

TWO NEW FRESHWATER CRABS IN *AUSTRALOCARCINUS* DAVIE, WITH
REMARKS ON TROGLOPLACINAE GUINOT AND GONEPLACIDAE MACLEAY
(CRUSTACEA:DECAPODA:BRACHYURA)

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Two new species, *A. kanaka* and *A. palauensis*, of the previously monotypic *Australocarcinus* Davie are described from New Caledonia and Palau Islands, respectively. The three species are separated on dentition of the anterolateral margins. Direct development of the young without free-living stages is confirmed for *A. kanaka*. *Australocarcinus* is placed in the previously monotypic almost completely freshwater Troglolacinae Guinot which is restricted to the tropical West Pacific. Their apparent closest relatives are marine, mostly deepwater Chasmocarcininae Serène (Gonoplacidae). *Trogloplax* has strong troglobitic adaptations and is presumed to have evolved from an *Australocarcinus*-like ancestor. The Troglolacinae is separated from the Chasmocarcininae by structure of the antennular region, and differences in length and shape of the male gonopods. □ *Brachyura*, *Goneplacidae*, *Australoplox*, *Trogloplax*, *freshwater*.

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Trogloplax Guinot, 1986, was erected for a freshwater troglobitic crab from New Britain. Its type, *T. jolivetii*, has a remarkable appearance, blind, and with many adaptive features for a cave environment. Because of its many peculiar features Guinot (1986) erected the Troglolacinae, in the Goneplacidae for it.

Australocarcinus Davie, 1988, was established for a north Queensland estuarine species, *A. riparius* Davie, 1988, also peculiar in the combination of morphological characters, in particular the unusual sternal plate, gonopods, and putative direct development of the young.

While *Trogloplax* shared the unusual structure of male sternite 8, its strong troglobitic adaptations made it difficult to be sure if the two genera were closely related. Close comparison shows the 2 genera to be related in the Troglolacinae. We provide a redefinition of the subfamily and better understanding of its relationships within the Goneplacidae.

Two additional species of *Australocarcinus* are described herein. One comes from a freshwater stream in northern New Caledonia and the second, from Palau, was discovered by P.J.F.D. amongst an unidentified collection of grapsids on loan from the USNM to Michael Türkay at the Senckenberg Museum, Frankfurt. Also a large population of *A. riparius* from a freshwater rainforest stream in north Queensland is reported.

This discovery, the records from freshwater of the New Caledonian species and the confirmation of direct development, show that troglolacinae are a very old freshwater group, probably derived from a marine ancestor, with at least *A. riparius*, showing estuarine tolerance. Jamieson & Guinot (1996) examine the ultrastructure of the spermatozoan of *A. riparius* and discuss possible generic relationships.

Abbreviations used in the text: c.b.=carapace width; G1,G2=male first and second gonopods; MNHN, Muséum national d'Histoire naturelle, Paris; QM, Queensland Museum, Brisbane; SMF, Senckenberg Museum, Frankfurt; USNM, United States National Museum, Washington.

Measurements given in the text are of the carapace breadth (measured at the widest point) followed by length. Leg segments were measured in a straight line to give maximum dorsal length, and so are not always the maximum possible length.

SYSTEMATICS

Family GONEPLACIDAE MacLeay, 1838
subfamily TROGLOPLACINAE Guinot, 1986

Troglolacinae Guinot, 1986:307; 1987:25; 1988:22;
1994:167; Guinot & Geoffroy, 1987:18.



FIG. 1. *Australocarcinus kanaka* sp. nov., ♀ paratype, 11.1 x 9.5 mm (QMW21389), dorsal view. Scale line in mm.

DIAGNOSIS (emended from Guinot, 1986). Carapace rounded; sometimes poorly calcified; anterolateral margin cristate, entire or toothed; front with or without shallow median indentation, without latero-external notch. Eyes relatively small. Antennules folded completely into fosset. Antenna lying in orbital hiatus. Buccal frame quadrangular; third maxilliped wide, together almost completely closing buccal cavity; exopod broad, with flagellum. Sternal plate very broad, with all sutures interrupted; large part of sternite 8 exposed; a supplementary transverse suture in middle of sternite 8, parallel to suture 7/8, forming a supplementary plate. Sterno-abdominal cavity deep. Male abdomen with segments 3-5 fused. Abdominal locking mechanism in normal position. Vulvae of female very large, occupying position near extremity of sternal suture 5/6. Penis very long, lying in covered channel on sternite 8, only uncovered next to the coxa of P5; finally protruding as long soft papilla. Chelipeds with minor heterochely and heterodonty. G1 stout, moderately tapering, with an apical aperture; G2 about as long as G1, with flagellum about same length as peduncle.

REMARKS. The Trogloplacinae belong to the Heterotremata showing a coxosternal disposition

of the male sexual opening (Guinot, 1978, 1979a).

Australocarcinus Davie, 1988

Australocarcinus Davie, 1988:259.

TYPE SPECIES. *Australocarcinus riparius* Davie, 1988, by original designation.

