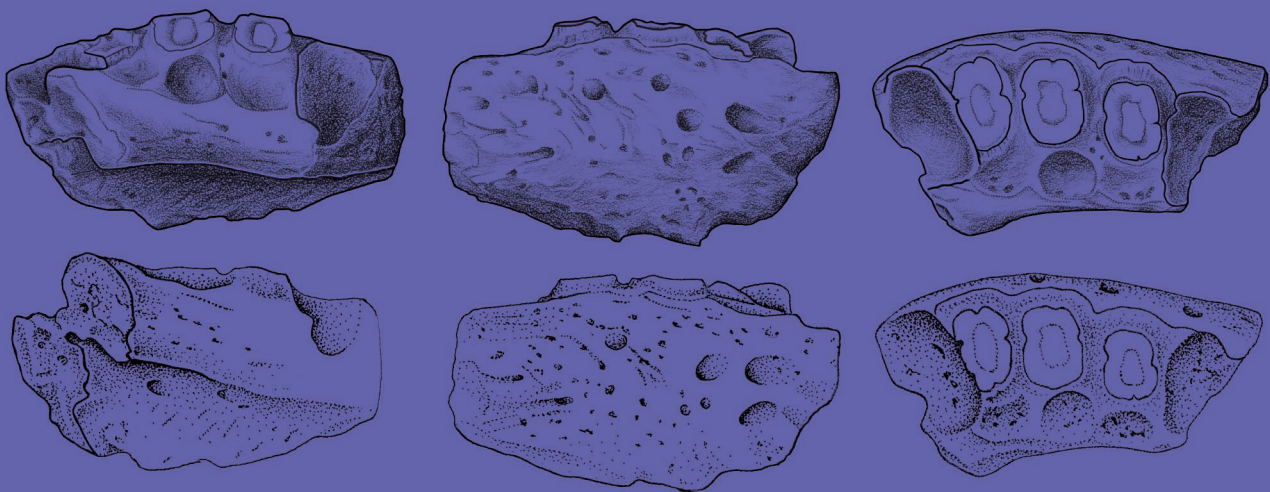


Visual methods for documenting the preservation of large-sized synapsids at Richards Spur

Tea MAHO, Robert HOLMES & Robert R. REISZ



THE IMPORTANCE OF SCIENTIFIC ILLUSTRATIONS IN PALEONTOLOGY: A TRIBUTE TO DIANE SCOTT

Edited by Michel LAURIN, Sean P. MODESTO & Robert R. REISZ

DIRECTEURS DE LA PUBLICATION / PUBLICATION DIRECTORS :
Gilles Bloch, Président du Muséum national d'Histoire naturelle
Étienne Ghys, Secrétaire perpétuel de l'Académie des sciences

RÉDACTEURS EN CHEF / EDITORS-IN-CHIEF (*, took charge of the editorial process of the article/a pris en charge le suivi éditorial de l'article) :
Michel Laurin* (CNRS), Philippe Taquet (Académie des sciences)

ASSISTANTE DE RÉDACTION / ASSISTANT EDITOR: Adenise Lopes (Académie des sciences; cr-palevol@academie-sciences.fr)

MISE EN PAGE / PAGE LAYOUT: Audrina Neveu (Muséum national d'Histoire naturelle; audrina.neveu@mnhn.fr)

RÉVISIONS LINGUISTIQUES DES TEXTES ANGLAIS / ENGLISH LANGUAGE REVISIONS: Kevin Padian (University of California at Berkeley)

RÉDACTEURS ASSOCIÉS / ASSOCIATE EDITORS:

Micropaléontologie/*Micropalaeontology*
Lorenzo Consorti (Institute of Marine Sciences, Italian National Research Council, Trieste)

Paléobotanique/*Palaeobotany*
Cyrille Prestianni (Royal Belgian Institute of Natural Sciences, Brussels)

Métazoaires/*Metazoa*
Annalisa Ferretti (Università di Modena e Reggio Emilia, Modena)

Paléoichthyologie/*Palaeoichthyology*
Philippe Janvier (Muséum national d'Histoire naturelle, Académie des sciences, Paris)

Amniotes du Mésozoïque/*Mesozoic amniotes*
Hans-Dieter Sues (Smithsonian National Museum of Natural History, Washington)

Tortues/*Turtles*
Walter Joyce (Universität Freiburg, Switzerland)

Lépidosauromorphes/*Lepidosauromorphs*
Hussam Zaher (Universidade de São Paulo)

Oiseaux/*Birds*
Eric Buffetaut (CNRS, École Normale Supérieure, Paris)

Paléomammalogie (mammifères de moyenne et grande taille)/*Palaeomammalogy (large and mid-sized mammals)*
Lorenzo Rook (Università degli Studi di Firenze, Firenze)

Paléomammalogie (petits mammifères sauf Euarchontoglires)/*Palaeomammalogy (small mammals except for Euarchontoglires)*
Robert Asher (Cambridge University, Cambridge)

Paléomammalogie (Euarchontoglires)/*Palaeomammalogy (Euarchontoglires)*
K. Christopher Beard (University of Kansas, Lawrence)

Paléoanthropologie/*Palaeoanthropology*
Aurélien Mounier (CNRS/Muséum national d'Histoire naturelle, Paris)

Archéologie préhistorique (Paléolithique et Mésolithique)/*Prehistoric archaeology (Palaeolithic and Mesolithic)*
Nicolas Teyssandier (CNRS/Université de Toulouse, Toulouse)

Archéologie préhistorique (Néolithique et âge du bronze)/*Prehistoric archaeology (Neolithic and Bronze Age)*
Marc Vander Linden (Bournemouth University, Bournemouth)

RÉFÉRÉS / REVIEWERS: <https://sciencepress.mnhn.fr/fr/periodiques/comptes-rendus-palevol/referes-du-journal>

COUVERTURE / COVER:

Made from the Figures of the article.

Comptes Rendus Palevol est indexé dans / *Comptes Rendus Palevol is indexed by:*

- Cambridge Scientific Abstracts
- Current Contents® Physical
- Chemical, and Earth Sciences®
- ISI Alerting Services®
- Geoabstracts, Geobase, Georef, Inspec, Pascal
- Science Citation Index®, Science Citation Index Expanded®
- Scopus®.

