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Cranial ornamentation of a large *Brachydectes newberryi* (Recumbirostra: Molgophidae) from Linton, Ohio, and effects of ontogeny on skull ornamentation in recumbirostrans

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Abstract: Although the cranial anatomy of the molgophid tetrapod *Brachydectes* has been reported in detail recently, many attributes of lysorophians are inadequately known. One under-described aspect of the genus is the development and variation of cranial ornamentation. Whereas the smallest skulls (<5 mm in length) lack sculpturing, ornamentation becomes more pronounced in progressively larger specimens and is conspicuous in the largest (>30 mm skull length) individuals. It includes rugose ornamentation on the anterior cranial roof elements (frontals and anterior parietals) and pustular ornamentation on the posterior elements (posterior parietals and postparietals). Such ornamentation, unique to recumbirostrans, is identified as an ontogenetic feature.

INTRODUCTION

Molgophids (Wellstead 1991, 1998; Pardo and Anderson 2016; Pardo et al. 2017) are highly elongated, limb-reduced, serpentine Permo-Carboniferous ‘lepospondyl’ tetrapods. The current understanding of the phylogenetic relationship of Molgophidae is as a highly derived recumbirostran group that constitutes the sister clade to the Brachystelechidae (Gleinke 2013, 2015; Pardo et al. 2015, 2017). Recently, micro-computed x-ray tomography (μCT) of the cranial anatomy of the molgophid *Brachydectes newberryi* Cope (1868) revealed the presence of derived amniote characters of the braincase and suspensorium (Pardo and Anderson 2016). Pardo and Anderson (2016) also argued that the highly reduced cranial morphology of molgophids is analogous to cranial morphology seen in extant fossorial reptiles, including microteiids, lacertoids, and some skinks. In this respect, molgophid morphology is consistent with functional adaptations to fossorial lifestyle common to Recumbirostra as a whole (Bolt and Wassersug 1975; Maddin et al. 2011; Huttenlocker et al. 2013; Szostakiwskyj et al. 2015). Moreover, Pardo and Anderson (2016) noted that features previously considered autapomorphic in the molgophid taxa *Brachydectes newberryi*, *Brachydectes elongatus*, and *Pleuroptyx clavatus* (Wellstead 1991, 1998) more likely represented ontogenetic morphological variants (ontogimorphs) rather than true taxonomic variation. This last point led the authors to provisionally assign all known material of *Brachydectes newberryi*, *B. elongatus*, and *Pleuroptyx clavatus* to a single taxon, *Brachydectes newberryi*, although as the authors themselves note, this is somewhat problematic given considerable vertebral variation among specimens collected from Upper Carboniferous cannel coal localities (Wellstead 1991, 1998; Pardo and Anderson 2016).

This paper addresses the cranial ornamentation or dermal sculpturing of a large specimen of the molgophid specimen *Brachydectes newberryi* from Linton, Ohio. YPM VPPU 20391 (Fig. 1), collected by G.R. Case in 1968, was previously described by Wellstead (1991) in his monograph on the ‘Lysorophia’; however, he did not comprehensively describe the morphology of its dermal ornamentation. More recent research on the well-preserved three-dimensional material of *Brachydectes* from the earliest Permian Eskridge Shale of Nebraska and Speiser Shale of Kansas from the Council Grove Group (Hembree et al. 2004; Huttenlocker et al. 2005, 2013; Pardo and Anderson 2016) permits a more in depth interpretation. Finally, the relationship between ontogeny and development of cranial ornamentation is discussed.

