

Locomotory abilities and habitat of the Cretaceous bird *Gansus yumenensis* inferred from limb length proportions

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Abstract

The relative length proportions of the three bony elements of the pelvic (femur, tibiotarsus and tarsometatarsus) and pectoral (humerus, ulna and manus) limbs of the early Cretaceous bird *Gansus yumenensis*, a well-represented basal ornithuromorph from China, are investigated and compared to those of extant taxa. Ternary plots show that the pectoral limb length proportions of *Gansus* are most similar to Apodiformes (swifts and hummingbirds), which plot away from all other extant birds. In contrast, the pelvic limb length proportions of *Gansus* fall within the extant bird cluster and show similarities with the neornithine families Podicipedidae (grebes), Diomedidae (albatross) and Phalacrocoracidae (cormorants). Although it does have some of the pelvic limb features of grebes and cormorants, the femur of *Gansus* is more gracile and is thus more consistent with an albatross-like shallow-diving mode of life than a strong foot-propelled diving movement pattern. The position of *Gansus* in pectoral limb ternary morphospace is largely due to its elongated manus. In contrast to apodiformes, where the humerus and ulna are short and robust, an adaptation, which provides a stiff wing for their demanding fast agile and hovering flight (respectively), the wing-bones of *Gansus* are slender, indicating a less vigorous flapping flight style. The suite of characters exhibited by *Gansus* mean it is difficult to completely interpret its likely ecology. Nevertheless, our analyses suggest that it is probable that this bird was both volant and capable of diving to some degree using either foot-propelled or, perhaps, both its wings and its feet for underwater locomotion.

Introduction

For more than 20 years, *Gansus yumenensis* has remained one of the most enigmatic fossil birds known from the entire Cretaceous. First described by Hou & Liu (1984) on the basis of an isolated left leg, this bird is considered to occupy a phylogenetic position much closer to modern birds (Neornithes) than to *Archaeopteryx*, as a member of the lineage Ornithuro-

morpha (Hou & Liu, 1984; You *et al.*, 2006; O'Connor *et al.*, 2010; O'Connor & Zhou, 2012). The type locality of *Gansus* is the Lower Cretaceous (Aptian-Albian) Xiagou Formation near Changma in Gansu Province, north-western China (Hou & Liu, 1984; You *et al.*, 2006).

Despite an explosion in the numbers of fossil avian taxa discovered in China over the last 15 years, new material of *Gansus* was not forthcoming until 2006 when You *et al.* (2006) reported a collection of five specimens all from the same Changma locality. Li *et al.* (2011) have since described nine additional fossils also referred to *Gansus*. So far, all regions of the skeleton of this bird are well represented in the fossil record, except

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for the skull, mandible and cranial cervical vertebrae. You *et al.* (2006) considered both the anatomical and phylogenetic position of *Gansus* to be consistent with a position close to the divergence of carinate birds (*Ichthyornis* + modern birds), a result that has been corroborated by more recent phylogenetic studies to also include this taxon (O'Connor *et al.*, 2010; O'Connor & Zhou, 2012).

In addition to its evolutionary relationships, *Gansus* is interesting because its pectoral anatomy (You *et al.*, 2006) and preserved primary feathers (Wang *et al.*, 2011) are consistent with powered flight, yet many of the known Changma specimens exhibit interdigital integumentary preservation implying webbed feet and other anatomical characteristics consistent with an aquatic lifestyle (i.e. a large tibiotarsal cnemial crest and elongate toes). One previous study (You *et al.*, 2006) concluded that the anatomical characteristics of *Gansus* were similar to foot-propelled diving birds such as the Cretaceous *Hesperornis* and living loons (Gaviidae) and grebes (Podicipedidae). Furthermore, it was postulated that *Gansus*'s association with an aquatic environment provides evidence for the antecedents of extant birds living in, or close, to water and using foot-propelled aquatic locomotion (You *et al.*, 2006). A more recent study, using sternal and hind-limb measurements of *Gansus*, concluded that the morphology of this fossil bird was actually similar to extant ducks (Li *et al.*, 2011). The study of Li *et al.* (2011), however, was limited in that it included just 12 species from five extant orders and grebes, and loons were not among these. Pertinently, the pectoral limb length proportions of *Gansus*, which are likely important indicators of both flight style and flight capability (see, e.g. Dyke & van Tuinen, 2004; Nudds *et al.*, 2004, 2007; Dyke & Nudds, 2009), have not been considered (Li *et al.*, 2011) or compared to extant taxa (You *et al.*, 2006). The relative length proportions of the pectoral limb bones determine the positions of the wrist and alula relative to the elbow and shoulder during a wing stroke, and hence, similar length proportions should reflect similar wing kinematics (Nudds *et al.*, 2007). Indeed, it has been well documented that focusing on the relative length proportions of the long bones alone in either the pectoral or pelvic limb, results in discrete clustering of extant taxa with similar flight styles or hindlimb locomotor styles (Gatesy & Middleton, 1997; Middleton & Gatesy, 2000).

