

Leptopalaemon gagadju* gen. nov., sp. nov., a new freshwater palaemonid shrimp from Arnhem land, and a re-evaluation of *Palaemonetes holthuisi* Strenth, with the designation of a new genus, *Calathaemon

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Abstract

A new palaemonid shrimp, *Leptopalaemon gagadju*, gen. nov., sp. nov., from the Arnhem Land plateau, Australia, is described and illustrated, and its systematic position discussed. The new genus most closely resembles *Leptocarpus* Holthuis, 1950, presently known only from India. *Palaemonetes holthuisi* Strenth is re-examined and excluded from the genus *Palaemonetes*. A new genus, *Calathaemon*, is designated for its accommodation.

Introduction

The freshwater caridean fauna of Australia is represented, as elsewhere, mainly by shrimps of the families Atyidae and Palaemonidae. Of the latter family, only one genus, *Macrobrachium* Bate, 1868, has been extensively reported from Australian freshwaters, with *Palaemonetes* Heller, 1869, and *Leandrites* Holthuis, 1950, occurring mainly in brackish waters, all genera with wide extra-Australian distributions, particularly in tropical regions. The discovery of a second genus in Australian freshwaters is therefore of interest. As *Palaemonetes holthuisi* Strenth appeared to have some similarities to *Leptopalaemon gagadju*, this

taxon was re-examined and a new genus is now designated for its inclusion.

Systematics

Leptopalaemon gen. nov.

Diagnosis

Small, slenderly built shrimps of subcylindrical body form; rostrum well developed, compressed, dorsal and ventral carinae dentate; carapace smooth, glabrous, supraorbital, epigastric and hepatic spines absent, orbit feebly developed, inferior orbital angle produced, antennal spine distinct,

branchiostegal and pterygostomial spines absent; branchiostegal suture absent, sulcus present, anterolateral angle rounded; abdomen smooth, glabrous, first to third pleura rounded, fourth and fifth pleura bluntly angular; telson with two pairs of dorsal spines, two pairs of posterior spines, central posterior margin setose; ophthalmic segment with 'bec ocellaire', upper antennular flagellum biramous, with rami fused proximally, epistome normal; mandible with 1-segmented palp, molar and incisor processes normal, metastoma with paragnaths proximally fused, forming 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, laciniae normal, lower lacinia broad; maxilla with broad palp, basal and coxal endites distinct, basal endite deeply bilobed, scaphognathite well developed, anterior lobe emarginate, plicate; first maxilliped with simple palp, basal endite elongate, coxal endite distinct, both with medial borders densely setose, exopod with large caridean lobe, epipod large, triangular; second maxilliped with dactylar segment narrow, propodal segment distomedially produced, coxal segment with setose medial carina, epipod with small podobranch; third maxilliped endopod moderately slender, coxa with small lateral plate, small, well developed outer arthrobranch and reduced inner arthrobranch; all maxillipeds with flagella of exopods densely setose distally. Fourth thoracic sternite without median process, with transverse triangular plate. Pereiopods without exopods. First pereiopods slender, chelate, fingers with minutely spatulate tips. Second pereiopods slender, distinctly more robust than first pereiopods, subequal and similar, or slightly unequal, dissimilar, chela with fingers unarmed, with small spatulate tips. Ambulatory pereiopods slender, dactyls simple. Second to fifth pleopods with appendix interna; male second pleopod endopod with elongate spinose subcylindrical appendix masculina. Exopod of uropod with distolateral tooth, without mobile spine medially.

Type species

Leptopalaemon gagadjuj, sp. nov.

Etymology

From 'leptos', Greek, smooth, and *Palaemon*, a generic name, first used by Weber, 1795. Gender: masculine.

Systematic Position

Leptopalaemon gen. nov., shows a general similarity to *Leptocarpus* Holthuis, 1950, rather than any other genus of the Palaemoninae, having the following features in common: rostrum well developed, slender, exceeding scaphocerite; carapace without supraorbital, hepatic and branchiostegal spines, antennal spine present; mandible with palp; second pereiopods slender, smooth, with carpus longer than chela; ambulatory pereiopods with simple dactyls. *Leptopalaemon* differs from *Leptocarpus* in lacking a slender median process on the fourth thoracic sternite and a distinct branchiostegal suture. It also lacks a markedly elevated basal rostral carina and has much more strongly developed second pereiopods. *Leptopalaemon* also shows some similarities to *Trogilindicus*, known only from a single species, *T. phreaticus*, described by Sankolli & Shenoy (1979). This genus may be distinguished from *Leptopalaemon* by the absence of a mandibular palp, coxal and basal endites of second maxillipeds without dense double fringe of long medial marginal setae, second pereiopods well developed, robust. Associated with its troglobitic habitat, the eye is greatly reduced, the obsolete cornea having only a small pigment spot, and the rostrum is also reduced, slightly exceeding the distal margin of the eye stalk.

Apart from its distinctive mouthparts, *Leptopalaemon* also shows a general resemblance to *Palaemon* Weber, 1875, but may be readily distinguished from that genus by the presence of a branchiostegal spine in all *Palaemon* species. The mouthparts of *Palaemon* species are similar to those of 'typical' palaemonine genera, such as *Leander* Desmarest, 1849, *Palaemonetes* Heller, 1869, or *Macrobrachium* Bate, 1868.

Remarks

The genus *Leptocarpus* is known only from India, Andaman Islands, Thailand, Malaya Java and Sumatra, from salt water, brackish and freshwater habitats. *Troglindicus phreaticus* is known only from its type locality.

Leptopalaemon gagadjui sp. nov. Figs 1–6*Material examined*

4 male, Barramundi Creek, Kakadu National Park, Northern Territory, 13° 20' S, 132° 27' E, 28 October 1984, coll. B. C. Russell; NTM.

Cr. 002013. 30 male, 8 female (7 ovig.), 23 immature, escarpment stream between Saw Cut Gorge and Deaf Adder Creek, Arnhem Land, Northern Territory, 21 February 1980, coll. P. Outridge, QM W16540–16544, (2 spms. NTM. Cr. 007569). 2 male, 7 female, Barramundi Creek, 22 June 1990, coll. J. Short, I. Brown, QM W16550. 1 female, ovig., 2 female, Graveside Gorge, 13° 18' S, 132° 34' E, 19 August 1990, coll. I. Brown, QM W16655. 1 male, 2 female, 1 immature, Whistle Wood Creek, S. of Twin Falls, Kakadu National Park, 5 August 1984, coll. H. E. Allison. 3 immature, Cooper Creek, Arnhem Land, 26 June 1984, coll. H. E. Allison.

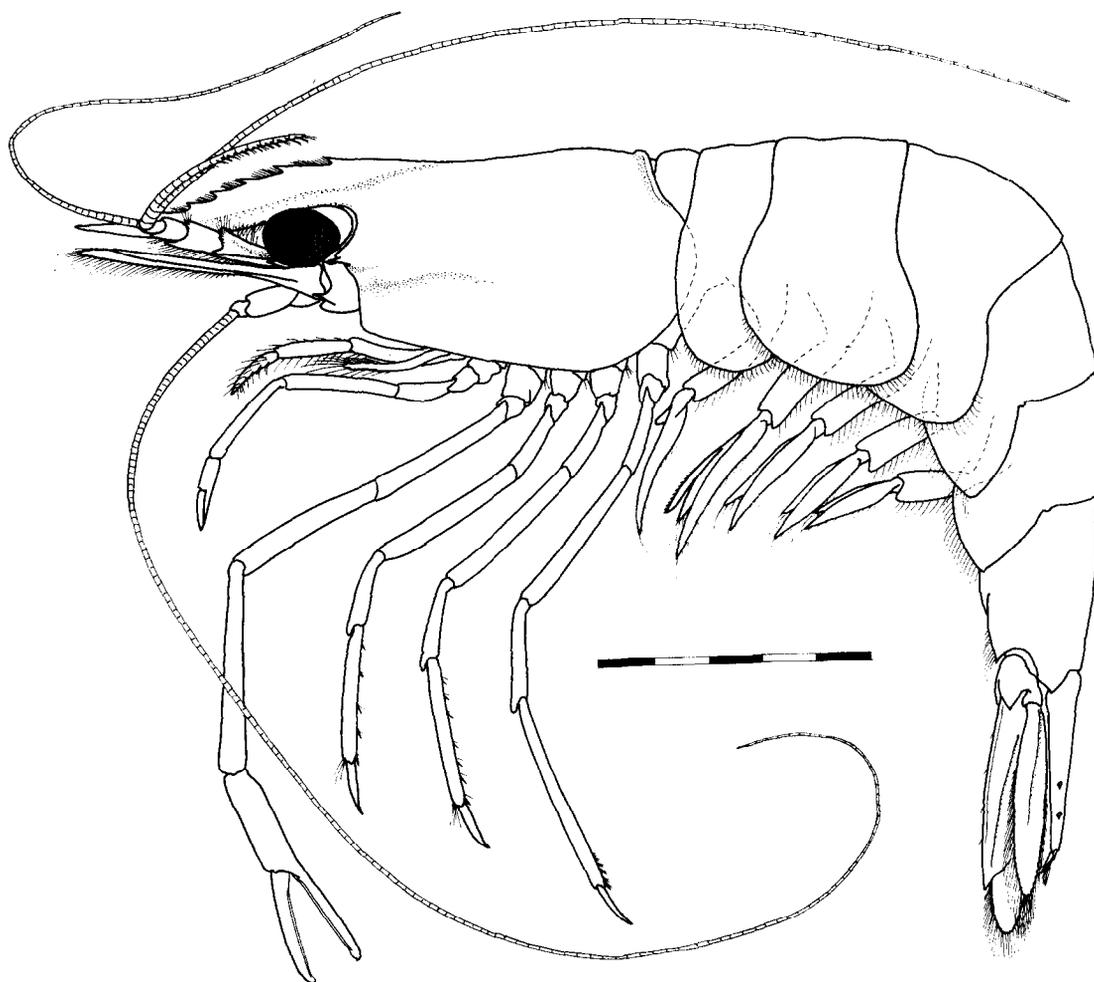
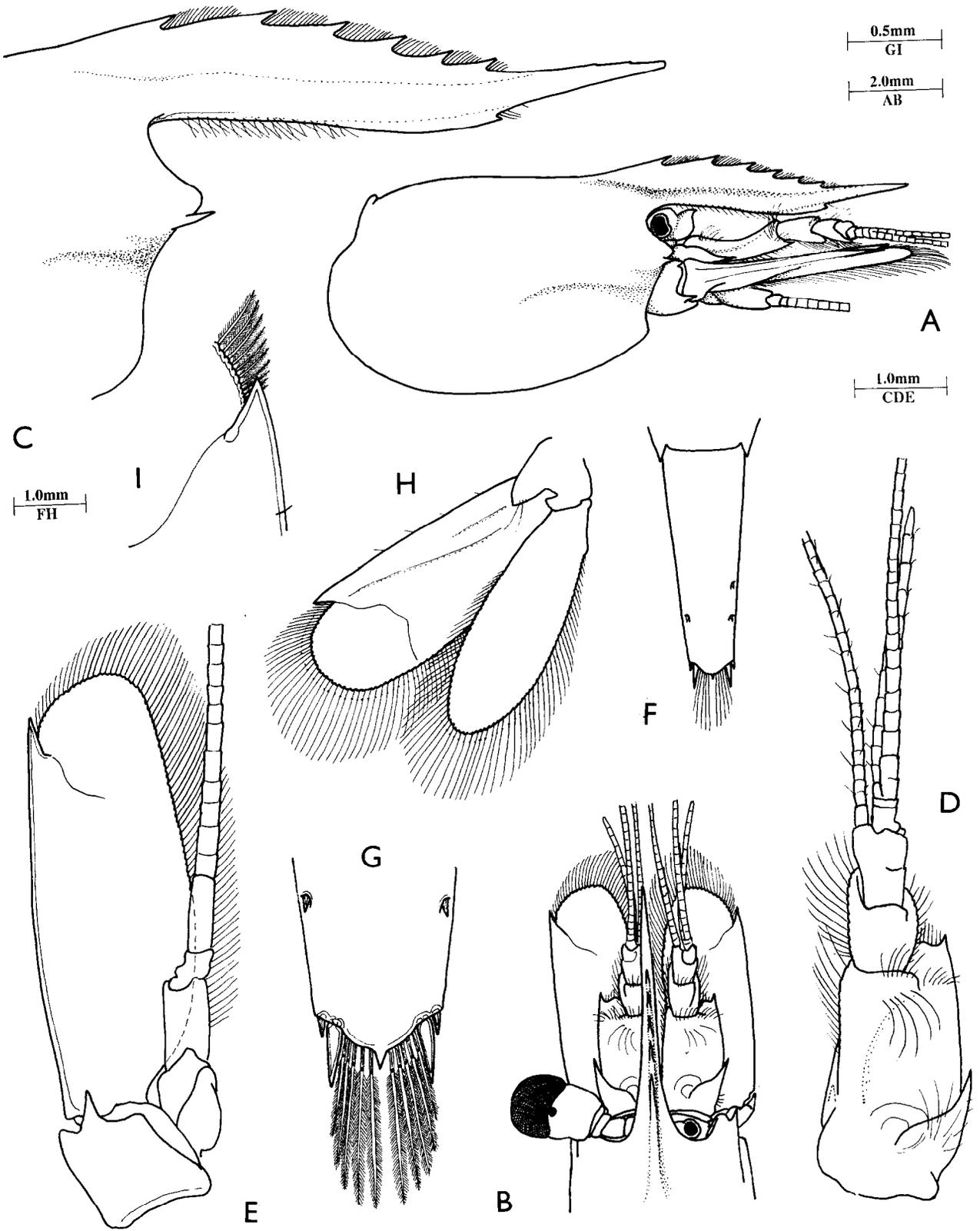


