

# Restudy of Permo-Carbouiferous synapsid *Edaphosaurus novomexicanus* Williston and Case, the oldest known herbivorous amniote

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Reexamination of the holotype and the description of new material of *Edaphosaurus novomexicanus* from the Permian-Pennsylvanian Cutler Formation of north-central New Mexico reveals that this species is the most primitive member of the *Edaphosaurus* clade. This assignment, based previously upon supposed plesiomorphies of the postcrania, is supported here by two primitive character states that occur in a derived form in the Texan species of *Edaphosaurus*. The presence of two autapomorphies in *E. novomexicanus* suggests that this species is probably not a morphological relict, as previously supposed, but may be part of a lineage that did not exhibit the level of diversification seen in its probable sister group, the clade of Texan edaphosaurids (*E. boanerges*, *E. cruciger*, and *E. pogonias*).

Un nouvel examen de l'holotype et de la description de nouveau matériel d'*Edaphosaurus novomexicanus* de la Formation de Cutler, d'âge permo-pennsylvanien, du centre-nord du Nouveau-Mexique, révèle que cette espèce représente le membre le plus primitif du clade d'*Edaphosaurus*. Cette assignation, fondée antérieurement sur de prétendues plesiomorphies post-crânielles, est renforcée ici par deux expositions de caractère primitif qui apparaissent dans une forme dérivée dans l'espèce texane d'*Edaphosaurus*. La présence de deux autapomorphies dans *E. novomexicanus* suggère qu'il est probable que cette espèce ne soit pas une relique morphologique, comme on le croyait antérieurement, mais qu'elle fait peut-être partie d'une lignée qui ne montre pas le niveau de diversification rencontré dans son présompu groupe soeur, le clade des édaphosaurides texans (*E. boanerges*, *E. cruciger* et *E. pogonias*).

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## Introduction

Vigorous collecting from the New Mexico redbeds has produced numerous genera and species of reptiles and amphibians endemic to the Four Corners area (Vaughn 1969). Localities in New Mexico, together with those in southeastern Utah and southern Colorado, are recognized as belonging to a vast paleogeographic area distinct from the midcontinental region of Oklahoma and Texas (Vaughn 1969).

*Edaphosaurus novomexicanus*, from the Cutler Formation near Arroyo de Agua in north-central New Mexico, is the only *Edaphosaurus* species known west of Texas. Described briefly by Williston and Case (1913), the holotype consists of a crushed skull, a nearly complete pectoral girdle, and a dozen anterior presacral vertebrae. Numerous fragmentary neural spines from El Cobre Canyon and caudal vertebrae from the type locality have been attributed to this species (Vaughn 1963; Reisz 1986), and several posterior dorsal vertebrae and ribs from Cottonwood Canyon in southern New Mexico have been referred tentatively to *E. novomexicanus* (Vaughn 1969). Because of the paucity of adequate material, the holotype remains the most useful specimen for comparison with other members of the family.

In their extensive review of early synapsids, Romer and Price (1940) remarked that there were no cranial features useful for diagnosing *E. novomexicanus*. They did, however, note that the cervical neural spines do not show the tendency towards enlarged distal ends, as seen in the Texan species, and also noted that there are no crossbars anterior to the sixth member of the series. Because the botanical evidence at the time implied that *E. novomexicanus* was contemporaneous with the oldest known Texan edaphosaurid *Edaphosaurus boanerges*, Romer and Price (1940) considered *E. novomexicanus* a morphological relict.

This review was undertaken after the descriptions of the most primitive edaphosaurid, *Ianthasaurus hardestii* (Reisz and Berman 1986; Modesto and Reisz 1990), demonstrated

that the rarity of lateral tubercles on the cervical vertebrae of *E. novomexicanus* was an autapomorphic feature. A casual examination of the holotype of *E. novomexicanus* revealed that much of the matrix remained on the skull, obscuring many sutures and other cranial features. These observations gave reason to doubt Romer and Price's belief that *E. novomexicanus* was merely a relict, and suggested that further study of the New Mexico species was warranted.

Recently, a scanning electron microscope study of tooth wear by Olson *et al.* (1991) provided strong support for the hypothesis that *Edaphosaurus* was a terrestrial herbivore. Hence, the study of edaphosaurid synapsids is important because this unusual family is one of the few Palaeozoic groups to document the morphological transition from insectivory to herbivory at a time when terrestrial vertebrate herbivores were making their first appearance. Because *E. novomexicanus* is the oldest known member of the genus *Edaphosaurus*, a thorough examination of this species should, therefore, expand our knowledge of this poorly documented but significant interval in the early diversification of amniotes.

In this paper the holotype of *E. novomexicanus* is redescribed. In addition, new postcranial materials, collected from the type locality and attributable to this species, are described. The description of these materials should firmly establish the systematic position of *E. novomexicanus* within the family.

## Systematic palaeontology

Synapsida Osborn 1903

Eupelycosauria Kemp 1982

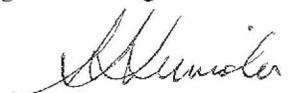
FAMILY Edaphosauridae Cope, 1882

GENUS *Edaphosaurus* Cope, 1882

*Edaphosaurus novomexicanus* Williston and Case, 1913

## Revised diagnosis

Distinguished from other members of the genus by the presence of anisodont tooth plate dentition, with at least one-quarter of the tooth plate teeth having a diameter greater than



