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Caridina biyiga sp. nov., a new freshwater shrimp (Crustacea: Decapoda: Atyidae) from Leichhardt Springs, Kakadu National Park, Australia, based on morphological and molecular data, with a preliminary illustrated key to Northern Territory *Caridina*

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Abstract

Caridina biyiga sp. nov. is described from Leichhardt Springs, Kakadu National Park, Northern Territory, Australia, based on morphological and molecular data. The new species is highly distinctive among its congeners in having the dactylus of pereiopod 5 similar to the dactyli of pereiopods 3–4 and lacking the comb-like row of spiniform setae typical of the genus. The branchial formula is also distinctive for the genus in lacking an arthrobranch at the base of pereiopod 1 and in having a vestigial epipod on maxilliped 1.

Despite the distinctive morphology of the new species, the molecular data did not provide strong support for the recognition of a new genus. Phylogenetic analyses of Australian *Caridina* using the mitochondrial 16S rDNA gene fragment placed the new species in a well-supported clade containing at least one typical species of *Caridina*. Within this clade, referred to as the 'thermophila' group, Kimura 2-parameter (K2P) genetic distances of 16S rDNA between the new species and sister taxa ranged from 5.1–6.0%. Analyses using the mitochondrial 3' COI gene fragment from species of the 'thermophila' group yielded K2P genetic distances between the new species and its sister taxa ranging from 10.4–15.1%.

A preliminary illustrated key to Northern Territory *Caridina* is provided. The conservation significance of Leichhardt Springs and its aquatic fauna are also briefly discussed.

Key words: taxonomy, systematics, DNA, phylogeny, genetics, new species, thermal springs.

Introduction

Bishop (1967) first reported *Caridina* from the Northern Territory in a paper discussing the zoogeography of Australian freshwater decapod Crustacea. Subsequently, Smith & Williams (1982) recorded *C. wilkinsi* (Calman, 1926) from Fogg Dam, Humpty Doo and near Jabiru in Kakadu National Park. Bruce (1983) reported *C. gracilirostris* De Man, 1892 (= *Caridina* 'sp. Gulf1' this study; sensu Page *et al.* 2007a) from Darwin River Dam. In a checklist of the Decapoda of Australian inland waters, Horwitz (1995) also listed *C. typus* H. Milne Edwards, 1837 and *C. serratirostris* (= *Caridina* 'sp. WA4' this study; sensu Page *et al.* 2007a) from the Northern Territory.

The most detailed treatment of the Northern Territory fauna to date was an extensive molecular phylogenetic study of Australian *Caridina* by Page *et al.* (2007a). Three undescribed species were reported from the Northern Territory: *Caridina* 'sp. NT 1' from Melville Island; *Caridina* 'sp. NT nilotica' from Bamboo Creek, Holmes Jungle and the Roper River at Roper River Bar; and *Caridina* 'sp. Gulf1' from Coomalie Creek (the same species previously listed from the Northern Territory as *C. gracilirostris* by Horwitz 1995). De Mazancourt *et al.* (2019) also recorded *C.* 'sp. NT nilotica' from the Blackmore River in the Northern Territory, as well as *C.* 'sp. WA4'. This last

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taxon had been originally reported from Western Australia (Page *et al*. 2007a) and was previously listed from the Northern Territory (as *C. serratirostris*) by Horwitz (1995). Wilson (2008) presented colour photographs, habitat information, colour pattern notes and life history details for the three undescribed Northern Territory species previously reported by Page *et al*. (2007a), and also recorded another undescribed species, *Caridina* 'sp. NT2'.

This study describes a new *Caridina* species from Leichhardt Springs, Kakadu National Park, Northern Territory, based on morphological and molecular data. Preliminary phylogenetic analyses of all known Australian *Caridina* species, including undescribed species, are also presented based on the mitochondrial 16S gene fragment. Relationships with the closest sister taxa of the Leichhardt Springs *Caridina* are further investigated using the 3' COI and 16S mitochondrial gene fragments. Key diagnostic characters for Northern Territory species, including undescribed taxa, are presented in the form of a preliminary illustrated key to Northern Territory *Caridina*.

In addition to the systematics of the new species, some features of the conservation significance of Leichhardt Springs and its aquatic fauna are also briefly described. Over the last decade, Leichhardt Springs has emerged as a significant 'hotspot' for narrow-range endemics amongst the freshwater ecosystems of Kakadu National Park (Cook *et al*. 2014; Unmack *et al*. 2013; Wilson *et al*. 2009). In common with a number of other springs and seeps associated with the ancient sandstone plateau and escarpment ('stone country') complex of the Park and western Arnhem Land, it shares high endemism of macrocrustaceans, including decapod shrimps (in other springs and seeps only endemic Palaemonidae) and phreatoicidean isopods. The fish fauna of the springs also contains distinctive elements.

Materials and methods

Specimens. The new species was collected from Leichhardt Springs on the headwaters of the northern branch of Burdulba Creek, approx. 12 km south of Jabiru and about 1 km west of a large, outlying, sandstone formation of the Kakadu-Arnhem Land plateau and escarpment complex (Fig. 1). Collections were made in May 2003 and May 2009 on the north arm of Leichhardt Springs by staff of the Supervising Scientist Branch (SSB), Department of Environment & Energy, Northern Territory. Both these collections were used for the taxonomic description and the latter collection for the molecular analyses. An additional collection of non-type material was made in June 2016 by Dr Michael Hammer (MAGNT) and Mike Ellis (SSB) near the head of the south arm of Leichhardt Springs and at the downstream confluence of the north and south arms.

The preliminary illustrated key to Northern Territory *Caridina* is based on preserved material from Northern Territory Monitoring River Health (NT MRH) surveys of the Northern Territory; SSB collections from the Alligator Rivers Region; specimens collected from the Darwin area by David Wilson; and the literature record of *C. typus* from the Northern Territory by Horwitz (1995).

Lodgement of types and molecular sequences. Type material is lodged at the Museum and Art Gallery of the Northern Territory, Darwin (registration numbers Cr019223–Cr019227). New gene sequences from all taxa sequenced for this paper are lodged on GenBank (http://www.ncbi.nlm.nih.gov; accession numbers KJ801318–KJ801334).

Terminology. In the description and illustrated key, the terms first cheliped and second cheliped refer to the first pereiopod (P1) and second pereiopod (P2) respectively. Similarly, the terms first and second chelae refer to the pincers of P1 and P2 respectively. Terminology for setae and spines follows Short (2004).

Measurements. Morphometric measurements were taken from drawings made using a camera lucida mounted on a stereomicroscope and were rounded to the nearest 0.05 mm.

Illustrations. Illustrations were made using a camera lucida mounted on a stereomicroscope.

Informal taxon names. Informal names for the undescribed Australian *Caridina* species in the molecular analyses and illustrated key follow Page *et al*. (2007a), Page *et al*. (2008b), Wilson (2008) and de Mazancourt *et al.* (2019).

Abbreviations. Aust., Australia; bp, base pairs; CE., central eastern; CL, postorbital carapace length; CW., central western; ERISS, Environmental Research Institute of the Supervising Scientist; MAGNT, Museum and Art Gallery of the Northern Territory; MDB, Murray-Darling Basin; NP, National Park; NSW, New South Wales; NT, Northern Territory; NT MRH, Northern Territory Monitoring River Health (subsequently known as AUSRIVAS); P, pereiopod; Qld, Queensland; SA, South Australia; SSB, Supervising Scientist Branch (Heritage, Reef and Marine Division), Department of Environment & Energy, Northern Territory; TL, total length measured from the tip of the rostrum to the tip of the telson; Vic., Victoria; WA, Western Australia; Water Res. Div. LPE, Water Resources Division, Lands, Planning and the Environment, Northern Territory (now Aquatic Health Unit, Water Resources Division, Department of Environment and Natural Resources, Northern Territory).

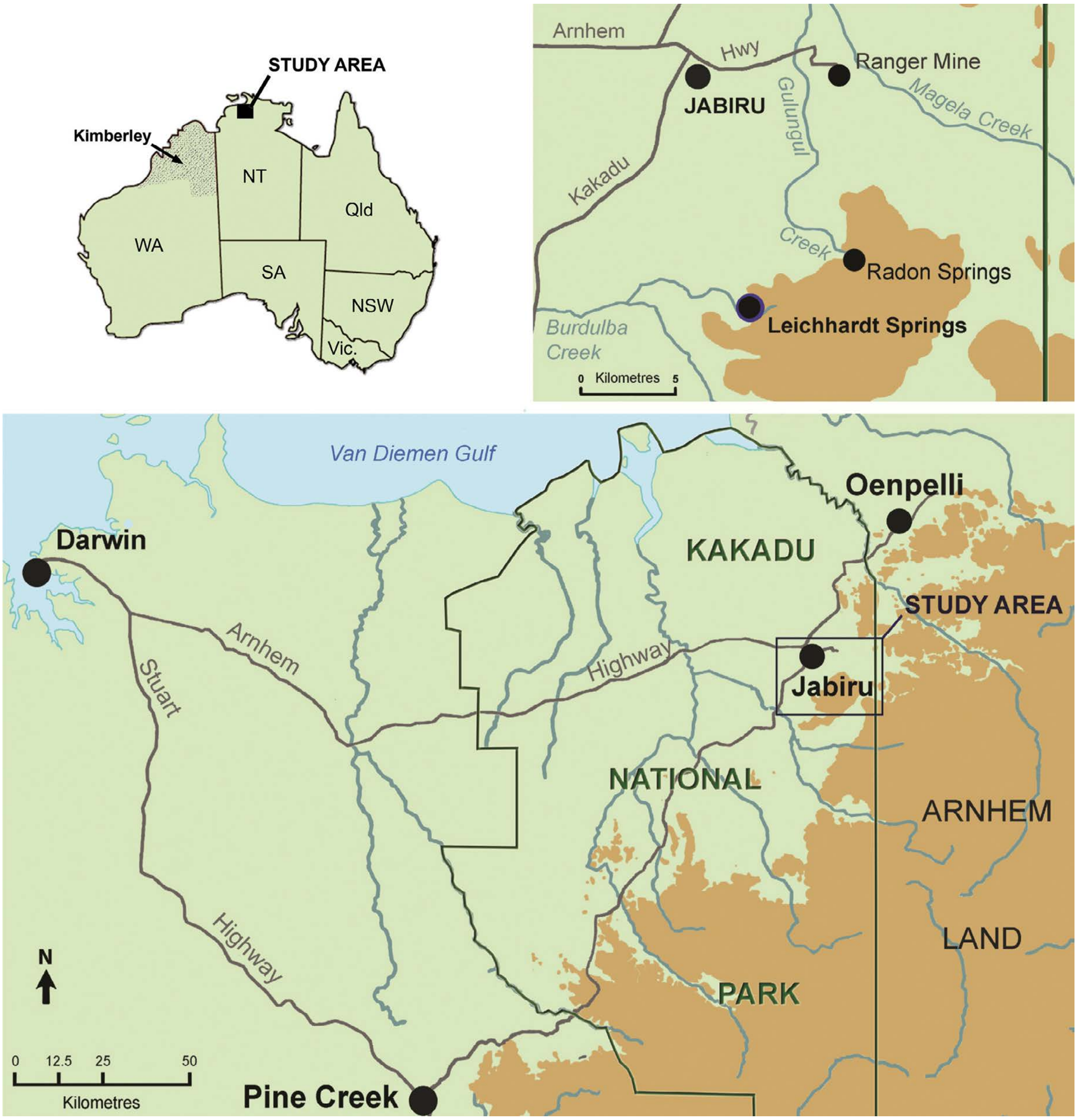

FIGURE 1. Maps showing the location of the study area. Upper left, location of the general study area within Australia; upper right, detailed view of the study area showing the location of Leichhardt Springs; main lower map, broader view of the study area showing its location within Kakadu NP and the Northern Territory.

Molecular analyses. Six specimens from the 2009 Leichhardt Springs collection were sampled for genomic DNA. Four genes were targeted for amplification and sequencing—three mitochondrial DNA (mtDNA) genes: 16S ribosomal DNA (**16S**), 3’ cytochrome c oxidase I (**3’ COI**) and 5’ cytochrome c oxidase I (**5’ COI**); and one nuclear DNA (nDNA) gene, 28S ribosomal DNA (**28S**). Five specimens were sampled for the 16S gene fragment and one specimen for the 3’ COI, 5’ COI and 28S gene fragments.

TABLE 1. Atyid species used in the 16S DNA sequence analyses.

