A JUVENILE SKELETON OF THE NECTRIDEAN AMPHIBIAN *DIPLOCAULUS* AND ASSOCIATED FLORA AND FAUNA FROM THE MITCHELL CREEK FLATS LOCALITY (UPPER WAGGONER RANCH FORMATION; EARLY PERMIAN), BAYLOR COUNTY, NORTH-CENTRAL TEXAS, USA

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Abstract—A well-preserved skeleton of a tiny individual of the nectridean amphibian *Diplocaulus* was found in association with other Early Permian animal remains and a flora in a gray mudstone at a site called Mitchell Creek Flats in Baylor County, north-central Texas. The locality has the sedimentological attributes of a pond deposit. The skeleton of *Diplocaulus* sp. is noteworthy for its completeness and small size, and appears to represent a juvenile individual. The associated plant material is beautifully preserved and comprises the sphenopsids *Annularia* and *Calamites*, the conifer? *Brachyphyllum*, possible cycads represented by one or possibly two forms of *Taeniopteris*, three gigantopterids—*Delnorta*, *Cathaysiopteris*, and *Gigantopteridium* —and three unidentified callipterids. Several unidentified narrow trunks were found at the base of the deposit, apparently washed up against the northern margin of the pond. Other faunal material from the deposit comprises myalinitid bivalves, conchostracans, a tooth of a xenacanthid shark, and a palaonisciform fish.

INTRODUCTION

Complete skeletons of Early Permian vertebrates are rare in north-central Texas, where much collecting has been done for about 150 years (Fig. 1). In addition, most vertebrate remains have been found by surface prospecting, a technique that generally precludes recovery of small skeletons. For these reasons, the discovery of a tiny skeleton of *Diplocaulus* (Figs. 2-3) is particularly significant. This specimen is nearly complete, lacking only the distal portion of the tail and a number of elements of the appendicular skeleton. It was discovered during quarrying of a site for fossil plants, which are noteworthy for the quality of their preservation and the peculiarity of some elements of the flora.

The nectridean amphibian *Diplocaulus* Cope, 1877 is common in the Early Permian in Texas and Early Permian in Oklahoma. It is also known from the Late Pennsylvanian of Illinois and Pennsylvania as well as the Permian of Morocco (Carroll et al., 1998). Adult specimens of this taxon are readily characterized by the “boomerang” shape of the skull due to the presence of long tabular processes or “horns” (Douthitt, 1917; Olson, 1951; Milner, 1996; Carroll et al., 1998).

The other animals and plants associated with this skeleton of *Diplocaulus* suggest that the local climate was humid but seasonally dry. The forest appears to have been of low diversity, which is typical of Leonardian floras, and comprises a mixture of canopy trees, vines, and ground cover.

North-central Texas has long been an area known for its richly fossiliferous Early Permian deposits, which have yielded numerous new animal and plant taxa and have begun to reveal much about the dynamics of Early Permian continental ecosystems. The plants from the Mitchell Creek Flats site are as important as the animal remains because of their exquisite preservation and the occurrence in the flora of at least one new form, a gigantopterid.

The acronym USNM denotes the collections of the Department of Paleobiology at the National Museum of Natural History, Smithsonian Institution, Washington, DC.

GEOLGY

Located in the northeast quarter of Baylor County, Texas, Mitchell Creek drains northward into the Wichita River. The highly fossiliferous outcrops along the Wichita have produced the majority of the known Early Permian vertebrates from North America over the past 150 years.
dominant mudstones are red in color and are interpreted at most levels to have been deposited under seasonally dry conditions.

Sediments at the Mitchell Creek Flats locality were deposited in a shallow (less than 3 m deep) channel-form depression. The channel at this location is oriented east-west and, based on preserved portions, appears to be asymmetrical, with the north side being the steepest. The sedimentary fill of the channel is light gray in color, distinguishing it from the pedogenically-overprinted, predominantly red silts and sands of the adjacent strata. The base of the channel fill is formed by a 3-5 cm thick layer of conglomerate composed of pedogenic carbonate nodules. These nodules were most likely reworked from soils developed on the landscape during hiatuses in the accumulation of the Waggoner Ranch Formation strata.

Fossils have been recovered from two levels in the deposit. Lying on the basal conglomerate were a number of “trunks.” The trunks were aligned east-west along the northern edge of the channel as if they had fallen into the water and accumulated there after having been moved around in the pond by air and/or water currents.

