

THE GENUS *GLYPTOCARCINUS* TAKEDA, 1973,
WITH DESCRIPTIONS OF A NEW SUBFAMILY,
TWO NEW GENERA AND TWO NEW SPECIES
FROM NEW CALEDONIA
(CRUSTACEA: DECAPODA: BRACHYURA: XANTHIDAE)

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ABSTRACT. - The poorly known western Pacific genus *Glyptocarcinus* Takeda, 1973, is revised. One genus and two new species, *Antrocarcinus petrosus*, new genus and species, and *Glyptocarcinus politus*, new species, are described from New Caledonia. The identities of *G. lophopus* Takeda, 1973, and *G. truncatus* (Rathbun, 1906) are clarified, and the latter is referred to a new genus, *Cyrtocarcinus*. *Glyptocarcinus*, *Antrocarcinus* and *Cyrtocarcinus*, previously placed in the Eumedonidae Dana, 1853, is shown to belong to the family Xanthidae MacLeay, 1838, *sensu* Serène, 1984, instead. A new subfamily, Antrocarcininae, is established for these three genera. Antrocarcinines are characterised mainly by their elongate second antennal segment, having pigmentation only on the tips and cutting edges of the fingers of the chelipeds, interrupted posterolateral margins, swollen cardiac regions, deep cardio-intestinal grooves, and presence of a postero-sub-branchial channel which joins the cardio-intestinal groove.

INTRODUCTION

The genus *Glyptocarcinus* was established by Takeda (1973) for *G. lophopus* Takeda, 1973, from Japan. Sakai (1974, 1976) however, synonymised *Glyptocarcinus* under *Harrovia* Adams & White, 1849 (type species *Harrovia albolineata* Adams & White, 1849), and *G. lophopus* under *Harrovia truncata* Rathbun, 1906 (type locality Hawaii). Takeda (1976) tentatively followed Sakai's action but later (Takeda, 1979), after examining specimens of *H. truncata* from Hawaii, provided sufficient evidence to resurrect *Glyptocarcinus* as a valid genus. He also showed that *G. lophopus* and *H. truncata* were not conspecific, and both should be classified in *Glyptocarcinus*. Takeda (1979) placed both *Glyptocarcinus* species in the Eumedoninae (family Parthenopidae MacLeay, 1838, *sensu* Serène *et al.*, 1958). Števcíć *et al.* (1988) recently recognised the eumedonines as a distinct family, and provisionally retained *Glyptocarcinus* in the Eumedonidae (no specimens examined), in a new subfamily, Ceratocarcininae (Števcíć *et al.*, 1988: 1318).

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Despite the peculiar features of *Glyptocarcinus*, no one has questioned its taxonomic position in the Parthenopidae. The form of the sternum and structure of the male pleopods have never been described or figured.

In the present paper, the genus *Glyptocarcinus* is revised after examining an important series of specimens from New Caledonia. The identities of *G. truncatus* (Rathbun, 1906) and *G. lophopus* Takeda, 1973, are clarified, two new genera, *Cyrtocarcinus* and *Antrocarcinus*, and two new species, *Glyptocarcinus politus* and *Antrocarcinus petrosus*, are also described from New Caledonia. *Glyptocarcinus* (and *Cyrtocarcinus* and *Antrocarcinus*) is removed from the Eumedonidae and transferred to a new subfamily, Antrocarcininae, in the family Xanthidae MacLeay, 1838, *sensu* Serène, 1984, instead.

The abbreviations cb and cl for the carapace width and length respectively. Specimens examined are deposited in the Muséum national d'Histoire naturelle (MNHN), Paris, France; Bernice P. Bishop Museum (BPBM), Honolulu, Hawaii, U.S.A.; National Science Museum, Tokyo (NSMT), Japan; and the Zoological Reference Collection (ZRC), Department of Zoology, National University of Singapore.

FAMILY XANTHIDAE MACLEAY, 1838, *sensu* Serène, 1984

NEW SUBFAMILY ANTROCARCININAE

Type genus. - *Antrocarcinus*, new genus, by present designation.

