

SECTION 1. SYSTEMATICS, FOSSIL RECORD, AND BIOGEOGRAPHY

Chapter 1 Pennaraptoran Systematics

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ABSTRACT

New and important pennaraptoran specimens continue to be discovered on a regular basis. Yet, with these discoveries the number of viable phylogenetic hypotheses has increased, including ones that challenge the traditional grouping of dromaeosaurids and troodontids within a monophyletic Deinonychosauria. This chapter will cover recent efforts to address prevailing phylogenetic uncertainties and controversies, both between and within key clades, including deinonychosaurian monophyly, the phylogenetic position of anchiornithines and scansoriopterygids, and the interrelationships of enantiornithines. While recent discoveries mainly from Asia have created much of the latest uncertainty and controversy, new material, particularly from Asia, promises to rather fittingly address these issues. Further curatorship of long-standing phylogenetic datasets and more prevalent use of extended analytical protocols will be essential to meeting this challenge, especially for groups whose boundaries have been blurred. As it becomes increasingly difficult to study all fossil materials, owing to their growing numbers and ever disparate locations, broader use of digital fossils and online character databases for character coding is acutely needed to ensure that errors arising from remote, rather than firsthand, scoring are reduced as far as possible, particularly at this time of rapid data accumulation.

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PENNARAPTORAN SYSTEMATICS TODAY

This chapter will cover clade definitions, the relationships within clades as well as the occasional controversial relationships between different clades. Phylogenies arising from a recent iteration of the Theropod Working Group (TwiG) matrix by Pei et al. (2020) and the recent Mesozoic avialan matrix of Wang et al. (2018a) are used as the main comparative backbones in this section (see Methods), with every effort made to incorporate key findings from all previous work. We opt to consider a range of crown bird phylogenies here given substantial disagreements between them (see Crown Birds section below).

PENNARAPTORA FOTH ET AL., 2014: A node-based clade defined as the last common ancestor of *Oviraptor philoceratops* Osborn, 1924, *Deinonychus antirrhopus* Ostrom, 1969, and *Passer domesticus* Linnaeus, 1758, and all its descendants (Foth et al., 2014). Pennaraptora was proposed by Foth et al. (2014) on the basis of a phylogenetic analysis using a modified TwiG data matrix with the Latin *penna* meaning “bird feather” in reference to the pennaceous feathering shared by these animals. While it is possible that such feathers may yet have a wider distribution among theropods (Foth et al., 2014), as hinted by evidence from earlier-diverging coelurosaurs such as ornithomimosaurians (Zelenitsky et al., 2012; but see Xu, 2020), a close phylogenetic relationship between Paraves and Oviraptorosauria has been recovered by a range of studies including with both clades as sister taxa (Senter et al., 2012; Turner et al., 2012; Xu et al., 2015; Lefèvre et al., 2017), with Paraves in a sister relationship with a (Therizinosauria + Oviraptorosauria) clade (Makovicky et al., 2005), and with Paraves, Therizinosauria, Oviraptorosauria and Alvarezsauroida in a polytomy (Choiniere et al., 2010). Agnolín and Novas (2013) recovered Alvarezsauroida as the most closely related clade to Paraves with Oviraptorosauria sister to this grouping. Therizinosaurians and alvarezsauroids have been consistently recovered as the closest relatives of

pennaraptorans. Each clade has been recovered as the most closely related to Pennaraptora (Therizinosauria: Senter et al., 2012; Turner et al., 2012; Xu et al., 2015; Alvarezsauroida: Senter, 2007; Zanno, 2010) as well as in a trichotomy with Pennaraptora (Brusatte et al., 2014).

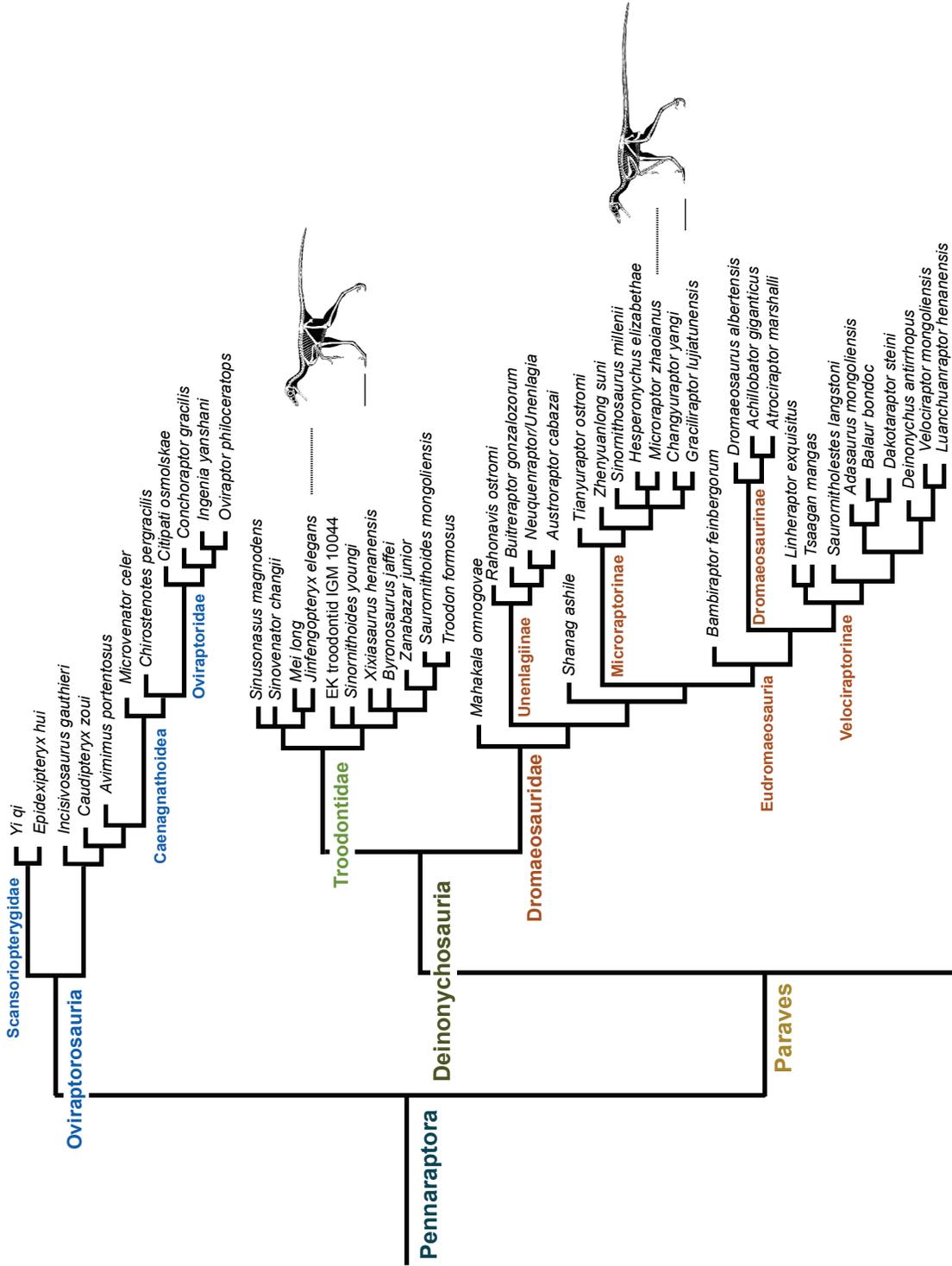
OVIRAPTOROSAURIA BARSBOLD, 1976: A stem-based taxon containing all maniraptorans closer to *Oviraptor philoceratops* Osborn, 1924, than to *Passer domesticus* Linnaeus, 1758 (sensu Sereno, 1998; Maryńska et al., 2002). Oviraptorosaurian fossils had been referred to ornithomimosaurians (e.g., Gauthier, 1986) and birds (e.g., Maryńska et al., 2002) largely due to their edentulous jaws, even though Oviraptorosauria had already been proposed as a new taxon (Barsbold, 1976). Despite being known from more than 40 reported genera, fully resolved interrelationships remain out of reach for a large portion of known oviraptorosaurian taxa, partly because some of them are missing significant amounts of data owing to their preservation as flattened and/or highly fragmentary specimens (Ji et al., 1998; Lü and Zhang, 2005; Zanno and Sampson, 2005; Sullivan et al., 2011; Longrich et al., 2013). Another obstacle to reconstructing fully resolved interrelationships is the lack of overlap between the elements preserved in specimens of different species. For example, several North American caenagnathid species are based solely on lower jaw remains whereas others are based on postcranial holotypes (Longrich et al., 2013), complicating the testing of taxonomic assignments and reconstruction of quantitative phylogenetic hypotheses (but see Funston and Currie, 2016, for an alternative view). *Incisivosaurus* has been recovered as the earliest-diverging oviraptorosaurian by a number of analyses that excluded oviraptorosaurian taxa known from poorly preserved specimens, e.g., *Protarchaeopteryx*, *Ningyuansaurus*, and *Luoyanggia* (Longrich et al., 2013; Brusatte et al., 2014; Lamanna et al., 2014; Lü et al., 2016, 2017; Pei et al., 2020) (figs. 1, 2A, C). However, if these poorly known taxa are included, early-diverging oviraptorosaurians collapse into a polytomy (Funston and Currie,

2016; Yu et al., 2018; fig. 2B, D). Oviraptorosauria has two main lineages, the Caenagnathidae and the Oviraptoridae, that are consistently recovered as monophyletic sister taxa (Longrich et al., 2013; Lamanna et al., 2014; Lü et al., 2015; Funston and Currie, 2016; Lü et al., 2016; Lü et al., 2017; Yu et al., 2018; fig. 2A–D). These two lineages together form the Caenagnathoidea, which is sister to *Avimimus* (Lamanna et al., 2014; Pei et al., 2020) (fig. 1). Within Caenagnathidae, *Microvenator* and the giant *Gigantoraptor* are consistently recovered as early-diverging members, whereas the interrelationships between later-diverging members remain unresolved largely due to the issue of nonoverlapping elements between specimens of different species (Lamanna et al., 2014; Lü et al., 2015; Lü et al., 2016; Lü et al., 2017; fig. 2C). Taxonomic revision of problematic taxa like *Caenagnathus sternbergi*, *Macrophalangia canadensis*, and “Alberta dentary morph 3” (fig. 2A) and the exclusion of poorly known taxa from the matrix like *Leptorhynchos gaddisi* and *Ojoraptorsaurus* has improved topological resolution among later-diverging caenagnathids (Funston and Currie, 2016; Yu et al., 2018; fig. 2B, D). *Elmisaurus*, *Apatortaptor*, and *Leptorhynchos elegans* are consistently recovered as the three latest-diverging caenagnathids, although the position of *Apatortaptor* and *Leptorhynchos gaddisi* interchanged in two recent analyses (Funston and Currie, 2016; Yu et al., 2018; fig. 2B, D). Previously, two sister clades have been recovered within Oviraptoridae, the Oviraptorinae and Ingeniinae (Longrich et al., 2010). Over the past decade, successive discoveries of new Chinese oviraptorids preserving interesting character combinations have unsurprisingly collapsed many parts of the phylogeny into different polytomies (Longrich et al., 2013; Lamanna et al., 2014; Lü et al., 2015, 2016, 2017). Funston and Currie (2016) and Yu et al. (2018) provide the most highly resolved interrelationships among oviraptorids to date: *Nankangia* is recovered as the earliest-diverging oviraptorid and all polytomies are resolved (fig. 2B, D). The oviraptorid interrela-

tionships of these two phylogenies are largely consistent with those of other recent analyses (Lamanna et al., 2014; Lü et al., 2015, 2016, 2017), except the placement of *Ganzhousaurus* at an earlier-diverging position (fig. 2B–D). However, this topological resolution may be short-lived as many newly reported Chinese specimens have yet to be included, e.g., *Huanansaurus*, *Tongtianlong*, *Beibeilong*, and *Corythoraptor* (Lü et al., 2015, 2016, 2017; Pu et al., 2017). Thus, while a phenomenal amount of oviraptorosaurian material is known, including specimens subject to detailed monographic work, future work combining and updating existing phylogenetic datasets is a much-needed priority (Funston and Currie, 2016; Lü et al., 2017).

