

# Cranial osteology of the Early Cretaceous *Sapeornis chaoyangensis* (Aves: Pygostylia)

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## ARTICLE INFO

### Article history:

Received 5 November 2019

Received in revised form

5 April 2020

Accepted in revised form 29 April 2020

Available online 12 May 2020

### Keywords:

*Sapeornis*

Cranial evolution

Jehol biota

Aves

## ABSTRACT

We describe the detailed cranial osteology of *Sapeornis chaoyangensis* based on information from previously described specimens and IVPP V19058, a specimen that was recently reported with regards to the palatal elements but not fully described. The skull in this specimen is entirely preserved in disarticulation, providing the most comprehensive glimpse into the morphology of the cranial bones and their articulations for this taxon. Based on the new information extracted from this specimen, we revise some interpretations of cranial elements in previously published *Sapeornis* specimens and provide a comprehensive description of the cranial osteology for this basal pygostylian. The results of this study demonstrate that the postorbital bar, jugal bar, nasal, quadrate, and palate in *Sapeornis* show the pleiomorphic rigid articulations among birds. The comparison of cranial features across Paraves suggests that major cranial modifications evolved at the base of Ornithothoraces, and primarily in the ornithur-omorph lineage.

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## 1. Introduction

During the evolution from non-avian dinosaurs towards crown birds, cranial morphology underwent a number of important transformations, such as the reduction of the circumorbital elements and related articulations, shortening of the face with enlargement of the braincase, reduction of teeth and appearance of the horny beak (Bhullar et al., 2016). These modifications provided birds with many evolutionary advantages, such as reducing the weight of the cranium, replacing the function of the forelimbs in food acquisition, and facilitating an increase in the brain size. The evolution of the beak structure has been heavily studied (Louchart and Viriot, 2011; Meredith et al., 2014; Wang et al., 2017c; Wang et al., 2017d), whereas other cranial transformations, from the rigid and largely akinetic skull of non-avian dinosaurs, to the light and flexible avian skull, are less well understood (Chiappe and Witmer, 2002; O'Connor and Chiappe, 2011; Zhou et al., 2013; Field et al., 2018).

The unparalleled Jehol Biota includes the world's most diverse known Cretaceous avifauna, revealing the second oldest record of fossil birds, which is exceeded in age only by *Archaeopteryx* from the Late Jurassic Solnhofen Limestone of Germany (Zhou, 2014). Although an unprecedented amount of data has been gleaned from the Jehol Biota regarding the origin and early diversification of Aves, limited details on cranial morphology have been revealed compared to that of postcranial elements. This is because the fragile cranial bones of birds were typically crushed during the fossilization process of the lacustrine Jehol deposits, which generally preserve fossils in two-dimensions. Consequently, the cranial morphology of individual avian taxa from Jehol Biota can only be fully reconstructed through a combination of information from multiple specimens. However, many species and genera of Early Cretaceous birds are only known from a single specimen e.g., *Jinguoortis*, *Longirostravis*, *Eogranivora*, *Yixianornis*, so that a comprehensive understanding of their cranial morphology is impossible at this time (Zhou and Zhang, 2001; Hou et al., 2004; Wang et al., 2018; Zheng et al., 2018). As a result, with the exceptions of *Archaeopteryx* (Elzanowski and Wellnhofer, 1996; Witmer, 2004; Alonso et al., 2004; Mayr et al., 2005, 2007; Rauhut, 2014), *Confuciusornis* (Peters and Ji, 1998; Chiappe et al., 1999; Hou et al.,

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1999; Rauhut et al., 2018; Wang et al., 2019) and a small number of enantiornithines (O'Connor and Chiappe, 2011), few attempts have been made to provide a comprehensive description of the cranial morphology of an Early Cretaceous avian taxon, and the skull remains poorly known even for some important basal lineages such as the Jeholornithiformes and Sapeornithiformes.

The Sapeornithiformes is a stem clade of Early Cretaceous pygostylians, commonly resolved in phylogenetic analyses as the sister taxon to the Ornithothoraces (Wang and Zhou, 2019; Wang et al., 2019). Eleven specimens have been described in detail to date with an additionally 90+ collection being reported without detailed descriptions (Zhang et al., 2014). All specimens come from the Jehol Group in northeastern China, known from the 125 Ma Yixian Formation and the 120 Ma Jiufotang Formation, with a majority of specimens coming from the latter (Swisher et al., 2002; He et al., 2004; Zhou, 2014). Several genera and species have been described (Zhou and Zhang, 2002a; Yuan, 2005; Yuan, 2008; Provini et al., 2009; Hu et al., 2010); however, it is now widely accepted all specimens belong to a single species, *Sapeornis chaoyangensis* (Gao et al., 2012). Among previously described specimens, the skull is best preserved and laterally exposed in articulation in LPM-B00018 (Hu et al., 2010) and STM 16–18 (Wang et al., 2017d). The medial surface of the unfused mandibles is also exposed in STM 16–18. Based on the large number of specimens housed in Shandong Tianyu Museum of Nature, Shandong, China (STM), it has been confirmed that the dentition of *Sapeornis* comprises four premaxillary teeth, three maxillary teeth and two tiny teeth in the dentary that are often lost during taphonomy (Wang et al., 2017d). However, another study considers the absence of dentary teeth to be a product of ontogeny based on other individual specimens of *Sapeornis* (Wang et al., 2017c). More evidence is needed to clarify this in the future (O'Connor, 2019).

Here we provide detailed cranial osteological information for *Sapeornis chaoyangensis* based on the review of previously described specimens and new information from a recently reported specimen IVPP V19058 (Fig. 1A; Hu et al., 2019). This specimen preserves the only known complete vomer among Early Cretaceous birds and was included in a recent 3D geometric morphometric analysis of paravian vomers. The results suggested that efficient cranial kinesis did not appear until relatively late in avian evolution with the appearance of neognaths, and that this feature may partly explain the extraordinary success of this clade (Hu et al., 2019). Except for the vomer, IVPP V19058 was not described in detail in that study (Hu et al., 2019). However, the disarticulated cranial elements preserved in this specimen not only reveals the morphology of the palatal elements, but also the complete morphology of individual cranial bones and their articular surfaces. Here, based on the new information from IVPP V19058, we revise previous interpretations in some articulated specimens. Combining information from seven key specimens (see Material and methods), we provide a comprehensive description of the skull of *Sapeornis* in lateral, ventral and medial (only mandible) views. The cumulative data shows that the skull of *Sapeornis* was unmodified with respect to most characters, largely retaining the plesiomorphic condition present in non-avian dinosaurs. Compared to the plesiomorphic condition in non-ornithothoracine stem avian lineages, more derived cranial features appeared at the base of the Ornithothoraces, and these were less specialised in the Enantiornithes relative to contemporary ornithuromorphs.

## 2. Material and methods

IVPP V19058 was collected from the Sihedang locality of the Lower Cretaceous, Yixian Formation in Lingyuan, Liaoning province (Fig. 2), and was assigned to *Sapeornis chaoyangensis* on the basis of

both cranial and postcranial characters (Hu et al., 2019). Other key specimens of *Sapeornis* involved in this study include IVPP V13275 (Zhou and Zhang, 2003), LPM B00018 (Hu et al., 2010), DNHM-D3078 (Gao et al., 2012), HGM 41HIII0405 (Pu et al., 2013) and STM 16–18 (Wang et al., 2017d).

Anatomical terminology primarily follows Baumel and Witmer (1993), using the English equivalents of the latinized osteological features.

