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NEW DECAPODA (CRUSTACEA) FROM THE MIDDLE AND LATE EOCENE OF PAKISTAN AND A REVISION OF *LOBONOTUS* A. MILNE EDWARDS, 1864

BY

CARRIE E. SCHWEITZER[1], RODNEY M. FELDMANN[2], AND PHILIP D. GINGERICH[3]

Abstract– Recovery of new decapod specimens from middle and late Eocene rocks of Pakistan prompted reevaluation of the known decapod fauna of the region. Specimens come from the Sulaiman Range in Balochistan, North-West Frontier, and Punjab provinces, and range temporally from the middle Lutetian through the Bartonian and possibly early Priabonian global marine ages. *Proxicarpilius planifrons*, *Portunus* sp., *Lobocarcinus indicus*, and a new hermit crab (unnamed) are the longest-ranging stratigraphically. *Gillcarcinus amphora* and *Hepatiscus sheranii* appear to be restricted to Lutetian strata, while *Hexapus pinfoldi* and *Bicarinocarcinus collinsi* are restricted to Bartonian-Priabonian strata. Additional Bartonian-Priabonian taxa include a new species of ghost shrimp, *Neocallichirus wellsi*, and a new genus, *Pakicarcinus*, to accommodate *Lobonotus orientalis* Collins and Morris, 1978.

Evaluation of the Pakistan species *Lobonotus orientalis* Collins and Morris, 1978, led to a revision of the extinct genus *Lobonotus* A. Milne Edwards, 1864. A new genus *Lobulata* is erected to accommodate *Lobonotus lobulata* Feldmann et al., 1995, from the Cretaceous-Danian of Argentina. *Lobonotus vulgatus* Quayle and Collins, 1981, is removed from the genus; however, examination of type material will be necessary to place that species within a genus. *Lobonotus* sensu stricto now embraces six North American species.

INTRODUCTION

Fossil decapod crustaceans from Pakistan and the surrounding area have received sporadic descriptive attention over the past 75 years (Table 1). Stoliczka (1871) and Noetling (1902) recorded new species from Pakistan and India, and Glaessner (1933) described several new species from what is now Pakistan and western India. Subsequently, Glaessner and Rao (1960) described a new Paleocene species from western India, and Glaessner and Secretan (1987) described a new genus

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TABLE 1 — Cretaceous, Paleocene, Eocene, and Miocene fossil decapods collected from Balochistan (southwestern Pakistan), Sind (southern Pakistan), and Kachh (western India), and other parts of modern Pakistan and India. Cretaceous, Paleocene, and Miocene occurrences are relatively few in number and marked as to age. Most records listed here are from the Eocene.

- Family Penaeidae Rafinesque, 1815
  - *Penaeus kapurdii* Prasad, 1966 (systematic placement not verified)
- Family Callianassidae Dana, 1852
  - *Callianassa* sp. (Mathur and Gangopadhyaya, 1967; Gingerich et al., 1979)
  - *Neocallichirus wellsi* new species (herein)
- Family Diogenidae Ortmann, 1892
  - Genus and species indeterminate (herein)
- Family Raninidae de Haan, 1839
  - *Laeviranina sinuosa* Collins and Morris, 1978
  - *Lophoranina bakeri* A. Milne Edwards, 1872 (in Withers, 1932; Glaessner, 1933; Sastry and Mathur, 1970)
  - *Ranina*? *griesbachi* Noetling, 1902 (Cretaceous)
- Family Necrocarcinidae Förster, 1968
  - *Hasaracancer cristatus* Jux, 1971 (Cretaceous)
- Family Majidae Samouelle, 1819
  - *Pyromaia inflata* Collins and Morris, 1978
- Family Cancridae Latreille, 1802
  - *Lobocarcinus indicus* Glaessner, 1933 (discussed herein)
- Family Cheiragonidae Ortmann, 1893
  - *Montezumella* sp. (in Sastry and Mathur, 1970; not confirmed)
- Family Hepatidae Stimpson, 1871
  - *Hepatiscus sheranii* Collins and Morris, 1978
- Family Portunidae Rafinesque, 1815
  - *Neptunus sindensis*? Stoliczka, 1871
- Family Carpiliidae Ortmann, 1893
  - *Palaeocarpilius bispinosus* Satsangi and Changkakoti, 1989
  - *Palaeocarpilius macrocheilus* (Desmarest, 1822) (in Sastry and Mathur, 1970; not confirmed)
  - *Palaeocarpilius simplex* Stoliczka, 1871
  - *Proxicarpilius planifrons* Collins and Morris, 1978 (discussed herein)
- Family Hexapodidae Miers, 1886
  - *Goniocypoda rajasthanica* Glaessner and Rao, 1960 (Paleocene)
  - *Goniocypoda sindensis* Glaessner, 1933
  - *Hexapus pinfoldi* Collins and Morris, 1978
- Family Goneplacidae MacLeay, 1838
  - *Bicarinocarcinus collinsi* Glaessner and Secretan, 1987
  - *Galenopsis murchisoni* A. Milne Edwards, 1865
  - *Galenopsis* cf. *G. typicus* A. Milne Edwards, 1865
  - *Galenopsis* sp. (Mathur and Gangopadhyaya, 1967)
  - *Gillcarcinus amphora* Collins and Morris, 1978
- Family Panopeidae Ortmann, 1893
  - *Glyphithyreus wetherelli* (Bell, 1858)
  - *Pakicarcinus orientalis* (Collins and Morris, 1978) (discussed herein)
- Family Potamidae Ortmann, 1896
  - *Potamon (Potamon) sivalense* Glaessner, 1933 (Neogene)
- Family Xanthidae MacLeay, 1838
  - *Xanthosia* sp. (in Gingerich et al., 1979; not confirmed)
  - Xanthid indet. (in Gingerich et al., 1979; not confirmed: probably representing several taxa)

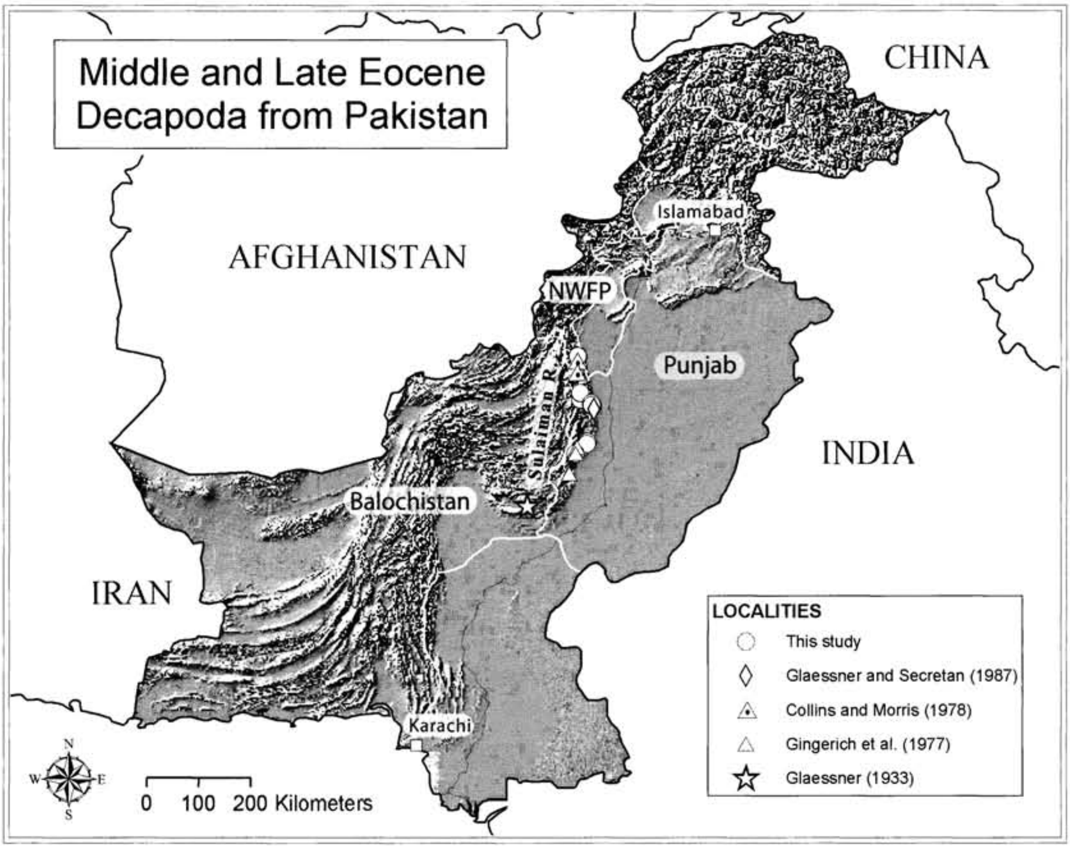

FIG. 1 — Location map showing middle and late Eocene decapod localities of Pakistan. All are concentrated in the Sulaiman Range in the central part of the country. Coordinates of localities are listed in the Appendix.

and species from Pakistan. Numerous other authors provided brief papers that mentioned or described material from Cretaceous to Miocene rocks in what are now Pakistan, Afghanistan, and India (Prasad, 1966; Mathur and Gangopadhyaya, 1967; Jux, 1971; Collins and Morris, 1978; Tiwari and Satsangi, 1988; Satsangi and Changkakoti, 1989). Localities yielding middle and late Eocene decapods of interest here are shown in Figure 1.

Collins and Morris (1978) contributed the most extensive work on Pakistan crabs to date. They reviewed all of the previously reported occurrences and described two new genera and eight new species, out of a total of ten species in the fauna. The current work includes a new occurrence of hermit crab, although it is not referred to a genus or species at this time, a new species of ghost shrimp, and description of one new genus from Pakistan.

Many of the decapod specimens described here come from Drug Lahar in the Sulaiman Range of easternmost Balochistan. The geographic and stratigraphic settings of Drug Lahar localities were described by Gingerich et al. (2001; see Fig. 2). Localities from other sections are correlated based on the regional continuity of Kirthar Group formations (Eames, 1952; Hemphill and Kidwai, 1973; Shah, 1991).

