



New decapod crustacean assemblage from the Upper Cretaceous (Cenomanian) of Chiapas, Mexico

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With 4 figures

Abstract: A rich decapod crustacean assemblage from the Upper Cretaceous (Cenomanian; Sierra Madre Formation) of El Chango quarry (Chiapas, Mexico) is reported here. Four new genera of shrimps, *Zoquepenaeus* nov., *Tzeltalpenaeus* nov. (Penaeidae RAFINESQUE-SCHMALTZ, 1815), *Mexicania* nov. (Sicyoniidae ORTMANN, 1898), and *Mokaya* nov. (Sergestidae DANA, 1852) are here described, representing the richest fossil shrimp community from the Mesozoic of the Americas. Moreover, the richness of El Chango assemblage is testified by the discovery of carideans, palinurids, and brachyurans in the study sample. Finally, *Mexicania* nov. represents the first unequivocal report of Sicyoniidae in the fossil record, extending the stratigraphic range of this family back to the Cenomanian. The systematic position of *Sicyonia roemeri* (VON DER MARCK, 1858), the only species previously interpreted as belonging to Sicyoniidae is here discussed, pointing out some morphological characters diagnostic of the Penaeidae.

Key words: Crustacea, Decapoda, Penaeoidea, Caridea, Achelata, Brachyura, Cenomanian, Upper Cretaceous, Mexico.

1. Introduction and geological setting

The El Chango quarry is located in Chiapas, Mexico, about 50 km SW of Tuxtla Gutiérrez (Fig. 1). The locality is becoming famous because of the presence of well-preserved remains of plants (GONZÁLEZ-RAMÍREZ et al. 2011, 2012; CEVALLOS-FERRIZ et al. 2012; HUERTA-VERGARA et al. 2012), crustaceans (VEGA et al. 2003, 2007) and fishes (OVALLES-DAMIÁN et al. 2006; ALVARADO-ORTEGA et al. 2009; ALVARADO-ORTEGA & THAN-MARCHESE 2012, 2013). Mollusks (ammonites) are not well-preserved, however, they appear to indicate a Cenomanian age (J. MORENO, pers. comm.) for the platy limestones of the Sierra Madre Formation at this locality (Fig. 2). Based upon the biostratigraphic range for some fishes, ALVARADO-ORTEGA & THAN-

MARCHESE (2012, 2013) confirmed a Cenomanian age for the Cintalapa Member of the Sierra Madre Formation. The regional geology was discussed in ALVARADO & THAN-MARCHESE (2012: 736).

2. Previous reports of penaeids and astacideans from the Cretaceous of Mexico

The decapod macrurans from the Lower and Upper Cretaceous of Mexico are very rare in the fossil record with only five reports documented to date. The first report was by ALENCASTER (1977), who described *Astacodes* sp. cf. *A. maxwelli* STENZEL, 1945, from the Lower Cretaceous (Hauterivian-Aptian) of Guerrero State. Later, FELDMANN et al. (1995) reported *Meye-*

