

## NEW MIDDLE EOCENE DECAPODS (CRUSTACEA) FROM CHIAPAS, MÉXICO

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**ABSTRACT**—Decapod crustacean specimens from the middle Eocene San Juan Formation in central Chiapas represent the first record of Eocene decapods in southern México. New taxa include: *Dardanus mexicanus* new species (Diogenidae), *Lophoranina cristaspina* new species, *Notopus minutus* new species (Raninidae); *Verrucoides stenohedra* new genus and new species (Xanthidae); *Stoaplax nandachare* new genus and new species (Goneplacidae); and *Viapinnixa alvarezii* new species (Pinnotheridae). *Verrucoides verrucoides* new genus and new combination from the Paleocene of Greenland represents a new combination. In addition, the fauna includes *Callianassa* sensu lato sp., *Laeviranina* sp., *Calappilia* cf. *C. hondoensis* Rathbun, 1930, *Eriosachila* sp., and indeterminate calappid and xanthoid taxa. This assemblage bears close relationship with coeval faunas in the Tethyan region of southern Europe and southern North America and with Paleocene faunas of Greenland, strengthening the evidence for previously described patterns of dispersal within the Decapoda.

### INTRODUCTION

**E**OCENE DEPOSITS of Chiapas State, México, contain a diverse fauna. Calcareous algae, large foraminifera, corals, gastropods, bivalves, nautiloids, annelids, spatangoid echinoderms, and fish remains have all been reported from central Chiapas. In particular, the Eocene San Juan Formation has been studied extensively. Except for the mention of arthropod remains from the San Juan Formation by Frost and Langenheim (1974, p. 315), fossil crustaceans from the Eocene of this region have not been formally reported. The lower Maastrichtian Ocozocuaula Formation, which crops out in the vicinity of Tuxtla Gutiérrez in Chiapas, contains several species of decapod crustaceans (Feldmann et al., 1996; Vega et al., 2001).

Numerous Eocene decapods previously have been described from other sites in México. These include *Calappilia hondoensis* Rathbun, 1930; *Callianassa tepetatis* Rathbun, 1930; and *Ranina* sp. from the Tepetate Formation (Rathbun, 1930). *Lobonotus mexicanus* Rathbun, 1930 and *Montezumella tubulata* Rathbun, 1930, are known from upper Eocene beds of Arrollo Colorado. Each of these occurrences is from Baja California Norte. *Ranina berglundii* Squires and Demetron, 1992, and *Lophoranina bishopi* Squires and Demetron, 1992, were described from the Bateque Formation, Baja California Sur. *Harpactocarcinus americanus* Rathbun, 1928, and *Callianassa pustulata* Withers, 1926, were reported from the states of Tamaulipas and Veracruz, respectively (Rathbun, 1930).

Several decapod taxa were recovered from the Eocene deposits under study. These include *Dardanus mexicanus* n. sp. of the Diogenidae; *Lophoranina cristaspina* n. sp. and *Notopus minutus* n. sp. of the Raninidae; *Verrucoides stenohedra* n. gen. and n. sp. of the Xanthidae sensu lato; *Stoaplax nandachare* n. gen. and n. sp. of the Goneplacidae; and *Viapinnixa alvarezii* n. sp. of the Pinnotheridae. In addition to these taxa, *Callianassa* sensu lato sp. (Callianassidae), *Laeviranina* sp. (Raninidae), *Calappilia* cf. *C. hondoensis* (Calappidae), *Eriosachila* sp. (Hepatidae), and calappid and xanthoid specimens of indeterminate identity were recovered from this unit.

The decapod fauna of the unit is quite diverse, encompassing members of at least eight families. This first report of Eocene decapods from Chiapas, México, is significant because the fauna bears close relationship with the Tertiary North Atlantic and Tethyan decapod faunas, strengthening the view that the Tethys may

have been an area of origin during the early Tertiary from which decapods dispersed to other regions. Southern México and Central America may have been a part of that area of origin for taxa, given the coeval occurrences of many taxa on each side of the Atlantic Ocean. Taxa may have been transported from Europe and the North Atlantic to North America and México, or vice versa, via ocean surface currents as has been previously suggested (Feldmann et al., 1998; Schweitzer and Feldmann, 2000a; Schweitzer and Salva, 2000).

### STRATIGRAPHY AND LOCALITIES

The type section for the San Juan Formation is located near El Bosque, Chiapas (Licari, 1960). Allison (1967) constructed a composite section for the San Juan Formation and subdivided the unit into three members; the Lower *Ostrea*-Siltstone Member; the Middle Sandstone-Grit Member; and the Upper Sandstone-Siltstone Member. The stratigraphic sequence at the type section was incomplete, however. Ferrusquía-Villafranca (1996) described the lithologic variation within the formation and estimated the probable composite thickness of the San Juan Formation to be 800 m. Fossil decapods have been collected from two localities, 1004 and 1005, within the San Juan Formation in the vicinity of Tuxtla Gutiérrez. These localities, described below, have been entered in the catalogue of localities of the Instituto de Historia Natural del Estado de Chiapas, Tuxtla Gutiérrez, Chiapas, México.

Locality 1004 is exposed on the northwest side of Mesa de Copoya, 5 km southeast from Tuxtla Gutiérrez, near the highway to Villa Flores (Fig. 1). These outcrops are included within the Middle Sandstone-Grit Member, which attains a thickness of 275 m (Allison, 1967). The rocks of the Middle Sandstone-Grit Member are tan sandstone interbedded with quartz-pebble conglomerates. The abundance of *Nummulites striatoreticulatus* prompted referring to these rocks as “*Nummulites* beds” (Pechaux, 1984; Aguilar, 1993). Other foraminifera reported by Durham et al. (1955) include: *Camerina guayabalensis*, *Eulinderina guayabalensis*, *Lepidocyclina (Polylepidina) antillea*, *Pseudophragmina (Proporocyclina) perpussilla*, *P. (Proporocyclina) zaragosensis*, *Helicostegina gyralis*, and *Ferayina coralliformis*. These species were used to document a middle Eocene age for the rocks in the upper part of Mesa de Copoya (Durham et al., 1955; Allison, 1967). Aguilar (1993) described *Amphistegina parvula*, *Pseudophragmina (Proporocyclina) teres*, *Helicostegina dimorpha*, *Eofabianina cushmani*, and *Quinqueloculina* sp. from this locality.

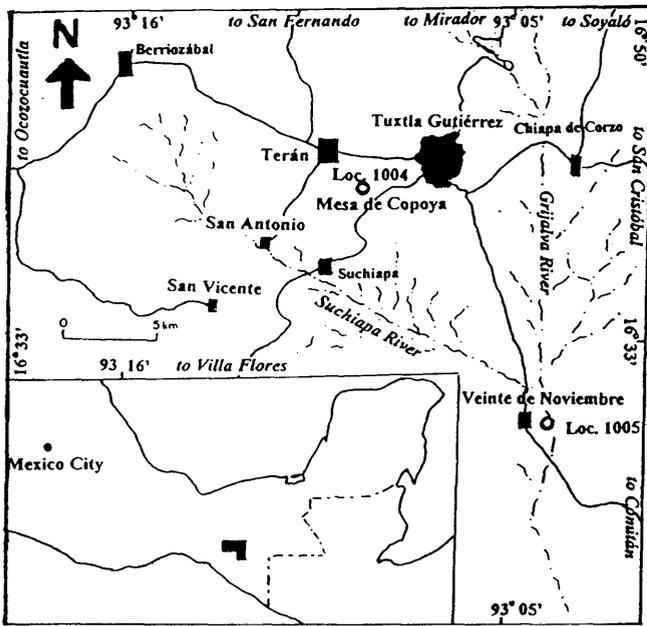


FIGURE 1—Location map of a portion of Chiapas, México, showing the position of the two sites in the San Juan Formation from which decapods were collected.

Frost and Langenheim (1974) found these same species in localities at Mesa de Copoya and, based upon the occurrence of *Lepidocyclus (Polylepidina) antillea* in the Middle Sandstone-Grit Member, proposed a middle Eocene age for this part of the San Juan Formation.

Frost and Langenheim (1974), and Ferrusquía-Villafranca (1996) proposed a correlation in age and lithology between the San Juan Formation and the Uzpanapa Conglomerate of northwestern Chiapas and Veracruz (Benavides, 1956; Contreras-Velázquez, 1956; Acevedo, 1960). A detailed description of stratigraphic units equivalent to the San Juan Formation is reported in Frost and Langenheim (1974, p. 37, 38).

Remains of *Dardanus mexicanus* n. sp., *Lophoranina cristaspina* n. sp., *Calappilia* sp., and *Eriosachila* sp. were found at locality 1004 (Fig. 1). This section has been identified as the Middle Sandstone-Grit Member of the San Juan Formation. The unit is a gray calcareous sandstone which weathers to a dark brown color. The abundance of foraminifera in association with gastropods, crustaceans, and fish causes some horizons to appear coquina-like (Fig. 2).

The rocks at Mesa de Copoya were suggested to have been deposited under shallow shelf conditions (Gutiérrez-Gil, 1956; Frost and Langenheim, 1974; Quezada-Muñetón, 1990). However, influence of continental waters was suggested by Aguilar (1993), based upon the presence of roots and wood remains. Alternation of carbonates with sandstones and siltstones may represent periodic influx of freshwater into a shallow marine environment. These conditions, along with sedimentary structures such as crossbedding, represent variable current directions and strength. At this locality, broken carapace fragments with angular margins of *Lophoranina cristaspina* n. sp. and *Calappilia* sp. were found. Only a single, small juvenile specimen of *Lophoranina cristaspina* n. sp. was found in nearly complete condition. We interpret these crab remains to be molts which were transported. Via (1965) suggested that species of *Lophoranina* inhabited areas with calcareous substrates containing benthic foraminiferans in warm, tropical, shallow environments. This was confirmed by the occurrence of *Lophoranina precocius* in lagoonal sediments of the Ocozocuaula Formation (Feldmann et al., 1996).

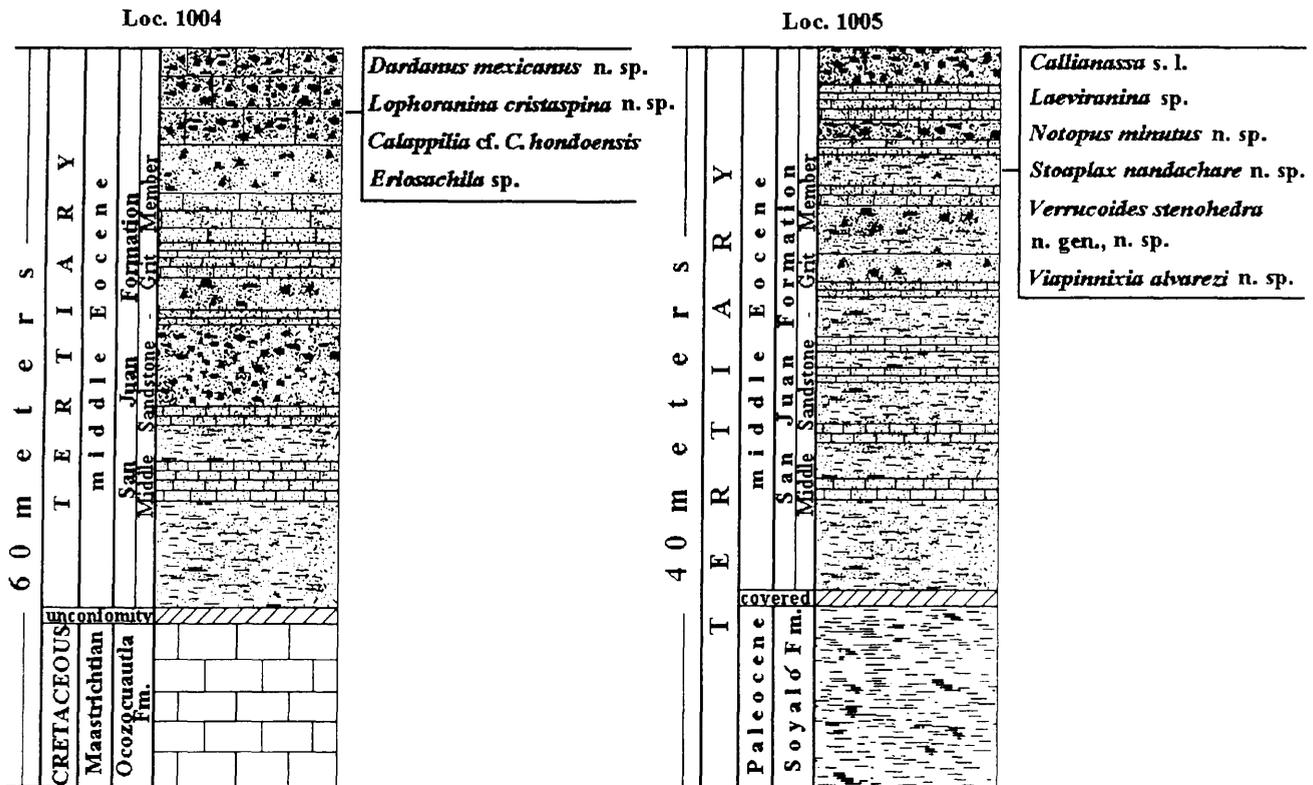


FIGURE 2—Stratigraphic sections from Mesa de Copoya and Veinte de Noviembre, Chiapas, México.