The main fossil-producing bed consists of 55 cm of gray claystone of uniform color and grain size. The bedding is very fine with little variation in grain size, imparting the appearance of massive bedding. Combined with the lack of bioturbation, this suggests continuous and constant accumulation of sediment in a quiet standing body of water. No evidence of desiccation of the pond (raindrop impressions, mud cracks) during the depositional interval was observed. There is a very thin (less than 1 mm thick), discontinuous silty parting. Other than the aforementioned trunks, all remains of plants and animals were recovered at this level. The remainder of the clay is devoid of macrofossils.

Above the gray clay, there is a 25 cm thick zone that coarsens upward and is composed of claystone and siltstone with limonitic staining. This zone forms the base of a weakly developed paleosol, which is rooted and mottled red and yellow.

Capping the deposit at the quarry site is a 25 cm thick layer of medium-ripple to cross-beded, white sandstone, which represents the return of a higher-energy depositional regime to the locality. The aerial extent of the “flats” is relatively small, about 4000 square meters. The relationship between the capping sandstone and the overlying strata is obscured by Recent soils and debris.

**FAUNA**

*Pseudestheria* sp.

(Fig. 4A)

Figured is an isolated specimen (USNM 528703) of the conchostracan, *Pseudestheria*, (identified by Dr. Thomas Martens); it is commonly found in clusters and is not uncommon at Mitchell Creek Flats. The conchostracans from all known localities in north-central Texas are being studied by Dr. Thomas Martens (Gotha, Germany). Paleoecologically, the presence of conchostracans indicates a fresh-water environment.

*Myalinid bivalve*

(Fig. 4B)

Myalinid clams are known from three specimens including USNM 528175. Members of this group of bivalves are known to have lived in fresh- or marine-water habitats.

*Xenacanthid shark*

(Fig. 4C)

Only one fragmentary tooth (USNM 528188) of a xenacanth shark, too incomplete to permit identification at lower taxonomic levels, has been recovered. Freshwater sharks of the genera *Xenacanthus* and *Orthocanthus* have been reported from the other Waggoner Ranch
Formation deposits by Johnson (1987).

**Palaeonisciforms**

(Fig. 4D)

The remains of a palaeonisciform fish (USNM 528192), missing only the tail, were recovered, but unfortunately the skull is poorly preserved, precluding more detailed assessment at the present time. One other fragmentary fish specimen was found in the quarry.

**Diplocaulus sp.**

(Figs. 2-3)

A well-preserved skeleton, part and counterpart, of a very small individual of the diplocaulid nektidean *Diplocaulus* (USNM 528201) was recovered from the light gray mudstone. Its principal preservational deficiencies are the loss of the more distal portion of the tail and loss of a number of limb-bones. Many girdle and limb elements are only partially preserved in bone or entirely as impressions in the claystone matrix. Most of the bones are quite delicate, and thus the entire specimen received a protective coating of a much diluted solution of Butvar in ethanol. Dark staining along the trunk region (Fig. 2) visible especially between the ribs probably represents traces of soft tissues. There is no trace of external gill filaments or gill arches.

The skull (Fig. 3) is only exposed in dorsal view. It is 8.3 mm long along the midline, only slightly larger than that of the smallest specimen of *Diplocaulus primus* (7.1 mm: Milner, 1996). The distance from a line across the anterior margins of the orbits to the tip of the snout is about 1.7 mm, so that the ratio of skull length to antorbital
length ("orbital-skull length" of Olson) is slightly less than 5; a ratio of less than 5 was deemed diagnostic of *D. magnicornis* by Olson (1970). However, Olson also observed ratios greater than 5 in some skulls less than 24 mm in length, and thus Milner (1996) questioned the diagnostic value of this ratio.

