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Proposal of *Arktourella* gen. nov., a new genus of the family Normanellidae Lang 1944 (Copepoda: Harpacticoida) from the Province of Cortez

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Abstract

A new genus, *Arktourella* gen. nov., is proposed to accommodate a new member of the harpacticoid family Normanellidae, *A. margarethae* gen. et sp. nov., from a polluted estuary in north-western Mexico. The new genus was attributed to the laophontoidean family Normanellidae on account of the lack of outer spinous processes on the second antennulary segment, one abexopodal seta on the antennary allobasis, four setae on the one-segmented antennary exopod, endopod of first swimming leg two-segmented with first segment elongated and with two distal elements on second segment, endopods of second to fourth legs two-segmented, distal setae on the male second endopodal segment of second and third legs reduced, and outer spine of the male second endopodal segment of third leg fused to segment. The new, so far monotypic genus, differs from the other normanellid genera in the presence of four elements on the third exopodal segment of the first leg, and two outer spines on the third exopodal segment of second to fourth legs. No synapomorphies were observed for *Arktourella* gen. nov. and *Normanella*, but they are unique within the Normanellidae in that the mandibular basis and endopod are not fused. Maximum parsimony analysis and Bayesian inference using 59 morphological characters to assess the relationships between the genera of the family Normanellidae confirmed the affinity of *Arktourella* gen. nov. and *Normanella*, and their sister group relationship with *Sagamiella*. *Paranaiara* and *Pseudocletodes* were shown consistently to be closely related and are the sister taxa of *Normanella*-*Arktourella* gen. nov.-*Sagamiella*. *Arktourella* gen. nov., *Paranaiara* and *Pseudocletodes* share the presence of a large spinulose spine on the fifth and sixth segments of the female antennule, but its significance is not clear. Additionally, we propose a key to the genera of the Normanellidae.

Keywords: Bayesian inference, maximum parsimony, new species, Mexico, phylogeny, taxonomy

Introduction

The family Normanellidae Lang, 1944 is one of the smallest families in Harpacticoida, but its establishment as a monophyletic group has been a long and complicated process. The history of the family began with the creation of the genus *Normanella* Brady 1880 for *Laophonte dubia* Brady & Robertson 1876, and with the subsequent inclusion of that genus in the Laophontidae Scott T. 1905 (Lang 1934). Since then, several authors have contributed importantly towards narrowing the boundaries of the Laophontidae through the removal of *Normanella* and *Cletopsyllus* Willey 1935 from the Laophontidae to the Canthocamptidae Brady 1880 (e.g. Nicholls 1941) and trough the removal of the Donsiellinae Lang 1944 from the Laophontidae to the Thalestridae Sars 1905 (e.g. Hicks 1988; Huys 1988), through the consolidation of the Normanellidae as a monophyletic taxon (e.g. Lang 1944, 1948; Nicholls 1945; Huys & Willems 1989; Huys 1990; Huys & Lee 1998; Lee & Huys (1999), and proposal of new normanellid genera (e.g. Lee & Huys 1999; Kihara & Huys 2009). At present, the Normanellidae is regarded as the sister taxon of the Laophontidae and the most basal taxon of the Laophontoidea Scott T. 1905 (Huys & Lee 1998), and is currently composed of four genera, *Normanella*, *Pseudocletodes* Scott T. & Scott A. 1893, *Sagamiella* Lee & Huys 1999, and *Paranaiara* Kihara & Huys 2009.

Several laophontoidean copepods were gathered during a short-term project on the effects of organic pollution on the distribution and diversity of meiofauna from a coastal estuary in north-western Mexico. The collected

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specimens fit the latest diagnoses for the Normanellidae by Lee & Huys (1999) and Kihara & Huys (2009), and the diagnosis for *Normanella* by Lee & Huys (1999), except for the armature complement of P1 EXP3, and outer armature complement of P2–P4 EXP3. The inclusion of the new Mexican species into *Normanella* would imply the expansion of the generic diagnosis of *Normanella*, and the new material is here attributed to a new genus instead. Here we propose *Arktourella* gen. nov. for the new Mexican normanellid species, *A. margarethae* gen. et sp. nov., based on maximum parsimony analysis and Bayesian inference. Also, we give some comments on the relationships amongst the genera of Normanellidae and propose an updated key to the genera of the family.

Materials and methods

Sample processing and taxonomy

Sediment samples were taken from ten sampling stations along Urías system, a polluted coastal system in north-western Mexico. The sediment samples were taken with an Eckman grab (sampling area 625 cm^2). Triplicate cores were taken with acrylic tubes (sampling area 24.6 cm^2) and the upper 3 cm layer of each tube was retrieved. Sediment samples were fixed in pure ethanol and sieved through 500 and 38 µm sieves. Meiofauna (the material retained in the 38 µm sieve) was extracted through centrifugation with Ludox® HS-40 following Burgess (2001) and Rohal *et al.* (2016), and preserved in pure ethanol. Meiofauna was separated manually from the fine grains of sediment using an Olympus SZX12 stereomicroscope equipped with DF PLAPO 1X objective and WHS10X eyepieces, at a magnification of 40x. Harpacticoid copepods were stored separately in 1 ml vials with pure ethanol. Illustrations and figures of the material presented herein were made from undissected individuals and dissected parts using a Leica DMLB microscope equipped with L PLAN 10X eyepieces, N PLAN 100X oil immersion objective, and drawing tube. The dissected parts were mounted on separate slides using lactophenol as mounting medium and sealed with Neo-Mount®.

Huys & Boxshall (1991) was followed for general terminology.

Abbreviations used in the text: acro, acrothek; ae, aesthetasc; BENP, baseoendopod; ENP, endopod; EXP, exopod; EXP (ENP)1–3, first–third exopodal (endopodal) segments, P1–P6, first to sixth legs.

Phylogenetic analyses

Fifty-nine characters were used for the phylogenetic analyses (Table 1). A general data matrix (Table 2) was prepared with Mesquite v. 3.61 (Maddison & Maddision 2019; http://www.mesquiteproject.org), based on the characters lists in Huys & Lee (1999) and Kihara & Huys (2009), and in the descriptions by Huys & Willems (1989), Huys (1990a, 1990b) and Lee & Huys (1999). Oligomerization was considered the dominant trend in copepod evolution for character coding (Huys & Boxshall 1991). Plesiomorphic character states inferred from out-group taxa were coded "0"; derived character states were coded "1" to "4" (see table 1). *Canthocamptus mirabilis* Sterba 1968 as described by Itô & Takashio (1980) was chosen as outgroup (Huys & Lee 1999). The position of the new genus within the Laophontoidea and within the Normanellidae was assessed through a maximum parsimony analysis and Bayesian inference.

The maximum parsimony analysis was performed using the Willi Hennig Society edition of Tree analysis using New Technology (TNT) v. 1.5 (Goloboff *et al.* 2008; Goloboff & Catalano 2016). Characters were considered to be non-additive and with equal weights (default), and the collapsing rule zero was followed (any branch with a minimum possible length of 0 was eliminated); missing data and gaps were coded '?'. With these settings, a traditional search was carried out using tree bisection and reconnection (TBR) branch swapping of Wagner trees, with random seed set 100; random addition sequence (RAS) was set 1000; trees were collapsed after the search. Photoshop was used for final editing of the trees.

The Bayesian inference-based phylogenetic analysis was performed using MrBayes (v. 3.2.5; Ronquist *et al.* 2012). All characters were unordered and with equal weights; unknown and missing data were coded as "?"; inapplicable data were coded as "–". The analysis was performed using the default options of the program except for rates which was set gamma (rates=gamma); posterior probabilities were set 3 000 000 generations (ngen=3

000 000; with which an average standard deviation of split frequencies of 0.004 was reached) with four Markov Chain Monte Carlo (MCMC) chains (nchains=4) with every 100th three saved (samplefreq=100), and "burn-in" was set 0.25% (burninfrac=0.25); default values were used for other parameters of the MCMC. Clades with around 95% posterior probability were accepted. A consensus tree was constructed with the "sumt" command using the "contype=allcompat" option with "burn-in" as for the MCMC. FIGTREE v.1.4.4 (Rambaut 2018; http://tree.bio.ed.ac.uk/software/figtree/) was used to visualize and to edit the resulting tree, and Photoshop was used for final editing.

Results

Systematics

Order Harpacticoida Sars 1903

Superfamily Laophontoidea Scott T. 1905

Family Normanellidae Lang 1944

Diagnosis (amended). As in Kihara & Huys (2009: 3–4) except for armature formula as follows:

	P1	P2	P3	P4
Exopod	0.1.02[2–3]	0.1.12[2–3]	0.1.22[2–3]	0.1.[1–2]2[2–3]
Endopod	[0–1].120 or absent	[0–1].[2–3]2[0–1]	[0–1].[2–3]21	[0–1].[1–2]21

Genus Arktourella gen. nov.

