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Kakaducaris glabra gen. nov., sp. nov., a new freshwater shrimp from the Kakadu National Park, Northern Territory, Australia, Crustacea: Decapoda: Palaemonidae with the designation of a new subfamily Kakaducaridinae

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Key words: Crustacea: Decapoda: Palaemonidae, *Kakaducaris glabra*, new genus, new species, freshwater, Northern Australia, new subfamily Kakaducaridinae (see addendum)

Abstract

A new species of palaemonid shrimp from the Northern Territory Kakadu National Park is described and illustrated. *Kakaducaris glabra*, gen, nov., sp. nov., can not be satisfactorily referred to the described subfamilies of the Palaemonidae and a new subfamily Kakaducaridinae is designated (see addendum).

Introduction

The Australian freshwater caridean fauna is dominated by two families, the Atyidae and the Palaemonidae. The latter is represented by the genus *Macrobrachium*, which has several species and is of widespread distribution, particularly in tropical waters. The genus *Leptopalaemon* Bruce & Short (1993), has been recently added to the Australia fauna. The discovery of a further presently endemic genus is of special interest, particularly as the new genus presents a number of characteristic morphological features that differentiate it from all subfamilies so far described and render necessary the designation of a new subfamily.

The following abbreviations are employed: NTM, Northern Territory Museum, Darwin; RMNH, Nationaal Natuurhistorisch Museum, Leiden; USNM, National Museum of Natural History, Washington; AM, Australian Museum, Sydney; BMNH, The Natural History Museum, London; QM, Queensland Museum, Brisbane. Carapace length (CL) refers to the postorbital carapace length.

Family PALAEMONIDAE

Genus *Kakaducaris* gen. nov.

Diagnosis. Rostrum well developed, short, dorsal carina well developed, unarmed, ventral carina obsolete, lateral carinae confluent with dorsal orbital margins. Carapace without antennal, hepatic or branchiostegal spines; branchiostegal groove present anteriorly. Telson without dorsal spines, two pairs of posterior spines. Eyes well developed. Antennae normal, scaphocerite well developed. Mandible with one-segmented palp, molar and incisor processes distinct; maxillula with laciniae broad; maxilla with basal endite bilobed, coxal endite obsolete, palp simple, scaphognathite with broad anterior lobe, first maxilliped with elongated basal endite, medial border of coxal

and basal endites with fringe of long setae, palp simple, caridean lobe normal, epipod anteriorly acute, posteriorly truncate; second maxilliped with dactylar segment narrow, propodal segment distomedially produced, coxal segment with broad medial lobe, all densely setose medially, epipod present, with small podobranch; third maxilliped slender, with small lateral coxal plate and 1 arthrobranch: all maxillipeds with well developed exopods, with strongly setose flagella. Pereiopods without exopods. First pereiopods slender, chelate; second pereiopods small, more robust than first, subequal, similar, chelate and unarmed; ambulatory pereiopods slender, dactyls simple. Second thoracic sternite with broad median triangular plate, fourth without median process. Pleurobranchs on pereiopods 1–5. Pleopods 2–5 with appendix interna, male pleopod 2 with elongate appendix masculina; exopod of uropod with distolateral tooth, lacking articulated spine medially.

Type species: Kakaducaris glabra *sp. nov.*

Etymology. From 'Kakadu', the locality of capture and the Greek '*karis*', shrimp. The gender is feminine.

Systematic position. The genus *Kakaducaris* is most closely related to the genus *Leptopalaemon* (Bruce & Short, 1993), also known from Arnhem Land, Australia. The two genera share the unusual morphology of the mouthparts, which appear similarly modified to form a filtratory basket. They also share the very characteristic greatly elongated, heavily spinose appendices masculinae on the endopods of the male second pleopods and not found in any other palaemonid shrimps. The genera many be readily distinguished by the features shown in Table 1.

Kakaducaris also shows a marked similarity in its mouthparts to the Mexican genus *Calathaemon* Bruce & Short (1993), a troglobitic species with strongly reduced eyes. The genera may be distinguished by the features shown in Table 2.

All three genera are also unusual, amongst palae = monid shrimps, in lacking a small mobile spinule medial to the distolateral tooth on the exopod of the uropod.

***Kakaducaris glabra*, sp. nov.**

(Figs 1–12)

Types. Holotype ♀ (non-ovig.), allotype ♂, 26 paratypes, Lightening Dreaming Creek, Nourlangi, Kakadu National Park, Arnhem Land, Northern Territory, 12°55.3'S, 132°55.8'E, 90 m alt., 8 September 1984, coll. P. J. Murray & G. Chaloupka. NTM Cr.001992a (holotype), NTM Cr.001992b (allotype), NTM Cr.001992c (dissected paratype), NTM Cr.001992 (paratypes), RMNH D36150, 36151 (paratypes), USNM 234303 (paratype), AM. P41845 (paratype), BMNH 1993:76.1 (paratype), QM W.16558 (paratype).

Diagnosis. With the characters of the genus.

Description. Medium sized palaemonid shrimp, with integument generally smooth, well calcified. Rostrum acute, compressed, extending anteriorly almost to base of intermediate antennular peduncular segment; dorsal carina well developed, convex, unarmed, with sparse short setae; ventral carina obsolete, convex, unarmed, nonsetose; lateral carina well developed posteriorly,

Table 1.

KAKADUCARIS gen. nov.	*LEPTOPALAEMON* Bruce and Short
1. Rostrum edentate (generally)	Rostrum strongly dentate
2. Antennal spine absent	Antennal spine present
3. Branchiostegal suture present	Branchiostegal suture absent
4. Telson without dorsal spines	Telson with two pairs of dorsal spines
5. Third maxilliped with single arthrobranch	Third maxilliped with two arthrobranchs

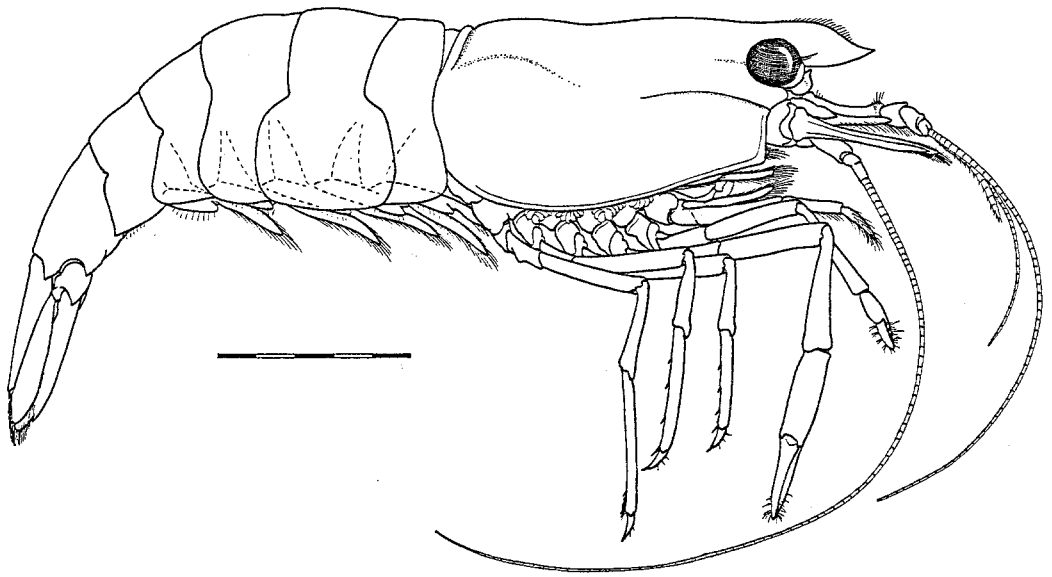

Fig. 1. Kakaducaris glabra, gen. nov., sp. nov., holotype female.

confluent with superior border of orbital notch. Carapace without supraorbital, antennal, hepatic or branchiostegal spines, inferior orbital angle slightly produced, rounded, branchiostegal groove distinct anteriorly, anterolateral angle of carapace rounded or rectangular.

Abdomen with somite 3 not posterodorsally produced, somite 5 about 0.6 of length of somite 6, somite 6 about 1.3 times longer than deep, with posteroventral and posterolateral angles acute, pleura of somites 1–3 rounded, somite 4 bluntly rectangular, somite 5 acute, slightly produced. Sternites forming raised transverse plates posteriorly on each segment, first sternite with small acute median process, second with larger acute median process, fifth with anterior rounded median longitudinal carina. Telson about 1.25 times length of somite 6, deeply cannulate ventrally, 3.2 times longer than broad, tapering posteriorly, sides straight, without dorsal spines, posterior border obtusely pointed, two pairs of posterior spines, small outer spines with larger adjacent sublateral spines, numerous ventrally submarginal plumose setae.

