Research article

A new species of *Breviconia* Conroy-Dalton & Huys, 2000 (Copepoda: Harpacticoida: Ancorabolidae Sars) from the Bering Sea, northern Pacific Ocean (Russia)

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Abstract. The finding of *Breviconia andrei* sp. nov. in the Russian Bering Sea enabled the clear-cut phylogenetic characterization of the former monotypic genus *Breviconia* Conroy-Dalton & Huys, 2000 as a monophylum. Comparison of the new species with *B. australis* (George, 1998) and other members of the subfamily Ancorabolinae Sars, 1909 yielded four autapomorphies that unambiguously support the monophyletic state of *Breviconia*: (1) an elongated and approximately 90°-curved mandibular gnathobase, (2) reduction of the maxillar endopod, (3) maxillar endites carrying 2 instead of 3 setae, and (4) loss of the minute seta on the maxillipedal claw. For *B. andrei* sp. nov., two autapomorphies could be detected, namely, (1) the development of dorsal tubercles on the P5-bearing body somite and (2) the remarkable elongation of the first endopodal segment of the first swimming leg that is twice as long as the whole exopod. Of particular interest is the presence of a 3-segmented endopod in the third swimming leg of the male of *B. andrei* sp. nov. It disproves the current assumption that the Ancorabolinae are characterized by (among others) the derived presence of an only 2-segmented endopod in the male's third swimming leg.

Keywords. Ancorabolinae, Bering Sea, *Breviconia andrei* sp. nov., phylogenetics, taxonomy.

Introduction

The Ancorabolinae Sars, 1909 (Copepoda, Harpacticoida, Ancorabolidae Sars, 1909) includes five genera, namely, *Ancorabolus* Norman, 1903, *Arthropsyllus* Sars, 1909, *Breviconia* Conroy-Dalton & Huys, 2000, *Juxtaramia* Conroy-Dalton & Huys, 2000, and *Uptionyx* Conroy-Dalton & Huys, 2000 (George 2020). The genus *Breviconia* was established by Conroy-Dalton & Huys (2000) to accommodate *Arthropsyllus australis* George, 1998, which was described by George (1998) from the Beagle Channel (Magellan Region, Chile). Furthermore, Conroy-Dalton & Huys (2000) placed *Laophontodes echinata* Brady, 1918, from the high Antarctic into *Breviconia* as a species inquirenda because Brady (1918) provided only a fragmentary, imprecise description and the type material was lost, so neither re-examination nor redescription of that species was possible (cf. Conroy-Dalton & Huys 2000: 373). Consequently, *Breviconia* is characterized this far by the features present in *B. australis*, thus actually resembling a monotypic genus.

George (1998) initially assigned the Magellan species to the genus *Arthropsyllus* due to its diagnostic similarities with *A. serratus* Sars, 1909, such as its general body shape, the lack of strong dorsal and dorsolateral cuticular body processes, and the number of setal elements on the swimming legs. Later, in their detailed phylogenetic analysis of the *Ancorabolus* lineage, Conroy-Dalton & Huys (2000) concluded that the assignment of the Magellan species to *Arthropsyllus* by George (1998) was unsubstantiated. They based their conclusion on an apparently erroneous homologation of the furcal setae by George (1998) as well as on "other anomalies in George's (1998) illustrations" – the maxillar endites equipped with only 2 instead of 3 setae, the mxp without a minute accessory seta on the endopod, and the presence of spinules instead of setular extensions on the posterior margins of the body somites except the penultimate one – and on the wide geographical separation of the respective species (cf. Conroy-Dalton & Huys 2000: 373, 395). Consequently, Conroy-Dalton & Huys (2000) foresaw a clear-cut phylogenetic characterization of *Breviconia*.

In the contribution at hand, we provide a description of a new *Breviconia* species, *B. andrei* sp. nov. It was collected in 2018 at a deapth of 402 m in the Khatyr Depression (Bering Sea, northern Pacific Ocean, Fig. 1). The discovery of *B. andrei* sp. nov. enables not only eliminating the discrepancies uncovered by Conroy-Dalton and Huys (2000) but also characterizing and confirming *Breviconia* as a monophylum. For that purpose, a detailed comparison of the new species, particularly with *Arthropsyllus serratus*, *Uptionyx verenae* Conroy-Dalton & Huys, 2000, and *Breviconia australis* – based on morphological characteristics – was undertaken. The results of that analysis are discussed in detail.

Materials and methods

Study area, sampling and imaging

The material was collected during the 82nd cruise of RV *Akademik M.A. Lavrentev* from 2nd June to 16th July 2018 to the Bering Sea around methane seep communities (Fig. 1). Sampling was performed using the remotely operated underwater vehicle (ROV) "Comanch-18". The sediment samples from the seafloor were collected using cylindrical push corers whose inner diameter was 48 mm. From the cylindrical corers, the upper 5 cm sediment layer was fixed with approximately 5% buffered formalin. The overlying water was filtered through a 40 mm mesh sieve, and the collected material was added to the sample. In the laboratory, the meiofauna samples were washed with tap water, passed through a 32 mm sieve and then centrifuged three times (4000 rpm, 6 min) with colloidal silica (Ludox HS40; Sigma-Aldrich). Meiofaunal animals (metazoan only) were identified and counted to higher taxa under a microscope (Carl Zeiss Stemi 2000) after staining with Rose Bengal. Copepods were picked up from every meiofauna sample and transferred to 96% ethanol.

The habitus was photographed, and body length measurements were made from whole specimens mounted in glycerine. The harpacticoids were dissected in glycerine, their parts were mounted individually in lactophenol, and the slides were sealed with transparent nail varnish. Observations were made with a Leica MZ APO and Olympus CX41. All drawings were made with a drawing tube attached to an Olympus CX41 light microscope.

Morphological study

Identification to the species level was performed with the tabular keys by Wells (2007), and the identifications were checked against the original literature.

Abbreviations used in the text
The morphological terminology follows Huys & Boxshall (1991).
A1   =   antennule
A2   =   antenna
aes   =   aesthetasc
cphth   =   cephalothorax
CR   =   caudal ramus/rami
enp1–3   =   first–third segment of endopod
exp-1–3   =   first–third segment of exopod
GDS   =   genital double somite
md   =   mandible
mx   =   maxilla
mxl   =   maxillula
mxp   =   maxilliped
P1–P6   =   swimming legs 1–6
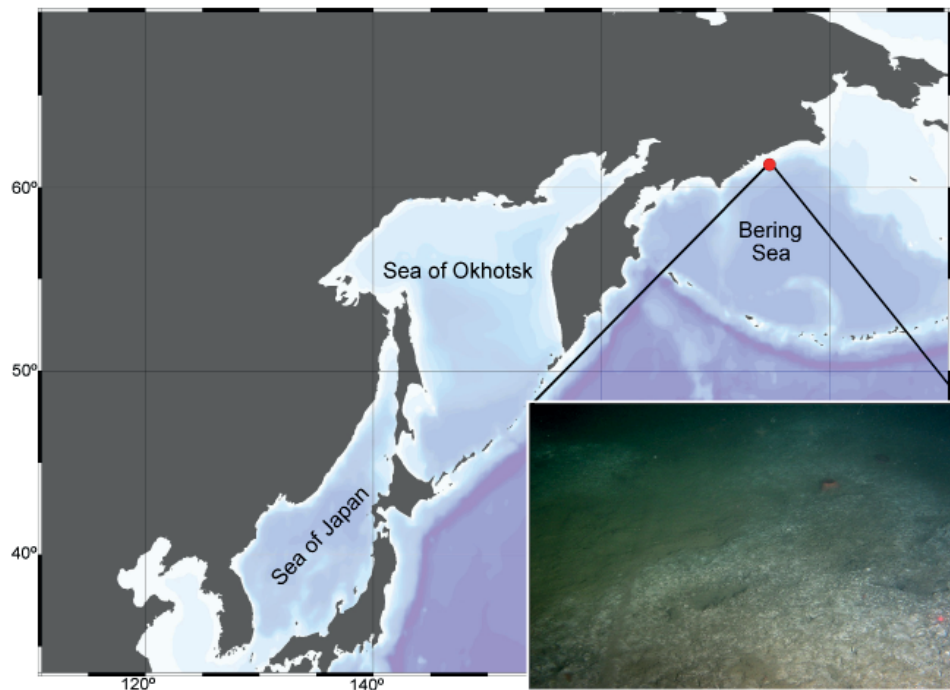
Fig. 1. Map of the Bering Sea (northern Pacific Ocean), showing the type locality at Khatyr Depression (red dot). The photo shows the sediment condition at the type locality. Map source: V. Morduchovich; photography: V. Morduchovich.