The presence of a fauna limited to fish, gastropods, and a few decapods, coupled with miliolid foraminifera, is suggestive of a restricted marine habitat at Mesa de Copoya. It is possible that organisms tolerant of normal salinities would be excluded. A lagoonal paleoenvironment for the sediments at Mesa de Copoya was previously suggested by Aguilar (1993). In marked contrast, the rocks at Locality 1005, described below, have a much more diverse fauna including corals and echinoderms which are often excluded from habitats characterized by elevated or reduced salinities.

Locality 1005 is located 5 km north of Veinte de Noviembre, which is 40 km southeast of Tuxtla Gutiérrez, on highway 190 between Tuxtla Gutiérrez and Angostura (Fig. 1). The lithology probably represents the middle part of the San Juan Formation, as it includes marl and calcareous sandstone. Coralline limestone and quartz conglomerate horizons are present at the top of the exposed section (Fig. 2). Presence of the foraminiferans *Lepidocyclina* (*Polylepidina*) *antillea*, *Storrsella* *haastersi*, *Sigmoilopsis* *centralamericana*, *Nummulites* (*Paleonummulites*) *panamensis*, and *Pellatospirella* *matleyi* suggest a middle Eocene age for the sediments of this locality. However, large foraminifera are not as abundant as they are at Mesa de Copoya. At this site, specimens of *Callianassa* *sensu lato* sp., *Laeviranina* sp., *Notopus* *minutus* n. sp., *Stoaplax* *nandachare* n. gen., n. sp., *Verrucoides* *stenohedra* n. gen., n. sp., *Viapinnixa* *alvarezii* n. sp., and indeterminate calappid and xanthoid taxa were collected. All decapods remains were partial or entire carapace exuvia; no ventral surfaces or appendages were present. Associated fauna include corals, gastropods, bivalves, nautiloids, annelids, and spatangoid echinoderms, representing a much more diverse assemblage than that at Mesa de Copoya. Most of the nautiloids exhibited broken shells; however, the rest of the mollusks were well preserved. The paleoenvironment probably represents an open marine, shallow shelf habitat.

#### SYSTEMATIC PALEONTOLOGY

- Order DECAPODA Latreille, 1802  
 Infraorder THALASSINIDEA Latreille, 1831  
 Superfamily CALLIANASSOIDEA Dana, 1852  
 Family CALLIANASSIDAE Dana, 1852  
 Genus CALLIANASSA Leach, 1814  
*CALLIANASSA sensu lato* sp.  
 Figure 3.1, 3.3

*Material examined.*—Specimens IHNCH-3424, 3425, 3426, and 3466, are deposited in the paleontological collection of the Instituto de Historia Natural de Chiapas, located in Tuxtla Gutiérrez, Chiapas.

*Occurrence.*—The specimens were collected from locality 1005 in the middle of the San Juan Formation, at Veinte de Noviembre, Chiapas, México.

*Discussion.*—Four fragments of claws (IHNCH-3424, 3425, 3478) are referable to *Callianassa* s.l. One of the specimens, IHNCH-3424, (Fig. 3.1) consists of what appears to be the outer surface of a left hand with a maximum height of 13.9 mm, measured just distal to the long, straight proximal joint which is oriented at right angles to the long axis of the hand. The upper half of the outer surface is smooth and the lower half is delicately scabrous. Another fragment, IHNCH-3425, (Fig. 3.3) consists of the mold of the interior of the cuticle forming the distal part of a hand and fixed finger. The surface of the hand seems to be weakly scabrous and there are two broad nodes marking the position of articulation of the dactylus. The fixed finger is long, slightly downturned, and tapers to a sharp, upturned terminus. The occlusal surface is finely serrated and bears a single, domed denticle about one-third the distance from the base of the finger to the tip.

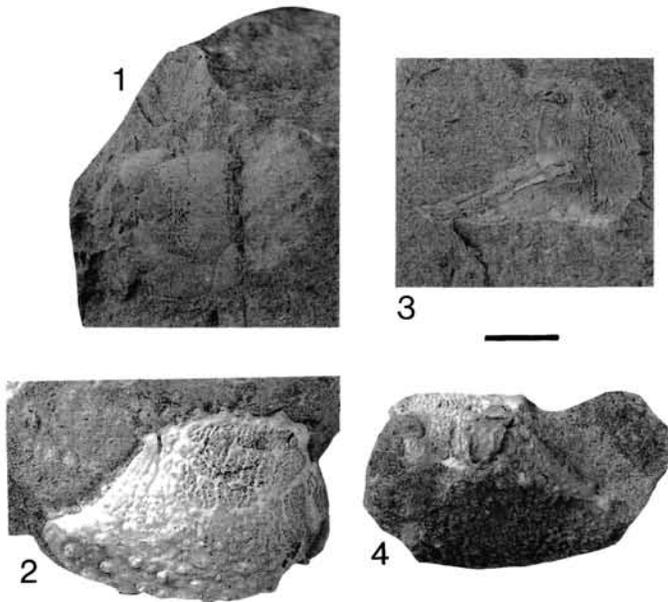


FIGURE 3—1, *Callianassa sensu lato* sp., outer surface of chela, IHNCH 3424; 2, *Dardanus mexicanus* n. sp., outer surface of propodus of holotype, IHNCH 3427; 3, *Callianassa sensu lato* sp., internal mold of chela, IHNCH 3425; 4, *Dardanus mexicanus* n. sp., inner surface of propodus of holotype, IHNCH 3427. Scale bar = 1 cm.

The third specimen, IHNCH-3426, is a fairly complete, smooth hand and the fourth specimen IHNCH-3466, associated with a calappid specimen, is a small minor chela with a slightly longer than high hand and a downturned, curved, slender, fixed finger.

None of the characters visible on the specimens permits confident generic placement. The American genera of the Callianassidae were recently revised and essential key characters were defined (Manning and Felder, 1991). At the same time, a closely related family, the Ctenochelidae, was named. Certain characters of the major chelae were recognized as being diagnostic of genera; however, many of those features were expressed on the meri. Unfortunately, the meri of the specimens in this collection are not preserved and, therefore, it is most judicious to refer them to *Callianassa sensu lato*.

- Infraorder ANOMURA MacLeay, 1838  
 Superfamily PAGOUIDEA Latreille, 1802  
 Family DIOGENIDAE Ortmann, 1892

*Discussion.*—Assignment of single propodi of decapods can be extremely difficult. The specimen under consideration is very similar in outline to species within the Paguroidea, Diogenidae, and Lithodidae in the Paguroidea. However, the Diogenidae are distinguished from the other two families, in part, because representatives of this family characteristically have the left cheliped developed as the larger one, rather than the right as is common in pagurids. Representatives of the Lithodidae tend to have claws that are circular to ovoid in cross-section. The material from Chiapas exhibits a triangular cross-section which would not be expected in the latter family. Although there is only one left claw as a representative of this species, it is robust and heavily ornamented and, therefore, it is assumed to be the major claw.

#### Genus DARDANUS Paulson, 1875

*Discussion.*—In a recent examination of *Trizopagurus*, Forest (1995a) presented a key to the 18 named genera within the Diogenidae. Although most of the key characters were morphologic

features exhibited on areas other than on the chelipeds, *Dardanus* was characterized by having a larger left claw than right, and a surface ornamented by granules, tubercles, spines, and occasionally by ciliated striae. Species referable to *Dardanus* never exhibit annulations, and the tips of both claws bear strong, corneous, non-denticled, occlusal surfaces. These characters are observed in the Chiapas specimen. Although the corneous tip of the fingers is not preserved, the termination of the fixed finger broadens and lacks calcified denticles. Thus, a corneous termination was most likely present.

Forest (1995a) excluded taxa from *Dardanus* that exhibited annulations as the primary ornamentation on the pereopods. Müller (1979) reassigned *Pagurites* [= *Paguristes*] *substriatiformis* Lórenthey in Lórenthey and Beurlen, 1929 to *Dardanus*. Forest (1995b) subsequently noted that *Dardanus substriatiformis* should be placed in *Cliopagurus* Forest, 1995a, based upon possession of annulations and development of a stridulatory apparatus on the inner surface of the cheliped. If one strictly applies the key characters presented by Forest (1995a), several other species previously referred to *Dardanus* must also be assigned to other genera. Species that require restudy, based upon their apparent similarity to *Cliopagurus* spp., include *D. hungaricus* (Lórenthey in Lórenthey and Beurlen, 1929) and *D. arrosor* (Herbst, 1794).

#### DARDANUS MEXICANUS new species

Figure 3.2, 3.4

*Diagnosis*.—Stout, left propodus with triangular cross-section and ornamentation on outer surface of hand that is reticulate near upper margin and becoming progressively more coarsely tuberculate toward lower and distal margins. Setal pits arranged as clusters prominent on distal and lower margins of propodus.

*Description*.—Propodus of left cheliped stout, rectilinear in outline, triangular in cross-section; height 17.2 mm measured at midlength of hand; length including all but tip of fixed finger, 25.5 mm; thickness of hand, 12.2 mm; length along upper surface, 14.4 mm; height of proximal articular region, 13.7 mm. Outer surface reticulated on the upper part and with small, distally directed nodes, nodes becoming larger and more closely spaced in lower half and along fixed finger; nodes along distal margin and along fixed finger with four to as many as 20 setal pits on apices. Articulation between propodus and dactylus inclined downward and distally at about 35 degree angle, curving to nearly parallel upper surface on occlusal surface. Upper surface straight with about eight prominent distally-directed spines generally arrayed in two rows. Lower surface narrow, convex, becoming more convex on base of fixed finger. Occlusal surface short, bearing a few dome-shaped denticles. Articulation with carpus smooth, inflated, separated from remainder of outer surface by prominent sulcus. Viewed from below, lower margin of hand and fixed finger convex outward in a smooth arch. Inner surface of chela composed of two nearly flat elements meeting at longitudinal crest extending from midpoint of carpus/propodus articulation to inner surface of fixed finger. Entire inner surface bearing moderate-sized, uniformly spaced nodes.

*Etymology*.—The trivial name notes the occurrence of the specimen in México.

*Type*.—The holotype, and sole specimen, IHNCH-3427, is deposited in the paleontological collection of the Instituto de Historia Natural de Chiapas, Tuxtla Gutiérrez, Chiapas.

*Occurrence*.—The specimen was collected at locality 1004, from the Middle Sandstone-Grit Member of the San Juan Formation at Mesa de Copoya, Chiapas, México.

*Discussion*.—The style of ornamentation of the propodus of the left cheliped distinguishes *Dardanus mexicanus* from previously named fossil species. *Dardanus subaequalis* Rathbun, 1926, from the Eocene of California, bears tubercles arrayed in rows on the

outer surface of the propodus, and *D. arnoldi* Rathbun, 1926, from the Pleistocene of California, has small, densely-spaced tubercles. In contrast to these two species, the outer surface of the propodus of *D. mexicanus* is reticulate near the upper margin and becomes more nodose toward the lower and distal margins. The geographic range of Eocene *Dardanus* sp. is herein extended from California to southern México; however, the new occurrence does not extend the geologic range because *Dardanus* has previously been reported from the Eocene of California.

Infraorder BRACHYURA Latreille, 1802  
Section EUBRACHYURA Saint Laurent, 1980  
Subsection RANINOIDA de Haan, 1839  
Superfamily RANINOIDEA de Haan, 1839  
Family RANINIDAE de Haan, 1839  
Subfamily RANININAE de Haan, 1839  
Genus LOPHORANINA Fabiani, 1910

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

*Diagnosis*.—Carapace obovate, longer than wide; carapace surface with transverse ridges ornamented with small, acute, needle-like spines; spines parallel to surface of carapace, directed forward; ridges parallel to one another or complex and bifurcating, often most complex on posterior portion of carapace; cervical groove usually indistinct; branchiocardiac grooves deeply incised. Front with anteriorly produced, axially sulcate, trifid rostrum. Orbits broad, with two open or closed fissures or v-shaped grooves; intra-orbital spine blunt and rectangular or sharp, bordered by orbital fissures/grooves; outer-orbital spine large, sharp, directed forward, sometimes with small spine on upper surface near base. Anterolateral margin short, with two or three spines; spines range in size from small, acute, and needle-like, to large and sharply triangular; last anterolateral spine may be bifid; posterolateral margin long, convex. Frontal area of carapace narrow, usually 10–15 percent maximum carapace length, but may occupy up to 20 percent maximum carapace length; surface granular or scabrous. Cardiac region bounded by deep, branchiocardiac grooves; remainder of carapace regions not differentiated. Chelae and elements of pereopods ornamented with short, spinose ridges or granular ridges.

