



A new clade of basal Early Cretaceous pygostylian birds and developmental plasticity of the avian shoulder girdle

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Early members of the clade Pygostylia (birds with a short tail ending in a compound bone termed “pygostyle”) are critical for understanding how the modern avian bauplan evolved from long-tailed basal birds like *Archaeopteryx*. However, the currently limited known diversity of early branching pygostylians obscures our understanding of this major transition in avian evolution. Here, we describe a basal pygostylian, *Jinguoformis perplexus* gen. et sp. nov., from the Early Cretaceous of China that adds important information about early members of the short-tailed bird group. Phylogenetic analysis recovers a clade (Jinguoformisidae fam. nov.) uniting *Jinguoformis* and the enigmatic basal avian taxon *Chongmingia* that represents the second earliest diverging group of the Pygostylia. Jinguoformisids preserve a mosaic combination of plesiomorphic nonavian theropod features such as a fused scapulocoracoid (a major component of the flight apparatus) and more derived flight-related morphologies including the earliest evidence of reduction in manual digits among birds. The presence of a fused scapulocoracoid in adult individuals independently evolved in Jinguoformisidae and Confuciusornithiformes may relate to an accelerated osteogenesis during chondrogenesis and likely formed through the heterochronic process of peramorphosis by which these basal taxa retain the scapulocoracoid of the nonavian theropod ancestors with the addition of flight-related modifications. With wings having a low aspect ratio and wing loading, *Jinguoformis* may have been adapted particularly to dense forest environments. The discovery of *Jinguoformis* increases the known ecomorphological diversity of basal pygostylians and highlights the importance of developmental plasticity for understanding mosaic evolution in early birds.

bird | development | Mesozoic | plasticity | phylogeny

Nonornithothoracine avian taxa constitute the earliest diverging lineages of birds before the first major diversification in avian evolution documented by the Early Cretaceous members of the Enantiornithes and Ornithuromorpha (including crown birds) (1–3). The currently known nonornithothoracine birds include *Archaeopteryx* and the Jeholornithiformes with a long bony tail and the short-tailed Confuciusornithiformes and Sapeornithiformes, which together with the Ornithothoraces form the clade Pygostylia (1). These early diverging taxa provide critical data regarding the extensive changes in morphology and bauplan from their theropod ancestors to a more derived set of features that eventually led to the evolutionary success of Ornithothoraces (2–4). Here, we report a nonornithothoracine pygostylian, *Jinguoformis perplexus*, gen. et sp. nov., based on a complete skeleton from the Dabeigou Formation in northeastern China dated to 127 Ma. We discuss the major changes to the shoulder girdle across the basal avian phylogeny and show how morphological diversification and flight apparatus likely were impacted by developmental plasticity in that early stage of avian evolution.

Systematic Paleontology

Aves Linnaeus, 1758; Pygostylia Chiappe, 2002; Jinguoformisidae fam. nov. (*SI Appendix, SI Text*); *Jinguoformis perplexus* gen. et sp. nov.

Holotype

A complete and articulated skeleton with feathers is housed at the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) under the collect number IVPP V24194 (Fig. 1 and *SI Appendix, Figs. S1–S7 and Table S1*).

Etymology

The generic name is derived from “jinguo” (Mandarin), referring to female warrior; the specific name is derived from Latin “perplexus,” referring to the combination of plesiomorphic and derived characters present in the holotype specimen.

Locality and Horizon

IVPP V24194 was collected near the village of Shixia, Weichang County, Hebei Province, China; Lower Cretaceous Dabeigou Formation of the Jehol Biota (127 ± 1.1 Ma; *SI Appendix, SI Text*).

Diagnosis

A large nonornithothoracine bird preserves the following autapomorphies among nonornithothoracine avian taxa: premaxillae toothed anteriorly; 9–10 dorsal vertebrae; boomerang-shaped

Significance

We report the second most basal clade of the short-tailed birds (Pygostylia) from the Early Cretaceous. The new family Jinguoformisidae exhibits a mosaic assembly of plesiomorphic nonavian theropod characteristics, particularly of the fused scapulocoracoid and more derived flight-related features, further increasing the known ecomorphological diversity of basal avian lineages. We discuss the evolution of the scapula and coracoid in major tetrapod groups and early birds and hypothesize that the fused scapulocoracoid in some basal avian lineages, although rare, results from an accelerated rate of ossification and that the avian shoulder girdle likely was transformed by developmental plasticity along an evolutionary lineage leading to the crown group of birds.

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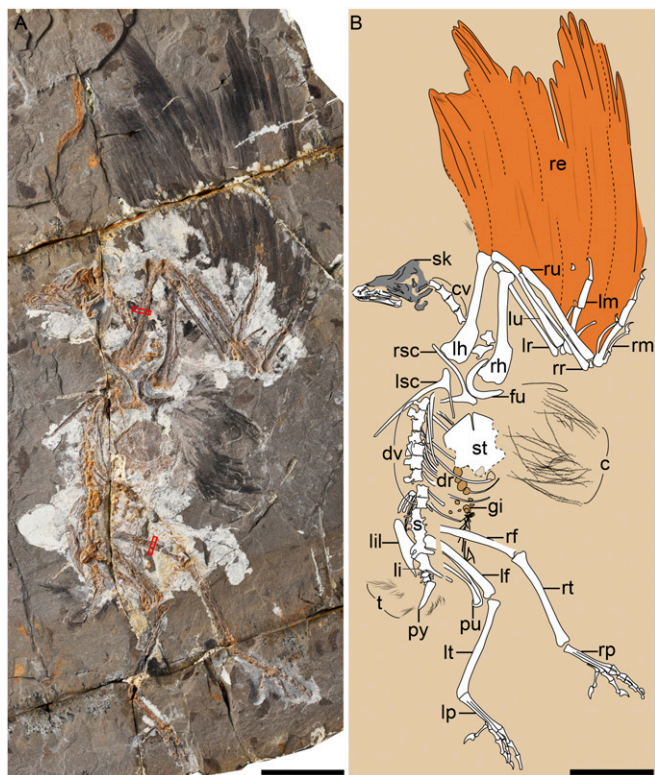