Species	Australian Distribution	GenBank Accession	Sequence Source
Australatya striolata	E. Aust.: NE.Qld to NE.Vic.	AY795035	Page *et al*. 2005b
Caridina appendiculata	NE.NSW to CE.NSW	AY795051	Page *et al*. 2005b
Caridina biyiga sp. nov.	Leichhardt Springs, NT	KJ801318-9	this study
Caridina confusa	NE.Qld	DQ478495	Page *et al*. 2007a
Caridina gracilipes	NE.Qld	DQ478497	Page *et al*. 2007a
Caridina gracilirostris	NE.Qld	KJ801329	this study
Caridina 'indistincta sp. A'	SE.Qld	DQ478499	Page *et al*. 2007a
Caridina 'indistincta sp. B'	E. Aust.: CE.Qld to NE.NSW. MDB: Qld to SA	AY795040	Page *et al*. 2005b
Caridina 'indistincta sp. C1'	SE.Qld	AY795045	Page *et al*. 2005b
Caridina 'indistincta sp. C4'	NE.NSW	AY795049	Page *et al*. 2005b
Caridina malanda	NE.Qld	MK189911	de Mazancourt *et al.* 2019
Caridina serratirostris	NE.Qld	KJ801331	this study
Caridina 'sp. D'	E.Aust.: CE.Qld to SE.Qld. MDB: Qld to SA	KJ801330	this study
Caridina 'sp. DG'	NW.Qld	DQ478520	Page *et al*. 2007a
Caridina 'sp. FK1'	Kimberley, WA	JN167232	Cook *et al*. 2011
Caridina 'sp. Gulf1'	N. Aust.: NT to NW.Qld	DQ478533	Page *et al*. 2007a
Caridina 'sp. Gulf2'	NW.Qld	KJ801320	this study
Caridina 'sp. LE'	Lake Eyre Basin, SA	DQ478534	Page *et al*. 2007a
Caridina 'sp. Moyle'	NW.NT	KJ801321	this study
Caridina 'sp. NT1'	Melville Island, NT	DQ478537	Page *et al*. 2007a
Caridina 'sp. NT2'	NW.NT	KJ801322	this study
Caridina 'sp. NT nilotica'	N. Aust.: Kimberley, WA to NE.NT	KJ801323	this study
Caridina 'sp. 3 Solomon'	NE.Qld	DQ478507	Page *et al*. 2007a
Caridina 'sp. WA2'	Kimberley, WA	DQ478551	Page *et al*. 2007a
Caridina 'sp. WA3'	Pilbara, WA	DQ478553	Page *et al*. 2007a
Caridina 'sp. WA4'	N. Aust.: Kimberley, WA to NT	KJ801324	this study
Caridina 'sp. WA5'	Kimberley, WA	JN167244	Cook *et al*. 2011
Caridina' sp. WA6'	Kimberley, WA	JN167245	Cook *et al*. 2011
Caridina spelunca	Kimberley, WA	DQ478548	Page *et al*. 2007a
Caridina spinula	NE.Qld	DQ478527	Page *et al*. 2007a
Caridina thermophila	CW.Qld	KJ801325	this study
Caridina typus	NE.Qld, CE.Qld, ? NT	DQ478561	Page *et al*. 2007a
Caridina wilkinsi	N. Aust.: NT to NE.Qld	DQ681272	Page *et al*. 2008a
Caridina zebra	NE.Qld	AY661486	Page *et al*. 2005a
Parisia gracilis	Cutta Cutta Caves, NT	EU123843	Page *et al*. 2008b
Parisia unguis	Cutta Cutta Caves, NT	DQ681288	Page *et al*. 2007b
Pycneus morsitans	Gibson Desert, WA	KJ801326	this study
Pycnisia raptor	Cutta Cutta Caves, NT	DQ681271	Page *et al*. 2007b
Stygiocaris stylifera	North West Cape, Barrow Is., WA	KJ801328	this study
Stygiocaris lancifera	North West Cape, WA	KJ801327	this study
Stygiocaris 'sp. Bundera'	North West Cape, WA	EU123842	Page *et al*. 2008b

Genomic DNA was amplified from tail muscle tissue and sequenced in both directions as per Page *et al.* (2008c). The following primer combinations were used; **16S**: 16S-F-Car and 16S-R-Car (von Rintelen *et al.* 2007); **3' COI**: CDC0.La (Page *et al.* 2005b) and COIa-H (Palumbi *et al.* 1991); **5' COI**: LCO-1490 and HCO-2198 (Folmer *et al.* 1994); **28S**: 28S-F-Cru and 28S-R-Met (von Rintelen *et al.* 2012). For comparative purposes, 12 additional Australian atyid species were also sequenced for 16S using the primer combination above or 16S-ar (Palumbi *et al.* 1991) and 16S-R1-Car (von Rintelen *et al.* 2007) (see Table 2 for sampling site details for specimens sequenced in this study). A specimen of *Caridina thermophila* was also sequenced for 3' COI using CRCOI-F and CRCOI-F (Cook *et al.* 2008).

As a quick preliminary scan for any closely related, Indo-West Pacific species, sequences of the four gene fragments from the Leichhardt Springs specimens were compared to all available DNA sequences on GenBank (http://blast.ncbi.nlm.nih.gov/) as of 12 June, 2019 and the 5' COI sequence compared to the BOLD database (http://www.boldsystems.org) on the same date.

The phylogenetic analyses focused on 16S ribosomal DNA (16S), the most widely sequenced gene fragment for atyid shrimps. From the 16S analyses, we identified a well-supported clade containing the new species and its most closely related taxa. We then constructed a smaller dataset using species from this clade and the second most common fragment sequenced for atyids, the 3' portion of cytochrome c oxidase I (COI). This was undertaken to explore relationships within the closely related species using the faster evolving COI gene.

The 16S dataset included all *Caridina* species so far reported from Australia and was compiled from the Leichhardt Springs sequences, 12 Australian atyid specimens sequenced for this study, and existing sequences downloaded from GenBank (Table 1). This dataset was aligned using Muscle (Edgar 2004) within Mega version 6 (Tamura *et al.* 2011). The most appropriate substitution model (lowest Bayesian Information Criterion score) was chosen with Mega for use in the phylogenetic analyses. Two forms of phylogenetic analyses were performed: maximum likelihood analyses in Mega using the appropriate model and bootstrapped 500 times; and Bayesian analyses using MrBayes version 3.2 (Huelsenbeck & Ronquist 2001) with the relevant molecular model for each dataset (parameters: 3 million generations, trees sampled every 1000 cycles, 25% burn in, two runs of four chains heated to 0.2). Genetic distances between species were calculated in Mega using the standard Kimura 2-parameter model (K2P). A smaller 3' COI dataset (species from the well-supported 16S clade containing *Caridina biyiga* sp. nov.), as well as a combined 16S/3' COI dataset, were also created, and analysed as above.

TABLE 2. Sampling sites for specimens sequenced in this study.

Species	Sampling Site	Latitude	Longitude
Caridina biyiga sp. nov.	Leichhardt Springs (north arm), NT	-12.7775	132.8583
Caridina gracilirostris	Johnstone River, Innisfail at main road crossing, NE.Qld	-17.5064	145.9926
Caridina serratirostris	Johnstone River, Innisfail at main road crossing, NE.Qld	-17.5064	145.9926
Caridina 'sp. D'	College's crossing, Brisbane River, SE.Qld	-27.5568	152.8042
Caridina 'sp. Gulf2'	Beatons Gully, Albert River, near Burketown (Nicholson Catchment), NW.Qld	-17.7335	139.5569
Caridina 'sp. Moyle'	Unnamed Creek, tributary of Moyle River, NT	-14.2721	130.0725
Caridina 'sp. NT2'	Blackmore River, Darwin Area, NT		
Caridina 'sp. NT nilotica'	Leanyer Swamp, Buffalo Creek, Darwin Area, NT		
Caridina 'sp. WA4'	Howard River, Gunn Point road crossing, Darwin Area, NT	-12.4625	131.0838
Caridina thermophila	Near Aramac, Qld		
Pycneus morsitans	Warburton Region, Canning Stock Route, Mujingerra Cave, WA	-22.5248	124.1636
Stygiocaris stylifera	L8, Barrow Island, WA	-20.8173	115.3951
Stygiocaris lancifera	C-24 Milyering Well, Cape Range, WA	-22.0200	113.9295

Results

Taxonomy

Family Atyidae De Haan, 1849

Caridina biyiga sp. nov.

(Figs 2–5, 7–9; Tables 1–3)

Type Material. Holotype, MAGNT Cr019223, ♀ (2.2 mm CL), Leichhardt Springs, north arm, Kakadu NP, Northern Territory, Australia, 12°46.6’ S, 132°51.5’ E, L. Chandler, D. Buckle, 26/5/2009. Paratypes, MAGNT Cr019224, 5 ovig. ♀, (2.15–3.05 mm CL), same collection data as holotype; MAGNT Cr019225, 2 ♂ (2.05–2.15 mm CL), same locality as holotype, SSB, 14/5/2003; MAGNT Cr019226, 2 ovig. ♀ (2.45–2.7 mm CL), same collection data; MAGNT Cr019227, 1 non-ovig. ♀ (2.25 mm CL), same collection data.

Non-type material: MAGNT Cr019228, 47 unsexed, Leichhardt Springs, south arm, Kakadu NP, Northern Territory, Australia, 12°46.7’ S, 132°51.3’ E, M. Hammer, M. Ellis, 8/6/2016; MAGNT Cr019229, 2 unsexed, Leichhardt Springs, downstream confluence of north and south arms, Kakadu NP, Northern Territory, Australia, 12°46.5’ S, 132°51.3’ E, M. Hammer, M. Ellis, 8/6/2016.

Comparative material: *Caridina wilkinsi*, MAGNT Cr019230, 1 ovig. ♀ (2.5 mm CL), Sandy Creek below Sandy Creek Falls, Northern Territory, 13°44.66’ S, 130°44.66’ E, NT MRH, Stn FN01, Water Res. Div. LPE, 30/10/1996.

Caridina typus, MAGNT Cr019231, 1 ♀ (3.2 mm CL), Ira Lafai, spring source, Timor-Leste, ERISS, 10/9/2006.

Caridina ‘sp. Gulf1’, MAGNT Cr019232, 1 ♀ (2.75 mm CL), Baralil Billabong, Kakadu NP, Northern Territory, ERISS, 29/5/2006.

Caridina ‘sp. NT1’, SAM 7904, 5 unsexed (1 specimen sequenced for Page *et al*. 2007a), Melville Island, Northern Territory, in creek approx. 2 km from river mouth, C. Watts, 23/5/1999; MAGNT Cr019233, 1 ovig. ♀ (3.25 mm CL), Takamprimili Creek downstream of Pickertaramoor Airstrip, Melville Island, Northern Territory, 11°46.9’ S, 130°52.7’ E, NT MRH, stn ML03, Water Res. Div. LPE, 17/9/1996.

Caridina ‘sp. NT2’, MAGNT Cr019234, 1 unsexed (2.25 mm CL), Casuarina Coastal Reserve, Tiwi Stormwater Drain, Darwin, Northern Territory, 12°21.9’ S, 130°52.4’ E, NT MRH, Stn DW12, Water Res. Div. LPE, 1/10/1996.

Caridina ‘sp. NT nilotica’, MAGNT Cr019235, 1 ♀ (7.25 mm CL), Leanyer Swamp, Buffalo Creek, Northern Territory, D. Wilson.

Caridina ‘sp. WA4’, MAGNT Cr019236, 1 unsexed (3.9 mm CL), Howard River at Gunn Point road crossing, Northern Territory, D. Wilson.

Etymology. An indigenous word from the Gundjeihmi language (pronounced bee-yee-ga) meaning ‘different’ or ‘other’, a reference to its unusual morphology compared to other species of *Caridina*. To be used as a noun in apposition.

Proposed vernacular name. Leichhardt Springs shrimp.

Description. *Habitus* (Fig. 2A). Small, subcylindrical, rotund species of the genus. Maximum size of females 3.05 mm CL ($n = 9$); males 2.15 mm CL ($n = 2$); minimum size of ovig. females 2.15 mm CL ($n = 7$).

Acron (Figs. 2A–B). Median carina absent, anteromedially with low, rounded, transverse carina, anteromedian projection (bec ocellaire) absent. Eyes well developed, cornea large, hemispherical, well pigmented.