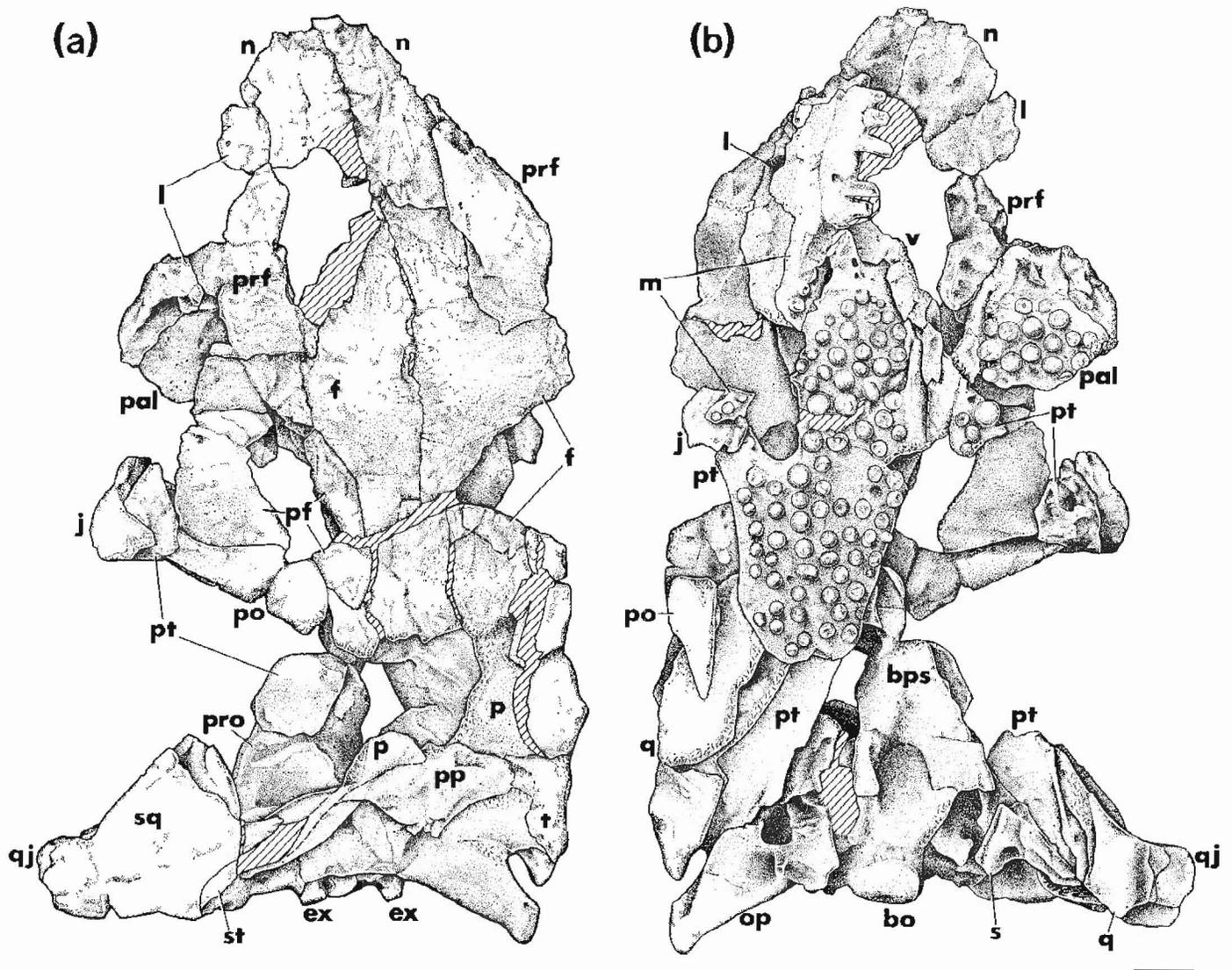


FIG. 1. *Edaphosaurus novomexicanus*, FMNH UC 674 (Field Museum of Natural History, University of Chicago), holotype. Dorsal (a) and ventral (b) views of skull. Abbreviations: bo, basioccipital; bps, basiparasphenoid; ex, exoccipital; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; op, opisthotic; p, parietal; pal, palatine; pf, postfrontal; po, postorbital; pp, postparietal; prf, prefrontal; pro, prootic; pt, pterygoid; q, quadrate; qj, quadratojugal; s, stapes; sq, squamosal; st, supratemporal; t, tabular; v, vomer. Hachure indicates areas of plaster or matrix. Scale = 1 cm.

that of the marginal teeth. Lateral tubercles, or crossbars, are rare on the anterior presacral neural spines. This species retains the primitive state of the frontal lateral lappet, which is approximately one-fifth the length of the frontal at midline. This character is found in a derived form in all other members of the genus for which cranial material is available.

#### Holotype

FMNH UC 674 (Field Museum of Natural History, University of Chicago) originally consisted of a partial skull with braincase, left scapula and cleithrum, right scapulocoracoid and clavicle, 15 anterior dorsal vertebrae (12 of which remain), and a dorsal rib. An associated right humerus and radius were very poorly preserved according to Williston and Case (1913) and, therefore, were not figured in their work; these appendicular elements are not described here. The specimen represents an adult animal, for the vertebral centra are fused to the neural arches.

#### Horizon and locality

Cutler Formation, Permo-Carboniferous. Near Poleo Creek, Arroyo de Agua, Rio Arriba County, New Mexico.

#### Attributed specimens

CM 34910 (Carnegie Museum of Natural History, Pittsburgh), described in this paper, consists of a partial tibia, two metatarsals, phalanges, and several anterior caudal vertebrae; collected from the type locality in 1979 by a field crew composed of members from the Carnegie Museum of Natural History and the University of Toronto.

#### Probable referred specimens

UCLA VP 1641 (University of California, Los Angeles) consists of several neural spine fragments from El Cobre Canyon in north-central New Mexico; collected from the "classic" collecting grounds of El Cobre, these specimens are Late Pennsylvanian in age (Berman *et al.* 1987a, 1987b).

UCLA VP 1719 consists of four closely associated posterior dorsal vertebrae and rib fragments from Cottonwood Canyon in southern New Mexico.

The cranial material of FMNH UC 674 is compared directly with those of better known Texan edaphosaurids because there are few adequate descriptions of edaphosaurid cranial materials. Skulls referred to *E. boanerges* MCZ 1762 and 1680 (Museum of Comparative Zoology, Harvard University) and, to a lesser extent, the holotype of *Edaphosaurus pogonias* AMNH 4009 (American Museum of Natural History, New York) were used for comparative purposes. Both MCZ specimens came from deposits in north-central Texas that are slightly younger than those of the New Mexico material and represent adults with approximately the same skull size as FMNH UC 674. AMNH 4009 was collected from a horizon considerably younger than that of the other material (Clear Fork Group) and represents a much larger animal.

### Description

There has been some minor loss of bone from the skull of FMNH UC 674 since the description by Williston and Case (1913). The left supraorbital region appears to have been originally reconstructed with plaster, but has since been disassembled. It has been reassembled for the present study, without the plaster. The skull appears to have been well preserved initially but many bone surfaces are damaged, especially those of the braincase. Much of this damage can be attributed to the original preparators.

The skull of FMNH UC 674 is crushed dorsoventrally and obliquely to the right (Fig. 1). Only the dorsal surfaces of most of the skull table elements and the ventral surfaces of the palatal elements and the braincase are visible. The premaxilla and the ectopterygoid remain unknown for *E. novomexicanus*. A reconstruction of the skull in dorsal and ventral views is shown in Fig. 2. Data not presently known for the skull of this species were taken from skulls referred to *E. boanerges* and are represented by broken lines in Fig. 2. A study of the cranial anatomy of *E. boanerges* revealed that the palatal tooth plates of *Edaphosaurus* are inclined about 30° posteroventrally to the long axis of the vomers and are slightly concave ventrally. Hence, the palatal tooth plates are foreshortened in ventral view (Fig. 2a). A reconstruction in lateral view is not offered, for the jugal and squamosal are fragmentary and the lacrimal is too distorted to provide a good estimate of skull height. The following redescription notes only characteristics of the holotype that were not identified in the original description.

