

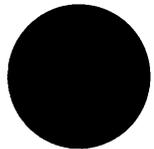
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NEW CRABS FROM THE EOCENE AND OLIGOCENE
 OF BAJA CALIFORNIA SUR, MEXICO AND AN ASSESSMENT
 OF THE EVOLUTIONARY AND PALEOBIOGEOGRAPHIC
 IMPLICATIONS OF MEXICAN FOSSIL DECAPODS

CARRIE E. SCHWEITZER, RODNEY M. FELDMANN,
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NEW CRABS FROM THE EOCENE AND OLIGOCENE OF BAJA CALIFORNIA SUR, MEXICO AND AN ASSESSMENT OF THE EVOLUTIONARY AND PALEOBIOGEOGRAPHIC IMPLICATIONS OF MEXICAN FOSSIL DECAPODS

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ABSTRACT—A new collection of fossil decapod crustaceans from the Cretaceous Rosario Formation, the Eocene Tepetate Formation and the Oligocene El Cien Formation, Baja California Sur, Mexico, has yielded two new genera and several new species, *Amydrocarcinus dantei* n. gen. and sp., *Levicyclus tepetate* n. gen. and sp., *Eriosachila bajaensis* n. sp., *Oregonia spinifera* n. sp., *Archaeopus mexicanus* n. sp., and *Necronectes nodosa* n. sp. Additionally, new occurrences of the previously described *Lophoranina bishopi*, *Xandaros sternbergi*, *Icriocarcinus xestos*, and *Lobonotus mexicanus* as well as *Dardanus* cf. *D. mexicanus* are reported. As part of ongoing work on global evolutionary and paleobiogeographic patterns within the Decapoda, the work has prompted a review and synthesis of decapod occurrences in the tropical and subtropical Americas including the southern United States, the Caribbean, Mexico, Central America, and northern South America. As a result of the systematic review, several new combinations are reported herein which include *Eriosachila bartholomaensis* (Rathbun, 1919), *Lobonotus sandersi* (Blow and Manning, 1996; 1998), and *Matutites americanus* (Rathbun, 1935). *Icriocarcinus* is transferred to the Goneplacidae, extending the range of that family into the Cretaceous. Most Cretaceous through Miocene tropical and subtropical American taxa appear to have originated within the area and a large number were endemic. Most of the immigrants to the central Americas appear to have evolved along North Atlantic shelves and subsequently dispersed to the Americas, probably via continental shelf routes. In addition, as demonstrated by several previous studies, decapod crustaceans appear to have evolved in numerous middle- and high- latitude areas with subsequent dispersal to lower latitudes, contrary to the long held notion that the tropics are areas of origin with subsequent dispersal to other regions. Low-latitude decapod taxa tend to remain in low-latitude areas. The Maastrichtian and the Eocene appear to have been times of elevated extinctions within the Decapoda; however, the extinction patterns for those two time intervals are very complex.

INTRODUCTION

FOSSIL DECAPOD crustaceans have previously been reported from the tropical and subtropical Americas; however, the record from the western coast of Mexico has been sparse. A small number of occurrences in Baja California were noted by Rathbun (1930b) and later by Bishop (1988a) and Squires and Demetron (1992). Grimm and Föllami (1994) reported the trace fossil *Thalassinoides*, commonly associated with decapods, from the Oligocene-Miocene San Gregorio Formation of Baja California Sur. The purpose of this work is to describe several new taxa as well as to provide expanded descriptions of some previously described taxa which were collected from the Eocene Tepetate Formation and the Oligocene El Cien Formation. These units are located in Baja California Sur, Mexico, northwest of La Paz. The decapod fauna now known from those units is diverse, containing eight genera in at least seven families. Additionally, new occurrences of previously described taxa from the Cretaceous Rosario Formation are noted. This work on the Eocene decapods of Baja California Sur complements recent work on Cretaceous and Eocene faunas of other regions in Mexico conducted by Vega, Feldmann, and others.

The discovery of these new fossil decapod crustaceans has prompted a review of their occurrences in the tropical and subtropical Americas. Specifically, the study area is restricted to decapod occurrences in the southern United States, including the Mississippi Embayment, the southern North Atlantic and Gulf Coastal Plain, and the southern North Pacific slope; Mexico; the Caribbean; Central America; and northern South America. Recently, several reviews of the occurrences and evolutionary and paleobiogeographic patterns within the Decapoda have been conducted, targeting such areas as South America (Feldmann, Casadío et al., 1995; Feldmann et al., 1997), New Zealand (Feldmann and McLay, 1993), Antarctica (Feldmann and Wilson, 1988; Feldmann et al., 1993), Japan (Karasawa, 1993), and the North Pacific (Schweitzer, 2001b). The tropical and subtropical Americas provide an important link between the North Atlantic and North

Pacific regions as well as between the high southern latitudes and the northern hemisphere; thus, the area is ideal for study.

The database for this study consists of 99 decapod genera and numerous species (Appendices A and B). The American region under study, especially Cretaceous and Eocene rocks, has received extensive attention by Bishop, Rathbun, Blow and Manning, and others, and the Caribbean has also received a moderate amount of study. Decapods of Mexico have received considerable attention in the last decade or so by Vega and Feldmann, and decapod occurrences in Central America and South America have been studied by one of us (Feldmann). Oligocene and Miocene occurrences within the study area are poorly known, probably due to vegetation covering the outcrops and the inhospitable climate (i.e., hot and humid) of the Caribbean areas where these rocks occur, which makes collecting less inviting and productive. Schweitzer and Feldmann have studied many of the most important North American collections and some of the collections in Japan and Europe, and they have also studied Antarctic decapods. Thus, generic identifications have been verified either through examination of type material or careful study of relevant literature. Decapods known only from chelae or other fragments that were not verifiable at the generic level by us were not included in the analysis. This includes most callianassid and hermit crab (paguroid) taxa as well as some other taxa known from fragmental material.

STRATIGRAPHY AND GEOLOGIC SETTING

All of the decapods described below were collected in Baja California. A brief synopsis of the lithology, age, and paleoenvironment and associated fauna are given for each unit.

Tepetate Formation.—Heim (1922) defined the Tepetate Formation as a sequence of several thousand feet of greenish sandstone, gray sandstone, and greenish to violet clay, exposed near Rancho El Tepetate in Arroyo Colorado, Baja California Sur (Figs. 1–3). Although Heim (1922) described several localities of the Tepetate Formation, he did not suggest a formal type locality.

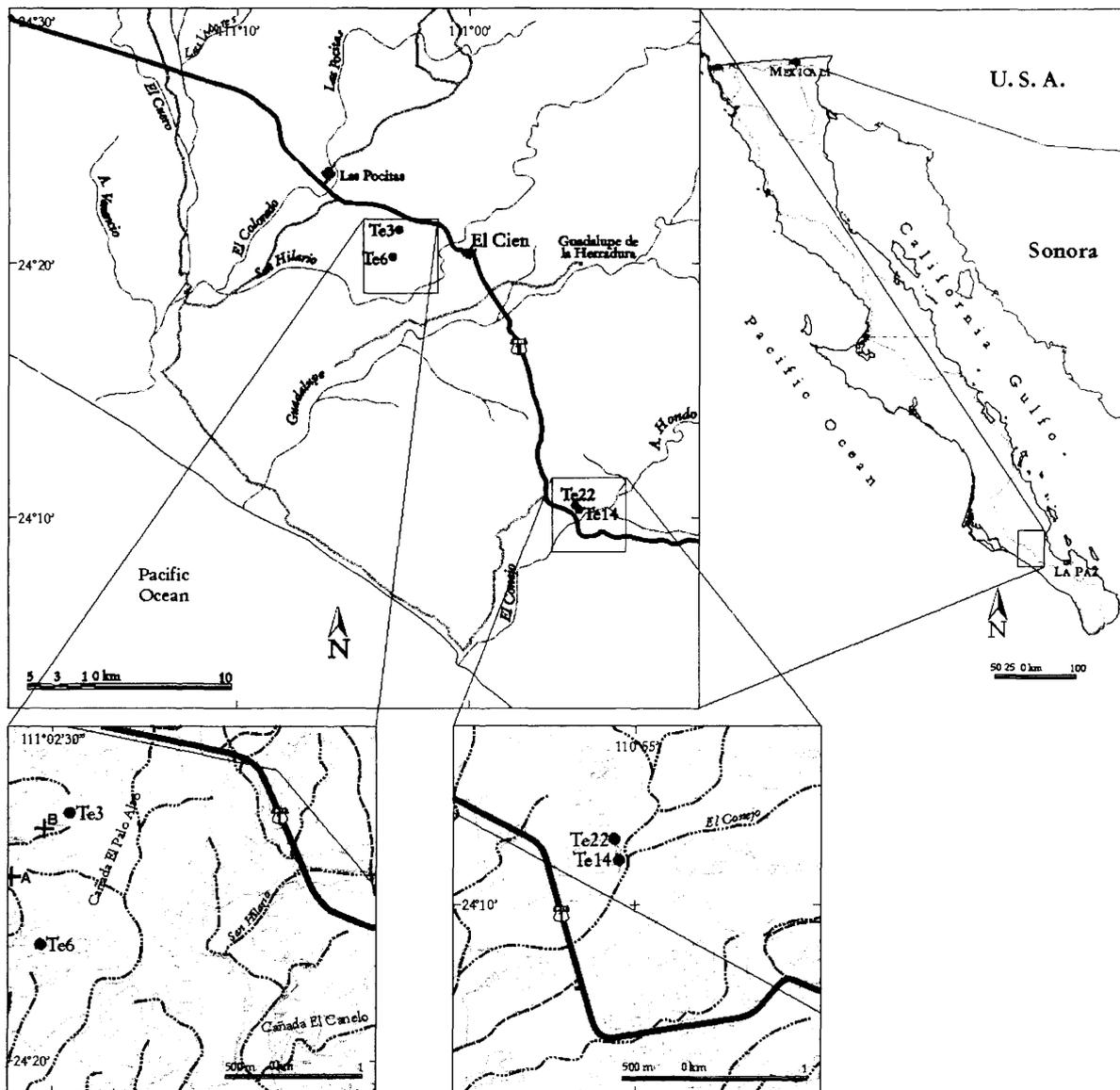


FIGURE 1—Location map of a portion of the isthmus of Baja California Sur, Mexico, surrounding La Paz, showing the position of the sites in the Tepetate Formation from which decapods were collected. Localities Te14 and Te22 are in the Arroyo El Conejo, in the lower right square. Localities A and B are in the lower left square, between localities Te3 and Te6, on the west bank of the Cañada El Palo Alto.

Beal (1948) described three outcrops for the Tepetate Formation; however, Lozano-Romen (1975) considered the rocks at these localities to be different from the Tepetate Formation. Mina-Uhink (1957) considered the Arroyo Colorado section as the type locality for the Tepetate Formation, although he did not describe the rocks or the upper and lower boundaries of the unit. Subsequently, numerous other studies have been conducted on the Tepetate Formation (Knappe, 1974; Fulwider, 1976; Minch and Leslie, 1979; Coleman, 1979; Galli-Oliver et al., 1986; López-Ferreira et al., 1991; Squires and Demetron, 1991, 1994; Vázquez-García et al., 1995; Perrilliat, 1996; Carreño, 2000; González and Thies, 2000; Ledesma-Vázquez et al., 2001). Knappe (1974) considered the unit to be early Eocene to early middle Eocene in age based upon planktic and benthic foraminiferans. In her work, Carreño (2000) defined a latest lower Eocene age for the outcrops of the Tepetate Formation at the Arroyo Colorado locality, based on the planktic foraminifers *Acarinina pentacamerata* and *Hankenina nuttalli*,

suggesting an age range of 51.2–48.4 Ma. Carreño (2000) also suggested the Arroyo Colorado section as the formal type section for the Tepetate Formation. Squires and Demetron (1992, 1994) considered the Tepetate Formation to be very similar to the Bateque Formation, also located in Baja California Sur, and correlated the Tepetate Formation with the middle part of the Bateque Formation.

El Cien Formation.—The El Cien Formation crops out to the west and northwest of La Paz, Baja California Sur in the area of San Juan de la Costa and El Cien (Fig. 4). Applegate (1986) defined the unit as 125–175 m of phosphatic mudstones, siltstones, sandstones, conglomerates, and tuff ranging in color from white to tan and from green to brown in the type section at Cerro Colorado (Fig. 5) (Applegate, 1986; Fisher et al., 1995). Applegate (1986) assumed that the same unit was found in the area of San Juan de la Costa, where the Oligocene material here reported was found. The unit contains granular phosphate which is mined

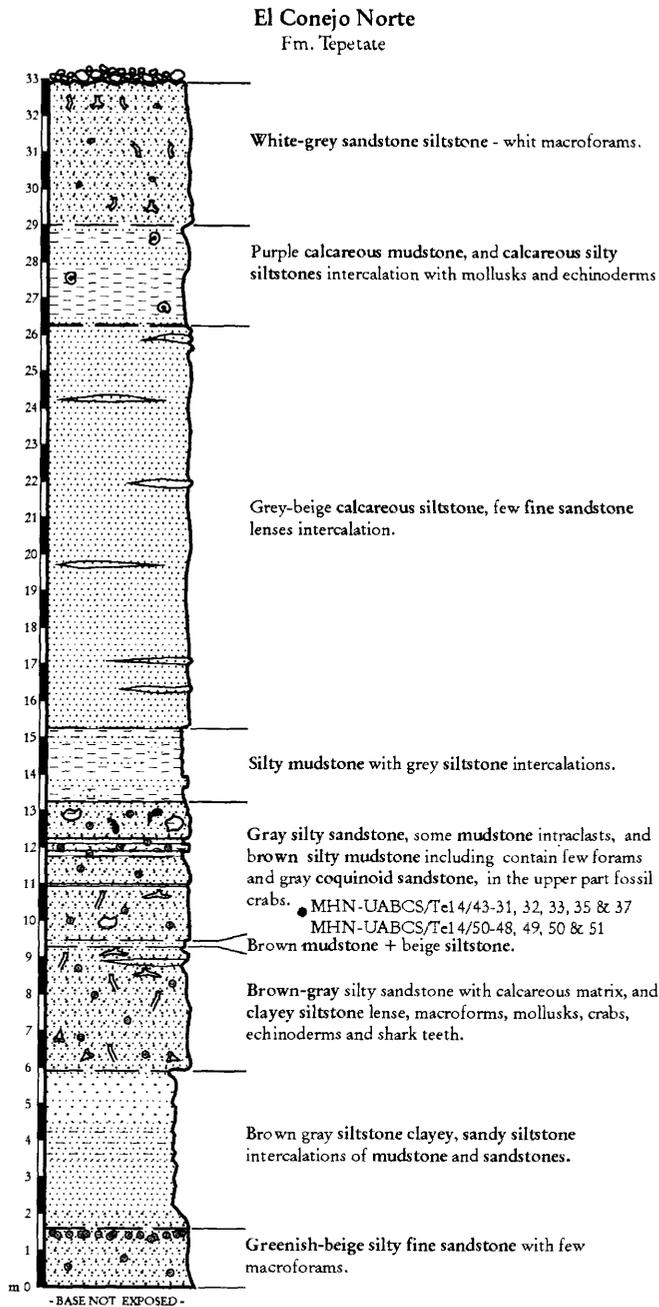


FIGURE 2—Stratigraphic section of the Tepetate Formation at the Conejo Norte locality Te14 (see Fig. 1) showing the stratigraphic position from which decapods were collected (based upon Schwennicke, unpublished data). See Figure 5 for key to lithologic symbols.

near San Juan de la Costa (Fischer et al., 1995). The unit has been subsequently well studied by several other workers, corroborating and expanding upon Applegate's work (Galli-Olivier et al., 1990; Gidde, 1991; Carreño et al., 1992; Grimm, 1992; Schwennicke, 1992; Galli-Olivier, 1993).

The fossil crabs collected from the El Cien Formation were recovered from spoil piles taken from the bed directly above the Humboldt phosphorite bed, at the Roca Fosforica Mexicana (RO-FOMEX) mine in San Juan de la Costa, a locality that has also yielded fossil whales. The lowermost El Cien is composed of a fossiliferous, sandy conglomerate that unconformably overlies the Tepetate Formation (Fischer et al., 1995). Fossils recovered from

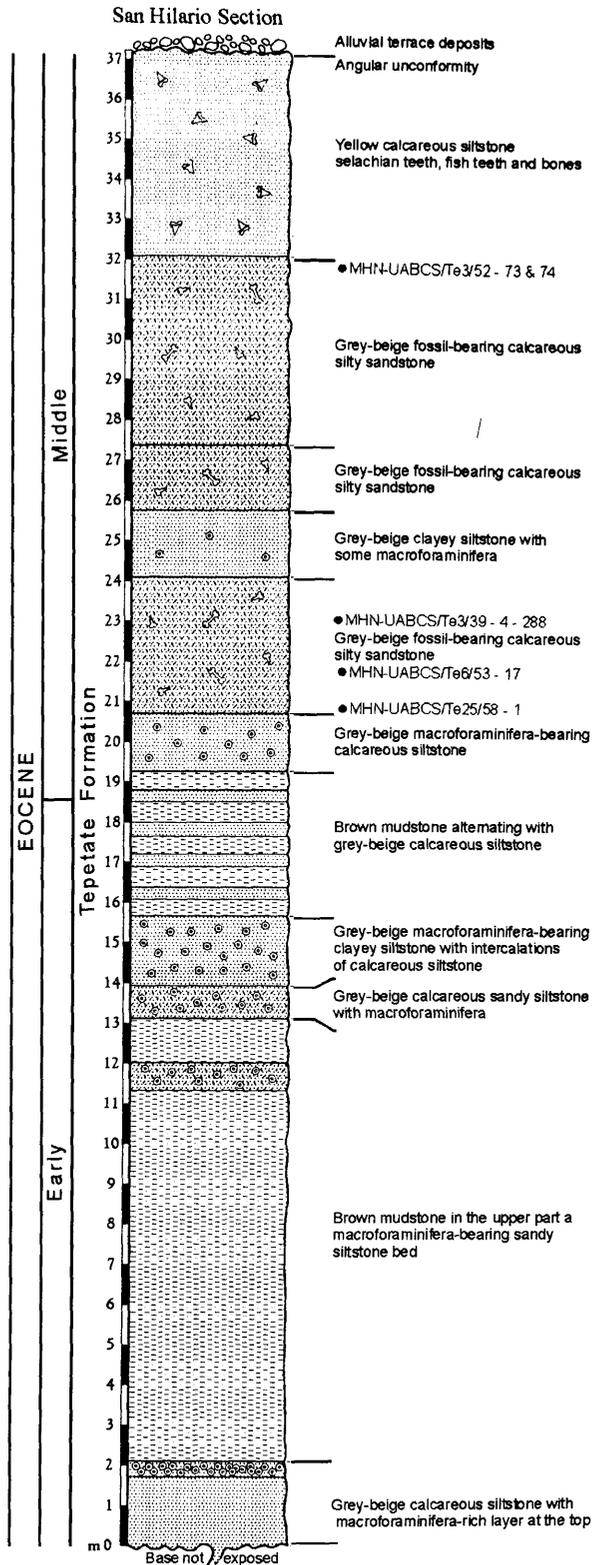


FIGURE 3—Composite stratigraphic section of the San Hilario locality (lower left inset in Fig. 1) of the Tepetate Formation showing the stratigraphic position from which decapods were collected. See Figure 5 for key to lithologic symbols. Bone and tooth symbols indicate positions where whale and other vertebrate bones as well as shark teeth were collected.



FIGURE 4—Location map of a portion of La Paz Bay, showing the position of the sites, Sj5, Sj2, and Sjl1, in the El Cien Formation from which decapods were collected.

this unit include shark's teeth, molluscs, fish scales, porpoises, desmostylids, and trace fossils including *Thalassinoides* and *Ophiomorpha* (Applegate, 1986), both of which are likely to have been constructed by decapods.

Applegate (1986) subdivided the El Cien Formation into three members, the Cerro Tierra Blanca, the San Hilario, and the Cerro Colorado members. However, Fischer et al. (1995) considered the lowermost El Cien to be composed of one unit, which they designated as the San Juan Member (corresponding to Applegate's Cerro Tierra Blanca and San Hilario members), and they concurred with Applegate (1986) in referring to the uppermost El Cien as the Cerro Colorado Member. The San Juan Member is late Oligocene based upon biostratigraphy and radiometric dating (Fischer et al., 1995). Kim and Barron (1986) and Kim (1987) reported the unit as containing diatoms indicative of *Rocella vigilans* to *Bogorovia veniamini* diatom zones. The Cerro Colorado Member is early Miocene in age (Fischer et al., 1995). Hausback (1982) measured a K/Ar radiometric age of 25.5 ± 0.4 Ma from a tuff bed located just below the main phosphorite bed near El

Cien, about 8 km southeast of Cerro Colorado in Arroyo San Hilario. The El Cien is overlain by volcanic rocks of the Miocene Comondú Formation.

Rosario Formation.—The Upper Cretaceous (Campanian-Maastrichtian) Rosario Formation is comprised of a variety of siliciclastic sediments, including conglomerates, sandstones, and mustones (Morris and Busby-Spera, 1990). The unit is interpreted as a submarine-fan complex including submarine channel fill, levees, and submarine slumps deposited in deep-marine slope and outer-shelf environments (Morris and Busby-Spera, 1988, 1990) as well as near-shore, rocky-coastal environments (Lescinsky et al., 1991; Johnson and Hayes, 1993). The type area for the Rosario Formation is located at El Rosario, approximately 200 km south of Ensenada, Baja California Norte, Mexico (Morris and Busby-Spera, 1990), and the unit is exposed along the coast as far north as Ensenada (Marincovich, 1975) and as far south as the north end of Vizcaino Bay (Webster, 1983). The Rosario Formation unconformably overlies a complex of nonmarine rocks of Cenomanian to early Campanian age of the Peninsular Ranges

Section of the San Juan Member
El Cien Formation (Upper Oligocene)

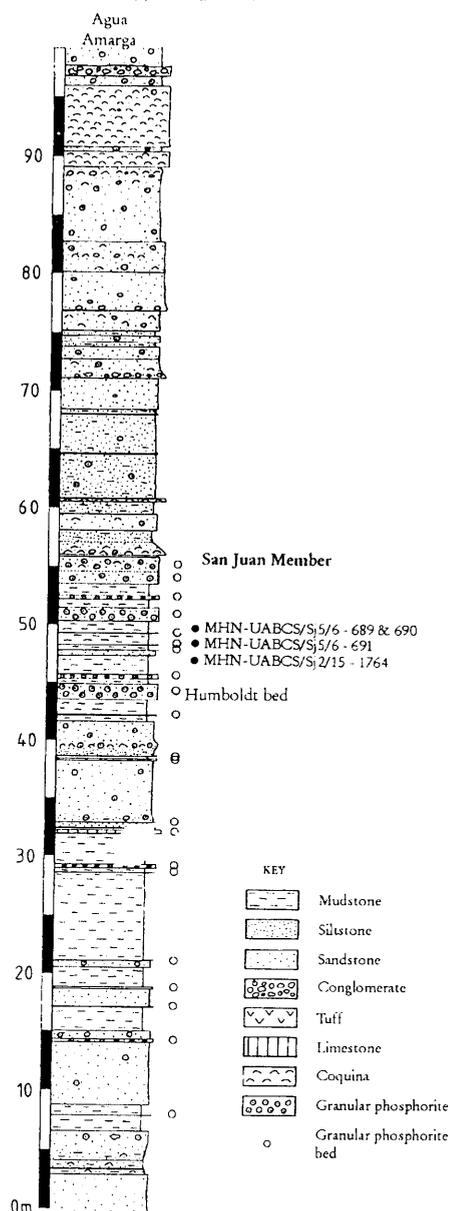


FIGURE 5—Stratigraphic section of the San Juan Member of the El Cien Formation near Mesa Agua Amarga (Fig. 4), eastern outcrop area (Fischer et al., 1995), showing the stratigraphic position just above the Humboldt Bed, from which decapods were collected.

forearc basin complex and is unconformably overlain by the Paleocene Sepultra Formation (Morris and Busby-Spera, 1990).

Numerous fossils have been described from the Rosario Formation. The Campanian-Maastrichtian age for the unit has been determined based upon molluscs and foraminiferans (Marincovich, 1975). Rudist biostromes (Marincovich, 1975), gastropods (Saul, 1970; Webster, 1983; Squires, 1993), oysters and crustose red algae (Johnson and Hayes, 1993), and boring sponges, corals, brachiopods, serpulid worms, and echinoids (Lescinsky et al., 1991). Bishop (1988a) described the crab *Xandoros sternbergi* (Rathbun, 1926a), preserved in concretions, from the Rosario Formation exposed at Punta San Jose in Baja California Norte. The decapods described here are preserved in dark mudstones; some

are preserved in concretions and some are not. Because the depositional environments for the Rosario Formation are so variable and because the stratigraphic position from which the decapods were collected is not known, it is difficult to speculate on where the decapods were living or how they were buried. Decapods preserved from active slope margins are typically preserved in concretions (see Feldmann et al., 1991; Schweitzer and Feldmann, 1999 for discussions). The decapods of the Rosario Formation may have been rapidly buried during downslope submarine movement or, alternatively, during storm events burying the animals in nearer shore environments.

SYSTEMATIC PALEONTOLOGY

Decapod morphology.—General morphology of a brachyuran decapod crustacean, a crab, is shown in Figure 6.

Repository information.—Specimens described in this study are deposited in the Museo de Historia Natural, Universidad Autónoma de Baja California Sur, La Paz, Baja California Sur, Mexico (MHN-UABCS) and the Museo de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México (UNAM IGM).

Order DECAPODA Latreille, 1802

Infraorder ANOMURA MacLeay, 1838

Superfamily PAGOUIDEA Latreille, 1802

Family DIOGENIDAE Ortmann, 1892b

Discussion.—Family-level assignment of paguroid material represented only by chelae can be facilitated by examining the relative size and symmetry of the right and left claws, the cross-sectional aspect of the manus, the ornamentation of the chelae, and the nature of the fingers (Vega, Cosma et al., 2001; Schweitzer and Feldmann, 2001b). The new material consists of the inner surface of a left chela and the outer surface of a right chela which are approximately equal in size. Within the Paguridae Latreille, 1802, and the Parapaguridae Smith, 1882, the right chela is always much larger than the left, thus excluding the material from those two families. The Coenobitidae Dana, 1851a, have extremely large mani, very high and stout fixed fingers, and very convex lower margin of the mani (Schweitzer and Feldmann, 2001b), none of which the new material exhibits. The Lithodidae Samouelle, 1819, have a circular to ovoid cross-section (Vega, Cosma et al., 2001), while the new material has a triangular cross-section of the manus. The Pylochelidae Bate, 1888, have symmetrical chelae, but the fixed finger is strongly flexed upwards, which is not a characteristic of the new material which has a weakly upturned fixed finger. The material here described consists of a right and a left manus, recovered from different localities. Because handedness is critical in family placement, and because the two mani are equal, the material is referred to the Diogenidae, which embraces genera with symmetrical, subequal, or asymmetrical chelae.

Genus DARDANUS Paulson, 1875

DARDANUS cf. DARDANUS MEXICANUS Vega, Cosma, Coutiño, Feldmann, Nyborg, Schweitzer, and Waugh, 2001b

Figure 7

Description.—Manus about as long as high, triangular in cross-section; inner surface moderately vaulted, coarsely granular; outer surface flattened, sparsely granular, granules poorly developed; proximal margin convex; upper margin weakly convex; lower margin convex, with blunt, spine-like projections; distal margin weakly concave, initially perpendicular to upper margin, then curving distally to merge with occlusal surface of fixed finger; fixed finger triangular, shorter than palm, upturned, occlusal surface with small tubercles.

