European Journal of Taxonomy 66: 1-59
http://dx.doi.org/10.5852/ejt.2013.66
ISSN 2118-9773
www.europeanjournaloftaxonomy.eu
2013 · Martens K., Halse S. & Schön I.

Monograph

urn:lsid:zoobank.org:pub:5270B024-84C1-4CD5-BC18-4AF37D2E1045

On the *Bennelongia barangaroo* lineage (Crustacea, Ostracoda) in Western Australia, with the description of seven new species

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[7] urn:lsid:zoobank.org:author:94232F10-7092-4E90-9071-64C4FDABE691

Abstract. The ostracod genus *Bennelongia* De Deckker & McKenzie, 1981 is endemic to Australia and New Zealand. Extensive sampling in Western Australia (WA) revealed a high specific and largely undescribed diversity. Here, we describe seven new species belonging to the *B. barangaroo* lineage: *B. timmsi* sp. nov., *B. gnamma* sp. nov., *B. hirsuta* sp. nov., *B. ivanae* sp. nov., *B. mcraeae* sp. nov., *B. scanloni* sp. nov. and *B. calei* sp. nov., and confirm the presence of an additional species, *B. dedeckkeri*, in WA. For five of these eight species, we could construct molecular phylogenies and parsimonious networks based on COI sequences. We also tested for cryptic diversity and specific status of clusters with a statistical method based on the evolutionary genetic species concept, namely Birky's 4 theta rule. The analyses support the existence of these five species and a further three cryptic species in the WA *B. barangaroo* lineage. The molecular evidence was particularly relevant because most species described herein have very similar morphologies and can be distinguished from each other only by the shape, size and position of the antero-ventral lapel on the right valve, and, in sexual populations, by the small differences in shape of the hemipenes and the prehensile palps in males. Four species of the WA *B. barangaroo* lineage occur in small temporary rock pools (gnammas) on rocky outcrops. The other four species are mainly found in soft bottomed seasonal water bodies. One of the latter species, *B. scanloni* sp. nov., occurs in both claypans and deeper rock pools (pit gnammas). All species, except for *B. dedeckkeri*, originally described from Queensland, have quite clearly delimited distributions in WA. With the seven new species described here, the genus *Bennelongia* now comprises 25 nominal species but several more await formal description.

Keywords. Taxonomy, evolution, cryptic species, biodiversity, Western Australia.

Martens K., Halse S. & 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

Introduction

The ostracod genus *Bennelongia* is endemic to Australia and New Zealand. Extensive sampling in Western Australia (WA) revealed a high specific and largely undescribed diversity of *Bennelongia* (Halse 2002), leading to the taxonomic research reported here. The present paper is the fourth in a recent series of taxonomic contributions on Australian *Bennelongia*. Martens *et al.* (2012) described nine new species in three different lineages within the genus, all based on collections from WA. Shearn *et al.* (2012) re-described several extant species and described three new species, all from Eastern Australia (mostly from Queensland). In addition, De Deckker & Martens (2013) described the unusually strong morphological changes in valve morphology during the last 3-4 ontogenetic stages in several *Bennelongia*-species, and showed that these changes can be different between the various lineages within the genus. The first two papers, together with the earlier work by De Deckker (1981a,b, 1982) and De Deckker & McKenzie (1981), brought the number of nominal species in the genus to 18, but both recent papers also recognised that some additional cryptic species exist, as determined by molecular methods.

Here, we describe seven new species of *Bennelongia* from WA and report on the occurrence of an additional described species in WA, namely *B. dedeckkeri* Shearn *et al.*, 2012. All of these eight species belong to the *B. barangaroo* lineage within the genus and for five of the species, their specific status is confirmed with molecular methods. Two of the new nominal species furthermore comprise several, sometimes sympatric, cryptic species that could not be recognised using either valve or soft part morphologies.

Material and methods

Collections

Ostracods were collected from pans, lakes and rock pools with a hand net with mesh size of 250 μm during several field trips (see below). Material for morphological analyses originated from both these 'new' collections and from earlier collections from all over WA, mostly collected by SH and preserved in a collection housed at the Department of Environment and Conservation, now DPaW (Woodvale, 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 five of the eight species (four of the seven new ones). 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, WA (WAM 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. Drawings of soft parts were made with a *camera lucida* with a compound microscope (Leica, DM 2500 at Bennelongia Environmental Consultants, Perth). Valves were illustrated and measured using scanning electron microscopy (Philips XL30 SEM at RBINS, Brussels).

Molecular analysis

The Qiagen Blood and Tissue extraction kit was used following the manufacturer's protocol to extract DNA from 99 ostracods representing four nominal and 2 cryptic species of the *Bennelongia barangaroo* lineage. Universal PCR primers (Folmer *et al.* 1994) were applied to amplify part of the mitochondrial COI region in a T personal Thermoblock (Biometra) with the following conditions: 25 μl volumes of the HotStar Master Mix (Qiagen; 1.5 mM $MgCl_2$, 0.1 μM primer, 200μM dNTP, Tris·Cl, KCl, $(NH_4)_2SO_4$, 1.25 U Taq) and 15 min at 95°C, 40 cycles of 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. Agarose gel electrophoresis and staining of gels with Gelred™ was carried out to check for successful PCR amplifications. PCR products were cleaned with the GFX™ PCR DNA and gel band purification kit (GE Healthcare) according to the manufacturer's protocol and sequenced in both directions with the universal COI primers and the Big Dye kit (ABI) on an ABI 3130X following the manufacturer's protocol.

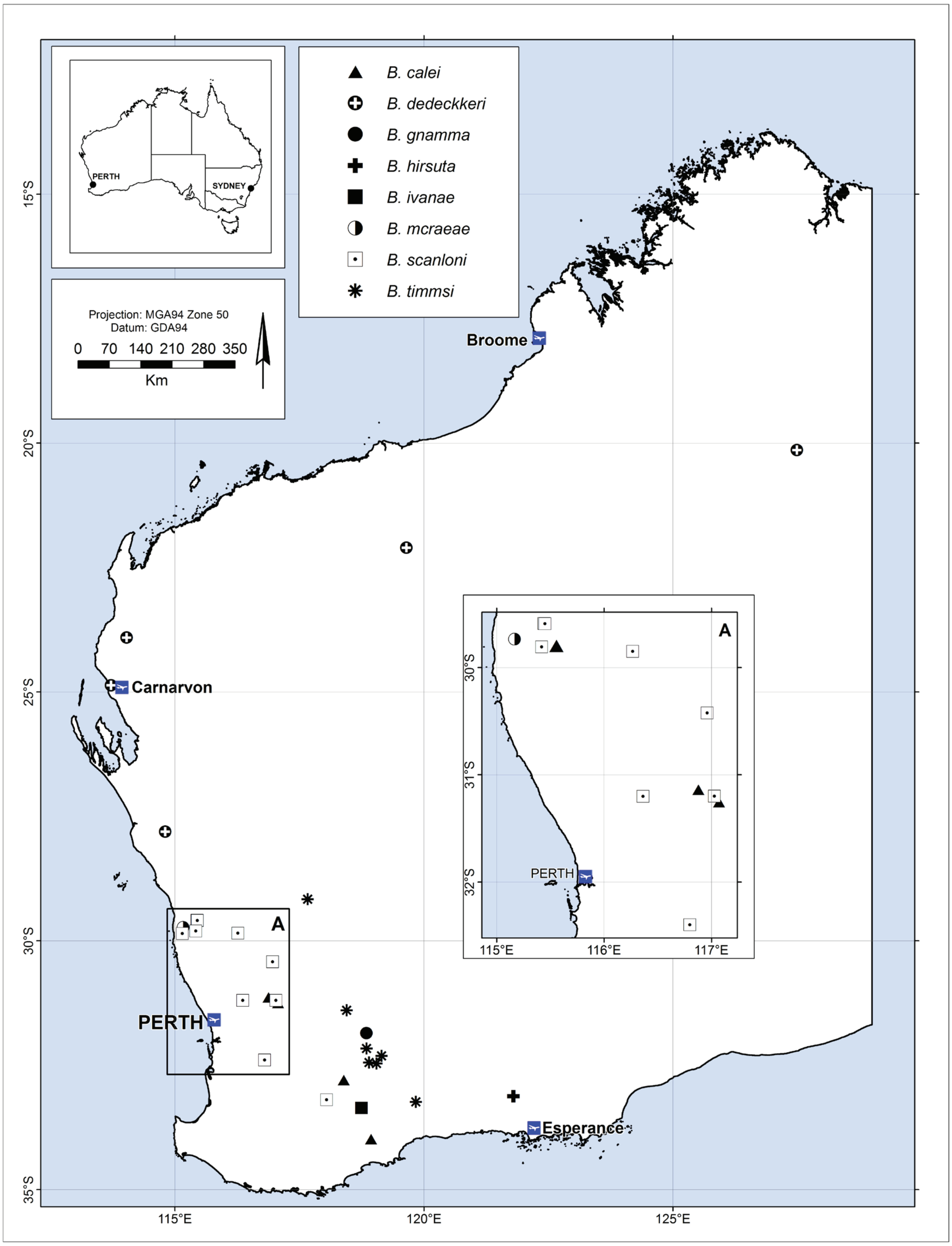

Fig. 1. Map of Western Australia with localities of *Bennelongia* - species described in the present paper.

No fresh (living) material of three of the seven new nominal species in the *barangaroo* lineage could be obtained (namely *B. gnamma* sp. nov., *B. hirsuta* sp. nov. and *B. mcraeae* sp. nov.); these species are not represented in the molecular phylogenetic tree and network.

Analyses of sequence data

Sequence chromatograms were visualised with BioEdit (Hall 2007). For each individual, the forward and reverse strand were aligned with ClustalX (Larkin *et al.* 2007), subsequently checked by eye for ambiguities, corrected and finally trimmed to obtain sequences of equal lengths. BLAST searches (Altschul *et al.* 1990) were used to confirm the identity of the obtained sequences in Genbank. We applied jModeltest 2.1.1 (Darriba *et al.* 2012) to identify the optimal model of molecular COI evolution using 88 or 24 models and the AICc criterion. Two different methods were used for phylogenetic reconstructions, Bayesian Inference (BI) in Mr Bayes 3.2 (Ronquist *et al.* 2011; with 4 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 bootstrap replicates and the parameters of jModeltest for all 88 models). We also constructed a parsimonious network at the 95% probability limit with TCS 1.21 (Clement *et al.* 2000) to connect different sequences (or haplotypes) and to illustrate genetic diversities and genetic relationships within and between populations. Selected sequences of all species have been submitted to Genbank (accession numbers KF724982-KF725015; see Table 1).

Testing for cryptic diversity

We applied the 4 theta rule (Birky *et al.* 2010; Birky 2011) based on the evolutionary genetic species concept (Birky & Barraclough 2009) to identify species boundaries and unravel cryptic diversities. This technique has been successfully used in bdelloid rotifers (Fontaneo *et al.* 2007, 2009; Birky & Barraclough 2009; Birky *et al.* 2011), asexual ostracods (Schön *et al.* 2012) including other *Bennelongia* ostracod species (Martens *et al.* 2012; Shearn *et al.* 2012), and a wide range of asexual prokaryotes (Birky *et al.* 2010).

We used the COI phylogenetic tree to identify statistically supported clades, which could potentially be different species according to the evolutionary genetic species concept. We then estimated sequence diversities within and between these phylogenetic clades with MEGA 5.0 (Tamura *et al.* 2011) using the number of differences (p) and the Tamura-3 parameter model with gamma distribution (allowing for multiple hits, different transition and transversion rates and GC bias) and 1000 bootstrap replicates. Following the procedure by Birky *et al.* (2010), sequence diversities were subsequently corrected for sample size and sequence lengths. In order to fulfill the criteria of the 4 theta rule, the sequence diversity between two sister clades must be at least 4 to 4.3 times larger than within the two clades, depending on the number of samples per clade (Birky *et al.* 2010).

Abbreviations used in text and figures

Cp = carapace
CpD/V = carapace in dorsal/ventral view
CpRL = carapace in right lateral view
F = female in Table 1
H = height of valves
il = inner list
KMWA = original working numbers given to specimens dissected and illustrated by the first author (KM)
K25 = electrical conductivity standardised to a water temperature of 25ºC
L = length of valves
Lpp = left prehensile palp

ls = lateral shield of hemipenis
LV/LVe/LVi = left valve/left valve exterior/left valve exterior
Mext/Fext = external views of valves of males/females
ms = medial shield of hemipenis
M = male in Table 1
NT = Northern Territory
OC = Ostracod Collection in the Royal Belgian Institute of Natural Sciences (Brussels, Belgium)
OS = ostracod slide dissected by Stuart Halse, retrieved from the voucher collection of DEC, now DPaW (Woodvale, Perth)
Rpp = right prehensile palp
RV/RVe/RVi = right valve/right valve exterior/right valve interior
SA = South Australia
QLD = Queensland
WA = Western Australia
WAMC = Western Australian Museum, Crustacean Collection (Perth, WA)

Specimens in bold in Table 1 are the holotypes of the species.

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

Results

Results of molecular screening

We obtained 680 nucleotide-long sequences for part of the mitochondrial COI region for all 99 ostracods subjected to DNA extraction. jModeltest selected the TPM1uf+I+G model with the following parameters among 88 models: freqA = 0.33; freqC = 0.19; freqG = 0.13; freqT = 0.35; [AC] = 1.00; [AG] = 24.84, [AT] = 2.91; [CG] = 2.91; [CT] = 24.84; [GT] = 1.00; p-inv = 0.56; gamma shape = 1.26. For Bayesian Inference, the HKY+I+G model was selected among 24 models.

The phylogenetic tree (Fig. 2) had a similar topology with ML and BI methods for tree construction. The two clades F1 and F2 (belonging to *B. ivanae* sp. nov. and *B.* sp. nov. F2 respectively) group together with high statistical support. They form the most basal branch and are separated from all other *Bennelongia* specimens. Within the phylogenetic cluster containing the other species, *B. dedeckkeri* forms the most basal branch, followed by clade B1 morphologically forming the new species *B. calei* sp. nov. The remaining specimens can be divided into three subgroups with strong statistical support for the tips but less support for the basal nodes of the subgroups themselves. Subgroup one consists of clade B2 as well as E1 and TST, which form sister clades and all belong morphologically to the new species *B. scanloni* sp. nov. The second subgroup is composed of clade E2, which is morphospecies *B.* sp. nov. E2 and sister clades A3 and A1, while the third subgroup contains clades A4, A2 and A5. According to their morphology, all A clades belong to the new species *B. timmsi* sp. nov.

We then used the topology of the phylogenetic tree (Fig. 2) to test whether clades phylogenetically closest to each other are in fact different genetic species by applying the 4 theta rule (see Table 2). Most sister clades represent different genetic species according to the criteria of the 4 theta rule (Birky *et al.* 2010), with the majority of these genetic species matching the morphologically identified species. This is the case for sister clades F1 and F2 representing *B. ivanae* sp. nov. and *B.* sp. nov. F2, respectively, and for B1 corresponding to *B. calei* sp. nov.. Likewise, morphology and genetics are concordant for the described species *B. dedeckkeri* and clade E2 (*B.* spec nov.). However, within *B. timmsi* sp. nov. and

B. scanloni sp. nov., there are phylogenetic clades representing different genetic species that cannot be distinguished morphologically. Of the five clades within *B. timmsi* sp.nov, only 3 are genetically distinct species (clades A1 and A3 on the one hand and A2+A4+A5 on the other). Within *B. scanloni* sp. nov., the cryptic clades E1/TST and B2 are good genetic species (see below for further remarks on species *B. timmsi* sp. nov. and *B. scanloni* sp. nov.).

If the topology of the tree in Fig. 2 is correct, then *B. timmsi* sp. nov. may be a polyphyletic species, as clades A1 and A3 on the one hand, and clades A2+A4+A5 on the other belong to different clusters of the tree. However, the support of the bifurcation between the two groups of *B. timmsi* clades is doubtful (bootstrap value of 77), so the apparent polyphyly of the species may be an artifact. As also no clear morphological characters, distinctive of the clusters, could be found (see below), we decided not to describe these two groups as distinct nominal species. If at some stage in the future this decision is to be reverted, then *B. timmsi* sp. nov. is defined by clade A5.

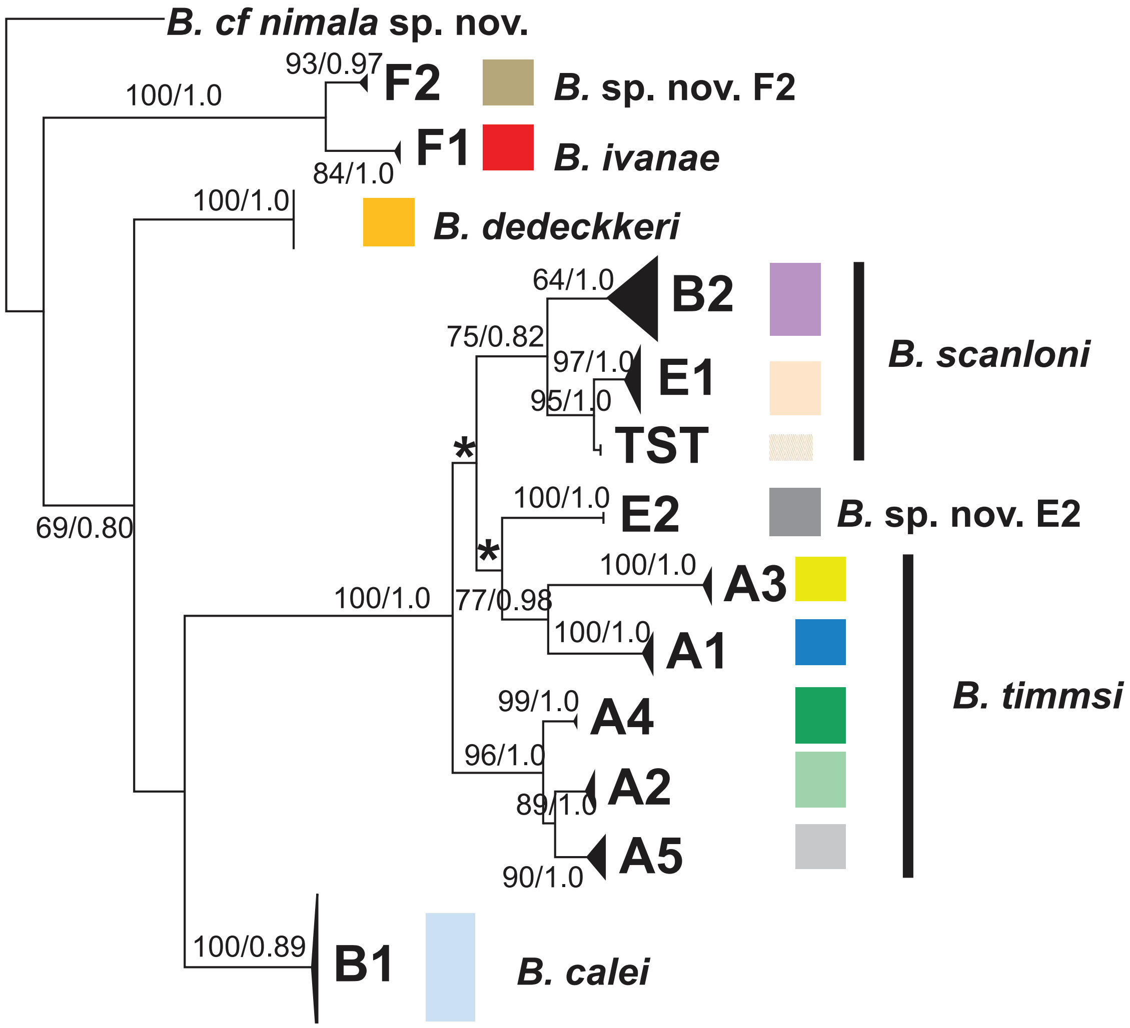

Fig. 2. Phylogenetic tree constructed with Bayesian Inference (BI) and Maximum Likelihood (ML) methods from COI sequences of 99 ostracods from the *Bennelongia barangaroo* lineage and with *B. nimala* as outgroup. Numbers above nodes illustrate statistical support for this particular node. Numbers before the hash (/) are % bootstrap values of ML analyses with 1000 replicates, numbers after the hash (/) are 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 (as in Fig. 3, page 15). The asterisks indicate two nodes (α1 and α2) that are weakly supported (see Discussion, p. 55).

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 99 specimens for which sequences are available. Specimens in bold are holotypes.

Mus Nr	**KMWA**	**Genbank accession number**	***Bennelongia* species**	**locality**	**M/F**	**RV**		**LV**		**CpRL**		**CpD/V**	
						L	H	L	H	L	H	L	W
WAMC52239	324		*timmsi*	BVT/010/1	F	1440	882	1520	907				
OC.3317	366		*timmsi*	BVT/10/02	F	1400	843	1480	874				
OC.3317	366		*timmsi*	BVT/10/02	Fext	1400	841	1460	883				
WAMC52240	434		*timmsi*	BVT/10/02	M	1190	730						
WAMC52240	434		*timmsi*	BVT/10/02	Mext	1190	727	1240	752				
WAMC52241	982	KF725001	*timmsi*	BVT/10/02	F	1420	849	1490	887				
WAMC52242	983	KF725002	*timmsi*	BVT/10/02	F	1480	903	1530	931				
WAMC52243	984	KF725003	*timmsi*	BVT/10/02	F	1510	905	1580	942				
WAMC52244	985		*timmsi*	BVT/10/02	M	1300	772	1340	823				
WAMC52245	998	KF725004	*timmsi*	BVT/10/03	F	1370	843	1440	841				
OC.3318	373		*timmsi*	BVT/10/04	F	1560	936	1630	989				
WAMC52246	435		*timmsi*	BVT/10/04	M	1340	818	1410	839				
WAMC52246	435		*timmsi*	BVT/10/04	Mext	1320	801	1380	829				
WAMC52247	436		*timmsi*	BVT/10/04	M	1380	812	1440	841				
WAMC52248	980		*timmsi*	BVT/10/04	F	1540	936	1650	974				
WAMC52249	981		*timmsi*	BVT/10/04	F	1580	960	1660	982				
OC.3319	986		*timmsi*	BVT/10/04	M	1370	821	1430	854				
WAMC52229	987	KF725005	*timmsi*	BVT/10/05	F	1510	913	1600	965				
OC.3314	988	KF725006	*timmsi*	BVT/10/05	F	1470	883	1530	929				
WAMC52233	989	KF725007	*timmsi*	BVT/10/05	F	1500	891	1550	925				
WAMC52234	990		*timmsi*	BVT/10/05	F							1580	951
WAMC52235	991		*timmsi*	BVT/10/05	F					1530	891		
OC.3315	992		*timmsi*	BVT/10/05	F							1550	931

Mus Nr	**KMWA**	**Genbank accession number**	***Bennelongia* species**	**locality**	**M/F**	**RV**		**LV**		**CpRL**		**CpD/V**	
						L	H	L	H	L	H	L	W
OC.3316	993		*timmsi*	BVT/10/05	M							1370	834
WAMC52236	994		*timmsi*	BVT/10/05	M					1330	770		
WAMC52237	995		*timmsi*	BVT/10/05	M							1380	840
WAMC52232	996		*timmsi*	BVT/10/05	M	1283	768						
WAMC52231	997		*timmsi*	BVT/10/05	M	1300	790	1375	812				
WAMC52228	**1073**		***timmsi***	**BVT/10/05**	**M**	**1318**	**783**	**1378**	**817**				
OC.3312	1074		*timmsi*	BVT/10/05	M	1320	798	1375	823				
WAMC52230	1075		*timmsi*	BVT/10/05	M	1285	768	1337	800				
OC.3313	379	KF725008	*timmsi*	BVT/10/05	F	1510	901	1570	950				
OC.3313	379		*timmsi*	BVT/10/05	Fext	1490	903	1550	943				
WAMC52250	381		*timmsi*	BVT/10/06	F	1500	892	1560	925				
WAMC52250	381		*timmsi*	BVT/10/06	Fext	1473	883	1535	919				
WAMC52251	999	KF725009	*timmsi*	BVT/10/06	F	1510	898	1535	919				
WAMC52252	1000		*timmsi*	BVT/10/06	M	1329	808	1404	848				
WAMC52253	888	KF725010	*timmsi*	BVT/10/08	M	/	/	1404	873				
OC.3320	889	KF725011	*timmsi*	BVT/10/08	F	1525	940	1619	981				
WAMC52254	890	KF725012	*timmsi*	BVT/10/08	F	1488	912	1548	948				
WAMC52255	891	KF725013	*timmsi*	BVT/10/08	M	1344	814	1402	829				
WAMC52256	892		*timmsi*	BVT/10/08	M							1387	848
WAMC52257	893		*timmsi*	BVT/10/08	M					1390	852		
WAMC52258	894		*timmsi*	BVT/10/08	M							1390	868
WAMC52259	895		*timmsi*	BVT/10/08	F							1613	987
WAMC52260	896		*timmsi*	BVT/10/08	F							1581	1015
WAMC52261	897		*timmsi*	BVT/10/08	F					1588	939		
WAMC52262	901		*timmsi*	BVT/10/08	M	1335	835	1396	840				
OC.3321	902		*timmsi*	BVT/10/08	M	1327	821	1398	842				
OC.3322	222		*gnamma*	OSTR012A	F	1450	973	1520	1050				