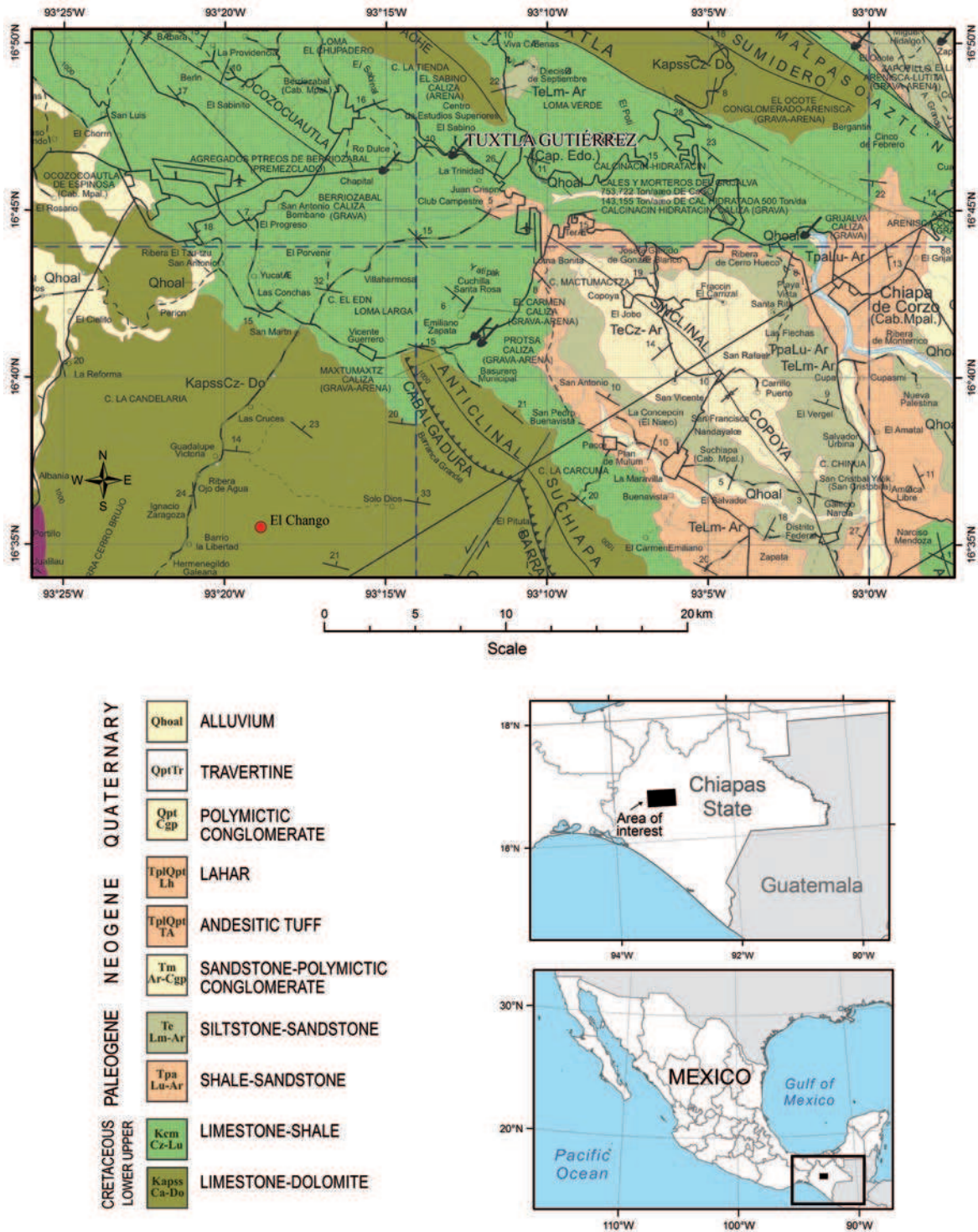


Fig. 1. Geographic and geologic map of the study area showing the location of the El Chango quarry. Modified from Servicio Geológico Mexicano, Carta Tuxtla Gutiérrez E 15-11.

ria pueblaensis FELDMANN & VEGA, 1995, from the Lower Cretaceous (Aptian) of Puebla State. Subsequently, VEGA et al. (2006) described *Palinurus pal-*

aciosi VEGA, GARCÍA-BARRERA, PERRILLIAT, COUTIÑO & MARIÑO-PÉREZ, 2006, from the Lower Cretaceous (Albian) of El Espinal quarry. Finally, FELDMANN et

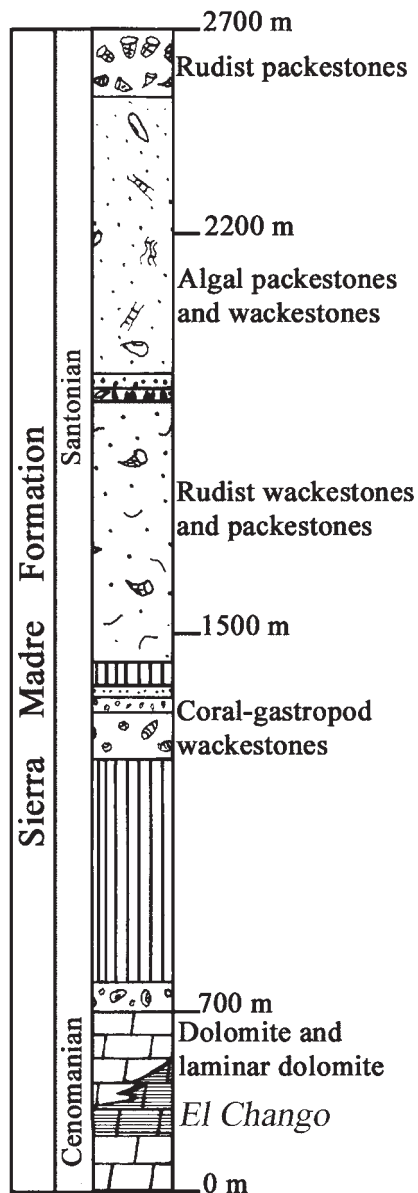


Fig. 2. Stratigraphic section of the Sierra Madre Formation, with approximate position of El Chango quarry sediments.

al. (2007) reviewed *M. pueblaensis* based upon some specimens discovered from the Muhi quarry (Albian-Cenomanian) in Hidalgo State. Moreover, FELDMANN et al. (2007) described from the same quarry *Aeger hidalguensis* FELDMANN, VEGA, MARTINEZ-LOPEZ, GONZÁLEZ-RODRÍGUEZ, GONZÁLEZ-LEÓN & FERNÁNDEZ-BARAJAS, 2007, representing the only fossil penaeid from Mexico known to date, and *Palinurus* sp.

