New prospects on the cranial evolution of non-avialan paravian theropods based on geometric morphometrics

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Abstract: The cranial morphology of theropod dinosaurs has been used to examine the phylogeny, ontogeny, ecology and biomechanics of the clade. Previous studies have recognized that paedomorphosis and peramorphosis occurred multiple times throughout theropod evolution, with skull paedomorphism being one of the major changes during the transition from non-avialan theropods to birds. This study supplemented previous works with more detailed sampling of the morphological data of non-avialan paravians. Principal component analyses based on the cranial geometry confirm that the small-bodied non-avialan paravians have paedomorphic skulls compared with the early-diverging theropods, but independent peramorphosis is also observed in various groups. The secondary elongation of the preorbital portion of the cranium was present in both the late-diverging troodontids and the late-diverging dromaeosaurids, but it was achieved through different morphological configurations in these two lineages.

Supplementary material: Landmark description and Procrustes transformed landmark coordinates of specimen-based samples are available at https://doi.org/10.6084/m9.figshare.c.5849285

The crania of vertebrate fossils usually provide crucial information in palaeontological studies, as the cranial morphology bears not only strong phylogenetic and ontogenetic signals, but also significant functional and ecological implications (Marugán-Lobón and Buscalioni 2003; Weishampel *et al.* 2004; Felice *et al.* 2020). Cranial heterochrony has been recognized as an important factor in theropod evolution. For example, an array of skull morphologies that display heterochrony have been documented in theropod species of a wide phylogenetic range and experimented with a wide variety of feeding strategies (Barrett 2005; Carrano 2006; Therrien and Henderson 2007; Zanno and Makovicky 2011; Zanno *et al.* 2016; Yoshikawa *et al.* 2019). Therefore, the cranial geometry interpreted with multivariate methods has been used to examine the functional constraints, dietary preferences, evolutionary relationships, ontogenetic trajectories and macroevolutionary patterns in theropods and birds in particular detail (Bhullar *et al.* 2012; Brusatte *et al.* 2012; Foth and Rauhut 2013; Foth *et al.* 2016; Felice *et al.* 2020). Based on the morphological diversity of theropod crania, the cranial geometry of theropod lineages may or may not be correlated with various functional and ecological proxies (Brusatte *et al.* 2012; Foth and Rauhut 2013; Foth *et al.* 2016; Felice *et al.* 2020). Interspecific variation of the facial morphology coupled with the ontogenetic interpretation suggests that paedomorphosis and peramorphosis occurred multiple times during the dinosaurian evolution (Bhullar *et al.* 2012; Foth *et al.* 2016). Even though the hypothetical ancestor of saurischians probably led to the early-diverging theropods mainly through peramorphosis (Foth *et al.* 2016), the paedomorphic trend of the cranial shape possibly occurred from the early evolution of avetheropods to recent birds (Bhullar *et al.* 2012; Foth *et al.* 2016). Furthermore, independent peramorphic trends in the cranial morphology have also been noticed in the late-diverging theropods, including birds (Bhullar *et al.* 2012, 2015, 2016; Plateau and Foth 2020).

In those studies, non-avialan paravian theropods were frequently mentioned as they have morphological and biological features of both stereotypical dinosaurs and living birds, which are reflected in the cranium and other parts of the skeleton (Xu *et al.* 2003, 2017; Brusatte *et al.* 2015; Pei *et al.* 2020). The non-avialan paravian lineages resemble their bird relatives in their skeletal morphology, plumage coverage and many behavioural and ecological aspects (Xu *et al.* 2003, 2017; Li *et al.* 2012; Wang *et al.* 2019; Pei *et al.* 2020). Discoveries of non-avialan paravians in recent decades provided increasing support to the framework of a dinosaurian origin of birds, but also revealed the complexity of

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the evolutionary details of the dinosaur–bird transition (Padian and Chiappe 1998; Xu *et al.* 2014; Brusatte *et al.* 2015; Pei *et al.* 2020). Unlike most typical non-paravian theropod dinosaurs, the non-avialan paravians possess both the typical theropod rectangular cranial profile with an elongate preorbital portion and a deep rostrum, and the triangular bird-like cranial profile with a shortened but shallow rostrum coupled with an enlarged orbit. Bhullar *et al.* (2012) demonstrated that recent birds have highly paedomorphic skulls compared with non-avialan theropods and Mesozoic birds, which evolved in a multistep transformation, and further implied that paedomorphic skulls might also exist in the early-diverging and small-bodied non-avialan paravians. However, these early-diverging and small-bodied non-avialan paravian samples were mostly missing from Bhullar *et al.'s* (2012) analyses (only including one *Anchiornis* without the osteohistology-based ontogenetic inference), and the cranial paedomorphosis of these taxa lacks quantitative support.