Diagnosis. - Carapace hexagonal; cardiac region swollen, may be expanded to form distinct fold which partly covers deep to very deep cardio-intestinal groove; intestinal region rectangular, raised, plate-like or depressed; anterolateral margin, with 3 lobiform teeth, continuous with supraorbital margin and external orbital angle, distinctly demarcated from cristate posterolateral margin; posterolateral margin interrupted, posterior part of sub-branchial region with distinct channel which connects to end of posterolateral margin, at junction which it curves into metabranchial region. Antennular fossa oblique, antennules folding obliquely. Basal antennal segment large, rectangular, subequal in length to elongate second segment. Epistome divided into two parts; anteromedian part depressed; posterior margin of epistome cristate, median part divided into 2 distinct truncate lobes which may be partially fused. Lateral margin of posterior part of epistome distinctly expanded to form granulose swelling. Endostome with weak oblique ridges. Ischium of third maxilliped with deep, broad median sulcus; antero-external angle of merus auriculiform. In both sexes: suture between sternites 1 and 2 absent but may be demarcated by row of granules; suture between sternites 2 and 3 distinct; suture between sternites 3 and 4 deep to very deep, interrupted medially. Only tips and cutting edges of fingers of chelipeds pigmented. Male abdominal segments 3-5 immovable, but sutures between segments deep, distinct. First male pleopod stout to relatively slender, distal margins lined with short, sharp spines, without long, setose subdistal hairs; second male pleopod short, distal segment 28-38% length of basal segment.

Remarks. - The external features of *Antrocarcinus*, *Glyptocarcinus* and *Cyrtocarcinus* are such that they preclude classification into any of the extant xanthid families. While the general facies of the three genera are xanthoid, they also possess many peculiar features, notably in the carapace, structure of the sternum, male abdomen and form of the fingers of the chelipeds. Takeda (1973), in describing *Glyptocarcinus*, commented on that in the "...

reticulated ornamentation of the carapace, chelipeds and ambulatory legs, the overhanging thin anterolateral border of the carapace, the imperfect orbits and the chelae with dark-coloured, blade-like cutting edges", the genus was characteristic of the Parthenopidae. The carapace and gonopods of parthenopids however, differs markedly from *Glyptocarcinus* (as well as *Antrocarcinus* and *Cyrtocarcinus*) (see later). The carapace and gonopods of *Glyptocarcinus* and its allies are closer to xanthoid crabs, especially of the Xanthidae MacLeay, 1838, *sensu* Serène, 1984, and these genera are here referred there.

The type of *Cyrtocarcinus truncatus* (Rathbun, 1906) (as a *Harrovia*) is a young specimen and bears a superficial resemblance to typical *Harrovia* species, the carapace being squarish in shape and the anterolateral teeth lobiform. It is thus not at all surprising that *C. truncatus* has remained in the genus *Harrovia* (Eumedoninae, Parthenopidae) for so long. Even with the discovery of larger specimens of *C. truncatus* by Edmondson (1951) and of *Glyptocarcinus lophopus* by Sakai (1974, 1976) (incorrectly as *Harrovia truncata*), the taxonomic position of these species has hardly been questioned.

The peculiar form of the interrupted posterolateral margin with the posterior sub-branchial channel, very swollen cardiac region which may overhang the deep cardio-intestinal groove, plate-like intestinal region, the fingers of the chelipeds being pigmented only at the tip and along the cutting edges, a sternite 4 with a transverse median ridge, elongate second antennal segment and the male abdominal segments 3-5 being immovable despite having all the sutures deep and distinct, are very unusual, and warrant the establishment of a separate subfamily for *Antrocarcinus*, *Glyptocarcinus* and *Cyrtocarcinus*.

The sternal structures of *Antrocarcinus*, *Glyptocarcinus* and *Cyrtocarcinus* are also unusual in that the lateral clefts demarcating sternites 3 and 4 are very deep, much more so than in any described xanthid subfamily.

The pigmentation of the fingers of the chelipeds is very distinctive for antrocarcinines in that only the tips and cutting edges are coloured dark brown. In xanthids, the fingers are either unpigmented, pigmented on the distal part only, and in some cases, on the entire finger and even onto the distal part of the palm. The pigmentation in antrocarcinines strongly resembles that of parthenopids, but whether this character has any phylogenetic importance cannot be ascertained at the moment.

