A LARGE MORADISAURINE TOOTH PLATE FROM THE LOWER PERMIAN OF TEXAS AND ITS BIOSTRATIGRAPHIC IMPLICATIONS

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Our knowledge of the tetrapod faunas of the youngest continental rocks of the North American Permain is due in great part to the research of E. C. Olson. Important paleoecological elements of these Early Permian faunas include moradisaurines of the Gzhelian–Wuchiapingian (303.7–254.1 Ma) reptile clade Captorhinidae. These multiple-tooth-rowed reptiles are the oldest eureptiles to adopt a high-fiber herbivorous diet.

In Texas, moradisaurines first appear in the Clear Fork Formation (sensu Nelson et al., 2013). Olson (1948) and his contemporaries used a system in which the Clear Fork was raised to the status of group and subdivided into the Arroyo, Vale, and Choza formations. Hentz (1988), however, concluded that there was no lithostratigraphic evidence to distinguish these formations and regarded the Clear Fork Group as undivided. Lucas (2006) demurred and continued to recognize Arroyo, Vale, and Choza formations. Nelson et al. (2013) restrict the use of these names to rocks cropping out to the southeast of the localities visited by Olson (1948, 1958) in Foard, Knox, and Wilbarger counties. Following Nelson et al. (2013), rocks of the former Arroyo, Vale, and Choza formations in north-central Texas are here referred to respectively as the ‘lower,’ ‘middle,’ and ‘upper’ units of the Clear Fork Formation.

Moradisaurine remains first appear in the middle Clear Fork Formation and are assigned to the genera Labidosaurikos and Captorhinicos. The associated tetrapod fauna includes the temnospondyl genera Cacops, Eryops, and Trimerorhachis, the lepospondyl genera Brachydeictes and Diplacaulus; the diadectomorph Diadectes, and the synapsid genera Casea, Dimetrodon, and Varanops (Olson, 1948, 1958; Campione and Reisz, 2010). Tetrapod fossils were collected from mudstones and conglomerates at 21 localities (Olson, 1958).

A particularly interesting fossil is a fragmentary tooth plate from the middle Clear Fork Formation that Olson (1956) attributed to an edaphosaurid synapsid. Olson (1956) noted that this fossil was appreciably larger than tooth plates of the genus Edaphosaurus (known from the lower Clear Fork Formation and underlying strata of the Wichita Group) and indicated that the teeth were arranged in rows, unlike the irregularly organized teeth that form the tooth plates in Edaphosaurus. Aware of these differences, Olson (1956) suggested that the middle Clear Fork Formation tooth plate represented a new genus of edaphosaurid. Interestingly, Olson (1956) also admitted that this specimen could belong to a ‘captorhinomorph’ reptile, but he did not compare it with the captorhinid materials he had previously described from the same strata ( Olson, 1954). We suspect that the large size of the incomplete tooth plate (116 mm long), which dwarfed the smaller tooth plates (ca. 20 mm long) of the Labidosaurikos and Captorhinicos specimens that Olson (1954) had described from the same formation, likely convinced him that the tooth plate did not belong to a middle Clear Fork Formation captorhinid. Olson upheld his assignment of the tooth plate to Edaphosauridae in his overview of the middle and upper Clear Fork Formation ( Olson, 1958).

Restudy of previously described moradisaurines (Dodick and Modesto, 1995; Modesto et al., 2014) and the descriptions of new moradisaurine fossils (Reisz et al., 2011; LeBlanc et al., 2015) have vastly expanded our knowledge of the cranial and dental anatomy of these early herbivorous reptiles. Coupled with research on edaphosaurid cranial and dental morphology (Modesto and Reisz, 1992; Modesto, 1995), the above advancements in moradisaurine research prompted us to reexamine the large middle Clear Fork Formation tooth plate. If this specimen is indeed attributable to an edaphosaurid synapsid, it would represent the last appearance datum for Edaphosauridae and thus have important implications for Early Permian vertebrate biochronology. If, instead, the tooth plate is referable to Moradisaurinae, it would represent the largest reptile from the Clear Fork Formation.

**Institutional Abbreviations—FMNH UR.** The Field Museum, Chicago, Illinois; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.

**MATERIALS AND METHODS**

The specimen, FMNH UR 29, was prepared mechanically by the authors using Microjack pneumatic airscribes and pin vises. Tooth basal diameters (n = 10) were measured directly from the specimen using a Mitutoyo ABS Digimatic caliper. The same was determined for the holotypes of Labidosaurikos meachami and Moradisaurus grandis, using Dodick and Modesto (1995:fig. 4) for the former species and photographs of the holotypic skull taken by R. R.R. (see Supplementary Data 1) for the latter (n = 10 for each).

**SYSTEMATIC PALEONTOLOGY**

REPTILIA Laurenti, 1758
CAPTORHINIDAE Case, 1911
MORADISAUROINAE de Ricqlès and Taquet, 1982

Gen. et sp. indet.