Table 2.

KAKADUCARIS gen. nov.	*CALATHAEMON* Bruce & Short
1. Rostrum edentate (generally)	Rostrum strongly dentate
2. Antennal spine absent	Antennal spine present
3. Telson without dorsal spines	Telson with dorsal spines
4. Telson with only two pairs of posterior spines	Telson with numerous pairs of posterior spines
5. Mandible with normal incisor process, with palp	Mandible with reduced incisor process, without palp
6. Maxillula with normal lower lacinia, laminar	Maxillula with lower lacinia enlarged, swollen
7. First maxilliped with reduced caridean lobe, moderately large epipod	First maxilliped with large caridean lobe, reduced epipod
8. Paragnaths with posteroventral corpus concave	Paragnaths with corpus bearing longitudinal median carina
9. Appendix masculina an elongate spinulate rod, reaching to or exceeding tip of endopod	Appendix masculina distinctly shorter than endopod

Eye with large globular hemispherical cornea with distinct accessory pigment spot dorsally; stalk short, about 1.2 times broader than long, slightly tapered proximally, distal width slightly less than corneal diameter. Ophthalmic somite with conspicuous 'bec ocellaire'.

Antennular penduncle reaching almost to level of distolateral tooth of scaphocerite; proximal segment about 1.55 times longer than central width, median border setose, without ventromedial tooth, anterolateral lobe well developed, rounded with minute distolateral tooth, stylocerite, short, broad, acute, reaching to middle of length of medial border, statocyst present, indistinct, dorsal flagellum biramous, rami with 3 proximal segments fused, lateral ramus long, slender, equal to 0.3 of carapace length, shorter ramus robust, 8 segmented, aesthetascs obsolete; lower ramus long, slender, about 1.6 of carapace length.

Antenna with basicerite armed with small ventrolateral tooth, carpocerite short and stout, slightly exceeding stylocerite, flagellum well developed, about 3.5 times carapace length; scaphocerite well developed, extending well beyond antennular peduncle, broad, about 2.2 times longer than wide, greatest width centrally, anterior margin broadly rounded, lateral border feebly convex, with small distolateral tooth, far exceeded by anterior lamina.

Epistome unarmed. Mandible normal, with small, one segmented non-setose palp, incisor process distally tridentate, molar process obliquely concave distally with small acute teeth and curved cutting edge. Maxillula with palp deeply bilobed, upper lacinia short, broad, about 15 short spines distally, with numerous setae, lower lacinia expanded, twice as long as deep, with dense setose fringe medially. Maxilla with slender non-

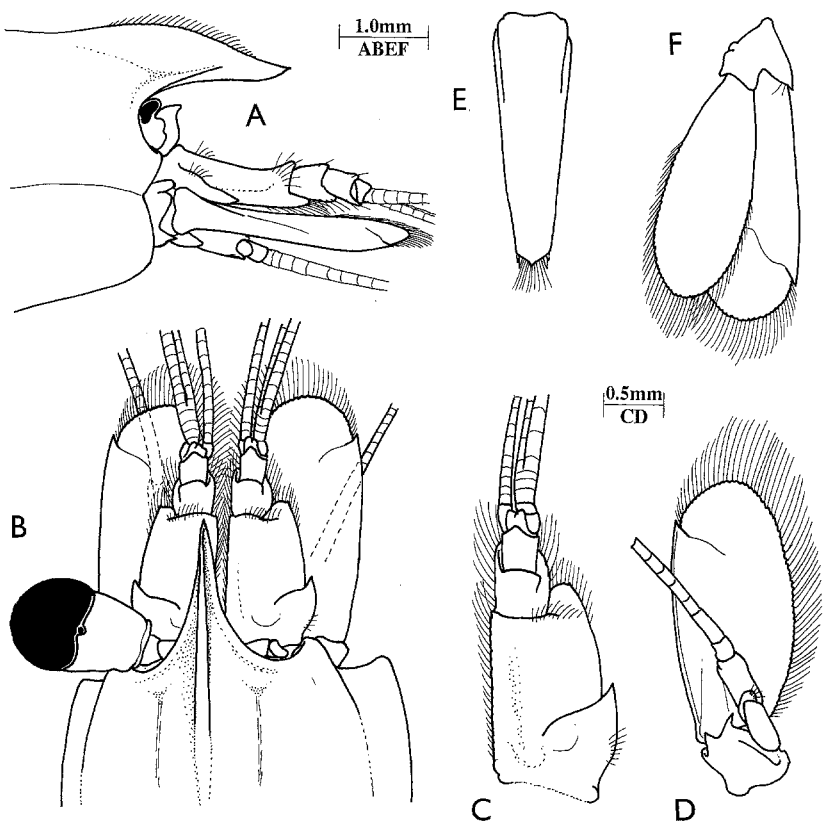

Fig. 2. Kakaducaris glabra, gen. nov., sp. nov. A, anterior carapace and antennal peduncles, lateral. B, same, dorsal. C, antennular peduncle. D, antenna. E, telson. F, uropod. A–B, male. C–F, female.

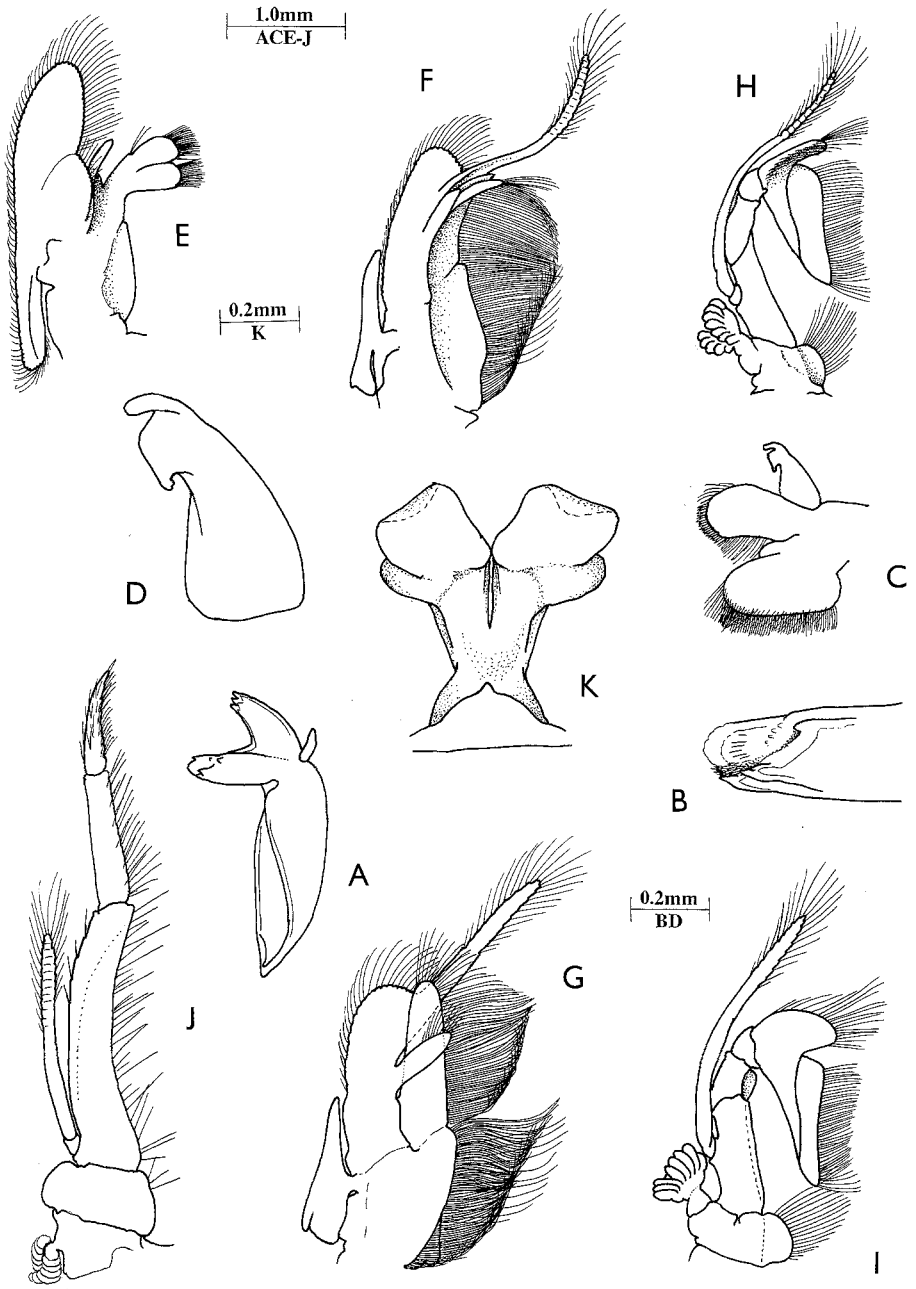

Fig. 3. Kakaducaris glabra, gen. nov., sp. nov., female. A, mandible. B, same, molar process. C, maxillula. D, same, palp. E, maxilla. F, first maxilliped. G, same, flattened. H, second maxilliped. I, same, flattened. J, third maxilliped, flattened.

