

Chapter 2

The Fossil Record of Mesozoic and Paleocene Pennaraptorans

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ABSTRACT

An unabated surge of new and important discoveries continues to transform knowledge of pennaraptoran biology and evolution amassed over the last 150+ years. This chapter summarizes progress made thus far in sampling the pennaraptoran fossil record of the Mesozoic and Paleocene and proposes priority areas of attention moving forward.

Oviraptorosaurians are bizarre, nonparavian pennaraptorans first discovered in North America and Mongolia within Late Cretaceous rocks in the early 20th century. We now know that oviraptorosaurians also occupied the Early Cretaceous and their unquestionable fossil record is currently limited to Laurasia. Early Cretaceous material from China preserves feathers and other soft tissues and ingested remains including gastroliths and other stomach contents, while brooding specimens and age-structured, single-species accumulations from China and Mongolia provide spectacular behavioral insights. Less specialized early oviraptorosaurians like *Incisivosaurus* and *Microvenator* remain rare, and ancestral forms expected in the Late Jurassic are yet to be discovered, although some authors have suggested *Epidexipteryx* and possibly other scansoriopterygids may represent early-diverging oviraptorosaurians.

Long-armed scansoriopterygids from the Middle-Late Jurassic of Laurasia are either early-diverging oviraptorosaurians or paravians, and some have considered them to be early-diverging avialans. Known from five (or possibly six) feathered specimens from China, only two mature individuals exist, representing these taxa. These taxa, *Yi* and *Ambopteryx*, preserve stylopod-supported wing membranes that are the only known alternative to the feathered, muscular wings that had been exclusively associated with dinosaurian flight. Thus, scansoriopterygid specimens—particularly those preserving soft tissue—remain a key priority for future specimen collection.

Dromaeosaurids and troodontids were first discovered in North America and Mongolia in Late Cretaceous rocks. More recent discoveries show that these animals originated in the Late Jurassic, were strikingly feathered, lived across diverse climes and environments, and at least in the case of dromaeosaurids, attained a global distribution and the potential for aerial locomotion at small size.

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China and Mongolia have yielded the most dromaeosaurid and troodontid specimens and taxa, but Gondwanan troodontids are almost unknown compared to southern dromaeosaurids, so the fidelity of this biogeographical signal is worth further exploration. Discovery of well-preserved Middle-Late Jurassic material will be crucial for understanding the origin of key dromaeosaurid and troodontid traits, with the controversial anchiornithines potentially already offering this if their troodontid status can be solidified.

In line with the preferences of most theropod palaeontologists, birds are defined herein as members of Avialae, including stem and crown taxa, whilst Aves herein refers to crown-group birds (see Pittman et al., chapter 1, for the precise definition of Avialae adopted; elsewhere, typically among ornithologists, Aves refers to stem and crown taxa whilst Neornithes refers to crown-group birds). Despite taphonomic bias against avialans in the fossil record, their Early Cretaceous record is fairly robust largely due to the high taxonomic and ecological diversity preserved within the rich Jehol deposits of northeastern China. *Archaeopteryx* (and possibly the controversial Middle-Late Jurassic anchiornithines) show what some of the earliest birds were like, but better-preserved soft tissues hold the key to understanding their substantially different anatomy and flight capabilities to crown-group birds (Aves).

The Late Cretaceous–early Paleocene fossil record of crown birds is especially poor, and improved sampling will be necessary to clarify our understanding of avialan survivorship, ecological selectivity, and recovery across the end-Cretaceous mass extinction. Deposits of Eocene age, such as Messel and Green River, have been especially useful for documenting the early evolutionary history of crown birds. However, the discovery of new Cretaceous and/or Palaeogene bird-bearing lagerstätten from Gondwana will be important for accurately determining ancestral biogeographic patterns.

BACKGROUND

Pennaraptorans are a clade of vaned feathered coelurosaurian dinosaurs that are comprised of the Oviraptorosauria, Scansoriopterygidae, Dromaeosauridae, Troodontidae, and Avialae (see Pittman et al., in the previous chapter for additional information). They include the only dinosaurs to have evolved flight and the only ones to have persisted to the present day.

OVIRAPTOROSAURIA

Oviraptorosaurian fossils were first discovered in the 1920s and are now represented by more than 40 genera spanning a size range across three orders of magnitude (table 1). The 1920s to 1940s, the 1970s, 1980s, 1990s, and the past 20 years have been key periods in our documentation of the oviraptorosaurian fossil record, which

is limited to Laurasian continents and dominated by discoveries from Asia and North America (fig. 1). The last 30 years have seen the discovery of most known oviraptorosaurian taxa, particularly from the Cretaceous of China and the Late Cretaceous of North America and Mongolia. These discoveries have greatly broadened our understanding of this group, including in regard to the evolution of their beaked and strangely pneumatized skulls, as well as the origin of brooding in theropod dinosaurs.

ASIA: This continent is the home of the first described oviraptorosaurian species (Osborn, 1924), the eponymous species *Oviraptor*. Asia is also home to more than 75% of valid oviraptorosaurian genera. The most important sources of Asian oviraptorosaurians are the Early Cretaceous (Hauterivian–Aptian) Jehol Lagerstätte of northeastern China, the Campanian–Maastrichtian Ganzhou oviraptorid fauna of southern

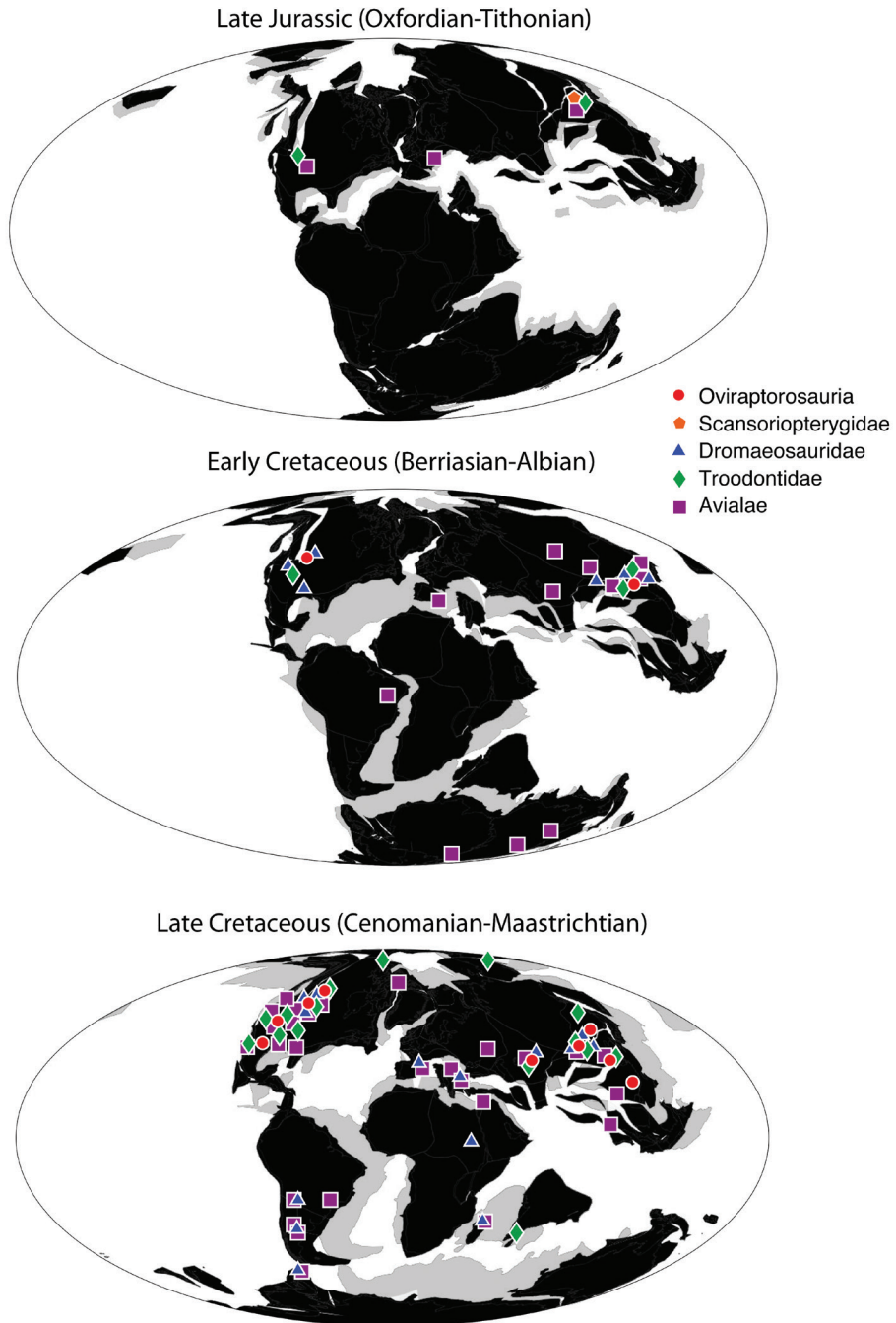


FIG. 1. Geographic distribution of pennaraptoran theropods illustrated on palaeogeographic globes of the Late Jurassic (Oxfordian-Tithonian), Early Cretaceous (Berriasian-Albian), and Late Cretaceous (Cenomanian-Maastrichtian). Palaeomaps modified from GPlates (www.gplates.org) (Müller et al., 2018).

TABLE 1
Oviraptorosauirian fossil record

Continent	Geological Unit	Country	Period	Age	Age Reference	Taxa	Reference	
Asia	Jehol Group (Yixian Formation; Jiufotang Formation)	China	Early Cretaceous	Barremian-Aptian	Chang et al., 2009, 2017; Pan et al., 2013	<i>Incisivosaurus</i> , <i>Caudipteryx</i> , <i>Ningyuansaurus</i> , <i>Protarchaeopteryx</i> , <i>Similicaudipteryx</i> (possibly <i>Incisivosaurus</i>), <i>Xinghiansaurus</i> ; <i>Similicaudipteryx</i>	Ji and Ji, 1997; Ji et al., 1998; 2012; Zhou et al., 2000; Xu et al., 2002a, 2010a; He et al., 2008; Balanoff et al., 2009; Qiu et al., 2019	
		China	Late Cretaceous	Campanian-Maastrichtian	Bureau of Geology and Mineral Resources of Jiangxi Province, 1984	<i>Banji</i> , <i>Corythoraptor</i> , <i>Ganzhousaurus</i> , <i>Huanansaurus</i> , <i>Jiangxisaurus</i> , <i>Nankangia</i> , <i>Tongtianlong</i>	Xu and Han, 2010; Lü et al., 2013a; Wang et al., 2013a; Wei et al., 2013; Lü et al., 2015, 2016, 2017	
	China	Early Cretaceous	Aptian/Albian	Xu et al., 2012a		<i>Luoyanggia</i>	Lü et al., 2009	
	China	Late Cretaceous	Maastrichtian	Bureau of Geology and Mineral Resources of Guangdong Province, 1988		<i>Heyuania</i>	Lü, 2003	
	China	Late Cretaceous	Maastrichtian	Zhao et al., 1991		<i>Shixinggia</i>	Lü and Zhang, 2005	
	China	Late Cretaceous	Campanian-Maastrichtian	Jiang et al., 2011		<i>Yulong</i>	Lü et al., 2013b	
	China	Late Cretaceous	Cenomanian-Turonian	Liang et al., 2009		<i>Beibeilong</i>	Pu et al., 2017	
	China	Late Cretaceous	Campanian-Maastrichtian	van Itterbeek et al., 2005; Bonnetti et al., 2014		<i>Avimimus</i> , <i>Caenagnathasia</i> , <i>Gigantoraptor</i>	Kurzanov, 1981; Xu et al., 2007; Yao et al., 2015; Ma et al., 2017	
	China	Late Cretaceous	Campanian	Godefroit et al., 2008		<i>Machairasaurus</i> , <i>Wulatelong</i>	Longrich et al., 2010; Xu et al., 2013b	
	China	Late Cretaceous	Campanian	An et al., 2016		<i>Anomalipes</i>	Yu et al., 2018	
	Mongolia	Djadokhia Formation	Late Cretaceous	Campanian	van Itterbeek et al., 2005; Dingus et al., 2008; Hasegawa et al., 2009		<i>Avimimus</i> , <i>Citipati</i> , <i>Khaan</i> , <i>Oviraptor</i>	Osborn, 1924; Kurzanov, 1981; Clark et al., 2001; Clark et al., 2002; Balanoff and Norell, 2012

TABLE 1 continued

Continent	Geological Unit	Country	Period	Age	Age Reference	Taxa	Reference
Asia	Barun Goyot Formation	Mongolia	Late Cretaceous	Campanian-Maastrichtian	Gradziński and Jerzykiewicz, 1974a, b; Fanti et al., 2012	<i>Ajancingenia/Ingenia/Heyuannia yanshini, Avimitus, Conchroraptor, Nemegetomaia</i>	Barsbold, 1981; 1986; Longrich et al., 2010; Fanti et al., 2012; Funston et al., 2017
	Nemegt Formation	Mongolia	Late Cretaceous	Maastrichtian	Jerzykiewicz and Russell, 1991; Shuvalov, 2000; van Isterbeek et al., 2005	<i>Avimitus, Elmisaurus, Gobiraptor, Nemegetomaia, Nomingia, Rinchenia</i>	Barsbold, 1981, 1986, 2000; Lü et al., 2004, 2005; Longrich et al., 2010; Osmólska, 1981; Fanti et al., 2012; Currie et al., 2015; Funston et al., 2017; Lee et al., 2019
	Bissekty Formation	Uzbekistan	Late Cretaceous	Turonian	Sues and Averianov, 2014, 2015	<i>Caenagnathasia</i>	Currie et al., 1993; Sues and Averianov, 2015
North America	Cloverly Formation	U.S.	Early Cretaceous	pre-Aptian-Albian	Oreska et al., 2013; Farke et al., 2014	<i>Microvenator</i>	Makovicky, 1998
	Aguja Formation	U.S.	Late Cretaceous	Campanian-Maastrichtian	Lehman, 1985; Sankey, 2001	<i>Leptorhynchos</i>	Longrich et al., 2013
	Two Medicine Formation	U.S.	Late Cretaceous	Campanian	Rogers et al., 1993; Foreman et al., 2008	<i>Chirostenotes?</i>	Osmólska et al., 2004
	Hell Creek Formation	U.S.	Late Cretaceous	Maastrichtian	Hoganson and Edward, 2002; Fastovsky and Bercovici, 2016	<i>Anzu, Chirostenotes?</i>	Osmólska et al., 2004; Lamanna et al., 2014
	Kaiparowits Formation	U.S.	Late Cretaceous	Campanian	Roberts et al., 2005; Jinnah et al., 2009; Zanno et al., 2011	<i>Hagryphus</i>	Zanno and Sampson, 2005
	Ojo Alamo Formation	U.S.	Late Cretaceous	Maastrichtian	Sullivan and Lucas, 2006; Sullivan et al., 2001	<i>Ojoraptorsaurus</i>	Sullivan et al., 2011
	Belly River Formation	Canada	Late Cretaceous	Campanian	Eberth, 2005	<i>Chirostenotes</i>	Gilmore, 1924
	Dinosaur Park Formation	Canada	Late Cretaceous	Campanian	Eberth, 2005; Brown et al., 2013	<i>Caenagnathus, Chirostenotes, Leptorhynchos</i>	Osmólska et al., 2004; Longrich et al., 2013; Funston and Currie, 2014; Funston et al., 2015
	Horseshoe Canyon Formation	Canada	Late Cretaceous	Campanian-Maastrichtian	Eberth and Braman, 2012; Quinney et al., 2013	<i>Epichirostenotes, Apatoraptor</i>	Sullivan et al., 2011; Funston and Currie, 2016

China (Nanxiong Formation) as well as the southern Mongolian Campanian Djadokhta Formation (and the similar Wulansuhai (Bayan Mandahu) Formation in China), Campanian-Maastrichtian Barun Goyot Formation, and the Maastrichtian Nemegt Formation.

