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MAASTRICHTIAN CRUSTACEA (BRACHYURA: DECAPODA) FROM THE OCOZOCUAUTLA FORMATION IN CHIAPAS, SOUTHEAST MEXICO

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ABSTRACT—More than thirty complete specimens of *Carcineretes planetarius* Vega, Feldmann, Ocampo, and Pope, 1997, a member of the extinct decapod family Carcineretidae, have been collected from the upper part of the Ocozocuautla Formation in Chiapas, southeast Mexico. Stratigraphic occurrences of *Carcineretes* in the Caribbean Province suggest that this crab should be regarded as an index fossil for the early Maastrichtian. Six samples of this species may represent individuals that died during molting. The sudden disappearance of this family at the end of the Maastrichtian and its restricted paleobiogeographic distribution in the vicinity of the impact site suggest that the Carcineretidae may have been affected by the Chicxulub impact. Other decapod specimens collected from the same localities were assigned to the Xanthidae; *Parazanthopsis meyapaquensis* new genus and species, and *Megaxantho zoque*, new genus and species, are described. They constitute the second and third reports of Cretaceous xanthid crabs from Mexico. A lagoonal paleoenvironment is suggested, based on associated fauna and flora. Occurrences of index species of benthic and planktic foraminifera along with that of diagnostic rudist species confirm an early Maastrichtian age.

INTRODUCTION

RECENT CONSTRUCTION of a new highway between Ocozocuautla and Cosoleacaque in central Chiapas State (Fig. 1) has exposed outcrops where several lithologic units can be observed. Paleontologic investigation of some of these outcrops has yielded several complete specimens of *Carcineretes planetarius* Vega, Feldmann, Ocampo, and Pope, 1997 (Pimentel et al., 1998), a carcineretid crab previously described from the early Maastrichtian dolomite of the Barton Creek Formation in Belize (Vega et al., 1997). Two other species of crab also were collected in the same outcrops, but they were much less abundant than *C. planetarius*. They represent new taxa of xanthoid crabs: *Parazanthopsis meyapaquensis* n. gen. and sp., and *Megaxantho zoque* n. gen. and sp.

The only decapod crustaceans previously reported from the Maastrichtian Ocozocuautla Formation are specimens of *Lophoranina precocious* Feldmann, Vega, Tucker, García-Barrera, and Avendaño, 1996, collected from limestones that crop out around Tuxtla Gutiérrez and Ocozocuautla, Chiapas.

STRATIGRAPHY AND FOSSIL LOCALITIES

The type section of the Ocozocuautla Formation is located northwest of the town of the same name. There the formation is 630 m thick, with red and brown prodeltaic sandstone and some conglomerate at the base. Toward the top of the formation the lithology changes to shale, marl, and limestone of beige color (Gutiérrez-Gil, 1956; Chubb, 1959; Frost and Langenheim, 1974). Channels are exposed at some localities. Lateral lithologic changes within the formation indicate changes in depth of the basin, from shallow, restricted, lagoonal conditions in the east to deeper, outer platform settings in the northwest.

The Ocozocuautla Formation is underlain by the Sierra Madre Limestone, which is Early to middle Cretaceous in age (Steele and Waite, 1986), and is comformably overlain by the Paleocene Soyaló Formation (Frost and Langenheim, 1974; López-Ramos, 1981; Quezada-Muñetón, 1987). The latter formation is absent in the area of study.

The localities under consideration here are exposed along the highway between Tuxtla Gutiérrez and Ocozocuautla, and in the new highway between Ocozocuautla and Cosoleacaque. They have been entered into the catalog of localities of the Instituto de Historia Natural del Estado de Chiapas as numbers 1001, 1002, and 1003 (Fig. 1). Locality 1001 is located approximately five km east of Ocozocuautla, latitude 16°48′58″N, longitude 93°17′25″W, where large blocks of light-brown calcarenite crop out. Locality 1002 is approximately 2 km east of Ocozocuautla, on a curve of the highway between Ocozocuautla and Cosoleacaque, latitude 16°46′32″N, longitude 93°18′30″W, and is an outcrop of calcarenite interbedded with thin layers of marl. Locality 1003 is an exposure on the east side of the same highway, 2.5 km northeast of Ocozocuautla, latitude 16°49′15″N, longitude 93°18′28″W. The lithology at this locality is light-brown calcarenite and marl. The stratigraphic position of the sites is equivalent to the upper part of the Ocozocuautla Formation (Fig. 2). Some limestone horizons adjacent to these localities contain abundant rudists, including *Titanosarcolites giganteus, Barretia gigas, Macgillavria nicholasi, Antillocaprina trilobata*, and *Birradiolites* sp. (García-Barrera et al., 1998). Some of these taxa were previously reported from the Maastrichtian of Jamaica (Chubb, 1971). Several reports of the rudist fauna from Upper Cretaceous rocks of Chiapas have been published (Sapper, 1894; Müllerried, 1931a, 1931b, 1933, 1934, 1936, 1947; Chubb, 1959; Alencáster, 1971; among others). Most have suggested a late Campanian–early Maastrichtian age for the Ocozocuautla Formation.

Abundant specimens of dasycladacean algae and larger benthic foraminifera were found in a sample of fossiliferous marl from just above the horizon including the carapace of *Megaxantho zoque* n. gen. and sp. at locality 1003. The most numerous algal remains are the cylindrical thalli of one species, *Neogyroporella*? *servaisi*. The original description of *N. servaisi* was based upon material from a locality near Ocuilapa, Chiapas. It is the only other noted occurrence of this species (Michaud, 1988). The type material of this alga was collected from the base of the lowermost carbonate unit in the Angostura Formation, which, at that locality, is at a horizon just above the contact with the Ocozocuautla Formation.

Foraminifera, including *Chubbina jamaicensis*, from the type horizon of *N. servaisi* indicate a Maastrichtian age (Michaud, 1988). The most conspicuous larger benthic foraminiferans in the marl sample from locality 1003 also are specimens of the alveolinid genus *Chubbina*. Members of *Chubbina* are known from Jamaica, Cuba and southern Mexico, and the genus reportedly has a stratigraphic range of upper Campanian to Maastrichtian. Three species were referred to *Chubbina* in the original generic

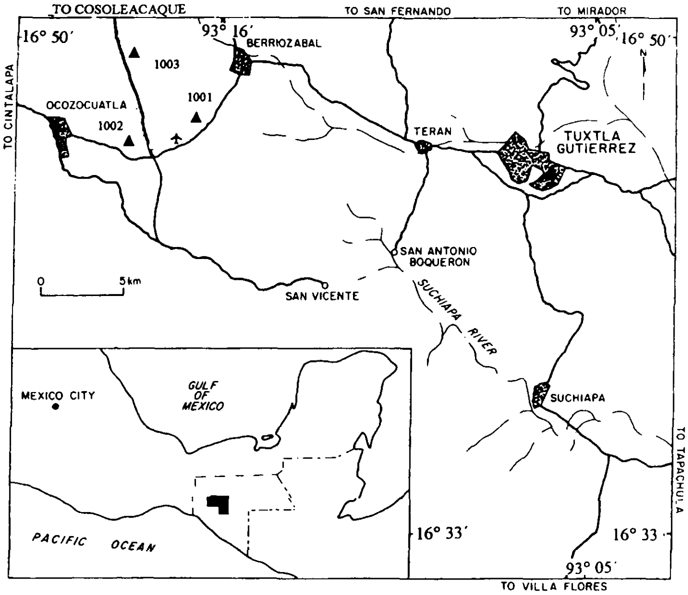

FIGURE *1*—Location map of studied area in Chiapas State, Southeast Mexico, showing localities 1001, 1002, and 1003, situated along the highway between Tuxtla Gutiérrez and Ocozocuautla, and between Ocozocuautla and Cosoleacaque, Chiapas.