Institutional abbreviations

The holotype, paratypes, and other specimens studied are housed in the following institutions:

IORAS   =   P.P. Shirshov Institute of Oceanology, Russian Academy of Science, Moscow, Russian Federation

MIMB   =   A.V. Zhirmunsky National Scientific Centre of Marine Biology Far East Branch, Russian Academy of Science, Vladivostok, Russian Federation

Results

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Phylum Arthropoda von Siebold, 1848

Subphylum Crustacea Brünnich, 1772

Superclass Multicrustacea Regier *et al.*, 2010

Subclass Copepoda Milne-Edwards, 1840

Order Harpacticoida Sars, 1903

Family Ancorabolidae Sars, 1909

Subfamily Ancorabolinae Sars, 1909

Genus *Breviconia* Conroy-Dalton & Huys, 2000

</div>

Generic diagnosis (amended from Conroy-Dalton & Huys 2000)

Ancorabolinae. Body slightly depressed dorsoventrally, tapering posteriorly, with no clear demarcation between prosome and urosome. Cphth slightly broader than long, with moderately developed sensillar groups I–V and with small conical processes. Rostrum small, fused to cphth, basally constricted, with rounded or bifid tips bearing 1 tube pore and 2 sensilla. All body somites except the penultimate somite and the telson with a pair of backwards produced lateral wing-like and spinulose processes and laterodorsally with paired tubercles or small conical processes. P2 and/or P3–P4 and/or P5-bearing somites additionally with dorsolateral and dorsal tubercles or processes. All tubercles/processes bearing a sensillum at their tips. The female's last thoracic and first abdominal somite fused, forming GDS. Anal operculum dorsally with small spinules laterally flanked by a pair of sensilla arising from small knob-like tubercles. A1 of female 3-, of male 7-segmented, subchirocer. Antennular segments smooth or densely covered with minute spinules. Aes on segments 2 and 3 (female) and 4 and 7 (male), respectively. A2 with allobasis, lacking exopods but carrying 2 abexopodal bipinnate setae. Endopod with 2 rows of spinules on the outer margin, and with spinulose frill subapically; apically with 1 short spine and 4 setae, 3 of which geniculate; additionally, with 1 small seta fused to the outermost apical seta. Md slender, with unarmed coxa, gnathobase elongated and curved by nearly 90°; md palp 1-segmented, with 1 (basal), 1 (exopodal) and 3 apical (endopodal) setae. Mxl with 1–2 setae on coxal endite; basis with 3 and 2 setae on proximal and distal endite, respectively; exo- and endopod completely reduced and represented by 2 and 1 setae, respectively. Mx with 2 syncoxal endites, each equipped with 2 apical setae; basis with 4 elements, the largest of which produced a strong claw-like spine; endopod represented by 2 setae. Mxp prehensile, slender; syncoxa unarmed or bearing few spinules subapically, without setae; basis longer than syncoxa, with a longitudinal row of long spinules; endopod drawn out into a long, slender lacking the usual accompanying minute seta. Swimming legs with slender, bow-like intercoxal sclerites and transversely elongated bases. P1 with 2-segmented exo- and endopod; basis carrying 1 inner and 1 outer bipinnate seta; exopod smaller than endopod, exp-1 with 1 outer spine, exp-2 with 2 outer spines and 3 geniculated setae. P2–P4 with 3-segmented exo- and endopods; basis with 1 outer bipinnate seta; exps-1 and -3 without inner setae, exps-3 with 2 outer spines/setae and 2 apical setae. In the female, endopods 2-segmented, with the first segment small and unarmed; enp-2 with 1 inner and 2 apical setae, in P3 and P4 additionally with 1 outer seta. Male P2 endopod like in the female; the P3 endopod is 3-segmented, with the first and third segment being small; enp-1 unarmed, enp-3 with 2 apical setae; enp-2 elongated, with strong curved apophysis on its inner apical edge. Male P4 enp-2 lacking inner seta. P5 of female

with endopod fused to basis, forming a baseoendopod, whose endopodal lobe is elongated and bears 2 inner and 2 apical setae. Exopod distinct, approximately twice as long as the endopodal lobe, with 2 outer spines, 2 apical setae, and 1 densely bipinnated inner seta. Female genital field with ventrally located gonopores in the middle of the somite. P6 small, forming genital operculum, with 2–3 setae. Caudal rami elongated, approximately 3–7 times as long as the broadest width and equipped with 7 setae.

Type species

Breviconia australis (George, 1998); additional species: *B. echinata* (Brady, 1918) (species inquirenda), *B. andrei* sp. nov. (present contribution).

Breviconia andrei sp. nov.
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Figs 2–9

Etymology

This species is named in honour of Professor Andrey Azovsky of Lomonosov Moscow State University, a Russian theoretical ecologist, our colleague, friend, and the husband of the first author.

Type material

Holotype
RUSSIAN FEDERATION • ♀, dissected on 4 slides; the Bering Sea, Khatyr Depression; 61°10'50.5" N, 174°51'3.2" E; depth 402 m; deep mud; 29 Jun 2018; V. Mordukhovich leg.; IORAS-Har229–232.

Allotype
RUSSIAN FEDERATION • ♂, dissected on 4 slides; same collection data as for holotype; IORAS-Har233–236.

Paratypes
RUSSIAN FEDERATION • 1 ♀, dissected on 4 slides; same collection data as for holotype; MIMB 42333–42336 • 1 ♂, dissected on 4 slides; same collection data as for holotype; MIMB 42337–42340 • 2 ♀♀, whole body specimens on 1 slide; same collection data as for holotype; IORAS-Har237 • 2 ♂♂, whole body specimens on 1 slide; same collection data as for holotype; IORAS-Har238.

Other material
RUSSIAN FEDERATION • 30 ♀♀ and 90 ♂♂, alcohol preserved; same collection data as for holotype; IORAS INV0000794 • 14 ♀♀ and 35 ♂♂, alcohol preserved; same collection data as for holotype; MIMB 42341.

Description of the adult female

Body (Fig. 2A–B). The total body length was 832 μm (mean 828 μm, n = 10) for the type specimen illustrated in Fig. 2A, measured from anterior tip of rostrum to posterior margin of the CR. Body slightly dorsoventrally depressed, tapering posteriorly, without clear demarcation between the prosome and urosome. Integument moderately sclerotized. Rostrum (Fig. 3A) small and prominent, having tube pore, laterally with 2 sensilla, inserting from the cuticular projection. Cphth wider than long, laterally with 5 pairs of moderate cuticular processes, each bearing sensillum terminally. Posterior margin with 4 small knob-like sensilla-bearing cuticular processes. Cphth dorsally and dorsolaterally with 4 pairs of sensilla. All body somites except penultimate somite and telson somite with pair of backwards produced lateral wing-like and spinulose processes and dorsolaterally produced paired, sensilla-bearing tubercles. P2–P5-bearing somites additionally with laterodorsal processes and with dorsal, sensilla-bearing tubercles.

Sensillar shape characteristic for the Ancorabolinae, arising from cup-shaped tip of respective process and inserting like ball-and-socket joint (Fig. 2E), as described by George (2020: 479). Anal operculum dorsally with small spinules laterally flanked by pair of sensilla arising from small knob-like bases.

CR (Fig. 2B–D). Approximately 3 times as long as broad, tapering distally, with 1 tube pore laterally (Fig. 2D; arrow) and the following setae: I and II laterally at half-length of ramus, II longer than I. III, IV, V, and VI terminally, VI very small, V being longest. VII arising dorsally, tri-articulated.

GDS (Fig. 2F). The last thoracic and first abdominal somite fused to form genital double somite, original separation indicated by row of small spinules and dorsal cuticular processes, and by position of lateral cuticular processes. Gonopore located ventrally in the middle of the somite. P6 small, forming genital operculum, with 3 setae.

