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Faunal overview of the Mud Hill locality from the early Permian Vale Formation of Taylor County, Texas

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Abstract.—The Texas red beds represent one of the richest series of early Permian deposits in the world. In particular, the Clear Fork Group has produced a diverse assemblage of temnospondyls, early reptiles, and synapsids. However, most of this material has been sourced from the oldest member, the Arroyo Formation, and the understanding of the paleoecosystem of the younger Vale and Choza formations is less well resolved. Here we present a previously undescribed Vale locality, the first vertebrate-bearing locality from the formation to be described in detail in several decades, from near Abilene, Texas with juvenile diplocaulids, captorhinids, abundant material of rare taxa such as *Varanops* and diadectids, and the first report of a recumbirostran 'microsaur' from the formation. This assemblage is atypical of early Permian deposits in the taxonomic and size distribution of the vertebrate fauna in comparison to other localities from the Vale Formation that preserve a greater abundance of aquatic taxa (e.g., fishes, *Trimerorhachis*) and synapsids (e.g., *Dimetrodon*). Minimal abrasion of the elements, relative articulation and association of the specimen of *Varanops*, and the paucity of aquatic taxa suggest an ephemeral pond deposit in which organisms were preserved essentially in situ. Our characterization of the locality also permits a revision and discussion of the vertebrate faunal assemblage of the Vale Formation.

Introduction

Studies of the early Permian fauna, flora, and geology of Texas date to the origins of vertebrate paleontology in North America. Some of the earliest discoveries were made in the mid-nineteenth century by B.F. Shumard, the state geologist (e.g., Shumard, 1858, 1859). Extensive collection and study of the vertebrate fauna was primarily undertaken in the late nineteenth century and into the twentieth century by classic paleontologists such as Cope, Williston, Case, and Olson and resulted in a significant expansion of the knowledge of the early Permian landscape with the discovery of many of the iconic taxa that typify the time period, such as *Eryops* Cope, 1877b, *Diplocaulus* Cope, 1877a, *Trimerorhachis* Cope, 1878, and *Dimetrodon* Cope, 1878 (Cope, 1877b, 1878). Even with exploration expanding into the southwest (e.g., New Mexico) and other areas of the midcontinent of North America (e.g., Oklahoma) from the mid-twentieth century to the present day, the described vertebrate fauna from Texas remains among the best characterized and the most diverse of early Permian assemblages. Many vertebrate taxa are known from the Clear Fork Group (Leonardian) of Texas, which has traditionally comprised three formations (from oldest to youngest): the Arroyo, the Vale, and the Choza (e.g., Lucas, 2006; Nelson et al., 2013, but see Hentz, 1988 for a different model). Of these, the Arroyo Formation was the first to produce vertebrate material (dating back to work in the nineteenth century by Cope) and has been extensively explored and studied, resulting in the most diverse vertebrate assemblage of the three formations (e.g., Olson, 1989, table 1). By contrast, material from the Vale and Choza formations was not reported until the mid-twentieth century (Olson, 1948, 1951c). Although these vertebrate assemblages contain significant overlap with the Arroyo assemblage at higher taxonomic levels, the documented taxonomic diversity is notably reduced.

Four relatively fossiliferous localities within the Vale Formation of Texas have been previously described (Table 1). The geology and faunal assemblage of the Vale Formation was first described in detail by Olson (1948) based on a locality near Vera (Knox County), often referred to as the 'northern Vale' by the author, and was later expanded on in a number of separate articles that included fauna of the Choza Formation (Olson, 1951b, c, 1952a, b, 1954a–c, 1955, 1956a–c, 1958). Although Olson (1948, p. 186) indicated that workers had been previously unable to recover vertebrate material from post-Arroyo sediments of the Clear Fork Group, this was in error. The earliest reported collection of significant vertebrate material from the Vale Formation was from 1939 – 1940 on the land of C.O. Patterson near Lawn (Taylor County) under the direction of a Works Projects Administration (WPA) excavation led by the University of Texas, Austin; this material was first noted in an abstract by Wilson (1948) but was not fully reported until 1953 by the same author, who limited the bulk of the description to a new paleoniscoid taxon, *Lawnia* Wilson, 1953. Wilson noted

Table 1. Major previously described early Permian vertebrate localities within the Vale Formation of Texas. The northern Vale localities described by Olson (1948) pertain to numerous sites spanning the entire stratigraphic section of the Vale.

Locality	County	Position	Primary reference
Northern Vale	Knox	lower–upper	Olson (1948)
Sid McAdams	Taylor	lower	Wilson (1953); Mead (1971)
Blackwood	Taylor	middle	Olson and Mead (1982)
Stamford	Haskell	middle	Dalquest and Mamay (1963)

the co-occurrence of well-known early Permian tetrapods (*Trimerorhachis*, *Diplocaulus*, *Seymouria* Broili, 1904*, Dimetrodon*) but stated that this material did not contribute novel information regarding these taxa (Wilson, 1953, p. 456) and thus did not describe, discuss, or figure any of this material. The locality's tetrapod fauna, which includes an unusually dense assemblage of *Dimetrodon* specimens, was redescribed in an unpublished master's thesis (Mead, 1971) that was incorporated into a summary of comparative Vale paleontology by Olson and Mead (1982). Material of *T. insignis* Cope, 1878 was collected from the same property but from a slightly younger horizon within the Vale Formation and was described by Olson (1979a). A large, nearly monotaxic assemblage of *Diplocaulus* was described by Dalquest and Mamay (1963) from the property of V.B. Rowland near Stamford (Jones County). Additionally, a new locality on the property of L.A. Blackwood near Buffalo Gap (Taylor County) was discovered in 1970 by David Berman and was described by Olson and Mead (1982). Brief lithological notes and faunal lists of less productive localities from the lower Vale (Baylor County) and the middle to upper Vale (Knox County) formation were compiled by Olson (1958). Since then, no new vertebrate localities have been reported, and general work on the tetrapod taxa has been extremely limited (e.g., Hunt and Lucas, 2005; Lucas and Hunt, 2005; Modesto et al., 2014). The ambiguity associated with some localities within the Clear Fork Group, particularly the Cacops Bone Bed from which the dissorophid *Cacops aspidephorus* Williston, 1910a, the caseid *Casea broilii* Williston, 1910b, and the varanopid *Varanops brevirostris* Williston, 1914 are known, and which occurs at either the top of the Arroyo Formation or at the bottom of the Vale Formation (Olson, 1989), suggests that material from the latter might have been collected prior to the WPA project, but none is confidently or explicitly referred to in the literature.

Here we describe the faunal assemblage of a vertebrate-bearing locality (Mud Hill) from the Olhausen Estate near Abilene, Texas (Taylor County) that occurs within the lower to middle Vale Formation (Figs. 1, 2). The locality is ~ 30 km north of the Patterson locality described by Wilson (1953). This site has been previously referenced in the locality details of two publications regarding a nearly complete varanopid (e.g., Reisz and Tsuji, 2006; Campione and Reisz, 2010) but has never been formally presented with an overview of the geology and the broader vertebrate assemblage. The assemblage includes some of the common early Permian forms (e.g., *Diplocaulus*) but is most notable for the absence of typical early Permian taxa (e.g., *Dimetrodon*, temnospondyls), for the presence of rare clades (e.g., diadectids, *Varanops*), and for the sole occurrence of some clades (e.g., recumbirostrans) within the Vale Formation. This unusual taxonomic composition and various aspects of the depositional environment, such as the articulation of much of the varanopid skeleton and the rarity of fully aquatic taxa commonly found in early Permian floodplain deposits, suggest in-situ preservation in an ephemeral aquatic setting. The description of this unusual assemblage contributes additional data regarding the Vale Formation, which is less well-characterized than the older Arroyo Formation, provides new insights regarding the paleobiology and the evolutionary history of forms that were previously rare or unknown from the formation, and permits the updating of the faunal list for the entire Vale Formation for the first time in 35 years.

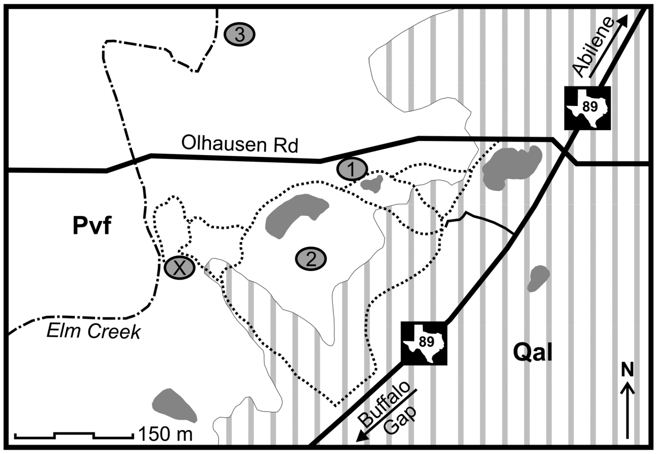

Figure 1. Mud Hill locality map. 1, 2, 3 = dig sites D1, D2, and D3; dotted lines = trails; unshaded area = exposure of the underlying Permian Vale Formation (Pvf); vertical striped area = Quaternary alluvium deposits (Qal); X = measured section site.