DIAGNOSIS. Carapace smooth, glabrous, regions poorly defined; anterolateral margins convex, with or without rounded teeth, posterolateral margins subparallel, posterolateral facet delimited. Frontal margin shallowly sinuous, formed of 2 rounded lobes, moderately deflexed, without preorbital lobes or teeth; fronto-orbital border c. 0.5-0.6 times carapace width. Orbits small, unarmed, with slightly raised rim. Eyestalks short, moveable, with well developed corneas; completely retractable within orbit. Chelae robust, similar but one slightly larger. Legs long, slender, hirsute, second pair longest. Male abdomen with segments 3-5 fused, segment 3 expanded laterally, subequal in width to segment one, neither covering sternum between last pair of legs. Sternal segment 8 in male with a closed, invaginated channel carrying penis, such

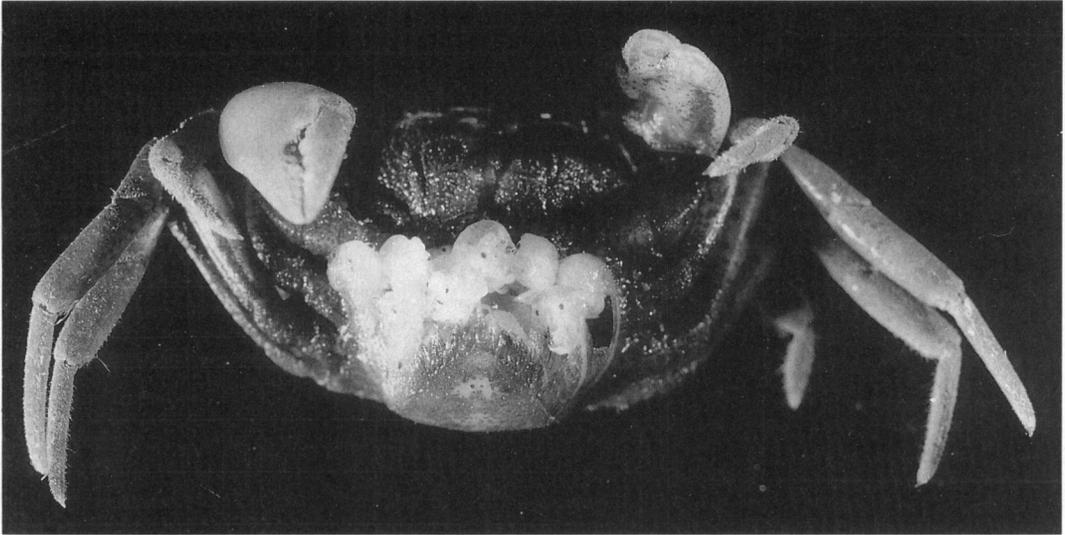


FIG. 2. *Australocarcinus kanaka* sp. nov., ♀ paratype, 11.1 x 9.5 mm (QMW21387), showing hatched megalopae under the abdomen. Scale line in mm.

that appears to be formed of 2 discrete plates; female of normal form. G1 stout, straight, tapering to simple apex; G2 as long as first, slender, narrowed in width over distal half, ending in simple apex.

***Australocarcinus riparius* Davie, 1988**
(Fig. 7)

Australocarcinus riparius Davie, 1988:260, figs 1-3.

MATERIAL EXAMINED. QMW18234, 12♂♂ (8.3x6.7-12.9x10.2 mm), 2♀♀ (10.2x8.2, 11.3x9.5mm), McIvor River at Isabella-McIvor road crossing, 15°07.2'S, 145°04.4'E, freshwater, under rocks in pools in drying river bed, fringing rainforest, DO₂ 0.9 ppm, altitude c. 30m, 18.11.1992, P. Davie & J. Short.

DESCRIPTION. See Davie (1988).

