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FOSSIL CRABS (CRUSTACEA: DECAPODA) FROM THE LATE CRETACEOUS CÁRDENAS FORMATION, EAST-CENTRAL MEXICO

FRANCISCO J. VEGA, RODNEY M. FELDMANN, AND FRANCISCO SOUR-TOVAR

Instituto de Geología, Universidad Nacional Autónoma de México,
 Ciudad Universitaria, 04510, México D.F., México,
 Department of Geology, Kent State University, Kent, Ohio 44242, and
 Facultad de Ciencias, Universidad Nacional Autónoma de México,
 Ciudad Universitaria, 04510, México D.F., México

ABSTRACT—Twenty-four nearly complete carapace samples were collected at three different localities of the Maastrichtian (Late Cretaceous) Cárdenas Formation in San Luis Potosí, east-central Mexico. The material has been assigned to five families: the Callianassidae, Dakoticancridae, Carcineretidae, ?Majidae, and Retroplumidae. Two genera of callianassid shrimp are described, *Cheramus* for the first time in the fossil record. *Dakoticancer australis* Rathbun is reported as the most abundant crustacean element; one new genus and species of carcineretid crab, *Branchiocarcinus cornatus*, is erected, and a single, fragmentary specimen is questionably referred to the Majidae. The three localities reflect paleoenvironmental differences, exhibited by different lithologies, within marginal marine, lagoon environments. The record of dakoticancrid crabs in the Cárdenas Formation extends the paleobiogeographic range of the family and the genus *Dakoticancer*. Carcineretid crabs, although not abundant, seem to have been a persistent element of crustacean assemblages in clastic environments during the Late Cretaceous of the ancestral Gulf Coast of Mexico.

INTRODUCTION

THE CÁRDENAS FORMATION is a clastic sedimentary sequence with an approximate thickness of 1,050 m that crops out at the western margin of the folded Sierra Madre Oriental in San Luis Potosí State, Mexico (Figure 1). The type section for the formation was described as the rocks exposed in an asymmetrical syncline east of Cárdenas railroad station (Myers, 1968). Here the Cárdenas Formation overlies the Tamasopo Limestone along a fault contact, and is unconformably overlain by the lower Tertiary red beds of the Tabaco Formation.

Cárdenas deposits extend northward from the type area, and the material described herein was collected by R. M. Feldmann, F. Sour-Tovar, and F. Vega at three different localities, near Ciudad del Maíz (Figure 1), along Federal Highway #80, which leads to the port city of Tampico. A more detailed description of the localities is given below. The fossil crabs were collected in rocks ranging from claystone to shales and sandy mudstones, which also contain an abundant fauna of gastropods, bivalves, and echinoderms. Most gastropod and bivalve species may be assigned to the *Exogyra costata* biozone. In fact, this gryphaeid

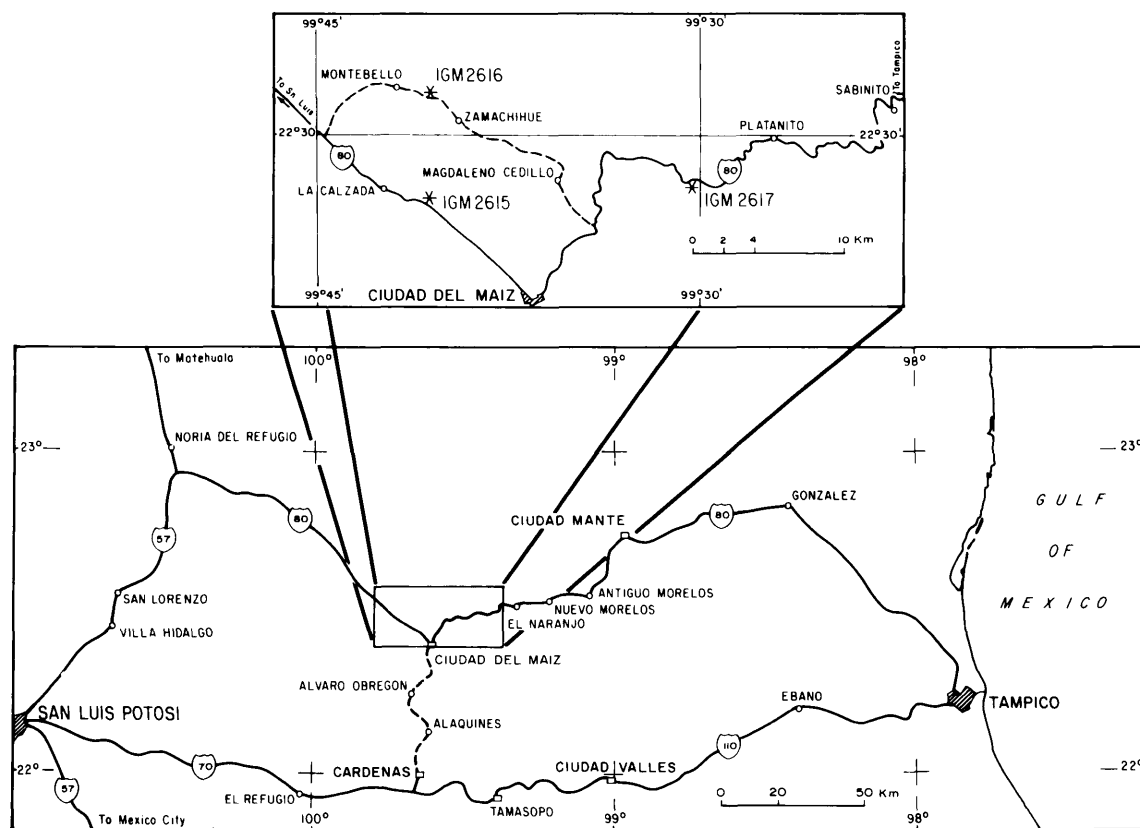


FIGURE 1—Location maps showing part of San Luis Potosí State from which fossil decapods were collected in the Cárdenas Formation. Crab-bearing fossil localities are indicated by stars.

is a common element in the Cárdenas Formation, and has been recognized as an index fossil of Late Cretaceous age for this unit by several authors (Böse, 1906; Böse and Cavins, 1927; Burckhardt, 1930; Heim, 1940; and Müllerried, 1941). Myers (1968) subdivided the Cárdenas Formation into three biozones (from base to top: *Durania ojanthalensis* Myers, *Arctostrea aguilerae* Böse, and *Tampsia floriformis* Myers) and proposed a Maastrichtian age for the formation. According to Myers' subdivision of the Cárdenas Formation, the fossil decapods were collected from the *Arctostrea aguilerae* biozone in the middle portion of the formation. The lithology of this unit, alternation of fine clastics and biogenic limestones (Figure 2), documents regressive conditions in a shallow environment on the Valles Platform. The pelagic equivalent of the Cárdenas Formation is the Méndez Formation of Maastrichtian age, which crops out along the eastern margin of the folded Sierra Madre Oriental (Gulf Coastal Plain of Mexico). Sources of sediment for the Cárdenas Formation were located to the west and northwest; the sediments filled an elongated shallow basin that was bordered to the east by a barrier that represented the beginning of folding and uplift of the Sierra Madre Oriental during the initial Laramide pulsations. Granulometric analysis, presence of decapod remains, and the associated molluscan fauna suggest subtidal and lagoon facies of low energy in this portion of the Cárdenas Formation.