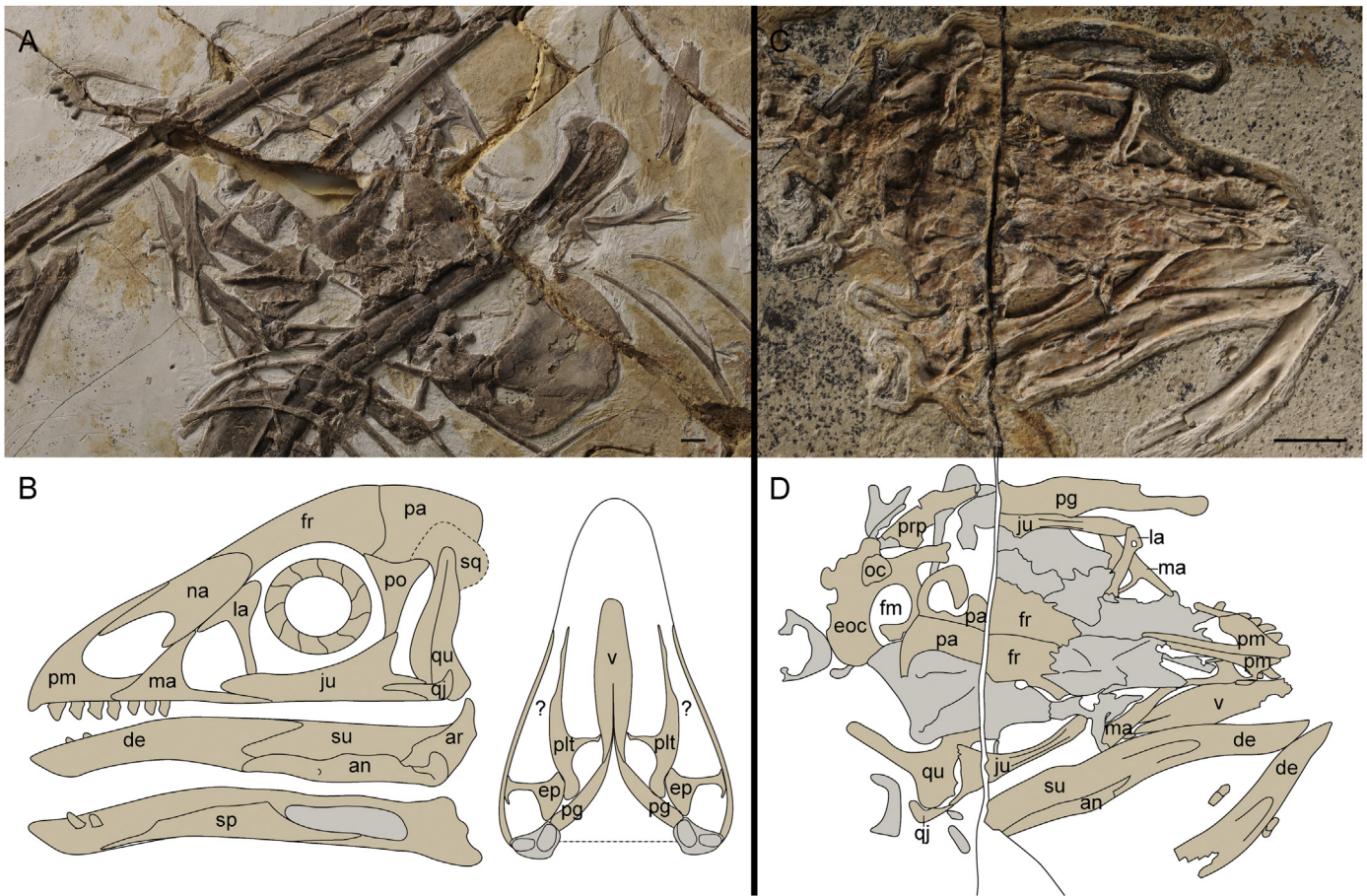
Institutional Abbreviations: DNHM, Dalian Natural History Museum, Dalian, Liaoning, China; HGM, Henan Geological Museum, Zhengzhou, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; LPM, Liaoning Paleontology Museum, Shenyang, Liaoning, China; STM, Shandong Tianyu Museum of Nature, Shandong, China.

## 3. Cranial osteology of *Sapeornis*

### 3.1. Skull in lateral

**Premaxilla.** The premaxilla is well preserved in lateral view in IVPP V19058 (left), STM 16–18 (left) and 41HIII0405 (right) (Fig. 3B; Fig. 4A, B). In these specimens, the rostral most tip of the robust premaxillary corpus is edentulous, forming a bluntly tapered and downturned bony projection (Wang et al., 2017d). This abrupt edentulous downturned projection in the tip of premaxilla is unique among Mesozoic birds, as the edentulous premaxillae in the Confuciusornithiformes (Wang et al., 2019) and Jeholornithiformes are gradually downturned throughout the ventral margin. The frontal process (or nasal process) is relatively short and sharply tapered caudally. Visible in IVPP V19058, a shallow groove is present along the caudodorsal margin of the premaxillary process of nasal for articulation with the premaxilla, indicating that the frontal process of the premaxilla extends caudally to just beyond the base of the premaxillary process (Fig. 3D), far from reaching the frontal as these processes do in neornithines and Confuciusornithiformes (Wang et al., 2019), as well as in some enantiornithines e.g. *Zhouornis* (Zhang et al., 2013). The angle between the frontal and maxillary process defines a cranium that is dorsoventrally deep (approximately 45°, Fig. 1B), similar to the condition in oviraptorosaurs (Xu et al., 2002a) and deeper than in other basal taxa e.g., *Archaeopteryx* (Rauhut et al., 2018). The maxillary process is short and the caudal 1/3 part is strongly inflected dorsally, so that the ventral surface articulates with the cranial portion of the premaxillary ramus of the maxilla. The premaxillary corpus is marked with tiny nutrient foramina, best preserved in STM 16–18 and 41HIII0405 (Fig. 4B; Wang et al., 2017d). Four teeth are present in the premaxilla, typical of the plesiomorphic condition in most Early Cretaceous toothed birds inherited from paravians (O'Connor and Chiappe, 2011); they are straight and spade-shaped, strongly expanded at the base of the crown as in previous descriptions (Fig. 4C, D; Zhou and Zhang, 2003; Hu et al., 2010; Gao et al., 2012), different from the morphology in enantiornithines (O'Connor, 2019). The teeth become reduced in size distally. Narrow grooves are present on the lingual surface (visible in STM 16–18, Fig. 4C; Wang et al., 2017d), and relatively shorter and wider grooves are present on the labial surface near the expanded base (visible in IVPP V19058, Fig. 4D).

**Maxilla.** The maxilla is complete in STM 16–18 (left) and the rostral half is preserved in LPM B00018 (right). It is relatively more slender than the remarkably robust and well developed jugal. The dorsal margin of the premaxillary process of the maxilla articulates with the ventral surface of the caudodorsally inflected maxillary process of the premaxilla (Wang et al., 2017d). The jugal process is more slender and much longer than the premaxillary process. The broad triangular ascending process (or nasal process) tapers



**Fig. 1.** A. Photograph of the skull of *Sapeornis* IVPP V19058 (following Hu et al., 2019); B. Cranial reconstructions of *Sapeornis* (lateral cranium, lateral mandible, medial mandible and ventral cranium, with crushed parts in grey, unknown areas in dashed lines, and '?' indicates the uncertain jugal process of palatine (following Hu et al., 2019); C. Photograph and D. Revised camera lucida drawing of the skull of *Sapeornis* IVPP V13275. Abbreviations: an, angular; ar, articular; de, dentary; eoc, exoccipital; ep, ectopterygoid; fm, foramen magnum; fr, frontal; hy, hyoid; ju, jugal; la, lacrimal; ma, maxilla; na, nasal; oc, occipital condyle; pa, parietal; pm, premaxilla; pg, pterygoid; po, postorbital; prp, paraoccipital process; qj, quadratojugal; qu, quadrate; sp, splenial; sq, squamosal; su, surangular; v, vomer. Scale bar equals 5 mm.