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Type and only species. *Arktourella margarethae* **gen. et sp. nov., by monotypy.**

Differential diagnosis. Normanellidae. Habitus semi-cylindrical, without clear demarcation between prosome and urosome. Cephalothorax covered with minute denticles, with areolated surface pattern, posterior margin serrated, lateral margin plain. Rostrum well-developed, discrete, triangular. P1-bearing somite fully incorporated to cephalothorax; P2–P4-bearing somites covered with minute denticles, serrated posterior margins progressively coarser posteriad. P5-bearing somite, and abdominal somite covered with surface denticles and with serrate posterior margin. Genital somite and third urosomite separated dorsolaterally but completely fused ventrally forming genital double-somite in the female. Anal somite with surface ornamentation as in previous somites; anal operculum semicircular, well-developed, with serrated posterior margin. Caudal rami twice as long as wide, with seven setae. Antennule five-segmented in the female. Antenna with allobasis, with one abexopodal seta; exopod one-segmented with four setae. Mandible biramous; basis with two setae; endopod one-segmented with four setae; exopod one-segmented with one seta. Maxillulary basis with two endites; endopod incorporated to basis, with two setae; exopod one-segmented, with two setae. Maxilla with three syncoxal endites; allobasis with two accompanying setae; endopod incorporated to allobasis, with three setae. Maxilliped subchelate; syncoxa with two setae; basis unarmed; endopod one-segmented, with long claw and accompanying seta. P1–P4 EXP three-segmented; P1–P4 ENP two-segmented, of P1 prehensile. P5 BENP and EXP not fused, elongate; endopodal lobe with five, exopod with six setae. P6 represented by one bipinnate seta. Sexual dimorphism expressed in separated genital somite and third urosomite, antennule, P2 and P3 ENP, P5 and P6. Male antennule subchirocer, seven-segmented. Inner seta of P2 ENP1, and distal, subdistal outer, and outer setae of ENP2 comparatively shorter than in the female. P3 ENP with comparatively shorter inner seta of ENP1, and with comparatively shorter distal inner and outer seta of ENP2, the latter segment with outer apophysis. P5 BENP and EXP not fused; both baseoendopods fused medially; endopodal lobe with two, exopod with four setae. P6 asymmetrical, only one leg functional, each leg with three setae. Armature formula of P1–P4 as follows:

	P1	P2	P3	P4
Exopod	0.1.022	0.1.122	0.1.222	0.1.222
Endopod	1.120	♀1.321 ♂slightly dimorphic (see above)	♀1.321 ♂1.32+Apophysis	1.221

Etymology. The generic name derives from the Greek given name Αρκτοῦρος, Arktouros (from ἄρκτος, arktos, bear, and οὖρος, ouros, guardian, meaning the Guardian of the Great Bear or Ursa Major constellation; Arktouros derived into the Latin given name Arcturus), and the Latin diminutive suffix *-ella*. The species is dedicated to the senior author's godfather Arturo Villanueva Robertson for his 74th birthday and for his 49th wedding anniversary with the senior author's godmother Margarita Noguera Farfán. It is to be treated as a noun in the nominative singular, gender feminine.

TABLE 1. List of characters used for phylogenetic analyses and explanation. Derived characters between brackets.

1. Habitus, with clear demarcation between prosome and urosome [habitus cylindrical]
2. Female antennule with 8 segments [1: with 7 segments; 2: with 6 segments; 3: with 5 segments; 4: with four segments]
3. Female antennule segments 3 and 4 free [fused forming double compound segment]
4. Female antennule segments 5–8 free [fused forming triple compound segment]
5. Male antennule segment 4 free [incorporated into segment 5]
6. Male antennule segments distal to geniculation free [fused forming single compound segment]
7. Female and male antennule without posterior spinous process on segment 2 [process present]
8. Antennary exopod two-segmented [1: one-segmented; 2: absent]
9. Antenna first exopodal segment when exopod two-segmented with one seta [unarmed]
10. Antenna second exopodal segment when two-segmented with three setae [with two setae]
11. Antenna exopod when one-segmented with four setae [1: with three setae; 2: with two setae]
12. Antenna with basis (basis and first endopodal segment separated) [with allobasis (basis and first endopodal segment fused)]
13. Antennary basis or basal component of allobasis with abexopodal seta (with two setae) [1: without abexopodal seta (with one seta); 2: without seta at all]
14. Mandibular basis with two setae [1: with one seta; 2: unarmed]
15. Mandibular basis and exopod separated [exopod incorporated to basis or absent]
16. Mandibular basis and endopod separated [endopod incorporated to basis or absent]
17. Maxillulary basis with two endites [with one endite]
18. Maxillulary endopod with three setae [1: with two setae; 2: with one seta]
19. Maxillulary exopod free with two setae [fused to basis with one seta]
20. Maxillary allobasis with two accessory setae [with one accessory seta]
21. Maxillipedal syncoxa with three setae [1: with two setae; 2: with one seta; 3: unarmed]
22. P1 EXP2 with inner seta [without inner seta]
23. P1 EXP 3 with three outer spines (five elements in all) [with two outer spines (four elements in all)]
24. P1 ENP present [absent]
25. P1 ENP when present three-segmented [two-segmented (ENP2 and ENP3 fused)]
26. P1 ENP non-prehensile [prehensile]
27. P1 ENP1 with inner seta [without inner seta]
28. P1 ENP3 (or ENP2 when ramus two-segmented) with inner lateral seta [without inner lateral seta]

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TABLE 1. (continued)

29. P1 ENP3 (or ENP2 when ramus two-segmented) with three distal elements [with two distal elements (inner seta absent)]
30. P2 EXP3 with three outer spines [with two outer spines]
31. P2 EXP3 outer elements spiniform [setiform]
32. P2 ENP three-segmented [two-segmented (ENP2 and ENP3 not separated)]
33. P2 ENP1 with inner seta [without inner seta]
34. P2 ENP2 when ramus three-segmented with inner seta [without inner seta]
35. P2 ENP3 when ramus three-segmented with two inner setae [with one inner seta]
36. P2 ENP2 (or ENP3 when ENP three-segmented) with outer spine/seta [element absent]
37. P2 ENP2 when ramus two-segmented with three inner setae [1: with two inner setae; 2: with one inner seta]
38. P3 EXP3 with three outer spines [with two outer spines]
39. P3 EXP3 outer elements spiniform [setiform]
40. P3 ENP three-segmented [1: two-segmented (ENP2 and ENP3 not separated); 2: one-segmented]
41. P3 ENP1 when ENP two-segmented with inner seta [without inner seta]
42. P3 ENP2 when ramus three-segmented with inner seta [without inner seta]
43. P3 ENP3 when ramus three-segmented with two inner setae [with three inner setae]
44. P3 ENP2 when ramus two-segmented with three inner setae [1: with two inner setae; 2: with one inner seta]
45. Male P3 ENP three-segmented [two-segmented (secondary separation of ENP2 failed)]
46. Male P3 ENP2 apical setae as long as in female [comparatively shorter than in female]
47. P4 EXP3 with three outer spines [with two outer spines]
48. P4 EXP3 outer elements spiniform [setiform]
49. P4 EXP3 with two inner setae [1: with one inner seta; 2: without seta]
50. P4 ENP three-segmented [1: two-segmented; 2: one-segmented]
51. P4 ENP1 when ENP three- or two-segmented with inner seta [without inner seta]
52. P4 ENP2 with two inner setae [with one inner seta]
53. Male P5 separated from ventral wall of somite [fused to ventral wall of somite]
54. Male P5 BENPs' separated [fused medially]
55. Male P5 ENP present [vestigial or absent]
56. Male P5 ENP lobe with four setae [1: with three setae; 2: with two setae; 3: with one seta; 4: without setae]
57. Male P6 with three setae [with two setae]
58. Caudal ramus cylindrical [lamelliform]
59. Caudal seta V well-developed [reduced or vestigial]

TABLE 2. General character matrix for the phylogenetic analyses.

Taxa \ Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Canthocamptus mirabilis	0	0	0	0	0	0	0	0	0	0	-	1	0	2	1	1	0	0	0	0	2	0	1	0	0	0	0	0	0
Pseudocletodes	0	2	1	0	?	?	0	1	-	-	1	1	0	1	0	1	0	0	0	1	3	0	0	1	-	-	-	-	-
Paranaiara	0	2	1	0	0	0	0	1	-	-	0	1	0	1	0	1	0	1	0	0	3	0	0	0	1	0	1	0	1
Sagamiella	0	2	1	0	0	0	0	1	-	-	1	1	1	0	0	1	1	0	0	0	1	0	0	0	1	1	0	0	1
Normanella	0	2&3	1	0	0	0	0	1	-	-	0	1	1	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	1
Arktourella gen. nov.	0	3	1	0	0	0	0	1	-	-	0	1	1	0	0	0	0	0	0	0	1	0	1	0	1	1	0	0	1
Adenopleurellidae	0	4	1	1	1	0	1	1	-	-	2	1	1	1	1	1	1	0	1	0&1	1	1	1	0	1	0	1	1	1
Cristacoxidae	1	4	1	1	1	1	1	2	-	-	-	1	2	2	1	0	0	0	1	0	1	1	1	0	1	1	0	1	1
Laophontidae	0	0&1	0	0	0	0	1	1	-	-	0&1&2	1	1	0	0&1	0&1	1	0&1	1	0	0	1	1	0	1	1	0	1	1
Laophontopsidae	1	4	1	1	1	1	1	1	-	-	0&1	1	1	1	1	1	0	0	0	0	2	1	1	0	1	1	0	1	1
Orthopsyllidae	1	4	1	1	1	0	1	1	-	-	0	1	1	0	1	1	1	2	1	0	2	1	1	0	1	1	1	1	1

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TABLE 2. (Continued)

Taxa \ Character	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49
Canthocamptus mirabilis	0	0	0	0	0	0	0	-	0	0	0	0	0	0	-	0	0	0	0	0
Pseudocletodes	0	0	1	1	-	-	1	1	0	0	1	1	-	-	1	1	1	0	0	1
Paranaiara	0	0	1	0	-	-	1	0	0	0	1	0	-	-	1	1	1	0	0	0
Sagamiella	0	0	1	0	-	-	0	1	0	0	1	0	-	-	0	1	1	0	0	0
Normanella	0	0	1	0	-	-	0	0&1	0	0	1	0	-	-	0	1	1	0	0	0
Arktourella gen. nov.	1	0	1	0	-	-	0	0	1	0	1	0	-	-	0	1	1	1	0	0
Adenopleurellidae	0&1	0	1	1	-	-	1	1	0&1	0	1	1	-	-	1	0	0	0&1	0	0
Cristacoxidae	1	1	1	0	-	-	1	2	1	1	2	-	-	-	2	1	0	1	1	0
Laophontidae	0	0	1	0&1	-	-	0	1	0	0	1	0&1	-	-	0	0	0	0	0	0&1&2
Laophontopsidae	0&1	1	1	1	-	-	1	2	0&1	1	1	1	-	-	2	1	0	0&1	1	0&1
Orthopsyllidae	0	0	1	1	-	-	1	2	0	0	1	1	-	-	2	0	0	0	0	2

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TABLE 2. (Continued)

Taxa \ Character	50	51	52	53	54	55	56	57	58	59
Canthocamptus mirabilis	1	0	0	0	1	0	2	0	0	0
Pseudocletodes	1	1	0	0	0	0	1	0	1	0
Paranaiara	1	0	1	0	1	0	0	0	1	1
Sagamiella	1	0	0	0	1	0	2	1	0	0
Normanella	1	0	0	0	1	0	2	0	0	0
Arktourella gen. nov.	1	0	0	0	1	0	2	0	0	0
Adenopleurellidae	1	1	1	1	-	1	2&3	1	0	0
Cristacoxidae	2	-	1	0	0	0	1	1	0	0
Laophontidae	1	0&1	1	0	1	0&1	2&3&4	1	0	0
Laophontopsidae	1	1	1	0	0	0	2	1	0	1
Orthopsyllidae	1	1	1	0	1	0	2	1	0	0

***Arktourella margarethae* gen. et sp. nov.**
(Figs. 1-8)

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Type locality. Urías estuary, Mazatlán, Sinaloa State, stn. 4 (23.1840°N, 106.3579°W; depth 0.7 m, organic carbon content 1.13%, organic matter content 1.94%, sand 82.44%, clay 8.27%, silt 9.29%.) (see also Gómez (2020: 43, figure 1).