Recent fossil discoveries have consistently revealed novel body plans and presumed ecological behaviours for paravians (Hu *et al.* 2009, 2018; Xu *et al.* 2011, 2015, 2017; Pei *et al.* 2017*b*, 2022; Wang *et al.* 2019), leading to an opportunity to re-examine the cranial disparity in these fossil organisms. The aim of this study is to investigate the geometric diversity of the crania of non-avialan paravians (and anchiornithines) and test the previously existing hypothesis on the paedomorphosis of these fossil taxa.

Non-avialan paravians and their cranial forms

Non-avialan paravians are typically represented by the traditionally recognized Deinonychosauria, as a union of Dromaeosauridae and Troodontidae (Makovicky and Norell 2004; Norell and Makovicky 2004; Turner *et al.* 2012). In addition, the phylogenetic affiliations of the Anchiornithinae, Scansoriopterygidae and Uenlagiinae are in debate as they have been recovered at multiple early-diverging branches within or outside Avialae (Hu *et al.* 2009, 2018; Xu *et al.* 2009, 2011, 2015; Senter *et al.* 2012; Godefroit *et al.* 2013; Foth and Rauhut 2017; Pei *et al.* 2017*a*, 2020; Wang *et al.* 2019). In this study we used the phylogenetic framework of Pei *et al.* (2020), in which the unenlagiines are recovered as dromaeosaurids, the scansoriopterygids recovered outside Paraves and the anchiornithines recovered as the earliest diverging branch of Avialae. Within this phylogenetic framework, *Anchiornis* is an early avialan, and can no longer represent the non-avialan paravians as in previous studies (e.g. Bhullar *et al.* 2012). Considering that anchiornithines have also been recovered as monophyletic or paraphyletic at the early-diverging branches of Troodontidae, Deinonychosauria or Avialae (Hu *et al.* 2009, 2018; Xu *et al.* 2011, 2015; Godefroit *et al.* 2013; Foth *et al.* 2014; Cau *et al.* 2017), we also treat Anchiornithinae as a separate assemblage in this study to investigate the early cranial changes leading to *Archaeopteryx* and later-diverging avialans. Regardless of the existing phylogenetic interpretations, each of these three groups of the anchiornithines, dromaeosaurids and troodontids (or non-anchiornithine troodontids in some alternative phylogenetic interpretations) has supposedly adult individuals with either a typical theropod-like elongate cranial profile or a bird-like shortened cranial profile (Fig. 1).

The majority of dromaeosaurids, including the unenlagiines and the eudromaeosaurians, have the typical theropod cranial forms that have rectangular outlines with elongate preorbital portions (referred to the region anterior to the orbit in this study) and deep rostrums (referred to the region anterior to the maxillary fenestra in this study) (Norell and Makovicky 2004; Turner *et al.* 2012). Eudromaeosaurians have the stereotypical hyper-carnivorous cranium with a robust premaxilla that forms a deep rostrum, and further makes the general shape of the skull rectangular (Fig. 1f). The preorbital portion of the unenlagiine skull appears even more elongate, but the cranium of the unenlagiine *Buitreraptor* is less robust than those of eudromaeosaurians (Makovicky *et al.* 2005), as the maxillary fenestra of *Buitreraptor* is more enlarged than in eudromaeosaurians. In contrast, the preorbital portion of most microraptorians such as *Microraptor*, *Zhenyuanlong*, *Tianyuraptor* and *Wulong* is relatively short and not as elongate as in other dromaeosaurids (Fig. 1e). The microraptorian *Sinornithosaurus*, however, has a slightly elongate preorbital region (Xu *et al.* 1999). The rostrums of small-bodied and possible juvenile microraptorian individuals (NGMC 91, *Microraptor*