Fig. 1. *Leptopalaemon gagadjui* gen. nov., sp. nov. Holotype male. Scale division in millimetres.



Description

Small, slenderly built shrimps of subcylindrical body form.

Rostrum well developed, slender, reaching to about distal margin of scaphocerite, slightly sinuous, distally styliform, dorsal carina well developed, raised, more elevated in females, with 6–7 acute, fixed teeth, all distal to posterior orbital margin, carina extending over anterior fourth of carapace, distal rostrum with 0–2 minute denticulations, all interspaces between teeth setose; lateral carina feebly developed; ventral carina feebly developed, obsolete proximally and distally, with 1–2 small acute teeth; proximal ventral border of rostrum with double row of short plumose setae. Carapace smooth, glabrous; epigastric, supraorbital, branchiostegal and hepatic spines absent; orbit feebly developed, inferior orbital angle produced, rounded, with narrow inner flange; antennal spine well developed, acute, marginal; anterolateral angle of branchiostegite rounded, branchiostegal groove distinct anteriorly, branchiostegal suture absent.

Abdomen slender, smooth, glabrous; third segment not posterodorsally produced, fifth segment about 0.85 of sixth segment length, sixth segment 1.42 times longer than deep, posteroventral angle acute, posterolateral angular; pleura of first three segments broadly rounded, fourth produced, bluntly angular, fifth produced, with minute posteroventral tooth. Telson about 1.15 times sixth segment length, about 2.75 times longer than anterior width, with two pairs of small dorsal spines at 0.6 and 0.7 of length, posterior margin about 0.5 of anterior width, angularly sinuous, with small acute median process, lateral spines small, similar to dorsal spines, inner spine robust, longer, about 0.1 telson length, medial border with five pairs of long plumose setae.

Antennule well developed, proximal segment about 1.9 times longer than broad, distolateral lobe large with small acute lateral tooth reaching to about middle of intermediate segment length,

medial margin with acute tooth ventrally, lateral margin feebly convex, stylocerite acute, reaching to about middle of segment length, statocyst normally developed, with oval statolith; intermediate segment about 1.5 times longer than broad, very obliquely articulated with distal segment, about 0.5 of proximal segment length, lateral margin laminar with numerous short plumose setae, medial margin setose; distal segment about 0.8 of proximal segment length, 1.5 times longer than wide, sparsely setose; upper flagellum biramous, proximal two segments of rami fused, upper free ramus with about 12 segments, about 0.75 of peduncle length, aesthetascs feebly developed, lower ramus long, slender, about 6.0 times length of short ramus; lower flagellum slender, about 3.5 times length of short upper ramus.

Antenna with basicerite robust, with strong acute, distolateral tooth; ischiocerite and mero-cerite normal, short; carpocerite robust, short, about –4 times longer than wide, flagellum well developed, about 5.0 times postorbital carapace length; scaphocerite large, extending far beyond antennular peduncles, about 2.7 times longer than broad, widest at about 0.3 of length, lateral margin feebly convex with strong distolateral tooth, far exceeded by bluntly angular distal lamella.

Eye with large globular well pigmented cornea, slightly compressed, with dorsal accessory pigment spot, stalk about 1.2 times broader than long, length about 0.75 of corneal diameter.

Ophthalmic somite with small acute ‘bec ocellaire’. Epistome without special features.

Mandible (left) with corpus moderately robust; palp present, short, single segmented, about 4.5 times longer than wide, with two slender simple distal setae; molar process robust, very oblique with low blunt teeth; incisor process robust, tapering, with three acute distal teeth. Maxillula with bilobed palp, upper lobe small, lower lobe broad, short, with single simple distal seta; upper lacinia moderately expanded, with about 21 short simple spines distally, with dense short plumose

Fig. 2. *Leptopalaemon gagadjui* gen. nov., sp. nov. Paratype male, CL. 6.1 mms. A, carapace, rostrum and antennae, lateral. B, same, dorsal. C, anterior carapace and rostrum. D, antennule. E, antenna, ventral. F, telson. G, same, posterior margin. H, uropod. I, same, exopod, disto-lateral tooth.

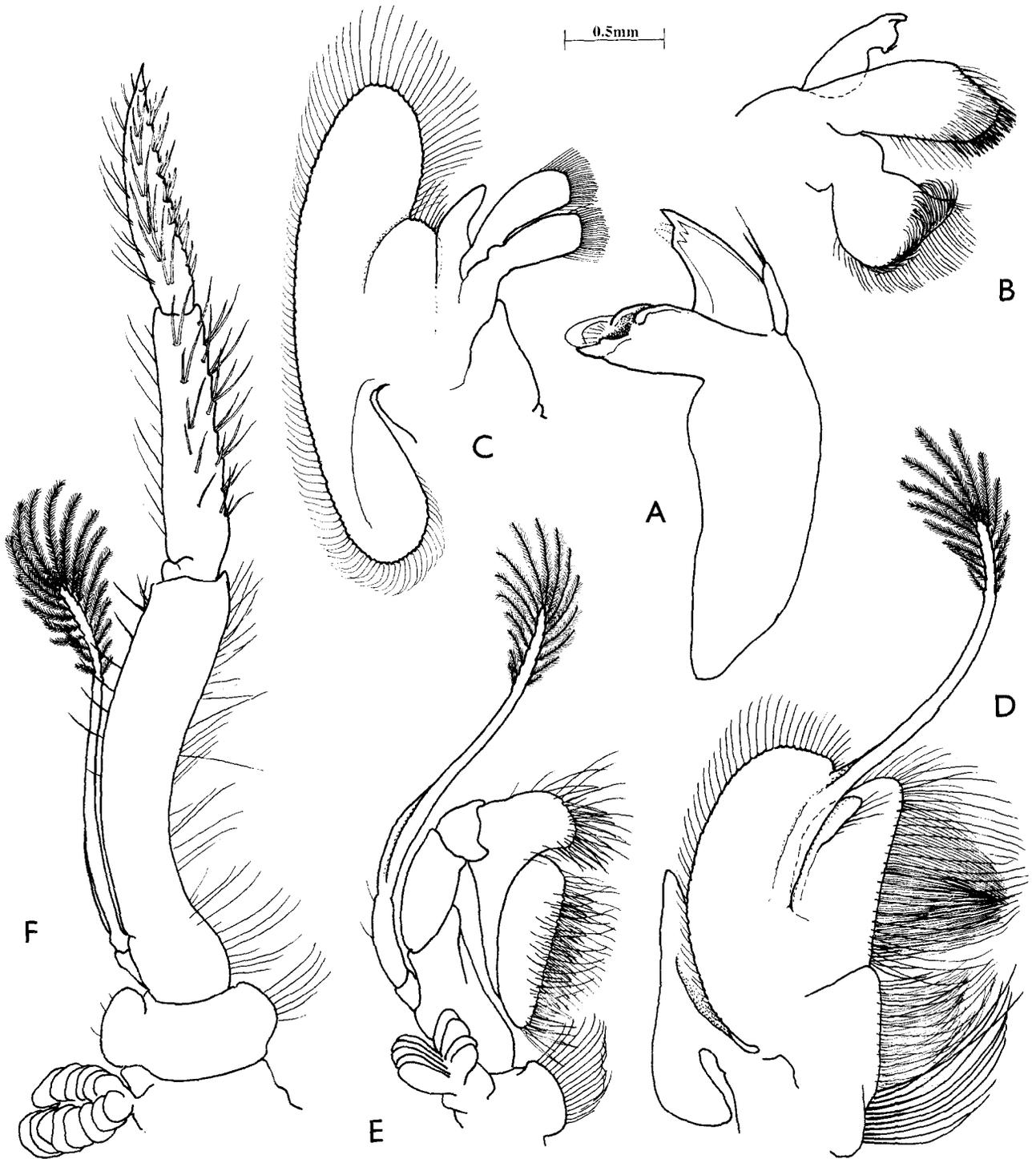


Fig. 3. *Leptopalaemon gagadjui* gen. nov., sp. nov. Paratype male, CL. 6.0 mms. A, mandible (left). B, maxillula. C, maxilla. D, first maxilliped, flattened. E, second maxilliped. F, third maxilliped.

