2–P4 with laterally elongated bases; female enps 2-segmented, enp-1 minute*, without setae/spines, enp-2 elongate, slender, in P2 and P3 with 2 apical setae, in P4 additionally with 1 inner, in some species also with 1 outer seta; male P2 and P4 as in female, but P3 enp* 3-segmented, the second segment with small triangular apophysis; enp-3 small, with 2 apical setae. P5 with endopodal lobe completely absorbed into benp, represented by 2 and 1 setae in female and male, respectively; female exp distinct, elongated, carrying 2 lateral and 3 (sub)apical setae; in male, exp fused to benp*, with 3–4 setae. Female P6 minute, located previous to copulatory pore, with former lobes each indicated by 1 small seta; male P6 absent*.

Bicorniphontodes clarae gen. et sp. nov.

Type material: Female holotype, embedded on 1 slide, coll. no. SMF 37200/1; paratype 1 (allotype): male, embedded on 1 slide, coll. no. SMF 37201/1; paratype 2: female, embedded on 1 slide, coll. no. SMF 37202/1; paratype 3: female, embedded on 1 slide, coll. no. SMF 37203/1; paratype 4: female, distributed over 4 slides, coll. no. SMF 37204/1–4; paratype 5: female, distributed over 3 slides, coll. no. SMF 37205/1–3; paratype 6: female, distributed over 4 slides, coll. no. SMF 37206/1–4; paratype 7: male, distributed over 3 slides, coll. no. SMF 37207/1–3.

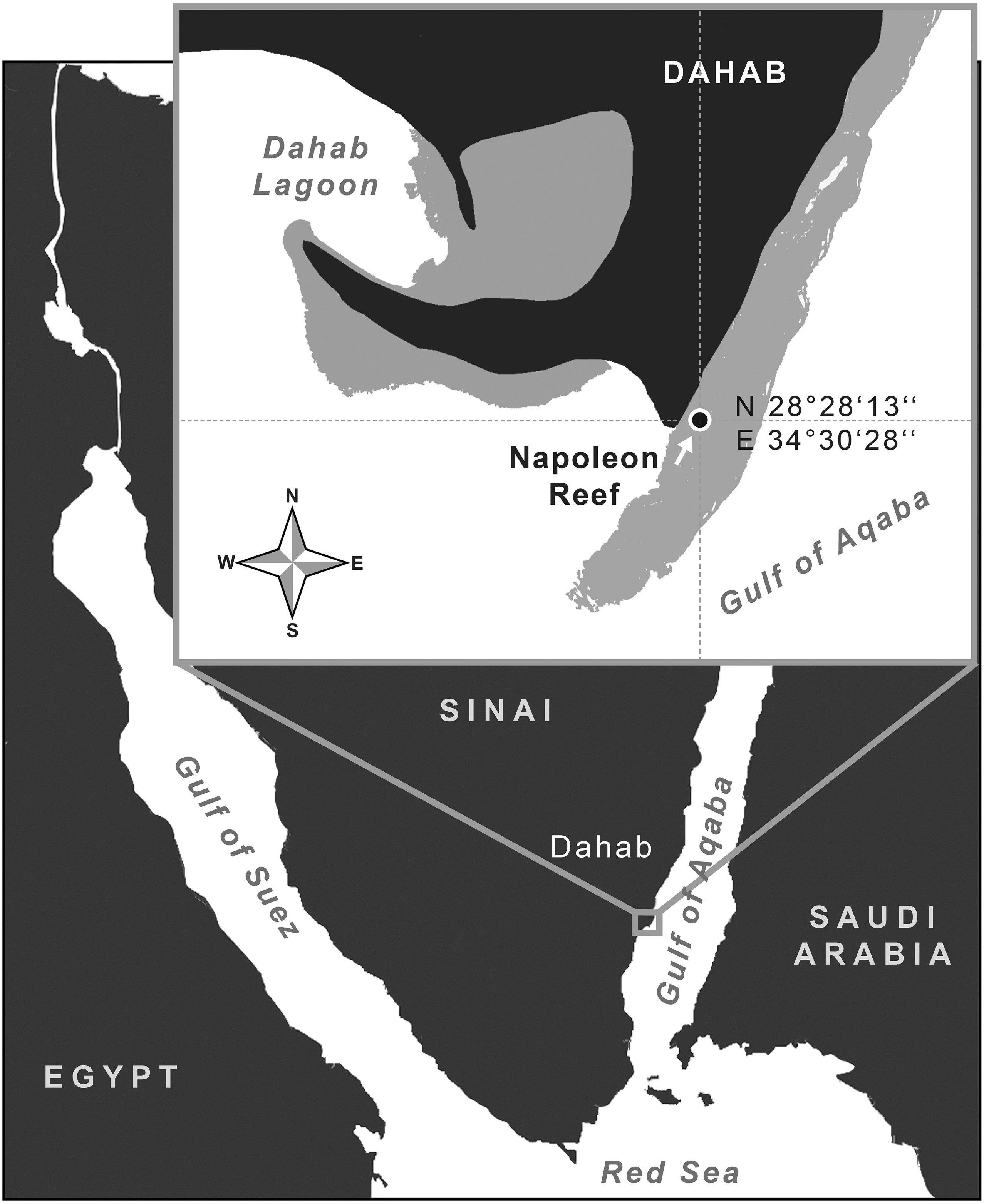

FIGURE 1. Napoleon Reef with sampling site, near the lagoon of Dahab. (map: D. Weinreich-Brunner)

Locus typicus: Napoleon Reef, Dahab, Gulf of Aqaba, Egypt, geographic location 28°28`13" N/34°30`28" E, littoral.

Etymology: The epitheton "*clarae*" is given in fondly dedication to TG's youngest daughter Clara (Hamburg, Germany).

Description of female. Habitus (Fig. 2A) slender, cylindrical, tapering distally, body length approximately 430µm (R to the end of FR). Rostrum (Fig. 3B) triangular, fused with cphth, with 2 pairs of sensilla, one of which apically, the other pair centrally. Cphth (Fig. 2A) comprising one third of total body length, with several sensilla, some of which arising from small socles; medio-laterally with paired triangular extensions; postero-laterally with pair of well-developed, backwardly curved cuticular processes; dorsally with cuticular ridges running in longitudinal direction. Free body somites clearly distinct. P2–P4-bearing somites (Fig. 2A) dorsally sclerotized, P2-bearing somite dorsally with 6, P3–P5 bearing somites each with 4 small socles carrying sensilla on their tips. All body somites except cphth with finger-like hyaline frill on the rear margin, P2-bearing somite–GDS dorsally with small tube pore. Telson small, broader than long and not reaching half of the length of the preceding somite. Anal operculum rounded, with row of fine spinules on posterior margin, and flanked by 2 sensilla.

FR (Fig. 7A) slender, about 5 times longer than their broadest parts, each ramus proximally with tube pore and distally with 7 bare setae: I and II subapically on outer margin, II somewhat longer than I. III subapically on dorsal outer edge, 3 times longer than I; IV and V apically, being IV about half as long as V; V double of the length of FR; VI apically on the inner margin, as long as III; VII dorsally, tri-articulated at base, slightly longer than IV.

A1 (Fig. 3A) 5-segmented. First segment with a cuticular "bump" on posterior margin bearing short spinules; anterior margin with long setules and 1 pinnate seta apically; second segment with a weak "bump" with several long setules on posterior margin, anteriorly with 9 bare setae; third segment longer as second, with 5 bare setae on anterior margin and 1 aes apically accompanied by 1 bare seta arising from acrothek, adjoining 1 extra bare seta; fourth segment smallest, overlapped by preceding segment, with 1 bare seta; fifth segment with 10 setae and 1 small aes.

Setal formula: 1/1; 2/9; 3/7 + aes; 4/1; 5/10 + aes.

A2 (Fig. 3D). Coxa small, without ornamentation; allobasis with row of spinules on abexopodal margin, lacking abexopodal setae; exp represented by 1 tiny bare seta; enp as long as allobasis, with row of spinules on anterior margin and 2 subapical spines, 1 of which bipinnate, the other bare; apically with 3 geniculated setae and 2 spines; subapically with spinulose frill.