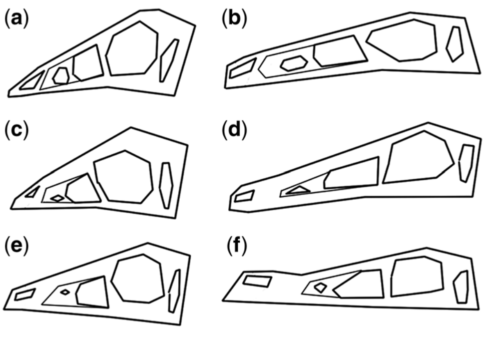

Fig. 1. Summary of skull shapes of short and long snouted anchiornithines, troodontids and dromaeosaurids. (**a**) *Anchiornis*; (**b**) *Caihong*; (**c**) *Mei*; (**d**) *Gobivenator*; (**e**) *Microraptor*; and (**f**) *Velociraptor*.

BMNHC PH881, *Wulong* DNHM D2933) are low and pointy (Pei *et al.* 2014; Poust *et al.* 2020). Slightly larger individuals including possible adult specimens of *Microraptor* and larger specimens of other microraptorians have a slightly deeper rostrum than the small-bodied microraptorian individuals (Xu *et al.* 1999; O'Connor *et al.* 2011; Xing *et al.* 2013), but it is not as deep as in eudromaeosaurians.

The troodontid crania are more lightly built than most eudromaeosaurians. The Early Cretaceous troodontids that are mostly known from the Jehol Biota generally have a triangular bird-like cranial profile with a short preorbital portion and a shallow rostral region (Fig. 1c). In *Sinusonasus*, the rostrum is moderately deep and not as pointy as in other Early Cretaceous troodontids (Xu and Wang 2004). This bird-like profile is retained in the relatively early-diverging Late Cretaceous troodontids *Almas* and *Papiliovenator* (Pei *et al.* 2017*b*, 2022). The later-diverging Late Cretaceous troodontids have an elongate face and a moderately deep rostrum (Fig. 1d), yet the rostrum of these troodontids is not as robust as in eudromaeosaurians (Makovicky *et al.* 2003; Makovicky and Norell 2004; Norell *et al.* 2009; Tsuihiji *et al.* 2014). The maxillary fenestra and the antorbital fossa are significantly anteroposteriorly elongate in these long-snouted troodontids, and become the most prominent features of these troodontids coupled with the elongation of the preorbital portion of their crania (Makovicky *et al.* 2003; Makovicky and Norell 2004; Norell *et al.* 2009; Tsuihiji *et al.* 2014; Pei *et al.* 2017*b*).

The cranial features of most anchiornithines are similar to *Archaeopteryx* and small-bodied deinonychosaurians like *Mei* and *Microraptor*. The crania of anchiornithines have short preorbital portions coupled with shallow and pointy rostrums (Fig. 1a; Hu *et al.* 2009; Xu *et al.* 2011; Godefroit *et al.* 2013; Pei *et al.* 2017*a*). The preorbital region of anchiornithines is fragile and pneumatic with enlarged maxillary and antorbital fenestrae, in addition to the promaxillary fenestra and the external naris (Hu *et al.* 2009; Xu *et al.* 2011; Godefroit *et al.* 2013; Pei *et al.* 2017*a*). Among the anchiornithines, *Caihong* is unique. The rostrum of *Caihong* is deep because of a distinct vertical section of the nasal process of the premaxilla, and the preorbital portion of the cranium is elongate like in eudromaeosaurians and late-diverging troodontids (Fig. 1b). As expected, the cranium of *Caihong* is still lightly built like other anchiornithines with an enlarged maxillary fenestra (Hu *et al.* 2018).