The nasal (Fig. 1) largely resembles those of other members of the genus, but the sculpturing on the dorsal surface is markedly more rugged than in any other edaphosaurid. The nasal is roughly 75% the length of the frontal at the midline. Slight telescoping of the right nasal has obscured the nature of its suture with the frontal.

As in other early synapsids, the lacrimal occupies the anterior part of the face between the external naris and the orbit (Fig. 1). Despite crushing and loss of bone, the posterior region of the lacrimal of FMNH UC 674 is very similar to that of *E. boanerges* MCZ 1762. This indicates that the lacrimal of *E. novomexicanus* probably contributed to a massive antorbital buttress along with the ventral process of the prefrontal and palatine.

The maxilla (Fig. 1) is similar to that of other *Edaphosaurus*

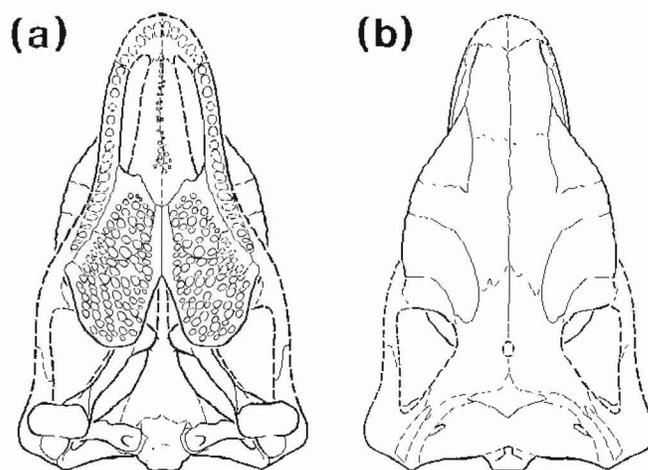


FIG. 2. *Edaphosaurus novomexicanus*. Reconstruction of skull in ventral (a) and dorsal (b) views based upon FMNH UC 674. Broken lines represent bone surfaces or edges taken from *Edaphosaurus boanerges*. Scale = 2 cm.

species. The right maxilla is reasonably well preserved, missing only the part of the posterior process that might have borne about 4 teeth. Hence, the maxilla would have accommodated 18 or 19 teeth. The marginal teeth are roughly cylindrical in form, with slightly swollen distal portions. None retain their apices, making it impossible to determine if the cutting edges of these teeth were inclined relative to the long axis of the tooth row, as seen in *E. boanerges*.

The prefrontal (Fig. 1) differs little from that of the Texan species, except that it is about 15% shorter anteroposteriorly. The ventral process of the prefrontal, quite prominent in *E. boanerges* MCZ 1762, cannot be observed because of extensive crushing. The frontal (Fig. 1) is essentially similar to that of other species of *Edaphosaurus*, except that its lateral lappet remains primitively broad anteroposteriorly, being roughly one-fifth the midline length of the frontal. The anteroposterior breadth of the lappet in *E. boanerges* and later edaphosaurids is slightly less than one-eighth the length of the frontal. The shape of the postfrontal (Fig. 1) is typical of the genus.

The jugal is very poorly preserved (Fig. 1). The suborbital process of the right jugal, missing much of the anterior portion, has been displaced by crushing such that its lateral surface faces ventrally (Fig. 1b). It maintains contact with the posterior tip of the right maxilla, which, when reconstructed, suggests that the posteriormost maxillary teeth project laterally as in the more derived members of the genus.

Both postorbitals are present (Fig. 1). The right element lacks the ventral process and was erroneously identified as the epipterygoid by Williston and Case (1913). It appears certain that the posterior process of the postorbital was overlain only by the parietal. Although relatively shorter than that of *Ianthasaurus*, the posterior process of the postorbital is longer than those of later edaphosaurids in which the squamosal has lost contact with the postorbital. The right postorbital of FMNH UC 674, however, shows no evidence of sutural scarring that would suggest contact with the squamosal. In the more derived Texan species of *Edaphosaurus* the postorbital-squamosal contact has been lost, perhaps in association with the expan-

sion of the lateral temporal fenestra. Since it cannot be determined if *E. novomexicanus* has also lost the contact between the postorbital and squamosal, the status of this character is ambiguous within the *Edaphosaurus* clade.

The parietals are poorly preserved (Fig. 1a), but the preserved portions differ little from those of other *Edaphosaurus* species. The same is true for the squamosals and quadratojugals (Fig. 1), although the fact that they are crushed makes it difficult to identify the squamosal-quadratojugal suture. Only the ventral flange of the left squamosal is present, and it appears no different from that of *E. boanerges*. The surface of the left quadratojugal has been damaged by excessive preparation. The stout, ventral foot of this bone, which formerly sat firmly above the lateral condyle of the quadrate, is visible in ventral view (Fig. 1b). The postparietal is a robust, diamond-shaped element (Fig. 1a). Displaced a little to the right, it appears to have been well preserved originally, but has suffered some superficial damage. Otherwise, the postparietal is not significantly different from that of other *Edaphosaurus* species.

A small sliver of bone (Fig. 1a) occupies a broad notch in the posterior margin of the left squamosal. Presumably, this is all that remains of the supratemporal. It formerly extended anterodorsally between the squamosal and parietal, where only matrix remains. Both tabulars (Fig. 1a) have been reduced by overpreparation to small, thin sheaths overlying the supraoccipital.

A wide but very short fragment of bone is all that remains of the right vomer (Fig. 1b). It has an irregular lateral border with the palatine and a short suture with the pterygoid posteriorly. There is no suggestion of the numerous tiny denticles that cover most of the palatal surface of the vomer in *E. boanerges*.

The palatine is represented by fairly well preserved elements (Fig. 1b). It differs from that of *E. boanerges* MCZ 1762 in two aspects. First, the toothless anterior shelf is about half as large as that in the Texas species, which suggests that the internal nares may have been relatively longer in *E. novomexicanus*. Secondly, the denticulate portion of the palatine of FMNH UC 674 accommodates roughly 25 teeth, as do most later edaphosaurids, except MCZ 1762, which possesses about 35 teeth. These teeth are simple, bulbous pegs of varying diameter. The tips of the teeth are worn, but whether such wear has resulted from normal food processing or postmortem loss is uncertain. The palatal teeth differ from those of *E. boanerges* and *E. pogonias* owing to their highly variable basal diameters and the presence of teeth with diameters greater than those of the marginal dentition. The pterygoid (Fig. 1b) differs from those of other edaphosaurids in that the plate portion of the pterygoid is more parabolic than U-shaped in outline and is slightly more narrow posteriorly. The pterygoid accommodated about 53 teeth. Replacement pits are visible, and a small area that could have borne at least two teeth is, curiously, not scarred by replacement pitting. The ectopterygoid is estimated to have accommodated 11 teeth, bringing the total tooth plate dentition to about 89 teeth.