3. Material

The studied sample includes 22 specimens collected in El Chango quarry. The specimens are preserved in laminated dolomitic limestones. The specimens are referred to *Zoquepenaeus* nov., with *Z. spinostratus* n. sp. (2 specimens) and *Tzeltalpenaeus* nov., with *T. exilichelatus* n. sp. (3 specimens) (Penaeidae RAFINESQUE-SCHMALTZ, 1815); to *Mexicania* nov., with *M. grijalvaensis* n. sp. (1 specimen) (Sicyoniidae ORTMANN, 1898); to *Mokaya* nov., with *Mokaya changoensis* n. sp. (12 specimens) (Sergestidae DANA, 1852). Moreover, one caridean, two palinurids, and one brachyuran (family, genus and species undetermined) are included in the study sample. For the higher-level classification, we follow the arrangement proposed by PÉREZ FARFANTE & KENSLEY (1997) and DE GRAVE et al. (2009).

The specimens are deposited in the palaeontological collection of the Museo Eliseo Palacios Aguilera, SEMAHN, Calzada de los Hombres Ilustres S/N, Colonia Centro, Tuxtla Gutiérrez, Chiapas, México (IHNFG).

Abbreviations: al: antennulae; a2: antennae; lcxp: carapace length (excluding rostrum); lr: rostrum length; P1-P5: pereopods 1 to 5; lt: body total length; sl-s6: pleonal somites 1 to 6; wcxp: carapace width.

4. Systematic palaeontology

Order Decapoda LATREILLE, 1802

Suborder Dendrobranchiata BATE, 1888

Superfamily Penaeoidea RAFINESQUE-SCHMALTZ, 1815

Family Penaeidae RAFINESQUE-SCHMALTZ, 1815

Genus *Zoquepenaeus* nov.

Etymology: From the Zoque people, who live mainly in the northern sector of Chiapas State.

Type species: *Zoquepenaeus spinostratus* n. sp.

Diagnosis: Carapace with hepatic spine; elongate pointed rostrum, with six dorsal teeth; cervical groove absent; P1-P3 chelate; uropodal exopod without diaeresis.

Zoquepenaeus spinostratus n. sp.

Fig. 3A-C

Etymology: The trivial name alludes to the spiny dorsal margin of the rostrum.

Types: Holotype: IHNFG-4714; Paratype: IHNFG-4715.

Material and measurements: Two specimens in lateral view (IHNFG-4714 – lcxp: 64.5 mm; wcxp: 17.7 mm; IHNFG-4715: lcxp: 36 mm; wcxp: 10.5 mm).

Diagnosis: As for the genus.