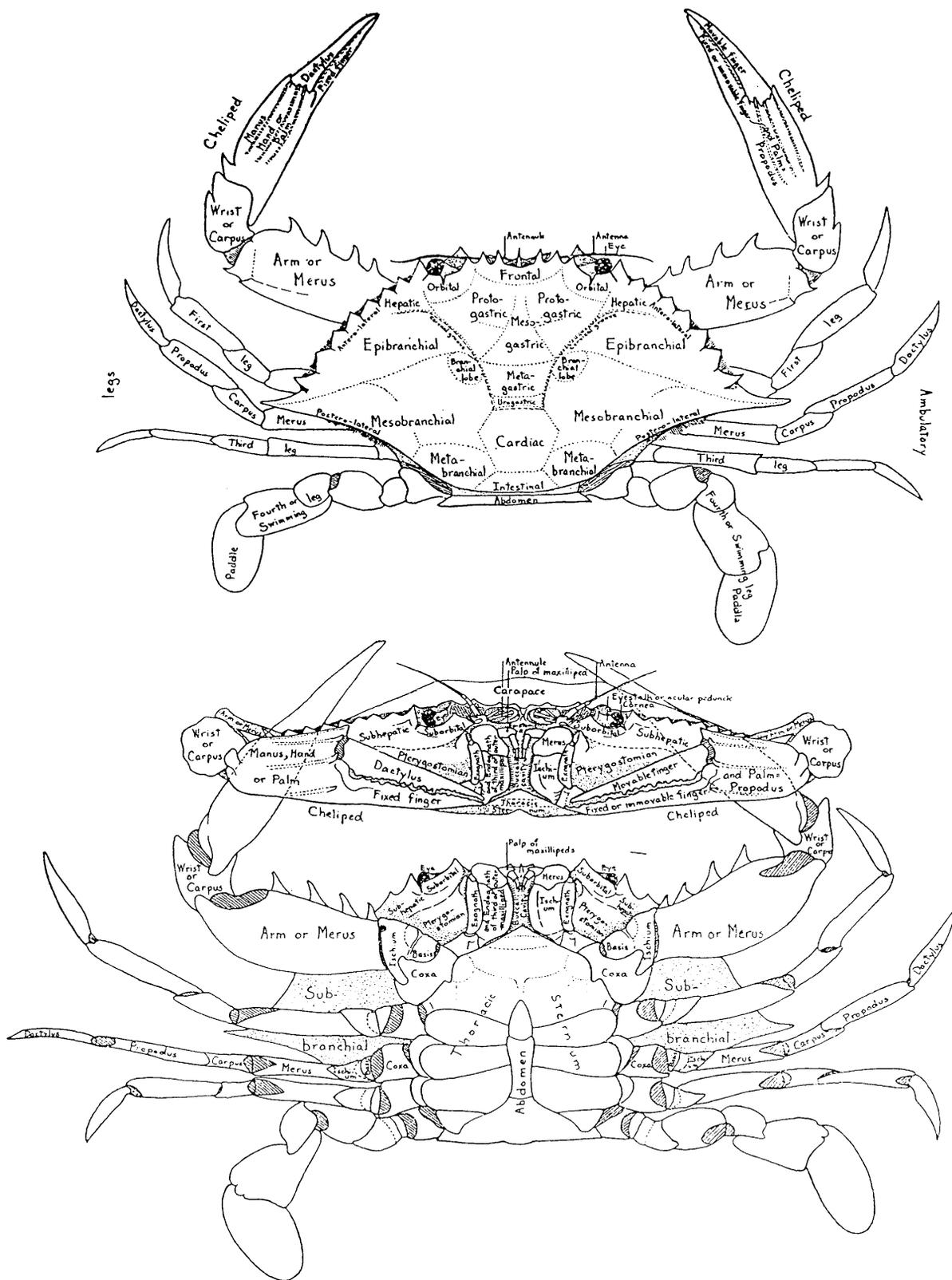


FIGURE 6—Line drawings of a typical brachyuran decapod, Portunidae, showing from top to bottom, dorsal, anterior, and ventral external morphology. From Rathbun, 1930.

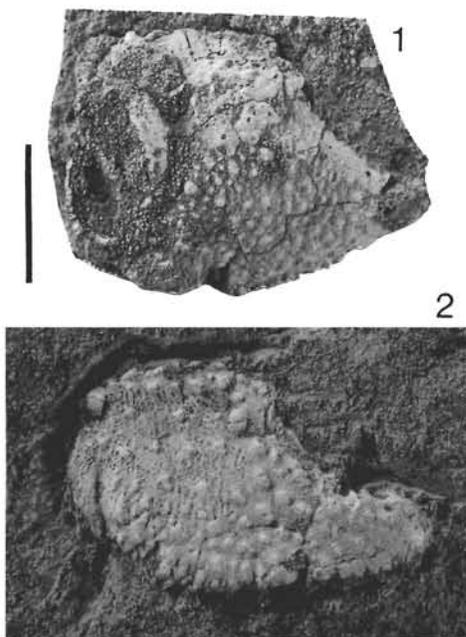


FIGURE 7.—*Dardanus* cf. *D. mexicanus* Vega, Cosma, et al., 2001. 1, MHN-UABCS/Te14/50-58, inner surface of chela; 2, MHN-UABCS/Te14/43-35, outer surface of chela. Scale bar equal to 1 cm.

Material examined.—Specimens MHN-UABCS/Te14/43-35 and MHN-UABCS/Te14/50-58.

Occurrence.—The specimens were collected from the Eocene Tepetate Formation, northwest of La Paz, Baja California Sur, Mexico, at Lat. N 24°10.240', Long. W 110°55.119'.

Discussion.—Vega, Cosma et al. (2001) described *Dardanus mexicanus* from Eocene deposits of Chiapas; that species was based upon only a left chela. The new material consists of both a right and left chela, which are approximately equal in size. The ornamentation on *Dardanus mexicanus* is very similar to that of the new material; however, the new specimens are poorly preserved and in one case broken, so that confident assignment of the material to *Dardanus mexicanus* is premature. Thus, the material is provisionally placed within that species until more and better specimens are collected.

Infraorder BRACHYURA Latreille, 1802
Section PODOTREMATA Guinot, 1977
Superfamily RANINOIDEA de Haan, 1833
Family RANINIDAE de Haan, 1833
Subfamily RANININAE de Haan, 1833
Genus LOPHORANINA Fabiani, 1910

Type species.—*Ranina marestiana* König, 1825.

Other species.—see Vega, Cosma et al., 2001 for complete list.

LOPHORANINA BISHOPI Squires and Demetron, 1992
Figure 8

Lophoranina bishopi SQUIRES AND DEMETRION, 1992, p. 44, fig. 130.

Diagnosis.—Carapace widened anteriorly, widest about one-third the distance posteriorly on carapace; outer-orbital spine medium sized for genus; two broad anterolateral spines, second with bifid tip; carapace ornamentation composed of short, discontinuous scabrous ridges on anterior 10 percent, followed by continuous, parallel transverse ridges to position of midlength, posterior half of carapace ornamented with sinuous, discontinuous transverse ridges.

Emendation to description.—Carapace longer than wide, obovate, widest about one-third the distance posteriorly on carapace; ornamented over most of carapace with closely spaced, sinuous, transverse ridges which bear broken bases of small spines; carapace flattened longitudinally and moderately vaulted transversely; ornamentation comprised of scabrous, short ridges on anterior one-tenth; these followed by continuous, parallel transverse ridges to about midlength of carapace; posterior half of carapace with discontinuous, sinuous ridges, not parallel to one another, with few to no bifurcations.

Rostrum unknown. Orbits broad, about two-thirds maximum carapace width. Orbital margin with 2 shallow, open fissures, inner located one-third the distance distally from inner orbital angle, outer located about two-thirds the distance distally from inner orbital angle. Small, sharp intra-orbital spine bounded by open fissures. Outer orbital spine broad, triangular, directed forward. Anterolateral margin with two spines; first spine triangular, directed forward; second spine broad, bifid near tip; entire spine and each bifurcation directed anterolaterally. Posterolateral margin convex, with beaded rim. Posterior margin unknown.

Carapace regions undifferentiated. Gastric areas with scabrous, discontinuous ornamentation; branchial regions with transverse ridges; cardiac region defined by deep branchiocardiac grooves.

Sternum narrow, complex; sternites 1–3 very reduced; sternites 4–6 broad for family.

Chelae appearing to be equal; manus with scabrous ridges aligned from upper to lower margin; upper margin of manus bearing triangular, distally directed spines.

Material examined.—Seven specimens, MHN-UABCS/Te14/50-48, 49, 50, 51, 52, 53, and 54.

Occurrence.—The specimens were collected from the Eocene Tepetate Formation, northwest of La Paz, Baja California Sur, Mexico, in the limestone walls of an arroyo, at Lat. N 24°10.240', Long. W 110°55.119'.

Discussion.—Squires and Demetron (1992) described *Lophoranina bishopi* from the Eocene Bateque Formation, which crops out along the west coast of Baja California Sur approximately 400 km from the Tepetate Formation localities from which the new material was collected. The molluscan and echinoderm faunas from the Bateque Formation and the Tepetate Formation appear to be quite similar upon preliminary inspection, and in fact, there has been some question as to whether or not the two units are distinct from one another (Squires and Demetron, 1992, p. 10). Thus, the discovery of a decapod species occurring in both formations is not surprising, and it appears that the two formations may have either been contemporaneous or deposited at different times in similar environments.

The new material permits a more complete description of the organism, including more details concerning the margins, the dorsal carapace, the venter, and the chelae. Especially important for species-level differentiation within the genus *Lophoranina* is the observation that the second anterolateral spine is in fact bifid, not singular as reported by Squires and Demetron (1992). Also, the anterolateral spines are much broader and longer than originally illustrated.

Lophoranina bishopi falls into the category of members of *Lophoranina* which are widened anteriorly (Vega, Cosma et al., 2001), and it may be easily differentiated from other species in the genus. Only two other species have a bifid second anterolateral spine, *L. cristaspina* Vega, Cosma et al., 2001, from the Eocene of Chiapas, and *L. marestiana* from the Eocene of Italy. *Lophoranina bishopi* is differentiated from *L. cristaspina* because *L. cristaspina* has much larger outer orbital spines and much more complex transverse ridges on the posterior portion of the carapace. *Lophoranina marestiana* is narrowed anteriorly and has much smaller orbital and anterolateral spines than does *L. bishopi*.

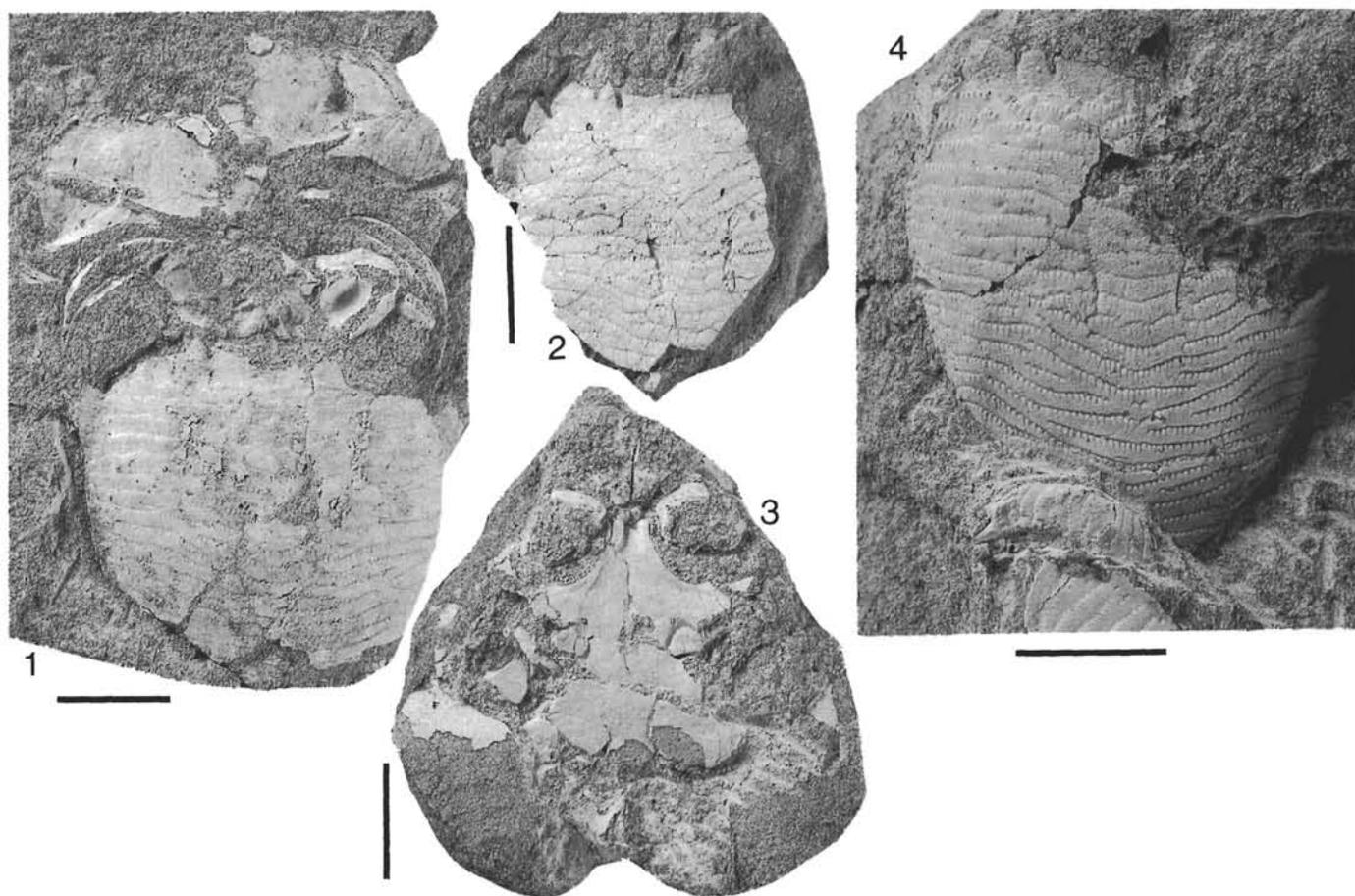


FIGURE 8—*Lophoranina bishopi* Squires and Demetrian, 1992. 1, MHN-UABCS/Te14/50-48, dorsal carapace and chelae; 2, MHN-UABCS/Te14/50-49, partial dorsal carapace showing anterolateral and orbital spines; 3, MHN-UABCS/Te14/50-50, partial sternum; 4, MHN-UABCS/Te14/50-51, dorsal carapace. Scale bars equal to 1 cm.

The other species known from Mexico, *Lophoranina precocious* Feldmann et al., 1996, has broadly spaced, linear, and parallel transverse ridges while those of *L. bishopi* are more closely spaced and have a much more complex pattern.

Section HETEROTREMATA Guinot, 1977
Superfamily CALAPPOIDEA de Haan, 1833
Family HEPATIDAE Stimpson, 1871

Discussion.—Schweitzer and Feldmann (2000a) referred both *Eriosachila*, to be discussed below, and *Matutites* Blow and Manning, 1996, to the Hepatidae sensu stricto. In that same work, they suggested that *Hepaticus americanus* Rathbun, 1935, might be referable to *Matutites*. *Hepaticus americanus* has a similar carapace shape, similar development of regions, and spiny carapace ornament that is typical of *Matutites* and not of *Hepaticus*, which lacks spiny ornamentation on the dorsal carapace and is overall more vaulted and has more inflated regions. Thus, the generic transferral is formalized herein, resulting in the new combination *Matutites americanus* (Rathbun, 1935).

Genus ERIOSACHILA Blow and Manning, 1996

Type species.—*Eriosachila petiti* Blow and Manning, 1996, by monotypy.

Other species.—*Eriosachila bartholomaeensis* (Rathbun, 1919, as *Zanthopsis*); *E. orri* Schweitzer and Feldmann, 2000a, (nomen novum of *Zanthopsis rathbunae* Kooser and Orr, 1973); *E. rossi*

Schweitzer and Feldmann, 2000a; *E. terryi* (Rathbun, 1937; as *Zanthopsis*); *Eriosachila* sp. Vega, Cosma et al., 2001.

Emendation to diagnosis.—Carapace about as wide as long, obovate, surface finely granular. Carapace regions poorly defined; protogastric, hepatic, mesogastric, cardiac, and branchial regions bearing large, spherical swellings. Front narrow, entire or with small projections, occupying about 20–30 percent maximum carapace width. Orbits circular, directed forward or slightly anterolaterally; sometimes with closed fissures; rimmed or with blunt inner and outer orbital spines; fronto-orbital width about half maximum carapace width. Anterolateral margin entire or with four spines or swellings; posterior margin with spines, or sinuous with blunt projections.

Discussion.—Schweitzer and Feldmann (2000a) described the genus *Eriosachila* as possessing an octagonal carapace, a crenulated anterolateral margin with four spines or swellings, large carapace swellings, and a posterolateral margin with spines. The new material is clearly referable to the genus based upon the carapace shape, position of the swellings on the dorsal carapace, shape and size of the orbits, and carapace dimensions. However, the new material differs from all other species within the genus in possessing two closed orbital fissures, an entire anterolateral margin and a posterolateral margin with broad, blunt projections instead of spines. The posterior-most branchial spine of *E. orri* Schweitzer and Feldmann, 2000a, is positioned very close to the posterolateral margin and projects from the carapace beyond the posterolateral margin so that it has the appearance of a posterolateral

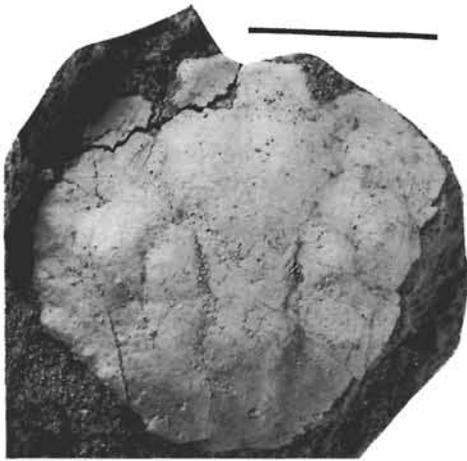


FIGURE 9—*Eriosachila bajaensis* n. sp., dorsal carapace of holotype, MHN-UABCS/Te25/58-1. Scale bar equal to 1 cm.

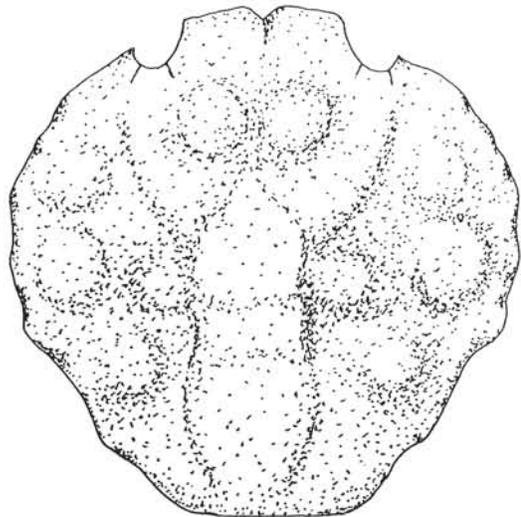


FIGURE 10—Reconstruction of *Eriosachila bajaensis* n. sp.

spine. The new species has a branchial spine in the same position as *E. rossi*; however, it does not project beyond the margin. *Eriosachila terryi* has a crenulated anterolateral margin, and that of the new species appears to be entire but sinuous, similar to that of *E. terryi*. Thus, the differences between the new species and other species of the genus are differences of gradation and are not sufficient to erect a new genus to accommodate the new material.

Rathbun (1919) described *Zanthopsis bartholomaeensis* from Eocene rocks of the West Indies. Examination of the description and illustrations of the holotype and sole specimen suggest that it must be referred to the genus *Eriosachila*. The species possesses the characteristic carapace shape and arrangement of regions and possesses large, blunt tubercles at the anterolateral corner and on the posterolateral margin, ornamentation typical of the genus. *Eriosachila bartholomaeensis* is most like *E. rossi* in possessing broadly inflated carapace regions and blunt ornamentation. The referral of *E. bartholomaeensis* to *Eriosachila* as well as the description of the new species suggests that the genus was well-established in the Americas by the Eocene.

ERIOSACHILA BAJAENSIS new species
Figures 9, 10

Diagnosis.—Carapace about as long as wide, L/W = 0.96; front weakly projected beyond orbits, with axial notch; orbits with two closed fissures; anterolateral margin entire; posterolateral margin sinuous, with two broad, blunt projections; protogastric, mesogastric, cardiac, hepatic, and branchial regions ornamented with large spherical swellings.

Description.—Carapace about as long as wide, L/W = 0.96, obovate, narrowing posteriorly, widest about half the distance posteriorly on carapace; regions poorly defined; protogastric, mesogastric, cardiac, hepatic, and branchial regions ornamented with large spherical swellings; carapace surface finely granular; strongly vaulted longitudinally and flattened transversely.

Front weakly triangular, projecting slightly beyond orbits, notched axially, margin slightly thickened, about 30 percent maximum carapace width. Orbits circular, directed forward; 2 closed fissures, inner fissure slightly longer and more deeply impressed; fronto-orbital width about half maximum carapace width.

Anterolateral margins strongly convex, appearing to be entire and weakly sinuous; small blunt projection at anterolateral corner,

extending short distance onto dorsal carapace. Posterolateral margin very sinuous; with two broad, blunt projections; rimmed. Posterior margin concave, rimmed, about 30 percent maximum carapace width, weakly developed blunt swellings at posterolateral corners.

Protogastric regions elevated, inflated; with prominent elongate central swelling, swelling oriented parallel to axis of carapace. Mesogastric region poorly delineated, with large spherical swelling situated between and posterior to protogastric swellings. Urogastric region depressed, short, defined laterally by relatively deep branchiocardiac grooves, margins concave. Cardiac region inflated, elongate, oriented parallel to axis, most inflated anteriorly. Urogastric region depressed, not well defined.

Hepatic regions flattened, with small swelling near anterolateral margin. Branchial regions narrow, elongate, narrowing distally; large swelling anteriorly, adjacent to protogastric swellings; small, sharp swelling posteriorly, adjacent to cardiac swelling.

Venter and appendages unknown.

Etymology.—The trivial name refers to the occurrence of the new species in Baja California, Mexico.

Types.—The holotype, MHN-UABCS/Te25/58-1 and one paratype, MHN-UABCS.

Measurements.—Measurements (in mm) taken on the dorsal carapace of the holotype of *Eriosachila bajaensis*: Maximum width (W1), 14.9; maximum length (L), 14.7; frontal width (W2), 4.4; fronto-orbital width (W3), 8.0; posterior width (W4), 5.0.

Occurrence.—The specimens were collected from the Eocene Tepetate Formation, at Cañada El Mangle, 2 km west of Cañada Palo Alto.

Discussion.—The new species is represented by two nearly complete dorsal carapaces. More complete specimens will be necessary to ascertain the true nature of the anterolateral margin. *Eriosachila bajaensis* differs from all other species of the genus in lacking spines on either the anterolateral or posterolateral margins and in possessing two closed orbital fissures. It differs from *Eriosachila* sp., reported by Vega, Cosma et al. (2001) because *Eriosachila* sp. has better developed and more inflated areas on the protogastric and branchial regions.

All known species of *Eriosachila* have been recovered from Eocene rocks. *Eriosachila petiti* was collected from the middle Eocene Santee Limestone of eastern North America; *Eriosachila* sp. is known from middle Eocene rocks of Chiapas, Mexico; *E.*

terryi is known from the late Eocene of Panama; *E. bartholomaeensis* is known from Eocene rocks of the Caribbean, and *E. rossi* and *E. orri* are known from the late Eocene west coast of North America.

Superfamily MAJOIDEA Samouelle, 1819
Family INACHIDAE MacLeay, 1838
Genus OREGONIA Dana, 1851b

Type species.—*Oregonia gracilis* Dana, 1852, by subsequent designation.

OREGONIA SPINIFERA new species
Figures 11, 12

Diagnosis.—Pyriform majoid with long rostrum of two contiguous elements, tiny preorbital spine, weakly defined regions, and row of meral spines on third pereiopod.

Description.—Carapace pyriform, about 1.5 times as long as wide, moderately inflated, regions weakly delineated.

Rostrum bifid, slender, tapering distally; rostral horns contiguous, about 9 percent total carapace length. Orbits on frontal prolongation with preorbital spine a small node, directed forward; postorbital hood about one half total orbital length, well developed, terminates posteriorly in laterally directed, triangular, postorbital spine. Hepatic spine well developed, triangular, directed anteriorly. Remainder of outline poorly preserved, appears to be smoothly rounded.

Frontal region flattened with 2 small axial spines. Protogastric regions subcircular, weakly inflated with single spine along inner margin; weakly distinguished from narrow, elongate mesogastric region which bears single large, axial spine at level of maximum width. Urogastric region very narrow, defined by deep, gently curved branchiocardiac furrows. Cardiac region depressed, poorly defined, with pair of nodes situated adjacent midline. Intestinal region weakly domed, narrower than cardiac. Branchial regions not subdivided, inflated with small nodes or spines situated on elevations. Prominent nodes at ends of posterior margin.

Venter and abdomen unknown.

Chelae not preserved. Pereiopods 2–5 partially preserved, long, slender; leg 2 poorly preserved; legs 3–5 become shorter posteriorly; leg 3 with row of at least 7 posteriorly-directed spines.

Etymology.—The trivial name alludes to the row of meral spines on the third pereiopod which distinguishes this species from other members of the genus.

Types.—The holotype, composed of a part and counterpart, MHN-UABCS/SJ2/15-1764a and b.

Measurements.—Carapace length, ca. 30.8 mm; carapace width, ca. 21.4.

Occurrence.—The specimen was collected from the Oligocene El Cien Formation near San Juan de la Costa.

Discussion.—Generic placement of fossil spider crabs is often difficult because definitive criteria are rarely available for study. In addition to the morphology of the male pleopod and the mouth parts, the form of the terminal segments of the male abdomen and the form of the basal articles of the antennae are extremely important in distinguishing *Oregonia* spp. from other crabs having a similar carapace outline (Garth, 1958). These features are not available in the specimen at hand and indeed are rarely preserved in fossils. However, there are several features that are present in the sole specimen referred to this new species that support placement in the genus. The elongate rostrum comprised of two slender, contiguous elements; the hood forming an incomplete orbit; and the distinct postorbital spine, well separated from the hood; and the absence of prehensile terminations on the pereiopods which decrease in size posteriorly are all characters that *Oregonia spinifera* shares with the type species, *O. gracilis* (Rathbun, 1925;

Garth, 1958; Sakai, 1976). The two features present on *O. spinifera* that are not seen on other species within the genus are the presence of a small preorbital node or spine and the row of meral spines on the third pereiopod. These are taken to be important species-level characters and, because this species is the only one known from the fossil record, may suggest that ancestral forms were more spinose than the extant ones.

Living representatives of the genus are known by two species in the eastern Pacific, *Oregonia gracilis* and *O. bifurca* Rathbun, 1902. Their combined geographic range extends from the Bering Sea to Monterey Bay, California (Garth, 1958, p. 136). The genus is also known from Japan, where the type species as well as *O. mutsuensis* Yokoya, 1928, have been described. This distributional pattern is typical of the North Pacific pattern of distribution noted for several other fossil decapod genera (Schweitzer, 2001b).