METHODS

Specimens studied are held in the collections of one of the following institutions: American Museum of Natural History (AMNH), New York; Carnegie Museum of Natural History (CM), Pittsburgh; Denver Museum of Nature and Science (DMNH), Denver; Field Museum of Natural History (FMNH), Chicago; University of Kansas

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Natural History Museum (KUVP), Lawrence; University of Nebraska State Museum (UNSM), Lincoln; Smithsonian Institution (USNM), Washington DC; Yale Peabody Museum (YPM), New Haven. Specimens from the British Museum of Natural History (BMNH), London, and the Harvard Museum of Comparative Zoology (MCZ), Cambridge, Museum für Naturkunde (MB), Berlin, were compared based on casts, latex peels, and existing literature. In this study, nearly all reported lysorophian material from Linton was examined, including cranial and postcranial remains. Lysorophian material was examined from the Francis Creek Shale of Mazon Creek, Illinois; the cannel coal below the Lower Kittanning coal of Five Points, Ohio; the Speiser Shale, Kansas; the Eskridge Shale, Nebraska; and a variety of material from Texas redbed localities. Cranial ornamentation was observed on a variety of 'microsaurs' and captorhinid eureptiles for comparative anatomical analysis. Photography was done with a Sony Alpha ILCE 5000 camera, F3.5 lens. All figures were drawn and formatted in Photoshop CS6 (Adobe, San Jose, CA).

CRANIAL ORNAMENTATION OF YPM VPPU 20391

The dorsal aspect of YPM VPPU 20391 preserves all dorsal cranial roof elements except the nasals and premaxillae (Fig. 1). The preserved skull length from the back of supraoccipital to the anterior edge of the frontals is 32.6 mm. Although the lateral and ventral components of the skull are well represented, only the dorsal cranial roof elements, including the supraoccipital, postparietals, parietals, frontals, prefrontals and the dorsal portion of the squamosals, bear ornamentation. There is no direct evidence of sutural obliteration through remodeling of the dermal bone.

The frontal ornamentation comprises long, raised ridges that flow into crenulations or small wrinkles toward the slightly raised midline frontal suture. This ornamentation, most pronounced on the lateral edges of the frontals, is continued onto the prefrontals. The crenulations of the frontal continue posteriorly onto the parietals. As in the frontals, the crenulations on the parietals are most pronounced along the lateral margins. Although multiple peels of the dorsal skull were examined, imperfections in the peels obscure the ornamentation on the dorsal surface of the parietals adjacent to the midline. A slightly raised interparietal ridge similar to that on the frontal occupies the inter-parietal suture. The bar-like squamosals bear very fine rugose sculpturing (Fig 1). No evidence of large supraorbital pits such as those in *Batropetes* (Glienke 2013, 2015) can be found.

The pustular ornamentation on the postparietals forms small raised domes and short ridges instead of long crenulations. These are particularly well-defined on the left postparietal (Fig. 1). This pustular ornamentation may have extended anteriorly onto the parietals, but poor quality of the peels (see above) makes it difficult to confirm this. The postparietal ornamentation dissipates toward the occiput. The supraoccipital (Fig. 1B), which wedges between the postparietals on molgophids, bears a distinct median depression, but is not significantly sculptured.

DISCUSSION

Recumbirostrans exhibit a few different patterns of cranial ornamentation. Rhynchonkids and brachystelechids show relatively smooth cranial elements, sometimes ornamented only with very fine radiating striae (Carroll and Gaskill 1978). Among brachystelechids, *Batropetes* is unique in bearing 3–4 enlarged supraorbital pits on the frontals (Glienke 2015). Cranial ornamentation in the ostodolepids such as *Micraroter* (BPI 3839), *Pelodosotis*, and *Nannaroter* consists of relatively deep pitting and radiating ridges that are most conspicuous on the dorsal skull roof elements. The radiating ridge ornamentation can be intensely excavated forming raised radiating ridges on areas of the skull roof as is the case in *Nannaroter* (Anderson et al. 2009). Some smaller individuals (under 5 cm skull length) including the holotype of *Micraroter erythrogeios* (Carroll and Gaskill 1978) and *Tambaroter* (Henrici et al. 2011) bear very weak cranial ornamentation conspicuously developed only on the parietals. Gymnarthrids exhibit a range of cranial ornamentation, ranging from light pitting on the otherwise smooth cranium of *Cardiocephalus* to the more deeply trenched striae and pits on the skull of *Euryodus* (Carroll and Gaskill 1978; pers. obs. A. Mann). The latter also bears rugosities on the lateral margins of the skull. *Pantylus cordatus* shows a very distinct mosaic of interweaving ridges and pitting across the entire skull and mandibles comparable to the dermal sculpturing found on temnospondyls (Romer 1969). This type of ornamentation is only shared with the putative pantylid *Trachystegos* from Joggins, and otherwise is unique among recumbirostrans. The skull of the tuditanomorph 'microsaur' *Tuditanus punctulatus* (Carroll and Baird 1968) bears grooves and rugose ridges on the lateral skull margins and mandibles, while the dorsal skull roof consists of pitted ornamentation similar to that seen in captorhinids (Fox and Bowman 1966). The pattern of cranial ornamentation in the specimen of *Brachydectes* (YPM VPPU 20391) described here has not been reported in other large recumbirostrans except molgophids. Unlike most recumbirostrans, molgophids possess no radiating striae in adult forms, and rugosities found on the dorsal skull roof bear more resemblance to sculpturing on coeval early amniote groups including pelycosaurian synapsids and eureptiles.