Geologic setting

The Vale Formation is early Permian (Leonardian) in age and is exposed along a roughly northerly trend through central Taylor County, Texas. In southern Taylor County, the Vale is truncated by a major unconformity that separates Permian strata from the Cretaceous strata of the Callahan Divide. The Callahan Divide (trending west to east) is composed of the Antlers Sandstone at its base and is capped by the Edwards Limestone. A deposit of alluvium (Quaternary) extends to the north, from the Callahan Divide, and was laid down directly on the underlying Permian Strata by northward flowing streams. The alluvium thins to the north, and in many areas has been eroded away. In western Taylor County, the Vale Formation is overlain by the Choza Formation, which in turn is truncated by the same unconformity that truncated the Vale Formation to the east. In eastern Taylor County, the underlying Arroyo Formation is exposed where it has been truncated by the unconformity.

The Vale Formation is exposed in road cuts, streams, and along many hillsides in the exposure area. Although the bulk of the Vale Formation could be considered monotonous red shale, there is some diversity in its deposits, especially south of the Mud Hill locality (described below). A small channel deposit composed of fine to medium plane-bedded quartz sand is found in one such exposure. The bounding shales at this locality have been known to produce fragmented plant impressions. A more productive fossil plant locality is found further to the west and has been known to produce several different plant species and trace fossils. Throughout the Vale exposure region, hematite nodules are commonly recovered after being weathered out of exposed shale deposits.

At the Mud Hill locality (Fig. 1), between six and eight meters of the Vale Formation are exposed along intermittent creeks and are capped by a half meter of alluvium (Figs. 2, 3). There are two lithofacies evident in the Vale at this locality. The dominant lithofacies is the red shale facies (Fig. S1.1). The shale is predominantly clay but can contain up to 3% very fine sand. The sandy constituent is dominated by iron-stained, translucent to transparent, subrounded quartz. Hematite and orthoclase account for less than 5% of the sand-sized grains. The siltstone-sandstone facies (Fig. S1.2) appears as distinctive white to light gray thin horizons within the shale. Grain-size varies substantially from horizon to horizon, ranging from dominantly silt to over 50% very fine to fine sands. The dominant subrounded to subangular quartz, along with minor amounts of subangular to angular hematite and orthoclase, is well cemented by calcite. The top of the siltstone-sandstone facies is associated with intermittent red caliche nodules (Fig. S1.3). The nodules are mostly calcite with up to ~25% silt and sand. Poorly preserved

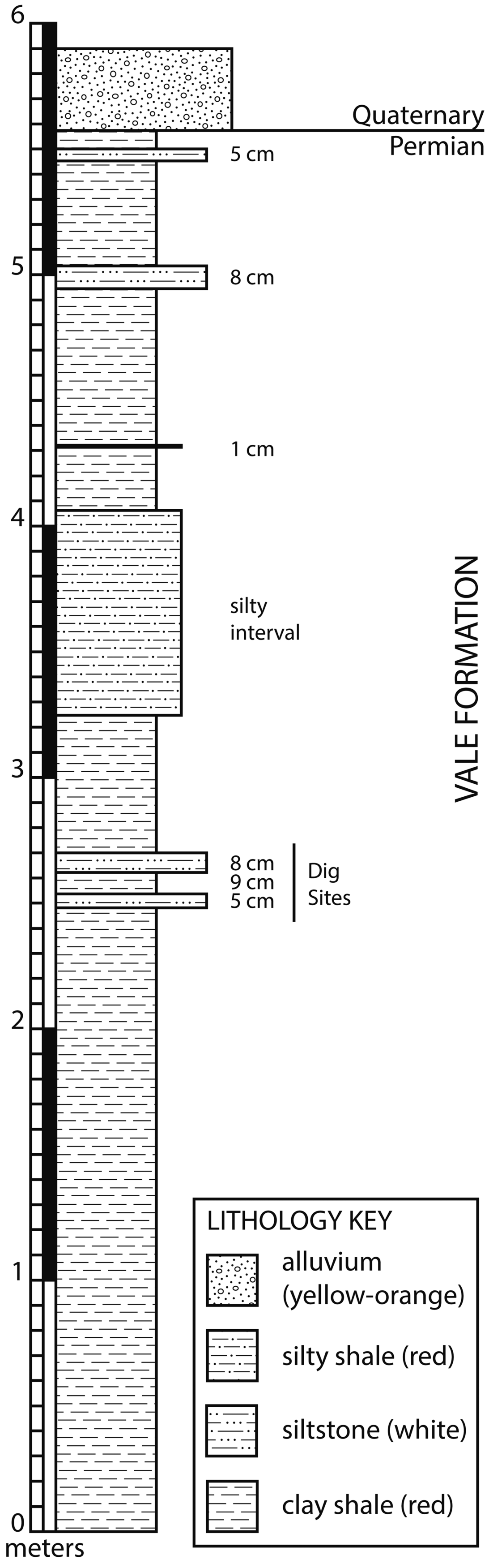

Figure 2. Measured section of the Vale Formation exposed along Elm Creek at the Mud Hill locality.

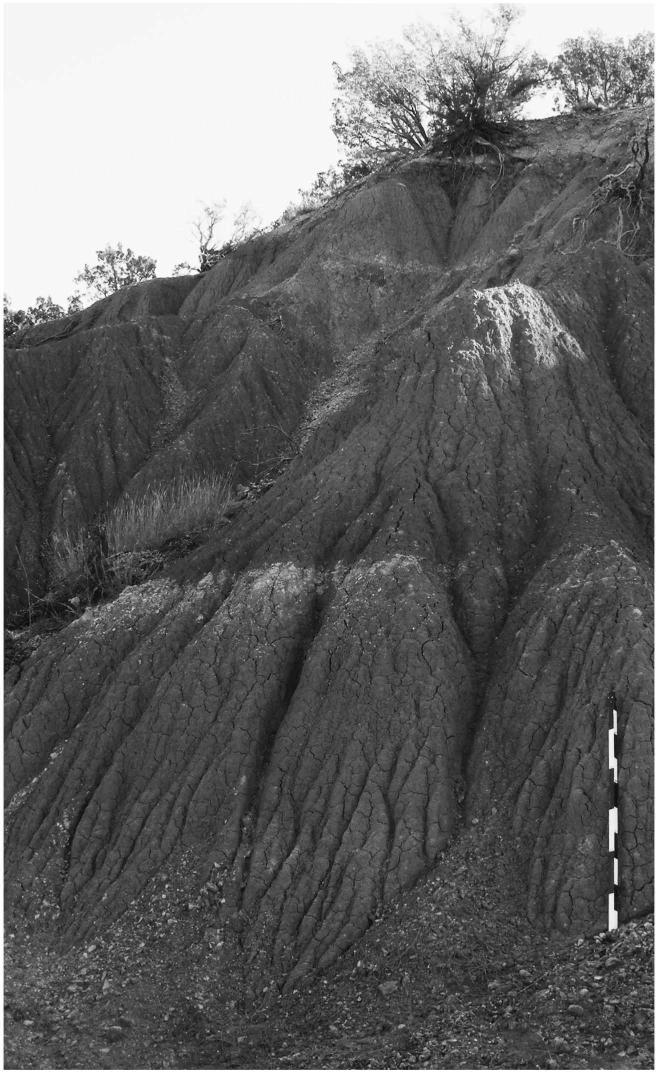

Figure 3. Site of the Elm Creek measured section at the Mud Hill locality. Photographic scale with 0.5-m divisions (left front) shown at lower right.

root traces and potential burrow fills are common and give the caliche nodules a 'vuggy' appearance. Frosted quartz grains dominate in the sand fraction with minor amounts of orthoclase and lithic fragments.

The alluvium that caps the Vale Formation at the Mud Hill locality is composed of Cretaceous material removed from the Callahan Divide, south of the locality. Clasts of conglomerates, sandstones, and limestones along with a diverse marine fossil assemblage are found in a matrix of loosely cemented quartz sand. The sands and conglomerates originate from the Antlers Sandstone, whereas the limestone and marine fossils are derived from the Edwards Limestone. The marine fossils are commonly fragmented and are representative of the molluscan dominated assemblage found in the Edwards Limestone.

Material at the Mud Hill locality was collected from several sites (Figs. 1, 3):

D1: vertebrate collection site in a bank northeast of an excavation for dam construction, north of a small water tank, south of Olhausen Road (32.335881°N, −99.799503°W); D2: vertebrate collection site in a bank south of a large tank, south of Olhausen Road (32.334817°N, −99.800989°W), which can be covered by an adjacent water tank in extremely wet weather; and D3: vertebrate collection site on a hillside exposure, north of Olhausen Road (32.337454°N, −99.801463°W). The D3 site is on private property that is not associated with the Olhausen Estates; collections were made under a private agreement with the landowner.

Materials and methods

All materials (Table 2) come from the Mud Hill locality on the Olhausen Estate near Abilene, Texas (Figs. 1–3, S1). An isolated diadectid centrum was collected from the estate by JO in the early 1970s, but the first bonebed site (D1) was not discovered until 1997 by Jacob and James Olhausen. The D2 site was found in 1998 by Robert Burt, and the D3 site was found in 2007 by Dale Ostlien. All three sites were periodically explored and partially excavated following their initial discovery. Because the sites were not excavated in a systematic fashion and without a quarry map, materials that are presently disarticulated could in fact have been associated at some point (e.g., right and left partial captorhinid mandibles).

Initial excavation, sorting, and preparation of some of the material was conducted by the family at the estate, primarily Jo Helen Cox, following collection; upon loan of the material to RRR, preparation of specimens in a formal laboratory was conducted with pin vises and air scribes by students at the University of Toronto Mississauga under the supervision of DS. Specimen photographs were taken by DS with a Canon EOS 40D digital SLR camera and a Leica DVM6 tilting microscope with Leica Application Suite X (LAS X) software; figures were compiled using Adobe Photoshop and Illustrator CS6.

