



Vertebrate fossils in the upper Pennsylvanian (Missourian) Tinajas Member of the Atrasado Formation, Socorro County, New Mexico

Susan K. Harris and Spencer G. Lucas

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VERTEBRATE FOSSILS IN THE UPPER PENNSYLVANIAN (MISSOURIAN) TINAJAS MEMBER OF THE ATRASADO FORMATION, SOCORRO COUNTY, NEW MEXICO

SUSAN K. HARRIS¹ AND SPENCER G. LUCAS¹

¹New Mexico Museum of Natural History, 1801 Mountain Road NW, Albuquerque, NM 87104; emailsharris@icloud.com

ABSTRACT—In the Quebradas area of Socorro County, New Mexico, the Middle-Late Pennsylvanian Atrasado Formation yields diverse non-marine and marine fossil assemblages. South of Arroyo del Tajo, NMMNH (New Mexico Museum of Natural History) locality 12323 is a recently discovered and unique fossil locality in floodplain deposits of the Upper Pennsylvanian (Missourian) Tinajas Member of the Atrasado Formation. The vertebrate fossil assemblage of NMMNH locality 12323 includes vertebral centra that pertain to a rhizodont sarcopterygian, cf. *Strepsodus*, postcranial elements comparable to the eupelycosaurian genus *Sphenacodon*, and a large number of elements of uncertain identity. Vertebrate coprolites and plant stems also occur in the deposit, which is a 1.3 m thick interval of red (moderate reddish-brown) mudstone 4–5 m above the black shale lake deposits of the Tinajas. This plant- and bone-bearing bed is at the top of a 3.4 m thick interval of moderate reddish-brown mudstone and intercalated laminar micaceous sandstone. The red mudstones are mottled, contain kaolinitic lenses, and are interpreted as pedogenically modified floodplain deposits. Fossils of NMMNH locality 12323 represent the oldest known assemblage of both aquatic and terrestrial vertebrates from New Mexico and document the oldest record of the eupelycosaur cf. *Sphenacodon*.

INTRODUCTION

The Pennsylvanian section in the Cerros de Amado and vicinity, northeast of Socorro, New Mexico, is approximately 800 m thick and consists of strata of marine and nonmarine origin assigned to the (in ascending order) Sandia, Gray Mesa, and Atrasado formations (Lucas et al., 2009a; Krainer et al., 2017). These are strata of Middle-Late Pennsylvanian (Atokan-Virgilian) age that contain a diversity of fossil assemblages of traces, terrestrial plants, marine micro- and macroinvertebrates and vertebrates (e.g., Lerner et al., 2009; Lucas et al., 2009a; Barrick et al., 2013; Berman et al., 2015; DiMichele et al., 2017; Harris et al., 2017; Hodnett and Lucas, 2017; Krainer et al., 2017). Most of the vertebrate fossils are fishes of marine origin (Hodnett and Lucas, 2017). Here, we document an unusual vertebrate fossil assemblage of freshwater fish and tetrapods recently discovered in the Tinajas Member of the Atrasado Formation, strata of Late Pennsylvanian (Missourian) age. This is the oldest known assemblage of both aquatic and terrestrial vertebrates from New Mexico and documents the oldest record of the eupelycosaur cf. *Sphenacodon*, a significant stratigraphic range extension. In this paper, NMMNH refers to the New Mexico Museum of Natural History in Albuquerque, New Mexico, and NHMUK refers to the Natural History Museum, United Kingdom, London.

STRATIGRAPHIC CONTEXT

The vertebrate fossils from locality 12323 are present in the upper 1.3 m of a 3.4 m thick interval of sandstone and red mudstone. These are strata of the Tinajas Member of the Atrasado Formation, Missourian age (Lucas et al., 2009a; Barrick et al., 2013). The bone-bearing strata at locality 12323 are about 4–5 m above the Tinajas black shale, a prominent marker bed in the

Tinajas Member (Fig. 1).

