

A NEW CRAB FROM THE MIDDLE EOCENE OF LIBYA

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ABSTRACT. A new species of carpilid crab, *Palaeocarpilius aquilinus*, is described from the Lutetian of Central Libya and comparisons are made with other members of the genus. The posterior margin of *P. aquilinus* is wider in the female than the male. This finding is compared with four species of xanthid crabs.

Palaeocarpilius is known to have ranged from the Lutetian (Middle Eocene) to the Lower Miocene and species have been described from north-west Africa to Saipan and from the Paris Basin to Zanzibar (Perrin Island). It is represented in north-east Africa (Egypt and the Somali Republic) by *P. macrochelus* (Desmarest) (Stubblefield 1946), which has a widespread distribution and ranges from the Lutetian to the Oligocene; by *P. simplex* Stoliczka from the Upper Eocene of Egypt (Glaessner 1929) and *P. straeleni* Remy from the lower Lutetian of Senegal.

The material described here forms part of the collection made by the 1964 Bristol University Expedition led by Dr. R. J. G. Savage from the area of Bu el Haderait; and collections made by oil-pipeline engineers from Beda Oilfield, Central Libya. The presence of *Nummulites laevigatus*, *Nonion* sp., *Elphidium* sp. in the accompanying fauna of corals, bryozoans, gastropods, lamellibranchs, nautiloids, echinoids, and marine mammals (Savage and White 1965, p. 91) indicates a late Lutetian age for the deposits, which consist of alternating micrites and shelly limestones. Goudarzi (1970, p. 38) assigns these beds to the two lower units of the Wadi Thamit Group, the Al Gata and T'med al K'sour Chalks. The Wadi Thamit Group is underlain by the *Orbitolites* Limestone of the Jabal Waddan Group, which is considered to be of Ypresian age, and is overlain by the Dur al Abd Formation of Upper Eocene to Oligocene age (Goudarzi 1970, p. 38).

The specimens from Bu el Haderait have been rolled and damaged, the outer layer of the dorsal carapace being lost; whereas the specimens from south-west of Beda were collected *in situ* and still retain the outer layer of shell. They are, however, sometimes covered by a dendritic encrustation which may possibly have been leached from the shell itself.

SYSTEMATICS

Section BRACHYRHYNCHA Borradaile, 1907

Superfamily XANTHOIDEA Dana, 1851

Family CARPILIIDAE Ortmann, 1894

Remarks. On the basis that *Palaeocarpilius* and some closely allied genera were derived from the Cretaceous *Caloxanthus* which had its origins in a different dynomenid stock from xanthid crabs *sensu stricto*, Wright and Collins (1972, p. 103) raised Ortmann's subfamily to family status.

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Genus PALAEOCARPILIUS A. Milne-Edwards, 1862

Type species. Cancer macrochelus Desmarest, 1822, subsequently designated by Glaessner (1929, p. 291).

P. aquilinus sp. nov.

Plate 29, figs. 1-8, Plate 30, figs. 1-8

Derivation of name. The trivial name, eagle-like, is suggested by the resemblance of the median ornament to a Roman standard-eagle (Pl. 30, fig. 1).

Diagnosis. A *Palaeocarpilius* with the front slightly produced; four almost coalescing bosses forming a low ridge, with a steep depression behind, across the posterior part of the mesogastric lobe.

Material. Thirty-three imperfectly preserved carapaces, some with parts of limbs associated, of which fifteen are males, six females, and the remainder indeterminate. Specimen In. 60890 from the Beda oilfield is designated holotype, which with paratypes In. 60891-In. 60899 is in the Department of Palaeontology, British Museum (Natural History). The other paratypes are: BU20286-BU20306 Department of Geology, Bristol University and 1691 JSHC Coll.

Occurrence. Middle Eocene, late Lutetian.

Localities. 1. Bu el Haderait, 28° 30' N. 18° 40' E.
2. 40 miles SW. of Beda oilfield, lat. 28° 10' N. long., 18° 47' E.

