

A Comparative Morphological Study of the Jugal and Quadratojugal in Early Birds and Their Dinosaurian Relatives

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ABSTRACT

The zygoma (called jugal bar) in modern birds accounts for a large portion of the ventral margin of the cranium. As a delicate and rod-like element, the jugal bar is functionally integrated into the avian cranial kinesis, a unique property that allows the beak to be elevated or depressed with respect to the braincase and thus distinguishes birds from all other modern vertebrates. Developmental studies show that the jugal bar of modern birds is formed by the fusion of the jugal and quadratojugal that are ossified from separated centers. However, those two bones are unfused and exhibit complicated morphological variations in basal birds and their dinosaurian relatives. Moreover, the jugal and quadratojugal form rigid articulations with the postorbital and squamosal, respectively, consequently hindering the movement of the upper jaw in most non-avian dinosaurs and some basal birds. A comparative study of the jugal and quadratojugal morphology of basal birds and their close relatives such as dromaeosaurids and oviraptorids elucidates how modern birds has achieved its derived jugal bar morphology, and sheds light on the evolution of the postorbital configuration of birds. We propose that numerous morphological modifications of those two elements (morphology changes and reduced articulation with other elements) took place in early bird history, and some of them pertinent to the refinement of the cranial kinesis. *Anat Rec*, 300:62–75, 2017. © 2016 Wiley Periodicals, Inc.

Key words: zygoma; function; evolution; jugal bar; quadratojugal; cranial kinesis; bird; Cretaceous

Birds stand out among living vertebrates in that can move the whole or part of their upper jaw relative to the braincase, an ability known as the cranial kinesis (Bock, 1964; Zusi, 1984, 1993). That functional property, among many other novelties, contributes to their extraordinary diversity of ecology in the modern world (Gill, 2007). In skull of living birds, the ventral margin of the orbit is formed by the jugal bar (*arcus jugalis*). The jugal bar is derived from the fusion of two bony elements—quadratojugal and jugal, which are ossified from separated centers that start to fuse into a single element in early embryonic developmental stage (Webb, 1957; Baumel and Witmer, 1993; Maxwell, 2008a). As one of the

Grant sponsors: National Natural Science Foundation of China; Grant number: 41502002; Youth Innovation Promotion Association (CAS); Grant number: 2016073; State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of Geology and Palaeontology, CAS); Grant number: 153111; National Basic Research Program of China 973 Program; Grant number: 2012CB821906.

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Received 25 January 2016; Revised 3 March 2016; Accepted 23 March 2016.

DOI 10.1002/ar.23446

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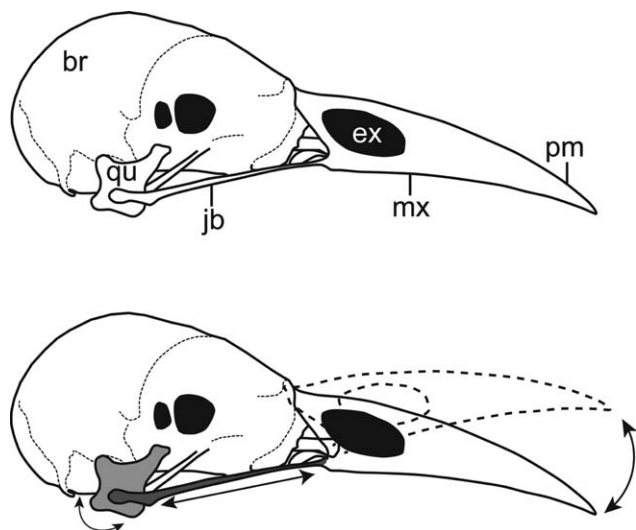


Fig. 1. Interpretative line drawing of modern bird's skull showing the avian cranial kinesis. The jugal bar acts as a lever that transmits the rotation of the quadrate to depress or elevate the upper beak, redrawn from Bock (1964).

connecting elements between the quadrate and the rostrum, the jugal bar is functionally integrated in avian cranial kinesis by transmitting the rotation of the quadrate during protraction or retraction of the upper jaw (Bock, 1964; Zusi, 1993; Fig. 1). Despite its functional importance, little is known about how jugal bar of modern birds has achieved its derived morphology. Over the last two decades, a wealth of spectacularly preserved feathered non-avian dinosaurs and basal birds, most from the Early Cretaceous Jehol Biota of northeastern China (130.7–120 million years ago), makes the dinosaurian origin of birds one of the best understood major transition in the history of life (Zhou et al., 2003; Zhou, 2004, 2014; Xu et al., 2011, 2014; Wang et al., 2015a). In most non-avian theropods, the jugal is a massive and triradiate element, considerably different from the morphology of jugal bar in modern birds (Paul, 1988; Elzanowski, 1999; Weishampel et al., 2004), indicating that marked modifications of this element, along with many other skeletal and physiological changes, took place in the early stage of bird history. The nearly complete and three dimensionally preserved cranial materials of the closest relatives of birds, such as dromaeosaurids, troodontids, and oviraptorosaurs, allow a rare chance to reconstruct the jugal morphology in those taxa, and further illuminate how this element had changed in morphology across the dinosaur-bird transition and its functional implications. The bizarre scansorioptergid theropods are considered to be phylogenetically more closely related to birds than dromaeosaurids by some studies (Zhang et al., 2008), but the jugal and quadratojugal in known specimens are all poorly preserved and thus are not included here. The jugal and quadratojugal were separated in non-avian dinosaurs and basal birds; therefore, both elements are considered in this study to fully understand the evolution of modern avian jugal bar.

MATERIALS AND METHODS

Anatomical Abbreviations Used in the Figures

af = antorbital fenestra; br = braincase; cqj = caudoventral process of quadratojugal; ex = external naris; fr = frontal; jb = jugal bar; jqj = jugal process of quadratojugal; ju = jugal; if = infratemporal fenestra; la = lacrimal; mf = maxillary fenestra; mju = maxillary process of jugal; mx = maxilla; or = orbital; pf = premaxillary fenestra; pju = postorbital process of jugal; pm = premaxilla; po = postorbital; pr = parietal; qf = quadrate foramen; qj = quadratojugal; qju = quadratojugal process of jugal; qu = quadrate; sf = supratemporal fenestra; sq = squamosal; sqj = squamosal process of quadratojugal. Specimens used in this study are listed in Table 1.

Institutional Abbreviations

AMNH = American Museum of Natural History, New York, USA; BMNHC = Beijing Museum of Natural History, Beijing, China; DNHM = Dalian Natural History Museum, Dalian, Beijing; GIN = Institute of Geology, Mongolian Academy of Sciences, Ulaan Bataar, Mongolia; GMV = National Geological Museum of China, Beijing, China; HGM = Henan Geological Museum, Zhengzhou, China; IGM = Institute of Geology, Mongolian Academy of Sciences, Ulaan Bataar, Mongolia; IVPP = Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; LP = Institut d'Estudis Ilerdencs, Lleida, Spain; MNHC = Beijing Museum of Natural History Collection, Beijing, China; PVL = Fundación-Instituto Miguel Lillo, Tucumán, Argentina; SMFAv = Forschungsinstitut Senckenberg, Frankfurt, Germany.

RESULTS

Anatomical Description of Jugal and Quadratojugal in Non-Avian Dinosaurs

Dromaeosauridae. The jugal in dromaeosaurids is typically triradiate with a maxillary process at the rostral end, a postorbital process projecting dorsocaudally, and a quadratojugal process extending caudally (Paul, 1988; Barsbold and Osmolska, 1999; Xu and Wu, 2001; Norell et al., 2006; Fig. 2). The bone is mediolaterally thin, dorsoventrally deep, and increases its depth caudally, giving the element a triangular appearance in lateral view (Fig. 2C). Rostrally, the jugal contacts the lacrimal on its dorsal margin and extends beyond the cranial margin of the latter bone (Fig. 2A,B), contributing to a small portion of the ventral margin of the antorbital fenestra (Barsbold and Osmolska, 1999). The rostral end of the jugal tapers to a blunt end and overlies the jugal process of the maxilla, preventing any contact between the maxilla and lacrimal. The ventral margin of the jugal is straight to slightly convex, whereas the dorsal margin slants dorsocaudally as a result of the distinctly elevated postorbital process. The caudal end of the jugal is bifurcated into the postorbital and the quadratojugal processes (Fig. 2C). The postorbital process of the jugal tapers and projects dorsocaudally, forming a large angle with the long axis of the jugal in *Linheraptor exquisitus* (62°), but smaller in *Velociraptor mongoliensis* (38°). The postorbital process articulates with the jugal process of the postorbital along its caudal

TABLE 1. Specimens used in this study and the preliminary description of the jugal and quadratojugal

