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The furculae of the dromaeosaurid dinosaur *Dakotaraptor steini* are trionychid turtle entoplastra.

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Abstract:

Dakotaraptor steini is a recently described dromaeosaurid dinosaur from the Upper Cretaceous (Maastrichtian) Hell Creek Formation of South Dakota. Included within the *D. steini* hypodigm are three elements originally identified as furculae: one which is part of the holotype specimen and two referred specimens. We show that the elements described as *D. steini* ‘furculae’ are not theropod dinosaur furculae, but rather trionychid turtle entoplastra. Given that the holotype ‘furcula’ is not referable to Dromaeosauridae and that the specimen is a disarticulated individual based on skeletal remains from a multitaxic bonebed, the holotype of *Dakotaraptor steini* is a chimera.

Dakotaraptor steini DePalma, Burnham, Martin, Larson, and Bakker, 2015, is a recently described dromaeosaurid dinosaur from the Upper Cretaceous (Maastrichtian) Hell Creek Formation of South Dakota. The holotype (PBMNH P.10.113.T) is given as an associated skeleton derived from a bonebed that purportedly contains the fossilized remains of other vertebrates including mammals, fish, amphibians, pterosaurs, reptiles, and birds (DePalma 2010; DePalma et al. 2015). Included within the *D. steini* hypodigm are three elements that DePalma and colleagues (2015) identify as furculae: one which is part of the holotype specimen and two referred specimens—NCSM 13170 and KUV 152429 (which was not figured)—the latter of which are considered “virtually indistinguishable” from and “identical” to the holotype ‘furcula’ (DePalma et al., 2015:p. 6). Here we demonstrate that the elements described as *D. steini* ‘furculae’ are not theropod dinosaur furculae, but rather trionychid turtle entoplastra. Given that the holotype ‘furcula’ is not referable to Dromaeosauridae and that the specimen is a disarticulated individual based on skeletal remains from a multitaxic bonebed, the holotype of *Dakotaraptor steini* is a chimera.

The furcula is a median, unpaired element present in extant birds and their non-avian theropod relatives (Nesbitt et al. 2009). Although the furcula is generally thought to have arisen through fusion of the clavicles, recent developmental studies suggest that the furcula is homologous with the interclavicle of early tetrapods (Vickaryous and Hall 2010). DePalma et al. (2015) themselves noted several differences between the putative ‘furculae’ of *Dakotaraptor steini* and those of other non-avian theropod

dinosaurs. We note that in *D. steini*, the 'furcula' is extremely craniocaudally compressed, and possesses flattened rami that bulge halfway along the length of the ramus, terminally asymmetrical 'epicleidia' with longitudinal striations, a medial juncture bearing a ventral tab (previously identified as the 'hypocleidium'), and transversely straight, rather than caudally bowed rami. Taken together this suite of characteristics is unknown in other theropod furculae (Nesbitt et al. 2009), yet is consistent with the structure of the entoplastron in trionychid (soft-shelled) turtles.

The entoplastron is a median, unpaired element in the plastron, and, like the furcula of theropods, is a homolog of the interclavicle (Gilbert et al. 2001). In many turtle clades, the entoplastron is a roughly diamond-shaped element; however, in trionychids (softshell turtles) it takes on a flattened slender V-shape with lateral projections that diverge at roughly 90 degrees (Hay 1908; Vitek 2012; Cadena et al. 2013; Hutchison 2013; Vitek and Joyce 2015), reminiscent of the shape of non-avian theropod furculae. In their description of the associated fauna DePalma et al. (2015) note that multiple turtles, including trionychids (as *Trionyx* sp.) are preserved at the holotype locality (DePalma 2010). Indeed, trionychids are common elements of Campanian-Maastrichtian North American ecosystems (Brinkman 2003) and at least five species are represented in the Hell Creek Formation from which *D. steini* derives (Holroyd et al. 2014; Vitek and Joyce 2015). Moreover, several Campanian to modern trionychine trionychids (terminology following Hummel 1928) have entoplastra that closely match the morphology of NCSM 13170 and the element figured as a 'furcula' in PBMNH P.10.113.T.

Among extinct North American trionychines, the taxonomic identity of the entoplastral elements within the *D. steini* hypodigm can be refined on the basis of comparative morphology and relative size (Vitek 2012). Here we follow the trionychid taxonomy of Danilov et al. (2014), but see Vitek and Joyce (2015) for a differing opinion. NCSM 13170 and PBMNH P.10.113.T exhibit an overall gracile morphology (narrow craniocaudally relative to the length of the lateral projections) as in *Axestemys splendida* (Gardner et al. 1995), other species of *Axestemys* (Vitek 2012), *Aspideretoides allani* (Gardner et al. 1995), and *Apalone* and relatives (Vitek 2011; Danilov et al. 2014).

