

Chapter 4

The Biogeography of Coelurosaurian Theropods and Its Impact on Their Evolutionary History

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ABSTRACT

The Coelurosauria are a group of mostly feathered theropods that gave rise to birds, the only dinosaurs that survived the Cretaceous-Paleogene extinction event and are still found today. Between their first appearance in the Middle Jurassic up to the end Cretaceous, coelurosaurians were party to dramatic geographic changes on the Earth's surface, including the breakup of the supercontinent Pangaea, and the formation of the Atlantic Ocean. These plate tectonic events are thought to have caused vicariance or dispersal of coelurosaurian faunas, influencing their evolution. Unfortunately, few coelurosaurian biogeographic hypotheses have been supported by quantitative evidence. Here, we report the first, broadly sampled quantitative analysis of coelurosaurian biogeography using the likelihood-based package BioGeoBEARS. Mesozoic geographic configurations and changes are reconstructed and employed as constraints in this analysis, including their associated uncertainties. We use a comprehensive time-calibrated coelurosaurian evolutionary tree produced from the Theropod Working Group phylogenetic data matrix. Six biogeographic models in the BioGeoBEARS package with different assumptions about the evolution of spatial distributions are tested against geographic constraints. Our results statistically favor the DIVALIKE+J and DEC+J models, which allow vicariance and founder events, supporting continental vicariance as an important factor in coelurosaurian evolution. Ancestral range estimation indicates frequent dispersal events via the Apulian route (connecting Europe and Africa during the Early Cretaceous) and the Bering land bridge (connecting North America and Asia during the Late Cretaceous). These quantitative results are consistent with commonly inferred Mesozoic dinosaurian dispersals and continental-fragmentation-induced vicariance events. In addition, we recognize the importance of Europe as a dispersal center and gateway in the Early Cretaceous, as well as other vicariance events such as those triggered by the disappearance of land bridges.

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INTRODUCTION

Coelurosauria is a clade of later-diverging theropod dinosaurians that includes Tyrannosauroidae, Compsognathidae, Ornithomimosauria, Alvarezsauroidae, Therizinosauria, Oviraptorosauria, Dromaeosauridae, Troodontidae, and Avialae (Brusatte et al., 2014). A large portion of coelurosaurians were feathered, while some of them, mainly members of Avialae, acquired powered flight ability (Xu et al., 2014). Most coelurosaurian clades lived from the Middle Jurassic to the end of the Cretaceous, with only a subset of avialan taxa (Aves) surviving the Cretaceous-Paleogene (K-Pg) extinction event (Xu et al., 2014). During the late Mesozoic, coelurosaurians and other dinosaurians lived through dramatic geographic changes (Upchurch et al., 2002): plate tectonic activity caused continents to break apart to form new oceans and seas, produced intermittent reconnections, and prompted fluctuations in sea level that further modified paleogeographic relationships (Condie, 1997). These geographic configurations and changes are presumed to have affected coelurosaurian populations and faunas, impacting their pattern and tempo of evolution (Benton and Harper, 2013). Evaluating this impact is crucial if we are to fully understand the most significant events in coelurosaurian evolution, including the acquisitions of herbivory and early theropod flight.

Biogeographic studies focus on the geography-dependent processes that lead to alterations in faunal distributions and speciation (Benton and Harper, 2013). Four of the most fundamental biogeographic processes are: (1) *dispersal*, when a fauna expands its distribution range; (2) *regional extinction*, when the distribution shrinks; (3) *sympatry*, when speciation happens within the ancestral distribution range of the fauna; and (4) *vicariance*, when speciation takes place due to the separation of two populations by a geographic barrier (Serenó, 1999a; Upchurch et al., 2002; Sanmartín and Ronquist, 2004). These processes play important roles in organismal evolution and are sensitive to geographic conditions.

Numerous biogeographic hypotheses have been proposed for clades within Coelurosauria, though the vast majority of these are narratives (by the definition of Ball (1975): 409) because they tend to read the fossil record literally. A few studies (e.g., Loewen et al. 2013) have applied quantitative phylogenetic biogeographic analyses to groups such as Tyrannosauroidae, but the majority of coelurosaurian subclades, and the group as a whole, have not been investigated using such approaches. At present, therefore, much of our knowledge of coelurosaurian biogeographic history comes from studies of Dinosauria as a whole (e.g., Bonaparte 1986; Upchurch et al. 2002; O'Donovan et al. 2018). To address these deficits, we perform the first quantitative biogeographic analysis focused on the Coelurosauria as a whole.

MESOZOIC PALEO GEOGRAPHY

The paleogeography of Pangaea provides an important backdrop to the evolution of coelurosaurians, and information on this topic is required in order to support the geographic constraints we apply in our biogeographic analyses. Below, therefore, we briefly outline key aspects of Mesozoic paleogeography.

The Mesozoic witnessed the breakup of the supercontinent Pangaea and the establishment of global geography close to the modern arrangement (Scotese, 2001). However, narrow land bridges connecting isolated landmasses did appear during short time intervals, and shallow epicontinental seas existed throughout the Mesozoic, especially within Laurasian landmasses (Poropat et al., 2016)

During the early Mesozoic all continents were joined together to form Pangaea, although the Laurasia-Gondwana connection was present only between North America and (Africa + South America) (Smith et al., 2004). The breakup of Pangaea began during the Middle Jurassic, starting with the separation of North America from South America, together with the opening of the Northern Atlantic Ocean (Bardet et al.,

2014). The complete separation of Laurasia and Gondwana dates back to the Kimmeridgian stage of the Late Jurassic (Gaina et al., 2013). Rifting and sea floor spreading among Africa, Indo-Madagascar, and Antarctica began later, during the Tithonian (Seton et al., 2012). The Turgai Sea existed between Asia and Europe throughout the late Mesozoic (especially the Late Cretaceous), although intermittent land connections occurred because of sea level fluctuations (Baraboshkin et al., 2003; Smith et al., 2004). During the Late Jurassic and earliest Cretaceous, Gondwana gradually separated into two large continents comprising South America + Africa (Samafrica) and Antarctica + Indo-Madagascar + Australia (East Gondwana) (Eagles and König, 2008). However, the sequence and timing of the breakup of Gondwana remain controversial (e.g., Sereno et al., 2004; Krause et al., 2006; Krause et al., 2007; Upchurch, 2008; Ali and Krause, 2011) and several workers have proposed that South America and Antarctica maintained a contact via Patagonia and the West Antarctic Peninsula throughout some or all of the Cretaceous (see review in Poropat et al. (2016)). During the earliest Cretaceous, the Apulian route was established (Zarcone et al., 2010). This connection between southwestern Europe and northwestern Africa was the first between Laurasia and Gondwana after the breakup of Pangaea (Ezcurra and Agnolín, 2012). The land connection between eastern North America and western Europe finally disappeared with the full establishment of the North Atlantic Ocean in the Barremian or Aptian (Seton et al., 2012). Later, in the late Aptian and Albian stages, the Bering land bridge connected northeastern Asia and northwestern North America for the first time (Plafker and Berg, 1994). This land bridge was probably absent during the Cenomanian-Santonian, but was potentially reestablished in the late Campanian and perhaps the Maastrichtian (Brikiatis, 2014). The Western Interior Seaway separating North America into eastern and western portions (known as Appalachia and Laramidia respectively) was present throughout much of

the Late Cretaceous until a possible reconnection during the Maastrichtian (Smith et al., 2004; Farke and Phillips, 2017). Africa and South America separated from each other at the end of the Albian Stage, after the isolation of Indo-Madagascar during the Aptian Stage (Eagles and König, 2008). India separated from Madagascar during the latest Cretaceous (Plafker and Berg, 1994). By the end of the Cretaceous, global geography had a configuration that resembled the modern one, though Africa and India did not collide with Eurasia, and the Patagonia-Antarctica connection might not have been severed, until the Cenozoic (Matthews et al., 2016).

GEOGRAPHIC AND TEMPORAL DISTRIBUTION OF COELUROSAURIANS

Most known fossil coelurosaurians are from Laurasia (1083 occurrences recorded at the time of writing in the Paleobiology Database, <https://paleobiodb.org/>), with only a few occurrences in Gondwana (59 recorded in the Paleobiology Database). Currently, the earliest-known coelurosaurians are the proceratosaurids *Proceratosaurus* (von Huene, 1926) and *Kileskus* (Averianov et al., 2010) from the Bathonian stage of the Middle Jurassic of southern England and central Russia respectively. The earliest-diverging coelurosaurians are *Bicentennaria* from Argentina (Novas et al., 2012), *Coelurus* from North America (Marsh, 1879), and *Zuolong* from China (Choiniere et al., 2010a). The occurrences of tyrannosauroids during the Middle Jurassic and early-diverging paravians during the early Late Jurassic (e.g., *Anchiornis*) imply that major lineages of coelurosaurians were established by the Middle to Late Jurassic (Rauhut et al., 2010; Choiniere et al., 2012). Some authors have argued that the clades, including Compsognathidae, Tyrannosauroidea, and Maniraptoriformes, probably originated during or even before the Middle Jurassic (Rauhut et al., 2010), and so predate the separation of Laurasia and Gondwana. The currently known geographic and temporal distributions of the major coelurosaurian clades Tyrannosauroidea, Compsognathidae, Ornitho-

mimosauria, Alvarezsaurioidea, Therizinosauria, Oviraptorosauria, Dromaeosauridae, Troodontidae, and Avialae are discussed in more detail below.