Repositories and institutional abbreviations.—All specimens are deposited in the Texas Memorial Museum (TMM) in Austin, Texas, USA. Other institutions referenced in the text are: CNHM-UR = Chicago Natural History Museum (Field Museum of Natural History), Chicago, Illinois; UCLA VP = University of California Los Angeles, Vertebrate Paleontology, Los Angeles, California; USNM = United States National Museum (now National Museum of Natural History, Smithsonian Institution), Washington, DC.

Table 2. Specimens from Mud Hill described herein, with site of recovery, taxonomic identification, and recovered material.

Specimen number	Site	Taxonomy	Elements
TMM 43628-1	D2	*Varanops brevirostris* (Williston, 1911)	Partial skeleton (see Campione and Reisz, 2010)
TMM 43628-2	D1	*Diadectes* sp. indet.	Premaxilla, maxilla, dentary
TMM 43628-3	D1	*Diadectes* sp. indet.	Dentary
TMM 43628-4	D1	cf. *Diadectes* sp. indet.	Postcrania (limbs, vertebrae, girdles)
TMM 43628-5	D2	cf. *Diadectes* sp. indet.	Postcrania (tarsus)
TMM 43628-6	D3	cf. *Diadectes* sp. indet.	Postcrania (vertebrae)
TMM 43628-7	D2	Nectridea indet.	Skull, partial mandible, clavicles
TMM 43628-8	D2	Diplocaulinae gen. indet. sp. indet.	Skull, mandibles, indet. tetrapod skull and vertebrae
TMM 43628-9	D2	cf. *Diplocaulus* sp. indet.	Skull, mandibles
TMM 43628-10	D3	Hapsidopareiontidae gen. indet. sp. indet.	Skull, mandibles
TMM 43628-11	D3	Captorhinidae gen. indet. sp. indet.	Humerus
TMM 43628-12	D3	Captorhinidae gen. indet. sp. indet.	Partial mandibles
TMM 43628-13	D3	cf. *Captorhinikos chozaensis* Olson, 1954c	Premaxilla, mandible

Systematic Paleontology

Superclass Tetrapoda Goodrich, 1930
Tetrapoda indet. and Diplocaulinae gen. indet. sp. indet.
Figure 4.1

Description.—This intriguing, although unfortunately poorly preserved, specimen is a diminutive partial skeleton of a tetrapod cemented to the skull roof of a diplocauline (TMM 43628-8) noted below from the D2 site (Fig. 4.2, 4.3). The general contours of an elongate, rounded skull with a posterolateral projection on the right side can be made out, but the small size of the specimen in conjunction with weathering and encrusting obscures all other details. A series of vaguely vertebrae-appearing elements is associated with the skull and extends posteriorly to the margin of the diplocaulid skull, but as with the former, no details can be resolved that would further inform the identification.

Subclass Lepospondyli Zittel, 1888
Order Nectridea Miall, 1875
Nectridea indet.
Figure 5

Description.—This specimen (TMM 43628-7) comprises the postorbital margin of a nectridean, with the fragment being roughly symmetrical, but with better preservation of the elements on the left side of the skull; it was collected from the D2 site. It is broken off anterior to the pineal foramen, and the

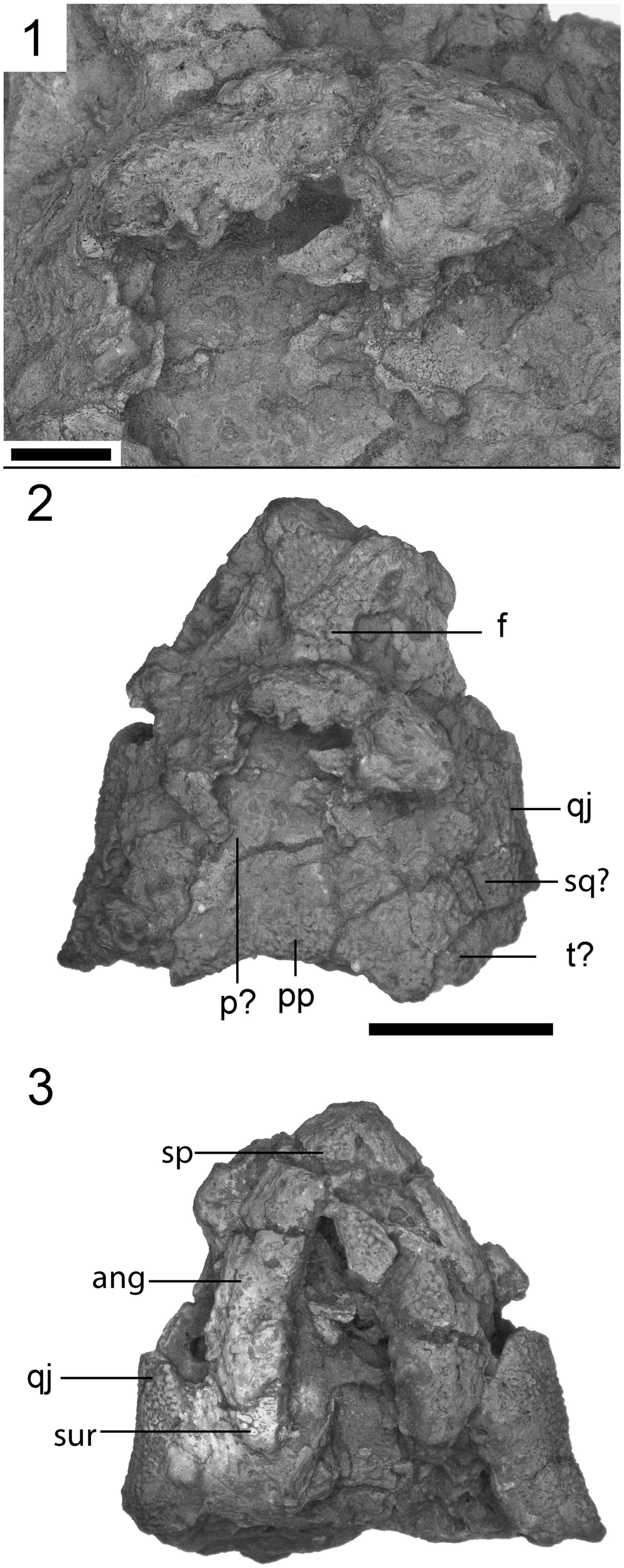

Figure 4. Tetrapoda indet. and Diplocaulinae gen. indet. sp. indet., a juvenile diplocauline with an indeterminate tetrapod on the dorsal skull roof (TMM 43628-8): (**1**) close-up of the indeterminate tetrapod; (**2**) dorsal profile of the diplocauline; (**3**) ventral profile of the diplocauline. ang, angular; f, frontal; p, parietal; pp, postparietal; qj, quadratojugal; sp, splenial; sq, squamosal; sur, surangular; t, tabular. Scale bars = 2.5 mm (1); 1 cm (2, 3).

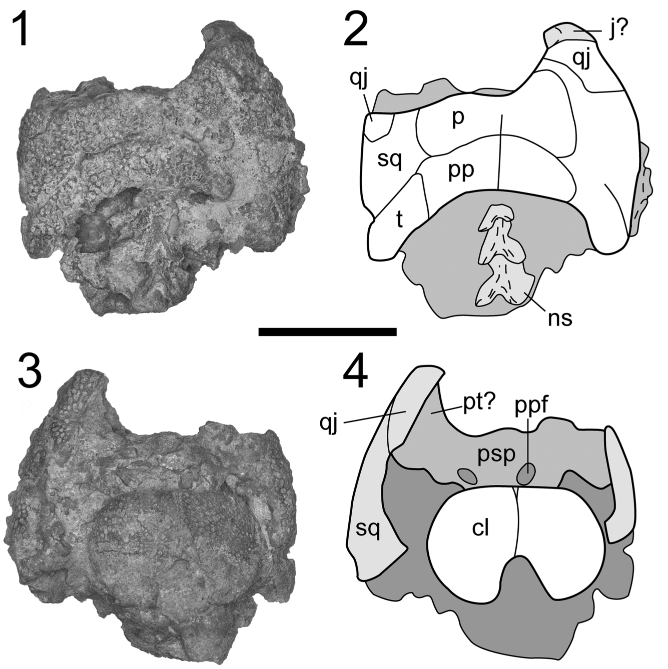

Figure 5. Nectridea indet. (TMM 43628-7): (**1**) photograph in dorsal profile; (**2**) illustration of Figure 5.1; (**3**) photograph in ventral profile; (**4**) illustration of Figure 5.3. cl, clavicle; j, jugal; ns, neural spine; p, parietal; pp, postparietal; ppf, postpterygoid fossa; psp, parasphenoid; pt, pterygoid; qj, quadratojugal; sq, squamosal; t, tabular. Scale bar = 1 cm.