Fig. 1. *J. perplexus* gen. et sp. nov., IVPP V24194. (A) Photograph of main slab. (B) Composed line drawing. Red-outline boxes denote the locations of histological samples. c, covert feathers; cv, cervical vertebrae; dr, dorsal ribs; dv, dorsal vertebrae; fu, furcula; gi, gizzard; lf, left femur; lh, left humerus; li, left ischium; lil, left ilium; lm, left manus; lp, left pes; lr, left radius; lsc, left scapulocoracoid; lt, left tibiotarsus; lu, left ulna; pu, pubis; py, pygostyle; re, remiges; rf, right femur; rh, right humerus; rm, right manus; rp, right pes; rr, right radius; rsc, right scapulocoracoid; rt, right tibiotarsus; ru, right ulna; s, synsacrum; sk, skull; st, sternum; t, tail feathers. (Scale bar, 5 cm.)

furcula with an interclavicular angle of 70°; postacetabular process of ilium that tapers rapidly to a point posteriorly; and elongate hallux about 70% as long as pedal digit II. *Jinguoformis* is distinguishable further from other stemward Aves in the unique combination of the following features: dentary with at least six closely packed teeth; scapula and coracoid fused into a scapulocoracoid in the adult; sternum ossified; deltopectoral crest of humerus large and not perforated; minor metacarpal strongly bowed caudally; minor digit reduced with manual phalangeal formula of 2–3–2; metatarsals III and IV subequal in distal extent; pedal phalanx II-2 with prominent heel proximally; and forelimb 1.15 times longer than hindlimb (see *SI Appendix, SI Text*, for differential diagnosis).

Description and Comparisons

The premaxillae and maxillae are toothed (Fig. 2*A* and *B* and *SI Appendix, Fig. S2*), but the exact tooth count cannot be determined. Two premaxillary teeth are visible, and the most anterior one is located near the tip of the rostrum, as in some dromaeosaurids and troodontids (5). In contrast, the tip of the premaxilla is edentulous in *Archaeopteryx* and stemward ornithothoracines (6–8), and the entire premaxilla is edentulous in *Jeholomis* and confuciusornithiforms (9, 10). The jugal is dorsoventrally tall as in nonornithothoracine birds (10), unlike the rod-shaped condition in crown birds. A mandibular symphysis is absent as in the most stemward avian taxa except confuciusornithiforms (9, 11). As in *Jeholomis* and *Sapeornis* (12), the mandible is dorsoventrally tall with a blunt anterior end,

contrasting with the slender form present in *Archaeopteryx* and ornithothoracines (8, 13). The mandible of *Jinguoformis* is straight in lateral view as in some enantiornithines and basal ornithuromorphs (8, 14), rather than the strongly dorsally convex condition occurring in *Jeholomis* and *Sapeornis* (12). Six teeth are exposed along the anterior one-third of the right lower jaw. The presence of additional dentary teeth cannot be ascertained due to preservation. Nevertheless, the dentary tooth count is greater than in most other nonornithothoracine birds, e.g., two to three in *Jeholomis*, two in *Sapeornis*, and none in confuciusornithiforms (10). In comparison, over 10 dentary teeth are present in *Archaeopteryx* and most nonavian paravians (5, 6). Those dentary teeth are closely packed in *Jinguoformis*, with the spacing less than one-quarter the mesiodistal width of the individual tooth, reminiscent of the condition seen in basal deinonychosaurs but dissimilar to that of stemward avian taxa (5, 6, 10). The splenial is triangular in outline, with the anterior ramus longer than the posterior one, contrasting with that of *Archaeopteryx* (6) and *Confuciusornis*. The anterior extent of the splenial terminates well posterior to the level of the sixth dentary tooth. Unlike troodontid, *Archaeopteryx*, and some enantiornithines (5, 6), the splenial is not perforated. In contrast to confuciusornithiforms (9), the external mandibular fenestra is absent as in other stemward avian clades (8, 12). There are 9 or 10 dorsal vertebrae, counted either by their associated dorsal ribs or their morphology (*SI Appendix, Figs. S3* and *S4*). Description of the vertebral column is provided in *SI Appendix, SI Text*.

