

Systematic revision and reappraisal of the Kakaducarididae Bruce (Crustacea : Decapoda : Caridea) with the description of three new species of *Leptopalaemon* Bruce & Short

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Abstract. The freshwater shrimp family Kakaducarididae Bruce, 1993 is revised and its familial status reappraised using morphological characters and the results of a complementary molecular study (Page *et al.* 2008). Based on combined morphological–molecular data, the Kakaducarididae is synonymised with the Palaemonidae Rafinesque, 1815 and the monotypic genus *Kakaducaris* Bruce, 1993 is synonymised with *Leptopalaemon* Bruce & Short, 1993. The Texan cave shrimp, *Calathaemon holthuisi* (Strenth, 1976), provisionally included in the Kakaducarididae by Bruce (1993), is re-assigned back to the Palaemonidae. *Leptopalaemon* is re-diagnosed and three new species, *L. gibbosus*, sp. nov., *L. gudjangah*, sp. nov. and *L. magelensis*, sp. nov., are described from the north-western edge of the Arnhem Land plateau/escarpment complex, Northern Territory, Australia. The two previously described species, *L. gagadjui* Bruce & Short, 1993 and *L. glabrus* (Bruce, 1993), comb. nov. are re-diagnosed. A key to the five presently recognised *Leptopalaemon* species is provided.

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Introduction

The Kakaducaridinae Bruce, 1993 was erected as a new subfamily of the Palaemonidae Rafinesque, 1815 by Bruce (1993) to accommodate two monotypic Australian freshwater shrimp genera, *Leptopalaemon* Bruce & Short, 1993 and *Kakaducaris* Bruce, 1993. In an addendum to the same study, Bruce (1993) elevated the subfamily to family rank to maintain parity with a re-classification of the Caridea by Chace (1992). The Texan cave shrimp, *Calathaemon holthuisi* (Strenth, 1976), was provisionally included in the Kakaducarididae by Bruce (1993), largely based on the shape of the first maxillipeds.

The type species of the two Australian kakaducaridid genera were originally described from the north-western edge of the Arnhem Land plateau, Northern Territory, Australia: *Leptopalaemon gagadjui* Bruce & Short, 1993, with a relatively wide distribution in the upper South Alligator River and East Alligator River catchments, and *Kakaducaris glabra* Bruce, 1993, from a single locality, Lightning Dreaming Creek, in the South Alligator River catchment.

In the late 1990s, new kakaducaridid material was collected from the north-western Arnhem Land plateau/escarpment complex that showed undocumented variation for the family. This new material could easily be sorted into two morphotypes, one resembling *L. gagadjui*, but with fewer rostral teeth and shorter second pereopods, and the other similar to *K. glabra*, but with an antennal spine. Encouraged by the possibility that other

new morphotypes might exist amongst the highly dissected topography of the Arnhem Land plateau/escarpment complex, one of the present authors (CLH) initiated a field collecting program in Kakadu National Park and adjacent areas of Arnhem Land.

Sampling focussed on target areas known to have spring-fed permanent water during the dry season period from May to October. Collections were made by staff of the Environmental Research Institute of the Supervising Scientist (ERISS) or by Kakadu National Park rangers. Fresh material was also collected from the general vicinity of the type localities of *L. gagadjui* and *K. glabra*.

The taxonomic status of the Kakaducarididae and relationships between genera and species within the family were investigated using an integrated molecular–morphological approach. The molecular component of the study was recently published by Page *et al.* (2008) and produced the following key findings:

- (1) Combined nuclear (18S rDNA, 28S rDNA, histone) and mitochondrial (16S rDNA) analyses indicated that *Leptopalaemon* and *Kakaducaris* represent a recently evolved, well-defined, Australian lineage within the Palaemonidae, rather than a distinct family within the Palaemonoidea. Net divergence estimates from mitochondrial COI data suggested a late Miocene or Pliocene origin for the lineage. More recently, an

independent molecular study by Bracken *et al.* (2009), using nuclear 18S rDNA and mitochondrial 16S rDNA, also placed *L. gagadju* within the Palaemonidae.

- (2) Mitochondrial COI data revealed that the new *Kakaducaris glabra*-like morphotype actually comprised two morphologically cryptic species of *Leptopalaemon*. Other mitochondrial groupings were largely congruent with morphotypes recognised during a preliminary morphological study.
- (3) Analyses of the mitochondrial COI data in relation to species and genus thresholds proposed by recent meta-analyses (Costa *et al.* 2007; Lefébure *et al.* 2006) were inconclusive as to whether *Leptopalaemon* and *Kakaducaris* should be retained as separate genera.

The present taxonomic revision concludes the review of the systematics of the Kakaducarididae using morphological data and the published findings of the molecular study (Page *et al.* 2008). Based on the combined morphological–molecular data, the Kakaducarididae will be synonymised with the Palaemonidae and the genus *Kakaducaris* with *Leptopalaemon*. As a result of these changes, *Leptopalaemon* and *Calathaemon* will now be included in the Palaemonidae. A new generic diagnosis will also be provided for *Leptopalaemon*, three new species of the genus described, and *L. gagadju* Bruce & Short, 1993, and *L. glabrus* (Bruce, 1993) re-diagnosed.

Materials and methods

Australian distributional records of the Kakaducarididae are presently limited to the broader Kakadu region as defined by Finlayson *et al.* (2006), with the exception of one record from the upper Mann River close to the eastern border of the region (Fig. 1). On a larger scale, the Kakadu region forms part of the wet–dry tropics of northern Australia (Finlayson *et al.* 1997, 2006).

Within the broader Kakadu region and adjacent areas of Arnhem Land, the Kakaducarididae are largely restricted to surface waters of the ancient plateau and escarpment ('stone country') complex (Russell-Smith *et al.* 1995). This highly dissected complex of landforms, the Mamadawerre Formation (previously known as the Kombolgie Formation), is composed predominantly of quartzose sandstone and rises to an average height of 300 m above the adjacent plains (Finlayson *et al.* 2006). Significantly, steep and abrupt escarpments form the north and west boundaries of this complex. The escarpments present a physical barrier of varying degree to the upstream dispersal of aquatic fauna onto the plateau from the surrounding lowlands. Deep dissection and fragmentation within the formation also present barriers to dispersal between many of its surface waters and streams.

As surface waters on the Mamadawerre Formation drain highly-leached sandstone, they are typically high in clarity, acidic, very soft and low in solutes. Key water quality variables measured at site 15 (see below) on the south arm of Magela Creek exemplify this: turbidity 1.7 NTU; pH 4.7; electrical conductivity 27 $\mu\text{S cm}^{-1}$; Ca and K < 0.1 mg L^{-1} ; Na 1 mg L^{-1} ; Mg 0.3 mg L^{-1} ; and SO_4 1.1 mg L^{-1} .

Specimens were examined from the 12 sites used in the molecular study (Fig. 1 in Page *et al.* 2008, adapted here as Fig. 1), with the exception of sites 7 and 10. Specimens from three new sites were also examined (Fig. 1): site 13 on the Arnhem Land plateau near Namarrgon Gorge (immediately adjacent to site 7 from the molecular study); site 14 from the western South Alligator River catchment (in the general area of sites 9 and 10 from the molecular study); and site 15 on the south arm of upper Magela Creek (~1 km upstream of site 3 from the molecular study).

Character selection

Characters and character states were initially compiled as relational tables in a Microsoft Access database using the original descriptions of *Kakaducaris glabra* by Bruce (1993) and *Leptopalaemon gagadju* by Bruce and Short (1993). A preliminary morphological study using this character set indicated that the new morphotypes and the two previously-described species were all similar in general morphology and that comparatively few characters would be useful for discriminating species. Of the characters that showed significant variation between species, most displayed a trend towards reduction. Some features that had previously been used as generic characters in the Kakaducarididae, and that had proven to be highly conservative elsewhere in the Palaemonoidea, were found to be highly variable within populations. For example, the presence of an antennal spine and spiniform setae on the dorsal surface of the telson were previously considered to be generic characters within the Kakaducarididae. However, these cuticular processes were greatly reduced in much of the new material and were highly variable within populations. In several specimens, the antennal spine was asymmetrically developed, being present on one side only. Similarly, the presence or absence of rostral teeth on both the upper and lower rostrum showed a high degree of variation in the new *K. glabra*-like material. The morphology of the second pereopods, although highly informative in many other palaemonoid genera, also provided relatively few characters for species discrimination.

Therefore, to discriminate species, detailed examination of subtle differences in the shape and relative length of body segments and appendages was necessary. A preliminary morphometric analysis using 25 proportional characters revealed that most were uninformative for the study group (Table 1). The remaining informative morphometric characters were incorporated into an expanded character list comprising 135 characters. The main diagnostic characters are summarised in Tables 2 and 3 respectively.

Measurement reference points for morphometric characters are illustrated in Fig. 2. All measurements were made from drawings using digital vernier calipers and a camera lucida and were rounded to the nearest 0.05 mm. Mean (\bar{x}) and sample size (n) were recorded for all metric characters. For meristic characters, e.g. the number of dorsal rostral teeth, the modal value and frequency (f) of the modal value within the sample (1.00 = 100%) were recorded.

In the systematic accounts and discussion, the terms 'cheliped' and 'second cheliped' refer to the second pereopod (P2) and 'first

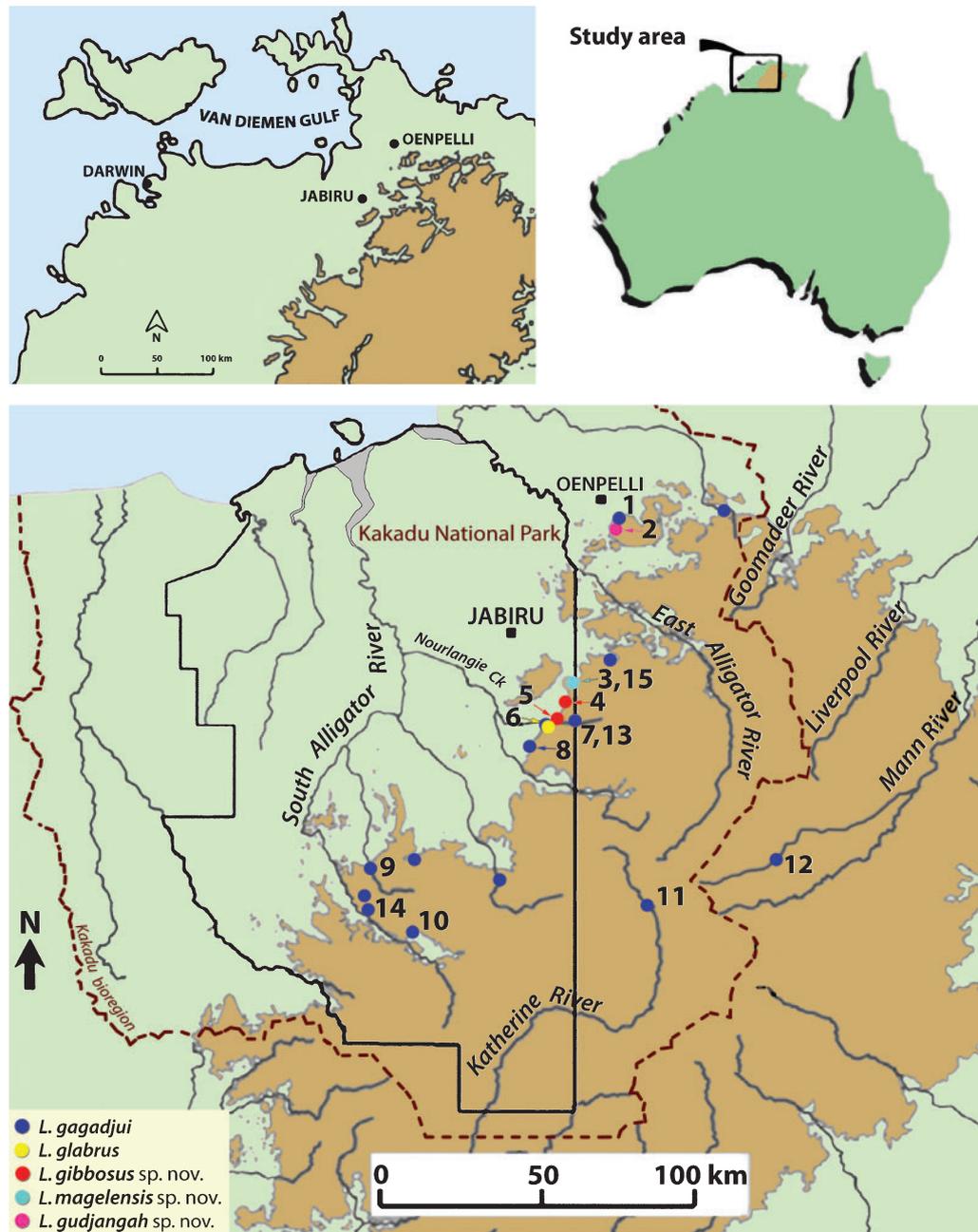


Fig. 1. Maps of the study area. Upper right, location of study area within Australia; upper left, enlarged view of study area within the north-west Northern Territory (Arnhem Land plateau highlighted in brown); main map, detailed view of study area showing the boundary of Kakadu NP (solid, black line), the broader Kakadu region (dashed, dark brown line), Arnhem Land plateau and associated outliers (light brown areas) and distributions of presently known species of *Leptopalaemon* (see legend at bottom left). Numbered sites 1–12 on the main map correspond with sites investigated in the molecular study (Page *et al.* 2008). Sites 13–15 are additional sites investigated during this revision.

cheliped' to the first pereopod (P1). Mouthpart terminology follows Bruce and Short (1993) and Bruce (1993). Terminology for setae and spines follows Short (2004).

All drawings were made using a camera lucida mounted on a stereomicroscope, digitised and then edited and composed in Adobe Photoshop.

Type material is deposited in the Queensland Museum, Brisbane and the Museum and Art Galleries of the Northern Territory, Darwin (formerly Northern Territory Museum of Arts and Sciences). Abbreviations used in the text include: CL, postorbital carapace length; ERISS, Environmental Research Institute of the Supervising Scientist; f.dev., fully developed;

Table 1. Uninformative morphometric characters

<i>Antennule</i>	
1.	peduncle proximal segment length versus breadth
2.	stylocerite length relative to CL
3.	stylocerite length relative to proximal segment length
<i>Antenna</i>	
4.	peduncle length relative to CL
5.	scaphocerite length versus breadth
<i>Pereiopod 1</i>	
6.	length relative to CL
7.	manus length relative to maximum depth
8.	carpus length relative to merus length
9.	carpus length relative to maximum breadth
<i>Pereiopod 2</i>	
10.	carpus length relative to maximum breadth
<i>Pereiopod 5</i>	
11.	carpus length relative to propodal length
<i>Abdomen</i>	
12.	fifth pleuron length relative to sixth pleuron length
13.	sixth pleuron length versus breadth
14.	sixth pleuron length relative to CL
15.	telson length relative to CL
16.	telson length relative to sixth pleuron length
17.	telson length versus breadth
18.	telson posterior margin width relative to anterior margin width

MAGNT, Museums and Art Galleries of the Northern Territory; NP, National Park; N.T., Northern Territory; P, pereiopod; QM, Queensland Museum; T, thoracic sternite.

Systematics

Family PALAEMONIDAE Rafinesque, 1815

Palaemonia Rafinesque, 1815: 98.

Palaemonidae. – Samouelle, 1819: 96.

Kakaducarididae Bruce, 1993: 44. (**syn. nov.**)

Diagnosis

Acron. Eyes visible, not concealed by carapace, without greatly elongated eyestalks.

Carapace. Rostrum variably developed (absent in *Paratypton* Balss, 1914), non-articulated. Postantennal longitudinal sutures absent on dorsolateral surfaces of carapace.

Antennule. Dorsal and ventral flagella present, distinctly separated; dorsal flagellum biramous, rami fused basally.

Mouthparts. Mandible bifurcate, molar process well developed, not flared, incisor process generally well developed, sometimes reduced. First maxilla with mesial coxal lobe not unusually large, mesial basal lobe not reduced. Second maxilla with 0–2 endites. First maxilliped with caridean lobe distinctly over-reaching endite, not acutely produced distally, exopodal lash fully developed, palp not unusually broad. Second maxilliped with segments articulating serially not side by side on penultimate segment, not markedly bilobate distally, last segment attached to penultimate, not touching antepenultimate. Third

maxilliped with antepenultimate segment neither articulated with, nor much wider than, next proximal segment.

Branchiae. Pereiopods without arthrobranchs or exopods; epipods, if present, not large, not extending dorsally into branchial chamber.

Pereiopods. First and second pereiopods chelate, chelae with movable dactylus and immovable propodus fused with manus, fingers not terminating in tufts of long setae, not pectinate without long slender teeth on both first and second chelae, first pereiopod with carpus entire (except in *Thaumastocaris* Kemp, 1922).

Abdomen. Second pleopod with appendix interna in both sexes and typically with appendix masculina in males (absent in some species of *Typton* Costa, 1844).

Remarks

Bruce (1993) erected the Kakaducarididae based on the highly modified, filtratory mouthparts and the distinctive form of the appendix masculina. He considered the specialised first maxillipeds in the Australian taxa *Leptopalaemon gagadju* and *Kakaducaris glabra* so similar in their unusual shape to the North American cave species, *Calathaemon holthuisi*, that it is 'difficult to avoid the conclusion that they are synapomorphic and there must be some close phylogenetic relationship'. He also suggested that the three taxa are 'relict species in specialized ecological niches, with few competitors or predators'. With some reservations, he provisionally assigned *Calathaemon* Bruce & Short, 1993 to the Kakaducarididae.

The hypothesis that the Kakaducarididae are an ancient group comprising relict species was not supported by analyses of the molecular data (Page *et al.* 2008), in which the two Australian genera were recovered together as a relatively-recent lineage originating in the Miocene or Pliocene from a *Macrobrachium*-like, palaemonid ancestor. In an independent molecular analysis of the infraorder Caridea, Bracken *et al.* (2009) also found *L. gagadju* embedded within the Palaemonidae, in a strongly supported clade containing *Cryphiops caementarius* (Molina, 1782) and two American species of *Macrobrachium* Spence Bate, 1868.

Although the first maxillipeds in the Australian taxa and in *Calathaemon* from North America are of similar shape and are highly atypical among the Palaemonoidea, there are also notable differences. In *Calathaemon* the basal and coxal endites are fused whereas in the Australian taxa they are distinct. There are also significant differences in the relative size and shape of the caridean lobe, exopod flagellum and epipod. Considering that the Australian taxa and *Calathaemon* also differ significantly in other aspects of their morphology, e.g. the form of the mandibles, metastoma, telson, chelipeds and presence or absence of the branchiostegal spine, the similarity of the first maxillipeds must be an example of convergence rather than synapomorphy. The complex mouthpart modifications required for filter feeding appear to have developed relatively quickly in the Australian taxa and in a similar, though not identical, way to those of *Calathaemon* from North America.

Bruce (1993) also considered the absence of an accessory spiniform seta mesial to the distolateral tooth on the uropodal

exopod a unique character shared by *Leptopalaemon*, *Kakaducaris* and *Calathaemon*. However, within the Palaemonoidea, the accessory spiniform seta on the uropodal exopod is also reduced or lost in several freshwater, North American species of *Palaemonetes* and several landlocked freshwater species of *Macrobrachium*, e.g. *M. koombooloomba* Short, 2004.

