CSIRO PUBLISHING
www.publish.csiro.au/journals/is *Invertebrate Systematics*, 2006, **20**, 9–41

Phylogenetic relationships within the genus *Atopobathynella* Schminke (Bathynellacea : Parabathynellidae)

Joo-Lae Cho[A,D], *W. F. Humphreys*[B] *and Sang-Don Lee*[C]

[A]International Drinking Water Center, San 6-2, Yeonchuk-Dong, Daedeok-Gu, Taejeon 306-711, Korea.
[B]Western Australian Museum, Locked Bag 49, Welshpool DC, Western Australia 6986, Australia.
[C]Department of Environmental Science and Engineering, Ewha Womans University, Seoul 120-750, Korea.
[D]Corresponding author. Email: parabath@hanmail.net

Abstract. The present study attempts to reconstruct the phylogenetic relationships among species of *Atopobathynella* Schminke, 1973 in order to elucidate their distributional patterns and to seek a mechanism for the worldwide colonisation of the limnic interstitial by the Parabathynellidae. We describe six new *Atopobathynella* recently discovered in Western Australia: *A. gascoyneensis*, sp. nov., *A. hinzeae*, sp. nov., *A. schminkei*, sp. nov., *A. wattsi*, sp. nov., *A. readi*, sp. nov. and *A. glenayleensis*, sp. nov. The phylogenetic relationships among these species and four previously known species in the genus are assessed using 28 morphological characters. The analysis yielded two most parsimonious trees 71 steps long with consistency index 0.5070, retention index 0.5270, and rescaled consistency index 0.2672. One of these trees supports the grouping of *A. readi*, sp. nov. + (((*A. wattsi*, sp. nov. + *A. glenaylensis*, sp. nov.) + (*A. hospitalis* Schminke, 1973 (*A. gascoyneensis*, sp. nov. (*A. schminkei*, sp. nov. + *A. hinzeae*, sp. nov.)))) + (*A. valdiviana* (Noodt, 1964) (*A. compagana* Schminke, 1973 + *A. chelifera* Schminke, 1973))). We discuss the monophyly of *Atopobathynella* and its phylogenetic position within the family Parabathynellidae. The results of the phylogenetic analysis and the biogeographical data suggest that the ancestors of *Atopobathynella* colonized groundwater via limnic surface water.

Introduction

Recent studies on the subterranean biotopes of the arid region of Western Australia have revealed a diversity of crustacean taxa belonging to ancient lineages (Poore and Humphreys 1992; Bruce and Humphreys 1993; Humphreys 1993; Yager and Humphreys 1996; Bradbury and Williams 1997; Wilson and Johnson 1999; Wilson and Keable 1999; Wilson 2001, 2003). Bathynellacean syncarids of great diversity have also been collected from limestone, calcrete, sedimentary and regolith substrata in fresh, saline and anchialine waters of the region (Humphreys 1999). This huge collection includes the six new species of *Atopobathynella* Schminke, 1973 described here.

The genus *Atopobathynella*, which belongs to the cosmopolitan family Parabathynellidae of the order Bathynellacea, was established by Schminke (1973) for those species characterised by: *1*, one-segmented antenna; *2*, half-spherical form of the male thoracopod VIII, and *3*, heterodonty of the labrum. The first described species came from South America (*Parabathynella valdiviana* Noodt, 1964). Two further species have been described from the Australian mainland (*A. chelifera* Schminke, 1973 and *A. compagana* Schminke, 1973), and one from Tasmania (*A. hospitalis* Schminke, 1973). One species, *A. compagana*, is known from New Zealand. This genus is also known from an undescribed species found in Madagascar (Schminke 1981). Thus, the genus displays a Gondwanan distribution.

New morphological and biogeographical information obtained from the new species permits appraisal of the phylogenetic relationships within the genus. Based on these results, we discuss the distribution of *Atopobathynella* and suggest a mechanism for the worldwide colonisation of the Parabathynellidae in the limnic interstitial.

Materials and methods

The species considered in this study are: *1*, *Atopobathynella hospitalis*; *2*, *A. compagana*; *3*, *A. chelifera*; *4*, *A. valdiviana*; *5*, *A. wattsi*, sp. nov.; *6*, *A. glenayleensis*, sp. nov., *7*, *A. readi*, sp. nov.; *8*, *A. gascoyneensis*, sp. nov.; *9*, *A. schminkei*, sp. nov., and *10*, *A. hinzeae*, sp. nov. The morphological comparison is based on our own observations of species *5–10*, as well as on the original descriptions of species *1–4* made by Schminke (1973).

The samples were prepared and mounted in a mixture of glycerin and formalin. For the drawings and morphological investigation, an Eclipse E600-microscope (Nikon, Tokyo, Japan) with differential interference contrast equipment was used with oil immersion. Male thoracopods VIII were compared using a S-3200N scanning electron microscope (Hitachi, Ibaraki, Japan).

The type material of the new species herein described is preserved as permanent preparations deposited in the collection of the Western Australian Museum, Perth (WAM) and the Museum and Art Galley of the Northern Territory, Darwin (NTM).

 10.1071/IS05019 1445-5226/06/010009

Abbreviations used in descriptions are: A. I, antennule; A. II: antenna ; Labr., labrum; Md., mandible; Mx. I, maxillule; Mx. II, maxilla; Th. I, II, etc., thoracopod I, II, etc.; Urp., uropod.

The characters used in the phylogenetic analysis and their character states are shown in Appendix 1.

Cladistic methods

Twenty-eight adult morphological characters were used to reconstruct the phylogenetic relationships among the ten species of *Atopobathynella*. The resulting data matrix is given in Table 1. A phylogenetic analysis was performed using the program PAUP 4.0b10 for Microsoft Windows (Swofford 2002), where a heuristic search for the most parsimonious trees was applied. Schminke (1973) suggested a close relationship between *Atopobathynella* and *Chilibathynella* Schminke, 1973, primarily based on the shared presence in these genera of one-segmented exopods on thoracopods I–VII. This character state has subsequently been reported for *Nunubathynella* Schminke, 1976. Therefore, *Chilibathynella* and *Nunubathynella*, were selected as outgroups to root the phylogenetic trees.

Taxonomy

Genus ***Atopobathynella*** Schminke

Parabathynella Chappuis, 1926 partim: 7–10.
Atopobathynella Schminke, 1973: 83–86.
Type species: *Parabathynella valdiviana* Noodt, 1964

Diagnosis

Antennule I often showing sexual dimorphism in inner margin of second segment: female has only one simple seta, while male bears an antennal organ with one or two setae, which can be modified. Antenna one-segmented. Labrum heterodont with numerous teeth, of which size decreases medially. Mandible with spine row of five spines. Maxilla four-segmented. Exopod of thoracopods I–VII one-segmented. Sympod of uropod usually with spines of equal size; exopod of uropod often with ventromedial seta. Male thoracopod VIII semicircular in lateral view, in form of a partially peeled tangerine in ventral view; protopod massive, cranial with lobus denticulatus, frontally often with slight protrusion; epipod drawn out into conical projection directed cranially; basipod triangular, as large as epipod; exopod and endopod in form of tiny spine located distally on basipod.

Table 1. Data matrix for phylogenetic analysis of the genus *Atopobathynella*
–, Inapplicable characters; ?, missing characters

Taxon	Characters		
	0000000001	1111111112	22222222
	1234567890	1234567890	12345678
A. wattsi	0100110010	1101000110	01000000
A. glenayleensis	0100110010	0100020100	11010001
A. readi	0110000003	0000110001	21011020
A. gascoyneensis	0100000030	0201120111	10011021
A. schminkei	1110011021	1211121011	01010021
A. hinzeae	0100110131	0211121111	20010020
A. hospitalis	0100??0010	01011201?1	10010020
A. compagana	0101011111	01011211?1	21100110
A. chelifera	1001101112	02011211?1	21100110
A. valdiviana	0000???0?0	0101121101	21100010
C. australiensis	0000001001	12010000?–	10001000
N. dimera	0000001000	01010100?–	21001100

Remarks

We propose a revised generic diagnosis for *Atopobathynella*, since that provided by Schminke (1973) does not cover the novelties within the six new species. For example, the sexual dimorphism seen in the inner margin of the second antennular segment is not identifiable in at least two new species. Schminke (1973) includes a three-segmented maxilla in the generic diagnosis, yet he refers to a four-segmented one, with a setal formula 2-4-9-7, when generally characterising the genus and in describing *A. hospitalis* and *A. chelifera*. In the six new species described here, the maxilla is four-segmented with a setal formula 2-4-n-7 (i.e. variation in the number of setae occurring on third endite).

Scanning electron micrographs of male thoracopods VIII are shown in Figs 2, 7, 12, 17 and 22. Remarkable is the small size of the basipod relative to that of the protopod, as well as the reduction of the endo- and exopod. One could interpret the protopod as the basipod. Thereafter, the epipod, the basipod, and the lobus denticulatus would be interpreted as a projection of the basipod, the exopod, and the endopod, respectively. However, this interpretation is not quite convincing because the projection of the basipod derives from the inner margin and is directed caudally in most other species of the Parabathynellidae.

The description of *A. valdiviana*, the type species of *Atopobathynella*, was first published in 1964 (Noodt 1964), not in 1965 as cited by Schminke (1973).

Atopobathynella wattsi, sp. nov.

(Figs 1–4)

Material examined

Holotype. ♂, Australia, Western Australia, Millbillillie Station, Main Roads bore north (26°41′04″S, 120°12′54″E), BES 6619, 5.v.2001, leg. W. F. Humphreys, C. H. S. Watts and S. J. B. Cooper. Dissected, on five slides (permanent preparation) (WAM C 34361).

Allotype. **Australia, Western Australia**: ♀, same data as for holotype. Dissected, on five slides (permanent preparation) (WAM C 34362).

Paratypes. **Australia, Western Australia**: 2 ♂, 1 ♀, same data as for holotype, each dissected, on five slides (WAM C 34363–34365). 10 ♂, 8 ♀, from type locality, each as whole specimens on a slide (WAM C 34366–34383).

Other material examined. **Australia**, **Western Australia**: Paroo Station, GSWA 15 south (26°24′01″S, 119°45′47″E), BES 5620, one female as a whole specimen on a slide (WAM C 34384).

Diagnosis

Body size up to 3 mm, 17× as long as wide; second antennular segment of male bearing antennal organ with two

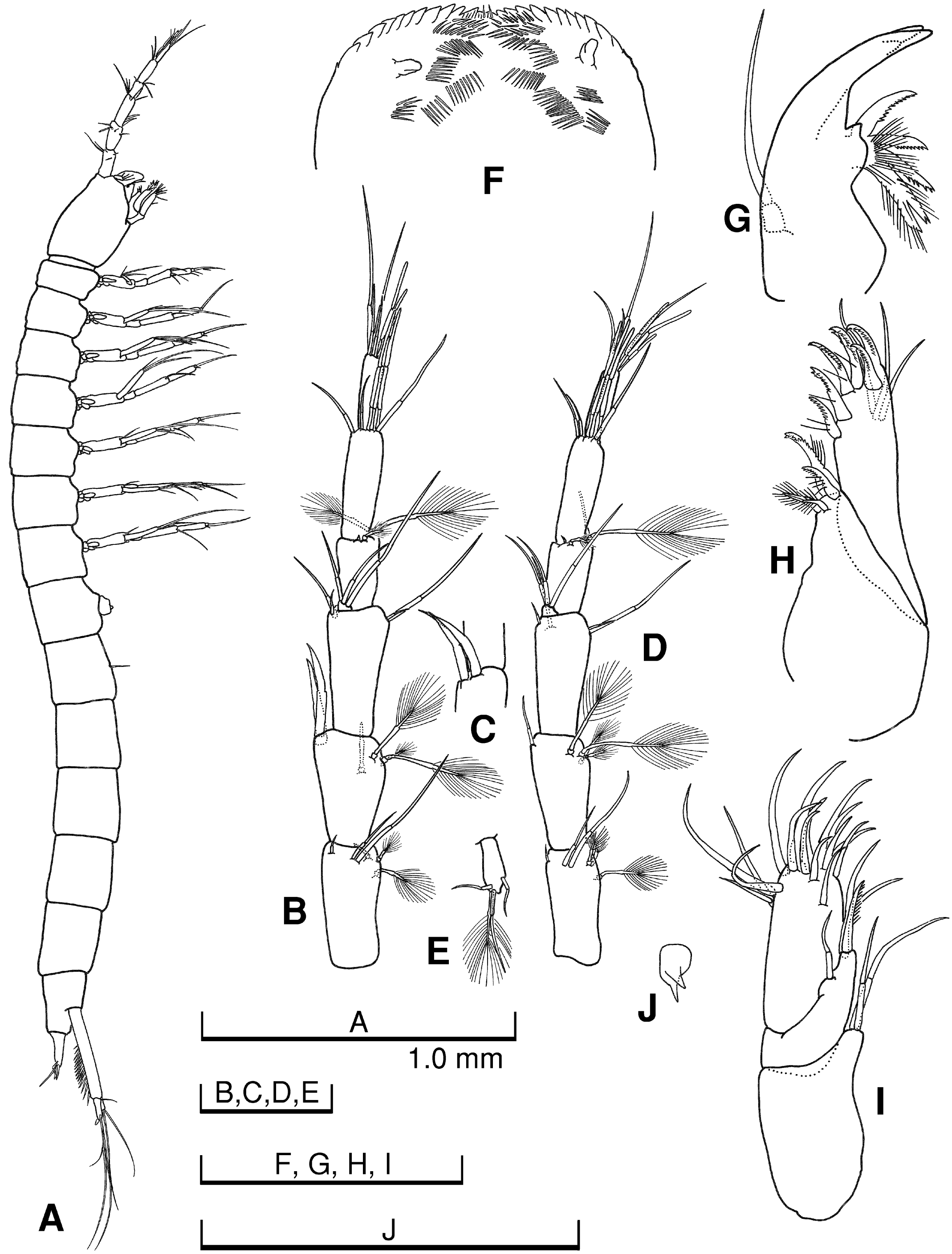

Fig. 1. *Atopobathynella wattsi*, sp. nov. (♂, holotype; ♀: allotype): *A*, general habitus ♂ (lateral); *B*, A. I ♂ (dorsal); *C*, antennal organ (lateral); *D*, A. I ♀ (dorsal); *E*, A. II ♂; *F*, Labr. ♂ (ventral); *G*, Md. ♂ (dorsal); *H*, Mx. I ♂ (dorsal); *I*, Mx. II ♂; *J*, Th. VIII ♀ (slightly ventral). Scale bars = 0.1 mm (unless otherwise specified).

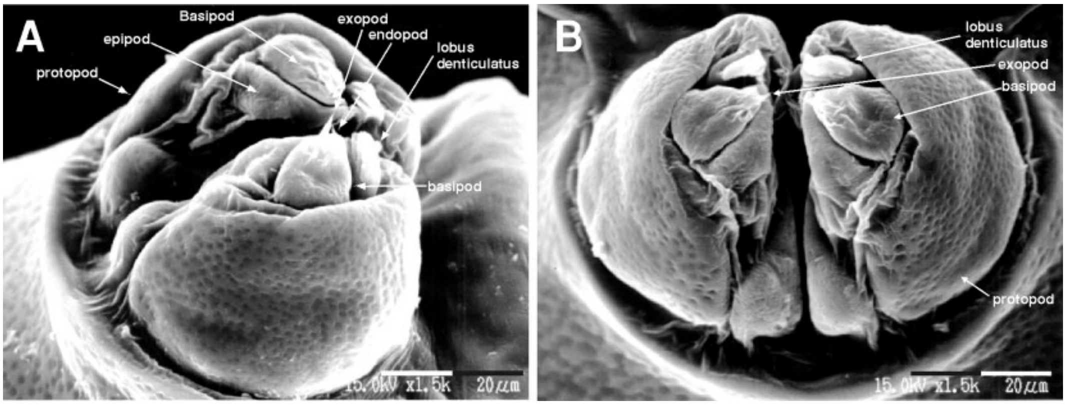

Fig. 2. *Atopobathynella wattsi*, sp. nov., thoracopod VIII (♂, paratype): *A*, lateroventral view; *B*, ventral view.

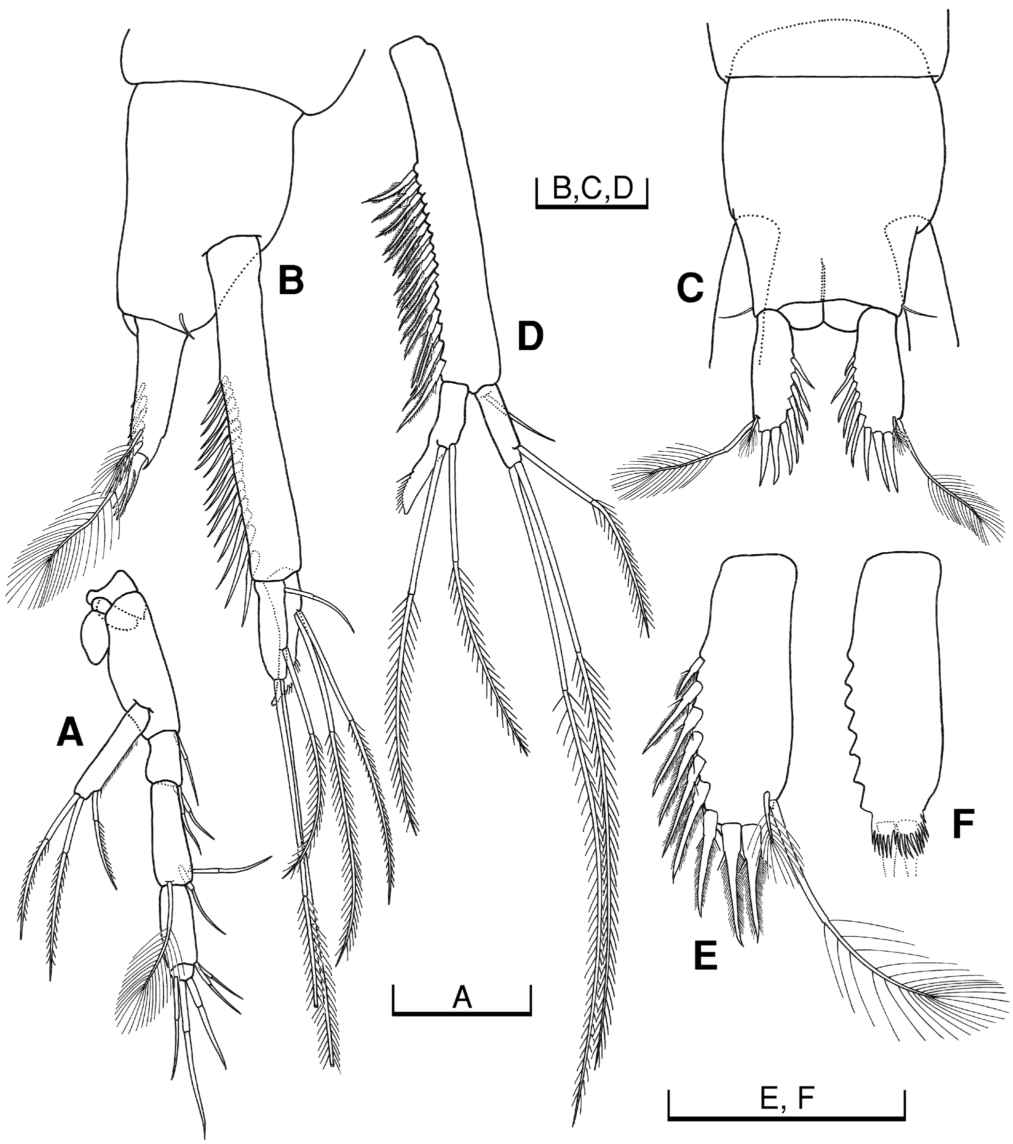

Fig. 3. *Atopobathynella wattsi*, sp. nov. (♂, holotype): *A*, Th. I (lateral); *B*, pleotelson, furcal rami and Urp. (outer lateral); *C*, pleotelson and furcal rami (dorsal); *D*, Urp. (lateral); *E*, furcal ramus (dorsal); *F*, furcal ramus without ornaments. Scale bar = 0.1 mm.

