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VERTEBRATES OF THE EL PELILLAL LOCALITY (CAMPANIAN, CERRO DEL PUEBLO FORMATION), SOUTHEASTERN COAHUILA, MEXICO

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ABSTRACT—A new locality named El Pelillal (Cerro del Pueblo Formation, Late Cretaceous, Campanian) in the southeastern area of the State of Coahuila, México yeilds an assemblage of vertebrates that is important for correlation due to its frequent occurrence in other localities along the Cerro del Pueblo Formation outcrops. It is located in the Municipio de Ramos Arizpe, Coahuila. Among the vertebrates found are: fishes (Lepisosteidae; Amiidae [cf. Melvius sp.]); turtles (Trionychidae, Chelydridae [cf. Protarchelydra sp.]), kinosternoidea [cf. Hoplochelys sp.], an undetermined kinosternoid genus, and ?Pleurosternidae [Compsemys viucta]); Crocodilians Neosuchia (Goniopholididae); and Eusuchia and a pterosaur (Pterodactyloidae). Dinosaurs found include a hadrosaurine hadrosaur, a new Troodontidae, and other indeterminate theropods. The El Pelillal Locality is interpreted as a freshwater environment possibly influenced by tides. The fauna of the El Pelillal locality, Cerro del Pueblo Formation, resembles southern U.S. Campanian-Maastrichtian faunas but lacks the prevalence of baenid, adocid, Basilemy and Nanhsuingchelyd turtles.

INTRODUCTION

The studied fossil record of Mesozoic terrestrial vertebrates in México is restricted to two main areas, the northern states bordering the United States of America, and the central and south-central parts of the country (Appendix 1).

Although some preliminary research work has been done with the vertebrates of the Cerro del Pueblo Formation in southeastern Coahuila (e.g., Hernández, 1992; Hernández and Kirkland, 1993; Hernández et al., 1995; Kirkland and Aguillon-Martinez, 1995; Rodríguez-de la Rosa, 1996), little is known about the vertebrates of the Cretaceous of this part of southern North America. In this paper the fossil vertebrates found in the El Pelillal locality are described because they are representative of those found elsewhere in the Cerro del Pueblo Formation outcrops, thus having local and regional importance for correlation.

Age and Locality

The Cerro del Pueblo Formation outcrops in the southeastern area of the State of Coahuila, México (Fig. 1). According to stratigraphic position, lithological features and the presence of the bivalve *Exogyra ponderosa* this sedimentary sequence is Late Cretaceous (Latest Campanian) in age (Murray et al., 1962; McBride et al., 1974; Vega-Vera et al., 1990). Among the fossils found in this sedimentary unit are angiosperm re-productive organs (flowers, fruits and seeds) and leaves, invertebrates, vertebrates and vertebrate coprolites (Cevallas-Ferriz et al., 1992; Cevallos-Ferriz and Rodríguez-de la Rosa, 1994; Rodríguez-de la Rosa and Cevallos-Ferriz, 1993, 1994, 1995; Rodríguez-de la Rosa, 1996).

The new locality named El Pelillal (Rodríguez-de la Rosa, 1996) is located at 101°7′W, 26°7′N in the northern face of Sierra Pinta, approximately 6 km from the nearby Francisco Coss Railroad Station, in the Municipio de Ramos Arizpe, Coahuila (Fig. 1). This locality is representative of the rich vertebrate fauna of the Cerro del Pueblo Formation.

MATERIAL AND METHODS

Most of the vertebrate material presented here was collected in a summer field season in 1995. Measurements were taken with the aid of a Scala vernier caliper. Since the material is black photographs were made after dusting with ammonium chloride and utilizing a NIKON (S-3) camera. The material is housed in the paleontological collection of the Instituto de Geología of the Universidad Nacional Autónoma de México under the collection numbers IGM-7657 to IGM-7716.

Institutional Abbreviations—IGM, Instituto de Geología, Ciudad Universitaria, Universidad Nacional Autónoma de México, México.

SYSTEMATIC PALEONTOLOGY

Class OSTEICHTHYES Huxley, 1880
Subclass ACTINOPTERYGI Cope, 1887
Order LEPISOSTEIFORMES Hay, 1929
Family LEPISOSTEIDAE Cuvier, 1825

Material—The most abundant material found are scales (67), but two operculums, twelve vertebrae, some of them fragmentary, and few skull fragments have also been collected. Material IGM-7657–IGM-7662.

Occurrence—El Pelillal locality and Agua de la Mula and Rincón Colorado areas.