Carapace (Figs. 2A, E, I–J). Smooth, glabrous; dorsum slightly to moderately humped in adult females, indistinctly humped in males. Rostrum short, at most reaching proximal 1/3 of intermediate antennular peduncle segment, 0.3–0.4 × CL ($\overline{x} = 0.35$, $n = 11$); slender, depressed, appearing triangular in dorsal view; lateral carina well developed, ventral carina obsolete, dorsal carina generally poorly developed, less commonly moderately developed; apex acute; dorsal carina slightly convex to almost straight, armed with 3–7 preorbital teeth (commonly 4–6), teeth variably distributed on dorsal margin, commonly unarmed near tip, interspaces between teeth setose; ventral carina unarmed. Antennal spine well developed, completely fused with, and indistinct from, inferior orbit. Pterygostome broadly rounded.

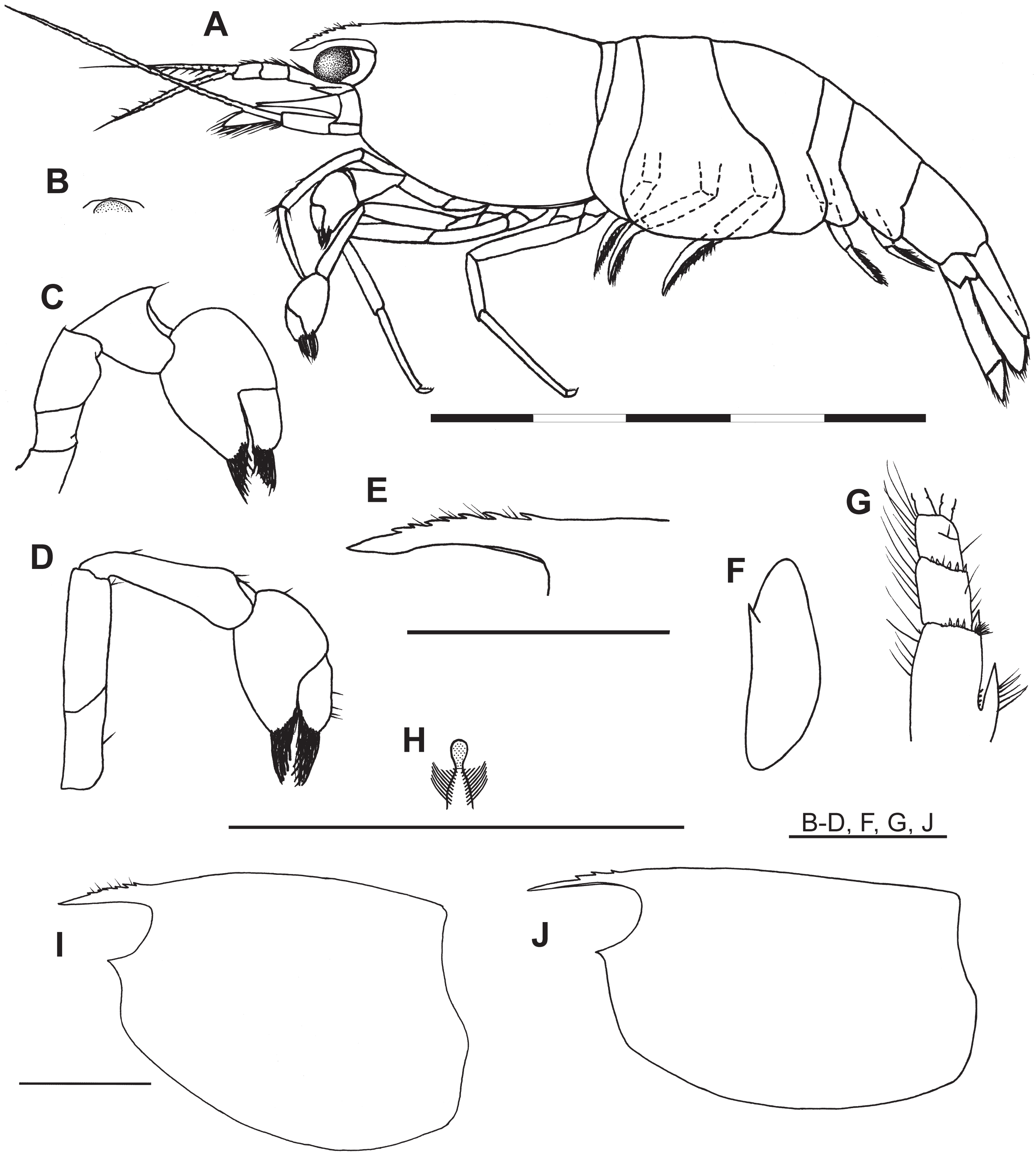

FIGURE 2. *Caridina biyiga* sp. nov. Holotype ♀ 2.2 mm CL (MAGNT Cr019223): A, habitus; C, right first pleopod; D, right second pereiopod; E, enlarged view of rostrum; H, dorsal view of tip of propodus of right first cheliped, setation cut to reveal tip. Paratype ovig. ♀ 2.45 mm CL (MAGNT Cr019226): B, posterodorsal view of anteromedial acron showing transverse carina; G, right antennule. Paratype ♂ 2.05 mm CL (MAGNT Cr019225): F, scaphocerite, setation omitted; J, carapace. Paratype non-ovig. ♀ 2.25 mm CL (MAGNT Cr019227): I, carapace. Scale bar for A = 5 mm, divisions = 1 mm. Remaining scale bars = 1 mm.

Antennule (Fig. 2G). Peduncle short, failing to reach distal margin of scaphocerite; distal margins of basal and intermediate segments with row of short spiniform setae; anterolateral angle of basal segment acutely pointed, reaching to around 1/3 length of intermediate peduncle segment; stylocerite short, failing to reach distal end of basal antennular peduncle segment, ca. 0.2 × CL.

Scaphocerite (Fig. 2F). Short, 0.6–0.65 × CL, length 2.75–3.0 × breadth, tapering strongly from broadest point to anterior margin, broadest point in proximal half, strongly produced anteromedially, lateral margin slightly concave.

Mouthparts (Figs. 3A–G). Labrum broadly rounded anteriorly, asetose. Metastoma with paragnatha incompletely fused basally to form weak corpus, basal paragnath with laterally revolute, semicircular carina, distolateral paragnath feebly alariform, distal margin rounded, distal and distomesial margins setose. Mandibles with well-developed incisor and molar processes, dimorphic, left and right mandible of similar size but differing in shape, left mandible with incisor process bearing 2 larger outer cusps and smaller, indistinct inner cusp, patch of long setae along margin leading to molar process, molar process strongly produced, ridged, right mandible incisor process with 2 outer cusps larger than inner pair, inner margin leading to molar process with 3 spiniform setae followed by patch of long setae, molar process ridged in semicircular arc. Maxillula with upper lacinia broadly elongate, mesial margin straight, with row of spiniform setae, lower lacinia bluntly angular distomesially, setose along distal margin and mesially; palp well developed, entire, bisetose, slightly expanded distally. Maxilla with distinct basal and coxal endites, inner margins densely setose; palp slender, tapering; scaphognathite well developed, with plumose setae distally, shorter setae laterally, proximal triangular process short and broad, terminating in several very long setae. First maxilliped with well separated basal and coxal endites, inner margins densely setose; palp broad, triangular, distally setose; caridean lobe well developed; rudimentary epipod present; exopod well developed, flagellum distinct, with few distal plumose setae. Second maxilliped with dactylar and propodal segments fused, slightly concave and densely setose mesially; coxa asetose, slightly produced mesially; exopod narrow, short, just over-reaching propodus, with marginal plumose setae distally; mesial margins of merus and ischium sparsely setose; carpus with few distal setae. Third maxilliped reaching slightly beyond scaphocerite; terminal segment ca. 0.8 × penultimate segment length, ending in sharply hooked unguis followed by row of ca. 9 large spiniform setae on distal third of segment; ischiomerus and basis fused, ischiomerus with few spiniform setae distolaterally; exopod a little shorter than ischiomerus, with long plumose setae on distal margin.

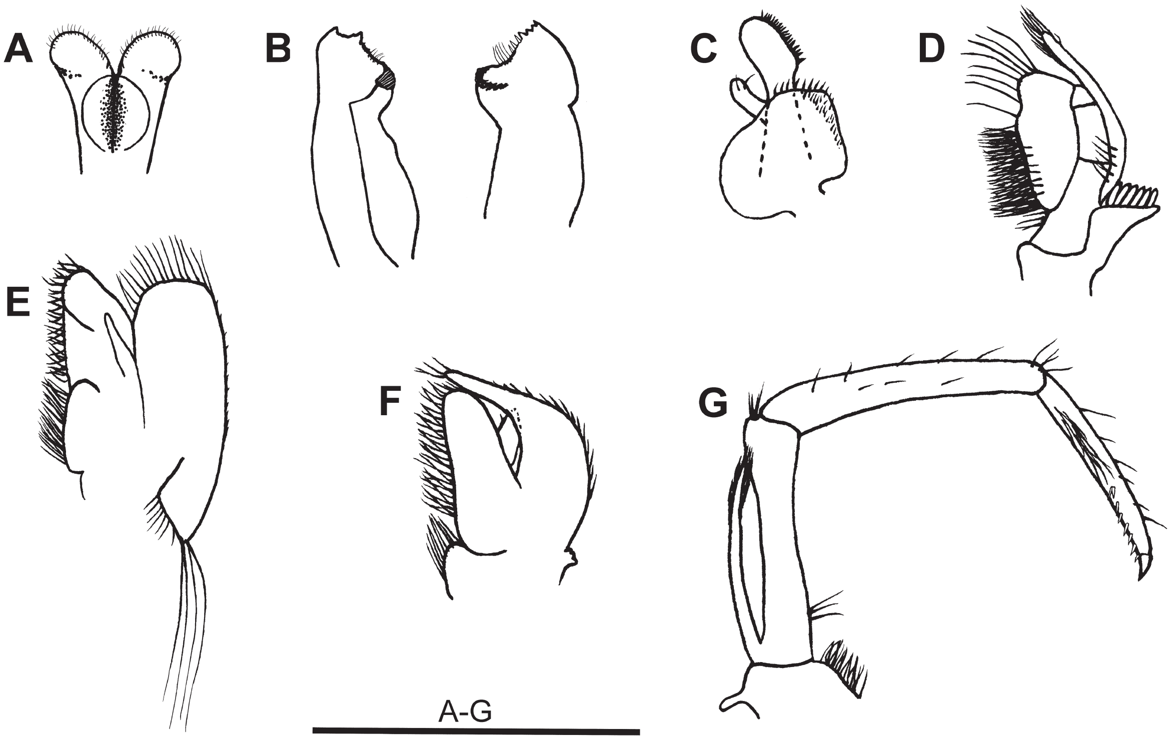

FIGURE 3. *Caridina biyiga* sp. nov. Paratype ♂ 2.05 mm CL (MAGNT Cr019225). A, metastoma; B, mandibles; C, maxillula; D, second maxilliped; E, maxilla; F, first maxilliped; G, third maxilliped (dorsal view of left maxilliped). Scale bar = 1 mm.

TABLE 3. Branchial formula of *Caridina biyiga* sp. nov.

	Maxillipeds			Pereiopods				
	I	II	III	1	2	3	4	5
Pleurobranchs	–	–	–	1	1	1	1	1
Arthrobranchs	–	–	2	–	–	–	–	–
Podobranchs	–	1	–	–	–	–	–	–
Epipods	1	1	1	1	1	1	1	–
Exopods	1	1	1	–	–	–	–	–

Branchiae (Figs. 3D, F–G; 4J; Table 3). Epipod rudimentary on first maxilliped, well developed on maxillipeds 2–3 and P1–4, bilobed on maxilliped 3 with bluntly elongate anterodorsal lobe and strap-like posteroventral lobe bearing distal hook, strap-like with distal hook on P1–4, bisetose setobranchs present on P1–5, well-developed, elongate, 6-lamellar podobranch present on epipod of maxilliped 2. Exopods present on maxillipeds, absent on pereiopods. Two arthrobranchs above maxilliped 3 (upper arthrobranch small, lower arthrobranch well developed), arthrobranch absent above P1. Pleurobranchs well developed above P1–5.

First cheliped (Figs. 2C, H). Short, at most reaching distal margin of intermediate segment of antennular segment; chela short, length 1.2–1.4 × breadth, fingers with flexible, sclerotinous, spatulate tips, dactylus slightly shorter to equal in length to manus; carpus deeply excavated distally for reception of chela, length 0.9–1.3 × breadth, 0.65–0.9 × chela length, equal in length to or slightly shorter than merus; merus compressed.

