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The gastral basket in basal birds and their close relatives: size and possible function

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Abstract Here we investigate the size and morphology of the gastral basket in non-neornithine Mesozoic birds and their close non-avian dinosaur relatives. The size of the gastral basket reportedly increases with body size in the Theropoda. However, *contra* earlier reports basal birds appear to have proportionately large gastral baskets compared to non-avian theropods, suggesting gastralia may have functioned as a compensatory feature for muscle attachment in the absence of a craniocaudally extensive sternum. As in crocodilians, the proximal row of gastralia in basal birds articulates with the sternum when present suggesting the two features may have functioned as a unit; this hypothesis is not supported by any scars to indicate the gastralia served as points of muscle attachment. Alternatively, the large size of the gastral basket may be related to its respiratory function and the high oxygen demands of powered flight in birds. Due to incomplete preservation of these delicate elements as a unit, sample size is too low to draw significant results from statistical analysis of this element.

Keywords Jehol Biota, Cretaceous, Paraves, Aves, gastralia, sternum, *Sapeornis*

1 Introduction

Gastralia, sometimes inaccurately referred to as 'abdominal ribs', are a series of small dermal ossifications. These dermal bones articulate to form an interlocking unit or 'basket' that is considered to protect the abdomen. Among extant taxa, this feature is only freely present in crocodilians and the tuatara (potentially also incorporated into the turtle plastron) (Claessens, 2004). However, gastralia may be plesiomorphic to tetrapods and are present in a number of extinct groups (e.g. plesiosaurs, ichthyosaurs) including theropod dinosaurs; although present in basal birds, this feature is lost in the neornithine lineage (Claessens, 2004). Claessens (2004) provided an excellent review of the distribution and function of this feature within Dinosauria, where they are found only in the Prosauropoda and Theropoda clades. However, due to the typically poor preservation of this delicate feature, which is free from the skeleton,

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little focus was put on reporting the exact number of pairs of gastralia forming the basket in various taxa. Overall, the number of gastralia is reported to increase with body size, with basal birds reportedly having very small gastral baskets, although only *Archaeopteryx* and two basal pygostylian confuciusornithiform taxa were included (Claessens, 2004).

The Late Jurassic Daohugou Formation and Lower Cretaceous Jehol Group, consisting of the lower Yixian and upper Jiufotang formations, are unique in providing numerous well preserved, nearly complete and fully articulated specimens (Zhou et al., 2003; Sullivan et al., 2014). These lithologic units, which outcrop in northeastern China, provide a taphonomic window through which to study many biological aspects typically elusive to paleontologists, such as feather morphology and color and the morphology of the alimentary canal and reproductive system (O'Connor et al., 2012; Zhang et al., 2010; Zheng et al., 2014a). The exceptional preservation of these faunas allows the size of the gastral basket to be closely examined across a broad range of taxa that cross the dinosaur-avian transition including all paravian clades and every clade of basal bird. The size of the gastral basket is reported to range from 8–21 pairs within Theropoda (Claessens, 2004). However, with 15–16 pairs, the basal pygostylian bird *Sapeornis* from the Jehol Group has the largest reported gastral basket within Paraves despite its relatively small size compared to larger cursorial taxa (Fig. 1) (Zhou and Zhang, 2002a, 2003). *Sapeornis* notably lacks an ossified sternum (Zhou and Zhang, 2002a), which is also absent in the basal most avian *Archaeopteryx* (Wellnhofer and Tischlinger, 2004) and the Troodontidae, a group of small, derived paravian maniraptoran theropods inferred to be very closely related to Aves (Makovicky and Norell, 2004; Turner et al., 2007). In extant birds the sternum provides the primary attachment surface for the two main flight muscles, the pectoralis and supracoracoideus (Gill, 2007), and ossified sternal plates are present in the Dromaeosauridae (Paraves), Oviraptorosauria (Maniraptora), and a number of other groups of dinosaurs (Chiappe et al., 2002; Galton and Upchurch, 2004; Norell and Makovicky, 2004; Osmólska et al., 2004) making their apparent absence at the base of the avian clade perplexing. The absence of any evidence of sternal plates and sternal ribs in all known specimens of *Sapeornis* (n=106) and the Daohugou troodontid *Anchiornis* (n=229), many of which preserve excellent soft tissue structures, has recently been cited as evidence that even a chondrified sternum was absent in these taxa and potentially also *Archaeopteryx* (Zheng et al., 2014b). We describe the gastral basket in basal birds in detail for the first time, document the size of the gastral basket in basal birds and their relatives, and explore the possibility the enlarged gastral basket in *Sapeornis* is related to the absence of ossified sternal plates as proposed by Zheng et al. (2014b).

Fig. 1 Close up of the complete or nearly complete gastral basket in *Sapeornis chaoyangensis*
A. IVPP V 13276; B. IVPP V 13396 (subadult specimen, former holotype of '*S. angustis*')
Scale bars equal 10 mm. Anatomical abbreviations: 1-16. pairs of gastralia; cor. coracoid; fem. femur; gas. gastralia; hum. humerus; pub. pubis; sca. scapula. Designations: l. left; r. right

2 Methods

We collected data on gastral basket size from across Paraves (Deinonychosauria+Aves) including representatives of all known clades of basal birds. Only specimens in which the gastral basket can be considered complete are reported (unfortunately encompassing quite a low number of non-avian taxa). When possible we used data collected directly from specimens in the collections of the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) and the Shandong Tianyu Museum of Nature (STM). In the case of taxa known from a single specimen or very limited material we only included those species known from exceptional holotype material (e.g. *Eopengornis*, *Mei long*) (Wang X et al., 2014; Xu and Norell, 2004); if a large number of specimens were available the highest preserved number was recorded (e.g. *Anchiornis*, *Sapeornis*, *Confuciusornis*, *Longipteryx*, *Yanornis*) (Zhang et al., 2001; Chiappe et al., 2008; Zheng et al., 2014a, b). For taxa outside the Daohugou or Jehol faunas we primarily relied on published data.