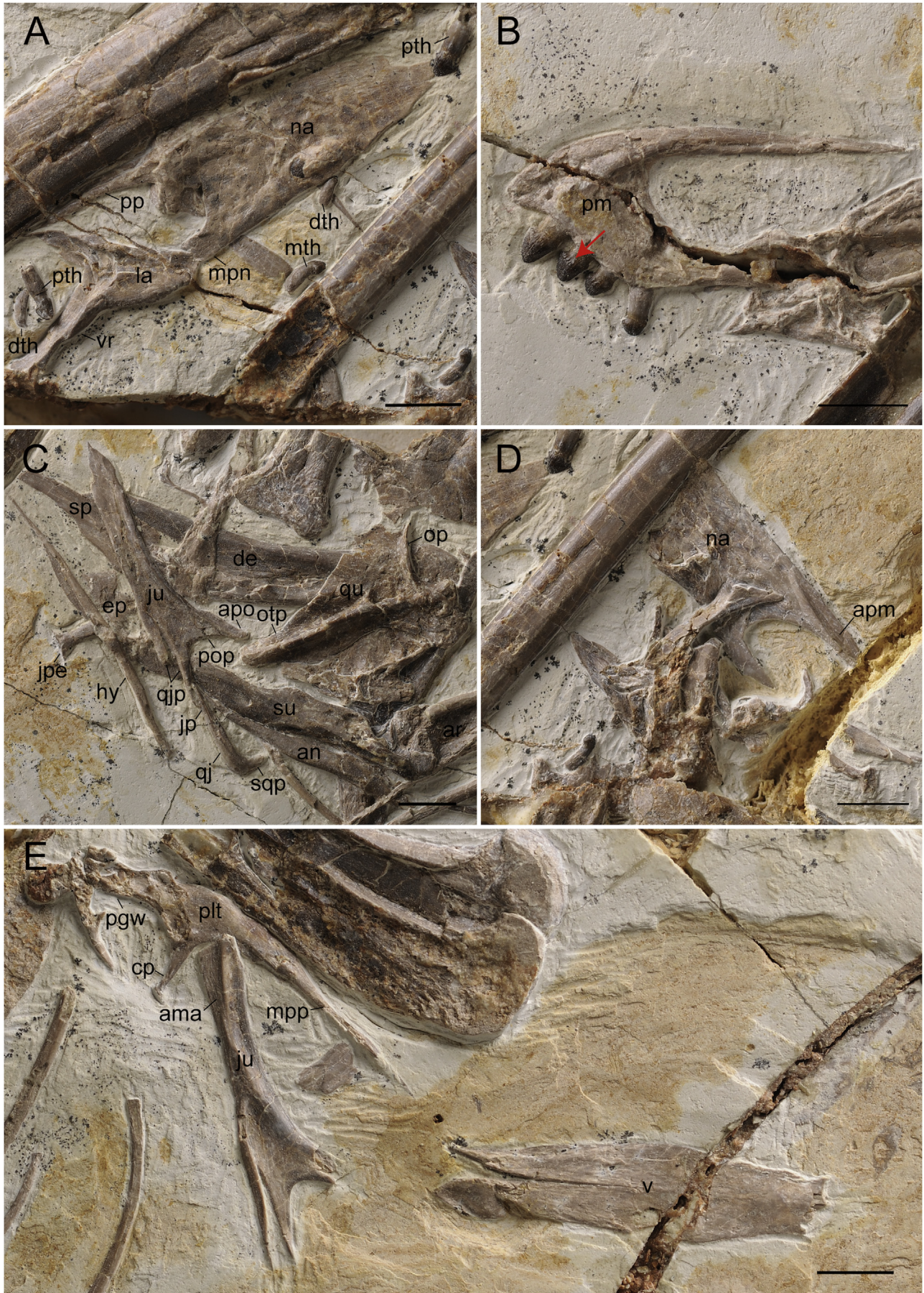


**Fig. 2.** Map of Liaoning, China showing the Sihedang locality of *Sapeornis* IVPP V19058 (indicated by the diamond, revised from Wang et al., 2017d).

caudodorsally and the distal one thirds of the dorsal margin contacts the nasal. It is equivocal if it contacts the lacrimal, whereas this process is forked distally in some enantiornithines, e.g., *Pengornis*, forming a tight contact with the ventral ramus of the

lacrimal (Zhou et al., 2008; O'Connor and Chiappe, 2011). The cranioventral portion of the maxillary corpus possesses several nutrient foramina, similar to, but larger than those in the premaxilla (Wang et al., 2017d). Three teeth are present in the maxilla, with a similar shape to the premaxillary teeth but nearly half the size of the latter (Pu et al., 2013; Wang et al., 2017d). No grooves or other forms of enamel ornamentation are present on the maxillary teeth on either the lingual or labial surface (Wang et al., 2017d). No maxillary fenestra was developed, and no antorbital fossa like that in *Archaeopteryx* or *Pengornis* appears to excavate the antorbital fenestra observed from the current published specimens (Mayr et al., 2007; Zhou et al., 2008; O'Connor and Chiappe, 2011; Mayr, 2018; Rauhut et al., 2018).

**Nasal.** The nasal is best preserved in IVPP V19058 (left and right) and 41HIII0405 (right) (Fig. 3A, D; Fig. 4G, H). Both the premaxillary and maxillary processes are tapered rostrally, and the latter is shorter than half of the former. The nasal corpus is large and mediolaterally broad. The rostral margin defined by the premaxillary process and maxillary process is deeply concaved. The incomplete morphology observed in STM 16–18 is probably due to breakage of the premaxillary process (Wang et al., 2017d). The short nature of the maxillary process strongly suggests that it did not contact the premaxilla, so that the maxilla participates in forming the caudal margin of the external nares, as in *Archaeopteryx* (Rauhut, 2014), most enantiornithines e.g. *Pengornis* (Zhou et al.,



**Fig. 3.** Details of the cranial elements of *Sapeornis* IVPP V19058. Abbreviations: ama, articular facet for maxilla; an, angular; apm, articular facet for premaxilla; apo, articular facet for postorbital; cp, choanal process; de, dentary; dth, dentary tooth; ep, ectopterygoid; hy, hyoid; jp, jugal process of quadratojugal; jpe, jugal process of ectopterygoid; ju, jugal; la,

2008) and some ornithuromorphs e.g. *Schizooura* (Zhou et al., 2012). The distal margin of the nasal is convex and articulates with the cranial margin of the frontal.

**Lacrimal.** A complete lacrimal is preserved in disarticulation near the nasal in IVPP V19058 (right, Fig. 3A, Fig. 4I). This element is also preserved in articulation with the jugal in LPM B00018 (right, Fig. 4J) and partially preserved (the ventral ramus only) in STM 16–18 (left). Based on the information from IVPP V19058 and LPM B00018, and observations from other *Sapeornis* specimens housed in STM, we re-identify the lacrimal, described originally in 41HIII0405 (Pu et al., 2013), as the postorbital (Fig. 5A). The lacrimal of *Sapeornis* is robust and T-shaped as in most non-avian maniraptorans (e.g., *Velociraptor*), with a sharply tapered rostradorsal ramus and a bluntly tapered caudodorsal ramus, similar to that of *Archaeopteryx* and some enantiornithines like *Pengornis*, *Parapengornis* and *Pterygornis* in overall shape (Mayr et al., 2005; Zhou et al., 2008; Hu et al., 2015; Wang et al., 2016a; Wang et al., 2017a). The rostradorsal ramus is rostroventrally inclined and the caudodorsal ramus is caudodorsally oriented. The rostrally inclined dorsal margin is straight, lacking the concavity present in *Pengornis* and *Parabohaiornis* (Zhou et al., 2008; Wang et al., 2014). The ventral ramus is robust with a slightly expanded ventral surface distally for articulation with the jugal. The rostralateral surface is excavated and the caudal margin of this excavation defines a ridge on the lateral surface (visible in IVPP V19058, Fig. 4I), which is also observed in *Archaeopteryx*, *Pengornis*, enantiornithine LP 4450 and *Zhouornis* (O'Connor and Chiappe, 2011; Zhang et al., 2014; Rauhut, 2018).

**Jugal.** The jugal and quadratojugal are well preserved in lateral view in IVPP V19058 (left, Fig. 3C), STM 16–18 (left, Fig. 4E), LPM B00018 (right, Fig. 4F), and 41HIII0405 (right). The disarticulated right jugal in IVPP V19058 is the only one that is exposed in medial view (right, Fig. 3E). The jugal of *Sapeornis* is robust even compared to that of *Archaeopteryx*, and closer to the plesiomorphic condition in non-avian dinosaurs (Fig. 6). The rostral end tapers to contact the maxilla ventrally. Visible in the medially preserved caudal half of the jugal in IVPP V19058, the articular facet for the maxilla of the jugal extends to nearly reach the base of the postorbital process (Fig. 3E), indicating tight dorso-ventral and medio-lateral articulations between the maxilla and the jugal. The medial surface of the caudal portion is concave, and the strongest concavity appears in the rostral base of the postorbital process. The caudal end forms a quadratojugal process that is bifurcated to form two delicate and sharply tapered processes. The deep notch defined by these two caudally oriented processes accepts the jugal process of the quadratojugal (Wang et al., 2017d). The postorbital process of the jugal is triangular with a broad base, caudodorsally oriented and tapered distally (Hu et al., 2010). In IVPP V19058, a shallow groove is visible extending along the caudal half of the dorsal margin of this process (Fig. 3C), which is identified as the articular surface for the postorbital, confirming the existence of a complete postorbital bar in this taxon. The dorsal margin of the cranial portion of the jugal is declined ventrally, inferred to represent the articulation with the ventral ramus of the lacrimal, such that the jugal partly forms the caudoventral margin of the antorbital fenestra similar to the dromaeosaurids (Barsbold and Osmolska, 1999).