Description—The scales (Fig. 2A) are rhomboidal and have an occasionally-pitted enameloid covering, they range in size from 0.99 to 2.01 cm (mean of 1.34 cm) in length and 0.61 to 1.38 cm (mean of 0.94 cm) in width; five subcircular scales (Fig. 2B, C) are 0.99 to 1.41 cm (mean of 1.12 cm) in diameter. The scarce skull fragments found have an ornamentation of fine tubercles (Fig. 2D). The vertebral centra are opisthocoelous (Fig. 2E, F), they preserve scars of the transversal hypophyses and range from 0.69 to 1.27 cm in length (mean of 1.02 cm). Of the two operculums, the most complete one measures 1.5 cm anteroposteriorly and its ornamentation is formed by fine tubercles that radiate posterocentrally (Fig. 2G).

Remarks—Ganoid scales, opisthocoelous vertebrae, and operculums shaped and ornamented like those reported here are found in the Family Lepisosteidae (Wiley, 1976). Additionally, most of the skull fragments found have the typical lepisosteid ornamentation of fine tubercles (Wiley, 1976). Five of the scales found are subcircular and they are thought to be scales of the...
middle lateral line of lepisosteids (Rodríguez-de la Rosa, pers. obs.). Until more material is collected and studied, the known material is referable to Lepisosteidae. However, the opercular is similar to *Lepisosteus* sp. in the general outline and surface ornamentation pattern and differs from *Atractosteus* in being more circular in outline and with a more finely tuberculate ornamentation (cf. Wiley, 1976:figs. 29, 30, 51, 52).

Fossil gars are known in North America from the Cretaceous to the Recent (Wiley, 1976). Other Cretaceous lepisosteid remains from Mexico comparable to the material presented here were reported from the State of Sonora (Lucas and González-León, 1993).

**Order Amiiformes Huxley, 1861**
**Family Amiidae Bonaparte, 1841**
**Genus *Melvius* Bryant, 1987**
cf. *Melvius* sp.

**Material**—Three complete vertebral centra (two of them in articulation) and vertebral fragments (Fig. 2H–J). Material IGM-7663–IGM-7664.

**Occurrence**—El Pelillal locality and La Rosa and Rincón Colorado areas.

**Description**—The vertebral centra are amphicoelous and strongly ossified. Both monospondylous and diplospondylous amiid centra are represented. The complete monospondylus vertebral centra are represented by two articulated centra, each one trapezoid in shape, with rectangular scars of the attachment of the neural arch and aortal facets and circular scars of the bas-apophyses. The centra are 1.94 cm dorsoventrally and 2.83 cm laterally.

The single diplospondylus centrum (Fig. 2H, I) is nearly sub-triangular in shape in anterior or posterior views. Dorsally the centrum has four scars of attachment with the neural arches (Fig. 2I). Each scar has the shape of an isosceles triangle with the base located toward the border (anterior and posterior) of the centrum. Each pair of scars correspond to a neural arch, one shared by this centrum and an anterior-located one and another neural arch was shared with a posterior-located centrum. It presents rectangular scars of the aortal facets and circular scars of the bas-apophyses. The areas between the bas-apophyses are concave ventrally and laterally (Fig. 2H). This diplospondylus centrum is 2.10 cm dorsoventrally, 2.78 cm laterally and 1.33 cm anteroposteriorly.

Most of the centra are fragmented radially (Fig. 2J). The anteroposterior length ranges from 0.97 cm to 2.04 cm, with a mean dimension of 1.38 cm.

**Remarks**—The amphicoelous, strongly ossified, monospondylus and diplospondylus vertebral centra are identified as amiid (Bryant, 1987; Patterson, 1994). The size and the concave surfaces between the aortal facets and the scars of the bas-apophyses make it comparable to *Melvius* (Fig. 2H; Bryant, 1987). This new material represents the southernmost occurrence of this genus in North America (Bryant, 1987), although more and complete material is needed for a better understanding of the taxonomic relationships this large amiid of the El Pelillal locality.
width. The costal plates (Fig. 3C, D) are incomplete but the anteroposterior width varies from 1.66 to 2.57 cm. The most conspicuous plastron fragment represents a portion of a left hypoplastron (Fig. 3E). The proximal end of a right femur is typically trionychid (Fig. 3F, G), and is characterized by having a hemispherical head 0.74 cm in diameter (Fig. 3F). Both the trochanter major and trochanter minor, are connected by a bony web enclosing a wide ventral fossa (Fig. 3G).

Remarks—The characteristic sculpture pattern of pits and ridges of the shell, and features of the portion of the right femur are found only within the Trionychidae (cf. Hay, 1908; Meylan, 1987). Due to the limited material a generic assignment cannot be made.

The presence of trionychids in the Late Cretaceous of Coahuila was noted first by Aguilera (1896) near División Peyotes in the Municipio de Parras; other Late Cretaceous trionychids have been also reported from the Campanian of the Cabullona Group in the State of Sonora, México (see Appendix 1).

