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New giant genus of Parabathynellidae (Crustacea: Bathynellacea): first record of Bathynellacea in an Australian cave

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Abstract. A new genus and species of Parabathynellidae (Crustacea: Bathynellacea), *Megabathynella totemensis* Camacho & Abrams gen. et sp. nov., is described from the Northern Territory, Australia. This species is the first to be described from an Australian cave. It is a new giant species (4 to 6 mm). The new species displays several unique morphological character states within Parabathynellidae and is the only known species with: more than 12 articles on antennules, with a short, curved barbed seta on each article from the fifth; eight setae on the last article of antennae; more than three setae on the mandibular palp; up to 17 articles on the exopod of the thoracopods, without ctenidia but with a strong spine on each article at the base of the external seta; strong row of pair of spines on latero-external side of second article of endopod in all thoracopods; the male thoracopod VIII is different from all those known; more than 50 spines on the sympod of the uropod and more than 35 spines on the furcal rami. Specimens of the new species are morphologically different from all known species, but more closely resemble some giant species of the genera *Kampucheabathynella* (Asia), and *Billibathynella* and *Brevisomabathynella* (Australia).

Keywords. Parabathynellidae, Crustacea, taxonomy, new taxa, cave, Australia.

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Introduction

The crustacean Malacostraca Latreille, 1802 family Parabathynellidae Noodt, 1965 has a worldwide distribution with 45 genera and 220 species recognized thus far (Camacho & Leclerc 2022). According to Abrams *et al*. (2013), 47 species were known from Australia (including two in Tasmania), distributed in 10 genera across mainland Australia. Since then, one more genus and species have been described, *Lockyerenella danschmidti* Camacho & Little, 2017 from Queensland, two new species of *Hexabathynella* Schminke, 1972 from Rottnest Island (Western Australia) (Perina *et al*. 2023a) and two new species of *Atopobathynella* Schminke, 1973 from the Pilbara region (Perina *et al*. 2023b). In addition, a recent paper by Matthews *et al*. (2020), using a combined approach of molecular species delimitation methods, identified between eight to 24 putative new species from remote subterranean habitats in the Pilbara region of Western Australia (WA). In the last 10 years, the delineation of parabathynellid species using molecular methods has focused on Queensland (QLD) (Cook *et al.* 2012; Little *et al*. 2016; Little & Camacho 2017), South Australia (SA) (Abrams *et al*. 2012, 2013), New South Wales (NSW) (Asmyhr & Cooper 2012), and the Yilgarn region, WA (Guzik *et al.* 2008; Abrams *et al.* 2012, 2013). Therefore, the diversity of species is much greater than the 52 species formally described and assigned to 11 genera.

As previously noted by Cho & Humphreys (2010), each new finding not only increases the known diversity in the area, but also the morphological novelties. The description of this new genus does not disappoint in this sense since it presents several morphological characters that have not been previously observed in the group and that expand the known morphospace of the Parabathynellidae family. It is a new giant genus and species, more than 4 mm long. Other genera that contain giant species include the Australian genera *Brevisomabathynella* Cho, Park & Ranga Reddy, 2006, and *Billibathynella* Cho, 2005, and the Cambodian genus *Kampucheabathynella* Cho, Kry & Chhenh, 2015. Here, we consider species larger than 4 mm to be 'giant' and those of 2.5–4 mm to be 'large'.

Unfortunately, despite multiple DNA extraction attempts on five specimens, we were unable to obtain sequences for this new genus, therefore, we were not able to place them in current global parabathynellid molecular phylogenetic frameworks (Little *et al.* 2016; Matthews *et al*. 2020; Camacho *et al.* 2021; Perina *et al.* 2023a, 2023b).

Material and methods

Study area

Totem Pole Cave is located in the Pungalina Karst area (-16°48′0.9972″ S, 137°27′1.0002″ E) on the eastern margin of the Northern Territory near the border with Queensland in the Gulf of Carpentaria. The karst is a Precambrian dolomite and stromatolite fossils are common throughout the karst area.

Specimens were collected from a shallow pool of clear water (15 cm deep and 1 m^2) in a cave passage approximately 150 m from the entrance and approximately 10 m above the phreatic zone. Numerous pools of water were present in the cave above the phreatic zone due to the recent cyclone and associated rainfall in the area. Specimens were collected by hand, using a forceps and placed into 70% ethanol. The small pool was densely populated with an estimated 80–100 individuals. Several adjacent pools of similar size contained individuals but in lower abundance. No other specimens were observed in the remainder of the cave.

Morphological study

Ten specimens used for the study are listed in Table 1. Two entire specimens (mounted completely) and eight completely dissected (all body appendages separately) were preserved as permanent slides (special metal slides, glycerine-gelatine stained with methylene blue and paraffin as the mounting medium (see Perina & Camacho 2016). Anatomical examinations were performed using an oil immersion lens

Table 1 (continued on next page). Variability between studied specimens with their museum voucher numbers. Abbreviations: art = articles; ARTP/MNCN = MNCN Arthropod collection; B = barbed; Bsp = basipod; D = distal; DE = distal end; Exp = exopod; L = lateral; MAGNT = Museum and Art Gallery of the Northern Territory; P = plumose; Symp = sympod; WAM = Western Australian Museum.

Voucher **Type series** **Sex**	**NTM Cr19142** **Allotype** **Female**	**NTM Cr19141** **Holotype** **Male**	**WAM C73466G** **Paratype** **Male**	**WAM C73466H** **Paratype** **Male**	**MNCN 20.04/20931** **Paratype** **Male**	**WAM C73466J** **Paratype** **Female**	**MNCN 20.04/20932** **Paratype** **Female**	**WAM C73466L** **Paratype** **Female**
Size	6.2	5.9	5.4	4.3	5.9	5.4	5.7	6.1
AI-articles	15	13	14	13	14	13	14	14
Md: pars distalis	12	12	8	10	9	10	8	10
Pars molaris	23	18	21	22	22	20	20	20
Setae Md palp	9	7	8	8	9	–	9	–
MxI: claws (D.end)	11	10	10	11	11	10	11	11
ThI: Bsp, setae	3	4	4	4	4	4	4	5
Exp: art number	12	14	11	11	13	12	13	13
art 1, setae	3+6	4+5	1+3	3+7	3+4	1+3	1+5	2+6
End: art 1, setae	8+2	2+1	7+1	9+1	5+1	8+1	9+1	6+1
art 2, setae	8+3	3+4	8+2	5+2	5+3	6+2	5+3	6+3
art 3, setae	8+1	3+1	5+1	5+1	6+1	4+1	6+1	5+1
ThII: Bsp, setae	5	4	4/5	4	4	4	4	5
Exp: art number	17	16	14	16	16	15	17	16
art 1, setae	2+4	4+4	2+3	3+5	3+4	2+3	5+3	3+5
End: art 1, setae	2+1	2+1	4+1	3+1	2+1	3+1	4+1	3+1
art 2, setae	3+5	3+4	3+4	4+4	3+4	3+4	5+4	3+4
art 3, setae	4+1	5+1	3–6+1	3–2+1	4+1	3+1	4+1	3+1
ThIII: Bsp, setae	5	4/5	4	4	4	4	4	5
Exp: art number	18	16	15	16	17	16	17	18
art 1, setae	3+4	4+4	2+3	2+4	3+4	2+2	3+4	2+4
End: art 1, setae	2+1	2+1	2+1	3+1	2+1	2+1	2+1	2+1
art 2, setae	4+4	3+4	3+3	3+3	3+5	3+4	3+5	3+4
art 3, setae	5+1	4+1	4+1	4+1	4+1	4+1	4+1	3+1
ThIV: Bsp, setae	4	4/5	4	4	4	4	4	5
Exp: art number	18	17	15	15	17	17	17	18
art 1, setae	3+4	2+5	3+3	3+4	3+4	2+3	2+3	3+4
End: art 1, setae	2+1	1+1	1–2+1	2+1	2+1	2+1	2-3+1	2+1
art 2, setae	3+5	4+2	3+4	4+5	3+5	3+4	3+5	3+4
art 3, setae	3+1	5+1	4+1	3–5+1	3+1	3+1	3+1	3+1
ThV: Bsp, setae	4	4/5	4	3	4	4	5	3
Exp: art number	18	17	15	15	17	16	16	18
art 1, setae	2+4	3+4	3+4	3+4	4+4	2+3	3+4	2+4
End: art 1, setae	2+1	1+1	1–2+1	2+1	2+1	2+1	2+1	2+1
art 2, setae	3+4	2+1	3+4	4+5	2+4	3+4	3+5	3+4
art 3, setae	3+1	3+1	4+1	3+1	3+1	3+1	3+1	3+1

Table 1 (continued). Variability between studied specimens with their museum voucher numbers. Abbreviations: art = articles; ARTP/MNCN = MNCN Arthropod collection; B = barbed; Bsp = basipod; D = distal; DE = distal end; Exp = exopod; L = lateral; MAGNT = Museum and Art Gallery of the Northern Territory; P = plumose; Symp = sympod; WAM = Western Australian Museum.

Voucher **Type series** **Sex**	**NTM Cr19142** **Allotype** **Female**	**NTM Cr19141** **Holotype** **Male**	**WAM C73466G** **Paratype** **Male**	**WAM C73466H** **Paratype** **Male**	**MNCN 20.04/20931** **Paratype** **Male**	**WAM C73466J** **Paratype** **Female**	**MNCN 20.04/20932** **Paratype** **Female**	**WAM C73466L** **Paratype** **Female**
ThVI: Bsp, setae	5	4	3	3	4	4	4	5
Exp: art number	17	17	17	15	16	16	16	17
art 1, setae	3+4	3+4	2+2	3+4	3+4	3+3	2+3	2+4
End: art 1, setae	2+1	2+1	1-2+1	1+1	1+1	1+1	2+1	2+1
art 2, setae	3+5	3+4	3+4	3+5	2+4	3+4	3+4	2+4
art 3, setae	4+1	4+1	3+1	3+1	3+1	4+1	4+1	5+1
ThVII: Bsp, setae	3	4	4	4	4	4	4	5
Exp: art number	18	16	17	17	15	16	17	17
art 1, setae	2+3	3+4	–	3+3	3+4	2+3	2+3	3+4
End: art 1, setae	1+1	1+1	1+1	1+1	1+1	1+1	1+1	1+1
art 2, setae	3+5	3+4	3+4	3+5	2+3	2+4	3+5	2+4
art 3, setae	4+1	3+1	3+1	4+1	3+1	3+1	4+1	3+1
ThI-V:								
Enp: art 4, setae	2+2	2+2	2+2	2+2	2+2	2+2	2+2	2+2
ThVI:								
Enp: art 4, setae	2+2	–	2+3	2+2	2+2	2+2	2+2	2+2
ThVII:								
Enp: art 4, setae	2+2	2+2	2+2	2+2	2+2	2+2	2+2	2+2
Uropod:								
Symp: spines	78	59	59	63	63	61	71	56
Exp: setae	3D+10L+5DE	3D+11L+4DE	3D+11L+4DE	3D+11L+4DE	3D+11L+4DE	3D+11L+4DE	3D+11L+4DE	3D+11L+4DE
End: spines	3+2	3+2	3+2	4+2	3+3	3+1	3+2	4+2
setae	3P+2B	3P+2B	3P+2B	3P+2B	3P+2B	3P+2B	3P+2B	3P+2B
Furca: spines	41+2	35+2	37+2	41+2	41+2	41+2	44+2	36+2

(100×) with a Zeiss interference microscope equipped with a drawing tube. Material is deposited in the Museum and Art Gallery of the Northern Territory (MAGNT) and Western Australian Museum (WAM) collections and two specimens of the type series are deposited in the Arthropod Collection of the Museo Nacional de Ciencias Naturales de Madrid (Spain) (MNCN).