Several changes should be noted concerning stratigraphy: (1) the Lutetian stage and age of earlier authors, representing the middle Eocene, is now divided into Lutetian and Bartonian stages and ages (Hardenbol and Berggren, 1978); (2) geodetic coordinates for the Ramak Kwar decapod locality given by Collins and Morris (1978) are the coordinates of the Ramak River on the Indus

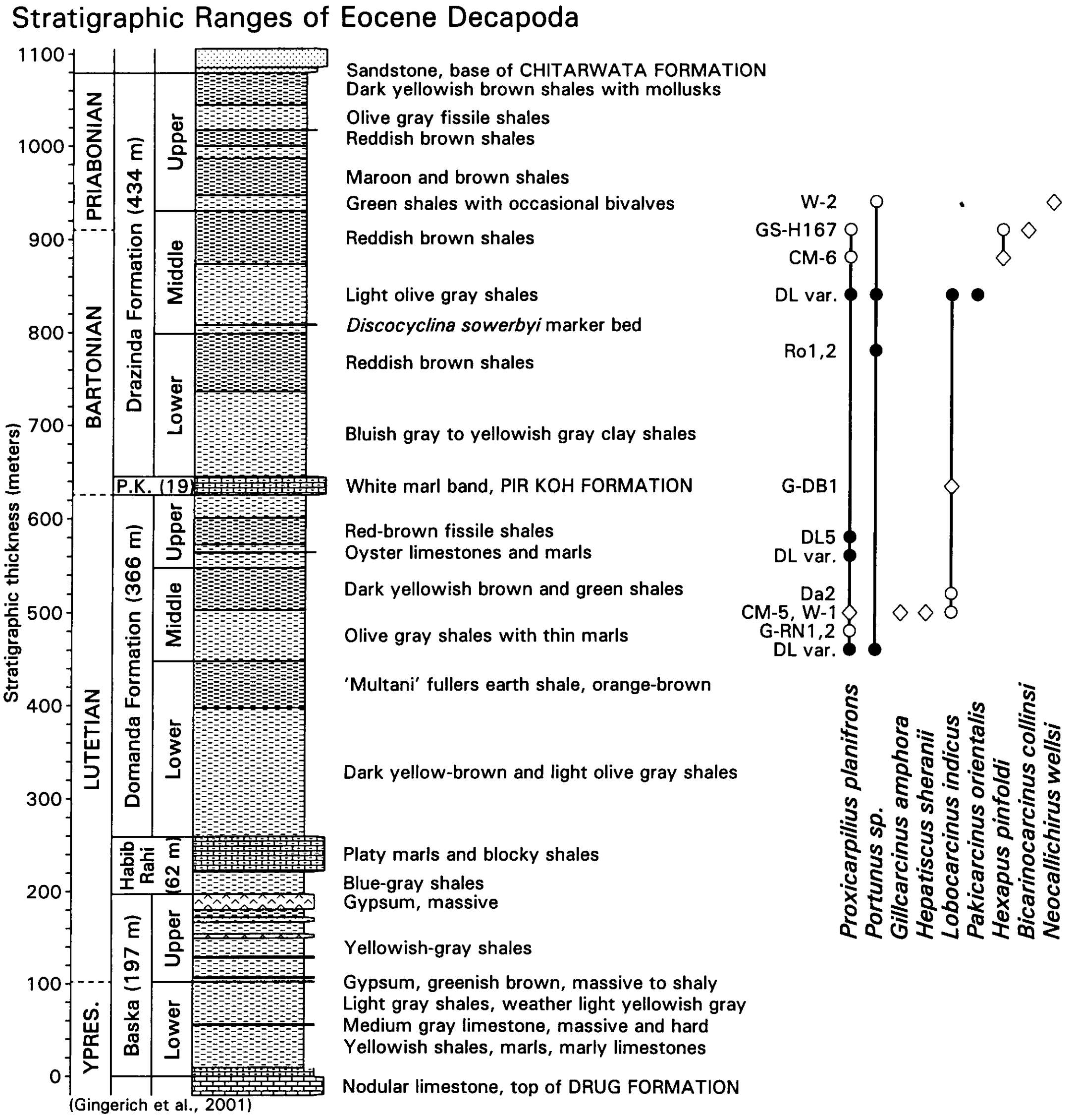

FIG. 2 — Stratigraphic ranges of middle to late Eocene decapod genera and species named from Pakistan. Habib Rahi, Domanda, Pir Koh, and Drazinda formations of the Kirthar Group (Hemphill and Kidwai, 1973; Shah, 1991) are equivalent to the Platy Limestone, Lower Chocolate Clays, White Marl Band, and Upper Chocolate Clays of Eames (1952). Formations are slightly more sand-rich in the northern Sulaiman Range, and more carbonate-rich in the southern Sulaiman Range. Stratigraphic section shown here was measured in the vicinity of Drug Lahar east of the village of Drug, Balochistan (30.86° N, 70.22° E; section is a composite of detailed sections described in Gingerich et al., 2001). This section is typical of Kirthar Group sections in the middle of the Sulaiman Range. Note that some decapod genera and species range through much of Lutetian, Bartonian, and possibly Priabonian time (*Proxicarpilius planifrons*, *Portunus* sp., and *Lobocarcinus indicus*), while others appear to be restricted to the Lutetian (*Gillcarcinus amphora* and *Hepatiscus sheranii*) or the Bartonian and/or Priabonian (*Pakicarcinus orientalis*, *Hexapus pinfoldi*, *Bicarinocarcinus collinsi*, and *Neocallichirus wellsi*). Type localities are represented by diamonds and other localities are represented by circles; solid symbols are tied directly to the Drug Lahar section shown at left, while open symbols are correlated and their position is less certain. Localities and locality abbreviations are listed in the Appendix.

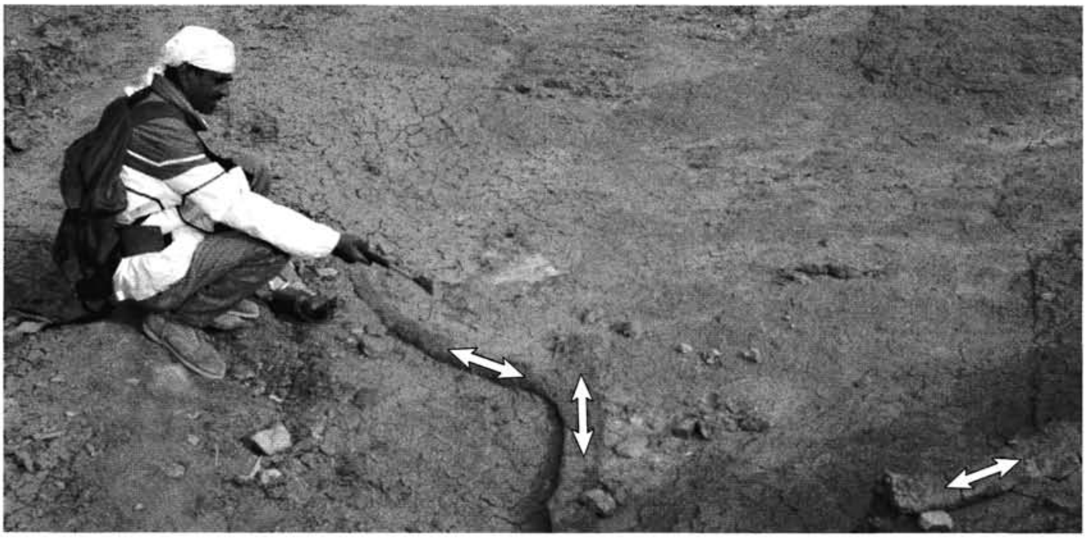

FIG. 3 — Partially-excavated natural cast of a branching decapod burrow complex attributed, questionably, to *Lobocarcinus indicus*. Burrow complex is in the middle Domanda Formation at locality Da2 (see Appendix). Burrow casts are on the order of 10 cm in diameter.

plain, and more accurate coordinates for the CM-5 fossil locality in Ramak anticline near Ramak village are those given in the Appendix here; (3) coordinates for locality 167 yielding the decapods described by Glaessner and Secretan (1987) have been corrected previously (Gingerich et al., 1995, p. 355; see entry for GS-167 in Appendix here).

Decapods were recovered in association with archaeocete cetaceans, as well as echinoids, gastropods and pelecypods. Systematic study of Decapoda is appropriately based on body fossils, but it is interesting to note that burrows are often preserved in the field (Fig. 3). With careful study these may eventually help to clarify how various crabs lived.

Study of the Pakistan species *Lobonotus orientalis* Collins and Morris, 1978, has led to revision of the extinct genus *Lobonotus* A. Milne Edwards, 1864. A new genus, *Lobulata* is erected to accommodate *Lobonotus lobulata* Feldmann et al., 1995, from the Cretaceous-Danian of Argentina, and *L. orientalis* is removed to a new genus, *Pakicarcinus*. *Lobonotus vulgatus* Quayle and Collins, 1981, is removed from the genus; however, examination of type material will be necessary to place that species within a genus. It may be allied with *Pulalius* Schweitzer et al., 2000. *Lobonotus* sensu stricto now embraces six North American species. All specimens described here are deposited in the Geological Survey of Pakistan-University of Michigan collection, Quetta, Pakistan. Casts of the type and figured specimens are available at the University of Michigan Museum of Paleontology, Ann Arbor. Collecting localities referred to in the text are listed in Appendix A.

ABBREVIATIONS

BMNH-In — Natural History Museum (British Museum; invertebrate collection), London, United Kingdom

GSP-UM — Geological Survey of Pakistan-University of Michigan collection, Quetta, Pakistan

SYSTEMATIC PALEONTOLOGY

Order DECAPODA Latreille, 1802
Infraorder THALASSINIDEA Latreille, 1831
Superfamily CALLIANASSOIDEA Dana, 1852
Family CALLIANASSIDAE Dana, 1852
Subfamily CALLICHIRINAE Manning and Felder, 1991

Genus *Neocallichirus* Sakai, 1988

Discussion.— Schweitzer and Feldmann (2002) recently reviewed the fossil members of the genus and provided a discussion of the key characters of the genus.

Neocallichirus wellsi, new species

Fig. 4A-F

Types.— Holotype, GSP-UM 3492; paratypes GSP-UM 3493-3498.

Type locality.— Locality W-2, north of Domanda Post in North-West Frontier Province (see Appendix).

Diagnosis.— Merus of major cheliped elongate, lower margin serrate; carpus of major cheliped longer than high, rounded; manus of major cheliped elongate, outer surface with row of setal pits along upper margin, distal margin with serrate projection with rounded mass of tubercles at lower edge; fixed finger slender, edentulous; movable finger stout, with sharp teeth on occlusal surface.

Etymology.— Species name honors Neil A. Wells, Kent State University, who collected the material and made it available for study.

Description.— Merus of major cheliped longer than high, highest proximally; inner surface with scattered granules, flattened; upper margin weakly convex; lower margin serrate, with small, sharp spines.

Carpus of major cheliped slightly longer than high, highest about one-fifth the distance proximally from distal margin, elliptical in shape. Proximal margin with small projection at upper corner for articulation with merus; projection followed by smooth, concave reentrant; remainder of margin convex, with small granules, continuous with lower margin. Lower margin granular, convex, sloping downward distally; upper margin slightly convex; distal margin nearly straight, at about 95° to upper margin. Outer surface inflated centrally, flattening toward upper and lower margins.

Manus of major cheliped longer than high, highest just distal to proximal margin, narrowing distally, elliptical in cross-section; inner and outer surfaces inflated centrally and flattened toward upper and lower margins; outer surface with row of setal pits parallel to and along upper margin. Proximal margin weakly concave centrally, upper and lower corners rounded; upper margin nearly straight; lower margin convex proximally and weakly concave near base of fixed finger. Distal margin initially straight, at about 85° angle to upper margin, straight segment followed by oblong, serrate projection with rounded mass of tubercles at lower edge; serrate projection followed by small indentation just above base of fixed finger.

Fixed finger round in cross-section, slender, appearing to be edentulous, with blunt keel on inner surface. Movable finger stout; with forward-directed spines on upper surface; large, sharp spine at base of occlusal surface; remainder unknown.

