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Source: Bulletin of the Peabody Museum of Natural History, 64(1) : 3-9

Published By: Peabody Museum of Natural History, Yale University

URL: https://doi.org/10.3374/014.064.0101

Lost and Found: Redescription of *Chamasaurus dolichognathus* Williston 1915 from the Permo-Carboniferous of New Mexico

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Abstract

Here we describe the "lost" holotype of *Chamasaurus dolichognathus* from the Permo-Carboniferous Cutler Group of El Cobre Canyon, New Mexico, USA. While *C. dolichognathus* has been suggested to be either an amniote or amphibian, we conclude that it is more likely a part of pan-Amniota. We also observe that there is little diagnostic material that would assign this specimen to a more specific clade, although the moderate degree of basal tooth infolding could prove to be of diagnostic utility if additional specimens are discovered. However, we declare the species as *nomen dubium* until such specimens are found.

Keywords

Carboniferous, El Cobre Canyon, Permian, tetrapod, amniote, reptile, synapsid, plicidentine, Captorhinidae, dentition

Introduction

Some of the most remarkable records of early pan-amniotes come from the Late Pennsylvanian to Early Permian strata of New Mexico (Berman 1993; Berman et al. 2015). These include stem amniotes such as *Limnoscelis paludis* Williston, 1911 (see Romer 1946 for a redescription) and well-preserved pelycosaur grade synapsids (e.g., Spielmann et al. 2010). Early expeditions to El Cobre Canyon, New Mexico (1877–1880) and the surrounding areas were led by David Baldwin, a fossil prospector who at the time was employed by O. C. Marsh of Yale University (Langston 1953; Vaughn 1963). These efforts produced numerous specimens from the Permo-Carboniferous Cutler Group of El Cobre Canyon, including a small jaw collected in 1880 within the same matrix as the holotype of *Limnoscelis* and named *Chamasaurus dolichognathus* Williston, 1915.

While many taxa from this area have been described in detail, the holotype and only known specimen of *Chamasaurus dolichognathus* was only briefly treated (Williston 1915). Williston (1915) took it to represent one of the earliest known "cotylosaurs" (broadly, early pan-reptiles). While later works made brief note of *C. dolichognathus* (Vaughn 1963; Langston and Reisz 1981), it was later reported as "lost" (Berman 1993; Lucas et al. 2010), and subsequently removed from taxonomic surveys of El Cobre Canyon (Berman et al. 2015). We recovered this lost holotype in the Division of Vertebrate Paleontology Collection of the Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA (YPM VP), and describe it herein.

Materials and Methods

Mechanical preparation of the holotype specimen of *Chamasaurus dolichognathus* (YPM VP 000827) was conducted to prepare the material for high-resolution CT scanning. It was scanned using a Nikon XT H 225 S micro-CT scanner, housed at Yale University, creating a series of 2,000 computed tomographs at a resolution of 18.2 μm. The stack of tomographs was then imported into VGSTUDIO MAX Version 3.5 (Volume Graphics 2021) to view internal anatomy. Additional high-resolution

Bulletin of the Peabody Museum of Natural History 64(1):3–9, April 2023.