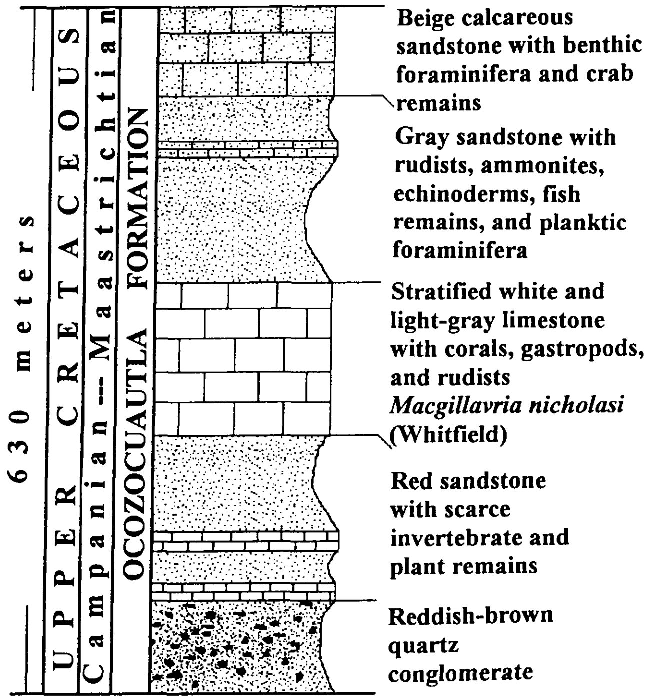

FIGURE 2—Stratigraphic section of the Ocozocuautla Formation, showing lithology and thickness.

description: *Chubbina jamaicensis, C. cardenasensis*, and *C. macgillavryi* (Barker and Grimsdale, 1937; Robinson, 1968). The type species, *C. jamaicensis*, previously has been reported from the Ocozocuautla and Angostura formations of Chiapas, where it occurs with *Neogyroporella servaisi*, and from the Guinea Corn Formation of Jamaica (Michaud, 1988). The second species, *C. cardenasensis*, has been reported from Cuba and the type locality near Cárdenas, in the State of San Luis Potosí, Mexico (Robinson, 1968). The third species, *C. macgillavryi*, has been reported only from the type locality, which is east of Ocozocuautla, along the road to Tuxtla Gutiérrez, Chiapas (Robinson, 1968). Mostly megalospheric forms of *Chubbina* were observed in thin sections of the rock sample examined in this study. The relatively large diameter of the proloculus and low rate of chamber enlargement observed in our samples are most similar to those same features of *C. macgillavryi*. The dasycladacean alga *N. servaisi* also is abundant in the same thin sections, as noted above.

Occurrences of other species of foraminifera in the sample from locality 1003 are uncommon. Only a few rotaliid specimens were observed in thin section. The morphology of the vertical section is most similar to that of *Smoutina cruysi* (Drooger, 1960, pl. 4., figs. 1–13). The latter species has been previously reported from Chiapas (García-Barrera et al., 1998, p. 132, fig. 6.4).

Overall, the benthic microbiota from locality 1003 indicates that the substrate was in warm, shallow, well-oxygenated water. The lack of abraded surfaces suggests that the fossils did not experience extensive transportation prior to deposition. Additionally, the presence of cysts preserved within the exterior regions of some of the thalli suggests a calm paleoenvironment.

The following benthic foraminifera were found associated with the crustaceans at localities 1001 and 1002 (identified by Lourdes Omaña, Instituto de Geología, UNAM): *Chubbina jamaicensis, Kathina jamaicensis, Sulcoperculina dickersoni, S. vermunti, S. globosa*, and *Rapidionina* sp. Other diagnostic Maastrichtian benthic foraminifera previously reported for the Ocozocuautla Formation are: *Omphalocyclus cubensis globosa, Torrenia torrei, Lepidorbitoides floridensis* (López-Ramos, 1981), and *Chubbina macgillavryi* (Robinson, 1968). Based upon the presence of calcareous algae, benthic foraminifera and rudists (Gutiérrez-Gil, 1956; Chubb, 1959; Robinson, 1968; Michaud, 1988), a lagoonal environment has been suggested for the upper part of the Ocozocuautla Formation. A recent report on planktic foraminifera collected approximately 40 m below the stratigraphic level of the crab localities includes the following species: *Globigerinelloides prairiehillensis, Globotruncana aegyptiaca, G. arca, G. bulloides, G. linneana, G. falsostuarti, Globotruncanita subspinosa, G. stuarti, Heterohelix globulosa, Rugoglobigerina hexacamerata, R. macrocephala, R. rugosa, R. reicheli, Rosita fornicata, Pseudoguembelina excolata, P. costulata*, and *Pseudotextularia elegans*. The stratigraphic ranges for these species suggest an early Maastrichtian age for the Ocozocuautla Formation. This portion of the section is interpreted to have been deposited in an outer platform environment (Omaña-Pulido, 1998). The Maastrichtian age is consistent with the stratigraphic ranges of the rudists and benthic foraminifera found at the crab localities. The type species of *Carcineretes, C. woolacotti*, was described from the Upper Cretaceous rocks of Jamaica (Withers, 1922, 1924). Similarity in faunal content and age suggest a correlation with the Barton Creek Formation of Belize (Pope et al., 1999), and the Guinea Corn Formation of Jamaica.

SYSTEMATIC PALEONTOLOGY

Order DECAPODA Latreille, 1802
Section HETEROTREMATA Guinot, 1977
Superfamily PORTUNOIDEA Rafinesque, 1815
Family CARCINERETIDAE Beurlen, 1930
Genus CARCINERETES Withers, 1922
CARCINERETES PLANETARIUS Vega, Feldmann, Ocampo, and Pope, 1997
Figure 3.1–3.7

Type species.—*Carcineretes woolacotti* Withers, 1922.

Carcineretes planetarius VEGA ET AL., 1997, p. 617, figs. 4.1, 4.2, and 5.