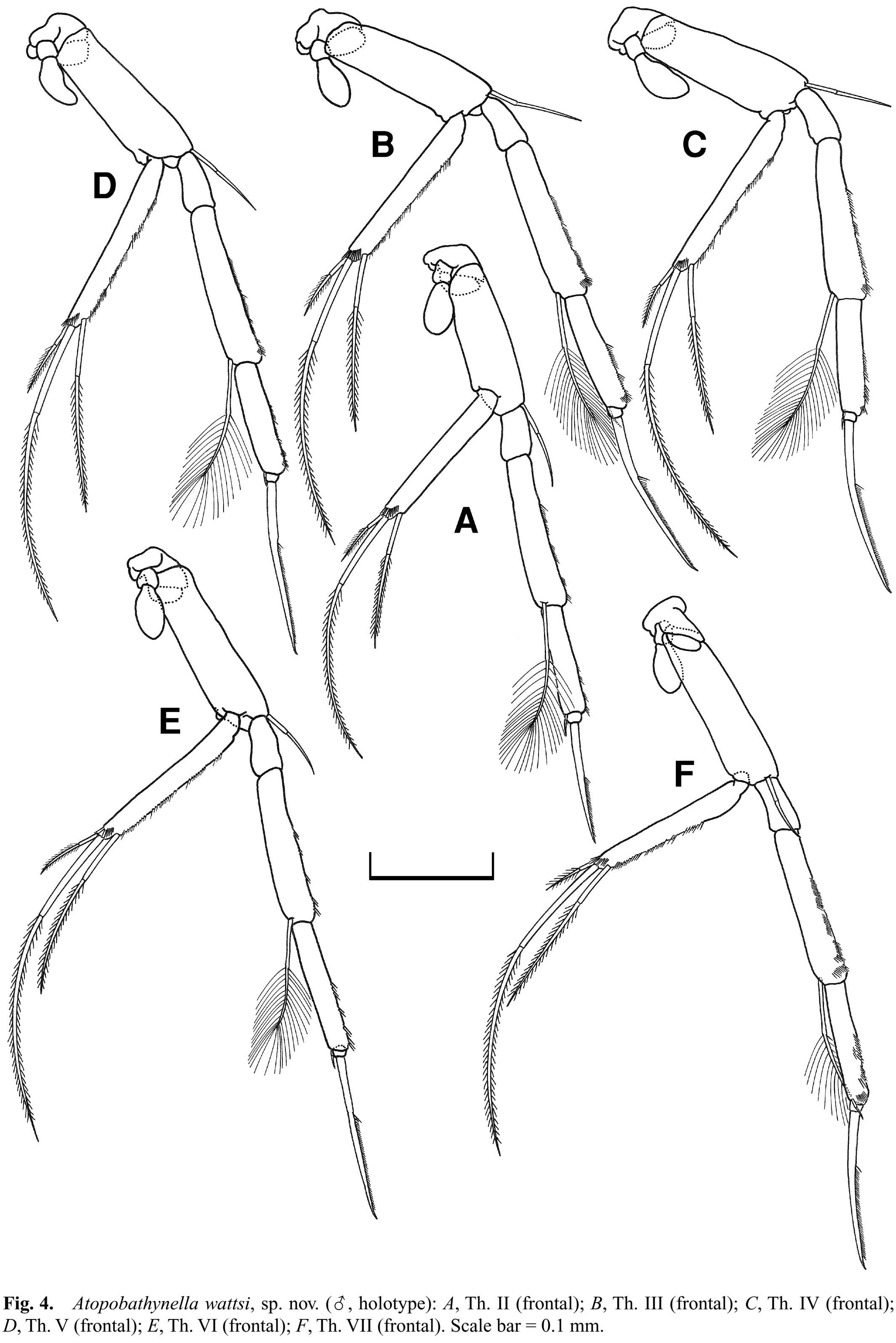

Fig. 4. *Atopobathynella wattsi*, sp. nov. (♂, holotype): *A*, Th. II (frontal); *B*, Th. III (frontal); *C*, Th. IV (frontal); *D*, Th. V (frontal); *E*, Th. VI (frontal); *F*, Th. VII (frontal). Scale bar = 0.1 mm.

claw-shaped setae; labrum with 26 teeth; male thoracopod VIII with balloon-shaped protopod with frontal protrusion; right and left thoracopods VIII of female fused to form single, tiny, bifurcated structure; uropodal sympod with 17 spines, exopod with ventral seta and subterminal seta; furcal rami 3× as long as wide, with nine spines; anal operculum flat.

Description

Male (holotype)

Body length (Fig. 1*A*) 2.95 mm, ~17× as long as wide. Head as long as segments 1–2 combined, with assemblage of mouthparts located in distal half of head.

Antennule (Fig. 1*B*) six-segmented. First segment with: one seta on inner distal margin, two simple dorsal setae and one dorsal, one lateral and one ventromedial plumose seta. Second segment with a group of four plumose setae and antennal organ. Antennal organ (Fig. 1*C*) represented by two setae of equal length on inner distal margin without protrusion. Both setae thick and claw-shaped, subdivided into stalk-shaped proximal and sharp-pointed distal parts. Third segment with two lateral setae: one seta on inner distal margin and one ventromedial seta. Inner flagellum of third segment with three simple setae. Fourth segment with one stub seta and one plumose seta on dorsal margin, and two plumose setae on outer distal apophysis. Fifth segment with two setae on inner margin, two aesthetascs and one simple seta dorsally, and one lateral aesthetasc. Sixth segment with four terminal setae and three subterminal aesthetascs.

Antenna (Fig. 1*E*) one-segmented, almost as long as sixth antennular segment, with two simple setae and one plumose seta distally, and one medial seta.

Labrum (Fig. 1*F*) with 26 teeth. Two median teeth flanked laterally by 12 teeth on each side.

Mandible (Fig. 1*G*) with incisor process of three teeth. Tooth on ventral edge triangular. Spine row consisting of five spines. Palp of one segment with one apical seta, 6× as long as palp.

Maxillule (Fig. 1*H*) two-segmented. Proximal segment with four setae on inner distal margin. Distal segment with two terminal claws, four claws on inner edge, and with three simple setae on outer distal margin.

Maxilla (Fig. 1*I*) four-segmented, setal formula 2-4-9-7.

Thoracopods I–IV (Figs 3*A*, 4*A–C*) increasing in length posteriorly. Thoracopods IV–VI (Fig. 4*C–E*) equal in length. Protopod of thoracopods I–VII each bearing one epipod. Basipod of thoracopods I–VII each bearing one seta. Exopod of thoracopods I–VII one-segmented, shorter than first and second segments of endopod, each with two terminal setae and with one subterminal seta on ventral margin. Outer terminal seta shorter than half length of inner one (except in exopod of thoracopod I). Endopod of thoracopods I–VII four-segmented, setal formulae:

Thoracopod I. 2+0/2+1/2+0/3(1)

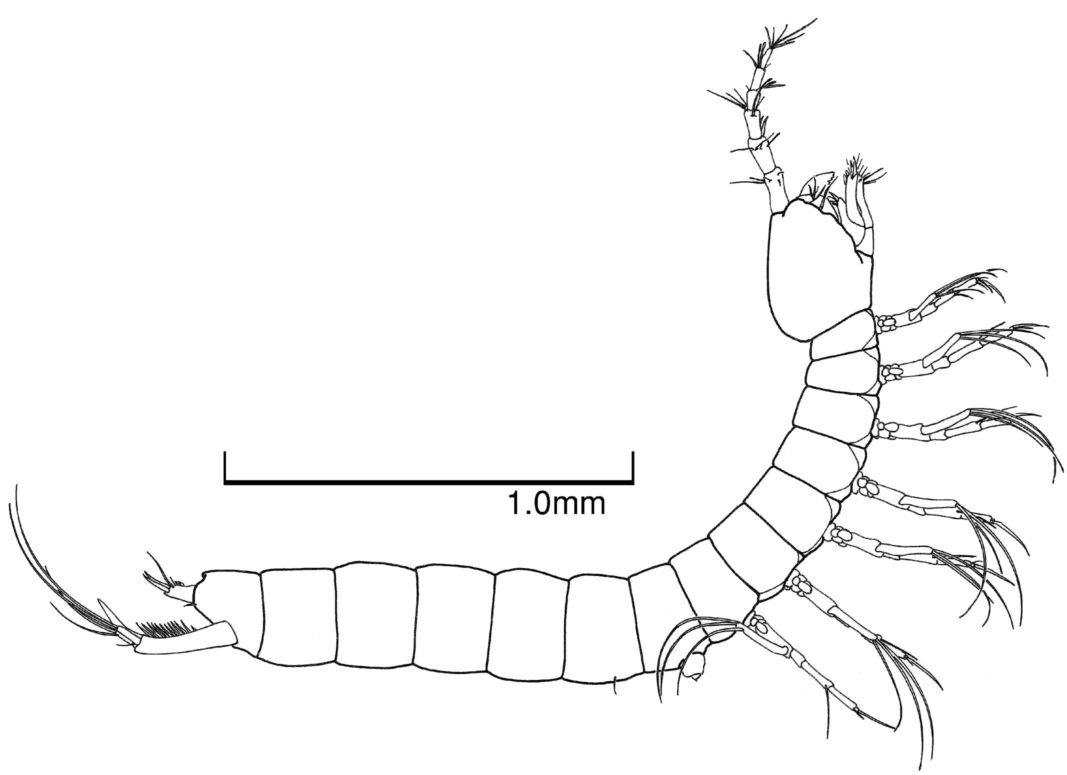

Fig. 5. *Atopobathynella glenayleensis*, sp. nov., general habitus, lateral (♂, holotype). Scale bar = 1 mm.

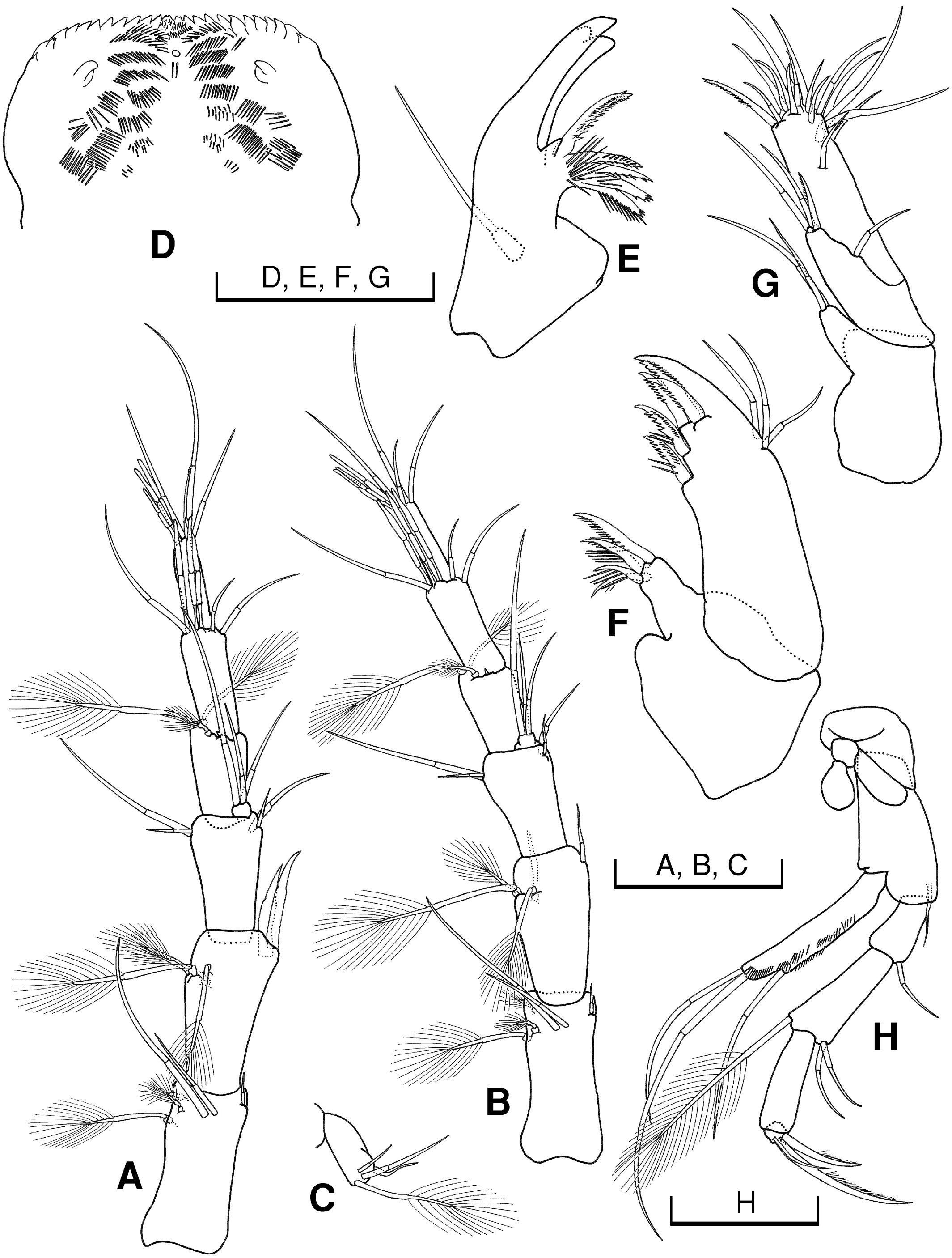

Fig. 6. *Atopobathynella glenayleensis*, sp. nov. (♂, holotype; ♀, allotype): *A*, A. I ♂ (dorsal); *B*, A. I ♀ (dorsal); *C*, A. II ♂ (dorsal); *D*, Labr. ♂ (ventral); *E*, Md. ♂ (ventral); *F*, Mx. I ♂ (dorsal); *G*, Mx. II ♂ (dorsal); *H*, Th. I ♂ (frontal). Scale bar = 0.1 mm.

Thoracopods II–VII. 0+0/0+1/0+1/1(0)

Thoracopod VIII (Fig. 2). Protopod massive, with frontal protrusion. Lobus denticulatus four-lobed. Epipod drawn out into conical projection and directed cranially. Basipod triangular, as large as epipod. Exopod and endopod in form of tiny spine located distally on basipod.

First pleopod seta-like.

Uropod (Fig. 3*B*, *D*) bearing 17 spines of equal size on inner margin of sympod. Endopod length 20% sympod length, drawn out distally in spur, with two lateral setae near base of spur. Exopod almost as long as endopod, with one ventromedial seta, one subterminal seta, and two terminal setae, of which inner seta is slightly longer than outer one.

Pleotelson (Fig. 3*B*, C) with one seta at base of furcal rami on both sides. Anal operculum slightly concave.

Furcal rami (Fig. 3*E*, *F*) 3× as long as wide, with 8–9 spines and two dorsal setae.

Female (allotype)

Female differs from male in second antennular segment and thoracopod VIII. Body length 2.90 mm, ~15× as long as wide. Second antennular segment (Fig. 1*D*) with one group of four plumose setae and simple seta on inner distal margin. Thoracopod VIII (Fig. 1*J*) unpaired, tiny, semicircular and bearing two distal spines.

Etymology

The species is named after one of the collectors, C. H. S. Watts.

Atopobathynella glenayleensis, sp. nov.

(Figs 5–9)

Material examined

Holotype. ♂, Australia, Western Australia, Glenayle Station, Gidgee Bore (25°23′10″S, 122°8′8″E), BES 9957, 6.vii.2003, leg. W. F. Humphreys and C. H. S. Watts. Dissected on five slides (permanent preparation) (WAM C 34395).

Allotype. **Australia, Western Australia**: ♀, same data as for holotype, Dissected on five slides (permanent preparation) (WAM C 34396).

Paratypes. **Australia, Western Australia**: 1 ♂, 1 ♀, from type locality, each dissected on five slides (WAM C 34397–34398). 10 ♂, 8 ♀, from type locality, each as whole specimens on a slide (WAM C 34399–34416).

Other material examined. **Australia**, **Western Australia:** Carnegie Downs Station, Site 247 nr Engine Bore (25°40′07″S, 122°22′07″E), BES 9962. 7.vii.2003, leg. W. F. Humphreys and C. H. S. Watts (WAM C 34417).

Diagnosis

Body size 2.3 mm, 15× as long as wide; second antennular segment of male bearing an antennal organ with two claw-shaped setae; labrum with 24 teeth; male thoracopod VIII with balloon-shaped protopod with frontal protrusion; right and left thoracopods VIII of female separated, each spine-like; uropodal sympod with 17 spines, exopod with ventral seta, and without subterminal setae; furcal rami 1.5× as long as wide, with eight spines; anal operculum protruded.

Description

Male (holotype).

Body length (Fig. 5) 2.22 mm, ~15× as long as wide. Head as long as segments 1–3 combined.

Antennule (Fig. 6*A*) as in *A. wattsi*.

Antenna (Fig. 6*C*) as in *A. wattsi*, almost as long as sixth antennular segment.

Labrum (Fig. 6*D*) with 24 teeth. Two median teeth (that are distally denticulate) flanked laterally by 11 teeth on each side. Size of teeth slightly increasing laterally (except last two).

Mandible (Fig. 6*E*) with incisor process of three teeth. Tooth of ventral edge triangular. Spine row consisting of five spines. Distal spine bearing two rows of spikes. Palp of one segment, with one apical seta, 6× as long as palp.