Other localities. Urías estuary, Mazatlán, Sinaloa State, stn. 9 (23.1904°N, 106.4121°W; depth 5.4 m, organic carbon content 1.41%, organic matter content 2.43%, sand 64.81%, clay 8.09%, silt 27.11%.), stn. 10 (23.1815°N, 106.4214°W; depth 6.0 m, organic carbon content 1.2%, organic matter content 2.07%, sand 69.12%, clay 7.91%, silt 22.97%.) (see also Gómez (2020: 43, figure 1).

Material examined. From the type locality: female holotype dissected (ICML-EMUCOP-180119-192), male allotype partially dissected (both antennules dissected, the rest left intact and preserved in alcohol) (ICML-EMUCOP-180119-195), one male paratype (ICML-EMUCOP-180119-193) and one CV female paratype (ICML-EMUCOP-180119-194) preserved in alcohol. **From other localities:** one female paratype (ICML-EMUCOP-180119-197) and one male paratype (ICML-EMUCOP-180119-196) from stn. 9 and 10, respectively. 18 Jan. 2019. S. Gómez leg.

Description of the female. Total body length ranging from 410 μm to 465 μm (n= 2; holotype, 465 μm) measured from anterior tip of rostrum to posterior margin of caudal rami.

Habitus (Fig. 1A, C) semi-cylindrical, without clear demarcation between prosome and urosome.

Prosome (Fig. 1A, C) consisting of cephalothorax, P1-bearing somite fully incorporated to the latter, and three free-pedigerous somites bearing P2–P4. Rostrum (Figs. 1A, C, 3A) well-developed, discrete, triangular, with wide base and pointed tip recurved upwards, reaching tip of second antennulary segment, covered with minute denticles and with two subdistal sensilla. Cephalothorax covered with minute denticles, with surface sensilla, pores, and with areolated surface pattern as shown, posterior margin serrated, lateral margin plain. P2–P4-bearing somites covered with minute denticles, with pores and tube-pores, and posterior sensilla as shown; posterior margin serrated, of P4-bearing somite comparatively coarser.

Urosome (Figs. 1A–D, 2A) comprising fifth pedigerous somite, genital double-somite, two free abdominal somites, and anal somite, all of which with minute surface denticles dorsally and laterally. P5-bearing somite largely as in previous somite. Second (genital somite) and third urosomites separated dorsolaterally but fully fused ventrally forming genital double-somite; both halves with tube-pores and posterior sensilla as shown, with posterior margin coarsely serrated; ventral surface of anterior half —genital somite— with P6, and one patch of small spinules close to lateral margin and one outer distal pointed projection on each side; each side of ventral surface of posterior half —third urosomite— with patch of small spinules at the base of outer distal projection, and short row of long slender spinules between pair of sensilla as depicted, medially with transverse row of small spinules between innermost pair of sensilla. Fourth urosomite largely as posterior half of genital double-somite dorsally and laterally; ventrally with additional pair of tube-pores and pattern of four crescentic sets of spinules between innermost pair of sensilla. Fifth urosomite largely as previous somite but without medial tube-pore dorsally, without sensilla; ventrally without tube-pores or sensilla, with pattern of surface minute spinules on posterior half, and with pattern of long posterior spinules as shown. Anal somite slightly wider than long; with one dorsolateral tube-pore on each side; with well-developed semicircular anal operculum ornamented with small denticles on surface and along posterior margin giving a serrated appearance and flanked by pair of sensilla; ventrally cleft medially, with pair of tube-pores medially and subdistally close to joint with caudal rami, with inner small spinules along inner margin of medial cleft and larger ones close to joint of caudal rami. Caudal rami twice as long as wide; dorsally with inner row of small spinules medially and at base of seta III, and with subdistal tube-pore; ventrally with comparatively longer spinules along posterior margin, and with two tube-pores as shown; with seven setae as follows: setae I and II aligned, issuing midway lateral margin, the former ventral to and about half as long as the latter; seta III displaced ventrally, slightly posterior to setae I and II, visibly longer than the latter; seta IV about half the length of seta V, slightly longer than supporting ramus; seta V nearly as long as anal somite and caudal ramus combined, posterior half rat-tail-like; seta VI issuing at inner distal corner, as long as seta II; dorsal seta VII triarticulated, as long as seta III.

Antennule (Fig. 3A) five-segmented; all segments smooth except for spinular row on first segment; all setae smooth except for one and three bipinnate setae on first and second segments, respectively, for one unipinnate strong element on third and fourth segments, and one unipinnate strong seta and one bipinnate distal element, the latter fused basally to slender seta and to short aesthetasc. Armature formula as follows: 1[1], 2[8], 3[7+(1+ae)], 4[3], 5[7+(2+ae)].

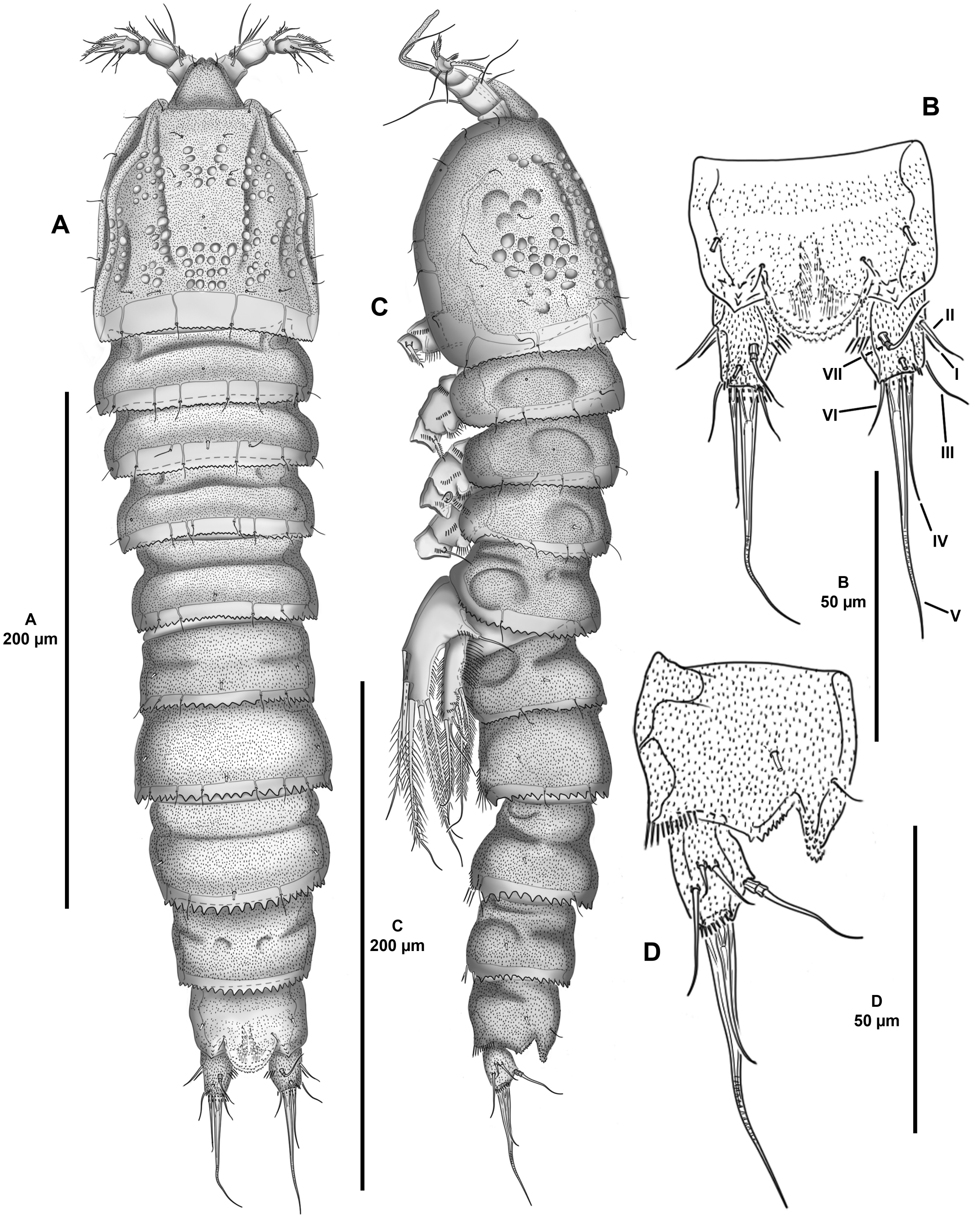

FIGURE 1. *Arktourella margarethae* gen. et sp. nov., female. A, habitus, dorsal; B, anal somite and caudal rami, dorsal; C, habitus, lateral; D, anal somite and left caudal ramus, lateral.