Several discrete features of NCSM 13170 and PBMNH P.10.113.T are shared with select trionychid species. In NCSM 13170 the craniomedial margin of the rami junction is broad and cranially convex, bearing distinct lateral notches for contact with the epiplastra (Fig. 1). This differs from the condition seen in *Axestemys montinsana* (Vitek 2012), yet closely matches the morphology seen in *Axestemys splendida* and other Late Cretaceous trionychids (Gardner et al. 1995). The distalmost one quarter of the ramus in PBMNH P.10.113.T (and in NCSM 13170, although the tip of the ramus is damaged) abruptly tapers asymmetrically, representing the end of the contact between the entoplastron and epiplastron (Fig. 1). This morphology is identical to that seen in *Axestemys splendida* (Gardner et al. 1995; Fig. 1), *Axestemys montinsana* (Vitek 2012) and possibly *Gobiapalone brevipastra* (Danilov et al. 2014).

The caudal margins of the rami in NCSM 13170 and PBMNH P.10.113.T bear a notch for the reception of the hyoplastron, which articulates with approximately two-thirds of the entoplastron ramus. The extent of this contact is similar in *Axestemys splendida* (Gardner et al. 1995; Fig. 1), *Axestemys montinsana* (Vitek 2012), *Axestemys cerevisia* (Vitek 2012), *Aspideretoides allani* (Gardner et al. 1995), and *Apalone* (Vitek 2012), yet differs in *Aspideretoides foveatus* (Gardner et al. 2015), *Oliveremys uintaensis* (Vitek

2011), and *Gobiapalone* (Danilov et al. 2014). It is noted by Vitek (2012) that this contact in *Axestemys* is not as extensive as in *Apalone* and that *Axestemys* lacks a hyoplastral shoulder locking the entoplastron in place.

Finally, a distinctive longitudinal fluting along the distal third of each ramus for the attachment of connective tissue mars the rami in NCSM 13170 and PBMNH P.10.113.T. This is also present in *Axestemys splendida* (Campanian-Maastrichtian, Fig. 1), *Axestemys montinsana* (Paleocene; Vitek 2012:fig. 17), and *Oliveremys uintaensis* (Vitek 2011).

The largest of the three trionychid entoplastra comprising the *D. steini* hypodigm (PBMNH P.10.113.T) pertains to a carapace approximately 60 cm in length based on comparisons with comparable materials (Fig 1A-D). This is consistent with the size range of *Axestemys* (Vitek 2012), and of similar proportions to the largest trionychid shells known from the Hell Creek Formation (Hutchison and Archibald 1986).

Taken together, the morphology and size of the PBMNH P.10.113.T "furcula" and NCSM 13170 indicate that they are most confidently identified as cf. *Axestemys splendida*. The holotype material of *Axestemys splendida* is Campanian in age, yet several specimens from the Late Maastrichtian have been referred to this taxon (Vitek 2012; Vitek and Joyce 2015) or are otherwise not identified to species (Holroyd et al. 2014) therefore, we refrain from referring these isolated elements beyond cf. *Axestemys splendida*.

As the holotype of *Dakotaraptor steini* is demonstrably a chimera, future authors should exercise caution when considering the taxon for comparative purposes or in phylogenetic analyses. Given that the coding of chimeric specimens as a single operational taxonomic unit in phylogenetic analyses can have misleading effects on character polarity and tree topology, a detailed element-by-element re-evaluation of the holotype and referred material should be conducted prior to the inclusion of *Dakotaraptor* in future studies.

Institutional abbreviations: KUV, University of Kansas Natural History Museum and Biodiversity Institute, Lawrence, Kansas, USA; NCSM, North Carolina Museum of Natural Sciences, Raleigh, North Carolina, USA; PBMNH, The Palm Beach Museum of Natural History; ROM, Royal Ontario Museum, Toronto, Ontario, Canada; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada.

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163 **Figures:**

164 Figure 1. Purported furculae for the holotype and referred specimens of *Dakotaraptor steini* compared
165 with the entoplastron of the trionychid turtle *Axestemys splendida*; anterior is up. **A-D**, *Axestemys*
166 *splendida* plastra in ventral view, showing the entoplastron in articulation with the other elements of
167 the plastron. **A** and **B**, ROM 1430; **C** and **D**, TMP 2015.012.0011. NCSM 13170 trionychid entoplastron
168 (formerly referred to *D. steini*) in **E**) dorsal and **F**) ventral views. **G**) PBMNH P.10.113.T ('furcula'
169 comprising part of the hypodigm for *D. steini*, adapted from DePalma et al. 2015.). Abbreviations: **hy**,
170 hypoplastron; **en**, entoplastron; **ep**, epiplastron.

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Purported furculae for the holotype and referred specimens of *Dakotaraptor steini* compared with the entoplastron of the trionychid turtle *Axestemys splendida*.

Figure 1. Purported furculae for the holotype and referred specimens of *Dakotaraptor steini* compared with the entoplastron of the trionychid turtle *Axestemys splendida*; anterior is up. **A-D**, *Axestemys splendida* plastra in ventral view, showing the entoplastron in articulation with the other elements of the plastron. **A** and **B**, ROM 1430; **C** and **D**, TMP 2015.012.0011. NCSM 13170 trionychid entoplastron (formerly referred to *D. steini*) in **E**) dorsal and **F**) ventral views. **G**) PBMNH P.10.113.T ('furcula' comprising part of the hypodigm for *D. steini*, adapted from DePalma et al. 2015.). Abbreviations: **hy**, hypoplastron; **en**, entoplastron; **ep**, epiplastron.