*Discussion*.—Members of *Lophoranina* (Table 1) are easily distinguished from other raninids by the spinose ridges and the shape and configuration of the front, orbits, and anterolateral margins. Species within the genus are distinguished from one another based upon the development and pattern of the carapace ridges, the shape of the rostrum, the size and shape of the orbital fissures and spines, and the shape and size of the anterolateral spines.

Spacing, continuity, and complexity of carapace ridges varies between species. The sole Cretaceous species, *Lophoranina precocious*, has parallel, continuous, and widely spaced ridges. This configuration is unique among members of the genus, and the Cretaceous age of that species suggests that a simple configuration of the ridges may be the ancestral form. Eocene species display a wide range of variation in ridge configuration. For example, *L. marestiana*, *L. bittneri*, *L. laevisformis*, *L. levantina*, and *L. cristaspina* n. sp. have simple, parallel ridges on the anterior portion of the carapace. The ridges become complex, discontinuous, and bifurcating on the posterior portion of the carapace. *Lophoranina raynoriae*, *L. bishopi*, and *L. reussi* have complex, discontinuous ridges on the entire carapace. The Oligocene species *L. georgiana* has simple, parallel, widely spaced ridges on the anterior portion of the carapace and *L. porifera* has simple ridges anteriorly and complex ridges posteriorly. Therefore, there does not seem to be an overall trend from simple to more complex ridge forms, although it appears that simple is the ancestral state.

The width measured between the bases of the last anterolateral spines (W1) as compared to the fronto-orbital width measured

TABLE 1—Species of *Lophoranina*, their age, and geographic distribution. Portions of this table were taken from Tucker (1995).

Taxon and age	Locality
LATE CRETACEOUS	
<i>Lophoranina precocious</i> Feldmann et al., 1996	Southern México
EARLY EOCENE	
<i>Lophoranina bishopi</i> Squires and Demetron, 1992	Baja California, México
<i>Lophoranina soembaensis</i> Van Straelen, 1938	Indonesia
EOCENE	
<i>Lophoranina aldrovandi</i> (Ranzani, 1820)	Italy
<i>Lophoranina bakerti</i> (A. Milne Edwards, 1872)	India
<i>Lophoranina barroisi</i> (Brocchi, 1887)	Cuenca de Paris
<i>Lophoranina bittneri</i> (Lörentz, 1902)	Italy
<i>Lophoranina cristaspina</i> n. sp.	Southern México
<i>Lophoranina laevifrons</i> (Bittner, 1875)	Italy
<i>Lophoranina levantina</i> Lewy, 1977	Israel
<i>Lophoranina persica</i> Withers, 1932	Iran
<i>Lophoranina raynoriae</i> Blow and Manning, 1996	North Carolina, USA
<i>Lophoranina reussi</i> (Woodward, 1866)	Europe
<i>Lophoranina rossi</i> Blow and Manning, 1996	South Carolina, USA
<i>Lophoranina straeleni</i> Via, 1959	Europe
<i>Lophoranina tchihatcheffi</i> (A. Milne Edwards, 1866)	Greece
<i>Lophoranina toyosimai</i> Yabe and Sugiyama, 1935	Japan
LATE EOCENE	
<i>Lophoranina marestiana</i> (König, 1825)	Europe, Egypt
OLIGOCENE AND YOUNGER	
<i>Lophoranina aculeata</i> (A. Milne Edwards, 1881)	Southwestern France
<i>Lophoranina georgiana</i> (Rathbun, 1935)	Alabama, USA
<i>Lophoranina kemmelingi</i> Van Straelen, 1924	Borneo
<i>Lophoranina perforata</i> Woodward, 1866	Trinidad
<i>Lophoranina? quinquespinosa</i> (Rathbun, 1945)	Lau, Fiji

between the tips of the outer-orbital spines (W2) differs among members of *Lophoranina*. *Lophoranina bittneri*, *L. bishopi*, *L. laeviformis*, *L. marestiana*, *L. precocious*, *L. reussi*, *L. rossi*, and *L. straeleni* have a W1/W2 ratio averaging 0.64 with a range of 0.61–0.68. *Lophoranina cristaspina* n. sp., *L. georgiana*, and *L. raynoriae* have a W1/W2 ratio averaging 0.78 with a range of 0.75–0.83. These latter three species are Gulf Coastal or East Coastal American species, suggesting that the wider fronto-orbital width was a regional evolutionary offshoot, and that the main lineage had narrow fronto-orbital widths as compared to the width between the bases of the last anterolateral spines. Members with a reduced fronto-orbital width occur throughout the geographic range of the genus.

The number of anterolateral spines in species of *Lophoranina* also varies. The earliest known species, *L. precocious*, has three anterolateral spines. Two Eocene species, *L. cristaspina* n. sp. and *L. marestiana*, have two anterolateral spines with the last being bifurcate, suggesting the possibility of fusion of the last two spines into one bifurcate spine. The remainder of the species have two anterolateral spines.

Beschin et al. (1988) and Feldmann et al. (1996) illustrated tiny needle-like spines on the carapace ridges of *L. laeviformis* and *L. precocious* respectively. Additionally, needle-like spines are easily observable on illustrations of *L. raynoriae* and *L. rossi* (Blow and Manning, 1996, pl. 2, figs. 3, 4). *Lophoranina cristaspina* n. sp. clearly exhibits such needle-like spines (Fig. 4.7). Additionally, in areas where the spines are broken, the ridges appear to be serrated or punctate, an artifact of the spines breaking near their bases. Other members of *Lophoranina* that do not exhibit preserved spines also have what appear to be serrated or punctate ridges. It is suggested here that the needle-like spines are, in fact, diagnostic for the genus; however, because of their delicate nature,

they have poor preservation potential. Therefore, the ridges typically appear serrate or punctate. Feldmann et al. (1996) suggested that members of the genus may use these spines as a means of anchoring the carapace in algal mats or debris accumulations in shallow marine environments. Most species of *Lophoranina*, including the new species described here, are found in shallow marine carbonate deposits within tropical to sub-tropical areas, so such an interpretation seems well founded.

The oldest known occurrence of *Lophoranina* is from the Late Cretaceous deposits in Chiapas, México (Feldmann et al., 1996). Numerous Eocene occurrences are known (Table 1), and three species are known from the Oligocene. It appears that the genus may have arisen in the vicinity of southern México and subsequently dispersed eastward to Europe, through the Tethys, and into the Indo-Pacific and Japan via the open Tethys seaway (Bice et al., 2000). *Lophoranina* is interpreted to have also dispersed westward to Baja California through the Central American passage, which was open during the late Mesozoic and Tertiary (Bice et al., 2000). The genus clearly had a Tethyan distribution and a preference for subtropical to tropical settings. The closing of the Tethys seaway and the Central American passage during the middle to late Paleogene may have affected the temperature regime in the world's oceans by distributing heat away from the tropics with the development of the North Pacific gyre (Bice, unpublished data; Bice et al., 2000), causing cooling of tropical waters and the extinction of the genus by the end of the Oligocene.

#### LOPHORANINA CRISTASPINA new species

Figures 4, 5

**Diagnosis.**—Carapace obovate; orbits broad, with two fissures and intra-orbital and outer-orbital spines; outer-orbital spine with small spine at base; anterolateral margins with two spines, outer spine bifurcate; anterior quarter of carapace ornamented with scabrous granules; remainder of carapace ornamented with spinose ridges; spinose ridges parallel to one another anteriorly, complex and bifurcate posteriorly.

**Description.**—Carapace obovate; slightly wider than long, maximum length (L1)/maximum width (W3) = 0.91, maximum width attained at position of last anterolateral spines; carapace weakly vaulted transversely and longitudinally, weak axial keel developed in some individuals; carapace surface ornamented with granules on anterior-most 10–20 percent of carapace, orbital spines, and anterolateral spines; remainder of carapace with transverse ridges ornamented with small, forward-directed spines; spines almost always broken so that ridges appear terraced; ridges parallel on anterior half of carapace, becoming more complex and with bifurcations on posterior half of carapace.

Rostrum broken, unknown. Orbits broad; fronto-orbital width (W2) about 65 percent maximum carapace width (W3). Orbits with two open fissures; proximal fissure located at about midwidth of orbit; distal fissure about midway between proximal fissure and outer margin of orbit, about half as deep as proximal fissure. Orbit with sharp intra-orbital spine bounded by fissures; outer-orbital spine large, directed forward, upper margin of spine concave, with small triangular spine near base, lower margin convex.

Anterolateral margin short, bearing two spines; proximal spine sharp, curving forward; distal spine bifurcate; inner bifurcation sharp, triangular, directed forward; outer bifurcation sharp, directed anterolaterally. Posterolateral margin long, convex, with granular rim. Posterior margin nearly straight, rimmed, posterior width (W4) about 30 percent maximum carapace width (W3).

Cervical groove interpreted to lie just anterior to first continuous ridge crossing entire carapace width. Gastric and hepatic regions undifferentiated; gastric regions with two concave, spiny ridges; remainder of gastric and hepatic regions ornamented with scabrous granules. Cardiac region with several parallel ridges well

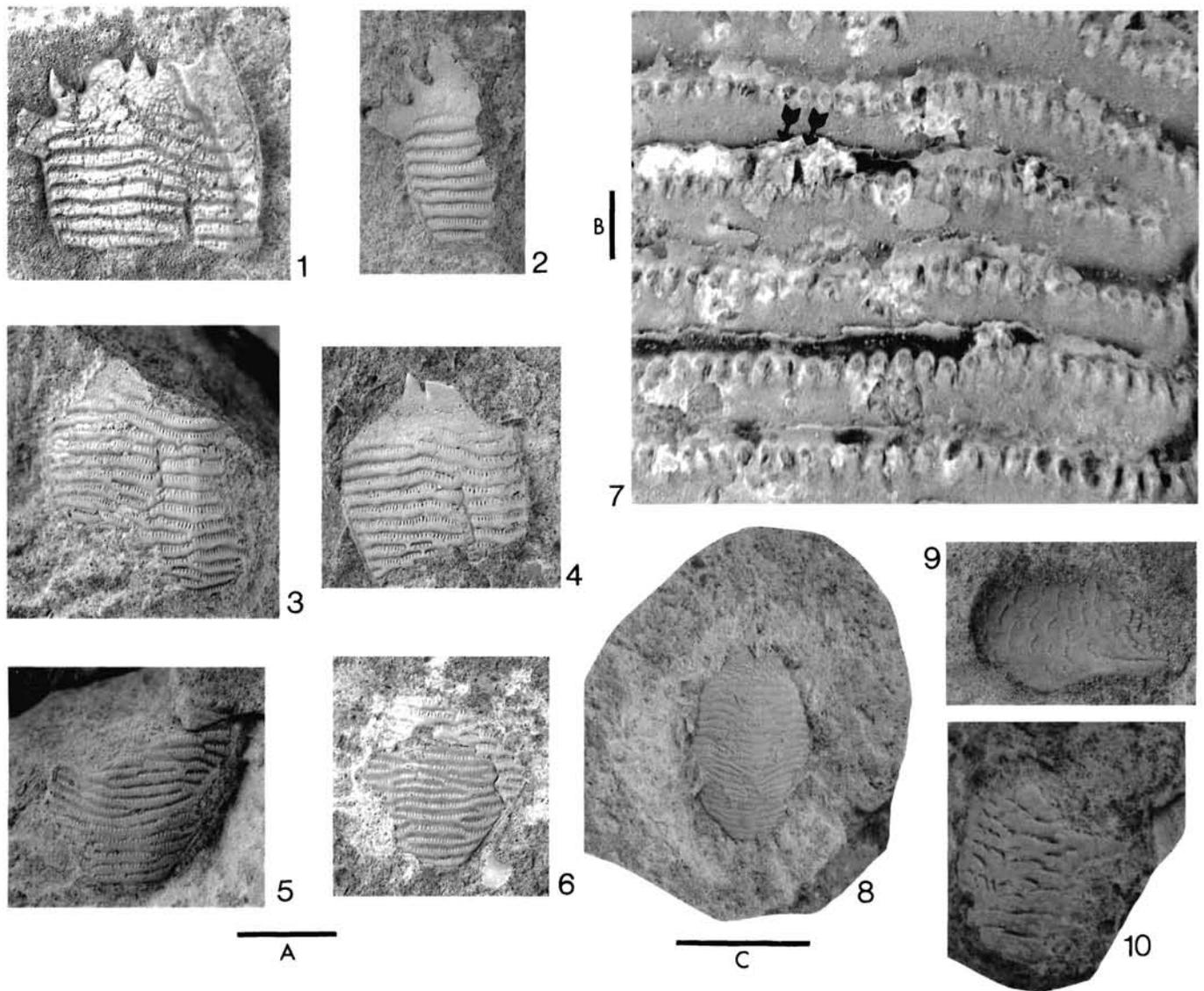


FIGURE 4.—*Lophoranina cristaspina* n. sp. 1, Anterior portion of dorsal carapace of holotype, IHNCH 3428; 2, anterior portion of dorsal carapace of paratype, IHNCH 3447; 3, central portion of dorsal carapace of paratype, IHNCH 3441; 4, central portion of dorsal carapace of paratype, IHNCH 3434; 5, posterior portion of dorsal carapace of paratype, IHNCH 3463; 6, posterior portion of dorsal carapace of paratype, IHNCH 3438; 7, enlargement showing spined projections (indicated by arrows) on transverse ridges of paratype, IHNCH 3441; 8, juvenile specimen and paratype, IHNCH 3429; 9, outer surface of appendage fragment of paratype, IHNCH 3441; 10, outer surface of propodus of paratype, IHNCH 3457. Scale bar A for 1–6 = 1 cm; scale bar B for 7 = 1 mm; scale bar C for 8–10 = 1 cm.

defined by deep branchiocardiac grooves. Branchial regions ornamented with parallel ridges anteriorly; ridges becoming complex and bifurcating posteriorly.