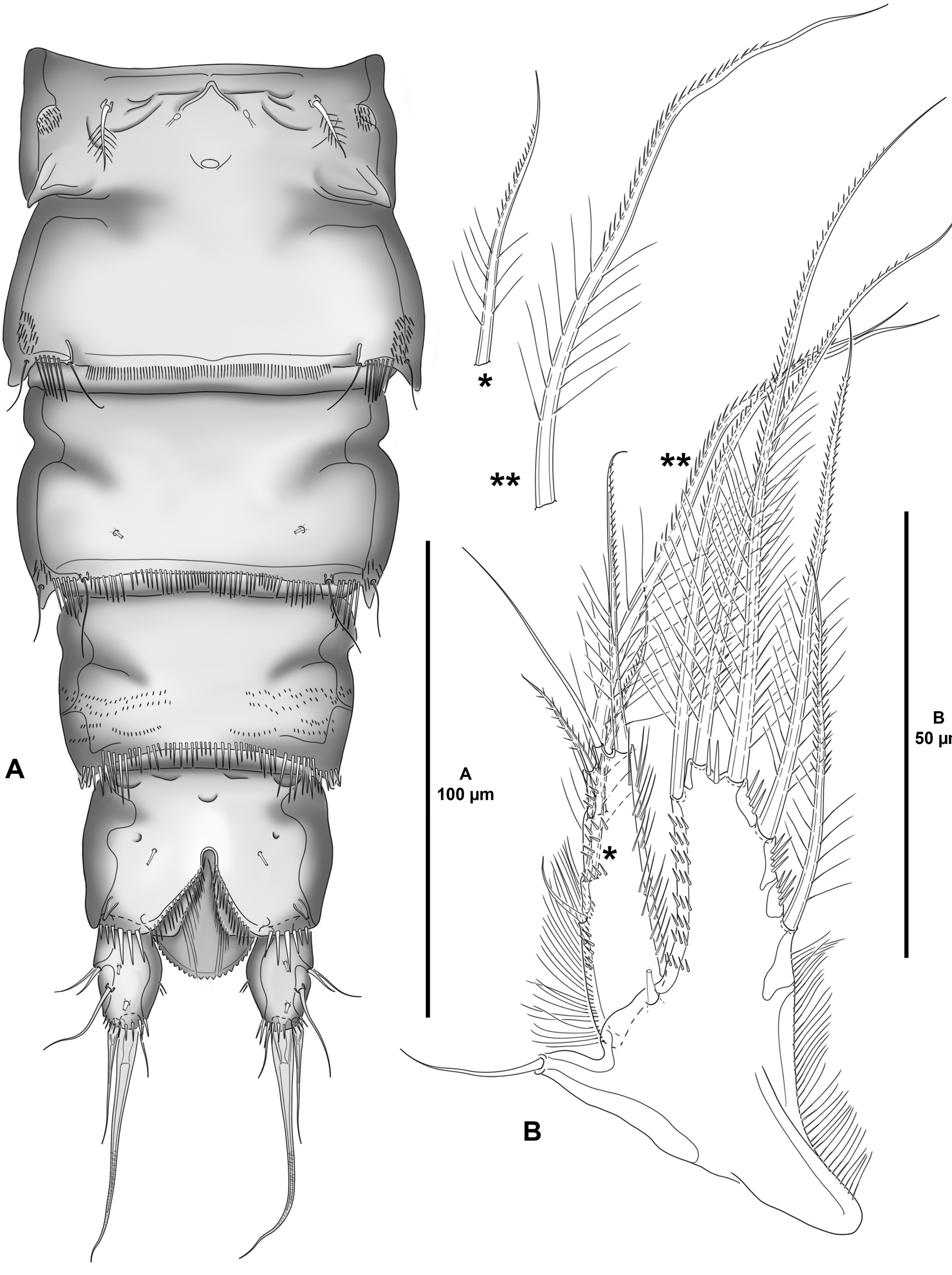

FIGURE 2. *Arktourella margarethae* gen. et sp. nov., female. A, urosome, ventral; B, P5, anterior (inserts show medial and distal outer setae for clarity).

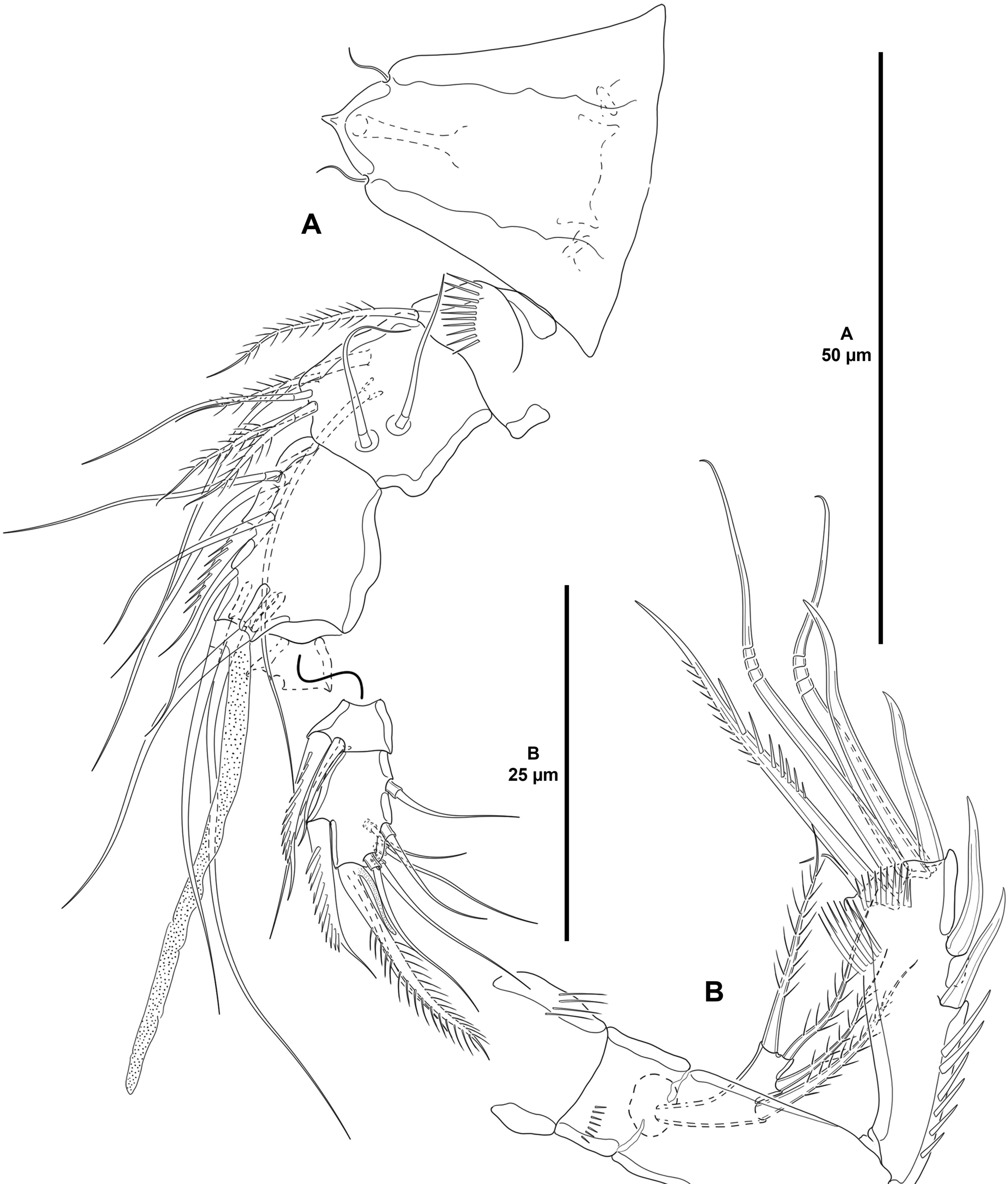

FIGURE 3. *Arktourella margarethae* gen. et sp. nov., female. A, rostrum and antennule; B, antenna.

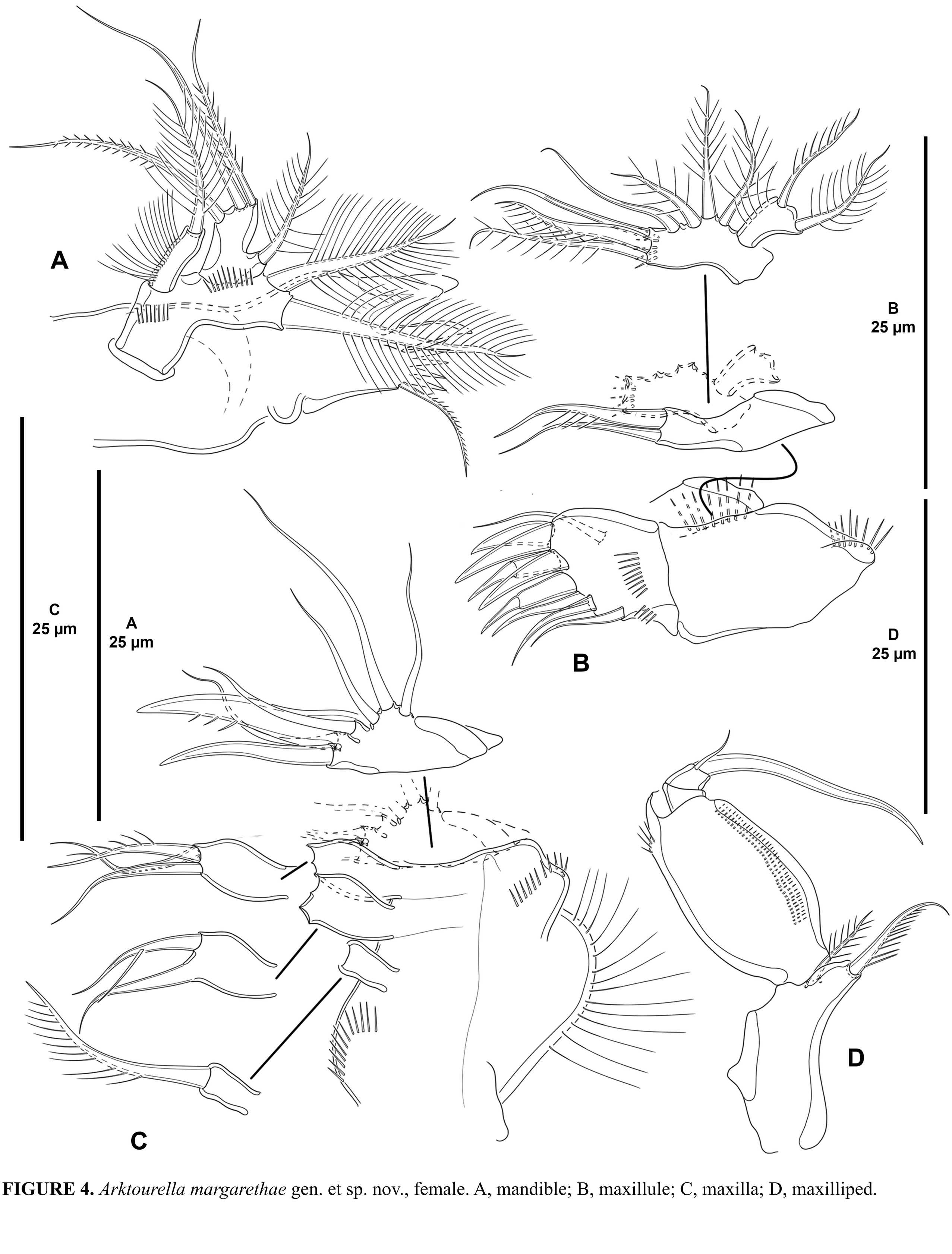

FIGURE 4. *Arktourella margarethae* gen. et sp. nov., female. A, mandible; B, maxillule; C, maxilla; D, maxilliped.