Second cheliped (Fig. 2D). Longer and slightly more slender than first pereiopods, reaching terminal segment of antennular peduncle; chela short, length 1.4–1.9 × breadth, dactylus about equal in length to clearly longer than manus, fingers with flexible, sclerotinous, spatulate tips; carpus slightly excavated distally for reception of chela, subconical, length 3.0–3.7 × breadth.

Third pereiopod (Fig. 4E). Short, distal third of propodus reaching distal scaphocerite; dactylus short, broad, length 2.1–2.3 × breadth, flexor margin armed with 3–4 spiniform setae generally decreasing in size proximally, distal spiniform seta sometimes subequal to unguis, unguis moderately developed; propodal length 7.7–9.1 × max. breadth, 4.7–4.8 × dactylar length, with 2 rows of moderate-sized spiniform setae along flexor margin; carpus with well-developed distal projection; merus with 2 large spiniform setae on flexor margin; coxa with semicircular, concave, lateral plate.

Fourth pereiopod (Figs. 4F, J). Short, reaching distal half of intermediate segment of antennular peduncle; dactylus short, broad, length 2.4–2.5 × breadth; propodus bearing 1 large spiniform seta on flexor margin, length 7.7–9.1 × max. breadth, 4.6–6.0 × dactylar length; coxa with semicircular, concave, lateral plate.

Fifth pereiopod (Fig. 4K). Short, failing to reach distal margin of basal antennular segment; dactylus similar to third and fourth pereiopods, short, length 2.1–2.4 × breadth, flexor margin armed with 3–4 spiniform setae, unguis feebly to moderately developed; propodus with 9–11 moderately large, spiniform setae on flexor margin, length 9.6–10.8 × max. breadth, 5.8–6.1 × dactylar length.

Abdomen (Figs. 4A–D, G). Smooth, glabrous, evenly rounded in lateral view; first to third pleura broadly rounded posteroventrally; fourth pleura produced and rounded posteroventrally; fifth pleura produced and bluntly angular posteroventrally, length ca. 0.5 × sixth pleura length; sixth pleura with posteroventral angle bluntly angular, posterolateral angle acute, non-spinate, length ca. 0.45 × CL, ca. 1.4 × depth. First male pleopod with endopod length ca. 0.5 × exopod length, ca. 2.0 × breadth, triangular, apex blunt, lateral margin setose, mesial margin with single seta; without appendix interna. Second male pleopod with endopod length 0.85–0.9 × exopod length; appendix interna reaching to about half appendix masculina length, with numerous retinaculae distally; appendix masculina spatulate, length 0.4–0.5 × endopod length, bearing ca. 11–13 long spiniform setae on mesial and distal margins. Uropodal exopod with well-developed diaeresis, diaeresis bearing 12–16 spiniform setae. Uropodal protopod with acutely pointed, short, posterior projection, protopod length 1.15–1.25 × breadth.

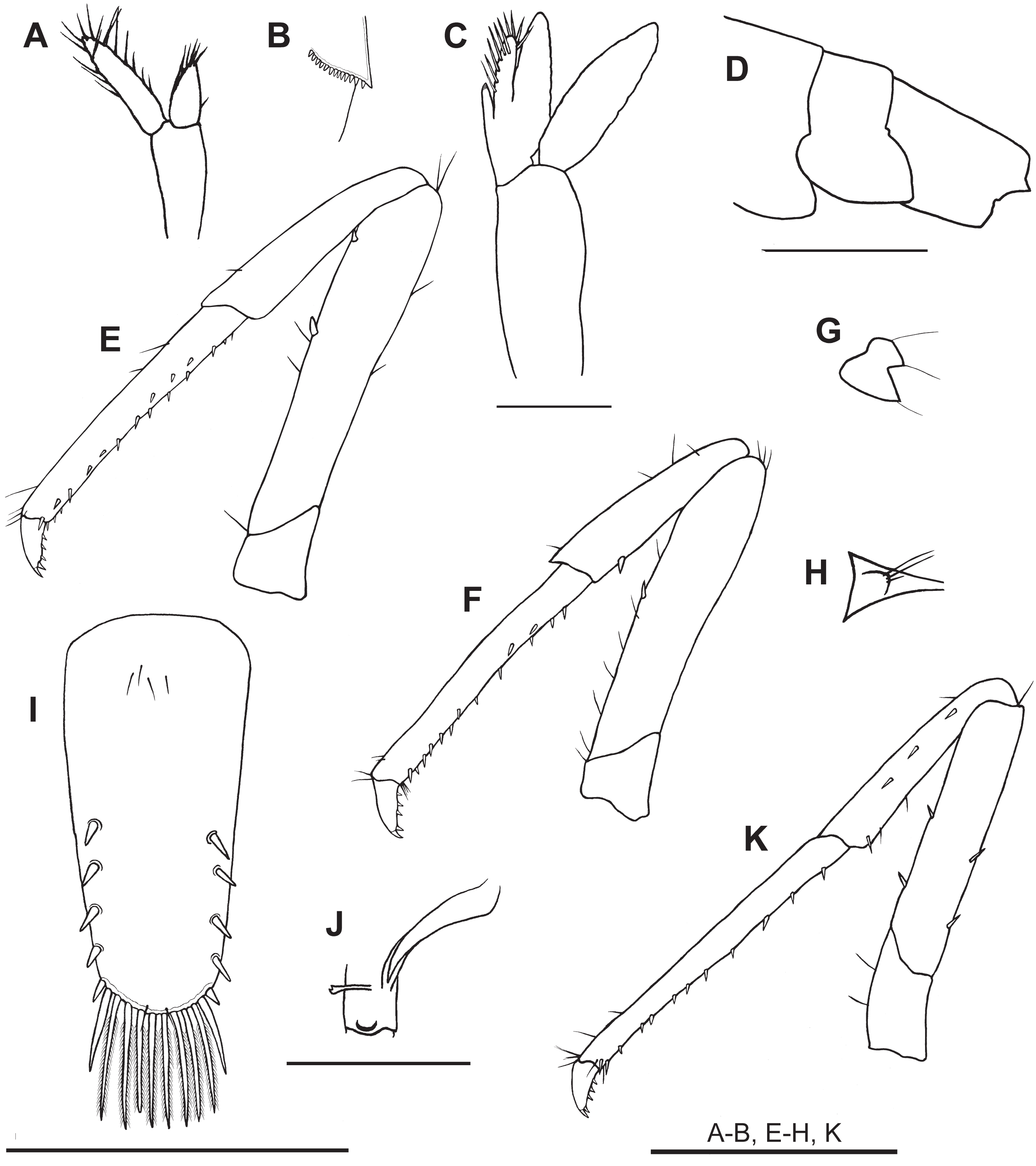

FIGURE 4. *Caridina biyiga* sp. nov. Paratype ♂ 2.05 mm CL (MAGNT Cr019225): A, first pleopod; D, abdominal pleura 4–6; G, left uropodal protopod. Paratype non-ovig. ♀ 2.25 mm CL (MAGNT Cr019227): B, right uropodal diaeresis, plumose setation omitted; H, ventrolateral view of pre-anal plate; I, telson. Paratype ♂ 2.15 mm CL (MAGNT Cr019225): C, second pleopod. Holotype ♀ 2.2 mm CL (MAGNT Cr019223): E, right third pereiopod; F, right fourth pereiopod; J, right coxa of fourth pereiopod showing epipod and setobranchs; K, fifth pereiopod. Scale bars = 1 mm.

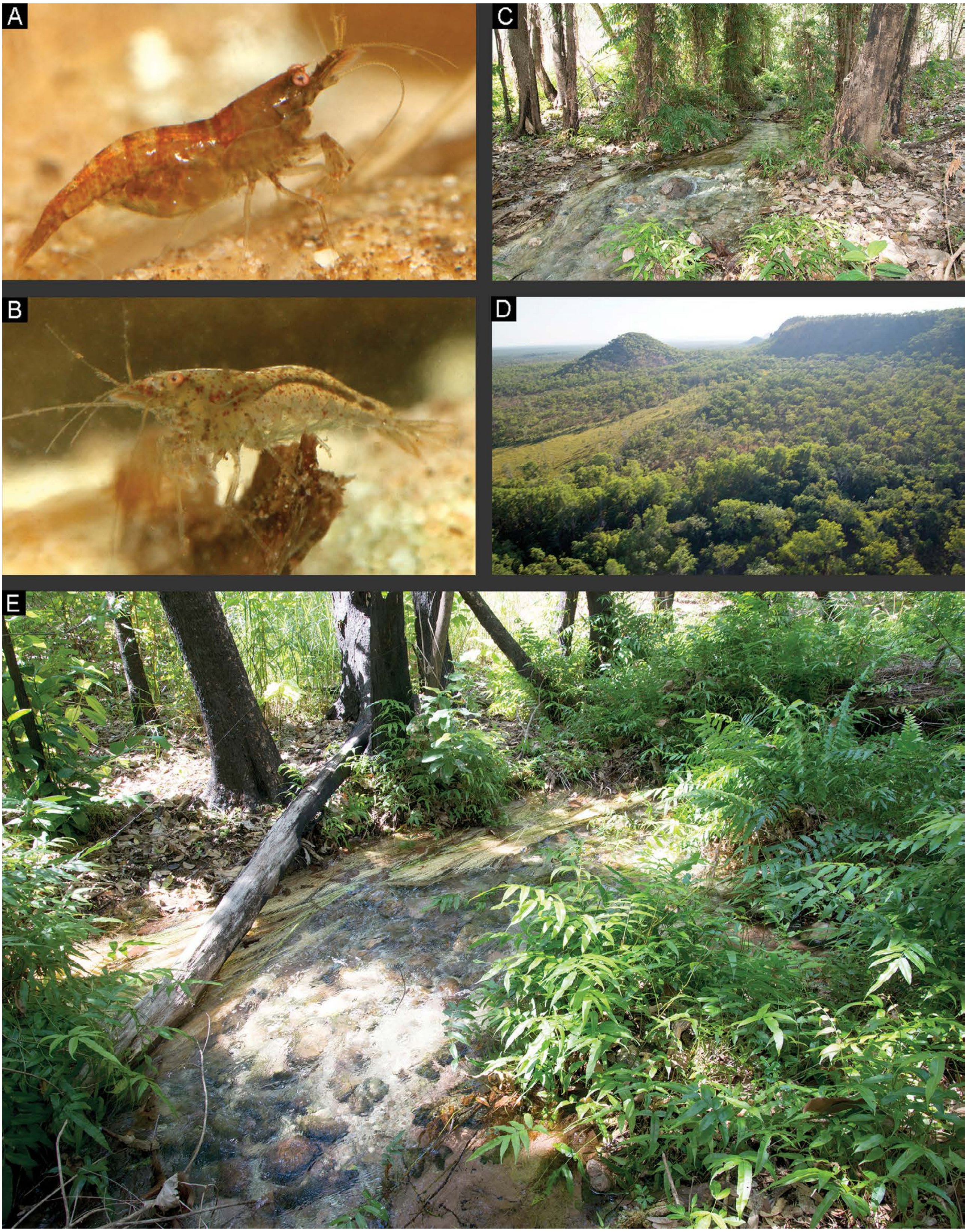

FIGURE 5. A–B, live colouration of *Caridina biyiga* sp. nov. (photos by Dave Wilson); C, South arm of Leichhardt Springs, riffle near head of spring (photo by Michael Hammer); D, aerial view of Leichhardt Springs (heavily vegetated area in foreground) (photo by Michael Hammer); E, North arm of Leichhardt Springs, type locality of *C. biyiga* sp. nov., riffle near head of spring (photo by Michael Hammer).

Telson (Fig. 4I). Short, length ca. 0.5 × CL, ca. 1.2 × sixth abdominal pleura length; broad, length ca. twice breadth; armed with 3–4 pairs of dorsal spiniform setae (holotype with 2 spiniform setae on left side, 3 on right side), usually subequal in size, generally located in posterior half of telson, posterior pair sometimes situated close to posterior telson margin; posterior margin of telson rounded, without medial projection, bearing 1 pair of small lateral spiniform setae, 1 pair of much longer, sublateral, spiniform, non-plumose setae and 8–12 equally spaced, intermediate, spiniform, plumose setae, intermediate plumose setae increasing in length medially, slightly thinner than sublateral setae, scattered simple setae above posterior telson margin.

