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EARLY CRETACEOUS ARTHROPODS FROM THE TLAYÚA FORMATION AT TEPEXI DE RODRÍGUEZ, PUEBLA, MÉXICO

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ABSTRACT—The arthropod macrofauna from the Middle Member of the lithographic limestones of the Tlayúa Formation, in quarries at Tepexi, México, is comprised of marine and nonmarine components. Marine taxa include a new species of flabelliferid isopod, a new genus and species of an anomuran, and a new genus and species of a brachyuran crab. Remains of an arachnid and an odonate nymph represent nonmarine constituents. Previous paleoenvironmental interpretations of a restricted lagoon, with periodic episodes of marine and freshwater influences are consistent with the nature of the arthropod fauna. Isopod remains, represented only by corpses, that resemble modern ectoparasites of fishes suggest that they are directly associated with the abundant fish remains found in the quarries, either as ectoparasites that released their hosts before they died or possibly as scavengers that fed on fish remains. The next most abundant arthropods are the crabs, most of which are corpses, suggesting that this group lived in or very near to the depositional site of the Tlayúa Formation. Based upon the new fossil material, the stratigraphic range for the Aeglidae has been extended to span Albian to Holocene time. Extant representatives of this family inhabit fresh water environments of South America.

INTRODUCTION

THE TLAYÚA QUARRY is located in the southern part of Puebla, approximately 200 km southeast of México City (Figure 1). the diverse and abundant fauna of more than a hundred taxa includes foraminifera, sponges, gorgonians, gastropods, ammonoids, belemnoids, bivalves, arachnids, crustaceans, insects, echinoids, asteroids, ophiuroids, fishes, and reptiles, as well as algae and remains of terrestrial plants. This assemblage is preserved in a red laminated limestone, which has been used commercially as flagstone by the Aranguthy family for many years. Since 1985, the quarry has been carefully collected, and the fossil material has been prepared, curated, and deposited in the Paleontological Museum of the Instituto de Geología, Universidad Nacional Autonomia de México (UNAM). The systematic and geologic study of the fauna has yielded several papers and field guides (Applegate and Espinosa-Arrubarena, 1982; Applegate et al., 1984; Applegate, 1987; Seibertz and Buitrón, 1987; Applegate, 1988; Martill, 1989; Pantoja-Alor et al., 1989; Applegate, 1992; Pantoja-Alor, 1992; Espinosa-Arrubarena and Applegate, 1995; Applegate, 1995, among others).

The purpose of this work is to describe the diverse arthropod fauna of the Tlayúa Formation and to discuss its paleoecological implications. Because work on the sedimentology and sedimentary geochemistry of the formation has not been concluded, it is not appropriate to speculate on the overall paleoecological setting beyond the scenarios that have been developed previously. Rather, it is intended that the information regarding the arthropod fauna be coupled with future sedimentological studies to refine the interpretation of the depositional setting.

The Tlayúa Formation was formally described by Pantoja-Alor (1992). It consists of at least 300 m of limestone (Figure 2), whose outcrops are located in a ravine known locally as Tlayúa. Since neither the top nor base of the sequence is exposed, the thickness for the formation remains unknown. The Tlayúa Formation was subdivided into three units, namely the Lower, Middle, and Upper Members (Pantoja-Alor, 1992). The Lower Member consists of a sequence of bioturbated, tightly folded bluish gray micritic limestone, with intraclasts, rudists, other bivalves, and abundant miliolids (Applegate, 1992). The Middle Member is a sequence of micritic, thinly laminated, yellow-brown limestones, 50 to 54 m thick. The bedding planes show red hematitic layers, which bear a large array of well-preserved fossils. All of the vertebrate fossils as well as many of the invertebrates, including the material here described, were collected from this member (Figure 2). Based upon some belemnoid and ammonoid species, the member has been assigned a middle to late Albian age (Seibertz and Buitrón, 1987; Buitrón and Malpica-Cruz, 1987). The Upper Member is a sequence of gray dolomites apparently barren of fossils (Applegate, 1992). The formation rests upon the Paleozoic Acatlán Complex which according to Ortega-Gutiérrez (1978) and Ortega-Guerrero (1989), represented a positive land surface during Jurassic times, that possibly existed until the Early Cretaceous (Applegate, 1987). The nature of that contact is not known.

Paleoenvironmental interpretations for the Tlayúa Formation depict a restricted shallow lagoon bordered by a large reef (Applegate, 1992). Presence of corals in limestones of Early Cretaceous age, located in outcrops to the east of the Tlayúa quarry, may define the position of the reef. Another barrier has been proposed to have existed landwards of the above mentioned reef separating the "normal" marine lagoon from the back lagoon area in which Tlayúa sediments were deposited (Applegate, 1992).

Exceptional preservation at Tlayúa was promoted by restricted circulation of water resulting in an anaerobic and/or hypersaline environment, coupled with the general absence of infaunal species. There were periods when the depositional site supported a rich planktic community. Large quantities of calcareous ooze were produced, resulting in rapid burial of the organisms. Presence of diagnostic terrestrial and freshwater organisms, including arachnids, insects, lizards, and chelonians, along with typical marine fauna, suggests that Tlayúa lagoon had periodic freshwater inflow, in addition to the strong marine, lagoonal, and reefal influence. Some organisms were transported into the lagoon when the barrier was breached, probably during periods of heavy rains and hurricanes, or during high tides (Applegate, 1992). Additionally, some fishes from Tlayúa have affinities with recent families known to inhabit brackish and freshwater environments. Some of these fish preserve gut contents. Preliminary analysis of the intestinal content of these fishes has resulted in identification of freshwater insects and fern fragments.

Cretaceous crustacean occurrences from México, compiled by Vega and Feldmann (1992), are rare. Since the time of that compilation, a few other species of fossil crustaceans have been described: *Meyeria pueblaensis* Feldmann and Vega, from the Aptian of the San Juan Raya Formation, Puebla (Feldmann et

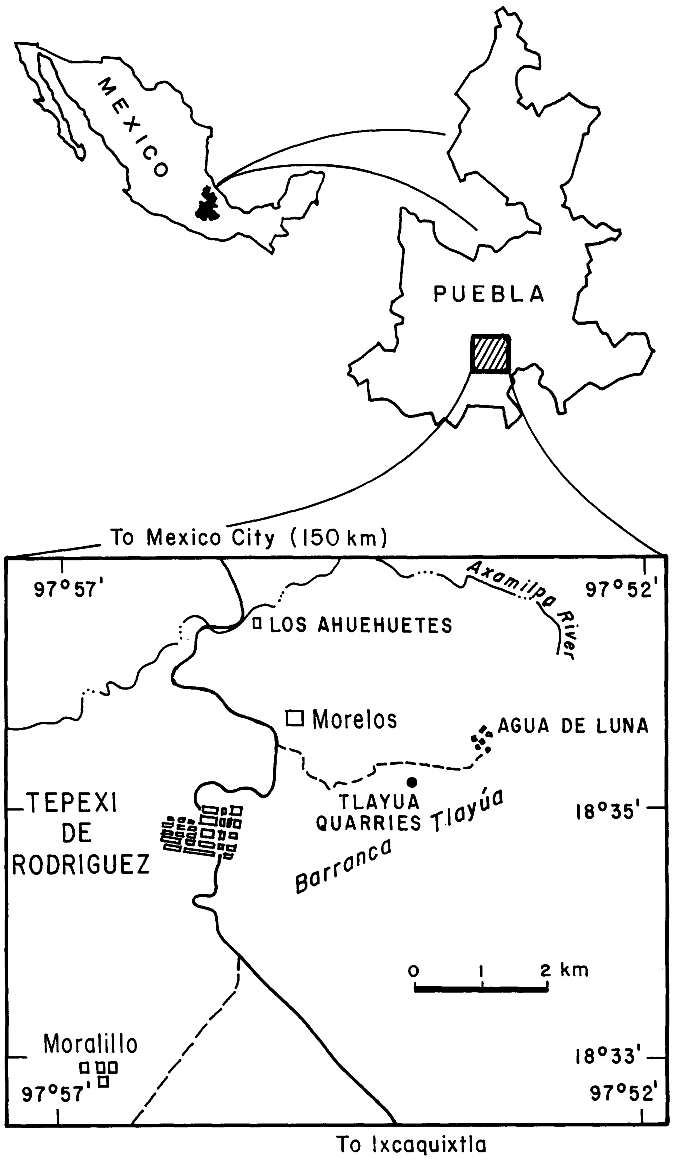

FIGURE *1*—Location map of the Tlayúa Quarry near Tepexi de Rodríguez, Puebla, southeast of México City.