Here, the relative length proportions of both the pectoral (humerus, ulna and manus length) and pelvic (femur, tibiotarsus and tarsometatarsus length) limb bones of *Gansus* were compared to an extensive data set of similar measurements from living birds using ternary plots. The hypothesis tested was that the relative length proportions of both limbs of *Gansus* occupy the same point in ternary morphospace as living

ducks and foot-propelled divers (i.e. grebes and loons).

Materials and methods

Comparative limb measurements of specimens referred with certainty to *G. yumenensis* as well as those less certain (referred to here as '*Gansus*?') were measured in the collections of the Chinese Academy of Geological Sciences, Institute of Geology (CAGS), Beijing and the Gansu Geological Museum (GSGM), Gansu (Tables 1 and 2). Additional fossil specimens recorded here are held in the collections of the Institute for Vertebrate Paleontology and Paleoanthropology (IVPP), Beijing, and in the Yale Peabody Museum (YPM), New Haven (USA). Although avialan fossils from Changma exhibit a high degree of articulation, many are very incomplete. Most of the specimens measured in this study were isolated limbs, or portions of incomplete skeletons, which included a pectoral or pelvic limb. Length measurements of pectoral limb elements [humerus, radius or ulna and manus (carpometacarpus + digits following Nudds 2007)] were taken from nine specimens and measurements of pelvic limb elements (femur, tibiotarsus and tarsometatarsus) from seven specimens (Tables 1 and 2). Pectoral limb data for the *Gansus*

Table 1 *Gansus* and *Hesperornis* pelvic limb length measurements (mm).

Specimen number	Species	Femur	Tibiotarsus	Tarsometatarsus
CAGS	<i>Gansus</i>	29.24	54.12	29.84
04-CM-010	<i>yumenensis</i>			
GSGM	<i>G. yumenensis</i>	28.73	67.72	40.41
05-CM-014				
GSGM	<i>G. yumenensis</i>	30.14	59.96	32.28
05-CM-090				
GSGM	<i>G. yumenensis</i>	29.14	65.88	37.19
07-CM-011				
GSGM	<i>G. yumenensis</i>	29.59	65.16	39.15
07-CM-012				
GSGM	<i>G. yumenensis</i>	28.73	55.38	29.32
07-CM-013				
GSGM	<i>G. yumenensis</i>	28.51	66.36	37.36
07-CM-014				
GSGM	<i>G. yumenensis</i>	27.29	56.37	31.98
07-CM-015				
IVPP V 15080*	<i>G. yumenensis</i>	31.6	56.2	30.1
YPM 1200†	<i>Hesperornis</i>	99	320	136
	<i>regalis</i>			
YPM 1476†	<i>H. regalis</i>	105	325	136

CAGS, Chinese Academy of Geological Sciences; GSGM, Gansu Geological Museum; IVPP, Institute for Vertebrate Paleontology and Paleoanthropology; YPM, Yale Peabody Museum.

Taken from *Li *et al.* (2011) and †Marsh (1880).

CAGS and GSGM measurements of *Gansus* were made by JA.

Table 2 *Gansus* pectoral limb length measurements (mm).