Md (Fig. 5A). Gnathobase apically with 4 multicuspidate teeth and 1 plumose seta. Md palp 1-segmented, carrying 6 bipinnate setae.

Mxl (Fig. 4B). Precoxal arthite with 5 strong bare spines and 2 setae apically. Two of the spines end in a double tip. Additionally with 2 surface setae. Coxa with 2 bare seta apically. Basis with 3 bare lateral spines and 3 bare apical setae.

Mx (Fig. 4C). Syncoxa and basis fused, with 2 endites and 3 rows of spinules, proximal endite apically with 2 bare setae and 1 strong unipinnate spine, distal endite with 1 fine seta and 1 strong bare spine; basis elongated, with 2 bare setae and apically with 1 strong unipinnate spine; enp represented by 2 bare setae.

Mxp (Fig. 4D) prehensile, syncoxa slender, with 1 rounded row of spinules, lacking apical seta; basis longer than syncoxa, with row of spinules on outer side; endopod produced into a long claw reaching length of basis and accompanied by minute seta.

P1 (Fig. 5A). Precoxa small, coxa elongated, as long as basis; basis with each 1 plumose seta on inner and outer side, respectively; enp long, 2 segmented, prehensile; enp-1 twice as long as whole exopod, with row of spinules on inner side, subapically with cuticular bulge; enp-2 reaching at most 1/3 of length of enp-1, apically with 1 strong unipinnate claw and 1 bare seta, subapically with 1 small bare seta. Exp 3-segmented, exp-1 with spinules on outer margin and 1 unipinnate strong spine; exp-2 with spinules on both the inner and outer margin and 1 bare geniculate outer seta; exp-3 apically with 4 geniculate setae, the innermost being plumose at distal half.

P2–P4 (Figs. 5B, 6A, B) with transversely elongated bases, 3-segmented exopods and 2-segmented endopods; bases with long tube pore on proximal margin, and with 1 outer biplumose (P2) respectively 1 bare seta (P4) (broken in P3). All exo- and endopodal segments except enps-1 with rows of spinules on inner and/or outer margin; first endopodal segments very small, second segments long and slender, apically with 2 long biplumose setae, in P4 additionally with 1 inner biplumose seta and 1 outer bipinnate spine. Exp-1 with 1 outer bipinnate spine; exp-2 with 1 inner biplumose seta and 1 bipinnate outer spine; exp-3 with 3 unipinnate, comb-shaped outer spines and 2 apical biplumose setae; P2 additionally with 1, P3 and P4 with 2 inner biplumose setae. Setal formula given in Tab. 1.

P5 (Fig. 5C). Endopodal lobe incorporated completely into benp and represented only by 2 setae of fish-bone aspect. Benp with 1 seta arising from long setophore, and with 1 row of spinules each on the inner and outer margin; additionally with 2 tube pores. Exp distinct, shorter than benp, with outer row of spinules, 1 outer spine and 2 inner setae, the proximal one being bare, the distal one bipinnate; apically with 1 bipinnate and 1 biplumose seta.

GF and P6 (Fig. 5D). Small, with single copulatory pore; P6 strongly reduced to a small seta, limbs fused to small single plate carrying each 1 minute seta.

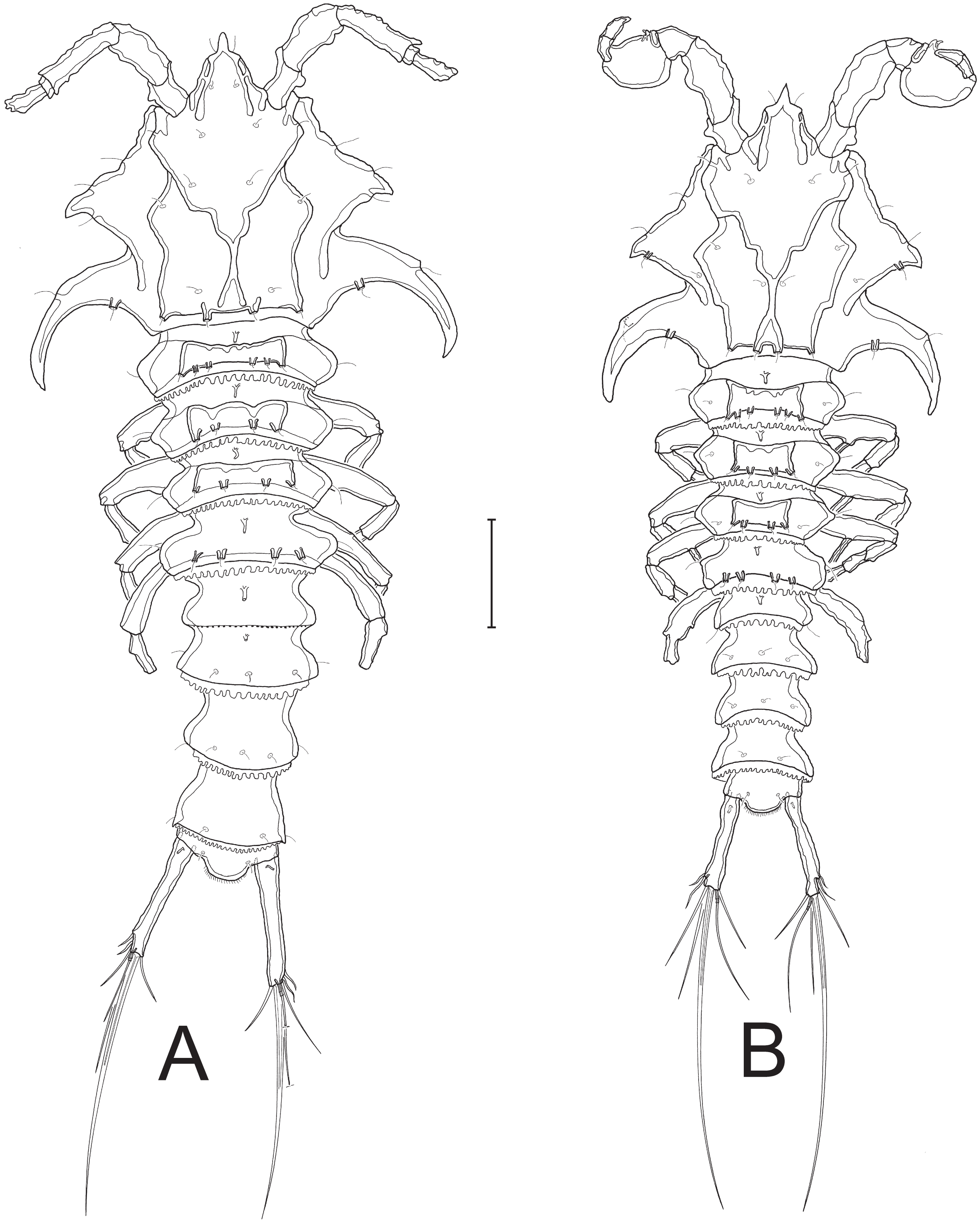

FIGURE 2. *Bicorniphontodes clarae* **gen. et sp. nov.**, **A.** female, dorsal habitus, **B.** male, dorsal habitus. Scale: 50µm.

Description of male. The male differs from the female in the following characters: body size, A1, P3 endopod, P5.

Habitus (Fig. 2B) smaller and slimmer, body length of described specimen from rostral tip to end of FR: 360µm.