Manus of first pereopod with spinose ridges; fixed finger smooth, sharp, triangular, directed perpendicular to long axis of manus. Other appendage elements ornamented with short ridges and granules.

*Etymology.*—The trivial name is derived from the Latin “*crista*,” meaning ridge, and “*spina*,” meaning spine, describing the spined transverse ridges on the carapace.

*Types.*—The holotype, IHNCH-3428, and 32 paratypes, IHNCH-3429–3460, are deposited in the paleontological collection of the Instituto de Historia Natural de Chiapas, located in Tuxtla Gutiérrez, Chiapas.

*Measurements.*—The line drawing of *Lophoranina cristaspina*

n. sp. (Fig. 5) is a composite of several incomplete specimens. It represents our best interpretation of the overall size, shape and dimensions of the carapace. Length and width ratios are based upon this reconstruction, and as such, are best approximations given the nature of the material. Position and orientation of measurements taken are illustrated in Figure 5. Ratio of fronto-orbital width (W2) to width between bases of last anterolateral spines (W1) = 0.82; maximum length (L1) to maximum width (W3) = 0.91; fronto-orbital width (W2) to maximum width (W3) = 0.65; posterior width (W4) to maximum width (W3) = 0.30; frontal length (L2) to point of maximum width = 0.19.

*Occurrence.*—More than 33 carapace and appendage fragments were collected from locality 1004 in the Middle Sandstone-Grit member of the San Juan Formation, near the top of Mesa de Copoya, south of Tuxtla Gutiérrez, Chiapas.

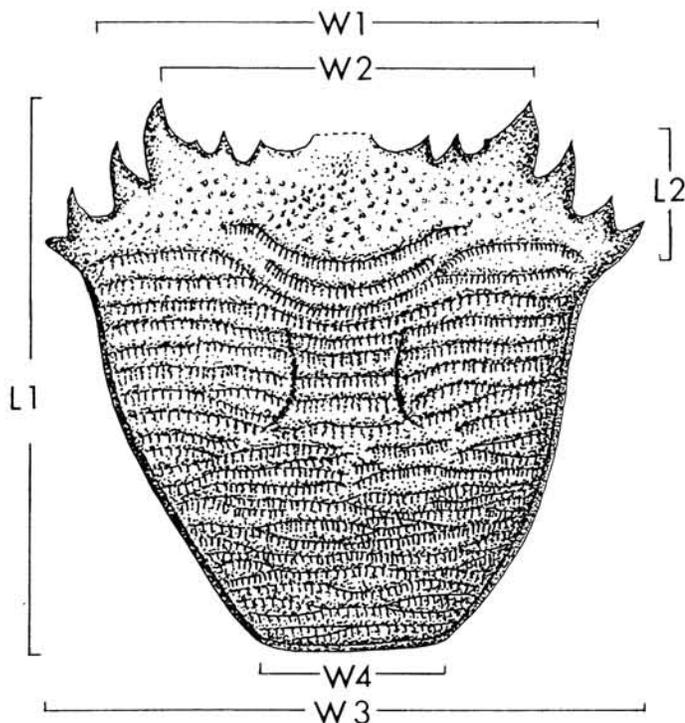


FIGURE 5—Composite reconstruction of *Lophoranina cristaspina* n. sp., showing position and orientation of measurements used to calculate various length and width ratios as indicated in the text.

**Discussion.**—Specimens of *Lophoranina cristaspina* n. sp. clearly demonstrate the spiny nature of the ridges traversing the carapace (Fig. 4.7). The spines are small, acute, and needle-like and are almost always broken at the base so that the carapace ridges appear terraced or serrate. The new species is distinct from all other species of the genus in possessing very large, produced outer-orbital spines with a triangular spine at the base; wide grooves in the orbits; a strongly bifurcate last anterolateral spine; large anterolateral spines; and a wide fronto-orbital area as compared to the width between the last anterolateral spines. Other species of the genus have small anterolateral spines that are simple or weakly bifurcate; relatively short outer-orbital spines; orbital fissures; and a narrower fronto-orbital width as compared to the width between the anterolateral spines. *Lophoranina cristaspina* n. sp. is most like *L. georgiana*, *L. raynorae*, and *L. rossi* in having a comparatively wide fronto-orbital area. However, *L. raynorae* and *L. rossi* have much more complex carapace ridge patterns and *L. georgiana* has much smaller anterolateral and orbital spines than does *L. cristaspina*. *Lophoranina porifera* has a similar configuration of carapace ridges as does *L. cristaspina*, but the terraces are more closely spaced and have less vertical relief than do those of *L. cristaspina*. The front of *L. porifera* is completely missing, making further comparisons between it and the new species difficult. *Lophoranina? quinquespina* from the Neogene of Fiji is known only from claw fragments, making comparison of it with *L. cristaspina* impossible.

This is the second notice of *Lophoranina* from the Eocene of México, as *L. bishopi* was previously reported from the Eocene Bateque Formation of Baja California Sur (Squires and Demetron, 1992). *Lophoranina precocious* was reported from Upper Cretaceous deposits in Chiapas (Feldmann et al., 1996).

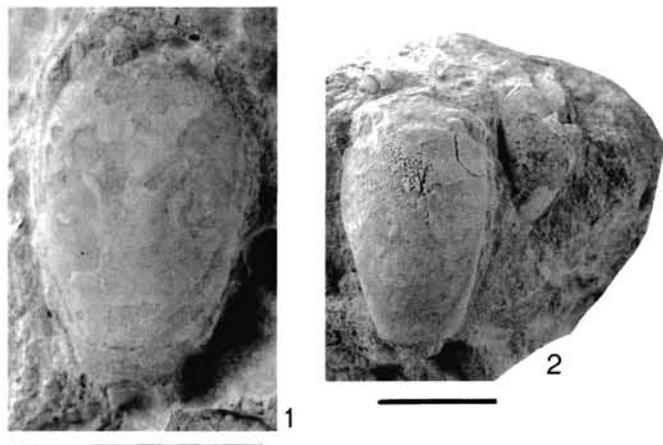


FIGURE 6—1, *Notopus minutus* n. sp., dorsal carapace of holotype, IHNCH 3462; 2, *Laeviranina* sp., dorsal carapace, IHNCH 3461. Scale bar = 1 cm.

Subfamily RANINOIDINAE Lörenthey  
(in Lörenthey and Beurlen, 1929)  
Genus LAEVRANINA Lörenthey  
(in Lörenthey and Beurlen, 1929)  
LAEVRANINA sp.  
Figures 6.2, 7

**Description.**—Carapace small for genus, spatulate in outline, length more than 1.5 times width, moderately vaulted transversely, nearly planar longitudinally, surface generally smooth.

Fronto-orbital margin incompletely preserved, about 88 percent maximum width measured at anterolateral corner. Outer orbital

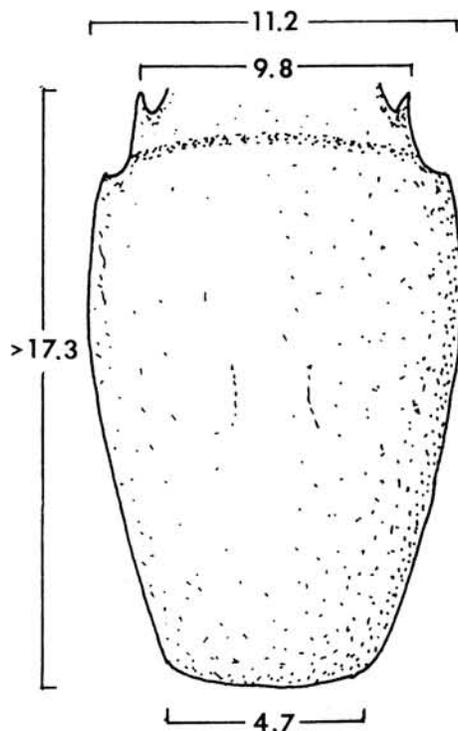


FIGURE 7—Line drawing of *Laeviranina* sp., indicating position and orientation of measurements taken.

spines acute, directed forward, remainder of frontal margin broken. Anterolateral corner with small, forward-directed spine defining maximum width. Lateral margin nearly straight anteriorly and tapers smoothly to well-defined posterolateral corner. Posterior margin about 42 percent maximum width, weakly convex.

Frontal region depressed below general carapace surface and defined along posterior by subtle convex-forward ridge. Remainder of carapace surface smooth. Branchiocardiac grooves weakly arcuate, subtle. Venter and appendages unknown.

*Material examined.*—The specimen referred to this genus, IHNCH-3461, is deposited in the paleontological collection of the Instituto de Historia Natural de Chiapas, located in Tuxtla Gutiérrez, Chiapas.

*Measurements.*—Measurements taken on the sole specimen referred to *Laeviranina* are given in Figure 7.

*Occurrence.*—The specimen was collected at locality 1005 from the middle part of the San Juan Formation at Veinte de Noviembre, Chiapas, México.

*Discussion.*—The genus *Laeviranina* belongs to a plexus of raninid genera, including *Raninoides* H. Milne Edwards, 1837, and *Quasilaeviranina* Tucker, 1998, that are extremely difficult to distinguish from one another in some cases. The “typical” members of each genus are readily characterized as is indicated in a key to the genera of the family (Tucker, 1998). However, examination of the entire spectrum of species assigned to the three genera indicates that there is an almost complete gradation in critical characters (Schweitzer et al., 2000). For example, *Raninoides* is distinguished from *Laeviranina* by the former having open orbital fissures and no post-frontal ridge whereas the latter has narrow orbital fissures and a well-developed post-frontal ridge. However, the orbital fissures exhibited by *L. vaderensis* (Rathbun, 1926), and *L. lewisiana* (Rathbun, 1926), among others, are open and well developed and the post-frontal ridge is subtle. Additionally, some extant members of *Raninoides* display weak frontal ridges, especially on larger specimens (Schweitzer et al., 2000). It seems clear the species within the three genera are closely related and that generic placement, especially within *Laeviranina* and *Raninoides*, can be quite arbitrary in some cases.

The specimen from Chiapas is referred to *Laeviranina* based upon possession of a well-developed post-frontal ridge. Because other diagnostic characters of the dorsal carapace, including the nature of the orbital and rostral regions, are not preserved, it is not appropriate to designate a new species.

The poor nature of the material argues against speculating on the biogeographic implications of the occurrence. The genus has a cosmopolitan distribution in the Eocene (Tucker, 1998) and appears to have had its earliest occurrence in the Paleocene of Greenland (Collins and Rasmussen, 1992).

#### Subfamily NOTOPODINAE Serène and Umali, 1972

##### Genus NOTOPUS de Haan, 1841

*Discussion.*—As with all raninids, many of the diagnostic features of this genus are found in the fronto-orbital region. Most raninids have a generally smooth carapace posterior to this area. *Notopus* is characterized by having a broad, nearly straight fronto-orbital margin with distinct orbital fissures and a small, triangular rostrum. The anterolateral spines are moderately well developed and lie at the same level as the orbital regions. The fronto-orbital region is separated from the remainder of the carapace by an ornamented, or serrated, ridge connecting the anterolateral spines (Glaessner, 1969). The specimen from Chiapas conforms to this definition and can be placed in the genus with reasonable certainty. Certainly, no other raninid genus can accommodate the species.

The distributional pattern of living and fossil species is Tethyan and the addition of a new species from Chiapas reinforces the

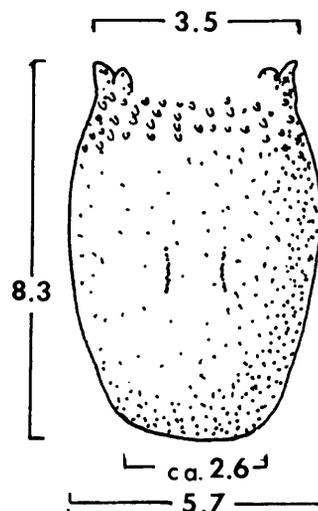


FIGURE 8—Line drawing of *Notopus minutus* n. sp. indicating position and orientation of measurements taken.

subtropical to tropical pattern. Two living species, *Notopus dorsipes* (Linnaeus, 1758), and *N. novemdentatus* Ortmann, 1892, are known from the Indo-Pacific region and the Red Sea (Tucker, 1995) and two, *N. beyrichi* Bittner, 1875, and *N. punctulatus* (Beschinn et al., 1988), have been described from the Eocene Tethyan localities of Hungary and Italy. Thus, this new species represents the first occurrence of the genus in the Western Hemisphere.

