J. Paleont., 73(3), 1999, pp. 407–413

0022-3360/99/0073-407$03.00

A NEW DECAPOD FAUNA FROM THE MIOCENE TUXPAN FORMATION, EASTERN MEXICO

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ABSTRACT—The first formal report of Tertiary portunid crabs for Mexico is based on two new species, *Portunus atecuicitli* and *Necronectes tajinensis*, from the middle Miocene beds of the Tuxpan Formation in Veracruz, east-central Mexico. Associated crustacean remains include fragments of calappid fingers, calappid carapace fragments possibly assignable to *Matuta* Fabricius, and callianassid hands. Low tolerance to osmotic variations of recent species of *Portunus* confirms paleoenvironmental interpretations for shallow, euryhaline, tropical waters during deposition of the Tuxpan Formation.

INTRODUCTION

As careful collecting yields new faunas, decapod crustaceans are becoming increasingly useful in paleoecological and biogeographic studies. However, with the exception of the Gulf Coastal Plain in the United States, the record of Cenozoic crabs and lobsters from the circum-Caribbean region is particularly sparse. For example, Vega and Feldmann (1992) compiled a list of only 14 Cenozoic species of macrocrustaceans reported for Mexico. Most of them are callianassids, and only one is a portunid, *Scylla costata*, from an unknown locality thought to be Oligocene. Thus, the discovery of a Miocene occurrence of decapods consisting of two species of portunids, one calappid, and callianassids contributes substantially to our knowledge of decapods in the region. This is the first well-documented report for portunid crabs from Tertiary deposits from anywhere in Mexico.

The Tuxpan Formation was defined by Dumble (1911) as "Tuxpan beds," based on a sequence of yellow sandstone, containing a diverse Miocene invertebrate fauna of gastropods, bivalves, and echinoderms collected from a series of small hills near the town of Tuxpan, Veracruz. Dumble (1918) also detailed the lithology of this formation. The type locality was designated by Thalmann (1935) as an outcrop within the town of Tuxpan. López-Ramos (1956) mapped the formation, which is defined by outcrops that extend generally parallel to the Gulf Coast. Width of the exposures ranges from 1 to 20 km, covered in part by Quaternary alluvium. López-Ramos also listed several diagnostic species of foraminiferans, molluscs, and echinoderms. Gío-Argáez (1982) listed the 15 most common species of ostracods for the Tuxpan Formation, among which are: *Actinocythereis exhantemata, Protocytheretta karlana, Murrayina gunteri, Actinocythereis grigsbyi, Actinocythereis waynensis, Bairdia* sp., *Protocytheretta inaequivalvis*, and *Peratocytheridea subovata*.

The localities from which the material herein described was collected are near San Pablo, located along Federal Highway 180, which extends between Papantla and Gutiérrez Zamora, in the eastern part of Veracruz State (Fig. 1). Locality 2989 is situated approximately 1 km west of San Pablo, at the base of a wall 50 m high, which represents the northern face of a normal fault. The second outcrop (Locality 2999) is located at km 7, on the north side of Federal Highway 180, near the town of Hermenegildo Galeana. It is a 22 m thick sequence of fine, cream colored sandstone. The localities are registered in the Locality Catalogus of the Instituto de Geología, UNAM.

The rocks of the Tuxpan Formation are cream colored sandstones, containing a relatively high diversity and abundance of gastropods, bivalves, annelid tubes, crustacean remains, and echinoids. The base of the formation includes conglomerates, and rests unconformably above the Mesón Formation. The thickness of the Tuxpan Formation reaches nearly 155 m at the type section. Based on a list of planktic foraminiferans, Barker et al. (1976) assigned a Miocene age to this formation. Particularly, the presence of *Operculinoides tuxpanensis* supported a correlation with the "*Operculinoides*" zone from the early Miocene of Louisiana (Burdigaliane to Langhiane stages). From the studied locality, Carreño (1979) reported the following ostracod species: *Actinocythereis grigsbyi, Cushmanidea ashermani, Cytherella hannai, Murrayina gunteri, Pterigocythereis americana*, and *Protocytherella karlana*, as well as the following foraminiferans: *Globigerinoides sacculifer, Globocuadrina altispira, Globocuadrina globosa, Globorotalia obesa*, and *Orbitulina universa*. Biostratigraphic ranges of these foraminiferans and ostracods suggest a middle Miocene age for the sediments where the crabs were collected.

