Chapter 8
Functional Morphology of the Oviraptorosaurian and Scansoriopterygid Skull

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ABSTRACT

Oviraptorosauria and Scansoriopterygidae are theropod clades that include members suggested to have partially or fully herbivorous diets. Obligate herbivory and carnivory are two ends of the spectrum of dietary habits along which it is unclear how diet within these two clades might have varied. Clarifying their diet is important as it helps understanding of dietary evolution close to the dinosaur-bird transition. Here, diets are investigated by conventional comparative anatomy, as well as measuring mandibular characteristics that are plausibly indicative of the animal's feeding habit, with reference to modern herbivores that may also have nonherbivorous ancestry. In general, the skulls of scansoriopterygids appear less adapted to herbivory compared with those of oviraptorids because they have a lower dorsoventral height, a smaller lateral temporal fenestra, and a smaller jaw-closing mechanical advantage and they lack a tall coronoid process prominence. The results show that oviraptorid mandibles are more adapted to herbivory than those of caenagnathids, early-diverging oviraptorosaurians and scansoriopterygids. It is notable that some caenagnathids possess features like an extremely small articular offset, and low average mandibular height may imply a more carnivorous diet than the higher ones of other oviraptorosaurians. Our study provides a new perspective to evaluate different hypotheses on the diets of scansoriopterygids and oviraptorosaurians, and demonstrates the high dietary complexity among early-diverging pennaraptorans.

INTRODUCTION

Scansoriopterygidae is a clade of theropod dinosaurs only known from the Middle to Late Jurassic Haifanggou/Jiulongshan Formation (Zhang et al., 2002, 2008) and Tiaojishan Formation (Xu et al., 2015) of China. To date, only four species of scansoriopterygids have been reported: *Ambopteryx longibrachium* (Wang et al., 2019), *Epidendrosaurus ninchengensis* (Zhang et al., 2002), *Epidexipteryx hui* (Zhang et al., 2008) and *Yi qi* (Xu et al., 2015). The most iconic feature of scansoriopterygids is perhaps their elongated third manual digit (Czerkas and Yuan, 2002; Zhang et al., 2002, 2008; Xu et al., 2015). It is generally thought that scansoriopterygids had an arboreal lifestyle (Zhang et al., 2002). *Yi* even possesses a rodlike bone extending from its forelimbs, believed to have sup-

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ported membranous wings, the only example among theropods (Xu et al., 2015). Despite having a bizarre body plan, scansoriopterygids share a number of cranial and postcranial osteological similarities with the theropod clades Oviraptorosauria and Avialae (Zhang et al., 2008; O'Connor and Sullivan, 2014). However, the phylogenetic placement of Scansoriopterygidae within Pennaraptora has been contentious: it has been placed at the base of Avialae (O'Connor and Sullivan, 2014) and as an early-diverging lineage within Oviraptorosauria (Agnolín and Novas, 2013; Brusatte et al., 2014; Pei et al., in press). Following the discovery of *Yi*, Scansoriopterygidae has also been recovered as a separate clade from Avialae and Oviraptorosauria, situated at the base of Paraves (Xu et al., 2015, 2017). However, this proposal involves a polytomy between Scansoriopterygidae, Avialae and Deinonychosauria (Xu et al., 2017).

Despite the unique osteology of scansoriopterygids and their importance in understanding the origins of birds and flight, the functional morphology of their skulls has yet to be studied in depth. Only *Epidexipteryx* and *Yi* preserve an articulated skull in lateral view (Zhang et al., 2008; Xu et al., 2015) and all scansoriopterygid fossils are preserved as fossil slabs (Czerkas and Yuan, 2002; Zhang et al., 2002, 2008; Xu et al., 2015) making three-dimensional modeling work difficult. Even for clades like Oviraptorosauria that have a number of taxa preserved in three dimensions, using these methods is still challenging as the sample size is heavily limited by time constraints and logistical difficulties associated with obtaining and restoring 3D models. Thus, analysis requiring 2D data is currently the most tenable for the study of cranial functional morphology in known scansoriopterygid specimens.

Scansoriopterygids and early-diverging oviraptorosaurians do not show obvious adaptations to either obligate herbivory or obligate carnivory, which has meant that their inferred diets remain controversial. The heavy-wear facets in the dentition of *Incisivosaurus* are an exception because they are a strong indicator of herbivory (Xu et al., 2002). Previous work on the dietary patterns among theropods inferred herbivory in both Scansoriopterygidae and Oviraptorosauria based on their osteological features (Zanno and Makovicky, 2011). Recent studies generally accept that at least some oviraptorosaurians were herbivorous (Xu et al., 2002; Longrich et al., 2010, 2013; Lü et al., 2013; Funston et al., 2016), whereas the diet of scansoriopterygids has not been commented on in other studies. As in modern bird groups and those of many other extant animals, it is likely that the diets of all scansoriopterygids and oviraptorosaurians were not entirely homogeneous, but displayed interclade, intraclade, and intraspecific variations.

A suite of differences in the mandibular morphology of caenagnathids and oviraptorids likely indicates distinct feeding styles and diets (Longrich et al., 2010, 2013; Funston and Currie, 2016; Ma et al., 2017, 2020). Most studies propose that oviraptorids had a herbivorous diet (Longrich et al., 2010, 2013; Lü et al., 2013), whereas the diet of caenagnathids is more controversial. The latter includes suggestions of a more predatory lifestyle (Funston and Currie, 2016) or alternatively a herbivorous diet consisting of plant materials softer than those consumed by oviraptorids (Longrich et al., 2013).

Investigating the dietary variation of closely related animals is challenging because their skull shape is usually very similar. Ancestral-state reconstruction analysis of herbivory-related anatomical characters (e.g., the possession of a downturned maxilla and/or dentary and the reduction of tooth count) has been effective in recovering broad patterns in the dietary evolution of theropods (Zanno and Makovicky, 2011), where "absence" or "presence" conditions for many of these characteristics are easily identified among a large sample of skulls with broad morphological and functional diversity. However, applying this method to differentiate the diets of oviraptorosaurians and scansoriopterygids is difficult because most of them possess these categorical "herbivorous characters," so uncovering patterns among these clades requires additional lines of evidence. Here we apply a conventional

comparative anatomy approach coupled with a quantitative, functional approach to study the dietary variation patterns among scansoriopterygids and oviraptorosaurians.

Numerous independently evolved modern herbivores show converging functional adaptations (Stayton, 2006). A series of cranial and mandibular characteristics show a functional link with herbivory in some extant and/or extinct animals, including birds (Greaves, 1974; Freeman, 1979; Emerson, 1985; Hanken and Hall, 1993; Thomason, 1997; Barrett, 2001; Sacco and Van Valkenburgh, 2004; Metzger and Herrel, 2005; Kammerer et al., 2006; Stayton, 2006; Grubich et al., 2008; Samuels, 2009; Olsen, 2017; Navalón et al., 2018). This is based on the idea that herbivores are likely to develop functional convergence, despite the fact that they may not show substantial morphological similarities (Stayton, 2006). For example, modern herbivores usually have a larger jaw-closing mechanical advantage than their carnivorous sister taxon (Stayton, 2006; Samuels, 2009). Thus, an increase in mechanical advantage along a lineage likely suggests an increasing adaptiveness to herbivory. Here we apply six of these characters to scansoriopterygid and oviraptorosaurian skulls, interpreting their variation patterns in terms of different levels of mandibular adaptation to herbivory (see Methods). This is the first in-depth study of the functional morphology of the early-diverging pennaraptorans and promises to provide new insights into their dietary variation that can help to clarify dietary evolution near the origin of birds.

MATERIALS AND METHODS

Materials

Twenty-six pennaraptoran mandibles were studied firsthand and from the literature (table 1). High-resolution photographs in lateral view were taken in person or from the literature (table 1) and then measured with the software ImageJ. The study sample included all available and usable mandibles of scansoriopterygids (2) and oviraptorosaurians (15). It also included six early-diverging avialans and three dromaeosaurids for comparative purposes, especially because of the controversial phylogenetic placement of Scansoriopterygidae at present (see Introduction).

Comparative Anatomy

Standard comparative anatomy methods are used to study the morphology and functional implications of scansoriopterygid and oviraptorosaurian skulls.

Functional Analysis

The six mandibular characteristics included in the functional analysis are: (1) anterior jaw-closing mechanical advantage (AMA); (2) posterior jaw-closing mechanical advantage (PMA); (3) jaw-opening mechanical advantage (OMA); (4) relative articular offset (RAO); (5) relative maximum mandible height (MMH); and (6) relative average mandible height (AMH). All these characters involve only two-dimensional measurements, which allows us to maximize our sample size from the slab specimens available while at the same time obtaining meaningful insights into the dietary habits of these early-diverging pennaraptorans. For the selection of each mandibular characteristic we identify a rationale.