Description. The carapace is sub-ovate in outline, the length being about two-thirds of the width; it is strongly arched transversely and more steeply rounded anteriorly in longitudinal section. There are nine (including the external orbital) sharp, triangular, slightly upturned spines increasing in size posteriorly on the rather thin antero-lateral margins. At the antero-lateral angle a rounded ridge extends on to and delimits the epibranchial lobe on a level with the rear of the urogastric; there is an upturned spine on the outer third of this ridge. The postero-lateral margins are short and deeply concave and lead by a broadly rounded angle and notches for the fifth coxae into the almost straight posterior margin which is bounded by a narrow marginal groove and is about a quarter of the maximum width. The posterior margin is delimited by two small processes. The orbito-frontal margin occupies half the carapace width. The orbits are large and open to the front. The upper orbital margin is thickened by a rounded ridge, which becoming sharper continues across the front.

EXPLANATION OF PLATE 29

Palaeocarpilius aquilinus sp. nov.

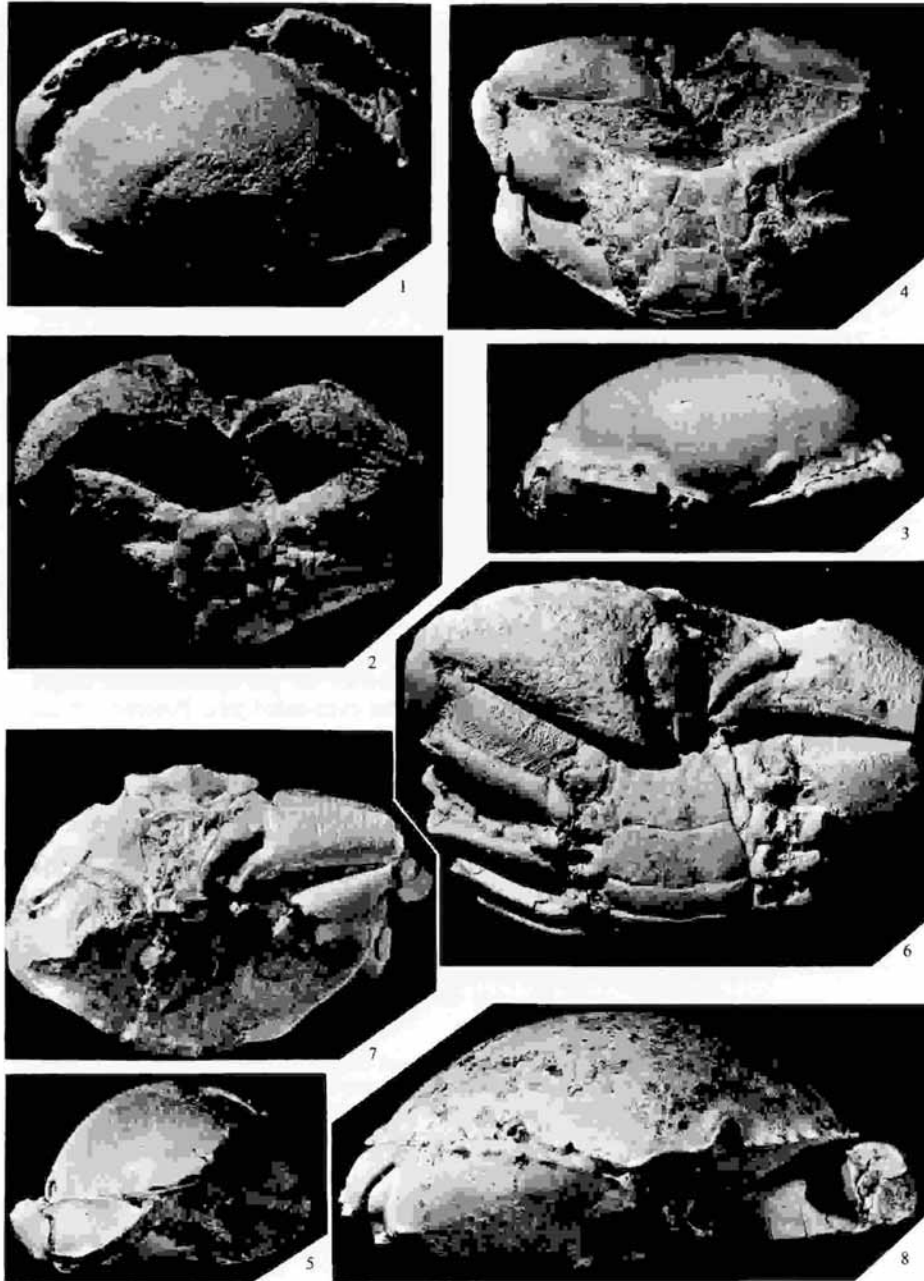
Figs. 1-3. Paratype BM. In. 60893 Lutetian, Bu el Haderait, Libya. Male $\times 1$. 1, Dorsal. 2, Ventral. 3, Anterior showing 2 rows of spines on chelae.