Pre-anal plate (Fig. 4H). Armed with well-developed pre-anal carina, apex setose, non-spinate.

Life history. Developed ova (with eye spots) large, 0.75–1.0 mm × 0.4–0.65 mm; few in number, 3–11 per brood (Fig. 5A). Ovigerous females collected in May during the early dry season.

The large ova are similar in size to the ova of *C. formosae* Hung, Chan & Yu, 1993 (ova 1.04 × 0.68 mm), a species with highly suppressed, larval development and an almost fully formed, benthic hatchling (Shy *et al*. 2001).

Colour. Translucent with rust brown chromatophores. Chromatophores either small and widely spaced giving speckled appearance (Fig. 5B) or forming large blotches (Fig. 5A), blotches tending to be grouped as transverse bands on abdomen and posterodorsal carapace, widely spaced on ventral carapace and pereiopods, closely spaced on anterodorsal carapace. Ova rust brown (Fig. 5A).

Habitat. Leichhardt Springs has two dominant outflows approx. 320 m apart—a north arm and a south arm, with a downstream confluence into the northern branch of Burdulba Creek (Fig. 6A). The new species has so far been collected from both the north arm and south arm as far downstream as the junction between the two streams. The total length of watercourse in which the species is presently known is approx. 700 m.

The heat source of Leichhardt Springs is presently undetermined although other thermal springs in the Alligator Rivers Region (including western Arnhem Land) are known to be associated with high heat-producing rocks in the basement of the crust (S. Marshall, Geosciences Australia, pers. comm.). No other thermal springs are presently known from Kakadu NP.

The thermal properties of Leichhardt Springs were investigated over a four to five-month period during the 2014 winter-spring dry season using two CTD-Diver multi-parameter dataloggers deployed on the north arm of Leichhardt Springs, one at the head of the spring and the other 160 m downstream (Figs. 6A–B). A third Diver was also deployed in Radon Springs, a non-thermal spring located approx. 6 km to the northeast on the large, outlying, sandstone formation above Leichhardt Springs (Fig. 1). Over the five-month period, water temperature at the head of the north arm spring was an invariant 30.2°C (SD = 0.005) and 160 m downstream, almost constant and only slightly cooler (mean 29.8°C, range 29.2–30.3°C). By comparison, Radon Springs showed a much higher temperature range (mean 26.0°C, range 22.1–29.3°C), thus 1–8°C cooler over the same period (Fig. 6B). A sampling trip to the south arm of Leichhardt Springs in June 2016 revealed thermal properties similar to the north arm.

Apart from its thermal properties, the location of Leichhardt Springs relative to the Kakadu-Arnhem Land plateau and escarpment complex is also interesting. Other sandstone-formation springs in Kakadu NP arise within small gorges and typically at the immediate base of escarpments. Leichhardt Springs is located approx. 900 m away from the western escarpment of an outlying sandstone formation and at a lower elevation (Fig. 5D).

Satellite imagery of Leichhardt Springs shows extensive rainforest vegetation along both arms associated with the permanent, spring-fed outflows (Fig. 6A). The head of the north arm outflows through a patch of small, abraded and bleached, sandstone cobbles. For at least 300 m downstream, the north arm is characterised by a sequence of pools with clean, quartzite sand substrate interspersed with swift-flowing runs and riffles of gravel and cobble (Fig. 5E). Riparian trees include *Melaleuca* spp., *Carallia brachiata*, *Pandanus aquaticus*, *Canarium australianum*, *Syzygium* spp. and the monsoon rainforest-specific species, *Nauclea orientalis* and *Melicope elleryana*. The understorey comprises climbing vines (*Flagellaria indica* and *Rhaphidophora australasica*), climbing ferns (*Stenochlaena palustris*), groundstorey ferns (*Blechnum orientale*) and the flowering shrub, *Melastoma* sp. The macrophyte, *Eleocharis* sp., is commonly interspersed amongst runs and riffles of the stream.

The new species is abundant amongst leaf litter and the fibrous roots of riparian trees and ferns along the edges of the stream. No shrimps were found in the clear, faster moving water in the runs and riffles.

The downstream distribution of the shrimps beyond the confluence between the north and south arm is presently unknown as is the dependence of the shrimps on constantly warm, spring waters.

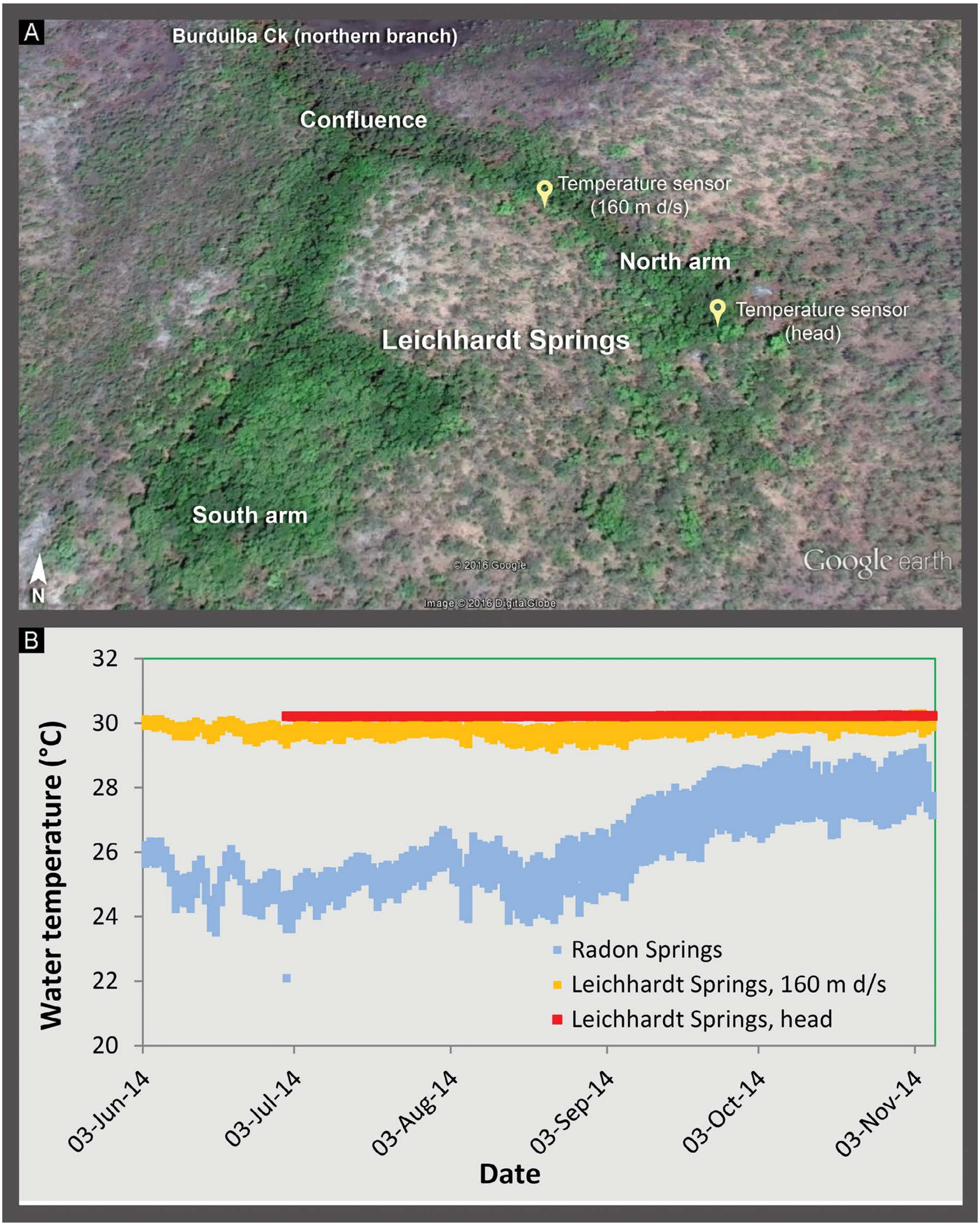

FIGURE 6. A, Google Earth image (2016) of Leichhardt Springs showing north and south arms, downstream confluence and the location of temperature sensors on the north arm (head and 160 m downstream); B, Seasonal, water temperature profiles for Leichhardt Springs (north arm: head and 160 m downstream) and Radon Springs, Kakadu NP.

Apart from water temperature, water quality of Leichhardt Springs is otherwise typical of surface waters draining the highly leached, sandstone formations of Kakadu NP and western Arnhem Land (Short *et al.* 2013) being high in clarity, acidic, very soft and low in solutes. Key physicochemical variables at Leichhardt Springs were measured on 14 May 2003 and were as follows: turbidity < 1 NTU; pH 5.2; electrical conductivity 16 µS cm^{-1}; Ca and K < 0.1 mg L^{-1}; Na 0.9 mg L^{-1}; Mg 0.3 mg L^{-1}; and SO_4 0.2 mg L^{-1}.

Distribution. Endemic to Leichhardt Springs, Kakadu NP, Northern Territory, Australia. The known distributional range within the watercourse and associated riparian zones of Leichhardt Springs is 0.05 km^2.

Molecular results. The five specimens of *Caridina biyiga* sp. nov. sequenced for 16S produced two very closely related haplotypes of 539 bp. The single individual sequenced for the three remaining genes produced the following sequences: 3' COI (557 bp), 5' COI (629 bp) and 28S (500 bp).

A BLASTN comparison of GenBank sequences resulted in the following closest matches to the new species; **16S**: *Caridina thermophila*—95% similar, *C.* 'sp. WA3'—94%, *C.* 'sp. NT1'—94%; **3' COI**: *C.* 'sp. NT1'—90%, *C. thermophila*—87%, *C.* 'sp. WA3'—87%, *C.* 'sp. WA2'—86%; **5' COI**: *C.* 'sp. 3 Solomon' - 85%, *C. similis* - 85%, *C. simoni* - 85%, *C.* 'indistincta sp. A' - 84%; **28S**: *C. similis* - 85%, *C. appendiculata* - 85%, *C. gracilipes* - 85%. The closest matches of the 5' COI sequence on the BOLD database were the same as those of the relevant GenBank results.

The best-fit models of molecular evolution for the molecular datasets were Hasegawa-Kishino-Yano with a gamma shape parameter and an estimated fraction of invariant sites for the 16S dataset, and Tamura 3-parameter with an estimated fraction of invariant sites for the 3' COI dataset. Bayesian and maximum likelihood trees were produced for both datasets and a Bayesian tree for a small combined 16S/3' COI dataset.

The topologies of both the Bayesian and maximum likelihood trees for the full 16S dataset (Bayesian arithmetric mean = –5050.72, maximum likelihood: log score = –4829.33) are very similar, in particular relating to the position of the new species (Figs. 7–8). Both analyses recover *C.* 'sp. WA3' (Pilbara, WA), *C. thermophila* Riek, 1953 (central western Qld), and *C.* 'sp. NT1' (Melville Island, NT) as forming a well-supported clade with *C. biyiga* sp. nov. (Bayesian posterior probability 1.00; maximum likelihood bootstrap 92%), a 'thermophila' species group. Analyses of the large 16S dataset (Figs. 7–8) are not clear on the relationships within the 'thermophila' group, whereas the 3' COI (Bayesian = –1584.72, maximum likelihood: –1580.05) (Figs. 9A–B) and combined 16S/3' COI (Bayesian = –2538.83) data (Fig. 9C) suggest *C.* 'sp. WA3' is sister to the other species in the group. The Kimura 2-parameter (K2P) genetic distances between *C. biyiga* sp. nov. and other species within the group ranged from 5.1–6.0% for the 16S dataset (closest *C. thermophila*) and 10.4–15.1% for the 3' COI dataset (closest *C.* 'sp. NT1').

The most closely related clade to the 'thermophila' group may be a moderately supported grouping of species all from the Kimberley, WA (Bayesian posterior probability 0.90; not supported by the maximum likelihood analysis). Within this clade, a grouping comprising *C. spelunca* Choy, 1996; *C.* 'sp. WA2'; *C.* 'sp. WA5'; and *C.* 'sp. WA6' was moderately supported by both the Bayesian and maximum likelihood analyses (Bayesian posterior probability 0.66; maximum likelihood bootstrap 74%) and is hereby referred to as the 'spelunca' group. K2P genetic distances between 16S sequences of *C. biyiga* sp. nov. and species from the 'spelunca' group ranged from 7.7–9.0% with a 3' COI distance of 15.9% to *C.* 'sp. WA2' from that group.