The purpose of this paper is to describe the first decapod remains to be collected from the Cárdenas Formation, including two species of callianassid mud shrimps, and southernmost occurrence of *Dakoticancer australis*, one new genus and species of carcineritid, the occurrence of *Costacopluma bishopi* Vega and Feldmann, and a single specimen assigned to the Majidae.

A comparison with the fauna of the Portrerillos Formation and some paleobiogeographic and paleoecologic interpretations are given.

LOCALITIES AND PALEOENVIRONMENTAL SETTINGS

The species described herein were collected at three localities within the Cárdenas Formation. The lithologies of these localities and the paleoenvironmental interpretations for each are different.

Locality IGM-2615, "La Calzada," is located 11 km northwest of Ciudad del Maíz (lat. 22°27'30"N, long. 99°41'W), beside Federal Highway #80 (Figure 1). There the exposures of the Cárdenas Formation are composed chiefly of gray, green, and gray-blue shales, mudstones, and siltstones, with a minor amount of sandstone and abundant evidence of bioturbation. A 420-m section, measured for the sequence (Figure 2.1), occurs within an asymmetric syncline. Several samples of *Dakoticancer australis* were collected in the lower portion of the section, associated with a diverse molluscan fauna and many chelae referable to *Protocallianassa*. A single mold of the exterior of a small crab was also collected and referred questionably to the Majidae. De la Mora-Vidal (1991) identified 10 species of gastropods, 16 bivalves, and spatangoid echinoderms from the section, and Hurtado-Gonzalez (1984) reported six gastropod species and 25 bivalve species from the same outcrop. She interpreted these sediments as shallow marine deposits, formed in a low-energy environment under a sub-humid climate, with dry episodes. Sedimentologic features and faunal composition suggest a marginal lagoon environment. Storm deposits are represented in the sequence as shell-rich horizons of about 10 cm thickness, be-

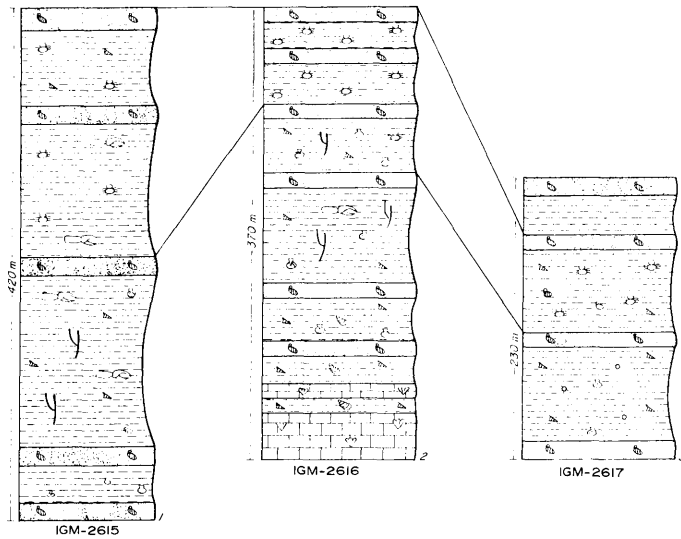


FIGURE 2—Generalized stratigraphic sections measured at three crab-bearing fossil localities. Upper part of sections consists of alternating brown sandstones and grayish-green shales; shale beds become finer toward top. Sandstones contain ostreids, whereas shales include articulated pelecypods and dakoticancrid crabs. Calcareous sandy shales are green and blue in color, with bioturbation and some pelecypods in life position dominating middle of section. Some callianassids and isolated crustacean appendages are also present. Lower part of siliclastic section includes brown calcareous sandstones, containing fragments of ostreids and gastropods, and calcareous grayish-green to grayish-blue shale with gastropods and pelecypods. Banks of *Exogyra costata* and *Pycnodonte mutabilis* as well as sedimentary structures suggest deposition in a lagoonal environment. Lowermost part of formation is comprised of silty gray-green limestone containing ostreids and rudists such as *Tampsia floriformis*.

tween gray shales and mudstones. These horizons are composed chiefly of disarticulated bivalves referable to *Idonearca*. Absence of breakage and lack of conspicuous abrasion suggest that these shells were subjected to minimal transport. Presence of *Exogyra costata* Say, as well as the entire molluscan assemblage, suggests a Maastrichtian age for these deposits.

Locality IGM-2616, "Montebello," is located 15 km northwest of Ciudad del Maíz. Outcrops of the Cárdenas Formation occur in an asymmetric syncline beside the road between the villages of Montebello and Zamachihue (Figure 1). The dirt road follows a main arroyo with lateral creeks (lat. 22°31'20"N, long. 99°40'W), in which 370 m of gray, green, and gray-blue mudstones and shales are exposed (Figure 2.2). Although lithologic features seen at this locality are similar to those of the previously described site, the sediments are more arenaceous and the rocks tend to be grayish blue. Although this could be a bias of collecting, the diversity and abundance of molluscan species is not as great as at locality IGM-2615. Some nautiloids, as well as some spatangoid echinoderms, are present. Hurtado-Gonzalez (1984) assigned these sediments to the Méndez Formation, previously defined by Dumble (1918). However, the original description for the Méndez Formation noted pelagic flysch-like sediments that crop out on the Mexican Gulf Coast Plain, where macroinvertebrate fossils are absent, and the biostratigraphy is based on foraminiferans. A Campanian–Maastrichtian age has been assigned for this formation (López-Ramos, 1985). For this reason, we do not consider these rocks as Méndez Formation, but rather as Cárdenas Formation, based upon lithologic, biostratigraphic, and paleoenvironmental similarities with the type section of this unit.

Evidence for bioturbation at this locality is scarce. Several complete carapaces and carapace fragments of *Dakoticancer australis* were collected. A single specimen of a new genus of carcineretid, *Branchiocarcinus cornatus*, was also found. Most carapace remains were found with appendages articulated and cuticle ornamentation preserved. However, all show deformation or displacement of the ventral portion. This suggests that all crab remains were exuviae, buried in a low-energy environment. A shallow part of a marginal lagoon is indicated.

Locality IGM-2617, "Santa Barbarita," located 12 km northeast of Ciudad del Maíz, is an outcrop on the south side of Federal Highway #80, near Santa Barbarita (Figure 1). The exposure lies in a syncline at the middle portion of the folded Sierra Madre Oriental (lat. 22°27'40"N, long. 99°30'45"W). It is the easternmost outcrop of the Cárdenas Formation containing macroinvertebrate remains. A 230-m-thick section of light-brown marls (mudstones, siltstones, and claystones, with a minor amount of sandstone) is exposed, containing a diverse assemblage of bivalves and gastropods toward the base, but no evidence of bioturbation (Figure 2.3). A few meters above the molluscan beds the diversity diminishes; at this point one complete carapace and three carapace fragments of *Dakoticancer australis* were found associated with *Pycnodonte mutabilis* (Morton), the sole accompanying faunal element. The carapaces were crushed or deformed with preserved cuticle but no appendages. Dislocation of the epimeral suture can be observed on one specimen, so these crab remains also are interpreted as exuviae. Toward the top of the section, the lithology changes to more sandy mudstones and shales of gray-blue color with no macroinvertebrate remains. The deposits of this locality are interpreted as subtidal shelf sediments. The easternmost synclines of the folded Sierra Madre Oriental are developed in continental slope and pelagic sediments, which belong to the correlative Méndez Formation.

