Cranial anatomy of Anchiornis huxleyi (Theropoda: Paraves) sheds new light on bird skull evolution postprint

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Abstract

From any perspective, dinosaur–bird evolution represents one of the most fascinating evolutionary events in Earth' s life history, involving extensive modifications of morphological and ecological characteristics. Compared with postcranial skeletal morphology, current understanding of the early evolution of the avian skull remains relatively limited, primarily constrained by the scarcity of well-preserved cranial fossil materials from early avialans. Anchiornis represents the earliest known paravian (approximately 160 million years old)—Paraves being defined as the most inclusive clade containing all extant birds but excluding oviraptorosaurs and scansoriopterygids. With over a hundred known Anchiornis specimens, this taxon constitutes the most ideal subject for investigating morphological transformations during the non-avian theropod dinosaur–bird evolutionary transition. Nevertheless, numerous aspects of Anchiornis cranial morphology remain poorly understood. Based on a well-preserved Anchiornis fossil, we provide a detailed description of the cranial morphological architecture of this taxon, including previously enigmatic regions (e.g., temporal and palatal areas). Our study demonstrates that Anchiornis retains the primitive diapsid and akinetic skull morphology characteristic of non-avian dinosaurs. Concurrently, the skull of Anchiornis also exhibits localized morphological features that are respectively similar to those of dromaeosaurids, troodontids, and basal avialans, revealing that modular evolution profoundly influenced the early evolution of the avialan skull.

Full Text

Preamble

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Cranial anatomy of Anchiornis huxleyi (Theropoda: Paraves) sheds new light on bird skull evolution

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Abstract

The origin of birds from theropod dinosaurs represents, by any measure, the most eye-catching evolutionary transition in the history of life, encompassing numerous extensive morphological and biological changes. Compared to the postcranium, little progress has been made regarding the evolutionary assemblage of the avian skull, primarily due to the scarcity of well-preserved early cranial materials from stem lineages. Anchiornis is the oldest known record of Paraves (~160 Ma), the most inclusive clade containing all living birds but not Caudipteryx or Epidexipteryx. With hundreds of known specimens, Anchiornis constitutes an ideal taxon for investigating morphological modifications across the theropod-bird transition, yet its cranial morphology remains enigmatic. Here we present an in-depth description of the cranial morphology of Anchiornis based on three-dimensional reconstruction of a well-preserved specimen, including elements from the temporal and palatal regions that were previously poorly recognized. Our study demonstrates that Anchiornis retains the plesiomorphic dinosaurian condition of a diapsid akinetic skull. The mixture of cranial characters shared with dromaeosaurids, troodontids, and stemward avialans present in Anchiornis reveals the complex history of early avialan cranial evolution.

Key words: Anchiornis, Avialae, cranium, kinesis, palatine, squamosal

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1 Introduction

Anchiornis is the first known Jurassic paravian stratigraphically older than Archaeopteryx, and its discovery has effectively reconciled the "temporal paradox" —a problem that has been used to argue against the theropod origin of birds (Zhou, 2004; Xu et al., 2014; Wang and Zhou, 2017; Rauhut and Foth, 2020). Over the last decade, several Jurassic paravians have been discovered, most of them unearthed from the Middle–Late Jurassic Yanliao biota of northeast China (Hu et al., 2009; Xu et al., 2011; Godefroit et al., 2013), where all Anchiornis specimens have been collected (Pei et al., 2017a; Zhou and Wang, 2017). These fossils have significantly filled the morphological gap between non-avialan and avialan bauplan, pushing back the initial appearances of many characteristic features of crown groups to the deep phylogeny of Avialae (Xu et al., 2014; Brusatte et al., 2015). However, systematic relationships among the earliest diverging paravians have been clouded by exceedingly rare fossil records and poor preservation (Agnolin and Novas, 2013; Rauhut and Foth, 2020). Specifically, known Jurassic paravians are preserved two-dimensionally, which hampers examination of skeletal element morphology, particularly the skull, which consists of delicate bones bearing phylogenetic and functional information. Here we provide a detailed morphological description and comparison of the skull of Anchiornis huxleyi based on X-ray CT scanning data. Our study not only revises previously misinterpreted cranial features but also documents previously unrecorded morphologies, which advance our understanding of early-diverging paravian cranial evolution.

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2 Materials and Methods

CT imaging. To optimize the resolution of computed tomography (CT) scanning, the skull of Anchiornis huxleyi (STM 0-47) and associated anterior cervical vertebrae were extracted from the slab. The skull was scanned using the industrial CT scanner Phoenix v-tome-x at the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (IVPP) in Beijing (Figs. 1–3). The experiment was conducted using beam energy of 130 kV and a flux of 100 A at a resolution of 12.163 m. The obtained scanned images were imported into Avizo (v. 9.2.0) for digital segmentation, rendering, and reconstruction.

Phylogenetic analysis. To explore the phylogenetic position of Anchiornis huxleyi in light of the revised cranial morphology, phylogenetic analysis was performed using the latest version of the Theropod Working Group matrix (Brusatte et al., 2014; Turner et al., 2021; Xu et al., 2023). All cranial characters of A. huxleyi were checked and revised based on the present study, but character scorings of postcranial regions remained unchanged. The phylogenetic analysis was conducted using the TNT v. 1.5 software package (Goloboff and Catalano, 2016), with the same settings as in previous studies (Xu et al., 2023). Specifically, all characters were equally weighted under parsimony. The New Technology search method, with sectorial search, ratchet, tree drifting, and tree fusion, was applied to perform a heuristic tree search, with the shortest tree found in 20 replicates to uncover as many tree islands as possible. Bootstrap and Bremer values were calculated as supporting indices. Absolute bootstrap values were calculated using 1000 replicates with the same settings as in the primary search. Bremer values were calculated using the script embedded in TNT.