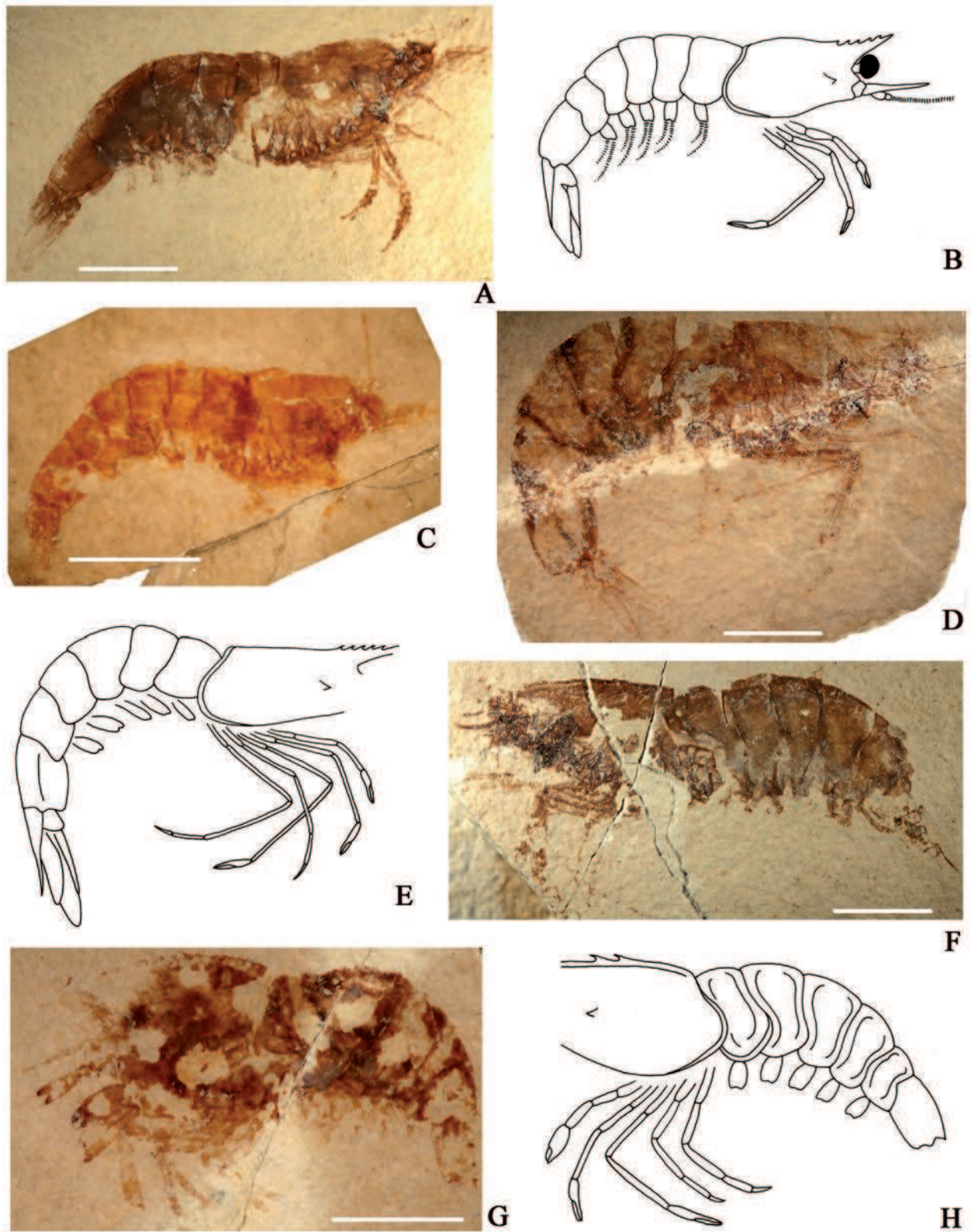


Fig. 3. A-C – *Zoquepenaeus spinirostratus* n. sp., A: holotype, IHNFG-4714, B: reconstruction, line drawing, C: paratype, IHNFG-4715. D-F – *Tzeltalpenaeus exilichelatus* n. sp., D: holotype, IHNFG-4717, E: reconstruction, line drawing, F: paratype, IHNFG-4718. G-H – *Mexicania grijalvaensis* n. sp., G: holotype, IHNFG-4716, H: reconstruction, line drawing. Scale bars equal 10 mm.

Description: Carapace: Subrectangular, elongate carapace; elongate pointed rostrum, with six dorsal teeth; posterior margin with a thin marginal carina; narrow ocular incision; weak antennal and pterigostomial angles; cervical groove absent; weak hepatic spine; postorbital spine absent.

Pleon: Subrectangular pleonal s1-s5 dorsally rounded, equal in size; pleonal s6 longer than the previous ones; smooth s1-s6 terga and pleurae; smooth triangular telson, with pointed tip, lacking lateral movable and fixed spines.

Cephalic appendages: Large eye with short eyestalk; elongate a1 peduncle; elongate slender scaphocerite, with a pointed tip.

Thoracic appendages: P1-P3 chelate, increasing in size; slender P1-P3 articles, bearing thin minute chelae; P4-P5 partially preserved.

Pleonal appendages: Well-developed basal segment of pleopods with flagella partially preserved; uropodal endopod and exopod slightly longer than the telson, both without median longitudinal carina; uropodal exopod without diaeresis.

Discussion: The specimens preserve diagnostic characters such as: compressed slender body; well-developed rostrum, armed with dorsal teeth; carapace without postorbital spine; hepatic spine present; posterior pleonal somites carinate; and telson sharply pointed, without lateral and fixed spines. All characters typical of the Penaeidae RAFINESQUE-SCHMALTZ, 1815, to which they are assigned (PÉREZ-FARFANTE & KENSLEY 1997). As reported by SCHWEITZER et al. (2010), this family includes to date 23 fossil genera from the Triassic to the Cretaceous, mostly reported from Europe (Austria, Belgium, Denmark, France, Germany, Great Britain, Italy, Switzerland), rarely from the Middle East (Lebanon), Africa (Morocco, Madagascar) and India. Based upon the above-mentioned fossil record, this family has previously never been reported from the Americas, except for the record of *Penaeus maddenii* FELDMANN et al., 1993, from the Miocene Loyola Formation in Ecuador (FELDMANN et al. 1993).

Genus *Tzeltalpenaeus* nov.

Etymology: From the Tzeltal people, who live in the highlands of Chiapas State.

Type species: *Tzeltalpenaeus exilichelatus* n. sp.

Diagnosis: Carapace with hepatic spine; elongate rostrum, with five to six dorsal teeth, including epigastric tooth; cervical groove absent; P1-P3 chelate, slender and elongate; P4-P5 achelate, slender and elongate, longer than the previous ones.