Mus Nr	KMWA	Genbank accession number	***Bennelongia* species**	locality	M/F	RV		LV		CpRL		CpD/V	
						L	H	L	H	L	H	L	W
OC.3322	222		*gnamma*	OSTR012A	Fext	1482	960	1497	1018				
WAMC52266	223		*gnamma*	OSTR012A	F							1560	1000
WAMC52263	**OS178**		***gnamma***	**OSTR012A**	**F**	**1550**	**915**	**1620**	**991**				
WAMC52275	224		*hirsuta*	OSTR012D	F							1430	896
WAMC52276	225		*hirsuta*	OSTR012D	F							1500	875
WAMC52277	226		*hirsuta*	OSTR012D	F					1430	826		
WAMC52272	227		*hirsuta*	OSTR012D	M					1450	837	1447	855
WAMC52270	1101		*hirsuta*	OSTR012D	F	1400	842	1470	845				
WAMC52274	1104		*hirsuta*	OSTR012D	F	1390	813	1450	824				
WAMC52269	**1105**		***hirsuta***	**OSTR012D**	**M**	**1260**	**738**	**1320**	**763**				
OC.3323	1106		*hirsuta*	OSTR012D	M	1240	743	1300	759				
WAMC52273	1103		*hirsuta*	OSTR012D	M					1300	737		
OC.3324	1102		*hirsuta*	OSTR012D	F					1410	803		
WAMC52279	903		*hirsuta*	BVT/10/09	F	1217	719	1302	719				
WAMC52280	**851**	KF725014	***ivanae***	**DJC/02**	**F**	**1475**	**915**	**1533**	**948**				
WAMC52280	**851**		***ivanae***	**DJC/02**	**Fext**	**1452**	**904**	**1512**	**940**				
OC.3326	852	KF725015	*ivanae*	DJC/02	F	1460	910	1542	947				
OC.3326	852		*ivanae*	DJC/02	Fext	1456	904	1513	935				
OC.3327	1001		*ivanae*	DJC/02	F					1488	931		
WAMC52281	1002		*ivanae*	DJC/02	F							1498	1025
WAMC52282	1003		*ivanae*	DJC/02	F							1452	/
WAMC52284	444		*ivanae*	OSTR013F	F	1400	842	1490	865				
WAMC52285	904		*spec F2*	BVT/10/09									
WAMC52286	**OS007**		***mcraeae***	**OSTR014B**	**M**	**1480**	**878**	**1560**	**896**				
WAMC52286	**OS007**		***mcraeae***	**OSTR014B**	**Mext**	**1465**	**871**	**1523**	**885**				
WAMC52287	180		*mcraeae*	OSTR014B	Fext	1608	1002	1663	1033				
OC.3328	1076		*mcraeae*	OSTR014B	M	1390	847	1450	859				

Mus Nr	**KMWA**	**Genbank accession number**	***Bennelongia* species**	**locality**	**M/F**	**RV**		**LV**		**CpRL**		**CpD/V**	
						L	H	L	H	L	H	L	W
WAMC52289	1078		*mcraeae*	OSTR014B	F					1650	1000		
WAMC52324	295		*scanloni*	BRYDE7	F	1460	873	1560	895				
WAMC52324	295		*scanloni*	BRYDE7	Fext	1448	863	1550	992				
WAMC52325	297		*scanloni*	BRYDE7	F	1460	863	1550	887				
WAMC52325	297		*scanloni*	BRYDE7	Fext	1438	860	1533	883				
WAMC52326	299		*scanloni*	BRYDE7	F					1489	878	1455	858
OC.3339	194		*scanloni*	BRYDE7	F	1330	807	1044	839				
OC.3339	194		*scanloni*	BRYDE7	Fext	1322	803	1412	822				
OC.3340	437		*scanloni*	OSTR013C	F	1310	775	1380	788				
OC.3340	437		*scanloni*	OSTR013C	Fext	1303	765	1350	782				
WAMC52327	438		*scanloni*	OSTR013C	M	1260	751	1310	761				
WAMC52327	438		*scanloni*	OSTR013C	Mext	1242	738	1303	749				
WAMC52328	1107		*scanloni*	OSTR013C	M	1230	688	1320	709				
OC.3338	916		*scanloni*	TST	M	1248	756	1331	769				
	917		*scanloni*	TST	F	1394	810	1487	833				
WAMC52322	918	KF724982	*scanloni*	TST	F	1294	752	1396	711				
WAMC52323	919		*scanloni*	TST	F							1352	744
OC.3334	855		*scanloni*	DJC/09	F	1438	900	1485	930				
OC.3334	855		*scanloni*	DJC/09	Fext	1446	890	1490	898				
WAMC52310	856		*scanloni*	DJC/09	F	1465	923	1525	933				
WAMC52310	856		*scanloni*	DJC/09	Fext	1421	898	1477	910				
WAMC52304	831	KF724983	*scanloni*	DJC/11	F	1380	797	1463	807				
WAMC52304	831		*scanloni*	DJC/11	Fext	1360	773	1433	796				
lost	832	KF724984	*scanloni*	DJC/11	F	1367	803	1458	807				
	832		*scanloni*	DJC/11	Fext	1352	789	1438	808				
WAMC52297	837		*scanloni*	DJC/11	F							1497	910
WAMC52298	838		*scanloni*	DJC/11	F							1448	832

Mus Nr	**KMWA**	**Genbank accession number**	***Bennelongia* species**	**locality**	**M/F**	**RV**		**LV**		**CpRL**		**CpD/V**	
						L	H	L	H	L	H	L	W
WAMC52299	839		*scanloni*	DJC/11	F					1493	867		
WAMC52295	841		*scanloni*	DJC/11	M					1290	730	1302	731
WAMC52296	842		*scanloni*	DJC/11	M							1222	745
OC.3329	1004		*scanloni*	DJC/11	M	1204	714	1277	737				
WAMC52291	**1005**		***scanloni***	**DJC/11**	**M**	**1223**	**694**	**1294**	**714**				
WAMC52293	1006		*scanloni*	DJC/11	M	1244	723	1327	735				
WAMC52294	1007		*scanloni*	DJC/11	M	1190	696	1263	708				
WAMC52292	1008	KF724985	*scanloni*	DJC/11	F	1263	752	1356	775				
OC.3331	1009		*scanloni*	DJC/11	F	1312	777	1398	792				
WAMC52300	1010		*scanloni*	DJC/11	F	1504	900	1583	919				
WAMC52301	1011		*scanloni*	DJC/11	F	1471	883	1562	889				
WAMC52302	1012	KF724986	*scanloni*	DJC/11	F	1383	827	1463	846				
WAMC52303	1013	KF724987	*scanloni*	DJC/11	F	1485	883	1588	906				
OC.3335	1022	KF724988	*scanloni*	DJC/19	F	1446	885	1519	906				
WAMC52311	1023	KF724989	*scanloni*	DJC/19	F	/	/	1660	broken				
WAMC52312	1025		*scanloni*	DJC/19	F					1515	887		
WAMC52313	1026		*scanloni*	DJC/19	F							1475	/
WAMC52314	1029		*scanloni*	DJC/19	F							1713	1038
WAMC52315	1030		*scanloni*	DJC/19	F							1721	1035
OC.3336	1031		*scanloni*	DJC/19	F					1625	983		
OC.3337	797		*scanloni*	DJC/23	F	1573	973	1670	1015				
OC.3337	797		*scanloni*	DJC/23	Fext	1560	979	1633	987				
WAMC52319	1018	KF724990	*scanloni*	DJC/23	F	1498	919	/	/				
WAMC52320	1020		*scanloni*	DJC/23	F							1608	948
WAMC52321	1021		*scanloni*	DJC/23	F					1502	898		
OC.3332	907	KF724991	*scanloni*	BVT/10/10	F	1460	929	1546	952				
WAMC52306	908		*scanloni*	BVT/10/10	F	1587	989	1646	998				

Mus Nr	**KMWA**	**Genbank accession number**	***Bennelongia* species**	**locality**	**M/F**	**RV**		**LV**		**CpRL**		**CpD/V**	
						L	H	L	H	L	H	L	W
WAMC52307	909	KF724992	*scanloni*	BVT/10/10	F	1415	885	1465	898				
WAMC52308	910	KF724993	*scanloni*	BVT/10/10	F	1602	994	1656	1015				
OC.3333	911		*scanloni*	BVT/10/10	M	1277	/	1350	831				
WAMC52336	822	KF724994	*calei*	DJC/18	F	1340	802	1432	818				
WAMC52336	822		*calei*	DJC/18	Fext	broken	792	1419	814				
WAMC52335	**823**	KF724995	***calei***	**DJC/18**	**F**	**1480**	**857**	**1555**	**865**				
WAMC52335	**823**		***calei***	**DJC/18**	**Fext**	**1452**	**844**	**1552**	**862**				
OC.3344	1014		*calei*	DJC/18	F	1446	835	1531	848				
WAMC52339	1015		*calei*	DJC/18	F	1490	864	1588	873				
WAMC52340	1016		*calei*	DJC/18	F	1335	775	1408	864				
WAMC52341	1017	KF724996	*calei*	DJC/18	F	1244	729	1337	748				
OC.3345	828		*calei*	DJC/18	F					1477	815		
WAMC52337	829		*calei*	DJC/18	F							1477	827
WAMC52338	830		*calei*	DJC/18	F							1518	802
WAMC52355	236		*calei*	SPM017B	F	1150	686	1240	711				
WAMC52355	236		*calei*	SPM017B	Fext	1145	682	1232	703				
WAMC52356	237		*calei*	SPM017B	F					1290	735	1290	729
	238		*calei*	SPM017B	F							1180	695
WAMC52353	195		*calei*	SPM017B	F					1330	756	1325	718
WAMC52354	196		*calei*	SPM017B	F	1170	699	1260	720				
WAMC52354	196		*calei*	SPM017B	Fext	1167	692	1252	713				
WAMC52349	870	KF724997	*calei*	DJC/10	F	1422	833	1522	855				
WAMC52349	870		*calei*	DJC/10	Fext	1400	837	1508	848				
OC.3346	807		*calei*	BVT/11/04	F	1307	792	1382	797				
OC.3347	808		*calei*	BVT/11/04	F							1427	782
WAMC52343	809		*calei*	BVT/11/04	F					1397	783		
WAMC52344	810		*calei*	BVT/11/04	F							1425	772

Mus Nr	KMWA	Genbank accession number	*Bennelongia* species	locality	M/F	RV		LV		CpRL		CpD/V	
						L	H	L	H	L	H	L	W
WAMC52345	813	KF724998	*calei*	BVT/11/05	F	1383	812	1460	832				
WAMC52345	813		*calei*	BVT/11/05	Fext	1371	812	1449	832				
WAMC52346	814		*calei*	BVT/11/05	F							1473	828
WAMC52347	815		*calei*	BVT/11/05	F							1417	773
WAMC52348	816		*calei*	BVT/11/05	F					1443	808		
WAMC52329	1080	KF724999	*calei*	DJC/15	F	/	/	1587	906				
OC.3343	1081		*calei*	DJC/15	F					1540	889		
WAMC52330	1082		*calei*	DJC/15	F							1546	842
WAMC52331	1083		*calei*	DJC/15	F							1506	842
OC.3348	874	KF725000	*calei*	DJC/36	F	1345	817	1433	833				
OC.3349	879		*calei*	DJC/36	F							1513	843
WAMC52350	880		*calei*	DJC/36	F					1497	850		
WAMC52351	881		*calei*	DJC/36	F							1430	830
WAMC52352	882		*calei*	DJC/36	F					1410	780		
OC.3350	190		*dedeckkeri*	KIES10	F					1110	650		
WAMC52359	191		*dedeckkeri*	KIES10	F							1100	641
WAMC52360	192		*dedeckkeri*	KIES10	F							1080	651
WAMC52357	193		*dedeckkeri*	KIES10	F	1110	676	1190	701				
OC.3351	678		*dedeckkeri*	SIKE9	F	1125	672	1188	715				
OC.3352	679		*dedeckkeri*	SIKE9	F					1210	717		
WAMC52364	680		*dedeckkeri*	SIKE9	F							1187	652
WAMC52365	681		*dedeckkeri*	SIKE9	F							1145	660

Table 2. Results of tests for genetic species boundaries using the 4 theta method for six species of the *Bennelongia barangaroo* lineage.

Phylogenetic sister clades	**Species**	**max. θ (within clades)**	**D (between clades)**	**Ratio D/θ**	**n^1, n^2**
A1-A3	*B. timmsi*	0.0076 *0.0078*	0.114 *0.139*	**15.00** ***17.82***	8, 7
A2-A4	*B. timmsi*	0.0138 *0.0141*	0.052 *0.058*	3.77 ***4.11***	9, 3
A2-A5	*B. timmsi*	0.0138 *0.0141*	0.048 *0.052*	3.48 *3.69*	8, 8
A4-A5	*B. timmsi*	0.0138 *0.0141*	0.049 *0.054*	3.55 *3.83*	3, 5
A1-E1	*B. timmsi* – *B. scanloni*	0.0133 *0.0138*	0.131 *0.169*	**9.85** ***12.25***	8, 13
A3-E1	*B. timmsi* – *B. scanloni*	0.0133 *0.0138*	0.140 *0.182*	**10.53** ***13.19***	7, 13
B1-*B. dedeckkeri*	*B. calei* - *B. dedeckkeri*	0.004 *0.004*	0.126 0.161	**31.5** ***40.25***	23, 25
B2-E1	*B. scanloni*	0.020 *0.021*	0.113 *0.141*	**5.65** ***6.71***	15, 13
B2-DJC11	*B. scanloni*	0.050 *0.053*	0.040 *0.044*	0.80 *0.83*	15, 2
E1-TST	*B. scanloni*	0.0133 *0.0138*	0.032 *0.034*	2.41 *2.46*	13, 2
B2-E2	*B. scanloni* – *B.* sp. nov. E2	0.020 *0.020*	0.103 *0.127*	**5.15** ***6.35***	15, 2
E2-TST	*B. scanloni* – *B.* sp. nov. E2	0.0015 *0.0015*	0.109 *0.135*	**72.67** ***90.00***	2, 2
F1-F2	*B. ivanae* – *B.* sp. nov. F2	0.0058 *0.0059*	0.061 *0.067*	**10.52** ***11.36***	3, 4

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 distance or with the Tamura-3 parameter model (in italics). Nearest neighbours or sister clades were defined from the COI tree constructed with Bayesian Inference and Maximum Likelihood methods (see Fig. 2). In order to fulfill the criteria of the 4 theta rule for species status, the ratio of the mean sequence diversity within as compared to between the two nearest neighbours of one sister clade 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.

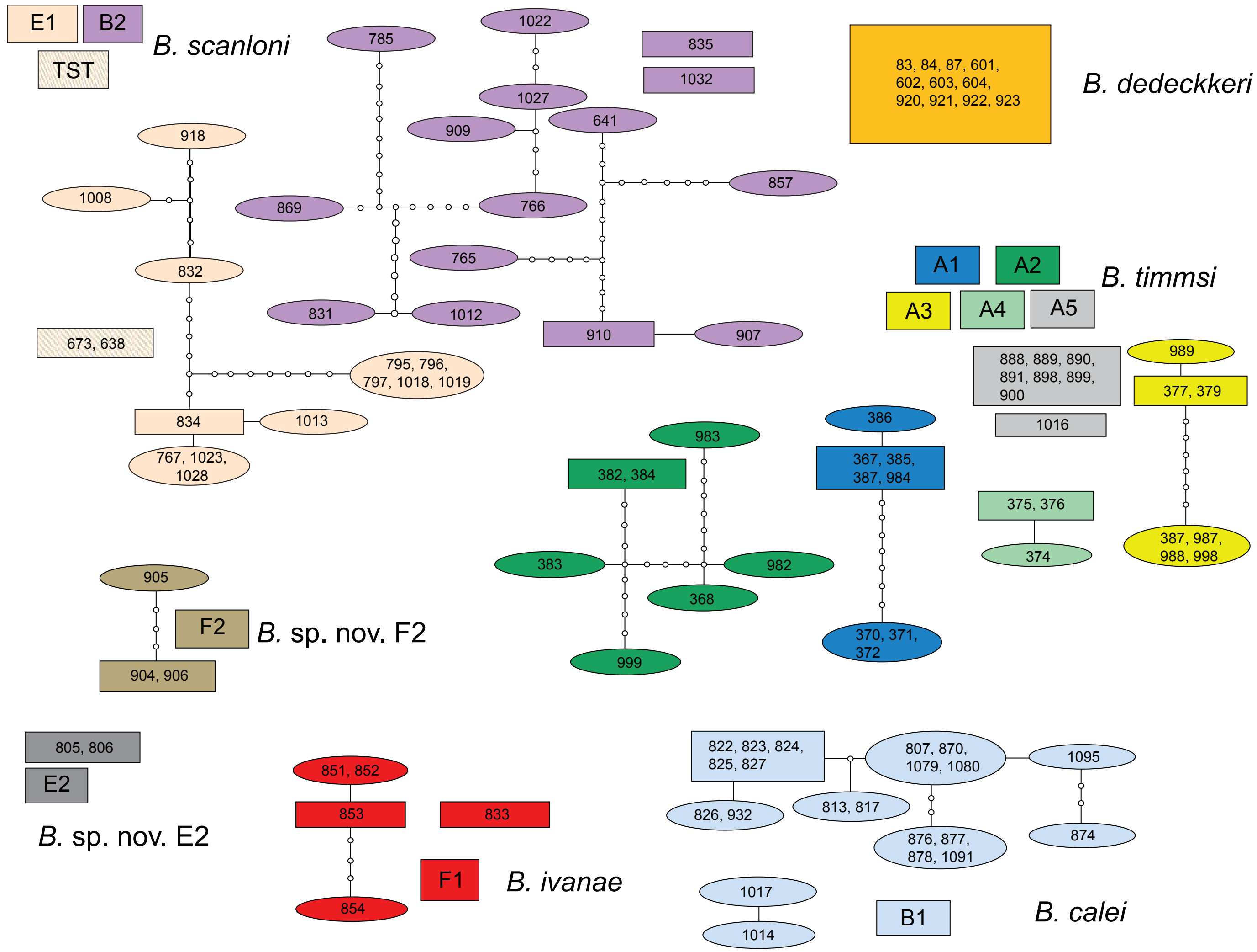

Fig. 3. Parsimonius network, based on COI sequences of the *Bennelongia barangaroo* lineage. Squares represent ancestral sequences (or haplotypes), small circles missing haplotypes. The size of squares and large ovals is proportional to the number of individuals with the same sequence in the analysed population. The network was constructed at the 95% probability limit, which includes up to 8 mutation steps for connecting different sequences or haplotypes. Different phylogenetic clades are indicated by different colours, which match those used in Fig. 2 (page 6).

The structure of the most parsimonious networks in Fig. 3 also reflects the higher genetic than morphological diversity. However, there are two species with a single haplotype each, *B. dedeckkeri* and *B. spec*. E2 sp. nov. (clade E2). For the latter, we obtained COI sequences of two individuals only while the same (identical) haplotype is found in 11 specimens of *B. dedeckkeri*. The three individuals in clade F2 (and *B. spec*. F2 sp. nov.) share two haplotypes, while the five specimens of *B. ivanae* sp. nov. possess 4 haplotypes, of which one remains unconnected. The remaining three species display two (*B. calei* sp. nov.) to five (*B. scanloni* sp. nov.) and six (*B. timmsi* sp. nov.) unconnected haplotype networks, respectively. The different genetic species within *B. timmsi* sp. nov. and *B. scanloni* sp. nov. form unconnected haplotype networks.

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 barangaroo lineage

Remarks

De Deckker (1981a) described *B. barangaroo* from Lake Buchanan (QLD – Type locality), but also reported the same species from other localities in QLD, NSW, SA, WA and New Zealand. However, as in De Deckker's (1981a) re-description of *B. australis* (Brady, 1886) (see Martens *et al.* 2012), at least two different species within this lineage were illustrated under the same name. The (type) specimens of *B. barangaroo* in De Deckker's (1981a) figure 7 from Lake Buchanan have a short, sub-quadrate, slightly ventrally pointed lapel on the antero-ventral side of the RV. The specimens from a pool 25 km N of Cue (WA) (De Deckker 1981a: fig. 9), however, appear to have an elongated lapel, much as is the case in *B. calei* sp. nov. (see below). We thus decided previously (Shearn *et al.* 2012) that the true *B. barangaroo* needs to be established based on new material from the type locality. Fortunately, De Deckker (1981a) illustrated the valves and soft parts of the holotype male, which facilitated identification, and allowed Shearn *et al.* (2012) to confidently describe *B. dedeckkeri* as a different species within the *B. barangaroo* lineage. Shearn *et al.* (2012) also described *B. mckenziei* as a second new species from QLD, characterised by a total absence of the lapel on the RV.

Diagnosis of the *B. barangaroo* lineage

All species of the *B. barangaroo* lineage (re-)described here share a number of features: all have relatively elongated and wide (in dorsal view) carapaces, mostly green in colour, relatively smooth (but hirsute) in adults. The RV has an internal eyelet at the posteroventral internal side, mostly situated directly internally of the lapel. This eyelet is best visible with transparent light; although in most species it is also visible on SEM micrographs (see various illustrations below).

Bennelongia timmsi sp. nov.

Figs 4-11

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Diagnosis

Valves in inner view (Fig. 4A-B, D-E) relatively high, with greatest height situated well in front of the middle; ventral margin anteriorly with well-pronounced mandibular curve. LV (Fig. 4A, D) with anterior il not overlapping. RV (Fig. 4B, E) with antero-ventral lapel subtriangular, asymmetrically produced with a ventral point (Fig. 4K-M). Carapace in dorsal and ventral views (Fig. 4G-J) with greatest width in the middle, hirsute, anteriorly with a mild rostrum; in lateral views (Fig. 4C, F) showing a clear anterior LV>RV overlap.

Hemipenes (holotype: Fig. 8F) mostly symmetrical, with ls protruding well beyond ventral tip of ms, ls with broad base, ventrally bluntly beak-shaped. Right prehensile palp (holotype: Fig. 8D) with distal segment elongated, with dorsal margin evenly rounded. Left prehensile palp (holotype: Fig. 8E) with distal segment elongated, reaching beyond ventro-apical margin of proximal segment with at least half of its length.

Etymology

This species is named after Prof. Brian V. Timms (Newcastle, Australia), in recognition of his vast contribution to the knowledge of Australian non-marine crustaceans in general, and of phyllopods from temporary pools in particular. Prof. Timms also collected the material of the present species from a series of pools on various rocky outcrops in WA.

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

Holotype ♂ (WAMC52228): RV: L = 1318, H = 783. LV: L = 1378, H = 817.
Allotype ♀ (WAMC52229): RV: L = 1510, H = 913. LV: L = 1600, H = 965.

Type locality

Rock pools on Wave Rock, WA, ca. 2 km E of Hyden. Approximate coordinates: 32º 27'S 118º 54' E (WGS 84). Material handpicked from pools by B.V. Timms on 23 Jul. 2010 (sample BVT/10/05).

Type material

Holotype

♂ (WAMC52228), with soft parts dissected in a sealed slide and valves stored dry in a micropalaeontological slide.

Allotype

♀ (WAMC52229), with soft parts dissected in a sealed slide, and valves stored dry in a micropalaeontological slide.

Paratypes

Numerous males and females from the type locality, either dissected and stored as the holotype, or as carapaces used for SEM (WAMC52230-52237, OC.3312-3316). Ca. 60 ♂♂ and ♀♀ in EtOH as bulk paratypes (WAMC52238).

Other material investigated

All material from WA, collected by B.V. Timms.

Fig. 4. *Bennelongia timmsi* sp. nov., all represent paratypes from Wave Rock (BVT/10/05 – type locality). **A**. ♀, LVi (OC.3313). **B**. ♀, RVi (idem). **C**. ♀, CpRL (WAMC52235). **D**. ♂ holotype, LVi (WAMC52228). **E**. ♂ holotype, RVi (idem). **F**. ♂, CpRL (WAMC52236). **G**. ♀, CpD (WAMC52234). **H**. ♀, CpV (OC.3315). **I**. ♂, CpV (OC.3316). **J**. ♂, CpD (WAMC52237). **K**. ♂ holotype, RVi, detail anterior (WAMC52228). **L**. ♂ holotype, RVi, detail anterior, tilted (WAMC52228). **M**. ♀, LVi, detail anterior, tilted (OC.3313). Scales: A-J = 1 mm; K-M = 200 µm.