Maxillule (Fig. 6*F*) as in *A. wattsi.*

Maxilla (Fig. 6*G*) as in *A. wattsi.*

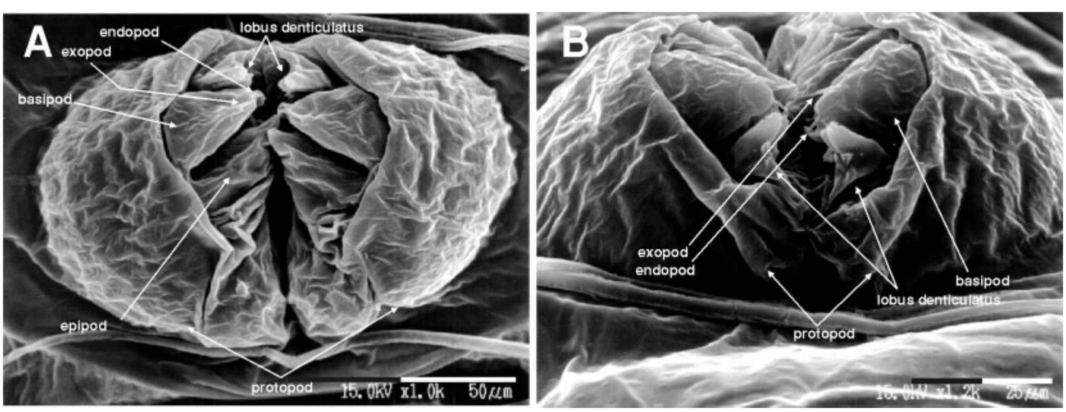

Fig. 7. *Atopobathynella glenayleensis*, sp. nov., thoracopod VIII (♂, paratype): *A*, ventral view; *B*, posterior view.

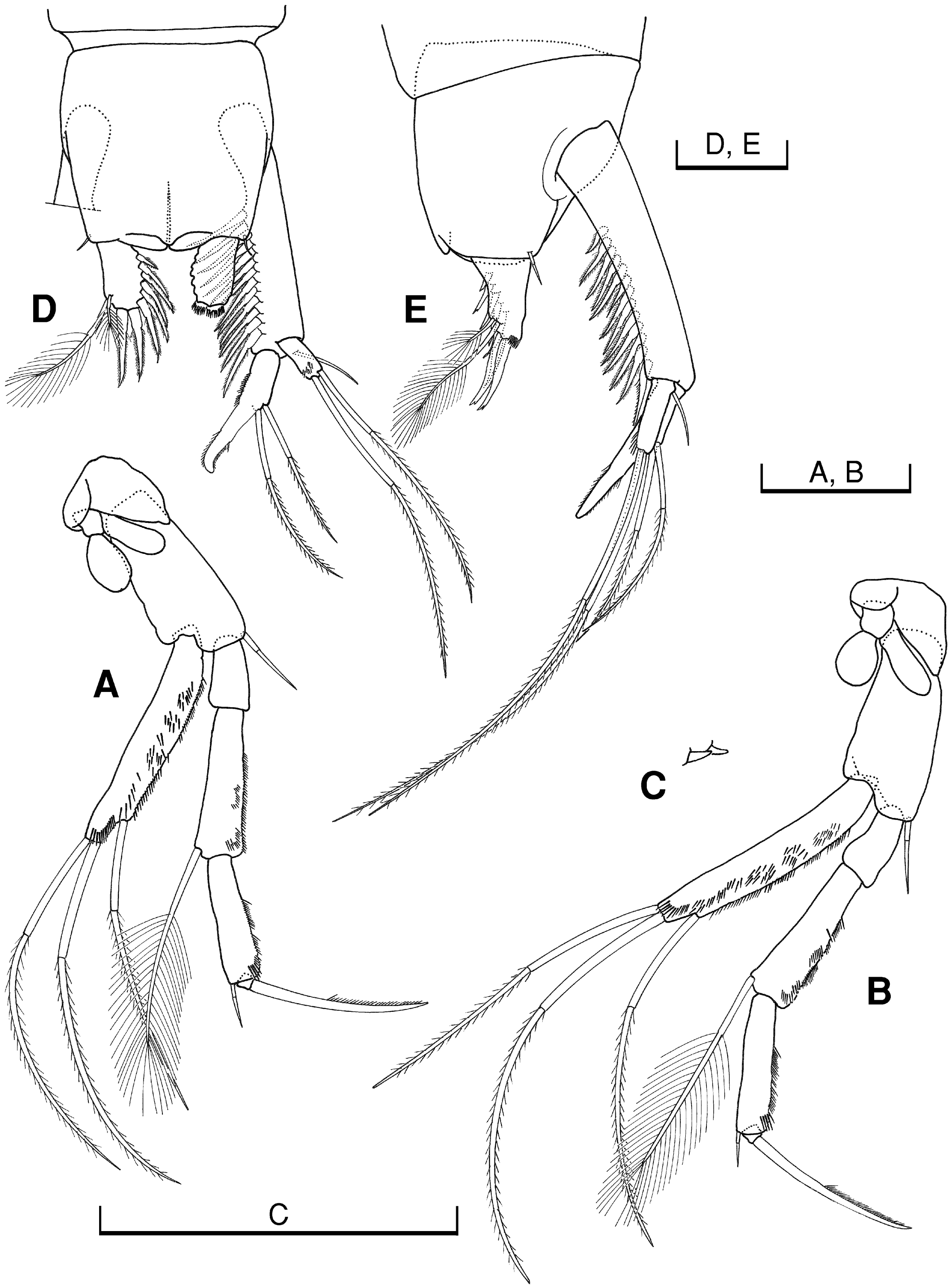

Fig. 8. *Atopobathynella glenayleensis*, sp. nov. (♂, holotype; ♀, allotype): *A*, Th. II ♂ (frontal); *B*, Th. III ♂ (frontal); *C*, Th. VIII ♀ (slightly ventral); *D*, pleotelson, furcal rami and Urp. (dorsal); *E*, pleotelson and furcal rami (lateral). Scale bar = 0.1 mm.

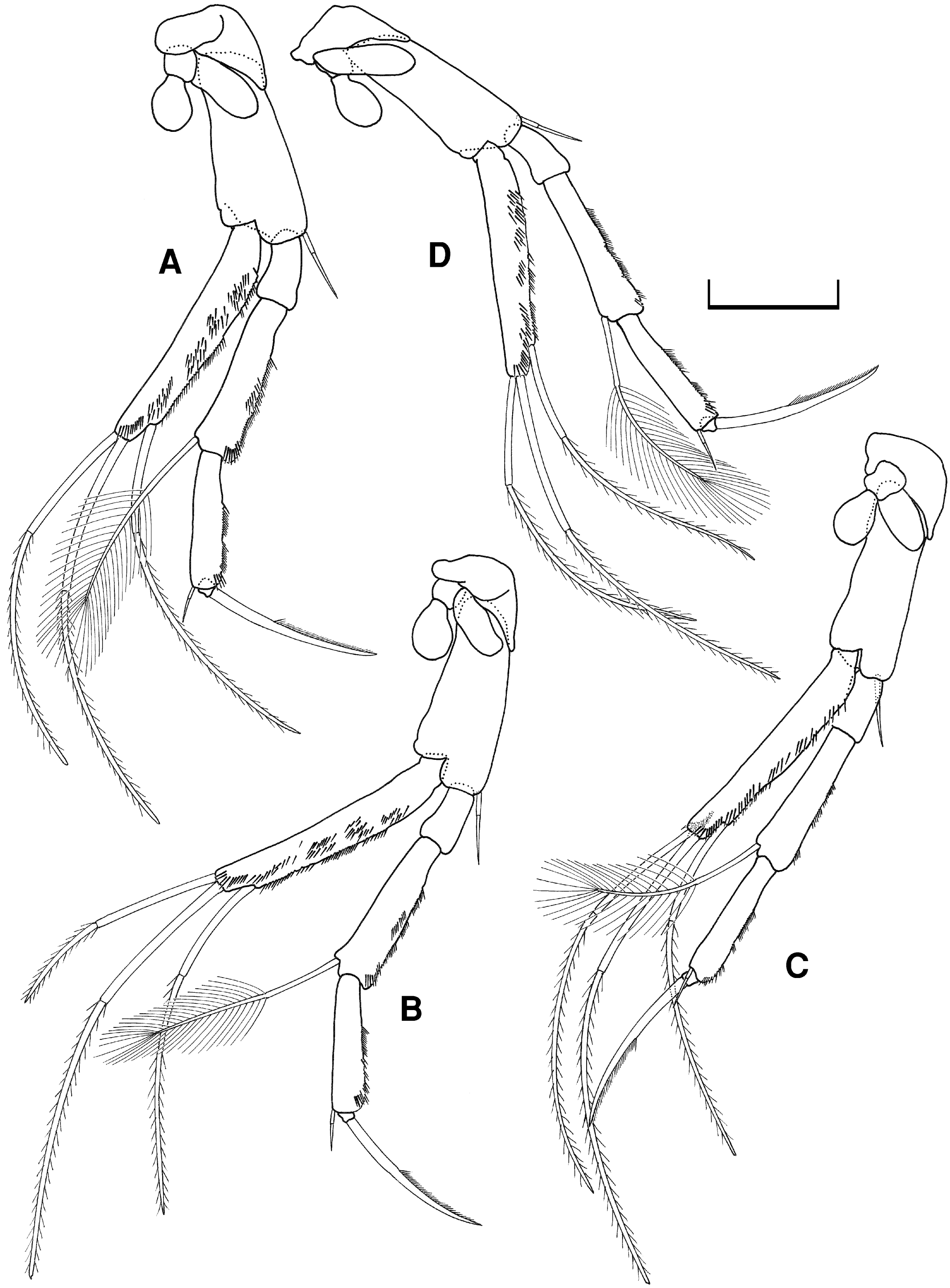

Fig. 9. *Atopobathynella glenayleensis*, sp. nov. (♂, holotype): *A*, Th. IV (frontal); *B*, Th. V (frontal); *C*, Th. VI (frontal); *D*, Th. VII (frontal). Scale bar = 0.1 mm.

Thoracopods I–IV (Figs 6*H*, 8*A*, *B*, 9*A*) increasing in length posteriorly. Thoracopods IV–VII (Fig. 9*A–D*) similar in length. Each protopod of thoracopods I–VII bears one epipod. Each basipod of thoracopods I–VII bears one seta. Exopod of thoracopods I–VII one-segmented, as long as first and second segments of endopod, bearing two terminal setae and one subterminal seta on ventral margin. Outer terminal seta longer than half length of inner one. Endopod of thoracopods I–VII four-segmented, setal formulae:

Thoracopod I. 1+0/2+1/0+0/3(1)

Thoracopods II–VII. 0+0/0+1/0+1/1(0)

Thoracopod VIII (Fig. 7). Protopod massive, with frontal protrusion. Lobus denticulatus three-lobed, epipod drawn out into conical projection directed cranially. Basipod triangular, as large as epipod; exopod and endopod in form of tiny spine located distally on basipod.

First pleopod seta-like.

Uropod (Fig. 8*D*, *E*) with 13 spines of similar size on inner margin of sympod. Endopod length 30% sympod length, drawn out distally into spur, with two lateral setae near base of spur. Exopod as long as endopod, with one ventromedial seta, group of ctenidia subterminally, and two terminal setae, of which inner one is slightly longer than outer one.

Pleotelson (Fig. 8*D*, *E*) with one seta at base of furcal rami on both sides. Anal operculum protruded.

Furcal rami 1.5× as long as wide, with eight spines and two dorsal setae.

Female (allotype)

Female differs from male in second antennular segment and thoracopod VIII. Body length 2.10 mm, ~15× as long as wide. Second antennular segment (Fig. 6*B*) with group of four plumose setae, and with simple seta on inner distal margin. Thoracopod VIII (Fig. 8*C*) paired, tiny, spine-like.

Etymology

This species is named after the type locality, Glenayle Station, Western Australia.

Atopobathynella readi, sp. nov.

(Figs 10–13)

Material examined

Holotype. ♂, Australia, Northern Territory, Newhaven Station, bore RN 15494 (22°56′04″S, 131°14′23″E), BES 9477, 19.viii.2002, leg. W. F. Humphreys and R. Read. Dissected on five slides (permanent preparation), coll. Museum and Art Galley of the Northern Territory, Darwin (NTM Cr 013924).

Allotype. **Australia, Northern Territory**: ♀, same data as for holotype, Dissected on five slides (permanent preparation) (WAM C 34386).

Paratypes. **Australia, Northern Territory**: 2 ♂, 6 ♀, same data as for holotype, each as whole specimens on a slide (WAM C 34387–34394).

Diagnosis

Body size 1.9 mm, fat-bellied, ~6–7× as long as wide; second antennular segment without antennal organ; labrum with 22 teeth; male thoracopod VIII with balloon-shaped protopod without frontal protrusion; right and left thoracopods VIII of female separated, each in form of raspberry fruit; uropodal sympod with 10 spines, exopod without ventral and subterminal setae; furcal rami 3× as long as wide, with three spines; anal operculum concave.

Description

Male (holotype)

Body length (Fig. 10*A*, *B*) 1.88 mm, ~6–7× as long as wide. Width and depth of body segments slightly increasing posteriorly to ninth segment, and then decreasing. Head as long as segments 1–3 combined.

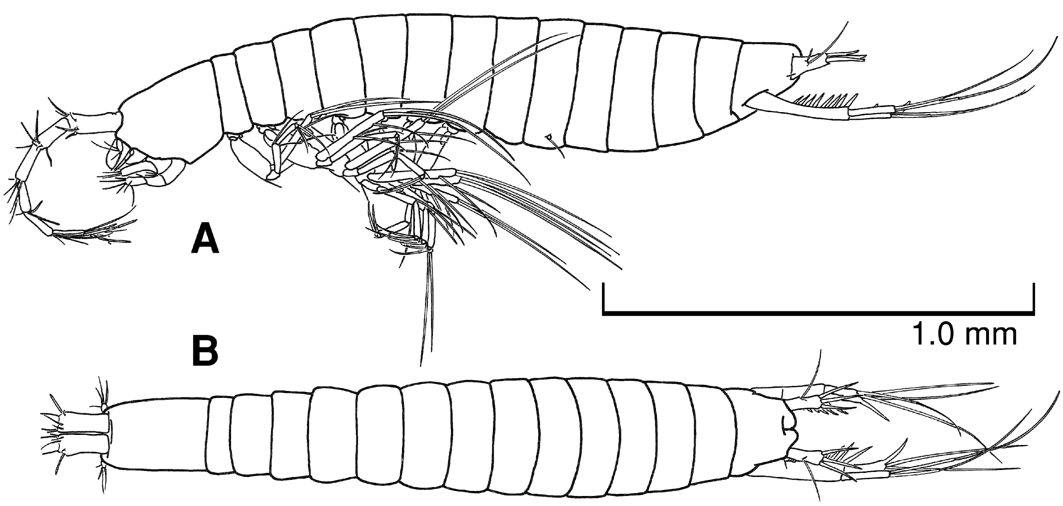

Fig. 10. General habitus of *Atopobathynella readi*, sp. nov. (♀, allotype): *A*, lateral; *B*, dorsal. Scale bar = 1 mm.

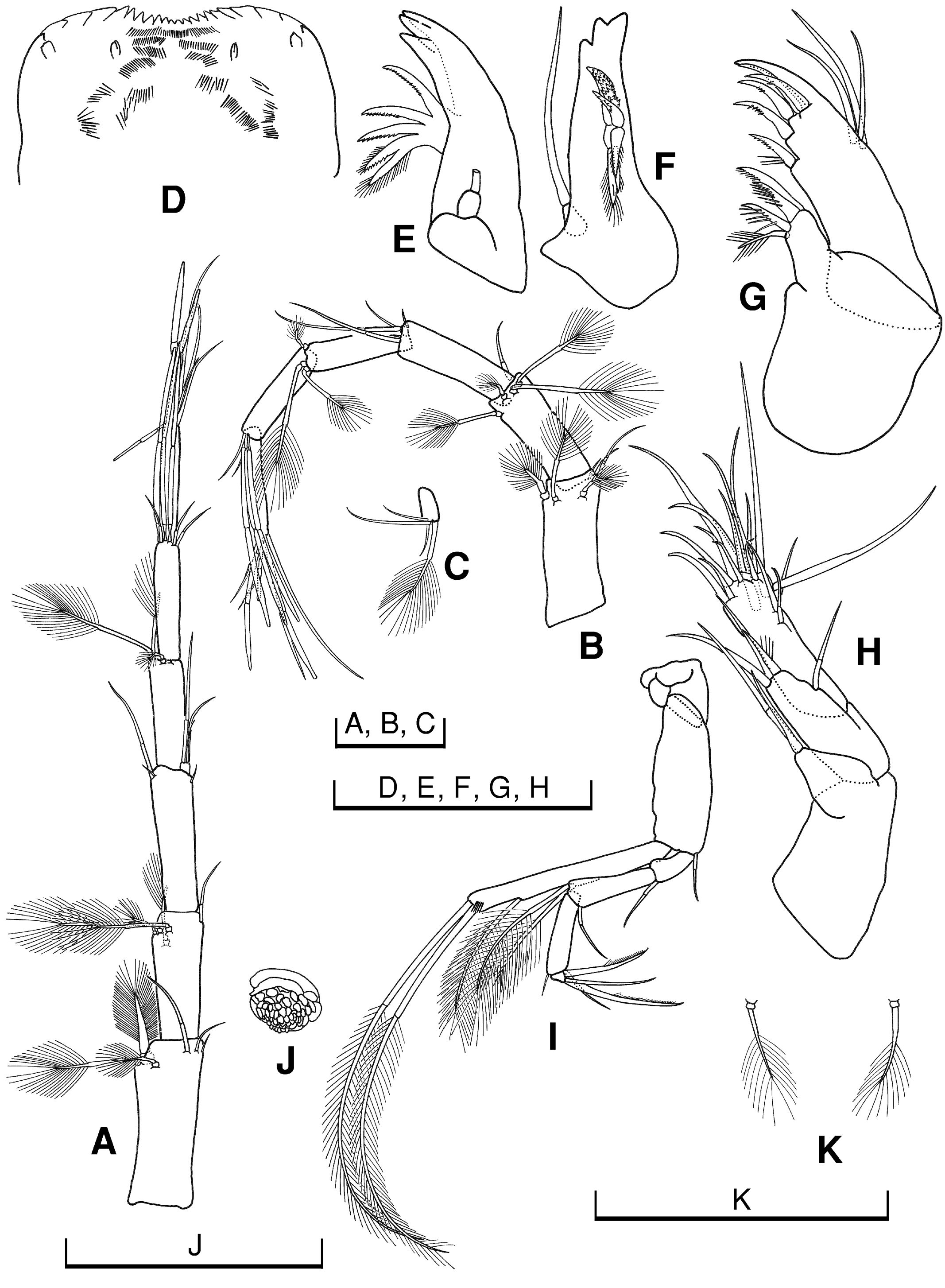

Fig. 11. *Atopobathynella readi*, sp. nov. (♂, holotype; ♀, allotype): *A*, A. I ♂ (dorsal); *B*, A. I ♀ (dorsal); *C*, A. II ♂ (dorsal); *D*, Labr. ♂ (ventral); *E*, Md. ♂ (ventral); *F*, Md. ♂ (inner lateral); *G*, Mx. I ♂ (dorsal); *H*, Mx. II ♂ (dorsal); *I*, Th. I ♂ (frontal); *J*, Th. VIII ♀ (ventral); *K*, pleopod I (ventral). Scale bar = 0.1 mm.

Antennule (Fig. 11*A*) as in *A. wattsi* except as follows: ventromedial plumose seta on first segment is 2× as thick as other setae; second segment without antennal organ; third segment without ventromedial seta. Each antennular segment elongated.

Antenna (Fig. 11*C*) as in *A. wattsi* except relative size, which measures one-third of sixth antennular segment.

