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A review of the Lower Cretaceous (Tlayúa Formation: Albian) Crustacea from Tepexi de Rodríguez, Puebla, Central Mexico

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Abstract

Crustacean specimens (Isopoda, Anomura and Brachyura) from the upper Albian lithographic limestone of the Tlayúa Formation are reviewed, providing new morphologic data for taxa previously reported from this locality. Description of mouth parts and other carapace details of the isopod *Archaeoniscus aranguthyorum* Feldmann, Vega, Applegate, and Bishop are provided for the first time. Following the recently proposed Brandt and Poore classification of the Isopoda, the Late Jurassic-Late Cretaceous monogeneric family Archaeoniscidae is placed into the suborder Sphaeromatidea. A right chela of *Pagurus* sp. is the first report for pagurid remains from this locality. The brachyuran crab *Tepexicarcinus tlayuaensis* Feldmann, Vega, Bishop and Applegate is moved to the Dorippidae, as previously suggested by Larghi. Dorsal carapace morphology, and fourth and fifth pereiopods are described and illustrated for this species. Based on preservation features of the crustaceans here described, paleoenvironmental interpretation of the site being a shallow restricted lagoon is reinforced.

Key words: Isopoda, Anomura, Brachyura, Albian, Tlayúa Formation, Mexico.

Introduction

Located in Puebla State, Central Mexico (Fig. 1), Tepexi de Rodríguez has become famous worldwide because of the nearby Tlayúa Quarry, where well-preserved fossils from lithographic limestone of unique red tones have been recovered. Since the discovery of this quarry, indicating its importance as a paleontological locality (Applegate and Espinosa-Arrubarrena, 1982), several papers have been published (for complete references see Applegate *et al*., 2005). A complete list of the higher taxa described to date includes cyanobacteria, foraminifera, algae, gymnosperms, sponges, cnidarians, annelids, gastropods, ammonites, bivalves, arachnids, insects, isopods, anomurans, brachyurans, crinoids, echinoids, holothuroids, stelleroids, ophiuroids, fishes, chelonians, pterosaurs, crocodiles, sphenodonts and lizards (Applegate *et al*., 2005).

The Tlayúa Formation was named for a limestone sequence of 300 m, subdivided in Lower, Middle and Upper Members (Pantoja-Alor, 1992). The most fossiliferous unit is the Middle Member, defined as finely laminated micritic limestone of yellow–brown color, with bedding planes defined by red hematitic layers and a total thickness of approximately 50 m (Fig. 2). The age of this unit was defined based on identification of belemnites and ammonites that indicate middle to late Albian age (Seibertz and Buitrón, 1987; Buitrón and Malpica-Cruz, 1987).

The paleoenvironment for deposition of the sediment of the Tlayúa Formation has been a matter of debate. The original interpretation was that it consisted of a shallow, restricted lagoon with anaerobic conditions and cyclic periods of freshwater influence (Applegate, 1987; Espinosa-Arrubarrena and Applegate, 1995). More recently, and open marine basin was proposed as the environmental setting for the Tlayúa Formation (Kashiyama *et al*., 2004). Kashiyama *et al*. (2004) considered that the sediments were dominated by storms and bottom waters had restricted circulation. As pointed out by Applegate *et al*. (2005), this model does not explain presence of shallow water elements such as algal mats and presence of freshwater and terrestrial elements such as an odonate nymph, arachnids and some reptiles (Feldmann *et al*., 1998). Crustacean remains are often transported from shallow environments to deeper basins, but this process would be reflected on the preservation quality of specimens. Most of crab specimens from Tepexi still preserve articulated appendages, which are long and thin and likely to detach with transport, and the abdomen that is also prone to being detached