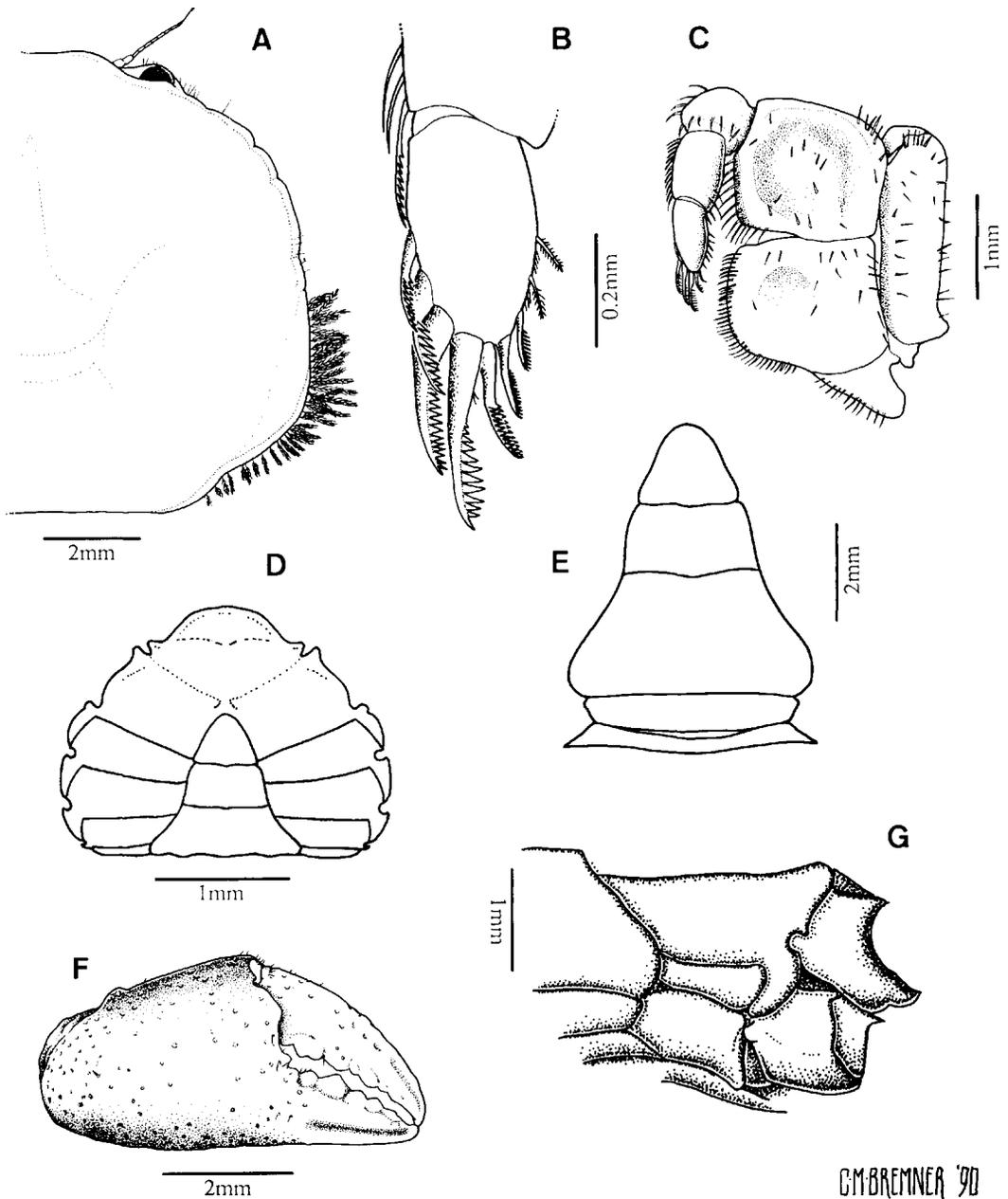
HABITAT. Freshwater and estuarine. The collection site at the McIvor River, is within rainforest at about 30m altitude, and they were found under rocks in pools in the drying river bed. Previous records were from estuaries where it is apparently common in salinities up to 20 p.p.t. (Davie, 1988).

DISTRIBUTION. This record extends the distribution 400km further north along the eastern Australian coast, from the Murray River, near Cardwell, and Hinchinbrook Island.

***Australocarcinus kanaka* sp. nov.**
(Figs 1-4, 6, 8)

MATERIAL EXAMINED. HOLOTYPE MNHNB25279, ♂ (11.1 x 9.5 mm), Col d' Amoss, near Ouégoa, New Caledonia, in freshwater stream, 100 m altitude, 13.11.1993, R. Raven. PARATYPES QMW21387, ♀ with megalopae (11.1 x 9.5 mm), data as for holotype. QMW21388, ♂ (10.5 x 9.0 mm), 2♀♀ (12.0 x 10.0; 13.1 x 10.8 mm), data as for holotype. QMW21389, ♀ (11.1 x 9.5 mm), ♂ (6.4 x 5.5 mm), Col d' Amoss, near Ouégoa, New Caledonia, in freshwater stream, 100 m altitude, 13.05.1984, G. Monteith and D. Cook. QMW20577, ♂ (3.6 x 3.1 mm), Ouekoulou, near Ouémou, upper drainage of the Ouémou River (draining to the west coast), small trickles originating from seeps, 230 m altitude, 13.07.1993, P. Bouchet. MNHN-B25280, 2♀♀ (11.2 x 9.2; 12.4 x 10.4 mm), Pangou, upper drainage of the Ouaième River (draining to the east coast), in wet mosses in splash zone of very small stream forming rapids, 300 m altitude, 13.07.1993, P. Bouchet. MNHNB25281, ♂ (8.7 x 7.3 mm), Ouéné, near Pangou, upper drainage of the Ouaième River, seepage and small trickle, under dense secondary vegetation, 400 m altitude, 14.07.1993, P. Bouchet. MNHNB25282, 3♂♂ (3.5 x 3.0; 4.0 x 3.6; 7.5 x 6.2 mm), 2♀♀ (7.2 x 6.3; 8.4 x 7.2 mm), Koumac, 3 Creeks, New Caledonia.

DESCRIPTION. Carapace subrectangular; greatest width behind exorbital angles; 1.16-1.17 times broader than long. Carapace convex anteriorly, flat from side to side posteriorly, slightly convex anteriorly. Regions poorly defined, cardiac and metagastric regions defined



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FIG. 3. *Australocarcinus kanaka* sp. nov. A-C, F, ♀ paratype, 11.1 x 9.5 mm. D, E, G, ♂ paratype, 6.4 x 5.5 mm (QMW21389). A, right side of carapace in dorsal view. B, dactylus of third maxilliped showing stout comb-like setae. C, third maxilliped. D, sternum of male. E, male abdomen. F, right chela. G, sternites 7 and 8 of male showing fissure to form a supplementary plate.