SYSTEMATIC PALEONTOLOGY

Order DECAPODA Latreille, 1803

Infraorder ANOMURA H. Milne Edwards, 1832

Superfamily THALASSINOIDEA Latreille, 1831

Family CALLIANASSIDAE Dana, 1852

Genus CHERAMUS Bate, 1888

CHERAMUS sp.

Figure 3.1

Referred material.—A single specimen, IGM-3311, collected from locality 2615, is deposited in the Museo de Paleontología, Instituto de Geología, Universidad Autónoma de México.

Remarks.—Callianassid remains are nearly ubiquitous elements of Cretaceous and Cenozoic marine decapod crustacean assemblages (Glaessner, 1969, p. R478). Thus, it is not surprising that remains of these animals have been collected from the Cárdenas Formation. Members of the Callianassidae typically have a weakly calcified carapace so that the majority of species in the fossil record are known only from isolated chelae. Because the morphology of the chelae is not complex, there are relatively few recognized descriptors for distinguishing genera and species. Therefore, it seems unwise to formally designate species.

Manning and Felder (1991) examined living American callianassids and recognized that *Callianassa*, as formerly defined, embraced a diverse assemblage of species. They erected three new genera to accommodate some of the species and assigned others to previously named genera. Although many of the important characters for recognition of the genera allied to *Callianassa* typically are not preserved in fossils, there are important differences in the major claw that are taxonomically useful.

Species of *Cheramus* do not exhibit a hook on the merus of the major claw and have a carpus that is triangular in outline, whereas species of *Callianassa* s.s. bear a prominent hook near the base of the merus and have a square or rectangular carpus. The propodi and dactyli of the chelae are similar in the two genera. Therefore, if only these two distal elements are preserved, it would be impossible to assign material to one of the two genera with confidence. However, one of the specimens from the Cárdenas Formation is represented by a preserved articulated major claw, and it can be noted (Figure 3.1) that the carpus is triangular. One edge of a poorly preserved merus shows no hook. For this reason, the Cárdenas callianassids of this type are referred to *Cheramus*. This represents the first notice of this genus in the fossil record.

Based upon the same criteria, *Callianassa symmetrica* Feldmann and Zinsmeister, 1984, might better be referred to *Cheramus*. The material basis for that species was collected from an erratic boulder from McMurdo Sound, Antarctica, inferred to be Eocene in age. Certainly, the fossil species referred to the Callianassidae are in need of intensive study and revision.

Genus PROTOCOLLIANASSA Beurlen, 1930

PROTOCOLLIANASSA sp.

Figure 3.2, 3.3

Referred material.—Specimens catalogued as IGM-3303, 3305, 3309, and 3310, collected from locality 2615, are deposited in the Museo de Paleontología, Universidad Nacional Autónoma de México, and CM 35029, collected from locality 2615, is deposited in the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

Remarks.—Species of *Cheramus*, and for that matter *Callianassa* s.l., can be distinguished from those of the related genus, *Protocallianassa*. Mertin (1941, p. 199) suggested that *Callianassa* s.l. and *Protocallianassa* differ in at least two ways. The carpus-propodus joint of the major cheliped in *Callianassa* lies at a right angle to the long axis of the segments of the limb whereas that joint is inclined at approximately 120 degrees to the long axis in *Protocallianassa*. The distal surface of the hand bears a prominent re-entrant just above the fixed finger in most species in the former genus, and the same area tends to lack a re-entrant in most species of *Protocallianassa*. Although these characters have not been applied consistently by systematists and some, including Glaessner (1969), have stated that the two genera cannot be distinguished with confidence, Manning (personal commun.) does believe that the angle of the carpus-propodus joint is a reliable character. We concur. Certainly, there are two distinct populations of callianassid claws in the Cárdenas Formation, based upon this feature, and those with the inclined joint are referred to *Protocallianassa*.

Infraorder BRACHYURA Latreille, 1803

Section PODOTREMATA Guinot, 1977

Subsection DROMIACEA Guinot, 1977

Superfamily DAKOTICANCROIDEA Rathbun, 1917

Family DAKOTICANCRIDAE Rathbun, 1917

Genus DAKOTICANCER Rathbun, 1917

DAKOTICANCER AUSTRALIS Rathbun, 1935

Figure 4.1–4.5

Referred material.—FCMP/N1-1088 is deposited in the Museo de Paleontología of the Facultad de Ciencias, Universidad Nacional Autónoma de México; IGM-3301, 3302, 3304, 3307, 3308, and 6236–6243 are deposited in the Museo de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México; and CM 35030–35040 are deposited in the Section of Invertebrate Paleontology, the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

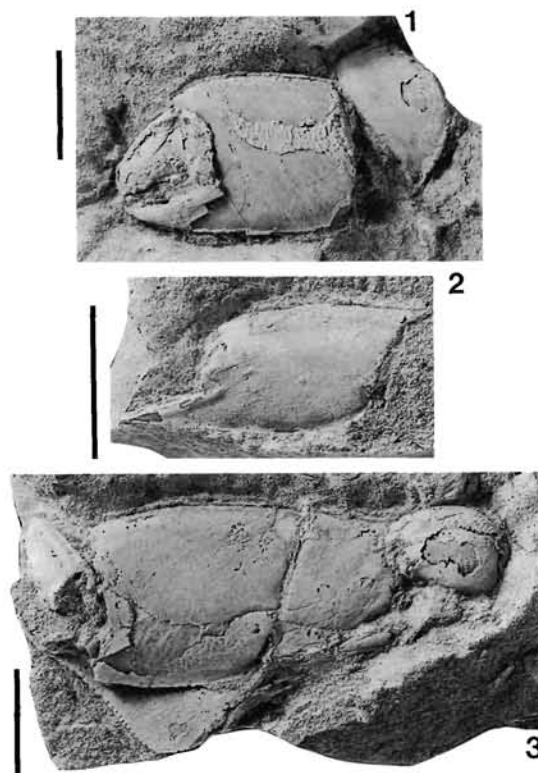


FIGURE 3—Callianassid shrimps. 1, *Cheramus* sp., IGM-3311, showing outer surface of left major chela. 2, outer surface of left chela of *Protocallianassa* sp., IGM-3310. 3, outer surface of left major chela, including merus, carpus, propodus, and dactylus, IGM-3309. Scale bars equal 1 cm.

Localities.—Specimens were collected at three localities, IGM-2615, IGM-2616, and IGM-2617, in the Cárdenas Formation in San Luis Potosí State, México.

