New species of crabs (Crustacea, Decapoda), one from the Middle Danian of Denmark, and three new species from the Upper Cretaceous of Nigeria

Joe. S. H. Collins

The Natural History Museum, Cromwell Road, London SW7 BD and 8, Shaw's Cottages, Perry Rise, London, SE23 2QN. U. K.

Abstract

Four new species of crabs (Crustacea, Decapoda) are described; a dynomenid, from the Middle Danian of Fakse, Denmark, is earlist known member of the genus; a necrocarcinid, *Paranecrocarcinus milbournei* sp. nov., from the Cenomanian of Calabar, Nigeria, represents the second known member of the genus from the African continent. Also from the Upper Cretaceous of Nigeria, *Cenomanocarcinus tenuicarinatus* sp. nov. (Lower Turonian, Eze Aku Formation), has characters in common with *Cenomanocarcinus cristatus* and *Campylostoma*, while *Cenomanocarcinus disimmilis* sp. nov. shares only basic characters with other known members of the genus.

Key words: Brachyura, Dynomenidae, Necrocarcinidae, Cenomanocarcinidae, Danian, Denmark, Upper Cretaceous, Nigeria

Introduction

A new species of dynomenid, *Kromtitis daniensis*, included in a collection of crabs deposited in the Department of Palaeontology, The Natural History Museum, London, by John Cooper from the Lower Danian of Fakse, is the earlist known member of the genus. A second collection, from the Upper Cretaceous of Nigeria, deposited by P. Zarbowsky, includes the new raninoids, *Paranecrocarcinus milbournei, Cenomanocarcinus tenuiscarinatus* and *Cenomanocarcinus dissimilis*.

Recent studies by Guinot (2008), indicate a close relationship of *Kromtitis* to Recent species of Paradynomeninae Guinot, 2008 (Guinot, 2008, p. 2) The new *Kromtitis* considerably extends the stratigraphic range of the genus to the Middle Danian and provides a notable contribution to the prolific crab fauna from the Coral/Bryozoa banks of Fakse, Denmark (Jakobsen and Collins, 1997).

All previously described species of *Kromtitis* are coral associates (Beschin *et al.*, 2007a, p. 27) — as are those assigned to *Paradynomene* (Guinot, 2008, p. 2) — and the new species from the coral/bryozoan banks of the Middle Danian is no exception. As known, with but one exception, species of *Kromtitis* are confined to the northern Tethys. With origins in the Middle Danian of Denmark there appears to have been a rapid southerly progression with *Kromtitis koberiformis* Beschin *et al.*, 2007a, *Kromtitis laevigatus* Beschin *et al.*, 2007a, and *Kromtitis subovatus* Beschin *et al.*, 2007a, reaching Vincenza, northern Italy, by the Early Eocene; *Kromtitis tuberculatus* Beschin *et al.*, 2007, was described from the Middle Eocene of the same region. *Kromtitis pentagonalis* Müller and Collins, 1991, from the Middle Eocene Priabonian of Hungary is much the same age as *Kromtitis* sp. 1, of Italy

(Beschin *et al.*, 2007b), while *Kromtitis* sp. 2 (De Angeli and Beschin, 2008) is from the Lower Oligocene of Italy. *Kromtitis koberi*, well known from the Miocene, Middle Badenian of Austria has since been recorded from deposits of similar age in the Holy Cross Mountains, Poland (Müller, 1984, p. 64; 1996, p. 9). The abovementioned exception, *Kromtitis spinulata* Portell and Collins, 2004, from the early Miocene Montpelier Formation of Jamaica, is among an assemblage containing three other genera common to European Tethyan forms. This species, misdeclined under Rule 30.1.4.4 of the International Commission on Zoological Nomenclature (1999) is here corrected to *Kromtitis spinulatus*.

Previous knowledge of fossil crabs from Nigeria has been limited to descriptions by Withers (1924) of the carpiliid *Halcocarcinus sulcatus* and a xanthid cheliped. Both species came from the Middle Eocene (Lutetian) of Ameki, southern Nigeria. To these early recordings Collins and Morris (1972) added the first Cretaceous species, *Costacopluma concava*, founded on carapaces from the Upper Campanian of Enugu Province, East Central Region, the Coniacian of Abakoliki Province, East Central Region and the ?Maastrichtian of Shendam of Benue Plateau Province. While *Paranecrocarcinus mozambiquiensis* Förster, 1970, has previously been recorded from the Cenomanian of Calabar, is the first of its genus to be recorded from Nigeria.