Labrum (Fig. 11*D*) with 22 teeth. Two tiny median teeth flanked laterally by ten teeth on each side. Teeth increasing in size laterally.

Mandible (Fig. 11*E*, *F*) with incisor process of three teeth. Tooth of ventral edge triangular. Spine row consisting of five spines. Distal spine wide, bearing three rows of denticles. Palp of one segment, with one apical seta, 6× as long as palp.

Maxillule (Fig. 11*G*) as in *A. wattsi.*

Maxilla (Fig. 11*H*) four-segmented, setal formula 2-4-10-7.

Thoracopods I–IV (Figs 11*I*, 13*A*, *B*, 14*A*) increasing in length posteriorly. Thoracopods IV–VII (Figs 13*C,* 14*A*–*C*) decreasing in length posteriorly. Each protopod of thoracopods II–VI bears one epipod. Each basipod of thoracopods I–VII bears one seta. Exopod of thoracopods I and VII one-segmented, longer than first and second segment of endopod. Exopod of thoracopods I–VI each with two terminal seta and two subterminal setae on ventral margin. Exopod of thoracopods VII with two terminal seta and one subterminal seta on ventral margin. Inner terminal seta slightly longer than outer one. Outer terminal seta slightly shorter than inner one. Endopod of thoracopods I–VII four-segmented, setal formulae:

Thoracopod I. 1+0/1+1/1+1/3(1)

Thoracopods II–VII. 0+0/0+1/0+1/2(0)

Thoracopod VIII (Fig. 12) semicircular in lateral view. Protopod massive, without frontal protrusion. Lobus denticulatus as cover plate with six rows of denticles. Epipod drawn out into conical projection directed cranially. Basipod triangular, as large as epipod; exopod and endopod in form of tiny spine located distally on basipod.

First pleopod (Fig. 11*K*) seta-like located on a tiny segment.

Uropod (Fig. 13*D*, *E*) rod-shaped, bearing 7–9 spines increasing in size distally on inner margin of sympod. Endopod length 50% sympod length, drawn out distally into spur, with two lateral setae near base of spur. Exopod as long as endopod, with two terminal setae, without ventromedial seta.

Pleotelson (Fig. 13*D*, *E*) with one seta at base of furcal rami on both sides. Anal operculum concave.

Furcal rami (Fig. 13*D*, *E*) rectangular, 3× as long as wide, with three distal spines and two dorsal setae.

Female (allotype)

Female differs from male in thoracopod VIII. Body length 1.80 mm. Both thoracopods VIII (Fig. 11*J*) separated, round, and in form of raspberry fruit.

Etymology

The species is named after one of the collectors, R. Read.

Atopobathynella gascoyneensis, sp. nov.

(Figs 15–19)

Material examined

Holotype. ♂, Australia, Western Australia, Carnarvon, Gascoyne River terrace, Water and Rivers Commission bore L71R (24°51′16″S, 113°42′13″E), BES 7420. 10.viii.1999, leg. W. F. Humphreys. Dissected on six slides (permanent preparation) (WAM C 34304).

Allotype. **Australia, Western Australia**: ♀, same data as for holotype. Dissected on five slides (permanent preparation) (WAM C 34305).

Paratypes. **Australia, Western Australia**: 13 ♂, 13 ♀, same data as for holotype, each as whole specimens on a slide. 3 ♂, 3 ♀ as whole specimens on a slide (WAM C 34306–34331).

Diagnosis

Body size 2.2 mm, 13× as long as wide; second antennular segment of male without antennal organ; labrum with

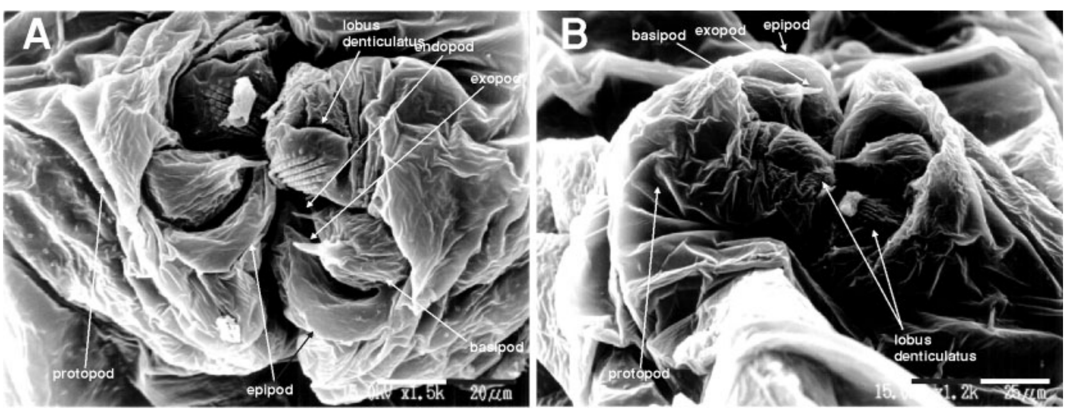

Fig. 12. *Atopobathynella readi*, sp. nov., thoracopod VIII (♂, paratype): *A*, ventral view; *B*, posterior view.

20 teeth; male thoracopod VIII with balloon-shaped protopod without frontal protrusion; right and left thoracopods VIII of female fused to single tiny structure with two distal spines; uropodal sympod with 12 spines, exopod without ventral and subterminal setae, endopod with tiny spine beneath spur; furcal rami 1.5× as long as wide, with three spines; anal operculum protruded.

Description

Male (holotype)

Body length 2.17 mm, ~13× as long as wide (Fig. 15). Head as long as segments 1–2 combined.

Antennule (Fig. 16*A*) as in *A. wattsi* except second segment lacks antennal organ.

Antenna (Fig. 16*C*) as in *A. wattsi.*

Labrum (Fig. 16*D*) with 20 teeth of dissimilar size.

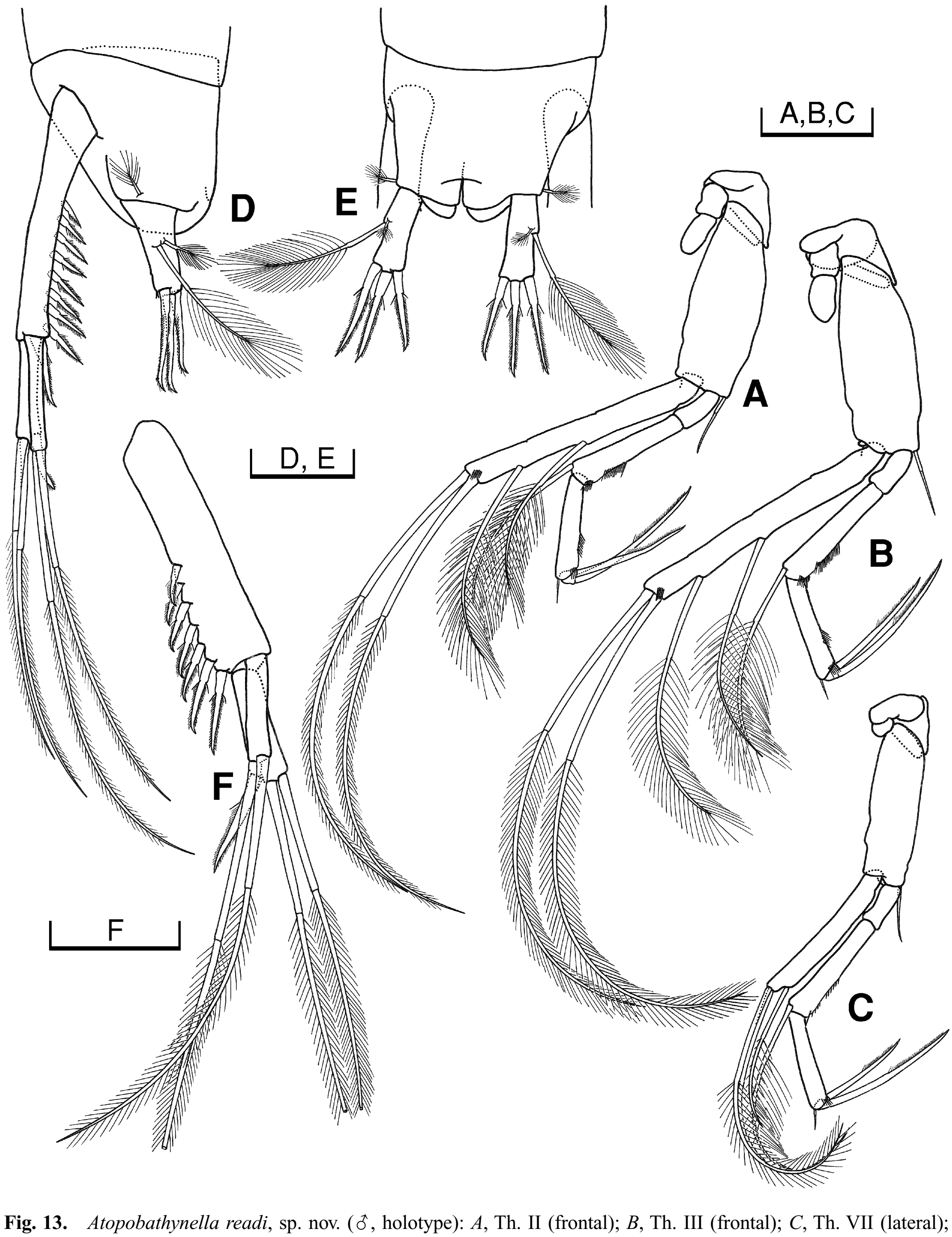

Fig. 13. *Atopobathynella readi*, sp. nov. (♂, holotype): *A*, Th. II (frontal); *B*, Th. III (frontal); *C*, Th. VII (lateral); *D*, pleotelson, furcal rami and Urp. (lateral); *E*, pleotelson and furcal rami (dorsal); *F*, Urp. (dorsal). Scale bar = 0.1 mm.

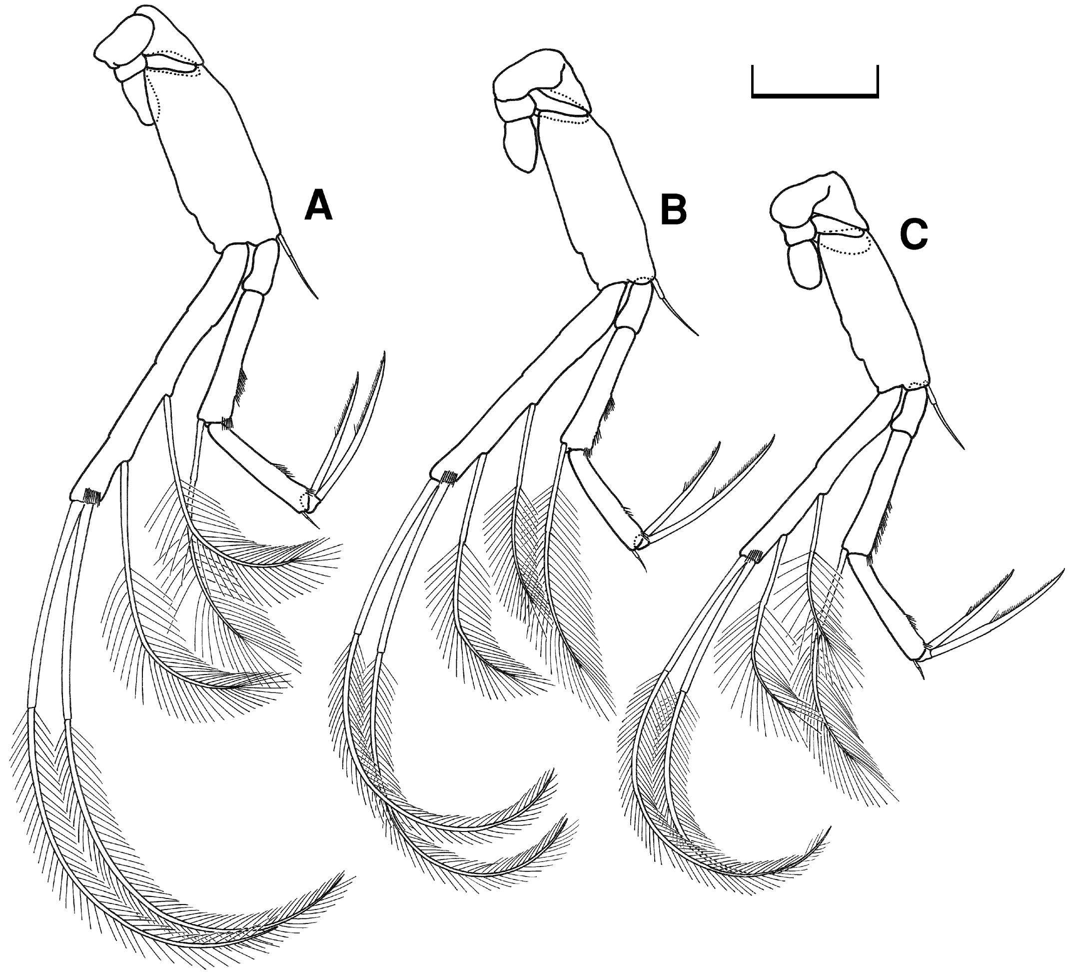

Fig. 14. *Atopobathynella readi*, sp. nov. (♂, holotype): *A*, Th. IV (frontal); *B*, Th. V (frontal); *C*, Th. VI (frontal). Scale bar = 0.1 mm.

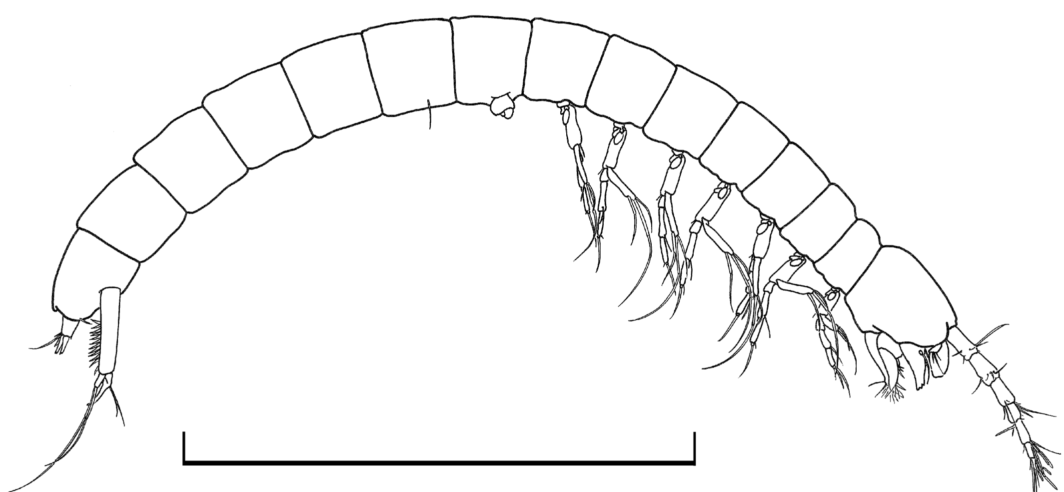

Fig. 15. General habitus of *Atopobathynella gascoyneensis*, sp. nov. (♂, holotype), lateral. Scale bar = 1 mm.

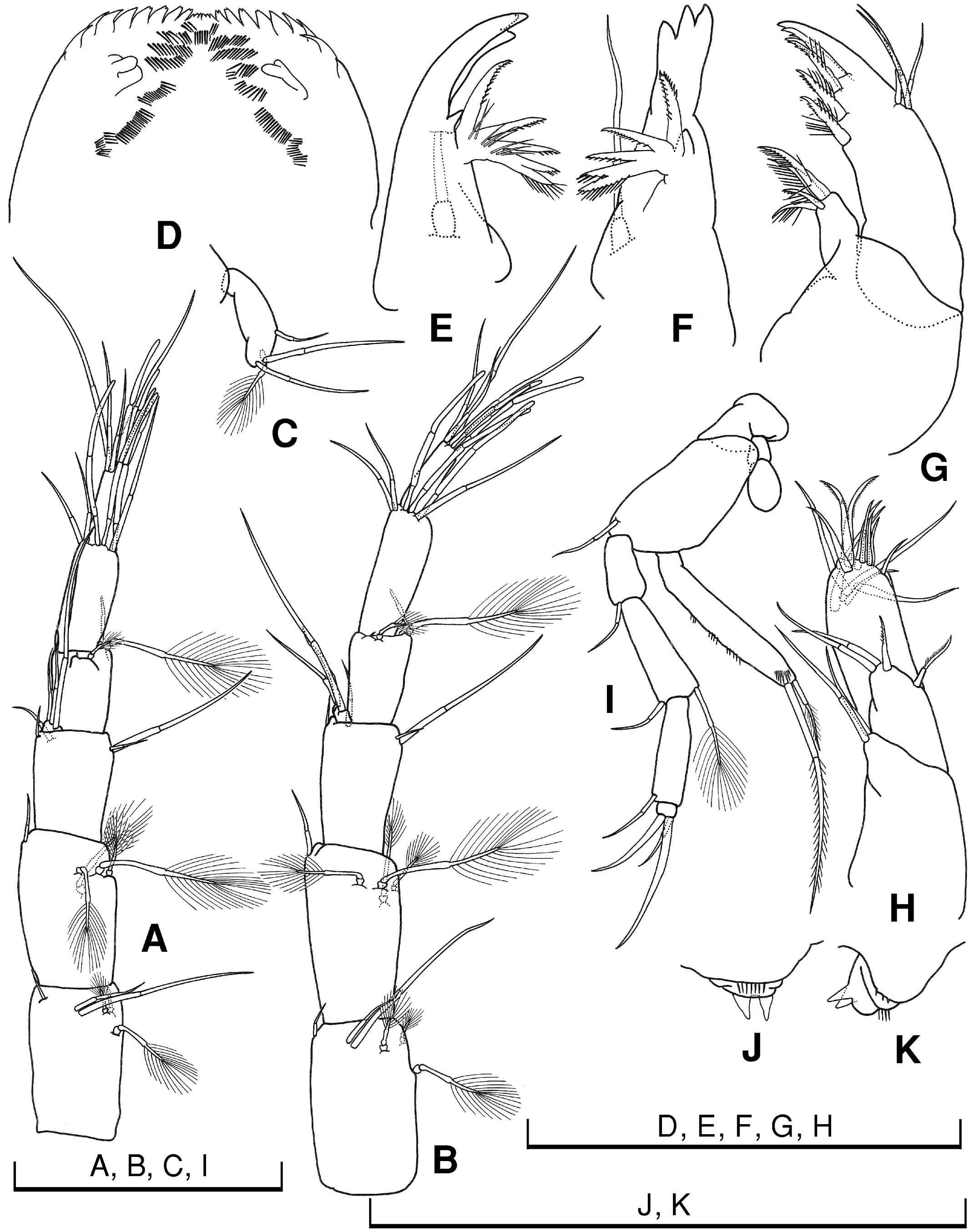

Fig. 16. *Atopobathynella gascoyneensis*, sp. nov. (♂, holotype; ♀, allotype): *A*, A. I ♂ (dorsal); *B*, A. I ♀ (dorsal); *C*, A. II ♂ (dorsal); *D*, Labr. ♂ (ventral); *E*, Md. ♂ (ventral); *F*, Md. ♂ (inner lateral); *G*, Mx. I ♂ (dorsal); *H*, Mx. II ♂ (inner lateral); *I*, Th. I ♂ (frontal); *J*, Th. VIII ♀ (ventral); *K*, Th. VIII ♀ (lateral). Scale bar = 0.1 mm.