Taxon	Group	Collection	Preservation	Key features
<i>Linheraptor exquisitus</i>	Dromaeosauridae	IVPP V16923	complete	quadratojugal: T-shaped; jugal: forked caudal end
<i>Velociraptor mongoliensis</i>	Dromaeosauridae	AMNH FR 6516	nearly complete	quadratojugal: T-shaped; jugal: forked caudal end
<i>Velociraptor mongoliensis</i>	Dromaeosauridae	GIN 11/25	nearly complete	quadratojugal: T-shaped; jugal: forked caudal end
<i>Sinornithosaurus millenii</i>	Dromaeosauridae	IVPP V12811	partial complete	quadratojugal: T-shaped; jugal: forked caudal end
<i>Microraptor zhaoianus</i>	Dromaeosauridae	BMNHC PH881	partial complete	quadratojugal: T-shaped; jugal: forked caudal end
<i>Erlikosaurus andrewsi</i>	Therizinosauria	IGM 100/111	nearly complete	quadratojugal: T-shaped; jugal: forked caudal end and the quadratojugal process forked
<i>Khaan mckennai</i>	Oviraptoridae	IGM 11/1127	partial complete	quadratojugal: T-shaped but the caudoventral process reduced; jugal: forked caudal end
<i>Yulong mini</i>	Oviraptoridae	HGM 41HIII-0107	incomplete	quadratojugal: T-shaped but the caudoventral process reduced; jugal: forked caudal end
<i>Incisivosaurus gauthieri</i>	Oviraptoridae	IVPP V13326	incomplete	quadratojugal: T-shaped; jugal: forked caudal end
<i>Archaeopteryx</i>	Archaeopterygidae	Munich specimen	largely incomplete	quadratojugal: L-shaped; jugal: forked caudal end with a corneal process on the caudal margin of the postorbital process
<i>Jeholornis prima</i>	Jeholornithiformes	IVPP V13274	incomplete	quadratojugal: missing; jugal: forked caudal end
<i>Sapeornis chaoyangensis</i>	Sapeornithiformes	IVPP V13275	partial complete	quadratojugal: T-shaped; jugal: forked caudal end
<i>Confuciusornis sanctus</i>	Confuciusornithiformes	IVPP V12644	nearly complete	quadratojugal: T-shaped; jugal: forked caudal end
<i>Confuciusornis sanctus</i>	Confuciusornithiformes	IGM-2153	partial complete	quadratojugal and jugal: poorly preserved
<i>Confuciusornis sanctus</i>	Confuciusornithiformes	IGM-2132	partial complete	quadratojugal and jugal: poorly preserved
<i>Confuciusornis sanctus</i>	Confuciusornithiformes	SMFAv-416	partial complete	quadratojugal and jugal: poorly preserved
<i>Bohaiornis guoi</i>	Enantiornithes	IVPP V17963	nearly complete	quadratojugal: missing; jugal: unforked caudal end
<i>Longusunguis kurochkini</i>	Enantiornithes	IVPP V17964	incomplete	quadratojugal: missing; jugal: forked caudal end
<i>Shenqiornis mengi</i>	Enantiornithes	DNHM D2950	incomplete	quadratojugal: missing; jugal: forked caudal end
Enantiornithes indet.	Enantiornithes	LP 4450	partial complete	quadratojugal: missing; jugal: forked caudal end
<i>Pterygornis dapingfangensis</i>	Enantiornithes	IVPP V20729	incomplete	quadratojugal: L-shaped; jugal: unforked caudal end
<i>Cathayornis yandica</i>	Enantiornithes	IVPP V9769	incomplete	quadratojugal: missing; jugal: unforked caudal end
<i>Pengornis houi</i>	Enantiornithes	IVPP V15336	nearly complete	quadratojugal: missing; jugal: poorly preserved
<i>Schizooura lii</i>	Ornithuromorpha	IVPP V16861	nearly complete	quadratojugal: missing; jugal: forked caudal end
<i>Yixianornis grabaui</i>	Ornithuromorpha	IVPP V13631	partial complete	jugal and quadratojugal fused
<i>Hongshanornis longicresta</i>	Ornithuromorpha	IVPP V14533	partial complete	jugal and quadratojugal fused
<i>Archaeorhynchus spathula</i>	Ornithuromorpha	IVPP V14287	incomplete	quadratojugal: L-shaped; jugal: caudal end poorly preserved

margin, and both processes together form the caudal boundary of the orbit. Unlike in most other non-avian dinosaurs (Currie and Zhao, 1993; Weishampel et al., 2004; Xu et al., 2006; Lautenschlager et al., 2014), the postorbital is excluded from the margin of the infratemporal fenestra as a result of the squamosal—jugal

contact (Fig. 2B), a feature unique to Dromaeosauridae (Norell et al., 2006; Xu et al., 2015). The quadratojugal process projects further caudally than the postorbital process. The lateral surface of the quadratojugal process bears a shallow wedged-like incision to accommodate the quadratojugal, and these two elements form the ventral

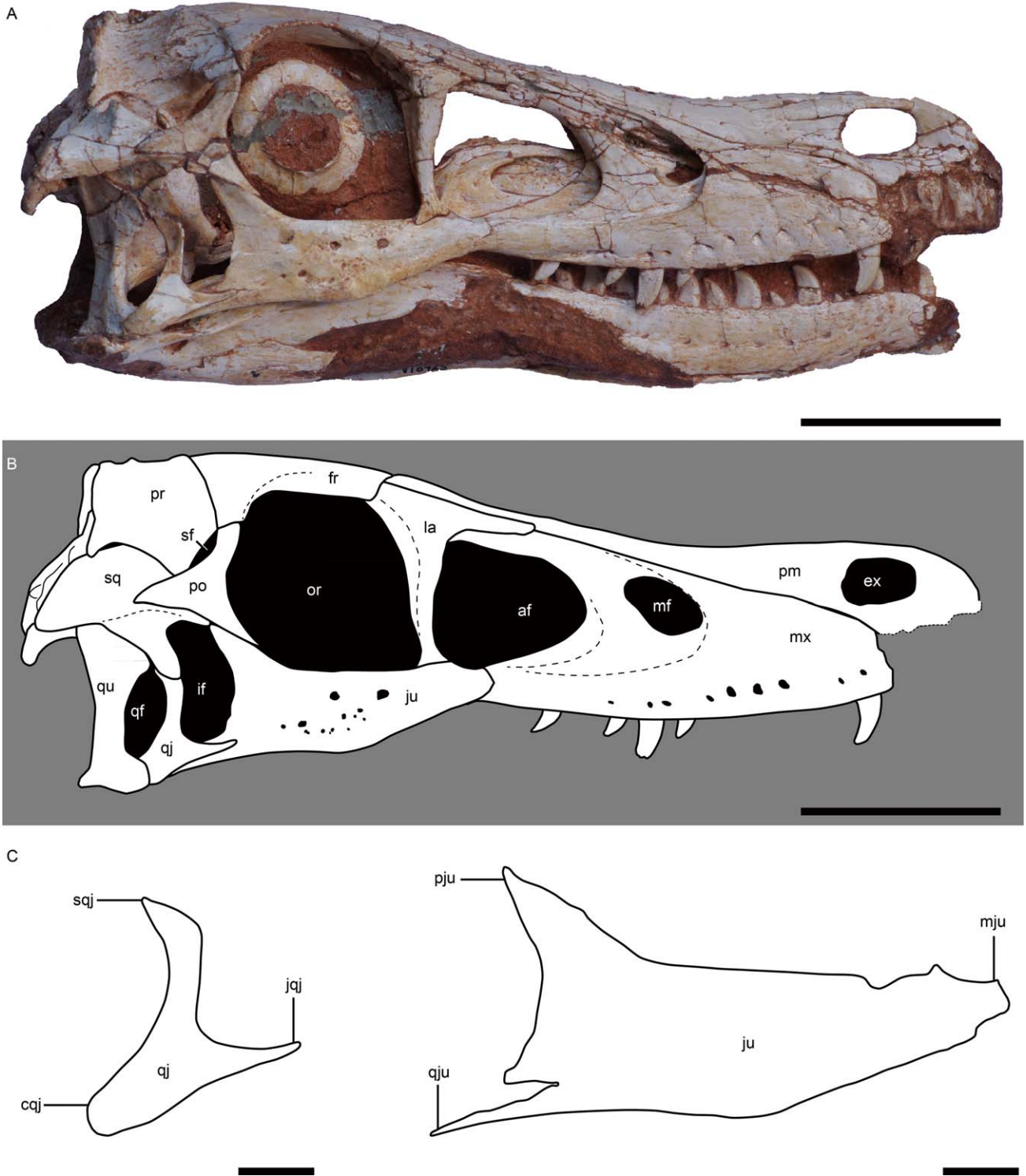


Fig. 2. Skull of *Linheraptor exquisitus* (Dinosauria: Dromaeosauridae) in right lateral view (holotype, IVPP V16923). (a) Photograph (courtesy of Xing Xu). (b) Line drawing. (c) Line drawing of the jugal and quadratojugal. Scale bars, 10 mm (a–c).

margin of the infratemporal fenestra (Fig. 2B). In some non-avian dinosaurs such as *Erlikosaurus andrewsi* (Theropod: Therizinosauria), the incision is highly

developed and the quadratojugal process is subdivided into two processes of equal length (Lautenschlager et al., 2014).