Les articles ainsi que les nouveautés nomenclaturales publiés dans *Comptes Rendus Palevol* sont référencés par /
Articles and nomenclatural novelties published in Comptes Rendus Palevol are registered on:

- ZooBank® (<http://zoobank.org>)

Comptes Rendus Palevol est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris et l'Académie des sciences, Paris
Comptes Rendus Palevol is a fast track journal published by the Museum Science Press, Paris and the Académie des sciences, Paris

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish:*

Adansonia, Geodiversitas, Zoosystema, Anthropolozologica, European Journal of Taxonomy, Naturae, Cryptogamie sous-sections *Algologie, Bryologie, Mycologie*.

L'Académie des sciences publie aussi / *The Académie des sciences also publishes:*

Comptes Rendus Mathématique, Comptes Rendus Physique, Comptes Rendus Mécanique, Comptes Rendus Chimie, Comptes Rendus Géoscience, Comptes Rendus Biologies.

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle
CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)
Tél. : 33 (0)1 40 79 48 05 / Fax: 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / <https://sciencepress.mnhn.fr>

Académie des sciences, Institut de France, 23 quai de Conti, 75006 Paris.

© This article is licensed under the Creative Commons Attribution 4.0 International License (<https://creativecommons.org/licenses/by/4.0/>)
ISSN (imprimé / print): 1631-0683/ ISSN (électronique / electronic): 1777-571X

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

Tea MAHO

Department of Biology, William G. Davis Building, University of Toronto Mississauga,
3359 Mississauga Road, Mississauga, ON, L5L 1C6 (Canada)
and International Center of Future Science, Dinosaur Evolution Research Center,
Jilin University, 2699 Qianjin Street, 130012 Changchun, Jilin Province (China)
tea.maho@mail.utoronto.ca (corresponding author)

Robert HOLMES

Department of Biological Sciences, University of Alberta, CW 405,
Biological Sciences Building, Edmonton, Alberta T6G 2E9 (Canada)

Robert R. REISZ

Department of Biology, William G. Davis Building, University of Toronto Mississauga,
3359 Mississauga Road, Mississauga, ON, L5L 1C6 (Canada)
and International Center of Future Science, Dinosaur Evolution Research Center,
Jilin University, 2699 Qianjin Street, 130012 Changchun, Jilin Province (China)

Submitted on 27 January 2023 | Accepted on 5 May 2023 | Published on 12 February 2024

urn:lsid:zoobank.org:pub:C8056FFB-EAC9-4754-B070-8D9F55F502CC

Maho T., Holmes R. & Reisz R. R. 2024. — Visual methods for documenting the preservation of large-sized synapsids at Richards Spur, in Laurin M., Modesto S. P. & Reisz R. R. (eds), The importance of scientific illustrations in paleontology: a tribute to Diane Scott. *Comptes Rendus Palevol* 23 (7): 95-105. <https://doi.org/10.5852/cr-palevol2024v23a7>

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 symphyseal 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. navajovicus* 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.

RÉSUMÉ

Méthodes visuelles pour documenter la préservation des synapsides de grande taille à Richards Spur.

De grands éléments squelettiques isolés, y compris ceux de synapsides sphénacodontidés et ophiacodontidés, provenant des systèmes de grottes des hautes terres de la localité de Richards Spur, en Oklahoma, sont décrits ici. De multiples formes de représentation visuelle, y compris des dessins au fusain sur papier coquille et au pointillisme, sont utilisées pour documenter et examiner les éléments isolés. Une partie antérieure fragmentaire d'un dentaire présente une fixation de la plicidentine de type « trèfle à quatre feuilles » caractéristique des sphénacodontidés à l'intérieur des racines dentaires, mais les dents sont toutes de taille uniforme, et la zone symphysaire est relativement mince et ne se courbe pas vers le haut, ce qui suggère que le spécimen n'appartient peut-être à aucun membre connu du clade. Un humérus plus grand, dont seule l'extrémité distale est conservée, et un astragale complet présentent des caractéristiques distinctes qui sont attribuables au sphénacodontidé *Dimetrodon* Cope, 1878. Un deuxième humérus, plus petit, a été identifié comme appartenant à *Ophiacodon* Marsh, 1878, cf. *O. navajovicus* et représente la première observation d'un ophiacodontidé à Richards Spur. Enfin, deux grandes interclavicules de sphénacodontidés ont été découvertes, l'une d'entre elles présente des excroissances inhabituelles représentant un état pathologique. En règle générale, les grands amniotes sont assez rares dans cet écosystème de hautes terres du Permien inférieur, mais la découverte de ce nouveau matériel montre que de grands synapsides sont présents à Richards Spur.

MOTS CLÉS

Amniotes,
grands synapsides,
début du Permien,
dépôt en grotte,
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 *Dolesepeton* Bolt, 1969 (Sigurdson & Bolt 2010; Gee *et al.* 2020), small microsaurians 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). Anamniote 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 trematopid *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

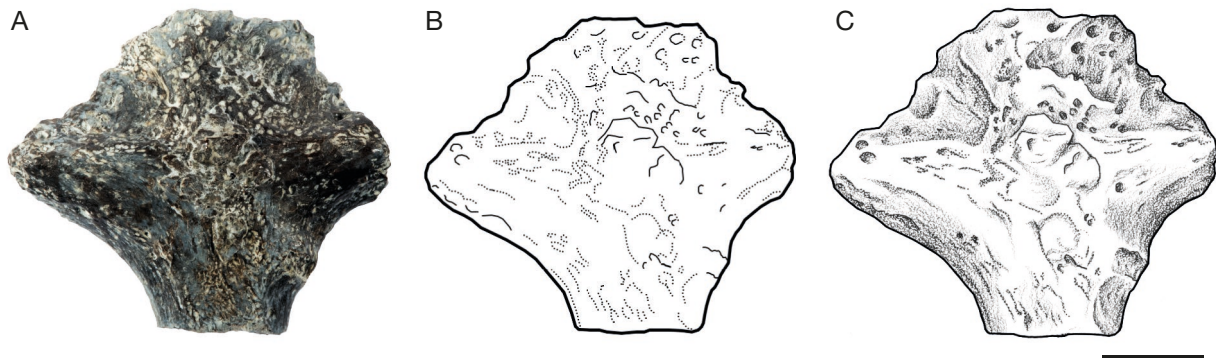


FIG. 1. — Coquille scientific illustrations method. Shown for the partial interclavicle (also in Figure 3): **A**, photograph; **B**, outline; **C**, final coquille drawing. Scale bar: 10 mm.

