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Research article

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On the *Bennelongia nimala* and *B. triangulata* lineages (Crustacea, Ostracoda) in Western Australia, with the description of six new species

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Abstract. The ostracod genus *Bennelongia* De Deckker & McKenzie, 1981 occurs in Australia and New Zealand. We redescribe *B. nimala* from the Northern Territory and describe six new species from Western Australia belonging to the *B. nimala* (five species) and *B. triangulata* sp. nov. (one species) lineages: *B. tirigie* sp. nov., *B. koendersae* sp. nov., *B. pinderi* sp. nov., *B. muggon* sp. nov., *B. shieli* sp. nov. and *B. triangulata* sp. nov. For six of these seven species, we could construct molecular phylogenies and parsimonious networks based on COI sequences. We tested for specific status and for potential cryptic diversity of clades with Birky's 4 theta rule. The analyses support the existence of these six species and the absence of cryptic species in these lineages. *Bennelongia triangulata* sp. nov. is a common species in the turbid claypans of the Murchison/ Gascoyne region. *Bennelongia nimala* itself is thus far known only from the Northern Territory. *Bennelongia tirigie* sp. nov., *B. pinderi* sp. nov. and *B. muggon* sp. nov. occur in the Murchison/ Gascoyne region, whereas *B. koendersae* sp. nov. and *B. shieli* sp. nov. are described from the Pilbara. With the six new species described here, the genus *Bennelongia* now comprises 31 nominal species.

Keywords. Taxonomy, evolution, biodiversity, Western Australia, Pilbara

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Introduction

The genus *Bennelongia* was originally described by De Deckker & McKenzie (1981) from Queensland, with *Bennelongia harpago* as type species. Subsequently, De Deckker (1981) redescribed and transferred *Chlamydotheca australis* Brady, 1886 to *Bennelongia* and added a further three species to the genus:

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Bennelongia barangaroo De Deckker, 1981, *Bennelongia nimala* De Deckker, 1981 and *Bennelongia pinpi* De Deckker, 1981. De Deckker (1982) then described *Bennelongia tunta* De Deckker, 1982 from Queensland. For about 30 years after those papers, nothing was added to the taxonomy of the genus *Bennelongia,* but Halse (2002) highlighted its high frequency of occurrence in Western Australia (WA). Then Martens *et al.* (2012, 2013) and Shearn *et al.* (2012) together added 19 new species, mostly from WA. De Deckker & Martens (2013) illustrated how different the valve morphologies of adult and juvenile *Bennelongia* species can be and how juvenile morphologies vary between the lineages within the genus.

Here, we redescribe *Bennelongia nimala* from the Northern Territory (NT) and describe six new species in the *B. nimala* and *Bennelongia triangulata* lineages within the genus, thus bringing the total number of species in the genus to 31 (see Discussion). This is the fifth contribution in the recent revision of the genus *Bennelongia*.

Material and methods

Collections

Ostracods were collected from pans and lakes with a hand net of mesh size of 250 µm during several field trips (see below) (Fig. 1). Material for morphological analyses originated from both these 'new' collections and from earlier samples from all over WA, mostly collected by the research group of one of us (SH) and preserved in a collection housed at the Department of Parks and Wildlife, Perth. The molecular analyses were successful only with newly collected material, using either living specimens or specimens sorted directly in the field and preserved in 100% ethanol. Consequently, molecular analyses were limited to six of the seven species (re-)described here. Locations of populations used for the present paper are indicated on the map in Fig. 1. Type material of the new species is deposited in the Western Australian Museum, Perth, Australia (WAMC numbers) and in the Ostracod Collection of the Royal Belgian Institute of Natural Sciences, Brussels, Belgium (OC numbers) (see Table 1).

Morphological analyses

Ostracods were dissected with valves stored dry in micropalaeontological slides and soft parts in glycerine in sealed slides, or with soft parts used for molecular analyses. Drawings of soft parts were made with a *camera lucida* on a compound microscope (Leica, DM 2500 at Bennelongia Environmental Consultants, Perth). Valves were illustrated and measured using scanning electron microscopy (Philips XL30 SEM at the Royal Belgian Institute of Natural Sciences, Brussels).

Molecular analysis

We used the Qiagen Blood and Tissue extraction kit following the manufacturer's protocol to extract DNA from 54 ostracods representing six species of the *Bennelongia nimala* and *B. triangulata* lineages. The universal PCR primers of Folmer *et al.* (1994) for amplifying part of the mitochondrial COI region were applied with the following conditions: 25 µl volumes of the HotStar Master Mix (Qiagen; 1.5 mM $MgCl_2$, 200 µM dNTP, Tris·Cl, KCl, $(NH_4)_2SO_4$, 1.25 U Taq) and 0.1 µM of each primer were applied. In a T personal Thermoblock (Biometra), we conducted PCRs with 15 min at 95°C, 40 cycles with 1 min at 95°C, 1 min at 44° C, 1 min at 72° C, followed by a final extension step for 10 min at 72° C. Success of PCR amplifications was verified by agarose gel electrophoresis and staining of gels with Gelred™. We cleaned PCR products with the GFX™ PCR DNA and gel band purification kit (GE Healthcare) and sequenced them in both directions with the universal primers and the Big Dye kit (ABI) on an ABI 3130X following the manufacturer's protocol.

No fresh (living) material of *B. shieli* sp. nov. was obtained and this species is not represented in the molecular phylogenetic tree and networks.

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Analyses of sequence data

We used BioEdit (Hall 2007) to visualize sequence chromatograms. Sequence editing included alignments of the forward and reverse sequence of each individual with ClustalX (Larkin *et al.* 2007), followed by manual checking and correcting of ambiguities and trimming the final alignment to equal length. We confirmed identity of the obtained sequences by BLAST searches (Altschul *et al.* 1990) in Genbank. The optimal model of molecular COI evolution was assessed with 88 or 24 models and the AICc criterion in jModeltest 2.1.1 (Darriba *et al.* 2012). We reconstructed phylogenies with two different methods, Bayesian Inference (BI) in Mr Bayes 3.2 (Ronquist *et al.* 2011; with 5 million generations, sampling every 100th generation, a burn-in of 25% and the parameters identified by jModeltest for 24 different models) and the Maximum-Likelihood method in PhyML (Guindon & Gascuel 2003; with 1000

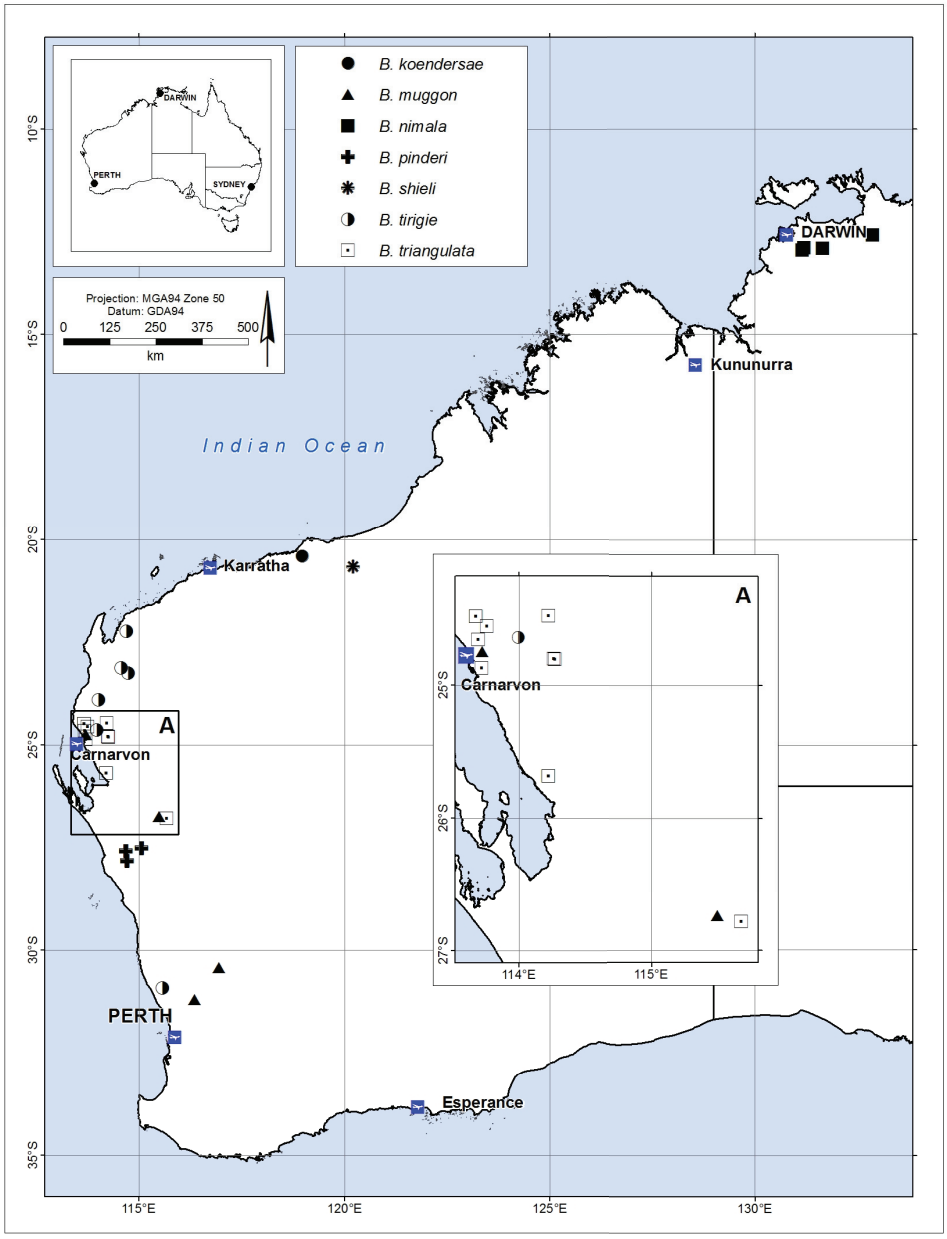

Fig. 1. Map of Western Australia with localities of *Bennelongia* species described in the present paper.

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Table 1. Individual measurements of specimens used for the present descriptions. All measurements were done using SEM (see Material and methods). If a molecular sequence was available for the same specimen, the GenBank registration number is also given. However, some specimens were used as whole animals for DNA sequencing, and thus no measurements are available. The present table therefore does not list all 54 specimens for which sequences are available. Specimens in bold are holotypes. Abbreviations: see Material and methods.

Museum nr	KMWA/OS	Genbank	*Bennelongia* species	Locality	♂/♀	RV		LV		CpRL		CPD/V	
						L	H	L	H	L	H	L	W
WAMC55564	**KMWA.1361**		***triangulata***	**SIKE07**	♂	**1850**	**1158**	**1923**	**1188**				
WAMC55565	KMWA.885		*triangulata*	SIKE07	♀	2192	1308	2286	1350				
WAMC55567	KMWA.886		*triangulata*	SIKE07	♂	1892	1161	1950	1158				
OC3368	KMWA.1364		*triangulata*	SIKE07	♀					2190	1338		
WAMC55569	KMWA.1365		*triangulata*	SIKE07	♀							2138	1122
WAMC55570	KMWA.1366		*triangulata*	SIKE07	♀							2168	1220
OC3369	KMWA.1367		*triangulata*	SIKE07	♂					1818	1100		
WAMC55571	KMWA.1368		*triangulata*	SIKE07	♂							1917	1038
WAMC55572	KMWA.1369		*triangulata*	SIKE07	♂							1933	1065
OC3367	KMWA.244		*triangulata*	CB54	♀	1931	1072	2147	1122				
WAMC55574	OS.254		*triangulata*	CB54	♂	1888	996	1990	1006				
WAMC55575	OS.122		*triangulata*	CB75a	♂	1800	1075						
WAMC55576	KMWA.884		*triangulata*	SIKE11	♂	1961	1022	2069	1061				
WAMC55577	KMWA.885		*triangulata*	SIKE11	♀	2339	1300	2486	1297				
WAMC55578	KMWA.701		*triangulata*	SIKE21	♀	2173	1360	2238	1377				
WAMC55579	KMWA.702		*triangulata*	SIKE21	♀					2178	1331		
WAMC55580	KMWA.703		*triangulata*	SIKE21	♀					2161	1350		
no nr	KMWA.1189	KP006594	*triangulata*	ESKI01	♀	1963	1230	2035	1255				
no nr	KMWA.229		*triangulata*	OSTR10B	♀	2030	1100						
no nr	KMWA.230		*triangulata*	OSTR10B	♀							2010	1030
no nr	KMWA.231		*triangulata*	OSTR10B	♀					2080	1160		
no nr	KMWA.232		*triangulata*	OSTR10C	♀							2260	1250
no nr	KMWA.234		*triangulata*	OSTR10C	♀	2160	1360	2270	1410				
OC3371	KMWA.1037	KP006566	*nimala*	NT/12/01	♀	1500	861	1640	962				
WAMC55585	KMWA.1038	KP006565	*nimala*	NT/12/01	♀	1520	872	1700	958				
OC3372	KMWA.1039		*nimala*	NT/12/01	♀							1730	1020
WAMC55586	KMWA.1040		*nimala*	NT/12/01	♀					1680	1710		
WAMC55587	KMWA.1043	KP006569	*nimala*	NT/12/03	♀	1510	863	1630	954				
WAMC55588	KMWA.1044	KP006570	*nimala*	NT/12/03	♀	1480	853	1630	946				
WAMC55589	KMWA.1047		*nimala*	NT/12/01	♀	1546	902	1700	994				
WAMC55590	KMWA.1048	KP006568	*nimala*	NT/12/08	♀	1554	906	1748	1012				
WAMC55591	KMWA.1111		*nimala*	CNJ R-109	♀	1383	781	1479	867				
WAMC55592	KMWA.1112		*nimala*	CNJ R-109	♀	1462	852	1567	904				
WAMC55593	KMWA.1113		*nimala*	CNJ R-109	♀	1450	840	1585	942				
WAMC55594	KMWA.1114		*nimala*	CORN 9/v/09	♀	1481	850	1594	937				
OC3373	KMWA.1116		*nimala*	CORN 9/v/09	♀					1627	1010		
WAMC55595	**KMWA.164**		***tirigie***	**SIEK4**	♂	**1080**	**603**	**1190**	**650**				
WAMC55596	KMWA.169		*tirigie*	SIEK4	♀	1180	692	1300	737				