Tzeltalpenaeus exilichelatus n. sp.

Fig. 3D-F

Etymology: The trivial name alludes to the very slender P1-P3 segments.

Types: Holotype: IHNFG-4717; Paratypes: IHNFG-4718, IHNFG-4719.

Material and measurements: Three specimens in lateral view (IHNFG 4717-4719; IHNFG-4717 – lcxp: 84.6 mm; wcxp: 18.8 mm; IHNFG-4718: lcxp: 67.4 mm; wcxp: 15 mm).

Diagnosis: As for the genus.

Description: Carapace: Subrectangular, elongate carapace; elongate rostrum, with five to six dorsal teeth, including epigastric tooth; posterior margin with a thin marginal carina; narrow ocular incision; weak antennal and pterigostomial angles; cervical groove absent; well-developed hepatic spine; postorbital spine absent.

Pleon: Subrectangular pleonal s1-s5 dorsally rounded, equal in size; subsquare pleonal s6 with deep longitudinal cicatrix; pleonal s6 longer than the previous ones; smooth s1-s6 terga and pleurae; smooth triangular telson, with pointed tip, lacking lateral movable and fixed spines.

Cephalic appendages: Large eye with short eyestalk; a1, a2 not preserved.

Thoracic appendages: P1-P3 chelate, increasing in size; very elongate slender P1-P3 articles, bearing thin minute chelae; P4-P5 achelate, with very elongate slender articles; P4-P5 longer than the previous ones.

Pleonal appendages: Well-developed basal segment of pleopods with flagella partially preserved; uropodal endopod and exopod slightly longer than the telson; uropodal endopod without longitudinal carina; uropodal exopod partially preserved.

Discussion: The specimens preserve diagnostic characters such as: compressed slender body; well-developed rostrum, armed with dorsal teeth; carapace without postorbital spine; hepatic spine present; cervical groove absent; posterior pleonal somites carinate; and telson sharply pointed, without lateral spines. All characters typical of the Penaeidae RAFINESQUE-SCHMALTZ, 1815, to which they are assigned (PÉREZ-FARFANTE & KENSLEY 1997). *Tzeltalpenaeus exilichelatus* n. sp. differs from *Zoquepenaeus spinirostratus* n. sp. in having a rostrum with five to six dorsal teeth, including the epigastric tooth, very elongate, slender P1-P3 articles, and telson with deep longitudinal cicatrix. Based upon the above-mentioned observations, we can attest that *Zoquepenaeus spinirostratus* n. sp. and *Tzeltalpenaeus exilichelatus* n. sp. are the first report of Penaeidae from the Cretaceous of the Americas, representing the first Mesozoic record of this family out of Europe.

Family Sicyoniidae ORTMANN, 1898

Genus *Mexicania* nov.

Etymology: From Mexica that, in Nahuatl language, designated a native people who lived in Central Mexico.

Type species: *Mexicania grijalvaensis* n. sp.

Diagnosis: Robust carapace with postrostral carina with at least two teeth; well-developed hepatic spine; cervical groove indistinct; pleonal somites marked by transverse sulci; P1-P3 chelate; P4-P5 achelate.

Mexicania grijalvaensis n. sp.
Fig. 3G-H

Etymology: The trivial name alludes to the Grijalva, one of the three most important rivers in Chiapas State.

Holotype: IHNFG-4716.

Material and measurements: One specimen in lateral view (IHNFG-4716 – lcxp: 29.9 mm; wcxp: 11.8 mm).

Diagnosis: As for the genus.

Description: Carapace: Subrectangular, stout carapace; carapace with postrostral carina with at least two middle teeth; cervical groove indistinct; well-developed hepatic spine; posterior margin with a thin marginal carina.

Pleon: Subrectangular pleonal s1-s5 dorsally rounded, decreasing in size posteriorly; subrectangular pleonal s6 longer than the previous ones; smooth s1-s5 terga and pleurae; pleonal s1-s5 with anterior and posterior tergal sulci, delimiting median shallow depressions; telson not preserved.

Cephalic appendages: Poorly preserved; only a 3rd segment with flagella preserved.

Thoracic appendages: P1-P3 chelate, increasing in size; P1 stout chela; P2 minute chela; P4-P5 achelate, longer than the previous ones.

Pleonal appendages: Well-developed basal segment of pleopods; uropodal endopod and exopod not preserved.