Jaw-closing Mechanical Advantage: Mechanical advantage refers to the ratio of the output force to the input force of a mechanical system. This is also equivalent to the ratio of the distance between the fulcrum and the effort (inlever) to the distance between the fulcrum and the load (outlever). Measuring the jaw-closing mechanical advantage (MA) allows us to compare the effectiveness of the jaw occlusal system of different mandibles. The value of MA is also likely to provide an indication of the diet of an animal. Animals that have a plant-based diet are likely to have a higher jaw-closing MA than their carnivorous sister taxa (sensu Stayton, 2006). In a mechanical system, there is a trade-off between

TABLE 1

List of specimens utilized in the functional analysis of this study

Institutional abbreviations: **AMNH,** American Museum of Natural History, New York; **BSP,** Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **CM,** Carnegie Museum of Natural History, Pittsburgh, PA; **CMN,** Canadian Museum of Nature, Ottawa, Ontario, Canada; **DYM,** Dongyang Museum, Dongyang City, Zhejiang, China; **FIP,** Florida Institute of Paleontology, Dania Beach, FL; **HGM,** Henan Geological Museum, Zhengzhou, Henan, China; **IVPP,** Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **LH,** Long Hao Institute of Geology and Paleontology, Hohhot, Nei Mongol, China; **MPC,** Paleontological Center, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; **STM,** Shandong Tianyu Museum of Nature, Pingyi, Shandong, China; **TMP,** Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; **YPM,** Yale Peabody Museum, New Haven, CT.

Clade	Taxon	Specimen	Data source	Reference
Scansoriopterygidae	*Epidexipteryx hui*	IVPP V15471	Firsthand	(Zhang et al., 2008)
	Yi qi	STM 31-2	Firsthand	(Xu et al., 2015)
Early-diverging oviraptorosaurians	*Incisivosaurus gauthieri*	IVPP V13326	Firsthand	(Xu et al., 2002)
	Caudipteryx sp.	IVPP V12430	Firsthand	(Ji et al., 1998)
Caenagnathidae	*Gigantoraptor erlianensis*	LH V0011	Firsthand	(Xu et al., 2007; Ma et al., 2017)
	Anzu wyliei	CM 78000	Firsthand	(Lamanna et al., 2014)
	Caenagnathus collinsi	CMN 8776	Literature	(Currie et al., 1993)
	Chirostenotes pergracilis	TMP 2001.12.12	Literature	(Funston and Currie, 2014)
Oviraptoridae	*Oviraptor philoceratops*	AMNH 6517	Firsthand	(Osborn et al., 1924)
	Rinchenia mongoliensis	MPC-D 100/32A	Literature	(Funston et al., 2017)
	Citipati osmolskae	IGM 100/978	Firsthand	(Clark et al., 2002)
	Huanansaurus ganzhouensis	HGM41HIII-0443	Firsthand	(Lü et al., 2015)
	Tongtianlong limosus	DYM-2013-8	Firsthand	(Lü et al., 2016)
	Banji long	IVPP V16896	Firsthand	(Xu and Han, 2010)
	Khaan mckennai	IGM 100/973	Firsthand	(Balanoff and Norell, 2012)
	Jiangxisaurus ganzhouensis	HGM41HIII0421	Firsthand	(Wei et al., 2013)
	Nemegtomaia barsboldi	MPC-D 100/2112	Literature	(Lü et al., 2004)
Avialae	*Jeholornis prima*	Reconstruction	Literature	(Xu et al., 2011)
	Sapeornis chaoyangensis	Reconstruction of IVPP V13275 and V13276	Firsthand	(Zhou and Zhang, 2003)
	Confuciusornis sanctus	Reconstruction	Literature	(Martin et al., 1998)
	Archaeopteryx lithographica	Reconstruction of BSP 1999 I 50	Firsthand	(Martin et al., 1998)
	Xiaotinggia zhengi	Reconstruction of STM 27-2	Firsthand	(Xu et al., 2011)
	Anchiornis huxleyi	Reconstruction	Literature	(Xu et al., 2011)
Dromaeosauridae	*Dromaeosaurus albertensis*	AMNH 5356	Firsthand	(Currie, 1995)
	Deinonychus antirrhopus	Reconstruction of YPM 5210 and YPM 5232	Firsthand	(Ostrom, 1969)
	Bambiraptor feinbergi	Reconstruction of FIP001	Firsthand	(Burnham et al., 2000)

jaw-closing velocity and MA—they cannot be maximized at the same time (i.e., increasing the jaw-closing velocity would reduce the MA). Velocity is important to carnivores that feed on elusive prey. Thus, carnivores need to take a balance between velocity and bite force as both factors influence hunting success. In contrast, it is expected that herbivores tend to maximize their jaw-closing MA because velocity is not a determining factor in plant procurement (Stayton, 2006). Increasing the MA allows herbivores to produce a larger bite force with the same input muscle force, and so exploit a wider range of vegetation (i.e., hard-fibered plants). This pattern is commonly seen in modern animals: herbivorous bird taxa convergently show increased jaw-closing MA compared to their omnivorous/carnivorous counterparts (Olsen, 2017; Navalón et al., 2018). Similar functional convergence is also observed in extant herbivorous lizards (Stayton, 2006), rodents (Samuels, 2009), and bears (Sacco and Van Valkenburgh, 2004). In this study, two characteristics of jaw-closing MA are applied:

Anterior Jaw-closing Mechanical Advantage: When measuring anterior jaw-closing mechanical advantage (AMA) (fig. 1A), the inlever is the distance from the midpoint of the articular glenoid to the midpoint of the adductor muscle attachment site (comprising the m. adductor mandibulae externus profundus [m. AMEP], m. adductor mandibulae externus medialis [m. AMEM], and m. adductor mandibulae externus superficialis [m. AMES]). The muscle-attachment sites were identified based on the reconstruction proposed by Holliday (2009). The outlever is defined as the distance between the midpoint of the articular glenoid and the most anterior point of the dentary or the tip of the first dentary tooth for toothed specimens. Oviraptorosaurians have a distinctive sliding joint that allows anteroposterior jaw movement (Clark et al., 2002), and thus measurements depending on glenoid location change as the jaw moves. The midpoint of the glenoid was chosen as the measurement point to facilitate comparisons with other taxa, although it should be noted that such measurements may not represent the full range of biomechanical performance of oviraptorosaurian jaws.

Posterior Jaw-closing Mechanical Advantage: For the measurement of posterior mechanical advantage (PMA), the inlever is the same as that of AMA (fig. 1A). However, the outlever here refers to the distance between the midpoint of the articular glenoid and the most posterior point of the occlusal margin (fig. 1B). For toothed specimens, the most posterior occlusal point is defined as the tip of the most posterior dentary tooth (fig. 1B). For edentulous specimens, this point is marked as the posteriormost point of the beak along the dorsal margin of the dentary. The posterior extent of the rhamphotheca in these specimens is reconstructed with reference to the proposed examples in Ma et al. (2017), which in turn follow the rationale suggested in Hieronymus and Witmer (2010) and Lautenschlager et al. (2014).

Jaw-opening Mechanical Advantage: In the calculation of jaw-opening mechanical advantage (OMA), the outlever refers to the distance between the midpoint of the articular glenoid and the anteriormost point of the mandible or the dorsal tip of the first tooth (fig. 1C). The inlever is measured from the midpoint of the articular glenoid to the posteriormost point of the retroarticular process (fig. 1C). The retroarticular process is the attachment point for the m. depressor mandibulae (m. DM), a muscle that is responsible for the jaw-opening action (Holliday, 2009).

OMA is related to the velocity of the jaw-opening action, with a smaller OMA indicating a faster jaw-opening action. Animals that feed on elusive prey would benefit from having a lower OMA, which increases the speed of the prey-capturing process. Thus, herbivores are likely to have a higher OMA than their carnivorous relatives. Previous studies on modern carnivorous lizards (Hanken and Hall, 1993), gars (Kammerer et al., 2006), and frogs (Emerson, 1985) indicate that skulls with a shorter retroarticular process have a higher jaw-opening speed, which suits the hunting of fast-moving prey.