Sediments of the Tuxpan Formation were deposited during a transgressive phase, followed by a regression which reached the present position of the northern Gulf Coast of Veracruz State. Based on the lithologic features and faunal content, tropical, euryhaline waters (32–36 parts per thousand salinity) with an approximate depth of 10–30 m is suggested.

SYSTEMATIC PALEONTOLOGY

Order DECAPODA Latreille, 1803
Infraorder BRACHYURA Latreille, 1803
Section HETEROTREMATA Guinot, 1977
Superfamily PORTUNOIDEA Rafinesque, 1815
Family PORTUNIDAE Dana, 1852
Genus PORTUNUS Weber, 1795
PORTUNUS ATECUICITLIS new species
Figures 2.1–2.6, 3.5, 3.6, 4

Diagnosis.—Typical *Portunus*, but with unique front comprised of axial portion with four triangular teeth and very wide orbits; carapace surface with two weakly developed transverse ridges.

Description.—Moderate sized portunid; width about 1.5 times length; gently arched transversely and longitudinally, most tightly arched in posterior half of carapace.

Front and anterolateral margins form a nearly smooth arch.

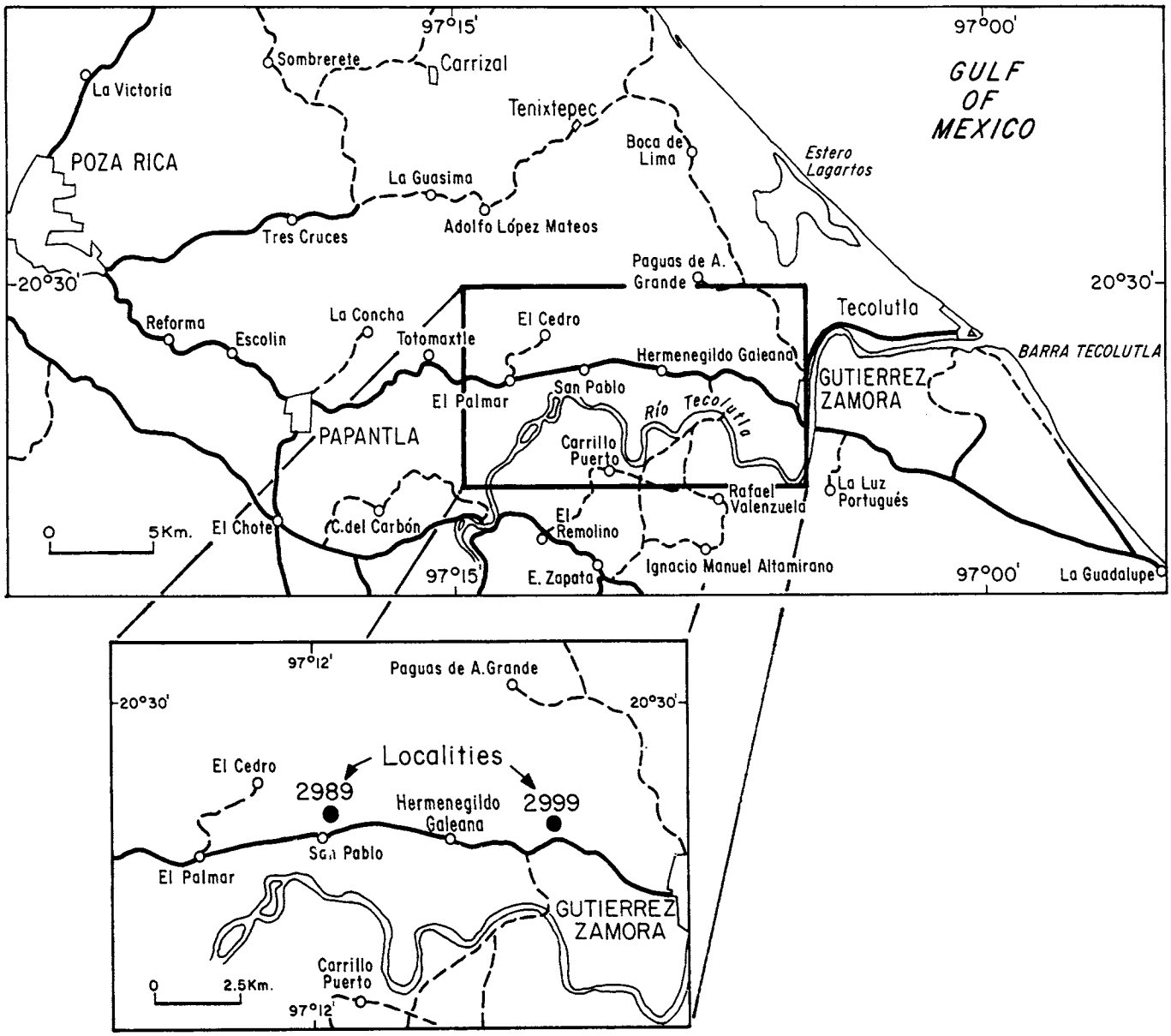

FIGURE 1—Location maps of the studied area in Veracruz State, east Central Mexico. Locality 2989 lies east of San Pablo, on the north side of the highway, at the base of a high cliff. Locality 2999 is located 7 km west of the town of Gutiérrez Zamora. It is an outcrop 20 m thick, located on the north side of the highway.

Front moderate width, about 15 percent carapace width with two short spines on either side of midline. Orbits well defined by triangular inner and outer orbital spines; broad, concave beaded margins axially and two orbital fissures situated in lateral third of orbit, near outer orbital spine. Anterolateral margin weakly upturned, with at least six approximately equal sized triangular spines, excluding outer orbital spine. Last spine apparently not elongated. Posterolateral margin smooth, sinuous, slightly convex anteriorly becoming concave posteriorly. Posterior margin straight, thickly rimmed, about 38 percent carapace width.

Carapace regions more distinctly defined on small specimens, not clearly defined on large specimens, only slightly elevated above broad, ill-defined grooves. Branchial regions most strongly swollen with broad ridge extending in convex-forward arc from cardiac region to lateral corner. Another ridge