parietals and squamosals are incomplete (Fig. 5.1, 5.2). Of the three nectridean specimens, the sutural contacts can be most readily defined in this specimen and are comparable to both those of a referred specimen of *Diplocaulus* sp. from this locality (below) and to previously described immature specimens of the genus (Olson, 1951a). The postparietals are transversely elongate rectangles, as in nectrideans with broader skulls. The quadratojugal has both dorsal and ventral exposures in association with the dorsoventral compression of the skull in diplocaulines. The tabular horns are incompletely developed but extend posteriorly and slightly laterally. The posterior margin of the skull forms a smooth concave curve, typical of diplocaulines in comparison to the squared-off margin of other nectrideans such as *Scincosaurus* Fritsch, 1876 and *Diceratosaurus* Jaekel, 1903 (Bossy and Milner, 1998; Milner and Ruta, 2009). The posterior portion of the palate is highly fragmentary but identifiable based on the presence of symmetrical, oval postpterygoid fossa. However, this specimen is the most difficult to further resolve because of the nature of a pair of clavicles that are preserved in the palatal region (Fig. 5.3, 5.4). The clavicles are of identical shape and comparable ornamentation to those of *Diplocaulus* (Williston, 1909b), but they contact each other anteriorly before being divided posteriorly by a small anterior process of the absent interclavicle in a similar fashion to that figured by Germain (2010, p. 38) for *Scincosaurus*; this relationship is not seen in any diplocauline and among nectrideans, is known only in *Scincosaurus* and *Diceratosaurus* (Bossy and Milner, 1998). That this disparity from previously described diplocauline material could be an ontogenetic shift cannot be excluded; the pectoral girdle of diplocaulines has not been extensively described or figured in articulation beyond that of

Williston (1909b, p. 129, pl. 4), who described much larger specimens. *Scincosaurus* is known only from the Carboniferous of Europe, lacks a dorsal exposure of the quadratojugal, and the posterior margin of the skull roof is squared-off, rather than markedly indented as in diplocaulines and in this specimen (Milner and Ruta, 2009). *Diceratosaurus* is known only from the Carboniferous of Ohio, features more equant postparietals, and lacks a dorsal exposure of the quadratojugal (Bossy and Milner, 1998). Three neural spines are exposed dorsally in articulation with the skull, but they are only partially exposed and are uninformative for improving the resolution of the taxonomic identification.

Family Diplocaulidae Cope, 1881
Subfamily Diplocaulinae Cope, 1881
Diplocaulinae gen. indet. sp. indet.
Figure 4.2, 4.3

Description.—An indeterminate diplocauline is represented by a nearly complete skull with articulated mandible on which the small indeterminate tetrapod material is preserved (TMM 43628-8); this was collected from the D2 site. Major features such as the orbits are identifiable, as are the posterior and lateral skull margins; the anteriormost portion of the snout appears to have been lost. The specimen can be referred to the Diplocaulinae based on an unpaired frontal that forms the entirety of the interorbital region (Fig. 4.2), but further taxonomic resolution is not possible because the palate is obscured by the mandible, most of the cranial sutures are obscured due to weathering and the overlying small-bodied tetrapod, and there is damage to the characteristically elongated tabular horns.

Genus *Diplocaulus* Cope, 1877a

Type species.—*Diplocaulus salamandroides* Cope, 1877a from the Bond Formation of Illinois, by original designation.

cf. *Diplocaulus* sp. indet.
Figure 6

Description.—A small skull with articulated mandible (TMM 43628-9) was collected from the D2 site. The skull is broken in several places, but the fragments remain in relative articulation, and much of the palate is well exposed from the exoccipitals to the left vomer (Fig. 6). The skull would have been subequal in length and width and does not appear to have had well-developed tabular horns with a strong posterolateral orientation. The posterior midline elements (parietal, postparietal) are proportionately short transversely relative to those of large-bodied individuals. The unpaired frontal (a diplocauline synapomorphy) constitutes the entirety of the interorbital region. A left postorbital is tentatively identified, separating it from *Peronedon* Olson, 1970 (Haglund, 1977). The proportions of the skull roof conform favorably with those of a small-bodied specimen of *Diplocaulus* sp. that was briefly described by Chaney et al. (2005) and the early stages of a detailed ontogenetic series described by Olson (1951a). In palatal view (Fig. 6.3, 6.4), the broad basal plate of the parasphenoid and the rectangular cultriform process are well preserved, as are several of the openings on the palate (e.g., subtemporal fossa, interpterygoid vacuity). The mandibles remain mostly articulated, although sutures are not clearly defined.

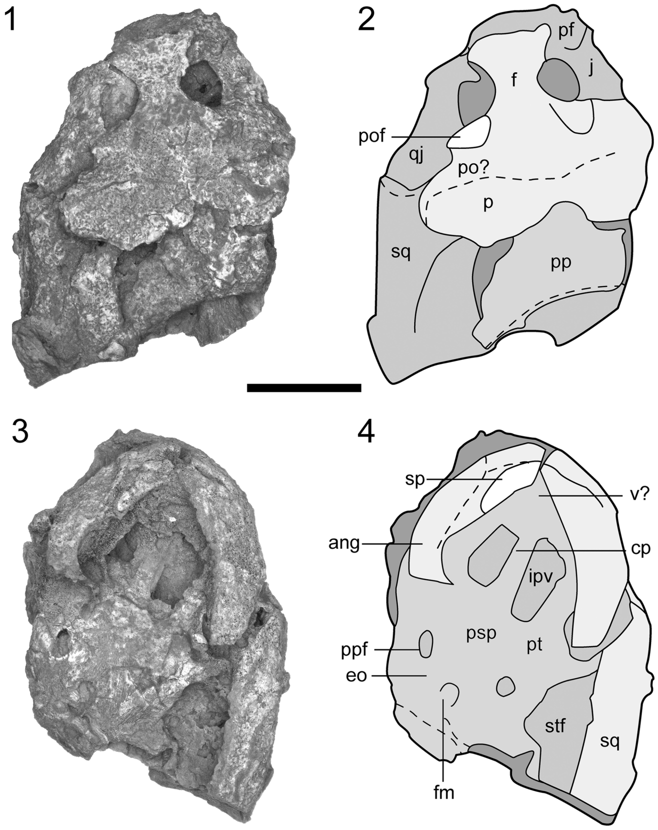

Figure 6. cf. *Diplocaulus* sp. indet., juvenile specimen (TMM 43628-9): (**1**) photograph in dorsal profile; (**2**) illustration of Figure 6.1; (**3**) photograph in ventral profile; (**4**) illustration of Figure 6.3. ang, angular; cp, cultriform process; eo, exoccipital; f, frontal; fm, foramen magnum; ipv, interpterygoid vacuity; j, jugal; p, parietal; pf, prefrontal; po, postorbital; pof, postfrontal; pp, postparietal; ppf, postpterygoid fossa; psp, parasphenoid; pt, pterygoid; qj, quadratojugal; sp, splenial; sq, squamosal; stf, subtemporal fenestra; v, vomer. Scale bar = 1 cm.

The specimen is not sufficiently preserved to confidently separate the specimen from the closely related *Diploceraspis* Beerbower, 1963 (unknown from Texas) based either on phylogenetic characters (e.g., Germain, 2010) or on informal differentiation (e.g., Beerbower, 1963; May and Hall, 2016). The immaturity of this specimen further confounds efforts to identify the subtle distinctions between them, and the referral is based on the indistinguishable nature from juvenile *Diplocaulus* and the abundance of *Diplocaulus* in Texas compared to the absence of *Diploceraspis*.

Remarks.—Differences between the various, highly-conserved species of *Diplocaulus* are relatively minor and characterized only for large-bodied specimens. Furthermore, Olson (1952a, p. 166) distinguished the two species that are found in the Vale Formation, *D. magnicornis* Cope, 1882 (Arroyo Formation and lower Vale) and *D. recurvatus* Olson, 1952a (upper Vale), only by the "frequency of occurrence of the recurved horn," which is not as developed in immature individuals and not well-preserved in these specimens, inhibiting further taxonomic resolution.

Subclass Lepospondyli Zittel, 1888
Order Microsauria Dawson, 1863
Microsauria indet.

Description.—Several poorly-preserved 'microsaurian' vertebrae are preserved within cylindrical segments of matrix, somewhat reminiscent of burrow-like structures. However, 'microsaurs' are highly conserved in their vertebral morphology, and the exposures are limited to different cross-sectional profiles, preventing further resolution of these specimens. Additionally, most early Permian 'microsaurs' are recovered within Recumbirostra, which is identified as having a number of synapomorphies for fossorial behavior, so the occurrence within a putative burrow is also uninformative.

Clade Recumbirostra Anderson, 2007
Family Hapsidopareiontidae Carroll and Gaskill, 1978
Hapsidopareiontidae gen. indet. sp. indet.
Figure 7

Description.—Recumbirostrans, a fossorially-adapted clade of tetrapods, are represented by a complete skull with articulated mandible (TMM 43628-10) measuring 16.3 mm from the premaxilla to the postparietal that was collected from the D3 site. The specimen is slightly compressed dorsoventrally on the left side, resulting in a slightly exaggerated width. In dorsal profile (Fig. 7.1, 7.2), the skull forms an equilateral triangle, with subequal width and length, similar to brachystelechids, pantylids, some ostodolepids, and microbrachomorphs. In lateral profile (Fig. 7.4, 7.5), the skull is nearly entirely flat, with the tip of the snout oriented vertically in a fashion reminiscent of gymnarthrids, pantylids, and hapsidopareiontids. The posterior skull margin extends slightly posteromedially, forming an inverted triangle relative to the main skull roof. The dorsal exposures of the nares and the orbits are limited. The maxillary tooth count, estimated on the left side, is ~19–21. Sutural patterns of the skull roof are difficult to confidently elucidate, particularly on the posterior skull table and on the left side. A noteworthy observation is that the specimen appears to have a large temporal emargination of comparable size and relationship to that of hapsidopareiontids, being open ventrally; framed anteriorly by a reduced postorbital and a posteriorly truncated jugal with a rounded posteroventral terminus; framed dorsally by some combination of the postfrontal, the postorbital, the supratemporal, and the tabular; and framed posteriorly by a tall, slender squamosal that meets a small quadratojugal ventrally. That this opening appears on both sides of the skull suggests that it is not a taphonomic artifact and thus forms the basis for the taxonomic assignment. The emargination in other hapsidopareiontids (Daly, 1973; Bolt & Rieppel, 2009) differs from that of most other emarginated recumbirostrans (e.g., ostodolepids) in its large size, which occupies most of the temporal region. This results from the greater reduction of the temporal elements that produces the narrow, vertically oriented squamosal; the posteriorly truncated jugal with a ventral margin dipping below the level of the maxilla; and the reduced lateral exposure of the tabular (e.g., Carroll & Gaskill, 1978; Anderson et al., 2009); these features are also seen in this specimen. The emargination of *Brachydectes* Cope, 1868 is comparable in size (Pardo & Anderson, 2016) but is open posteriorly. The lacrimal is blocky and tapers anteriorly; it joins both the narial and orbital margins. Two perforations for the lacrimal duct are present on the right side. The frontals are narrowly excluded from the orbital margins by the pre- and postfrontal and posteriorly; they feature two slender processes that incise into the postfrontal and the parietal and a prominent medial flange from the left element that incises into the right counterpart. The dorsal exposure of the premaxillae is minimal. Aspects of the palate and mandibles are mostly unidentifiable. Because of the poor preservation of the material, further taxonomic resolution is not possible. The specimen likely represents a new taxon insofar as it is distinct from all known 'microsaurs' and given the current absence of any 'microsaurs' in the Vale Formation, but because of the poor preservation and the difficulty in characterizing many aspects of the specimen, we refrain from erecting a new taxon at present.

