Article

Description of *Bradyetes paramatthei* sp. nov. (Copepoda: Calanoida), a new aetideid species from the deep Pacific Ocean with notes on the genus *Bradyetes*

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Abstract

A new and rare aetideid species of the benthopelagic genus *Bradyetes* Farran, 1905 is described from female specimens collected near the seafloor from the abyss of the Pacific, Atlantic and Southern Oceans between 2000 and 2014. The new species, *Bradyetes paramatthei* **sp. nov.,** is described from the Kurile-Kamchatka Trench (Pacific Ocean) and is additionally reported from the Angola and Guinea basins and from the Meteor Seamount of the Atlantic Ocean. *Bradyetes paramatthei* **sp. nov.** is related to the species *B. matthei* Johannessen, 1976, but differs in the shape of the prosome posterior corners, which are oval-rounded, and in the proximal segment of the antennal exopod, which is supplied with one seta. These two species are shown to constitute a separate species group within the genus *Bradyetes*. The other species group contains the remaining congeners including *Bradyetes inermis* Farran, 1905, for which morphological variability is discussed. Specimens of this species show diverse morphology and comprise 3 morphotypes distinguished by the P1, with a developed or absent lateral lobe , the P1 basal medial seta, which is either nude or supplied with setules, and by the different number of setae of the maxillule praecoxal arthrite.

Key words: Clausocalanoidea, *Bradyetes*, taxonomy, benthopelagic, biogeography

Introduction

Studies on the biodiversity of the deep-sea, near-bottom habitats have intensified in recent decades leading to the discovery of many new calanoid taxa (e.g., Schulz 2005; Markhaseva *et al.* 2008; Bradford-Grieve *et al.* 2014; Renz & Markhaseva 2015; Renz *et al.* 2018, etc.). Nevertheless, despite these research efforts the composition of the demersal calanoid fauna is still rather poorly known and each expedition that sampled in the vicinity of the sea bed shed new light on the taxonomic diversity of this biotope. Studies of the benthopelagic samples recently collected from the abyss of the World Ocean have demonstrated that the Aetideidae is one of the key families of the near-bottom calanoid community. Quite a few new and rare benthopelagic aetideid species were recently described or redescribed (e.g., Schulz & Markhaseva 2000; Schulz 2002; Bradford-Grieve 2003; Othsuka *et al.* 2005; Markhaseva & Schulz 2006, 2008; Markhaseva *et al.* 2017a, b).

The aim of the present study was to describe a new aetideid species that belongs to the rare benthopelagic genus *Bradyetes* (*B. paramatthei* **sp. nov.)** and to revise the taxonomic status of another species of *Bradyetes, B. inermis* Farran, 1905. These two representatives of *Bradyetes* were found in abyssal samples collected during expeditions carried out between 2000 and 2014. Both species were present in the samples from the Kurile-Kamchatka Trench and were also recorded from the Atlantic Ocean. *Bradyetes* cf. *inermis* was also registered from the South Sandwich Trench of the Southern Ocean (Markhaseva & Schulz (2006) and Table 1). *Bradyetes inermis* warrants a taxonomic revision, because this species was found to be morphologically heterogeneous, containing at least 3

morphotypes in the studied samples. In the present study, this apparent species complex is denoted *B.* cf. *inermis* following Markhaseva & Schulz (2006). The genus *Bradyetes* currently includes 5 species: *Bradyetes curvicornis* Markhaseva & Schulz, 2006, *B. inermis*, *B. matthei*, *B. pacificus* Ohtsuka, Boxshall & Shimomura, 2005, *B. weddellanus* Markhaseva & Schulz, 2006, and the new species described herein. Morphological comparison and the phylogenetic analyses were conducted to evaluate relationships among the known species of *Bradyetes*.

TABLE 1. The list of recorded specimens of *Bradyetes* cf. *inermis*

Reference and expedition	Abbreviation of information source, or expedition	Station	Date	Locality	Depth (m)	Number of specimens, body length (mm), morphotype number
Farran (1905)	F	-	24.08.1901	53°58'N 12°28'W	358	1 female, 2.57, morphotype ?
Grice (1972)	G	281-282	09.07.1968 10.07.1968	39°46.45'N 70°34.25'W 39°49.25'N 70°34.55'W	1465–1500 992-1000	5 females, 3.00-3.20; 2 males, 2.44, 2.52, morphotype 1
DIVA–3, ME 79–1	D3	Sta. 554	22.07.2009	26°34.70'S 35°12.79'W Brazil Basin	4485	1 female, 2.60, morphotype 1
	D3	Sta. 636	18.08.2009	29°19.24'N 28°37.94'W Meteor Seamount	4338	1 female, 3.00, morphotype 1
ICE AGE, ME 85–3	IA	Sta. 1054	07.09.2011	61°36.19'N, 31°22.60'W Irminger Basin	2537	1 female, 2.50, morphotype 2
DIVA–1, ME 48–1	D1	Sta. 348	27.07. 2000	16°16.98'S 05°27.27'E Angola Basin	5390	2 females, 2.80, 2.90, morphotype 3
DIVA–2, ME 63–2	D2	Sta. 40	04.03.2005	28°03.07'S 07°19.81'E Cape Basin	5062	4 females, 2.50, 2.60, 2.65, 2.65, morphotype 3
ANDEEP–2, ANT XIX-4	A2	Sta. 140	22.03.2002	58°15.98'S 24°53.73' W South Sandwich Trench	2970	2 females, 2.50, 2.65, morphotype 3
ANDEEP–3, ANT XXII-3	A3	Sta. 016	26.01.2005	41°07.02'S 09°55.94'E Cape Basin	4720	1 female, 2.95, morphotype 3
KuramBio, SO 223	KB	Sta. 6–12	15.08.2012	42°28.49'N 153°59.54'E	5304	1 female, 2.90, morphotype 3
		Sta. 7–10	17.08.2012	43°01.82'N 152°58.55'E	5223	6 females, 2.75–2.95, morphotype 3
		Sta. 8–12	21.08.2012	42°14.38'N 151°43.12'E	5127	3 females, 2.50-2.80, morphotype 3
Vema-Transit, cruise SO 237	VT	Sta. 2–7	20.12.2014	10°42.89'N 25°03.21'W E Mid Atlantic Ridge	5507	1 female, 2.90, morphotype 3

Material and methods

Collection and descriptions. Females of *B. paramatthei* **sp. nov.** (12 specimens) and *Bradyetes* cf. *inermis* (23 specimens) were sorted from abyssal near-bottom collections of the World Ocean (Table 1). Collections were obtained between 2002 and 2014 during expeditions ANDEEP 2–3 (ANTarctic benthic DEEP-sea biodiversity), DIVA 1–3 (Latitudinal Gradients of Deep-Sea Biodiversity in the Atlantic Ocean), ICE AGE 1 (Icelandic marine Animals: Genetics and Ecology), Vema-TRANSIT and KuramBIO 1 (Kurile-Kamchatka Biodiversity Study), which incorporated a deep benthopelagic sampling programme using an epibenthic sledge (Brenke 2005).

The material was fixed in either 96% pure ethanol or 4% buffered formalin and later stained by adding a solution of chlorazol black E dissolved in 70% ethanol/30% water. Oral parts and legs were dissected in glycerine and figures were prepared using a *camera lucida*.

The following abbreviations are used in the descriptions: Pd1–5, pedigerous somites 1–5; Gns, genital double somite; A1, antennule, A2, antenna, Mdp, mandibular palp; Mx1, maxillule, Mx2, maxilla; Mxp, maxilliped; Exp, exopod, Exp 1–3, exopod segments 1–3; Enp, endopod; Enp 1–3, endopod segments 1–3; Epi, epipodite; P1–P5, legs 1–5. Articulating segments of the antennules are designated by Arabic numerals, ancestral segments by Roman numerals. One seta and 1 aesthetasc on a segment of the antennule are designated as 1s + 1ae. The number of antennule segments follows Huys & Bosxhall (1991). The antennal exopod setation formula is given according to Markhaseva & Ferrari (2006) and Markhaseva *et al.* (2014). Maxilla segments are labeled after Ferrari & Ivanenko (2008) as: praecoxal endite; coxal endite; basal endites; enditic-like lobe of proximal endopodal segment. The syncoxa of the maxilliped is presumed to have 3 praecoxal endites and 1 coxal endite after Ferrari & Markhaseva (2000 a, b) and Ferrari & Ivanenko (2001).

The expeditions are abbreviated as: D1–D3 for DIVA 1–3; A2–3 for ANDEEP 2–3; IA for ICE AGE 1; VT for Vema-Transit; and KB for the KuramBIO 1 expedition.

The type material and additional specimens are deposited in the Zoological Museum Hamburg (ZMH) and Senckenberg Museum Frankfurt (SMF), Germany and the Zoological Institute, Russian Academy of Sciences, St. Petersburg (ZIN).

Outgroup taxa. The outgroup taxa were chosen in the context of the current phylogenetic hypotheses concerning the order Calanoida (e.g., Bradford-Grieve & Boxshall, 2014: fig. 12). *Monacilla typica* Sars, 1920 and *Spinocalanus usitatus* Park, 1970 (synonym *S. pteronus* Park, 1970), members of the closely related superfamily Spinocalanoidea (fam. Spinocalanidae), were chosen as monophyletic outgroup. *Pseudochirella obesa* Sars, 1920, which belongs to the same family as *Bradyetes* (fam. Aetideidae, Clausocalanoidea), was used for comparative reasons as an additional ingroup taxon. *Pseudochirella hirsuta* (Wolfenden 1905) was also examined for information on the most primitive setation of the aetideid antennal exopod.

The character set. The character (chars) list was assembled (Table 2) based on the emended diagnostic characters presented by Grice (1972), Markhaseva (1996), Othsuka *et al*. (2005), Markhaseva & Schulz (2006), and Von Vaupel Klein & Rijerkerk (1996, 1997) and on defensible hypotheses of primary homology. We assume that evolutionary processes in copepods proceed towards a reduction in the segmentation, usually by failure of arthrodial membranes to form, and reduction in the armature of the appendages (Dogiel 1954; Boxshall, Ferrari & Tiemann 1984). Our failure to arrive at hypotheses of primary homologies for some mouthpart characters / states is evaluated in the section below.

Posterior metasome (chars 1, 2). The posterior corners of the metasome of aetideids may be rounded or drawn out into a triangular point (Fig. 1D–G). In some cases the drawn out corners may be bifurcate distally at the top as they are in *Bradyetes pacificus* (Fig. 1E).

Rostrum (char. 3). The rostrum of aetideids never has rostral filaments although the frontal margin may be drawn out into bifurcate points, one point or take the form of a blunt plate (Figs 1A–C).

Genital double-somite (chars 4, 5). The genital double-somite may be a globular shape or be more elongate and barrel-like (Figs. 1D–E). The spermathecae, situated dorsal to the genital atrium, in lateral view, are connected to a narrow duct that opens into the genital atrium. The spermathecae may be large, round to oval round (Fig. 1G) or narrow, being not much wider than the duct leading to the genital atrium (Fig. 1F).

Antennule (chars 6, 7). The possession of three setae is the plesiomorphic state of setation of ancestral segment I. During the development of *Aetideopsis armata* (Boeck, 1872), by copepodid stage II there are three setae which are retained in the adult female (Matthews 1964). Most *Bradyetes* species have lost 2 of these setae, but at least *B. paramatthei* has retained all 3 ancestral setae (see Table 3).