Superfamily CANCROIDEA Latreille, 1802
Family ATELECYCLIDAE Ortmann, 1893

Discussion.—The Atelecyclidae has recently been re-examined (Salva and Feldmann, 2001) and restricted to the genera *Atelecyclus* Leach, 1814, *Peltarion* Jacquinet, 1847, *Krunopeltarion* Števčić, 1993, *Pteropeltarion* Dell, 1972, and *Trichopeltarion* A. Milne Edwards, 1880 (= *Trachycarcinus* Faxon, 1893). Unifying characteristics of the family members were identified on the basis of a cladistic analysis of these genera as well as those in the closely related Belliidae Dana, 1852, Thiidae Dana, 1852, and Cheiragonidae Ortmann, 1893. The characters of the dorsal carapace that were identified in the cladistic analysis, and that are relevant to the study of fossil atelecyclids, include development of an ovoid to pentagonal outline of the dorsal carapace, possession of spinose orbital margins, and lateral margins bearing typically compound spines. The specimen under consideration herein clearly bears the characteristics of the family; however, the outline is markedly ovoid and wider than long. Only species of *Atelecyclus* are markedly wider than long. Although a few species within the family are slightly wider than long, typically they are equant or somewhat longer than wide. The front of typical atelecyclids is trifid (Schweitzer and Salva, 2000), an additional character exhibited by the Mexican material. Of these characters of the dorsal carapace, the ones that are most distinctive are the development of compound spines on the anterolateral margin and the presence of a trifid front. A cursory examination of representative crabs in other decapod families indicates that compound spines are common in the Atelecyclidae, present in some genera within the Cancridae (Nations, 1975) and Majidae (Rathbun, 1925), and very rare or absent in other families. The combination of compound spines and a trifid front, although the specimen under consideration is represented only by a single broken specimen, permits certain placement within the Atelecyclidae.

Genus LEVICYCLUS new genus

Type species.—*Levicyclus tepetate* new species, by monotypy.

Etymology.—The generic name is derived from the Latin words, *levis* = smooth, or bald, alluding to the generally smooth nature of the carapace; and *cyclus*, the Latin equivalent of the Greek *kyklos* = circle, one of the root words of the family name.

Description.—Atelecyclid much wider than long, with thickened orbital rim, very large suborbital spine at outer corner of orbit, reduced compound anterolateral spines, and generally smooth carapace surface with undefined regions.

Discussion.—Although the characters described above clearly place *Levicyclus* within the Atelecyclidae, other aspects of the morphology preclude assignment to any of the recognized genera. The outline of *L. tepetate* is very much like that of species of *Atelecyclus*; however, the latter have anterolateral margins bearing

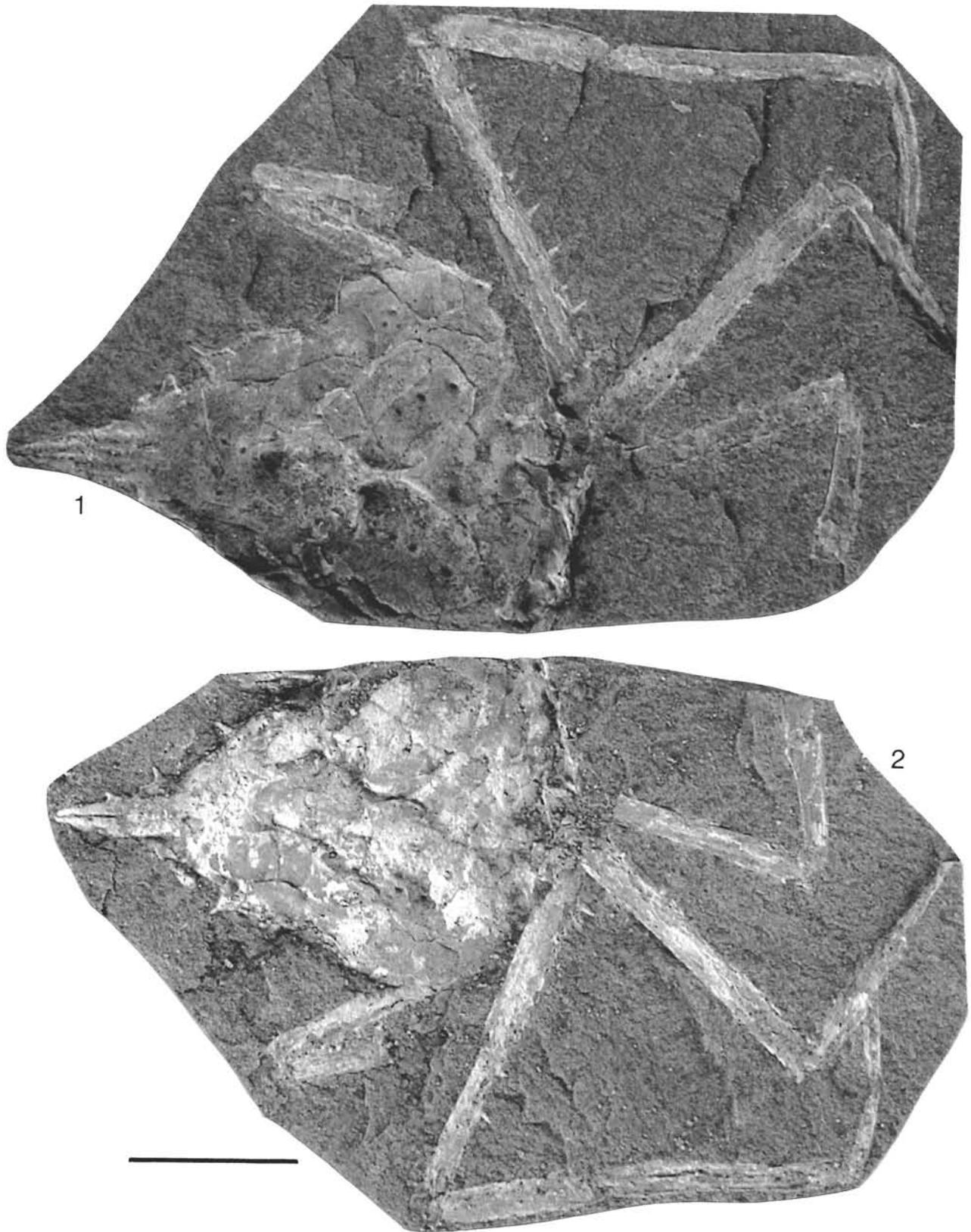


FIGURE 11—*Oregonia spinifera* n. sp., holotype, MHN- UABCS/SJ2/15-1764a and b. 1, counterpart (a) and, 2, part (b). Scale bar equal to 1 cm.

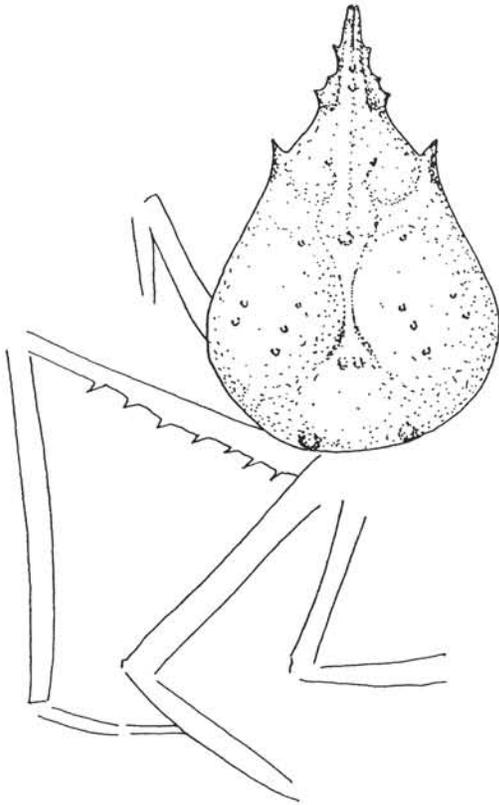


FIGURE 12—Reconstruction of *Oregonia spinifera* n. sp.

very regular, large, triangular compound spines and carapace surfaces that are granular. The prominent, thickened, orbital rim developed on *L. tepetate*, although fundamentally a modified spine, is unlike the orbital structure seen on representatives of other genera. Likewise no other atelecyclids are known that bear such

a prominent suborbital spine as does the new species. Anterolateral spines are reduced in size in *Levicyclus* as they are in *Peltarion* spp. but the genus *Peltarion* is characterized by very well defined carapace regions. In fact, the smooth nature of the carapace surface in *L. tepetate* immediately distinguishes it from species in any of the other atelecyclid genera. *Trichopeltarion greggi* Dell, 1969, can range from nearly smooth to coarsely granular; however, the branchiocardiac groove is always very deep and well defined in that species. Therefore, the combination of characters defining *Levicyclus* readily distinguish it from all other genera within the family.

LEVICYCLUS TEPETATE new species
Figures 13, 14

Diagnosis.—As for the genus.

Description.—Moderate-sized brachyuran; carapace transversely ovoid, carapace length estimated to be 65 percent maximum width, moderately vaulted longitudinally, weakly vaulted transversely; generally smooth; anterolateral margin finely spinose.

Front narrow, approximately 11 percent maximum width measured at posterior corner of anterolateral margin, trifid, extending slightly beyond orbits. Axial spine short, broad, downturned almost at right angles to carapace surface, axially sulcate; lateral rostral spines circular in cross section, prominent, directed anteriorly. Orbits large, fronto-orbital width 41 percent maximum width, directed anterolaterally; prominent, narrow, upturned rim developed as broad triangular projection from outer rostral spine to shallow, open fissure situated laterally from midpoint of orbit; second fissure situated at outer corner of orbit. Large, forward-directed spine situated ventral to outer orbital margin; remainder of ventral orbital margin not preserved.

Anterolateral margin smoothly concave between orbit and first anterolateral spine, then weakly convex and spinose throughout remainder of length; spines developed as small, simple forms or as larger, complex spines bearing from one to seven tiny spines. Posterolateral margin smoothly convex, not spinose. Posterior margin not preserved.

Carapace generally smoothly convex. Epibranchial regions defined as transversely ovoid swellings between axial sulcus and

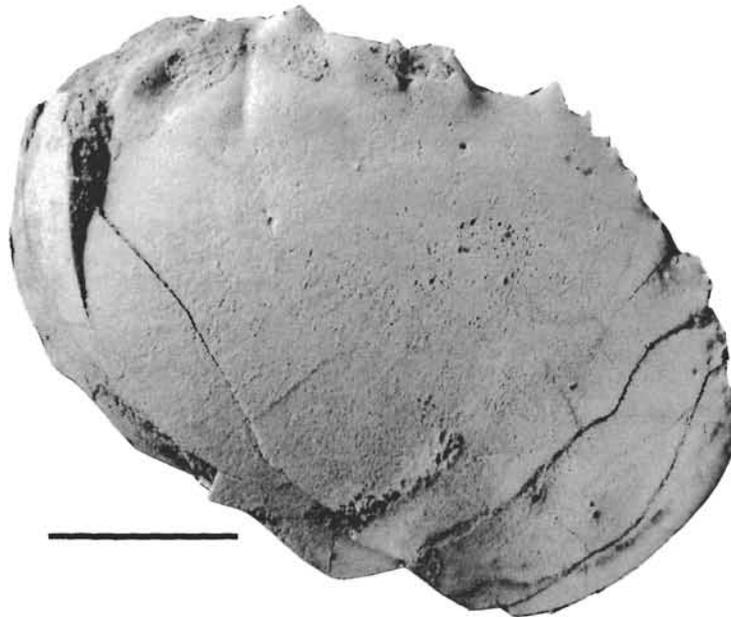


FIGURE 13—*Levicyclus tepetate* n. sp., holotype, MHN-UABCS/Te3/39-4-288. Scale bar equal to 1 cm.

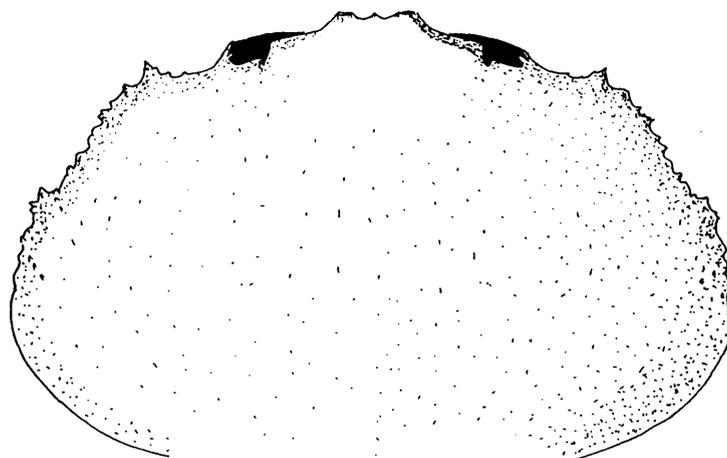


FIGURE 14—Reconstruction of *Levicyclus tepetate* n. sp.

depressed region posterior to orbital rim; remainder of carapace regions undefined.

Etymology.—The trivial name refers to the Eocene Tepetate Formation from which the holotype was collected.

Type.—The holotype, and sole specimen, MHN-UABCS/Te3/39-4-288.

Measurements.—Carapace length, ca. 27.6 mm; carapace width, ca. 53.4 mm; frontal width, 5.9 mm; fronto-orbital width, 21.6 mm.

Occurrence.—The sole specimen was collected from Cañada Palo Alto, Arroyo Palo Alto, Baja California Sur, Mexico, from the top of the Campanile Bed, in the middle Eocene Tepetate Formation, 5 November 1999, by Gerardo González-Barba.

Discussion.—The measurements of width and length of the specimen must be taken as estimates owing to the broken and incomplete condition of the carapace. Of particular note, the reconstruction of the carapace, from which it was concluded that the width was much greater than the length, was prepared by replicating and reversing the outline and features of the right side. Extreme care was exercised to assure as accurate a reconstruction as possible; but, slight rotation of the two sides when preparing the drawing would result in a different outline. However, no matter how the outline is reconstructed, the carapace would be much wider than long.

The occurrence of *Levicyclus tepetate* in middle Eocene rocks of Baja California Sur represents the first record of the family Atelecyclidae in the fossil record of Mexico. Living atelecyclids are, however, known from the region. *Trichopeltarion nobile* A. Milne Edwards, 1880, is known from the Gulf of Mexico as are *Peltarion spinulosum* (White, 1843) and *P. dextrum* (Rathbun, 1898); *T. corallinus* Faxon, 1893, occurs along the Pacific coast south of Baja California (Salva and Feldmann, 2001).

Family PORTUNIDAE Rafinesque, 1815

Genus NECRONECTES A. Milne Edwards, 1881

[=*Gatunia* Rathbun, 1919 (type species, *Gatunia proavita*)]

Type species.—*Necronectes vidalianus* A. Milne Edwards, 1881, p. 1, pl. 21, fig. 1, by original designation.

Included species.—*Necronectes beaumonti* (A. Milne Edwards, 1864), as *Cancer*; *N. drydeni* Rathbun, 1935; *N. nodosa* new species herein; *N. proavitus* (Rathbun, 1919), as *Gatunia*; *N. schafferi* Glaessner, 1928; *N. summus* Collins and Donovan, 1995; *N. tajinensis* Vega, Feldmann, Villalobos-Hiriart, and Gío-Argíez, 1999; *N. vicksburgensis* (Stenzel, 1935), as *Portunites* = *N. vaughani* Rathbun, 1935 (fide Rathbun, 1936). *Necronectes?* *boeckhi* (Lörenthey, 1898), as *Cancer* is probably better referred

to the Cancridae; however, confirmation must await examination of the type material.

NECRONECTES NODOSA new species

Figures 15, 16

Diagnosis.—Typical *Necronectes* with anterolateral spines triangular anteriorly and rectilinear posteriorly; weak branchial ridge defined by arcuate row of discrete swellings.

Description.—Moderate-sized portunid; approximately 1.6 times as wide as long; weakly vaulted transversely and longitudinally; regions poorly defined.

Front moderately broad, approximately 22 percent maximum width measured at last anterolateral spine situated at 68 percent of length measured from front; axially sulcate and bearing 6 small, triangular spines, including inner orbital spine, decreasing in size slightly laterally. Orbits arcuate, deepest near lateral margin at position of shallow orbital fissure; fronto-orbital width about 41 percent maximum width. Anterolateral margin long, arcuate, bearing eight anterolateral spines including outer orbital spine; outer orbital and adjacent spines closely spaced, triangular; third spine rounded, apex directed anteriorly; fourth and fifth spines triangular with sharp, forward directed tips; sixth and seventh spines rectilinear with forward curving, rounded terminations; eighth spine triangular with laterally directed, sharp termination and distinct axial ridge extending onto branchial region. Posterolateral margins strongly convergent with subtle reentrant lateral to straight posterior margin which is approximately 18 percent total width; narrow, distinct rim borders posterolateral and posterior margins.

Carapace regions subtly expressed. Frontal region slightly depressed below carapace surface, defined by arcuate transverse ridge extending in width approximately between midpoints of orbits. Mesogastric region vase-shaped; anterior portion narrow, parallel sided; posterior portion widens abruptly then narrows in broader arc. Urogastric region narrow. Cardiac region circular, slightly narrower than maximum width of mesogastric region. Hepatic and branchial regions undifferentiated. Arcuate row of four subtle swellings extend in convex-forward arc from base of anterolateral spine 6 to gastric muscle scars. Pair of subtle, broadly arched nodes situated adjacent urogastric region and another, similar pair situated near margin just lateral to posterolateral inflection.

Venter and abdomen unknown.

Appendages represented by small basal elements of antennae and antennules and partial remains of pereiopods. Chelae long, slender, fingers appear to be shorter than hand, gently curved,

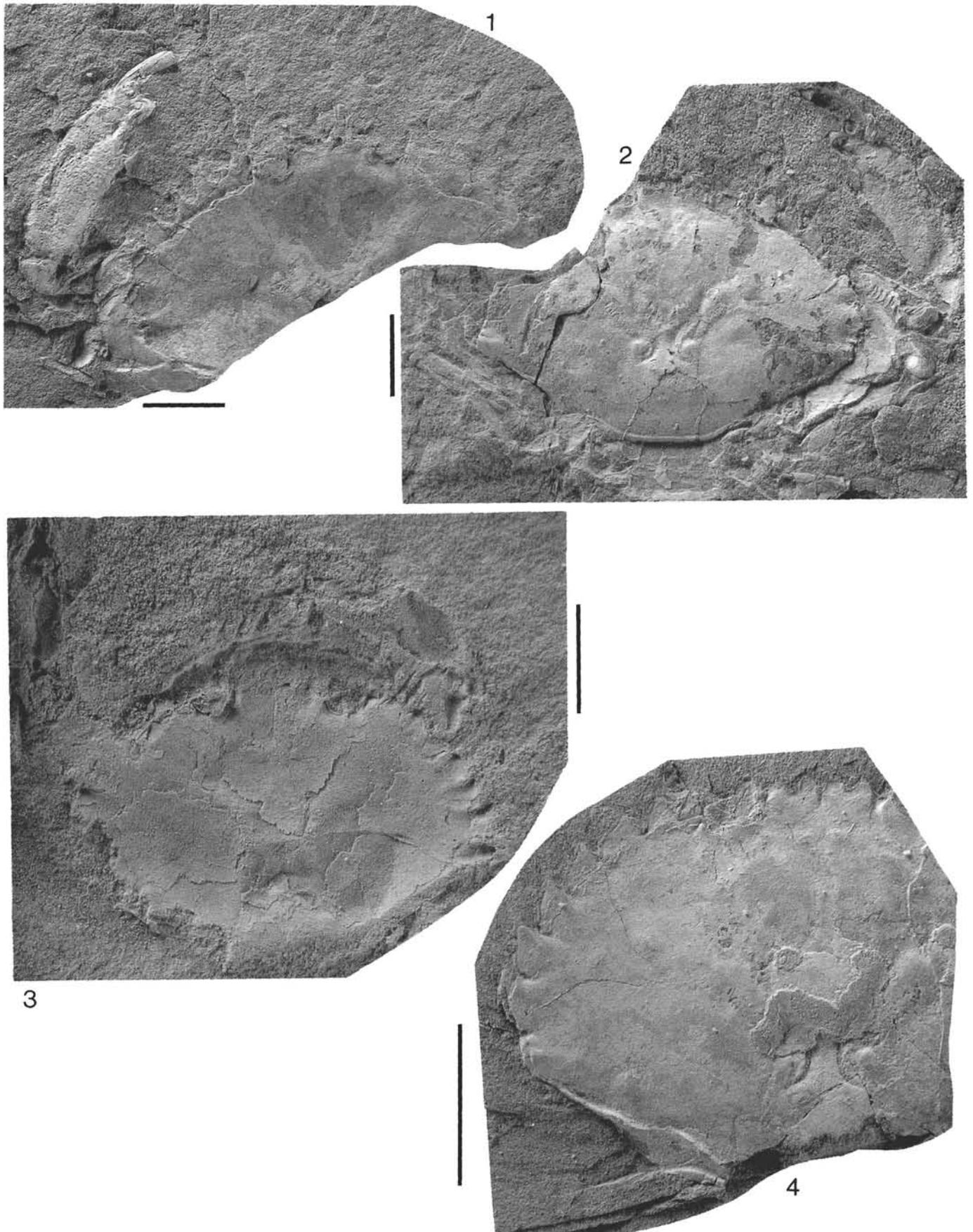


FIGURE 15—*Necronectes nodosa* n. sp. 1, counterpart of paratype, MHN-UABCS/SJ5/6-689a; 2, part of paratype, UABCS/SJ5/6-689b; 3, paratype MHN-UABCS/SJ5/6-691, showing detail of orbits and anterolateral spines; 4, holotype MHN-UABCS/SJ5/6-690, showing excellent anterolateral margin. Scale bars equal to 1 cm.

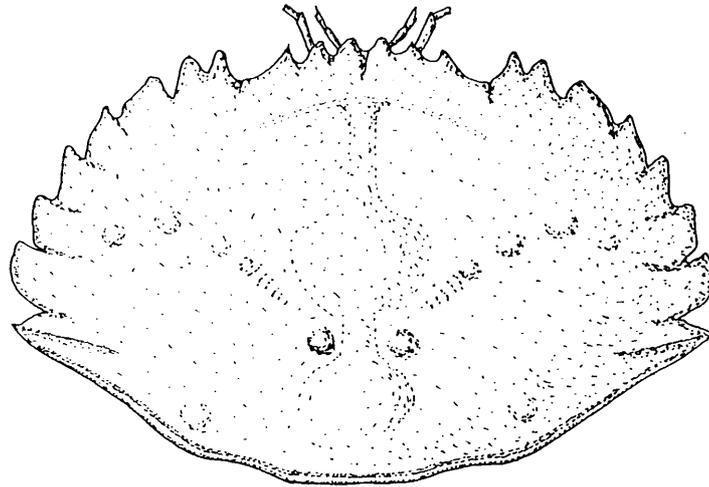


FIGURE 16—Reconstruction of *Necronectes nodosa* n. sp. Excellent preservation makes reconstruction of the antennae and antennules possible.

apparently not keeled. Basal elements of pereopods 2–5 slender. Propodus and dactylus of pereopod 5 strongly broadened and flattened into paddle-shape.

Etymology.—The trivial name *nodosa* is the Latin feminine form of *nodosus* meaning “full of knots” alluding to the diagnostic subtle row of nodes that crosses the branchial region.

Types.—The holotype is MHN-UABCS/SJ5/6-690 and three paratypes are MHN-UABCS/SJ5/6-689 and 691.

Measurements.—MHN-UABCS/SJ5/6-690 carapace length, ca. 30.2 mm; carapace width, 48.2 mm; frontal width, 10.4 mm; fronto-orbital width, 8.6 mm. MHN-UABCS/SJ5/6-689b carapace length, 32.6 mm; carapace width, ca. 52.2 mm. Paratype MHN-UABCS/SJ5/6-691 carapace length, 17.9 mm; carapace width, ca. 30.9 mm.

Discussion.—The genus *Necronectes* is characterized by species bearing eight anterolateral spines, including the outer orbital spine, four frontal spines in addition to the inner orbital spines, and a relatively smooth carapace on which the axial regions are best developed. The last anterolateral spine is either the smallest or nearly the smallest of the anterolateral spines. The transverse ridge, characteristic of many portunid genera, is either absent or very weakly developed. Finally, the anterolateral margin tends to be longer than the posterolateral margin and the latter is nearly straight and steeply inclined toward the posterior margin. Of the characters that distinguish *Necronectes* from other portunids, perhaps the three that are most distinctive are the absence of a well-developed transverse ridge, the number of spines on the anterolateral margin, and the degree of development of the last anterolateral spine. In these characters, *Necronectes nodosa* fits the definition well and the placement is certain.

All of the species assigned to this genus are represented by carapace material, with the exception of *N. summus*. *Necronectes summus* does exhibit the very massive, generally smooth claws suggesting affinities with *N. proavitus*. In making comparisons with the species represented by carapace material, *N. nodosa* is quite distinctive in having a series of subtle nodes in an array that is similar to the transverse ridges of some other portunids, thus, the species is certainly distinct. The relative development of the spines is also distinctive on the new species. The first two spines, the outer orbital and first anterolateral spine, are bluntly triangular and the next five spines exhibit short anterior margins and longer, often flattened posterior margins which is unique among the known species.

In comparing *Necronectes nodosa* to the other recognized species, it would appear that *N.? boeckhi* is probably not appropriately placed within this genus. The placement was originally questioned by Lörenthey and Beurlen (1929). It would appear that the original placement within the genus *Cancer* is more appropriate. Although the specimen, with paired anterolateral spines, distinct carapace regions, and a long, sinuous posterolateral margin, probably does not belong to *Cancer* sensu stricto, it probably is a member of the Cancridae (Schweitzer and Feldmann, 2000c).

The description of this new species represents the second species of *Necronectes* known from Mexico and the first certain notice of the genus in the Eocene. The late lower Eocene occurrence in the Tepatete Formation firmly extends the genus into the Eocene. Glaessner (1969) indicated a geological range of ?upper Eocene to Miocene for the genus; however, the sole Eocene species was *N.? boeckhi* which cannot be referred to the genus with any confidence. Thus, the earliest record of *Necronectes* is from the Eocene of Baja California, Mexico. In the Oligocene, the genus is known from *N. vicksburgensis* in Mississippi and Florida (Rathbun, 1935) and *N. summus* from Antigua (Collins and Donovan, 1995). The remainder of the verified occurrences of the genus are Miocene in age. By that time, the genus had dispersed to include a broadly Tethyan distribution in Ecuador (Feldmann, Chirino-Galvez et al., 1993), Panama (Rathbun, 1919), Mexico (Vega et al., 1999), Maryland (Rathbun, 1935), France (A. Milne Edwards, 1881), Austria (Glaessner, 1928), and Hungary (Lörenthey, 1898; Müller, 1984).

No post-Miocene occurrences are now known.

Family RETROPLUMIDAE Gill, 1894
Genus ARCHAEOPUS Rathbun, 1908

Type species.—*Archaeopus antennatus* Rathbun, 1908.

Other species.—*Archaeopus ezoensis* (Nagao, 1941); *A. lunicarina* Schweitzer and Feldman, 2001b; *A. vancouverensis* (Woodward, 1896); *A. mexicanus* new species herein.

ARCHAEOPUS MEXICANUS new species
Figures 17, 18

Diagnosis.—Carapace quadrate, widest about three-quarters the distance posteriorly on carapace; post-orbital spine directed forward; transverse carapace ridges discontinuous, protogastric, mesogastric, and branchial ridges well-developed; epibranchial region with one spherical and one ovate swelling; posterior margin concave.