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WAMC55597	KMWA.168		*tirigie*	SIEK4	♂					1090	603	1100	659
WAMC55598	KMWA.165		*tirigie*	SIEK4	♀							1290	800
WAMC55599	KMWA.166		*tirigie*	SIEK4	♀							1300	755
WAMC55600	KMWA.167		*tirigie*	SIEK4	♀					1280	724		
WAMC55605	KMWA.1169	KP006532	*tirigie*	ESKI06	♂	1029	593						
WAMC55606	KMWA.1170		*tirigie*	ESKI06	♀							1196	740
WAMC55607	KMWA.1171		*tirigie*	ESKI06	♀					1136	638		
WAMC55608	KMWA.1172		*tirigie*	ESKI06	♂					1063	603		
WAMC55609	KMWA.1173		*tirigie*	ESKI06	♂							1042	597
WAMC55610	KMWA.1176	KP006539	*tirigie*	ESKI08	♀	1129	660						
OC3374	KMWA.1178		*tirigie*	ESKI08	♀					1178	663		
OC3375	KMWA.1179		*tirigie*	ESKI08	♂					1086	615		
WAMC55611	**KMWA.171**		***koendersae***	**KIES1A**	♂	**1110**	**587**	**1210**	**621**				
WAMC55612	KMWA.174		*koendersae*	KIES1A	♀					1353	767	1340	845
WAMC55613	KMWA.172		*koendersae*	KIES1A	♂					1190	629	1189	672
WAMC55614	KMWA.175		*koendersae*	KIES1A	♀	1240	689	1340	729				
OC3376	KMWA.176		*koendersae*	KIES1A	♀	1260	714	1380	749				
WAMC55617	KMWA.1260		*koendersae*	KIES1A	♀							1321	804
WAMC55618	KMWA.1261		*koendersae*	KIES1A	♀							1309	725
WAMC55620	**KMWA.664**		***pinderi***	**SIKE03**	♀	**1395**	**810**	**1507**	**840**				
WAMC55621	KMWA.665		*pinderi*	SIKE03	♀							1508	898
WAMC55622	KMWA.666		*pinderi*	SIKE03	♀					1450	810		
OC3378	KMWA.667		*pinderi*	SIKE03	♀							1433	865
WAMC55624	KMWA.671		*pinderi*	SIKE05	♀	1410	813	1533	875				
WAMC55625	KMWA.672		*pinderi*	SIKE05	♀							1528	927
WAMC55626	**KMWA.181**		***shieli***	**PSW036**	♀	**1380**	**807**	**1467**	**888**				
WAMC55627	KMWA.290		*shieli*	PSW036	♀	1311	745	1475	852				
OC3379	KMWA.293		*shieli*	PSW036	♀					1480	888		
WAMC55628	KMWA.183		*shieli*	PSW036	♀							1500	933
WAMC55629	KMWA.184		*shieli*	PSW036	♀							1470	984
WAMC55630	KMWA.294		*shieli*	PSW036	♀	1370	813	1480	907				
WAMC55632	**KMWA.1090**		***muggon***	**SIKE20**	♀	**1015**	**603**	**1078**	**638**				
WAMC55633	KMWA.1084		*muggon*	SIKE20	♀	1018	606						
WAMC55634	KMWA.1085		*muggon*	SIKE20	♀							1107	654
WAMC55635	KMWA.1086		*muggon*	SIKE20	♀					1117	668		
WAMC55636	KMWA.1087		*muggon*	SIKE20	♀							1119	685
WAMC55637	KMWA.690		*muggon*	SIKE20	♀	1040	629	1108	655				
WAMC55638	KMWA.691		*muggon*	SIKE20	♀							1111	699
WAMC55639	KMWA.692		*muggon*	SIKE20	♀							1101	681
WAMC55640	KMWA.693		*muggon*	SIKE20	♀					1078	660		
WAMC55641	KMWA.1345		*muggon*	SIKE20	♀	1082	636						
WAMC55642	KMWA.1346		*muggon*	SIKE20	♀	1021	603						
WAMC55643	KMWA.1347		*muggon*	SIKE20	♀	1043	621	1111	650				
OC3382	KMWA.1348		*muggon*	SIKE20	♀	1058	629	1124	667				
OC3383	KMWA.1349		*muggon*	SIKE20	♀	1049	621	1121	672				
WAMC55644	KMWA.1350		*muggon*	SIKE20	♀	1004	600	1056	631				

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bootstrap replicates and the parameters of jModeltest for all 88 models), respectively. Genetic diversities and relationships within and between populations were illustrated with parsimonious networks at the 95% probability limit with TCS 1.21 (Clement *et al.* 2000). Selected sequences of all species have been submitted to Genbank (accession numbers KP006531–KP006599; see Table 1).

Testing for cryptic diversity

In the COI phylogenies of *Bennelongia*, well-supported phylogenetic clades (with bootstraps above 75% or posterior probabilities above 0.85) were identified, which could represent different species following the evolutionary genetic species concept (Birky & Barraclough 2009). We then used MEGA version 6.0 (Tamura *et al.* 2013) to estimate sequence diversities within and between these phylogenetic clades, either using the number of differences (p) or the Tamura-3 parameter model with gamma distribution and 1000 bootstrap replicates. Following Birky *et al.* (2010), we then corrected the obtained estimates of sequence diversities for sample size. According to the 4 theta rule, sequence diversities between two sister clades must be no less than 4 to 4.3 times larger than within the two clades, depending on the number of sequences per clade (Birky *et al.* 2010). The 4 theta rule has been used previously on bdelloid rotifers (Fontaneto *et al.* 2007, 2009; Birky & Barraclough 2009; Birky *et al.* 2011), sexual and asexual ostracods (Bode *et al.* 2010; Schön *et al.* 2012), including other *Bennelongia* species (Martens *et al.* 2012, 2013; Shearn *et al.* 2012), asexual prokaryotes (Birky *et al.* 2010) and sexual vertebrates and invertebrates (Birky 2013).

Abbreviations used in text and figures

Cp = carapace
CpD/CpV = carapace in dorsal/ ventral view
CpRL = carapace in right lateral view
DPaW = Department of Parks and Wildlife
F = female
H = height of valves
il = inner list
K25 = electrical conductivity standardised to a water temperature of 25ºC
KMWA = original working numbers given to specimens dissected and illustrated by the first author (KM)
L = length of valves
Lpp = left prehensile palp
ls = lateral shield of hemipenis
LV = left valve
LVe = left valve, external view
LVi = left valve, internal view
M = male
ms = medial shield of hemipenis
NT = Northern Territory
OC = Ostracod Collection in the Royal Belgian Institute of Natural Sciences (Brussels, Belgium)
OS = Ostracod Slide dissected by Stuart Halse (SH), retrieved from the voucher collection of DPaW (Perth)
QLD = Queensland
Rpp = right prehensile palp
RV = right valve
RVe = right valve, external view
RVi = right valve, internal view
SA = South Australia

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Temp = temperature in °C
W = width of carapace
WA = Western Australia
WAMC = Western Australian Museum, Crustacean Collection (Perth, Australia)

Specimens in bold in Table 1 represent the holotypes of the new species.

Chaetotaxy of the limbs follows the model proposed by Broodbakker & Danielopol (1982), revised for A2 by Martens (1987). Higher taxonomy of the Ostracoda follows the synopsis by Horne *et al.* (2002).

Results

Results of molecular screening

Both phylogenetic methods generated COI trees with similar topologies consisting of seven well-supported phylogenetic clades (see the consensus tree in Fig. 2). Of these seven clades, five, namely *B. triangulata* sp. nov., *B. muggon* sp. nov., *B. koendersae* sp. nov., *B. pinderi* sp. nov. and *B. tirigie* sp. nov., match with the novel species described here from morphological data (see below). A sixth clade

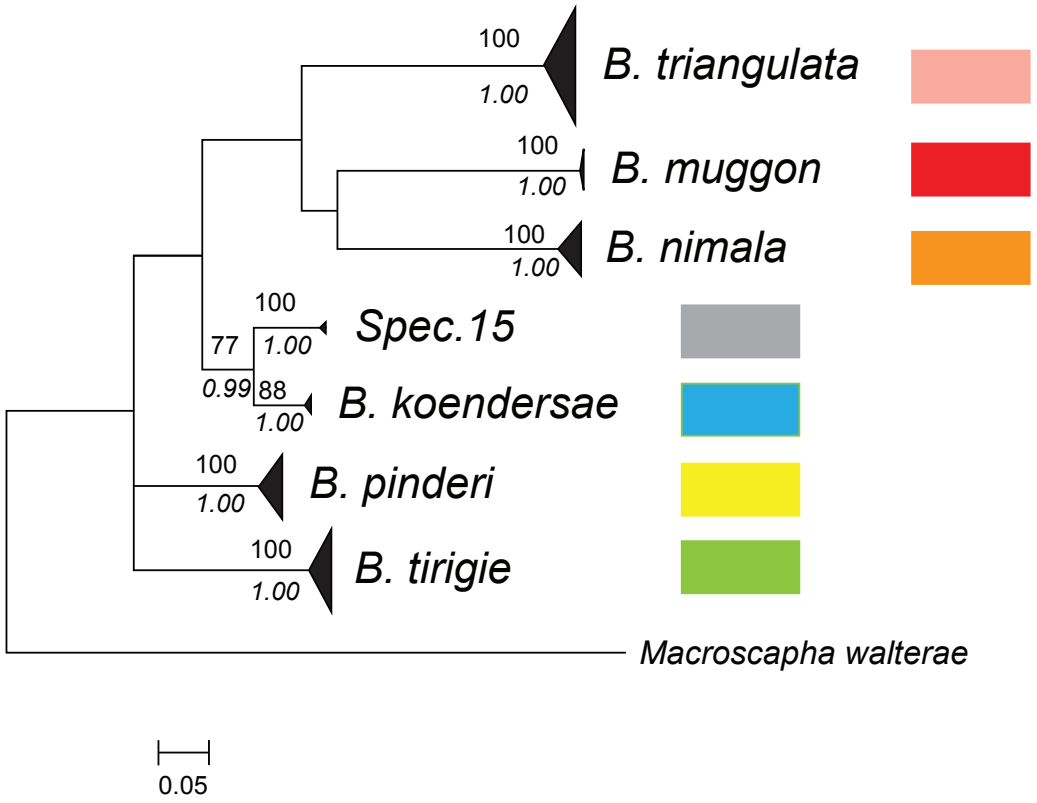

Fig. 2. Phylogenetic tree constructed with Bayesian Inference (BI) and Maximum Likelihood (ML) methods from COI sequences belonging to a total of 54 ostracods from the *Bennelongia nimala and B. triangulata* lineages, respectively, with the marine ostracod *Macroscapha walterae* from Genbank (accession number GU566887) as outgroup. Numbers above and below nodes illustrate statistical support for this particular node. Numbers above nodes are % bootstrap values of ML analyses with 1000 replicates, numbers below nodes in italics represent Bayesian posterior probabilities (ranging from 0 to 1). Both methods, BI and ML, resulted in the same tree topology. Different phylogenetic clades are indicated by different colours.

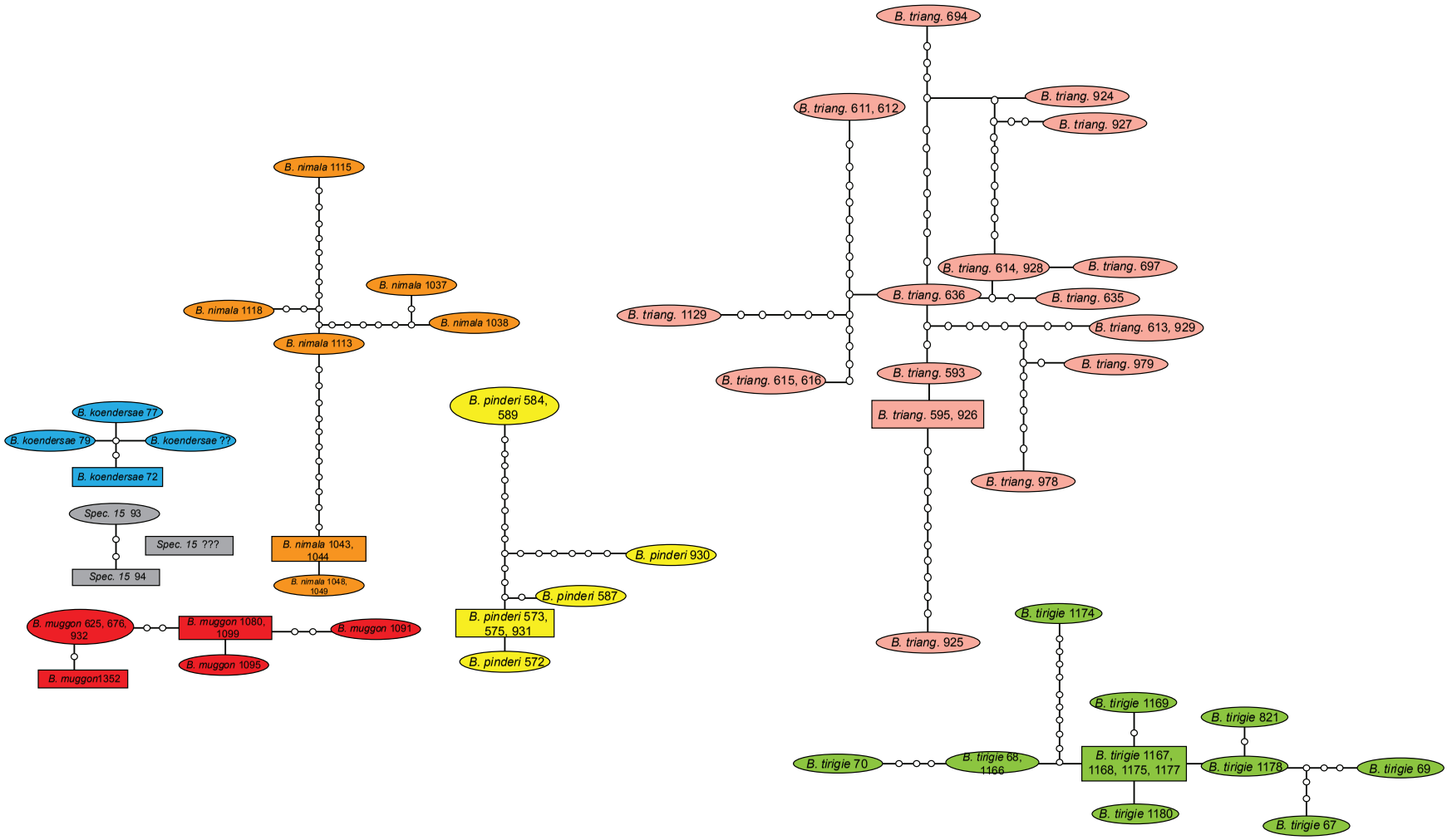

Fig. 3. Parsimonius networks, based on COI sequences of the *Bennelongia nimala* and *B. triangulata* lineages. Squares represent ancestral sequences (or haplotypes), small circles missing haplotypes. The size of squares and large ovals is proportional to the number of individuals with the same sequence in the analysed population. The networks were constructed with up to 14 mutations steps connecting different sequences or haplotypes. Different phylogenetic clades are indicated by different colours (see Fig. 2).

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Table 2. Results of tests for genetic species boundaries using the 4 theta rule for species of the *Bennelongia nimala* and *B. triangulata* lineages, respectively. θ = population genetic parameter theta, indicating genetic variability within populations. D = genetic distance between sister clades. n^1, n^2 = number of sequences for each sister clade. θ and D were either calculated as p distances or with the Tamura-3 parameter model (in italics). With the exception of *B. koendersae* sp. nov. and Spec. 15 (see Fig. 2), no sister clades with high statistical support could be identified in the obtained COI trees; therefore, all phylogenetic clades were compared to each other. In order to fulfil the criteria of the 4 theta rule for genetic species status, the ratio of the mean sequence diversity within a phylogenetic clade (theta, θ) as compared to the sequence diversity between this clade and its nearest phylogenetic neighbour (D) needs to be 4 or more, depending on the number of specimens per clade (Birky *et al.* 2010). Comparisons, for which these criteria are fulfilled, are printed in bold. (Table continued on next page.)