Discussion.— The new material fits the diagnosis of *Neocallichirus* in almost every regard. *Neocallichirus wellsi* possesses a serrate merus; a rounded carpus; a rectangular manus with a serrate projection on the distal margin; a distal margin with a shallow notch above the fixed finger; an edentulous, slender fixed finger; and a stout, toothed, movable finger. These features taken together are diagnostic for *Neocallichirus* (Manning and Felder, 1991; Schweitzer and Feldmann,

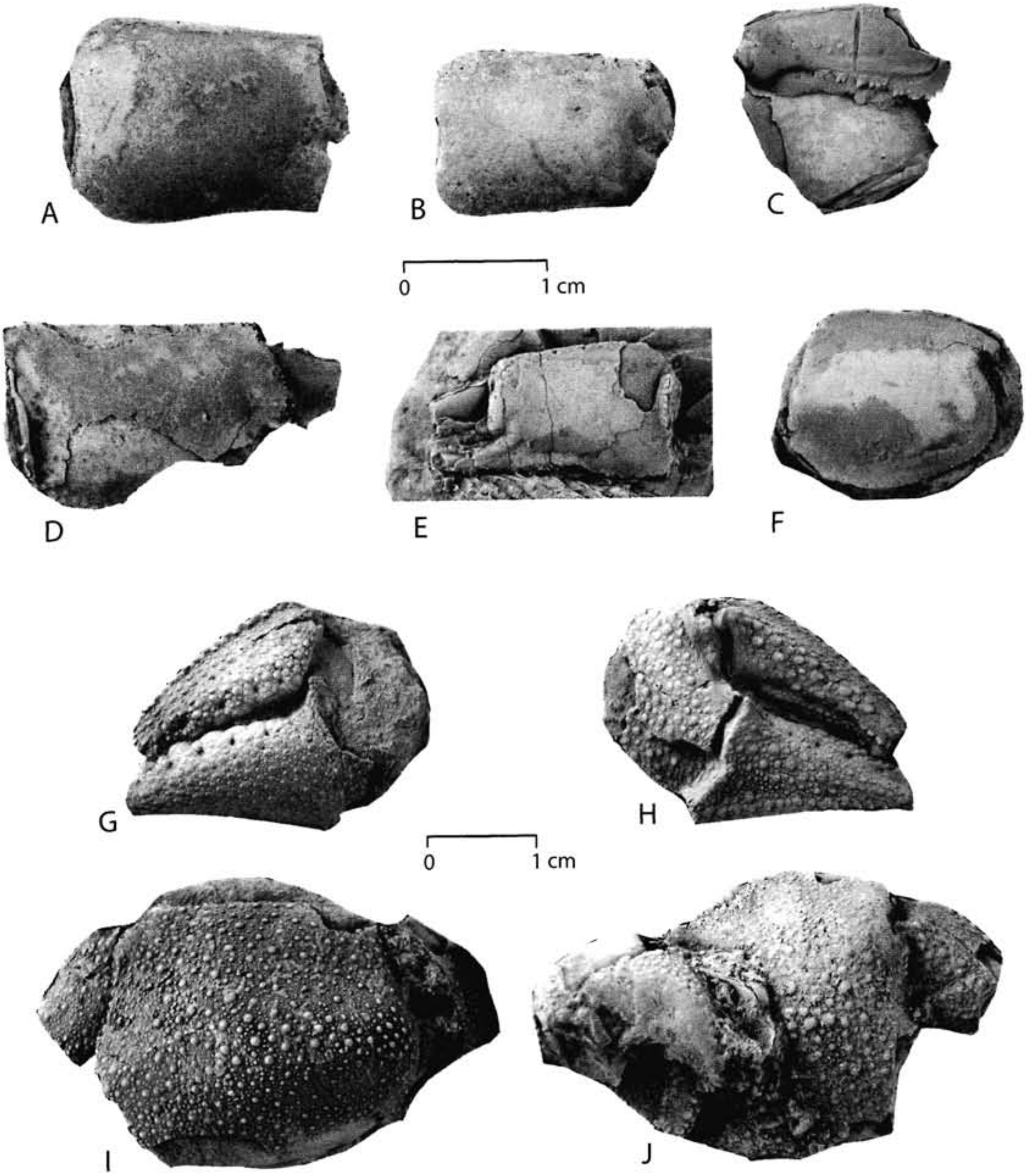

FIG. 4 — *Neocallichirus wellsi* new species (A-F); Diogenidae genus and species indeterminate (G-J). A, outer surface of manus of major cheliped, holotype GSP-UM 3492. B, outer surface of manus of major cheliped, paratype GSP-UM 3493. C, outer surface of merus of major cheliped, paratype GSP-UM 3496. D, outer surface of manus and portion of movable finger of major cheliped, paratype GSP-UM 3495. E, inner surface of manus and fingers of major cheliped, paratype GSP-UM 3494. F, outer surface of carpus of major cheliped, paratype GSP-UM 3497. G, outer surface of major chela, GSP-UM 3510. H, inner surface of major chela, GSP-UM 3510. I, outer surface of manus, portion of movable finger, and carpus of major cheliped, GSP-UM 3517. J, inner surface of manus, movable finger, and carpus of major cheliped, GSP-UM 3517.

2002). The only regard in which *N. wellsi* does not resemble other members of the genus is that *N. wellsi* is characterized by an elongate merus. Other species, including *N. rhinos* Schweitzer and Feldmann, 2002, and *Neocallichirus grandimana* (Gibbes, 1850), for example, have shorter, more stout meri. However, no other callianassoid taxon has a serrate merus and a serrate distal margin of the manus. Thus, we herein place the new material in *Neocallichirus*.

Neocallichirus wellsi differs from all other species in the genus in having an elongate merus. The mani of *Neocallichirus wellsi* and *Neocallichirus rhinos* appear to be nearly identical; both have the same overall shape and a rounded tuberculate area at the base of the serrate projection on the distal margin. Without the other articles of the cheliped, it would be difficult to distinguish them from one another; the differences between the movable finger and merus of each species are quite sufficient, however, to permit distinction between the two species. In addition to the stouter merus of *N. rhinos*, the movable finger is very stout in *N. rhinos* and clearly distinguishable from the movable finger in *N. wellsi*.

The earliest known occurrences of *Neocallichirus* are the occurrence herein; *N. rhinos* from the Eocene of southern California (Schweitzer and Feldmann, 2002); and *N. fortisi* Beschin et al., 2002, from the Eocene of Italy (Beschin et al., 2002). Other occurrences are in the Oligocene of Japan (Karasawa and Fudouji, 2000); middle Miocene of Japan (Karasawa, 1993, 1997); and Pleistocene of Japan and the Caribbean (Karasawa and Goda, 1996; Collins et al., 1996). The genus appears to have exhibited a Tethyan distribution in its early history, with localities in Pakistan, Italy, and southern California. Although the Indian subcontinent was not in its present position, it was certainly well into the Tethyan region (Scotese, 1997), and the present occurrences of the genus in subtropical and warm temperate areas world wide are likely a relic of a Tethyan dispersal route.

Infraorder ANOMURA MacLeay, 1838
Section PAGURIDEA Latreille, 1802
Superfamily COENOBITOIDEA Dana, 1851

Discussion.— Forest et al. (2000) subdivided the Paguridea into two superfamilies, the Coenobitoidea and the Paguroidea. Members of the Coenobitoidea have chelipeds in which the left is generally larger, and if the chelae are equal or subequal, the claws are similar in structure (Forest et al., 2000). In the Paguroidea, members generally have larger right chelae, and if the chelae are equal or subequal, they are not similar structurally (Forest et al., 2000). The specimens reported here from Pakistan are each left chelae, suggesting that it is the major one; thus, we have placed them within the Coenobitoidea.

Family DIOGENIDAE Ortmann, 1892

Discussion.— The specimens are placed within the Diogenidae for several reasons. The other two families within the Coenobitoidea cannot embrace the new fossils. Members of the Pylochelidae Bate, 1888, inhabit wood, scaphopods, or rocks, and have equal appendages (Forest et al., 2000). In addition, the family is not robust, composed of only seven extant genera. Members of the Coenobitidae are semi-terrestrial, and there are only two extant genera. The shape of the chelae of members of the Coenobitidae is large and rounded, with convex margins (Glaessner, 1969; Schweitzer and Feldmann, 2001b), much like the chelae described here. However, it is highly unlikely that a semi-terrestrial species would be preserved in the fossil record, because of the lack of proximity of the animals to the water and because of the high energy conditions in near-shore areas, which would easily destroy cuticle material. By contrast, the Diogenidae inhabit tropical to temperate waters (Forest et al., 2000) and are widespread and diverse. Thus, we believe it most likely that the new specimens belong to the Diogenidae. The Diogenidae have a well-documented fossil record, known from Eocene rocks of the Pacific west coast of North America as well as other locations worldwide (Glaessner, 1969; Vega et al., 2001; Schweitzer and Feldmann, 2001b; Schweitzer et al., 2002).

Genus indeterminate

Discussion.— Making generic level determinations within the Paguroidea and Coenobitoidea is difficult when working with fossils. Fossil hermit crabs are almost exclusively known only from chelae. As in most other decapods, biological classifications are based primarily on soft-part anatomy, which in the hermit crabs includes the dorsal carapace, which has never been found fossilized. Features of the chela morphology are rarely used for generic diagnoses, and in fact, chelae of species within the same genus often are remarkably different from one another morphologically (R. Lemaitre, personal commun.; illustrations in Williams, 1984; Forest et al., 2000). Thus, placement of fossils into genera must be done with extreme caution. Because the material described here consists only of two broken chelae, a carpus, and a merus, we have opted to identify the fossils only to the family level.

Genus and species indeterminate

Fig. 4G-J

Material examined.— GSP-UM 3510, 3517.

Occurrence.— Localities DL01 and Ro1 (see Appendix).

Description.— Carpus of left cheliped about as long as high, becoming higher distally, triangular in shape, inner and outer surfaces extremely convex, each with broad, blunt keels extending longitudinally at about mid-height; proximal margin rounded; distal margin long, weakly concave; upper and lower margins nearly straight, converging proximally; all surfaces covered with large granules with dense smaller granulation in between them.

Manus of left cheliped circular, not much longer than high, highest at about midlength; proximal margin nearly straight, with pronounced collar for articulation with carpus; lower margin convex; upper margin convex; distal margin oblique to upper margin, granular. Outer surface very convex, maximum convexity just below mid-height, bluntly keeled at maximum convexity; inner margin weakly convex, with broad swelling at articulation with movable finger, swelling with reentrant centrally to articulate with projection on movable finger.

Fixed finger triangular, directed upward, arcuate, narrowing distally; lower margin concave, with blunt, forward directed spines; outer surface convex, occlusal surface with large, blunt teeth; inner surface weakly convex, with granules and row of setal pits; lower margin with very blunt, forward-directed spines; all surfaces ornamented with pavement of coarse and fine granules.

Movable finger granular on all surfaces; proximal margin oblique, granular at articulation with manus; outer surface composed of flattened, oblique element and vertical element merging with occlusal surface; occlusal surface with large blunt teeth; upper margin with crest bearing double row of forward-directed small spines; inner surface with longitudinal keel centrally, extending about half the length of the finger, large node extending from the keel distally to articulate with proximal margin of manus; inner surface with forward-directed nodes surrounded by pavement of granules.