The stratigraphical and geographical distribution of *Paranecrocarcinus* appears to have been limited to the Cretaceous Tethys. From, as far as known, an origin in the Hauterivian of France (*Paranecrocarcinus hexagonalis* Van Straelen, 1936), the genus made a rapid westerly migration to reach the Lower Albian of Texas, as

Paranecrocarcinus stenzeli Bishop, 1983; in the Upper Albian of Texas it is represented by Paranecrocarcinus graysonensis (Rathbun, 1935) and Paranecrocarcinus moseleyi Stenzel 1945. Paranecrocarcinus gamma Roberts, 1962, extended the range in the Western Hemisphere to the Campanian of New Jersey. The genus is unknown among the prolific Albian decapod fauna of Europe. By the Cenomanian, migration once again seems to have favoured an easterly dispersal, encompassing the Lebanon, Paranecrocarcinus libanoticus Förster, 1968, and Mozambique, Paranecrocarcinus mozambiquiensis Förster, 1970; Paranecrocarcinus milbournei sp. nov. reached Nigeria by the late Cenomanian, early Turonian. The most northerly Cenomanian species, reaching southern England, were Paranecrocarcinus biscissus Wright and Collins, 1972, Paranecrocarcinus foersteri Wright and Collins, 1972, and Paranecrocarcinus digitatus Wright and Collins, 1972; the latter, together with Paranecrocarcinus sp., occur in contemporary deposits of northern France. The last known occurrences, Paranecrocarcinus quadriscissus (Noetling, 1881) and Paranecrocarcinus vanbirgeleni Fraaije, 2002, from the Maastrichtian of The Netherlands, lay on much the same latitude as the European Cenomanian species.

According to Guinot *et al.* (2008, p. 707) *Paranecrocarcinus kennedyi* Wright, 1997, from the Barremian, Makatini Formation of Zululand has characters, 'different from those of typical Necrocarcininae' and was excluded from that subfamily.

All aspects of Cenomanocarcinidae and related families are fully documented by Guinot et al. (2008). With apparent origins (Cenomanocarcinus oklahomensis Rathbun, 1935) in the Upper Albian of the Western Interior of the USA, the genus remained in the USA during the Cenomanian (Cenomanocarcinus vanstraeleni Stenzel, 1945) and also migrated eastward reaching Nigeria (Cenomanocarcinus dissimilis sp. nov. and Cenomanocarcinus tenuicarinatus sp. nov.) by the Lower Cenomanian and Lower Turonian respectively, and became established in northern Europe by the Upper Cenomanian (Cenomanocarcinus inflatus Van Straelen, 1936). The genus persisted into the late Turonian-Coniacian of Vancouver Island, Canada (Cenomanocarcinus bairdi Schweitzer et al., 2003) and the Upper Campanian of Afghanistan (Cenomanocarcinus cristatus (Jux, 1971)). Cenomanocarcinus tenuicarinatus sp. nov. has a superficial similarity to Cenomanocarcinus cristatus and possesses characters indicating a relationship with Campylostoma Bell, 1858, from the Lower Eocene, London Clay of England, tentatively included in Cenomanocarcinidae (Guinot et al., 2008, p. 684).

Local stratigraphy

The stratigraphy of the Coral/Bryozoan banks of the Palaeocene Middle Danian *Typilobus bruennichi* Zone of Fakse, Denmark was thoroughly documented by Asgaard (1968), Bernecker and Wiedlich (1990) and Floris (1980).

Restricted to the southeastern portion of the basin around Calabar, southeastern Nigeria, beds of Cenomanian age rest directly on Pre-Cambrian basement rocks. The beds have been assigned to the Odukani Formation, dated to Cenomanian to Lower Turonian age (Kogbe, 1975b, p. 273). About 600 m thick, the beds are of shallow water origin and have been described as having been deposited as typical near-shore sediments (Reyment, 1965, *vide* Kogbe, 1975a, p. 273) consisting of arkose sandstone, limestone and shales, becoming gradually more prominently shaly (Reyment, 1956, *vide* Kogbe, 1975a, p. 276). The beds have a regional dip of c. 60 degrees to the south. The type locality is situated at Odupani, Calabar. The ammonite assemblage from the district around Calabar was listed by Zaborski (1985, 1990).

All new specimens are deposited in the Department of Palaeontology, The Natural History Museum, London.