Relationships of the remaining Australian *Caridina* species were partially resolved using the 16S dataset. Two species groups, which were also easily recognised using morphological characters, were recovered as strongly supported clades in both the Bayesian and maximum likelihood analyses; viz. a 'gracilirostris' group (Bayesian posterior probability 1.00; maximum likelihood bootstrap 99%) and a 'serratirostris' group (Bayesian posterior probability 1.00; maximum likelihood bootstrap 95%).

The *Caridina zebra* species complex (sensu Choy *et al*. 2019) also formed a strongly supported clade in both the Bayesian and maximum likelihood analyses (Bayesian posterior probability 0.99; maximum likelihood bootstrap 86%). This complex comprises three, highly similar species from the Tablelands and Cardwell Range areas of the wet tropics, viz. *C. zebra* Short, 1993, *C. confusa* Choy & Marshall, 1997 and a recently described species, *C. malanda* Choy, Page, de Mazancourt & Mos, 2019.

Another strongly supported clade included the species *C.* 'sp. Gulf2' from northwest Qld and *C.* 'sp. NT2' from the Darwin area, Northern Territory (Bayesian posterior probability 1.0; maximum likelihood bootstrap 100%), although the comparative morphology of the two species was not investigated in the present study.

Two representatives of the *Caridina* 'sp. D' complex, *C.* 'sp. D' and *C.* 'sp. DG', were recovered as a well-supported clade (1.00 Bayesian posterior probability; 100% maximum likelihood bootstrap). This species complex, which requires further study to resolve relationships between putative species, shows an extensive distribution across much of northern, eastern and central Australia. Material from east Queensland has previously been reported as *C. nilotica aruensis* (J. Roux 1926; Riek 1953; Glaister 1976) although the genetic relationship between Australian material and *C. aruensis* J. Roux, 1911 from the Aru Islands, Indonesia, is presently undetermined.

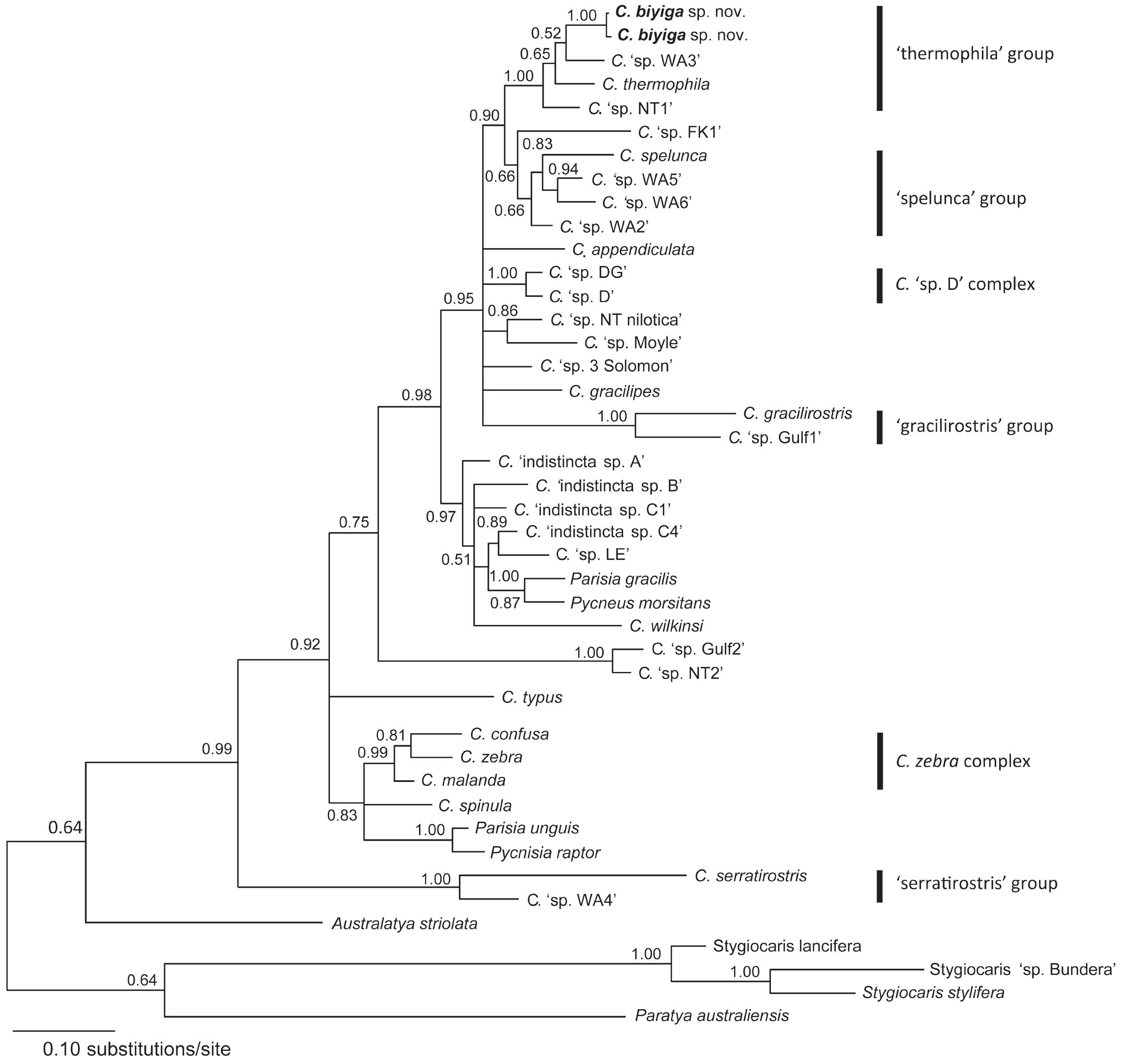

FIGURE 7. Bayesian majority rule consensus topology of Australian *Caridina* 16S rDNA dataset with Bayesian posterior probability values. Nodes with probability values < 0.50 have been collapsed.

Two moderately to strongly supported clades containing species of *Caridina* as well as representatives of hypogeal genera were also recovered. The first of these clades (Bayesian posterior probability 0.97; maximum likelihood bootstrap 69%) comprised *Caridina wilkinsi* (Calman), a wide-ranging, northern Australian species, with the eastern and central Australia species, *C.* 'indistincta sp. A', *C.* 'indistincta sp. B', *C.* 'indistincta sp. C1', *C.* 'indistincta sp. C4', *C.* 'sp. LE' and the northwest Australian, hypogeal species, *Parisia gracilis* Williams, 1964 (NT) and *Pycneus morsitans* Holthuis, 1986 (WA). The second clade (Bayesian posterior probability 0.83; maximum likelihood bootstrap 97%) included species of the *Caridina zebra* complex, *C. spinula* and the NT subterranean species, *Parisia unguis* Williams, 1964 and *Pycnisia raptor* Bruce, 1992. Although presently not supported by morphological data, most of these relationships were also reported in the 16S analyses of Page *et al*. (2008b).

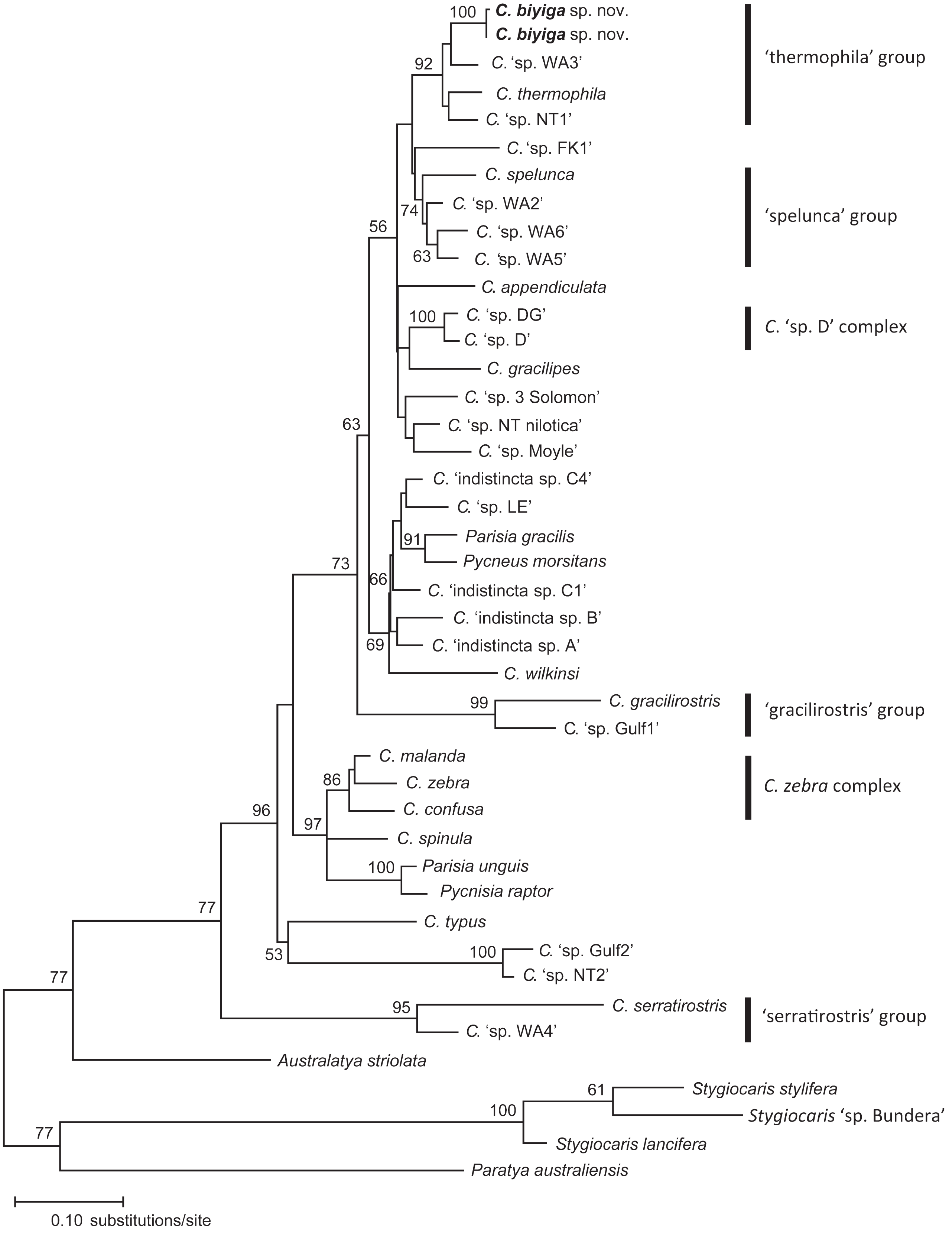

FIGURE 8. Maximum likelihood topology of Australian *Caridina* 16S rDNA dataset with bootstrap values >50% shown.

Within the two hypogeal-epigeal species clades reported above, strong relationships between *P. gracilis* and *Pycneus morsitans* (Bayesian posterior probability 1.0; maximum likelihood bootstrap 87%) and *P. unguis* with *Pycnisia raptor* (Bayesian posterior probability 1.0; maximum likelihood bootstrap 100%) were also recorded. These relationships have previously been reported in the 16S analyses of Page *et al*. (2008b) and von Rintelen *et al*. (2012). The close relationship of *P. gracilis* and *Pycneus morsitans* was also confirmed in the combined 16S/28S/H3 and 16S/28S analyses of von Rintelen *et al*. (2012). The molecular data strongly suggest that Australian *Parisia* are non-monophyletic and that the current generic classification of Australian species of *Parisia*, *Pycneus* and *Pycnisia* requires re-appraisal.

Systematic Position. Although the general morphology of the new species is typical of *Caridina*, the branchial formula, fingertips of the chelae and fifth pereiopod dactylus are unusual for the genus.

The new species lacks an arthrobranch at the base of the first cheliped and has 8 pairs of branchiae rather than the full complement of 9 branchiae normally associated with *Caridina*. There is also a vestigial epipod on the first maxilliped (Fig. 3F) in addition to the epipods on maxillipeds 2–3 (Figs. 3D, G) and pereiopods 1–4 (Fig. 4J) typical of *Caridina*. Under the subfamilial and generic classification of Holthuis (1993), these differences would exclude the new species from *Caridina* and would assign the species to a different subfamily (Caridellinae rather than Atyinae). However, recent studies (von Rintelen *et al.* 2008; von Rintelen *et al*. 2012; De Grave & Page 2014) indicate that the branchial formula is less conservative within the Atyidae than previously accepted and minor differences in the development of the branchiae are not reliable for defining genera and subfamilies. For example, *Caridinides wilkinsi* Calman, which was recently transferred to *Caridina* by De Grave & Page (2014), has an exopod on the first pereiopod and a small epipod on the first maxilliped. Similarly, Cai & Shokita (2006) noted that the arthrobranch at the base of the first cheliped is sometimes reduced in *C. serratirostris*, and invariably absent in *C. celebensis* De Man, 1892. In *C. thomasi* von Rintelen, Karge & Klotz, 2008, there is only one arthrobranch rather than the usual two arthrobranchs at the base of the third maxillipeds. The branchial formula for *C. biyiga* sp. nov. falls within the wide range of variation now reported for *Caridina* sensu lato.