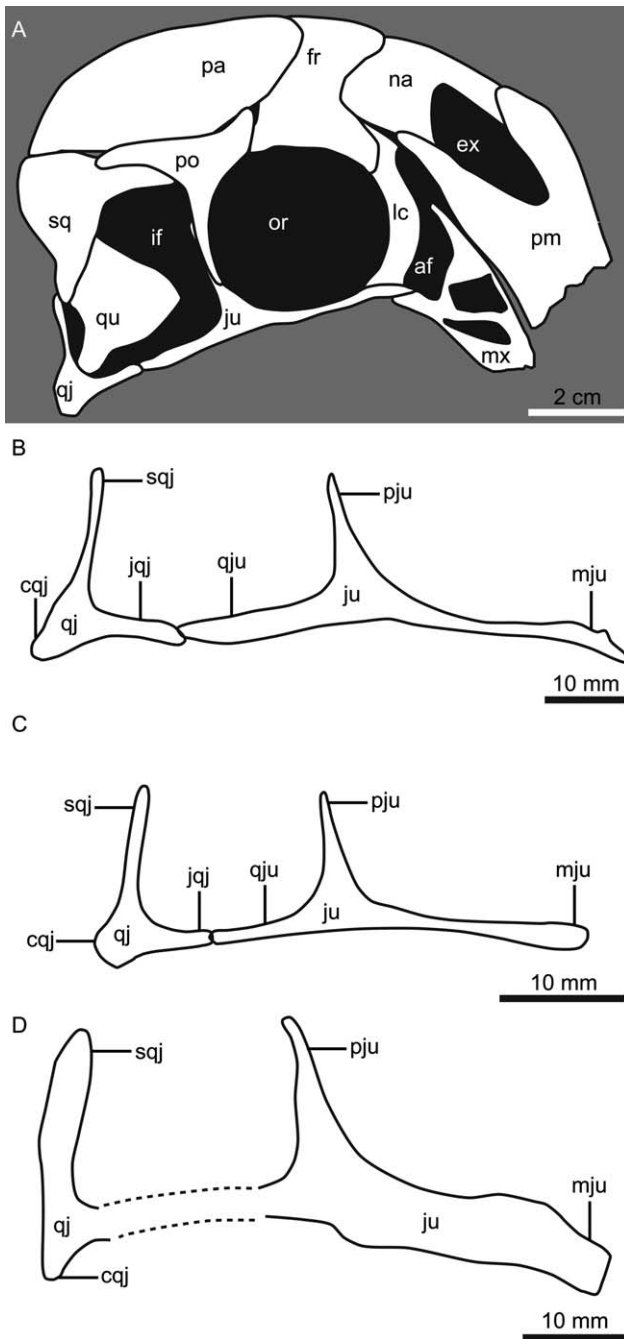


Fig. 3. Interpretative drawings of select oviraptorid cranial elements. (a) Reconstructed skull of *Khaan mckennai* (holotype, IGM 100/1127). (b–d) Line drawings of the jugal and quadratojugal: (b) *K. mckennai*, (c) *Yulong mini* (holotype, HGM 41HIII-0107), and (d) *Incisivosaurus gauthieri* (holotype, IVPP V13326). Scale bars, 20 mm (a), 10 mm (b–d).

The quadratojugal is shaped as an inverted T, consisting of three distinct processes, that is, the jugal, squamosal and caudoventral processes (Fig. 2C). The ventral margin of the quadratojugal is nearly straight, whereas the caudal margin is concave. Typically, the caudoventral process is the most robust one, and the jugal process is slender than the other two (Barsbold and Osmolska, 1999). The squamosal process is elongated and extends

dorsorostrally to meet the squamosal, consequently isolating the infratemporal fenestra from the quadrate foramen (Fig. 2B). The caudoventral process articulates with the quadrate at its mandibular condyle. Among dromaeosaurids, the development of the caudoventral process exhibits large variations: specifically, the ratio of the caudoventral process length to the jugal process length is less than one third in *Sinornithosaurus milnii* and *Microraptor zhaoianus*, greater than 0.5 in *V. mongoliensis*, *Bambiraptor feinbergorum*, and *Deinonychus antirrhopus* (Xu and Wu, 2001), and approaches 1.0 in *L. exquisitus*.

Oviraptoridae. Compared with most other non-avian dinosaurs, the jugal and quadratojugal of oviraptorosaurs are more bird-like in the slender outline, standing out in their massive skulls (Elzanowski, 1999; Xu et al., 2011). For instance, in oviraptorosaurs such as *Caudipteryx zoui*, *Khaan mckennai*, *Avimimus portentosus*, and *Yulong mini*, the jugal is thin and rod-like (Elzanowski, 1999; Zhou et al., 2000; Balanoff and Norell, 2012; Lü et al., 2013; Fig. 3A–C), but it is strap-like and massive in the basal oviraptorosaur *Incisivosaurus gauthieri* (Xu et al., 2002; Fig. 3D). As in most other non-avian dinosaurs, the postorbital process is elongated and articulates with the postorbital (Fig. 3A), forming the postorbital bar that delimitates the orbital from the infratemporal fenestra completely (Clark et al., 2002; Xu et al., 2002; Lü et al., 2013). Unlike the condition in dromaeosaurids (Norell et al., 2006), the postorbital process of the jugal fails to meet the squamosal and thus the postorbital forms the craniodorsal margin of the infratemporal fenestra as in many other non-avian dinosaurs (Clark et al., 2002; Balanoff and Norell, 2012; Fig. 3A). Compared with that of dromaeosaurids, the caudoventral process of the quadratojugal is reduced and the caudal end of the quadratojugal weakly protrudes caudally (Figs. 2 and 3). The squamosal process projects dorsally and defines an angle approaching 90° with the jugal process. Dorsally, the squamosal process of the quadratojugal contacts the squamosal, enclosing the caudal margin of the infratemporal fenestra.

Anatomical Description of Jugal and Quadratojugal in Early Birds

Archaeopterygidae. The jugal is preserved in five specimens of *Archaeopteryx*—the Berlin, Eichstätt, Munich, Thermopolis and the 11th specimen (Elzanowski and Wellnhofer, 1996; Elzanowski, 2002; Mayr et al., 2007; Foth et al., 2014). Unless indicated elsewhere, the following description is based on the Munich specimen, given its good preservation (Fig. 4). The jugal is transversely thin, plate-like and gently bowed ventrally (Fig. 4B), considerably more delicate than in non-avian dinosaurs, in which the bone is massive and strap-like in lateral view. The jugal tapers and projects cranially, and its caudal end is bifurcated into a larger postorbital process and a smaller quadratojugal process as in most non-avian dinosaurs (Weishampel et al., 2004; Norell et al., 2006; Fig. 4C). As in dromaeosaurids, the postorbital process projects caudodorsally and sharply tapers to a distal extremity. The caudal margin of the postorbital process convexes caudoventrally and forms a small corneal process (Elzanowski and Wellnhofer, 1996; Fig. 4C),