Description.—Carapace large, quadrate, wider than long, flattened transversely and longitudinally. Regions well defined by broad, distinct grooves. Cervical groove separates hepatic from epibranchial regions, and these are separated from fused mesobranchial and metabranchial regions by shallow groove, parallel to cervical groove. Front projected in advance of orbital region. Rostrum broad, downturned, with elevated axial region widening anteriorly between two divergent sulci forming U-shaped depression extending onto mesogastric region. Base of antenna subrectangular. Anterior margin inclined, raised, limited by intersection of hepatic groove and anterior margin, forming a small notch. Orbital margins long, concave-forward directed anteriorly or slightly anterolaterally, with two distinct, open fissures, one near mid-length, and one near anterolateral spine; anterolateral corner with strong, acute, triangular, forward-directed spine. Anterolateral margins slightly curved, with two short, acute, forward directed spines; one arises at level of epibranchial lobe; smaller spine arises at level of mesobranchial lobe. Posterolateral margin curved toward relatively short, straight posterior margin, one half maximum carapace width. Mesogastric region with narrow, parallel-sided anterior portion, pointed toward rostrum but becoming obscure posterior to ridges of protogastric region; mesogastric region broadens abruptly at level of epibranchial region to become 25 percent total carapace width, narrowing posteriorly to distinct, ovate, swollen urogastric region which is about 20 percent carapace width. Protogastric regions represent fifty percent carapace width, bordered by curved cervical and hepatic grooves, widest at mid-length, tapering uniformly to intersection with widest part of mesogastric region. Protogastric region with distinct, concave-forward transverse crest extending across region just in advance of point of maximum carapace width. Metagastric region fused with mesogastric at posterior slope of ovate lobe. Cervical groove 33 percent carapace width, convergent posteriorly to urogastric region, to complete general "V" shape; curved posterolaterally at level of hepatic regions. Hepatic regions swollen with subtle medial protuberance. Epibranchial lobes swollen, twice as wide as long, slightly inclined toward posterolateral margin, where small, anteriorly-directed spine is present. Metabranchial region slightly elevated, with prominent posterior slope, parallel to posterior margin. Branchial lobe distinct, forming small boss at level of urogastric lobe. Short, curved, deep grooves separate cardiac region from branchial lobes. Cardiac region becomes indistinctly defined posteriorly.

Subhepatic regions rectangular, with raised posterior ridge; pointed anterior margin. Sternum subquadrate, smooth. Thoracic sternites 1–4 fused into subtrapezoidal anterior unit with straight posterior margins. Sternites 5 to 7 rectangular, distal portion posteriorly curved, forming a sharp, inverted triangle. Eighth sternite subtrapezoidal, slightly narrower and longer than the rest; anterolateral margin directed forward; posterior margin broadly curved. Male abdomen pointed. First abdominal somite subdorsal, transversely elongated and slightly wider than posterior margin. Second abdominal somite slightly longer than first. Somites 3 to 5 fused into trapezoidal plate, posterior margin wider than sternum and covering coxae of P5. Fused sternites 3 to 5, 33 percent of plastron length. Sixth sternite subquadrate, anterior margin slightly concave; about 20 percent of plastron length. Telson triangular, shorter than somite 6, base convex and about 17 percent length of plastron. Female abdomen broadly triangular. First three abdominal somites subdorsal, of equal size and narrower than posterior margin. Fourth and fifth somites rectangular, 75 percent width of plastron. Sixth somite subtrapezoidal, twice as long as fifth somite. Telson broadly triangular, with straight posterior margin as long as sixth somite.

Buccal cavity quadrate. Endopodite of third maxilliped long, rectangular, slightly concave on external surface and convex on internal margin; exopodite acute, elongate, pointed.

Chelipeds relatively strong and acute. Right cheliped in males larger than left cheliped. Difference in size more evident in larger, presumably older, specimens. Chelipeds about equal size in females. Coxae strongly concave, narrower but as long as merus. Basis small, embraced by distal portion of coxa. Ischium smooth, subquadrate, 1/4 the length of merus. Merus long; quadrate upper surface with small but distinct spine on interior proximal corner. Lower surface acute, with three sharp, aligned spines directed outwards. Proximal two spines of equal size, placed at mid-length, third spine larger and placed 66 percent length from base of merus. Carpus strong, inflated, subquadrate. Propodus inflated, strong, attains maximum thickness below mid-length. A strong node present on proximal third of upper, outer surface. Sharp spine at mid-length on upper surface, directed inwards. Strong longitudinal ridge at outer edge on lower surface. Left fixed finger acutely triangular, slightly longer than right fixed finger; curves upwards at its tip, forming acute hook; upper surface dentate, with several sharp teeth. Dactylus more acute than fixed finger, dentate lower surface with fine, sharp teeth. Right cheliped in mature males 33 percent larger than left cheliped. Strong fixed finger, curved at tip with few, blunt strong teeth on upper margin; excavated surface at proximal portion holds massive, rounded tooth of dactylus. Dactylus sharp, curved downward; teeth strong and blunt.

Coxae of second to fourth pereiopods subtrapezoidal; basis short, rectangular; ischium subtriangular with elongate anterolateral corner; merus long, smooth, flattened dorsoventrally, anterior edge acute; carpus short, inflated, 25 percent length of merus; propodus long, flattened dorsoventrally, half length of merus; dactylus acute, 50 percent length of merus. Coxae of P5 inflated, subtrapezoidal, with strong, concave surface toward subtrapezoidal smaller basis, with "V" shaped surface toward small and subhexagonal ischium. Merus flattened, relatively long; carpus ovate, with excavated concave surface at articulation with propodus largest element of P5, subquadrate in shape, with triangular projection and broadly rounded outer proximal margin; one small fissure at upper portion of outer margin, where it articulates with oval, flat dactylus.

Material examined.—Thirty-seven nearly complete specimens. Specimens IHNCH-3412 to IHNCH-3417 are deposited in the paleontological collection of the Instituto de Historia Natural de Chiapas, located in Tuxtla Gutiérrez, Chiapas.

Measurements.—Measurements of the most complete specimens are given in Table 1.

Occurrence.—The material was collected from the upper part of the early Maastrichtian Ocozocuautla Formation near Tuxtla Gutiérrez, Chiapas, Mexico, at localities 1001, 1002, and 1003.

Discussion.—*Carcineretes planetarius* was first reported from the early Maastrichtian dolomite of the Barton Creek Formation on Albion Island, Belize. Just three incomplete specimens were collected then, but differences between *C. planetarius* and *C. woolacotti* were sufficient to propose a new species (Vega et al., 1997). Because the new material from Chiapas is so much better preserved than the type material, a complete description is provided to strengthen the understanding of the species.