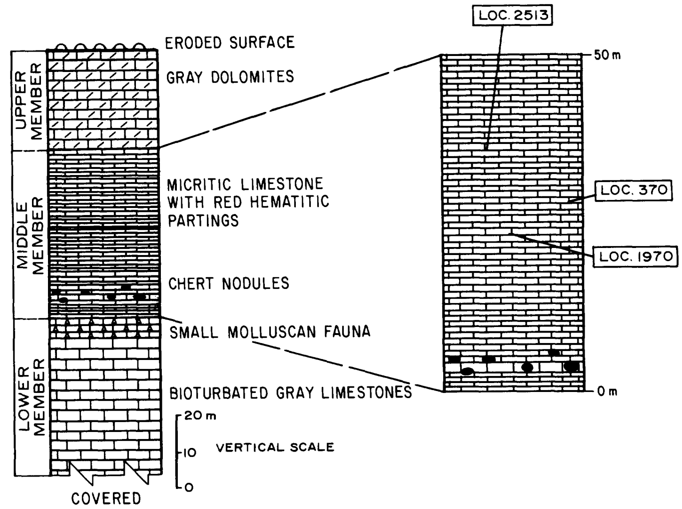

FIGURE *2*—Stratigraphic section of the Tlayúa Formation, showing lithology and thickness of the three members of this formation, as well as detailed location of samples herein described.

al., 1995); *Cheramus* sp., *Protocallianassa* sp., *Dakoticancer australis* Rathbun, *Branchiocarcinus cornato* Vega and Feldmann, *Costacopluma bishopi* Vega and Feldmann, and a possible member of the Majidae, were described for the Maastrichtian Cárdenas Formation, San Luis Potosí (Vega, Feldmann, and Sour-Tovar, 1995); ?*Callianassa* sp., *Paleopagurus* cf. *P. pilsbryi*, *Sodakus mexicanus* Vega and Feldmann, and *Prehepatus harrisi* Bishop, were reported for the Maastrichtian Potrerillos Formation, Nuevo León (Vega, Feldmann, and Villalobos-Hiriart, 1995); and, *Lophoranina precocious* Feldmann and Vega, from the Maastrichtian Ocozocuautla Formation, Chiapas (Feldmann et al., 1996).

To date, crustaceans are one of the most abundant macroinvertebrate fossils known from the Middle Member of the Tlayúa Formation, represented by over fifty specimens. Most specimens were collected from the upper portion of this member. As will be discussed below, preservational conditions of some of the specimens hampered the observation of diagnostic features; but, the observations and data of only the best preserved specimens could be used to describe many features of the new taxa here proposed.

Most fossil insects and arachnids described from México date from the upper Oligocene-lower Miocene deposits of Simojovel, Chiapas (Petrunkevitch, et al., 1963; Perrilliat, 1989). A pair of tipulid wings were found in the Middle Member of the Albian Tlayúa Formation (Pantoja-Alor, 1992). Other members of the Tipulidae range from Hauterivian (Early Cretaceous)-Holocene (Labandeira, 1994). Poor preservation and lack of more diagnostic features made it impossible to develop a more detailed description and identification of this dipteran. Other important records of Mexican fossil insects include an Upper Permian species from Valle Las Delicias, Coahuila, that Carpenter and Miller (1937) described based on a single wing. Recently, another insect has been found from the Upper Cretaceous deposits in Coahuila, and its description is in preparation.

SYSTEMATIC PALEONTOLOGY

Class ARACHNIDA Lamarck, 1801
Order ARANEA Clerck, 1757
Family Uncertain
ATOCATLE new genus

Type species.—*Atocatle ranulfoi* new species

Diagnosis.—As for species.

Etymology.—The name of the genus is derived from the prehispanic Náhuatl language, and means "spider that lives near the water," from *atl* = water, and *tocatl* = spider.

ATOCATLE RANULFOI new species
Figure 3.1, 3.2

Diagnosis.—Body of medium size, suboval longitudinally. Prosoma triangular, opisthosoma suboval, divided into four abdominal segments, the third bears a pair of long spinnerets. First and second segments bear a pair of backward directed spurs. Chelicerae adaxial. Three posterior pairs of legs preserved, with long, pointed tarsi.

Description.—Spider preserved in ventral position, suboval in shape. Prosoma triangular, with last three pairs of legs preserved, two-fifth of the maximum length. Three posterior pairs of legs with long, acute tarsi. Possible left pedipalp bears tarsus with broad shape, typical for males. Pair of adaxial chelicerae visible, displaced beyond anterior margin of sternum. Chelicerae com-

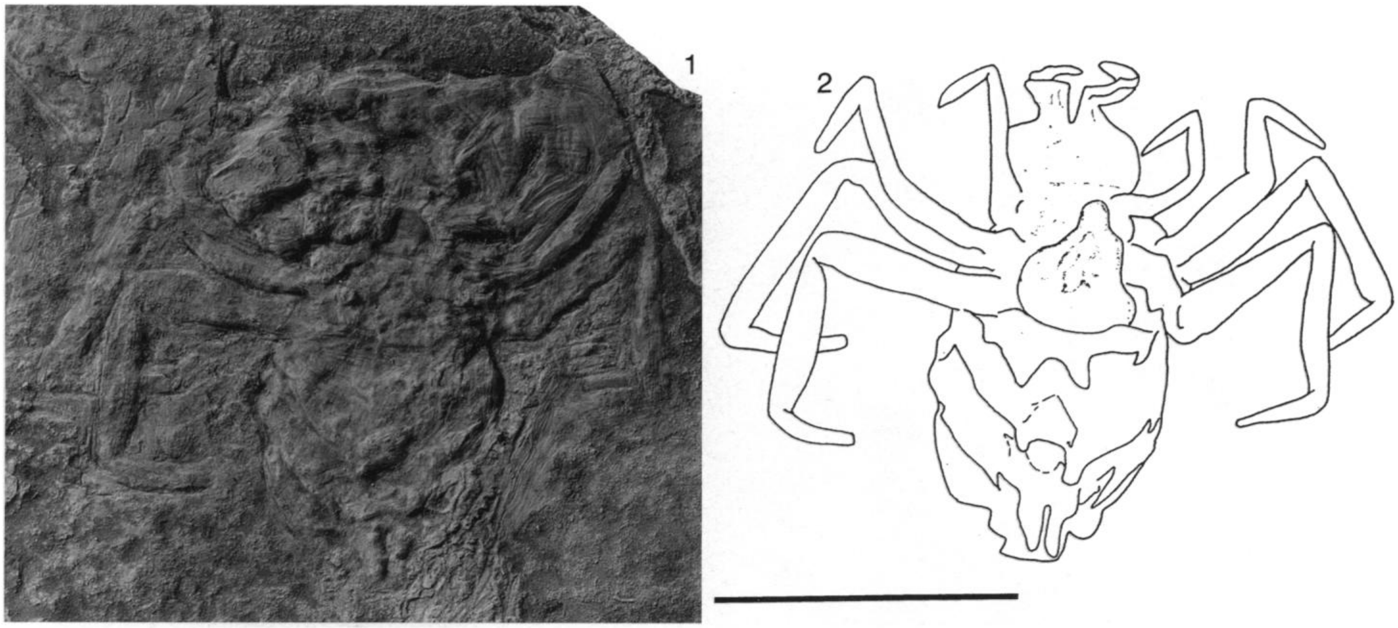

FIGURE 3—*Atocatlis ranulfoi* new genus and species. *1*, holotype, IGM–6535; *2*, line drawing. Scale bar equals 1 cm.

posed of broadly triangular basal segment, and acute, curved fang. Sternum triangular; labium also triangular, possibly bordered by raised internal margins of maxillae. Opisthosoma suboval, one-half maximum length, slightly constricted, three-fifth maximum width, with four visible segments. First segment with two central spurs, directed backwards, but displaced to right, perhaps a result of preservation. Second segment also bears pair of shorter spurs. Third segment with pair of straight, pronounced spinnerets, that extend almost to posterior margin of fourth segment, which exhibits a notch at right posterolateral margin. A possible displaced fragment of the carapace preserved on the anterior left margin of specimen.