Measurements.— Measurements (in mm) taken on specimens described here: GSP-UM 3517, maximum length of carpus, 14.8; maximum height of carpus, 25.3; maximum length of manus, 28.3; maximum height of manus, 26.3; GSP-UM 3510, length of movable finger, 20.0 (minimum); length of fixed finger, 22.0 (minimum).

Discussion.— Only two specimens are known. The ornamentation and other features of the cuticle are well-preserved, but unfortunately, both specimens are broken. More material will be needed to attempt generic level placement and to confirm placement at the family and superfamily level. A sample size of only two specimens, in a group in which handedness is extremely important at the family and superfamily level, cannot form the basis for confident identification.

Infraorder BRACHYURA Latreille, 1802
Section HETEROTREMATA Guinot, 1977
Superfamily CANCROIDEA Latreille, 1802
Family CANCRIDAE Latreille, 1802
Subfamily LOBOCARCINIDAE Beurlen, 1930

Genus *Lobocarcinus* Reuss, 1857

Type species.— *Lobocarcinus paulinowurtenburgensis* von Meyer, 1847.

Lobocarcinus indicus Glaessner, 1933
Fig. 5

Lobocarcinus indicus Glaessner, 1933, p. 14; pl. 3: 6, 7; pl. 4: 1. Anderson and Feldmann, 1995, p. 922. Schweitzer and Feldmann, 2000b, p. 249.

Material examined.— GSP-UM 3505 and 3508.

Occurrence.— The type material was collected from the "white marly nummulitic limestone (Kirthar)" said to be Lutetian in age, at an unspecified locality in the Dera Bugti District, Balochistan (Glaessner, 1933: 14). This is almost certainly the Pir Koh Formation of early Bartonian age. New specimens described here were collected from locality Da-3 in the middle part of the Drazinda Formation (Bartonian; see Fig. 2 and Appendix). Crab burrows of ca. 10 cm diameter at locality Da2 may belong to *Lobocarcinus indicus* (Fig. 3).

Diagnosis.— Carapace much wider than long; fronto-orbital width appearing to be no more than 40 percent maximum carapace width; anterolateral margin with long spines, appearing to have been paired (Glaessner, 1933, pl. 4); posterolateral margin with at least six spines; posterior margin with five spines; branchial region with large tubercles posteriorly (after Glaessner, 1933).

Emendation to description.— Fronto-orbital width 40 percent or less maximum carapace width. Posterolateral margins with six spines; spines round in cross-section, robust; small tubercles on margin between spines. Posterior margin with five spines; largest at posterolateral corners; one positioned axially; others situated between axial spine and corner spines.

Carapace regions not well defined, generally smooth; branchial regions with large tubercles posteriorly; lateral margins of protogastric, posterior-most mesogastric, cardiac, and intestinal regions delimited by deep, narrow groove; axial regions not well-differentiated, narrow.

Male sternum narrow; fourth sternite long, with long episternal projections; fifth and sixth sternites very short, fifth sternite with long episternal projections. Male abdomen elongate, somites 3-5 appearing to be fused, sutures visible; sixth somite longer than any exposed somites, about as long as telson; telson triangular, blunt, elongate.

Buccal cavity long, about one-third length of carapace.

Measurements.— Measurements (in mm) taken on the dorsal carapace of GSP-UM 3508: width, 70.0 (minimum); length, 47.0 (minimum); posterior width, 23.7; buccal cavity length, 15.0.

Discussion.— The new specimens are clearly referable to *Lobocarcinus indicus*, which Glaessner (1933) described from Balochistan. Specimens described here were collected in Punjab, about 160 km along strike to the NE of the type locality. The material upon which the species is based is damaged, as is the material described here, but some observations and emendations may be added. Glaessner (1933) described the species as having four spines on the posterolateral margin; the new material clearly exhibits six. The material upon which Glaessner (1933, pl. 3: 6) based that observation is damaged; thus the new observation is more accurate although the new specimen is also broken. There may be even more posterolateral spines. The posterior margin has five spines,

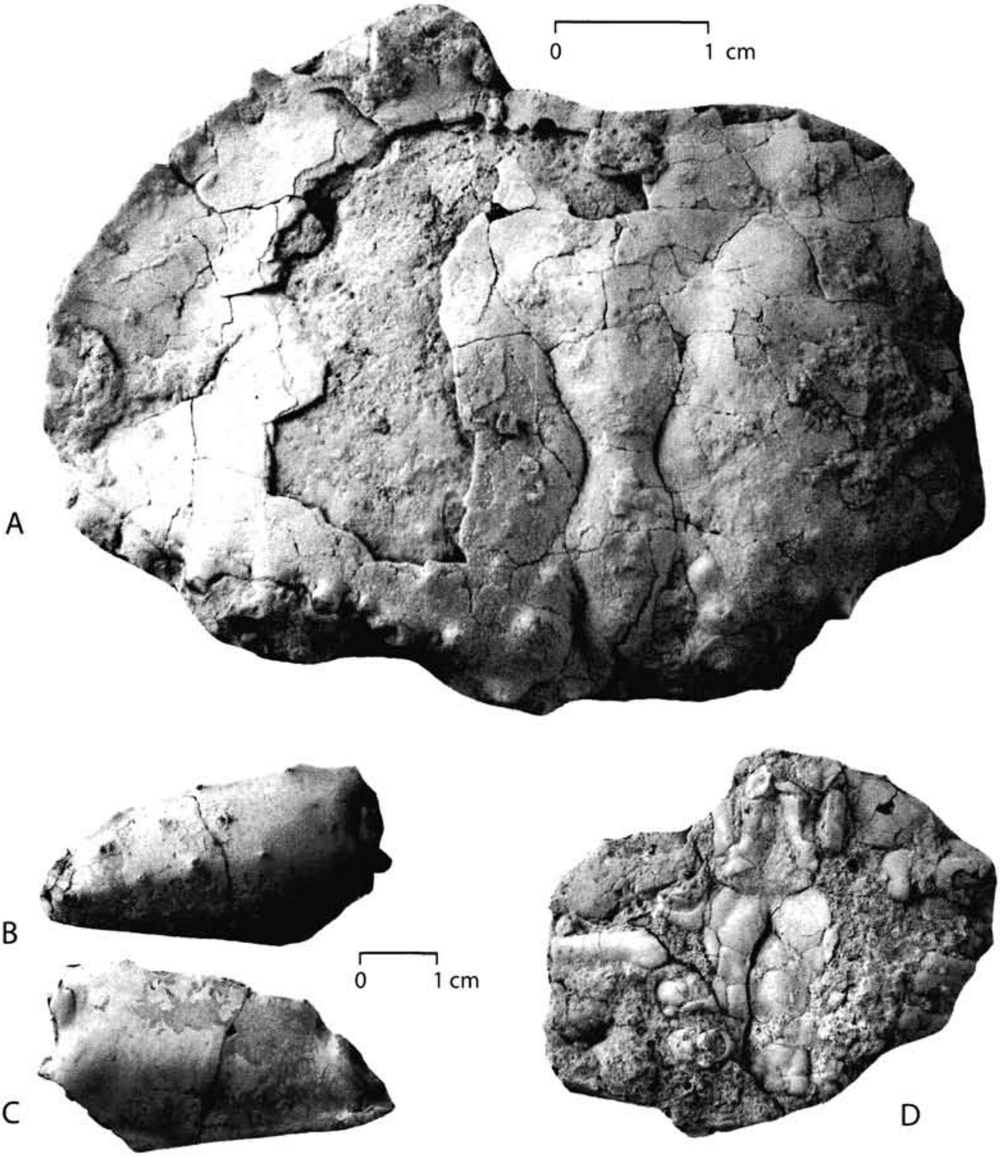

FIG. 5 — *Lobocarcinus indicus* Glaessner, 1933, GSP-UM 3508. A, dorsal carapace; B, outer surface of manus of major chela; C, inner surface of manus of major chela; D, ventral surface of male.

illustrated by Glaessner, (1933, pl. 4) but not discussed. The carapace surface was described by Glaessner (1933) as being smooth; however, the branchial regions have large tubercles posteriorly, and these are clearly visible in his illustrations (pls. 3, 4). The description for the species is therefore so emended.

Glaessner (1933) compared *Lobocarcinus indicus* directly with *Lobocarcinus paulinowurtembergensis* citing numerous differences. Summarized, *Lobocarcinus paulinowurtembergensis* has a less ornamented dorsal carapace than does *L. indicus*; only five spines on the posterolateral margin, while *L. indicus* has at least six; and spines on the cardiac region, which *L. indicus* lacks. *Lobocarcinus lumacopius* Anderson and Feldmann, 1995, has large tubercles on the dorsal carapace and spines on the cardiac region, which *L. indicus* lacks. *Lobocarcinus lumacopius* has smaller anterolateral spines than does *L. indicus*. *Lobocarcinus indicus* is most similar to *L. aegypticus* Lõrenthey, 1909, but *L. aegypticus* has smooth chelae, as opposed to the spinose chelae of *L. indicus*, and anterolateral spines of a different shape than *L. indicus*. *Lobocarcinus pustulosus* Feldmann and Fordyce, 1996, has rounded anterolateral spines and granular ornamentation on the branchial regions not characteristic of *L. indicus*. A diagnosis and a paleobiogeographic discussion for *Lobocarcinus* was given by Schweitzer and Feldmann (2000b); this occurrence supports the hypothesis of a Tethyan distribution for the subfamily and genus.

Superfamily PORTUNOIDEA Rafinesque, 1815
Family PORTUNIDAE Rafinesque, 1815
Subfamily PORTUNINAE Rafinesque, 1815

Genus *Portunus* Weber, 1795 (= *Neptunus* de Haan, 1833) sensu lato

Type species.— *Cancer pelagicus* Linneaus, 1758.

Portunus sp.

Material examined.— GSP-UM 3206, 3209, 3499, 3506, 3518, 3520, 3548.

Occurrence.— Localities DL02-DL04, Da3, Ro2, Ro3, W-2 (see Appendix). One additional specimen was collected from Bari Nadi, Punjab Province, near the top part of the lower Drazinda Formation.

Description of material.— Manus longer than high, highest distally, ovate in cross-section; proximal surface rounded; outer surface convex, with two long, distinct keels; inner surface flattened, with one long keel; distal margin at about 85° angle to upper margin, with large tubercles at articulation with movable finger.