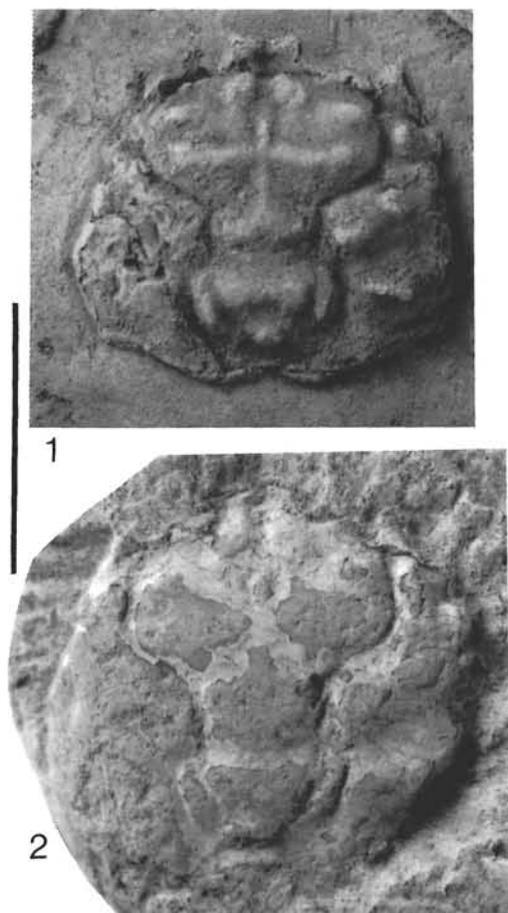


FIGURE 17—*Archaeopus mexicanus* n. sp. 1, holotype IGM-7953, dorsal carapace with detailed ornamentation; 2, paratype IGM-7954, badly weathered dorsal carapace showing much less ornamentation. Scale bar equal to 1 cm.

Description.—Carapace quadrate, wider than long, L/W about 0.85, widest about three-quarters the distance posteriorly on carapace; weakly vaulted transversely, moderately vaulted longitudinally; regions well-defined by deep grooves; regions ornamented by elevated tubercles and ridges.

Rostrum projected well in advance of orbits, concave margin, axially sulcate, weakly downturned. Orbital margins wide, sinuous, with blunt medial projection, terminating laterally in prominent, forward-directed postorbital spine. Lateral margins convex, sinuous, with blunt protuberance posterior to postorbital spine. Posterolateral margins converging distally, sinuous, weakly rimmed. Posterior margin concave, sinuous.

Protogastric regions with 2 anterior swellings just posterior to rostrum and to midlength of orbit; transverse ridge situated about three-quarters distance posteriorly on region, ridges very weakly concave forward. Mesogastric region with long, straight, anterior process; posterior portion of region inflated transversely. Urogastric region short, poorly defined. Cardiac region widest of all axial regions; triangular, apex directed posteriorly; with lobose swellings parallel to lateral margins. Intestinal region flattened, poorly developed. Cervical groove deepest at midwidth, indistinct near lateral margins and across axial regions.

Hepatic regions with longitudinal ovoid swellings centrally, small. Epibranchial region with 2 swellings; outer swelling spherical; inner swelling ovate, transverse, at same level as transverse swelling of mesogastric regions, forming discontinuous transverse

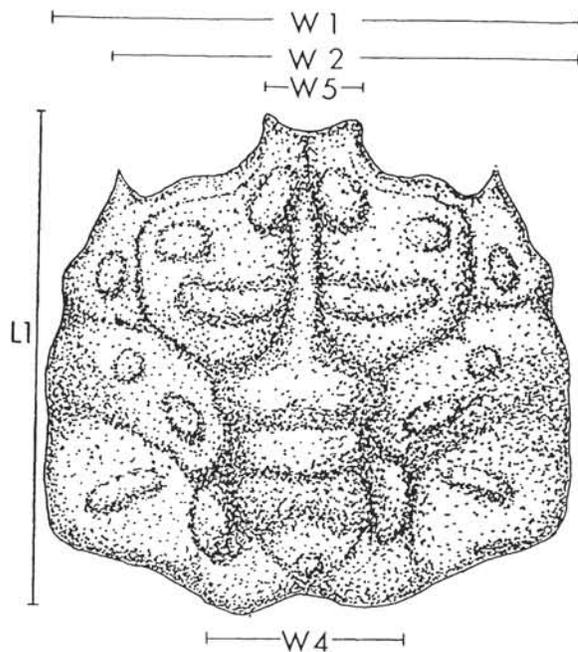


FIGURE 18—Reconstruction of *Archaeopus mexicanus* n. sp., showing position and orientation of measurements taken.

carapace ridge. Mesobranchial and metabranchial regions not differentiated, with transverse swelling at level with transverse swelling on cardiac region, forming discontinuous transverse carapace ridge.

Venter and appendages unknown.

Etymology.—The trivial name denotes the occurrence of the specimens in Baja California Norte, Mexico.

Types.—Three specimens, the holotype UNAM IGM-7953, and two paratypes, UNAM IGM-7954 and 7955.

Measurements.—Measurements (in mm) taken on the dorsal carapace of the holotype, IGM-1953: maximum width (W1), 15.4; maximum length (L1), 13.0; fronto-orbital width (W2), 11.0; frontal width (W5), 2.6; posterior width (W4), 6.6. Position and orientation of measurements taken are illustrated on Figure 18.

Occurrence.—The specimens were collected from Sal Sipuedes, Ensenada area, Baja California Norte, Mexico, from Upper Cretaceous rocks questionably referred to the Rosario Formation.

Discussion.—*Archaeopus* has not previously been reported from a locality as far south as Baja California. The new species extends the range of the genus from the cool temperate, northern North Pacific Rim to the warm temperate, mid-Pacific area. Both specimens are probably molts, as only the dorsal carapace is preserved.

Archaeopus mexicanus is distinguished from all other members of the genus in having a quadrate carapace that attains its maximum width approximately three-quarters the distance posteriorly on the carapace. The transverse ridges of *A. vancouverensis* are much better developed and are more continuous than those of *A. mexicanus*. *Archaeopus antennatus* is markedly wider than long, and the transverse carapace ridges are more poorly developed than are those of *A. mexicanus*. The protogastric ridges of *A. lunicarina* are markedly concave forward, while those of *A. mexicanus* are weakly concave forward. The transverse carapace ridges of *A. ezoensis* are poorly developed and the carapace is sub-circular, both of which differentiate that species from *A. mexicanus* which has well-developed transverse carapace ridges and a quadrate carapace.

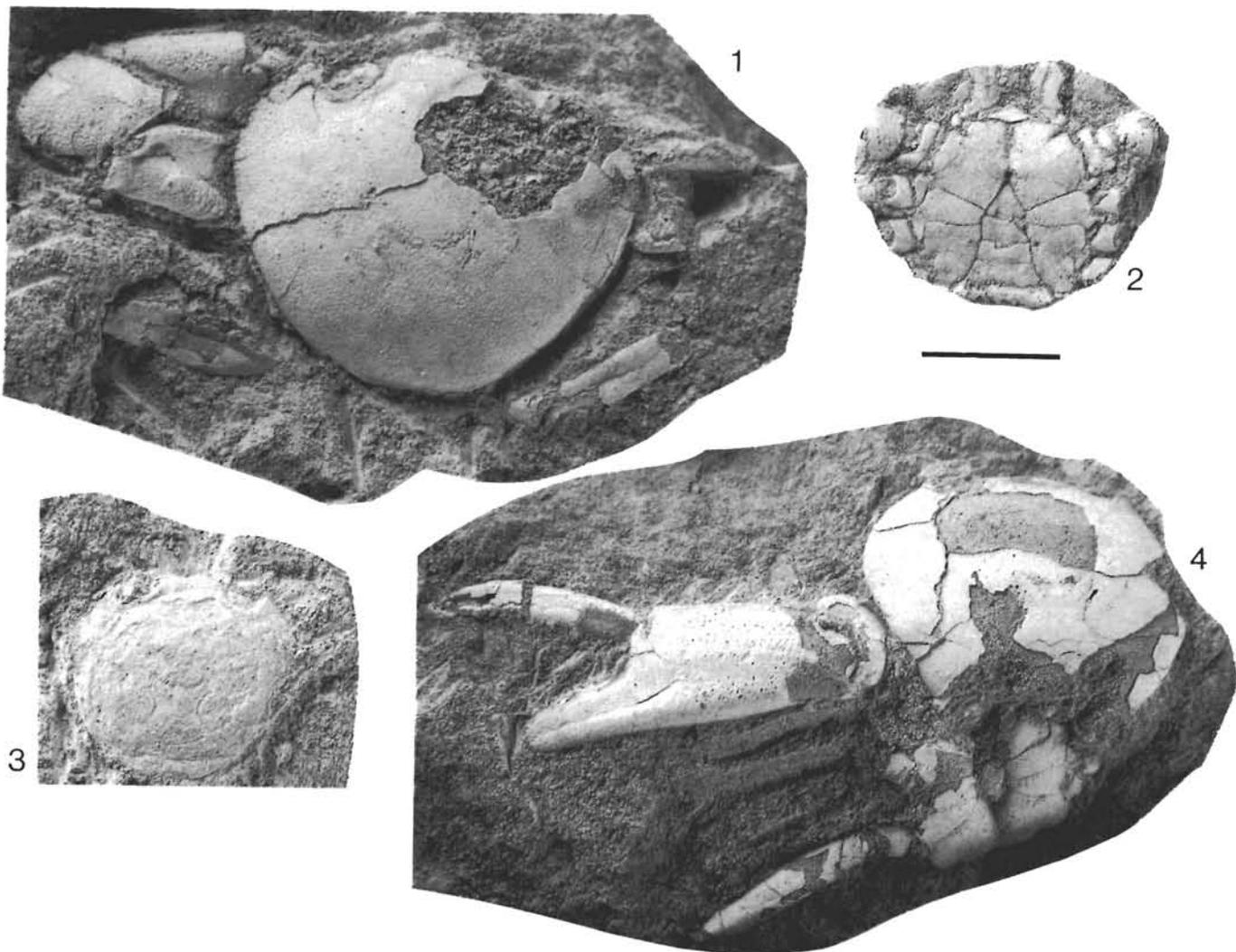


FIGURE 19—*Amydrocarcinus dantei* n. gen. and sp. 1, holotype, MHN-UABCS/Te14/43-32; 2, paratype, MHN-UABCS/Te14/43-33, male sternum and abdomen; 3, paratype, MHN-UABCS/Te14/43-37, badly weathered carapace with well preserved orbital margins; 4, paratype, MHN-UABCS/Te14/43-30, dorsal carapace, major chela, and ventral surface in molt position. Scale bar equal to 1 cm.

Superfamily XANTHOIDEA MacLeay, 1838
 Family XANTHIDAE sensu lato MacLeay, 1838
 AMYDROCARCINUS new genus

Diagnosis.—As for species.

Description.—As for species.

Etymology.—The name is derived from the Greek word *amydros*, meaning indistinct, and the Greek word *karkinos*, meaning crab, referring to the indistinct ornamentation of the dorsal carapace, carapace margins, and claws of the new taxon.

Occurrence.—As for species.

Discussion.—The new genus is clearly referable to the Xanthoidea based upon its shape, the development of the carapace regions, the straight front, the shape of the sternum as a whole and the individual sternites, the shape of the chelae, and the relative size of pereopods 2–5. However, placement within a family of the Xanthoidea is difficult. Examination of numerous works on fossil and extant xanthids indicates that *Amydrocarcinus* cannot be reasonably accommodated in any existing family (see Rathbun, 1930a; Sakai, 1976; Serène, 1984; Williams, 1984; numerous works by Karasawa, Müller, Collins, Glaessner, Guinot). The relatively smooth carapace and poorly developed carapace regions

are typical of the Carpiliidae Ortmann, 1893, and the Trapeziidae Miers, 1886; however, the new genus cannot be placed within either of those families. The Trapeziidae are characterized by having male abdominal somites 3–5 fused (Serène, 1984), while the new genus has all male abdominal somites free. Within the Trapeziidae, the front and anterolateral margins are serrate or spined, and the orbits are located on the frontal corners of the carapace and are directed anterolaterally. In *Amydrocarcinus*, the front and anterolateral margins are smooth or finely granular and the orbits are not located on the margins of the frontal region of the carapace. Within the Carpiliidae, the dorsal carapace is strongly convex and usually completely smooth, the front is spined or triangular, and there is a swelling at the anterolateral corner that often extends onto the dorsal carapace (Serène, 1984; Schweitzer, 2001a). In *Amydrocarcinus*, the dorsal carapace is only moderately vaulted, the regions are defined albeit weakly, the front is straight, and there is no swelling at the posterolateral corner.

Other families within the Xanthoidea cannot accommodate the new genus. The Xanthidae MacLeay, 1838 sensu stricto; Panopeidae Ortmann, 1893, Pilumnidae Samouelle, 1819; Menippidae Ortmann, 1893; Platyxanthidae Guinot, 1977; Goneplacidae

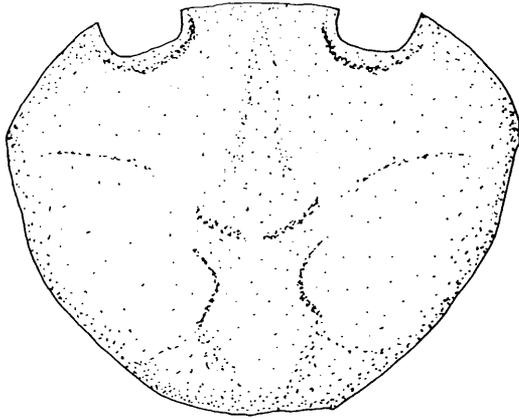


FIGURE 20—Reconstruction of *Amydrocarcinus dantei* n. gen. and sp.

MacLeay, 1838; Hexapodidae Miers, 1886 each have characteristics that preclude placement of the new genus within them. All except the Hexapodidae and the Goneplacidae typically have well-defined carapace regions and spined or lobate fronts and anterolateral margins, which the new genus lacks. The Hexapodidae are characterized by rectangular carapaces, fused male abdominal somites, and possession of only four pairs of walking legs and seven sternites (Manning and Holthuis, 1981; Schweitzer and Feldmann, 2001a). *Amydrocarcinus* has eight sternites, no fusion of abdominal somites, and an ovate carapace, thus excluding it from the Hexapodidae. The Goneplacidae encompasses two general morphologies: those crabs with a hexagonal carapace, extremely broad orbits, a very narrow front, and usually at least one anterolateral spine, and those that resemble xanthids *sensu lato* in the shape of the carapace and carapace regions and the spiny nature of the anterolateral margins (Schweitzer, 2001a). *Amydrocarcinus* lacks extremely elongate orbits and spines on the anterolateral margins and has a broad front, excluding it from the Goneplacidae. However, more work is needed on the definitional bases of the Goneplacidae to fully resolve the placement of this genus. Thus, we have placed the new genus within the Xanthidae *sensu lato* awaiting further work on the fossil xanthoids, currently in progress by Schweitzer and Feldmann.

AMYDROCARCINUS DANTEI new species
Figures 19, 20

Diagnosis.—Carapace ovoid; surface finely granular; regions poorly developed; frontal margin nearly straight; orbits square, no fissures; anterolateral margin granular, entire; sternum narrow; no fusion of male abdominal somites.

Description.—Carapace ovoid, wider than long, $L/W = 0.84$, widest about 40 percent distance posteriorly on carapace; surface very finely granular, granules coarsest along front and anterolateral margins; regions very poorly developed if at all; moderately vaulted longitudinally and weakly vaulted transversely.

Frontal margin nearly straight, about 28 percent maximum carapace width; granular, projected somewhat beyond orbits. Orbits squared, fairly deep, no fissures, directed weakly anterolaterally, with weakly developed rim, fronto-orbital width about two-thirds maximum carapace width. Anterolateral margin short, granular, convex, merging smoothly with posterolateral margin. Posterolateral margins long, smooth, entire, weakly convex, converging posteriorly, with shallow posterolateral reentrants. Posterior margin short, nearly straight, about one-quarter maximum carapace width.

Most carapace regions poorly defined. Mesogastric region very faintly defined, with long anterior process. Urogastric region

TABLE 1—Measurements (in mm) taken on the dorsal carapace of *Amydrocarcinus dantei* n. gen and sp. L1 = maximum length. W1 = maximum width. W2 = fronto-orbital width. W3 = posterior width. W4 = frontal width. L2 = length posteriorly on dorsal carapace to position of maximum width.

MNH-UABCS specimen number	L1	W1	W2	W3	W4	L2
Te14/43-32	20.4	25	16.4	6.7	7.4	8.7
Te14/43-30	22.1	27.7	16.6	—	7.2	8.7
Te14/43-33	16.3	19.4	12.1	4.9	4.9	7
Te14/43-37	13.9	15.7	10.7	—	4.6	5.2

bounded by branchiocardiac groove. Cardiac region faintly defined, triangular, apex directed posteriorly. Intestinal region depressed, flattened. Branchial region weakly inflated, posterior portion depressed to level of intestinal region.

Sternum rectangular, longer than wide; sternites 1–2 fused, triangular; sternites 3–4 fused, with small indentation in lateral margin at point of fusion, sternite 3–4 with episternal projections, directed anterolaterally; sternite 5 wider than long, directed anterolaterally, with “bouton-presson” and episternal projections; sternite 6 less wide than sternite 5, directed weakly posterolaterally, with episternal projections; sternite 7 small, directed posterolaterally; sternite 8 apparently obscured by abdomen.

Male abdomen narrow, with concave lateral margins; somites appearing to be free but somites 1–2 not preserved; somite 3 much wider than long; somite 4 wider than long, with weakly concave lateral margins; somite 5 less wide than 4, with weakly concave lateral margins; somite 6 rectangular, with straight lateral margins; telson an equilateral triangle.

Buccal cavity rectangular wider than long; third maxillipeds longer than wide. Merus of first pereiopod granular, with blunt spine on outer surface. Carpus equidimensional, granular. Manus longer than high, height increasing distally; proximal margin with projections articulating with carpus, upper and lower margins nearly straight, distal margin at about 80 degree angle to lower margin. Fixed finger narrowing distally, with blunt tubercles on occlusal surface. Movable finger slender, arcuate, with small tubercles on occlusal. Meri of pereiopods long and slender.

Etymology.—The new species is named for Dante J. Morán Zenteno, Instituto de Geología, Universidad Nacional Autónoma de México, in recognition for the support he has provided for paleontological studies in México.

Types.—Holotype, MHN-UABCS/Te14/43-32 and six paratypes, MHN-UABCS/Te14/43-30, 33, and 37 and MHN-UABCS/Te14/50-55, 56, and 57.

Measurements.—Measurements (in mm) taken on the dorsal carapace are listed in Table 1.

Occurrence.—The specimens were collected from the Eocene Tepetate Formation, from cliffs in a broad arroyo northwest of La Paz, Baja California Sur, México, at Lat. N 24°10.240', Long. W 110°55.119'.

Discussion.—The new taxon is represented by moderately well-preserved specimens comprised of three molts and two probable corpses. One specimen, MHN-UABCS/Te14/43-30, displays both the dorsal carapace and ventral surface of the animal which was clearly buried while in the process of molting. The dorsal carapace material is rather fragile, as each specimen displays damage to some portions of the margins and the dorsal surface. The pereiopods also appear to have been delicate as very few elements from pereiopods 2–5 are preserved.

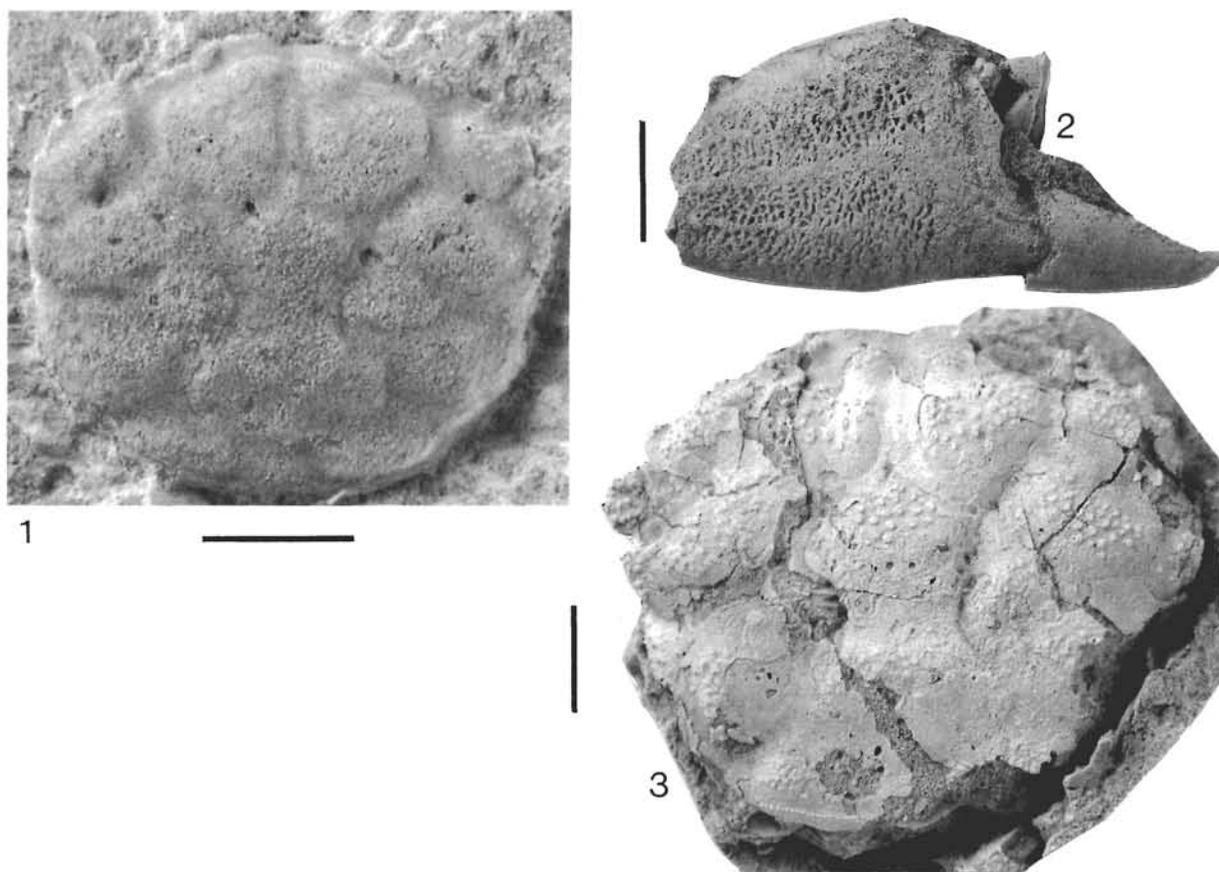


FIGURE 21—*Lobonotus mexicanus* Rathbun, 1930b. 1, MHN-UABCS/Te6/53-17, weathered dorsal carapace with little ornamentation; 2, MHN-UABCS/Te3/52-74, major chela found associated with MHN-UABCS/Te3/52-73; 3, MHN-UABCS/Te3/52-73, dorsal carapace with excellent preservation of ornamentation. Scale bars equal to 1 cm.

Genus LOBONOTUS A. Milne Edwards, 1864
(=ARCHAEOPIUMNUS Rathbun, 1919)

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

Included species.—*Lobonotus?* *australis* Fritsch, 1878; *L. bakeri* (Rathbun, 1935, as *Plagiolophus*); *L. brazoensis* Stenzel, 1935 (known only from claw fragments); *L. mexicanus* Rathbun, 1930b; *L. natchitochensis* Stenzel, 1935; *L. orientalis* Collins and Morris, 1978; *L. sculptus*; *L. sandersi* (Blow and Manning, 1996; as *Eohalimede sandersi*; Blow and Manning, 1998; as *Eohalimede sandersi nom. corr.*); *L. vulgatus* Quayle and Collins, 1981.

Diagnosis.—Carapace not much wider than long; with deep grooves and clearly defined regions ornamented with large, densely spaced granules; front nearly straight with central notch; orbits with two fissures and sometimes with one intraorbital spine bounded by fissures; anterolateral margin long, with four or five anterolateral spines excluding outer orbital spine, last very small or absent; cardiac region three-lobed; intestinal region wide, short, linear when developed; mani of chelae with rows of granules on outer surface.

Discussion.—Both *Lobonotus* and the superficially similar genus *Titanocarcinus* A. Milne Edwards, 1863, were named by A. Milne Edwards, who did not provide a basis for differentiation between the two genera. Some authors have considered the two to possibly be synonymous (Collins and Morris, 1978), based upon the overall similarity of the carapace shape and ornamentation and the nature of the front and anterolateral spines. Both *Titanocarcinus* and *Lobonotus* have a distinctive tri-lobed cardiac

region and well-defined, densely granular carapace regions. According to Collins and Morris (1978), the major criterion used to differentiate between the two genera is the geographic location of occurrences; *Titanocarcinus* has been considered to be a European genus whereas *Lobonotus* has been described as an American genus. This observation is clearly insufficient to make generic determinations. The two genera are, in fact, very similar; however, re-examination of the type species of *Titanocarcinus*, *T. serratifrons* A. Milne Edwards, 1863, is required to determine the status of the two genera. That work is in progress by two of us (Schweitzer and Feldmann). Herein, the two genera will be retained, and *Lobonotus* is used as is consistent with the precedent set by other workers.

Several American, one British, and one Middle Eastern species have been assigned to *Lobonotus*, and, as discussed herein, nearly all are clearly congeneric based upon their distinctive carapace ornamentation and development of carapace regions. *Lobonotus brazoensis* was named for claw material only; thus, its status in the genus is questionable. Feldmann, Casadío et al. (1995) named *L. lobulata* from Maastrichtian and Danian rocks of Argentina; however, that species lacks the carapace ornamentation and distinctive development of carapace regions characteristic of *Lobonotus*. That species is herein removed from *Lobonotus*. Placement of that species into a genus, probably within the Xanthoidea, is currently underway by Schweitzer and Feldmann. *Lobonotus?* *australis* Fritsch, 1878, reported from the Eocene of Borneo, has not been examined by the authors; thus, its placement in the genus remains questionable.

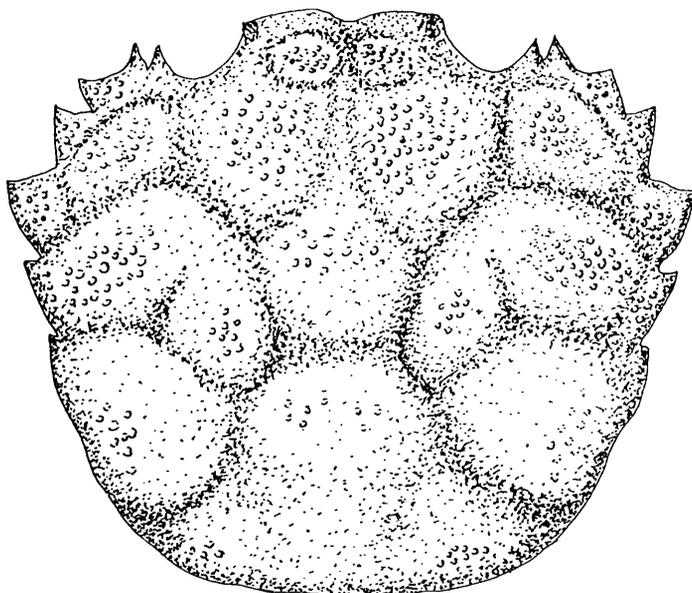


FIGURE 22—Reconstruction of *Lobonotus mexicanus* Rathbun, 1930.

Blow and Manning (1996; 1998) assigned a new species to *Eohalimede*, *E. sandersi*. However, that species is quite different from the type species of *Eohalimede*, *E. walleri* Blow and Manning, 1996, in the development of carapace regions, ornamentation of the carapace regions, and the shape of the carapace. *Eohalimede walleri* has weakly developed carapace regions and weakly developed carapace ornamentation; in fact, the regions appear to be smooth except for the large, fungiform projections on the carapace. By contrast, *E. sandersi* has carapace regions which are densely ornamented and has very well-defined carapace regions, typical of *Lobonotus*. Further, the carapace of *E. walleri* is widest about one quarter the distance posteriorly on the carapace, while that of *E. sandersi* is widest about half the distance posteriorly, typical of species of *Lobonotus*. The carapace of *E. walleri* narrows posteriorly beginning at the point of maximum width, while the carapace of *E. sandersi* is rectangular, typical of *Lobonotus*. Based upon these characters, *E. sandersi* is herein placed within *Lobonotus*.

