



Short communication

Remarks on the evolution of the avian sternum, dinosaur gastralia, and their functional significance for the respiratory apparatus



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ABSTRACT

The sternum is a central part of the avian skeleton and, among other functions, it serves as a key element of their locomotor apparatus by providing the origin site for the primary flight musculature. Understanding the evolutionary history of the sternum is critical for understanding the origin of active flight: a fundamental characteristic of one of the most diverse extant tetrapod lineages. It recently has been proposed that the sternal elements in extinct basal bird radiations may not be homologous and that the stem species of Aves lacked a sternum. Here we show that sternal elements were indeed present in the stem line throughout the evolutionary transformation from non-avian theropod dinosaurs to modern birds. We further demonstrate a trade-off between sternal elements and gastralia, dermal bones of the belly wall that at least partially overlapped with the respiratory functions of the sternum. As long as gastralia were present and functioned in ventilation, the sternum could become completely reduced such as possibly in Troodontidae, *Archaeopteryx* and *Sapeornis*. However, once gastralia became lost in Neornithes, even the flightless species needed to retain their sternum: no animal needs to fly, but all need to breathe.

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1. Introduction

The sternum is frequently considered to be one of the most important elements of the avian skeleton because of its central role in the flight apparatus (e.g., Zheng et al., 2012, 2014). Active flight most likely is plesiomorphic for the extant avian crown-group and those living birds that are flightless doubtlessly reduced this capability secondarily, sometimes even convergently in closely related groups (e.g., Harshman et al., 2008; Phillips et al., 2010). However, the situation is far from resolved, and there still is much debate on when and how active flight actually evolved during the Mesozoic origin of birds as derived theropod dinosaurs (e.g., Dial, 2003; Nudds and Dykes, 2010; Foth et al., 2014; Koschowitz et al., 2014; Feo et al., 2015).

Zheng et al. (2014) recently provided a detailed analysis focusing on the sternal morphology in a variety of paravian taxa and concluded that because sternal elements are absent in Troodontidae, *Archaeopteryx* von Meyer, 1861 and *Sapeornis* Zhou and Zhang, 2002 'it is most parsimonious to interpret that this feature was

the plesiomorphic avian condition' and that 'basal bird sterna may not be truly homologous'. Using the commonly accepted phylogenetic relationships that these authors employed, this hypothesis would require (a) the complete reduction of sternal elements at the base of Paraves, because the closest related outgroups as well as more basal theropod taxa possessed sternal elements (Zheng et al., 2012, 2014), and (b) the separate re-evolution of sternal elements in Dromaeosauridae, Jeholornithiformes, and those Pygostylia more crownward than *Sapeornis*.

The aim of the present study is to reappraise the evolution of the avian sternum and to place these findings into a functional context with particular emphasis on the respiratory function of the sternum and gastralia.

2. Materials and methods

We used the data published by Zheng et al. (2014) on the presence and absence of sternal elements in a variety of paravian taxa to reconstruct the ancestral states of this trait, employing the commonly accepted phylogenetic relationships used by these authors. The analysis was run using the software Mesquite 3.01 (www.mesquiteproject.org) and one of two possible discrete states was assigned to each terminal taxon: 0, sternal elements absent; 1, sternal elements present. Terminal taxa were (character states

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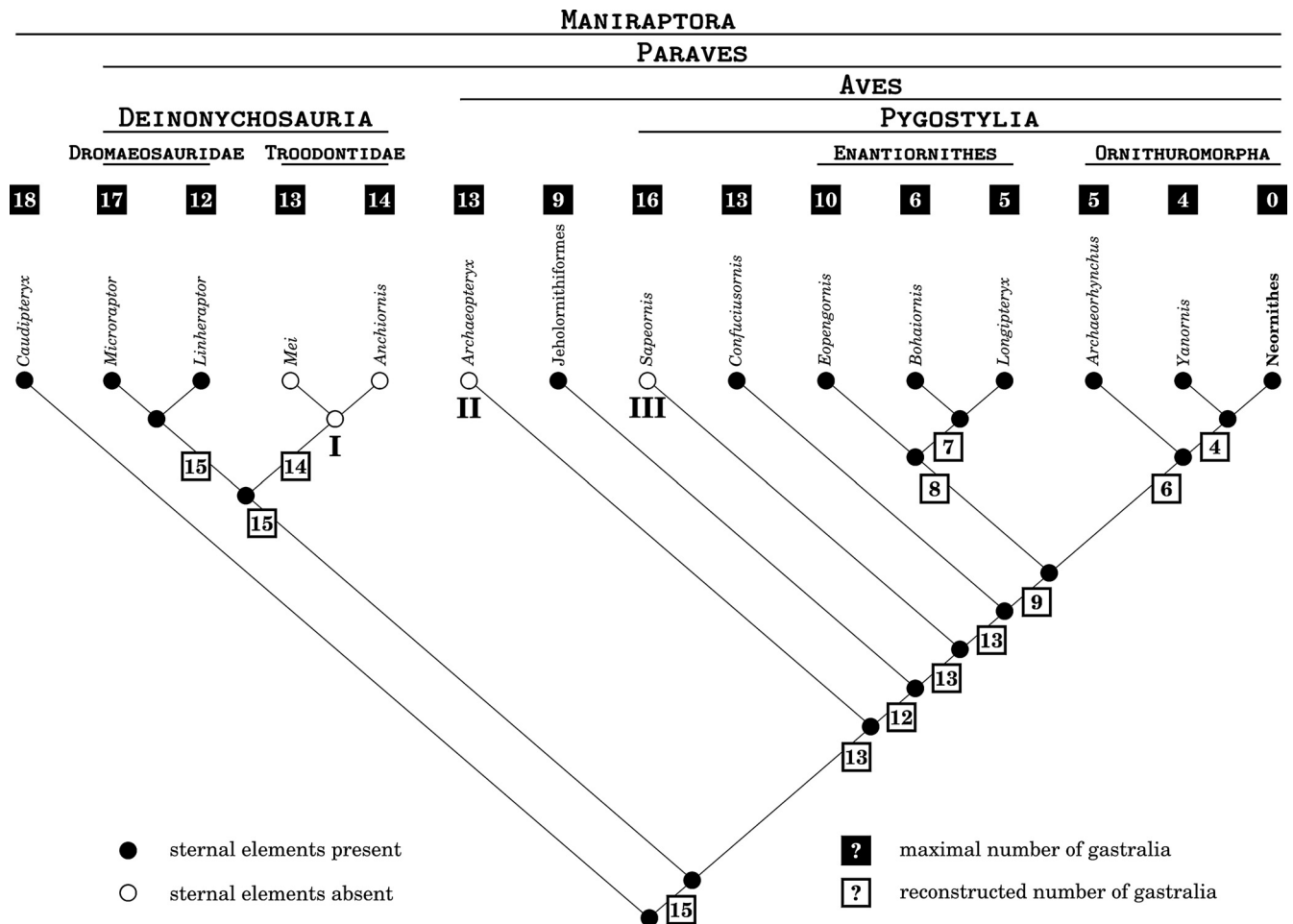