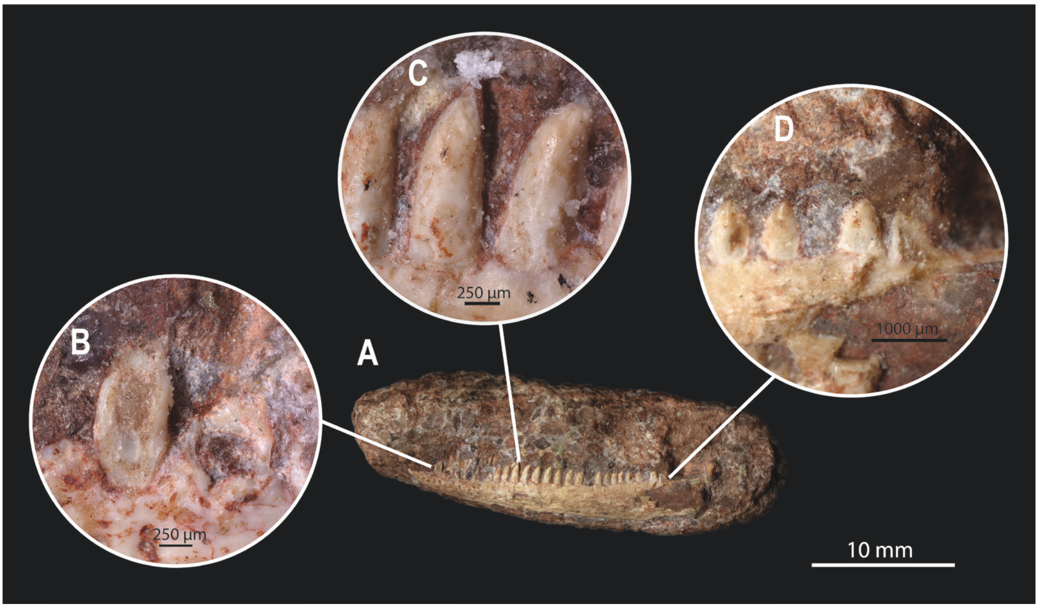

FIGURE 1. Holotype of *Chamasaurus dolichognathus,* YPM VP 000827. **A.** Full specimen post-mechanical preparation. Close-up views: **B.** Anterior dentition with exposed pulp cavities. **C.** Dentition approximately halfway down the lower jaw. **D.** Posterior dentition.

photographs were taken using a Keyence VHX-7000 digital microscope (Kayence, Itasca, IL, USA), and tooth measurements were taken directly with the Keyence as well.

Results

The specimen YPM VP 000827 is a small left lower jaw with only the dentary preserved (Figure 1A), as confirmed by CT scanning (Figure 2). It contains 27 tooth positions, with the first nine teeth either missing or badly broken. Another two tooth positions, toward the middle (position 19) and end (position 27) of the tooth row, are also badly preserved. The first two preserved teeth are broken laterally, exposing wide pulp cavities that span the dorsoventral height of the teeth (Figure 1B). The teeth are closely spaced and taper to a sharp apical cusp. They bear no serrations, accessory cusps, cutting edges, or other obvious distinguishing features, though the labial profiles of the teeth are reminiscent of basal captorhinids (Modesto 1996; Reisz et al. 2016). No fluting is visible on the tooth surfaces, though crenulations are present at the base of the teeth as seen in transverse section (Figure 3A). Those crenulations appear more evident within the pulp cavities than on the outer surfaces. The bases of the teeth become relatively wider toward the posterior end of the dentary, taking on a slightly bulbous appearance (Figure 1D, Table 1). Tooth implantation is difficult to interpret owing to poor CT contrast between the specimen and the surrounding matrix (Figure 2). The firm attachment of the teeth to the jawbone suggests that the mode of attachment is by ankylosis (i.e., fusion). However, the delimitation between the teeth and the surrounding jawbone approximately midway through the height of the teeth suggests that the ankylosis occurs only at the tooth bases (Figure 3B). This is unlike the more extensive ankylosis seen in derived captorhinids (e.g., LeBlanc and Reisz 2015).

While Williston (1915) noted a series of rugosities along the lateral wall of the dentary, we observe that the jaw is heavily weathered with some fracturing occurring along the anterior half. As such, the surface texture of the specimen *in vivo* is indeterminable. However, pitting in the anterior portion of the jaw ventral