TABLE 2. Characters and character states used in the morphological cladistics analysis

1. Prosome posterior corners (Pd5): **(0)** rounded; **(1)** drawn out into a triangular point.
2. Prosome posterior corners (Pd5) in dorsal view: **(0)** bifurcate; **(1)** not bifurcate.
3. Rostrum : **(0)** drawn out into bifurcate points; **(1)** drawn into one point; **(2)** in form of blunt plate; **(3)** absent.
4. Genital somite of a globular shape: **(0)** yes; **(1)** no.
5. Spermathecae shape: **(0)** narrow, not much wider than the duct leading to the genital atrium ; **(1)** large, round to oval round.
6. A1 ancestral I segment with: **(0)** 2 or 3 setae; **(1)** 1 seta.
7. A1 ancestral XII segment with: **(0)** 2 setae; **(1)** 1 seta.
8. A2 Exp proximal fusions: **(0)** Exp1-2 fused; **(1)** Exp1-2 separate.
9. A2 seta on Exp penultimate segment: **(0)** long; **(1)** vestigial, or absent.
10. Mdp basis with: **(0)** 4 setae; **(1)** 3 setae; **(2)** 2 setae; **(3)** 1 seta.
11. Mdp Enp1 with: **(0)** 3 or 4 setae; **(1)** 2 setae; **(2)** 1 seta; **(3)** 0 setae.
12. Mdp Enp2 terminal setae number: **(0)** 9; **(1)** 5; **(2)** 4.
13. Mx1 praecoxal arthrite posterior setation: **(0)** both 3rd and 4th setae present; **(1)** 3rd or 4th seta present; **(2)** both setae absent.
14. Mx1 praecoxal artrite with 2 anterior setae: **(0)** yes; **(1)** no.
15. Mx1 coxal endite with: **(0)** 6 or 5 setae; **(1)** 4 setae.
16. Mx1 proximal basal endite with: **(0)** 4 setae; **(1)** 3 setae.
17. Mx1 distal basal with: **(0)** 5 setae; **(1)** 4 setae.
18. Mx1 outer coxal endite with 1 seta: **(0)** present; **(1)** absent.
19. Mx1 Enp setation: **(0)** 15-16 setae; **(1)** less than 15 setae.
20. Mx1 Exp with: **(0)** 11 setae; **(1)** 10 setae.
21. Mx1 praecoxal arthrite 2nd terminal seta: **(0)** well developed, spine-like; **(1)** rudimentary; **(2)** absent.
22. Mx2 Enp 1 setation: **(0)** 2 setae; **(1)** 1 seta.
23. Mx2 outer seta present: **(0)** yes; **(1)** no.
24. Maxilliped coxa with: **(0)** 4 setae; **(1)** 3 setae.
25. Mxp coxa additionally to setae supplied with: **(0)** conical tubercle; **(1)** aesthetasc-like appendage.
26. Mxp coxal aesthetasc-like appendage 6 times shorter relative to the longest distal seta: **(0)** yes; **(1)** no.
27. Mxp coxal aesthetasc-like appendage as long as, or 1.5 longer relative to the longest distal seta: **(0)** yes; **(1)** no .
28. Mxp coxal aesthetask-like appendage 2 times longer relative to the longest distal seta: **(0)** yes; **(1)** no .
29. Mxp coxal aesthetask-like appendage 3 times longer relative to the longest distal seta: **(0)** yes; **(1)** no .
30. P1 Exp lateral setae number: **(0)** 4 setae; **(1)** 3 setae.
31. P1 Exp 2 lateral spine length: **(0)** not reaching the base of lateral spine Exp 3; **(1)** reaching or exceeding base of lateral spine Exp3.
32. P1 lateral lobe present, moderately, or well developed: **(0)** yes; **(1)** no.
33. P2-P4 Exp3 with: **(0)** 5 setae; **(1)** 4 setae.
34. P2 Enp 2 and usually P3-P4 Enp 3 posterior surface supplied with spinules: **(0)** yes; **(1)** no.
35. P4 coxa with row of spines: **(0)** no; **(1)** yes .

Antenna (chars 8, 9). The antenna morphology is interpreted according to Markhaseva & Ferrari (2006) and Markhaseva *et al.* (2014). In Aetideidae, the antenna exopod is typically 10-segmented and primitively, each segment other than the terminal segment is supplied with 1 seta (*B. weddellanus*). Some proximal segments are usually fused. Interpretation of proximal segment fusions is not in question when each of the fused segments retains its seta, which marks the segment (Fig. 1H–I). However, when seta(e) have been lost, it is difficult to postulate whether segments I-II were fused and 1 seta lost, or whether segments II-IV were fused and 1 seta lost, this state is scored "unknown" (Fig. 6A–C). Another modification found in *Bradyetes* is the state of the seta on ancestral segment IX of the exopod (penultimate segment). In some species, this seta is long and well-developed or it may be vestigial or absent (char. 9) (Fig. 1H–I, 6A).

Mandible palp (chars. 10–12). The mandible palp plesiomorphically has 4 setae on the basis and endopod segment 1, and 9 long terminal and 2 short posterior setae on endopod segment 2 (Fig. 1J) (see Park 1970 for spinocalanids). Aetideids primitively share the same setation on endopod segment 2 and have a primitive maximum of 3

setae on the basis and endopod segment 1 (Markhaseva 1996). Bradford-Grieve & Boxshall (2019) found it difficult to determine individual setal homologies for these segments and proposed to trace their losses by considering their placement. In aetideids and spinocalanids it is especially difficult to analyse the placement of setae on the basis, because there is no clear link to a specific part of the segment. The set of 4 setae in spinocalanids may be located along the basis in its proximal and middle parts (*S. usitatus*), all setae can be concentrated in the middle (*S. longispinus* Brodsky, 1950), or may extend onto its distal part (*S. elongatus* Brodsky, 1950) (Park 1970; Brodsky *et al.* 1983). When some seta(e) are lost it is difficult to determine which one was lost and it is especially difficult in *Bradyetes* species, some of which have lost a large proportion of the ancestral setae from the basis and endopod segment 1, with only 1 or 2 setae retained (Table 3) at different locations (Fig. 1J, 6D, Fig. 1J, Markhaseva & Schulz 2006; Fig. 2C, Ohtsuka *et al.* 2005; Fig. 6, Grice 1972). Similar difficulties arise in the determination of individual homologies of 1 or 2 setae retained on endopod segment 1 in *Bradyetes* species. *B. paramatthei* and *B. matthei* retain the primitive presence of 9 terminal setae on endopod segment 2, typical for 23 aetideid genera, while other *Bradyetes* species are supplied by 4, or 5 terminal setae (*B. curvicornis*) and share this state with the aetideid genera *Crassantenna* Cole *et al.*, 1972, *Lutamator* Bradford, 1969, *Prolutamator* Markhaseva & Schulz, 2008, *Mesocomantenna* Alvarez, 1986, *Paracomantenna* Campaner, 1978 (part.), and *Comantenna* Wilson, 1924. The group of these aetideid taxa with only 4–5 terminal setae retained may suggest to display paedomorphosis, when the remaining setae fail to develop in the adult individuals. Their mandible segment 2 setation corresponds to that of CI–CII stages of *Jaschnovia tolli* (Linko, 1913) and *Bradyidius similis* (Sars, 1902), while the adults of *J. tolli* and *B. similis* possess the complete set of 9 terminal setae at mandible endopod segment 2 as is typical of the most aetideid genera (Markhaseva 1980, Shih *et al.* 1981). Therefore, we assume that when smaller number of setae is found in the respective genera they are homologous so that when setae have failed to develop it is the same setae in each species.

Maxillule (chars. 13–21). Plesiomorphically, the maxillule praecoxal arthrite is supplied with 9 terminal spines, 2 anterior and 4 posterior setae (Schulz 1989 and Fig. 2A) but only 1 anterior seta is retained in aetideids. Further reductions and losses are observed in *Bradyetes* among the 9 terminal spines (herein numbered from proximal to distal as 1 to 9, Fig. 2A). Proximal spine number 2 can be partially reduced (Fig. 4, morphotype 1) or completely lost (Figs. 3–4 morphotypes 2-3). Homologies were determined for individual posterior setae (herein numbered 1 to 4 from proximal to distal, Fig. 2A) according to their placement in congeners and compared to the outgroup because the development data on aetideids are uncertain. The single posterior seta retained in some *Bradyetes* species is interpreted as being in the position of either seta 3 or 4 (Fig. 2A, Table 3). This interpretation is possible because in the taxa with the complete set of 4 posterior setae present (the outgroup taxa *B. matthei* Johannessen*, 1976, B. paramatthei* **sp. n.** and *B. pacificus* Ohtsuka *et al.*, 2005), the posterior setae in positions 3 and 4 are placed opposite or distal to terminal spine 3 (Fig. 2A) as observed in *B.* cf. *inermis*, *B. curvicornis* and *B. weddellanus*. The setation of the coxal endite, basal endites, outer coxal exite, and exopod have 2 states, so it is assumed that the lesser number of setae represents the loss of the same seta. Bradford-Grieve (2010) suggested for the case of the coxal epipodite that during development setae are added proximally, with the most recently added setae very small and it is assumed that where there are fewer than 9 setae, it is the proximal setae that have failed to develop. The complete set of setae at the maxillule epipodite (9) is observed in some *Bradyetes* species (Table 3), however for the others it is uncertain what setae were lost and this uncertainty concerning the setation of some species necessitated the omission of this character and its state. The endopod is difficult to interpret because all three endopod segments are fused and it is impossible to determine which setae belong to which segment. Here, we assume that the same total number of setae are homologous so that when there are fewer setae it is the same setae that are missing. Thus character 19 has two states: total setae 15-16 versus 14 setae or fewer.

Maxilla (chars. 22–23). Plesiomorphically, the aetideid maxilla endopod has 2, 2, 2 and 3 setae on endopod segments 1–4 (Von Vaupel Klein & Rijerkerk 1997) and this state is shared with the spinocalanid outgroup taxa. *Bradyetes paramatthei* **sp. nov.** retains this setation type and endopod segment 1 is supplied by 1 long and 1 thin short setae, segments 2 and 3 bear one long and 1 short, vestigial seta each, and the terminal segment is supplied with 3 long setae (Fig. 1K, 7B). The other *Bradyetes* species have lost the thin short seta from endopod segment 1 and retain 1 seta here (3C). We assume it is the same seta lost in all species. Another plesiomorphic character (Schulz 1989), the presence or absence of a seta on the coxal epipodite, is additionally used (Fig. 1K).