In light of the relatively recent, late Tertiary origin of the Australian lineage, its close relationship to *Macrobrachium* in the Palaemonidae (Page *et al.* 2008) and the lack of defining synapomorphic characters for the family, we believe the Kakaducarididae should no longer be recognised as a distinct family and it is hereby synonymised with the Palaemonidae. The North American genus, *Calathaemon*, provisionally assigned to the Kakaducarididae by Bruce (1993), is also included in the Palaemonidae.

Although *Leptopalaemon* and *Calathaemon* comprise freshwater, free-living species and would be expected to show affinities with the Palaemoninae rather than the Pontoniinae, neither genus fits neatly within the current definition of the subfamily, i.e. two pairs of spines (= spiniform setae) on the posterior margin of the telson, two arthrobranches above the third maxilliped and usually a podobranch above the second maxilliped (Davie 2002).

Bruce (1994) provided a detailed historical account of the changing definitions of the two subfamilies provided by various authors and considered the morphological dividing line between the Palaemoninae and the Pontoniinae to be a very fine one. Currently, there are several palaemonids (other than species of *Leptopalaemon* and *Calathaemon*), that are not accommodated by the present definitions of the two subfamilies, e.g. *Coutierella tonkinensis* Sollaud, 1914. Despite several problems with the current subfamily definitions, *Leptopalaemon* and *Calathaemon*

appear to be more closely related to genera that clearly belong to the Palaemoninae as currently defined.

Genus *Calathaemon* Bruce & Short, 1993

Calathaemon Bruce & Short, 1993: 85.

Type species: *Palaemonetes holthuisi* Strenth, 1976, by monotypy.

Gender: masculine.

Diagnosis

Acron. Eyes reduced, cornea unpigmented.

Carapace. Smooth, glabrous; dorsum moderately humped. Rostrum short, slender; dorsal carina well developed, convex, dentate; ventral carina obsolete. Anterior branchiostegite inflated. Branchiostegal groove present. Branchiostegal suture absent. Inferior orbital margin moderately produced. Antennal spine small or absent, postmarginal and distinct from inferior orbit when present. Branchiostegal spine present, postmarginal, situated well below branchiostegal groove. Supraorbital, hepatic and pterygostomial spines absent.

Antennule. Fused portion of dorsal flagellum less than half length of shorter free ramus; proximal segment of peduncle with distolateral spine; stylocerite moderately developed.

Antennal somite. Scaphocerite moderately long, length almost twice breadth; lamina distinctly tapering from broadest point to anterior margin, lateral margin straight; anterior margin produced forward at mesial angle.

Mouthparts. Mandible with incisor process reduced, triangular, non-dentate, molar process well developed; palp absent. Metastoma with paragnaths proximally fused to form long slender corpus, corpus with well developed median carina, paragnaths distally bilobed, upper lobe large, broadly rounded. Maxillula with bilobed palp, upper lobe small, lower

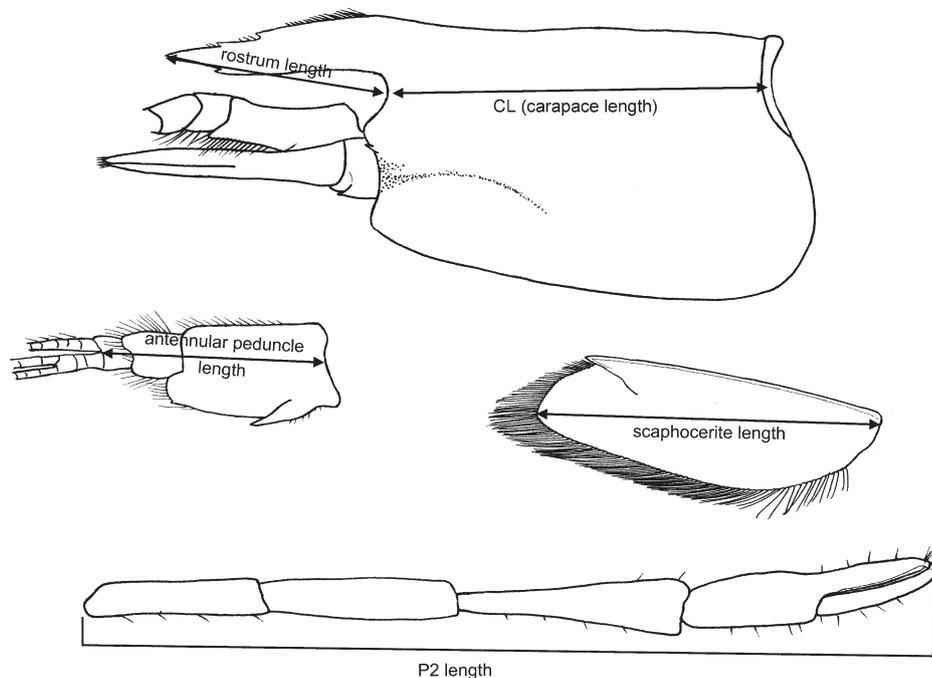


Fig. 2. Measurement reference points for morphometric characters.

lobe broad; upper lacinia broad, scoop-shaped, densely setose; lower lacinia enlarged swollen, tapering distally, densely setose. Maxilla with simple palp; basal endite bilobed, broad; coxal endite distinct; scaphognathite well developed, broad, elongate. First maxilliped with short, simple palp; basal and coxal endites fused, elongate, with dense median fringe of long filtratory setae; exopod with large, broad caridean lobe, flagellum short, with plumose setae distally; small, simple, triangular epipod. Second maxilliped with endopod enlarged, elongate, strongly compressed; dactylar segment large, broad, densely setose mesially, deeply concave dorsally; basis elongate, compressed; coxa with rudimentary epipod; exopod flagellum densely setose distally with plumose setae. Third maxilliped with slender, elongate endopod; ischiomerus and basis distinct; terminal segment slender, with stout unguis, with numerous groups of setae ventrally and mesially, subequal in length to penultimate segment; exopod flagellum densely setose distally; coxa with small plate laterally.

Thoracic sternum. First three sternites each with pair of low transverse ridges, without median processes; fourth and fifth sternites each with small median protuberance; sixth to eighth sternites unarmed.

Branchiae. Vestigial podobranch and rudimentary epipod on second maxilliped. One small arthrobranch present on articular membrane at base of third maxilliped.

First pereopod. Fingers longer than manus; chela small, fingertips semispatulate.

Second pereopods. Short, exceeding scaphocerite by part of chela only; slender; slightly longer than first pereopods; chela small, fingers longer than manus, fingertips semispatulate.

Ambulatory pereopods. Dactyli simple.

Abdomen. Fourth and fifth pleura acutely to bluntly angular. Appendices internae present on pleopods 2–5, absent on first male pleopod; endopod of first male pleopod distomesially expanded, ovate. Appendix masculina on second male pleopod subcylindrical, slightly compressed, shorter than endopod, with long, slender setae ventrally. Uropodal exopod with distolateral tooth, without accessory spiniform seta mesially.

Telson. Elongate; expanded distally; anterodorsally without semicircular median clump of simple setae; two pairs of dorsolateral spiniform setae; posterior margin convex, with 5–6 pairs of spiniform setae, sublateral setae elongate, without median process.

Remarks

Palaemonetes holthuisi was described from Ezell's Cave, San Marcos, Texas by Strenth (1976) and later transferred to a new genus, *Calathaemon*, by Bruce & Short (1993), based on the distinctive morphology of the filtratory mouthparts and chelae.

As noted above, a close phylogenetic relationship between *Calathaemon holthuisi* from North America and the two Australian species previously assigned to the Kakaducarididae, viz. *Leptopalaemon gagadjuui* and *Kakaducaris glabra*, is unlikely based on overall morphology and the relatively-recent, late Miocene/Pliocene origin of the Australian lineage suggested by the molecular data (Page *et al.*, 2008).

Although highly distinctive among North American freshwater palaemonids in possessing filtratory mouthparts, semispatulate fingertips on the chelae and in the shape of the telson, *Calathaemon holthuisi* most closely resembles the sympatric hypogeal species, *Palaemonetes antrorum* Benedict, 1896. In a cladistic analysis of the Palaemonidae using morphological characters, Pereira (1997) recovered the two species as a strongly supported clade. The two species are unique among North American freshwater palaemonids in the following combination of characters:

- (1) Eyes strongly degenerated and without pigment;
- (2) First and second pereopods similar in relative size;
- (3) The absence of teeth on the lower rostrum;
- (4) The absence of a movable spine (= spiniform seta) on the inner side of the tooth of the uropodal exopod;
- (5) A branchiostegal spine on the carapace; and
- (6) Mandible without palp.

Characters 1–4 were used by Holthuis (1952a) to define the subgenus, *Palaemonetes (Alaocaris)*. Characters 5 and 6 distinguish *Calathaemon holthuisi* and *Palaemonetes antrorum* from *Creaseria* Holthuis, 1950, *Cryphiops* Dana, 1852, *Macrobrachium*, *Neopalaemon* Hobbs, 1973 and *Troglocabanus* Holthuis, 1949.

Strenth (1976) considered characters 1–3 to be regressive characters associated with the subterranean lifestyle of *Calathaemon holthuisi* and *Palaemonetes antrorum*. He also noted that character 4 showed a high degree of variability in three of the North American species of *Palaemonetes*. Accordingly, he considered all four characters to be of low taxonomic weight and synonymised the subgenus *Palaemonetes (Alaocaris)* with *Palaemonetes*. Notwithstanding the possibility that the similarity of *Calathaemon holthuisi* to *Palaemonetes antrorum* may be superficial and the result of convergent evolution through similar subterranean lifestyles, their highly restricted sympatric distributions suggest there may be a phylogenetic link between the two species. Unfortunately, molecular data are presently not available for either species to test this hypothesis.

Genus *Leptopalaemon* Bruce & Short, 1993

Leptopalaemon Bruce & Short, 1993: 73.

Kakaducaris Bruce, 1993: 27. (syn. nov.)

Type species: *Leptopalaemon gagadjuui* Bruce & Short, 1993 by original designation. Gender: masculine.

Diagnosis

Acron. Eyes well developed, cornea large, well pigmented, with accessory pigment spot. Bec ocellaire small or obsolete, acute or bluntly pointed when present.

Carapace. Smooth, glabrous, dorsum flat to moderately humped. Rostrum with dorsal and lateral carinae well developed, ventral carina variably developed; dorsal carina sinuous or convex, unarmed or dentate, all teeth (when present) immovable, interspaces between teeth setose; ventral carina (when present) unarmed or dentate, with double row of short plumose setae proximally (except in *L. glabrus*). Antennal spine absent to well developed, marginal and situated below

and distinct from inferior orbit when present. Hepatic, branchiostegal, supraorbital and pterygostomial spines absent (except in one aberrant paratype of *L. gagadjui* that has well developed branchiostegal spines). Branchiostegal groove curved, well developed in hepatic region, extending to carapace margin. Branchiostegal suture absent. Inferior orbital margin moderately produced, bluntly angular or rounded. Pterygostome bluntly angular or rounded.

Antennule. Fused portion of dorsal flagellum less than half length of shorter free ramus; proximal segment of peduncle usually with small to minute distolateral spine (sometimes absent); stylocerite moderately developed, reaching to about half length of proximal segment of peduncle.

Antennal somite. Scaphocerite with lamina distinctly tapering from broadest point to anterior margin, anterior margin produced forward at mesial angle or in middle third (*L. glabrus*), lateral margin straight to moderately convex. Epistome divided, submedian lobes rounded, well separated.

Mouthparts. Mandible with well developed molar process; incisor processes well developed, isomorphic, tricuspidate; palp present or absent, when present consisting of single segment of variable size. Metastoma with paragnaths proximally fused to form robust corpus, corpus with broad medial depression, without carinae, paragnaths distally alariform, alae sinuously rolled into upper and lower lobes, upper lobe distally revolute, extending over mandibular incisor process, lower lobe well developed. Maxillula with bilobed palp, upper lobe small, lower lobe broad; upper lacinia moderately expanded; lower lacinia broad. Maxilla with well developed palp, basal and coxal endites distinct, basal endite deeply bilobed, scaphognathite well developed, anterior lobe emarginate, plicate. First maxilliped with basal and coxal endites distinct, endites forming hemispherical filtratory basket, exopod with broad caridean lobe, flagellum densely setose distally, epipod well developed. Second maxilliped densely setose mesially; distodorsal angle of propodal segment enlarged, with numerous spiniform setae, mesial margin of coxal segment broadly expanded, densely setose, exopod flagellum densely setose distally with plumose setae. Third maxilliped with moderately slender endopod, ischiomerus and basis completely fused, bowed, mesial margin with sparse, long, simple setae; terminal segment slender, tapering strongly with well developed unguis, with numerous groups of setae ventrally and mesially, clearly shorter than penultimate segment, flagellum densely setose distally, coxa with small, oval, lateral plate.

Thoracic sternum. Second sternite with large, transverse triangular plate; third sternite with low, transverse ridge with median notch; fourth sternite with large triangular plate with median notch; eighth male sternite without anterolateral lobes or median process.

Branchiae. Podobranch well developed on second maxilliped. Small upper (absent in *L. glabrus*) and large lower arthrobranch present on articular membrane at base of third maxilliped. Exopods absent from all pereopods. Pleurobranchs present on all pereopods.

First pereopod. Fingers about equal in length to manus (rarely shorter than manus), fingertips with small accessory lateral cutting edge distally forming minutely spatulate tip.

Second pereopods. Longer and more strongly developed than first pereopods; sexually dimorphic, longer in fully developed males with fingers much longer than manus (fingers shorter or about equal in length to manus in undeveloped males and females); generally isomorphic or similar in shape, subequal in length; relatively short, at most exceeding scaphocerite by part of carpus; non-setose except for scattered clumps of simple setae; without grooves; fingers without gape, cutting edges unarmed, carinate, fingertips minutely spatulate distally, with feeble unarmed lateral cutting edge, tips hooked; maximum manus breadth clearly greater than maximum merus breadth; carpus generally longer than merus (commonly about equal in length to merus in *L. glabrus*).

Ambulatory pereopods. Third pereopod short, reaching to around distal margin of scaphocerite, dactylus simple, with moderately developed ventral carina. Fourth pereopod similar to third but with longer propodus. Fifth pereopod similar to fourth but with longer propodus and brush of grooming setae posteroventrally on distal propodus.

Abdomen. Smooth, glabrous, without pitting; first to third pleura broadly rounded; fourth pleura rounded to bluntly angular; fifth pleura produced, bluntly angular with or without minute posteroventral tooth; sixth pleura with posteroventral angle acute, posterolateral margin angular; third tergite slightly convex antero-posteriorly (abdomen evenly rounded in lateral view). Appendices internae present on pleopods 2–5, absent on first male pleopod; endopod of first male pleopod mesially curved, distally ovate or rounded. Appendix masculina on second pleopod elongate, subcylindrical in basal half, spatulate distally, straight, rigid, feebly tapering distally, shorter to longer than endopod, in adult males with ~11–26 spiniform setae around distal margins of mesial face, increasing in size apically. Uropodal exopod with distolateral tooth, without accessory spiniform seta mesially.

Telson. Moderately long, tapered distally; armed with 0–2 pairs of minute to small dorsal spiniform setae; anterodorsally with semicircular median clump of simple setae; posterior margin generally angularly sinuous or angular, typically armed with small to moderately developed acute median process, two pairs of spiniform setae laterally (three pairs in one aberrant paratype of *L. gibbosus*, sp. nov.; Fig. 12D); 6–10 plumose setae between innermost lateral spiniform setae. Pre-anal carina absent.

Remarks

Bruce (1993) distinguished *Kakaducaris* from *Leptopalaemon* using the following characters:

- (1) Rostrum generally edentate in *Kakaducaris* versus strongly dentate in *Leptopalaemon*;
- (2) Antennal spine absent in *Kakaducaris* versus present in *Leptopalaemon*;
- (3) Branchiostegal suture present in *Kakaducaris* versus absent in *Leptopalaemon*;
- (4) Telson without dorsal spines (=spiniform setae) in *Kakaducaris* versus with two pairs of dorsal spines (=spiniform setae) in *Leptopalaemon*;

- (5) Third maxilliped with single arthrobranch in *Kakaducaris* versus third maxilliped with two arthrobranches in *Leptopalaemon*.

Characters 1, 2 and 4 show a high degree of variation within the study material, with the notable exception of *L. gagadjuui*, and are regressive characters in *Leptopalaemon*. Character 3 may have been erroneously reported by Bruce (1993). Among ~50 topotypical specimens of *K. glabra* examined during this study, no branchiostegal suture could be seen. Bruce (1993) mentioned this character in his Table 1, but not in the diagnosis of *Kakaducaris* nor in the description of *K. glabra*.

Only character 5 consistently separates *K. glabra* from *L. gagadjuui* and the new species of *Leptopalaemon* described below. However, the value of this character for defining genera in the Palaemonidae is questionable. In marine palaemonids, particularly symbiotic species currently assigned to the Pontoniinae, there is a clear regressive trend in the development of arthrobranches on the third thoracic somite. Furthermore, the genera *Hamodactylus* Holthuis, 1952b, *Periclimenes* Costa, 1844 and *Periclimenaeus* Borradaile, 1915, show infrageneric variation in this character and have either a single, reduced arthrobranch or no arthrobranch (Bruce 1994).

Other than relatively minor differences, such as subtle differences in the shape of the scaphocerite and a relatively shorter P2 carpus in *K. glabra*, no other morphological characters were found to separate *K. glabra* from *L. gagadjuui* and the new species of *Leptopalaemon*.

As the molecular data were inconclusive as to whether *K. glabra* should be retained in a monotypic genus (Page *et al.* 2008) and we were unable to find significant, defining, morphological differences, *Kakaducaris* is hereby synonymised with *Leptopalaemon*.

In morphology, *Leptopalaemon* has diverged significantly from all extant palaemonid genera, including *Macrobrachium*, and its relationships within the family remain obscure. Like *Macrobrachium*, *Leptopalaemon* has isomorphic, tricuspidate, mandibular incisor processes, a well developed branchiostegal groove and lacks an appendix interna on the first male pleopods. Together these characters separate *Leptopalaemon* and *Macrobrachium* from other extant palaemonine genera occurring in estuarine or freshwater environments in northern Australia, e.g. *Palaemon* Weber, 1795, *Leandrites* Holthuis, 1950 and *Palaemonetes*. At the same time, *Leptopalaemon* differs significantly from *Macrobrachium sensu stricto* in the following features:

- (1) Second pereopod of fully developed males glabrous, lacking protective modified setae;
- (2) Fingers of second pereopod elongated, medially carinate and lacking teeth on the cutting edges in fully developed males;
- (3) First pereopod with sub-spatulate fingertips *v.* non-spatulate in *Macrobrachium*;
- (4) Filtratory mouthparts;
- (5) Mandibular palp (if present) composed of a single segment versus a 3-segment palp in *Macrobrachium*;
- (6) Male thoracic sternite 8 without anterolateral lobes versus with well developed, anterolateral lobes in *Macrobrachium*;

- (7) Thoracic sternite 4 with a triangular median plate versus a rounded or spinate median process or unarmed sternite 4 in *Macrobrachium*;
- (8) No branchiostegal suture (present in *Macrobrachium*); and
- (9) A rigid, basally-subcylindrical appendix masculina bearing short spiniform setae along the margins of the distomesial face versus a flexible, sub-spatulate appendix masculina covered in short simple setae on the mesial face in *Macrobrachium*.