Figure 1 [**Figure 1: see original paper**] Photograph of Anchiornis huxleyi (STM 0-47) from Jianchang, Liaoning. Scale bar = 10 cm.

Figure 2 [**Figure 2: see original paper**] Photograph of the skull of Anchiornis huxleyi (STM 0-47) from Jianchang, Liaoning. Scale bar = 10 mm.

Institutional abbreviations. BMNHC, Beijing Museum of Natural History, Beijing, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; LPM, Liaoning Paleontological Museum, Shenyang, China; PKUP, Peking University Paleontological Museum, Beijing, China; STM, Shandong Tianyu Museum of Nature, Shandong, China.

Figure 3 [**Figure 3: see original paper**] Digital reconstruction of the skull of Anchiornis huxleyi (STM 0-47) from Jianchang, Liaoning in right (A) and left (B) lateral views showing cranial anatomy. Abbreviations: hy, hyoid; lan, left angular; lde, left dentary; lec, left ectopterygoid; lfr, left frontal; lju, left jugal; llc, left lacrimal; lma, left maxilla; lna, left nasal; lpa, left palatine; lpm, left premaxilla; lpo, left postorbital; lqj, left quadratojugal; lqu, left quadrate; ls, left squamosal; lsp, left splenial; lsu, left surangular; pa, prearticular; par, parietal; pr, parasphenoid rostrum; ran, right angular; rde, right dentary; rec, right ectopterygoid; rfr, right frontal; rlc, right lacrimal; rma, right maxilla; rna, right nasal; rpa, right palatine; rpm, right premaxilla; rpo, right postorbital; rqj, right quadratojugal; rqu, right quadrate; rsu, right surangular; vo, vomer. Scale bars = 10 mm.

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3 Description

As in early-diverging paravians (Ostrom, 1969; Makovicky and Norell, 2004; Turner et al., 2012; Wang and Zhou, 2017), the premaxillae of Anchiornis are unfused (Fig. 4A [Figure 4: see original paper]). The rostrum is more pointed than in most deinonychosaurs (Norell and Makovicky, 2004), comparable to that of Archaeopteryx (Elżanowski and Wellnhofer, 1996). The rostral tip curves anterodorsally, in stark contrast to the straight condition present in other paravians (Xu et al., 2011; Sullivan and Xu, 2017), including Sinovenator (Xu et al., 2002), Dromaeosaurus (Currie, 1995), and Archaeopteryx (Elżanowski and Wellnhofer, 1996). In contrast, the rostral end bends ventrally in Sapeornis and Jeholornis (Hu et al., 2019, 2022). Like Archaeopteryx and other non-avialan paravians (Norell et al., 2006; Tsuihiji et al., 2014; Xu et al., 2015), the nasal processes are short, rather than elongate and contacting the frontal as in confuciusornithids and some ornithothoracines (O' Connor and Chiappe, 2011; Wang et al., 2019, 2021, 2022). The maxillary process curves posterodorsally with a tapering end (Fig. 3A), contrasting with the blunt form seen in other paravians such as Archaeopteryx and Sinovenator (Xu et al., 2002; Mayr et al., 2005). The maxilla is probably excluded from participation in the margin of the external naris, given the length of the maxillary process of the premaxilla and the ventral process of the nasal. This condition present in Anchiornis is widely distributed in dromaeosaurids (Norell and Makovicky, 2004; Xu et al., 2015), but absent in stemward avialans (e.g., Archaeopteryx, enantiornithines) and troodontids such as Byronosaurus, Almas, and Sinovenator (Xu et al., 2002; Makovicky et al., 2003; Mayr et al., 2005; O' Connor and Chiappe, 2011; Pei et al., 2017b; Wang et al., 2021). As in early-diverging avialans and some troodontids such as Mei (Mayr et al., 2005; Turner et al., 2012; Pei et al., 2017a; Wang et al., 2021), the external naris extends posteriorly beyond the anterior margin of the antorbital fossa in Anchiornis, opposite to the condition seen in dromaeosaurids and some troodontids such as Byronosaurus (Makovicky et al., 2003; Makovicky and Norell, 2004; Norell and Makovicky, 2004).

Figure 4 [**Figure 4: see original paper**] Anatomy of facial elements of Anchiornis huxleyi (STM 0-47) from Jianchang, Liaoning. Digital reconstruction of the left premaxilla (A), right maxilla (B), left lacrimal (C, D), and left nasal (E, F). A–C, E, lateral views; D, F, medial views. The blue arrowhead indicates the recess at the juncture of the anterior and ventral processes, and the orange arrowhead denotes the lateral fossa on the ventral process. Abbreviations: afl, articular facet for lacrimal; apl, anterior process of lacrimal; ib, interfenestral bar; jm, jugal process of maxilla; mf, maxillary fenestra; mp, maxillary process; np, nasal process; pf, promaxillary fenestra; pm, premaxillary process; pn, premaxillary process of nasal; pp, promaxillary pila; ppl, posterior process of lacrimal; vn, ventral process of nasal; vpl, ventral process of lacrimal. Scale bars = 5 mm.