Discussion.— The material consists of only five mani, one with remnants of the two fingers. The chelae are clearly portunid, bearing the typical keels on the outer and upper surface; elongate shape; and large nodes at the articulation of the movable finger and the manus. Glaessner (1933) described *Neptunus (Achelous) withersi* from the Miocene of Sulabadar, Persia (now presumably Iran); *Neptunus* has been synonymized with *Portunus* (Glaessner, 1969). Tiwari and Satsangi (1988) subsequently described *Portunus* sp. from lower Miocene rocks of eastern India. The chelae of *Portunus withersi* are similar to those illustrated here, but the new material is clearly a different species. The new material possesses two keels on the outer surface, while *P. withersi* has only one. The new material is much older than that referred to *P. withersi* and to *Portunus* sp. by Tiwari and Satsangi (1988) as well; thus we refer the new material to *Portunus* sp. Interestingly, neither Sastry and Mathur (1970) nor Collins and Morris (1978) described portunids from Paleocene or Eocene rocks of India and neighboring areas. Glaessner and Secretan (1987) similarly described no portunids from Eocene rocks of Pakistan; Eocene portunid material is apparently rare in these deposits. More material, including the dorsal carapace, will be necessary before referring the material to a new or previously known species.

Superfamily XANTHOIDEA MacLeay, 1838
Family CARPILIIDAE Ortmann, 1893

Genus *Proxicarpilius* Collins and Morris, 1978

Type species.— *Proxicarpilius planifrons* Collins and Morris, 1978.

Diagnosis.— Carapace ovate, wider than long; front downturned, bluntly triangular in shape; anterolateral margin with four spines or protuberances including outer orbital spine; posterolateral margin at about 32° angle to posterior margin; see Schweitzer (2003).

Discussion.--The genus is clearly assignable to the Carpiliidae based upon characters of the dorsal carapace and the articulation of the merus of the major cheliped directly with the coxa (Schweitzer, 2003).

Proxicarpilius planifrons Collins and Morris, 1978
Fig. 6

Proxicarpilius planifrons Collins and Morris, 1978, p. 972, pl. 117: 5, 7; pl. 118: 1-4, 7.

Proxicarpilius minor Collins and Morris, 1978, p. 976, pl. 117: 6, 8, 9; pl. 118: 5, 6, 11. Glaessner and Secretan, 1987, p. 5, pl. 1: 1.

Material examined.— GSP-UM 3153, 3501, 3503, 3509, 3511-3516, 3519, 3521-47, 3549, 3550.

Occurrence.— The type material was collected from middle Eocene rocks from the Kirthar Formation and the Domanda Shale, Ramak Kwar, near Dera Ismail Khan, North West Frontier Province, Pakistan (Collins and Morris, 1978). The specimens examined in this report were collected from localities G-RN2, DL02-DL19, Da1, Ro4, Ro5 (see Appendix), as well as one specimen from an unknown locality.

Diagnosis.— as for genus (Schweitzer, 2003).

Emendation to description.— Carapace moderately vaulted transversely, strongly vaulted longitudinally. Front projected well-beyond orbits; outer-orbital spine narrowly triangular, directed forward. Anterolateral margin with three spines excluding outer-orbital spine; first spine blunt, low, broad; second spine triangular, sharp, directed anterolaterally; third spine long, attenuated, directed laterally.

Protogastric region not differentiated from anterior-most mesogastric region, inflated; hepatic region weakly depressed. Posterior-most mesogastric region and anterior-most branchial region inflated, forming sinuous ridge across axial portion of carapace; ovate inflations on hepatic region placed lateral to and slightly anterior to ridge. Posterior-most mesogastric, urogastric, and cardiac regions inflated, forming narrow axial ridge, not differentiated from one another, bounded by branchiocardiac groove; cardiac region very narrow, triangular.

Merus of major cheliped articulating directly with coxa.

Measurements.— Measurements (in mm) on specimens of *Proxicarpilius planifrons* are presented in Table 2.

Discussion.— Collins and Morris (1978) erected a new genus and two new species to accommodate Eocene carpiliid material collected from Pakistan. *Proxicarpilius planifrons* was described in detail, and *P. minor* was described as being like *P. planifrons* except that it was smaller, had slightly different dorsal carapace length/width ratios, and lacked the mesogastric-branchial ridge across the axis (Collins and Morris, 1978, p. 976).

Examination of twenty-nine new specimens of *Proxicarpilius* collected from Pakistan suggests that the two species are synonymous. The two species originally described by Collins and Morris (1978) were recovered from the same rocks as one another. In addition, the differences in the dorsal carapace morphology were clearly correlated to specimen size, suggesting that ontogenetic changes could explain the differences. Changes in carapace length and width ratios, as well as changes in dorsal carapace ornamentation and definition of regions, are well-known within the brachyuran decapods and have been attributed to allometric growth (Wright and Collins, 1972; Guinot, 1989; Schweitzer and Feldmann, 2000a). Schweitzer and Feldmann (2000a) showed that

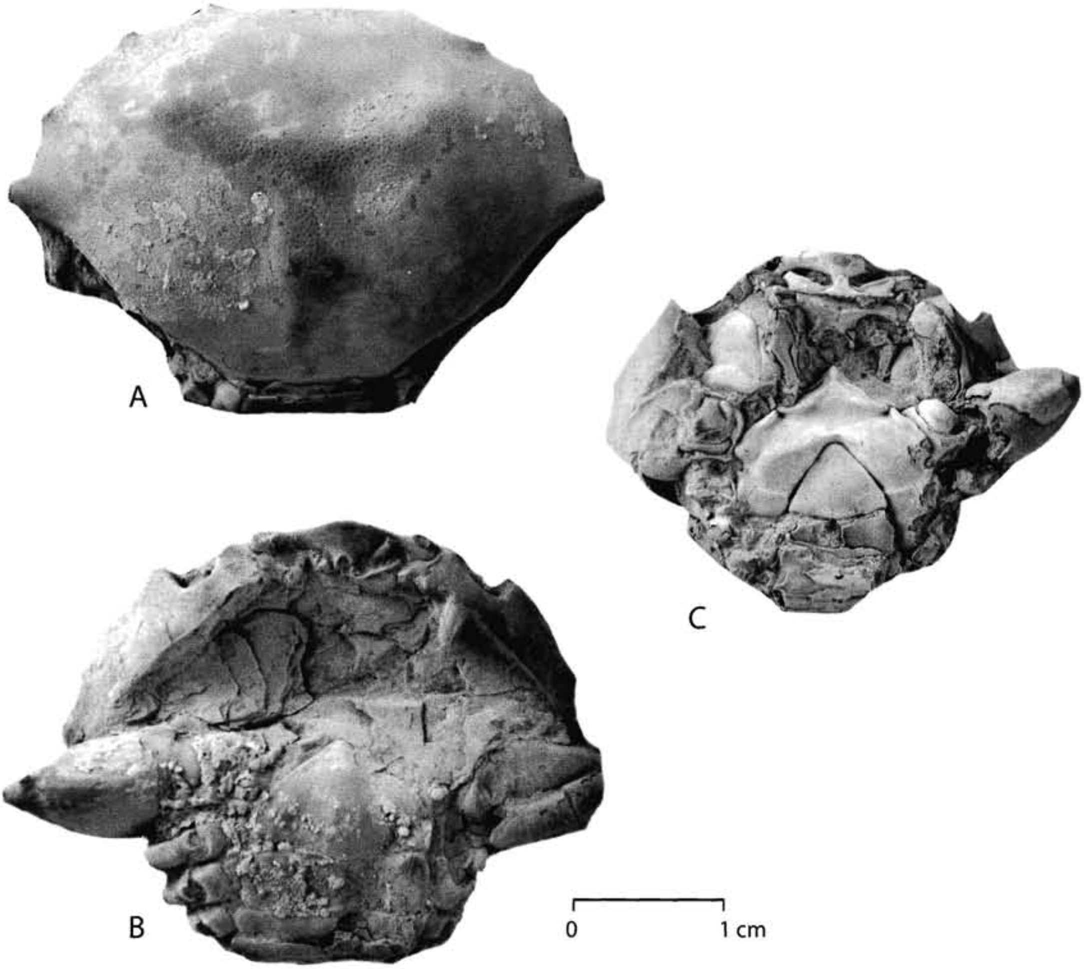

FIG. 6 — *Proxicarpilius planifrons* Collins and Morris, 1978. A, dorsal carapace, GSP-UM 3512. B, female ventral surface, GSP-UM 3512. C, immature female ventral surface, GSP-UM 3550.

the carapace regions and ratios changed with growth in *Chaceon peruvianus* (d'Orbigny, 1842). In juveniles of that species, regions were better defined than in adults. Guinot (1989) showed that the number of anterolateral spines and the length of the anterolateral margin can change with growth in species of *Carcinoplax* A. Milne Edwards, 1852. The differences in the length/width ratio and the ratio of the fronto-orbital width to the total width in *P. planifrons* and *P. minor* are easily explained as a product of allometric growth, and the poor development or absence of the mesogastric ridge in *P. minor* may also be explained as a product of change through ontogeny. Thus, the two species are synonymous and only one species of *Proxicarpilius* is known.

Family GONEPLACIDAE MacLeay, 1838
Subfamily CHASMOCARCININAE Serène, 1964

Discussion.— Schweitzer and Feldmann (2001a) placed two exclusively fossil genera, *Falconoplax* Van Straelen, 1933, and *Orthakrolophos* Schweitzer and Feldmann (2001a), into the

TABLE 2 — Measurements (in mm) on the dorsal carapace of specimens of *Proxicarpilius planifrons* Collins and Morris, 1978. L, maximum carapace length; L2, length to position of maximum width; W1, maximum carapace width; W2, fronto-orbital width; W3, frontal width; W4, posterior width; angle, angle of posterolateral margin to posterior margin. Asterisk indicates minimum measurement. Gender is listed when known.

Specimen number	L1	L2	W1	W2	W3	W4	Angle	Gender
3509	26.7	20.4	35.8	25.7	14.3	11.9	35°	—
3512	26.1	17.9	35.2	23.0	13.7	11.1	—	female
3513	27.9	19.0	36.7	24.5	12.7	—	—	—
3514	21.3	15.8	30.6	19.6	11.1	10.6	—	male
3515	19.3	13.0	27.4	20.0	—	9.7	—	—
3516	28.8	20.1	38.3	29.4	14.2	—	—	male
3519	24.6	19.1	31.0	24.2	13.0	12.3	35°	female
3523-A	24.4	16.9	34.0	23.6	12.0	13.1	—	—
3523-B	26.0*	—	37.1	24.7	14.2	12.7	—	—
3524	—	—	34.6	—	—	—	—	female
3525	17.4	13.9	24.4	18.0	9.0	9.5	35°	—
3528	—	—	—	—	—	—	—	female
3529	18.5	—	26.4	—	—	—	35°	male
3531	21.4	16.0	28.7	20.2	11.6	10.4	—	female
3532	23.1	16.6	33.2	22.0	11.9	11.0	—	female
3533	—	—	30.3	22.1	12.5	—	—	—
3534	—	—	23.0	15.5	—	—	—	male
3535	19.0	12.6	26.1	17.2	9.9	9.0	—	male
3536	20.1	13.3	31.0	19.6	11.1	—	—	female
3543	22.6	—	15.9	29.3	20.9	11.1	—	female
3544	25.9	17.8	34.7	24.4	13.6	11.0	—	male
3545	—	—	38.9	25.1	—	—	—	male
3546	—	—	28.2	18.6	—	—	—	—

Chasmocarcininae, in addition to the extant genera recognized by Serène (1964). Of the extant genera, only *Chasmocarcinus* Rathbun, 1898, has a fossil record. Karasawa and Kato (2003a) subsequently provided a diagnosis and a list of included genera for the Chasmocarcininae as well as a cladistic analysis of the Goneplacidae. They added the extinct genera *Gillcarcinus* Collins and Morris, 1978, and *Mioplax* Bittner, 1884, to the Chasmocarcininae. We concur with their definition of the Chasmocarcininae.