#### NOTOPUS MINUTUS new species

Figures 6.1, 8

*Diagnosis.*—Very tiny for genus, strongly vaulted transversely, with post-frontal, serrated ridge developed as narrow field of pustules; remainder of carapace smooth.

*Description.*—Carapace very small for genus, ovoid in outline, length more than 1.6 times maximum width, strongly vaulted transversely, moderately vaulted longitudinally with maximum elevation of carapace in anterior one-third, surface with fine setal pits overall and granular frontal region.

Fronto-orbital margin incompletely preserved, about 61 percent maximum width measured approximately at midlength. Outer orbital spines broad, curved anterolaterally with acute terminations. Orbital regions with two nearly fused fissures. Remainder of frontal region not preserved. Lateral margins smoothly convex; posterolateral corner defined by increase in curvature into convex posterior margin, about 46 percent maximum width.

Frontal region with fine granular surface curving downward from highest carapace elevation. Remainder of carapace surface with very fine punctae. Branchiocardiac grooves nearly straight, weakly expressed.

Venter and appendages unknown.

*Etymology.*—The trivial name alludes to the very small size of the individual referred to the holotype.

*Types.*—The holotype, and sole specimen referred to this species, IHNCH-3462, is deposited in the paleontological collection of the Instituto de Historia Natural de Chiapas, located in Tuxtla Gutiérrez, Chiapas.

*Measurements.*—Measurements taken on the sole specimen referred to this species are given in Figure 8.

*Occurrence.*—The specimen was collected at locality 1005 from the middle part of the San Juan Formation, at Veinte de Noviembre, Chiapas, México.

*Discussion.*—*Notopus minutus* n. sp. differs from other species of the genus by having rounded rather than acute tips on the

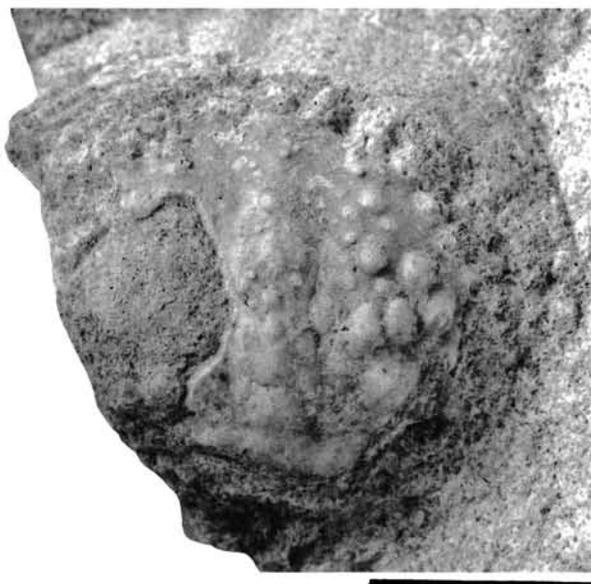


FIGURE 9—*Calappilia* cf. *C. hondoensis*, dorsal carapace of IHNCH 3463. Scale bar = 1 cm.

anterolateral and outer orbital spines. Further, the anterolateral spines curve anterolaterally rather than being straight-sided. Finally, the serrated ridge is broader than on previously described members of the genus and, instead of being serrated, consists of just a field of small granules. The characteristics serve to distinguish the species from previously named forms.

Section HETEROTREMATA Guinot, 1977  
 Superfamily CALAPPOIDEA de Haan, 1833  
 Family CALAPPIDAE de Haan, 1833  
 Genus CALAPPILIA A. Milne Edwards, 1873

*Type species.*—*Calappilia verrucosa* A. Milne Edwards, 1873.

CALAPPILIA cf. *C. HONDOENSIS* Rathbun, 1930  
 Figures 9, 10

*Description.*—Carapace moderate size for genus; transversely oval, pustulose; greatest width at mid-length; more strongly vaulted longitudinally than transversely; fronto-orbital margin estimated to be approximately 30 percent of total carapace width; anterolateral margin convex, crenulate, with four blunt projections, projections smoothly convex, projections with pronounced pustules; posterolateral margin unknown; posterior margin straight, downturned.

Rostrum weakly developed, deflected; orbits small, sub-circular. Protogastric region defined by smooth, shallow, irregular grooves; mesogastric region inflated, with four small pustules; metagastric region inflated, oval swelling directed axially; urogastric region with one large, blunt, circular node; two small pits between mesogastric and metagastric regions represent posterior gastric muscle scars. Cardiac region defines highest point on carapace, with pronounced ovoid axial swelling bearing four small pustules; intestinal region arched transversely, with two oval axial pustules extending length of intestinal region. Hepatic region flat, depressed, with four small pustules. Branchial regions poorly differentiated; numerous epibranchial nodes and pustules; five pronounced mesobranchial swellings in addition to numerous nodes and pustules; one pronounced metabranchial swelling.

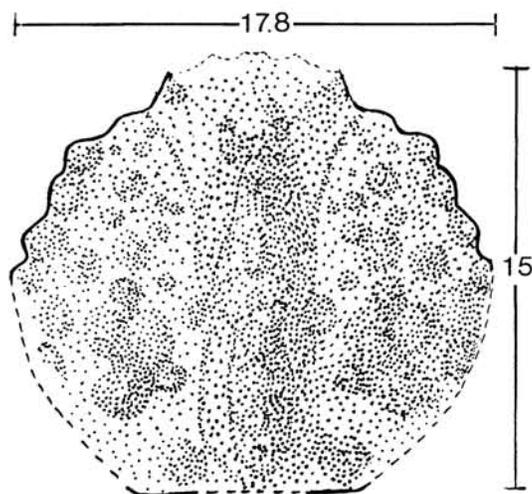


FIGURE 10—Line drawing of *Calappilia* cf. *C. hondoensis* showing position and orientation of measurements taken.

*Material examined.*—The three specimens referred to this taxon, IHNCH-3463–3465, are deposited in the paleontological collection of the Instituto de Historia Natural de Chiapas, in Tuxtla Gutiérrez, Chiapas.

*Measurements.*—Measurements taken on specimen IHNCH-3463 are provided in Figure 10.

*Occurrence.*—The specimens were collected at locality 1004 from the Middle Sandstone-Grit Member of the San Juan Formation, at Cerro de Copoya, Chiapas, México.

*Discussion.*—These specimens, exhibiting the external dorsal carapace surface, lack the posterolateral margin and much of the posterior dorsal surface so that it is impossible to determine whether or not a posterolateral flange was developed. Other diagnostic morphologic characters also are incompletely preserved, including the weakly projecting rostrum and small, forward-directed, sub-circular orbits. The well-preserved axial regions are narrow, with pronounced swellings and smaller pustules. The maximum width of this specimen occurs at the mid-length, and the anterolateral margin is crenulate. These characters are diagnostic of *Calappilia* (Schweitzer and Feldmann, 2000a) and form the basis for assignment to that genus.

Species of *Calappilia* are distinguished from one another based upon details of the fronto-orbital region, relative development and arrangement of pustules, and nature of the posterolateral flange. Poor preservation of the rostrum and complete lack of the posterolateral margin make assignment beyond the generic level difficult. However, *Calappilia hondoensis* Rathbun, 1930, has previously been described from upper Eocene rocks of the Tepetate Formation; the new material is provisionally referred to that species until better preserved material can be collected.

Representatives of *Calappilia* are known only from the fossil record. The genus exhibits widespread distribution, both geologically and geographically (Schweitzer and Feldmann, 2000a). Species of *Calappilia* have been recovered from strata ranging in age from Eocene to Miocene (Glaessner, 1969; Feldmann, 1993; Feldmann et al., 1998; Schweitzer and Feldmann, 2000a). Eocene occurrences of *Calappilia* have been noted from North America, the Caribbean, Europe, and the Indo-Pacific. Later occurrences have been recorded from European and Indo-Pacific sedimentary deposits (Schweitzer and Feldmann, 2000a). The genus appears to have inhabited both tropical and temperate waters.



FIGURE 11—Calappidae, genus and species indeterminate, dorsal view of fragmentary carapace, IHNCH 3466. Scale bar = 1 cm.

Family CALAPPIDAE de Haan, 1833  
Genus and species indeterminate  
Figures 11, 12

*Description of material.*—Moderate-sized calappid with transversely oval carapace, pustulose, wider than long; greatest width at mid-length; more strongly vaulted longitudinally than transversely; fronto-orbital margin estimated to be approximately 20 percent of total carapace width; anterolateral margin smoothly convex; posterolateral and posterior margins unknown. Rostrum projected, deflected; one outer-orbital spine directed anterolaterally; orbits small, sub-circular, directed anterolaterally.

Gastric regions defined by smooth, shallow grooves, axial regions bearing pronounced carapace swellings; mesogastric region inflated with one circular swelling; metogastric region inflated with one circular swelling, larger than mesogastric swelling; urogastric region with one small swelling; posterior gastric pits situated on either side of axis between mesogastric and metogastric regions. Cardiac region with one large, circular swelling surrounded by smaller pustules; intestinal region vaulted transversely, downturned, with one circular swelling. Hepatic region with one large swelling and four smaller pustules near the posterior hepatic border. Branchial regions not well differentiated, traversed by two prominent nodose ridges, directed anterolaterally. Outer ridge appears to parallel lateral carapace margin, consists of five discrete blunt nodes. Inner ridge parallels outer ridge, contains six prominent blunt nodes, nodes decrease in size posteriorly. Single large branchial node at elevation of urogastric region is largest carapace swelling. Numerous small pustules occur on surface of branchial regions.

*Material examined.*—The specimen referred to this genus, IHNCH-3466, is deposited in the paleontological collection of the Instituto de Historia Natural de Chiapas, Tuxtla Gutiérrez, Chiapas.

*Measurements.*—Measurements taken on the sole specimen are provided in Figure 12.

*Occurrence.*—The specimen was collected at locality 1004 from the middle part of the San Juan Formation, at Mesa de Copoya, Chiapas, México.

*Discussion.*—Assignment of the specimen to the Calappidae is based on the well-developed nodose linear ridges; narrow, flattened rostrum; and convex anterolateral margin. This specimen lacks the posterolateral and posterior margins, and characters of

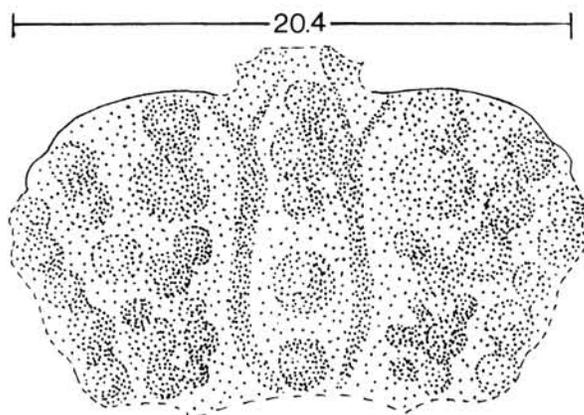


FIGURE 12—Line drawing of Calappidae genus and species indeterminate showing position and orientation of estimated width measurement.

the rostrum are indistinctly preserved. The linear ridges are characteristic of *Mursia* Desmarest, 1823, as are the convex anterolateral margin, narrow rostrum, and pronounced tubercles (Schweitzer and Feldmann, 2000a). These characters are also diagnostic for *Calappa* Weber, 1795, which differs from *Mursia* in possessing a spined flange on the posterolateral margin. Species of *Mursia* possess a straight posterolateral margin and often have an attenuated spine at the anterolateral corner. Because the posterolateral margins are missing and the anterolateral margins are poorly preserved, it is impossible to assign the specimen to a genus. However, note that *Calappa zurcheri* Rathbun, 1930, was described from Oligocene rocks of México. That species possesses well-developed linear ridges on the carapace, and it is suggested that the new material may be allied with that taxon. Definitive placement must await the collection of better material.

Family HEPATIDAE Stimpson, 1871  
Genus ERIOSACHILA Blow and Manning, 1996  
*ERIOSACHILA* sp.  
Figures 13, 14

*Description.*—Carapace ovate, slightly wider than long, rostrum projecting beyond orbits, carapace flattened longitudinally, moderately vaulted transversely; regions characterized by swellings and subtle grooves.

Fronto-orbital region depressed, broad for family, occupying



FIGURE 13—*Eriosachila* sp., dorsal view of partial carapace, IHNCH 3467. Scale bar = 1 cm.