Remarks.—Specimens of *Dakoticancer australis* are interpreted to be exuviae. Most specimens show some degree of deformation of the carapace. This could be the result of lateral compression, or, most probably, deformation of the weak exuviae as they were filled and covered by the fine mud in which they were buried. In some specimens, the ventral portion is crushed, and dislocation of epimeral sutures is evident (Bishop, 1986a). However, proportions and carapace features were preserved well enough to assign the specimens to *Dakoticancer australis*.

Previously, dakoticancrid crabs from Mexico had been reported exclusively from the Maastrichtian Potrerillos Formation, where Vega and Feldmann (1991) recognized *Dakoticancer australis*. Since that report, more than 40 complete carapaces referable to this species have been collected. Until the identification of the species in San Luis Potosí State, this was the southernmost report for *D. australis* in North America. The presence of this species in the Cárdenas Formation expands the paleobiogeographic range for the family and for the genus *Dakoticancer* to east-central Mexico. Although the distance between Upper Cretaceous deposits of the Potrerillos Formation and the Cárdenas Formation is not great, about 400 km, it does represent a latitudinal increase in range of about 4 degrees.

Dakoticancrids in Maastrichtian deposits from Mexico are comparatively sparse as compared to some localities in the United States, such as in the Coon Creek Formation. Bishop (1986b)

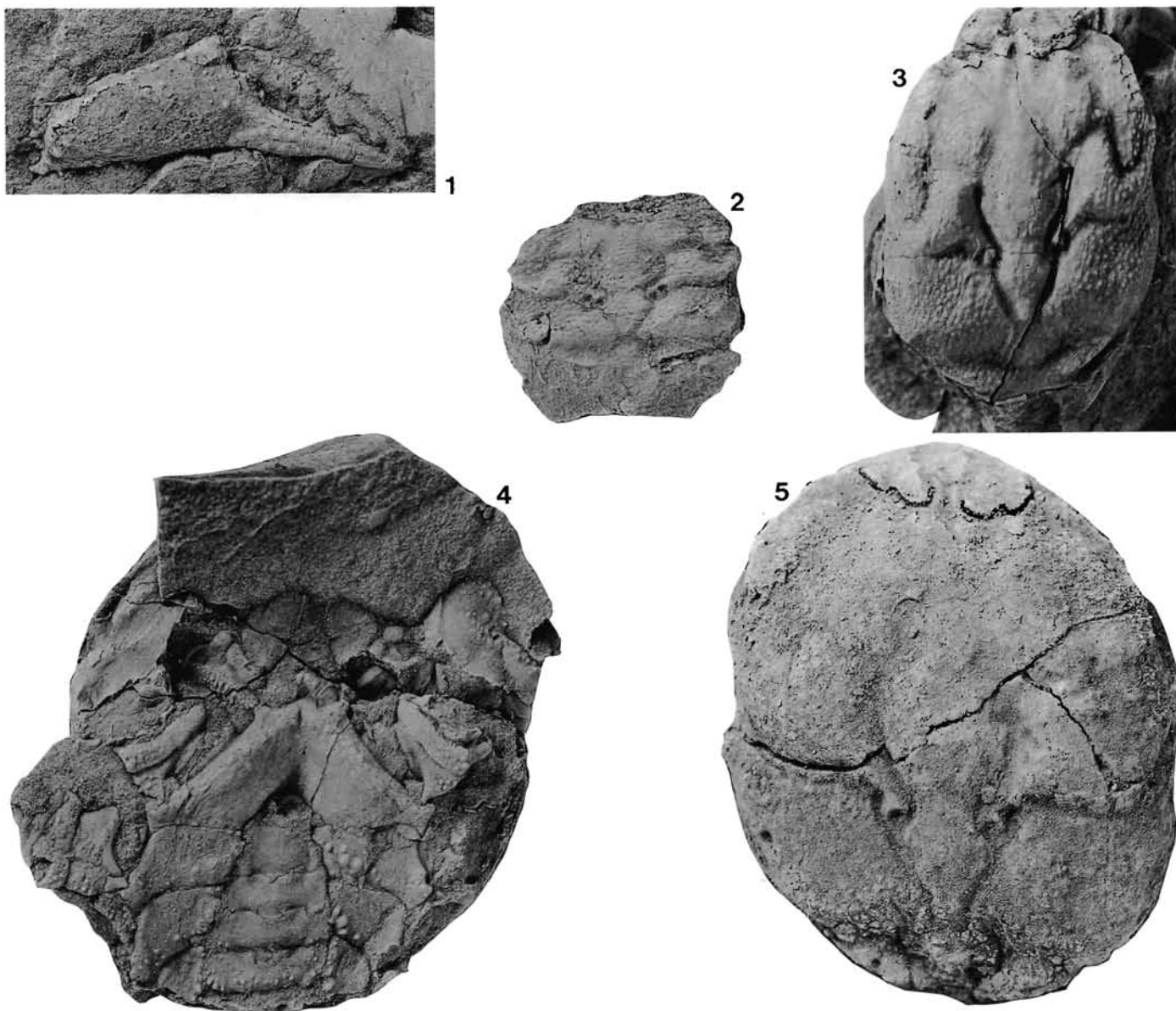


FIGURE 4—*Dakoticancer australis* Rathbun. 1, outer surface of right chela, IGM-3302. 2, cast of dorsal surface of undistorted carapace, CM 35030. 3, dorsal surface of deformed carapace, CM 35038. 4, 5, ventral and dorsal surfaces of deformed carapace, IGM-3301. Scale bar equals 1 cm.

reported 637 specimens from that unit. In one outcrop of the Potrerillos Formation, Vega and Feldmann (1991) found evidence that *D. australis* molted within burrows. This observation has not been repeated in the Cárdenas Formation, possibly due to different molting behavior, or, more likely, to different taphonomic histories.

Bishop (1988a) observed that Late Cretaceous dakoticancrid crabs from North America exhibited a relatively high degree of endemism, with limited overlap of the boundaries between distinct taxa. These species inhabited shallow marginal marine environments of the epicontinental seaway and the Gulf Coastal region. Occurrence of *Dakoticancer australis* from the Cárdenas Formation confirms Bishop's conclusions with respect to paleobiogeography and habitat of dakoticancrids. Presence of *D. australis* in northeastern Mexico was expectable, in view of the distribution of this species in the Mississippi Embayment (Bishop, 1983).

Late Cretaceous paleogeography for this portion of Mexico is still unclear. First pulsations of the Laramide Orogeny resulted in uplift of the Sierra Madre Oriental to the east and northeast of the Cárdenas depocenter. A physical barrier may have formed and isolated Cárdenas crab populations that inhabited shallow marginal environments. The regressive phase that ended at the closure of the Cretaceous Period may have affected these populations, reducing habitat areas (Beurlen, 1931), resulting, in many instances, in extinction of the taxa.

Section HETEROTREMATA Guinot, 1977
 Superfamily PORTUNOIDEA Rafinesque, 1815
 Family CARCINERETIDAE Beurlen, 1930
 BRANCHIOCARCINUS n. gen.