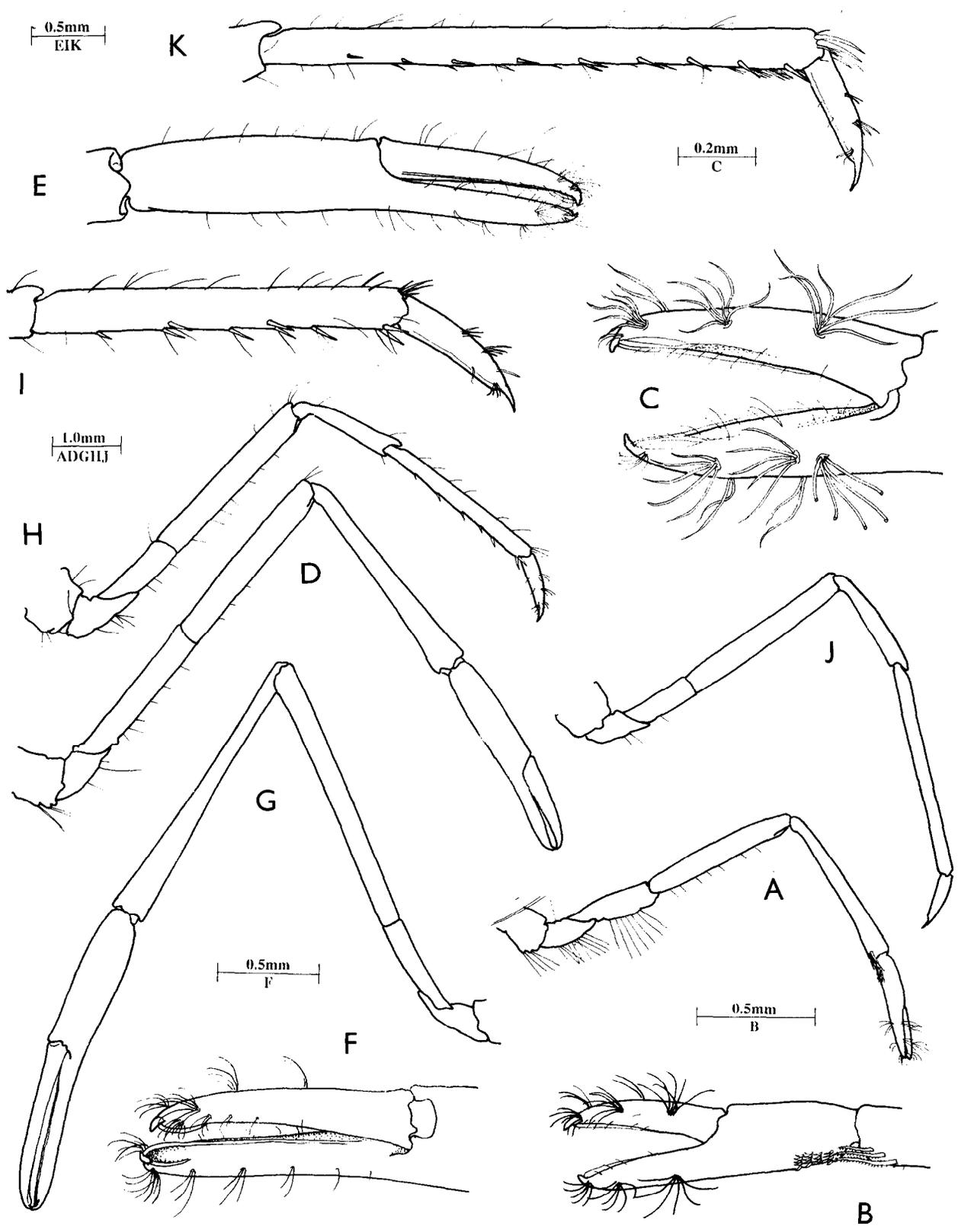
setae distolaterally and ventrally; lower lacinia broad, distoventral border with dense double row of short marginal plumose setae. Maxilla with short broad, distally emarginate, non-setose palp; basal endite well developed with two clearly separated distally setose lobes; coxal endite distinctly separated from basal, without medial lobes; scaphognathite well developed, about 3.4 times longer than broad, posterior lobe about 0.3 of length, anterior lobe with medial border deeply notched with distinct fold, plane of scaphognathite perpendicular to rest of segment. First maxilliped with elongated simple palp, proximally fused with basal endite, distal half with medial margin with several short plumose setae; basal endite simple, elongate, exceeding palp, with medial margin with dense dorsal row of long setulose setae, with ventral row of longer setae, more widely spaced, feebly setulose distally only, exopod well developed, with broad caridean lobe, flagellum broad, with numerous plumose setae distally; coxal endite well developed, simple, distinctly demarkated from base, with similar setae to basis distally and extra long simple setae only proximally; epipod well developed, triangular, anterior lobe acutely pointed, posterior lobe rounded; coxal and basal endites perpendicular to plane of caridean lobe and epipod. Second maxilliped with dactylar segment about 3.2 times longer than broad, medial border with rows of setulose setae, coarsely serrulate spines and long feebly serrulate setae, propodal segment expanded distomedially, with slender spines and setae, distal articular portion narrow, carpus, ischiomerus and basis normal, exopod well developed, flagellum broad, with numerous plumose setae distally, coxa with carinate medial border with numerous long simple setae, small oval epipod with podobranch laterally. Third maxilliped with moderately slender endopod, extending to about distal end of carapocerite, ischiomerus and basis completely fused, bowed, combined segment about 5.5 times longer than central width, uniform, medial margin with sparse long simple setae, lateral margin with several spiniform setae; penultimate segment straight, about 4.2 times longer than proximal width, slightly tapered dis-

tally, about 0.6 of antepenultimate segment length, sparsely setose laterally, with groups of spiniform setae ventrally and medially; terminal segment about 0.8 of penultimate segment length, 5.0 times longer than central width, tapering strongly with stout terminal spine, with numerous groups of serrulate spines ventrally and medially; exopod as second maxilliped, as long as antepenultimate segment; coxa with medial margin convex, setose, laterally with oval plate and small upper and large lower arthrobranch.

Second thoracic sternite with large transverse triangular plate. Third sternite with low transverse ridge. Fourth thoracic sternite without acute median process, with transverse triangular plate with small median notch.

First pereopods slender, reaching to about end of antennular peduncle; chela slender, palm about 2.0 times longer than deep, slightly compressed, with four transverse rows of short serrulate cleaning setae proximally; fingers subequal to palm length, dactyl about 5.0 times longer than proximal depth, with several groups of coarsely serrulate setae, with small acute hooked distal spine, cutting edges medial, with small accessory lateral cutting edge distally forming minute spatulate tip; carpus about 1.5 times chela length, slender, about 7.0 times longer than distal width, with several long, serrulate cleaning setae distoventrally; merus subequal to carpus length, about 7.0 times longer than wide, broadest centrally; ischium about 0.55 of merus length, ventrally carinate, setose; basis 0.4 of merus length, ventrally setose; coxa with small setose ventral process.

Second pereopods well developed, slender, subequal and similar or feebly unequal and slightly dissimilar, exceeding scaphocerite by half carpus length. Major chela about 0.8 of carapace length, with palm subcylindrical, slightly swollen proximally, about 3.7 times longer than central depth, smooth; fingers slender, slightly exceeding palm length in males, slightly shorter than palm in females, dactyl about 5.2 times longer than proximal depth, with small acute hooked tip, minutely spatulate distally, with feeble unarmed lateral cutting edge; fixed finger similar; carpus about 0.93 of chela length, 2.0 times palm length; 8.3 times



longer than distal width, tapering proximally, smooth, unarmed; merus about 0.9 of carpal length, 0.8 of chela length, slender, about 10.0 times longer than distal width, slightly tapering proximally, unarmed; ischium about 0.3 of meral length, 5.0 times longer than distal width; basis and coxa without special features. Minor chela generally similar, chela about 0.75 of major chela length, fingers 0.45 of palm length; carpus 1.15 of chela length; merus 0.8 of carpal length; ischium 0.85 of meral length.

Ambulatory pereopods slender, third reaching to distal margin of scaphocerite; dactyl slender, compressed, unguis distinct, curved, about 3.0 times longer than basal width, carpus about 4.0 times longer than proximal depth, simple, dorsal border convex, ventral margin straight, sharp, with several groups of spiniform setae; propod about 2.3 times dactyl length, about 8.5 times longer than wide, uniform, with pair of strong distoventral spines, 5 ventral spines and 2 ventrolateral spines, with scattered setae and group of spiniform setae distodorsally; carpus about 0.58 of propod length, with distodorsal lobe unarmed; merus subequal to propod length, about 7.4 times longer than wide, uniform, unarmed; ischium about 0.45 of merus length, 3.2 times longer than distal width; basis and coxa without special features. Fourth pereopod generally similar, to third. Fifth pereopod longer and more slender than third; dactylus similar, less setose; propod 3.8 times dactyl length, 15.5 times longer than central width, 1.5 times length of third propod, with 1 distoventral spine, 6 ventral spines, 8 ventrolateral spines, with several groups of short stout serrulate setae distomedially; carpus 0.5 of propod length; merus about 0.8 of propod length.