Stratigraphic occurrence of *C. woolacotti* in the upper part of the Maastrichtian Guinea Corn Formation of Jamaica (Withers, 1922, 1924; Sohl, 1992; Verdenius, 1993; Krijnen et al., 1993; Morris, 1993), nerineid gastropods associated with the specimens from Belize, and $^{87}Sr/^{86}Sr$ isotope ratios (0.70786–0.70796) for the dolomite at Albion Island (Ocampo et al., 1996; Pope et al., 1999), indicate an early Maastrichtian age for *C. planetarius*. A similar age is indicated for the occurrence of *Carcineretes* in the Ocozocuautla Formation. This is documented by the presence of *Globotruncana aegyptiaca* in the upper part of the Ocozocuautla


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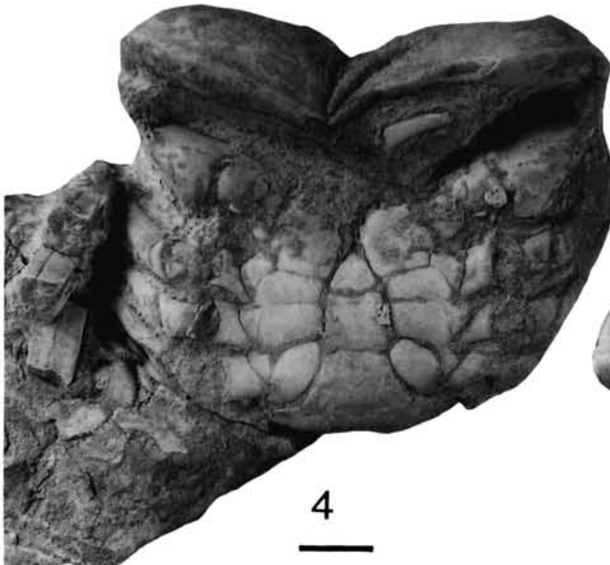
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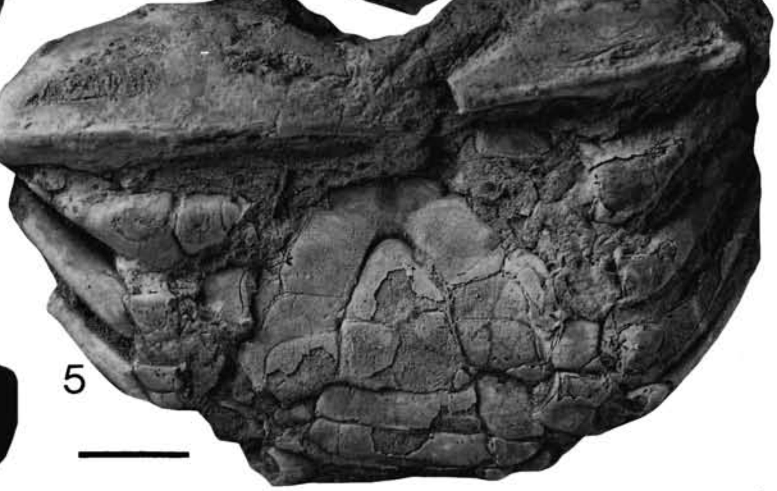
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Formation, near the localities where the material here described was collected (Omaña-Pulido, 1998). Thus, the stratigraphic range of *Carcineretes* in the Caribbean Province seems to be restricted to the lower Maastrichtian.

A lagoonal paleoenvironment has been suggested for the limestones of the Guinea Corn Formation, from which *Carcineretes woolacotti* was reported (Flores, 1952; Robinson, 1968; Withers, 1922; Sohl, 1992; Morris, 1993). A similar paleoenvironment has been suggested for the Barton Creek Formation on Albion Island, Belize (Vega et al., 1997; Pope et al., 1999). The presence of miliolids, rudists, calcareous algae and nerineid gastropods at the studied localities of the Ocozocuautla Formation indicates a lagoonal paleoenvironment. Morris (1993) suggested that the narrow posterior end of the carapace and flattened fifth pereiopods in *Carcineretes woolacotti* were an adaptation for digging backwards into the sediment instead of swimming. However, in all probability the appendages served both for swimming and burrowing.

Most of the 37 examined specimens from the Ocozocuautla Formation were males; only three were determined to be females. However, this could be due to late appearance of sexual characteristics in females; in most brachyurans, immature females resemble males. Also, most specimens are molts, based on thickness of the carapace and posterior displacement of the sternal plastron. Only six specimens are corpses. It is important to note that six pairs of specimens were found together, and that each paired sample included one specimen that is slightly larger than the other (Fig. 3.6, 3.7). In every case the smaller specimen represents a molt, the larger a corpse. Measurements of linear dimensions on the molt and associated corpse indicates that the corpse is about 16 percent larger than the molt. This is well within the normal range of size increase during molting (Warner, 1977), suggesting that the two specimens were produced by the same individual. Death shortly after molting is suggested by these occurrences. It would seem more than coincidental that six specimens illustrating this phenomenon were found at one site; however, because there is no evidence for any type of lethal event, the cause remains unknown.

Extinction of carcineretid crabs has been explained in relation to their paleobiogeographic distribution. They are restricted to the Caribbean Province, near the Chicxulub impact site (Feldmann et al., 1998). Four genera of carcineretids were present in the early Maastrichtian: *Ophthalmoplax* in Texas and Brazil (Rathbun, 1935; Beurlen, 1958); *Mascaranada* and *Branchiocarcinus* in northeast Mexico (Vega and Feldmann, 1991; Vega et al., 1995); and *Carcineretes* in the Caribbean Province (Withers, 1922; Vega et al., 1997). Carcineretids in the Caribbean Province have also been recorded from the Turonian of Colombia, where *Ophthalmoplax spinosus* Feldmann, Villamil, and Kauffman, 1999, was an abundant element, related to mass mortality (Feldmann et al., 1999). Of these, the most abundant is *Carcineretes planetarius*, with 43 specimens at various localities. None of these genera is known from the Cenozoic.

Superfamily XANTHOIDEA Dana, 1851
Family XANTHIDAE Dana, 1851 sensu lato
Genus PARAZANTHOPSIS new genus

Type species.—*Parazanthopsis meyapaquensis* new species.

Diagnosis.—Carapace medium size, subhexagonal, wider than long; anterolateral and posterolateral margins of equal length, anterolateral margins with four short, slightly raised spines of approximately equal size; fronto-orbital margin narrow; orbits small; rostrum narrow, sulcate, with two small spines at margin of sulcus. Regions of carapace well defined by bluntly rounded elevations, posterior part of carapace with steep slope, posterior margin short; chelae massive, right chela larger than left; sternum small.

Etymology.—The first part of the generic name indicates the similarity (Greek *para* = near) of the new genus to *Zanthopsis* M'Coy 1849.

Discussion.—The new genus is most similar to *Zanthopsis* M'Coy (1849) in the general shape of the carapace, in possessing a short frontal margin, and on the presence of four spines on the anterolateral margin. However, *Zanthopsis* has an almost equidimensional carapace; its front has four spines; and its regions, particularly of the epigastric and mesogastric lobes, are proportionally smaller.

Palaeoxanthopsis Beurlen, 1958, described from the Maastrichtian of Brazil is also similar to this new genus. However, *Palaeoxanthopsis* has much shorter posterolateral margins, its anterolateral margins have fissures instead of spines, and there is a long lateral spine which separates the anterolateral and posterolateral margins. *Xanthilites* Bell, 1858, is also similar, except that it has longer posterolateral margins and shorter anterolateral margins, its carapace is not much wider than long, and the regions of the carapace are not as strongly marked as in *Parazanthopsis*. Finally, *Lobonotus* Milne Edwards, 1864, is similar to *Parazanthopsis* because it has four broadly lobose teeth on the anterolateral margins, but the regions of *Lobonotus* are subdued and not as distinct, and the frontal margin is wider than in *Parazanthopsis*.

The reported distribution of xanthoid crabs in Mexico during Maastrichtian time suggests that they were restricted to the Pacific and Caribbean Provinces exclusively. No xanthoids have been reported from the Maastrichtian sequences of northeast and central Mexico. The only Cretaceous xanthoid crab described previously from Mexico is *Xandaros sternbergi* (Rathbun, 1926) from the Maastrichtian of Baja California Norte (Bishop, 1988).