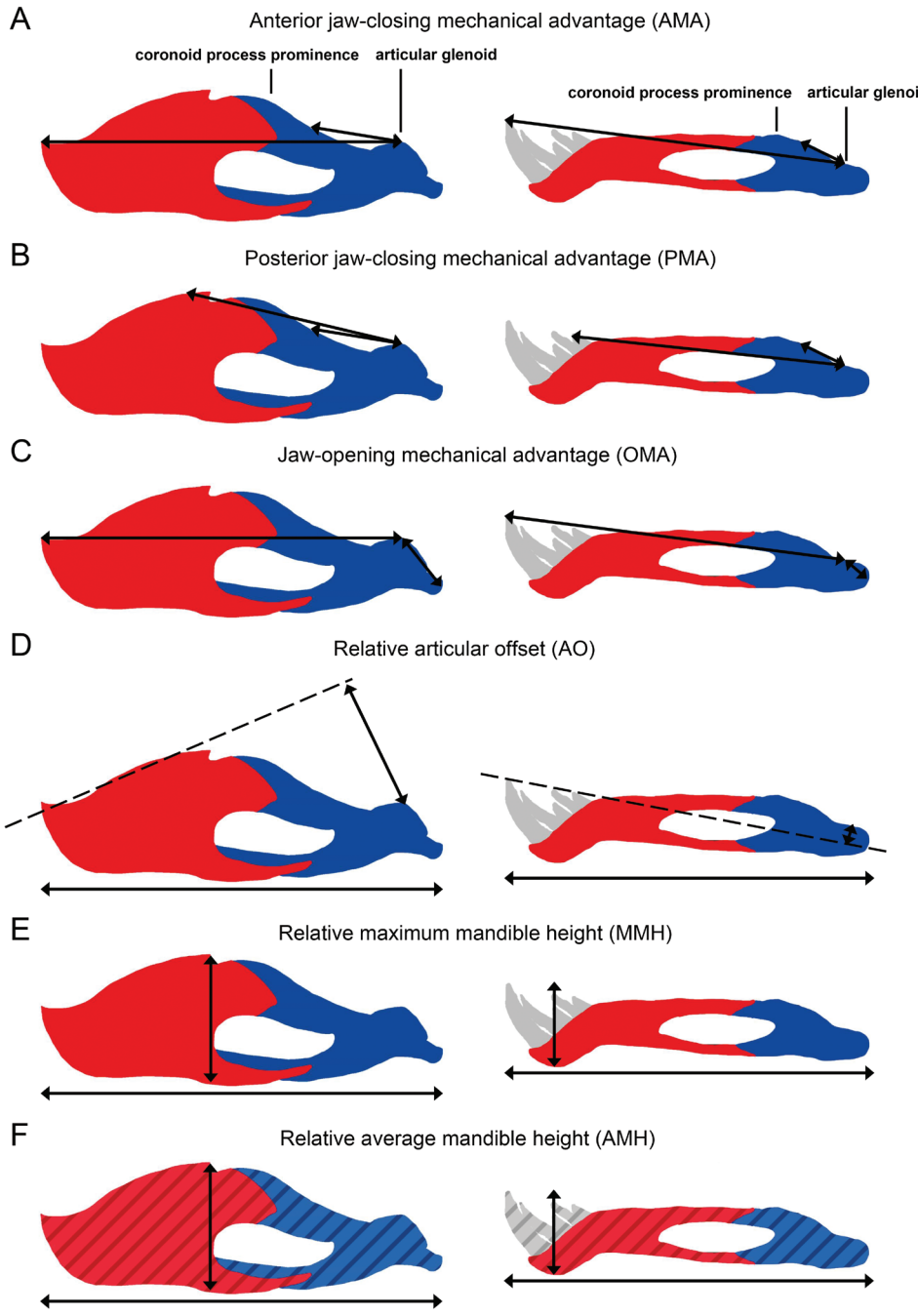


FIG. 1. Schematic diagram showing how the six functionally related mandibular characteristics were measured in the oviraptorosaurians and scansoriopterygids studied. **A.** Anterior jaw-closing mechanical advantage, AMA. **B.** Posterior jaw-closing mechanical advantage, PMA. **C.** Jaw-opening mechanical advantage, OMA. **D.** Relative articular offset, AO. **E.** Relative maximum mandible height, MMH. **F.** Relative average mandible height, AMH.

Relative Articular Offset: Relative articular offset (AO) is measured as the perpendicular distance between the tangent line of the occlusal margin and the midpoint of the articular glenoid, divided by the anteroposterior length of the mandible (fig. 1D). The purpose of dividing the articular offset by the total mandibular length is to make the measurement size independent, as body size varies among scansoriopterygids and oviraptorosaurians.

Differences in this character represent different modes of occlusion. A large AO suggests that different locations of the occlusal margin of the mandible contact with the upper jaw nearly simultaneously (Greaves, 1974). In contrast, a small AO suggests that different locations of the mandible occlude with the upper jaw at different instants, starting from the posteriormost point to the anterior tip (i.e., a "scissorlike" occlusal mode) (Greaves, 1974; Grubich et al., 2008). Herbivores usually have a large AO whereas carnivores tend to have a small one (Freeman, 1979; Thomason, 1997). This increases the effectiveness of the plant-cropping and meat-slicing procedures in herbivores and carnivores respectively (Freeman, 1979). This pattern can be observed extensively in both extant and extinct animals, such as ornithischian dinosaurs (Barrett, 2001), modern mammals (Greaves, 1974), and fish (Grubich et al., 2008).

Relative Maximum Mandible Height: Relative maximum mandible height (MMH) refers to the maximum height of the mandible divided by its total length (fig. 1E). To ensure the orientation of the mandibles are standardized when measurements are made, the horizon here refers to the "best fit" of the ventral margin of the mandible, as defined in the studies of therizinosaurian (Zanno et al., 2016) and oviraptorosaurian jaws (Ma et al., 2017). The height is measured as perpendicular to the horizon. This character relates to the stiffness of a mandible along the dorsoventral direction (the direction along which stress is applied on the jaw during occlusion). It is observed that animals with a feeding style that requires a larger bite force have a more robust mandible (i.e., a larger MMH) to resist the stress (Sacco and Van Valkenburgh, 2004). With an expected increase in MA and bite force in herbivores, having a stiffer mandible allows them to mitigate the stress experienced by the mandibles during plant cropping. Herbivorous bears are known to have a more rigid mandible than the nonherbivorous ones, a trait that may be linked to an increase in MA (Sacco and Van Valkenburgh, 2004). Different lineages of extant herbivorous lizards convergently show an increase in skull height, whereas their carnivorous counterparts have a relatively elongated skull (i.e., lower in height) (Metzger and Herrel, 2005). Extant rodents specialized in herbivory are observed to have a taller skull than the generalist herbivorous rodents (Samuels, 2009).

Relative Average Mandible Height: Relative average mandible height (AMH) can be obtained by dividing the average mandible height by the total mandible length (fig. 1F). Average mandible height is defined as the total area of the mandible in lateral view divided by its total mandible length. The total area of the mandible excludes the area of the external mandibular fenestra to ensure only the parts that contribute to jaw stiffness are considered. Based on the same principle as MMH, a larger AMH is likely to represent a stiffer jaw, which suggests a feeding style that requires a stronger bite. Thus, animals having a larger AMH are likely to be more adapted to herbivory.

Ancestral-State Reconstruction: Ancestral-state reconstruction of functional characters was conducted in the software Mesquite v. 3.4 with the function "Parsimony ancestral state reconstruction method" under "Trace character history" (Maddison and Maddison, 2018). This allows us to visualize the evolutionary trends of different characters in Pennaraptora, especially across those well-sampled lineages such as Oviraptoridae and Caenagnathidae. As there is no single phylogeny that includes all the pennaraptorans involved in the study, we have produced a hypothetical phylogenetic tree by integrating the trees of different pennaraptoran clades (Lü et al., 2017; Pei et al., in press).

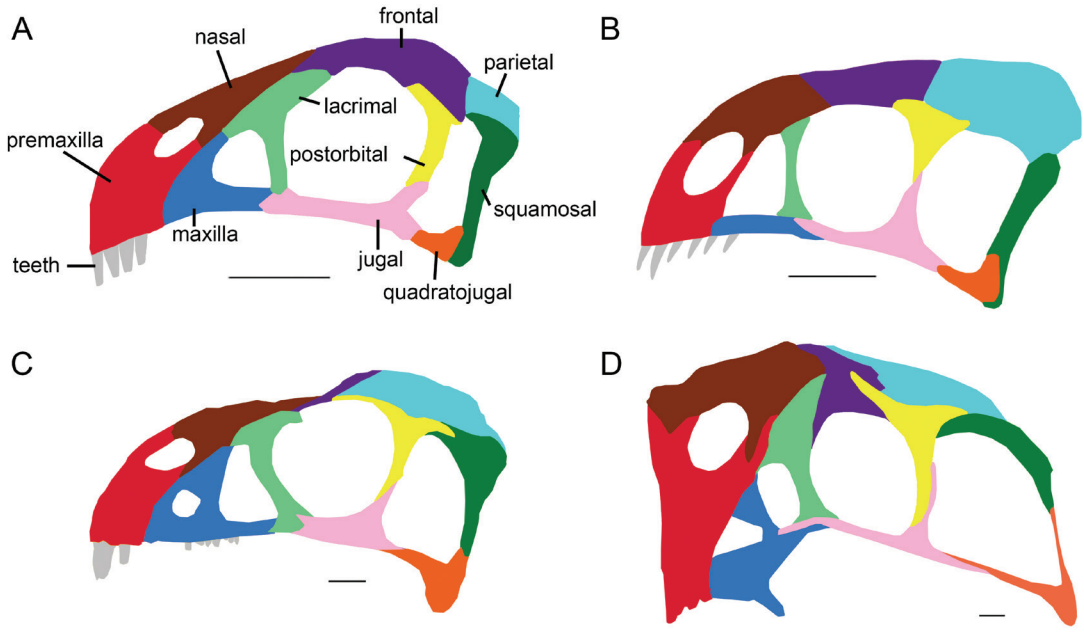


FIG. 2. Simplified drawings of the crania of early-diverging pennaraptorans. **A.** *Yi.* Qualitative reconstruction of STM 31-2, modified from Xu et al. (2015). **B.** *Epidexipteryx.* Qualitative reconstruction of IVPP V15471, modified from Zhang et al. (2008). **C.** *Incisivosaurus.* Qualitative reconstruction of IVPP V13326, modified from Xu et al. (2002). **D.** *Citipati.* Qualitative reconstruction of IGM 100/978, modified from Clark et al. (2002). Scale is 1 cm.