The sandstone beds in this interval are laminar and micaceous, and the red mudstones are color mottled and locally kaolinitic, features we take to indicate pedogenesis (e.g., Lucas and Tanner, 2021). The strata that yield the vertebrate fossils at locality 12323 thus are floodplain deposits of pedogenically modified mudstone and sheetflood deposits of laminar sandstone. They represent a rare example of probable floodplain deposits in the Tinajas Member, which is mostly composed of laminated siltstones and shales of lacustrine and estuarine origin, marine limestones, and river-channel sandstones and conglomerates (Lucas et al., 2009a; DiMichele et al., 2017; Krainer et al., 2017).

VERTEBRATE FOSSILS

More than 50 fragmentary, iron-permineralized vertebrate fossils were recovered from NMMNH locality 12323 over a surface area of approximately 10–12 square meters. Many specimens are heavily encrusted with a dense overlay of iron oxide that makes both mechanical and chemical preparation largely unsuccessful. Therefore, the following identifications are provisional.

cf. *Strepsodus sauroides*

More than 20 thin, disc-like vertebral centra (Fig. 2A–F), some of which are articulated in short strings of two to four elements (Fig. 2F), were recovered from NMMNH locality 12323. NMMNH P-83787 (Fig. 2A–D) is a large, bipartite centrum consisting of a separate pleurocentrum (Fig. 2D) and intercentrum (Fig. 2C). Where not occluded by matrix, each of these elements bears a large notochordal foramen with a

diameter of 10–12 mm at its center. The intercentrum has a maximum transverse diameter of 37 mm, and the somewhat larger pleurocentrum is 41 mm in the same dimension. The height of the pleurocentrum (47 mm) is also slightly greater than that of the intercentrum (41 mm) because of a low, rounded prominence positioned at its dorsal center, which is likely the attachment surface for the neural arch. Both elements are very thin: the anteroposterior length of the pleurocentrum is

6 mm, and the intercentrum is only 4 mm (these values are somewhat inflated by an adhering layer of iron oxide). The articular faces of both central elements (Fig. 2C–D) are slightly beveled. This is more clearly seen on the articular face of the intercentrum where a shallow emargination is positioned on either side of its lateral border. The articular face of the pleurocentrum has small complementary prominences for reception of the intercentrum.

NMMNH P-83788 (Fig. 2E) is a somewhat smaller, isolated notochordal pleurocentrum (transverse width 32 mm; dorsoventral height 41 mm; anteroposterior length 5 mm). It differs from the pleurocentrum of NMMNH P-83787 in its overall oval shape, but bears a low, rounded prominence at its dorsal center, as does NMMNH P-83787.

NMMNH P-83785 (Fig. 2F) is a short string of four articulated central elements: one pleurocentrum and the dorsal portion of a second, as well as two intervening intercentra. The maximum transverse diameter of these articulated elements is 42 mm, whereas their maximum dorsoventral height in articulation is 25 mm, and their maximum anteroposterior length in articulation is 25 mm. Although the overall dimensions of the central elements of NMMNH P-83785 and P-83787 are similar, the maximum notochordal diameter of the articulated elements of NMMNH P-83785 (21 mm) is approximately twice that of NMMNH P-83787.