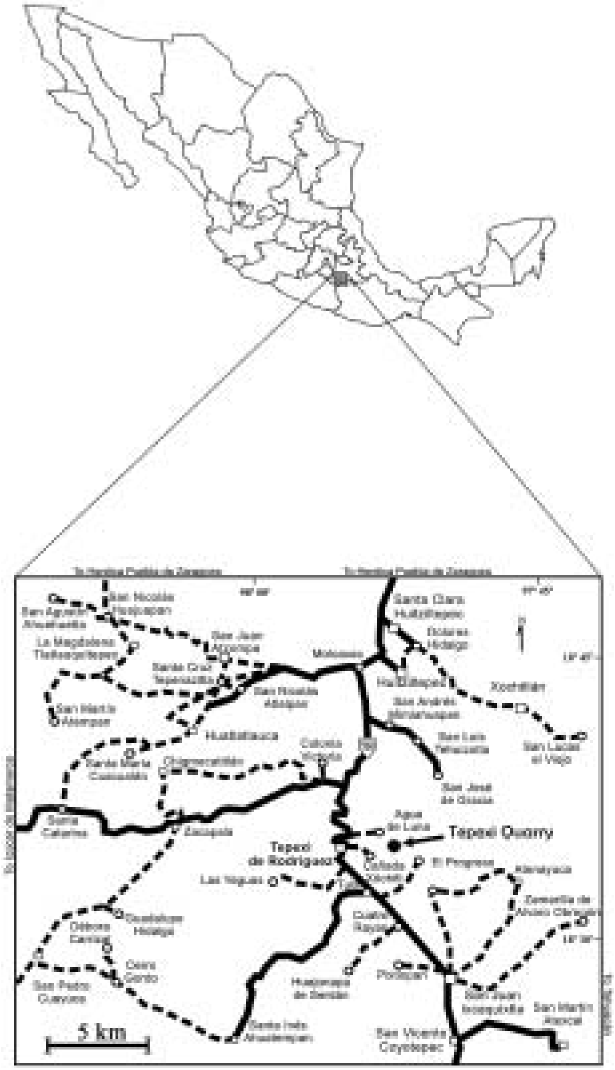

Fig. 1. Location map of the Tlayúa Quarries near Tepexi de Rodríguez town, south part of Puebla State, Central Mexico.

during transport. Furthermore, many specimens seem to be molts, as displacement of plastron is evident in those crabs preserved in ventral position. In contrast, isopods are represented almost exclusively by entire bodies that show different levels of decomposition, as interpreted from three-dimensional specimens to delicate "slides" of dorsal and ventral views, where some appendages and mouth parts can be observed (Feldmann *et al*., 1998).

The typical red color of the fossiliferous planes was interpreted to be the result of authigenic hematite deposition, precipitated by decaying organic matter and trapped by algal mats (Espinosa-Arrubarrena and Applegate, 1995). However, Kashiyama *et al*. (2004) suggested that the hematite was deposited secondarily during diagenesis. As observed by Espinosa-Arrubarrena and Applegate (1995), irregular topographic relief of fossils is completely covered by the hematite coat, and this can be observed also in some crustaceans described here. Thus, we agree with the hypothesis that the hematite was suspended in the shallow water column, and its deposition propitiated by chemical reactions in turn of decomposing corpses and organic matter.

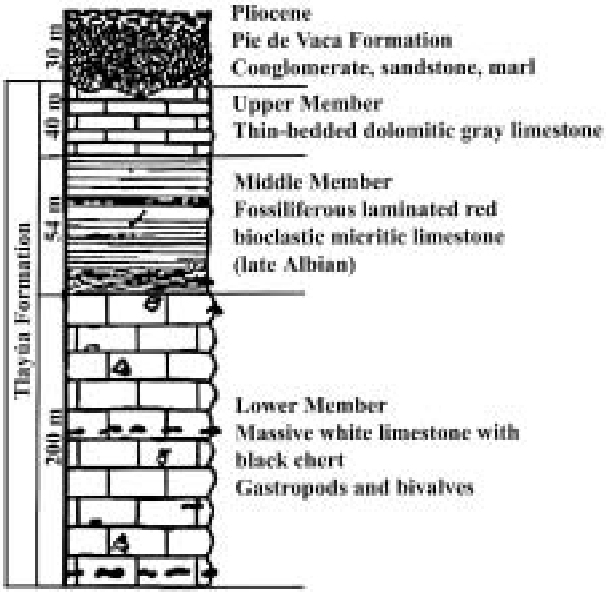

Fig. 2. Composed stratigraphic section of the Tlayúa Formation (Cretaceous: Albian). Modified from Applegate *et al*. (2005).

Studied material is deposited in the Colección Nacional de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México. Types are included in the Type Collection and registered under the acronym IGM.

Systematic Paleontology

Order Isopoda Latreille, 1817
Suborder Sphaeromatidea Wägele, 1989
Superfamily Sphaeromatoidea Latreille, 1825
Family Archaeoniscidae Haack, 1918
Genus *Archaeoniscus* Milne Edwards, 1843

Type species: *Archaeoniscus brodiei* Milne Edwards, 1843, by original designation.