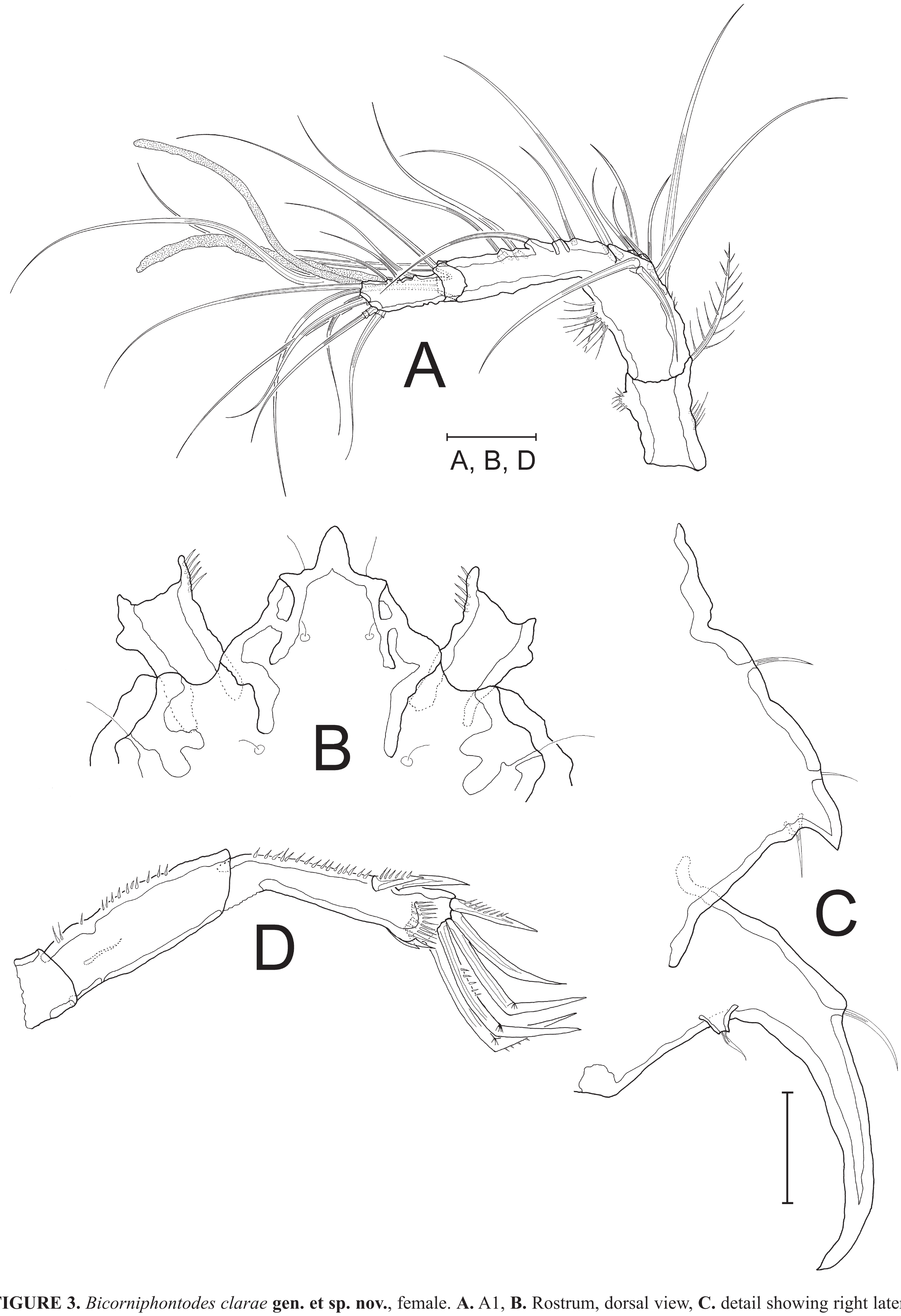

FIGURE 3. *Bicorniphontodes clarae* **gen. et sp. nov.**, female. **A.** A1, **B.** Rostrum, dorsal view, **C.** detail showing right lateral triangular extension and cuticular process, **D**. A2. Scales: 20µm.

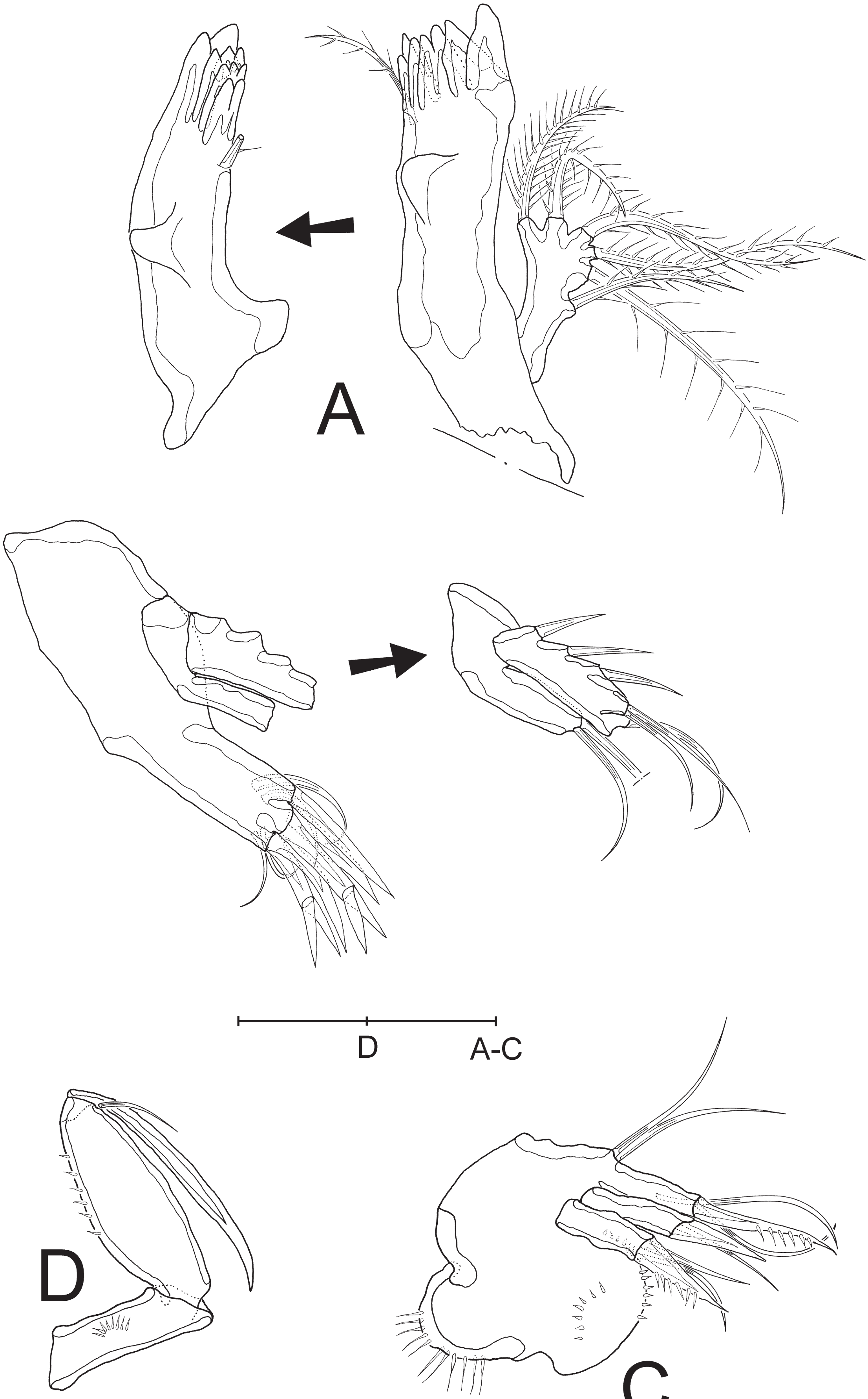

FIGURE 4. *Bicorniphontodes clarae* **gen. et sp. nov.**, **A.** Md, A'. Md of counterpart, **B.** Mxl, **C.** Mx, **D.** Mxp. Scales: 20µm.