We used the terminology proposed by Serban (1972, 1980, 1985) to describe the mandible and male thoracopod VIII.

Abbreviations used in text and figures

Morphology

AI	=	antennule
AII	=	antenna
Art	=	article
BSP, Bsp	=	basipod
Crst Bsp	=	crest of the basipod
D.Lb, D. Lb, D. lob	=	dentate lobe
Endp	=	endopod
Exp	=	exopod
I.Lb, , I. Lb, I. lob	=	inner lobe
Md	=	mandible
Mx.I	=	maxillule
Mx.II	=	maxilla
O.Lb, O. Lb, O. lob	=	outer lobe
Symp	=	sympod
Th I-VIII	=	thoracopods I-VIII
Urp	=	uropod

Acronyms

ARTP/MNCN	=	MNCN Arthropod Collection
CSIC	=	Consejo Superior de Investigaciones Científicas, Spain
MAGNT	=	Museum and Art Gallery of the Northern Territory, The Gardens, NT, Australia
MNCN	=	Museo Nacional de Ciencias Naturales de Madrid, Madrid, Spain
NTM	=	Northern Territory Museum (see MAGNT)
WAM	=	Western Australian Museum, Perth, WA, Australia

Results

Systematic account

Class Malacostraca Latreille, 1802
Order Bathynellacea Chappuis, 1915
Family Parabathynellidae Noodt, 1965

Genus ***Megabathynella*** Camacho & Abrams gen. nov.
urn:lsid:zoobank.org:act:0A114DE6-1E02-47CF-A1B0-366CE8EE03F7

Type species

Megabathynella totemensis Camacho & Abrams gen. et sp. nov. (here designated).

Diagnosis

AI multisegmented with more than 12 articles with terminal aesthetascs present on fifth to last segments. AII 7-segmented. Labrum flat, free margin dentate. Md pars molaris (molar process) protruding; proximal tooth present; mandibular palp bi-segmented with several setae (more than six). Proximal endite of MxI with four claws; ten to 11 claws present on distal endite. Exopod of ThI to ThVII multisegmented (more than 11 articles); epipod present from ThI to ThVII; first and second article of endopod of ThI to ThVII each with a plumose dorsal seta. Male ThVIII unusually large, twice as long as wide; basal region of penial complex supports three independent lobes: inner lobe, outer lobe and dentate lobe; dentate lobe as inner lobe, rounded and as long as the outer lobe; very long curved outer lobe, as a finger; large basipod with a seta and a pronounced crest-like on internal face; dentate small exopod; endopod large with two setae and with the distal end rounded with four teeth and two setae of different sizes, the longest barbed. Female ThVIII one-segmented, almost triangular with three long barbed terminal setae. Pleopods absent. Inhomonomous sympod of uropod, with more than 50 spines, distalmost 25% longer than the rest; endopod with spines, the two terminal spines stronger than the rest, and setae, two barbed apical setae and one subterminal and two basal plumose setae; exopod with more than 16 setae. Furca very enlarged with more than 35 spines. Giant species, more than 4 mm long.

Differential diagnosis

Megabathynella Camacho & Abrams gen. nov. bears some resemblance to the giant genera *Billibathynella*, *Brevisomabathynella* and *Kampucheabathynella* (see Table 2). The new genus has more than 12 segments in AI, while the other genera have seven or 10; however, the new genus shows few teeth on the labrum, 12 to 14 with few lateral denticles, less than the other giant genera (between 12 and 63 teeth); the new genus presents a two-segmented mandibular palp with more than six setae, the general condition is one or up to three setae found in some species of *Billibathynella* and *Brevisomabathynella*; the new genus has up to 18 articles in the exopod of the Ths and always more than 10, while the largest number found never exceeded 13 articles. The maximum number of spines found in the furca of giant species is 23, while the new genus always has more than 35. Similarly, the sympod of the uropod of the new genus has more than 50 spines, in comparison, the maximum counted to date is 28 spines in species of *Billibathynella*. The male ThVIII of the new genus also shows several significant differences: it is very large, with a very special endopod, the rounded and protruded distal end with small teeth and setae is totally novel.

Etymology

This prefix '*Mega-*' comes from the Greek 'μέγας', which means 'big'. The name *Megabathynella* refers to the unusually large size of the new genus.

Distribution

Australia, Northern Territory (present study).

Megabathynella totemensis Camacho & Abrams gen. et sp. nov.
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Figs 1–8, 9F

Diagnosis

AI multisegmented, 12–15 articles with terminal aesthetascs present on fifth to last segments. AII 7-segmented. Labrum flat, free margin with 17–21 teeth. Md pars molaris (molar process) protruding with many well-developed claws (18–23); with strong triangular proximal tooth; mandibular palp bi-segmented with several setae (7–9). Proximal endite of MxI with four claws; 9–11 claws present on distal endite. Exopod of ThI to ThVII multisegmented (11–18 articles); epipod present from ThI to

Table 2 (continued on next page). Character variability in different genera of the 'big' and 'giant' (2.5–4 mm and >4.0 mm in length, respectively) Australian and Asian Parabathynellidae and genera with more than four-segmented exopod of some thoracopods in the world. 1. *Billibathynella* Cho, 2005; 2. *Brevisomabathynella* Cho, Park & Ranga Reddy, 2006; 3. *Octobathynella* Camacho & Hancock, 2010; 4. *Arkaroolabathynella* Abrams & King, 2013; 5. *Lockyerenella* Camacho & Little, 2017; 6. *Kampucheabathynella* Cho, Kry & Chhenh, 2015; 7. *Sinobathynella* Camacho, Trontelj & Zagmajster, 2006; 8. *Allobathynella* Morimoto & Miura, 1957; 9. *Paraeobathynella* Camacho, 2005; 10. *Sketinella* Camacho, 2005; 11. *Notobathynella* Schminke, 1973; and 12. *Megabathynella* Camacho & Abrams gen. nov. Abbreviations: A = absent; AI = antennule; AII = antenna; art = article; C = cave; D.end = distal endite; End = endopod; Exp = exopod; Hom = Homonomous; Inhom = Inhomonomous; Min-max = minimum and maximun length in mm; L = Large; M = Medium-sized; Md = mandible; MxI = maxillule; N = number of; NPr = not pronounced; P = present; Pr = pronounced; R = river bank; Rect = rectangular; S = small; Sp = spring; st = setae; Symp = sympod; Th = thoracopod; ThI = thoracopod 1; ThVIII = thoracopod 8; Urp = uropod; W = well; XL = extralarge. In red character states present only in the new genus.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12. gen. nov.**
AI : N. art	7	7	8	7	7	10	10	6–8	7–9	8	6–8	13–15
Male antennal organ	A	A	A	A	A	A	A	A	A	A	A	A
AII : N. art	7	5	7	5	6	7	6	5–7	6–7	6	5–6	7
Labrum:	Flat	Flat	Convex	Flat	Flat	Flat	Concave	Concave	Concave	Concave	Concave	Flat
N. teeth	22–28	12–63	18–20	8–22	30	21	20	10–22	12–16	12	14–28	17–21
Md: pars distalis	4–6	4–7	4	4	4	4	3	3–6	5–8	6	4–6	7–14
Pars molaris	9–14	5–20	8	6–13	11	13	14	4–12	7–14	8	7–10	18–23
St Md palp	1–3	1–3	1	1	1	1	1	1–2	1	1	1	7–9
MxI: claw (D.end)	7–10	5–7	7	6–9	7	7	7	5–8	7	7	6–8	9–11
ThI–VII:												
N. plumose st endp	2–3	2	2	2	2	2	2	2	2	2	2	2
N st 4th art endp	3–6(1–4)	2–6(0–4)	3(1)	3–4(1–2)	4(2)	3(1)	3(1)	3–4(1–2)	3(1)	3(1)	3–4(1–2)	4–5(2)
ThI: epipod	P	P	A	P	P	A	A	A/P	A	A	A/P	P
Exp: N art	4–8	2–9	3–4	1–4	2	8	7	2–4	3–5	3	1–3	11–17
ThII: epipod	P	P	P	P	P	A	A	A/P	A	A	P	P
ThIII: epipod	P	P	P	P	P	P	P	A/P	A/P	P	P	P
Exp N art: ThII	5–11	3–6	4	2–5	3	9	9	2–6	4–7	4	2–4	13–17
ThIII–V	5–12	3–12	4–5	2–6	4	10	10	2–7	5–8	5	3–5	15–18
ThVI–VII	4–12/5–13	3–9	3–5	2–6	4	10–11	10	2–7	5–9	5	2–5	15–18
ThVIII male: size	L	L	L	L	L	L	L	L	M	M	M	XL
Forme	Rect	Square/Rect	Rect	Rect	Rect	Rect	Square	Rect	Square	Square	Square	Rect

Table 2 (continued). Character variability in different genera of the 'big' and 'giant' (2.5–4 mm and > 4.0 mm in length respectively) Australian and Asian Parabathynellidae and genera with more than four-segmented exopod of some thoracopods in the world.