the stipple drawings. Either a camera with a macro lens or a digital microscope connected to a software that includes an image stacking setting can be used to produce high-quality photographs of the specimens. The image stacking will reduce any focus and depth of field issues. The initial drawings include the general outer outline of a particular view for the specimen that is represented as a thicker solid line, with any major interior features being represented as either a thin solid line when the feature is an edge or as a thin dotted line for any distinct features that needed to be highlighted as landmarks for the coquille drawings. By having these landmarks within the specimen outline, it allows for the artist to be able to precisely locate the features while shading the final coquille drawing (Fig. 1C). After the outline has been completed in Photoshop, it is then printed directly on the coquille board in order to begin drawing. By convention, the illustration is shaded as though the light was originating from the upper left. At the start, having an external light source at a low angle is helpful in observing the high and low points of the specimens while shading. It is important to leave the highest points of the specimen completely white, so no shading should be done to obtain the highlight. Begin lightly shading the darker areas first, gradually getting darker at the deeper depressions of the specimen. For sharp edges, the shading on the lower surface should come right up to the line defining, whereas a narrow band of highlight (not shaded) should be left on the edge of the upper surface to define the edge and distinguish the height of the two surfaces from each other. The illustrations are produced using conté black stone pencils. A kneaded eraser can be used to lightly remove any extra shading from a specific area that needs to be lighter.

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

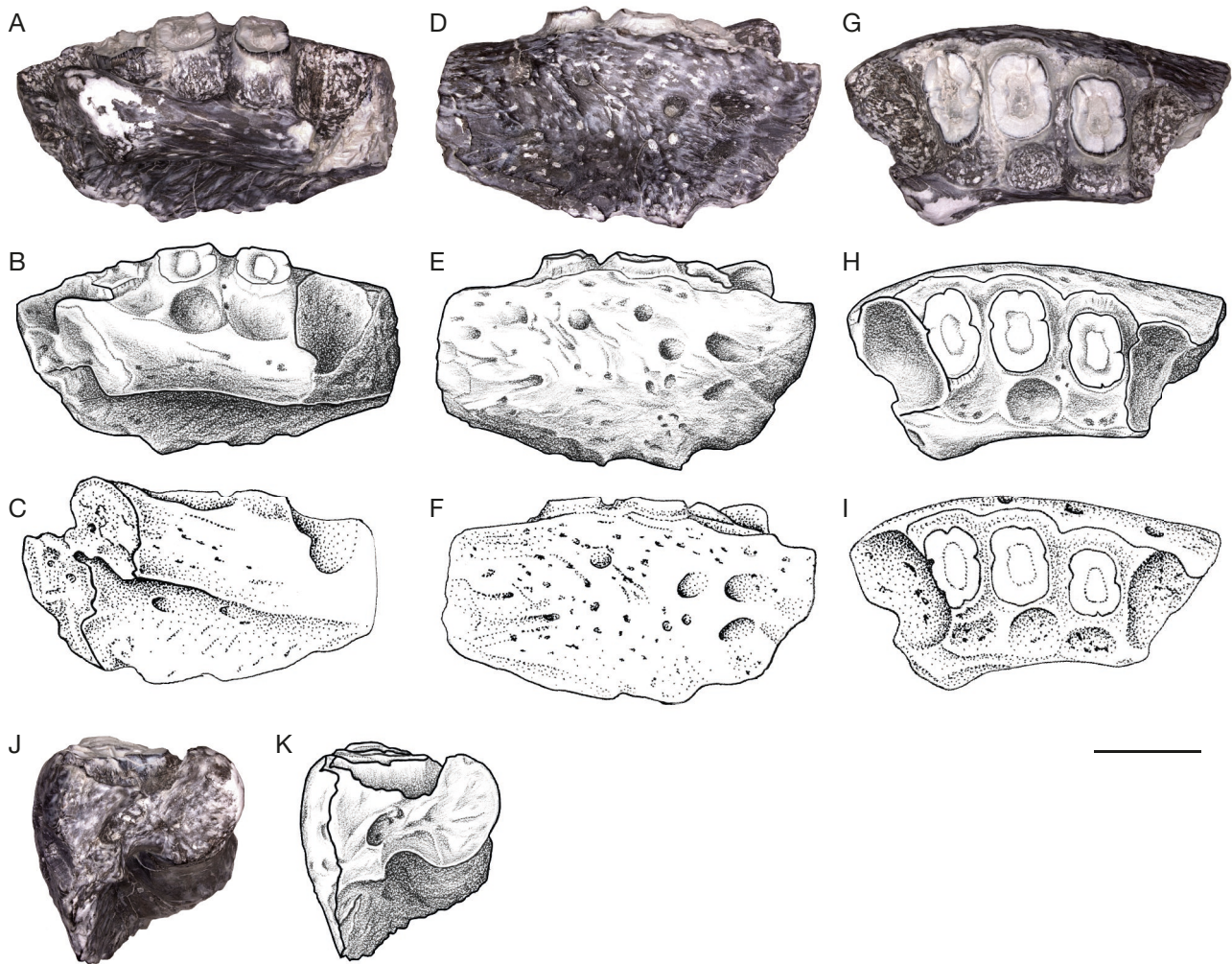


FIG. 2. — Sphenacodontid partial dentary (OMNH 81932): **A, B**, lingual view shown as: **A**, photograph; **B**, coquille drawing; **C**, anterior-ventral view on an angle shown as a stipple drawing; **D-F**, labial view shown as: **D**, photograph; **E**, coquille; **F**, stipple drawing; **G-I**, occlusal view shown as: **G**, photograph; **H**, coquille; **I**, stipple drawing; **J, K**, anterior view shown as: **J**, photograph; **K**, coquille drawing. Scale bar: 5 mm.