The epipterygoid is present as a poorly preserved fragment of bone lying on the tooth plate and next to the basiptyergoid process of the basiparasphenoid (Fig. 1b). A thin sheet of bone, sandwiched between the right quadrate and quadrate process of the pterygoid, probably represents the basal portion of this same element.

The quadrate (Fig. 1) differs from those of other members

of the genus in that the condylar portions are wider in transverse dimension and are less robust, with sharply lipped margins.

The complete supraoccipital (Fig. 1a) is indistinguishable from those of other members of the genus. However, the nature of its contact with the tabular is unclear because of the poor preservation of the latter, and the extent of the contribution to the foramen magnum by the supraoccipital is similarly uncertain. The ventral margin bordering the exoccipitals and the foramen magnum appears slightly raised, but not to the extent seen in *E. boanerges* MCZ 1762. A broad and low vertical ridge marks the midline just ventral to the postparietal.

Despite surface scoring, the basioccipital is nearly complete (Fig. 1b). The condyle is more kidney shaped than those of other edaphosaurids, with broadly rounded edges. The ventral median ridge that lies between the anterior processes, weakly developed in sphenacodontids but well-developed in *E. boanerges* MCZ 1762, is absent; it may have been removed during the original preparation. The poorly preserved exoccipitals are indistinguishably fused with the basioccipital (Fig. 1a). The ascending rami are distinct from the adjacent opisthotics, but little else may be noted about the exoccipital except that it is similar to those of other species of *Edaphosaurus*.

Both opisthotics also bear damage due to excessive preparation (Fig. 1). The paroccipital process is slightly more narrow, and its lateral surface less deep dorsoventrally, than that of *E. boanerges* MCZ 1762. The severely marred dorsal surface of the left prootic (Fig. 1a) and the ventral surface of the right (Fig. 1b) are visible, but again, little can be said about the prootic except that it does not appear to differ from those of other *Edaphosaurus* specimens.

Only the parasphenoid portion of the basiparasphenoid complex can be seen (Fig. 1b), and much of this has been lost in preparation. The basal tubera appear quite thin, having been compressed transversely, and beyond the broad convexity of the ventral surface observed for the braincase of *E. boanerges*. The right basiptyergoid process and the base of the cultriform process are present and appear no different from those seen in *E. boanerges* MCZ 1762.

The stapes (Fig. 1b) is indistinguishable from those of other edaphosaurids in which this element is known.

The holotypic series of 12 anterior presacral vertebrae and 1 dorsal rib are shown in right lateral view (Fig. 3); Williston and Case (1913) had figured the anterior seven presacrals and the twelfth vertebra only. These vertebrae are embedded in a plaster block (for display purposes), such that the opposite side could not be examined. Williston and Case (1913) described these elements at length, and only the following additional observations will be noted. The lateral tubercles are not as prominent as figured by Williston and Case (1913) and instead appear as mere nubbins and slight swellings on the lateral surfaces of the neural spines. Only the tubercles of the ninth and tenth presacrals may have been substantial in size, but these have been lost and their bases have been damaged. Long tubercles, however, are found on isolated fragments of dorsal neural spines from the type locality (Williston and Case 1913) and on the lumbar spines from El Cobre Canyon (Vaughn 1963) that have been attributed to *E. novomexicanus*. In all other edaphosaurids, well-developed lateral tubercles are always present on anterior presacral neural spines. As noted by Berman (1979), the neural spines are relatively slender compared with those of other species of *Edaphosaurus*. The dorsal rib, probably associated with the seventh presacral

