Visual methods for documenting the preservation of large-sized synapsids at Richards Spur

Tea MAHO, Robert HOLMES & Robert R. REISZ
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ABSTRACT

Large isolated skeletal elements, including those of sphenacodontid and ophiacodontid synapsids from the upland cave systems of the Richards Spur locality, Oklahoma, are described. Multiple forms of visual representation, including coquille and stipple drawings, are used to document and examine the isolated elements. A fragmentary anterior portion of a dentary has the sphenacodontid four-leaf clover plicidentine attachment within the tooth roots, but the teeth are all of uniform size, and the symphysial area is relatively slender and does not curve upward, suggesting that the specimen may not belong to any known member of the clade. A larger humerus with only the distal end preserved and a complete astragalus have distinct characteristics which are attributable to the sphenacodontid *Dimetrodon* Cope, 1878. A second, smaller humerus was identified to belong to *Ophiacodon* Marsh, 1878, cf. *O. navajojicus* and represents the first record of an ophiacodontid at Richards Spur. Finally, two large sphenacodontid interclavicles were discovered, with one having unusual growths representing a pathological condition. Typically, large amniotes are quite rare in this early Permian upland ecosystem, but the discovery of the new material shows that large synapsids are present at Richards Spur.

KEY WORDS

Amniotes, large synapsids, early Permian, cave deposit, coquille drawing, stipple drawing, pathology.
MOTS CLÉS
Amniotes, grands synapsides, début du Permien, dessin de coquille, dessin au pointillé, pathologie.

INTRODUCTION

The early Permian cave deposits of the Richards Spur locality, Oklahoma, has preserved a unique upland tetrapod fauna (MacDougall et al. 2017). Vertebrate fossils, preserved in the poorly consolidated carbonaceous claystones and conglomerate infill, were first reported in 1932 by the operators of the Dolese Brothers limestone quarry (Gregory et al. 1956). Since then, thousands of isolated bones, as well as numerous articulated skeletons, have been recovered. The vast majority of material found at Richards Spur pertain to small tetrapods, with the most common elements belonging to small temnospondyls like Doleroserpeton Bolt, 1969 (Sigurdson & Bolt 2010; Gee et al. 2020), small microsaurs like Cardiocephalus Broili, 1904 and Llistrofus Carroll & Gaskill, 1978 (Anderson & Reisz 2003; Gee et al. 2019), captorhinids of various kinds (Kissel et al. 2002; deBraga et al. 2019), as well as two mycterosaurine varanopids (Reisz et al. 1997; Maho et al. 2019). However, more than 30 taxa have been named, and additional taxa await description (MacDougall et al. 2017). Amniote tetrapods, parareptiles, and captorhinomorphs comprise most of the taxa at Richards Spur, while diapsids and synapsids are comparatively rare (Reisz 2005; Maddin et al. 2006; Evans et al. 2009; Brink et al. 2019). The remains of larger individuals include a Dimetrodon Cope, 1878 neural spine and isolated teeth (Brink et al. 2019), the tetrapod Acheloma Cope, 1882 cranial materials and some complete limb bones (Sullivan et al. 2000; Polley & Reisz 2011), and various isolated elements of a large varanopid (Maddin et al. 2006). Recently, we have uncovered new articulated and isolated material of the large varanopid Varanops Williston, 1914, confirming its presence at Richards Spur (Maho et al. 2023). With the exception of Mesenosaurus Efremov, 1938, synapsids are rare at this locality, with some infrequent discoveries of sphenacodontids (Evans et al. 2009; Brink et al. 2019), including Dimetrodon, being reported. Here we describe isolated elements of larger tetrapods belonging to synapsids that contribute significantly to our knowledge of a relatively rare faunal component at Richards Spur. We are using three forms of visual representation, including photography, stipple drawings, and coquille drawings, to document the presence of large synapsids and to exemplify the value of scientific illustrations in research.

MATERIAL AND METHODS

The materials used in the present study are early Permian synapsid taxa from the Dolese Brothers Limestone Quarry near Richards Spur, Oklahoma, United States. All materials were photographed using a Leica DVM6 digital microscope with the LAS X software: incomplete right humerus, OMNH 81929, assignable to Ophiacodon Marsh, 1878, cf. O. navajovicus (Case, 1907); incomplete left humerus, OMNH 81930, and complete right astragalus, OMNH 91831, assignable to Dimetrodon sp.; incomplete right dentary, OMNH 81932, and one interclavicle, OMNH 81933, identified as large sphenacodontids of unknown species; lastly, one interclavicle, OMNH 81934, was unidentifiable at this time. All materials were illustrated using either one or both methods, coquille and stippled drawings.