Figs. 4-5. Paratype BM. In. 60894. 4, Flattened male abdomen. 5, Left lateral view showing epibranchial ridge spine.

Fig. 6. Paratype BM. In. 60895, ventral view of female abdomen.

Fig. 7. Paratype BM. In. 60896, ventral view.

Fig. 8. Holotype BM. In. 60890 Lutetian, 40 miles SW. of Beda Oilfield, Central Libya. Anterior view showing orbit, notched front and sculpture. Male $\times 1$.



COLLINS and MORRIS, Eocene crab

The inner supra-orbital spine is broadly triangular and somewhat larger than the external one. The lower orbital margin is thin, with a sharp sub-orbital spine (Pl. 29, fig. 8) and the second segment of the antenna completes the lower orbital margin. The front is set a little in advance of the general curve produced by the antero-lateral margins so that it can be seen when viewed directly from above; it is divided into three nearly equal parts. The central portion is produced, slightly upturned and notched medially; the portion on either side is concave.

The lobes are barely differentiated on the anterior part of the carapace. A gently curving ridge, formed by four transversely elongated, almost coalescing bosses extends across the posterior part of the mesogastric lobe and adjacent portion of the protogastrics; anteriorly this ridge is barely raised above the general surface of the carapace, but posteriorly it is steeply depressed. The urogastric lobe is quadrate and tumid, but not higher than the ridge before it; the cardiac lobe is pentagonal with concave lateral margins and rounded base. The small intestinal region is rounded and hardly differentiated from the metabranchial lobes. The lateral portion of the metabranchials is deeply deflected under the epibranchial ridge.

A V-shaped mass of 'wedge-shaped' pits scarifies the mesogastric anterior to the bosses and a single row of similar pits curves back, round and under the bosses to the centre of the epimeral adductor muscle scars, immediately above which the posterior gastric pits are generally prominent. A row of circular pits extends in a broad semicircle from near the mesogastric pits back to the epibranchial ridge, and other pits of several diameters are scattered within the area enclosed. A further row begins below the epibranchial ridge and extends ventrally close to the pleural suture to a small kidney-shaped mass of pits marking the attachment of the adductor testis muscle. The sculpture of the carapace anterior to the epibranchial ridges (Pl. 29, fig. 8, Pl. 30, fig. 5), is composed of regular even-sized pits. Postero-lateral, metabranchial, and intestinal areas are mostly smooth with sporadic pits. As with many carpiids the pits are deepest and densest nearest to the margins. The pits continue, but much less densely, on to the sub-orbital and sporadically over the sub-hepatic regions (Pl. 30, fig. 6). A lower shell layer is composed of numerous flattened, somewhat reticulate nodes, many overlapping one another.