Included species: *Archaeoniscus brodiei* Milne Edwards, 1843, Late Jurassic of Europe; *A. aranguthyorum* Feldmann, Vega, Applegate and Bishop, 1998, late Albian, Mexico; *A. texanus* Wieder and Feldmann, 1992, Late Cretaceous, Texas.

Archaeoniscus aranguthyorum Feldmann, Vega, Applegate and Bishop, 1998

(Fig. 3; P l. 1, Figs. 1–11)

Description: Semi-oval, elongate carapace of medium size. Cephalon subquadrate, embedded into first pereonite, $^1/_7$ the total length.

Pereon $^2/_3$ the total length; first pereomere twice as long as, but narrower than other pereonites. Pereonites 2 and 3 straight; 4 and 5 the widest; 6 and 7 posteriorly slightly convex on median portion. Epimeres on pereonite 2 subtriangular; subquadrate on 3 and 4; ovate and posteriorly inclined on 5 to 7. Width of each epimere $^1/_5$ of total pleonite width. Coxal plates present on pereonites 2 to 7, separated from terguites by distinct sutures.

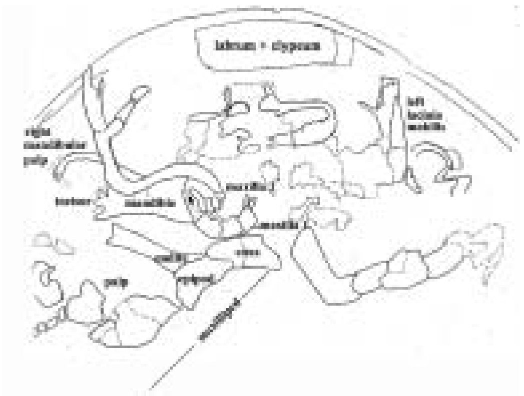

Fig. 3. Drawing of mouthparts, based on plate 1, figure 9.

Labrum and clypeus form a rectangular plate on anterior part of cephalon.

Pleon $1/5$ the maximum length, with five free pleonites and pleonite 6 fused to telson. Pleonite 1 reduced, not extended to lateral body margins. Pleonites 2–4 of similar width and length. Pleonite 5 narrow but longer. Pleonites arched 45° on median part. Pleotelson semicircular, $1/5$ maximum length.

Females with ventral axial ridge that extends from middle portion of pleotelson to base of fourth pleonite. Illustration of holotype IGM-6486 clearly shows the pocket shape of this structure (Feldmann *et al*., 1998, fig. 5.1).

Left mandible narrow, incisor process with 4 indistinct cusps; mandibular palp long, curved, formed by 3 articles. Right lacinia mobilis with 3 cusps and elongate projection. Exopod and endopod of maxilla 1 thin, elongated, connected to a semiquadrate article, preceeded by another of similar shape and size; coxa semirectangular, $1/5$ longer than proceeding article. Right maxilla 2 with 2 semirectangular articles of equal size and a third article with protuberance formed by fusion of lobes. Right maxilliped with semirectangular coxa, twice as long as wide; epipod as long as coxa, shape irregular; semirectangular endite, twice as long as epipod but narrower; palp composed of at least 3 indistinct articles. Third segment with an apparent copulatory spine.

Posterior pereopods ambulatory, $1/5$ the total length. Basis rectangular, elongate, slightly wider than other articles; ischium rectangular, $2/3$ longer than basis; merus rectangular, slightly shorter than ischium; carpus short, rectangular; propodus rectangular, as long as merus, becoming narrow toward dactylus, which is twice as long as carpus, half the width of propodus, becomes narrow to distal end.

Uropods as long as telson. Peduncle elongate, semitriangular, wider at junction with rami and with one posteriorly projecting distolateral spine. Both rami lamellar; endopod flat, semirectangular; exopod $1/3$ as long as endopod, triangular, 5 times as long as basal width.

Material examined: Holotype IGM-6486; Paratypes IGM-6479, 6489, 6490, 6497, hypotypes IGM-6608 and 6637.

Remarks: Feldmann *et al*. (1998) provided a nearly complete description of *Archaeoniscus aranguthyorum*. New data reported here, revealed morphologic details that complete description of this isopod. Mouth parts are often necessary for diagnostic identification of families and genera of recent isopods. Epimeres are also an important addition to the diagnosis. These new data permit a confident placement of the genus into the Sphaeromatidea.