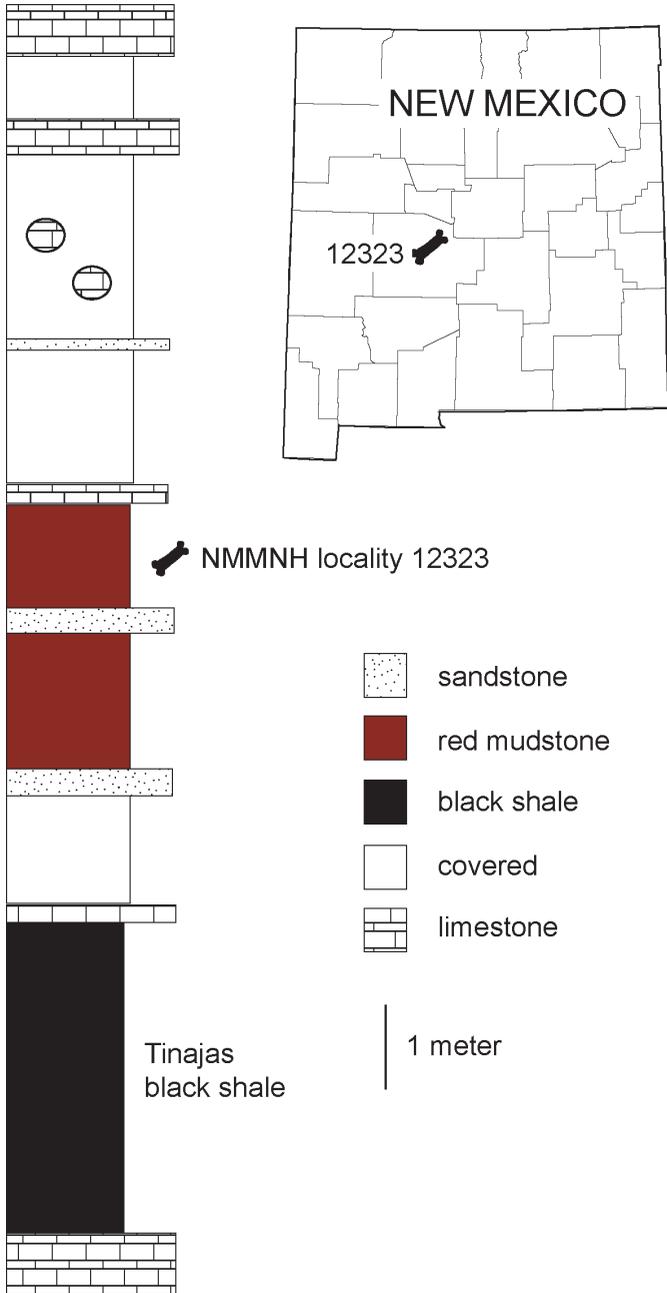


FIGURE 1. Index map and stratigraphic section locating the fossil site (locality 12323) discussed in this paper. The Tinajas Member of the Atrasado Formation is a Missourian interval of that unit, which consists of eight members that range in age from Desmoinesian to Virgilian (see, e.g., Lucas et al., 2009a). The fossils discussed here were collected from the lower-middle part of the Tinajas Member a short distance above the “Tinajas black shale” that provides a locally distinctive marker bed (see Lucas et al., this volume, fig. 4a, top of right-hand column).