Measurements.—Maximum length: 19.1 mm, maximum width: 10.2 mm, thoracic length: 6.7 mm, thoracic width: 8.1 mm, abdominal length: 10.1 mm, abdominal width: 10.2 mm.

Type and locality.—Holotype IGM-6535, deposited in the collection of the Museo de Paleontología, Instituto de Geología, UNAM. Tlayúa quarry, site IGM–2513.

Etymology.—The species name honors Mr. Ranulfo Aranguthy Contreras, Scientific Assistant at the Tlayúa quarry.

Remarks.—Presence of segmented spinnerets on the last abdominal segment confirmed placement in the Arachnida. Presence of four, clearly defined abdominal segments, place the specimen near the suborder Liphistiina. However, poor preservation of the material makes it difficult to provide a more detailed systematic treatment. Stratigraphic distribution of primitive spiders with segmented abdomen is largely confined to the upper Paleozoic. This is the oldest spider reported from Mexico to date. The large size and terrestrial habit of spiders confirms the interpretation of periodic influence of fresh-water into the Tlayúa environment. Presumably the spider was washed into the depositional site by stream activity.

A second specimen, presumed to be a spider, has also been recognized. The preservation of that specimen is sufficiently poor that photography and description are not warranted. Suffice it that there is potential for further discovery of additional arachnids in the formation.

Class INSECTA Linné, 1758
Order ODONATA Fabricius, 1793
Suborder ?ANISOPTERA Selys-Longchamps, 1854
Family uncertain
IXTAHUA new genus

Type species.—*Ixtahua benjamini* new species.

Diagnosis.—Same as for species.

Etymology.—The name of the genus is the translation for dragonfly in the Náhuatl language.

IXTAHUA BENJAMINI new species
Figure 4.1, 4.2

Diagnosis.—Medium sized nymph. Head rectangular; large rounded eyes beside trapezoidal labium. Abdomen elongated, nearly rectangular longitudinally; ten abdominal segments. Three pairs of legs preserved, first two directed forward. Tarsus flexed, perpendicular to length of the body.

Description.—Odonate nymph of medium size, preserved in ventral view. Head rectangular, with prominent rounded eyes; its length is about one-tenth total length, width four-fifth maximum width (abdomen). Labium trapezoidal. Prothorax one-fifth length of body. Abdomen two-third length, apparently with ten segments. A pair of anal gills visible, one-tenth maximum length of abdomen. First and second pair of legs directed forward. Left metathoracic coxa rectangular. Femur of first pair of legs almost half total length of leg, second and third pairs with femur one-third length of leg. No hairs on tibiae are visible.

Measurements.—Total length: 20.5 mm; width of head: 5.2 mm; length of head: 2.8 mm; width of prothorax: 5.0 mm; length of prothorax: 3.3 mm; width of abdomen: 6.2 mm; length of abdomen: 12.2 mm; length of caudal filaments: 2.2 mm; width: 1.9 mm.

Type.—Holotype IGM-6536, deposited in the collection of the Museo de Paleontología, Instituto de Geología, UNAM. Tlayúa quarry, site IGM-2513.

Etymology.—The name of species honors Benjamin Aranguthy, Scientific Assistant at the Tlayúa quarry.

Remarks.—The systematics of fossil Odonata are based on the structure of adult wings. There are very few descriptions and illus-

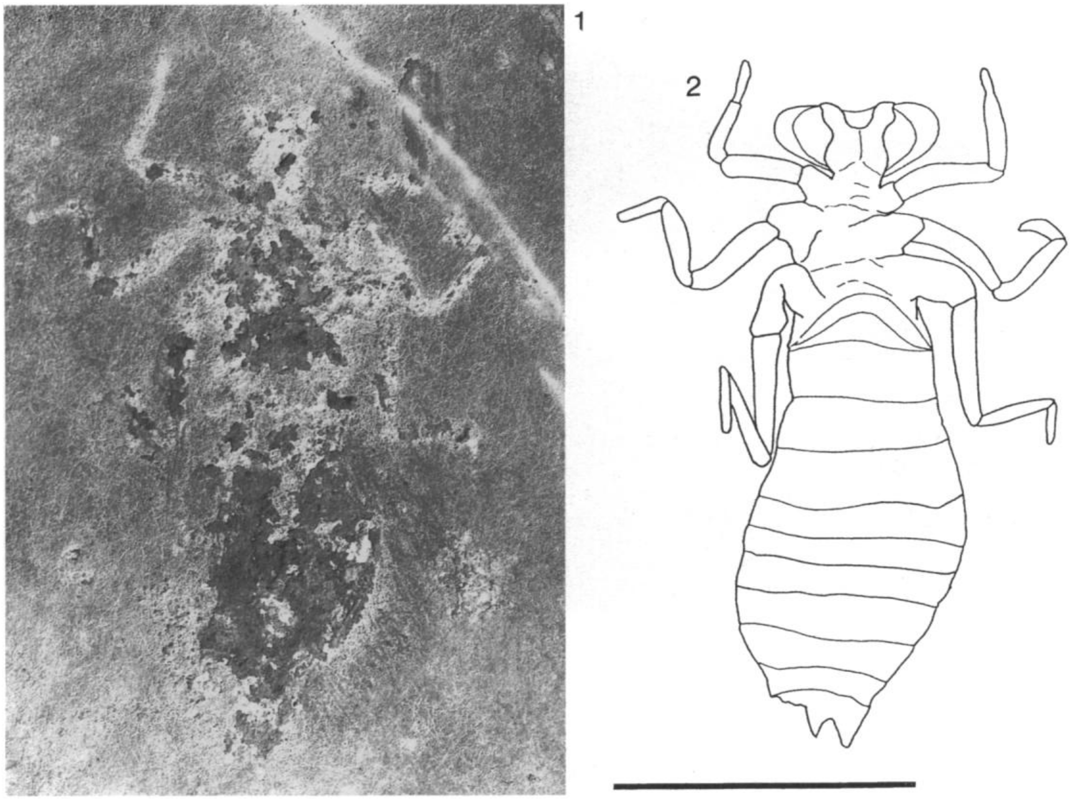

FIGURE 4—*Ixtahua benjamini* new genus and species. *1*, holotype, IGM–6536; *2*, drawing. Scale bar equals 1 cm.

trations of immature stages (e.g., Whalley and Jarzembowski, 1985). However, the following features in the nymph specimen seem to be diagnostic of the Odonata: acute shape of legs, legs directed forward, short separation between each pair of legs (shorter than in hemipterans), and well developed eyes. The large eyes on this specimen are difficult to discern (Figure 4.1, arrow) as is the segmentation of the abdomen. Attempts at cleaning and preparation destroyed some of the detail observed when the specimen was initially collected.

From the six odonate suborders described in the literature, there are only three which have Cretaceous representatives, Anisozygoptera, Anisoptera, and Zygoptera. Only the last two suborders have a fossil record of immature stages. The general shape of our sample resembles immature stages of the suborder Anisoptera. However, lack of more diagnostic features make it nearly impossible to develop a more detailed identification.