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12. gen. nov.**
N st endp	2–3	1–3	2	2	2	2	2	2	2	2	2	2+2/teeth (4)
N st exp	2–4	0–3	0	1	0	1	0	0	0	0	0	0
ThVIII female	S (0 st)	M (0 st)	S (0 st)	S (0 st)	M (0 st)	(3 st)	L (2 st)	M (0–1 st)	L (2 st)	–	M (0 st)	XL (3 st)
Pleopod	A/P	A/P	A	A/P	A	A	A	A/P	A	P	A	A
Urp: Symp: spines	13–28	6–20	10–12	7–18	13	25	20	5–18	7–13	12	6–13	56–85
Type spines	Hom/Inhom	Hom/Inhom	Inhom	Inhom	Inhom	Inhom	Hom	Hom/Inhom	Hom/Inhom	Inhom	Inhom	Inhom
Exp: N st	8–23	4–12	6	1–8	4	9	8	3–7	6–8	7	2–6	15–18
Basiventral st	A/P	A	A	A	A	P	P	P	P	P	A	P
Endp: N spines	3–9	3–6	3–4	1–4	3–4	2	4	0/2/5/6/7	2	2	0–5	4–6
N st	2–6	5	4	4	4	4	4	2–5	4	4	4–5	5
Furca: N spines	10–23	5–20	10–13	7–15	10	7–8	9–10	3–8	4–7	7	7–14	37–46
Anal operculum	NPr	NPr	Pr(S)	NPr	NPr	Pr(M)	Pr(S)	Pr(S–L)/NPr	Pr(S–XL)	Pr(M)	Pr(S–M)/NPr	NPr
Length Min–max	2.2–6.3	1.1–4,6	1.3–2.1	0.8–3.3	1.6–2.0	4.5–4.7	3.5–3.7	1.6–3.3	2.6	1.9	1.3–2.7	4.4–5.9
Habitat	W	W	R	Sp/R/	R	W	C	R/W/C	C	C	R/W/C	C

ThVII; first and second article of endopod of ThI to ThVII each with a plumose dorsal seta. Male ThVIII unusually large, twice as long as wide; basal region of penial complex supports three independent lobes: inner lobe, outer lobe and dentate lobe; dentate lobe as inner lobe, rounded and as long as the outer lobe; very long curved outer lobe, as a finger; large basipod with a seta and a pronounced crest on internal face; dentate small exopod; endopod large with two basal setae and with the distal end rounded with four teeth and two setae of different length, the longest barbed. Female ThVIII one-segmented, almost triangular with three long barbed terminal setae. Pleopods absent. Inhomonomous sympod of uropod, with many long spines (56–85), distalmost 25% longer than the rest; endopod with four to six spines, the two terminal spines stronger than the rest, and setae, two barbed apical ones, one subterminal and two basal plumose setae; exopod with 15 to 18 setae. Furca very enlarged with 37 to 46 spines, the two distal ones twice as long as the rest. Anal operculum not pronounced. Giant species, more than 4 mm long.

Etymology

The specific name '*totemensis*' is dedicated to the Totem Pole Cave where the new species was found.

Material examined

Holotype

AUSTRALIA • ♂ (all appendages dissected in glycerine and preserved as permanent slides, special metal slides, glycerine-gelatine stained and paraffin as mounting medium); Northern Territory, Pungalina Karst area, Totem Pole Cave; 16°48′ S, 137°27′ E; 24 Jul. 2006; T.A. Moulds leg.; NTM Cr19141.

Allotype

AUSTRALIA • ♀; same collection data and storage as for holotype; NTM Cr19142.

Paratypes

AUSTRALIA • 5 ♀♀, 3 ♂♂; same collection data and storage as for holotype; WAM C73466E (in toto, 5.6 mm, not in Table 1), WAM C73466F (in toto, 5.6 mm, not in Table 1), WAM C73466J, WAM C73466L (females), WAM C73466G, WAM C73466H (males) • 1 ♀, 1 ♂; same collection data and storage as for holotype; MNCN 20.04/20932 (female), MNCN 20.04/20931 (male).

Type locality

Ten specimens, six females and four males, were collected at the type locality by T.A. Moulds on 24 Jul. 2006.

Fig. 1. Habitus of male *Megabathynella totemensis* Camacho & Abrams gen. et sp. nov., paratype (WAM C73466H).

Description

Measurements and appearance. Body total length of male holotype 5.9 mm, allotype 6.2 mm. Body elongated (Figs 1–2), segments widening towards posterior end ~8 × as long as wide. Head slightly longer than broad. All drawings are of the holotype, except ThVIII (Fig. 5C), labrum (Fig. 3D), mandibular palp (Fig. 3F) and ThI (Fig. 4B) which are of the allotype.

Antennules (Figs 3A, 6A) (AI). Almost 35% longer than AII. 13-segmented; first three articles as long as the next six and slightly longer than the last four articles combined; first article longest, similar to third, second slightly shorter, but just as thick; the fourth article is the shortest; the fifth to eighth articles are similar in length, short and thick, and the last five are longer and narrower than all the previous ones. First article with three smooth dorsal setae and three plumose ones (Fig. 3A, I). Second article with four plumose setae and eight smooth setae on inner margin. Inner flagellum on third article, small and almost square with three smooth setae. Third article (Fig. 3J) with two smooth and one plumose outer lateral setae and eight smooth setae of different sizes on inner margin. Fourth article with two plumose setae on outer distal apophysis, one more dorsal plumose seta and one small, plumose stub on dorsal margin. Fifth to ninth articles (Fig. 3A, K) with three smooth setae, one strong and short curved seta with long setules and two aesthetascs, of similar size, on inner margin, and one smooth dorsal seta. Articles 10 to 12 with similar setation as previous ones but with three terminal aesthetascs instead of two. Last article with three subterminal aesthetascs and four terminal smooth setae.

Antennae (Figs 3B, 6B) (AII). Seven-segmented, the fifth article longest, 20% longer than first three together and fourth, sixth and seventh similar in length. Thickness gradually decreases from fourth to seventh. All setae smooth. Setal formula: 0+0/0+0/3+0/4+1/4+1/2+1/8.

Labrum (Figs 3C, 6C). Almost flat**,** with 12 main teeth, and two smaller teeth at each angle; ventral surface with several rows of strong spinules.

Mandibles (Figs 3E, 6D–F) (Md). Pars distalis with six well-developed teeth and six small and one triangular strong proximal tooth as in figures 3E and 6D; pars molaris (molar process) very big, with row of 18 claws, all strong and denticulate, with two more distal setulose ones, joined basally (Figs 3E, 6E); exceptional two-segmented mandibular palp with seven setae (Figs 3E, 6D, F) not exceeding distal part of Md.

Fig. 2. Habitus of female *Megabathynella totemensis* Camacho & Abrams gen. et sp. nov., paratype (WAM C73466J).

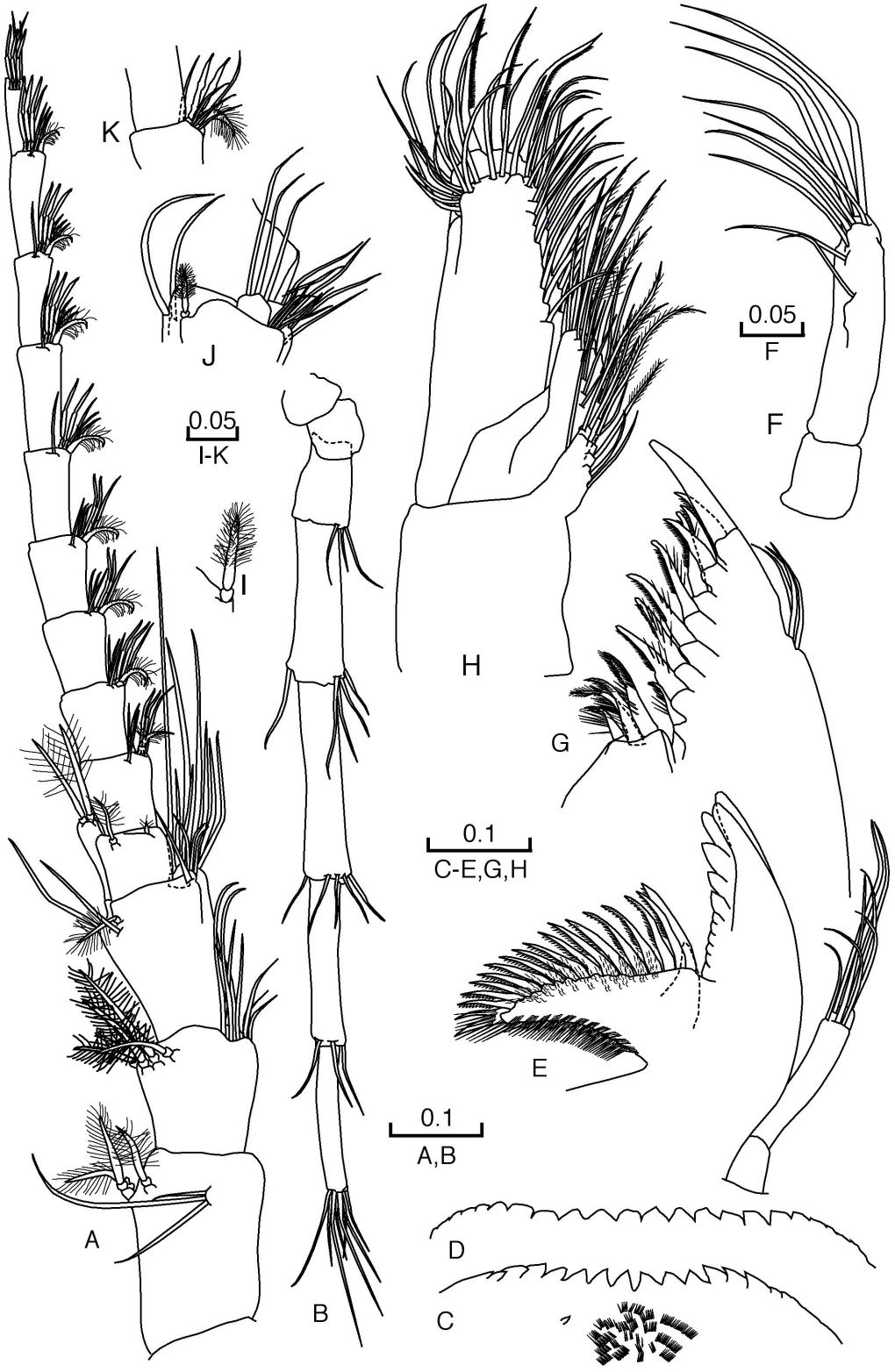

Fig. 3. *Megabathynella totemensis* Camacho & Abrams gen. et sp. nov. **A–C, G–K**. Holotype, ♂ (NTM Cr19141). **A**. Antennule (dorsal view). **B**. Antenna (dorsal view). **C**. Labrum. **D–E**. Paratype, ♀ (MNCN20.04/20932). **D**. Labrum. **E**. Mandible. **F**. Allotype, ♀ (NTM Cr19142), mandibular palp of female. **G**. Maxillule. **H**. Maxilla. **I**. Plumose seta of the first articles of AI. **J**. Article three of AI. **K**. Article eight of AI, with special plumose seta and two aesthetascs. Scale bars in mm.