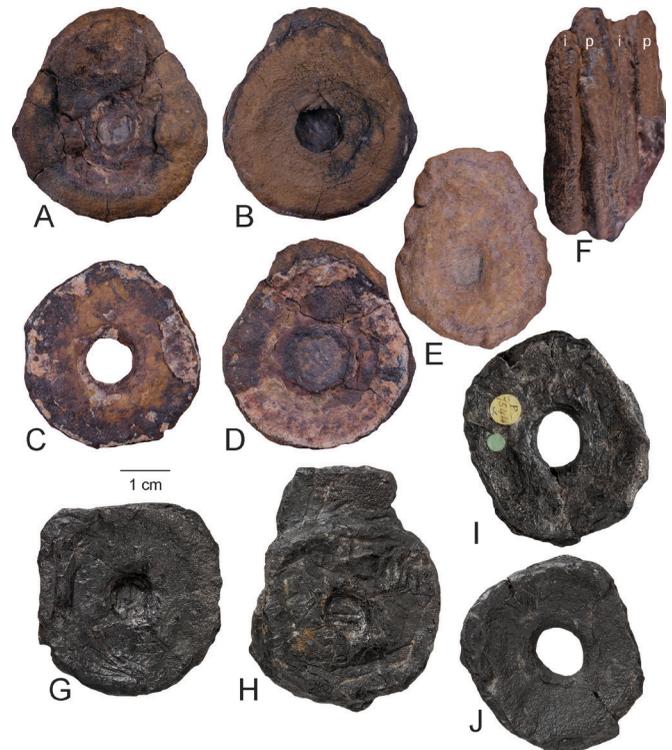


FIGURE 2. Central elements pertaining to cf. *Strepsodus sauroides* collected from NMMNH locality 12323 and from North Staffordshire, England. A–D, NMMNH P-83787, articulated bipartite centrum in A, posterior view, B, anterior view, C, articular face of intercentrum, D, articular face of pleurocentrum. E, NMMNH P-83788, isolated central element. F, NMMNH P-83785, four articulated central elements. G–J, four isolated central elements collected by John Ward from North Staffordshire, England, NHMUK PV 7544a–d. Abbreviations: i, intercentrum; p, pleurocentrum.

Discussion: Defining characters (autapomorphies) of the genus *Strepsodus* are limited to those of its sigmoid teeth with raised striae on the enamel (Jeffery, 2006). Therefore, because NMMNH P-83785, P-83787, and P-83788 were not collected in close association with diagnostic *Strepsodus* teeth, attribution to the genus is uncertain. However, the NMMNH central elements described above strongly resemble multiple *Strepsodus sauroides* centra collected more than a century ago from a locality in North Staffordshire, England (Ward, 1890, pl. II, fig. 25), and later accessioned into the Natural History Museum, London, as NHMUK PV P 7544a–d (Fig. 2G–J). The North Staffordshire locality has special significance for the genus *Strepsodus* because it is the locality from which Jeffery (2006) selected a tooth as the neotype specimen for *Strepsodus sauroides*. Cylindrical centra attributed to *Strepsodus sauroides* from two localities in Scotland, Ballagan Formation (Tournasian) at Burnmouth (Otoo et al., 2018), and the Coal Measures ironstone pit of Palace Craig in Airdrie (Andrews and Westoll, 1970), do not co-occur with diagnostic *Strepsodus* teeth.

cf. *Sphenacodon* sp.

NMMNH P-83790 is a small (preserved length 12 mm), notochordal centrum and attached neural arch (Fig. 3A) and associated centrum (Fig. 3B–C). The centra are V-shaped in cross section and bear a sharp ventral keel, characteristic of the Sphenacodontidae (Romer and Price, 1940). In left lateral view (Fig. 3A), a slender transverse process is posteroventrally directed and lies adjacent to the centrum, indicating it is likely from the caudal region.

NMMNH P-83797 (Fig. 3E–G) is a large neural arch and preserved base of the neural spine. The maximum anteroposterior length of the neural arch is 39 mm, and its preserved height is 51 mm. Many features of NMMNH P-83797 are obscured by crushing and iron oxide encrustation. However, the cross section exposed at the base of the broken neural spine is visible and forms an oval to triangular outline similar to that of a transverse section through the proximal region of a *Sphenacodon* dorsal neural spine illustrated by Huttenlocker et al. (2010, fig. 6A).

NMMNH P-83794 (Fig. 3D) consists of two broken neural spine segments attached by iron oxide to the surface of an oval concretion. The height of the longer segment is 65 mm, and the shorter segment is 39 mm. The longer spine segment increases in anteroposterior length from 16 mm at one end to 20 mm at the opposite end, and its transverse width is 4 mm. Blade-like neural spines, in which the anteroposterior length is four times that of the distal width, are indicative of the eupelycosaurian genus *Sphenacodon* (Romer and Price, 1940).