Maxilliped (chars. 24–29). Plesiomorphically, in some spinocalanids (Schulz 1989) (Fig. 2F), the maxilliped coxa is supplied with 4 sclerotized articulated setae but 3 sclerotized setae typically are present in all aetideids. The only exception is *Paracomantenna wishnerae* Markhaseva, 1995, which is described as possessing 4 setae, but

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TABLE 3. Selected character states of species included in *Bradyetes* (Females)

Character	B. cf. inermis	B. pacificus	B. weddellanus
Total length (mm)	2.95	2.96–2.98	4.75–5.50
Shape of posterior corners of prosome	rounded	drawn out into a triangular point	rounded
Shape of genital double somite	barrel-like	barrel-like	barrel-like
Proportions of genital double somite	longer than wide	longer than wide	longer than wide
Shape of spermathecae	narrow, not much wider than the duct leading to the genital atrium	narrow, not much wider than the duct leading to the genital atrium	narrow, not much wider than the duct leading to the genital atrium
Posterior corners of prosome dorsally	not bifurcate	bifurcate	not bifurcate
Antennule ancestral segment 1 setation	1	1	1
Antenna: Exp setation formula	1-1,1-1,1,1,1,0,3	1?0?1?1,1,1,1,1,3**	1-1,1-1,1,1,1,1*,3
Mandible: setation of basis/Enp1/Enp2	1/1/4***	1/0/4	1/1/4
Maxillule:			
setation of praecoxal endite	9–11	13	11
setation of coxal endite	4	4	4
setation of proximal basal endite	3	3	3
setation of distal basal endite	4	4	4
setation of Enp	12	12	12
setation of Exp	11	11	11
setation of epipodite	7+?	6	9
Maxilla endopod setation	6 +1(2)	6+2	6+2
Maxilliped coxal appendage	aesthetask-like	aesthetask-like	aesthetask-like
Length of maxilliped coxal aesthetask-like appendage relative to the longest distal seta	nearly as long as, or about 1.5 times longer	2 times longer	6 times shorter
P1 Enp lateral lobe	developed or absent	well developed	moderately or poorly developed
P2–P4 Enp segments posterior surface	nude	nude	nude

TABLE 3. (Continued)

Character	B. curvicornis	B. matthei	B. paramatthei
Total length (mm)	4.15	1.19–1.32	1.90–2.30
Shape of posterior corners of prosome	drawn out into a triangular point	drawn out into a triangular point	rounded
Shape of genital double somite	barrel-like	globular shape	globular shape
Proportions of genital double somite	longer than wide	wider than long	wider than long
Shape of spermathecae	narrow, not much wider than the duct leading to the genital atrium	large, round to oval round	large, round to oval round
Posterior corners of prosome dorsally	not bifurcate	not bifurcate	not bifurcate
Antennule ancestral segment 1 setation	1	2?	3
Antenna: Exp setation formula	1-1,1-1,1,1,1*,3	0?0?1?1,1,1,1,1,3**	1?0?1?1,1,1,1,1,3**
Mandible: setation of basis/Enp1/Enp2	1/1/5	2/2/9	2/2/9+1
Maxillule:			
setation of praecoxal endite	11	13	14
setation of coxal endite	4	5	5
setation of proximal basal endite	3	4	4
setation of distal basal endite	4	5	5
setation of Enp	14	15	16
setation of Exp	11	10	9–10
setation of epipodite	9	9	9
Maxilla endopod setation	6+2	?	6+3
Maxilliped coxal appendage	aesthetask-like	not aesthetask-like conical tubercle	not aesthetask-like conical tubercle
Length of maxilliped coxal aesthetask-like appendage relative to the longest distal seta	3 times longer	-	-
P1 Enp lateral lobe	well developed	well developed	well developed
P2–P4 Enp segments posterior surface	nude	P2–P4 Enp 3 spinulated, P4 Enp1–2 spinulated	P3 Enp 3, sometimes P4 Enp 2–3 spinulated

* Seta vestigial;

question marks (in bold**) designate ambiguity on whether proximal Exp 1 and 2, or Exp 2 and 4 are fused;

***in one limb in 2 specimens 5/6 setae

re-examination suggests this may be an artifact of the orientation of the mounted limb. Distally to the group of 3 sclerotized setae, some aetideid genera (*Gaetanus, Pseudochirella*) have an unarticulated conical tubercle, which is an outgrowth of the segment (Fig. 2E) (Markhaseva 1996) that Von Vaupel Klein & Rijerkerk (1997) indicated in *P. obesa* as possessing glandular pore. The conical tubercle is placed on the maxilliped coxa where the aesthetasc-like sensory appendage sits in other genera and is here considered to be homologous with the aesthetasc-like sensory appendage. The aesthetasc-like sensory appendage was earlier interpreted as an attenuation of the maxillipedal coxal lobe edge, not as a transformed sclerotized seta (Markhaseva & Schnack-Schiel 2003). Characters 26-29 are species-specific (Fig 2 B–D).

Legs (chars 30–35). All aetideids have leg 1 exopod segment 3 with 3 inner/medial border setae, whereas two of the outgroup taxa (the spinocalanids *Monacilla typica* and *Spinocalanus usutatus*) have 4 setae on this border (char. 30). Leg 1 (Fig. 1L) exopod segment 2 lateral spine may be short or long (char. 31) and the endopod may have a lateral lobe or not (char. 32). All aetideids have exopod segment 3 of legs 2–4 with 4 inner/medial border setae whereas *Monacilla* and *Spinocalanus*, the spinocalaids in the outgroup, have 5 setae on this border (Char. 33). Endopod segment 2 of leg 2 and endopod segments 2 and 3 of legs 3 and 4 may or may not be decorated with posterior surface spinules.

Phylogenetic analysis. The data set comprises 11 operational taxonomic units (OTUs) and 35 morphological characters. *Bradyetes* cf. *inermis* was treated as a species complex represented by at least 3 morphotypes; each morphotype is included into the data matrix as a separate OTU. The characters and character states are listed in Table 2, and their distribution in the taxa is given in Table 4.

The data matrix was analysed using maximum parsimony and Bayesian inference. Maximum parsimony analysis was performed with PAUP v. 4.3 (Swofford 2002) using the branch-and-bound algorithm. All characters were equally weighted; 20 characters (3, 6, 7, 10–21, 23–25, 30, and 33) were scored as ordered and 15 characters as unordered (see "The character set" above for the rationale of character scoring). Eight characters were autapomorphic and were excluded from the parsimony analysis. Branch support was evaluated through bootstrap and Bremer support values. The bootstrap analysis was conducted using the branch-and-bound algorithm, with 10000 replicates. Bremer decay indices of individual clades (Bremer 1994) were calculated for the strict consensus tree using a batch file produced by TreeRot v. 3 (Sorenson 1996). The bootstrap values are shown at branches and the decay indices at nodes in the strict consensus tree (Fig. 10A).

The Bayesian phylogenetic analysis was performed using MrBayes 3.2 (Huelsenbeck & Ronquist 2001) with the standard discrete (MK1) model (Lewis 2001). All characters were used in the analysis. Parameters were set to equal rates of change among character states and characters. Two independent simultaneous runs with four chains each (three hot and one cold) were used with 20 million generations and a sampling frequency of 1000. At the end of the runs the average split frequencies of the standard deviations were well below 0.05. The first 25% of the trees were discarded as burn-in and the remaining trees were used to construct a 50% majority-rule consensus tree (Fig. 10B).

TABLE 4. Distribution of characters and their coding in the taxa. Explanations: ? = not known, – = not applicable

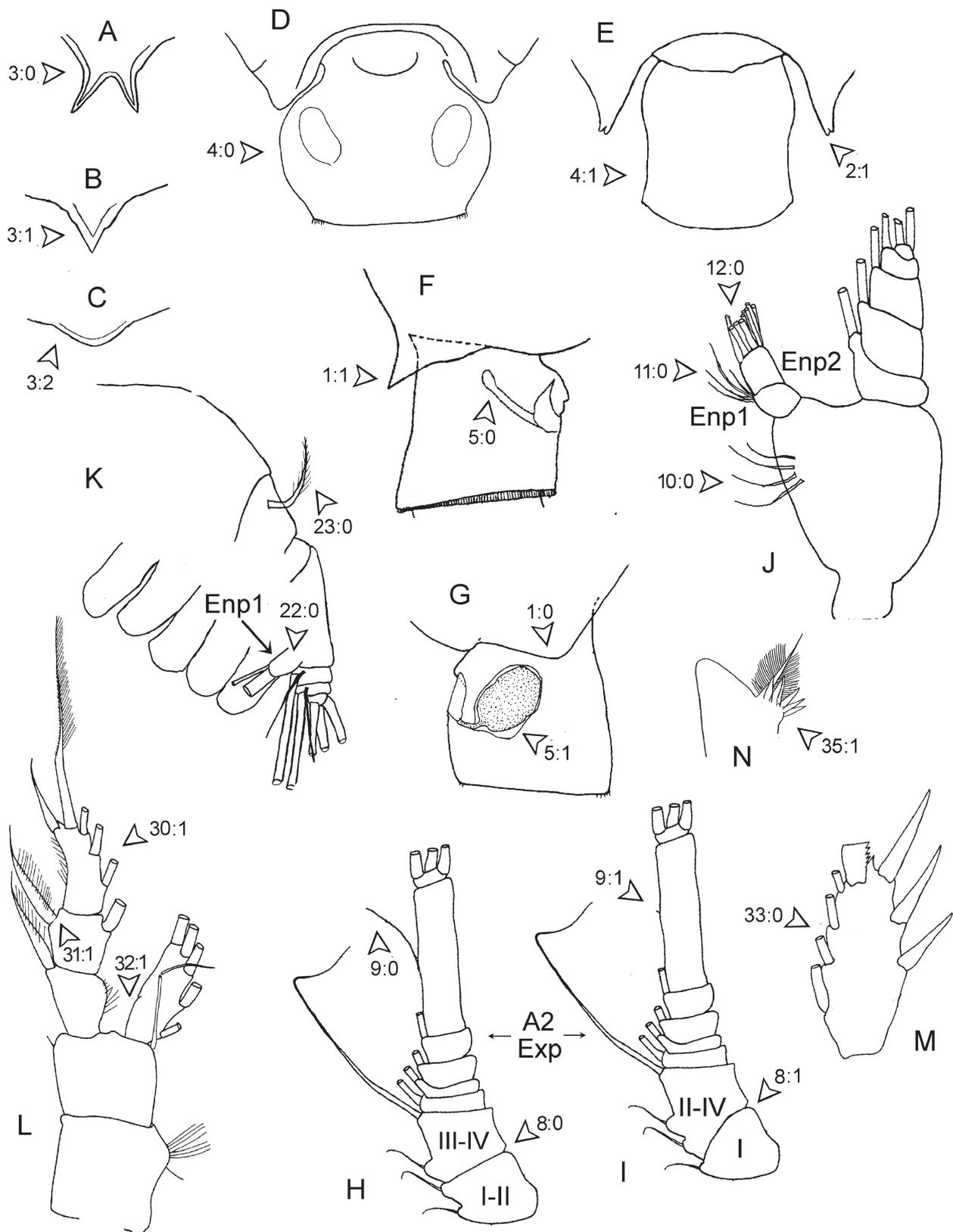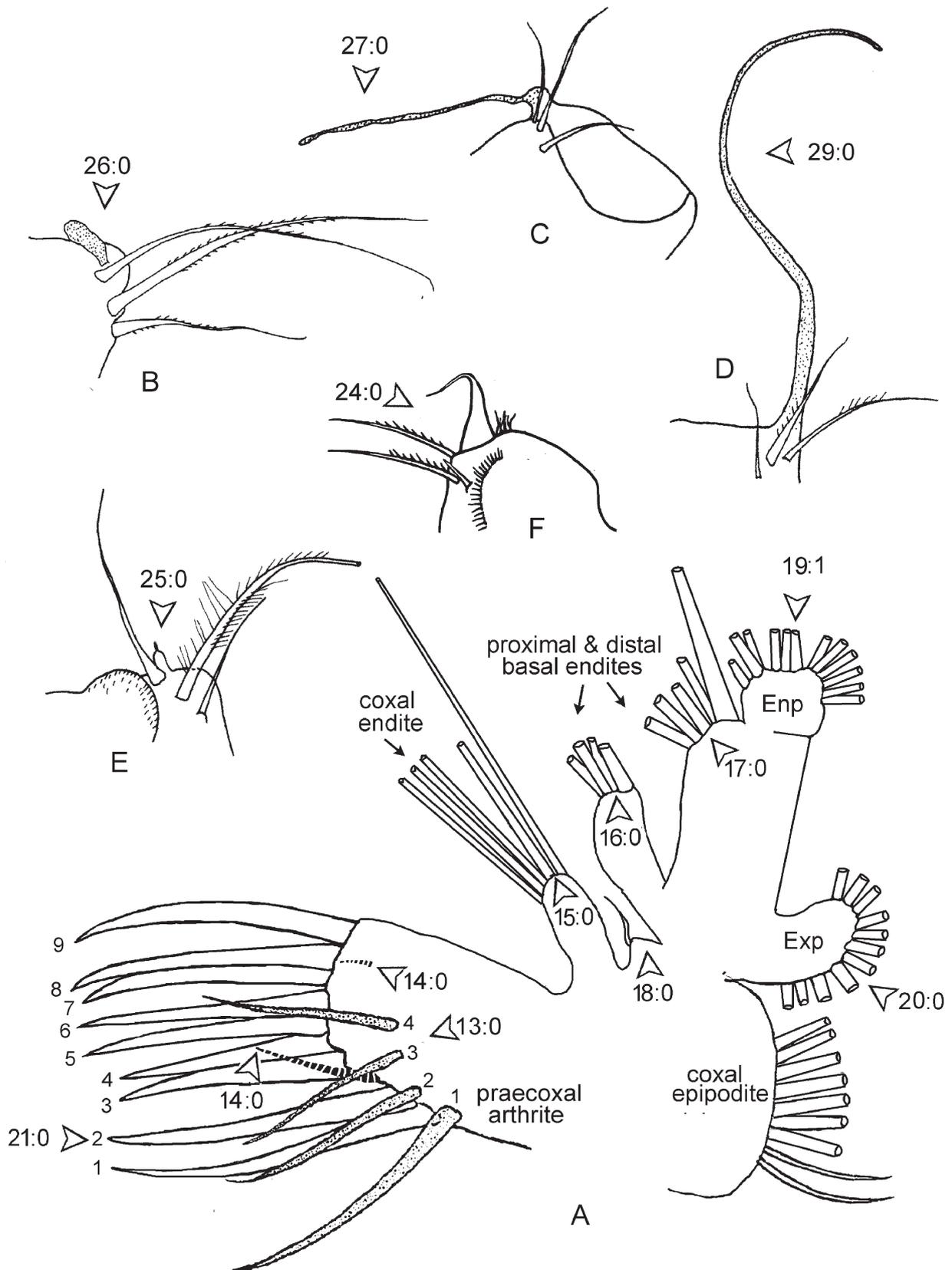| Taxa	Characters			
	1–9	10–19	20–29	30–35
Monacilla typica	0101?0110	0000000000	00000-----	000000
Spinocalanus usitatus	013100110	0000100010	00001-----	0000??
Pseudochirella obesa	0111?0110	1000100010	000110----	110101
B. inermis morpho1	012101001	3221111111	01?1111011	110110
B. inermis morpho2	012101001	3222111111	0211111011	111110
B. inermis morpho3	012101001	3221111111	0211111011	111110
B. pacificus	102101010	3320111111	0?11111101	110110
B. weddellanus	012101001	3221111111	0111110111	100110
B. curvicornis	112101001	3211111111	0111111110	110110
B. matthei	1120100?0	2100100010	10?110----	110100
B. paramatthei	0120100?0	2100100010	100110----	110100