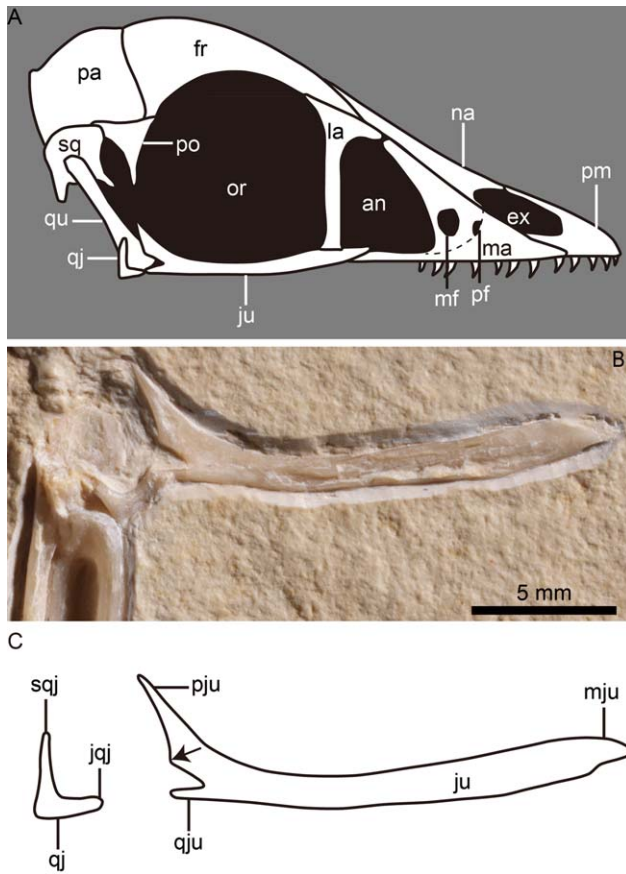


Fig. 4. Skull of *Archaeopteryx* (Aves: Archaeopterygidae). (a) Reconstruction of *Archaeopteryx* skull in right lateral view, modified from Elzanowski (2001) combined information from Mayr et al. (2005). (b) Photographs (courtesy of Oliver Rauhut) and (c) line drawings of the jugal and quadratojugal of the Munich specimen. The arrow indicates a corneal process in the caudal margin of the postorbital process of the jugal. Scale bar, 5 mm (b).

a feature otherwise unknown among non-avian dinosaurs, in which the caudal margin is simply concave, such as in *L. exquisitus* (Fig. 2C), *Xiaotingia zhengi*, *V. mongoliensis*, and *C. zoui*. The postorbital process is separated from the jugal process by a triangular notch. The quadratojugal process is rod-like, more slender than the postorbital process, and these two processes are subequal in caudal extension; whereas the former projects further caudally in most other non-avian dinosaurs, including *Sinoraptor hepingensis* (Theropod: Carnosauria), *L. exquisitus* and *C. zoui* (Currie and Zhao, 1993; Zhou et al., 2000; Xu et al., 2015).

The quadratojugal is small and shaped like an inverted L (Fig. 4C), lacking a caudoventral process of the kind present in dromaeosaurids (Paul, 1988; Fig. 2C). The squamosal and the jugal processes are subequal in length, and the latter appears to be stouter. The squamosal process is straight and perpendicular to the jugal process, rather than curved in lateral view as in dromaeosaurids. Unfortunately, no specimen of *Archaeopteryx* allows confident reconstruction of the postorbital region due to the preservation. However, the postorbital process of the jugal, the squamosal process of the

quadratojugal, and the quadratojugal process of the squamosal are so short that direct postorbital-jugal and quadratojugal-squamosal contacts are unlikely present (Martin et al., 1998; Chiappe et al., 1999; Elzanowski, 2002; Fig. 4A). Those paired elements were likely connected by ligaments in *Archaeopteryx* (Elzanowski and Wellnhofer, 1996; Elzanowski, 2001).

Jeholornithiformes. Jeholornithiformes are the only known avian clade that has a long bony tail except for *Archaeopteryx* (Zhou and Zhang, 2003a). Over the last decade, several long tailed specimens of Jeholornithiformes, including *Jeholornis prima* (Zhou and Zhang, 2002a), *Shenzhouraptor sinensis* (Ji et al., 2003), *Jixiangornis orientalis* (Ji et al., 2002), *Dalianraptor cuhe* (Gao and Liu, 2005), *Jeholornis palmapenis* (O'Connor et al., 2011), and *Jeholornis curvipes* (Lefèvre et al., 2014), have been reported exclusively from the Early Cretaceous Jehol Biota. However, some of these species were poorly diagnosed and their taxonomies remain controversial. For instance, *S. sinensis* and *J. orientalis* were considered as junior synonyms of *J. prima* (Zhou and Zhang, 2006a; Zhou and Wang, 2010), but not by everyone (Lefèvre et al., 2014). Therefore, taxonomical reappraisal of these putative taxa is mostly in need and central to our understanding of early avian evolution, but it is beyond the scope of this article. Detailed features of the jugal can only be appreciated in the holotype of *J. prima* (IVPP V13274; Fig. 5). As in *Archaeopteryx*, the bone is rod-like and caudally bifurcated into the postorbital and the quadratojugal processes (Fig. 5B). The jugal is more bowed ventrally than in *Archaeopteryx*. As in some oviraptorosaurs, the postorbital process projects dorsally (Xu et al., 2011), lacking the caudal inclination present in *Archaeopteryx* and dromaeosaurids (Figs. 2C and 4C). In contrast to the condition in *Archaeopteryx* and most other non-avian dinosaurs, the postorbital process barely narrows and gently curves caudally. The caudal margin between the postorbital and the quadratojugal processes are concave and continuous without a notch of the kind in *Archaeopteryx* (Elzanowski, 2002). The quadratojugal process is longer than the postorbital process, but the opposite is true in *Archaeopteryx* and many non-avian dinosaurs (Elzanowski and Wellnhofer, 1996; Barsbold and Osmolska, 1999; Norell et al., 2006). The known skull materials of Jeholornithiformes are severely compressed and detailed morphologies of the quadratojugal, squamosal or postorbital cannot be determined.

Sapeornithiformes. As one of the most basal pygostylians—birds with a pygostyle formed by the fusion of last few caudal vertebrae—*Sapeornis chaoyangensis* is the largest known Early Cretaceous bird with prominently elongated forelimb (the forelimb/hindlimb ratio ~ 1.5 , but that ratio is slightly > 1.0 in other Cretaceous birds; Zhou and Zhang, 2002b,b; Wang, 2014). The jugal is rod-like, and caudally bifurcated into the postorbital and the quadratojugal processes (Fig. 5D). In *S. chaoyangensis* (IVPP V13275), both the postorbital and the quadratojugal processes appear to be short. The distal end of the postorbital process is overlain by the quadratojugal in that specimen, but it is unlikely to reach the length of that in *J. prima*, *Archaeopteryx*, and non-

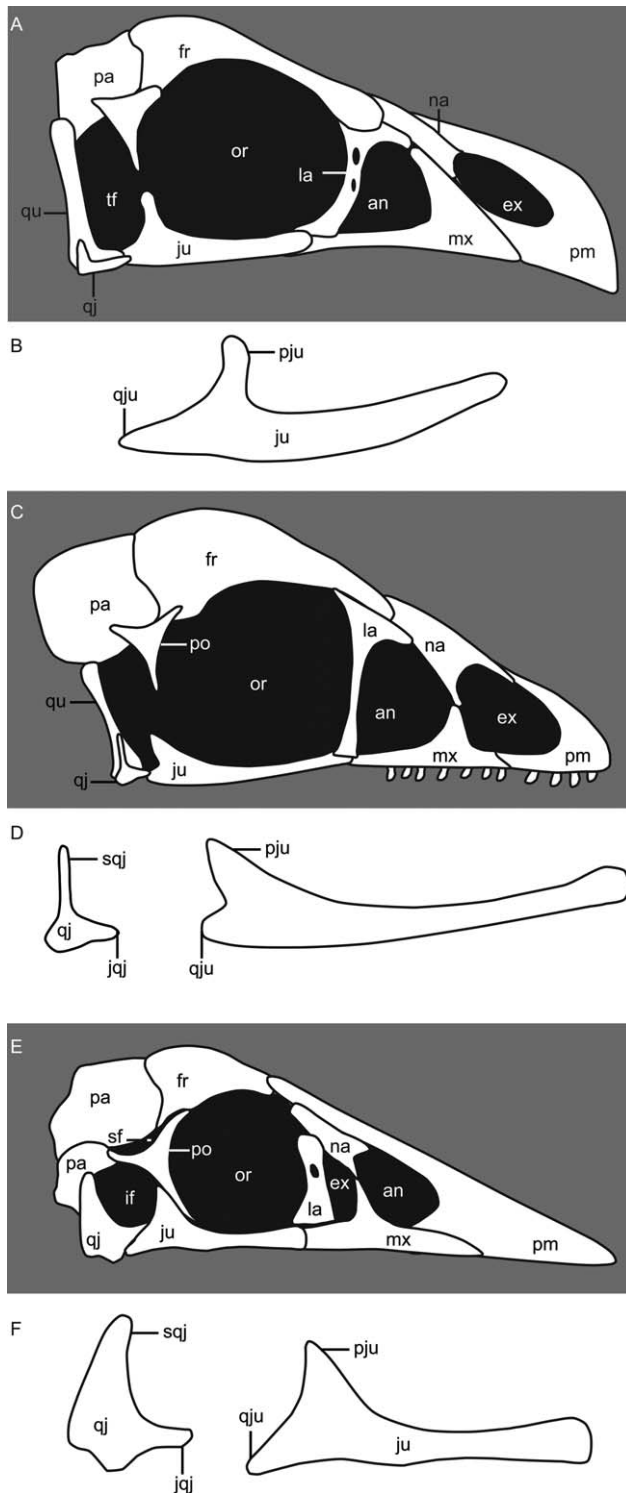


Fig. 5. Interpretative drawings of non-ornithothoracine bird skulls. (a) Reconstruction of *Jeholornis prima* skull (Aves: Jeholornithiformes). (b) Jugal preserved in *J. prima* holotype (IVPP V13274). (c) Reconstruction of *Sapeornis chaoyangensis* skull (Aves: Sapeornithiformes). (d) Jugal and quadratojugal preserved in *S. chaoyangensis* specimen (IVPP V13275). (e) Reconstruction of *Confuciusornis sanctus* skull (Aves: Confuciusornithiformes), modified from Chiappe et al. (1999). (f) Jugal and quadratojugal of *C. sanctus*.