A1 (Fig. 3A–C). 3-segmented segments lacking coverage with tiny spinules. First segment medially on outer side with 2 rows of spinules and 1 bipinnate seta, located half-length on outer margin, with 9 bare setae inserting on distal half. Second segment almost as long as first segment, bearing 6 bare setae and 1 aesthetasc, which is fused with 1 bare seta. Third segment shortest, with 7 bare setae, 1 small aesthetasc, and 3 additional setae. Setal formula: 1-[10], 2-[6+(1+ae)], 3-[7+(3+ae)].

A2 (Fig. 3D). With allobasis, exopod absent. Allobasis almost as long as enp, on outer margin with 2 bipinnate setae; additionally, 4 spinules situated proximally and 4 spinules distally. Endopod with 3 bare setae and row of long spinules on outer margin. Inner margin with 5 rows of short spinules. Apically with 1 short spine, 1 long seta and 3 geniculate setae, the longest basally fused with 1 small bare seta.

Md (Fig. 4C). Coxa unarmed, cutting edge elongate and bent at nearly 90°, with 5 teeth. Basis, endopod and exopod fused to 1-segmented mandibular palp carrying 5 setae and 5 spinules apically.

Mxl (Fig. 4A). Arthrite of praecoxa terminally with 4 bare setae, one of which very strong, and 1 strong bipinnate seta. Subapically on surface with 1 bare and 1 bipinnate seta. Coxa with 1 bare and 1 strong bipinnate seta. Basis, enp and exp fused to 1-segmented palp with 2 rows of spinules. Proximal part of basal endite with 3 bare setae, one of which short and strong. Distal part of basal endite with 2 bare setae. Endopod represented by 1 bipinnate seta, exopod by 2 bare setae.

Mx (Fig. 4B). Syncoxa with row of strong spinules and 2 endites, each with 1 bipinnate and 1 smaller, bare seta. Basis fused with syncoxa, bearing 3 bare setae, one of which fused to basis and transformed into long claw-like element, to which a fourth seta is fused. Endopod reduced, represented by 2 bare setae.

Mxp (Fig. 4D). Prehensile, syncoxa unarmed. Basis with row of long spinules. Endopod transformed into large claw, which is longer than basis, without accompanying minute seta.

P1 (Fig. 5A). With transversely elongated basis bearing 1 inner and 1 outer pinnate seta. Exopod 2-segmented, exp-1 with row of long spinules on outer border and 1 outer spine. Exp-2 with patches of spinules on both borders and 2 outer bipinnate spines, terminally with 2 long bipinnate geniculate setae and 1 very long plumose geniculate seta. Endopod 2-segmented, first segment being twice as long as exopod, with row of long spinules on distal half of inner border. Enp-2 terminally with 2 long geniculate setae, 1 short bare seta subterminally on inner side, and 2 rows of long spinules on outer and inner margins.