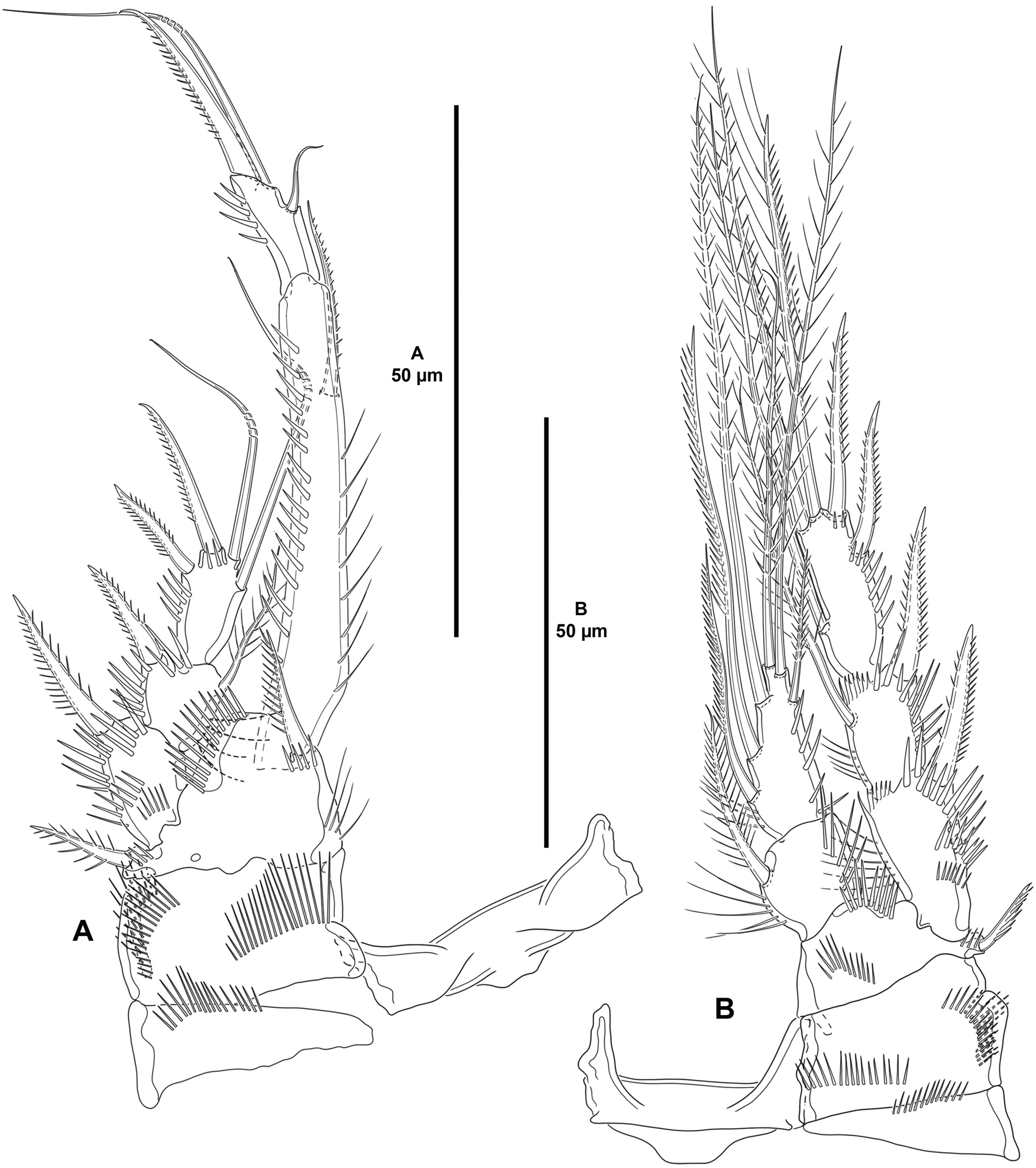

FIGURE 5. *Arktourella margarethae* gen. et sp. nov., female. A, P1, anterior; B, P2, anterior.

Antenna (Fig. 3B) with small coxa furnished with few outer spinules. Allobasis with short row of spinules proximally, armed with one abexopodal seta, with outer and inner remainder of original division between basis and first endopodal segment. Free endopodal segment as long as allobasis, with outer spinules and two subdistal inner frills; with two inner lateral spines, distally with two inner spines, two medial geniculate setae, and one outer spinulose element fused basally to outer small seta. Exopod one-segmented, armed with four setae —two lateral and two distal.

Mandible (Fig. 4A) with well-developed coxa; gnathobase well-developed, with two bicuspidate teeth, set of four spines, and one long ventral unipinnate seta. Palp biramous. Basis with spinules proximally and at base of endopod, with two strong bipinnate setae. Endopod one-segmented, with one lateral and three distal elements. Exopod one-segmented, elongate, with slender long outer spinules and armed with one distal seta.

Maxillule (Fig. 4B) with robust praecoxa ornamented with spinules proximally and at base of coxal endite; arthrite with short rows of surface spinules as shown, with one surface seta, seven distal elements —five strong and two thinner spines—, and one lateral element. Coxal endite with two setae. Basis with few spinules distally, with two endites of which distal with three, proximal with two setae. Endopod fully incorporated to basis and represented by two setae. Exopod one-segmented, with two setae.

Maxilla (Fig. 4C) with syncoxa ornamented with small proximal inner, outer small subdistal, and outer medial long slender spinules; with three endites of which proximal with one, medial with two, distal with three elements. Allobasis drawn out into claw accompanied by one posterior and one anterior accompanying seta, additionally with strong proximal claw. Endopod completely incorporated to basis, represented by three setae.

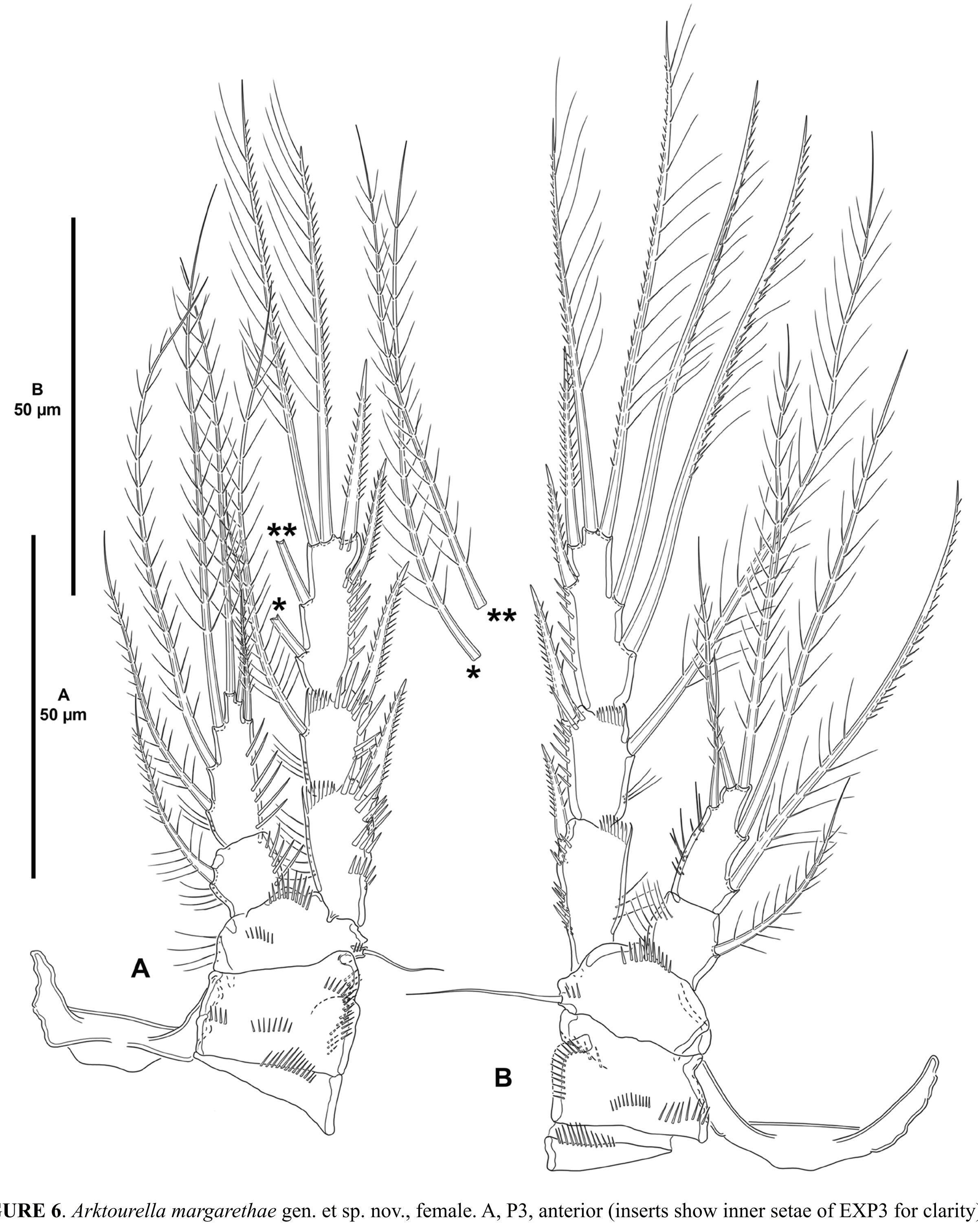

FIGURE 6. *Arktourella margarethae* gen. et sp. nov., female. A, P3, anterior (inserts show inner setae of EXP3 for clarity); B, P4, anterior.