The furcula has a plesiomorphical boomerang shape, as in other nonornithothoracine birds except *Sapeornis* in which a hypocleidium is present (13, 15, 16) (Fig. 2*C* and *SI Appendix, Fig. S5A*). The bone is more robust than in *Archaeopteryx* and Ornithothoracines, but more slender than that of *Chongmingia*. The furcula has an interclavicular angle of about 70°, which is smaller than in other nonornithothoracine birds. As in *Archaeopteryx* and *Chongmingia* (13), the furcula has tapered omal ends, without the expansion seen in *Confuciusornis* (11). The coracoid and the scapula are fused into a scapulocoracoid (*SI Appendix, Fig. S3 A and B*), which is known only in confuciusornithiforms and *Chongmingia* among Mesozoic birds (13, 15, 16) (Fig. 3). A fused scapulocoracoid is rarely present among crown birds with the exception of some flightless birds, e.g., paleognathous ratites (17, 18), but the condition is distributed widely among nonavian dinosaurs, pterosaurs, and amphibians (19, 20). As in other nonornithothoracine birds, the angle defined by the coracoid and the scapula is ~90°, giving the scapulocoracoid an L-shaped contour in lateral view, as opposed to the acute angle present among more crownward birds (17, 18). Similar to enantiornithines, the scapula is straight, slender, tapers distally, and differs from the stout, blunt-ended morphology seen in *Archaeopteryx* and confuciusornithiforms (11, 13). The sternum is broad, formed by two bilaterally fused plates with an anterior cleft (Figs. 1 and 2*C*), similar to *Confuciusornis* (4).

The humerus is the most robust appendicular element (Fig. 2*D* and *SI Appendix, Fig. S5*), a feature shared by most Mesozoic birds crownward of *Archaeopteryx*. As in *Chongmingia* (15), the deltopectoral crest lacks any perforation, contrasting with the state in *Sapeornis* and confuciusornithiforms (9, 16). The humerus has a concave proximal margin, a characteristic absent in other basal avian clades except *Chongmingia* and enantiornithines (15). The ulna is longer than the humerus, as in the majority of volant birds, as opposed to *Archaeopteryx* and most nonavian theropods (13, 19). The semilunate carpal is fused with the proximal ends of the major and minor metacarpals, forming a carpometacarpus, as in other Aves except *Archaeopteryx* (21, 22). The alular metacarpal is only fused proximally with the major metacarpals similar to most other Early Cretaceous avian clades (21). The alular metacarpal is rectangular and bears no extensor process. The minor metacarpal is strongly bowed caudally and,