Feldmann *et al*. (1998) suggested that *Archaeoniscus* was sexually dimorphic, based on presence in some specimens of a brood pouch. Several genera of the Sphaeromatidae have brood pouch (Harrison, 1984), and the presence of such a brood pouch in *Archaeoniscus* taken to suggest an affinity to the Sphaeromatidae. Some specimens of *Archaeoniscus brodiei* from the Late Jurassic of England (deposited on the Colección de Referencia, Museo de Paleontología, Instituto de Geología, UNAM), also exhibit this feature (Plate 1, Figure 4). According to Wieder and Feldmann (1992), the single posterior exuvium of *A. texanus* from the Late Cretaceous of Texas exhibits an axial ridge, similar to but wider than the ones present in the females of *A. aranguthyorum*.

Brandt and Poore (2003) proposed a new classification for the former suborder Flabellifera Sars, 1882, with the suborders Cymothoida Wägele, 1989 and Sphaeromatidea Wägele, 1989 being formally accepted. Extant representatives of the former Flabellifera were assigned to seven suborders, two of them new (Brandt and Poore, 2003). Some of the character states observed in *A. aranguthyorum* support the family Archaeoniscidae being placed in the Sphaeromatidea: pleonite 1 narrower than others, mandibular lacinia mobilis present on left side and uropodal rami lateral to margin of pleotelson. The presence of brood pouch in females (Feldmann *et al*., 1998), further reinforces a relation of *Archaeoniscus* with the Sphaeromatidae Latreille, 1825. However, the biramous uropods with articulated exopod specifically excludes *Archaeoniscus* from the family Sphaeromatidae. The Serolidae have biramous uropods, and this character state does not therefore exclude the Archaeoniscidae from the suborder Sphaeromatidea. Brandt *et al*. (1999) also consider the Archaeoniscidae not related to the Sphaeromatidae, but probably ancestors of oniscid terrestrial isopods, but presented no justification for this opinion. For these reasons, we propose to retain the Archaeoniscidae as a monogeneric extinct family, included into the Sphaeromatidea.

Certain similarities can be seen in the shape and form of the extant, *incertae sedis* genus *Paravireia* Chilton, 1925, but this genus lacks uropods and telson is much smaller in size (Brökeland *et al*., 2001). As pointed by Feldmann *et al*. (1998), it is important to note that *Archaeoniscus* was distributed in Europe (England, France and Germany) during the Late Jurassic (Gaillard *et al*., 2005), they were present in central Mexico during Early Cretaceous, and the last occurrence of the genus recorded for the Late Cretaceous of Texas. This is probably the longest stratigraphic range recorded for an isopod genus, that migrated west and probably became extinct at the end of the Cretaceous Period. General morphology and habitat of the genus remained relatively constant during 80 Ma.

Order Decapoda Latreille, 1802
Infraorder Anomura MacLeay, 1838
Superfamily Paguroidea Latreille, 1802
Family Paguridae Latreille, 1802
Subfamily Pagurinae Latreille, 1802
Genus *Pagurus* Fabricius, 1775

Type species: *Cancer bernhardus* Linnaeus, 1778, by subsequent designation of Latreille (1810).

Pagurus sp.

(P l. 2, Fig. 1)

Description: Right cheliped major claw (?). Merus stout, semirectangular, twice as long as high; upper margin convex, tuberculate; lower surface straight and smooth; inner surface flat, smooth, except for distal lower angle, with three strong spines. Carpus short, semiovate, $1/4$ the length of merus, upper margin convex. Propodus slightly higher than long, semisquare in lateral view; inner surface flat, smooth; upper margin convex; lower margin straight. Movable finger triangular, stronger and slightly longer than fixed finger; occlusal surface smooth, straight. Fixed finger triangular, acute distal end; occlusal surface smooth, inclined 45˚; lower margin straight, smooth.

Second and third pereopods of equal size and shape. Merus subrectangular, four times as long as high, inner surface smooth; carpus rectangular, twice as long as high, distal articulation inclined; propodus rectangular, as long as merus, evenly covered by uniformly spaced setal pits; dactylus as long as propodus but narrower, arcuate, evenly covered by setal pits.

Left merus rectangular, $2/3$ the length of right merus and half as high; upper and lower margins nearly straight; outer surface covered with small tubercles. Carpus square, smaller than right carpus; outer surface with small tubercles.