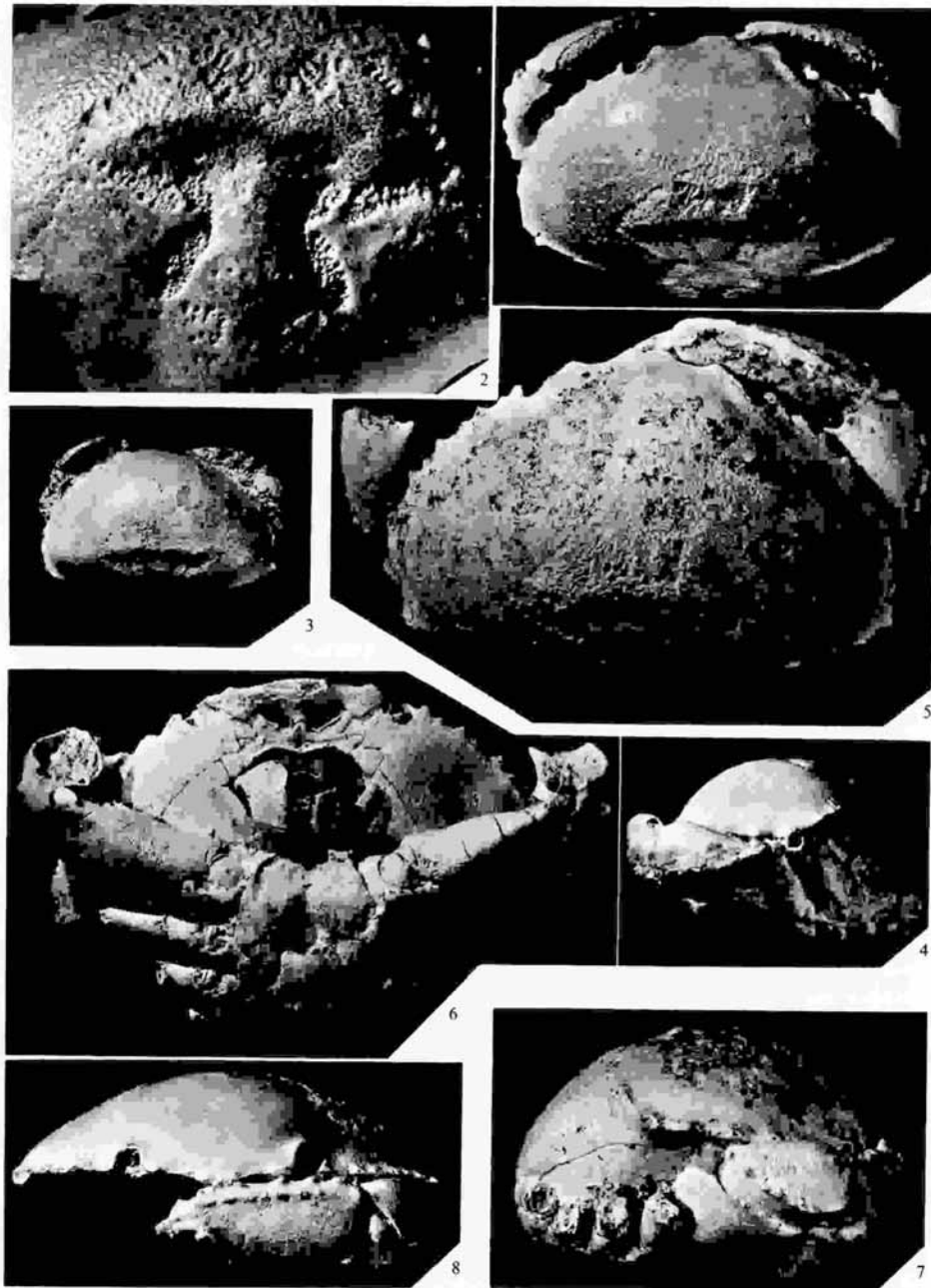
On the ventral surface the front curves downward and backward to meet the head of the rather narrow epistome, which has a thickened margin round a median pit. The basal segment of the antennules is half-moon shaped with the distal margin

EXPLANATION OF PLATE 30

Palaeocarpilius aquilinus sp. nov.

Figs. 1-4. Lutetian, Bu el Haderait, Central Libya. 1, Dorsal view, Paratype BM. In. 60894 male $\times 1$. 2, Enlarged view of branchial and cardiac areas to show sculpture $\times 2$. 3, Paratype BM. In. 60897 immature juvenile male showing main characters of adults, $\times 1$. 4, Lateral view of paratype BM. In. 60893, $\times 1$.