Oviraptorosauria is generally seen as the sister clade of Paraves, together forming the more inclusive clade Pennaraptora (Brusatte et al., 2014; Foth et al., 2014; Xu et al., 2017; Pei et al., 2020) (see Pennaraptora and Paraves sections below). However, the phylogenetic placement of Scansoriopterygidae within Pennaraptora has been contentious. Scansoriopterygids have been placed within Avialae (Xu et al., 2011; Senter et al., 2012; O’Connor and Sullivan, 2014), as an early-diverging lineage within Oviraptorosauria (Agnolín and Novas, 2013; Brusatte et al., 2014; Agnolín et al. 2019; Pei et al., 2020), as an early-diverging paravian clade outside the traditional (Deinonychosauria + Avialae) clade (Turner et al., 2012; Xu et al., 2015; Lefèvre et al., 2017), and in a polytomy with Deinonychosauria and Avialae (Xu et al., 2017). Herein we consider Scansoriopterygidae to be early-branching oviraptorosaurians (fig. 1). More exhaustive descriptions of scansoriopterygid specimens as well as application of developmental insights to the study of nonadult scansoriopterygids may help to give this group a more stable phylogenetic position. This is sorely needed to deepen our understanding of oviraptorosaurians and early-diverging pennaraptorans more broadly.

PARAVES SERENO 1997: A stem-based taxon containing *Passer domesticus* Linnaeus, 1758, and all coelurosaurians closer to it than to *Ovi-*



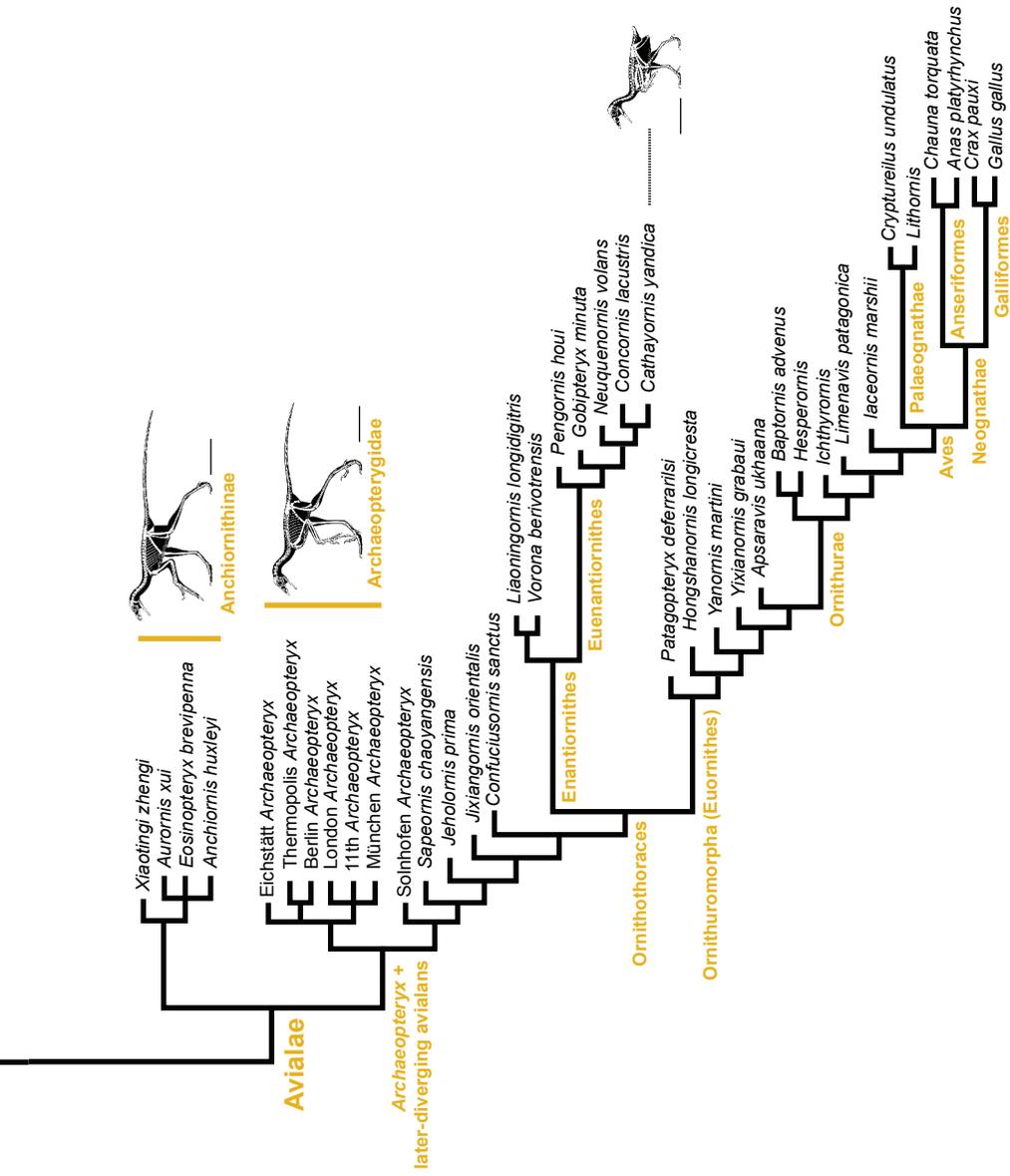
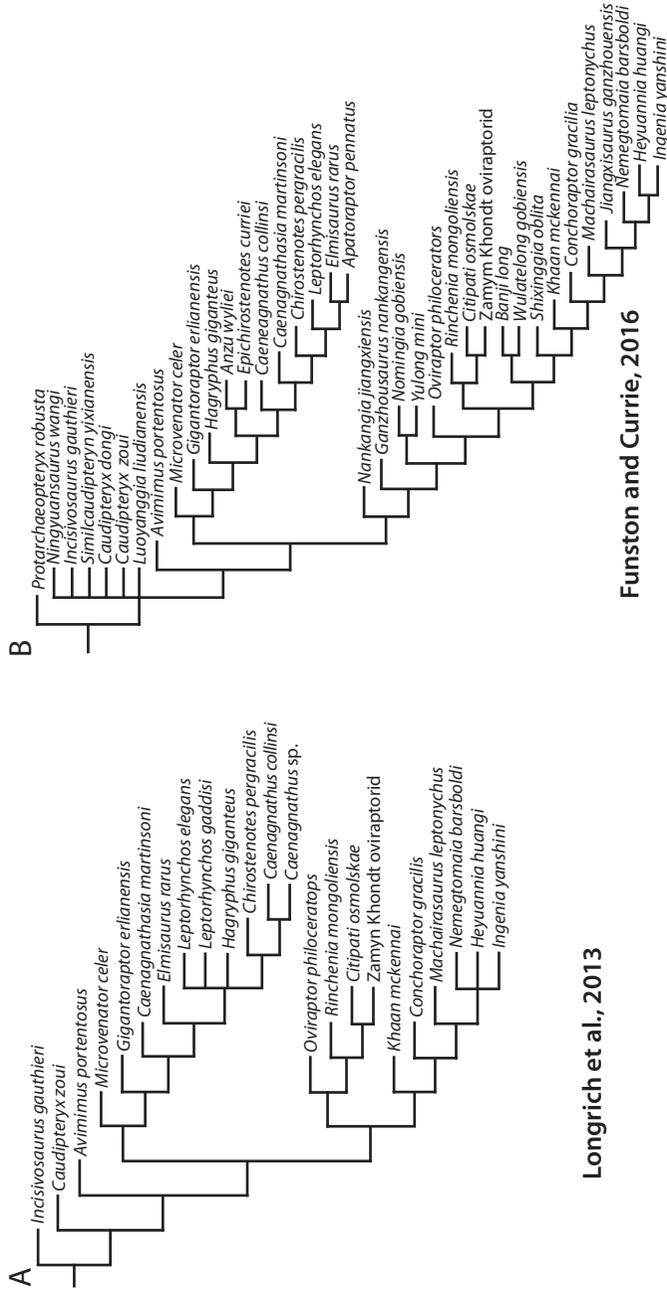


FIG. 1. Pennaraptoran reduced strict consensus tree using extended implied character weighting in analysis of updated TWiG dataset (modified from Pei et al., 2020). Skeletal reconstructions used with the permission of Scott A. Hartman. Scale bars = 10 cm.