Specimen number	Species	Humerus	Ulna	Carpometacarpus	Digit I	Digit II
CAGS 04-CM-004	<i>Gansus yumenensis</i>	47.72	49.06	23.65	12.40	24.41
GSGM 05-CM-005	<i>G. yumenensis</i>	49.86	53.16	24.83	13.39	23.53
GSGM 05-CM-014	<i>G. yumenensis</i>	48.10	50.82	23.75	11.84	22.55
GSGM 06-CM-003	<i>Gansus?</i>	50.33	53.81	25.36	12.17	21.65
GSGM 06-CM-005	<i>G. yumenensis</i>	48.17	51.78	25.38	13.92	24.16
GSGM 06-CM-013	<i>Gansus?</i>	48.74	52.81	27.02	17.63	28.53
GSGM 06-CM-092	<i>Gansus?</i>	50.42	56.91	24.02	14.13	24.39

CAGS, Chinese Academy of Geological Sciences.

CAGS and GSGM measurements of *Gansus* were made by JA.

specimen studied by Li *et al.* (2011) were also included for comparison (Table 1). The extant bird data set comprised measurements for 447 species of neognathae from 24 orders (including ducks, grebes and loons) and was that derived from Nudds (2007), which in turn was used in the ternary plots in figure 3 of Dyke & Nudds (2009). Pelvic limb data for *Hesperornis* were also included (Table 1).

Ternary diagrams were used (see Fig. 2 of Gatesy & Middleton, 1997 for a detailed explanation of the application of these diagrams) to visualize the limb proportion diversity of *Gansus* in ternary morphospace relative to the diversity seen in extant birds. Segment lengths for each limb were summed – pectoral limb (humerus length + ulna length + manus length = total forelimb length) and pelvic limb (femur length + tibiotarsus length + foot = total hindlimb length), divided by total limb length and then multiplied by 100 to produce a percentage of total limb length for each segment. The percentage of each segment was plotted on one of the three ternary diagram (Figs 1 and 2) axes orientated at 120°.

Results

The pectoral limb length proportions of *Gansus* (and specimens of previously uncertain identity) occupy a similar area in ternary morphospace (Fig. 1). One point representing a '*Gansus* ?' specimen does plot slightly away from the others, but all the fossils cluster among the Apodiformes (living swifts and hummingbirds), which are the only group that plot away from the main cluster of extant neognaths (Fig. 1). In contrast, the pelvic limb length proportions of *Gansus* (and indeterminate specimens) are positioned within the main extant taxa cluster (Fig. 2). Unlike the pectoral limb, there are no extreme outliers among the neognathae in terms of pelvic limb length proportions. Within the pelvic limb cluster, *Gansus* has similar limb length proportions to the neognathae families Podicipedidae (grebes) and Diomedidae (albatross). There is also some degree of overlap with Phalacrocoracidae (cormorants). Similarity to loons and ducks, however, was not sup-

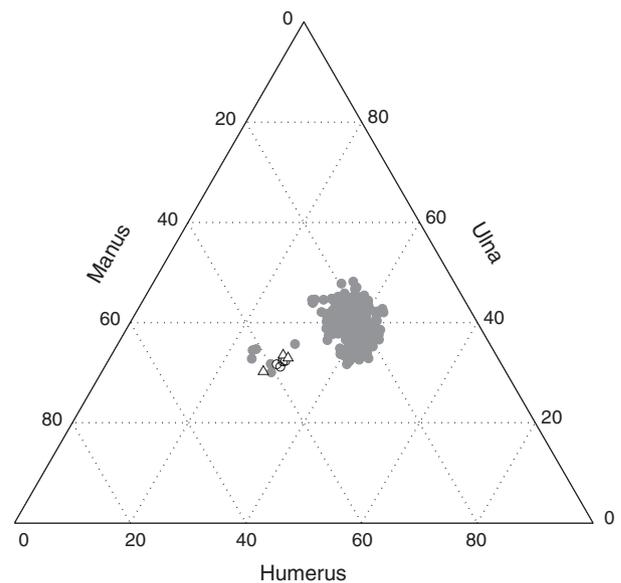


Fig. 1 Ternary diagram comparing the pectoral limb length proportions of *Gansus* (open circles) and indeterminate, but *Gansus*-like, specimens (open triangles) to those of extant birds (grey circles). Both *Gansus* and all indeterminate specimens plot together in ternary morphospace amongst the Apodiformes (swifts and hummingbirds) and away from the main cluster of extant taxa.

ported here (Fig. 2). Nor are the *Gansus* pelvic limb length proportions similar to those of *Hesperornis*, which occupies morphospace well away from the living bird cluster. The *Gansus* specimen investigated by Li *et al.* (2011) occupies ternary morphospace on the edge of the cluster of *Gansus* specimens measured in this current study, between grebes, albatrosses and cormorants, and ducks.