TYRANNOSAUROIDEA: Tyrannosauroids include the infamous *Tyrannosaurus rex* and its closest relatives (Brusatte et al., 2010). Early-diverging Jurassic tyrannosauroids had a wide distribution in Laurasia as indicated by *Guanlong* from Asia (Xu et al., 2006), *Juratyran* from Europe (Brusatte and Benson, 2013), and *Stokesosaurus* from North America (Benson, 2008). It is inferred that dispersal events within Laurasian landmasses occurred during that period of time (Rauhut et al., 2010). On the other hand, tyrannosaurids are known mostly from the Late Cretaceous of Asia and western North America (Brusatte et al., 2010). The existence of closely related taxa in both Asia and western North America just before the end of the Cretaceous, as in other coelurosaurian clades, may suggest faunal exchange events between these landmasses at that time (Brusatte et al., 2010). Traditionally, it was thought that tyrannosauroids were restricted to Laurasian landmasses, including North America, Europe, and Asia, but Gondwanan material challenges this (Benson et al., 2010). The Australian occurrence of a possible tyrannosauroid is inferred based on a late Early Cretaceous pubis described in 2010 (Benson et al.), although the material's affinity to megaraptorids was proposed later (Novas et al., 2013). Some authors (Novas et al., 2013; Porfiri et al., 2014, 2018) put megaraptorids within Tyrannosauroidea, which may imply a wider distribution of the clade within Gondwanan landmasses.

COMPSOGNATHIDAE: Compsognathids are comparatively small early-diverging coelurosaurians known from the Late Jurassic to Early Cretaceous (Hwang et al., 2004). Laurasian compsognathids occur in North America (Osborn, 1903), Europe (Göhlich and Chiappe, 2006), and Asia (Hwang et al., 2004), but only one Gondwanan taxon, *Mirischia*, from the Albian of South America is known (Naish et al., 2004). Since *Mirischia* is the youngest and latest-

diverging compsognathid, a dispersal event from Laurasia to Gondwana seems likely, most probably from Europe to South America, via Africa (Naish et al., 2004). If this in fact occurred, later-diverging compsognathids are expected to be found in Africa in the future.

ORNITHOMIMOSAURIA: The slender "ostrich-like" ornithomimosaurians are known only from the Cretaceous period (Xu et al., 2011a). Ornithomimosaurians are found in all Laurasian landmasses, with most frequent occurrences in Asia (Xu et al., 2011a). *Nqwebasaurus* from South Africa is the earliest-diverging ornithomimosaurian and also the only one from Gondwana (De Klerk et al., 2000; Choiniere et al., 2012). Given the close relationship between *Nqwebasaurus* and early-diverging Laurasian ornithomimosaurians, the clade is inferred to have achieved a wide distribution before the breakup of Pangaea (Allain et al., 2014). The Late Cretaceous North American ornithomimids, including *Ornithomimus* and *Struthiomimus*, form a monophyletic group (Xu et al., 2011a). This phylogenetic and geographic pattern has been explained by a single dispersal event from Asia to North America via the Bering land bridge during the latest Cretaceous (Ji et al., 2003; Liyong et al., 2012).

ALVAREZSAUROIDEA: Alvarezsauroids are known for their small, later-diverging forms that have especially large first fingers (Xu et al., 2011b). Until recently, alvarezsauroids were known only from the Late Cretaceous, including earlier-diverging forms from South America (e.g., *Alvarezsaurus*: Bonaparte 1991) and later-diverging forms from Asia and North America (e.g., *Mononykus*: Altangerel et al., 1993; and *Albertonykus*: Longrich and Currie, 2009a). This led to a South American origin being proposed for the clade (Longrich and Currie, 2009a). The discovery of the early-diverging alvarezsauroid *Haplocheirus* from the Late Jurassic of China overturned this origin hypothesis (Choiniere et al., 2010b). On the basis of a quantitative analysis (Xu et al., 2011b), it was later proposed that if alvarezsauroids originated in central Asia

shortly before the breakup of Pangea, a dispersal from Asia to South America probably occurred before the Late Cretaceous, most likely via Europe and Africa. This dispersal hypothesis is also supported by two recently discovered Early Cretaceous alvarezsaurids from China (Xu et al., 2018a). A distal tibiotarsus from Romania is the only suspected record of the group in Europe (Naish and Dyke, 2004), and no African records are yet known. The dispersal of Patagonian alvarezsaurids to Asia has become a consensus recently (Xu et al., 2011b; Averianov and Sues, 2017). An additional Late Cretaceous dispersal event from Asia to North America has been inferred to explain the occurrence of the Late Cretaceous North American alvarezsaurid *Albertonykus*, which is closely related to Asian forms (Longrich and Currie, 2009a; Agnolín et al., 2012).

THERIZINOSAURIA: Therizinosaurians are a Cretaceous coelurosaurian clade that evolved herbivory, as also seen in Ornithomimosauria and Oviraptorosauria (Zanno and Makovicky, 2011). Most therizinosaurians are from the Cretaceous of Asia, especially China and Mongolia (Zanno, 2010). The earliest-diverging therizinosaurian, *Falcarius* from the Barremian of Utah, potentially indicates a vicariance event resulting from the separation of North America and Asia during the Early Cretaceous, or a dispersal of early-diverging therizinosaurians from North America to Asia via the controversial land connections proposed across the proto-Atlantic and Turgai Sea (Zanno, 2010). More fossil evidence, such as earlier and/or confirmed European records are required to address this issue further. The other non-Asian therizinosaurians are later-diverging forms from the early Late Cretaceous of North America (e.g., *Nothronychus*) whose ancestors potentially dispersed from Asia via the Bering land bridge during its establishment in the later stages of the Early Cretaceous (Kirkland and Wolfe, 2001; Zanno, 2010; Fiorillo and Adams, 2012). This dispersal event has received further support in the form of a potential therizinosaurian track found in Alaska, which is on

one side of the modern Bering Strait (Fiorillo and Adams, 2012; Fiorillo et al., 2018).

OVIRAPTOROSAURIA: Oviraptorosaurians are known for the preservation of evidence of their brooding behavior, and include later-diverging forms with short, elaborate skulls (Clark et al., 2001). Early-diverging oviraptorosaurians, including *Incisivosaurus*, caudipterygids and *Avimimus*, are solely Asian taxa that lived before the Late Cretaceous (Funston and Currie, 2016). Later-diverging taxa have parrotlike beaks, with or without bony skull crests, and have been divided into two subclades, Caenagnathidae and Oviraptoridae (Lü et al., 2015). Whereas known oviraptorids are restricted to Asia, the Caenagnathidae include both North American and Asian taxa (Xu et al., 2007; Funston and Currie, 2016). The presence of *Microvenator* in North America during the late Early Cretaceous is probably attributable to a dispersal event of early-diverging oviraptorosaurians from Asia via the Bering land bridge (Makovicky and Sues, 1998). Like several other coelurosaurian clades, the Late Cretaceous caenagnathids spread across Asia and North America (Funston and Currie, 2016).

DROMAEOSAURIDAE: Dromaeosaurids together with troodontids are the closest relatives of birds (Turner et al., 2012). Dromaeosaurids and troodontids have a hyperextendable second toe, while dromaeosaurids include taxa with rod-like tails comprising caudal vertebrae bound by elongated prezygapophyses (Turner et al., 2012). Dromaeosaurids have a broad geographic distribution across Laurasia and Gondwana throughout the Cretaceous (Turner et al., 2012). Laurasian taxa include early-diverging forms such as *Mahakala* (Turner et al., 2007) as well as later-diverging ones such as the renowned *Velociraptor* (Osborn et al., 1924). Early-diverging dromaeosaurids from Gondwanan landmasses, including *Rahonavis*, *Buitreraptor*, *Neuquenraptor*, and *Austroraptor*, form a single clade (Turner et al., 2012), but alternative relationships have been proposed (Novas et al., 2018). This may indicate a vicariance event due to the separation of Laurasia and Gondwana during the Middle

Jurassic (Makovicky et al., 2005; Novas and Pol, 2005). Antarctic occurrences of dromaeosaurids were also inferred from some pedal fossil fragments, which, together with other Gondwanan taxa, might imply a cosmopolitan distribution of the clade before the breakup of Pangea (Case et al., 2007). Although Jurassic teeth from Laurasia have been referred to Dromaeosauridae (Goodwin et al., 1999; Vullo et al., 2014), more substantial fossil evidence is needed to confirm this important early record. The establishment of the Bering land bridge during the later stages of the Early Cretaceous and again in the latest Cretaceous has been proposed as a potential explanation of the flourishing of the Velociraptorinae in Asia and the occurrences of microraptorines (*Hesperonychus*) in North America (Longrich and Currie, 2009b; Turner et al., 2012). Faunal exchange between Europe and Asia is also thought to have occurred during the Cretaceous based on the close relationship between the European dromaeosaurid *Balaur* and other Laurasian dromaeosaurids (Csiki et al., 2010; Brusatte et al., 2013). While flight capabilities have been proposed in the microraptorine *Microraptor*, these relate to flights of relatively short distances and probably did not affect the dispersal ability of dromaeosaurids over continental scales, but perhaps came into play in archipelago settings (Chatterjee and Templin, 2007).

TROODONTIDAE: Troodontids can be distinguished from dromaeosaurids by their numerous, closely packed teeth (Currie, 1987). Most of these close avialan relatives are from Asia (Lü et al., 2010). North American occurrences of the clade are restricted to *Geminiraptor* from the Early Cretaceous of Utah (Senter et al., 2010) and several later-diverging taxa from the Late Cretaceous (Leidy, 1856; Zanno et al., 2011). While the occurrence of later-diverging North American troodontids, represented by *Troodon*, can be attributed to a dispersal from Asia via the Bering land bridge during the Campanian and Maastrichtian stages of the Late Cretaceous (Dodson et al., 2004), *Geminiraptor* and abundant teeth referred to troodontids from Europe

indicate that multiple dispersal events might have happened within Laurasia even before the Late Cretaceous (Senter et al., 2010). The first reported Gondwanan troodontid was based on a tooth found in the Late Cretaceous of India, with this occurrence reflecting either a dispersal event from Laurasia, or a much wider distribution of the clade before the breakup of Pangea (Goswami et al., 2013). However, this identification should be considered as provisional. Even though troodontids have reasonably diagnostic teeth among theropods, this record would be more convincing with additional confirmatory skeletal material (Makovicky and Norell, 2004).