Mandible (Fig. 16*E*, *F*) with incisor process of three teeth. Tooth of ventral edge triangular. Spine row consisting of five spines. Palp of one segment with one apical seta, 9× as long as palp.

Maxillule (Fig. 16*G*) as in *A. wattsi.*

Maxilla (Fig. 16*H*) four-segmented, setal formula 2-4-6-7.

Thoracopods I–IV (Figs 16*I*, 18*A*, *B* 19*A*) increasing in length posteriorly. Thoracopods IV–VII (Figs 18*B*, *C*, 19*B*, *C*) similar in length. Each protopod on thoracopods I–VII bears one epipod; each basipod bears one seta. Exopod of thoracopods I–VII one-segmented, at least as long as first and second segments of endopod. Exopod of thoracopod I with two terminal setae. Exopod of thoracopods II–VI each with two terminal setae and with one subterminal seta on ventral margin. Outer terminal seta of exopod of thoracopods I–VII shorter than the half length of inner one. Endopod of thoracopods I–VII four-segmented, setal formulae:

Thoracopod I. 1+0/1+1/1+0/3(1)

Thoracopods II–VII. 0+0/0+1/0+1/1(0)

Thoracopod VIII (Fig. 17) semicircular in lateral view. Protopod massive, without frontal protrusion. Lobus denticulatus as a wide plate with six distal teeth. Epipod drawn out into conical projection and directed cranially. Basipod triangular, as large as epipod; exopod and endopod in form of tiny spine located distally on basipod.

First pleopod seta-like.

Uropod (Fig. 18*D*, *E*) bearing 11 or 12 spines of equal size on inner margin of sympod. Endopod length 25% sympod length, drawn out distally into spur, with tiny spine beneath spur and with two lateral setae near base of spur. Exopod as long as endopod, without ventromedial seta, with two terminal setae, of which inner seta is 1.5× as long as outer one.

Pleotelson (Fig. 18*D*, *E*) with one seta at base of furcal rami on both sides. Anal operculum slightly projected, divided in three parts distally.

Furcal rami 1.5× as long as wide, with three spines and with two dorsal setae.

Female (allotype)

Female differs from male only in body length and thoracopod VIII. Body length 2.11 mm, ~15× as long as wide. Thoracopod VIII (Fig. 16*J*, *K*) unpaired, tiny, semicircular, with short hairs at base and two distal spines.

Etymology

The species is named after the type locality (Gascoyne River, Western Australia, Australia).

Atopobathynella schminkei, sp. nov.

(Figs 20–23)

Material examined

Holotype. ♂, Australia, Western Australia, Pilbara, Fortescue River road bridge (21°17′52″S, 116°08′23″E), BES 4997, 5.viii.1997, Bou-Rouch pump, leg. W. F. Humphreys and S. M. Eberhard. Dissected on five slides (permanent preparation) (WAM C 34348).

Allotype. **Australia, Western Australia**: ♀, same data as for holotype, Dissected on five slides (permanent preparation) (WAM C 34349).

Paratypes. **Australia, Western Australia**: 1 ♀ dissected on five slides. 5 ♂, 3 ♀ each as whole specimens on a slide (WAM C 34350–34358). Two juveniles as whole specimens on a slide (WAM C 34359–34360).

Diagnosis

Body size 1.3 mm, 11× as long as wide; second antennular segment of male bearing an antennal organ with strong simple seta; labrum with 16 teeth; male thoracopod VIII with balloon-shaped protopod without frontal protrusion; right and left thoracopods VIII of female fused to form tiny, bifurcated structure; uropodal sympod comb-like, with 16 spines, exopod with ventral seta, and without subterminal setae; furcal rami 1.5× as long as wide, with three spines; anal operculum protruded.

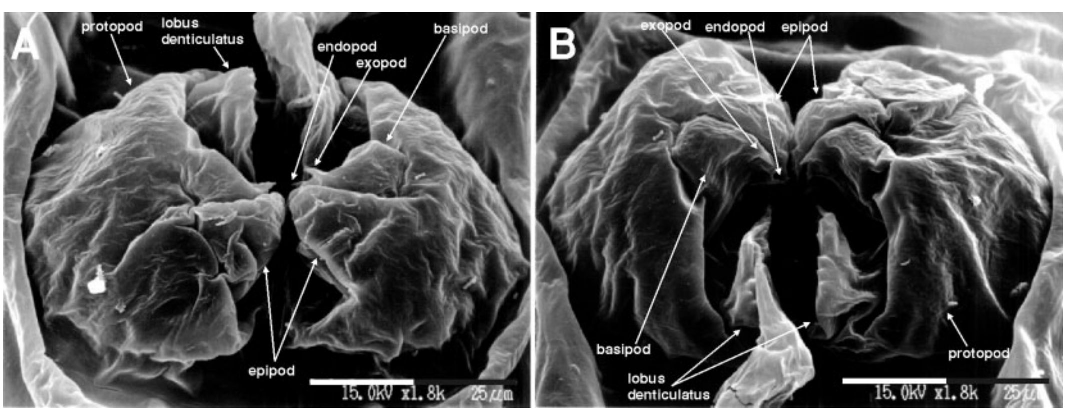

Fig. 17. *Atopobathynella gascoyneensis*, sp. nov., thoracopod VIII (♂, paratype): *A*, ventral view; *B*, posterior view.

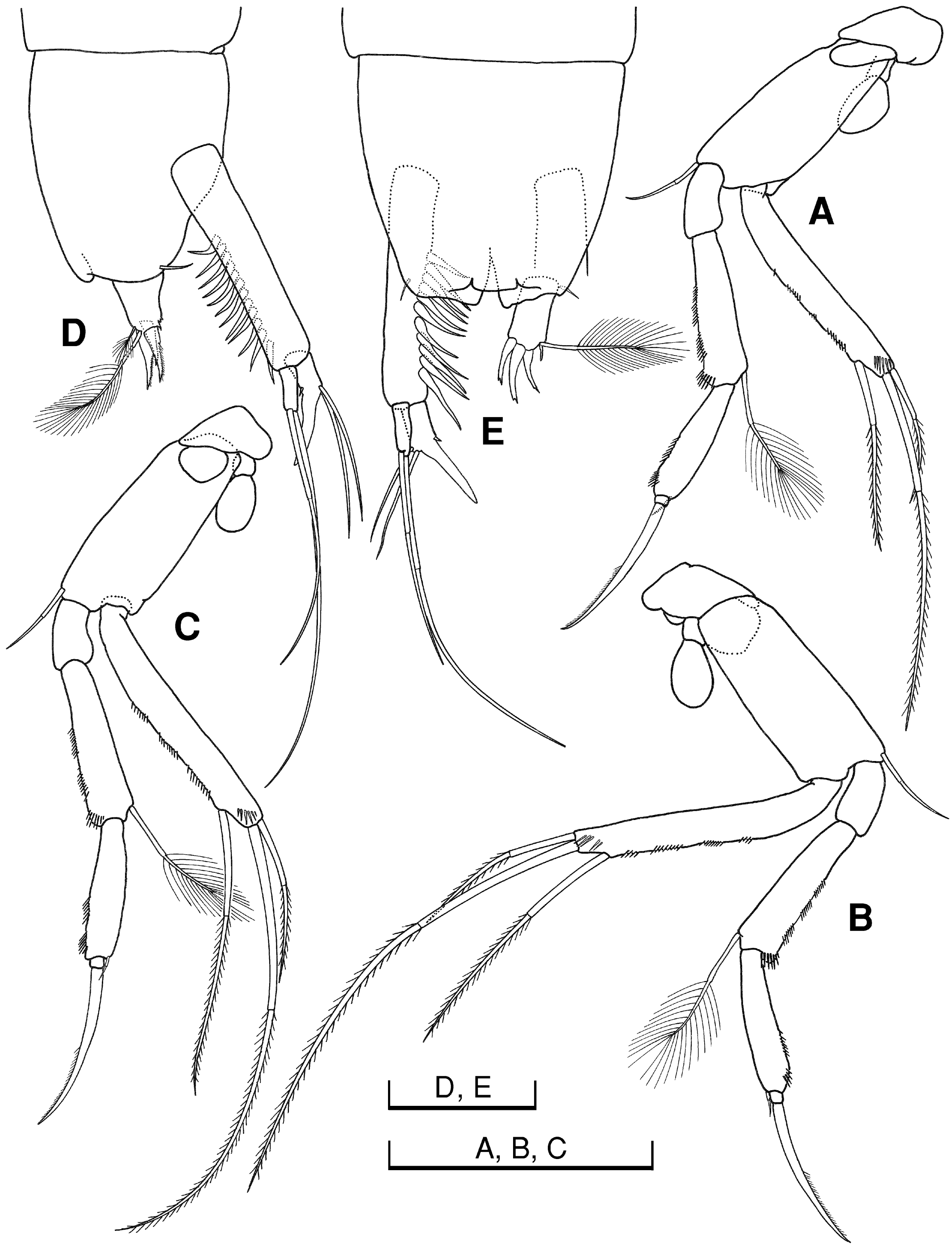

Fig. 18. *Atopobathynella gascoyneensis*, sp. nov. (♂, holotype): *A*, Th. II (frontal); *B*, Th. IV (frontal); *C*, Th. V (lateral); *D*, pleotelson, furcal rami and Urp. (lateral); *E*, pleotelson and furcal rami (dorsal). Scale bar = 0.1 mm.

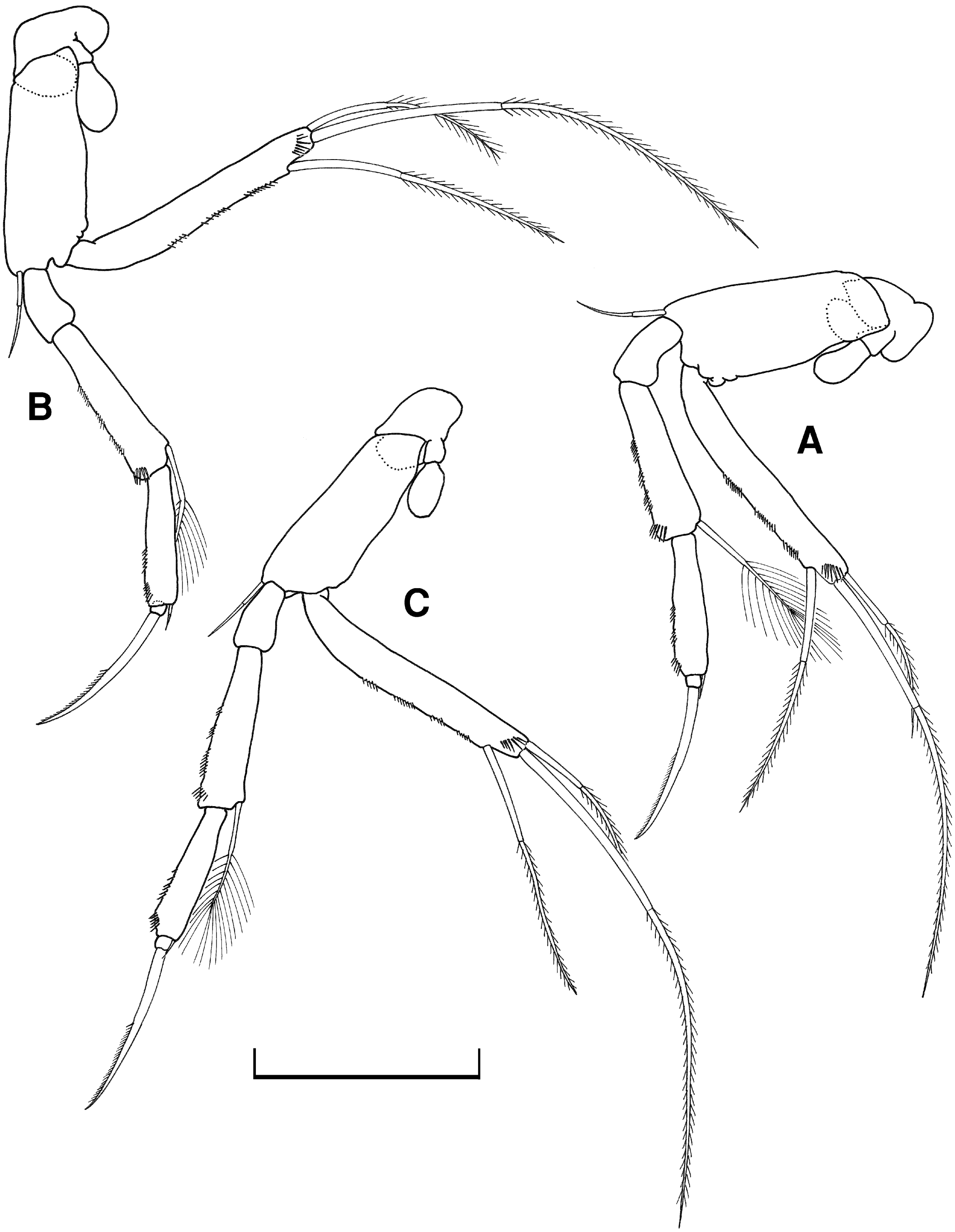

Fig. 19. *Atopobathynella gascoyneensis*, sp. nov. (♂, holotype): *A*, Th. III (frontal); *B*, Th. VI (frontal); *C*, Th. VII (frontal). Scale bar = 0.1 mm.

Description

Male (holotype)

Body length 1.34 mm, ~11× as long as wide (Fig. 20). Head as long as segments 1–2 combined.

Antennule (Fig. 21*A*) as in *A. wattsi* except as follows: first segment with one simple dorsal seta instead of two; antennal organ of second segment represented by one long and thick seta on inner distal margin and without protrusion; third segment without ventromedial seta.

Antenna (Fig. 21*C*) as in *A. wattsi*, almost as long as sixth antennular segment.

Labrum (Fig. 21*D*) with 16 teeth. Two tiny median teeth flanked by seven teeth on each side.

Mandible (Fig. 21*E*) with incisor process of three teeth. Tooth of ventral edge round. Spine row consisting of five spines. Palp of one segment, with one apical seta, 9× as long as palp.

Maxillule (Fig. 21*F*) two-segmented. Proximal segment with four setae on inner distal margin. Distal segment with two terminal claws, three claws on inner edge and three simple setae on outer distal margin.

Maxilla (Fig. 21*G*) four-segmented, setal formula 2-4-8-7.

Thoracopods I–IV (Figs 21*H–J*, 23*A*) increasing in length posteriorly. Thoracopods IV–VI (Fig. 23*A–C*) similar in length. Each protopod of thoracopods II–VII bears one epipod. Each basipod of thoracopods I–VII bears one seta. Exopod of thoracopods I–VII one-segmented, shorter than first and second segments of endopod. Exopod of thoracopods I and VII with two terminal setae, whereas that of thoracopods II–VI with one subterminal seta on ventral margin and two terminal setae. Outer terminal seta is shorter than half length of inner one. Endopod of thoracopods I–VII four-segmented, setal formulae:

Thoracopod I. 1+0/1+1/1+0/2(0)

Thoracopods II–III. 0+0/0+1/0+1/2(0)

Thoracopods IV–VII. 0+0/0+1/0+1/1(0)

Thoracopod VIII (Fig. 22*A*, *B*) semicircular in lateral view. Protopod massive, without frontal protrusion. Left and right protopods fused through basal bar. Epipod drawn out into conical projection and directed cranially. Lobus denticulatus conical with three distal denticles. Basipod round, somewhat larger than epipod; exopod and endopod in form of tiny spine.

First pleopod seta-like.

Uropod (Fig. 23*E*, *F*) with comb-shaped sympod bearing 16 spines of equal size on inner margin. Endopod length 15% sympod length, drawn out distally into spur, with two lateral setae near base of spur. Exopod half as long as endopod, with one ventromedial seta and two terminal setae, of which inner seta twice as long as outer one.

Pleotelson (Fig. 23*E*, *F*) with one seta at base of furcal rami on both sides. Anal operculum protruded with round tip.

Furcal rami 1.5× as long as wide, with three spines and two dorsal setae.

Female (allotype)

Female differs from male in second antennular segment and thoracopod VIII. Second antennular segment (Fig. 21*B*) with one group of four plumose setae and simple seta on inner distal margin. Thoracopod VIII (Fig. 21*K*) fused to form only one tiny bifurcated structure.

Etymology

The species is named after Prof. Dr H. K. Schminke (University Oldenburg, Germany), who established the genus.

Atopobathynella hinzeae, sp. nov.

(Figs 24–27)

Material examined

Holotype. ♂, Australia, Western Australia, Depot Springs Station, Bore 03 (27°58′01″S, 120°00′04″E), BES 8369, 26.vi.2000, leg. W. F. Humphreys and S. Hinze. Dissected on five slides (permanent preparation) (WAM C 34332).

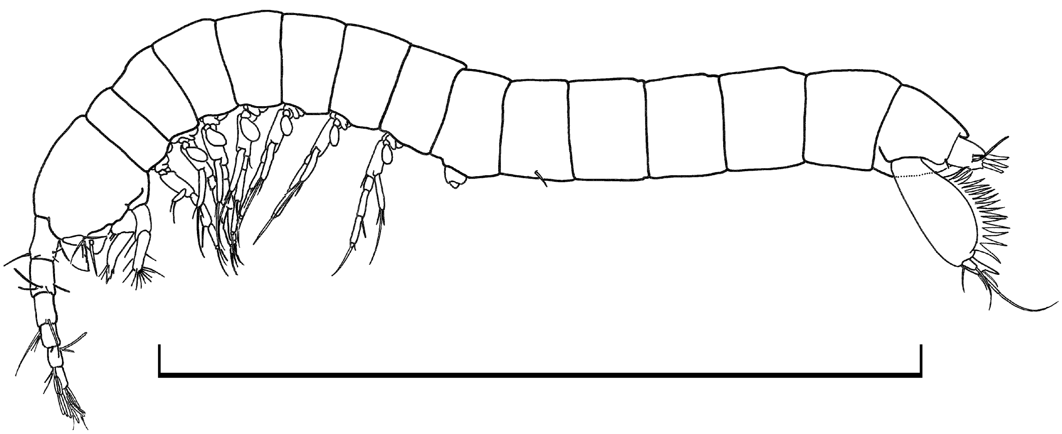

Fig. 20. General habitus of *Atopobathynella schminkei*, sp. nov. (♂, holotype), lateral. Scale bar = 1 mm.