Discussion

Based on the analyses here, *Gansus* possesses hindlimbs with similar relative length proportions to those of grebes, albatrosses and cormorants, but not ducks, and forelimb length proportions similar to those of swifts and hummingbirds. Therefore, only one of the two

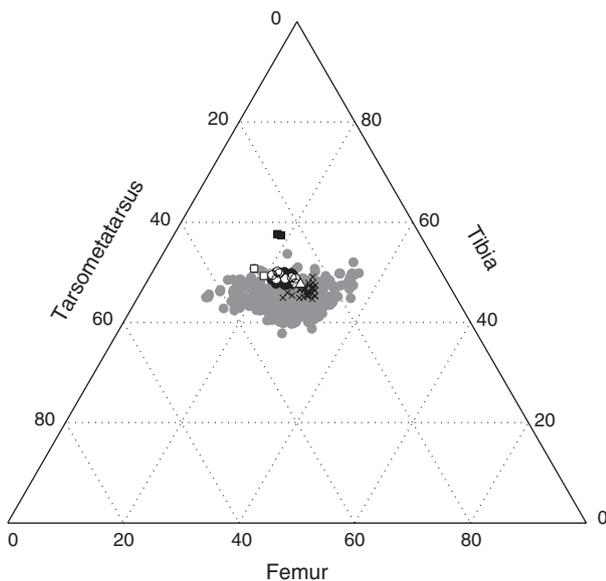


Fig. 2 Ternary diagram comparing the pelvic limb length proportions of *Gansus* (open circles & specimen Institute for Vertebrate Paleontology and Paleoanthropology Institute for Vertebrate Paleontology and Paleoanthropology IVPP V 15080, open triangle) with the range of extant birds (grey circles), ducks (crosses), loons (open squares) and *Hesperornis* (black squares). *Gansus* plots within the cluster for extant taxa and has similar hind-limb length proportions to the neornithine families Podicipedidae (grebes), Phalacrocoracidae (cormorants) and Diomedidae (albatross), represented by black circles.

previously proposed hypotheses about the movement of this bird can be supported. When the first specimen of *Gansus* was reported by Hou & Liu (1984), it was originally reconstructed as being similar to an extant shorebird. Indeed, Hou (1997) likened *G. yumenensis* to a sandpiper (Scolopacidae), birds that wade in near-shore habitats. Later, as more materials became available, You *et al.* (2006) inferred that *Gansus* possessed powered flight capability because of its pectoral and alular features, whereas at the same time the pelvic anatomy of *Gansus* was thought typical of an amphibious bird. The fact that interdigital telae are partly preserved in one specimen, however, also suggested that *Gansus* was probably adapted to both terrestrial and aquatic environments (You *et al.*, 2006). In accordance with and based on more *Gansus* material, Li *et al.* (2011) showed that the sternum width-to-depth ratio was indicative of swimming birds, whereas the sternum length-to-keel depth ratio is more like that of terrestrial birds. Moreover, based on a ternary plot of pelvic limb length proportions and characters of the distal tarsometatarsus, Li *et al.* (2011) suggested *Gansus* was closest to ducks (Anatidae), a swimming bird analogue with some powered flight capability. The small data set of extant birds used in Li *et al.* (2011), without representatives of the Podicipedidae (grebes), Diomedidae

(albatross) or Phalacrocoracidae, however, precluded a closer match being identified. The fact that their specimen (Li *et al.*, 2011) plots between the grebes and cormorants, and the ducks in the analyses presented here (Fig. 2), might suggest that IVPP V 15080 is not necessarily a typical *Gansus*.