avian dinosaurs. The quadratojugal is more robust than in *Archaeopteryx*, and bears a long squamosal process and a short jugal process (Fig. 5D). The squamosal process is more than three times as long as the jugal process, but is more slender than the latter. The squamosal process projects dorsally and is perpendicular to the ventral margin of the quadratojugal. As in *Archaeopteryx*, the caudoventral corner of the quadratojugal weakly protrudes rather than forms a distinct caudoventral process as in dromaeosaurids. No postorbital or squamosal can be ascertained in the known specimens of Sapeornithiformes, and thus the configuration of the postorbital region is largely unknown.

Confuciusornithiformes. As the most primitive birds that have an edentulous beak (Hou et al., 1996; Chiappe et al., 1999), Confuciusornithiformes are the most abundant Mesozoic avian clade represented by more than thousands of specimens (Chiappe et al., 2008). The jugal is nearly straight, and rod-like (Fig. 5F); the bone narrows along its middle third length and weakly expands rostrally. In Martin et al. (1998), the jugal was reconstructed to contact the lacrimal at its rostral end; whereas, Chiappe et al. (1999) alternatively suggested that the lacrimal contacted the maxilla rather than the jugal. Unfortunately, few specimens in perfect preservation are available to test either hypothesis. Regardless the minor differences among those reconstructions, both studies demonstrated that the jugal had been excluded from the antorbital fenestra (Fig. 5E), recalling the condition in more advanced birds such as Enantiornithes, for example, *Bohaiornis guoi* (IVPP V17963) and *Zhouornis hani* (BMNH Ph756). By contrast, the jugal forms a small portion of the ventral margin of the antorbital fenestra in *Archaeopteryx* (Mayr et al., 2005) and most non-avian dinosaurs (Currie and Zhao, 1993; Barsbold and Osmolska, 1999; Norell et al., 2006; Figs. 2A and 4A). *Confuciusornis sanctus* has a large T-shaped postorbital with a long jugal process, and several specimens show the direct contact between the postorbital and the jugal (GMV-2132, GMV-2153, SMFAv-416), indicating that the orbital and the infratemporal fenestra are separated from each other (Martin et al., 1998; Chiappe et al., 1999; Hou et al., 1999; Fig. 5E). Previously, the articulation of the jugal for the postorbital was described as a round projection (Martin et al., 1998; Hou et al., 1999). This inaccurate description is most likely resultant from the lack of exposure (overlain by the postorbital). In IVPP V12644, the exposed caudal end of the jugal reveals that such projection is actually the postorbital process. That process is short and triangular (Li, 2010), morphologically similar to that of *S. chaoyangensis*. The quadratojugal process of *C. sanctus* is tapered and short, rather than elongated as in *Archaeopteryx* and *J. prima*. The quadratojugal is larger than that of *Archaeopteryx*. As in *S. chaoyangensis*, the caudoventral process is absent and the squamosal process is longer than the quadratojugal process (Fig. 5F). It is still unclear whether the quadratojugal articulates with the squamosal. The squamosal contacts the postorbital directly, indicating that the supratemporal and the infratemporal fenestrae were completely separated (Chiappe et al., 1999; Li, 2010). Collectively, all these observations demonstrate that Confuciusornithiformes unequivocally represent the first known

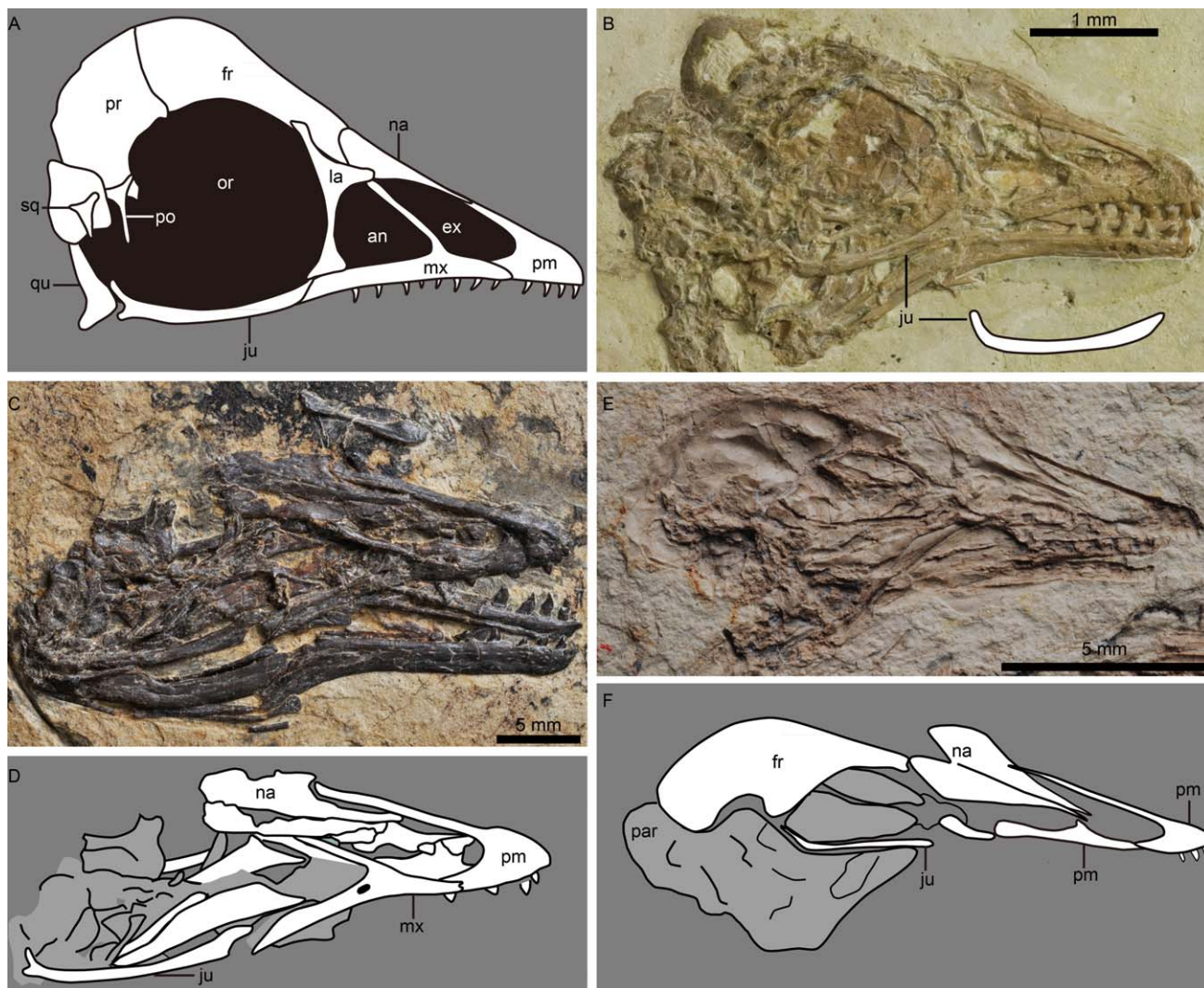


Fig. 6. Photographs and line drawings of select enantiornithine skulls. (a) Enantiornithine indet. LP4450, modified from Chiappe and Walker (2002); (b) *Bohaiornis guoi* (IVPP V17963) with line drawing of the jugal. (c,d) *Longusunguis kurochkini* (holotype, IVPP V17964). (e,f) *Cathayornis yandica* (holotype, IVPP V9769). Scale bars, 10 mm (b), 5 mm (c,e).

avian clade that retains the primitive diapsid skull (Chiappe et al., 1999; Fig. 5E).