The fifth pereiopod dactylus of the new species is also atypical for the genus and is similar in shape to the dactyli of the third and fourth pereiopods (Figs. 4E–F, K). In other species of *Caridina*, the fifth pereiopod dactylus is usually more slender and elongate than the preceding ambulatory pereiopods, as illustrated by Cai *et al*. (2006; Figs. 13F–I, 14E–H, 15G–J) for the type species, *C. typus*. In the new species, the number of spiniform setae on the flexor margin of the dactylus is also similar to the preceding two pereiopods. At most, there are four, widely spaced, claw-like spiniform setae on the flexor margin (Fig. 4K). In other *Caridina* species, including *C. typus* (see Cai *et al*. 2006; Figs. 13I, 14H, 15J), there is a comb-like row of numerous, closely spaced setae.

In the new species, the fingers of the first and second chelae are distinctive for the genus in having flexible, spatulate tips (Fig. 2H). In the type species of the genus, *C. typus*, the fingertips bear a rigid, hooked, nail-like unguis as illustrated by Bouvier (1925; Fig. 282).

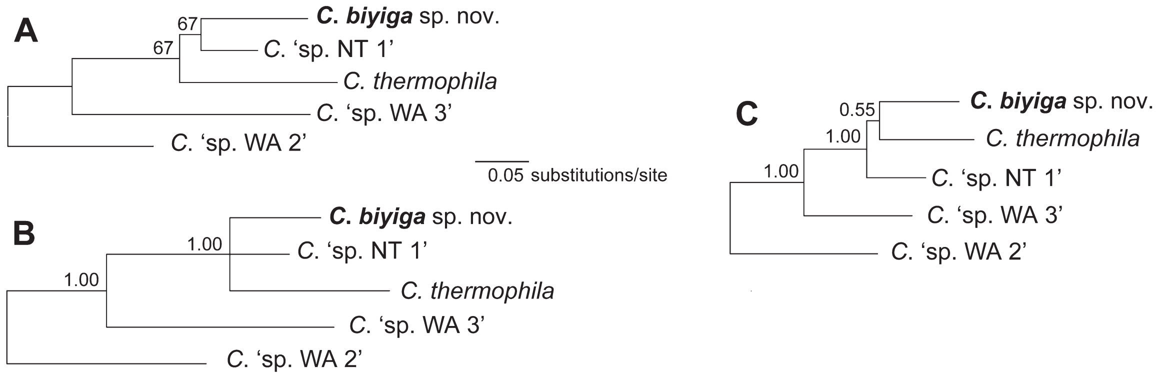

FIGURE 9. Maximum likelihood and Bayesian majority rule consensus topologies of 'thermophila' group using 3' COI or combined 3' COI/16S gene fragments with *C*. 'sp. WA2' ('spelunca' group) as outgroup. A, maximum likelihood (3' COI) topology with bootstrap values >50% shown; B, Bayesian (3' COI) majority rule consensus topology with Bayesian posterior probability values, nodes with probability values < 0.50 have been collapsed; C, Bayesian combined (3' COI/16S) majority rule consensus topology with Bayesian posterior probability values.

Within the described Australian *Caridina* fauna, the new species is easily recognised by the short, slender, depressed rostrum bearing 3–7 longitudinally compressed, preorbital, dorsal teeth but lacking ventral teeth (Figs. 2A, E, I–J); the anteromedially produced scaphocerite lamina (Fig. 2F); and the relatively short, first and second chelae which have length/breadth ratios less than 1.5 and 2.0 respectively (Figs. 2C–D).

In regard to the short, slender, depressed rostrum, the new species shows some resemblance to *C. confusa*, *C. malanda*, *C. spinula*, and *C. zebra* from northeast Qld, but differs in having 3 or more dorsal teeth (Figs. 2A, E, I–J). It also differs in having the scaphocerite lamina anteromedially produced *vs*. anteromesially produced; 4 or fewer spiniform setae on the flexor margin of P5 dactylus *vs*. 45 or more spiniform setae on the flexor margin of P5 and in lacking an arthrobranch at the base of the first chelipeds.

Although the 16S molecular analyses placed the new species in a strongly supported clade, the 'thermophila' species group, these relationships are not readily apparent using morphological characters. In addition to the characters mentioned above for distinguishing the new species from its Australian congeners in general, the new species can easily be distinguished from *C. thermophila* and C. 'sp. NT1' within the 'thermophila' group, by the following characters:

1. rostrum depressed, with 7 or fewer dorsal teeth and lacking postorbital teeth (Figs. 2A, E, I–J) *vs*. a laterally compressed rostrum with 12 or more dorsal teeth including 1–4 postorbital teeth;

2. antennal spine fused with, and indistinct from, inferior orbit (Figs. 2A, I–J) *vs*. antennal spine situated below and distinct from inferior orbit in *C. thermophila and C.* 'sp. NT1' (Fig. 14B);

3. flexor margin of P5 dactylus with 3–4, widely spaced, spiniform setae (Fig. 4K) *vs*. a comb-like row of 45–49 closely spaced, spiniform setae on the flexor margin of P5 in *C. thermophila* and a similar row of ca. 40 closely spaced, spiniform setae in *C*. 'sp. NT1';

4. flexor margin of P3 dactylus bearing 3–5 spiniform setae (Fig. 4E) *vs*. 8–11 spiniform setae in *C. thermophila* and ca. 7 spiniform setae in *C*. 'sp. NT1'.

Recent COI meta-analyses for the Decapoda are helpful to some degree regarding genetic evidence for or against the recognition of a new genus to accommodate the new species. The closest sister taxon to the new species based on the 3' COI fragment was *C*. 'sp. NT1' in the 'thermophila' species group with a K2P distance of 10.4%. This is slightly below the 11.27–49.93% range of genetic difference between genera within a family reported by Costa *et al*. (2007) and significantly lower than the 19.75% average they reported. It is also lower than the 22.33% average reported by Matzen da Silva *et al.* (2011) for decapods but falls within the large overall range between genera of 6.69–48.35%.

Although both the genetic and morphological data indicate that *C. biyiga* sp. nov. is a highly distinctive species within the Australian *Caridina* fauna, there does not appear to be sufficient evidence at this point to warrant the recognition of a new monotypic genus. The genetic analyses placed the new species in the 'thermophila' group, a strongly supported clade including at least one typical species of *Caridina*, viz. *C. thermophila*. The K2P genetic distances between the new species and other species within the clade are also towards the lower end of the range recorded between genera in decapod meta-analyses (Costa *et al*. 2007; Matzen da Silva *et al*. 2011). We therefore assign the new species to the genus *Caridina*.

The following illustrated key can be used to identify the new species from other Northern Territory *Caridina*. The inclusion of *C. typus* in the key is based solely on the Australian distribution given by Horwitz (1995), 'Northeastern Queensland to Northern Territory', which is possibly erroneous. Although the species is known from eastern Queensland, we have so far been unable to find other records or material of the species from the Northern Territory.

Preliminary illustrated key to Northern Territory *Caridina*

1. First pereiopod (and occasionally second pereiopod) with well-developed exopod (Fig. 10A); adult rostrum reaching to at least distal end of antennular peduncle, dorsal rostral margin with sub-equally spaced teeth along length, without distinct unarmed region (Fig. 10B) . . . . *C. wilkinsi* (Fig. 10A–B)
[Northern Australia: NT to NE.Qld. Eggs moderately large, ca. 0.85 mm long, egg size indicative of highly abbreviated larval development or direct development in fresh water.]

– All pereiopods without exopods; adult rostrum not as above 2

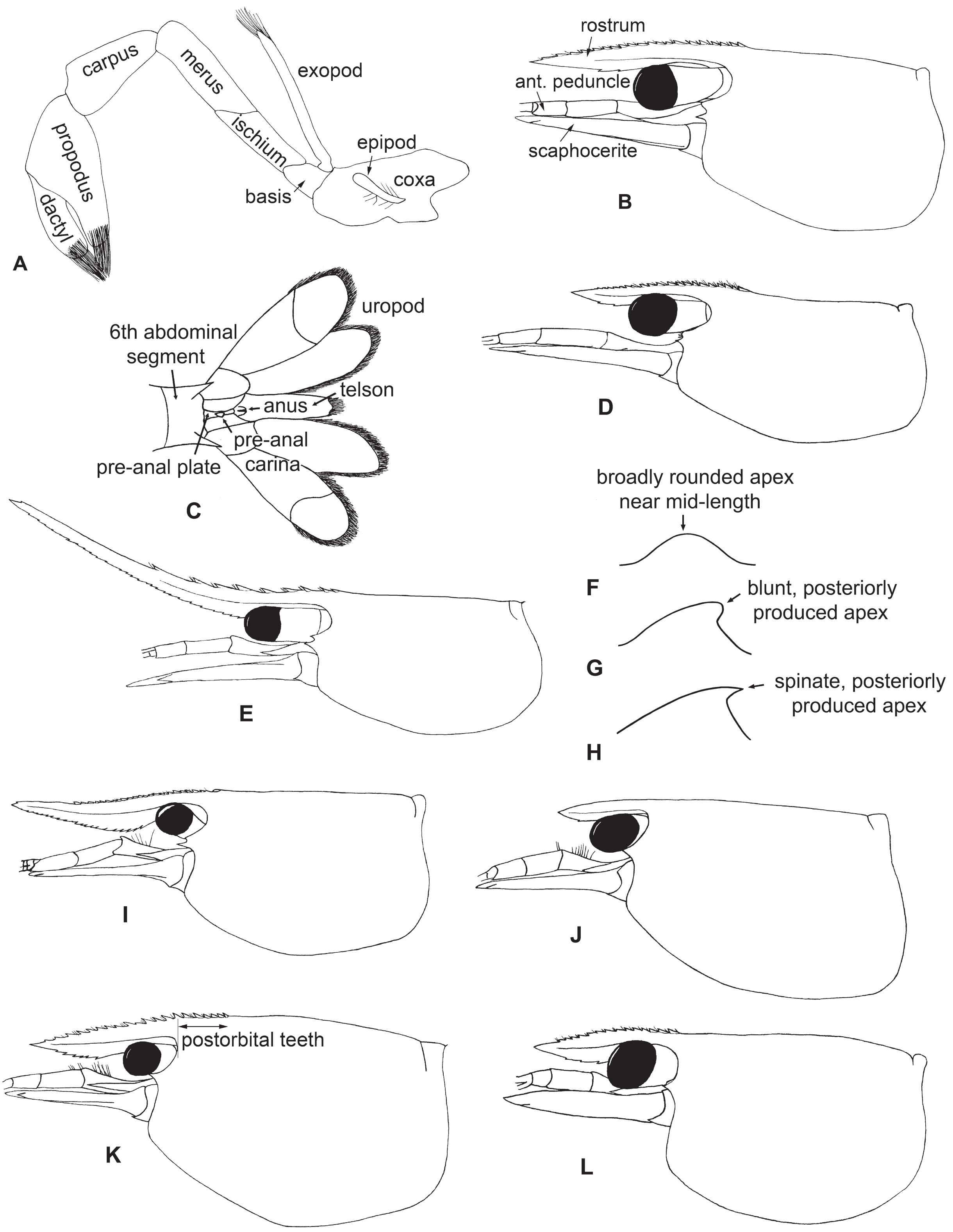

FIGURE 10. A, first pereiopod of *Caridina wilkinsi* (MAGNT Cr019230); B, cephalothorax of same; C, location of pre-anal carina; D, *Caridina* 'sp. NT2' (MAGNT Cr019234); E, *Caridina* 'sp. Gulf1' (MAGNT Cr019232); F–H, pre-anal carina variation in lateral view (setation omitted); I, *Caridina* 'sp. NT nilotica' (MAGNT Cr019235); J, *Caridina typus* (MAGNT Cr019231); K, *Caridina* 'sp. WA4' (MAGNT Cr019236); L, *Caridina* 'sp. NT1' (MAGNT Cr019233).