(Figs. 1–2)
Specimen—FMNH UR 29, a large tooth-plate fragment with eight rows of teeth. Associated with this fragment are two smaller fragments (45 × 29 mm; 37 × 19 mm) of occluded tooth plates that bear teeth with the same basal diameter as those in FMNH UR 29, but do not fit onto it or to each other.

Locality and Horizon—Olson’s (1948) ‘KB’ locality, in the upper part of the middle Clear Fork Formation, Knox County, Texas; Leonardian, Lower Permian. Although Olson (1956:331) stated that FMNH UR 29 was collected from locality ‘KC’ (also in the upper part of the Clear Fork Formation; Olson, 1958: table 1), this is likely a lapsus calami, judging from his statement that this specimen was preserved in association with Captorhinus, and from his faunal lists for localities KB and KC in Olson (1958:430), which list Captorhinus and “Edaphosaurid, n. gen., unnamed” for the locality KB, whereas neither taxon is listed for KC in the 1958 publication.

DESCRIPTION

Specimen FMNH UR 29 comprises a partial tooth plate (Fig. 1) that is 116 mm long and 49 mm broad and consists of two pieces: a small, triangular anterior fragment and a larger posterior, quadrangular fragment, that were glued together (presumably by E. C. Olson); the fit is excellent, but much bone, including a large medial wedge, was lost to weathering. The anterior and posterior ends are heavily eroded, and it is unclear how much bone is missing from either end. The labial and lingual margins are, however, well preserved and conform to the subtriangular occlusal profile of a moradisaurine maxillary tooth plate (Dodick and Modesto, 1995; Modesto et al., 2014), and are dramatically different from the oval occlusal profile of the palatal tooth plate of Edaphosaurus (Modesto, 1995). We consider that the straight margin is the lateral, or labial, margin of the tooth plate and the opposite, weakly convex margin is the medial, or lingual, margin, and that the tooth plate represents the greater part of a right maxilla. In addition, the missing anterior end would have preserved the single-rowed tooth region characteristic of multiple-tooth-rowed captorhinid maxillae (Dodick and Modesto, 1995; Reisz et al., 2011).

Nearly the entire ventral surface of the maxilla is studded with the stumps of teeth. These teeth are subcircular to oval in basal cross-section and subequal in size. The crown of each tooth is damaged, and the pulp cavity is exposed in the majority of teeth. The teeth are clearly organized into longitudinal, subparallel rows, as are moradisaurine tooth rows (Reisz et al., 2011; Modesto et al., 2014). This organization contrasts sharply with the irregular arrangement of the tooth-plate teeth in Edaphosaurus (Modesto, 1995). Eight rows of teeth are present. As preserved, the labial-most row is the longest and the lingual-most row is the shortest. The first, or mesial-most, tooth of the lingual-most row is well posterior to the longitudinal midpoint of the tooth plate, as in Labidosaurikos meachami (Dodick and Modesto, 1995) and Moradisaurus grandis (S.P.M. and R.R.R., pers. observ.).

Olson (1956) described the teeth as ‘bullet-shaped,’ but none of the teeth have crowns complete enough to assess their profiles. Included in the collections tray with FMNH UR 29, but neither described nor illustrated by Olson (1956), are fragments of occluded tooth plates that presumably were associated with FMNH UR 29 at the time of collection. In the better preserved of these fragments (Fig. 2), stout ‘bullet-shaped’ teeth, from

FIGURE 1. FMNH UR 29, Moradisaurinae indet., maxillary tooth plate in occlusal view. A, drawing and B, photograph. Anterior is to top of page.
what we infer to be the posterior ends of the occluded (left?) pair of tooth plates, can be seen in lingual/distal aspect. These teeth are indistinguishable in morphology from those of *Labidosaurikos meachami* (Dodick and Modesto, 1995).

**FIGURE 2.** FMNH UR 29, Moradisaurinae indet., occluded tooth-plate fragment with teeth in lingual/distal view.

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**DISCUSSION**

For over half a century, FMNH UR 29 was the only record of an edaphosaurid synapsid known from post-early Clear Fork Formation strata (i.e., above the former ‘Arroyo Formation’). Olson (1948:197) originally inferred the presence of edaphosaurids in the middle Clear Fork Formation on the basis of “pterigoid plates studded with Edaphosaurus-like teeth” and “two large palates with teeth arranged in regular rows” and suggested that several other, partial lower jaws from the same formation could be attributed to an edaphosaurid. Olson (1948) was, however, puzzled that no fragments of the neural spines that are so distinctive of *Edaphosaurus* were present in the middle Clear Fork Formation. In the same discussion, Olson (1948) remarked that the specimen with the teeth arranged in rows (presumably FMNH UR 29, but no specimen numbers were provided) resembled a small tooth plate (MCZ 1352) attributed by Romer and Price (1940) to *Trichasaurus*, a genus then assigned tentatively to Edaphosauridae. Interestingly, Olson (1954) assigned MCZ 1352 to the captorhinid *Labidosaurikos barkeri*. Two years later, Olson (1956) described FMNH UR 29 and attributed it to Edaphosauridae. That assignment was upheld by Olson (1958), who listed only a single occurrence of Edaphosauridae in the middle Clear Fork Formation. Olson (1958) also described the teeth as “bullet-shaped” and comparable to those in tooth plates of *Edaphosaurus*, but ‘bullet-shaped’ teeth are also known to form the tooth plates of the moradisaurines *Labidosaurikos meachami* (Dodick and Modesto, 1995) and *Captorhinikos valensis* (Modesto et al., 2014). The dentition of FMNH UR 29, particularly the arrangement of the teeth into eight distinct rows, allows us to remove this specimen from Edaphosauridae and assign it to Moradisaurinae.