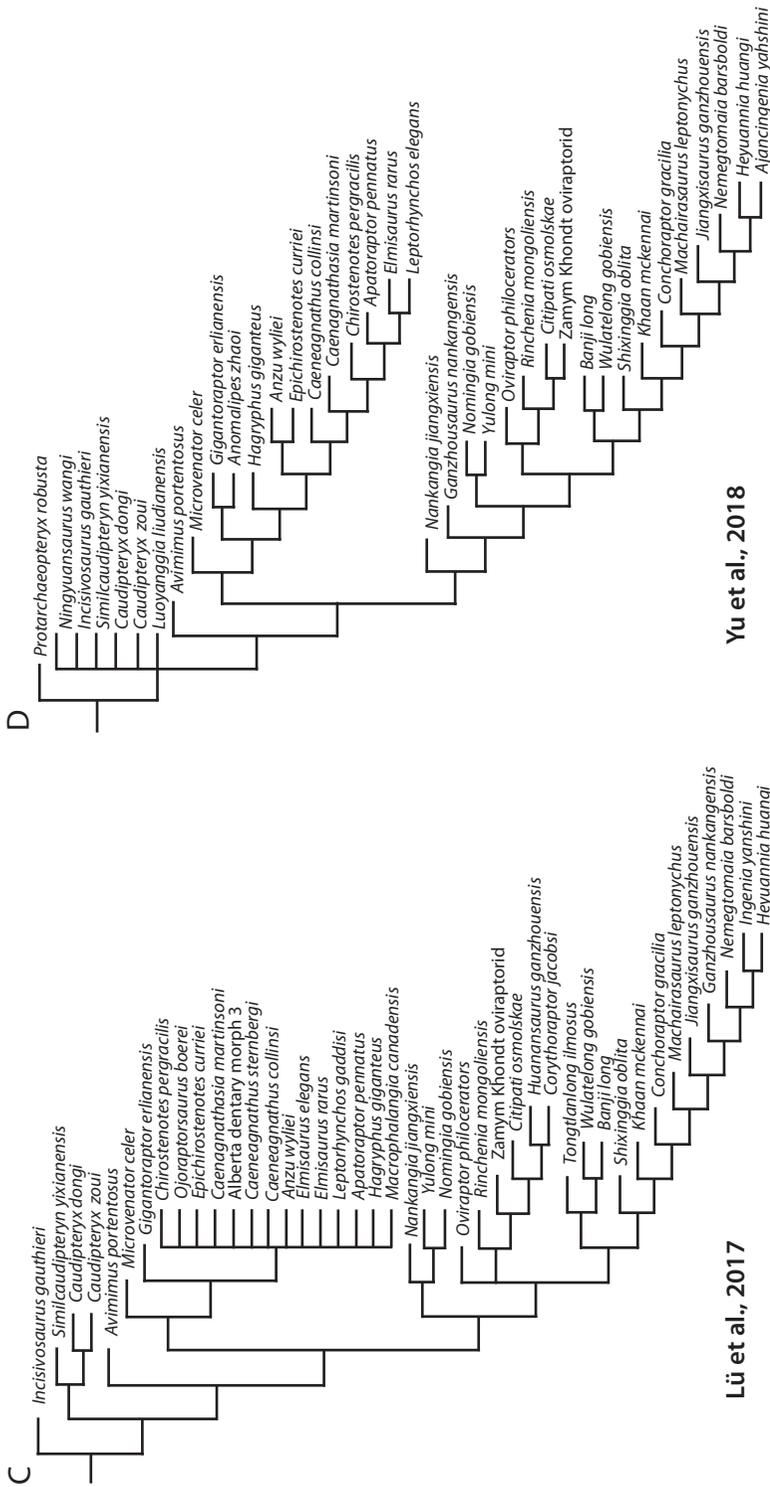


FIG. 2. Existing oviraptorosaurian phylogenies. **A.** Adams consensus tree of Longrich et al. (2013). **B.** Strict consensus tree of Funston and Currie (2016). **C.** Strict consensus tree of Lü et al. (2017). **D.** Strict consensus of Yu et al. (2018).

raptor philoceratops Osborn, 1924 (sensu Holtz and Osmólska, 2004; after Turner et al., 2012). The last main iteration of the TWiG matrix (Pei et al., 2020) produced a pruned, reduced consensus tree that reaffirmed that Paraves comprises exclusively of Deinonychosauria and Avialae (Gauthier, 1986; Sereno, 1997; Norell et al., 2001; Senter et al., 2004, 2012; Turner et al., 2007a, 2012), bringing recent uncertainty associated with the Brusatte et al. (2014) matrix iteration to a close. Disregarding the most unstable taxa, reasonable group supports (frequency differences between 76 and 100) were calculated by means of no-zero-weight symmetric resampling (Goloboff et al., 2003) for Paraves and the key internal nodes Troodontidae, Dromaeosauridae, Unenlagiinae, and Eudromaeosauria in a recent TWiG study (Pei et al., 2020). The no-zero-weight resampling increases or decreases character weights, but never eliminates characters. With no-zero-weight resampling, support is lowered only because of conflict among characters and not just because of absence of information; it is thus an appropriate resampling scheme for palaeontological datasets. The identification of rogue taxa was carried out in two steps, first identifying a list of possible rogues with a heuristic procedure (the *chkmoves* command of TNT), then selecting taxon subsets from that list with an optimality-based method (the *prupdn* command of TNT). This combined routine was implemented in a script called *bothprunes* (see Pei et al., 2020, for additional details). Other datasets generally have low nodal supports for paravian nodes (Senter et al., 2012; Turner et al., 2012; Brusatte et al., 2014; Foth et al., 2014; Xu et al., 2015), with Bremer supports typically between 1 and 2 for most of them (but see Xu et al., 2015). Despite the differences in pennaraptoran interrelationships recovered in previous studies (Zheng et al., 2009; Xu et al., 2010, 2011, 2015; Senter et al., 2012; Turner et al., 2012; Evans et al., 2013; Godefroit et al., 2013a, 2013b; Brusatte et al., 2014; Foth et al., 2014; Cau et al., 2015; DePalma et al., 2015) there are some seemingly robust paravian synapomorphies: a laterally facing glenoid fossa was

recovered by Pei et al. (2020) and at the equivalent node by Turner et al. (2012) and Brusatte et al. (2014) and is related to the extension of the glenoid floor onto the external surface of the scapula, a paravian synapomorphy of Agnolín and Novas (2013), Senter et al. (2012), and Xu et al. (2015), and a synapomorphy of Foth et al. (2014) for the node (*Jimfengopteryx* + Paraves). Agnolín and Novas (2013), Brusatte et al. (2014), and Pei et al. (2020) recover paravians as sharing a proximal surface of ulna that is divided into two distinct fossae. At the paravian node in Pei et al. (2020) and at the node (Deinonychosauria + Avialae) in Turner et al. (2012) and Brusatte et al. (2014), an acromion margin of the scapula with a laterally everted anterior edge is also shared. Three equivalent paravian synapomorphies were recovered by Pei et al. (2020), Brusatte et al. (2014), and Senter et al. (2012), one of which was also recovered by Xu et al. (2015) and Agnolín and Novas (2013): basiptyergoid process absent or very subtle; carotid process present on posterior cervical vertebrae; posterior trochanter is developed as a slightly projected tubercle or flange. Additionally, short and stout proximal chevrons were recovered as a common synapomorphy in this study and in Brusatte et al. (2014) and Xu et al. (2015). Some paravian synapomorphies have been shown to have a more inclusive distribution. For example, large maxillary and dentary teeth and an astragalus fused to the calcaneum but not to the tibia were paravian synapomorphies in the analysis of Turner et al. (2012), but Pei et al. (2020) found these to be avialan and deinonychosaurian synapomorphies respectively. However, some reconstructed tree topologies have been so seemingly different that their synapomorphies have no overlap with other studies. For example, Foth et al. (2014) found that avialans share closer affinities to troodontids than to dromaeosaurids and recovered anchiornithines as early-diverging birds.

DEINONYCHOSAURIA COLBERT AND RUSSELL, 1969: A node-based taxon containing the last common ancestor of *Troodon formosus* Leidy, 1856, and *Velociraptor mongoliensis* Osborn,

1924, and all its descendants (sensu Sereno, 1998; after Turner et al., 2012). Dromaeosaurids and troodontids have been traditionally united as the Deinonychosauria by the “sickle claw” on their second toe among other characteristics and considered the sister group of birds (Gauthier, 1986; Sereno, 1997; Norell et al., 2001, 2009; Makovicky et al., 2005; Novas and Pol, 2005; Senter, 2007; Senter et al., 2012; Turner et al., 2012). A deluge of discoveries over the last decade has called this status quo into question (Lü et al., 2007; Senter et al., 2012; Evans et al., 2013; Godefroit et al., 2013a; Godefroit et al., 2013b; Foth et al., 2014; DePalma et al., 2015; Lü and Brusatte, 2015; Pittman et al., 2015), seemingly supporting every combination of taxa and demonstrating that historically diagnostic features of the clade have more inclusive distributions than once thought or have parallel origins (Zheng et al., 2009; Xu et al., 2010, 2015; Xu et al., 2011; Senter et al., 2012; Turner et al., 2012; Evans et al., 2013; Godefroit et al., 2013a, 2013b; Brusatte et al., 2014; Foth et al., 2014; Cau et al., 2015; DePalma et al., 2015). Deinonychosaurian monophyly was reaffirmed in a recent TWiG study under both extended implied-weighting and equal-weighting searches and in the strict consensus trees (Pei et al., 2020; fig. 1), as well as independently (Lefèvre et al., 2017). Seemingly robust synapomorphies of this clade include: a splenial exposed as a broad triangle in the lateral surface of the dentary between the dentary and angular (Senter et al., 2012; Turner et al., 2012; Pei et al., 2020); dorsal vertebrae with interspinous ligament scars that terminate below the apex of the neural spine (Turner et al., 2012; Pei et al., 2020); an astragalus fused to the calcaneum but not to the tibia (Turner et al., 2012; Brusatte et al., 2014; Pei et al., 2020); penultimate phalanx of digit II highly modified for extreme hyperextension, and its ungual is larger and more curved than that of digit III (Turner et al., 2012; Pei et al., 2020), but a dromaeosaurid synapomorphy in Brusatte et al. (2014) and equivalent to synapomorphies of Senter et al. (2012) and

Xu et al. (2015); slightly raised bicipital scar of the ulna (Turner et al., 2012; Pei et al., 2020).