As in deinonychosaurs (Ostrom, 1969; Xu and Wu, 2001; Xu et al., 2015), but unlike stemward avialans such as Archaeopteryx (Mayr et al., 2005; Wang et al., 2021; Hu et al., 2022), the anterior process of the maxilla is substantially shorter than its posterior counterpart (Fig. 4A). The posterior process terminates with a sharply tapering end, contrasting with the blunt form present in troodontids (Makovicky and Norell, 2004; Tsuihiji et al., 2014), dromaeosaurids (Norell and Makovicky, 2004), and early avialans (O' Connor and Chiappe, 2011; Rauhut et al., 2018; Wang et al., 2019). The lateral surface of the maxilla is concave. The dorsal process of the maxilla is inset from the labial surface and is largely occupied by the antorbital fossa (Fig. 4A). As in dromaeosaurids and basal troodontids (e.g., Sinovenator; Xu et al., 2002, 2015; Norell and Makovicky, 2004), both maxillary and promaxillary fenestrae are laterally exposed (Fig. 4A). In contrast, the promaxillary fenestra is absent in later-diverging troodontids (e.g., Zanabazar and Saurornithoides; Norell et al., 2009) and avialans except for Archaeopteryx (Rauhut et al., 2018; Wang et al., 2021; Li et al., 2023). Our digital reconstruction shows that both fenestrae differ greatly from previous descriptions (Hu et al., 2009; Pei et al., 2017a). The promaxillary fenestra is elliptical with the long axis posterodorsally oriented, rather than rounded as depicted in Hu et al. (2009). As in Sinovenator (Xu et al., 2002), the promaxillary fenestra is level with, rather than more ventrally positioned than, the maxillary fenestra (contrary to Pei et al., 2017a). The promaxillary fenestra is proportionately much larger than in dromaeosaurids (Norell and Makovicky, 2004; Xu et al., 2015) and Archaeopteryx, in which the fenestra is more ventrally located relative to the maxillary fenestra (Xu and Wu, 2001; Norell et al., 2006; Rauhut et al., 2018). The promaxillary and maxillary fenestrae are separated by the rod-like, posterodorsally oriented promaxillary pila (Fig. 4A), contrasting with the anteroposteriorly broad form present in some troodontids such as Sinovenator (Xu et al., 2002; Makovicky et al., 2003; Pei et al., 2017b) and most dromaeosaurids (e.g., Bambiraptor, Velociraptor, and Sinornithosaurus; Barsbold and Osmólska, 1999; Xu and Wu, 2001; Norell and Makovicky, 2004). The maxillary fenestra has a straight ventral margin and its anteroventral corner is constricted, rather than rounded as described previously (Hu et al., 2009; Pei et al., 2017a). It extends as far ventrally as the antorbital fenestra, unlike in dromaeosaurids where it is more dorsally located (Norell and Makovicky, 2004). As in other troodontids except Byronosaurus (Makovicky et al., 2003; Norell et al., 2009), the interfenestral bar is inset from the lateral surface of the maxilla (Fig. 4A). An interfenestral canal of the kind present in Byronosaurus is absent in Anchiornis (Makovicky et al., 2003).

The T-shaped lacrimal is distinguishable from other paravians (Fig. 4C, D). Specifically, the anterior process is less than half the length of the ventral process, proportionately much shorter than in early avialans (e.g., Archaeopteryx, Aurornis) and dromaeosaurids (Mayr et al., 2005; Godefroit et al., 2013; Rauhut et al., 2018), whereas the former is subequal to or longer than the latter in some troodontids such as Jianianhualong, Gobivenator, and Almas (Tsuihiji et al., 2014; Pei et al., 2017b; Xu et al., 2017). As in troodontids (Makovicky et al., 2003), dromaeosaurids (Norell et al., 2006), and Archaeopteryx (Rauhut et al., 2018), a recess is developed at the juncture of the three processes (Fig. 4C). Pei et al. (2017a) described a recess on the ventral surface of the anterior process, which is absent in STM 0-47. This recess is absent in crownward avialans such as enantiornithines (Wang et al., 2022; Wang, 2023). The recess is overhung by the dorsoventrally compressed anterior process. The short posterior process deflects dorsally and forms an L-shaped dorsal margin with the anterior process (Fig. 4D). In contrast, the posterior process is straight and extends posterodorsally in other paravians (Norell et al., 2006; O' Connor and Chiappe, 2011; Tsuihiji et al., 2014; Rauhut et al., 2018), and a similar morphology was erroneously adopted for Anchiornis huxleyi (Hu et al., 2009; Pei et al., 2017a). Reexamination of previously described specimens of A. huxleyi reveals that the posterior process is either heavily compressed (BMNHC PH804, PH823 in Pei et al., 2017a) or overlain by other elements (LPM-B00169 in Hu et al., 2019; PKUP V1068, BMNHC PH822 in Pei et al., 2017a), making the original description problematic. The lacrimal lacks a pneumatic fossa between the posterior and ventral processes, but this structure is widely distributed in deinonychosaurs and some early-diverging avialans such as Jeholornis and Parabohaiornis (Norell et al., 2009; Tsuihiji et al., 2014; Xu et al., 2015; Hu et al., 2022; Wang, 2023). As in Archaeopteryx and dromaeosaurids (Norell and Makovicky, 2004; Rauhut et al., 2018), the robust ventral process is expanded anteroposteriorly at the ventral end, forming a large articular facet for the jugal. In contrast, the ventral end tapers or is blunt in some troodontids such as Sinovenator and Jianianhualong (Xu et al., 2017; Yin et al., 2018) and some stemward avialans (Hu et al., 2022; Wang et al., 2022; Wang, 2023). Like Archaeopteryx and dromaeosaurids (Norell and Makovicky, 2004; Rauhut et al., 2018), the ventral process is perpendicular to the anterior process, rather than curving anteroventrally as in some troodontids such as Gobivenator, Saurornithoides, and Byronosaurus (Makovicky et al., 2003; Norell et al., 2009; Tsuihiji et al., 2014). The lateral surface of the ventral process is deeply excavated by a fossa along its ventral third (Fig. 4C), a unique feature otherwise unknown among early-diverging paravians (Norell and Makovicky, 2004; O' Connor and Chiappe, 2011; Rauhut et al., 2018; Yin et al., 2018; Wang et al., 2021).