Materials and methods

Previous geometric studies of the theropod crania focused primarily on the general evolutionary trends of the early-diverging theropods or avialans, and only included limited taxa of non-avialan paravians with typical theropod cranial profiles, while the typical small-bodied and short-snouted dromaeosaurids, troodontids and anchiornithines with bird-like crania were either missing from the analyses (Brusatte *et al.* 2012; Foth *et al.* 2016) or were only represented by a single *Anchiornis* specimen without osteohistology-based ontogenetic inference (Bhullar *et al.* 2012; Foth and Rauhut 2013). To fill this gap, this study focuses on the variations of the non-avialan paravians and anchiornithines by constructing an expanded dataset of Dromaeosauridae, Troodontidae and Anchiornithinae, which includes more detailed sampling of non-avialan paravians. Thirty-one specimen-based samples of Dromaeosauridae, Troodontidae and Anchiornithinae are included in this study (Supplementary material), while six samples of these three groups were included in the previous study (Bhullar *et al.* 2012). New landmarks are selected for each sample, especially at the preorbital portion of the skull that is more sensitive for the testing of facial changes (Supplementary material). Selected samples from other theropod groups are included in this study, with both mature and immature specimens incorporated to test the hypothetical paedomorphosis in non-avialan paravians. The ontogenetic stage of each sample is summarized from previous studies of each specimen based on morphological and/or osteohistological information. Only early-diverging oviraptorosaurians are included in this analysis as late-diverging oviraptorosaurians have highly specialized skulls that may hinder the recognition of other meaningful morphological changes of other theropod dinosaurs (Bhullar *et al.* 2012; Brusatte *et al.* 2012).

The methods of geometric morphometrics could be used to quantify the landmark-based shape variations related to phylogeny, ontogeny and polymorphy within a multivariate framework (Mitteroecker and Gunz 2009). We encapsulated the cranial geometry of 66 theropod species/specimens using 21 type 1 and 2 homologous landmarks (Fig. 2a; Supplementary material), which were plotted on photographs and reconstructions using the programs ImageJ and TPSDig2 (Rohlf 2005). The coordinates of landmarks were then superimposed using Generalized Procrustes Analysis in the programs PAST (Hammer 2009) and MorphoJ (Klingenberg 2011) to generate a covariance matrix, which was eventually subjected to principal component analysis. The selected landmarks are mainly focused on the regions anterior to the orbit (Fig. 2a; Supplementary material), as the aim of this study is to investigate the morphological changes in the preorbital portion of the cranium. These rostral and facial bones are also better preserved and less distorted to reflect the actual morphology in small-bodied paravians than bones from

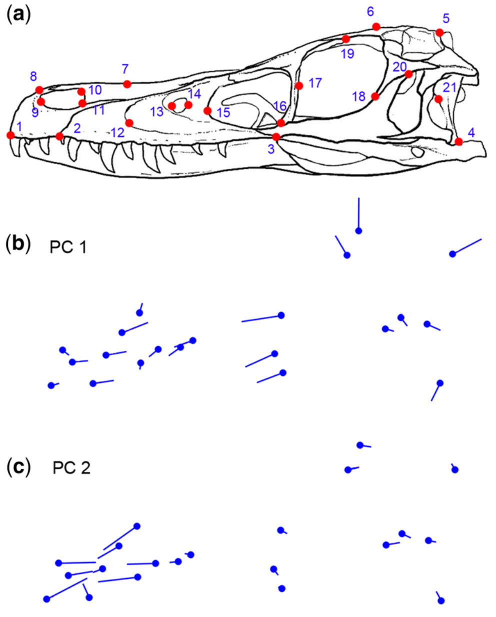

Fig. 2. Theropod cranial shape analysed using geometric morphometrics. (**a**) Landmarks plotted on all skulls in the study; (**b**) major changes in cranial shape on PC 1; (**c**) major changes in cranial shape on PC 2. Skull depicted in (a) is *Velociraptor* (modified from Turner *et al.* 2012).

the posterior portion of the cranium. The preservation of the posterior portion of the cranium (e.g. the temporal region) is heavily influenced by the taphonomy, especially considering that many small-bodied paravian fossils are vulnerable to compression and usually preserved flattened.

Results

The first two principal component (PC) axes (29.7 and 14.1% of total variance, respectively) can summarize the major facial shape variations of the samples. PC 1 mostly describes the variation in the relative size of the orbit as well as the elongation of the preorbital region of the cranium (Fig. 2b). PC 2 mostly describes the relative size of the rostrum (Fig. 2c). The general distribution of the theropods in the morphospace (PC 1 v. PC 2, Fig. 3) confirms the hypothesis of the previous studies that small-bodied non-avialan paravians have paedomorphic skulls compared with the early-diverging theropods, and independent peramorphosis is also observed in various groups.