Maxillules (Figs 3G, 6G–H) (MxI). Proximal endite with four unequal strong claws with strong setation; distal endite with ten claws (as spines), along inner edge, one apical smooth and very large and strong, remaining claws denticulate with strong row of denticles and setae, basal claw smallest, half length of others; three smooth setae subdistally on outer margin of endite as figured.

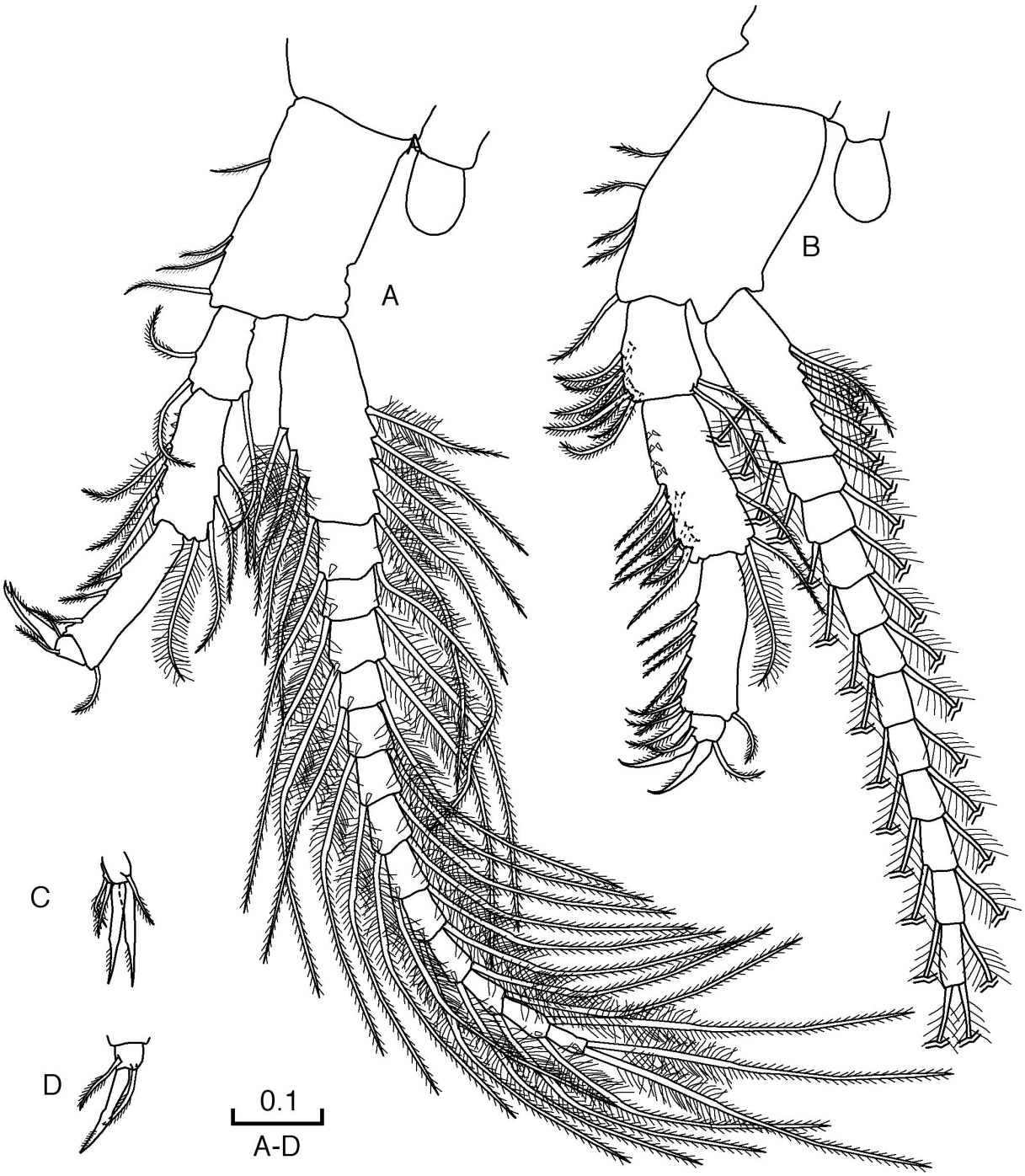

Fig. 4. *Megabathynella totemensis* Camacho & Abrams gen. et sp. nov. **A**. Holotype, ♂ (NTM Cr19141) thoracopod I. **B**. Allotype, ♀ (NTM Cr19142), thoracopod I. **C–D**. Last article of endopod of ThVII of two male paratypes (WAMC73466H and MNCN 20.04/20931). Scale bar in mm.

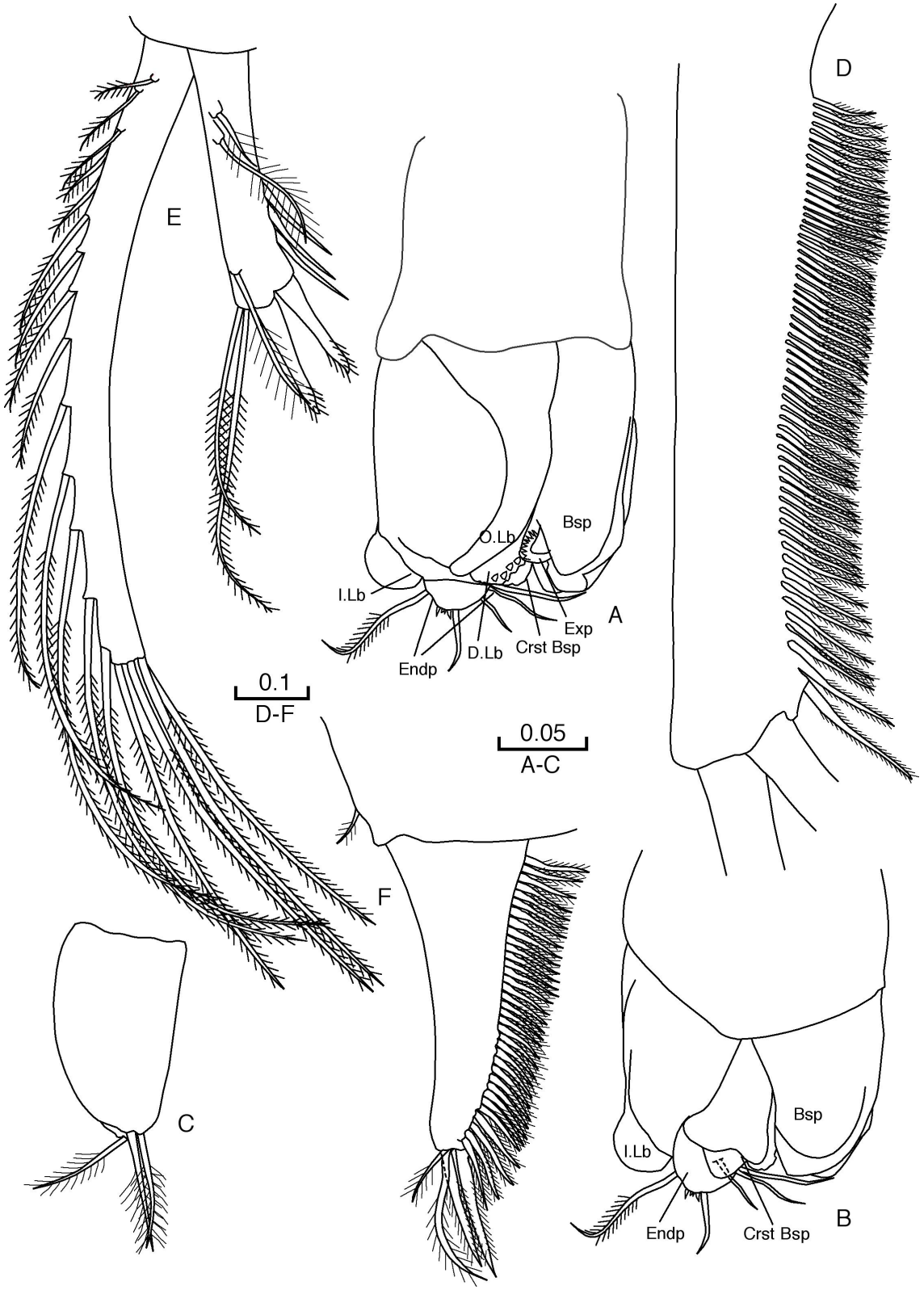

Fig. 5. *Megabathynella totemensis* Camacho & Abrams gen. et sp. nov. **A–B**. Holotype, ♂ (NTM Cr19141). **A**. Thoracopod VIII (latero-external view). **B**. Thoracopod VIII (latero-internal view). **C–F**. Allotype, ♀ (NTMCr19142). **C**. ThVIII. **D**. Sympod of uropod (dorsal view). **E**. Exopod and endopod of the uropod (dorsal view). **F**. Furca (dorsal view). Scale bars in mm.

Maxillae (Figs 3H, 6I). Four-segmented, setal formula: 8, 16, 31, 8.

Thoracopods (Figs 4A–B, 7A–D) (ThI to VII). Well developed; length gradually increasing from ThI to ThIV (Figs 1–2), ThV to VII similar in length; small epipod on ThI (Figs 4A, 7A) to VII, each about ⅓ of length of corresponding basipod. Basipod of all Ths with several (three to five) distolateral, barbed setae. Exopods multi-segmented, 14 to 17 articles; number of exopodal articles of thoracopods I to VII: 14-16-16-17-17-17-16; basal article very long and wide with several barbed setae plumose at base on each side; following eight articles almost square and last ones elongated, all with barbed seta (plumose at base) on each side and one strong spine at base of inner seta. Endopod 4-segmented; first article short, second and third long and similar in length and fourth article reduced with two smooth strong spinulose claws and two simple setae; first article with distal plumose inner seta as second article; second article with inner and outer barbed setae, and cluster of pairs of strong spinules along inner margin from base to first seta; third article with barbed setae on inner margin and one barbed distoventral seta. All thoracopods similar to ThI, but varying in number of articles of exopod, number of setae in basal article, number of setae on basipod and on first three articles of endopod. Size ratios between articles, of exopod and endopod, similar to those of ThI (Fig. 4A).

Setal formula of endopod.