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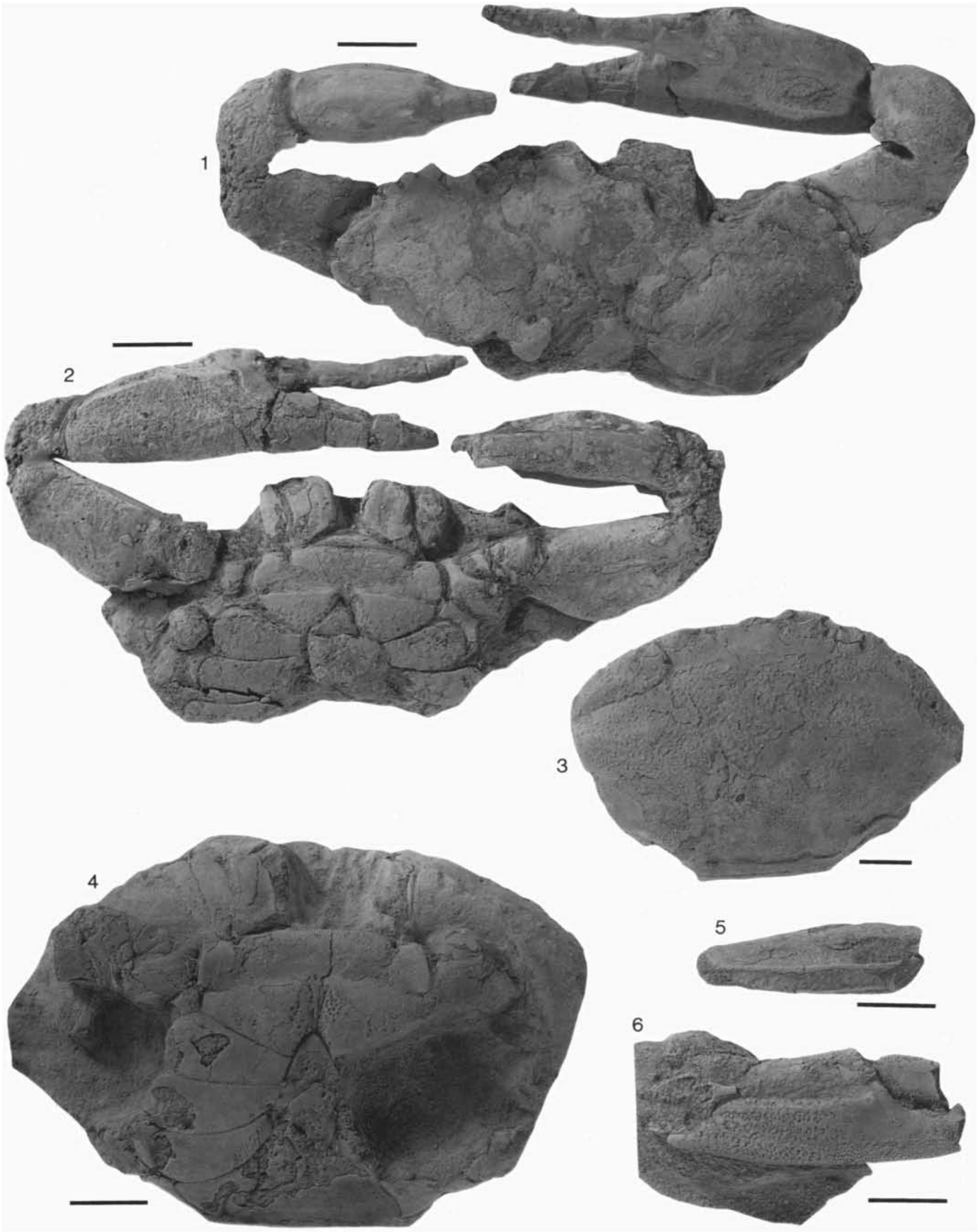
FIGURE 2—*Portunus atecuicitlis* n. sp. *1,* dorsal view of anterior half of carapace, including chelipeds, paratype IGM-7654; *2,* ventral view of anterior half of carapace, including chelipeds, paratype IGM-7654; *3,* dorsal