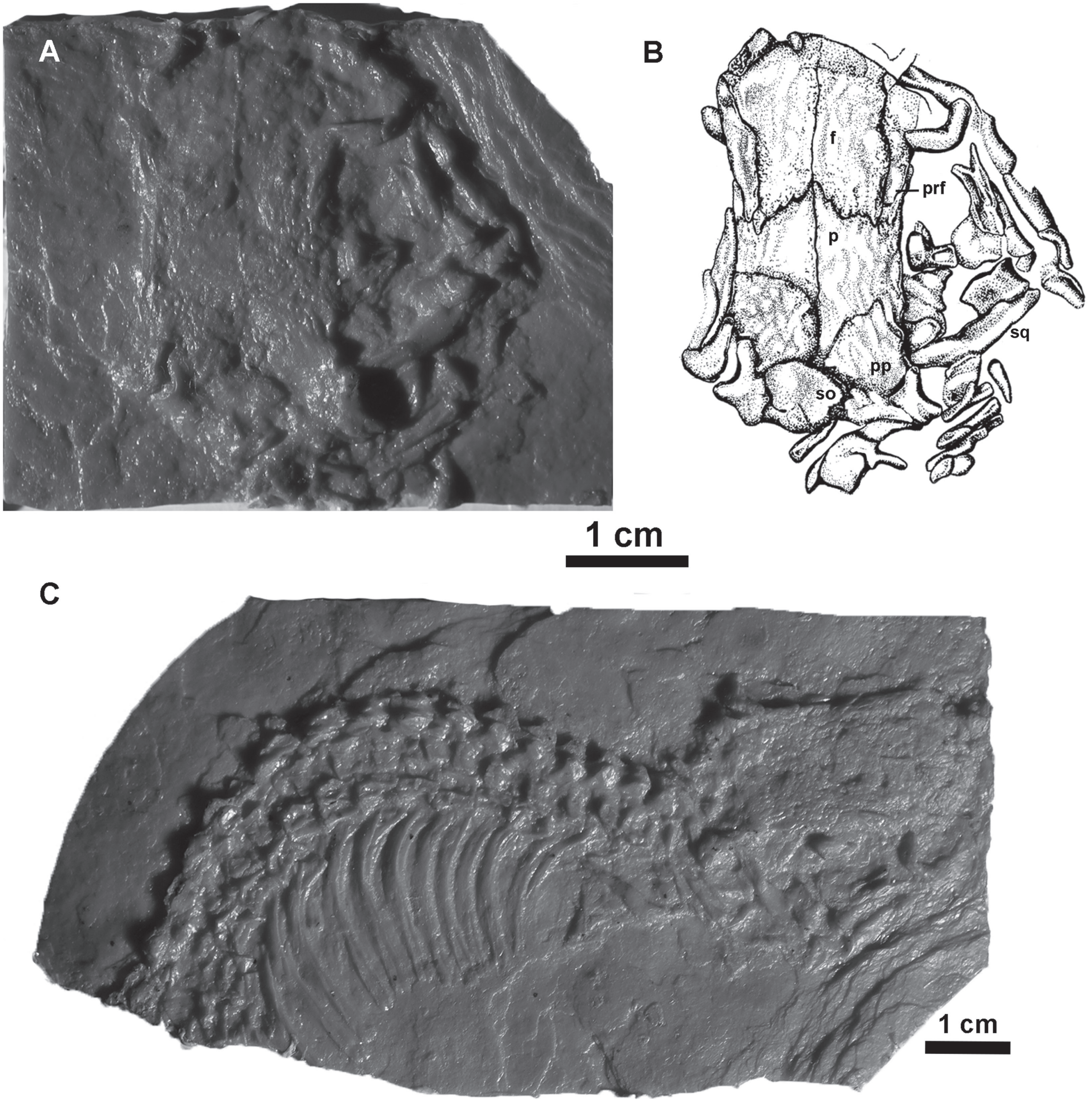

Figure 1. *Brachydectes newberryi* YPM VPPU 20391. A, latex cast of cranium in dorsal aspect. B, line drawing of the cranium showing well-developed dermal sculpturing. C, latex cast of full dorsal view.

Ontogenetic development of cranial ornamentation in molgophids, in which only large specimens show well-developed ornament, was observed by Wellstead (1991). Further examination of a variety of size classes outlined below reveals that cranial ornamentation is pronounced in skulls only greater than 2 cm in cranial length. The smallest molgophid specimens examined in this study, the diminutive '*Lysorophus minutus*' (CM 8564) and an even smaller undescribed specimen from Mazon Creek, FMNH PR 1031 (approx. 50 mm total body length), represent nearly complete juvenile specimens based on the level of ossification and lack of sutural closure between skull elements. Neither shows any indication of sculpture on any of the cranial elements. Small (under 20 mm cranial length) *Brachydectes* from Linton, Ohio (including AMNH 6925 '*Cocytinus gyrinoides*', AMNH 6861, and AMNH 2156), show weak dermal ornamentation on their crania that include very fine striae and developing pits. From Linton, only larger (30 mm cranial length) molgophids such as YPM VPPU 20391 (*Brachydectes newberryi*) and MCZ 2303 '*Pleuroptyx clavatus*' show well-developed rugose ornamentation, suggesting this feature becomes increasingly conspicuous through ontogeny. These observations are further substantiated by three-dimensionally preserved *Brachydectes* specimens from the Early Permian Speiser shale, Kansas, Eskridge shale, Nebraska (Fig. 2), where small individuals approximately 10 mm in cranial length (Fig. 2A) bear only a rough cranial surface lacking raised ridges. Larger specimens (Fig. 2B, C) show progressively more developed dermal sculpturing. Specimens with skulls attaining 20 mm or more in length, including UNSM 32149 (Fig. 2C), show cranial ornamentation comparable to that of YPM VPPU 20391, including rugosity on the anterior cranial roof elements and pustular ornamentation and pits on the posterior elements. Similar trends in growth of cranial ornamentation through ontogeny have been observed in other 'lepospondyl' taxa, such as *Microbrachis*, and temnospondyls alike (Boy 1988; Schoch 2002, 2003; Vallin and Laurin 2004).

CONCLUSION

The morphology of cranial ornamentation in the molgophid *Brachydectes newberryi*, described here for the first time in detail based on YPM VPPU 20391 (Fig 1), reveals unique patterns of rugose ornamentation on the skull