AVIALAE: This clade includes early birds and their modern descendants (Padian, 2004). By the Late Cretaceous avialans had achieved a global geographic distribution (Brocklehurst et al., 2012). The controversial Late Jurassic early-diverging paravians, the anchiornithines, proposed as both early-diverging birds and troodontids, were previously known only from Liaoning, China (Godefroit et al., 2013), but have recently been confirmed in Europe (*Ostromia*) (Foth and Rauhut, 2017). This might indicate a Late Jurassic dispersal event from Asia to Europe (Foth and Rauhut, 2017), given that *Archaeopteryx*, the most widely accepted oldest and earliest-diverging bird, is from Germany (Wellnhofer, 2009; Foth et al., 2014). The second oldest avifaunas are in the Early Cretaceous Hauteriverian-Barremian, during which the later-diverging clades Ornithuromorpha and Enantiornithes first appear, and are found in China (Zhou and Zhang, 2006) and in Mongolia (O'Connor and Zelenkov, 2013; Zelenkov and Averianov, 2016), where both clades are represented, as well as in Spain, where only enantiornithines have been found (Sanz, 1990; Sanz et al., 1995; Sanz et al., 1996). Until recently, the only recognized Cretaceous non-ornithothoracines were from the Hauteriverian-Aptian Jehol Biota (*Jeholornis* with its long bony tail and early-diverging pygostylians such as *Sapeornis* and *Confuciusornis*; Zhou and Zhang, 2006) although recently a non-ornithothoracine pygostylian was recovered from the

Aptian Kitadani Formation in Japan (Imai et al., 2019). Slightly younger deposits have yielded enantiornithines with an even wider distribution, present in Brazil (de Souza Carvalho et al., 2015) and Australia (Close et al., 2009), with the earliest hesperornithiforms preserved in late Albian deposits in the U.K. (Galton and Martin, 2002). During the Late Cretaceous, enantiornithines and later-diverging ornithuromorphs (ornithurines) had a global distribution, with records in Asia (e.g., *Gobipteryx*), South America (e.g., *Patagopteryx*), North America (e.g., *Ichthyornis*), Europe (e.g., *Baptornis*), Madagascar (*Vorona*), and Antarctica (*Vegavis*) (Elzanowski, 1974; Martin and Bonner, 1977; Alvarenga and Bonaparte, 1992; Forster et al., 1996; Clarke, 2004; Clarke et al., 2005).

Theropod flight appeared in the Middle or Late Jurassic at the latest (Xu et al., 2014), but the exact time(s) when powered flight was acquired is still under debate (Brocklehurst et al., 2012; Allen et al., 2013; Zheng et al., 2013; Xu et al., 2014; Dececchi et al., 2016). Modern avialan flight ability varies widely from species to species (Tobalske et al., 2003). Some extant birds are flightless, while others (like terns, e.g., *Sterna*) are capable of migrating across oceans (Tobalske et al., 2003). Given the general absence of functionally informative soft tissue evidence in avialan fossils, the dispersal ability of Mesozoic avialans is even harder to estimate than modern birds, providing major challenges to biogeographic analysis of this clade. However, the distribution of Late Cretaceous taxa such as the enantiornithine *Martinavis*, found in North and South America and in Europe (Walker et al., 2007), if in fact all specimens have been correctly referred to a single genus, may suggest at least some taxa were able to disperse long distances, and were unrestricted in their dispersal relative to nonavialan dinosaurians.

ANCESTRAL CROWN AVIALAN BIOGEOGRAPHY

The Mesozoic biogeographic history of coelurosaurians set the stage for early spatial distribution patterns of crown birds. Although the

stunning diversity of living birds and their easily observable nature would seem to simplify robust biogeographic inferences for their major extant subclades, deep crown bird biogeography has emerged as one of the most contentious issues in contemporary avialan macroevolution (Cracraft and Claramunt, 2017; Mayr, 2017; Field and Hsiang, 2018; Saupe et al., 2019).

Opposing views on crown bird historical biogeography relate to the observation that their early Cenozoic fossil record frequently reveals unforeseen complexity in the distributions of major clades. For example, many major clades of extant birds are restricted to vestiges of Gondwana (South America, Africa, and Australasia). As a result, quantitative ancestral biogeographic reconstructions invariably infer a Gondwanan origin for crown birds, and for many of the deepest nodes within the avian tree of life (fig. 5) (Cracraft, 2001; Claramunt and Cracraft, 2015). However, the earliest known fossil stem group representatives of many such “Gondwanan” clades derive from the Paleogene of the northern hemisphere, entirely outside the modern geographic distributions of their crown clades, casting doubt on what the ancestral geographic distributions for these groups really were. This holds true for clades currently restricted to Africa, such as Musophagiformes (Field and Hsiang, 2018) and Coliiformes (Houde and Olson, 1992; Mayr and Peters, 1998; Mayr, 2001; Zelenkov and Dyke, 2008; Ksepka and Clarke, 2009, 2010a); Madagascar, such as Leptosomiiformes (Mayr, 2002a, 2002b, 2008); South America, such as Cariamiformes (Mourer-Chauviré and Cheneval, 1983; Peters, 1995; Mourer-Chauviré, 1999; Mayr, 2000, 2002b; Mourer-Chauviré, 2006) and Opisthocomiformes (Mayr and De Pietri, 2014); and Australasia, such as Podargiformes (Nesbitt et al., 2011; Mayr, 2015). Indeed, the dynamic nature of crown bird biogeography is further evinced by the early Old World fossil record of clades presently restricted to the New World such as hummingbirds (Trochilidae) (Karhu, 1988; 1992; 1999; Mayr, 2003, 2004; Bochenski and Bochenski, 2008; Louchart et al.,

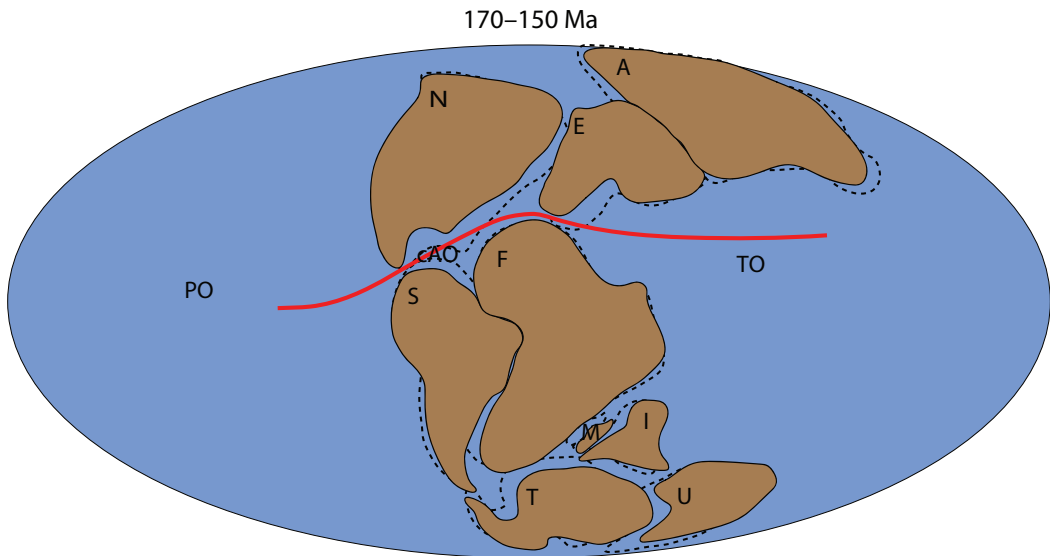


FIG. 1. Hypothesis 1, Laurasia-Gondwana vicariance event during the Late Jurassic. The separation between Laurasia and Gondwana was established in the Kimmeridgian Stage. The red line denotes the approximate position of the hypothesized biogeographical barrier: the central Atlantic Ocean (cAO) and Tethys Ocean (TO); Dotted lines denote paleogeography at 170 Ma, while solid lines denote it at 150 Ma. Paleomap after (Matthews et al., 2016). Abbreviations: A, Asia; cAO, central Atlantic Ocean; E, Europe; F, Africa; I, India; M, Madagascar; N, North America; PO, Pacific Ocean; S, South America; T, Antarctica; TO, Tethys Ocean; U, Australia.

2008), and the early New World fossil record of clades presently restricted to the Old World such as the roller + ground roller clade (Coraciiformes) (Mayr et al., 2004; Clarke et al., 2009; Ksepka and Clarke, 2010b).

Inclusion of early Cenozoic crown bird fossils in biogeographic analyses therefore has potential to erode confidence in erstwhile robust analytical reconstructions of crown bird historical biogeography (fig. 5). Moreover, as the evolutionary timescale of crown birds has come into clearer focus (Feduccia, 2014; Jarvis et al., 2014; Prum et al., 2015; Berv and Field, 2018; Field, et al., on timing the extant avian radiation, this volume), attempts to reconcile the “trans-Antarctic” distributions of many groups of crown birds through Gondwanan vicariance (Cracraft, 2001) have emerged as untenable since Gondwanan breakup was largely complete by the time crown birds arose (Mayr, 2009). Recently,

the hypothesis that large-scale climatic changes throughout the Cenozoic were implicated in driving major contractions in the distributions of “tropical” avian clades gained support from quantitative ecological and environmental modeling (Saupe et al., 2019). Additionally, the oldest crown-bird fossil yet identified, *Asteriornis*, comes from the latest Cretaceous of Belgium (Field et al., 2020). As a result, the true biogeographic origins of crown birds may be best regarded as uncertain at present; only future fossil discoveries of the earliest crown birds from the latest Cretaceous and earliest Cenozoic have potential to shed direct light on ancestral biogeographic distributions of crown birds (Field and Hsiang, 2018). As such, this article will not treat the biogeographic history of crown birds (the “living coelurosaurians”) and will instead focus solely on the Mesozoic biogeography of the major nonavian coelurosaurian clades.