A surprising find during the course of this study was the presence of male morphotypes in *Leptopalaemon*. Male morphotypes linked to social dominance have been well documented for *Macrobrachium rosenbergii* (De Man, 1879) (Barki *et al.* 1991a, 1991b; Kuris *et al.* 1987; Ra'anan and Sagi 1985) and appear to be typical of the genus (Short 2004). However, in contrast to *Macrobrachium s.s.*, which are typically solitary, largely nocturnal, aggressive species with well developed agonistic behaviour, species of *Leptopalaemon* are active during daylight away from shelter and are highly gregarious (Fig. 19F).

Most of the male specimens studied were highly similar to females, but a few males in *L. gagadjuui*, *L. glabrus* and one of the new *Leptopalaemon* species described below, had markedly different second chelipeds. In these males, the second chelipeds were more elongated with the fingers clearly longer than the manus. In general, the manus was also more inflated. The third pereopods were also significantly longer. Males with the more developed second chelipeds were not always among the largest males in a population and fully grown males sometimes had undeveloped chelipeds similar to females. Development of the male chelipeds in *Leptopalaemon*, therefore, appears to be correlated with social dominance rather than directly to age or size, similar to cheliped development in *Macrobrachium* (Short 2004).

Unlike *Macrobrachium*, allometric growth of the chelipeds in developed male *Leptopalaemon* was largely restricted to elongation of the fingers. Apart from the form of the chelae, the second chelipeds of developed males are otherwise highly similar to undeveloped males and females. Curiously, the developed male P2 chela in *Leptopalaemon* is most similar to the undeveloped male P2 chela of *Macrobrachium*. In most species of *Macrobrachium*, the swollen manus and elongated fingers of undeveloped males are lost as the chelipeds develop, the reverse of development in *Leptopalaemon*.

As mentioned above, fully developed males have only been recorded for three of the five *Leptopalaemon* species. In the remaining two species, the sample sizes were smaller and it is quite likely that fully developed males will be found with further collecting. Among the material of *L. gagadjuui*, which is by far the most commonly collected species, some males were intermediate between undeveloped males and fully developed males and had slightly elongated chelipeds with the fingers equal in length or shorter than the manus.

In regard to the swollen manus and elongated fingers, the second chela of fully developed male *Leptopalaemon* resembles the second chela of several palaemonine genera, e.g.

Leander Desmarest, 1849, *Nematopalaemon* Holthuis, 1950, *Pseudopalaemon* Sollaud, 1911, *Creaseria* Holthuis, 1950, *Troglocubanus* Holthuis, 1949, *Urocaridella* Borradaile, 1915 and *Exopalaemon* Holthuis, 1950.

To highlight the close association of *Leptopalaemon* with the broader Kakadu region, the common name 'Kakadu shrimps' is hereby proposed for the genus.

***Leptopalaemon gagadjui* Bruce & Short, 1993**

(Figs 1, 3, 4F–J, 5B, 19G; Tables 2–4)

Leptopalaemon gagadjui Bruce & Short, 1993: 75–85, figs 1–6. – Davie, 2002: 270. – Page *et al.*, 2008: 1006.

Material examined

Paratypes. QM W16550, 1 f.dev.♂ (5.3 mm CL), 1♂ (3.70 mm CL), 7♀ (3.60–7.30 mm CL), upper Barramundie Ck, Kakadu NP, N.T., Australia, 13°20' S, 132°27' E, J. W. Short, I. Brown, 22.vi.1990.

Other material examined. MAGNT Cr17062, 1♂ (5.20 mm CL) 4♀ (4.30–5.20 mm CL), site 13, Arnhem Land plateau near Namarrgon Gorge, Kakadu NP, N.T., Australia, 12°55'08.9' S, 132°58'44.8' E, G. Spiers, R. Muller, 3.vi.1999; QM W24755, 8♂ (5.05–5.75 mm CL), 5♀ (5.70–6.50 mm CL), site 1, above Mandjawuril Falls, Oepelli outlier, Arnhem Land, N.T., Australia, sandy pool with rocks and leaf litter, 12°21.62' S, 133°05.49' E, J. W. Short, 26.x.1998; MAGNT Cr17063, 1 f. dev.♂ (6.20 mm CL), 3♂ (4.80–5.20 mm CL), 2♀ (5.80, 6.00 mm CL), site 14, Gunlom above Waterfall Creek Falls, Kakadu NP, N.T., Australia, 13°25'50.9' S, 132°25'4.8' E, C. L. Humphrey, 7.x.1997; MAGNT Cr17064, 4♂ (4.15–5.00 mm CL), 3♀ (4.95–6.80 mm CL), site 12, upper Mann R, Arnhem Land, N.T., Australia, 13°17.94' S, 133°32.34' E, C. L. Humphrey, 9.ix.2000; MAGNT Cr17065, 3♂ (4.15–4.60 mm CL), 4♀ (5.10–5.55 mm CL), site 11, upper Katherine R, Arnhem Land, N.T., Australia, 13°24.84' S, 133°11.04' E, C. L. Humphrey, 7.ix.2000; MAGNT Cr17066, 7♀ (4.30–5.20 mm CL), site 8, Arnhem Land plateau S of Namarrgon Gorge, Kakadu NP, Australia, 12°59.9' S, 132°54.06' E, G. Spiers, 15.vii.1999.

Diagnosis

Carapace dorsum flat, appearing more or less straight in lateral view. Rostrum of medium length to long (short in one paratype), reaching between distal end of antennular peduncle and distal end of antennal scale or slightly beyond, $0.65\text{--}1.10 \times \text{CL}$ ($\bar{x}=0.80$, $n=57$); sinuous; dorsal carina armed with 5–10 teeth (mode = 7, $f=0.41$); ventral carina with 1–4 teeth (mode = 2, $f=0.63$) and double row of plumose setae proximally. Antennal spine well developed (rarely moderately developed). Antennular peduncle with well developed spine on distolateral margin of proximal segment. Scaphocerite $0.50\text{--}1.00 \times \text{CL}$ ($\bar{x}=0.75$, $n=50$), anterior margin produced forward at mesial angle, lateral margin straight or slightly convex. Mandible with one-segment palp. Two arthrobranchs (small upper and large lower arthrobranch) on articular membrane at base of third maxilliped. P2 of undeveloped males and females $1.80\text{--}2.25 \times \text{CL}$ ($\bar{x}=2.00$, $n=23$), fully developed males $2.55\text{--}3.10 \times \text{CL}$ ($\bar{x}=2.80$, $n=6$); carpus clearly longer than merus; manus subcylindrical or slightly to moderately inflated. Ova large, 1.8 mm maximum length, maximum width 1.1 mm.

Size

Small, maximum length 7.30 mm CL.

Colour

Generally transparent, feebly speckled with small red–brown chromatophores (Bruce and Short 1993).

Life history

Larval development in this species has not been studied. At 1.8 mm maximum length, the ova are relatively large for a freshwater palaemonid, but still significantly smaller than those of *L. glabrus*, which are 2.5 mm in length. This suggests that larval development is likely to be abbreviated, although the first larval stage is possibly less developed than the benthic first larval stage of *L. glabrus* (see below).

Habitat

The habitat of the species at the type locality, upper Barramundie Creek, was well described by Bruce and Short (1993) and is typical of escarpment and plateau streams over the broad geographic range of the species. Most of these streams have spring-fed permanent pools but little flow during the dry season months (May until October).

The species often co-exists with fishes and *Macrobrachium bullatum*, although the fish faunas are highly depauperate compared with localities below the escarpment and are often dominated by the northern purple-spotted gudgeon, *Mogurnda mogurnda*. Larger, more active predatory fish, such as grunters (Teraponidae spp.), are usually absent, although at site 11 on the upper Katherine River, eel-tail catfish (Plotosidae spp.) are present, and at site 12 on the upper Mann River, the species co-exists with banded grunter (*Amniataba percoides*), spangled grunter (*Leiopotherapon unicolor*) and sooty grunter (*Hephaestus fuliginosus*). In terms of water physicochemistry, flow regimes, fringing vegetation and substrates, the localities where *L. gagadjui* occurs are otherwise similar to those of its congeners.

One atypical habitat for the species was a small side pool on the bank above the main watercourse of Lightning Dreaming Creek (Fig. 19G). The pool was located below the Arnhem Land escarpment ~100 m downstream of the type locality of *L. glabrus* and below the series of shallow glides that present a barrier to the upstream dispersal of fishes. No fish were seen in the pool.

This represents one of just three records of the species below the Arnhem Land plateau/escarpment complex. As *L. gagadjui* has not been found further upstream in sympatry with *L. glabrus*, the pool must have been colonised from downstream. Lightning Dreaming Creek is a headwater tributary of Namarrgon Creek, which is also fed by several other escarpment tributaries draining into Namarrgon (Saw Cut) Gorge. The population in the small side pool of Lightning Dreaming Creek is likely to have originated from another headwater tributary of Namarrgon Creek inhabited by *L. gagadjui*.

Behaviour

Like its congeners, *L. gagadjui* is highly gregarious and active during daylight away from shelter. When disturbed, the shrimps show the typical backward escape response of other carideans, but do not seek shelter.

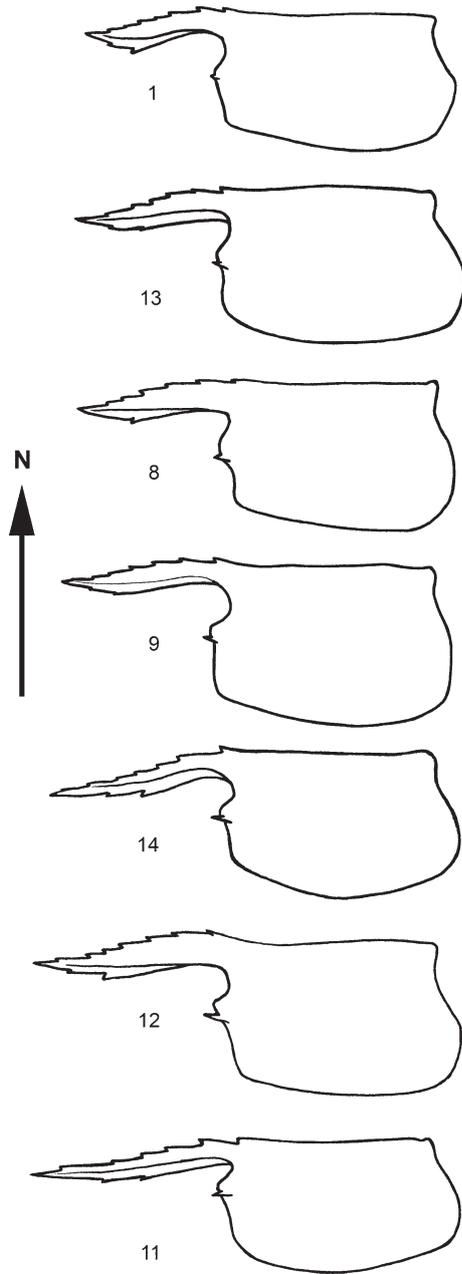


Fig. 3. Geographic variation in rostral length in *Leptopalaemon gagadjui* Bruce & Short, 1993. Numbers are site numbers as indicated on the map of the study area (Fig. 1). Figured specimens are individuals most typical of each site based on mean rostrum length and modal values for dorsal and ventral rostral teeth number for each population (see also Table 3). Carapace lengths equalised to highlight relative rostral length. The arrow indicates a general trend towards shorter rostra between sites moving northward towards the coast. Figured specimens for each site: site 1, QM W24755, ♂ 5.30 mm CL; site 8, MAGNT Cr17066, ♀ 5.00 mm CL; site 9, type locality, QM W16550, paratype ♀, 3.60 mm CL; site 11, MAGNT Cr17065, ♂ 4.25 mm CL; site 12, ♂ 4.25 mm CL, MAGNT Cr17064; site 13, ♀ 4.30 mm CL, MAGNT Cr17062; site 14, MAGNT Cr17063, ♂ 6.20 mm CL.

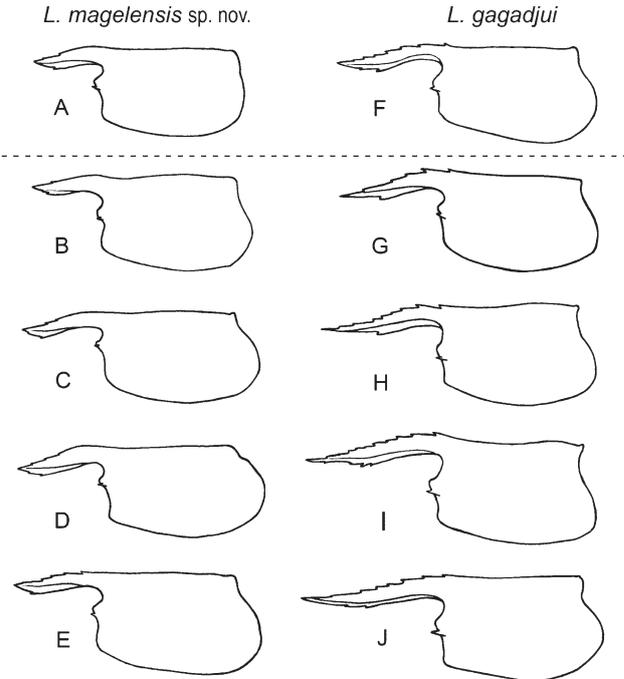


Fig. 4. Carapace variation in *Leptopalaemon* species with medium and long rostra. Carapace lengths equalised to highlight relative rostral length. Drawings above the dashed line are the most typical individuals for each species based on mean rostrum length and the modal values for dorsal and ventral rostral teeth number (see also Table 2). *L. magelensis*, sp. nov.: A, paratype ♂, 5.50 mm CL, site 15, MAGNT Cr017060; B, paratype ♀, 6.15 mm CL, site 3, type locality, QM W24748; C, paratype ♀, 6.20 mm CL, site 15, MAGNT Cr01760; D, paratype ♀, 6.50 mm CL, site 15, MAGNT Cr01760; E, paratype ♂, 3.85 mm CL, site 15, MAGNT Cr01760. *L. gagadjui* Bruce & Short, 1993: F, ♀ 5.00 mm CL, site 13, MAGNT Cr17062; G, ♀ 6.00 mm CL, site 14, MAGNT Cr17063; H, ♂ 5.20 mm CL, site 14, MAGNT Cr17063; I, ♂ 5.00 mm CL, site 12, MAGNT Cr17064; J, ♀ 5.11 mm CL, site 11, MAGNT Cr17065.

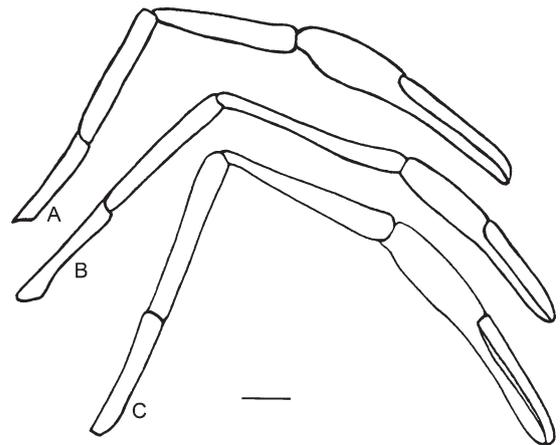


Fig. 5. Fully developed male second pereiopods. A, *Leptopalaemon glabrus* (Bruce, 1993), ♂ 5.75 mm CL, QM W24749; B, *L. gagadjui* Bruce & Short, 1993, ♂ 6.2 mm CL, site 14, MAGNT Cr17063; C, *L. gudjangah*, sp. nov., paratype ♂, 6.85 mm CL, site 2, QM 24754. Scale bar = 1 mm.

Midwater aggregations of the species have been observed at Graveside Gorge (I. Brown, pers. comm.), the upper Katherine River and above Gunlom (Waterfall Creek Falls) (CLH). These aggregations typically involve a large number of individuals and are usually more or less stationary in the water column. Individuals appear motionless but are presumably swimming using the swimmerets. The aggregation behaviour is not presently understood, but may involve group filter-feeding on plankton.

Distribution

Widely distributed in the 'stone country' and adjacent areas of the broader Kakadu region from the South Alligator River catchment to Cooper Creek, East Alligator River catchment. Also recorded from the upper Katherine and Mann Rivers on the central Arnhem Land plateau, the latter lying just outside the eastern border of the broader Kakadu region as defined by Finlayson *et al.* (2006).

Proposed common name

Common Kakadu-shrimp.

Remarks

The species was described by Bruce and Short (1993) based on 22 specimens from the type locality, upper Barramundie Creek, as well as material from several escarpment tributaries in the South Alligator River catchment in Kakadu NP. Three immature

specimens were also recorded from Cooper Creek in Arnhem Land. The above diagnosis is based on a re-examination of paratypes from the type locality, as well as 45 additional specimens from a much broader geographic range, including new material from the upper Mann and Katherine Rivers in the central Arnhem Land plateau and from above Mandjawuril Falls in the East Alligator River catchment.

The species sometimes occurs in close proximity to the localities of the other four species of *Leptopalaemon*, although it has not yet been recorded in sympatry with its congeners. In Lightning Dreaming Creek it was collected only 100 m downstream of the type locality of *L. glabrus*, as noted above.

In contrast to the results of the molecular study (Page *et al.* 2008), which recorded relatively low levels of COI divergence (2.13–5.5%) between *L. gagadjui* and the three new species (*Leptopalaemon* sp. 1, sp. 2 and sp. 3 in Page *et al.* 2008), *L. gagadjui* shows distinctive morphology throughout its relatively broad geographic range, including areas adjacent to the new species. It is immediately recognisable by the relatively long, well developed rostrum, which reaches to around the distal margin of the scaphocerite and bears five or more well developed teeth on the dorsal margin.