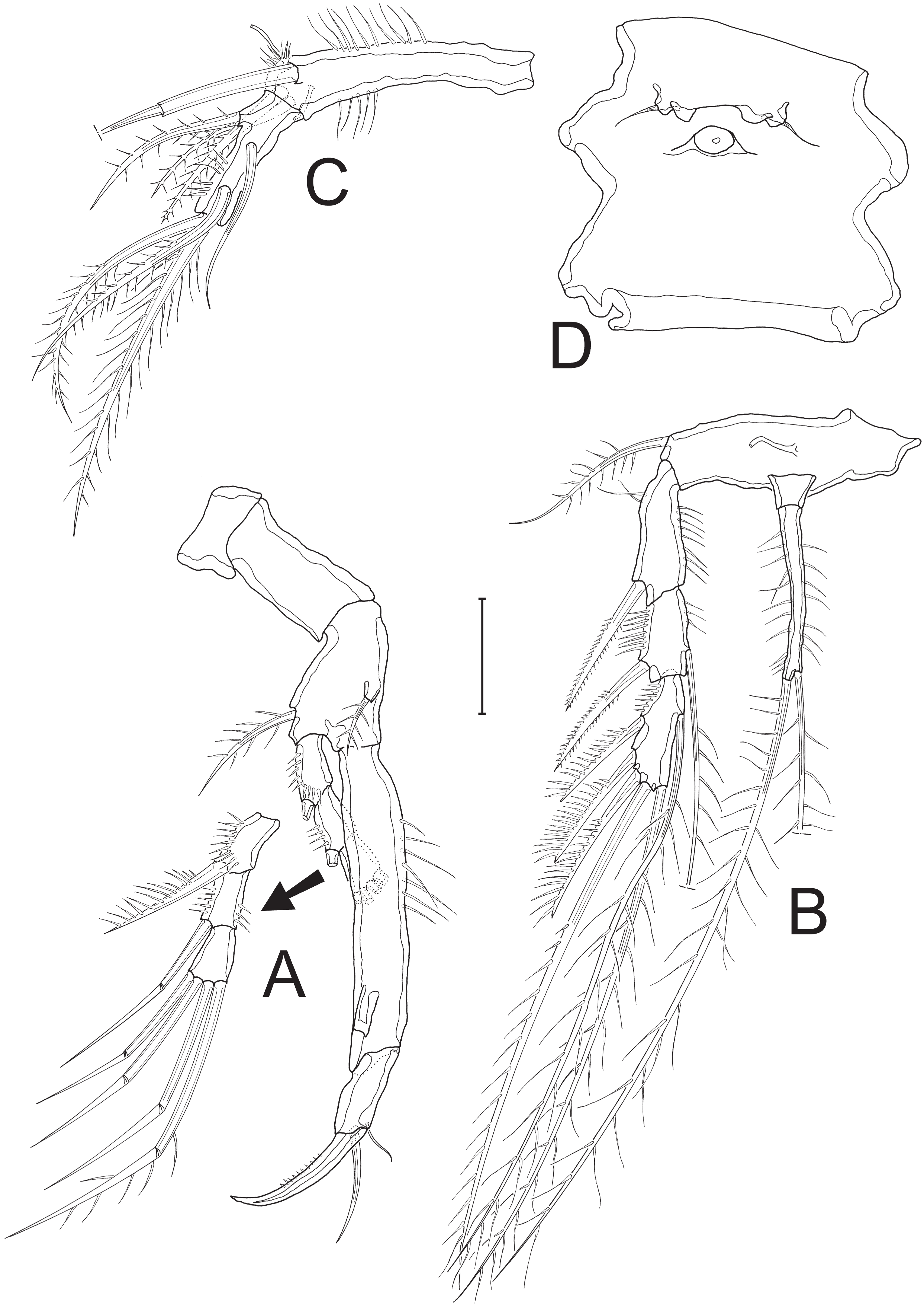

FIGURE 5. *Bicorniphontodes clarae* **gen. et sp. nov.**, female. **A.** P1, **B.** P2, **C.** P5, **D.** GDS with P6 and copulatory pore. Scale: 20μm.

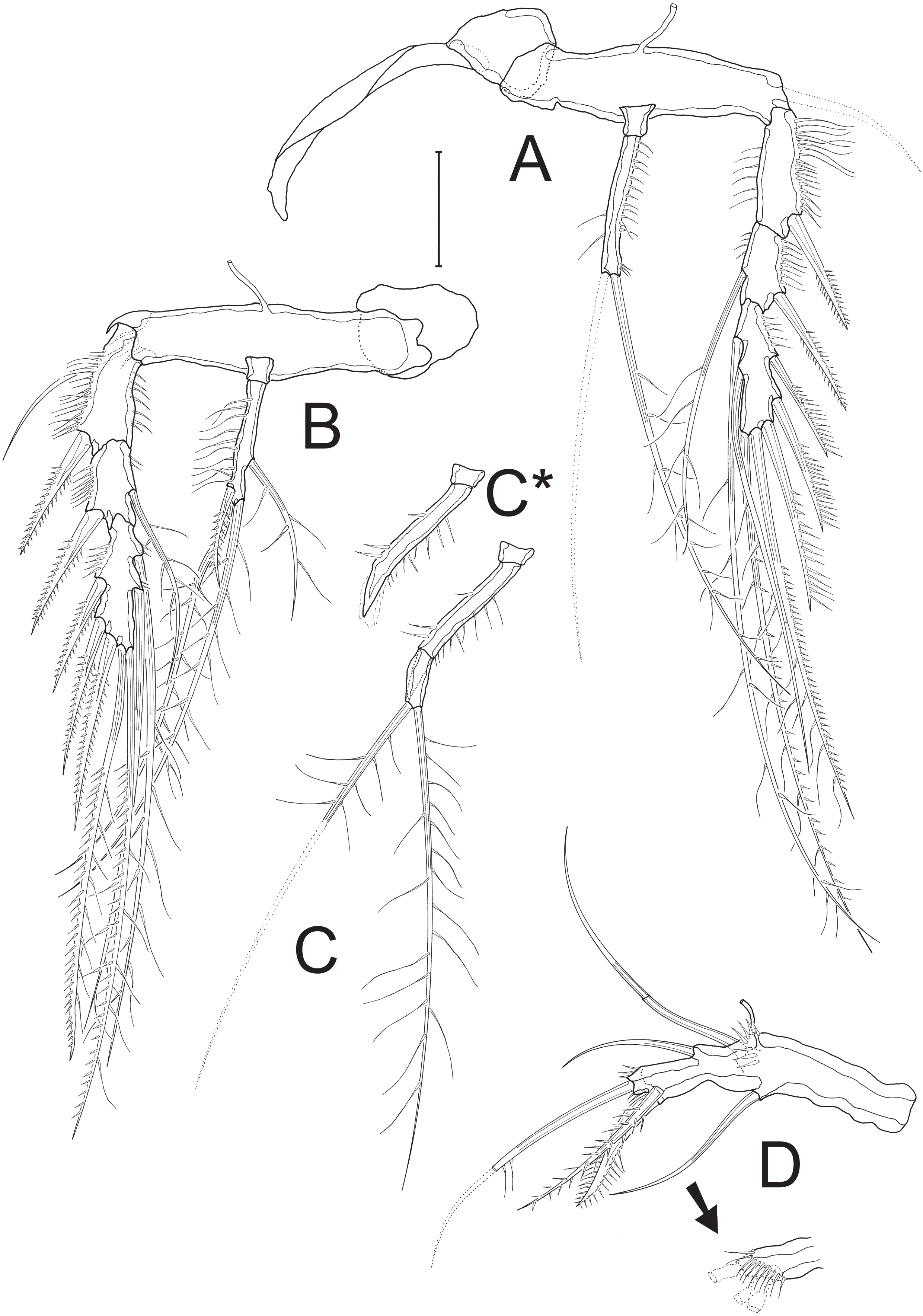

FIGURE 6. *Bicorniphontodes clarae* **gen. et sp. nov.**, **A.** Female P3, **B.** Female P4, **C.** Male P3 enp, **C*.** Male P3 endopod showing apophysis (enp-3 omitted), **D.** Male P5, arrow pointing to subapical row of spinules. Scale: 20µm.