Species	**max. θ (within clades)**	**D (between clades)**	**Ratio D/θ**	**n^1, n^2**
B. koendersae – Spec. 15	0.0091 *0.0091*	0.049 *0.053*	**5.38** ***5.82***	4, 2
B. koendersae – B. tirigie	0.0081 *0.0083*	0.114 *0.135*	**14.07** ***16.27***	4, 14
B. koendersae – B. pinderi	0.0148 *0.0154*	0.106 *0.124*	**7.16** ***8.05***	4, 10
B. koendersae – B. nimala	0.0200 *0.0204*	0.124 *0.148*	**6.20** ***7.25***	4, 9
B. koendersae – B. muggon	0.0050 *0.0052*	0.137 *0.168*	**27.40** ***32.31***	4, 8
B. koendersae – B. triangulata	0.0189 *0.0196*	0.129 *0.157*	**6.83** ***8.01***	4, 21
Spec. 15 – *B. tirigie*	0.0091 *0.0091*	0.113 *0.133*	**12.42** ***14.62***	2, 14
Spec. 15 – *B. pinderi*	0.0148 *0.0154*	0.097 *0.112*	**6.55** ***7.27***	2, 10
Spec. 15 – *B. nimala*	0.0200 *0.0204*	0.140 *0.171*	**7.00** ***8.38***	2, 9
Spec. 15 – *B. muggon*	0.0091 *0.0091*	0.143 *0.177*	**15.71** ***19.45***	2, 8
Spec. 15 – *B. triangulata*	0.0189 *0.0196*	0.137 *0.170*	**7.25** ***8.67***	2, 21
B. pinderi – B. tirigie	0.0148 *0.0154*	0.109 *0.128*	**7.36** ***8.31***	10, 14
B. pinderi – B. nimala	0.0200 *0.0204*	0.159 *0.204*	**7.95** ***10.00***	10, 9

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B. pinderi – B. muggon	0.0148 *0.0157*	0.148 *0.186*	**10.00** ***11.85***	10, 8
B. pinderi – B. triangulata	0.0189 *0.0196*	0.144 *0.181*	**7.62** ***9.23***	10, 21
B. tirigie – B. nimala	0.0200 *0.0204*	0.146 *0.184*	**7.30** ***9.02***	14, 9
B. tirigie – B. muggon	0.0081 *0.0083*	0.142 *0.177*	**17.53** ***21.33***	14, 8
B. tirigie – B. triangulata	0.0189 *0.0196*	0.136 *0.167*	**7.20** ***8.52***	14, 21
B. nimala – B. muggon	0.0200 *0.0204*	0.144 *0.177*	**7.20** ***8.68***	9, 8
B. nimala – B. triangulata	0.0200 *0.0204*	0.142 *0.175*	**7.10** ***8.58***	9, 21
B. muggon – B. triangulata	0.0189 *0.0196*	0.146 *0.179*	**7.72** ***9.13***	8, 21

contains the sequences of *B. nimala* (see below). Two additional sequences in the tree belonging to clade Spec. 15 could not be investigated morphologically because the entire specimens had been used for the molecular analyses. The sequences of Spec. 15 cluster together with *B. koendersae* sp. nov. with good statistical support while the relationships among the other phylogenetic clades cannot be derived from the COI tree because of lack of statistical support (Fig. 2). The seven phylogenetic clades are completely congruent with seven isolated parsimonious networks (Fig. 3). Among the network structures, it appears that *B. triangulata* sp. nov. is genetically most diverse, as this species contains 16 different haplotypes (sequences) being separated by up to 15 mutational steps. With 10 haplotypes, the network of *B. tirigie* sp. nov. is genetically the second most diverse species while the other species contain 7 (*B. nimala*), 5 (*B. pinderi* sp. nov.) and 4 (*B. koendersae* sp. nov. and *B. muggon* sp. nov.) haplotypes, respectively, and their network structures are more simple. When comparing genetic diversities between and within each phylogenetic clade, the genetic distances between all seven phylogenetic clades clearly exceed the distances within each clade by more than 4 times (Table 2), thus fulfilling the criterion of the 4 theta rule (Birky *et al.* 2010). The seven phylogenetic clades and networks can thus be regarded as different genetic species according to the phylogenetic species concept. We found no evidence for cryptic genetic diversity as all genetic species matched the morphological species with the exception of Spec. 15, for which no morphological data are available.

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Taxonomic descriptions

Class Ostracoda Latreille, 1806
Subclass Podocopa G.O. Sars, 1866
Order Podocopida G.O. Sars, 1866
Suborder Cypridocopina Baird, 1845
Superfamily Cypridoidea Baird, 1845
Family Cyprididae Baird, 1845
Subfamily Bennelongiinae Martens *et al.*, 2012

Genus ***Bennelongia*** De Deckker & McKenzie, 1981

Diagnosis

See Martens *et al.* (2012).

Bennelongia nimala - lineage

Diagnosis of the *B. nimala*-lineage

All species in this lineage with strongly calcified and heavily ornamented valves, also in adults external valve surfaces set with large pustules, spines and short but stiff setae. Nearly all species with yellowish-brownish colour. Most species also with very pronounced anterior LV/RV overlap, most pronounced of all lineages in this genus. Some species with an inner 'eyelet' in the anterior part of the RV, close to the lapel, just as in the species of the *B. barangaroo* lineage (see Martens *et al.* 2013), to which this lineage is most closely related.

Bennelongia nimala De Deckker, 1981
Fig. 4A–N

Bennelongia nimala n. sp. – De Deckker, 1981: 105–108, figs 10–11.

Abbreviated redescription.

Valves in inner view (Fig. 4A–B) relatively high, with almost straight dorsal margin and greatest height situated well in front of the middle; ventral margin anteriorly without mandibular curve. LV (Fig. 4A) with antero-distal il running all the way down into the beak, but not connecting with ventral inner list; antero-proximal il running slightly over halfway along the anterior margin; posterior il tuberculate and running halfway up the posterior margin, next to the pointed valve margin. RV (Fig. 4B) with antero-ventral lapel large, ventrally pointed and heavily serrated (Fig. 4L–N). Both valves with heavy external ornamentation, consisting of pits, smaller and larger tubercles (Fig. 4C–D, F–G, K).

Cp (Fig. 4G, K, M) with LV overlapping RV on all sides, but moderately so; CpRL with LV forming an antero-dorsal hump over RV. CpD with greatest width situated in the middle in females (Fig. 4G), anteriorly with strong and slightly asymmetrical rostrum, dorsally set with parallel rows of tubercles.

From De Deckker (1981): Soft parts as typical of the genus. Hemipenis with lobe ls broad and plump, antero-ventral extremity broadly rounded; lobe ms with antero-ventral extremity broad and rounded. Rpp with unusually long and narrow distal segment. Lpp with sickle-shaped terminal segment, relatively long and slender, also proximal segment long and narrow.

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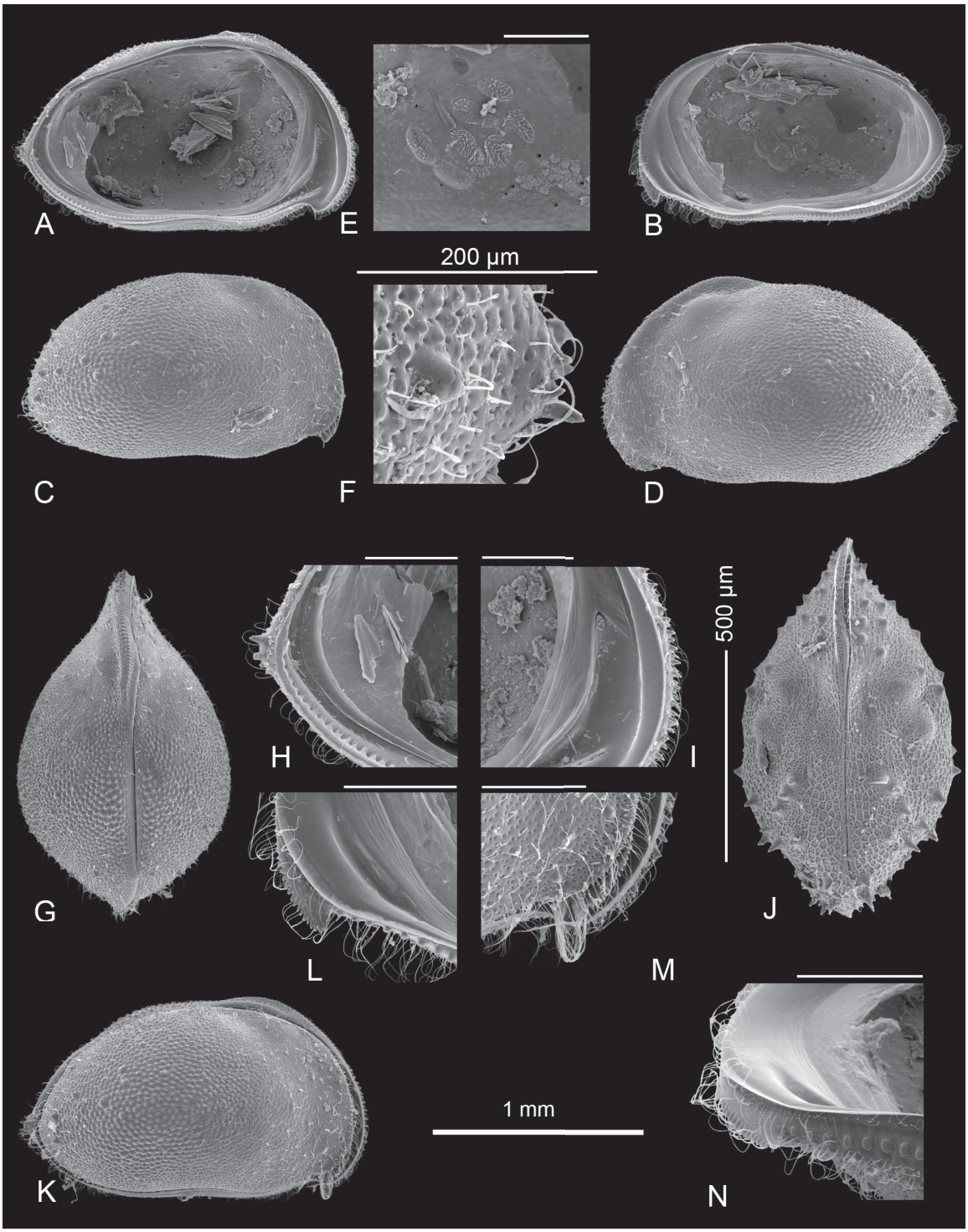

Fig. 4. *Bennelongia nimala* De Deckker, 1981 (all ♀, all from Kakadu National Park, NT). **A**. LVi (WAMC55593). **B**. RVi (WAMC55593). **C**. RVe (WAMC55589). **D**. LVe (WAMC55589). **E**. RVi, detail of central muscle scars (WAMC55593). **F**. LVe, detail of surface ornamentation (WAMC55589). **G**. CpD (OC3373). **H**. LVi, detail of caudal side (WAMC55593). **I**. LVi, detail of anterior side (WAMC55593). **J**. CpD (juvenile A-3, specimen lost). **K**. CpRL (OC3373). **L**. RVi, detail of anterior margin (WAMC55593). **M**. CpRL, detail of anterior margin, showing external view of lapel (OC3373). **N**. RVi, tilted, detail of anterior margin and of lapel (WAMC55593). Scale = 1 mm for A–D, G, K; 500 µm for J; 200 µm for E–F, H–I, L–N.

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New material investigated

Kakadu National Park, Coonjimba Billabong, Gulungul Creek, Ranger, Jabiru region, NT (sample CNJ-R-109). Approximate coordinates: 12°34'37" S, 132°52'30.1" E. Collected by Russell Shiel on 9 May 2009. Several females (WAMC55591–55593).

Kakadu National Park, Corndori Billabong, Gulungul Creek, Ranger, Jabiru region, NT (sample CORN 9/v/09). Approximate coordinates: 12°37'50" S, 120°53'06" E. Collected by Russell Shiel on 9 May 2009. Several females (WAMC55594, OC3373).

Unnamed lagoon, Adelaide River Floodplain, NT (sample NT/12/01). Approximate coordinates: 12°53'06.5" S, 131°12'03.0" E. Collected by the authors on 28 Jul. 2012. Several females (OC3371–3372, WAMC55585–55586, 55589). K25 = 58 µS/cm, Temp = 30,2°C, pH = 8.0, depth = *ca*. 0.3 m.

Bennett Dam, Adelaide River Floodplain, NT (sample NT/12/03). Approximate coordinates: 12°57'08.3" S, 131°09'59.7" E. Collected by the authors on 25 Jul. 2012. Several females (WAMC55587–55588). K25 = 58 µS/cm, Temp = 28°C, pH = 7.2, depth = *ca*. 0.5 m.

Unnamed lagoon, Mary River Park, NT (sample NT/12/08). Approximate coordinates: 12°54'52.1" S, 131°39'23.7" E. Collected by the authors on 26 Jul. 2012. Several females (WAMC55590).

Type locality

Georgetown Lagoon, Jabiru, NT.

Measurements (all measurements in µm – see Table 1 for measurements of all newly collected specimens illustrated with SEM)

Measurements of type material from De Deckker (1981):
Holotype ♂: RV: L = 1340, H = 760, LV: L = 1500, H = 840.
Paratype ♀: RV: L = 1540, H = 860; LV: L = 1640, H = 960.

Measurements of new material (only ♀♀):
RV: L = 1450–1550, H = 780–900; LV: L = 1480–1750, H = 870–1010, W = *ca*. 1020.

Differential diagnosis

The species can be separated from all other congeners belonging to the *B. nimala* lineage by the pointed caudal section of the LV and by the large, pronounced and heavily serrated lapel on the RV. The moderate antero-ventral LV/RV overlap distinguishes this species specifically from *B. tirigie* sp. nov., *B. koendersae* sp. nov. and *B. muggon* sp. nov.

Ecology and distribution

Bennelongia nimala is an NT species. It occurs in vegetated and unvegetated freshwater lagoons, from which it derives its name.

Bennelongia tirigie sp. nov.
urn:lsid:zoobank.org:act:7323D117-25B3-4059-B42C-079286494218
Figs 5A–N, 6A–D

Abbreviated description

Valves in inner view (Fig. 5A, C–D, F) relatively elongated, with rounded dorsal margin and greatest height situated well in front of the middle; ventral margin with pronounced mandibular curve anteriorly.

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LV (Fig. 5A, D) with antero-distal il running only halfway along the anterior valve margin, antero-proximal il running almost all the way up along the valve margin; posterior il tuberculate and running halfway up the posterior margin. RV (Fig. 5C, F) with antero-ventral lapel relatively large, but bent closely to valve surface and therefore less conspicuous (Fig. 5K–N). Valves with heavy external ornamentation, mostly consisting of small tubercles (Fig. 5B, E, G–J).