Enantiornithes. Ever since recognized by C.A. Walker (1981), enantiornithine birds (“opposite birds,” referring to their coracoid-scapula articulation opposite to that of modern birds) have been collected from nearly all continents with a temporal span of the whole Cretaceous, making Enantiornithes the most speciose clade of Mesozoic birds (Chiappe and Walker, 2002; Wang et al., 2015b). Over 60 taxa have been named and more than half of them are from the Early Cretaceous Jehol Biota (Wang et al., 2015b). The numerous fossils provide a spectacular window into various aspects of the biology of those birds, and detailed morphologies of the jugal and quadratojugal can be appreciated from several specimens. As in more basal birds, these two bones are not

fused (Fig. 6). The jugal is rod-like, bowed ventrally, and forms the entire ventral margin of the orbit. Rostrally, the ventral margin of the jugal slants rostr dorsally to a tapered maxillary process, and forms a rostr dorsol-caudoventral articulation with the jugal process of the maxilla, for example, *Z. hani*, *B. guoi*, and *Longusunguis kurochkini* (Fig. 6B,C). Above the jugal-maxilla articulation, the lacrimal reaches down to the level of the jugal on its dorsal margin, for example, *Z. hani* and Enantiornithes indet. LP 4450 (Fig. 6A). As in *C. sanctus* but unlike most non-avian dinosaurs, the jugal has been completely excluded from the antorbital fenestra (Fig. 6). The caudal end of the jugal among Enantiornithes exhibits considerable variations. As in non-avian dinosaurs and more basal birds such as *Archaeopteryx*, *J. prima*, *S. chaoyangensis*, and *C. sanctus*, the caudal end of the jugal bears a postorbital and a quadratojugal processes, for example, *L. kurochkini*, *Shenqiornis mengi*,

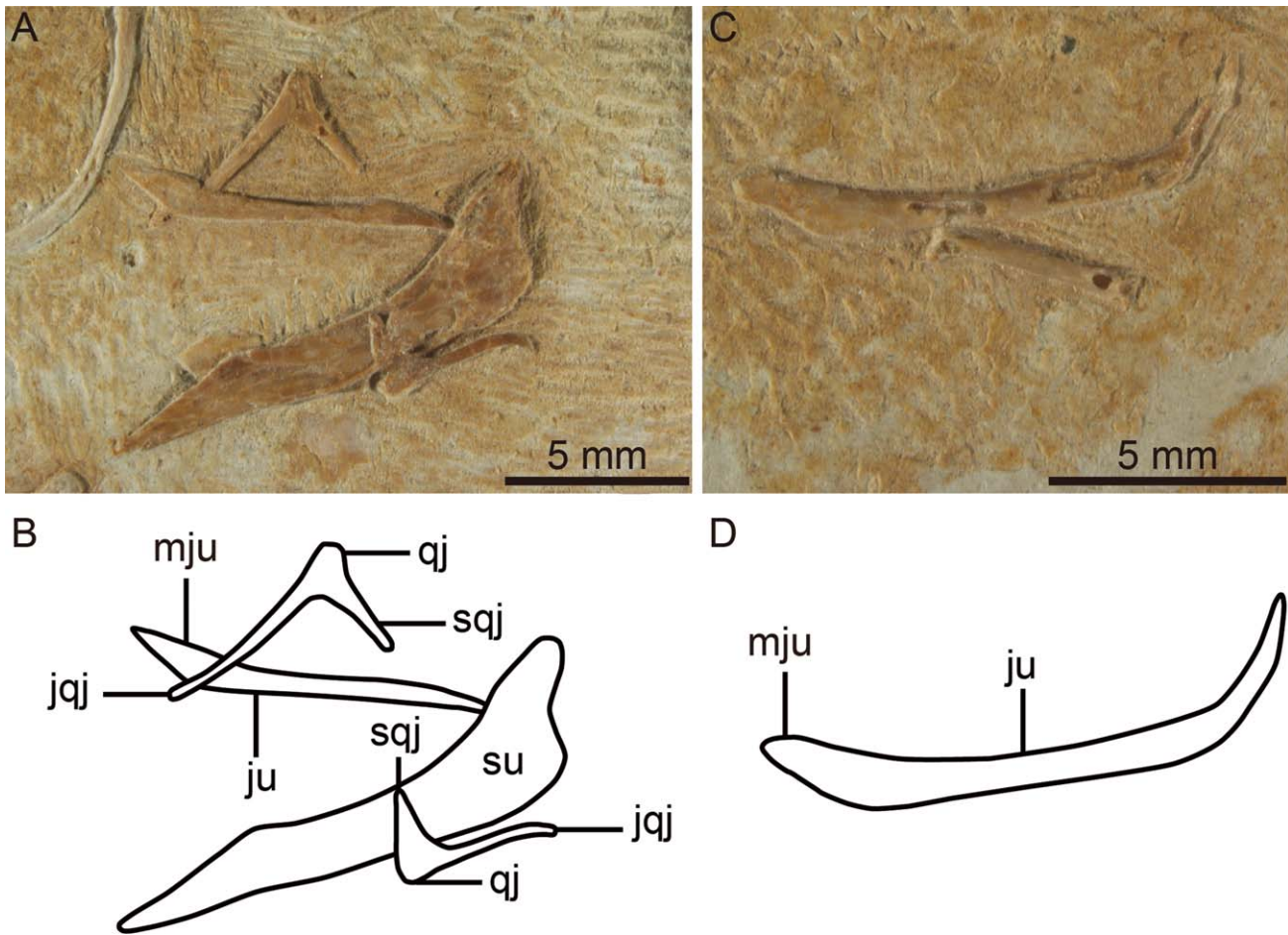


Fig. 7. Photographs and line drawings of the jugal and quadratojugal of *Pterygornis dapingfangensis* (Aves: Enantiornithes), holotype, IVPP V20729. Scale bars, 5 mm (a,b).

and Enantiornithes indet. LP 4450 (O'Connor and Chiappe, 2011; Wang et al., 2014; Fig. 6). By contrast, the jugal is unforked caudally but simply curves dorsally in some species, including *Pterygornis dapingfangensis*, *Cathayornis yandica*, and *B. guoi* (Wang et al., 2016; Figs. 6 and 7). In those taxa, the caudal end of the jugal resembles the morphology of the postorbital process of the bifurcated jugal, suggesting that the quadratojugal process has simply been lost in those taxa. In specimens with a forked caudal end, the postorbital process is considerably longer than the quadratojugal process (Fig. 6). The postorbital process extends caudodorsally and surpasses the quadratojugal process in caudal extension. The quadratojugal process protrudes caudoventrally, and defines an obtuse angle slightly over 90° with the postorbital process, for example, *L. kurochkini* and Enantiornithes indet. LP 4450. Only three enantiornithine specimens are informative with respect to the postorbital configuration, including the holotypes of *S. mengi* (DNHM D2950), *Pengornis houi* (IVPP V15336), and Enantiornithes indet. LP 4450. In *S. mengi*, the postorbital is T-shaped with a long and tapered jugal process (only slightly shorter than the dorsoventral height of its quadrate). Despite that, the postorbital is displaced from its natural position in this specimen, O'Connor and

Chiappe (2011) interpreted that it contacted the jugal directly on basis of the length of its jugal process. In Enantiornithes indet. LP 4450 (Fig. 6A), the postorbital is also T-shaped but terminates before reaching the jugal (O'Connor and Chiappe, 2011). The postorbital of *P. houi* differs from that of Enantiornithes indet. LP 4450 and *S. mengi* significantly in that the bone is shaped as an inverted L with a slender jugal process. In the holotype of *P. houi* (IVPP V15336), the postorbital is preserved in its natural position, and its jugal process terminates far away from the jugal, demonstrating that the temporal fenestra is confluent with the orbit.

So far, the quadratojugal of enantiornithines can only be identified in a single specimen, the holotype of *P. dapingfangensis* (IVPP V20729). The specimen is disarticulated with some cranial elements well preserved, including the jugal, quadratojugal, and splenial, allowing a rare chance to reconstruct morphologies for those elements (Wang et al., 2016). The quadratojugal is inverted L-shape with jugal and squamosal processes (Fig. 7), and it is considerably smaller than in *C. sanctus* and *S. chaoyangensis*. As in *Archaeopteryx*, the squamosal process is shorter than the jugal process, but the opposite is true in *S. chaoyangensis*, *C. sanctus*, and many non-avian dinosaurs. This squamosal process

projects dorsally and thus defines an angle close 90° with the jugal process. The jugal process is slender, more than twice as long as the squamosal process. The squamosal can only be definitively determined in one enantiornithine specimen (LP 4450), in which, unfortunately, the quadratojugal is not preserved. Therefore, whether the squamosal and quadratojugal contact directly or not is unknown at this point.