Male first pleopod with basipodite about 2.7 longer than distal width; exopod well developed, about 1.1 times basipodite length; endopod small, about 0.5 of exopod length, about 3.6 times longer

than central width, medially curved, distally rounded, medial margin with numerous stout coarsely serrulate setae proximally, distal half with 5 small simple spinules, with short plumose setae distally, extending to middle of lateral margin, proximal lateral margin with simple spines. Female first pleopod with basipodite about 3.3 times longer than distal width; exopod well developed, about 1.3 times basipodite length; endopod small, about 0.3 of exopod length, about 3.0 times longer than central width, medially curved, distally ovate, with long plumose setae. Second pleopod with basipodite about 1.1 of first basipodite length, 2.5 times longer than distal width in males, 3.3 times longer in females; male exopod well developed, 1.1 times basipodite length; endopod subequal to exopod length; appendix masculina elongate, subcylindrical, rigid, feebly tapering distally, slightly exceeding, subequal to, or slightly shorter than endopod, with about 21 short simple spines medially; appendix interna short, reaching to about 0.3 of appendix masculina length, with few cincinnuli.

Uropod with protopodite posterolaterally acute; exopod far exceeding telson, about 2.5 times longer than broad, lateral margin almost straight, sparsely setose, with strong distolateral tooth, without median mobile spine, diaeresis well marked; endopod about 0.9 of exopod length, 3.0 times longer than wide.

Types

A male, CL 5.50 mm. is selected as holotype and deposited in the collections of the Northern Territory Museum, Darwin, catalogue number NTM. Cr. 002103A. Two further males, CL 6.0, 6.1 mm, are designated as paratypes, NTM. Cr. 002103B-C. A male paratype is also deposited in the collection of the Nationaal Natuurhistorisch Museum. Five males and five females are selected from the Queensland Museum material and designated as paratypes.

Fig. 4. *Leptopalaemon gagadjui* gen. nov., sp. nov. Paratype male. A, first pereopod. B, same, chela. C, major second pereopod. D, minor second pereopod. E, same, chela. F, same, fingers, oblique. G, same, lateral. H, third pereopod. I, same, propod and dactyl. J, fifth pereopod. K, same, propod and dactyl.

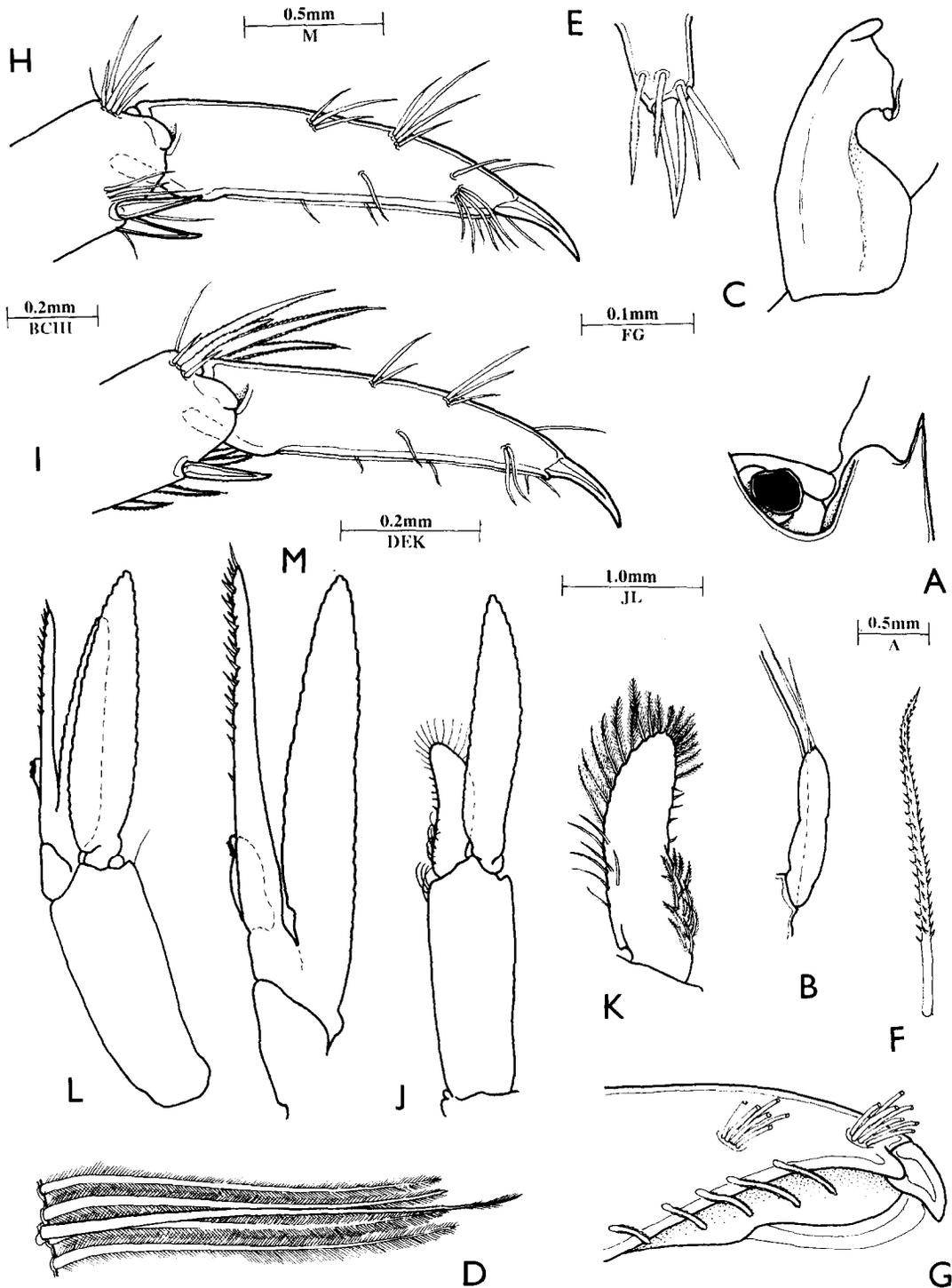


Fig. 5. *Leptopalaemon gagadju* gen. nov., sp. nov. Paratype male. A, inferior orbital angle, dorsal aspect. B, mandibular palp. C, maxillular palp. D, first maxilliped, basal endite, medial setae. E, third maxilliped, terminal spine. F, first pereopod, dactylar seta. G, second pereopod, distal dactyl. H, third pereopod, dactyl. I, fifth pereopod, dactyl. J, first pleopod. K, same, endopod. L, second pleopod. M, same, endopod.

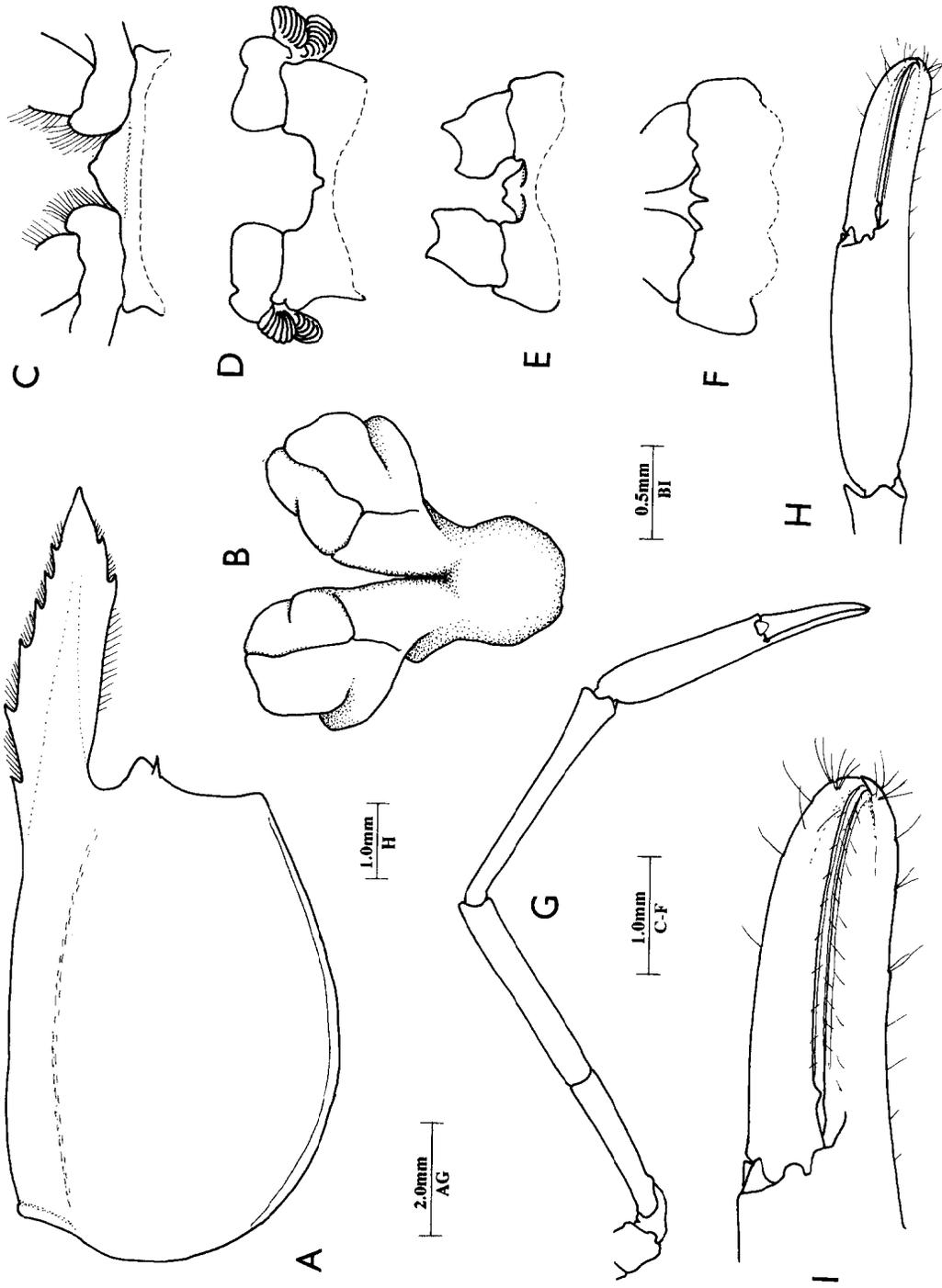


Fig. 6. *Leptopalaeomon gagadju* gen. nov., sp. nov. Paratype female. A, carapace and rostrum. B, paragnath. Thoracic sternites. C, second, D, third, E, fourth, F, fifth, G, second pereopod. H, same, chela. I, same, fingers.