RESULTS

Comparative Anatomy

Cranium

The skulls of scansoriopterygids are short and high when compared with those of typical theropods (fig. 2). Scansoriopterygids share a similar skull shape to early-diverging oviraptorosaurians such as *Incisivosaurus* (fig. 2C) and *Caudipteryx* (O'Connor and Sullivan, 2014). The skulls of *Yi* and *Epidexipteryx* have a height of about 40% and 60% (Zhang et al., 2008) of their anteroposterior lengths respectively (fig. 2A, B). The height/length ratio of the skull of *Epidexipteryx* is comparable to those of some oviraptorids, such as *Banji*, *Citipati*, and *Khaan* (fig. 2B, D). However, some late-diverging oviraptorosaurians have a taller skull because of the presence of a tall crest (Lamanna et al., 2014; Funston et al., 2017; Lü et al., 2017). Oviraptorids, such as *Rinchenia*, have a skull length and height that are nearly identical (Tsuihiji et al., 2016: fig. 8). *Yi* was described with a crestlike structure above its nasal (Xu et al., 2015) that is lower than those of crested caenagnathids and oviraptorids (fig. 2D). However, cranial crests are not known in early-diverging oviraptorosaurians (fig. 2C). The dorsal margin of the external naris of scansoriopterygids is positioned at a comparable level to that of the antorbital fenestra, as in *Incisivosaurus* and possibly *Caudipteryx* (fig. 2A–C). In late-diverging oviraptorosaurians, the relative position of the external naris and antorbital fenestra is highly variable (Lü et al., 2017: fig. 6; Ma et al., 2020). When compared to scansoriopterygids and early-diverging oviraptorosaurians, late-diverging oviraptorosaurians generally have an elevated external naris (fig. 2). The orbit of scansoriopterygids is large relative to the lateral profile of the crania (about 25% of the total area of the crania in lateral view; fig. 2A, B). The relative size of the orbit is smaller in oviraptorosaurians (about 14% and 20% in oviraptorids and

Incisivosaurus respectively; fig. 2C, D). The orbit of scansoriopterygids and oviraptorosaurians are circular in shape (fig. 2), similar to those of closely related theropods like early-diverging avialans, therizinosaurians, and ornithomimosaurians. The lateral temporal fenestra of scansoriopterygids is smaller than their orbits in lateral view, unlike the condition in oviraptorosaurians where the two fenestrae are usually comparable in size (fig. 2). The lateral temporal fenestra of scansoriopterygids is longer dorsoventrally than anteroposteriorly (fig. 2), similar to those of typical theropods. This condition is also present in some oviraptorosaurians such as *Incisivosaurus*, *Tongtianlong*, and *Corythoraptor*. However, some oviraptorids have a more squarelike lateral temporal fenestra, including *Rinchenia*, *Conchoraptor*, and *Citipati* (fig. 2D). The upper jaw of scansoriopterygids is toothed, a condition absent in oviraptorids and caenagnathids but present in some early-diverging oviraptorosaurians including *Incisivosaurus*, *Caudipteryx*, and *Protarchaeopteryx*. *Yi* possesses at least four premaxillary teeth on each side whereas no maxillary tooth is visible in the only known specimen of *Yi* (Xu et al., 2015). *Epidexipteryx* has at least seven teeth on each side of its upper jaw (Zhang et al., 2008), although the exact number of premaxillary and maxillary teeth cannot be determined due to poor preservation. In general, toothed oviraptorosaurians seem to possess more teeth in their upper jaw than scansoriopterygids: *Incisivosaurus* has at least four and nine teeth on each side of the premaxilla and maxilla respectively (Balanoff et al., 2009); *Protarchaeopteryx* displays eight teeth on each side of its upper jaw (Ji et al., 1998). However, the maxilla of *Caudipteryx* is edentulous and each of its premaxillae possesses only four teeth (Ji et al., 1998). A heterodont condition with anterior teeth enlargement is present in both scansoriopterygids and toothed oviraptorosaurians. In scansoriopterygids, anterior premaxillary teeth are larger than the ones located more posteriorly (Zhang et al., 2008; Xu et al., 2015). This condition is especially evident in *Epidexipteryx*: its robust second premaxillary tooth is about 1.5× the lengths of the other teeth (Zhang et al., 2008: fig. 1). In comparison, the anterior enlargement of teeth is less obvious in *Yi* as the size difference between its teeth is not prominent. The dentition-variation patterns in *Incisivosaurus* and *Protarchaeopteryx* are slightly different from those of scansoriopterygids. The first premaxillary tooth of *Incisivosaurus* is the largest tooth, which is about double the length of the other teeth. In *Protarchaeopteryx*, the first four teeth seem to be comparable in their sizes but they are all longer than the more posterior ones (Ji et al., 1998: fig. 2).

Compared to oviraptorosaurians, the frontals of scansoriopterygids are relatively long in general (fig. 2). *Epidexipteryx*, *Yi*, and *Epidendrosaurus* have fairly long frontals, which make up approximately 40% of their skull lengths (the skull length of *Epidendrosaurus* is estimated from its mandible length) (Zhang et al., 2002: fig. 1; 2008: fig. 2; Xu et al., 2015: fig. 3). The relative length of the frontals of *Incisivosaurus* is longer than those of other oviraptorosaurians (about 20% of the skull length) (Xu et al., 2002; Balanoff et al., 2009), although it is still shorter than those of scansoriopterygids. In scansoriopterygids, the parietals are anteroposteriorly shorter than the frontals (Zhang et al., 2002: fig. 1; 2008: fig. 2; Xu et al., 2015: fig. 3). Both *Epidexipteryx* and *Epidendrosaurus* have a parietal/frontal ratio of approximately 0.8, whereas the ratio is about 0.25 for *Yi* (Zhang et al., 2002: fig. 1; 2008: fig. 2; Xu et al., 2015: fig. 3). In the early-diverging oviraptorosaurians *Incisivosaurus* and *Caudipteryx*, the lengths of parietals are similar to and shorter than the frontals respectively (Ji et al., 1998; Balanoff et al., 2009). However, in oviraptorids, the parietals are anteroposteriorly longer than the frontals (Osmolska et al., 2004).

Mandible

The overall shape of the mandible of scansoriopterygids is more similar to those of early-diverging oviraptorosaurians (especially

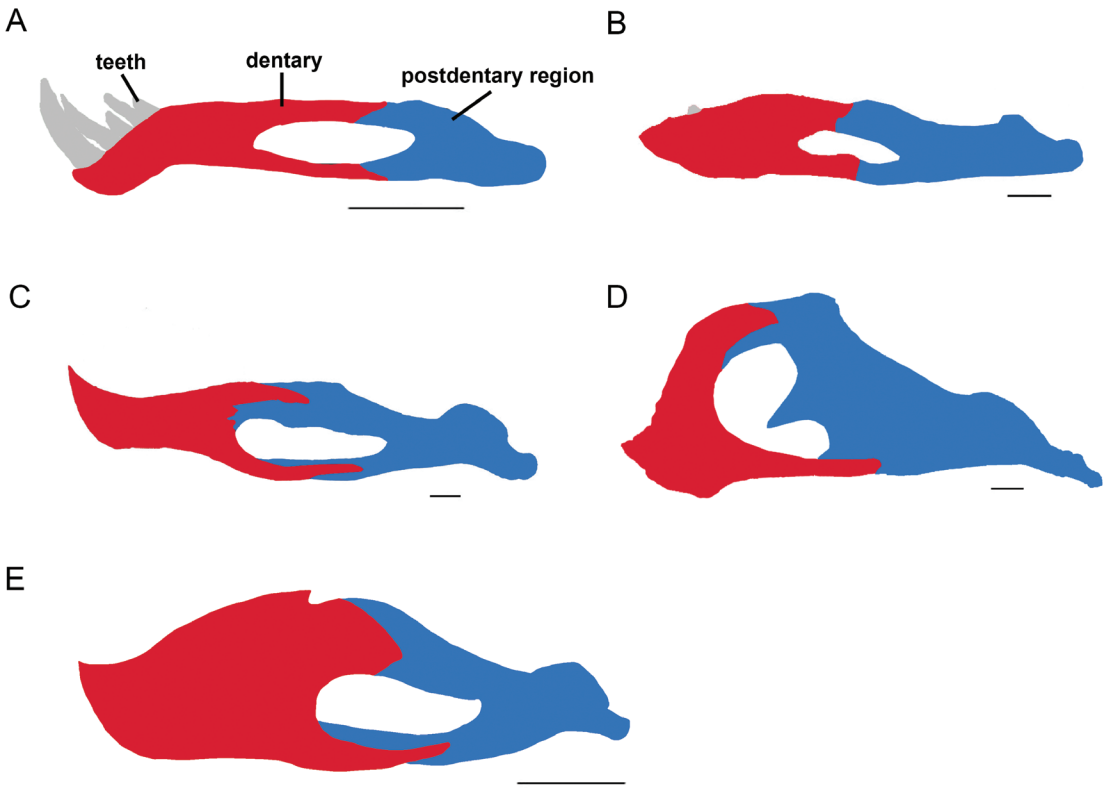


FIG. 3. Mandible of early-diverging pennaraptorans. **A.** *Epidexipteryx.* Qualitative reconstruction of IVPP V15471, modified from Zhang et al. (2008). **B.** *Incisivosaurus.* Qualitative reconstruction of IVPP V13326, modified from Xu et al. (2002). **C.** *Chirostenotes.* Qualitative reconstruction of TMP 2001.12.12, modified from Funston and Currie (2014). **D.** *Citipati.* Qualitative reconstruction of IGM 100/978, modified from Clark et al. (2002). **E.** *Gigantoraptor.* Qualitative reconstruction of LH V0011, modified from Ma et al. (2017). Scale is 1 cm in A–D; 10 cm in E.