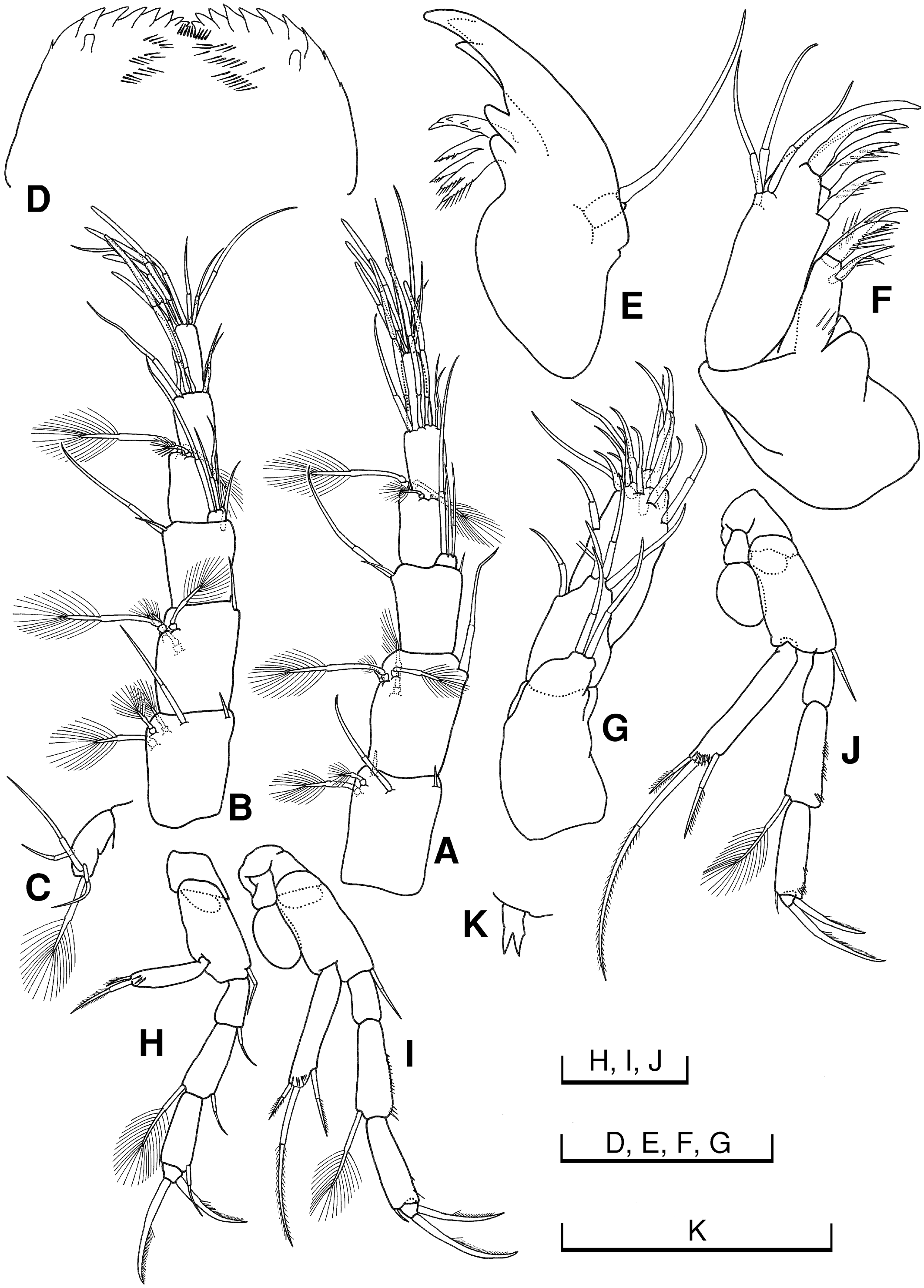

Fig. 21. *Atopobathynella schminkei*, sp. nov. (♂, holotype; ♀, allotype): *A*, A. I ♂ (dorsal); *B*, A. I ♀ (dorsal); *C*, A. II ♂ (dorsal); *D*, Labr. ♂ (ventral); *E*, Md. ♂ (ventral); *F*, Mx. I ♂ (dorsal); *G*, Mx. II ♂ (inner lateral); *H*, Th. I ♂ (frontal); *I*, Th. II ♂ (frontal); *J*, Th. III ♂ (ventral); *K*, Th. VIII ♀ (ventral). Scale bar = 0.05 mm.

Allotype. **Australia, Western Australia**: ♀, same data as for holotype, Dissected on four slides (permanent preparation) (WAM C 34333).

Paratypes. **Australia, Western Australia**: 5 ♂, 5 ♀, from type locality, each as whole specimens on a slide (WAM C 34334–34343). 2 ♀ (intact) and 1 ♀ (mutilated), from type locality, on a slide (WAM C 34344). 1 ♂, 2 ♀, from 27°55′48″S, 120°03′31″E, each as whole specimens on a slide (WAM C 34345–34347).

Diagnosis

Body size 1.6 mm, 15× as long as wide; second antennular segment of male bearing an antennal organ with two club-shaped setae; labrum with 25 teeth; male thoracopod VIII balloon-shaped protopod without frontal protrusion; right and left thoracopods VIII of female fused to form tiny, bifurcated structure; uropodal sympod with nine spines, exopod with ventral seta, and without subterminal setae, endopod with tiny spine beneath spur; furcal rami 1.2× as long as wide, with three spines; anal operculum flat.

Description

Male (holotype)

Body length 1.58 mm, ~15× as long as wide (Fig. 24). Head as long as segments 1–3 combined.

Antennule (Fig. 25*A*) as in *A. wattsi* except antennal organ (Fig. 25*B*) represented by two club-shaped setae of equal length on inner distal margin without protrusion.

Antenna (Fig. 25*D*) as in *A. wattsi*.

Labrum (Fig. 25*E*) with 25 teeth. Three median teeth flanked laterally by 11 teeth on each side.

Mandible (Fig. 25*F*) with incisor process of three teeth. Tooth of ventral edge round. Spine row consisting of five spines. Distal claw wide and hand-shaped. Palp of one segment, with one apical seta, 11× as long as palp.

Maxillule (Fig. 25*G*) as in *A. wattsi.*

Maxilla (Fig. 25*H*) four-segmented, setal formula 2-4-6-7.

Thoracopods I–IV (Fig. 26*A–D*) increasing in length posteriorly. Thoracopods IV–VII (Fig. 27*A–C*) similar in length. Each protopod of thoracopods II–VII bear one epipod. Each basipod of thoracopods I–VII with one seta. Exopod of thoracopods I–VII one-segmented, as long as first and second segments of endopod. Exopod of thoracopod I with two terminal setae, whereas that of thoracopods II–VI each with two terminal setae and with one subterminal seta on ventral margin. Outer terminal seta shorter than half length of inner one. Endopod of thoracopods I–VII four-segmented, setal formulae:

Thoracopod I. 1+0/1+1/1+0/2(0)

Thoracopods II–VII. 0+0/0+1/0+1/1(0)

Thoracopod VIII (Fig. 25*I*) semicircular in lateral view. Protopod massive, without frontal protrusion. Left and right protopods separated. Epipod drawn out into conical projection and directed cranially. Lobus denticulatus with two denticulate teeth. Basipod triangular; exopod and endopod in form of tiny spine.

First pleopod seta-like.

Uropod (Fig. 26*E*, *F*) bearing eight to nine spines of equal size on inner margin of sympod. Endopod length 25% sympod length, drawn out distally in spur, with tiny spine beneath spur and two lateral setae near base of spur. Exopod as long as endopod, with one ventromedial seta and two terminal setae, of which inner seta is 1.2× as long as outer one.

Pleotelson (Fig. 21*E*, *F*) with one seta at base of furcal rami on both sides. Anal operculum straight.

Furcal rami 1.5× as long as wide, with three spines and two dorsal setae.

Female (allotype)

Female differs from male in second antennular segment and in thoracopod VIII. Second antennular segment (Fig. 25*C*) with one group of four plumose setae and simple seta on inner distal margin. Thoracopod VIII (Fig. 25*J*, *K*) unpaired, tiny, semicircular and bearing two distal spines.

Etymology

The species is named after one of the collectors, S. Hinze (Adelaide, South Australia, Australia).

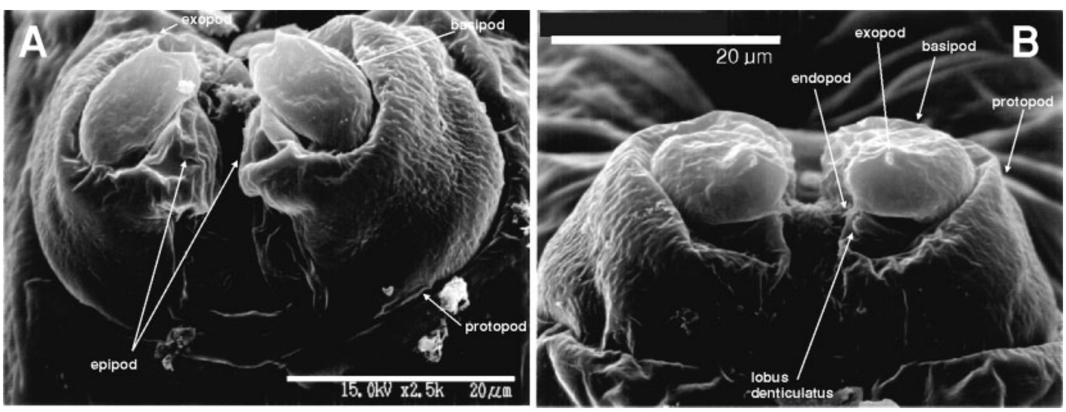

Fig. 22. *Atopobathynella schminke*, sp. nov. thoracopod VIII (♂, paratype): *A*, ventral view; *B*, posterior view.

Results of the phylogenetic analysis

The analysis of 28 unordered characters yielded two most parsimonious trees each of 71 steps, consistency index (*CI*) 0.5070, retention index (*RI*) 0.5270 and rescaled consistency index (*CI*) 0.2672. The strict consensus of these trees is shown in Fig. 28*a* with Bremer support values for each clade. Synapomorphic (closed circles) and homoplastic characters (open circles) are mapped on one of the two trees (Fig. 28*b*). This tree shows *A. readi* as the basal representative of *Atopobathynella*, displaying a sister relationship to all the remaining species. Table 2 summarises the clades within the genus and their supporting characters. Note that a phylogenetic analysis using a set of 28 ordered characters results in a single most parsimonious tree having a similar topology to that shown in Fig. 28*b*. However, this tree is 76 steps long with consistency index (*CI*) 0.4737, retention index (*RI*) 0.5294 and rescaled consistency index (*CI*) 0.2508.

Discussion

Bathynellaceans are adapted to the confined interstitial space of subterranean groundwater and so their 'Bauplan' tends to be simplified (Schminke 1973). This trend is manifest in the reduced number of ornaments on appendages, of segments of appendages, and even of the appendages themselves. Consequently, a phylogenetic analysis of this animal

Table 2. The clades within *Atopobathynella* and their supporting characters
Unique characters are shown in italics

Clade	Species	Characters and character states
A	*A. wattsi* *A. glenayleensis* *A. gascoyneensis* *A. schminkei* *A. hinzeae* *A. hospitalis* *A. compagana* *A. chelifera* *A. valdiviana*	*6–1: Seta(e) on inner margin of second antennular segment of male similar to those of female* *9–1: Number of setae on third endite of maxilla: 9* *16–2: Number of setae on inner margin of third endopodal segment of thoracopod I: 0* *18–1: Number of setae on fourth endopodal segment of thoracopod II–III: 1* *25–1: Ventromedial seta on uropodal exopod present*
B	*A. wattsi* *A. glenayleensis* *A. gascoyneensis* *A. schminkei* *A. hinzeae* *A. hospitalis*	*19–1: Protopod without frontal protrusion* 21–1: Number of spines on uropodal sympod 11–13
C	*A. wattsi* *A. glenayleensis*	5–1: Number of setae on inner margin of second antennular segment of male: 2 *15–0: Number of setae on inner margin of second endopodal segment of thoracopod I: 2* *20–0: Thoracopods of female VIII separated* *27–0: Number of spines of furcal rami: 8*
D	*A. gascoyneensis* *A. schminkei* *A. hinzeae* *A. hospitalis*	22–0: Additional spine beneath endopodal stiletto of uropodal endopod present
E	*A. gascoyneensis* *A. schminkei* *A. hinzeae*	*9–3: Number of setae on third endite of maxilla: 6* 12–2: Number of subterminal seta on exopod of thoracopod I: 0 28–1: Anal operculum convex
F	*A. schminkei* *A. hinzeae*	10–1: Epipod present in thoracopods I–VII *13–1: Subterminal seta on exopod of thoracopod VII absent* 17–1: number of setae on fourth endopodal segment of thoracopod I: 2 *21–0: number of spines on uropodal sympod: more than 16*
G	*A. compagana* *A. chelifera* *A. valdiviana*	*2–0: Ventromedial seta of second antennular segment present* 7–1: Number of teeth on free margin of labrum: less than 16 17–1: Number of setae on fourth endopodal segment of thoracopod I: 2 *23–1: Outer seta of two terminal setae on uropodal exopod longer than inner one* 24–0: Lateral subterminal setae of uropodal exopod present *27–1: Number of spines on furcal rami: 5*
H	*A. compagana* *A. chelifera*	*4–1: Number of aesthestascs on sixth antennular segment: 2* 8–1: Distal spine of spine row modified to wide hand-shaped structure 10–1: Epipod present in thoracopods II–VII 26–1: Setae on endopod shorter than endopodal spur

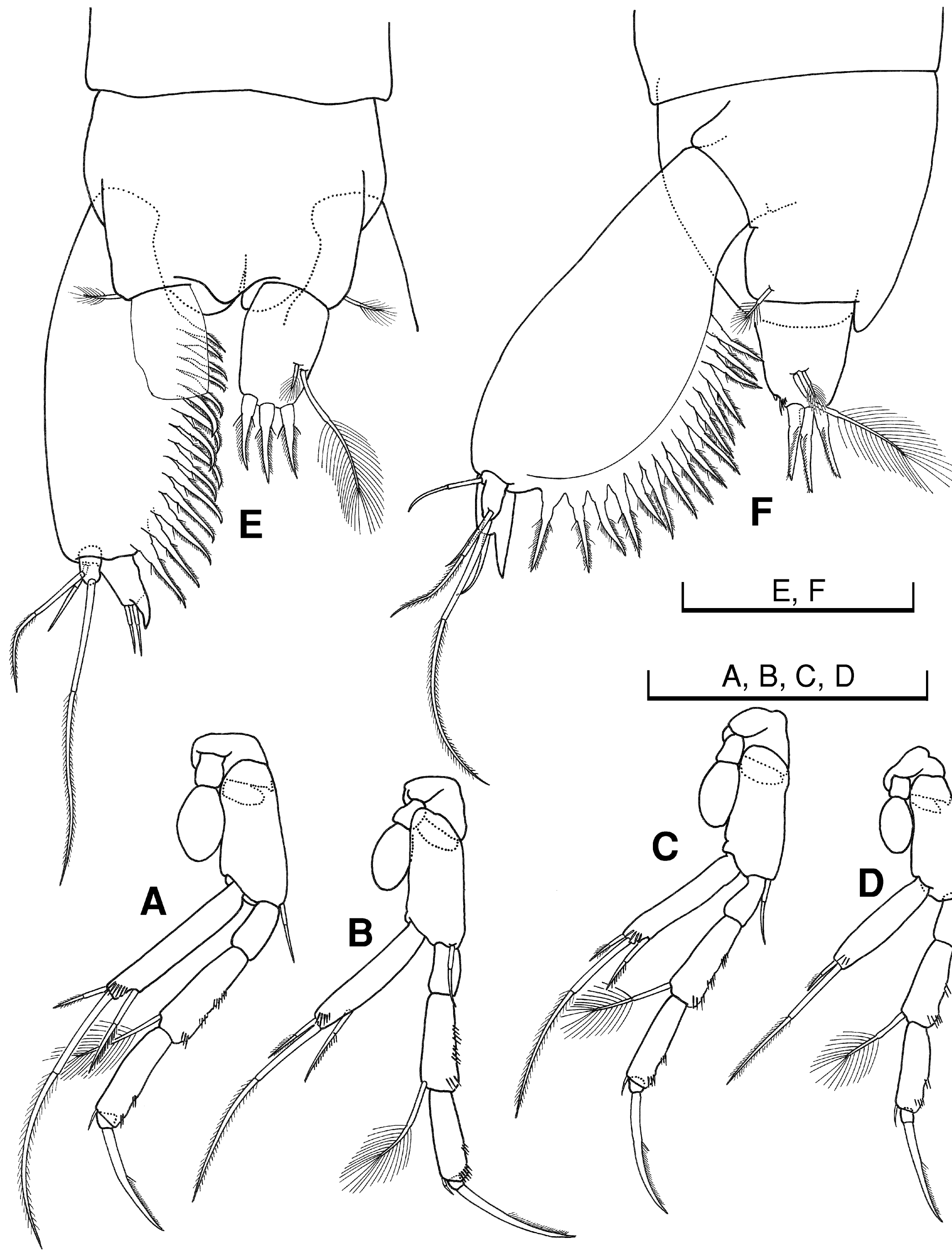

Fig. 23. *Atopobathynella schminkei*, sp. nov. (♂, holotype): *A*, Th. IV (frontal); *B*, Th. V (frontal); *C*, Th. VI (frontal); *D*, Th. VII (frontal); *E*, pleotelson, furcal rami and Urp. (dorsal); *F*, pleotelson, furcal rami and Urp. (lateral). Scale bar = 0.05 mm.

group is dependent on characters relating to the reduction of a structure. This holds true also for the genus *Atopobathynella*, so that the relationships among species are poorly resolved. In many characters, state reversal occurs several times (characters 2, 5–7, 9, 12, 14–22, 24 and 27). Only the relationships between the three species of clade G (*A. compagana*, *A. chelifera* and *A. valdiviana*) retain their topology in less parsimonious trees and thus seem to be well supported.

The monophyly of *Atopobathynella* was not tested in this analysis. However, it could be supported by at least two characters: the one-segmented antenna and the male thoracopod VIII with its specific features, particularly the small basipod and the reduced endo- and exopods. The first character is present in all known species of *Atopobathynella* and may be an autapomorphic character of the genus, as it is otherwise unknown within the Parabathynellidae. The second character also seems to be another peculiarity of *Atopobathynella*. However, the presence of this condition is not clearly demonstrated in *A. valdiviana*, *A. hospitalis*, *A. compagana* and *A. chelifera* (cf. Schminke 1973).

As in many genera of the Parabathynellidae, the position of *Atopobathynella* within the family is uncertain. Schminke (1973) considered *Atopobathynella* to be closely related to the genus *Chilibathynella* based on the one-segmented exopods of the thoracopods I–VII, the furcal rami ornamented with numerous spines, and by only one seta being associated with the formation of the antennal organ. The genus *Nunubathynella* could be included in this relationship based on the first of these characters, but not on the latter two characters. Numerous spines on the furcal rami is one of the plesiomorphic character states widely distributed in species considered primitive in the family. In addition, four species of *Atopobathynella* (*A. chelifera*, *A. wattsi*, *A. glenayleensis* and *A. hinzeae*) have an antennal organ bearing two setae. Schminke (1973) further considered that the phylogenetic lineage including *Atopobathynella* and *Chilibathynella* also contains *Notobathynella* and *Hexabathynella* Schminke, 1972, based on the tendency for the formation of a complex antennal organ. Testing this hypothesis and revealing the position of the *Atopobathynella* within the family Parabathynellidae must await a cladistic analysis at the generic level.