Systematic descriptions

Infraorder Brachyura Linnaeus, 1758 Section Podotremata Guinot, 1977 Subsection Dromioidea De Haan, 1833 Family Dynomenidae Ortmann, 1892 Subfamily Paradynomeninae Guinot, 2008

Genus Kromtitis Müller, 1984

(non Papp et al., 1978, nomen nudum)

Type species: Dromilites koberi Bachmeyer and Tollmann, 1953, by monotypy.

Range: Palaeocene to Upper Miocene.

Kromtitis daniensis sp. nov.

(Figs. 1.1, 1.2)

Diagnosis: Carapace subcircular, subglobose, margins lobate with a spine at the posterolateral angle; dorsal surface bilaterally tuberculate, those on the metabranchial lobes fused into short ridges.

Material: Holotype, carapace and counterpart, BMNH IC500 from the Middle Danian, *T. bruennichi* Zone of Fakse, Denmark.

Derivation of name: Indicating origin in both the Danian and Denmark.

Description: Carapace subcircular in outline, length about four fifths of width, widest posteriorly (c. 86%), strongly arched transversely, longitudinally more steeply so anteriorly. The front is damaged, but, as indicated by the inclined upper orbital margin, is triangular and slightly produced. The strongly raised upper orbital margins are entire. Of five flattened nodes lining the antero- and posterolateral margins, the first (outer-orbital) and third (epibranchial) are the smallest; all lobes overlap the carapace edge and there is scarred evidence of another such node at the posterior angle. The cervical furrow, straight across the midline, curves weakly forwards and outwards to the margin between the second and third nodes. Dorsal lobes are well defined and composed of tubercles of varying size. There is a pair of small epigastric tubercles at the base of the rostrum, one tubercle on each hepatic lobe and one on each protogastric lobe form a transverse row with two basal tubercles, of three in a triangle, on the mesogastric lobe. Epi- and mesobranchial lobes, each with two tubercles are transversely separated by a distinct postcervical furrow; those on the epibranchial lobe are in line with two on the narrow urogastric lobe, while those on the mesobranchial lobe

line with two anterior tubercles on the sub-triangular cardiac region. Of two rounded ridges on the metabranchial lobes, the anterior is the smaller. The branchiocardiac furrow runs almost straight between the ridges to the margin and a thin ridge bounds the posterior margin.

Minute, even-sized granules crowd the dorsal surface.

Discussion: Fused metabranchial tubercles into ridges immediately distinguish *Kromtitis daniensis* sp. nov. from *K. koberi* and *K. koberiformis*, the latter of which, also has secondary granules. There is a tendency of fusion in metabranchial tubercles in *K. spinulatus*, which otherwise differs in the absence of urogastric tubercles and in having three pairs of tubercles on each epibranchial lobe. The angular outline of *K. pentagonalis* and ovate outline of *Kromtitis* sp. 1 (Beschin *et al.*, 2007b) readily distinguish those species. Sparse dorsal tuberculation distinguishes *K. laevigatus. Kromtitis daniensis* sp. nov. appears to have a stronger relationship with *K. tuberculatus*, from the Lower Eocene, Ypresian, of Vicenza, Italy, particularly in orbitofrontal characters and dorsal outline, but that species differs in having distinct metabranchial tubercles. A coarser surface ornament immediately distinguishes *Kromtitis* sp. 2 (De Angeli and Beschin, 2008) from the Oligocene of Italy.

Subsection Raninoidia De Haan, 1833

Family Cenomanocarcinidae Guinot, Vega and van Bakel, 2008

Genus Cenomanocarcinus Van Straelen, 1936

Type species: By original designation, *Cenomanocarcinus inflatus* Van Straelen, 1936, from the Cenomanian of France.

Range: Upper Albian to Campanian.

Cenomanocarcinus tenuicarinatus sp. nov. (Fig. 1.3)

Diagnosis: Carapace subhexagonal, a little wider than long, orbitofrontal margin rather less than half carapace width, rostrum trifid; anterolateral margin rounded with five spines distally and straight to the epibranchial spine; posterolateral margins convergent to rounded posterolateral angles; posterior margin wide, weakly concave; tuberculate hepatic ridges; median ridge broad medially, tapering as a smooth ridge from cardiac region to posterior margin; lateral ridges not quite reaching posterior margin.

Derivation of name: Referring to the comparatively narrow ridges.

Material: Holotype, a decorticated carapace, BMNH In. 61075 from the Lower Turonian, Ezu-Aku Formation of Ezilla, S. E., Nigeria. P. Zaborski Coll.