view of carapace, holotype, IGM-7653; *4,* ventral view of carapace, holotype IGM-7653; *5,* dorsal view of left palm, paratype, CM 45600 ; *6,* posterior view of left palm, paratype, CM 45601. Scale bars equal 1 cm.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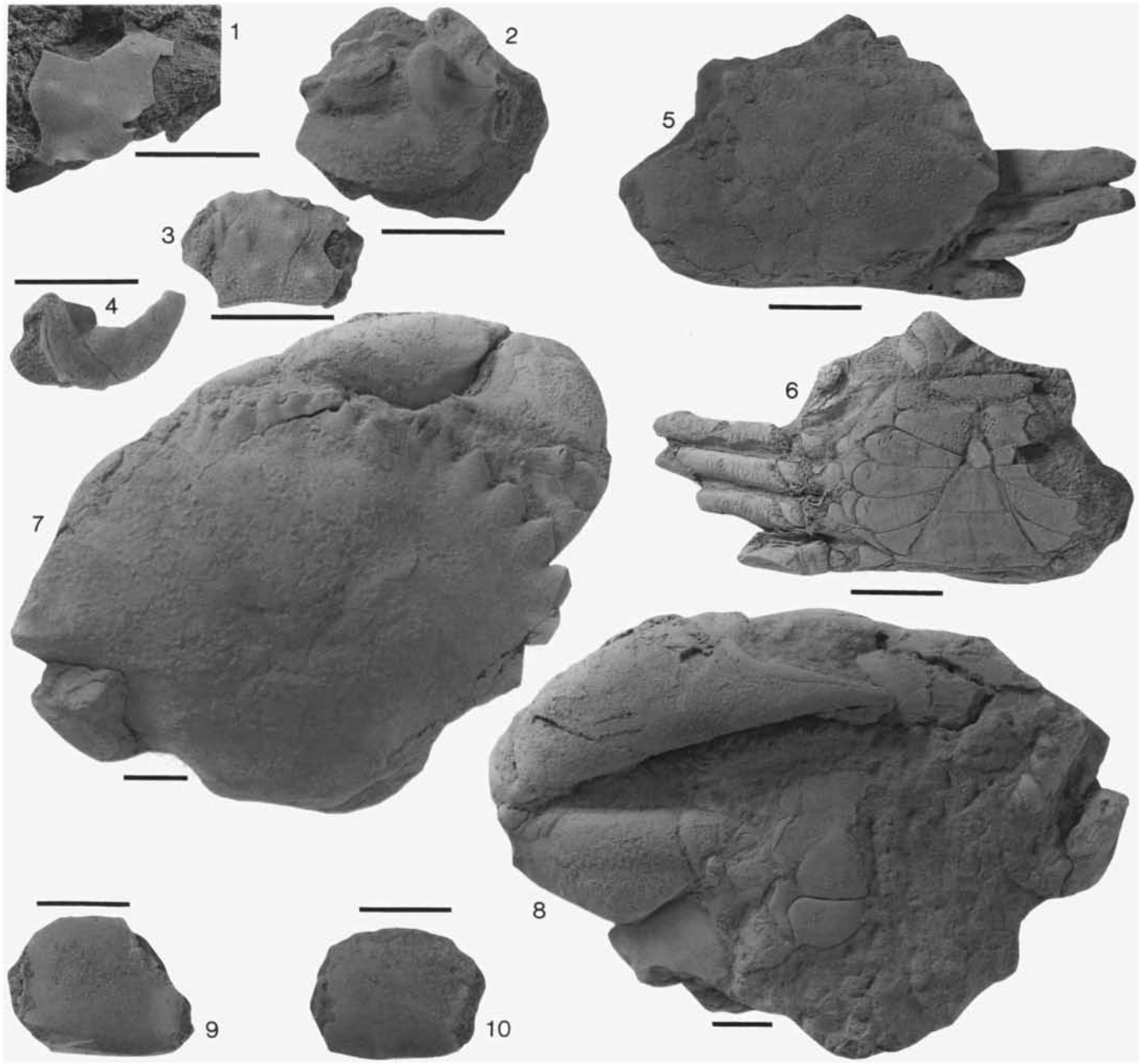