The fossil occurrences of the Chasmocarcininae suggest a Tethyan distribution in the early history of the family. Eocene occurrences are known from Antarctica (*Chasmocarcinus*); the Caribbean (*Falconoplax*); and Pakistan (*Gillcarcinus*) (respectively, Feldmann and Zinsmeister, 1984; Van Straelen, 1933; Collins and Morris, 1978); a Tethyan mode of transport clearly accommodates the Caribbean and Pakistan occurrences. The Antarctic occurrence suggests the possibility of an extra-tropical origin of the genus. Miocene occurrences include Japan (*Collinsius*), the Caribbean (*Falconoplax*), east-coastal USA (*Chasmocarcinus*); and Central Europe (*Mioplax*) (respectively, Karasawa, 1993; Collins and Morris, 1976; Blow and Bailey (1992); Glaessner, 1969); the Miocene occurrences also indicate a Tethyan distribution.

Genus *Gillcarcinus* Collins and Morris, 1978

Gillcarcinus amphora Collins and Morris, 1978

Fig. 7

Gillcarcinus amphora Collins and Morris, 1978, p. 967, pl. 117, figs. 2-4.

Material examined.— GSP-UM 3500.

Occurrence.— The type material was collected from the middle Eocene Kirthar Formation, Domanda Shale in Ramak Kwar, about 85 km southwest of Dera Ismail Khan, North West Frontier Province, Pakistan (Collins and Morris, 1978, p. 968). The new specimen was collected from locality W-1 (see Appendix).

Diagnosis.— Length about two-thirds carapace width; orbits square, directed forward; fronto-orbital width about 42 percent maximum carapace width; posterior width about equal to fronto-orbital width; carapace with distinctive granular, arcuate ridge extending from the left branchial region forward on the carapace, then arcing across the hepatic, protogastric, and mesogastric regions, then arcing posteriorly to terminate on right branchial region; cardiac region with transverse ridge anteriorly; male abdominal somites 3-5 fused.

Measurements.— Measurements (in mm) taken on the dorsal carapace of *Gillcarcinus amphora*: width, 13.1; 11.5 (minimum).

Discussion.— The distinctive arcuate ridge extending from branchial region to branchial region by way of the anterior part of the carapace clearly demonstrates that the specimen is a member of the genus and species. To date, Eocene occurrences in Pakistan are the only known localities at which specimens of *Gillcarcinus amphora*, the sole species of the genus, have been collected.

Family PILUMNIDAE Samouelle, 1819

Discussion.— To date, *Lobonotus* sensu lato has been placed within the Xanthidae sensu lato. Because several specimens in species of the genus have well-preserved sterna and abdomina, it is possible to attempt further refinement of the family-level placement of the genus. In the course of this work, the genus has been restricted by removing those species with morphologies markedly divergent from that of the type species. *Lobonotus* sensu stricto resembles genera within the Pilumnidae, specifically the Pilumninae Samouelle, 1819, and the Galeninae Alcock, 1898, as defined by Davie (2002), in having a strongly longitudinally vaulted rectangular carapace, well-defined regions; a bilobed front; and a male abdomen that does not reach the level of the anterior edge of the coxa of the first pereiopod; as well as having the same general arrangement of carapace regions as members of the Pilumninae and Galeninae. In addition, members of the family have male abdomina with all seven somites free and movable, and the abdomen does not entirely cover sternite 8 (Davie, 2002). Both features are seen in *L. mexicanus* Rathbun, 1930b (pl. 1, fig. 3). *Lobonotus mexicanus* closely resembles the type species in terms of the dorsal carapace morphology; thus, we are confident in using the characters of the sternum of *Lobonotus mexicanus* as generic level characters for *Lobonotus*.

Other xanthoid families cannot accommodate *Lobonotus*. The orbits of members of the Eriphiidae MacLeay, 1838 are much more broadly spaced than those of *Lobonotus*, and the general arrangement of carapace regions and shape in eriphiids differs from that of *Lobonotus*. Members of the Goneplacidae MacLeay, 1838, while possessing a rectangular carapace similar to that of *Lobonotus*, lack heavy ornamentation and have much more poorly defined regions than does *Lobonotus*. The Zanthopsidae Via, 1959, have much more poorly defined regions, longer anterolateral margins, and markedly quadrilobed fronts, not typical of *Lobonotus*. The Palaeoxanthopsidae Schweitzer, 2003, have very large nodes on the carapace and posteriorly directed lateral spines, not seen in *Lobonotus*. Other families, including the Carpiliidae Ortmann, 1893; Trapeziidae Miers, 1886; Pseudoziidae Alcock, 1898; and the Pseudorhombiliidae Alcock, 1900, have an altogether differ-

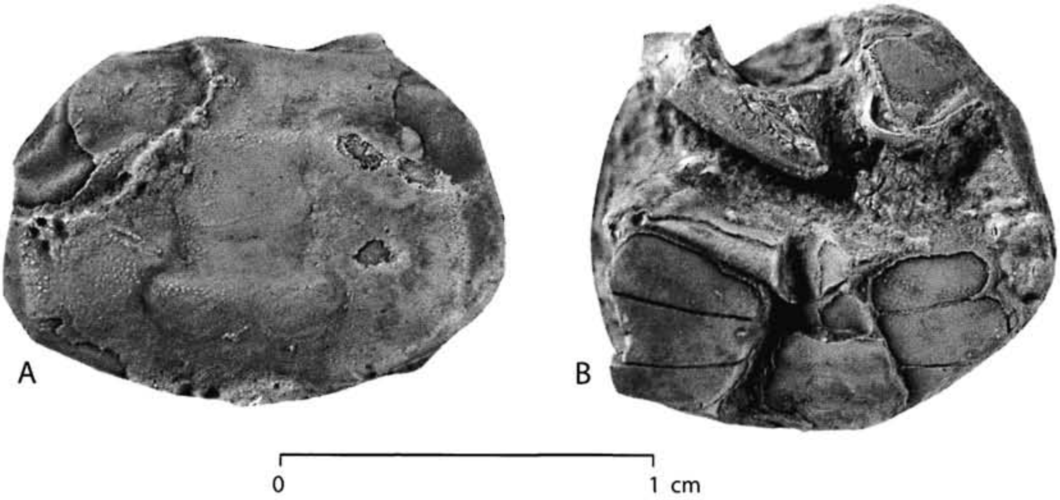

FIG. 7 — *Gillcarcinus amphora* Collins and Morris, 1978, GSP-UM 3500. A, dorsal carapace; B, male ventral surface.

ent shape of the dorsal carapace and much smoother carapaces than *Lobonotus*. Thus, the genus is best placed within the Pilumnidae.

Genus *Lobonotus* A. Milne Edwards, 1864

Archaeopilumnus Rathbun, 1919, p.177, pl. 7, fig. 10-13.

Type species.— *Lobonotus sculptus* A. Milne Edwards, 1864.

Other species.— *Lobonotus bakeri* (Rathbun, 1935); *L. brazoensis* Stenzel, 1935 (known only from claws); *L. mexicanus* Rathbun, 1930b; *L. natchitochensis* Stenzel, 1935; *L. sandersi* Blow and Manning, 1997.

Diagnosis.— Carapace not much wider than long, length about 84 percent maximum width, widest about one-third the distance posteriorly on carapace; grooves deep; regions clearly defined, ornamented with coarse granules; front nearly straight with central notch, about one-third maximum carapace width; orbits with two fissures and sometimes one intraorbital spine bounded by fissures, fronto-orbital width about two-thirds maximum carapace width; anterolateral margin with four or five spines excluding outer-orbital spine, last spine reduced or absent; cardiac region distinctively three-lobed, distal two lobes arcuate, inflated extensions from anterior-most cardiac region; intestinal region wide, short, linear when developed; mani of chelae with rows of granules on outer surface; male abdominal somites free, not covering entire space between bases of fifth pereiopods, not extending to level of anterior edge of bases of first pereiopods (modified after Schweitzer et al., 2002).

Discussion.— During the course of this work, all species referred to *Lobonotus* were reevaluated; only those that fit the diagnosis above were retained in the genus. The fragmentary nature of the material upon which *L. foerstei* Rathbun, 1935, is based will make it necessary to examine type material to determine its generic placement. Outliers have been removed to other genera or families. Schweitzer et al. (2002) had already suggested that *Lobonotus lobulata* Feldmann et al., 1995, was not a member of the genus; we have erected a new genus, *Lobulata*, to accommodate that species (see below). *Lobonotus australis* Fritsch, 1878, is based on fragmentary material (Fritsch, 1878, pl.18: 7a) that is very difficult to interpret from the drawing; type material will need to be examined in order to determine its most appropriate generic placement. It does not appear to possess the arcuate lateral extensions on the cardiac region that are typical of species of *Lobonotus*.

TABLE 3 — Dimensions and other aspects of the carapace and ventral surface in selected species of *Lobonotus* as well as *Pakicarcinus orientalis*, formerly referred to *Lobonotus*. Important carapace features are listed in the left column; taxa and their features are listed in the remainder of the columns. Taxa in **bold** have been removed from the genus.

Carapace feature	*Lobonotus sculptus* (type)	*Lobonotus bakeri*	*Lobonotus mexicanus*	***Lobonotus vulgatus***	*Lobonotus saundersi*	***Pakicarcinus orientalis***
L/W	0.81	0.85	0.88	**0.95**	0.86	**0.97**
FOW/W	0.58	0.70	0.57	**0.71**	0.70	**0.60**
F/W	0.34	0.27	0.30	**0.40**	0.37	**0.35**
Front	Straight, central notch	Straight, central notch	Straight, central notch	**Two long spines, axial notch**	Straight, central notch	**Straight, central notch**
Cardiac region	Lateral extensions	Lateral extensions	Lateral extensions	**Much reduced lateral extensions**	Lateral extensions	**Lateral extensions**
Front projects (beyond orbits)	No	No	No	**Yes**	No	**No**
Sternites	Unknown	Unknown	3-4 with no suture	**Unknown**	Unknown	**3-4 with clear suture**
Male somites	Unknown	Unknown	All free	**Unknown**	Unknown	**3-5 fused**

In addition to these two species, it is clear that *Lobonotus vulgatus* Quayle and Collins, 1981, is not a member of the genus. Numerous differences between the type species, *L. sculptus*, and *L. vulgatus*, are presented in Table 3. In addition to all of the features listed therein, especially important being the nature of the front, the carapace of *L. vulgatus* is bulbous and inflated, and each region is convex; in authentic *Lobonotus*, the carapace and regions are flattened. Thus, we remove *L. vulgatus* from *Lobonotus*. *Lobonotus vulgatus* appears to strongly resemble members of *Pulalius* in the shape of the carapace regions; inflation of the carapace; and the spinose nature of the front; however, examination of type material will be necessary to confirm generic placement of *Lobonotus vulgatus*.