ThI (4 basipod setae): 2+1/3+4/3+1/4(2)
ThII (4 basipod setae): 2+1/3+4/5+1/4(2)
ThIII (4–5 basipod setae): 2+1/3+4/4+1/4(2)
ThIV (4–5 basipod setae): 1+1/4+2/5+1/4(2)
ThV (4-5 basipod setae): 1+1/2+1/3+1/4(2)
ThVI (4 basipod setae): 2+1/3+4/4+1/4(2)
ThVII (4 basipod setae): 1+1/3+4/3+1/4(2)

Male thoracopod VIII (Figs 5A–B, 8A–J, 9F). Unusually large, twice as long as wide; basal region of penial complex supports three independent lobes: inner lobe, outer lobe and dentate lobe**;** inclined dentate lobe, as long as outer lobe, with rounded distal end and big teeth (Fig. 5A–B); inner lobe rounded and longer than outer lobe; very long (6× as long as wide) and curved outer lobe (as a finger) (Fig. 5A, 8B) that covers end of dentate lobe and not extending beyond basipod; large basipod with seta and pronounced crest-like protuberance (Fig. 5A–B, 8C) on internal face, and small almost triangular exopod with several denticles; endopod large with two basal setae and with distal end rounded, like skullcap or "helmet" (Figs 5A–B, 8F–G, J) with four teeth and two setae of different length, longest one barbed.

Pleotelson. Small ventral plumose seta. Anal operculum not pronounced, almost flat.

First pleopods. Absent.

Uropods (Figs 5D–E, 7F–G). Sympod 6.5 times as long as wide, 15% longer than exopod and almost three times as long as endopod, with 59 barbed spines subequal, except distalmost spine, slightly longer than rest. Endopod 2.5 times as long as exopod, with three spines along distal half of inner margin and two stronger and enlarged distal ones; distolateral angle of ramous with one subterminal plumose and two terminal barbed setae; basal part of ramous with two plumose setae of different length. Exopod with 18 barbed setae, 14 lateral and four terminal.

Furcal rami (Figs 5F, 7F). Each ramus almost triangular, very enlarged, with 37 barbed spines, six distal ones of different sizes, four slightly longer than first 31 and two terminal ones two times as long as others; two plumose setae of different lengths oriented dorsally, shorter one without reaching tip of terminal spines.

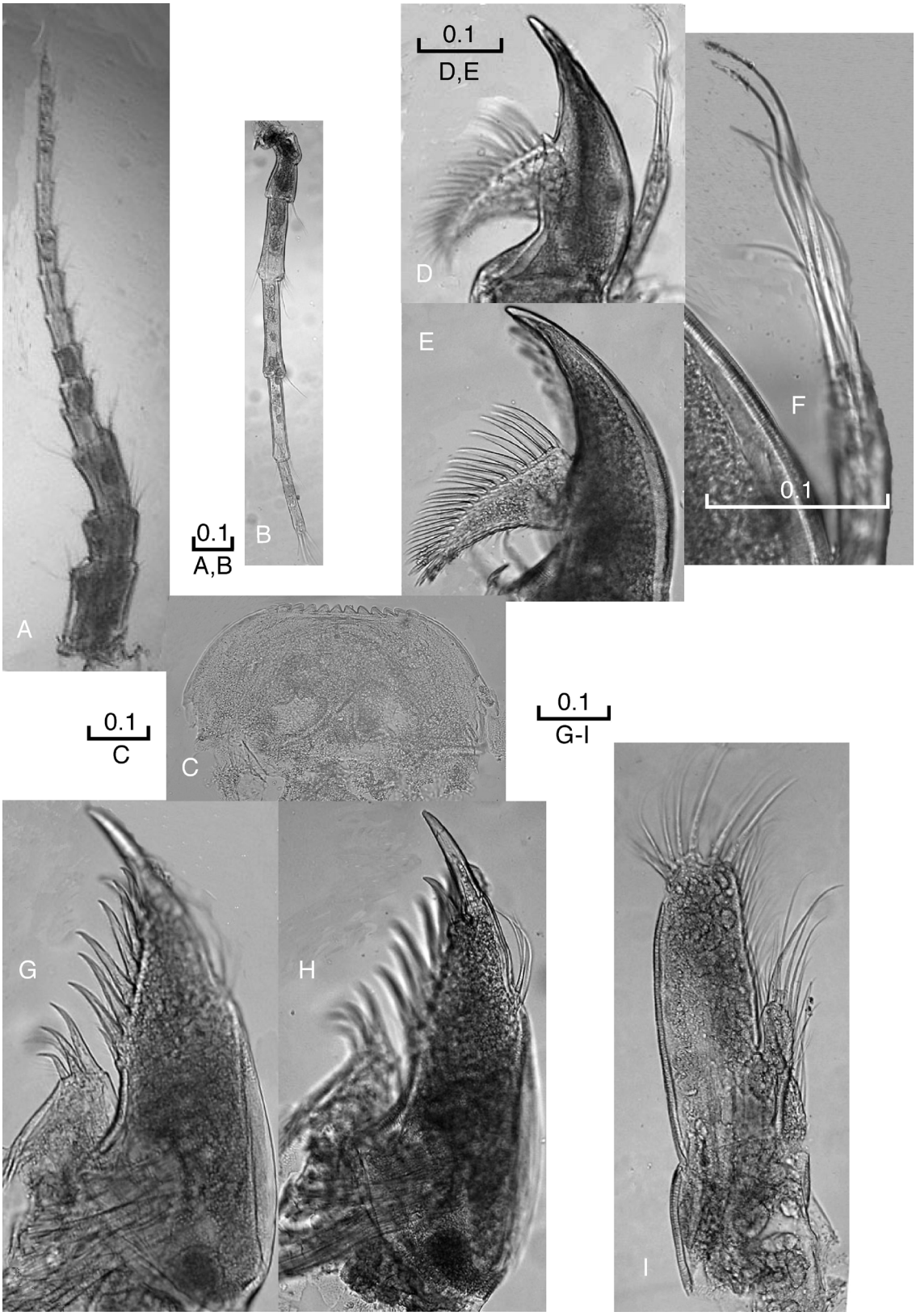

Fig. 6. *Megabathynella totemensis* Camacho & Abrams gen. et sp. nov., holotype, ♂ (NTM Cr19141), microscope photographs. **A**. AI. **B**. AII. **C**. Labrum. **D**. Md. **E**. Md. **F**. Mandibular palp. **G**. MxI. **H**. MxI. **I**. MxII. Scale bars in mm.

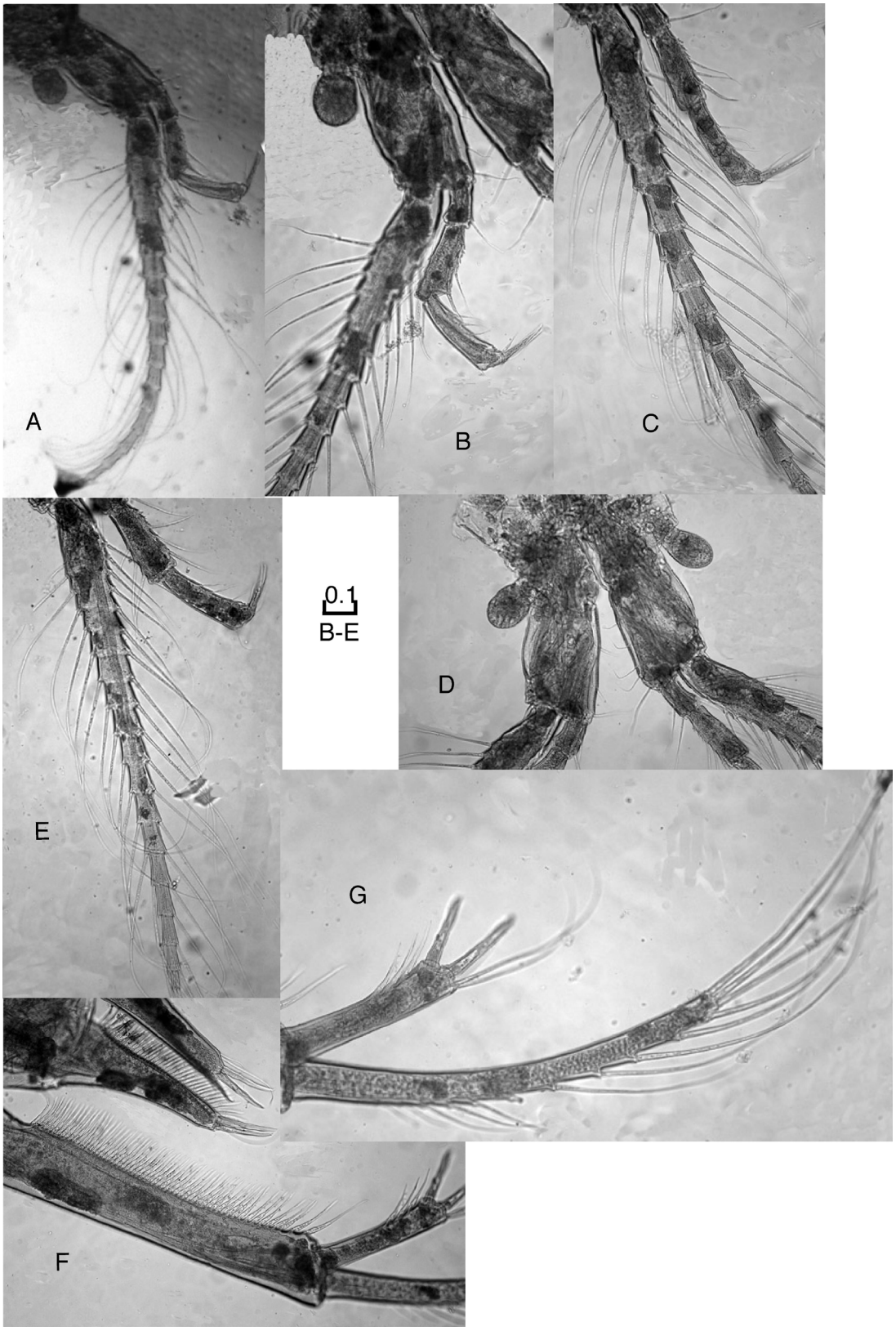

Fig. 7. *Megabathynella totemensis* Camacho & Abrams gen. et sp. nov., holotype, ♂ (NTM Cr19141), microscope photographs. **A**. ThI. **B**. ThI details. **C**. ThIII. **D**. Details of basipod and epipod of ThV. **E**. ThV. **F**. Furca and uropod. **G**. Exopod and endopod of uropod. Scale bar in mm.