Lobonotus as restricted herein is primarily an Eocene genus with one occurrence in Miocene rocks. Middle Eocene occurrences include *Lobonotus orientalis* from Pakistan; *L. natchitochensis*, *L. brazoensis*, *L. bakeri*, and *L. sandersi* from the Gulf Coastal Plain of the United States; *L. mexicanus* from Baja California, Mexico; and *L. vulgatus* from Britain. *Lobonotus sculptus* is known from Miocene rocks of the Caribbean. Thus, the genus clearly exhibits a Tethyan distribution, either originating in the eastern Tethys and dispersing westward to the Americas or vice-versa.

LOBONOTUS MEXICANUS Rathbun, 1930b
Figures 21, 22

Lobonotus mexicanus RATHBUN, 1930b, p. 2, pl. 1.

Diagnosis.—*Lobonotus* with weakly developed tri-lobed cardiac region, long hepatic regions; with intraorbital spine bounded by two orbital fissures; front lacking granules.

Description.—Carapace hexagonal, wider than long, L/W = 0.86, widest about half the distance posteriorly on carapace; regions well-defined by broad, shallow, smooth grooves; regions inflated, coarsely granular; moderately vaulted longitudinally, especially anteriorly and flattened transversely.

Front granular, nearly straight, notched axially, slightly downturned, about one-third maximum carapace width. Orbits circular, directed forward, with two open fissures closely spaced near outer orbital corner, fissures occur on either side of sharp, narrow intraorbital spine; outerorbital spine small, sharp, directed forward. Anterolateral margins with four spines excluding outerorbital spine; first spine smallest, triangular, directed forward; second spine broad, triangular, granular on dorsal surface, directed anterolaterally; third spine largest, granular on dorsal surface, broad, directed anterolaterally; fourth spine short, triangular, granular on dorsal surface, directed nearly laterally. Posterolateral margin sinuous, convex, granular. Posterior margin weakly convex, rimmed, about 60 percent maximum carapace width.

Dorsal surface of frontal region smooth. Epigastric regions inflated, tabular, granular. Protogastric regions large, moderately inflated, coarsely granular centrally. Mesogastric region with long, narrow, smooth anterior process; posterior portion of region wide, pentagonal in shape, granular. Urogastric region with concave lateral margins, depressed, smooth. Cardiac region broader than urogastric and mesogastric regions, with broad circular swellings anteriorly and depressed posteriorly. Intestinal region broadest of all axial regions, depressed, flattened centrally, granular swellings on either side of flattened central area. Hepatic regions strongly inflated, granular. Epibranchial region arcuate, arc extending from base of fourth anterolateral spine to lateral margin of urogastric region; separated into two parts, one ovate and oriented transversely and one triangular and directed at urogastric region. Remainder of branchial region undifferentiated, inflated, granular.

Manus of major chela becoming higher distally; moderately vaulted outer surface; inner surface flattened; proximal margin at about 80° angle to lower margin; upper margin convex; lower margin weakly convex; distal margin nearly straight; fixed finger slightly deflexed, with upturned tip, occlusal surface with blunt tubercles.

Ventral surface and remainder of appendages unknown.

Material examined.—Four specimens, MHN-UABCS/Te3/52-73 and 74; MHN-UABCS/Te6/53-17; and MHN-UABCS/Te14/50-59.

Measurements.—Measurements (in mm) taken on the dorsal carapace of the MHN-UABCS/Te3/52-73 and MHN-UABCS/Te6/53-17, listed respectively. Maximum carapace length: 34.5, 21.6; maximum carapace width: 40.0, 25.0; fronto-orbital width: 26.4, 14.8; frontal width: 14.0, 8.3; posterior width: 23.6, 14.0; length to position of maximum carapace width: 16.2, 11.3.

Occurrence.—All of the specimens were collected from the Eocene Tepetate Formation, northwest of La Paz, Baja California Sur, Mexico. Two specimens, MHN-UABCS/Te3/52-73 and 74, were collected near the top of a small hill at Lat. N 24°21.120', Long. W 111°02.807'. Specimen MHN-UABCS/Te6/53-17 was collected in the bed of a dry arroyo at Lat. N 24°21.369', Long. W 111°02.603'. Specimen MHN-UABCS/Te14/50-59 was collected from an unknown locality in the Tepetate Formation.

Discussion.—The new specimens permit more detailed description of the nature of the front and orbits of *Lobonotus mexicanus*. The species is distinguishable from other members of the genus because of its poorly developed tri-lobed cardiac region and its possession of an intraorbital spine bounded by orbital fissures. Other species of the genus possess fissures, but in no other species do the fissures bound a spine. The type species, *L. sculptus*, has much better developed regions, a broader intestinal region, and a much more clearly trilobed cardiac region than does *L. mexicanus*. *Lobonotus vulgatus* has much more inflated and vaulted regions than does *L. mexicanus*, and *L. orientalis* has a more lobate cardiac region and a more depressed intestinal region than does *L. mexicanus*. The ornamentation of *L. natchitochensis* is much coarser than that of *L. mexicanus*, and the intestinal region and

cardiac regions are much better developed in *L. natchitochensis*. *Lobonotus bakeri* has much deeper carapace grooves, much more densely ornamented regions, and better developed cardiac and intestinal regions than does *L. mexicanus*. *Lobonotus sandersi* has much better developed intestinal and cardiac regions, and it has a better developed anterior process of the mesogastric region than does *L. mexicanus*.

Both dorsal carapace specimens appear to be molts, because they do not retain the ventral surface or appendages. Specimen MHN-UABCS/Te3/52-73 has preserved cuticle, permitting observation of ornamentation, while specimen MHN-UABCS/Te6/53-17 lacks cuticle and has been highly weathered so that the surface is smooth. Two isolated chelae were collected from the same locality as the dorsal carapace specimens and are interpreted as the claws of *L. mexicanus*. One chela specimen appears to display a pathological condition on the fixed finger, which is strongly deflexed into a position unusual in the brachyurans, and has a bulbous swelling at the base of the finger. There is no sign of damage to the chela nor is there evidence of a repaired break.

Genus XANDAROS Bishop, 1988a
XANDAROS STERNBERGI (Rathbun, 1926a)

Zanthopsis sternbergi RATHBUN, 1926a, p. 55, pl. 39, figs. 1-4; BISHOP AND WHITMORE, 1986, p. 128, fig. 10a, b.

Xandaros sternbergi BISHOP, 1988a, p. 252, figs. 3E-H, 4.

Material examined.—One chela, UNAM IGM-7956.

Occurrence.—IGM-7956 was collected from sea cliffs directly west of Victors Ranch, Punta San Thomas, Baja California, Mexico, from rocks questionably referred to the Rosario Formation.

Family GONEPLACIDAE MacLeay, 1838
Genus ICRIOCARCINUS Bishop, 1988a
ICRIOCARCINUS XESTOS Bishop, 1988a

Icriocarcinus xestos BISHOP, 1988a, p. 247, figs. 2, 3A-D.

Material examined.—One dorsal carapace, UNAM IGM-7957.

Occurrence.—IGM-7957 was collected from rocks associated with IGM-7956, discussed under *Xandaros*.

Discussion.—Bishop (1988a) originally assigned *Icriocarcinus* to the Carcineretidae Beurlen, 1930, based upon its shape, long, slender eyestalks, transverse ridges, and unequal chelipeds (p. 247). Vega et al. (1997) restricted the Carcineretidae, considering *Branchiocarcinus* Vega, Feldmann, and Sour-Tovar, 1995; *Cancrinxantho* Van Straelen, 1934; *Carcinertes* Withers, 1922; *Lithophylax* A. Milne Edwards and Brocchi, 1879; *Mascaranada* Vega and Feldmann, 1991; *Ophthalmoplax* Rathbun, 1935; and *Woodbinax* Stenzel, 1953, to be true carcineretids. The family as restricted by Vega et al. (1997) is known primarily from United States Western Interior, Mexican, and Caribbean occurrences and was suggested to have become extinct at the time of the end-Cretaceous Chixculub event (Feldmann, Vega, and Villamil, 1998). Vega and Feldmann (1991) and Vega et al. (1997) proposed that the two Pacific slope genera previously assigned to the Carcineretidae, *Icriocarcinus* and *Longusorbis* Richards, 1975, might be better placed within the Xanthidae based upon their gross morphology, a position with which we concur.

It is suggested here that *Icriocarcinus* may be best placed within the Goneplacidae, based upon the broad orbits; narrow rostrum; posteriorly sloping orbital margins; long, attenuated, laterally directed outer-orbital spine at the anterolateral corner; transverse ridges on the epigastric region; and slender pereopods. All of these features are remarkably reminiscent of the goneplacid genera *Goneplax* Leach, 1814, and *Ommatocarcinus* White, 1852, of the Goneplacidae Macleay, 1838 (see Glaessner, 1969; Jenkins,

1975; Sakai, 1976). *Icriocarcinus* falls into the broad category of fossil goneplacids defined by Schweitzer (2000) as possessing an angular carapace, elongate orbits, and attenuated outer-orbital spines directed laterally, which includes members of the Goneplacidae. *Icriocarcinus* differs from other members of the Goneplacidae in possessing well-developed carapace regions; goneplacids typically have poorly developed carapace regions. However, *Ommatocarcinus*, particularly specimens of *Ommatocarcinus corioensis* (Cresswell, 1886), has inflations on the carapace that correspond with the well-developed regions of *I. xestos*. Both *I. xestos* and *Ommatocarcinus* have a transverse ridge extending across the epibranchial areas and the mesogastric region of the carapace. Additionally, *O. corioensis* has an ornamented posterolateral ridge as does *I. xestos*. The carapace posterior to the cardiac region is depressed in both *Icriocarcinus* and *Ommatocarcinus*. *Icriocarcinus* has small intra-orbital spines which are not typical of most members of the Goneplacidae; however, *O. corioensis* has a granular orbital margin, indicating that ornamentation of that area does occur within the family. Thus, because *Ommatocarcinus* is clearly a member of the Goneplacidae and because *Icriocarcinus* is clearly related to *Ommatocarcinus*, *Icriocarcinus* is placed within the Goneplacidae with confidence. This occurrence of *Icriocarcinus* extends the geologic range of the Goneplacidae into the Late Cretaceous.

GENERAL STATEMENT OF PURPOSE

Systematic work in all areas of paleontology, including the decapod crustaceans, is experiencing a renaissance as workers are increasingly embracing the value and absolute necessity of systematic work in synthetic treatments of any kind. Thus, the data are changing rapidly as the volume of systematic work conducted by authors worldwide increases. This is as true for the decapods as for any other group. While decapods do not have as robust a record as, for example, some molluscan groups, they are much more abundant than vertebrate remains, upon which many major paleobiogeographic conclusions are drawn. In addition, the presence of fossils in a rock unit indicates unequivocally that the animals were in fact living in the geographic region in which the rocks were deposited; thus, whether there is one fossil decapod or 100, paleobiogeographic, evolutionary, and paleoecological conclusions may be drawn from them. We recognize that the fossil record of all groups, not just decapods, is growing, and as new records are made available, conclusions may change. It is with that in mind that we have written the following interpretive sections.

AREAS OF ORIGIN FOR TROPICAL AND SUBTROPICAL AMERICAN DECAPODS

General.—The areas of origin for the decapod taxa discussed here are based upon known first occurrences (Table 2; Appendices A and B). The decapods of the tropical and subtropical Americas region display a very different pattern with regard to areas of origin at the generic level than the decapods of the North Pacific (Schweitzer, 2001b), the high southern latitudes (Feldmann et al., 1997), or New Zealand (Feldmann and McLay, 1993). Over half (59, or 58 percent) of the decapods occurring in the tropical to subtropical Americas during the Cretaceous through the Miocene appear to have originated within the area; there is also a significant number of genera, 21 or 21 percent, that originated in the North Atlantic region (Greenland, Iceland, the British Isles, Scandinavia, northern continental Europe). However, note that most of the rock occurrences of these ages, and much of the collecting activity, has occurred in these regions. Collections from underrepresented areas such as Africa, the Middle East, Central Asia, and China will be necessary to adequately test this problem. Due to the political instability of these regions, it may be some time

TABLE 2.—Areas of origin, based upon known first occurrence, of genera collected from the tropical and subtropical Americas. Data from which the values in this table are derived may be found in Appendix B. The number in parentheses following age of origin indicates number of genera originating in the respective time periods. CAM = tropical and subtropical Americas; NATL = North Atlantic and epicontinental Northern Europe; TETH = Tethyan region; NPAC = North Pacific; HSL = High Southern Latitudes; WI = Western Interior of North America; EQ = equivocal area of origin.

Age of origin	CAM	NATL	TETH	NPAC	CAM or TETH	HSL	WI	EQ
Triassic (2)	0	2 (100%)	0	0	0	0	0	0
Jurassic (6)	0	6 (100%)	0	0	0	0	0	0
Lower Cretaceous (19)	10 (53%)	6 (32%)	0	1 (5%)	0	0	0	2
Upper Cretaceous (20)	14 (70%)	3 (15%)	0	0	0	0	1 (5%)	3
Paleocene (12)	8 (67%)	2 (17%)	0	0	1 (8.3%)	1 (8.3%)	0	0
Eocene (35)	21 (60%)	2 (6%)	6 (17%)	1 (3%)	2 (6%)	1 (3%)	0	2
Oligocene (4)	3 (75%)	0	1 (25%)	0	0	0	0	0
Miocene (4)	3 (75%)	0	0	1 (25%)	0	0	0	0

before these areas are comprehensively studied. Numerous genera and two families appear to have been endemic to the tropical and subtropical Americas, most notably during the Late Cretaceous and Eocene. This pattern of high endemism parallels that seen in the decapod fauna of the Pacific Northwest of North America (Schweitzer, 2001b).

Triassic and Jurassic.—All of the decapods known from the tropical and subtropical Americas that have first occurrences in the Triassic or Jurassic appear to have originated in the North Atlantic region. Many of these first occurrences are from Britain, which may be an artifact because the North Atlantic region has a large number of rock outcrops and the rocks of Britain have a long history of detailed study. Dispersal from the North Atlantic to the tropical and subtropical Americas would have been facilitated during the Triassic and Jurassic as well as the early Cretaceous by proximity of Europe to North America and the narrowness of the Atlantic Ocean, permitting larval dispersal or dispersal along the continental shelves.

Lower Cretaceous.—Lower Cretaceous decapods of the tropical and subtropical Americas originated either within the region

(53%) or in the North Atlantic region (32%) with only three exceptions (Fig. 23). Clearly, faunal exchange between the tropical and subtropical Americas and the North Atlantic region was active during this time. Of nineteen decapod genera known from the tropical and subtropical Americas during the Lower Cretaceous, six dispersed from the North Atlantic to the Americas, and six genera dispersed from the Americas to the North Atlantic. Eastward exchange appears to have been facilitated by ocean surface currents and westward movement probably occurred through range expansion along the continental shelf. The narrow Atlantic Ocean would have enhanced the probability of this exchange. One crab taxon, *Homola*, appears to have originated in the North Pacific and subsequently dispersed to the tropical and subtropical Americas, probably via the open Central American Seaway (Bice et al., 2000; Schweitzer, 2001b). Four of the nineteen decapod genera known from the tropical to subtropical Americas were endemic to the region; of the decapod fauna from the Pacific Northwest of North America, 2 of 4 known genera were endemic to the region. Influx of decapod genera from other regions was undoubtedly higher in the tropical and subtropical Americas because

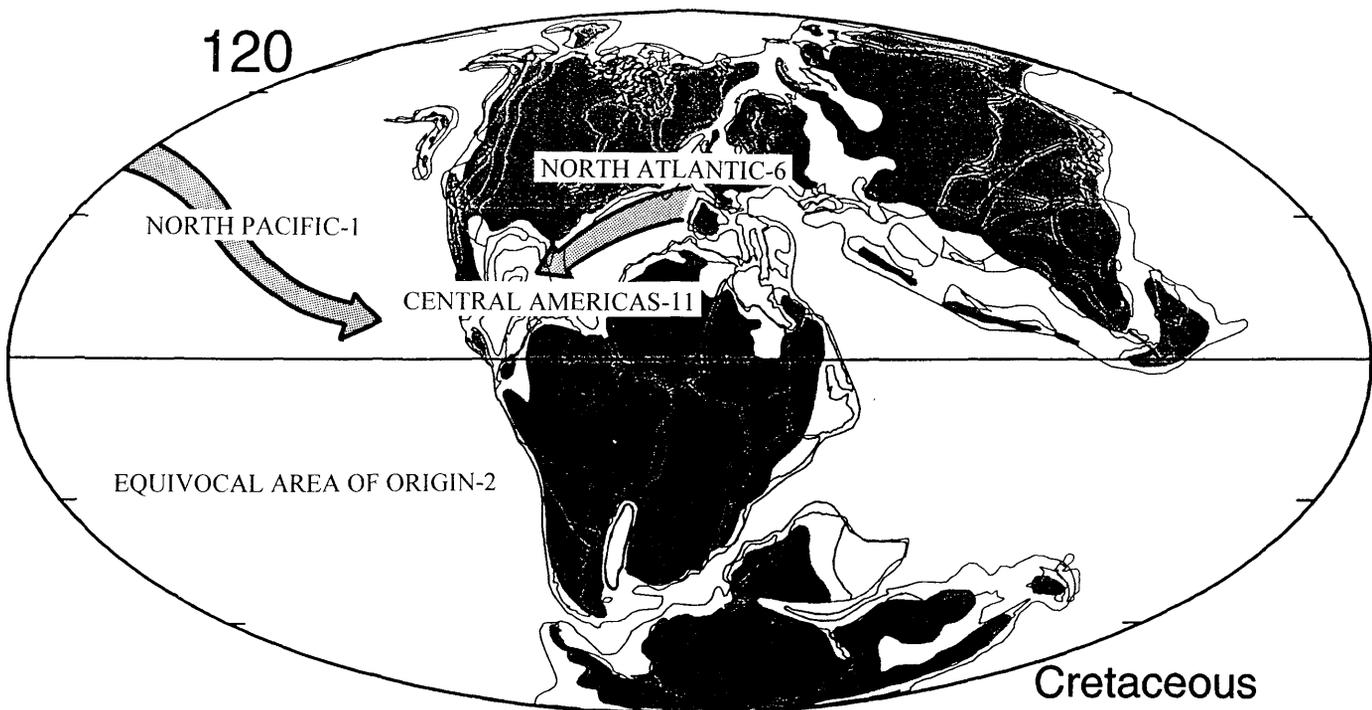


FIGURE 23.—Areas of origin of the Early Cretaceous decapod fauna of the tropical and subtropical Americas, designated Central Americas on this and all subsequent maps. Dispersal avenues for decapods during this time interval are shown with large arrows. Numbers following areas of origin on this and all subsequent maps indicate the number of genera with that area of origin. Base map for 120 Ma from Scotese (1997).

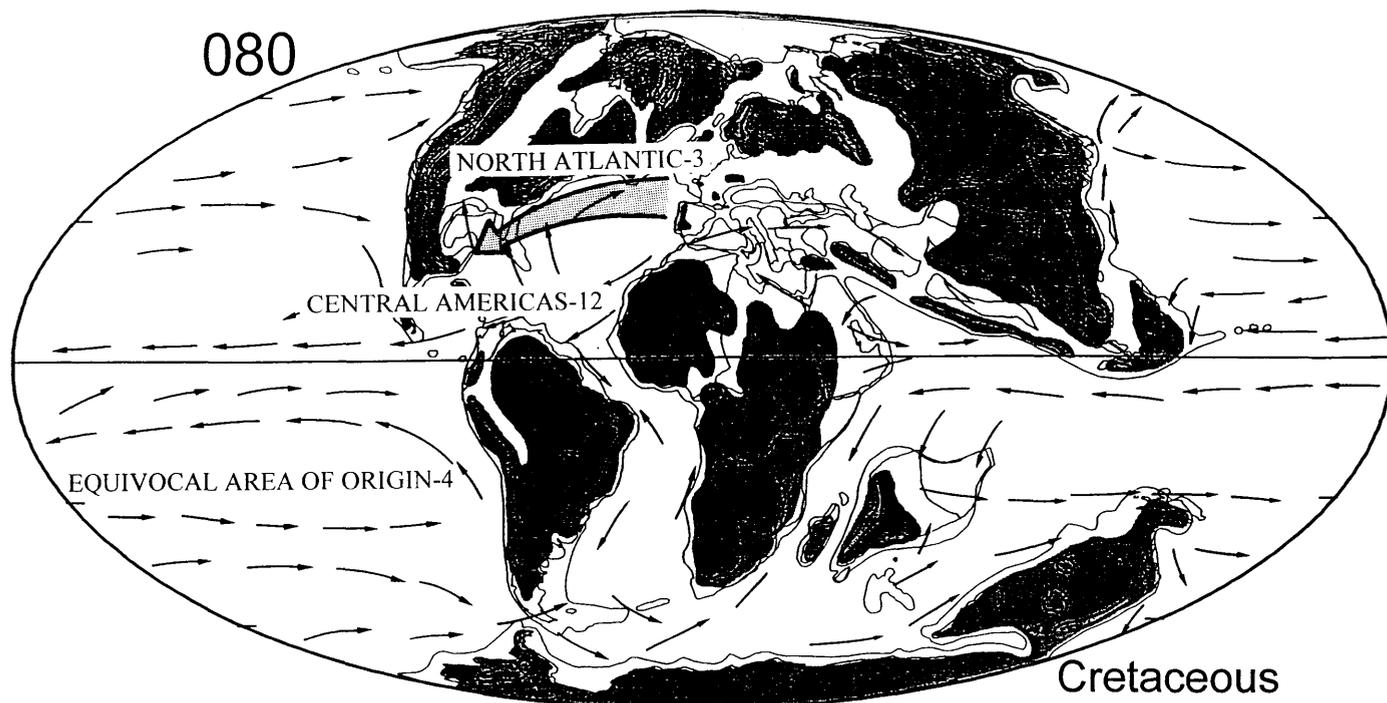


FIGURE 24—Areas of origin of the Late Cretaceous decapod fauna of the tropical and subtropical Americas. Dispersal avenues for decapods during this time interval are shown with large arrows. Base map from Scotese (1997, 80 Ma) and paleocurrent data from Bice (unpublished data, 93 Ma).

of the narrow Atlantic Ocean and open Tethys Seaway, while the North Pacific region was much more isolated. Endemism may also be an artifact of collecting bias; for example, specimens recently received for study by two of us (CES and RMF) from the Cretaceous of British Columbia are remarkably similar to some forms from Britain and Continental Europe. Thus, as more material is studied, these patterns will likely be reinterpreted.

Upper Cretaceous.—In a pattern similar to that of the Lower Cretaceous, fourteen of twenty decapod genera known from the tropical and subtropical Americas originated within the region (70% of total) or in the North Atlantic (15% of total) (Fig. 24). Three other genera have equivocal areas of origin. Undoubtedly the same factors controlling Early Cretaceous origin and dispersal of decapods operated during the Late Cretaceous as well. Eleven of twenty decapod genera (55%) known from the tropical and subtropical Americas were endemic to the region, and of these, six belonged either to the Dakotancridae or the Carcineretidae, families endemic to the area.

Paleocene.—Paleocene decapods maintain the same pattern as do the Cretaceous decapods; eight of twelve genera recorded from the tropical and subtropical Americas appear to have originated in the area (Fig. 25). Two (17%) originated in the North Atlantic, in Greenland specifically (Collins and Rasmussen, 1992), and probably reached the Americas via the continental shelf. One genus recorded from the tropical and subtropical Americas originated in the high southern latitudes and probably reached the central Americas via the continental shelf; ocean currents do not appear to have been favorable for transport in a northerly direction (Bice, unpublished data; Schweitzer, 2001b). Endemism was lower during the Paleocene; only two genera appear to have been endemic to the tropical and subtropical Americas.

Eocene.—The Eocene appears to have been a time of high mobility in terms of faunal dispersal worldwide (Fig. 26). Two (6%) originated in the North Atlantic, and for the first time, a Tethyan component of six genera (17%) arrived in the central

Americas. Additionally, one of the genera occurring in the tropical and subtropical Americas originated in the high southern latitudes, and one originated in the North Pacific. The influx of decapods from a wider variety of areas than at any other time may have been due to the high sea levels and favorable climate during the Eocene, although the same should have been true during the Late Cretaceous when most of the decapods are endemic (P. Harries, personal commun.). However, twenty-one of thirty-five genera known from the tropical and subtropical Americas originated within the region, and of these, sixteen were endemic. The relatively high number of endemic genera is consistent with findings for the Pacific Northwest of North America, in which about half of the Eocene genera were endemic to the North Pacific Ocean (Schweitzer, 2001b). Otte (1981) also observed a high degree of endemism in the benthic fauna of the Eocene Castle Hayne Limestone, indicating that endemism, at least in the tropical and subtropical Americas, was not restricted to the Decapoda.

Based upon the decapods of the Cretaceous and Tertiary of the North Pacific, many of which originated in the Tethys and subsequently dispersed to the region, it was expected that the decapod fauna of the tropical and subtropical Americas would also have been strongly influenced by Tethyan immigration during the Cretaceous and Tertiary. However, the Eocene was the only time that there appears to have been significant faunal exchange between the Tethys and the tropical and subtropical Americas. The decapod fauna of the North Pacific shows a substantial Tethyan influence during the Eocene and Oligocene (Schweitzer, 2001b), during which at least seven genera were believed to have arrived in the North Pacific from the Tethys via the Central American Seaway (Schweitzer and Salva, 2000; Schweitzer and Feldmann, 2000a; Schweitzer, 2001b). Clearly, some genera arose in the Tethyan region and dispersed to the Americas, facilitated by westward flowing currents in the western-most Tethyan region (Feldmann, Bice et al., 1998). These taxa would have then reached the Pacific via the

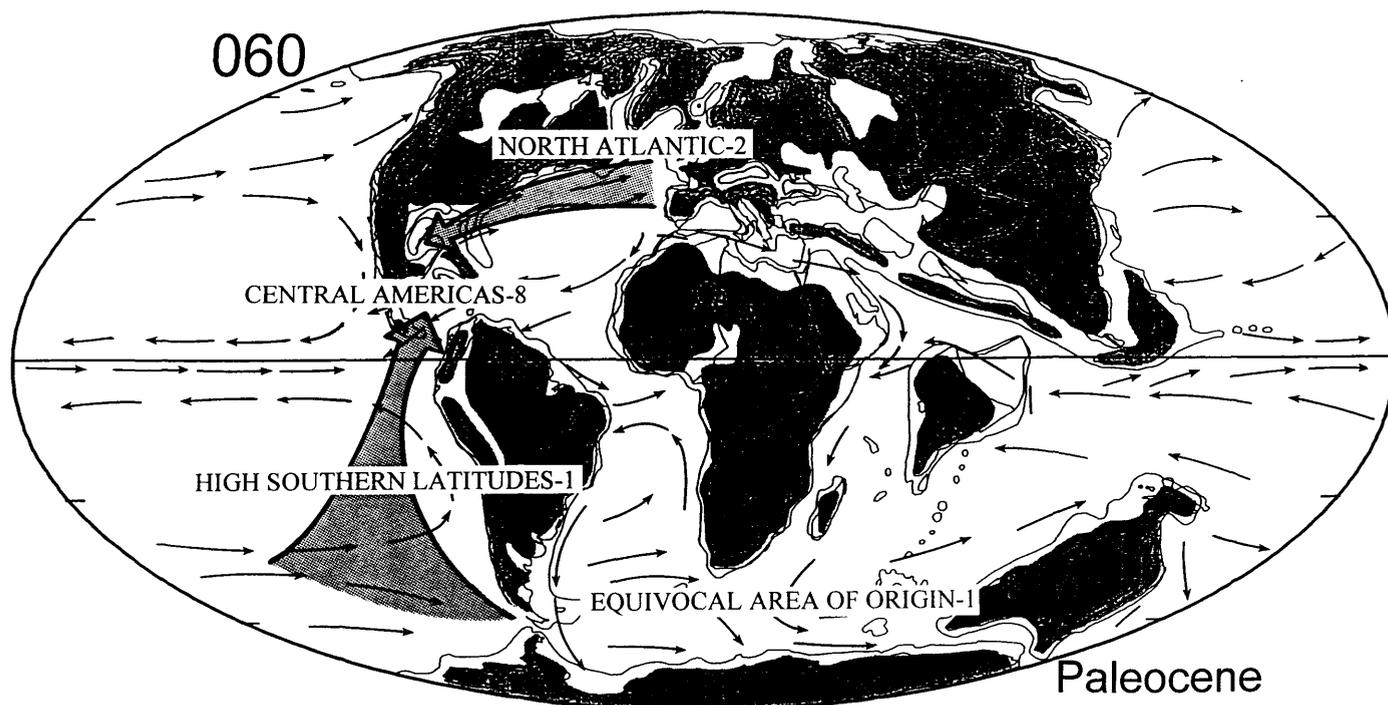


FIGURE 25—Areas of origin of the Paleocene decapod fauna of the tropical and subtropical Americas. Dispersal avenues for decapods during this time interval are shown with large arrows. Base map from Scotese (1997, 60 Ma) and paleocurrent data from Bice (unpublished data, 55 Ma).