P2–P4 (Figs 5B, 6A–B). With transversely elongated bases, 3-segmented exopods and 2-segmented endopods. Exp-1 and exp-2 with 2 rows of long spinules on inner and outer margins, exp-3 with 1 row
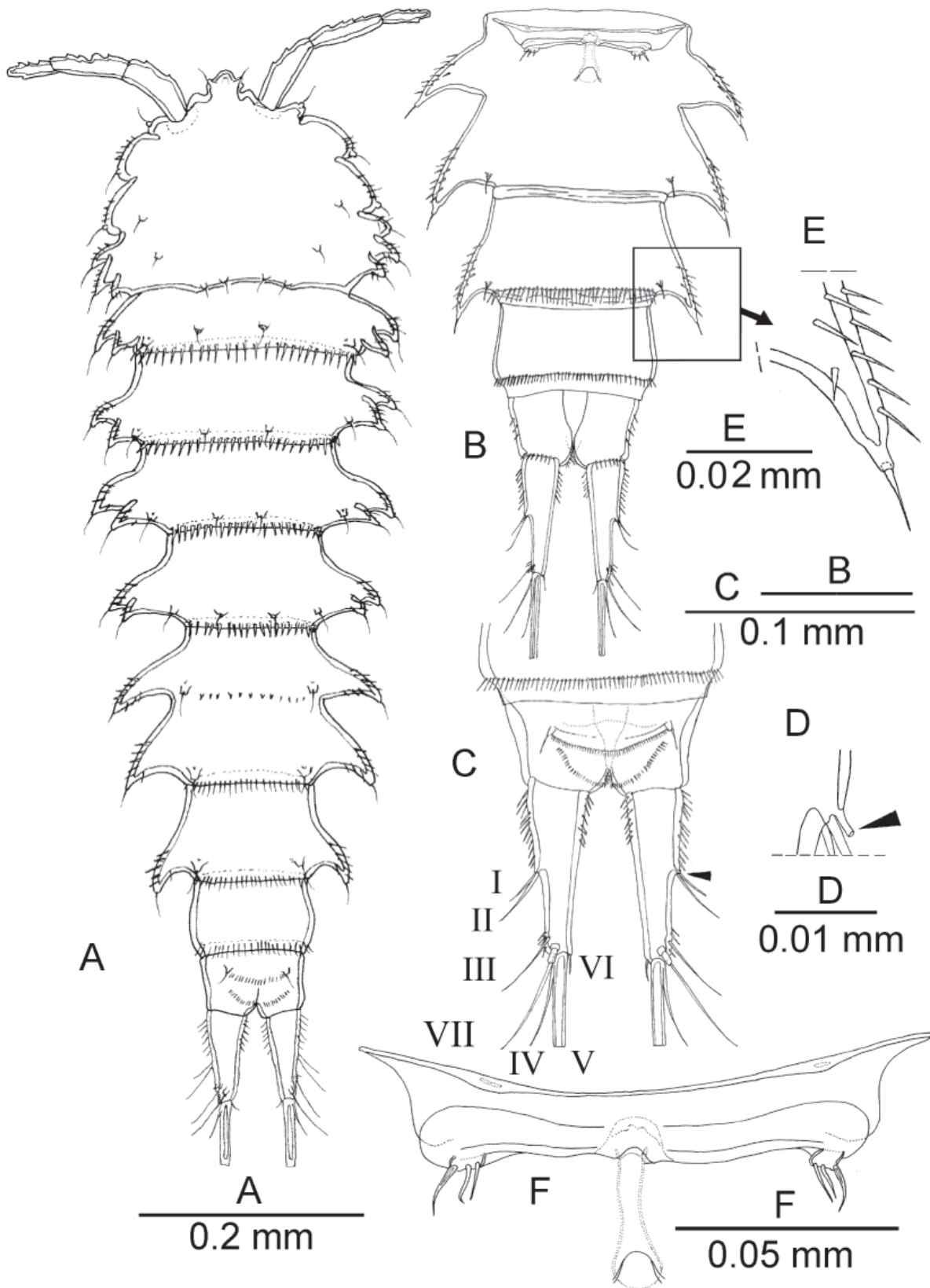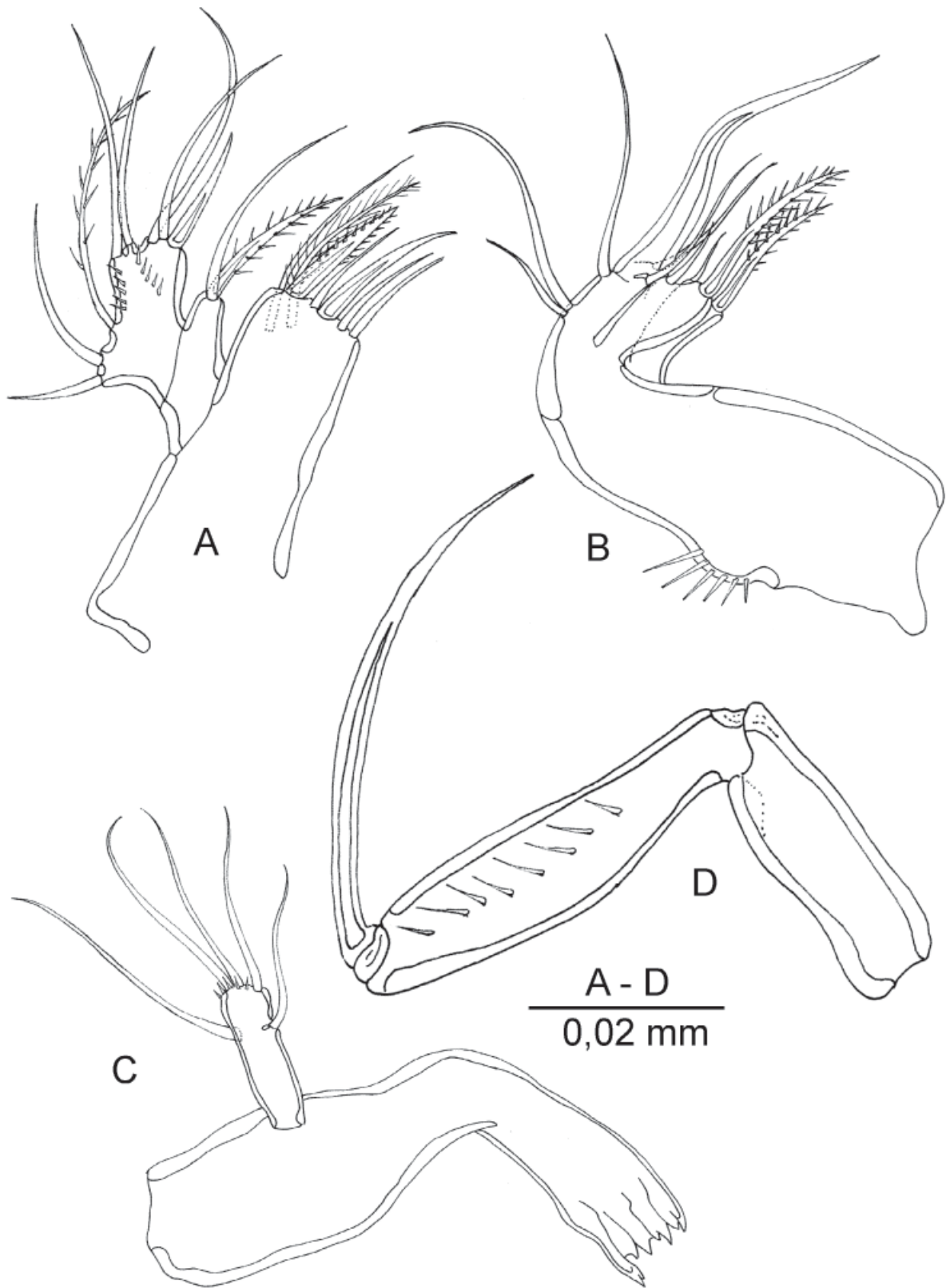
Fig. 2. *Breviconia andrei* sp. nov., ♀. **A**. Habitus, dorsal view. **B**. Abdomen, ventral view. **C**. CR, dorsal view. **D**. Tube on CR. **E**. Cuticular body processes. **F**. Genital field.
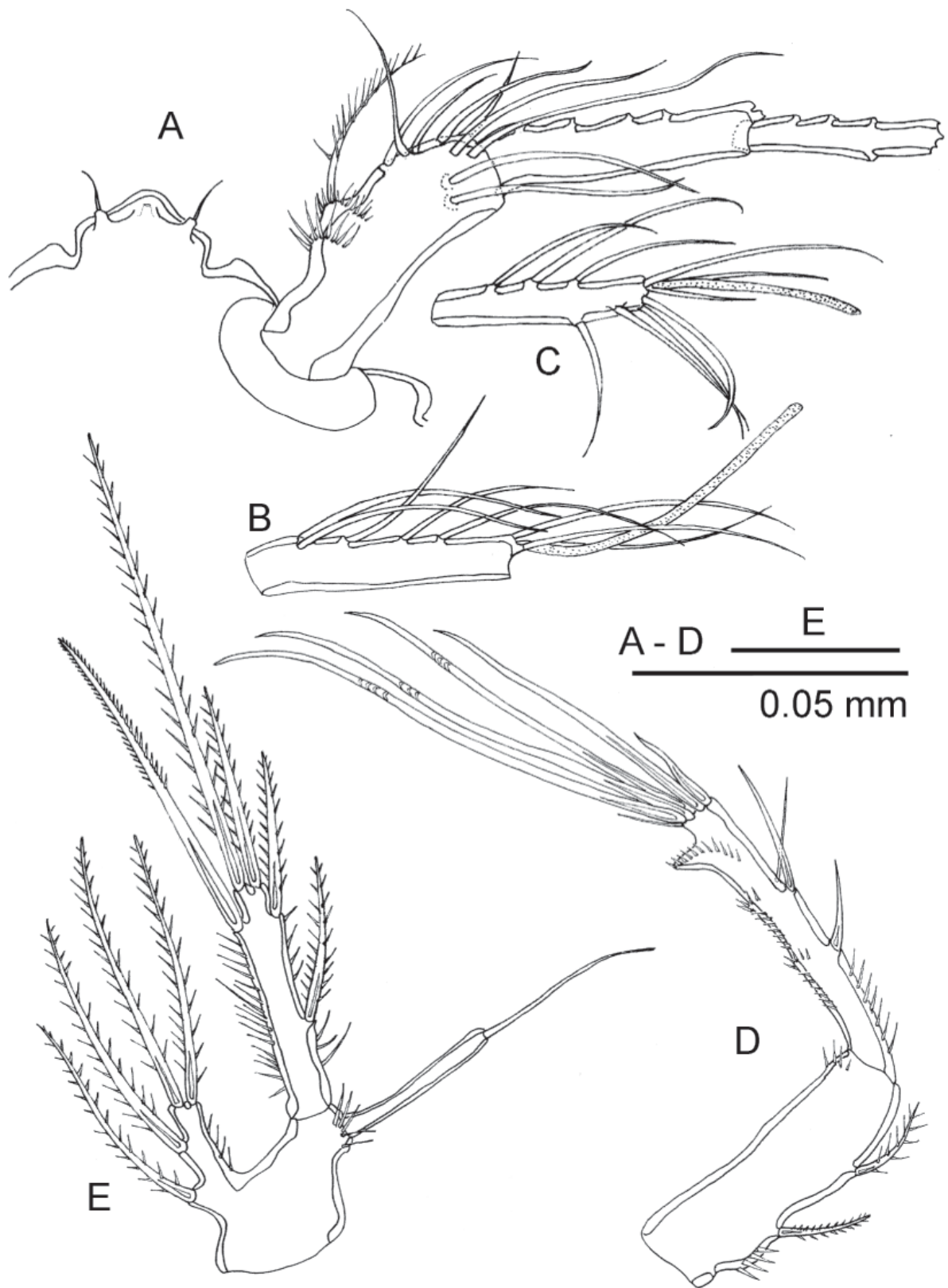
Fig. 3. *Breviconia andrei* sp. nov., ♀. **A**. Rostrum and A1. **B**. 2nd segment of A1. **C**. 3rd segment of A1. **D**. A2. **E**. P5.

Fig. 4. *Breviconia andrei* sp. nov., ♀. **A**. Mxl. **B**. Mx. **C**. Md. **D**. Mxp.

Table 1. Setal formula of the swimming legs P1–P4 of both the female and the male of *Breviconia andrei* sp. nov.

	Exopod	Endopod
P1	1:230	0:120
P2	0:1:022	0:120
P3 female	0:1:022	0:121
P3 male	0:1:022	0:0 (apophysis):2
P4 female	0:1:022	0:121
P4 male	0:1:022	0:021

of spinules on outer border. Exp-2 of P2–P4 with very long inner plumose seta; exp-3 of P2–P4 without inner seta, with 2 outer and 2 terminal setae. Enp-1 of P2–P4 small and unarmed. Enp-2 of P2 with row of long spinules on outer margin and 2 patches of spinules on inner margin. Additionally, with 1 long plumose inner seta on proximal half and 2 very long terminal plumose setae. Enp-2 of P3–P4 with rows of spinules on outer margins; with 1 inner seta on proximal half, 1 subterminal outer seta and 2 terminal setae; all setae biplumose. The setal formula is given in Table 1.