Other xanthoids from Mexico include *Lobonotus mexicanus* Rathbun and *Xanthosia americana* Rathbun from the upper Eocene and Oligocene respectively, of the Tepetate Formation of Baja California Norte, and *Harpactocarcinus americanus* Rathbun from the Eocene of Tamaulipas (Rathbun, 1930a). These occurrences must be carefully evaluated. The Xanthidae sensu lato has been subdivided into several subfamilies and assignment of fossil species to the new systematic arrangement of families is under way. Recent re-appraisal of the genus *Xanthosia* led Schweitzer et al. (1999) to conclude that the type material of *X. americana* was incomplete, and that no firm placement was possible. *Harpactocarcinus americanus* may be referrable to the xanthoid family Carpiliidae.

PARAZANTHOPSIS MEYAPAQUENSIS new species
Figure 4.1–4.3

Diagnosis.—As for genus.

Description.—Carapace medium size, subhexagonal to ovate, strongly convex in longitudinal section; 33 percent wider than long; anterolateral and posterolateral margins of equal length; anterior margin short, slightly raised, less than half the maximum

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FIGURE 3—*Carcineretes planetarius*. *1*, Dorsal view of carapace, female. IHNCH-3412, locality 1001; *2*, ventral view of carapace, male. Note shape of maxillipeds. IHNCH-3413, locality 1003; *3*, ventral view of carapace, male. Note flattened, semioval, left propodus. IHNCH-3414, locality 1001; *4*, ventral view of carapace, male. Note flattened, oval, right dactylus. IHNCH-3415, locality 1001; *5*, ventral view of carapace, female. IHNCH-3416, locality 1001; *6*, *7*, dorsal and ventral views of paired specimens IHNCH-3417 showing a molt (smaller specimen) and corpse (larger specimen). Note that only the corpse exhibits the sternum, abdomen, and appendages. Scale bars equal 1 cm.

TABLE *1*—Measurements and features of *Carcineretes planetarius*, from the Ocozocuautla Formation.

	Specimen				
Measurement/Feature	3412	3413	3414	3415	3416
Carapace Length	33.5	16.4	42.7	41.7	38.1
Carapace Width	37.1	23.4	48.1	47.6	44.8
Carapace Height	13.1	7.3	14.5	14.5	11.6
Carapace W/L	1.07	1.42	1.12	1.14	1.17
Orbital Margin Width	10.1	~	11.3	10.4	10.7
Fronto-orbital Width	16.6	~	20.9	20.4	18.8
Right Cheliped Length	20.4	20.4	43.3	43.6	32.2
Right Cheliped Width	6.7	~	11.4	~	~
Right Cheliped Height	~	~	24.1	21.3	17.9
Right Cheliped L/H	~	~	1.79	2.04	1.79
Left Cheliped Length	28.1	~	42.7	39.5	35.3
Left Cheliped Width	6.4	~	10.3	10.2	~
Left Cheliped Height	12.2	~	17.6	17.3	14.3
Left Cheliped L/H	2.3	~	2.42	2.28	2.46
Abdomen Length	21.4	13.2	23.6	23.6	21.8
Abdomen Width	10.7	4.9	7.5	8.2	11.1
Abdomen L/W	2	2.69	3.14	2.87	1.96
Male/Female	Female	Male	Male	Male	Female
Corpse/Molt	Corpse	Corpse	Corpse	Molt	Molt

width; orbits small and circular, their diameter 12 percent maximum width; orbital margin weakly rimmed; rostrum very small, bifid, with two short, forward-projected divergent spines; anterolateral margins a broadly rounded, undulate surface with four upturned small spines which become slightly longer toward midlength of carapace; fourth anterolateral spine perpendicular to longitudinal axis of carapace, length 20 percent maximum width of carapace; posterolateral margins straight, 66 percent maximum length, inclined about 45 degrees to long axis, reaching the short, straight, slightly raised posterior margin, which is about 25 percent maximum width. Regions with rounded bosses and well defined grooves. Mesogastric region lowest elevation on carapace, subpentagonal, with subparallel axial sulci directed forward, converges before reaching frontal margin. Fused epigastric and protogastric lobes form tricuspate boss, of inverted triangular shape, delimited by cervical groove, with a small projection toward the frontal margin, parallel to furrow of mesogastric region. Cervical groove deeply impressed, convergent behind mesogastric lobe, one-third maximum length. Hepatic lobes small, elongated and inclined, almost parallel to anterolateral margin, with sharp, centrally-located spine. Epibranchial lobe ovate, inclined toward fourth anterolateral spine, 17 percent maximum width. Mesobranchial lobe elongate, smaller than epibranchial and perpedicular to it, situated at mid-length of carapace, at level of maximum width. Metabranchial lobes relatively large and prominent, located near mid-length of posterolateral margin, bearing low spine near lateral margin. Cardiac lobe subtrapezoidal, with transverse ridge at midlength, width 25 percent maximum carapace width, separated from short posterior margin by steep slope.

Buccal frame quadrate, endopodite of third maxilliped rectangular, straight-sided. Sternum relatively small, subovate in longitudinal section. Fused sternites 1–3 forming a triangle, with deep longitudinal groove in middle part. Fourth sternite rectangular, longer than wide, with deep groove slightly inclined in middle part; sharp, episternal process at posterolateral corner overlaps fifth sternite. Fifth sternite subquadrate, much smaller than fourth, with episternal process at lower part of lateral margin, which overlaps sixth sternite. Sixth sternite smaller than fifth and subquadrate. Remaining sternites not preserved. Abdomen partially preserved. Sixth somite large, subrectangular, length equivalent to sternites 4 and 5; telson triangular, with curved posterior margin, two-thirds length of sixth sternite.

Ischium of cheliped small, subtriangular; merus strong, subrectangular, with sharp, ventral longitudinal keel; carpus subquadrate, massive, with short, sharp spine projecting from anterolateral dorsal surface; right cheliped larger than left; palm massive, surface ventricose, keel on dorsal surface, distal external surface with rounded boss at insertion of dactylus; propodus strongly pigmented on distal two thirds, relatively short, triangular, with three rounded teeth on occlusal surface; dactylus completely pigmented, slightly curved toward carapace, triangular and with five rounded teeth on occlusal surface.

Fourth and fifth pairs of pereiopods very long. Ischium of P5 short, subquadrate; merus very long, ovate in transverse section; carpus short, subtriangular. Carpus of P4 twice as long as in P5.

Etymology.—The name is derived from the Meyapac region, where the most fossiliferous outcrops of the upper part of the Ocozocuautla Formation are located.

Types.—Four specimens: two juveniles and one adult, and an incomplete specimen. Holotype IHNCH-3418, and Paratypes IHNCH-3419, and IHNCH-3420, are deposited in the paleontological collection of the Instituto de Historia Natural de Chiapas, located in Tuxtla Gutiérrez, Chiapas.

Measurements.—Measurements of holotype and paratypes are given in Table 2.

Occurrence.—The material was collected from the upper part of the early Maastrichtian Ocozocuautla Formation near Tuxtla Gutiérrez, Chiapas, Mexico, at localities 1001 and 1003.