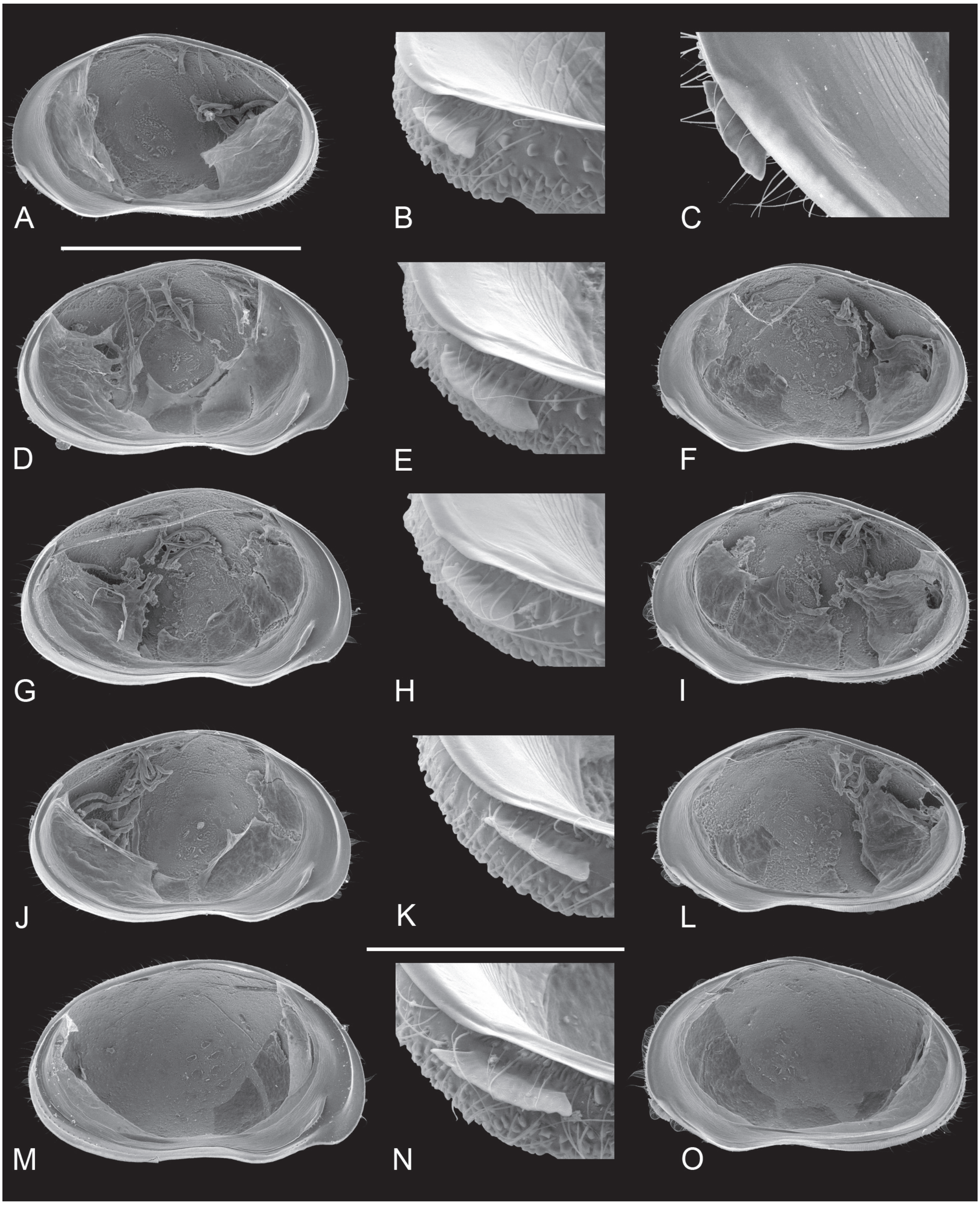

Fig. 5. *Bennelongia timmsi* sp. nov., all males with hemipenes and prehensiles palps illustrated (see Figs 8-10). A-L = paratypes from Wave Rock (BVT/10/05), M-O = non-types from King Rocks (BVT/10/06). — **A-C**. WAMC52232: **A**. RVi. **B**. RVi, detail anterior, tilted. **C**. RVi, detail anterior. — **D-F**. WAMC52231: **D**. LVi. **E**. RVi, detail anterior, tilted. **F**. RVi. — **G-I**. OC.3312: **G**. LVi. **H**. RVi, detail anterior, tilted. **I**. RVi. — **J-L**. WAMC52230: **J**. LVi. **K**. RVi, detail anterior, tilted. **L**. RVi. — **M-O**. WAMC52252: **M**. LVi. **N**. RVi, detail anterior, tilted. **O**. RVi. Scales: A, D, F-G, I-J, L-M, O = 1 mm; B-C, E, H, K, N = 200 µm.

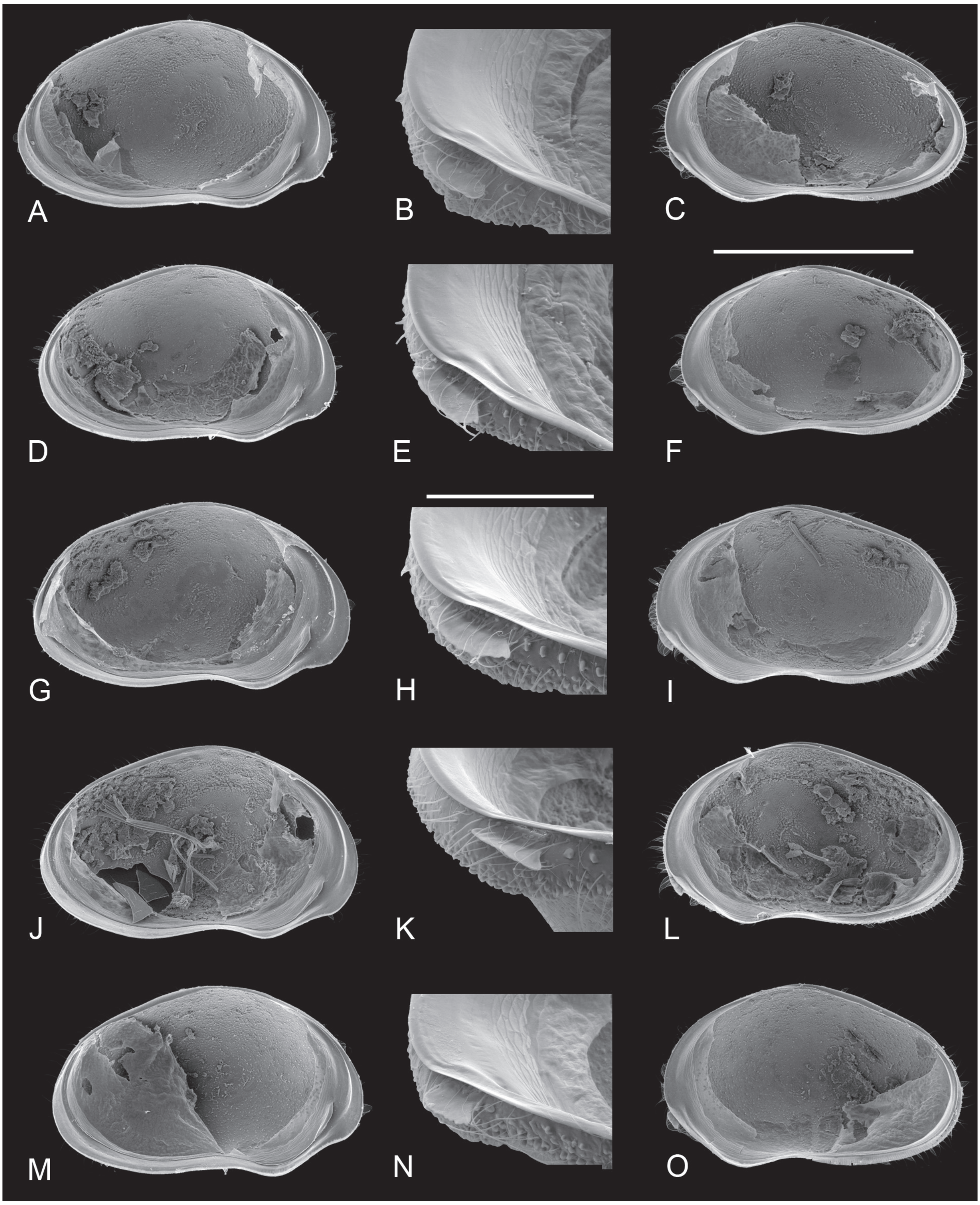

Fig. 6. *Bennelongia timmsi* sp. nov., all represent females with molecular data available. — **A-C**. Grahams Rock (BVT/10/02 – WAMC52243 – cryptic species A1): **A**. LVi. **B**. RVi, detail anterior, tilted. **C**. RVi. — **D-F**. Grahams Rock (BVT/10/02 – WAMC52241 – cryptic species A2): **D**. LVi. **E**. RVi, detail anterior, tilted. **F**. RVi. — **G-I**. King Rocks (BVT/10/06 – WAMC52251 – cryptic species A2): **G**. LVi. **H**. RVi, detail anterior, tilted. **I**. RVi. — **J-L**. Wave Rock (BVT/10/05 – allotype WAMC52229 – cryptic species A3): **J**. LVi. **K**. RVi, detail anterior, tilted. **L**. RVi. — **M-O**. Mt Madden Rocks (BVT/10/08 – WAMC52254 – cryptic species A5): **M**. LVi. **N**. RVi, detail anterior, tilted. **O**. RVi. Scales: A, C-D, F-G, I-J, L-M, O = 1 mm; B, E, H, K, N = 200 µm.

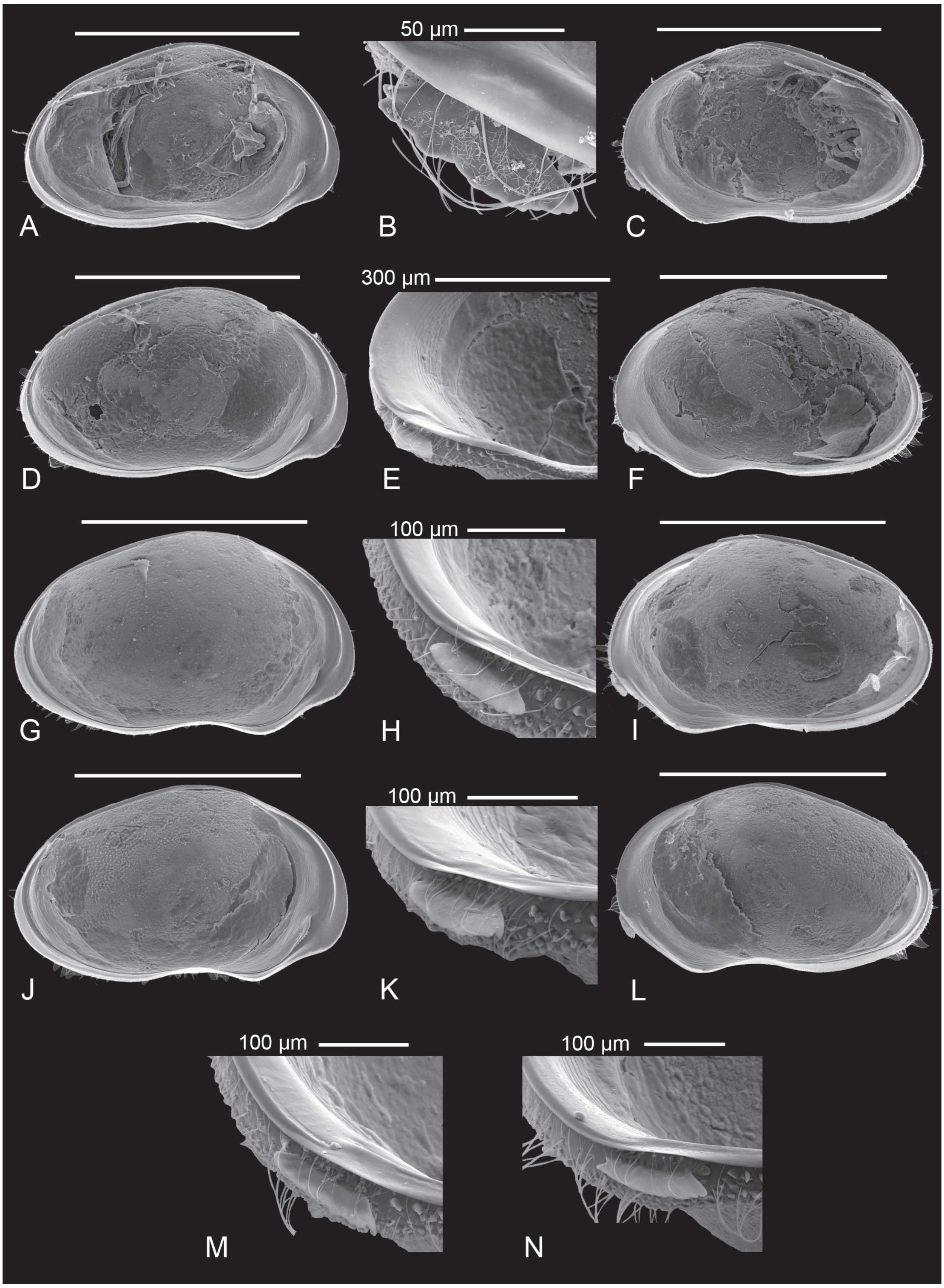

Fig. 7. *Bennelongia timmsi* sp. nov. — **A-C**. Mt Madden Rocks (BVT/10/08 – ♂, WAMC52255 – cryptic species A5). **A**. LVi. **B**. RVi, detail anterior, tilted. **C**. RVi. — **D-F**. Anderson Rock (BVT/10/03 – ♀, WAMC52245). **D**. LVi. **E**. RVi, detail anterior, tilted. **F**. RVi. — **G-I**. Paynes Find Rock (BVT/10/01 – ♀, WAMC52239). **G**. LVi. **H**. RVi, detail anterior, tilted. **I**. RVi. — **J-L**. Grahams Rock (BVT/10/02 – ♀, OC.3317). **J**. LVi. **K**. RVi, detail anterior, tilted. **L**. RVi. — **M**. Burracopin Rock (BVT/10/04 – ♀, OC.3318), RVi, detail anterior, tilted. — **N**. King Rocks (BVT/10/06 – ♀, WAMC52250), RVi, detail anterior, tilted. Scales = 1 mm unless otherwise indicated.

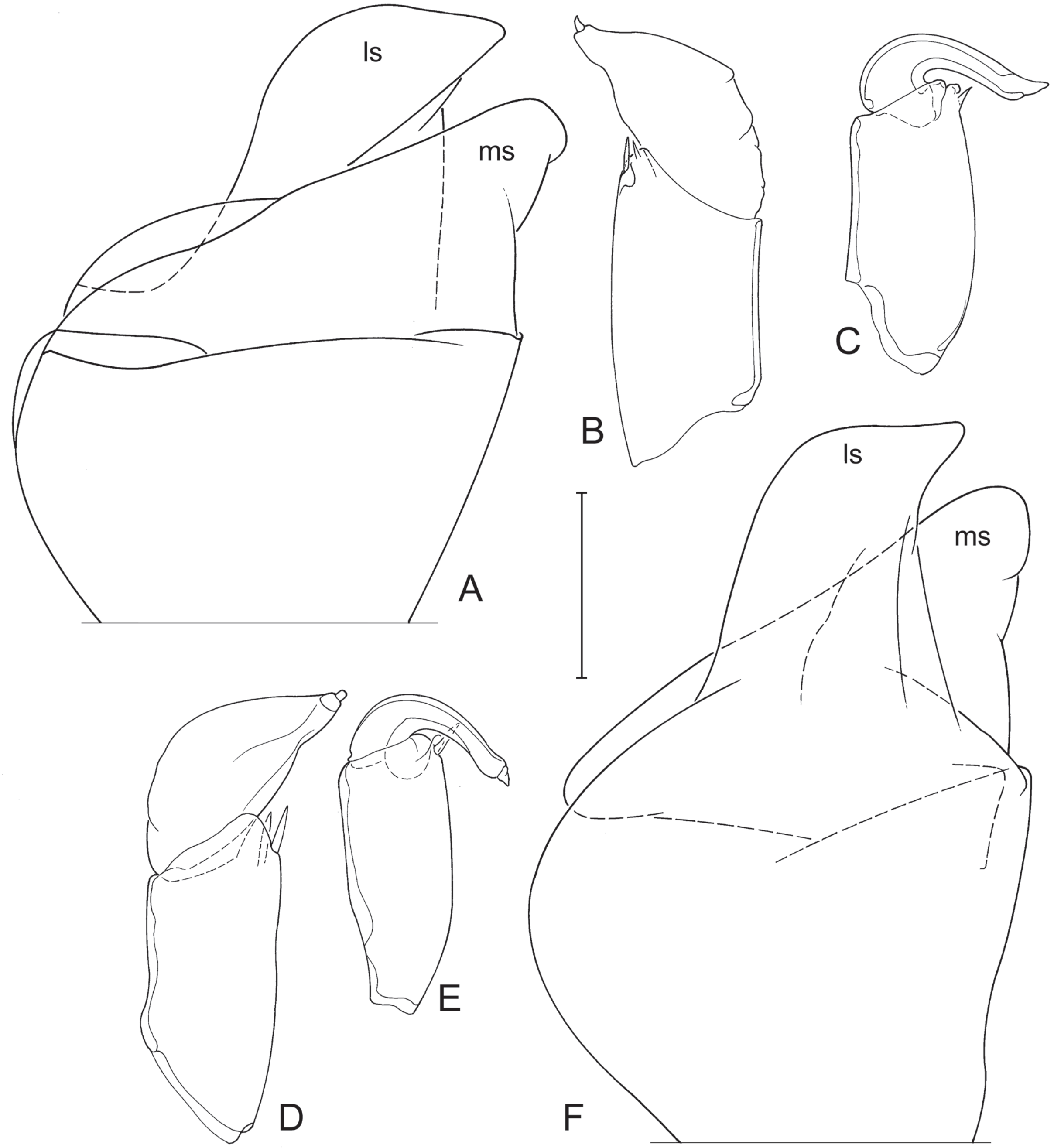

Fig. 8. *Bennelongia timmsi* sp. nov., male type specimens from type locality (Wave Rock, BVT/10/05). — **A-C**. Paratype M (OC.3312): **A**. Hemipenis (both hemipenes symmetrical in this specimen). **B**. Right prehensile palp. **C**. Left prehensile palp. — **D-F**. Holotype ♂ (WAMC52228): **D**. Right prehensile palp. **E**. Left prehensile palp. **F**. Hemipenis (both hemipenes symmetrical in this specimen). Scale: A-F = 92 µm.

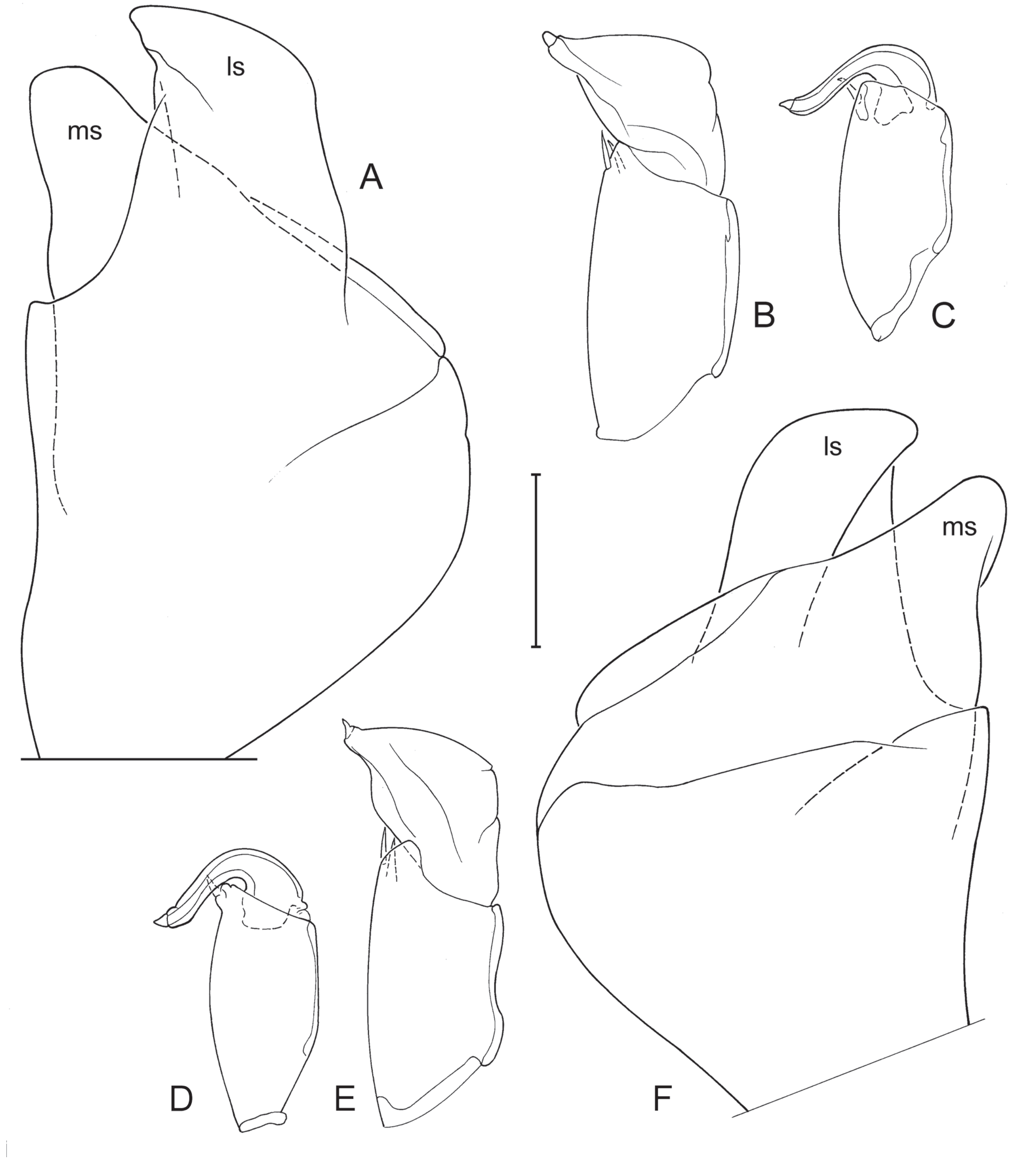

Fig. 9. *Bennelongia timmsi* sp. nov., paratypes from type locality (Wave Rock, BVT/10/05). — **A-C**. Paratype ♂ (WAMC52231): **A**. Hemipenis (both hemipenes symmetrical in this specimen). **B**. Right prehensile palp. **C**. Left prehensile palp. — **D-F**. Paratype ♂ (WAMC52230): **D**. Left prehensile palp. **E**. Right prehensile palp. **F**. Hemipenis (both hemipenes symmetrical in this specimen). Scale: A-F= 92 µm.