DROMAEOSAURIDAE MATTHEW AND BROWN, 1922: A stem-based taxon containing *Dromaeosaurus albertensis* Matthew and Brown, 1922, and all deinonychosaurians closer to it than to *Troodon formosus* Leidy, 1856, or *Passer domesticus* Linnaeus, 1758 (sensu Sereno, 1998; after Turner et al., 2012). This clade is consistently supported by robust synapomorphies, particularly in relation to the paroccipital process of the skull. The dromaeosaurid paroccipital process is: elongate and slender with nearly parallel dorsal and ventral edges (Turner et al., 2012; Brusatte et al., 2014; Foth et al., 2014; Pei et al., 2020); has a dorsal edge twisted anterolaterally at its distal end (Turner et al., 2012; Brusatte et al., 2014; Foth et al., 2014; Pei et al., 2020); possesses a ventral flange at its distal end (Brusatte et al., 2014; Pei et al., 2020); and has a ventral edge at its base that is situated at the midheight of the occipital condyle or further ventrally (Brusatte et al., 2014; Pei et al., 2020). Other cranium-based synapomorphies include dentary and maxillary teeth with confluent tooth crowns and roots (Turner et al., 2012; Brusatte et al., 2014; Foth et al., 2014; Pei et al., 2020) as well as an anterior location of the anterior tympanic recess and anterior tympanic crista, with little or no development of the recess posterior to the basiptyergoid processes (Turner et al., 2012; Brusatte et al., 2014; Foth et al., 2014; Pei et al., 2020). Past studies are contradictory on the absence/presence of the accessory tympanic recess dorsal to the crista interfenestralis: absent according to Turner et al. (2012) and Pei et al. (2020) but present according to Brusatte et al. (2014) and Foth et al. (2014). Two of the few robust postcranial synapomorphies are: posterior trunk vertebrae with parapophyses projected distinctly on pedicels (Turner et al., 2012; Brusatte et al., 2014; Foth et al., 2014; Pei et al., 2020) and a well-developed ginglymus on the distal end of metatarsal II (Turner et al., 2012; Agnolín and Novas, 2013; Brusatte et al., 2014; Foth et al., 2014; Pei et al., 2020). Rogue taxa can significantly impact

support for previously recovered dromaeosaurid synapomorphies, e.g., many synapomorphies are shared with the analysis of Foth et al. (2014) only if *Pyroraptor* is pruned. The basic dromaeosaurid topology places unenlagiines at an earlier-diverging position and microraptorines and Eudromaeosauria at later-diverging positions (Senter, 2007; Senter et al., 2012; Turner et al., 2012; Evans et al., 2013; Brusatte et al., 2014; Foth et al., 2014; Han et al., 2014; DePalma et al., 2015; Lü and Brusatte, 2015; Pei et al., 2020; fig. 1). However, some analyses have suggested that unenlagiines and microraptorines are early-branching members of Averaptora, a paravian clade that includes avialans and is most closely related to dromaeosaurids (Agnolín and Novas, 2011; Agnolín and Novas, 2013). *Mahakala* is typically recovered as the earliest-diverging dromaeosaurid (Turner et al., 2007a, 2012; Brusatte et al., 2014; Pei et al., 2020) potentially forming a clade with an additional dromaeosaurid from the Djadokhta Formation, *Halszkaraptor escuilliei* (Cau et al., 2017). This early-diverging clade is then followed by the Unenlagiinae. Unenlagiinae Bonaparte, 1999, is a stem-based taxon containing *Unenlagia comahuensis* Novas and Puerta, 1997, and all coelurosaurs closer to it than to *Velociraptor mongoliensis* Osborn, 1924, *Dromaeosaurus albertensis* Matthew and Brown, 1922, *Microraptor zhaoianus* Xu et al., 2000, and *Passer domesticus* Linnaeus, 1758 (sensu Sereno et al., 2005; after Turner et al., 2012). Within the group, *Austroraptor* is typically recovered as a sister taxon of *Unenlagia*, which are both in turn sister to *Buitreraptor* (Turner et al., 2012; Agnolín and Novas, 2013; Pei et al., 2020). *Rahonavis*, originally described as a long, bony-tailed bird (Forster et al., 1996), has been identified as a member of the Unenlagiinae (Makovicky et al., 2005) with additional referred material and anatomical work continuing to support that relationship (Forster et al., 2020), but some authors still find it to be an early-diverging avialan (Agnolín and Novas, 2013; Agnolín et al. 2019). Unenlagiine synapomorphies shared by some recent studies include

a pubic shaft that is vertically oriented when articulated and an ilium with a reduced supraacetabular crest that is still separate from the antitrochanter (Foth et al., 2014; Pei et al., 2020) and has a postacetabular process with a concave dorsal edge (Agnolín and Novas, 2013; Pei et al., 2020). (Microraptorinae + Eudromaeosauria) is usually recovered as the latest-diverging dromaeosaurid clade (Senter et al., 2012; Turner et al., 2012; Brusatte et al., 2014; Xu et al., 2015; Pei et al., 2020; fig. 1). Pei et al. (2020) found this clade to lack a deep and sharp groove on the lateral side of the dentary and to have a relatively reduced maxillary fenestra.

Microraptorinae Senter et al., 2004, is a stem-based taxon containing *Microraptor zhaoianus* Xu et al., 2000, and all coelurosaurs closer to it than to *Dromaeosaurus albertensis* Matthew and Brown, 1922, *Velociraptor mongoliensis* Osborn, 1924, *Unenlagia comahuensis* Novas and Puerta, 1997, and *Passer domesticus* Linnaeus, 1758 (sensu Sereno et al., 2005; after Turner et al., 2012). Microraptorine interrelationships have been elusive in main TWiG dataset studies (Turner et al., 2012; Brusatte et al., 2014) as well as related ones (Lü and Brusatte, 2015), but some datasets relying on TWiG data as its backbone have recovered resolved microraptorine topologies (Senter et al., 2012; Xu et al., 2015). Both Pei et al. (2020) and Gianechini et al. (2018) extended this improved resolution to a main TWiG study by recovering the two largest microraptorines, *Tianyuraptor* and *Zhenyuanlong*, as the earliest-diverging microraptorines (fig. 1), as suggested by Senter et al. (2012) for *Tianyuraptor*, but contrary to the eudromaeosaurian affinity recovered by DePalma et al. (2015). This is supported by the lack of prominent median posterior process along the posterior edge of the ischium in *Tianyuraptor* and *Zhenyuanlong*, unlike other microraptorines and some early-diverging paravians (Pei et al., 2020). Clarifying the character state distributions of several potentially important features will help to test this phylogenetic hypothesis. For example, a posteriorly curved pubis and a radial shaft

less than half of the ulnar width were recovered as synapomorphies of smaller-bodied microraptorines excluding *Tianyuraptor* (Pei et al., 2020), but as microraptorine synapomorphies by Xu et al. (2015) and Agnolín and Novas (2013). Pei et al. (2020) found a proximally pinched metatarsal III was shared by a more inclusive group of microraptorines excluding *Tianyuraptor* and *Zhenyuanlong*, whereas Senter et al. (2012) recovered this as a microraptorine synapomorphy. Small-bodied microraptorines have a subarctometatarsalian foot that is absent in *Zhenyuanlong* and has an uncertain condition in *Tianyuraptor*. The plesiomorphic unspecialized pedal phalanx II-2 appears to be present in small-bodied microraptorines whereas the specialized condition exists in *Zhenyuanlong* but is unknown in *Tianyuraptor*. Pruning incomplete specimens like IVPP V22530 substantially improves the resolution of later-diverging microraptorine interrelationships (Pei et al., 2020). Using automated phylogenetic analysis pipelines (Pei et al., 2020) to further explore the impact of rogue taxa on microraptorine phylogeny would therefore be worthwhile. It is important to bear in mind that some studies have recovered microraptorines as the closest avialan relatives as part of a paravian clade called Avertora, rather than as dromaeosaurids (Agnolín and Novas, 2011, 2013). Thus, more work is clearly needed to bridge this large discrepancy.

Eudromaeosauria Longrich and Currie, 2009, includes the vast majority of dromaeosaurids. It is a node-based taxon containing the last common ancestor of *Saurornitholestes langstoni* Sues, 1978, *Deinonychus antirrhopus* Ostrom, 1969, *Dromaeosaurus albertensis* Matthew and Brown, 1922, and *Velociraptor mongoliensis* Osborn, 1924, and all its descendants (Longrich and Currie, 2009; sensu Turner et al., 2012). Long-standing eudromaeosaurian synapomorphies include: a sharp demarcation between the postorbital process and the frontal orbital margin in dorsal view (Turner et al., 2012; Pei et al., 2020); a pedal phalanx II-2 with a long and lobate flexor heel with the midline ridge extend-

ing onto its dorsal surface (Turner et al., 2012; Pei et al., 2020); thoracic centra approximately equal in anteroposterior length and midpoint mediolateral width (Foth et al., 2014, after *Pyroraptor* is pruned; Pei et al., 2020); lateral surfaces of dorsal vertebrae possess pneumatic foramina (Pei et al., 2020; equivalent node in Xu et al., 2015; clade with equivalent taxa in Agnolín and Novas, 2013).

A relatively early-diverging position was recovered for the diminutive *Bambiraptor* within Eudromaeosauria (Senter et al., 2012; Agnolín and Novas, 2013; DePalma et al., 2015; Pei et al., 2020; fig. 1), but *Bambiraptor* and *Saurornitholestes* were nested within Velociraptorinae in recent main TWiG dataset studies (Turner et al., 2012; Brusatte et al., 2014), and indeed their taxonomic distinction is based on a few traits that are known to change ontogenetically. The long-standing monophyletic subclades Dromaeosaurinae and Velociraptorinae are still maintained, but not without pruning several species known from fragmentary remains (*Yurgovuchia*, *Acheroraptor*, *V. osmolskae*, and *Utahraptor*) (Pei et al., 2020; fig. 1). Dromaeosaurinae Matthew and Brown, 1922, is a stem-based taxon containing *Dromaeosaurus albertensis* Matthew and Brown, 1922, and all coelurosaurians closer to it than to *Velociraptor mongoliensis* Osborn, 1924, *Microraptor zhaoianus* Xu, 2000, *Unenlagia comahuensis* Novas and Puerta, 1997, and *Passer domesticus* Linnaeus, 1758 (sensu Sereno et al., 2005; after Turner et al., 2012). Dromaeosaurines appear to share serrations on all premaxillary and maxillary teeth and have premaxillary teeth that all have a D-shaped cross section (Turner et al., 2012; Pei et al., 2020). However, Pei et al. (2020) recovered these synapomorphies despite pruning *Utahraptor*. That study found *Dromaeosaurus* in a sister relationship with (*Achillobator* + *Atrociraptor*) as in Turner et al. (2012), but unlike Xu et al. (2015), where *Dromaeosaurus* is later diverging than *Achillobator* and *Atrociraptor* and also unlike Brusatte et al. (2014) where these taxa are paraphyletic. Velociraptorinae Barsbold, 1983, is a stem-based taxon containing *Velocirap-*