The male pleopods of both species of *Glyptocarcinus* are not known, both being represented only by females. As for the male pleopod structures of *Cyrtocarcinus* and *Antrocarcinus*, the stout first male pleopod lined with short, stout spines, second male pleopod structure and immovable male abdominal segments 3-5 necessitate the transfer of these genera out of the Eumedonidae. Eumedonids have long, sinuous, relatively slender first male pleopods lined with hairs, as do their closest relatives, the Pilumnidae. Eumedonids and pilumnids also have very short second male pleopods, which are proportionately much shorter than those of *Glyptocarcinus* and *Antrocarcinus*. The first male pleopods of *Cyrtocarcinus* and *Antrocarcinus* however, closely resemble those of some xanthids (especially members of the Euxanthinae, Xanthidae). The peculiar structure of the cardiac region and posterolateral margin of the carapace however, argues against including *Antrocarcinus*, *Glyptocarcinus* and *Cyrtocarcinus* in the Euxanthinae for the time being. Moreover, euxanthines typically have the "... antero-lateral margins of the carapace are poorly indicated behind the exorbital angles; a feeble crest (line) in a sub-orbital position (sub-hepatic) is directed not towards the orbit but towards the frame of the buccal cavity" (Serène, 1984: 16). In antrocarcinines, the

anterolateral margin is cristate throughout its length and clearly reaches the orbits. It must be noted however, that the definition of the Euxanthinae is still quite unsatisfactory and must be revised (Ng, 1993), during which time it may be necessary to redefine the subfamily so that it includes *Antrocarcinus*, *Glyptocarcinus* and *Cyrtocarcinus* as well. For the moment, the authors feel that it is better to separate these three genera into a group of their own considering their distinctive characters.

The male abdomen of *Cyrtocarcinus truncatus* has been figured by Edmondson (1951: fig. 21f) and shows seven clearly demarcated segments, typical of the xanthoid families Menippidae, Pilmunidae, Eumedonidae and Platyxanthidae. The male abdominal segments 3-5 of *Antrocarcinus* and *Cyrtocarcinus* however, are immovable, effectively forming a single structure. The sutures between the segments are evident only externally. Internally, the sutures are incomplete, with several parts of the sutures of all three segments ankylosed. In larger male specimens, the entire suture is ankylosed and from the internal view, appears completely fused. In *Antrocarcinus petrosus*, segments 3-5 are partly ankylosed, along the inner surfaces and externally. These three segments seem to be free but are effectively immovable. The male abdominal segments 3-5 of the Parthenopidae s. str. (Parthenopoidea) are fused, and the rather broad male abdomen of *Cyrtocarcinus* and *Antrocarcinus* bear a distinct similarity. The first and second male pleopods of parthenopids however, are very different, with the first male pleopod usually being very stout and cylindrical and the second male pleopod long.

The Antrocarcininae also bears a resemblance to some members of the Liomerinae Sakai, 1976 (Xanthidae s. str.), especially to *Actites* Lanchester, 1901. *Glyptocarcinus* and *Antrocarcinus* resemble *Actites* in the form of the carapace, front and structure of the cristate ambulatory legs. There is also a distinct but shallow transverse groove separating the cardiac and intestinal regions in *Actites*, which could be a "precursor" to the much more extreme condition present in *Glyptocarcinus* and *Antrocarcinus*. Antrocarcinines however, differ from *Actites* in that the 2M region is entire and not divided longitudinally into two halves by a groove, the anterolateral margin consists of three distinct teeth (rounded lobes in *Actites*), the posterolateral margin stops abruptly two-thirds from the start and curves downwards towards the intestinal region (normal and entire in *Actites*), the cardiac region is swollen and separated from the intestinal region by a deep transverse groove with the posterior part overhanging the groove (against a normal cardiac region which is separated from the intestinal region by shallow groove in *Actites*), the intestinal region is raised and plate-like or distinctly depressed and sloping anteriorly (gently convex in *Actites*), the second antennal segment is elongate and subequal in length to the basal segment (second segment very small and reduced in *Actites*), the antero-external angle of the merus of the third maxilliped is auriculiform (rounded and not expanded in *Actites*), the posterior margin of the epistome consists of two median truncate lobes with a deep median fissure (against a triangular median lobe in *Actites*), the margins of the ambulatory legs are more strongly cristate, the tips of the fingers are sharp (tips dilated and somewhat spoon-like in *Actites*), pigmentation on the fingers are along the cutting edges and tips only (distal pigmentation or entire finger faintly pigmented in *Actites*), the sutures of male abdominal segments 3-5 are deep and distinct (only the edges of the sutures are still visible in *Actites*), the distal part of the first male pleopod is not covered with long, setose hairs, and the second male pleopod basal segment is proportionately longer (distal segment length 28-38% that of basal segment vs. 28-29% in *Actites*).