The importance of this insect, aside from its taxonomic affinities, stands in the paleoenvironmental interpretation of the Tlayúa Formation. Odonate nymphs inhabit freshwater, while developing to the flying adult stage. In extant species, the nymph can live in that stage for as long as five years (Carpenter, 1992) before developing into the predacious flying adult stage. The presence of this kind of insect in the Tlayúa sediments reinforces the interpretation of periodic influx of freshwater into a restricted lagoon. Although poorly preserved, the flexure of some legs and the twisted body is suggestive of a partially decomposing animal.

Class MALACOSTRACA Latreille, 1805
Order ISOPODA Latreille, 1817
Suborder FLABELLIFERA G. O. Sars, 1882
Family ARCHAEONISCIDAE Haack, 1918
Genus ARCHAEONISCUS Milne Edwards, 1843

Type species.—*Archaeoniscus brodiei* Milne Edwards, 1843

Diagnosis.—"Body broad, oval, only moderately vaulted; cephalon subquadrate, sunk deeply into 1st pereionite; eyes located dorsolaterally, of moderate size, prominent; 7 pereionites alike except for 1st; epimeres not defined; pleon as wide as pereion; 4 free pleonites subequal, essentially like pereionites; pleotelson large, subsemicircular" (Hessler, 1969, p. R379). To this diagnosis, it must be added that there may be 4 or 5 free pleonites, and that an axial elevation extends from the pleotelson anteriorly onto the pleonites, based upon the morphology of *Archaeoniscus texanus* Wieder and Feldmann, 1992, and *A. aranguthyorum* new species, described below.

Range.—The genus *Archaeoniscus* was first described from Wealden rocks in Wiltshire, England (Milne Edwards, 1843). The age of the Weald sequence in that area is Barremian-lower Aptian (Rawson et al., 1978). Hessler (1969) indicated that the type species was known from the Jurassic of England and Germany. The basis for this determination is unknown. More recently, the stratigraphic range of the genus was extended to the Late Cretaceous with the report of *A. texanus* from the Austin Chalk, Texas (Weider and Feldmann, 1992). An isopod, identified as *Archaeoniscus brodii* [sic] (British Museum (Natural History), 1983, p. 126, pl. 40, fig. 1) was reported from lowermost Cretaceous nonmarine beds of the Durlston Formation, Wiltshire, England. The illustration bears little resemblance to *Archaeoniscus*, however, and no more can be said about this occurrence until the specimen is examined and the identification is confirmed. Clearly, questions regarding the total range and environmental preference of members of the genus remain unresolved.

Remarks.—Isopods from the Albian Tlayúa quarry show typical features of the extinct Archaeoniscidae. The posterior sagittal ridge which extends from the central portion of the pleotelson to the base of the first pereionite seems to be characteristic of this family. This ridge is interpreted to be the dorsal reflection of a ventral structure present on females?, probably a brood pouch. Indeed, the axial pouchlike structure is apparently unique among isopods and excludes the genus from all known extant families.

Although *Sphaeroma burkartii,* known from the Tertiary, is the sole fossil isopod described previously from México, the differences between the Tepexi isopods and species of *Sphaeroma* are very clear. Sphaeromids tend to have a wider and more prominent head, with large marginal eyes, and the pleonites tend to be smaller and not as conspicuous as in the Archaeoniscidae.

ARCHAEONISCUS ARANGUTHYORUM new species
Figure 5.1–5.7

Diagnosis.—Body bilaterally symmetrical, oval, elongate. Head short, situated within middle portion of first pereionite, width about half that of pereionite 1. Eye spots situated at base of head. Pereion formed of 7 somites that are concave forward medially. Five pleonites are crossed medially by conspicuous axial ridge which extends forward from axial portion of pleotelson. Pleotelson rounded posteriorly, anterior edge convex forward. No epimeres present on either pleonites or pereionites.

Description.—Body ovate, elongate, length of males? about 1.8 times width, females? length about 1.5 times width, moderately vaulted transversely. Head with rounded anterior margin; lateral margins form a sigmoidal curve with eyes at posterior base. Head width more than half first pereionite maximum width in males? and just slightly less than half in females?; three-fourths maximum length of first pereionite. Sigmoidal margin of first pereionite forms an acute border along posterior portion of cephalon. Pereion of seven overlapping pereionites with weakly concave forward margins in central portion of carapace. First pereionite largest, with broadly rounded lateral margin, represents 21 percent of total carapace length and nearly maximum carapace width. First pereionite slightly overlaps second pereionite and so successively to fourth pereionite, which is overlapped by third and fifth pereionites. Second to fourth pereionites with nearly straight to gently rounded lateral margins, whereas fifth to seventh pereionites bear more acutely rounded lateral margins, posterior edge of each overlaps the next somite. Posterior margins of pereionites 5 to 7 recurved backward. Pleon with 5 articulated pleonites and pleotelson. First to third pleonites with gently curved posterior margins and nearly straight lateral margins, giving impression of a single segment. Fourth and fifth pleonites wider, with straight, rather than curved, posterior margins and straight lateral margins. First pleonite overlapped by posterior margin of seventh pereionite, and by anterior margin of second pleonite. Anterior margins of pleonites overlap immediate anterior pleonite, except for fifth pleonite, which is overlapped anteriorly by fourth pleonite, and posteriorly by pleotelson. Pleonite five generally obscured except in counterpart molds. Pleotelson nearly as broad as the pereional segments, 26 percent of length of dorsal shield; anterior margin medially produced forward to parallel curvature of pereional and anterior pleonal segments; posterior margin evenly rounded into semicircular curve in males? and somewhat straighter posterior margin in females?

Ventral surface with axial structure in females? and none in males?. Anterior medial portion of pleotelson of females? with axial pouch whose shape varies from a pair of ridges extending parallel to each other, to a main ridge with two small bosses at its base. Length of axial ridge about 25 percent of total carapace length, and extends anteriorly to posterior margin of first pleonite. Epimeres lacking.

Appendages poorly preserved. Fragments of uniramous, elongate, slender appendages preserved on pleonite. Uropods formed of elongated basis, fused to edges of pleotelson. An elongated endopod and short exopod project posteriorly from uropodal basis.

Measurements.—Measurements taken on the best preserved specimens are presented in Table 1.

Types.—The holotype, a female, IGM-6486, male allotype, IGM-6478, and the paratypes, IGM-6477, 6479-6485, and 6487-6501 are deposited in the collections of the Museo de Paleontología of the Instituto de Geología, Universidad Nacional Autónoma de México. All specimens have been collected at the Tlayúa Quarry subsequent to 1985.

Preservation, sample size, and occurrence.—To date, 30 specimens have been collected from three different sites within the Tlayúa Formation in the Tlayúa quarry (Figure 2). The Early Cretaceous flaggy limestone beds preserve the isopods mostly as compressions along laminations within the rock. However, some samples do preserve the typical convex shape of the isopods, comprising some of the best preserved and most complete specimens. Many of the compressions are of extremely low relief and hardly contrast in color or tone from the enclosing sediment.

Etymology.—The trivial name is derived in honor of the Aranguthy family, who have unselfishly allowed and actively pursued the collection of specimens from the Tlayúa quarry. They have assured their preservation as a Mexican national treasure.

Comparison.—The Tepexi specimens show nearly all features of the Archaeoniscidae, including a subquadrate head, deeply embraced by the first pereionite; presence of 7 similar pereionites, and a pleon as wide as the pereion. The pleotelson is semicircular. There tends to be a dorsal axial ridge extending from the pleotelson onto the pleon.

The Sphaeromidae tend to have a much reduced pleon, when compared to the pereion. In this family, the head is usually larger and more conspicuous, and the axial ridge of the pleotelson, if present, does not extend beyond the anterior margin of this last segment. Finally, the uropods in the Sphaeromidae are larger, with endopods nearly as large as exopods. Therefore, the new species does not belong in this family.