Discussion: The specimen preserves diagnostic characters such as: carapace with postrostral carina bearing some median teeth; well-developed hepatic spine; and pleonal s1-s5 with anterior and posterior tergal sulci, delimiting median shallow depressions. All characters typical of the Sicyoniidae ORTMANN, 1898, to which they are assigned (PÉREZ-FARFANTE & KENSLEY 1997). As reported by SCHWEITZER et al. (2010), this family is represented in the fossil record only by *Sicyonia roemeri* (VON DER MARCK, 1858) from the Upper Cretaceous (Senonian) of Germany (VON DER MARCK 1858). However, we question the assignment of this species to Sicyoniidae, based upon the diagnostic characters of the type genus *Sicyonia* H. MILNE EDWARDS, 1830, according to PÉREZ-FARFANTE & KENSLEY (1997). Indeed, three characters of the fossil species, the rostrum with ventral teeth (*versus* rostrum with only dorsal teeth in *Sicyonia*), postrostral carina absent (*versus* postrostral carina present in *Sicyonia*), and pleonal s1-s6 with smooth terga and pleurae (*versus* pleonal s1-s6 with anterior and posterior tergal sulci, delimiting median shallow depressions in *Sicyonia*) exclude its belonging to this genus. Based on these observations, a review of *S. roemeri* is warranted to establish its true systematic assignment. Indeed the line drawing of this species

by VON DER MARCK (1858, pl. 6, fig. 1) points out some characters, such as the rostrum with dorsal and ventral teeth, pleonal s1-s6 with smooth terga and pleurae, pointed telson without lateral movable spines that are all typical of Penaeidae. *Mexicania grijalvaensis* n. sp. represents the first unequivocal report of the Sicyoniidae in the fossil record, extending the stratigraphic range of this family back to the Cenomanian. On the other hand, the presence of sicyoniids in the fossil record from Mexico is not so unusual, thus reflecting the extant rich sicyoniid community, widespread in the Gulf of Mexico (PÉREZ-FARFANTE 1985; PÉREZ-FARFANTE & KENSLEY 1997).

Superfamily Sergestoidea DANA, 1852
Family Sergestidae DANA, 1852

Genus *Mokaya* nov.

Etymology: From Mokaya, pre-Olmec cultures of the Soconusco region in Chiapas State.

Type species: *Mokaya changoensis* n. sp.

Diagnosis: Carapace without hepatic spine; short rounded toothless rostrum; weak cervical groove; supraorbital and hepatic spines absent; well-marked branchiocardiac carina; pleonal somites dorsally rounded; telson lacking lateral movable and fixed spines; P1-P5 achelate; reduced P4-P5 shorter than P1-P3.

Mokaya changoensis n. sp.
Fig. 4A-D

Etymology: From El Chango quarry, where the specimens were collected.

Types: Holotype: IHNFG-4702; Paratypes: IHNFG-4703, IHNFG-4704.

Material and measurements: 12 specimens in lateral view (IHNFG 4702-4713; IHNFG-4702 – lcxp: 25.6 mm; wcxp: 5.7 mm; IHNFG-4703: lcxp: 25 mm; wcxp: 5.7 mm; IHNFG 4705: lcxp: 21.8 mm; wcxp: 5.7 mm; IHNFG-4706: lcxp: 25.9 mm; wcxp: 7.5 mm).

Diagnosis: As for the genus.

Description: Carapace: Subrectangular, elongate carapace; short rounded toothless rostrum; posterior margin with a thin marginal carina; narrow ocular incision; weak antennal and pterigostomial angles; weak cervical groove; supraorbital and hepatic spines absent; well-marked branchiocardiac carina.

Pleon: Subrectangular pleonal s1-s5 dorsally rounded, equal in size; pleonal s6 longer than the previous ones; smooth s1-s6 terga and pleurae; smooth triangular telson,

with pointed tip, lacking lateral movable and fixed spines.

Cephalic appendages: Large cornea, with very elongate eyestalk; a1 and a2 poorly preserved.

Thoracic appendages: P1-P5 achelate; P1-P3 equal in size; elongate slender P1-P3 articles, bearing stiff setae; reduced P4-P5, equal in size and shorter than the previous ones.

Pleonal appendages: Well-developed basal segment of pleopods, bearing elongate flagella; uropodal endopod and exopod longer than the telson, both without median longitudinal carina; uropodal exopod without diaeresis.

