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SHORT COMMUNICATION

POSTCRANIAL ANATOMY OF THE ‘MICROSAUR’ *CARROLLA CRADDOCKI* FROM THE LOWER PERMIAN OF TEXAS

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Carrolla craddocki Langston and Olson, 1986, is a diminutive recumbirostran tetrapod known from a unique specimen collected from the Lower Permian of Texas in 1977 by Kenneth W. Craddock. In their original description, Langston and Olson (1986) made the single, well-preserved skull with attached jaws the holotype (Texas Memorial Museum [TMM] 40031-54) of the taxon. More recently, application of micro-computed tomography (μ CT) to the skull revealed previously undescribed aspects of the internal cranial anatomy of *C. craddocki*, including features further implicating its fossorial habits, as well as traits likely associated with miniaturization (Maddin et al., 2011). It was during that study that a small fragment of matrix containing a short string of dorsal vertebrae and associated ribs was noticed within the box containing the holotype skull.

The fragment possesses the holotypic specimen number. The elements preserved within the small fragment are consistent with what would be expected for the postcrania of a brachystelechid recumbirostran such as *C. craddocki*, including holospondylous vertebrae and long, broad ribs of an appropriate size. Despite this, no mention of the piece is made in the original description, and no notes describing an association between it and the holotype skull exist in the TMM archives. Without any data confirming a biological association of the two pieces, Maddin et al. (2011) refrained from referring these postcranial remains to *C. craddocki*.

On our behalf, Robert W. Hook, a research associate with the University of Texas Vertebrate Paleontology Laboratory, which houses the TMM vertebrate collections, recently contacted K. W. Craddock, who recalled in detail the discovery of both the skull and the postcranial fragment. The two pieces were found almost in direct contact with one another, within a space of less than 5 cm in diameter. Thus, there is no longer any doubt regarding the association of the skull and postcranial remains.

Also in the course of the current work, we were able to clarify previous observations (Gliénke, 2015) about the cuspate anatomy of the marginal dentition. Here, we describe the associated postcranial material of the holotype that, together with the new dental features, provides an updated diagnosis for the taxon.

METHODS

Specimens were studied at the Vertebrate Paleontology Laboratory of the Jackson School of Geosciences, The University of Texas at Austin. Comparative material, including casts of

Batropetes and lysorophians, was studied at the Redpath Museum at McGill University, Montreal; the American Museum of Natural History, New York; the Carnegie Museum of Natural History, Pittsburgh; and the Yale Peabody Museum, New Haven. Photographs were taken using a Sony Alpha ILCE 5000 camera with an F3.5 lens. All figures were drawn and formatted in Adobe Photoshop CS6 (San Jose, California).

SYSTEMATIC PALEONTOLOGY

LEPOSPONDYLI Zittel, 1888

RECUMBIROSTRA Anderson, 2007

BRACHYSTELECHIDAE Carroll and Gaskill, 1978

CARROLLA Langston and Olson, 1986

CARROLLA CRADDOCKI Langston and Olson, 1986

Holotype—TMM 40031-54, a skull, attached lower jaws, and associated vertebrae and ribs (Fig. 1).

Locality and Horizon—South side of Tit Mountain, approximately 4.8 km northeast of Dundee, in northwest Archer County, Texas; collected by K. W. Craddock on November 6, 1977. Petrolia Formation, Wichita Group, Wolfcampian Series, Lower Permian. Artinskian–Sakmarian.

Comments—Langston and Olson (1986) considered *C. craddocki* to be unique among known microsaur at the time in that the marginal dentition possessed bifurcated crowns. Thus, this aspect of the dental anatomy has been included in the diagnosis of *Carrolla* (Maddin et al., 2011). Following Gliénke’s (2015) observations that *Carrolla craddocki* (TMM 40031-54) possesses at least one tricuspid tooth, we reexamined the holotype to confirm this feature. On the lingual side of the dentary, two to three well-exposed teeth are present, two of which show a clear tricuspid morphology. The cusps would have been mesiodistally arranged, with the lingual-most cusp showing the weakest development (Fig. 2). These findings indicate that tricuspid dentition may have been a more widespread trait within Brachystelechidae, being known in *Batropetes* and now in *Carrolla*, the only two brachystelechid taxa that preserve dentition.

DESCRIPTION

Postcranial Anatomy

The fragment of TMM 40031-54 that preserves postcranial remains includes a series of three nearly complete, holospondylous vertebrae (and posteriorly, possibly fragments of a fourth) in left lateral view, and a series of dorsal ribs (Fig. 1C, D). Weathering of the specimen has damaged the lateral surfaces of the

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centra such that partial internal surfaces are exposed. The exposed surface reveals an hourglass-shaped cavity that may be a remnant of the notochordal canal. The centra are longer than they are tall and appear weakly dumbbell-shaped, similar to those of *Batropetes* and lysorophians. The neural arches may have been fused to the centra; however, cracks between the two elements raise uncertainty. Each neural spine is approximately the same height as its centrum, is shallowly excavated, and bears a slight dorsolateral lip along the distal-most margin of the spine.