Caudipteryx) and most caenagnathids (except *Gigantoraptor*) than the late-diverging ones (fig. 3A–C compared with 3D, E). The mandible of scansoriopterygids is shallow relative to those of oviraptorids (fig. 3A compared to 3D). Their dentary does not expand dorsoventrally posterior to the symphyseal region, in contrast to the condition in caenagnathids, oviraptorids, and *Avimimus*. The dentary of oviraptorosaurians is likely to be covered with rhamphotheca, as indicated by the presence of foramina and fossa on the outer surface of the dentary (Ma et al., 2017), whereas the condition in scansoriopterygids is unclear as no foramina are visible in known specimens.

The anterior portion of the dentary of scansoriopterygids is downturned (fig. 3A), as in theropods like oviraptorosaurians, ornithomimosaurians, therizinosaurians, and some early-diverging avialans (Zanno and Makovicky, 2013). Dentary teeth are present in *Epidexipteryx* (Zhang et al., 2008), *Epidendrosaurus* (Zhang et al., 2002) and *Yi* (Xu et al., 2015). In Oviraptorosauria, *Incisivosaurus* (Xu et al., 2002), *Protarchaeopteryx* (Ji et al., 1998), and *Ningyuansaurus* (Ji et al., 2012) are known to have dentary teeth. *Protarchaeopteryx*, *Incisivosaurus*, and *Ningyuansaurus* have at least seven (Ji et al., 1998), nine (Balanoff et al., 2009), and 14 (Ji et al., 2012) dentary teeth respectively. In

scansoriopterygids, *Epidexipteryx*, *Yi*, and *Epidendrosaurus* have at least five (Zhang et al., 2008), three (Xu et al., 2015) and 12 (Zhang et al., 2002) dentary teeth respectively.

Scansoriopterygids and *Incisivosaurus* both possess unserrated teeth, whereas all the dentary teeth of *Protarchaeopteryx* are anteriorly and posteriorly serrated (Ji et al., 1998). The teeth of scansoriopterygids are generally straight (i.e., not recurved), although the distal margin of the first dentary tooth of *Epidexipteryx* appears to be curved (Zhang et al., 2008: fig. 1; Xu et al., 2015: fig. 1). Anterior enlargement of the dentary teeth is observed in scansoriopterygids (Zhang et al., 2002, 2008; Xu et al., 2015). This condition is especially obvious in *Epidexipteryx* as its first dentary tooth is about 2× the length of its third and fourth teeth (Zhang et al., 2008: fig. 1; fig. 3A). Due to missing teeth, it is unclear whether anterior teeth enlargement is also present in *Incisivosaurus* and *Protarchaeopteryx*, although the sizes of their preserved teeth do not show strong variation. The dentary teeth of scansoriopterygids are highly procumbent (Zhang et al., 2002, 2008; Xu et al., 2015), unlike the condition in *Incisivosaurus* where its teeth are only slightly procumbent (Balanoff et al., 2009; fig. 3A, B). In *Epidexipteryx*, the first dentary tooth is highly recurved and the more posterior teeth are relatively long and thin (Zhang et al., 2008: fig. 1; fig. 3A). In contrast, the preserved dentary teeth of *Incisivosaurus* (Balanoff et al., 2009) and *Protarchaeopteryx* (Ji et al., 1998) are more bulbous and none of them are recurved. The dentary teeth of *Epidexipteryx* are tightly packed, unlike those of *Incisivosaurus* where the distances between subsequent teeth are similar to half of the width of the teeth themselves (Xu et al., 2002: fig. 1e) (fig. 3A, B).

Scansoriopterygids do not possess a tall coronoid process prominence, unlike most oviraptorosaurians. Oviraptorids, in general, have a taller coronoid process prominence than other oviraptorosaurians (Ma et al., 2017). The shape of the external mandibular fenestra of scansoriopterygids is similar to those of early-diverging oviraptorosaurians and caenagnathids, which are all relatively long and dorsoventrally low (fig. 3A–C, E). This is different from the condition in oviraptorids, in which the external mandibular fenestra is more circular (fig. 3D). The articular glenoid of oviraptorosaurians is dorsally convex in lateral view, unlike that of scansoriopterygids where it is relatively flat (Zhang et al., 2008: figs. 1, 2; fig. 3).

Functional Comparison

Six functional characters were measured and subjected to ancestral-state reconstruction analysis using squared-change parsimony and a tree topology (fig. 4; table 2) based on Lü et al. (2017) and Pei et al. (in press). The reconstructed nodal value of mechanical advantage (MA) of the jaw-closing system (average of AMA and PMA) of scansoriopterygids (~0.179) is lower than those of oviraptorosaurians. MA varies largely within Oviraptorosauria: oviraptorids have the largest MA of ~0.311 whereas caenagnathids have a value of ~0.272. The MAs of early-diverging avialans and dromaeosaurids are smaller than those of oviraptorosaurians. Scansoriopterygids have a lower AMA than oviraptorosaurians. The AMAs of caenagnathids and early-diverging oviraptorosaurians are similar, which is ~0.190. Oviraptorids have the greatest AMA, which is ~0.267. Oviraptorids have the largest PMA among the studied taxa (~0.355). Caenagnathids and early-diverging oviraptorosaurians have PMAs of ~0.341 and ~0.291 respectively. The PMA of scansoriopterygids is smaller than that of oviraptorosaurians, which is ~0.202. PMA is always larger than AMA because when the position of the load moves from the front tip of the occlusal margin to the posteriormost point, the outlever decreases and eventually results in a larger MA. It is noteworthy that some taxa display a more significant variation in MA than others (i.e., percentage difference between AMA and PMA). The MA of scansoriopterygids shows the smallest increase among the studied taxa, which is only ~30.3%. The percentage increases in MA of oviraptorids is relatively small, which is ~33.0%. The