COQUILLE DRAWINGS

The coquille drawings were completed using the methods perfected by Diane Scott. Initially, Diane used a camera lucida mounted on a dissection microscope to outline the specimens on tracing paper, but later on, Diane began using high-quality photographs of the specimens (Fig. 1A) to produce outlines using Adobe Photoshop software (Fig. 1B), which can also be used for generating the initial outlines for...
Stipple drawings
Specimens are first drawn in pencil (best results are obtained by drawing the specimen at about twice the intended publication size) on tracing paper using a camera lucida mounted on a dissecting scope for small specimens; larger specimens are photographed, and the image is transferred onto tracing paper. In all cases, the preliminary sketches are checked against the specimen, and any major adjustments to proportions and details are made at this point. The image is then transferred to Strathmore Bristol (smooth surface). Inking is performed using a drafting pen (e.g. Koh-I-Noor Rapidograph®). For most drawings, a 0-gauge (0.35 mm diameter) nib is optimal. These pens are becoming somewhat difficult to obtain. If you can’t find one, Rapidograph® manufactures an inexpensive disposable pen with a similar nib; however, the lines and dots are not as crisp, but they will do in a pinch. By convention, the illustrations are shaded as though the light was originating from the upper left. Training a light source at a low angle across the specimen from this direction is helpful, particularly while first practicing the technique. Becoming proficient in shading is largely a matter of practice, although referring to a selection of stippled figures assembled from the literature will be useful. Begin by stippling lightly, and then add them slowly. Adding a few more dots is much easier than removing superfluous dots later. Pay particular attention to sharp edges; the stipples on the lower (more heavily stippled) surface should come right up to the line defining the edge, but leave a very narrow band along the edge of the upper (more lightly stippled) surface free of dots. Deeper depressions should be stippled more densely, in particular to the upper left, as this part of the depression will be, by the convention given above, in the deepest shade. Major errors can be corrected if you can find an ink eraser (either manual or electric if you can find one). Often errors can be corrected using an image-manipulating program like Photoshop® or GIMP.

Institutional Abbreviation
OMNH Sam Noble Oklahoma Museum of Natural History, University of Oklahoma, Norman, OK.

Description and Comparison
Dentary
A partial right dentary, including the symphysis as well as the sockets and roots of the anterior-most five tooth positions, is preserved (OMNH 81932; Fig. 2). The root structure is visible for tooth positions two through four, but the crowns are missing, preventing us from determining the tooth size, shape, and presence or absence of ziphodonty (true denticles) on the mesial and distal edges of the teeth. An alternating
tooth replacement pattern is apparent, with tooth positions one and five having an empty tooth socket showing that the tooth has been lost during replacement and tooth position three having a large resorption pit on the lingual side of the root. Plicidentine organized in a “four-leaf clover” pattern is apparent within each tooth base. This specific morphology has been reported in *Dimetrodon*, *Sphenacodon* Marsh, 1878 (Brink et al. 2014), and *Shashajaia bermani* Huttenlocker et al., 2021 (Huttenlocker et al. 2021). However, the species of *Dimetrodon* previously noted from Richards Spur was not found to have plicidentine and four-leaf clover-shaped roots (Brink et al. 2019), showing that this specimen might be a different taxon. The roots appear anteroposteriorly compressed and are all of approximately the same diameter, with no indication of an enlarged dentary “canine” seen in either *Dimetrodon* or *Sphenacodon* (see, e.g. Romer & Price 1940; Reisz 1986: figs 38, 39). The anterior portion of the dentary does not curve upward and is relatively slender, in contrast to the characteristics of the aforementioned sphenacodontids. Additionally, the shape of the lower jaw suggests that it may not be any of the known *Dimetrodon* or *Sphenacodon* species, because it is slender and does not have a concave outline in lateral view (Romer & Price 1940), nor is it likely to be *Secodontosaurus* Romer, 1936 since the dentary OMNH 81932 is more robust anteriorly than that species (Brink et al. 2014). There is a large and broad symphysis within the anterior region of the bone.