While characters like the structures of the 2M carapace region, posterior margin of the epistome, margins of the ambulatory legs, fingers of the chelipeds, distal part of the first

male pleopod, shape of the antero-external angle of the merus of the third maxilliped, degree of fusion of the male abdominal segments 3-5, and proportions of the second antennal segment, are generic in level, the unusual structures of the sternum (with deep clefts between sternites 3 and 4), very swollen cardiac region, interrupted posterolateral margin and presence of a posterior sub-branchial channel are more difficult to assess, and suggest that *Antrocarcinus*, *Glyptocarcinus* and *Cyrtocarcinus* are not closely related to *Actites* and not consubfamilial.

Serène (1984: 55) regarded *Actites* as a subgenus of *Liomera* Stimpson, 1859, and to this taxon assigned two species, *Actites erythrus* Lanchester, 1901 (type species), and *Carpilodes lophopus* Alcock, 1898 (including *Carpilodes lophopus* var. *boninensis* Odhner, 1925). In these species, two characters, the shape of the carapace and the stout first male pleopod combine to form a distinct group within the Liomerinae. Therefore, *Actites* should be assigned full generic status.

General biology. - As far as is known, antrocarcinines are free-living. This fact had created doubt about the placement of the genus *Glyptocarcinus* in the Eumedonidae which are otherwise, strict symbionts of echinoderms (Števíć *et al.*, 1988). The available evidence makes it extremely unlikely that antrocarcinines are associated with any organisms. Xanthoid symbionts like trapeziids, cymoines, chlorodiinines, and certainly all eumedonids (unpublished data) have a specialised dactylo-propodal process on their ambulatory legs, in which a knob on each side of the proximal part of the dactylus is able to lock into a depression on each side of the inner distal edge of the propodus. Once the knob on the dactylus is locked into its corresponding process on the propodus, both segments become very rigid. The process presumably helps the eumedonid crabs maintain a strong grip on their hosts. Antrocarcinines lack this dactylo-propodal process.

The peculiar structure of the posterolateral margin and cardiac region in antrocarcinines might be associated with respiration. In antrocarcinines, the posterolateral margin curves suddenly inwards towards the metabranchial region and cardio-intestinal groove, with the intestinal region forming a separate plate or structure. The posterior part of the outer margin of the metabranchial region is thus no longer distinct from dorsal view. In xanthoid crabs, the posterolateral margins form the outer lateral margins of the metabranchial regions, and join the posterior margin of the carapace; and the metabranchial regions are separated from the intestinal region by a shallow oblique groove.

In antrocarcinines, below the cristate posterolateral margin, on the posterior part of the sub-branchial region, is a distinct channel, lined with scattered spines and sharp tubercles on its anterior part. This channel is linked to the end of the posterolateral margin, at the junction which it curves into the metabranchial region. The deep cardio-intestinal groove is thus connected to the posterior sub-branchial channels via the end of the posterolateral margins. It seems likely that water currents are brought in via the posterior dorsal part of the carapace, via the posterior sub-branchial channels to the Milne Edwards' openings. The sculpture and form of the carapace of antrocarcinines strongly suggest that they have cryptic habits and probably hide under mud or rubble. Most of the recent specimens of *Glyptocarcinus politus* and *Antrocarcinus petrosus* collected from New Caledonia are covered in mud and other sediments. With such habits, a specialised mechanism for bringing in oxygenated water would be an advantage. Some xanthid crabs (e.g. *Hypocolpus*, *Carpoporpus*, *Hepatoporus*, *Euxanthinae*) have a special depression on the anterior part of their sub-branchial region

which is also believed to aid respiration. In a similar fashion, burrowing crabs like *Trichia* (Trichiinae, Xanthidae) and *Calappa* (Calappidae) use their chelipeds to help channel in the afferent respiratory current.