Central American Seaway. However, it now appears that the number of Tethyan-derived decapods in the central Americas was smaller than originally believed. At least some of the taxa that display a Tethyan/low-latitude distribution are equivocal in their area of origin and may have originated either in the Tethys or in tropical

to subtropical America. Further, at least one of the genera, *Montezumella*, originally believed to have had a Tethyan area of origin and distribution (Schweitzer and Salva, 2000), appears to have actually originated in the North Atlantic and may have reached the Tethys of southern Europe and the tropical to subtropical Americas

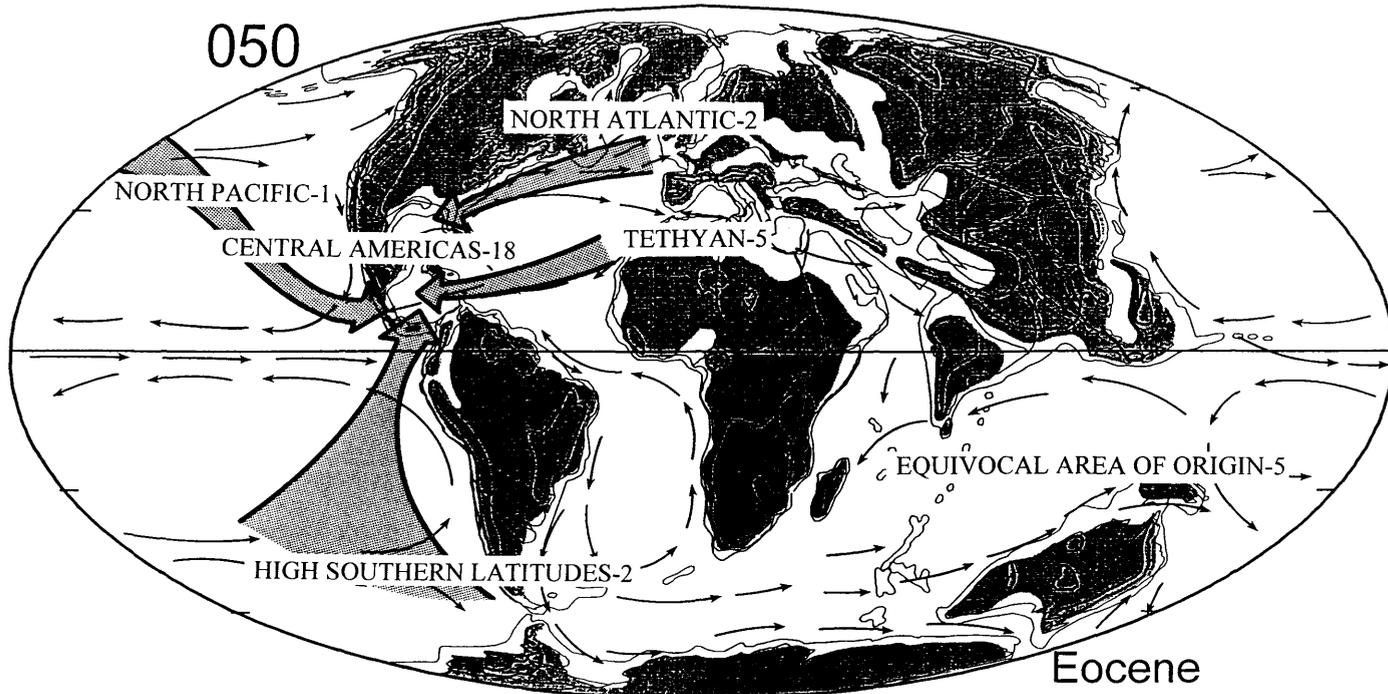


FIGURE 26—Areas of origin of the Eocene decapod fauna of the tropical and subtropical Americas. Dispersal avenues for decapods during this time interval are shown with large arrows. Base map from Scotese (1997, 50 Ma) and paleocurrent data from Bice (unpublished data, 40 Ma).

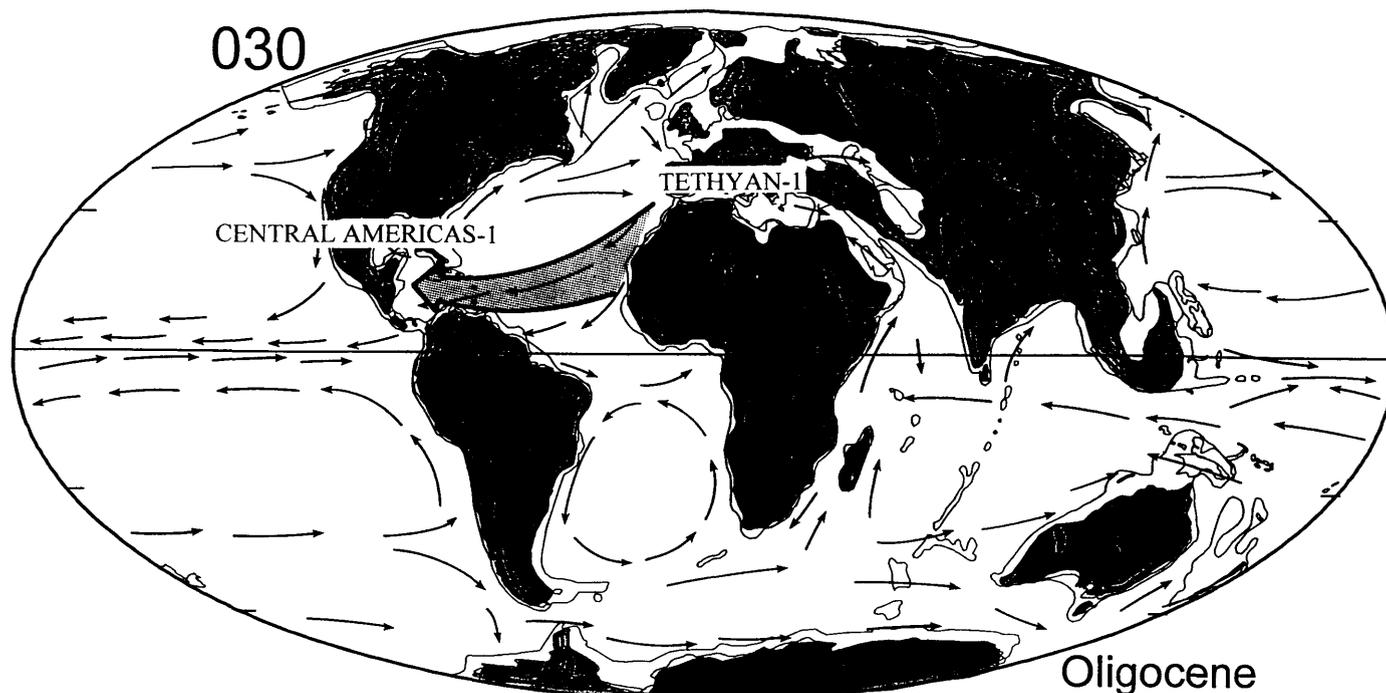


FIGURE 27—Areas of origin of the Oligocene decapod fauna of the tropical and subtropical Americas. Dispersal avenues for decapods during this time interval are shown with large arrows. Base map from Scotese (1997, 30 Ma) and paleocurrent data from Bice (unpublished data, 33 Ma).

in independent dispersal events following the continental shelves. Feldmann, Bice et al. (1998) noted that ocean current velocities may not have been sufficiently fast to permit dispersal to the Americas from the Tethyan region, as was previously observed by Adams (*in* Berggren and Hollister, 1974). Many of the decapod genera known from the North Pacific that had a Tethyan origin probably reached the area by moving eastward through the Tethys, which is supported by the ocean surface currents in the eastern part of the Tethys (Bice, unpublished data) and occurrences in Japan (Karasawa, 1993; Schweitzer, 2001b).

Oligocene and Miocene.—Few decapods are recorded from Oligocene and Miocene rocks of the tropical and subtropical Americas. Of these, most originated within the area (Figs. 27 and 28). This observation is attributable to the paucity of rocks of this age in the area. Oligocene and especially Miocene faunas of other areas which contain large outcrops of rocks of these ages are relatively rich in decapod taxa, including rocks in Japan (Karasawa, 1993), Europe (Müller, 1984), and the Pacific Northwest of North America (Schweitzer, 2001b).

Endemicity.—The pattern of endemicity at the generic level within the decapods of the tropical and subtropical Americas mirrors that seen for the North Pacific region (Schweitzer, 2001b). Both the Cretaceous and the Eocene decapod faunas of the Pacific Northwest of North America display a high degree of endemicity, 50% and 56%, respectively, while the tropical and subtropical Americas contain 33% and 49%, respectively. Both the Cretaceous and the Eocene appear to have been times of rapid evolution and appearance of new genera within the Decapoda; thus, it is not surprising that genera may have been specialized for the area in which they arose and thus remained endemic. Further, the high sea levels and favorable climate during much of the Cretaceous and Eocene undoubtedly created a large variety of niches and habitats to which the decapods were very specifically adapted. Endemicity is not restricted to the tropical and subtropical Americas. The decapod faunas of the Cretaceous and Tertiary of Chile and Argentina are very different from one another and from other

geographic regions, probably due to both thermal and tectonic barriers (Feldmann et al., 1997). In contrast, only 17% of genera known from Recent waters surrounding New Zealand are endemic (Feldmann and McLay, 1993). This is a very isolated geographic area of continental shelf sediments compared to the size of the areas discussed herein. If expanded to include Australian or South Pacific waters, the number of endemic genera might well be higher. Thus, it does not appear that endemicity was higher in the past as compared to Recent oceans.

Summary.—Overall, the vast majority of decapods occurring in the tropical and subtropical Americas of Cretaceous through Miocene rocks appear to have evolved within the region. The North Atlantic region was also a major area of origin for these decapods, and the Tethys, high southern latitudes, and North Pacific region were minor contributors. The decapod fauna of the Pacific Northwest of North America was also dominated by those decapods originating within the area into the Miocene and even into the Recent for the North American Pacific slope (Schweitzer, 2001b). The pattern in Japan was somewhat different, because that region shows that by the Miocene, decapods of Tethyan origin dominated the fauna (Schweitzer, 2001b). Each geographic area for which the occurrences of decapod crustaceans have been studied and summarized (Japan, the North Pacific, Argentina, Chile, Antarctica, and New Zealand) displays very different patterns of origin and dispersal of decapods from one another.

EVOLUTION AND EXTINCTION PATTERNS

The evolution and extinction patterns documented for decapods in the tropical and subtropical Americas are, in general, similar to those reported for decapods and other faunas; however, there are a few interesting patterns that have not been well documented (Tables 3–5).

It is widely acknowledged that the end-Cretaceous was marked by a mass extinction event; however, the cause and magnitude are still debated. Within the decapods, there is clearly a marked decline in the number of genera by the end of the Cretaceous;

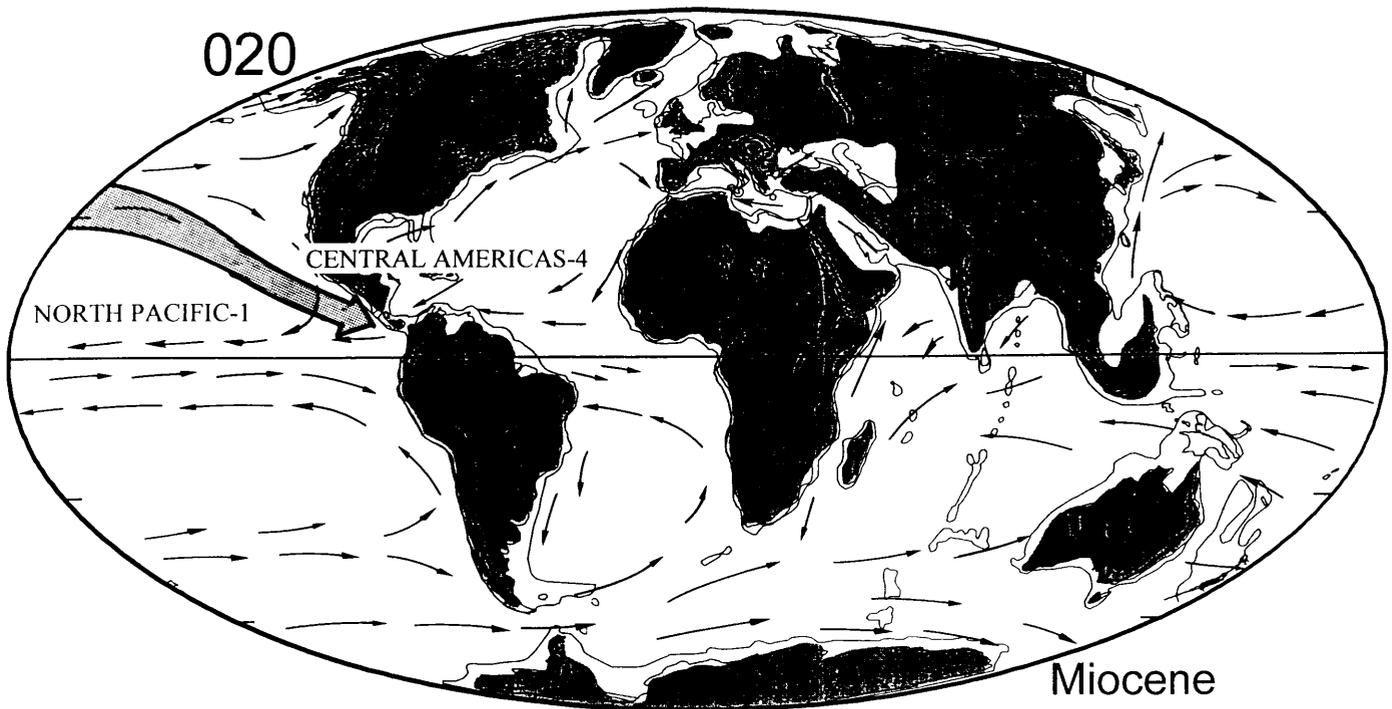


FIGURE 28—Areas of origin of the Miocene decapod fauna of the tropical and subtropical Americas. Dispersal avenues for decapods during this time interval are shown with large arrows. Base map from Scotese (1997, 20 Ma) and paleocurrent data from Bice (unpublished data, 20 Ma).

however, the cause(s) of this decline and the timing of the decline are not known with certainty. Of 45 decapod genera occurring in the Central American region during the Cretaceous, fourteen (31%) crossed the K/T boundary (Fig. 29). Of these, three become extinct within the Paleocene, and six became extinct within the Eocene. Five of the decapod genera crossing the boundary have congeners in the Recent, a large number compared with other regions. Of the Cretaceous decapod genera of the North Pacific and New Zealand, only one genus per region has a modern congener (Schweitzer, 2001b; Feldmann and McLay, 1993).

Significantly, 31 decapods of 45 total (69%) known from the tropical and subtropical Americas that originated before or during the Cretaceous were extinct by the end of the Cretaceous. However, when examined by stage within the Cretaceous, nineteen of these 31 decapod taxa were extinct before the beginning of the Maastrichtian. Thus, only 12, or 27% of the total number of Cretaceous-occurring decapods became extinct at some time during the Maastrichtian, a significantly smaller number than when reported as 69% of the Cretaceous-occurring decapods becoming extinct by the end of the Cretaceous. Thus, the end Cretaceous extinction appears significantly smaller when viewed in this more constrained context.

The pattern is even more complex. Of the 45 genera known from before or during the Cretaceous, 24 (53%) last occurred in the Upper Cretaceous, while the percentage of taxa with Eocene records becoming extinct by the end of the Eocene is even higher (68% with last occurrences in the Eocene). A literal reading of the data would suggest that a mass extinction comparable to the end-Cretaceous event occurred at the end of the Eocene. An alternate suggestion is that the Cretaceous and the Eocene were each times of rapid evolution within the Decapoda. The large numbers of extinctions at the ends of these two time intervals may simply be a reflection of turnover in the fauna as a consequence of the rapid evolution and therefore heightened competition that was occurring at those times. Many niches existed during these two times, and the decapods radiated to fill them. As the climate and environments changed during each of

these time intervals, decapods became extinct over a long interval of time, not necessarily cataclysmically because of a discrete event or cause. The Cretaceous record shows just this, because 19 genera with Cretaceous records, which is 61% of the total number of decapods that became extinct during the Cretaceous, became extinct before the Maastrichtian. A compounding factor in resolving this problem is that Paleocene occurrences are scarce; thus, it is difficult to determine if decapods recovered rapidly after the K/T event(s).

A problem with our knowledge of Eocene decapods is that the occurrences are not well-constrained chronologically. They are typically known as either lower, middle, or upper Eocene, or simply as Eocene occurrences. This is obviously problematic when attempting to determine whether or not the Eocene turnover was just that, occurring throughout the Eocene, or a part of the Eocene-Oligocene extinction event. Additionally, the Eocene spans approximately 20 million years whereas the Upper Cretaceous was about 35 million years long. Thus, comparisons of the Eocene and Upper Cretaceous are inherently complicated by the difference in time spans. More constrained ages and age ranges for decapod occurrences during the Eocene are necessary to resolve this problem.

The rates of origination of decapod genera and extinction of decapod genera during a single time unit in the tropical and subtropical Americas from the Cretaceous through the Miocene are very similar to one another, suggesting that through most of the Cretaceous and Cenozoic, the decapod fauna experienced a relatively constant turnover of genera (Table 5). During the entire Upper Cretaceous, Eocene, Oligocene, and Miocene, the rates of origination and extinction of genera within each time unit are identical to one another or nearly so. During the Lower Cretaceous, more genera originated than became extinct, probably because the Lower Cretaceous marks the beginning of the radiation of the Brachyura, or true crabs. The Maastrichtian origination and extinction rates differ somewhat from those of the Late Cretaceous as a whole. At least seven, and possibly eleven, genera

TABLE 3.—Detailed analysis of differential occurrence of decapod taxa within the Mesozoic and Cenozoic. Only those decapods occurring in the Central American region as defined in this report were analyzed. Data used for these calculations may be obtained from Appendix B. All decapod taxa were analyzed, including macrurans, anomurans, thalassinideans, and brachyurans, unless noted otherwise. Inferred occurrences are used when a genus is known from two time units separated by a third time unit. For example, a taxon known from the Cretaceous and Eocene is inferred to have existed during the Paleocene as well.

Total number originating before or during Cretaceous	45
Of these 45 genera, number crossing K/T Boundary	14 (31%)
Of these 45 genera, number surviving into Paleocene only	3 (6.7%)
Of these 45 genera, number surviving into Eocene only	6 (13%)
Of these 45 genera, number surviving into Recent	5 (11%)
Of these 45 genera, number extinct by end of Lower Cretaceous	7 (16%)
Of these 45 genera, number extinct by the end Cretaceous	31 (69%)
Of these 45 genera, number extinct before the Maastrichtian	19 (42%)
Total number with only or last record in Upper Cretaceous	24 (53%)
Of these 24, number in the Carcineretidae or Dakoticancridae	8 (33%)
Total number with only Cretaceous records (Upper and/or Lower)	26 (58%)
Of these 26, number of carcineretids or dakoticancrids	8 (31%)
Total number originating in the Paleocene	13
Of these 13, number with only or last record in Paleocene	5 (38%)
Of these 13, number surviving into Eocene only	5 (38%)
Of these 13, number surviving into Oligocene only	1 (8%)
Of these 13, number surviving into Miocene only	1 (8%)
Of these 13, number surviving into the Recent	1 (8%)
Total number with records or inferred occurrence in the Paleocene	27
Of these 27, total number extinct by end of Paleocene	9 (33%)
Total number originating in the Eocene	35
Of these 35, number surviving into Oligocene only	1 (3%)
Of these 35, number surviving into Miocene only	3 (9%)
Of these 35, number surviving into Recent	8 (23%)
Of these 35, number with only or last record in Eocene	26 (74%)
Total number with records or inferred occurrence in the Eocene	53
Of these 53, total number extinct by end of Eocene	36 (68%)
Total number originating in the Oligocene	3
Number with only Oligocene record	2
Number surviving into Recent	2
Total number with records or inferred occurrence in the Oligocene	13
Of these 13, total number extinct by end Oligocene	3 (23%)
Total number originating in the Miocene	5
Number with only Miocene record	1
Number surviving into Recent	4
Total number with records or inferred occurrence in the Miocene	21
Of these 21, total number extinct by end of Miocene	6 (29%)
Total number originating in Triassic or Jurassic	8
Of these, number of non-brachyurans	6 (75%)
Total number originating in Cretaceous	39
Of these, number of non-brachyurans	7 (18%)
Total number originating before or during the Cretaceous	45
Of these, number of non-brachyurans	14 (31%)
Total number originating post-Cretaceous	56
Of these, number of non-brachyurans	2 (4%)
Total number of brachyurans originating in Triassic or Jurassic	2
Of these, number of Podotremata	2
Total number of brachyurans originating before or during the Cretaceous	34
Of these, number of Podotremata	21 (62%)
Of these, number of Heterotremata	13 (38%)
Total number of brachyurans originating post-Cretaceous	54
Of these, number of Podotremata	14 (26%)
Of these, number of Heterotremata	39 (72%)
Of these, number of Thoracotremata	1 (2%)

originated during the Maastrichtian. Thus, depending on the number used, it appears that either a large extinction or simple faunal turnover occurred during the Maastrichtian. During the Paleocene, the origination rate is higher than the extinction, perhaps marking the beginning of the second brachyuran radiation usually ascribed to the Eocene. Thus, the second major radiation of the Brachyura may have begun earlier than previously thought, demonstrating the need for intensive study of Paleocene rocks and fossils.

Two decapod families, the Carcineretidae and the Dakoticancridae, appear to have been endemic to the tropical and subtropical Americas and the Western Interior of the United States. These two families have almost exclusively Late Cretaceous occurrences. Of the tropical or subtropical American decapods with last or only records in the Late Cretaceous, 33% belong to one of these two families, and of those decapods with only Cretaceous records,

31% belong to one of those two families. Further, of the 31 decapod genera extinct by the end of the Cretaceous, about one-quarter, belonged to one of those families. The Western Interior and Gulf Coastal Plain habitats, which had been flooded by epeiric seas, were eliminated by the end of the Cretaceous, possibly resulting in the extinction of these families. Furthermore, Feldmann, Vega, and Villamil (1998) suggested that the Carcineretidae became extinct as a possible victim of the Chixculub impact in the Yucatan Peninsula, Mexico, which could also account for the disappearance of the Dakoticancridae.

ORIGINATION OF HIGHER LEVEL TAXA

The patterns of origin for higher level taxa mirror those seen for the decapods worldwide (Table 3). For example, of the decapods originating in the Triassic or Jurassic, 75% were non-brachyurans—the shrimps and lobsters. It has long been known that

TABLE 4—Geologic ranges of genera occurring in the tropical and subtropical Americas. The range is listed for the world-wide range of the genus; it is not restricted to the occurrence of the genus only in the central Americas.

Genus	Geologic range
<i>Eryma</i>	Triassic-Upper Cretaceous
<i>Glyphea</i>	Triassic-Eocene
<i>Cyphonotus</i>	Jurassic-Lower Cretaceous
<i>Diaulax</i>	Jurassic-Lower Cretaceous
<i>Palaeastacus</i>	Jurassic-Upper Cretaceous
<i>Astacodes</i>	Jurassic-Upper Cretaceous
<i>Enoploclytia</i>	Jurassic-Paleocene
<i>Upogebia</i>	Jurassic-Recent
<i>Meyeria</i>	Lower Cretaceous
<i>Protaegla</i>	Lower Cretaceous
<i>Tepexicarcinus</i>	Lower Cretaceous
<i>Graptocarcinus</i>	Lower Cretaceous
<i>Hillius</i>	Lower Cretaceous
<i>Feldmannia</i>	Lower Cretaceous
<i>Cenomanoarcinus</i>	Lower Cretaceous-Upper Cretaceous
<i>Paraneocarcinus</i>	Lower Cretaceous-Upper Cretaceous
<i>Xanthosia</i>	Lower Cretaceous-Upper Cretaceous
<i>Ophthalmoplax</i>	Lower Cretaceous-Upper Cretaceous
<i>Cretacorantina</i>	Lower Cretaceous-Upper Cretaceous
<i>Prehepatus</i>	Lower Cretaceous-Upper Cretaceous
<i>Caloxanthus</i>	Lower Cretaceous-Paleocene
<i>Necrocarcinus</i>	Lower Cretaceous-Eocene
<i>Protocallianassa</i>	Lower Cretaceous-Eocene
<i>Hoploparia</i>	Lower Cretaceous-Eocene
<i>Linuparus</i>	Lower Cretaceous-Eocene
<i>Galathea</i>	Lower Cretaceous-Recent
<i>Homarus</i>	Lower Cretaceous-Recent
<i>Homola</i>	Lower Cretaceous-Recent
<i>Rathbunopon</i>	Upper Cretaceous
<i>Sodakus</i>	Upper Cretaceous
<i>Dakoticancer</i>	Upper Cretaceous
<i>Avitelmessus</i>	Upper Cretaceous
<i>Seorus</i>	Upper Cretaceous
<i>Tetracarcinus</i>	Upper Cretaceous
<i>Carcineretes</i>	Upper Cretaceous
<i>Branchiocarcinus</i>	Upper Cretaceous
<i>Mascaranada</i>	Upper Cretaceous
<i>Archaeopus</i>	Upper Cretaceous
<i>Icriocarcinus</i>	Upper Cretaceous
<i>Megaxantho</i>	Upper Cretaceous
<i>Palaeoxanthopsis</i>	Upper Cretaceous
<i>Xandaros</i>	Upper Cretaceous
<i>Hemioon</i>	Upper Cretaceous-Paleocene
<i>Costacopluma</i>	Upper Cretaceous-Paleocene
<i>Titanocarcinus</i>	Upper Cretaceous-Eocene
<i>Lophoranina</i>	Upper Cretaceous-Eocene
<i>Penaeus</i>	Upper Cretaceous-Recent
<i>Scyllarella</i>	Paleocene
<i>Dromilites</i>	Paleocene
"Xanthilites"	Paleocene
<i>Kieronopsis</i>	Paleocene
<i>Tehuacana</i>	Paleocene
<i>Viapinnixa</i>	Paleocene-Eocene
<i>Quasilaeviranina</i>	Paleocene-Eocene
<i>Raninella</i>	Paleocene-Eocene
<i>Cyclocorystes</i>	Paleocene-Eocene
<i>Verrucoides</i>	Paleocene-Eocene
<i>Laeviranina</i>	Paleocene-Oligocene
<i>Palaeopinnixa</i>	Paleocene-Miocene
<i>Dromidia</i>	Eocene
<i>Prohomola</i>	Eocene
<i>Notopus</i>	Eocene
<i>Titanodorippe</i>	Eocene
<i>Eriosachila</i>	Eocene
<i>Matutites</i>	Eocene
<i>Wilsonimaia</i>	Eocene
<i>Eoinachoides</i>	Eocene
<i>Acantholambrus</i>	Eocene
<i>Pororaria</i>	Eocene
<i>Ocalina</i>	Eocene
<i>Santeexanthus</i>	Eocene
<i>Amydrocarcinus</i> n. gen.	Eocene
<i>Eohalimede</i>	Eocene
<i>Harpactocarcinus</i>	Eocene
<i>Levicyclus</i> n. gen.	Eocene
<i>Glyphithyreus</i>	Eocene

TABLE 4—Continued.