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

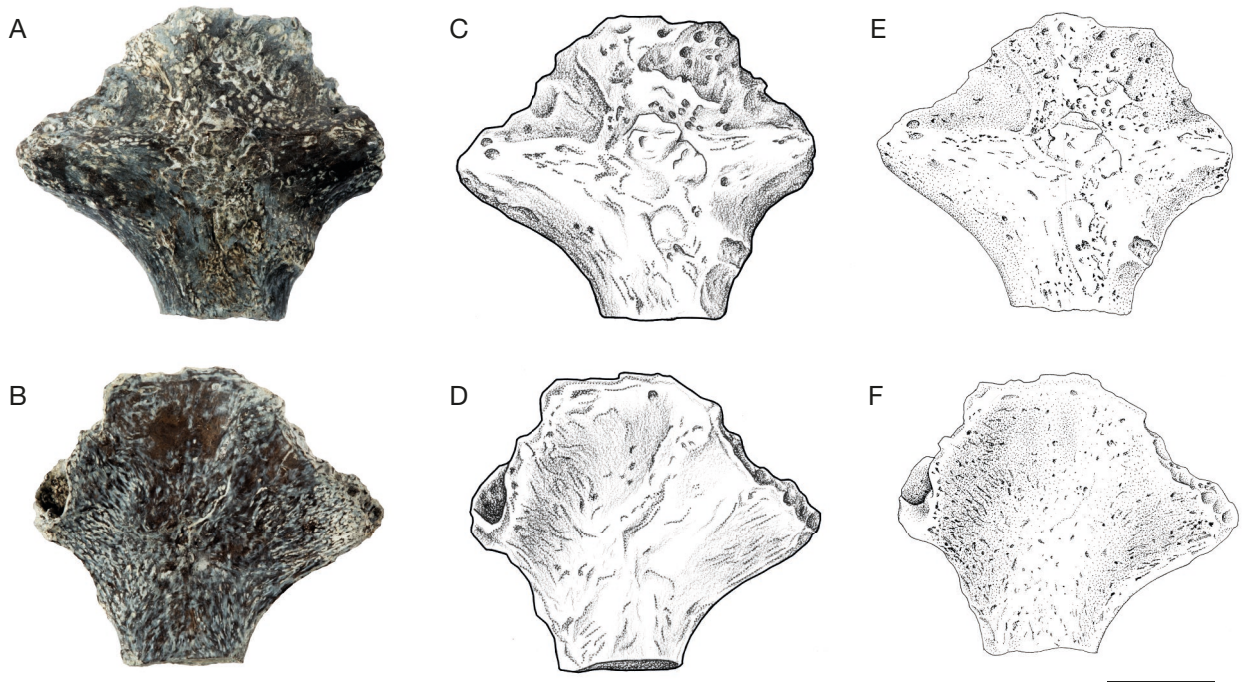


FIG. 3. — Partial interclavicle with pathology (OMNH 81933): **A, B**, photograph of: **A**, ventral; **B**, dorsal view; **C, D**, coquille drawing of: **C**, ventral; **D**, dorsal view; **E, F**, stipple drawings of: **E**, ventral; **F**, dorsal view. Scale bar: 10 mm.

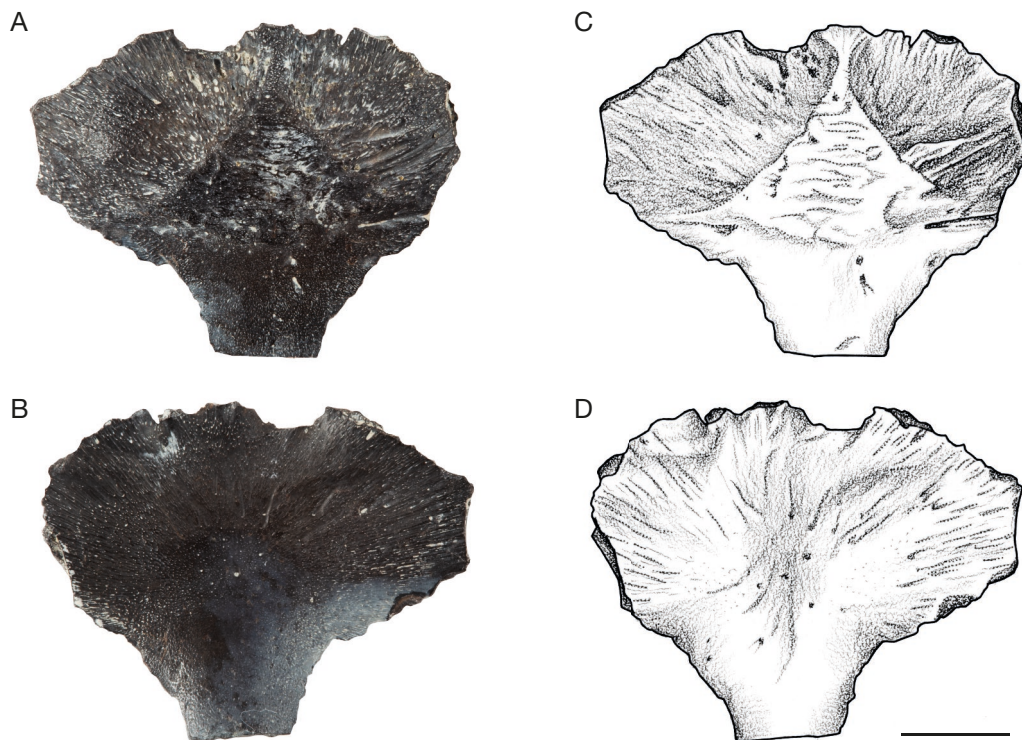


FIG. 4. — Partial interclavicle (OMNH 81934): **A, B**, photograph of: **A**, ventral; **B**, dorsal view; **C, D**, coquille drawing of: **C**, ventral; **D**, dorsal view. Stipple drawings of this interclavicle were not completed because the specimen was not available to R.H. Scale bar: 10 mm.