Family Chelyridae Agassiz, 1857
Genus *Protochelydra* Erickson, 1973
cf. *Protochelydra* sp.

Material—Four peripheral plates (Figs. 4A–D). Material IGM-7671 to IGM-7674.

Occurrence—The El Pelillal locality.

Description—Two posterior peripheral plates (Fig. 4A, B) with uprolled distal borders, ranging from 2.79 to 2.97 cm anteroposteriorly by 2.19 to 3.29 cm mediolaterally. These posterior peripheral plates have a rugose surface, and well marked dermal sulci. Two other peripheral plates (Fig. 4C, D) have a concave, smooth, dorsal surface. They range from 2.04 to 2.89 cm anteroposteriorly, by 1.49 to 1.93 cm mediolaterally.

Remarks—According to Hutchison (pers. comm., 1995) these peripheral plates show similarities in size and general shape to those of *Protochelydra*. However, more material is needed before a close identification can be made.

Family Kinosternidae Baur, 1893
Genus *Hoplochelys* Hay, 1908
cf. *Hoplochelys* sp.

Material—Eight complete neurals, two costals, and peripheral and plastron fragments (Fig. 5A–I). Material IGM-7675 to IGM-7683.

Occurrence—All the areas considered in this study (Table 1).

Description—The neurals (Fig. 5A–C) possess a strong middle longitudinal keel and smaller lateral keels that diverge anteriorly. Some of these neurals suggest a rather radial pattern of the keels over the carapace (e.g., Fig. 5B, H). Some of the neurals are six-sided or typically coffin-shaped, these elements are 2.47 cm (2.23 to 2.95 cm) anteroposteriorly and 1.70 cm in width (1.44 to 1.79 cm). However, in other neurals the width (1.81 to 2.45 cm, mean of 2.10 cm) is greater or equal to the anteroposterior dimension (1.63 to 2.83 cm, mean of 2.09 cm), and they appear to be four-sided (e.g., Fig. 5B). In these more rectangular elements the radial pattern of the keels over the carapace is more evident. Two small neurals of equal length–width dimensions (1.37 cm by 1.30 cm respectively), similar to those presented here, were found at the La Rosa area (Fig. 5H, I). Some of the costals found possess longitudinal keels that vary in number from two to four (Fig. 5E, F). Some neurals and costal fragments present the characteristic abrupt dermal sulci of *Hoplochelys* (Fig. 5B, D). A single peripheral plate characterized by a thick margin, dermal sulci, and presence of longitudinal keels is also present (Fig. 5G).

Remarks—Based on the similarities in carapace elements, such as keeled plates and abrupt or rough dermal sutures, it is

FIGURE 2. Fish remains from the El Pelillal locality. A-G, Lepisosteidae; H-J, Amiidae. A, ganoid scale (IGM-7657); B, C, nearly circular scales interpreted as scales of the middle lateral line (IGM-7658, IGM-7659 respectively); D, lepisosteid skull fragment (IGM-7660); E, F, lepisosteid vertebra in dorsal (E) and ventral (F) views (IGM-7661); G, opercular in lateral view (IGM-7662). H, I, Amiid diplospondylous vertebral centrum in anterior (H) and dorsal (I) views (IGM-7663); J, vertebral centrum in medial section (IGM-7664). Scale bars equal 0.5 cm.
identified as cf. Hoplochelys sp. However, some neural plates have a distinctive radial pattern of the keels (Fig. 5B, H), suggesting the presence of a new kinosternoid taxon perhaps related to Hoplochelys. The small size of the neural elements from the La Rosa area (Fig. 5H, I) suggests juvenile individuals of this taxon. However, it is premature to suggest a nesting area for this turtle based on the limited evidence. This material represents the first report of this genus for the Cretaceous of México.

Kinosternoidea gen. indet.

Material—A single neural plate, four costals, nine peripherals, two pygals and five plastron fragments (Fig. 6A–K). Material IGM-7684 to IGM-7694.

Occurrence—The El Pelillal locality.

Description—Generally all the carapace elements have a smooth surface. A single subrectangular neural shows two small projections that represents the other two sides of a six-sided chelonian neural. In addition to its smooth surface this element possesses two small parallel, medial, longitudinal ridges.

Four costals (Fig. 6B, C), 1.59 to 1.87 cm mediolaterally (mean of 1.76 cm) by 0.85 to 1.75 cm anteroposteriorly (mean of 1.18 cm), have well defined grooves left by the sulci of the dermal scutes (two laterals and one marginal).

There are two kinds of peripherals (Fig. 6D–G). The first type has blunt distal margins, show sulci impressions of between three and four dermal scutes (Fig. 6D, E). In addition, these peripherals present sutures, of the plastral joint, in the medial sides suggesting lateral peripherals, and some of them represent transition peripherals (Fig. 6D). The second type has an uprolled distal margin, show sulci impressions of between four dermal scutes (Fig. 6F, G), and are interpreted as posterior peripherals.