Figs. 5-8. Lutetian, 40 miles SW. of Beda Oilfield, Central Libya. 5, Dorsal view of holotype BM. In. 60890 to show surface sculpture, $\times 1$. 6, Ventral view of holotype with right chela removed at wrist joint to show buccal cavity and antennular areas, $\times 1$. 7, Lateral view of holotype showing outer marginal spines of carpus and upper distal spines of merus, $\times 1$. 8, Anterior view of paratype BM. In. 60892.



COLLINS and MORRIS, Eocene crab

ridged. The second segment of the antenna is of moderate length, shaped like an arrow-head at its base with the 'shaft' parallel sided, terminating in the orbit. A moderate ridge extends across the endostome. The buccal margins converge a little posteriorly and the distal angles are broadly rounded. The pterygostomial region is finely pitted; a fine groove bounds the buccal margin and, becoming broader, continues round the anterior and lateral border of that part of the process enclosing the chelipeds. The ischial endognath of the third maxillipeds is rhomboidal and medially depressed; the exognath is about two-thirds of the width of the endognath and rounded transversely; both members are pitted.

The part of the sternum corresponding to the third thoracic sternite is flattened and ridged at the postero-lateral angle where a deep marginal cleft separates it from the fourth sternite. The cleft continues as a broad groove towards the midline where there is a small pit. The lateral edge of the fourth sternite is raised and the posterior part is tumid; the anterior part of the abdominal 'trough' is densely pitted and a few fine pits extend on to the tumid area. The remaining sternites are flattened, with a few scattered pits, particularly round the edges.

The 1st and 2nd abdominal somites of the male (Pl. 29, figs. 2, 4) are of about equal length; the 3rd-5th are fused, but their positions are marked by short notches on the lateral margins and a few pits extend further towards the centre; the lateral thirds of the '3rd' and '4th' are tumid, the '5th' is almost flat; the 6th is quadrate and about as long as the triangular telson; a shallow groove extends round the lateral margin leaving a broad median portion. In the female abdomen the lower margin of the 1st somite is deeply concave and medially about half the length of the 2nd; the 3rd-5th become slightly longer, the 6th is triangular, about twice the length of the 5th and somewhat shorter than the more or less sub-oval telson; the median and almost equal-sized lateral portions are separated by shallow depressions.

The chelipeds are robust and the larger claw, where preserved, is on the right. The merus is triangular with fairly sharp angles; there are two spines in line on the upper distal angle; on the inner distal angle is a large quadrate node with a pit behind into which fits a node on the proximal end of the palm. The carpus is half the length of the merus, sub-triangular in section; dorsally it is triangular with a sharp tooth on the inner distal angle and a carinated tubercle between it and the rounded articulating knob; there are generally four sharp, carinated spines on the rim-like outer margin. The palm of the right claw is heavy, about half the carapace width in length, and increasing in width from the proximal to the distal end. The fixed finger is half the length of the palm, squat, and with the lower margin almost in line with that of the palm; the opposing margin has a single broad cusp and a lower terminal 'pad'. The movable finger is broadly curved with three evenly spaced cusps on the opposing margin. The palm of the left claw is shorter and much less tapered from distal to proximal end; the fixed finger is longer, more slender, and inclined downwards forming a distinct curve with the basal margin of the palm. The movable finger is straighter. Both the opposing margins are sharper, with fine, almost granular cusps.

Both the claws share the same character of a row of strong, almost conical spines increasing in size distally on the upper margin of the palm; the number on the larger claw varies from nine to seven, while on the smaller there may be only six or seven. The spines are separated by a shallow groove from a prominent node-lined ridge

extending nearly the whole length of the upper outer margin. The lower margin of the palm is lined with a thin ridge (beginning at the node which fits into the meral pit) which becomes thickened at the junction with the fixed finger and extends a short way along it, tapering rapidly. There is a large tubercle, with a smaller one beside it, on the proximal upper margin of the movable finger and a shallow groove extends about half the length of the upper outer margin. The lower articulating knob is protected by a short process and above this is a prominent tubercle, sometimes forming part of a short rounded ridge.

The walking legs are long and stout; the meri are elliptical in section and a strong ridge lines the upper (and possibly lateral) margin of the slender dactylus. The fingers on both hands are markedly dark coloured, a feature which, according to Stoliczka (1871, p. 9) is typical of this group.