Institutional abbreviations BPM, Beipiao Paleontological Museum, Liaoning, China; DINO, Dinosaur National Monument, Utah, USA; GMV, National Geological Museum of China, Beijing; IGM, Mongolian Institute of Geology, Ulaanbaatar, Mongolia; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; JMP, Jinzhou Museum of Paleontology, Jinzhou, Liaoning, China; STM, Shandong Tianyu Museum of Nature, Pingyi, Shandong, China.

3 Gastralia description

Troodontidae (Paraves: Deinonychosauria) The most common troodontid is *Anchiornis* with a huge published collection of over 200 specimens (n=229) (Zheng et al., 2014b); 78% preserve gastral elements but in only 10% is the basket even moderately well preserved. Based on STM 0-120, we estimate the complete gastral basket of *Anchiornis* consisted of 13–14 pairs of gastralia (Zheng et al., 2014b: fig. 1). Each pair is formed by four curved elements except for the cranial-most pair, which is more robust and appears to be fused on each side and consisting of only two elements (STM 0-165, 0-120; Zheng et al., 2014b: fig. 1). Midline fusion of elements is reported in *Troodon formosus* (Russell, 1969). Fusion of cranial and caudal gastral elements is common although typically the rostral pair fuses into a single chevron shaped element (Claessens, 2004), which is not observed here. In *Anchiornis* the proximal most gastralium is level with the third thoracic rib (Zheng et al., 2014b: fig. 1). The proximal three pairs are more robust; caudally the gastralia are thin and delicate and the distal pair is less than a third the length of the proximal pair. This is different from previous reports for theropods, which are described to range in length by only 50% (Claessens, 2004); this may suggest that the very small caudal rows are lost in many specimens as a result of their delicate morphology. The morphology of the gastral basket is otherwise consistent with previous descriptions for this clade (Claessens, 2004).

Mei long, a younger taxon from the Yixian Formation that is slightly larger than *Anchiornis*, preserves 13 pairs of gastralia in the holotype specimen (Fig. 2C). Fifteen pairs are reported in the similarly well-preserved nearly complete holotype of the larger taxon *Sinornithoides youngi* (IVPP V 9612) from the Early Cretaceous Ejinhoro Formation (Russell and Dong, 1993) (Table 1). Troodontidae encompasses a considerable size range (Makovicky and Norell, 2004; Turner et al., 2007); however, taxa from the upper size limit are typically very incomplete and do not preserve this delicate feature in its complete form, if at all.

Table 1 Comparative data regarding body size, size of gastral basket, proportions of the coracoid, and presence of a sternum in derived maniraptorans (mm)

Taxon	Clade	Sternum	Femur L	Spec. No.	Gastralia (pairs)	Gastralia/ Femur L	Coracoid W/L
Allosaurus	Certatosauria	absent	880	DINO 11541	18	0.02	1.64
Sinocalliopteryx	Compsognathidae	unknown	236.1	JMP-V-05-8-01	12	0.051	0.99
Caudipteryx	Oviraptorosauria	unfused	195	STM 22-1	17–18	0.087	0.82
Velociraptor	Dromaeosauridae	potentially fused late in ontogeny	238	IGM 100/985	12	0.05	0.60
Sinornithoides youngi	Troodontidae	absent	140	IVPP V 9612	15	0.10	1.11
Microraptor gui	Dromaeosauridae	fused	51	STM 5-28	14–15	0.255	0.66
Anchiornis	Troodontidae	absent	73	STM 0-120	13–14	0.178	1.01
Mei long	Troodontidae	absent	81	IVPP V 12733	13	0.161	1.04
Archaeopteryx lithographica	Aves	absent	52.2	Berlin Specimen	12–13	0.239	0.91
Jeholornis	Aves: Jeholornithiformes	fused, add’l ossifications	75	STM 2-47	8-9	0.161	0.35
Confuciusornis	Aves: Confuciusornithiformes	fused	45	STM 13-52	12–13	0.267	0.67
Sapeornis	Aves: Sapeornithiformes	absent	74	IVPP V 13276	15–16	0.20	0.84
Eopengornis	Aves: Enantiornithes	fused	27	STM 24-1	10	0.37	0.58
Parabohaiornis	Aves: Enantiornithes	fused, keeled	37	IVPP V 18690	6	0.147	0.35
Archaeorhynchus	Aves: Ornithuromorpha	fused, keeled	34	IVPP V 17075	5	0.077	0.71

Note: Femoral length (L) is used as a proxy for size and was typically measured from the specimen preserving the most complete gastral basket for each taxon. We normalized the number of gastralia for size by dividing the minimum number of gastral pairs by the length of the femur in the associated specimen (when possible).

Dromaeosauridae (Paraves: Deinonychosauria) The dromaeosaurid known from the greatest number of specimens is *Microraptor* from the Jehol Group (Xu et al., 2000; 2003). Despite its rostrocaudally elongate sternum, this small volant dromaeosaurid (only slightly smaller than the average *Anchiornis*, Table 1) preserves an estimated 14–17 pairs of gastralia in one specimen (STM 5-28); however, the largest number observed in any other specimen is 13–14 in STM 5-101 (Fig. 2A) thus we estimate 14–15 pairs were present. The cranial row is twice the length of the caudal row. The rostral row of gastralia appears to be level with approximately the fourth thoracic rib; despite the presence of a well developed sternum, this position is comparable to *Anchiornis* (estimated to be level with the third rib). Dromaeosauridae encompasses a large size range and *Microraptor* is the smallest known taxon in the clade (Xu et al., 2000; Turner et al., 2007); unfortunately most specimens are plagued by incomplete preservation. Reports from larger dromaeosaurids vary and also may underestimate the true number of gastralia, especially if gastral baskets are truly considered to increase with body size (Claessens, 2004; Norell and Makovicky, 1997). Only twelve rows are reported preserved in *Velociraptor* IGM 100/985, a much larger cursorial taxon from the Late Cretaceous (Norell and Makovicky, 1997); a similar number is reported in the well-preserved holotype of *Linheraptor* (Xu et al., 2010; 2015) (Fig. 2B), which is purportedly very closely related to *Velociraptor*. This may indicate that this is an accurate representation of the gastral basket in these taxa; if so, that would indicate a unique trend within this clade.