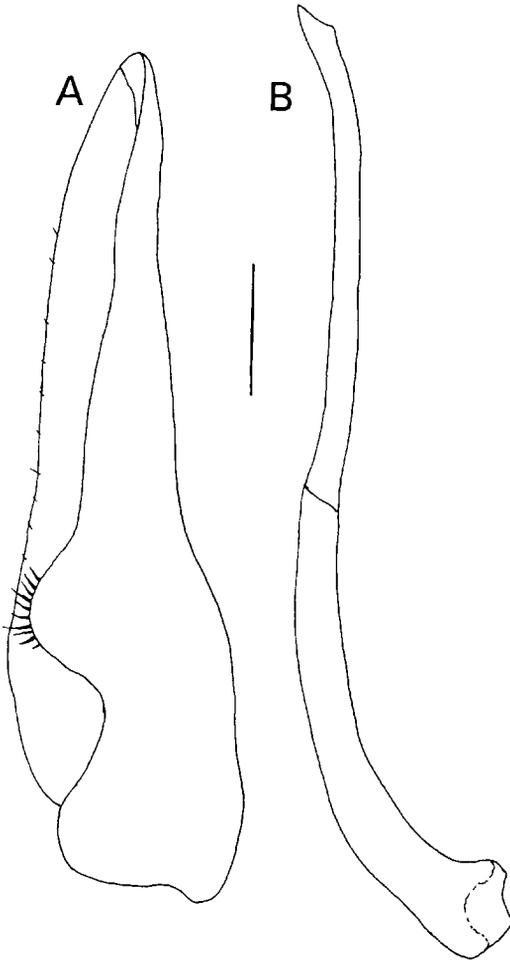


FIG. 4. *Australocarcinus kanaka* sp. nov., ♂ holotype, 11.1 x 9.5 mm, QMW20577. A, gonopod 1. B, gonopod 2. Scale line = 0.5 mm.

by shallow grooves; posterolateral facet delimited from behind last anterolateral tooth. Lateral margins subparallel, or slightly divergent posteriorly; straight. Anterolateral margins regularly convex; cristate; with two teeth behind the exorbital angle. Exorbital angle effaced. First anterolateral tooth blunt, placed about halfway along anterolateral margin. Second anterolateral tooth blunt; similar in size to first in small male but less obvious on holotype. Front moderately deflexed; with or without shallow median emargination; lateral angles rounded; no pre-orbital teeth; lateral margins diverging posteriorly; front-orbital border c. 0.5 times width. Carapace

surface evenly punctate, smooth, naked, long feathered setae restricted to side walls. Upper orbital border smooth; moderately concave. Lower orbital border straight, slightly concave at inner end; smooth. Inner angle of lower orbital border effaced, reaching about halfway up basal antennal segment; lower orbital border continuous with lower edge of outer orbital tooth as a slightly raised rim. Antennal flagellum entering orbit c. 1.5 times length of orbit. Orbital hiatus open. Basal antennal segment short, not touching front; unarmed. Inter-antennular septum narrow.

Third maxilliped with merus and ischium subequal. Merus slightly wider than long; outer margin straight; antero-external angle not produced, broadly rounded; about equal in length to ischium. Suture between merus and ischium horizontal. Ischium quadrate; inner margin smooth. Palp articulating at inner distal margin of merus; relatively long, dactylus armed with long, stout, comb-like bristles apically. Exopod moderately broad.

Chelipeds subequal, right slightly the larger on holotype; large and robust; borders granulate; row of longer feathered setae on anterior and posterior borders; carpus with a broad spine at inner angle. Outer surface of palm smooth, with coarse punctations. Outer surface of palm naked. Inner surface of palm smooth. Immobile finger moderately long; flattened on outer surface; with a broad, shallow, longitudinal groove, bearing close cropped setae; length cutting edge c. 0.4 times length propodus. Ventral border of chela straight. Dorsal surface of dactyl smooth, rounded; distal third of dactyl with broad groove like fixed finger. Fingers pointed, slightly curved inwards; a narrow gape between cutting margins proximally.

Walking legs relatively long, compressed, slender; second pair the longest. Longest leg c. 1.8-1.9 times maximum carapace width. Merus of third leg c. 3.7-4.25 times as long as wide (paratype and holotype respectively); carpus c. 2.7-2.8 times as long as wide; propodus c. 2.5-2.7 times as long as wide; dactylus c. 1.5-1.6 times length of propodus. Dactyli cylindrical, densely covered in felt of setae; terminating in acute chitinous tips. Anterior margin of merus with a subdistal shoulder; unarmed terminally. Leg segments smooth; fringed with short, feathered, setae, longer on infero-distal borders of propodi.