FIGURE 1. Illustrations of character location and selected character states (Table 2) used in the morphological cladistic analysis. First digit designates character number in the list of characters and the other designates character state. A, B, C, rostrum drawn out into bifurcate points, drawn into one point and in form of a blunt plate; D, E, prosome posterior corners and genital double-somite in dorsal view; F, G, prosome posterior corners and genital double-somite in lateral view; H, I, antenna exopod, different kind of segmentation of proximal segments; J, mandibular palp; K, maxilla; L, P1; M, P2-P4 exopod segment 3; N, P4 basipod.

FIGURE 2. Illustrations of character location and selected character states (Table 2) used in the morphological cladistic analysis. First digit designates character number in the list of characters and the other designates character state. A, maxillule; B, maxilliped coxa (part.) of *Bradyetes weddellanus*; C, maxilliped coxa (part.) of *Bradyetes* cf. *inermis*; D, maxilliped coxa (part.) of *Bradyetes curvicornis*; E, maxilliped coxa (part.) of *Bradyetes paramatthei* **sp. n.**; F, maxilliped coxa (part.) of *Monacilla typica* (after Schulz 1989 with changes).
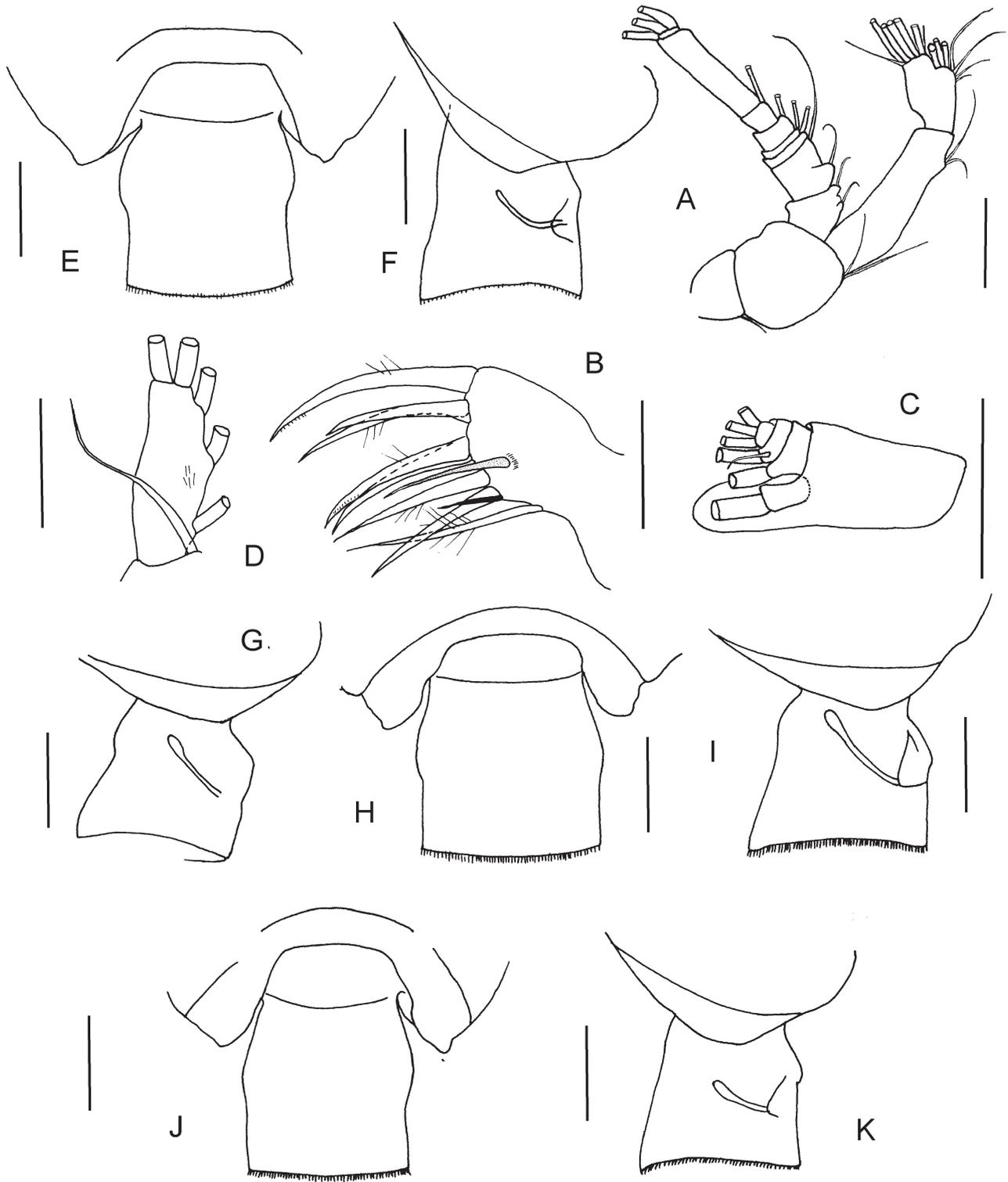
FIGURE 3. *Bradyetes* cf. *inermis*. Female, morphotype 3 specimens from the Kurile-Kamchatka Trench, KuramBIO 1 expedition. Sta. 7–10. A–E, specimen 1, A, antenna; B, maxillule, praecoxal arthrite; C, maxilla, endopod; D, P1 endopod; E, F, pedigerous somite 5 & genital double-somite in dorsal and lateral views; G, specimen 2, 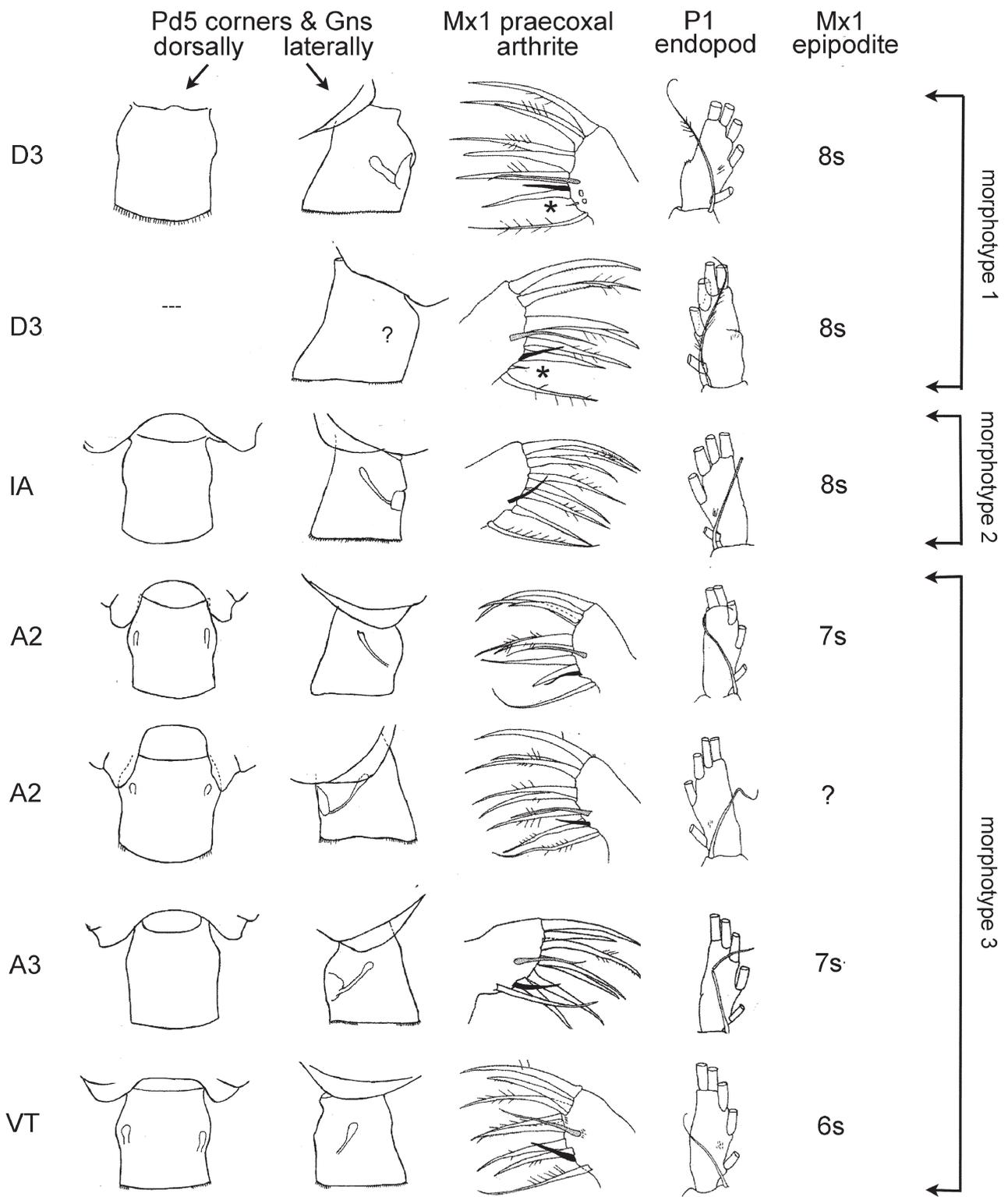pedigerous somite 5 & genital double-somite in lateral views; H–I, specimen 3, pedigerous somite 5 & genital double-somite in dorsal and lateral views; J–K, specimen 4, pedigerous somite 5 & genital double-somite in dorsal and lateral views. Scale bars 0.1 mm.