Jehol oviraptorosaurians represent the oldest unequivocal oviraptorosaurian records, and the six described taxa include some articulated specimens preserving feathers, gastroliths, and stomach contents. The early-diverging oviraptorosaurians *Incisivosaurus*, *Protarchaeopteryx*, *Similicaudipteryx*, *Caudipteryx*, *Xingtianosaurus*, and *Ningyuansaurus* are the only known toothed forms and have less specialized skulls compared to later oviraptorosaurians (Ji et al., 1998; Zhou et al., 2000; Xu et al., 2002a; Balanoff et al., 2009; Qiu et al., 2019). *Caudipteryx* is known for its pennaceous feathered arms, gastroliths, and a tail plume probably used for display purposes (Ji et al., 1998; Zhou et al., 2000; Pittman et al., 2013; Persons et al., 2014). It is known from two species (Ji et al., 1998; Zhou et al., 2000), although this is contested. Both specimens were recovered from the ~125 Ma Yixian Formation in Liaoning province, with both 2-D and 3-D preservations. Two specimens of *Similicaudipteryx*, another Yixian Formation genus, show radical changes to feather morphology during ontogeny (Xu et al., 2010a). However, these two specimens might be specimens of *Incisivosaurus* (Xu, 2020). *Ningyuansaurus* possibly preserves seeds within its body cavity (Ji et al., 2012). *Xingtianosaurus* is the most recently named Jehol genus, which is known from an articulated postcranial skeleton (Qiu et al., 2019). *Luoyangia* is an Aptian- to Albian-aged oviraptorid from the Haoling Formation of Henan, central China, which was previously thought to be Late Cretaceous in age (Lü et al., 2009; Xu et al., 2012a).

The Late Cretaceous Ganzhou fauna of Jiangxi, southern China, has the greatest known diversity of oviraptorid oviraptorosaurians with seven reported genera in the Campanian-Maastrichtian Nanxiong Formation: *Banji*, *Huanansaurus*, *Jiangxisaurus*, *Tongtianlong*, *Ganzhousaurus*, *Nankangia*, and *Corythoraptor* (Xu and Han, 2010; Lü et al., 2013a,

2015, 2016, 2017; Wang et al., 2013a; Wei et al., 2013). Embryos of an oviraptorid have also been recovered from this formation (Wang et al., 2016a). *Heyuannia* is an oviraptorid genus described from a partial skeleton from the Maastrichtian Dalangshan Formation of Guangdong, southern China (Lü, 2003). “*Ingenia*,” or *Ajancingenia yanshini*, from the Campanian-Maastrichtian Barun Goyot Formation of southern Mongolia (Barsbold, 1981; Easter, 2013) has been referred to this genus as a second species, *H. yanshini*, but this involves a very large geographical and temporal separation between species (Funston et al., 2017). *Shixinggia* is another described Guangdong oviraptorid from the Maastrichtian Pingling Formation (Lü and Zhang, 2005). *Yulong* is a chicken-sized oviraptorid represented by excellent fossil material from the Upper Cretaceous Qiupa Formation of Henan, central China (Lü et al., 2013b), while *Beibeilong* is a caenagnathid known from a perinate skeleton and some eggs from the Cenomanian-Turonian Gaogou Formation of the same province (Pu et al., 2017). *Anomalipes* is a recently reported caenagnathid from the Campanian Wangshi Group of Shandong Province, known only from hind-limb elements (Yu et al., 2018). The largest known oviraptorosaurian—the caenagnathid *Gigantoraptor*—was recovered in the northernmost frontier of China from the Campanian-Maastrichtian Erlian (Iren Dabasu) Formation of Nei Mongol (Inner Mongolia) (Xu et al., 2007). This is also the locality for one of the smallest oviraptorosaurians, *Avimimus*, which was first reported from similarly aged rocks in Mongolia (Kurzanov, 1981), although these assignments would benefit from review, as they may represent different taxa. The Campanian Wulansuhai (Bayan Mandahu) Formation, also in the Gobi Desert region, is the home to the oviraptorids *Machairasaurus* and *Wulatelong* and some other indeterminate oviraptorid material (Longrich et al., 2010; Xu et al., 2013b).

Mongolian oviraptorosaurians are dominated by oviraptorids, with three genera from the Campanian Djadokhta Formation (*Oviraptor*, *Citipati*, and *Khaan*) (Osborn, 1924; Clark et al., 2001, 2002; Balanoff and Norell, 2012), four genera from

the Maastrichtian Nemegt Formation (*Gobiraptor*, *Nomingia*, *Rinchenia*, and *Nemegtomaia*) (Barsbold, 1986; Barsbold et al., 2000; Lü et al., 2004, 2005; Fanti et al., 2012; Funston et al., 2017; Lee et al., 2019) and three from the Campanian-Maastrichtian Barun Goyot Formation (“*Ingenia*”/ *Ajancingenia*/*Heyuannia yanshini*, *Conchoraptor*, and *Nemegtomaia* [also from the Nemegt]; see Fanti et al., 2012, for details of Maastrichtian portion) (Barsbold, 1981; 1986; Longrich et al., 2010; Funston et al., 2017). Several skeletons are known for *Khaan* and *Citipati* from the rich fossil beds of Ukhaa Tolgod, including brooding specimens, single species group associations and embryos (Norell et al., 1995, 2001; Clark et al., 2001).

Avimimus is a small, early-diverging oviraptorosaurian closer to Caenagnathidae and Oviraptoridae that is known from multiple formations in Mongolia, including the Djadokhta, Nemegt, and Barun Goyot (Kurzanov, 1981; Longrich et al., 2010). *Elmisaurus* is a caenagnathid from the Nemegt Formation (Osmólska, 1981; Currie et al., 2016). The holotype of the caenagnathid *Caenagnathasia* is a pair of dentaries from a single individual recovered from the Turonian Bissekty Formation of Uzbekistan (Currie et al., 1993). A partial dentary referred to *Caenagnathasia* is known from the Erlian (Iren Dabasu) Formation of Nei Mongol, China (Yao et al., 2015). Few caenagnathid skull elements have been reported in Asia; these are from the perinate *Beibeilong* and the mandible of *Gigantoraptor* and a similarly sized specimen from the Gobi Desert (Xu et al., 2007; Tsuihiji et al., 2015; Ma et al., 2017; Pu et al., 2017).

NORTH AMERICA: The early-diverging caenagnathid *Microvenator* was recovered from the Aptian-Albian Cloverly Formation and is a historically important specimen and likely that of a juvenile. It is the continent’s oldest oviraptorosaurian (Makovicky and Sues, 1998). Late Cretaceous caenagnathids dominate the North American oviraptorosaurian fossil record. *Chirostenotes*, currently known from the species *C. pergracilis*, was the first discovered caenagnathid as well as the first described North American

oviraptorosaur (Gilmore, 1924). The Campanian Dinosaur Park Formation of Canada is the most important source of North American caenagnathids including *Chirostenotes* (also referred to possible material in the Campanian Two Medicine and Maastrichtian Hell Creek formations of the northern United States [Osmólska et al., 2004]), *Leptorhynchos* (Longrich et al., 2013) (also the Campanian-Maastrichtian Aguja Formation of the southern United States) as well as *Caenagnathus*, the caenagnathid that lends its name to the clade (Currie et al., 1993). *Hagryphus* is a caenagnathid from the Campanian Kaiparowits Formation of Utah, known from forelimb material (Zanno and Sampson, 2005). Moving into the latest Cretaceous, *Epichirostenotes* and *Aptoraptor* are caenagnathids from the Campanian-Maastrichtian Horseshoe Canyon Formation of Canada. Both have preserved skull elements, and the holotype of *Aptoraptor* is a largely articulated partial skeleton. *Ojoraptorsaurus* is a caenagnathid known from pubic bones recovered from the Maastrichtian Ojo Alamo Formation of the southwestern United States (Sullivan et al., 2011; Funston and Currie, 2016). *Anzu* is the largest described caenagnathid from North America and is one of the best-preserved North American oviraptorosaurians (Lamanna et al., 2014). It is known from the Maastrichtian Hell Creek Formation of North and South Dakota (Lamanna et al., 2014). Fossil eggshell material and undescribed skeletal material from the top of the Cedar Mountain Formation (Cenomanian-Turonian) of Utah represents an even larger taxon that was similarly sized to *Gigantoraptor* (Makovicky et al., 2015; Tucker et al., 2020).

EUROPE: Oviraptorosaurians are poorly known from Europe with representation from only isolated postcranial material (Naish et al., 2001; Csiki and Grigorescu, 2005) whose referrals have been subsequently challenged (Csiki et al., 2010; Allain et al., 2014).

Isolated elements from Cretaceous strata of Gondwana have been interpreted as deriving from oviraptorosaurians, but these records have

not withstood subsequent reevaluation. An isolated cervical from the Maastrichtian El Brete Formation of Argentina was described as an oviraptorosaurian (Frankfurt and Chiappe, 1999), but has since been reinterpreted as a noasaurid theropod (Agnolín and Martinelli, 2007). Elements from the Lower Cretaceous Otway Group of Australia described as an oviraptorosaurian lower jaw fragment and dorsal vertebra (Currie et al., 1996), have since been attributed to Unenlagiinae or other theropod clades (Agnolín et al., 2010). To date, no unambiguous records of oviraptorosaurians from Gondwanan continents exist.

SCANSORIOPTERYGIDAE

Scansoriopterygids are a bizarre group of early-diverging Laurasian oviraptorosaurians or paravians, known only from the Middle and Late Jurassic Haifanggou Formation and Late Jurassic Tiaojishan Formation of north China so far (~168–155 Ma) (Czerkas and Yuan, 2002; Zhang et al., 2002; Zhang et al., 2008a; Turner et al., 2012; Brusatte et al., 2014; Xu et al., 2015a; Wang et al. 2019a; Pei et al., in press) (fig. 1; table 2). Known from five (or six: O'Connor and Sullivan, 2014) feathered Chinese specimens, only one definitive and possibly two somatically mature individuals exist. Two of these specimens (*Yi qi* and *Ambopteryx longibrachium*) possess feathered, membranous wings (Xu et al., 2015a; Wang et al., 2019a) and one possesses a pygostyle (Wang et al., 2019a). *Epidendrosaurus* and *Epidexipteryx* are two well-accepted genera, but *Scansoriopteryx* may be the same genus as *Epidendrosaurus*. The Early Cretaceous *Zhongornis*, originally described as a bird (Gao et al., 2008), may be a scansoriopterygid instead (O'Connor and Sullivan, 2014), but this has been contested (Rashid et al., 2018). The notion that scansoriopterygids are early-branching avialans (Xu et al., 2011a; Czerkas and Feduccia, 2014) has been replaced by anatomical evidence grouping some or all scansoriopterygids with oviraptorosaurians (Turner et al., 2012; Agnolín and Novas, 2013; Brusatte et al., 2014; Pei

TABLE 2
Scansoriopterygid fossil record

Continent	Geological Unit	Country	Period	Age	Age Reference	Taxa	Reference
Asia	Haifanggou and Tiaojishan formations	China	Middle-Late Jurassic	Kimmeridgian-Bathonian	Liu et al., 2012; Wang et al., 2013c; Sullivan et al., 2014; Tian et al., 2015	<i>Ambopteryx</i> , <i>Epidendrosaurus</i> , <i>Epidexipteryx</i> , <i>Scansoriopteryx</i> (possibly a synonym of <i>Epidendrosaurus</i>), <i>Yi</i> , possibly <i>Zhongornis</i>	Czerkas and Yuan, 2002; Zhang et al., 2002; Gao et al., 2008; Zhang et al., 2008a; O'Connor and Sullivan, 2014; Xu et al., 2015b; Rashid et al., 2018; Wang et al., 2019a

TABLE 3
Dromaeosaurid fossil record

Continent	Geological Unit	Country	Period	Age	Age Reference	Taxa	Reference
Asia	Bayan Gobi Formation	China	Early Cretaceous	Aptian-Albian	Pitman et al., 2015	IVPP V22530	Pitman et al., 2015
	Jehol Group (Yixian Formation; Jiufotang Formation)	China	Early Cretaceous	Barremian-Aptian	He et al., 2004; Chang et al., 2009, 2017; Pan et al., 2013	<i>Changyuraptor graciliraptor</i> , <i>Sinornithosaurus Tianyuraptor</i> , <i>Zhenyuanlong</i> , <i>Zhongjiansaurus</i> , <i>Microaptor</i> , <i>Wulong</i>	Xu et al., 1999, 2000, 2003; Xu and Wang, 2004a; Hwang et al., 2002; Longrich and Currie, 2009; Zheng et al., 2009; Gong et al., 2012; Han et al., 2014; Lü and Brusatte, 2015; Xu and Qin, 2017; Pei et al., 2014; Poust et al., 2020
	Wulansuhai/Bayan Mandahu Formation	China	Late Cretaceous	Campanian	Godefroit et al., 2008	<i>Linheraptor</i> , <i>Velociraptor osmolskae</i>	Godefroit et al., 2008; Xu et al., 2010b, 2015a
	Qiupa Formation	China	Late Cretaceous	Campanian-Maastrichtian	Jiang et al., 2011	<i>Luanchuanraptor</i>	Lü et al., 2007
	Bayan Shireh Formation	Mongolia	Late Cretaceous	Senomanian-Santonian	Shuvalov, 2000; van Itterbeek et al., 2005; Kurumada et al., 2020	<i>Achillobator</i>	Perle et al., 1999
	Djadokhta Formation	Mongolia	Late Cretaceous	Campanian	van Itterbeek et al., 2005; Dingus et al., 2008; Hasegawa et al., 2009	<i>Halszkanaptor</i> , <i>Mahakala</i> , <i>Tsaagan</i> , <i>Velociraptor mongoliensis</i>	Osborn, 1924; Norell et al., 2006; Turner et al., 2007b, 2011; Cau et al., 2017
	Barun Goyot Formation	Mongolia	Late Cretaceous	Campanian-Maastrichtian	Gradzinski and Jerzykiewicz, 1974a, 1947b; Fanti et al., 2012	<i>Hulsanpes</i> (possibly not a dromaeosaurid)	Osmólska, 1982; Turner et al., 2012; Cau and Madzia, 2018
	Nemegt Formation	Mongolia	Late Cretaceous	Maastrichtian	Jerzykiewicz and Russell, 1991; Shuvalov, 2000; van Itterbeek et al., 2005	<i>Adasaurus</i>	Barsbold, 1983
	Öösh Formation	Mongolia	Early Cretaceous	Berriasian-Barremian	Turner et al., 2007c	<i>Shanag</i>	Turner et al., 2007c
	Jinju Formation	South Korea	Early Cretaceous	Aptian	Kim et al., 2018	suspected microraptorine tracks	Kim et al., 2018
	Bissekty Formation	Uzbekistan	Late Cretaceous	Turonian	Sues and Averianov, 2014, 2015	<i>Itemirus</i>	Kurzanov, 1976; Sues and Averianov, 2014

