

# THE PERMIAN COTYLOSAUR *DIADECTES* *TENUITECTUS*.

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ABSTRACT. A skeleton of the Permian reptile *Diadectes tenuitectus* from the Clear Fork group of Texas is described and figured, with particular regard to the atlas-axis complex and the fused astragalo-calcaneum.

THE anatomy of the Permo-Carboniferous reptile *Diadectes* is well known in many regards, due to the work of Cope, Case, Williston and other writers. Most of the material described, however, has been obtained from the lower fossiliferous beds of Texas, those of the Wichita group; little is known of the representatives of the genus in the later Texas horizon, the Arroyo formation of the Clear Fork group. The skeleton discussed below (No. 1035, Museum of Comparative Zoölogy) is from the Clear Fork and is thus not without interest.

The specimen was collected by Sternberg in 1882, during his first trip to Texas.<sup>1</sup> It had, however, lain unnoticed in the Harvard collections for nearly half a century until in 1929 it was rediscovered and then prepared and mounted for exhibition. It is now being remounted in panel form; this has made it both possible and necessary to inquire into its anatomy.

The exact place of collection is unknown, but it is certainly from the Arroyo formation and presumably from the Coffee Creek region of Baylor County, Texas. From this horizon were, apparently, derived all the materials collected by Sternberg at that time, and most of his finds were from Coffee Creek.

The skull is imperfect, the region posterior to the orbits having been lost except for the basioccipital region and imperfect quadrates. The jaws are nearly completely preserved. The dentition is poorly preserved, with little of the crown of the "molars" remaining. The jaw rami have a length of about 23 cm. From the guide given by the position of the jaw articulation, the length of the skull can be estimated as having been approximately 24.5 cm. Other described Clear Fork skulls are the type of *D. huenei*, which is of about the same length (25.8 cm.),<sup>2</sup> and the type of "*Bolbodon*" *tenuitectus* which is

<sup>1</sup> Sternberg, C. H.: 1909, The life of a fossil hunter, pp. 205-229.

<sup>2</sup> Broom, R.: 1914, Some points in the structure of the diadectid skull. Bull. Amer. Mus. Nat. Hist., XXXIII, p. 110.

28.4 cm. in length.<sup>3</sup> The size of these skulls is considerably above that of the other Texas diadectid skulls described from various localities in the Wichita group, as may be seen by the comparative figures on dentitions given by Broom.<sup>4</sup> Our specimen is presumably conspecific with *D. huenei* and this in turn with the earlier described *D. maximus*, founded on vertebrae from this horizon.<sup>5</sup> '*Bolbodon*' *tenuitectus* seems quite certainly to be a *Diadectes* from the same horizon, which has priority over the other two available names. The size differences are not great. The presumed specific character of *D. tenuitectus* is the thinness and lesser degree of sculpture of the cranial roof elements in that form. Because of imperfections in our skull close comparisons cannot be made; however, these features are not improbably to be associated with age and sex differences. I believe that all Clear Fork diadectid material should be assigned to *Diadectes tenuitectus* until valid specific differences are available.

Twenty-one presacral vertebrae are preserved, including several series of articulated elements, but with a number of breaks, so that the presacral count may have been somewhat higher. The sacrals are represented by their centra, and there are 11 caudals present—not, however, articulated. The centra are in general well preserved, but the neural spines are without exception broken off and relatively few are present. Typical dorsal and lumbar vertebrae average about 4.5 cm. in length; anterior dorsals are slightly shorter. The transverse diameter of mid-dorsal centra (taken at the end of the centrum) averages about 5.0 cm. The height of the vertebra to the zygopophyses is 5.6 cm. in an anterior dorsal, and 5.0 and 4.8 cm. in a typical mid-dorsal and lumbar respectively. The width across the zygopophyses in the same regions is 11.7, 10.4, and 12.8 cm.

Except for imperfect spines the first three vertebrae are preserved in articulated fashion. With spines restored and a few slight details added from other material these vertebrae are shown in Text Fig. 1. There is a facet on the atlantal neural arch for a pro-atlas, but that element is not preserved.<sup>6</sup> Presum-

<sup>3</sup>Case, E. C.: 1911, A revision of the Cotylosauria of North America. Carnegie Inst., Washington, Pub. No. 145, p. 23.