Type species.—*Branchiocarcinus cornatus* n. sp.

Diagnosis.—Carapace hexagonal to inverted trapezoidal, one-

fourth wider than long, widest portion in anterior portion of carapace. Dorsal surface bears two oblique ridges and one posterior straight ridge. Deeply impressed cervical groove extends posteriorly and medially from anterolateral corners. Surface smooth. Two large anteriorly curved sharp spines, forming widest portion of carapace at level of epibranchial ridges, delimit anterolateral from posterolateral margins. Anterolateral margins slightly curved. Posterolateral margins straight and steep, posteriorly convergent to gently concave posterior margin. Small, transverse protogastric, and central plateau-like mesogastric region, extending anteriorly in narrow, parallel-sided projection, does not reach anterior margin. Hepatic lobes small, protuberant. Metagastric region a posterior steep slope behind protogastric ridge. Transversely elongated urogastric lobe at central portion of carapace. Posterior small transverse ridge defines transverse axis of cardiac region. Branchial regions with straight, acute ridges; epibranchial ridges shorter and steeply inclined from cervical groove posterolaterally toward lateral spine; metabranchial ridges longer, less steeply inclined, longest subparallel to posterior margin. Cervical groove deeply impressed, converging posteriorly at central portion of carapace, then becoming straight to converge again behind cardiac ridge.

Etymology.—The generic name refers the broad branchial areas of the carapace, and to the conspicuous epi-, meso-, and metabranchial ridges.

Comparison.—Carcineretid crabs from the Late Cretaceous have been referred to the following genera: *Carcineretes* Withers, 1922; *Cancrinxantho* Van Straelen, 1934; *Ophthalmoplax* Rathbun, 1935; *Woodbinax* Stenzel, 1952; *Longusorbis* Richards, 1975; *Icriocarcinus* Bishop, 1988b; *Mascaranada* Vega and Feldmann, 1991; and probably *Lithophylax* Milne Edwards and Brocchi, 1879. The diagnosis of the Carcineretidae is as follows (Glaessner, 1969, p. R514): "Carapace square to transversely extended, flat to convex longitudinally, with straight lateral margins converging posteriorly, . . . regions well marked by grooves and transverse ridges." There is great variation in carapace shape and ornamentation among the Heterotremata, and many similarities can be observed between our specimen and certain Xanthidae Dana, 1851; Geryonidae Colosi, 1923; and Goneplacidae MacLeay, 1838, especially the Carcinoplacinae Milne Edwards, 1852. However, *Branchiocarcinus* has strong, straight acute ridges and deep grooves, a feature that is not seen in the Goneplacidae. The Xanthidae tend to have a transversely oval carapace, and smoothly rounded lobes. The Geryonidae have a wider front, and the dorsal regions are weakly marked.

Bishop (1988b, p. 247) proposed the existence of two natural groups within the Carcineretidae, based upon carapace shape, rostrum features, and presence or absence of areolation. However, Vega and Feldmann (1991, p. 173) suggested that differentiation between these two groups is not always possible, as the different carcineretid genera may vary, and share many common features. Within the Carcineretidae, *Branchiocarcinus* differs from *Woodbinax* in having a more posterior and more curved protogastric ridge. The cervical grooves of *Woodbinax* seem to begin at the level of the orbital regions. *Carcineretes* is larger, lacks spined lateral margins, and lacks definition of the median anterior extension of the mesogastric region. This same difference distinguishes *Branchiocarcinus* from *Ophthalmoplax*, which is subquadrate in outline and bears a cervical groove that begins at the internal side of the orbital margin. *Ophthalmoplax* has large, acute postorbital spines at the edge of the supraorbital margins, and a pair of straight, anterolateral spines, projecting at the level of the epibranchial regions. *Lithophylax* has less pronounced transverse ridges, and seems to lack lateral spines.

Longusorbis has spiny supraorbital margins, and the dorsal surface of the carapace has many tubercles. Its transverse ridges

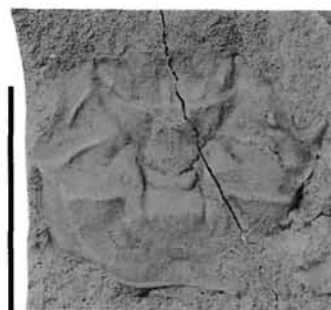


FIGURE 5—Dorsal view of carapace of holotype specimen of *Branchiocarcinus cornatus* n. sp., IGM-6244. Scale bar equals 1 cm.

are not as well marked nor as sharp as those on *Branchiocarcinus*. The same differences can be observed with respect to *Icriocarcinus*, which has an extremely wide, spiny supraorbital margin. The transverse ridges are not as inclined as in *Branchiocarcinus*. *Mascaranada* has a wider protogastric ridge, and lacks spines on the anterolateral margins. *Cancrinxantho* most resembles our specimen; however, it lacks the great anterolateral spines of *Branchiocarcinus*, and the carapace tends to be rectangular. Although shape of cervical groove is very similar, configuration of gastric regions is quite different in these two genera.

BRANCHIOCARCINUS CORNATUS
Feldmann and Vega n. sp.

Figure 5

Diagnosis.—As for genus.

Description.—Carapace hexagonal to trapezoidal inverted, 20 percent wider than long, widest portion above mesobranchial and behind epibranchial areas. Dorsal regions well defined by transverse and inclined acute ridges and deep grooves. Anterolateral margins rounded, delimited by sharp, prominent acute spines that project 1.2 mm anterolaterally from base of mesobranchial ridges. Inner margin of spines slightly curved. Outer margin continuous with straight, converging posterolateral margins, which represent 75 percent of total length. Posterior margin weakly concave, comprising half of maximum width. Posterolateral corners broadly rounded. Anterior margin straight, half of greatest width. Anterolateral corners apparently short and acute, poorly preserved. Protogastric transverse ridge extending distally near cervical groove. Hepatic lobes as small protuberances at inner side of cervical groove, inclined toward anterolateral corners. Epibranchial ridges parallel to anterolateral margins. Mesogastric lobe elevated, forming small, semicircular platform, from which a narrow, well-marked ridge extends anteriorly. Metagastric region a steep slope, delimited posterolaterally by cervical groove. Branchial lobes as small protuberances beside transversely elongated urogastric lobe, located at central portion of carapace. Cardiac region with short transverse ridge bearing rounded crest, slightly behind metabranchial ridges, the most prominent on carapace, subparallel to posterior margin. Mesobranchial ridges inclined 45 degrees with respect to metabranchial ridges, and extending toward metagastric slope, reaching deeply impressed cervical groove, beginning at anterolateral corners, then converging toward base of metagastric slope, and extending in longitudinal straight lines, converging again behind cardiac ridge. Carapace surface smooth.

No appendages, nor ventral portion were preserved.

Measurements and condition of specimen.—Carapace length, 10.6 mm; width, 13.1 mm. The right posterolateral and left anterolateral portions of the carapace are eroded. The specimen shows no deformation, but lack of appendages and ventral por-



FIGURE 6—Cast of part of the dorsal surface of an indeterminate genus and species, probably referable to the Majidae, FCMP/N1-1089. Scale bar equals 1 cm.