The species most similar to our material is *Archaeoniscus brodiei* Milne Edwards, which has a head of similar shape and size, seven pereionites, a pereion as wide as pleon, a semicircular pleotelson with axial ridge, and lateral uropods. However, this species, from England and Germany, has four pleonites (Milne Edwards, 1843) and the axial ridge is broader and weaker than in the Puebla specimens. There also may be a size discrepancy; however, the size of the type specimens has not been validated by us. Henri Milne Edwards (1843, p. 327) indicated that *Archaeoniscus brodiei* ranged from 9–12 cm in length whereas the illustration of the taxon in the Treatise on Invertebrate Paleontology indicates that individuals would be about 2.4 cm in length (Hessler, 1969, p. R379).

More recently, *Archaeoniscus texanus* Wieder and Feldmann was described from the Late Cretaceous of Texas (Wieder and Feldmann, 1992). Although this species has seven pereionites and five pleonites, and the size of the specimens is similar to the size of our samples, the axial ridge is wider and bordered laterally by deep grooves. Additionally, the fifth pleonite is twice as long as the preceeding fourth pleonite. Description of *A. texanus* is based on posterior exuviae; therefore, comparison of the cephalon or first pereionites is impossible. However, differences in the pleon are sufficient to distinguish this species from the Tepexi isopods.

The axial ridge, seen in dorsal aspect on species referred to the family, may reflect the position of a ventral structure in some cases. Fortuitously, the Tepexi isopods are preserved with both dorsal and ventral aspects of the carapaces exposed on the bedding planes. When the ventral surface is exposed a large, ob-

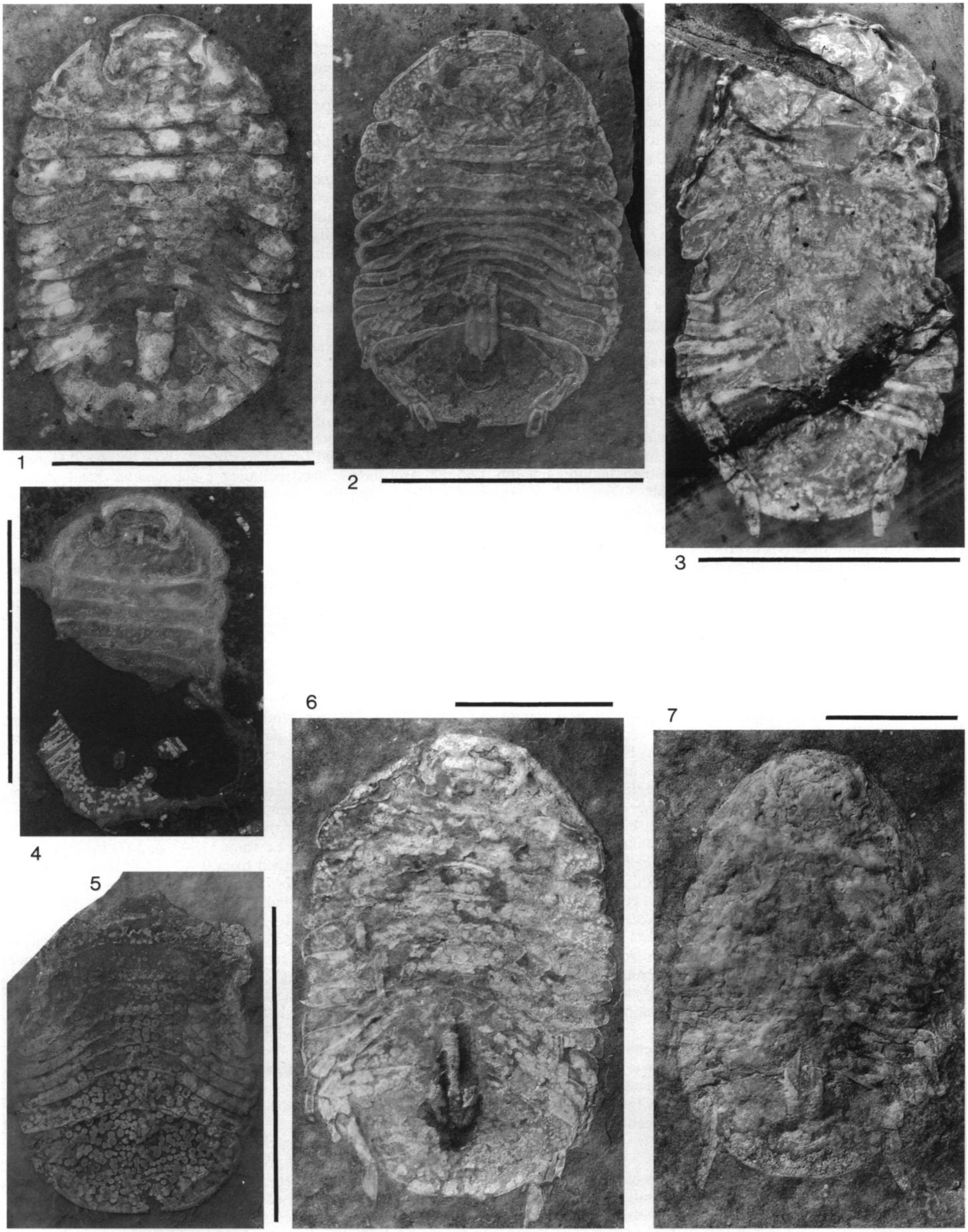
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TABLE 1—Measurements, in millimeters, taken on specimens of *Archaeoniscus aranguthyorum.*

	Total animal		Head		Pleotelson	
Specimen	Length	Width	Length	Width	Length	Width
Females						
Holotype IGM–6486	16.0	10.6	2.7	4.1	4.0	—
Paratype 1 IGM–6477	28.2	18.3	—	—	7.0	14.6
Paratype 3 IGM–6484	30.7	2.6	—	—	8.3	16.0
Paratype 4 IGM–6479	15.0	10.0	—	3.9	3.1	6.0
Males						
Allotype IGM–6478	20.1	10.7	—	—	5.1	8.8
Paratype 2 IGM–6480	12.6	6.8	2.3	2.6	—	—
Paratype 5 IGM–6497	20.1	11.9	—	—	—	—

vious, elongate pouch is observed on the specimens that are broader, have proportionately smaller heads, and exhibit a more rounded posterior margin. It is likely that the structure is some form of brood pouch, unique to the Archaeoniscidae, and that the individuals bearing the pouch are most likely females.

The variations in brooding structures in the closely related, extant family Sphaeromatidae White, have recently been described by Harrison (1984). These structures are comprised of one or more of three different ventral structures; an anterior pocket, a posterior pocket, and oostegites. The pockets arise as folds of cuticle extending along the midline, and the oostegites are paired flaps of cuticle arising from near the base of the pereiopods. One or more pairs of oostegites may be present. Invariably, these structures are situated on the pereion; none of the brooding structures is associated with the pleotelson or the pleon. However, the pouches on the new species, *A. aranguthyorum,* do not fit this morphology and cannot be assigned to this family.

The structure preserved on the ventral surface of *Archaeoniscus aranguthyorum* would be most closely analogous to the posterior pocket seen in the Sphaeromatidae in that it is an unpaired, axial pouch. However, its posterior position clearly sets it apart from any previously described structure in isopods. Although the structure has not been observed directly on the other species within the Archaeoniscidae, it is likely that the axial ridge represents the dorsal expression of such a structure. If this interpretation can be confirmed, the position of an axial brood structure on the pleon will form an important definitional character for the family.

Remarks.—Today, marine isopods occupy a wide variety of ecological niches, including scavenging upon corpses of fish and invertebrates and parasitization on fish and invertebrates. Presence of a large number of fossil isopods at the Tlayúa quarry, where fish are the most common element, is suggestive that some relationship existed between the fish and the isopods. Two scenarios are possible, parasitization and scavenging.