FIGURE 3—Miocene decapods from Tuxpan Formation. *1–4, Mursia?* sp.; *1,* carapace fragment, CM 45604. *5, 6,* dorsal and ventral views of incomplete carapace and second through fourth meri of *Portunus atecuicitlis* n. sp., paratype, CM 45602. *7, 8,* dorsal and ventral views of carapace of *Necronectes tajinensis* n. sp., holotype, IGM-7721. *9, 10,* callianassid hands; *9,* inner surface of left propodus, CM 45608; *10,* inner surface of left propodus, CM 45609. Scale bars equal 1 cm.

extends transversely across protogastric and mesogastric regions. Carapace surface with widely spaced granules over entire surface except frontal region which is smooth to very finely pustulose.

Buccal cavity rectangular, wider than long. Maxillipeds do not cover axial portion of cavity. Thoracic sternites typical for family, not fused except elements 1–3. Anterior half of sternite 4 of male markedly lower than posterior half. Sternum widest, about 50 percent carapace width, at sternite 7. Telson and at least two abdominal somites of male form broad isosceles triangle, broadest element probably represents fusion of somites 3–5. Proximal abdominal somites reduced, carried in subvertical position.

Chelipeds greatly elongated and much larger than walking legs. Width from one carpus to the other about 1.4 times carapace width. Merus triangular in cross section, with at least three spines on inner margin. Carpus with prominent spine at inner articulation with merus and nodose prominences at articulations with propodus. Propodus long, stout, strongly keeled; three keels on outer surface, two keels terminating in small spines define upper surface; one keel on inner surface. Fingers slightly shorter than palm, bearing broad, domal teeth proximally and narrower, sharper teeth distally. Remaining pereiopods represented only by long, slender proximal elements.

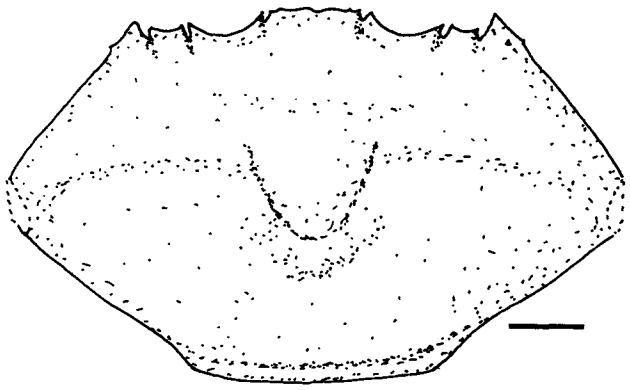

FIGURE 4—Line drawing of carapace in dorsal view of holotype, IGM 7653, of *Portunus atecuicitlis* n. sp. The anterolateral margin is generalized as it is not well preserved. Scale bar equals 1 cm.

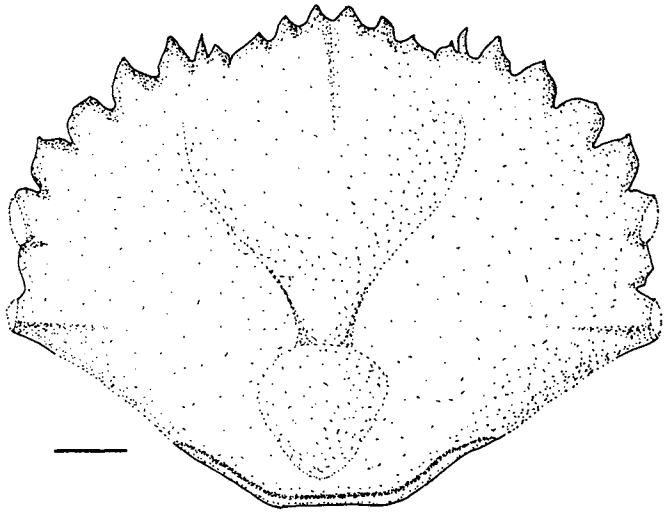

FIGURE 5—Line drawing of carapace in dorsal view of holotype, IGM 7721, of *Necronectes tajinensis* n. sp. Scale bar equals 1 cm.

Etymology.—The trivial name of the species refers to the translation from the Nahuatl language for blue-crab, *atecuicitli.*

Types.—The holotype, IGM-7653, and paratype, IGM-7654, and six isolated claw fragments presumed to represent the same species are deposited in the Paleontological Museum of the Instituto de Geología, UNAM. Paratypes, CM 45600, 45601, and 45602, are deposited in the Department of Invertebrate Paleontology, Carnegie Museum of Natural History, Pittsburgh, Pa.

The carapace material represents males exclusively.

Measurements.—Holotype IGM-7653, carapace width, 74.5 mm; length 47.8 mm. Paratype IGM-7654, carapace width, 65.0 mm; right propodus length, 50.3 mm, height, 18.7 mm. Paratype, CM 45602, carapace width, 40.0 mm; length, ca. 30mm. Paratype, CM 45603, carapace width, 34.0 mm, height, 20.0 mm.

Occurrence.—The material was collected from the middle Miocene Tuxpan Formation in Veracruz State, Mexico at Locality 2989 (Fig. 1).