NMMNH P-83800 (Fig. 3H) is a moderately large left femur and probable fibula preserved together within a dense iron oxide concretion. Although the femur is heavily encrusted along its length of 98 mm, the outline of its slender shaft and distal condyles is visible. NMMNH P-83800 strongly resembles distal femora with well-ossified posterior and anterior condyles illustrated and identified as sphenacodontine (Harris et al., 2004, fig. 12C–D, NMMNH P-32089) and *Sphenacodon*

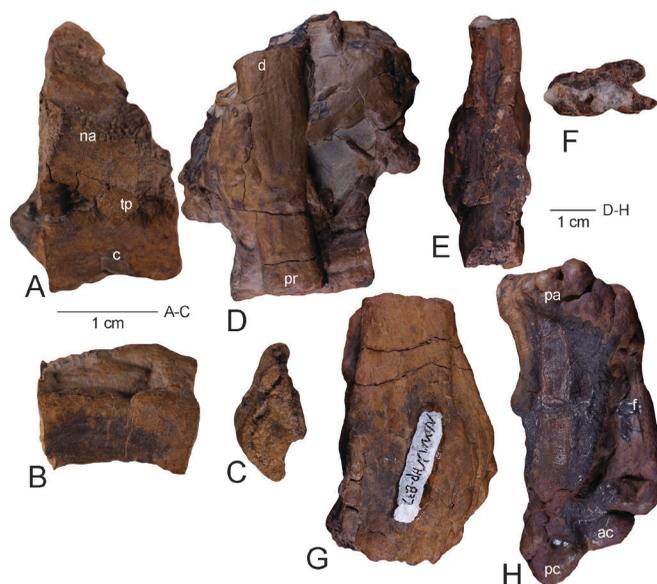


FIGURE 3. Sphenacodontid elements from NMMNH locality 12323. A–C, NMMNH P-83790, associated caudal vertebrae in A–B, lateral views, and C, cross sectional view of B. D, NMMNH P-83794, cf. *Sphenacodon* neural spine segments on concretion. E–G, NMMNH P-83797, cf. *Sphenacodon* neural arch in E, anterior view, F, cross sectional view at neural spine break, and G, lateral view. H, NMMNH P-83800, sphenacodontid femur and probable fibula in ventral view. Abbreviations: ac, anterior condyle; c, centrum; d, distal end; f, fibula; na, neural arch; pa, proximal articular surface; pc, posterior condyle; pr, proximal end; tp, transverse process.

sp. (Lucas et al., 2005, fig. 7H–J, NMMNH P-46534). Its lack of a supracondylar process on the posterior condyle, however, indicates NMMNH P-83800 may represent a juvenile or perhaps a relatively gracile *Sphenacodon* species.

Indeterminate Vertebrate Elements

The fossil assemblage from NMMNH P-12323 includes more than 20 elements of uncertain taxonomic affinity, of which three were selected for illustration. These specimens include NMMNH P-83792 (Fig. 4A–B), a large, enigmatic partial maxilla with 14 empty alveoli in which closely spaced, cylindrical teeth of uniform size were apparently attached to its lingual surface; NMMNH P-83798 (Fig. 4C–D), a rectangular pectoral element, possibly the dorsal lamina of a cleithrum; and NMMNH P-83799 (Fig. 4E), a partial pelvic girdle, preserving only the ischium and pubis.

Coprolites

Coprolites are common at NMMNH locality 12323 and range from small, spiral forms produced by chondrichthyans (NMMNH P-83779, Fig. 5F) to those of large, ovoid to amorphous form, likely of tetrapod origin (NMMNH P-83774, Fig. 5E; see Harris et al., 2017).