P5 (Fig. 3E). Baseoendopod elongate, with 2 inner and 2 apical setae. Outer basal seta arising from long setophore that reaches ⅔ of length of exopod, with 5 long spinules at base. Exopod 6 times as long as wide, with 2 outer spines, 2 terminal biplumose setae, and 1 densely bipinnated inner seta.

Description of the adult male

Body (Fig. 7A–B). Total body length 505 µm (mean 498 µm, n = 10) for the specimen illustrated in Fig. 7A, measured from anterior tip of rostrum to posterior margin of CR. Body with pattern of processes and sensilla same as for female, except: Cphth terminally with pair of moderate cuticular processes, each bearing sensillum; first 4 thoracic somites with cuticular processes; P6-bearing somite and first abdominal somite (equivalent to the female GDS) with dorsolateral processes being stronger developed than in female; thoracic and abdominal somites except penultimate without rows of spinules on posterior margins.

A1 (Fig. 8A–D). Seven-segmented and subchirocer geniculation between segments 4 and 5; aesthetascs on segments 4 and 7; segment 4 swollen. Segment 1 anteriorly with 2 rows of spinules and with 1 dorsal seta. Segment 2 small, with 6 elements. Segment 3 represented by U-shaped sclerite. Segments around geniculation without modified elements. Setal formula: 1-[9], 2-[6], 3-[2], 4-[10+(2+ae)], 5-[1], 6-[1], 7-[7+(1+ae)].

A2, mouthparts, P1 and P2 as in female.

P3 (Fig. 9A). Exp as in female, enp modified, 3-segmented; enp-2 with row of spinules on outer margin and distal anterior surface produced into smooth recurved apophysis; enp-3 with 2 apical setae.

P4 (Fig. 9B). Exp as in female; enp 2-segmented, sexually dimorphic: broader than in female; enp-2 with row of spinules on outer margin, 2 terminal setae and 1 pinnate subterminal outer seta; inner seta lost.

P5 (Fig. 8E). Exp and benp separate. Outer basal seta arising from long setophore. Endopodal lobe reduced, bearing 2 setae of different lengths, inner seta strong and pinnate. Exp smaller than in female, nearly 3 times longer than broad, with 2 outer and 2 apical setae, and with 1 pinnate inner seta.
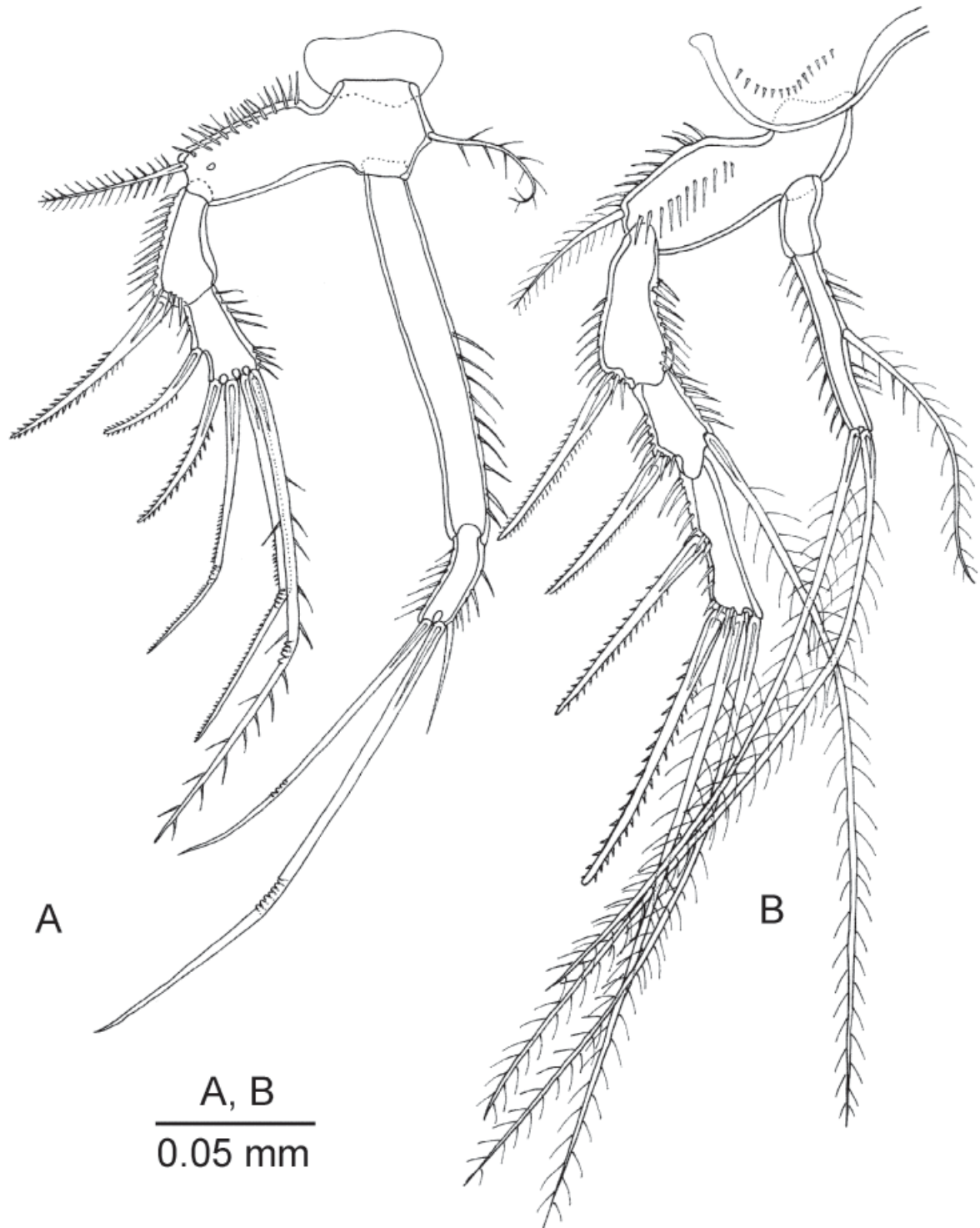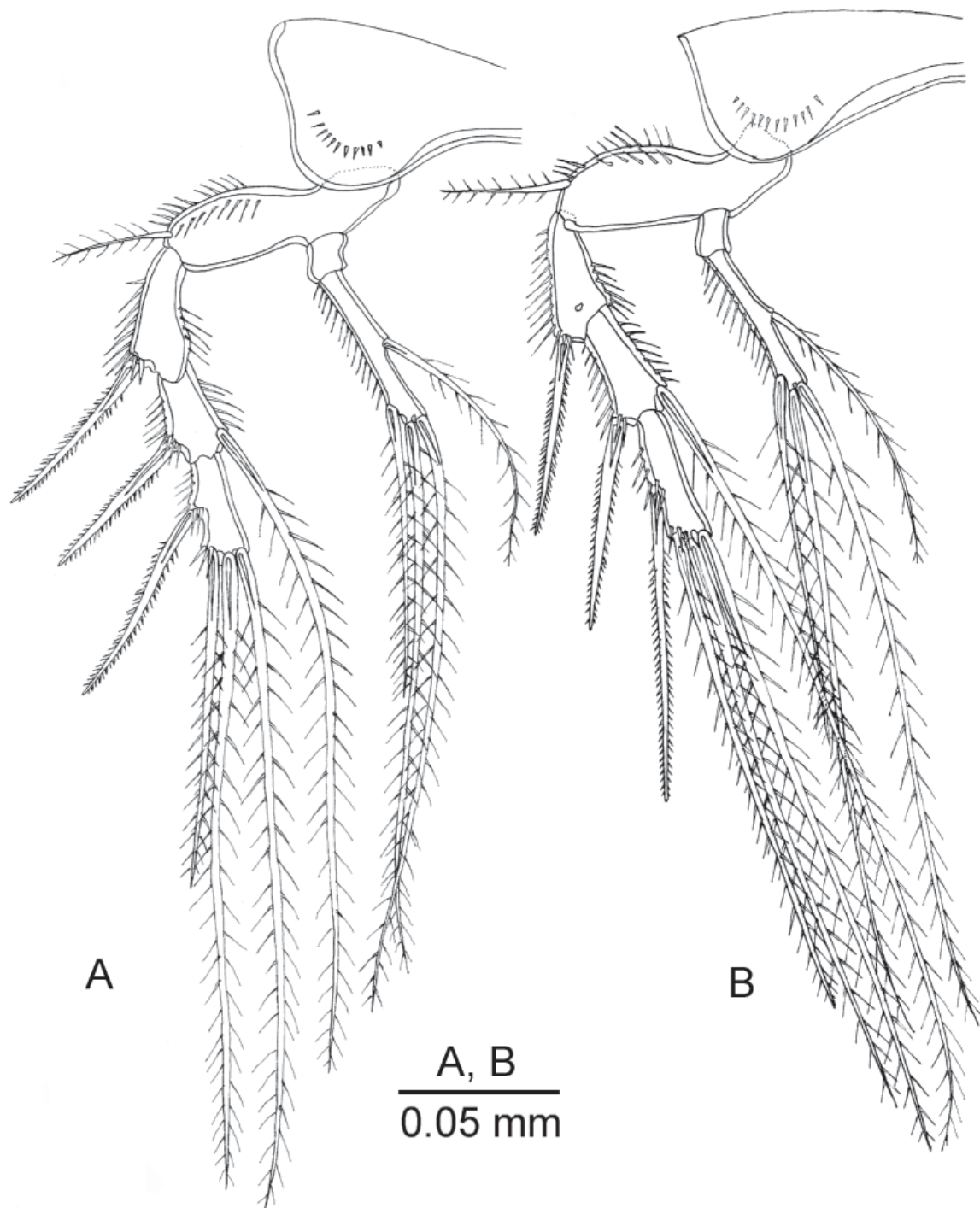
Fig. 5. *Breviconia andrei* sp. nov., ♀. **A**. P1. **B**. P2.