Male abdomen moderately broad; 5 free segments; 3-5 fused; 1 and 3 widest, subequal. First segment not covering entire width of sternum between 4th pereopods; narrow. Segments 3-5

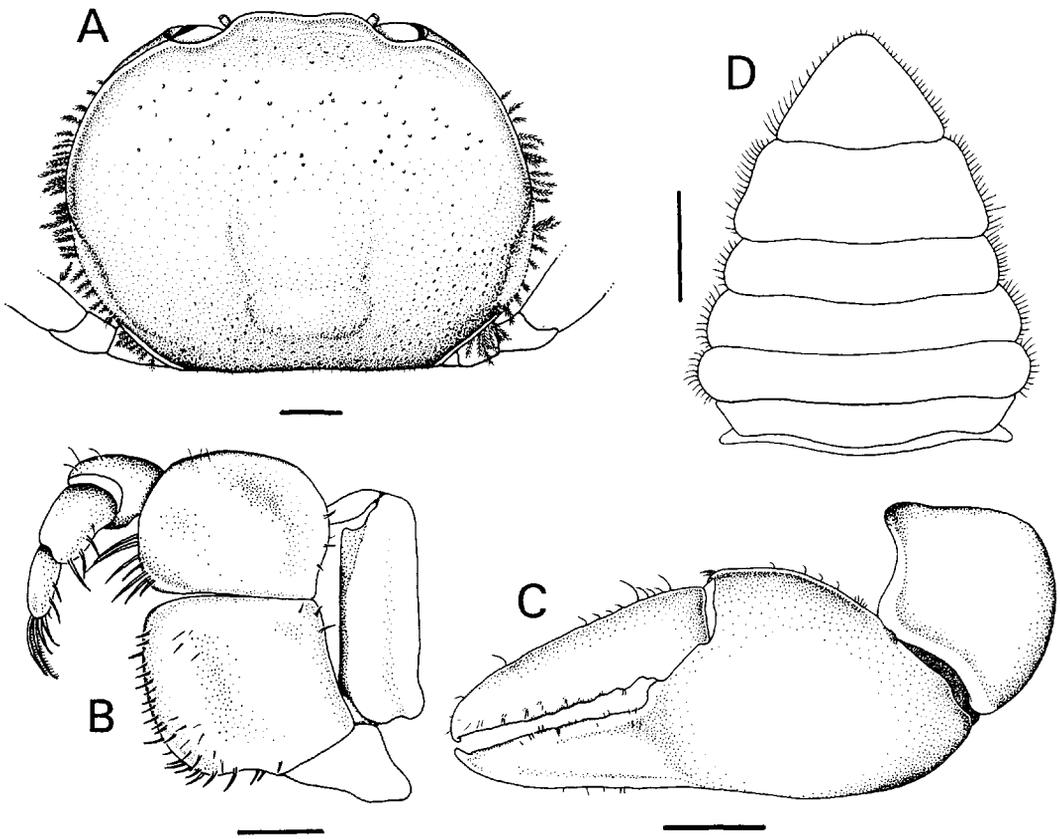


FIG. 5. *Australocarcinus palauensis* sp. nov., ♀ holotype, 7.1 x 5.8 mm (USNM). A, carapace in dorsal view. B, third maxilliped. C, left chela. D, abdomen. Scale line = 1 mm.

tapering, basally bulbous. Segment 6 c. 2 times wider than long. Telson longer than penultimate segment; c. 0.8 times longer than wide; apically rounded. Male gonopods Fig. 4. Sternum broad.

HABITAT. Freshwater habitats - in a freshwater stream; in small trickles originating from seeps; in wet mosses in splash zone of very small stream forming rapids; and in seepage and small trickles under dense secondary vegetation. Recorded up to 400m above sea level.

ETYMOLOGY. A noun in apposition for the native peoples of the islands of the South West Pacific.

***Australocarcinus palauensis* sp. nov.**
(Figs 5, 8)

MATERIAL EXAMINED. HOLOTYPE USNM, ♀

(7.1 x 5.8 mm), Addeido River, in small fast tributary, Babelthuap Id., Palau Islands, 05.03.1946, D.S. Frey.

DESCRIPTION. Carapace subrectangular; greatest width behind exorbital angles; 1.22 times broader than long. Carapace convex anteriorly, flat from side to side but slightly convex towards the margins. Regions poorly defined, cardiac and metagastric regions indistinctly defined; posterolateral facet not defined. Lateral margins subparallel; straight. Anterolateral margins regularly convex; cristate; without teeth. Exorbital angle effaced. Front moderately deflexed; bilobed; lateral angles rounded; no pre-orbital teeth; lateral margins diverging posteriorly; fronto-orbital border c. 0.55 times carapace width. Carapace surface evenly punctate, smooth. Dorsal surface naked, long feathered setae on side-walls. Upper orbital border smooth; moderately