Discussion.—*Xandaros sternbergi* (Rathbun, 1926) differs from *Parazanthopsis meyapaquensis* n. sp. in being slightly wider than long, having a wider frontal margin, lacking spines on the anterolateral margins, and possessing lower bosses on the regions. Also, *X. sternbergi* has rows of tubercles on the chelipeds, whereas chelipeds of *Parazanthopsis meyapaquensis* n. sp. are smooth. *Palaeoxanthopsis cretacea* (Rathbun, 1902) from the Maastrichtian of Brazil (Beurlen, 1958) has two large lateral spines, and the anterolateral margins have two fissures and lack spines. The posterior margin of *Palaeoxanthopsis cretacea* is slightly curved, with a sharp edge at its union with the posterolateral margin. In *Parazanthopsis meyapaquensis* n. sp., the posterior margin is straight and broadly rounded at its junction with the posterolateral margins. *Xanthilites verrucoides* Collins and Rasmussen, 1992, from the Paleogene of West Greenland has anterolateral margins with four spines, and carapace regions that are similar to those of

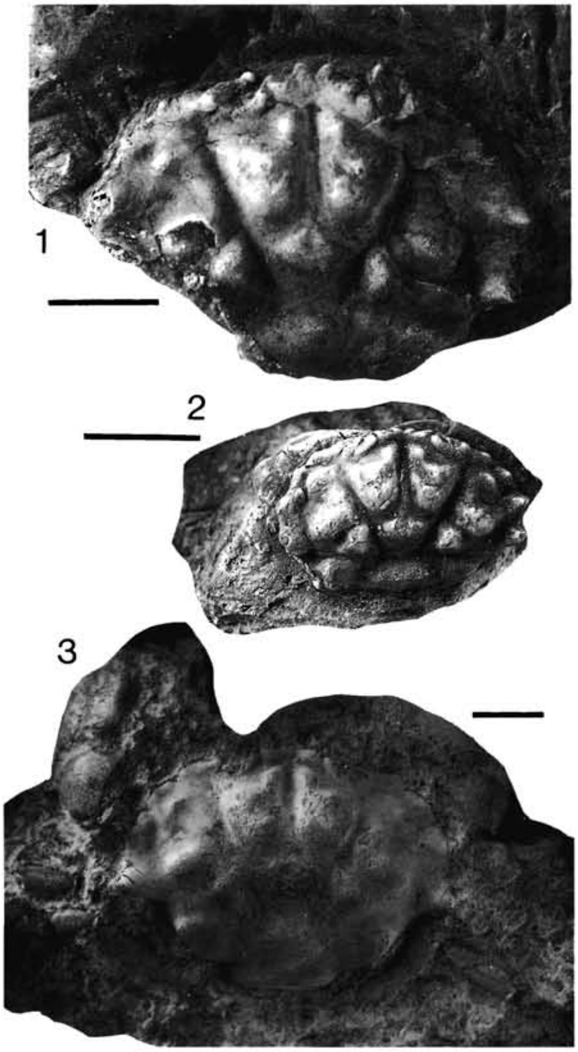

FIGURE 4—*Parazanthopsis meyapaquensis* n. gen. and sp. *1*, Dorsal view of incomplete specimen. Paratype IHNCH-3420, locality 1003; *2*, dorsal view of juvenile specimen. Paratype IHNCH-3419, locality 1003; *3*, dorsal view. Holotype IHNCH-3418, locality 1001. Scale bars equal 1 cm.

Parazanthopsis meyapaquensis n. sp. However, the species from Greenland has a carapace that is not as convex; it has a larger lateral spine; the carapace has proportionally longer posterolateral margins; the widest part of the carapace is located more anteriorly; and the carapace regions are represented by low tubercles. *Xanthilites gerthi* Glaessner, 1930, and *Lobonotus lobulata* Feldmann et al., 1995, from the Upper Cretaceous and lower Paleocene of Argentina are different from *Parazanthopsis meyapaquensis* n. sp. in having anterolateral margins with four lobes, instead of four spines. Also, the carapaces of *X. gerthi*, and *L. lobulata* are not as convex in longitudinal section, and their posterolateral margins are proportionally longer than those of *P. meyapaquensis* n. sp. The distribution of the regions is different, and the regions are defined by elevated spines on *X. gerthi*, whereas in *P. meyapaquensis* n. sp. the regions are defined by blunt, massive bosses, the most prominent of which occupy the epigastric-protogastric and metabranchial regions. *Lobonotus lobulata* differs from *P. meyapaquensis* n. sp. in having an almost flat, equant carapace.

TABLE 2—Measurements and features of *Parazanthopsis meyapaquensis*, from the Ocozocuautla Formation.

	Specimen		
Measurement/Feature	3418	3419	3420
Carapace Length	34.8	14.8	27.2
Carapace Width	47.2	21.1	33.9
Carapace Height	16.6	~	~
Carapace W/L	1.35	1.42	1.24
Orbital Margin Width	6.3	3.2	4.3
Fronto-orbital Width	10.8	5.4	8.6
Right Cheliped Length	37.8	14.7	22.9
Right Cheliped Width	12.9	5.2	~
Right Cheliped Height	14.4	~	10.6
Right Cheliped L/H	2.6	~	2.16
Left Cheliped Length	27.3	12.5	17.1
Abdomen Length	17.4	~	7.9
Abdomen Width	8.6	~	4.7
Abdomen L/W	2.02	~	1.68
Male/Female	Male	~	Male
Corpse/Molt	Corpse	Corpse	Molt

Two Cretaceous specimens from Jamaica, referred to *Necrocarcinus* sp. and *Paranecrocarcinus*? sp. by Morris (1993, fig. 1.5 and 1.6) are more similar to xanthoid crabs than to calappoids. One specimen (Morris, 1993, fig. 1.5) resembles *Parazanthopsis meyapaquensis*, although it is incomplete and difficult to compare with the new species from Chiapas.

Genus MEGAXANTHO new genus

Type species.—*Megaxantho zoque* new species.

Diagnosis.—Carapace large, subhexagonal, wider than long; front wide, orbits large; anterolateral margins broadly rounded, with three semirectangular broad lobes and one subtriangular lobe which is most prominent, located at mid-length of carapace. Posterior to the last lobe, a much smaller spine is present defining anterior part of posterolateral margin which is straight and inclined toward short, straight posterior margin. Dorsal surface apparently flat, pitted; cervical groove and regions weakly defined; heterochelous, chelipeds massive and large, right cheliped much larger than left; plastron subrectangular, relatively small; abdomen triangular, longer than wide.

Etymology.—The Greek generic name recognizes the unusually large size of the Cretaceous xanthid crab (*mega* = large).