One interpretation is that members of the new species were ectoparasites. Comparison of the Tlayúa isopods and recent members of the Family Cymothoidae reveals some resemblances, and, although the Tepexi specimens cannot be placed within that family, might serve as an ecological analogue. Recent Cymothoidae are exclusively ectoparasites on marine, freshwater, and brackish water fishes. Although gill parasites are rather asymmetrical, ectoparasites on the rest of the body may be perfectly symmetrical, as is *Archaeoniscus aranguthyorum.* Marine representatives of this family occur in shallow, tropical and subtropical areas (Kensley and Schotte, 1989). The juveniles can swim and attach to any convenient fish host, but eventually they will go to the preferred host-species. At that stage, the juvenile develops into a functional male, losing the swimming setae of the pleopods. Juveniles and males feed actively on the host's blood. In some species the female is nonfeeding. The male eventually becomes a female (Kensley and Schotte, 1989). Archeoniscid isopods from Tepexi have similar gross morphology to members of the Cymothoidae and may have been ecological equivalents. The Tepexi specimens cannot be placed in the Cymothoidae, however, because the ventral structure, described above as a possible brooding structure, is not present on members of this family.

The isopods represent the most numerous population of archeoniscids ever found and, because they are associated with a large number and diversity of fishes, we suggest that they might have been ectoparasites on some fishes, perhaps releasing from the host before the host died. The isopods may not have been able to locate another host, nor were they capable of reaching a more suitable environment, and consequently they were buried. Some show evidence of decomposition and/or of scavenger attack.

Alternatively, it is quite possible that, upon death of the fish, the isopods scavenged on their corpses. The general paleoecological setting of the sediments of the Middle Member of the Tlayúa Formation is an alteration between tolerable and lethal conditions for pelagic organisms such as the fish. The benthic fauna of the formation is limited to a few decapod crustaceans, and perhaps several groups of echinoderms, including holothuroids, asteroids, and ophiuroids. Periodic rapid changes in water conditions, possibly as a result of rapid influx of fresh water, would kill both pelagic and benthic forms that were not tolerant of rapid changes in salinity. This sort of killing would account for the accumulation of beds of fish, and the associated isopods may have been the scavengers on this abundant food resource.

As with many other arthropods, it may be anticipated that some of the fossil remains will represent deceased organisms whereas others will consist of molted exoskeletons. Distinguishing between molted and deceased remains of isopods is straightforward because representatives of this arthropod order exhibit biphasic molting. During this process, the posterior portion of the exoskeleton, typically consisting of the entire pleon and the last few segments of the pereion, is shed as much as several days in advance of molting of the anterior part of the pereion. The process is well described by Tait (1917) and George (1972). Whereas the posterior portion of the molt is shed as a single unit, it is common that the anterior portion tends to be fragmented during ecdysis so that the shed segments are disarticulated and fragmented.

Examination of the remains of fossil isopods from North America (Wieder and Feldmann, 1989, 1992) has led to the conclusion that molted remains are indicated when the fossil consists solely of the posterior portion of the integument. If the entire skeleton is preserved, the fossil likely represents a corpse.

←

FIGURE 5—*Archaeoniscus aranguthyorum* new genus, and species. *1,* holotype, IGM–6486; *2,* paratype, IGM–6479; *3,* allotype male IGM–6478; *4,* paratype, IGM–6480; *5,* paratype, IGM–6481; *6,* paratype IGM–6477; *7,* paratype IGM–6484. Scale bars equal 1 cm.

Based upon this criterion, none of the fossil isopods at Tepexi are molts.

Most assemblages of fossil crustaceans are dominated by exuviae, so it is surprising that the isopod assemblage at Tlayúa is represented mostly by corpses. The low energy which prevailed at the Tlayúa lagoon preserved the corpses as articulated, entire animals.

The preservation of corpses at Tepexi seems to suggest three different stages of decomposition. A few of the specimens are strongly convex (Figure 5.7), suggesting the original convexity of the animal. These organisms may have been killed and buried rather quickly. Burial may have occurred prior to extensive decomposition and scavenging. All of these specimens are preserved with the dorsal side of the organism upward on the bedding surface.

Most of the isopod remains, however, are flattened onto the rock surface, suggesting that the soft tissue had decomposed and the cuticle had softened to the point that it was very thin and flexible. The cuticle of a portion of these remains may be folded so that one part of the skeleton lies beneath another part (Figure 5.2, 5.3). Specimens exhibiting this type of preservation are oriented on rock surfaces with either the dorsal or the ventral surface upward. It is the specimens that are preserved with the ventral surface upward that have provided the opportunity to see some of the appendages and to describe the brood pouch. The orientation of the specimens, venter upward, can be readily confirmed by noting that the somites overlap one another with the trailing edge of the more anterior somite of any pair lying beneath the leading edge of the more posterior somite. The appendages can be seen to lie above the level of the carapace as well.

In other specimens, tiny, spherical fecal pellets are preserved within the confines of the carapace (Figure 5.5). This suggests that the corpses may have been scavenged by some other organism that produced the pellets.

Order Decapoda Latreille, 1803
Infraorder Anomura H. Milne Edwards, 1832
Family Aeglidae Dana, 1852

Remarks.—The known Aeglidae have a unique geographic and geologic distribution. The family was known only from a single genus, *Aegla* Leach, embracing numerous species confined to recent freshwater habitats in southern South America (Schmitt, 1942; Morrone and Loprette, 1994; and a series of papers by C. G. Jara) until Feldmann (1984) described *Haumuriaegla glaessneri* from Late Cretaceous marine rocks in New Zealand. Description of this new genus and reference to the Aeglidae raises the number of genera to three and extends the geologic range into the Early Cretaceous.

Several aspects of the morphology of aeglids is so distinct that placement of the new form herein described in the family can be done with a high level of certainty. All the previously described species exhibit a dorsoventrally flattened, triangular cephalothorax traversed by transverse and longitudinal lineae. All have very short chelipeds that tend to lie parallel to the long axis of the animal and that bear stout chelae with a prominent, flabellate projection developed on the inner margin of the propodus. All extant forms, and presumably *Haumuriaegla glaessneri* as well, carry the abdomen in such a way that the first three somites are visible dorsally, much in the manner of the galatheids, and the fifth pair of pereiopods are strongly reduced. All of these attributes are present on the specimen described below, except the lineae on the cephalothorax. That region is crushed and broken, the sternum is pressed into the dorsal carapace and the details of the linea morphology cannot be determined. Despite this, the remainder of the characters are so much like the other aeglids, and so different from other decapod taxa, that the familial placement is certain.

Identification of an aeglid in the Tlayúa Formation extends the range of the Aeglidae from Maastrichtian back to the middle to late Albian. The occurrence in a restricted marine sedimentary sequence corroborates the observation made previously (Feldmann, 1984) that the family arose in a marine setting and subsequently adapted to freshwater habitats.

Genus Protaegla new genus

Type species.—*Protaegla miniscula* n. sp.

Diagnosis.—Same as for species.

Etymology.—The generic name combines the Greek, *protos* = first, with the generic name *Aegla,* as a reflection of the early geologic occurrence of this taxon.

Protaegla miniscula new species
Figure 6

Diagnosis.—Extremely small aeglid with flabellate swelling on inner surface of hand of cheliped and keeled pereiopods.

Description.—Extremely small for family, preserved in dorsoventral plane. Carapace triangular, wider than long, attaining greatest width at posterolateral corner. Sternum reflected through cephalothorax, triangular, with nodes on posterolateral corners of each somite.

Parts of four abdominal somites visible dorsally. Surfaces smooth except for raised anterior and posterior borders.