The much flattened skull bears an external ornament composed of small, round pits. In the region of the squamosal, these pits are aligned between radiating ridges. Sutures are, for the most part, clearly visible. The snout is rounded anteriorly and short. The nasal is absent. At least the maxilla bears long, slender teeth, which are best visible in the posterior portion of the left element. This condition is typical of juvenile individuals of *Diplocaulus* and differs from the short, blunt teeth present in adult specimens (Milner, 1996). The prefrontal and lacrimal separate the maxilla from the frontal. The fused frontals form the interorbital region of the skull roof and are slightly expanded at their anterior contact with the premaxillae. The orbits face dorsally. The postorbital contacts the squamosal laterally and the postfrontal anteromedially. The squamosal forms most of the cheek region, but does not meet the large postparietal. The postparietal is large but does not participate in the formation of the horn. The tabular only contacts the postrolateral corner of the parietal; contra Milner (1996), such a contact is also present in some other small skulls of *Diplocaulus* illustrated by Olson (1951). Unlike in *D. primus* (Milner, 1996), there is no boss on the posterior margin of the tabular; instead the margin is slightly convex in this region. As in other juvenile skulls referred to *Diplocaulus*, the tabular horns are short, rather than long and posterolaterally directed as in the adults.

The vertebræ have long, spool-shaped holospicynous centra and well-developed horizontal rib articulations. The ribs are straight and have double proximal heads with vertically aligned articular facets.

The interclavicle is long and has a squared-off posterior edge. Little detail concerning the structure of the limbs is discernible. Neither carpus nor tarsus are represented by ossifications.

Given the uncertainty in using cranial proportions for species identification and the fact that it represents a juvenile individual, USNM 528201 cannot be readily assigned to one of the named species of *Diplocaulus* and we refer to it as *Diplocaulus* sp. in this account.

**FLORA**

**Indeterminate trunks**

(Fig. 5 H)

Several trunks were found at the base of the deposit, aligned with the long axis of the paleochannel. Although three-dimensionally preserved, the trunks were flattened, and no cellular structure is preserved. The longest specimen measured nearly 6 m, as exposed in excavation. An additional 3+ m is indicated by fragments, aligned with the excavated portion, on the present-day weathering surface. In the lower meter, this trunk was 6.5 cm wide (USNM 528492). At the trunk intersection with the weathering surface, 5.81 m from the base, the width of the trunk had decreased to 4 cm. The base of this specimen was festooned with small, branch-like structures that appeared to be roots, suggesting that it may have entered the water body by bank collapse. All other trunks, although shorter and narrower, had similar diameters but varied in preserved length. One was significantly more contorted than the others and may have represented a different taxon. The bases and/or tops of all trunks were missing, so that the total length cannot be determined for any. There was no evidence of branching or jointing, and the trunks appeared to have been "cheaply" constructed, as they are flattened to a thickness of 1 cm. In addition, when viewed in cross section, the specimens appear to be composed of interlaminated carbon and inorganic matrix. It is quite possible that the trunks of these trees were not constructed of secondary xylem. Unfortunately no foliar material was found connected to any of them.

Two specimens identifiable as *Annularia* were recovered, one of which, USNM 528170, consists of a part and counterpart. Leaves are grouped in whorls, spatulate, with bluntly rounded tips, up to 3.5 mm in length, and 1.1 mm at maximum width, with strong midvein that terminates at the leaf tip. Whorls are spaced approximately 5 mm apart on the lateral branches. Lateral branches arise from the main stem in whors spaced 10-14 mm apart. The largest number of leaves observed in a whorl is 12. This form differs from *A. spicata* (Gutbier) Schimper, 1869 in having smaller leaves that do not have parallel straight-sided margins.

**Calamites sp.**

(Fig. 5B)

A single specimen (USNM 528176) attributable to *Calamites* was found in the deposit. It is a short portion of a stem with one node. Preservation of the specimen precludes meaningful comparison with known species.

**?Brachyphyllum densum** Mamay, 1967

(Fig. 5C)

Mamay (1967) questionably referred material from north-central Texas to the Triassic genus *Brachyphyllum*. The preservation of his original material was not good enough to determine if the leaves were in fact wider than long, although they appeared to be. In gross appearance, the conifer foliage (USNM 528181) from the Mitchell Creek Flats locality is very similar to Mamay’s *Brachyphyllum densum*. However, the few leaves that could be measured have lengths that exceed widths by approximately 1.33 times. Allowing for preservational vagaries, these plants appear to be the same as those identified by Mamay (1967) from what is now considered the Luaders Formation (not the Arroyo Formation, as interpreted at that time).

**Pteridosperm foliage**

(Fig. 5D-G)

Two forms of pteridosperm foliage are present at Mitchell Creek Flats. These differ strongly in pinnule shape and venation.