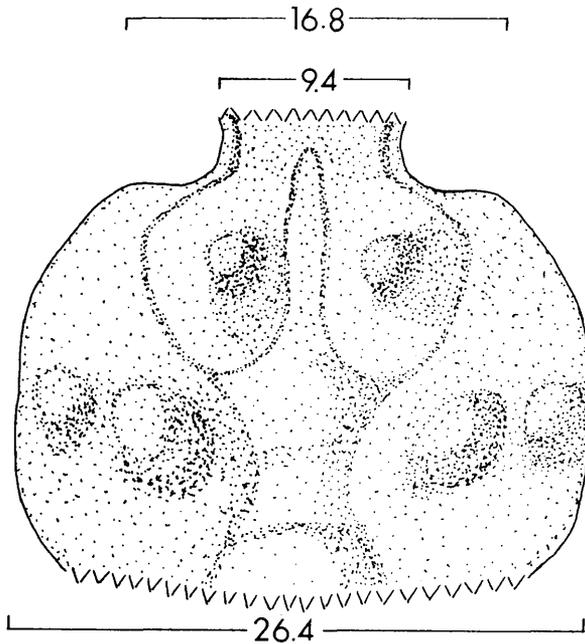


FIGURE 14—Line drawing of *Eriosachila* sp. showing position and orientation of measurements taken.

63 percent maximum carapace width. Fronto-orbital margin incompletely preserved. Orbits upturned, broad, arcuate, and complete, directed slightly anterolaterally. Remainder of frontal margin broken. Anterolateral margin incomplete, weakly convex. Posterolateral margin incomplete. Posterior margin missing. Protogastric regions elevated and inflated, narrowing posteriorly, each with broad conical swellings adaxially. Mesogastric region narrow, depressed anteriorly, widening posteriorly, abruptly wider at level of posterior part of protogastric region, most strongly swollen posteriorly. Metagastric region slopes and narrows posteriorly to cardiac region. Cardiac region incomplete, swollen. Shallow cervical groove separates branchial regions from gastric regions. Hepatic region weakly arched at midpoint. Epibranchial and mesobranchial regions not clearly distinguished; with two conical swellings; epibranchial swelling smaller; mesobranchial swelling larger, located posterior and mesial to epibranchial swelling; mesobranchial region depressed posterolaterally. Small depression between epibranchial and mesobranchial swellings. Gastric muscle scars weakly impressed as a series of lines and pits directed anteriorly and mesially.

**Material examined.**—The specimen referred to this genus, IHNCH-3467, is deposited in the paleontological collection of the Instituto de Historia Natural de Chiapas, located in Tuxtla Gutiérrez, Chiapas.

**Measurements.**—Measurements taken on the sole specimen referred to *Eriosachila* are given in Figure 14.

**Occurrence.**—The specimen was collected at locality 1004 from the Middle Sandstone-Grit Member of the San Juan Formation, at Mesa de Copoya, Chiapas, México.

**Discussion.**—*Eriosachila* was originally assigned to the subfamily Matutinae of the Calappidae sensu lato (Blow and Manning, 1996). Subsequent to that work, Bellwood (1996) included the Matutinae within the superfamily Leucosiidea, based upon a phylogenetic study, supporting the divisions proposed by Rice (1980) based upon larval studies. *Eriosachila* was subsequently assigned to the Hepatidae (Schweitzer and Feldmann, 2000a), based upon its broad carapace and convex anterolateral margins

and lack of pronounced lateral spines and discrete carapace nodes or tubercles.

The specimen from Chiapas is placed within the family Hepatidae because the carapace is wider than long, the carapace surface exhibits inflated regions, discrete tubercles are absent, and the front extends well beyond the orbits. It is most appropriately placed within the genus *Eriosachila* because *Hepatus* Latreille, 1802, and *Hepatella* Smith, 1869, have smooth carapaces that do not have distinctly swollen regions, species of *Hepatus* Bittner, 1875, possess entire anterolateral and posterolateral margins, and members of *Osachila* Stimpson, 1871, possess entire, crenulated anterolateral margins. Although the anterolateral and posterolateral margins are broken on the Chiapas specimen, there is no indication of crenulations.

Because other diagnostic characters of the dorsal carapace, including the nature of the frontal and posterior regions, are not preserved, it is not appropriate to designate a new species. Members of the genus are known from Eocene rocks of both the east and west coasts of North America, and an east-west dispersal through the Central American Seaway has been proposed for this taxon (Schweitzer and Feldmann, 2000a). The occurrence of an Eocene member of the genus in Chiapas supports this interpretation.

Superfamily XANTHOIDEA MacLeay, 1838

Family GONEPLACIDAE MacLeay, 1838

Subfamily CARCINOPLACINAE H. Milne Edwards, 1852

Genus STOAPLAX new genus

**Type species.**—*Stoaplax nandachare* n. sp., by monotypy.

**Diagnosis.**—As for the species.

**Etymology.**—The generic name is derived from the Greek “*stoa*,” meaning porch, referring to the significant frontal projection, and from “*plax*,” Greek for tablet. The latter is a common root used for generic names of members of the Goneplacidae which have a flattened carapace.

**Occurrence.**—As for the species.

**Discussion.**—The Xanthidae sensu lato and the Goneplacidae exhibit quite similar morphologies. Morphologic characters narrowing possible familial assignment to the two preceding families are the ovoid carapace outline; wide, projected front; broad, deep orbits; flattened carapace; and dentate anterolateral margins. Assignment of *Stoaplax nandachare* n. sp. to the Goneplacidae is based on the extreme width of the fronto-orbital margin (80 percent of total carapace width), flattened carapace, and wide orbits. These morphologic characters are typical of taxa within the Goneplacidae, but are not typical of the Xanthidae s.l. (Tucker and Feldmann, 1990).

The new genus is most similar to *Orbitoplax* Tucker and Feldmann, 1990. Species of both of these genera share similar fronto-orbital margin dimensions and wide orbits. Both genera are characterized by pronounced swellings on the branchial regions and smooth, shallow grooves defining the carapace regions. However, representatives of *Orbitoplax* and *Stoaplax* display marked morphologic differences. *Orbitoplax* spp. are widest in the anterior third of the carapace, whereas the maximum width for *Stoaplax* occurs at the mid-length of the carapace. The anterolateral and posterolateral margins of *Stoaplax* are far more convex than those of *Orbitoplax*. *Stoaplax* exhibits pronounced gastric swellings, whereas *Orbitoplax* has none. The frontal margin of *Stoaplax* is much more projected than that of *Orbitoplax* and the orbits are much more deeply excavated in *Stoaplax*. *Carcinoplax* H. Milne Edwards, 1852, shares some morphologic similarities with *Stoaplax*; however, *Carcinoplax* spp. possess narrower orbits and a straighter fronto-orbital margin than does *Stoaplax*. Species of *Coeloma* A. Milne Edwards, 1865, have a much less produced front than members of *Stoaplax*, and the carapace regions are

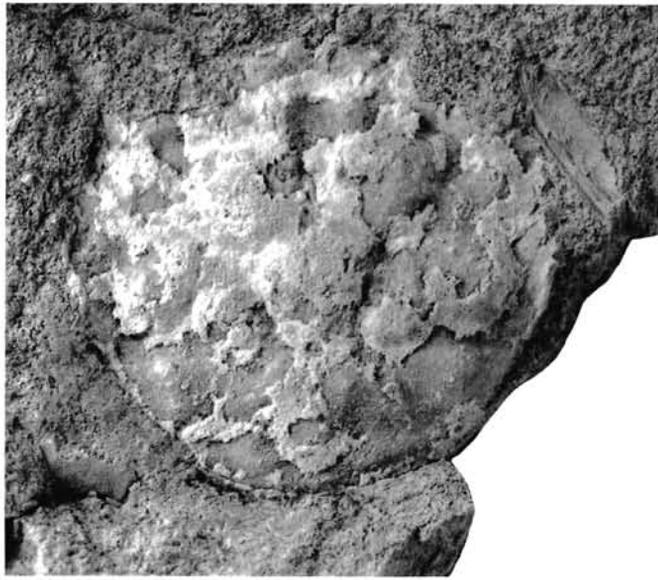


FIGURE 15—*Stoaplax nandachare* n. gen. and sp., dorsal view of carapace, IHNCH 3468. Scale bar = 1 cm.

flattened in *Coeloma* and inflated in *Stoaplax*. The carapace regions of *Glyphithyreus* Reuss, 1859, are much better developed and the grooves are much deeper than those of *Stoaplax*. No recognized genera within the Goneplacidae can accommodate this extremely unusual frontal morphology. Assignment of the new material to a new genus is based upon these unique morphologic characters.

STOAPLAX NANDACHARE new species  
Figures 15, 16

**Diagnosis.**—Diminutive goneplacid with ovoid carapace, slightly wider than long, weakly vaulted longitudinally and transversely; front produced, slightly deflected, axis sulcate; single anterolateral spine directed anterolaterally; orbits broad, arcuate, notched axially; outer-orbital spine directed anterolaterally.

**Description.**—Diminutive goneplacid with transversely ovoid carapace. Carapace granular, slightly wider than long; greatest width of carapace attained at mid-length. Carapace weakly vaulted longitudinally and transversely. Fronto-orbital margin approximately 80 percent maximum carapace width.

Front well-developed, projected, slightly deflected, axis sulcate, bounded by small blunt spines; frontal width 20 percent total carapace width measured between tips of anterolaterally directed lateral spines. Orbits broad, deep, arcuate, with shallow notch near mid-point; orbital margin sinuous; orbital width measured between blunt spine of front and outer-orbital spine 24 percent of maximum carapace width; outer-orbital spine projecting anteriorly. Anterolateral margin with two spines including outer-orbital spine, both spines triangular. Posterolateral margin convex, rimmed. Posterior margin convex.

Gastric regions defined by shallow grooves. Epigastric region with small swelling; prominent swelling in protogastric region; ovoid, axially elongated, mesogastric swelling; urogastric swelling weakly inflated; cardiac region narrow, inflated, longitudinally ovoid; intestinal region depressed. Hepatic region flattened, slightly downturned. Branchial regions separated from axial regions by smooth, shallow, irregular grooves and prominent swellings; one epibranchial, two mesobranchial, and one metabranchial swelling.

**Etymology.**—The trivial name is based upon the original name,

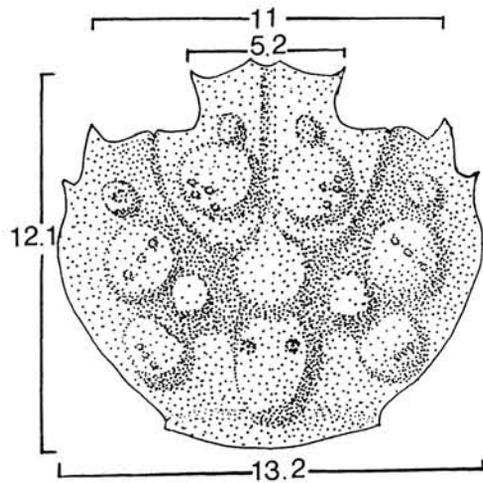


FIGURE 16—Line drawing of *Stoaplax nandachare* n. sp. showing position and orientation of measurements taken.

Nandachare, for the town of Veinte de Noviembre. Nandachare means “yellow river” in the Nahuatl language.

**Types.**—The holotype and sole specimen, IHNCH-3468, is deposited in the paleontological collection of the Instituto de Historia Natural de Chiapas, Tuxtla Gutiérrez, Chiapas.

**Measurements.**—Measurements taken on the sole specimen referred to this species are given in Figure 16.

**Occurrence.**—The specimen was collected at locality 1005 in the middle part of the San Juan Formation, at Veinte de Noviembre, Chiapas, México.

**Discussion.**—Only one specimen of this taxon has been discovered. This specimen is preserved as a nearly complete internal mold of the carapace with some heavily weathered cuticle adhering to it. Neither appendages nor ventral characters are preserved. Collection of additional material will be necessary to frame a more complete description of the taxon.

Family XANTHIDAE sensu lato MacLeay, 1838  
Genus VERRUCOIDES new genus

**Type species.**—*Xanthilites verrucoides* Collins and Rasmussen, 1992, by original designation.

**Other species.**—*Verrucoides stenohedra* new species.

**Diagnosis.**—Xanthid with hexagonal carapace, wider than long; front with four spines; four spines on anterolateral margin; tubercles defining epigastric, protogastric, metagastric, and cardiac regions, other regions indistinct. Fronto-orbital margin less than half maximum width, front slightly less than half the fronto-orbital width. Front projects beyond orbits. Orbits notched and defined by outer orbital spine. Anterolateral margin with four spines; last spine prominent, longer than wide, directed slightly upward and posteriorly, marking maximum width of carapace. Posterolateral margin straight to slightly convex. Cardiac region tuberculate, inflated and hexagonal; hepatic regions triangular; branchial region indistinct, two tubercles posterior to cervical groove at level of large lateral spine, one positioned behind the other on an axis between anterolateral spine three and four and cardiac tubercle, tubercle closest to anterolateral margin slightly larger.

**Etymology.**—The generic name is taken from the trivial name of *Xanthilites verrucoides* (Collins and Rasmussen, 1992) in reference to the wart-like appearance of the ornamentation of the two species in this genus.