**INTERCLAVICLES**

Two large interclavicles have been discovered (OMNH 81933 and 81934; Figs 3; 4); the former is missing the posterior part of the parasternal process and the left lateral edge of the central plate (Fig. 3). Missing bone associated with the latter exposes a large cavity contained within the thickened transverse ridge that runs parallel to the posterior edge of the facet for the clavicle. Given its morphology and relatively large size compared with other known synapsid material from the Richards Spur locality, this is unlikely to belong to a varanopid and may belong to a large sphenacodontid. The typical four quadrants of the bone are not as apparent...
Fig. 3. — Partial interclavicle with pathology (OMNH 81933): A, B, photograph of: A, ventral; B, dorsal view; C, D, coquille drawing of: C, ventral; D, dorsal view; E, F, stipple drawings of: E, ventral; F, dorsal view. Scale bar: 10 mm.

Fig. 4. — Partial interclavicle (OMNH 81934): A, B, photograph of: A, ventral; B, dorsal view; C, D, coquille drawing of: C, ventral; D, dorsal view. Stipple drawings of this interclavicle were not completed because the specimen was not available to R.H. Scale bar: 10 mm.
within the specimen. There is no discernible organization to the ornamentation pattern on the external surface—mostly randomly arranged pits and extensive growths with no apparent radiation from an ossification center on the central nob of the ventral surface. This unique external structure, with the addition of the bizarre “braided” texture on the internal surface and the presence of the large internal cavity, signify that this bone has been greatly altered by pathology, making more precise identification difficult.

A second large interclavicle (OMNH 81934) appears to have a more typical appearance with no unusual growths or pathologies (Fig. 4). The specimen lacks the lateral edges of the central plate and the posterior portion of the parasternal process. The preserved anterior portion of the shaft is 10.2 mm wide and thicker near the midline. The dorsal surface appears slightly concave, with no apparent features, while the ventral surface is convex. The ventral surface of the central plate bears two large, well-preserved facets for articulation with the clavicles that are separated by a very small gap, suggesting that the clavicles had broad proximal heads, but did not make contact with each other at the midline. As in the pathological specimen, the gently concave outline of the posterior edge of the head transitions smoothly into the shaft and is distinct from varanopids, where the posterior edge of the head is strongly concave and clearly demarcated from the shaft (Reisz & Laurin 2004).

Although similar in size to the largest known varanopid Watongia, it is more lightly built and dorsoventrally more slender. Rather than four distinctive quadrants on the ventral surface, as in Dimetrodon (Romer & Price 1940), only the equivalents of the two anterior quadrants are apparent for articulation with the clavicles, with the anteroposterior ridges being well-developed. Long radially aligned striae that extend laterally are apparent on the two surfaces of articulation with the clavicles. The central plate has a raised, cruciform-like outline, and its surface bears a few striae running mediolaterally. Across the central part of the head, the transverse ridge is well-developed and posterior to this ridge, the shaft transitions quite smoothly without any sculpturing. The distinctive morphology of this interclavicle makes it difficult to identify its affinities among synapsids, and we refrain from assigning this to any particular taxon.

**Humeri**

The distal ends of two synapsid humeri of relatively large size are preserved. OMNH 81929 (Fig. 5), a right humerus, is similar to that seen in the ophiacodontid synapsid Ophiacodon, cf. O. navajovicus (Harris et al. 2010: fig. 7).
The ectepicondyle and supinator processes are complete and well preserved, but the entepicondyle appears to be incomplete distally, causing it to appear proximodistally short. In distal-dorsal aspect, the supinator process is separated from the ectepicondyle by a groove which appears deep and narrow. Although it is possible that this was the result of incomplete ossification, postmortem damage is unlikely because the bone is otherwise well ossified (compare, e.g. Shelton & Sander 2017: fig. 1). Both the ectepicondyle and entepicondyle appear to be well-ossified laterally, allowing us to determine that the width of the distal end of this humerus is 40.3 mm. There is a small but distinct notch separating the proximal portion of the entepicondyle from the rest of the preserved posterior margin (Fig. 5E). The preserved morphology is reminiscent of Ophiacodon (Shelton & Sander 2017: fig. 1), and this distinct notch is clearly present in Ophiacodon navajovicus (Harris et al. 2010: fig. 7), known from the Early Permian of New Mexico.