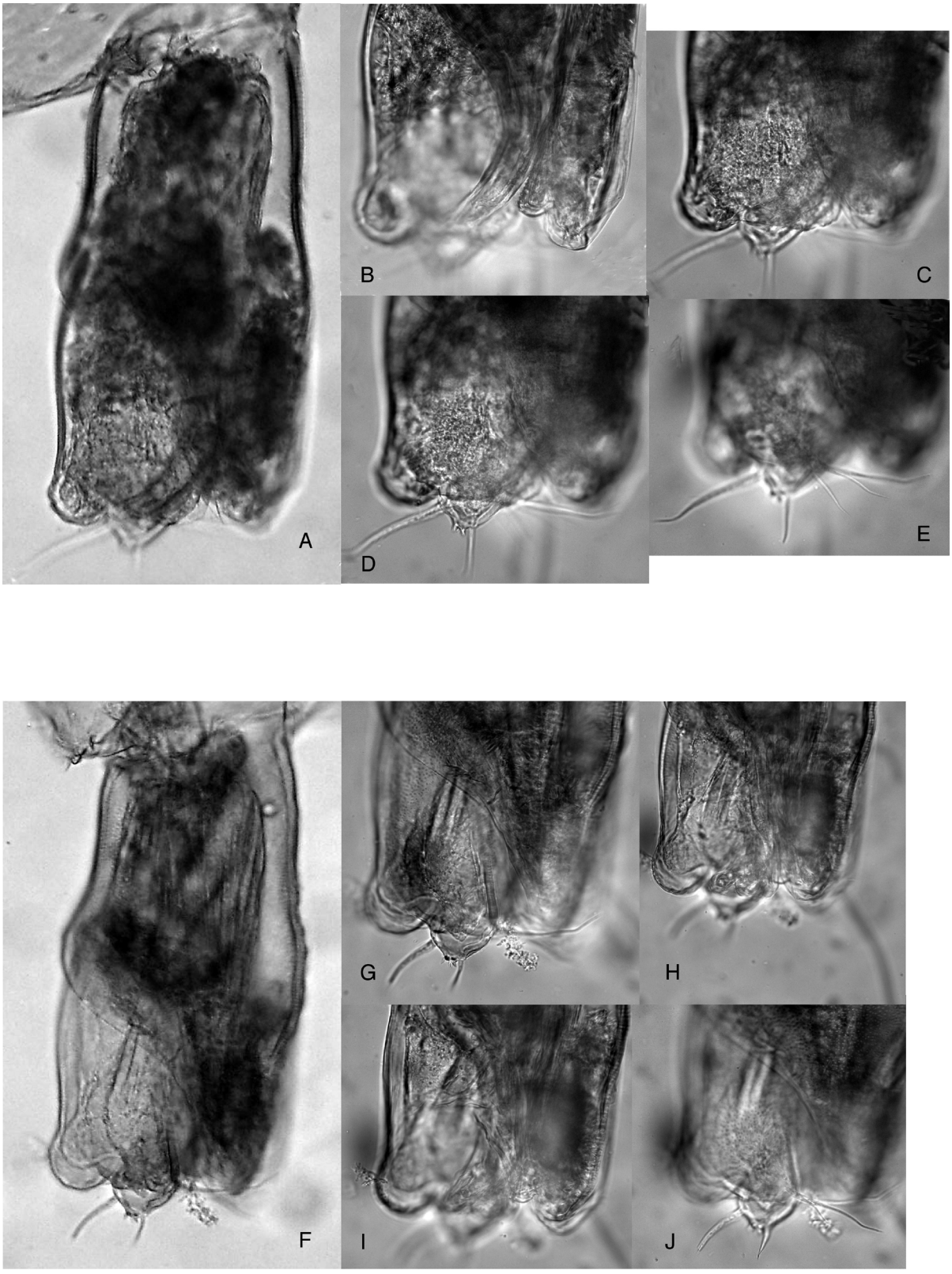

Fig. 8. *Megabathynella totemensis* Camacho & Abrams gen. et sp. nov., holotype, ♂ (NTM Cr19141), microscope photographs. **A**. ThVIII (latero external view). **B–E, G–J**. Details of ThVIII. **F**. ThVIII (latero internal view).

Female (allotype)

The female allotype is similar to the holotype, except for the ThVIII (Fig. 5C), the number of articles of AI and exopod of Ths; teeth of labrum; claws on Md and MxI; setae on Md palp, and spines on sympod of the uropod and furcal rami. See Table 1.

Antennules. Similar to male but with more segments, 15.

Labrum (Fig. 3D). With 14 main teeth and several lateral denticles on each side.

Mandibles. Pars molaris with 23 teeth and mandibular palp with nine setae (Fig. 3F).

Maxillules. Distal endite with 11 claws.

Thoracopods. Number of exopodal articles of thoracopods I to VII: 12-17-18-18-18-17-18.

Setal formula of endopod.

ThI (3 basipod setae) (Fig. 5B): 8+2/8+3/8+1/4(2)
ThII (5 basipod setae): 2+1/3+5/4+1/4(2)
ThIII (5 basipod setae): 2+1/4+4/5+1/4(2)
ThIV (4 basipod setae): 2+1/3+5/3+1/4(2)
ThV (4 basipod setae): 1+1/2+1/3+1/4(2)
ThVI (5 basipod setae): 2+1/3+5/4+1/4(2)
ThVII (3 basipod setae): 1+1/3+5/4+1/4(2)

Thoracopod VIII (Fig. 5C). One-segmented; almost triangular with three long barbed terminal setae.

Uropod. Sympod with 78 spines

Furcal rami. With 43 spines.

Variability

The size varies among the studied paratypes: females 5.4–6.1 (n = 5) and males 4.3–5.9 (n = 2). There is variation in the number of: articles of AI (13–15); claws on pars molaris (18–23), teeth on pars distalis (8–12) and setae on mandibular palp (7–9) of Md; claws on distal endite of MxI (10–11); spines on the furcal rami (37–46), spines on sympod of uropod (56–78); articles of exopod of Ths (11–18) and setation of three first articles of endopod, first article of exopod and basipod on all Ths. See Table 1 for details of the six studied paratypes and holotype and allotype also, of *Megabathynella totemensis* gen. et sp. nov.

Discussion

Worldwide, there are 33 species in 18 genera that are larger than 2.5 mm (Table 3). *Megabathynella totemensis* gen. et sp. nov is a new giant species, larger than 4 mm long. The Australian genera *Brevisomabathynella* and *Billibathynella* and the Cambodian genus *Kampucheabathynella*, also present giant species. In common with these genera, the new species shares a multisegmented exopod of the thoracopods and the presence of two plumose setae on the endopod of the thoracopods (Table 2). These two striking features are also shared with other Australian genera (*Arkaroolabathynella* Abrams & King 2013, *Octobathynella* Camacho & Hancock, 2010, *Lockyerenella* Camacho & Little, 2017 and *Notobathynella* Schminke, 1973) and the Asian genera (*Sinobathynella* Camacho, Trontelj & Zagmajster, 2006, *Allobathynella* Morimoto & Miura, 1957, *Paraeobathynella* Camacho, 2005 and *Sketinella* Camacho, 2005) some of which also have large (between 2.5 and 4 mm) but not giant (>4 mm) species (Table 3). Among the European genus *Parabathynella* Chappuis, 1926 and the North

Table 3. Big and giant species of the world (2.5–4 mm 'large' or >4 'giant'): species list and maximum size. *Afrobathynella* Schminke, 1976; *Allobathynella* Morimoto & Miura, 1957; *Arkaroolabathynella* Abrams & King, 2013; *Atopobathynella* Schminke, 1973; *Billibathynella* Cho, 2005; *Brevisomabathynella* Cho, Park & Ranga Reddy, 2006; *Chilibathynella* Noodt, 1963; *Kampucheabathynella* Cho, Kry & Chhenh, 2015; *Kimberleybathynella* Cho, Park & Humphreys, 2005; *Iberobathynella* Schminke, 1973; *Megabathynella* Camacho & Abrams gen. nov.; *Montanabathynella* Camacho, Stanford & Newell, 2009; *Lockyerenella* Camacho & Little, 2017; *Nipponbathynella* Schminke, 1973; *Notobathynella* Schminke, 1973*; Onychobathynella* Camacho & Hancock, 2011; *Paraeobathynella* Camacho, 2005; *Parabathynella* Chappuis, 1926; *Paraiberobathynella* Camacho & Serban, 1998; *Sinobathynella* Camacho, Trontelj & Zagmajster, 2006. In bold the 'giant' species.

Genera	Species	Size	Country
Afrobathynella	*A. trimera*	2.7	South Africa
Allobathynella	*A. donggangensis*	2.54	South Korea
	A. gigantea "pluto"	3.3	Japan
	A. maseongensis	2.55	South Korea
	A. munsui	3.41	South Korea
	A. okcheonensis	2.73	South Korea
Arkaroolabathynella	*A. remkoi*	2.2–3.3	Australia (South Australia)
Atopobathynella	*A. wattsi*	3.0	Australia (Western Australia)
Billibathynella	*B. humphreysi*	5.45–6.30	Australia (Western Australia)
	B. ilgarariensis	3.0–3.17	Australia (Western Australia)
	B. wolframnoodti	4.56–5.12	Australia (Western Australia)
Brevisomabathynella	***B. changjini***	4.24	Australia (Western Australia)
	B. clayi	3.52	Australia (Western Australia)
	B. jundeeensis	3.42	Australia (Western Australia)
	B. magna	4.62	Australia (Western Australia)
	B. uramurdahensis	3.62	Australia (Western Australia)
Chilibathynella	*C. joshuai*	2.8	Australia (Queensland)
Kampucheabathynella	***K. khaeiptouka***	4.52–4.72	Cambodia
Kimberleybathynella	*K. gigantea*	3.91	Australia (Western Australia)
Iberobathynella	*I. barcelensis*	3.4	Portugal
	I. gracilipes	4.0	Portugal
	I. lusitanica	3.0	Portugal
	*I. paragracilipe*s	3.2	Spain
Megabathynella gen. nov.	***M. totemensis*** sp. nov.	4.1–5.9	Australia (Northern Territory)
Montanabathynella	*M. salish*	3.0	USA (Montana)
Nipponbathynella	*N. pectina*	2.57	South Korea
Notobathynella	*N. lemurum*	2.5	Madagascar
	N. octocamura	2.7	Australia (Queensland)
Onychobathynella	*O. bifurcata*	2.54	Australia (Queensland)
Paraeobathynella	*Pe. siamensis*	2.60	Thailand
Parabathynella	*P. badenwuerttembergensis*	2.5	Germany
Paraiberobathynella	*Pi. fagei*	2.8	Spain, France
	Pi. maghrebensis	2.8	Morocco
Sinobathynella	*S. decamera*	3.70	China

American *Montanabathynella* Camacho, Stanford & Newell, 2009, as well as the Moroccan and French-Spanish species of the genus *Paraiberobathynella* Camacho & Serban, 1998 (*Pi. maghrebensis* Boutin & Coineau, 1987 and *Pi. fagei* Delamare Debouttéville & Angelier, 1950, respectively) there are also large species (Table 3) with multisegmented exopods in thoracopods, but only *Parabathynella badenwuerttembergensis* Fuchs, Hahn & Cho, 2012 and *Montanabathynella salish* Camacho, Stanford & Newell, 2009 share two plumose setae on the endopod of thoracopods. The Spanish genus *Iberobathynella* Schminke, 1973 with large species (Table 3) and the large Australian species (Table 3), *Atopobathynella wattsi* Cho, Humphreys & Lee, 2006, *Kimberleybathynella gigantea* Cho, Park & Humphreys, 2005, *Chilibathynella joshuai* Camacho & Hancock, 2012, *Onychobathynella bifurcata* Camacho & Hancock, 2012 and the South Korean *Nipponbathynella pectina* Cho, Hwang & Num, 2009 are the other side of the coin, because although large, they only have one article in the exopod of the thoracopods (two in the case of *Iberobathynella*) and they do not have a great profusion of setae, spines or teeth. The distribution of all large and giant species of Parabathynellidae in the world is shown in Figure 11.

