Reply to Foth: Preserved cartilage is rare but not absent: Troodontid sternal plates are absent, not rare

Foth (1) critiques the conclusions of a previous work by Zheng et al. (2), which describes the complete absence of sternal elements in *Anchiornis* and *Sapeornis*. Although initially we were equally skeptical, we feel that the evidence continues to be strongly compelling, and we thank Foth (1) for giving us the opportunity to further address potential skepticism. First, it is argued that most theropod dinosaurs lack ossified sternal elements; this may be true of basal members of the clade and indeed these elements are rare. However, recent work on derived maniraptoran theropods strongly suggests that these elements are present in most taxa but ossify late in skeletal ontogeny and even fuse in mature specimens (3). Unfortunately, sternal plates are very thin and not strongly attached to the rest of the skeleton and thus are not commonly preserved. For these reasons, sternal elements have always been described as not preserved in the Troodontidae, rather than "absent" (4); it is only through the Zheng et al. (2) dataset and histological analysis that the complete absence of ossified sternal elements could be confirmed in at least one troodontid, *Anchiornis*, and implied for others. Second, feathers are not always preserved as melanosomes (often as amorphous carbon or simply as impressions); there is a huge diversity of preservational types in the Yanliao and Jehol biotas, representing a multitude of taphonomic microenvironments, most of which are poorly understood (5). Some specimens do preserve impressions or a stain of the cartilaginous skeletal elements (*Eoconfuciusornis* IVPP V11977, juvenile enantiornithines, e.g., IVPP V14238); therefore, we considered the absence of any such indicator in 224 specimens of *Anchiornis* to strongly suggest a chondrified element was absent. Admittedly, preserved cartilage is strangely far less frequent than the preservation of soft tissue (numerous fish and amphibians; bird feathers and ovarian follicles) (5). However, considering the rapid appearance of derived skeletal features during the 10 million years of evolution encapsulated by the Jehol, the mechanical stresses of powered flight, and the ease at which a cartilaginous element can become ossified through bone morphogenetic protein signaling, we consider the absence of an ossified sternum in Jiufotang sapeornithids to be further evidence that this element was entirely absent in this clade (2). We are aware of the calcitic mass preserved in the Berlin *Archaeopteryx*; however, the position of the mass (between the scapula and coracoid) is inconsistent with its interpretation as the sternum. The ribs are slightly expanded in *Anchiornis*, *Sapeornis*, and *Jeholornis*, and variably in neornithines, but we suggest that the bulbous expansion present in *Archaeopteryx* may be a derived feature of this volant lineage, perhaps related to strengthening this area for muscle attachment in the absence of a sternum.

Although cartilage is rarely preserved its traces are not absent, and in light of our large sample size we remain confident that a cartilaginous sternum was absent in *Anchiornis* and *Sapeornis*. Although exploring specimens through fluorescent light can be useful, notably there is no trace of this element revealed by a recent UV study on *Archaeopteryx* (1).

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1 Foth C (2014) Comment on the absence of ossified sternal elements in basal paravian dinosaurs. *Proc Natl Acad Sci USA* 111:E5334.

2 Zheng X, et al. (2014) On the absence of sternal elements in *Anchiornis* (Paraves) and *Sapeornis* (Aves) and the complex early evolution of the avian sternum. *Proc Natl Acad Sci USA* 111(38): 13900–13905.

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4 Xu X, et al. (2009) A new feathered maniraptoran dinosaur fossil that fills a morphological gap in avian origin. *Chin Sci Bull* 54(3): 430–435.

5 Zhou Z, Barrett PM, Hilton J (2003) An exceptionally preserved Lower Cretaceous ecosystem. *Nature* 421:807–814.

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The authors declare no conflict of interest.

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