FIGURE 7—Dorsal view of carapace of *Costacopluma bishopi* Vega and Feldmann, IGM-3306. Scale bar equals 1 cm.

tion suggests that it is an exuvium preserved in gray-green shale of a marginal lagoon environment.

Type.—Holotype, IGM-6244, is deposited in the Museo de Paleontología of the Instituto de Geología, Universidad Nacional Autónoma de México.

Locality and stratigraphic position.—The holotype was collected at the basal portion of the section at locality IGM-2616 (Montebello) of the Maastrichtian Cárdenas Formation (Figure 2).

Etymology.—The species name refers to the horn-shaped anterolateral spines of the carapace, which seems to be the most conspicuous feature of this species.

Comparison.—As stated above, *Branchiocarcinus cornatus* has similarities with some Xanthidae, Geryonidae, and Goneplacidae, chiefly in carapace shape. However, clear differences can be noted with respect to position and number of anterolateral spines and development of dorsal regions. Within the Carcinetidae, the most similar species is *Cancrinoxantho pyrenaicus* Van Straelen (1934), from the Upper Cretaceous deposits of Spain, of which there is only one specimen, deposited in the Dalloni Collection, at Marsella (Solé and Via, 1989, p. 25). It differs from *B. cornatus* in having a nearly rectangular carapace shape, three pairs of posterolateral spines, and a much wider supraorbital margin, which is divided into three lobes. Although its epi- and mesobranchial ridges are directed posterolaterally, they are not as inclined as in *B. cornatus*. *Cancrinoxantho pyrenaicus* lacks a metagastric slope, and the fingerlike projection of the mesogastric region is shorter than in *B. cornatus*.

Superfamily ?MAJOIDEA Samouelle, 1819

Family ?MAJIDAE Samouelle, 1819

Genus and species indeterminate

Figure 6

Description.—Moderately small crab, pyriform outline, widest in mesobranchial region; moderately vaulted longitudinally and transversely. Regions well defined, swollen, separated by deep depressions. Entire surface coarsely pustulose.

Frontal and anterolateral regions missing. Lateral margin smoothly convex, attaining greatest carapace width at level of mesobranchial swelling. Width at level of epibranchial swelling about 75 percent maximum width. Posterolateral corner well defined, strongly convex. Posterior margin smoothly and gently concave, bordered by well-defined raised rim which continues at least onto posterior portion of lateral margins.

Metagastric region an ovoid swelling, longer than wide, about

23 percent maximum width. Urogastric region poorly defined, separated from mesogastric region by weak constriction. Cardiac region elongate oval swelling about 27 percent maximum width. Intestinal region elongate, well defined by lateral sulci, widest at midlength. Epibranchial and mesobranchial regions prominent swellings separated by a moderately broad depression extending from lateral margin posteriorly then curving anteriorly to terminate at narrow posteromedial protuberance of epibranchial lobe. Metabranchial region reduced, transversely elongate.

Entire surface ornamented by relatively coarse, uniform-sized pustules, about six pustules per square mm.

Measurements.—Length, greater than 13.6 mm. Maximum width, doubling width from midline to right margin, 12.2 mm. Width of posterior margin, doubling width from midline to right margin, 9.7 mm.

Referred specimen.—The sole specimen upon which the above description is based is a partial mold of the exterior, FCMP/N-1089, deposited in the Museo de Paleontología, Facultad de Ciencias, Universidad Nacional Autónoma de México.

Locality and stratigraphic position.—The specimen was collected from the Cárdenas Formation, at locality IGM-2615, San Luis Potosí State, Mexico.

Remarks.—The specimen forming the basis for this description differs markedly from other decapods collected in the Cárdenas Formation. The coarse, pustulose ornamentation, the definition of regions as swollen areas separated by narrow depressions, and the relative size and configuration of the preserved regions are all bases for distinction. The overall pyriform outline, inferred from the change in width along the branchial margins, further documents distinction.

Unfortunately, the specimen cannot be assigned with any confidence to a taxon below the level of infraorder. It is possible that the specimen belongs in the Prosopidae, perhaps close to *Rathbunopon* Stenzel. Relative proportions of the carapace regions do not seem to permit placement in any of the presently known genera, however.

The overall appearance of the carapace, with inflated regions and pyriform outline, most strongly suggests placement with the spider crabs, in the Majidae. We suggest that this is the most likely placement but we do so with caution. The Cretaceous record of majid crabs is very limited (Glaessner, 1969) and the Cárdenas specimen does not readily conform to any of the previously described Cretaceous spider crabs. In order to assign the specimen confidently to the Majidae, it will be necessary to find specimens in which at least the frontal region and the orbital areas are preserved.

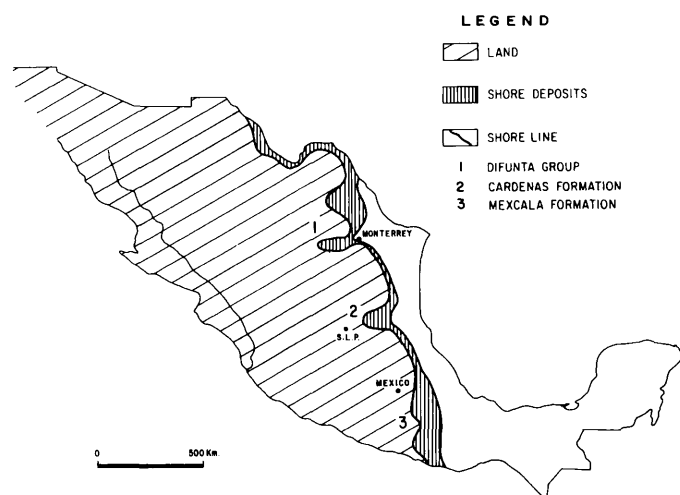


FIGURE 8—Inferred shoreline of the Gulf coast of Mexico during Maastrichtian time, based upon distribution of shore deposits (Cserna, 1976).

Section THORACOTREMATA Guinot, 1977
 Superfamily OCYPODOIDEA Rafinesque, 1815
 Family RETROPLUMIDAE Gill, 1894
 Genus COSTACOPLUMA Collins and Morris, 1975
 COSTACOPLUMA BISHOPI Vega and Feldmann, 1992
 Figure 7

Referred specimen.—A single specimen, IGM-3306, was collected from locality 2616.

Remarks.—Two species of *Costacopluma* have been recognized in Mexico, *C. mexicana* Vega and Perrilliat-Montoya, 1989, from the Potrerillos Formation in Nuevo Leon, Mexico, and *C. bishopi* in the Mexcala Formation from Guerrero, southern Mexico. Both units are Maastrichtian in age. Although the latter was described solely on juvenile specimens, Vega and Feldmann (1992) suggested that the two species could be distinguished on the basis of the angularity and ornamentation of the transverse carinae, which are characteristic of the genus, and carapace outline. *Costacopluma mexicana* exhibits distinct, flattened, pustulose crests whereas those of *C. bishopi* are smoother and more rounded. The outline of the former tends to be more angular than that of *C. bishopi*. Based upon these criteria, the Cárdenas specimen must be referred to the latter species.