The pygal (Fig. 6I) is subrectangular, 0.99 cm in length by 1.98 cm in width. It has a V-shaped anterior margin and an uprolled posterior margin.

The hypoplastron fragments have a smooth surface and sutural impressions of the abdominal and femoral dermal scutes (Fig. 6H).

Some of the elements, either carapace and/or plastron fragments, of this turtle taxon bear marks that are interpreted as tooth marks due, perhaps, to predation and/or scavenging (Fig. 6J, K); these tooth marks have surfaces where the bone is damaged and/or crushed.

Remarks—This kinosternoid turtle belongs to an undescribed group of small kinosternoid-like turtles (Hutchison, pers. comm., 1998). The material presented here does not allow a more accurate identification.

Several fungal and/or parasites may leave pits in the shell similar to those presented by some of the elements of this turtle material, however due to the presence of damaged bone in the surfaces of the marks, the suggestion that these are tooth marks seems more likely.

Fossil kinosternoids in México are mainly known from Late Tertiary sediments (Barrios-Rivera, 1985).
FIGURE 5. cf. *Hoplochelys* sp. A–C, neurals (IGM-7675–7677); D–F, costal plates (IGM-7678–7680); G, marginal scute (IGM-7681); H, I, neural plates collected in the La Rosa area that are thought to belong to young individuals (IGM-7682 and IGM-7683 respectively). Scale bars equal 0.5 cm.

FIGURE 6. Kinosternoida. A, neural plate with two longitudinal ridges (IGM-7684); B, C, costal plates (IGM-7685 and IGM-7686 respectively); D, E, peripheral plates with blunt distal margins (IGM-7687 and IGM-7688 respectively); F, G, peripheral plates with uprolled distal margins (IGM-7689 and IGM-7690 respectively); H, fragment of a right hypoplastron (IGM-7691); I, pygal (IGM-7692); J, K, carapace (J, IGM-7693) and plastron (K, IGM-7694) fragments bearing tooth marks occasioned by a predator or a scavenger. Scale bars equal 0.5 cm.
Family Incertae sedis

**Compsemys victa** (Leidy, 1856)

**Material**—Two neural plates, two costal plates and a hypoplastron fragment (Fig. 7A–E). Material IGM-7695 to IGM-7699.

**Occurrence**—The El Pelillal locality and Agua de la Mula areas.

**Description**—The shell ornamentation pattern is composed of compactly arranged small pustulae. The neural plates are six-sided (Fig. 7A, B), and vary from 1.59 to 1.70 cm anteroposteriorly by 1.68 to 1.80 cm in maximum width. The costal plates are subrectangular in shape and have well-defined dermal sulci (Fig. 7C, D). The single left hypoplastron fragment has a similar ornamentation of compactly arranged small pustulae (Fig. 7E).

**Remarks**—Ornamentation pattern is characteristic of *Compsemys victa* (Hay, 1908:pl. 34, figs. 2, 3). A similar sculpture pattern is also seen in *Helopanoplia* (Hay, 1908:pl. 88, figs. 4, 5), but this taxon is a trionychid and lacks scales and the pustulae are of a larger size and not densely arranged as in *C. victa* and the El Pelillal material.

Hay (1910) and Gaffney (1972) placed *Compsemys* within the Baenidae based on characters of the mesoplastra, but Hutchinson and Archibald (1986), due to the mesoplastral weak characters, stated this taxon as Incertae sedis. However, Hutchison (pers. comm. 1998) places *Compsemys victa* within ?Pleurosternidae.
Order CROCODYLIFORMES Clark, in Benton and Clark, 1988
Suborder NEOUCHIA Benton and Clark, 1988
Family GONIOPHOLIDIDAE Cope, 1875

Material—A single tooth crown, a sacral vertebra, and a fragmented osteoderm are known (Fig. 8A–C). Material IGM-7700 to IGM-7702.

Occurrence—The El Pelillal locality and La Rosa and Rincon Colorado areas.

Description—The tooth crown is 3.64 cm in height, it is nearly cylindrical, with a blunt tip and it has longitudinal striae (Fig. 8A). The sacral vertebrae is 2.39 cm anteroposteriorly. It presents a flat anterior face while the posterior one is rather slightly concave (Fig. 8B). The osteoderm seems to be circular, but is fragmented (Fig. 8C). It has an unpitted area parallel to its margin.

Remarks—The features mentioned for the tooth crown are characteristic of goniopholidids (Lucas, 1992). The osteoderm has similarities to those of these neosuchians and compares positively with osteoscutes identified as goniopholidids (e.g., those in Lucas, 1992). The vertebra is platycoelous indicating a goniopholidid relationship and is similar to the first of the two sacral vertebrae of these neosuchians (Mook, 1933). This material represents the first report of this group of neosuchians in Mexico.