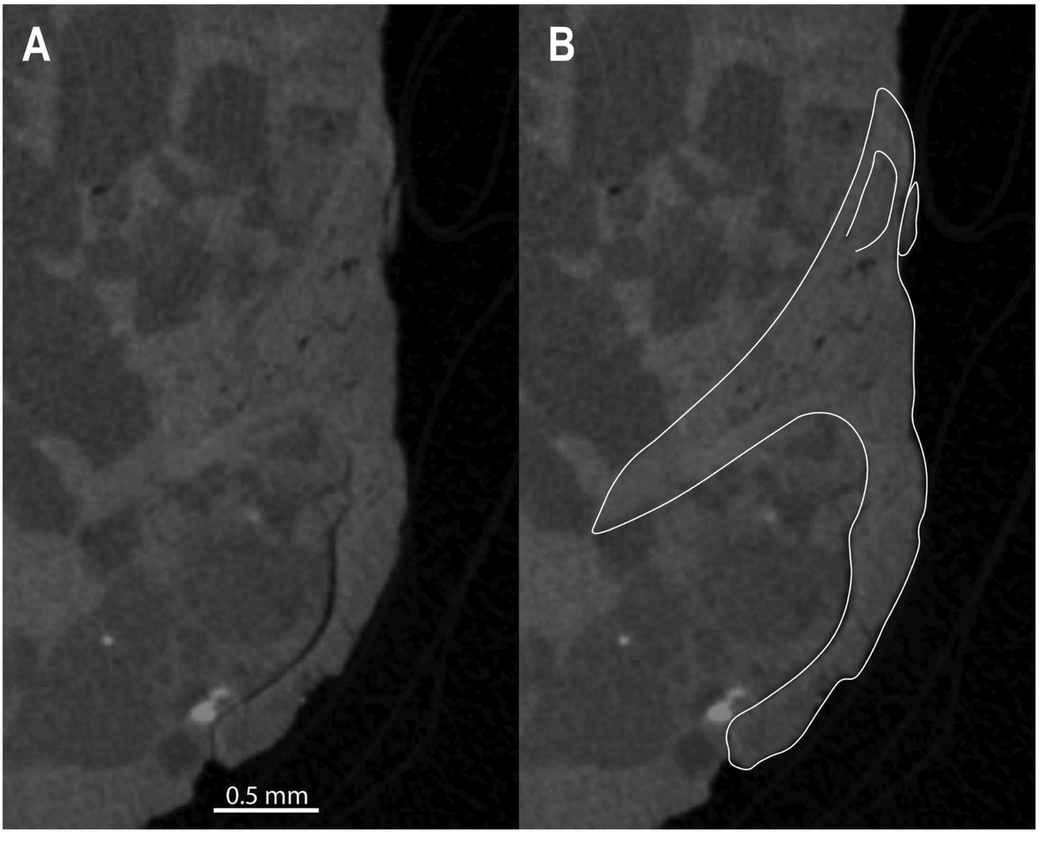

FIGURE 2. Coronal slice through the jaw of *Chamasaurus dolichognathus,* YPM VP 000827. Slice captures the 18th tooth position (9th tooth preserved in sequence). **A.** Slice shown as is. **B.** Slice is superimposed with outline of the jaw, tooth, and pulp cavity.

to the first eight tooth positions may be associated with foramina or bony sculpturing.

Discussion

There are few diagnostic characters pertaining to the dentary teeth of near-crown and early amniotes that would aid in determining the taxonomic affinity of *Chamasaurus dolichognathus.* Those characters that do relate to mandibular dentition, such as procumbency or the presence of an enlarged caniniform tooth (Huttenlocker et al. 2021), concern the first few teeth implanted in the lower jaw, which are broken or missing here. However, several features of *C. dolichognathus* are worth discussing in regard to its taxonomic affinity, including tooth implantation and the presence of dental infolding. Williston (1915) first suggested that *C. dolichognathus* had a cotylosaurian affinity owing to the slenderness of the jaw and its "thecodont or protothecodont" tooth implantation. However, this form of tooth implantation is present in early stem mammals (e.g., Modesto 1995; Reisz et al. 2022) in addition to early stem reptiles such as captorhinids (LeBlanc and Reisz 2015). Furthermore, it is difficult to discern the mode of tooth implantation in *C. dolichognathus*. While the crenulations at the base of the teeth in *C. dolichognathus* are reminiscent of plicidentine, the morphology of these crenulations do not narrow the diagnosis of this taxon any further. Plicidentine evolved multiple times across vertebrata, including just within and just outside the crown node of Amniota (Maxwell et al. 2011). It is present in