**Occurrence.**—The genus is known from Paleocene rocks of Greenland and from the Eocene of México.

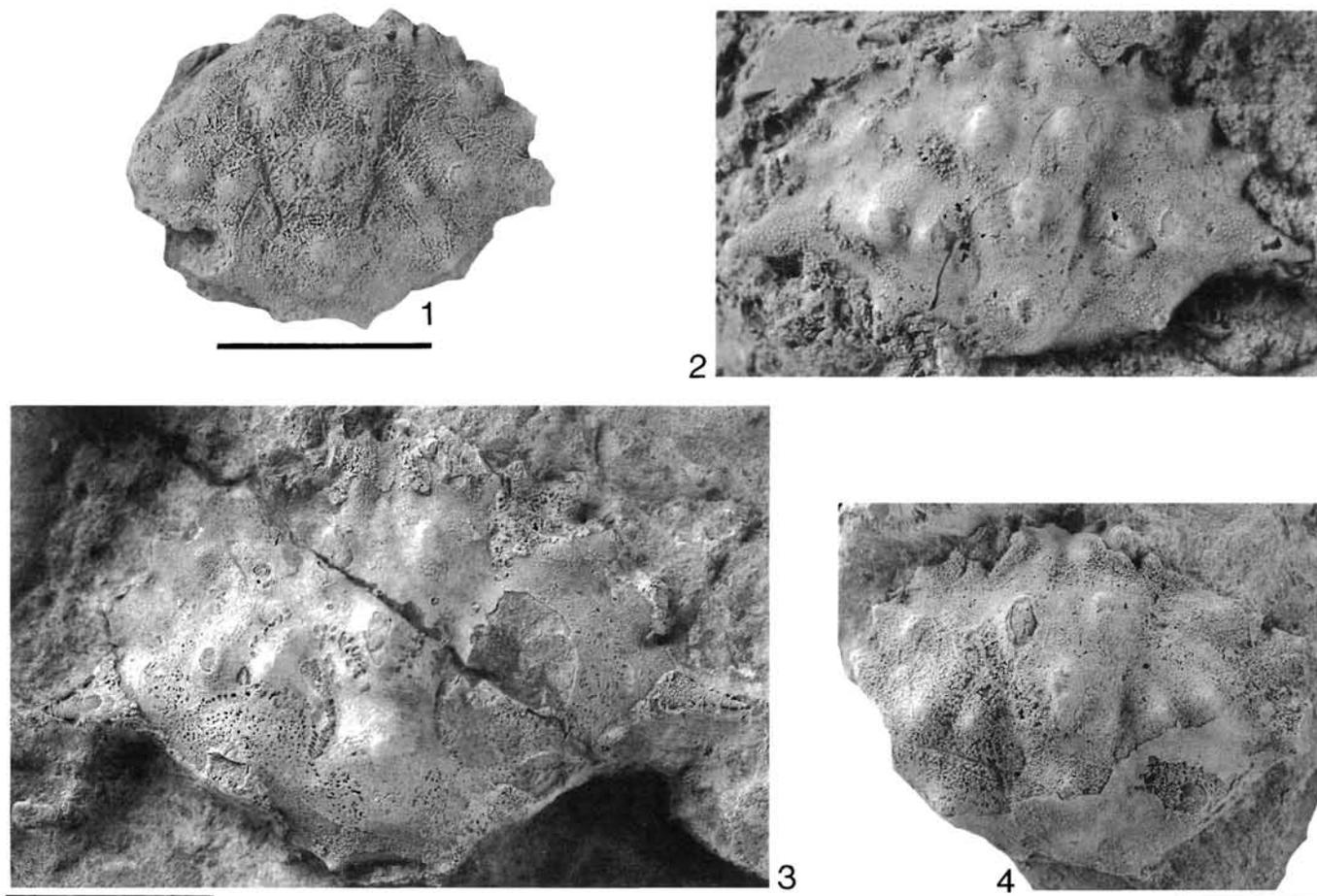


FIGURE 17—*Verrucoides stenohedra* n. gen. and sp. 1, Dorsal view of carapace of paratype, IHNCH 3472; 2, dorsal view of external mold of carapace of paratype IHNCH 3470. Note that orbits and granular surface are well preserved but that the posterior margin is missing; 3, dorsal view of carapace of holotype, IHNCH 3469; 4, dorsal view of carapace of paratype, IHNCH 3471. Scale bars = 1 cm.

*Discussion.*—*Xanthilites verrucoides* Collins and Rasmussen, 1992, was originally described from Paleocene rocks of Greenland. Referral to the genus *Xanthilites* Bell, 1858, was based upon comparison with *Xanthilites gerthi* Glaessner, 1930, and *X. alabamensis* Rathbun, 1935. New material referable to a new xanthid species from Chiapas, bearing striking similarity to *X. verrucoides*, warrants the creation of a new genus to embrace the Greenland and Mexican material. The genus *Xanthilites*, as presently constituted, is a collection of species referable to several genera. *Xanthilites verrucoides* and the material from Chiapas form the basis for one of these distinct genera.

*Xanthilites verrucoides* and the new material differ from the type species of *Xanthilites*, *X. bowerbanki* Bell, 1858, in several respects. The well-defined regions of *X. bowerbanki* and other species currently placed within that genus are distinctly different from the more poorly defined regions of *X. verrucoides* and the new material. The carapaces of *X. verrucoides* and the new material have a greater width to length ratio than *X. bowerbanki*, primarily due to the extreme length of the last anterolateral spine in those two species. The last anterolateral spine is longer than wide in *X. verrucoides* and in the new material, whereas that spine is reduced in *X. bowerbanki*. The anterolateral spines are sharper and more pronounced in *X. verrucoides* and the new material than those of *X. bowerbanki*. *Xanthilites verrucoides* and the new material also differ significantly from *X. gerthi* and from *X. alabamensis*. The carapace of *X. gerthi* is much more flattened and the

ornamentation is not nearly as well developed as that of *X. verrucoides* and the new material. Further, the last anterolateral spine is much better developed in *X. verrucoides* and the new material than in *X. gerthi*. *Xanthilites alabamensis* is similar to *X. verrucoides* and the new material; however, the carapace regions, front, and orbits are different in *X. alabamensis*. Further, it is clear that *X. gerthi* and *X. alabamensis* are themselves quite different from *X. bowerbanki*; each of those three species probably belong to different genera separate from the new genus described here, *Verrucoides*. Those decisions must await examination of type material of species assigned to *Xanthilites*.

The new genus *Verrucoides* is here established to accommodate *Xanthilites verrucoides* and the new material collected from Chiapas. The new genus is characterized by possession of a frontal margin with four spines; well-developed orbits with two fissures; well-developed, wart-like carapace ornamentation; four anterolateral spines, the last of which is hypertrophied and longer than wide; a convex and narrow posterior margin; and poorly developed carapace regions. *Xanthilites verrucoides* is designated as the type species of *Verrucoides*, and *Verrucoides stenohedra*, the new species described herein, is placed within this new genus.

Familial placement of *Verrucoides* is difficult. Ventral characters are absent as far as is known. The carapaces of *V. stenohedra* n. sp. and *V. verrucoides* are both wider than long and hexagonal. These characters, along with overall morphologic similarity to

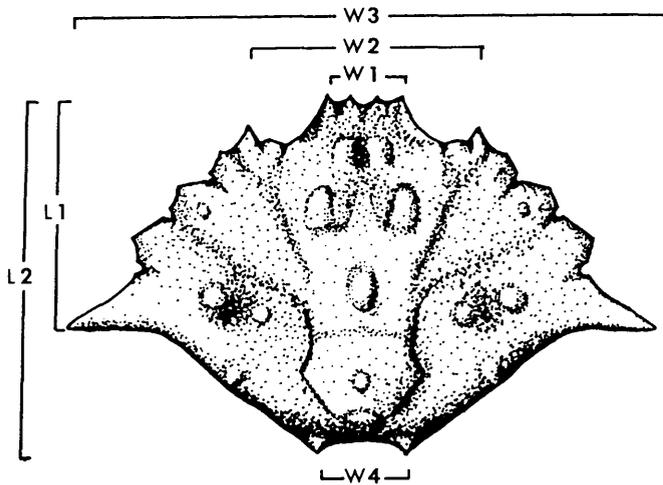


FIGURE 18—Line drawing of *Verrucoides stenohedra* n. gen. and sp. showing position and orientation of measurements taken.

other fossil xanthids such as *Etyus* Leach in Mantell, 1822; *Palaeoxanthopsis* Beurlen, 1958; *Xanthosia* Bell, 1863; *Xanthilites*, and *Zanthopsis* sensu stricto McCoy, 1849, make placement of *Verrucoides* within the Xanthidae sensu lato appropriate. Assignment to any of the ten families now considered to be assignable to the Xanthoidea is impossible, because the preserved characters do not seem to fall into any established family. The new genus is clearly allied with the xanthoids, however, and is therefore placed within the Xanthidae s.l.

*Verrucoides* is known from Paleocene rocks of Greenland and middle Eocene rocks of southern México. This suggests that the genus arose in the North Atlantic region during the Paleocene and subsequently dispersed to México via ocean surface currents or along the continental shelf. A similar pattern is demonstrated by *Viapinnixa*, to be described below.

#### VERRUCOIDES STENOHEDRA new species

Figures 17, 18

**Diagnosis.**—*Verrucoides* with four spines excluding outer-orbital spines separated by U-shaped fissures on anterolateral margin, posteriormost spine longer than wide, directed slightly posterolaterally; front axially sulcate with four equally spaced spines, orbits interrupted by small spines bounded by open fissures; posterior margin concave, narrow, defined by posteriorly directed tubercles; regions, except cardiac, relatively indistinct; epigastric and protogastric regions separate, mesogastric region terminates at level of protogastric tubercles; cardiac region hexagonal with vertically-directed tubercle.

**Description.**—Carapace hexagonal, about 1.5 times as wide as long including lateral spines, moderately vaulted transversely and strongly vaulted longitudinally. Lateral margins well-defined, folded beneath carapace. Dorsal surface finely punctate. Regions defined by low, broad swellings separated by shallow grooves, swellings often crested with round to oblong tubercles. Prominent lateral spine terminates anterolateral margin, spine directed slightly upward and posterolaterally. Cardiac and gastric regions inflated to form broad raised axis.

Fronto-orbital margin defined by postorbital spines, about 38 percent maximum carapace width. Front projecting beyond orbits, axially sulcate, slightly downturned, about 12 percent maximum carapace width; with four equally spaced spines, equal in size, directed anteriorly. Orbital rim elevated on lateral margins of the front. Orbits well-developed; orbits with two narrow, shallow,

TABLE 2—Measurements (in mm) taken on the dorsal carapace of specimens of *Verrucoides stenohedra* n. gen. and sp. W1 = frontal width, W2 = fronto-orbital width, W3 = maximum carapace width, W4 = posterior width, L1 = length from front to maximum width, L2 = carapace length, \* = based on half measurement of one half specimen.

Specimen Number	W3	W2	W1	W4	L2	L1
3470	265	117	44	—	>15.2	93
3469	345	132	52	59	213	106
3471	>30.4	144	49	77	>21.7	—
3472	>20.7	86	—	54	>14.8	>9.7
3473	>39.8	—	—	90	>30.7	—
3474	>22.0	—	—	—	>15.0	—

open fissures, one at midpoint and one at base of acute, forward-directed outer-orbital spine; fissures bounded by small intraorbital spine. Anterolateral margin weakly convex with four spines excluding outer-orbital spine. First three spines wider than long, increasing in size posteriorly, spines two and three bounded by U-shaped fissures. Fourth and last spine long, slightly up-turned, about 12 percent maximum carapace width, defining position of maximum width of carapace, drawn into sharp termination, anterior edge directed posterolaterally, posterior edge directed laterally. Posterolateral margin slightly convex, spine at midpoint of margin directed upward and posteriorly. Posterolateral corner defined by acute spine. Posterior margin concave, 16 percent maximum carapace width.

Carapace grooves generally indistinct. Cervical groove deep axially, becoming indistinct laterally, crossing midline at right angles to axis, curving sharply anteriorly at metagastric margin, then directed toward anterolateral margin; becoming shallow, broad, indistinct before reaching anterolateral margin between spines two and three.

Epigastric regions small, defined by reniform lobes that border central ovate depression, lobes distinct anteriorly, becoming indistinct posteriorly. Protogastric regions inflated, prominent, broad, longitudinally elongate, tubercles becoming indistinct posteriorly. Mesogastric region triangular, terminated by small tubercle at level of protogastric tubercles. Metagastric region defined laterally by deep cervical groove, inflated; large, low, ovate spine located centrally. Urogastric region narrow and poorly defined. Cardiac region inflated, well defined, hexagonal, tubercle located centrally. Intestinal region separated from cardiac region by broad, laterally elongate tubercle; depressed posteriorly. Hepatic region triangular with small tubercle axial to second anterolateral spine. Branchial regions indistinct; two tubercles posterior to cervical groove at level of large lateral spine, one positioned behind the other on an axis between anterolateral spine three and four and cardiac tubercle, tubercle closest to anterolateral margin slightly larger than others; tubercle at midpoint of posterolateral margin directed laterally.

**Etymology.**—The trivial name of *Verrucoides stenohedra* refers to the narrow posterior margin of this species. It is derived from the Greek root “*stenos*,” meaning narrow, and “*hedra*,” meaning base.