setose palp, medially excavate, basal endite bilobed, lobes expanded distally with dense tufts of short setae distally, coxal endite obsolete, medial border feebly convex; scaphognathite about 3.3 times longer than broad, anterior lobe broad, medial border intended, posterior lobe narrow. First maxilliped with short palp, distolaterally setose; basal endite long and narrow, 3.4 times longer than proximal width, exceeding distal margin of caridean lobe, densely fringed with long slender finely setulose setae along whole of straight medial border, coxal endite separated from basal

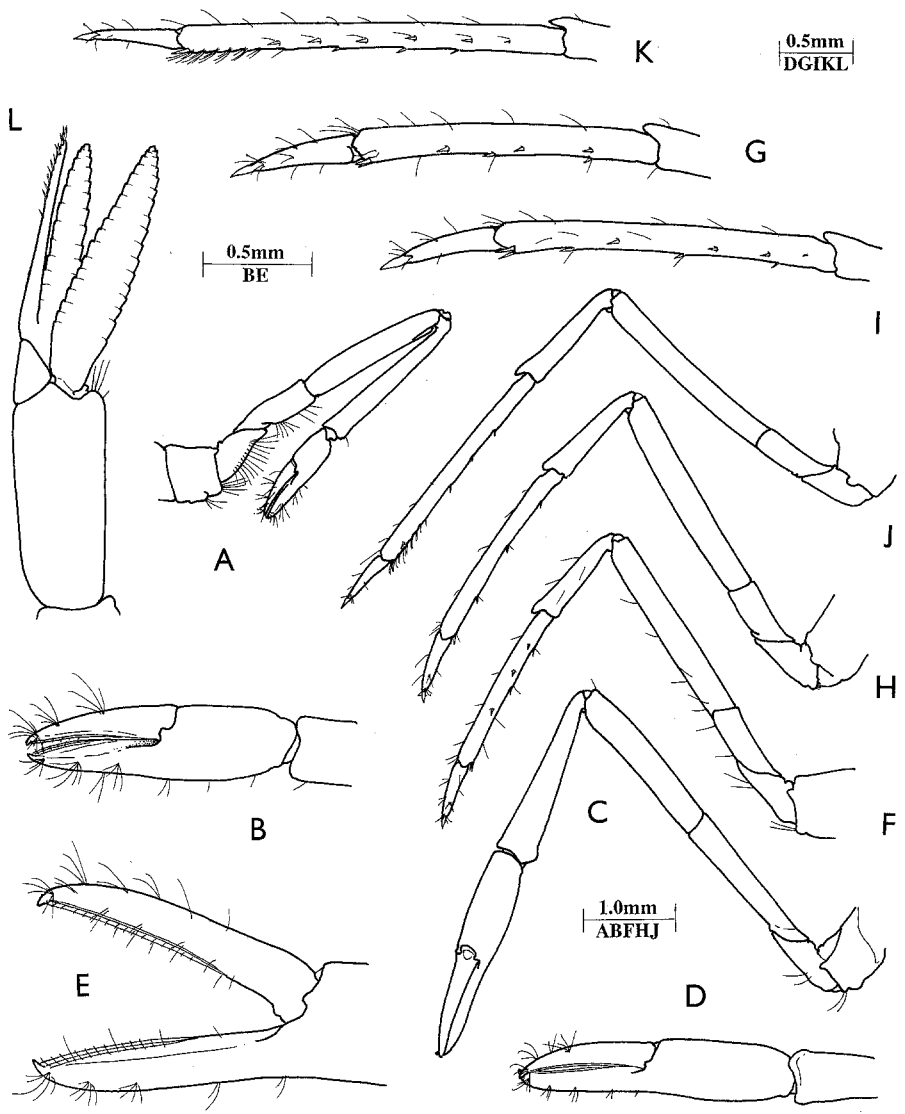

Fig. 4. Kakaducaris glabra, gen. nov., sp. nov. A, first pereiopod. B, same, chela. C, second pereiopod. D, same, chela. E, same, fingers. F, third pereiopod. G, same, propodus and dactyl. H, fourth pereiopod. I, same, propodus and dactyl. J, fifth pereiopod. K, same, propodus and dactyl. L, second pleopod, male.

endite by slight notch, feebly convex, densely fringed as basal endite; caridean lobe well developed, broadest distally; epipod with anterior lobe slender, tapering, posterior lobe short, broad, posteriorly truncated. Second maxilliped, endopod with dactylar segment long, narrow, about 7.5 times longer than central width, densely setose medially, propodal segment narrow distally, broadly expanded anteromedially, anteromedial lobe densely setose, carpus and ischiomerus relatively slender, ischiomerus deeply excavate medially, basis elongate, feebly excavate medially, coxa with broad, round, densely setose lobe medially, with small epipod laterally, with well developed small podobranch. Third maxilliped with endopod slender, slightly exceeding carpocerite; ischiomerus fused to basis, combined antipenultimate segment about 5.3 times longer than proximal width, tapering slightly distally, medial border with numerous setae, lateral border with 3–4

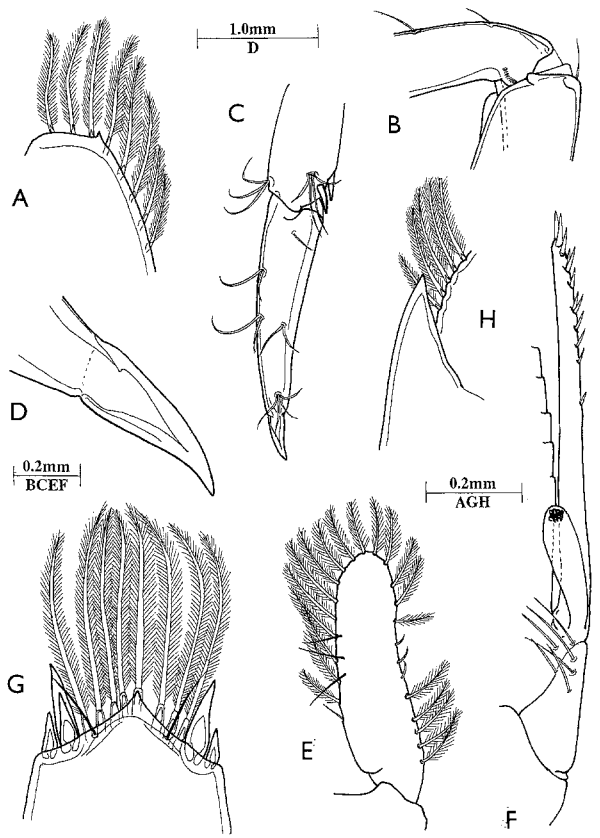

Fig. 5. Kakaducaris glabra, gen. nov., sp. nov. A, distolateral lobe of proximal segment of antennular peduncle. B, third pereiopod, carpo-meral joint, lateral. C, same, dactylus. D, same, ungius. E, male first pelopod, endopod. F, male second pleopod, appendices interna and masculina. G, posterior telson spines. H, exopod of uropod, distolateral angle.

spiniform setae distally; penultimate segment 0.5 of antepenultimate segment length, 4.0 times longer than proximal width, tapering, densely setose medially; terminal segment 0.8 of penultimate segment length, 4.5 times longer than proximal width, tapering, with stout distal spine and numerous groups of short serrulate setae ventromedially, coxa without medial process, sparsely setose, small rounded plate laterally, with small developed arthrobranch. All maxilliped with well developed exopods, flagella with numerous plumose setae distally.