Discussion: The specimens preserve diagnostic characters such as: carapace moderately compressed; rostrum shorter than the eyestalk; well-marked branchiocardiac carina; and reduced P4-P5. All characters typical of Sergestidae DANA, 1852, to which they are assigned (PÉREZ-FARFANTE & KENSLEY 1997). However, the combination of the short, rounded, toothless rostrum, the absence of supraorbital and hepatic spines, and the P1-P3 achelate is unique and are the enough to justify the introduction of a new genus *Mokaya*, distinct from all other fossil and extant genera within this family. The representatives of Sergestidae are very rare in the fossil record. Indeed, as listed by SCHWEITZER et al. (2010), to date only two species are known from the Cretaceous: *Pa-leomattea deliciosa* MAISEY & DE CARVALHO, 1995, from the Lower Cretaceous (Aptian-Albian) Santana Formation of Brazil, and *Cretasergestes sahelalmaensis* GARASSINO & SCHWEIGERT, 2006, from the Upper Cretaceous (Cenomanian) of Lebanon (MAISEY & DE CARVALHO 1995; GARASSINO & SCHWEIGERT 2006). *Mokaya changoensis* n. sp. differs from both species in having a short, rounded, toothless rostrum (*versus* short, pointed rostrum, with three dorsal spines in *P. deliciosa*; *versus* short, pointed, toothless rostrum in *C. sahelalmaensis*) and P1-P3 achelate (*versus* P1-P3 chelate in *P. deliciosa* and *C. sahelalmaensis*). *Mokaya changoensis* n. sp. is the first representative of Sergestidae in North America and the youngest representative of this family in the Americas.

Infraorder Caridea DANA, 1852

Family, genus and species indet.

Fig. 4E-F

Material and measurements: One specimen in dorsal view (IHNFG-4723 –lt: 28 mm; wcxp: 7.2 mm).

Description: Carapace: Any morphological characters can be observed.

Pleon: Subrectangular pleonal s1-s5 decreasing in size distally; pleonal s6 smaller than the previous ones; smooth s1-s6 terga and pleurae; smooth triangular telson, with two longitudinal marginal carinae; lateral margins with three fixed spines; and restricted distal extremity, bearing two elongate flagella.

Cephalic appendages: a1 not preserved; a2 short segments; a2 elongate multiarticulate flagellum.

Thoracic appendages: Not preserved.

Pleonal appendages: Pleopods not visible; uropodal endopod and exopod longer than the telson, both without median longitudinal carina; uropodal exopod without diaeresis.

Discussion: The dorsal view preservation of the study specimen makes difficult to observe the main morphological characters, even though the probable rounded s2 pleura could suggest its assignment to the infraorder Caridea DANA, 1852. As reported in the description, the most peculiar character is the well-preserved telson, never found both in the fossil penaeids and in the fossil carideans. Only the discovery of most complete specimens will make possible to clarify the systematic position of this specimen.

Infraorder Achelata SCHOLTZ & RICHTER, 1995

Family Palinuridae LATREILLE, 1802

Genus and species indet.

Fig. 4G

Material and measurements: Two specimens in lateral and ventral view (IHNFG-4721 –lt: 20.5 mm; wcxp: 3.6 mm; IHNFG-4722 –lt: 15 mm; wcxp: 3.5 mm).

Description: Carapace: Any morphological characters can be observed.

Pleon: Subrectangular pleonal s1-s5 decreasing in size distally; pleonal s6 smaller than the previous ones; smooth s1-s6 terga and pleurae; smooth subrectangular telson.

Cephalic appendages: a1-a2 not preserved; a2 elongate multiarticulate flagellum.

Thoracic appendages: P1-P5 achelate; P4 probably longer than the P1-P3 and P5.

Pleonal appendages: Pleopods not visible; uropodal endopod and exopod longer than the telson, both without median longitudinal carina; uropodal exopod with diaeresis.

Discussion: The small palinurids are preserved in lateral and ventral views respectively and the poor state of preservation does not allow closer comparison with *Palinurus palaciosi* VEGA et al., 2006, and *Palinurus* sp., reported from El Espinal and Muhi quarries respectively (VEGA et al. 2006; FELDMANN et al. 2007).

Infraorder Brachyura LINNAEUS, 1758

Section Eubrachyura DE SAINT LAURENT, 1980

Family, genus and species indet.

Fig. 4H-I

Material and measurements: One specimen in dorsal view (IHNFG-4720 –lcp: 18.1 mm; wcxp: 20.2 mm).

Description: Carapace subhexagonal, widest at anterior third; posterolateral margin inclined, two-thirds the maxi-