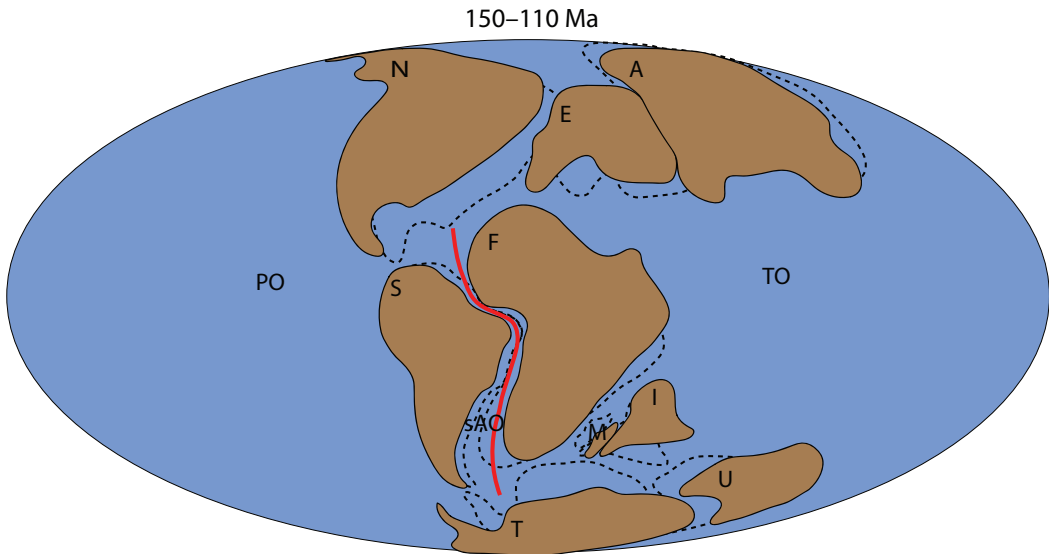


FIG. 2: Hypothesis 2, South America-Africa vicariance event during the late Early Cretaceous. The separation between South America and Africa was established in the Albian Stage. The red line denotes the approximate position of the hypothesized biogeographical barrier: the south Atlantic Ocean (sAO); Dotted lines denote paleogeography at 150 Ma, while solid lines denote it at 110 Ma. Paleomap after (Matthews et al., 2016). Abbreviations: A, Asia; E, Europe; F, Africa; I, India; M, Madagascar; N, North America; PO, Pacific Ocean; S, South America; sAO, south Atlantic Ocean; T, Antarctica; TO, Tethys Ocean; U, Australia.

MAJOR COELUROSAURIAN BIOGEOGRAPHIC HYPOTHESES

Besides the clade-level biogeographic hypotheses summarized above (see Geographic and Temporal Distribution of Coelurosaurians), analyses of dinosaurian biogeography as a whole, including coelurosaurians, have given varying emphasis to particular biogeographic processes, namely vicariance events, regional extinction events, and dispersal events.

Many authors attach particular importance to vicariance events because of the global continental fragmentation that occurred during the late Mesozoic (Serenó, 1999b; Upchurch et al., 2002; Choiniere et al., 2012). The Middle Jurassic occurrences of tyrannosauroids (e.g., *Kileskus* and *Proceratosaurus*) and Late Jurassic avialans (e.g., *Archaeopteryx* and possible avialan *Anchiornis* [also proposed as a troodontid]), are consistent with the idea that major coelurosaurian lineages were established at least before the Late

Jurassic (Rauhut et al., 2010; Choiniere et al., 2012). Together with several early-diverging coelurosaurian Gondwanan occurrences (e.g., *Bicentenaria* from South America and *Nqwebasaurus* from Africa), a geographically widespread distribution of coelurosaurian lineages before the breakup of Pangaea has been inferred, which makes vicariance possible upon separation of the continents (Choiniere et al., 2012). Proposed continental scale vicariance events include the Laurasia-Gondwana separation during the Late Jurassic (as shown in fig. 1: Hypothesis 1) and the final disconnection of South America and Africa during the Early Cretaceous (as shown in fig. 2: Hypothesis 2) (Serenó, 1999b). Possible vicariance-induced phylogenetic patterns have been identified in the distributions of maniraptoran lineages (Makovicky et al., 2005) and Ornithomimosauria (De Klerk et al., 2000). However, other workers have seen continental-scale vicariance as a rare occurrence, and argue that regional extinctions were primarily responsible for late Meso-

TABLE 1
Biogeographic hypotheses tested in this study

Number	Hypothesis
1	Laurasia-Gondwana vicariance event during the Kimmeridgian Stage of the Late Jurassic (Sereno, 1999a; Choiniere et al., 2012).
2	South America-Africa vicariance event during the Albian stage of the Early Cretaceous (Sereno, 1999a).
3	Late Early Cretaceous Europe-Africa faunal exchange via the Apulian route (Naish et al., 2004; Ezcurra and Agnolín, 2011; Dal Sasso et al., 2016). Modified to include dispersal events of both directions.
4	Cretaceous North America-Asia faunal exchanges relating to Early and Late Cretaceous establishments of the Bering land bridge (Sereno, 1999a; Dodson et al., 2004; Zanno, 2010).

zoic dinosaurian distributions. This latter view is often based on the observation that vicariancelike repeated area relationships can also be explained by regional extinction events and that many clades were widespread early in their evolutionary history and seem to become more geographically restricted subsequently (Sereno, 1997; 1999a; Barrett et al., 2011; Benson et al., 2012; Carrano et al., 2012). Most authors agree that intercontinental dispersal played a key role in creating dinosaurian (coelurosaurian) biogeographic patterns (Bonaparte, 1986; Sereno, 1999b; Brusatte et al., 2013; Dunhill et al., 2016). Such dispersal events are implied from the fossil record and phylogenetic relationships. Faunal dispersal events in both directions via the Early Cretaceous Apulian route were inferred by different authors: faunal assemblages from the Santana Formation of northern South America that are similar to Laurasian ones suggest possible Asian dinosaurian dispersal to Africa via Europe (Naish et al., 2004); and the presence of Gondwanan faunas in Europe indicates dispersal events in the opposite direction (Ezcurra and Agnolín, 2012; Dal Sasso et al., 2016). These ideas are unified here as an Africa-Europe faunal exchange hypothesis (Hypothesis 3), as shown in figure 3. Frequent dispersal events within coelurosaurian lineages (including Tyrannosauroidae, Therizinosauria, and Dromaeosauridae), enabled by the Bering land bridge are well documented and accepted (Makovicky and Sues, 1998; Ji et al., 2003; Dodson et al., 2004; Longrich and Currie, 2009a; Bru-

satte et al., 2010; Zanno, 2010; Turner et al., 2012), as discussed in the last section (see Geographical and Temporal Distribution of Coelurosaurians) (Hypothesis 4: fig. 4): this includes the impacts of both the Early Cretaceous and Late Cretaceous establishments of the land bridge.

The dinosaurian biogeographic hypotheses we propose to test in this study include the existing hypotheses outlined above, as well as ones that we have modified or developed ourselves (table 1). Existing hypotheses are mostly based on narrative or qualitative approaches, which have limited their accuracy as well as their ability to undergo statistical testing. To address this issue, a quantitative biogeographic method with multiple biogeographic models is implemented in this study.

METHODOLOGY

Quantitative biogeographic methods are mainly used for inferring the ancestral geographic distributions of species and clades, as well as the biogeographic processes that produced the observed species distribution. Quantitative analyses require phylogenetic trees of the target clades and some models or assumptions about the evolution of faunal distribution (Ronquist and Sanmartín, 2011). A statistical framework, including parsimony (to a wider extent) and likelihood, is used for formulating an analysis (Ronquist, 1997; Ree, 2005; Landis et al., 2013; Matzke, 2013).

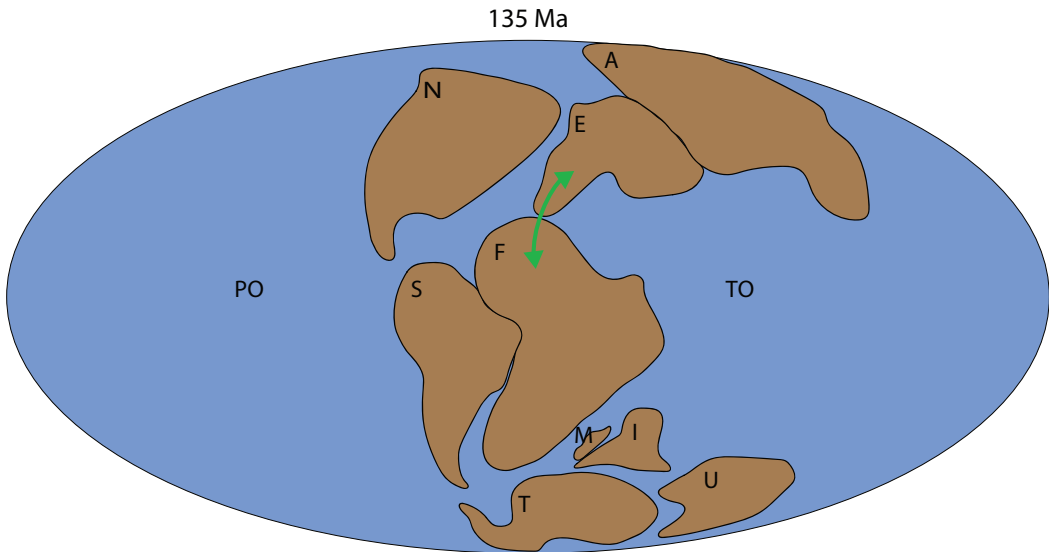


FIG. 3. Hypothesis 3, late Early Cretaceous Europe-Africa faunal exchange via the Apulian route. The green arrowed lines denote the approximate dispersal directions and dispersal routes; Solid lines denote paleogeography at 135 Ma. Paleomap after (Matthews et al., 2016). Abbreviations: A, Asia; E, Europe; F, Africa; I, India; M, Madagascar; N, North America; PO, Pacific Ocean; S, South America; T, Antarctica; TO, Tethys Ocean; U, Australia.