FIGURE 4. *Bradyetes* cf. *inermis*. Females. Selected characters differentiating morphotypes 1–3. Names of the expeditions are abbreviated as: DIVA 3 (D3); ANDEEP 2–3 (A 2–3); ICE AGE 1 (IA); Vema-Transit (VT). Specimens from D1 and D2 (DIVA 1, 2) are not included and share characters as given for morphotype 3.

Taxonomy

Superfamily Clausocalanoidea Giesbrecht, 1893

Family Aetideidae Giesbrecht, 1893

Genus *Bradyetes* Farran, 1905

***Bradyetes paramatthei* sp. nov.**
(Figs 5–8)

Holotype. Adult female, dissected, body length 2.10 mm. ZMH 45138. Collected above the sea bed in the Kurile-Kamchatka Trench at Sta. 2–10, 46° 14.76' N 155° 32.81' E, on 3 August 2012 by the KuramBio 1 expedition, Sonne cruise SO 223, at depths between 4859 and 4865 m.

Paratypes. 5 adult females, partly dissected, body length 2.20, 2.20, 2.20, 2.30 and 2.30 mm. SMF 37208–37212, collected above the sea bed in the Kurile-Kamchatka Trench, by the KuramBio 1 expedition, Sonne cruise SO 223 at Sta. 9–12 on 24 August 2012, 40°34.49' N 150°59.85' E, at depths between 5399 and 5392 m; 2 adult females, 1 in poor condition, body length 2.00, 2.15 mm, ZIN 91147, Sta. 11–12, 31 August 2012, 40°12.32 ' N 148° 05.73' E, at depths between 5350 to 5348 m.

Type locality. 46°14.77' N 155°32.79' E.

Additional material. Four females from the Atlantic Ocean: 1 female, body length 2.15 mm, collected in the Angola Basin, Sta. 348, 27 July 2000, 16°16.98' S 005°27.27' E, by the DIVA–1 expedition, Meteor cruise ME 48–1, at a depth of 5390 m; 2 females collected in the Guinea Basin by the DIVA–2 expedition, Meteor cruise ME 63–2 from 2 stations – 1 female, body damaged, not measured, Sta. 64–5, 15 March 2005, 00°13.27' S 002°29.91' W, depth 5055 m and 1 female, body length 2.05 mm, Sta. 89–6, 20 March 2005, 00°45.30' S 005°35.00' W, depth 5154 m; 1 female, body length 1.90 mm, collected at Meteor Seamount, Sta. 636, 18 August 2009, 29°19.24' N 28°37.94' E, by the DIVA–3 expedition, Meteor cruise ME 79–1, at a depth of 4338 m. One female from the Pacific Ocean, body length not measured, collected above the sea bed in the Kurile-Kamchatka Trench, at Sta. 7–10 on 17 August 2012, 40°01.82' N 152°58.55' E, by the KuramBio 1 expedition, Sonne cruise SO 223, at depths between 5223 and 5221 m.

Description. Female. Body length 1.90–2.30 mm. Prosome 2.7–3.3 times as long as urosome (Fig. 5A–B). Rostrum as a significantly reduced blunt plate (Fig. 5C). Cephalosome and pedigerous somite 1 and pedigerous somites 4–5 incompletely separate; posterior corners oval-triangular in dorsal view; rounded in lateral view (Fig. 5A–B, E–H). Urosome of 4 somites (Fig. 5A–B). Genital double somite globular shape. Spermathecae large, round to oval round with very narrow duct leading to the genital atrium (Fig. 5B, F–H). Caudal rami with 1 lateral seta, 1 ventral seta, and 4 terminal setae (Fig. 5D).

Antennule (Fig. 5J–L) reaching pedigerous somite 3, of 24 articulating segments; armature as follows: I–3s, II–IV–6s+1ae (ae absent in holotype), V–2s+1ae, VI–2s, VII–2s+1ae, VIII and IX–2s each, X–XI–4s+1ae, XII and XIII–2s each, XIV–2s+1ae, XV–2s, XVI–2s+1ae, XVII to XXI–2s each, XXII and XXIII–1s each, XXIV–XXVI–2s each, XXVII–XXVIII–5s+1ae, aestethasc long, nearly as long as 3 preceding segments together.

Antenna (Fig. 6A–C), coxa with 1 seta, basis with 2 setae; exopod of 8 segments, setation formula 1?0?1?1, 1, 1, 1, 1, 1, and 3 setae (uncertain whether proximal Enp 1 and 2, or Enp 2 and 4 are fused), all terminal setae long, of nearly the same length; first endopodal segment with 2 setae, second with 8–9 + 7 setae.

Mandible (Fig. 6D–E), gnathobase with 4 large and 4 small teeth near dorsal seta; basis with 2 setae; exopod 5-segmented with 1, 1, 1, 1, and 2 setae; endopod segment 1 with 2 setae, segment 2 with 9+1, or 9 setae in paratype.

Maxillule (Fig. 6F), praecoxal arthrite with 9 terminal, 4 posterior and 1 anterior setae, coxal endite with 5 setae; coxal epipodite with 7 long+2 short setae; proximal basal endite with 4 setae, distal basal endite with 5 setae; endopod with 16 setae; exopod with 9–10 setae.