Measurements (mms)

Holotype: total body length (approx.), 16.5; carapace and rostrum, 10.5; postorbital carapace, 5.50; second pereopod chela, left, 4.4; right, 4.3. Ova, 1.1×1.8 .

Colouration

Generally transparent, feebly speckled with small red brown chromatophores.

Habitat and Behaviour

This species appears to be confined to upper lotic, freshwater habitats and is presently known from escarpment streams draining the northwest portion of the Arnhem Land plateau. The sandstone plateau is thought to have formed in the middle Proterozoic between 1800 and 1400 million years ago and rises 50–250 m above the lowland hill country, floodplains and tidal flats (Christian & Aldrick, 1977).

L. gagadju typically occurs above major waterfalls along the escarpment. The fish communities of these areas appear to be relatively depauperate. In upper Barramundi Creek, at an altitude of 70–95 m, one of the authors (J.S.) observed only the Norther Purple-spotted Gudgeon, *Mogurnda mogurnda* and species of rainbow fish, *Melanotaenia*.

When visited during the dry season, the water in Barramundi Creek above Barramundi Falls was clear and acidic (pH 4.5–6.0), with surrounding seepage areas. The creek immediately above the falls was formed into a deep gorge but further upstream there were numerous shallow pools connected by riffle areas. Many of these pools contained large amounts of filamentous green algae but were largely free of rooted macrophytes. The substrates were solid bedrock, rocks on bedrock or sand, or clear sand. *L. gagadju* was active during the day and most easily located on sandy substrates in water less than two metres deep, but was also observed on solid bedrock. Only when disturbed did the animals seek shelter. In contrast, *Macrobrachium bullatum* Fincham, was usually located sheltering under rocks and the atyid, *Caridina nilotica* (P. Roux) in exposed root mats of vegetation along the banks of

larger pools. *L. gagadju* appears to be widely distributed in upper Barramundi Creek and was observed up to three kilometres above the falls.

Remarks

The mouthparts of *L. gagadju* are generally similar to those of most other palaemonine shrimps. One significant difference is in the first maxilliped in which basal and coxal endites are distinct, but markedly dorsally concave, (flattened in Fig. 3d) with a double fringe of long setae along the whole medial margin, with very dense but slightly shorter dorsal plumose marginal setae, with longer setae, only feebly setose at the tip, along the ventral margin. These setae appear to form a filtratory basket. The second maxilliped has the dactylar segment also provided with a dense medial fringe of unusually long slender, feebly serrulate setae and serrulate spines, the distodorsal angle of the propodal segment is enlarged, with numerous spiniform setae, and the medial margin of the coxa also broadly expanded and densely setose, all together forming an outer palisade of setae. The maxillula has the basal endites well developed. The maxillula has both laciniae moderately enlarged. The mandible has a functional incisor process, and the molar process is dentate. The third maxilliped has a robust endopod. This combination of features suggests a dual function for the mouthparts, a compromise between a micro-predatory or scavenging life style, with a capability of some form of filter feeding. The necessary water current may be derived from the movements of the scaphognathite and caridean lobe, sucking a current through the abducted first and second maxillipeds.

The appendix masculina of the male second pleopod is a particularly distinctive feature of *Leptopalaemon gagadju*. Some specimens of *Troglindicus phreaticus* show an appendix masculina which is very variable but may, in some larger specimens, be almost as long as the endopod, with numerous long spines along the ventromedial margin. Some other palaemonid shrimps, such as *Periclimenes elegans*, have appendices masculinae that exceed the endopod (Holthuis, 1952) but these usually arise from about the mid-

point of the medial margin of the endopod and not near its base, as in *Leptopalaemon* and *Troglindicus*.

It may also be noted that a single non-ovigerous female specimen (Graveside Gorge, CL 7.1 mm) was provided with well developed branchiostegal spines, but in all other respects resembled the other specimens. Also, in the males, the genital pore is located on a papilla arising from the inner articular membrane of the fifth pereopod, and has a moderately developed rounded terminal operculum.

Calathaemon gen. nov.

Diagnosis

Small sized shrimps of subcylindrical body form. Rostrum distinct, dorsally dentate; carapace smooth, epigastric, supraorbital and hepatic spines absent, inferior orbital angle distinct, antennal and branchiostegal spines present, anterior branchiostegite inflated, branchiostegal suture absent; abdomen smooth; pleura of first three segments rounded, fourth and fifth angular, blunt; telson with two pairs of dorsal spines, three to six pairs of posterior spines; antennae normal; upper antennular flagellum biramous, rami fused proximally; eyes reduced, cornea unpigmented; mandible without palp, incisor process reduced, molar process normal, metastoma with paragnaths proximally fused forming long slender corpus, with well developed median carina, paragnaths distally bilobed, upper lobe large, broadly rounded; maxillula with lower lacinia enlarged, swollen, densely setose; maxilla with simple palp, bilobed endite, broad scaphognathite; first maxilliped with basal and coxal endites fused, elongate, deeply concave, with dense medial fringe of long filtratory setae, exopod with caridean lobe large, broad, flagellum short, with plumose setae distally, epipod small, simple, triangular; second maxilliped with endopod enlarged, elongate, strongly compressed, dactylar segment, large, broad, with dense fringe of fine setae medially, deeply concave dorsally, basis elongate, compressed, with slender exopod, with plumose setae

distally, coxa with rudimentary epipod, with vestigial podobranch; third maxilliped with slender elongate endopod, ischiomerus distinct from basis, coxa with small lateral plate, with single small arthrobranch, without pleurobranch; third and fourth thoracic sternites with small median rounded protuberances; first and second pereopods feeble, chelae small, subequal, semispatulate; ambulatory pereopods slender, dactyls simple; appendix masculina short, not exceeding endopod of pleopod, with numerous simple spines; uropod normal, exopod without distolateral mobile spine.

Type species

Palaemonetes holthuisi Strenth, 1976.

Etymology

From *calathus*, Latin (*kalathos*, Greek), a basket, referring to the endites of the first maxillipeds, and *Palaemon*, a generic name first used by Weber, 1795.

Systematic Position

The assessment of the systematic relationship to other palaemonid genera presents some difficulty. As its previous placement in the genus *Palaemonetes* Heller, 1869, indicates, its general morphology shows a close similarity to that genus. It seems unlikely that *Calathaemon* is actually closely related as indicated by the radically different structure of the mouthparts, apparently highly modified for filtratory feeding. These are quite unlike those of any of the other species placed in the genus *Palaemonetes*, particularly including two other troglobitic species, *P. antrorum* Holthuis, under which name *C. holthuisi* was initially included, and *P. cummingi* Chace, 1954. Both of these species have mouthparts closely resembling those of the epigeal species of the genus, which are adapted to the micropredatory or scavenging feeding methods found in most other palaemonine shrimps. *Calathaemon* is therefore considered to occupy an isolated systematic position in the Palaemonidae, possibly most closely related only to *Leptopalaemon*, which also has mouthparts adapted to filtratory feeding.

Table 1.

	LEPTOCARPUS (<i>L. potamiscus</i>)	LEPTOPALAEON (<i>L. gagadjui</i>)	PALAEONETES (<i>P. varians, P. atrinibes</i>)	CALATHAEMON (<i>C. holhuisi</i>)	PALAEON (<i>P. semmelincki</i>)
Mandible					
palp	present	present	absent	absent	present
molar process	robust, dentate	robust, dentate	robust, dentate	feebly dentate	robust, dentate
incisor, process	normal, dentate	normal, dentate	normal, dentate	reduced, non dentate	normal, dentate
Maxillula					
palp	bilobed	bilobed	bilobed	simple	bilobed
upper lacinia	slender, spinose	slender, spinose	slender	scaphoid, setose	slender, spinose
lower lacinia	slender	broadened	slender	swollen, densely setose	slender
Maxilla					
scaphognathite	anterior lobe narrow, emarginate	normal	normal	expanded	normal
First Maxilliped					
coxal and basal endites	very distinct, basal lobe enlarged, with short medial setae, coxal lobe reduced	distinct, narrow, densely fringed with double rows of long setae	distinct, broad, normally setose	fused, narrow, deeply concave, very densely fringed with single row long setae long	distinct, broad, normally setose
caridean lobe	normal, broad	long, narrow	short, broad	broad reduced	short, broad
epipod	large, deeply bilobed	large, triangular	medium sized, simple or feebly bilobed	single row of very small, triangular	short, broad medium sized deeply bilobed
Second maxilliped					
endopod	robust	robust	robust	slender	robust
dactylar segment	normal	normal	normal	narrow	normal
propodal segment	broad, with large distomedial lobe	broad, with large distomedial lobe	broad, with feeble distomedial lobe	narrow, very slender	broad with feeble distomedial lobe
basis	?	medially excavate	medially excavate	not medially excavate, reduced	medially excavate
podobranch	well developed	well developed	well developed	vestigial	well developed
Third maxilliped					
endopod	slender	robust	robust	slender	robust
arthrobranchs	two	two	two	one	two
Paragnaths					
corpus	?	short, without carina	short, with opposing curved submedian cavinae	long, with median carina	short, with opposing curved submedian carinae
alae	?	broad, complex	broad, bilobed	broad, bilobed	broad, bilobed
Thoracic sternites					
second segment	?	large transverse triangular plate	unarmed	transverse ridge, with median anterior process	unarmed
third segment	?	low transverse ridge, with median notch	unarmed	low transverse angulate ridge	unarmed
fourth segment		transverse plate, with small acute median process	median spine, with submedian plates posteriorly	small median tubercle	median spine, with submedian plate
fifth segment		transverse plate with median notch	submedian rounded plates	larger rounded median tubercle	submedian plate posteriorly
Branchiostegal suture	distinct	absent	distinct	absent	distinct, short

Calathaemon holthuisi comb. nov. Figs 7–10

Material examined

Palaemonetes (Alaocaris) antrorum – Holthuis, 1951: 203–207, *partim*, pl. 50, 51a–d.

Palaemonetes holthuisi Strenth, 1976: 3–5, fig. 1. Holthuis, 1986; 607.

2 male, Edzell's Cave, San Marcos, Texas, 21 November 1971, coll. N. Strenth, NTM. Cr. 008410.