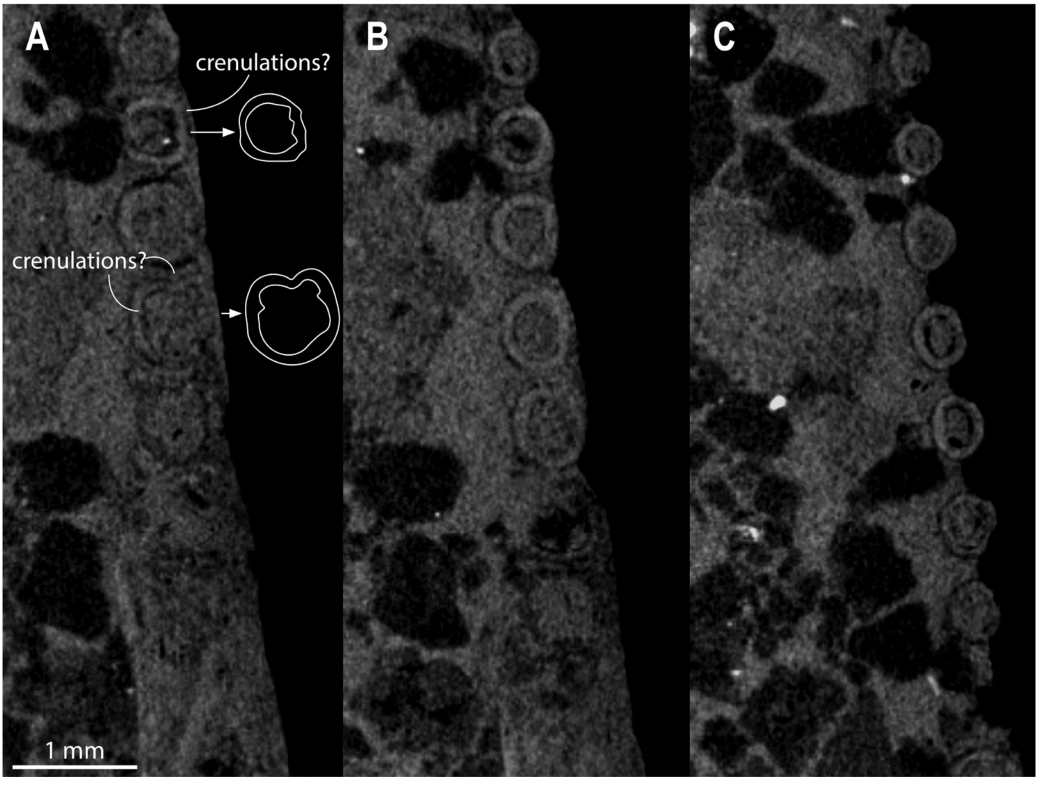

FIGURE 3. Transverse slices through the jaw of *Chamasaurus dolichognathus,* YPM VP 000827. **A.** Slice taken near the tooth bases, showing crenulations. **B.** Slice taken approximately halfway through the height of the teeth. **C.** Slice taken near the apex of the teeth. Slices are taken toward the posterior end of the jaw, featuring the last seven teeth in the tooth row.

several Permo-Carboniferous clades, including the near-crown clade of Diadectomorpha (LeBlanc and Reisz 2013), early synapsids (Brink et al. 2014; Huttenlocker et al. 2021), and several clades within the reptilian lineage (Maxwell et al. 2011; MacDougall et al. 2014). Plicidentine also occurs in captorhinids (de Ricqlès and Bolt 1983), which were long considered basal stem reptiles, though recent phylogenetic analyses place them outside of crown Amniota (Simões et al. 2022). The widespread occurrence of plicidentine around the crown node, as well as the volatility of this portion of the phylogeny at present, hinders the diagnostic utility of this trait at the clade level.