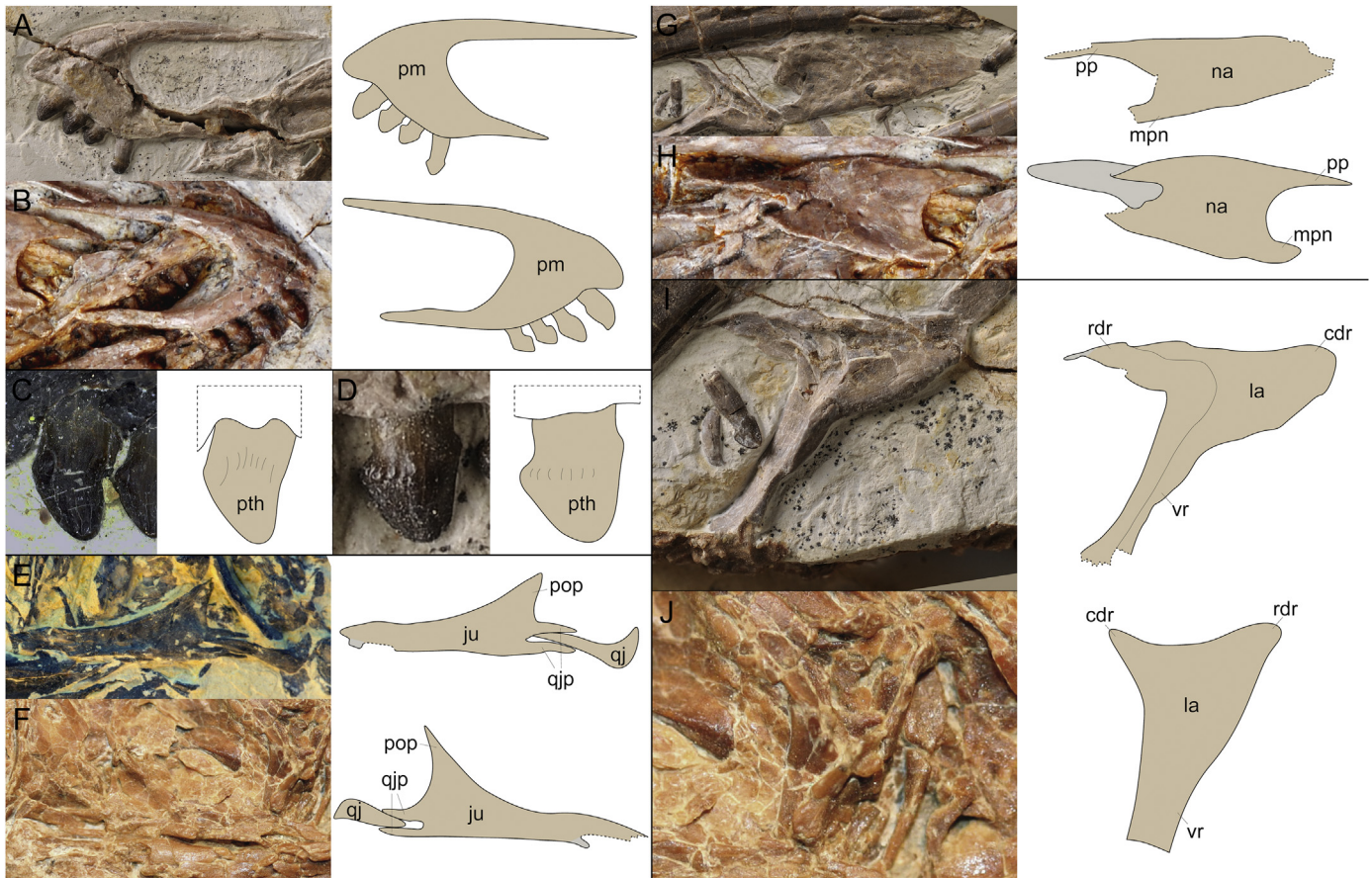
**Quadratojugal.** The L-shaped quadratojugal is preserved in IVPP V19058 (left, Fig. 3C), STM 16–18 (left, Fig. 4E), 41HIII0405 (right), DNHM-D3078 (left), IVPP V13275 (right) and LPM B00018

(right, Fig. 4F). The elements originally described as the quadratojugal in 41HIII0405 and IVPP V13275 are reinterpreted as the quadrate according to their shape and size (Pu et al., 2013; Zhou and Zhang, 2003) (Fig. 1D). As described in Wang et al. (2017d), the jugal process of the quadratojugal is elongated and sharply tapered rostrally, inserting into the deep notch in the forked quadratojugal process of the jugal to form a tight articulation. The squamosal process bluntly tapers dorsally and is much shorter, being less than one-third the length of the jugal process, prohibiting its contact with the squamosal. The relative length of the squamosal process is shorter in *Sapeornis* than in *Archaeopteryx* (Rauhut, 2014), but similar to that of the enantiornithines *Rapaxavis pani* (O'Connor et al., 2011) and *Cruralispennia multidonta* (Wang et al., 2017b).

**Postorbital.** The postorbital is preserved in LPM B00018 (right, Fig. 5A) and 41HIII0405 (right, Fig. 5B), originally identified as the lacrimal in Pu et al., 2013). It is a large, broad, triangular and plate-like bone with slightly concave margins, similar to the morphology in non-avian dinosaurs (Xu and Wu, 2001), and more robust than that in *Archaeopteryx* (Rauhut et al., 2018) (Fig. 6). The squamosal (caudodorsal) and frontal (craniodorsal) processes are nearly in the same length, which are slightly shorter than the jugal process. All the processes are tapered sharply in the distal ends. The postorbital is only preserved in the 12th specimen of *Archaeopteryx* (Rauhut et al., 2018): the triradiate processes of this element are slightly more slender than that of *Sapeornis* and non-avian dinosaurs, resembling the condition in the enantiornithine juvenile LP4450. As in *Sapeornis*, the articular surface on the postorbital process of the jugal preserved in the 10th (Thermopolis) specimen of *Archaeopteryx* also indicates that a complete postorbital bar was present in this stem-most bird (Rauhut, 2014). The postorbital is also well-developed in other basal pygostylian lineages, such as *Confuciusornis* (Peters and Ji, 1998; Wang et al., 2019).

**Quadrate.** The quadrate is preserved *in situ* in LPM B00018 (right, Fig. 5F) and dislocated in IVPP V19058 (left, Fig. 3C, Fig. 5E). Similar to *Archaeopteryx*, the quadrate is overall broad and robust. The orbital process is broadly triangular in shape with the rostral tip directed cranioventrally, similar to the condition in enantiornithines, e.g., *Zhouornis* and *Pterygornis* (Zhang et al., 2013; Wang et al., 2016a), but different from the extruded morphology of this process in modern birds and Late Cretaceous *Ichthyornis* (Elzanowski and Stidham, 2010; Field et al., 2018). The single headed otic process is nearly perpendicular to the ventral margin of the corpus, and dorsoventrally elongated compared to the typical stout condition in modern birds and *Ichthyornis* (Elzanowski and Stidham, 2010; Field et al., 2018). A longitudinal ridge is developed from the distal end of the otic process and extends to the ventral margin of the corpus (Fig. 5E), also similar to that in *Zhouornis* and *Pterygornis* (Zhang et al., 2013; Wang et al., 2016a). The mandibular process of the quadrate projects caudally and appears to be bicondylar, with the medial condyle slightly larger than the lateral one. No pneumatic foramen is observed in the quadrate of *Sapeornis*, whereas it is present in modern birds and *Ichthyornis* (Elzanowski and Stidham, 2010; Field et al., 2018).