Costacopluma seems to be an important component of near-shore marine deposits in the Maastrichtian of Mexico. Indeed, recent work on fossil crabs from Greenland (Collins and Rasmussen, 1992), as well as work in progress on crabs from Brazil and Argentina (Feldmann and others), suggests that the genus has a much wider distribution than previously recognized.

PALEOBIOGEOGRAPHY

The potential and limits of fossil decapod occurrences in small sample sizes were broadly discussed by Feldmann (1990). There is no doubt that the presence of one organism in a fossil assemblage represents a clue in proposing paleobiogeographic models. However, one must take care not to extend such conclusions too far beyond the data.

In this case, occurrence of dakoticancrid crabs in the Cárdenas Formation of east-central Mexico expands the paleobiogeographic range for that family, and for the genus *Dakoticancer*, far to the south from where members of Dakoticancridae were previously described, the Northern Atlantic Coastal Plain (Weller, 1905), Western Interior Seaway (Bishop, 1981), Southern

TABLE 1—List of species at localities of the Potrerillos Formation, where *Dakoticancer australis* has been collected.

Species	IGM-2444	IGM-1582
Phylum Porifera		
<i>Cliona</i> sp.	x	
Phylum Cnidaria		
<i>Siderastrea</i> sp.	x	
Phylum Mollusca		
Class Gastropoda		
<i>Architectonica (Granosolarium) voragiformis</i> Stephenson	x	
<i>Turritella vertebroides</i> Morton	x	x
<i>T. triliria</i> Conrad		x
<i>Pugnellus densatus</i> Conrad		x
<i>Gyrodos abyssinus</i> (Morton)	x	
<i>Gyrodos</i> sp.		x
<i>Stantonella</i> sp.	x	
<i>Pyropsis</i> sp.	x	x
Class Cephalopoda		
<i>Eutrephoceras planoverter</i> Stephenson	x	x
<i>Baculites ovatus</i> Say		x
<i>B. undatus</i> Stephenson		x
<i>Baculites</i> sp.	x	x
<i>Solenoceras</i> sp.	x	
<i>Sphenodiscus pleurisepta</i> (Conrad)	x	x
Class Pelecypoda		
<i>Nuculana chatfieldensis</i> Stephenson		x
<i>Nucula</i> sp.	x	
<i>Nemodon</i> sp.		x
<i>Cucullaea (Idonearca) capax</i> (Conrad)		x
<i>Glycymeris</i> sp.		x
<i>Pinna laqueata</i> Conrad	x	x
<i>Inoceramus</i> sp.		x
<i>Anomia argentaria</i> Norton		x
<i>Paranomia scabra</i> (Morton)	x	
<i>Pecten</i> sp.	x	
<i>Neithea youngi</i> Myers	x	
<i>Arctostrea aguilerae</i> Böse	x	
<i>Pycnodonte mutabilis</i> (Morton)	x	
<i>Exogyra costata</i> Say	x	x
<i>Lopha</i> sp.	x	
<i>Trigonia castrovillensis</i> Stephenson	x	
<i>Trigonia</i> sp.		x
<i>Crassatella</i> sp.	x	
<i>Trachycardium eufaulense</i> (Conrad)		x
<i>Pachycardium</i> sp.		x
<i>Leptosolen biplicatus</i> Conrad		x
<i>Linearia</i> sp.		x
<i>Veniella conradi</i> (Morton)	x	
<i>Aphrodina</i> sp.	x	
<i>Cyprimeria coonensis</i> Stephenson	x	
<i>Panopea decisa</i> Conrad		x
<i>Pholadomya occidentalis</i> Morton	x	x
<i>P. coahuilensis</i> Imlay		x
<i>P. tippiana</i> Conrad	x	
Phylum Annelida		
<i>Hamulus</i> sp.	x	
Phylum Arthropoda		
<i>Callianassa</i> sp.		x
Phylum Bryozoa		
<i>Conopeum</i> sp.		x
Phylum Echinodermata		
<i>Hemiaster bexari</i> Clark	x	
<i>Micraster (Plesiaster) americanus</i> Stephenson	x	

Atlantic Coastal Plain (Rathbun, 1923), Northern Mississippi Embayment (Bishop, 1983), and Southern Mississippi Embayment or northeastern Mexico (Vega and Feldmann, 1991). The presence of dakoticancrid crabs in east-central Mexico was somewhat unexpected as the *Dakoticancer australis* populations from the Maastrichtian in northeastern Mexico (Vega and Feldmann, 1991) are represented by relatively few specimens compared with the large sample sizes of the Late Cretaceous Western Interior and Gulf and Atlantic Coastal Plains.

TABLE 2—List of species at localities of the Cárdenas Formation, where *Dakoticanter australis* has been found.

Species	IGM-2615	IGM-2616	IGM-2617
Phylum Cnidaria			
<i>Trochocyathus</i> sp.	x		
Phylum Mollusca			
Class Gastropoda			
<i>Turritella vertebroides</i> Morton	x	x	x
<i>T. potosiana</i> Böse	x	x	
<i>T. trilira</i> Conrad	x	x	
<i>Turritella</i> sp.	x	x	x
<i>Drepanochilus</i> sp.	x	x	x
<i>Anchura lamari</i> (Stephenson)	x		x
<i>Anchura</i> sp.	x		x
<i>Puanellus densatus</i> Conrad	x		
<i>Gyrodes supraplicatus</i> Conrad	x	x	
<i>Gyrodes</i> sp.			x
<i>Polinices</i> sp.	x		x
<i>Euspira rectilabrum</i> (Conrad)	x		x
<i>Stantonella riplejana</i> Conrad	x		x
<i>Stantonella</i> sp.	x		
<i>Pyrifusus</i> sp.	x	x	
<i>Deussenia</i> sp.		x	x
<i>Dolicholatus</i> sp.			x
<i>Graphidula</i> sp.			x
<i>Fusinus</i> sp.			x
<i>Pyropsis proxima</i> Wade		x	
<i>Pyropsis</i> sp.	x	x	x
<i>Volutoderma</i> (Longoconcha) sp.	x		
<i>Volutomorpha</i> sp.		x	
<i>Liopleplum leioderium</i> Conrad	x		
<i>Beretra</i> sp.	x		x
<i>Epitonium pondi</i> Stephenson			x
Class Cephalopoda			
<i>Eutrephoceras</i> sp.		x	
<i>Solenoceras</i> sp.		x	
<i>Scaphites</i> sp.		x	x
Class Pelecypoda			
<i>Nucula</i> sp.	x		x
<i>Cucullaea</i> (<i>Idonearca</i>) <i>neglecta</i> (Weller)	x		
<i>C. (Idonearca) capax</i> (Conrad)		x	
<i>Glycymeris</i> sp.	x		
<i>Pinna lacueata</i> Conrad	x	x	
<i>Inoceramus</i> sp.	x		
<i>Paranomia scabra</i> (Morton)			x
<i>Neitheia youngi</i> Myers		x	x
<i>Ostrea plumosa</i> Morton			x
<i>Arctostrea aguilerae</i> Böse			x
<i>Pycnodonte mutabilis</i> (Morton)		x	x
<i>Exogyra costata</i> Say		x	
<i>Trigonia castrovillensis</i> Steph.	x		
<i>Trigonia</i> sp.			x
<i>Lucina</i> sp.		x	x
<i>Crassatella vadosa</i> <i>manorensis</i> Stephenson	x	x	x
<i>C. vadosa</i> <i>bexarensis</i> Stephenson	x		x
<i>Crasstella</i> sp.		x	
<i>Cardium</i> sp.	x		x
<i>Cardium</i> (<i>Granocardium</i>) <i>bowenae</i> (Stephenson)			x
<i>Cardium</i> (<i>Granocardium</i>) sp.		x	
<i>Pachycardium</i> sp.		x	
<i>Leptosolen biplicatus</i> Conrad	x		
<i>Veniella conradi</i> (Morton)	x		
<i>Veniella</i> sp.			x
<i>Legumen</i> sp.	x		
<i>Corbula</i> sp.	x		x
<i>Panopea subplicata</i> Shumard		x	
<i>Panopea</i> sp.		x	
<i>Pholadomya occidentalis</i> Morton		x	
<i>Pholadomya</i> sp.	x		
<i>Cuspidaria</i> sp.			
Phylum Annelida			
<i>Serpula</i> sp.			x
<i>Hamulus</i> sp.	x		x