Sternite of second thoracic somite broad, with triangular median projection. Fourth thoracic sternite without median process, broad, with low

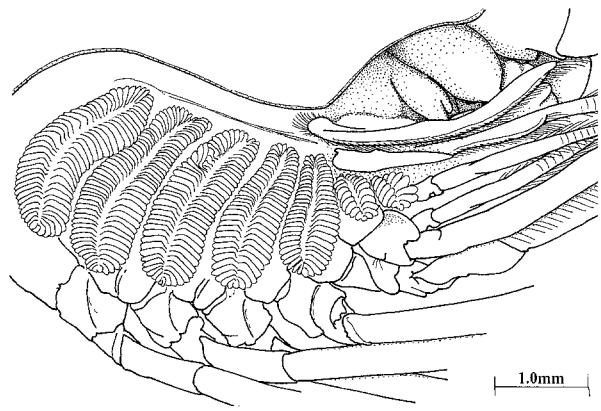

Fig. 6. Kakaducaris glabra, gen. nov., sp. nov., female paratype, right branchial region.

transverse ridge with small median notch, fifth sternite similar but more robust.

First pereiopods slender, extending slightly beyond antennular peduncle; palm of chela slightly compressed, about 1.7 times longer than deep, fingers about 1.1 times palm length, slender, tapering, about 4.5 times longer than proximal depth, with small acute hooked tips and laterally situated entire cutting edges; carpus about 1.5 of chela length, slightly tapered proximally, about 6.3 times longer than distal width; merus subequal to carpus, 6.0 times longer than central width, ischium 0.45 of merus length, sparsely setose medially, basis 0.8 of ischium length, with submedian row of setae, coxa robust with small ventromedian lobe.

Second pereiopods subequal and similar, with chelae equal to about 0.6 of carapace length in females, palm subcylindrical, slightly compressed, about 2.5 times longer than deep, smooth; fingers slender, tapering, about 0.9 of palm length and 5.5 times longer than deep, with small, acute, hooked tips, cutting edge entire, laterally situated, without teeth; in males, fingers about 1.2 times palm length, about 8.0 times longer than proximal depth, palm about 2.6 times longer than deep; carpus about 0.8 of chela length, about 4.5 times longer than distal width, tapered proximally, slightly excavate distally, unarmed; merus subequal to carpal length, uniform, about 5.5 times longer than central width, unarmed; ischium subequal to merus, about 6.0 times longer than dis-

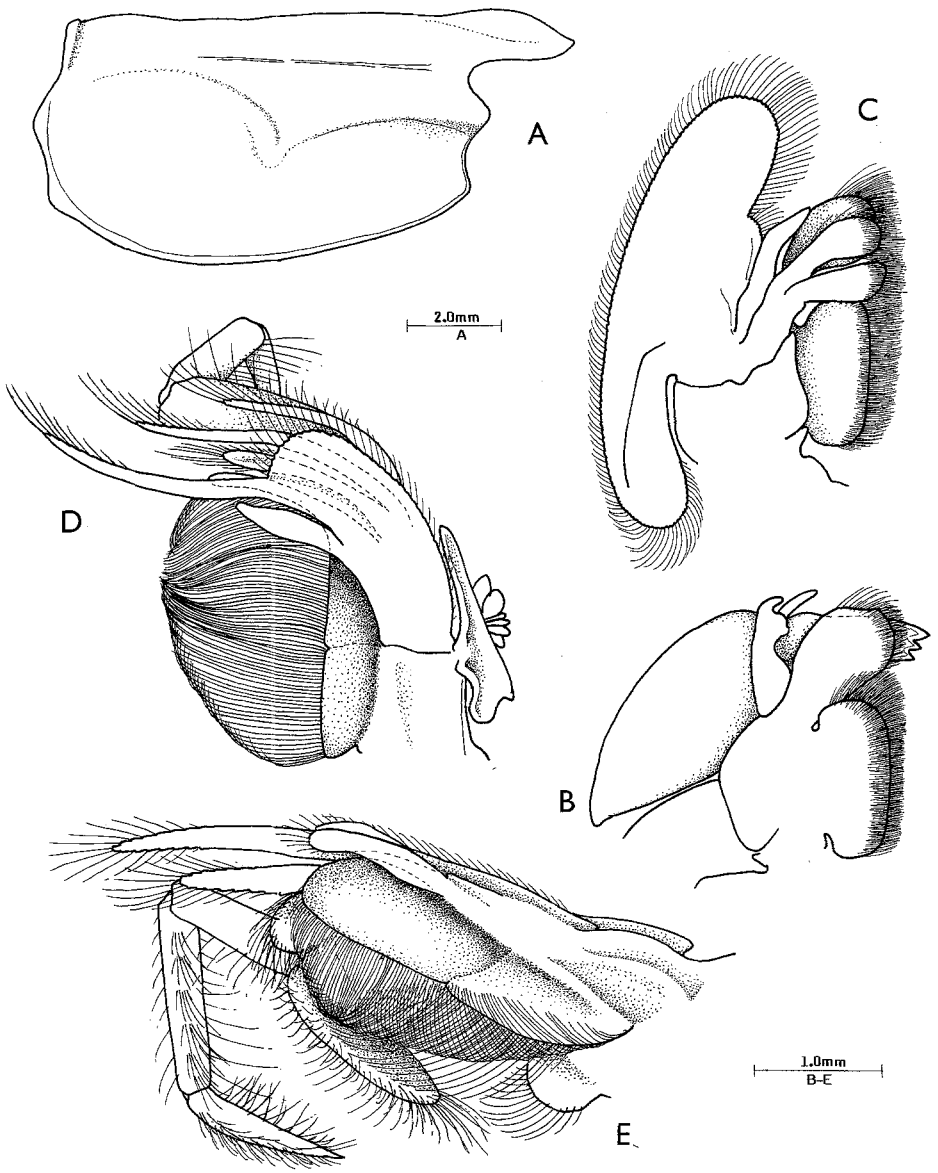

Fig. 7. Kakaducaris glabra, gen. nov., sp. nov. A, carapace, female. B, mandible and maxillula, right, ventral aspect. C, maxillula and maxilla, right, ventral aspect. D, maxilliped, right, dorsal. E, same, medial.

tal width, tapering proximally, unarmed; basis slender, unarmed, about 0.5 of meral length; coxa robust, without ventromedial process.

Third pereiopod slender, extending anteriorly to end of antennular peduncle; dactylus robust, simple, corpus compressed, about 3.5 times longer than deep, feebly curved, with stout, feebly demarkated unguis, equal to 0.2 of corpus length, corpus with dorsal, lateral and distolateral setae; propodus about 2.4 times dactylar length, uniform, about 10.0 times longer than wide, with a pair of distoventral spines and ventral and ventromedial rows each of 3 spines; carpus about 0.55 of propodal length about 4.8 times longer than distal width, with small curved row of about 10 short minute ridges proximomedially; merus slightly longer than propodus, about 7.0 times longer than deep, uniform, unarmed; ischium

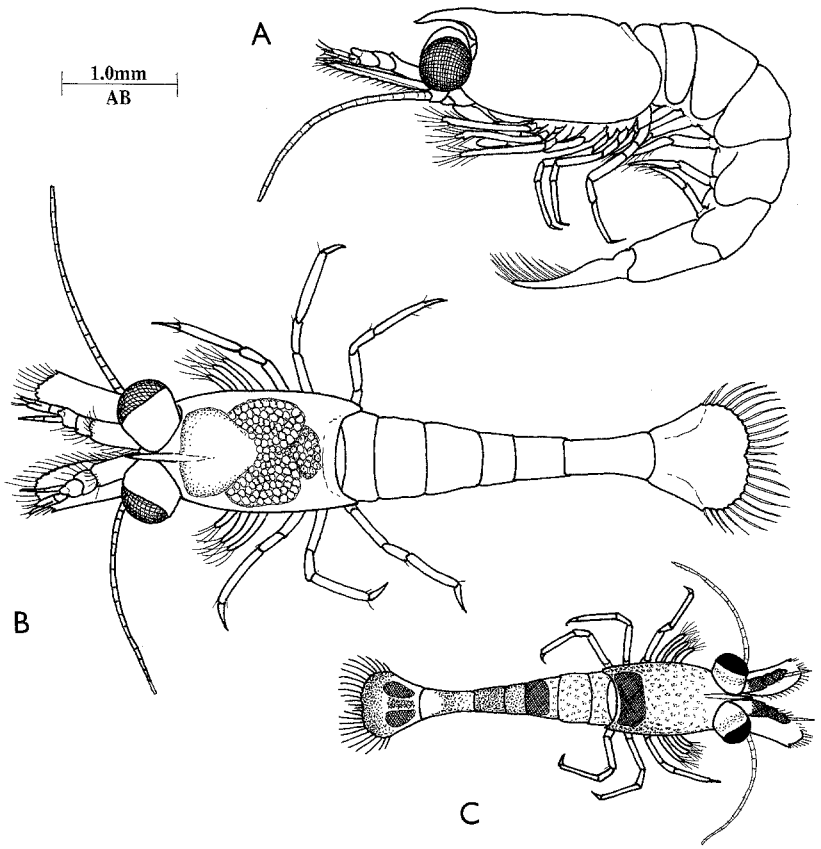

Fig. 8. Kakaducaris glabra, gen. nov., sp. nov. A, hatchling, dorsal. B, same, lateral. C, same, colour pattern. Cross hatched, white; dotted, reddish brown.