***Archaeopteryx* (Aves)** There are eleven known specimens of *Archaeopteryx*, seven of which are nearly complete and articulated (Foth et al., 2014). *Archaeopteryx* reportedly has 12−13 pairs of gastralia (well preserved in the Berlin, Eichstätt, Munich, Solnhofen, and Thermopolis specimens) (Elzanowski, 2002; Wellnhofer, 1993) and no ossified sternum, comparable to *Anchiornis*. The basket is reported to extend caudally from the level of the longest thoracic rib, which we estimate is the third thoracic rib, back to the pubis (Wellnhofer, 1993), also consistent with *Anchiornis*.

***Jeholornis* (Aves: Jeholornithiformes)** Nearly 100 specimens of *Jeholornis* (n=95) are available; slightly less than half preserve gastralia (44%). The greatest number of pairs of gastralia preserved in any specimen is eight to nine (STM 2-47; Fig. 3A). Based on comparisons with other taxa (13–14 preserved in one specimen of *Microraptor* STM 5-101 and nearly as many in *Confuciusornis* STM 13-52; Fig. 3B), as well as discrepancies between published reports (Chiappe et al., 1999) and our observations for other taxa (e.g. *Confuciusornis*), potentially the true number of gastralia was much higher. In support of the gastral basket being potentially incomplete, the size range between the first and last pair is smaller than in our observations of *Anchiornis* and *Sapeornis*. However, given the large number of available specimens we consider the small size of the gastral basket to be a true feature of *Jeholornis* pending new discoveries. Although preservation is equivocal in all specimens, the first pair of gastralia may also be fused. As reported in derived non-avian maniraptorans (Claessens, 2004), the medial gastralium is more than twice the length of the lateral gastralium.

***Sapeornis* (Aves: Pygostylia: Sapeornithiformes)** In over 100 specimens of *Sapeornis* (n=106) 50% preserve gastralia but only 13% preserve complete or nearly complete baskets (Zheng et al., 2014b: table S2). The complete gastral basket, best preserved in the holotype of '*S. angustis*' (reinterpreted as a juvenile *S. chaoyangensis*, see Gao et al. 2012, Pu et al., 2013) contains 15−16 pairs of interlocking gastralia (IVPP V 13276, V 13396; Fig. 1) (Provini et al., 2008; Zhou and Zhang, 2003). The most proximal gastral ribs are approximately level with the fourth thoracic rib and the caudal-most pair is preserved caudoventral to the synsacrum (Fig. 1). The ribs are fatter proximomedially and taper distally. The gastralia decrease in size caudally so that the cranial pair is twice as long as the caudal pair (Zhou and Zhang, 2003). The distalmost five-six pairs are relatively small and delicate. Potentially the first pairs are also fused into two elements, as in *Anchiornis*.

Fig. 2 Comparative gastral baskets in derived maniraptorans

A. *Microraptor gui* STM 5-101 (Dromaeosauridae), scale bar equals 2 cm; B. *Linheraptor exquisitus* IVPP V 16923 (Dromaeosauridae), scale bar equals 3 cm; C. *Mei long* IVPP V 12733 (Troodontidae), scale bar equals 1 cm; D. *Caudipteryx* STM 22-1 (Oviraptorosauria), scale bar equals 4 cm

Anatomical abbreviations (not listed in Fig. 1 caption): 1–18. pairs of gastralia; f. fibula; mtII 2. second phalanx of second digit; mtIII 2. second phalanx of third digit; stn. sternum; tb. tibia; uln. ulna

Fig. 3 Gastralia in basal birds

A. *Jeholornis* STM 2-47; B. *Confuciusornis* STM 13-52; C. pengornithid enantiornithine *Eopengornis* STM 24-1; D. bohaiornithid enantiornithine *Parabohaiornis* IVPP V 18690, note cranial pair of gastralia articulates with the xiphoid process of the sternum. Scale bars equal 10 mm

Anatomical abbreviations (not listed in caption of Figs. 1 and 2): 1-12. pairs of gastralia; cav. caudal vertebrae; ili. ilium; isc. ischium; lt. lateral trabeculae; sr. sternal rib; syn. synsacrum

***Confuciusornis* (Aves: Pygostylia: Confuciusornithiformes)** The gastral basket in this taxon was described in a short monograph on the skeletal morphology of this taxon (Chiappe et al., 1999); however, upon reviewing the large collection available at the STM we describe the complete gastral basket as formed by approximately 13 pairs of gastralia (STM 13-52; Fig. 3B) compared to previous reports of eight pairs of gastralia (Chiappe et al., 1999). This is approximately the same number as in troodontids *Anchiornis* and *Mei*, which are nearly twice the average size of this pygostylian bird (femur length roughly 45 mm in *Confuciusornis* compared to 70−80 mm in *Anchiornis* and *Mei*; Table 1). The rostral row of gastralia clearly articulates with the caudal margin of the sternum (GMV-2152; STM 13-52; Fig. 3B) (Chiappe et al., 1999).