These historical biogeographic methods are analogous to phylogenetic analysis for inferring character evolution, in that the characters of the taxa are replaced with geographic distributions (Ree, 2005). Therefore, they share similar statistical frameworks, with parsimony, likelihood, and Bayesian methods, all of which are applied in different quantitative biogeographic techniques (Ronquist, 1997; Ree, 2005; Landis et al., 2013). Although the debate on the justification of different statistical frameworks in phylogenetic methods is heated (Goloboff et al., 2018a, 2018b; O'Reilly et al., 2018), the selection of methodological approach is more straightforward and constrained than in historical biogeography. To date, no single method has yet been shown to have better performance in historical biogeographic analyses. Validation of the plethora of biogeographic techniques is beyond the scope of this project, though this work should be a priority in the future.

In most analytical approaches the whole geographic range of interest is divided into multiple

smaller areas and taxa are assigned to one or more of these areas. Faunal distribution evolution models are simplified versions of biogeographic processes that operate on the defined geographical areas (Ronquist, 1997; Ree, 2005; Landis et al., 2013; Matzke, 2013). For example, a dispersal event for a taxon corresponds to an increase in the number of distribution areas at a node and/or along a branch in a taxon phylogeny. Other distribution evolution models include regional extinction, sympatry, vicariance, and founder-event speciation (the latter occurring when one of the two daughter lineages of an ancestor acquires a different area to that ancestor, usually through dispersal across a barrier). Different quantitative biogeographic methods take different models into consideration, which directly affect the results obtained (Matzke, 2013). Thus, a multimodel approach is recommended for more accurate identification of biogeographical patterns.

The first widely used quantitative biogeographic analysis approach was dispersal-vicari-

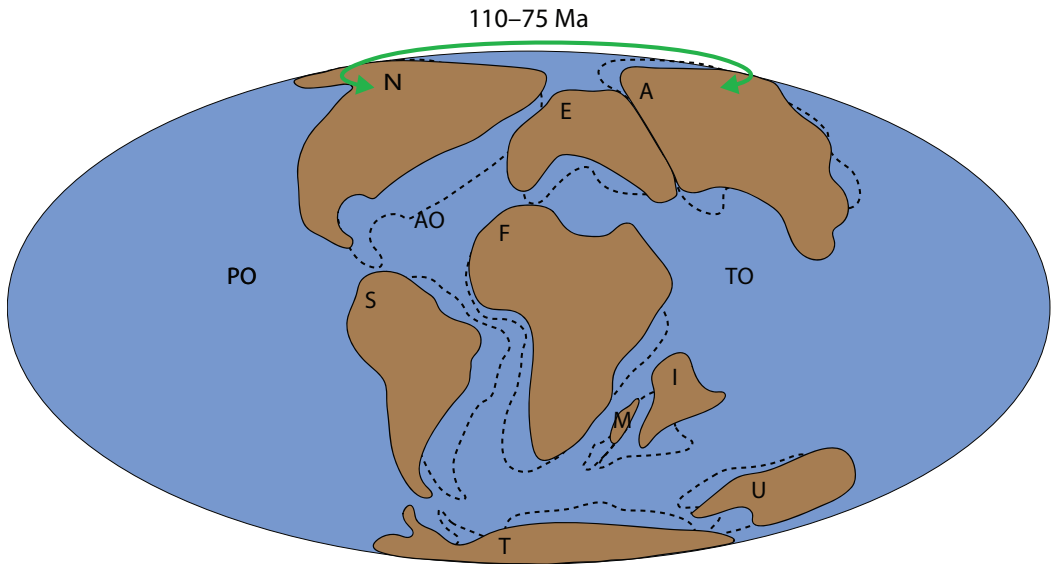


FIG. 4. Hypothesis 4, Cretaceous North America–Asia faunal exchanges. This includes both the Early and Late Cretaceous establishments of the Bering land bridge. The green arrowed line denotes the approximate dispersal directions and route. Dotted lines denote paleogeography at 110 Ma, solid lines denote paleogeography at 75 Ma. Paleomap after (Matthews et al., 2016). Abbreviations: A, Asia; AO, Atlantic Ocean; E, Europe; F, Africa; I, India; M, Madagascar; N, North America; PO, Pacific Ocean; S, South America; T, Antarctica; TO, Tethys Ocean; U, Australia.

ance analysis or DIVA (Ronquist, 1997), as implemented in the program FigTree. This parsimony-based approach utilizes phylogenetic character optimization methods and models dispersal, extinction, and vicariance events. Each event is assigned with a cost (the cost of dispersal and regional extinction events is 1 while the cost of vicariance events is 0). The overall biogeographic history with the lowest cost is favored (Ronquist, 1997). However, the time dimension is not considered in the analysis. Subsequently, a likelihood framework was introduced in the form of the dispersal-extinction cladogenesis model (DEC) by assigning dispersal and extinction rates as free parameters, which can vary to give different overall likelihoods (Ree and Smith, 2008). Subset sympatry (one of the daughter lineages lives in a subset of the ancestral range, while the other continues to occupy the whole ancestral range) and a limited form of vicariance (one of the daughter lineages occupies only one ancestral area, while the other occupies the rest

of the ancestral range) are permitted, but widespread sympatry or vicariance are prohibited. By varying free parameter values, the ancestral state is reconstructed by maximizing the overall likelihood of the whole biogeographic process. This approach incorporates information on the branch lengths in phylogenetic trees (i.e., evolutionary time is taken into consideration). Historical geographic changes can also be incorporated into the analysis using this method (Ree and Smith, 2008). Finally, in order to enhance the computational speed of biogeographic analysis, the program BayArea was developed with a Bayesian approach based on a likelihood framework, in which vicariance was prohibited (Landis et al., 2013).

In this project, we adopt the R package, BioGeoBEARS (Matzke, 2013), for analyzing coelurosaurian biogeography. Likelihood versions of the biogeographic models in DIVA, DEC, and BayArea are incorporated into BioGeoBEARS, which allows the results of several

models to be more easily compared. DEC is the original dispersal-extinction cladogenesis model (Ree and Smith, 2008). DIVALIKE is a likelihood version of dispersal-vicariance analysis (Ronquist, 1997). Unlike DEC, the DIVALIKE model disallows subset sympatry, but permits widespread vicariance (i.e., two daughter lineages divide up the ancestral range and both share more than one area). BAYAREALIKE is a likelihood-based version of BayArea (Landis et al., 2013). In BAYAREALIKE, the two daughter lineages of a given ancestor inherit the same area distribution as that ancestor. As a consequence, the BAYAREALIKE model allows widespread sympatry (i.e., for any ancestral range occupying more than one area, a daughter lineage copies it), which is prohibited in both the DEC and DIVALIKE models. Like BayArea, BAYAREALIKE also disallows vicariance events. All three models assume narrow sympatry (i.e., spontaneous range copying of single area ancestral ranges) and set dispersal and regional extinction rate as free parameters. In BioGeoBEARS, founder events are included as a separate range-switching process (termed the J parameter), which can be considered as a rapid dispersal event. This creates three new variants of the three models, giving a total of six possible model comparisons per biogeographic dataset: DEC, DIVALIKE, BAYAREALIKE, DEC+J, DIVALIKE+J, and BAYAREALIKE+J (Matzke, 2013). Standard statistical comparison with natural log of the process likelihood (LnL) and the Akaike information criterion (AIC) can be performed to identify the model(s) that best fits the data

Applying BioGeoBEARS has three notable advantages over existing methods: (1) different models are compared based on the same dataset (as mentioned above); (2) geological time spans are considered in calculating the likelihood of faunal distribution evolution; and (3) paleogeographic constraints can be implemented to inform the analysis about area connectedness during the Mesozoic. At this stage, these three features cannot be achieved by any current soft-

ware based on a parsimony framework or Bayesian approach.

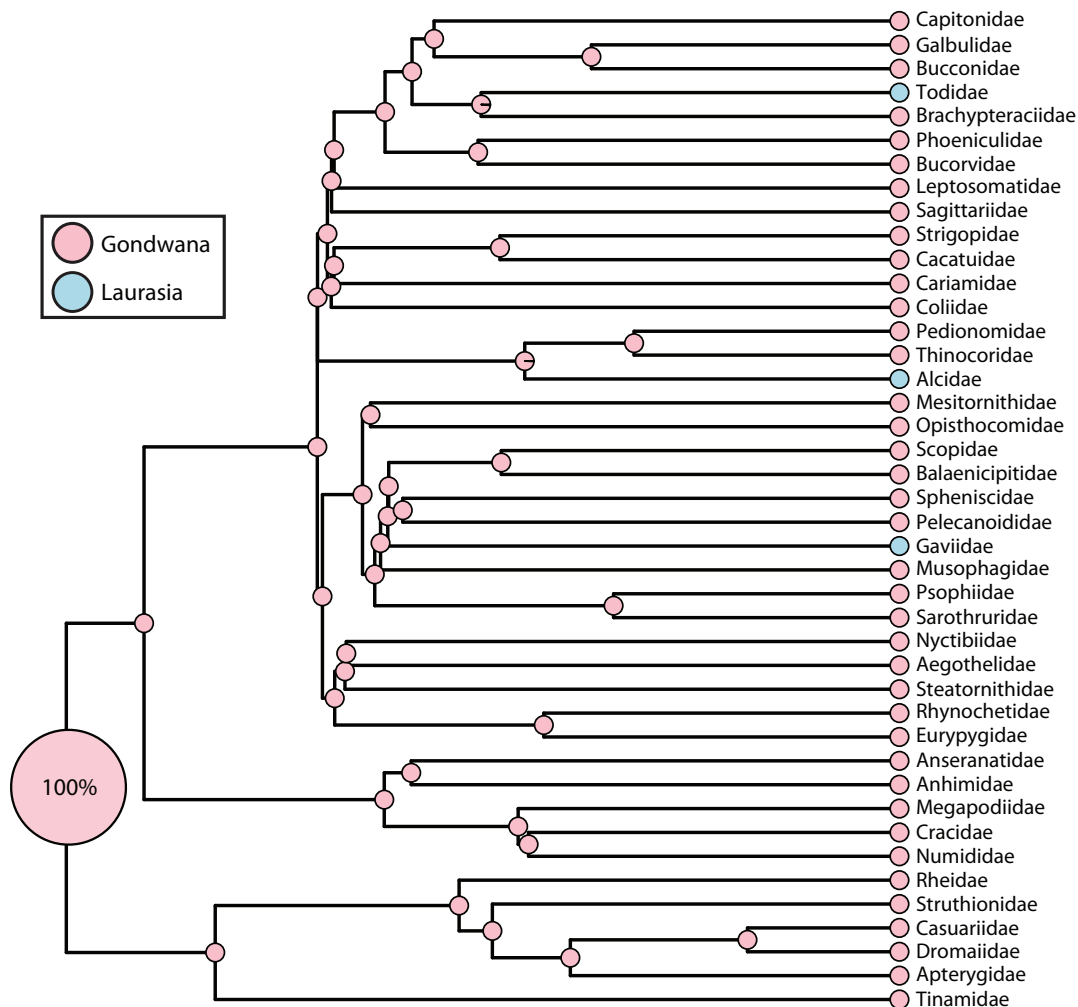
BioGeoBEARS considers time in calculating the likelihood of faunal distribution evolution. All things being equal, a biogeographic event should have a higher probability of occurring over a longer period of time. This time span, which is the branch length of each lineage, is taken into consideration within the likelihood framework through the relationship:

$$P_{ij}(t) = \exp(-Q_{ij} * t)$$

Where P is the event likelihood, Q is the universal event rate (dispersal, local extinction, vicariance, founder event) and t is the branch length (Matzke, 2013). Although assigning one universal rate value to each biogeographic event is still overly simplistic, the consideration of time, which is not achievable within a parsimony framework at this time, remains an important advantage over other current methods of analysis.

BioGeoBEARS allows paleogeographic constraints with known temporal ranges to be incorporated into an analysis (Matzke, 2013). This ensures that dispersals between areas that are connected or separated are assigned different dispersal probabilities despite one universal dispersal rate. To do so, dispersal multipliers are introduced, whose product with the universal dispersal rate will be the new regional dispersal rate used to calculate the likelihood of the dispersal event in question. The dispersal multipliers for connected geographic ranges are set to 1 while those for separated ranges are set to 0.000001 (a low value does not rule out such dispersal events but implies that they are highly unlikely). Here, we follow the protocol of Poropat et al. (2016). When dealing with regions that are separated by shallow seas or uncertain geographic barriers, the value 0.5 is assigned to the dispersal multiplier between those regions, which act as our starting (or normal) constraints (see Poropat et al., 2016, for further details).

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Within each analysis, the overall likelihood of reproducing the dataset given the model is computed, and the overall biogeographic process with the maximum probability (likelihood) will be the best-fit result. The Akaike information criterion (AIC) and natural log of the process likelihood (LnL) are calculated to infer the quality of data fit. A smaller AIC and a larger (less negative) LnL indicate a better fit of the data given the model tested.

We divide land areas on the Earth's surface into eight geographic units, namely Africa, Asia, Australia, Europe, India, Madagascar,

North America, and South America (although there are no taxa from India or Australia in our dataset). Each taxon is assigned to the areas according to data reviewed above in Geographic and Temporal Distributions of Coelurosaurians. These data were obtained by referring back to holotype descriptions and other literature (the dataset is available in the appendix of this paper).

The coelurosaurian phylogenetic tree with time calibration applied in the analysis is a maximum agreement subtree of a recent analysis of the Theropod Working Group (TWiG)

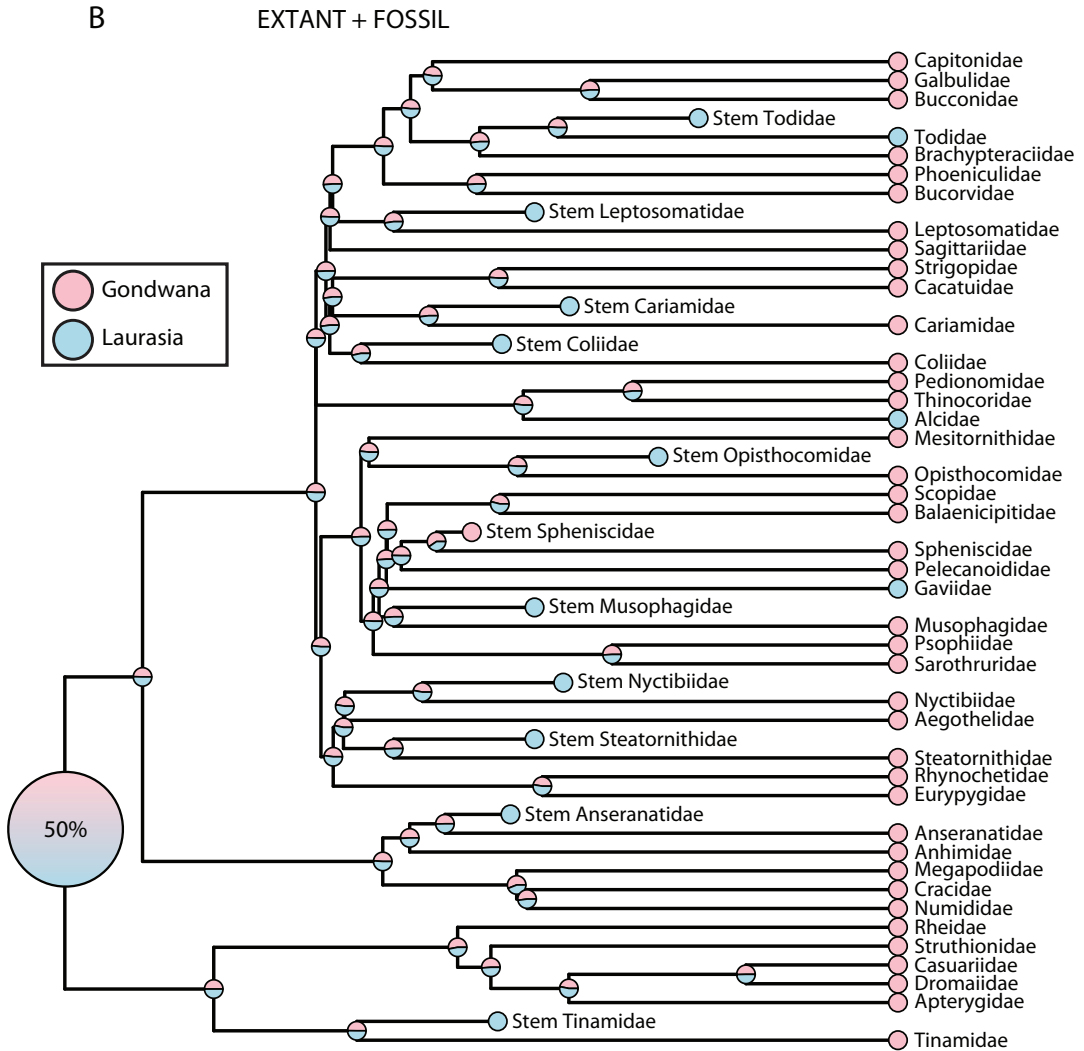


FIG. 5. Illustration (*opposite page and above*) of conflict between “extant only” biogeographic reconstructions for crown birds, and the crown bird fossil record (modified from Field and Hsiang, 2018). **A**, Extant-only reconstructions infer a Gondwanan origin of crown birds with strong probability, whereas **B**, identical analyses incorporating the earliest fossil stem group representatives infer a markedly less robustly supported result.

phylogenetic matrix (see Brusatte et al., 2014, for further details). The paleogeographic constraints are those used by Xu et al. (2018a), as modified from those summarized by Poropat et al. (2016) by better constraining the opening and closing of the Russian Platform Sea between Asia and Europe during the Jurassic (Xu et al., 2018b). They are represented by 23 dispersal multiplier matrices corresponding to

23 time slices from the Middle Jurassic to the Late Cretaceous. Four analyses with “starting”, “relaxed”, “harsh”, or “no paleogeographic constraints” were carried out. Relaxed constraints set all 0.5 dispersal multiplier values to 1, harsh constraints set all 0.5 dispersal multipliers to 0.000001. These analyses were repeated for all six biogeographic models giving a total of 24 comparisons.

TABLE 2

Relative performance of the six biogeographic models under the unconstrained and three palaeogeographically constraint conditions

Abbreviations: **Alt**, alternative model; **null**, null model; **LnL**, natural log of the process likelihood; **p-value**, p-value of the likelihood ratio test; **AIC**, Akaike information criterion.

Analysis		Alternative	Null	LnL _{alt}	LnL _{null}	AIC _{alt}	AIC _{null}	p-value
Unconstrained	1	DEC+J	DEC	-177.3	-241.8	360.6	487.6	6.60E-30
	2	DIVALIKE+J	DIVALIKE	-177.2	-232.8	360.5	469.7	5.30E-26
	3	BAYAREALIKE+J	BAYAREALIKE	-179.9	-294.6	365.8	593.3	7.60E-52
Starting	1	DEC+J	DEC	-263	-278.4	532	560.9	2.80E-08
	2	DIVALIKE+J	DIVALIKE	-261.8	-275.1	529.6	551.9	2.60E-07
	3	BAYAREALIKE+J	BAYAREALIKE	-282.9	-317	571.7	638.1	1.30E-16
Relaxed	1	DEC+J	DEC	-262.7	-277.5	531.4	558.9	5.70E-08
	2	DIVALIKE+J	DIVALIKE	-261.4	-273.9	528.8	551.9	5.70E-07
	3	BAYAREALIKE+J	BAYAREALIKE	-278.1	-318.5	562.2	641	2.50E-19
Harsh	1	DEC+J	DEC	-338.1	-344.8	682.3	693.5	0.0003
	2	DIVALIKE+J	DIVALIKE	-372.5	-383	751	770.1	4.60E-06
	3	BAYAREALIKE+J	BAYAREALIKE	-311.4	-329.7	628.7	663.4	1.40E-09

RESULTS

The relative fit of the 24 analyses to the data are summarized in table 2, with the corresponding parameter values listed in table 3.