Fig. 6. *Breviconia andrei* sp. nov., ♀. **A**. P3. **B**. P4.
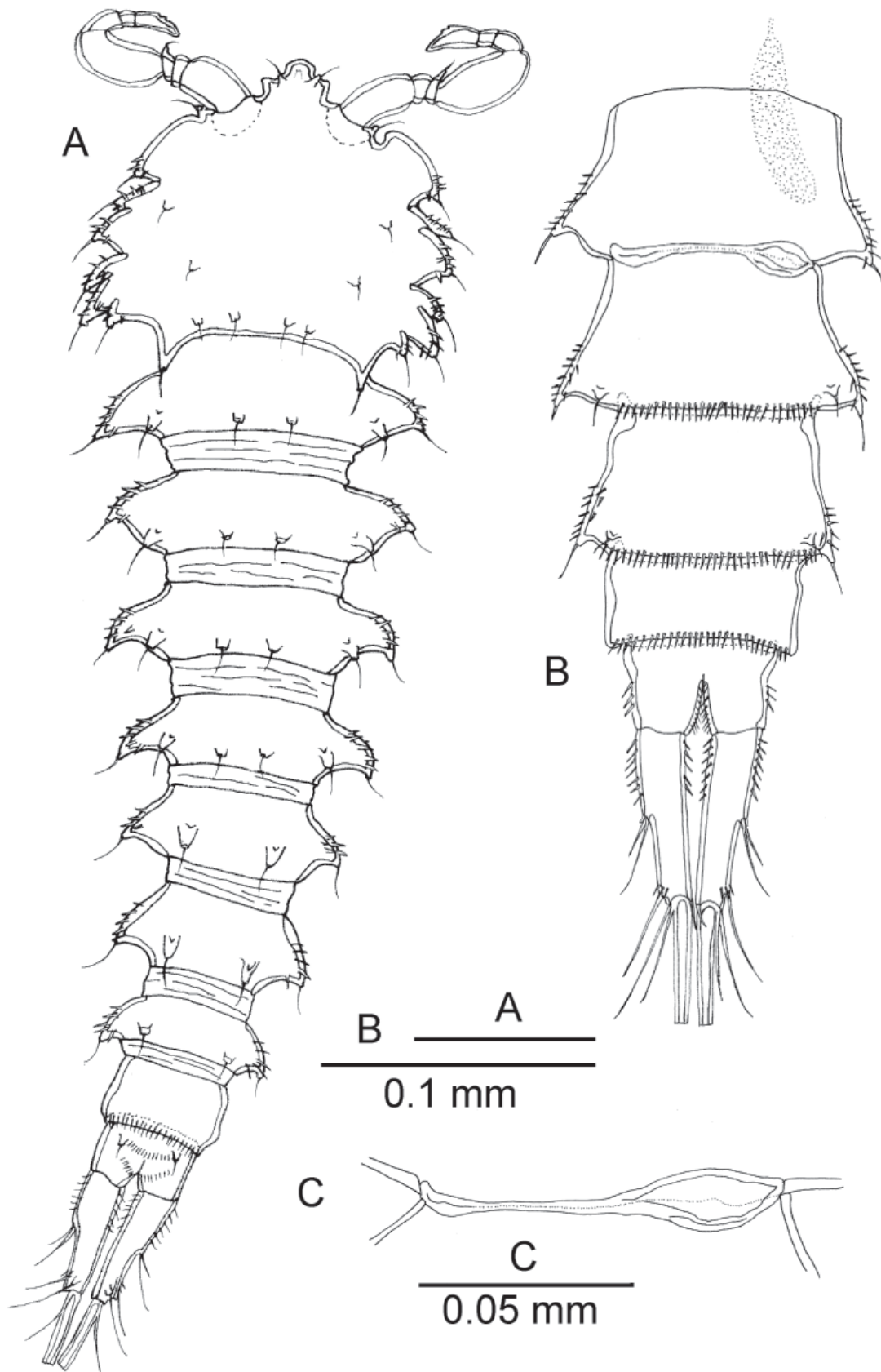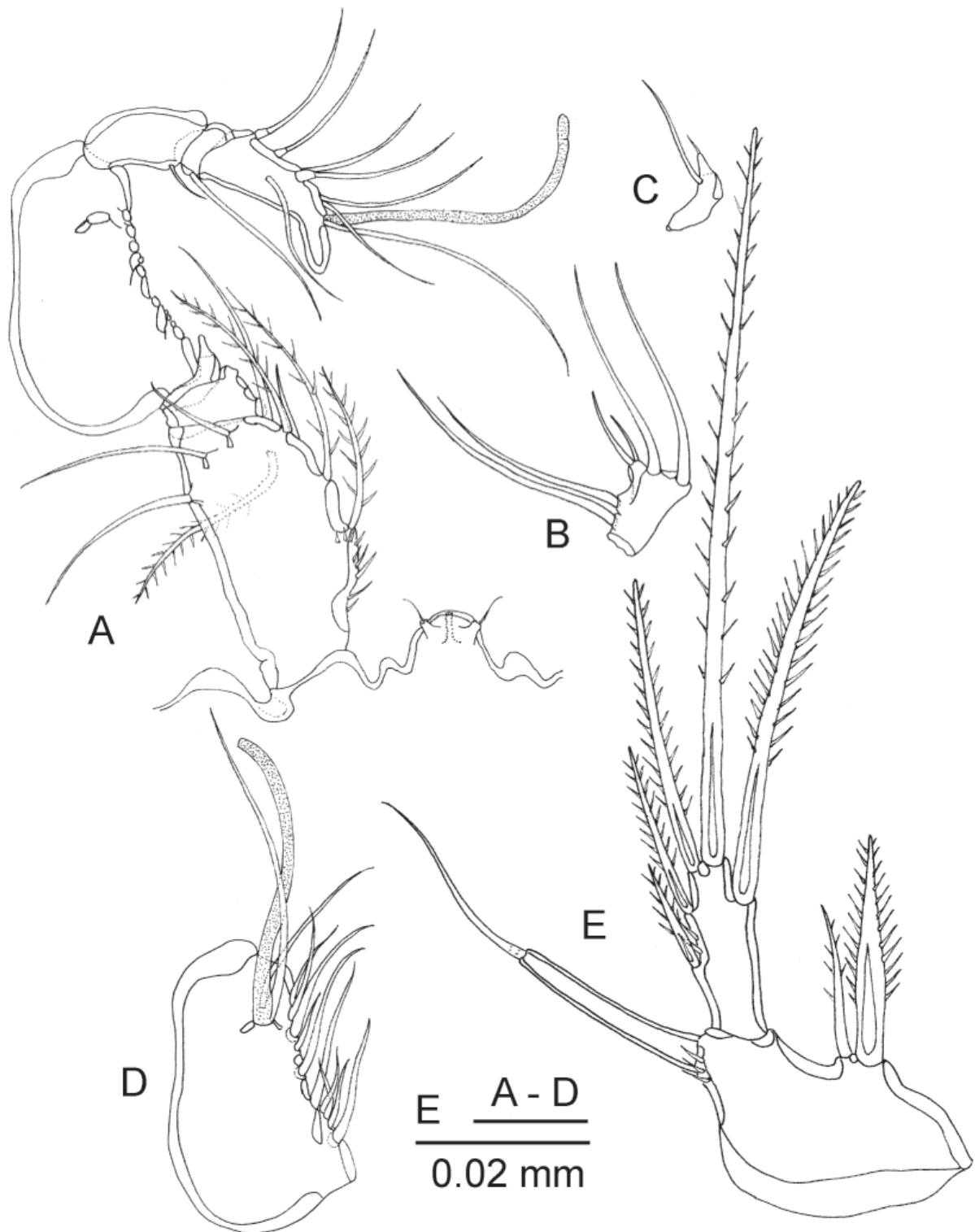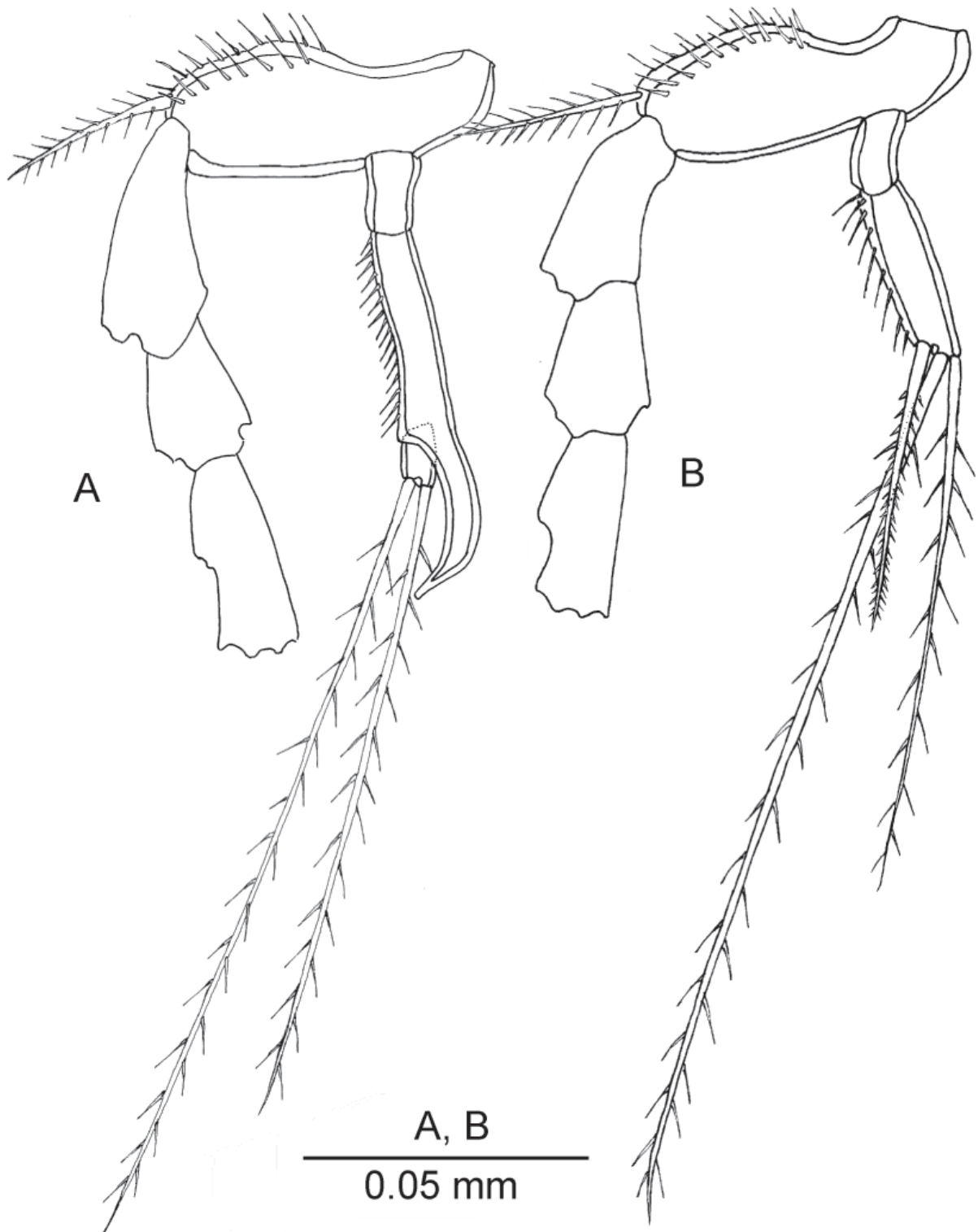
Fig. 7. *Breviconia andrei* sp. nov., ♂. **A**. Habitus, dorsal view. **B**. Abdomen, ventral view. **C**. P6.