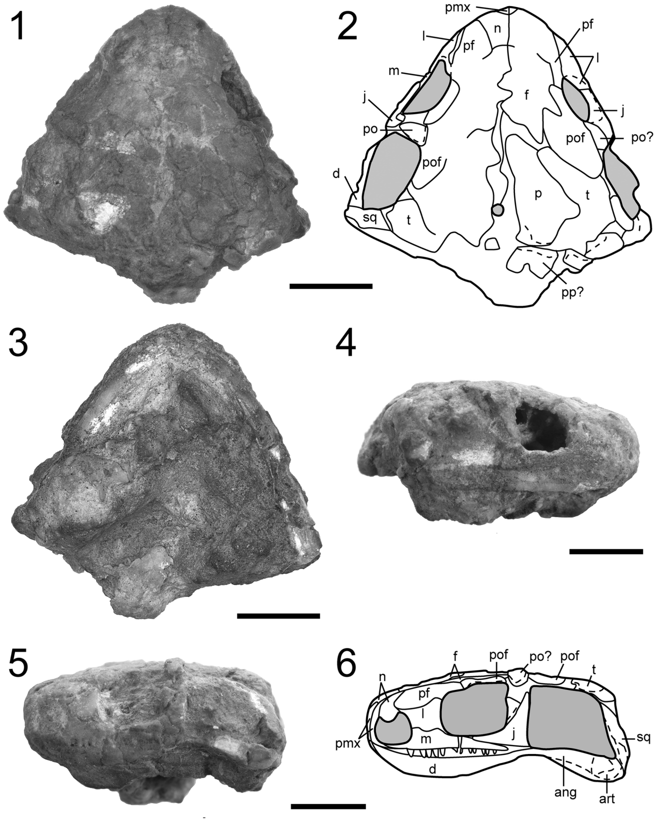

Figure 7. Hapsidopareiontidae gen. indet. sp. indet. (TMM 43628-10): (**1**) photograph in dorsal profile; (**2**) illustration of Figure 7.1; (**3**) photograph in ventral profile; (**4**) photograph in right lateral profile; (**5**) photograph in left lateral profile; (**6**) illustration of Figure 7.5. ang, angular; art, articular; d, dentary; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; pf, prefrontal; pmx, premaxilla; po, postorbital; pof, postfrontal; pp, postparietal; sq, squamosal; t, tabular. Scale bars = 1 cm.

Clade Eureptilia Olson, 1947
Family Captorhinidae Case, 1911
Captorhinidae gen. indet. sp. indet.
Figures. 8.1–8.3, S2

Description.—Indeterminate captorhinid material comprises both postcranial material consisting of several thoracic vertebrae and a right humerus (TMM 43628-11, Fig. S2) and mandibular

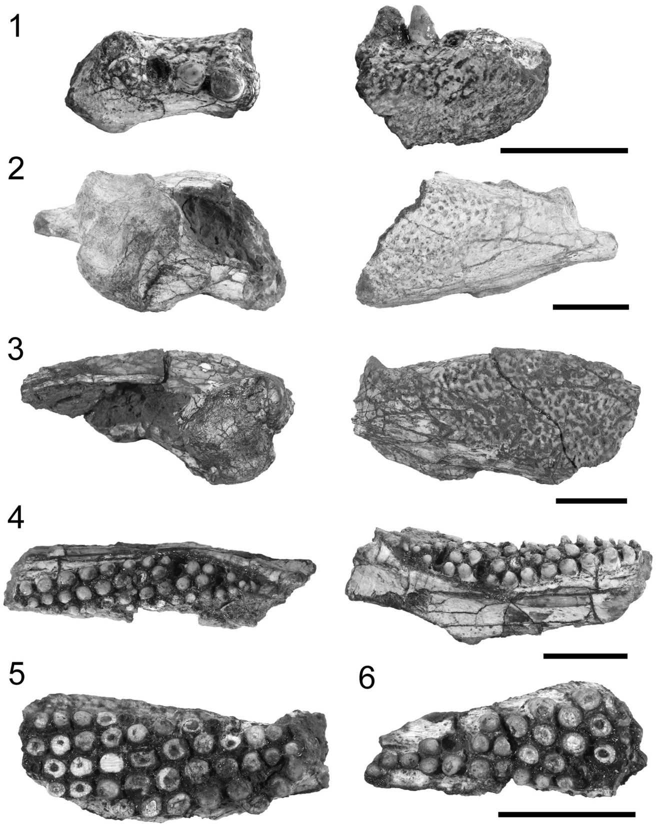

Figure 8. Dentulous fragments of captorhinids: (**1–3**) Captorhinidae gen. indet. sp. indet. (TMM 43628-12): (**1**) right mandibular symphysis in dorsal profile (left) and labial profile (right); (**2**) posterior right lower jaw in dorsal profile (left) and labial profile (right); (**3**) posterior left lower jaw in dorsal profile (left) and labial profile (right); (**4–6**) cf. *Captorhinikos chozaensis* Olson, 1954c (TMM 43628-13): (**4**) partial right dentary in dorsal profile (left) and labial profile (right); (**5**) posterior maxillary fragment in dorsal profile; (**6**) anterior maxillary fragment in dorsal profile. Scale bars = 1 cm.

material consisting of partial left and right mandibles and a partial symphysis with two enlarged (caniniform) teeth (TMM 43628-12, Fig. 8.1–8.3) from the D3 site.

The two partial mandibles (Fig. 8.2, 8.3) are of an identical size but are also of markedly different preservation and cannot be confidently assigned to the same individual. Only the posterior and labial regions are preserved, including portions of the articular, surangular, and possibly the angular; no teeth are present, which inhibits further resolution. The medial wall of the adductor chamber is lost in both specimens. The labial surface is ornamented with the shallow ridging and pitting typical of captorhinids, being less developed and more irregular in patterning than in coeval temnospondyls. The glenoid region is slightly wider than long and consists of medial and lateral facets that are divided by a slight ridge, as in *Labidosaurus* Cope, 1896 (Modesto et al., 2007) and in contrast to *Captorhinus* Cope, 1895 (e.g., Fox and Bowman, 1966). Conversely, the greater development of the retroarticular process and the posterior boss rising dorsally to frame the glenoid are more comparable to *Captorhinus.* Shallow bosses also frame the glenoid anteriorly and laterally. The partial symphysis appears to comprise only the dentary and features two complete teeth with circular cross sections and pointed tips. Positioned anterior to these are an additional empty socket and a lateral protuberance that houses two teeth broken at the level of the jaw. The lateral surface is lightly ornamented with a few pits.

The vertebrae consist mostly of the amphicoelous centra that are tightly sutured to the expanded bases of the neural arches. All of the vertebrae pertain to the presacral region, but some feature prominent, laterally directed transverse processes, indicating a more anterior position, whereas others lack them entirely, indicating a more posterior position. The pre- and postzygapophyses are mostly anteroposteriorly directed, with the facets parallel to each other in the dorsoventral axis. The base of the neural arch is a rough square and becomes slightly longer posteriorly in the column. The spines are frequently damaged so that determining their original height for additional axial determination is not possible. The humerus is typical of early reptiles, featuring expanded ends set at approximate right angles; a thin shaft; a small, oval entepicondylar foramen; and a prominent deltoid process. It is more comparable to the humerus of small captorhinids such as *Captorhinus aguti* Cope, 1895 (Fox and Bowman, 1966) in which the features are less robust than in a large taxon like *Labidosaurus* (Sumida, 1989), but to cite one differential feature, the ectepicondyle of TMM 43628-11 is intermediate between the two. Both elements are relatively conserved among captorhinids and cannot be further resolved in isolation. Because the material comes from the same site as the moradisaurine material described below, it might all pertain to the same individual, or at least to the same taxon, but this cannot be demonstrably proven, hence the separate specimen numbers and taxonomic identifications.

Subfamily Moradisaurinae de Ricqlès and Taquet, 1982
Genus cf. *Captorhinikos* Olson, 1954c

Type species.—*Captorhinikos valensis* Olson, 1954c from the Vale Formation, Texas, by original designation.

cf. *Captorhinikos chozaensis* Olson, 1954c
Figure 8.4–8.6

Holotype.—Cranial and mandibular fragments (CNHM UR 97) from the lower part of the Choza Formation, Texas (Olson, 1954c, fig. 86A–E).