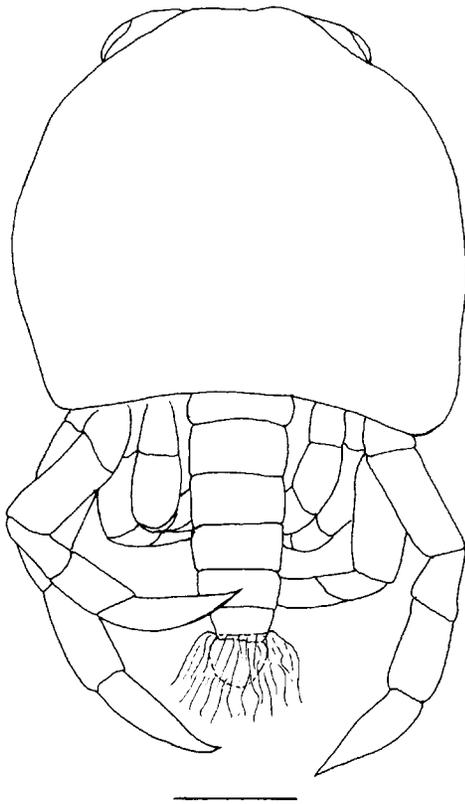


FIG. 6. *Australocarcinus kanaka* sp. nov., megalopa (QMW21387). Pleopodal membrane still attached around base of telson. Scale line = 0.5 mm.

concave. Lower orbital border shallowly sinuous; smooth; inner angle effaced, reaching about halfway up basal antennal segment; continuous with lower edge of outer orbital tooth as a slightly raised rim. Antennal flagellum entering orbit; both flagellums missing. Orbital hiatus open. Basal antennal segment short, not touching front, unarmed. Inter-antennular septum narrow.

Third maxilliped with merus and ischium subequal. Merus wider than long; outer margin slightly convex; antero-external angle not produced, broadly rounded; c. 0.85 times length of ischium. Suture between merus and ischium horizontal. Ischium quadrate; inner margin smooth. Palp articulating at inner distal margin of merus; relatively long, dactylus armed with long, stout, comb-like bristles apically. Exopod moderately broad.

Chelipeds slightly unequal, right slightly the larger; large and robust; borders granulate; row

of long feathered setae on anterior and posterior borders; carpus with a broad, blunt spine at inner angle. Outer surface of palm smooth, with coarse punctations; naked. Inner surface of palm smooth. Immobile finger moderately long, flattened on outer surface; without obvious longitudinal groove. Length cutting edge c. 0.4 times length propodus. Ventral border of chela slightly concave at base of fixed finger. Dorsal surface of dactyl smooth, rounded. Fingers pointed; slightly curved inwards; a narrow gap between cutting margins proximally, fingers with teeth poorly differentiated, but large, backwardly directed molar near base of dactyl.

Walking legs relatively long; compressed; slender; second pair the longest, c. 1.8 times maximum carapace width. Merus of third leg c. 3.5 times as long as wide; carpus c. 2.6 times as long as wide; propodus c. 2.4 times as long as wide; dactylus c. 1.4 times length of propodus. Dactyli cylindrical, densely covered in a felt of setae; terminating in acute chitinous tips. Anterior margin of merus with subdistal shoulder; unarmed terminally. Leg segments smooth; fringed with short, feathered setae, longer on infero-distal borders of propodi.

HABITAT. From a fast flowing tributary of the Adeido River suggesting a freshwater habitat.

ETYMOLOGY. For the Palau Islands.

REMARKS ON *AUSTRALOCARCINUS* DAVIE

The three known species are very similar but differ conspicuously by the dentition of the anterolateral margins. *Australocarcinus riparius* has 4 large, prominent blunt teeth; *A. kanaka* has only 2 low, hardly projecting, blunt lobes; and *A. palauensis* has no anterolateral teeth, but simply a continuous crest. The telson of *A. kanaka* is much shorter than on *A. riparius*. *A. riparius* also differs from the other two species by having the outer margin of the merus of maxilliped 3 much more strongly convex.

Davie (1988) speculated that direct development occurred in *A. riparius* because 18 juvenile crabs were collected with the adult female. This reproductive strategy has now been confirmed for *A. kanaka* as one female (QMW21387) has 17 megalopae still attached to its pleopods (Figs 2,6). The megalopae have no obvious yolk reserve. Oviparous females of *A. riparius* carry about 70 eggs, so there seems to be significant attrition during the developmental stages. The

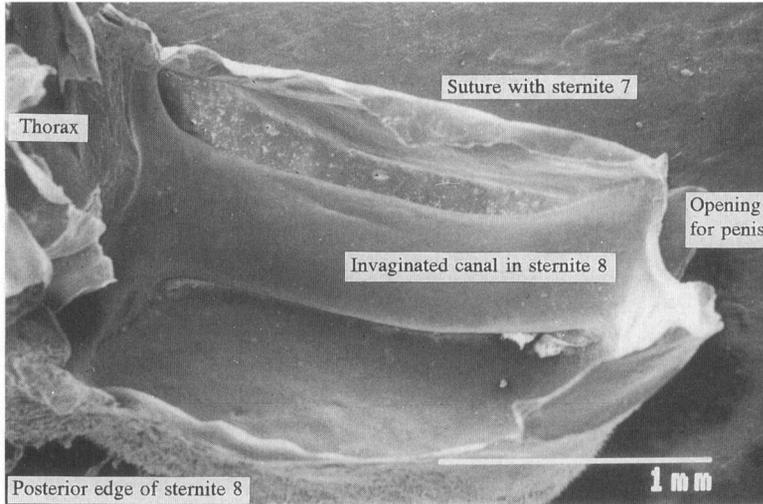


FIG. 7. *Australocarcinus riparius* Davie, 1988 (♂, 11.6 mm c.b., QMW18234), scanning electron micrograph of the inside of sternite 8, showing invaginated channel in which the penis lies.

holotype female of *A. palauensis* also shows large vulval openings and therefore direct development can similarly be inferred for this species.