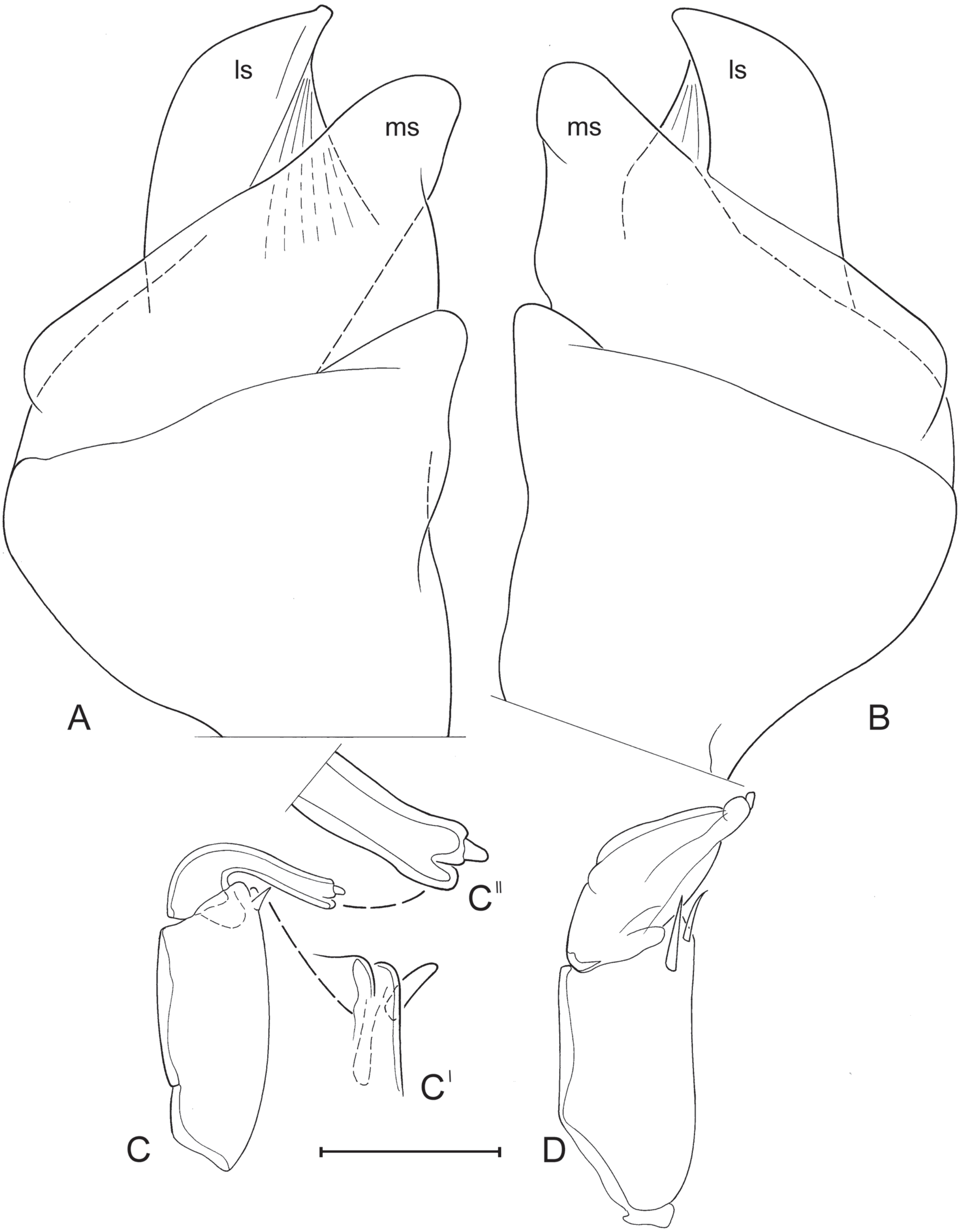

Fig. 10. *Bennelongia timmsi* sp. nov., male paratype (WAMC52232) from type locality (Wave Rock, BVT/10/05) Aberrant specimen. **A**. Hemipenis. **B**. Hemipenis. **C**. Left prehensile palp. **C'**. Idem, detail of ventroapical part of first segment, showing two lobes and a sensory organ. **C"**. Idem, detail of distal part of second segment, showing aberrant, bilobed morphology. **D**. Right prehensile palp. Scale: A-D = 92 µm; C', C" = 37 µm.

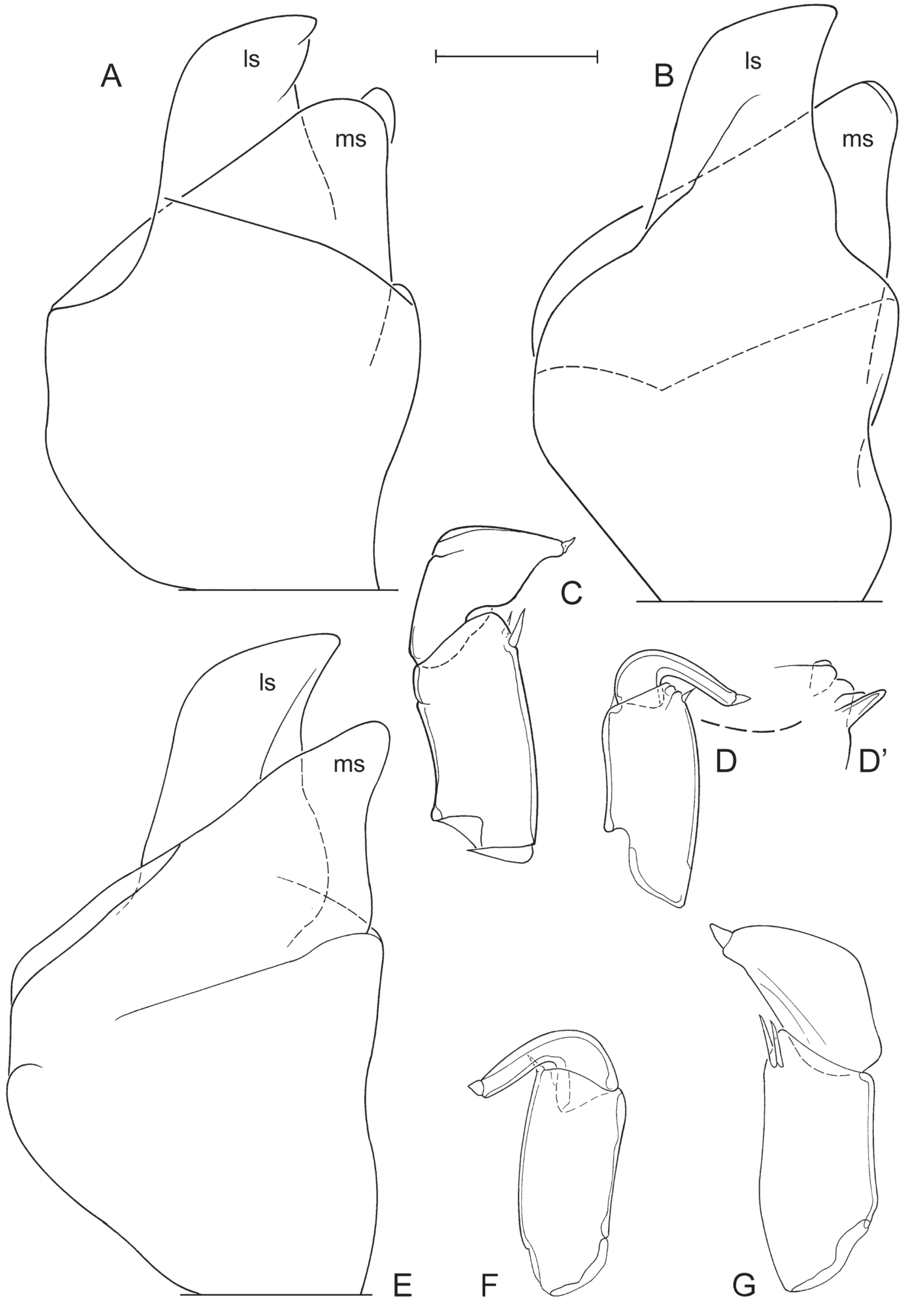

Fig. 11. *Bennelongia timmsi* sp. nov., non-type males. — **A-D**. Grahams Rock (WAMC52240, BVT/10/02): **A**. Hemipenis. **B**. Hemipenis. **C**. Right prehensile palp. **D**. Left prehensile palp. **D’**. Idem, detail of ventro-apical part of first segment. — **E-F**. King Rocks (WAMC52252, BVT/10/06): **E**. Hemipenis. **F**. Left prehensile palp. **G**. Right prehensile palp. Scale: A-G = 92 µm; D’ = 37 µm.

Paynes Find Rocks. Approximate coordinates: 29º10’ S, 117º40’ E (sample BVT/10/01), collected by B.V. Timms on 23 Jul. 2010 (one ♀ - WAMC52239).
Grahams Rock. 32º28’ S, 119º03’ E (sample BVT/10/02), collected by B.V. Timms on 23 Jul. 2010 (six ♂♂ and ♀♀, WAMC52240-52244; OC.3317).
Anderson Rock. 32º10’ S, 118º51’ E (sample BVT/10/03), collected by B.V. Timms on 23 Jul. 2010 (one ♂, WAMC52245).
Burracopin Rock. 31º24’ S, 118º27’ E (sample BVT/10/04), collected by B.V. Timms on 26 Jul. 2010 (six ♂♂ and ♀♀, WAMC52246-52249; OC.3318-3319).
King Rocks. 32º19’ S, 119º09’ E (sample BVT/10/06), collected by B.V. Timms on 23 Jul. 2010 (one ♂ and two ♀♀, WAMC52250-52252).
Yorkrakine Rocks. 31º25’ S, 117º30’ E (sample BVT/10/07), collected by B.V. Timms on 27 Jul. 2010.
Mt Madden Rock. 33º14’ 22” S, 119º50’ 33” E (sample BVT/10/08), collected by B.V. Timms on 01 Aug. 2010 (11 ♂♂ and ♀♀, WAMC52253-52262; OC.332-3321).

Differential diagnosis

Bennelongia timmsi sp. nov. can be distinguished from most species of the *B. barangaroo* lineage by the triangular and ventrally pointed lapel on the RV and the strongly sinuous ventral valve margins. The lapel of *B. scanloni* sp. nov. is also subtriangular and ventrally protruding, but it is rounded, thus looking drop-shaped in internal (non-tilted) view.

Bennelongia timmsi sp. nov. can moreover be distinguished from *B. gnamma* sp. nov. by the less high and less rounded valves and by the ls of the hemipenes, which protrudes well beyond the ms (subequal in *B. gnamma* sp. nov.).

Additional notes on cryptic species

As was described above, five genetic clusters are recognised in this species (A1-5, Fig. 2). According to the calculations of the 4 theta rule, three cryptic species were found in *B. timmsi* sp. nov. with molecular methods, but no morphological diagnostic features could be found. Cryptic species A1 occurred in BVT/10/02, 03 and 07. Cryptic species A3 was found in BVT/10/02, 04, 06 and 08. Cryptic species A2+A4+A5 occurred in BVT/10/03 and 05 and is used here to characterize *B. timmsi* sp. nov. with BVT/10/05 (Wave Rock) as type locality. Note that BVT/10/02 (Grahams Rock) and BVT/10/03 (Anderson Rock) hold at least two sympatric clades/cryptic species each. In order to establish beyond reasonable doubt that the specimens belonging to these clusters and cryptic species are indeed morphologically indistinguishable, long series of specimens are illustrated.

Sample BVT/10/05 from pools on Wave Rock appeared to contain only one genetic cluster and cryptic species and, for this reason, Wave Rock was chosen as type locality. We then proceeded with two different approaches: (1) to dissect a series of males from this sample to test whether male reproductive organs (hemipenes, prehensile palps) showed uniformity within one cluster/cryptic species; (2) we checked for potential differences in the morphology of the valves of specimens belonging to different populations and/or shown to belong to different clusters/cryptic species.

Type specimens

Valves and carapaces of males and females of the type population (in sample BVT/10/05) were illustrated (Fig. 4) and this morphology defines the species. We then dissected several males from the same sample and population and illustrated the soft part and valve morphology. Shape of valves and size and shape of the antero-ventral lapel on the RV were most similar and indeed almost indistinguishable (Fig. 5). In all male specimens the valves have the shape described in the diagnosis above. The lapels are all elongated subtriangular, with a more or less serrated distal margin. In tilted perspective some lapels appear to be shorter than others (e.g., the lapel in Fig. 5B appears shorter than in 5E), but this is almost entirely a matter of distorted perspective depending on how the valves were positioned when the photographs were taken (the same lapels appear almost equally long in non-tilted views - Fig. 5A and 5F, respectively).

However, there are significant differences in soft part morphology. Whereas the shapes of the hemipenis-outline and of the left prehensile palps are fairly uniform in the different specimens (Figs 8A, C, E-F; 9A, C-D, F), the second segment of the right prehensile palps ranges from elongated sub-triangular with almost equally rounded distal margin (Fig. 8B, D), to sub-rectangular with a clear blunt corner in this margin (Fig. 9B, E). It is not clear to what extend these differences are a biological reality, or whether the differences are distortions of the limbs caused by different positions in the slides. The differences are sufficiently small to be accepted as part of intra-specific variability, yet future investigations should take this variability into account. The morphology in the holotype (WAMC52228 – right prehensile palp in Fig. 8D) determines the specific morphology.

One male (WAMC52232 – Fig. 10A-D) had an aberrant morphology, with the terminal segment of the right prehensile palp (Fig. 10D) being even more elongated and with especially the terminal segment of the left prehensile palp being distally bilobed (Fig. 10C, C"), a morphology never before encountered in Cyprididae. Nevertheless the valves of this male show no differences with other type specimens (Fig. 5A-C).

Morphology within different clades/cryptic species

Valve morphology of specimens for which molecular clades are known (A1: Fig. 6A-C; A2: Fig. 6D-I; A3: Fig. 6J-L; A5: Fig. 6M-O, 7A-C) and for specimens from different populations for which no molecular data were available (Fig. 7D-N) again show no constant differences that could be used as identifying characters. There is some variability in size, shape and degree of crenulation of the lapel, but insufficiently so to use such features to characterise different clades/cryptic species.

One male specimen from BVT/10/02 and thus belonging to either cryptic species A1 or A3, had a right prehensile palp with a terminal segment clearly showing a blunt angle on the distal margin (Fig. 11C), while a male from BVT/10/06, and thus most likely belonging to clade A2, had a more elongated segment there with a more rounded distal margin (Fig. 11G) as in the holotype. In both of these specimens, the terminal segment of the left prehensile palp is slightly shorter than in the type specimens (Fig. 11D, F). Hemipenis outlines (Fig. 11A-B, E) are indistinguishable from those in the types.

Ecology and distribution

Bennelongia timmsi sp. nov. is a typical rock pool species and occurs in fresh water in gnammas on various rocky outcrops in the south/central part of western Australia. Although it appears to be limited to this restricted area, it seems to be quite common there.

Bennelongia gnamma sp. nov.

Figs 12, 13A-E

urn:lsid:zoobank.org:act:6931D617-1443-4776-891B-C02752E6C0BE

Diagnosis

Valves in internal view (Fig. 12A-B, E-F) high, with greatest height situated in front of the middle; ventral margin almost evenly curved except for middle third. LV (Fig. 12A, E) with anterior il slightly overlapping. RV (Fig. 12B, F) with antero-ventral lapel subtriangular, asymmetrically produced with a dorsal point (Fig. 12H-K).

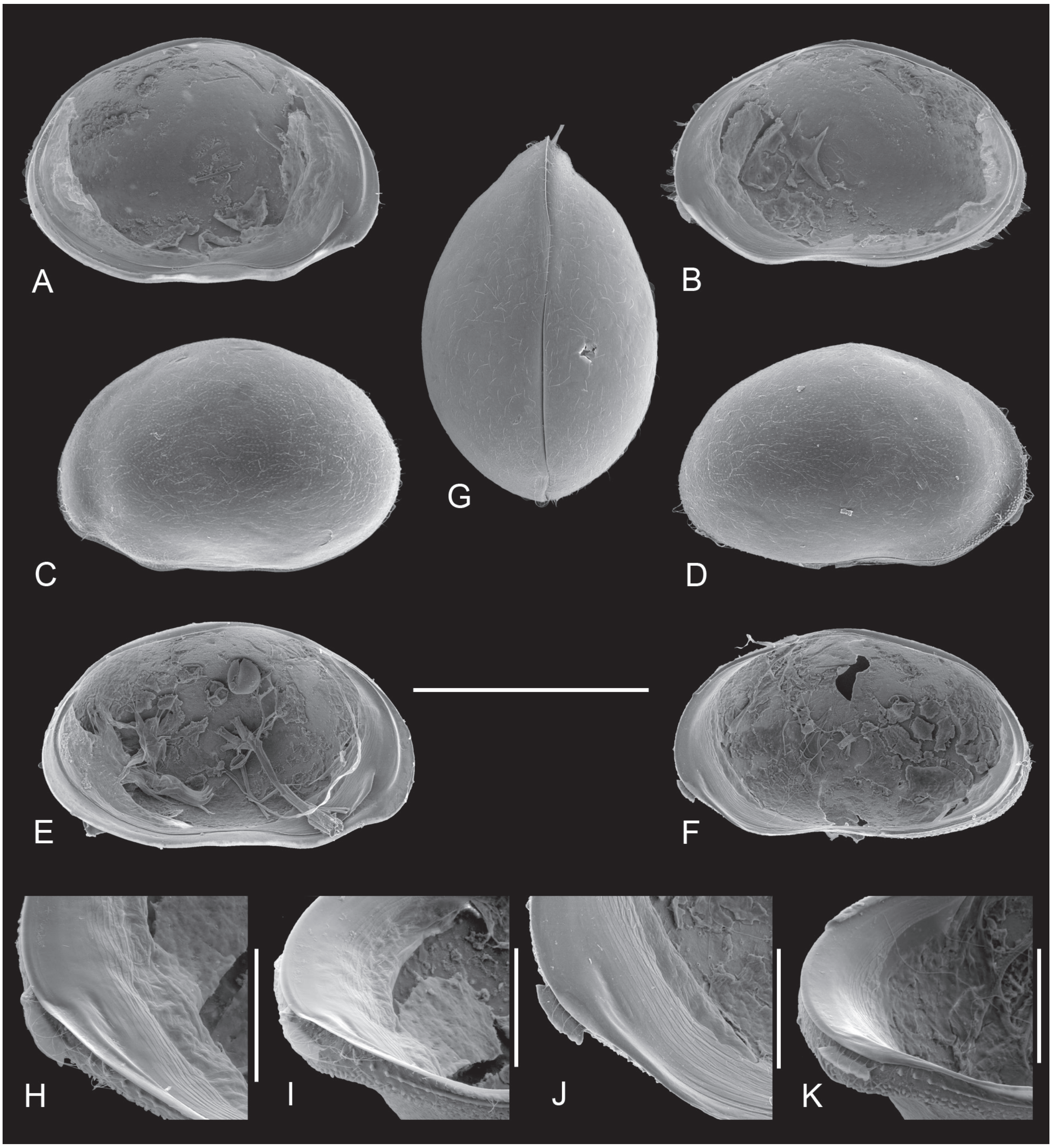

Fig. 12. *Bennelongia gnamma* sp. nov., type material from type locality (Cairn Rock, OSTR012A). **A**. ♀ paratype, LVi (OC.3322). **B**. ♀ paratype, RVi (idem). **C**. ♀ paratype, LVe (idem). **D**. ♀ paratype, RVe (idem). **E**. ♀ holotype, LVi (WAMC52263). **F**. ♀ holotype, RVi (idem). **G**. ♀ paratype, CpD (WAMC52266). **H**. ♀ paratype, RVi, detail anterior (OC.3322). **I**. ♀ paratype, RVi, detail anterior, tilted (idem). **J**. ♀ holotype, RVi, detail anterior (WAMC52263). **K**. ♀ holotype, RVi, detail anterior, tilted (idem). Scales: A-G = 1 mm; H-K = 200 μm.

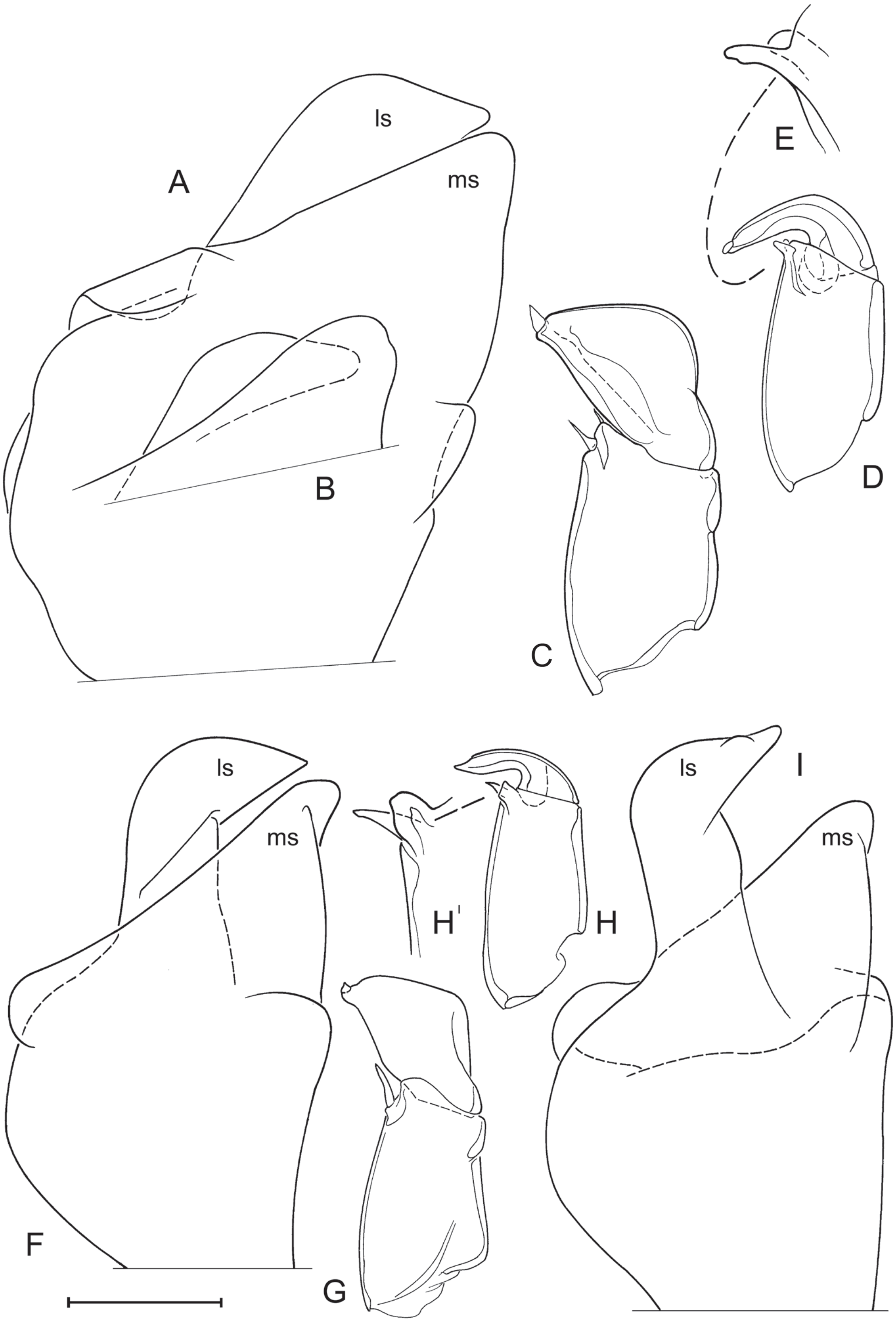

Fig. 13. *Bennelongia gnamma* sp. nov. (A-E, type specimens from type locality, Cairn Rock, OSTR012A) and *Bennelongia hirsuta* sp. nov. (F-I type specimens from type locality, Styles Rock, OSTR012D). Males. — **A-E**. *B. gnamma* sp. nov.: **A**. Hemipenis (both hemipenes symmetrical in this specimen, WAMC52264). **B**. Apical part of hemipenis (WAMC52265). **C**. Right prehensile palp (WAMC52264). **D**. Left prehensile palp (WAMC52264). **E**. Idem, detail of ventro-apical part of first segment (different specimen, WAMC52265). — **F-I**. *B. hirsuta* sp. nov. (WAMC52271): **F**. Hemipenis. **G**. Right prehensile palp. **H**. Left prehensile palp. **H'**. Idem, detail of ventro-apical part of first segment. **I**. Hemipenis. Scale: A-D, F-I = 92 µm; E, H' = 37 µm.

Valves in external lateral view (Fig. 12C-D) high and rounded on all sides, even ventrally to some extent; hirsute and weakly pitted. Carapace in dorsal view (Fig. 12G) anteriorly with a mild rostrum.

Hemipenes (Fig. 13A) mostly symmetrical, with length of ls subequal to that of ms, in one specimen tip of ms even extending beyond that of ls (Fig. 13B); ls with broad base, ventrally bluntly beak-shaped. Right prehensile palp (Fig. 13C) with distal segment broad, with anterior margin straight, distal margin bilobed. Left prehensile palp (Fig. 13D-E) with distal segment short, reaching beyond ventro-apical margin of proximal segment with less than half its length.

Etymology

The present species is named after the Australian term for small to middle-sized rock pools, namely gnammas, in which it occurs.

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

Holotype ♀ (WAMC52264): RV: L = 1550, H = 915. LV: L = 1620, H = 991.

Type locality

Rock pools (gnammas) on Cairn Rock, WA, ca. 67 km SE of Merredin. Approximate coordinates: 31º51’31” S, 118º50’39” E (WGS 84). All material (voucher sample OSTR012A; locality code SPS059) collected by J. McRae & A. Pinder on 24 Sep. 1997 with a sweep net.

Type material

Holotype

♀ (WAMC52263), with soft parts dissected in a sealed slide and valves stored dry in a micropalaeontological slide.

Allotype

♂ (WAMC52264), with soft parts dissected in a sealed slide, and valves stored dry in a micropalaeontological slide.

Paratypes

2 ♀♀ (WAMC52266; OC.3322) and one ♂ (WAMC52265); 3 ♀♀ in bulk in EtOH (WAMC52267).

Other material investigated

? 1 ♀ (WAMC52268) from Yanneymooning Rocks (identification uncertain).