TABLE 3 continued

Continent	Geological Unit	Country	Period	Age	Age Reference	Taxa	Reference
Europe	Jydegaard Formation	Denmark	Early Cretaceous	Berriasian-Valanginian	Bonde and Christiansen, 2003	<i>Dromaeosauroides</i>	Bonde and Christiansen 2003; Christiansen and Bonde, 2003
	Lulworth Formation	U.K.	Early Cretaceous	Berriasian	Milner, 2002	<i>Niuhetes</i>	Owen, 1854; Milner, 2002; Sweetman 2004; Rauhut et al., 2010
	Wessex Formation	U.K.	Early Cretaceous	Barremian	Howse and Milner 1993	<i>Ornithodesmus</i>	Seeley, 1887; Howse and Milner, 1993; Norell and Makovicky, 1997
	Grès à Reptiles Formation	France	Late Cretaceous	Campanian-Maastrichtian	Walker et al., 2007	<i>Pyroraptor</i>	Allain and Taquet, 2000; Turner et al., 2012
	Sebeş Formation	Romania	Late Cretaceous	Maastrichtian	Brusatte et al., 2013	<i>Balaur</i>	Csiki et al., 2010; Brusatte et al., 2013
South America	Allen Formation	Argentina	Late Cretaceous	Campanian-Maastrichtian	Armas and Sánchez, 2015	<i>Austroraptor</i>	Novas et al., 2009; Currie and Paulina-Carabajal, 2012
	Candeleros Formation	Argentina	Late Cretaceous	Cenomanian-Turonian	Leanza et al., 2004	<i>Buitreraptor</i>	Makovicky et al., 2005; Novas et al., 2018; Gianechini et al., 2018
	Portezuelo Formation	Argentina	Late Cretaceous	Turonian-Coniacian	Calvo et al., 2007	<i>Neuquenraptor</i> , <i>Unenlagia</i> , <i>Pamparaptor</i>	Novas and Puerta, 1997; Calvo et al., 2004; Makovicky et al., 2005; Novas and Pol, 2005; Porfiri et al., 2011; Brissón Egli et al., 2017; Novas et al., 2018
	Huincul Formation	Argentina	Late Cretaceous	Cenomanian-Turonian	Garrido, 2010; Motta et al., 2020	<i>Overoraptor</i> (nonavianian paravian, possibly unenlagiine dromaeosaurid)	Motta et al., 2020
	Los Blanquitos Formation	Argentina	Late Cretaceous	Maastrichtian	Martínez and Novas, 2006	<i>Unquillosaurus</i>	Powell, 1979; Novas and Agnolin, 2004; Martínez and Novas, 2006
North America	Dinosaur Park Formation	Canada	Late Cretaceous	Campanian	Eberth, 2005; Brown et al., 2013	<i>Dromaeosaurus</i> , <i>Hesperonychus</i> , <i>Saurornitholestes</i>	Matthew and Brown, 1922; Sues, 1978; Currie, 1995; Longrich and Currie, 2009; Turner et al., 2012; Currie and Evans, 2020

TABLE 3 continued

Continent	Geological Unit	Country	Period	Age	Age Reference	Taxa	Reference
North America	Horseshoe Canyon Formation	Canada	Late Cretaceous	Campanian-Maastrichtian	Eberth and Braman, 2012; Quinney et al., 2013	<i>Atrociraptor</i>	Currie and Varricchio, 2004
	Wapiti Formation	Canada	Late Cretaceous	Campanian	Bell and Currie, 2015	<i>Boreonykus</i>	Bell and Currie, 2015
	Antlers Formation	U.S.	Early Cretaceous	Aptian-Albian	Brinkman et al., 1998	<i>Deinonychus</i>	Brinkman et al., 1998
	Cedar Mountain Formation	U.S.	Early Cretaceous	Barremian?-Aptian	Senter et al., 2012	<i>Utahraptor, Yurgovuchia</i>	Kirkland et al., 1993; Senter et al., 2012
	Cloverly Formation	U.S.	Early Cretaceous	pre-Aptian-Albian	Oreska et al., 2013; Farke et al., 2014	<i>Deinonychus</i>	Ostrom, 1969
	Hell Creek Formation	U.S.	Late Cretaceous	Maastrichtian	Hoganson and Edward, 2002; Fastovsky and Bertovici, 2016	<i>Acheronaptor, Dakotaraptor</i>	Evans et al., 2013; DePalma et al., 2015
	Morrison Formation	U.S.	Late Jurassic	Kimmeridgian-Tithonian	Trujillo and Kowallis, 2015	teeth of dromaeosaurids?	Foster and Heckert, 2011
	Ojo Alamo Formation	U.S.	Late Cretaceous	Maastrichtian	Sullivan and Lucas, 2006; Sullivan et al., 2001; Jasinski et al., 2020	<i>Dineobellator</i>	Jasinski et al., 2020
	Two Medicine Formation	U.S.	Late Cretaceous	Campanian	Rogers et al., 1993; Foreman et al., 2008	<i>Bambiraptor</i>	Burnham et al., 2000
	Africa	Maevarano Formation	Madagascar	Late Cretaceous	Maastrichtian	Rogers et al., 2013	<i>Rahonavis</i>
	Wadi Milk Formation	Sudan	Early to Late Cretaceous	Albian-Cenomanian	Turner et al., 2012	Wadi Milk dromaeosaurid	Rauhut and Werner, 1995
Antarctica	Snow Hill Island Formation	-	Late Cretaceous	Maastrichtian	Case et al., 2007	<i>Imperator</i> (indeterminate deinonychosaurian material or nondromaeosaurid paravian)	Case et al., 2007; Turner et al., 2012; Ely and Case, 2019

et al., in press) or as early-branching paravians (Turner et al., 2012; Godefroit et al., 2013a, 2013b; Xu et al., 2015a; Wang et al., 2019a).

DROMAEOSAURIDAE

Dromaeosaurid fossils have been found on almost all modern continental landmasses including members that appear to have had volant capabilities (Turner et al., 2012; Pei et al., in press; fig. 1; table 3).

NORTH AMERICA: In 1922, *Dromaeosaurus*, from the Campanian Dinosaur Park Formation of Alberta, Canada, was the first dromaeosaurid to be described. It lends its name to the clade and is known from partial cranial and very fragmentary postcranial material (Matthew and Brown, 1922; Currie, 1995). The Dinosaur Park Formation has also yielded *Saurornitholestes*, a relatively completely known taxon thought to be from only one species, *Saurornitholestes langstoni* (Sues, 1978; Turner et al., 2012). This taxon lacked a proper diagnosis until recently and is likely represented by multiple partial skeletons. Recently, an exquisite skull and skeleton from Dinosaur Provincial Park were recovered allowing for a revised diagnosis (Currie and Evans, 2020). Evidence of tooth-marked bones and a broken tip of a tooth still embedded in a bone suggest that this taxon ate azhdarchid pterosaurs on occasion (Currie and Jacobsen, 1995). *Hesperonychus elizabethae* is known from a single incomplete pelvis and referred pedal bones recovered from the Dinosaur Park Formation (Longrich and Currie, 2009). This taxon is North America's only named microraptorine and the youngest one worldwide by almost 45 million years (Longrich and Currie, 2009). *Atrociraptor marshalli* is a fragmentary taxon recovered from the similarly aged Horseshoe Canyon Formation from the same part of Canada (Currie and Varricchio, 2004). It consists of a partial rostrum, including both premaxillae, a right maxilla, and both dentaries. The snout of this dromaeosaurid appears to be quite short and deep, given the abbreviated nature of the facial process of the maxilla. Across the border in neighboring

Montana, the Campanian Two Medicine Formation is home to the relatively well-preserved dromaeosaurid *Bambiraptor* (Burnham et al., 2000). The holotype of *Bambiraptor feinbergi* is quite small and typically considered a juvenile to subadult (Currie and Varricchio, 2004; Norell and Makovicky, 2004). However, attempts at histologically sampling the single known skeleton of this taxon have been unsuccessful. It is possible that *Bambiraptor* is a juvenile specimen of *Saurornitholestes* (Burnham et al., 2000; Norell and Makovicky, 2004): both taxa lack detailed and adequate diagnoses and differ only in the length of the suborbital process of the frontal, a feature that is undoubtedly influenced by ontogeny. Furthermore, the *Bambiraptor feinbergi* type specimen is known to be a chimera, as there are elements of three different similarly sized lower legs included in the holotype. The youngest North American dromaeosaurids are from the Maastrichtian Hell Creek and Ojo Alamo formations of the United States. From the Hell Creek Formation: the velociraptorine *Acheroraptor temertyorum*, which is known from a complete right maxilla and a referred right dentary (Evans et al., 2013) as well as the significantly larger *Dakotaraptor steini*, which was originally described as a dromaeosaurine (DePalma et al., 2015), but recently recovered as a velociraptorine (Pei et al., in press). From the Ojo Alamo Formation: the velociraptorine *Dineobellator notohesperus*, which is known from fragmentary cranial and postcranial material (Jasinski et al., 2020). *Deinonychus*, *Utahraptor*, and *Yurgovuchia* are the oldest widely accepted dromaeosaurids from North America with an Aptian/Albian age for the former (Ostrom, 1969) and a Barremian age for the latter two taxa (Kirkland et al., 1993; Senter et al., 2012). *Deinonychus* and *Utahraptor* are known from a large amount of material, much of it undescribed (personal commun., J. Kirkland), and *Utahraptor ostrommaysorum* remains the largest dromaeosaurid known. *Yurgovuchia doellingi* is represented by associated postcranial remains. The oldest record of Dromaeosauridae in North America relates to controversial fragmentary material from the Late Jurassic Morrison Formation (Heckert and Foster, 2011). *Deinonychus antirrhopus* remains the best-

represented dromaeosaurid from North America. It is known from at least eight partially articulated and disarticulated skeletons from the Cloverly and Antlers formations. A partial egg associated with an adult has also been recovered (Grellet-Tinner and Makovicky, 2006). The osteology of this taxon was described in detail in Ostrom's monograph (Ostrom, 1969) and has been revisited by subsequent studies (Norell and Makovicky, 1997, 1999; Norell et al., 2006).

ASIA: *Velociraptor*, arguably the most famous dromaeosaurid, was the second dromaeosaurid to be described, in 1924 (Osborn, 1924). It is one of the best-known genera, with several complete or near-complete skeletons, and lends its name to the subfamily Velociraptorinae. *Velociraptor* was recovered from the Campanian Djadokhta Formation of southern Mongolia, which is among the most productive strata for dromaeosaurids anywhere on Earth. Several specimens of *Velociraptor* tell us much about its palaeobiology. The famous "fighting dinosaurs" appears to preserve *Velociraptor* attacking a large *Protoceratops* (Kielan-Jaworowska and Barsbold, 1972). Another specimen shows the presence of quill knobs on the ulna (Turner et al., 2007a), and yet another preserves stomach contents that include the remains of a pterosaur (Currie and Jacobsen, 1995). A second species, *V. osmolskae*, is known from paired maxillae and a left lacrimal described from similar rocks across the border in Nei Mongol, China (Wulansuhai (Bayan Mandahu) Formation) (Godefroit et al., 2008). This appears to be a valid taxon despite the paucity of its preserved fossil material (Turner et al., 2012). Djadokhta Formation outcrops at Ukhaa Tolgod have yielded *Tsaagan mangas*, a velociraptorine larger than *Velociraptor* (Norell et al., 2006) that is closely related to *Linheraptor exquisitus*, with a nearly complete holotype skeleton from the Wulansuhai Formation (Xu et al., 2010b, 2015b). The Djadokhta Formation has also yielded the earliest diverging noneudromaeosaurian dromaeosaurid *Mahakala omnogovae*, which is known from a partial skeleton including the back of the skull (Turner et al., 2007b; Turner et al., 2011). It was recovered from the Tögrögiin Shiree locality in Mongolia. Recent work described

an additional dromaeosaurid from the Djadokhta Formation, *Halszkaraptor escuilliei*, and recovered it as the sister taxon to *Mahakala*, although parts of the sole specimen have been forged (Cau et al., 2017). *Hulsanpes* is another enigmatic specimen purported to be a dromaeosaurid (Osmólska, 1982). It is from the Campanian -Maastrichtian Barun Goyot Formation at the Khulsan locality in Mongolia. It consists only of a partial right metatarsus and pes (and possibly an associated braincase). Although considered a dromaeosaurid by recent analyses (Cau et al., 2017; Cau and Madzia, 2018), because of the extremely fragmentary nature of the material this identification has been repeatedly challenged (Turner et al., 2012).

The Gobi Desert has yielded a number of taxa occupying other parts of the Late Cretaceous: *Achillobator* from the Cenomanian-Santonian Bayan Shireh Formation (Perle et al., 1999) and *Adasaurus* from the Maastrichtian Nemegt Formation (Bayankhongor) of southwestern Mongolia (Barsbold, 1983). *Adasaurus* was only recently well figured and described (Turner et al., 2012). IGM 100/20 is the only specimen considered to be *Adasaurus* and is known from a partial skull and postcranial skeleton. Additional cranial and postcranial remains (IGM 100/22 and 100/23) likely pertain to a different taxon from the older Baynshiree Formation. *Shanag* is the only Early Cretaceous Mongolian dromaeosaurid, belonging to the Berriasian-Barremian Öösh Formation (Turner et al., 2007c).

In contrast, China has a large number of Early Cretaceous forms, but fewer Late Cretaceous ones. The Barremian-Aptian Yixian Formation and Aptian Jiufotang Formation of northeastern China, which yield part of the Jehol Biota, are home to many microraptorines, a non-eudromaeosaurian subclade that is known only from one fragmentary specimen outside Asia (Longrich and Currie, 2009). Despite their name, microraptorines were not all small and appear to be reasonably large ancestrally (Pei et al., in press). Their well-known arm and leg feathers are exemplified in the group's namesake *Microraptor*, where they are extremely long and are thought to have enabled volant capabilities, although this remains an area of intense study

(Dyke et al., 2013; Dececchi et al., 2016; Pei et al., in press). *Microraptor* is from the Aptian Jiufotang Formation and is known from three species *M. zhaoianus*, *M. gui*, and *M. hanqingi* (Xu et al., 2000, 2003; Gong et al., 2012); however, the status of *M. gui* (Senter et al. 2004) and *M. hanqingi* have been questioned (Turner et al., 2012; Pei et al., 2014). The other known Jiufotang microraptorine is *Wulong* (Poust et al., 2020). The Yixian Formation has the microraptorines *Changyuraptor* (Han et al., 2014), *Graciliraptor* (Xu and Wang, 2004a), *Sinornithosaurus* (Xu et al., 1999), *Zhongjianosaurus* (Xu and Qin, 2017) and the larger seemingly early-diverging forms *Tianyuraptor* and *Zhenyuanlong* (Zheng et al., 2009; Lü and Brusatte, 2015; Pei et al., in press). Microraptorines are otherwise rare in Asia: IVPP V22530 is from the younger Aptian-Albian Bayan Gobi Formation of Nei Mongol, northern China (Pittman et al., 2015) and suspected microraptorine tracks have been discovered in the Aptian Jinju Formation of Gyeongsangnamdo, South Korea (Kim et al., 2018). *Shanag* is possibly a microraptorine as well, as found in some phylogenetic analyses (Gianechini et al., 2018). *Luanchuanraptor*, known from a partial skeleton, was discovered from the Campanian-Maastrichtian Qiupa Formation of Henan, central China (Lü et al., 2007), and a recent analysis found it closely related to its Late Cretaceous Mongolian relative *Velociraptor* (Pei et al., in press). Tracks of two differently sized coeval deinonychosaurs have been found in the Barremian-Aptian Tianjialou Formation of Shandong, eastern China, but the identity of their makers remains elusive (Li et al., 2008a).

A small partial braincase forms the type of *Itemirus medullaris* from the Turonian Bissekty Formation of Uzbekistan, which was originally described as an earlier-diverging theropod (Kurzanov, 1976). More recently, two phylogenetic analyses have recovered it as a velociraptorine (Longrich and Currie, 2009) and dromaeosaurine (Sues and Averianov, 2014).