The present material includes a series of subdeveloped and fully developed males ranging in size from 4.15 to 6.20 mm CL. The adult male holotype, measuring 5.50 mm CL, has undeveloped second chelae and is of similar morphology to adult females. The male paratype figured in the original description has the major cheliped fully developed (Bruce and

Table 2. Summary of the main distinguishing features for *Leptopalaemon* species

	<i>L. gagadjui</i>	<i>L. magelensis</i> , sp. nov.	<i>L. gudjangah</i> , sp. nov.	<i>L. gibbosus</i> , sp. nov.	<i>L. glabrus</i>
Rostrum					
Length v. CI	0.65–1.10 × CL (\bar{x} = 0.80, n = 57)	0.50–0.70 × CL (\bar{x} = 0.60, n = 24)	0.45–0.60 × CL (\bar{x} = 0.50, n = 20)	0.30–0.60 × CL (\bar{x} = 0.40, n = 18)	0.30–0.35 × CL (\bar{x} = 0.30, n = 10)
Length relative to antennular peduncle	longer	generally shorter	shorter	shorter	shorter
Dorsal teeth	5–10 (mode = 7, f = 0.41)	1–4 (mode = 2, f = 0.50)	0–1 (mode = 0, f = 0.75)	0–1 (mode = 0, f = 0.89)	0–1 (mode = 0, f = 0.80)
Ventral teeth	1–4 (mode = 2, f = 0.63)	0–2 (mode = 1, f = 0.63)	0–1 (mode = 0, f = 0.95)	0–2 (mode = 0, f = 0.63)	0 (mode = 0, f = 1.00)
Dorsal carapace					
	flat	flat	flat	moderately humped	flat to moderately humped
Antennal spine					
	generally well developed	absent or poorly developed	poorly to moderately developed	poorly to moderately developed	absent
Antennule peduncle					
length	0.55–0.75 × CL (\bar{x} = 0.65, n = 49)	0.45–0.55 × CL (\bar{x} = 0.50, n = 10)	0.45–0.55 × CL (\bar{x} = 0.50, n = 14)	0.40–0.50 × CL (\bar{x} = 0.45, n = 18)	0.40–0.45 × CL (\bar{x} = 0.40, n = 10)
Distolateral spine on proximal segment	well developed	poorly developed	absent or poorly developed	poorly developed	poorly developed
Scaphocerite length					
	0.50–1.00 × CL (\bar{x} = 0.75, n = 50)	0.60–0.70 × CL (\bar{x} = 0.65, n = 10)	0.55–0.65 × CL (\bar{x} = 0.60, n = 14)	0.45–0.60 × CL (\bar{x} = 0.55, n = 18)	0.45–0.55 × CL (\bar{x} = 0.50, n = 10)
Mandibular palp					
	1 segment	absent	1 segment	1 segment	0–1 segments
Pereiopod 2					
Length in ♀ and undeveloped ♂	1.80–2.25 × CL (\bar{x} = 2.00, n = 23)	1.55–1.90 × CL (\bar{x} = 1.75, n = 14)	1.55–1.85 × CL (\bar{x} = 1.65, n = 12)	1.40–1.90 × CL (\bar{x} = 1.65, n = 9)	1.30–1.45 × CL (\bar{x} = 1.40, n = 5)
Length in fully developed ♂	2.55–3.10 × CL (\bar{x} = 2.80, n = 6)	–	2.30 × CL (n = 1)	–	2.25–2.35 × CL (\bar{x} = 2.30, n = 3)
Carpus v. merus	clearly longer	clearly longer	clearly longer	clearly longer	about equal in length

Table 3. Geographic variation in *Leptopalaemon gagadju* Bruce & Short, 1993

	<i>Katherine River</i>	<i>Mann River</i>	<i>S. Alligator River</i>				<i>E. Alligator River</i>
	Site 11 Upper Katherine River	Site 12 Upper Mann River	Site 14 Gunlom	Site 9 Barramundie Creek (type locality)	Site 8 Arnhem Land plateau S of Namarrgon Gorge	Site 13 Arnhem Land plateau near Namarrgon Gorge	Site 1 Above Mandjawuril Falls
Rostrum							
Length	0.90–1.10 × CL (\bar{x} = 1.00, n = 7)	0.90–1.05 × CL (\bar{x} = 0.95, n = 7)	0.75–0.95 × CL (\bar{x} = 0.90, n = 6)	0.75–1.10 × CL (\bar{x} = 0.85, n = 12)	0.70–0.80 × CL (\bar{x} = 0.75, n = 7)	0.70–0.80 × CL (\bar{x} = 0.75, n = 7)	0.65–0.85 × CL (\bar{x} = 0.65, n = 13)
Dorsal teeth	5–7 (mode = 6, f = 0.71)	6–10 (mode = 7, f = 0.57)	5–8 (mode = 7, f = 0.50)	6–8 (mode = 7, f = 0.50)	6–7 (mode = 6, f = 0.71)	6–7 (mode = 6, f = 0.50)	6–8 (mode = 7, f = 0.54)
Ventral teeth	2–3 (mode = 2, f = 0.71)	1–4 (mode = 2, f = 0.71)	1–3 (mode = 1, f = 0.50)	1–3 (mode = 2, f = 0.88)	1–2 (mode = 1, f = 0.57)	1–2 (mode = 2, f = 0.80)	2–4 (mode = 2, f = 0.62)
Antennule							
Peduncle length	0.60–0.70 × CL (\bar{x} = 0.65, n = 7)	0.60–0.75 × CL (\bar{x} = 0.65, n = 7)	0.55–0.65 × CL (\bar{x} = 0.60, n = 6)	0.55–0.75 × CL (\bar{x} = 0.65, n = 6)	0.55–0.65 × CL (\bar{x} = 0.60, n = 7)	0.60 × CL (\bar{x} = 0.60, n = 3)	0.55–0.70 × CL (\bar{x} = 0.60, n = 13)
Scaphocerite							
Length	0.70–0.95 × CL (\bar{x} = 0.85, n = 7)	0.75–0.95 × CL (\bar{x} = 0.85, n = 7)	0.75–0.85 × CL (\bar{x} = 0.80, n = 6)	0.75–1.00 × CL (\bar{x} = 0.85, n = 7)	0.55–0.85 × CL (\bar{x} = 0.70, n = 7)	0.70–0.80 × CL (\bar{x} = 0.75, n = 3)	0.50–0.75 × CL (\bar{x} = 0.65, n = 13)
Pereiopod 2							
length in ♀ and undeveloped ♂	1.90–2.70 × CL (\bar{x} = 2.00, n = 3)	1.95–2.25 × CL (\bar{x} = 2.15, n = 3)	1.90–2.50 × CL (\bar{x} = 2.10, n = 5)	1.80–2.20 × CL (\bar{x} = 2.15, n = 8)	1.90–2.00 × CL (\bar{x} = 1.95, n = 2)	2.00 × CL (\bar{x} = 2.00, n = 2)	1.60–2.05 × CL (\bar{x} = 1.95, n = 13)
Length in fully developed ♂	2.70–3.10 × CL (\bar{x} = 2.90, n = 2)	2.75–3.05 × CL (\bar{x} = 2.90, n = 2)	–	2.70 × CL (n = 1)	–	–	–

Short 1993; Fig. 4G) and the minor cheliped undeveloped, possibly regenerated (Bruce and Short 1993; Fig. 4D).

Although some geographic variation was recorded during this study (Table 3, Figs 3, 4F–J), it was not sufficient to establish clearly defined subspecies. In general, geographic morphological variation was consistent with limited contemporary gene flow, recent genetic bottlenecks or founder effects and a small effective population size at each site, as indicated by the molecular study (Page *et al.* 2008). There was some evidence of clinal variation in relative rostral length along the western Arnhem Land escarpment, with a gradual decrease in rostral length in a northward direction towards the coast (Fig. 3; Table 3). However, specimens at sites 11 and 12 on the central Arnhem Land plateau (Fig. 1), representing the southernmost populations, had the shortest rostra for the species. Clinal variation in rostral length was most apparent when the mean values for relative rostral length were compared amongst sites (Table 3; Fig. 3), rather than range values, which showed significant overlap between sites. Variation in the relative length of the scaphocerite (Table 3) also partially mirrored this pattern.

Unlike rostral length, the two rostral dentition characters showed considerable variation among sites, as demonstrated by the modal values (Table 3), emphasising the unique haplotypes at each site revealed by the molecular study (Page *et al.* 2008).

In general morphology, specimens from the adjacent sites 7 and 8 in the South Alligator River basin, paired closely

(Table 3). Similarly, specimens from sites 9 and 14, both proximate headwater tributaries of the upper South Alligator River, showed high similarity in general morphology. The latter pairing of sites provided further support for a western grouping comprising sites 9 and 10 which was recognised in the molecular study. The two central plateau sites, 11 and 12, the upper Mann and Katherine rivers respectively, were also generally similar.

Leptopalaemon glabrus (Bruce, 1993), comb. nov.

(Figs 1, 5A, 6M–R, 20B; Tables 2, 4)

Kakaducaris glabra Bruce, 1993: 28–40, figs 1–12. – Davie, 2002: 270. – Page *et al.*, 2008: 1006.

Material examined

Topotypical material. QM W24749, 1 f.dev. ♂ (5.75 mm CL), Lightning Dreaming Creek, plunge pool below waterfall, Kakadu NP, N.T., Australia, 12°55.3' S, 132°55.8' E, J. W. Short, C. L. Humphrey, 25.x.1998; QM W24750, 1 f.dev. ♂ (5.70 mm CL), Lightning Dreaming Creek, pool on first ledge of waterfall, Kakadu NP, N.T., Australia, J. W. Short, C. L. Humphrey, 25.x.1998; QM W24751, 1 f.dev. ♂ (5.40 mm CL), Lightning Dreaming Creek, plunge pool below waterfall, Kakadu NP, N.T., Australia, J. W. Short, C. L. Humphrey, 25.x.1998.

Other material examined. MAGNT Cr17067, 3♀ (5.60–6.10 mm CL), site 6, Lightning Dreaming Creek, above falls, Kakadu NP, N.T., Australia, 12°54.76' S, 132°56' E, G. Spiers, T. Hillman, 15.vi.1999; MAGNT Cr17068, 1♂ (5.65 mm CL), 2♀ (5.35–5.70 mm CL), same locality and collection data.

Diagnosis

Carapace dorsum flat to humped, straight to moderately convex in lateral view. Rostrum short, failing to reach base of intermediate antennular peduncle segment, $0.30\text{--}0.35 \times \text{CL}$ ($\bar{x}=0.30$, $n=10$); convex or slightly sinuous; dorsal carina with 0–1 teeth (mode=0, $f=0.80$); three minute denticles in one female; ventral carina obsolete, ventral margin unarmed, without plumose setae proximally. Antennal spine absent. Antennular peduncle with poorly developed spine on distolateral margin of proximal segment. Scaphocerite $0.45\text{--}0.55 \times \text{CL}$ ($\bar{x}=0.50$, $n=10$), anterior margin generally produced forward in middle third (rarely produced forward at mesial angle), lateral margin slightly to moderately convex. Mandibular palp variably developed, absent to well developed as long, single segment. One well developed arthrobranch present on articular membrane at base of third maxilliped. P2 of undeveloped males and females $1.30\text{--}1.45 \times \text{CL}$ ($\bar{x}=1.40$, $n=5$), fully developed males $2.25\text{--}2.35 \times \text{CL}$ ($\bar{x}=2.30$, $n=3$); carpus about equal in length to slightly longer than manus; manus inflated in middle third. Ova large, 2.5 mm maximum length, maximum width 1.5 mm.

Size

Small, maximum length 8.5 mm CL.

Colour

Although the colour pattern of the species was described in detail by Bruce (1993), the description does not appear to be based on live specimens in their natural habitat. No mention was made of the distinctive, white, transverse bands on the dorsum of the body present in live specimens at the type locality (Fig. 20B). Captive individuals quickly lose the banding pattern when kept in a laboratory environment (CLH, pers. obs.) and develop a speckled brown appearance.

Life history

The first larval stage was described by Bruce (1993) and is largely of benthic appearance, resembling a miniature adult but with some natatory larval features retained such as well developed natatory exopods on thoracopods 3–5 and a telson of natatory form (broadly rounded with numerous plumose setae on the posterior margin).

Habitat

The type locality is a rocky, waterfall plunge pool with minimal dry season flow and is located at approx. 100 m elevation. Bruce (1993) noted that there were no fish or other decapod crustaceans inhabiting the pool, although phreatoicid isopods of the genus *Eophreatoicus* Nicholls, 1926 were present.

The plunge pool at the type locality is separated from lower Lightning Dreaming Creek by a series of shallow bedrock glides, which appear to form a barrier to the upstream migration of fishes and other decapod crustaceans. As mentioned above, a small isolated side pool near Lightning Dreaming Creek below this series of glides contains a population of *L. gagadjui*.

The new material studied from Lightning Dreaming Creek includes samples from a pool on the first ledge of the waterfall and specimens from the creek above the waterfall at an elevation of

approx. 200 m (site 6). The total dry-season distribution of the species in upper Lightning Dreaming Creek is extremely restricted, being limited to an approx. 2 km section immediately above the falls (G. Spiers, pers. comm.).

Behaviour

The species shows general behaviour similar to other species of the genus and like its congeners is gregarious and active away from shelter during daylight.

Distribution

Restricted to Lightning Dreaming Creek, a headwater tributary of Namarrgon Creek in the South Alligator River basin.

Proposed common name

Smooth Kakadu-shrimp.

Remarks

This species was well described and illustrated by Bruce (1993), based on a collection of 50 specimens from the plunge pool below the waterfall on Lightning Dreaming Creek. In addition to new topotypical material, the present collections include specimens from above the falls and a pool on the first ledge on the waterfall. The present material also includes the first fully developed males recorded for the species. The form of the fully developed male cheliped is shown in Fig. 5.

Leptopalaemon glabrus differs from its congeners in having only one arthrobranch at the base of the third maxilliped. In terms of the reduction of the rostrum, antennal spine and second chelipeds, *L. glabrus* shows the greatest expression of this common evolutionary trend within the genus. It also shows the least variation in proportional morphometric and meristic characters (Table 2).

Leptopalaemon gudjangah, sp. nov.

(Figs 1, 5C, 6A–F, 7–10, 19C, E; Tables 2, 4)

Leptopalaemon sp. 1 Page et al., 2008: 1006.

Material examined

Holotype. QM W29091, ♂ (5.60 mm CL), site 2, seasonally-flowing stream, Oenpelli outlier, approx. 9 km SSE of Oenpelli, Arnhem Land, N.T., Australia, 12°23.9' S, 133°05' E, pool in small bedrock gorge, J. W. Short, C. L. Humphrey, I. Brown, 24.x.1998.

Paratypes. QM W24754, 1 f.dev. ♂ (6.85 mm CL), 10 ♂ (4.55–6.70 mm CL), 9 ♀ (5.15–6.65 mm CL), same collection data as holotype.

Diagnosis

Carapace dorsum flat, straight to slightly convex in lateral view. Rostrum typically short (of medium length in one paratype), reaching from distal end of basal segment of antennular peduncle to almost distal margin of terminal segment of antennular peduncle, $0.45\text{--}0.60 \times \text{CL}$ ($\bar{x}=0.45$, $n=20$); slightly sinuous or convex (rarely), dorsal carina with 0–1 teeth (mode=0, $f=0.75$), ventral carina with 0–1 teeth (mode=0, $f=0.95$), with double row of plumose setae proximally. Antennal spine poorly to moderately developed. Antennular peduncle with spine on distolateral margin of proximal segment absent or poorly

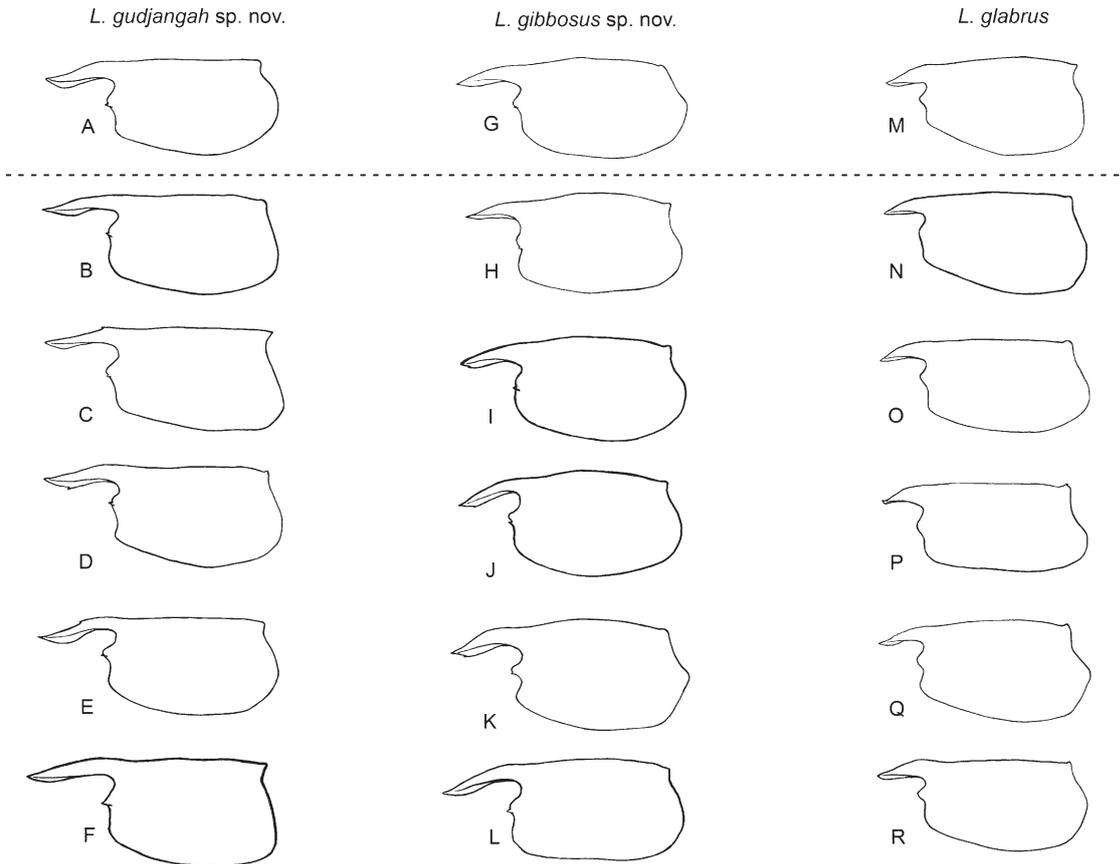


Fig. 6. Carapace variation in species of *Leptopalaemon* with short rostra. Carapace lengths equalised to highlight relative rostral length. Drawings above the dashed line are the most typical individuals for each species based on mean rostrum length and the modal values for dorsal and ventral rostral teeth number (see also Table 2). *L. gudjangah*, sp. nov., all site 1, type locality: A, paratype ♂, 5.40 mm CL, QM W24754; B, Holotype ♂, 5.60 mm CL, QM W24754; E, paratype ♂, 6.85 mm CL, QM W24754; F, paratype ♂, 4.8 mm CL, QM W24754. *L. gibbosus*, sp. nov., all site 5, QM W26845: G, paratype ♂, 5.70 mm CL; H, paratype ♂, 5.65 mm CL; I, paratype ♂, 5.00 mm CL; J, paratype ♀, 5.00 mm CL; K, paratype ♀, 5.60 mm CL; L, paratype ♀, 4.00 mm CL. *L. glabrus* (Bruce, 1993): M, ♀, 6.10 mm CL, site 6, MAGNT Cr17067; N, ♀, 5.35 mm CL, site 6, MAGNT Cr17068; O, ♂, 5.40 mm CL, QM W24751; P, ♂, 5.70 mm CL, QM W24750; Q, ♀, 5.60 mm CL, site 6, MAGNT Cr17067; R, ♂, 5.75 mm CL, QM W24750.

developed. Scaphocerite $0.55\text{--}0.65 \times \text{CL}$ ($\bar{x}=0.60$, $n=14$), anterior margin produced forward at mesial angle, lateral margin straight or slightly convex. Mandible bearing one-segment palp. Two arthrobranchs (small upper and large lower arthrobranch) at base of third maxilliped. Second pereopod of undeveloped males and females $1.55\text{--}1.85 \times \text{CL}$ ($\bar{x}=1.65$, $n=12$), fully developed male $2.30 \times \text{CL}$ ($n=1$); carpus clearly longer than merus; manus inflated in middle third. Size and number of ova not yet recorded.

Description of holotype male

Acron. Bec ocellaire small, acute.