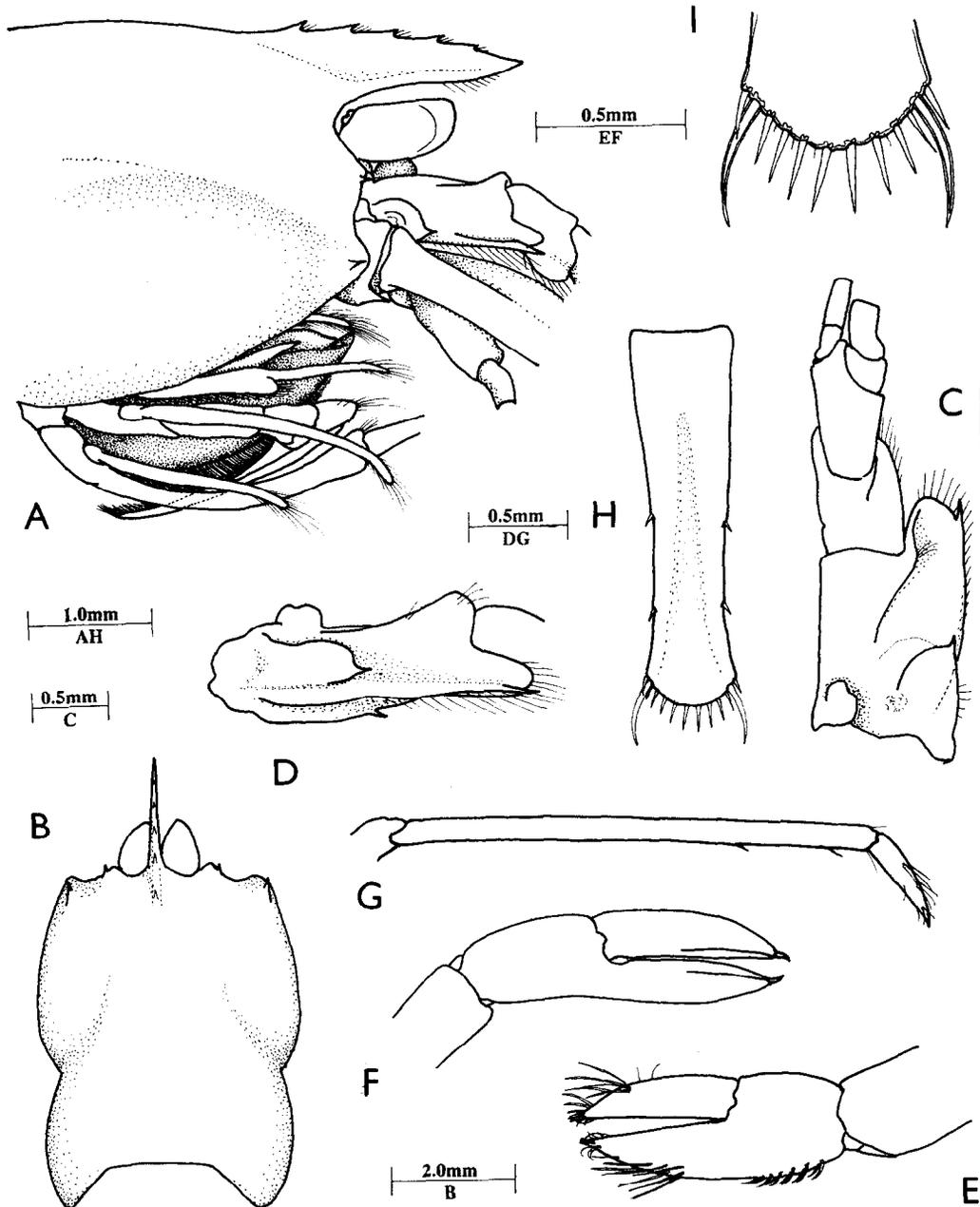


Fig. 7. *Calathaemon holthuisi* comb. nov., male, Edzell's Cave, Texas, CL 5.0 mms. A, anterior carapace, mouthparts, bases of antennal peduncles, lateral. B, carapace, dorsal. C, antennular peduncle. D, same, proximal segment, lateral. E, first pereiopod, chela. F, second pereiopod, chela. G, third pereiopod (?), propod and dactyl. H, telson. I, same, posterior spines.

Description

The general morphology has been well described by Holthuis (1951) and Strenth (1976). Examination of the present specimens, which are rather damaged, confirms the accuracy of these descriptions and allows amplification of some details, several of which are included above in the generic diagnosis. The following points may also be noted:

No branchiostegal suture could be detected in the single specimen in which the carapace was entire, but the pterygostomial region of each branchiotebite presented on inflated appearance, exactly symmetrical on the two sides and apparently natural, not due to *post mortem* swelling.

Mandibles with incisor process consistently reduced to small triangular non-dentate process, anterior margin of molar process finely carinate; maxillula with palp bilobed, large lower lobe with two short curved setae, upper lacinia broad, scoop-shaped, medially concave, densely setose with short simple setae distomedially, lower lacinia enlarged, swollen, tapering distally, with ventral and medial surfaces densely setose, devoid of spines; maxilla with slender, tapering palp, with few short setae on central medial margin, basal endite bilobed, lobes curved medially, slender, distal lobe slightly larger than proximal, both with sparse simple setae distally, coxal endite distinct, endites obsolete, medial margin convex, scaphognathite broad, elongate, at right angle to plane of endopod, 3.5 times longer than broad, posterior lobe about 0.3 of length, 2.0 times longer than wide, 0.6 of anterior lobe length, anterior lobe 1.7 times longer than broad, tapering distally, medial border near straight; first maxilliped with short simple non-setose tapering palp, basal and coxal endites fused, elongate, narrow, curved anteroposteriorly, deeply concave dorsomedially, with very dense fringe of long curved simple setae medially, forming deep basket-like arrangement, exopod with short broad flagellum with numerous plumose setae distally, caridean lobe large, sub-oval, broad, 3.0 longer than wide, 0.6 of scaphognathite length, coxa small, stout, feebly separated from basis, with small triangular epipod laterally, second maxilliped large, with slender endopod,

with distal segments expanded, all parts forming dorsomedially concave surface with central hiatus, dactylar segment about 3.75 times longer than broad, tapering slightly distally, medial margin sublinear, densely setose with simple medially curved setae; propodal segment with slender elongate proximal portion extending along dactyl, with very small distomedial lobe, carpus, ischiomerus and basis elongate, compressed, basis not markedly excavate medially, coxa distinct, without median process, with small epipod laterally with rudimentary prodobranth; third maxilliped with slender endopod, reaching to about distal end of antennal peduncle, ischiomerus and basis distinct, ischiomerus compressed, feebly tapering distally, about 5.0 times longer than proximal width, bowed, dorsally concave, slightly produced distomedially with tuft of setae, medial margin sparsely setose, penultimate segment subcylindrical, about 0.6 of ischiomerus length, about 7.0 times longer than wide, very sparsely setose, terminal segment subequal to penultimate segment length, slender, bowed, about 9.0 times longer than central width, with stout terminal spine, numerous transverse groups of shorter spines medially; basis with width subequal to maximum length, medial margin longer, broadly convex with long simple setae, exopod normal, with numerous plumose setae distally, coxa short, without medial process, with large rounded lateral plate, with single small arthrobranch.

First three thoracic sternites not clearly distinguishable in available material, with two low anteriorly angulated transverse ridges, not projecting ventromedially; fourth and fifth sternites broad, with small rounded median protuberances, fourth slightly smaller than fifth; sixth to eight narrow, unarmed.

Pereiopods as previously described; first pereiopod with chela short, about 0.15 of carapace length, 0.4 of carpus length, deep, palm about as long as broad, dactyl about 1.3 times palm length, 3.8 times longer than proximal depth, stout, with pair of small distally projecting spines with lamellar expansions; distomedially, lateral cutting edge sharp, fixed finger similar, 2.3 times longer than proximal depth, with three small

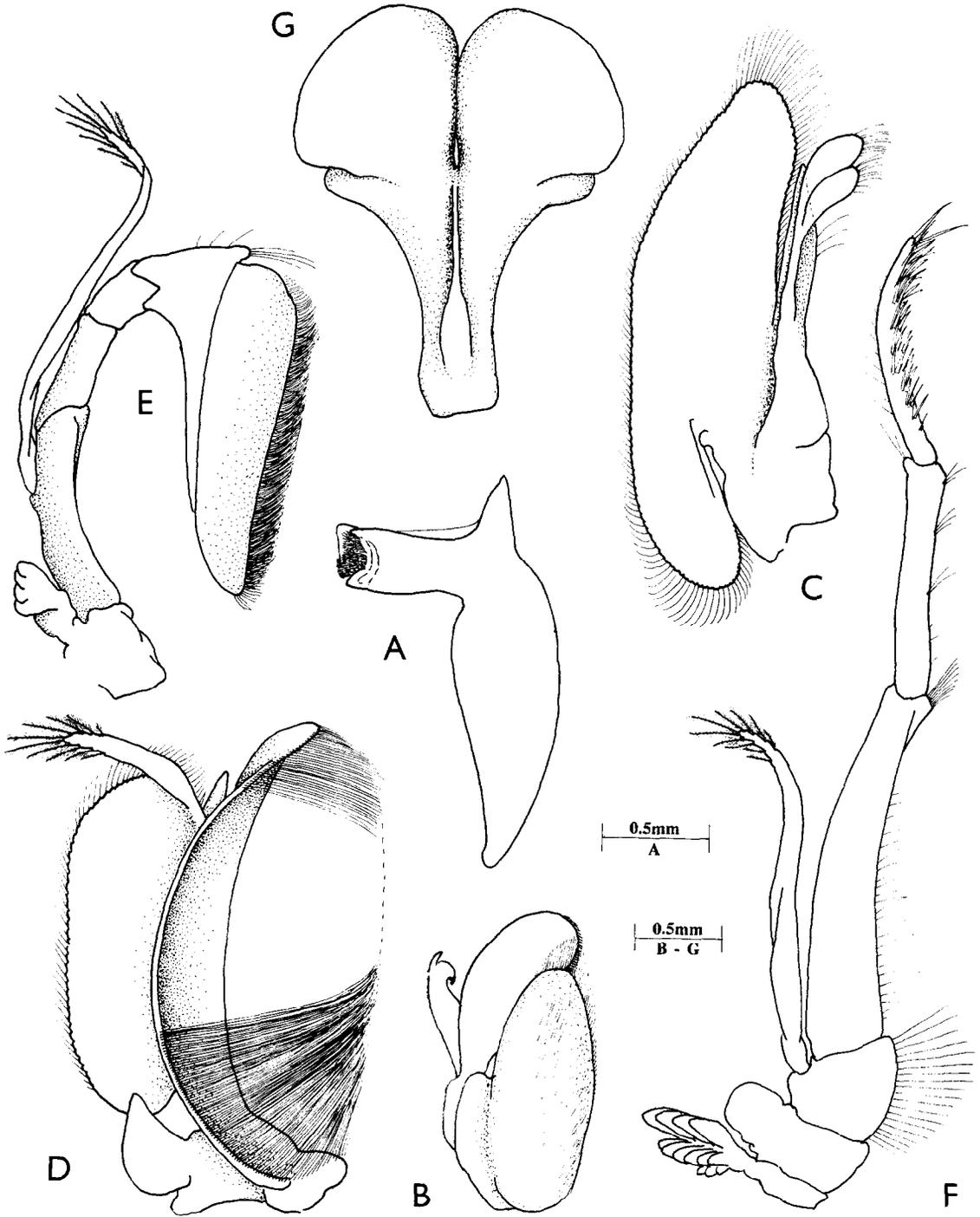


Fig. 8. *Calathaemon holthuisi* comb. nov. Mouthparts, ventral aspect, unflattened. A, mandible. B, maxillula. C, maxilla. D, first maxilliped. E, second maxilliped. F, third maxilliped. G, paragnaths. A, male, CL 5.0 mm. B-G, male, CL 5.0 mm.