EUROPE: *Variraptor* was named as a dromaeosaurid from the Late Campanian–Early Maastrichtian Grès à Reptiles Formation of France (LeLoeuff and Buffetaut, 1998). However, it was

shown to lack dromaeosaurid synapomorphies and was superseded by *Pyroraptor* (Late Campanian–Early Maastrichtian of La Boucharde, France) as the only known Late Cretaceous European dromaeosaurid taxon (Allain and Taquet, 2000; Turner et al., 2012). Prior to the discovery of *Pyroraptor*, only indeterminate Late Cretaceous dromaeosaurid material had been known in Europe (Allain and Taquet, 2000) from elsewhere in France (Buffetaut et al., 1986; LeLoeuff et al., 1992; LeLoeuff and Buffetaut, 1998) and from Portugal (Antunes and Sigogneau, 1992) and Romania (Weishampel and Jianu, 1996). Despite being represented by only extremely fragmentary remains, the unique biogeography of *Pyroraptor* and its near contemporaneity with Late Cretaceous taxa from neighboring continents (Campanian and Maastrichtian of Provence, France) made it an important taxon (Allain and Taquet, 2000). Understanding of Late Cretaceous European dromaeosaurids dramatically increased with the discovery of *Balaur*, a more complete partial skeleton of an island-dwelling velociraptorine from the Maastrichtian Sebeş Formation of Alba county, Romania (Csiki et al., 2010; Brusatte et al., 2013). The animal is perhaps most distinctive for its double sickle claw on the foot, due to the unusual hypertrophy of the first pedal ungual in addition to the typically enlarged and trenchant second pedal ungual of dromaeosaurids and other deinonychosaurs. Although recently argued to be an avialan (Cau et al., 2015), its status as a velociraptorine was recently reaffirmed (Pei et al., in press).

Knowledge of Early Cretaceous European dromaeosaurids is sparse and superficial. Reexamination of historic reptilian tooth and fragmentary jaw material from the Berriasian Lulworth Formation of the U.K. led to *Nuthetes* being reassigned as a dromaeosaurid taxon (Milner, 2002), and then being narrowed to the subfamily Velociraptorinae (Sweetman, 2004). However, this assignment was later contested by one of the original authors as possible tyrannosaurid material instead (Rauhut et al., 2010). Six fused sacral vertebrae from the Berriasian-Barremian Wessex Formation of the U.K.

TABLE 4
Troodontid fossil record

Continent	Geological Unit	Country	Period	Age	Age Reference	Taxa	Reference
Asia	Ejinhoru Formation	China	Early Cretaceous	Aptian-Albian	Sereno, 2010	<i>Sinornithoides</i>	Russell and Dong, 1993
	Huajiying Formation	China	Early Cretaceous	Hauterivian-Barremanian	Pan et al., 2013	<i>Jinfengopteryx</i>	Ji et al., 2005
	Majiacun Formation	China	Late Cretaceous	Coniacian-Santonian	Tan et al., 2015	<i>Xixiasaurus</i>	Lü et al., 2010
	Wulansuhai/Bayan Mandahu Formation	China	Late Cretaceous	Campanian	Godefroit et al., 2008	<i>Linthevenator</i> , <i>Philovenator</i>	Xu et al., 2011b, 2012b
	Jehol Group (Yixian Formation)	China	Early Cretaceous	Barremanian-Aptian	Chang et al., 2009, 2017; Pan et al., 2013	<i>Daliansaurus</i> , <i>Jianianhualong</i> , <i>Liaoningvenator</i> , <i>Mei</i> , <i>Sinovenator</i> , <i>Sinusomasus</i> , <i>Yixianosaurus</i> (possibly an avialan)	Xu et al., 2002b, 2017; Xu and Wang, 2003, 2004b; Xu and Norell, 2004; Chang et al., 2017; Shen et al., 2017a, 2017b; Yin et al., 2018
	Kallamedu Formation	India	Late Cretaceous	Maastrichtian	Goswami et al., 2013	troodontid tooth	Goswami et al., 2013
	Khamareen Us locality	Mongolia	Early Cretaceous	Cenomanian	Makovicky and Norell, 2004	MPC-D 100/44	Barsbold et al., 1987; Makovicky and Norell, 2004
	Khamaryn Ar locality	Mongolia	Early Cretaceous	Barremanian-Albian	Tsuihiji et al., 2016; Lucas, 2006	MPC-D 100/140	Tsuihiji, et al., 2016
	Djadokhta Formation	Mongolia	Late Cretaceous	Campanian	van Ifferbeck et al., 2005; Dingus et al., 2008; Hasegawa et al., 2009	<i>Almas</i> , <i>Byronosaurus</i> , <i>Gobivenator</i> , <i>Sauromnithoides</i>	Osborn, 1924; Norell et al., 2000; Makovicky et al., 2003; Bever and Norell, 2009; Tsuihiji et al., 2014; Pei et al., 2017a
	Nemegt Formation	Mongolia	Late Cretaceous	Maastrichtian	Jerzykiewicz and Russell, 1991; Shuvalov, 2000; van Ifferbeck et al., 2005	<i>Borogovia</i> , <i>Tochisaurus</i> , <i>Zanabazar</i>	Barsbold, 1974; Osmólska, 1987; Kurzanov and Osmólska, 1991; Norell et al., 2009

TABLE 4 *continued*

Continent	Geological Unit	Country	Period	Age	Age Reference	Taxa	Reference
Asia	Kakanaut Formation	Russia	Late Cretaceous	Maastrichtian	Herman et al., 2016	<i>Troodon</i> ?	Godefroit et al., 2009
	Udurchukan Formation	Russia	Late Cretaceous	Maastrichtian	Averianov and Sues, 2007	<i>Troodon</i> ?	Averianov and Sues, 2007
	Dzharakuduk Formation	Uzbekistan	Late Cretaceous	Cenomanian	Averianov and Sues, 2007	<i>Urbacodon</i>	Averianov and Sues, 2007
North America	Dinosaur Park Formation	Canada	Late Cretaceous	Campanian	Eberth, 2005; Brown et al., 2013	<i>Latenivenatrix</i> , <i>Polyodontosaurus</i> / <i>Stenonychosaurus</i> / <i>Troodon</i> ?	Gilmore, 1932; Sternberg, 1932; Brown et al., 2013; Evans et al., 2017; van der Reest and Currie, 2017
	Horseshoe Canyon Formation	Canada	Late Cretaceous	Campanian-Maastrichtian	Eberth and Braman, 2012; Quinney et al., 2013	<i>Albertavenator</i> , <i>Troodon</i>	Ryan et al., 1998; Evans et al., 2017
	Old Man Formation	Canada	Late Cretaceous	Campanian	Eberth, 2005	<i>Troodon</i>	Ryan and Russell, 2001
	Scollard Formation	Canada	Late Cretaceous-Palaeogene	Maastrichtian-Palaeocene	Khidir and Catuneanu, 2010	<i>Troodon</i>	Weishampel et al., 2004
	St. Mary River Formation	Canada	Late Cretaceous	Maastrichtian	Jackson and Varricchio, 2017	<i>Troodon</i>	Weishampel et al., 2004
	Wapiti Formation	Canada	Late Cretaceous	Campanian-Maastrichtian	Fanti et al., 2013	<i>Troodon</i>	Ryan and Russell, 2001
	El Gallo Formation	Mexico	Late Cretaceous	Campanian	López-Conde et al., 2018	<i>Troodon</i>	Weishampel et al., 2004
	Cedar Mountain Formation	U.S.	Early Cretaceous	Berremian?-Aptian	Senter et al., 2012	<i>Geminiraptor</i>	Senter et al., 2010
	Dakota Formation	U.S.	Early to Late Cretaceous	Albian-Cenomanian	Barclay et al., 2015	<i>Troodon</i>	Eaton et al., 1999
	Ferris Formation	U.S.	Late Cretaceous-Palaeogene	Maastrichtian-Palaeocene	Lillegraven and Eberle, 1999	<i>Troodon</i>	Lillegraven and Eberle, 1999

TABLE 4 continued

Continent	Geological Unit	Country	Period	Age	Age Reference	Taxa	Reference
North America	Hell Creek Formation	U.S.	Late Cretaceous	Maastrichtian	Hoganson and Edward, 2002; Fastovsky and Bercovici, 2016	<i>Troodon</i>	Fastovsky and Bercovici, 2016
	Judith River Formation	U.S.	Late Cretaceous	Campanian	Lawver and Jackson, 2017	<i>Troodon</i>	Leidy, 1856; Varricchio and Jackson, 2004
	Kaiparowits Formation	U.S.	Late Cretaceous	Campanian	Roberts et al., 2005; Jinnah et al., 2009; Zanno et al., 2011	<i>Talos</i> , <i>Troodon</i>	Eaton et al., 1999; Zanno et al., 2011
	Kirtland Formation	U.S.	Late Cretaceous	Campanian	Sullivan and Lucas, 2006	' <i>Sauromitholestes</i> '	Sullivan, 2006; Evans et al., 2014
	Lance Formation	U.S.	Late Cretaceous	Maastrichtian	Elizanowski et al., 2000	<i>Pectinodon/Troodon</i> ?	Carpenter, 1982
	Morrison Formation	U.S.	Late Jurassic	Kimmeridgian-Tithonian	Trujillo and Kowallis, 2015	<i>Hesperornithoides</i> , <i>Koparion</i>	Chure, 1994; Hartman et al., 2019
	Prince Creek Formation	U.S.	Late Cretaceous	Maastrichtian	Fiorillo et al., 2016	<i>Troodon</i>	Fiorillo et al., 2016
	Wahweap Formation	U.S.	Late Cretaceous	Campanian	Moran et al., 2010	<i>Troodon</i>	Eaton et al., 1999
	Two Medicine Formation	U.S./Canada	Late Cretaceous	Campanian	Rogers et al., 1993; Foreman et al., 2008	<i>Troodon</i> ?	Foreman et al., 2008
	Europe	Painten Formation	Germany	Late Jurassic	Tithonian	Foth and Rauhut, 2017	<i>Ostromia</i> (anchiornithine; possibly an early-diverging avialan)
Antarctica	Snow Hill Island Formation	-	Late Cretaceous	Maastrichtian	Case et al., 2007	<i>Imperobator</i> (indeterminate deinonychosaurian material or nondromaeosaurid paravian)	Case et al., 2007; Turner et al., 2012; Ely and Case, 2019

form the type of *Ornithodesmus cluniculus* (Seeley, 1887), which probably belongs to a dromaeosaurid (Norell and Makovicky, 1997; Naish and Martill, 2007). However, this specimen has a complex taxonomic history including past identifications as a bird, pterosaur, troodontid, and earlier-diverging theropod (Anonymous, 1887; Seeley, 1887; Howse and Milner, 1993; Naish et al., 2001). *Dromaeosauroides bornholmensis* is a taxon known from a tooth from the Early Cretaceous of Denmark (Bonde and Christiansen, 2003).

AFRICA: *Rahonavis ostromi* of the Maastrichtian Maevarano Formation (Rogers et al., 2013) of Madagascar's Mahajanga Basin was first described as an avialan (Forster et al., 1998) as supported by others (Agnolín and Novas, 2013; Cau, 2018; Novas et al., 2018). However, it has also been recognized as one of the first discovered Gondwanan dromaeosaurids (Makovicky et al., 2005; Turner et al., 2012; Pei et al., in press), which we follow in this volume. A dromaeosaurid from the Albian-Cenomanian Wadi Milk Formation of Sudan (Dromaeosauridae incertae sedis (Turner et al., 2012)) is the first and only African record reaching into the Early Cretaceous (Rauhut and Werner, 1995).

SOUTH AMERICA: The discovery of *Unenlagia* from the Turonian-Coniacian Portezuelo Formation of Patagonia, Argentina (Calvo et al., 2007) provides strong support that dromaeosaurids were not exclusively Laurasian, but occupied Gondwana as well (Novas and Puerta, 1997). This landmark discovery was followed by recognition of a second species, *U. paynemili*, in addition to the original *U. comahuensis* from the same formation (Calvo et al., 2004) as well as the new genus *Neuquenraptor* (Novas and Pol, 2005). However, the latter might be a junior synonym of *Unenlagia* (Makovicky et al., 2005), but this remains unclear (Brissón Egli et al., 2017). *Buitreraptor* from the Cenomanian-Turonian Candeleros Formation of Patagonia extended the South American record of dromaeosaurids into the earliest Late Cretaceous (Makovicky et al., 2005) and also provided evidence for a monophyletic Unenlagiinae in Gondwana, while *Austroraptor* demonstrated that their record extended to the end of the Cretaceous (Campan-

ian-Maastrichtian Allen Formation) (Novas et al., 2009) and solidified Patagonia, Argentina, as a hotspot for dromaeosaurid fossils. *Pamparaptor* is based on a deinonychosaurian foot from the Portezuelo Formation that is distinct from specimens of *Unenlagia* (Porfiri et al., 2011). This material has possible unenlagiine affinities, but does not nest exclusively with that clade in phylogenetic analyses (Gianechini et al., 2018). *Overoraptor* of the Cenomanian-Turonian Hiuncul Formation of Patagonia is known from fragmentary postcranial material (Motta et al., 2020). Described as a paravian, it was recovered as a stem avialan in a phylogenetic analysis (Motta et al., 2020). However, the closeness of its phylogenetic position to contemporaneous Patagonian unenlagiine dromaeosaurids as well as its highly modified deinonychosaurian digit II-2, suggests that *Overoraptor* might instead be an unenlagiine. *Unquillosaurus* is based on a left pubis from the Maastrichtian Los Blanquitos Formation of Patagonia (Powell, 1979). It may be a dromaeosaurid (Martínez and Novas, 2006) and was previously proposed as an indeterminate maniraptoran theropod (Novas and Agnolín, 2004) and as an earlier-diverging theropod (Powell, 1979). South American records outside Argentina are rare, but possible unenlagiine elements have been reported from the Late Cretaceous Bauru group of Brazil (Candeiro et al., 2012; Delcourt and Grillo, 2017).

ANTARCTICA: Two isolated teeth associated with a partial left foot and fragments from the right foot from the Maastrichtian Snow Hill Island Formation of James Ross Island, Antarctica were referred to Dromaeosauridae (Case et al., 2007). These were subsequently reinterpreted as indeterminate deinonychosaurian material (Turner et al., 2012). Ely and Case (2019) have recently described this specimen as *Imperobator antarcticus*, and recovered it as a nondromaeosaurid paravian.

TROODONTIDAE

Troodontids were first recognized in the late 19th century in North America and it is on that continent and in Asia where most fossils have been found (fig. 1; table 4). Troodontids are oth-

erwise scarce and have been traditionally thought of as a Laurasian group, but a single tooth now suggests that troodontids were possibly present in Gondwana (fig. 1; table 4).