tor mongoliensis Osborn, 1924, and all coelurosaurians closer to it than to *Dromaeosaurus albertensis* Matthew and Brown, 1922, *Microraptor zhaoianus* Xu, 2000, *Unenlagia comahuensis* Novas and Puerta, 1997, and *Passer domesticus* Linnaeus, 1758 (sensu Sereno et al., 2005; after Turner et al., 2012). Pei et al. (2020) recovered (*Linheraptor* + *Tsaagan*) as the earliest-diverging velociraptorine clade, but remaining velociraptorine interrelationships were controversial as they differed between the two weighting schemes adopted. Later-diverging velociraptorine interrelationships were better resolved at the expense of *Luanchuanraptor* and *V. osmolskae*: *Deinonychus* was recovered as a later-diverging velociraptorine than (*Linheraptor* + *Tsaagan*), which has a sister relationship with *Adasaurus* and the clade (*Balaur* + *Dakotaraptor*). *Balaur*, a strange double-sickle-clawed velociraptorine (Csiki et al., 2010; Turner et al., 2012; Brusatte et al., 2013; Lü and Brusatte, 2015), has also been recovered as an avialan (Cau et al., 2015). *Dakotaraptor* is a eudromaeosaurian that has been recovered as both a velociraptorine (Pei et al., 2020) and as a dromaeosaurine (DePalma et al., 2015). Recent analyses have not converged on the same velociraptorine synapomorphies (Turner et al., 2012; Brusatte et al., 2014; Pei et al., 2020), but some potential ones are worth bearing in mind: cranial nerve X–XII openings located in a shallow bowl-like depression; basal tubera dorsoventrally deeper than the occipital condyle. Pei et al. (2020) recovered *Yurgovuchia*, *Acheroraptor*, *V. osmolskae*, and *Utahraptor* as rogue taxa in their analysis. This is not unexpected as they are all based on fragmentary material that is missing the anatomy relating to dromaeosaurine and velociraptorine synapomorphies. *Utahraptor* is the best preserved among these four taxa but still has a poorly resolved phylogenetic position despite possessing at least one dromaeosaurine synapomorphy (Pei et al., 2020). Ongoing descriptive work on a range of different-sized *Utahraptor* individuals (Jim Kirkland, personal commun.) has particular promise in further elucidating eudromaeosaurian phylogeny. Drom-

aeosaurids are known for their “rodlike” tails that deviate from the typical coelurosaurian tail condition (Senter et al., 2012; Pittman et al., 2013), but unlike Senter et al. (2012), Pei et al. (2020) did not recover tail-based synapomorphies at any internal dromaeosaurid nodes except as a trait of *Luanchuanraptor*. This hints that their tail evolution may be more complex than previously appreciated or that a more sequential evolutionary pattern may yet emerge as more anatomical data becomes available in the future.

TROODONTIDAE GILMORE, 1924: This group is defined as a stem-based taxon containing *Troodon formosus* Leidy, 1856, and all coelurosaurians closer to it than to *Velociraptor mongoliensis* Osborn, 1924, or *Passer domesticus* Linnaeus, 1758 (sensu Sereno, 1998; after Turner et al., 2012). Troodontid phylogeny is probably the least resolved of the paravian groups and does not have subclades established to the same degree as in dromaeosaurid and avialan phylogeny. Seemingly persistent troodontid synapomorphies include a laterally expanded supraorbital crest of the lacrimal anterior and dorsal to the orbit (Turner et al., 2012; Foth et al., 2014; Pei et al., 2020) (excluding anchiornithines); an asymmetrical foot with a slender metatarsal II and a very robust metatarsal IV (Turner et al., 2012; Foth et al., 2014; Pei et al., 2020) (excluding anchiornithines); metatarsal IV wider than either II or III (Turner et al., 2012; Pei et al., 2020) (excluding anchiornithines); smaller, more numerous and more closely appressed anterior dentary teeth compared to those in the middle of the tooth row (Senter et al., 2012; Brusatte et al., 2014; Pei et al., 2020) (in Brusatte et al., 2014, the anchiornithines are included); metatarsal II shorter than IV, but reaching distally further than the base of the metatarsal IV trochlea (Foth et al., 2014; Pei et al., 2020); absence of the basisphenoid recess between the basisphenoid and basioccipital (Xu et al., 2015; Pei et al., 2020); oval foramen magnum taller than wide (Xu et al., 2015; Pei et al., 2020); dentary teeth set in an open groove (Xu et al., 2015; Pei et al., 2020); postorbital process of the lat-

erosphenoid with pneumatic depression on ventral surface (Xu et al., 2015; Pei et al., 2020); and conjoined basal tubera narrower than the occipital condyle (Xu et al., 2015; Pei et al., 2020). In Brusatte et al. (2014) the concave step in the anterior margin of the maxilla is a troodontid synapomorphy, but this same anatomical feature was recovered as a paravian synapomorphy by Pei et al. (2020). In general, some Jehol troodontids such as *Sinovenator* and *Jingfengopteryx* are often recovered as the earliest-diverging members of the group, sometimes including a pair of small-bodied Mongolian troodontids as well in a Jingfengopterygid clade (Turner et al., 2012). Other taxa like *Sinusonasus* and *Jianianhualong*, which have transitional features, are later diverging in their systematic positions, and most Late Cretaceous troodontids are the latest-diverging within the group. In some analyses the transitional taxa collapse nodes into polytomies and produce a single nested troodontid clade with no distinction between Jehol or Mongolian groups (Xu et al., 2017). Main TWiG datasets recover at least two troodontid clades of varying composition (reduced strict consensus tree: Brusatte et al., 2014; Pei et al., 2020; fig. 1; strict consensus tree: Turner et al., 2012) near the base of the troodontid phylogeny, but have yet to include *Jianianhualong* and other new taxa that seem to be blurring traditional clade lines. Anchiornithines have been recovered as the earliest-diverging troodontids in some analyses of past TWiG dataset iterations (e.g., Turner et al., 2012; Brusatte et al., 2014; Gianechini et al., 2018) as well as modified versions of them (Agnolín et al. 2019) whilst other studies have resolved them with early-diverging avialans (e.g., Agnolín and Novas, 2013; Pei et al., 2020; fig. 1) or as early-diverging paravians (e.g., Lefèvre et al., 2017). *Anchiornis* is known from hundreds of fossils preserved in different postures (Hu et al., 2009; Pei et al., 2017; Wang et al., 2017a), offering the most complete picture of anchiornithine anatomy currently available. This taxon has a key role to play in further investigating the taxonomic status of anchiornithines. In this study *Xiaotingia*

maintains its close affinities with *Anchiornis* as part of the Anchiornithinae (fig. 1). Its phylogenetic position has also been contentious, since it was originally recovered as part of a deinonychosaurian subclade with *Anchiornis* and *Archaeopteryx* (Xu et al., 2011) and later recovered as a troodontid (Turner et al., 2012).

MESOZOIC AVIALAE: Avialae Gauthier, 1986, is a stem-based taxon containing *Passer domesticus* Linnaeus, 1758, and all coelurosaurians closer to it than to *Dromaeosaurus albertensis* Matthew and Brown, 1922, or *Troodon formosus* Leidy, 1856 (sensu Maryańska et al., 2002; after Turner et al., 2012). Although our understanding of the phylogenetic relationships of Mesozoic birds has improved enormously over the past three decades, there remain major challenges as systematists scramble to keep up with the rapidly expanding species diversity primarily coming out of the Jehol deposits in northeastern China. Current analyses targeted at Mesozoic bird relationships have experienced a decline in overall support as new taxa with unusual character combinations blur the distinction between major clades (Zhou et al., 2012). This is primarily because character matrices have failed to keep abreast of new morphological diversity through revision and expansion of the character set. This is not to say that character matrices have not been expanded, but with new species and even clades identified every year, it is unsurprising that most analyses fail even to keep up with new operational taxonomic units (OTUs).

Most, but not all, 21st-century descriptions of new taxa have included a phylogenetic analysis to support taxonomic inferences based on morphological observations. All major analyses stem from either the Norell and Clarke (2001) data set, which consists of 201 characters, or the Chiappe (2002) data set, consisting of 169 characters. Generally, Norell and Clarke's (2001) matrix includes more characters targeted at resolving later-diverging avialans derived from their work on *Apsaravis* (Clarke and Norell, 2002) and Clarke's (2004) revision of *Ichthyornis*, whereas the Chiappe (2002) character list focuses more

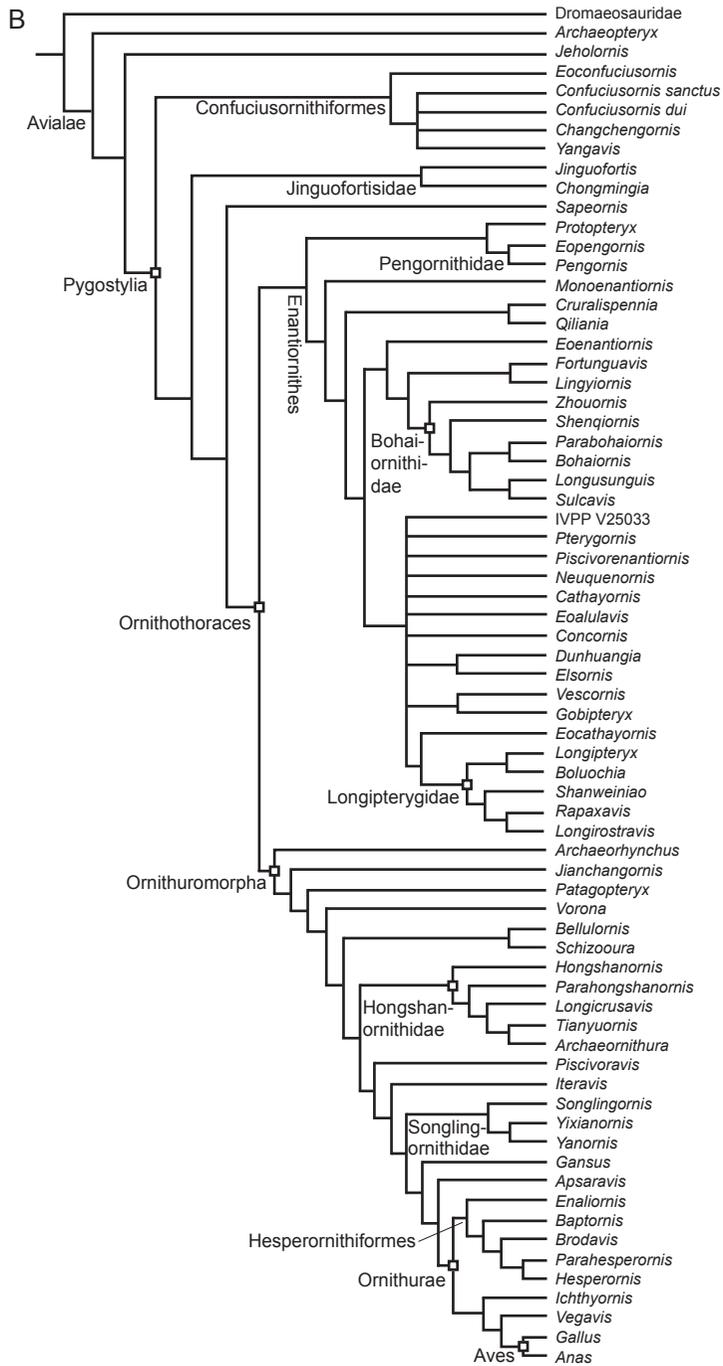


FIG. 3. Wang et al. (2018a) analysis of 70 taxa scored across 280 morphological characters. Published results using **A.** new technologies; **B.** traditional search using implied weighting, $k = 16$.

heavily on early-diverging birds based on his work on the El Brete enantiornithines and the early-diverging ornithuromorph *Patagopteryx* (Chiappe, 1995). Chiappe (2002) included Allosauroidea, Velociraptorinae, and the Troodontidae as outgroups but did not illustrate their relative relationships. The Alvarezsauroidea, at one time considered to be a clade of flightless birds (Suzuki et al., 2002), were also initially included (Chiappe, 2002). In contrast, Norell and Clarke (2001) used the OTU Dromaeosauridae to root their analysis. Following their usage, all subsequent analyses born from the Chiappe (2002) list have also used the Dromaeosauridae as the outgroup (O'Connor et al., 2011; Zhou et al., 2014; Wang et al., 2018a) (fig. 3).