Differential diagnosis

Bennelonga gnamma sp. nov. can be distinguished from all other species in the lineage by the high and rounded shape of the valves and especially by the subequal ls and ms in the hemipenes.

Ecology and distribution

This species is thus far known with certainty only from its type locality, a set of rock pools on Cairn Rock.

Bennelongia hirsuta sp. nov.

Figs 13F-I, 14

urn:lsid:zoobank.org:act:CDE0D1E7-52E6-4F18-B6FF-B3AD48C6E4B4

Diagnosis

Valves elongated, with greatest height situated well in front of the middle, dorsal margin evenly sloping towards the posterior side; ventral margin anteriorly with pronounced mandibular curve. LV (Fig. 14A, D) with antero-ventral inner list large, well-overlapping the dorsal il. RV (Fig. 14B, E) with antero-ventral lapel long, narrow and weakly crenulated (Fig. 14J-M).

Carapace in dorsal and ventral view (Fig. 14G-I) with greatest width in the middle, most hirsute, anteriorly with a clear rostrum; in lateral views (Fig. 14C, F) anteriorly with a clear LV>RV overlap.

Hemipenes asymmetrical (Fig. 13F, I), ls with slender base, ventrally sharply beak-shaped and pointed, only slightly protruding beyond ventral tip of ms. Right prehensile palp (Fig. 13G) with distal segment stout and subquadrate, anterior margin straight, dorsal margin sinuous. Left prehensile palp (Fig. 13H, H') with distal segment short and sickle-shaped, reaching beyond ventro-apical margin of proximal segment with less than a third of its length.

Etymology

Named after the hirsute ('hairy') nature of this species. All species of the *B. barangaroo* lineage are hirsute to some extent, but the present species is more so, with the entire carapace set with long and stiff setae.

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

Holotype ♂ (WAMC52269): RV: L = 1260, H = 738. LV: L = 1320, H = 763.
Allotype ♀ (WAMC52270): RV: L = 1400, H= 842. LV: L = 1470, H = 845.

Type locality

Rock pools (gnammas) on Styles Rock, WA, ca. 80 km N of Esperance. Approximate coordinates: 33º07'35" S, 121º48'02" E (WGS 84). All specimens (voucher sample OSTR012D; locality code SPS139), collected on 07 Sep. 1998 by J. McRae & A. Pinder with a sweep net.

Type material

Holotype

♂ (WAMC52269), with soft parts dissected in a sealed slide and valves stored dry in a micropalaeontological slide.

Allotype

♀ (WAMC52270), with soft parts dissected in a sealed slide, and valves stored dry in a micropalaeontological slide.

Paratypes

Numerous ♂♂ and ♀♀, as valves or carapaces (WAMC52271-52277; OC.3323-3325). Nine ♂♂ and ♀♀ in bulk in EtOH (WAMC52278).

Other material investigated

? One ♀ (WAMC52279) from Lilian Stokes Rocks (BVT/10/09) (identification uncertain).

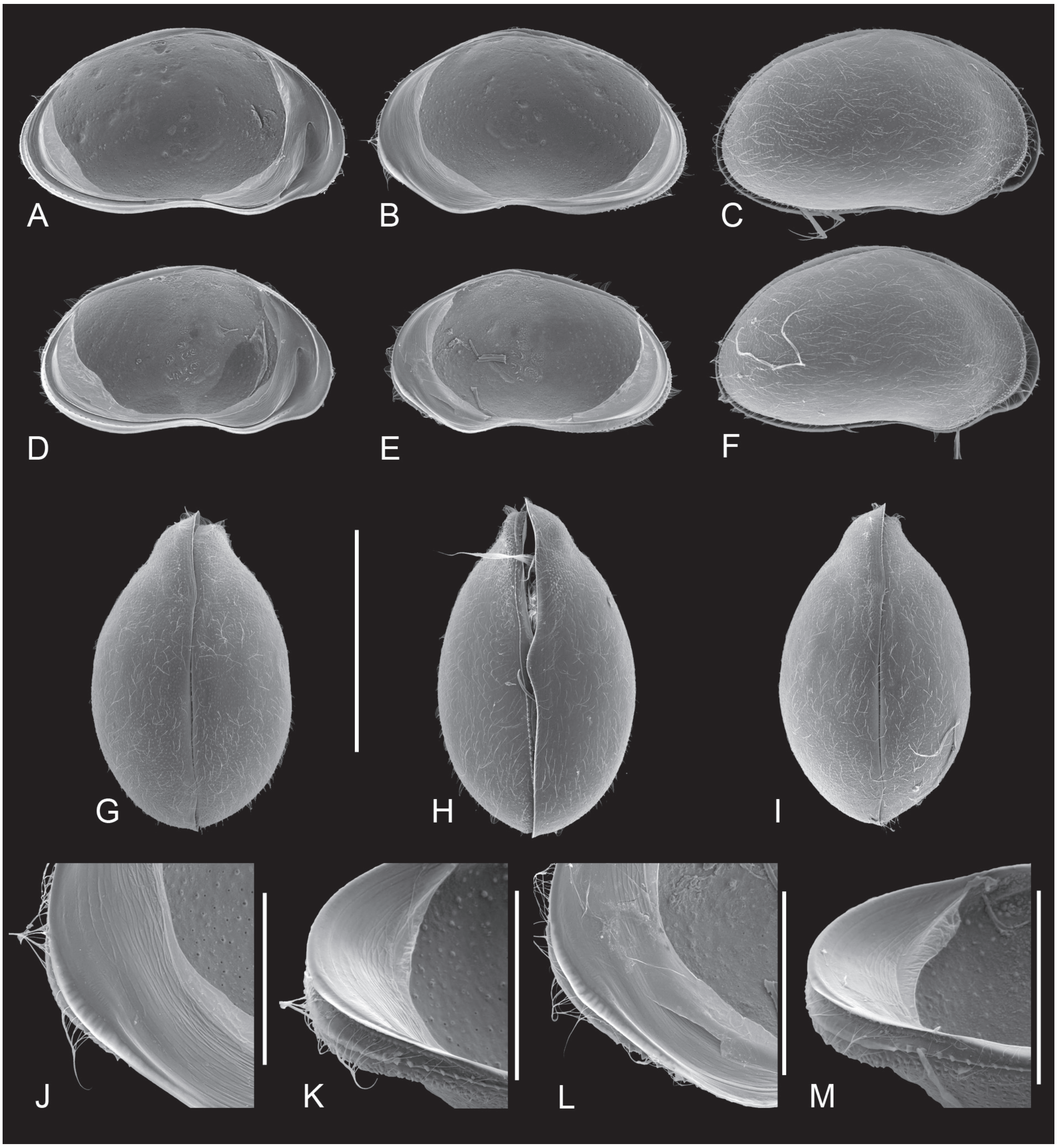

Fig. 14. *Bennelongia hirsuta* sp. nov., type specimens from type locality (Styles Rock, OSTR012D). **A**. ♀ allotype, LVi (WAMC52270). **B**. ♀ allotype, RVi (idem). **C**. ♀ paratype, CpRL (WAMC52277). **D**. ♂ holotype, LVi (WAMC52269). **E**. ♂ holotype, RVi (idem). **F**. ♂ paratype, CpRL (WAMC52272). **G**. ♀ paratype, CpD (WAMC52275). **H**. ♀ paratype, CpV (WAMC52276). **I**. ♂ paratype, CpD (WAMC52272). **J**. ♀ allotype, RVi, detail anterior (WAMC52270). **K**. ♀ allotype, RVi, detail anterior, tilted (idem). **L**. ♂ holotype, RVi, detail anterior (WAMC52269). **M**. ♂ holotype, RVi, detail anterior, tilted (idem). Scales: A-I = 1 mm; J-M = 300 µm.

Differential diagnosis

Bennelongia hirsuta sp. nov. can be distinguished from all other species in the *B. barangaroo* lineage by the pointed shape of the ls in the hemipenis. Also the shapes of the distal segments of the prehensile palps are distinctive. In valve morphology, the species is easily recognisable by the long and narrow lapel on the RV (which is nevertheless very difficult to see with a normal binocular microscope) and the large antero-ventral il.

Ecology and distribution

The species is thus far only known with certainty from its type locality, a set of rock pools on Styles Rock.

Bennelongia ivanae sp. nov.

Fig. 15

urn:lsid:zoobank.org:act:2D60FC82-0938-475A-AF4E-E2DBE24D1D8D

Diagnosis

Valves (Fig. 15A-B) high and rounded, with greatest height situated well in front of the middle; dorsal margin with blunt angle towards the posterior side; ventral margin almost straight, without pronounced mandibular curve. LV (Fig. 15A) with antero-ventral il well-developed in lower third of the valve, dorsal il descending almost to ventral side, thus clearly overlapping with ventral il. RV (Fig. 15B) without antero-ventral lapel (Fig. 15H-J). Carapace in dorsal and ventral views (Fig. 15D-F) with greatest width in the middle, medium hirsute and slightly pitted, anteriorly with a hint of a rostrum; in lateral view (Fig. 15C, G) anteriorly with a clear LV>RV overlap.

Male unknown.

Etymology

This species is named after Dr Ivana Karanovic (South Korea), in recognition of her contributions to the knowledge of the subterranean candonids of the Pilbara area.

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

Holotype ♀ (WAMC52280): RV: L = 1475, H = 915. LV: L = 1533, H = 948.

Type locality

Rock pools (gnammas) on Holland Rocks, WA. Approximate coordinates: 33°21’35.66” S, 118°44’48.55” E (WGS 84) (sample DJC/02). All specimens collected and handpicked by D.J. Cale on 30 Aug. 2011.

Type material

Holotype

♀ valves stored dry (WAMC52280).

Allotype

As males are unknown, no allotype is designated.

Paratypes

Four ♀♀ with valves or carapaces stored dry (WAMC52281-52282; OC.3326-3327); *ca.* 25 ♀♀ stored dry as bulk in one micropalaeontological slide.

Other material investigated

? ♀♀ valves stored dry (WAMC52284) from Yanneymooning Rocks (OSTR013F).

Differential diagnosis

Bennelongia ivanae sp. nov. differs from all other WA species within the *B. barangaroo* lineage in the total absence of an antero-ventral lapel on the RV and in the fact that the antero-dorsal il in the LV runs almost entirely to the ventral margin. *Bennelongia mckenziei* Shearn *et al.*, 2012 from Queensland also lacks the antero-ventral lapel on the RV completely, but it has a notably different valve and carapace

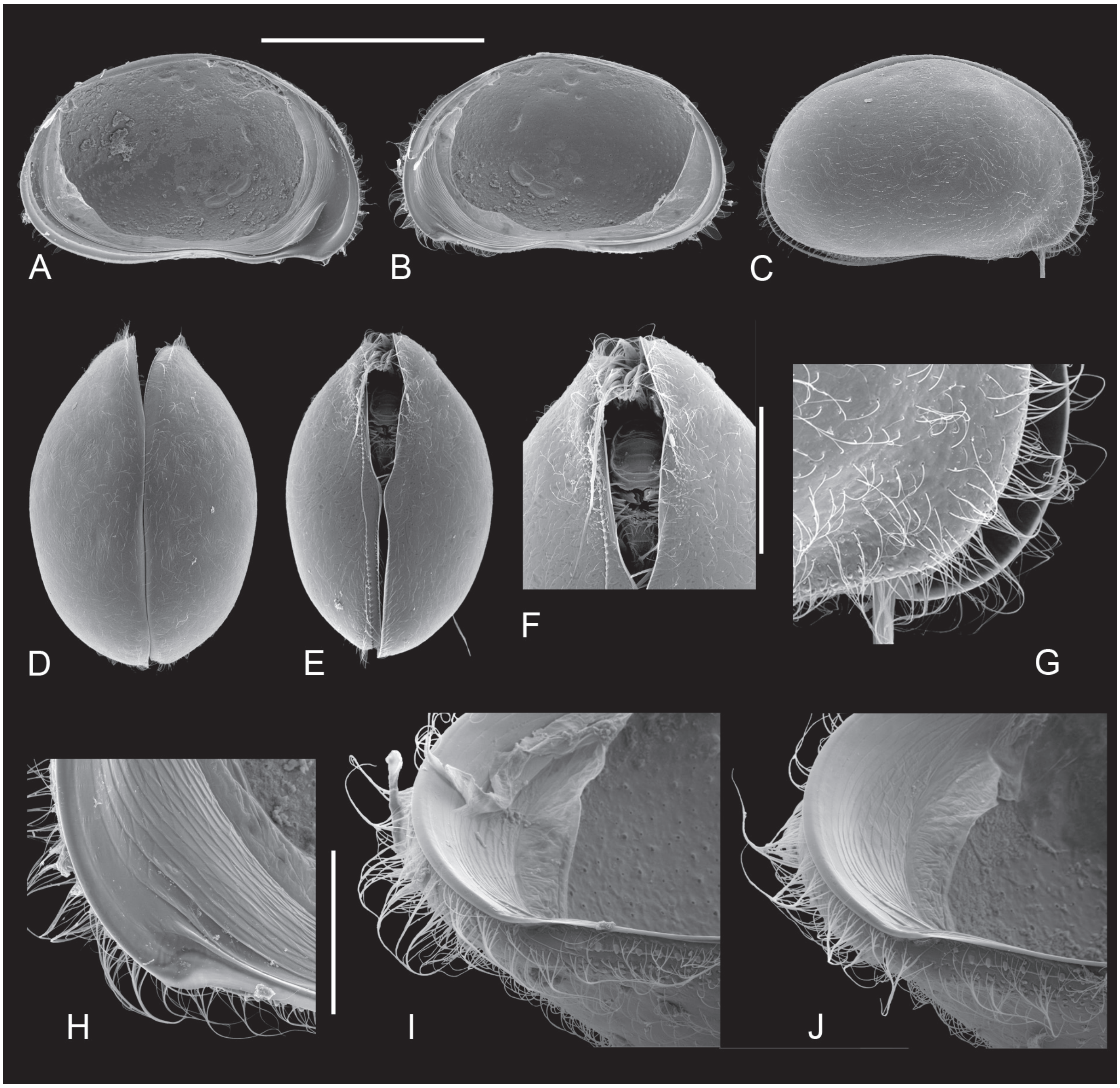

Fig. 15. *Bennelongia ivanae* sp. nov., type specimens from type locality (Holland Rocks, DJC/02). **A**. ♀ holotype, LVi (WAMC52280). **B**. ♀ holotype, RVi (idem). **C**. ♀ paratype, CpRL (OC.3327). **D**. ♀ paratype CpD (WAMC52281). **E**. ♀ paratype, CpV (WAMC52282). **F**. ♀ paratype, CpV, detail anterior (idem). **G**. ♀ paratype, CpRL, detail anterior (OC.3327). **H**. ♀ holotype, RVi, detail anterior (WAMC52280). **I**. ♀ holotype, RVi, detail anterior, tilted (idem). **J**. ♀ paratype, RVi, detail anterior, tilted (OC.3326). Scales: A-E = 1 mm; F = 400 μm; G-J = 200 μm.

shape, with a more pointed caudal margin and an evenly sloping dorsal margin in both valves, a shorter antero-dorsal il in the LV and an anterior LV>RV overlap in a carapace in right lateral view which is twice as large as in *B. ivanae* sp. nov.

Remark

Bennelongia ivanae sp. nov. and *B. mckenziei* have pronounced molecular differences, when the present sequences of *B. ivanae* sp. nov. are compared with those of Shearn *et al.* (2012). Because of the shorter lengths of the sequences provided by Shearn *et al.* (2012), the alignment of COI sequences from *B. ivanae* sp. nov. and *B. mckenziei* are not shown in the present paper.

Ecology and distribution

The species has thus far been found with certainty only from rockpools at Holland Rocks. Two tentatively identified females also originated from rock pools on another outcrop.

Bennelongia sp. nov. F2

Material investigated

Two ♀♀ (KMWA.905, 906) *in toto* used for molecular screening, one ♀ with soft parts used for molecular screening and with broken RV stored dry in micropalaeontological cavity slide (WAMC52285 = KMWA.904).

Locality

Lilian Stokes Rocks (eastern Wheatbelt – BVT/10/09), coordinates: 33º4’06” S, 120º05’49” E. Collected on 25 Aug. 2010 by B.V. Timms.

Remarks

The specimens of the F2-group cluster close to those of *B. ivanae* sp. nov. in the phylogenetic tree (Fig. 2), but still constitute a separate genetic species (Table 2). A broken RV could be saved from only one of these specimens (KMWA.904), and it could be ascertained that the antero-ventral lapel on the RV is also fully absent (not shown). It is possible that cluster F2 will turn out to be a cryptic species within *B. ivanae* sp. nov., but this remains to be tested with new material. Note that the same sample (BVT/10/09) also contained one putative female of *B. hirsuta* sp. nov. (see above).

Bennelongia mcraeae sp. nov.

Figs 16-17

urn:lsid:zoobank.org:act:DFD1A720-E602-46CC-AABF-C6EDD63CD70E

Diagnosis

Valves (Fig. 16A-B, E-F) high and rounded, with greatest height situated on or close to the middle, dorsal margins almost evenly rounded; ventral margin weakly sinuous. LV (Fig. 16A, E) with antero-ventral il large, reaching over half of the anterior margin; dorsal il descending along ca. 4/5 of anterior margin, both lists thus clearly overlapping. RV (Fig. 16B, F) with antero-ventral lapel fairly ventrally inserted, large and pronounced, with rounded, weakly crenulated margin (Fig. 16D, I-L). Carapace in lateral view (Fig. 16C- D) pitted, especially along anterior and posterior margins, and set with few setae.

Hemipenes (Fig. 17A, F) largely symmetrical, ls with broad base, ventrally bluntly beak-shaped, only protruding significantly beyond ventral tip of ms. Right prehensile palp (Fig. 17C, E) with distal segment stout, but of somewhat variable shape, either strongly subquadrate or with rounded dorsal and anterior

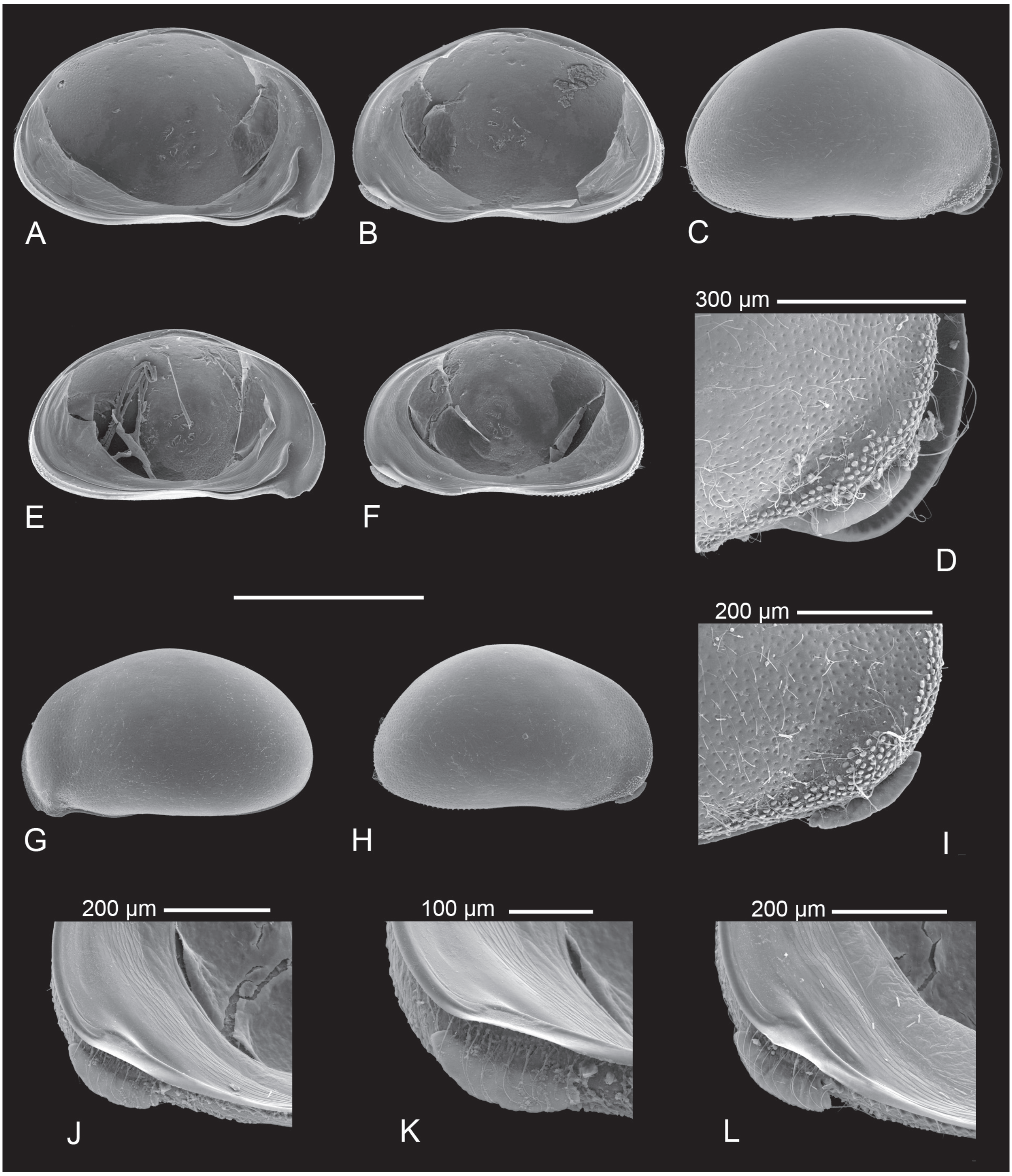

Fig. 16. *Bennelongia mcraeae* sp. nov., type specimens from type locality (Arro Lake, OSTR014). **A**. ♀ allotype, LVi (WAMC52287). **B**. ♀ allotype, RVi (idem). **C**. ♀ paratype, CpRL (WAMC52289). **D**. ♀ paratype, CpRL, detail anterior (idem). **E**. ♂ holotype, LVi (WAMC52286). **F**. ♂ holotype, RVi (Idem). **G**. ♂ holotype, LVe (idem). **H**. ♂ holotype, RVe (idem). **I**. ♂ holotype, RVe, detail anterior (idem). **J**. ♂ holotype, RVi, detail anterior (idem). **K**. ♂ holotype, RVi, detail anterior, tilted (idem). **L**. ♀ allotype, RVi, detail anterior, tilted (WAMC52287). Scales = 1 mm unless otherwise indicated.

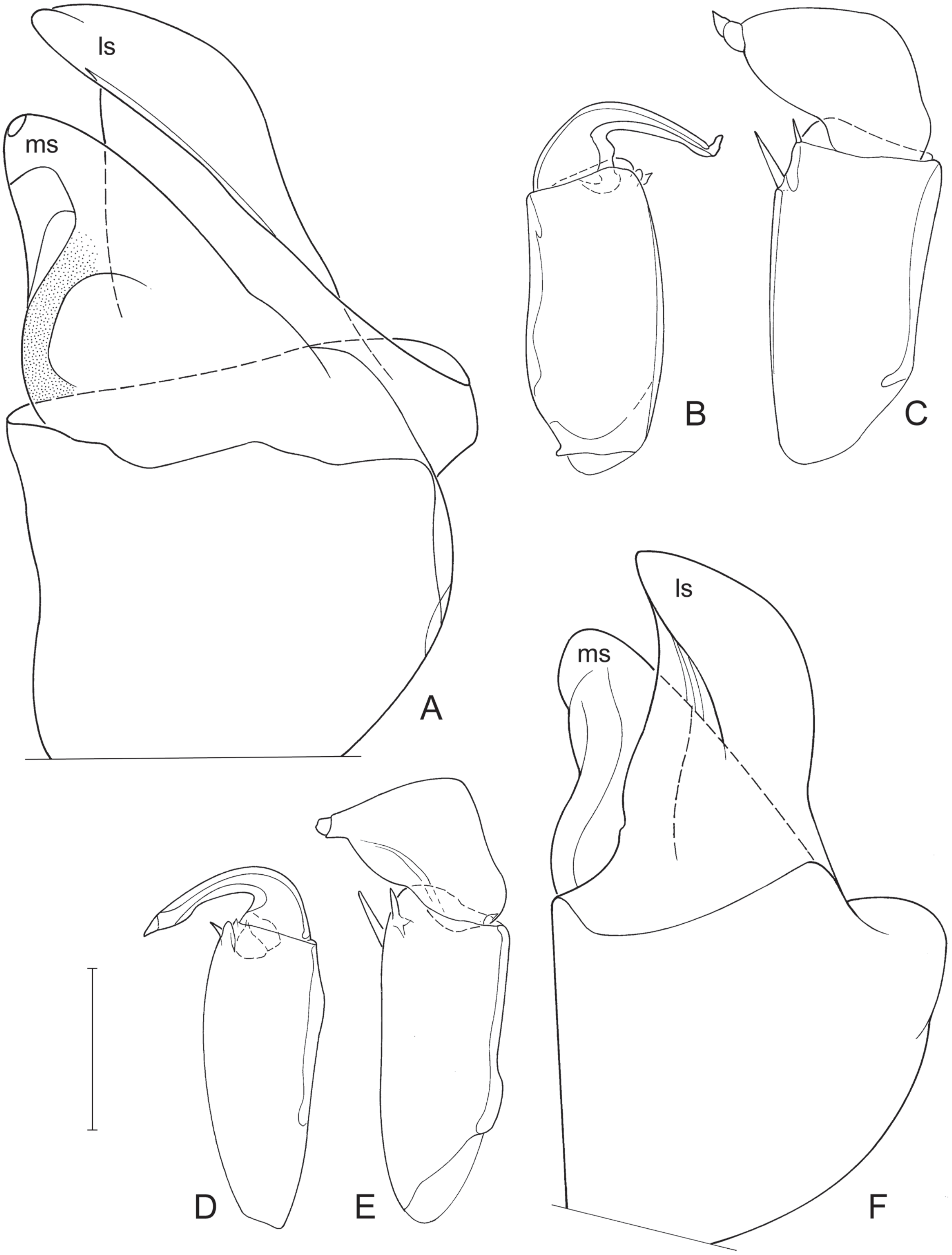

Fig. 17. *Bennelongia mcraeae* sp. nov., type males from type locality (Arro Lake, OSTR014B). — **A-C**. Holotype ♂ (WAMC52286). **A**. Hemipenis. **B**. Left prehensile palp. **C**. Right prehensile palp. — **D-F**. Paratype ♂ (OC.3328). **D**. Left prehensile palp. **E**. Right prehensile palp. **F**. Hemipenis. Scale: A-F = 92 µm.

margins. Left prehensile palp (Fig. 17B, D) with distal segment long and slender, reaching beyond ventro-apical margin of proximal segment with at least half of its length.