Second and third meri semirectangular, of equal length, as long as cheliped merus.

Remarks: Preservation of specimen as a two dimensional remains and a partial left cheliped prevents a more complete description and identification. However, it seems that left cheliped is larger and that suggests affinity with the Pagurinae. *Pagurus banderensis* Rathbun, 1935 and *P. travisensis* Stenzel, 1945 from the Albian of Texas differs from the Mexican specimen in having a more elongate shape of the claw, the fixed and movable fingers being longer and being larger in general size, as illustrated by Bishop (1983, 1986). *P. pilsbryi* Roberts, 1962 and *P. convexus* Whetstone and Collins, 1982 from the Campanian of New Jersey and Alabama respectively, are also of larger size and the palm is comparatively longer. *P. alabamensis* Rathbun, 1935 from the Eocene of Alabama has also a small size but differs with the Mexican specimen in having movable finger narrow and curved.

Material examined: Hypotype IGM-6634.

Infraorder Brachyura Latreille, 1802
Section Heterotremata Guinot, 1977
Superfamily Dorippoidea MacLeay, 1838
Family Dorippidae MacLeay, 1838
Subfamily Telamonocarcininae Larghi, 2004
Genus *Tepexicarcinus* Feldmann, Vega, Applegate and Bishop, 1998

Type species: *Tepexicarcinus tlayuaensis* Feldmann, Vega, Applegate and Bishop, 1998, by original designation.

Tepexicarcinus tlayuaensis Feldmann, Vega, Applegate and Bishop, 1998

(Fig. 4; P l. 2, Figs. 2–12)

Description: Carapace subrectangular, widest at level of hepatic regions. Anterior margin wide; rostrum square, sulcate, bifid on anterior margin. Orbits semicircular, narrow, with 2 fissures between triangular orbital notch. Anterolateral margins slightly convex, with 3 teeth, anterior teeth larger, sharply triangular. Lateral margins inclined toward straight posterior margin. Posterior margin $3/4$ maximum width, medially convex. Cervical groove wide, straight, reaching anterolateral margin at widest part of carapace, concave at median portion of carapace. Branchial groove shallow, inclined toward cardiac region, parallel to cervical groove.

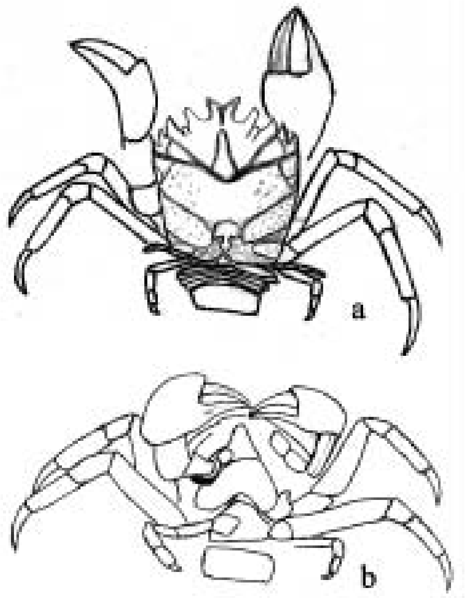

Fig. 4. Reconstruction of *Tepexicarcinus tlayuaensis* Feldmann, Vega, Applegate and Bishop, 1998, dorsal and ventral views.

Surface of carapace nearly smooth on anterior $2/3$; acute spines on posterior third. Hepatic regions semitriangular, prominent boss at proximal portion, separated from gastric regions by curved shallow groove, directed to anterior margin. Protogastric regions subovate, with weak tubercles. Epi- and mesogastric regions not clear. Epibranchial areas wide, subrectangular, inclined, represent about $1/3$ of carapace area: sharp, prominent spine at lateral margin, prominent boss on middle portion. Mesobranchial regions parallel to epibranchial areas, shorter, covered by sharp, short spines. Metabranchial areas shorter, smooth, subtriangular. Cardiac region subtrapezoidal. Intestinal region subtriangular inverted.

Sternum suboval. Sternites 1–4 subtriangular; sternites 5–7 subrectangular; sternite 8 subquadrate, smaller. Female abdomen rectangular, 3/4 surface of plastron; segments 1–5 rectangular, narrow; segments 3 and 4 narrow, semicircular lateral margins; segment 5 twice as long as wide; telson semicircular, twice as long as segment 5. Male abdomen smaller, subtriangular, composed of 5 trapezoidal segments, becoming narrower toward telson.