As shown in table 2, the AIC and LnL values indicate that the unconstrained analysis performs “better” than the constrained ones, an expected result for three reasons: first, without geographic constraints, the dispersal rate remains constant between any two geographic areas throughout coelurosaurian evolutionary history. Under these conditions, unlikely dispersal events will not be prohibited or penalized, and will have the same probability of occurring as paleogeographically more plausible dispersals. For example, Asian taxa may be able to directly disperse to South America,

which to a large extent simplifies the biogeographic processes. As a result, the overall likelihood of the unconstrained processes should be expected to be higher than the constrained ones because of oversimplification of the biogeographic processes. Second, vicariance events can take place whenever a fauna is distributed across more than one geographic area. Since the overall dispersal rate is low between continents, any fauna having cross-continent biogeographic ranges is separated by “geographic barriers” as understood by the statistical framework. Due to the high flexibility for vicariance events in an unconstrained analysis, low-probability regional extinction events will frequently be replaced by “must-happen” vicariance, which boosts the overall process likelihood (in models that allow vicariance, the vicariance rate is set close to 1).

TABLE 3

Parameter values for the six biogeographic models under the unconstrained and three palaeogeographically constraint conditions

Abbreviations: **LnL**, natural log of the process likelihood; **d**, dispersal rate; **e**, regional extinction rate; **j**, founder-event rate; **AIC**, Akaike information criterion; **AICweight**, Akaike information criterion weight.

Model	LnL	d	e	j	AIC	AICweight
Unconstrained						
DEC	-241.8	0.001	0.0021	0	487.6	1.20E-28
DEC+J	-177.3	1.00E-12	1.00E-12	0.023	360.6	0.47
DIVALIKE	-232.8	0.0012	2.00E-09	0	469.7	9.50E-25
DIVALIKE+J	-177.2	1.00E-12	1.00E-12	0.024	360.5	0.49
BAYAREALIKE	-294.6	0.0011	0.015	0	593.3	1.40E-51
BAYAREALIKE+J	-179.9	1.00E-12	1.00E-12	0.024	365.8	0.035
Starting						
DEC	-278.4	0.014	0.0084	0	560.9	1.30E-07
DEC+J	-263	0.0083	0.0059	0.1	532	0.23
DIVALIKE	-275.1	0.016	0.0077	0	554.1	3.70E-06
DIVALIKE+J	-261.8	0.0099	0.0062	0.1	529.6	0.77
BAYAREALIKE	-317	0.013	0.022	0	638.1	2.10E-24
BAYAREALIKE+J	-282.9	0.0013	0.015	0.051	571.7	5.50E-10
Relaxed						
DEC	-277.5	0.011	0.0081	0	558.9	2.30E-07
DEC+J	-262.7	0.0068	0.0059	0.083	531.4	0.21
DIVALIKE	-273.9	0.013	0.0075	0	551.9	7.90E-06
DIVALIKE+J	-261.4	0.0083	0.0062	0.082	528.8	0.79
BAYAREALIKE	-318.5	0.011	0.022	0	641	3.50E-25
BAYAREALIKE+J	-278.1	0.0063	0.0082	0.12	562.2	4.50E-08
Harsh						
DEC	-344.8	0.021	0.0086	0	693.5	8.60E-15
DEC+J	-338.1	0.015	0.0072	0.082	682.3	2.40E-12
DIVALIKE	-383	0.023	0.008	0	770.1	2.00E-31
DIVALIKE+J	-372.5	0.015	0.0065	0.1	751	2.70E-27
BAYAREALIKE	-329.7	0.0056	0.024	0	663.4	2.90E-08
BAYAREALIKE+J	-311.4	0.0037	0.019	0.049	628.7	1

Third, founder events, as a fast version of dispersal, will be more frequently applied in an unconstrained analysis. A founder event is similar to instant range switching of an ancestral state, which shares the same rate as a dispersal event. In an unconstrained analysis, it not only mimics the process of dispersal, but also does not need low-probability regional extinction events to account for taxa that occupy just a single area. Therefore, founder events can accommodate any taxon that occupies an area that differs from its ancestral state, and this will be more statistically favorable than the estimate of vicariance events to explain the observed distributions. The large LnL contrasts between models with (+J models) and without founder-event speciation are also expected because of the statistical preference for models that include this parameter. The predicted high likelihoods achieved by the unconstrained analyses are confirmed in table 2 where the LnL values for all six biogeographic models are less negative than those in any constrained analyses. Thus, in spite of the low AIC and high LnL values, the results of the unconstrained analysis should be treated with caution because they do not consider paleogeographic constraints. The absence of such information relevant to the direction and probability of faunal dispersal is ultimately likely to lead to less accurate estimations of dispersal events, e.g., direct dispersal events from Asia to South America across the Mesozoic Pacific Ocean.

Within the constrained analyses, the starting and relaxed constraints give results that agree on the most preferred model, DIVALIKE+J, while the harsh constraints suggest a preference for BAYAREALIKE+J. Here, we accept DIVALIKE+J as the best-supported model based on the following reasons:

1. DIVALIKE+J is preferred in the analysis with the starting constraints, which to our knowledge best reflects Mesozoic geography. Such model preference is also supported in the analysis with the relaxed constraints.
2. The ancestral area estimations proposed by the DIVALIKE+J model yield more plausible interpretations of evolutionary history and biogeographic processes for coelurosaurians. This will be discussed in more detail in the Discussion.
3. The results of the BAYAREALIKE+J model (including the one under the harsh geographic constraints) estimate several occurrences of ancestors that were present solely in South America and Asia during the Cretaceous. Such ancestral area estimates are not realistic since the two continents were separated by large oceans during that time (Scotese, 2001) and it is highly unlikely that faunal exchange ever happened. Events of this type are frequent in the BAYAREALIKE+J model, because a high value (nearly 1) is assigned to the widespread sympatry process rate. Some authors (Poropat et al., 2016; Xu et al., 2018b) interpret such unlikely ancestral distributions as resulting from the impacts of uneven sampling of the fossil record. In reality, such widespread sympatry cannot happen without faunal exchange across these areas, but this is neglected in the model. The unrealistic results and oversimplified biogeographic processes justify the rejection of this model.
4. The harsh biogeographic constraints might not accurately reflect paleogeography and the true dispersal capabilities of coelurosaurians. The reason is that they treat all uncertain connections and shallow seas as geographic barriers, which largely isolates the individual continents throughout the Cretaceous. The harsh constraints could therefore be underestimating the dispersal ability of coelurosaurians. Analogous to the modern Madagascan fauna (Ali and Huber, 2010), coelurosaurians—particularly small ones, with or without aerodynamic capabilities—might have been