In the morphospace (PC 1 v. PC 2, Fig. 3), most juvenile non-paravian theropods are located in the large-orbit (greater PC 1) and the short-rostrum (greater PC 2) morphospace. While the juveniles of *Tarbosaurus* and *Dilong* have relatively small orbits and long preorbital regions (lesser PC 1), they still have comparatively larger orbits and shorter preorbital regions than adult tyrannosauroids. Unsurprisingly, most small-bodied dromaeosaurids, troodontids and anchiornithines are also clustered in the large-orbit and the short-rostrum morphospace with *Archaeopteryx* and juveniles of the relatively early-diverging theropods (Fig. 3). This confirms that, like early avialans such as *Archaeopteryx*, the small-bodied paravians also have paedomorphic skulls compared with their theropod ancestors. The small-bodied troodontid *Mei* (DNHM D2514, adult inferred from osteohistology, Gao *et al.* 2012), the anchiornithine *Xiaotingia* (STM 27-2, possible adult inferred from morphology) and the Berlin *Archaeopteryx* locate close to each other with enlarged orbits (greater PC 1) (Fig. 3), but the rostrum is longer (lesser PC 2) in *Archaeopteryx* than in *Mei* and *Xiaotingia*. The small-bodied dromaeosaurid *Microraptor* (QM V1002, possible adult inferred from morphology) also locates within the typical juvenile-like cluster, while it has a slightly elongate preorbital portion (lesser PC 1) compared with *Mei* and *Xiaotingia*.

The majority of non-paravian theropod adults are clustered in the small-orbit (lesser PC 1) morphospace (Fig. 3). Most late-diverging and larger-bodied dromaeosaurids and troodontids are also distributed in the small-orbit (lesser PC 1) morphospace, while these late-diverging troodontids have shorter rostrums (greater PC 2) than late-diverging dromaeosaurids. The majority of tyrannosauroids (except for the long snouted form *Xiongguanlong*) are clustered with the late-diverging dromaeosaurids (Fig. 3). Most anchiornithines for which no definite ontogenetic stages have been identified are clustered with the small-bodied dromaeosaurid and troodontid individuals in the large-orbit (greater PC 1) and the short-rostrum (greater PC 2) morphospace, while *Caihong* is unexpectedly clustered with the smaller-orbited (lesser PC 1) late-diverging troodontids (Fig. 3). *Archaeopteryx* and other late-diverging avialans are distributed in the large-orbit (greater PC 1) and the long-rostrum (lesser PC 2) morphospace, drifting away from the typical theropods. *Yi* and *Caudipteryx* are also located in the morphospace with the enlarged orbit (greater PC 1), close to avialans, but away from the typical theropod cluster.

Discussion

With the rapid increase in the diversity of Mesozoic paravians described in recent decades, more and more studies suggest that paravians have paedomorphic skulls compared with their theropod ancestors

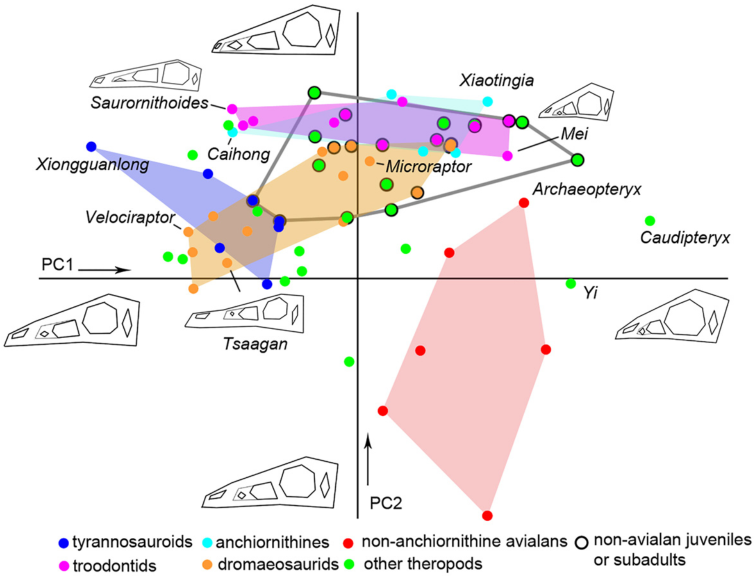

Fig. 3. Two-dimensional theropod cranial shape morphospace (PC 1 v. PC 2). Black circled dots represent juveniles or subadults of non-avialan theropods.