KEY TO THE GENERA AND SPECIES OF ANTROCARCININAE

- 1a. Frontal margin with deep, broad, V-shaped cleft, frontal lobes usually directed obliquely outwards, inner supraorbital lobes present; anterolateral margin normal, not strongly lamelliform and plate-like from frontal view; cardio-intestinal groove deep, cardiac fold not over-reaching groove; dorsal margin of chela with inward folding crest, median part with several spines or teeth; surfaces of male and female abdominal segments 2-4 with three large, transverse, granulated swellings, median one largest, segments 5 and 6 with large median granulated swelling*Antrocarcinus*, new genus (monotypic, *A. petrosus*, new species)
- b. Frontal margin with deep, narrow fissure, frontal lobes directed anteriorly, inner supraorbital lobes indistinct or absent; anterolateral margin strongly lamelliform and plate-like from frontal view; cardio-intestinal groove very deep, cardiac fold over-reaching and partly covering groove; dorsal margin of chela not distinctly cristate, median part without spines or teeth; surfaces of all male and female abdominal segments smooth, without large swellings2
- 2a. Anterolateral teeth low, broadly triangular, lobiform; posterior part of cardiac fold in adults subtruncate in shape; intestinal region appears depressed and sloping anteriorly into cardio-intestinal groove, posterior margin of carapace sunken below margin of last abdominal segment; inner surface of chela distinctly swollen, surfaces rounded; carpus with only 1 broad, blunt tooth at inner distal angle; posterior part of sternite 4 sloping suddenly downwards forming strong transverse ridge and deep median depression*Cyrtocarcinus*, new genus (monotypic, *C. truncatus*)
- b. Anterolateral teeth well developed, acutely triangular, sharp; posterior part of cardiac fold in adults broadly triangular in shape; intestinal region raised, plate-like, margins appear cristate, posterior margin of carapace raised well above margin of last abdominal segment; inner surface of chela raised, with median part forming a low longitudinal ridge; carpus with 1 large, sharp tooth at inner distal angle and 1 small but distinct sub-basal tooth; posterior part of sternite 4 sloping gradually anteriorly, forming low transverse ridge and median depression*Glyptocarcinus*
- 3a. Dorsal surface of carapace uneven, with numerous small granules and punctations, especially on epibranchial, gastric and branchial regions forming reticulate-pattern; intestinal region with distinct median groove; fourth ambulatory merus stout, length ca. 1.8 times width*G. lophopus*
- b. Dorsal surface of carapace appears smooth, without distinct granules, or reticulate-pattern, punctations sparse; intestinal region entire, without median longitudinal cleft or groove; fourth ambulatory merus slender, length ca. 2.1 times width*G. politus*, new species

Antrocarcinus, new genus

Type species. - *Antrocarcinus petrosus*, new species, by present designation, monotypy.

Diagnosis. - Carapace transverse, broader than long; regions very distinct, well defined, grooves deep; surfaces distinctly punctate to rugose; front distinctly bilobed, with deep, broad, V-shaped cleft, frontal lobes usually directed obliquely outwards, supraorbital lobe low but clearly demarcated; cardiac region swollen, with distinct transverse median ridge, does not form cardiac fold, does not cover deep cardio-intestinal groove from dorsal view; intestinal region rectangular, plate-like, posterior margin with distinct median longitudinal cleft; posterior margin of carapace distinctly raised above margin of last abdominal segment; anterolateral margin with 3 distinct teeth, anterior 2 larger; posterolateral margin distinctly converging, not continuous, anterior two-thirds straight, then curving sharply into metabranchial region forming low, short transverse ridge; posterior part of sub-branchial region with distinct channel which connects to end of posterolateral margin (at junction which it curves into metabranchial region). Posterior margin of epistome truncate, median lobes usually fused marginally. Ischium of third maxilliped rectangular, width ca. 65% length; antero-external angle of merus auriculiform. Dorsal margin of chela with inward folding crest lined with several spines or teeth, median part of inner surface of chela gently convex. Suture between sternites 2 and 3 prominent, lined with small granules; suture between sternites 3 and 4 interrupted medially; sternite 4 with low transverse median ridge. Male abdomen 7-segmented; sutures between segments 3-5 distinct on external surface but incomplete internally, with segments partially ankylosed and completely immovable; external surfaces of male and female abdominal segments 2-4 with 3 large, transverse, granulated swellings, median one largest, segments 5 and 6 with large truncate median granulated swelling. First male pleopod stout, proximal half almost straight, distal margins lined with short, strong spines; second male pleopod relatively short, distal segment ca. 38% length of basal segment.