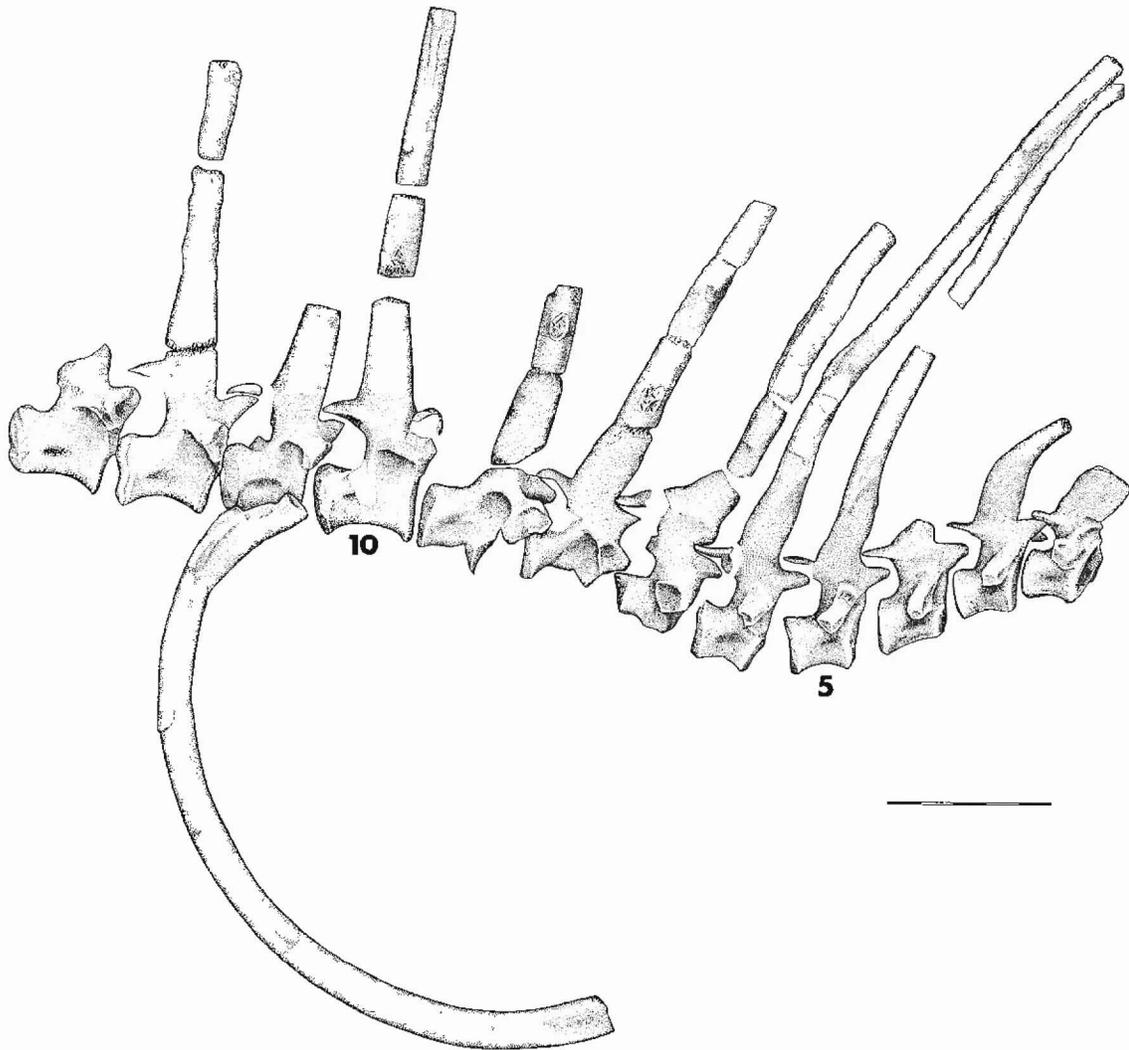


FIG. 3. *Edaphosaurus novomexicanus*, FMNH UC 674, holotype. Articulated series of anterior presacral vertebrae 2–13 in right lateral view, and a dorsal rib. Scale = 5 cm.

vertebra, shows the strong curvature and the reduced tuberculum characteristic of *Edaphosaurus*. Williston and Case (1913) remarked on the presence of several intercentra, but apparently these have been lost.

The pectoral girdle is fairly well preserved in FMNH UC 674. The left cleithrum, maintaining its suture with its associated scapulocoracoid, is missing only the distal 5 mm or so (Fig. 4). It is virtually identical to that of *E. boanerges*, as reconstructed by Romer and Price (1940, p. 524). The clavicle (Fig. 5) also closely resembles that of *E. boanerges*, differing primarily in its slightly smaller size and remarkably more slender dorsal shaft. The latter feature is probably size related; the clavicular shafts of edaphosaurids larger than the New Mexico form are notably thicker relative to shaft length (Romer and Price 1940). The scapulocoracoid (Figs. 4, 6) is represented by the partial left scapular blade and the more complete right element. With the exception of its slightly smaller size, the scapulocoracoid of FMNH UC 674 is similar to those of all species of *Edaphosaurus* in which scapulocoracoids are known to exist.

The new material, CM 34910, consists of diverse elements of the tail and hind limb. The caudal vertebrae (Fig. 7) generally resemble those of other species of *Edaphosaurus*. The

exact location of these vertebrae within the caudal series is uncertain, but there is a slight difference in neural spine morphology between the larger proximal and the smaller, more distal spines. The latter are approximately the same size as the caudal vertebra of *E. boanerges* identified by Romer and Price (1940, p. 524) as the probable 35th member of the series. The proximal caudals display the distinctive leaf-shaped distal ends of the neural spines that are generally attributed to the genus (Fig. 7a), whereas the tips of the more distal caudal neural spines have thickened anterior edges and thinner, rudder-like posterior edges (Fig. 7b). None are laterally bowed, like those of *E. boanerges* figured by Romer and Price (1940). This bowing appears to be an exception among caudals of this species, for examination of caudals referred to *E. boanerges* (Royal Ontario Museum (ROM), uncatalogued) do not exhibit such a deformity. Two caudal intercentra and a single fragmentary haemal spine are present (Fig. 7). The anterior and posterior margins of the intercentra are deeply notched between the bases of the ankylosed haemal arches. The slightly swollen tip of the haemal spine is faintly rugose in the same manner as those of the caudal neural spines. Although a complete haemal arch is not present, the chevrons appear to have been about two-thirds the height of the caudal neural arches.

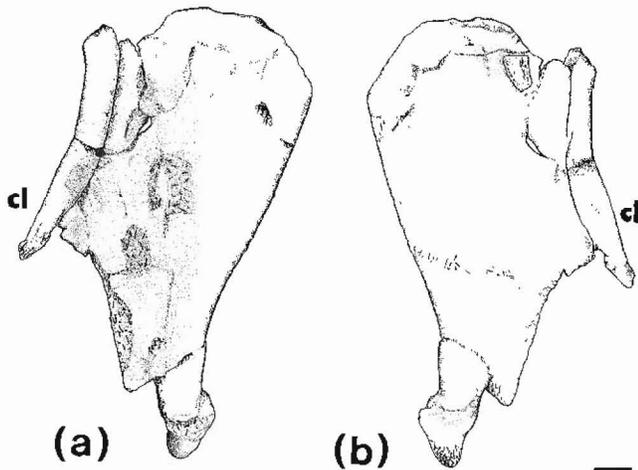


FIG. 4. *Edaphosaurus novomexicanus*, FMNH UC 674, holotype. Lateral (a) and medial (b) views of left cleithrum (cl) and scapular blade. Scale = 1 cm.

The left tibia, of which only the proximal two-thirds remains (Fig. 8), resembles that of other *Edaphosaurus* species, with one exception. The tibia more closely resembles that of a sphenacodontid than that of *E. boanerges* because it has a lateral articulating surface with an elliptical outline (Fig. 8a) instead of a tear-shaped, anteriorly expanded proximal articulating surface (Romer and Price 1940).

Two complete metapodials are present (Figs. 9a, 9b). Edaphosaurid metapodials have not been described heretofore. The shorter and highly flattened metapodial is probably the left first metatarsal, as the proximal and distal articulating surfaces are expanded transversely compared with the other metapodial. It closely resembles that of *Dimetrodon* (Romer and Price 1940) in its strongly lunate lateral border. The larger metapodial is one of the remaining metatarsals, although which one is uncertain. It is indistinguishable from a metapodial (ROM, uncatalogued) that is referred to *E. boanerges*. The proximal end in the New Mexico specimen is slightly larger dorsoventrally than the distal end, which suggests that this bone may be the second metatarsal, if the similarity to *Dimetrodon* is carried further. There are several phalanges, presumably also from the pes; however, no unguals are preserved. These phalanges do not differ greatly from those of other primitive synspsids.