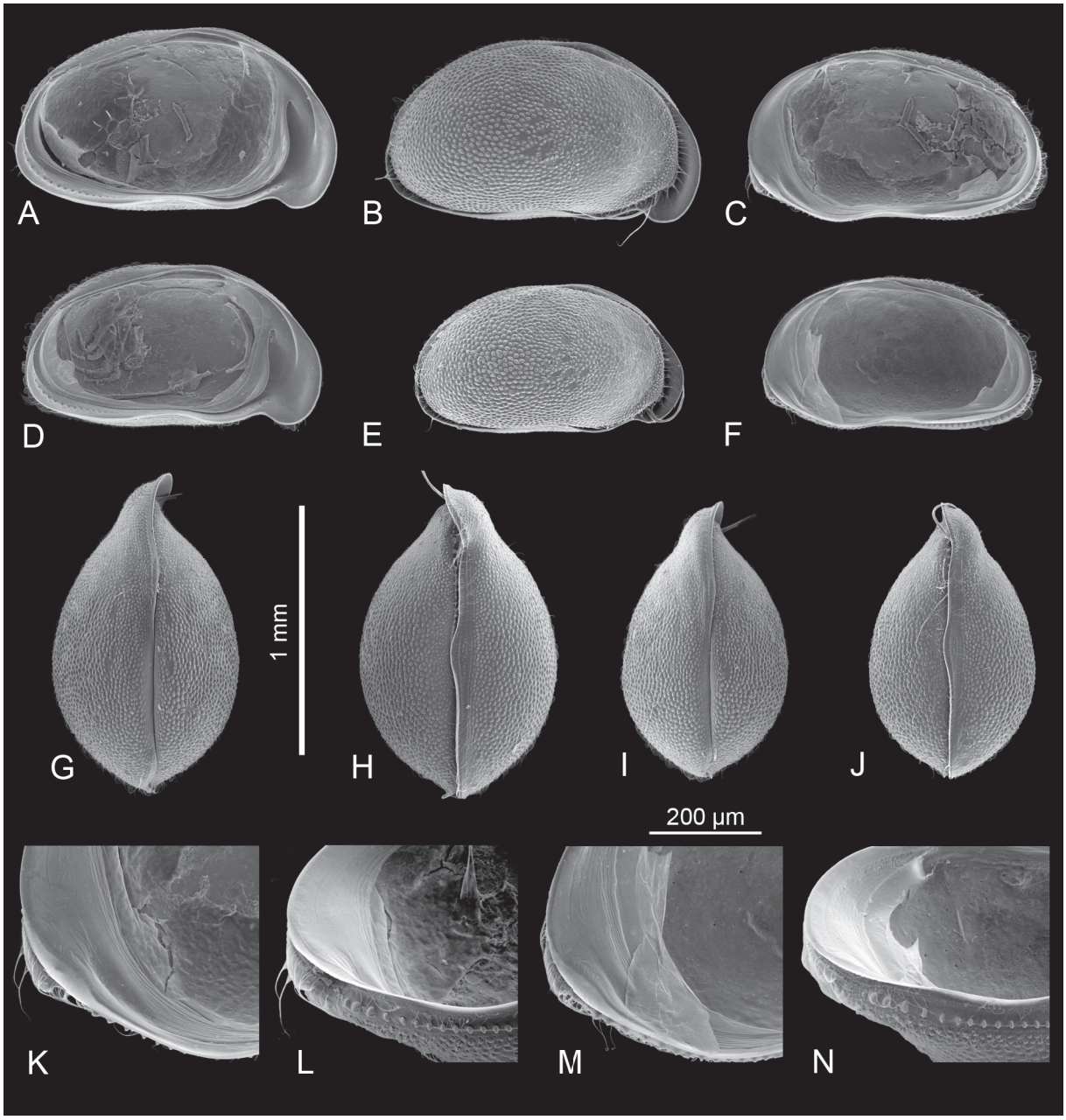

Fig. 5. *Bennelongia tirigie* sp. nov. (all from type locality: Tirigie Claypan, Murchison/Gascoyne, WA). **A**. LVi (allotype ♀, WAMC55596). **B**. CpRL (♀, WAMC 55600). **C**. RVi (♀, WAMC55596). **D**. LVi (holotype ♂, WAMC55595). **E**. CpRL (♂, WAMC55597). **F**. RVi (♂, WAMC55595). **G**. CpD (♀, WAMC55599). **H**. CpV (♀, WAMC55598). **I**. CpD (♂, WAMC55597). **J**. CpV (♂, WAMC55597). **K**. RVi, detail anterior margin (♀, WAMC55596). **L**. RVi, tilted, detail anterior margin (♀, WAMC55596). **M**. RVi, detail anterior margin (♂, WAMC55595). **N**. RVi, tilted, detail anterior margin (♂, WAMC55595). Scale = 1 mm for A–J; 200 µm for K–N.

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Cp (Fig. 5B, E, G–J) with largest LV/RV overlap of all *Bennelongia* species known to date. CpD and CpV with greatest width situated slightly behind the middle in males (Fig. 5I–J), in the middle in females (Fig. 5G–H), anteriorly with strong and asymmetrical rostrum.

Soft parts as typical of the genus. Hemipenes (Fig. 6A–B) almost symmetrical, edge of lobe ms almost straight, lobe ls with extremity ventrally pointed. Lpp (Fig. 6C) with distal segment rather narrow. Rpp (Fig. 6D) with distal segment rather broad, elongated and distally rounded, sensory organ on first segment stout.

Etymology

The species is named after its type locality, Tirigie Claypan in Gascoyne, WA.

Type material

Holotype

♂ (WAMC55595), with soft parts dissected in a sealed slide and valves stored dry in a micropalaeontological slide.

Allotype

♀ (WAMC55596), with valves stored dry in a micropalaeontological slide and soft parts used for molecular screening.

Paratypes

Numerous females and males from the type locality, either dissected or stored as the holotype, as carapaces used for SEM or in alcohol. See Table 1 for listing of specimens (WAMC5597–55601).

Other material investigated

Crackers Swamp, Dandaragan, WA (sample SIEK1). Approximate coordinates: 30°54'36" S, 115°35'30.2" E. All material collected by the authors on 5 Apr. 2006. Several females.

Minilya Pool, Gascoyne, WA (sample SIKE19). Approximate coordinates: 23°54'25" S, 114°01'47.3" E. All material collected by the authors on 7 Jul. 2011. K25 = 693 µS/cm, Temp = 17.3°C, pH = 7.3.

Unnamed crabhole swamp on Winning Station, Gascoyne, WA (sample ESKI05). Approximate coordinates: 23°15'22" S, 114°44'57.8" E. All material collected by the authors on 6 Apr. 2013. Several females (WAMC55602–55604).

Dam on Winning Station, Gascoyne, WA (sample ESKI06). Approximate coordinates: 22°14'16.0" S, 114°42'34.0" E. All material collected by the authors on 6 Apr. 2013. Several males and females (WAMC556055–55609).

Unnamed large claypan on Winning Station, Gascoyne, WA (sample ESKI08). Approximate coordinates: 23°07'39.6" S, 114°34'41.3" E. All material collected by the authors on 6 Apr. 2013. Several males and females (WAMC55610, OC3374–3375).

Type locality

AUSTRALIA: Tirigie Claypan, Gascoyne, WA (sample SIEK4), approximate coordinates: 24°38'29" S, 113°59'44" E. All material collected by the authors on 7 Apr. 2006.

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Differential diagnosis

The large frontal LV/RV overlap and the shape of the lapel on the RV distinguish this species from all others in the *B. nimala* lineage. The shape of the ls on the hemipenes and of the distal segment of the Rpp enables this species to be distinguished from others of the *B. nimala* lineage for which males are known: *B. nimala* has a broader ls and an even narrower distal segment on the Rpp; *B. koendersae* sp. nov. has an ls that is longer, more robust and not so pointed, while the distal segment of its Rpp is broadly triangular, with almost straight margins; in *B. regina* Shearn *et al*., 2012 the distal segment of the Rpp is evenly rounded while the ls of the hemipenes end in small, birdhead-like lobes.

Measurements (all measurements in µm – see Table 1 for measurements of all specimens illustrated with SEM)

Holotype ♂ (WAMC55595): RV: L = 1080, H = 603; LV: L = 1190, H = 650.
Allotype ♀ (WAMC55596): RV: L = 1180, H = 692; LV: L = 1300, H = 737.

Ecology and distribution

Bennelongia tirigie sp. nov. is a common species in turbid seasonal water bodies of the Gascoyne region of WA. Its range extends south to the northern Swan Coastal Plain, where it has been collected from a seasonal freshwater swamp of low turbidity.

Bennelongia koendersae sp. nov.
urn:lsid:zoobank.org:act:6CA91421-02FF-4A2E-A0E6-89F417057C81
Figs 6E–H, 7A–N

Abbreviated description

Valves in inner view (Fig. 7A, C–D, F) relatively elongated, with rounded dorsal margin and greatest height situated well in front of the middle; ventral margin anteriorly without pronounced mandibular curve. LV (Fig. 7A, D) with antero-distal il running only halfway along the anterior valve margin, antero-proximal il running slightly higher along the anterior valve margin; posterior il tuberculate and running halfway up the posterior margin. RV (Fig. 7C, F) with antero-ventral lapel large, rounded and strongly serrated (Fig. 7K–N). Valves with heavy external ornamentation, mostly consisting of small tubercles (Fig. 7B, E, G–J).

Cp (Fig. 7B, E, G–J) with large LV/RV overlap, but less so than in *B. tirigie* sp. nov. CpD and CpV with greatest width situated in the middle in males (Fig. 7G–H), slightly behind the middle in females (Fig. 7I–J), anteriorly with strong and asymmetrical rostrum.

Soft parts as typical of the genus. Hemipenes (Fig. 6E–F) almost symmetrical, edge of ms slightly sinuous, ls with extremity rounded. Lpp (Fig. 6G) with distal segment rather broad, distal half of second segment with parallel margins. Rpp (Fig. 6H) with distal segment large, subtriangular and with almost straight margins, sensory organ on first segment stout.

Etymology

The species is named after Dr Annette Koenders (Edith Cowan University, Joondalup, WA), in recognition of her contribution to our knowledge of the genetic diversity of various Australian invertebrate groups.

Type material

Holotype

♂ (WAMC55611), with soft parts dissected in a sealed slide and valves stored dry in a micropalaeontological slide.

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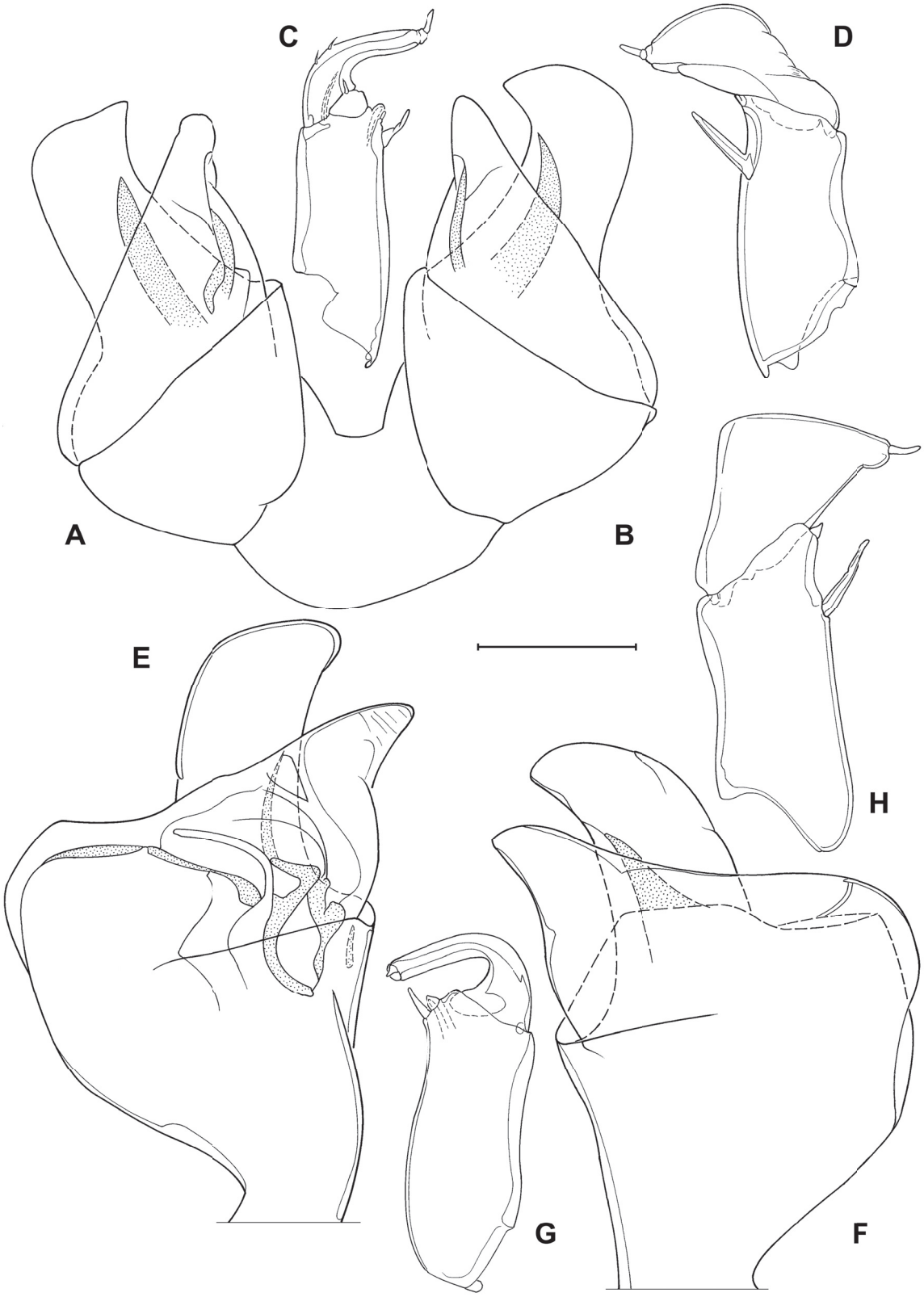

Fig. 6. *Bennelongia tirigie* sp. nov. (A–D, WAMC55595, holotype) and *B. koendersae* sp. nov. (E–H, WAMC55615, paratype), all ♂. **A–B**. Outlines of hemipenes. **C**. Lpp. **D**. Rpp. **E–F**. Outlines of hemipenes. **G**. Lpp. **H**. Rpp. Scale = 73 μm for A, D–E; 31 μm for B–C, F–H.

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Allotype

♀ (WAMC55612) carapace stored dry in a micropalaeontological slide.

Paratypes

Numerous males and females from the type locality, either dissected and stored as the holotype, as carapaces used for SEM or in alcohol (WAMC55613–55619, OC3376–3377). See Table 1 for listing of specimens.

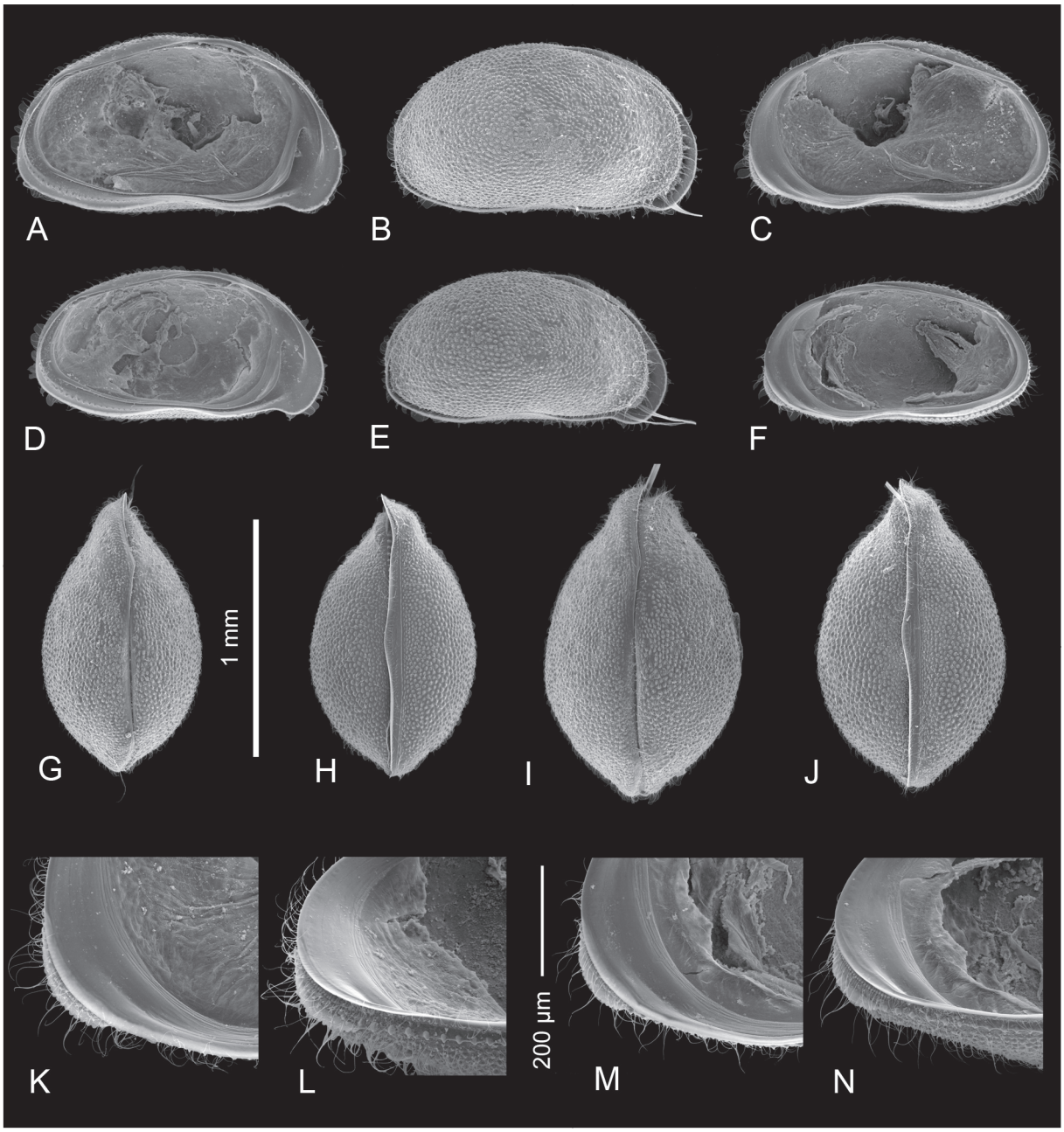

Fig. 7. *Bennelongia koendersae* sp. nov. (all from type locality: claypan at Strelley Station, Pilbara, WA). **A**. LVi (♀, OC3376). **B**. CpRL (♀, WAMC55618). **C**. RVi (♀, OC3376). **D**. LVi (holotype ♂, WAMC55611). **E**. CpRL (♂, WAMC55613). **F**. RVi (♂, WAMC55611). **G**. CpD (♂, WAMC55613). **H**. CpV (♂, specimen lost). **I**. CpD (allotype ♀, WAMC55612). **J**. CpV (♀, WAMC55617). **K**. RVi, detail anterior margin (♀, OC3376). **L**. RVi, tilted, detail anterior margin (♀, OC3376. **M**. RVi, detail anterior margin (♂, WAMC55611). **N**. RVi, tilted, detail anterior margin (♂, WAMC55611). Scale = 1 mm for A–J; 200 µm for K–N.