**Frontal.** The frontals are preserved in dorsal view in IVPP V19058 and DNHM-D3078, and in dorsolateral view in STM 16–18 and 41HIII0405. The rostral half is narrow and the caudal half is expanded (Fig. 1A), as in other Mesozoic birds (O'Connor and Chiappe, 2011). The medial margin is straight, and the two frontals remain unfused throughout ontogeny from early subadult STM



**Fig. 4.** Detailed paragraphs and lucida drawings of selected cranial elements in *Sapeornis* specimens, with crushed parts in grey and broken margin in dashed lines: premaxilla in IVPP V19058 (A) and HGM 41HIII0405 (B); premaxillary tooth in STM 16–18 (C, lingual surface) and IVPP V19058 (D, labial surface); jugal and quadratojugal in STM 16–18 (E) and LPM-B00018 (F); nasal in IVPP V19058 (G) and HGM 41HIII0405 (H); and lacrimal in IVPP V19058 (I) and LPM-B00018 (J). Abbreviations: cdr. caudodorsal ramus of lacrimal; pth. premaxillary tooth; rdr. rostradorsal ramus of lacrimal; other abbreviations see Fig. 1 and Fig. 3.

16–18 to adult IVPP V13275. However, the frontals contact each other much more tightly to form a longitudinal suture in IVPP V13275 compared to the completely free condition in sub-adult specimens (Fig. 1D). The ventrolateral margin is strongly concave, defining the dorsal margin of the orbit. The expanded caudal portion is obviously vaulted in IVPP V19058 with a slightly convex caudal margin to contact the parietals.

**Parietal.** The parietals are best preserved in IVPP V13275 (Fig. 1C, D). They have an overall rectangular shape with rounded margins and are smaller than the frontals (Zhou and Zhang, 2003). Similar to the condition in the frontals, the left and right parietals are not entirely fused but tightly contact with each other to form a suture in the probable adult IVPP V13275. The whole body of the parietal is vaulted such that the external surface is convex. This convexity reaches strongest near the caudal margin. The rounded caudal margin is convex caudally, with the area near the interparietal suture slightly concave.

**Occipital bones.** The occipital elements are partially preserved in STM 16–18 and IVPP V13275 (Fig. 1C, D), in which they reveal limited information due to poor preservation. The exoccipital is perforated by a small circular foramen in STM 16–18 (Wang et al., 2017d) probably for one of the cranial nerves. Part of the exoccipital contributes to the occipital condyle, as in *Shenqiornis* (Wang et al., 2010; O'Connor and Chiappe, 2011).

**Sclerotic ring.** The sclerotic ring is partially preserved in DNHM-D3078 (right, Fig. 5H). The ossicles are narrow such that the inner diameter of the ring is only slightly smaller than the outer

diameter. The sclerotic bones are not fused, but tightly overlap each other. One isolated ossicle reveals a rounded rectangular shape, with the outer margin approximately half the length of the margin that contacts the adjacent ossicle. The exact number of included sclerotic ossicles cannot be determined, but it could be inferred that the ring was formed by more than 11 ossicles based on information from DNHM-D3078.

### 3.2. Palatal elements

Palatal elements are preserved in IVPP V19058 (vomer and potential palatine), STM 16–18 (vomer) and IVPP V13275 (vomer and potential pterygoid). They were previously well described in Hu et al. (2019) and are expanded here to provide more details and comparisons.

**Vomer.** The vomer is completely preserved in disarticulation in IVPP V19058 (Fig. 3E, Hu et al., 2019) and partially preserved *in situ* in STM 16–18 and IVPP V13275 (originally described as the splenial in Zhou and Zhang, 2003) (Fig. 1C, D). The two elements are fused in their cranial portion and strongly dorsoventrally compressed forming a long, plate-like morphology (Hu et al., 2019). This morphology indicates a dorsoventrally overlapping contact with the maxillae, as in non-avian dinosaurs and paleognathous birds (Tsuihiji et al., 2014; Hu et al., 2019). The lateral margin is weakly convex near the point where the fused cranial portion diverges into two unfused caudal flanges. A triangular leaf-like caudodorsal process is present on the dorsal surface of the distal end of each



**Fig. 5.** Detailed paragraphs and lucida drawings of selected cranial elements in *Sapeornis* specimens, with crushed parts in grey and broken margin in dashed lines: postorbital in HGM 41HIII0405 (A) and LPM-B00018 (B); dentary in STM 16–18 (C) and STM 15–7 (D); quadrate in IVPP V19058 (E) and LPM-B00018 (F); splenial in STM 16–18 (G); and scleral ring in DNHM-D3078 (H). Abbreviations: fpo, frontal process of postorbital; jpo, jugal process of postorbital; scl, scleral ring; spo, squamosal process of postorbital; other abbreviations see Fig. 1 and Fig. 3.

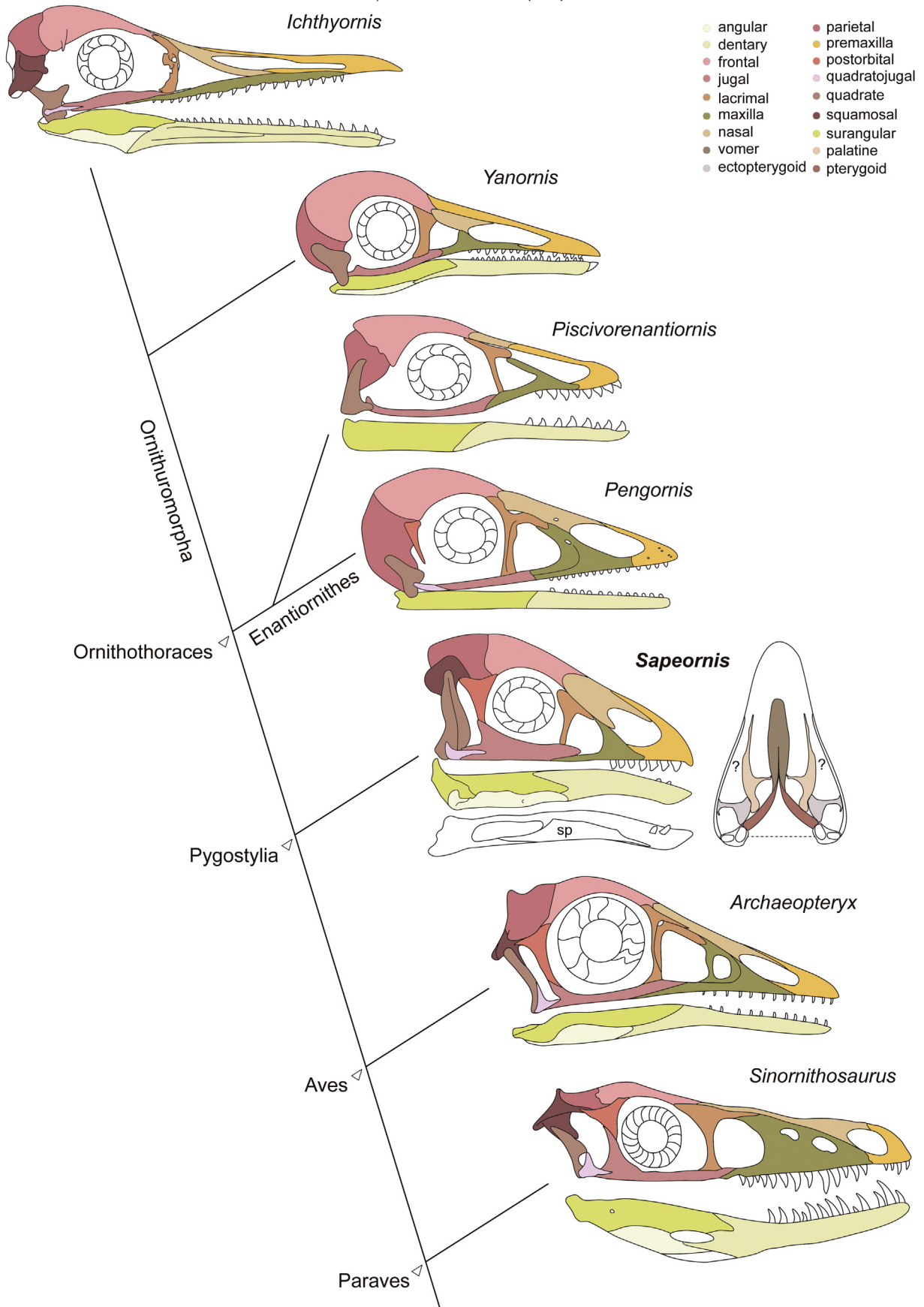
caudal flange, which are buried in the matrix and only visible through CT scanning data. This process is laterally compressed and interpreted as oriented at nearly a right angle to the main body of the vomer (Hu et al., 2019). The cranial end of this process is strongly tapered, and the medial surface has a well-defined concavity which presumably accommodates the parasphenoid rostrum (Hu et al., 2019).