An analysis of the oligomerization of appendages in relation to the size of the species, as a whole, would be required to determine whether it can be explained by simple allometry; however, this is outside the scope of this study

The new species is most similar overall to species in the genera *Billibathynella*, *Brevisomabathynella* and *Kampucheabathynella* and shares characters with some species of the other Australian and Asian genera as shown in Table 2.

The new species has the highest number of articles known to date in AI, viz. 15. *Kampucheabathynella* and *Sinobathynella* have the next highest number of articles (10). The new species is unique in having a very strong, recurved, short, thick and plumose seta from the fifth to the penultimate article (Fig. 3A, K).

The new genus has few teeth on the labrum like *Sketinella* Camacho, 2005. However, in the pars incisiva of the Md, *Megabathynella* gen. nov. has more teeth than most genera, as in the pars molaris, but species of *Brevisomabathynella* are close (20) to the 23 shown by *Megabathynella totemensis* gen. et sp. nov. The new species and *Brevisomabathynella uramurdahensis* Cho & Humphreys, 2010 exhibit groups of strong spines at the base of the claws and on the clawless edge. The bisegmented mandibular palp of the new species is unusual, and only known in one other species, *Billibathynella humphreysi* Cho, 2005, but *B. humphreysi* only has three setae whereas the new species always has more than the double the number of setae (7–11). A one-segmented palp, but with more than one seta (usually only one seta on the palp is present in the family), is found in *Brevisomabathynella magna* Cho & Humphreys, 2010, and some species of *Allobathynella* described by Park & Cho (2016) (*A. imjinensis*, *A. maseongensis*, *A. munsui*, *A. hongcheonensis*, *A. okcheonensis*, *A. buronensis*, *A. bangokensis*, *A. yecheonensis*, *A. cheongdoensis*), but they only have a maximum of three setae.

The new genus has numerous claws in the distal endite of the MxI, up to 11, and only some species of *Billibathynella* come close, with 10 claws, but the most common state is seven claws.

Brevisomabathynella uramurdahensis has a great profusion of setae in MxII but not as many as the new species.

The number of articles of the Th exopods of *Megabathynella totemensis* gen. et sp. nov. is unusually high (18 in some Th) in comparison with other genera, for example some species of *Billibathynella*, *Brevisomabathynella* and *Kampucheabathynella* have 10 or 12 articles. *Sinobathynella decamera* Camacho, Trontelj & Zagmajster 2006 also has a relatively high number of articles of the exopod of some Ths (9–10). The new species has an epipod on all Ths, as all species of the genera *Billibathynella*, *Brevisomabathynella*, *Arkaroolabathynella* and *Lockyerenella*, and some species of *Allobathynella* and

Notobathynella, but the absence of the first and second epipods is common in Asian and Australian genera as in *Kampucheabathynella*, and even in the third epipod as occurs in some species of *Paraeobathynella* and *Allobathynella*. *Megabathynella totemensis* has several setae on the basipod of all Ths, which is also found in *Kampucheabathynella*. However, the new species has a large number of setae on the first article (Table 1) of the exopod of all Ths, which makes it difficult to see where the second article begins. In other genera, there are few setae, 1 or 2 on each side only. Another exclusive character is the lack of the ubiquitous ctenidia at the base of the setae (which are plumose at the base and barbed elsewhere) of all articles of the exopod that all other species of the family Parabathynellidae show; instead, it presents a strong spine at the base of the outer seta of all articles, at the inner margin. The new species shows a cluster of pairs of strong spinules along the inner margin from the base to the first seta on the second article of the endopod of the Ths; both the second and third articles can have barbed setae on the inner face in a variable number (Tables 1–2); in *Brevisomabathynella uramurdahensis*, *B. magna* and some other species of this genus and in *Notobathynella octocamura* Camacho & Hancock, 2011 there are also barbed setae on the inner face of the second article and some species of *Allobathynella* have a small seta, as a spinula, but never on the third article as in the new species.

The female ThVIII of the new species is very large with three distal setae as only occurs in *Kampucheabathynella khaeiptouka* Cho, Kry & Chhenh, 2015. The male ThVIII (Fig. 10C) is distinctive in comparison with all other genera, as it is much larger and more elongated than that of any known species (Figs 9A–B, 10). Some examples of male ThVIII in Australian and Asian species are shown in Figs 9 and 10 for comparison. Perhaps the greatest resemblance of this appendage is to the genus *Lockyerenella* (Fig. 9C) due to the similarities of the long, curved, finger-shaped outer lobe and the crest-like protuberance on the internal face of the basipod, smaller than those of *Megabathynella totemensis* gen. et sp. nov. Due to its elongated appearance, male thoracopod VIII resembles Australian genera (Fig. 9) more than Asian genera (Fig. 10), in which the general appearance is more square. However, the gigantic size and unique morphology of the endopod of the male ThVIII of the new species makes it completely different from all other male ThVIIIs of other species.

The absence of the first pair of pleopods in the new species is quite common in most species of Parabathynellidae.

No species known to date shows such a large number of spines on the sympod of the uropod, nor on the furca as the new species. However, some species of *Billibathynella* outnumber the new species in the number of setae on the uropod exopod (Table 2).

The unique combination of characters along with the exclusive characters we have listed justifies the erection of a new genus with similarities to Australian and Asian genera. Elucidating whether the oligomerization of AI and the Th exopods is correlated with size is beyond the scope of this study but will be an interesting question for future comprehensive analyses of the family Parabathynellidae.

Distribution of bathynellaceans of northern Australia

The diversity and distributions of bathynellaceans of the Northern Territory are poorly known, with only a single described species, *Atopobathynella readi* Cho, Humphreys & Lee, 2005, recorded in the Ngalia Basin, approximately 941 km south-west of the type locality of *Megabathynella totemensis* gen. et sp. nov. (Fig. 11). However, there are records of a likely new species of possibly *Brevisomabathynella* from the Cambrian Limestone Aquifer in the Beetaloo Sub-basin (Oberprieler *et al*. 2021) (Fig. 11). The region has not been extensively sampled for stygofauna and it is likely that new taxa will be collected with further survey. Far west of Totem Pole Cave, near the border with Western Australia, a rich parabathynellid assemblage has been recorded from the eastern Kimberley, with five species of *Kimberleybathynella* occurring in alluvial and regolith substrata in the Ord River catchment (Cho

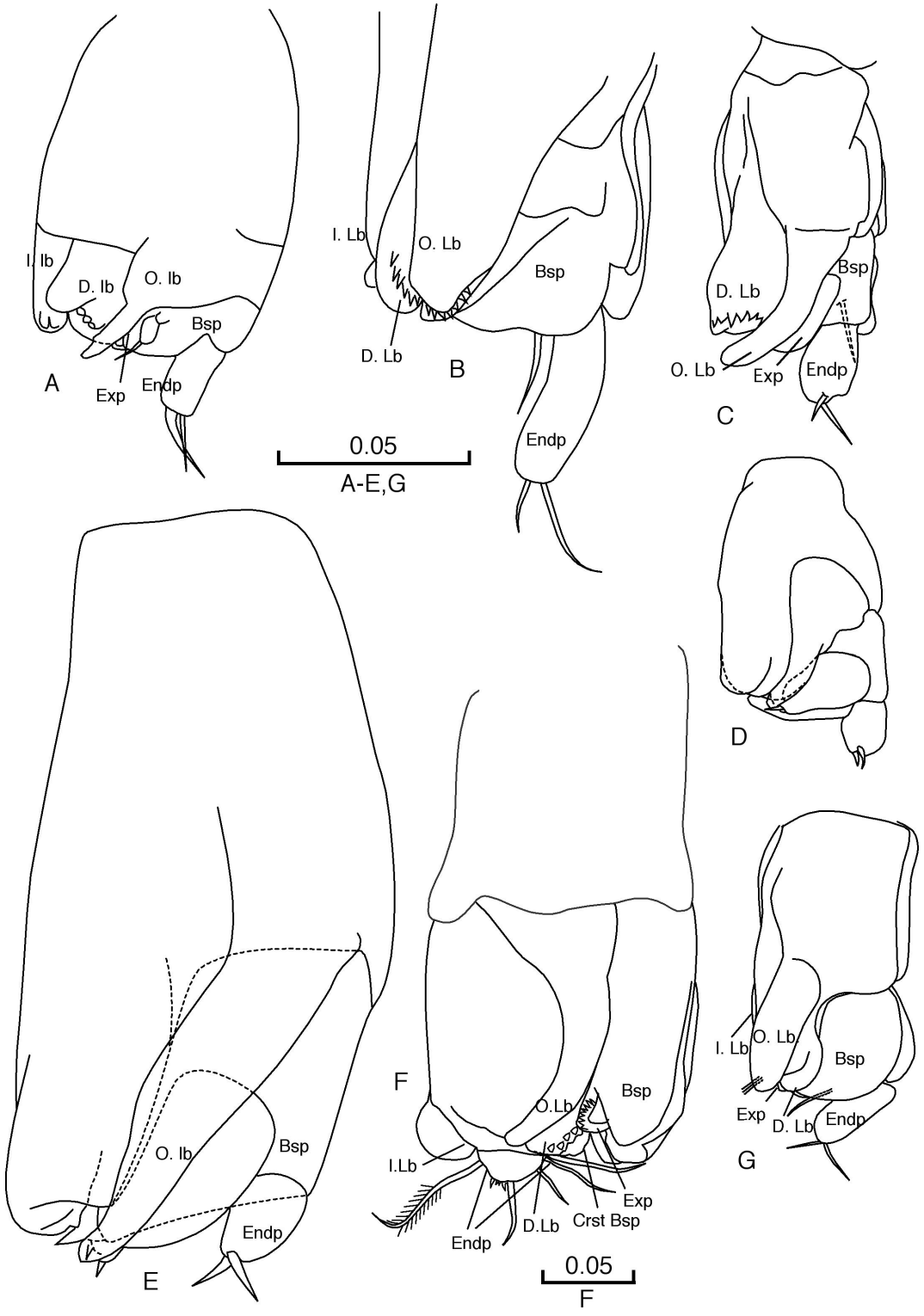

Fig. 9. Male ThVIII of different species from Australia. **A**. *Arkaroolabathynella bispinosa* Abrams & King, 2013. **B**. *Notobathynella octocamura* Camacho & Hancock, 2011. C. *Lockyerenella danschmidti* Camacho & Little, 2017. **D**. *Brevisomabathynella cooperi* Cho, Park & Ranga Reddy, 2006. **E**. *Billibathynella wolfrannodti* Hong & Cho, 2009. **F**. *Megabathynella totemensis* Camacho & Abrams gen. et sp. nov. **G**. *Octobathynella peelensis* Camacho & Hancock, 2010. Original and redrawings by AIC. Scale bars in mm.