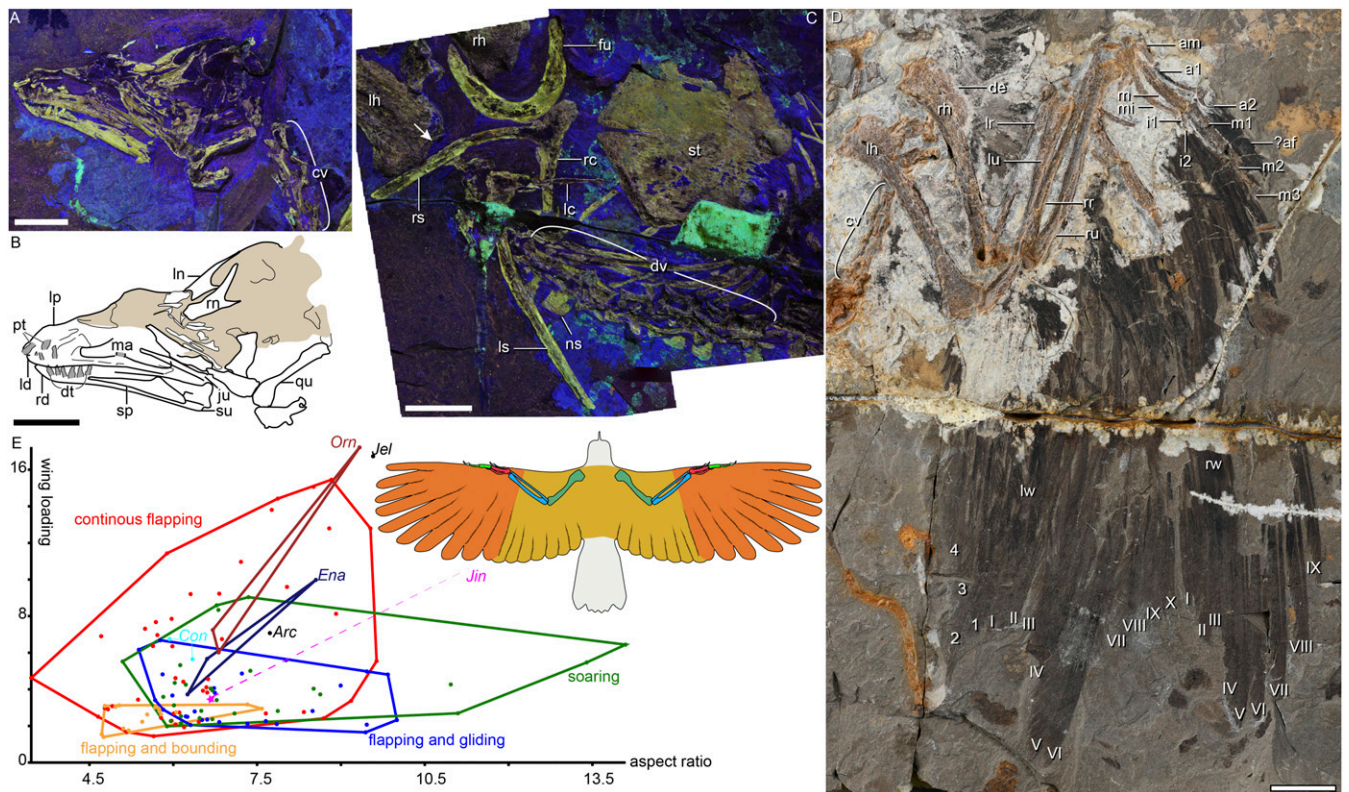


Fig. 2. Skeleton anatomy and morphometric analysis of *Jinguoformis*. (A and B) LSF photograph and line drawing of the skull in the main slab (IVPP V24194a). (C) LSF photograph of the pectoral girdle in the main slab. (D) Forelimb showing the preserved primary (numbered I–X) and secondary (numbered 1–4) remiges in the counterslab (IVPP V24194b). (E) Binary plotting of the aspect ratio and wing loading of basal avian clades (*Arc*, *Archaeopteryx*; *Con*, *Confuciusornis*; *Ena*, *Enantiornithes*; *Jel*, *Jeholornis*; *Jin*, *Jinguoformis*; *Orn*, stemward ornithuromorphs) under the context of modern avian flight styles. Arrow in C indicates the concave proximal margin of the humerus. am, alular metacarpal; a1-2, proximal and distal phalanges of alular digit; cv, cervical vertebrae; de, deltopectoral crest; dt, dentary teeth; dv, dorsal vertebrae; fu, furcula; i1-2, first and distal phalanges of the minor digit; ju, jugal; lc, left coracoid; ld, left dentary; lh, left humerus; ln, left nasal; lp, left premaxilla; lr, left radius; ls, left scapula; lu, left ulna; lw, left wing; m, major metacarpal; ma, maxilla; mi, minor metacarpal; m1-3, proximal, intermediate, and distal phalanges of the major digit; ns, neural spine; pt, premaxillary teeth; rc, right coracoid; rd, right dentary; rh, right humerus; rn, right nasal; rr, right radius; rs, right scapula; ru, right ulna; rw, right wing; sp, splenial; st, sternum; su, surangular. [Scale bars: 1 cm (A–C) and 2 cm (D).]

along with the straight major metacarpal, forms a wide inter-metacarpal space. That space distinctly exceeds the craniocaudal width of the minor metacarpal, a crown bird-like feature only known in *Chongmingia* and *Jeholornis* among stemward Aves (15, 17) (Fig. 3). The distal ends of the major and minor metacarpals are separated, and the former extends further distally as in other nonenantiornithine birds (13, 15). *Jinguoformis* has a highly reduced hand with a phalangeal formula of 2–3–2 shared with *Sapeornis* (16). That reduction contrasts with the presence of three-clawed fingers with a formula of 2–3–4 in *Archaeopteryx*, *Jeholornis*, and confuciusornithiforms (11, 13, 23) (Fig. 3). The alular and major digits have strongly recurved claws that are subequal in size. The proximal phalanx of the alular digit terminates at the level of the distal end of the major metacarpal, as in *Chongmingia* (15). In contrast, the digit projects further distally in *Archaeopteryx* and confuciusornithiforms (11, 13), but ends far proximally in *Sapeornis* and *Jeholornis* (15). Similar to *Chongmingia* and *Sapeornis* (15, 16), the proximal phalanx of the major digit is longer than the intermediated one, contrasting with *Archaeopteryx* and *Jeholornis* (13, 23). The minor digit is extremely reduced, having a wedged-shaped proximal phalanx and a vestigial distal phalanx, similar to some stemward ornithothoracines (22, 24). *Sapeornis* bears two rod-like phalanges in the minor digit, which together are more than half the length of the proximal phalanx of the major digit, but that ratio is less than one-third in *Jinguoformis*.

The ilium has a less convex dorsal margin compared with other nonornithothoracine birds (6, 16, 25). The preacetabular process of the ilium is anteriorly convex and longer than the postacetabular process. The postacetabular process has an abruptly constricted posterior end (SI Appendix, Fig. S4 A and B). The straight ischium bears a distinct proximal dorsal process, as in *Jeholornis*, *Sapeornis*, and enantiornithines (16, 22), but not in *Archaeopteryx* (13). The ischium decreases in anteroposterior width distally and lacks both the swelling seen in *Confuciusornis* (9) and the obturator process in *Archaeopteryx* and basal deinonychosaurs (12, 19). The pubes are retroverted posteriorly to a greater degree than in *Archaeopteryx* and *Jeholornis*. The pubic shafts are nearly straight and distally form a symphysis that extends approximately a quarter of the length of the pubis, and that length is proportionally shorter than the symphysis in other nonornithothoracine birds (6, 11, 13). A description of the hindlimb is provided in SI Appendix, SI Text.

The wings remain semifolded and are preserved in great fidelity (Fig. 2D and SI Appendix, Fig. S7 A and B). We estimate that there are 10 primary remiges, and at least four secondary remiges are preserved. Primary remiges IV–VI are the longest, and the lengths of remiges VII–X decrease toward the distal end of the limb. The remiges are highly asymmetrical, particularly the primaries in which the trailing vane is approximately four times the width of the leading vane. The rachises curve, narrow distally, and terminate well proximal to the rounded distal margins. Long