Genus	Geologic range
<i>Martinetta</i>	Eocene
<i>Santeella</i>	Eocene
<i>Falconoplax</i>	Eocene
<i>Stoaplax</i>	Eocene
<i>Viacarcinus</i>	Eocene
<i>Sarahcarcinus</i>	Eocene
<i>Montezumella</i>	Eocene-Oligocene
<i>Calappilia</i>	Eocene-Miocene
<i>Eocarpilius</i>	Eocene-Miocene
<i>Lobonotus</i>	Eocene-Miocene
<i>Laevicarcinus</i>	Eocene-Miocene
<i>Albunea</i>	Eocene-Recent
<i>Ranina</i>	Eocene-Recent
<i>Cyrtorhina</i>	Eocene-Recent
<i>Raminoides</i>	Eocene-Recent
<i>Calappa</i>	Eocene-Recent
<i>Mursia</i>	Eocene-Recent
<i>Parthenope</i>	Eocene-Recent
<i>Portunus</i>	Eocene-Recent
<i>Scylla</i>	Eocene-Recent
<i>Necronectes</i>	Oligocene-Miocene
<i>Hepatus</i>	Oligocene-Recent
<i>Oregonia</i>	Oligocene-Recent
<i>Sandomingia</i>	Miocene
<i>Euphyllax</i>	Miocene-Recent
<i>Persephona</i>	Miocene-Recent
<i>Cancer</i>	Miocene-Recent
<i>Podophthalmus</i>	Miocene-Recent
<i>Speocarcinus</i>	Miocene-Recent

the shrimps and lobsters are the most primitive of the decapods and, in fact, have the oldest fossil records (Glaessner, 1969). Of the decapods originating in the Cretaceous, 18% were non-brachyurans and of the number with post-Cretaceous origins, only 4% were non-brachyurans. This is strong evidence that the lobsters and shrimps evolved very early in decapod history, and notably, many survived the K/T extinction to proliferate in Tertiary and modern oceans. Brachyurans evolved at least by the Jurassic and radiated in the Cretaceous and again during the Eocene (Glaessner, 1969; Schram, 1986), clearly mirrored in the data from the tropical and subtropical Americas.

Several family-level range extensions have resulted from recent work. The placement herein of the Cretaceous genus *Icriocarcinus* within the Goneplacidae extends the geologic range of that family into the Cretaceous. Other xanthoids have previously been reported from Late Cretaceous rocks (Glaessner, 1969); however, the history of the superfamily and its constituent families is poorly understood (Schweitzer, 2000). Recent work on fossil members of the group is beginning to address these deficiencies (Karasawa, 1993; Schweitzer, 2000). The extension of the Goneplacidae into the Cretaceous parallels the range extension into the Cretaceous for the Chirostylidae Ortmann, 1892a, a family previously known only in Recent oceans (Schweitzer and Feldmann, 2000d). Additionally, the ranges of the Cheiragonidae Ortmann, 1893; Cycloporippidae Ortmann, 1892a; Cancridae Latreille, 1802; Geryonidae Colosi, 1923; and Asthenognathinae Stimpson, 1858b, within the Pinnotheridae de Haan, 1833, have been extended into the Eocene (Schweitzer and Feldmann, 2000b, 2000c, 2001a, 2001b; Schweitzer and Salva, 2000; Schweitzer, 2001a). The range of the Portunidae Rafinesque, 1815, has been extended with certainty into the Paleocene and possibly into the Cretaceous (Feldmann et al., 1995; Schweitzer and Feldmann, 2000b). Thus, recent work continues to extend the known time of origin of decapod families and the apparent timing of the major adaptive radiation within the Decapoda, and especially the Brachyura, further and further into geologic time. While it appears clear that the Eocene was a time of major evolutionary innovation within the

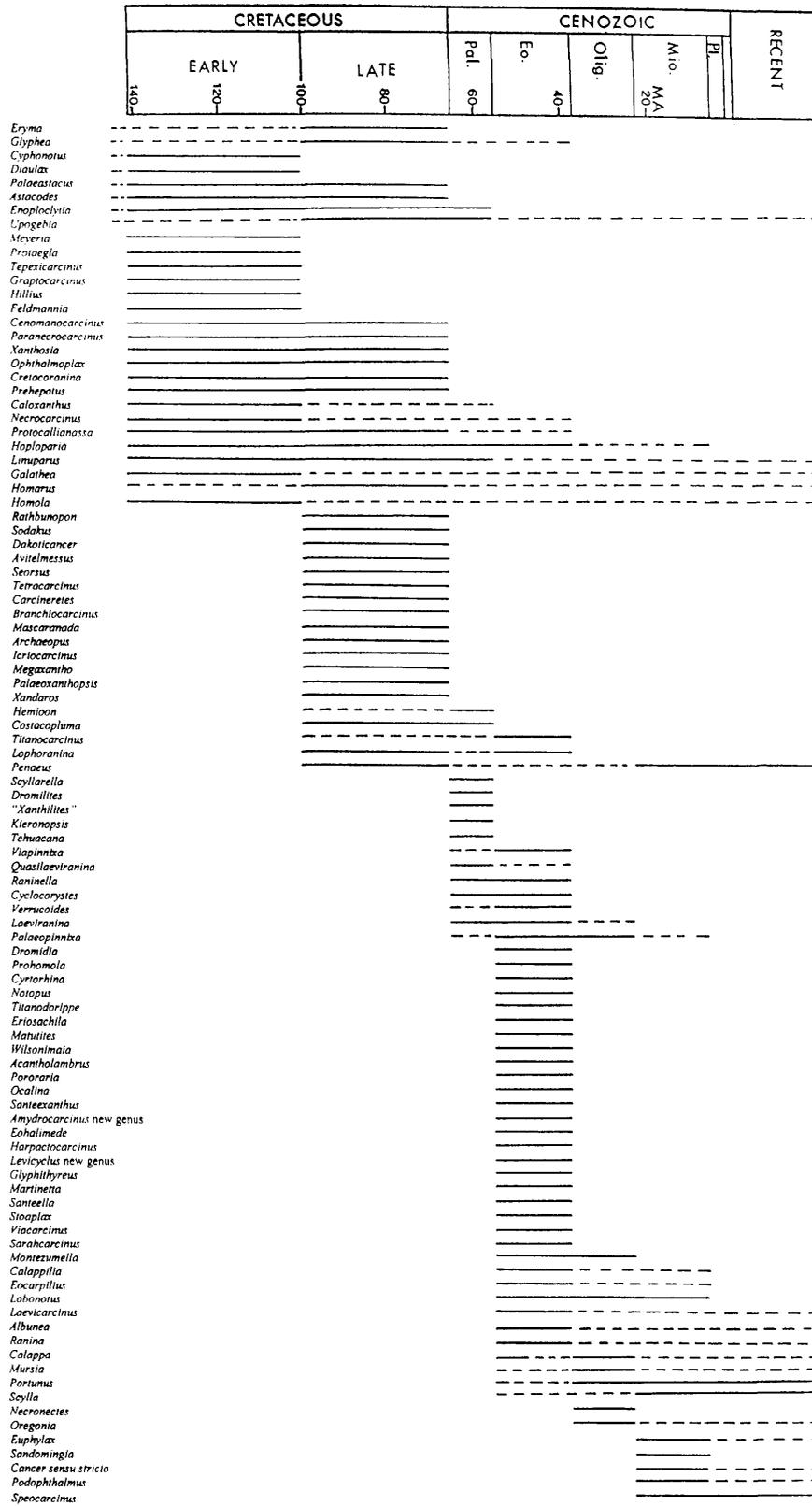


FIGURE 29—Geographic ranges of decapod taxa known from the tropical and subtropical Americas from the Early Cretaceous through the Recent. Dashed lines indicate occurrence outside of the tropical and subtropical Americas. Those decapods with temporally discontinuous ranges within the tropical and subtropical Americas (so-called Lazarus taxa) are shown with a continuous solid line during the interval in which no fossils are known for that taxon. Those taxa with temporally discontinuous ranges but that do not occur in the tropical and subtropical Americas on one or the other end of the range are shown with dashed lines during the interval in which no fossils are known for that taxon.

TABLE 5.—Origination and extinction rates for decapod genera. Rates were calculated by dividing the number of genera originating or becoming extinct during a particular time interval by the number of millions of years in that time interval. Number in parentheses is length of time interval in millions of years.

Time interval	Genera originating	Rate of originating (per Ma)	Genera becoming extinct	Rate of extinction (per Ma)
Miocene (19 Ma)	5	0.26	6	0.32
Oligocene (10 Ma)	3	0.3	3	0.32
Eocene (21 Ma)	35	1.67	36	1.71
Paleocene (10 Ma)	13	1.3	9	0.9
Maastrichtian (7.5 Ma)	7 or 11	0.9 or 1.5	12	1.6
Upper Cretaceous (34 Ma)	20	0.59	24	0.71
Lower Cretaceous (45 Ma)	19	0.42	7	0.16

Decapoda at both the generic and family levels (Glaessner, 1969; Warner, 1977; Schram, 1986), many families may have appeared well before that time based upon preliminary work by two of us (CES and RMF).

Evolutionary patterns at the Section level.—Within the Brachyura, or true crabs, there are three generally recognized categories, usually assigned as sections (Guinot, 1977). The Section Podotremata consists of the most primitive crabs which possess genital openings on the appendages in both males and females. Within the Section Heterotremata, the males possess genital openings on the appendages while females have genital openings on the sternum. In the Section Thoracotremata, both males and females have genital openings on the sternum. The Podotremata evolved by the Jurassic and proliferated in the Cretaceous. All tropical and subtropical American brachyurans that originated during the Triassic or Jurassic, and 62% of those originating during the Cretaceous, belong to this most primitive group of crabs. By post-Cretaceous time, approximately three-quarters of the decapods were heterotremes and only one thoracotreme, a member of the most derived group of crabs, is known from the fossil record of the tropical and subtropical Americas. This pattern parallels the pattern that was demonstrated in southern South America (Feldmann et al., 1997) and the North Pacific Ocean (Schweitzer, 2001b).

PALEOECOLOGY

Distinctive paleoecological trends, specifically, with regard to substrate preference of the decapods studies, are apparent for time periods as well as at various taxonomic levels (Appendix A). It is assumed here that decapods preferred a substrate similar to that which enclosed the fossils, and that large distances of post-mortem transport are absent, because such transport would destroy the delicate decapod carapace. Records for substrate preference were compiled from the literature and are thus based upon the rock type reported for each fossil occurrence.

Most tropical and subtropical American decapod occurrences during the Cretaceous were recovered from fine siliciclastic sediments; however, a substantial minority were recovered from carbonate sediments. The abundance of siliciclastic sediment was apparently due to the fine siliciclastics derived from mountains to both the east and west that were being deposited in the epeiric seas that existed in the Americas during this time. Carbonates developed in the areas starved of siliciclastic sediments in low latitudes and as a result of the warm climate during most of the Cretaceous. During the Paleocene, almost all of the decapod occurrences were in fine siliciclastic sediments. Eocene occurrences are nearly completely restricted to carbonate rocks, probably as a consequence of the warm climate and high sea level stand during the Eocene, absence of siliciclastic sediment, as well as the proximity of the area to the equator. Oligocene and Miocene occurrences have been recovered from both fine siliciclastics and carbonates, and a few Miocene decapods are known from coarse siliciclastic rocks.

Almost all of the macruran (lobster) genera display a pattern

of occurrence in either fine siliciclastic sediment or carbonate environments. *Homarus* and *Linuparus* are recorded only from fine siliciclastics, and *Hoploparia* is known from both types of sediments. The remainder of the macruran genera, *Astacodes*, *Palaeastacus*, *Enoploclytia*, *Glyphea*, *Eryma*, and *Meyeria* are known only from carbonate rocks. However, many of these taxa are known from siliciclastics from other regions of the world. Most of the anomuran genera were restricted to carbonate environments as well, including *Protocallianassa* and most of the paguroid taxa. However, these taxa are known from clastic deposits in other areas as well. *Upogebia* was recovered from both types of deposits, and *Galathea* was found in fine siliciclastics. It is possible that apparent substrate preferences are explainable by the occurrence of many carbonate rocks in the area due to its tropical and subtropical location.

Substrate preference within some brachyuran families is evident. The dakoticancrids are almost exclusively limited to fine siliciclastics, probably related to their occurrence in the Western Interior of the United States and the interior of Mexico. The Etyiidae, Retroplumidae and the Necrocarcinidae are also restricted to fine siliciclastic rocks. Most of the raninids were recovered from carbonate rocks, except during the Paleocene when all of the occurrences were in fine siliciclastic sediments. Other families do not seem to display a preference for a particular substrate.

SUMMARY

The decapod fauna of the tropical and subtropical Americas is largely composed of taxa that appear to have evolved within the region. A minority of genera appear to have dispersed to the area from such areas as the North Atlantic Ocean, the Tethys, the North Pacific Ocean, and the high southern latitudes. Many of the genera that evolved in the tropical and subtropical Americas remained endemic to the region. The patterns of evolution and extinction of decapods during the Cretaceous and Eocene are complicated; however, an extinction event appears to have occurred during both time intervals. The paucity of Oligocene and Miocene records is probably due to collecting bias and limited area of outcrop. The rates of origination and extinction of genera during the Upper Cretaceous, Eocene, Oligocene, and Miocene are identical or nearly so, while the rate of origination of genera is higher than the rate of extinction during the Lower Cretaceous and the Paleocene. The Maastrichtian shows either a high rate of extinction as compared to origination, or the rates are approximately equal, depending on the data used. Macrurans, anomurans, and the most primitive brachyuran genera appeared during the Triassic, Jurassic, and Cretaceous, while many of the more derived brachyurans evolved much later, during the Tertiary. That said, the range of the Goneplacidae, a more derived brachyuran family, has been extended from the Eocene into the Cretaceous. Thus, although it remains clear that the Eocene was a time of generic level radiation within the Brachyura, many of the derived families may have first appeared during the Cretaceous. Previous works have also extended the geologic record of several decapod families into the

Eocene or even into the Cretaceous, and the biogeographic history of the Decapoda is complex and differs markedly depending on the studied region. Thus, the evolutionary history of the Decapoda, especially the Brachyura, may be more ancient than previously believed. Further, as more decapods are described and more synthetic works conducted, this has revealed evolutionary and dispersal patterns within the Decapoda to be complex and highly dependent on regional geography and oceanographic factors.

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APPENDIX A

Occurrences of fossil decapods in the Gulf Coast-Mexico-Central America region, by periods and stages (where possible) and geographic location. Taxa belonging to the Callianassidae and those known only from claws were excluded, unless generic verification was determined by the authors. Partial specimens previously placed within the Nephropidae but considered questionable by Tshudy (1993), and partial or damaged specimens within the Raninidae considered by Tucker (1995) to be of indeterminate genus also were excluded from the study. Gulf Coastal Plain includes occurrences in Texas, Louisiana, Mississippi, Alabama, Georgia, and Tennessee. F = occurrence in fine siliciclastic sediments; CS = occurrence in coarse siliciclastic sediments; C = occurrence in carbonate rocks. Substrate preference was determined using the literature and may be approximate.

MAASTRICHTIAN

Belize

C *Carcineretes planetarius* Vega, Feldmann, Ocampo, and Pope, 1997

Northeastern Mexico

F *Costacopluma mexicana* Vega and Perrilliat, 1989

F *Dakoticancer australis* Rathbun, 1926b

F/C *Enoploclytia tumimanus* Rathbun, 1935

F *Mascaranada difuntaensis* Vega and Feldmann, 1991

F *Sodakus mexicanus* Vega, Feldmann and Villalobos-Hiriart, 1995

East-central Mexico

F *Branchiocarcinus cornatus* Vega, Feldmann, and Sour-Tovar, 1995

F *Costacopluma bishopi* Vega and Feldmann, 1992

F *Dakoticancer australis* Rathbun, 1926b

Southern Mexico

C *Carcineretes planetarius* Vega, Feldmann, Ocampo, and Pope, 1997

F *Costacopluma bishopi* Vega and Feldmann, 1992

C *Lophoranina precocious* Feldmann, Vega, Tucker, García-Barrera, and Avendaño., 1996

C *Megazantho zoque* Vega, Feldmann, García-Barrera, Filkorn, Pimentel, and Avendaño, 2001

C *Palaeozanthopsis meyapaquensis* (Vega, Feldmann, García-Barrera, Filkorn, Pimentel, and Avendaño, 2001); as *Parazanthopsis*

United States: Gulf Coastal Plain and the Carolinas

C *Avitelmessus grapsoides* Rathbun, 1923a

C *Prehepatus harrisi* Bishop, 1985

F *Seorsus wadei* Bishop, 1988b

F *Tetracarcinus subquadratus* Weller, 1905

CAMPANIAN

United States: Gulf Coastal Plain and the Carolinas

C *Astacodes maxwelli* Stenzel, 1945

C *Enoploclytia* sp. Beikirch and Feldmann, 1980

C *Notopoides (?) pflugervillensis* Beikirch and Feldmann, 1980 (indet. Tucker, 1995)

C *Palaeastacus kimzeyi* Rathbun, 1935

C *Protocallianassa pleuralum* Beikirch and Feldmann, 1980

SANTONIAN

United States: Gulf Coastal Plain and the CarolinasC *Astacodes maxwelli* Stenzel, 1945C *Enoploclytia* sp.F *Hoploparia blossomana* Rathbun, 1926b

CONIACIAN

United States: Gulf Coastal Plain and the CarolinasC *Enoploclytia triglypta* Stenzel, 1945

TURONIAN

ColombiaC *Ophthalmoplax spinosus* Feldmann, Villamil, and Kauffman, 1999C *Ophthalmoplax triambonatus* Feldmann and Villamil, 2002C *Pinnotheres?* sp. Feldmann, Villamil, and Kauffman, 1999**United States: Gulf Coastal Plain and the Carolinas**F *Astacodes davisi* Stenzel, 1945F *Cenomanocarcinus vanstraeleni* Stenzel, 1945F *Cretacoranina dichrous* (Stenzel, 1945); as *Notopocorystes*F *Homarus brittonestrus* Stenzel, 1945F *Homarus davisi* Stenzel, 1945F *Linuparus grimmeri* Stenzel, 1945F *Linuparus watkinsi* Stenzel, 1945F *Paranecrocarcinus ovalis* (Stenzel, 1945); as *Necrocarcinus*F *Upogebia racheochir* Stenzel, 1945

CENOMANIAN

United States: Gulf Coastal Plain and the CarolinasC *Graptocarcinus texanus* Roemer, 1887C *Palaeastacus walkeri* (Whitfield, 1878); as *Paramithrax?*C *Rathbunopon polyakron* Stenzel, 1945

UPPER CRETACEOUS (UNDIFFERENTIATED)

BrazilC *Ophthalmoplax brasiliانا* (Maury, 1930); as *Zanthopsis*C *Palaeozanthopsis cretacea* (Rathbun, 1902); as *Zanthopsis***Mexico: Baja California Norte**F *Archaeopus mexicanus* n. sp.F *Xandaros sternbergi* Bishop, 1988a**United States: California**F *Icriocarcinus xestos* Bishop, 1988a**United States: Gulf Coastal Plain and Carolinas**C *Avitelmessus grapsoides* Rathbun, 1923aF *Caloxanthus americana* Rathbun, 1935C *Cretacoranina testacea* (Rathbun, 1926b); as *Raninella*F *Dakoticancer overanus* Rathbun, 1917C *Enoploclytia sculpta* Rathbun, 1926bC *Eryma flecta* Rathbun, 1926bC *Eryma stantoni* Rathbun, 1935C *Glyphea(?) carolinensis* Rathbun, 1935C *Hoploparia mcnairensis* Rathbun, 1926bC *Hoploparia tennesseensis* Rathbun, 1926bF *Hoploparia blossomana* Rathbun, 1926bF *Linuparus canadensis* (Whiteaves, 1884); as *Hoploparia?*C *Ophthalmoplax stephensi* Rathbun, 1935C *Palaeastacus kimzeyi* Rathbun, 1935C *Palaeastacus selmaensis* Rathbun, 1935C *Penaeus wenasogensis* Rathbun, 1926bC *Petrochirus taylori* Rathbun, 1935C *Cretacoranina testacea* (Rathbun, 1926b)

ALBIAN

Puebla State, MexicoC *Protaegla miniscula* Feldmann, Vega, Applegate, and Bishop, 1998C *Tepexicarcinus tlayuensis* Feldmann, Vega, Applegate, and Bishop, 1998**United States: Gulf Coastal Plain and Carolinas**F *Cenomanocarcinus renfroae* (Stenzel, 1945); as *Necrocarcinus*F *Cenomanocarcinus oklahomensis* (Rathbun, 1935); as *Necrocarcinus*F *Cretacoranina punctatus* (Rathbun, 1935); as *Notopocorystes*C *Cyphonotus naglei* (Bishop, 1983); as *Palaeodromites*C *Diaulax roddai* Bishop, 1983C *Dioratiopus scotti* Bishop, 1983C *Enoploclytia wenoensis* Rathbun, 1935C *Enoploclytia wintoni* Stenzel, 1945F *Galathea cretacea* Stenzel, 1945C *Hillius youngi* Bishop, 1983C *Hoploparia dentonensis* Rathbun, 1935F *Linuparus vancouverensis* (Whiteaves, 1895); as *Podocrates*F *Linuparus adkinsi* Rathbun, 1935F *Necrocarcinus texensis* Rathbun, 1935F/C *Ophthalmoplax comancheensis* Rathbun, 1935C *Pagurus travisensis* Stenzel, 1945C *Pagurus banderus* Rathbun, 1935C *Palaeastacus walkeri* (Whitfield, 1878); as *Paramithrax?*F *Paranecrocarcinus graysonensis* (Rathbun, 1935); as *Necrocarcinus*F *Paranecrocarcinus moseleyi* (Stenzel, 1945); as *Necrocarcinus*C *Prehepatus hodgesi* Bishop, 1983C *Prehepatus cretaceous* Rathbun, 1935C *Protocallianassa klofi* Bishop, 1983C *Pseudonecrocarcinus stenzeli* Bishop, 1983C *Roemerus robustus* Bishop, 1983F *Feldmannia wintoni* (Rathbun, 1935); as *Xanthosia*F *Xanthosia reidi* Schweitzer Hopkins, Salva, and Feldmann, 1999F *Xanthosia pawpawensis* Schweitzer Hopkins, Salva, and Feldmann, 1999F *Xanthosia aspera* Rathbun, 1935

APTIAN

Puebla State, MexicoC *Astacodes maxwelli* Stenzel, 1944C *Graptocarcinus muiri* Stenzel, 1944C *Meyeria mexicana* Rathbun, 1935C *Meyeria pueblaensis* Feldmann, Vega, García-Barrera, Rico-Montiel, and Martínez-López, 1995

NEOCOMIAN (BARREMIAN)

ColombiaC *Necrocarcinus? olsoni* (Rathbun, 1937); as *Dakoticancer* (see Feldmann, Villamil, and Kauffman, 1999)

LOWER CRETACEOUS (UNDIFFERENTIATED)

United States: Gulf Coastal Plain and CarolinasF *Necrocarcinus texensis* Rathbun, 1935F *Ophthalmoplax comancheensis* Rathbun, 1935F *Prehepatus pawpawensis* Rathbun, 1935F *Feldmannia wintoni* (Rathbun, 1935); as *Xanthosia*

PALEOCENE

BrazilC *Costacopluma nordestina* Feldmann and Martins-Neto, 1995**United States: Gulf Coastal Plain and Carolinas**F *"Xanthilites" alabamensis* Rathbun, 1935F *Dromilites americana* Rathbun, 1935F *Hemioon bidentata* (Rathbun, 1935); as *Symmista*F *Hoploparia johnsoni* Rathbun, 1935F *Kierionopsis nodosa* Davidson, 1966F *Laeviranina bournei* (Rathbun, 1935); as *Notosceles*F *Linuparus wilcoxensis* Rathbun, 1935F *Matutites americanus* (Rathbun, 1935); as *Hepatisiscus*F *Paguristes johnsoni* Rathbun, 1935F *Pagurus alabamensis* Rathbun, 1935F *Quasilaeviranina ovalis* (Rathbun, 1935); as *Raninoides*F *Raninella eocenica* Rathbun, 1935F *Scyllarella aspera* Rathbun, 1935F *Scyllarella gibbera* Rathbun, 1935F *Symethis johnsoni* Rathbun, 1935C *Tehuacana tehuacana* Stenzel, 1944aF *Upogebia midwayensis* Rathbun, 1935**United States: West Coast**F *Cyclocorystes alderstoni* Squires, 1980

EOCENE

United States: Gulf Coastal Plain and CarolinasC *Santeexanthus wardi* Blow and Manning, 1996C *Acantholambrus baumi* Blow and Manning, 1996C *Albunea hahnae* Blow and Manning, 1996