(Xu *et al.* 2003; Xu and Norell 2006; Bever and Norell 2009; Bhullar *et al.* 2012; Choiniere *et al.* 2014; Pei *et al.* 2014, 2017*b*, 2022; Poust *et al.* 2020). Bhullar *et al.* (2012) indicated that *Archaeopteryx* and early avialans had paedomorphic skulls, and also implied that paedomorphic skulls may have existed in the early-diverging and small-bodied non-avialan paravians, even though no quantitative evidence was provided for the latter in their study. This hypothesis, however, is supported and therefore confirmed in our analysis based on the expanded morphological dataset with the small-bodied non-avialan paravians, in which the small-bodied non-avialan paravians do cluster with the juveniles of earlier-diverging theropods such as *Coelophysis*, *Compsognathus*, *Scipicnyx*, *Haplocheirus* and *Sinosauropteryx* (Fig. 3). As expected, the juvenile and subadult troodontids and dromaeosaurids are also plotted in this juvenile cluster (Fig. 3). The morphospace occupied by non-avialan juveniles is fairly large as the samples come from the taxa of a wide phylogenetic range. The specific morphospace (at least the first two PCs) of these young animals (juveniles and subadults) does not correlate well with body size. This is possibly because even though all of these individuals are inferred to be immature, they are still on quite different ontogenetic stages with relatively fast growth rates.

The ontogeny of the sampled specimens is a crucial factor in the interpretation of heterochronic evolutionary patterns. Unfortunately, only a fraction of the sampled specimens have an osteohistology-based ontogenetic interpretation, while the ontogenetic stages of other specimens are either unknown or inferred only based on the morphological information (such as fusion of bones, bone ratios, texture of bone surface and relative size of specimens), which may or may not reflect the real condition (Choiniere *et al.* 2014; Poust *et al.* 2020). Many small-sized paravians sampled in our dataset do not have osteohistology-based developmental interpretation, which may hinder the analysis of this study. The interpretation of the heterochrony should be treated carefully without comprehensive and reliable ontogenetic information of all of the sampled specimens. Owing to the limited information on the ontogenetic series that is available for theropod dinosaurs, this current work will need to be complemented with further studies in the future.

Unlike the typical theropod-like cranial profile (i.e. the cranial profile with a rectangular outline and a relatively long pre-orbital region) found in the late-diverging troodontids and the late-diverging dromaeosaurids, the early-diverging non-avialan paravians and anchiornithines usually have a pointy rostrum, a relatively short preorbital region and an enlarged orbit. The crania of these taxa usually have triangular outlines in lateral view, preorbital regions of around half the entire cranial anteroposterior length and enlarged antorbital fenestrae. The maxillary fenestra is also more enlarged than in later-diverging forms and the lateral lamina of the ascending process of the maxilla is reduced, both of which depict a relatively gracile cranial profile. Taxa with such a profile are usually small-bodied and are often inferred to juveniles or subadults based on their cranial shape and the lack of fusion of bones (e.g. Xu and Norell 2004; Pei *et al.* 2017*b*). However, osteohistological evidence suggests that the small-bodied troodontid *Mei* DNHM D2514 is a mature individual (Gao *et al.* 2012), yet this individual is also located in the juvenile cluster (Fig. 3) and this therefore indicates that the paedomorphic cranium of the small-bodied non-avialan paravians is a real phenomenon rather than merely a reflection of the young ontogenetic stage. This may also imply that the ontogenetic trajectory of this taxon with early somatic maturation is shorter than that in early-diverging theropods. Therefore the paedomorphic cranial profile of the non-avialan paravians is probably a result of the truncation of the heterochronic transformation as suggested previously in avialans (Alberch *et al.* 1979; Bhullar *et al.* 2012). Interestingly, in the relatively later-diverging troodontid *Almas* and *Papiliovenator*, the paedomorphic cranial outline is retained from their ancestors, but the detailed morphology of the preorbital region of these animals bears a strong phylogenetic signal and becomes similar to those of other closely related Late Cretaceous troodontids with elongate preorbital portions (Pei *et al.* 2017*b*, 2022).