Form 1 appears to be a callipterid. It is characterized by pinnules that are essentially dimorphic in size. The specimen (USNM 528158) is illustrated in Figure 5E1-2, and has a pinn with large pinnules, including the initial stages of progressive pinnule lobation in the middle and lower portions of the pinn. Pinnules are subopposite, broad, somewhat obovate, with rounded tips. In the upper portions of the pinna, pinnules are acroscopically constricted with a basiscopic auricle. Venation is typically callipterid: the midvein is strong and displaced angularly through the laminae with lateral veins that are strongly acute, broadly "S" shaped, slightly inflected immediately beyond the point of insertion with the midvein and inflected upward just prior to meeting the lamina margin. Pinnules have rachial veins that enter the auricle from the main axis of the pinna. In those pinnules with lobed margins, the venation is fasciculate, each fascicle corresponding to a marginal lobe. The individual fascicles are representative of the venation of a single free pinnule. Smaller specimens, such as those illustrated (Figure 5F; USNM 528154) have similar pinnule shape to the large specimens, with broadly rounded tips, although the acroscopic constriction and auricle are less well developed because of the fusion of the base of the lamina between successive pinnules. Pinnule venation is essentially the same as that in the larger, non-lobed pinnules. The apical pinnule of large and small pinnae consists of a bluntly and broadly rounded terminal pinnule that is basiscopically fused to the adjoining lateral pinnules. An isolated pinnule (Figure 5G; USNM
Taeniopteris spp.

(Fig. 6 A-C, E-H)

Taeniopteris in the sample are all incomplete and vary in width, including some very small specimens (Figure 6C; USNM 528173) and those of more typical size (Figure 6A; USNM 528165). Width variation is typical of most Taeniopteris populations sampled in north-central Texas and is not necessarily a good determinate of species affinities (Remy and Remy, 1975). The veins in the Mitchell Creek Flats specimens arise from the midvein at a high angle with a slight concave upward curve (Figure 6F; USNM 528184) or at 90° bifurcate immediately and run straight to the leaf margin (Figure 6B; USNM 528178). They end with a small upward inflection at the leaf margin. Leaf tips vary from bluntly rounded (Figure 6G; USNM 528151) to acutely rounded (Figure 6E; USNM 528194) to acute (Figure 6H; USNM 528152), appearing to form a continuum. Associated reproductive organs assignable to Phasmatocycas (Figure 6D; USNM 528172) occur in association with the foliage and have been attributed to Taeniopteris due to similarities in lamina venation (Mamay, 1976).

Gigantopterids

(Fig. 7 and Table 1)

The gigantopterids are a group that has received intense scrutiny. Described primarily from China and North America, there are several names in common use between these two areas, which were widely separated biogeographically during the Permian. In all cases, application of names used originally for Chinese material for American specimens is based solely on similarity of venation, despite often considerable differences in frond architecture. The differences and similarities between these plants remain to be worked out fully. The characters that have been used to distinguish one genus of gigantopterid from another are summarized in Table 1, based on the literature. In some genera, such as Evolsionia texana Mamay, 1989 and Delnortea abbottiae Mamay 1988, leaves were described as unforked in specimens of all known sizes. In others, such as Cathaysiopteris yochelsonii Mamay, 1986 and Zeilleropteris wattii Mamay, 1986, larger specimens were forked but smaller, unforked specimens are also known. Similar patterns are known in the genus Comia.