The left nasal is relatively well-preserved, compensating for anatomical information that has remained elusive thus far (Fig. 4E, F; Hu et al., 2009; Xu et al., 2009; Pei et al., 2017a). As in other troodontids (Makovicky et al., 2003; Pei et al., 2017b), the bone is proportionately much more slender than in some early avialans such as Archaeopteryx, Sapeornis, and some enantiornithines (O' Connor and Chiappe, 2011; Rauhut et al., 2018; Hu et al., 2019). The triangular ventral process is stout and longer than previously appreciated (Hu et al., 2009). The premaxillary process is anteriorly forked with a longer ventral and shorter dorsal branch (Fig. 4E). Similar morphology is otherwise unknown among Mesozoic paravians (Makovicky and Norell, 2004; Norell and Makovicky, 2004; O' Connor and Chiappe, 2011; Wang et al., 2021). The nasal has a forked posterior end to articulate with the lacrimal, contrasting with the simply tapering or blunt form present in most other early paravians (Norell et al., 2009; Xu et al., 2015; Rauhut et al., 2018; Wang et al., 2019).

As in troodontids and stemward avialans, the T-shaped postorbital has three slender processes (Fig. 5A [Figure 5: see original paper]; Tsuihiji et al., 2014; Rauhut et al., 2018; Yin et al., 2018; Wang et al., 2021), contrasting with the broad form in dromaeosaurids (Currie, 1995; Norell and Makovicky, 2004). The jugal and frontal processes are subequal in length, contrasting with the large difference present in early-diverging troodontids and some stemward avialans (Tsuihiji et al., 2014; Rauhut et al., 2018; Yin et al., 2018; Wang et al., 2021). Specifically, the former is >1.5 times longer than the latter in Almas, Sinovenator, Archaeopteryx, and Yuanchuavis, whereas in dromaeosaurids the three processes are of equal length (Hu et al., 2009; Pei et al., 2017b; Rauhut et al., 2018; Yin et al., 2018; Wang et al., 2022). The articulated right postorbital and jugal show that a complete postorbital bar is present in Anchiornis (Fig. 3B), as in other non-avialan theropods and stemward avialans (Currie, 1995; Weishampel et al., 2004; Wang et al., 2021).

The squamosal is an enigmatic element that is rarely well-preserved in Jurassic paravians, and to our knowledge is preserved intact in no other reported specimens of Anchiornis huxleyi (Hu et al., 2009; Pei et al., 2017a). The squamosal shares features with Archaeopteryx and Deinonychus in having a postorbital process that is anteriorly deeply forked, an elongate quadratojugal process, and a paroccipital process that is flexed ventrally (Fig. 5B, C; Ostrom, 1969; Elżanowski and Wellnhofer, 1996). In contrast, the postorbital process is not forked in some stemward avialans such as Jeholornis and enantiornithines (Wang et al., 2021; Hu et al., 2022), and the paroccipital process protrudes posterolaterally in some dromaeosaurids (e.g., Linheraptor) and enantiornithines such as Parabohaiornis and Yuanchuavis (Xu et al., 2015; Wang et al., 2022; Wang, 2023). The quadratojugal process projects less anteriorly than in Archaeopteryx and Deinonychus (Ostrom, 1969; Elżanowski and Wellnhofer, 1996), and it forms a right angle with the postorbital process (Fig. 5B). The preserved left squamosal and quadratojugal approach each other but do not contact directly (Fig. 3B), which we interpret as a preservational artifact because the left squamosal has been posteriorly displaced and thus offset from the postorbital, resulting in the short distance between the squamosal and quadratojugal. Therefore, we suggest that the squamosal contacts the quadratojugal, demonstrating that Anchiornis retained the archosaurian plesiomorphy of having the quadrate foramen fully separated from the infratemporal fenestra. Pei et al. (2017a) argued that Anchiornis probably lacked the squamosal-quadratojugal articulation as in some troodontids, including Almas, Mei, and Sinovenator (Pei et al., 2017b; Yin et al., 2018). Our study suggests that some of these interpretations should be reconsidered given the poor preservation of these paravians.

Our three-dimensional reconstruction of the jugal (Fig. 5D, E) reveals morphologies largely consistent with previous studies (Pei et al., 2017a). The bone is much more slender than in most non-avialan theropods. The straight suborbital process is excavated laterally (Fig. 5E), a feature absent in early avialans (e.g., Jeholornis, confuciusornithids) and some troodontids (e.g., Almas and Sinovenator; Pei et al., 2017b; Yin et al., 2018). A previous study recognized a longitudinal groove along the dorsomedial margin of the jugal as a diagnostic character of Anchiornis (Hu et al., 2009). However, our three-dimensional reconstruction of both jugals shows no sign of this groove (Fig. 5D), indicating that this feature cannot be considered a valid diagnostic character. As in many paravians including Archaeopteryx (Norell and Makovicky, 2004; Mayr et al., 2005; Wang and Hu, 2017), the jugal tapers anteriorly, rather than being forked (contrary to Turner et al., 2012), whereas an anteriorly forked jugal is present in some troodontids such as Gobivenator, Jinfengopteryx, and Almas (Tsuihiji et al., 2014; Pei et al., 2017b). The postorbital process projects posterodorsally and lacks the corneal process on the posterior margin that is present in Archaeopteryx and the enantiornithine IVPP V17901 (Wang and Hu, 2017; Wang et al., 2021). The posterior margin between the postorbital and quadratojugal processes is rounded, contrasting with the deeply notched condition present in Archaeopteryx (Rauhut et al., 2018). The quadratojugal process lacks the posterior incisure present in many non-avialan theropods such as Sinovenator and some dromaeosaurids (Xu et al., 2015; Sullivan and Xu, 2017; Yin et al., 2018).