The dorsal rib morphology of TMM 40031-54 is very similar to that of *Batropetes*, the sister taxon of *Carrolla* (Glienke, 2015). On the left side of TMM 40031-54, approximately four dorsal rib fragments are present; on the right side, three or more complete dorsal ribs are represented. Each dorsal rib is relatively broad and spatulate, similar to those of *Batropetes* and lysorophians, but different from those of *Microbrachis*, *Hyloplezion*, and *Odontopteron*, close to which *Carrolla* has been traditionally placed (Carroll, 1998; see also Carroll and Gaskill, 1978). The dorsal ribs exhibit a mild degree of distal curvature and do not appear to taper distally at all. The estimated maximum dorsal rib length, based upon the more complete right dorsal ribs

(Fig. 2C), would be 3–4 times the lengths of the dorsal centra, similar to that of *Batropetes* (Glienke, 2013, 2015).

DISCUSSION

Recumbirostran postcranial remains are known comprehensively from a diverse array of taxa, such as *Pantylus*, *Micraroter*, *Pelodosotis*, *Batropetes*, and various lysorophians (Carroll, 1968; Carroll and Gaskill, 1978; Wellstead, 1991). Among brachystelechids, postcranial remains were previously known only from the Early Permian *Batropetes*, which is found in the Lower Rotliegend of the Saar-Nahe Basin in western Germany (Carroll, 1991; Glienke, 2013, 2015). Our documentation of *Carrolla craddocki* increases the postcranial diversity known for Brachystelechidae.

Current understanding of recumbirostran phylogeny is that brachystelechids form a sister-clade relationship with lysorophians, largely supported by cranial characters (Pardo et al., 2017). This is somewhat surprising based on the radically different bauplans unique to each group. Lysorophians have highly elongated (up to 97 presacrales), snake-like bodies and are among the largest of recumbirostrans, likely reaching lengths of

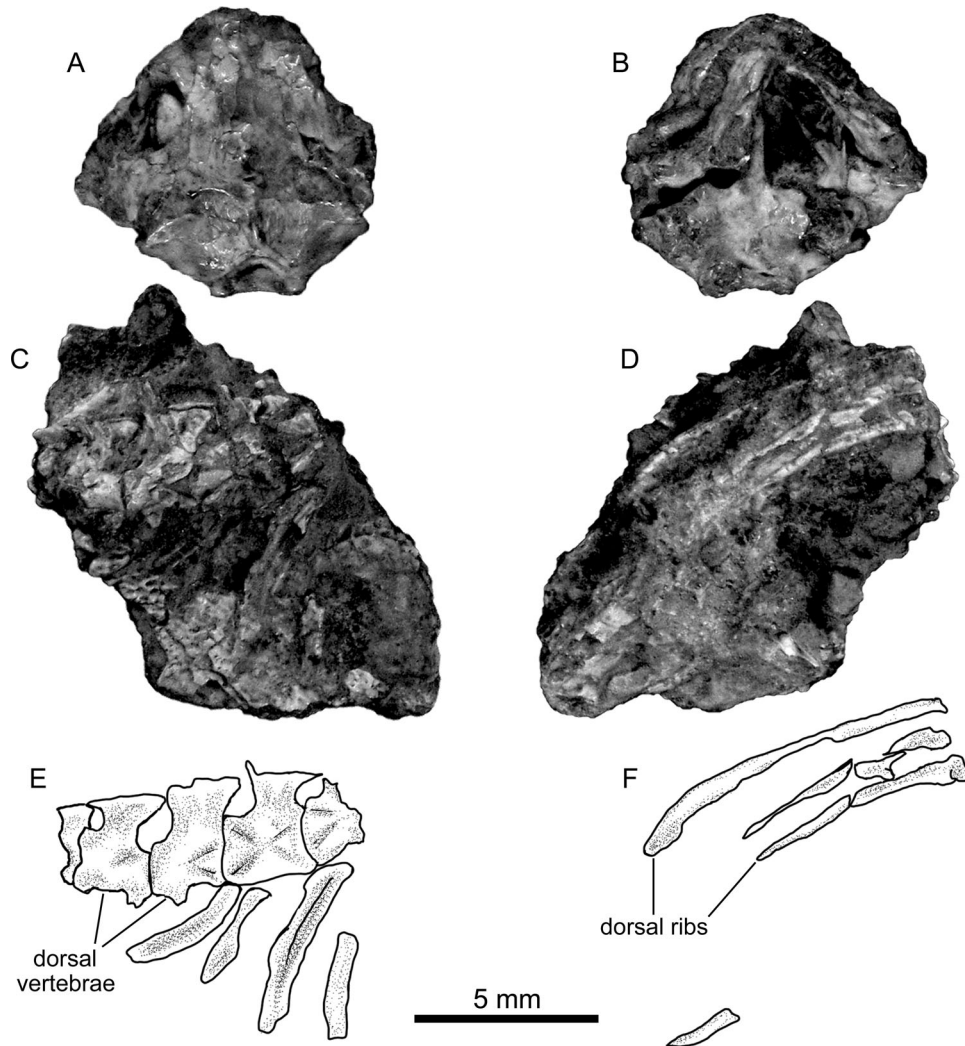


FIGURE 1. *Carrolla craddocki*, TMM 40031-54, cranial and associated postcranial remains. **A**, dorsal and **B**, ventral views of the skull. **C**, one side of the fragment containing the postcranial remains, with dorsal vertebrae and some rib fragments exposed in left lateral view. **D**, the other side of the fragment showing more long dorsal ribs.