Carapace. Dorsum flat, appearing straight in lateral view. Rostrum short, $0.50 \times \text{CL}$, just over-reaching intermediate segment of antennular peduncle, slender, maximum depth clearly less than dorso-ventral diameter of cornea; with well developed dorsal and lateral carinae, ventral carina reduced; dorsal carina slightly sinuous, unarmed; ventral carina unarmed, with double row of short plumose setae proximally.

Antennal spine moderately developed, situated below and distinct from inferior orbit, marginal. Inferior orbital margin moderately produced, bluntly angular. Pterygostome bluntly angular.

Antennule. Peduncle length $0.50 \times \text{CL}$, distolateral margin of proximal segment with small spine.

Antennal somite. Scaphocerite short, $0.65 \times \text{CL}$, lamina widest in proximal half, anterior margin produced forward at mesial angle, lateral margin more or less straight.

Mouthparts. Mandible with one-segment, non-setose palp. Maxillula with upper lacinia moderately expanded, with setal rows distally; lower lacinia broad, with dense double row of setae distally. Maxilla with coxal endite without mesial lobes, basal endite distally setose, palp elongate, distally pointed, emarginate, non-setose, scaphognathite with mesial border deeply notched with distinct fold. First maxilliped with basal and coxal endites densely setose mesially; palp simple, elongate, proximally fused with basal endite, distal half with short plumose setae along mesial margin; epipod triangular, anterior lobe rounded, posterior lobe rounded. Second maxilliped with dactylar segment narrow, mesial border with

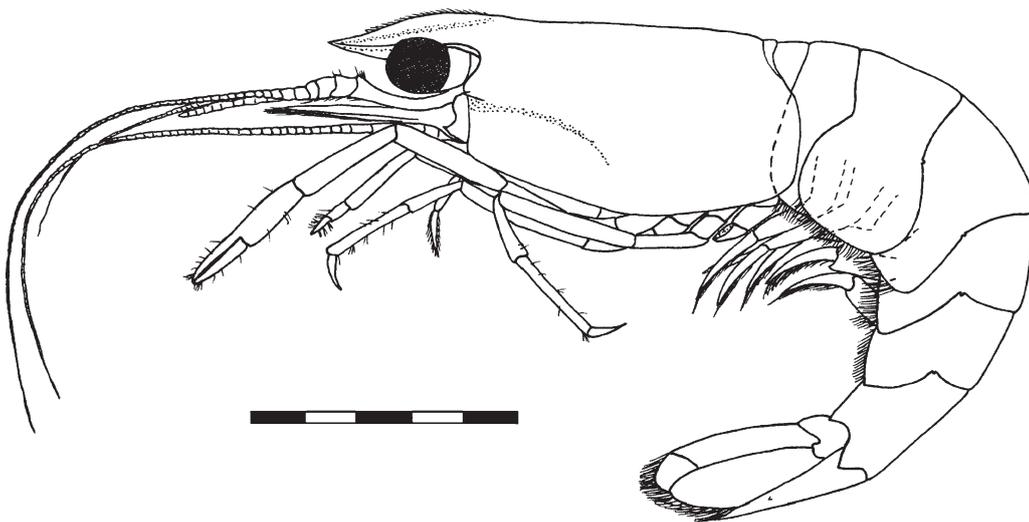


Fig. 7. *Leptopalaemon gudjanganh*, sp. nov. Holotype ♂, 5.60 mm CL, QM W29091. Scale divisions = 1 mm.

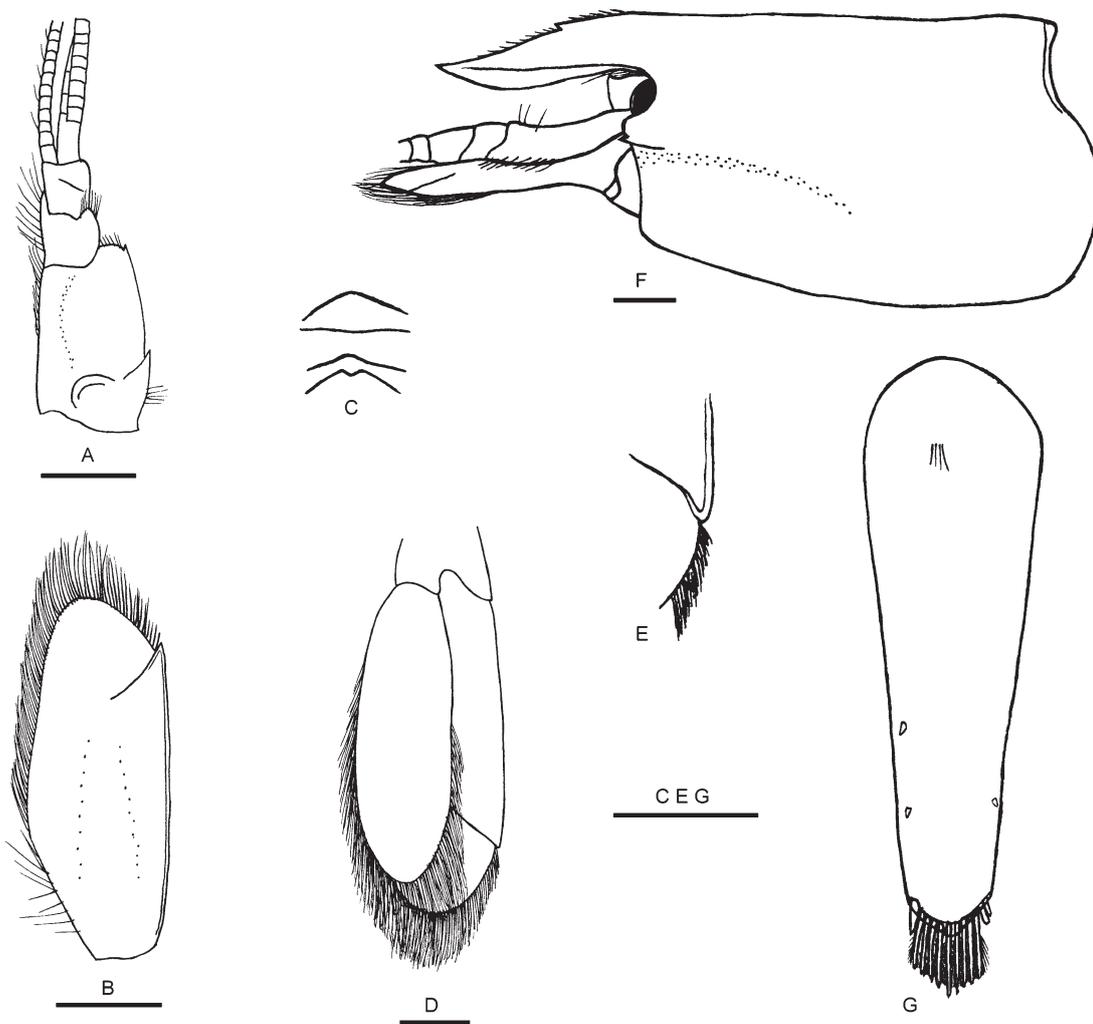


Fig. 8. *Leptopalaemon gudjanganh*, sp. nov. Holotype ♂, 5.60 mm CL, QM W29091; A, dorsal antennular peduncle. B, dorsal view of scaphocerite. Paratype ♂, 6.85 mm CL, QM W24754; C, thoracic sternites 2–4, ventroposterior view. D, uropod. E, distolateral tooth on uropodal exopod. F, lateral view of cephalothorax with eye removed to show bec ocellaire. G, telson. Scale bars = 1 mm.

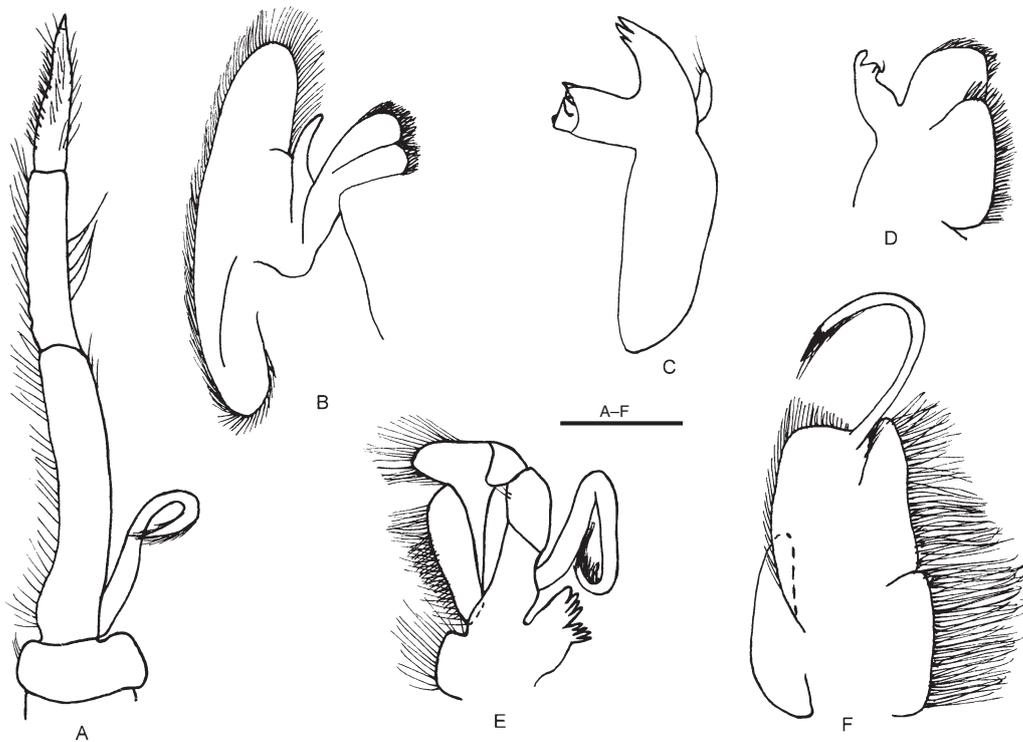


Fig. 9. *Leptopalaemon gudjangah*, sp. nov. Paratype ♂, 6.85 mm CL, QM W24754; A, third maxilliped (left). B, maxilla (right), flattened. C, mandible (left). D, maxillula (right). E, second maxilliped (left). F, first maxilliped (right), flattened. Scale bars = 1 mm.

rows of setae; propodal segment distomesially produced, setose distomesially, distal articular portion narrow; coxal segment with carinate mesial border with numerous long, simple setae.

Thoracic sternum. Second sternite armed with large, transverse, triangular plate with blunt apex; third sternite with low transverse ridge with broad shallow median notch; fourth sternite armed with two plates, posterior transverse triangular plate with well developed median notch and anterior slightly raised plate with median process.

Branchiae. Two arthrobranchs (small upper and large lower arthrobranch) present on articular membrane at base of third maxilliped.

Second pereopod. Isomorphic; short, $1.80 \times \text{CL}$; distal 1/3 of carpus exceeding scaphocerite; fingers without gape, cutting edges unarmed; manus about equal in length to fingers, length $2.50 \times \text{max. depth}$, slightly inflated at mid-length; carpus clearly shorter than chela, clearly longer than merus, moderately long, tapering proximally; merus subcylindrical; ischium compressed, tapered subproximally.

Third pereopod. Short, just reaching past distal margin of dactylus.

Abdomen. Fourth pleura rounded. Fifth bluntly angular, without minute posteroventral tooth. Endopod of first male pleopod distally rounded. Second pleopod with appendix masculina about equal in length to endopod, ~ 21 spiniform setae around distal margin of mesial face, setae increasing in size apically.

Telson. Armed with three dorsal spiniform setae (left distalmost seta absent); posterior margin unevenly rounded, armed with minute submedian process, nine long plumose setae between innermost pair of lateral spiniform setae and medial projection.

Type series variation

Carapace. Dorsum flat, not distinctly humped, appearing straight to slightly convex in lateral view. Rostrum short (of medium length in one paratype only), $0.45\text{--}0.60 \times \text{CL}$ ($\bar{x} = 0.45$, $n = 20$; $\bar{x} = 0.50$ in females, $n = 10$; 0.60 in males, $n = 10$), reaching from distal margin of basal segment of antennular peduncle to almost distal margin of terminal segment of antennular peduncle, most commonly reaching slightly beyond intermediate segment of antennular peduncle; dorsal carina typically slightly sinuous, convex in one paratype, typically unarmed, with single tooth in five paratypes and four teeth in one aberrant specimen (mode = 0, $f = 0.75$); ventral carina unarmed (with single tooth in distal half in one paratype; mode = 0, $f = 0.95$). Antennal spine poorly to moderately developed (asymmetrically developed in two paratypes). Inferior orbital margin bluntly angular or obtusely rounded. Pterygostome bluntly angular or obtusely rounded.

Antennule. Peduncle length $0.45\text{--}0.55 \times \text{CL}$ ($\bar{x} = 0.50$, $n = 14$), distolateral margin of proximal segment with distolateral spine absent or poorly developed.

Antennal somite. Scaphocerite short, $0.55\text{--}0.65 \times \text{CL}$ ($\bar{x} = 0.60$, $n = 14$).

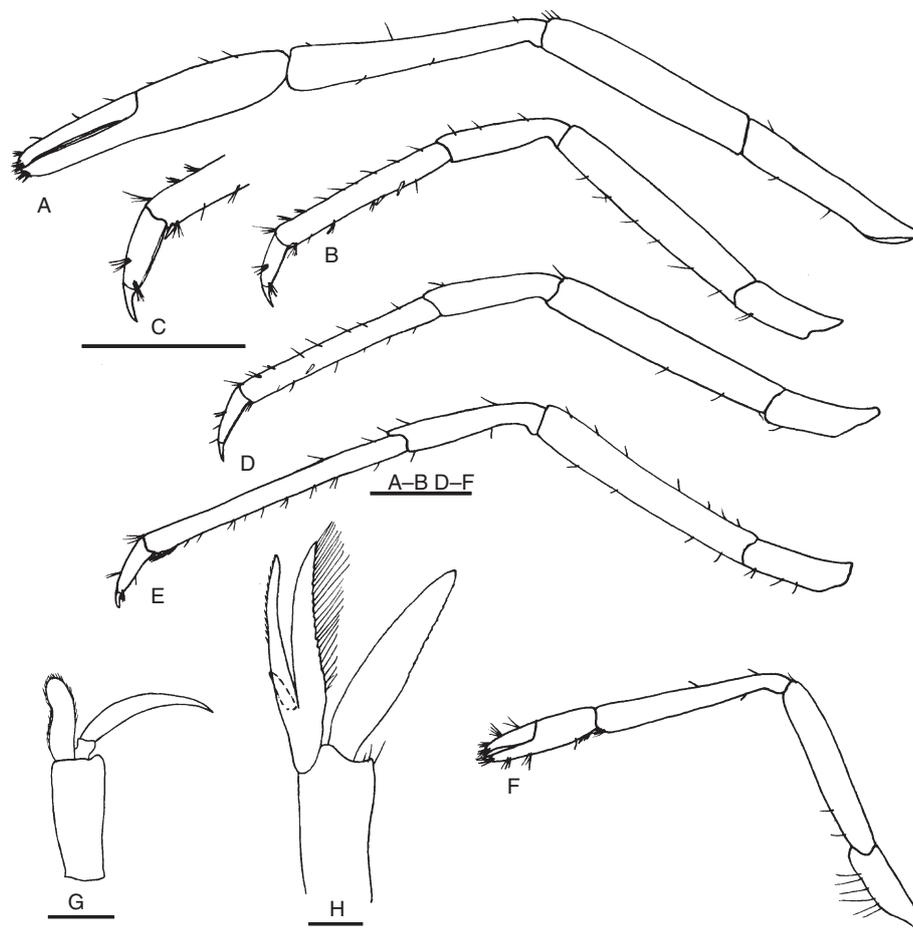


Fig. 10. *Leptopalaemon gudjangah*, sp. nov. Holotype ♂, 5.60 mm CL, QM W29091; A, isomorphic second pereiopod. B, third pereiopod. C, same, dactylus and distal propodus. D, fourth pereiopod. E, fifth pereiopod. F, first pereiopod. Paratype ♂, 6.85 mm CL, QM W24754; G, first pleopod. H, second pleopod. Scale bars = 1 mm.

Mouthparts. Mandibular palp sometimes with single seta.

Second pereiopod. Isomorphic or subequal to unequal in length; $2.30 \times$ CL in fully developed male paratype, $1.55\text{--}1.85 \times$ CL in undeveloped male and female paratypes (for type series excluding fully developed male paratype $\bar{x}=1.65$, $n=12$); carpus just exceeding scaphocerite in undeveloped males and females to $2/3$ carpus exceeding scaphocerite in fully developed male paratype; manus clearly shorter to clearly longer than fingers, length $2.20\text{--}3.05 \times$ max. depth ($\bar{x}=2.30$, $n=13$), slightly to moderately inflated at mid-length or in middle third; carpus clearly shorter to about equal in length to chela, tapering proximally or subproximally; merus subcylindrical, slightly inflated near mid-length or tapered proximally; ischium compressed, tapered subproximally or proximally.

Third pereiopod. Exceeding scaphocerite by $1/2$ propodus in fully developed male paratype, reaching to around distal margin of scaphocerite in undeveloped male and female paratypes.

Abdomen. Appendix masculina with ~ 25 spiniform setae around distal margin of mesial face in fully developed male paratype, setae increasing in size apically.

Telson. Typically with two pairs of minute dorsal spiniform setae (absent in one paratype); posterior margin angularly sinuous; typically with moderately developed, acute median process (blunt median process in one paratype, process absent in one paratype); posterior margin with 8–11 long plumose setae between innermost pair of lateral spiniform setae.

Ova. Egg size not yet recorded.

Size

Small, maximum length 6.85 mm CL.

Colour

Translucent, indistinctly speckled.

Habitat

The type locality is a large, narrow, pool approx. 20 m in length and up to 5 m wide in a small, bedrock gorge. At the head of the pool was a small waterfall, which at the end of the dry season was limited to seepage down the rock face. The northern side of the gorge had a sheer rock face approx. 6 m high whereas the

southern side was more accessible and only ~4 m high. The substrate of the pool was solid bedrock with few loose rocks or stones. No other decapod crustaceans or fish were present in the pool. The pool was located approx. 100 m above the level of the East Alligator River floodplain.

When visited in October 1998, the watercourse immediately downstream of the type locality was largely dry and consisted mostly of rocks and sand with small areas of solid bedrock. A few individuals were observed in a small bedrock pool ~1 km downstream of the type locality, but were not captured.

Behaviour

Like its congeners, *L. gudjanganh*, sp. nov. is gregarious and active away from shelter during daylight. A large, stationary, midwater aggregation of the species was observed at the type locality in October at the end of the dry season by two of the present authors (JWS, CLH).

Etymology

From the indigenous name (pronounced *good-jung-are*) for the patrilineal clan estate which includes the area of the type locality. To be used as a noun in apposition.

Distribution

Presently known from the type locality, a small, seasonally-flowing stream on the Oenpelli outlier approx. 9 km SSE of Oenpelli, Arnhem Land, Northern Territory, Australia. The stream is a tributary of another small stream that feeds directly to the East Alligator River floodplain at Oenpelli; this floodplain connects with estuarine reaches of the East Alligator River during the wet season.

Proposed common name

Gudjanganh shrimp.