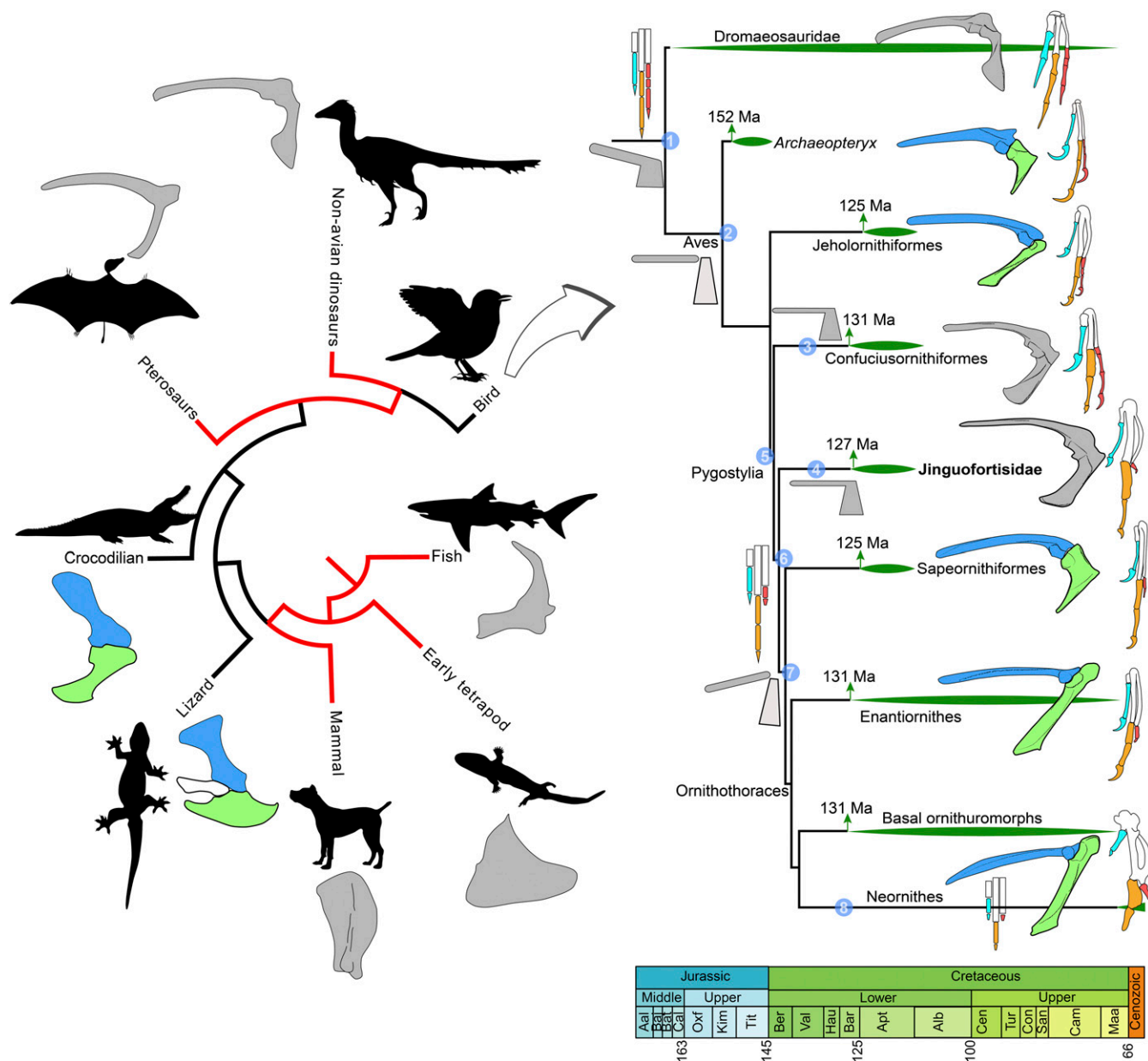


Fig. 3. Changes to the scapula and coracoid in vertebrates with a focus on basal avian clades. A simplified tree of vertebrates (Left) shows the scapula (colored in blue) and coracoid (in green) fused into a scapulocoracoid (in gray) in most major tetrapod clades (see *SI Appendix, SI Text*, for details). Simplified cladogram of basal Aves (Right) shows the changes to the shoulder girdle and manus (see *SI Appendix, Fig. S8*, for complete phylogenetic result). Thick green lines near each clade denote temporal range with the first-appearance datum denoted. Major changes to the shoulder girdle and manus across basal avian phylogeny are summarized: (1) in most nonavian theropods, the scapula and coracoid are fused into a scapulocoracoid at an obtuse angle, and they have a manual phalangeal formula of 2–3–4; (2) scapula and coracoid become separated and form an angle of ~90°; (3, 4) independent evolution of a fused scapulocoracoid in the Confuciusornithiformes and Jinguoformitidae; (6) minor digit is reduced resulting in a manual phalangeal formula of 2–3–2; (7) scapula and coracoid are decoupled and form an acute angle with further manual digit reduction evolving in derived ornithuromorphs; (8) alternatively, it is equally parsimonious that a fused scapulocoracoid evolved at the base of Pygostylia and was lost in pygostylians crownward of Jinguoformitidae (5).

rachis-less covert feathers extend off and line the ventral side of the body (*SI Appendix, Fig. S7C*). The rectrices are poorly preserved, with a few short rachis-less feathers and pennaceous ones extending off the pygostyle. There is no sign of an extensive tail fan of feathers.