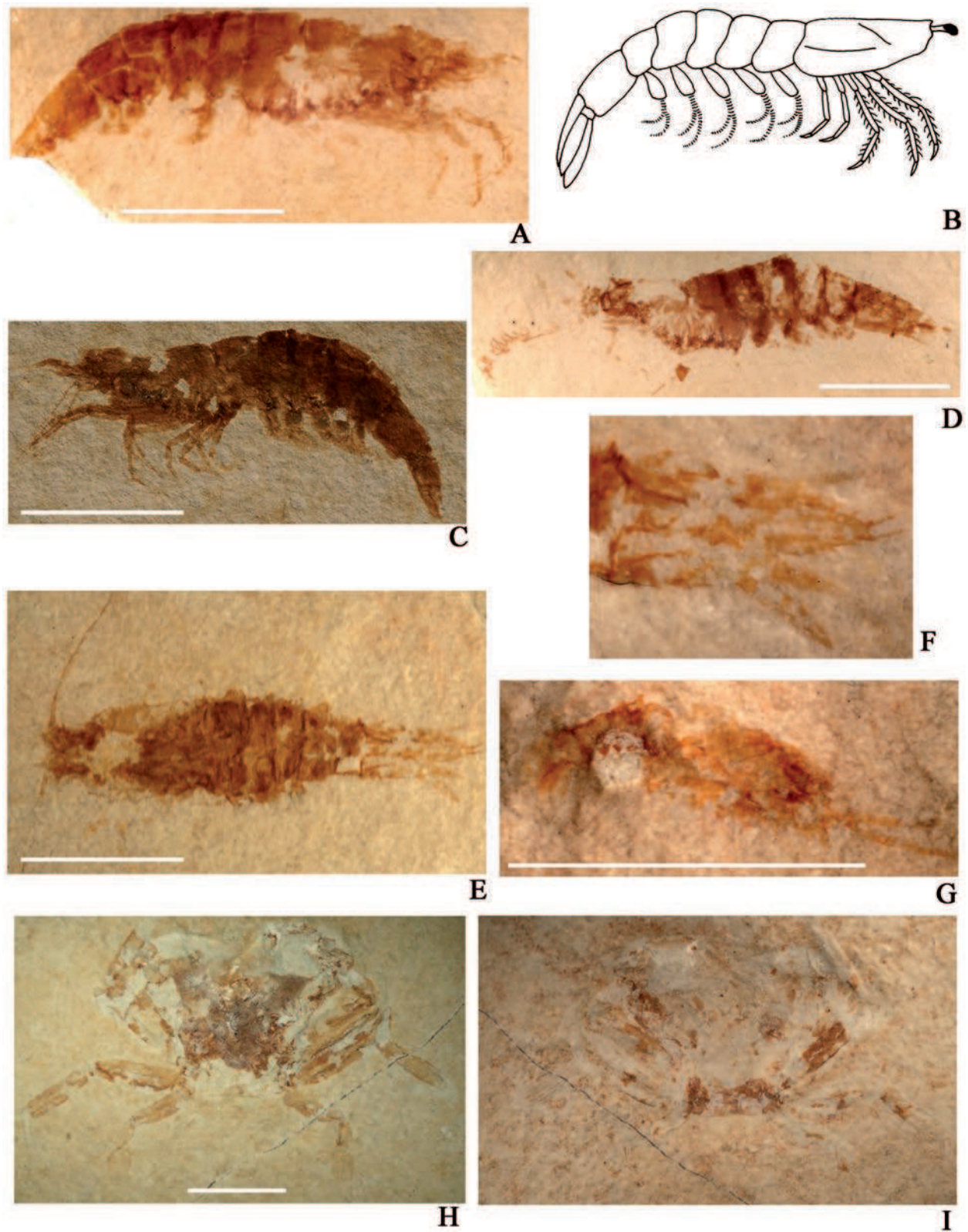


Fig. 4. **A-D** – *Mokaya changoensis* n. sp., **A**: holotype, IHNFG 4702, **B**: reconstruction, line drawing, **C**: paratype, IHNFG-4703, **D**: paratype, IHNFG-4704. **E-F** – Undetermined ?caridean, **E**: specimen IHNFG-4723, **F**: detail of tail fan, same specimen. **G** – Undetermined palinurid, specimen IHNFG-4721. **H-I** – Undetermined crab, part and counterpart, specimen IHNFG-4720. Scale bars equal 10 mm.

mum carapace length; posterior margin straight, two-thirds the maximum carapace width; chelae subequal, robust; P2 to P4 elongate, with slender merus; P4 elongate subrectangular merus, with rounded lower margin, carpus inverted subtrapezoidal, one-third the length of merus, subrectangular propodus, half the merus length; unciform dactylus; P5 slightly reduced, subquadrate ischium, subrectangular merus, with rounded lower margin, inverted subtrapezoidal carpus, rounded lower margin, half the merus length, subovate propodus, slightly longer than carpus but twice its height, lanceolate dactylus; short rectangular pleonal sl.

Discussion: The preservation of the specimen prevents a more detailed taxonomic placement. It bears similarities to one specimen from the Albian of Colombia (VEGA et al. 2010, fig. 8.7-8.9), reported as *Cenomanocarcinus renfroae* (STENZEL, 1945). The elongate, slender pereopods resemble also those of *Corazzatocarcinus hadjoulae* (ROGER, 1946), from the Cenomanian of Lebanon. The main problem is that the Chiapas specimen has a slightly reduced P5, whereas in the Colombia and Lebanon specimens it is more reduced. Better preserved specimens are needed before a more detailed systematic position.

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