**Types.**—The holotype, IHNCH-3469, and six paratypes, IHNCH-3470–3475, are deposited in the paleontological collection of the Instituto de Historia de Chiapas, located in Tuxtla Gutiérrez, Chiapas.

**Measurements.**—Measurements taken from specimens of *Verrucoides stenohedra* are given in Table 2. The position and orientation of dorsal carapace measurements are shown in Figure 18. Specimen IHNCH-3475 was too fragmentary for measurement, but appears to be significantly larger than the other measured specimens.

**Occurrence.**—The specimens were collected from locality

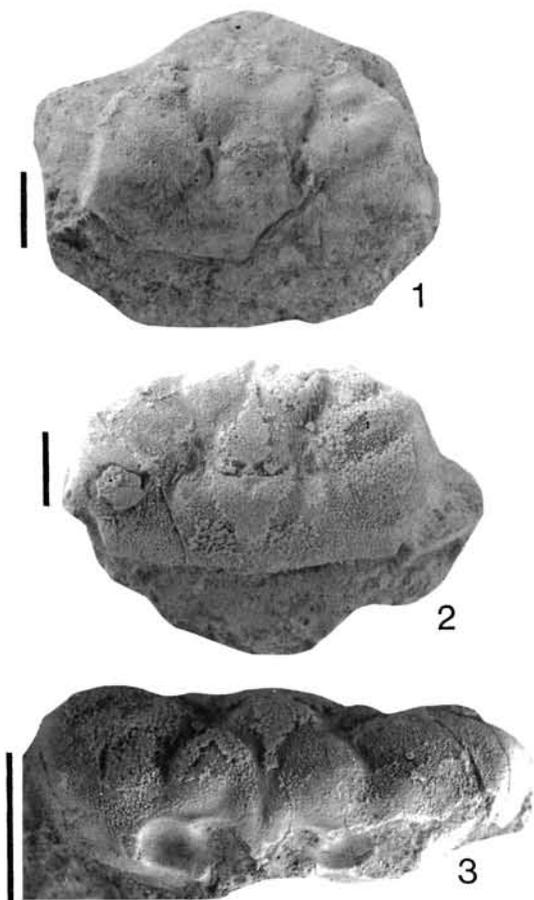


FIGURE 19—*Viapinnixa alvarezii* n. sp. 1, Dorsal view of carapace of paratype, IHNCH 3477; 2, dorsal view of carapace of holotype, IHNCH 3476; 3, anterior view of holotype, IHNCH 3476. Scale bars = 1 cm.

1005 from the middle part of the San Juan Formation, at Veinte de Noviembre, Chiapas, México.

**Discussion.**—*Verrucoides stenohedra* and *V. verrucoides* are sufficiently different to assign *V. stenohedra* to a separate species. The posterior margin of *V. stenohedra* lacks a prominent posterior rim, is narrow (no wider than the cardiac region) and is bounded by prominent, posteriorly directed tubercles; the posterior of *V. verrucoides* is wider than the cardiac region, is not defined by tubercles, and possesses a posterior rim. The epigastric and proto-gastric regions are distinct in *V. stenohedra*, but are indistinguishable in *V. verrucoides*; the mesogastric region extends to the front of *V. verrucoides* and terminates at the level of the proto-gastric regions in *V. stenohedra*. The metagastric region of *V. verrucoides* is pentagonal, unlike that of *V. stenohedra*, in which the region is not well-defined. The tubercle on the cardiac region of *V. verrucoides* is laterally elongate, unlike the round cardiac tubercle of *V. stenohedra*. A cast made from a well-preserved external mold of *V. stenohedra* shows the surface to be covered with fine granules; however, other specimens do not have the granules preserved. "A few widely scattered granules appear on the surface of *V. verrucoides* (Collins and Rasmussen, 1992, p. 39).

Superfamily PINNOTHEROIDEA de Haan, 1833

Family PINNOTHERIDAE de Haan, 1833

Genus VIAPINNIXA Schweitzer and Feldmann, 2000c

*Type species.*—*Pinnixa (Palaeopinnixa) nodosa* Collins and Rasmussen, 1992, by original designation and monotypy.

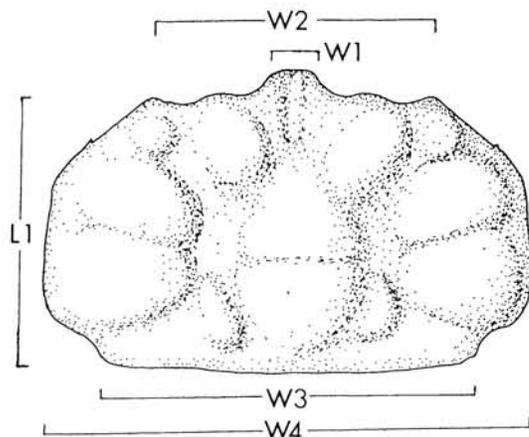


FIGURE 20—Line drawing of *Viapinnixa alvarezii* n. sp. showing position and orientation of measurements taken.

**Diagnosis.**—Carapace much wider than long, average L/W 0.63; front projected beyond orbits, frontal width to fronto-orbital width ratio 0.23–0.25; fronto-orbital width to maximum width ratio about 0.57–0.70; orbital rim complete, upper orbital margin sinuous; lateral margins rounded, with small erect spine immediately posterior to cervical groove; posterolateral margin straight, posterior width to maximum width ratio about 0.75; fronto-orbital width to posterior width ratio about 0.69–0.89; posterolateral corner with reentrant.

**Discussion.**—Schweitzer and Feldmann (2000c) erected the genus *Viapinnixa* to accommodate material previously referred to *Pinnixa (Palaeopinnixa)* (Collins and Rasmussen, 1992). New material from southern México is referable to *Viapinnixa* based upon possession of a carapace that is wider than long (L/W = 0.63); and has a rounded-rectangular shape; a narrow, flared rostrum extending well beyond the orbits; wide orbits; a small anterolateral spine, and posterolateral reentrants. The new material differs from the type species, *Viapinnixa nodosa* (Collins and Rasmussen, 1992) in the ratio of the fronto-orbital width to posterior width, which averages 0.89 in *Viapinnixa nodosa* and 0.69 in the new species to be described below. Further, the fronto-orbital width to maximum width ratio in *Viapinnixa nodosa* averages 0.70 while that ratio is 0.51 in the new material. Therefore, the diagnosis for the genus has been emended herein to reflect those ranges.

#### VIAPINNIXA ALVAREZII new species

Figures 19, 20

**Diagnosis.**—Carapace strongly vaulted, transversely ovate; posterolateral margins straight with flanks inclined; cardiac region triangular; surface ornamentation granular; fronto-orbital width to maximum width about 0.51; fronto-orbital width to posterior width about 0.69.

**Description.**—Carapace much wider than long, average L/W 0.63, transversely ovate, strongly vaulted longitudinally and flattened transversely. Orbits broadly ovate. Front occupies medial third of fronto-orbital margin. Front downturned, projected beyond orbits, with shallow median depression. Average frontal width to fronto-orbital width ratio 0.23. Orbital rim complete, terminating in broad orbital node. Upper orbital margin sinuous with projection at midlength marking dorsal termination of ridge extending ventrally and axially, dividing orbits into two concavities. Lower orbital margin with prominent suborbital spine at termination of ridge. Average fronto-orbital width to maximum width ratio 0.51.

Anterolateral margin shorter than posterolateral margin. Small, rounded, erect spine situated immediately posterior to cervical groove. Posterolateral margins straight; flanks inclined outward, wider than fronto-orbital margin. Average posterior width to maximum width ratio 0.74. Shallow concave reentrant at posterolateral corner, greatest carapace width at posterolateral corner. Posterior margin very wide, slightly convex. Average fronto-orbital width to posterior width ratio 0.69.

Epigastric region small, circular, elevated. Protogastric region ovate, tumid; regions widen anteriorly. Mesogastric region subtriangular; separated from protogastric region by shallow grooves. Urogastric region obscure. Cardiac region triangular, apex directed posteriorly. Intestinal region flattened, not well developed.

Hepatic region rounded, weakly tumid, defined by broad, shallow cervical groove and shallow hepatic groove. Branchial regions tumid, with two transversely ovate swellings converging towards cardiac region; separated by shallow groove. Small branchial lobes longitudinally ovate, adjacent to cardiac region. Prominent, deeply-incised branchiocardiac groove curves broadly. Shallow grooves separate intestinal, cardiac, and branchial regions; grooves converge at branchiocardiac groove. Surface ornamentation granular where visible.

*Types*.—The holotype, IHNCH-3476, and paratype, IHNCH-3477, are deposited in the Paleontological Collection of the Instituto de Historia Natural de Chiapas, Tuxtla Gutiérrez, Chiapas.

*Measurements*.—Measurements taken from two specimens within the type series are: length of IHNCH-3476, 13.4 mm and IHNCH-3477, 13.2 mm; width of IHNCH-3476, 22.3 mm and IHNCH-3477, 20.3 mm; frontal width of IHNCH-3476, 2.4 mm, and IHNCH-3477, 2.5 mm; fronto-orbital width of IHNCH-3476, 12.0 mm, and IHNCH-3477, 9.7 mm; posterior width of IHNCH-3476, 17.0 mm and IHNCH-3477, 14.7 mm. Positions and orientations of the measurements are given in Figure 20. The following average ratios and their ranges are: length to width, 0.63 (0.60 and 0.65); frontal width to carapace width, 0.23 (0.20 and 0.26); fronto-orbital width to carapace width, 0.51 (0.54 and 0.48); posterior width to carapace width, 0.74 (0.76 and 0.72); fronto-orbital width to posterior width, 0.69 (0.71 and 0.66).

*Occurrence*.—The specimens were collected from locality 1005 in the middle part of the San Juan Formation, at Veinte de Noviembre, Chiapas, México.

*Etymology*.—The species name honors Don Miguel Alvarez del Toro, who provided strong support for the paleontological research in Chiapas.

*Discussion*.—*Viapinnixa alvarezzi* is similar to the only other known species, *V. nodosa*. However, the carapace of *V. alvarezzi* is strongly vaulted and transversely ovate, whereas in *V. nodosa* it is moderately rounded longitudinally and almost flat in transverse section. The posterolateral margins are straight with flanks inclined outward in *V. alvarezzi* whereas the posterolateral margins are nearly straight in *V. nodosa*. The cardiac region in *V. alvarezzi* is triangular, and in *V. nodosa* is ligulate. Surface ornamentation is granular on the entire carapace in *V. alvarezzi* and is only visible on the gastric, hepatic and branchial regions as well as on the anterolateral margin in *V. nodosa*. Three tubercles are present on the cardiac region of *V. nodosa* which are not visible on *V. alvarezzi*. The fronto-orbital width to maximum width ratio is about 0.51 in *V. alvarezzi* and 0.70 in *V. nodosa*. The fronto-orbital width to posterior width ratio in *V. alvarezzi* is 0.69 and in *V. nodosa* is 0.89.

#### PALEOBIOGEOGRAPHY

Numerous recent works have suggested that decapod taxa were dispersed from the Tethyan region of Europe westward to North America or vice versa beginning as early as the Cretaceous and extending at least into the Eocene (Feldmann et al., 1998;

Schweitzer, 2001; Schweitzer and Feldmann, 2000a, 2000b, 2000c; Schweitzer and Salva, 2000). The region of southern México and Central America is therefore crucial for understanding the veracity and the timing of these dispersal events. The decapod fauna described here supports the view that decapods were dispersed from the Tethys of Europe and North Atlantic region to Central and North America or vice versa, and suggests that the Central American Seaway, developed in what is now México and Central America, was an important Tertiary avenue for dispersal of decapods.

Of the decapods described here, *Calappilia*, *Laeviranina*, *Lophoranina*, and *Notopus* appear to have had Tethyan distributions during the Eocene, with known localities in southern Europe and North America (Tucker, 1995; Schweitzer and Feldmann, 2000a). *Montezumella* Rathbun, 1930, displays a similar distributional pattern (Schweitzer and Salva, 2000). It is difficult to determine whether dispersal operated primarily from east to west or from west to east; examples of both exist. For example, *Lophoranina* is first known from Cretaceous deposits in México and so appears to have dispersed eastward to Europe and the Tethys. Conversely, *Montezumella* appears in the early Eocene of the Tethys and the middle and late Eocene of Central and North America, suggesting a westward dispersal. In either case, the area of southern México and Central America was clearly an important avenue for decapod dispersal.

Other taxa support the view that the regions of México and Central America were important crossroads for decapod dispersal. *Eriosachila* is known from Eocene rocks of both the east and west coasts of North America. The earlier occurrences in North Carolina suggest that the genus dispersed westward through the Central American seaway (Schweitzer and Feldmann, 2000a). Two genera, *Verrucoides* and *Viapinnixa*, first occurred during the Paleocene in Greenland and appeared during the Eocene in southern México. This suggests that these taxa dispersed westward across the Atlantic, perhaps via ocean currents or by movement along the continental shelf of North America. Continued work in this region will undoubtedly clarify the timing and efficacy of the dispersal events within this region.

#### ACKNOWLEDGMENTS

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