2. Rostrum of medium length to very long, reaching beyond distal end of antennular peduncle, armed dorsally and ventrally . . 3
– Rostrum generally short, often failing to reach distal end of antennular peduncle, if reaching beyond antennular peduncle, unarmed dorsally 5

3. Dorsal rostrum with less than 12 teeth, teeth widely spaced on proximal half (Fig. 10E); pre-anal carina (Fig. 10C) with spinate, posteriorly produced apex (Fig. 10H) . . . . *C.* 'sp. Gulf1' (Figs. 10E, 11C)
[An undescribed species of the 'gracilirostris' group. Recorded from the NT as *C. gracilirostris* by Bruce (1983) and Horwitz (1995). Daly River, NT to Wenlock River, Qld. Commercially cultured for the aquarium industry as the Darwin Red Nose Shrimp (Wilson, 2008).]
– Dorsal rostrum with more than 12 teeth, teeth closely spaced on proximal half (Fig. 10I); pre-anal carina (Fig. 10C) with broadly rounded apex near mid-length (Fig. 10F) or with blunt, posteriorly produced apex (Fig. 10G) 4

4. Pre-anal carina (Fig. 10C) with blunt, posteriorly produced apex (Fig. 10G); ova small, <0.5 mm in length … *C.* 'sp. NT nilotica' (Figs. 10I, 11E–F)
[A euryhaline species presently known from coastal localities from the Kimberley, WA to the Roper River, NT. The species has been cultured for the aquarium industry as the Darwin Algae Shrimp (Wilson, 2008). A closely related species, *Caridina* 'sp. Moyle', formed a well-supported clade with *Caridina* 'sp. NT nilotica' in the molecular analyses but was not available for morphological study.]
– Pre-anal carina (Fig. 10C) with broadly rounded apex near mid-length (Fig. 10F); ova medium-sized, >0.5 mm in length.. . . . . *C.* 'sp. D' complex (NT form)
[A widely distributed species complex in fresh waters across northern, eastern and inland Australia. Larval development studied by Glaister (1976; as *C. nilotica aruensis*).]

5. Rostrum with dorsal teeth 6
– Rostrum without dorsal teeth (Fig. 10J) . . . . *C. typus* (Fig. 10J)
[Wide-ranging Indo-West Pacific: east Africa to Japan, Australia and Polynesia. Eggs small (0.45–0.48 mm length) and numerous, indicative of lengthy larval development in tidal waters.]

6. Rostrum without ventral teeth, ventral carina obsolete (Figs. 2A, E, I–J). *C. biyiga* sp. nov. (Figs. 2–5)
[Endemic to Leichhardt Springs, Kakadu NP, NT. Eggs large (ca. 1.0 mm in length) and few (<12 per brood), indicative of highly abbreviated larval development or direct development in fresh water.]
– Rostrum generally with ventral teeth, ventral carina well developed 7

7. Epipods (Figs. 4J, 10A) absent on pereiopods 2–4; ventral rostral carina with less than 3 teeth (Fig. 10D) . . . . *C.* 'sp. NT2' (Figs. 10D, 11D)
[Northwest NT: Holmes Jungle; the Blackmore River; Marlow Lagoon, Palmerston; and Casuarina. Eggs medium-sized, ca. 0.65 mm. Larval development completed in fresh water (Wilson, 2008). Commercially cultured for the aquarium industry as the Blackmore River Caridina (Wilson, 2008).]
– Epipods (Figs. 4J, 10A) well developed on pereiopods 2–4; ventral rostral carina generally with 3 or more teeth 8

8. Rostrum with 4 or more postorbital teeth (Fig. 10K) . . . . *C.* 'sp. WA4' (Figs. 10K, 11A–B)
[An undescribed species of the 'serratirostris' group. First recorded from the NT as *C. serratirostris* by Horwitz (1995). Northwest Australia: Fitzroy River catchment, WA to Alligator Rivers, NT. Eggs moderately large, ca. 0.9 mm long, indicative of highly abbreviated larval development or direct development in fresh water. Commercially cultured for the aquarium industry as the North Australian Chameleon Shrimp (Wilson, 2008).]
– Rostrum with less than 4 postorbital teeth (Fig. 10L) . . . . *C.* 'sp. NT1' (Fig. 10L)
[Presently known from Melville Island. Eggs large, ca. 1.0 mm in length, indicative of highly larval abbreviated or direct development in fresh water. An ovigerous female of a similar species was collected from upstream Magela Creek, Kakadu NP in 1990 by Peter Dostine and examined by the first author. The specimen was deposited in the MAGNT collection but could not be located during this study.]

Discussion

The Australian *Caridina* fauna now comprises approx. 33 species based on the results of the phylogenetic analyses (Figs 7–8, Table 1). Six of these species show Australian distributions limited to east coast drainages but are also wide-ranging in the Indo-West Pacific region, viz. *C. appendiculata* Jalihal and Shenoy, 1998, *C. gracilipes* De Man, 1892, *C. gracilirostris*, *C. serratirostris*, *C. typus* and *C.* 'sp. 3 Solomon' (sensu de Mazancourt *et al*. 2019; previously recorded from Australia as *C. longirostris* H. Milne Edwards, 1837). The remaining 27 species appear to be endemic to the Australian continent (with the possible exception of the *Caridina* 'sp. D' complex which has yet to be compared to *C. aruensis* J. Roux, 1911 from the Aru Islands, Indonesia, using molecular data). At least 15 of the endemics are presently undescribed. It is also very likely that additional species are yet to be discovered in the Kimberley region of Western Australia and the Alligator Rivers-Arnhem Land regions of the Northern Territory.

Eight species are presently known from the Northern Territory, including four endemics, viz. *C. biyiga* sp. nov., *C*. 'sp. NT1', *C*. 'sp. NT2' and *C*. 'sp. Moyle'. By comparison, 19 species (10 endemic) are known from Queensland (Gulf of Carpentaria catchments: 4 species, 2 endemic) and 7 species (5 endemic) from the Kimberley region of Western Australia.

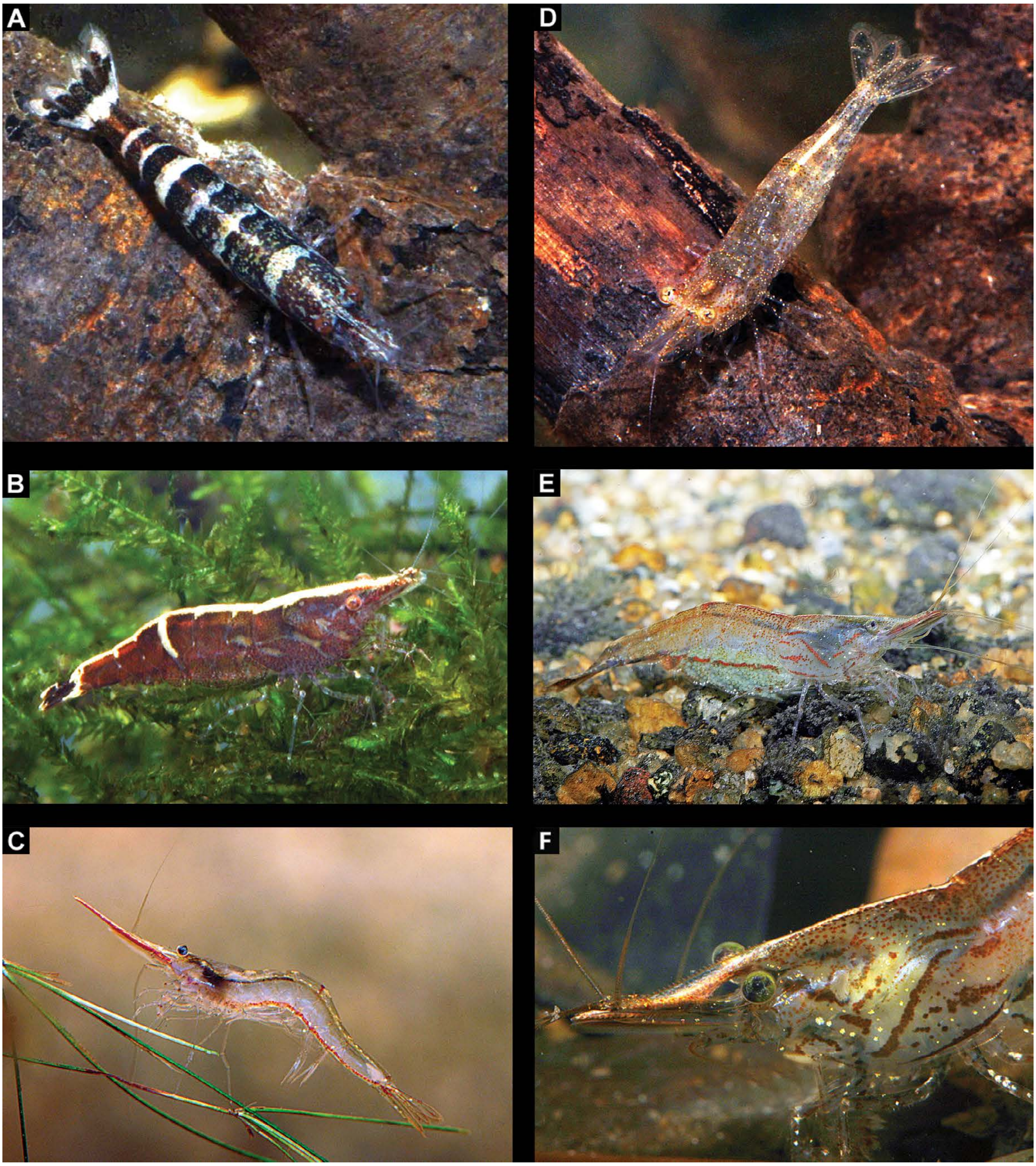

FIGURE 11. Live colouration of selected NT *Caridina* species**.** A, transversely banded colour form of *C*. 'sp. WA4' from the Blackmore River, Darwin area, NT; B, longitudinally banded colour form of same; C, *C*. 'sp. Gulf1' from the Howard R, Darwin area, NT; D, *C*. 'sp. NT2' from the Blackmore River, Darwin area, NT; E, *C*. 'sp. NT nilotica' from Leanyer Swamp, Buffalo Creek, Darwin Area; F, closeup view of cephalothorax of same. All photos courtesy of Dave Wilson.

A surprising feature of the Northern Territory fauna (and northwest Australian fauna in general), is the apparent absence of widely distributed, euryhaline, Indo-West Pacific species (apart from an uncertain record of *C. typus*). By comparison, five wide-ranging, euryhaline, Indo-West Pacific species are presently known from northeast Queensland, viz. *C. gracilipes*, *C. gracilirostris*, *C.* 'sp. 3 Solomon', *C. serratirostris* and *C. typus*. The 16S analyses suggest that at least two of these wide-ranging species are closely related to species in the Northern Territory fauna: *C. gracilirostris* with *C.* 'sp. Gulf1' in the 'gracilirostris' group and *C. serratirostris* with *C.* 'sp. WA 4' in the 'serratirostris' group. In comparison to these euryhaline species, the Northern Territory species in each group have relatively large eggs, normally an indication of abbreviated larval development in fresh water.

Among the endemic Northern Territory *Caridina*, *C. biyiga* sp. nov. shows by far the most restricted distribution and specialised habitat requirements. The new species also shows 16S genetic distances from other species in the 'thermophila' group of 5.1–6.0%. This roughly equates to a late Miocene origin, based on a commonly used divergence rate for decapod crustaceans of 0.65–0.9% per million years (Schubart *et al*. 2000). In addition to its distinctive genetics, the new species also displays highly distinctive morphology compared to its congeners.

To further highlight the distinctive fauna and conservation significance of Leichhardt Springs, two freshwater fishes with distinctive genetics have also been collected from the same locality: a highly divergent, infraspecific lineage of the Spotted Blue Eye, *Pseudomugil gertrudae* (Cook *et al*. 2014) and a cryptic species of rainbowfish related to *Melanotaenia trifasciata* (Unmack *et al*. 2013). A current phylogenetic study of the phreatoicidean isopod families Amphisopidae and Mesamphisopidae (Wilson and Humphrey in prep.) has also revealed a new genus and species from Leichhardt Springs. The species was previously reported in Wilson *et al*. (2009) as 'sp. 21' among a large flock of undescribed *Eophreatoicus* species (>30 species) from the Alligator Rivers Region.

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