Discussion.—In terms of their large size, fossil xanthoid crabs similar to *Megaxantho* n. gen. include: *Neptocarcinus, Tumidocarcinus, Harpactocarcinus, Harpactoxanthopsis, Menippe, Palaeocarpilius*, and *Ocalina*, all from the Cenozoic. However, none of these bears close morphological affinities. *Neptocarcinus* has similar anterolateral margins with four rounded lobes, but its carapace is much wider than long, the fourth lateral spine seems to be longer, and the orbital margins lack fissures (Lőrenthey, 1898). *Tumidocarcinus* lacks lobes and spines on the anterolateral margins and the front is more narrow (Glaessner, 1960). *Harpactocarcinus* and *Palaeocarpilius* differ from the new genus in having more inflated and semicircular carapace, and in having denticulate anterolateral margins and dorsal margins of palms, and in fact, may be referred to the Carpiliidae (Milne Edwards, 1862). *Harpactoxanthopsis* has blunt teeth on the anterolateral margins, a much narrower front, and smaller orbits without fissures (Vía, 1969; de Haan, 1833). *Menippe* has a transversely oval carapace, smaller orbits, and a narrower distance between orbits than the new genus from Chiapas. *Ocalina* has a semicircular carapace, tuberculate front, and anterolateral margins with ten thick lobules (Rathbun, 1929), and is also referrable to the Carpiliidae (Schweitzer et al., 2000). Another genus which might be similar is *Laevicarcinus* Lőrenthey. It has similar anterolateral margins,

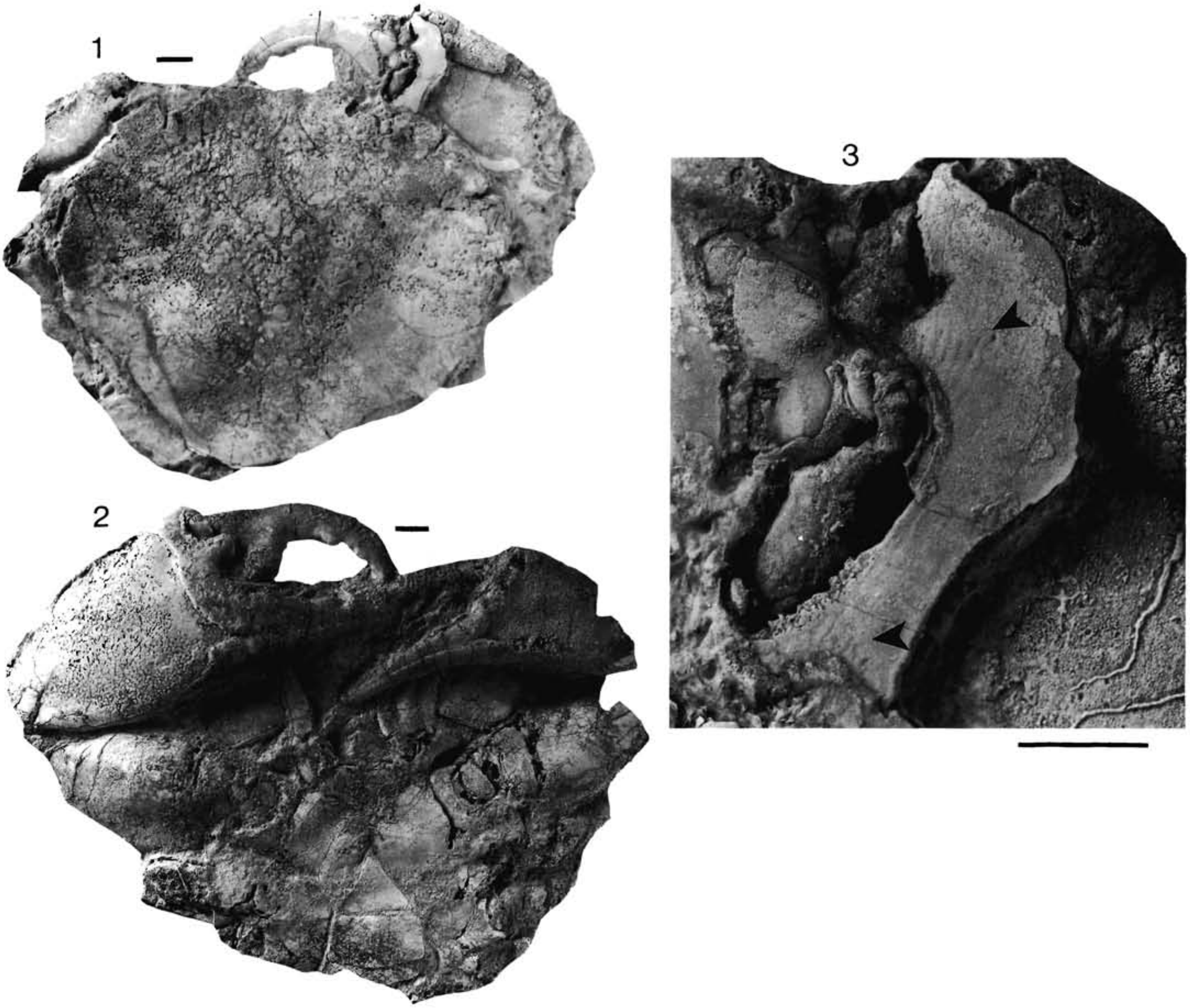

FIGURE 5—*Megaxantho zoque* n. gen. and sp. Holotype IHNCH-3421, locality 1003. *1*, Ventral view; *2*, detail of parallel grooves on the inner surface of the distal portion of right palm, possible stridulatory mechanism; *3*, dorsal view. Scale bars equal 1 cm.

but differs from the new genus in having much stronger dorsal regions and in being much smaller (Lőrenthey and Beurlen, 1929). Although Glaessner (1969) placed *Laevicarcinus* in the Goneplacidae, it was suggested by Vía (1969) that the species of this genus should be regarded as a xanthoid related to *Titanocarcinus*. This placement remains in question, and Schweitzer (personal commun.) proposed that *Laevicarcinus* is referrable to the Panopeidae.

The only Cretaceous crab that attains a size comparable to that of *Megaxantho* is *Ophthalmoplax* Rathbun, 1935. A single specimen from Colombia, currently under study, attains a carapace width of more than 35 cm. However this genus is characterized by a very broad, straight front, nearly parallel sides and transverse ridges on the carapace surface. It is referrable to the Carcineretidae. Thus, the genus cannot be confused with any known crab taxa.

The familial placement of *Megaxantho* within the Xanthoidea cannot be determined with certainty. The extremely flattened carapace surface is reminiscent of the Goneplacidae; however, the surface is crushed and the degree to which it was originally vaulted cannot be determined. Until better preserved specimens are found, it is judicious to place *Megaxantho* in the Xanthidae s.l.

MEGAXANTHO ZOQUE new species
Figures 5.1–5.3, 6

Diagnosis.—As for genus.