Enantiornithes (Aves: Ornithothoraces) The gastral basket in this clade, where clearly preserved, is very similar to that of other paravians except that the rostral row does not appear fused in any taxon. More often than not the gastral basket in these small birds is incomplete and doesn't reveal clear morphological details. The gastral basket is best preserved in the holotype specimen of *Eopengornis martini* (Wang X et al., 2014); the most common enantiornithine in the STM collection, *Longipteryx*, was examined to determine the upper size limit of the gastral basket in this species (estimated four pairs preserved in the holotype IVPP V 12325). The small basal enantiornithine *Eopengornis* has approximately ten pairs of gastralia that decrease in size caudally and a simple sternum with elongate lateral trabeculae (Fig. 3C) (Wang X et al., 2014). The cranialmost row of gastralia appears to be level with the fifth or sixth thoracic rib and reaches the caudal margin of the sternum. The larger, more derived bohaiornithid enantiornithine *Parabohaiornis* (Wang M et al., 2014) has approximately six pairs of gastralia with the cranial pair preserved in articulation with the xiphoid process of the sternum (IVPP V 18690; Fig. 3D; Table 1). The greatest number observed in any specimen *Longipteryx* is five to six pairs (STM 8-128). In the latter two taxa the sternal morphology is relatively more advanced than *Eopengornis* with distally expanded lateral trabeculae, intermediate trabeculae, and a xiphoid process.

Ornithuromorpha (Aves: Ornithothoraces) The derived lineage of Cretaceous birds, Ornithuromorpha, which includes Neornithes nested within, still retain gastralia in basal members. The basal ornithuromorph *Archaeorhynchus*, known from three excellent specimens, preserves five pairs of very delicate gastralia (Zhou et al., 2013). Compared to derived Jehol ornithuromorphs, this taxon is characterized by a comparatively simple sternal morphology: deep incisions are present between the two pairs of caudal trabeculae so that the imperforate corpus is limited to the rostral half of the sternum. The gastralia do not appear to articulate with the sternum in this taxon or any other ornithuromorph and are small and caudally restricted to the area ventral to the preacetabular ilium. Although Early Cretaceous ornithuromorphs are typically larger than sympatric enantiornithines, the gastral basket is smaller than that of enantiornithines; *Yanornis* preserves approximately four pairs. Ornithuromorphs typically have two short pairs of sternal trabeculae that are subequal in length but not thickness (except in

Archaeorhynchus and *Jiuquanornis*) and a craniocaudally elongate sternal corpus. Gastralia are absent in all specimens of the more derived non-ornithurine Xiagou ornithuromorph, *Gansus* (You et al., 2006). Gastralia are also not reported in the larger Late Cretaceous ornithurines *Ichthyornis* and *Hesperornis*, however a preservational bias cannot be ruled out. Neornithines do not preserve gastralia (Claessens, 2004; Gill, 2007).

4 Statistical analysis

In order to test observations regarding differences in the size of the gastral basket between clades we attempted to quantify these trends statistically. Unfortunately the complete gastral basket is only known in a handful of derived theropod taxa (n=15) leaving any resultant trends highly subject to distortion due to preservational bias – addition or removal of a single taxon greatly affects perceived trends. We normalized the data for size by dividing the minimum number of pairs of gastralia by femur length (Table 1). We compared this information for maniraptorans (including birds) with a sternum (n=9) versus those without (n=5) using a t-test (Hammer and Harper, 2006). The results produced a high p-value (0.614) indicating a lack of statistical significance. Although this could be due to the very small sample size, this corroborates our observations that taxa of comparable size with and without sterna have similarly sized gastral baskets. The means of the two populations are not well separated (0.172 in taxa with sternal elements vs. 0.146 in taxa with none). When birds (n=7) are compared to non-avian maniraptorans (n=7), the results are similar with a p-value greater than 0.05 (0.138) suggesting there is no significant difference between the size of the gastral basket in birds and closely related dinosaurs. However, the average of each group (0.126 in non-avians, 0.196 for birds) differs more than between taxa with and without a sternum and a larger sample size may show different conclusions. The low p-value in this instance probably results from the low sample size given observable differences between the two populations.

5 Discussion

Gastralia have received fairly little attention in recent taxonomic descriptions of dinosaurs other than to note that they are preserved. Understanding these small dermal ossifications is obfuscated by their incomplete preservation in the fossil record. Gastralia are very delicate elements and complete gastral baskets are rarely preserved – even in a collection of over two hundred largely complete specimens of *Anchiornis*, only a few specimens preserve what can be considered a complete or nearly complete set. We consider most reported information to underestimate the true number of gastralia. For example, 11 pairs of gastralia are reported in the oviraptorosaur *Caudipteryx* BPM 001 (Zhou and Wang, 2000); however, observations from an unpublished specimen at the STM indicates the number was much higher (estimated minimum 17–18 pairs in STM 22-1) (Fig. 2D). Similarly, despite the fact *Confuciusornis* is the most numerous fossil in the Jehol Group, previous descriptions greatly underestimated the size of the gastral basket in this taxon (Chiappe et al., 1999). This complicates any attempts to study these features and compare between a range of taxa, which in turns obfuscates potential correlations between the number of gastralia and other features (Claessens, 2004) and precludes significance in any statistical analysis. These limitations must be considered in any attempt to derive information from the published record of these dermal ossifications.

Preservational biases In context of the description, preservational biases have been indirectly discussed. The large collection of *Anchiornis* specimens available at the STM provides a case study in preservational biases. This collection consists of over 200 slab specimens (n=226); the collection was purchased, not collected, and thus is heavily biased towards exceptionally preserved material – all specimens are more than 50% complete with most being around 90% complete and all specimens are largely articulated. Despite this bias, less than ten percent preserve complete or nearly complete gastral baskets. Given that the size of the gastral basket is often underestimated in published reports based on limited material, this puts forth the possibility that any gastral basket estimate based on a small number of specimens may not represent the true size of this feature, even in cases of exquisite three-dimensional preservation (e.g. *Sinornithoides*, *Mei long*). This inference is supported somewhat by the fact that the size difference between the cranial and caudal gastralia observed in *Anchiornis* is greater than that reported for other theropods (Claessens, 2004). However, taxa based on isolated specimens are usually not from the lacustrine Daohugou or Jehol deposits and are typically three-dimensional specimens that were rapidly buried and thus with no post-mortem disturbance (e.g. *Sinornithoides* IVPP V 9612). Although the holotype of *Mei long* (IVPP V 12733) is from the Yixian Formation of the Jehol Group it was collected in the fluvial volcanoclastic deposits at the Liujiatun locality (Xu and Norell, 2004); perfectly preserved in an avian resting posture, this specimen was clearly rapidly buried while sleeping. The very different taphonomic conditions between the two general types of preservation (rapid burial vs. lacustrine) suggest that perhaps in such rare rapid burial conditions a large number of specimens are not needed to infer the size of the gastral basket and that these specimens accurately record this feature. This is supported by the fact that the gastral basket in the holotype of *Mei long* preserves approximately the same number as in the comparably sized *Anchiornis*. This strongly suggests that the preservation of 15 rows of gastralia in *Sinornithoides* IVPP V 9612 represents either the complete or nearly complete basket.