Derivation of name: With reference to the thin lateral carinae.

Description: Carapace subhexagonal in outline, one sixth wider (measured behind epigastric spine) than long (83.0 %), moderately arched in both longitudinal and transverse sections, highest at cardiac region. The orbitofrontal margin occupies rather less than half the width (45.0 %) with the circular orbits taking up the outer thirds. The rostrum is sulcate, broadly trilobed and produced slightly beyond the outer orbital spines, the tip is obscured; the blunt post-rostral spines lead back to rounded inner orbital spines. There are two notches in the thickened upper orbital margins and the outer orbital angles are bluntly triangular. On the anterolateral margins five forwardly directed, upturned spines increase in size posteriorly, then, lined with a few granules, the margins are straight to the epibranchial angle; basal scars of which suggesting it was produced to a narrow elongate, upwardly inclined spine. Weakly convex posterolateral margins, converging to rounded posterolateral angles, lead to a weakly concave posterior margin bounded by a thin ridge.

Lobes are weakly tumid. The cervical furrow, almost straight and shallow across the midline is broader towards the margins. Branchiocardiac furrows are moderately deep. Two tubercles crown a low ridge on each hepatic region, and there are two larger tubercles on each protogastric lobe. There is a tubercle at the base of the anteromesogastric process which extends to the post-rostral spines and the median carina is comparatively wide across the tuberculated mesogastric lobe, the median of three tubercles set in a triangle on the urogastric lobe is the largest, and two are on the lingulate cardiac region, which tapers in a smooth ridge to the posterior margin. Curving epibranchial ridges, lined with three or four small tubercles, are conjoined medially with subparallel metabranchial ridges lined with eight or nine tubercles, the first the largest, terminating just before the posterior margin. Terminal 'damage' of the left lateral ridge is limited to a chip in the cutical and there is no evidence of a terminal spine.

Discussion: There is a superficial resemblance to *C. cristatus*, but the sole specimen, "is squeezed transversely and deformed" (Guinot *et al.*, 2008, p. 693), thus, probably rendering similarity more apparent than real; while both species lack the 'H-shape', the sharper median angle of the cervical furrow and straighter, thicker, more tuberculated lateral ridges, readily distinguish *C. cristatus*. The smooth branchial part of the median ridge is similar to that of *Cenomanocarcinus vanstraeleni* as figured by Guinot *et al.* (2008, fig. 5d) and suggests a transient step towards *Campylostoma matutiforme* Bell, 1858, from the Lower Eocene, London Clay of England, a genus provisionally included in the Cenomanocarcinidae.

Strictly speaking, the referred to 'epibranchial' spines in *Campylostoma* project from the metabranchial region posterior to the dorsal epibranchial ridge. As such, they are the equivalent of the first of 'two teeth on the posterolateral margin' of *Cenomanocarcinus* (Guinot *et al.*, 2008, p. 684).

The controversial species, *Campylostoma pierrense* var. *multituberculatus* [sic] Joleaud and Hsu, 1935, from the Upper Cretaceous of Tanout, Niger, differs in all respects from the two new species as it does from Cenomamocarcinidae (see Guinot *et al.*, 2008, p. 697).

Cenomanocarcinus dissimilis sp. nov.

(Fig. 1.4)

Diagnosis: Carapace wider than long, hepatic and protogastric tubercles not in line, 'H-shape' indistinct, a gap before penultimate and last lateral carinal tubercles.

Derivation of name: Different from other known species.

Material: A carapace lacking details of the front and lateral spines, BMNH In. 63710 from the Lower Cenomanian Odukpani Formation, Calabar-Ikam road, 1 km north of Ikot Ekpeni Junction, S. E. Nigeria.