Etymology. - The genus name is derived from the Greek "antrum" for cave or hollow, in combination with "carcinus" (for crab), alluding to the deep grooves on the carapace of the type species. Gender masculine.

Remarks. - The genus is monotypic. The differences between *Antrocarcinus* and other antrocarcinine genera have been outlined in Table 1 and in the key. *Antrocarcinus* seems to be the least specialised of all antrocarcinine genera, and bears the closest resemblance to more typical xanthid genera, especially in its well defined regions, less inflated cardiac region which does not overhang the more shallow cardio-intestinal groove, and possession of distinct inner supraorbital lobes.

Antrocarcinus petrosus, new species

(Figs. 1-4, 10A)

Material examined. - Holotype - male (cb 12.0 mm, cl 8.8 mm) (MNHN), SMIB 8: station DW 174, 23°39.94'S, 168°00.55'E, New Caledonia, 235-240 m depth, coll. B. Richer de Forges, 29.i.1993.

Paratype - 1 female (cb 12.3 mm, cl 9.3 mm) (MNHN), same data as holotype. — 1 young female (cb 8.8 mm, cl 6.5 mm) (ZRC), 1 female (cb 13.6 mm, cl 9.5 mm) (specimen dismembered, only carapace intact) (MNHN), station DW 170, 23°41.23'S, 168°00.56'E, New Caledonia, 241-244 m depth, coll. B. Richer de Forges, 29.i.1993.

Ng & Chia: The Genus *Glyptocarcinus* Takeda

Table 1. Differences between *Glyptocarcinus*, *Cyrtocarcinus* and *Antrocarcinus*

Character	<i>Glyptocarcinus</i>	<i>Antrocarcinus</i>	<i>Cyrtocarcinus</i>
Carapace	distinctly broader than long; carapace width 1.34-1.39 times carapace length	squarish, carapace width 1.32-1.36 times carapace length	distinctly broader than long; carapace width ca. 1.41 times carapace
Frontal margin	with deep, narrow fissure, frontal lobes directed anteriorly outwards	with deep, broad, V-shaped cleft, frontal lobes directed obliquely	with deep, narrow fissure, frontal lobes directed anteriorly
Cardio-intestinal region	very deep, cardiac fold groove over-reaching and partly covering groove	shallow, cardiac fold not over-reaching groove	very deep, cardiac fold over-reaching and partly covering groove
Intestinal region	raised, plate-like, margins cristate	raised, plate-like, margins cristate	depressed, not raised, sloping anteriorly into cardio-intestinal groove, not plate-like, margins not distinct or cristate
Sternum	posterior part of sternite 4 sloping gently towards anterior part	posterior part of sternite 4 sloping gently towards anterior part	posterior part of sternite 4 slopes very suddenly downwards, forming distinct transverse ridge and depression in median part of sternite
Third maxilliped	relatively long, width of ischium ca. 60% length	relatively short, width of ischium ca. 65% length	relatively long, width of ischium ca. 63% length
Chela	dorsal margin of chela slightly cristate; inner surface gently convex but not distinctly swollen	dorsal margin of chela with inward folding crest, median part with several spines or teeth; inner surface gently convex, not distinctly swollen	dorsal margin of chela rounded, not cristate; inner surface strongly swollen
Male and female abdomina	surfaces of all segments smooth, without large swellings	surfaces of segments 2-4 with three large, tranverse, truncate swellings, median one largest, segments 5 and 6 with large median truncate swelling	surfaces of all segments smooth, without large swellings
First male pleopod	not known	relatively stout, proximal half almost straight	relatively slender, C-shaped
Second male pleopod	not known	relatively short, distal segment ca. of basal segment	relatively long, distal segment ca. 28% length of basal segment