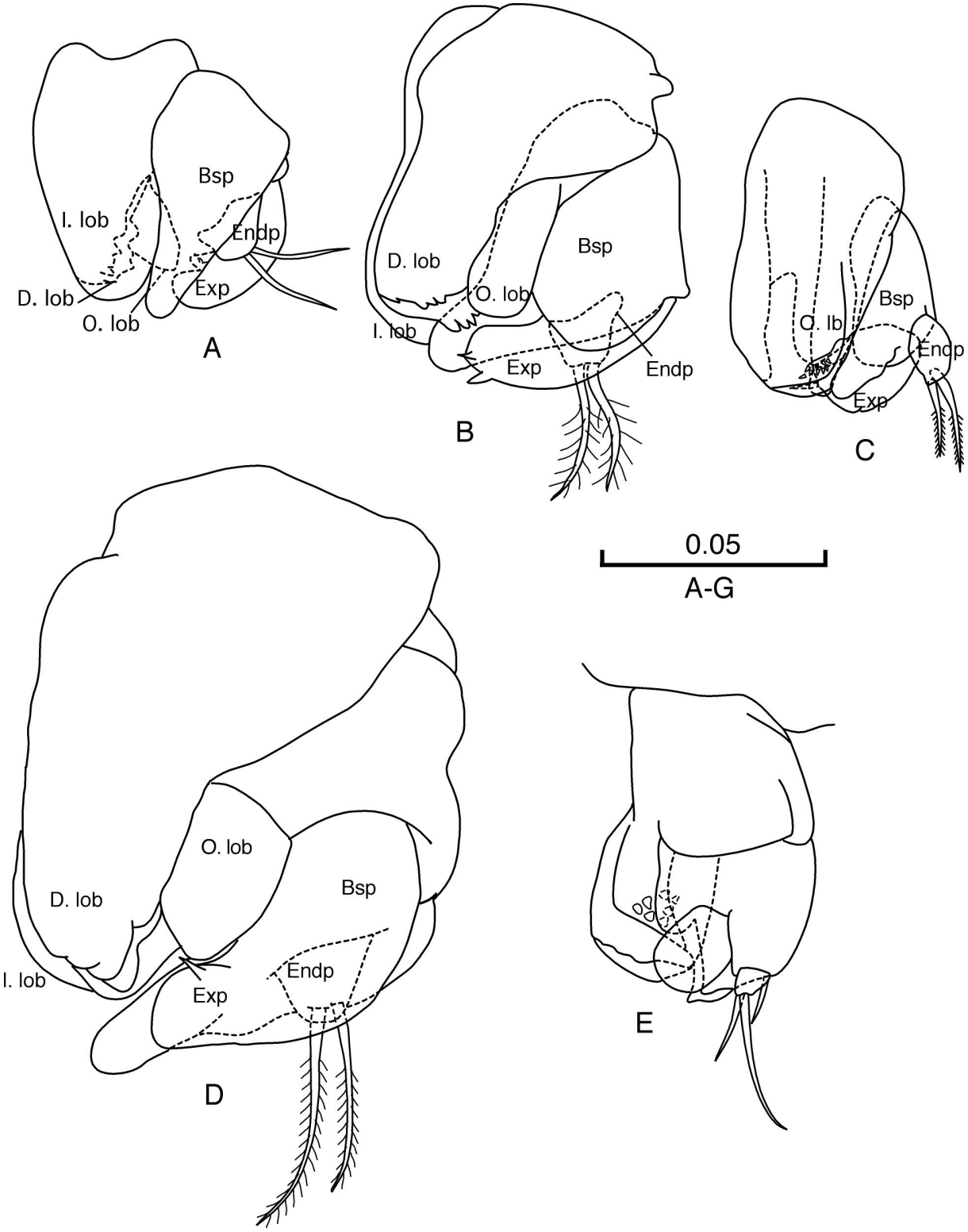

Fig. 10. Male ThVIII of different species from Asia. **A**. *Paraeobathynella vietnamensis* Camacho, 2005. **B**. *Sketinella trontelji* Camacho, 2005. **C**. *Kampucheabathynella* Cho, Kry & Chhenh, 2015. **D**. *Sinobathynella decamera* Camacho, Trontelj & Zagmajster 2006. **E**. *Allobathynella coreana* Morimoto, 1970. Original and redrawing by AIC. Scale bar in mm.

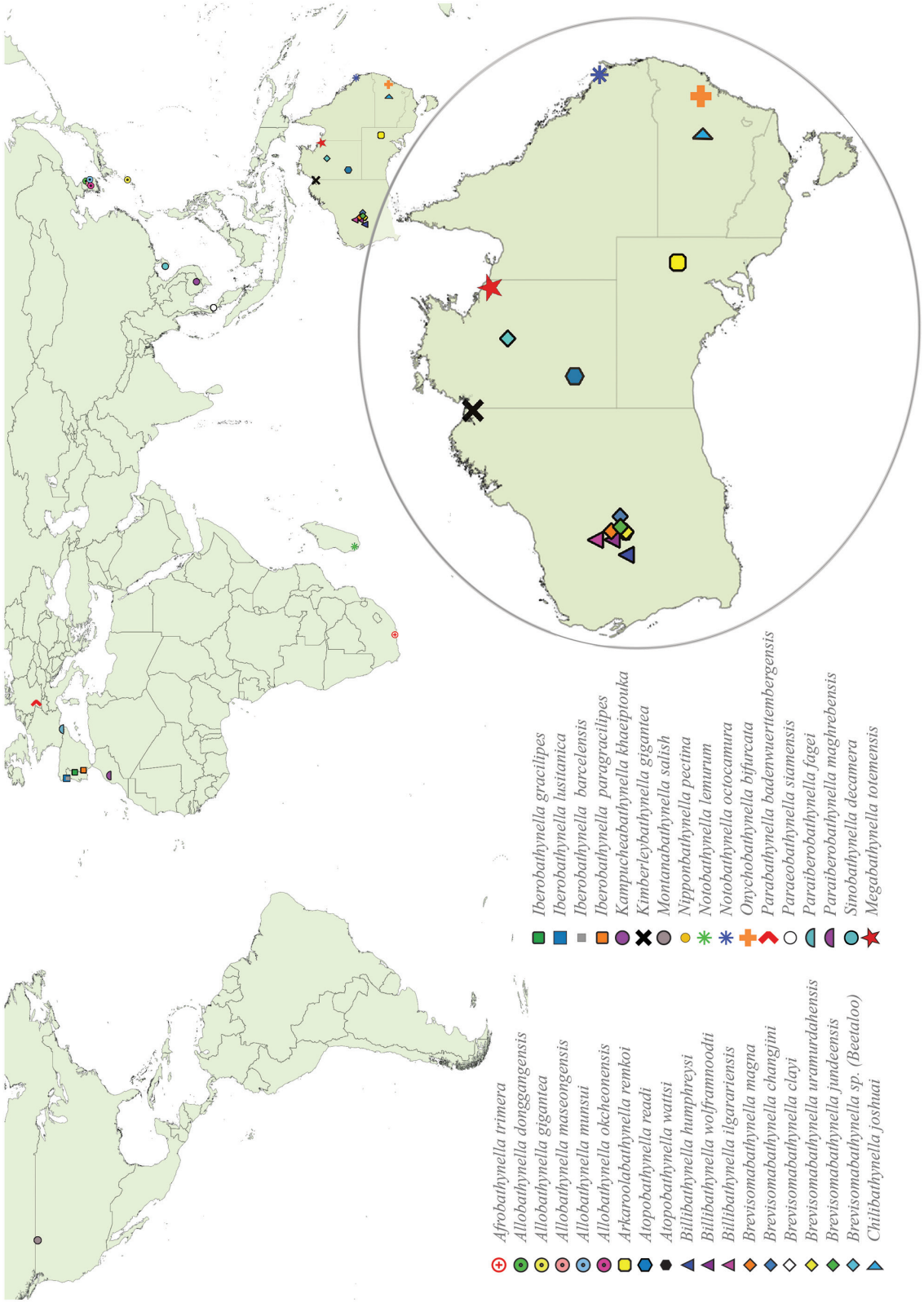

Fig. 11. World distribution of 'large' (2.5–4 mm) and 'giant' (>4 mm) parabathynellid species.

et al. 2005), and multiple undescribed species have been collected from environmental impact surveys (Humphreys 1999; Bennelongia 2012).

As new species continue to be discovered and described in Australia and around the world, it is interesting to observe that large and giant species occur on every continent (Table 3) (Fig. 11). Although almost half of them (15 species) have been recorded from Australia, five occur in Europe (Portugal, Spain and France) and five occur in South Korea. One large species has been collected each from Thailand, China, South Africa, USA, Madagascar, Morocco, Cambodia and Japan to date. It is likely that numerous new species will be discovered in these and other countries with further survey of prospective habitats, as is the case in Australia. Future studies could explore the factors that lead to this unusually large size and proliferation of articles and setae observed. It would also be interesting to investigate the paleobiogeographic aspects that have led to this worldwide distribution of genera with large species on all continents when more comprehensive and robust phylogenies based on both molecular and morphological data will have become available.

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