Measurements in mm.

	<i>Carapace length</i>	<i>Width*</i>	<i>Orbito-frontal width</i>
Holotype In. 60890	61	82	40
Paratype In. 60893	41	57	29
Paratype In. 60898	66	86	46
Paratype In. 60894	45	64	32
Paratype In. 60897	28	38	20

* Between 8th/9th antero-lateral spines.

Discussion. While most of the specimens are to some degree damaged or rolled, the diagnostic characters are generally sufficiently well preserved, although the antero-lateral spines often appear rounded and almost globular, and the additional spine on the epibranchial ridge is much reduced, as is the ornament on the upper margin of the hand. Traces of the endophragmal skeleton are preserved on specimen BU. 20297.

The new species has affinities with *P. macrochelus* (Desmarest), but may at once be distinguished by its slightly produced front, the arrangement of the bosses and the depression caused by them, and the presence of the additional spine on the epibranchial ridge. The nature of the tubercles on the upper margin of the hand of *P. aquilinus* is of solid individuals rising directly from the margin and not fringed like *P. macrochelus* as stated and figured by Stubblefield (1946, pl. 8, fig. 5); also the carina on the upper outer margin is nodose and does not extend the whole length of the hand. The strong ridge figured by Stubblefield (1946, pl. 8, figs. 2b, 6) extending the length of the movable finger (and to some extent on to the immovable finger) is not developed in *P. aquilinus*. One of the specimens (C11,113 Sedgwick Museum) described by Stubblefield from British Somaliland, is a juvenile which nearly corresponds in size with paratype BM. In. 60897 of *P. aquilinus*; each shows the distinctive specific characters of the adult which do not appear to alter to any great extent during ontogeny. On Bittner's subspecies, *P. m. coronata* (1886, pl. 1), from the Priabonian of Verona, the bosses are prominent, individual, and arranged in a distinct semicircle. Bittner also stated that a second row of tubercles is developed near the 'upper hump' of a chela of one large male. The specimens from the Upper Eocene of Rumania (Ghiurca and Givulescu 1964, figs. 2-5) appear to belong to this subspecies. Milne-Edwards figured (1862, pl. 6, figs. 2, 2a) a specimen from the

neighbourhood of Verona; this compares favourably with Bittner's description and figure (1886, pl. 1) and evidently belongs to *P. m. coronata*, as does the specimen BM. 39355, formerly considered by Stubblefield (1946, p. 516) to be *P. macrochelus*. In this specimen, however, the bosses are somewhat more subdued than Bittner's figure (op. cit.) would indicate. The front is produced in *P. stenurus* (Reuss) (vide Milne-Edwards 1862, pl. 1, fig. 3) from the 'terrine nummulitique' near Verona, but in this form only two bosses are present and the epibranchial ridge extends much further towards the midline of the carapace. Milne-Edwards (1862) and Glaessner (1929) consider *P. stenurus* is a juvenile of *P. macrochelus*. The unique specimen of *P. stenurus* is an internal mould and appears to differ in certain aspects from small specimens assigned to *P. macrochelus* in the British Museum (Natural History). The nature of the preservation of *P. stenurus* may account for these differences, but more material may show it to be a valid species. Antero-lateral spines are reduced to nodes on *P. straeleni* and are not developed on *P. simplex* Stoliczka which is also recorded from the Upper Eocene of Egypt. There is a close similarity between the antero-lateral spines of *P. aquilinus* and *P. rugifer* Stoliczka, and some specimens of the former show a similar rugose ornament of the cheliped on a subsurface shell layer, but among other differences the bosses are lacking and the orbito-frontal width is much greater on *P. rugifer*.

Six female specimens were determined from their broader abdominal somites. Further to distinguish male and female forms two parameters were measured; the dorsal carapace width (trs.) and posterior margin width (trs.). The dorsal carapace width measurement was taken from between the 8th-9th antero-lateral spines. The posterior margin width was taken between the tips of the two spiny processes that delimit the posterior margin. These processes form the lateral extent of the 1st abdominal somite. The percentage ratios of the two measured parameters of the small population (only six females) of *P. aquilinus* indicated a substantially wider abdomen in the female of 14.4% as compared with the male. Hu (1971, p. 36) has indicated similar but unquantified results from the ocypodid *Uca pugilator* (Bosc.).