**Palatine.** A slender bone preserved between the right jugal and humerus in IVPP V19058 is identified as the palatine (Fig. 3E, Hu et al., 2019). This probable palatine is avian in morphology, being triradiate with the jugal process absent, similar to *Hesperornis*, but different from the tetradactylate palatine present in non-avian dinosaurs (Fig. 7). The choanal process is hooked in *Archaeopteryx* and *Hesperornis*, contacting the vomer to enclose the choana, whereas it appears to be nearly straight in *Sapeornis*. Divided by the choanal process, one end of this element is much more slender and strongly tapered than the other end. Compared to the palatine morphology of modern birds, the slender portion of the palatine with the pointed end is most likely the maxillary process pointing

to the rostrum, and the short and blunt end is the pterygoid wing contacting with the pterygoid caudally (Fig. 1B; Fig. 3E; Hu et al., 2019).

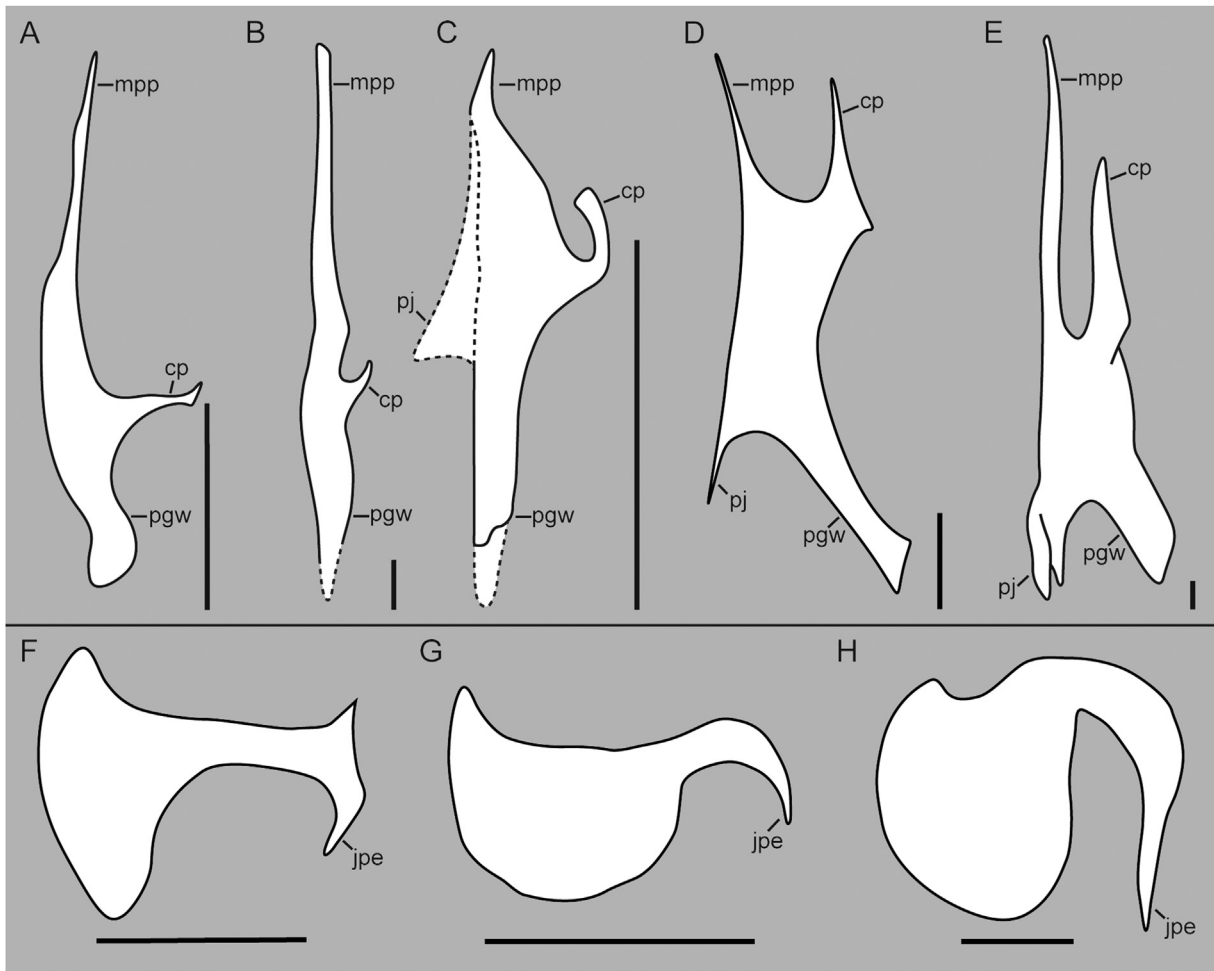
**Pterygoid.** An element tentatively identified as the pterygoid is preserved in IVPP V13275 (Fig. 1C, D; Hu et al., 2019). This element is strut like and more robust than the probable palatine. The slender rostral end is inferred to contact the parasphenoid rostrum, and possibly the caudodorsal process of the vomer as well (Fig. 1).

**Ectopterygoid.** The dislocated ectopterygoid preserved in IVPP V19058 is the only unequivocal evidence of this element among all the post-Jurassic birds (Hu et al., 2019), although it may also be present in *Confuciusornis* (Chiappe et al., 1999) (Fig. 7F). The overall shape of this element is similar to that in *Archaeopteryx* (Fig. 7G) and non-avian dinosaurs (Fig. 7H). However, the main body is laterally narrower with a sharply angled caudal margin, differing from the semicircular shape in *Archaeopteryx* and more rounded shape in non-avian theropods. The jugal process has a hooked distal end similar to that in *Archaeopteryx* and non-avian dinosaurs, but this process is relatively straighter in *Sapeornis* compared to the



**Fig. 6.** Comparisons of the skulls of selected Paraves: *Sinornithosaurus millenii* (modified from Xu and Wu, 2001), *Archaeopteryx lithographica* (modified from Elzanowski, 2001 and Rauhut, 2014), *Sapeornis chaoyangensis* (lateral cranium, lateral mandible, medial mandible, ventral cranium, followed Hu et al., 2019), *Pengornis houi* (modified from O'Connor and Chiappe, 2011), *Piscivorenantiornis inusitatus* (modified from Wang et al., 2016b), *Yanornis grabaui* and *Ichthyornis dispar* (followed Field et al., 2018). Abbreviations: ep. ectopterygoid; pg. pterygoid; plt. palatine; sp. splenial; sq. squamosal; v. vomer.





**Fig. 7.** Comparisons of palatines in A. *Sapeornis chaoyangensis*, IVPP V19058; B. *Hesperornis*; C. *Archaeopteryx* (the seventh skeleton); D. *Dromaeosaurus albertensis*; E. *Allosaurus*; and ectopterygoids in F. *Sapeornis chaoyangensis*, IVPP V19058; G. *Archaeopteryx* (the seventh skeleton); H. *Sinovenator changii* (B, C, E, G modified from [Elzanowski and Wellnhofer, 1996](#) and [Mayr et al., 2007](#); D modified from [Witmer, 1997](#) and [Tsujihi et al., 2014](#); H modified from [Yin et al., 2018](#)). Abbreviations: cp, choanal process; mpp, maxillary process of palatine; jpe, jugal process of ectopterygoid; pgw, pterygoid wing; pj, jugal process of palatine. Scale bar equals 1 cm in A–E and 5 mm in F–H.

latter. The hooked jugal process indicates that the ectopterygoid of *Sapeornis* maintains contact with the jugal as in the plesiomorphic non-avian dinosaurian condition ([Hu et al., 2019](#)).