Remarks

The new species closely resembles *L. glabrus* from Lightning Dreaming Creek in the South Alligator River catchment. It differs from *L. glabrus* in having two arthrobranches on the third maxilliped. The latter species also has a distinctively banded colour pattern (Fig. 20B) whereas *L. gudjanganh*, sp. nov. is lightly speckled without banding. The COI data from the molecular study (Page *et al.* 2008) indicated that *L. gudjanganh*, sp. nov. is more closely allied to the remaining *Leptopalaemon* species than to *L. glabrus*, although it did not clade strongly with one particular species.

Leptopalaemon gibbosus, sp. nov.

(Figs 1, 6G–L, 11–14, 19A, D, F, 20A; Table 2, 4)

Leptopalaemon sp. 3 Page *et al.*, 2008: 1006.

Material examined

Holotype. QM W29094, ♂ (4.80 mm CL), site 5, small headwater tributary of Namarrgon Creek north of Namarrgon Gorge, Arnhem Land plateau, Kakadu NP, N.T., Australia, 12°54.2' S, 132°57.3' E, G. Spiers, 24.v.1999.

Paratypes. QM W26845, 7♀ (4.00–5.60 mm CL), 3♂ (5.00–5.70 mm CL), same collection data as holotype; MAGNT Cr017061, 5♂ (4.75–7.00 mm CL), 3♀ (4.70–8.45 mm CL), site 4, small headwater tributary of Namarrgon Creek north of Namarrgon Gorge, approx. 8 km N of site 5, Arnhem Land plateau, Kakadu NP, N.T., Australia, 12° 51.76' S, 132° 59.47' E, G. Spiers, 18.vi.1999.

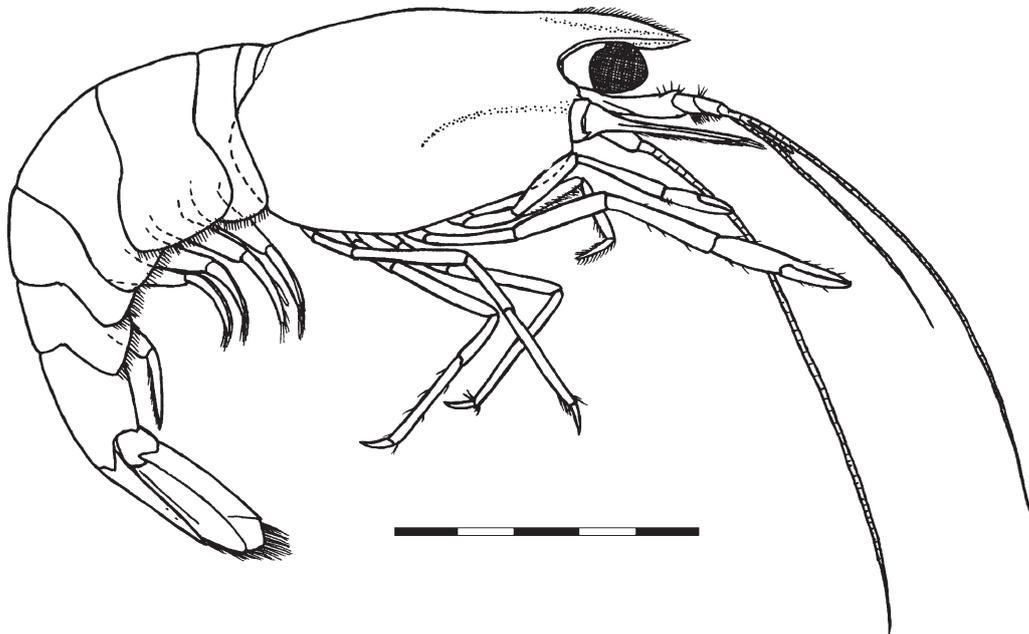


Fig. 11. *Leptopalaemon gibbosus*, sp. nov. Holotype ♂, 4.80 mm CL, QM W29094. Scale divisions = 1 mm.

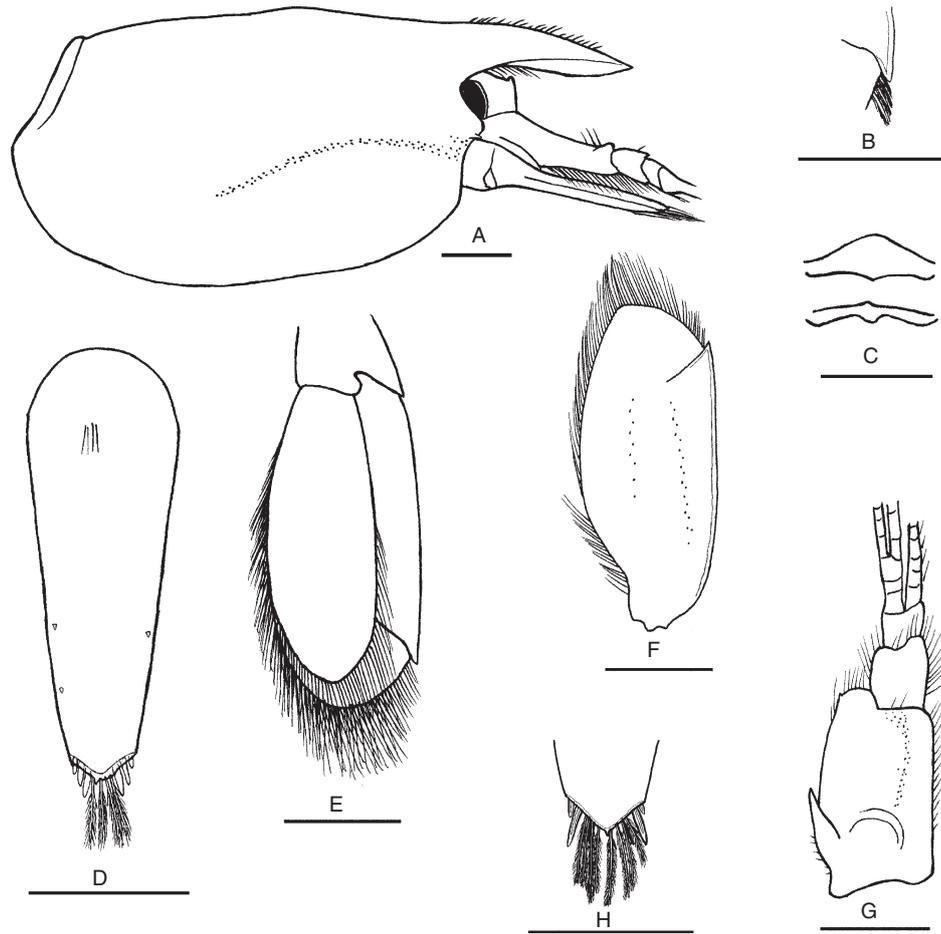


Fig. 12. *Leptopalaemon gibbosus*, sp. nov. Paratype ♂, 5.70 mm CL, QM W26845; A, lateral view of cephalothorax with eye removed to show bec ocellaire. B, distolateral tooth on uropodal exopod. C, thoracic sternites 2–4, ventroposterior view. D, telson with abnormal number of spiniform setae on posterior margin. E, uropod. F, dorsal view of scaphocerite. G, dorsal antennular peduncle. Holotype ♂, 5.70 mm CL, QM W29094. H, telson, posterior margin and setae. Scale bars = 1 mm.

Diagnosis

Carapace dorsum humped, convex in lateral view. Rostrum short, just reaching to slightly exceeding intermediate segment of antennular peduncle segment; $0.30\text{--}0.60 \times \text{CL}$ ($\bar{x}=0.40$, $n=18$); convex or slightly sinuous; dorsal carina typically unarmed, at most with small postorbital denticle (mode=0, $f=0.89$); ventral carina typically unarmed, at most with one small denticle or tooth (mode=0, $f=0.63$), with double row of plumose setae proximally. Antennal spine poorly to moderately developed (absent on one side in one specimen). Antennular peduncle with small to minute spine on distolateral margin of proximal segment. Scaphocerite $0.45\text{--}0.60 \times \text{CL}$ ($\bar{x}=0.55$, $n=18$), anterior margin produced forward at mesial angle, lateral margin straight or slightly convex. Mandible bearing one-segment palp. Two arthrobranchs (small upper and large lower arthrobranch) at base of third maxilliped. P2 of females and undeveloped males $1.40\text{--}1.90 \times \text{CL}$ ($\bar{x}=1.65$, $n=9$); carpus clearly longer than merus; manus inflated in middle third. Ova size not yet recorded.

Description of holotype male

Acron. Bec ocellaire small, acute.

Carapace. Smooth, glabrous; dorsum humped, convex in lateral view. Rostrum short, $0.45 \times \text{CL}$, reaching middle of intermediate segment of antennular peduncle; slender, maximum depth clearly less than dorso-ventral diameter of cornea; with well developed dorsal, ventral and lateral carinae; dorsal carina setose along most of length; ventral carina unarmed, double row of short plumose setae proximally. Antennal spine poorly developed, situated below and distinct from inferior orbit, marginal; inferior orbital margin moderately produced, postantennular carapace margin evenly rounded; pterygostome evenly rounded.

Antennule. Peduncle length $0.45 \times \text{CL}$, distolateral margin of proximal segment with minute spine.

Antennal somite. Scaphocerite short, $0.55 \times \text{CL}$, lamina widest in proximal half, anterior margin produced forward at mesial angle, lateral margin more or less straight.

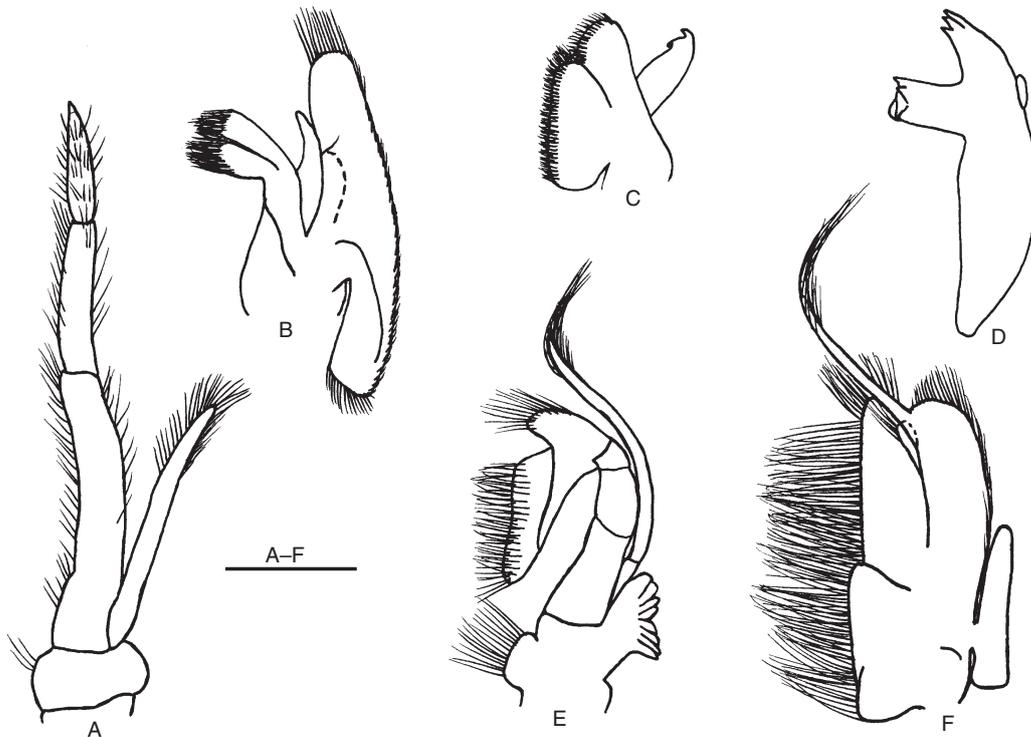


Fig. 13. *Leptopalaemon gibbosus*, sp. nov. Paratype ♂, 5.70 mm CL, QM W26845; A, third maxilliped. B, maxilla. C, maxillula. D, mandible (left). E, second maxilliped. F, first maxilliped, flattened. Scale bar = 1 mm.

Mouthparts. Mandible with one-segment, non-setose palp. Maxillula palp with upper lacinia moderately expanded, with setal rows distally; lower lacinia broad, with dense double row of setae. Maxilla with coxal endite without mesial lobes; distally setose; palp elongate, distally pointed, emarginate, non-setose; scaphognathite with anterior lobe with mesial border deeply notched with distinct fold. First maxilliped with basal and coxal endites distinct, densely setose mesially; palp simple, elongate, proximally fused with basal endite, distal half with short plumose setae along mesial margin; epipod triangular, anterior lobe rounded, posterior lobe rounded. Second maxilliped dactylar segment narrow, mesial border with rows of setae; propodal segment distomesially produced, setose distomesially, distal articular portion narrow; coxal segment with carinate mesial border with numerous long simple setae.

Thoracic sternum. Second sternite armed with large, transverse, triangular plate with blunt apex; third sternite with low transverse ridge with broad shallow median notch; fourth segment with two plates, posterior transverse triangular plate with well developed median notch and anterior slightly raised triangular plate bearing median process.

Branchiae. Two arthrobranchs (small upper and large lower arthrobranch) present on articular membrane at base of third maxilliped.

Second pereopod. Isomorphic; short, $1.70 \times \text{CL}$, distal carpus reaching end of scaphocerite; fingers without gape, cutting edges unarmed; manus slightly longer than fingers, length $2.55 \times \text{max. depth}$, slightly inflated around mid-length;

carpus clearly shorter than chela, moderately long, tapering proximally; merus slightly inflated near mid-length; ischium compressed, slightly tapered proximally.

Third pereopod. Short, reaching to around distal margin of scaphocerite.

Abdomen. Fourth pleura rounded. Fifth pleura without minute posteroventral tooth. Endopod of first pleopod distally rounded, almost ovate. Second pleopod with appendix masculina undeveloped, clearly shorter than endopod.

Telson. Armed with two pairs of minute dorsal spiniform setae; posterior margin angularly sinuous; median process moderately developed, acute; two pairs of long plumose setae between innermost pair of lateral spiniform setae.

Type series variation

Acron. Bec ocellaire small or obsolete (in two paratypes), acute or bluntly angular.

Carapace. Rostrum short, $0.30\text{--}0.60 \text{ CL}$ ($\bar{x}=0.40$, $n=18$; only one specimen above 0.50), just reaching to slightly exceeding intermediate segment of antennular peduncle; dorsal carina convex or slightly sinuous, typically unarmed (one small postorbital denticle in two paratypes); ventral carina reduced or moderately developed, typically unarmed (one minute subapical denticle in one paratype and one small tooth in distal third in three paratypes). Antennal spine poorly to moderately developed (absent on one side in one paratype); postantennular carapace margin evenly rounded or bluntly angular.

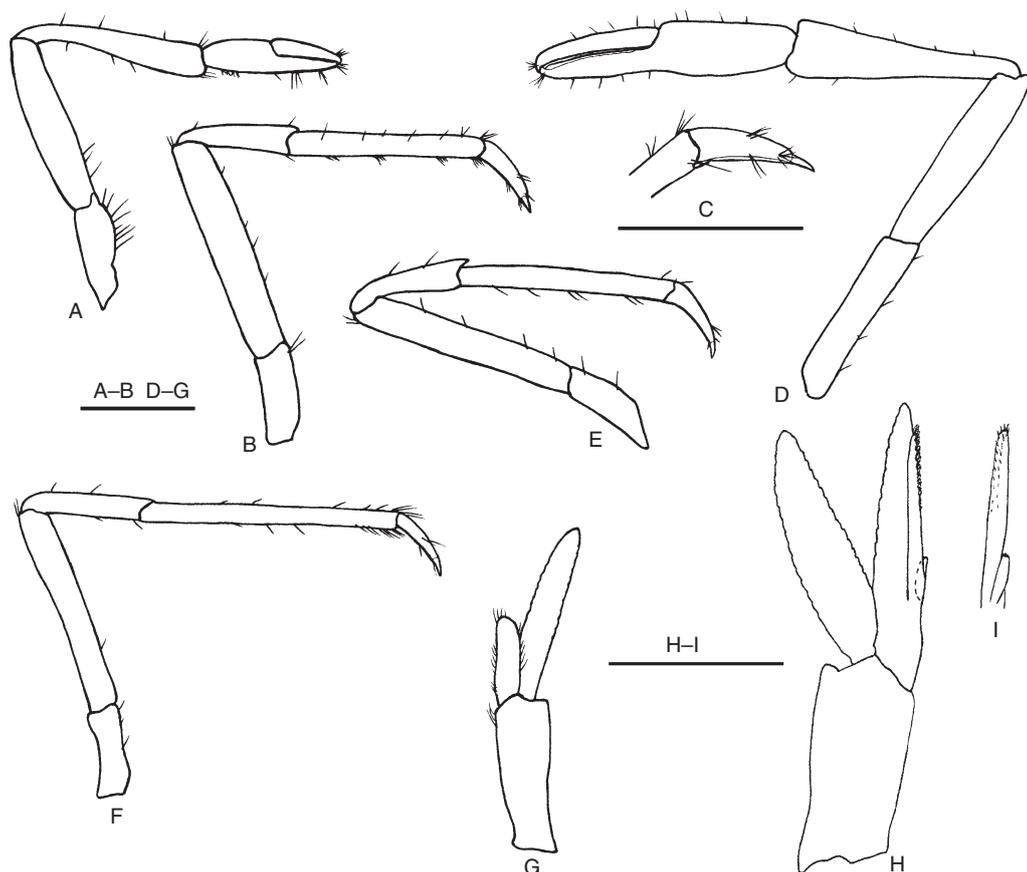


Fig. 14. *Leptopalaemon gibbosus*, sp. nov. Paratype ♂, 5.70 mm CL, QM W26845; A, first pereiopod. B, third pereiopod. C, same, dactylus and distal propodus. D, isomorphic second pereiopod. E, fourth pereiopod. F, fifth pereiopod. G, first pleopod. H, second pleopod. I, mesial view of appendix masculina and appendix interna of same. Scale bars = 1 mm.

Antennule. Peduncle length $0.40\text{--}0.50 \times \text{CL}$ ($\bar{x}=0.45$, $n=18$), distolateral margin of proximal segment with small to minute spine.

Antennal somite. Scaphocerite short to moderately long, $0.45\text{--}0.60 \times \text{CL}$ ($\bar{x}=0.55$, $n=18$).

Second pereiopod. Isomorphic (slightly unequal in size in one paratype); $1.40\text{--}1.90 \times \text{CL}$ in undeveloped male and females ($\bar{x}=1.70$, $n=9$), distal margin or distal 1/4 of carpus reaching distal margin of scaphocerite; generally with manus clearly longer than fingers (slightly longer in some paratypes), length $2.50\text{--}2.90 \times \text{max. depth}$ ($\bar{x}=2.65$, $n=11$), generally with carpus clearly shorter than chela (about equal in length to chela in some paratypes); merus slightly inflated near mid-length or in distal third (one paratype only); ischium untapered to slightly tapered proximally.

Third pereiopod. Typically reaching to around distal margin of scaphocerite (exceeding scaphocerite by $\sim 2/3$ dactylus in one paratype).

Abdomen. Fifth pleura typically without minute posteroventral tooth, with minute tooth in one paratype. Endopod of first male pleopod evenly rounded distally. Appendix masculina on second male pleopod not fully developed in type series, with 11–22 spiniform setae around distal margin of mesial face, increasing in size apically.

Telson. Typically with two pairs of minute dorsal spiniform setae (right posterior seta missing in one paratype; Fig. 12D); posterior margin typically with moderately developed, acute, median process (absent in two paratypes), typically with two pairs of spiniform setae (three pairs progressively increasing in size medially in one aberrant paratype; Fig. 12D), 4–10 plumose setae between innermost lateral spiniform setae.