With exaggerated ancestral morphologies, some paravians have also been suggested to have peramorphic cranial features (Bhullar *et al.* 2012, 2015; Foth *et al.* 2016). The late-diverging dromaeosaurids (such as *Velociraptor*, *Linheraptor* and *Tsaagan*) and the late-diverging troodontids (such as *Saurornithoides*, *Zanabazar* and *Gobivenator*) have relatively small orbits and long preorbital regions like the relatively early-diverging theropods (Fig. 3). The orbits are relatively small as the preorbital region is significantly elongate and the cranium is more rectangular in outline with a deep and expanded rostrum in both the late-diverging dromaeosaurids and the late-diverging troodontids (e.g. Norell *et al.* 2006, 2009; Xu *et al.* 2011; Tsuihiji *et al.* 2014). The premaxilla usually has a deep main body and the nasal process of the premaxilla has a near vertical base and then curves anterodorsally to become confluent with the near horizontal dorsal surface of the nasal. The lateral lamina of the ascending process of the maxilla is also expanded with a distinctly anterodorsal convex margin, forming a strong and solid upper jaw.

As indicated in our analysis (Fig. 3), even though both the late-diverging dromaeosaurids and the late-diverging troodontids are located in the small-orbit and long-preorbital-portion morphospace like many relatively early-diverging theropods, these two types of deinonychosaurians are still in separate clusters with different morphologies of the rostral region. This indicates that the late-diverging dromaeosaurids and the late-diverging troodontids employed different strategies to achieve a secondarily elongate cranial profile. In the late-diverging dromaeosaurids, such as the eudromaeosaurians *Velociraptor*, *Tsaagan* and *Linheraptor*, the maxillary fenestra is small and dorsally displaced, as is typical for dromaeosaurids, leaving a large unperforated area between the naris and the antorbital fenestra. This structure may provide strong resistance to the skull of these animals, coupled with the deep anterior portion of the ventral lamina of the maxilla, the enlarged lateral lamina of the ascending process of the maxilla and the deep main body of the premaxilla. Many tyrannosauroids also share this robust facial configuration and are clustered with the eudromaeosaurians in our results (Fig. 3). In contrast, the maxillary fenestra in the late-diverging troodontids, such as *Zanabazar*, *Saurornithoides* and *Gobivenator*, is relatively large and elongate, and the area between the pneumatic maxillary fenestra and the naris is relatively smaller than in their dromaeosaurid counterparts. Therefore, the late-diverging troodontids usually have a less robust cranial profile. The prominent dental variations between the late-diverging dromaeosaurids and late-diverging troodontids are probably coupled with the variations of the teeth and the facial region and therefore impact the dietary preferences of these animals. The dromaeosaurids have loosely packed and relatively large-sized maxillary teeth with hyper-carnivorous features similar to those of tyrannosauroids, while the densely packed maxillary teeth of troodontids are often numerous and relatively smaller-sized than in dromaeosaurids. The early-diverging theropod *Coelophysis*, which may feed on small prey (Nesbitt *et al.* 2006), is closely clustered with these late-diverging troodontids in our analysis.

Although most anchiornithines have typical paedomorphic crania like *Archaeopteryx* and the small-bodied deinonychosaurians, the anchiornithine *Caihong* also shows an unusual peramorphic cranial feature with an elongate preorbital region (Fig. 3). The general outline of the cranium of *Caihong* is rectangular like the late-diverging troodontids and dromaeosaurids, but it retains the primitive paravian features of a very large maxillary fenestra and a significantly reduced lateral lamina of the maxillary ascending process. *Archaeopteryx* and other later-diverging avialans also show long rostrums through having elongate premaxillae. A peramorphic feature of the elongation of the premaxilla is also reported in previous studies in stem birds (Bhullar *et al.* 2012, 2015), but our results show that this trend occurs much earlier in avialans than is previously thought and is already present in the Late Jurassic *Archaeopteryx*.

Previous studies with the cranial geometry suggested a general correlation between certain cranial