Maxilla (Fig. 7A–B), praecoxal to basal endites with 3 setae each, all endites decorated with denticles; enditic-like lobe of proximal endopod segment with 3 setal elements, two thicker, spine-like; endopod with 9 (2+2+2+3) setae.
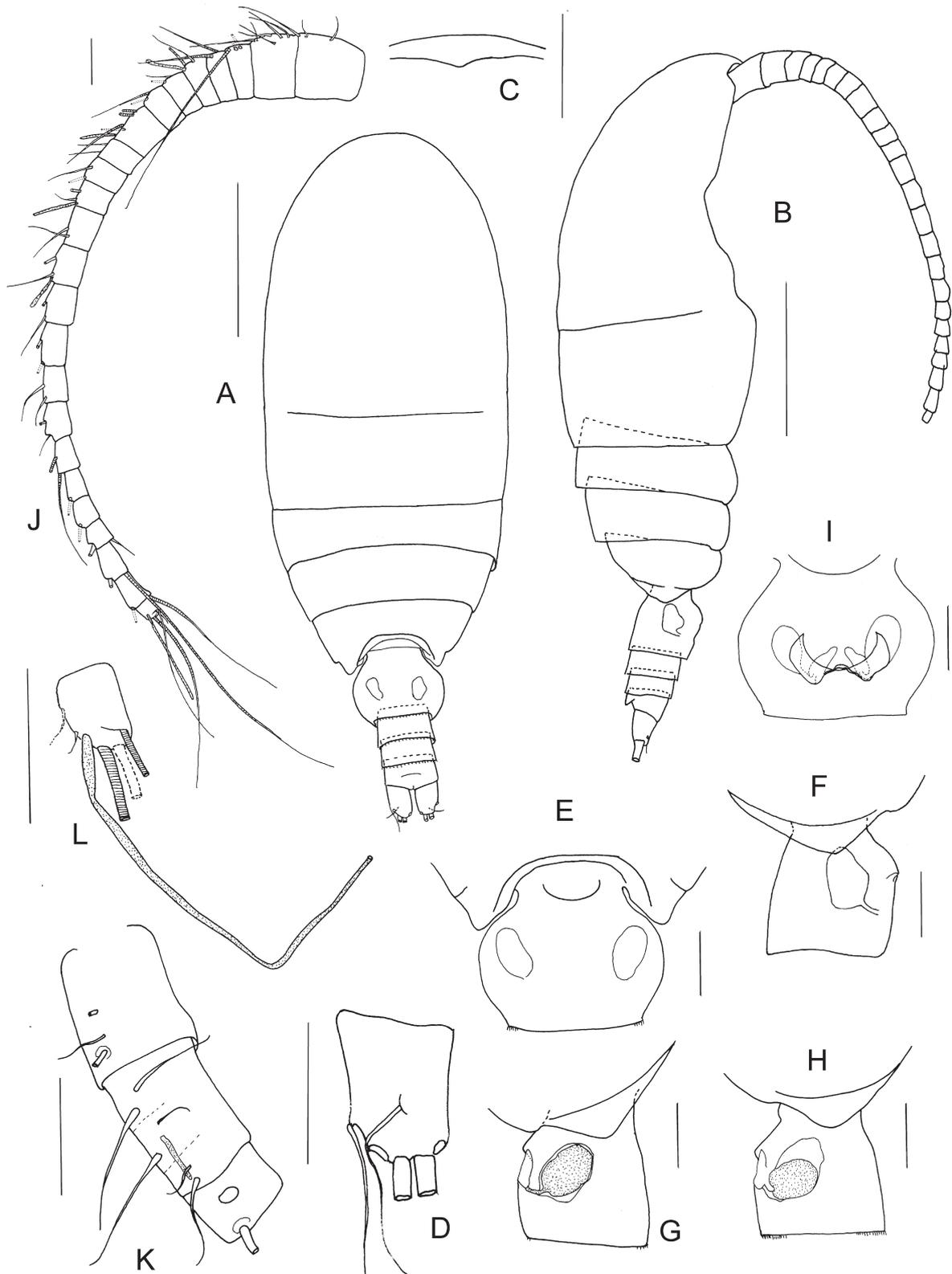
FIGURE 5. *Bradyetes paramatthei* **sp. nov.** Female, A, habitus, dorsal view; B, habitus, lateral view; C, rostrum, ventral view; D, caudal ramus, ventral view; E, posterior prosome and genital double-somite, dorsal view; F–H, posterior prosome and genital double-somite, lateral view; I, genital double-somite, ventral view; J, antennule, dotted line marks additions from another holotype limb and paratypes; K, antennule, ancestral segments I–V; L, antennule, ancestral segments XXVII–XXVIII, dotted line marks additions after additional specimen. A–C, F, I–J, L, holotype; E, G–H, K, paratypes (SMF) and D, additional material (DIVA–2, Sta. 89). Scale bars: A–B 0.5 mm, C–L 0.1 mm.
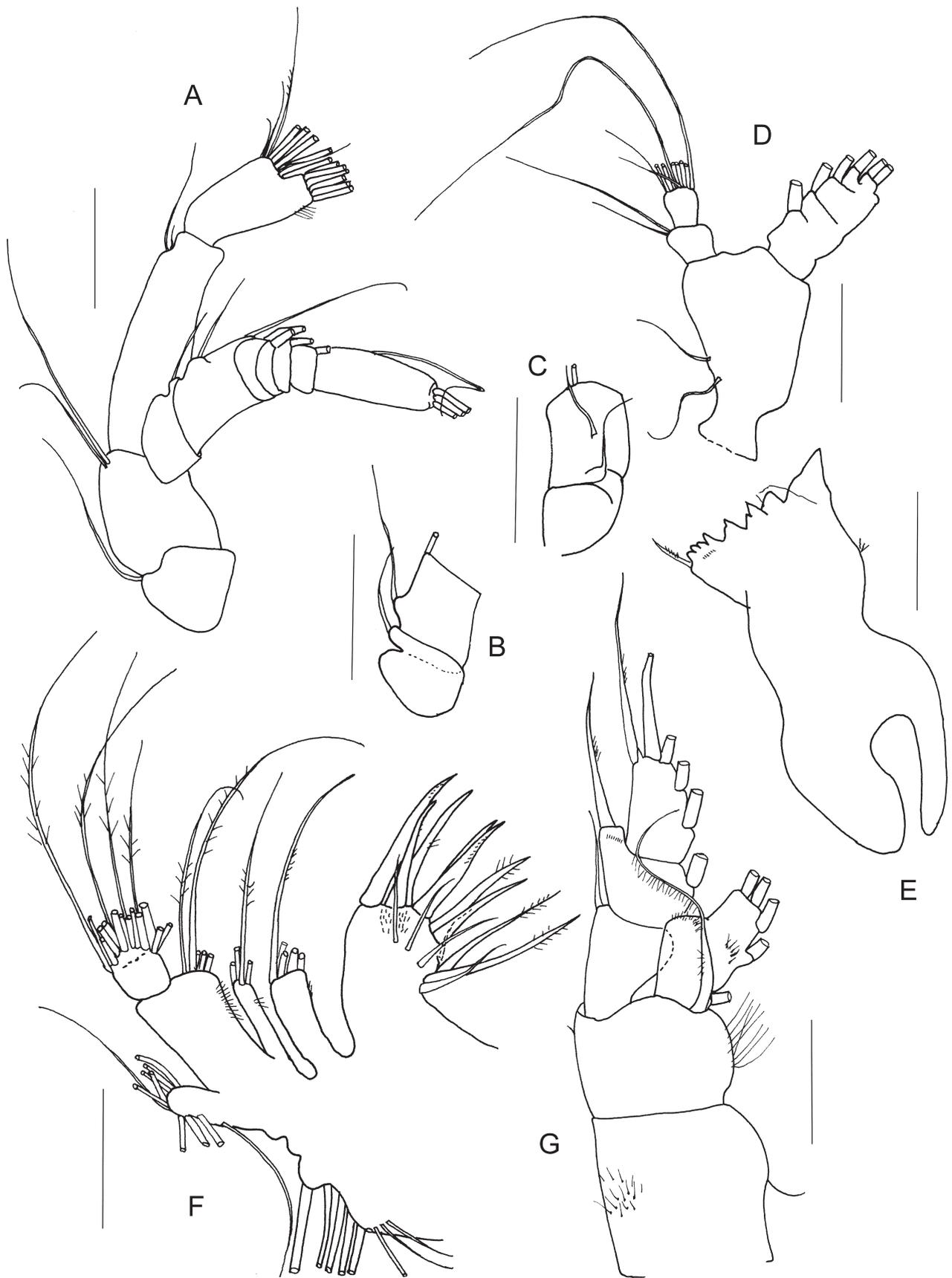
FIGURE 6. *Bradyetes paramatthei* **sp. nov.** Female. A, antenna; B, C, antenna exopod (part.), different positions; D, mandible, palp; E, mandible, gnathobase; F, maxillule, dotted line marks additions from paratype; G, P1. A, D–G holotype, B, C, additional material (DIVA1, Sta. 348 and DIVA 3, Sta. 636 respectively). Scale bars 0.1 mm.
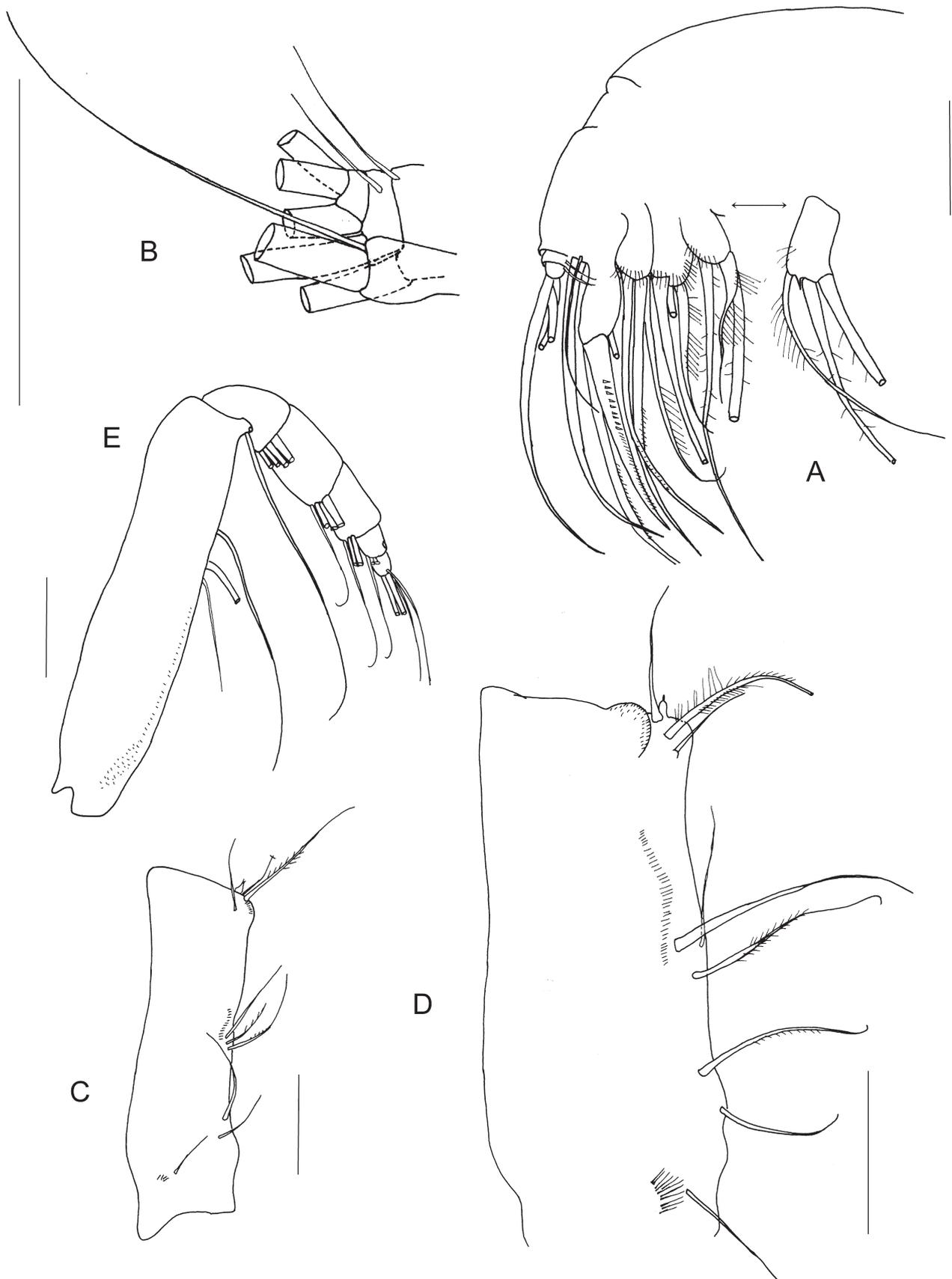
FIGURE 7. *Bradyetes paramatthei* **sp. nov.** Female. A, maxilla, 2 endopod setae broken, not figured; B, maxilla, endopod; C–D, maxilliped, syncoxa; E, maxilliped, basis and endopod. A, C, E - holotype, B, D – paratype (SMF). Scale bars 0.1 mm.
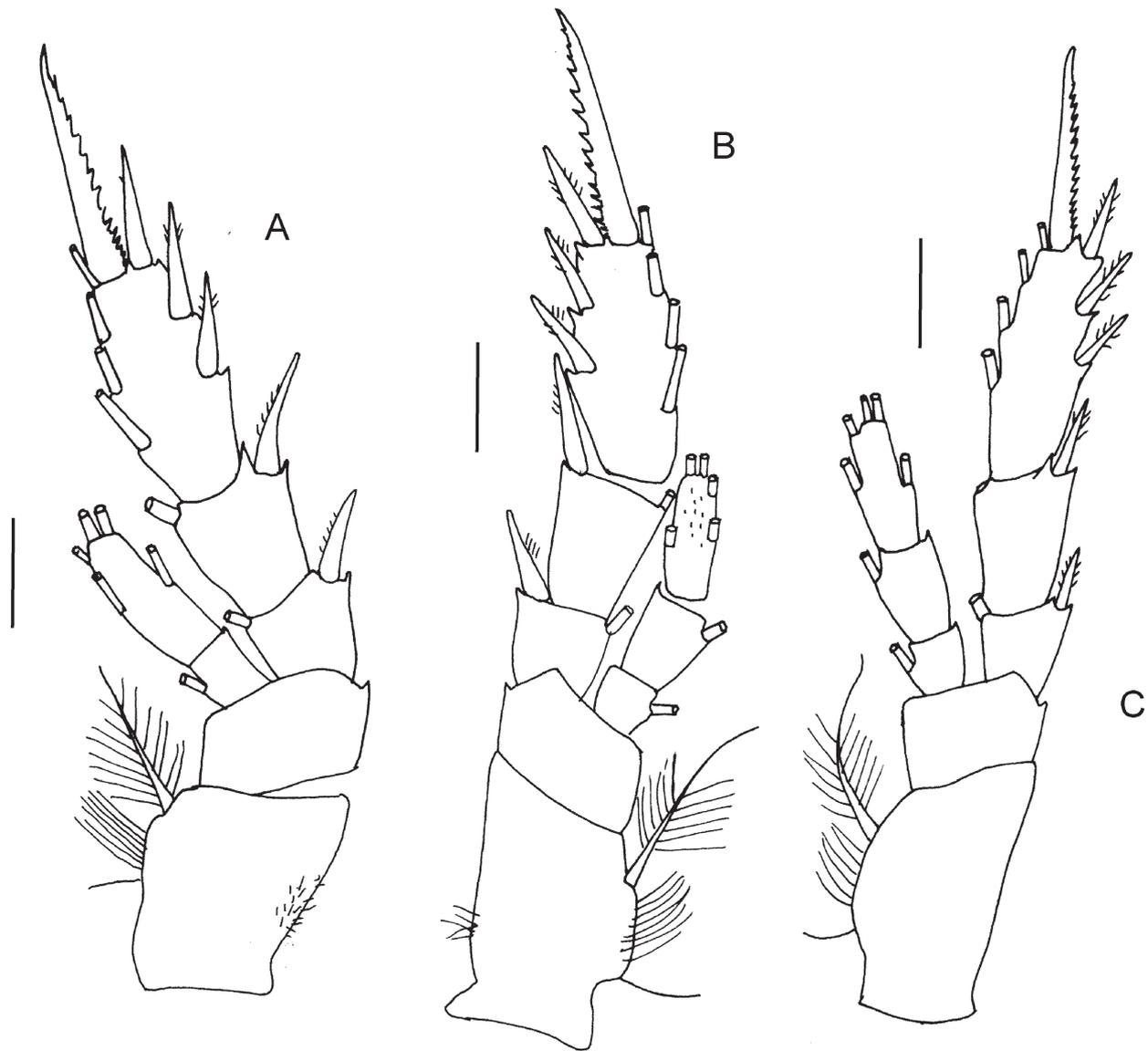
FIGURE 8. *Bradyetes paramatthei* **sp. nov.** Female, holotype. A, P2; B, P3, C, P4. Scale bars 0.1 mm.