### Discussion

On the basis of the palaeobotanical evidence available to them, Romer and Price (1940) believed that the distinctive New Mexico Arroyo de Agua assemblage was contemporaneous with that of the Wolfcampian Series of north-central Texas. However, recent studies have shown this to be an oversimplification. The Cutler Formation strata of Arroyo de Agua are largely thought to be Wolfcampian in age (Berman *et al.* 1987a, 1987b). However, the lowermost beds of this locality are believed to be Virgilian (Berman *et al.* 1988). Since the exact vertical position of the holotype of *E. novomexicanus* within the Cutler section at Arroyo de Agua is uncertain, its age is best referred to as Permo-Carboniferous. In contrast, the north-central Texas localities (those that have produced edaphosaurid material that have been identified to species) are positioned within the upper half of the Texas Wolfcampian

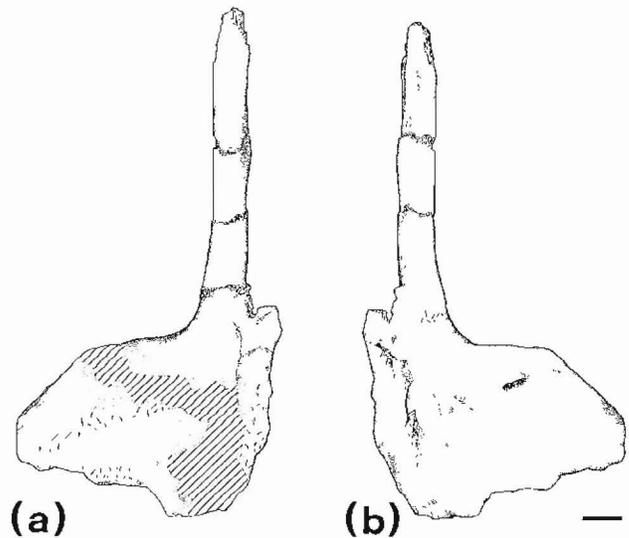


FIG. 5. *Edaphosaurus novomexicanus*, FMNH UC 674, holotype. Posteromedial (a) and anterolateral (b) views of right clavicle. Hachure indicates matrix remaining between the clavicle and associated fragment of interclavicle. Scale = 1 cm.

(Hentz 1988), suggesting that these collecting grounds are younger than the lowermost beds of Arroyo de Agua. Fragments of edaphosaurid neural spines are known from the Cutler Formation of El Cobre Canyon and the Markley Formation (terminology following Hentz 1988) of north-central Texas; the lower portions of both formations have been identified as Virgilian in age. Neural spines from the former formation have been assigned to *E. novomexicanus* (Vaughn 1963), whereas those from the latter, although attributed to *Edaphosaurus*, have not been identified to species (Hook 1989). Unfortunately, it is not clear whether the Markley specimens are of Wolfcampian age, Virgilian age, or both (Hook 1989). Regardless, the stratigraphic ranges of *E. novomexicanus* and the Texan edaphosaurids overlap, albeit only slightly, but certainly not to the extent suggested by Romer and Price (1940). If it is no longer clear that *E. novomexicanus* was a contemporary of the Texan species *E. boanerges*, then Romer and Price's (1940) hypothesis that the New Mexico edaphosaurid is a morphological relict is greatly weakened. Furthermore, their hypothesis that the New Mexico edaphosaurid was the most primitive member of the genus was based in part on the supposed presence of a plesiomorphy not found in the Texan edaphosaurids. This character, the rarity of lateral tubercles on the cervical neural spines of *E. novomexicanus*, now appears to be autapomorphic, for the anterior two-thirds of the dorsal sail of *Ianthasaurus*, the oldest-known, most primitive edaphosaurid, displays normally developed lateral tubercles (Reisz and Berman 1986). Romer and Price (1940) considered the presence of slender cervical neural spines as the second plesiomorphy marking the Arroyo de Agua edaphosaurid as the most primitive species of *Edaphosaurus*. This latter character is indeed primitive for the genus, as the cervical neural spines also taper gradually in *Ianthasaurus* (Reisz and Berman 1986). We consider the use of the term "relict species" to describe *E. novomexicanus* as incorrect in light of the presence of its two autapomorphies. *Edaphosaurus novomexicanus* has undergone the same number of character transformations as its sister lineage (*E. boanerges*

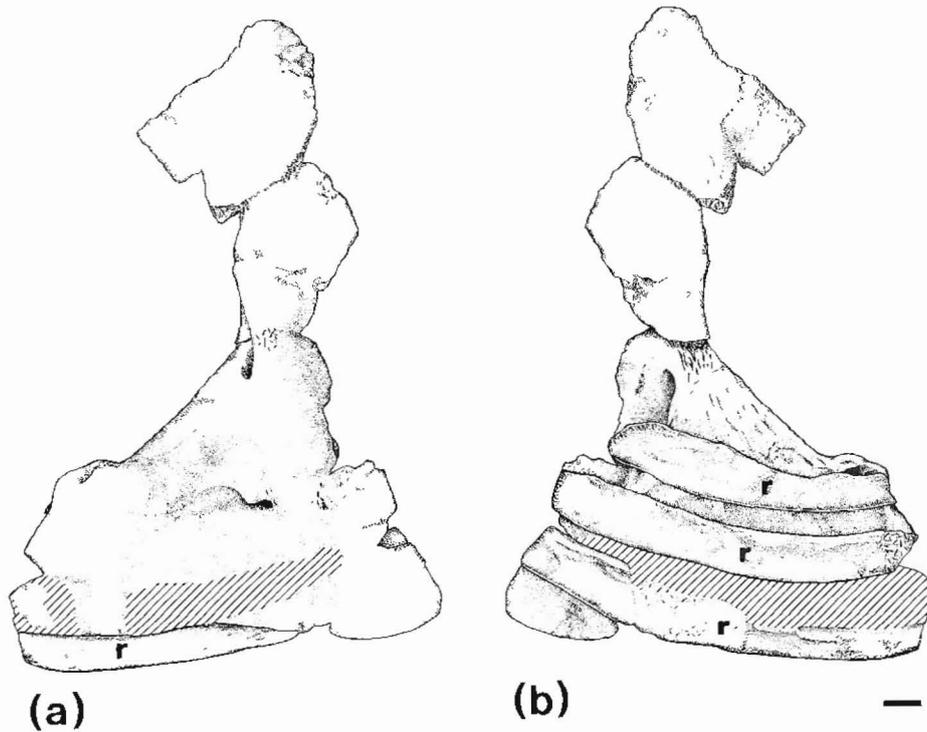


FIG. 6. *Edaphosaurus novomexicanus*, FMNH UC 674, holotype. Lateral (a) and medial (b) views of right scapulocoracoid. Portions of dorsal ribs (r) obscure the ventral half of the medial surface. Hachure indicates matrix and plaster. Scale = 1 cm.