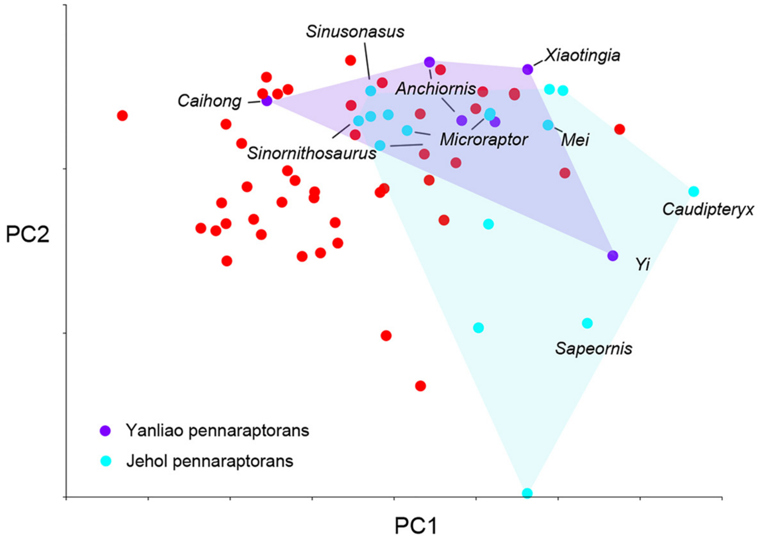

Fig. 4. Two-dimensional theropod cranial shape morphospace (PC 1 v. PC 2) with coloured scheme indicating the Yanliao and Jehol biotas.

shape and the body size in theropod dinosaurs (see Bhullar *et al.* 2012; Brusatte *et al.* 2012; Foth and Rauhut 2013), as small or immature individuals tend to have larger orbits and triangular crania, while large or mature individuals often show relatively small orbits and rectangular crania. Although most specimens follow this pattern in our analysis, several exceptions exist. The relatively large bodied and possible subadults of *Zhenyuanlong* and *Tianyuraptor* possess a paedomorphic cranial profile with a relatively short preorbital portion and relatively large orbits that are typical for the small-bodied microraptorians, which indicates that phylogeny and/or ontogeny plays a more important role than the body size in shaping the crania of these taxa. In contrast, the small-bodied and possible adult individual of *Caihong* has an elongate preorbital portion and a rectangular cranium like most larger-bodied theropods, which may indicate an ecological partitioning between *Caihong* and other small-bodied anchiornithines.

The pennaraptorans from the Jehol Biota occupy a larger morphospace than those from the Yanliao Biota (PC 1 v. PC 2, Fig. 4), yet the morphospace of the two biotas will generally overlap with the late-diverging avialans from the Jehol Biota excluded. *Anchiornis* and *Xiaotingia* from the Yanliao Biota have similar cranial profiles like most dromaeosaurids and troodontids from the Jehol Biota, while *Caihong*, *Sinusonasus* and *Sinornithosaurus* all tend to have an elongate preorbital region and probably occupy different ecological niches (Fig. 4). *Yi* of the Yanliao Biota occupies a cranial morphospace between *Caudipteryx* and avialans of the Jehol Biota, although the morphospace of the Jehol avialans is quite large considering their high taxonomic and ecological diversity. The general overlap of the morphospace of the Yanliao pennaraptorans and the Jehol non-avialan pennaraptorans indicates that these animals of both biotas generally have conservative cranial geometry, and some later-diverging Jehol taxa (mainly avialans) succeed in experimenting with new bauplans and occupy expanded ecological niches. The postcranial morphology also varies significantly despite the cranial outlines being conservative in these animals of the Yanliao and the Jehol biotas. For example, *Caihong*, the small-bodied Jehol troodontids and the larger-bodied Jehol dromaeosaurids have relatively short forelimbs, while the forelimbs of other anchiornithines, *Yi* and small-bodied microraptorians are proportionally longer. The Yanliao biota also lacks larger theropod taxa to take the ecological niches of the Jehol tyrannosauroids and therizinosauroids, which may or may not be taphonomically biased.

Conclusions

Both the typical theropod-like small-orbited cranial profile and the bird-like large-orbited profile exist in all three lineages of the Dromaeosauridae, Troodontidae and Anchiornithinae. Our updated analysis confirms that the early-diverging and small-bodied non-avialan paravians have paedomorphic skulls like the early-diverging avialans. The secondary elongation of the preorbital portion of the cranium occurred independently in the late-diverging deinonychosaurians, but the late-diverging troodontids and the late-diverging dromaeosaurids achieved this feature through different morphological changes. The peramorphic premaxilla of birds was developed as early as in the Late Jurassic *Archaeopteryx* compared with its theropod ancestors. However, comprehensive and reliable ontogenetic information is still needed to carefully examine the heterochronic changes of theropod dinosaurs.

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Data availability All data generated or analysed during this study are included in this published article (and its supplementary information files).

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