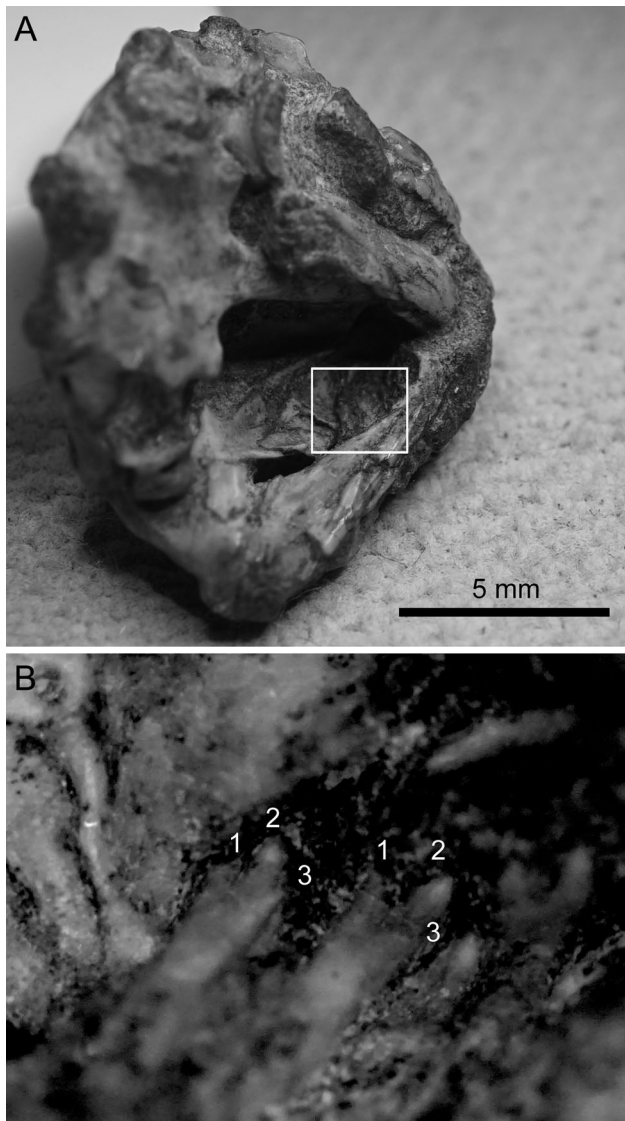


FIGURE 2. *Carrolla craddocki*, TMM 40031-54. **A**, lingually exposed tricuspid teeth on the dentary. **B**, close-up view of the dentary teeth in **A** showing the three distinct cusps (labeled 1, 2, and 3) in two teeth.

around 1 m (Wellstead, 1991). Body elongation in lysorophians is likely indicative of increased fossoriality (Bolt and Wassersug, 1975; Pardo and Anderson, 2016). Conversely, brachystelechids are amongst the smallest Paleozoic tetrapods, often described as miniaturized (Maddin et al., 2011; Pardo et al., 2015). Their numbers of presacral vertebrae are among the lowest of any Paleozoic tetrapod, sometimes reaching as few as 17 (Glienke, 2015). Brachystelechids also show well-ossified girdle elements, and well-developed limbs, supporting terrestrial interpretations of the group (Glienke, 2015; contra Carroll, 1991). Despite evident postcranial differences between lysorophians and brachystelechids, they seem to share robust ribs that can be spatulate; it is possible that this is an autapomorphy of an exclusive or nearly exclusive clade containing these two groups; such a clade was found, on different evidence, by Vallin and Laurin (2004), Pardo et al. (2017), and Marjanović and Laurin (2018).

The postcranial remains of *Carrolla craddocki* presented here show a high degree of similarity to vertebral and dorsal rib

morphology in *Batropetes*. Most notable is that the long dorsal ribs seem to hint at a rotund body shape similar to that of *Batropetes fruttschi* (Carroll, 1991). If the body construction of *C. craddocki* is in fact similar to that of *Batropetes*, in addition to their unique cranial morphology (Maddin et al., 2011; Glienke, 2013; Pardo et al., 2015), a suite of unique postcranial traits also may be diagnostic for Brachystelechidae. Proposed postcranial characters uniting Brachystelechidae would include elongated ribs (3–4 times the thoracic centra length), shortened vertebral series (17–21 presacral vertebrae), and well-ossified robust limbs and girdle elements. Unfortunately, the last of these traits remain to be confirmed in *C. craddocki* until additional postcrania can be identified.

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