Discussion

Our phylogenetic analysis recovered *Jinguoformitis* as the sister to *Chongmingia* (Fig. 3 and *SI Appendix, Fig. S8*). Given the incomplete preservation of *Chongmingia*, its phylogenetic position is elusive (15). The previously unrecognized clade uniting

Jinguoformitis and *Chongmingia*, named the Jinguoformitidae here (*SI Appendix, SI Text*), constitutes the second most basal pygostylian lineage, as the outgroup to Sapeornithiformes and Ornithothoraces. The bauplan of Jinguoformitidae demonstrates previously undocumented ecomorphological specialization among basal pygostylians and also adds to our knowledge of the widespread occurrences of mosaic evolution characterizing early avian diversification. The holotype of *Jinguoformitis* is subadult or adult given the presence of a fused carpometacarpus, tarsometatarsus, and pygostyle, in addition to analysis of its bone histology (*SI Appendix, Fig. S9*; see *SI Appendix, SI Text* for histology). We

estimate the holotype individual to have had a body mass of 250.2 g, a wing span of 69.7 cm, and a wing area of 730 cm² (*SI Appendix, SI Text*). To infer the flight style, we calculated the aspect ratio and wing loading of *Jinguoformis*, which directly relate to aerodynamic performance (26, 27), and compared those data with those of stemward avian taxa and crown birds. The results place *Jinguoformis* in the overlapping morphospaces of modern birds that are adapted to continuous flapping, flapping and gliding, and soaring (Fig. 2E). The aspect ratio (6.665) in *Jinguoformis* is low or average, and the wing loading is quite low (3.43 kg/m²), lower than all of the sampled basal avian taxa and many modern flapping or flapping/gliding fliers. This combination of aspect ratio and wing loading commonly occurs among crown birds that require high maneuverability to fly in dense habitats (26, 27), and the reconstruction of wing dynamics is consistent with the reconstructed forested paleoenvironment of the Jehol Biota that includes *Jinguoformis* and other early avian clades (28). *Jinguoformis* preserves a few stones in the posteroventral side of the abdominal cavity (Fig. 1 and *SI Appendix, Fig. S3*), consistent with the position of the gizzard in crown birds (29), and thus are considered gastroliths. Gastroliths have been reported in many stemward avian groups (1, 14–16, 24), revealing herbivory-dominant feeding in early avian diversification.

Jinguoformis is the most basal and earliest avian taxon showing manual digit reduction with two rudimentary and nonfunctional phalanges in the minor digit (Fig. 3). That same phalangeal formula is widely distributed in taxa that are crownward of *Jinguoformis* with a few exceptions (1, 7, 22, 24) until further reduction is seen in more crownward birds. *Archaeopteryx*, jeholornithiforms, and confuciusornithiforms retain a 2–3–4 phalangeal formula (9, 13, 23) as in most nonavian theropods (19, 30), and the widespread occurrence and retention of that count indicates a unidirectional constraint in favoring of lateral reduction of the manual digit during avian evolution. This lateral reduction-first pattern possibly reflects that the minor digit is overlain dorsally by the primary remiges and therefore experiences little or no physical contact with substrate in *Jinguoformis* and more crownward taxa.

The forelimb and shoulder of *Jinguoformis* demonstrate a high degree of mosaic assembly of plesiomorphic nonavian theropod and derived crown bird features. The elongate forelimb, large deltopectoral crest [increasing the area for the attachment of the pectoralis muscle that is responsible for flight downstroke (18)], and a distinctly bowed minor metacarpal as in crown birds [increasing the metacarpal's lever arm to increase support of the overlying primary remiges (15)] are all derived characters contributing to the refinement of the flight capability in *Jinguoformis*. *Jinguoformis* retains several plesiomorphic features absent among crown birds and their flight mechanism: the furcula is stout as in nonavian theropods, possessing little or no flexibility, which is needed to aid in avian respiration during flight via its elastic deformation (31); and the proximal margin of the humeral head is concave centrally, as in nonavian theropods but more similar to enantiornithines, but unlike the bulbous form seen in ornithuromorphs, constraining rotation against the glenoid during the flight strike (18). The most notable primitive feature present in the flight apparatus of *Jinguoformis* is the fused scapulocoracoid, a feature absent in most other Mesozoic birds (13, 15, 16) and also rarely seen within the crown groups (32).

The fused scapulocoracoid is a plesiomorphical feature that evolved before the origin of limb digits and was retained among stem tetrapods (33) (Fig. 3). A sutural contact between the scapula and coracoid evolved in basal amniotes and then became widely distributed among reptiles (33), although a fused scapulocoracoid independently evolved in a few lineages (19, 20). The tendency for fusion between the coracoid and scapula stems from their developmental origins as a unified homogenous condensation (34). However, that coalescence becomes detached

during chondrogenesis because the osteogenic pattern and/or the differentiation of the preskeletogenic cells is delayed (33), resulting in a sutural contact between the elements. In paleognathous ratites, such as kiwi, the coracoid and scapula are never separated since chondrification (32). It is generally thought that the presence of a fused scapulocoracoid in an adult is achieved by an acceleration of osteogenesis (33). Genetic mechanisms underlying the occurrence of a fused scapulocoracoid likely relates to the homeobox (*Hox*) genes given their crucial role involved in the morphogenesis of the pectoral girdle (35). Specifically, developmental research shows that expansion of *Hoxc6* expression could result in the fusion of the scapula and coracoid in chicks (36).