Description.—Dentulous maxillary fragments and a partial dentary (TMM 43628-13) from the D3 site are confidently referable to the Moradisaurinae on the basis of a high number of tooth rows arranged in parallel, and on the basis of the shape of the teeth. Five tooth rows arranged in parallel are present on one maxillary fragment (Fig. 8.5), likely representing a more posterior region of the element, whereas the second fragment (Fig. 8.6) preserves a transition from one to four rows, likely representing the anterior region. The dentary (Fig. 8.4) features the typical torsion along its length and a transition from one to four rows, with teeth arranged in parallel. The teeth are worn and often lacking the tip of the crown, but when intact, they are generally circular in cross section, without any compression, and with rounded tips. An intact anterior dentary tooth from the single-tooth-row region, and a lingual (younger) tooth from the mid-region of the multiple-tooth-row area each have the typical moradisaurine conical shape. The captorhinids from the Arroyo Formation, *Captorhinus* and *Labidosaurus* (Olson, 1989), have up to four rows of somewhat randomly arranged teeth and one row, respectively; both are found in the Vale Formation in addition to *Captorhinikos* Olson, 1954c (Olson and Mead, 1982). An indeterminate moradisaurine tooth plate was described from the Vale Formation by Modesto et al. (2016), but that specimen possesses eight tooth rows and is evidently distinct from TMM 43628-12. The presence of five tooth rows on the maxilla is shared with *Rothianiscus* Olson, 1965, *Gansurhinus* Reisz et al., 2011, and *Captorhinikos*. There is no evidence of the slight cusp and recurvature seen in *Gansurhinus*, which is known from middle Permian deposits (Reisz et al., 2011). *Rothianiscus* is said to have up to seven tooth rows on the dentary (Olson, 1965). The maxillary teeth do not appear to be radiating insofar as the rows remain equally spaced throughout their length in the larger fragment, contrary to those of *Captorhinikos valensis* (see Modesto et al., 2014).

The material is tentatively assigned to *Captorhinikos chozaensis* because the taxon is known to occur in the same geographic region and because it does not display any differences from previously described material (Olson, 1954c; Vaugh, 1958). It should be noted that although Vaughn (1958) did not figure any of the specimens that he referred to this taxon, photographs of Vaughn's specimen (USNM 21275) are publicly available on the Smithsonian Institution's website.

Remarks.—The study of *Captorhinikos valensis* and broader phylogenetic analysis of captorhinids by Modesto et al. (2014) recovered *C. chozaensis* as the sister taxon to a clade containing *Labidosaurus hamatus* Cope, 1895 and the Moradisaurinae and suggested that it could warrant placement in a new genus. Because we have not reappraised the type or previously referred material of *C. chozaensis* and because the referral of the Mud Hill specimens is more tentative given the disparity in stratigraphic occurrence, we utilize the traditional taxonomic standing sensu Olson (1954c).

Order Diadectomorpha Watson, 1917
Family Diadectidae Cope, 1880
Genus cf. *Diadectes* Cope, 1878

Type species.—*Diadectes sideropelicus* Cope, 1878 from the Admiral Formation, Texas, by original designation.

cf. *Diadectes* sp. indet.
Figures. 9, S3–S5

Description.—The vast majority of the well-preserved diadectid is postcranial material, mostly vertebrae, with limb and girdle elements also being represented. An extremely fragmentary parabasisphenoid is also present. Because most diadectid diagnoses are based solely on cranial material, resolution for disarticulated remains is difficult. Most of this material was collected from the D1 site (TMM 43628-4). A large portion of the material pertains to isolated thoracic and caudal centra that are characterized by markedly amphicoelous morphology and the lack of fusion to the neural arches (Fig. S3.1); at least 65 centra have been collected from Mud Hill. The centra are slightly wider than they are long and with concave ventrolateral surfaces that meet at a shallow ventral midline ridge, differing from the centra of coeval synapsids (e.g., *Dimetrodon*), which are narrower and with a sharp ridge. The haemal arches are mostly lost. Neural arches are rare and fragmentary, which is again an indication of immaturity. A pair of articulated neural arches (TMM 43628-6) with the characteristic 'swollen' morphology was collected from the D3 site (Fig. S3.2). A large number of fragmentary ribs are also present. The appendicular material of TMM 43628-4 comprises three humeri (Fig. S4), a femur, a fibula, an ulna, and a radius. Extremely fragmentary limb material is also present. The limbs are characterized by unfinished bone at the ends, indicative of relative immaturity. A significant number of isolated phalanges, elements pertaining to the carpus and tarsus, and a complete left astragalus with a partial, articulated calcaneum are present (Fig. 9); some of these were collected from the D2 site (catalogued as TMM 43628-5). Association between any of these elements is unknown. Pectoral material is represented by a dorsal fragment of a scapulacoracoid with a partial cleithrum (Fig. S5.1) and a partial clavicular stem. Pelvic material is represented by an ilium, a pubis, and an ischium (Fig. S5.2–S5.4); all three are of an appropriate size to pertain to a single individual, but they display a range of preservation and cannot be confidently fit together. At least two individuals were present based on the humeri count, but an association with more diagnostic cranial material (listed below) is unclear. The material cannot be confidently referred to *Diadectes* in the absence of preserved autapomorphies, but the taxon is abundant in the early Permian of North America and is confidently documented at the site (see below).

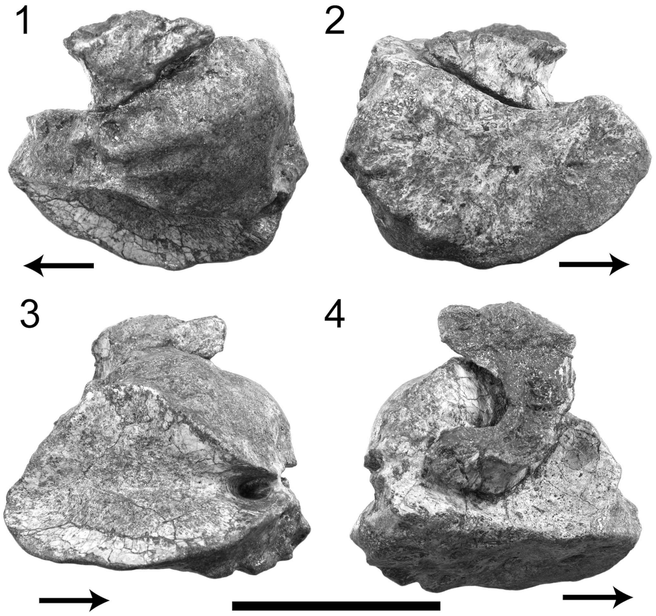

Figure 9. cf. *Diadectes* sp. indet., astragalus and partial tarsal bone (TMM 43628-5) from the D2 site: (**1**) ventral profile; (**2**) posterolateral profile; (**3**) anterior profile; (**4**) medial profile. Arrows point distally. Scale bar = 5 cm.

Diadectes Cope, 1878
Diadectes sp. indet.
Figure 10

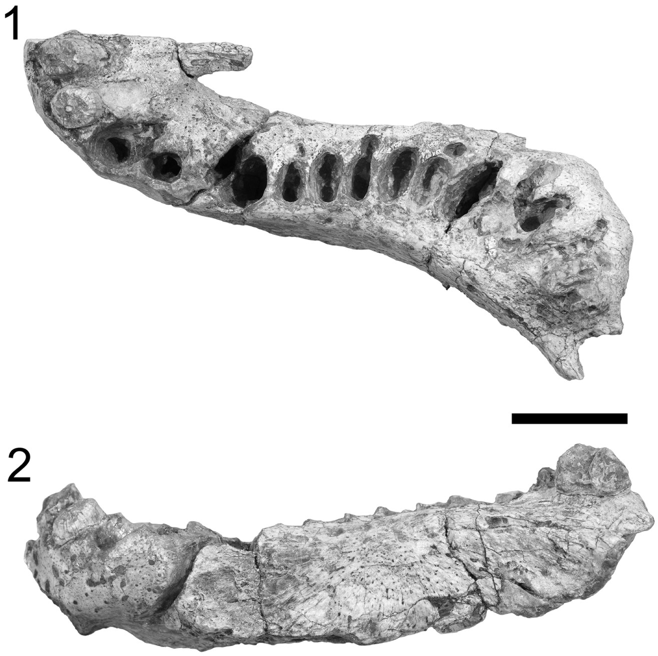

Figure 10. *Diadectes* sp. indet., upper jaw (premaxilla and maxilla) (TMM 43628-2): (**1**) dorsal profile; (**2**) lateral profile. Scale bar = 2 cm.

Description.—Diagnostic material referable to the genus is limited to a right premaxilla articulated with a partial maxilla and associated with a pair of dentaries (TMM 43628-2), which are referred to the genus on the basis of the tooth count and mandibular morphology. The maxilla features a concave dorsal margin and a mostly flat ventral margin that is upturned only at the posterior region. The lateral surface is irregularly ornamented in small pits and shallow grooves. Four tooth positions are present in the premaxilla, two with partial incisiform teeth in place. The incisiform teeth found in diadectids typically feature cusps, but the teeth here are broken off at the level of the jaw. A slight decrease in size posteriorly is noted. Eleven tooth positions are present on the maxilla, which informs its taxonomic identification; most other diadectids possess 12 (e.g., *Orobates* Berman et al., 2004). Only the vacant sockets for the anterior molariform teeth are preserved, but they are compressed into oval cross sections, as in diadectids. The posteriormost teeth are weathered but preserve the general cusped morphology (Fig. 10.2). The tooth sockets increase in width to the seventh position and then decrease posteriorly.