Atopobathynella hospitalis is reported from the Tasmanian high plateau, whereas *A. compagana*, *A. chelifera* and *A. valdiviana* came from the lowlands of New Zealand, Victoria (Australia), and Chile respectively (Schminke 1973). Vicariance owing to continental drift could be argued as being responsible for the apparent Gondwanan distribution of the four known species of *Atopobathynella*. In contrast, the six new species described here are widely distributed in western Australia from aquifers of the coastal plains (*A. schminkei* from the Fortescue River and *A. gascoyneensis* from the Gascoyne River) to the arid interior of the continent (*A. wattsi*, *A. glenayleensis* and *A. hinzeae* from calcrete aquifers formed in palaeodrainage channels of the Yilgarn Craton and *A. readi* from the Ngalia Basin, Northern Territory) (Fig. 29). Whereas *A. schminkei* and *A. gascoyneensis* inhabit coastal areas inundated by shallow seas several times since mid-Cretaceous (cf. Frakes *et al*. 1987), *A. readi*, *A. wattsi*, *A. glenayleensis* and *A. hinzeae* occur in the region which has not been submerged by the sea since the Proteozoic (Hocking *et al*. 1987), raising a question about the mechanisms of colonisation by the Parabathynellidae of the limnic interstitial.

Many bathynellaceans in the Australian arid zone occur in moderately saline waters, even up to marine salinities (Humphreys *et al*., unpublished data). However, the waters inhabited by the *Atopobathynella* species reported here occur in waters of only moderate salinity (60–4600 mg L^{-1} TDS). Mapping ecological association of habitat onto a cladogram (Fig. 28) suggests two alternative evolutionary scenarios that may account for the origin of *Atopobathynella*. First, a marine ancestor could have

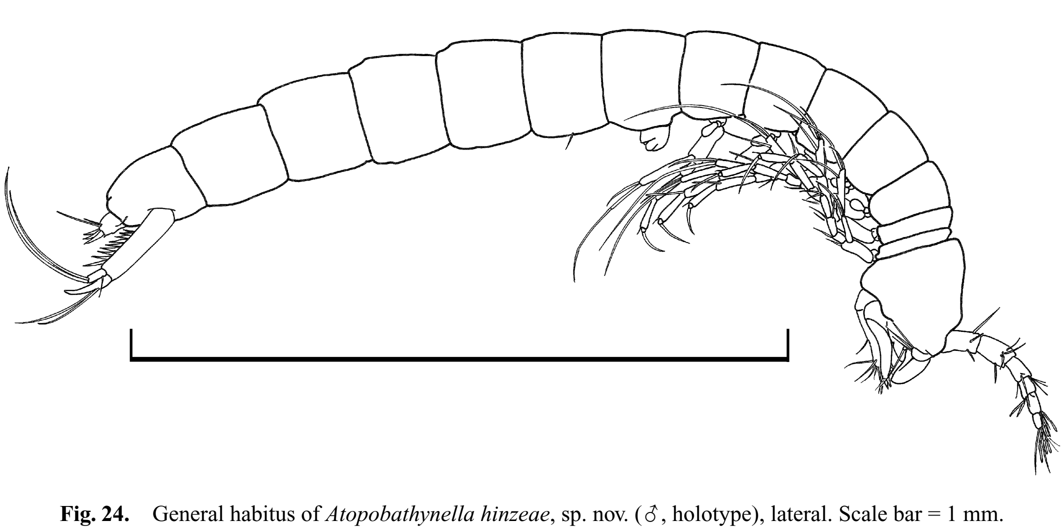

Fig. 24. General habitus of *Atopobathynella hinzeae*, sp. nov. (♂, holotype), lateral. Scale bar = 1 mm.

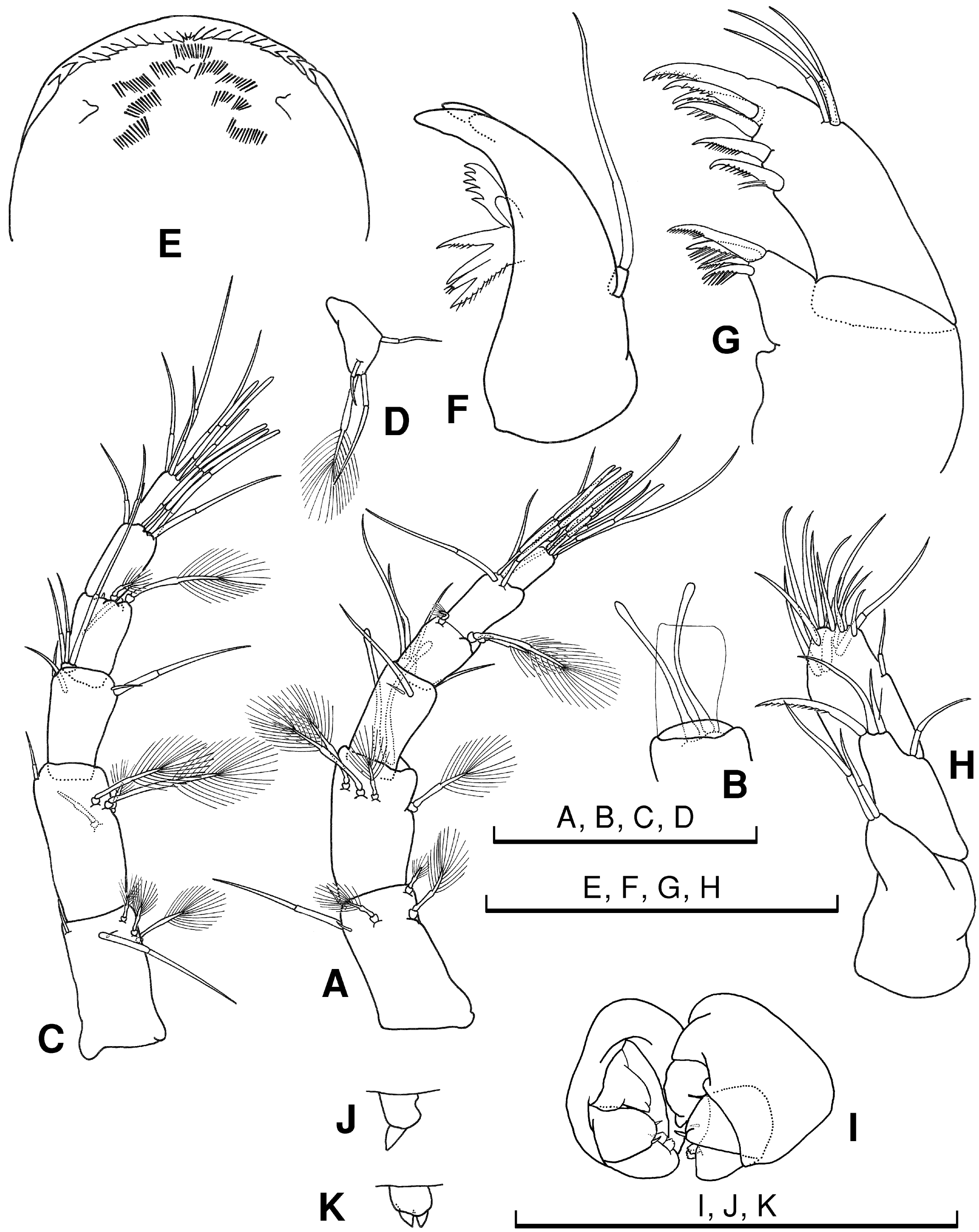

Fig. 25. *Atopobathynella hinzeae*, sp. nov. (♂, holotype; ♀, allotype): *A*, A. I ♂ (outer lateral); *B*, antennal organ ♂; *C*, A. I ♀ (dorsal); *D*, A. II ♂ (lateral); *E*, Labr. ♂ (ventral); *F*, Md. ♂ (ventral); *G*, Mx. I ♂ (dorsal); *H*, Mx. II ♂ (inner lateral); *I*, Th. VIII ♂ (ventral); *J*, Th. VIII ♀ (lateral); *K*, Th. VIII ♀ (ventral). Scale bar = 0.1 mm.

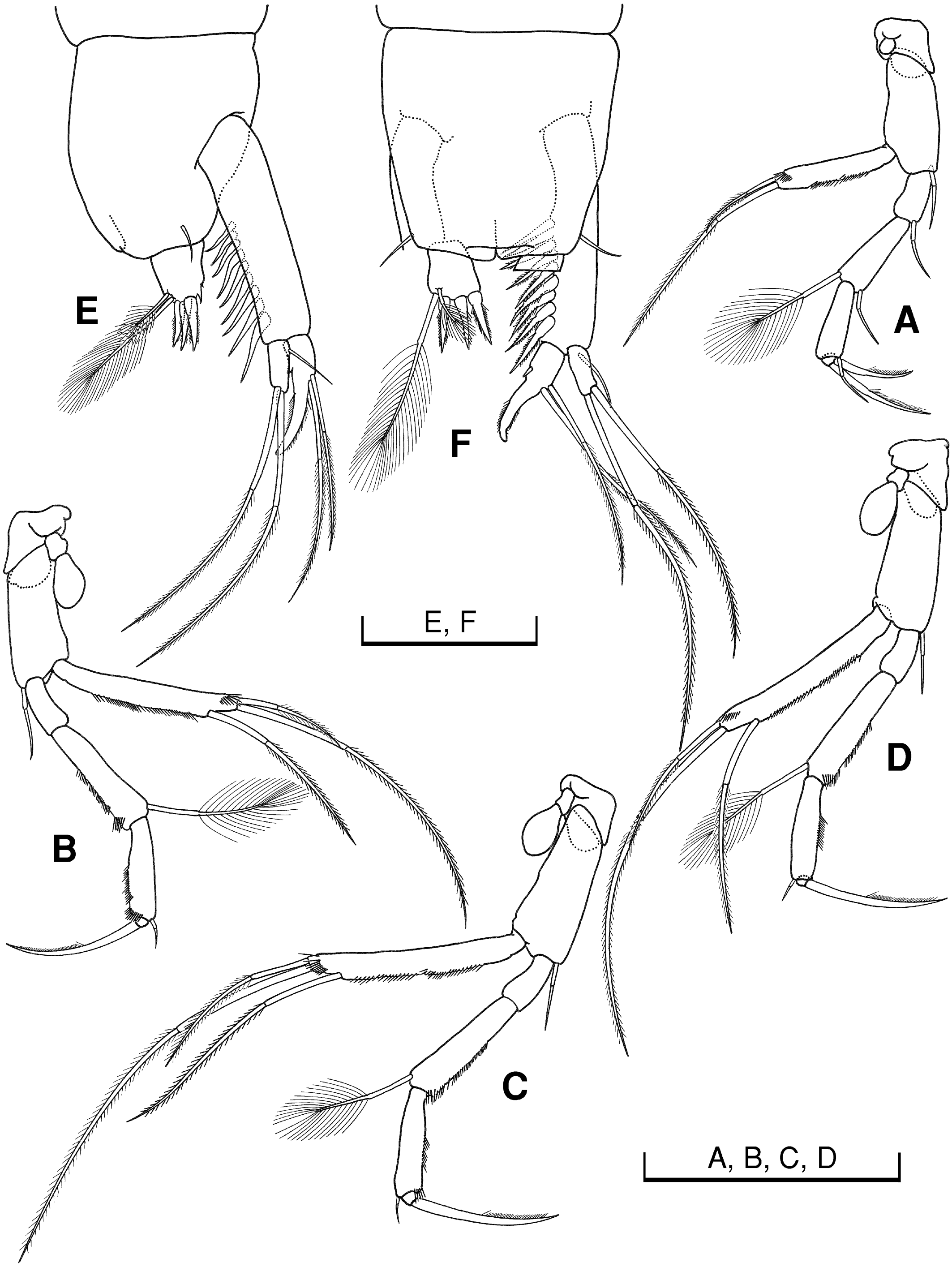

Fig. 26. *Atopobathynella hinzeae*, sp. nov. (♂, holotype): *A*, Th. I (frontal); *B*, Th. II (frontal); *C*, Th. III (lateral); *D*, Th. IV (lateral); *E*, pleotelson, furcal rami and Urp. (lateral); *F*, pleotelson and furcal rami (dorsal). Scale bar = 0.1 mm.

actively colonised the interstitial of marine littoral and then invaded the underground freshwater environment, following marine regression. Since dispersal is not regarded as being responsible for the distribution in this hypothesis, the invasion should have happened several times. Accordingly, those species occurring in near-coastal habitats could be regarded as relictual elements of a fauna that would have been widely distributed in the Pangaean marine littoral. Second, a marine ancestor could have colonised limnic surface water and from there colonised groundwater to disperse along hyporheic corridors to the inland aquifer. Consequently, the occurrence of species in near-coastal habitat would result from the secondary transition.

The first hypothesis is promulgated widely (Stock 1993; Humphreys 1999; Holsinger 2000; Coineau 2000), but it does not adequately explain the occurrence of species of *Atopobathynella* in far-inland continental areas long removed from marine influence. In addition, it neglects to consider the number of invasions (at least four times) necessary to account for the observed distributional and the phylogenetic relationships. Hence, the first hypothesis is not parsimonious, contrary to Camacho (2003), who argued this case for the *Hexabathynella*, a cosmopolitan genus of the Parabathynellidae having an ecological distribution similar to that of *Atopobathynella*. Therefore, we prefer the second hypothesis, which was earlier formulated by Schminke (1972, 1973): the species of the Parabathynellidae are derived from the ancestors that invaded groundwater via limnic surface water. In the case of *Atopobathynella* the transitions of species to near coastal habitat could have

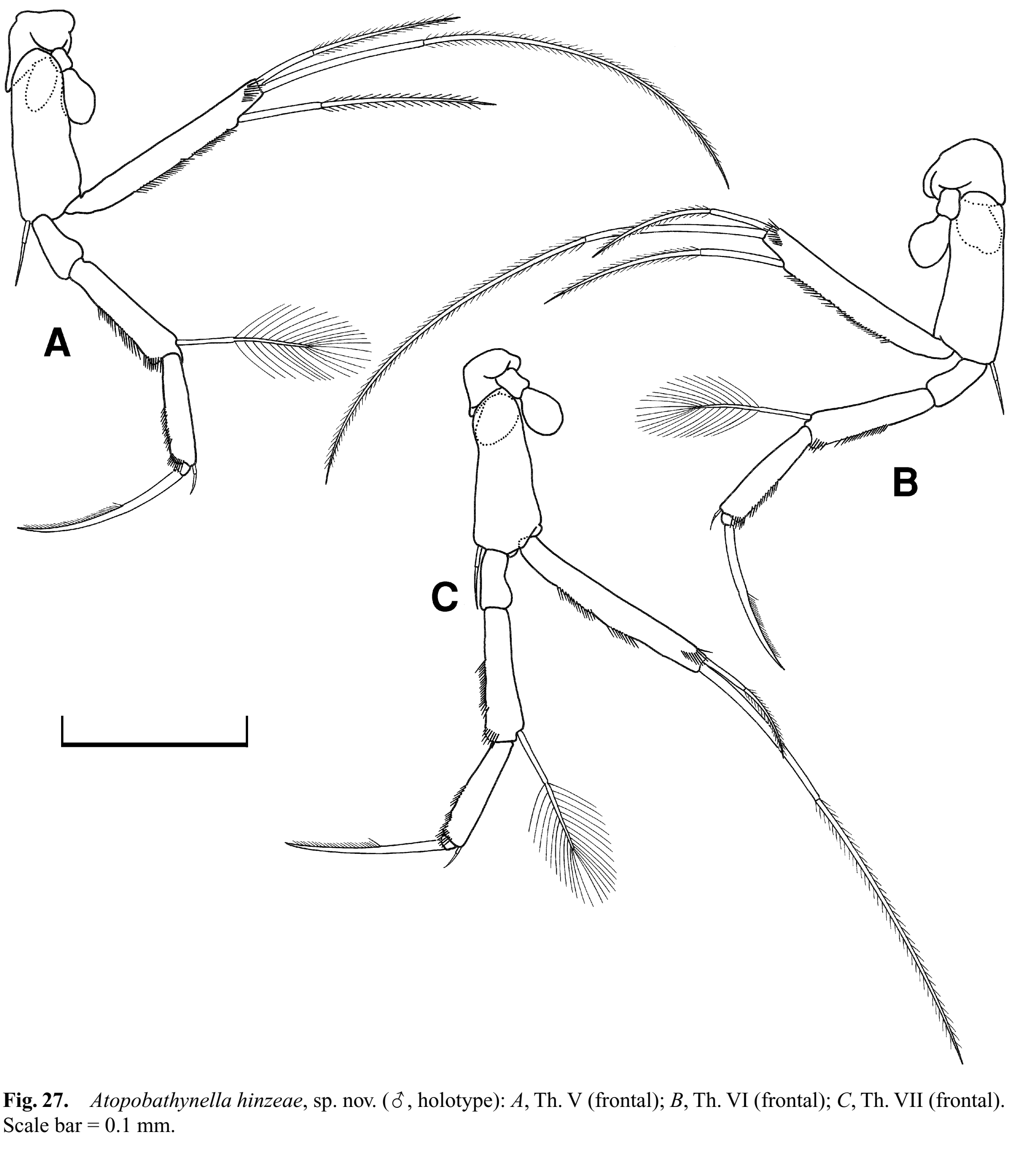

Fig. 27. *Atopobathynella hinzeae*, sp. nov. (♂, holotype): *A*, Th. V (frontal); *B*, Th. VI (frontal); *C*, Th. VII (frontal). Scale bar = 0.1 mm.