Lobonotus orientalis Collins and Morris, 1978, is more problematic. In many regards, it clearly resembles authentic *Lobonotus* (Table 3). However, there are some very important differences. *Lobonotus orientalis* is almost exactly equidimensional, while authentic *Lobonotus* are slightly longer than wide. The regions of *L. orientalis* are more tumid than those of authentic *Lobonotus*, and the cardiac and metabranchial regions of *L. orientalis* are transversely raised so as to form a nearly continuous transverse ridge across the carapace, not seen in authentic *Lobonotus*. The intestinal region of *L. orientalis* is deeply depressed below the level of the cardiac region and the metabranchial region, a condition not seen in authentic *Lobonotus*. Most importantly, the nature of the sternum and male abdomen differs from members of authentic *Lobonotus*. In *L. orientalis*, sternites 3/4 have a very clear suture separating them, while in *L. mexicanus*, those sternites have no visible suture between them. In addition, male abdominal somites 3-5 are fused in *L. orientalis*, while in *L. mexicanus*, those sternites are free and appear to have been movable (Rathbun, 1930b, pl. 1, fig. 3). Differences in the fusion and sutures in the sternum and abdomen are important

TABLE 4 — Dorsal carapace length and width ratios of *Pakicarinus orientalis* (bold) compared to those for various species of *Lobonotus* and *Titanocarcinus*. Measurements were taken from illustrations in A. Milne Edwards (1864), Collins and Morris (1978), and Schweitzer et al. (2002). L, maximum carapace length; W, maximum carapace width; FOW, fronto-orbital width; FW, frontal width; PW, posterior width.

Species	L/W	FOW/W	FW/W	PW/W
Lobonotus sculptus A. Milne Edwards, 1864 (type):	0.61	0.33	0.42	0.78
Lobonotus mexicanus Rathbun, 1930b	0.71	0.33	0.60	0.86
***Pakicarcinus orientalis* (Collins and Morris, 1978)**	**0.67**	**0.34**	**0.67**	**0.83**
***Pakicarcinus orientalis* (specimen examined herein)**	**0.58**	**0.32**	—	**0.88**
Titanocarcinus serratifrons A. Milne Edwards, 1864	0.66	0.37	0.46	0.86
Titanocarcinus pulchellus A. Milne Edwards, 1864	0.68	0.43	0.38	0.75
Titanocarcinus raulinianus A. Milne Edwards, 1864	0.71	0.38	0.48	0.79
Titanocarcinus edwardsi A. Milne Edwards, 1864	0.69	0.38	0.66	0.79

family and subfamily level characters in the Xanthoidea; thus, these differences cannot exist within the same genus according to recent work on the Xanthoidea (Guinot, 1977; 1978; Ng, 1998; Davie, 2002). We remove *L. orientalis* to a new genus, discussed below.

Collins and Morris (1978) and Schweitzer et al. (2002) discussed the marked similarity between *Titanocarcinus* and *Lobonotus*. Upon revisiting that issue in the course of this work, many observations can be made. Various ratios of carapace lengths and widths for each genus fall into the same range (Table 4). Further, the position, development, and areolation of the various dorsal carapace regions are very similar among members of the two genera. In A. Milne Edwards (1864), in which he erected the two genera, *Titanocarinus* is illustrated as having a moderately to poorly developed epigastric region and possessing a groove extending from the anterior edge of the protogastric region about one-third the distance posteriorly on that region. In that same work, *Lobonotus* is depicted as possessing a well-defined epigastric region and no groove dividing the protogastric region. However, specimens of *Lobonotus mexicanus* Rathbun, 1930b, have well-defined epigastric regions and a groove dividing the protogastric region. As illustrated by A. Milne Edwards (1864) and in the other authentic species of the genus, *Lobonotus* has a much more quadrate carapace than does *Titanocarcinus*; however, some species of *Titanocarcinus*, including *T. edwardsi*, are nearly as quadrate as species of *Lobonotus*. As discussed by Collins and Morris (1978) and Schweitzer et al. (2002), there is a largely geographic pattern in the usage of the two generic names; *Titanocarcinus* has been used for European forms, and *Lobonotus* has been used mostly for American forms. It seems distinctly possible that the two genera are synonymous; however, we reiterate the decision of Schweitzer et al. (2002) that synonymy must await examination of type material.

Family PALAEOXANTHOPSIDAE Schweitzer, 2003

Included genera.— *Lobulata* new genus; *Palaeoxanthopsis* Beurlen, 1958; *Paraverrucoides* Schweitzer 2003; *Remia* Schweitzer, 2003; *Verrucoides* Vega et al., 2001.

Diagnosis.— Carapace length about three-quarters carapace width, widest about two-thirds the distance posteriorly on carapace; fronto-orbital width about half maximum carapace width; deep, v-shaped groove separating gastric regions from hepatic and branchial regions; regions usually with large spherical swellings but may be small swellings; anterolateral margin with four or five spines, last longest, directed laterally or posterolaterally; spines triangular, separated from one another by notches or fissures (modified after Schweitzer, 2003).

Genus **Lobulata** new genus

Lobonotus A. Milne Edwards, 1864 (part). Feldmann, Casadío, Chirino-Gálvez, and Aguirre-Urreta, 1995, p. 11, fig. 7.

Type species.— *Lobonotus lobulata* Feldmann, Casadío, Chirino-Gálvez, and Aguirre-Urreta, 1995.

Types.— The types originally referred to *Lobonotus lobulata* are deposited in the Geology Collections at the Universidad Nacional de La Pampa, Santa Rosa, La Pampa, Argentina.

Occurrence.— The sole species of the genus is known from Maastrichtian to Danian rocks of Río Negro and La Pampa provinces, Argentina (Feldmann et al., 1995).

Diagnosis.— Carapace wider than long, L/W about 0.77; widest over half the distance posteriorly on carapace; fronto-orbital width about half maximum carapace width; anterolateral margin with four spines excluding outer-orbital spine, spines triangular, separated by notches; last spine longest, directed laterally; relatively deep grooves separating protogastric from branchial and hepatic regions; protogastric regions with central spherical swellings; mesogastric region with long anterior process, with two swellings positioned alongside one another; epibranchial regions arcuate, with two large swellings, one positioned near base of third and fourth anterolateral spines, other positioned between first swelling and urogastric region; cardiac region with broad, bilobed swelling; branchial regions inflated centrally; sternum narrow; immature female abdominal somites free; chela stout; fixed finger with large denticles; movable finger with very large denticle near base and at least two smaller denticles on occlusal surface.

Etymology.— The genus name is taken from the trivial name of *Lobonotus lobulata*, the type and sole species of the new genus, in reference to the lobate nature of the anterolateral margin.

Discussion.— *Lobonotus lobulata* cannot be accommodated within *Lobonotus* as defined above. *Lobonotus lobulata* lacks the well-defined carapace regions; granular ornamentation; well-developed subhepatic and epigastric regions; lateral arcuate extensions on the cardiac region, and nearly equidimensional carapace of *Lobonotus* sensu stricto. In addition, the spherical swellings on the branchial, protogastric, and mesogastric regions of *L. lobulata* are not typical of authentic species of *Lobonotus*. The lobate nature of the anterolateral margin and large, triangular spines separated by notches that are found in *L. lobulata* are not seen in authentic *Lobonotus*. The sternum of *L. lobulata* is much more narrow and straighter than that of typical *Lobonotus*. Thus, we herein remove it from *Lobonotus* and place it within the new genus *Lobulata*.

Lobulata new genus may be referred to the Palaeoxanthopsidae for several reasons. It possesses nearly all of the diagnostic characters for the family, including a carapace about 75 percent as long as wide; a fronto-orbital width of about half the carapace width; large, triangular anterolateral spines separated by notches or grooves; a longest last anterolateral spine directed laterally; spherical swellings on the protogastric, mesogastric, and branchial regions; and relatively deep grooves separating the protogastric region from the hepatic and branchial regions. In addition, *Lobulata* has anterolateral margins that are flared upward in frontal view (Feldmann et al., 1995, fig. 7.3), as in *Paraverrucoides* (Schweitzer, 2003, fig. 6.1, 6.3, 6.6). The only character that is slightly different from other palaeoxanthopsids is the double swellings on the mesogastric region; the other genera within the family have a single swelling on that region.

The Palaeoxanthopsidae are known from Maastrichtian to Eocene rocks; the new genus is known from the Maastrichtian to Danian and thus does not change the geologic range of the family. The family exhibits an Atlantic distribution, with its earliest occurrences in Maastrichtian rocks of Brazil and Mexico (*Palaeoxanthopsis*) (Rathbun, 1902; Maury, 1930; Beurlen, 1958; Vega et al., 2001); Senegal (*Remia*) (Remy and Tessier, 1954); and southern Argentina *(Lobulata)* (Feldmann et al., 1995). The family subsequently dispersed throughout the central and northern Atlantic (Schweitzer, 2003), becoming extinct by the end of the Eocene.

Family PANOPEIDAE Ortmann, 1893

Discussion.— The new genus described below clearly displays a xanthoid appearance, and it is best placed within the Panopeidae Ortmann, 1893, based upon the morphology of the dorsal carapace, the sternum, and the male abdomen. The material referred here to *Pakicarcinus* new genus cannot be accommodated within the Pilumnidae, nor can it be placed within the Eriphiidae, because members of those families have all seven male abdominal segments free, while *Pakicarcinus* has male abdominal somites 3-5 fused. The Goneplacidae MacLeay, 1838, cannot accommodate *Pakicarcinus* either. Members of the Goneplacidae may have all male segments movable, as in the Euryplacinae Stimpson, 1871; *Pakicarcinus* cannot be referred to that subfamily. Members of the Chasmocarcininae Serène, 1964, have male abdominal somites 3-5 fused, but the quadrate carapace and supplementary plate on thoracic sternite 8 are not present in *Pakicarcinus*. The Goneplacinae MacLeay, 1838, also have seven free somites of the male abdomen, but the extremely elongate orbits typical of that subfamily are not present in *Pakicarcinus*. Karasawa and Kato (2003a) synonymized the Goneplacinae and the Carcinoplacinae H. Milne Edwards, 1852, while Davie (2002) maintained them as separate subfamilies. According to Karasawa and Kato (2003a, b), the sterno-abdominal cavity reaches the anterior of sternite 4 in the Goneplacinae (= Carcinoplacinae). The sterno-abdominal cavity only reaches to the middle of sternite 4 in *Pakicarcinus*, thus excluding it from the Goneplacinae and Carcinoplacinae, as recognized by Davie (2002). Further, the distinctive ornamentation, well-defined carapace regions, inflated carapace regions, and transverse ridges on the cardiac and branchial regions are not typical of goneplacid ornamentation. The Xanthidae MacLeay, 1838, sensu stricto, and the Platyxanthidae Guinot, 1977, cannot accommodate *Pakicarcinus* because the sterna of members of those two families are narrower and more straight-sided. In addition, the fourth sternite of those two families is extremely long. *Pakicarcinus* has a rounded, relatively broad sternum and has a short fourth sternite; thus, it is excluded from the Xanthidae and Platyxanthidae. Members of the Pseudorhombilidae Alcock, 1900, generally have smooth carapaces and short anterolateral margins with sharp spines; neither condition is seen in *Pakicarcinus*.