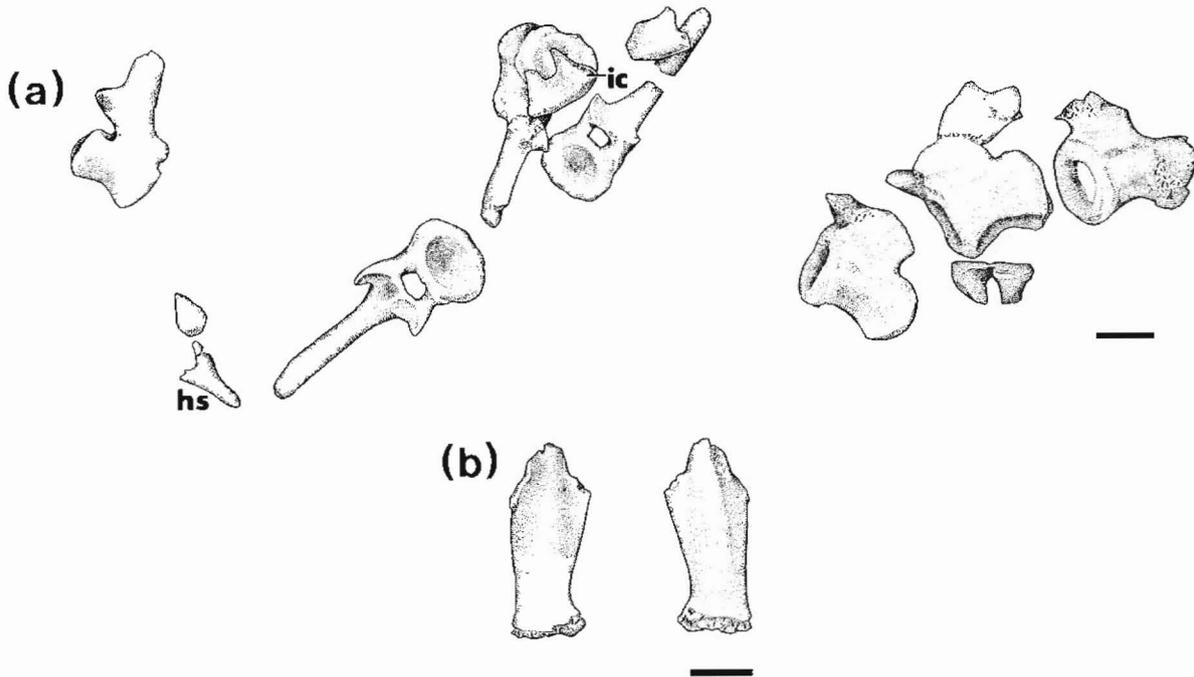


FIG. 7. *Edaphosaurus novomexicanus*, CM 34910 (Carnegie Museum of Natural History, Pittsburg), referred specimen. (a) Caudal vertebrae. (b) A caudal neural spine in left and right lateral views. Abbreviations: ic, intercentrum; hs, haemal spine. Scales = 1 cm.

plus *E. cruciger* and *E. pogonias*), raising the possibility that its rate of evolution may have been equal to that of the lineage leading to the clade of Texan edaphosaurids. Relict species fall into three categories. The first two, taxonomic and geographic relicts, may be identified with relative ease. Morphological relicts, including taxa that persist over long geologic periods

of time and show little morphological change, are relatively difficult to characterize. It is possible that the relict status currently assigned to some taxa may be found to be inappropriate once these taxa are examined in closer detail. The identification of taxa as "morphological relicts" should be based upon sister-group comparisons, where evolutionary rates (anagene-

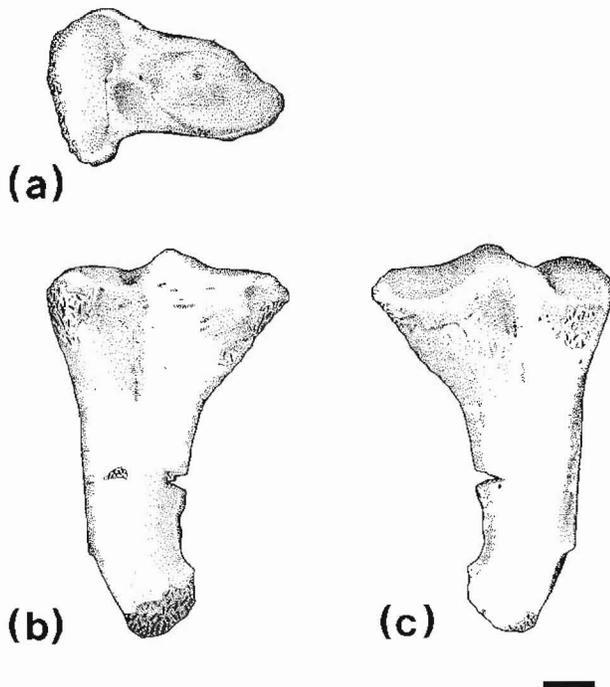


FIG. 8. *Edaphosaurus novomexicanus*, CM 34910, referred specimen. Proximal (a), dorsal (b), and ventral (c) views of the left tibia. Scale = 1 cm.

sis) can be evaluated quantitatively in terms of the number of character transformations.

*Edaphosaurus novomexicanus* is the most primitive known member of the genus *Edaphosaurus*. In addition to the presence of cervical neural spines that taper gradually to slender tips, it retains a relatively broad lateral lappet of the frontal, a character shared with *Ianthasaurus hardestii*. *Edaphosaurus boanerges*, *E. cruciger*, and *E. pogonias* from the Texas Lower Permian are more advanced in that the lateral lappet of the frontal is notably slender. Although recognized as a species of *Edaphosaurus* (Modesto and Reisz 1990), the taxonomic position of *E. colohistion* from the Pittsburgh Formation of West Virginia (Berman 1979) is problematic. Known from a single partial skeleton, it shares no apomorphies with the Texan edaphosaurids. Although the distal tips of the cervical neural spines of this species are not expanded anteroposteriorly to the degree seen in the Texan edaphosaurids, they demonstrate slightly greater anteroposterior expansion than does *E. novomexicanus* (Berman 1979). However, the taxonomic affinities of this edaphosaurid must await the discovery of cranial material.

Romer and Price (1940) remarked that there is little difference between the skulls of the various species of *Edaphosaurus*. The results of this study refute this contention. In addition to the presence of a primitively broad frontal lateral lappet in *E. novomexicanus*, the tooth plate morphology differs among the various species of *Edaphosaurus*. The palatal tooth plates of *E. pogonias* and *E. boanerges* are 6 and 11–16% longer (relative to tooth plate width), respectively, than that of *E. novomexicanus*. However, with such a small sample size it is difficult to determine how significant these differences truly are. Perhaps more importantly, each palatal tooth plate in *E. novomexicanus* accommodated about 90 teeth, whereas that of *E. pogonias* carried about 100 teeth. *Edaphosaurus*

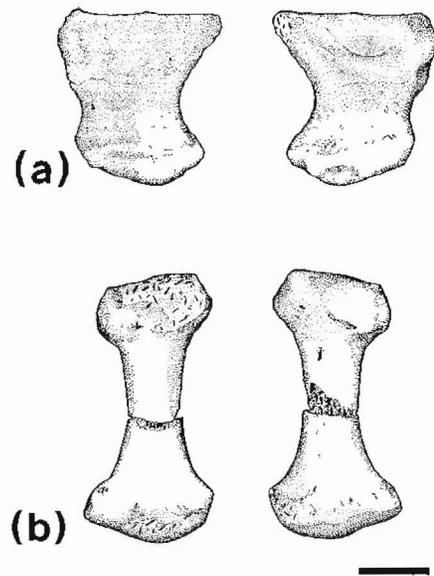


FIG. 9. *Edaphosaurus novomexicanus*, CM 34910, referred specimen. (a) First metatarsal in dorsal and ventral views. (b) Second (?) metatarsal in dorsal and ventral views. Scale = 1 cm.