For comparison four Recent species belonging to genera related to *Palaeocarpilius* were studied. Six specimens of each sex of *Carpilius corallinus* (Herbst), *C. maculatus* (Linn.), *C. convexus* (Forskål), and *Atergatis floridus* (Linn.) were used. In all the species the female abdomens are wider than the males. The increase in size ranged from 8.5% in *C. convexus* to 15.8% in *C. maculatus*. The ratios do not overlap but in *C. convexus* the upper limit of the male range just coincides with the lower limit of the range of the females. Their average ratios are quite dissimilar. One male specimen of *A. floridus* had the unusually low ratio of 14.7%. The ratio was so low that it has been excluded from the average rather than produce an abnormally low figure. Generally, but by no means uniformly, the larger the specimens the greater difference between the ratios of the sexes.

Using the measurements of Ghiurca and Givulescu (1964, table 1) from an unknown population, the ratios fall into two groups 23.2-24.3%, average 23.9% (specimens 1-4) and 26.0-27.5%, average 26.6% (specimens 5-8, 10). One specimen, 9, had a ratio of 25% and cannot be assigned to either group. We can now assume that specimens 1-4 are males and specimens 5-8 and 10 are females. Specimens 1 and 3 are in fact figured as males.

Thus, by using the method described above it is possible to determine with some degree of accuracy the sex of an individual when no abdominal somites are present, provided that the carapace width and posterior margin are entire.

Habits and ecology

The family Carpiliidae is common around the shores of tropical countries and especially the Indo-Pacific islands. They are free-living, bottom-crawling inhabitants of the tropical littoral. Early workers considered that they were the inhabitants of the fringes of coral reefs. Recent work by Macnae and Kalk (1958), Taylor (1968, 1971) suggests that in fact larger members of the family are mostly found in the sublittoral zone or the algal ridge of the eulittoral zone of wave-cut platforms. These wave-cut platforms are frequently associated with pre-existing coral colonies. Tweedie (1950) and Guinot (1967) observe that carpiliids are normally nocturnal and Macnae and Kalk state that the large carpiliids are to be found under large stones during daylight. But Taylor (1968, p. 174) has observed them to move about during daylight, when their bright yellow and orange spots make them difficult to see.

To date nobody has studied the habits and ecology of these crabs in any detail and it has been assumed that they are general scavengers as well as possibly preying on molluscs and worms that inhabit the same environment. In the Seychelles the swimming crab *Thalamita* has been seen to prey upon *Carpilius* (Taylor 1968). Abundant molluscs have been found in association with *Palaeocarpilius*, but without more work on the recent genera it is impossible to give any idea of the prey of *Palaeocarpilius*.

In his work on shoreline sedimentation in the Miocene of Libya, Selley (1966, p. 3) points out that the Miocene deposition is the continuation of a facies that started in the Cretaceous. The facies consists of an alternation of shallow-water limestones and shales and the limestones are generally of detrital organic origin. It would seem that *Palaeocarpilius* occupied an environment not very different from the recent *Carpilius*. No swimming crabs have been found in association with *Palaeocarpilius* in Libya, but the portunids are thin-shelled animals and are not often preserved.

None of the characteristic coloured spots of the dorsal carapace of the recent genera have been found on the fossil material, but the spots usually fade fairly rapidly after death in *Carpilius*. It would seem that the strong spinosity of the antero-lateral margins of *Palaeocarpilius* similar to that on portunid crabs, although less exaggerated, would act as a defence mechanism against predators.

It seems likely that *Palaeocarpilius* lived in the high-energy environment of a shallow water hard bottom, probably at the seaward edge of a wave-cut platform, living by scavenging at night and sheltering under rocks by day.

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Repositories. BM., British Museum (Natural History), London; BU., Geology Department, Bristol University; J.S.H.C. Collection.

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