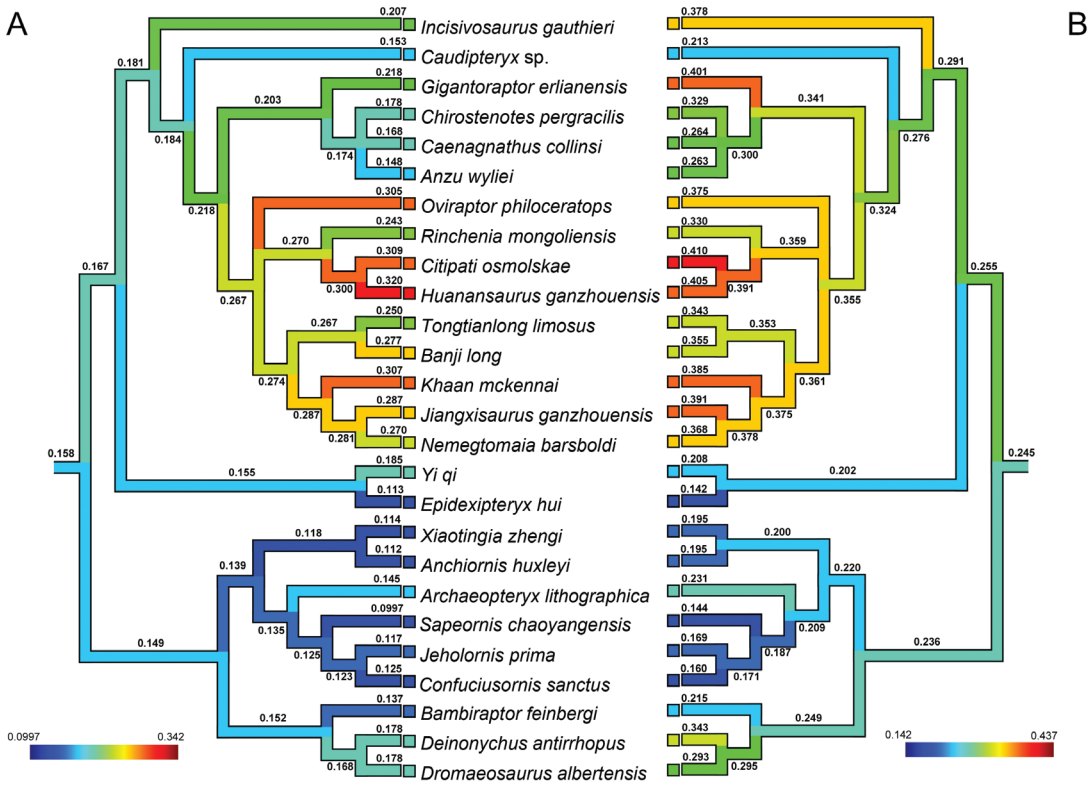
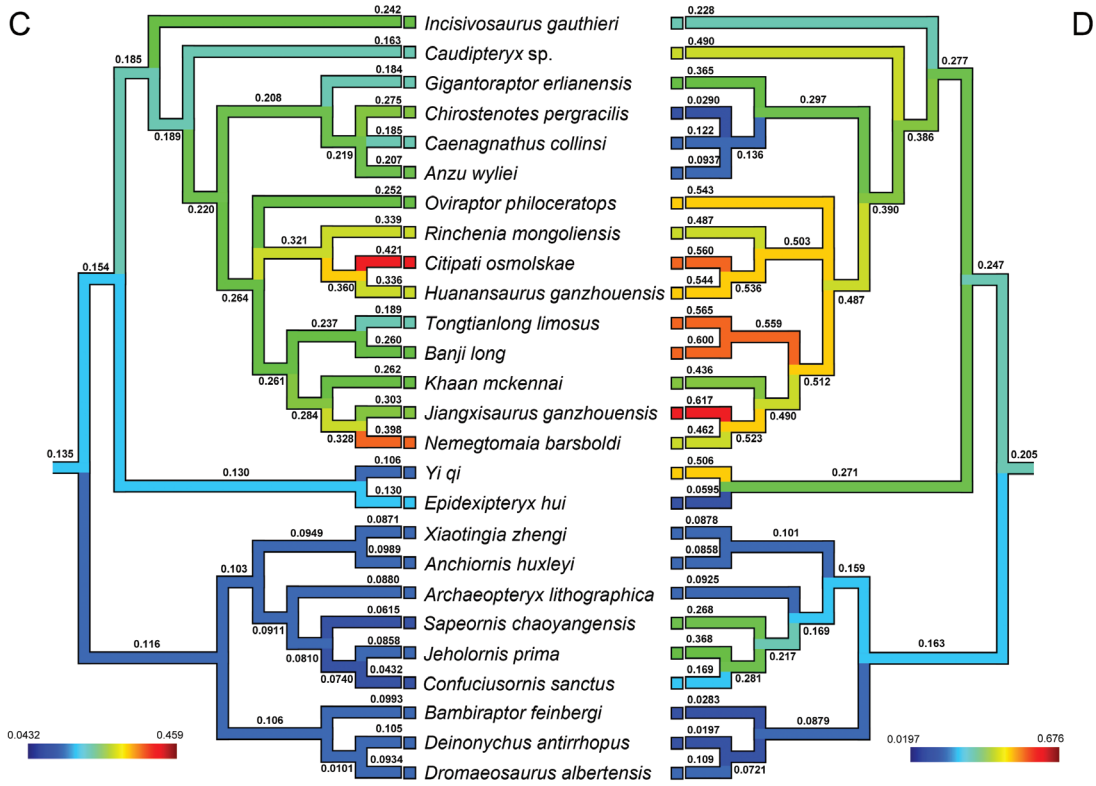


FIG. 4. Ancestral-state reconstruction (*above and following two pages*) of the six functional characters across Pennaraptora under squared-change parsimony (above and on next two pages). **A.** Anterior jaw-closing mechanical advantage, AMA. **B.** Posterior jaw-closing mechanical advantage, PMA. **C.** Jaw-opening mechanical advantage, OMA. **D.** Relative articular offset, AO. **E.** Relative maximum mandible height, MMH. **F.** Relative average mandible height, AMH. Tree topology based on Lü et al. (2017) and Pei et al. (in press). Reconstructed nodal values for select nodes are given in table 2.

percentage increase in MA in early-diverging oviraptorosaurians is ~60.8%, which is intermediate between those of oviraptorids and caenagnathids. Caenagnathids and dromaeosaurids show a large increase in MA of ~68.0% and ~63.8% respectively.

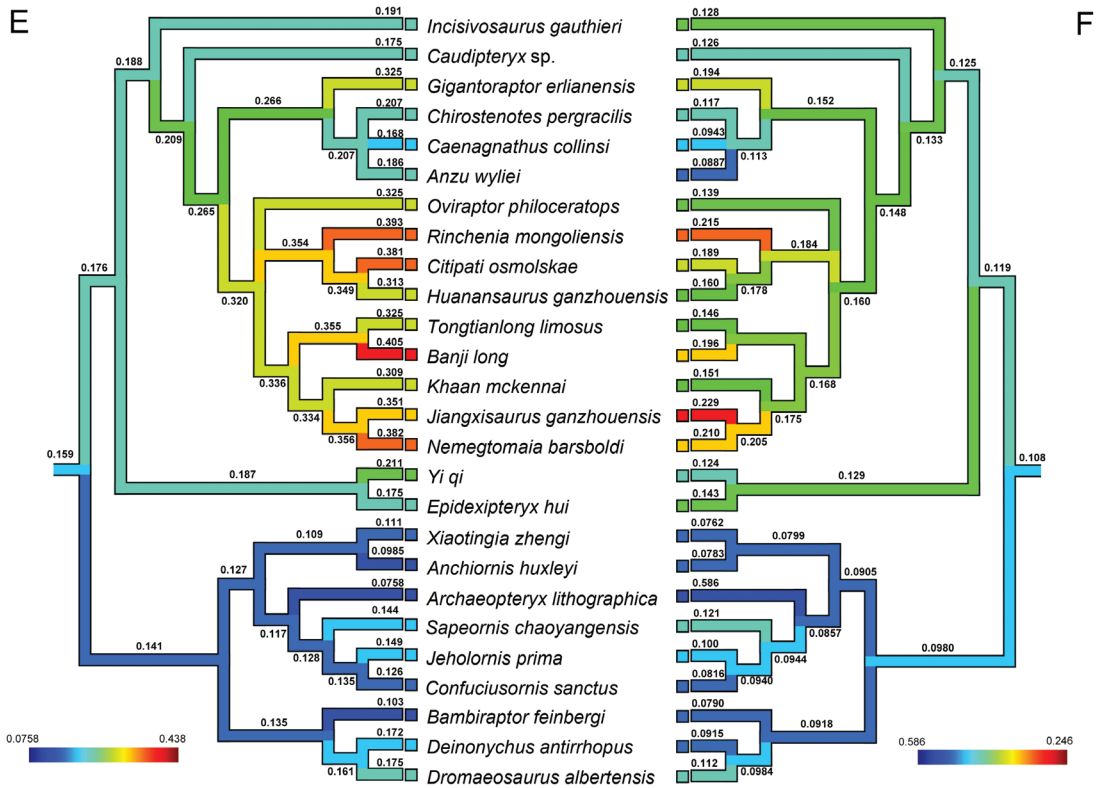
Ancestral-state reconstructions of MA reveal that there is an overall increase in AMA and PMA from early-diverging oviraptorosaurians to the oviraptorid lineage (AMA: from ~0.181 to ~0.267; PMA: from ~0.291 to ~0.355). Both AMA and PMA show an increasing trend along the oviraptorid lineage, whereas the caenagnathid lineage displays a decreasing trend (fig. 4). Paravians, in general, have relatively uniform AMAs, whereas their PMAs are more variable: members such as dromaeosaurids have an increased PMA.

The reconstructed opening mechanical advantage (OMA) of scansoriopterygids (~0.130) is lower than that of oviraptorosaurians. Early-diverging oviraptorosaurians and caenagnathids have a similar OMA (~0.185 & ~0.208 respectively). Oviraptorids have the highest OMA, which is ~0.264. Early diverging avialans and dromaeosaurids have a small OMA of ~0.103 and ~0.106 respectively. Ancestral-state reconstruction reveals an increase in OMA along the oviraptorosaurian lineage, whereas the OMA is relatively uniform among paravians (fig. 4).