Suborder EUSUCHIA Huxley, 1875

Material—Fragments of osteoderms, two procoelus dorsal and cervical vertebral centra and a distal end of a left femur (Fig. 8D–J). Material IGM-7703 to IGM-7707.

Occurrence—The El Pelillal locality and the Agua de la Mula area (Fig. 8J), its entire dorsal surface is coarsely pitted. The preserved portion of the interorbital plate is moderately broad and flat, with the lateral edges not uprolled. The widest, posterior part of the frontal is 2.49 cm in width and bears a completely sutured border, the least width is 1.51 cm between the orbits. The posterior border seems not to participate in formation of the anterior border of the supratemporal fenestrae, thus, probably allowing contact between the parietal and postorbital which is suggestive of an eusuchian affinity, although it lacks the uprolled lateral edges of the frontal (Norell and Clark, 1990).

Remarks—Among the crocodilians, the procoelous cervical and dorsal vertebrae are diagnostic to the Eusuchia (Norell and Clark, 1990; Clark and Norell, 1992).

The rugose surface of the sutures between the centrum and neural arch suggest immature individuals (Brochu, 1996).

Although primitive eusuchians lack keeled osteoderms, and even some mesosuchians (e.g., Bernissartia) had osteoderms with a pair of keels (Norell and Clark, 1990), one of the osteoderms of El Pelillal locality could be identified as eusuchian due to the presence of a weakly developed dorsal keel. It is also likely for the fragmentary femur, although more material is need for corroboration.

Recovering more complete material will shed more light on the evolution of eusuchians during the Late Cretaceous. The material represents the first report of Eusuchia from Coahuila, and the second from Mexico (Lucas and González-León, 1993; Appendix 1). Other Mesozoic crocodiles from Mexico are known from the Late Cretaceous of Baja California (Lillegraven, 1976) and from the Early Cretaceous of Puebla, but the former is of unknown affinity and the later seems to be a mesosuchian.

Class ARCHOSAURIFORMES Huene, 1946
Order PTEROSAURIA Kaup, 1834
Suborder PTERODACTYLOIDEA Plieninger, 1901

Material—A single proximal end of a left tibia (Fig. 9). Material IGM-7708.

Occurrence—The El Pelillal locality.

Description—The specimen represents a portion, 3.08 cm in length, of the proximal end of a left tibia, the bone is crushed and the epiphyseal end is incompletely ossified.

Remarks—The bone is crushed due probably to the pneumaticism of pterosaur bones. The ossification degree of the epiphyseal end suggests an immature individual (Fig. 9). The material is referred to Suborder Pterodactyloidea and is com-
FIGURE 11. Troodontidae. II-2 pes phalanx in right lateral (A), dorsal (B), proximal (C), and distal (D) views (IGM-7710).

TABLE 1. Faunal list of the vertebrates found in the El Pelillal Locality (Campanian, Cerro del Pueblo Formation, EPL). A, B, C and D are other areas where the formation outcrops thus permitting a correlation of the vertebrate taxa found in the El Pelillal Locality with the vertebrates found in other sites along the Cerro del Pueblo Formation. A longitudinally-ribbed coprolite morphotype has been added for the same correlative purpose. EPL, El Pelillal Locality; A, Presa San Antonio area; B, Agua de la Mula area; C, La Rosa area; D, Rincón Colorado area.

<table>
<thead>
<tr>
<th>Order</th>
<th>Family</th>
<th>Material</th>
<th>Occurrence</th>
<th>Description</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ornithischia</td>
<td>Hadrosauridae Cope, 1869</td>
<td>Hadrosaurid dinosaurs</td>
<td>all areas</td>
<td>seem robust</td>
<td>in contrast to those more dorsally situated found in Dromaeosauridae.</td>
</tr>
<tr>
<td>Ornithischia</td>
<td>Cerro del Pueblo Formation</td>
<td>ready to Pteranodon sp. in size (compare with Eaton, 1910: pl. 27, figs. 2, 5a).</td>
<td>A local</td>
<td>robust</td>
<td>in contrast to those more dorsally situated found in Dromaeosauridae.</td>
</tr>
<tr>
<td>Ornithischia</td>
<td>Neosuchia</td>
<td>Eusuchia</td>
<td>A local</td>
<td>robust</td>
<td>in contrast to those more dorsally situated found in Dromaeosauridae.</td>
</tr>
<tr>
<td>Ornithischia</td>
<td>Troodontidae Gilmore, 1924</td>
<td>Troodontidae</td>
<td>A local</td>
<td>robust</td>
<td>in contrast to those more dorsally situated found in Dromaeosauridae.</td>
</tr>
<tr>
<td>Ornithischia</td>
<td>Theropoda Indet. family</td>
<td>Theropoda Indet. family</td>
<td>A local</td>
<td>robust</td>
<td>in contrast to those more dorsally situated found in Dromaeosauridae.</td>
</tr>
</tbody>
</table>
Another fact that supports this interpretation is that in most dromaeosaurids the ginglymous arch is more robust and projects more dorsally than in troodonts; a situation that does not occur in the specimen from Coahuila. In a bivariate plot of the shaft diameter against the dorsoventral width of the ginglymous arch, two groups can be distinguished, each formed by a family (Troodontidae and/or Dromaeosauridae; Fig. 12). The plotting of the measurements taken from the phalanx from the El Pelillal Locality, place it within the Troodontidae. In the case of *Troodon formosus* (Fig. 12C), it is closer to Dromaeosauridae due to the robustness of the II-2 pedal phalanx (i.e., the shaft diameter is more or less similar to the dorsoventral width of the ginglymous arch).