about 0.45 of merus length, unarmed; basis and coxa without special features. Fourth pereiopod similar to third, propodus 1.15 times length of third pereiopod propod, carpus with proximal row of minute transverse ridges. Fifth pereiopod similar to third, propodus 1.25 times length of third pereiopod propodus, about 16.0 times longer than deep, with 6 transverse rows of cleaning setae distoventrally, with 1 spine, ventral margin with 3 spines, ventromedial with 6, carpus with proximal row of minute transverse ridges.

Pleopods well developed. Endopod of male first pleopod about 3.6 times longer than wide, uniform, without distomedian lobe, medial border with 5 short plumose setae proximally, 3 short simple spines centrally, 5 plumose setae distally, lateral border with 10 plumose setae and proximal spiniform seta. Endopod of male second pleopod with elongated appendix masculina, exceeding tip of endopod, corpus about 13.5 times longer than proximal width, cylindrical, rigid, tapering slightly distally, distal half of medial border armed with numerous short simple spines, of increasing size distally. Appendix interna about 3.5 times longer than distal width, slightly swollen distally, with few cincinnuli, equal to 0.3 of length of appendix masculina.

Uropods with protopodite posterolaterally acute; exopod about 1.2 times length of endopod, about 2.5 times longer than wide, lateral border unarmed, feebly convex, with acute posterolateral tooth, without articulated spine medially; endopod about 2.6 times longer than wide.

Material examined. Known only from the type material listed above, and 50 spms (25 ♂, 2 ovig. ♀, 21 ♀, 2 juv.) from the same locality, collected on 2 October 1984, NTM Cr.002051.

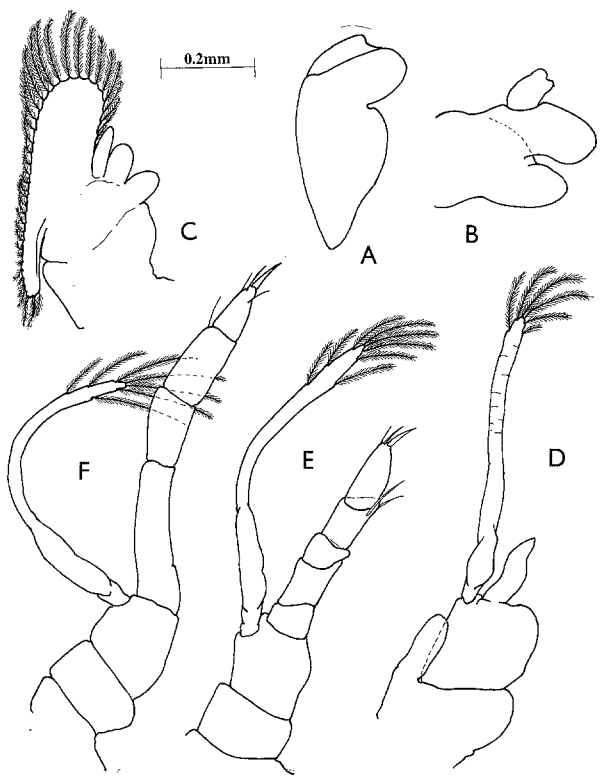

Fig. 9. Kakaducaris glabra, gen. nov., sp. nov., hatchling. A, mandible. B, maxillula. C, maxilla. D, first maxilliped. E, second maxilliped. F, third maxilliped.

Variations. Several specimens show small variations in the form of the rostrum, presumably due to minor injury. Two specimens differed from the rest on the presence of a single small acute tooth on the anterior region of the raised part of the dorsal rostral carina.

Colouration. Generally semitransparent with fine speckling of red dots. Dorsal surface of carapace and abdomen with series of conspicuous white patches; anterior and posterior median gastric, median intestinal, dorsolateral hepatic and dorsolateral intestinal; first abdominal somite with median and dorsolateral pair, fourth with large oval or rectangular median patch, fifth and sixth with median posterior spots; telson with central median spot; bases of antennular peduncle around statocyst also white. Rostrum transparent. Eyes with cornea rimmed with white. Abdomen with band of dark red-blue along upper edges of pleura to anterior of sixth segment, extending across dorsum of fifth somite; similar bands along anterior sides of telson. Similar red-blue colouration along thoracic and abdominal sternites and branchiae, first and second abdominal sternites with median white spot in large females. Antennular peduncle finely red speckled, also anterior uropod and telson, which has darker posterior end. Scaphocerite and distal ends uropodal rami colourless. Pereiopods colourless, translucent; tips of fingers of second pereiopods orangeish. Gastric mill dark maroon speckled with red and white, hepatopancreas pinkish, intestine dark brown, conspicuous, ovary and ova dark olive green. White spots vary considerably in size and distribution, frequently lacking in varying degrees in smaller specimens, the antennular, posterior gastric, first and fourth abdominal and telsonic spots being most consistent.

Measurements. (See Table 3, p. 38.)

Habitat. The shrimps were collected in a large rock pool in the downfall of a waterfall at the eastern edge of the Arnhem Land escarpment. The pool was situated at an altitude of 90 m above mean sea level, about 60 m above flood plain level and 150 m below the general level of the plateau surface. No fish or other decapod crustaceans were noted in the pool, in which water flow was minimal and little vegetation was present. Shrimps were absent from pools lower in the water course. Some unidentified phreatoicid isopods, *Eophreatocius* sp., were present. The associated insect fauna consisted of hemipterid water bugs, *Anisops* sp. (Notonecidae) and caddis-fly larvae of the families Leptoceridae and Helicopschidae.

Ovum. The ova are relatively large and few, length about 1.5 × 2.5 mm, about 10 in number.

Description of hatching. Rostrum acute, reaching to about 0.3 of first segment of antennular peduncle, dorsal carina convex, without teeth; carapace without spines. Abdominal segments unarmed dorsally, pleura all rounded. Telson about