At the Mitchell Creek Flats locality, three distinct types of

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Lamina Forked</th>
<th>orders Venation</th>
<th>Secondary Forked</th>
<th>lobe</th>
<th>Mesh</th>
<th>Final veins</th>
<th>Suture vein</th>
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<tr>
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<td>0</td>
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<td>Fine straight</td>
<td>27</td>
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<tr>
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<td>1</td>
<td>3</td>
<td>1</td>
<td>0</td>
<td></td>
<td>Herring-bone</td>
<td>Fine straight</td>
<td></td>
</tr>
<tr>
<td>Zeilleropteris wattii Mamay, 1986</td>
<td>1</td>
<td>4</td>
<td>1</td>
<td>0</td>
<td></td>
<td>Mesh</td>
<td>Zig-zag</td>
<td>27</td>
</tr>
<tr>
<td>Gigantopteridium americanum (White) Koidzumi, 1936</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>0</td>
<td></td>
<td>Variable Herring-bone</td>
<td>Fine straight</td>
<td></td>
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<tr>
<td>cf. Gigantopteridium USNM 528185</td>
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<td>3</td>
<td>1</td>
<td>0</td>
<td></td>
<td>Mesh</td>
<td>none</td>
<td>3</td>
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<tr>
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<td>Margin not lobed</td>
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</table>
gigantopterids can be recognized. All specimens are small, the significance of which, with regard to whole plant architecture, is not understood. None of the small specimens in the Mitchell Creek Flats collection is known to be forked, which, because of their small size, should not be taken as diagnostic. Of the three types, only USNM 528159 (Figure 7E) has character states that match a previously described form, Delnortea abbottiae, if size is disregarded. If the identification is correct, this would be the earliest reported occurrence of D. abbottiae. USNM 528185 (Figure 7C) is most similar to Gigantopteridium americanum (White) Koidzumi 1936, if its unforked state is disregarded. Gigantopteridium is a common element of the Waggoner Ranch Formation flora. USNM 528169 (Figure 7B) has a very straight margin with no or only minor lobing making it difficult to determine the position of secondary vein endings, in lobes or in sinuses. If the secondary veins were to terminate in the sinuses, this leaf could be confidently assigned to Cathaysiopteris, which is well represented in this part of the stratigraphic succession in north-central Texas. However, there is some suggestion that these secondary veins may in fact end in the lobes, in which case this specimen would belong to a previously undescribed genus. At this time Cathaysiopteris seems to be the most prudent taxo-

nomic determination. USNM 528183 (Figure 7A) and USNM 528166 (Figure 7D) have been referred to cf. Cathaysiopteris based solely on having three orders of venation in a strong herring bone pattern.

**Miscellaneous reproductive organs**

(Fig. 8)

Mitchell Creek Flats is noteworthy for the occurrence of a large number of seeds and other kinds of reproductive structures. In many cases, seeds formed dense accumulations as if after a seasonal release they have been blown or washed together.

Strobili of ?noeggerathialean form (Fig. 8A-B: USNM 528155 and 528162, respectively) occur rarely. These structures have whorled sporophylls with densely packed abaxial sporangia. They appear to have been quite flexulose.

Winged seeds of samaropsid morphology are common (Fig. 8G-I; USNM 528187, 528517, and 528171). These seeds are characterized by a central nucule surrounded by a broad, generally symmetrical
wing. In some of these seeds, the nucule is offset, so that the wing is asymmetrical. Such seeds have generally been attributed to the gigantopterids, through patterns of co-occurrence rather than by any positive evidence of attachment or of similarity in such features as epidermal anatomy, which has not been investigated. Small, ovoid, faintly ribbed and unwinged seeds (Fig. 8D, F; USNM 528193 and 528190, respectively) are commonly and often found in dense accumulations. Several kinds of indeterminate, possibly reproductive structures are found in abundance in some layers of the deposit. These include distinctly bifid, elongate structures that may be pollen organs (Fig. 8E, USNM 528177 and 528190, respectively) of uncertain affinities.

**CONCLUSIONS**

The Mitchell Creek Flats locality is most distinctive for being a fossiliferous, gray, fine-grained, freshwater pond deposit in the midst of otherwise red mottled paleosols. Plant bearing deposits are generally rare within this lithologic sequence. The biotic-association may, in fact, represent a not uncommon component of the original landscape, which was lost by the broad overprinting of the landscape by pedogenesis. Preservation of both plant and animal remains is exceptionally good, revealing fine details, and suggests quiet depositional conditions with little bottom disturbance. This is consistent with Olson's (1951) inference that Diplacodus lived primarily in quiet waters. Additionally, the presence of tall and narrow trunks is unknown in other Permian deposits of north-central Texas, other than very large coniferous trunks found in the brackish-water tidal channels, stratigraphically just below the Mitchell Creek Flats locality. Both the large and narrow trunks suggest a forest close to the pond.

Despite substantial sampling, the flora of the Mitchell Creek Flats locality is notably low in diversity. This is consistent with other Permian conifer-dominated floras both in north-central Texas and other parts of the southwestern United States (e.g., New Mexico: Hunt, 1983; Lucas et al., 1995; DiMichele et al., submitted) and other areas such as nova Scotia, Canada (Ziegler et al., 2002). The significance of this low diversity is not fully understood. It does suggest fairly restricted species pools, but is also in keeping with much lower global biodiversity in the tropics of the late Palaeozoic than in the present-day tropics (Niklas et al., 1980).

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