Little was known about the morphology of the quadratojugal in Anchiornis, and this element is exquisitely preserved here (Fig. 5D, E). As in troodontids and early avialans (Wang and Hu, 2017; Yin et al., 2018), the bone is L-shaped, without the posterior process present in non-avialan theropods including dromaeosaurids (Turner et al., 2012; Sullivan and Xu, 2017). Hu et al. (2009) reconstructed a V-shaped quadratojugal with a prominent posterior end in Anchiornis, resembling the condition of some dromaeosaurids such as Linheraptor. Our study shows that this reconstruction is inaccurate. The squamosal and jugal processes are subequal in length, and together they form a right angle. The squamosal process extends as far dorsally as the postorbital process of the jugal (Fig. 5D). In contrast, the postorbital process of the jugal extends more dorsally in early-diverging avialans (e.g., Archaeopteryx, Jeholornis; Wang and Hu, 2017) and troodontids such as Mei, Sinovenator, and Gobivenator (Tsuihiji et al., 2014; Yin et al., 2018).

As in non-avialan dinosaurs and most stemward avialans (Hendrickx et al., 2015; Wang et al., 2022), the quadrate has a bicondylar mandibular process, and an orbital process that is dorsoventrally deep and broadly convex anteriorly (Fig. 6 [Figure 6: see original paper]). In contrast, the orbital process is transformed into a pointed structure in crownward avialans such as Ichthyornis (Baumel and Witmer, 1993; Field et al., 2018). As in non-avialan paravians and Archaeopteryx (Elżanowski and Stidham, 2011; Hendrickx et al., 2015; Stidham and O' Connor, 2021), the anterior apex is near the dorsoventral midpoint of the orbital process (Fig. 6A, E), rather than more ventrally located as in some Cretaceous avialans such as Sapeornis and Yuanchuavis (Hu et al., 2019; Wang et al., 2022). Like non-avialan dinosaurs and stemward avialans (e.g., Archaeopteryx, Yuanchuavis) (Norell et al., 2006; Hendrickx et al., 2015; Wang et al., 2022), the dorsal margin that extends from the orbital process to the otic process is straight. In contrast, that margin is deeply concave dorsally in most crownward avialans (Baumel and Witmer, 1993). As in early-diverging avialans, the single-headed otic process bears a low lateral ridge that extends down to the lateral condyle (Fig. 6A; Stidham and O' Connor, 2021; Wang et al., 2022). In contrast, in dromaeosaurids a prominent triangular process (Norell et al., 2006:fig. 10c [Figure 10: see original paper]) projects laterally from the otic process and contacts the squamosal and quadratojugal (Hendrickx et al., 2015; Xu et al., 2015). The posterior surface of the quadrate shaft is not perforated by a foramen as in some troodontids such as Troodon, Sinovenator (Fig. 6C), and some enantiornithines (e.g., Pengornis) (Makovicky et al., 2003; O' Connor and Chiappe, 2011; Yin et al., 2018). The straight quadrate ridge extends anteroventrally (Fig. 6F), rather than being bowed anteriorly as in Sinovenator and Parabohaiornis (Yin et al., 2018; Wang, 2023). Like early avialans (Wang et al., 2021, 2022), the lateral and medial mandibular condyles are posteriorly located relative to the quadrate shaft, rather than being level with it as in non-avialan theropods (Hendrickx et al., 2015; Xu et al., 2015). As in most non-avialan theropods (Hendrickx et al., 2015), the lateral condyle is larger than the medial one (Fig. 6D), opposite to the condition present in Linheraptor, Archaeopteryx, and some enantiornithines (O' Connor and Chiappe, 2011; Xu et al., 2015; Kundrát et al., 2019). The lateral condyle is more posteriorly and ventrally located relative to the medial condyle, whereas they are roughly co-planar in some non-avialan theropods (e.g., Tsaagan; Norell et al., 2006; Hendrickx et al., 2015), and the medial condyle is more posteriorly positioned in Yuanchuavis and Jeholornis (Hu et al., 2022; Wang et al., 2022). As in non-avialan and early avialan theropods (Hendrickx et al., 2015; Xu et al., 2015; Wang, 2023), a pterygoid condyle is absent, a derived feature that evolved later along the line to crown birds (Wang et al., 2021, 2022).

Figure 6 [Figure 6: see original paper] Anatomy of the quadrate of Anchiornis huxleyi (STM 0-47) from Jianchang, Liaoning. A–D, right quadrate in lateral (A), medial (B), posterior (C), and ventral (D) views; E, F, left quadrate in lateral (E) and medial (F) views. Abbreviations: afq, articular facet for quadratojugal; lc, lateral condyle; mc, medial condyle; mp, mandibular process; orp, orbital process; otp, otic process; qr, quadrate ridge. Scale bars = 5 mm.

Morphology of the palatal elements remains obscure in Anchiornis, as well as in many other Jurassic paravians. The pterygoid exhibits the typical non-avialan maniraptoran condition, with a large quadrate ramus that projects far dorsal to the palatal surface in a position posterior to the orbit (Fig. 7A [Figure 7: see original paper], B; Ostrom, 1969; Norell et al., 2006; Holliday and Witmer, 2008). This plesiomorphic condition is retained in stemward avialans such as enantiornithines (Wang et al., 2021). As in dromaeosaurids and enantiornithines (Ostrom, 1969; Wang et al., 2021, 2022), but unlike Sinovenator and Jeholornis (Yin et al., 2018; Hu et al., 2022), the quadrate ramus is forked posteriorly (Fig. 7A). An ectopterygoid wing, present in Archaeopteryx and some non-avian theropods (Elżanowski and Wellnhofer, 1996; Eddy and Clarke, 2011; Rauhut et al., 2018), is absent here as in Sinovenator and enantiornithines (Yin et al., 2018; Wang et al., 2021). The palatine ramus is as long as the quadrate ramus, whereas the former is twice as long as the latter in other non-avialan paravians and some early avialans (Yin et al., 2018; Wang et al., 2021; Hu et al., 2022). The pterygoid in Anchiornis is notably shorter than in other Mesozoic paravians. Specifically, the bone is slightly longer than the dorsoventral height of the quadrate in Anchiornis, whereas the pterygoid is substantially longer in other non-avialan theropods and early avialans (Ostrom, 1969; Yin et al., 2018; Wang et al., 2021, 2022; Hu et al., 2022). We suggest a short pterygoid as a diagnostic character of Anchiornis.