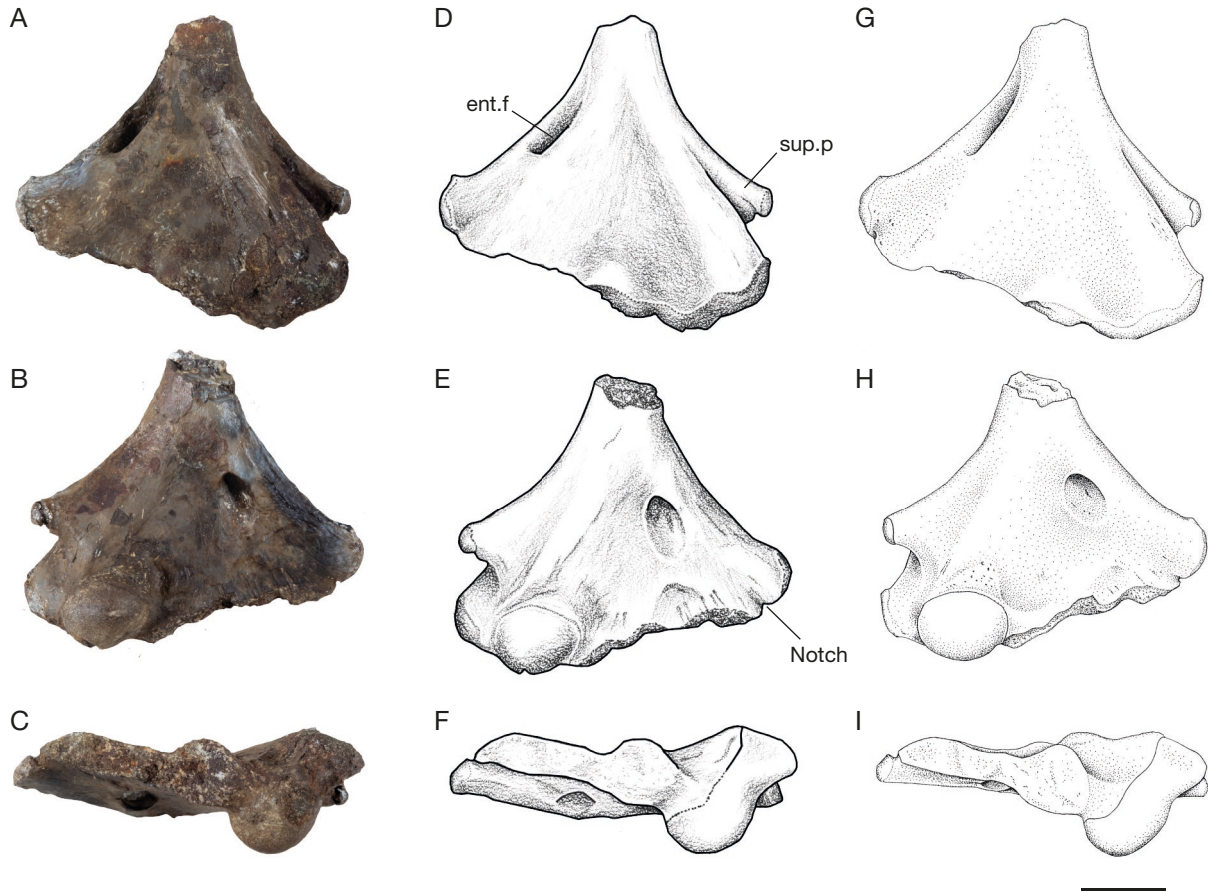


FIG. 5. — *Ophiacodon* Marsh, 1878 partial humerus (OMNH 81929): **A-C**, photograph of: **A**, distal-dorsal; **B**, distal-ventral; **C**, distal end views; **D-F**, coquille drawing of: **D**, distal-dorsal; **E**, distal-ventral; **F**, distal end views; **G-I**, stipple drawings of: **G**, distal-dorsal; **H**, distal-ventral; **I**, distal end views. Abbreviations: **ent.f.**, entepicondylar foramen; **sup.p.**, supinator process. 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 synsapsids, and we refrain from assigning this to any particular taxon.

HUMERI

The distal ends of two synsapsid humeri of relatively large size are preserved. OMNH 81929 (Fig. 5), a right humerus, is similar to that seen in the ophiacodontid synsapsid *Ophiacodon*, cf. *O. navajovicus* (Harris *et al.* 2010: fig. 7).