### 3.3. Mandible

The mandible is well preserved in lateral view in LPM B00018, 41HIII0405, and IVPP V19058 ([Fig. 3C](#)), and in medial view in STM 16–18 ([Fig. 5C, G](#)). The dentary, surangular and angular are not fused with each other, with the sutures clearly observable in IVPP V19058.

The dentary is robust and not fused to form a mandibular symphysis. The corpus is remarkably downturned along the rostral half, which is unique in Early Cretaceous birds. The dentary in *Sapeornis* is forked caudally, similar to, but not as strongly as in confuciosornithids and neornithines ([Wang et al., 2019](#)). The dentary is unforked and slopes ventrally in most enantiornithines, with the exception of *Gobipteryx* ([Elzanowski, 1977](#); [O'Connor and Chiappe, 2011](#); [Wang and Zhou, 2017](#)). The surangular is robust and perforated by a small central foramen, with the cranial portion slightly tapered. Visible in IVPP V19058, the angular is thin and rod like. The caudal portion of the articular is strongly deflected dorsally.

The medial surface of the mandible is exposed in STM 16–18 ([Fig. 5C, G](#)), and related descriptions were provided in detail in [Wang et al. \(2017d\)](#): Meckel's groove extends to the level of the rostral-most tooth and is overlapped caudally by the splenial; the triangular splenial is tightly attached to the medial surface of the dentary; the dorsal margin of the splenial defines an obtuse angle with the tapered rostral and caudal wing; the rostral wing is dorsoventrally expanded near the apex of the dorsal margin and the caudal wing is concave dorsally ([Fig. 1B](#)), while the dorsal margins of both the rostral and caudal wings are concave or nearly straight in *Archaeopteryx* ([Elzanowski and Wellnhofer, 1996](#)) and the enantiornithines *Pterygornis dapingfangensis* ([Wang et al., 2017a](#)), *Piscivorenantiornis inusitatus* ([Wang and Zhou, 2017](#)), and *Junornis hou* ([Liu et al., 2017](#)).

The dentary dentition was also described in detail in [Wang et al. \(2017d\)](#) based on the medial exposed dentary of STM16–18: Two tiny dentary teeth are present preceded by three empty aveoli; these teeth are much smaller than and different from the premaxillary and maxillary teeth in shape; the dentary teeth are straight and peg-like, without the constriction at the base of the crown present in the premaxillary and maxillary teeth. Besides this, in IVPP V19058, several teeth preserved near the nasal are identified as the dislocated dentary teeth according to their shape

(Fig. 3A), supporting the existing hypothesis that these teeth have a loose contact with the dentary bone (Wang et al., 2017d).

#### 4. Discussion

*Sapeornis* has been described as typifying the 'mosaic evolution' that characterizes the early evolutionary stage of birds: its forelimbs have become highly derived with remarkably long wings and fused caudal vertebrae forms an abbreviated, neornithine-like pygostyle, whereas the skull retains mostly plesiomorphic features inherited from non-avian dinosaurs (Chiappe, 2007; Gao et al., 2012). In our detailed study of cranial morphology, several previously unknown features are identified to confirm the plesiomorphic and akinetic skull of *Sapeornis*.

The reduction of the postorbital bar (or infratemporal bar) and the resultant loss of the infratemporal fenestra is thought to be the key modification of the modern avian skull (Bhullar et al., 2016). The well-preserved articular facet for the postorbital in the jugal provides unequivocal evidence of a complete postorbital bar in *Sapeornis*. The similarity of the postorbital of *Sapeornis*, *Archaeopteryx* and *Confuciusornis* to the non-avian dinosaurs (Fig. 6), indicates that all the non-ornithuromorph lineages of early birds likely retained a plesiomorphic postorbital bar and diapsid skull inherited from their dinosaurian ancestors (Chiappe et al., 1999; Hou et al., 1999; Hu et al., 2010; Rauhut, 2014; Rauhut et al., 2018; Wang et al., 2019). In the Enantiornithes, the postorbital is still retained although strongly reduced in *Pengornis*, one of the basal-most enantiornithines (Zhou et al., 2008; O'Connor and Chiappe, 2011). Besides this, the jugal process of the postorbital remains elongate in Enantiornithine indet. LP4450 (Sanz et al., 1997), and a complete postorbital bar is newly indicated for a specimen of the bohaiornithid *Longusunguis* (Hu et al., 2020). In addition, disarticulated elements are tentatively identified as the postorbital in other bohaiornithids, e.g., *Shenqiornis* and *Sulcavis*, in which this element appears to be unreduced (O'Connor and Chiappe, 2011; O'Connor et al., 2013). Notably, in contrast, no postorbital is reported for any known ornithuromorphs, even in the basal taxa e.g. *Archaeorhynchus* (Zhou and Zhang, 2006; Zhou et al., 2013; Wang and Zhou, 2016).

The broad jugal in *Sapeornis* is remarkably robust even compared to *Archaeopteryx* especially considering the presence of a broad postorbital process, providing further evidence of the widespread homoplasy thought to characterize early avian evolution. The interdigitating articulation between the jugal and quadratojugal in *Sapeornis* is plesiomorphic, being present in non-avian dinosaurs (Xu et al., 2015). In *Archaeopteryx*, a notch is also present in the caudal end of the jugal, but it cannot be determined if it accommodates the quadratojugal to form an interdigitating articulation, since it could also represent the separation between the postorbital process and the quadratojugal process (Elzanowski and Wellnhofer, 1996; Rauhut, 2014; Wang and Hu, 2017; Rauhut et al., 2018). The articulation between the jugal and quadratojugal is not clear in *Jeholornis* and *Confuciusornis* at this time (Zhou and Zhang, 2002b; Wang and Hu, 2017; Elzanowski et al., 2018; Wang et al., 2019), thus *Sapeornis* provides the only unequivocal evidence of this plesiomorphic articulation among birds. Compared to the primitive and robust condition in *Sapeornis*, the jugal bar is more slender and rod-like in ornithothoracines (Wang and Hu, 2017). Notably, the jugal in ornithuromorphs e.g. *Schizooura* and *Yanornis* (Liu, 2009; Zhou et al., 2012), appears to be even more slender and reduced than that of the enantiornithines e.g. *Pterygornis* and *Bohaiornis* (Li et al., 2014; Wang et al., 2016a; Wang and Hu, 2017).

The postorbital process of the jugal is present in known enantiornithines (e.g., *Longusunguis*, *Shenqiornis*, *Bohaiornis* and Enantiornithes indet. LP 4450, and tentatively in *Pterygornis* and *Cathayornis*) (Hu et al., 2020; Li et al., 2014; O'Connor and Chiappe, 2011; Sanz et al., 1997; Wang et al., 2014, 2016; Wang and Hu, 2017), indicating the presence of a complete postorbital bar in enantiornithines together with the presence of postorbitals (Hu et al., 2020; O'Connor and Chiappe, 2011). Although the jugal bar is rarely preserved in ornithuromorphs, the limited evidence indicates that the postorbital process of the jugal is strongly reduced in *Schizooura* (Zhou et al., 2012) and completely lost in *Yanornis* and the Late Cretaceous ornithurine *Ichthyornis* (Liu, 2009; Field et al., 2018), suggesting that the postorbital bar has been lost. This along with the presence of the more slender morphology, are indicative of derived features only observed in the Ornithuromorpha and represent early stages in the evolution of the crown avian condition.

The nasal in *Sapeornis* is relatively short and broad similar to the condition in non-avian dinosaurs. In modern birds this element is typically elongated and narrow, a morphology that allows bending and facilitates cranial kinesis (Holliday and Witmer, 2008). Compared to that, the mediolateral broad nasal in *Sapeornis* have broader articulation with the frontal, which would likely prohibit any significant flexibility of the nasofrontal region, further indicating that its rostrum was incapable of moving independently relative to the rest of the cranium, together with the unreduced postorbital bar and ectopterygoid.