Fig. 1. Evolution of sternal elements and gastralia among Paraves. Parsimony-based ancestral state reconstruction for the presence (black circles) or absence (white circles) of sternal elements in paravians using *Caudipteryx* as outgroup. All internal nodes except for that of Troodontidae indicate that sternal elements were present, which suggests three independent complete reductions of this trait (I–III). Parsimony-based ancestral state reconstruction for gastralial number (squares, rounded up to the nearest integer) indicates a general trend for a reduction along the stem line, and further separate reductions within Enantiornithes and Ornithuromorpha.

given in parentheses): *Microraptor* Xu et al., 2000 (1), *Linheraptor* Xu et al., 2010 (1), *Mei* Xu and Norell, 2004 (0), *Anchiornis* Xu et al., 2009 (0), *Archaeopteryx* (0), *Jeholornithiformes* (1), *Sapeornis* (0), *Confuciusornis* Hou et al., 1995 (1), *Eopengornis* Wang et al., 2014 (1), *Longipteryx* Zhang et al., 2001 (1), *Bohaiornis* Hu et al., 2011 (1), *Archaeorhynchus* Zhou and Zhang, 2006 (1), *Yanornis* Zhou and Zhang, 2001 (1) and *Neornithes* (1). *Caudipteryx* Ji et al., 1998 (1) was used as outgroup. The analysis was run with unordered character states and employing parsimony. The final figure was compiled in the software Inkscape 0.48.4 (www.inkscape.org).

In addition, we evaluated the character history of the number of gastralia for the same taxon sampling in Mesquite, employing continuous characters and parsimony. We chose the maximal number of gastralia reported for each taxon by Zheng et al. (2014) to account for the most conservative estimate of maximal gastralial number in each lineage. These were (maximal gastralial number in parentheses): *Microraptor* (17), *Linheraptor* (12), *Mei* (13), *Anchiornis* (14), *Archaeopteryx* (13), *Jeholornithiformes* (9), *Sapeornis* (16), *Confuciusornis* (13), *Eopengornis* (10), *Longipteryx* (5), *Bohaiornis* (6), *Archaeorhynchus* (5), *Yanornis* (4) and *Neornithes* (0). *Caudipteryx* (18), again, was used as outgroup. We also performed a corresponding analysis for the minimal number of gastralia as reported by Zheng et al. (2014), but since the overall result did not differ from that using the maximal number of gastralia, the analysis is not shown here.

Several specimens from the teaching collection of the Institut für Zoologie, Rheinische Friedrich-Wilhelms-Universität Bonn (*Balearica pavonina* (Linnaeus, 1758): isolated sternal apparatus with reconstructed flight musculature made out of wax; *Casuaris* Brisson, 1760: isolated sternal apparatus; *Struthio camelus* Linnaeus, 1758: mounted skeleton; all specimens without voucher numbers) were used to illustrate our functional discussion. All photographs were made with a Canon EOS 5D Mark II digital single lens reflex camera equipped with a Canon Lens EF 50 mm 1:1.8. Photographs were edited (color-corrected, background eliminated) with the software GIMP 2.8 (www.gimp.org) and imported to Inkscape to finalize the figure.

3. Results and discussion

Ancestral state reconstructions reveal that the most parsimonious explanation is three independent, complete reductions of sternal elements, i.e., in Troodontidae, *Archaeopteryx*, and *Sapeornis*. All internal nodes, except for that of troodontids, are reconstructed to have sternal elements present (Fig. 1). Based upon the data at hand, we see no parsimony-based reason to question that the avian stem species possessed sternal elements. Furthermore, there are no parsimony-based reasons to question the homology of these structures in basal birds.

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