The entepicondyle of the second humerus (OMNH 81930; Fig. 6) is mostly incomplete below the entepicondylar foramen, which prevents us from precisely measuring the total width of the distal end, but it is estimated to have been at least 65 mm wide. There is a mediolaterally elongated, well-developed entepicondylar foramen with a thicker lateral edge that tapers distally, compared to the medial edge. Interestingly, small pits and ridges are present on the dorsal wall of the foramen. The supinator process is well-developed and ossified, and in distal-dorsal aspect, a groove separates it from the entepicondyle that extends more distally. The groove is wider and less deep compared to that seen in OMNH 81929. Along the length of the anterior edge, the supinator process has a sharp well-developed ridge. On the ventral surface, the radial and ulnar articulations are ossified and well-developed. The radial articular surface, the capitellum, is large and only visible on the ventral surface. It is thick but not as rounded and bulbous as seen in OMNH 81929. The preserved morphology
of these humeri suggests that OMNH 81929 pertains to an ophiacodontid, and OMNH 81930 belongs to a sphenacodontid, likely *Dimetrodon* (Romer & Price 1940: 521, pl. 34; Brinkman 1988: fig. 3; Shelton et al. 2013).

**Astragalus**

The right astragalus (OMNH 81931) has an overall L-shape (Fig. 7). The general shape and proportions are consistent with the astragalus of *Dimetrodon*. According to Henrici et al. (2005), the transverse width of the astragalus of *Dimetrodon* at the distal surface is roughly 50% of the proximodistal length measured along its suture with the calcaneum. Our specimen shows essentially the same ratio. The medial margin proximal to the tibial facet is also straighter than in *Sphenacodon*, although the more concave margin in *Sphenacodon* is probably just a byproduct of the wider distal portion of the bone (Henrici et al. 2005: fig. 2). Laterally, the gap in the surface of articulation between the astragalus and calcaneum and the astragalar articulation with the fibula seen in *Sphenacodon* is absent in both OMNH 81931 and *Dimetrodon* (Romer & Price 1940: 520, pl. 33). Thus, the distal and lateral articulation surfaces, although oriented in different directions, are contiguous in both OMNH 81931 and in *Dimetrodon*, unlike the condition in *Sphenacodon*, which has a small rectangular notch present (Henrici et al. 2005). The astragalus’s contribution to the foramen between the astragalus and calcaneum for the presumed perforating artery is positioned more distally in *Sphenacodon* and ophiacodontids (Romer & Price 1940), whereas in OMNH 81931, it is slightly more anterior, closer to the center of the element. In strong contrast, the perforating foramen is almost entirely enclosed by the astragalus in large varanopids like *Varanops* (Campione & Reisz 2010). The two articular surfaces for the calcaneum on the lateral side of OMNH 81931 are well-developed, with the anterior one being longer and having a flatter surface, whereas the posterior one appears transversely convex. The distal articular surfaces on the lateral and medial sides are connected through the elongated, flat articular surface that would typically be in articulation with the lateral centrale. The dorsal surface is nearly flat, with some striae and pits located at the base of the raised dorsal margins of the articular surfaces. In contrast, the ventral surface has a deep groove extending proximo-medially from the foramen to the notch separating the tibial and fibular surfaces of articulation, with a well-developed ridge formed on the distal portion.

**DISCUSSION**

Although the Richards Spur locality shares some taxa with the approximately coeval (Permain, Artinskian, MacDougall et al. 2017) Texas red beds, its fauna is dominated by distinctly terrestrial vertebrates indicative of an upland depositional environment (Sullivan et al. 2000) rarely preserved in the fossil record. Large synapsids are quite rare in the upland ecosystem of the Dolese Limestone Quarry in Oklahoma (MacDougall et al. 2017), but the presence of the new material represented here shows that large synapsids are present at Richards Spur in addition to the cacopine and trematopid materials previously described from this locality. The larger tetrapods now include sphenacodontid, ophiacodontid, and varanopid (Maho et al. 2023) synapsids. The ophiacodontid material represents the first record of this family at Richards Spur, and the size of the humerus suggests that this specimen belonged to an animal somewhat smaller than the better-known materials of *Ophiacodon navajovicus*, possibly slightly larger than 1 m in total length.

Some of the sphenacodontontid material, such as the humerus, likely belongs to *Dimetrodon* based on morphology and large size, but assignment to species is not possible. The partial dentary suggests that there is a distinct sphenacodontid of uncertain relationships at this locality. Brink et al. (2014) found the clover leaf plidicidentine pattern among sphenacodontids, including Secodontosaurus, *Sphenacodon*, and *Dimetrodon*, whereas Huttenlocker et al. (2021) identified it for the sphenacodontid *Shashajaita bennemi*. Although the four-leaf clover plidicidentine implantation of the dentition is present, this jaw is unlike those of Secodontosaurus, *Sphenacodon*, *Shashajaita*, and *Dimetrodon* in that all of the anterior teeth in the lower jaw are roughly the same size (no evidence of a dentary “canine”) and there is no development of a deepened symphysis, suggesting that the new specimen may fall outside the clade encompassing the three sphenacodontids. Additionally, the jaw is unlike that in *Dimetrodon*, previously recorded at Richards Spur, which lacks plidicidentine in the form of clover leaf-shaped roots (Brink et al. 2019). Thus, the presence of the four-leaf clover plidicidentine pattern and absence of “canine” and deepened symphysis suggests that the OMNH 81932 most likely pertains to another sphenacodontid, possibly more basal than the known species due to the less sophisticated jaw morphology.