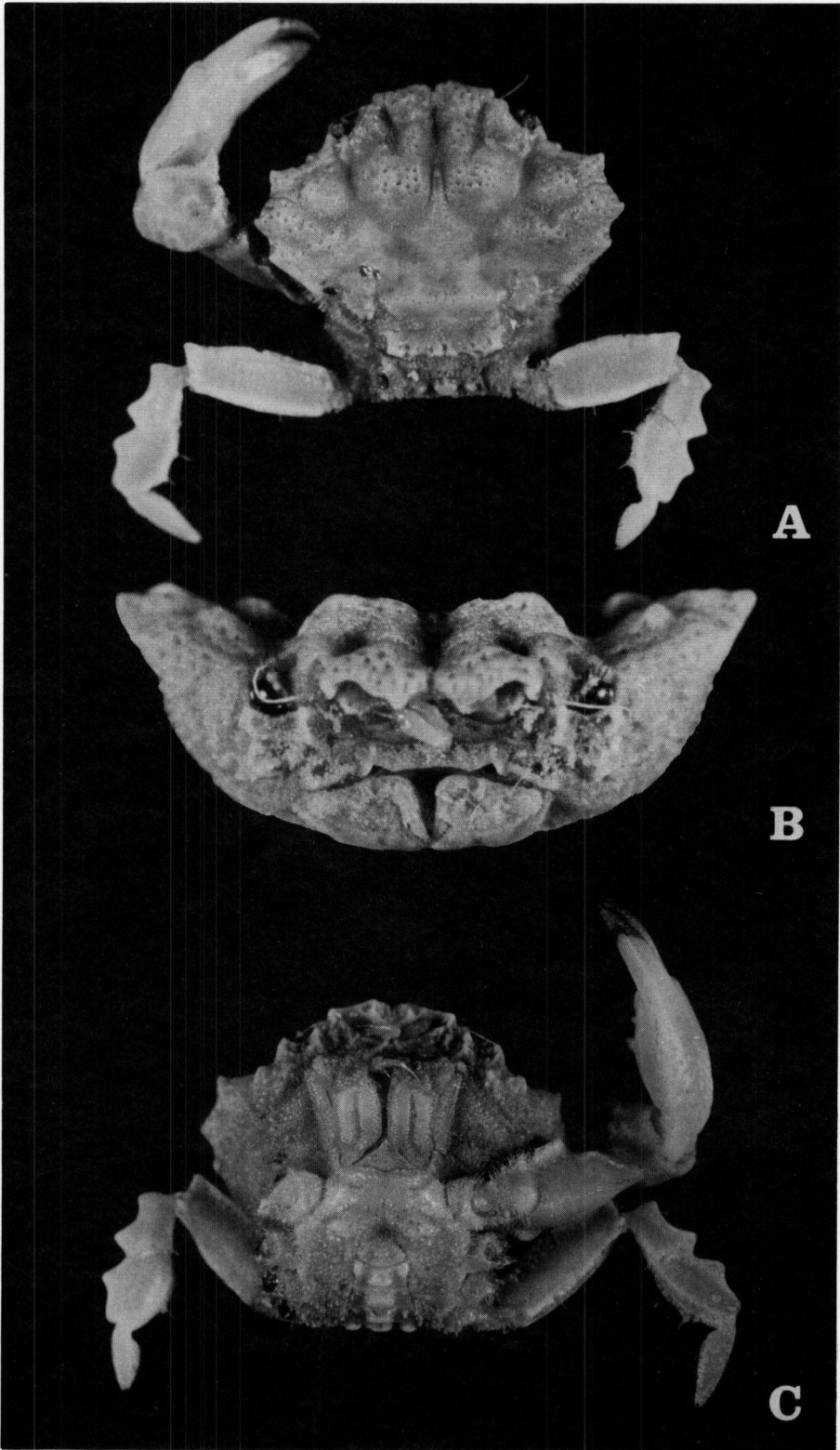


Fig. 1. *Antrocarcinus petrosus*, new genus and species. Holotype male, cb 12.0 mm, cl 8.8 mm (MNHN). A, dorsal view; B, frontal view; C, ventral view.