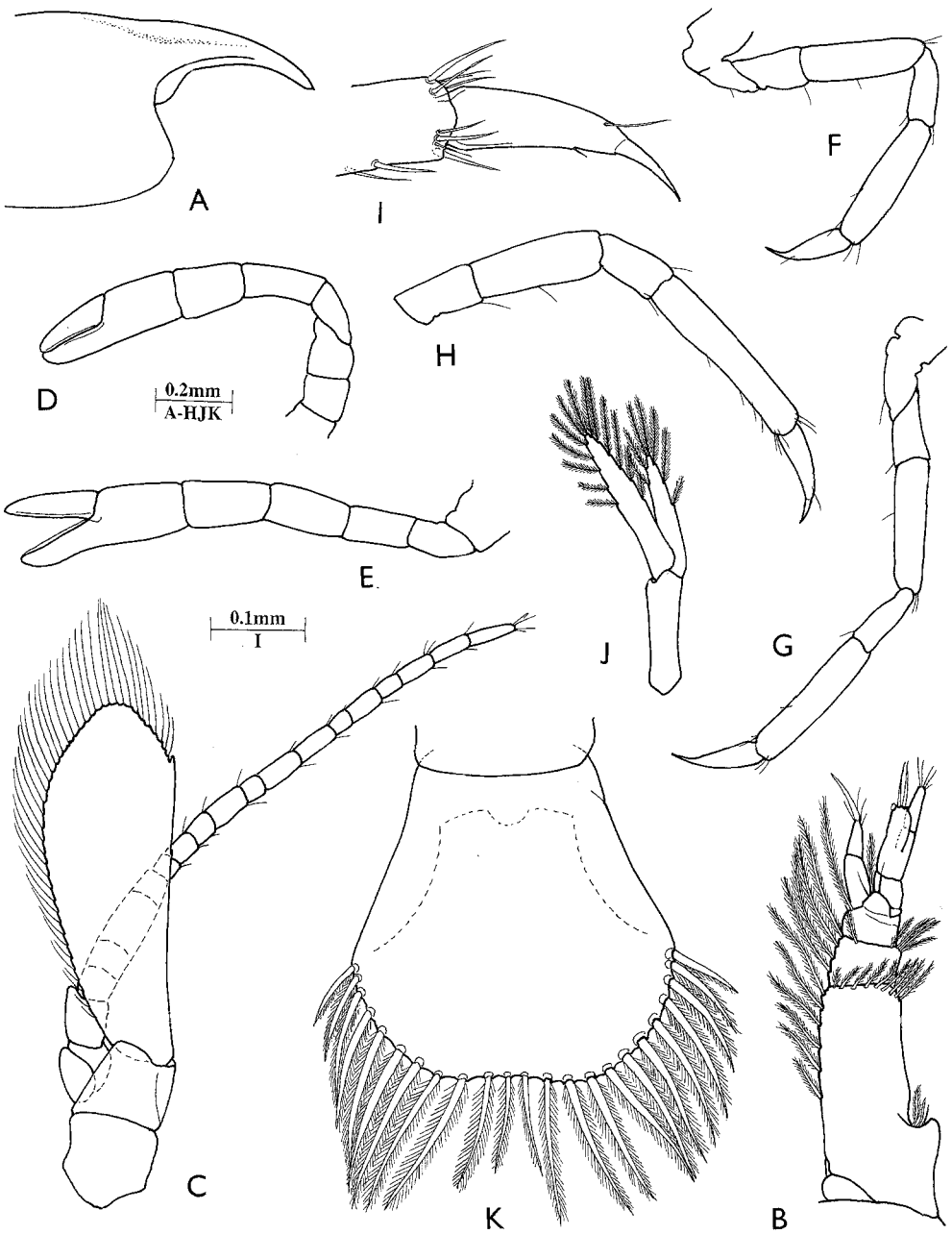

Fig. 10. Kakaducaris glabra, gen. nov., sp. nov., hatchling. A, anterior carapace and rostrum. B, antennule. C, antenna. D, first pereiopod. E, second pereiopod. F, third pereiopod. G, fourth pereiopod. H, fifth pereiopod. I, dactyl of fifth pereiopod. J, third pleopod. K, telson.

1.1 times broader than long, posterior border biconvex, with 11 + 11 setae, biplumose except for lateral seta, plumose on medial border only. Uropods of next stage feebly discernible within cuticle.

Antennular peduncle three-segmented. Proximal segment 2.0 times longer than wide, with small stylocerite with 3 setae medially, 6 plumose setae along distomedial border, 9 plumose setae along anterior dorsal margin. Statocyst not evi-

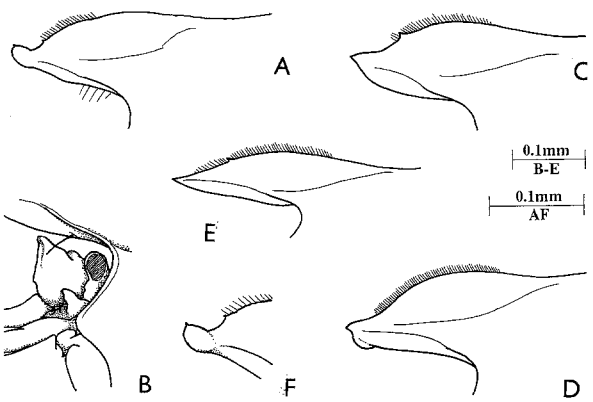

Fig. 11. Kakaducaris glabra, gen. nov., sp. nov. A, ophthalmic somite. B–E, rostral variations. F, tip of A, further enlarged. A–C, female; D, male.

dent. Second segment 0.2 of length of first, with 4 plumose setae medially, 1 anteriorly and 4 distolaterally. Distal segment with 1 distolateral plumose seta, 1 distodorsal plumose and 2 simple setae. Outer flagellum with short proximal segment and fused proximal segment of longer and shorter rami. Short ramus bearing 2 terminal aesthetascs, longer ramus with single free segment with 5 simple setae distally. Inner flagellum consisting of 2 segments, distal segment with terminal spine and 4 short simple setae.

Antenna with short unarmed basicerite; flagellum with 17 segments, carpocerite short and stout. Scaphocerite 2.8 times longer than broad, lateral border feebly concave with small distolateral tooth, anterior margin of lamella rounded, with medial margin bearing numerous plumose setae.

Eyes with short cylindrical stalks of same diameter as cornea.

Mandible with molar and incisor processes feebly differentiated, unarmed; without palp. Maxillula with feebly bilobed palp; upper and lower laciniae feebly developed unarmed. Maxilla with well developed scaphognathite, with about 40 plumose marginal setae; palp subcylindrical, basal endite bilobed, coxal endite obsolete, all devoid of setae. First maxilliped with small simple epipod; palp subcylindrical, basal and coxal endite distinct, rounded, devoid of setae; exopod with 6 plumose setae distally, caridean lobe not developed. Second maxilliped without epipod; exopod with 8 plumose setae distally; endopod 5 segmented, terminal segment with spine and 2 simple setae distally, penultimate segment with 2 distoventral spines, other segments unarmed; basis and coxa devoid of setae. Third maxilliped without epipod; exopod with 7 plumose setae distally; endopod 4 segmented, ischio-meral segments fused, terminal segment with distal spine and 3 simple setae, penultimate segment with single distodorsal spine, basal segment slightly produced medially, basis and coxa devoid of setae.

First and second pereiopods 7 segmented, with chelae distinct, dactylus free but immobile; proximal segments devoid of setae. Ambulatory

Table 3. Measurements (mm)

	Holotype	Allotype	Largest ♀	Largest ♂
Postorbital carapace length	8.0	5.6	7.5	8.5
Carapace and rostrum	10.3	6.4	9.5	10.0
Total body length (approx.)	–	–	23.0	26.0
Second pereipod chela, L:R	5.0:4.8	5.2:5.9	6.0:?	5.4:5.3
fingers, L:R	2.5:2.5	2.8:3.3	3.2:?	3.3:3.4
fingers: chela, L:R	0.50:0.52	6.53:0.56	0.53:?	0.46:0.37
carpus, L:R	3.3:3.1	3.2:3.5	3.5:?	3.3:3.4
merus, L:R	3.2:3.2	2.8:3.3	3.5:?	3.3:3.1
ischium, L:R	2.7:2.6	1.8:2.6	3.0:?	3.1:2.9
Third pereiopod, propod	2.9	3.6	2.6	2.7
Fourth pereiopod, propod	3.3	4.2	3.0	3.3
Fifth pereiopod, propod	4.0	3.0	3.3	4.4