Chelipeds very short, total length less than length of cephalothorax and exposed abdomen, stout. Proximal segments poorly differentiated. Propodus with hand wider than long and fixed finger an equilateral triangle, about equal in length to length of hand. Inner surface of hand with smoothly arcuate, flabellate projection just in advance of articulation with dactylus. Occlusal margin of fixed finger may be thickened. Dactylus nearly an equilateral triangle, slightly curved distally. Both fingers edentate. Chelipeds preserved in horizontal plane with dactyli situated toward midline. Pereiopods 2–4 about equal in size; merus about twice as long as broad, carpus short, equidimensional with gently curved inner and outer margins; propodus as long as merus but more slender, dactylus an acute triangle; all elements with a longitudinal keel extending along midline of upper surface. Fifth pereiopod reduced or absent, not observed.

Measurements.—Length of entire holotype specimen, 10.3 mm; carapace width of holotype, measured at posterolateral corner, 5.3 mm; length of propodus of left cheliped, 2.1 mm; height of propodus of left cheliped, 1.9 mm.

Types.—The holotype, IGM-6502, and paratype, IGM-6503, are deposited in the collections of the Museo de Paleontología of the Instituto de Geología, Universidad Nacional Autónoma de México.

Etymology.—The trivial name alludes to the very small size of the individuals in this species.

Infraorder Brachyura Latreille, 1803
Family ?Homolidae White, 1847
Genus Tepexicarcinus new genus

Type species.—*Tepexicarcinus tlayuaensis* new species.

Diagnosis.—Carapace rectangular, longer than wide, with nearly parallel lateral margins. Front broad; with long, bifid, sulcate rostrum and three teeth between rostrum and anterolateral corner. Posterior margin straight, not covering the first abdominal somites. Entire dorsal surface covered by fine punctae. No ridges or grooves were preserved. Abdomen short. Female abdomen as wide as posterior margin of carapace, telson semicircular; wider than triangular male telson. Chelipeds short and

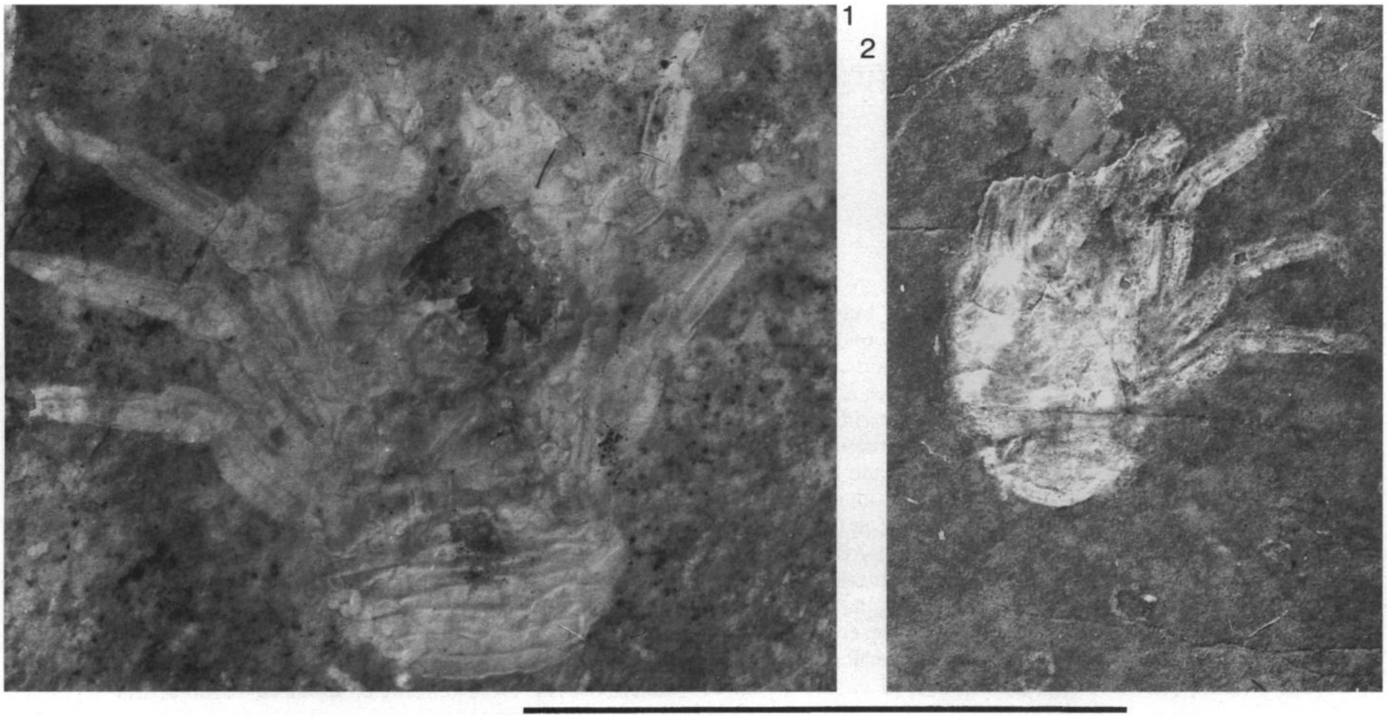

FIGURE 6—*Protaegla miniscula* new genus and species. *1,* holotype IGM–6502; *2,* paratype IGM–6503. Scale bar equals 1 cm.

small. Second, third, and fourth pereiopods very large, with acute dactylus. Fifth pereiopods reduced and subdorsal.

Etymology.—The name of the genus is compound, formed from Tepexi + carcinus, denoting that this is a crab from Tepexi de Rogríguez.

TEPEXICARCINUS TLAYUAENSIS new species
Figure 7

Description.—Carapace rectangular, longer than wide, widest in anterior one-third. Front broad. Rostrum wide and long, bifurcated at tip, sulcate. Remainder of front with three teeth decreasing in size toward anterolateral corner, 68 percent of carapace width; outer tooth forming greatest width of carapace. Lateral margins subparallel, somewhat convergent posteriorly tightly rounding onto straight to slightly concave posterior margin. Dorsal carapace regions not discernable except for suggestion of swollen mesogastric and metagastric areas; but a finely punctate surface can be observed under microscope, covering entire dorsal portion of carapace, including rostrum. Carapace surface does not cover first abdominal somites.

Venter dominated by sternum. Abdomen short, telson large. Sternum ovoid. First sternal segment forms a small equilateral

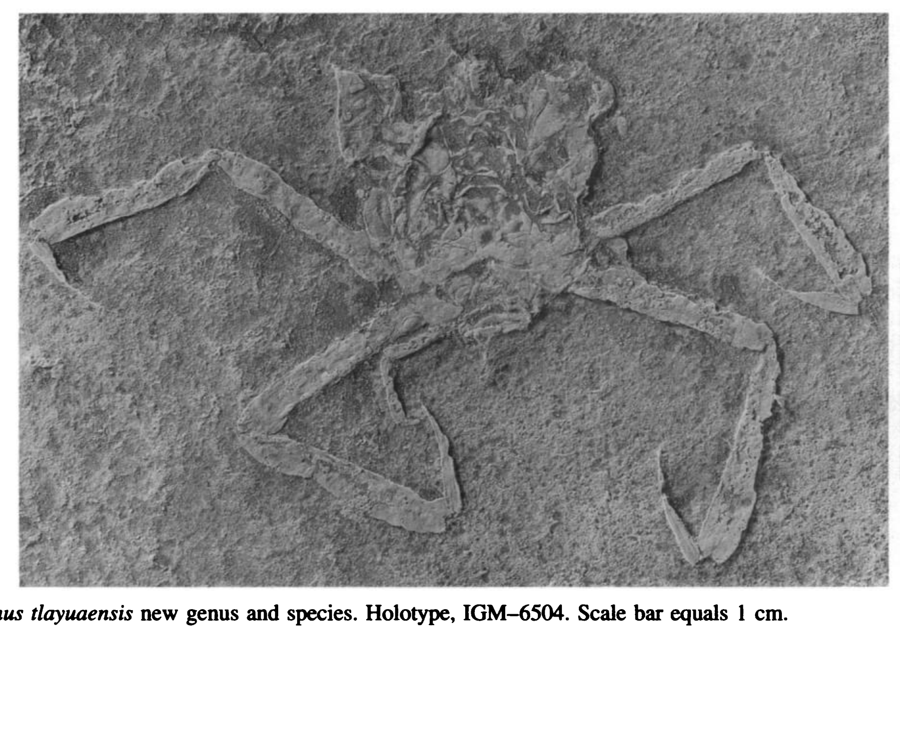

FIGURE 7—*Tepexicarcinus tlayuaensis* new genus and species. Holotype, IGM–6504. Scale bar equals 1 cm.