<sup>4</sup>Broom, R.: 1914, op. cit., p. 110.

<sup>5</sup>Romer, A. S., and Byrne, F.: 1931, The pes of *Diadectes*. *Palaeobiologica*, IV, p. 26.

<sup>6</sup>Cf. Olson, E. C.: 1936, Dorsal axial musculature of certain primitive Permian tetrapods. *Jour. Morph.*, LIX, Fig. 8.

ably correlated with the maturity of the individual, there is a high degree of fusion of elements in the atlas region, in contrast to the discrete arch and centrum figured by Olson. The atlantal neural arches have the characteristic shape seen in many other early reptiles, a slender process passing backward and upward on either side of the base of the axial spine, and with a facet facing downward for articulation with that element. The base of the arch on either side is expanded, bears a distinct raised circular facet for the rib tubercle, and anteriorly forms with the adjacent intercentrum a deep subcircular socket for the skull condyle. Ventrally and posteriorly the arches are fused to a mass of bone which extends backward without break to the axis centrum and bears on either side two facets for rib attachments. It is obvious that this mass includes both intercentrum and centrum of the atlas and the axial intercentrum as well. Faint rugose lines, shown in our figure, appear to indicate the position of sutures between the elements. These, if correctly interpreted, indicate that the major ventral portion of this fused mass consists merely of the two intercentra, and that the atlantal centrum failed to reach the ventral surface of the column (cf. the pelycosaur *Ophiacodon*), being represented by only a small postero-dorsal portion of the fused mass.

As noted, the spine of the axis is not preserved. The arch

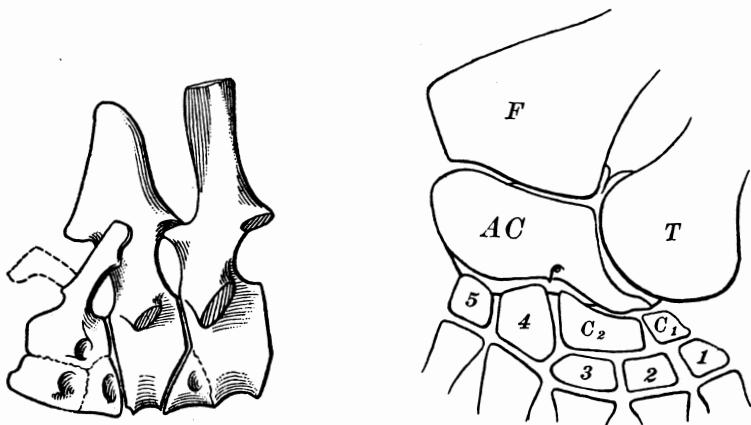


Fig. 1. Diagrammatic restoration of the first three vertebrae. x 1/6.

Fig. 2. Sketch to show assumed relations of astragalo-calcaneum (AC) to adjacent elements. The tarsals are restored as if completely ossified. C<sub>1</sub>, C<sub>2</sub>, Centralia; F, Fibula; T, Tibia, 1-5, distal tarsals.

bears an oval rib facet. Ventrally, the centrum is thin antero-posteriorly, with a pronounced median ventral pit at the anterior margin. The *Diadectes* axis, as noted elsewhere, is well represented by the isolated type vertebrae of *Metamosaurus*.<sup>7</sup> The third intercentrum is large and appears to be fused to the centrum.

A considerable amount of rib material is present, but for the most part disarticulated. Atlantal and axial ribs are present and articulated. Both are slender, although flattened and slightly dilated distally, and are distinctly two-headed. The first measures 82 mm. in length; the second is incomplete.