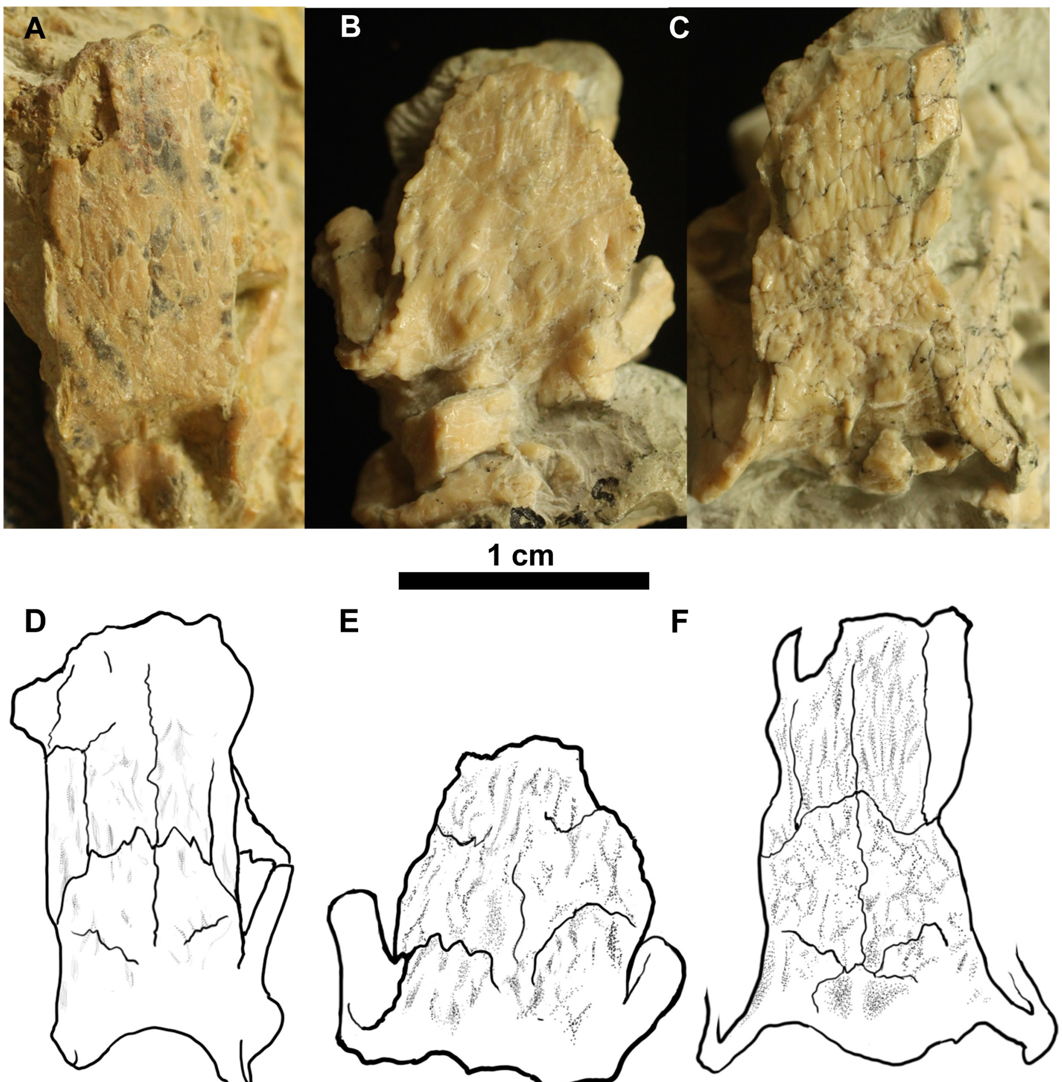

Figure 2. Photographs and drawings of skulls of *Brachydectes* from the earliest Permian Eskridge Shale of Nebraska (UNSM 32100, UNSM 32149) and Speiser Shale of Kansas (KUVP 49541), Council Grove Group. A and D, KUVP 49541, an immature individual showing only small crenulations on the cranium. B and E, UNSM 32100, posterior skull roof, showing the beginning of dermal rugose sculpture forming. C and F, UNSM 32149, a larger skull roof showing well developed cranial ornamentation comparable to patterns observed in PU 20391 (Photos courtesy of J. D. Pardo).

roof and pustular ornamentation on the postparietals. In addition, the ontogenetic pattern of cranial ornamentation is identified in *Brachydectes newberryi* from Linton, Ohio, where cranial ornamentation is pronounced only in individuals with a cranial length greater than 2 cm.

Going forward, a more in-depth specimen-based study of molgophid from all known Permo-Carboniferous localities is required in order to decouple factors that may be muddling alpha taxonomy, including taphonomy, ontogeny, and intraspecific variation. Given that postcranial variation, including variation in presacral vertebrae and rib morphology, provides the most promising character support for multiple taxa within Molgophidae, it remains the next area of research to be conducted.

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