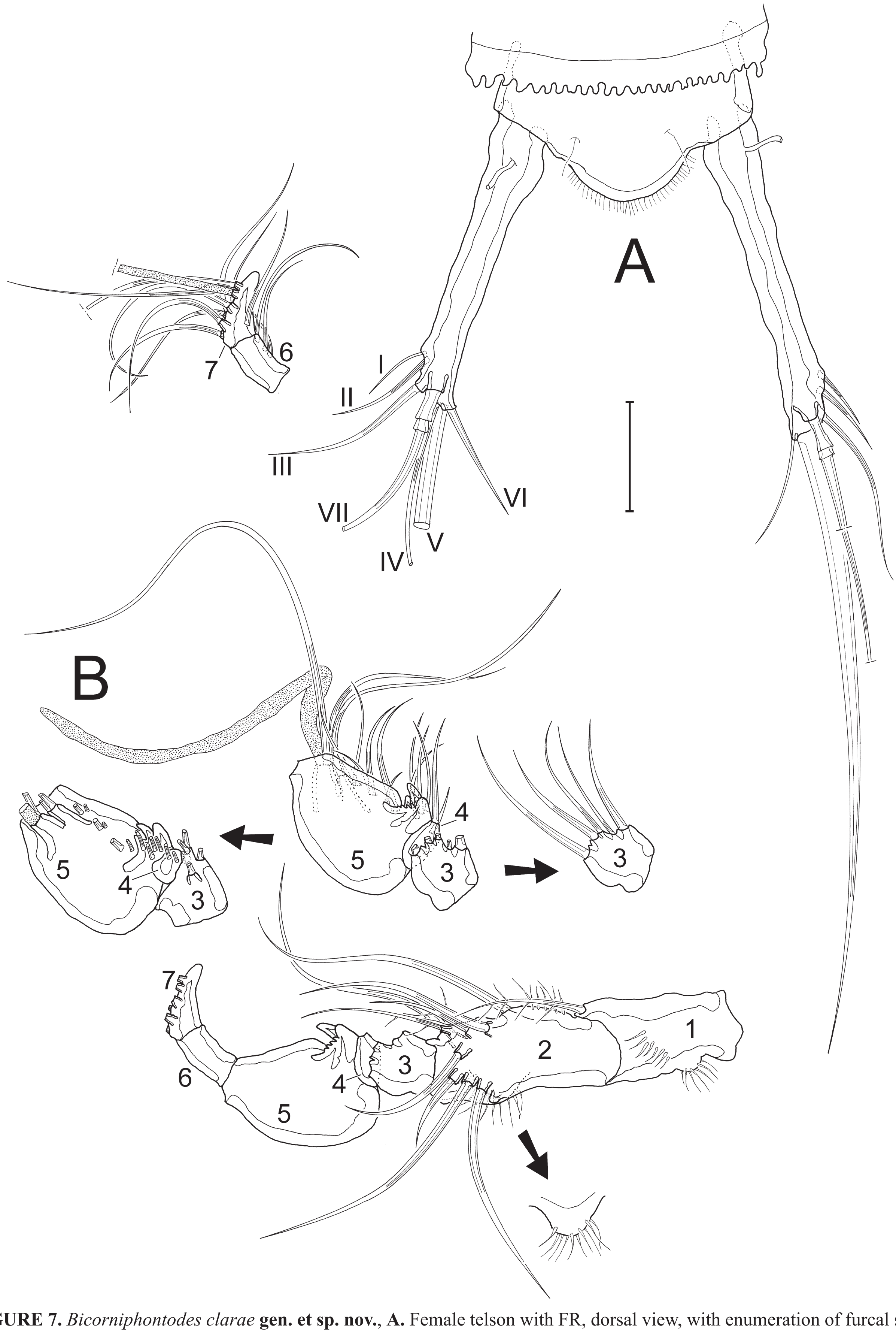

FIGURE 7. *Bicorniphontodes clarae* **gen. et sp. nov.**, **A.** Female telson with FR, dorsal view, with enumeration of furcal setae I–VII on left FR, **B.** Male A1, segments numbered; arrow at segment 2 showing spinulose "bump"; additionally, single numbered segments show setation. Scale: 20µm.

TABLE 1. *Bicorniphontodes clarae* **gen. et sp. nov.**, setation of P2–P4. Roman numerals indicate outer spines.

	Exp-1	Exp-2	Exp-3	Enp-1	Enp-2	Enp-3
P2	I-0	I-1	III-2-1	0	0-2-0	–
P3 female	I-0	I-1	III-2-2	0	0-2-0	–
P3 male	I-0	I-1	III-2-2	0	0 (apophysis)	0-2-0
P4	I-0	I-1	III-2-2	0	1-2-1	–

A1 (Fig. 7B) 7-segmented, subchirocer. First segment longer than broad, apically with 2 rows of spinules and 1 bipinnate seta; second segment with spinulose bump on the posterior margin, and with 9 setae, 4 of them longer than the remaining 5; third segment smaller than the preceding segments, with 5 smooth setae apically; fourth segment very small, with 2 smooth setae; fifth segment swollen, with 2 hook-shaped spines on its ventral surface, and with 4 setae, followed by 6 setae; apically with acrothek formed by aes and 1 seta, accompanied by pedestal with 2 setae; sixth segment with 3 setae; seventh segment tapering posteriorly, with 8 setae on outer side and 1 small aes with 1 accompanying seta.

Setal formula: 1/1; 2/9; 3/5; 4/2; 5/13 + aes; 6/3; 7/9 + aes.

P3 (Fig. 6C, C*). Exp as in female. Enp 3-segmented: enp-1 small and unarmed, enp-2 longest, with row of spinules on inner and outer margin, apically with a short triangular apophysis (Fig. 6C*) that reaches the end of enp-3; enp-3 with 2 biplumose apical setae.

P5 (Fig. 6D) small, benp and exp fused. Benp with outer basal seta arising from setophore accompanied by row of spinules and 1 tube pore; endopodal lobe represented by 1 bare seta; exopodal lobe with 1 bare outer seta, apically with 3 pinnate spines.

Discussion

Establishment of *Bicorniphontodes* gen. nov. Recently, the genus *Laophontodes* T. Scott, 1894, type genus of the taxon Laophontodinae Lang, 1944 (Copepoda, Harpacticoida, "Ancorabolidae" Sars, 1909), became object of intensive phylogenetic re-examination (e.g. Conroy-Dalton 2004; Gheerardyn & Lee 2012; George & Gheerardyn 2015; George 2017, 2018). In this regard *Laophontodes* was recognized as mixture of species, many of which actually not being closer related. Consequently, several species were excluded from *Laophontodes* and displaced into newly established genera (*Paralaophontodes* Lang, 1965, *Lobopleura* Conroy-Dalton, 2004, *Calypsophontodes* Gheerardyn & Lee, 2012 (Lang 1965; Conroy-Dalton 2004; Gheerardyn & Lee 2012; George 2017). Thus, the number of species assigned to *Laophontodes* suffered a remarkable fluctuation (cf. Boxshall & Halsey 2004; Wells 2007; George & Gheerardyn 2015; George 2017, 2018). The most recent counting lists 18 species plus 1 species *incertae sedis* assigned to *Laophontodes* (George 2018) (cf. Tab. 2).

The description of the here presented new species and its subsequent comparison with remaining *Laophontodes* species revealed its close relationship particularly with *Laophontodes bicornis*, *L. horstgeorgei* and, with reservation, also with *L. hamatus* and *L. ornatus*. These species share (at least part of) the following set of six derived characters that are missing in the remaining *Laophontodes* species and therefore considered as synapomorphies for the species [plesiomorphic states in square brackets]:

1. Cphth medio-laterally with triangular extensions [cphth medio-laterally not extended];
2. Cphth postero-laterally with pair of cuticular processes [cphth without postero-lateral processes];
3. All free body somites except telson dorsally with hyaline frill ending in rounded lappets [such hyaline frills not developed];
4. Furcal setae I and II displaced subapically [furcal setae I and II inserting laterally];
5. A2 allobasis without abexopodal seta [abexopodal seta on endopodal half of allobasis still present];
6. Outer spines of P2 and P3 exp-3 unipinnate and comb-like, pinnae extremely long and set widely apart [outer spines bipinnate, pinnae small and located densely together].