Chelipeds unequal, smooth; right cheliped 1/3 bigger than left cheliped; fixed finger down-turned; movable finger curved, slender; both fingers with longitudinal straight groove. Coxae of chelipeds subcilindrical; merus semitriangular; carpus rectangular; palm semiquadrate, rounded superior margin. Pereopods 2 and 3 the longest, pereopod 3 longer than pereopod 2. Ischium subquadrate, short; merus rectangular, as long as carapace width; carpus short, semitriangular; propodus long, subrectangular, wider than merus; dactylus acute, unciniform, half the length of merus. Pereopod 4 much shorter; merus robust, subrectangular; carpus short, semiovate; propodus elongate, rectangular, 1/3 longer than carpus; dactylus short, unciniform. Pereopod 5 subdorsal, thin; its length half of carapace width; merus, carpus and propodus of equal length, rectangular; dactylus not clear, but probably curved and as long as propodus.

Material: Holotype IGM-6504 ; Paratypes IGM-6506, 6520, hypotypes IGM-6607, 6609, 6631, 6632, 6633, 6635. One figured specimen (Pl. 2, Fig. 13) is lost.

Remarks: Larghi (2004) transferred the genus *Tepexicarcinus* to the subfamily Telamonocarcininae which he erected to include the older dorippids from the Cenomanian-Maastrichian of the Tethys and Pacific areas, including *Telamonocarcinus*, *Eodorippe* and *Tepexicarcinus*. *Telamonocarcinus* includes the species *T. gambalatus* Larghi, 2004 from Lebanon and *T. binodosus* (Collins, Kanie and Karasawa, 1993) from Japan, both from Cenomanian deposits. Larghi (2004) indicate the need to emend diagnosis of *Tepexicarcinus* in order to include presence of pereopods 4 and 5 as subdorsal, reduced appendages and that systematic position of *Tepexicarcinus aranguthyorum* needed to be reviewed. Although there are clear differences between these two genera, we agree with Larghi (2004) that the affinities of the Mexican specimens lie with the Dorippidae, based on shape and size of pereiopods, as well as on ventral and dorsal carapace morphology. We were able to confirm that pereopods 4 are reduced, and pereopods 5 are poorly preserved in one specimen (Pl. 2, Fig. 6), but clearly subdorsal. The description provided by Feldmann *et al*. (1998) for *T. aranguthyorum* was complete as based on material available at that time. Those authors suggested that the pereiopod morphology of the Tlayúa specimens indicate a reef environment as the original habitat of these crustaceans. *Telamonocarcinus gambalatus* Larghi from the Cenomanian of Lebanon was probably also an inhabitant of shallow seas, associated to reefs.

Based on documented occurrences of the genera that composed the Telamonocarcininae, *Tepexicarcinus aranguthyorum* represents the oldest known record of members of a widely distributed subfamily during the Late Cretaceous (Glaessner, 1980; Collins *et al*., 1993; Schweitzer, 2001; Larghi, 2004).

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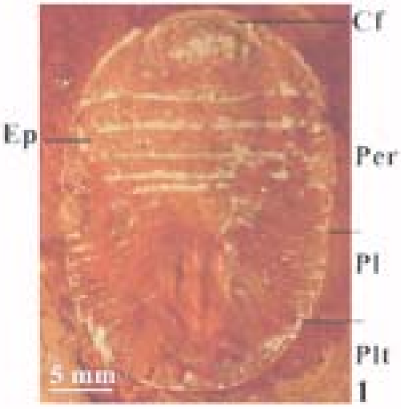
Plates 1, 2

Plate 1

Figs. 1–10. *Archaeoniscus aranguthyorum* Feldmann, Vega, Applegate and Bishop, 1998, and *A. brodiei* Milne Edwards, 1843. Abbreviations for morphological features: Cf = cephalon, Ep = epimere, En = endopod, Ex= exopod, Md = mandible:, Mpt = mouthparts, Ped = peduncle, Per = pereon, Pl = pleon, Plp = pleopod, Plt = pleotelson, Po = brood pouch, Ur = uropod.