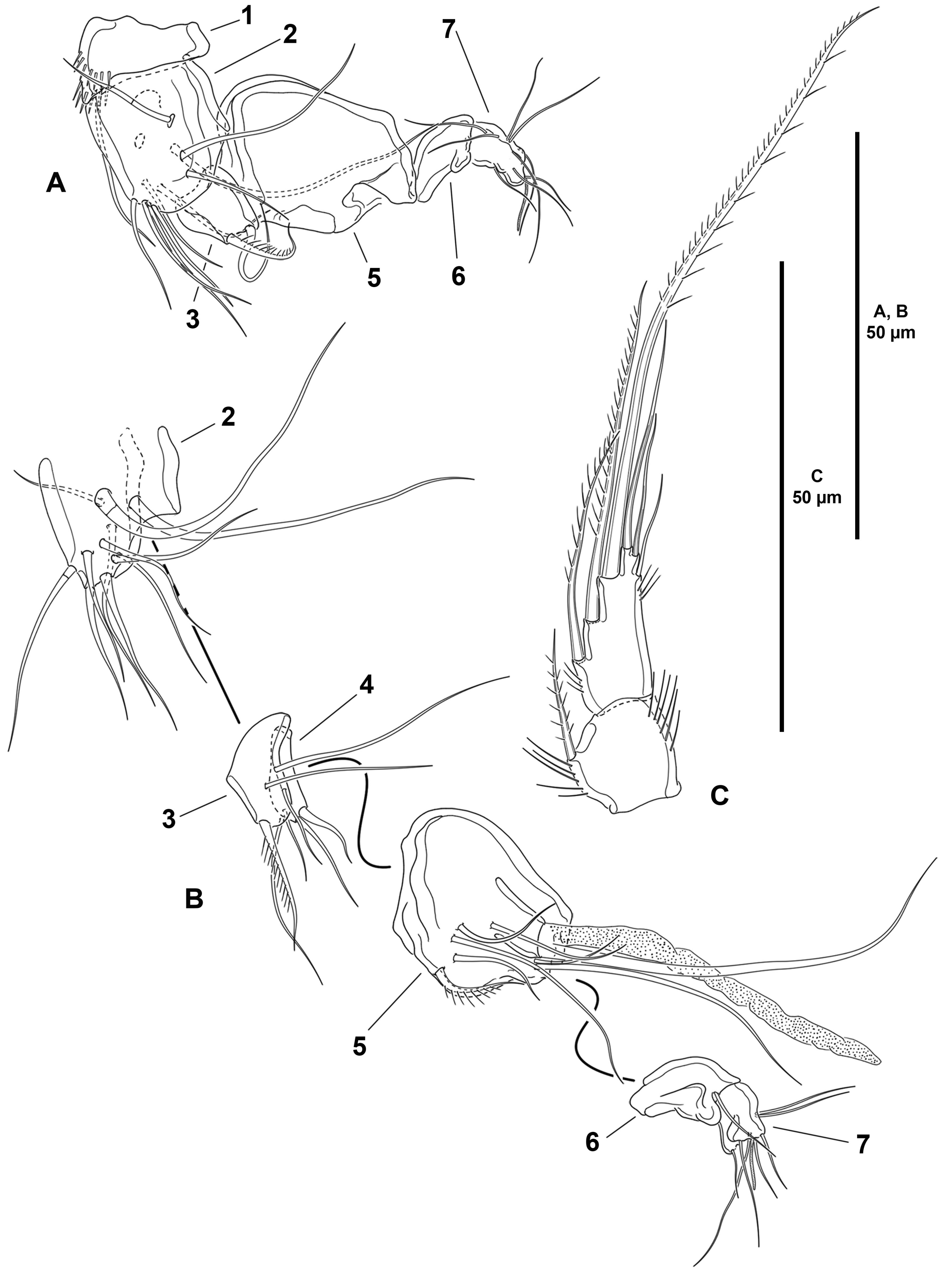

FIGURE 7. *Arktourella margarethae* gen. et sp. nov., male. A, antennule (actual segments are numbered with Arabic numerals); B, P2 ENP.

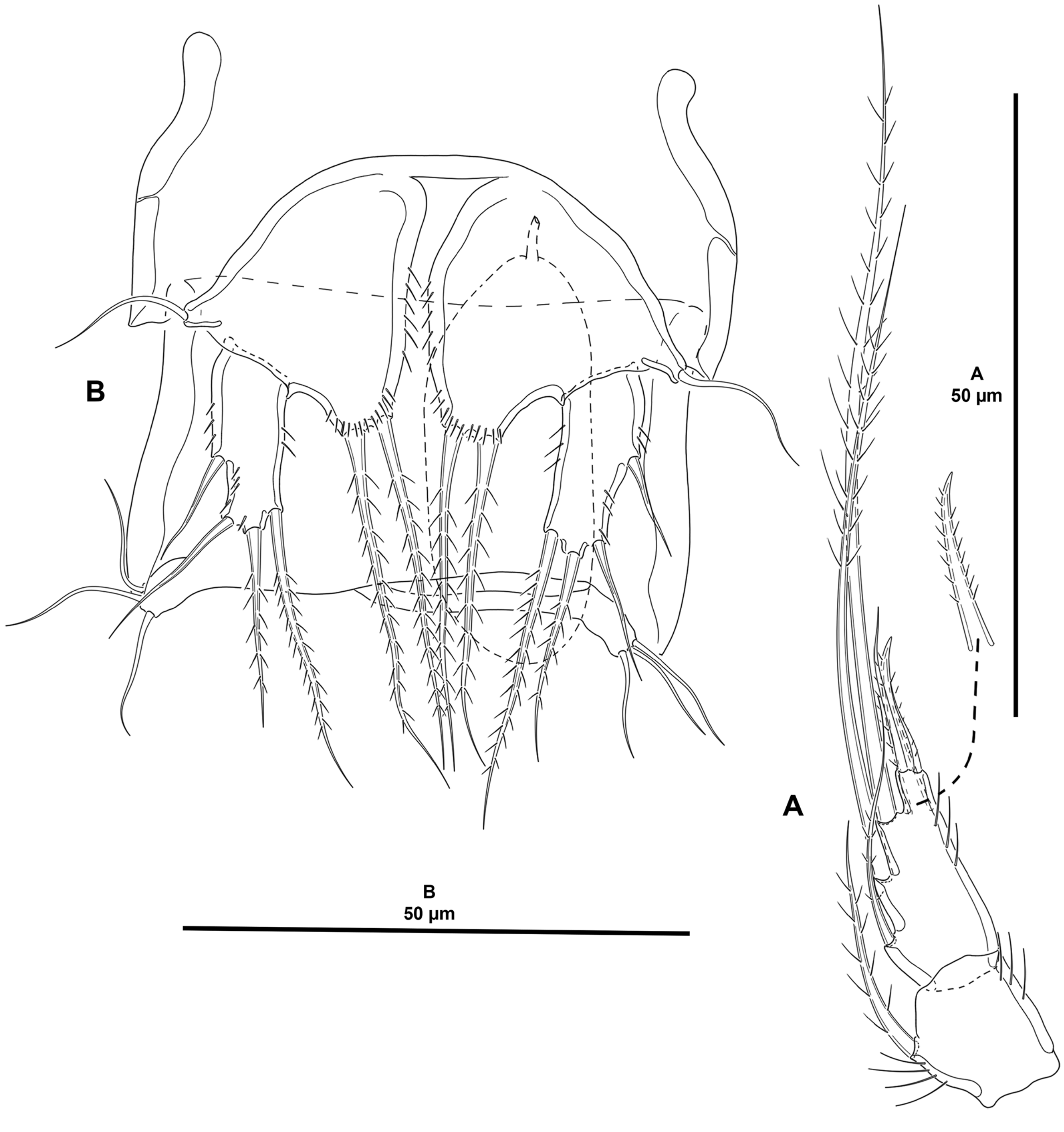

FIGURE 8. *Arktourella margarethae* gen. et sp. nov., male. A, P3 ENP, anterior; B, P5 and P6, anterior.

Maxilliped (Fig. 4D) subchelate. Syncoxa unornamented, with two distal setae. Basis with longitudinal row of small spinules, and with few subdistal outer spinules, unarmed. Endopod one-segmented, with long claw accompanied by short seta.

P1 (Fig. 5A) with elongate bare intercoxal sclerite, the latter with distal outer short extension on each side. Praecoxa triangular, with distal row of spinules. Coxa rectangular, with one medial transverse and one outer longitudinal row of anterior spinules, and with one outer longitudinal row of posterior spinules. Basis largely triangular, with one proximal pore, with long slender outer spinules proximally, with stronger shorter ones at the base of inner and outer spines, and with longer spinules between rami. Exopod situated at a lower level than the endopod and reaching proximal third of first endopodal segment, three-segmented; segments subequal in length, spinular ornamentation as shown; first segment without, second segment with inner seta, third segment with four elements —two outer spines, and two distal geniculate setae of which innermost displaced to inner margin. Endopod two-segmented; first segment elongate, about five times as long as wide —widest part measured proximally— with inner slender and outer strong spinules longitudinally, with one subdistal inner seta; second segment short, three times as long as wide and 0.25 times as long as first segment, with one inner short seta, and two distal elements —one distal inner geniculate seta and one distal outer unipinnate spine.

P2–P4 (Figs. 5B, 6A, B) with elongate smooth intercoxal sclerites, the latter with distal outer extension on each side, U-shaped; of P2 thickest, of P4 slenderest. Praecoxa triangular, with transverse row of medial spinules distally. Coxa rectangular, with anterior and posterior spinules as shown. Basis trapezoid; of P2 and P3 with spinules medially, at base of outer element, and between rami, of P4 with spinules at the base of outer element and between rami, and P2 and P4 seemingly without, of P3 with long slender inner spinules; outer element of P2 a unipinnate spine, of P3 and P4 a slender naked seta. Exopods three-segmented; first and third segments subequal in length, second segment shortest; first and second segments with, third segment without inner distal frill; spinular ornamentation of segments as shown; first segment without, second segment with inner well-developed seta; third segment with two outer spines, two distal setae, and one (P2), and two (P3 and P4) inner setae of which proximal inner seta of P4 EXP3 visibly thicker. Endopods two-segmented, of P2 and P3 reaching slightly beyond, of P4 reaching middle of EXP2; first segment shorter than second one, of P2 and P3 with long slender inner spinules and comparatively stronger outer ones, of P4 with long slender inner spinules only, with one inner seta; second segment with outer spinules as shown, with one outer subdistal and two distal elements —outermost of which at a lower level—, and three (P2 and P3) and two (P4) inner setae.