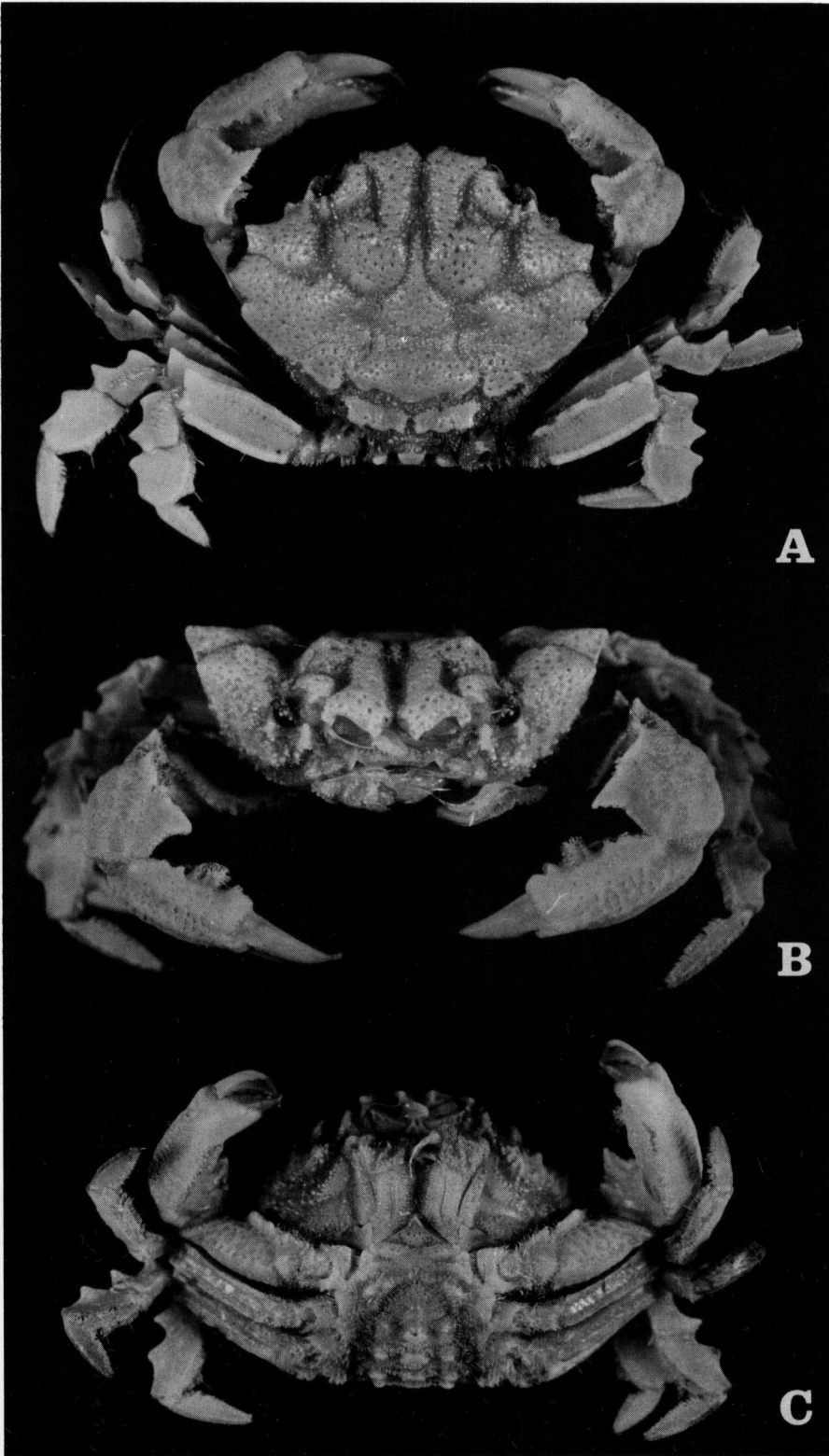


Fig. 2. *Antrocarcinus petrosus*, new genus and species. Paratype female, cb 12.3 mm, cl 9.3 mm (MNHN). A, dorsal view; B, frontal view; C, ventral view.