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Type locality

AUSTRALIA: Strelley Station, shallow unnamed claypan, Pilbara, WA (sample KIES1A), approximate coordinates: 20°24'58" S, 118°59'4" E. All material collected by the authors on 21 Apr. 2006.

Measurements (all measurements in µm – see Table 1 for measurements of all specimens illustrated with SEM)

Holotype ♂ (WAMC55611): RV: L = 1110, H = 587; LV: L = 1210, H = 621.
Paratype ♀ (WAMC55612): RV: L = 1240, H = 689; LV: L = 1340, H = 729.

Differential diagnosis

Bennelongia koendersae sp. nov. can be distinguished from all other species in the *B. nimala* lineage by the size and shape of the antero-ventral lapel on the RV, and from *B. tirigie* sp. nov. by the less pronounced anterior LV/RV overlap. *Bennelongia koendersae* sp. nov. can be distinguished from those species in the lineage where males are known (*B. nimala*, *B. regina*, *B. tirigie* sp. nov.) by the large and triangular second segment of the Rpp.

Ecology and distribution

The species is only known from its type locality, which is a small, ephemeral, turbid claypan.

Remarks

In a second sample from the 2006 KIES collecting expedition in Pilbara, a species close to *B. koendersae* sp. nov. was recognised with molecular methods only. This species (as *Spec. 15* in Fig. 2) looked very much like *B. koendersae* sp. nov. and the only two specimens available were both screened *in toto* by molecular methods to establish conspecificity. Although these specimens cluster close to *B. koendersae* sp. nov. in the phylogenetic COI tree, they are considered to represent a second species (Fig. 2). As no further specimens are available, it could not be checked whether the species is cryptic or morphologically distinguishable from *B. koendersae* sp. nov. We thus leave this clade in open nomenclature.

Locality of *Spec. 15*

Ethel Creek claypan*, *east of Roy Hill Station, Pilbara, WA (sample KIES15). Approximate coordinates: 22°41'28" S, 119°58'45" E. Specimens collected by the authors on 24 Apr. 2006.

Bennelongia pinderi sp. nov.
urn:lsid:zoobank.org:act:B2630A2B-D21E-4A5E-8B15-D5E0D9C13FAF
Figs 8A–G

Abbreviated description

Valves in inner view (Fig. 8A, C) relatively elongated, with rounded dorsal margin and greatest height situated slightly in front of the middle; ventral margin anteriorly without pronounced mandibular curve. LV (Fig. 8A) with antero-distal il running over halfway along the anterior valve margin, antero-proximal il running about 4/5 way up along the anterior valve margin; posterior il tuberculate, but more delicately so than in the preceding three species, and running halfway up the posterior margin. RV (Fig. 8C) with antero-ventral lapel pronounced and rounded but with a smooth edge (Fig. 8F–G). Valves with external ornamentation mostly consisting of small tubercles, less pronounced than in the three preceding species (Fig. 8C–E).

Cp (Fig. 8C–E) with large LV/RV overlap, but less so than in the two preceding species. CpD and CpV with greatest width situated in the middle in females, anteriorly with strong and asymmetrical rostrum.

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Soft parts as typical of the genus.

Male unknown.

Etymology

The species is named after Adrian M. Pinder (DPaW, Science and Conservation Division, Kensington, WA) in recognition of his substantial contribution to our knowledge about the taxonomy and ecology of freshwater invertebrates of Australia, especially freshwater Oligochaeta.

Type material

Holotype

♀ (WAMC55620), valves stored dry in a micropalaeontological slide and soft parts used for molecular screening.

Paratypes

Numerous females from the type locality, either stored as the holotype, as carapaces used for SEM or in alcohol (WAMC55621–55623, OC3378). See Table 1 for listing of specimens.

Other material investigated

Unnamed claypan near Murchison River, Murchison, WA (sample SIKE01). Approximate coordinates: 27°50'03" S, 114°43'37" E. All material was collected by the authors on 5 Jul. 2011. K25 = 28 µS/cm, Temp = 8.3°C, pH = 5.8.

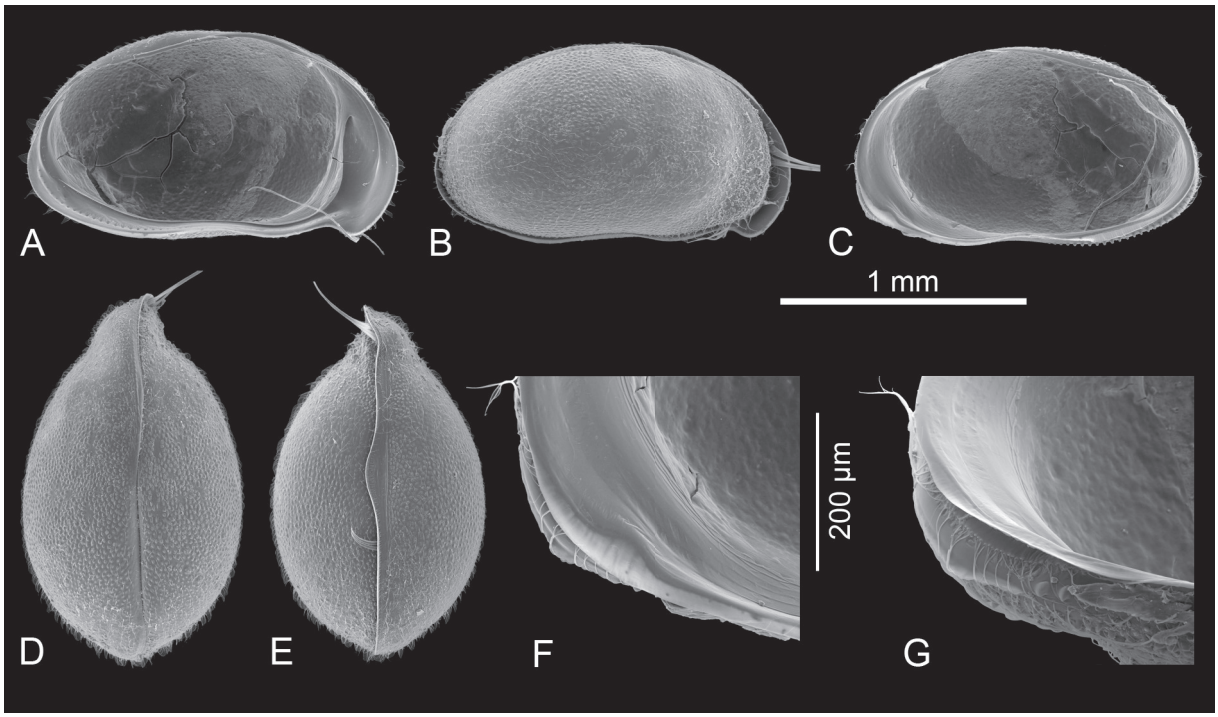

Fig. 8. *Bennelongia pinderi* sp. nov. (all ♀, all from type locality: unnamed claypan in Murchison/Gascoyne, WA). **A**. LVi (holotype, WAMC55620). **B**. CpRL (WAMC55622). **C**. RVi (WAMC55620). **D**. CpD (WAMC55621). **E**. CpV (OC3378). **F**. RVi, detail anterior margin (WAMC55620). **G**. RVi, tilted, detail anterior margin (WAMC55620). Scale = 1 mm for A–E; 200 µm for F–G.

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Roadside ditch on Euardy Station, Murchison, WA (sample SIKE05). Approximate coordinates: 27°35'31" S, 114°41'43" E. All material was collected by the authors on 5 Jul. 2011. Several females (WAMC55624–55625). K25 = 31 µS/cm, Temp = 14°C, pH = 6.7.

Type locality

AUSTRALIA: Unnamed swamp, Coolcalalaya Station, Murchison, WA (samples CB06a, SIKE 3). Approximate coordinates: 27°31'22" S, 115°04'23" E. All material collected by the authors on 5 Jul. 2011. K25 = 33 µS/cm, Temp = 13.6°C, pH = 7.8.

Measurements (all measurements in µm – see Table 1 for measurements of all specimens illustrated with SEM)

Holotype ♀ (WAMC55620): RV: L = 1395, H = 810; LV: L = 1507, H = 840.

Differential diagnosis

Bennelongia pinderi sp. nov. is most closely related to *B. koendersae* sp. nov., but is *ca*. 15–20% larger, has a less pronounced valve ornamentation and has a less-developed antero-ventral lapel with a smooth edge on the RV rather than serrated as in *B. koendersae* sp. nov.

Ecology and distribution

Bennelongia pinderi sp. nov. has thus far been found in three seasonal or ephemeral water bodies in the Murchison region of WA.

Bennelongia muggon sp. nov.
urn:lsid:zoobank.org:act:38D3B6B7-30B5-4F70-AE39-A46A3213719C
Fig. 9A–N

Bennelongia cf. *nimala* nov. sp. – De Deckker & Martens 2013: 6–7, figs 2–10.

Abbreviated description

Valves in inner view (Fig. 9A ,C) relatively high, with rounded dorsal margin and greatest height situated well in front of the middle; ventral margin anteriorly with slight mandibular curve. LV (Fig. 9A) with antero-distal il running over halfway along the anterior valve margin, antero-proximal il running less than halfway up along the anterior valve margin; posterior il running more than halfway up the posterior margin, but mostly smooth, not tuberculate. RV (Fig. 9C) with antero-ventral lapel pronounced and droplet-shaped, with delicately serrated edge (Fig. 9C, H–I, K–N). Valves with external ornamentation mostly consisting of small tubercles (Fig. 9B, D–H).

Cp (Fig. 9C–G) with strong LV/RV overlap, almost as large as in *B. tirigie* sp. nov. CpD and CpVwith greatest width situated in the middle in females, anteriorly with less pronounced, asymmetrical rostrum.

Soft parts as typical of the genus.

Male unknown.

Etymology

The species is named after its type locality, a large lake on Muggon Station, Murchison, WA.

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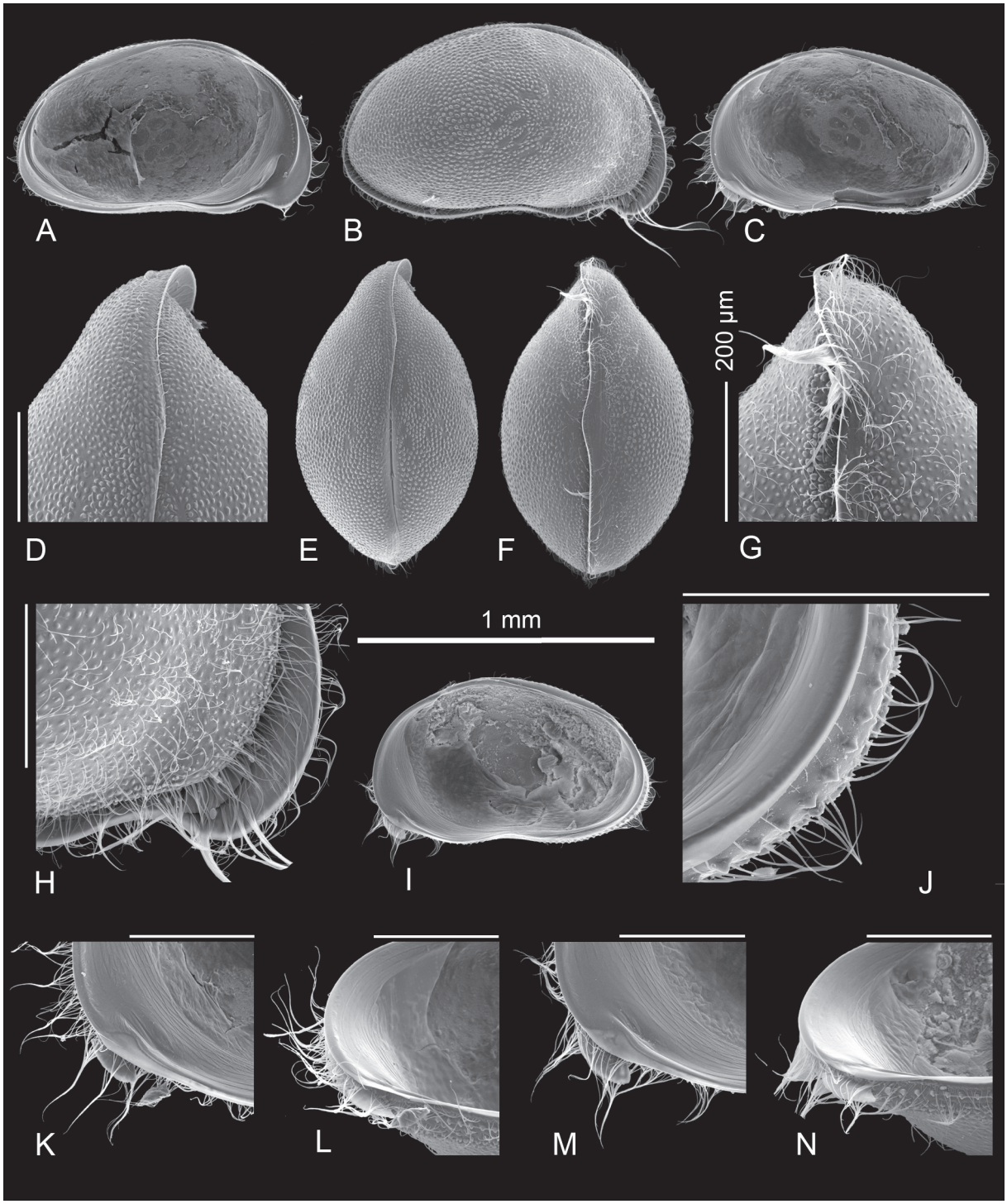

Fig. 9. *Bennelongia muggon* sp. nov. (all ♀, from type locality: Lake Muggon, Murchison/Gascoyne, WA). **A**. LVi (holotype, WAMC55632). **B**. CpRL (WAMC55635). **C**. RVi (WAMC55632). **D**. CpD, detail anterior margin (WAMC55634). **E**. CpD (WAMC55634). **F**. CpV (WAMC55636). **G**. CpV, detail anterior margin (WAMC55636). **H**. CpRL, detail anterior margin (WAMC55635). **I**. RVi (WAMC55633). **J**. RVi, detail posterior margin (WAMC55633). **K**. RVi, detail anterior margin (WAMC55632). **L**. RVi, tilted, detail anterior margin (WAMC55632). **M**. RVi, detail anterior margin (WAMC55633). **N**. RVi, tilted, detail anterior margin (WAMC55633). Scales = 1 mm for A–C, E–F, I; 200 µm for D, G–H, J–N.

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Type material

Holotype

♀ (WAMC55632), valves stored dry in a micropalaeontological slide, with soft parts used for molecular screening.