Character 1, cphth medio-laterally with triangular extensions: almost all *Laophontodes* species (e.g. *L. gertraudae* George 2018, *L. maccklintocki* Schizas & Shirley, 1994, *L. mourois* Arroyo, George, Benito & Maldonado, 2003, *L. sabinegeorgeae* George & Gheerardyn 2015, *L. spongiosus* Schizas & Shirley, 1994, *L. typicus* T. Scott, 1894, *L. whitsoni* T. Scott, 1912) show a cephalothorax whose lateral margins are not extended laterally but run more or less longitudinally towards their posterior margin (cf. Schizas & Shirley 1994; Arroyo *et al.* 2003; George & Gheerardyn 2015; George 2018). As such shape of the cphth is common within Laophontodinae and even Harpacticoida, it is regarded as the plesiomorphic state; in contrast, the lateral extension in *L. bicornis*, *L. horstgeorgei*, *L. hamatus*, *L. ornatus* and the here described new species is interpreted as the derived, i.e. apomorphic condition.

Character 2, cphth postero-laterally with pair of cuticular processes: apart from the here compared species, no other *Laophontodes* species but only the genus *Ancorabolina* George, 2006 is characterized by the presence of such postero-lateral processes on the cphth. That circumstance has already been discussed intensively by Gheerardyn & George (2010), when they referred to an apparent similarity between *Ancorabolina* and *Laophontodes bicornis*. Nonetheless, these authors listed 10 clear morphological differences between the two taxa, coming to the conclusion that they are not closely related. Therefore, the formation of the cephalothoracic lateral processes has to be seen as convergent development of *Ancorabolina* and *L. bicornis*. However, that deviation is considered as synapomorphic for the here treated species.

Character 3, all free body somites except telson dorsally with hyaline frills ending in rounded lappets: the forming of special hyaline frills on the dorsal margins of the body somites (except cphth and telson) is a feature being unique within *Laophontodes* and even all “Ancorabolidae”. It is therefore regarded as synapomorphy for *L. bicornis*, *L. horstgeorgei*, *L. ornatus*, and *B. clarae* **gen. et sp. nov.** (not confirmed for *L. hamatus*).

Character 4, furcal setae I and II displaced subapically: in comparison with remaining species of *Laophontodes*, in *L. bicornis*, *L. hamatus*, *L. horstgeorgei*, *L. ornatus*, and *B. clarae* **gen. et sp. nov.** the furcal setae I and II are no longer located laterally as being usual in Copepoda (Huys & Boxshall 1991); instead, these setae are displaced subapically, so all furcal setae arise from the (sub)apical part of the furcal rami. That condition is interpreted as apomorphic.

Character 5, A2 allobasis without abexopodal seta: the primary condition in the A2 allobasis of derived Podogennonta Lang, 1944 (e.g. Ameiridae Boeck, 1865, Laophontoidea T. Scott, 1904, Tetragonicipitidae Lang, 1944) is the existence of 2 abexopodal setae, the proximal one representing the former basal seta, and the distal one representing the former endopodal element. That condition is retained also in certain “ancorabolid” taxa, like e.g. the *Ancorabolus*-lineage *sensu* Conroy-Dalton & Huys (2000). In *Laophontodes*, however, the basal representative is lost, whilst the endopodal one is still present. Three of the here treated species (confirmed neither for *L. hamatus* nor *L. ornatus*), however, lost that seta, too, being that a shared deviation.

Character 6, outer spines of P2 and P3 exp-3 unipinnate and comb-like, pinnae extremely long and set widely apart: the outer spines of the swimming legs commonly are of a moderate length and bipinnate, with the pinnae being small and staying densely together (cf. Huys *et al.* 1996). This applies to most *Laophontodes* species and other “Ancorabolidae” and is considered as the plesiomorphic state. In contrast, *L. bicornis*, *L. horstgeorgei*, *L. ornatus* and the here described new species (not confirmed for *L. hamatus*) present different outer spines on P2 and P3 exp-3, with the spines being unipinnate and comb-like, with remarkably long pinnae that are not staying close together (e.g. Figs. 5B, 6A, see also George & Gheerardyn 2015). That deviation is seen as synapomorphic.

Characters 1–6 unambiguously confirm a monophyletic status of at least *L. bicornis*, *L. horstgeorgei*, and the here described new species (Fig. 8). In addition, *L. hamatus* and *L. ornatus* share characters 1, 2, and 4, the latter presenting also the very peculiar hyaline frills on the body somites (character 3) and the peculiar outer spines on P2 exp-3 (character 6) (cf. Thomson 1883; Lang 1934; Monard 1935; Krishnaswamy 1957). Nonetheless, it has to be asserted that the respective species descriptions are incomplete and of a quite low quality. Moreover, the type material neither of *L. hamatus* nor of *L. ornatus* is available for re-examination. Thus, a re-description of both species as well as a detailed comparison with *L. bicornis*, *L. horstgeorgei* and *Bicorniphontodes clarae* **gen. et sp. nov.** has to be postponed until new findings of both *L. hamatus* and *L. ornatus*. However, as both species share the most outstanding synapomorphies (characters 1, 2) plus at least part of the other derived features, their close relationship with *L. bicornis*, *L. horstgeorgei*, and the here described new species is not doubted here.

These conditions clearly point towards a close phylogenetic relation of the species *L. bicornis*, *L. horstgeorgei*, *L. hamatus*, *L. ornatus*, and *Bicorniphontodes clarae* **gen. et sp. nov.**, which is illustrated in Fig. 8. On the other hand it is not possible to ascertain the relationship of that monophylum with the remaining *Laophontodes* species. Contrary to the expectation “towards an increasingly unambiguous phylogenetic characterization of a monophylum “*Laophontodes*” expressed by George (2018: 2), so far no clear autapomorphy for a monophylum *Laophontodes* could be found. Against that background it appears to be reasonable displacing the above named five species into a newly erected, undoubtedly monophyletic taxon, which is named *Bicorniphontodes* **gen. nov.** It includes the here described new species *Bicorniphontodes clarae* **gen. et sp. nov.**, *B. bicornis* (A. Scott, 1896) **comb. nov.** as designated type species, *B. hamatus* (Thomson, 1883) **comb. nov.**, *B. horstgeorgei* (George & Gheerardyn, 2015) **comb. nov.**, and *B. ornatus* (Krishnaswamy, 1957) **comb. nov.** (Fig. 8). Ongoing phylogenetic research attempts to elucidate the phylogenetic position and relationship of *Bicorniphontodes* **gen. nov.** within Laophontodinae.

Justification of *Bicorniphontodes clarae* gen. et sp. nov. as distinct species. As verified above, the allocation of the here described new species into a new genus *Bicorniphontodes* **gen. nov.** is doubtless, as the new species fits all six autapomorphies (characters 1–6) of the new genus. Because of insufficient information about *B. hamatus* **comb. nov.** and *B. ornatus* **comb. nov.**, in the following comparison *B. hamatus* **comb. nov.** is excluded, whilst *B. ornatus* **comb. nov.** can be considered only partly.

Bicorniphontodes clarae **gen. et sp. nov.** differs from its congeners in several features. For instance, the cephalothoracic lateral triangular extensions are much more developed in the new species than in *B. bicornis* **comb. nov.** and *B. horstgeorgei* **comb. nov.**, being larger and turning their tips into cuspidate tips (Figs. 2A, B, 3C) (character 7). Moreover, the postero-lateral processes are much stronger than in the compared species, and distinctly curved backwardly (character 8). Furthermore, in *B. clarae* **gen. et sp. nov.** the socles carrying the dorsal sensilla on P2–P4-bearing body somites arise from a prominent, sclerotized area, which is not the case in its congeners (character 9). The FR are longer, more slender and slightly diverging (character 10). Another apomorphy is detectable in the A2 endopod. The presence of a very slim seta on that lobe is present in many harpacticoid species, e.g. in Laophontidae T. Scott, 1904 (part.) (e.g. Willen 1992; Lee & Huys 1999); within *Laophontodes*, that seta is still present e.g. in *L. gertraudae*, *L. sarsi*, and *L. whitsoni* (cf. George & Gheerardyn 2015; George 2017), and also in *B. bicornis* **comb. nov.** and *B. horstgeorgei* **comb. nov.** (George & Gheerardyn 2015). In contrast, *Bicorniphontodes clarae* **gen. et sp. nov.** lacks that seta (character 11), which is regarded as apomorphic for that species.