Permineralized Plant Fossils

More than 100 fragmentary iron-permineralized plant fossils occur together with the vertebrate fossils at NMMNH

locality 12323. These include a large stem with narrow vertical ribs and horizontal nodes characteristic of the sphenop-sid “horsetail” genus *Calamites* (NMMNH P-83781, Fig. 5A; Lucas et al., 2009b; DiMichele et al., 2017), an axis segment with a pattern of regular-shaped leaf scars comparable to those of the coniferophyte *Dicranophyllum* (NMMNH P-83784, Fig. 5D; Van Der Pas et al., 2017), woody axes of small diameter (NMMNH P-83780, Fig. 5C), likely conifers (W. DiMichele, pers. commun., 2018), and radially symmetrical seed casts (NMMNH P-83783, Fig. 5B), which are generally associated with pteridosperms (primitive seed plants; DiMichele et al., 2017). Considered together, these plant fossils point to a seasonally dry landscape with calamitaleans living near the water body (W. DiMichele, pers. commun., 2018).

DISCUSSION

Most of the pre-Permian fossil vertebrates from New Mexico are fishes of marine origin (Hodnett and Lucas, 2015). Pennsylvanian tetrapod fossils are mostly amphibians, but also include amniotes known from the Virgilian strata of the Cutler Group in the Cañon del Cobre of Rio Arriba County in the northern part of the state (Berman et al., 2015). The vertebrate-fossil assemblage documented here is the oldest known assemblage of both aquatic and terrestrial vertebrates from New Mexico.

Fossils of large, freshwater, predatory tetrapodomorph fish-

es of the family Rhizodontidae are rare in New Mexico, where, to date, only one record other than the record documented here is known. Lerner et al. (2009) reported rhizodontiform scales, teeth, and skull bones, also likely referable to *Strepsodus*, from the lacustrine Tinajas black shale unit in the Tinajas Member of the Atrasado Formation east of Socorro.

The Sphenacodontidae is a carnivorous family of pelycosaurian-grade synapsids with sprawling to semi-erect posture. The genus *Sphenacodon* is known principally from New Mexico and is distinguished from the better-known and closely related *Dimetrodon* by the shape of its neural spines. In *Sphenacodon*, blade-like neural spines of its vertebrae formed a low crest along its back, whereas elongate neural spines (with a figure eight cross section) formed a sail-like structure in the genus *Dimetrodon*.

The genus *Sphenacodon* includes two species, *S. ferox* and *S. ferocior*, both of which have abundant records in early Permian (Wolfcampian) strata of New Mexico (see Romer, 1937; Vaughn, 1969; Eberth, 1985; Lucas et al., 2005, 2010, 2012; Spielmann et al., 2010; Rinehart et al., 2007; Berman et al., 2015). Records of *Sphenacodon* from Upper Pennsylvanian (Virgilian/Gzhelian) strata are rare, but are known from both New Mexico (Red Tanks Member of the Bursum Formation: Harris et al., 2004; Cutler Group in the Cañon del Cobre) and Colorado (Halgaito Formation of the Cutler Group: Sumida, 1999a, 1999b; Huttenlocker et al., 2018, 2020). Lucas (2006, 2018, 2021) used the first appearance datum (FAD) of *Sphenacodon* to define the beginning of the