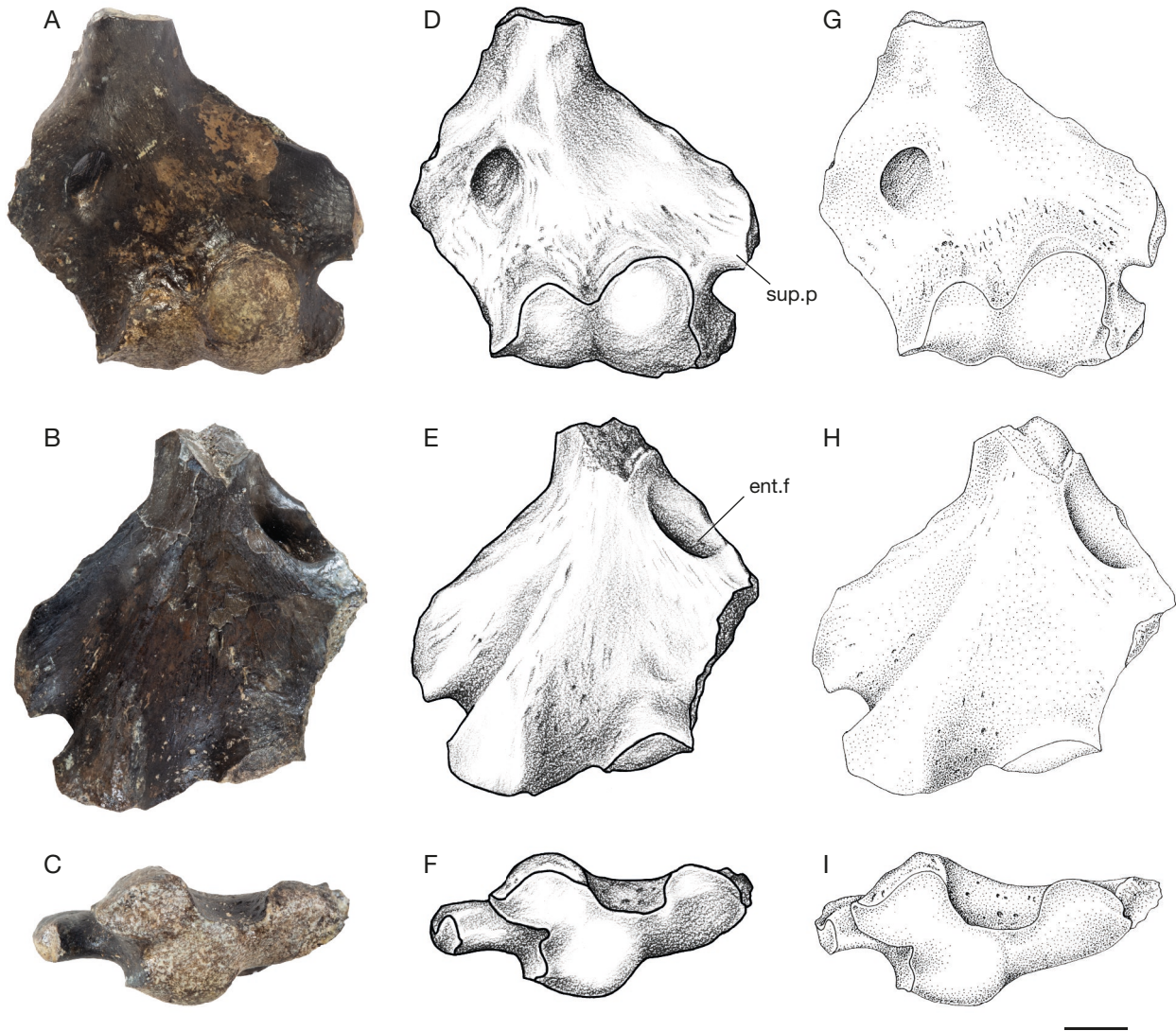


FIG. 6. — *Dimetrodon* Cope, 1878 partial humerus (OMNH 81930): **A-C**, photograph of: **A**, distal-ventral; **B**, distal-dorsal; **C**, distal end views; **D-F**, coquille drawing of: **D**, distal-ventral; **E**, distal-dorsal; **F**, distal end views; **G-I**, stipple drawings of: **G**, distal-ventral; **H**, distal-dorsal; **I**, distal end views. Abbreviations: **ent.f**, entepicondylar foramen; **sup.p**, supinator process. Scale bar: 10 mm.

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 ectepicondyle 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 astragular 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* (Campioni & 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 (Permian, 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 mate-

rial 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 sphenacodontid 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 plicidentine pattern among sphenacodontids, including *Secodontosaurus*, *Sphenacodon*, and *Dimetrodon*, whereas Huttenlocker *et al.* (2021) identified it for the sphenacodontoid *Shashajaia bermani*. Although the four-leaf clover plicidentine implantation of the dentition is present, this jaw is unlike those of *Secodontosaurus*, *Sphenacodon*, *Shashajaia*, 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 plicidentine in the form of clover leaf-shaped roots (Brink *et al.* 2019). Thus, the presence of the four-leaf clover plicidentine 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 aspidephorus* 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

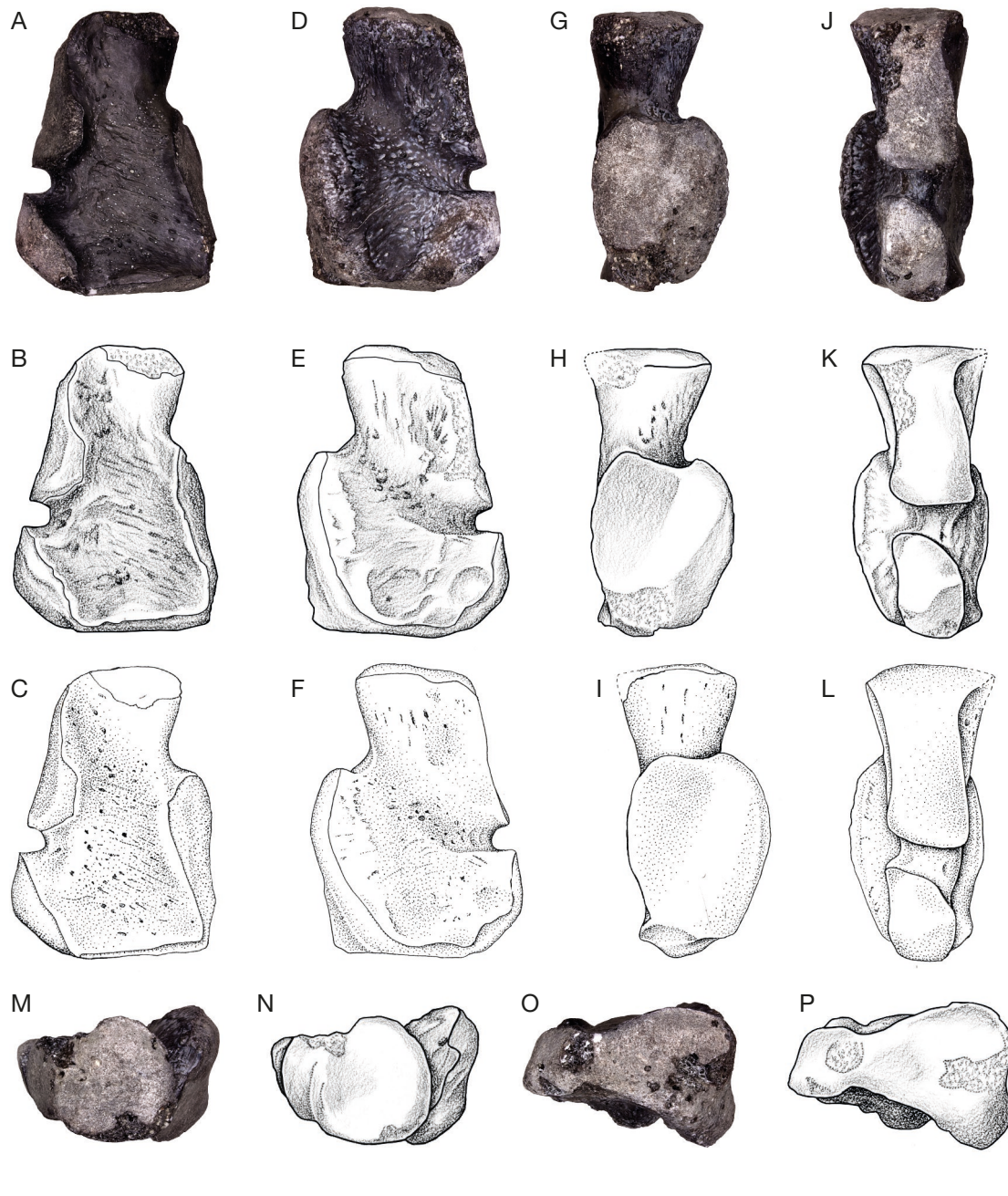


FIG. 7. — *Dimetrodon* Cope, 1878 astragalus (OMNH 81931): **A-C**, dorsal view shown as: **A**, photograph; **B**, coquille; **C**, stipple drawing; **D-F**, ventral view shown as: **D**, photograph; **E**, coquille; **F**, stipple drawing; **G-I**, medial view shown as: **G**, photograph; **H**, coquille; **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.