Another dentary (TMM 43628-3) was histologically sampled in a study of dental tissues by LeBlanc and Reisz (2013). Both specimens are from the D1 site and thus indicate the presence of at least two individuals, as with the humeri.

Remarks.—The specific identity of the diadectid material is unresolved, as all previous material recovered from the Vale Formation was undiagnostic below the genus (and in some cases might not even warrant referral below the family level). Olson (1956c) suggested possible affinities of this material with *Diadectes tenuitectus* Cope, 1896, the highest occurring taxon at the time, but the extent of faunal overlap at the specific level between the Vale and the Choza formations remains poorly defined, and the material described here is only sufficient to merit referral to *Diadectes* sp.; the same assignment was utilized in the histological sampling of this material by LeBlanc and Reisz (2013).

Class Synapsida Osborn, 1903
Clade Eupelycosauria Kemp, 1982
Family Varanopidae Romer and Price, 1940
Genus *Varanops* Williston, 1914

Type species.—*Varanosaurus brevirostris* Williston, 1911 from the Arroyo Formation, Texas, by subsequent designation (Williston, 1914).

Varanops brevirostris (Williston, 1911)

1911 *Varanosaurus brevirostris* Williston, p. 85, pls. 1–13.

1914 *Varanops brevirostris* Williston, p. 387.

Holotype.—Nearly complete skull with mandibles and articulated skeleton (FMNH UC 644) from the Arroyo Formation, Texas (Williston, 1911, pls. 1–13).

Description.—Material of *Varanops* from the locality has been previously described with a focus on scavenging of the postcrania of a large, nearly complete skeleton (TMM 43628) from the D2 site by Reisz and Tsuji (2006), and in greater detail in the description of the same specimen (referred to as TMM 43628-1) by Campione and Reisz (2010) in a broader review of *V. brevirostris*. The cranial material comprises a partial skull with a braincase and associated mandible. The postcranial skeleton consists of both humeri, an ulna, a complete femur and one comprising the distal and proximal ends, both tibiae, the pectoral girdle (interclavicle, partial clavicles, and scapulacoracoid), the pelvic girdle (pubis, ilia, and ischia), vertebrae from all major regions (cervical, thoracic, lumbar, sacral, and caudal), ribs, gastralia, and portions of the left manus and left pes. All materials pertaining to this specimen were figured and described in detail by Campione and Reisz (2010).

Remarks.—The revised osteology by Campione and Reisz (2010) was primarily based on the Mud Hill specimen, and no new information is contributed here.

Discussion

Depositional environment and paleoenvironment at Mud Hill.—The geology and paleoenvironmental interpretations of the Vale Formation have been frequently discussed in descriptions of vertebrate taxa (e.g., Olson, 1948; Wilson, 1953), but more extensive discussions have also been presented by Olson (1958) and were well-summarized by Nelson et al. (2013). The red shale facies (Fig. S1.1) is interpreted as alluvial plain deposits resulting from the settling of suspended clay from shallow overbank sheet floods. The absence of well-developed laminations and of varves suggests that perennial lacustrine deposition can be ruled out. The red color strongly supports the early oxidation of clay and indicates prolonged subaerial exposure. Diagenesis associated with early oxidation of the clays results in the formation of nodular hematite. The siltstone-sandstone facies (Fig. S1.2) is interpreted to represent deposition immediately following flood events. The thick laminations of coarse silt and fine sands, and subrounding of the quartz grains in association with orthoclase and granite clasts, indicate flux from a fluvial source. The associated caliche nodules (Fig. S1.3) are almost always found just above or within the siltstone-sandstone facies discussed above and are directly associated with the vertebrate dig sites found on the property. Further characterization of the facies (e.g., paleosol classification) is confounded by the absence of pedogenic structures. The early diagenesis required for caliche development, the presence of calcified root/burrow structures, and frosted subrounded quartz grains in this facies indicate a prolonged period of subaerial exposure. The frosted quartz grains recovered from caliche nodules are indicative of the input of windblown quartz during the period of exposure. Subaerial exposure is also supported by the surface characteristics of the bones. They are uniformly cracked, which is usually caused by prolonged exposure to the sun and strong desiccation (e.g., Behrensmeyer, 1978). Prolonged subaerial exposure of remains would also explain the prevalence of scavenging marks on many of the elements (Reisz and Tsuji, 2006; Flear et al., 2017).

Any determination of the relation of the section at Mud Hill with those of other localities in the Vale Formation, particularly those of a greater distance away, is limited at present without a high-resolution dataset of stratigraphic sections and without more detailed lithological and petrographic descriptions of those localities. As noted by Wilson (1953), most beds appear fairly localized and nontraceable over broad distances, and the fossil record is not sufficient to provide reliable correlation. Similar concerns about the possible scope of extrapolation from a limited localized dataset were noted by Olson (1958, p. 422, 423). The lack of any exposures of the underlying Arroyo Formation and the loss of the overlying Choza Formation at Mud Hill presents additional challenges. Furthermore, the Vale Formation is noted to be several hundred meters thick in some areas (Olson, 1958), whereas the exposure at Mud Hill (Figs. 2, 3) does not exceed 8 m. The general position can be determined based on the stratigraphic patterns listed by Olson (1958) and Olson and Mead (1982). Red shales are persistent throughout the Vale Formation, but there is a pronounced coarsening upward in the upper Vale that results in widespread conglomeratic deposits with clasts that are sourced from the incised strata (Olson and Mead, 1982). The dominance of finer-grained shales and sandstones at Mud Hill suggests that the locality is relatively low, and Mead (1971) suggested that calcareous clasts at the Sid McAdams locality (situated in the lower Vale) were caliche nodules and hematite concretions, both of which are found at Mud Hill.

Previous paleoenvironmental interpretations of the Vale Formation, both on local and regional scales, are consistent with those presented here. The conditions necessary to form caliche, as well as aspects of the facies at Mud Hill (e.g., frosting of the quartz), reflect subaerial exposure that was likely associated with periodic desiccation at the site (further discussed below). Pronounced seasonality, likely associated with the development of a monsoon system around the equatorial regions (e.g., Tabor and Montañez, 2002; Tabor et al., 2002, 2008; Woodhead et al., 2010), would have resulted in episodic inundation and overflowing of stream channels that would have provided both the lithological material and the transport for many of the fossils that are preserved. Subsequent desiccation would result in subaerial weathering of the fossils and their encapsulating horizons and the formation of pedogenic carbonates. Because the section at Mud Hill does not capture any higher-energy depositions such as channel fills, it is unclear whether the localized environment contained perennial bodies of water.

Comparison of Mud Hill with other Vale Formation localities.—Mud Hill is characterized by a relatively abnormal faunal assemblage for the early Permian of Texas (Table 3). Some of the represented taxa (e.g., *Diplocaulus*, captorhinids) are commonly recovered constituents of other deposits, but others are significantly rarer (*Diadectes, Varanops*) or previously unknown (the recumbirostran). Additionally, many of the common constituents of other Vale Formation localities, such as xenacanthid sharks, temnospondyls (e.g., *Trimerorhachis, Eryops*), and *Dimetrodon* are absent at Mud Hill. The specimens of the sole aquatic constituent, *Diplocaulus* (and the other nectridean specimens), are small and likely represent early stages of ontogeny. The lack of a more precise context for the locality within the Vale Formation and relative to the other localities prevents any confident characterization of these faunal trends as faunal turnover, because taphonomic bias remains a likely contributor to some degree; the presence of only extremely small-bodied *Diplocaulus* is one line of evidence in this regard. The disarticulation but general association of some of the specimens at each of these localities is indicative of relatively little transport, and in the case of Mud Hill, in situ preservation with minimal disturbance of skeletal remains.

The Sid McAdams locality features a significant skew toward *Dimetrodon*; Mead (1971) estimated a minimum number of individuals (MNI) of 22, and even relatively common taxa such as *Diplocaulus* and *Trimerorachis* are represented only by a handful of fragmentary specimens at the site. Mead's interpretation, as was the classic interpretation of many Paleozoic and Mesozoic mass death assemblages of a particular taxon, was that some sort of abnormal event produced an unusually dense concentration of fossilized individuals. Because Mud Hill has not been extensively quarried, more individuals, particularly of diadectids affinities, might be preserved but are presently unknown. Whether the general paucity of aquatic forms is associated with a small size and isolation or with ephemerality of the aquatic environment in which the localities formed is unclear. The hypothesis of an ephemeral body of water could explain the Mud Hill site, as it would account for the general paucity of aquatic forms and the relative immaturity of such forms when they occur; it could, for example, have been utilized as a habitat by small diplocaulids. The extreme abundance of *Diplocaulus* at the Stamford locality, which otherwise preserves only the similarly aquatic *Trimerorhachis* and *Xenacanthus* Beyrich, 1848, suggests in situ preservation of an isolated, desiccating aquatic environment (Dalquest and Mamay, 1963). The Blackwood locality features a more even distribution of various taxa with significant

Table 3. Comparison of vertebrate assemblages between major described Vale Formation localities, derived from original locality descriptions (Olson, 1948; Wilson, 1953; Dalquest and Mamay, 1963; Mead, 1971; Olson and Mead, 1982) and the faunal lists of Olson (1958, table 2) and Olson and Mead (1982, table 1). Taxa that occur within the Vale but that are not found at any of these localities are excluded. The sole occurrence of *Cacops* is predicated on the synonymizing of *Trematopsis seltini* Olson, 1956b with *Cacops* cf. *C. aspidephorus* Williston, 1910a by Milner (1985). + = present; − = absent.