RELATIONSHIP OF *AUSTRALOCARCINUS* AND *TROGLOPLAX*

Many of the most unusual characteristics of monotypic *Trogloplax* (Guinot, 1986, 1987) (type *T. jolivetii*), can be attributed to its cavernicolous adaptations. These are common, to a greater or lesser extent, in all cave dwelling arthropods. They are: 1) the soft, poorly calcified carapace; 2) dorsoventral flattening; 3) the reduced narrow eyestalks with the corneas lacking faceting and pigment (Guinot, 1988, fig. 16A-C); 4) the loss of pigmentation of the carapace and pereopods; 5) exceptionally elongated and thin pereopods, especially the ambulatory legs; 6) the two long spines of the chelipeds. (Guinot, 1986:165).

Despite strong superficial differences there are fundamental characters that mark a close relationship between *Trogloplax* and *Australocarcinus*: 1) the carapace lacks setae, is rounded, and the anterolateral borders are anteriorly converging and cristate. 2) the buccal cavity is large and quadrangular. 3) the maxillipeds are short and broad, with the exopods relatively broad and with a flagellum. 4) the sternal plate is broad with the sutures 4/5 to 7/8

interrupted, and with sternite 8 broadly uncovered. 5) the G1 is stout and straight, and with an apical opening. 6) the G2 is subequal in length to G1, and with the two parts (flagellum and peduncle) subequal in length. 7) the male abdomen has segments 3-5 fused. 8) the sterno-abdominal cavity is deep in the male. 9) there is feeble heterochely and feeble heterodonty. 10) the antennular flagellae fold transversely into fossae under the frontal margin. 11) a sternal crest surrounds the telson of the male. 12) the outer face of sternite 8 is composed of two plates separated by a suture which marks a medial invaginated canal,

in which the penis lies.

REMARKS ON THE GONEPLACIDAE

Guinot (1969a,b,c, 1971) showed that the Goneplacidae MacLeay, 1838, *sensu* Balss (1957) constitutes an heterogeneous assemblage, and must be re-appraised. Evolutionary lineages in the family are the goneplacine (=carnioplacine) line, a pilumnine line, the panopeine line, and the euryplacine line. The Geryonidae were considered very distant from the Goneplacidae. The Rhizopinae Stimpson, 1858, still needs to have some questions resolved. This subfamily may need to be restricted to the type species, *R. gracilipes* Stimpson, 1858, which appears to constitute a separate lineage, a little different from the pilumnine line (*sensu stricto*) because the male G1, while similar, is not of typical pilumnid form with the strongly recurved tip (Guinot, 1969a, fig. 110), but the G2 is effectively the same as in the Pilumnidae. Ng (1987) reviewed the constitution of the Rhizopinae, and it appears that all the genera he included have the G1 with a pilumnine recurved tip, and the short sinuous G2 also typical of pilumnids. We think it possible that the Rhizopinae (*sensu* Ng, 1987) may still be heterogeneous with *Rhizopa* itself forming a separate lineage. If this is so, then the name Typhlocarcinopsinae Rathbun, 1909, is

available for *Typhlocarcinops* and perhaps some other genera. *Typhlocarcinops* has gonopods that are not of the classical pilumnid type (sensu Ng, 1987).

We consider that primitive goneplacid genera of the pilumnine line cannot be separated phylogenetically from the xanthoid Pilumnidae (*Pilumnus*). In the same way the panopeids *Cyrtoplax* Rathbun, 1914, *Tetraplax* Rathbun, 1901, *Glyptoplax* Smith, 1870, and *Cycloplax* Guinot, 1969, etc., cannot be separated phylogenetically from the panopeids like *Panopeus* H. Milne Edwards, 1834, but they form a natural grouping for which the name Eucratopsinae Stimpson, 1871 (= Prionoplacinae Alcock, 1900) may be used.

The Goneplacidae contains the Goneplacinae Miers, 1886, Carcinoplacinae, Miers, 1886, Chasmocarcininae Serène, 1964, Troglolacinae Guinot, 1986, and the Euryplacinae Stimpson, 1871. Many genera are still not satisfactorily placed in these subfamilies and a revision is urgently needed.

AFFINITIES OF THE TROGLOPLACINAE.

The most revealing character in helping to understand the affinities of the Troglolacinae is the disposition of the penis and gonopore. Typically in coxosternal crabs (sensu Guinot, 1978, 1979a), the ejaculatory canal opens on the coxa of P5 and there is a long penis sometimes visible near the aperture on the coxa but with most of its length covered by the complete junction of sternites 7 and 8 and with the distal part long and emerging to enter the base of the G1 (Guinot, 1979a, fig. 51F; 1979b, figs 2,3). Sternite 8 of the Troglolacinae has an invaginated channel in which the penis lies (Fig. 7).