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

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.

Acknowledgements

Thanks to Bill and Julie May for collection of specimens and Jacqueline Lungmus (OMNH) for assistance with the fossil materials. Special thanks to Diane Scott for fossil preparation and thorough training for the coquille drawings. Diane has contributed to the training of several generations of students and postdocs who have worked or spent time in the Reisz lab, and her attention to detail and her dedication to the study of fossils have had a major impact on the field. We hope that this short manuscript meets her expectations of quality and her standards of scientific illustration. We also thank the two reviewers, and the editor-in-chief, Michel Laurin, for their comments on the manuscript.

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.

REFERENCES

- ANDERSON J. S. & REISZ R. R. 2003. — A new microsauro (Tetrapoda, Lepospondyli) from the Lower Permian of Richards Spur (Fort Sill), Oklahoma. *Canadian Journal of Earth Sciences* 40 (4): 499-505. <https://doi.org/10.1139/e02-066>
- BOLT J. R. 1969. — Lissamphibian origins: possible protolissamphibian from the Lower Permian of Oklahoma. *Science* 166 (3907): 888-891. <https://doi.org/10.1126/science.166.3907.888>
- BRINK K. S., LEBLANC A. R. H. & REISZ R. R. 2014. — First record of plicidentine in Synapsida and patterns of tooth root shape change in Early Permian sphenacodontians. *Naturwissenschaften* 101: 883-892. <https://doi.org/10.1007/s00114-014-1228-5>
- BRINK K. S., MACDOUGALL M. J. & REISZ R. R. 2019. — *Dimetrodon* (Synapsida: Sphenacodontidae) from the cave system at Richards Spur, OK, USA, and a comparison of Early Permian-aged vertebrate paleoassemblages. *Die Naturwissenschaften* 106 (2): 2-10. <https://doi.org/10.1007/s00114-018-1598-1>
- BRINKMAN D. 1988. — Size-independent criteria for estimating relative age in *Ophiacodon* and *Dimetrodon* (Reptilia, Pelycosauria) from the Admiral and lower Belle Plains formations of west-central Texas. *Journal of Vertebrate Paleontology* 8 (2): 172-180. <https://doi.org/10.1080/02724634.1988.10011695>
- BROILI F. 1904. — Permische Stegocephalen und Reptilien aus Texas. *Palaeontographica* 51: 1-120.
- CAMPIONE N. E. & REISZ R. R. 2010. — *Varanops breviostris* (Eupelycosauria, Varanopidae) from the Lower Permian of Texas, with discussion of varanopid morphology and interrelationships. *Journal of Vertebrate Paleontology* 30 (3): 724-746. <https://doi.org/10.1080/02724631003762914>
- CARROLL R. L. & GASKILL P. 1978. — The order Microsauria. *Memoirs of the American Philosophical Society* 126: 1-211.
- CASE E. C. 1907. — *Revision of the Pelycosauria of North America*. Carnegie Institute of Washington, Publication 55, Washington, D.C., 176 p. <https://doi.org/10.5962/bhl.title.45536>
- COPE E. D. 1877. — Descriptions of extinct vertebrata from the Permian and Triassic formations of the United States. *Proceedings of the American Philosophical Society* 17 (100): 182-195. <https://biostor.org/reference/203094>
- COPE E. D. 1878. — Descriptions of extinct Batrachia and Reptilia from the Permian Formation of Texas. *Proceedings of the American Philosophical Society* 17: 505-530. <https://doi.org/10.5962/bhl.title.104569>
- COPE E. D. 1882. — Third contribution to the history of the Vertebrata of the Permian formation of Texas. *Proceedings of the American Philosophical Society* 20 (112): 447-461. <https://biostor.org/reference/202900>
- DEBRAGA M., BEVITT J. J. & REISZ R. R. 2019. — A new captorhinid from the Permian cave system near Richards Spur, Oklahoma, and the taxic diversity of *Captorhinus* at this locality. *Frontiers in Earth Science* 7: 112. <https://doi.org/10.3389/feart.2019.00112>
- EFREMOV J. A. 1938. — Some new Permian reptiles of the USSR. *Academy of Sciences URSS. Comptes Rendus (Doklady)* 19: 121-126.
- EVANS D. C., MADDIN H. C. & REISZ R. R. 2009. — A re-evaluation of sphenacodontid synapsid material from the Lower Permian fissure fills near Richards Spur, Oklahoma. *Palaeontology* 52 (1): 219-227. <https://doi.org/10.1111/j.1475-4983.2008.00837.x>
- GEE B. M. & REISZ R. R. 2018. — Postcrania of large dissorophid temnospondyls from Richards Spur, Oklahoma. *Fossil Record* 21 (1): 79-91. <https://doi.org/10.5194/fr-21-79-2018>
- GEE B. M., BEVITT J. J., GARBE U. & REISZ R. R. 2019. — New material of the "microsaur" *Llistrofus* from the cave deposits of Richards Spur, Oklahoma and the paleoecology of the Hapsidopareiiidae. *PeerJ* 7 (1): e6327. <https://doi.org/10.7717/peerj.6327>
- GEE B. M., HARIDY Y. & REISZ R. R. 2020. — Histological skeltochronology indicates developmental plasticity in the early Permian stem lissamphibian *Doleserpeton annectens*. *Ecology and Evolution* 10 (4): 2153-2169. <https://doi.org/10.1002/ece3.6054>
- GREGORY J. T., PEABODY F. E. & PRICE L. I. 1956. — Revision of the Gymnarthridae American Permian microsaur. *Peabody Museum of Natural History Bulletin* 10: 77.
- HARRIS S. K., LUCAS S. G. & SPIELMANN J. A. 2010. — A partial skeleton of *Ophiacodon navijovicus* (Eupelycosauria: Ophiacodontidae) from the Upper Pennsylvanian of Cañon Del Cobra, New Mexico. *New Mexico Museum of Natural History and Science Bulletin* 49: 137-150.