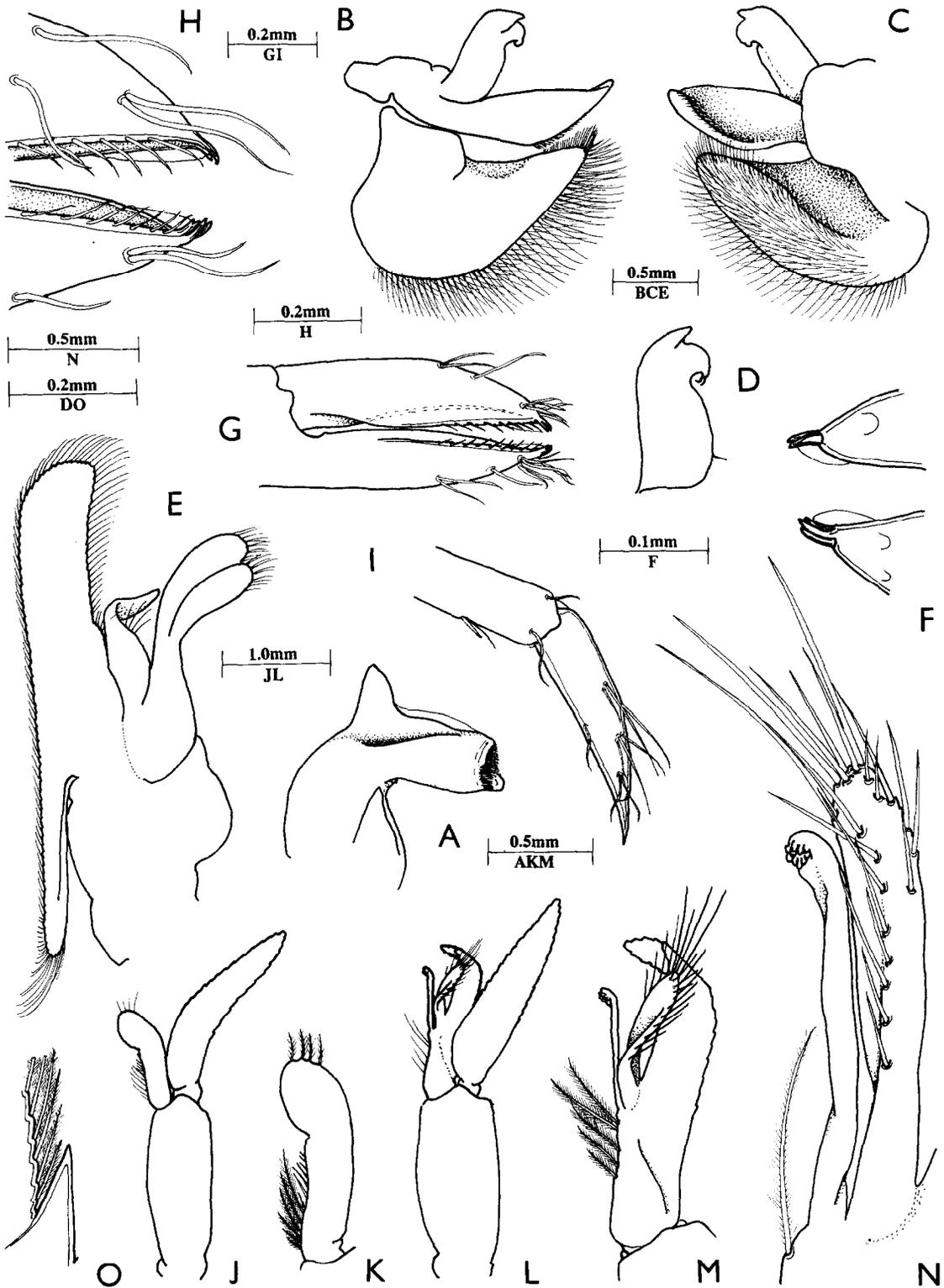


Fig. 9. *Calathaemon holthuisi* comb. nov. A, mandible, dorsal aspect. B, maxillula, lateral. C, same, medial. D, same palp. E, maxilla, lateral. F, first pereiopod, chela, tips of fingers. G, second pereiopod chela, fingers. H, same, tips of fingers. I, third pereiopod, and distal propod dactyl. J, first pleopod. K, same, endopod. L, second pleopod. M, same, endopod. N, same, appendix masculina, appendix interna. O, exopod of uropod, distolateral tooth.

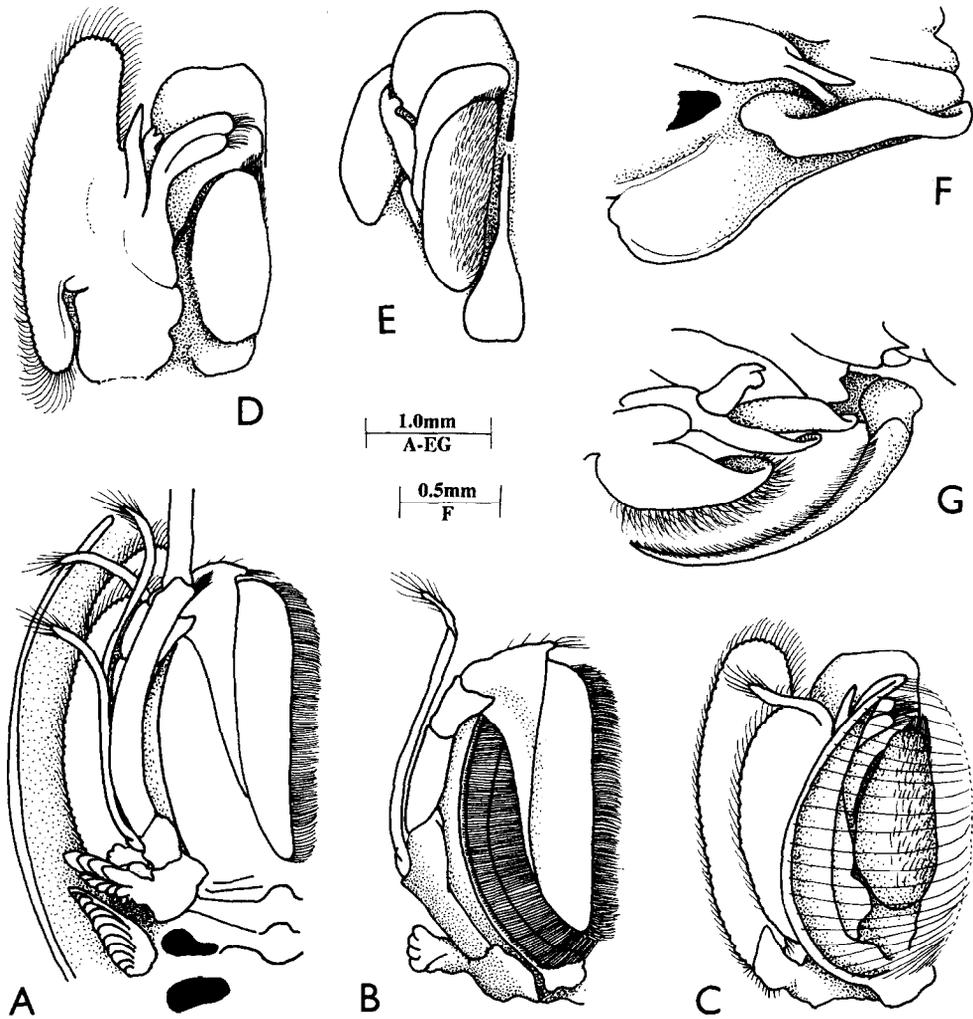


Fig. 10. *Calathaemon holthuisi* comb. nov., right mouthparts, ventral aspect. A, first, second and third maxillipeds (first maxilliped setae omitted), ventral margin of branchiostegite. B, first and second maxillipeds. C, paragnath, maxillula, maxilla and first maxilliped. D, paragnath, maxillula, maxilla. E, mandible, maxillula, paragnath. Right lateral. F, labrum, mandible, paragnath. G, labrum, mandible, paragnath, maxillula, left second maxilliped endopod.

spines distally, opposing surfaces of fingers semi-spatulate (see below); second pereopod with chela short, about 0.35 of carapace length, 0.33 of carpus length, 1.2 times first pereopod chela length, more slender, with palm 2.0 times longer than deep, fingers similar, about 1.2 times palm length, semispatulate; ambulatory pereopods with propod sparsely spinose, dactyl of third pereopod about 0.2 of propod length, unguis distinct, about 0.18 of corpus length, corpus with several groups of setae dorsolaterally, ventral margin blunt.

Male first pleopod with endopod about 0.55 of basipodite length, 5.0 times longer than central width, distomedially expanded, without medial lobule, distal margin with four short plumose setae, proximal medial border with six plumose setae proximally, seven shorter simple spines distally; second pleopod with endopod about 0.9 of basipodite length, with appendices at about 0.4 of medial margin length, appendix masculina sub-cylindrical, slightly compressed, about 6.5 times longer than broad, with nine ventromedial spines, six distal ventrolateral spines, five terminal spines,

all simple, of increasing length distally, appendix interna slender, with few distal cincinnuli, reaching to about 0.9 of appendix masculina length.