Paratypes

Numerous females from the type locality, either stored as the holotype, as carapaces used for SEM or in alcohol (WAMC55633–55645, OC3381–3383). See Table 1 for listing of specimens.

Other material investigated

Unnamed canegrass pan on Boolathana Station, Gascoyne, WA (sample SIKE 12). Approximate coordinates: 24°44'41" S, 113°43'22" E. All material collected by the authors on 6 Jul. 2011. K25 = 1020 µS/cm, pH = 8.7, Temp = 16.9°C.

Dam at Solomon's Well, Victoria Plains, WA (sample DJC/04). Approximate coordinates: 31°11'59" S, 116°21'47.7" E. All material collected by David J. Cale (DPaW, Kensington) on 9 Sep. 2011. K25 = 120 µS/cm, pH = 6.8, Temp = 14.4°C.

Petrudor Dam, Wheatbelt, WA (sample DJC/15). Approximate coordinates: 30°25'19" S, 116°57'40" E. All material collected by David J. Cale (DPaW, Kensington) on 11 Sep. 2011. K25 = 162 µS/cm, pH = 7.85, Temp = 22.0°c.

Type locality

AUSTRALIA: Unnamed large lake at Muggon Station, Murchison, WA (sample SIKE 20). Approximate coordinates: 26°44'15" S, 115°29'59" E. All material collected by the authors on 8 Jul. 2011. K25 = 475 µS/cm, pH = 8.9, Temp = 13.4°C.

Measurements (all measurements in µm – see Table 1 for measurements of all specimens illustrated with SEM)

Holotype ♀ (WAMC55632): RV: L = 1015, H = 603; LV: L = 1078, H = 638.

Differential diagnosis

This is the smallest of all species described in the present paper. *Bennelongia muggon* sp. nov. can further be distinguished from other members of the *B. nimala* lineage by the size and shape of the antero-ventral lapel on the RV, the smooth posterior il and the short anterior inner il in the LV.

Ecology and distribution

This is one of the more common species in this lineage, as it has been found in several freshwater dams and pans from the Gascoyne region south to the Wheatbelt, WA. It occurs in fresh turbid water.

Bennelongia shieli sp. nov.

urn:lsid:zoobank.org:act:3739DA56-41CC-47FA-93A6-44BBFBFFB52E

Fig. 10A–M

Abbreviated description

Valves in inner view (Fig. 10A–B, G, I) relatively high, with almost straight dorsal margin, parallel to ventral margin in RV, sloping caudally in LV; greatest height situated well in front of the middle; ventral margin anteriorly with slight mandibular curve. LV (Fig. 10A, G) with antero-distal il running almost along the entire anterior valve margin, almost connecting with ventral inner list; antero-proximal

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il reaching halfway up along the anterior valve margin; posterior il running more than halfway up the posterior margin, tuberculate for most of its length. LV with 2-3 spines halfway up the posterior margin (Fig. 10A, D, G). RV (Fig. 10B, I) with antero-ventral lapel elongated and slightly serrate, with a large tooth (Fig. 10B, I, K–M). Valves with external ornamentation mostly consisting of small tubercles (Fig. 10C–F, H). (Remark: one specimen showed a larger tooth on the antero-ventral lapel on the RV; this may be an aberrant individual).

Cp (Fig. 10E–F, H) with strong LV/RV overlap, but less so than in *B. tirigie* sp. nov., *B. koendersae* sp. nov. and *B. muggon* sp. nov. CpRL with LV forming an antero-dorsal hump over RV. CpD and CpV with greatest width situated slightly behind the middle in females, anteriorly with strongly pronounced, asymmetrical rostrum, dorsally set with parallel rows of tubercles, as in *B. nimala*.

Soft parts as typical of the genus.

Male unknown.

Etymology

The species is named after Dr Russell Shiel (University of Adelaide, Adelaide) in recognition of his substantial contribution to the taxonomy and ecology of freshwater invertebrates, especially rotifers and cladocerans, of Australia.

Type material

Holotype

♀ (WAMC55626), with soft parts dissected in a sealed slide and valves stored dry in a micropalaeontological slide.

Paratypes

Numerous females from the type locality, either stored as the holotype, as carapaces used for SEM or in alcohol (WAMC55627–55631, OC3379–3380). See Table 1 for listing of specimens.

Type locality

AUSTRALIA: Munreemya Billabong, Pilbara, WA (sample PSW036 = OSTR133). Approximate coordinates: 20°40’12” S, 120°13’33.6” E. Material collected by Adrian Pinder and Harley Barron on 19 May 2004. K25 = 194 µS/cm, pH = 8.54, Temp = 23°C.

Measurements (all measurements in µm – see Table 1 for measurements of all specimens illustrated with SEM)

Holotype ♀ (WAMC55626): RV: L = 1380, H = 807; LV: L = 1467, H = 888.

Differential diagnosis

In shape and valve ornamentation, the species differs from all others described here except *B. nimala*, which it resembles. However, *B. shieli* sp. nov. has a much wider anterior LV/RV overlap than *B. nimala* and is also about 10% smaller. In *B. nimala,* the anterodorsal inner list almost connects with the ventral list and clearly overlaps with the anteroventral inner list. In addition, the antero-ventral lapel on the RV is also different in both species.

Ecology and distribution

The species is known from its type locality only, a freshwater semi-permanent billabong in the northern Pilbara.

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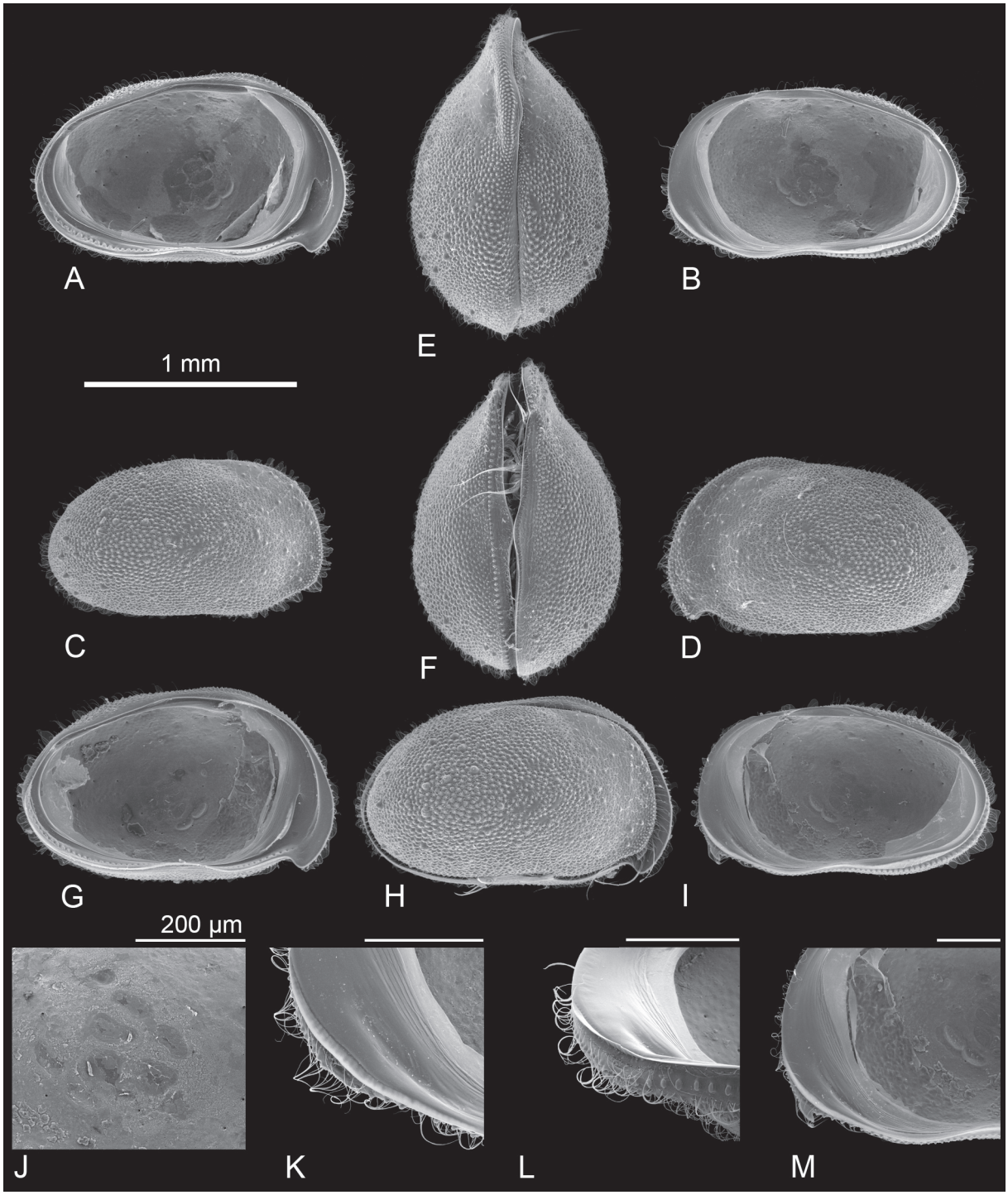

Fig. 10. *Bennelongia shieli* sp. nov. (all ♀, all from type locality: Munreemya Billabong, Pilbara, WA). **A**. LVi (holotype, WAMC55626). **B**. RVi (WAMC55626). **C**. RVe (WAMC55627). **D**. LVe WAMC55627). **E**. CpD (WAMC55628). **F**. CpV (WAMC55629). **G**. LVi (WAMC55630). **H**. CpRL (OC3379). **I**. RVi (WAMC55630). **J**. RVi, detail central muscle scars (WAMC55627). **K**. RVi, detail anterior margin (WAMC55626). **L**. RVi, tilted, detail anterior margin (WAMC55626). **M**. RVi, detail anterior margin (WAMC55630, aberrant specimen). Scales = 1 mm for A–I; 200 µm for J–M.

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Bennelongia triangulata lineage

Diagnosis of the *B. triangulata* lineage

Large (L > 2 mm) and triangular species, with ventral margins nearly smooth, without an antero-ventral beak on the LV. Anterior LV/RV overlap moderate. CpD and CpV without pronounced anterior rostrum. Last 3 juvenile stages with fully flat ventral side, not so in adults.

Remarks

De Deckker & Martens (2013) described the morphology of the last 3 instar juveniles of *B. triangulata* sp. nov. (as *B.* sp. 414) and found that they have, unlike juveniles of any other *Benelongia* species, a fully flat ventral side. This feature is an important part of the diagnosis of the lineage.

This lineage and species are atypical for *Bennelongia*, in that some of the obvious features, such as the long beak in the *B. australis* lineage or the large LV/RV overlap in the *B. nimala* lineage, are missing. Nevertheless, the structure of the valve margins of both valves is most similar to the other species in the genus, and also the soft parts, apart from being slightly more elongated, show no structural differences. We thus maintain this species in *Bennelongia*.

Bennelongia triangulata sp. nov.
urn:lsid:zoobank.org:act:2EE84F9D-40BD-4866-9E42-5B6815D95E1A
Figs 11A–M, 12A–M, 13A–G

Bennelongia sp. nov. 414 – Halse *et al.* 2000: table 4, appendix 4.
Bennelongia n. sp. 414 – Pinder *et al.* 2010: appendix 2.
Bennelongia sp. 414 nov. sp. – De Deckker & Martens 2013: 7–8, figs 11–12.

Abbreviated description

Valves in inner view (Figs 11A, C, H, J; 12A, C, H, J) subtriangular, with greatest height situated either in the middle or just before the middle; ventral margin almost straight, with weak mandibular curve. LV (Figs 11A, H; 12A, H) with antero-distal il running only halfway along the anterior valve margin, antero-proximal il running slightly beyond halfway up along the valve margin, this list dorsally strongly S-shaped; posterior il smooth, not tuberculate, and running only along ventral margin. RV (Figs 11C, J; 12C, J) with antero-ventral lapel a very narrow ridge, but valve margin protruding beyond selvage as in the *Bennelongia pinpi* lineage (Figs 11C, I–M; 12C–D, G, I–J, L–M). Valves with delicate external ornamentation, consisting of small tubercles (Figs 11D, G, L; 12G, I, M).

Cp (Fig. 11B, D–G, L) with moderate LV/RV overlap. CpD and CpV with greatest width situated in the middle in both males and females (Figs 11E–F; 12E–F), without anterior rostrum.

Soft parts as typical of the genus, but generally more elongated than in the other species of *Bennelongia*. Hemipenes (Fig. 13A, E) symmetrical, edge of ms almost straight, ls with ventral extremity strongly pointed. Lpp (Fig. 13B, F) with distal segment narrow, tapering towards the point and rather long (the specimen in Fig. 13C is an exception). Rpp (Fig. 13D, G) with distal segment narrowly subtriangular, with apical margin straight, sensory organs on first segment unequal, one long, one short.

Etymology

The species is named after its most striking character, the triangular shape of the valves in lateral view.

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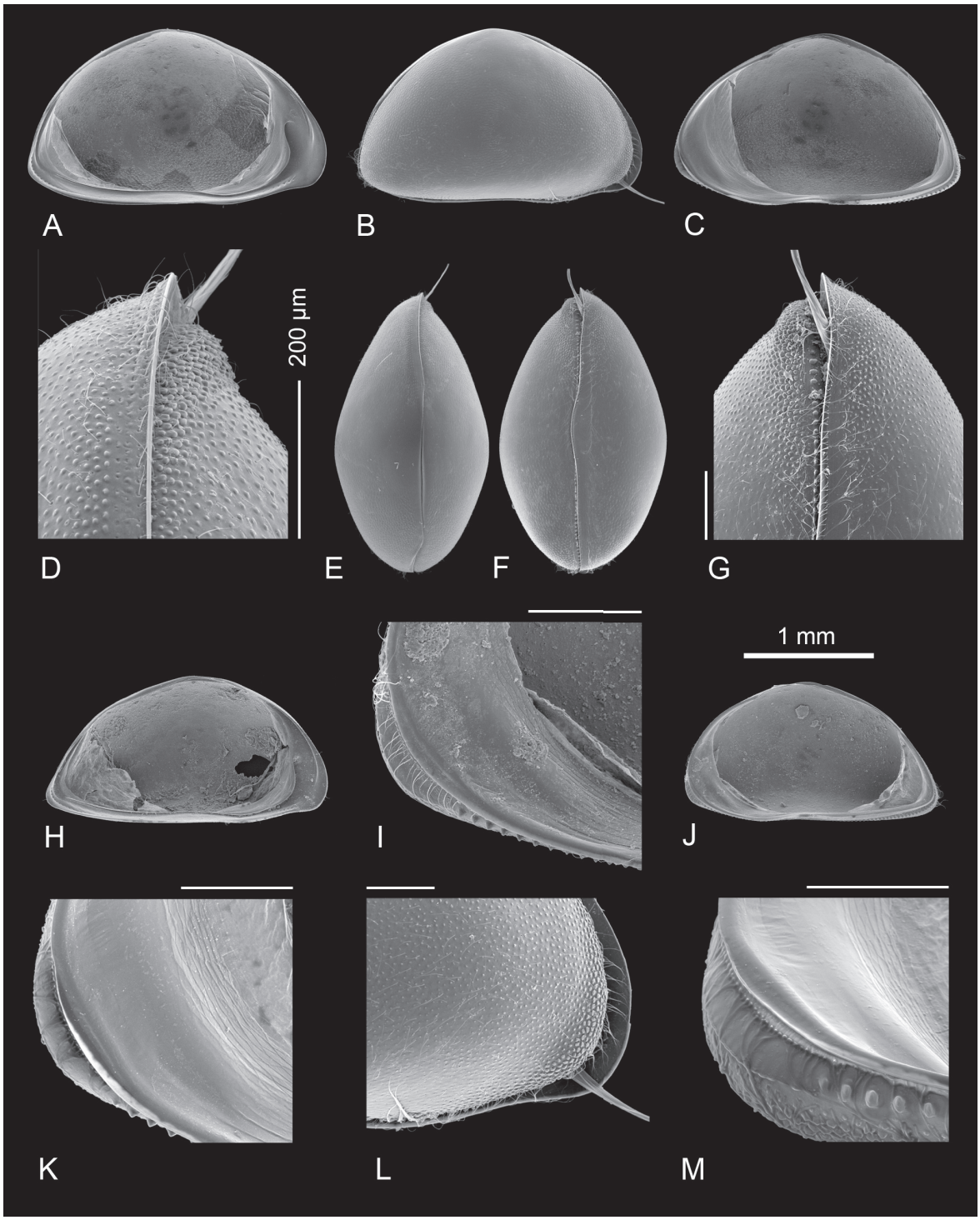

Fig. 11. *Bennelongia triangulata* sp. nov. (all ♀, A–G & K–M from type locality: canegrass pan on Wooramel Station, Murchison/Gascoyne, WA; H–J from CB54, Boolathana Station, Carnarvon Basin, WA). **A**. LVi (allotype, WAMC55565). **B**. CpRL (OC3368). **C**. RVi (WAMC55565). **D**. CpD, detail anterior margin (WAMC55569). **E**. CpD (WAMC55569). **F**. CpV (WAMC55570). **G**. CpV, detail anterior margin (WAMC55570). **H**. LVi (OC3370). **I**. LVi, detail posterior margin (OC3370). **J**. RVi (OC3370). **K**. RVi, detail anterior margin (WAMC55565). **L**. CpRL, detail anterior margin (OC3368). **M**. RVi, tilted, detail anterior margin (WAMC55565). Scales = 1 mm for A–C, E–F, H, J; 200 µm for D, G, I, K–M.