The only xanthoid family which can accommodate *Pakicarcinus* is the Panopeidae. Panopeids are characterized by having generally 'xanthoid' carapaces that are hexagonal or tranversely ovate; a bilobed frontal margin; anterolateral margins with two to four spines or entire; a narrow sternum that is nonetheless rounded and wider than members of the Xanthidae or Platyxanthidae (see illustrations in Rathbun, 1930a, for example); and male abdominal somites 3-5 fused (after Davie, 2002). *Pakicarcinus* fits all of these criteria. The carapace regions of panopeids range from poorly defined to well-defined; *Pakicarcinus* has well-defined regions. In addition, the shape of the sternum in *Pakicarcinus* is very similar to some members of the Panopeidae (see Rathbun, 1930a). The sutures between sternites 2-3 and 3-4 in species of *Panopeus* are very clear; this condition is also true of *Pakicarcinus*. In xanthids and platyxanthids, sternites 3 and 4 appear to be fused with little evidence of a suture. The male abdomen of *Pakicarcinus* entirely fills the space between the fifth pereiopods. Davie (2002) indicated that in the Eucratopsinae Stimpson, 1871, the space was not entirely filled by the abdomen, but did not list this as a feature of the family. By implication, then, some members of the family do have the entire space covered, as in *Pakicarcinus*. Guinot (1978, p. 276) was similarly vague, discussing a tendency toward more and more of sternite 8 being uncovered, suggesting that in some panopeids, it may be completely covered. Guinot (1979, p. 206) stated that in the majority of the xanthid panopeines, the second abdominal somite is separated from the coxa of the fifth pereiopod by the outer-lateral part of sternite 8" (translated from French). This implies that in some panopeids, the entire sternite 8 is covered. Guinot (1979, p. 206) went on to state that in the type species of *Panopeus* H. Milne Edwards, 1834, *P. herbsti* H. Milne Edwards, 1834, only a small portion of sternite 8 is visible. We suggest that it is possible that more primitive members of the Panopeidae possess a completely covered sternite 8, and more derived members exhibit exposure of a portion of that sternite, possibly more and more of sternite 8 is exposed the more derived the form is. Clearly, the antiquity of *Pakicarcinus* places it as one of the more primitive members of the lineage.

There are a few features of *Pakicarcinus* which do not seem to fall within the range of extant panopeids. *Pakicarcinus* is nearly equidimensional; this condition is seen in some panopeids of the subfamily Eucratopsinae, like *Homoioplax* Rathbun, 1914, but it is not typical of panopeids with well-defined carapace regions, as in *Panopeus* of the Panopeinae Ortmann, 1893. In addition, the carapace regions of *Pakicarcinus* are better developed than in extant panopeids, even those taxa that are defined as having well-defined regions, and *Pakicarcinus* has granular ornamentation and transverse ridges on the branchial and cardiac regions that are not typical of extant panopeids. However, it should be noted that many extant panopeids do in fact have transverse ridges on the hepatic and protogastric regions (Schweitzer, 2000). We view these differences as less important than the very important features of the sternum and male abdomen and place *Pakicarcinus* within the Panopeidae. That it should differ somewhat from extant members is not surprising, given its Eocene age.

Karasawa and Kato (2003a) suggested that *Glyphithyreus* Reuss, 1859, may belong within the Eucratopsinae; that genus is under review (by CS and H. Karasawa). Review of the status of all Panopeidae in the fossil record is beyond the scope of this paper but is sorely needed.

Subfamily PANOPEINAE Ortmann, 1893

Discussion.— *Pakicarcinus* is placed within the Panopeinae, based upon its relatively narrow orbits and the fact that sternite 8 is completely covered by the abdomen. These features exclude *Pakicarcinus* from the Eucratopsinae.

Genus **Pakicarcinus** new genus

Lobonotus A. Milne Edwards, 1864 (part). Collins and Morris, 1978, p. 970, pl. 116: 10, 11, pl. 117: 1; Schweitzer et al., 2002, p. 19.

Type species.— *Lobonotus orientalis* Collins and Morris, 1978.

Occurrence.— as for species.

Diagnosis.— as for species.

Etymology.— The generic name is a contraction of Pakistan, the country from which the material is known, and the Greek root *karkinos*, meaning crab.

Discussion.— The material originally referred to *Lobonotus orientalis* has been referred to a new species as there are none known that can accommodate it. The reasons for removing the species from *Lobonotus* sensu stricto have been discussed above. Some members of *Glyphithyreus*, of which one species is known from Pakistan, *Glyphithyreus wetherelli* (Bell, 1858), are similar to *Lobonotus orientalis* in the well-defined, granular carapace regions and a ridge on the cardiac and branchial regions; however, the orbits of *Glyphithyreus* sensu stricto are extremely broad, occupying nearly the entire front margin of the carapace. Thus, *Glyphithyreus* cannot accommodate *L. orientalis*, and the new species *Pakicarcinus* has been erected to embrace it.

Pakicarcinus orientalis (Collins and Morris, 1978) new combination

Fig. 8A,B

Lobonotus orientalis Collins and Morris, 1978, p. 970, pl. 116: 10, 11, pl. 117: 1.

Material examined.— GSP-UM 3507.

Occurrence.— The holotype, BMNH-In. 48245, was collected from the "lower Eocene Ghazij Formation, south of Nila Kund, Dera Ghazi Khan, 29 30' N, 69 45' E, Punjab Province, Pakistan"

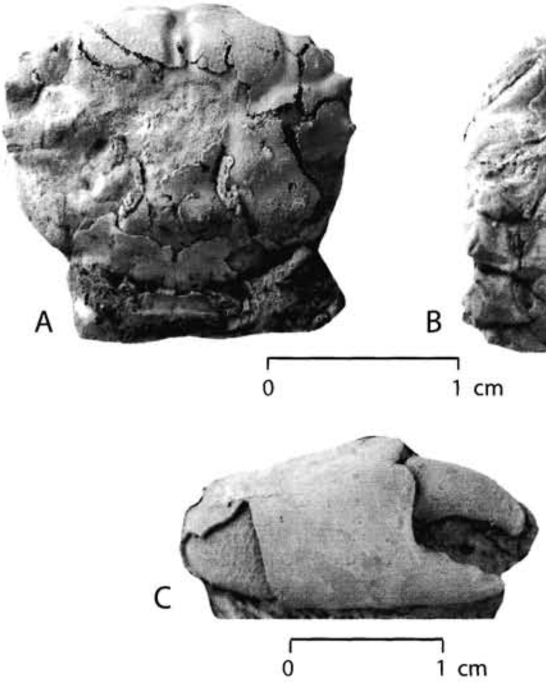

FIG. 8 — *Pakicarcinus orientalis* (Collins and Morris, 1978) new genus and new combination, GSP-UM 3507 (A, B); and Xanthoidea, genus and species indeterminate, GSP-UM 3504 (C). A, dorsal carapace. B, male venter (arrow 1 indicates clear suture between sternites 3 and 4; arrow 2 indicates fused abdominal somites 3-5). C, outer surface of chela.

(Collins and Morris, 1978, p. 971). The new specimen was collected from locality Da3 (see appendix).

Diagnosis.— Carapace about as wide as long, length/width about 0.97; regions well-defined by grooves, granular; front bilobed, with median notch, about 30 percent maximum carapace width; orbits small, circular, fronto-orbital width about 60 percent maximum carapace width; anterolateral margin with 4 spines excluding outer-orbital spine; epigastric regions small, weakly inflated; protogastric regions broad; hepatic regions small; epibranchial region arcuate, relatively long; branchial and cardiac regions with transverse ridge that is nearly continuous across entire carapace; intestinal region flattened, depressed below level of remainder of carapace; male sternum relatively broad, ovate, sutures between sternites 2-3 and 3-4 clear; sternite 4 short; male abdomen with somites 3-5 fused, telson reaching lower edge of base of first pereiopods, sterno-abdominal cavity reaching to middle of fourth sternite, abdomen entirely filling space between fifth pereiopods.

Discussion.— The new specimen permits description and illustration of the male sternum and abdomen, which were only briefly described by Collins and Morris (1978) and were not illustrated. It was these important features that spurred reevaluation of the species and the genus.

Superfamily XANTHOIDEA family, genus and species indeterminate
Fig. 8C

Material examined.— GSP-UM 3504.

Occurrence.— Locality Ro6 (see Appendix).

Discussion.— The specimen consists of a xanthoid claw and some articles of the cheliped. The claw is stout, relatively smooth, and without spines on the upper margin, which makes it typical of many xanthoid families. In addition, the fingers are darker than the remainder of the carapace, also seen in many xanthoid groups. The merus and what appear to be the carpus and ischium are spinose. The claw may be excluded from two xanthoids known from the region. The morphology of the claw excludes it from *Proxicarpilius*, in which the claws are spinose on the upper margins, and the claws of *Gillcarcinus amphora*, which are elongate and granular. The claw morphology of *Pakicarcinus orientalis* is unknown. More material, associated with a dorsal carapace, will be needed to determine the placement of this xanthoid chela.

DISCUSSION

Many of the decapods from the Domanda and Drazinda formations of Pakistan are typical of what would be expected in an Eocene fauna from the Tethyan region. Members of the Carpiliidae had an exclusively Tethyan distribution during the Eocene, and the tropical and subtropical occurrences of extant forms suggest a relict Tethyan distribution (Schweitzer, 2003). The Pakistan occurrence of *Proxicarpilius* fits this model for the family. *Lobocarcinus* similarly displays a Tethyan distribution, with occurrences in southern Europe, Egypt, India, and New Zealand in addition to the Pakistan occurrence described here (Schweitzer and Feldmann, 2000b). Portunids and paguroids are cosmopolitan in modern oceans and also have widespread Eocene records; little paleoecological information can be gleaned from their Pakistan occurrences. Extant *Neocallichirus* species are known from subtropical locales, as are other fossil occurrences (Schweitzer and Feldmann, 2002); thus, species of the genus clearly could have thrived in the Eocene Tethyan region. Two other species described here, *Gillcarcinus amphora* and *Pakicarcinus orientalis*, belong to monotypic genera; thus, paleoecological inferences at the generic level cannot be drawn from them. At the subfamily level, the Chasmocarcininae, to which *Gillcarcinus* belongs, exhibits a subtropical to tropical, generally Tethyan distribution (Schweitzer and Feldmann, 2001a), with the exception of one occurrence in Antarctica (Feldmann and Zinsmeister, 1984). Too little is known about Panopeidae in the fossil record to make any inferences about the occurrence of *Pakicarcinus*. A high degree of endemism at the generic level is seen in Eocene decapod occurrences of North America (Blow and Manning, 1996; Feldmann et al., 1998; Schweitzer, 2001; Schweitzer et al., 2002), suggesting that the warm, equable climate of the Eocene was conducive to rapid evolution and radiation, resulting in high levels of endemism at the generic level. The Pakistan decapod occurrences described herein clearly support the interpretation that the Tethyan Seaway was a major avenue of dispersal of decapod crustaceans during the Paleogene and early Neogene.

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