It has been suggested that a taxonomic relationship exists between Troodontidae and Dromaeosauridae due to the presence of a raptorial second digit (Osmolska and Brasbold, 1990). However, it has been mentioned that this feature could have evolved as a convergence (Currie and Peng, 1993). Of the elements that form the second raptorial digit, the second phalanx is the most conspicuous and diagnostic (apart from the ungual, Fig. 13).

Currie and Peng (1993) suggested that the degree of ossification in some troodonts is not suggestive of the stage of maturity, and that size or differences in proportion are not diagnostic for the troodontid species. The II-2 phalanx of El Pelillal locality is very slender compared to that of other troodonts (Fig. 14). The proximal border of the heel is complete and the two small processes form part of this structure representing a remarkable difference with respect to other troodontid species and to Dromaeosauridae (Fig. 13). Therefore, the presence of a new species of a medium-sized troodont is suggested.

Suborder **Theropoda** Marsh, 1881

*Indeterminate family*

**Material**—Pes phalanges (complete and fragmentary), as well as few fragments of manus phalanges and caudal vertebrae (Fig. 15A–F). Material IGM-7711 to IGM-7716.

**Occurrence**—All the areas considered.

**Description**—A first phalanx (Fig. 15A) measures 1.76 cm in dorsal length and 1.88 cm in ventral length. Laterally, the phalanx is 1.04 cm in width at the proximal articular surface and 0.93 cm at the ginglymous arch. Dorsoventrally the proximal portion of the shaft is 0.94 cm and 0.86 cm distally. A second phalanx (Fig. 15B) is 1.77 cm in dorsal length and 2.17 cm in ventral length. Laterally, the phalanx is 1.11 cm in width at the proximal articular surface and 0.96 cm at the ginglymous arch. Dorsoventrally, the proximal portion of the shaft is 1.12 cm and 0.99 cm distally. Both phalanges have ginglymoid distal articulation and foveae centrally situated with respect to a moderate ginglymous arch.

A complete distal portion of a manus phalanx (Fig. 15C) measures 0.81 cm in dorsoventral length and 0.64 cm laterally. It has a ginglymoid distal articulation and foveae centrally situated, and the ginglymous arch is projected slightly dorsally.

A fragmented caudal vertebral centrum (Fig. 15D) measures 1.12 cm dorsoventrally and 1.14 cm laterally and only preserves the scars of the attachment with the neural arch.

The distal portion of two other pes phalanges of two different
DISCUSSION

The El Pelillal locality contains a moderately diverse Late Cretaceous (Campanian) vertebrate assemblage, from which some of the taxa are reported for the first time from Mexico (Table 1).

Some of the vertebrate taxa reported occur with other vertebrates known from other, previously described, areas of the Cerro del Pueblo Formation (Table 1), and are important for the correlation of previously unidentified outcrops of this formation. Among the turtle taxa that support this correlation are Trionychidae and the kinosternoid Hoplochelys, whose remains are found along the Cerro del Pueblo Formation outcrops. Goniocephalid remains are known to occur in the La Rosa and Rincón Colorado areas. In addition to the eusuchian material from El Pelillal locality, remains of these crocodilians are known in the Agua de la Mula and in Rincón Colorado areas. Additional support for correlation is given by the presence in most outcrops of a longitudinally ribbed coprolite morphotype (Table 1).

Further support of the correlation between the fossiliferous outcrops in the Cerro del Pueblo Formation may be given by other vertebrate groups, but more detailed studies are needed before this can be done. For example, hadrosaurid dinosaurs are known in almost all the localities (Table 1), but they cannot be used as correlation tools since their remains are well known from the overlying Cerro Huerta Formation of Maastrichtian age. Similarly, it is necessary to make a definitive identification of the theropod material in order to assess their utility for correlation.