Like some dromaeosaurids such as Velociraptor (Ostrom, 1969; Barsbold and Osmólska, 1999), the tetraradiate palatine is mediolaterally broad (Fig. 7C, D), contrasting with the elongate and slender condition present in some troodontids (e.g., Sinovenator, Gobipteryx; Tsuihiji et al., 2014; Yin et al., 2018), Archaeopteryx, and more crownward avialans (Elżanowski and Wellnhofer, 1996; Zusi and Livezey, 2006; Torres et al., 2021; Wang et al., 2022). As in dromaeosaurids and Archaeopteryx (Currie, 1995; Eddy and Clarke, 2011), the choanal process is hooked anteriorly, contrasting with both the medially oriented form, as in Sapeornis and Yuanchuavis (Hu et al., 2019; Wang et al., 2022), and the straight and anteriorly directed condition, as in Sinovenator and Allosaurus (Madsen, 1976; Yin et al., 2018). The pterygoid process is slightly longer than the choanal process, representing an intermediate stage from the ancestral theropod condition to the further elongate form in later-diverging avialans (Madsen, 1976; Elżanowski and Wellnhofer, 1996; Hu et al., 2019; Wang et al., 2022). The jugal process is present, a plesiomorphic condition for theropods (Zusi and Livezey, 2006; Wang et al., 2022). This structure is weakly developed in Archaeopteryx (Rauhut et al., 2018; but see Elżanowski and Wellnhofer, 1996) and absent in other avialans (Torres et al., 2021; Wang et al., 2022). The maxillary process is proportionately shorter than in Sinovenator and early avialans such as Archaeopteryx and Yuanchuavis. As in dromaeosaurids (e.g., Velociraptor and Dromaeosaurus; Currie, 1995; Barsbold and Osmólska, 1999), the posterior margin of the internal naris (between the choanal and maxillary processes) is parabolic, contrasting with the deeply notched condition present in Sinovenator and Archaeopteryx (Rauhut et al., 2018; Yin et al., 2018). The dorsal surface of the palatine bears three depressions at the base of the pterygoid and choanal processes and along the lateral margin, respectively, which are separated from one another by a triradiate embossment (Fig. 7C). This feature is absent in Sinovenator, Deinonychus, and early avialans such as Archaeopteryx and Ichthyornis (Ostrom, 1969; Rauhut et al., 2018; Yin et al., 2018; Torres et al., 2021). Unlike Archaeopteryx and Deinonychus (Ostrom, 1969; Rauhut et al., 2018), the lateral margin of the palatine is not thickened.

As in non-avialan theropods and Archaeopteryx (Currie, 1995; Elżanowski and Wellnhofer, 1996; Barsbold and Osmólska, 1999), the ectopterygoid has a posteriorly recurved jugal process (Fig. 7E, F), contrasting with the straight form observed in Sapeornis and Yuanchuavis (Wang et al., 2022). The lateral end of the jugal process is not expanded anteroposteriorly as in some non-avialan theropods (e.g., Allosaurus) and early avialans (e.g., Yuanchuavis and Sapeornis; Madsen, 1976; Godefroit et al., 2013; Wang et al., 2022). The jugal process terminates proximal to the midpoint of the pterygoid process, but it approaches the posterior margin of the pterygoid process in Archaeopteryx and some non-avialan theropods such as Sinovenator and dromaeosaurids (Currie, 1995; Elżanowski and Wellnhofer, 1996; Yin et al., 2018). The subtemporal fenestra defined by the jugal and pterygoid processes is relatively wider than in non-avialan theropods including Sinovenator and Deinonychus (Ostrom, 1969; Yin et al., 2018). Like some basal non-avialan theropods (e.g., Sinoraptor, Allosaurus) (Madsen, 1976; Currie and Zhao, 1993), the pterygoid flange is prominent and hooked posteriorly (Fig. 7E). In contrast, this flange is reduced in other paravians such as Archaeopteryx and some troodontids (Elżanowski and Wellnhofer, 1996; Tsuihiji et al., 2014; Yin et al., 2018). As in Sinovenator (Yin et al., 2018), the pterygoid process is rectangular, contrasting with the semicircular shape present in stemward avialans such as Archaeopteryx and Yuanchuavis (Elżanowski and Wellnhofer, 1996; Tsuihiji et al., 2014; Wang et al., 2022). The pterygoid process lacks both the ventral pocket present in other non-avialan theropods and Archaeopteryx (Currie, 1995; Rauhut et al., 2018) and the dorsal depressions present in Sinovenator and Deinonychus (Ostrom, 1969; Yin et al., 2018).

The basicranial elements are severely crushed, leaving only the parasphenoid rostrum identifiable. As in some non-avialan theropods and the enantiornithine IVPP V12707 (Currie and Zhao, 1993; Wang et al., 2021), the ventral surface of the rostrum is concave (Fig. 7G), rather than convex as in Cratonavis, Parabohaiornis, and crown groups (Baumel and Witmer, 1993; Li et al., 2023). A spatulate element preserved adjacent to the left palatine is interpreted as the anterior part of the vomer (Figs. 3, 7H). If this is the case, the asymmetric shape of this element indicates that the paired vomers are not fused as in some non-avialan and avialan theropods (e.g., Archaeopteryx, Sapeornis; Elżanowski and Wellnhofer, 1996; Hu et al., 2019).