Comparisons between the Richards Spur locality and the multitude of typical lowland localities of the Lower Permian confirm that there are some limited similarities, with temnospondyls and synapsids constituting the largest known members of each community. The lowland localities frequently preserve the semi-aquatic temnospondyl *Eryops* Cope, 1877 and various dissorophoid temnospondyls, including *Acheloma* and *Cacops* Williston, 1910. At the terrestrial Richards Spur locality, *Eryops* is absent, and only the terrestrial temnospondyls *Acheloma* and *Cacops* have been recorded. The largest known *Cacops* from Richards Spur has a skull size of 13.5 cm (Reisz et al. 2009; Gee & Reisz 2018). *Cacops aspidopherus* Williston, 1910 from Texas appears to have grown to a slightly larger size. However, the level of ossification of the braincases of *Cacops* from Richards Spur suggests that these are not full adults. Among amniotes, members of the Ophiacodontidae Nopska, 1923, *Sphenacodontidae Williston, 1912*, and Varanopidae Romer & Price, 1940 have now been confirmed to be present in both typical lowland and Richards Spur localities, but the specimens at Richards Spur are somewhat smaller in size. This is particularly true of the very small caseid synapsids found at Richards Spur and the total absence of any edaphosaurids. Richards Spur has also produced diadectids that are distinctly
smaller than most coeval early Permian members of this clade of stem amniotes (Reisz & Sutherland 2001; Reisz & Fröbisch 2014). The discovery of the new material shows that large synapsids are present at Richards Spur and are not as rare as previously thought.

Using three forms of visual representation, including photography, stipple drawings, and coquille drawings, allows us to represent much more information about the specimens compared to only using photographs. The scientific illustration, as perfected by Diane Scott throughout her career, allows us to show the depths of structures and important fine details that could have been missed with photographs, because coquille drawings are more visually arresting. The illustrations eliminate the effect of variation in color and other diagenetic features of the fossils, allowing us to graphically distinguish relevant anatomical features from taphonomic effects. The process of drawing is already a form of interpretation of the specimens, in which the researcher and artist must evaluate and show where the natural cracks and blemishes of the bone are while also showing which areas of the fossil are intact or

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**Fig. 7.** — Dimetrodon Cope, 1878 astragalus (OMNH 81931): A-C, dorsal view shown as: A, photograph; B, coquille; C, stipple drawing; D-F, ventral view shown as: D, photograph; E, coquille; F, stipple drawing; G-I, medial view shown as: G, photograph; H, coquille; I, stipple drawing; J, K, lateral view shown as: J, photograph; K, coquille; L, stipple drawing; M, N, proximal view shown as: M, photograph; N, coquille drawing; O, P, distal view shown as: O, photograph; P, coquille drawing. Scale bar: 5 mm.
damaged. Coquille and stipple drawings of these areas are represented by incorporating different textures and boundaries, such as areas where the cartilage would have been located and details where various tendons and ligaments may have attached to the bones. Additionally, distinguishing sutures within elements (i.e., cranial) from cracks is more easily and clearly done through drawings than photographs. The drawings also allow us to focus on features of the specimen that enhance the scientific description and interpretation of the specimen being studied, providing a better match between the description and the visual depiction from the perspective of the author. If the illustration is of sufficient quality, it adds significantly to the overall understanding of the anatomy of the relevant bone. For example, the astragalus represented in the figure has damage on a few surfaces of the bone, and the coquille drawing shows it as a broken, stippled area, whereas the photograph itself does not clearly show that this is a damaged area. Overall, a combination of high-quality photographs and illustrations is the ideal method of representation since it presents the material as it is observed in real-life and also includes the interpretation of the unique morphology of the fossils.

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Author contributions
R.R.R. conceptualized the study. R.H. drew the stipple illustrations. T.M. photographed the specimens, drew the coquille illustrations, and prepared the figures. T.M. and R.H. analyzed the data and wrote the initial draft of the manuscript. All authors reviewed, edited, and approved the final draft of the manuscript.

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