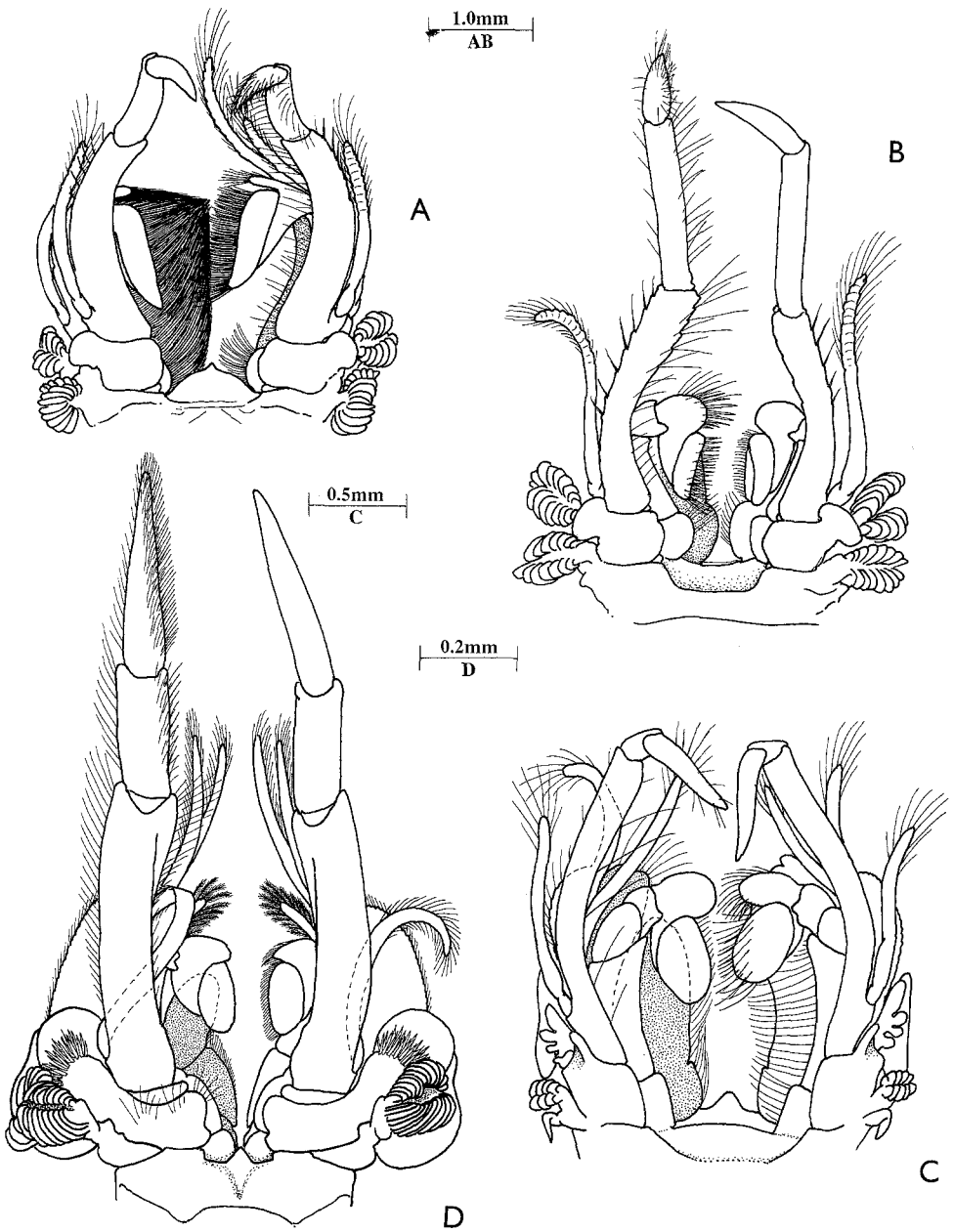

Fig. 12. Maxillipeds, ventral aspect. A, *Kakaducaris glabra*, gen. nov., sp. nov. B, *Macrobrachium* sp. C, *Typhlocaris galilea* Calman. D, *Desmocaris trispinosa* (Aurivillius).

pereiopods well developed, without exopods; dactylus about 4 times longer than proximal depth, simple, with unguis distinct, dorsal and ventral setae present on corpus; propodus 3.0 times longer than wide (P3) to 5.5 times (P5), with setae distally and sparsely along ventral border; carpus 0.5 times length of propodus (P3) to 0.4 (P5), with distal dorsal and ventral setae; merus subequal in P3–5, most robust in P5; basis and coxae unarmed.

Pleopods all biramous, with exopod and endopod with numerous plumose setae.

Measurements of hatchling. Total body length, 5.3 mm; carapace length, 1.5 mm.

Discussion

The mouthparts of the genus *Kakaducaris* present a suite of morphological features that show only minimal differences from those of *Leptopalaemon* and are almost without parallel in the other genera of the Palaemonidae. These clearly indicate that these shrimps conform to radically different life styles and emphasizes their isolated systematic position.

The mandibles (Fig. 3a) present few special features, other than the presence of a rudimentary, single segmented palp. The incisor process is not reduced and is typical of many palaemonid shrimps. The molar process (Fig. 3b) is rather scoop-like, with a few small teeth, quite lacking the transverse ridges of minute teeth as found in *Desmocaris*. The maxillula (Fig. 3c) overlies the mandible in such a way that the gap between the distal lobes of the palp appears to almost engage with the mandibular palp and suggests that its function may be to clean the palp (Fig. 7b). The lacinae are densely setose along their ventral margins, forming an almost complete brush. The maxilla (Fig. 3e) overlies the maxillula in such a way (Fig. 10c) that the similarly setose lobes of the basal endite occlude the small gap between the maxillular laciniae to form an almost continual dense ventromedial brush. The broad elongate lower lacinia of the maxillula would appear to render a large coxal endite on the maxillula superflous, which may correlate with its absence. The first maxilliped (Fig. 3fg) is most remarkable and highly characteristic, with its elongate basal endite and distinctly demarkated coxal endite, both with a dense medial fringe of very long fine setae, forming a basket-like arrangement (Fig. 7de), with the endites forming the lateral and distals walls and the setae the ventromedial part of the unit. The endites are deeply concave dorsomedially and the fine inner setal fringes on each side curve to meet in the midline and are reflected dorsally inwards, with the lower ventral row of marginal setae projecting more outwards, possibly to protect the finer inner setae. The inner mouthparts project into this cup-shaped basin, which is anterodorsally closed by the palp of the first maxilliped. The broad caridean lobe lies in a plane approximately at right angles to that of the endites. The endopod of the second maxilliped (Fig. 3hi), with its narrowed dactylar segment and medially produced propodal segment, forms another deeply concave arrangement that covers the outer ventral surface of the setal basket of the first maxilliped, possibly also protecting it from damage by, or separating off the coarser food particles from those retained by the fine inner setae. The dense medial fringe setae may function also to clean the outer surface of the setal basket, pushing the accumulated particles through the opposed tips of the long filtratory setae to be collected up by the endites of the maxillae, passed over the ventral surface of the paragnaths and between the mandibles. When the second maxillipeds are adducted, with the distal segments flexed, the setae of the distomedial lobe of the propodal segment, medial margin of the dactylar segment and of the rounded medial coxal lobe, form a continuous band, effectively a ventromedial enclosure over the setal basket (Fig. 12a). The third maxilliped endopods are relatively robust and strongly bowed, gaping widely around the setal basket, the posterior end of which is firmly closed by the rounded transverse plate of the second thoracic sternite.

The different arrangements of the maxillipeds in *Kakaducaris*, *Macrobrachium*, *Typhlocaris* and *Desmocaris* are illustrated in Fig. 12, as viewed from the ventral aspect, with many setae omitted. It is immediately apparent that only *Kakaducaris* possesses the setal-basket arrangement, based on the first maxilliped and protected by the second maxillipeds. The closest resemblance is shown by *Desmocaris*. In this genus the first maxilliped endites are comparatively feebly developed (Powell, 1977) and relatively sparsely setose, with shorter setae. The prodopal segment of the second maxilliped shows a distomedial lobe which is similar to that of *Kakaducaris*, but the dactylar segment is short and oval, with a spinulose medial margin,

not elongate and setose, and the coxa is without a well rounded setose medial lobe. The ischiomerus is provided with long setae, but these are coarsely and more widely spaced than the filtratory setae of *Kakaducaris* and are probably of a protective nature.

The systematic position of the genus *Kakaducaris* raises some interesting problems, as it does not fit well into the presently used schemes of subgenera (Holthuis, 1955; Balss, 1957, or Bruce, 1986). The genus is clearly very closely related to *Leptopalaemon* Bruce and Short, on account of the characteristic morphology of the mouthparts, radically modified for filtratory feeding, and without precise parallel elsewhere in the Palaemonidae. A close relationship of the two genera is also supported by their occurrence in the same geographical region, – Arnhem Land. The appendix masculina is also characteristic of the two genera and unique in the Palaemonidae. With two pairs of spines on the posterior telson margin, the genera show a relationship to the Palaemonidae rather than the Pontoniinae, and their general morphology also closely resembles other genera of the Palaemoninae. Following Sollaud (1910), one of the features generally used to distinguish the Palaemoninae from the Pontoniinae has been the presence of a pleurobranch on the third thoracic somite in the former and its absence in the latter (Borradaile, 1917; Kemp, 1922; Holthius, 1950, 1955). Some subsequent authors have pointed out that in a number of palaemonine shrimps the third thoracic somite appears to lack a pleurobranch, but possesses two arthrobranches, rather than the 'normal' complement of one (Padwardhan, 1937; Abele & Felgenhauer, 1986; Bruce & Short, 1993). In these cases, there is usually a larger lower outer arthrobranch and smaller upper inner arthrobranch. Except for the Euryrhynchinae, all other palaemonid subfamilies have, at the most, only a single arthrobranch, often small, and in many of the Pontoniinae reduced, vestigial or absent. The utility of the number of arthrobranch on the third somite in assessing the systematic position of the clearly closely related genera *Kakaducaris* and *Leptopalaemon* is complicated by the presence of one arthrobranch on the third somite in the former, but two in the latter.