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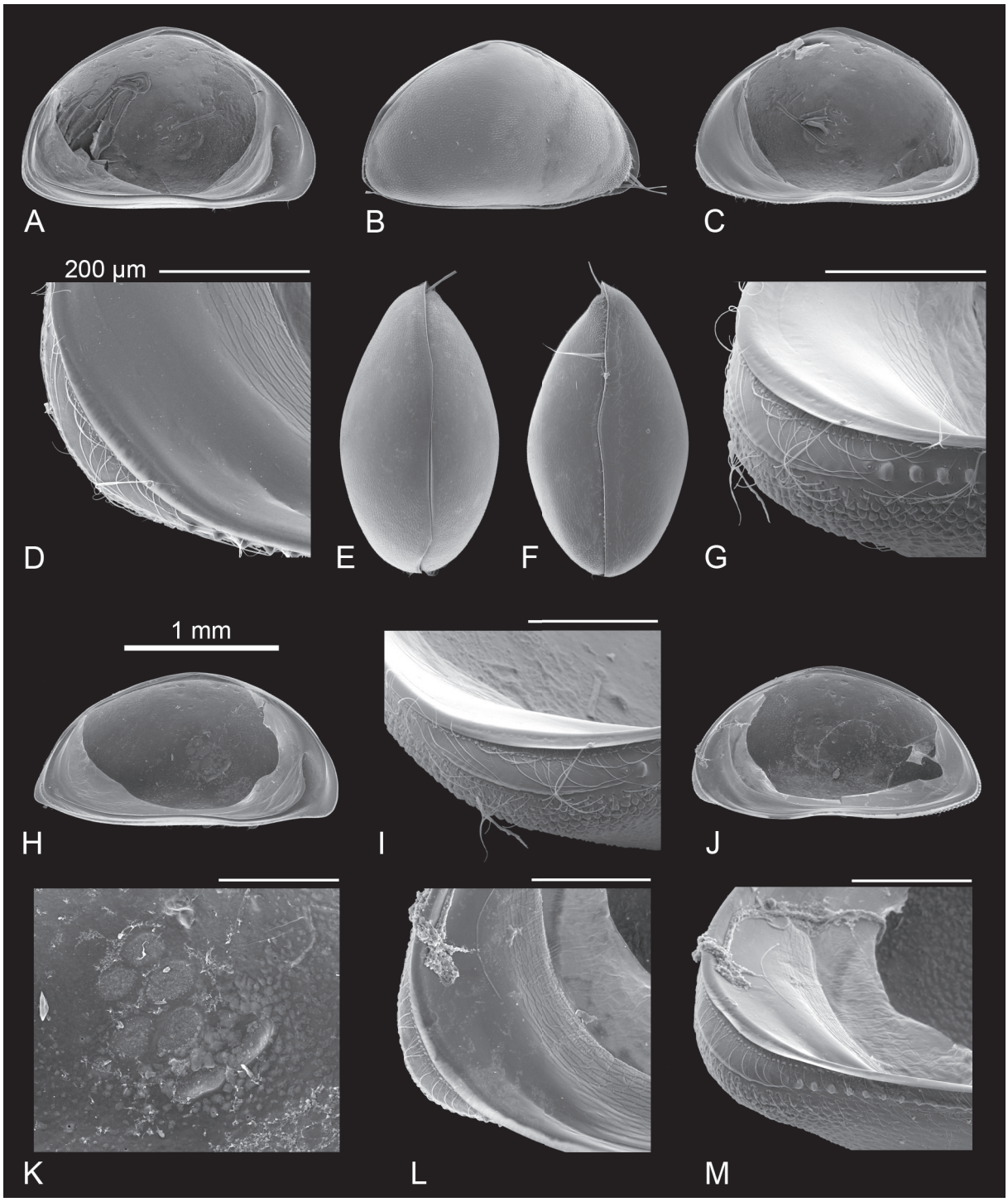

Fig. 12. *Bennelongia triangulata* sp. nov. (all ♂, A–G from type locality: canegrass pan on Wooramel Station, Murchison/Gascoyne, WA; H–M from CB54, Boolathana Station, Carnarvon Basin, WA). **A**. LVi (holotype, WAMC55564). **B**. CpRL (OC3369). **C**. RVi (WAMC55564). **D**. RVi, detail anterior margin (WAMC55564). **E**. CpD (WAMC55571). **F**. CpV (WAMC55572). **G**. RVi, tilted, detail anterior margin (WAMC55564). **H**. LVi (WAMC55574). **I**. RVi, tilted, detail anterior margin (WAMC55564). **J**. RVi (WAMC55574). **K**. LVi, detail central muscle scars (WAMC55574). **L**. RVi, detail anterior margin (WAMC55574). **M**. RVi, tilted, detail anterior margin (WAMC55574). Scale = 1 mm for A–C, E–F, H, J; 200 µm for D, G, I, K–M.

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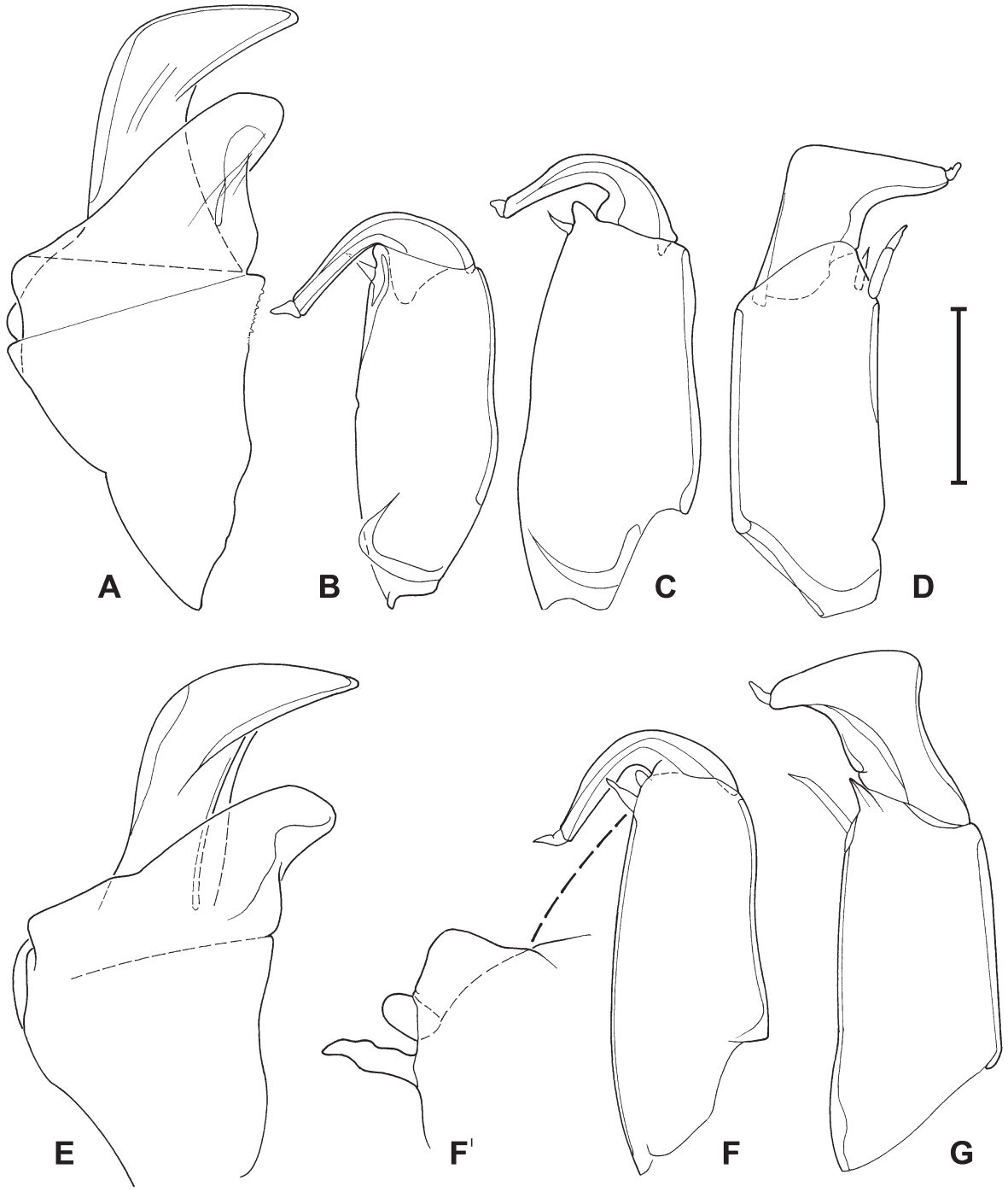

Fig. 13. *Bennelongia triangulata* sp. nov. (all ♂, A–D from CB75a, Cattle Camp Pan, Gascoyne, WA; E–G holotype (WAMC55564): cane grass pan on Wooramel Station, Murchison/Gascoyne, WA). **A**. Outline of hemipenis (WAMC55584). **B**. Lpp (WAMC55584). **C**. Lpp (WAMC55575). **D**. Rpp (WAMC55584). **E**. Outline of hemipenis. **F**. Lpp. **F'**. Lpp, detail of distal part of first segment. **G**. Rpp. Scale = 156 µm for A, E; 73 µm for B–D, F–G.

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Type material

Holotype

♂ (WAMC55564), with soft parts dissected in a sealed slide and valves stored dry in a micropalaeontological slide.

Allotype

♀ (WAMC55565), with valves stored dry in a micropalaeontological slide and soft parts used for molecular screening.

Paratypes

Numerous ♂♂ and ♀♀ from the type locality, either dissected and stored as the holotype, as carapaces used for SEM or in alcohol (WAMC55566–55573, OC3367–3369). See Table 1 for listing of specimens.

Other material investigated

Unnamed claypan, Gascoyne, WA (sample SIKE11). Approximate coordinates: 24°47'49" S, 114°15'42" E. All material collected by the authors on 6 Jul. 2011. Several males and females (specimens WAMC55576–55577). K25 = 434 µS/cm, Temp = 15.4°C, pH = 7.6.

Unnamed claypan, ***Muggon Station,*** Murchison, WA (sample SIKE21). Approximate coordinates: 26°46'54" S, 115°40'53" E. All material collected by the authors on 8 Jul. 2011. Several males and females (specimens WAMC55578–55583). K25 = 154 µS/cm, Temp = 13.3°C, pH = 8.0.

Homestead dam, Boolathana Station, Gascoyne, WA (sample ESKI/01). Approximate coordinates: 24°39'15" S, 113°41'37" E. All material collected by the authors on 5 Apr. 2013. Several females (specimens WAMC55584).

Unnamed canegrass pan, Wooramel Stn, Gascoyne, WA (sample CB35a). Approximate coordinates: 25°40'52" S, 114°13'14" E. Material collected by Stuart Halse on 24 Aug. 1994 (specimen OS256).

Near Cardabia Swamp, Gascoyne, WA (sample CB54). Approximate coordinates: 24°33'10" S, 113°45'35" E. Material collected by Stuart Halse on 18 Mar. 1995 (specimen OC3370).

Unnamed claypan, Doorawarrah Stn, Gascoyne, WA (sample CB58b). Approximate coordinates: 24°48'8" S, 114°16'15" E. Material collected by Stuart Halse on 23 Aug. 1994 (specimen WAMC55574).

Boolan Pool, Gascoyne, WA (sample CB73). Approximate coordinates: 24°28'38" S, 113°40'36" E. All material collected by Stuart Halse on 18 Aug. 1994 (specimens OS121, OS391).

Cattle Camp Pan, Gascoyne, WA (sample CB75a). Approximate coordinates: 24°28'25" S, 114°13'27" E. Material collected by Stuart Halse on 19 Aug. 1994 (specimen WAMC55575).

Nicabay Flats, Gascoyne, WA. Approximate coordinates: 24°52'7" S, 113°43'3" E. Material collected by Stuart Halse on 15 Aug. 1995 (specimen OS258).

Type locality

AUSTRALIA: Unnamed canegrass pan on Wooramel Station, Gascoyne, WA (samples CB35a and SIKE07). Approximate coordinates: 25°40'53" S, 114°13'17" E. All material collected by the authors on 5 Jul. 2011. K25 = 307 µS/cm, Temp = 15.5°C, pH = 7.4.

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Measurements (all measurements in µm – see Table 1 for measurements of all specimens illustrated with SEM)

Holotype ♂ (WAMC55564): RV: L = 1850, H = 1158; LV: L = 1923, H = 1188.
Allotype ♀ (WAMC55565): RV: L = 2192, H = 1308; LV: L = 2286, H = 1350.

Differential diagnosis

This species is unlike any other species in the genus, because of the features cited in the diagnosis to the *B. triangulata* lineage, especially the large size, triangular shape and lack of an antero-ventral beak on the LV.

Remark

The species comes in two forms, one with valves high (Figs 11A–C; 12A–C) and one with valves more elongated (Figs 11H, J; 12H, J). In the soft parts, both forms are almost identical, with the exception of the shape of the second segment of the Rpp. In the high form, this segment is subtriangular, with both dorsal and distal margins straight (Fig. 13D). In the more elongated form, this segment has a straight distal, but more sinuous dorsal margin (Fig. 13G).

Morphology, ecology and distribution

Bennelongia triangulata sp. nov. is common in the Murchison region north to the southern Pilbara region of WA and occurs in turbid claypans. As outlined above, the valve shape can be quite different (either rather high, or quite elongated), and originally it was thought that these two forms were either seasonally determined or constituted two species.

New sampling and screening of older collections showed that both forms occur in both summer and winter. Laboratory cultures reared at different temperatures, day length etc. may show which, if any, aspects of the environment may affect valve shape in this species. Males with different valve shape have slightly different morphologies in the Rpp, but as this could be part of a normal range of variability, its occurrence should be checked on longer series of dissections. *Bennelongia timmsi* Martens *et al.*, 2013 also showed significant variability in the shape of the Rpp (Martens *et al.* 2013).

Sadly, all specimens with elongated valves originated from old collections, on which no molecular work could be done. In spite of several attempts, we have not been able to collect fresh material of the elongated form. Future work will have to examine whether genetic data suggest that the two forms are different species. For the moment we retain both forms as being conspecific.