Etymology

The species is named in honour of Jane McRae (Perth, WA) in acknowledgement of her vast knowledge of the taxonomy and morphology of many invertebrate groups of Western Australia. She also collected the type material of the present species and has unrelentingly provided technical help towards the present revision of *Bennelongia* since 2006.

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

Holotype ♂ (WAMC52286): RV: L = 1480, H = 878. LV: L = 1560, H = 896.
Allotype ♀ (WAMC52287): RV: L = 1608, H = 1002. LV: L = 1663, H = 1033.

Type locality

Arro Lake, *ca*. 11 km NW of Eneabba, WA. Approximate coordinates: 29º44'11" S, 115º09'58" E (WGS 84). All specimens collected by J. McRae & A. Pinder (voucher OST14B; locality code SPS182) on 23 Sep. 1999 with a sweep net. Arro Lake is an open lake with a *Melaleuca/Casuarina* fringe. Water chemistry at the time of collecting: Salinity = 0.15 g/l, pH = 7.32. Nutrient levels were fairly high: total N = 1700 µg/l; total P = 220 µg/l. The milky-white colour of the water equates to a high level of turbidity (2200 NTU).

Type material

Holotype

♂ (WAMC52286), with soft parts dissected in a sealed slide and valves stored dry in a micropalaeontological slide.

Allotype

♀ (WAMC52287), with soft parts dissected in a sealed slide, and valves stored dry in a micropalaeontological slide.

Paratypes

Two ♂♂ (dissection: OC.3328; valves: WAMC52288) and one ♀ carapace (WAMC52289). Three females in bulk in EtOH (WAMC52290).

Differential diagnosis

The species is characterised especially by the large and stout lapel on the RV but also by the large antero-ventral il on the LV.

Ecology and distribution

Lake Arro (*ca.* 300 km N of Perth) is a large flat-bottomed body of water with episodic inflow that holds water for about 4-24 months after inflow. The lake has a clay base and sediment-driven turbidity. This species is known only from the type locality. From the same sample as the one that yielded *B. macraeae* sp. nov., Timms (2002) described a new species of Anostraca, *Branchinella complexidigitata* Timms, 2002.

Bennelongia scanloni sp. nov.

Figs 18-20

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Diagnosis

Valves (Fig. 18A-B, D-E) high, with greatest height situated close to the middle, dorsal margin evenly sloping towards the posterior side; ventral margin sinuous. LV (Fig. 18A, D) with antero-ventral il of medium size, covering lower third of valve, antero-dorsal il descending to about halfway along antero-ventral il. RV (Fig. 18B, E) with antero-ventral lapel tear-shaped in untilted lateral view; in tilted view, lapel subtriangular with rounded ventral point (Fig. 18K-N). Carapace in dorsal and ventral views (Fig. 18G-J) with greatest width in the middle, hirsute and pitted, anteriorly with a clear rostrum; in right lateral view (Fig. 18C, F) with large anterior LV>RV overlap, anterior margins of RV and LV not parallel.

Hemipenes (holotype: Fig. 20F) asymmetrical, ls with broad base, ventrally bluntly pointed (more so in one hemipenis than in the other), largely protruding beyond ventral tip of ms. Right prehensile palp (holotype: Fig. 20D) with distal segment stout and subquadrate, with sharp angle between anterior and dorsal margins, both of these margins almost straight. Left prehensile palp (holotype: Fig. 20E) with distal segment sickle-shaped and of intermediate length, reaching beyond ventro-apical margin of proximal segment with about half of its length.

Etymology

The species is named in honour of Mike Scanlon (Perth, WA) in acknowledgement of his unrelenting technical help since 2006 towards the present revision of *Bennelongia*.

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

Holotype ♂ (WAMC52291): RV: L = 1223, H = 694. LV: L = 1294, H = 714.
Allotype ♀ (WAMC52292): RV: L = 1263, H =752. LV: L = 1356, H = 775.

Type locality

One Tree Hill Creek, *ca.* 62 km SE of Dongara, WA. Approximate coordinates: 29º35'19.0" S, 115º26'31.0" E (WGS 84). All specimens (sample DJC/11; locality code SPS180) collected by D.J. Cale on 10 Sep. 2011 with a sweep net. Water chemistry at time of collecting: K25 5.62 mS/cm, pH 6.68, water temperature 20.8 ºC.

Type material

Holotype

♂ (WAMC52291), with soft parts dissected in a sealed slide and valves stored dry in a micropalaeontological slide.

Allotype

♀ (WAMC52292) valves stored dry in a micropalaeontological slide.

Paratypes

Numerous males and females either as dissection, or as valves or carapaces stored dry (WAMC52293-52304; OC.3329-3331). *Ca.* 30 ♂♂ and ♀♀ stored as bulk in EtOH (WAMC52305).

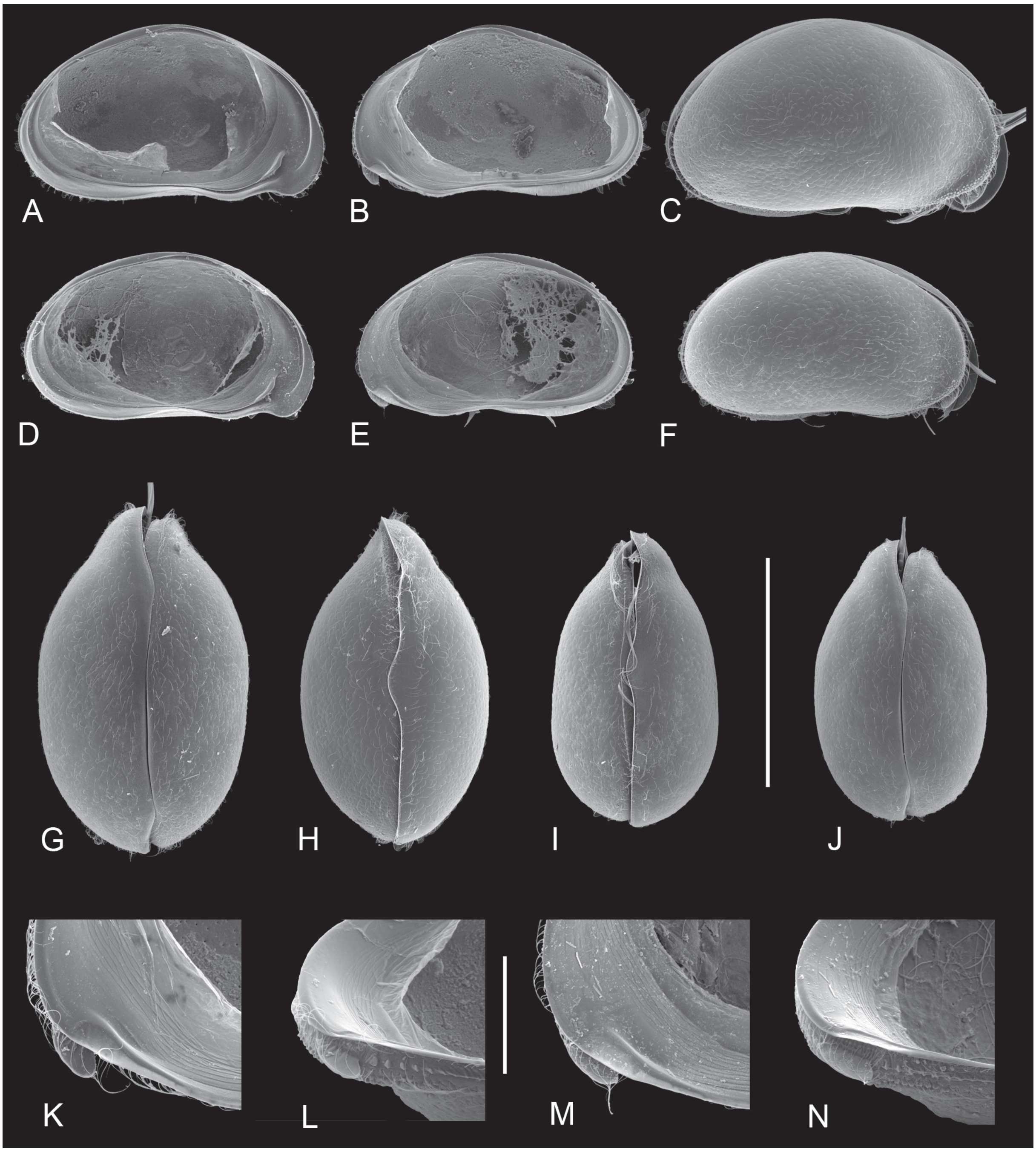

Fig. 18. *Bennelongia scanloni* sp. nov., type specimens from type locality (One Tree Hill Creek, DJC/11). **A**. ♀ allotype, LVi (WAMC52292). **B**. ♀ allotype, RVi (idem). **C**. ♀ paratype, CpRL (WAMC52299). **D**. ♂ paratype, LVi (OC.3329). **E**. ♂ paratype, RVi (idem). **F**. ♂ paratype, CpRL (WAMC52295). **G**. ♀ paratype, CpD (WAMC52297). **H**. ♀ paratype, CpV (WAMC52298). **I**. ♂ paratype, CpV (WAMC52295). **J**. ♂ paratype, CpD (WAMC52296). **K**. ♀ allotype, RVi, detail anterior (WAMC52292). **L**. ♀ allotype, RVi, detail anterior, tilted (idem). **M**. ♂ paratype, RVi, detail anterior (OC.3329). **N**. ♂ paratype, RVi, detail anterior, tilted (idem). Scales: A-J = 1 mm; K-N = 200 μm.

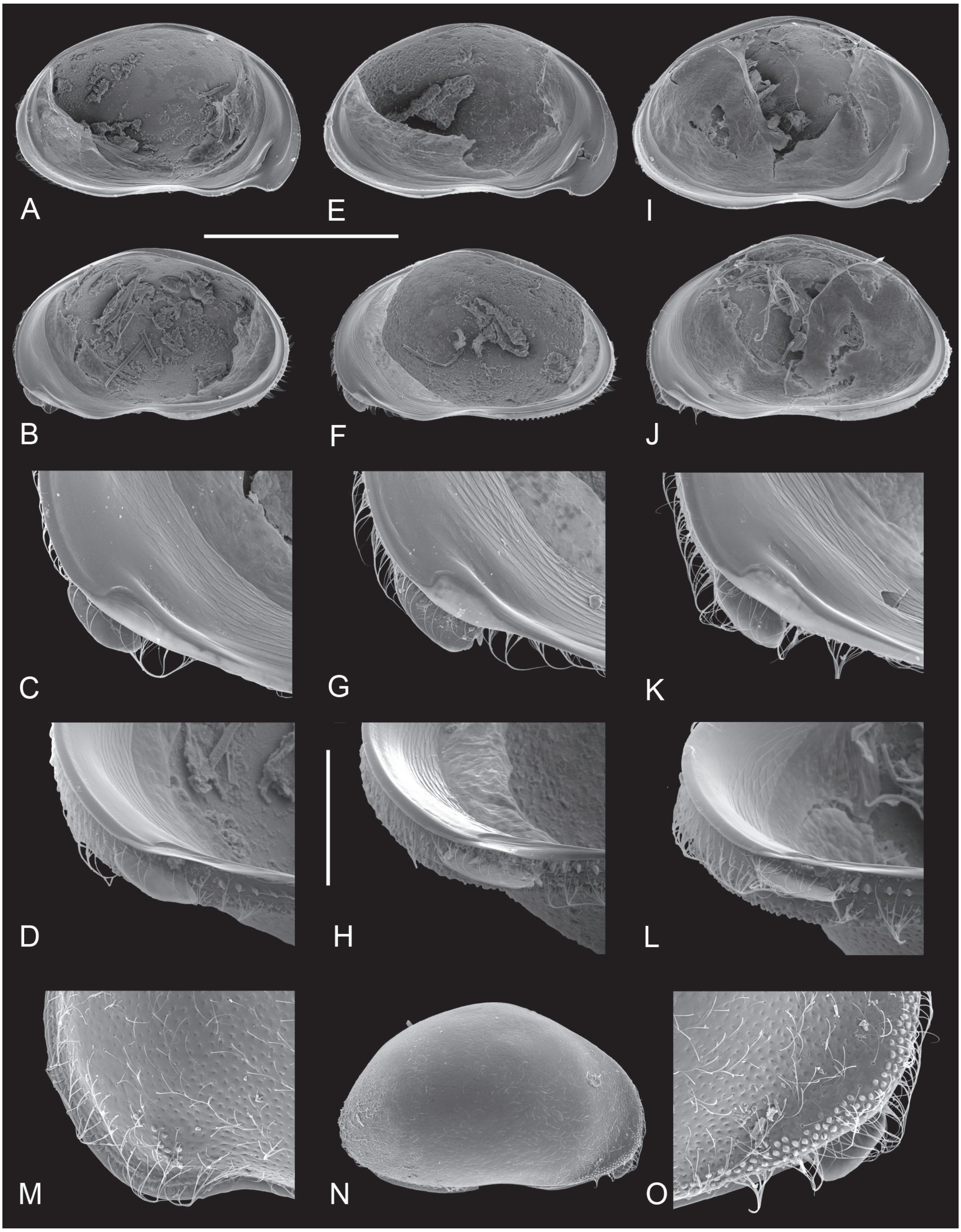

Fig. 19. *Bennelongia scanloni* sp. nov., non-type specimens. — **A-D**. Pool at Latham-Coorow Rd (BVT/10/10, ♀, WAMC52307)). **A**. LVi. **B**. RVi. **C**. RVi, detail anterior. **D**. RVi, detail anterior, tilted. — **E-H**. Tin Dog Creek (DJC/19, ♀, OC.3335). **E**. LVi. **F**. RVi. **G**. RVi, detail anterior. **H**. RVi, detail anterior, tilted. — **I-O**. Pool at Brookton Hwy (Warrine Park) (DJC/23, ♀, OC.3337). **I**. LVi. **J**. RVi. **K**. RVi, detail anterior. **L**. RVi, detail anterior, tilted. **M**. LVe, detail anterior. **N**. RVe. **O**. RVe, detail anterior. Scales: A-B, E-F, I-J, N = 1 mm; C-D, G-H, K-M, O = 200 µm.

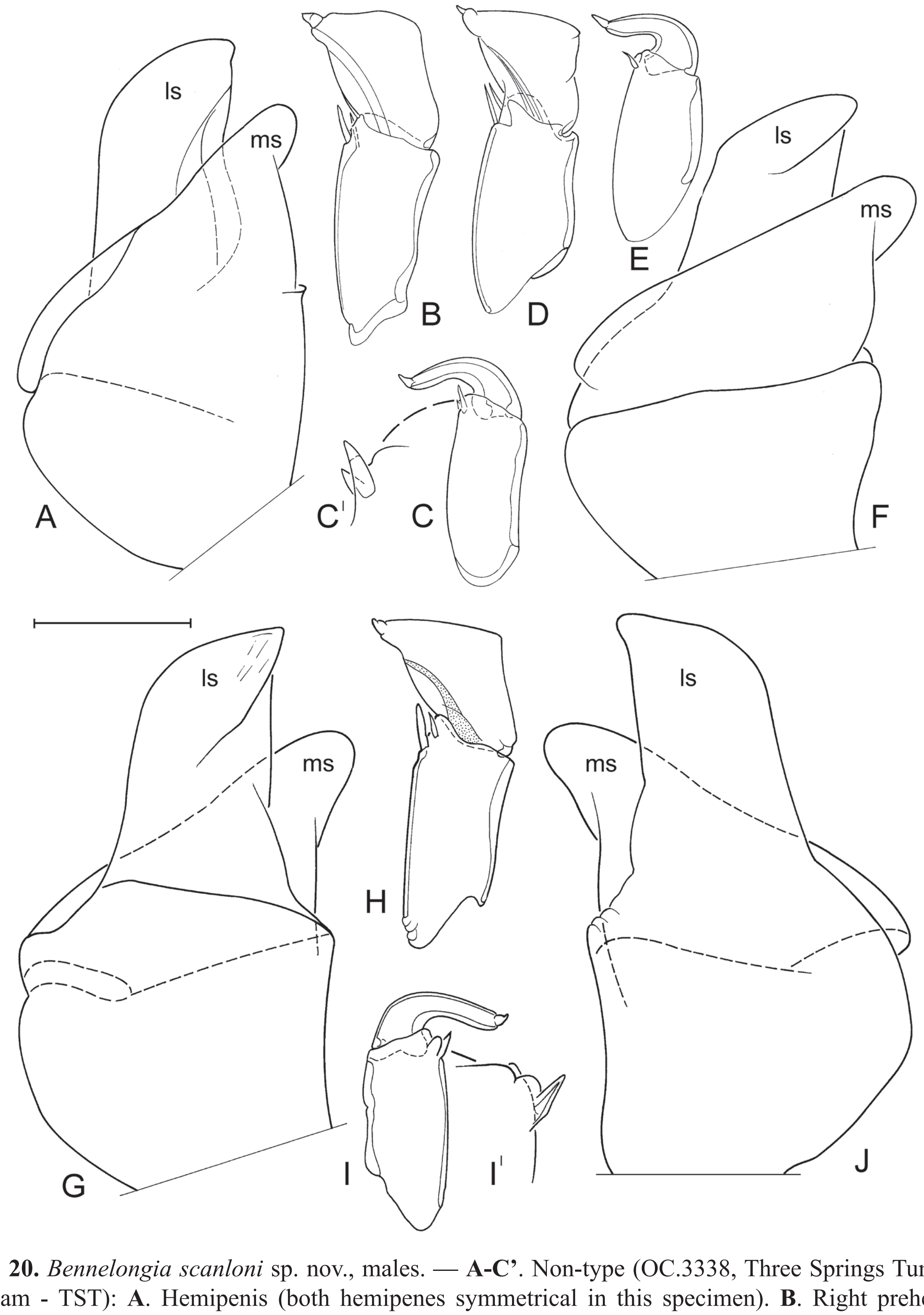

Fig. 20. *Bennelongia scanloni* sp. nov., males. — **A-C'**. Non-type (OC.3338, Three Springs Tumulus Stream - TST): **A**. Hemipenis (both hemipenes symmetrical in this specimen). **B**. Right prehensile palp. **C**. Left prehensile palp. **C'**. Idem, detail of ventro-apical part of first segment. — **D-F**. Holotype (WAMC52291, One Tree Hill Creek – DJC/11): **D**. Right prehensile palp. **E**. Left prehensile palp. **F**. Hemipenis (both hemipenes symmetrical in this specimen). — **G-J**. Non-type (WAMC52327, from OSTR013C): **G**. Hemipenis. **H**. Right prehensile palp. **I**. Left prehensile palp. **I'**. Idem, detail of ventro-apical part of first segment. **J**. Hemipenis. Scale: A-J = 92 µm; C', I' = 37 µm.

Other material investigated

One Tree Hill Creek. 29º35’19.0” S, 115º26’31.0” E, collected by S. Halse and A. Pinder on 11 Aug. 1999 (OSTR013C), see Fig. 20G-J (WAMC52327). Water chemistry at time of collecting: K25 3.12 mS/cm, pH 7.65, water temperature 19.4 ºC.

Pools at Latham-Coorow Rd. 29º51’S, 116º16’ E (sample BVT/10/10), collected by B.V. Timms on 10 Sep. 2010 (WAMC52306-52308; OC.3332-3333).

Dam at Solomons Well. Approximate coordinates: 31°11’58.8” S, 116°21’47.7” E (sample DJC/04), collected by D.J.Cale on 09 Sep. 2011 (4 ♀♀: WAMC52332-52334; OC.3343). Water chemistry at time of collecting: K25 0.12 mS/cm, pH 7.85, water temperature 14.4 ºC.

Three Pools along Eneabba-Carnamah Rd. Approximate coordinates: 34°18’32.80” S, 115°39’16.44” E (sample DJC/09), collected by D.J. Cale on 10 Sep. 2011 (2 ♀♀: WAM52310; OC.3334). Water chemistry at time of collecting: K25 8.7 mS/cm, pH 7.2, water temperature 20.3 ºC.

Second pool along Carnamah-Eneabba Road on south side (Eneabba Springs). Approximate coordinates: 29°48’23.62” S, 115°25’6.11” E (sample DJC/10), collected by D.J. Cale on 10 Sep. 2011. Water chemistry at time of collecting: K25 3.19 mS/cm, pH 6.6, water temperature 20.9 ºC.

Petruder Dam. Approximate coordinates: 30°25’20.87” S, 116°57’39.43” E (sample DJC/15), collected by D.J. Cale on 11 Sep. 2011 (5 ♀♀: WAMC52329-52331, OC.3341-3342). Water chemistry at time of collecting: K25 0.16 mS/cm, pH 7.85, water temperature 22.0 ºC.

Tin Dog Creek. Approximate coordinates: 31°11’53.5” S, 117°01’41.4” E (sample DJC/19), collected by D.J. Cale on 23 Sep. 2011 (♀♀: WAMC52311-52315, OC.3335-3336. Juveniles: WAMC52316-52318). Water chemistry at time of collecting: K25 1.56 mS/cm, pH 7.06, water temperature 24.2 ºC.

Pools near Brookton Hwy (in Warrine Park). Approximate coordinates: 32°23’50.4” S, 116°48’00.4” E (sample DJC/23), collected by D.J. Cale on 01 Oct. 2011 (4 ♀♀: WAMC52319-52321, OC.3337). Water chemistry at time of collecting: K25 0.44 mS/cm, pH 8.1, water temperature 21.6 ºC.

Three Springs Tumulus Stream. 29º35’31” S, 115º27’1” E, collected by A. Pinder on 29 Sep. 2010 (1 male: OC.3338; 2 ♀♀: WAMC52322-52323).

East Lake Bryde. 33º21’ S, 118º49’ E (sample BRYDE7), collected by D.J. Cale on 22 Mar. 2006 (4 ♀♀: WAMC52324-52326; OC.3339). Water chemistry at time of collecting: K25 0.17 mS/cm, pH 6.91, water temperature 25.8 °C.

Lake Cronin. Episodically filled waterbody with extensive shrub and *Melaleuca* fringe, collected by S. Halse and A. Pinder on 25 Sep. 1997. Approximate coordinates: 32°23’02” S, 119°45’51” E. Water chemistry at time of collecting: K25 0.23 mS/cm, pH 9.48, water temperature 18.0 °C. *Material investigated:* one dissected ♀ (nr OS.544), with soft parts in a sealed slide and valves stored dry in micropalaeontological cavity slide (illustrated: Fig. 24E-H).

Reserve Esperance 26140 near Munglinup. Seasonally filled lake with trees across most of flooded area, collected 27 Oct. 1986 by S. Halse. Approximate coordinates: 33°26’24” S, 120°31’48” E. Water chemistry: salinity 0.27 mg/L TDS, pH 6.93. *Material investigated:* one dissected ♀ (nr OS.604), with soft parts in a sealed slide and valves stored dry in a micropalaeontological cavity slide (illustrated: Fig. 25I-L).