Fig. 8. *Breviconia andrei* sp. nov., ♂. **A**. Rostrum and A1. **B**. 2nd segment of A1. **C**. 3rd segment of A1. **D**. 4th segment of A1. **E**. P5.

Fig. 9. *Breviconia andrei* sp. nov., ♂. **A**. P3. **B**. P4.

P6 (Fig. 7C). Asymmetrical, with only 1 functional member, represented by membranous flap, and its counterpart fused to somite.

Discussion

Assignment of *B. andrei* sp. nov. to *Breviconia* and phylogenetic characterization of the genus

As demonstrated by Conroy-Dalton & Huys (2000) and subsequently underlined by George (2020), *Breviconia* can unambiguously be allocated to Ancorabolinae, as it shares all corresponding autapomorphies of the subfamily. Conroy-Dalton & Huys (2000) also presented a phylogenetic evaluation within Ancorabolinae (at that time named "*Ancorabolus* lineage" by these authors). They concluded that *Breviconia* might constitute "…a morphological intermediate between *Uptionyx* and the *Juxtaramia–Ancorabolus* clade" (Conroy-Dalton & Huys 2000: 395). However, a clear-cut phylogenetic characterization of *Breviconia* was not possible because George (1998) examined only a single female of *B. australis*, so sexual dimorphism data were unavailable. Subsequently, Conroy-Dalton & Huys (2000) doubted about the correctness of some of George's (1998) described characters (e.g., the setation of the maxillar endites).

The new species strongly resembles *B. australis* and fits the generic diagnosis given above. Compared with the remaining Ancorabolinae, both species share the following derived features as synapomorphies [plesiomorphic state in square brackets]:

1. the md gnathobase is elongated and curved by approximately 90° [gnathobase straight];
2. the mx without endopod, which is represented by 2 setae [mx endopod 1-segmented, knob-like, with 2 setae];
3. the mx endites with 2 setae/spines [with 3 setae/spines];
4. the mxp lacks the minute seta on its endopodal claw [accompanying minute seta present].

The mandibular gnathobase of *Breviconia* is remarkably elongated and bent by approximately 90° (character 1; cf. George 1998: fig. 3e; present contribution, Fig. 4C); such a derived md is found neither in the remaining Ancorabolinae nor in their sister group Laophontodinae Lang, 1944 and therefore is interpreted here as autapomorphic for *Breviconia*. Likewise, characters 2–4, which constitute exclusive novelties within Ancorabolinae, whose remaining taxa in all three cases retain the ancestral state (cf. Conroy-Dalton & Huys (2000) for detailed character description), are hypothesized here to be synapomorphic for *B. australis* and *B. andrei* sp. nov. and thus, as autapomorphies of *Breviconia*. Consequently, characters 1–4 clearly confirm the assignment of *B. andrei* sp. nov. to *Breviconia*.