Ornithuromorpha. Ornithuromorpha are the most inclusive clade containing all living birds but not the Enantiornithes (Wang et al., 2015a). Over the last two decades, our understanding of the basal ornithuromorphs has been greatly refined as the increasing discoveries of many exceptionally preserved specimens from the Jehol Biota (Zhou et al., 2013; Chiappe et al., 2014). Complete and articulated Jehol specimens and in some cases with feathers and other soft tissues have provided critical information about the basal ornithuromorphs, such as morphology, ecology and phylogeny (Zheng et al., 2011, 2014; Zhou et al., 2013, 2014). Unfortunately, these Jehol birds are largely preserved in two-dimensions and the cranial elements are overlain by one another, severely limiting the amount of cranial features that can be discerned. The jugal is frequently described as a thin, rod-like element in basal ornithuromorphs, but its caudal end is only visible in a few taxa, including the holotypes of *Schizooura lii*, *Yixianornis grabau*, and *Hongshanornis longicresta* (Zhou and Zhang, 2005; Clarke et al., 2006; Zhou et al., 2012). In *S. lii* (Fig. 7A,B), the jugal is more slender than in enantiornithines and more basal birds such as *C. sanctus* and *Archaeopteryx*. Caudally, the bone is forked with the postorbital and quadratojugal processes (Zhou et al., 2012). The postorbital and the quadratojugal processes are subequal in length, but the latter is more robust and approaches the dorsoventral depth of the main body of the jugal (Fig. 7B). By contrast, the quadratojugal process is considerably thinner than the jugal in Enantiornithes and more basal birds (Figs. (4 and 6)–). The postorbital process projects caudodorsally, and terminates shortly of the caudal end of the quadratojugal process. In stark contrast to *S. lii*, the jugal in *Y. grabau* and *H. longicresta* is unforked, and the bone is simply rod-like and bowed ventrally as in crown birds (Zhou and Zhang, 2005; Clarke et al., 2006). Apart from the Jehol ornithuromorphs, the jugal can only be confidently determined in *Ichthyornis dispar* and *Hesperornis gracilis* among Cretaceous ornithuromorphs, and the bone is morphological indistinguishable from that of living birds (Gregory, 1952; Gingerich, 1973; Fig. 8D).

The fossil record of the quadratojugal in basal Ornithuromorpha is even sparser than that of the jugal, being limited to a single specimen—the holotype of *Archaeorhynchus spathula* (IVPP V14287; Fig. 8C). The quadratojugal is shaped as an inverted L, comprising two processes (Zhou and Zhang, 2006b). Due to disarticulation, the identity of those two processes (jugal and squamosal processes) cannot be ascertained. However, these two processes are of equal length, without the length disparity observed in *P. dapingfangensis*, *S. chaoyangensis*, *C. sanctus*, and *Archaeopteryx*. The jugal and quadratojugal processes define an angle about 73° . So far no postorbital or squamosal have been preserved

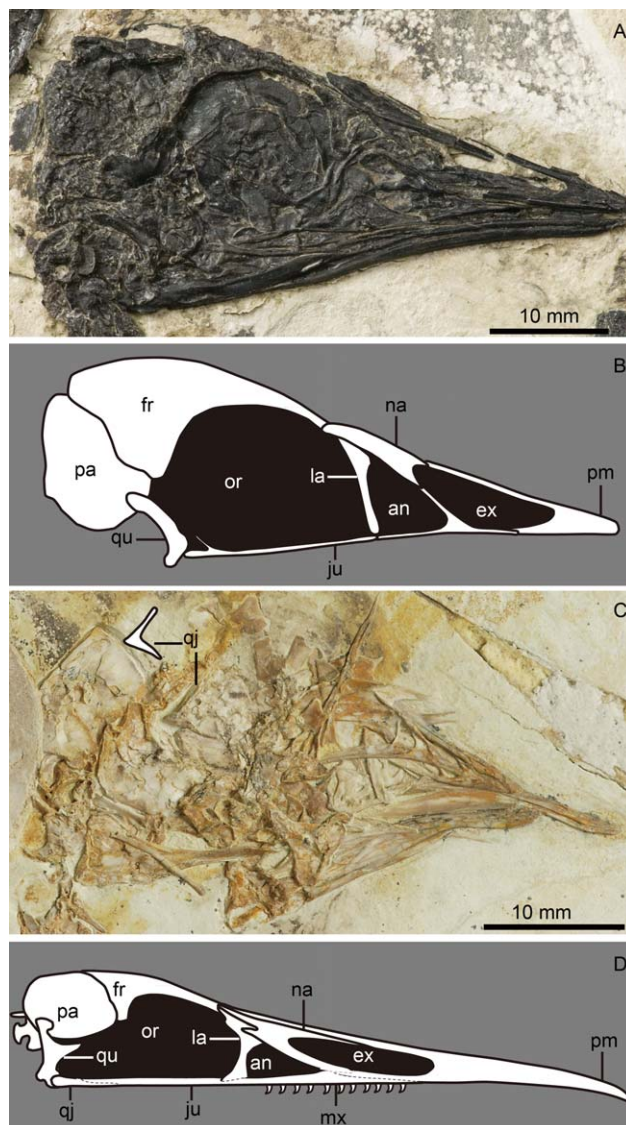


Fig. 8. Photographs and line drawings of select Cretaceous ornithuromorph skulls. (a,b) Holotype of *Schizooura lii*, IVPP V16861. (c) Holotype of *Archaeorhynchus spathula* (IVPP V14287) with the interpretative drawing of the quadratojugal. (d) Reconstructed skull of *Hesperornis regalis*, modified from Gingerich (1973), showing that the jugal and quadratojugal are fused to form the jugal bar. Scale bars, 10 mm (a,c).

in basal ornithuromorphs, suggesting that the squamosal had already been fused with the braincase and the postorbital might have been reduced or lost. In addition, the reduced postorbital process of the jugal (e.g., *S. lii*) and the squamosal process of the quadratojugal (e.g., *A. spathula*) strongly indicate that the postorbital bar was absent, and that the temporal fenestra was confluent with the orbit in basal ornithuromorphs (Fig. 8A).

Modern bird-like jugal bar can be at least traced back to the Ichthyornithiformes and Hesperornithiformes, the basal members of the Ornithurae—the clade that also encompass all living birds. Developmental studies of living birds demonstrate that the quadratojugal and jugal are among the cranial elements to be ossified early in