McBride et al. (1971) mentioned that the Difunta Group is the result of deltaic sedimentation in a shallow embayment of what is now the Parras Basin. This embayment was part of the ancestral Gulf of México. The El Pelillal locality is here interpreted as a freshwater environment based on its vertebrate fauna (fishes, turtles, crocodilians, etc.). Most of the reports of lepisosteid fishes have been made from freshwater deposits (Wiley, 1976); however, there are few reports from marine deposits (e.g., Cuvancara and Hoganson, 1993) and even it has been noted that some living species frequent waters of coastal brackish and marine environments (Suttkus, 1963 in Cuvancara and Hoganson, 1993). A similar situation is mentioned for the amsid Melvius (Bryant, 1987).

In addition, most of the fossil trionychids known have been recovered from sediments that represent freshwater environments; however, it is well known that a few extant species enter into brackish coastal waters and they have even been observed in the sea (Hay 1908; Ernst and Barbour, 1989).

The extant representatives of the turtle fauna found in the El
Pelilall locality (Trionychidae, Chelydridae and Kinosternoidea) are mostly freshwater, but some species are known to enter into brackish waters (Ernst and Barbour, 1989). Hutchison and Archibald (1986) suggested that *Compsemys victa* may have preferred fresh and shallow waters.

The crocodylian remains agree with the environments suggested by the turtles. For example, with some exceptions (e.g., *Alligator mississippiensis, A. sinensis*) many living crocodylians live typically in tropical to subtropical ecosystems, inhabiting rivers, lakes, ponds, marshlands, swamps and estuaries (Alcalá and Dy-Liacco, 1989). Thus, in addition to lepisosteoid and amid fishes, a tidal riverine system with a coastline closely situated is suggested by some elements of the reptilian fauna. Other elements (e.g., dinosaurs) were surely hydrodynamically brought to the depositional setting.

The presence of pterosaur remains is interesting because they are frequently found in marine deposits (Wellnhofer, 1978, 1991; Langston, 1981); however, pterosaur remains are also reported from lagoonal or marginal marine deposits, and even, their remains have been found in areas that represent inland desert plains (Bell and Padian, 1994; Kellner, 1994).

Although the fauna of the El Pelilall locality, and in fact that of the Cerro del Pueblo Formation, agrees with a Late Cretaceous age, it shows significant differences from other regional vertebrate faunas of the same age found elsewhere in North America. For example, goniopholidids lived in the Late Jurassic to the Early Cretaceous of Europe and North America. Their Late Cretaceous occurrence known at the moment is from the San Juan Basin in New Mexico, the Aguja Formation of Texas and Karpowits Formation of Utah (Lucas, 1992; Rowe et al., 1992; Hutchison et al., in press). Thus, another Late Cretaceous (Campanian) occurrence of goniopholidids is represented by the material presented here.

The presence of *Compsemys* in the Late Campanian of the El Pelilall locality and in the Fruitland Formation in New Mexico (Hunt and Lucas, 1992, 1993) plus the absence of this taxon in the Campanian of Alberta, Montana and Wyoming and its presence in the Maastrichtian of these last three localities suggests an extending biogeographic area for *Compsemys* through northwestern North America during the Late Cretaceous.

The presence of *Hoplochelys* in the El Pelilall locality and through the Cerro del Pueblo Formation outcrops agree with a Late Cretaceous age due to the fact that this taxon is well known to the Paleocene elsewhere in North America. However, other typical Late Cretaceous taxa are absent in the El Pelilall assemblage, among these are Nanhsiungchelyd turtles, Baenidae, *Basilemys* and *Adocus*, although an isolated neural collected shows similarities to those presented by this later taxon but more material is needed to confirm its presence. Additionally, kinosternid turtles are absent or they are rare in the Late Cretaceous of several North American localities such as Alberta, Montana and Wyoming.

The El Pelilall locality vertebrate fauna differs, respect other localities of similar age in North America, in the kinds and relative abundance of taxa present that make the assemblage, strikingly, more similar to a Paleocene assemblage than to a Campanian one. It has been suggested in particular by the turtle assemblage (McCord, 1996; Hutchison et al., in press; Brinkman, pers. comm., 1998), indicating that the changes from the Cretaceous to the Early Tertiary are most likely a reflection of environmental changes with the turtle assemblages tracking environments.

A preliminary comment that must be mentioned, is that the paleogeographic location of the El Pelilall locality, as seen in aerial photographs, suggests that the preserved fauna developed in a freshwater lacustrine environment close to a small bay in the western margin of the Late Cretaceous epicontinental seaway. However, more paleontological work is needed for the better understanding of the biodiversity, paleobiogeography and the implications of this Cretaceous area of southern North America.