Description: Carapace subhexagonal in outline, about one third (66.0 %) broader (measured behind epigastric spine) than long, moderately arched in both longitudinal and transverse sections. The poorly preserved front occupies rather less than half carapace width (45.0 %), with circular orbits taking up the outer thirds; the sulcate basal part of the rostrum suggests rounded inner orbital angles. Only the outer notch close to the outer angle is preserved in the raised upper orbital margin. Notched at the outer orbital angles, the lower orbital margins extend marginally beyond the upper. Basal scars suggest spinular outer orbital angles and three small, weakly upturned spines on the convex anterolateral margins, whereas the epigastric basal scars suggest more robust spines. Weakly concave posterolateral margins have two close set granules about midlength, then run almost straight to broadly rounded, posterolateral angles leading to an almost straight posterior margin. Hepatic ridges have three tubercles set distal to two on each protogastric lobe. The cervical furrow crosses the midline in a broad V, loops round the outer protogastric tubercle and recurves to the margin. Commencing with a tubercle posterior to the outer protogastric one, three or four tubercles line curving epibranchial ridges. Adjacent to the same tubercle are weakly divergent lateral ridges, irregularly lined with four to six tubercles; there is a gap before the penultimate and last which overhang the posterior angles. The median ridge rises with a tubercle on the ovate mesogastric lobe, there is a tubercle on the crescentic urogastric lobe, a depression between deep epimeral adductor muscle scars, the elongate cardiac region has two tubercles and there is one on the intestinal lobe. The H-shape is produced by a low, convex eminence either side of the cardiac region.

Discussion: Cenomanocarcinus dissimilis sp. nov. is shorter in proportion to width than Cenomanocarcinus inflatus with which, apart from a gap before the terminal one on the lateral ridges and non-aligned hepatic/protogastric ridges, it approximates in surface ornament. Much the same can be said for Cenomanocarcinus vanstraeleni.

The epibranchial ridges of *Cenomanocarcinus oklahomensis* are straighter, thus producing a sharper angle with the lateral ridges.

Cenomanocarcinus beardi differs in having a minute tubercle on the anteromesogastric process, a smooth hepatic ridge and a more conspicuous 'bar' to the 'H-shape'. Elongate carapace length/width proportions immediately distinguish *Cenomanocarcinus cristatus*.

Family Necrocarcinidae Förster, 1968 Subfamily Paranecrocarcininae Förster, 1968 Genus Paranecrocarcinus Van Straelen, 1936 Type species: Paranecrocarcnus hexagonalis Van Straelen, 1936, by monotypy, from the Hauterivian of Yonne, France. *Range:* Aptian to Maastrichtian.

Paranecrocarcinus milbournei sp. nov.

(Figs. 1.5-1.8)

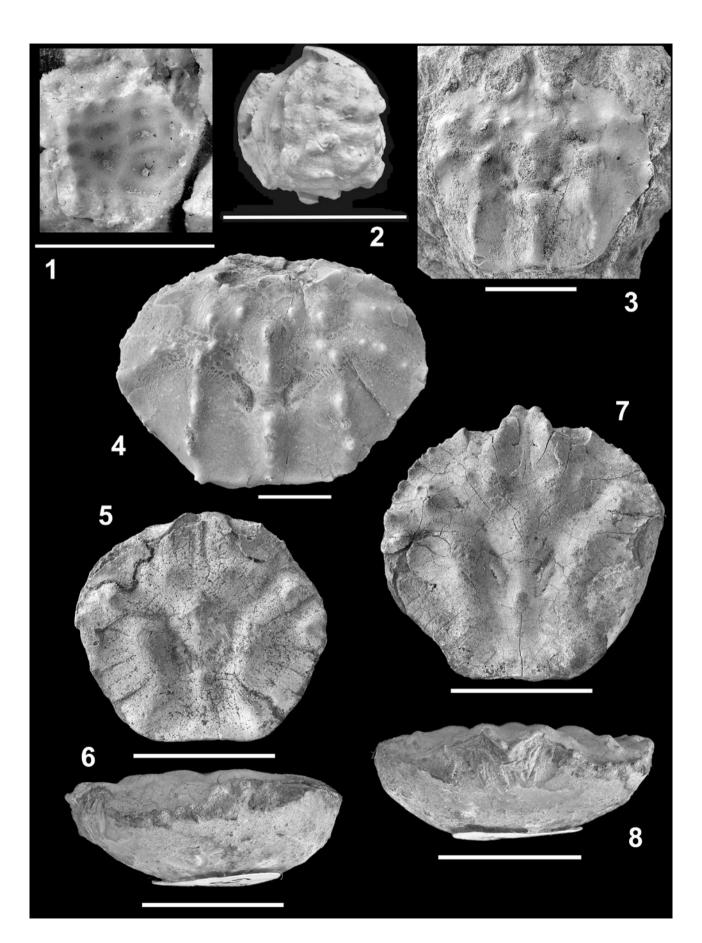
Diagnosis: Carapace subpentagonal in outline; a little wider than long, orbitofrontal margin narrow; one pair of post-rostral slits; anterolateral margins granulate, protogastric, epibranchial, mesobranchial and cardiac lobes tumid; a longitudinal ridge on metabranchial lobes.