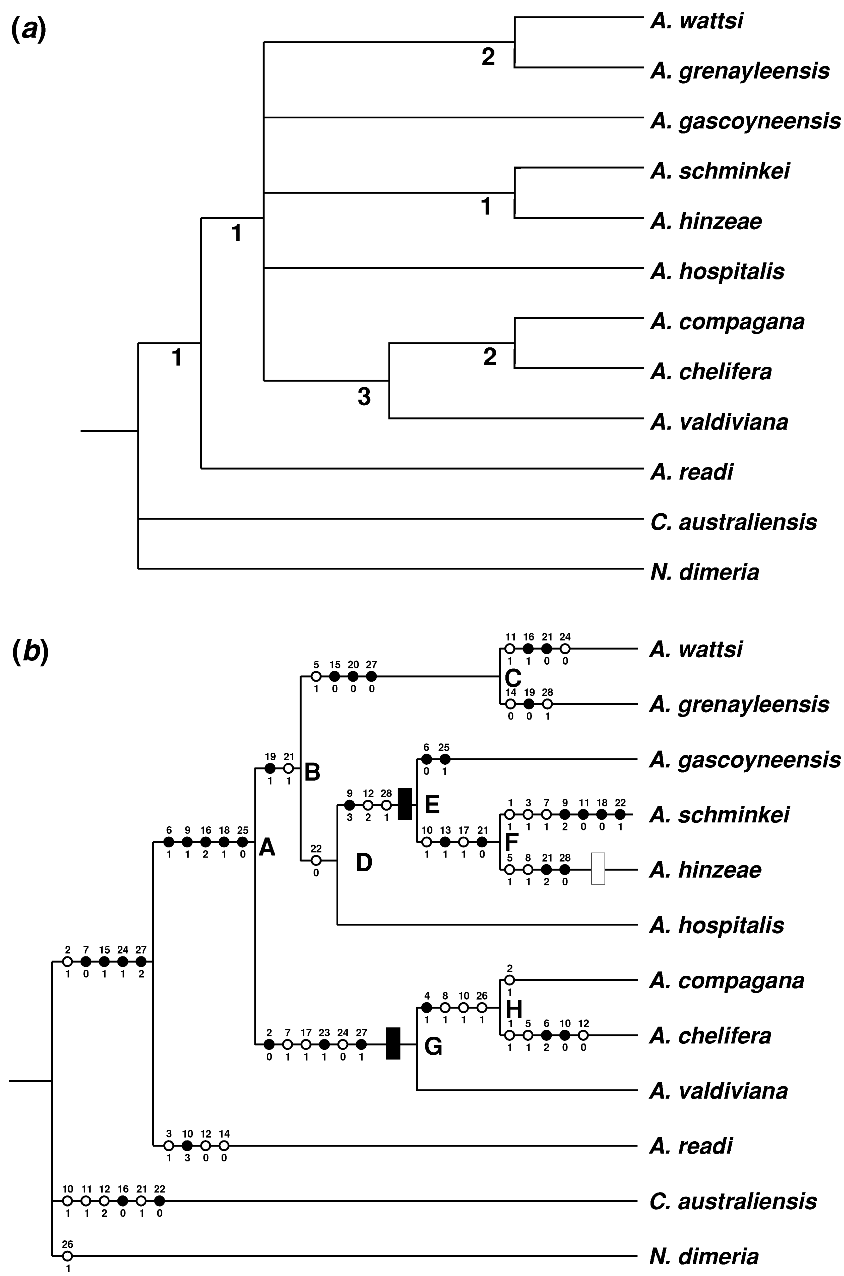

Fig. 28. Cladograms depicting hypothesised relationships of ten species of the genus *Atopobathynella. a*, Strict consensus tree of two most parsimonious cladograms with Bremer support values; *b*, one of two most parsimonious cladograms. Unique characters are indicated by closed circles, homoplasies by open circles. Black rectangular marks indicate the secondary transition to near-coastal habitat. White rectangular mark indicates secondary transition to far inland.

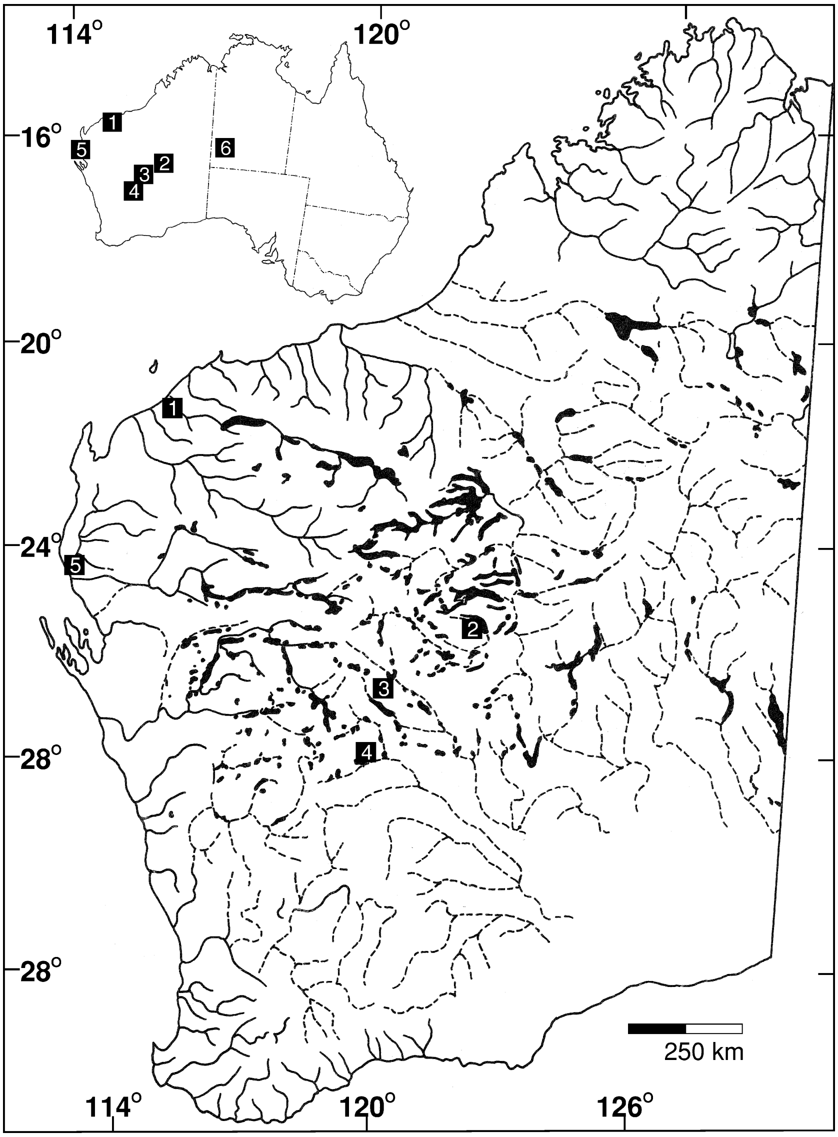

Fig. 29. The distribution of the six new species of the genus *Atopobathynella* in Australia. Modern and palaeo-drainage (respectively continuous and dashed line) and calcrete areas (black) are shown. (Modified after Humphreys 1999). *1*, *A. schminkei*, sp. nov.; *2*, *A. glenayleensis*, sp. nov.; *3*, *A. wattsi*, sp. nov.; *4*, *A. hinzeae*, sp. nov.; *5*, *A. gascoyneensis*, sp. nov.; 6, *A. readi*, sp. nov.

happened in the two lineages represented by the clades E and G. Given that clade B, which includes clade E, covers the full extent of the continent, from Tasmania in the south-east to the Pilbara in the north-west, and clade G (*A. compagana*, *A. chelifera* and *A. valdiviana*) clearly displays a Gondwanan distribution, the transitions would have occurred, despite the great age of the landscape and the longevity of the palaeodrainage systems of the Australian western plateau, in a landscape radically different from that now present, with denudation of up to *c.* 12 km since Permian and *c.* 6 km since Jurassic (Belton *et al.* 2004). Marine incursions would also have intruded up to the lower parts of palaeodrainage systems in the Eocene that could have allowed derived species access from coastal areas (e.g. *A. hinzeae* (a sister group of *A. schminkei*) on Yilgarn Craton). We recognise that this is a preliminary examination of the diversity of *Atopobathynella* in Australia. The most specious habitat for Australian bathynellaceans seems to be the groundwater calcrete aquifers common through the arid western plateau. Material from five calcrete aquifers occurring in four palaeodrainage systems (Carnegie, Carey, Raeside, Ngalia) is studied in this paper, but bathynellaceans are known in this region from at least 49 discrete calcrete bodies occurring in 13 palaeodrainage systems.

This material is likely to include numerous additional species of *Atopobathynella* whose descriptions may considerably aid resolution of the phylogeny and zoogeography of this apparently ancient lineage. In this context, detailed interpretation of the biogeographic patterns and phylogeny of the group is premature at this time. These issues may be more adequately resolved when data becomes available from a broader range of sites. However, given the apparent extreme age of the lineages, the historical biogeography may still be difficult to resolve.

The new species of *Atopobathynella* have a wide range of associated species, from anchialine fauna (e.g. *Stygiocaris*, Atyidae; *Halosbaena*, Thermosbaemacea), through to strictly freshwater taxa such as Hydracarina, Phreodrilidae, crangonytoid amphipods and Candoninae, as well as a range of taxa that are euryhaline (Dytiscidae, Coleopteran; Hyalidae, Amphipoda). They occur in neutral to alkaline waters of fresh to brackish quality and generally low in dissolved oxygen. The stygofauna of the western plateau appears to have a complex and varied origin. There have been multiple independent invasions of groundwater by Dytiscidae during the Tertiary (Cooper *et al*. 2002; Leys *et al*. 2003), whereas the largely marine harpacticoid copepod families Diosaccidae and Ameirinae occur widely, even in inland areas long emergent from the sea (Karanovic 2004). Among Amphipoda, the near coastal areas are dominated by Melitidae, whereas on the western plateau Hyalidae dominate the more saline waters of the south, giving way to Paramelitidae in the central and northern regions (Bradbury *et al*., personal communication).

Acknowledgments

Fieldwork was facilitated and enlivened by the participation of Steve Cooper, Stefan Eberhard, Susan Hinze, Bob Read and Chris Watts. Material for this study was collected under funding from the Australian Biological Resources Study (Humphreys and Watts), the Butler Trust, Western Australian Museum, and the Waterhouse Club, South Australian Museum. Collection in the Northern Territory was facilitated by Northern Territory Power and Water especially through R. Read. One of us (Cho) is very grateful to the Sustainable Water Resources Research Center of the 21st Century Frontier for providing funding (Project 3–4–2), and to the Korea Institute of Geoscience and Mineral Resources for funding the project 'Prediction of contaminant transport and ecological application of microbial species in subsurface environments for remediation of groundwater systems' (Project Code 03-8103).

References

Belton, D. X., Brown, R. W., Kohn, B. P., Fink, D., and Farley, K. A. (2004). Quantitative resolution of the debate over antiquity of the central Australian landscape: implications for the tectonic and geomorphic stability of cratonic interiors. *Earth and Planetary Science Letters* **219**, 21–34. doi:10.1016/S0012-821X(03)00705-2

Bradbury, J. H., and Williams, W. D. (1997). Amphipod (Crustacea) diversity in underground waters in Australia: an Aladdin's Cave. *Memoirs of the Museum of Victoria* **56**, 513–519.

Bruce, N. L., and Humphreys, W. F. (1993). *Haptolana pholeta*, sp. nov., the first subterranean flabelliferan isopod crustacean (Cirolanidae) from Australia. *Invertebrate Taxonomy* **7**, 875–884. doi:10.1071/IT9930875

Camacho, A. I. (2003). Historical biogeography of *Hexabathynella*, a cosmopolitan genus of groundwater Syncarida (Crustacea, Bathynellacea, Parabathynellidae). *Biological Journal of the Linnean Society* **78**, 457–466. doi:10.1046/j.0024-4066.2002.00149.x

Coineau, N. (2000). Adaptation to groundwater life. In 'Ecosystems of the world. Vol. 30. Subterranean ecosystems'. (Eds S. Wilkens, D. C. Culver and W. F. Humphreys.) pp. 189–210. (Elsevier: Amsterdam, The Netherlands.)

Cooper, S. J. B., Hinze, S., Leys, R., Watts, C. H. S., and Humphreys, W. F. (2002). Islands under the desert: molecular systematics and evolutionary origins of stygobitic water beetles (Coleoptera: Dytiscidae) from central Western Australia. *Invertebrate Systematics* **16**, 589–598. doi:10.1071/IT01039

Frakes, L. A., McGowran, B., and Bowler, J. M. (1987). Evolution of Australian Environments. In 'Fauna of Australia. Vol. 1A. General Articles'. (Eds G. R. Dyne and D. W. Walton) pp. 1–16. (Australian Government Publishing Service: Canberra, Australia.)

Hocking, R. M., Moors, H. T., and van de Graaff, W. J. E. (1987). Geology of the Carnarvon Basin, Western Australia. *Western Australia Geological Survey Bulletin* **133**, 1–289.

Holsinger, J. (2000). Ecological derivation, colonization, and speciation. In 'Ecosystems of the world. Vol. 30. Subterranean ecosystems'. (Eds S. Wilkens, D. C. Culver and W. F. Humphreys.) pp. 399–416. (Elsevier: Amsterdam, The Netherlands.)

Humphreys, W. F. (1993). Stygofauna in semi-arid tropical western Australia: A tethyan connection? *Memoires de Biospeologie* **20**, 111–116.

Humphreys, W. F. (1999). Relict stygofauna living in sea salt, karst and calcrete habitats in arid northwestern Australia contain many ancient lineages. In 'The Other 99%. The Conservation and Biodiversity of Invertebrates'. (Eds W. Ponder and D. Lunney.) pp 219–227. (Transactions of the Royal Society of New South Wales: Mosman, Australia.)

Karanovic, T. (2004). Subterranean copepods (Crustacea: Copepoda) from arid Western Australia. *Crustaceana Monograph* **3**, 1–366.

Leys, R., Watts, C. H. S., Cooper, S. J. B., and Humphreys, W. F. (2003). Evolution of subterranean diving beetles (Coleoptera: Dytiscidae: Hydroporini, Bidessini) in the arid zone of Australia. *Evolution* **57**, 2819–2834.

Noodt, W. (1964). Natürliches System und Biogeographie der Syncarida (Crustacea, Malacostraca). *Gewässer und Abwässer* **37/38**, 151–167.

Poore, G. C. B., and Humphreys, W. F. (1992). First record of Thermosbaenacea (Crustacea) from the Southern Hemisphere: a new species from a cave in tropical Western Australia. *Invertebrate Taxonomy* **6**, 719–725. doi:10.1071/IT9920719

Schminke, H. K. (1972). *Hexabathynella halophila* gen. n., sp. n. und die Frage nach der marinen Abkunft der Bathynellacea (Crustacea: Malacostraca). *Marine Biology* **15**, 282–287. doi:10.1007/BF00383559

Schminke, H. K. (1973). Evolution, System und Verbreitungsgeschichte der Familie Parabathynellidae (Bathynellacea, Malacostraca). *Mikrofauna Meeresboden* **24**, 1–192.

Schminke, H. K. (1981). Perspectives in the study of zoogeography of interstitial Crustacea. Bathynellacea (Syncarida) and Parastenocarididae (Copepoda). *International Journal of Speleology* **11**, 83–89.

Stock, J. H. (1993). Some remarkable distribution patterns in stygobiont amphipoda. *Journal of Natural History* **23**, 807–819.

Swofford, D. (2002). PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4.0 (Sinauer Associates: Sunderland, MA, USA.)

Wilson, G. D. F. (2001). Australian groundwater-dependent isopod crustaceans. In 'Subterranean Biology in Australia 2000'. (Eds W. F. Humphreys and M. S. Harvey.) *Records of the Western Australian Museum*, Supplement No. 64, 239–240.

Wilson, G. D. F. (2003). A new genus of Tainisopidae fam. nov. (Crustacea: Isopoda) from the Pilbara, Western Australia. *Zootaxa* **245**, 1–20.

Wilson, G. D. F., and Johnson, R. T. (1999). Ancient endemism among freshwater isopods (Crustacea, Phreatoicidea). In 'The Other 99%. The Conservation and Biodiversity of Invertebrates'. (Eds W. Ponder and D. Lunney.) pp 264–268. (Transactions of the Royal Society of New South Wales: Mosman, Australia.)

Wilson, G. D. F., and Keable, S. J. (1999). A new genus of phreatoicidean isopod (Crustacea) from the north Kimberley Region, Western Australia. *Zoological Journal of the Linnean Society* **126**, 51–79. doi:10.1006/zjls.1998.0180

Yager, J., and Humphreys, W. F. (1996). *Lasionectes exleyi*, sp. nov., the first remipede crustacean recorded from Australia and the Indian Ocean, with a key to the world species. *Invertebrate Taxonomy* **10**, 171–187. doi:10.1071/IT9960171

Manuscript received 11 May 2005, revised and accepted 23 December 2005.

Appendix 1. Character coding and scoring

Antennule

(*1*) *Number of dorsal simple setae on first antennular segment:* (0) 2, (1) 1.
(*2*) *Ventromedial seta of second antennular segment:* (0) present, (1) absent.
(*3*) *Ventral seta of third antennular segment:* (0) present, (1) absent.
(*4*) *Number of aesthestascs on sixth antennular segment:* (0) 3, (1) 2.
(*5*) *Number of setae on inner margin of second antennular segment of male:* (0) 1, (1) 2.
(*6*) *Seta(e) on inner margin of second antennular segment of male:* (1) similar to those of female, (2) different from or significantly greater than that of female.

Labrum

(*7*) *Number of teeth on free margin of labrum:* (0) more than 16 teeth, (1) less than 16 teeth.
The two states of character seven result from a simple gap-coding. In three species (*A. compagana*, *A. chelifera* and *A. schminkei)* the labrum is equipped with 16 teeth, whereas in the remaining species the number of teeth varies between 20–26. The gap between 16 and 20 exceeds the standard deviation (3.98) about the mean value for the number of teeth of each species.

Mandible

(*8*) *Distal spine of spine row:* (0) simply dentate, (1) modified to wide, hand-shaped structure.

Maxilla

(*9*) *Number of setae of third endite of maxilla:* (0) 10 and more, (1) 9, (2) 8, (3) 6.

Epipods of thoracopods I–VII

(*10*) *Epipod present on thoracopods:* (0) I–VII, (1) II–VII, (2) III–VII, (3) II–VI.

Exopods of thoracopods I–VII

(*11*) *Length of exopod of thoracopods II–VII (a), and that of first and second segments of endopod (b): (*0) a > b (1) a < b.
(*12*) *Number of subterminal setae of exopod of thoracopod I:* (0) 2, (1) 1, (2) 0.
(*13*) *Subterminal seta of exopod of thoracopod VII:* (0) present, (1) absent.
(*14*) *Outer one of two terminal setae:* (0) longer than half length of inner one, (1) shorter than half length of inner one.

Endopods of thoracopods I–VII

(*15*) *Number of setae on inner margin of second endopodal segment of thoracopod I:* (0) 2, (1) 1.
(*16*) *Number of setae on inner margin of third endopodal segment of thoracopod I:* (0) 2, (1) 1, (2) 0.
(*17*) *Number of setae on fourth endopodal segment of thoracopod I:* (0) 3, (1) 2.
(*18*) *Number of setae on fourth endopodal segment of thoracopod II–III:* (0) 2, (1) 1.

Male thoracopods VIII

(*19*) *Protopod:* (0) with frontal protrusion, (1) without frontal protrusion.

Female thoracopods VIII

(*20*) *Thoracopods of female VIII:* (0) separated, (1) fused to single structure.

Uropod

(*21*) *Number of spines on uropodal sympod:* (0) more than 16, (1) with 11–13, (2) with 4–9.
Among the species, the number of spines varies between 5 and 17 according to species. The gap between each character state does not exceed the standard deviation (3.97) about the mean value for the number of teeth of each species.
(*22*) *Additional spine beneath endopodal stiletto of uropodal endopod:* (0) present, (1) absent.
(*23*) *Outer one of two terminal setae on uropodal exopod:* (0) shorter than inner one, (1) longer than inner one.
(*24*) *Lateral subterminal setae on uropodal exopod:* (0) present, (1) absent.
(*25*) *Ventromedial seta of uropodal exopod:* (0) present, (1) absent.
(*26*) *Setae on endopod:* (0) longer than endopodal spur, (1) shorter than endopodal spur.

Furcal rami

(*27*) *Number of spines on furcal rami:* (0) 8 and more, (1) 5, (2) 3.

Anal operculum

(*28*) *Anal operculum:* (0) flat to concave, (1) convex.