NORTH AMERICA: The first troodontid genus *Troodon* was given to a tooth discovered in the Campanian Judith River Formation of Montana in the mid-19th century (Leidy, 1856). Originally thought to belong to a fossil lizard and then a pachycephalosaur, this is one of three historic North American troodontid genera, alongside *Polyodontosaurus* (Gilmore, 1932) and *Stenonychosaurus* (Sternberg, 1932). North American Campanian- and Maastrichtian-aged troodontids have experienced a prolonged period of taxonomic instability, including the role of *Troodon* as a wastebasket taxon (see Zanno et al., 2011, for further details) once it was recognized as a theropod (Sternberg, 1945). Campanian material referred to this genus comes from the Judith River Formation (Lawver and Jackson, 2017) as well as the Dinosaur Park (Brown et al., 2013) and Oldman formations of Alberta, Canada (Ryan and Russell, 2001), the Two Medicine Formation of Alberta, Canada, and Montana (Foreman et al., 2008), the Kaiparowits and Wahweap formations of Utah (Eaton et al., 1999), the El Gallo Formation of Baja California, Mexico (Weishampel et al., 2004) and the Campanian-Maastrichtian Wapiti, Horseshoe Canyon and St. Mary River formations of Alberta, Canada (Ryan et al., 1998; Ryan and Russell, 2001). The Two Medicine material includes eggs, some with embryos, and nests (Varricchio and Jackson, 2016) as well as skeletons. *Troodon* has been reported from Maastrichtian strata including the Ferris Formation of Wyoming (Lillegraven and Eberle, 1999), the Hell Creek Formation of Montana, Wyoming, North Dakota, and South Dakota (Fastovsky and Bercovici, 2016), the Prince Creek Formation of Alaska (Fiorillo et al., 2016), the Lance Formation of Wyoming (Carpenter, 1982), and the Scollard Formation of Alberta, Canada (Weishampel et al., 2004). *Troodon* has even been assigned to material from the Lower Cretaceous Dakota Formation of Utah (Eaton et al., 1999),

although this rock unit, now known as the Naturita Formation, has been reassigned to the early Late Cretaceous (Tucker et al., 2020). Material from the Dinosaur Park Formation has been assigned a different species name, *T. inequalis*, from the original *T. formosus* (Currie, 2005). The discovery of *Talos*, a partial postcranial skeleton from the Campanian Kaiparowits Formation of Utah, provided a chance to reappraise North American troodontid material, which led to the suggestion that *Troodon* is a nomen dubium and support for the genus *Pectinodon* (Longrich, 2008; Zanno et al., 2011). The latter, known from teeth and juvenile skeletal material from the Maastrichtian Lance Formation of Wyoming, was originally described as an additional species of *Troodon*, *T. bakkeri* (Carpenter, 1982). Continued efforts to address the taxonomic confusion arising from North America's problematic, highly fragmentary historic holotypes led to the resurrection of the genus *Stenonychosaurus* for some troodontid skeletal material from the Dinosaur Park Formation (Evans et al., 2017). This analysis was supported by subsequent work that assigned some of this *Stenonychosaurus* material to the new genus *Latenivenatrix* (van der Reest and Currie, 2017). *Albertavenator* was named from a distinctive partial left frontal recovered from the Maastrichtian Horseshoe Canyon Formation of Alberta, Canada (Evans et al., 2017). "*Saurornitholestes*" *robustus* from the Campanian Kirtland Formation of San Juan Basin, New Mexico, is an indeterminate troodontid frontal (Evans et al., 2014), originally referred to a new species of the dromaeosaurid *Saurornitholestes* (Sullivan, 2006). *Geminiraptor*, an incomplete maxilla from the Cedar Mountain Formation of Utah is arguably one of the most important North American troodontid specimens because, as the only Early Cretaceous record, it provides a crucial point of comparison with better-known Chinese contemporaries (Senter et al., 2010). A tooth that is the holotype of *Koparion* (Chure, 1994), and the partial articulated skeleton that forms the type of *Hesperornithoides miessleri* (Hartman et al., 2019) are possible Jurassic troodontid records, both

from the Morrison Formation of the western United States.

ASIA: The Gobi Desert of Mongolia provided the first Asian record of troodontids: *Saurornithoides* from the Campanian Djadokhta Formation of southern Mongolia (Osborn, 1924). Its reasonably complete skull and partial postcranium was particularly important in the early days of troodontid research. This animal was known from one species, *S. mongoliensis*, that was later joined by a second species, *S. junior*, from the younger Maastrichtian Nemegt Formation (Barsbold, 1974), although *S. junior* is now ascribed to *Zanabazar* (Norell et al., 2009). Other Djadokhta taxa include *Byronosaurus*, which is known from a large amount of cranial material and some postcranial material (Norell et al., 2000; Makovicky et al., 2003) including, perhaps, two perinates (Bever and Norell, 2009; but see Pei et al., 2017a). *Gobivenator* and *Almas* are well-preserved, recently described specimens from this formation, with *Gobivenator* one of the best three-dimensionally preserved troodontids in existence (Tsuihiji et al., 2014; Pei et al., 2017a). *Linhevenator tani*, known from a partial, eroded skeleton, was discovered from the similar Campanian Wulansuhai (Bayan Mandahu) Formation across the border in Nei Mongol, northern China (Xu et al., 2011b, 2012b). A single leg from the same formation was originally identified as a juvenile *Saurornithoides* specimen (Currie and Peng, 1993) and was later assigned to the new taxon *Philoventator* (Xu et al., 2012b). Mongolia and Russia provide the latest Cretaceous records. *Borogovia* and *Tochisaurus* are known from fragmentary hind-limb elements (Osmólska, 1987; Kurzanov and Osmólska, 1991), and like *Zanabazar*, were recovered from the Maastrichtian Nemegt Formation of southern Mongolia. “Troodon” records from the Maastrichtian Kakanaut and Udurchukan formations of Russia are expected to belong to one or more new genera given the recent revisions to *Troodon* taxonomy in North America (Averianov and Sues, 2007; Zanno et al., 2011; Evans et al.,

2017; van der Reest and Currie, 2017). A single tooth from the Maastrichtian Kallamedu Formation of India potentially represents the only troodontid record from Gondwana (Goswami et al., 2013), despite the group being known for over 150 years. Occurrences from China and Uzbekistan extend the Asian troodontid record back into the earliest Late Cretaceous as well as the Early Cretaceous, providing the only described taxa from these time intervals worldwide. *Xixiasaurus* is from the Coniacian-Santonian Majiacun Formation (Lü et al., 2010) of Henan, China, and *Urbacodon* is from the Cenomanian Dzharakuduk Formation of Navoi Viloyat, Uzbekistan (Averianov and Sues, 2007). The Early Cretaceous troodontid record of Asia is well represented in China by at least eight named genera. The oldest record is *Jinfengopteryx* from the Hauterivian-Barremian Huajiying (Qiaotou) Formation of Hebei, China, that was originally described as an avialan and whose stomach may contain preserved seeds (Ji et al., 2005; Pan et al., 2013). *Sinovenator*, *Mei*, *Sinuserosaurus*, *Daliansaurus*, *Liaoningvenator*, and *Jianianhualong* were all discovered from the Barremian-Aptian Yixian Formation of northern China (Xu et al., 2002b, 2017; Xu and Norell, 2004; Xu and Wang, 2004b; Pan et al., 2013; Chang et al., 2017; Shen et al., 2017a, 2017b). This formation and the Djadokhta Formation represent the most important sources of troodontid material globally. *Sinovenator* was the first troodontid reported from the Yixian Formation (Xu et al., 2002b). Initially represented by a partial skull and a few incomplete postcranial skeletons (Xu et al., 2002b), later material included a partial skull with a well-preserved braincase (Yin et al., 2018). *Mei* was first described on the basis of an exquisitely-preserved skeleton with a bird-like sleeping posture, which is arguably the most complete Early Cretaceous troodontid specimen known (Xu and Norell, 2004; Pan et al., 2013). *Sinuserosaurus*, *Daliansaurus*, and *Liaoningvenator* all have a similar size as *Sinovenator*, and each of them were reported from a single, near com-

TABLE 5
Mesozoic avialan fossil record

Continent	Geological Unit	Country	Period	Age	Age Reference	Taxa	Reference
Asia	Haifanggou and Tiaojiashan formations	China	Middle-Late Jurassic	Bathonian-Oxfordian	Gao and Shubin, 2012; Liu et al., 2012; Wang et al., 2013c; Sullivan et al., 2014; Tian et al., 2015	<i>Anchiornis</i> , <i>Aurornis</i> (possibly a synonym of <i>Anchiornis</i>), <i>Cailong</i> , <i>Eosinopteryx</i> , <i>Pedopenna</i> , <i>Serikornis</i> , <i>Xiaotingia</i> (possibly all troodontids)	Xu and Zhang, 2005; Xu et al., 2009, 2011a; Hu et al., 2009, 2018; Godefroit et al., 2013a, 2013b; Lefèvre et al., 2017; Pei et al., 2017b
	Dabeigou Formation	China	Early Cretaceous	Hauterivian-Barremian	Zhang et al., 2008b	<i>Jingguofortis</i> , <i>Eoconfuciusornis</i>	Zhang et al., 2008b; Wang et al., 2018
	Huajiying Formation	China	Early Cretaceous	Hauterivian-Barremian	Pan et al., 2013	<i>Archaeornithura</i> , <i>Cruralispemnia</i> , <i>Eoconfuciusornis</i> , <i>Eopengornis</i> , <i>Hebeiornis</i> (<i>Vescornis</i>), <i>Jibeinia</i> , <i>Orientalius</i> , <i>Protopteryx</i>	Hou, 1997a; Zhang and Zhou, 2000; Zhang et al., 2004; Jin et al., 2008; Wang et al., 2014a,, 2015a, 2017; Pan et al., 2016; Zheng et al., 2017; Navalón et al., 2018, Chiappe et al., 2019a; Liu et al., 2019
	Qiaotou Formation	China	Early Cretaceous	Barremian	Wang et al., 2010	<i>Shenoptornis</i>	Wang et al., 2010
	Jehol Group (Yixian Formation; Jiufotang Formation)	China	Early Cretaceous	Barremian-Aptian	Chang et al., 2009, 2017; Pan et al., 2013	<i>Archaeorhynchus</i> , <i>Changchengornis</i> , <i>Confuciusornis</i> , <i>Dalingheornis</i> , <i>Dingavis</i> , <i>Eoenantiornis</i> , <i>Eogranivora</i> , <i>Grabauornis</i> , <i>Gretcheniao</i> , <i>Hongshanornis</i> , <i>Iteravis</i> , <i>Jeholornis</i> , <i>Jixiangornis</i> (likely a synonym of <i>Jeholornis</i>), <i>Jurornis</i> , <i>Liaoningornis</i> , <i>Longicrusavis</i> , <i>Longirostravis</i> , <i>Mirusavis</i> , <i>Monocnantiornis</i> , <i>Paraprotopteryx</i> , <i>Sapeornis</i> , <i>Shanweiniiao</i> , <i>Sulcavis</i> , <i>Tianyuanis</i> , <i>Xinghaiornis</i> , <i>Yangavis</i> , <i>Yanornis</i> , <i>Zhongornis</i> (possibly a scansoriopterygian)	Hou et al., 1995, 1996, 1997b, 1999a, 1999b, 2002, 2004; Hou, 1996, 1997b; Chiappe et al., 1999, 2007, 2014, 2019b; Ji et al., 1999, 2002a, 2002b; Xu et al., 1999; Zhang et al., 2006, 2009; Zhou and Zhang, 2005, 2006a, 2006b; Gao et al., 2008, 2012; O'Connor et al., 2009, 2010, 2011a, 2013, 2016c; Li et al., 2010; Wang et al., 2013d, 2013e, 2019c; ; Zheng et al., 2007, 2013, 2014, 2018; Dalsätt et al., 2014; Lefèvre et al., 2014; Zhou et al., 2014a; Hu and O'Connor, 2017; Liu et al., 2017; Wang and Zhou, 2018

TABLE 5 continued

Continent	Geological Unit	Country	Period	Age	Age Reference	Taxa	Reference
Asia							
						<i>Alethodactornis</i> , <i>Archaeorhynchus</i> , <i>Bellatornis</i> , <i>Bohaiornis</i> , <i>Boluochia</i> , <i>Cathayornis</i> (<i>Largirostornis</i> , <i>Longchengornis</i>), <i>Chaoyangia</i> , <i>Chiappeavis</i> , <i>Chongningia</i> , <i>Confuciusornis</i> , <i>Dalianraptor</i> (might be a chimera), <i>Dapingfangornis</i> , <i>Eocathayornis</i> , <i>Fortunguavis</i> , <i>Gracilornis</i> , <i>Houornis</i> , <i>Huoshanornis</i> , <i>Jeholornis</i> (<i>Shenzhouraptor</i>), <i>Jianchiangornis</i> , <i>Linyiornis</i> , <i>Longipteryx</i> , <i>Longusunguis</i> , <i>Mengciusornis</i> , <i>Parabohaiornis</i> , <i>Parahongshanornis</i> , <i>Parapengornis</i> , <i>Pengornis</i> , <i>Piscivoravis</i> , <i>Piscivorenantiornis</i> , <i>Pterygornis</i> , <i>Rapaxavis</i> , <i>Sapeornis</i> , <i>Schizoostra</i> , <i>Shangyang</i> , <i>Shengfingornis</i> , <i>Sinornis</i> , <i>Songlingornis</i> , <i>Xiangornis</i> , <i>Yanornis</i> , <i>Yixianornis</i> , <i>Yuanjiaawaornis</i> , <i>Zhongjianornis</i> , <i>Zhouornis</i>	Sereno and Rao, 1992; Zhou et al., 1992, 2004, 2008, 2009, 2010, 2012, 2013, 2014; Hou and Zhang, 1993; Zhou, 1995, 2002; Hou, 1997a; Hou et al., 2002; Czerkas and Ji, 2002; Ji et al., 2002a; Zhou and Hou, 2002; Zhou and Zhang, 2001, 2002a, 2002b, 2003a, 2003b, 2006a; Gong et al., 2004; Dalsätt et al., 2006; Li et al., 2006, 2007, 2008, 2010a, 2010b, 2011, 2012, 2014b; Morschhauser et al., 2009; Yuan, 2010; Hu et al., 2010, 2011, 2015a, 2015b; Li and Hou, 2011; O'Connor et al., 2011a, 2012, 2016a; Pu et al., 2013; Wang et al., 2010b, 2014b, 2014d, 2014e, 2016b, 2016c, 2016d, 2019d; Zhang et al., 2001, 2013; Wang and Zhou, 2018, 2019
	Jingchuan Formation	China	Early Cretaceous	Barremian-Aptian?	Lockley et al., 2012	<i>Otogornis</i> (originally assigned to the Yijinhuluo Formation), enantiornithines	Hou, 1994; Li et al., 2008b; Zhang et al., 2010; Wang and Liu, 2015
	Xiagou Formation	China	Early Cretaceous	Aptian	O'Connor et al., 2016b	<i>Avimata</i> , <i>Changmaornis</i> , <i>Dunhuangia</i> , <i>Feitianius</i> , <i>Gansus</i> , <i>Jiuquanornis</i> , <i>Qiliania</i> , <i>Yumenornis</i>	Hou and Liu, 1984; You et al., 2006, 2010; Ji et al., 2011; Wang et al., 2013b, 2013f, 2015b; O'Connor et al., 2016b; Baillieu et al., 2019
	Jiangdihe Formation	China	Late Cretaceous	Turonian-Santonian	Wang et al., 2014c	<i>Paravis</i>	Wang et al., 2014c
	Qiupa Formation	China	Late Cretaceous	Campanian-Maastrichtian	Jiang et al., 2011	enantiornithines	Xu et al., 2011c
	Kuwajima Formation	Japan	Early Cretaceous	Barremian	Sano and Yabe, 2017	enantiornithines	Matsuoka et al., 2002