Discussion.—The specimens from Veracruz closely fit the definition of *Portunus* (Rathbun, 1930; Williams, 1984). Development of a front with four teeth; arcuate anterior and anterolateral margins whose radii originate approximately at the posterior margin; triangular male abdomen; and spines on merus, carpus, and propodus of the cheliped are particularly distinctive features of the genus. It is not certain that the anterolateral margin exhibits nine spines, including the outer orbital spine, as this region is incomplete in all specimens. Likewise, it is not possible to determine whether or not the last of these spines is elongated because none is preserved.

The species differs from all other described species in development of the front and the very wide orbits. In this regard, the species most closely resembles *Portunus viai* Secretan, 1971, from upper Burdigalien sandstones of the Rhone Valley, France. In this latter species the front is about 16.6 percent of maximum width, and the fronto-orbital width is about 56 percent, whereas they are 15 and 53 percent, respectively, in the Veracruz species. The appearance of the fronts is quite different in the two species, however, because that of *P. viai* is projected well in advance of the orbits whereas in *P. atecuicitlis* the front does not extend appreciably in advance of the orbits. The two species may be further distinguished because the carapace regions of *P. viai* are much more inflated and distinct than on the Mexican specimens. Finally, the sternum of *Portunus viai* attains its greatest width at the sixth, rather than the seventh somite.

The specimens of *Portunus* are associated with isolated callianassid hands (Fig. 3.9, 3.10) and a carapace fragment, dactylus, and fragmentary propodi of a calappid, possibly *Mursia* Desmarest (Fig. 3.1, 3.2, 3.3, 3.4). The calappid carapace fragment is generally smooth and bears at least two rows of rather large nodes. The claw fragments have densely nodose surfaces and the dactylus bears the distinctive swollen hook near its base, which is used to fragment shells of prey. The callianassid hands do not exhibit any distinctive morphological characters that would permit identification, even to the generic level.

Living species of *Portunus* inhabit inner and outer shelf environments. Along the coasts of Mexico, nearly 20 species have been described, collected at depths from 1 to 500 m (Rathbun, 1930; Garth and Stephenson, 1966; Powers, 1977; Williams, 1984; Abele and Kim, 1986), although they are more frequent between 4 to 100 m. These crustaceans show a preference for relatively consolidated coarse sands, including bioclasts of corals, shells, and small rocks. They are associated with seaweed and burrow into the substrate or seek shelter beneath corals and rocks (Britton and Morton, 1989). Members of the genus have a rather low tolerance to osmotic variations, unlike their relatives of the genus *Callinectes* Stimpson.

Genus NECRONECTES A. Milne Edwards, 1881

NECRONECTES TAJINENSIS new species

Figures 3.7, 3.8, 5

Diagnosis.—Typical *Necronectes* with outer orbital teeth elongate and slender, and remainder of anterolateral teeth with recurved posterior margins and apices directed more laterally than anteriorly. Carapace regions very weakly developed.

Description.—Carapace slightly wider than long, width 1.24 times maximum length; dorsal surface smoothly granulated; weakly convex transversely, more strongly so longitudinally.

Frontal margin 0.19 maximum width, with four triangular spines with rounded apices, separated by deep "U" shaped grooves; lateral frontal spines more robust, mesial ones slightly more projected. Orbits narrow, about 0.10 maximum width of carapace, two well-defined fissures; orbits bordered axially by triangular subacute spine with wide base, separated from frontolateral spine by rounded notch which continues posteriorly onto dorsal portion of carapace as defined depression. Orbits defined laterally by subacute, wide-based triangular external orbital spine. Anterolateral margin 1.1 times longer than posterolateral margin, with regular convex outline bearing eight subacute to acute triangular spines. First spine, the outer orbital

spine, acute with narrow base, spines 2–7 wide-based. Width of each spine increases from second to fifth; their bases separated by narrow grooves. First spine three times longer than wide; second 1.45 times wider than long with sides regularly convergent towards tip. Third 1.42 times wider than long, with straight anterior margin, slightly shorter than posterior margin, which is straight in basal portion becoming abruptly convergent toward apex to form shoulder. Fourth spine 1.5 times as wide as long, with similar convex anterior and posterior margins. Fifth spine similar to third in shape of anterior and posterior margins, width 1.38 times length. Sixth spine incomplete, but similar to fifth. Seventh and eighth also incomplete; eighth bears subtle ridge which continues onto carapace a short distance. Posterolateral margin weakly concave. Marginal rim extends along posterior and posterolateral margins.