Figure 7 [**Figure 7: see original paper**] Anatomy of the palatal elements of Anchiornis huxleyi (STM 0-47) from Jianchang, Liaoning. A, B, right pterygoid in medial (A) and lateral (B) views; C, D, left palatine in dorsal (C) and ventral (D) views; E, F, right ectopterygoid in dorsal (E) and ventral (F) views; G, parasphenoid rostrum in ventrolateral view; H, possible right vomer in dorsal view. The blue arrowheads in (C) denote the dorsal depressions, and the green arrowhead in (G) denotes the concave ventral surface of the parasphenoid rostrum. Abbreviations: afp, articular facet for basipterygoid process; chp, choanal process; jue, jugal process of ectopterygoid; jup, jugal process; mxp, maxillary process; pfe, pterygoid flange of ectopterygoid; plr, palatine ramus; pte, pterygoid process of ectopterygoid; ptp, pterygoid process of palatine; qur, quadrate ramus. Scale bars = 5 mm.

As in many non-avialan theropods, the dentary is ventrally convex (Fig. 8A [Figure 8: see original paper], B; Weishampel et al., 2004; Sullivan and Xu, 2017), which contrasts with both the dorsally convex condition, as in Jeholornis and Sapeornis (Hu et al., 2019, 2022), and the straight form, as in Archaeopteryx and some ornithothoracines (Elżanowski and Wellnhofer, 1996; O' Connor and Chiappe, 2011; Wang and Zhou, 2017). The lateral surface of the dentary bears a groove that widens posteriorly and houses nutritional foramina (Fig. 8B), a derived feature shared by Anchiornis and troodontids (Hu et al., 2009). Pei et al. (2017a) described that the dentary ended with a sheet-like posteroventral process. Although we cannot reexamine these specimens firsthand, the posterior end is only fully visible in the right dentary of PKUP V1068 in that study, and it is broken and compressed with other elements (Pei et al., 2017a:fig. 5). Our CT scanning shows that both dentaries have a posteroventrally sloping posterior margin (Fig. 8A, B), as in other non-avialan theropods and some early-diverging avialans (O' Connor and Chiappe, 2011; Sullivan and Xu, 2017; Wang and Zhou, 2017). We posit that the "sheet-like" structure reported in Pei et al. (2017a) in fact represents another element (e.g., prearticular, splenial?).

The teeth of STM 0-47 are complete and most remain in situ, enabling us to determine the tooth count for the first time in Anchiornis. There are 4, 12, and 16 premaxillary, maxillary, and dentary teeth, respectively (Figs. 4A, B, 8A, B), which differ from previous estimates (Hu et al., 2009; Pei et al., 2017a). For instance, Hu et al. (2009) reconstructed 21 dentary teeth but provided no direct evidence. The dentary tooth count is more than in many stemward avialans and dromaeosaurids (e.g., Velociraptor and Tsaagan; Barsbold and Osmólska, 1999; Norell et al., 2006; Wang and Zhou, 2017; Zhou et al., 2019) but fewer than in most troodontids (Makovicky and Norell, 2004; Norell et al., 2009). As in early avialans (Elżanowski and Wellnhofer, 1996; O' Connor and Chiappe, 2011; Zhou et al., 2019), the tooth crowns are recurved distally. Like dromaeosaurids and early avialans (Elżanowski and Wellnhofer, 1996; Norell and Makovicky, 2004; Rauhut et al., 2018), the premaxillary teeth are closely packed, and the maxillary and dentary teeth are relatively sparsely spaced. In contrast, troodontids are characteristically characterized by closely packed anterior dentary teeth (Currie, 1987). The tooth row approaches the posterior end of the dentary, proportionately much longer than in many dromaeosaurids (Barsbold and Osmólska, 1999; Norell and Makovicky, 2004), troodontids (Tsuihiji et al., 2014; Xu et al., 2017), and stemward avialans (Rauhut et al., 2018; Zhou et al., 2019; Wang et al., 2022). Like dromaeosaurids and avialans (Turner et al., 2012; Wang and Zhou, 2017), the teeth are placed in individual sockets, rather than in a continuous groove as in troodontids (Fig. 8A; Currie, 1987). Contrary to Pei et al. (2017a), the interdentary plate is absent in STM 0-47, as in other paravians except Archaeopteryx (Currie, 1987; Elżanowski and Wellnhofer, 1996; Wang and Zhou, 2017). The anterior four dentary teeth are smaller and more recurved than the succeeding ones.

The triangular splenial lacks the foramen present in early avialans such as Archaeopteryx and Pterygornis (Fig. 8C; Rauhut et al., 2018; Wang et al., 2021). Unlike dromaeosaurids and troodontids (Makovicky and Norell, 2004; Norell and Makovicky, 2004), but as in early avialans (O' Connor and Chiappe, 2011; Turner et al., 2012), the bone is not visible laterally.

The surangular has a convex dorsal margin that thickens transversely close to the articular facet for the upper jaw (Fig. 8D–F). The angular is bowed ventrally and has an anterior process that curves dorsally and separates the dentary from the external mandibular fenestra (Fig. 8D), a diagnostic feature of Deinonychosauria (Xu et al., 2017). The dorsal margin of the angular rises dorsally to form the posteroventral margin of the external mandibular fenestra. As in other deinonychosaurs (Currie, 1995; Makovicky and Norell, 2004; Norell and

Makovicky, 2004; Xu et al., 2015), but unlike early avialans except confuciusornithids (O' Connor and Chiappe, 2011; Wang and Zhou, 2017; Wang et al., 2022), the external mandibular fenestra is laterally exposed (contradicting Pei et al., 2017a). Like Byronosaurus and Xiaotingia (Makovicky et al., 2003; Xu et al., 2011), the surangular fenestra of Anchiornis is anteroposteriorly longer than dorsoventrally high, as in previous reconstructions (Hu et al., 2009; Pei et al., 2017a).