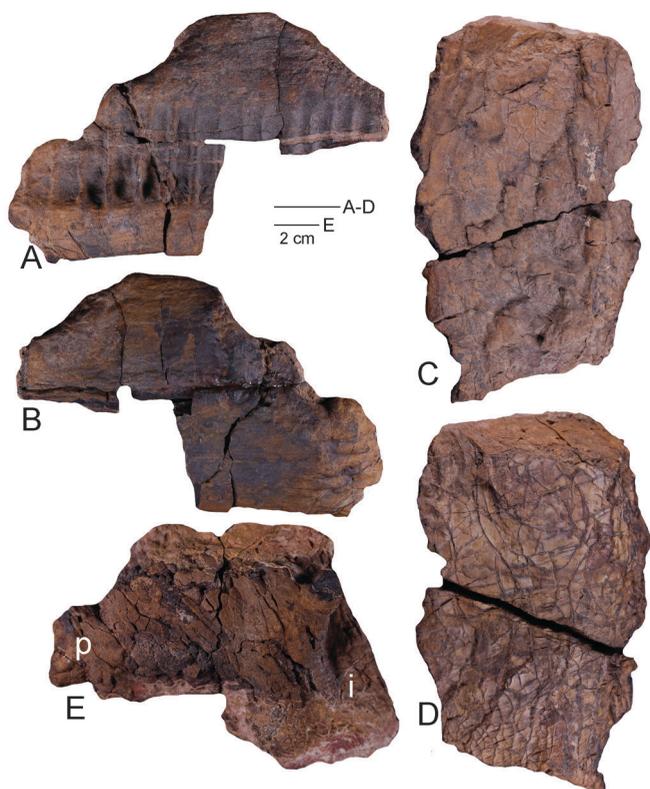


FIGURE 4. Indeterminate vertebrate elements from NMMNH locality 12323. A–B, maxilla, NMMNH P-83792, in A, medial and B, lateral views. C–D, cleithrum, NMMNH P-83798, in C, internal and D, external views. E, partial pelvis, NMMNH P-83799, in lateral view. Abbreviations: i, ischium; p, pubis.

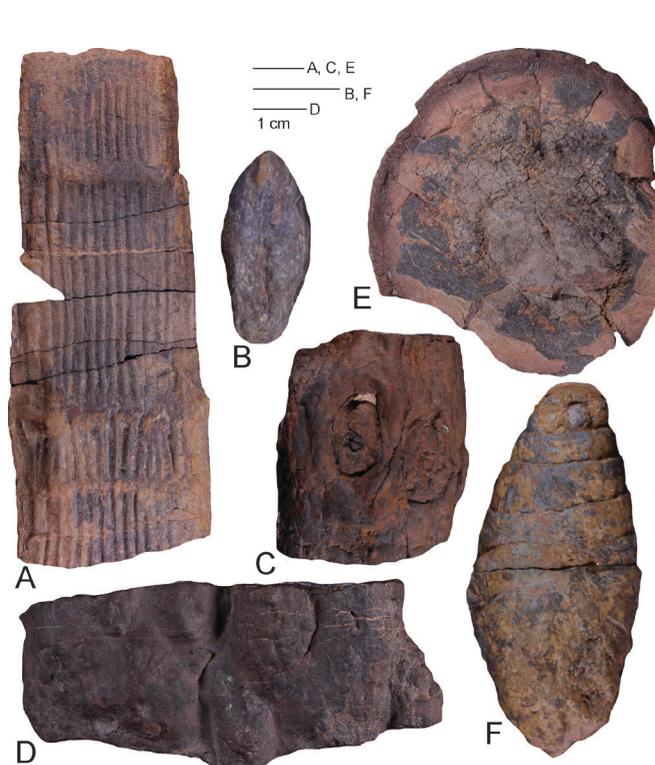


FIGURE 5. Iron permineralized plant fossils and coprolites from NMMNH locality 12323. A, NMMNH P-83781, *Calamites* stem. B, NMMNH P-83783, seed cast. C, NMMNH P-83780, conifer axis segment. D, *Dicranophyllum* axis segment. E, NMMNH P-83774, amorphous coprolite in concretion. F, NMMNH P-83779, spiral coprolite.

Coyotean land-vertebrate faunachron, an interval of time that crosses the Pennsylvanian-Permian boundary. Thus, the lowest occurrence (LO) of *Sphenacodon* in New Mexico (and in the Halgaito Formation) was understood to be in strata of Virgilian/Gzhelian (latest Pennsylvanian) age. The occurrence of cf. *Sphenacodon* in Missourian/Kasimovian age strata of the Tinajas Member of the Atrasado Formation represents a possible stratigraphic range extension for the genus and likely positions *Sphenacodon* as a denizen of both the Cobrean and Coyotean land-vertebrate faunachrons. If this is correct, it necessitates a new criterion to define the beginning of Coyotean time, a role perhaps best filled by the FAD of the diadectomorph *Diadectes* (cf. Lucas, 2006, fig. 7).

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