Ova. Egg size not yet recorded.

Size

Small, maximum length 8.50 mm CL.

Colour

Dark olive brown with light blotches on the dorsal abdomen and between the eyes (Fig. 20A).

Habitat

The habitat of *L. gibbosus*, sp. nov. is similar to that of its congeners in terms of water physicochemistry, hydrology, fringing vegetation and substrates. No fish or other decapod Crustacea were observed at the type locality. The two known localities for the species, sites 4 and 5, are situated at approx. 160–240 m elevation.

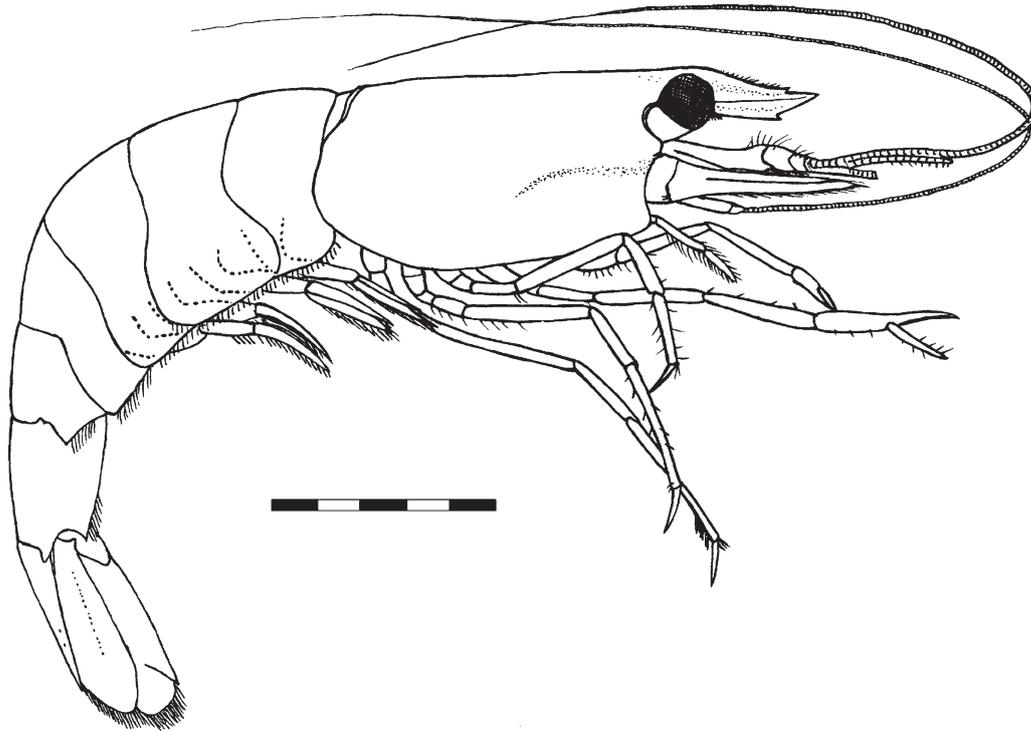


Fig. 15. *Leptopalaemon magelensis*, sp. nov. Holotype ♀, 6.5 mm CL, QM W29092. Scale divisions = 1 mm.

Behaviour

Like its congeners, the species is gregarious, active during daylight, and does not seek shelter when disturbed. Large midwater aggregations, similar to those observed in *L. gagadjuui* and *L. gudjangah*, sp. nov., have been observed and photographed (Fig. 19F).

Etymology

Derived from the Latin adjective, 'gibbosus' (humped) and referring to the humped dorsum of the species.

Distribution

Presently known from two small headwater tributaries of Namarrgon Creek approx. 8 km apart on the Arnhem Land plateau north of Namarrgon Gorge, Kakadu NP, Northern Territory, Australia. The two streams flow independently over the Arnhem Land escarpment and drain into Namarrgon Creek below the escarpment. Namarrgon Creek is a northern arm of Nourlangie Ck, the latter connecting with the upper estuarine reach of the South Alligator River via the Nourlangie floodplain during the wet season.

Proposed common name

Humped Kakadu-shrimp.

Remarks

Although the above description is based on a type series of 19 specimens, including large adult males and females, none of the males appear to have fully developed second pereopods and they

lack the elongated chelae typical of fully developed males in *L. gagadjuui*, *L. glabrus* and *L. gudjangah*, sp. nov.

The two known populations of the species are highly similar in their general morphology but show some divergence in the relative length of the rostrum and scaphocerite. Individuals at site 4 (Fig. 1) generally have a shorter rostrum, $0.32\text{--}0.43 \times \text{CL}$ ($\bar{x}=0.38$, $n=8$) versus $0.39\text{--}0.58 \times \text{CL}$ ($\bar{x}=0.46$, $n=11$; holotype, 0.44) at site 5, although the range of variation overlaps. Similarly, the scaphocerite is generally shorter in individuals at site 4, $0.47\text{--}0.53 \times \text{CL}$ ($\bar{x}=0.50$, $n=8$) versus $0.50\text{--}0.58 \times \text{CL}$ ($\bar{x}=0.55$, $n=10$, holotype = 0.55) at site 5. This degree of morphological divergence is consistent with the findings of the molecular study (Page *et al.* 2008), which, although placing both sites in a strongly supported terminal clade in all of the analyses, found no shared haplotypes between the two sites, indicative of a lack of contemporary gene flow.

The new species most closely resembles *L. gudjangah*, sp. nov. from the Oenpelli outlier approx. 50 km to the north-east in the East Alligator River catchment. Although the two species are well isolated geographically, they are highly cryptic in morphology and only differ significantly in the shape of the dorsal carapace and their live colouration. In the present species, the dorsum of the carapace is strongly humped and distinctly convex in lateral view (Figs 6G–L, 11), whereas in *L. gudjangah*, sp. nov., the dorsum of the carapace is typically flat and more or less straight in lateral view (Figs 6A–F, 7). In *L. gibbosus*, sp. nov. the general body colour is also a dark olive brown and there are distinctive light blotches on the dorsal abdomen and on the acron between the eyes whereas *L. gudjangah*, sp. nov. is translucent and indistinctly speckled.

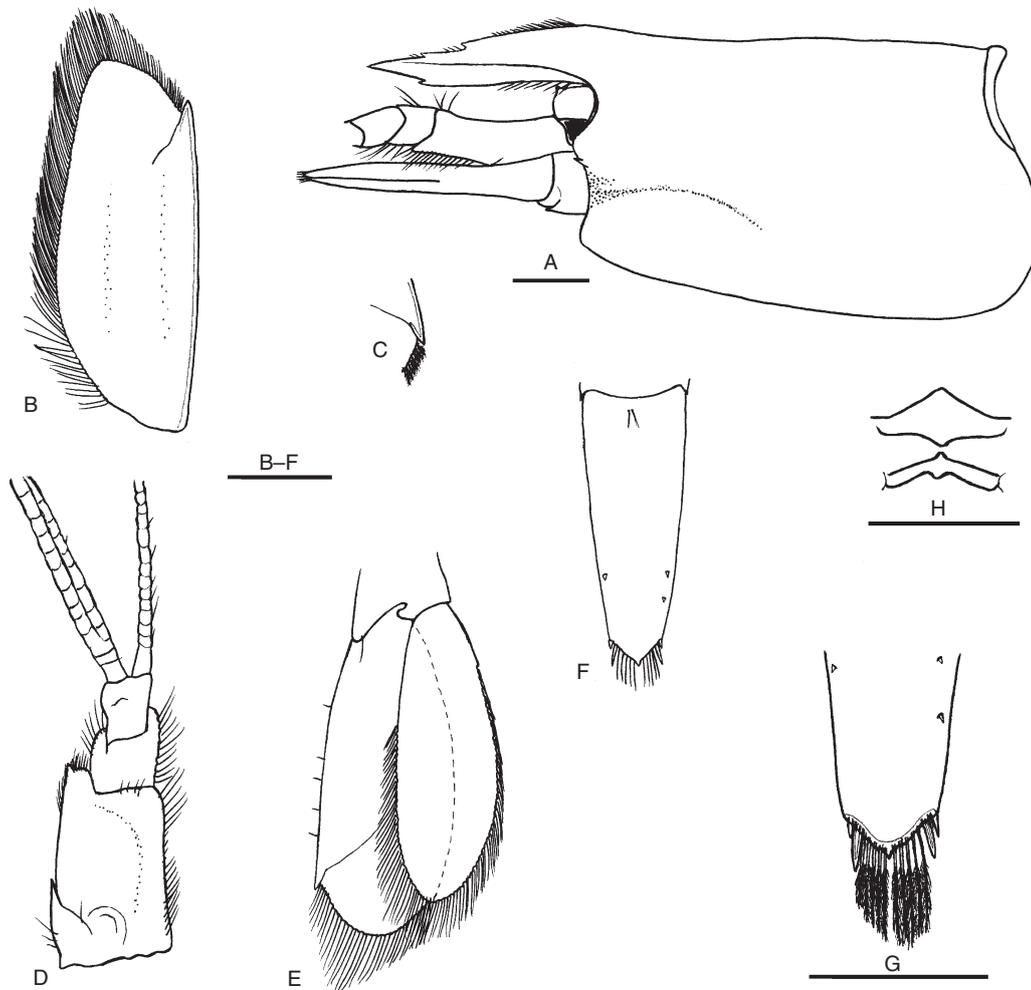


Fig. 16. *Leptopalaemon magelensis*, sp. nov. Allotype ♂, 5.75 mm CL, QM W29093; A, lateral view of cephalothorax with eye removed to show bec ocellaire. B, dorsal view of scaphocerite. C, distolateral tooth on uropodal exopod. D, dorsal antennular peduncle. E, uropod. F, telson. G, same, posterior margin and setae. H, thoracic sternites 2–4, ventroposterior view. Scale bars = 1 mm.

In contrast to morphology, the COI data from the molecular study (Page *et al.* 2008) did not provide strong evidence of a close relationship between *L. gudjangah*, sp. nov. (= *Leptopalaemon* sp. 1 of Page *et al.* 2008) and *L. gibbosus*, sp. nov. (= *Leptopalaemon* sp. 3 of Page *et al.* 2008).

***Leptopalaemon magelensis*, sp. nov.**

(Figs 1, 4A–E, 15–18, 19B; Table 2, 4)

Leptopalaemon sp. 2 Page *et al.*, 2008: 1006.

Material examined

Holotype. QM W29092, ♀ (6.50 mm CL), site 3, upper south arm of Magela Creek, Kakadu NP, N.T., Australia, 12°48.6' S, 132°59.8' E, K. McAlpine, 17.ix.1998.

Allotype. QM W29093, ♂ (5.75 mm CL), same collection data as holotype.

Paratypes. QM W24748, 1♂ (5.50 mm CL), 3♀ (5.60–6.70 mm CL), same collection data as holotype; MAGNT Cr017060, 12♂ (3.80–6.00 mm CL), 5♀ (4.80–6.50 mm CL), site 15, south arm of Magela Creek, Kakadu NP, N.T., Australia, 12°48.1' S, 132°59.6' E, A. Cameron, 16.viii.2004.

Diagnosis

Carapace dorsum flat, appearing more or less straight in lateral view. Rostrum of short to medium length, reaching from distal margin of intermediate segment of antennular peduncle to slightly exceeding antennular peduncle, $0.50\text{--}0.70 \times \text{CL}$ ($\bar{x}=0.60$, $n=24$); typically slightly sinuous (strongly sinuous in one paratype); dorsal carina with 1–4 teeth (mode=2, $f=0.50$), ventral carina with 0–2 teeth (mode=1, $f=0.63$), with double row of plumose setae proximally. Antennular spine absent or poorly developed. Antennular peduncle with small spine on distolateral margin of proximal segment. Scaphocerite $0.60\text{--}0.70 \times \text{CL}$ ($\bar{x}=0.65$, $n=10$), anterior margin produced forward at mesial angle, lateral margin straight or slightly convex. Mandible

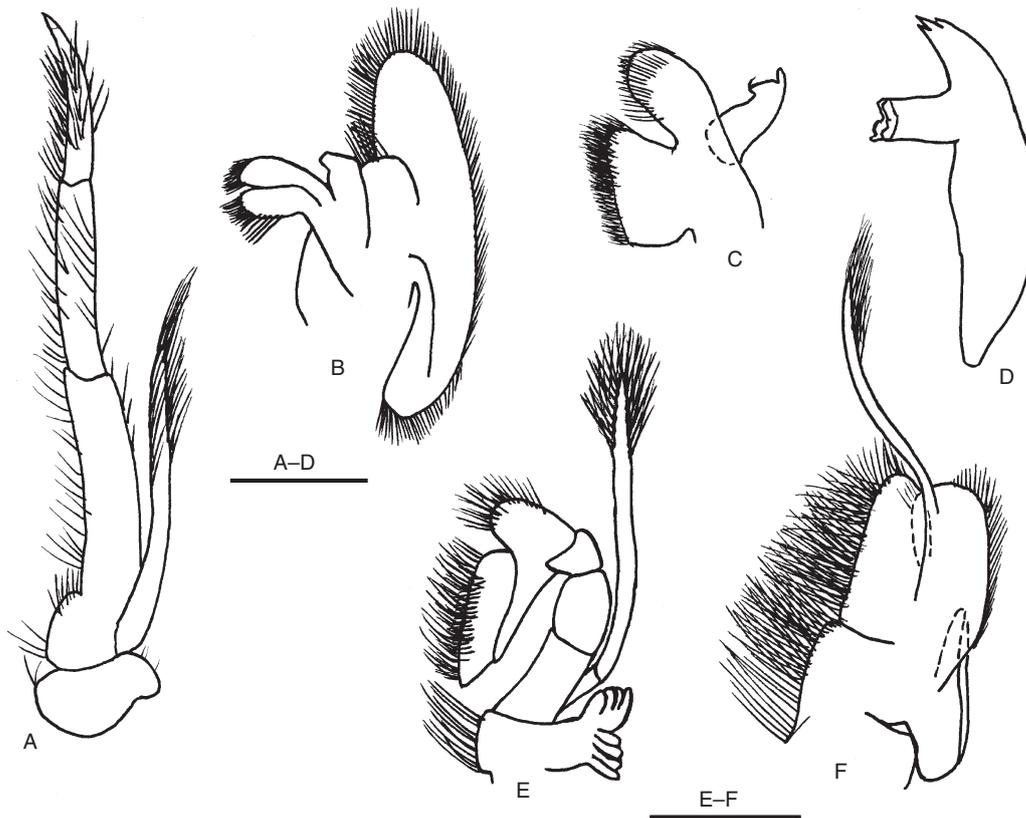


Fig. 17. *Leptopalaemon magelensis*, sp. nov. Allotype ♂, 5.75 mm CL, QM W29093; A, third maxilliped. B, maxilla. C, maxillula. D, mandible (left). E, second maxilliped. F, first maxilliped, flattened. Scale bars = 1 mm.

without palp. Two arthrobranchs (small upper and large lower arthrobranch) present on articular membrane at base of third maxilliped. P2 of undeveloped males and females $1.55\text{--}1.90 \times \text{CL}$ ($\bar{x} = 1.75$, $n = 14$); carpus clearly longer than merus; manus subcylindrical to moderately inflated. Size of ova not yet recorded.

Description of holotype female

Acron. Bec ocellaire small, acute.

Carapace. Dorsum flat, more or less straight in lateral view. Rostrum of medium length, $0.60 \times \text{CL}$, just over-reaching antennular peduncle; slender, maximum depth clearly less than dorso-ventral diameter of cornea; with well developed dorsal and lateral carinae, ventral carina moderately developed; dorsal carina slightly sinuous, dentate in distal half, single immovable preorbital tooth, setose along most of length; ventral carina dentate, single tooth in distal half, double row of short plumose setae proximally. Antennal spine absent on left side, poorly developed on right side, situated below and distinct from inferior orbit, marginal. Inferior orbital margin moderately produced, bluntly angular. Pterygostome bluntly angular.

Antennule. Peduncle length $0.50 \times \text{CL}$, distolateral margin of proximal segment with small spine.

Antennal somite. Scaphocerite short, $0.60 \times \text{CL}$, lamina widest in proximal half, anterior margin produced forward at mesial angle, lateral margin more or less straight.

Mouthparts. Mandible without palp. Maxillula upper lacinia moderately expanded, with rows of setae distally; lower lacinia broad, distally with dense double row of setae. Maxilla coxal endite without mesial lobes; distally setose; palp short broad, distally emarginate, non-setose; scaphognathite anterior lobe with mesial border deeply notched with distinct fold. First maxilliped with basal and coxal endites distinct; basal endite with mesial margin with rows of long setae; coxal endite with rows of similar setae distally, single row of long setae proximally; palp simple, elongate, proximally fused with basal endite, distal half with several short plumose setae along mesial margin; epipod triangular, anterior lobe acutely pointed, posterior lobe rounded. Second maxilliped dactylar segment narrow, mesial border with rows of setae; propodal segment distomesially produced, setose distomesially, distal articular portion narrow; coxal segment with carinate mesial border with numerous long simple setae.

Thoracic sternum. Second sternite armed with large, transverse, triangular plate, acute; third sternite armed with low transverse ridge with shallow to moderately defined median notch; fourth segment armed with two plates, posterior transverse triangular plate with small median notch and anterior slightly raised triangular plate.

Branchiae. Two arthrobranchs (small upper and large lower arthrobranch) present on articular membrane at base of third maxilliped

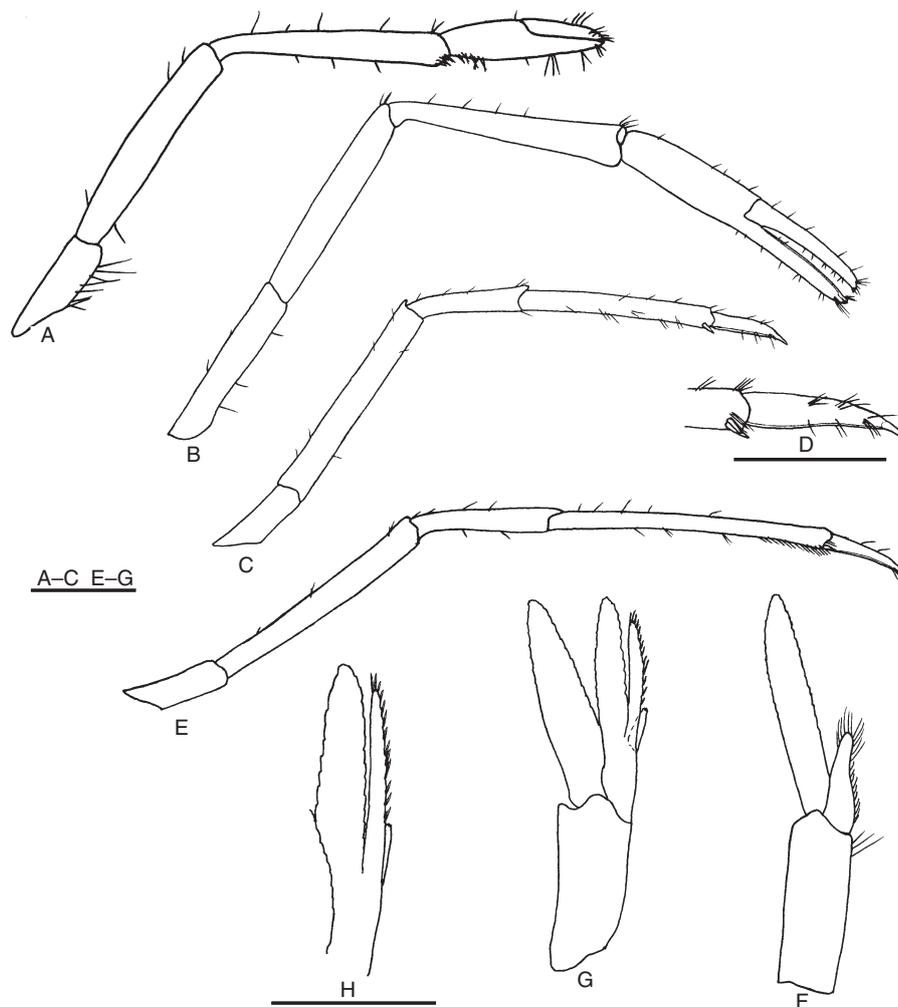


Fig. 18. *Leptopalaemon magelensis*, sp. nov. Allotype ♂, 5.75 mm CL, QM W29093; A, first pereiopod. B, isomorphic second pereiopod. C, third pereiopod. D, same, dactylus and distal propodus. E, fifth pereiopod. F, first pleopod. G, second pleopod. H, same, endopod. Scale bars = 1 mm.