Caudal fan as previously described; telson with two pairs of dorsal spines laterally, at 0.50 and 0.74 of length, posterior margin expanded, convex, with six pairs of spines, sublateral spines elongate, curved; exopod of uropod with distinct diaeresis, with acute distolateral tooth, without mobile spinule medially.

Measurements (mms)

Total length (approx.), 17.5, (without rostrum); carapace and rostrum, 6.6; postorbital carapace, 5.0.

Remarks

The mouthparts in *Calathaemon* are radically different from those of the species of *Palaemonetes* with which it was formerly included. In the troglobitic species *P. cummingi* Chace, the mouthparts are essentially similar to the epigeic species of *Palaemon*, as they are also in *P. antrorum* Benedict. In *Palaemonetes* species, as in other palaemonines, the mouthparts are adapted for micro-predatory or scavenging feeding methods. In *Calathaemon*, the whole complex is arranged to act as a filtratory system, although this has not been observed in life. The inflated anterior branchiostegal region forms a cavity which allows extensive movements of the scaphognathite and caridean lobe. These movements would combine to develop a strong exhalant water current. This current would suck a foodbearing current through the mesh formed by the dense fringe of long slender setae on the endites of the first maxillipeds, which are contiguous and inflected in the midline. The inhalant current passes through these setae after having passed through the hiatus outlined by the proximal and distal components of the endopod of the second maxilliped, the dactylar segments of which are also in contact in the midline. In many palaemonine shrimps the dactylar and propodal segments of the second maxilliped endopod are often mobile and flex to form a pseudo-operculum, fitting into a deep concavity on the

medial aspect of the ischiomerus and, particularly, the basis. This does not occur in *Calathaemon*, where the segments lack easy mobility and are semi-rigid, so that the central hiatus remains open. The endopod and basis are capable of adduction and abduction at the coxo-sternal articulation. These movements can enable the dense fringe of dactylar setae to sweep any food particles on the outer surface of the first maxillepedal basket towards the midline and between the inwardly turned tips of these setae, towards the large lacinae of the maxillula. The movements of these are not certain but it appears that a horizontal anterior-posterior motion, guided by the median carina of the posterior paragnath, would drive food material towards the deep median fissure between the distal paragnaths. It would then come into contact with the molar processes, which could comminute any more solid fragments, the incisor process being redundant, and any forward escape of food being hindered by the basal endites of the maxillula, posterior escape prevented by the swollen posterior part of the median carina of the metastomal corpus.

The chelae of the first, and also second pereopods, in *Calathaemon* are also unusual, possibly without parallel in the Palaemonidae. In most palaemonid shrimps, the chelae of the first pereopod have a simple central cutting edge on each finger. In some taxa, this may be somewhat laterally situated, in others, markedly so, with the inner surfaces distinctly concave, giving rise to a subspatulate shape when the fingers are in apposition. In yet other taxa, this may be even more marked, with the medial and lateral edges of the fingers carinate (and sometimes pectinate) and distally confluent, with a deep central concavity, so that each finger is scoop-shaped, giving rise to a fully spatulate condition when the fingers are opposed. In *Calathaemon*, the fingers of both pairs of chelae are basically similar, with distinct low medial and lateral cutting edges, but with the central region not concave, being flattened or even feebly convex, a condition referred to as semispatulate. The arrangement appears to resemble that of a minute nut-cracker, rather than of a scoop, shears or forceps, as found in other palaemonines.

monids, in which the fingers of the second pereopod are generally distinctly different to those of the first pereopods.

Discussion

The analysis of the systematic positions of *Leptopalaemon* and *Calathaemon* within the family Palaemonidae has presented some unexpected problems. These stem largely from the available definitions of the family Palaemonidae. Recent discussions of this family (Holthuis, 1955; Balss, 1957) have separated the palaemonine genera from the pontoniine genera on the basis of two features: the presence of a pleurobranch on the third thoracic somite and two pairs of posterior telson spines in the former subfamily and absence of a pleurobranch on the third thoracic somite and three pairs of posterior telson spines in the latter. These features were first reported by Sol-laud (1910) and have been accepted by most subsequent authors. Kemp (1922) is less than clear as he states that in the Palaemoninae 'six large branchiae' are found. As usually seen, the Palaemoninae present six large branchiae consisting of five pleurobranches and the outer arthrobranch of the third maxilliped.

In a detailed study, Patwardhan (1937) has reported the branchial formula of *Macrobrachium malcolmsonii* as consisting of five pairs of pleurobranches, with each third maxilliped having a pair of arthrobranches. Recently Abele & Felgenhauer (1986) have confirmed this in *Macrobrachium* sp. Similarly, Hobbs (1978), in designating the genus *Neopalaemon* and placing it in the Palaemoninae, reports the presence of pleurobranches on somites bearing pereopods and two arthrobranches on that supporting the third maxilliped.

In *Macrobrachium rosenbergii* (De Man) the third maxilliped is provided with a larger outer arthrobranch and a smaller more dorsally situated inner arthrobranch that is largely concealed beneath the outer arthrobranch, and is without a pleurobranch on the third somite (personal observation). In a cleared and stained specimen a distinct foramen is present on each of the fourth to

eight thoracic pleurites at the origin of each pleurobranch but is lacking on that of the third pleurite. This arrangement appears to be common to many palaemonine genera, despite observations on *Palaemon* in Bruce (1990), now considered erroneous, and is also the condition found in *Leptopalaemon*.

The situation of *Calathaemon* is even less clear. The present specimens also lack a pleurobranch on the third thoracic somite, but have only a single small functional arthrobranch on the third maxilliped. Dr F. A. Chace has recently indicated (pers. comm.) that there appear to be two arthrobranches on each side of the third thoracic somite or possibly a single forked gill, in the paratype specimen of *C. holthuisi*. These features should place *Calathaemon* in the subfamily Pontoniinae, but its filtratory feeding mechanism is without parallel in that subfamily and is sufficiently distinctive to suggest that it may need to be placed in its own subfamily. The extent to which radical changes of feeding methods and mechanisms can be accommodated within a single taxon, other morphological features remaining similar, is debatable, and the variations within 'Gnathophyllidae', provide a particular source of difficulty. *Calathaemon* has a small epipod on the second maxilliped which bears a feebly developed podobranch. Within the Pontoniinae, this epipod is almost invariably without a podobranch, and in the vast majority of taxa, the third maxilliped is without an arthrobranch and is provided with, at the most, only a small or rudimentary arthrobranch in the others. A few pontoniines, such as *Palaemonella rotumana* (Borradaile) may have a very small rudimentary podobranch on the second maxilliped (Holthuis, 1952).

The impression is left that in the course of evolution, the branchiae associated with the third thoracic somite are of decreasing functional importance. There seems no reason why their loss should not have occurred more than once in taxa that are not closely related. None the less, the structure of the mouthparts in *Calathaemon* is of a basically palaemonid nature. Clearly, the division of the Palaemonidae into subfamilies is a subject in need of further investigation.

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References

- Abele, L. G. & B. E. Felgenhauer, 1986. Phylogenetic and phenetic relationships among the lower Decapoda. *J. Crustacean Biol.*, 6: 385–400.
- Balss, H., 1957. Decapoda. VIII. Systematik. In H. G. Bronn (ed.), *Klassen und Ordnungen des Tierreichs (V)* (1) 7(2): 1505–1672.
- Borradaile, L. A., 1917. On the Pontoniinae. The Percy Sladen Trust Expedition to the Indian Ocean in 1905, under the leadership of Mr J. Stanley Gardiner. *Trans. Linn. Soc. London*, 17: 323–396.
- Bruce, A. J., 1990. Redescriptions of five Hong Kong caridean shrimps first described by W. Stimpson, 1860. In B. Morton (ed.), *Proceedings of the Second International Marine Workshop: The Marine Fauna of Hong Kong and Southern China*, Hong Kong, 1986, Hong Kong University Press: 569–610.
- Christian, C. S. & J. M. Aldrick, 1977. The department of the Northern Territory and the Australian Mining Industry Council Alligator Rivers Study. A review report of the Alligator Rivers Region environmental fact finding study. Australian Government Publishing Service: Canberra.
- Hobbs, H. H., Jr., 1973. Three new troglobitic decapod crustaceans from Oaxaca, Mexico. *Ass. Mexican Cave Stud. Bull.* 5: 25–38.
- Holthuis, L. B., 1950. Subfamily Palaemoninae. The Palaemonidae collected by the Siboga and Snellius Expeditions with Remarks on other species. I. The Decapoda of the Siboga Expedition, X. *Siboga Expedition Monogr.*, 39a: 1–268.
- Holthuis, L. B., 1952a. Subfamily Palaemoninae. A general Revision of the Palaemonidae of the Americas, II. Allan Hancock Foundation Occasional Papers, 12: 1–396.
- Holthuis, L. B., 1952b. The Decapoda of the Siboga Expeditions, XI. The Palaemonidae collected by the Siboga and Snellius Expeditions with remarks on other species II. Subfamily Pontoniinae. *Siboga Expedition Monogr.*, 39a¹⁰: 1–152.
- Holthuis, L. B., 1955. The Recent Genera of the Caridean and Stenopodidean Shrimps (Class Crustacea, Order Decapoda, Supersection Natantia) with Keys for their Determination. *Zool. Verh. Leiden*, 26: 1–157.
- Holthuis, L. B., 1986. Decapoda. In: Botosaneanu, L. (ed.), *Stygiofauna Mundi*, Leiden: 589–615.
- Kemp, S., 1922. Notes on Crustacea Decapoda in the Indian Museum. XV. Pontoniinae. *Records of the Indian Museum*, 24: 113–288.
- Patwardhan, S. S., 1937. *Palaemon* (The Indian River Prawn). In Bahl, K. N. (ed.), *The Indian Zoological Memoirs on Animal Types*, 6: i–xi, 1–100.
- Sankolly, K. N. & Shenoy, 1979. On a new genus and a new species of subterranean prawn *Troglindicus phreaticus* (Caridea, Palaemonidae). *Bull. Fish. Fac. Konkan Agricul. Univ., India*, 1: 83–91.
- Sollaud, E., 1910. Sur les affinité des genres *Urocaris* (Stimpson) et *Palaemonella* (Dana), et considerations sur l'évolution des Crevettes de la Famille des Pontoniidés. *Comptes Rendus de l'Académie des Sciences, Paris*, 151: 1158–1161.
- Strenth, N. E., 1976. Review of the Systematics and Zoogeography of the Freshwater Species of *Palaemonetes* Heller of North America. *Smithsonian Contributions to Zoology*, 228: 1–27.