Remarks on the latter two localities: the lapels of both specimens are slightly larger than in most specimens of *B. scanloni* sp. nov. and as (1) no males are at hand to check for the morphology of the hemipenes and the prehensile palps in these populations and (2) no molecular data are available, the identifications of these two specimens are tentative.

Additional notes on cryptic species

Specimens from the type locality (One Tree Hill Creek, sample DJC/11) all belong to cryptic species E1, which is thus the true *B. scanloni* sp. nov. *s.s.* Also specimens from sample DJC/23 (pools near Brookton Hwy in Warrine Park) belong to this lineage (Fig. 19I-O). Two specimens from cryptic species

B2 are also illustrated here, one female from pools beside Latham-Coorow Rd (western Wheatbelt) **(**BVT/10/10) (Fig. 19A-D) and one female from Tin Dog Creek (DJC/19) (Fig. 19E-H). There are no clear differences between the two cryptic species in valve morphology.

The soft parts of the male from Three Springs Tumulus Stream (TST) (Fig. 20A-C) are slightly different from those of the holotype (Fig. 20D-F). Yet, within the molecular phylogeny the TST specimens cluster closely with the cryptic species E1, which is the same as for the type specimens. The hemipenis outline and the prehensile palps of the male from OSTR013C (Fig. 20G-J) are almost identical to those of the holotype, though no molecular data on this population are available, and it is thus also not clear to which of the two cryptic species within *B scanloni* sp. nov. this specimen belongs.

Thus far, the two molecular species cannot be distinguished morphologically. Interestingly, these two cryptic lineages occur sympatrically in no less than 4 localities (DJC/09, DJC/11, DJC/19 and BVT/10/10).

Differential diagnosis

The drop-shaped lapel on the RV and the sharp angle on the distal margin of the terminal segment of the right prehensile palp distinguish *B. scanloni* sp. nov. from all other species within the *B. barangaroo* lineage.

Ecology and distribution

This is arguably the most common species in this lineage in the south-western part of WA. It typically occurs in pools, dams and lakes with soft sediments.

Bennelongia calei sp. nov.

Figs 21-22

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Bennelongia barangaroo – De Deckker 1981a: 104, fig. 9 (partim).

Diagnosis (based on type specimens)

Valves (Fig. 21A-B, E-F) elongated, with greatest height situated close to the middle, dorsal margin evenly sloping towards the posterior side; ventral margin almost straight. LV (Fig. 21A, E) with antero-ventral il large and reaching beyond middle of valve, antero-dorsal il descending to about halfway along antero-ventral il. RV (Fig. 21B, F) with antero-ventral lapel large, elongated and wide, with crenulated edge (Fig. 21C-D, G-H). Carapace in dorsal and ventral views (Fig. 21K-L) with greatest width in the middle, most slender of all species described here, external surface rather smooth to weakly pitted, set with only few short setae; anteriorly with a clearly delimited rostrum. Carapace in right lateral view (Fig. 21I-J) with greatest height in the middle, dorsal margin evenly sloping to bluntly rounded posterior margin; anteriorly with the widest LV>RV overlap of all species described here.

Males unknown.

Etymology

This species is named after D.J. Cale (Woodvale, WA) in honour of his longstanding contribution to the knowledge of freshwater invertebrates in WA, including at Fraser Lake which is the type locality of the present species (Cale *et al.* 2004), and also in recognition of the fact that he has collected so many of the samples used for the present revision of the *Bennelongia barangaroo* lineage.

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

Holotype ♀ (WAMC52335): RV: L = 1480, H = 857. LV: L = 1555, H = 865.

Type locality

Fraser Lake, *ca*. 8 km SE of Dowerin, WA. Approximate coordinates: 31º15’18.0” S, 117º4’22.0” E (WGS 84). All material (sample code DJC/18) collected on 23 Sep. 2011 by D.J. Cale with a sweep net. Water chemistry at time of collecting: K25 1.76 mS/cm, pH 8.1, water temperature 23.9 ºC.

Type material

Holotype

♀ (WAMC52335) valves stored dry in a micropalaeontological slide.

Allotype

As males are unknown, no allotype is designated.

Paratypes

Eight ♀♀, either as dried valves or carapaces (WAMC52337-52341; OC.3344-3345). *Ca*. 45 females stored as bulk in EtOH (WAMC52342).

Other material investigated

Fraser Lake (type locality). Four ♀♀ valves and carapaces stored dry (WAMC52353-52356) from the same locality, but collected on another date (sample nr SPM017B, collected by D.J. Cale, 24 Nov. 2000), were also used during the present assessment of this species but are not considered as type material here.
Second pool along Carnamah-Eneabba Road on south side (Eneabba Springs). Approximate coordinates: 29°48’23.62” S, 115°25’6.11” E (sample DJC/10), collected by D.J. Cale on 10 Sep. 2011 (one ♀ WAMC52349). Water chemistry at time of collecting: K25 3.19 mS/cm, pH 6.6, water temperature 20.9 ºC.
Jerramungup West. Approximate coordinates: 33°59’16.03” S, 118°56’28.15” E (sample DJC/36), collected by D.J. Cale on 21 Oct. 2011 (five ♀♀ valves and carapaces stored dry WAMC52350-52352; OC.3348-3349). Water chemistry at time of collecting: K25 0.73 mS/cm, pH 8.74, water temperature 25.8 ºC
Oak Flat W pit gnamma via Goomalling. Approximate coordinates 31º08’21” S, 116º52’46” E (sample BVT/11/04), collected by B.V. Timms on 16 Aug. 2011 (four ♀♀ valves and carapaces stored dry WAMC52343-52344; OC.3346-3347).
***Horse Collar gnamma*, *on Magee Rd via Kulin*.** Approximate coordinates: 32º48’04” S, 118º23’34” E (sample BVT/11/05), collected by B.V. Timms on 4 Sep. 2011 (four ♀♀ valves and carapaces stored dry WAMC52345-52348).

Additional illustrations

Several other populations of this species were found and for four of these (listed above), valves of female specimens are also illustrated here (Fig. 22). All of these specimens comply with the above diagnosis, and where specimens were available for molecular analyses, they also fell into the *B. calei* sp. nov. – cluster. No cryptic species were identified in this species.

Differential diagnosis

Bennelongia calei sp. nov. can easily be distinguished from all other species in the *B. barangaroo* lineage by the elongated and stout antero-ventral lapel on the RV, which is slightly rounded and has a

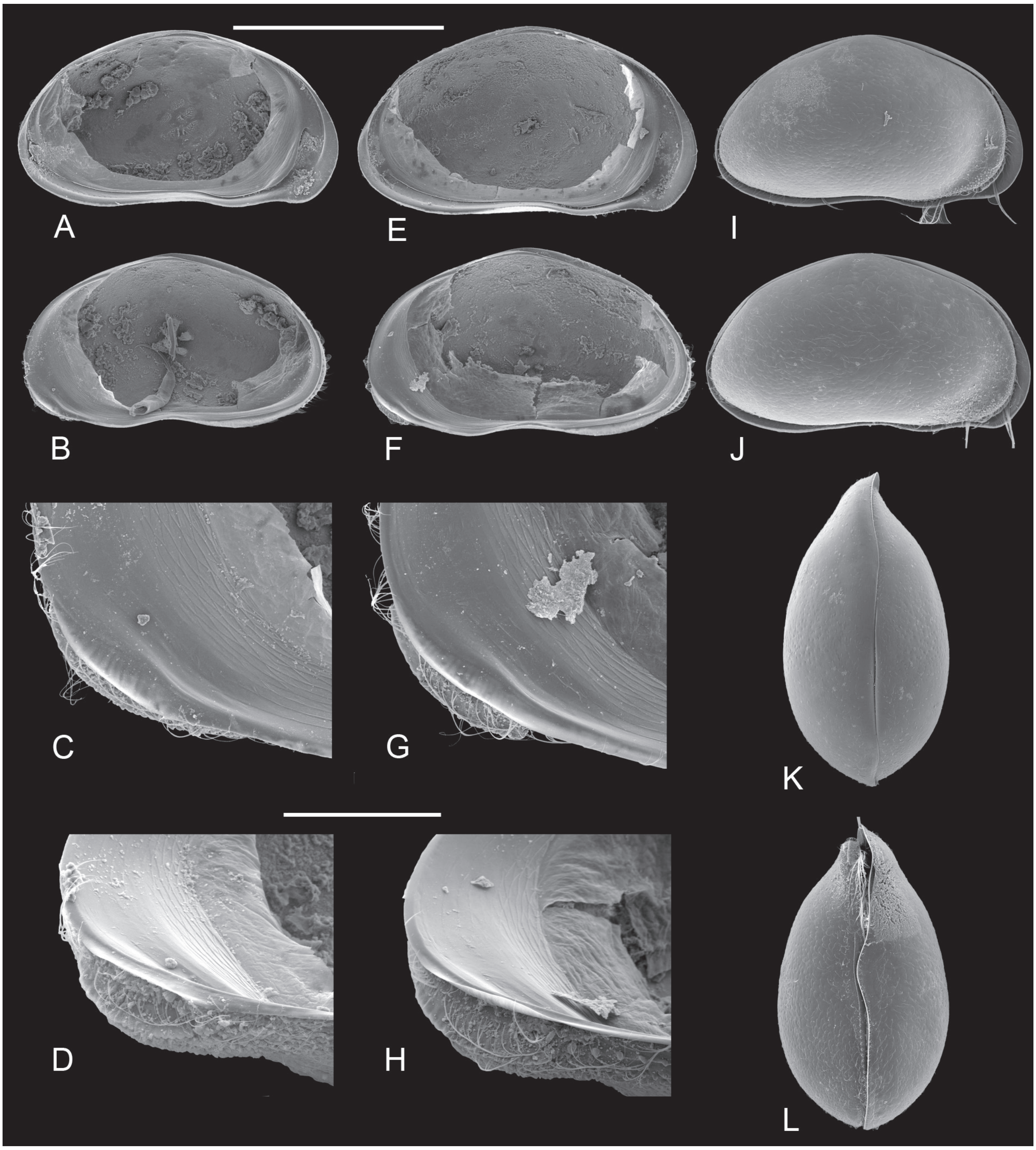

Fig. 21. *Bennelongia calei* sp. nov. — **A-H**, **J-L**. Fraser Lake (type locality, females, DJC/18): **A**. Paratype, LVi (OC.3344). **B**. Paratype, RVi (idem). **C**. Paratype, RVI, detail anterior (idem). **D**. Paratype, RVI, detail anterior, tilted (idem). **E**. Holotype, LVi (WAMC52335). **F**. Holotype, RVI (idem). **G**. Holotype, RVi, detail anterior (idem). **H**. Holotype, RVi, detail anterior, tilted (idem). **J**. Paratype, CpRL (OC.3345). **K**. Paratype, CpD (WAMC52338). **L**. Paratype, CpV (WAMC52337). — **I**. Oak Flat W pit gnamma, via Goomalling (BVT/11/04, non-type female, WAMC52343). CpRL. Scales: A-B, E-F, I-L = 1 mm; C-D, G-H = 200 µm.

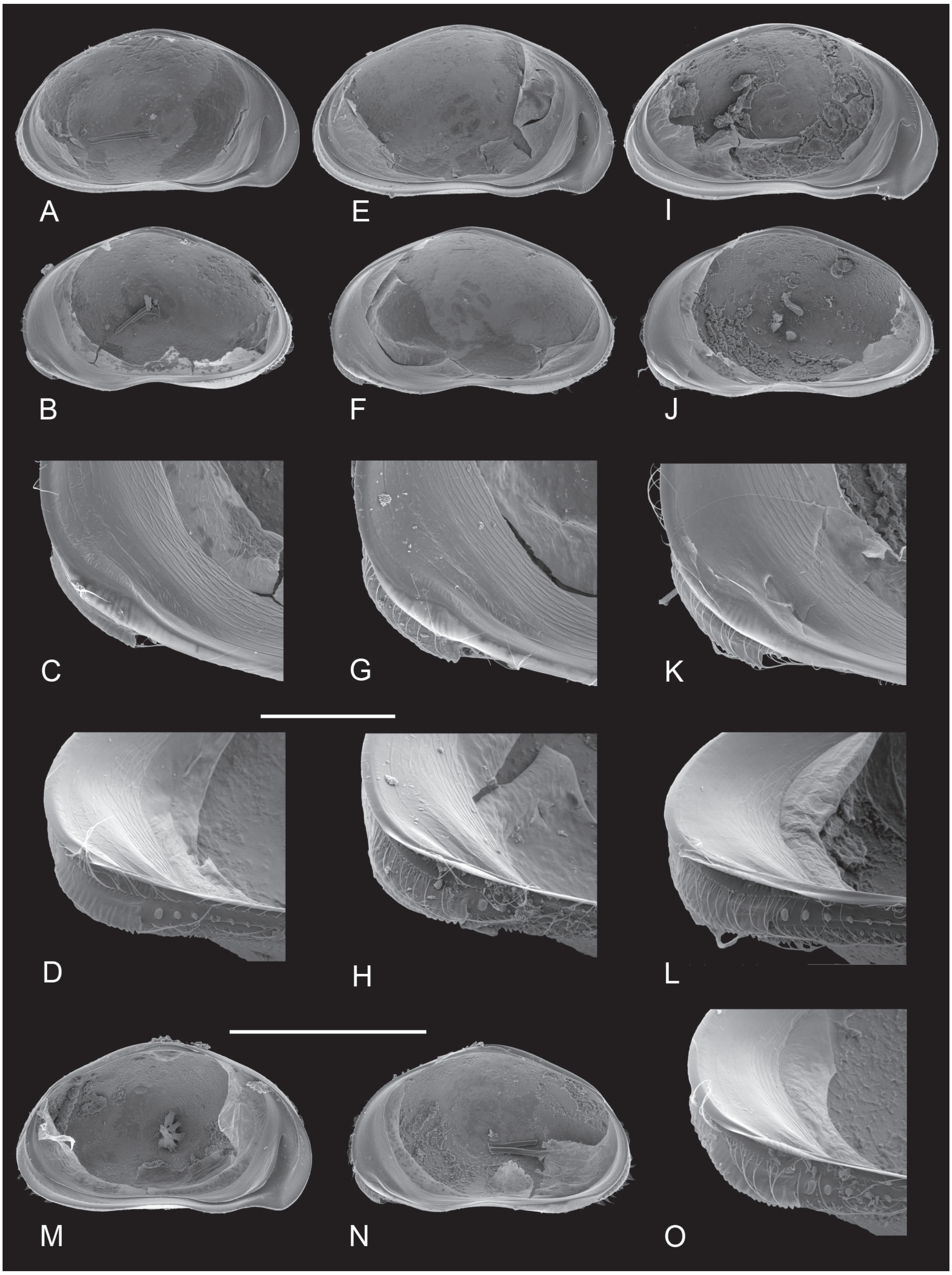

Fig. 22. *Bennelongia calei* sp. nov., non-type specimens. — **A-D**. Oak Flat W pit gnamma, via Goomalling (BVT/11/04, ♀, OC.3346). **A**. LVi. **B**. RVi. **C**. RVi, detail anterior. **D**. RVi, detail anterior, tilted. — **E-H**. Horse Collar gnamma, on Magee Rd via Kulin (BVT/11/05, ♀, WAMC52345). **E**. LVi. **F**. RVi. **G**. RVi, detail anterior. **H**. RVi, detail anterior, tilted. — **I-L**. Second pool along Carnamah-Eneabba Road on south side, Eneabba Springs (DJC/10, ♀, WAMC52349). **I**. LVi. **J**. RVi. **K**. RVi, detail anterior. **L**. RVi, detail anterior, tilted. — **M-O**. Pool at Jerramungup West (DJC/36, ♀, OC.3348). **M**. LVi. **N**. RVi. **O**. RVi, detail anterior, tilted. Scales: A-B, E-F, I-J, M-N = 1 mm; C-D, G-H, K-L, O = 200 µm.

crenulated distal margin, the large anterior LV>RV overlap, the stout antero-ventral il on the LV and the clear anterior rostrum on the carapace in dorsal or ventral view.

Ecology and distribution

The species is most common in pools and lakes in the southwest of WA. However, *B. calei* sp. nov. was also recovered from a totally different kind of habitat, namely pit gnammas near Goomalling (BVT/11/04) and Kulin (BVT/11/05). Whereas the other species in this lineage apparently occur either in rock pools or in soft bottomed pools and lakes, *B. calei* sp. nov. can apparently survive in both (very different) types of habitats. *Bennelongia calei* sp. nov. is, together with *B. timmsi* sp. nov. and *B. scanloni* sp. nov., one of the more common species in its area.

Bennelongia dedeckkeri Shearn *et al.*, 2012

Figs 23, 24I-L

Bennelongia dedeckkeri sp. nov. – Shearn *et al.*, 2012: 10-14, figs 4-5.

Material investigated

Dam at Kylena Well **(Pilbara).** Approximate coordinates: 22°06’00” S, 119°39’00” E (sample KIES10). Collected on 23 Apr. 2006 by the authors.
Unnamed saline billabong N of Coolcalaya Rd **(Murchinson, Gascoyne).** Approximate coordinates: 27°48’28” S, 114°48’18” E (sample SIKE2). Collected on 5 Jul. 2011 by the authors. Water chemistry at time of collecting: K25 8.8 mS/cm, pH 8.8, water temperature 11.0 ºC.
McNeil Claypan, ***Carnarvon*** **(Murchinson, Gascoyne).** Approximate coordinates: 24°52’06” S, 113°42’56” E (sample SIKE9). Collected on 6 Jul. 2011 by the authors. Water chemistry at time of collecting: K25 0.19 mS/cm, pH 9.4, water temperature 10.8 ºC.
Roadside ditch 1, ***North-West Coastal Hwy***, ***Minilya Station*** **(Murchinson, Gascoyne).** Approximate coordinates: 23°54’25” S, 114°01’45” E (sample SIKE18). Collected on 7 Jul. 2011 by the authors. Water chemistry at time of collecting: K25 0.66 mS/cm, pH 7.4, water temperature 17.3 ºC.
Roadside ditch 2, ***North-West Coastal Hwy***, **(Murchinson, Gascoyne).** Approximate coordinates: 23°54’25” S, 114°01’47” E (sample SIKE19). Collected on 7 Jul. 2011 by the authors. Water chemistry at time of collecting: K25 0.69 mS/cm, pH 7.3, water temperature 17.3 ºC.
Lake Gregory, ***south of Halls Creek.*** Approximate coordinates: 20º12’ S, 127º27’ E. Collected by S. Halse on 29 May 1991 in fresh water (see Halse *et al.* 1998). One dissected ♀ (nr OS.260), with soft parts in a sealed slide and valves stored dry in micropalaeontological cavity slide (illustrated in Fig. 24I-L).

Brief redescription

Smallest of the species described here, with females being only slightly longer than 1 mm.

Valves (Fig. 23A-B, E-F) high, with greatest height situated well in front of the middle, dorsal margin evenly sloping towards the posterior side; ventral margin nearly straight. LV (Fig. 23A, E) with antero-ventral il of medium size in lower half of valve, antero-dorsal il descending to about halfway along the antero-ventral il. RV (Fig. 23B, F) with antero-ventral lapel almost rectangular, but slightly skewed and bluntly pointed towards the ventral side (Fig. 23C-D, G-H).

Carapace in dorsal and ventral views (Fig. 23K-L) with greatest width in the middle, hirsute and heavily pitted, anteriorly without a rostrum.

Males not yet found in WA.

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

♀ (Pilbara, KIES10, WAMC52357): RV: L= 1110, H= 676. LV: L= 1190, H= 701.
♀ (Murchinson/Gascoyne, SIKE9, OC.3351): RV: L= 1125, H= 672. LV: L= 1188, H= 715.

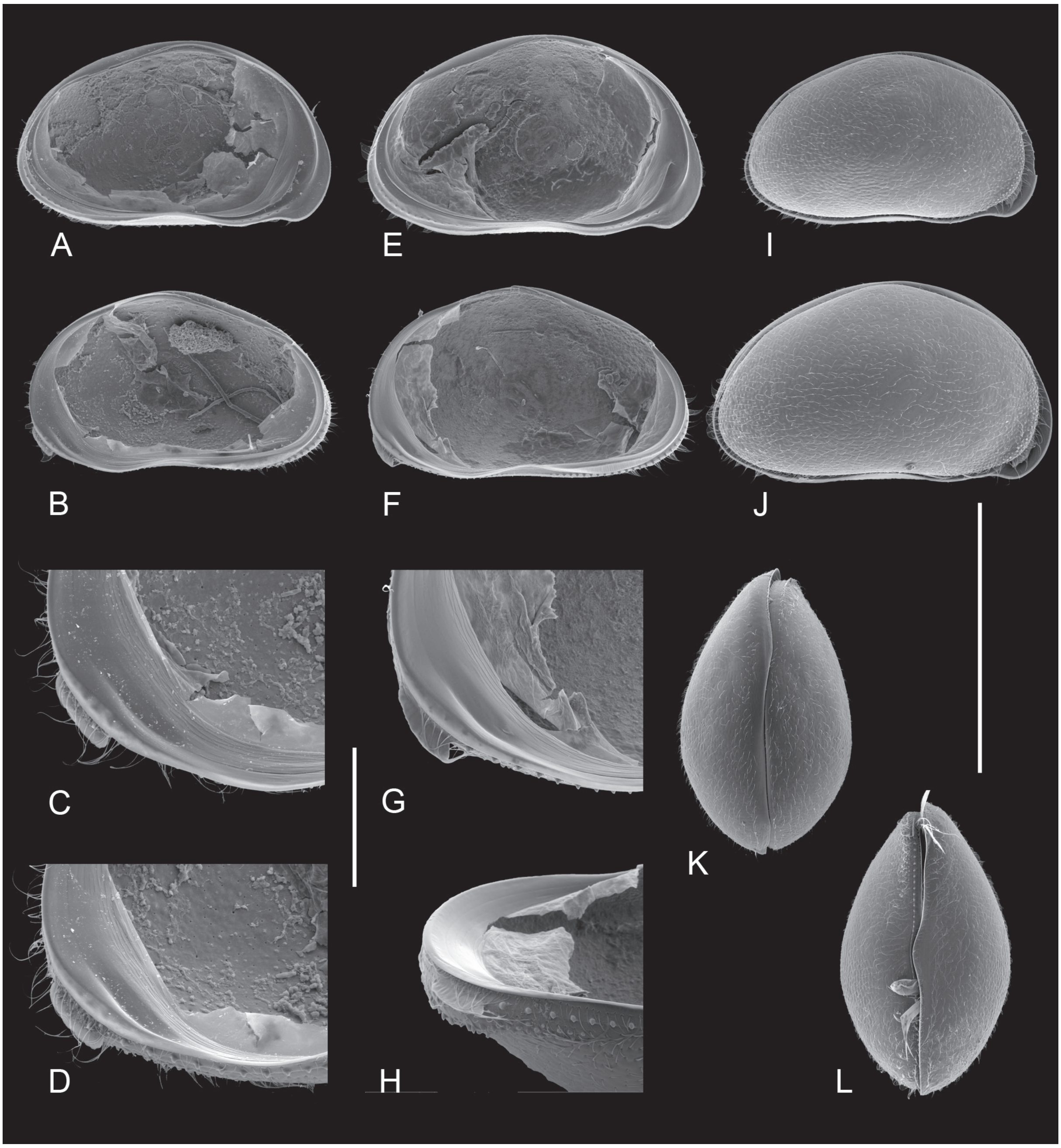

Fig. 23. *Bennelongia dedeckkeri*, non-type females. — **A-D**, **I**, **K-L**. Dam at Kijlena Well, Pilbara (KIES/10). **A**. LVi (WAMC52357). **B**. RVi (idem). **C**. RVi, detail anterior (idem). **D**. RVi, detail anterior, slightly tilted (idem). **I**. CpRL (OC.3350). **K**. CpD (WAMC52360). **L**. CpV (WAMC52359). — **E-H**, **J**. McNeil Claypan, Murchinson/Gascoyne (SIKE9). **E**. LVi (OC.3351). **F**. RVi (idem). **G**. RVi, detail anterior (idem). **H**. RVi, detail anterior, tilted (idem). **J**. CpRL (OC.3352). Scales: A-B, E-F, I-L = 1 mm; C-D, G-H = 200 µm.

Ecology and distribution

Bennelongia dedeckkeri Shearn *et al*, 2012 was first described from Queensland, from a sexual population. In WA it is not uncommon, but thus far only asexual populations have been found. To date *B. dedeckkeri* is the only species of the *B. barangaroo* group found in both the eastern and the western parts of Australia.