P1–P4 armature formulae as follows:

	P1	P2	P3	P4
Exopod	0.1.022	0.1.122	0.1.222	0.1.222
Endopod	1.120	1.321	1.321	1.221

P5 (Fig. 2B) with baseoendopod and exopod distinct, elongate and narrow, ornamented with spinules as depicted. Baseoendopod with outer seta arising from setophore; endopodal lobe with tube-pore close to exopod, with two inner —one medial, one subdistal—, two distal, and one outer seta. Exopod with three outer setae of which proximal very short, and three distal setae.

Genital field (Fig. 2A) with median copulatory pore on first half of genital double-somite; each P6 represented by one bipinnate seta.

Description of the male. Total body length ranging from 330 µm to 360 µm (mean= 341.6 µm, n= 3; allotype, 360 µm) measured from anterior tip of rostrum to posterior margin of caudal rami. Habitus (not shown) as in female. Sexual dimorphism expressed in separated genital somite and third urosomite, antennule, P2 and P3 ENP, P5 and P6.

Antennule (Fig. 7A, B) subchirocer, seven-segmented, with geniculation between fourth and fifth, and fifth and sixth segments, with two segments distal to second geniculation. Armature formula difficult to define, most probably as follows: 1[1], 2[11], 3[6], 4[2], 5[7+(1+ae)], 6[1], 7[5+ (1+ae)].

Mandible, maxillule, maxilla and maxilliped (not shown) as in female.

P1 (not shown) as in female.

P2 EXP (not shown) as in female; ENP (Fig. 7C) as in female except for comparatively shorter inner seta of ENP1, and comparatively shorter distal, subdistal outer and outer setae of ENP2.

P3 EXP (not shown) as in female; ENP (Fig. 8A) as in female except for comparatively shorter inner seta of ENP1, comparatively shorter distal inner and outer seta of ENP2, and for outer apophysis of ENP2.

P4 (not shown) as in female.

P5 (Fig. 8B) with baseoendopod and exopod distinct; both baseoendopods fused medially; outer seta arising from setophore. Endopodal lobe reaching proximal third of exopod, with two setae. Exopod elongate, about three times as long as wide, with two outer setae —one medial, one subdistal—, and two distal setae of which innermost displaced to inner margin.

P6 (Fig. 8B) asymmetrical, only one leg functional, the other fused to somite; each leg with three setae.

Variability. No variability was detected in the specimens inspected.

Etymology. The species is named after the senior author's godmother Margarita Noguera Farfán for her 73rd birthday. The binomen is for the 49th wedding anniversary of the senior author's godfather Arturo Villanueva Robertson with the senior author's godmother Margarita Noguera Farfán. It is a noun in the genitive case, gender feminine.

Phylogenetic analyses

The parsimony analysis yielded two equally parsimonious trees (Fig. 9A, B) (tree length 99) and a consensus tree (Fig. 9C). The topology of the laophontoidean families in these trees are as in Huys (1990b) and Huys & Lee (1999), being Normanellidae the most basal family and the sister taxon of Laophontidae. The superfamily was supported by a high bootstrap value (100%) (Fig. 9D); the Laophontidae-Cristacoxidae clade (see Fig. 9D) was supported by a bootstrap value of 82%. The topology of the Normanellidae is similar in trees 1 and 2, and in the consensus tree, with a polytomy in *Normanella*-*Sagamiella*-[*Paranaiara*-*Pseudocletodes*] (tree 1; Fig. 9A), *Sagamiella*-[*Arktourella* gen. nov.-*Normanella*]-[*Paranaiara*-*Pseudocletodes*] (tree2; Fig. 9B), and *Arktourella* gen. nov.-*Normanella*-*Sagamiella*-[*Paranaiara*-*Pseudocletodes*] (consensus tree; Fig. 9C). *Paranaiara* and *Pseudocletodes* were shown consistently as sister taxa. The bootstrap tree (Fig. 9D) is more similar to tree 2 (Fig. 9B) than to tree 1 (Fig. 9A) and the consensus tree (Fig. 9C), in that *Sagamiella* appears as the sister taxon of all remaining genera; also, *Paranaiara* and *Pseudocletodes* appears consistently as the most closely related taxa. The bootstrap analysis yielded a relatively low bootstrap value for Normanellidae (43%); *Sagamiella* is shown as the sister taxon of *Arktourella* gen. nov.-*Normanella* (the latter with a low bootstrap value of 12%) and *Paranaiara*-*Pseudocletodes* (the latter with a bootstrap value of 69%). The Bayesian inference analysis yielded a fully resolved tree for the Laophontoidea supported by a high Bayesian posterior probability value (BPP) (Fig. 9E). The Normanellidae appears as the first offshoot within the superfamily and is supported by a relatively high BPP value (0.73); the lowest BPP value was shown for the clade Cristacoxidae-Laophontopsidae-Orthopsyllidae (0.67). Within the Normanellidae, *Pseudocletodes* is most closely related to *Paranaiara*; this clade appears as the first offshoot within the family and is supported by a BPP value of 0.93 and appears as the sister taxon of [*Normanella*-*Arktourella* gen. nov.]-*Sagamiella* (the latter clade is supported by a low BPP value of 0.25). *Normanella* and *Arktourella* gen. nov. are closely related to each other; this clade is supported by a BPP value of 0.51 and appears as the sister taxon of *Sagamiella*.

Discussion

Historical background

The history of the family Normanellidae can be traced back to the creation of the genus *Normanella* by Brady (1880) to reallocate *Laophonte dubia*. He (Brady 1880) placed *Normanella* in his newly proposed subfamily Cathocamptinae Brady 1880. Lang (1934) included *Normanella* into the Laophontidae, but Monard (1935a) believed that *Normanella* was not related to *Laophonte* Philippi 1840, but to the Canthocamptidae¸ and proposed to allocate *Mesochra minuta* Boeck 1872 (=*N. minuta* (Boeck 1872)), *N. mucronata* Sars 1909, *N. tenuifurca* Sars 1909, *N. incerta* Lang 1934, *N. quarta* Monard 1935b, and *N. semitica* Monard 1935a in a separate subfamily for which he did not give a name nor a diagnosis. In an attempt to narrow the boundaries of the Laophontidae, Nicholls (1941) believed that *Normanella* occupied an intermediate position between the Cletodidae Scott T. 1905 and the Canthocamptidae, and proposed to remove *Normanella* and *Cletopsyllus* from the Laophontidae and to reallocate them into the Canthocamptidae. Lang (1944) did not follow Nicholls' (1941) view and subdivided the Laophontidae into three subfamilies, Laophontinae Lang 1944, Donsiellinae Lang 1944, and Normanellinae Lang 1944, the latter for *Cleta* Claus 1863, *Normanella*, *Cletopsyllus*, and *Pseudocleta* Lang 1944. Probably unaware of Lang's (1944) proposal of the Normanellinae, and inspired in the similarity of the first leg of *Normanella* and *Cletopsyllus* noted by Willey (1935), Nicholls (1945) proposed and diagnosed the family *Normanellidae* for *Cletopsyllus* and *Normanella*. Lang (1948) did not add Nicholls' (1945) paper in his monograph, and followed his own scheme of 1944 regarding the subdivision of the Laophontidae. Lang (1948) believed that *Normanella* and *Cletopsyllus* are closely related, and that *Cleta* and *Pseudocleta* can be regarded as more specialized forms within *Normanella*. The Donsiellinae was recognized as the closest relative of the Pseudotachidiinae Lang 1936 and was reallocated into the Thalestridae (Hicks 1988; Huys 1988). At the time of publication of Lang's (1948) monograph, the Normanellinae included the genera *Cleta*, *Pseudocleta*, *Normanella*, and *Cletopsyllus*. The taxonomic concept of the subfamily Normanellinae was revised by Huys & Willems (1989) who proposed the family Laophontopsidae Huys & Willems 1989 for *Laophontopsis* Sars 1908, *Aculeopsis* Huys & Willems 1989 and *Telodocus* Huys & Willems 1989, and revised Lang's (1948) subdivision of the Normanellinae into the *Cleta* and *Normanella* groups on the basis of the armature of P1 and P2 ENP. As a result, they (Huys & Willems 1989) upgraded provisionally the Normanellinae to family level to further narrow the diagnosis of the Laophontidae, and subdivided the Normanellidae into two subfamilies, Normanellinae (*Normanella*) and Cletopsyllinae Huys & Willems 1989 (*Cletopsyllus–Pseudocletopsyllus* Vervoort 1964; the latter considered as *incertae sedis* within the Cletopsyllinae), and relegated *Pseudocleta* to *incertae sedis* within the Laophontoidea. At this point, *Normanella* (with 13 species, and one species inquirenda) was the only genus within the Normanellidae (Huys & Willems 1989). One year later, Huys (1990) gave a list of apomorphies for the Laophontoidea, excluded the Normanellidae and Cletopsyllidae from that superfamily, and recognized the Laophontidae as the first offshoot within the Laophontoidea. Huys & Lee (1998) re-assessed the phylogenetic relationships of the families of the Laophontoidea and noted that the Normanellidae actually bears a sister-group relationship with the other laophontoidean genera as evidenced by several synapomorphies (Huys & Lee 1998: 270–271), and re-incorporated the former into the latter. Additionally, Huys & Lee (1998) relegated the genus *Pseudocletopsyllus* as *genus inquirendum*, and formally gave full family rank to Cletopsyllinae. In their review of the genus *Normanella,* Lee & Huys (1999) recognized five evolutionary lineages within the genus, and created the genus *Sagamiella* for *S. latirostrata* Lee & Huys 1999 and *S. aberrans* (Bodin 1968). More recently, Kihara & Huys (2009) added the monotypic genus *Paranaiara*, removed *Pseudocletodes* from the Nannopodidae Brady 1880 and reallocated it into the Normanellidae, and presented an amended diagnosis for the latter family. At this point, the Normanellidae included the type genus *Normanella* (18 valid species; *N. quarta*, *N. semitica*, and *N. serrata* Por 1959, and the records of *N. minuta* by Willey (1930) and Bodin (1972), *N. serrata* by Božić (1964) and Marinov & Apostolov (1985), and *N. mucronata* by Marinov (1977) were relegated to *species inquirendae*) (Lee & Huys 1999), *Pseudocletodes* (monotypic) (Kihara & Huys 2009), *Sagamiella* (two species) (Lee & Huys 1999), and *Paranaiara* (monotypic) (Kihara & Huys 2009).