TABLE 2—Continued.

Species	IGM-2615	IGM-2616	IGM-2617
Phylum Arthropoda			
<i>Cheramus</i> sp.		x	
<i>Protocallianassa</i> sp.		x	
<i>Costacopluma bishopi</i> Vega and Feldmann			x
<i>Branchiocarcinus cornatus</i> n. sp.			x
Majidae, genus indet.			
Phylum Echinodermata			
<i>Hemiaster bexari</i> Clark			x
<i>Hemiaster</i> sp.	x	x	x
<i>Micraster</i> sp.		x	

IGM-2615 = La Calzada; IGM-2616 = Montebello (Ca-22, Ca-26, Ca-27); IGM-2617 = Santa Barbarita.

In the Maastrichtian Potrerillos Formation of northeastern Mexico, the most abundant decapod is *Costacopluma mexicana*, which has been collected in large numbers and which exhibits excellent preservation (Vega and Perrilliat-Montoya, 1989). Recent discovery of *C. bishopi* Vega and Feldmann from the Maastrichtian Mexcala Formation of southern Mexico and now the discovery of this species in the Cárdenas Formation lead to a preliminary conclusion that the retroplumids were also significant elements in the Maastrichtian clastic sequences of the Gulf Coastal Plain of Mexico (Vega and Feldmann, 1992).

The record for Late Cretaceous carcineretid crabs is frequently scarce and fragmentary. Descriptions of the following species were based on single specimens: *Woodbinax texanus* (Stenzel, 1952); *Cancrinxantho pyrenaicus* (Van Straelen, 1934); and *Mascaranada difuntaensis* (Vega and Feldmann, 1991). This is not to say that populations of such species were small but that, at least for the Maastrichtian of Mexico, preservation of these

TABLE 3—List of shared genera between Potrerillos and Cárdenas Formations, at localities with *Dakoticanter australis*.

Genus	Potrerillos Fm.	Cárdenas Fm.
Phylum Mollusca		
Class Gastropoda		
<i>Turritella</i>	x	x
<i>Pugnellus</i>	x	x
<i>Gyrodes</i>	x	x
<i>Stantonella</i>	x	x
<i>Pyrifusus</i>	x	x
Class Cephalopoda		
<i>Eutrephoceras</i>	x	x
<i>Solenoceras</i>	x	x
Class Pelecypoda		
<i>Nucula</i>	x	x
<i>Cucullaea</i>	x	x
<i>Glycymeris</i>	x	x
<i>Pinna</i>	x	x
<i>Inoceramus</i>	x	x
<i>Paranomia</i>	x	x
<i>Neitheia</i>	x	x
<i>Arctostrea</i>	x	x
<i>Pyonodonte</i>	x	x
<i>Exogyra</i>	x	x
<i>Trigonia</i>	x	x
<i>Crassatella</i>	x	x
<i>Pachycardium</i>	x	x
<i>Leptosolen</i>	x	x
<i>Veniella</i>	x	x
<i>Panopea</i>	x	x
<i>Pholadomya</i>	x	x
Phylum Annelida		
<i>Hamulus</i>	x	x
Phylum Echinodermata		
<i>Hemiaster</i>	x	x
<i>Micraster</i>	x	x

TABLE 4—List of shared species between Potrerillos and Cárdenas Formations, at localities with *Dakoticaner australis*.

Species	Potrerillos Fm.	Cárdenas Fm.
Phylum Mollusca		
Class Gastropoda		
<i>Turritella vertebroides</i> Morton	x	x
<i>T. trilira</i> Conrad	x	x
<i>Pugnellus densatus</i> Conrad	x	x
Class Pelecypoda		
<i>Cucullaea (Idonearca) capax</i> (Conrad)	x	x
<i>Pinna laqueata</i> Conrad	x	x
<i>Paranomia scabra</i> (Morton)	x	x
<i>Neitheia youngi</i> Myers	x	x
<i>Arctostrea aguilerae</i> Böse	x	x
<i>Pycnodonte mutabilis</i> (Morton)	x	x
<i>Exogyra costata</i> Say	x	x
<i>Trigonia castrovillensis</i> Stephenson	x	x
<i>Leptosolen biciplicatus</i> Conrad	x	x
<i>Veniella conradi</i> (Morton)	x	x
<i>Pholadomya occidentalis</i> Morton	x	x
Phylum Echinodermata		
<i>Hemiaster bexari</i> Clark	x	x

populations was biased by biologic and/or taphonomic factors. Decapod families described for the Upper Cretaceous deposits from Mexico include: Erymididae (Rathbun, 1935); Dakoticaneridae (Vega and Feldmann, 1991); Portunidae (Rathbun, 1930); Carcineretidae (Vega and Feldmann, 1991); Xanthidae (Bishop, 1988b); and Retroplumidae (Vega and Perrilliat-Montoya, 1989; Vega and Feldmann, 1992). Dakoticanerid and carcineretid crabs are both present in the Potrerillos and Cárdenas Formations.

Thus, the decapod faunas of the Potrerillos and Cárdenas Formations are quite similar to one another. In fact, the similarity extends well beyond the decapods. Tables 1–4 provide a comparison of the invertebrate faunas at localities in the two formations from which *Dakoticaner australis* has been collected. The two formations share 51 percent of the genera and 21 percent of the species, based upon totals from the most speciose formation, the Cárdenas. These faunal similarities, coupled with the lithologic similarities, suggest that the two formations were part of the same nearshore depositional complex lying along the eastern Maastrichtian paleocoastline of Mexico (Figure 8). More detailed paleobiogeographic and paleoecologic conclusions must await more field work and more complete specimens.

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