TABLE 2. List of so far known *Laophontodes* species (nos. 1–15); in addition, the species here assigned to *Bicorniphontodes* **gen. nov.** are listed (1–5). From these, nos. 1–4 were formerly placed in *Laophontodes* (see discussion in the text).

No.	Species
	***Laophontodes* T. Scott, 1894**
1	*Laophontodes typicus* T. Scott, 1894 (**type species**)
2	*Laophontodes propinquus* Brady, 1910
3	*Laophontodes whitsoni* T. Scott, 1912
4	*Laophontodes antarcticus* Brady, 1918 (**species *incertae sedis***)
5	*Laophontodes gracilipes* Lang, 1936
6	*Laophontodes maccklintocki* Schizas and Shirley, 1994
7	*Laophontodes spongiosus* Schizas and Shirley, 1994
8	*Laophontodes mourois* Arroyo, George, Benito and Maldonado, 2003
9	*Laophontodes multispinatus* Kornev and Chertoprud, 2008
10	*Laophontodes sabinegeorgeae* George and Gheerardyn, 2015
11	*Laophontodes gertraudae* George, 2018
12	*Laophontodes monsmaris* George, 2018
13	*Laophontodes norvegicus* George, 2018
14	*Laophontodes sarsi* George, 2018
15	*Laophontodes scottorum* George, 2018
	***Bicorniphontodes* gen. nov.**
1	*Bicorniphontodes hamatus* (Thomson, 1883) **comb. nov.**
2	*Bicorniphontodes bicornis* (A. Scott, 1896) **comb. nov.** (**type species**)
3	*Bicorniphontodes ornatus* (Krishnaswamy, 1957) **comb. nov.**
4	*Bicorniphontodes horstgeorgei* (George and Gheerardyn, 2015) **comb. nov.**
5	*Bicorniphontodes clarae* **gen. et sp. nov.** (present contribution);

Characters 7–11 represent derived stages if compared with *B. bicornis* **comb. nov.** and *B. horstgeorgei* **comb. nov.** as well as with remaining *Laophontodes* species. Thus, they are considered as meaningful autapomorphies, justifying the establishment of *Bicorniphontodes clarae* **gen. et sp. nov.** as distinct species (Fig. 8).

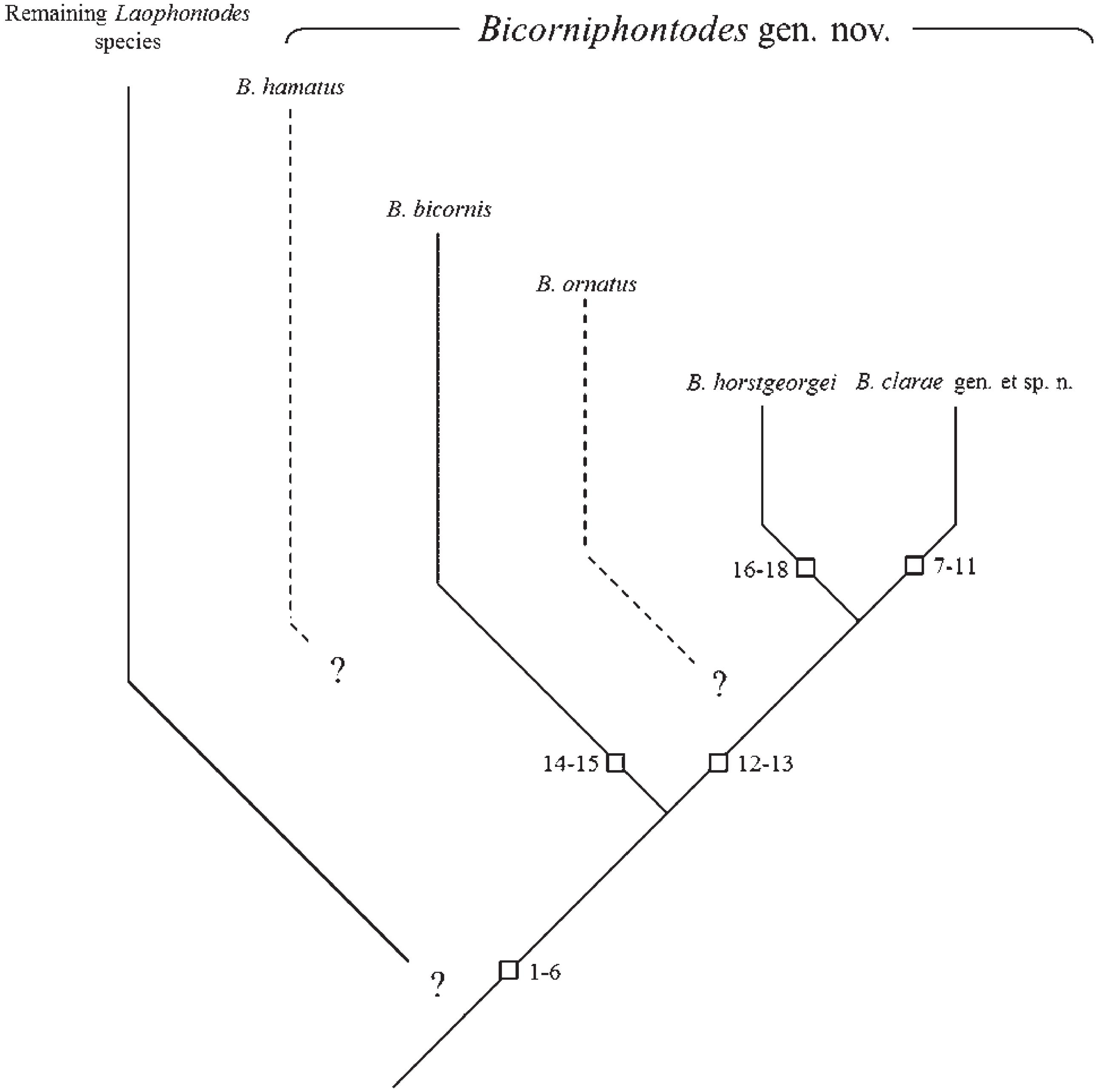

FIGURE 8. Phylogenetic relationships within *Bicorniphontodes* **gen. nov.**. Dashed lines and question marks point to the uncertain systematic position of *B. hamatus* and *B. ornatus*. Numbers 1–16 refer to the apomorphies discussed in the text.

Inside that genus, *B. bicornis* **comb. nov.** may be the most plesiomorphic representative (*B. hamatus* **comb. nov.** not considered further) (Fig. 8). Compared with *B. clarae* **gen. et sp. nov.**, *B. horstgeorgei* **comb. nov.** and (in parts) *B. ornatus* **comb. nov.**, the former lacks the cuticular ridges on the cphth, which are clearly developed in the latter species (cf. Figs. 2A, B, and Krishnaswamy 1957; George & Gheerardyn 2015) (character 12). That shared derived character points towards a closer relationship of *B. clarae* **gen. et sp. nov.**, *B. horstgeorgei* **comb. nov.** and *B. ornatus* **comb. nov.**. Moreover, at least *B. clarae* **gen. et sp. nov.** and *B. horstgeorgei* **comb. nov.** (confirmed neither for *B. hamatus* **comb. nov.** nor for *B. ornatus* **comb. nov.**) share the derived loss of the maxillar endopod, being represented by 2 setae only (character 13), whereas in *B. bicornis* **comb. nov.** the mx still retains a small endopod carrying 2 setae. On the other hand, *B. bicornis* **comb. nov.** presents two apomorphies: the male A1 consists of 6 segments and is chirocer (George & Gheerardyn 2015; error in their fig. 18A) (character 14), while both *B. clarae* **gen. et sp. nov.** and *B. horstgeorgei* **comb. nov.** still retain a 7-segmented subchirocer male A1; the md palp of *B. bicornis* **comb. nov.** bears only 4 setae (Fig. 4A; character 15), whilst the other two species still retain 6 setae (George & Gheerardyn 2015).