Evolutionary trajectories in the size of the gastral basket All clades of Cretaceous birds possess gastralia; the size of the gastral basket does not appear especially reduced in basal birds, *contra* previous reports (Claessens, 2004). In theropods the number of pairs of gastralia is reported to range from eight to 21 pairs, but did not include ornithothoracine birds (Enantiornithes + Ornithuromorpha); plesiomorphically, theropods are reported to have a large number of gastralia that decreases with body size (Claessens, 2004). However, our observations of Cretaceous birds, including ornithothoracines, reveal a range from four to 16 pairs of gastralia (Figs. 1, 3). Ornithothoracines range from four to ten pairs. The lower limit of eight reported by Claessens (2004) was based on *Confuciusornis*, which our observations reveal had a much larger gastral basket formed by 13 pairs of gastralia; however, the long boney-tailed bird *Jeholornis* (not included in the 2004 study by Claessens) apparently had a gastral basket formed by eight to nine, as previously reported for *Confuciusornis*, thus technically the range reported by Claessens (2004) is correct for non-ornithothoracine theropods. Differences in the size range encompassed by Theropoda (ranging a whole order of magnitude) versus Mesozoic Aves indicate that two groups did not share the same relationship (if any) between size and number of gastralia, indicating different evolutionary trajectories (Fig. 4).

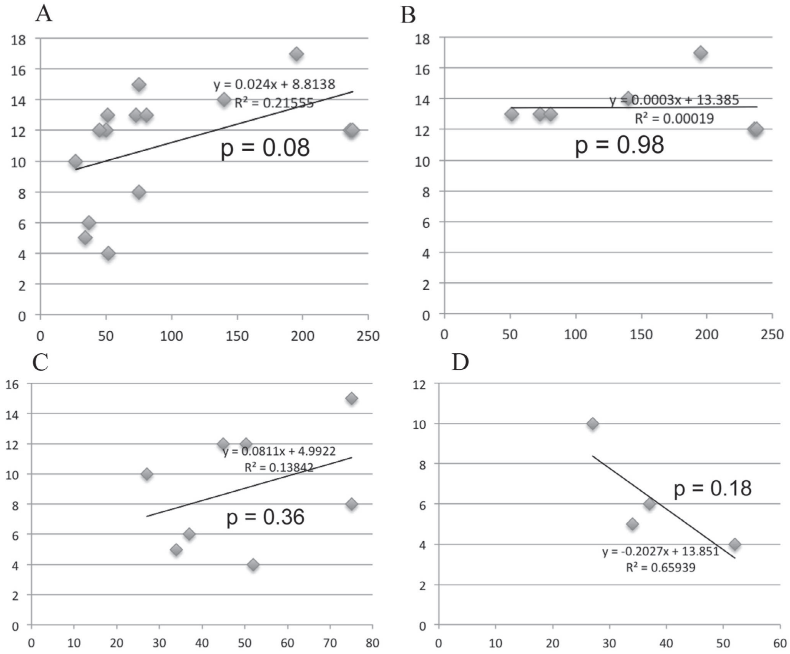

Fig. 4 Correlation plots between size and number of gastralia
x-axis is femur length (in cm); y-axis is number of pairs of gastralia
A. all derived theropods including birds; B. non-avian derived theropods only; C. Mesozoic birds; D. Ornithothoraces. Data in Table 1. The sample size is very small in each correlation, and p-values are high (> 0.05) indicating no statistical significance

Although intuitively we may infer the presence of a sternum might limit the number of gastralia, restricting them caudally, observations between non-avian paravians and basal birds with and without sterna of similar size are comparable (Table 1). The complete gastral basket of *Anchiornis* appears to be composed of approximately 13–14 pairs of gastralia. Despite its rostrocaudally elongate sternum, we estimate the gastral basket in the similarly sized taxon *Microraptor gui* was formed by 14–15 pairs of gastralia (Fig. 2A). In both taxa the first row of gastralia appears to be level with the third or fourth thoracic rib. The sample size of derived theropod taxa (including birds) preserving 'complete' gastral baskets is too small to produce significant results (n=15); however, when taxa with and without sterna were compared the high calculated p value (p=0.614) tentatively supports our observations that there is no relationship between the presence of a sternum and the number of gastralia among derived maniraptorans (Fig. 4).