- C Ameridromia hyneorum* Blow and Manning, 1996
C Calappa robertsi Ross, Lewis, and Scolaro, 1964
C Calappilia brooksi Ross and Scolaro, 1964
F Calappilia diglypta Stenzel, 1934
C Calappilia sitzi Blow and Manning, 1996
C Cyrtorhina füsseli Blow and Manning, 1996
C Dromidia bedetteae Blow and Manning, 1996
C Eocarpilius carolinensis Blow and Manning, 1996
C Eocarpilius blowi Feldmann, Bice, Schweitzer, Salva, and Pickford, 1998
C Eohalimede walleri Blow and Manning, 1996
C Eriosachila petiti Blow and Manning, 1996
C Glyphithyreus sturgeonii Feldmann, Bice, Schweitzer, Salva, and Pickford, 1998
C Harpactocarcinus rathbunae Stenzel, 1934
C Harpactocarcinus americanus Rathbun, 1928 (= *Zanthopsis peytoni* Stenzel, 1934)
C Harpactocarcinus carolinensis Rathbun, 1935
C Harpactocarcinus mississippiensis Rathbun, 1935
C Laevicarcinus dockeryi Blow and Manning, 1996
C Lobonotus natchitochensis Stenzel, 1934
C Lobonotus sandersi nom. corr. Blow and Manning, 1998
C Lobonotus bakeri (Rathbun, 1935); as *Plagiolophus*
C Lophoranina raynorae Blow and Manning, 1996
C Lophoranina georgiana (Rathbun, 1935); as *Ranina*
C Lophoranina rossi Blow and Manning, 1996
C Martinetta palmeri Blow and Manning, 1997
C Matutites anthonyae Blow and Manning, 1996
C Matutites miltonorum Feldmann, Bice, Schweitzer, Salva, and Pickford, 1998
C Ocalina floridana Rathbun, 1929
C Palaeocarpilius brodkorbi Lewis and Ross, 1965
C Pororaria? granulosa Feldmann, Bice, Schweitzer, Salva, and Pickford, 1998
C Prohomola katunai Blow and Manning, 1996
C Santeella lillyae Blow and Manning, 1996
C Sarahcarcinus campbellorum Blow and Manning, 1996
C Titanocarcinus purdyi Blow and Manning, 1996
C Titanocarcinus euglyphos Bittner, 1875
C Titanodorippe eocenica Blow and Manning, 1996
C Viacarcinus druidi Blow and Manning, 1996
C Wilsonimaia schneiderorum Blow and Manning, 1996
C Wilsonimaia ethelae Blow and Manning, 1996
- Caribbean**
- C Eriosachila bartholomaeensis* new comb. (Rathbun, 1919); as *Zanthopsis*
C Lophoranina porifera (Woodward, 1866); as *Ranina*
Montezumella rutheni Van Straelen, 1934
- Southern Mexico**
- C Calappilia* cf. *C. hondoensis* Rathbun, 1930b
C Dardanus mexicanus Vega, Cosma, Coutiño, Feldmann, Nyborg, Schweitzer, and Waugh, 2001
C Eriosachila sp.
C Laeviranina sp.
C Lophoranina cristaspina Vega, Cosma, Coutiño, Feldmann, Nyborg, Schweitzer, and Waugh, 2001
C Notopus minutus Vega, Cosma, Coutiño, Feldmann, Nyborg, Schweitzer, and Waugh, 2001
C Stoaplax nandachare Vega, Cosma, Coutiño, Feldmann, Nyborg, Schweitzer, and Waugh, 2001
C Verrucoides stenohedra Vega, Cosma, Coutiño, Feldmann, Nyborg, Schweitzer, and Waugh, 2001
C Viapinnixa alvarezii Vega, Cosma, Coutiño, Feldmann, Nyborg, Schweitzer, and Waugh, 2001
- Eastern Mexico**
- Harpactocarcinus americanus* Rathbun, 1928
- Baja California Sur, Mexico**
- C Amydrocarcinus dantei* n. gen. and sp.
C Calappilia hondoensis Rathbun, 1930b
- C Dardanus* cf. *D. mexicanus* Vega, Cosma, Coutiño, Feldmann, Nyborg, Schweitzer, and Waugh, 2001
C Eriosachila bajaensis n. sp.
C Levicyclus tepetate n. gen. and sp.
C Lobonotus mexicanus Rathbun, 1930b
C Lophoranina bishopi Squires and Demetron, 1992
Montezumella tubulata Rathbun, 1930b
C Ranina berglundi Squires and Demetron, 1992
- Panama**
- CS/C *Cancer santosi* (Rathbun, 1937); as *Lobocarcinus*
 CS *Eriosachila terryi* (Rathbun, 1937); as *Zanthopsis*
- Venezuela**
- F Eriosachila rathbunae* (Maury, 1930); as *Zanthopsis*
F Eoinachoides senni Van Straelen, 1933
F Falconoplax kugleri Van Straelen, 1933
F Raninoides rathbunae Van Straelen, 1933
- Caribbean**
- C Falconoplax bicarinella* Collins and Morris, 1976
C Palaeopinnixa perornata Collins and Morris, 1976
- OLIGOCENE**
- Eastern Mexico**
- Calappa flammea* (Herbst, 1794); as *Cancer*
Calappa zurcheri Bouvier, 1899
- Baja California Sur, Mexico**
- C Oregonia spinifera* n. sp.
C Necronectes nodosa n. sp.
- Panama**
- F Montezumella casayetensis* Rathbun, 1937
F Mursia obscura Rathbun, 1918
C Palaeopinnixa prima (Rathbun, 1918); as *Thaumastoplax*
- Venezuela**
- Calappa laraensis* Van Straelen, 1933
- Caribbean**
- C Calappa earlei* Withers, 1924
Necronectes summus Collins and Donovan, 1995
- United States: Gulf Coastal Plain and Carolinas**
- C Necronectes vaughni* Rathbun, 1935
Portunus (?) vicksburgensis Stenzel, 1935
- MIOCENE**
- Ecuador**
- F ?Penaes maddenii* Feldmann, Chirino-Galvez, Mason, Anderson, Duncan, Ward, and Salem, 1993
F ?Necronectes proavitus (Rathbun, 1918); as *Gatunia*
- Panama**
- Euphyllax callinectias* Rathbun, 1918
Euphyllax fortis Rathbun, 1918
?Necronectes proavitus (Rathbun, 1918)
- Venezuela**
- Parthenope venezuelensis* Van Straelen, 1933
- F Portunus oblongus* Rathbun, 1920
- Caribbean**
- Hepatus nodus* Collins and Morris, 1976
C Lobonotus sculptus (see Rathbun, 1919); as *Archaeopilumnus*
Necronectes proavitus (Rathbun, 1919); as *Gatunia*
Palaeopinnixa intermedia (Collins and Morris, 1976)
Persephona cf. *P. punctata* (Linnaeus, 1758)
C Podophthalmus domingensis Rathbun, 1919
C Portunus oblongus Rathbun, 1920
C Portunus gabbi Rathbun, 1919
Portunus haitensis Rathbun, 1923b
C Sandomingia yaquiensis Rathbun, 1919
C Scylla costata Rathbun, 1919
- United States: West Coast**
- CS *Speocarcinus berglundi* Tucker, Feldmann, and Powell, 1994
- Eastern Mexico**
- CS *Necronectes tajinensis* Vega, Feldmann, Villalobos-Hiriart, and Górguez, 1999
 CS *Portunus atecuicilis* Vega, Feldmann, Villalobos-Hiriart, and Górguez, 1999

APPENDIX B

Systematic list of decapod crustaceans, arrayed by time interval, occurring in the region of southeastern United States, Mexico, the Caribbean, Central America, and northern South America (CAM), during the Cretaceous and Tertiary. All localities from which the taxon has been collected are given for each listed taxon during each time interval and at each geographic location from which it has been reported. 1 indicates presence in an area; 0 indicates absence in an area; * indicates generic first occurrences; and † indicates genera endemic to the indicated geographic area; ∞ indicates origin in either of two places in which case both places will be so marked; ? indicates questionable occurrence in a region. Those entries marked with T or J indicate presence of the genus in that region during the Triassic and Jurassic, respectively. Abbreviations as for Table 2; WI = Western Interior of the United States; NATL includes some Northern European epicontinental occurrences.

Lower Cretaceous	CAM	NPAC	WI	NATL	TETH	HSL
Family Erymidae Van Straelen, 1924[1925]						
<i>Enoploclytia</i> McCoy, 1849	1	0	0	1 J*	0	1
<i>Eryma</i> von Meyer, 1840	0	0	0	1 J, T*	0	1
<i>Palaeastacus</i> Bell, 1850	1	0	0	0 J*	0	1
Family Nephropidae, Dana, 1852						
<i>Homarus</i> Weber, 1795	0	0	0	1*	0	0
<i>Hoploparia</i> McCoy, 1849	1	1	0	1∞	1∞	1
Family Glypheidae Zittel, 1885						
<i>Glyphea</i> von Meyer, 1835	0	0	0	1 J, T*	0	1
Family Callianassidae Dana, 1852						
<i>Protocallianassa</i> Beurlen, 1930	?1	0	0	?1	0	0
Family Mecochiridae Van Straelen, 1924[1925]						
<i>Meyeria</i> McCoy, 1849	1	0	0	1*	1	1
Family Palinuridae Latreille, 1802						
<i>Astacodes</i> Bell, 1863	1	0	0	1 J*	0	0
<i>Linuparus</i> White, 1847	1∞	0	0	1∞	0	0
Family Aeglididae Dana, 1852						
<i>Protaegla</i> Feldmann, Vega, Applegate, and Bishop, 1998	1*†	0	0	0	0	0
Family Galatheidae Samouelle, 1819						
<i>Galathea</i> Fabricius, 1793	1*	0	0	0	0	0
Family Homolidae White, 1847						
<i>Homola</i> White, 1847	1	1*	1	0	0	0
<i>Tepeixcarinus</i> Feldmann, Vega, Applegate, and Bishop, 1998	1*†	0	0	0	0	0
Family Dynomenidae Ortmann, 1892a						
<i>Cyphonotus</i> Bell, 1863	1	0	0	1 J*	0	0
<i>Diaulax</i> Bell, 1863	1	0	0	1 J*	0	0
<i>Graptocarcinus</i> Roemer, 1887	1*	0	0	0	0	0
Family Dorippidae MacLeay, 1838						
<i>Hillius</i> Bishop, 1983	1*†	0	0	0	0	0
Family Necrocarcinidae Förster, 1968						
<i>Cenomanocarcinus</i> Van Straelen, 1936	1*	0	0	0	0	0
<i>Necrocarcinus</i> Bell, 1863	1	1	1	1*	0	0
<i>Paranecrocarcinus</i> Förster, 1968	1	0	0	1*	0	0
Family Etyiidae Guinot and Tavares, 2001						
<i>Feldmannia</i> Guinot and Tavares, 2001	1*	0	0	0	0	0
<i>Xanthosia</i> Bell, 1863	1	0	1	1*	0	0
Family Raninidae de Haan, 1839						
<i>Cretacoranina</i> Mertin, 1941	1	0	0	1*	0	0
Family Hepatidae Stimpson, 1871						
<i>Prehepatus</i> Rathbun, 1935	1*	0	0	0	0	0
Family Carcineretidae Beurlen, 1930						
<i>Ophthalmoplax</i> Rathbun, 1935	1*†	0	0	0	0	0
Family Xanthidae s. l. MacLeay, 1838						
<i>Caloxanthus</i> A. Milne Edwards, 1864	1*	0	0	0	0	0
Upper Cretaceous	CAM	NPAC	WI	NATL	TETH	HSL
Family Penaeidae Rafinesque, 1815						
<i>Penaeus</i> Fabricius, 1798	1∞	0	0	1∞	0	0
Family Erymidae Van Straelen, 1924[1925]						
<i>Enoploclytia</i> McCoy, 1849	1	0	0	1	1	1
<i>Eryma</i> von Meyer, 1840	1	0	0	1	0	0
<i>Palaeastacus</i> Bell, 1850	1	0	0	1	0	0
Family Nephropidae Dana, 1852						
<i>Homarus</i> Weber, 1795	1	0	0	0	0	0
<i>Hoploparia</i> McCoy, 1849	1	1	1	1	1	1

APPENDIX B—Continued.

Upper Cretaceous	CAM	NPAC	WI	NATL	TETH	HSL
Family Glypheidae Zittel, 1885						
<i>Glyphea</i> von Meyer, 1835	1(?)	0	0	1	0	1
Family Callianassidae Dana, 1852						
<i>Protocallianassa</i> Beurlen, 1930	1	0	0	1	0	0
Family Upogebiidae Borradaile, 1903						
<i>Upogebia</i> Leach, 1814	1	0	0	1 J*	0	0
Family Palinuridae Latreille, 1802						
<i>Astacodes</i> Bell, 1863	1	0	0	0	0	0
<i>Linuparus</i> White, 1847	1	1	1	1	0	1
Family Prosopidae von Meyer, 1860						
<i>Rathbunopon</i> Stenzel, 1945	1	0	0	1*	0	0
Family Dynomenidae Ortmann, 1892a						
<i>Graptocarcinus</i> Roemer, 1887	1*	0	0	1	0	0
Family Homolidae De Haan, 1839						
<i>Homola</i> Leach, 1815	0	0	1	1	0	0
Family Raninidae de Haan, 1839						
<i>Cretacorantina</i> Mertin, 1941	1	0	0	1	1	1
<i>Hemioon</i> Bell, 1863	0	0	0	1*	0	0
<i>Lophoranina</i> Fabiani, 1910	1*	0	0	0	0	0
Family Dorippidae MacLeay, 1838						
<i>Sodakus</i> Bishop, 1978	1	0	1*	0	0	0
Family Necrocarcinidae Förster, 1968						
<i>Cenomanocarcinus</i> Van Straelen, 1936	1	0	0	1	1	0
<i>Necrocarcinus</i> Bell, 1863	0	0	0	1	0	1
<i>Paranecrocarcinus</i> Förster, 1968	1	0	1	0	1	0
Family Dakoticancridae Rathbun, 1917						
<i>Dakoticancer</i> Rathbun, 1917	1 ∞	0	1 ∞	0	0	0
<i>Avitelmessus</i> Rathbun, 1923a	1*†	0	0	0	0	0
<i>Seorsus</i> Bishop, 1988b	1*†	0	0	0	0	0
<i>Tetracarcinus</i> Weller, 1905	1*†	0	0	0	0	0
Family Etyiidae Guinot and Tavares, 2001						
<i>Xanthosia</i> Bell, 1863	1	0	1	1	1	0
Family Hepatidae Stimpson, 1871						
<i>Prehepatus</i> Rathbun, 1935	0	1	0	1	1	0
Family Carcineretidae Beurlen, 1930						
<i>Carcineretes</i> Withers, 1922	1*†	0	0	0	0	0
<i>Branchiocarcinus</i> Vega, Feldmann, and Sour-Tovar, 1995	1*†	0	0	0	0	0
<i>Mascaranada</i> Vega and Feldmann, 1991	1*†	0	0	0	0	0
<i>Ophthalmoplax</i> Rathbun, 1935	1†	0	0	0	0	0
Family Retroplumidae Gill, 1894						
<i>Archaeopus</i> Rathbun, 1908	1 ∞	1 ∞	0	0	0	0
<i>Costacopluma</i> Collins and Morris, 1975	1*	0	0	1	1	0
Family Goneplacidae MacLeay, 1838						
<i>Icriocarcinus</i> Bishop, 1988a	1*†	0	0	0	0	0
Family Xanthidae s. l. MacLeay, 1838						
<i>Caloxanthus</i> A. Milne Edwards, 1864	1	0	0	1	0	0
<i>Megaxantho</i> Vega, Feldmann, García-Barrera, Filkorn, Pimentel, and Avendaño, 2001	1*†	0	0	0	0	0
<i>Palaeozanthopsis</i> Beurlen, 1958	1*†	0	0	0	0	0
<i>Titanocarcinus</i> A. Milne Edwards, 1863	0	0	0	1*	0	0
<i>Xandaros</i> Bishop, 1988a	1*†	0	0	0	0	0
Paleocene	CAM	NPAC	WI	NATL	TETH	HSL
Family Penaeidae Rafinesque, 1815						
<i>Penaeus</i> Fabricius, 1798	0	0	0	0	?1	0
Family Erymidae Van Straelen, 1924[1925]						
<i>Enoploclytia</i> McCoy, 1849	1	0	0	0	0	0
Family Nephropidae Dana, 1852						
<i>Hoploparia</i> McCoy, 1849	1	0	1	1	0	0
Family Glypheidae Zittel, 1885						
<i>Glyphea</i> von Meyer, 1835	0	0	0	0	0	1

APPENDIX B—Continued.

Paleocene	CAM	NPAC	WI	NATL	TETH	HSL
Family Callianassidae Dana, 1852						
<i>Protocallianassa</i> Beurlen, 1930	0	0	0	0	0	1
Family Upogebiidae Borradaile, 1903						
<i>Upogebia</i> Leach, 1814	1	0	0	0	0	0
Family Palinuridae Latreille, 1802						
<i>Linuparus</i> White, 1847	1	0	0	0	0	1
Family Scyllaridae Latreille, 1825						
<i>Scyllarella</i> Rathbun, 1935	1*†	0	0	0	0	0
Family Dromiidae de Haan, 1833						
<i>Dromilites</i> H. Milne Edwards, 1837	1*	0	0	0	0	0
Family Raninidae de Haan, 1839						
<i>Hemioon</i> Bell, 1863	1	0	0	0	0	0
<i>Laeviranina</i> Lörenthey and Beurlen, 1929	1*	0	0	1	0	0
<i>Quasilaeviranina</i> Tucker, 1998	1*	0	0	0	0	0
<i>Raninella</i> A. Milne Edwards, 1862	1∞	0	0	0	1∞	0
Family Symethidae Goeke, 1981						
<i>Symethis</i> Weber, 1795	1*	0	0	0	0	0
Family Corystidae Samouelle, 1819						
<i>Cyclocorystes</i> Bell, 1858	1*	0	0	0	0	0
Family Retroplumidae Gill, 1894						
<i>Costacopluma</i> Collins and Morris, 1975	1	0	0	0	1	0
Family Hexapodidae Miers, 1886						
<i>Palaeopinnixa</i> Via, 1966	0	0	0	0	0	1*
Family Xanthidae s. l. MacLeay, 1838						
<i>Caloxanthus</i> A. Milne Edwards, 1862–1865	0	0	0	1	0	0
<i>Verrucoides</i> Vega, Cosma, Coutiño, Feldmann, Nyborg, Schweitzer, and Waugh, 2001	0	0	0	1*	0	0
"Xanthilites" <i>alabamensis</i> Rathbun, 1935	1*	0	0	0	0	0
Family Pinnotheridae de Haan, 1833						
<i>Viapinnixa</i> Schweitzer and Feldmann, 2001	0	0	0	1*	0	0
Indeterminate Family						
<i>Kieronopsis</i> Davidson, 1966	1*†	0	0	0	0	0
<i>Tehuacana</i> Stenzel, 1944b	1*†	0	0	0	0	0
Eocene	CAM	NPAC	WI	NATL	TETH	HSL
Family Penaeidae Rafinesque, 1815						
<i>Penaeus</i> Fabricius, 1798	0	0	0	0	1	0
Family Nephropidae Dana, 1852						
<i>Homarus</i> Weber, 1795	0	0	0	1	0	0
<i>Hoploparia</i> McCoy, 1849	1	0	0	1	1	0
Family Glypheidae Zittel, 1885						
<i>Glyphea</i> von Meyer, 1835	0	0	0	0	0	1
Family Callianassidae Dana, 1852						
<i>Protocallianassa</i> Beurlen, 1930	0	0	0	0	0	1
Family Palinuridae Latreille, 1802						
<i>Linuparus</i> White, 1847	0	0	0	0	0	1
Family Albuneidae Stimpson, 1858a						
<i>Albunea</i> Weber, 1795	1∞	0	0	0	1∞	0
Family Dromiidae de Haan, 1833						
<i>Ameridromia</i> Blow and Manning, 1996	1*†	0	0	0	0	0
<i>Dromidia</i> Stimpson, 1859	1*	0	0	0	0	0
Family Homolidae de Haan, 1839						
<i>Prohomola</i> Karasawa, 1992	1∞	1∞	0	0	0	0
Family Raninidae de Haan, 1839						
<i>Cyrtorhina</i> Monod, 1956	1	0	0	0	1*	0
<i>Laeviranina</i> Lörenthey and Beurlen, 1929	1	1	0	1	1	1
<i>Lophoranina</i> Fabiani, 1910	1	1	0	0	1	0
<i>Notopus</i> de Haan, 1841	1	0	0	0	1*	0
<i>Quasilaeviranina</i> Tucker, 1998	0	0	0	0	1	1
<i>Ranina</i> Lamarck, 1801	1*	1	0	0	1	0
<i>Raninella</i> A. Milne Edwards, 1862–1865	1	0	0	0	0	0
<i>Raninoides</i> H. Milne Edwards, 1837	1	1	0	0	0	0

APPENDIX B—Continued.

Eocene	CAM	NPAC	WI	NATL	TETH	HSL
Family Dorippidae MacLeay, 1838						
<i>Titanodorippe</i> Blow and Manning, 1996	1*†	0	0	0	0	0
Family Calappidae de Haan, 1833						
<i>Calappa</i> Weber, 1795	0	0	0	0	0	1*
<i>Calappilia</i> A. Milne Edwards, 1873	1∞	0	0	0	1∞	0
<i>Mursia</i> Leach, in Desmarest, 1823	0	1*	0	0	0	0
Family Hepatidae Stimpson, 1871						
<i>Eriosachila</i> Blow and Manning, 1996	1*	1	0	0	0	0
<i>Matutites</i> Blow and Manning, 1996	1*†	0	0	0	0	0
Family Majidae s. l. Samouelle, 1819						
<i>Eoinachoides</i> Van Straelen, 1933	1*†	0	0	0	0	0
<i>Wilsonimaia</i> Blow and Manning, 1996	1*†	0	0	0	0	0
Family Parthenopidae MacLeay, 1838						
<i>Acantholambrus</i> Blow and Manning, 1996	1*†	0	0	0	0	0
<i>Parthenope</i> Weber, 1795	0	0	0	0	1*	0
Family Atelecyclidae Ortmann, 1893						
<i>Levicyclus</i> n. gen.	1*†	0	0	0	0	0
Family Cheiragonidae Ortmann, 1893						
<i>Montezumella</i> Rathbun, 1930b	1	1	0	1*	1	0
Family Cancridae Latreille, 1802						
<i>Cancer</i> s. l. Linnaeus, 1758	1?	0	0	0	0	0
Family Corystidae Samouelle, 1819						
<i>Cyclocorystes</i> Bell, 1858	0	0	0	1	0	0
Family Portunidae Rafinesque, 1815						
<i>Pororaria</i> Glaessner, 1980	1?	0	0	0	0	1
<i>Portunus</i> Weber, 1795	0	0	0	0	1*	0
Family Carpiidae Ortmann, 1893						
<i>Eocarpilus</i> Blow and Manning, 1996	1*	0	0	0	0	0
<i>Ocalina</i> Rathbun, 1929	1*†	0	0	0	0	0
<i>Santeexanthus</i> Blow and Manning, 1996	1*†	0	0	0	0	0
Family Hexapodidae Miers, 1886						
<i>Palaeopinnixa</i> Via, 1966	1	1	0	0	0	0
Family Xanthidae s. l. Macleay, 1838						
<i>Amydrocarcinus</i> n. gen.	1*†	0	0	0	0	0
<i>Eohalimede</i> Blow and Manning, 1996	1*†	0	0	0	0	0
<i>Falconoplax</i> Van Straelen, 1933	1*†	0	0	0	0	0
<i>Harpactocarcinus</i> A. Milne Edwards, 1862	1	0	0	0	1*	0
<i>Laevicarcinus</i> Lörenthey and Beurlen, 1929	1∞	0	0	1∞	1∞	0
<i>Lobonotus</i> A. Milne Edwards, 1864	1*	0	0	0	0	0
<i>Glyphithyreus</i> Reuss, 1859	1	0	0	1*	1	0
<i>Martinetta</i> Blow and Manning, 1997	1*†	0	0	0	0	0
<i>Santeella</i> Blow and Manning, 1996	1*†	0	0	0	0	0
<i>Stoaplax</i> Vega, Cosma, Coutiño, Feldmann, Nyborg, Schweitzer, and Waugh, 2001	1*†	0	0	0	0	0
<i>Titanocarcinus</i> A. Milne Edwards, 1863	1	0	0	1	1	0
<i>Verrucoides</i> Vega, Cosma, Coutiño, Feldmann, Nyborg, Schweitzer, and Waugh, 2001	1	0	0	0	0	0
Family Eumedonidae Neumann, 1878						
<i>Viacarcinus</i> Blow and Manning, 1996	1*†	0	0	0	0	0
Family Pinnotheridae de Haan, 1833						
<i>Viapinnixa</i> Schweitzer and Feldmann, 2001	1	0	0	0	0	0
<i>Sarahcarcinus</i> Blow and Manning, 1996	1*†	0	0	0	0	0
Oligocene	CAM	NPAC	WI	NATL	TETH	HSL
Family Nephropidae Dana, 1852						
<i>Homarus</i> Weber, 1795	0	0	0	1	0	0
Family Raninidae de Haan, 1839						
<i>Raninoides</i> H. Milne Edwards, 1837	0	1	0	0	0	0
Family Calappidae de Haan, 1833						
<i>Calappa</i> Weber, 1795	1	1	0	1	1	0
<i>Calappilia</i> A. Milne Edwards, 1873	0	0	0	0	1	0
<i>Mursia</i> Leach in Desmarest, 1823	1	1	0	0	0	0
Family Hepatidae Stimpson, 1871						
<i>Hepatus</i> Latreille, 1802	0	0	0	0	1*	0

APPENDIX B—Continued.

Oligocene	CAM	NPAC	WI	NATL	TETH	HSL
Family Majidae Samouelle, 1819						
<i>Oregonia</i> Dana, 1851b	1*†	0	0	0	0	0
Family Cheiragonidae Ortmann, 1893						
<i>Montezumella</i> Rathbun, 1930b	1	0	0	0	0	0
Family Portunidae Rafinesque, 1815						
<i>Euphylax</i> Stimpson, 1860	1*†	0	0	0	0	0
<i>Necronectes</i> A. Milne Edwards, 1881	1*	0	0	0	0	0
<i>Portunus</i> Weber, 1795	1	0	0	1	1	0
Family Hexapodidae Miers, 1886						
<i>Palaeopinnixa</i> Via, 1966	1	0	0	0	0	0
Family Xanthidae s. l. MacLeay, 1838						
<i>Lobonotus</i> A. Milne Edwards, 1864	1	0	0	0	0	0
Miocene	CAM	NPAC	WI	NATL	TETH	HSL
Family Penaeidae Rafinesque, 1815						
<i>Penaeus</i> Fabricius, 1798	1	0	0	0	0	0
Family Nephropidae Dana, 1852						
<i>Homarus</i> Weber, 1795	0	0	0	1	0	0
Family Raninidae de Haan, 1839						
<i>Raninoides</i> H. Milne Edwards, 1837	1	0	0	0	1	0
Family Calappidae de Haan, 1833						
<i>Calappa</i> Weber, 1795	1	0	0	1	1	0
<i>Calappilia</i> A. Milne Edwards, 1873	0	0	0	0	0	1
<i>Mursia</i> Leach in Desmarest, 1823	0	1	0	1	0	0
Family Hepatidae Stimpson, 1871						
<i>Hepatus</i> Latreille, 1802	1	0	0	0	0	0
Family Leucosiidae Samouelle, 1819						
<i>Persephona</i> Leach, 1817	1*	0	0	0	0	0
Family Parthenopidae MacLeay, 1838						
<i>Parthenope</i> Weber, 1795	1	0	0	0	1	0
Family Cancridae Latreille, 1802						
<i>Cancer</i> s. s. Linnaeus, 1758	0	1*	0	0	0	0
Family Portunidae Rafinesque, 1815						
<i>Euphylax</i> Stimpson, 1860	1†	0	0	0	0	0
<i>Necronectes</i> A. Milne Edwards, 1881	1	0	0	0	1	0
<i>Podophthalmus</i> Lamarck, 1801	1*	0	0	0	0	0
<i>Portunus</i> Weber, 1795	1	0	0	0	1	0
<i>Scylla</i> de Haan, 1833	1	0	0	0	1	1
Family Carpiliidae Ortmann, 1893						
<i>Eocarpilius</i> Blow and Manning, 1996	0	0	0	0	1	0
Family Hexapodidae Miers, 1886						
<i>Palaeopinnixa</i> Via, 1966	0	1	0	0	0	0
Family Xanthidae s. l. MacLeay, 1838						
<i>Laevicarcinus</i> Lörenthey and Beurten, 1929	0	0	0	0	1	0
<i>Lobonotus</i> A. Milne Edwards, 1864	1	0	0	0	0	0
<i>Speocarcinus</i> Stimpson, 1859	1*	0	0	0	0	0
Family Ocypodidae Rafinesque, 1815						
<i>Sandomingia</i> Rathbun, 1919	1*	0	0	0	0	0