Description.—Carapace large, subhexagonal, 25 percent wider than long; anterolateral margins broadly rounded and with three semirectangular lobes; one triangular lobe near mid-length of carapace. Front relatively wide, orbits large, curved inward, 20 percent width of frontal margin, with two parallel fissures situated lateral to orbital midline. Posterolateral margins smooth, 66 percent maximum length, inclined toward relatively short posterior margin, which is straight, 33 percent maximum width. Regions

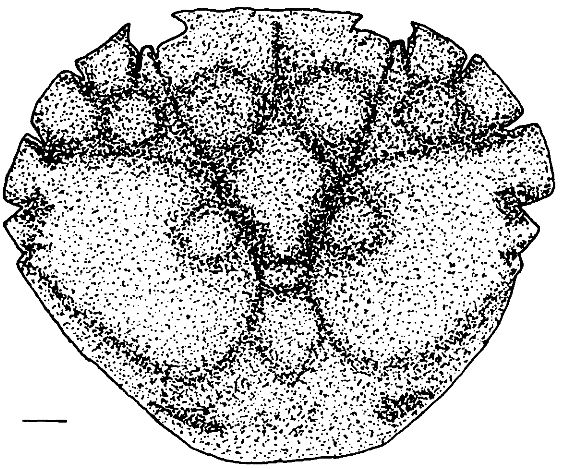

FIGURE 6—Line drawing of *Megaxantho zoque* n. gen. and sp. Dorsal view. Scale bar equals 1 cm.

of carapace weakly marked; surface pitted. Mesogastric and metagastric regions subrhombic, with shallow furrow projected toward rostrum. Protogastric lobes circular, low, rounded protuberances. Cervical groove "V" shaped, weakly marked, inclined and convergent toward posterior portion of metagastric region; hepatic lobes relatively small, slightly raised and circular; cardiac regions subtrapezoidal; branchial regions undifferentiated; posterior slope of carapace gently inclined toward posterolateral and posterior margins.

Sternum relatively small, elongate and subrectangular, 66 percent maximum length, and 33 percent maximum width of carapace; sternites 1–4 fused with shallow, straight grooves, directed anterolaterally, defining junction of somites 3 and 4; anterior margin broadly rounded, surface smooth and flat; male abdomen triangular, 33 percent maximum length, and 25 percent maximum width of carapace; fifth somite subrectangular, much wider than long; sixth somite rectangular, 3 times longer but slightly narrower than fourth somite; telson triangular. Subhepatic regions smooth, rectangular, with straight, slightly raised posterior margin. Buccal frame widens anteriorly, longer than wide; third maxillipeds strong, endopodite subquadrate, proximal margin convex, distal margin concave.

Chelipeds massive; basis wide and short, distal margin concave; ischium subrectangular, short; merus very strong, 66 percent carapace length and 25 percent maximum width, lower surface smooth, with broadly rounded keel; carpus not preserved; chelipeds strong and massive, heterochelous, right cheliped much larger and morphologically different than left cheliped. Palm of right cheliped pitted, twice as long as high; distal inside surface of right palm shows patches of oblique, parallel striae, possibly some kind of stridulating organ (Fig. 5.3). Fixed finger strong, triangular, with short longitudinal keel on inner surface and longitudinal groove on outer surface, curved inward, with five blunt teeth on occlusal surface; movable finger broadly curved, with smooth upper surface, and shallow, curved longitudinal groove on inner surface, four teeth on occlusal surface, large basal tooth, articulates with large subbasal tooth, arising on distal margin of palm. Left cheliped half the height of right cheliped, palm surface pitted, fixed finger triangular, curved inward, with longitudinal groove on outer margin, more than five blunt teeth on occlusal surface; movable finger almost straight, slightly curved inward, dorsal and distal surfaces each with longitudinal grooves. Basis of P3 subtrapezoidal, distal margin concave. Meri of P4 to P3 elongate, subrectangular, surface with small granules.

Etymology.—The name honors the Zoque people, who inhabited the study area more than eight hundred years ago.

Types.—One specimen, the holotype IHNCH-3421, is deposited in the paleontological collection of the Instituto de Historia Natural de Chiapas, located in Tuxtla Gutiérrez, Chiapas.

Measurements.—Holotype IHNCH-3421. Carapace: length = 109.4 mm, width = 126.7 mm, height = 26.3 mm, W/L ratio = 1.15; orbital margin width = 16.2 mm; fronto-orbital width = 35.1 mm; right chela: length = 108.1 mm, width = 24.9 mm, height = 57.1 mm, length of dactylus = 53.7 mm, height of dactylus = 28.2 mm, length of propodus = 42.9 mm, height of propodus = 19.5 mm; left chela: length (incomplete) = 79.8, width = 14.4 mm, heigth = 37.8 mm, length of dactylus = 35.6 mm, height of dactylus = 12.9 mm, length of propodus = 45.8 mm, height of propodus = 13.8 mm; sternum (incomplete): length = 66.5 mm, width = 44.9 mm; abdomen (incomplete): length = 36.1 mm, width = 26.3 mm.

Occurrence.—The material was discovered by H. Filkorn in the upper part of the early Maastrichtian Ocozocuautla Formation near Tuxtla Gutiérrez, Chiapas, Mexico, at locality 1003.

Discussion.—Previously reported Cretaceous xanthoids are different from the new species from Chiapas, particularly in carapace shape and size, and in the shape and distribution of regions, as noted above in the discussion given for the genus. *Menippe mercenaria* from the Pleistocene and Recent of the Atlantic Ocean, Gulf of Mexico and Caribbean is similar in shape of the carapace, and lack of development of carapace regions (Say, 1818; Rathbun, 1935; Williams, 1984). The anterolateral margins of *Mennipe mercenaria* are similar to *Megaxantho zoque* in having three wide lobes, and a small lateral spine located in the widest portion of carapace. The posterior margin of *Menippe mercenaria* is relatively wider, its orbits are smaller with indistinct fissures, and the distance between them is relatively shorter than in *Megaxantho zoque. Laevicarcinus egerensis* Lőrenthey and Beurlen, 1929, from the Eocene of Europe, is very similar to *M. zoque* in its carapace shape, including frontal and anterolateral margins, but the carapace is smaller, the regions of the carapace are strongly defined, and some of the regions have ridges on them (Lőrenthey and Beurlen, 1929; Müller and Collins, 1991). *Neptocarcinus millenaris* from the Upper Eocene of Hungary is also similar to *M. zoque* n. sp. in its anterolateral margins, but it differs from *M. zoque* in having a carapace that is much wider than long (Lőrenthey, 1898; Lőrenthey and Beurlen, 1929). The systematic position of *Neptocarcinus* was considered uncertain by Vía (1969), who stated that there are similarities between it and *Palaeocarpilius*. However, Müller and Collins (1991) preserved the original generic name.

The peculiar curved shape of the right movable finger of the specimen from Chiapas might represent a deformation related to the regenerative process. The strongly curved dactylus is unusual among members of the Xanthoidea.

Patches of parallel striae on the inner surface of the chelipeds of the Recent menippid crab *Menippe mercenaria* can be observed in adult specimens. This crab strokes these striae against the second and third anterolateral spines and outer suborbital spine in order to create sound, a process called stridulation (Williams, 1984). Stridulation has been reported by several authors in xanthoids, portunids, ocypodids, and other families (Rathbun, 1930b; Guinot-Dumortier and Dumortier, 1960; Bender, 1971; Warner, 1977, among others). Stridulatory organs in the fossil record are scarce. Feldmann and Bearlin (1988) reported a stridulatory mechanism, developed on the frontal region of the cephalothorax and in the basal elements of the antennae of the palinurid *Linuparus korura* Feldmann and Bearlin, 1988. The possible function of this kind of structure has been related to agonistic behavior and attraction of mates (Warner, 1977).

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