Specimen FMNH UR 29 preserves no autapomorphies of its own, nor does it exhibit (or preserve) those of described moradisaurine species. Accordingly, we regard it as Moradisaurinae indet. The presence of 115 tooth positions suggests placement within the moradisaurine clade that includes *Labidosaurikos meachami*, *Moradisaurus grandis*, *Gansurhinos qingtoushanensis*, and *Rothianicus multidontus*, because this clade is diagnosed (in part) by the presence of 40 or more teeth on the maxillary dental field (Reisz et al., 2011). Because the tooth-plate teeth of *G. qingtoushanensis* feature distinctly recurved tips, and *R. multidontus* exhibits less than 40 tooth-plate teeth arranged into four rows (Reisz et al., 2011), it seems unlikely that FMNH UR 29 is a close relative of either moradisaurine; accordingly, we restrict the following comparisons to *L. meachami* and *M. grandis*. The teeth in FMNH UR 29 are arranged into eight tooth rows, a figure that is two more and two fewer than the number of rows in *L. meachami* (six rows) and *M. grandis* (10 rows), respectively. In addition, posterior teeth of FMNH UR 29 average 5.7 mm in maximum basal diameter, a figure that is intermediate between those of *L. meachami* (averaging 4.8 mm) and *M. grandis* (averaging 7.4 mm). At 116 mm, FMNH UR 29 is longer than that of *L. meachami* (ca. 86 mm long), but shorter than that of *M. grandis* (ca. 157 mm long). These metrics together suggest that FMNH UR 29 is all that remains of a skull that is intermediate in size between the holotypic skulls of *L. meachami* (ca. 30 cm long) and *M. grandis* (ca. 40 cm long), yielding an estimated skull length of roughly 35 cm. Thus, FMNH UR 29 represents the largest reptile known from the Clear Fork Formation.

Modesto et al. (2014) regarded moradisaurines and species of the genus *Edaphosaurus* as ecological analogues, because members of both groups are high-fiber herbivores that independently evolved dental batteries consisting of upper and lower pairs of tooth plates, which were ground against each other via propalinal jaw action. As the chronologically younger group, Moradisaurinae could be considered a candidate replacement clade (‘CCR’) sensu Benton (1996a, 1996b). The transfer of FMNH UR 29 from Edaphosauridae to Moradisaurinae, however, removes the only record of the synapsid family from rocks of the middle Clear Fork Formation (i.e., the former ‘Arroyo Formation’). As a result, the stratigraphic range of Edaphosauridae now terminates within the lower Clear Fork Formation (the former ‘Arroyo Formation’). The dijunct biostatigraphy of Moradisaurinae and Edaphosauridae rules out the former as a CCR; i.e., it is unlikely that competition with edaphosaurids played any role in the evolutionary radiation of moradisaurines (and the extinction of edaphosaurids).

If competition was not a factor, what agency may have fostered moradisaurine diversification? The available phylogenetic, stratigraphic, and palaeoclimatological evidence suggests that climate change promoted moradisaurine evolution. Stratigraphic calibrations of captorhinid evolutionary relationships (Modesto et al., 2007, 2014) indicate that, whereas Moradisaurinae makes its first stratigraphic appearance in the middle Clear Fork Formation, this clade—as the sister taxon of the lower Clear Fork Formation captorhinid *Labidosaurus hamatus*—must have been contemporaneous with *Edaphosaurus pogonius*. Olson (1952:182) inferred an equable climate (“temperatures appear to have been moderate” with “rainfall sufficient to support ferns, seed ferns, and conifers”) for the lower Clear Fork Formation, which transitioned to drier, monsoonal climate in the middle Clear Fork Formation (see also Nelson et al., 2001). Accordingly, the extinctions of edaphosaurids, ophiacodontid synapsids, single-toothed-rowed captorhinids (e.g., *La. hamatus*), and microsaurs in the lower Clear Fork Formation may have been triggered by drying climatic conditions in the Permian Basin of North America. The succeeding fauna, which included moradisaurines and caseid synapsids as the dominant high-fiber herbivores, may have originated in drier, highland regions (as suggested by recent research on caseids, captorhinids, and other tetrapods from the upland Richards Spur and Bally Mountain sites of Oklahoma; Reisz and Sutherland, 2001; Reisz, 2005; LeBlanc et al., 2015) and thus were exapted to the arid, monsoonal climate inferred for the middle Clear Fork Formation.
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