- HENRICI A. C., BERMAN D. S., LUCAS S. G., HECKERT A. B., RINEHART L. F. & ZEIGLER K. E. 2005. — The carpus and tarsus of the Early Permian synapsid *Sphenacodon ferox* (Eupelycosauria: Sphenacodontidae). *New Mexico Museum of Natural History and Science Bulletin* 30: 106-110.
- HUTTENLOCKER A. K., SINGH S. A., HENRICI A. C. & SUMIDA S. S. 2021. — A Carboniferous synapsid with caniniform teeth and a reappraisal of mandibular size-shape heterodonty in the origin of mammals. *Royal Society Open Science* 8 (12): 211237. <https://doi.org/10.1098/rsos.211237>
- KISSEL R. A., DILKES D. W. & REISZ R. R. 2002. — *Captorhinus magnus*, a new captorhinid (Amniota, Eureptilia) from the Lower Permian of Oklahoma, with new evidence on the homology of the astragalus. *Canadian Journal of Earth Sciences* 39 (9): 1363-1372. <https://doi.org/10.1139/e02-040>
- MACDOUGALL M. J., TABOR N. J., WOODHEAD J., DAOUST A. R. & REISZ R. R. 2017. — The unique preservational environment of the Early Permian (Cisuralian) fossiliferous cave deposits of the Richards Spur locality, Oklahoma. *Palaeogeography, Palaeoclimatology, Palaeoecology* 475: 1-11. <https://doi.org/10.1016/j.palaeo.2017.02.019>
- MADDIN H. C., EVANS D. C. & REISZ R. R. 2006. — An Early Permian varanodontine varanopid (Synapsida, Eupelycosauria) from the Richards Spur locality, Oklahoma. *Journal of Vertebrate Paleontology* 26 (4): 957-966. <https://doi.org/b236kv>
- MAHO S., GEE B. M. & REISZ R. R. 2019. — A new varanopid synapsid from the early Permian of Oklahoma and the evolutionary stasis in this clade. *Royal Society Open Science* 6 (10): 191297. <https://doi.org/10.1098/rsos.191297>
- MAHO T., BEVITT J. J. & REISZ R. R. 2023. — New specimens of the early Permian apex predator *Varanops brevirostris* at Richards Spur, Oklahoma, with histological information about its growth pattern. *PeerJ* 11: e14898. <https://doi.org/10.7717/peerj.14898>
- MARSH O. C. 1878. — Notice of new fossil reptiles. *American Journal of Science* s3-15 (89): 409-411. <https://doi.org/10.2475/ajs.s3-15.89.409>
- POLLEY B. P. & REISZ R. R. 2011. — A new lower permian trematopid (Temnospondyli: Dissorophoidea) from Richards Spur, Oklahoma. *Zoological Journal of the Linnean Society* 161 (4): 789-815. <https://doi.org/10.1111/j.1096-3642.2010.00668.x>
- REISZ R. R. 1986. — *Pelycosauria*. *Handbuch der Paläherpetology*. Teil 17A. Fischer, Stuttgart, 102 p.
- REISZ R. R. 2005. — *Oromycter*, a new caseid from the Lower Permian of Oklahoma. *Journal of Vertebrate Paleontology* 25 (4): 905-910. <https://doi.org/bwv8kn>
- REISZ R. R. & LAURIN M. 2004. — A reevaluation of the enigmatic Permian synapsid *Watongia* and of its stratigraphic significance. *Canadian Journal of Earth Sciences* 41 (4): 377-386. <https://doi.org/10.1139/e04-016>
- REISZ R. R. & SUTHERLAND T. E. 2001. — A diadectid (Tetrapoda: Diadectomorpha) from the Lower Permian fissure fills of the Dolese Quarry, near Richards Spur, Oklahoma. *Annals of Carnegie Museum* 70: 133-142. <https://doi.org/10.5962/p.316106>
- REISZ R. R. & FRÖBISCH J. 2014. — The oldest caseid synapsid from the Late Pennsylvanian of Kansas, and the evolution of herbivory in terrestrial vertebrates. *PLoS ONE* 9: e94518. <https://doi.org/10.1371/journal.pone.0094518>
- REISZ R. R., WILSON H. & SCOTT D. 1997. — Varanopseid synapsid skeletal elements from Richards Spur, a Lower Permian fissure fill located near Fort Sill, Oklahoma. *Geology Notes* 57: 160-170.
- REISZ R. R., SCHOCH R. R. & ANDERSON J. S. 2009. — The armoured dissorophid *Cacops* from the Early Permian of Oklahoma and the exploitation of the terrestrial realm by amphibians. *Die Naturwissenschaften* 96: 789-796. <https://doi.org/10.1007/s00114-009-0533-x>
- ROMER A. S. 1936. — Studies on American Permo-Carboniferous reptiles. *Problems of Paleontology* 1: 85-93.
- ROMER A. S. & PRICE L. W. 1940. — *Review of Pelycosauria*. Geological Society of America, Boulder: 493-521. <https://doi.org/10.1130/SPE28-p1>
- SHELTON C. D. & SANDER P. M. 2014. — Long bone histology of *Ophiacodon* reveals the geologically earliest occurrence of fibrolamellar bone in the mammalian stem lineage. *Comptes Rendus Palevol* 16 (4): 397-424. <https://doi.org/10.1016/j.crpv.2017.02.002>
- SHELTON C. D., SANDER P. M., STEIN K. & WINKELHORST H. 2013. — Long bone histology indicates sympatric species of *Dimetrodon* (Lower Permian, Sphenacodontidae). *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* 103 (3-4): 217-236. <https://doi.org/10.1017/S175569101300025X>
- SIGURDSEN T. & BOLT J. R. 2010. — The Lower Permian amphibamid *Doleserpeton* (Temnospondyli, Dissorophoidea); the interrelationships of amphibamids, and the origin of modern amphibians. *Journal of Vertebrate Paleontology* 30 (4): 1360-1377. <https://doi.org/10.1080/02724634.2010.501445>
- SULLIVAN C., REISZ R. R. & MAY W. J. 2000. — Large dissorophid skeletal elements from the Lower Permian Richards Spur fissures, Oklahoma, and their paleoecological implications. *Journal of Vertebrate Paleontology* 20 (3): 456-461. <https://doi.org/bvmg8h>
- WILLISTON S. W. 1910. — *Cacops*, *Desmospondylus*; new genera of Permian vertebrates. *Geological Society of America Bulletin* 21 (1): 249-284. <https://doi.org/10.1130/GSAB-21-249>
- WILLISTON S. W. 1914. — The osteology of some american permian vertebrates. *The Journal of Geology* 22 (4): 364-419. <https://doi.org/10.1086/622158>

Submitted on 27 January 2023;
accepted on 5 May 2023;
published on 12 February 2024.