Of the shoulder girdle there are only fragmentary remains. The left side of the pelvis, of characteristic diadectid form, is well preserved. Its height is 21 cm., its length 26 cm.; the length of the iliac blade is 10.5 cm. The humeri are somewhat imperfect in the "shaft" region. As restored, the measurements are: length, 23.5 cm., proximal width 10.5 cm., distal width 16.2 cm. Radius and ulna are nearly complete. The radius has a length of 13 cm., proximal width 6.7 cm., distal width 7.2 cm.; the ulna has a length of 18.8 cm., width across articular region 7.8 cm., distal width 6.1 cm. Except for the proximal end of one tibia, the major bones of the hind legs are well preserved. Their measurements in centimeters are as follows:

	Femur	Tibia	Fibula
Length .....	22.9	16.2	18.9
Proximal width .....	10.4	8.2	6.0
Distal width .....	11.1	7.7	9.7

These limb measurements exceed by 20 per cent or so those of characteristic Wichita specimens.<sup>8</sup> On the other hand, isolated elements of individuals of still larger size are occasionally found in the Clear Fork.

It seems certain that in the case of *Diadectes*, as of various pelycosaurs studied in detail by the writer and Price, there was a steady increase in size within species phyla during that period of the early Permian covered by the Wichita and early Clear Fork deposits; a type of phyletic "drift" observable in the case of most common types throughout the history of vertebrates. It is unfortunate that the absence of fossil remains in beds

<sup>7</sup> Romer, A. S., and Price, L. I.: 1940, Review of the Pelycosauria. Geol. Soc. Amer., Special Papers No. 28, p. 428.

<sup>8</sup> Cf. for example, the figures given by Case, 1911, p. 83.

higher than those of the lower Clear Fork does not permit us to observe the end results of this trend towards gigantism.

A considerable amount of foot material was found, but unfortunately not articulated, so that identification is difficult. One pair of elements, however, is readily identified and well preserved—the fused astragalo-calcaneum (Text Fig. 3).

In the few previously described examples of diadectid foot remains, astragalus and calcaneum are distinct, as in early reptiles in general. Here, presumably in correlation with the advanced age of the individual, the two elements are almost indistinguishably fused. The condition suggests that in diadectids in general there was no motion possible between these

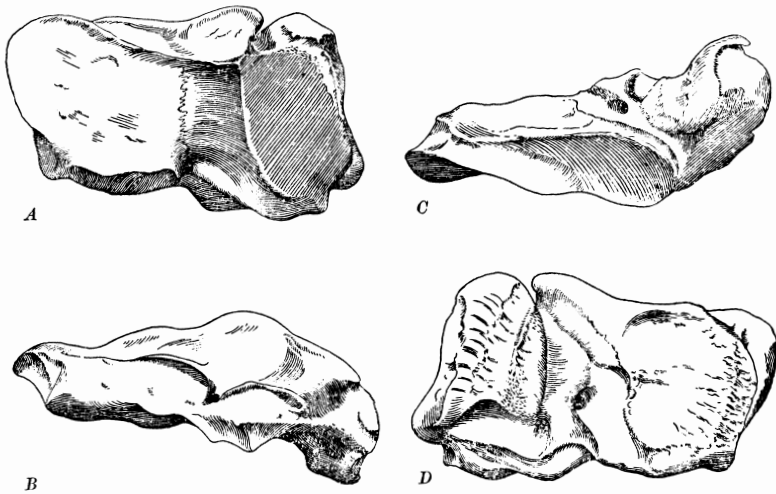


Fig. 3. Right astragalo-calcaneum. A, dorsal; B, distal; C, proximal, and D, ventral aspects.  $\times 2/5$ .

bones, and it may be that even in cases where two separate ossifications are seen, astragalus and calcaneum were continuous in cartilage. The line of fusion is indicated by rugosities along the region of sutural obliteration, and by the presence of the foramen for a perforating vessel; a foramen represented in typical early reptiles by a pair of apposed notches on the two elements.

The calcaneal portion of the bone is a relatively thin plate, with nearly smooth upper and lower surfaces. Proximally there is a broad facet for the lateral portion of the fibula.

The lateral surface is unossified. The distal margin is occupied by an articular surface whose principal contact was presumably with the fourth distal tarsal. A slight projection along the dorsal surface of this margin suggests that the relatively smaller area lateral to this point articulated with a fifth distal element.