The Chiappe (2002) character list was expanded by Gao et al. (2008), whose new matrix included 15 new taxa and 73 additional characters (total 242 characters), some of which were new and others taken from Norell and Clarke (2001). This list was further expanded to include three new characters and a large number of additional taxa (O'Connor et al., 2009, 2011). The O'Connor et al. (2011) character list has since been expanded independently by Wang et al. (2014, 2018a) and Atterholt et al. (2018). Wang et al. (2014) added 17 new characters (262 characters) and Atterholt et al. (2018) added seven (252 characters). In both cases the added characters were targeted towards increasing resolution in the Enantiornithes. The Wang et al. (2014) matrix was modified by Chiappe et al. (2019), in which some characters were added while others were deleted and some scorings were modified (212 characters). Wang and colleagues expanded their matrix again in 2018, and it has 70 taxa scored over 280 (18 new) characters (Wang et al., 2018a; fig. 3). In 2014, Li's group added 19 characters to the Norell and Clarke (2001) matrix but included only 36 taxa (Li et al., 2014).

All these aforementioned analyses stem from careful firsthand observation of almost all the analyzed OTUs. However, they all fail at one critical level: in only using the OTU Dromaeosauridae as

the outgroup, these analyses included only one potential avialan ancestor. This made it impossible to test hypotheses regarding the closest dinosaurian relatives of Avialae. A notable recent difference between the analyses of these various workers is the parameters utilized for the analysis. For example, although Wang et al. (2017b) and O'Connor et al. (2016) both use the TNT software (Goloboff et al., 2008a), Wang et al. (2018a) have recently shifted to using "new technology" search algorithms (fig. 3A). O'Connor et al. (2014; Atterholt et al., 2018) continue to use traditional search terms and have more recently started applying implied weighting (Goloboff et al., 2008b) to account for the extreme homoplasy observed during early avialan evolution because this method more strongly weights characters that have more homology (less homoplasy) (Wang and O'Connor, 2017; Xu, 2018). Here, the Wang et al. (2018a) analysis is rerun with a traditional search using implied weighting (Goloboff et al., 2008b) with a gentle concavity (Goloboff et al., 2018), $k = 16$ (fig. 3B) (see Methods). The results are presented together with the results published by Wang et al. (2018a) based on "new technology" search algorithms in TNT (fig. 3A).

There are a few other matrices that have been utilized in attempts to resolve the phylogeny of Mesozoic birds (Cau and Arduini, 2008; Lefèvre et al., 2014). However, these appear to rely heavily on published information, which is often incomplete if taxa are not monographed and can at times be inaccurate (e.g., "*Dalingheornis*": Zhang et al., 2006; Lockley et al., 2007). Controversial taxa that have received only preliminary study can produce erroneous results in analyses when their purported morphologies are taken at face value (e.g., *Jixiangornis* (Ji et al., 2002; Lefèvre et al., 2014)).

There are several relationships in Mesozoic avialan phylogeny that have stabilized in recent analyses, and other regions of the tree where recent analyses still fail to find consensus. *Archaeopteryx* is the earliest-diverging avialan according to the definition above followed by most Mesozoic ornithologists (possible troodontids such as

Anchiornis are not included in these analyses) and *Jeholornis*, another long bony-tailed bird, is typically resolved as later diverging than *Archaeopteryx* but earlier diverging than the Pygostylia, all birds whose abbreviated tail ends in a fused, compound element, the pygostyle (Li et al., 2014; Atterholt et al., 2018; Wang et al., 2018a). The Enantiornithes and the Ornithuromorpha (node-based definition that we follow in this volume because of the preference of our authors; Euornithes Sereno et al., 1998, is the stem-based definition) are consistently resolved as sister taxa, forming the Ornithothoraces (Chiappe, 2002; Clarke, 2004; Gao et al., 2008; Wang et al., 2018a). The relative placement of the two major recognized early-diverging pygostylian clades, the Sapeornithiformes and Confuciusornithiformes, is unstable; the two groups have both been resolved as the sister taxon to the Ornithothoraces (Li et al., 2014; Wang et al., 2014). The “mosaic” distribution of derived avialan features within Paraves obscures attempts at resolving aspects of early avialan phylogeny. For example, while the absence of an ossified sternum suggests *Sapeornis* is earlier diverging, it has a more reduced (and thus derived) manus with only two manual unguals, whereas in *Confuciusornis* the manus retains the plesiomorphic condition of three manual unguals, and these are hypertrophied relative to most other paravians (Chiappe et al., 1999; Zhou and Zhang, 2002; Zheng et al., 2014) (fig. 4). The Wang et al. (2018a) analysis suggests that the Confuciusornithiformes are the earliest-diverging pygostylians known, even more primitive than the recently identified Jinguoformisidae (fig. 3).

Enantiornithine phylogeny is poorly resolved (O'Connor et al., 2011; Wang et al., 2018a), but several groups have become apparent in recent analyses. *Protopteryx*, *Iberomesornis*, and the Pengornithidae are fairly consistently resolved as very early-diverging taxa (Wang et al., 2017b; Atterholt et al., 2018; Wang et al., 2018a). Jehol “longirostrine” taxa are commonly resolved into two clades, one formed by *Longirostravis*, *Shanweiniao*, and *Rapaxavis*, and the other by *Longipteryx* and *Boluochia* (O'Connor et al., 2009,

2016; Wang et al., 2014; Zhou et al., 2014). These two clades are often but not always resolved forming a larger clade (the Longipterygidae; fig. 3) (Wang et al., 2014, 2018a). The most diverse and reasonably resolved clade of enantiornithines is the Bohaiornithidae, although its recognition through cladistic analysis required additional characters to be added and scored in relevant phylogenetic data matrices (Wang et al., 2014, 2018a) and a recent analysis included in the description of a new bohaiornithid-like species failed to resolve this clade (Chiappe et al., 2019). The only recognized Late Cretaceous family is the Avisauridae (Chiappe, 1992). Through the support of seven additional characters targeted at avisaurid relationships, this clade has recently been demonstrated to consist of North American and South American subclades, each consisting of three taxa (Atterholt et al., 2018).

The Ornithuromorpha is slightly more resolved than the Enantiornithes, probably due to its lesser diversity (fig. 3). *Archaeorhynchus* and *Patagopteryx* are consistently resolved as among the earliest-diverging taxa (You et al., 2006; Li et al., 2014; O'Connor et al., 2016; Wang et al., 2017b), although in the enlarged analysis of Wang et al. (2018a) *Patagopteryx* has a later-diverging position. The secondary loss of flight in the Late Cretaceous *Patagopteryx* may be creating a false signal interpreted by some analyses as indicative of an earlier-diverging position (fig. 1B). *Vorona*, *Chaoyangia*, *Jianchangornis*, and *Zhongjianornis* are also consistently resolved as early-diverging taxa (Wang et al., 2014; Zhou et al., 2014; O'Connor et al., 2016). The most diverse family is the Hongshanornithidae (Wang et al., 2015; 2017b; 2018a). *Yanornis*, *Yixianornis*, and *Songlingornis* are often grouped together based on sternal morphology forming a clade referred to as the Songlingornithidae (Clarke et al., 2006; Li et al., 2014; Wang et al., 2018a). *Gansus* from the slightly younger Xiagou Formation is typically resolved as later diverging than Jehol ornithuromorphs (Zhou et al., 2014; Wang et al., 2018b).