Discussion

***B. nimala* lineage**

The *Bennelongia nimala* lineage presently consists of seven species, which are united by the presence of heavily calcified and heavily ornamented adult valves. Valve ornamentation consists of large pustules, spines and short and stiff setae. It is in the *B. nimala* lineage that the heavily ornamented valves of the juveniles of the last instars of most *Bennelongia* species, as described by De Deckker & Martens (2013), are strongly retained in the adults. With regard to these features, the species in this lineage show the most retarded heterochronic development. However, in other features, for example the strongly developed anterior LV/RV overlap, the species show the most derived valve characters.

Two species of the *B. nimala* lineage (*B. pinderi* sp. nov. and *B. muggon* sp. nov.) have an eyelet in the anteroventral part of the RV, much as in the *B. barangaroo* lineage (see Martens *et al.* 2013), indicating that these lineages are more closely related to one another than the valve morphology might indicate at first glance. Species of the *B. barangaroo* lineage have valves that are much smoother and only weakly pitted, although they can in some species be quite hirsute. As is usual in ostracods (Tsukagoshi 1988;

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Martens *et al.* 2004), morphology of the different lineages of *Bennelongia* shows a mixture of different heterochronic processes.

As in the other lineages of *Bennelongia* (Martens *et al.* 2012, 2013; Shearn *et al.* 2012), the antero-ventral lapel on the RV proved to be a species-specific feature, allowing distinction between species in the lineage and genus. In the *B. nimala* lineage, the lapel is most strongly developed in *B. nimala*, where it has the appearance of a toothed comb, and weakest in *B. pinderi* sp. nov., where it is a small smooth ridge. *Bennelongia muggon* sp. nov. has a pronounced triangular lapel, reminiscent of some of the species in the *B. barangaroo* lineage (*B. timmsi*, *B. scanloni*).

The *B. nimala* lineage occurs in the NT (the nominal *B. nimala*) as well as in the western part of WA, between Pilbara and Perth. Additional information about the frequency of occurrence of the lineage (though not individual species) is available from Pinder *et al.* (2010). No representatives of the lineage have been found to date in Kimberley or south of Perth. One would expect the lineage to occur in Kimberley to bridge the gap between the occurrence of *B. nimala* in the NT and *B. koendersae* sp. nov. and *B. shieli* sp. nov. in the Pilbara, but thus far the only *Bennelongia* species known from Kimberley is *B. kimberleyensis* within the *B. australis* lineage (Martens *et al.* 2012).

In line with earlier findings in other *Bennelongia* lineages, most species of the *B. nimal*a lineage have restricted distributions, with *B. nimala* being known only from the NT, *B. koendersae* sp. nov. and *B. shieli* sp. nov. being restricted to Pilbara and *B. pinderi* sp. nov. occurring only in the Murchison region. In contrast, *Bennelongia muggon* sp. nov. is widespread, being recorded from Carnarvon to south of Perth, a distance of 800 km. *Bennelongia tirigie* sp. nov. appears to be even more widespread, with most records being from north of Carnarvon in the Gascoyne region and an outlying population occurring at Crackers' Swamp about 1000 km to the south. In addition to this surprising disjunct distribution, there are also ecological differences with northern localities all being turbid water claypans, while Crackers' Swamp is a clear-water body. Nevertheless, the specimens of all localities, including from Crackers' Swamp, cluster tightly together in the COI-tree and have a very similar morphology, so conspecificity cannot be doubted at this stage.

The results for genetic species boundaries of the *B. nimala* lineage match the morphological species descriptions. With the possible exception of the enigmatic "species 15" from Pilbara, the morphology of which remains unknown, no cryptic species were discovered with molecular methods in this lineage.

***B. triangulata* sp. nov.**

Bennelongia triangulata sp. nov. is an aberrant species in the genus, as its triangular shape is different from all other congeneric species. The morphology of the latest instar juveniles is even more different, with a ventral side that is completely flattened (De Deckker & Martens 2013). Nevertheless, marginal valve structures are typical of the genus and the soft parts are very similar to those of other *Bennelongia* species, albeit slightly more elongated. Accordingly, we have decided to maintain this species within the genus *Bennelongia*, despite its different habitus.

This species is common in the turbid clay pans of Murchison, Gascoyne and coastal southern Pilbara with a latitudinal range of approximately 550 km. More information on the species range and habitat preferences is available from the collecting records in Halse *et al.* (2000) and Pinder *et al.* (2010).

Bennelongia triangulata sp. nov. can occur in highly arched and more elongated forms (see Figs 11–12) and both forms have been found in both warmer and colder seasons. In addition, male soft parts (hemipenes, prehensile palps) are similar in both forms. Rpp (Fig. 13D, G) appear to have a different morphology according to valve shape, but intermediate shapes of the distal segment have been found in

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Table 3. Species presently described in *Bennelongia*, their lineage and their distribution (species in bold are newly described here). Only certain distributions, based on type localities and documented range extensions, are given here. * indicates the type species.

1. **Bennelongia harpago* De Deckker & McKenzie, 1981: QLD
2. *Bennelongia tunta* De Deckker, 1982: QLD

***B. australis* lineage**

3. *Bennelongia australis* (Brady, 1886): SA (uncertain species)
4. *Bennelongia bidgelangensis* Martens *et al*., 2012: WA, Gascoyne
5. *Bennelongia coondinerensis* Martens *et al*., 2012: WA, Pilbara
6. *Bennelongia cuensis* Martens *et al*., 2012: WA, Yilgarn
7. *Bennelongia gwelupensis* Martens *et al*., 2012: WA, Perth, southwest coast
8. *Bennelongia lata* Martens *et al*., 2012: WA, Gascoyne-Murchinson region

***B. barangaroo* lineage**

9. *Bennelongia barangaroo* De Deckker, 1981: WA
10. *Bennelongia calei* Martens *et al*., 2013: WA
11. *Bennelongia dedeckkeri* Shearn *et al*., 2012: QLD, WA
12. *Bennelongia gnamma* Martens *et al*., 2013: WA
13. *Bennelongia hirsuta* Martens *et al*., 2013: WA
14. *Bennelongia ivanae* Martens *et al*., 2013: WA
15. *Bennelongia mckenziei* Shearn *et al*., 2012: QLD
16. *Bennelongia mcraeae* Martens *et al*., 2013: WA
17. *Bennelongia scanloni* Martens *et al*., 2013: WA
18. *Bennelongia timmsi* Martens *et al*., 2013: WA

***B. cygnus* lineage**

19. *Bennelongia cygnus* Martens *et al*., 2012: WA, Swan Valley
20. *Bennelongia frumenta* Martens *et al*., 2012: WA, Wheatbelt

***B. nimala* lineage**

21. *Bennelongia koendersae* sp. nov.: WA
22. *Bennelongia muggon* sp. nov.: WA
23. *Bennelongia nimala* De Deckker, 1981: NT
24. *Bennelongia pinderi* sp. nov.: WA
25. *Bennelongia regina* Shearn *et al*., 2012: QLD
26. *Bennelongia shieli* sp. nov.: WA
27. *Bennelongia tirigie* sp. nov.: WA

***B. pinpi* lineage**

28. *Bennelongia kimberleyensis* Martens *et al*., 2012: WA, Kimberley
29. *Bennelongia pinpi* De Deckker, 1981: QLD
30. *Bennelongia strellyensis* Martens *et al*., 2012: WA, Pilbara

***B. triangulata* lineage**

31. *Bennelongia triangulata* sp. nov.: WA

some specimens, so that the observed differences may be artefacts of the dissected limb's position on a slide. Unfortunately, only older material of the elongated forms was available so that molecular data cannot be compared for the two morphological forms. From the network in Fig. 3 it can be seen that *B. triangulata* sp. nov. is genetically highly variable, but there are no indications of the existence of cryptic species, as all haplotypes remain connected.

With the six new species described here, the genus *Bennelongia* now comprises 31 nominal species, divided over at least 7 lineages (Table 3), but several new species still await description.

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References

Altschul S.F., Gish W., Miller W., Myers E.W. & Lipman D.J. 1990. Basic local alignment search tool. *Journal of Molecular Biology* 215: 403–410. http://dx.doi.org/10.1016/S0022-2836(05)80360-2

Birky C.W. Jr. 2013. Species detection and identification in sexual organisms using population genetic theory and DNA sequences. *PLoS ONE* 8: e52544. http://dx.doi.org/10.1371/journal.pone.0052544

Birky C.W. Jr. & Barraclough T.G. 2009. Asexual speciation. *In*: Schön I., Martens K. & van Dijk P. (eds) *Lost sex*: 201–216. Springer Scientific Publishers, Dordrecht.

Birky C.W. Jr., Adams J., Gemmel M. & Perry J. 2010. Using population genetic theory and DNA sequences for species detection and identification in asexual organisms. *PLoS ONE* 5: e10609. http://dx.doi.org/10.1371/journal.pone.0010609

Birky Jr. C.W., Ricci C., Melone G. & Fontaneto D. 2011. Integrating DNA and morphological taxonomy to describe diversity in poorly studied microscopic animals: new species of the genus *Abrochtha* Bryce, 1910 (Rotifera: Bdelloidea: Philodinavidae). *Zoological Journal of the Linnean Society* 161: 723–734. http://dx.doi.org/10.1111/j.1096-3642.2010.00674.x

Bode S.N.S., Lamatsch D.K., Martins M.J.F., Schmit O., Vandekerkhove J., Mezquita F., Namiotko T., Rossetti G., Schön I., Butlin R.K. & Martens K. 2010. Exceptional cryptic diversity and multiple origins of parthenogenesis in a freshwater ostracod. *Molecular Phylogeny and Evolution* 54: 542–552. http://dx.doi.org/10.1016/j.ympev.2009.08.022

Broodbakker N.W. & Danielopol D.L. 1982. The chaetotaxy of Cypridacea (Crustacea, Ostracoda) limbs: proposals for a descriptive model. *Bijdragen tot de Dierkunde* 52: 103–120.

Clement M., Posada D. & Crandall K. 2000. TCS: a computer program to estimate gene genealogies. *Molecular Ecology*, 9: 1657–1660. http://dx.doi.org/10.1046/j.1365-294x.2000.01020.x

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Darriba D., Taboada G.L., Doallo R. & Posada D. 2012. jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9: 772. http://dx.doi.org/10.1038/nmeth.2109

De Deckker P. 1981. Taxonomy and ecological notes of some ostracods from Australian inland waters. *Transactions of the Royal Society of South Australia* 105: 91–138.

De Deckker P. 1982. On *Bennelongia tunta* De Deckker sp. nov. *A Stereo-Atlas of Ostracod Shells* 9: 117–124.

De Deckker P. & McKenzie K.G. 1981. *Bennelongia*, a new cyprididid ostracod genus from Australasia. *Transactions of the Royal Society of South Australia* 105: 53–58.

De Deckker P. & Martens K. 2013. Extraordinary morphological changes in valve morphology during the ontogeny of several species of the Australian ostracod genus *Bennelongia* (Crustacea, Ostracoda). *European Journal of Taxonomy* 36: 1–37. http://dx.doi.org/10.5852/ejt.2013.36

Folmer O., Black M., Hoeh W., Lutz R. & Vrijenhoek R. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3: 294–299.

Fontaneto D., Herniou E.A., Boschetti C., Caprioli M., Melone G., Ricci C. & Barraclough T. 2007. Independently evolving species in asexual bdelloid rotifers. *PLoS Biology* 5: e87. http://dx.doi.org/10.1371/journal.pbio.0050087

Fontaneto D., Kaya M., Herniou E.A. & Barraclough T.G. 2009. Extreme levels of hidden diversity in microscopic animals (Rotifera) revealed by DNA taxonomy. *Molecular Phylogenetics and Evolution* 53: 182–189. http://dx.doi.org/10.1016/j.ympev.2009.04.011

Guindon S. & Gascuel O. 2003. PhyML – a simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Systematic Biology* 52: 696–704. http://dx.doi.org/10.1080/10635150390235520

Hall T. 2007. BioEdit: Biological sequence alignment editor for Win95/98/NT/2K/XP [Online]. Website last modified on 27 June 2007 (accessed on 13 September, 2011). Available at http://www.mbio.ncsu.edu/BioEdit/bioedit.html

Halse S.A., Shiel R.J., Storey A.W., Edward D.H.D., Lansbury I., Cale D.J., & Harvey M.S. 2000. Aquatic invertebrates and waterbirds of wetlands and rivers of the southern Carnarvon Basin, Western Australia. *Records of the Western Australian Museum, Supplement* 61: 217–267.

Halse S.A. 2002. Diversity of Ostracoda (Crustacea) in inland waters of Western Australia. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie* 28: 914–918.

Horne D.J., Cohen A. & Martens K. 2002. Taxonomy, morphology and biology of Quaternary and living Ostracoda. *In*: Holmes J.A. & Chivas A.R. (eds) *The Ostracoda: Application in Quaternary Research.* Geophysical Monograph 131: 5–36. American Geophysical Union, Washington, DC.

Larkin M.A., Blackshields G., Brown N.P., Chenna R., McGettigan P.A., McWilliam H., Valentin F., Wallace I.M., Wilm A., Lopez R., Thompson J.D., Gibson T.J. & Higgins D.G. 2007. Clustal W and Clustal X version 2.0. *Bioinformatics* 23: 2947–2948. http://dx.doi.org/10.1093/bioinformatics/btm404

Martens K. 1987. Homology and functional morphology of the sexual dimorphism in the antenna of *Sclerocypris* Sars, 1924 (Crustacea, Ostracoda, Megalocypridinae). *Bijdragen tot de Dierkunde* 57: 183–190.

Martens K., Rossetti G. & De Deckker P. 2004. On a new terrestrial genus and species of Scottiinae (Crustacea, Ostracoda) from Australia, with a discussion on the phylogeny and the zoogeography of the subfamily. *Zoologischer Anzeiger* 243: 21–36. http://dx.doi.org/10.1016/j.jcz.2004.05.001

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Martens K., Halse S. & Schön I. 2012. Nine new species of *Bennelongia* De Deckker & McKenzie, 1981 (Crustacea, Ostracoda) from Western Australia, with the description of a new subfamily. *European Journal of Taxonomy* 8: 1–56. http://dx.doi.org/10.5852/ejt.2012.8

Martens K., Halse S.A. & Schön I. 2013. On the *Bennelongia barangaroo* lineage (Crustacea, Ostracoda) in Western Australia, with the description of seven new species. *European Journal of Taxonomy* 66: 1–59. http://dx.doi.org/10.5852/ejt.2013.66

Pinder A.M., Halse S.A., Shiel R.J., & McRae J.M. 2010. An arid zone awash with diversity: patterns in the distribution of aquatic invertebrates in the Pilbara region of Western Australia. *Records of the Western Australia Museum, Supplement* 78: 205–246.

Ronquist F., Teslenko M., van der Mark P., Ayres D., Darling A., Hohna S., Larget B., Liu L., Suchard M.A. & Huelsenbeck J.P. 2011. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542. http://dx.doi.org/10.1093/sysbio/sys029

Schön I., Pinto R.L., Halse S.A., Smith A.J., Martens K. & Birky C.W. Jr. 2012. Cryptic species in putative ancient asexual darwinulids (Crustacea, Ostracoda). *PLOS One* 7: e39844. http://dx.doi.org/10.1371/journal.pone.0039844

Shearn R., Koenders A., Halse S., Schön I. & Martens K. 2012. A review of *Bennelongia* De Deckker & McKenzie, 1981 (Crustacea, Ostracoda) species from eastern Australia, with the description of three new species. *European Journal of Taxonomy* 25: 1–35. http://dx.doi.org/10.5852/ejt.2012.25

Tamura K., Stecher G., Peterson D., Filipski A. & Kumar A. 2013. MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. *Molecular Biology and Evolution* 30: 2725–2729. http://dx.doi.org/10.1093/molbev/mst197

Tsukagoshi A. 1988. Reproductive character displacement in the ostracod genus *Cythere*. *Journal of Crustacean Biology* 8: 563–575. http://dx.doi.org/10.2307/1548693

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