Contra reports that basal birds, being small relative to non-avian theropods, have fewer gastralia (Claessens, 2004), *Sapeornis* has a complete gastral basket formed by 15−16 pairs of gastralia, among the largest previously reported within Paraves (Fig. 1). Within Aves this is generally consistent with the larger size of this taxon relative to most other Mesozoic birds: *Confuciusornis sanctus*, a smaller basal pygostylian, preserves approximately 13 pairs of gastralia (STM 13-52; Fig. 3B) and a plate-like sternum with large lateral processes. However, the gastral basket of *Sapeornis* is larger than that of larger non-avian paravians (e.g. *Anchiornis*, *Microraptor*). Incongruous with other Early Cretaceous birds, *Jeholornis* only preserves eight to nine pairs of gastralia (Fig. 3A), despite the fact it is roughly the same size as *Sapeornis* and has a sternum fairly similar to that of *Confuciusornis*. Although this is potentially a true feature of this taxon given the fairly large available sample size, in light of the much larger gastral baskets observed in other basal birds we cannot rule out a preservational bias. Similarly, the preserved gastral basket formed by 15 pairs of gastralia in *Sinornithoides* may potentially be incomplete, considering the difference in size in this taxon versus *Sapeornis* and *Microraptor*. Basal birds show a weak correlation between pairs of gastralia and femur size (R^2=0.14; Fig. 4) and the size of the gastral basket does not appear affected by the presence of a fairly simple sternum.

Within the derived clade Ornithothoraces (Enantiornithes+Ornithuromorpha) there is an apparent trend towards smaller gastral baskets in more derived taxa with increasingly complex sternal morphologies, with an inverse correlation to body size (R^2=0.66; Fig. 4). Ornithothoracines are on average much smaller than more basal taxa, which increases the likelihood preservation of the gastral basket will be incomplete or not preserved at all (n=four), potentially skewing evolutionary trends. Despite its small size the basal enantiornithine *Eopengornis* STM 24-1 has the largest ornithothoracine gastral basket consisting of approximately ten pairs of gastralia (Fig. 3C). However, the small body size of this taxon is probably exaggerated by the subadult status of the only known specimen, potentially obscuring inferred trends. Adult *Pengornis*, a younger relative of *Eopengornis*, is the largest known Early Cretaceous enantiornithine; unfortunately gastralia are not well preserved in this taxon. More derived enantiornithines of equal and larger size to *Eopengornis* have four to six pairs and in *Parabohaiornis* (Bohaiornithidae) (Wang M et al., 2014) the cranial pair articulates with the xiphoid process of the sternum (IVPP V 18690; Fig. 3D; Table 1). Thus within Enantiornithes the size of the gastral basket decreases in more phylogenetic derived taxa. This is also matched by a trend towards increasing sternal complexity.

The basal ornithuromorph *Archaeorhynchus*, known from three subadult specimens, despite its relatively simple sternal morphology has only five pairs of very delicate gastralia (Zhou et al., 2013); more derived Jehol ornithuromorphs, all of which are larger than *Archaeorhynchus* and most enantiornithines, preserve even fewer (*Yanornis*, approximately four pairs). Ornithuromorphs have more caudally extensive sterna compared to more basal birds (O'Connor et al., 2011; Zheng et al., 2012); this restricts the gastral basket caudally, making this feature increasingly redundant as in neornithines. However, in the presence of a superficially modern sternum (e.g. *Yanornis*) gastralia are reduced but still present. Gastralia are unknown in the Early Cretaceous non-ornithurine taxon *Gansus* and the Ornithurae, which may suggest they were rapidly lost during ornithuromorph evolution.

Gastral basket function in early birds It has been proposed that the proportionately large gastral basket in basal birds may be related to flight (Zheng et al., 2014b). It is commonly accepted that *Archaeopteryx* and *Sapeornis* were volant (Burgers and Chiappe, 1999; Zhou and Zhang, 2002a), thus they may have compensated for the absence of a sternum through other morphological innovations. In crocodilians several muscles attach to the gastralia and the cranial pair of gastralia articulates with the sternum (Claessens, 2004). This plesiomorphic condition is retained and the gastralia are observed to articulate with the sternum in some basal birds (*Jeholornis*, *Confuciusornis*, *Eopengornis*, *Parabohaiornis*; Fig. 3). Gastralia are notably highly modified within Theropoda compared to other groups of amniotes, and proximally fused gastralia have been proposed to function similarly to the sternum in tyrannosaurids (Claessens, 2004). Gastralia are absent in living birds, considered functionally redundant in the presence of the large ossified sternum that characterizes Neornithes (Claessens, 2004), thus bridging the possibility that the large gastral basket in *Sapeornis* may have functioned as a compensatory feature in the absence of a sternum and that the extensive gastral basket of basal birds with sterna may also have participated in supporting or reinforcing the sternum and the flight muscles (Zheng et al., 2014b). Given that the gastral basket is comparable in troodontids and the similar sized *Microraptor* that has a sternum, the gastral basket does not appear specialized in *Archaeopteryx* (Table 1); notably, the presence of a sternum does not appear associated with a trend in reduction of the gastral basket. Trend towards smaller gastral baskets only occur within the derived ornithothoracine lineages, which are carinate birds. The large number of gastralia in volant taxa even with ossified sternal elements puts forth the possibility that in the absence of a morphologically complex, keeled sternum, gastralia were functionally important to basal birds. This would suggest that gastralia may have been especially important in taxa without sterna, consistent with the fact that *Sapeornis* does have a greater number of gastralia compared to other small, derived maniraptorans of equivalent and even slightly greater size (e.g. *Mei*, *Anchiornis*). Potentially the gastral basket may have provided additional attachment surface for the flight muscles, in particular the m. *pectoralis* (Fig. 5). Because the gastral basket is centered in a more distal location (relative to the position of the sternum), this would have greatly elongated the moment arm of the flight muscles by moving the line of action further from the center of rotation of the shoulder joint, increasing muscular leverage and the resultant size of the force generated by the flight muscles. This would have served a similar function to the lateral trabeculae in ornithothoracines (and potentially also in *Jeholornis* and the non-avian dromaeosaurid *Linheraptor*). The much greater caudal extension of the attachment surface provided by the gastralia relative to caudal extensions of the sterna in even derived neornithines may have facilitated the enormous size achieved by *Sapeornis* relative to other volant Cretaceous birds such as the confuciusornithiforms and ornithothoracines, despite the overall primitive flight apparatus of this taxon (Zhou and Zhang, 2002a). Although caudal attachment of the flight muscles in living birds would potentially make the flight stroke less effective, the keel is notably restricted to the caudal half of the sternum in Enantiornithes (O’Connor et al., 2011). This provides a precedent for the existence of more caudally located musculature in some basal birds relative to the neornithine configuration. *Confuciusornis* lacks sternal trabeculae but has a relatively large number of gastralia for its size (Fig. 3B). In this taxon, gastralia and the sternum may both have provided attachment surface for the flight muscles. Notably, *Jeholornis* has an additional pair of sternal ossifications (Fig. 3A) that are unfused to the sternal plates but inferred to have functioned similar to the lateral trabeculae (Zhou and Zhang, 2002b) – this may account for the smaller number of gastralia in this taxon, although the gastral basket still appears to meet the sternum rostrally thus not strongly supporting this hypothesis (Fig. 3A). Muscle attachment has not previously been suggested as a function of the gastral basket in theropods although in crocodilians there are several muscles that are anchored on the gastralia (Claessens, 2004); the basket is formed of delicate elements and is ‘free’ in the skeleton, features that would not make this feature suitable for the attachment of large muscles. However, because the gastralia clearly brace against the sternum – as they do in crocodilians – in non-avian theropods (Clark et al., 1999; Norell and Makovicky, 1997), confuciusornithiforms (Fig. 3B), and at least one enantiornithine (Fig. 3D), it is possible that this offered greater rigidity to the gastral basket, potentially allowing the wing muscles to extend their attachment surfaces at least partially onto the gastral basket in at least some taxa (Fig. 5). However, the absence of a sternum in *Sapeornis* and *Anchiornis* would have left the gastral basket free, suggesting it would have lacked the rigidity to support large flight muscles. Although the first pair of gastralia may have been fused, the gastral basket in these taxa does not otherwise show modifications to suggest it was the attachment site of robust musculature. However, although also largely unmodified, where fusion of the cranial row occurs in tyrannosaurids, this fused element is considered to have functioned similar to the sternum of more derived theropods (Claessens, 2004), providing precedent for this muscle attachment hypothesis. In addition, broad areas of muscle attachment, including that of the supracoracoideus muscle on the sternum, coracoid, and sternocoraclavicular membrane in living birds, are commonly not clearly demarcated by distinct scars or rugose surfaces (although in the case of the avian supracoracoideus, intermuscular lines are present) (Vanden Berge and Zweers, 1993). We do not fully understand how the gastralia may have supported the musculature necessary for volant activity but in the absence of a sternum these muscles clearly would have had to find attachment elsewhere.