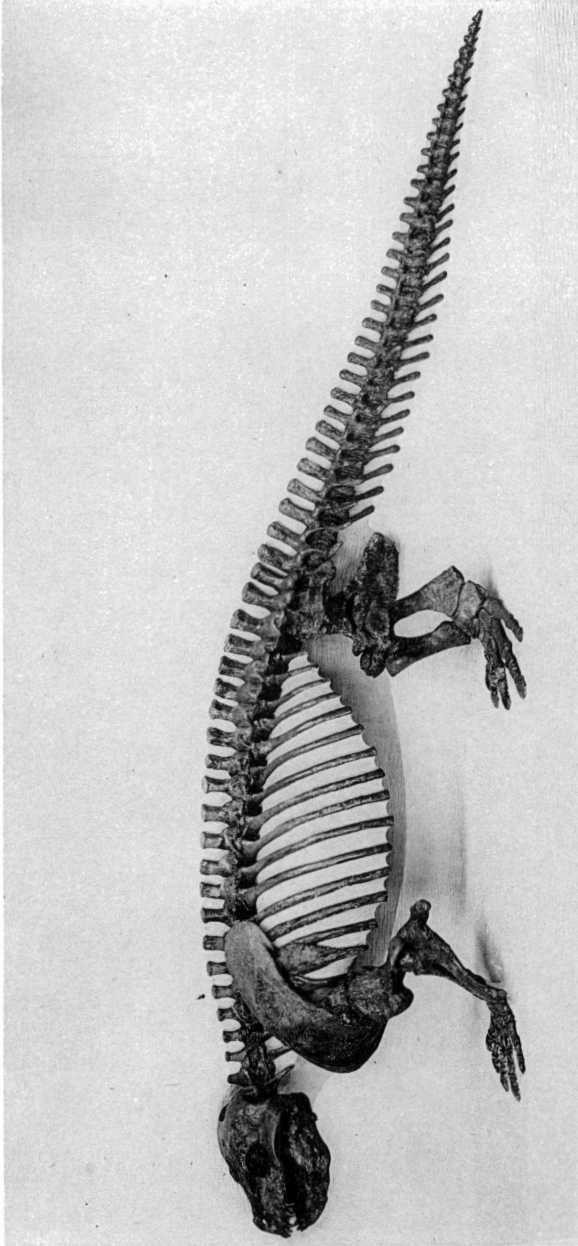
The astragalar portion of the bone is much thicker. Proximally it bears an articular face for the fibula, continuous with that above the calcaneal portion; this face is turned somewhat dorsally as well as proximally. The lateral margin is covered in great measure by a large oval surface upon which the tibia was supported; this faces somewhat anteriorly and proximally as well as laterally. Ventral to this there is, as usual in early reptiles, a thickened rugose area presumably associated with muscle tendons. The distal surface is occupied by an articular face for more distal tarsal elements, presumably two centralia. The medial portion of this surface is flat, the lateral area, close to the foramen, markedly convex and essentially hemispherical.

Apart from the fusion of the elements, the structure is essentially similar to that of the astragalus and calcaneum of captorhinomorph cotylosaurs.

This tarsal fusion is of possible significance with regard to the relationships of the diadectids. A similar situation is found in certain later reptiles: Rhynchocephalia and many Lacerilia and Chelonia. Among early types it is found, however, only in certain other cotylosaurs: the pareiasaurs and *Telerpeton*, a member of the procolophonid group. The structure seen in pareiasaurs is seemingly similar to that here described in *Diadectes*, although Hartmann-Weinberg<sup>9</sup> believes the large tarsal to include elements other than astragalus and calcaneum. Watson<sup>10</sup> believes that diadectids, pareiasaurs and procolophonids are related groups of cotylosaurs, which he unites as the Diadectomorpha. The tendency toward tarsal fusion now seen to be present in all three types is evidence supporting his conclusion.

<sup>9</sup> Hartmann-Weinberg, A.: 1929, Ueber Carpus und Tarsus der Pareiasauriden. Anat. Anz., LXVII, S. 401-428.

<sup>10</sup> Watson, D. M. S.: 1917, A sketch classification of the Pre-Jurassic tetrapod vertebrates. Proc. Zool. Soc., Lond., 1917, p. 171.



Mounted skeleton of *Diadectes tenuitectus*. Length as mounted, 235 cm.