TABLE 5 continued

Continent	Geological Unit	Country	Period	Age	Age Reference	Taxa	Reference
Asia	Kitadani Formation	Japan	Early Cretaceous	Aptian	Sano and Yabe, 2017	<i>Fukuipteryx</i>	Imai et al., 2019
	Sinuju series	North Korea	Early Cretaceous	-	Gao et al., 2009	confuciusornithiforms, enantiornithines	Gao et al., 2009
	"Burmese Amber"	Myanmar	Late Cretaceous	Cenomanian	Xing et al., 2017	enantiornithines; <i>Elektorornis</i>	Xing et al., 2016, 2017, 2019a,b,c
	Khodzhakul Svita	Uzbekistan	Early Cretaceous	Albian	Kurochkin, 2000	<i>Horeznavis</i>	Kurochkin, 2000
	Bissetky Formation	Uzbekistan	Late Cretaceous	Coniacian	Pantelev, 2018	enantiornithines, ornithuromorphs (<i>Zhyraornis</i>)	Nesov, 1984; Kurochkin, 2000; Pantelev, 2018
	"Kushmurun"	Kazakhstan	Late Cretaceous	Maastrichtian	Dyke et al., 2006	<i>Asiahesperornis</i>	Nesov and Prizemlin, 1991; Dyke et al., 2006
	Ilek Formation	Russia	Early Cretaceous	Barremian-Aptian	O'Connor et al., 2014	<i>Evgenavis</i> , <i>Mystiornis</i>	Kurochkin et al., 2011; O'Connor et al., 2014
	Rybuskha Formation	Russia	Late Cretaceous	Campanian	Kurochkin, 2000	<i>Hesperornis</i>	Marsh, 1872; Kurochkin, 2000
	"Ouadi al Gabour"	Lebanon	Late Cretaceous	Cenomanian	Cau and Arduini, 2008	<i>Enantiophoenix</i>	Cau and Arduini, 2008
	Andaikhudag Formation	Mongolia	Early Cretaceous	Hauterivian-Barremian	Zelenkov and Averianov, 2016	<i>Ambiortus</i> , <i>Holbotia</i>	Kurochkin, 1982; O'Connor and Zelenkov, 2013; Zelenkov and Averianov, 2016
	Barun Goyot Formation	Mongolia	Late Cretaceous	Campanian-Maastrichtian	Gradzinski and Jerzykiewicz, 1974a, 1974b	<i>Gobipteryx</i> , <i>Hollandia</i> , nests of enantiornithines?	Elzanowski, 1974; Elzanowski, 1977; Bell et al., 2010; Varricchio and Barta, 2015
	Djadokhta Formation	Mongolia	Late Cretaceous	Campanian?	van Ifferbeck et al., 2005; Dingus et al., 2008; Hasegawa et al., 2009	<i>Apsaravis</i> , <i>Gobipteryx</i> , nests of enantiornithines?	Chiappe et al., 2001; Norell and Clarke, 2001; Varricchio and Barta, 2015
	Nemegt Formation	Mongolia	Late Cretaceous	Maastrichtian?	Jerzykiewicz and Russell, 1991; Shuvalov, 2000; van Ifferbeck et al., 2005	<i>Brodavis</i> , <i>Gurilynia</i> , <i>Judimornis</i>	Nesov and Borkin, 1983; Kurochkin, 1999; Martin et al., 2012
Australia	Wonthaggi Formation	Australia	Early Cretaceous	Barremian-Aptian	Close et al., 2009	enantiornithines	Rich et al., 1999; Close et al., 2009

TABLE 5 continued

Continent	Geological Unit	Country	Period	Age	Age Reference	Taxa	Reference
Australia	Toolebuc Formation	Australia	Early Cretaceous	Albian	Close et al., 2009	enantiornithines	Molnar, 1986
	Griman Creek Formation	Australia	Early Cretaceous	Albian	Close et al., 2009	enantiornithines	Molnar, 1999
Europe	Solnhofen Limestone (Altmühlal Formation)	Germany	Late Jurassic	Tithonian	Rauhut et al., 2018	<i>Archaeopteryx</i>	Owen, 1863; Dames, 1884; Heller, 1959; Wellnhofer, 1974, 1988, 1993, 2009; Mayr et al., 2005; Wellnhofer and Röper, 2005; Tischlinger, 2009; Foth et al., 2014; Rauhut et al., 2018; Kunderát et al., 2019.
	Painten Formation	Germany	Late Jurassic	Tithonian	Foth and Rauhut, 2017	<i>Ostromia</i> (anchiornithine; possibly a troodontid; formerly <i>Haarlem Archaeopteryx</i>)	Foth and Rauhut, 2017
	Mörnsheim Formation	Germany	Late Jurassic	Tithonian	Foth and Rauhut, 2017	<i>Archaeopteryx</i>	Tischlinger, 2009; Kunderát et al., 2019
	La Pedrera de Rubies Lithographic Limestones Formation	Spain	Early Cretaceous	Barremian	Szwedo and Ansoorge, 2015	<i>Noguerornis</i> , enantiornithines	Lacasa-Ruiz, 1989; Sanz et al., 1997
	Calizas de la Huérguina Formation	Spain	Early Cretaceous	Barremian	Buscalioni and Fregenal-Martínez, 2010	<i>Concornis</i> , <i>Eoalulavis</i> , <i>Iberomesornis</i>	Sanz and Bonaparte, 1992; Sanz and Buscalioni, 1992; Sanz et al., 1996, 2002; Sereno, 2000; Navalon et al., 2015
	Melovatskaya Formation	Russia	Late Cretaceous	Cenomanian	Kurochkin et al., 2007	<i>Cerebravis</i>	Kurochkin et al., 2007
	Cselbánya Formation	Hungary	Late Cretaceous	Santonian	Dyke and Ösi, 2010	<i>Bauxiornis</i>	Dyke and Ösi, 2010
	Grès à Reptiles Formation	France	Late Cretaceous	Campanian-Maastrichtian	Walker et al., 2007	<i>Gargantuavis</i> , <i>Martiniavis</i>	Buffetaut, 1998; Walker et al., 2007
	"Fox-Amphoux basin"	France	Late Cretaceous	Maastrichtian?	Buffetaut et al., 1995	unnamed taxon	Buffetaut et al., 1995

TABLE 5 continued

Continent	Geological Unit	Country	Period	Age	Age Reference	Taxa	Reference
Europe	Sebeş Formation	Romania	Late Cretaceous	Maastrichtian	Brusatte et al., 2013	nests and bones of enantiornithines	Dyke et al., 2012
	"Hateg Basin"	Romania	Late Cretaceous	Maastrichtian	Wang et al., 2011	enantiornithines	Wang et al., 2011
	Maastricht Formation	Belgium	Late Cretaceous	Maastrichtian	Keutgen, 2018	<i>Ichthyornis</i> -like bird, <i>Asteriornis</i>	Dyke et al., 2002; Field et al., 2020
South America	Crato Formation	Brazil	Early Cretaceous	Aptian	de Souza Carvalho et al., 2015	enantiornithines; <i>Cratoavis</i> (valid?)	Naish et al., 2007; de Souza Carvalho et al., 2015
	Portezuelo Formation	Argentina	Early Cretaceous	Turonian-Coniacian	Agnolin et al., 2006	ornithuromorph	Agnolin et al., 2006
	Bajo de la Carpa Formation	Argentina	Late Cretaceous	Santonian	Fernández et al., 2013	<i>Neuquenornis</i> , <i>Patagopteryx</i> ; nests with embryonic remains	Alvarenga and Bonaparte, 1992; Chiappe and Calvo, 1994; Schweitzer et al., 2002; Fernández et al., 2013
	Las Curtiembres Formation	Argentina	Late Cretaceous	Campanian	Novas et al., 2010	<i>Iniornis</i>	Novas et al., 2010
	Allen Formation	Argentina	Late Cretaceous	Campanian-Maastrichtian	Armas and Sánchez, 2015	<i>Limenavis</i>	Clarke and Chiappe, 2001
	Los Alamitos Formation	Argentina	Late Cretaceous	Campanian-Maastrichtian	Agnolin and Martinelli, 2009	<i>Alamitornis</i>	Agnolin and Martinelli, 2009
	Bauru Group	Brazil	Late Cretaceous	Campanian-Maastrichtian	Nava et al., 2015	enantiornithines	Nava et al., 2015
	Quiriquina Formation	Chile	Late Cretaceous	Campanian-Maastrichtian	Olson, 1992	<i>Neogaornis</i>	Lambrecht, 1929; Olson, 1992; Mayr, 2016
	Lecho Formation	Argentina	Late Cretaceous	Maastrichtian	Walker and Dyke, 2009	<i>Elbretornis</i> , <i>Enantiornis</i> , <i>Lectavis</i> , <i>Martinavis</i> , <i>Yungavolucris</i> , <i>Soroavisaurus</i>	Walker, 1981; Chiappe, 1993; Walker et al., 2007; Walker and Dyke, 2009
	La Colonia Formation	Argentina	Late Cretaceous	Maastrichtian	Lawver et al., 2011	enantiornithines	Lawver et al., 2011
North America	Ashville Formation	Canada	Late Cretaceous	Cenomanian	Tokaryk et al., 1997	<i>Pasquiaornis</i>	Tokaryk et al., 1997

TABLE 5 continued

Continent	Geological Unit	Country	Period	Age	Age Reference	Taxa	Reference
North America	Belle Fourche Formation	Canada	Late Cretaceous	Cenomanian	Clarke, 2004	<i>Ichthyornis</i> -like material	Clarke, 2004
	Woodbine Formation	U.S.	Late Cretaceous	Cenomanian	Tykoski and Fiorillo, 2010	<i>Flexornornis</i>	Tykoski and Fiorillo, 2010
	Kaskapau Formation	Canada	Late Cretaceous	Turonian	Clarke, 2004	<i>Ichthyornis</i> -like material	Clarke, 2004
	"Canadian Arctic circle"	Canada	Late Cretaceous	Turonian	Bono et al., 2016	<i>Tingniatornis</i>	Bono et al., 2016
	Mancos Shale Formation	U.S.	Late Cretaceous	Turonian	Clarke, 2004	<i>Ichthyornis</i>	Lucas and Sullivan, 1982; Clarke, 2004
	Austin Chalk Formation	U.S.	Late Cretaceous	Coniacian-Santonian	Clarke, 2004	<i>Ichthyornis</i>	Clarke, 2004
	Niobrara Formation	U.S.	Late Cretaceous	Coniacian-Campanian	Da Gama et al., 2014	<i>Apatornis</i> , <i>Baptornis</i> , <i>Hesperornis</i> , <i>Iaceornis</i> , <i>Ichthyornis</i> , <i>Parahesperornis</i> , hesperornithiforms	Marsh, 1872, 1877, 1880; Martin and Tate, 1976; Martin, 1984; Clarke, 2004; Bell and Chiappe, 2015; Field et al., 2018b
	Belly River Group	Canada	Late Cretaceous	Campanian	Longrich, 2009	ornithurines	Longrich, 2009
	Dinosaur Park Formation	Canada	Late Cretaceous	Campanian	Brown et al., 2013	enantiornithines	Buffetaut, 2010
	Northumberland Formation	Canada	Late Cretaceous	Campanian	McLachlan et al., 2017	<i>Maaqwi</i>	Morrison et al., 2005; McLachlan et al., 2017
	La Bocana Roja Formation	Mexico	Late Cretaceous	Campanian	Peacock and Sidor, 2015	<i>Alexornis</i>	Brodtkorb, 1976
	Kaiparowits Formation	U.S.	Late Cretaceous	Campanian	Zanno et al., 2011	<i>Mirarce</i>	Atterholt et al., 2018
	Mooreville Chalk Formation	U.S.	Late Cretaceous	Campanian	Clarke, 2004	<i>Haltornis</i> , <i>Ichthyornis</i>	Chiappe et al., 2002; Clarke, 2004; Field et al., 2018b
	Two Medicine Formation	U.S.	Late Cretaceous	Campanian	Foreman et al., 2008	<i>Gettyia</i>	Atterholt et al., 2018

TABLE 5 continued

Continent	Geological Unit	Country	Period	Age	Age Reference	Taxa	Reference
North America	Pierre Shale	U.S.	Late Cretaceous	Campanian-Maastrichtian	Aoisuka and Sato, 2016	hesperornithiforms	Bell and Chiappe, 2015
	Frenchman Formation	Canada	Late Cretaceous	Maastrichtian	Martin et al., 2012	enantiornithines, hesperornithiforms, ornithurines	Longrich et al., 2011; Martin et al., 2012
	“Canadian Arctic Circle”	Canada	Late Cretaceous	Maastrichtian	Hou, 1999	<i>Canadaga</i>	Hou, 1999
	Hell Creek Formation	U.S.	Late Cretaceous	Maastrichtian	Fastovsky and Bercovici, 2016	<i>Avisaurus</i> , hesperornithiforms, ornithurines	Brett-Surman and Paul, 1985; Longrich et al., 2011
	Lance Formation	U.S.	Late Cretaceous	Maastrichtian	Elzanowski et al., 2000	ornithurines	Longrich et al., 2011
Africa	Maevarano Formation	Madagascar	Late Cretaceous	Maastrichtian	Rogers et al., 2013	<i>Vorona</i> , enantiornithines, <i>Rahonavis</i> ?	Forster et al., 1996; O’Connor and Forster, 2010; Agnolín and Novas, 2013
Antarctica	López de Bertodano Formation	-	Late Cretaceous	Maastrichtian	Olivero et al., 2007	<i>Vegavis</i> , <i>Polaravis</i> ; <i>Ichthyornis</i> -like material	Zinsmeister, 1985; Noriega and Tambussi, 1995; Chatterjee, 2000; Clark et al., 2005a
	Snow Hill Island Formation	-	Late Cretaceous	Maastrichtian	Cordes-Person, 2020	<i>Antarcticavis</i> ; <i>Imperovator</i> (indeterminate deinonychosaurian material or nondromaeosaurid paravian)	Case et al., 2007; Turner et al., 2012; Ely and Case, 2019; Cordes-Person, 2020

plete skeleton (Xu and Wang, 2004b; Shen et al., 2017a, 2017b). *Jianianhualong* is only known from a single flattened specimen from the Yixian Formation, which preserves the first record of asymmetrical feathers in troodontids (Xu et al., 2017). *Sinornithoides* is known from the Aptian-Albian Ejinhoru Formation of Nei Mongol, China, based on a near complete skeleton (Russell and Dong, 1993). Across the border in Mongolia, unnamed Early Cretaceous troodontids have been reported, including the well-known “Early Cretaceous troodontid” MPC-D 100/44 and MPC-D 100/140 (Barsbold et al., 1987; Tsuihiji et al., 2016).

In northeastern China, the Middle Jurassic Bathonian Haifanggou Formation yields *Pedopenna* (Xu and Zhang, 2005), while the Late Jurassic Oxfordian Tiaojishan Formation yields *Anchiornis*, *Auronis*, *Caihong*, *Eosinopteryx*, *Serikornis*, and *Xiaotingia* (Xu et al., 2008, 2011a; Godefroit et al., 2013a, 2013b; Lefèvre et al., 2017; Hu et al., 2018). These taxa have been proposed as members of the Anchiornithinae, a controversial clade of long-tailed, early-diverging paravians. Anchiornithines were first described as early avialans, but their phylogenetic placement lacks consensus (Hu et al., 2009; Lee and Worthy, 2011; Xu et al., 2011a; Agnolín and Novas, 2013; Godefroit et al., 2013a, 2013b; Foth and Rauhut, 2017; Lefèvre et al., 2017; Pei et al., 2017b, in press). If they are troodontids as recovered in some recent works, they would be the oldest fossils of these animals (Hu et al., 2009). *Hesperornithoides*, from the Morrison Formation of Wyoming, is also a potential Jurassic troodontid (Hartman et al., 2019). Two Early Cretaceous taxa from the Yixian Formation, *Liaoningvenator* and *Yixianosaurus*, have been recovered as anchiornithines and are the only anchiornithine taxa besides *Ostromia* (previously an archaeopterygid) that have been found outside the Tiaojishan Formation (Cau et al., 2017; Foth and Rauhut, 2017; Shen et al., 2017b). However, the phylogenetic placement of *Yixianosaurus* remains controversial (Dececchi et al., 2012; Xu et al., 2013a; Cau et al., 2017; Foth and Rauhut, 2017; Lefèvre et al., 2017).