Claessens (2004) consider the highly modified gastralia in Theropoda to be related to a respiratory function. Compared to the Troodontidae, which also lack an ossified sternum, the gastral basket in *Sapeornis* is the same size as that reported for the much larger *Sinornithoides* and larger than that reported in comparably sized taxa (*Anchiornis*, *Mei*); this may suggest that this feature is specialized in *Sapeornis* relative to larger cursorial troodontids whom also lack sternal plates. Because the gastral basket may serve as part of the respiratory apparatus in theropods, this feature may have had increasing importance in Aves because of the heavy oxygen demands of powered flight (Gill, 2007). Thus a simple respiratory function may be responsible for the relatively large size of the gastral basket in basal birds.

The morphology of the coracoid in *Sapeornis* also differs from that of other basal birds in which this bone definitively articulates with a sternum and may potentially also have compensated for the absence of the sternum in some way (O'Connor et al., 2011). Compared to other Cretaceous birds, the coracoid is proportionately wide and short (Fig. 1). The morphology in *Sapeornis*, which is similar to that of *Anchiornis* and *Archaeopteryx*, is plesiomorphic to a larger group of theropods, including some non-avian maniraptorans with an ossified sternum. *Caudipteryx*, with its simple oval sternal plates also has a plesiomorphic proportionately short coracoid and the sternal margin is greater than the craniocaudally length of the coracoid in *Bambiraptor*, despite the fact the coracoids articulate with a pair of medially articulating craniocaudally elongate sternal plates (Burnham et al., 2000). In contrast, *Microraptor* has a proportionately more narrow coracoid relative to other derived maniraptorans, somewhat resembling that of basal birds such as *Jeholornis* (Table 1). It is interesting to note that in all supposedly volant taxa with sterna (*Microraptor*, *Jeholornis*, Confuciusornithiformes, and ornithothoracines), the coracoid is elongated relative to the plesiomorphic condition, suggesting these two features are correlated. Where a sternum is absent the coracoid is not elongated, even in supposedly volant taxa (*Archaeopteryx* and *Sapeornis*); this may indirectly support inferences that even a chondrified sternum was absent in these taxa (Zheng et al., 2014b).

In the plesiomorphic theropod coracoid morphology, present in *Archaeopteryx* and *Sapeornis*, the distal margin is convex, especially along the distolateral margin, whereas in other paravian taxa the sternal margins are straight for articulation with the sternum (e.g. *Microraptor*, *Jeholornis*, *Confuciusornis*, ornithothoracines). This convexity is particularly pronounced in troodontids (e.g. *Mei long*, *Anchiornis*), which also have proportionately short coracoids (slightly wider than long: Table 1). The sternolateral margin of the coracoid is also typically expanded. Such expansions are similar to the sternolateral process in most ornithuromorph birds but are proportionately larger in *Sapeornis* (Fig. 1); potentially this expanded surface may also have served to provide a larger proximal attachment surface for the pectoral muscles. This may suggest the pectoralis muscle in sapeornithiforms may have had two distinct attachment points, one on the coracoid and another on the gastralia (Fig. 5). In living birds the supracoracoideus attaches to coracoid, sternum, and sternocoraclavicular membrane (Vanden Berge and Zweers, 1993), and thus the hypothetical muscle attachment sites described here are not totally inconsistent with information regarding Aves. Similar sternolateral processes are reduced in most dromaeosaurids, which have well-developed sterna. Unfortunately, this hypothesis is not further supported by the presence of any local rugosity, tubercle, or other indicator on the coracoid to suggest that this was in fact a site of muscle attachment.