TABLE 2—Measurements, in millimeters, taken on specimens of *Tepexicarcinus thayuaensis*.

Specimen	Carapace length	Carapace width
Holotype IGM-6504	10.5	8.3
Paratype 1 IGM-6509	10.8	10.1
Paratype 2 IGM-6506	15.7	14.2

triangle; next segment is about half the length but much wider; third segment is longer but narrower than second, with trapezoidal shape. Fourth segment nearly square, shorter and narrower. Fifth segment small, trapezoidal. Blunt bosses arise at corners between each sternal segments, forming sharp ridge which extends toward lateral margin. Some regions of the sternum seem to be covered by a fine granulation. Sharp, acute epimere, surrounded by relatively broad antennular grooves. Antennar grooves parallel and nearly as wide as those of antennulae, separated by prominent bosses. Pterygostomial regions prominent, buccal frame nearly square, slightly broader anteriorly.

Abdomen about 40 percent of carapace length, composed of at least five segments. All specimens which preserve abdomens are females; only one male preserves all five abdominal segments. Male abdomen about 40 percent total carapace width. First male abdominal segment longest of all segments, semicircular with straight posterior margin. Second segment as wide as first, but shorter, with sharp ridge that extends transversely at midpoint of segment. Third abdominal segment rectangular, shorter than wide, lacking complete transverse ridge, but with three small ridges. Trapezoidal fourth segment, narrower and slightly shorter than third one, with transverse ridge reduced to three small bosses. Last segment triangular in shape, longer than fourth segment and conforming to shape of plastron. Female abdomen much wider than that of male. Segments 2–5 preserved. Second segment wider than long, with acute lateral margins. Third segment as wide as second, with rounded lateral edges. Fourth segment longer than previous one, lateral margins nearly straight. Fifth segment semicircular, as wide as fourth but much longer, nearly twice as long as fourth segment.

Chelipeds short; proximal segments short, propodus triangular with downturned fixed finger. Dactylus slim, curved, and triangular. Occlusional surfaces of fingers toothless, but perhaps sharp; fingers calcified and touching only at tips. Second, third, and fourth pereiopods very long, slender, almost equal in size and shape, including a large merus, short carpus, a propodus almost as long as merus, and a long pointed dactylus. Fifth pereiopods reduced, subdorsal, slender, about one-third of the length of third pereiopods; merus long, carpus short, propodus not as long as merus, and rather short, pointed dactylus.

Measurements.—Measurements taken on well preserved specimens are given in Table 2.

Types.—The holotype, a male, IGM-6504, female allotype, IGM-6505, and 27 paratypes, IGM-6506-6532, are deposited in the collections of the Museo de Paleontología of the Instituto de Geología, Universidad Nacional Autónoma de México.

Localities and stratigraphic position.—Specimens were collected from the Tlayúa Formation at localities 370, 1970, and 2513.

Etymology.—The trivial name is derived from the locally know ravine, Tlayúa, meaning "dawn."

Remarks.—Placement of this new genus and species within the Homolidae is based upon the overall quadrate outline of the carapace, the presence of a bilobed rostrum, the spinose frontal margin, and the shape of the chelipeds and pereiopods, all characteristics of the Homolidae. In these regards, the specimens closely resemble species of *Homolopsis* Bell and *Homola* White. However, in both these genera the carapace regions are quite well delineated, and even the compression to which the Tepexi specimens have been subjected should not have obliterated all traces of the regions. Thus, it would appear that the specimens are best referred to a new species within a new genus and questionable referred to the Homolidae. No other assignment is warranted.

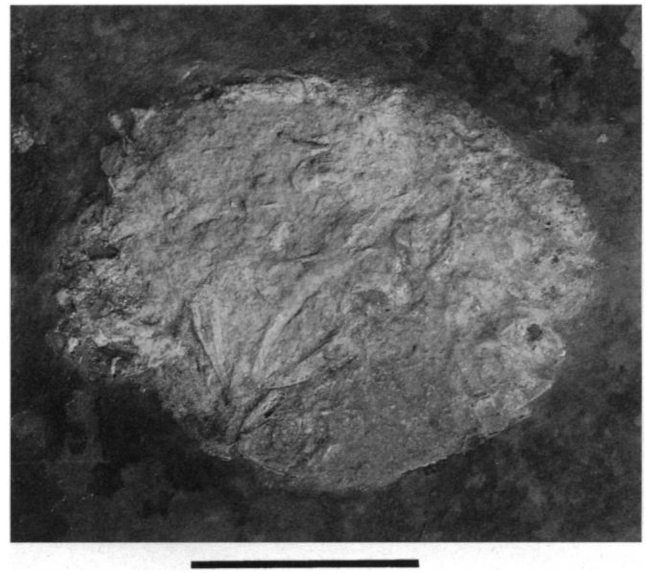

FIGURE 8—Pelleted remains containing decapod fragments, UGM-6534. Scale bar equals 1 cm.

The several specimens assigned to *Tepexicarcinus tlayuaensis* are all preserved as crushed, flattened fossils. Apparently the carapace material was somewhat brittle as fracturing of the cuticle is common. In all probability, the specimens are largely corpses, rather than molts, because the legs are articulated and in the living orientation relative to the carapace. However, in all but two specimens, one of the pereiopods, probably the fourth, is missing. The absence of the leg may result from its having been separated from the body during burial or from having been folded beneath the carapace and, thus, not recognized. Additionally, when ventral surfaces are exposed, the abdomens are in position as is the sternum. Because it would be extremely unlikely that such a delicate structure as a crab carapace could have been transported any distance without becoming disarticulated, these crabs possibly constitute a vagile benthic component of the environment of deposition.

ARTHROPODS OF INDETERMINATE AFFINITIES

Two additional specimens are worth noting, despite our inability to identify the organisms. A single pellet is preserved in which fragments of the cheliped and perhaps some walking legs of a decapod can be identified (Figure 8). The pellet closely resembles the product of regurgitation or, less likely, a fecal pellet of a large organism preying upon the crabs.

Another specimen provides evidence of an arthropod that differs entirely from anything described above. The organism (Figure 9) is clearly segmented, and appears to have relatively poor differentiation of metameres, each of which seems to bear a stubby, uniramous appendage constructed of at least 5 articles. The cuticle appears to be very thin and delicate. It may represent some form of insect larva; however, no more precise identification is possible at this time.

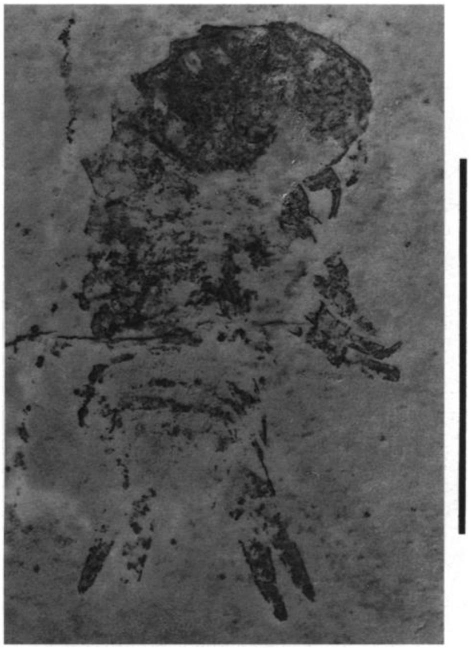

FIGURE 9—Unidentified arthropod, possibly an insect larva, UGM–6533. Scale bar equals 1 cm.

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