Fig. 1. Ventral view, female. Paratype IGM-6489.
Fig. 2. Dorsal view, male. Paratype IGM-6497.
Fig. 3. Ventral view, male. Hypotype IGM-6637.
Fig. 4. *Archaeoniscus brodiei* Milne Edwards. Late Jurassic, England. Dorsal view, female. Colección de referencia, Instituto de Geologóa, UNAM.
Fig. 5. Ventral view, female. Paratype IGM-6479.
Fig. 6. Ventral view, male. Allotype IGM-6478.
Fig. 7. Left uropod, male. Allotype IGM-6478.
Fig. 8. Dorsal view, male. Hypotype IGM-6608.
Fig. 9. Cephalic region with mouth parts, female. Paratype IGM-6479.
Fig. 10. Ventral view, female. Paratype IGM-6490.
Fig. 11. Cephalic region with mouth parts, female. Paratype IGM-6490.



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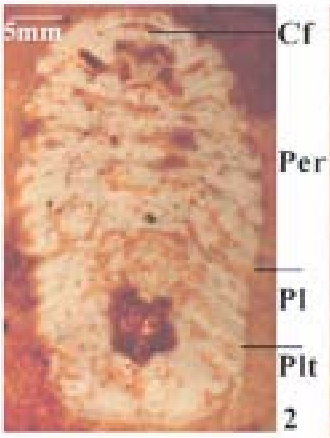

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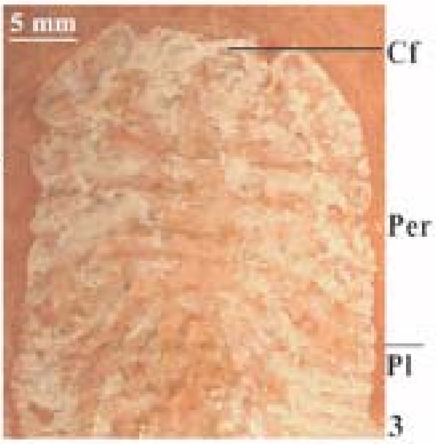

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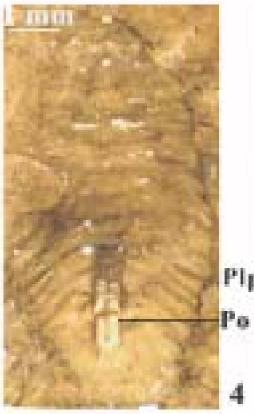

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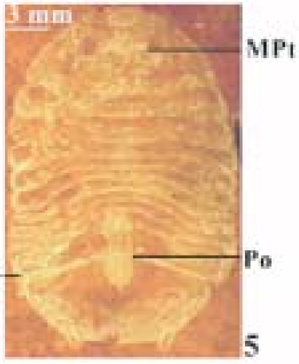

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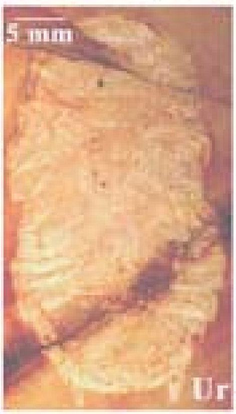

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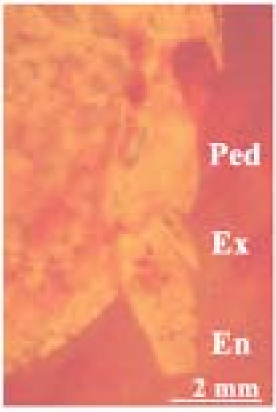

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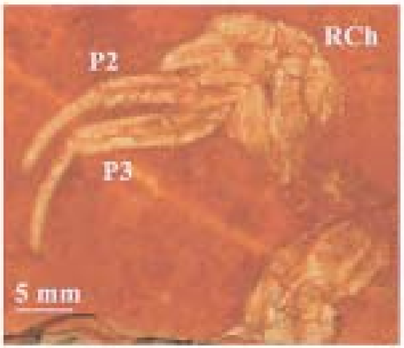
Plate 2