Maxilliped (Fig. 7C–E), syncoxa with 1 seta on proximal praecoxal endite, 2 setae on middle praecoxal endite and 3 setae on distal praecoxal endite; coxal lobe with 3 setae and conical tubercle. Basis with 3 setae. Endopod 6-segmented with 2, 4, 4, 3, 3+1, and 4 setae, first segment very small and fused to basis.

Legs. P1 (Fig. 6G), coxa with lateral spinules; basis with small lateral spinule distally and medial distal seta curved with setules; endopod 1-segmented with lateral lobe, its lateral margin with spinules, anterior segment surface with distal spinules; exopod segments 1 to 3 with 1 lateral spine each; spine of exopod segment 1 usually exceeding base of segment 2 lateral spine, sometimes, reaching base of segment 2 lateral spine. P2–P4 (Fig. 8A–C), coxa with 1 medial seta and medial spinules; basis without seta; endopod 2-segmented in P2, 3-segmented in P3–P4; posterior surface spinules present on P2 endopod segment 2 (nude in holotype), P3 endopod segment 3, and P4 endopod segments 2–3 (nude in holotype); exopods 3-segmented. P5 absent.

Male unknown.

Etymology. The species name "*paramatthei*" refers to a close relation of the species to *Bradyetes matthei* Johannessen, 1976.

Remarks. The new species is closely related to *B. matthei* and shares with this species a significant number of morphological features (Table 3), but differs from *B. matthei* in the shape of the posterior corners of Pd5, which are rounded (*vs* drawn out into the triangular points in *B. matthei*) and in the armament of the proximal segment of the antennal exopod, which bears a seta (*vs* seta absent in *B. matthei*).

While *Bradyetes paramatthei* **sp. nov.** and *B. matthei* both inhabit the near-bottom biotope, they are widely separated geographically and live in distant depth zones. *Bradyetes matthei* is recorded only from its type locality (Fensfjord, about 60° N 05° E) at depths between 548 and 580 m (Johannessen 1976, Markhaseva 1996), whereas the new species was collected at abyssal depths between 4338 and 5399 m in the North and South Atlantic Ocean (several localities between 29° N and 16° S: Angola and Guinea basins, Meteor Seamount) and in the Pacific Ocean (Kurile-Kamchatka Trench).
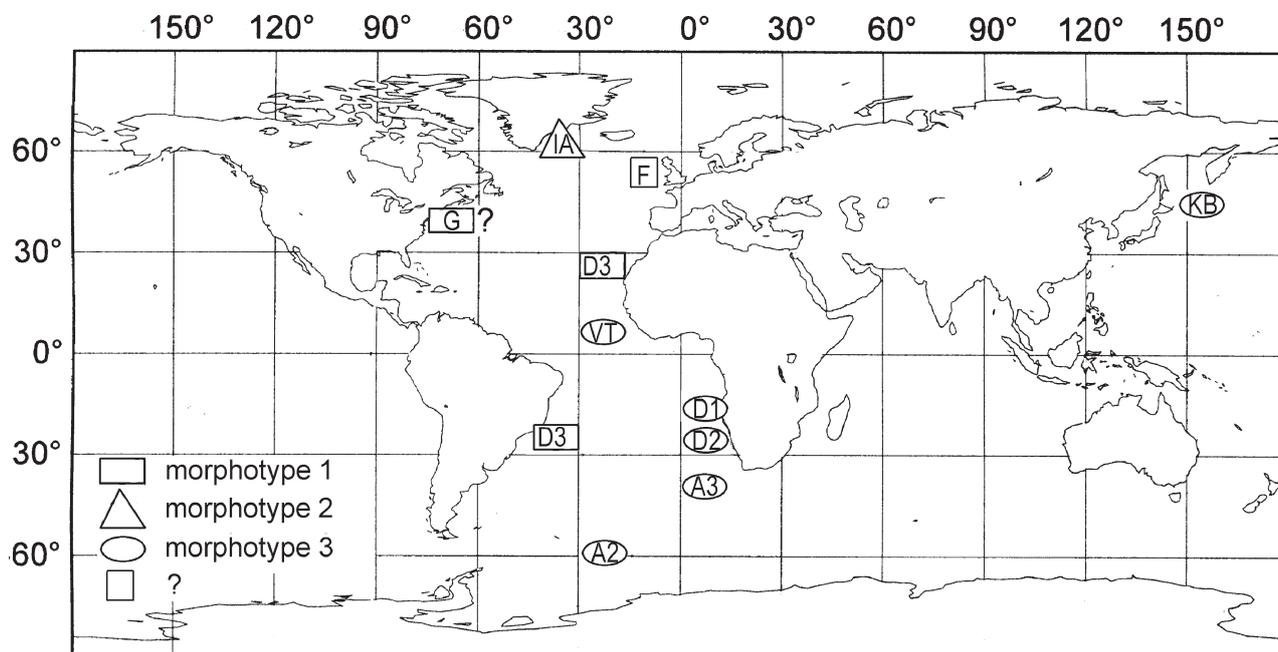

FIGURE 9. Geographical distribution of *Bradyetes* cf. *inermis* and its morphotypes 1, 2 and 3. Records of Farran (1905) and Grice (1972) are given as letters F and G respectively. Expeditions are abbreviated as: D1–D3 (DIVA 1–3); A2–3 (ANDEEP 2–3); IA (ICE AGE 1); VT (Vema-Transit) and KB expedition (KuramBIO 1). Morphotype 1 is designated by a rectangle, morphotype 2 by a triangle, and morphotype 3 by an oval (abbreviations for respective expeditions are included inside the symbol).

Bradyetes cf. *inermis*
(Figs 3–4)

Material. Twenty three *Bradyetes* cf. *inermis* females attributed herein to 3 morphological types were sorted from the samples (Table 1).

   Description. *Bradyetes* cf. *inermis* morphotypes 1–3 share the general characters described for the species by Markhaseva and Schulz (2006: 143–146), e.g., the body segmentation and caudal rami structure; the rostrum, which is formed as a rudimentary blunt plate, the genital double-somite, which is barrel-like and usually wider anteriorly, and the general details of the armament of oral parts (Table 3).

   Bradyetes cf. *inermis* morphotypes 1–3 differ in the combination of the following characters (Figs 3–4): morphotype 1 (Fig. 4), body length 2.60–3.00 mm, is characterized by 1) a sausage-like spermatheca that has nearly the same width proximally and distally, 2) a maxillule praecoxal arthrite with 11 setae: 8 long plus 1 short terminal setae (marked by a star in Fig. 4), 1 anterior and 1 posterior setae (this short terminal seta is absent in morphotypes 2 and 3), and 3) a P1 with a well-developed lateral lobe on the endopod and a plumose basal medial seta (this lobe is poorly developed or absent and the medial seta is nude in morphotypes 2 and 3). Morphotype 1 shares with morphotype 2 the maxillular epipodite which is equipped with 8 setae (6–7 setae are present in morphotype 3).

   Morphotype 2 (Fig. 4), body length 2.50 mm, is characterized by a maxillule praecoxal arthrite with 9 setae: 8 long terminal setae plus 1 anterior seta, short terminal seta and posterior seta are absent. Morphotype 2 shares the setation of the maxillule epipodite with morphotype 1. Morphotype 2 shares with morphotype 3 a narrow-elongate spermathecae that is slightly widened in the distal part, the P1 that lacks the lateral lobe at the endopod, and a nude basal medial seta at P1.
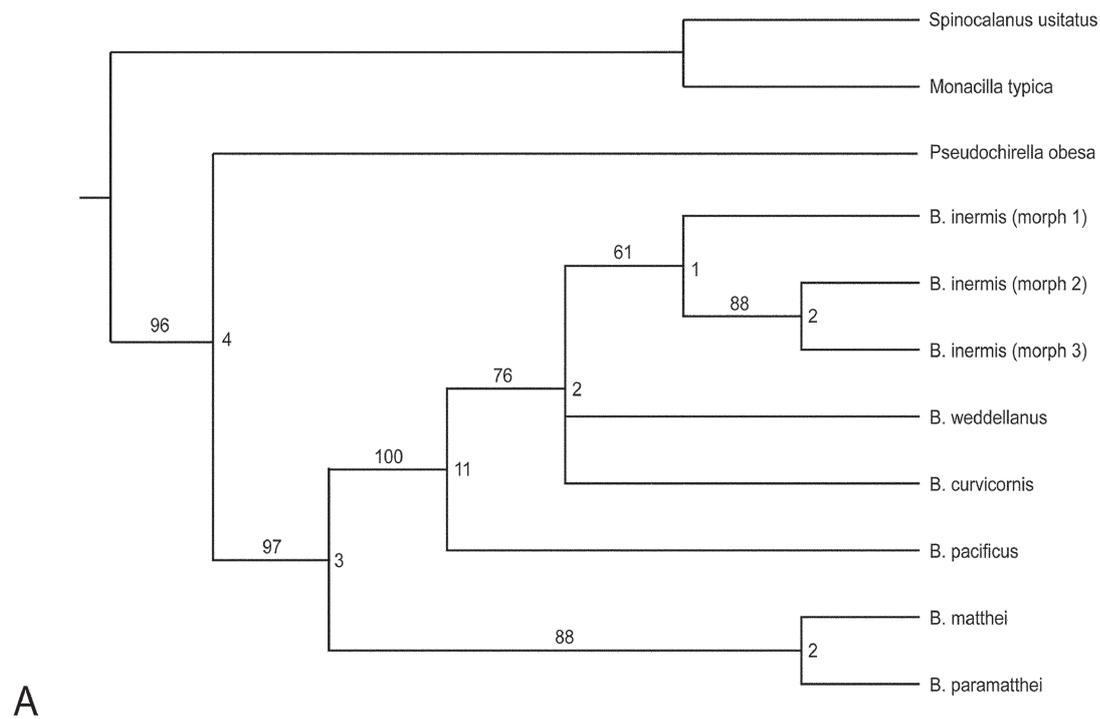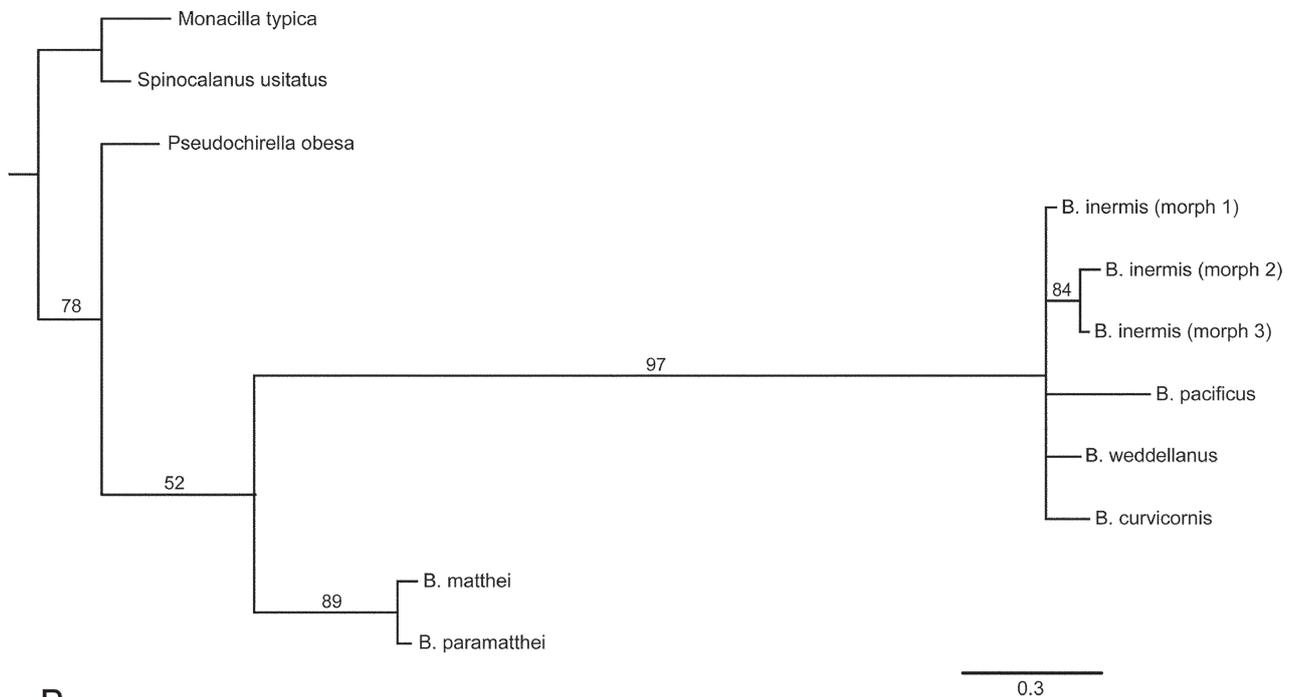
FIGURE 10. Phylogenetic reconstructions showing the relationships among the species of *Bradyetes*. A, strict consensus of 2 most parsimonious trees. Bremer support values and bootstrap values > 50% are shown adjacent to the nodes and above the branches, respectively. B, MrBayes majority-rule consensus. Numbers at the nodes indicate posterior probability percentages. The branch lengths are proportional to the expected changes per character as indicated by the scale bar at the lower right.