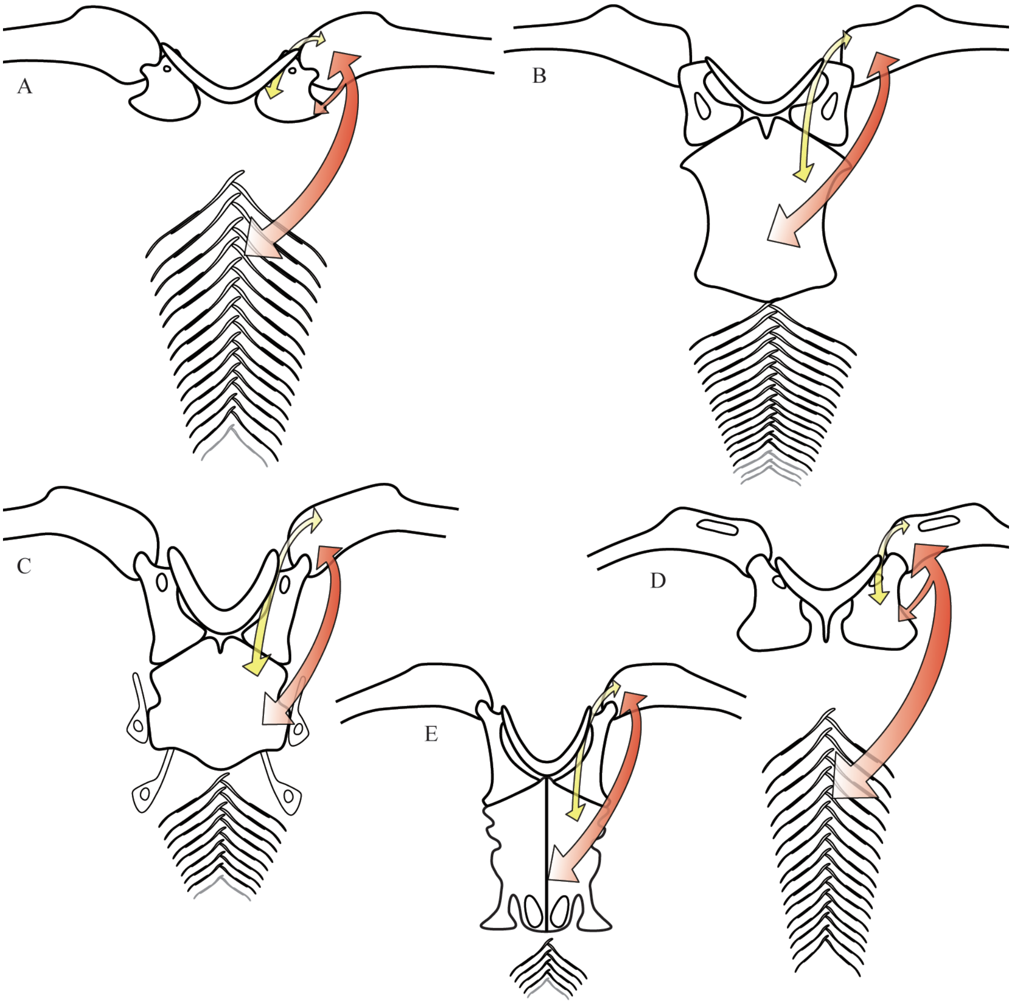

Fig. 5 Interpretative drawing of paravian pectoral girdles showing suggested point of muscle attachment of the two major flight muscles, the pectoralis (red) and supracoracoideus (yellow)
A. *Anchiornis*; B. *Microraptor*; C. *Jeholornis* (showing two potential orientations of the accessory sternal ossifications); D. *Sapeornis*; E. *Yanornis* (superficially modern configuration)

6 Conclusions

Because gastralia are absent in living birds with large sterna, we explored the possibility that this feature compensated for the sternum in basal taxa without this feature or with a simple sternum. Although *Sapeornis* does have the largest gastral basket within Aves, statistical analysis indicates that body and gastral basket size are not strongly correlated among basal birds, nor is the presence of a sternum correlated with the number of gastralia; trends are obfuscated by low sample size, ontogenetically immature specimens, smaller lineage specific trends, and poor preservation of these small elements. *Sapeornis* has a larger gastral basket than larger non-volant troodontids, which also lack an ossified sternum; thus it is likely that the enlarged gastral basket is flight related. This may have served to increase the surface area available for muscle attachment or to increase respiratory efficiency. The large gastral basket in small basal birds with sterna supports the former hypothesis whereas the absence of any indicators of muscle attachment supports the latter hypothesis.

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早期鸟类及其近亲的腹肋腔：大小和功能

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摘要：对中生代鸟类及与其亲缘关系密切的非鸟兽脚类腹肋腔的大小和形态进行了研究。据报道，在兽脚类中，腹肋腔的大小与个体大小正相关。然而与早期报道相反，基于鸟类的腹肋腔按个体大小比例似乎比非鸟兽脚类的大，这表明在缺乏前后向充分发育的胸骨时，腹肋可能作为一种补偿性结构，具有附着肌肉的功能。像鳄鱼一样，具有胸骨的早期鸟类的近端一排腹肋与胸骨相关联，表明这两种结构在功能上可能是一个整体；但在所有腹肋结构中都没有发现任何用来附着肌肉的痕迹，所以这一观点还没有此方面证据的支持。或者，大型的腹肋腔可能与呼吸功能以及鸟类飞翔需要的大量氧气供应有关。由于这些细弱骨骼结构的保存往往不完整，好的样本太少，以至于无法从对腹肋资料的统计分析中得出重要的结论。

关键词：热河生物群，白垩纪，Paraves, 鸟纲，腹肋，胸骨，会鸟

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