Derivation of name: In rememberance of the late Raymond A. Milbourne, staunch friend and colleague of 60 years standing, and dedicated palaeontologist.

Material: Holotype, a carapace, BMNH In. 63771, Calabar-Ikam road, 1 km North of Ikot Ekpeni Junction, Nigeria; paratype, a carapace, BMNH In. 61076, Calabar-Ikam road, 1 km north of Ikot Ekpene Junction, S. E. Nigeria. Both specimens are from the Cenomanian, Odukpani Formation; P. Zaborski Coll.

Description: Carapace subhexagonal in outline, almost as long as wide (93 %), longitudinally and transversely flattened. The orbitofrontal margin occupies about a half (51.6 %) of the width, of which the produced front takes up the median third. Ovate orbits are directed slightly upwards and the lower orbital margin is visible from above. The deeply sulcate rostrum is bifid, strongly downturned at its tip, the horns, crowned by a tubercle, are separated by a rounded notch; thickened sides run back in two arcs to thin, slightly raised upper orbital margins which have two equidistant notches, the inner one closed. The outer orbital spine is bluntly triangular. Inclined, weakly convex anterolateral margins are lined with six minute granules increasing in size posteriorly before the cervical notch and two behind, the larger at the lateral angle. The posterolateral margins are almost straight for about half their length before curving to the weakly concave posterior margin, which is narrower than the orbitofrontal margin and bounded by a weak groove, separating a narrow, triangular intestinal lobe. A pair of short post-rostral slits lay alongside a tapering anteromesogastric process extending almost to the front. There is a pair of gastric pits a little more than half (59 %) distant from the front, the cervical furrow, broadly V-shaped to the outer angle of the mesogastric lobe, runs forwards and outwards, then turns sharply to reach the margin at a slightly wider gap between the 6th/7th anterolateral margin granules. Each protogastric lobe has a transverse pair of tubercles, the inner one the larger. Defined by weak lateral grooves, a subtriangular mesogastric lobe has a low basal node. The urogastric lobe is depressed, bounded laterally by deep attractor epimeralis muscle scars and weakly separated from the narrow, elongated ovate cardiac region which has a median node.

→Fig. 1. 1, 2. Kromtitis daniensis sp. nov. dorsal view of holotype, carapace and counterpart, BMNH IC500 from the Middle Danian, T. bruennichi Zone of Fakse, Denmark. 3. Cenomanocarcinus tenuicarinatus sp. nov. Dorsal view of holotype, BMNH In. 61075 from the Lower Turonian, Ezu-Aku Formation of Ezilla S. E., Nigeria. P. Zaborski Coll. 4. Cenomanocarcinus dissimilis sp. nov. A carapace lacking details of the front and lateral spines, BMNH In. 63710 from the Lower Cenomanian Odukpani Formation, Calabar-Ikam road, 1 km north of Ikot Ekpeni Junction, S. E. Nigeria. 5, 6. Paranecrocarcinus milbournei sp. nov. Dorsal and left lateral views of holotype, BMNH In. 63771, Calabar-Ikam road, 1 km North of Ikot Ekpeni Junction, Nigeria. 7, 8. Paranecrocarcinus milbournei sp. nov. Dorsal and left lateral views of paratype, BMNH In. 61076, Calabar-Ikam road, 1 km north of Ikot Ekpene Junction, E. S. Nigeria. Both specimens from the Cenomanian, Odukpani Formation, P. Zaborski Coll. Scale bars in mm.



Faint branchiocardiac furrows curve to the base of the urogastric lobe and recurve sharply to run parallel with the bounding grooves of the urogastric lobe. Each epibranchial lobe has three tubercles in a triangle, and a narrow ridge on the mesobranchial lobes is almost continuous with a broadly rounded, crescentic ridge extending to the posterior angles on the metabranchial lobes. Densely, crowded granules cover the dorsal surface, those on the nodes and ridges varied in diameter.

Discussion: Paranecrocarcinus milbournei sp. nov. differs from the type species in having a subpentagonal outline with granulated anterolateral margins and metabranchial ridges. Paranecrocarcinids with a single mesogastric tubercle in common with *P. milbournei* are: *P. graysonensis, P. foersteri, P, kennedyi, P. libanoticus,* and *P. mozambiquensis.* However, in none of these species are the branchial lobes fused into ridges, a condition approached only in *P. digitatus* and *P. moseleyi.*

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