The fusion between the coracoid and scapula is present predominantly in nonavian theropods (19, 30). However, these two elements are separated in *Archaeopteryx* (13) and in more crownward avian clades (18, 24, 33) (Fig. 3). The convergently evolved scapulocoracoid (an apparent reversal to the plesiomorphic theropod condition) in jinguornithids and confuciusornithiforms suggests that these basal clades likely reacquired a similar level of osteogenesis (or gene expression) present in their nonavian theropod ancestors that is responsible for the coossification of the pectoral girdle. Presumably, the absence of fusion in other avian clades is the result of a decline in the rate of osteogenesis or a change in gene expression patterns during development. This evolutionary developmental hypothesis is supported by the slower growth rate inferred for *Archaeopteryx* (37), *Jeholornis* (38), and *Sapeornis*, compared with *Confuciusornis* (39), *Chongmingia* (15), *Jinguoformis* (*SI Appendix, Fig. S9*), and similar sized nonavian theropods in terms of their bone microstructure (37). The rapid growth rate, on one hand, shortens the time to reach adult size and morphology, and that is conceivably important for these relatively large basal avian clades (here jinguornithids and confuciusornithiforms), given their limited flight capability. On the other hand, a rapid growth rate could accelerate the osteogenesis that induces bone fusion (in this case the scapulocoracoid). In addition, the evolutionarily sudden abbreviation of the long bony tail in jinguornithids and confuciusornithiforms (i.e., Pygostylia) drastically changes their bauplan and locomotion, and tissue have been reallocated during development. The combination of selection for flight, rate of growth, and potentially plesiomorphic developmental/genetic pathways may have resulted in developmental plasticity in terms of fusion of the scapulocoracoid that we see in basal pygostylians (see *SI Appendix, SI Text*, for further discussion).

The fact that the separation of the coracoid and scapula becomes evolutionarily “fixed” (with a few exceptions in the crown groups) across Ornithothoraces is intriguing, and we suggest some possible explanations. The basal members of the Ornithothoraces generally are smaller than nonornithothoracine birds (40), which may shorten the time to reach adult size without necessarily inducing the acceleration in osteogenesis. Furthermore, their earliest members exhibit a slower growth rate (demonstrated by bone histology) compared with jinguoformis and confuciusornithiforms (*SI Appendix, Fig. S9*). Ornithothoraces further refined the flight-related musculoskeletal system (1, 4), and the chondrified scapula and coracoid are acted upon by different muscles and thus move in different ways (41). These combined factors delay (or stop) the fusion of the cartilaginous germs of these two bones, and a separated coracoid and scapula are to be expected. We further posit that the scapulocoracoid in jinguoformis and confuciusornithiforms may be derived through the heterochronic process of peramorphosis (42). The absence of a scapulocoracoid in *Archaeopteryx*, *Jeholornithiformes*, and taxa crownward of *Jinguoformis* indicates that a scapulocoracoid is not plesiomorphic within Aves. The development of the shoulder girdle in these basal pygostylians not only retains the phenotype of the fused scapulocoracoid of

nonavian theropod ancestors, but exhibits that fused bone has new morphologies (1, 11, 18). In Enantiornithes and Ornithomorphs, the developmental strategy of the shoulder is modified with the fusion of the coracoid and scapula being impeded and with the addition of changes to other parts of the skeleton including an ossified sternal keel and formation of the triosseal canal. These developmental changes to the skeleton likely correspond to intense selective pressure to improve flight capability that eventually leads to the musculoskeletal system present among volant crown birds, suggesting developmental plasticity (43). The discovery of *Jinguoformis* further highlights the importance of plasticity of development for mosaic evolution as a driver of the diversification of early birds.

Materials and Methods

To explore the phylogenetic relationships of *Jinguoformis* with respect to other Mesozoic birds, we added IVPP V24194 to the dataset of Wang et al.