*boanerges* may be more derived in that at least 120 teeth were present in each palatal plate; one individual (MCZ 1762) possessed 153 palatal plate teeth. However, as the number of tooth plate teeth is unknown for *E. cruciger*, it is unclear whether a tooth plate that accommodates approximately 90–100 teeth indeed represents the primitive condition for the genus. The tooth plate dentition of *E. novomexicanus* differs further from those of *E. boanerges* and *E. pogonias* in the variation of the basal diameters of the tooth plate teeth and the presence of several of these teeth with a diameter greater than that of the largest marginal teeth. In *E. boanerges* and *E. pogonias*, tooth plate dentition is generally isodont (although small teeth fringe the plates in all species), and the basal diameters of the tooth plate are never greater than those of the marginal dentition. Since the basal diameters of the palatal teeth of other advanced eupelycosaurids (sensu Reisz 1986) are never larger than those of marginal teeth, the presence of palatal teeth with basal diameters greater than those of marginal teeth probably represents a second autapomorphy for *E. novomexicanus*. Although the palatal teeth of most synapsids can vary greatly in relative diameter, the largest palatal teeth are restricted to the transverse flange of the pterygoid. This condition is probably not homologous to that seen in *E. novomexicanus*, where large and small teeth are randomly positioned on the tooth plate. Therefore the variation in the diameter of the tooth plate teeth may represent the third autapomorphy for the New Mexico edaphosaurid. It is apparent that the cranial morphology of *Edaphosaurus* displays considerably more variation than Romer and Price (1940) presumed.

The new postcrania sheds a little more light on the phylogenetics of the genus *Edaphosaurus*. The morphology of the caudal vertebrae demonstrates that the presence of leaf-shaped neural spines is a synapomorphy uniting all species of *Edaphosaurus*. The marginal thickening of the tips of these neural spines suggests that the caudal series may have supported a horny protuberance in life. Interestingly, because the haemal spines similarly display slight apical expansion, they may have also been extended further by heavily keratinized scales. The

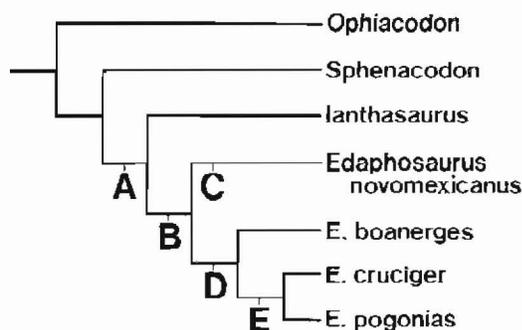


FIG. 10. A tentative cladogram illustrating a hypothesis of the interrelationships of the Edaphosauridae. *Ophiacodon* and *Sphenacodon* are outgroups. A more extensive phylogenetic analysis of the family is the subject of a forthcoming paper. The branches are defined as follows: *A*, presence of lateral tubercles, elongated neural spines sub-circular in cross section distal to laterally compressed proximal portion, cervical neural spines lean anteriorly, and posterior neural spines arch posteriorly; *B*, presence of tooth plates on palate and inner aspect of lower jaw, isodont marginal dentition, jaw articulation offset ventrally, and skull small relative to trunk; *C*, anisodont tooth plate dentition, lateral tubercles on anterior presacral neural spines rare; *D*, lateral lappet of frontal slender, distal ends of cervical neural spines expanded anteroposteriorly; *E*, cervical neural spines club-like, dentary reduced to 66% total mandibular length.

tibia, though only partially preserved, differs from that of *E. boanerges* in size and the shape of the lateral proximal facet only. The latter feature may represent another plesiomorphy retained by *E. novomexicanus*, but, as tibiae have not been described for the remaining five edaphosaurid taxa, it would be inappropriate to recognize it as such at this time. The presence of metatarsals that closely resemble those of sphenacodontids is interesting, for it suggests that the edaphosaurid pes had changed little since the edaphosaurid lineage separated from that leading to sphenacodontids and therapsids. The strongly lunate lateral border of the first metatarsal may represent a synapomorphy of edaphosaurids and sphenacodonts; it is uncertain whether this apomorphy is size related, as the pes of the small edaphosaurid *Ianthasaurus hardestii* remains unknown. However, the primitive state is present in the small eupelycosaur *Haptodus garnettensis* (Laurin 1990), which suggests that a deeply embayed first metatarsal lateral border may have been acquired independently by *Edaphosaurus* and sphenacodontids.

Figure 10 illustrates a hypothesis of relationships within the Edaphosauridae; this hypothesis is a condensed account of a more extensive phylogenetic analysis of the family, which is the subject of a forthcoming paper on the cranial anatomy of *E. boanerges*. The ophiacodontid *Ophiacodon* and the sphenacodontid *Sphenacodon* serve as outgroups; as the interrelationships of the Eupelycosauria are well established (Reisz 1986), only characters concerning edaphosaurid interrelationships are dealt with. The following phylogenetic scheme is suggested for the Edaphosauridae: (*Ianthasaurus hardestii* (*E. novomexicanus* (*E. boanerges* (*E. cruciger*, *E. pogonias*))))). The New Mexico edaphosaurid is more derived than the Late Pennsylvanian edaphosaurid *Ianthasaurus hardestii*, but falls out of the clade of Texan edaphosaurids owing to the absence of two apomorphies: (i) the frontal lateral lappet is slender; and (ii) the cervical neural spines are expanded anteroposteriorly. As noted above, Romer and Price (1940) were correct in their assumption that the New Mexico edaphosaurid

was the most primitive member of the genus, but for the wrong reasons.

During the past decade, most students of Palaeozoic tetrapods have targeted their systematic studies on unravelling the interrelationships of higher taxa (Brinkman and Eberth 1983; Gauthier *et al.* 1988; Reisz and Laurin 1991; Reisz *et al.* 1992). These studies are now beginning to produce robust hypotheses concerning higher-group interrelationships, and the next task will be to examine the phylogeny of the constituent members of these taxa. This study represents a step in this direction, a preliminary investigation of the Edaphosauridae. However, a full appreciation of the evolution of this group must await the reexamination of the remaining edaphosaurid species.

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