The reconstructed relative articular offset (AO) of oviraptorids is ~0.488, which is the highest among the studied taxa. Scansoriopterygids, caenagnathids, noncaenagnathoid oviraptorosaurians, and early-diverging avialans have a much smaller AO than oviraptorids, which are only ~0.271, ~0.297, ~0.277, and ~0.159 respectively. However, it should be noted that *Gigantoraptor erlianensis* has a high AO (~0.365), which strongly deviates from those of other caenagnathids. If only caenagnathids diverging later than *Gigantoraptor* are considered, the nodal value drops to ~0.136. A high disparity in AO is also noticed among scansoriopterygids, e.g., the AO of *Yi* (~0.506) is about 10 times that of *Epidexipteryx* (~0.0595). Dromaeosaurids have the smallest AO, ~0.0879. Ancestral-state reconstruction shows an increasing trend in AO from early-diverging oviraptorosaurians to oviraptorids (fig. 4). In contrast, AO decreases across the caenagnathid lineage (fig. 4). Similar to oviraptorosaurians, the AOs among paravians also display high variability (fig. 4).

The relative maximum mandibular height (MMH) of scansoriopterygids and early-diverging oviraptorosaurians are similar, ~0.187 and ~0.188 respectively. The MMH of caenagnathids is ~0.266, with the value for *Gigantoraptor* the largest (~0.325). Oviraptorids have the highest MMH, ~0.320. The MMHs of early-diverging avialans and dromaeosaurids are both smaller than those of oviraptorosaurians and scansoriopterygids, which are ~0.127 and ~0.135 respectively. Similar patterns are also observed in the AMH measurements. The AMHs of scansoriopterygids and early-diverging oviraptorosaurians show similar values of ~0.129 and ~0.125 respectively. Caenagnathids have an AMH of ~0.152. As in average MMH, oviraptorids show the greatest average AMH value (~0.160). The AMH of early-diverging avialans and drom-



aeosaurids are ~0.0905 and ~0.0918 respectively, which are all smaller than those of oviraptorosaurians and scansoriopterygids.

Ancestral-state reconstructions show that there is an increase in MMH and AMH from early-diverging oviraptorosaurians to oviraptorids, and along oviraptorid lineage. For both MMH and AMH, there is a decreasing trend along Caenagnathidae, due to the large values of *Gigantoraptor* (fig. 4). The MMH and AMH of paravians are fairly similar without large variations (fig. 4).

DISCUSSION

The results of the functional comparison, with reference to comparative anatomy, suggest that different levels of adaptation to herbivory existed among early-diverging pennaraptorans. These variation patterns are likely to be indicative of the level of herbivory among these animals. Based on this inference, a number of dietary-related trends can be identified along different lineages of early-diverging pennaraptorans.

The most obvious pattern that can be inferred is that oviraptorids are likely to be more adapted to herbivory than other early-diverging pennaraptorans. Oviraptorids have the largest mean values for all the six characteristics compared to other early-diverging pennaraptorans (table 1). For all the six functional characteristics, the larger the value, the more likely the animal is to be adapted to herbivory (see Methods for detailed explanations). Oviraptorids have a large jaw-closing mechanical advantage (MA), a low jaw opening speed, an occlusal style similar to modern herbivores, and a rigid mandible. The large jaw-closing MA of oviraptorids favors the production of a large bite force, which facilitates plant cropping. However, this also increases the stress experienced by the jaw during jaw occlusion. Thus, increasing the rigidness of the jaw by

TABLE 2

Reconstructed nodal values of the six diet-related functional characteristics of the major clades of pennaraptorans

Abbreviations: **AMA,** anterior mechanical advantage; **AMH,** average mandibular height; **AO,** relative articular offset; **MA,** mechanical advantage; **MMH,** maximum mandibular height; **OMA,** jaw-opening mechanical advantage; **PMA,** posterior mechanical advantage.

Taxon	AMA	PMA	MA	% increase in MA	OMA	AO	MMH	AMH
Scansoriopterygids	0.155	0.202	0.179	30.3	0.130	0.271	0.187	0.129
Oviraptorosaurians (excluding scansoriopterygids)	0.181	0.291	0.236	60.8	0.185	0.277	0.188	0.125
Caenagnathids	0.203	0.341	0.272	68.0	0.208	0.297	0.266	0.152
Oviraptorids	0.267	0.355	0.311	33.0	0.264	0.487	0.320	0.160
Early-diverging avialans	0.139	0.220	0.180	58.3	0.103	0.159	0.127	0.0905
Dromaeosaurids	0.152	0.249	0.201	63.8	0.106	0.0879	0.135	0.0918

increasing its height is a likely adaptive outcome. Since animals with a high-level herbivorous diet are likely to rely less on hunting, they do not experience large selective pressure to increase the velocity of jaw movement for food procurement. Evidence from comparative anatomy also suggests that oviraptorids are likely to be more adapted to herbivory than other early-diverging pennaraptorans. Oviraptorids in general have a taller skull, a relatively larger lateral temporal fenestra, and a taller coronoid process prominence. Having a taller skull probably increases its rigidity and reduces the risk of bone fracturing during feeding (Metzger and Herrel, 2005; Samuels, 2009). The possession of a tall coronoid process prominence provides a larger area for inserting adductor muscles, increasing the jaw-adducting force (Nogueira et al., 2009; Lü et al., 2013; Ma et al., 2017). The crania of oviraptorids have relatively long parietals and a large lateral temporal fenestra compared to other early-diverging pennaraptorans. The expansion of the posterior region of the crania is likely to provide more space to accommodate thicker adductor muscles, which allow oviraptorids to produce a stronger bite. Evidence from both functional analysis and comparative anatomy consistently shows that the skulls of oviraptorids are well suited for feeding that requires a stronger bite force but less demand on speed than other early-diverging pennaraptorans, and its jaw occlusion is similar to that of modern herbivores. This suggests that oviraptorids are likely the most adapted to herbivory among early-diverging pennaraptorans, strengthening the hypothesis that oviraptorids included a large amount of plants in their diets (Longrich et al., 2013).

Scansoriopterygids appear to be less adapted to herbivory compared to oviraptorids, although scansoriopterygid stomach contents remain unknown. The mandibles of scansoriopterygids have a relatively low jaw-closing MA and lack a tall coronoid process prominence, in contrast to those of oviraptorids. Also, the mandible and crania of scansoriopterygids appear to be less robust due to their relatively long length. Scansoriopterygids have a smaller lateral temporal fenestra than oviraptorids, which probably constrains the space available for muscle attachment and reduces its bite force. If they were herbivorous to some degree, the adaptiveness of their skull to herbivory was probably similar to early-diverging oviraptorosaurians, which preserve direct evidence of herbivory (Ji et al., 1998, 2012;

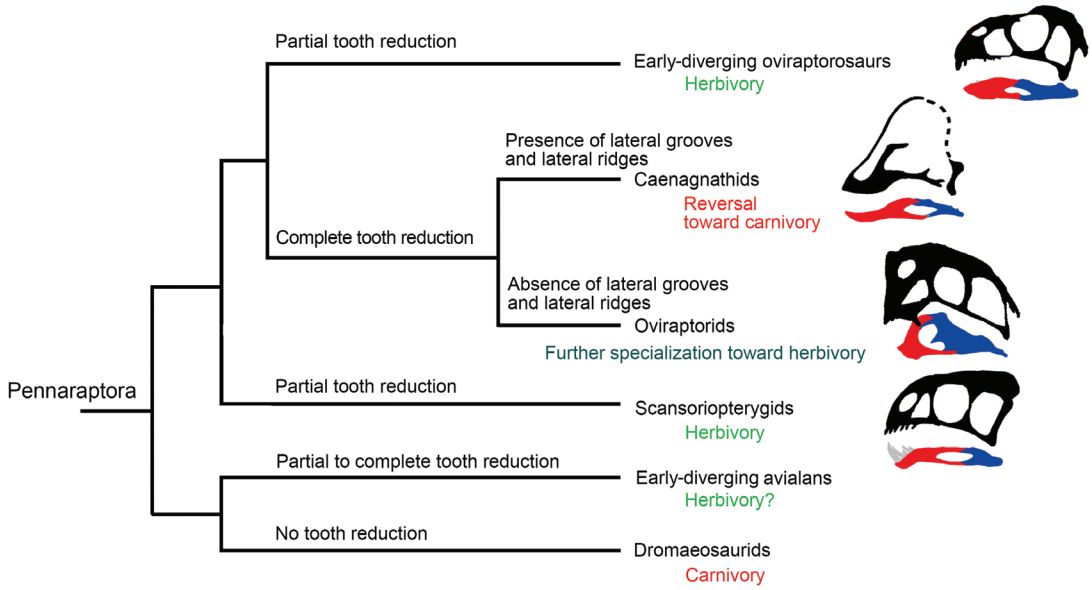


FIG. 5. Patterns of tooth reduction and inferences of dietary evolution in Pennaraptora based on the results of the functional analysis (fig. 4). Tree topology based on Lü et al. (2017) and Pei et al. (in press). Skull drawings modified from Clark et al. (2002), Xu et al. (2002, 2011) and Lamanna et al. (2014).