Although our results confirm that *Gansus* does show pelvic limb length proportions similar to those of grebes, they do not support a similarity with ducks and loons. Interestingly, for the first time, our results also show that the pelvic limb length proportions of *Gansus* are similar to those of albatrosses and cormorants. Among these extant analogues, grebes and cormorants have robust hind-limb skeletons, and both are strong foot-propelled divers using lift-based and drag-based propulsion, respectively (Habib & Ruff, 2008). In contrast, albatross are specialized for soaring supplemented by shallow plunge and surface dives (Pennycuik, 1987). *Gansus*' similarity to strong foot-propelled divers is supported by axial skeleton morphology (i.e. sternum width-to-depth ratio and hypapophyses on thoracic vertebrae extending inward between the lungs) and pelvic limb anatomical characters (e.g. proximally projecting cnemial crests on the tibiotarsus for the attachment of large swimming muscles; elongated pedal digits with elongate proximal phalanges, unrecurved unguis and webbed feet) (Cracraft, 1982; Duzler *et al.*, 2006; Li *et al.*, 2011). The femur of *Gansus*, however, is more gracile (long and narrow) than that of strong underwater swimmers (IVPP V 15080 has a femur mid-shaft/length ratio of approximately 0.08 – see Figure 4A in Li *et al.*, 2011), and although this bird does not appear albatross-like based on its size alone, it may nevertheless have had an albatross-like shallow diving habit. *Gansus* may also have used its wings for some underwater propulsion as it possessed somewhat flattened pectoral limb bones, which is typical of more aquatic species, whereas in aerial species the humerus is more rounded (Habib & Ruff, 2008).

Although the results presented here for pelvic limb measurements support a waterbird categorization, the finding that the pectoral limb length proportions of *Gansus* cluster among swifts and hummingbirds is novel (Fig. 2). The position of *Gansus* in pectoral limb ternary morphospace is largely due to the possession of a relatively long manus. In contrast to apodiformes, where the lengths of the proximal wing bones (humerus and radius, and ulna) are greatly abbreviated (Mayr, 2003), it appears that manus elongation alone is responsible for the relatively large proportion of wing length this element contributes in *Gansus*.

Interestingly, Dyke & Nudds (2009) reported a similar result for the forelimbs of the enantiornithine *Otogornis*. Given the primitive forelimb characters (e.g. thick-walled long bones and undeveloped deltoid crest), the flight capability of *Otogornis* was thought to be more advanced than that of *Archaeopteryx*, but more primitive than that of other enantiornithines, such as *Sinornis* and

Cathayornis (Hou, 1994). Although *Gansus* possesses more derived forelimb skeletal characters than *Archaeopteryx* and the enantiornithines, some characters are still primitive compared with Neornithes (e.g. weakly developed extensor process of the alular metacarpal; fused distal tips of pubic bones; unreduced fibula; the lack of a supratendinal pons). The humerus and ulna in swifts and hummingbirds are short and robust, an adaptation, which provides a stiff wing for their demanding fast agile and hovering flight, respectively (Savile, 1950). Contrariwise, the wing bones of *Gansus* are slender, indicating a less vigorous flapping flight style. Furthermore, the ratio between primary feather length and total arm length (humerus + ulna + manus length) in *Gansus* was similar (low compared to extant birds) to *Caudipteryx*, some *Archaeopteryx* specimens and some primitive species in enantiornithines (e.g. *Sinornis*, *Concornis*), again perhaps implying a more limited flight capability (Wang *et al.*, 2011). The relatively long hand of *Gansus* might be interpreted as a plesiomorphic character, consistent with recent phylogenetic studies, which have resolved this bird outside Ornithurae (You *et al.*, 2006; O'Connor & Zhou, 2012), or alternatively there might be functional explanations for this adaptation including perhaps wing-propelled diving (M. Habib, personal communication).

The pelvic limb anatomy and length proportions of *Gansus* suggest that it was probably a foot-propelled shallow-diving bird. The pectoral (e.g. cranially projecting bicapital crest, completely co-ossified carpal trochlea and reduced alular digit) and sternal features (e.g. large, sickle-shaped keel) of *Gansus* indicate powered flight. Although the forelimb length proportions are similar to extant swifts and hummingbirds, flight capabilities (fast agile flight and hovering, respectively) similar to these are unlikely. A volant bird, however, capable of foot-propelled or, perhaps, both wing and foot-propelled diving are two possibilities for *Gansus*. Interpreting the life style of *Gansus* is of paramount importance, because as a "mosaic" taxon of as yet unstable phylogenetic position (*Gansus* has remained unresolved with respect to node Ornithurae in phylogenetic hypotheses), its ecology will have an influential role in our interpretation of the evolution of avian flight and birds in general.

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