Cervical groove well defined along lateral and posterior margins of mesogastric region, becoming obscure toward anterolateral margins. Regions poorly marked; gastric region weakly inflated; protogastric regions defined by two broad, rounded elevations, separated anteriorly by shallow axial depression. Cardiac region slightly inflated, defined by weakly marked grooves.

Thoracic sternites narrow, first four fused. Fourth sternite triangular, slightly elevated above rest of plate. Lateral sternal process well defined, strongly concave and curving around anterolateral angle of fifth somite, two straight marginal faces distally. Fifth sternite separated from anterior sternal plate by distinct groove. Sternum does not appear to widen significantly posteriorly.

Abdomen not preserved.

Right cheliped strong; surface with fine granulations similar to those of dorsal carapace. Coxa, basis, and ischium visible in ventral view, freely articulated. Coxa subquadrate, slightly wider distally, articulated at posterolateral corner of sternal plate. Basis small, triangular. Ischium triangular, anterior margin slightly curved. Merus of right cheliped with strong, projecting carpal articulation on lower surface and smooth, rounded distal posterior angle; ventrally smooth, posterior margin convex, widest at midlength; anterior margin straight, thicker and more regularly curved than posterior margin; distal margin with rounded articular condyle on upper surface. Carpus robust, triangular, with rounded anterior margin; internal, acute spine prominent on upper surface; dorsal surface finely granulated. Chela strong and moderately inflated, length including fixed finger 2.33 times maximum height attained at distal end of palm; dorsal portion of palm rounded, with fine granulations; external and lower surfaces smooth; proximal articulation with a lobe-shaped condyle on lower margin. Fingers robust, moderately long and slightly curved fixed finger 0.4 times length of total chela. Dactylus approximately as long as fixed finger; denticles broad, flattened, decreasing in size distally.

Etymology.—The trivial name refers to the famous archaeological zone El Tajín, located relatively near to the localities here reported.

Type.—The holotype, and sole specimen (IGM-7721), is deposited in the Instituto de Geología, UNAM.

Measurements.—Maximum carapace length, 61.5 mm; maximum carapace width, 84.4 mm; frontal width, 15.8; fronto-orbital width, 40.3 mm; posterior margin width, 20.1 mm; length of right cheliped, 60.8 mm; maximum height of right cheliped, 26.2 mm.

Occurrence.—The specimen was collected from the middle Miocene Tuxpan Foramation in Veracruz State, Mexico at Locality 2999 (Fig. 1).

Discussion.—*Necronectes tajinensis* rather closely resembles the middle Miocene Panamanian species *N. proavita* (Rathbun); however, the latter exhibits anterolateral spines that do not have complexly curved margins and whose apices are directed more anteriorly than laterally. Furthermore, the carapace regions on *N. proavita* are much more distinct than on *N. tajinensis,* particularly in development of the protogastric region.

It is interesting to note that Rathbun (1918) recognized that the morphology of the specimens from Panama that she was studying bore striking resemblance in one character or another to representatives of the Portunidae, the Cancridae, and the Xanthidae. As a result she erected a new genus, *Gatunia* Rathbun, and considered it the sole representative of a new family, Gatuniidae Rathbun. Although subsequent authors have not recognized the family and, instead, have placed *Gatunia proavita* in *Necronectes* A. Milne Edwards, within the Portunidae, the confusing array of characters is still of interest. It is likely that dissociated parts of this organism would be misidentified.

ACKNOWLEDGMENTS

We are grateful to V. M. Malpica-Cruz, from the Department of Geology, Instituto de Geología, UNAM, for his valuable help during the prospection in the field. F. Vega made the location figures. Useful reviews were provided by D. Tshudy and J. S. H. Collins. Our thanks to these gentlemen.

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ACCEPTED 5 OCTOBER 1998