Morphotype 3 (Figs. 3–4), body length 2.50–2.95 mm, is characterized by 1) a maxillule praecoxal arthrite with 10 setae: 8 long terminal, 1 anterior and 1 posterior setae; 2) a maxillule epipodite with 6–7 setae. Morphotype 3 is similar to morphotype 2 in lacking the P1 endopod lateral lobe and in having a nude basal medial seta and elongate spermathecae, which is slightly widened distally. The shape of the spermathecae varies slightly among the specimens of morphotype 3.

Remarks. The species *Bradyetes inermis* was established by Farran (1905) based on a single specimen from the North Atlantic (at about 53° N 12° W) collected from a depth of 358 m. The other taxonomic notes on *B. inermis* records are brief comments on the first finding of its male with incompletely detailed figures of both sexes in Grice (1972) and a recent record by Markhaseva & Schulz (2006) with an illustrated description of females.

Markhaseva & Schulz (2006), however, postponed a final decision on the specific status of their specimens and referred to them as *Bradyetes* cf. *inermis*, because of inconsistent and insufficiently detailed existing descriptions of *B. inermis*.

In 2016 it was clarified that the type specimen of *B. inermis* was most likely lost (Paolo Viscardi, National Museum of Ireland, Natural History, personal communication) and none of the newly obtained specimens were found in or close to the *B. inermis* type locality. Therefore, due to the incomplete species description (Farran 1905) and until possible specimens of this species are found in the type locality, it remains impossible to confirm or disprove that the available *B.* cf. *inermis* specimens belong to *B. inermis sensu* Farran.

All recently captured *B.* cf. *inermis* individuals were collected in deep waters (Table 1) and were regarded as belonging to 3 different morphotypes. Specimens identified as morphotypes 1 and 2 (Table 1, Figs. 4, 9) were found in the Atlantic Ocean only. *Bradyetes inermis sensu* Grice (1972), also found in the Atlantic, more probably belongs to morphotype 1 (e.g., similar shape of spemathecae and P1 endopod supplied with a lateral lobe).

Bradyetes cf. *inermis* morphotype 3 appears to be the most widely distributed morphotype, as it was recorded from the Atlantic, Southern and Pacific Oceans (Table 1, Figs. 3–4, 9). Morphotype 3 specimens from different geographical regions share the setation of maxillule and mandible and a similar P1 morphology. They demonstrate variability of the shape of the genital double somite and the spermathecae, but this variability among the Pacific specimens from one region (Kurile-Kamchatka Trench) is at least as high as between specimens from different oceans (Figs. 3–4).

In regard to the identity of *Bradyetes* cf. *inermis* specimens from the Atlantic and Southern Oceans with the individuals from the Pacific Ocean we rely only on their morphological comparisons as molecular data is currently impossible to obtain, because of a lack of specimens from the Atlantic and Southern oceans, which are suitably preserved for molecular analysis.

Species groups in *Bradyetes*. Classical morphological analysis shows that the genus *Bradyetes* is subdivided into two species groups.

Group I includes the species *B. curvicornis*, *B.* cf. *inermis*, *B. pacificus* and *B. weddellanus*. Females of this group share 1) a body size of 2.50–5.50 mm; 2) a genital double-somite that is longer than wide, of a barrel-like or close to barrel-like shape; 3) a narrow spermathecae, which is not much wider than the duct leading to the genital atrium, or sausage-like; 4) an antennule with ancestral segment I with 1 seta; 5) an antenna with a setal formula of 1-1,1-1,1,1,1,1(0) and 3 setae, and fused proximal exopod segments 1–2 and 3–4 (differs in *B. pacificus*); 6) a mandible basis with 1 seta, and an endopod segment 1 with 1 seta (or seta absent), and endopod segment 2 with less than 6 setae; 7) a maxillule coxal endite with 4 setae, proximal basal endite with 3 setae, distal basal endite with 4 setae, endopod with fewer than 15 setae, and an exopod with 11 setae; 8) a maxilla endopod with 7 or 8 setae; 9) a maxilliped coxa with an aesthetasc-like appendage, and 10) a nude posterior surface of segments of the P2–P4 endopods. Males are defined by one-segmented left P5 endopod (Table 3).

Group II includes the species *B. matthei* and the new species *Bradyetes paramatthei* **sp. nov**. The females of this group are defined by: 1) a body size of 1.19–2.30 mm; 2) a genital double-somite of globular shape; 3) a large spermathecae, round to oval-round with a narrow duct leading to the genital atrium; 4) an antennule ancestral segment I with 2? or 3 setae; 5) unclear antenna exopod fusions and uncertain setal formula interpretation 0(1)?0?1?1,1,1,1,1,1 and 3, with at least one seta lost from proximal exopod segments 1–4 ; 6) a mandible basis and endopod segment 1 with 2 setae each and endopod segment 2 with 9 or 9+1 setae; 7) a maxillule coxal endite with 5 setae, proximal basal endite with 4 setae, distal basal endite with 5 setae, endopod with 15–16 setae, and an exopod with 9–10 setae; 8) a maxilla endopod with 9 setae; 9) a maxilliped coxa without an aesthetasc-like appendage, but equipped with a conical tubercle; 9) posterior surface spinules that are present at least on some of the P2–P4 endopod segments. Males are defined by a two-segmented left endopod in P5.

Cladistic analysis. The parsimony analysis recovered two most parsimonious trees with 49 steps (consistency index = 0.898, retention index = 0.938). The 50% majority rule topology was identical with the strict consensus tree (Fig. 10A). The analysis confirms that *Bradyetes* falls into two clades: one comprising *B. curvicornis*, the three morphotypes of *B.* cf. *inermis*, *B. pacificus*, and *B. weddellanus* (Group I) and the other containing *B. matthei* and the new species *B. paramatthei* (Group II). The monophyly of Group I is very strongly supported (bootstrap value [BV] = 100%, Bremer index [BI] = 11), whereas Group II has a relatively weak support (BV = 88%, BI = 2). Both groups together form a well-supported clade (BV = 97%, BI = 3). Within Group I, *B. pacificus* is robustly resolved as sister to the remaining species. The three morphotypes of *B. inermis* form a weakly-supported monophyletic clade (BV = 61%, BI = 1), with morphotypes 2 and 3 being more closely related than morphotype 1.

The Bayesian analysis yielded a similar, but less resolved topology compared to the parsimony analysis (Fig. 10B). Groups I and II were recovered as monophyletic, with Group I being highly robust (posterior probability [PP] = 97%) and Group II only weakly supported (PP = 89%). The relationships within Group I are mostly unresolved, except for morphotypes 2 and 3 of *B. inermis*, which form a monophyletic group, albeit with a weak support (PP = 84%).

Discussion

The family Aetideidae includes more than 200 species in 30 genera of diverse morphology. The most recent taxonomic review of the family produced a key for the genera and species (Markhaseva 1996), that is useful for the practical purposes of identification, but does not resolve phylogenetic relationships within the Aetideidae. Although the family Aetideidae has a long history of studies (Giesbrecht 1893), the descriptions of many aetideid species and genera remain insufficient and generic differential diagnoses are still lacking. This leads to an uncertainty in the aetideid intergeneric relationships. Furthermore, some genera are not taxonomically homogeneous and contain morphologically different species groups (e.g., *Bradyetes, Gaetanus, Paracomantenna*) (Markhaseva & Renz 2019).

The taxonomic heterogeneity of the genus *Bradyetes* was demonstrated in this study by classical taxonomic analysis and a cladistic analysis, both of which showed the presence of two separate species groups within this genus. Compared to the *Bradyetes* species Group I (*B. curvicornis*, *B.* cf. *inermis*, *B. pacificus* and *B. weddellanus*), the congeners of Group II (*B. paramatthei* **sp. nov.** and *B. matthei*) are defined by primitive characters (according to the classical taxonomic analysis). In general, their oral parts, e.g., mandible, maxillule and maxilla are supplied with a greater number of setae and the maxilliped coxa lacks a derived structure, i.e. a sensory-like appendage (Table 3). Most likely, the species *B. paramatthei* **sp. nov.** and *B. matthei,* that comprise Group II, represent a separate taxonomic unit that should be excluded from the genus *Bradyetes*.

The phylogenetic analyses based on the maximum parsimony and Bayesian methods support the monophyly of *Bradyetes* and the exclusion of *B. paramatthei* and *B. matthei*. Both methods resolved Group I as a monophyletic clade, with a very high support. The monophyly of Group II is less certain and its relationships with Group I remains unclear. A comprehensive analysis of the aetideid morphological characters is required to clarify the phylogenetic relationships among the aetideid genera. Furthermore, no apomorphy for the *Bradyetes* species of Group II, *B. paramatthei* **sp. nov.** and *B. matthei,* was identified. Therefore, a final decision on the taxonomic position of this species group should be postponed.

Acknowledgments

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