AVIALAE

The fossil record of stem birds (those members of Avialae falling outside the crown group Aves; alternatively crown group birds are referred to as Neornithes, with Aves consisting of stem and crown birds) has rapidly expanded since the 1980s (table 5). Prior to this, the record of Mesozoic birds consisted almost entirely of the Late Jurassic *Archaeopteryx* from the Solnhofen Limestone of southern Germany (Owen, 1863) and the Late Cretaceous “Odontornithes” (ornithurines *Ichthyornis* and the Hesperornithiformes) from marine deposits in North America (Marsh, 1880), with little to no evidence documenting the evolution of the avian postcranium from the primitive condition in *Archaeopteryx* to the nearly modern condition in *Ichthyornis* (fig. 1; table 5). Since the 1980s the number of species has more than doubled and the number of specimens has increased more than tenfold. In addition to the overwhelming collections uncovered in the Jehol Lagerstätte of northeastern China, important specimens have been discovered in Cretaceous deposits all over the world (O'Connor et al., 2011a) (fig. 1).

ASIA: The greatest concentration of non-avian avialan fossils is found in Asia. More than half of all known species of Cretaceous birds are from the Early Cretaceous Hauterivian - Aptian Jehol lagerstätten, preserved in northeastern China, which occurs in three successive formations (and their stratigraphic equivalents): the Huajiyang, Yixian, and Jiufotang formations, deposited from about 131 to 120 Ma (Zhou and Zhang, 2006a; Pan et al., 2013). This includes the only lineage of long bony-tailed birds other than the Archaeopterygiformes, the Jeholornithiformes (Zhou and Zhang, 2002a); almost the entire record of non-ornithothoracine pygostylians, including the Sapeornithiformes, Confuciusornithiformes, and the Jinguoortisidae (Hou et al., 1995; Zhou and Zhang, 2002b; Wang et al., 2016b, 2018); and the earliest-known record of the Enantiornithes and Ornithuromorpha (together Ornithothoraces) in the Huajiyang Formation (Zhang and

Zhou, 2000; Wang et al., 2014a, 2015). We adopt the node-based definition for the Ornithuromorpha because of the preference of our authors: Euornithes Sereno et al. 1998 is the stem-based definition. Two species of *Jeholornis* are currently recognized, *J. prima* and *J. palmapenis* (the holotype of "*J. curvipes*" is thought to be tampered) (O'Connor et al., 2012). The Sapeornithiformes is currently monospecific with all reported specimens purportedly ontogimorphs of *Sapeornis chaoyangensis* (Pu et al., 2013). *Jeholornis* and *Sapeornis* clades occur predominantly in the Jiufotang Formation with a few specimens also collected in the Yixian. The Confuciusornithiformes is much more diverse (*Eoconfuciusornis*, *Confuciusornis*, *Changchengornis*, and *Yangavis*: Wang and Zhou, 2018; Wang et al., 2019b). The early-diverging *Eoconfuciusornis zhengi* and another indeterminate confuciusornithiform have been reported from the Huajiyang Formation (Zhang et al., 2008b; Navalón et al., 2018). Most confuciusornithiform specimens are referable to *Confuciusornis sanctus* and are found in the Yixian Formation with a few specimens from the Jiufotang. *C. dui* (Hou et al., 1999), *Changchengornis hengdaoziensis* (Chiappe et al., 1999), and *Yangavis confucii* (Wang and Zhou, 2018) are known only from single specimens. Enantiornithines and ornithuromorphs are found throughout the entirety of the Jehol Biota, with diversity increasing through time, peaking in the Jiufotang Formation. Currently, approximately 41 valid species of enantiornithines are recognized compared to approximately 19 species of ornithuromorphs. Diverse subclades are also recognized, such as the enantiornithine Pengornithidae (e.g., *Eopenornis*, *Chiappeavis*: O'Connor et al., 2016a), Bohaiornithidae (e.g., *Sulcavis*, *Longsunguis*: Wang et al., 2014b), and Longipterygidae (e.g., *Boluochia*, *Longipteryx*: O'Connor et al., 2011b), and the ornithuromorph lineage, the Hongshanornithidae (e.g., *Archaeornithura*, *Longicrusavis*: O'Connor et al., 2010). The Pengornithidae and Hongshanornithidae lineages persisted for the entire duration of the Jehol Biota (Wang et al., 2014a, 2015). Jehol equivalent deposits in

nearby basins also preserve enantiornithines (e.g., Qiaotou, Dabeigou, and Yijinhuoluo formations).

The slightly younger Aptian Xiagou Formation in Gansu, northwestern China, has also produced a small diversity of enantiornithines (e.g., *Feitianius*, *Qiliania*: Ji et al., 2011; O'Connor et al., 2016b) and ornithuromorphs (*Jiuquanornis*, *Changmaornis*: Wang et al., 2013b) with a majority of the collected specimens assigned to the ornithuromorph *Gansus yumenensis* (You et al., 2006). The Late Cretaceous record consists of only two isolated specimens referable to the Enantiornithes: *Parvavis* from the Turonian-Santonian Jiangdihe Formation (Wang et al., 2014c) and an unnamed taxon from the upper Upper Cretaceous Qiupa Formation.

Fukuipteryx prima is the first nonornithothoracine pygostylian to be found outside of the Jehol Biota basins (Imai et al., 2019). Its partial skeleton as well as a single enantiornithine humerus have been reported from the Lower Cretaceous Tetori Group in Japan (Matsuoka et al., 2002; Imai et al., 2019) from the Barremian Kuwajima Formation and Aptian Kitadani Formation respectively. Confuciusornithiforms and enantiornithines have been reported in the North Korean Lower Cretaceous Sinuiju series (Gao et al., 2009). In southeastern Asia, Cenomanian (~99 Ma) age amber from Myanmar has recently become an unlikely major source of Cretaceous birds, recording a fauna of very small precocial enantiornithines including the taxon *Elektorornis* (Xing et al., 2016, 2017, 2019a,b,c). In Central Asia, a large number of fragments have been collected from the Turonian Bissekty Formation in Uzbekistan (Panteleev, 2018). These are apparently referable to enantiornithines and ornithuromorphs, including forms related to *Ichthyornis* (Kurochkin, 2000). The controversial and fragmentary enantiornithine taxon *Horezmavis* comes from Albian deposits of the Khodzshakul Formation, also in Uzbekistan (Kurochkin, 2000). A hesperornithiform, *Asiahesperornis*, has been described from numerous fragments collected from Maastrichtian deposits

in Kazakhstan (Dyke et al., 2006). A few specimens have been collected in Russia including *Evgenavis* and *Mystiornis* from the Barremian Ilek Formation, both of uncertain phylogenetic affinity (Kurochkin et al., 2011; O'Connor et al., 2014), and *Hesperornis rossicus* from the Campanian Rybuskha Formation (Kurochkin, 2000). In western Asia, a single enantiornithine specimen (*Enantiophoenix*) has been collected from Cenomanian marine limestones in Lebanon (Dalla Vecchia and Chiappe, 2002).

Several early-diverging avialan skeletons as well as nests have been discovered in Mongolia. The enantiornithine *Holbotia* and the ornithuromorph *Ambiortus* were collected from the Hauterivian-Barremian Andaikhudag Formation in the Central Mongolian Altai, both preserving soft tissue (O'Connor and Zelenkov, 2013; Zelenkov and Averianov, 2016). All other specimens are from Late Cretaceous deposits. The early Late Cretaceous Javkhlant Formation has yielded enantiornithine embryos (Varricchio et al., 2015). The Campanian-Maastrichtian Barun Goyot Formation has produced several specimens of the enantiornithine *Gobipteryx* (Elzanowski, 1977) and the only known specimen of the ornithuromorph *Hollanda* (Bell et al., 2010). The Ukhaa Tolgod locality, which is attributed to the Campanian Djadokhta Formation, has produced a skull of the enantiornithine *Gobipteryx* (Chiappe et al., 2001) and the only known specimen of the ornithuromorph *Apsaravis* (Norell and Clarke, 2001; Clarke and Norell, 2002). The Tögrögiin Shiree locality of the Campanian Djadokhta Formation has yielded the enantiornithine *Elsornis*, which is represented by a partial articulated skeleton (Chiappe et al., 2007). Both the Barun Goyot and Djadokhta formations have also produced nests probably belonging to enantiornithines (Varricchio and Barta, 2015). Fragmentary hesperornithiforms including *Brodavis mongolensis* and *Judinornis* and the enantiornithine *Gurilynia* were collected in the Maastrichtian Nemegt Formation (Kurochkin, 2000; Clarke and Norell, 2004).

The Oxfordian-aged anchiornithines were first described as early birds and this phylogenetic placement has been recovered by several independent studies (Xu et al., 2008, 2011a; Agnolín and Novas, 2013; Godefroit et al., 2013a; 2013b). However, until consensus is reached (see Pittman, et al., chapter 1), *Archaeopteryx* of Germany remains the oldest unequivocal bird (see Europe section below).

AUSTRALIA: Fragmentary enantiornithines are reported from the Barremian-Aptian Wontaggi Formation (Close et al., 2009) and the Albian Toolebuc and Griman Creek formations (Molnar, 1986; Kurochkin and Molnar, 1997; Molnar, 1998; 1999). Contra Molnar (1999), reports of ornithuromorphs are likely misidentified enantiornithines (J. O'C., personal obs.).

EUROPE: Outside China, the greatest concentration of exceptionally well-preserved specimens of nonavian avialans occurs in the Early Cretaceous (Barremian) Las Hoyas lagerstätte (La Huerquina Formation) near Cuenca, Spain. These deposits have produced half a dozen enantiornithines, several of which represent distinct taxa (*Concornis*, *Eoalulavis*, and *Iberomesornis*), with most preserving at least some soft tissue (Sanz et al., 2002; Navalón et al., 2015). A pellet containing several juveniles and a perinate has also been collected (Sanz et al., 2001; Knoll et al., 2018). Two enantiornithine specimens (including the holotype of *Noguerornis*) have also been collected from the lithographic limestones of the Hauterivian-Barremian La Pedrera de Rúbies Formation near Montsec, Spain (Lacasa-Ruiz, 1988; Sanz et al., 1997; Szwedo and Ansoerge, 2015). Fragmentary enantiornithines including the holotype of *Martinavis cruzyensis* and the ornithothoracine *Gargantuavis* have been collected from late Campanian–early Maastrichtian deposits in southern France (Buffetaut et al., 1995; Buffetaut, 1998; Walker et al., 2007). In Romania, an enantiornithine nesting colony that also preserved bones has been found in the Maastrichtian Sebeş Formation (Dyke et al., 2012), and an enantiornithine humerus has been described from Upper Cretaceous deposits in the

Hateg Basin (Wang et al., 2011). Several enantiornithine elements have been described from the Santonian Csehbánya Formation in Hungary, including a tarsometatarsus used to erect the taxon *Bauxitornis* (Dyke and Ösi, 2010). A cranial endocast inferred to be avialan (*Cerebavis*) was collected from Cenomanian deposits in European Russia (Kurochkin et al., 2007). Fragmentary remains of Hesperornithiformes are known from Campanian marine deposits of southern Sweden (Rees and Lindgren, 2005). A historically important specimen is *Enaliornis* from the Cambridge Greensand member of the West Melbury Marly Chalk Formation of south-east England. This specimen was one of the first Mesozoic avialans ever collected and is now considered a hesperornithomorph (Elzanowski and Galton, 1991).

SOUTH AMERICA: In 1981 the Enantiornithes was named from a large collection of isolated elements found in the Maastrichtian Lecho Formation of northwestern Argentina (Walker, 1981). Several taxa have been named, consisting of a few elements or less (e.g., *Enantiornis*, *Elbretornis*, and *Yungavolucris*) (Chiappe, 1993; Walker and Dyke, 2010). The partial skeletons of the avisaurid enantiornithine *Neuquenornis* (Chiappe and Calvo, 1994) and the early-diverging ornithuromorph *Patagopteryx* (Alvarenga and Bonaparte, 1992) were found soon after in the Santonian Bajo de la Carpa Formation of central Argentina, which has also yielded nests with embryonic remains (Schweitzer et al., 2002; Fernández et al., 2013). Fragmentary enantiornithines have been reported in the Campanian Las Curtiembres Formation of northwestern Argentina (*Intiornis*) (Novas et al., 2010) and the Upper Cretaceous La Colonia Formation of southern Argentina (Lawver et al., 2011). Fragmentary ornithuromorph taxa have also been published from the Campanian-Maastrichtian Allen Formation (*Limenavis*) (Clarke and Chiappe, 2001) and the similarly aged Los Alamitos Formation (*Alamitornis*) (Agnolín and Martinelli, 2009), both located in central Argentina. A partial ornithuromorph coracoid was described from the Turonian-Coniacian Portezu-

elo Formation, also in central Argentina (Agnolín et al., 2006). In Brazil several important enantiornithines have been described from the Lower Cretaceous Crato Formation (Naish et al., 2007; de Souza Carvalho et al., 2015). More recently a diverse but as yet undescribed enantiornithine avifauna is being excavated in the Campanian-Maastrichtian Bauru Group (Nava et al., 2015). *Neogaeornis*, from the Campanian-Maastrichtian Quiriquina Formation of Chile (Lambrech, 1929), was identified as an early representative of Gaviiformes (loons) (Olson, 1992); however, it is based on a single tarsometatarsus and its identification as a crown bird is highly uncertain (Mayr, 2009, 2016).

NORTH AMERICA: Only Late Cretaceous birds have been collected in North America. *Alexornis* (Enantiornithes) from the Campanian Roja (La Bocana Roja) Formation in Baja California is the only specimen known from Mexico (Brodkorb, 1976). In the United States, fragmentary remains of enantiornithines have been collected in the Campanian Kaiparowits (*Mirarce*) and Two Medicine (*Gettyia*) formations (Atterholt et al., 2018), the Campanian Mooreville Chalk (*Halimornis*) (Chiappe et al., 2002), and the Cenomanian Woodbine Formation (*Flexomornis*) (Tykoski and Fiorillo, 2010). The Maastrichtian Hell Creek Formation has yielded fragmentary remains of enantiornithines (*Avisaurus*), indeterminate (non-hesperornithiform or ichthyornithiform) ornithurines, and hesperornithiforms (Longrich et al., 2011). Hesperornithiforms have also been collected from the late Coniacian-early Campanian Smoky Hill Chalk Member of the Niobrara Formation and the Campanian-Maastrichtian Pierre Shale (Bell and Chiappe, 2015). Numerous specimens of the ornithurine *Ichthyornis* have been collected from the Smoky Hill Chalk Member of the Niobrara Formation, with additional remains found in Turonian and Campanian deposits belonging to the Mancos Shale, Mooreville Chalk, and other formations (Clarke, 2004). The fragmentary ornithurines *Apatornis* and *Iaceornis* are also known from the Smoky Hill Chalk Member (Clarke, 2004). The Maastrichtian

Lance Formation has also yielded indeterminate ornithurine fragments (Longrich et al., 2011).

Fragmentary specimens of enantiornithines and ornithuromorphs have been collected across Canada, reported in the Campanian Northumberland Formation (Nanaimo Group, from which the Ornithurine *Maaqwi* is reported) (Morrison et al., 2005; McLachlan et al., 2017) and Cenomanian Ashville Formation (Tokaryk et al., 1997), the latter including the hesperornithiform *Pasquiaornis*. An enantiornithine fragment has been reported from the Campanian Dinosaur Park Formation (Buffetaut, 2010), and the Campanian Belly River Group has produced a fragmentary fauna consisting primarily of ornithurine birds (Longrich, 2009). Enantiornithines, indeterminate ornithurines, and hesperornithiform fragments are reported from the Maastrichtian Frenchman Formation (Longrich et al., 2011; Martin et al., 2012). Fragmentary *Ichthyornis*-like material has been reported from the Turonian Kaskapau Formation and Cenomanian Belle Fourche Formation (Clarke, 2004). From within the Canadian Arctic circle two species have been named: *Tingmiatornis*, a large ornithurine from Turonian age deposits (Bono et al., 2016) and *Canadaga*, a Maastrichtian hesperornithiform (Hou, 1999).