The mouthpart morphology of *Leptopalaemon* and *Kakaducaris*, together with the form of the appendix masculina, is without parallel in other palaemonid subfamilies and together are sufficiently distinctive enough to justify the designation of a further subfamily within the Palaemonidae. The suite of morphological characters involved in converting the mouthparts into a filtratory mechanism, not without parallel in some of the Atyidae, indicate that these shrimps have adopted a radically different life style and confirms their rather isolated systematic position. The systematic relationship of the genera *Kakaducaris* and *Leptopalaemon* in relation to the currently recognized subfamilies of the Palaemonidae is also ambiguous and their isolated position requires that a further subfamily is designated.

Subfamily Kakaducaridinae nov.

Palaemonid shrimps with distinct compressed rostra; carapace without longitudinal dorsolateral suture, branchiostegal suture present or absent, lacking supraorbital and hepatic spines; mandible with palp; first maxilliped with endites forming hemispherical filtratory basket; third maxilliped with ischio-merus fused, ischium distinct from basis, with 1–2 arthrobranchs; 5 pairs of pleurobranchs, first pereiopods slender, with simple fingers; second pereiopods with well developed chelae; ambulatory pereiopods with simple dactyls, appendices internae on second to fifth pleopods; appendix masculina elongate, tapering, subcylindrical, rigid, with numerous short spines; exopod of uropod with distolateral tooth, without articulated spine medially; telson with 2 pairs of posterior spines.

Provisionly included in the subfamily Kakaducaridinae, is the genus *Calathaemon*. Although there is a close general resemblance between *Calathaemon* and *Leptopalaemon*, which may be readily distinguished by the branchiostegal spine of the former genus, the paragnaths are radically different, the mandible lacks a palp and has a

reduced incisor process; the posterior margin of the telson also bears numerous pairs of spines. The third maxilliped has at least one arthrobranch, but may possibly have a second, albeit rudimentary. The appendix masculina of *Calathaemon* does not show the characteristic features of *Kakaducaris* or *Leptopalaemon*. *Calathaemon holthuisi* (Strenth) is known from only a few specimens, generally not in perfect condition, and the details of some parts of its morphology are still obscure. To include *Calathaemon*, the above definition would require significant modification. Examination of further material of *Calathaemon* may indicate that it is sufficiently distinct to require its own subfamily. Despite these differences, the first maxillipeds in the three taxa are so similar in their unusual shape, that it is difficult to avoid the conclusion that they are synapomorphic and there must be some close phylogenetic relationship. Both *Calathaemon holthuisi* in a Mexican cave, and *Leptopalaemon gagadjui* and *Kakaducaris glabra* on the Arnhem Land escarpment, would appear relict species in specialized ecological niches, with few competitors or predators. The abbreviated larval developed occurring in *Kakaducaris* would appear to be a further adaptation to its waterfall habitat.

Recent keys to the subfamilies of the Palaemonidae (Holthuis, 1950; 1952a; 1955; Balss, 1957; Bruce, 1986) have utilized the number of branchiae as an important character in separating some taxa. All subfamilies possess a pleurobranch on each of the somites bearing a pereiopod. As discussed above, the Palaemoninae appear to have two arthrobranchs on the third thoracic somite, rather than an arthrobranch and pleurobranch, a feature that is shared only with the subfamily Desmocaridinae (Powell, 1977). The Kakaducaridinae, as defined above, may have one or two arthrobranchs in this position. The Euryrhynchinae and Typhlocardinae both possess only a single arthrobranch on this somite (Powell, 1976; Calman, 1909). The Pontoniinae may have a single arthrobranch, often rudimentary, or may lack an arthrobranch on this somite. The Gnathophyllinae and the Anchistioidinae are always without arthrobranchs on the third thoracic somite. The presence of two arthrobranchs is considered to be the plesiomorphic condition, with the Palaemoninae as the least specialized taxon. Other taxa show progressive reductions in the number of branchiae, with the loss of the podobranch from the second maxilliped and, in the Pontoniinae, even considerable reductions in the size of the pleurobranchs, *i.e.* in *Paratypton* (Bruce, 1969). However, the number of branchiae in many genera of the Palaemoninae should be re-examined for confirmation that the presence of two arthrobranchs only is a constant feature as many generic or species descriptions are not precise on this point. A key for the separations of the subfamilies of the Palaemonidae is provided below.

A provisional key to the subfamilies of the family Palaemonidae Samouelle

1. Third maxilliped with ischium and merus distinctly articulated.. **Hymenocerinae** Ortmann, 1890
– Third maxilliped with ischium and merus completely fused 2
2. Carapace with complete longitudinal dorsolateral suture present, eyes reduced; third maxilliped with sagittate setae on coxal lateral plate . **Typhlocaridinae** Annandale and Kemp, 1913
– Carapace without longitudinal dorsolateral suture 3
3. Pleopods without appendices internae; carapace with supraorbital spines; telson without dorsal spines .... **Desmocaridinae** Borradaile, 1915
– Second to fifth pleopods with appendices internae 4
4. First maxilliped with endites modified to form filtratory basket, densely fringed medially with numerous fine long setae; appendix masculina elongate, subcylindrical,tapering, rigid, reaching to distal end of endopod, with numerous short spines; exopod of uropod with disloteral tooth, without articulated spinule ... **Kakaducaridinae** nov.

- First maxilliped not forming filtratory basket; appendix masculina not as above; exopod of uropod usually with distolateral tooth and articulated spinule (except in some Pontoniinae) 5
5. Upper antennular flagellum with two completely free rami; male second pleopod without appendix masculina . **Euryrhynchinae** Holthuis, 1950
- Upper antennular flagellum with rami partly fused proximally; male second pleopod with appendix masculina 6
6. Third maxilliped with two arthrobranchs; posterior margin of telson generally with two pairs of spines only ..... **Palaemoninae** Dana, 1852
- Third maxilliped with not more than one arthrobranch, frequently reduced or absent .. 7
7. Third maxilliped generally broadened, at least proximally, often operculate with ischiomerus fused to basis, mandible with incisor process reduced or absent, telson with ten pairs of spines ..... **Gnathophyllinae** Dana, 1852
- Third maxilliped generally slender, ischiomerus usually distinct from basis, non-operculate; incisor process of mandible usually distinct 8
8. Mandible with normal or reduced molar process; telson generally with 10 pairs of spines ..... **Pontoniinae** Kingsley, 1878
- Mandible with molar process distally flared or excavate; telson generally with 3–4 pairs of posterior spines only ... **Anchistioidinae** Gurney, 1938

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Addendum

Subsequent to the acceptance of this report for publication, an important review of the classification of the Caridae has become available (Chace, 1992).

This report requires readjustment of the classification of the Palaemonoidea as proposed in the present paper. In his review Chace recognizes the Anchistioididae, Desmocarididae, Typhlocarididae, Palaemonidae, Hymenoceridae and Gnathophyllidae as families of the Palaemonoidea. To maintain parity with this classification, the Kakaducaridinae should be elevated also to familial rank, as the Kakaducarididae.

In Chace's report the Palaemonidae contains the traditional subfamiles Palaemoninae and Pontoniinae. The Typhlocarididae is also subdivided into two subfamilies, the Typhlocaridinae and the Euryrhynchinae. In the present author's opinion these two taxa are not closely related and should also receive independent familial status. The characters that separate them in Chace's key, the presence of a longitudinal branchiostegal suture on the carapace and the proximally fused biramous upper antennal flagellum in the Typhlocarididae and the absence of any longitudinal carapace suture and completely biramous upper antennal flagellum in the Euryrhynchinidae, are of much greater systematic importance than the character used to unite them, the acute anterior margin of the caridean of the first maxilliped. This character could have readily evolved independently in taxa that are not otherwise closely related. Another feature that conspicuously distinguishes the Euryrhynchinidae from the Typhlocaridinidae is the lack of an appendix masculina on the endopod of the second pleopod in the former family.

Additional reference:

Chace, F. A., 1992. On the classification of the Caridea (Decapoda). Crustaceana 63: 70–80.