Second pereiopod. Isomorphic in shape, subequal in size; short, minor P2 $1.55 \times$ CL, major P2 $1.85 \times$ CL, exceeding scaphocerite by half propodus; finger tips minutely spatulate distally, with feeble unarmed lateral cutting edge and small acute hooked tips; fingers without gape, cutting edges unarmed; manus slightly longer than fingers, length $3.05 \times$ max. depth, subcylindrical, slightly inflated near mid-length; carpus clearly shorter than chela, moderately long, tapering proximally; merus slightly inflated near mid-length; ischium compressed, slightly tapered proximally.

Third pereiopod. Short, reaching to about distal margin of scaphocerite.

Abdomen. Fourth pleura bluntly angular. Fifth pleura with minute posteroventral tooth. Endopod of first pleopod distally ovate.

Telson. Armed with two pairs of small to minute dorsal spiniform setae; posterior margin angularly sinuous, moderately developed acute median process, five pairs of long plumose setae between innermost pair of lateral spiniform setae.

Ova. Size of ova not yet recorded.

Type series variation

Carapace. Rostrum of short to medium length, $0.50\text{--}0.70 \times$ CL ($\bar{x} = 0.60$, $n = 24$), reaching from distal margin of intermediate segment of antennular peduncle to slightly exceeding antennular peduncle; ventral carina poorly to moderately developed; generally with dorsal carina slightly sinuous (strongly sinuous in one paratype); 1–4 dorsal teeth (mode = 2, $f = 0.50$); four teeth plus two minute distal denticles in one paratype); ventral carina unarmed or dentate, 0–2 teeth (mode = 1, $f = 0.63$). Antennal spine absent or poorly developed (asymmetrically developed in allotype male and 10 of 14 paratypes). Inferior orbital margin evenly rounded in allotype male.

Antennule. Peduncle length $0.45\text{--}0.55 \times$ CL ($\bar{x} = 0.50$, $n = 10$).

Antennal somite. Scaphocerite short to moderately long, $0.60\text{--}0.70 \times$ CL ($\bar{x} = 0.65$, $n = 10$).

Thoracic sternum. Transverse, triangular plate on second sternite typically acute (bluntly pointed in allotype male and one paratype); anterior plate on fourth segment armed typically



Fig. 19. A, Site 4, small headwater tributary of Namarrgon Creek north of Namarrgon Gorge, approx. 8 km N of Site 5, Arnhem Land plateau, habitat of *L. gibbosus*, sp. nov. (photo: G. Spiers); B, Upper south arm of Magela Creek, habitat of *L. magelensis*, sp. nov. (photo: C. L. Humphrey); C, aerial view of habitat of *L. gudjangah*, sp. nov. upstream of type locality (photo: J. Matthews); D, Site 5, small headwater tributary of Namarrgon Creek north of Namarrgon Gorge, type locality of *L. gibbosus*, sp. nov. (photo: G. Spiers); E, Site 2, type locality of *L. gudjangah*, sp. nov. (photo: J. W. Short); F, midwater aggregation of *L. gibbosus*, sp. nov. at the type locality (photo: G. Miles); G, small side pool above main watercourse of lower Lightning Dreaming Creek, habitat of *L. gagadju* Bruce & Short, 1993 (photo: J. W. Short).

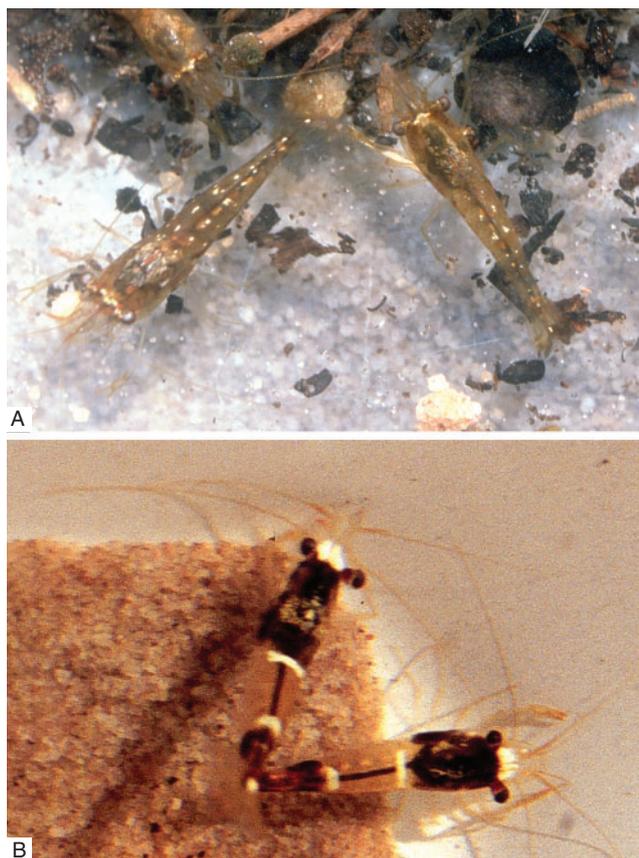


Fig. 20. A, live colouration of *L. gibbosus*, sp. nov. (photo: G. Miles); B, live colouration of *L. glabrus* (Bruce, 1993) (photo: C. L. Humphrey).

without median process (present in allotype male and one paratype).

Second pereopod. Typically isomorphic (subequal in size in some paratypes); $1.55\text{--}1.90 \times \text{CL}$ ($\bar{x} = 1.75$, $n = 14$); distal carpus reaching distal end of scaphocerite; manus length $2.90\text{--}3.35 \times \text{max. depth}$ ($\bar{x} = 3.05$, $n = 11$).

Abdomen. Fifth pleura typically with minute posteroventral tooth (absent in one paratype). Endopod of first pleopod distally rounded in allotype male. Appendix masculina on second male pleopod clearly shorter than endopod, with 13–18 spiniform setae around distal margin of mesial face, setae increasing in size apically.

Telson. Left distalmost dorsal spiniform seta absent in allotype male.

Ova. Size of ova not yet recorded.

Size

Small, maximum length 6.70 mm CL.

Colour

Iridescent in the water with patches of colour (K. McAlpine, pers. comm.).

Habitat

The upper south arm of Magela Creek is well isolated from other tributaries of Magela Creek and drains an area of the Arnhem Land plateau bordered by sheer escarpments to the north and west. Only one other species of freshwater shrimp, *Macrobrachium bullatum* Fincham, 1987, is present. There are no large predatory fish, e.g. grunters (Teraponidae). In terms of microclimate, substrates, flow regime, water physicochemistry and fringing vegetation, the upper south of Magela Creek is similar to localities inhabited by other species of the genus. Apart from the two collection dates listed above, the upper south arm of Magela Creek was also visited on 15 December 2003, following early wet season rains and stream flows. Despite an intensive search, only *M. bullatum* was found on that occasion, suggesting *L. magelensis*, sp. nov. (and possibly species of *Leptopalaemon* in general) display behavioural traits during the wet season that prevent them being washed downstream during seasonal flooding events.

Etymology

Derived from Magela Creek. The species is restricted to the upper south arm of the Magela Creek catchment.

Distribution

Presently known from two localities ~1 km apart on the upper south arm of Magela Creek, East Alligator River catchment, Kakadu NP, the Northern Territory, Australia. Both localities are at an elevation of approx. 100 m and lie near the eastern boundary of Kakadu NP. The south arm of Magela Creek feeds into the main branch of Magela Creek, which is connected during the wet season with the mid-estuarine reach of the East Alligator River via the Magela floodplain.

Proposed common name

Magela shrimp.

Remarks

Although the above description is based on a type series of 24 specimens, including large adult males and females, none of the males have the elongated second chelae typical of fully developed males in *L. gagadjuui*, *L. glabrus* and *L. gudjangah*, sp. nov.

The new species most closely resembles *L. gagadjuui*, but differs in lacking a mandibular palp and in having a shorter rostrum that at most reaches to around the distal margin of the antennular peduncle versus to the distal margin of the scaphocerite in the latter species. The present species also has only 1–4 well developed teeth on the dorsal rostrum versus 5–10 well developed teeth in *L. gagadjuui*. In general, the antennal spine is also less developed than in *L. gagadjuui*.

In contrast to the morphological resemblance to *L. gagadjuui*, the molecular data (Page *et al.* 2008) indicated a close genetic relationship to the geographically proximate, *L. gibbosus*, sp. nov. (= *Leptopalaemon* sp. 3 of Page *et al.* 2008). The latter species is known from adjacent areas to the immediate south on the Arnhem Land plateau and has been recorded as close as 2 km to the type locality of the present species. Despite their close proximity, the two species are separated geographically by the

drainage divide between the South and East Alligator River catchments.

A key to the species of *Leptopalaemon* currently recognised is provided below. Due to the high variability and regressive trend shown by most of the key characters, some caution should be exercised when using the key. Species identifications made using the key should be verified using the relevant species diagnosis, geographic distribution and, where available, notes on live colouration. Species of the genus may also be confused with juveniles of *Macrobrachium bullatum*, which occurs sympatrically at several locations, but can easily be distinguished by the lack of a hepatic spine.

Key to *Leptopalaemon* species

1. Rostrum with five or more well developed dorsal teeth (Fig. 4F–J), long, reaching to about distal margin of scaphocerite, always clearly over-reaching antennular peduncle..... *L. gagadju*
Rostrum with less than five well developed dorsal teeth (Figs 4A–E, 6A–R), of short to medium length, clearly shorter than scaphocerite, at most just over-reaching antennular peduncle (Figs 7, 8F, 11, 12A, 15, 16A)...2
2. Rostrum with dorsal and ventral teeth (Fig. 4A–E).....
..... *L. magelensis*, sp. nov.
Rostrum typically without teeth, never with both dorsal and ventral teeth (occasionally with either a single dorsal tooth or a single ventral tooth) (Fig. 6A–R)..... 3
3. One arthrobranch at base of third maxilliped; live specimens with four, large, white bands on dorsum of body (Fig. 20B)..... *L. glabrus*
Two arthrobranches (large, lower arthrobranch and small, upper arthrobranch behind larger arthrobranch) on articular membrane at base of third maxilliped; live specimens without large white bands on dorsum of body, at most with small light blotches..... 4
4. Dorsum of carapace humped (Figs 6G–L, 11, 12A); live specimens dark olive brown with light blotches between the eyes and on the dorsal abdomen (Fig. 20A)..... *L. gibbosus*, sp. nov.
Dorsum of carapace not humped (Figs 6A–F, 7, 8F); live specimens translucent and indistinctly speckled..... *L. gudjangah*, sp. nov.

Discussion

The genus *Leptopalaemon* now comprises five species, all endemic to the western half of the Arnhem Land plateau/escarpment complex and immediate surrounds in northern Australia. This area lies largely within the broader Kakadu region, as defined by Finlayson *et al.* (2006). The only record of the genus outside the Kakadu region is from the upper Mann River immediately to the east.

Within the Kakadu region, distributional records of *Leptopalaemon* are predominantly from the north-west rim of the Arnhem Land plateau/escarpment complex, an area that is also a hotspot for species diversity in another freshwater macrocrustacean group, the isopod genus *Eophreatoicus* (Wilson *et al.* 2009), as well as for terrestrial plants (Woinarski *et al.* 2006). The high levels of endemism and species diversity on the north-west rim have been attributed to multiple factors:

- (1) The highly dissected nature, complex topography and general isolation of the Mamadawerre sandstone formations (Woinarski *et al.* 2006);

Table 4. Sequences of *Leptopalaemon* currently available on GenBank (15 August 2012)

All sequences from Page *et al.* (2008) except those marked with * (from Bracken *et al.*, 2009)

Species	Gene	GenBank Accession Number
<i>L. gagadju</i> Bruce & Short, 1993	COI	EF588279–EF588282, EF588285–EF588290, EF588296
	16S	EF588304–EF588309, EF588314–EF588315, EU868693*
	18S	EF588298, EU868787*
	28S	EF588299–EF588300, EF588302–EF588303
<i>L. gibbosus</i> , sp. nov.	COI	EF588291–EF588293
	16S	EF588312–EF588313
	18S	EF588297
	28S	EF588301, EU249465
	H3	EU249459
<i>L. glabrus</i> (Bruce, 1993)	COI	EF588295
	16S	EF588318
	18S	EU249463
	28S	EU249464
	H3	EU249461
<i>L. gudjangah</i> , sp. nov.	COI	EF588283–EF588284
	16S	EF588310
<i>L. magelensis</i> , sp. nov.	COI	EF588294
	16S	EF588311

- (2) The geological stability of the area (further south the plateau has eroded much more quickly) and recent immunity to major climatic and sea level variation (Wilson *et al.* 2009); and
- (3) Relatively elevated topography and higher rainfall compared with areas to the south and east (Wilson *et al.* 2009) resulting in more reliable dry season surface water.

Apart from one wide-ranging species, *L. gagadju*, *Leptopalaemon* is characterised by narrow-range endemism, similar to that reported for *Eophreatoicus* by Wilson *et al.* (2009). Of the four highly localised species, three are each confined to a single stream and have longitudinal distributions of 2 km or less during the dry season. All *Leptopalaemon* species are highly reliant on spring-fed permanent pools, which act as refugia during the extended dry season. The availability of permanent water largely determines the distribution of the genus on the Arnhem Land plateau/escarpment complex.

The evolution of *Leptopalaemon* appears to have been strongly influenced by the presence or absence of predatory fish and to a lesser degree, opportunistically feeding shrimps of the genus *Macrobrachium*. Most of the streams where *Leptopalaemon* have been collected on the Arnhem Land plateau/escarpment complex have highly depauperate fish faunas or are totally devoid of fish. Similarly, the north-west Australian river prawn, *Macrobrachium bullatum*, a common inhabitant of headwater streams in the Northern Territory and potential predator/competitor of *Leptopalaemon*, is often absent in streams where there are no fish.

Species occurring where fish, and to a lesser degree *Macrobrachium*, are absent show a regressive trend in the development of the rostrum, second chelipeds, antennal spine and spiniform setae on the dorsal telson. These features would be expected to have an important defensive role in freshwater shrimps, with the possible exception of the dorsal spiniform setae on the telson. In *Leptopalaemon*, which are highly gregarious and lack well developed agonistic behaviour, they would be largely redundant where aquatic predators/competitors are absent.

In general, these regressive characters also displayed a higher degree of infraspecific variation than normally encountered in other freshwater palaemonid shrimps. Some characters, such as the development of the antennal spine and, to a lesser extent, the development of the dorsal spiniform setae on the telson, also showed a significant degree of asymmetric variation.

Strong correlations between the development of defensive cuticular structures or appendages and the presence or absence of predatory freshwater fishes have been documented elsewhere for freshwater caridean shrimps and insect larvae. Covich *et al.* (2009) identified large infraspecific variation in rostrum length in the Caribbean shrimp, *Xiphocaris elongata* (Guérin-Méneville, 1855), associated with the presence or absence of fish predators. Similarly, Mikolajewski and Johansson (2004) discussed the development of abdominal spines in species of freshwater dragonfly larvae associated with the presence or absence of fishes. Increased rostral length and dentition in the cavernicolous atyid shrimps of the genus *Troglocaris* in response to the presence of an amphibian predator, *Proteus anguinus*, has also been reported by Jugovic *et al.* (2010).

Other than regressive characters, there were few morphological features that were useful for discriminating species of *Leptopalaemon*. As a result, revising the systematics of the group proved to be highly challenging. The molecular data and analyses (Page *et al.* 2008; *Leptopalaemon* sequences currently available on GenBank as of 15 August 2012 listed in Table 4) were helpful in establishing the age of the group, elucidating relationships within the Palaemonoidea and revealing cryptic speciation, but were sometimes inconclusive regarding the relationships between putative species and genera. In particular, the DNA barcode approach, as an objective method for defining species and genera (Hebert and Gregory 2005), was found to be ineffective for the study group (Page *et al.* 2008).

Net divergence estimates from the molecular study (Page *et al.* 2008) using the 16S gene fragment, placed the split between *L. glabrus* (as *K. glabra*) and the lineage including the remaining species in the late Miocene/Pliocene. This time period has been shown to be highly significant in the evolution of the northern Australian freshwater shrimp fauna (*Macrobrachium*: Short 2000; Murphy and Austin 2005; de Bruyn *et al.* 2004; *Caridina*: Chenoweth and Hughes 2003; Page *et al.* 2007; *Paratya*: Cook *et al.* 2006) and coincides with initial contact between the northern edge of the Australian continent plate and the Sunda Arcs in the mid-Miocene 10–15 mya (Powell *et al.* 1981; Archer *et al.* 1991).

Another important geological event following first contact between Australia and Asia was the development of the central highlands of New Guinea during the Pliocene (Raven and

Axelrod 1972; Flannery 1990). Within far northern Australia, the late Miocene/early Pliocene also coincided with the development of a monsoonal climate and marked rainfall seasonality (Russell-Smith *et al.* 1995) as discussed by Wilson *et al.* (2009) in regard to the rapid radiation of *Eophreatoicus* in the Kakadu region.

The close association of the genus with the stone country of the Kakadu region, and the narrow range endemism of four of the five species of *Leptopalaemon*, highlight the high conservation value of the group. Even the relatively wide-ranging species *L. gagadjui* appears to comprise highly isolated populations with limited contemporary gene flow (Page *et al.* 2008). Dry season refugia, in particular, represent key *Leptopalaemon* habitats in need of management and protection. Habitats of four of the five species currently have a degree of protection from anthropic disturbance within the confines of Kakadu NP. The remaining species, *L. gudjangah*, sp. nov., occurs in the proposed Warddeken Indigenous Protected Area. A management plan for the area is currently under development (Northern Territory Government, Department of Natural Resources, Environment, The Arts and Sport 2009). Despite the relatively low risk of anthropic disturbance, the four highly localised species remain highly vulnerable to other foreseeable threats, such as the recent invasion of cane toads, *Bufo marinus*, into the Kakadu region (van Dam *et al.* 2002) and the long-term effects of climate change.

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