AFRICA: Avialan remains are yet to be discovered on the African continent although a large number of avialan bones have been collected from the Maastrichtian Maevarano Formation in nearby Madagascar, consisting of a diversity of enantiornithines (O'Connor and Forster, 2010) as well as the ornithuromorph, *Vorona* (Forster et al., 1996). *Rahonavis* was also described as an avialan from this formation, but although this was supported by some subsequent analyses (Agnolín and Novas, 2013; Cau, 2018; Novas et al., 2018), *Rahonavis* has also been recognized as a dromaeosaurid by several studies (Makovicky et al., 2005; Turner et al., 2012; Pei et al., in press).

ANTARCTICA: Latest Cretaceous deposits in Antarctica have produced some avialan remains, including the ornithurines *Vegavis* (Noriega and Tambussi 1995; Clarke et al. 2005), *Polarornis*

(Chatterjee, 2002) and *Antarcticavis* (probable ornithurine; Cordes-Person et al., 2020). Preliminary descriptions have placed *Vegavis* in the Anatoidea (Clarke et al., 2005) and some cladistic analyses suggest this taxon may be an early stem-group anseriform (Agnolín et al., 2017; Worthy et al., 2017). However, others have argued that *Vegavis* falls outside the avian crown clade (Wang et al., 2014b; Mayr et al., 2018), so its status as a crown bird is contentious. *Polarornis* was described as a stem loon (Chatterjee, 2002), but the only available images of this specimen appear to be heavily reconstructed making any interpretations equivocal. *Antarcticavis* was described as an ornithuromorph that probably belongs to the Ornithurae (Cordes-Person, 2020). Some undescribed *Ichthyornis*-like material is also known (Zinsmeister, 1985).

EARLY FOSSIL RECORD OF CROWN BIRDS (AVES)

Much of our contemporary understanding of crown-bird macroevolution has come from large-scale molecular phylogenies, which are ever improving in light of the development of new sequencing technologies and analytical methods (Hackett et al., 2008; McCormack et al., 2013; Jarvis et al., 2014; Prum et al., 2015; Reddy et al., 2017; Kimball et al., 2019; see also Pittman, et al., chapter 1). However, the only direct evidence of crown-bird evolutionary history comes from the fossil record, placing a premium on the discovery of early fossil representatives of crown birds that can shed light on when (see Field et al.'s divergence time section in chapter 5) and where (see Ding et al.'s biogeography section, chapter 4) the major groups of crown birds originated.

Unfortunately, the earliest fossil record of crown birds is extremely sparse, as is the Late Cretaceous fossil record of the crownwardmost portion of the avialan stem group (fig. 1; table 5) (Mayr, 2016). The crownwardmost stem avialans known include classic Mesozoic taxa such as *Ichthyornithiformes* and *Hesperornithiformes*

(Marsh, 1880), both of which persisted into the terminal Maastrichtian (Dyke et al., 2002; Longrich et al., 2011; Dumont et al., 2016), as well as more poorly known marine taxa such as *Iaceornis* (Clarke, 2004), and the single specimen of the Campanian *Apsaravis* (Clarke and Norell, 2002), whose phylogenetic position is controversial and often unstable in recent analyses (Field et al., 2018a). Recent work on the anatomy and phylogeny of this portion of the avialan tree has revealed a multitude of anatomical plesiomorphies exhibited by these closest Mesozoic relatives of crown birds (e.g., in *Ichthyornis*, a strongly anteriorly projecting squamosal, primitive beak lacking a palatal shelf, extensive dentition throughout the upper and lower jaws; Field et al., 2018b). Clearly, our current knowledge of the closest-known stem-group relatives of crown birds must be incomplete: a range of hierarchically interrelated taxa crownward of Hesperornithiformes and Ichthyornithiformes must have existed, and their discovery will be necessary to document the acquisition of a fully crownlike avian skeleton. It is hoped that the coming years will reveal such fossils and clarify how, when, and where crown birds themselves originated.

The latest Cretaceous fossil record of crown birds is even more sparse. Total-clade loons (Gaviiformes) were long regarded as present in the latest Cretaceous on the basis of *Neogaeornis* (Olson, 1992) and *Polarornis* (Chatterjee, 2002), although the status of these taxa as gaviiforms is dubious (Mayr, 2016) and at least *Polarornis* may be closely related to, if not synonymous with, *Vegavis* (Clarke et al., 2016). Until recently, only one comparatively well-supported crown-bird fossil has emerged from the entirety of the Mesozoic and, even then, from within approximately one million years of the end-Cretaceous mass-extinction event (Noriega and Tambussi, 1995; Clarke et al., 2005). The phylogenetic position of this taxon, *Vegavis iaai*, is debated (Agnolín et al., 2017; Mayr et al., 2018), with recent analyses recovering it as an early stem-group anseriform (Worthy et al., 2017) and others questioning its validity as a crown bird (Mayr et al., 2018).

Moreover, the stem lineages of the deepest clades within crown birds—Palaeognathae and Neognathae—are entirely unknown. This lack of stem palaeognaths and stem neognaths, which must have been present in the latest Cretaceous, has contributed to ongoing uncertainty regarding the antiquity of the avian crown group (Cracraft et al., 2015; Ksepka and Phillips, 2015; Mitchell et al., 2015; Prum et al., 2015; Berv and Field, 2018; see also Field et al.'s molecular rate variation section in chapter 5), precluding the application of a hard-minimum age for the avian root in node-dating analyses. Recently, the oldest clear evidence of a crown neognath was described from the Maastrichtian of Belgium (Field et al., 2020), and appears to represent an early galloanseran. This taxon, *Asteriornis maastrichtensis*, suggests that even earlier crown bird fossils are likely to be discovered from sediments in the Northern Hemisphere.

Although definitive representatives of Aves are exceedingly rare in Mesozoic sediments, isolated, often fragmentary remains from the latest Maastrichtian of North America (Hope, 2002; Longrich et al., 2011) may derive from crown-group birds. The only phylogenetic analysis to test the position of these specimens recovered several of them in a large polytomy with Aves and *Iaceornis*, crownward of Ichthyornithiformes and Hesperornithiformes. However, given the substantial presumed phylogenetic distance between these stem birds and Aves as discussed above, these isolated remains may instead be more likely to derive from the crownwardmost portion of the avian stem. With luck, continued exploration in the Late Cretaceous of North America may reveal more complete remains of these fragmentary avialans, and help clarify their phylogenetic affinities.

Beyond the Mesozoic, the earliest Paleocene fossil record of crown birds is also extremely sparse. Bird-producing lagerstätten comparable to the famous Eocene localities of Messel, Green River, and Fur have not been discovered in Paleocene sediments. Considering that a major diversification of crown birds, including Neoaves

(which comprises >95% of extant avialan diversity) may have taken place within a narrow temporal window during the Paleocene (see Field et al.'s molecular rate variation section in chapter 5), avian fossils from this interval have strong potential to reveal important insights into the pattern and timing of the extant avian radiation, and will help shed light on the ancestral morphologies and biogeography of major avian lineages. With the exception of a handful of important fossil discoveries providing divergence time constraints across the bird tree of life (e.g., the earliest stem penguin *Waimanu*, the possible stem tropicbird *Australornis*, the earliest pelagornithid *Protodontopteryx* from New Zealand, as well as the stem mousebird *Tsidiyazhi* from the southwestern United States (Slack et al., 2006; Mayr and Scofield, 2016; Ksepka et al., 2017; Mayr et al., 2019)), the early Paleocene avialan fossil record remains greatly undersampled with respect to subsequent epochs.

Importantly, the oldest of these discoveries, the stem-lineage mousebird *Tsidiyazhi abini* from New Mexico (Ksepka et al., 2017) is approximately 62.5 million years old—dating to more than three million years after the end-Cretaceous mass extinction. Where are the diagnosable bird fossils closer in age to the K–Pg boundary? The Chicxulub asteroid impact 66.02 million years ago is hypothesized to have devastated avialan population sizes (Robertson et al., 2004; Field, 2017; Field et al., 2018a), which may help explain the rarity of birds in the lowermost Paleocene. Additionally, avialan body sizes are hypothesized to have been reduced in the wake of the K–Pg mass extinction event (Berv and Field, 2018), potentially adding a taphonomic bias against the preservation and discovery of birds from this time interval.

Furthermore, the early Cenozoic crown-bird fossil record is strongly biased towards remains from the northern hemisphere. Although considerable dissent regarding the biogeographic origins of crown birds and the major avian subclades is ongoing (Mayr, 2009; Claramunt and Cracraft, 2015; Cracraft and Claramunt, 2017;

Mayr, 2017; Field and Hsiang, 2018; Saupe et al., 2019; see also Ding et al.'s biogeography section in chapter 4), analytical reconstructions have supported a scenario in which many lineages of crown birds originated in the southern hemisphere—specifically, South America and west Antarctica—and expanded northward following the end-Cretaceous mass extinction (Claramunt and Cracraft, 2015). If this scenario is accurate, then the scarcity of crown-bird fossils from the latest Cretaceous and earliest Paleocene may be at least partly explained by sparse sampling from relevant geographic regions (Claramunt and Cracraft, 2015).

DISCUSSION

The pennaraptoran fossil record has expanded phenomenally since they were first discovered in the mid 19th century, bringing about huge leaps in our understanding of the group. Archaeopterygiformes, anchiornithines, and scansoriopterygids tell us that the clade had originated by the Late Jurassic, with other pennaraptoran groups either unknown at that time as in oviraptorosaurians (Osmólska et al., 2004) or based on fragmentary specimens as in dromaeosaurids (Heckert and Foster, 2011). The anchiornithines are the best represented group of Jurassic paravians after Archaeopterygiformes, but their status as birds, troodontids, early-diverging deinonychosaurs, or sister to Paraves remains controversial, even though consensus for their near-avialan status is emerging (Pei et al., in press). The search for Jurassic-aged pennaraptorans should therefore remain a priority moving forward, both from lagerstätten that have recovered them already, like the Solnhofen Limestone of southern Germany and the Tiaojishan Formation of northern China, and from new localities. Although Konservat Lagerstätten are few and far between, it is heartening to note that new exposures containing Jehol and Yanliao biota fossils are cropping up across northern China with increasing collection

efforts. They are also present, but undersampled in Mongolia, where only a few feathers have been excavated (Kurochkin, 2000). In general, the uneven nature of the pennaraptoran record, which is biased toward key formations like the Yixian and Djadokhta, needs to be better counterbalanced to ensure our understanding of this group is not being biased by potential local or regional factors. This is easier said than done, but a healthy awareness of this issue will at least help to minimize any chance of conflating separate evolutionary signals.

OVIPTOROSAURIA: Tooth-bearing early-diverging oviraptorosaurians like *Incisivosaurus* and *Caudipteryx* remain rare and oviraptorosaurians with more ancestral theropod body plans are expected in the Late Jurassic, but have not been found. This is potentially the most important priority for future work because it should shed more light on the evolution of the beak and the changes involved in skull specialization. Future finds of later-diverging taxa that could better characterize the caenagnathid and oviraptorid split would also be very useful, especially as early-diverging caenagnathids are not known from complete cranial material and include giant, evidently specialized forms like *Gigantoraptor* (Ma et al., 2017). Oviraptorosaurians and Scansoriopterygidae are currently exclusively Laurasian groups, but experience in other pennaraptoran groups, including those with a longer collection history, suggests that future Gondwanan finds are possible. Thus, efforts to seek such material whether in the field or in existing collections could be fruitful.

SCANSORIOPTERYGIDAE: Scansoriopterygids are among the least known early-diverging pennaraptorans because of their representation by a small pool of specimens. More specimens, particularly from adult growth stages, will be critical in solidifying the taxonomic status of the group and uncovering key events in their evolutionary history as well as their correct phylogenetic position. *Yi* preserves feathered, membranous wings that appear to be an alternative dinosaurian volant strategy to feathered, muscular wings (Xu

et al., 2015a; Wang et al., 2019a). This astonishing discovery warrants extensive further study that will require additional soft-tissue-preserving specimens. Further discoveries are also needed to determine whether scansoriopterygids were a short-lived experiment or they persisted to the terminal Cretaceous like oviraptorosaurians.

DROMAEOSAURIDAE: Dromaeosaurids are among the most widely distributed pennaraptorans after birds. This, coupled with their generally more ground-based lifestyle compared with early birds (early birds could probably cross barriers more easily), provides the best opportunity to understand the impact of Mesozoic biogeography on pennaraptoran evolution. This is examined in the next chapter on coelurosaurian biogeography. Encouraging potential for further finds in underrepresented parts of Gondwana, e.g., the Wadi Milk Formation of Sudan and James Ross Island, Antarctica, underscores the importance of Dromaeosauridae in understanding pennaraptoran biogeography more generally. The reconstruction of flight capabilities in *Microraptor* makes microraptorines an obvious subclade to focus more attention on (Pei et al., in press). However, the unenlagiine *Rahonavis* also has similar flight potential, and so this clade should also be studied more intensively, especially given that it represents the only detection of nonavian flight potential in Gondwana (Pei et al., in press).

TROODONTIDAE: Troodontids are thought to be a Laurasian clade, but the discovery of a possible troodontid tooth from the Kallamedu Formation of India (Goswami et al., 2013) justifies further search efforts to confirm this Gondwanan record and explore biogeographic differences among troodontids in more detail (see Ding et al., chapter 4). The taxonomic status of Anchiornithinae should be another study priority and will benefit from Jurassic nonavian paravian finds, particularly from the Solnhofen and Tiaojishan as well as the sparse Early Cretaceous of North America. The discovery of more troodontid specimens with transitional anatomical features between

longer-armed earlier-diverging forms and shorter-armed later-diverging forms (e.g. *Sinusonasus* and *Jianianhualong* (Xu et al., 2017)) would also shed more light on troodontid character evolution.

AVIALAE: Despite the incredible number of new specimens unearthed within the past four decades, there remain numerous major gaps in the fossil record of stem avialans. There is a 20 million year gap in the record between the 155–150 Ma *Archaeopteryx* and the beginning of the Jehol avifauna captured by the 131 Ma Huajiying Formation. Specimens from this 20 Ma gap are critical to understanding early skeletal transitions such as the evolution of the pygostyle and the evolution of the first avialan edentulous beak, let alone a host of other features like solidification of the pectoral girdle and plumage specialization. Notably, non-ornithothoracines are almost exclusively found in the Solnhofen limestones (*Archaeopterygiformes*) and in the Early Cretaceous Jehol lagerstätten, which may suggest early-diverging lineages went extinct fairly early, being unable to compete with ornithothoracines. No Mesozoic avialan has been collected from the African continent, despite its great potential (although remains are known from Madagascar). Globally, the Early Cretaceous record is far stronger than the Late Cretaceous record (mostly due to the Jehol Biota), but there are currently no Early Cretaceous avialan fossils known from North America. A major gap in the avialan fossil record consists of the conspicuous absence of fossils documenting the crownwardmost portion of the avian stem lineage, i.e., crownward of the Late Cretaceous ornithurine groups *Hesperornithiformes*, *Ichthyornithiformes*, and *Iaceornis*. Similarly, the earliest stages of crown-bird evolution are poorly known at present, and many of the greatest questions regarding the early evolutionary history of Aves will be resolved by new discoveries of crown birds from the Late Cretaceous and early Paleogene, including questions related to avialan survivorship, ecological selec-

tivity, and recovery across the end-Cretaceous mass extinction. It is hoped that the coming years will yield avialan fossils filling the critical temporal and geographic gaps discussed above—and in the process, shed important new light on the Mesozoic and Cenozoic evolutionary history of avialan pennaraptorans.

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