- Wang M, Zhonghe Z (2017) The evolution of birds with implications from new fossil evidences. *The Biology of the Avian Respiratory System*, ed Maina NJ (Springer International Publishing, New York), pp 1–26.
- Brusatte SL, O'Connor JK, Jarvis ED (2015) The origin and diversification of birds. *Curr Biol* 25:R888–R898.
- Chiappe LM, Meng Q (2016) *Birds of Stone: Chinese Avian Fossils from the Age of Dinosaurs* (Johns Hopkins Univ Press, Baltimore).
- O'Connor JK, et al. (2015) Evolution and functional significance of derived sternal ossification patterns in ornithothoracine birds. *J Evol Biol* 28:1550–1567.
- Makovicky PJ, Norell MA (2004) Troodontidae. *The Dinosauria*, eds Weishampel D, Dodson P, Osmólska H (Univ California Press, Berkeley, CA), 2nd Ed, pp 184–195.
- Rauhut OWM, Foth C, Tischlinger H (2018) The oldest *Archaeopteryx* (Theropoda: Avialae): A new specimen from the Kimmeridgian/Tithonian boundary of Schanhaupten, Bavaria. *PeerJ* 6:e4191.
- Clarke JA, Zhou Z, Zhang F (2006) Insight into the evolution of avian flight from a new clade of Early Cretaceous ornithurines from China and the morphology of *Yixianornis grabaui*. *J Anat* 208:287–308.
- O'Connor JK, Chiappe LM (2011) A revision of enantiornithine (Aves: Ornithothoraces) skull morphology. *J Syst Palaeontol* 9:135–157.
- Wang M, O'Connor JK, Zhou Z (2018) A taxonomical revision of the Confuciusornithiformes (Aves: Pygostylia). *Vertebr Palasiat*, 10.19615/vj.cnki.1000-3118.180530.
- Wang Y, et al. (2017) A previously undescribed specimen reveals new information on the dentition of *Sapeornis chaoyangensis*. *Cretac Res* 74:1–10.
- Chiappe LM, Ji S, Ji Q, Norell MA (1999) Anatomy and systematics of the Confuciusornithidae (Theropoda: Aves) from the Late Mesozoic of northeastern China. *Bull Am Mus Nat Hist* 242:1–89.
- Xu X, You H, Du K, Han F (2011) An *Archaeopteryx*-like theropod from China and the origin of Avialae. *Nature* 475:465–470.
- Mayr G, Pohl B, Hartman S, Peters DS (2007) The tenth skeletal specimen of *Archaeopteryx*. *Zool J Linn Soc* 149:97–116.
- Zhou S, O'Connor JK, Wang M (2014) A new species from an ornithomorph (Aves: Ornithothoraces) dominated locality of the Jehol Biota. *Chin Sci Bull* 59:5366–5378.
- Wang M, Wang X, Wang Y, Zhou Z (2016) A new basal bird from China with implications for morphological diversity in early birds. *Sci Rep* 6:19700.
- Zhou Z, Zhang F (2003) Anatomy of the primitive bird *Sapeornis chaoyangensis* from the Early Cretaceous of Liaoning, China. *Can J Earth Sci* 40:731–747.
- Baumel J, Raikow R (1993) Arthrologia. *Handbook of Avian Anatomy: Nomina Anatomica Avium*, eds Baumel JJ, King AS, Breazile JE, Evans HE, Berge JCV (Nuttall Ornithological Club, Cambridge, MA), 2nd Ed, pp 133–187.
- Jenkins FA (1993) The evolution of the avian shoulder joint. *Am J Sci* 293:253–267.
- Turner AH, Makovicky PJ, Norell MA (2012) A review of dromaeosaurid systematics and paravian phylogeny. *Bull Am Mus Nat Hist* 371:1–206.
- Padian K (1983) A functional analysis of flying and walking in pterosaurs. *Paleobiology* 9:218–239.
- Wang M, Li Z, Zhou Z (2017) Insight into the growth pattern and bone fusion of basal birds from an Early Cretaceous enantiornithine bird. *Proc Natl Acad Sci USA* 114:11470–11475.
- O'Connor JK (2009) A systematic review of Enantiornithes (Aves: Ornithothoraces). PhD thesis (Univ of Southern California Press, Los Angeles).
- Zhou Z, Zhang F (2002) A long-tailed, seed-eating bird from the Early Cretaceous of China. *Nature* 418:405–409.
- Zhou S, Zhou Z, O'Connor JK (2013) Anatomy of the basal ornithomorph bird *Archaeorhynchus spathula* from the Early Cretaceous of Liaoning, China. *J Vertebr Paleontol* 33:141–152.
- Zhou Z, Zhang F (2003) Jeholornis compared to Archaeopteryx, with a new understanding of the earliest avian evolution. *Naturwissenschaften* 90:220–225.
- Norell M, Makovicky PJ, Akademi MSU (1999) Important features of the dromaeosaurid skeleton. 2: Information from newly collected specimens of *Velociraptor mongoliensis*. *Am Mus Novit* 3282:1–45.
- Norberg UM (1990) *Vertebrate Flight: Mechanics, Physiology, Morphology, Ecology and Evolution* (Springer, Berlin).
- Lindhe Norberg UM (2002) Structure, form, and function of flight in engineering and the living world. *J Morphol* 252:52–81.
- Zhou Z, Barrett PM, Hilton J (2003) An exceptionally preserved Lower Cretaceous ecosystem. *Nature* 421:807–814.
- Gill FB (2007) *Ornithology* (W. H. Freeman, New York), 3rd Ed.
- Jenkins FA, Jr, Dial KP, Goslow GE, Jr (1988) A cineradiographic analysis of bird flight: The wishbone in starlings is a spring. *Science* 241:1495–1498.
- Parker TJ (1891) Observations on the anatomy and development of *Apteryx*. *Philos Trans R Soc B* 182:25–134.
- Vickaryous MK, Hall BK (2006) Homology of the reptilian coracoid and a reappraisal of the evolution and development of the amniote pectoral apparatus. *J Anat* 208:263–285.
- Romanoff AL (1960) *The Avian Embryo: Structural and Functional Development* (The Macmillan Company, New York).
- Williams MS (2003) Developmental anomalies of the scapula—the “omo”st forgotten bone. *Am J Med Genet A* 120A:583–587.
- Oliver G, De Robertis EM, Wolpert L, Tickle C (1990) Expression of a homeobox gene in the chick wing bud following application of retinoic acid and grafts of polarizing region tissue. *EMBO J* 9:3093–3099.
- Erickson GM, et al. (2009) Was dinosaurian physiology inherited by birds? Reconciling slow growth in *Archaeopteryx*. *PLoS One* 4:e7390.
- O'Connor JK, Wang M, Zheng X, Wang X, Zhou Z (2014) The histology of two female Early Cretaceous birds. *Vertebr Palasiat* 52:112–128.
- De Ricqlès AJ, Padian K, Horner JR, Lamm ET, Myhrvold N (2003) Osteohistology of *Confuciusornis sanctus* (Theropoda: Aves). *J Vertebr Paleontol* 23:373–386.
- Liu D, Zhang Y, Zhou Z (2012) Mass estimation and evolutionary trend in Chinese Mesozoic fossil birds. *Vertebr Palasiat* 50:39–52.
- Jasinowski SC, Russell AP, Currie PJ (2006) An integrative phylogenetic and extrapolatory approach to the reconstruction of dromaeosaur (Theropoda: Eumaniraptora) shoulder musculature. *Zool J Linn Soc* 146:301–344.
- Laudet V (2011) The origins and evolution of vertebrate metamorphosis. *Curr Biol* 21:R726–R737.
- Moczek AP, et al. (2011) The role of developmental plasticity in evolutionary innovation. *Proc Biol Sci* 278:2705–2713.
- Goloboff PA, Catalano SA (2016) TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics* 32:221–238.