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APPENDIX I.—Localities with Mesozoic terrestrial vertebrates in México.

NORTHERN MEXICO

State of Baja California

Amphibia
Anura
Anuran indet.

Reptilia
Chelonia
Fam. et gen. indet.
Squamata
Fam. et gen. indet.
Crocodilia
Fam. et gen. indet.

Archosauria
Theropoda
Tyrannosauridae
cf. Albertosaurus sp.

?Tyrannosaurid indet.
Ornithomimid indet.

Tyrannosauridae
Troodon formosus
Dromeosauroidae
Saurornitholestes sp.
Dromeosaurus indet.

Ornithopoda
Hadasauridae
?Lambeosaurus laticeps
?Lambeosaurus sp.

Hadasaurinae indet.

Ankylosauria
Ankylosaurus indet.

Nodosauridae
cf. Euplocephalus sp.

Ceratopsia
Ceratopsid indet.

Mammalia
Allotheria
Multituberculata
Neoplaugiaulacidae
Mesodma cf. M. formosa
Eucoelodontidae

?Syrignys sp.

Theria
Metatheria
Marupilia
Didelphoidea
Pediomyidae

Pediomys sp.

Eutheria
Insectivora
Fam. Indet.

Galloxlestes pachymanellaris

B. La Bocana Roja Formation: Campanian (Brodkorb, 1976; Chieppe, 1991; Molnar, 1974);

Archosauria
Theropoda
Fam. indet.

Labocania anomala

?Labocaniasaurid indet.

Hadasauridae indet.

Aves
Enantiornithes
Alectronis antecedens

State of Sonora
A. Snake Ridge Formation: Maastrichtian (Lull and Wright, 1942);

Ornithopoda
Hadasaurid indet.

B. Corral de Enmedio Formation (Cabullona Group): Campanian--Maastrichtian (Taliaferro, 1933; Lucas and Gonzalez-Leon, 1993, 1996); Osteichthyes

Actinopterygii
Amiiformes

Aves

Enantiornithes

Alexorns antecedens

APPENDIX 1.—(Continued)

Archosauria

Theropoda
Tyrannosauridae
cf. Albertosaurus sp.

Ornithopoda
Hadasauridae

Hadasauridae indet.
APPENDIX 1.—(Continued)

Ceratopsia

Ceratopsidae indet.

Theropoda

Tyrannosauridae
cf. Albertosaurus sp.

Ornithopoda

Hadrosauridae


Actinopterygii

Lepisosteiformes

Lepisosteidae

Reptilia

Sauria

Scincomorpha

Teiidae

Chamops segnis

Archosauria

Ornithopoda

Hadrosauridae


Eusuchia

Eusuchia indet.

Archosauria

Ornithopoda

Hadrosauridae

D. El Pelillal Locality, Cerro del Pueblo Formation: Campanian (Rodriguez-de la Rosa, 1996; Table 1).

State of Tamaulipas

A. La Boca Formation, Huizachal Canyon: Middle Jurassic (Clark et al. 1994; Clark et al., 1996; Fastovsky et al. 1995; Reynoso, 1996): Diapsida

Tamaulipasaurus morenoi

Lepidosauria

Sphenodonta

Cynosphenodon huizachalensis

New sphenodontid
cf. Cleosaurus

Archosauria

Crocodyliformes

New crocodyliform 1
New crocodyliform 2

Dinosauria

Ornithischia

Theropoda

Pterosauria

Rhamporphynochond pterosaur

Therapsida

Tritylodontidae

Bocantherium mexicanum

?Ictidosauria

Mammaliaformes

Triconodontidae

„Amphilestidae”

Theria

CENTRAL AND SOUTH-CENTRAL MEXICO

State of Puebla

A. San Felipe Otlaltepec in the State of Puebla: Early Cretaceous (Ferrusquia-Villafranca et al., 1995; Ortega-Guerrero, 1989; Applegate, pers. comm., 1988):

Archosauria

Sauropoda

Sauropod indet. gen.


Lepidosauria

Rhyncocephalia

Sphenodontia

Sphenodontidae

Pantzinusaurus tlayuaensis

Testudines

Crocodilia

?Mesosuchia

Archosauria

Pterosauria

Pterodactyloidea

C. Mitepec: Maastrichtian (Ferrusquia-Villafranca et al., 1993, 1995): Ornithopod and sauropod footprints

State of Michoacán

A. Near Playa Azul: Late Jurassic (Ferrusquia-Villafranca et al., 1978a, b, 1995): Ornithopod and theropod footprints

State of Oaxaca

A. Xochitzlapilco: Middle Jurassic (Ferrusquia-Villafranca et al., 1995, 1996a, b): Sauropod, ornithopod and theropod footprints.