Figure 8 [**Figure 8: see original paper**] Anatomy of the lower jaw elements of Anchiornis huxleyi (STM 0-47). A, B, left dentary in medial (A) and lateral (B) views; C, left splenial in medial view; D, E, left post-dentary elements in medial (D) and lateral (E) views; F, right post-dentary elements in lateral view. Abbreviations: ang, angular; emf, external mandibular foramen; saf, surangular foramen; san, surangular. Scale bars = 5 mm.

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4 Discussion

Jurassic paravians offer critical anatomical information for piecing together the evolutionary acquisition of the avian "blueprint" (Xu et al., 2009, 2014; Brusatte et al., 2015), and Anchiornis stands out among Jurassic taxa given its rich fossil record and phylogenetic position (Zheng et al., 2018). Despite previous efforts to comprehend the skeletal morphology of Anchiornis (Hu et al., 2009; Xu et al., 2009; Pei et al., 2017a), much remained unknown regarding its cranial anatomy because two-dimensional preservation severely limits available data. This gap in knowledge of cranial morphology impacts our understanding of the phylogenetic affinity and functional anatomy of Anchiornis. The well-preserved skull of STM 0-47, visualized via high-resolution X-ray CT scanning, enables digital reconstruction of the cranial morphology of Anchiornis with great fidelity. Our study not only amends previous results but, more importantly, demonstrates the three-dimensional configuration of some cranial elements for the first time. For Anchiornis, the following morphologies are revised: the promaxillary fenestra is elliptical and level with the maxillary fenestra in ventral extent (Fig. 4B); the lacrimal bears a recess at the juncture between the anterior and ventral processes (Fig. 4C); the jugal lacks the groove on its dorsomedial margin (Fig. 5D); the squamosal likely contacts the quadratojugal; the quadrate lacks the lateral flange (Fig. 6); the posterior end of the dentary slopes posteroventrally (Fig. 8A); the interdentary plates are absent (this structure appears variously present in other Anchiornis specimens, personal communication with Pei Rui) (Fig. 8A); and the external mandibular fenestra is laterally exposed (Fig. 8D-E).

Our digital reconstruction reveals a great deal of cranial morphology of Anchiornis, including the temporal and palatal regions that are relevant to deciphering the functional performance of this taxon (e.g., cranial kinesis). Specifically, the quadrate lacks the quadrate condyle (Fig. 6), indicating the absence of condyle-based articulation between the quadrate and the pterygoid. Instead, the broad orbital process of the quadrate and the elongate quadrate ramus of the pterygoid reveal the presence of a scarf joint between the two elements, an ancestral dinosaurian condition retained by avialans stemward of ornithuromorphs (Holliday and Witmer, 2008; Wang et al., 2022). The tetraradiate palatine has a well-developed jugal process that forms a large articular facet for the jugal (Fig. 7C, D). The squamosal is morphologically more similar to that of Archaeopteryx than to other paravians in having an anteriorly forked postorbital process and a ventrally flexed paroccipital process (Fig. 5B). All these features, combined with the complete postorbital bar, show that Anchiornis preserves much of the ancestral dinosaurian condition of a diapsid and almost akinetic skull, despite derived avialan-like features in postcranial regions. This observation is in agreement with recent studies (Wang et al., 2021; Li et al., 2023), revealing that the skull was evolutionarily conservative along the line to early-diverging avialans.

The phylogenetic affinity of Anchiornis remains unsettled, with competing hypotheses identifying Anchiornis as either avialan or troodontid (Hu et al., 2009; Xu et al., 2011; Turner et al., 2012; Agnolín and Novas, 2013; Pei et al., 2017a). On one hand, this controversy is ascribed to the sparse fossil record, which is further complicated by preservation that hinders direct observation (new analytical methods such as CT scanning can help resolve this issue). On the other hand, evolutionary mosaicism always impacts morphology-based phylogenetic inference. Previous studies show that the early evolution of avialans has been deeply shaped by mosaicism (Clarke and Middleton, 2008; Xu et al., 2014; Wang and Zhou, 2017), attested by the Anchiornis skull which exhibits mixed morphologies shared with dromaeosaurids, troodontids, and avialans. Although beyond the scope of this paper, we tentatively investigated to what degree the revised cranial anatomy could affect the phylogenetic position of Anchiornis, using the latest version of the Theropod Working Group matrix with modifications. Forty cranial character states of Anchiornis have been revised here. We performed maximum parsimony-based phylogenetic analyses using the same settings as in Xu et al. (2023) (see Materials and Methods). The strict consensus tree is consistent with the previous result (Xu et al., 2023), in which Anchiornis was resolved in a polytomy that unites Xiaotingia, Fujianvenator, Eosinopteryx, and Aurornis (Fig. 9 [Figure 9: see original paper]). This clade is poorly supported (Bootstrap value <50%; Bremer value = 0). The seemingly unchanged phylogenetic topology is not surprising, considering that the revised cranial characters account for <5% of the total characters. On the other hand, over 70% of the cranial characters in that data matrix cannot be determined for most other early-diverging paravians, which prevents comparison and offsets much phylogenetic significance introduced by the revised cranial anatomy of Anchiornis. Therefore, much effort is needed to extract detailed and genuine cranial features of early-diverging paravians, particularly using techniques such as CT scanning, which together with discoveries of new fossils can help reconcile phylogenetic controversies of the earliest diverging avialans.

Figure 9 [Figure 9: see original paper] Evolutionary tree showing the position of Anchiornis. The tree is the strict consensus derived from the phylogenetic analysis based on revised cranial characters of Anchiornis. Bootstrap and Bremer support values are indicated in normal and bold italic formats, respectively.

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Note: Figure translations are in progress. See original paper for figures.