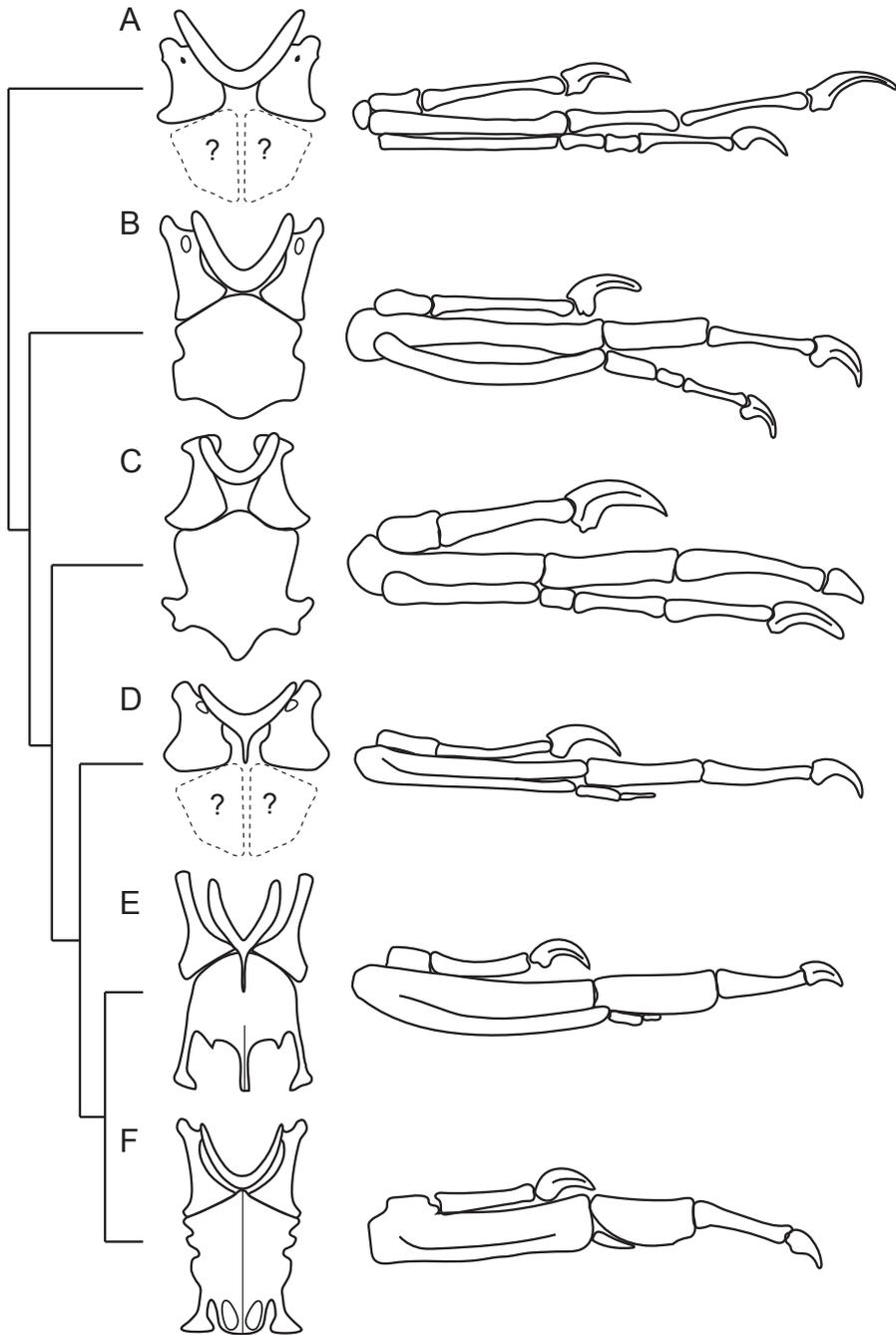


FIG. 4. Major evolutionary transformations in the avian furcula, coracoid and sternum, and manus in context of a simplified phylogeny, as documented in **A.** *Archaeopteryx*, **B.** *Jeholornis*, **C.** *Confuciusornis*, **D.** *Sapeornis*, **E.** Early Cretaceous Enantiornithes (*Parabohaiornis*), and **F.** Early Cretaceous Ornithuromorpha (*Yanornis*). Generally during early avian evolution, the furcula, coracoid, and sternum become more craniocaudally elongate, while the manual digits become reduced and fusion between the metacarpals increases. Illustrations not to scale.

The Ornithurae generally consists of *Ichthyornis*, *Hesperornis*, and Aves, although whether the *Ichthyornis* lineage or the Hesperornithiformes is more closely related to modern birds is unresolved (Clarke, 2004; O'Connor et al., 2011; Li et al., 2014; Wang et al., 2018a). Since the most common definition of Ornithurae is node based with *Hesperornis* and living birds as reference taxa (Gauthier and de Queiroz, 2001), this means that *Ichthyornis* may or may not be a member of this clade. It is for this reason that stem-based definitions may better serve until early avialan relationships are better understood. Although *Ichthyornis* was traditionally resolved as later diverging (Chiappe, 2002; Clarke, 2004; You et al., 2006), increased character sampling in the Hesperornithiformes resulted in this clade moving crownward (O'Connor et al., 2011). New cranial information on *Ichthyornis* supports the earlier-diverging position of this taxon (Atterholt et al., 2018; Field et al., 2018). However, the position resolved for this taxon using the Wang et al. (2018a) matrix is quite different depending on how the data is analyzed, further highlighting the uncertainty that surrounds the relative placement of these later-diverging lineages (fig. 3).

In recent analyses, Bremer support is typically very low (O'Connor et al., 2017; Wang et al., 2018a). This likely reflects similarities between early-diverging ornithuromorphs and enantiornithines that have blurred the distinction between these two major clades and not missing data (O'Connor and Zhou, 2013). Take, for example, the taxon *Schizooura lii*: although clearly a member of the Ornithuromorpha, this species possesses a Y-shaped enantiornithine-like furcula; the coracoid lacks a lateral process (at one time a synapomorphy of the Ornithuromorpha); and the cranial surface of the humerus is flat (Zhou et al., 2012). *Chaoyangia* preserves two features observed clearly only in ornithuromorphs, but sometimes is resolved in the Enantiornithes, and thus a well-resolved tree can be found only if it is excluded (O'Connor et al., 2014). In many recent analyses, Ornithothoraces forms a single clade in trees only one or two steps longer than the most parsimoni-

ous solution (O'Connor and Zhou, 2013; Wang et al., 2018a). This mosaic distribution of morphologies among taxa and the dwindling number of clear morphological differences between the Enantiornithes and the Ornithuromorpha as early-diverging taxa are uncovered has diminished the number of synapomorphies in support of each node, resulting in weak support for most traditional clades (O'Connor et al., 2014; Zelenkov, 2017). The only way to increase support is to identify new synapomorphies for each clade and increase the amount of morphological data incorporated into the character matrix, no easy task given the varying preservational limitations set by the known diversity and the rapid rate of discovery principally in China (O'Connor and Zhou, 2013), but also elsewhere (de Souza Carvalho et al., 2015; Atterholt et al., 2018). Currently, all synapomorphies in support of Ornithothoraces, Enantiornithes, and Ornithuromorpha are ambiguous because of the large number of taxa and substantial amount of preservational variability between specimens. Although the rate of discovery has outpaced the rate at which character sets have been expanded, the Wang et al. (2018a) dataset exemplifies the continual efforts that are being made to encapsulate greater morphological variation. This dataset has roughly 100 more characters than datasets from 15 years ago and double the number of OTUs.

It is often difficult to compare results of various analyses due to differences in the included taxa. Nearly half of all Mesozoic avialans are not even included in phylogenetic analyses because of their highly fragmentary nature (O'Connor, 2009; O'Connor et al., 2014). With the exception of specimens from a few key deposits, most of the Mesozoic fossil record consists of incomplete taxa based on a small number of incomplete elements (e.g., *Flexomornis*, *Limenavis*), a single bone (e.g., *Avisaurus*, *Yungavolucris*), or sometimes less (e.g., *Lectavis*, *Almatiornis*). Such incomplete OTUs in already weakly supported phylogenies can result in the collapse of the Ornithothoraces (e.g., *Chaoyangia*), and some (e.g., *Mystiornis*, *Flexomornis*) even cause the Pygostylia to collapse (O'Connor

and Zhou, 2013; O'Connor et al., 2014; Atterholt et al., 2018).

Zhongornis is known only from a single young juvenile specimen and, given the extreme ontogenetic changes likely experienced by most paravians, its phylogenetic affinities cannot be determined with any certainty at this time. Originally considered a member of a distinct lineage of birds characterized by a tail morphology intermediate between that of *Archaeopteryx* and that of pygostylians (Gao et al., 2008), the specimen was later suggested to be a juvenile scansoriopterygid (O'Connor and Sullivan, 2014). New data on pygostyle formation suggests that *Zhongornis* may in fact be a juvenile pygostylian (Rashid et al., 2018).

Anchiornithine taxa—*Anchiornis*, *Aurornis*, *Eosinopteryx*, and *Xiaotingia*—have been gathered into a distinct clade of early branching avialans (Anchiornithinae: we use this stem-based taxon containing *Anchiornis* instead of Anchiornithidae because the former was proposed earlier [Xu et al. 2016]) either all together (Agnolín and Novas, 2011; Agnolín and Novas, 2013; Foth et al., 2014; Pei et al., 2017, 2020; Rashid et al., 2018) or as a subset of the four taxa (Xu et al., 2011). This contrasted with past analyses involving the main TWiG data matrix or modified versions, which recovered anchiornithines or a subset of them as part of the Troodontidae (Turner et al., 2012; Brusatte et al., 2014; Agnolín et al., 2019), as well as previous studies that found them to be early-diverging deinonychosaurians (Senter et al., 2012; Xu et al., 2015) or early-diverging paravians (Lefèvre et al., 2017). Despite such major differences in the phylogenetic position of this clade these avialan synapomorphies stand out (Turner et al., 2012; Brusatte et al., 2014; Foth et al., 2014): transition point proximal to caudal 7; in lateral view, the dorsal border of the antorbital fossa is formed by the lacrimal and nasal.

Eight individual *Archaeopteryx* specimens (of 11 published) were recently recovered in a polytomous clade that is sister to the nonanchiornithine avialans (Pei et al., 2020; fig. 1). With the Haarlem specimen pruned (recently

proposed as an anchiornithine: Foth and Rauhut, 2017), six *Archaeopteryx* specimens (the London, Berlin, Munich, Thermopolis, Eichstätt, and 11th specimens) form a group sister to a large avialan clade comprising of the Solnhofen specimen and remaining later-diverging avialans. However, the former group was supported by synapomorphies that cannot be scored in the Solnhofen specimen, so additional data may yet show a monophyletic *Archaeopteryx* group (although some fragmentary specimens are probably only referable to more inclusive Mesozoic avialan clades: Rauhut et al., 2018).

Rahonavis was originally described as an early-diverging avialan (Forster et al., 1996) and has been found in a later-diverging position than *Archaeopteryx* (Cau, 2018; Novas et al., 2018). However, it has also been recovered as a dromaeosaurid by a range of other studies (Makovicky et al., 2005; Turner et al., 2012), which is the position favored in this volume.

CROWN BIRDS (AVES): The last decade has seen a great deal of progress with regard to resolving the interrelationships of the major groups of living birds. A series of large-scale “phylogenomic” studies has iteratively brought us closer than ever to a complete picture of crown bird interordinal relationships (e.g., Ericson et al., 2006; Hackett et al., 2008; McCormack et al., 2013; Jarvis et al., 2014; Claramunt and Cracraft, 2015; Prum et al., 2015; Kimball et al., 2019). Ongoing work seeks to continue progress on resolving recalcitrant portions of the bird tree of life, as well as achieving the goal of sequencing and analyzing the whole genomes of all known extant avialan species.

Crown birds (Aves) comprise nearly 11,000 described extant species, and are divided into two major subclades: Palaeognathae and Neognathae (Gill and Donsker, 2017). Palaeognathae comprises the paraphyletic, flightless ratites (i.e., the extant ostriches, rheas, kiwis, emus, and cassowaries), and the volant tinamous of the New World. Over the last decade, the surprising hypothesis that ratites are paraphyletic

with respect to tinamous has received accumulating support from molecular phylogenetic data sets (Hackett et al., 2008; Harshman et al., 2008; Phillips et al., 2010; Haddrath and Baker, 2012; Smith et al., 2013; Baker et al., 2014; Jarvis et al., 2014; Mitchell et al., 2014; Prum et al., 2015; Yonezawa et al., 2016; Grealy et al., 2017; Reddy et al., 2017) and is corroborated by embryological data (Faux and Field, 2017), suggesting that flightlessness and large body size have arisen repeatedly throughout palaeognath evolutionary history. Neognathae are divided into Galloanserae (chickenlike and ducklike birds) and the major clade Neoaves, which represents over 95% of living bird diversity. The earliest fossil crown bird yet identified, *Asteriornis* from the Maastrichtian of Belgium, appears to represent an early galloanseran (Field et al., 2020). This implies that at least the stem lineages of Palaeognathae, Galloanserae, and Neoaves were present in the Late Cretaceous.

