

**A peer-reviewed version of this preprint was published in PeerJ on 9 February 2016.**

[View the peer-reviewed version](https://doi.org/10.7717/peerj.1691) (peerj.com/articles/1691), which is the preferred citable publication unless you specifically need to cite this preprint.

Arbour VM, Zanno LE, Larson DW, Evans DC, Sues H. 2016. The furculae of the dromaeosaurid dinosaur *Dakotaraptor steini* are trionychid turtle entoplastra. PeerJ 4:e1691 <https://doi.org/10.7717/peerj.1691>

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

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*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.

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

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8

9 *Abstract:*

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

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

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

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

43 The entoplastron is a median, unpaired element in the plastron, and, like the furcula of theropods, is a  
44 homolog of the interclavicle (Gilbert et al. 2001). In many turtle clades, the entoplastron is a roughly  
45 diamond-shaped element; however, in trionychids (softshell turtles) it takes on a flattened slender V-  
46 shape with lateral projections that diverge at roughly 90 degrees (Hay 1908; Vitek 2012; Cadena et al.  
47 2013; Hutchison 2013; Vitek and Joyce 2015), reminiscent of the shape of non-avian theropod furculae.  
48 In their description of the associated fauna DePalma et al. (2015) note that multiple turtles, including  
49 trionychids (as *Trionyx* sp.) are preserved at the holotype locality (DePalma 2010). Indeed, trionychids  
50 are common elements of Campanian-Maastrichtian North American ecosystems (Brinkman 2003) and at  
51 least five species are represented in the Hell Creek Formation from which *D. steini* derives (Holroyd et al.  
52 2014; Vitek and Joyce 2015). Moreover, several Campanian to modern trionychine trionychids  
53 (terminology following Hummel 1928) have entoplastra that closely match the morphology of NCSM  
54 13170 and the element figured as a 'furcula' in PBMNH P.10.113.T.

55 Among extinct North American trionychines, the taxonomic identity of the entoplastral elements within  
56 the *D. steini* hypodigm can be refined on the basis of comparative morphology and relative size (Vitek  
57 2012). Here we follow the trionychid taxonomy of Danilov et al. (2014), but see Vitek and Joyce (2015)  
58 for a differing opinion. NCSM 13170 and PBMNH P.10.113.T exhibit an overall gracile morphology  
59 (narrow craniocaudally relative to the length of the lateral projections) as in *Axestemys splendida*  
60 (Gardner et al. 1995), other species of *Axestemys* (Vitek 2012), *Aspideretoides allani* (Gardner et al.  
61 1995), and *Apalone* and relatives (Vitek 2011; Danilov et al. 2014).

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

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

76 2011), and *Gobiapalone* (Danilov et al. 2014). It is noted by Vitek (2012) that this contact in *Axestemys* is  
77 not as extensive as in *Apalone* and that *Axestemys* lacks a hyoplastral shoulder locking the entoplastron  
78 in place.

79 Finally, a distinctive longitudinal fluting along the distal third of each ramus for the attachment of  
80 connective tissue mars the rami in NCSM 13170 and PBMNH P.10.113.T. This is also present in  
81 *Axestemys splendida* (Campanian-Maastrichtian, Fig. 1), *Axestemys montinsana* (Paleocene; Vitek  
82 2012:fig. 17), and *Oliveremys uintaensis* (Vitek 2011).

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

87 Taken together, the morphology and size of the PBMNH P.10.113.T "furcula" and NCSM 13170 indicate  
88 that they are most confidently identified as cf. *Axestemys splendida*. The holotype material of *Axestemys*  
89 *splendida* is Campanian in age, yet several specimens from the Late Maastrichtian have been referred to  
90 this taxon (Vitek 2012; Vitek and Joyce 2015) or are otherwise not identified to species (Holroyd et al.  
91 2014) therefore, we refrain from referring these isolated elements beyond cf. *Axestemys splendida*.

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

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

## 102 103 **Acknowledgements**

104 Thanks are extended to D. Brinkman (TMP) for access to TMP 2015.012.0011 and G. Housego (TMP) for  
105 photographs, and to D. Dufault (ROM) for photographing ROM 1430. NCSM 13170 was donated to the  
106 North Carolina Museum of Natural Sciences by W. Stein (PaleoAdventures).

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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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## 1

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.