Taxon	Northern Vale	Sid McAdams	Blackwood	Stamford	Mud Hill
Chondricthyes					
Xenacanthus Beyrich, 1848	+	+	+	?	−
Actinopterygii					
Lawnia Wilson, 1953	+	+	−	-	−
Sarcopterygii					
Gnathorhiza Cope, 1883	+	+	−	−	−
‘Microsauria’	−	−	−	−	+
Nectridea	−	−	−	−	+
Diplocaulus Cope, 1877a	+	+	+	+	+
Lysorophus Cope, 1877b	+	−	−	−	−
Temnospondyli					
?*Tersomius* Case, 1910	−	+	−	−	−
Cacops Williston, 1910a	+	−	−	−	−
Eryops Cope, 1877b	+	?	+	?	−
Trimerorhachis Cope, 1878	+	+	−	+	−
Reptiliomorpha					
Diadectes Cope, 1878	+	+	+	−	+
Seymouria Broili, 1904	+	+	+	−	−
Reptilia					
Araeoscelis Williston, 1910b	−	+	−	−	−
Captorhinikos Olson, 1954c	−	−	−	−	?
Captorhinus Cope, 1895	−	+	−	−	−
Labidosaurikos Stovall, 1950	+	+	+	−	−
Synapsida					
?*Ophiacodon* Marsh, 1878	−	+	−	−	−
Dimetrodon Cope, 1878	+	+	+	−	−
Varanops Williston, 1914	−	−	−	−	+

Table 4. Revised vertebrate faunal list of the Vale Formation derived from Olson and Mead (1982). Although we have eliminated taxa that have since been synonymized with other Vale taxa (e.g., *Trematopsis seltini* with *Cacops* cf. *C. aspidephorus*) and updated nomenclature for taxa synonymized with non-Vale taxa (e.g., *Trematops milleri* Williston, 1909a with *Acheloma cumminsi* Cope, 1882), the original taxonomic assignments, including somewhat tentative referrals to particular species, e.g., ‘*Xenacanthus*’ *platypternus* (Cope, 1884), remain unchanged unless figures provide strong evidence to contradict Olson and Mead’s classification.

Chondrichthyes
  Xenacanthus cf. *X. platypternus* Cope, 1884
Actinopterygii
  Lawnia taylorensis Wilson, 1953
Sarcopterygii
  Gnathorhiza dikeloda Olson, 1951b
  Gnathorhiza serrata Cope, 1883
Lepospondyli
  Diplocaulus magnicornis Cope, 1882
  Diplocaulus recurvatus Olson, 1952a
  Hapsidopareiontidae gen. indet. sp. indet.
  Lysorophus tricarinatus Cope, 1877b
  Peronedon primus Olson, 1970
Temnospondyli
  Cacops cf. *C. aspidephorus* Williston, 1910a
  Eryops megacephalus Cope, 1877b
  ?*Tersomius* sp. indet.
  Trimerorhachis insignis Cope, 1878
Reptiliomorpha
  Diadectes sp. indet.
  Seymouria baylorensis Broili, 1904
  Seymouria grandis Olson, 1979b
  Waggoneria knoxensis Olson, 1951b
Reptilia
  Araeoscelis gracilis Williston, 1910b
  Captorhinikos valensis Olson, 1954c
  Captorhinoides valensis Olson, 1954c
  Captorhinus aguti Cope, 1895
  Labidosaurikos meachami Stovall, 1950
  cf. *Rothianiscus* sp. indet.
Synapsida
  Casea broilii Williston, 1910b
  Casea nicholsi Olson, 1954a
  Dimetrodon giganhomogenes Case, 1907
  Edaphosauridae gen. indet. sp. indet.
  ?*Ophiacodon* sp. indet.
  Varanops brevirostris (Williston, 1911)

disarticulation and abrasion of the material, indicative of greater transport and sorting (Olson and Mead, 1982).

Several aspects of the taxonomic assemblage merit further exploration as well in the broader context of the vertebrate assemblage characterized from the Vale Formation (Tables 3, 4). ‘Microsaurs’ have a well-documented record from the early Permian of Texas, including taxa such as *Pantylus* Cope, 1881; the gymnarthrids *Cardiocephalus* Broili, 1904, *Euryodus* Olson, 1939, and *Pariotichus* Cope, 1878; and the ostodolepids *Ostodolepis* Williston, 1913, *Pelodosotis* Carroll and Gaskill, 1978, and *Micraroter* Daly, 1973 (BPI 3839), but all of these taxa occur in the Arroyo Formation or older units (Carroll and Gaskill, 1978). The hapsidopareiontid skull noted here thus represents the first ‘microsaur’ of the Vale Formation and possibly one of the youngest ‘microsaurs’ known to date. Early Permian localities within North America and outside of Texas that preserve ‘microsaurs’ are limited to two sites, each bearing a number of taxa. A locality near Norman, Oklahoma that is considered equivalent to the Choza Formation includes the recumbirostrans *Rhynchonkos* Schultze and Foreman, 1981, *Aletremyti* Szostakiwskyj, Pardo, and Anderson, 2015, and *Dvellecanus* Szostakiwskyj, Pardo, and Anderson, 2015 (Olson, 1970; Szostakiwskyj et al., 2015), and the site at South Grandfield, Oklahoma that is considered equivalent to the Arroyo Formation includes *Hapsidopareion* Daly, 1973, *Cardiocephalus*, *Micraroter*, and possibly *Pariotichus* (Daly, 1973). However, suggested biostratigraphic correlation of the latter site has often been made with the well-known Richards Spur locality, which was similarly proposed as being equivalent to the Arroyo Formation until it was resolved as being Sakmarian in age based on radioisotopic work (Woodhead et al., 2010); this could accordingly pull back the age of South Grandfield. Because of the poor preservation of sutural contacts, it is difficult to refine the taxonomic identity of TMM 43628-10, but it appears distinct from the clade comprising the three taxa from the Choza Formation equivalent on several grounds (e.g., weakly recumbent snout, higher maxillary tooth count).

The diadectid material represents the most complete assemblage of material from the clade known from the entirety of the Vale Formation. In all likelihood, all of the diadectid material belongs to *Diadectes*; the size of all materials is consistent for a few modestly large (but still immature) individuals, but the postcrania of diadectids is relatively conserved and thus non-referable under an apomophy-based identification system. Even when considering only the material that is properly referable, the *Diadectes* from Mud Hill is still quite significant in the context of the Vale Formation. Prior to this study, *Diadectes* was represented only by a single tooth (TMM 30966-321) from the Sid McAdams locality (lower Vale), one vertebra from the lower Vale Formation of Baylor County (CNHM-UR 270), and two fragments, an incomplete quadrate (UCLA VP 558) and an incomplete vertebra from the Blackwood site (middle Vale) (Olson, 1956c; Olson and Mead, 1982); under an apomorphy-based identification, most of this material is probably referable only to Diadectidae gen. indet. sp. indet. In general, the taxonomy of *Diadectes* needs revision, because taxonomic separation at the species level is often on the basis of relative differences in size and proportions of the skeleton and stratigraphic occurrence within the early Permian. *Diadectes tenuitectus* is the highest occurring taxon within Texas, but referable material is also known only from the Arroyo Formation (Olson, 1956c). Despite a significantly improved record of diadectids in the Vale Formation via the Mud Hill material, the general paucity of the clade could still be correlated with a decline in abundance of these large herbivores, possibly as a result of increased aridity and subsequent changes to the local environment. The preservation of diadectids at this particular locality is probably associated with the nuances of the depositional environment; low-energy aquatic settings were likely conducive for vegetation.

The documentation of *Varanops brevirostris* at Mud Hill in contrast to other Vale Formation localities is more difficult to explain. No varanopid material has ever been confidently reported from the Vale Formation, although the lack of stratigraphic resolution of the Cacops Bone Bed to the upper Arroyo Formation or to the lower Vale Formation might alter this pattern. The specimen from Mud Hill is the first unequivocal documentation of the taxon in the Vale. Varanopids where they occur are typically restricted to a single taxon, but this does not explain the general absence of *Varanops* from other localities in the Vale Formation; the taxon is otherwise known only from the Cacops Bone Bed and tentatively from the Richards Spur locality (Maddin et al., 2006; Campione and Reisz, 2010). Beyond inference of in situ preservation based on the exceptional articulation of much of the skeleton, little more can be confidently proposed regarding explanations for its apparent paucity. It might simply be that varanopids were exceedingly rare in Texas throughout the early Permian; younger varanopids (e.g., *Varanodon* Olson, 1965; *Watongia* Olson, 1974) are found outside of Texas.

Conclusion

The Mud Hill locality described here is the first major vertebrate-bearing locality to be described from the Vale Formation in several decades. Preservation of rare forms (diadectids), previously undocumented forms (hapsidopareiontid), and forms only tentatively reported from the formation (*Varanops*) expand both the biostratigraphic ranges of these clades and the tetrapod assemblage of the Vale at large (Table 4), and augment the morphological characterizations of these groups. The unusual taxonomic assemblage at Mud Hill is indicative of an atypical depositional environment and probably represents a low-energy aquatic environment in which most organisms were preserved in situ and in which obligately aquatic taxa (e.g., temnospondyls, fishes) were not abundant or permanent constituents.

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Accessibility of supplemental data

Data available (Figs. S1 – S5) from the Dryad Digital Repository: https://doi.org/10.5061/dryad.4rc74sp.

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