Derived features of *Bicorniphontodes horstgeorgei* **comb. nov.** refer to the armouring of several appendages. The presence of spinules on the mxp (character 16), P1 exp-1 and exp-2 (character 17), and enp-1 (character 18) observable in both *B. clarae* **gen. et sp. nov.** and *B. bicornis* **comb. nov.** correspond to the plesiomorphic state that is present in most Harpacticoida including "Ancorabolidae". However, the named appendages and segments are absolutely unarmoured in *B. horstgeorgei* **comb. nov.**, which is regarded as derived condition compared with the remaining species within *Bicorniphontodes* **gen. nov.** (Fig. 8).

Future findings of *B. hamatus* **comb. nov.** and *B. ornatus* **comb. nov.** may sharpen and refine the systematic relationships within that genus.

Key to the species of *Bicorniphontodes* gen. nov.
(*B. hamatus* excluded, due to the insufficient species description)

1. Cphth dorsally with longitudinal cuticular ridges; mandibular palp with >4 setae; male A1 7-segmented. 2
- Cphth lacking dorsal cuticular ridges; mandibular palp with 4 setae; male A1 6-segmented . . . . ***Bicorniphontodes bicornis*** (A. Scott, 1894) **comb. nov.**
2. Lateral transverse extensions on cphth large, cuspidate; postero-lateral processes on cphth large, distinctly curved backwardly; A2 endopod lacking slim seta accompanying subapical spines . . . . ***B. clarae*** **gen. et sp. nov.**
- Lateral transverse extensions on cphth moderately developed, not cuspidate; posterolateral processes on cphth moderately developed, not curved; A2 endopod bearing slim seta that accompanies the subapical spines 3
3. P2 exp-2 with inner seta; P4 enp-2 with outer seta . . . . ***B. horstgeorgei*** (George & Gheerardyn, 2015) **comb. nov.**
- P2 exp-2 without inner seta; P4 enp-2 lacking outer seta . . . . ***B. ornatus*** (Krishnaswamy, 1957) **comb. nov.**

Remarks on the geographical distribution of *Bicorniphontodes* gen. nov. Whilst several "ancorabolid" representatives have been reported in the Mediterranean Sea (cf. George *et al.* 2018 for review), only two findings are documented for the Red Sea: *Laophontodes hamatus* found by Gurney (1927) in the Suez Canal, and the here described *Bicorniphontodes clarae* **gen. et sp. nov.**

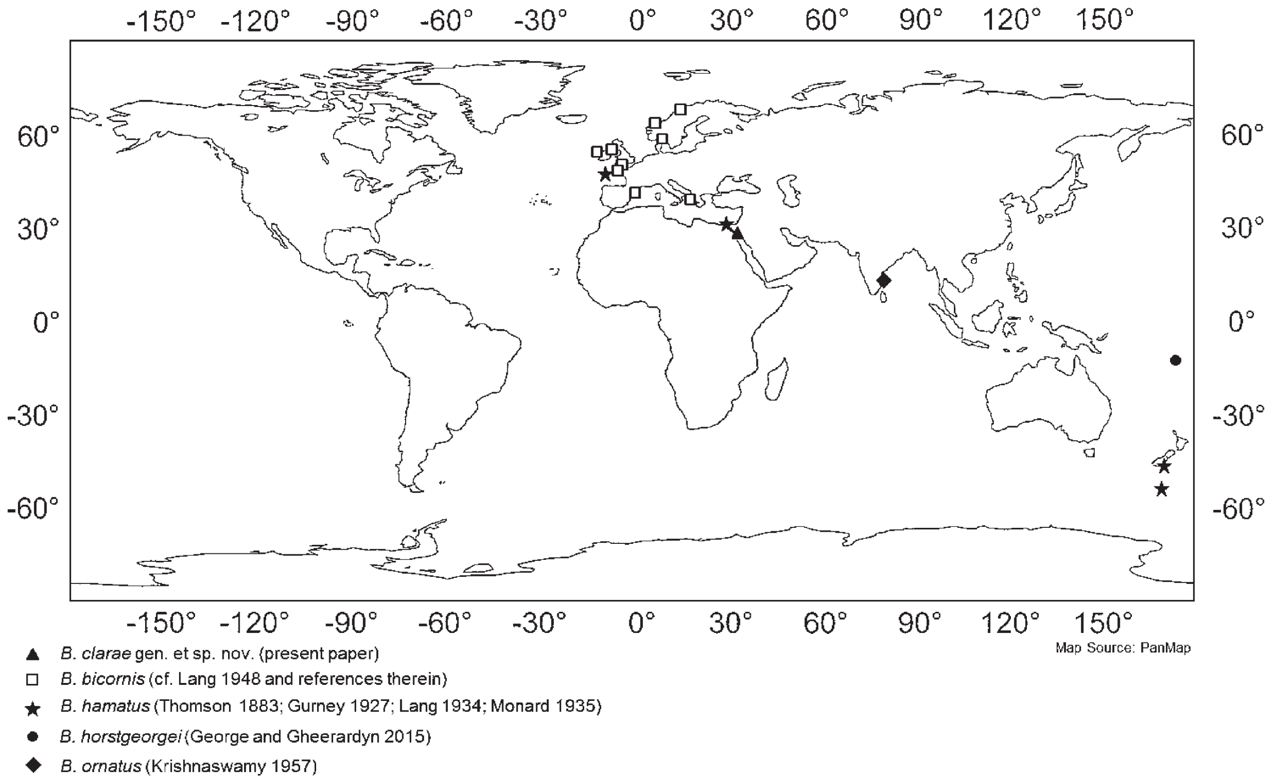

FIGURE 9. Distribution patterns of the five so-far known *Bicorniphontodes* **gen. nov.** species in the world's oceans.

Bicorniphontodes **gen. nov.** seems to be restricted to shallow waters and even to the littoral (Fig. 9). All species have been reported from littoral to sub-littoral locations (e.g. Lang 1948 and references therein; Krishnaswamy 1957; George & Gheerardyn 2015). Of the five so far known species, three were found at single locations (Fig. 9): *B. horstgeorgei* **comb. nov.** at Viti Levu, Fiji Islands (George & Gheerardyn 2015), *B. ornatus* **comb. nov.** in Madras, India (Krishnaswamy 1957), and *B. clarae* **gen. et sp. nov.** at the Napoleon Reef (present contribution). In contrast, *B. bicornis* **comb. nov.** has so far been discovered in several European areas, i.e. in Norwegian, Swedish, Scottish, Irish, and French waters (cf. Lang 1948 and references therein); moreover, that species was found in the Mediterranean Sea, i.e. in Banyuls (France; Monard 1928), and Dodekanes (Greece; Brian 1927). However, the widest distribution is apparently presented just by *B. hamatus* **comb. nov.**, the species exhibiting the poorest description: it ranges from eastern New Zealand (Dunedin Harbour; Thomson 1883) to the eastern Atlantic Ocean (Roscoff, France: Monard 1935), with findings also from the southern Pacific Campbell Island (Lang 1934) and the Suez Canal (Egypt; Gurney 1927). Up to date, no reports from the Americas nor from Easter Asia are documented.

Regarding the distribution at species level (Fig. 9), it seems obvious that the observed distribution patterns may rather reflect a sampling artefact that the true distribution patterns. Thus it is expected that increasing sampling may lead to further findings of *Bicorniphontodes* **gen. nov.**.

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