Justification and relationships of *Arktourella* gen. nov.

The phylogenetic relationships amongst the laophontoidean families have been outlined before in Huys (1990a), Huys (1990b), Huys & Lee (1999) and Kihara & Huys (2009) and won't be discussed here. *Arktourella* gen. nov. was attributed to the Laophontoidea and to the Normanellidae in particular on account of the lack of outer spinous processes on the second antennulary segment, antennary allobasis with one abexopodal seta, one-segmented antennary exopod armed with four setae, P1 ENP two-segmented with elongate ENP1 and with two distal elements on ENP2, two-segmented P2–P4 endopods, distal setae on the male P2 ENP2 and P3 ENP2 reduced, and outer spine of the male P3 ENP2 fused to segment (the two latter autapomorphic for Normanellidae; Lee & Huys 1999). However, the Mexican specimens could not be attributed to any of the known normanellid genera due to the presence of four elements on the P1 EXP3 (character 23), and reduction of the outer armature on P2–P4 EXP3 from three to two spines (characters 30, 38, and 47, respectively). The reduction of the outer armature of P1 EXP3 from three to two spines (four elements in all) seems to have occurred independently in all laophontoidean families except for the Normanellidae, and such reduction is considered here apomorphic for *Arktourella* gen. nov. Similarly, all the normanellid genera except for *Arktourella* gen. nov. possess three outer spines on P2–P4 EXP3; the loss of one outer spine on P2–P4 EXP3 seems to have occurred also independently in Cristacoxidae, in some adenopleurellids and in some laophontopsids (Laophontidae and Orthopsyllidae Huys 1990a possess three outer spines on P2–P4 EXP3), and the reduction in outer armature on P2–P4 EXP3 is considered here as another apomorphy for the new genus within the Normanellidae.

Within Normanellidae, *Paranaiara* and *Pseudocletodes* were shown consistently as closely related (see Fig. 9) and are the sister taxa of *Normanella*-*Arktourella* gen. nov.-*Sagamiella*. The *Paranaiara*-*Pseudocletodes* clade is supported by a relatively high bootstrap value of 69%, and a high BPP value of 0.93%. These two genera share the synapomorphic unisetose mandibular basis (character 14), the unarmed maxillipedal syncoxa (character 21), the absence of an outer element on the P2 ENP2 (character 36), the reduction from three to two inner setae on P3 ENP2 (character 44), and the lamelliform caudal rami (character 58; the latter being autapomorphic for this clade), but also the lack of spinular ornamentation on the maxillipedal basis and the bisetose maxillulary endopod (Kihara & Huys 2009). These two genera also share the plesiomorphic presence of two abexopodal setae (one basal, one endopodal) on the antennary allobasis (character 13). The unisetose mandibular basis is also present in Adenopleurellidae Huys 1990b and in Laophontopsidae; the lack of inner armature on P2 ENP occurs also in

Adenopleurellidae, Cristacoxidae Huys 1990a, Laophontopsidae, and in Orthopsyllidae; two inner setae on P3 ENP2 occur also in Adenopleurellidae.

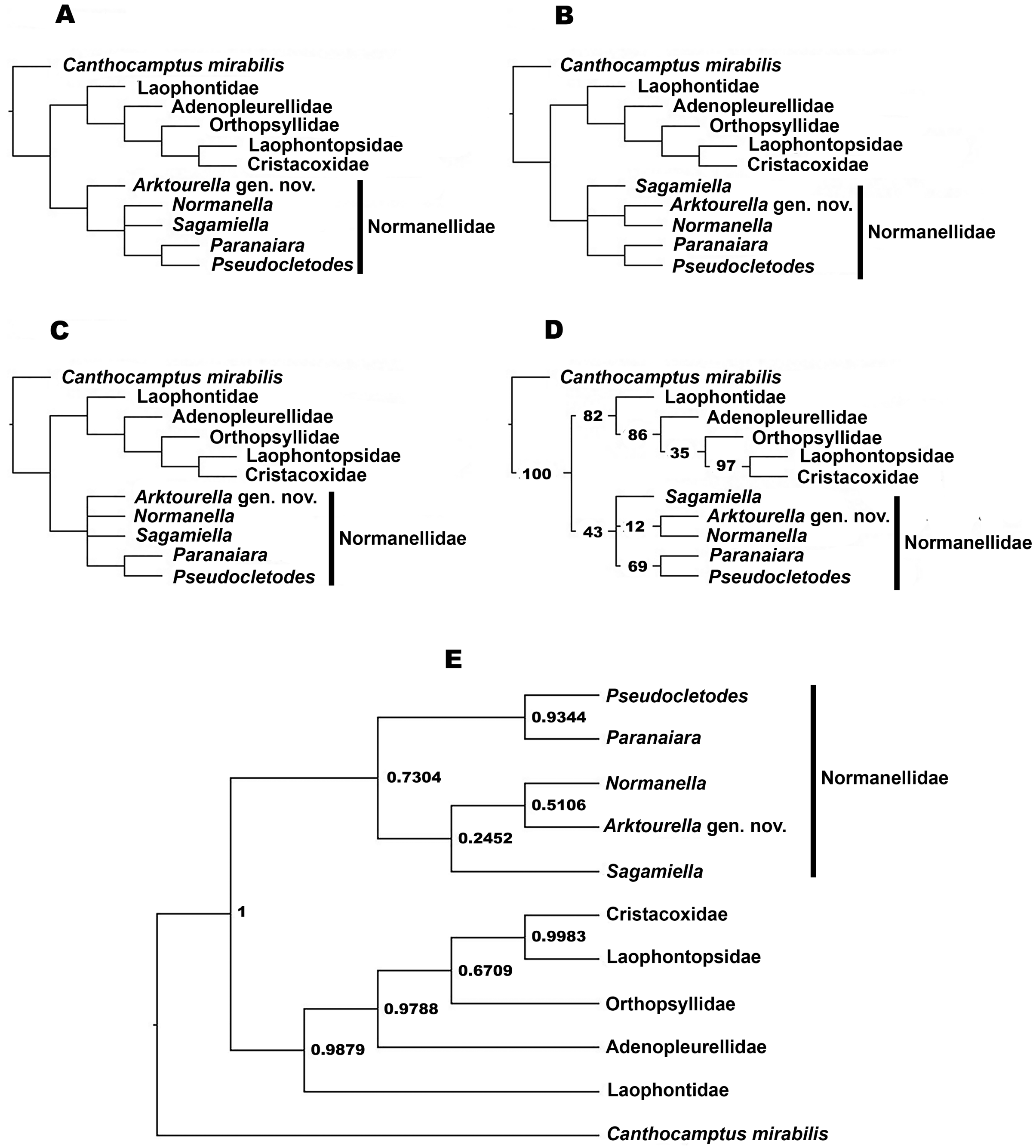

FIGURE 9. Cladograms showing relationships amongst the families of the Laophontoidea, and amongst the genera of the family Normanellidae. A, tree 1 obtained with TNT (maximum parsimony); B, tree 2 obtained with TNT (maximum parsimony); C, strict consensus tree obtained with TNT (maximum parsimony); D, bootstrap tree obtained with TNT (numbers indicate bootstrap values); E, strict consensus tree obtained with Bayesian inference (numbers indicate posterior probabilities of nodes).

The relationships amongst *Sagamiella*, *Normanella*, and *Arktourella* gen. nov. are not clear, but *Sagamiella* seems to be the sister taxon of *Arktourella* gen. nov.-*Normanella*. These three genera share the plesiomorphic bisetose mandibular basis (character 14), the presence of two setae on the maxillipedal syncoxa (character 21), and the presence of an outer element on P2 ENP2 (character 36), and the (syn) apomorphic prehensile P1 ENP (character 26) and loss of the basal abexopodal seta of the antennary allobasis (character 13), i.e., only one instead of two setae on the antennary allobasis. *Sagamiella* differs from *Arktourella* gen. nov.-*Normanella* in the reduced armature complement of the antennary exopod (three setae in *Sagamiella*, but four elements in *Arktourella* gen.

nov.-*Normanella*) (character 11), in the mandibular endopod incorporated into basis (separated in *Arktourella* gen. nov.-*Normanella*; this character appears also in *Pseudocletodes* and *Paranaiara*) (character 16), and in the maxillulary basis with one endite (two endites in the other Normanellidae) (character 17); the latter is apomorphic for *Sagamiella*, and is also present in Adenopleurellidae, Laophontidae, and Orthopsyllidae. We did not detect any synapomorphy for *Arktourella* gen. nov.-*Normanella*, but these two genera are unique within the Normanellidae in the —plesiomorphic— mandibular basis and endopod separated (character 16), which occurs also in Cristacoxidae and in some Laophontidae.

Kihara & Huys (2009) noted that a large spinulose spine is present on the fifth and sixth segments of the female antennule in *Paranaiara* and *Pseudocletodes*. Similar spines are also present in *Arktourella* gen. nov., but its significance is not clear.

Key to the genera of the family Normanellidae

1a. P1 endopod absent . . . . ***Pseudocletodes***

1b. P1 endopod present, two-segmented **2**

2a. P1 endopod prehensile; P1 ENP1 elongate bearing inner seta, ENP2 short; male P5 with two elements on endopodal lobe . . **3**

2b. P1 endopod not prehensile; P1 ENP1 as long as ENP2, and without inner seta; male P5 with four elements on endopodal lobe . . . . ***Paranaiara***

3a. Antennary exopod with three setae; maxillulary basis with one endite; male P6 with two setae; cephalothorax without areolated pattern . . . . ***Sagamiella***

3b. Antennary exopod with four setae; maxillulary basis bearing two endites; male P6 with three setae; cephalothorax with areolated pattern **4**

4a. P1 EXP3 with five elements; P2–P4 EXP3 with three outer spines.. . . . . ***Normanella***

4b. P1 EXP3 with four elements; P2–P4 EXP3 with two outer spines... . . . . ***Arktourella*** **gen. nov.**

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