The Troglolacinae as Guinot (1986) has already indicated, belongs to the Goneplacidae and is most closely related to the Chasmocarcininae Serène, 1964 (*Chasmocarcinus* Rathbun, 1898) a marine, mostly deepwater group (Serène, 1964a,b). All Chasmocarcininae (*Chasmocarcinus*, *Camatopsis* Alcock & Anderson, 1899, *Chasmocarcinops* Alcock, 1900, *Hepthopelta* Alcock, 1899, *Scalopidia* Stimpson, 1858) have the penis lying in either an enclosed or open groove in sternite 8 (Felder & Rabelais, 1986), such that sternite 8 has an intercalated plate anteriorly, a fact first observed for *Chasmocarcinus* by Rathbun (1914).

The type species of *Hepthopelta* (*H. lugubris* Alcock) is a female, and not well known, but a new species of *Hepthopelta* we have examined (being described by Davie & Richer de Forges)

has an open suture in sternite 8, such that the penis is visible. Glaessner & Secretan (1987) and Tavares (1992) described exactly such a condition for the fossil American Eocene crab *Falconoplax* Van Straelen, 1933. This genus had been attributed to the 'Tymolinae' by Glaessner (1969) (= Cyclodorippidae), but Tavares (1992) re-attributed this fossil to the Goneplacidae sensu lato, agreeing with Van Straelen's (1933) original placement. We believe that *Falconoplax* belongs to the Chasmocarcininae. The first record of a fossil *Chasmocarcinus* was reported from the Eocene of Antarctica, in shallow water sediments (Feldmann & Zinsmeister, 1984).

Serène (1964a), with some reserve, placed *Megaesthesius* Rathbun, 1909, in the Chasmocarcininae. We exclude it from the subfamily but acknowledge its relationships must be investigated further.

In spite of the similarity in the coxosternal plate between the Troglolacinae and the Chasmocarcininae, there are some notable differences. The major difference is that in the Chasmocarcininae the basal antennular segment is very swollen and completely fills the antennular fossa, such that the flagellum is excluded and cannot be folded. The gonopods of the two subfamilies are similar in that the G1 is stout and tapering and the G2 is long and not sigmoid, however there are also differences. In the Chasmocarcininae the G2 is noticeably shorter than the G1 and the flagellum is short (length varies a little depending on the species). In the Troglolacinae the G2 is as long or slightly longer than the G1, and the flagellum occupies about half or slightly more of the length.

Considering the close relationships with the exclusively marine Chasmocarcininae, and the presence of at least one estuarine tolerant species in *Australocarcinus*, derivation of the completely freshwater *Troglolax* from a marine stock is a logical assumption.

BIOGEOGRAPHY. The troglolacines are so far only known from the western Pacific (Fig. 8). *Troglolax* occurs in two freshwater subterranean caves on New Britain, PNG (Guinot & Geoffroy, 1987). The two caves are 250 km apart, and the crabs were found 300m into the caves. *Australocarcinus* is now known from three species in north Queensland, New Caledonia, and Palau; it seems probable that other species will be found on the West Pacific Islands. Although little is known of the reproductive patterns of the troglolacines, Davie's (1988) supposition of direct development for *Australocarcinus riparius*

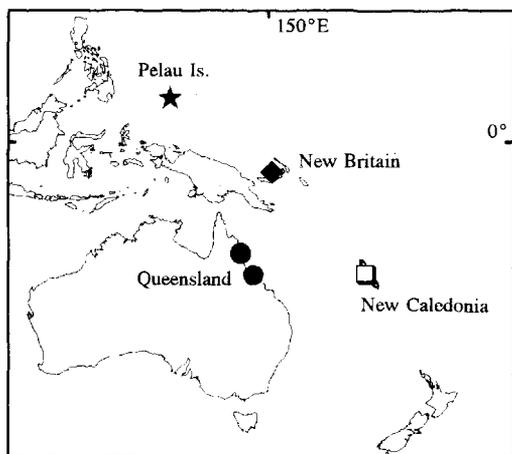


FIG. 8. Distribution of *Australocarcinus* and *Troglolpax*. Star = *A. palauensis* sp. nov.; hollow box = *A. kanaka* sp. nov.; solid circle = *A. riparius* Davie, 1988; diamond = *Troglolpax jolivetii* Guinot, 1986.

has been confirmed for *A. kanaka*. If the other species of *Australocarcinus* and *Troglolpax* also have direct development, this should reinforce their allopatric distributions and contribute to small area speciation. One factor which could allow genetic interchange over a limited range is the high salinity tolerance exhibited by *A. riparius*, which allows it to survive under estuarine conditions. Estuarine corridors along the coast between river systems, during flood conditions, could allow dispersal of adults and the maintenance of the species over long distances, as occurs on the NE coast of QLD. Such a dispersal method however is only likely to be of local importance. There seems to be no obvious dispersal or vicariant explanation that conveniently explains the observed distribution patterns of the genera and species of the Troglolpaxinae.

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