The quadrate is another element that underwent strong modification during the evolution of the modern avian skull. This element connects the upper and lower jaws and controls the lifting of the cranium relative to the mandibles during cranial kinesis. In the Neornithes, the otic process of the quadrate is double-headed, differentiated into the prootic capitulum and squamosal capitulum, and the orbital process is elongated and sharply tapered (Baumel and Witmer, 1993). In contrast, the quadrate in *Sapeornis* again retains the plesiomorphic condition of a single headed otic process and a short and broad orbital process, resembling the condition in non-avian dinosaurs, e.g., *Sinovenator* (Xu et al., 2002b; Yin et al., 2018). Those plesiomorphic features are also retained in the Enantiornithes, visible in *Pterygornis* (Wang et al., 2016a), *Monoenantiornis* (Hu and O'Connor, 2017), *Zhouornis* (Zhang et al., 2013), and *Pengornis* (Zhou et al., 2008) and are present in the non-ornithurine ornithuromorph *Archaeorhynchus* and *Yixianornis* (Zhou and Zhang, 2006; Clarke et al., 2006). However, the divided otic process and the narrow and elongate orbital process evolved later in this clade, at this time known only in Late Cretaceous ornithurines e.g. *Ichthyornis* and the isolated quadrate of *Potamornis* (Elzanowski et al., 2001; Field et al., 2018).

The morphology of the stem avian palate is poorly known due to the rare preservation of the delicate elements that form the palatal complex. Other than *Archaeopteryx* (Elzanowski and Wellnhofer, 1996), the best preserved palatal information is from *Sapeornis*. Although known from hundreds (if not thousands) of specimens, the only putative palatal elements reported for *Confuciusornis* are a palatine, a pterygoid, and an ectopterygoid reported by Chiappe et al. (1999) and a palatine described by Elzanowski et al. (2018). However, the palatal elements described by Chiappe et al. (1999) are poorly figured so that no morphological information can be confirmed. The craniocaudally elongate and triangular element identified as the palatine by Elzanowski et al. (2018) is more consistent with a splenial based on morphology and its close association with the surangular. The identification of the palatine in

*Sapeornis* IVPP V19058 is not unequivocal; however, with the limited available data it was tentatively suggested to have the triradiate shape typical of crown birds (Hu et al., 2019). In the plesiomorphic condition in non-avian dinosaurs, this element is tetradiate with a jugal process that contacts the jugal (Fig. 7D, E). In *Sapeornis*, the jugal process appears to be absent so that contact with the jugal is lost (Fig. 7A). However, due to the relatively poor preservation, the possibility that the jugal process is broken rather than reduced in IVPP V19058 cannot be excluded, which may produce an artificial triradiate morphology (Hu et al., 2019). Based on the dislocated palatine preserved in the Munich specimen, the palatine of *Archaeopteryx* was first described as triradiate and lacking a jugal process (Elzanowski and Wellnhofer, 1996; Elzanowski, 2001). In the more recently published Thermopolis specimen, the palatine of *Archaeopteryx* was reinterpreted as tetradiate, as in non-avian theropods (Fig. 7C; Mayr et al., 2007). However, the palatine in the Thermopolis specimen is only partly exposed through the antorbital fenestra, providing insufficient detail to be certain about the reinterpretation of this element.

It has been demonstrated, both qualitatively and quantitatively, that the vomer of *Sapeornis* shares striking similarities with that of non-avian dinosaurs (Hu et al., 2019). Its broad overlapping contact with the maxilla cranially and embracing contact with the parasphenoid rostrum caudally, indicate that the skull of *Sapeornis* was largely akinetic, as in non-avian dinosaurs and palaeognaths (Hu et al., 2019). This is also inferred from the morphology of the postorbital bar and the ectopterygoid identified in IVPP V19058 (Hu et al., 2019). The ectopterygoids in *Archaeopteryx* (Fig. 7G, Elzanowski and Wellnhofer, 1996) and *Sapeornis* (Fig. 7F) are the only strong evidence of this element in Aves, although this element may also be present in *Confuciusornis* (Chiappe et al., 1999). The disappearance of this element in more derived birds decoupled the palate and cranium, increasing the flexibility of the palatal complex. The distal expansion in the jugal process of the ectopterygoid in *Sapeornis* demonstrates the existence of a contact between the ectopterygoid and the jugal, indicating a rigid palate with limited flexibility as in non-avian dinosaurs (Hu et al., 2019).

Palatal elements are rarely described in non-neornithine ornithothoracines. The palatine is reported in the holotype specimens of *Pterygornis dapingfangensis* (Wang and Hu, 2016) and *Hebeiornis fengningensis* (Xu et al., 1999; commonly known by its junior synonym “*Vescornis hebeiensis*,”; Zhang et al., 2004). However, this element is incompletely preserved in both specimens, and thus its morphology is ambiguous. The pterygoids are only reported in *Parapengornis* IVPP V18687 and *Longsunguis* IVPP V17964 (Wang et al., 2014; Hu et al., 2015). In these taxa the pterygoids appear to be relatively long, broad, and plate-like, similar to the condition in *Sapeornis*, but very different from that of the more abbreviated morphology of this element in neornithines. Evidence of the vomer is preserved in two enantiornithines, *Chiappeavis* (O'Connor et al., 2016, 2017) and *Gobipteryx* (Elzanowski, 1995; Chiappe et al., 2001), and their overall mediolaterally extensive morphology show similarity to the morphology in *Sapeornis*, indicating that this element remained unreduced in at least one lineage of Late Cretaceous enantiornithines (Hu et al., 2019). Very little unequivocal information of the palatal has been reported for any Early Cretaceous non-ornithurine ornithuromorph. The remnants described as the palatine in *Eogranivora* STM 35-3, *Schizoura* IVPP V16861 and *Zhongjianornis* IVPP V15900 are too badly crushed to be informative, despite that they are in the right locations of palatines (Zhou et al., 2010; Zhou et al., 2012; Zheng et al., 2018). The palatine preserved in *Archaeorhynchus* IVPP V14287 is largely overlapped by other cranial elements (Zhou and Zhang, 2006). The lack of palatal information for Early Cretaceous non-ornithurine ornithuromorphs may be partly due to the relative rarity of specimens, but may also

be a consequence of the particularly delicate and specialized nature of these bones in this lineage.

## 5. Conclusions

The well-developed postorbital bar, tightly articulated jugal bar (jugal and quadratojugal), short and broad nasal, single-headed quadrate with broad orbital process, dorsoventrally overlapping vomer-maxilla contact, and unreduced ectopterygoid-jugal contact, together all demonstrate the primitive and rigid construction of the skull of *Sapeornis*. Compared to this, preliminary interpretations of the very limited cranial evidence available for Early Cretaceous ornithothoracines suggests that some important derived cranial features evolved only in the Ornithothoraces with some further restricted to the Ornithuromorpha. The skull of enantiornithines is in some ways more primitive relative to that of sympatric ornithuromorphs, as indicated by the potential existence of a complete postorbital bar, a relatively robust jugal, a broad quadrate, a vomer that resembles the plesiomorphic condition retained in *Sapeornis*, and the absence of edentulous forms. Although the dentition is reduced in some enantiornithine lineages, e.g., the Longipterygidae (O'Connor et al., 2011), the complete loss of teeth does not occur in the Enantiornithes until the Late Cretaceous (*Gobipteryx*, Chiappe et al., 2001), whereas complete tooth loss evolved independently several times among Early Cretaceous ornithuromorphs (Zhou and Zhang, 2005; Zhou and Zhang, 2006; Zhou et al., 2012). The more flexible and lightweight morphology of the derived ornithuromorph skull may have been a determining factor in the ultimate success of this clade over other stem avian lineages.

## CRediT authorship contribution statement

**Han Hu:** Conceptualization, Data curation, Methodology, Writing - original draft. **Jingmai K. O'Connor:** Conceptualization, Methodology, Writing - original draft. **Paul G. McDonald:** Methodology, Writing - review & editing. **Stephen Wroe:** Methodology, Writing - review & editing.

## Acknowledgments

We acknowledge D. Li for specimen preparation and W. Gao for photography, and H. Chang and D. Hu for providing high-resolution photographs of *Sapeornis* 41HIII0405 and LPM B00018. We are grateful to two anonymous reviewers and the editor for their helpful comments to improve the manuscript. This research was supported by an UNE Postdoctoral Research Fellowship awarded to Han Hu, the State Key Laboratory of Precision Spectroscopy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences grant number 183110, and the National Natural Science Foundation of China grant No. 41688103.

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