The El Cobre Canyon Formation (Cutler Group) contains a diverse array of vertebrate fauna found largely within two outcrops, summarized elsewhere (Berman et al. 2015). *Chamasaurus dolichognathus* appears distinct from most other described members of that fauna. Diadectids from the formation possess the characteristically labiolingually expanded dentition associated with the clade (Case 1908; Case and Williston 1912; Kissel and Lehman 2002) and/or are of much larger body size than *C. dolichognathus* (Romer 1946; Langston 1966; Moss 1972). Most of the amniote material known from the El Cobre Canyon Formation belongs to pelycosaur-grade synapsids and has been described in detail. *C. dolichognathus* lacks the pronounced recurvature seen in the varanopids and eothyridids described from the vicinity (Langston 1965; Langston and Reisz 1981). Others synapsids are larger-bodied and/or do not have dentition preserved (Romer and Price 1940; Eberth 1985; Spielmann et al. 2010). One smaller-bodied ophiacodont, *Ophiacodon*

TABLE 1. Tooth measurements from *Chamasaurus dolichognathus* YPM VP 000827.

Tooth position	Dorsoventral height (µm)	Anteroposterior length (µm)	Ratio of tooth height to width
1	Missing	Missing	—
2	Missing	Missing	—
3	Missing	Missing	—
4	Broken	Broken	—
5	Broken	Broken	—
6	Broken	Broken	—
7	Broken	Broken	—
8	Missing	Missing	—
9	Broken	Broken	—
10	1,041	465	2.24
11	1,153	482	2.39
12	1,300	518	2.51
13	1,344	528	2.55
14	1,232	632	1.95
15	1,209	609	1.99
16	1,048	646	1.62
17	1,210	627	1.93
18	967	527	1.83
19	Missing	Missing	—
20	1,043	539	1.94
21	992	456	2.18
22	970	501	1.94
23	855	366	2.34
24	822	491	1.67
25	785	441	1.78
26	694	620	1.12
27	Broken	Broken	—

navajovicus Case, 1907, is known from a partial dentary with striated tooth bases, though from the description it is difficult to determine whether these striations represent mild infolding of the tooth bases, like what is seen in *C. dolichognathus*, or whether they represent carinae (Harris et al. 2010). Similarly, *Baldwinonus trux* Romer and Price, 1940, and *Edaphosaurus novomexicanus* Williston and Case, 1913, possesses marginal teeth that lack diagnostic characters that would link them to *C. dolichognathus* (Brinkman and Eberth 1986; Modesto and Reisz 1992). Within the reptilian lineage, the parareptile *Bolosaurus striatus* Cope, 1878, possesses apomorphic, cusped dentition that does not resemble that of *C. dolichognathus* (Lucas et al. 2005). There is an assortment of poorly described and unnamed captorhinid material that could plausibly bear resemblance to *C. dolichognathus* should more descriptive work be conducted (Berman and Reisz 1986). Cranial material associated with the araeoscelid *Zarcasaurus tanyderus* Brinkman et al., 1984 is limited to a small portion of a lower jaw (Brinkman et al. 1984), though the few teeth present are of a similar size and shape as *C. dolichognathus*. However, there is not enough material of *Z. tanyderus* to synonymize the two taxa.

Despite the lack of diagnosable material, still others have made attempts to place *Chamasaurus dolichognathus* within a clade. It was said that *C. dolichognathus* "almost certainly" does not represent a pelycosaur, and it could possibly be amphibian (Langston and Reisz 1981:93). However, no justification was given for either argument. While a more specific placement of *C. dolichognathus* is impossible at present based on the only known specimen, the lack of pedicellate teeth or highly labyrinthodont dental infolding calls into question an amphibian affinity (Warren and Davey 1992; Anderson et al. 2008). Given its conservative morphology, certainly it is far from either the mammalian or the reptilian crown. However, we cannot place *C. dolichognathus* specifically within or outside the crown node of Amniota. As such, we declare it *nomen dubium* until more specimens are found.

Acknowledgments

We thank Vanessa Rhue for access to specimens. Mechanical preparation and CT scanning was conducted by Marilyn Fox. Training for Keyence microscopy was provided by Elizabeth Sibert. Constructive reviews that improved the quality of this manuscript were provided by Sean Modesto and Tiago Simões, with additional comments provided by the editor, Patrick Sweeney.

Received 12 October 2022; revised and accepted 17 December 2022.

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