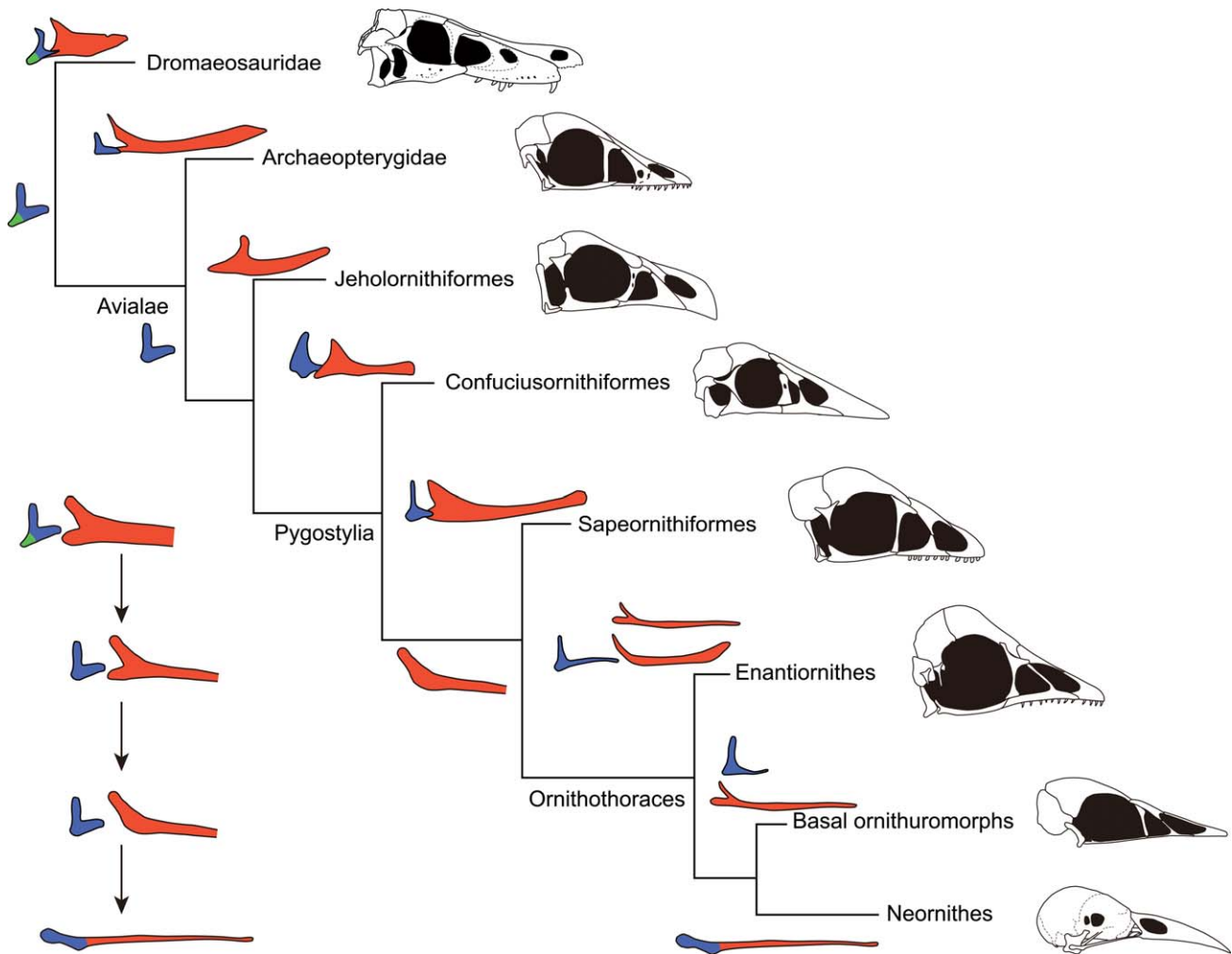


Fig. 9. Distribution of jugal and quadratojugal morphologies in early birds and the hypothetical evolution of modern avian jugal bar. The cladogram of Mesozoic birds is simplified after Wang et al. (2015a). Both jugal (red) and quadratojugal (blue) became slender in basal

birds with respect to their dinosaurian relatives; the caudoventral (green) and the squamosal processes of the quadratojugal were sequentially reduced early in avian history, and eventually the jugal and quadratojugal were fused in more advanced birds.

embryonic development, for example, 11–13 days of incubation in *Anas platyrhynchos* (Aves: Anseriformes) and *Meleagris gallopavo* (Aves: Galliformes; Maxwell, 2008a,b), eight days of incubation in *Coturnix japonica* (Aves: Galliformes; Nakane and Tsudzuki, 1999). The fusion between the bony jugal and quadratojugal takes place prior to hatching, for example, around 15 days of incubation in *Sterna hirundo* (Aves: Charadriiformes; Simonetta, 1960), and the suture between those two bones are invisible in adult. The jugal bar forms the ventral boundary of the orbit. Rostrally, it is articulated or more commonly fused with the maxilla, and caudally with the quadrate (Simonetta, 1960; Livezey and Zusi, 2006; Fig. 1).

DISCUSSION

Despite that numerous fossil birds come to light over the last two decades, the evolutionary pathways of cranial morphologies of basal birds can only be pieced

together from temporally and taxonomically sparse materials. The available fossil evidences show that numerous modifications took place early in avian evolution, many of which contribute to the refinement of the cranial kinesis (Chiappe et al., 1999; O'Connor and Chiappe, 2011; Wang et al., 2016). Observations of jugal and quadratojugal in basal birds and their closest relatives in present work allow us to arrive at some conclusions about how the massive, strap-like jugal and quadratojugal in non-avian dinosaurs were transformed to the delicate jugal bar in living birds. In dromaeosaurids and some other non-avian dinosaurs, the quadratojugal is shaped as an inverted T element with elongated caudoventral, squamosal, and jugal processes (Figs. 2 and 3). The squamosal process contacts the postorbital and thus separates the infratemporal fenestra from the quadrate foreman (Figs. 2A, 3A, and 9). The caudoventral process articulates with the quadrate, which together enclose the ventral boundary of the quadrate foramen. The quadratojugal in basal birds changed

substantially in morphology relative to that of dromaeosaurids and oviraptorosaurs. The most conspicuous modification is the absence of the caudoventral process in all basal birds, for example, *Archaeopteryx*, Sapeornithiformes, Enantiornithes, and Ornithuromorpha (Figs. (4 and 9)–). Although retained, the squamosal process in basal birds is heavily reduced, which likely fails to reach the squamosal (Fig. 9). Therefore, the quadrate foramen is confluent with the infratemporal fenestra. In living birds, before ankylosed with the jugal, the quadratojugal is a short rod-like element without the squamosal process. All these observations reveal that reduction of the caudoventral process took place prior to the reduction of the squamosal process in early bird evolution.

In most non-avian dinosaurs such as dromaeosaurids and oviraptorosaurs, the jugal is massive and strap-like, with prominent postorbital and quadratojugal processes at its caudal end (Figs. 2 and 3). The postorbital process projects dorsocaudally to contact the jugal process of the postorbital, rendering the orbit fully isolated from the infratemporal fenestra (Figs. (2 and 3), and 9). The caudal end of the jugal in non-ornithothoracine birds is also bifurcated, but the postorbital process is considerably short, compared to the state in dromaeosaurids and oviraptorosaurs. Except for *C. sanctus* in which the jugal contacts the postorbital directly (Martin et al., 1998; Chiappe et al., 1999), those two bones were probably connected indirectly by ligament in other basal birds, for example, *Archaeopteryx*, enantiornithines, and ornithuromorphs (Elzanowski and Wellnhofer, 1996; Elzanowski, 2002; O'Connor and Chiappe, 2011; Fig. 9). Therefore, the infratemporal fenestra had already been confluent with the orbit in those early birds. Within Enantiornithes, the jugal is forked caudally except for *P. dapingfangensis*, *B. guoi*, and *C. yandica*, in which the caudal end of the jugal is unforked (Figs. 6B and 7). Only one ornithuromorph taxon *S. lii* has a caudally forked jugal as in enantiornithines (Fig. 8A). All these observations indicate that the unforked morphotype of jugal occurred after the origin of Ornithothoraces, and that such derived morphology occurred in parallel among independent lineages of Enantiornithes and Ornithuromorpha (Wang et al., 2016; Fig. 9).

The modifications in jugal and quadratojugal make the postorbital region light and flexible in basal birds. Living birds are distinguished from other tetrapods in having a highly kinetic skull in which the upper jaw can move relative to the braincase (Bock, 1964; Zusi, 1993). Such avian cranial kinesis involves the free movements of the jugal bar, quadrate and palate; when the quadrates rotates cranially and dorsally, the jugal bar, acting as a lever, can be pushed rostrally and dorsally, which in turn enables the beak to be elevated or depressed relative to the cranium (Bock, 1964; Zusi, 1984, 1993; Fig. 1B). This unique property is evolved at the expense of losing several bones and processes, among which are the postorbital, the postorbital process of the jugal, the squamosal process of the quadratojugal and the ectopterygoid. Obviously, losing these elements could lighten the skull and enlarge the orbit by fusion with the temporal fenestra (housing large eyes and enhanced visual capability); on the other hand, the presence of jugal-postorbital and the quadratojugal-squamosal contacts would otherwise severely reduce or even prevent any degree of kinesis (the movement of the jugal is restricted

by its contact with the postorbital). Therefore, the observed modifications in jugal and quadratojugal among basal birds reveal that the refinement for cranial kinesis took place early in bird history. Meanwhile, it is also likely that the evolution of cranial kinesis represents an exadaptation of the reduction of cranial elements under the selective pressure of the reduction of body weight and/or enlargement of the orbit. The modified skeletal morphologies in turn change their articulations with other elements, which also contribute to the cranial kinesis. However, the typical two-dimensional preservations of the quadrate and quadratojugal in most early birds hinder our understanding about how those articulations changed (or not) during their early history. Despite that, the lacrimal becomes slender in early birds than in non-avian dinosaurs, it still articulates with the jugal through the suture joint, the same way as in non-avian dinosaurs, which impairs the movement of the rostrum. The absence of lacrimal-jugal articulation appears to happen relatively later in bird evolution, given that this bony contact is still present in *Hesperornis* (Chiappe et al., 1999), the closest relative of crown birds. The fusion of quadratojugal and jugal would represent another evolutionary novelty that further increases such kinesis by allowing the jugal bar to move rostrocaudally as a single unit rather two interdigitating components. Unfortunately, little is known about when and how such fusion occurred due to the lack of fossil materials with adequate preservation, which would further advance our knowledge about the evolution of jugal bar of modern birds.

ACKNOWLEDGEMENTS

The authors thank Jie Zhang for photographs and Yutong Li for fossil preparation. They are grateful to Xing Xu and Oliver Rauhut for kindly sharing photographs of *Linheraptor exquisitus* and the Munich specimen of *Archaeopteryx*. They thank Zhonghe Zhou and Corwin Sullivan for discussion. They are grateful to two anonymous reviewers for their constructive comments on this manuscript. They thank Qian Wang and Paul Dechow for inviting us to participate in this special issue.

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