Notably, as confirmed for males of *B. andrei* sp. nov. (not confirmed yet for *B. australis*), the male P3 endopod in *Breviconia* still retains 3 segments (Fig. 9A), with the second segment presenting a strong curved apophysis on its distal inner edge. This is relevant because both Conroy-Dalton & Huys (2000) and George (2020) hypothesized a 2-segmented male P3 endopod as autapomorphic for the "*Ancorabolus* lineage", viz. the Ancorabolinae. The finding of males of *B. andrei* sp. nov. indicates, however, that the reduction from 3 to 2 endopodal segments occurred within the Ancorabolinae but not in their supposed common ancestor. As *Uptionyx* is supposed to have branched off before *Breviconia* (Conroy-Dalton & Huys 2000), it is assumed here that the males of that taxon, which are not yet known, may also present a 3-segmented P3 endopod.

Establishment of *Breviconia andrei* sp. nov.

Despite the strong similarity between *B. australis* and *B. andrei* sp. nov. (*B. echinata* not considered here), each species can clearly be characterized by exclusively derived features. *B. australis* presents the following autapomorphies:

5. further pronunciation of the dorsal and dorsolateral processes on the female cphth and the bodysomites [dorsal/dorsolateral processes weakly developed only];
6. development of a bifid rostral tip [rostrum retaining a rounded tip];
7. A1 is densely covered with minute spinules [A1 with a smooth surface];
8. the coxa of the mxl bears 1 apical seta [coxa with 2 apical elements];
9. the outer setophore of the female P5 baseoendopod is remarkably elongated, twice as long as the exopod [setophore moderately elongated, not reaching the exopodal length];
10. female P6 with 2 setae [female P6 retaining 3 setae].

Comparison of both species of *Breviconia* by means of characters 5–11 reveals that *B. andrei* sp. nov. forms the ancestral taxon within the genus. Its dorsal and dorsolateral processes on the cphth and body somites (character 5) are less developed than in *B. australis*; its rostrum retains a rounded tip (Fig. 3A) similar to *Uptionyx* (Conroy-Dalton & Huys 2000: figs 24, 26c), whereas *B. australis* presents a clearly bifid rostrum (George 1998: fig. 2a) (character 6); its A1 lacks the dense coverage with minute spinules found in *B. australis* (George 1998: fig. 3a) (character 7); its maxillular coxa (Fig. 4a) retains the ancestral state of 2 apical setae as found in *Arthropsyllus* and *Uptionyx* (Conroy-Dalton & Huys 2000: figs 12c, 26b) (character 8); the outer setophore of its female P5 baseoendopod does, unlike being elongated, not reach the length of the endopod (Fig. 3E), which in contrast is the case in *B. australis* (George 1998: fig. 6) (character 9); its female P6 (Fig. 2D) retains – as in *Arthropsyllus*, *Uptionyx*, and *Juxtaramia* (cf. Conroy-Dalton & Huys 2000) – 3 minute setae, whilst in *B. australis* only 2 setae are present (George 1998: fig. 2c) (character 10).

In contrast, for *B. andrei* sp. nov., two clear-cut autapomorphies could be detected:

11. P5-bearing body somite with a pair of sensilla-bearing dorsal tubercles [no tubercles developed; the sensilla arise directly from the cuticular surface];
12. P1 enp-1 twice as long as the exopod [P1 enp-1 as long as the exopod].

While both species of *Breviconia* carry paired dorsal tubercles on the P2–P4-bearing somites, *B. australis* lacks such structures on the P5-bearing somites (cf. George 1998: fig. 1), reflecting the ancestral state found in *Uptionyx* (cf. Conroy-Dalton & Huys 2000: fig. 24A). In contrast, *B. andrei* sp. nov. presents such dorsal tubercles (Fig. 2A) (character 11), which are therefore regarded here as autapomorphic for that species.

In *Breviconia andrei* sp. nov., the first endopodal segment of P1 is almost twice as long as the whole exopod (character 12), while in *B. australis,* P1 enp-1 and the exopod they are nearly the same length. The remarkable elongation of the first endopodal segment, which is unique within all Ancorabolinae, constitutes an unambiguous autapomorphy of *B. andrei* sp. nov.

Doubts remain with respect to the caudal rami. They differ in size and shape between *B. andrei* sp. nov. and *B. australis*, but it remains unclear which may form the comparatively derived state. In *B. australis,* the CR is slender, cylindrical in shape, and approximately 6 times as long as their broadest width. That condition is observable in the further derived *Ancorabolus* but also in the rather ancestral *Arthropsyllus* (cf. Conroy-Dalton & Huys 2000). It might therefore be concluded that *B. australis*, *Arthropsyllus*, and *Ancorabolus* retain a CR that had evolved in the stem lineage of Ancorabolinae and thus have to be weighted as the plesiomorphic state. In contrast, the CR in *B. andrei* sp. nov. are only 3 times longer as long as their broadest width, and they taper distally, becoming a triangular shape (Fig. 1A–C). However, this type of CR is also present in the rather ancestral *Uptionyx* (Conroy-Dalton & Huys 2000: figs 24a, 25d); actually, the CR of the latter and *B. andrei* sp. nov. are almost identical. Nevertheless, as in the Ancorabolinae, *Uptionyx* forms the second branch-off after *Arthropsyllus* and before *Breviconia* (cf. Conroy-Dalton & Huys 2000), and thus the development of a triangular CR in the former might

be autapomorphic. As *B. australis* retains the supposed plesiomorphic long and cylindrical CR, the development of shorter and triangular CR in *B. andrei* sp. nov. might – although morphologically almost identical to those in *Uptionyx* – constitute a convergent autapomorphy of *B. andrei* sp. nov. It is admitted, however, that currently, the monophyletic evaluation of the caudal rami remains somewhat speculative and is therefore not considered in the present evaluation.

It is not the purpose of the contribution on hand to provide a detailed re-evaluation of Conroy-Dalton's & Huys' (2000) ancorabolin phylogeny. This demands further morphological insight than available thus far from Conroy-Dalton & Huys' (2000) unquestionably excellent and detailed species descriptions. In particular, the males of *Uptionyx verenae* Conroy-Dalton & Huys, 2000 and of *B. australis* as well as findings of additional species of *Arthropsyllus* and *Uptionyx* may provide helpful and important information, enabling us to unambiguously clear the systematic relationships within the Ancorabolinae.

Biogeographical remarks

The report of *B. andrei* sp. nov. from the Russian Bering Sea points towards a quite wide geographical distribution of *Breviconia* that nonetheless seems to be restricted exclusively to the (sub)polar regions, as *B. australis* was described from the Beagle Channel in the south-Chilean Magellan Region (George 1998). This circumstance contradicts Conroy-Dalton & Huys' (2000) insinuation of a distinct geographical separation constituting a barrier for the existence of close phylogenetic relationships. That these can persist at the species level has recently been confirmed, e.g., for several deep-sea and shallow-water harpacticoid Copepoda, such as the argestid *Mesocletodes abyssicola* (T. & A. Scott, 1901) (cf. Menzel *et al.* 2011), the ancorabolid *Paralaophontodes exopoditus* Mielke, 1981 (cf. George 2017), the cletodids *Stylicletodes longicaudatus* (Brady & Robertson, 1880) and *Tauroceratus steiningeri* (George, 2006) (cf. Mahatma 2009; George 2013), the normanellid *Normanella pallaresae* Lee & Huys, 1999 (cf. Packmor & Riedl 2016), and several species of the Paramesochridae Lang, 1944 (cf. Gheerardyn & Veit-Köhler 2009; Packmor *et al.* 2015). These findings are of increasing interest for phylogenetic and biogeographic research, and they have been the object of a growing number of chorological and biogeographical studies (e.g., Gheerardyn & Veit-Köhler 2009; Koller & George 2011; Menzel *et al.* 2011; George 2013, 2017; Pointner *et al.* 2013, George *et al.* 2014, 2018; Packmor *et al.* 2015; Packmor & Riedl 2016; Richter & George 2019; Azovsky *et al.* 2020). Some of the above-named species demonstrate disjunct distribution patterns, although *Breviconia* is the only known harpacticoid genus with a widely separated (bi-subpolar) distribution. For many other taxa, however, enhanced sampling enabled us to expand their known distribution patterns, revealing that a former apparent disjunct distribution became increasingly continuous, thereby leading to a diminution of the formerly supposed large geographical separation. Thus, it might not be too speculative to assume that *Breviconia* may also be much more continuously distributed than is currently known.

Acknowledgements

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