Fig. 1. *Pagurus* sp. Right chela. Hypotype IGM-6634.
Figs. 2–12. *Tepexicarcinus tlayuaensis* Feldmann, Vega, Applegate and Bishop, 1998. Abbreviations for morphologic features: Ab = abdomen, LCh = left chela, RCh = right chela, P2 = second pereopod, P3 = third pereopod, P4= fourth pereopod, P5 = fifth pereopod, S3 = third segment, S4 = fourth segment, S5 = fifth segment, Te = telson.
Fig. 2. Dorsal view of carapace. Hypotype IGM-6607.
Fig. 3. Dorsal view of nearly complete specimen. Hypotype IGM-6632.
Fig. 4. Dorsal view of nearly complete specimen. Hypotype IGM-6633.
Fig. 5. Right chela. Hypotype IGM-6633.
Fig. 6. Dorsal view, showing abdomen and fifth pereopods. Hypotype IGM-6632.
Fig. 7. Abdomen of a female specimen showing segments 3-5 and telson. Paratype IGM-6520.
Fig. 8. Ventral view of nearly entire male specimen. Hypotype IGM-6609.
Fig. 9. Ventral view showing left fourth pereopod. Hypotype IGM-6609.
Fig. 10. Ventral view of male specimen showing abdomen with segments 4, 5 and telson. Paratype IGM-6506.
Fig. 11. Ventral view of female specimen showing second and third pereopods and abdomen. Hypotype IGM-6635.
Fig. 12. Dorsal view of lost specimen.



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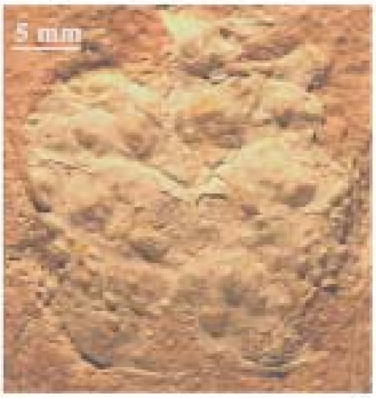

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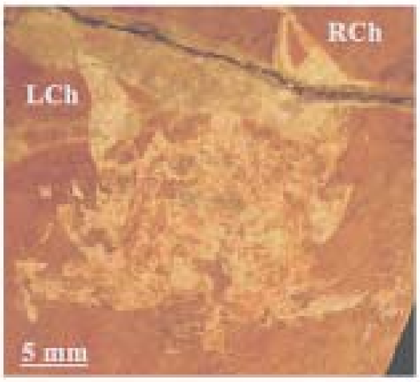

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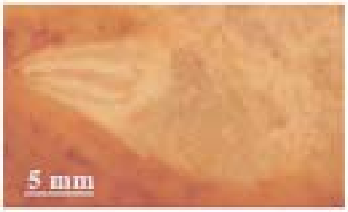

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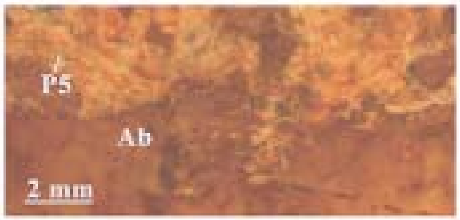

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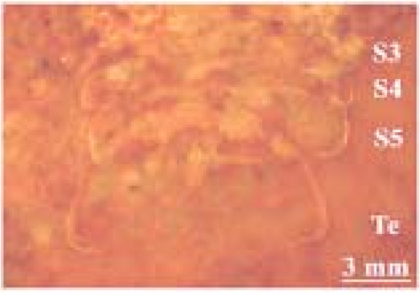

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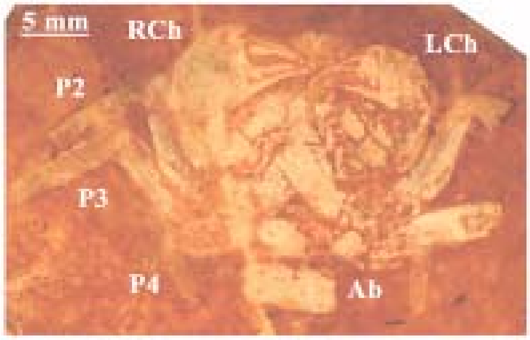

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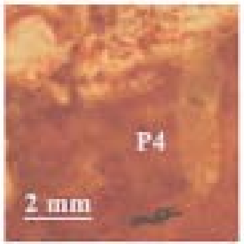

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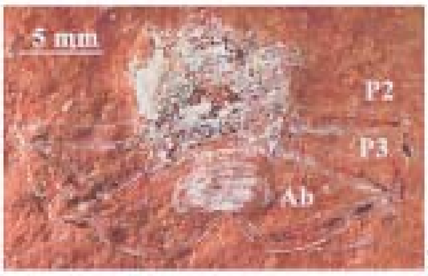

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