Xu et al., 2002). The large relative articular offset in the mandible of *Yi* suggests a jaw-occlusal mode similar to extinct and extant herbivores (e.g., ornithischian dinosaurs and herbivorous mammals and fish), *Caudipteryx*, and oviraptorids. However, *Epidexipteryx* has a small relative articular offset that is comparable to those of late-diverging caenagnathids and dromaeosaurids. This suggests that the modes of occlusion might not be homogeneous within scansoriopterygids. The crania of scansoriopterygids also share a number of similarities with those of early-diverging oviraptorosaurians, such as their relative heights and sizes of cranial fenestra. It is noteworthy that scansoriopterygids have a low jaw-opening MA, which suggests that they have a more rapid jaw-opening movement than oviraptorosaurians. This may give them advantages during occasional hunting. In general, this functional and morphological evidence suggests that scansoriopterygids are unlikely to be as adapted to herbivory as oviraptorids, but their diets were probably similar to early-diverging oviraptorosaurians in being mostly made up of plants. Preserved scansoriopteryid stomach contents are unknown, but they will be essential in validating these findings to complement the direct dietary information currently known in early-diverging oviraptorosaurians.

Our results show that caenagnathids are more adapted to predation than other oviraptorosaurians and scansoriopterygids, implying a possible dietary reversal back to the typical carnivorous diet. Unlike oviraptorids, caenagnathids do not display apparent adaptations to herbivory—they have a smaller anterior jaw-closing mechanical advantage (AMA) and a less robust mandible than oviraptorids. Instead, caenagnathids show a number of features that facilitate a carnivorous feeding style. The extremely low relative articular offset of caenagnathids points to a more carnivorous diet compared to oviraptorids and early-diverging oviraptorosaurians. It is noteworthy that dromaeosaurids, which are dominated by carnivorous theropods, also have a very small relative articular offset that is comparable to caenagnathids. Caenagnathids also have a smaller opening mechanical advantage than oviraptorids, which can be

interpreted as having a higher jaw-opening velocity for prey capture. Caenagnathids and dromaeosaurids have a high posterior mechanical advantage relative to their anterior mechanical advantage. This pattern can be interpreted as an indication of carnivory as carnivores usually have a "scissorlike" occlusal style (Greaves, 1974; Grubich et al., 2008), such that the posterior part of the dentary is also actively involved in food processing. The anteriormost tip of the mandibles of caenagnathids appears to be more recurved and sharper compared with those of oviraptorids. Having a pointed beak tip is favourable for slashing meat (Funston et al., 2016) and prey capturing—the tip allows bite force to be concentrated at one point for killing the prey effectively. The mandibles of caenagnathids are likely adapted to shearing action, which could actually benefit both cutting of foliage and meat (Funston and Currie, 2014; Ma et al., 2017). In modern carnivores, shearing is the dominant food-processing mechanism whereas crushing plays only a minor role (Sanson, 2016). The carnivorous affinity of caenagnathids is also supported by their postcranial anatomy. Although the recurved claws of oviraptorids have been considered an indication of carnivory (Osmolska et al., 2004), geometric morphometric analysis shows that oviraptorosaurian claws are morphologically similar to those of therizinosaurians (Lautenschlager, 2014), suggesting that the possession of recurved claws may not necessarily be a sign of carnivory. Despite this, the arctometatarsalian condition in caenagnathids suggests that they are more cursorial than oviraptorids, which is possibly linked to predation (Funston et al., 2016). The hands and feet of caenagnathids are also more elongated than those of oviraptorids, which shows grasping and prey capture ability that is not commonly seen in herbivorous dinosaurs (Longrich et al., 2013). It was hypothesized that their limbs may be suited for tree climbing or grasping of vegetation for feeding (Longrich et al., 2013). However, considering the mandibular features and postcranial anatomy of caenagnathids, it seems more likely that the limbs of caenagnathids are primarily adapted for predation. All this evidence suggests that caenagnathids are likely to have had an omnivorous diet that was more carnivorous than that of oviraptorids and possibly other oviraptorosaurians and scansoriopterygids.

Although the six functional characteristics were developed based on the fact that they have shown convergence in independently evolved modern herbivores, including birds, we still need to be careful when interpreting the results—distinct diets may share similar functional demands. Similar to herbivory, the evolution of a durophagous diet results in an animal's larger bite force with less selective pressure on the speed of food procurement compared with a nonherbivorous sister taxon. By solely considering the results of the functional analysis, one may conclude that oviraptorids were more specialized in durophagy than any other early-diverging pennaraptorans. Durophagy, in particular feeding on freshwater molluscs, has long been suggested as a feeding mode of oviraptorids (Barsbold, 1983). However, this hypothesis is weakly supported by their environmental preferences—oviraptorids are discovered mainly in arid environments, although they have also been found in fluvial deposits (Longrich et al., 2010, 2013; Funston et al., 2017). Freshwater molluscs are less likely to be abundant in drought-prone environments (García et al., 2010), and so it is doubtful that the skulls of oviraptorids are primarily adapted for consuming them. An herbivorous diet is a more probable hypothesis for the diet of oviraptorids. Despite this, we cannot rule out the possibility that oviraptorids occasionally included molluscs or other items in their diets, as their robust skulls may have allowed them to do so. The robust mandibles of parrots, which are morphologically similar to those of oviraptorosaurians (Longrich et al., 2010, 2013; Funston and Currie, 2014; Ma et al., 2017), are capable of procuring a wide range of food items including nuts, seeds, fruits, leaves, stems, and bark (Benavidez et al., 2018). We suggest that the highly specialized skulls of oviraptorids allowed them to consume not only tough vegetation, but also harder plant materials such as stems, seeds, and nuts. This might have provided them with an additional

advantage in an arid environment, as plant materials (e.g., leaves, seeds) tend to be thicker and harder in a dry environment to prevent water loss (Jones, 2013).

Various degrees of tooth reduction can be observed among early-diverging pennaraptorans—early-diverging oviraptorosaurians, scansoriopterygids, and some early-diverging avialans exhibit partial tooth loss; late-diverging oviraptorosaurians (*Avimimus*, caenagnathids and oviraptorids) are edentulous; dromaeosaurids do not show tooth loss. An extensive study on tooth reduction in theropod dinosaurs clarified the mechanisms involved, suggesting that tooth reduction involves a series of transformations and further tooth reduction is associated with the formation of a more extensive rhamphotheca (Wang et al., 2017: fig. 4). The possession of a rhamphotheca has been demonstrated to have a stress mitigation effect on the skull (Lautenschlager et al., 2013). Developing a rhamphotheca is beneficial to herbivores as it reduces the risk of skull failure during plant procurement (Lautenschlager et al., 2013). This may explain why different dental anatomies are observed among late-diverging oviraptorosaurians—lingual grooves are present in some caenagnathids but absent in all known oviraptorids. Lingual grooves are likely to be vestigial alveoli (Wang et al., 2017) and their presence in caenagnathids suggests that rhamphothecae are likely to be less extensive in caenagnathids than in oviraptorids. The reason may be that oviraptorids are more specialized in herbivory, and hence they have experienced a larger selective pressure in increasing their skull stability.

Early-diverging members of several theropod lineages have evolved beaklike structures, and are likely to have undergone development of different morphological strategies in response to functional demands possibly related to dietary shifts (Lautenschlager et al., 2013). Early-diverging oviraptorosaurians experienced partial tooth reduction and developed a complete edentulous beak in their late-diverging forms. Instead of developing an edentulous beak like late-diverging oviraptorosaurians, the scansoriopterygid *Epidexipteryx* evolved a different dentition pattern: it has tightly packed mandibular teeth that are reminiscent of the shape of a beak. By possessing anteriorly enlarged and densely packed procumbent teeth, the dentary of *Epidexipteryx* is morphologically and possibly functionally similar to those of beaked oviraptorosaurians. Although Oviraptorosauria and Scansoriopterygidae are closely related clades, their members have shown distinct strategies in adapting to herbivory (observed or suspected), the former by developing an edentulous beak, the latter by modifying the size and the arrangement of teeth. This adds to the known diversity of mandibular morphology in theropod dinosaurs and highlights the innovations in the feeding apparatus accompanying the dietary shift by pennaraptorans closely related to avialans.

CONCLUSIONS

This study presents the first comprehensive analysis of the dietary habits of scansoriopterygids and oviraptorosaurians from both anatomical and functional perspectives, with reference to dietary patterns observed in extant animals. The results of the comparative anatomy and functional analyses consistently suggest that oviraptorid skulls are more adapted to herbivory than caenagnathids, early-diverging oviraptorosaurians, and scansoriopterygids. Scansoriopterygids are less adapted to herbivory than oviraptorids because they have a lower dorsoventral height, a smaller lateral temporal fenestra, a smaller jaw-closing mechanical advantage and lack a tall coronoid process prominence. Some caenagnathids possess features like an extremely small relative articular offset and small average mandible height that may imply a more carnivorous diet than those of other oviraptorosaurians. Our study provides a new perspective to evaluate various hypotheses on the diets of scansoriopterygids and oviraptorosaurians, and demonstrates the high dietary complexity among early-diverging pennaraptorans. Future work involving other approaches such as geochemical proxies of diet and 3D biomechanical modeling would provide additional opportunities to test these hypotheses. However,

this study provides insights that are important to our understanding of the dietary evolution of theropods close to the origin of birds.

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