The phylogenetic interrelationships of the major subclades of Neoaves are hotly contested, and according to one recent high-profile phylogenomic study, represent “the greatest unresolved challenge in dinosaur systematics” (Prum et al., 2015). While several recent studies have sought to clarify the deep branching pattern among the major neoavian clades (e.g., Hackett et al., 2008; Jarvis et al., 2014; Prum et al., 2015; Reddy et al., 2017; Kimball et al., 2019), these studies have recovered incompatible neoavian topologies, raising questions about the influence of data type, taxon sampling, and analytical approach in driving topological results. Indeed, recent work (Suh, 2016) hypothesises that a consistent, bifurcating branching pattern along much of the backbone of Neoaves may never be obtained, since the early evolutionary history of Neoaves may have been characterized by extremely rapid cladogenesis and high rates of incomplete lineage sorting. Although the subject is still controversial (see Field et al., chapter 5, on molecular rate variation), the hypothesis of a rapid radiation of Neoaves in the aftermath of the end-Cretaceous mass extinction

has gained mounting support in recent years (Feduccia, 1995; Ericson et al., 2006; Longrich et al., 2011; Feduccia, 2014; Jarvis et al., 2014; Prum et al., 2015; Berv and Field, 2018). Importantly, uncertainty regarding the precise origination times of the deepest clades of crown birds, as well as Aves itself, has clouded understanding of the influence of the end-Cretaceous mass extinction on avialan evolution. However, the known neoavian fossil record is entirely post-Cretaceous at present (Longrich et al., 2011; Field, 2017; Ksepka et al., 2017), consistent with the idea that lingering topological uncertainty at the base of Neoaves may indeed be related to rapid early Cenozoic cladogenesis (see Field et al., chapter 5, on molecular rate variation).

Despite ongoing controversy related to the branching pattern at the base of Neoaves, recent phylogenetic studies are consistent in recognizing about 10 major constituent neoavian subclades (Reddy et al., 2017; Field et al., chapter 5). Figure 5 depicts competing topological hypotheses presented by two recent avialan phylogenomic studies (Jarvis et al., 2014; Prum et al., 2015), illustrating that despite some topological uncertainty, the composition of most major clades is consistent across studies. Major outstanding topological controversies influencing our understanding of avialan macroevolution include:

1. Which clade is the sister taxon to the rest of Neoaves? Some recent studies (e.g., Jarvis et al., 2014) recovered a monophyletic “Columbea” comprising Mirandornithes (Podicipediformes and Phoenicopteriformes) and Columbimorphae (Columbiformes, Pteroclidiformes, and Mesitornithiformes) in this position, although Prum et al. (2015) recovered Strisores (which comprises a paraphyletic “Caprimulgiformes” and Apodiformes) as sister to all other Neoaves. In turn, the monophyly of Columbea was not recovered by Prum et al. (2015), and the interrelationships of Strisores are still hotly contested (Chen et al., 2019).

2. Are most aquatic avialan lineages part of a monophyletic aquatic radiation? Prum et al. (2015) recovered a topology in which most aquatic birds (with the exception of Anseri-

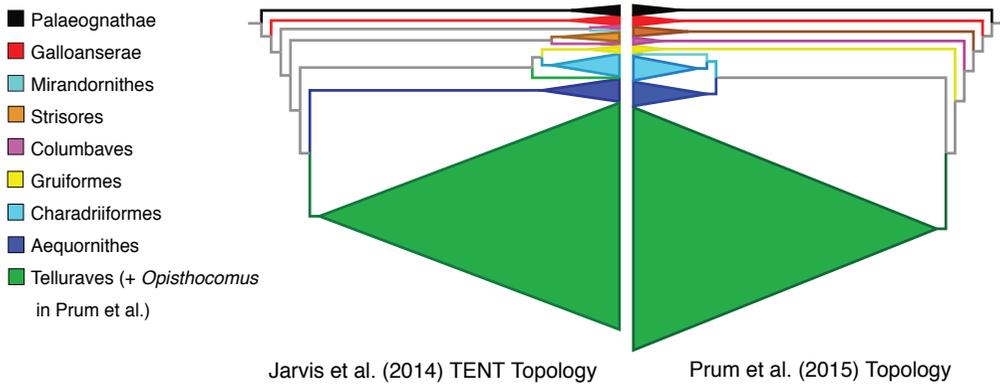


FIG. 5. Competing phylogenetic topologies for crown birds from recent phylogenomic studies of Jarvis et al. (2014) and Prum et al. (2015). Both topologies support Palaeognathae (black) and Galloanserae (red) as successive sister taxa to the rest of extant birds (Neoaves). Interrelationships within Neoaves differ, but the same major constituent clades are largely supported (see legend). The monotypic hoatzin (*Opisthocomus hoazin*) is inferred to be the sister taxon of Telluraves in Prum et al. (2015), and sister to a Charadriiformes + Gruiformes clade in Jarvis et al. (2014). Prum et al. (2015) supports a monophyletic Columbaves (fuscia), uniting Otidimorphae (bustards, cuckoos, turacos) and Columbimorphae (doves, mesites, sandgrouse), whereas Jarvis et al. (2014) find Columbimorphae as the sister taxon to Mirandornithes, and Otidimorphae as sister to Strisores.

formes, kingfishers, and aquatic gruiforms and passerines like dippers) formed a large monophyletic clade. This clade, dubbed Aequorlitor-nithes, united Aequornithes, Charadriiformes, and Mirandornithes, suggesting that adaptation to aquatic habits may have taken place fewer times throughout avialan evolutionary history than previously thought. However, the monophyly of this clade has not been obtained by other large-scale phylogenomic studies (Jarvis et al., 2014; Reddy et al., 2017; Kimball et al., 2019).

While ongoing large-scale phylogenetic studies are likely to shed light on these and other questions related to neoavian phylogeny in the relatively short-term, targeted phylogenomic studies of major avialan subclades are continuously illuminating finer-scale phylogenetic relationships across the bird tree of life. For example, a recent phylogenomic study of passerines (a massive avian subclade comprising over 6000 living species) represents the first effort to sequence representatives of all extant passerine families, revealing important insight into this charismatic superradiation (Oliveros et al., 2019).

DISCUSSION

Pennaraptoran systematics has dramatically improved over the past few decades through immense efforts from all corners of the globe, but there remain areas to improve in all clades, particularly the enigmatic Scansoriopterygidae and Anchiornithinae.

CONTENTIOUS GROUPS AND GROUPS WITH 'BLURRY' BOUNDARIES: For groups with contentious phylogenetic positions like the Anchiornithinae and Scansoriopterygidae and for groups with "blurry" boundaries, an automated pipeline of phylogenetic analysis, like the one described in Methods, will be helpful in further exploring phylogenetic placement through easier and more efficient running of analyses using alternative character codings and considering all phylogenetically informative but highly fragmentary specimens.

POWERED-FLIGHT ORIGINS: The topology in figure 1 provided the context to determine that only paravians meet the minimum thresholds of modern powered flight (in terms of wing loading and specific lift estimates seen in today's flying birds: see Pei et al. (2020) for details). This is despite the

reduced body size, pennaceous feathers, and capable respiratory system among nonparavian pennaraptorans (Turner et al., 2007a; Dececchi and Larsson, 2013; Benson et al., 2014; Foth et al., 2014; Lee et al., 2014; Xu et al., 2014; Brusatte et al., 2015). Powered flight potential among microraptorines and unenlagiines underscores the need for more intensive systematic study of these groups, particularly the more enigmatic unenlagiines (Pei et al., 2020). Recovered early-diverging positions of the larger microraptorines *Tianyuraptor* and *Zhenyuanlong* imply a decrease in body size and an increase in relative forelimb length across Microraptorinae (Pei et al., 2020). Discovering microraptorines that cover temporal and geographical ranges outside the currently known Early Cretaceous Asian forms and Late Cretaceous North American ones may yet reveal the drivers and development of this flight potential.

METHODS

MAIN NONAVIALAN PENNARAPTORAN ANALYSIS DISCUSSED (Pei et al., 2020)

The study of Pei et al. (2020) was based on the Theropod Working Group dataset [TWiG dataset] of Brusatte et al. (2014), which was significantly expanded with data pertinent to paravian phylogeny, including nine dromaeosaurid terminals (Late Cretaceous microraptorine IVPP V22530, *Changyuraptor*, *Zhenyuanlong*, *Luanchuanraptor*, *Acheroraptor*, *Linheraptor*, *Yurgovuchia*, *Dakotaraptor*, and *Velociraptor osmolskae*), revised codings and data obtained from laser-stimulated fluorescence (LSF) imaging (Kaye et al., 2015; Wang et al., 2017a). The phylogenetic analysis was automated using a master script executed in TNT version 1.5 (Goloboff et al., 2008a; Goloboff and Catalano, 2016), which helped identify and correctly score errors/problems more quickly and easily. This script automated thorough searches, as well as the subsequent diagnosis and characterization of results. All the scripts and batch files for initial

analysis, diagnosis, and other tasks, are available (with full descriptions) in Pei et al. (2020). Tree searches used the extended search algorithms of TNT (“new technologies”), initially using 5 random addition sequence Wagner trees followed by TBR, sectorial searches [CSS, RSS, and XSS], and 5 cycles of tree-drifting, followed by tree-fusing (see Goloboff, 1999, for details). The search calculated the consensus as trees of optimal score were repeatedly found (eliminating branches of minimum length zero (Coddington and Scharff, 1994); subsequent consensus calculation after pruning rogue taxa more conservatively collapsed trees with TBR branch-swapping (Goloboff and Farris, 2001)), stopping the search only when the consensus becomes stable to new hits, thereby validating the accuracy of the consensus for the corresponding dataset and optimality criterion. The optimal score was therefore independently found as many times as needed to obtain a stable consensus; this validation procedure was performed three times for greater reliability. All our analyses included implied weighting (XIW) (Goloboff, 1993), with modifications proposed by Goloboff (2014) that prevent improper inflation of weights due to missing entries (characters with missing entries have their weights downweighted faster). Missing entries were assumed to have 0.8 of the homoplasy in observed entries, but not extrapolating beyond 5 times the observed homoplasy. The analyses used a concavity of 10, which mildly weights against characters with homoplasy. For the complete methodological details see Pei et al. (2020).

MAIN EARLY-DIVERGING AVIALAN ANALYSIS DISCUSSED (after Wang et al., 2018a)

The Mesozoic avialan analysis of Wang et al. (2018a) was rerun using a traditional search (heuristic search using tree-bisection reconnection retaining the single shortest tree from every 1000 replications, followed by a second round of tree-bisection reconnection) using implied weighting with the k value of 16 (fig. 3B). The

results of this analysis are presented together with those of Wang et al. (2018a), which used extended search algorithms (“new technologies”) in TNT (fig. 3A).

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