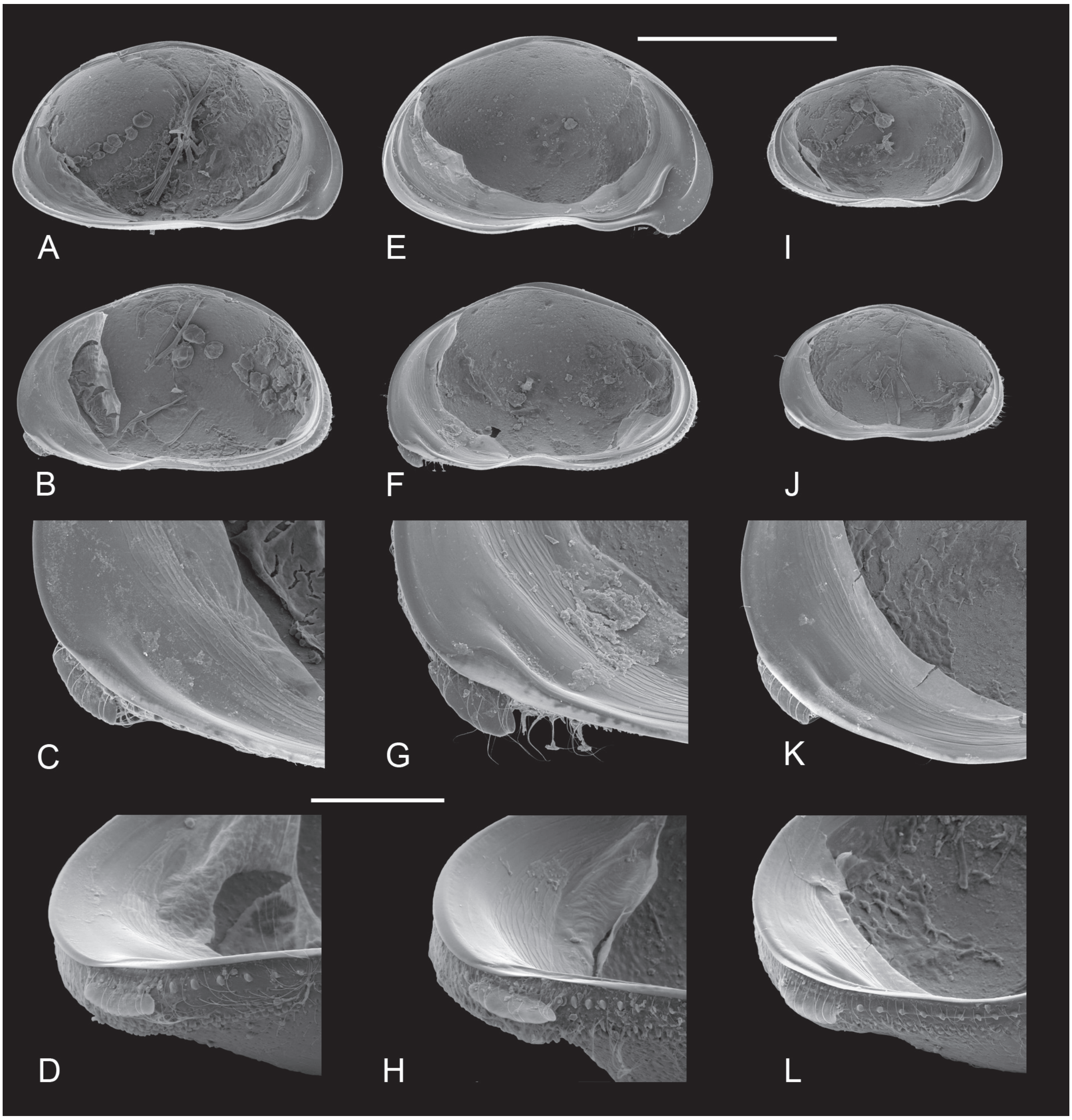

Fig. 24. *Bennelongia* spp. (no museum nrs), females. — **A-D**. *Bennelongia* sp. X1. Crane Pan (OS.255). **A**. LVi. **B**. RVi. **C**. RVi, detail anterior. **D**. RVi, detail anterior, tilted. — **E-H**. *? Bennelongia scanloni* sp. nov., Lake Cronin (OS.544). **E**. LVi. **F**. RVi. **G**. RVi, detail anterior. **H**. RVi, detail anterior, tilted. — **I-L**. *Bennelongia dedeckkeri*, Lake Gregory (OS.260). **I**. LVi. **J**. RVi. **K**. RVi, detail anterior. **L**. RVi, detail anterior, tilted. Scales: A-B, E-F, I-J = 1 mm; C-D, G-H, K-L = 200 µm.

Bennelongia sp. indet.

There are several single specimens, mostly female, from various (older) collections that could not be identified with certainty. Some of these are here illustrated to allow for future reference, in case new collections will become available. It is entirely possible that some of these specimens represent hybrid clades within the *B. barangaroo*-group. As none of these specimens have as yet been identified with certainty, no museum numbers have been allocated to them.

Bennelongia sp. X1

Fig. 24A-D

Material investigated

One dissected ♀ (nr OS.255), with soft parts in a sealed slide and valves stored dry in a micropalaeontological cavity slide.

Locality

Canegrass covered claypan beside North-West Coastal Highway on Wooramel Station (CB35a), 25°40’52” S, 114°13’14” E, collected by S. Halse and A. Clarke on 24 Aug. 1994.

Morphology and affinities

The specimen is characterised by (1) a large antero-ventral lapel on the RV, subquadrate and only weakly crenulated, i.e., a shape unlike that of any of the other species (re-) described in the present paper, (2) a relatively small antero-ventral il on the LV and, (3) the bluntly pointed posterior margin of the LV, with a pronounced flange. The latter character is unique within the *B. barangaroo* lineage. If this character is stable and also occurs in other specimens, it could be indicative at a specific level.

Bennelongia sp. X2

Fig. 25A-D

Material investigated

One dissected ♀ (nr KMWA.917), with soft parts in a sealed slide and valves stored dry in a micropalaeontological cavity slide.

Locality

Three Springs Tumulus stream, 29º35’31”S, 115º27’1” E, collected by A. Pinder on 29 Sep. 2010.

Morphology and affinities

The specimen has some affinity with *B. scanloni* sp. nov., but the antero-ventral il on the LV is smaller and the antero-ventral lapel of the RV is of a different shape, being larger and almost rectangular.

Remarks

Several other specimens from the same sample belong to cryptic species E1 of *B. scanloni* sp. nov., as shown by morphological and molecular evidence (see above).

Bennelongia sp. nov. E2

Fig. 25E-H

Material investigated

One dissected ♀ (nr KMWA.806), with soft parts used for molecular analysis and valves stored dry in a micropalaeontological cavity slide.

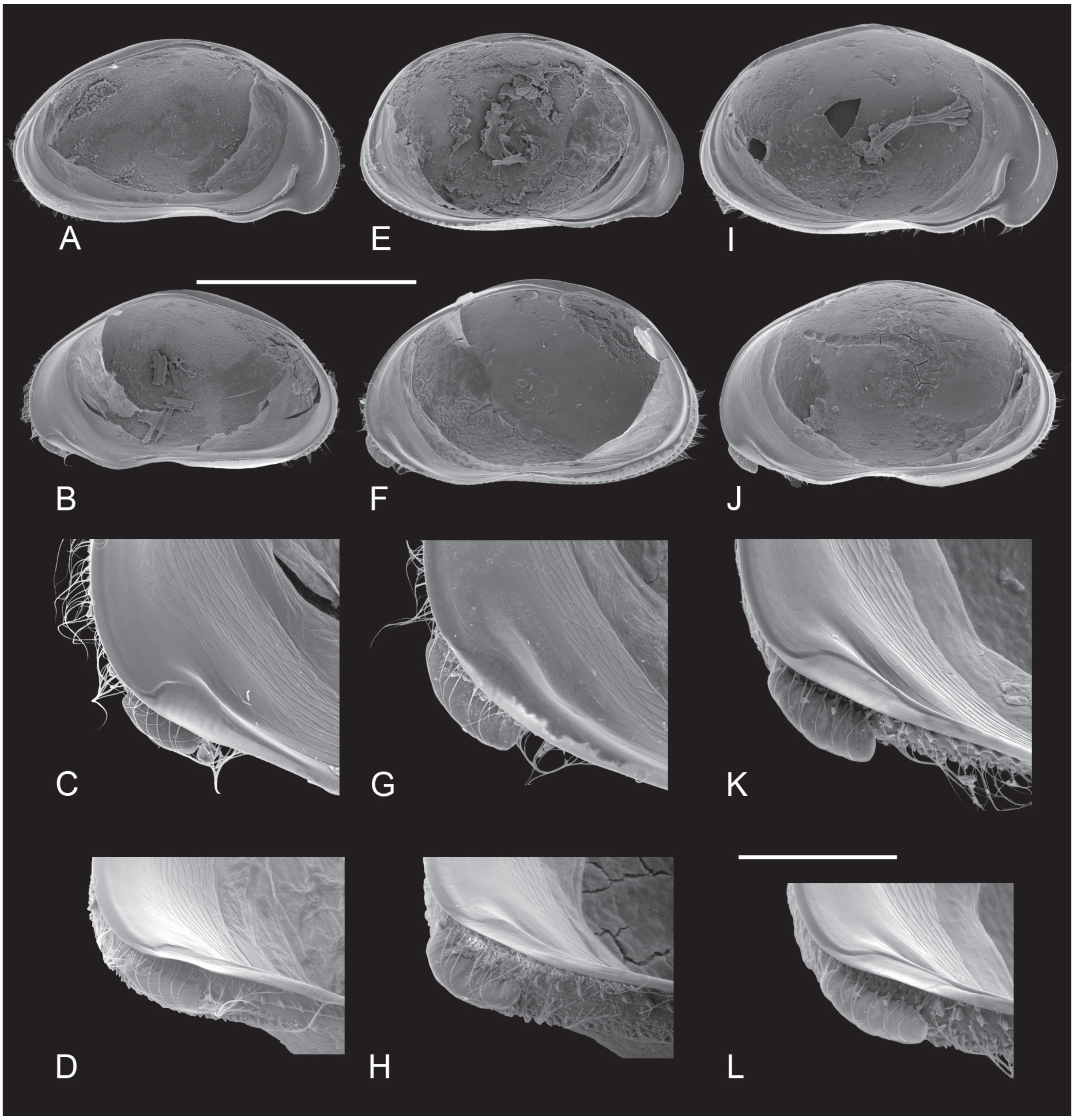

Fig. 25. *Bennelongia* spp. (no museum nrs). — **A-D**. *Bennelongia* sp. X2, Three Springs Tumulus Stream (♀, KMWA.917). **A**. LVi. **B**. RVi. **C**. RVi, detail anterior. **D**. RVi, detail anterior, tilted. — **E-H**. *Bennelongia* sp. nov. E2, BYK (♀, KMWA.806) = Species E2 in Figs 2-3. **E**. LVi. **F**. RVi. **G**. RVi, detail anterior. **H**. RVi, detail anterior, tilted. — **I-L**. *? Bennelongia scanloni* sp. nov., pool near Esperance (♀, OS.004). **I**. LVi. **J**. RVi. **K**. RVi, detail anterior. **L**. RVi, detail anterior, tilted. Scales: A-B, E-F, I-J = 1 mm; C-D, G-H, K-L = 200 µm.

Locality

Yakabindie Claypan, approximately 27°34' S, 120°31' E (sample LN3006), collected by Outback Ecology on 24 Mar. 2011.

Morphology and affinities

Although general valve appearance again shows some affinities to *B. scanloni* sp. nov., the different shape of the antero-ventral il on the LV (less pronounced and evenly rounded) and the large and subquadrate anteroventral lapel on the RV distinguishes this specimen from all other species (re-)described here. Molecular analysis of the soft parts of the same specimen shows that it clusters outside of the *B. scanloni* sp. nov. group (including cryptic species B2 and E1), and constitutes a different genetic species. Lack of additional material and males prevents us from formally describing this new species here.

General Discussion

De Deckker (1981a) reported two species of *Bennelongia* from WA: *B. australis* (Brady, 1886) and *B. barangaroo* De Deckker, 1981. Meanwhile, Martens *et al.* (2012) described nine new species from three separate lineages within this genus from WA (the *B. australis* lineage, the *B. cygnus* lineage and the *B. pinpi* lineage) and showed that *B. australis* is actually a species group with at least seven nominal species and potentially more. Shearn *et al.* (2012) contributed to the knowledge of the genus *Bennelongia* in eastern Australia by confirming the validity of *B. pinpi* De Deckker, 1981 and *B. harpago* De Deckker & McKenzie, 1981, using genetics to identify the occurrence of a cryptic lineage within a species of the *B. australis* lineage (*B. cuensis* Martens *et al.*, 2012), and by describing two new species in the *B. barangaroo* lineage (*B. dedeckkeri* Shearn *et al.*, 2012 and *B. mckenziei* Shearn *et al.*, 2012) and one new species within the *B. nimala* lineage (*B. regina* Shearn *et al.*, 2012). The previous work of De Deckker (1981a,b, 1982) and De Deckker & McKenzie (1981) as well as these two new papers (Martens *et al*, 2012; Shearn *et al.*, 2012) show that the genus *Bennelongia* has extensive radiations in both eastern and western Australia. The present paper formally describes seven new species within the *B. barangaroo* lineage, redescribes *B. dedeckkeri* and indicates the putative presence of several other species within the *B. barangaroo* lineage, all from WA. With the seven new species described here, the genus *Bennelongia* now comprises 25 nominal species (Table 3) but several more await formal description.

Morphological features

Once again, the size and shape, and in some cases the sheer presence or absence, of the antero-ventral lapel on the RV has proven to be indispensable to characterize species of *Bennelongia*. The plasticity of this feature within the *B. barangaroo* lineage is amazing and ranges from being fully absent through being small and triangular, to large and drop-like and to a large, elongated and heavily serrated structure. Whereas Martens *et al.* (2012) hypothesized that the function of the lapel is to lock the sulcus in the LV when valves need to be closed tightly (*e.g.*, when attacked by predators, or in cases where habitat is rapidly desiccating), one could ask why such a wide range of morphologies of the lapel is necessary for highly similar functions in the different lineages and species. When homologous structures have widely different morphologies in closely related species, sexual selection is often invoked as causality. Several authors have indeed already mentioned the potential of sexual selection in ostracod radiations (for example Tsukagoshi 1988; Martens 2000). However, such structures must usually (1) display sexual dimorphism and be most common in males, (2) be accessible during pre-copulation by putative partners, i.e., females, to determine whether or not to accept the male as a partner for reproduction, and (3) occur only in the adult stage, i.e., after the final moult. Only the latter of these three conditions is fulfilled in *Bennelongia* because there is no apparent sexual dimorphism in lapel-shape and lapels are in general not easily available for inspection by females during the pre-copulatory stage. It is therefore unlikely that lapel morphology has evolved through sexual selection.

Table 3. Species presently described in *Bennelongia* 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.

Bennelongia australis (Brady, 1886): SA
Bennelongia barangaroo De Deckker, 1981: WA
Bennelongia bidgelangensis Martens *et al.*, 2012: WA, Gascoyne
***Bennelongia calei* sp. nov.: WA**
Bennelongia coondinerensis Martens *et al.*, 2012: WA, Pilbara
Bennelongia cuensis Martens *et al.*, 2012: WA, Yilgarn
Bennelongia cygnus Martens *et al.*, 2012: WA, Swan Valley
Bennelongia dedeckkeri Shearn *et al.*, 2012: QLD, WA
Bennelongia frumenta Martens *et al.*, 2012: WA, Wheatbelt
***Bennelongia gnamma* sp. nov.: WA**
Bennelongia gwelupensis Martens *et al.*, 2012: WA, Perth, southwest coast
**Bennelongia harpago* De Deckker & McKenzie, 1981: QLD
***Bennelongia hirsuta* sp. nov.: WA**
***Bennelongia ivanae* sp. nov.: WA**
Bennelongia kimberleyensis Martens *et al.*, 2012: WA, Kimberley
Bennelongia lata Martens *et al.*, 2012: WA, Gascoyne-Murchinson region
Bennelongia mckenziei Shearn *et al.*, 2012: QLD
***Bennelongia mcraeae* sp. nov.: WA**
Bennelongia nimala De Deckker, 1981: NT
Bennelongia pinpi De Deckker, 1981: QLD
Bennelongia regina Shearn *et al.*, 2012: QLD
***Bennelongia scanloni* sp. nov.: WA**
Bennelongia strellyensis Martens *et al.*, 2012: WA, Pilbara
***Bennelongia timmsi* sp. nov.: WA**
Bennelongia tunta De Deckker, 1982: QLD

This leaves the possibility that lapels have evolved by chance (not a very parsimonious solution) or that natural selection is acting on the evolution of this morphological feature and that selection pressures are quite stringent. The morphological differences between species living in similar environments (pools, lakes) can be either substantial, as is the case for *B. macraeae* sp. nov., *B. scanloni* sp. nov. and *B. calei* sp. nov., or almost non-existent as in the case of the rock pool dwelling species, which are either cryptic species without morphological differences or have very small differences (*B. timmsi* sp. nov. with 3 cryptic species and *B. gnamma* sp. nov.).

Bennelongia timmsi sp. nov. as a biological reality?

Recent research has shown that cryptic species are not uncommon in non-marine ostracods, as Shearn *et al.* (2012) found a genetically distinct eastern Australian lineage within the otherwise western Australian *B. cuensis* Martens *et al.*, 2012, and confirmed that both clades within this species are morphologically indistinguishable. Schön *et al.* (2012) found several cryptic species within putative ancient asexual darwinulid ostracods, while Bode *et al.* (2010) revealed no less than 40 cryptic species within the Palaearctic ostracod species *Eucypris virens* (Jurine, 1820).

In the *B. barangaroo* lineage, both *B. timmsi* sp. nov. and *B. scanloni* sp. nov. comprise cryptic species as identified by molecular phylogenies based on the mitochondrial COI gene (Fig. 2) and the 4 theta rule (Table 2). *Bennelongia scanloni* sp. nov. comprises three clusters and three unconnected genetic networks (Fig. 3) of which two are identified as separate genetic species by the 4 theta rule, and the two clusters together form a monophyletic clade within the tree. The smaller TST-clade is phylogenetically slightly separate from the E1 clade, forms an additional network, but does not constitute a separate genetic species. The situation in *B. scanloni* sp. nov. is thus a classic case of a monophyletic species consisting of diverged, but morphologically unrecognisable, clades.

In *B. timmsi* sp. nov., however, the situation is less straightforward. Five clades are recognised in the phylogenetic tree (Fig. 2 – A1-5) and there are six unconnected networks (Fig. 3), of which three are considered valid genetic species (A1, A3, A2+4+5). However, unlike the situation in *B. scanloni* sp. nov., *B. timmsi* sp. nov. does not appear as a monophyletic taxon in the phylogenetic analysis, because A1 and A3 cluster together in a different clade than A2+4+5. Extensive morphological comparisons (Figs 4-11) could not reveal any specific differences in valve or soft part morphology between the clusters (though see below), excluding the possibility that even clades A1+A3 on the one hand and clades A2+4+5 on the other could be described as different monophyletic species. We considered it of little use to describe two different species when they cannot be identified, except with molecular techniques.

Adding complexity to the phylogenetic uncertainty described above, the morphology of the antero-ventral lapel on the RV shows some variability in length and position on the valve among specimens within the *B. timmsi* sp. nov. clades, but this limited variability could not be linked to the phylogenetic position of the specimens. While the shape of the terminal segment of the right prehensile palp was variable within what is assumed to be the same cryptic species (in clade A5), it differed little between cryptic species. Whether or not the differences observed in clade A5 specimens are real or artefacts remains to be seen. The morphologies of the hemipenis-outlines and of the left prehensile palp were fairly constant across all five clades and three cryptic species.

The situation in *B timmsi* sp. nov. is the first case within the revision of the genus *Bennelongia* where morphological and molecular data are incongruent. At this stage, we have chosen to follow the results of the morphological analyses, as it seems that, within the tree, the nodes indicated by an * (Fig. 2) are weakly or not statistically supported, and if those nodes are collapsed into a polytomy, the virtual polyphyletic position of *B. timmsi* sp. nov. would disappear. As soon as we have described and screened all new species of *Bennelongia* from our collections, the molecular phylogeny of the genus as a whole will be reconstructed and it is hoped that this more complete analysis will shed light on the presumed polyphyletic status of *B. timmsi* sp. nov. In the meantime, *Bennelongia timmsi* sp. nov. is proposed here as a valid biological species.

Distribution and Ecology

The continental-scale distribution of *Bennelongia* as a whole and phylogeography of selected species will be dealt with elsewhere. At this stage, however, it is useful to point out that almost all species in this genus have fairly restricted distributions: this appears to be so for the species within the *B. australis* and *B. cygnus* lineages (Martens *et al.* 2012), as well as in the *B. pinpi* and the *B. barangaroo* lineages (Martens *et al.* loc. cit; Shearn *et al.* 2012). One notable exception appears to be *B. dedeckkeri*, which has meanwhile been reported from Queensland in eastern Australia (Shearn *et al.* 2012) and from both northern and central Western Australia (present paper - Fig. 1). Molecular screening has shown that specimens from WA and from QLD even have (near to) identical COI-sequences, showing that this species must have a very efficient means of dispersal compared to its congeners. So far, only parthenogenetic populations have been found in WA, which would be one way to explain a potentially recent expansion from the east (where sexual populations do appear to exist) to the west. Indeed, parthenogens are assumed to be more efficient dispersers, as one egg is potentially enough to establish a viable population, whereas sexual groups must have both genders colonising the same habitat, and these moreover must find each other in a spatially and temporally diluted environment (Horne & Martens 1999). All screened specimens from WA had identical COI sequences (Fig. 3), and the apparent absence of genetic diversity between localities more than 1000 km apart supports this hypothesis of parthenogens.

Bennelongia dedeckkeri was recovered from both ephemeral lakes and pans (*e.g.*, the McNeil Claypan in Carnarvon), as well as semi-permanent lakes (e.g., the remote Lake Gregory, in the Tanami Desert, but see Halse *et al.* 1998), and thus seems to be able to thrive in different types of environments. The species might very well have a General Purpose Genotype (Van Doninck *et al.* 2003). The remainder of the species of the *B. barangaroo* lineage are distributed in more particular habitat types: *B. timmsi* sp. nov., *B. gnamma* sp. nov., *B. hirsuta* sp. nov. and *B. ivanae* sp. nov. occur only in rock pools, and this diversity within a single lineage confirms the rock pools on the granite outcrops in southwestern Australia as foci of diversification of aquatic animals (Pinder *et al.* 2000). *Bennelongia mcraeae* sp. nov. and *B. scanloni* sp. nov. were sampled in seasonal or episodic soft-sediment lakes and pools only. *Bennelongia calei* sp. nov. occurs mainly in the latter types of habitats, but was also found in at least two localities in pit-gnammas, which are deep and narrow rock pools. Populations from both types of habitats were also shown to belong to one and the same genetic species (Fig. 2), and this species thus has a puzzling autecology.

Acknowledgements

The authors gratefully acknowledge the financial support by an ABRS-grant (nr RF211-33: 'Biodiversity and taxonomy of Ostracoda (Crustacea) from temporary water bodies of inland Western Australia') and by an Edith Cowan University Industry Collaboration grant. KM & IS acknowledge the Western Australian Department of Parks and Wildlife (2006) and Bennelongia Pty Ltd (2008, 2009, 2010) for financial support during several scientific stays in Perth, as well as the financial contribution of the FWO Vlaanderen (Fund for Scientific Research, Flanders) in the form of travel grants in 2010 (V4.172.10N & V4.173.10N) and the projects 1.5.172.09 (Krediet aan Navorsers) and G.0118.03N (projectonderzoek). KM and IS also thank the people of Bennelongia Pty Ltd (Perth, WA) for continuous logistic support (lab space, use of microscopes, etc.) and for unfailing companionship in the lab and their son Emrys for invaluable help with sorting living specimens in the field as well as in the lab. David J. Cale, A. Clarke and Adrian Pinder (DEC, Woodvale, Australia), Brian V. Timms (Newcastle, Australia), Outback Ecology (Perth, Australia) and Jane McRae (Bennelongia Pty Ltd, Perth, Australia) are acknowledged for collecting most of the material described in the present paper.

Julien Cilis and Claudine Behen (RBINS, Brussels, Belgium) provided technical assistance with the SEM micrographs and with the line drawings, respectively. Kristiaan Hoedemakers (RBINS, Brussels, Belgium) produced the SEM plates and supervised the entire production of the manuscript. Mike Scanlon (Bennelongia Pty Ltd, Perth, WA) produced the map. IS thanks Annette Koenders (Edith Cowan University, Perth) and Mike Johnson (University of Western Australia, Perth) for providing laboratory space for the molecular part of this research. Dr Finn Viehberg (Köln, Germany) and Dr David J. Horne (London, U.K.) are thanked for their valuable comments as referees.

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Manuscript received: 29 July 2013
Manuscript accepted: 9 October 2013
Published on: 25 November 2013
Topic editor: Rudy Jocqué
Desk editor: Kristiaan Hoedemakers