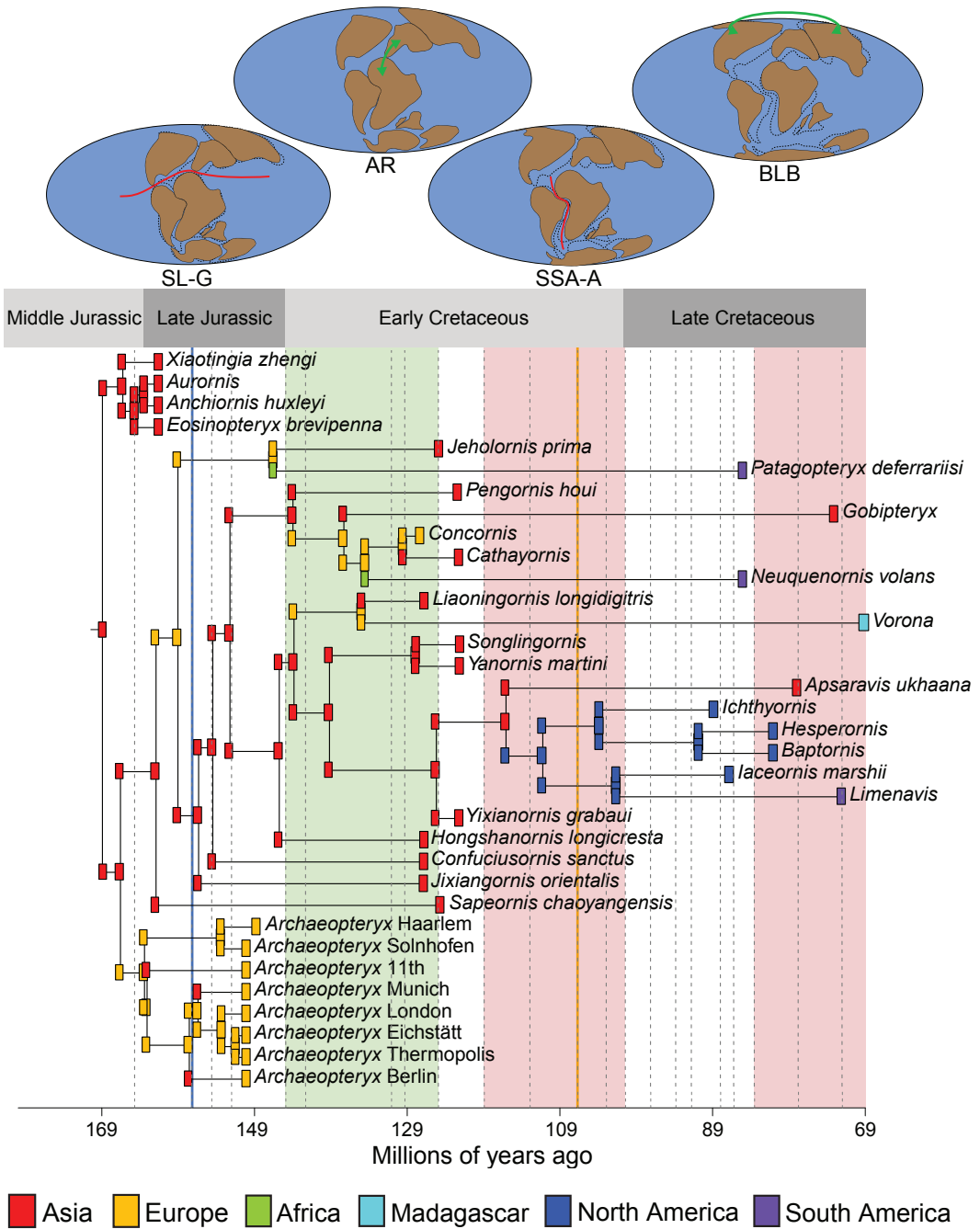
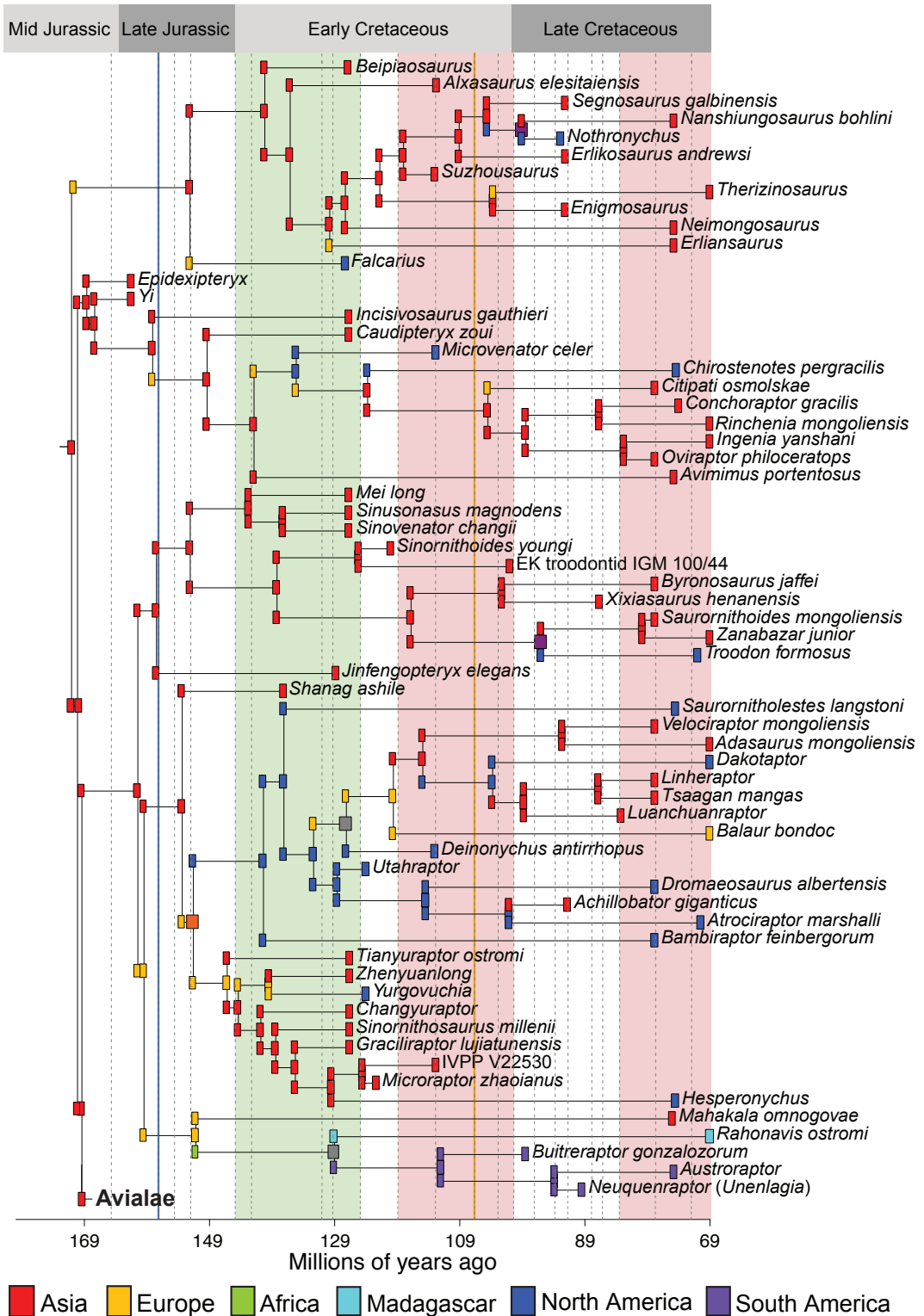
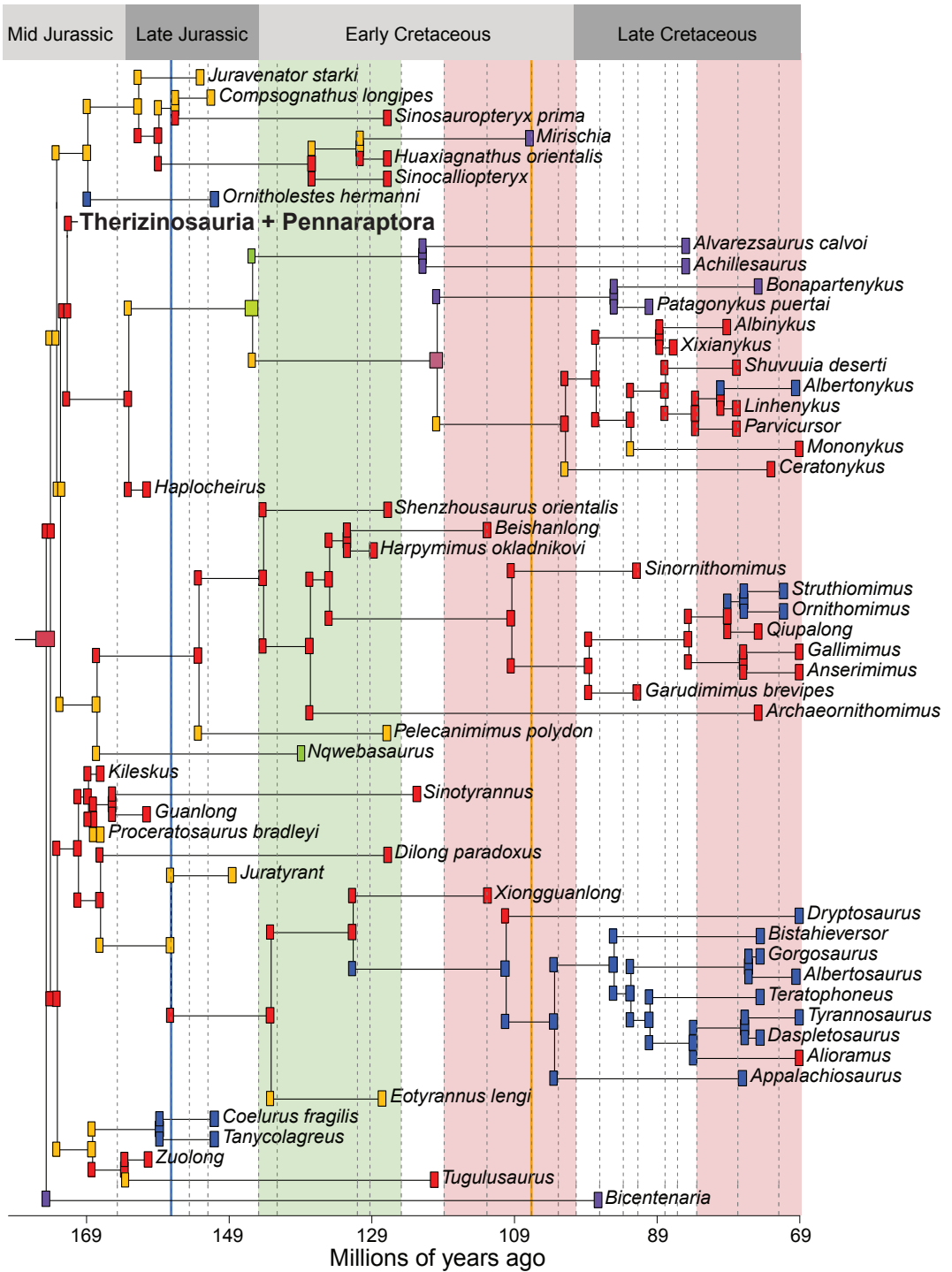


FIG. 6. Ancestral area estimation applying the DIVALIKE+J model with starting constraints to a dated coelurosaurian phylogeny (above and following two pages). Green shading denotes the period when the Apulian route (AR) connected northeast Africa and southwest Europe, while red shadings denote Bering land bridge (BLB) connections. The blue line denotes the time of separation between Laurasia and Gondwana (SL-G), while the yellow line denotes the time of separation between South America and Africa (SSA-A).





■ Asia ■ Europe ■ Africa ■ Madagascar ■ North America ■ South America

capable of crossing relatively narrow channels or shallow waterways over geological time scales.

In the various constrained analyses, the +J models still perform better than non+J models, although the differences are not as large as in the unconstrained analysis (as suggested by p-values in table 2). This phenomenon also occurs because founder-event speciation, as an alternative explanation for area switching, is statistically more favorable than other forms of dispersal. With the implementation of paleogeographic constraints, this flexibility is to some extent restricted and vicariance events are preferred if no feasible dispersal route is allowed, thereby reducing the likelihood gap of +J models and corresponding non+J models. However, which particular events happened during coelurosaurian evolution, whether founder events or dispersals, cannot be determined by these analyses.

In the analyses with the starting and relaxed constraints, the DIVALIKE+J and the DEC+J models perform nearly equally well with close AIC and LnL values. Both of the models allow narrow vicariance and founder events, while DIVALIKE+J allows widespread vicariance but DEC+J allows subset sympatry. Because nearly all taxa in our analysis occupy only single geographic areas and large-scale connections of these units were absent after the breakup of Pangaea, biogeographic processes that result in widespread ancestral species probably did not play a major role in coelurosaurian evolution. This might explain the similar results of the DIVALIKE+J and DEC+J models. The ancestral area estimates of the two models also provide similar interpretations of biogeographic history. Because the DIVALIKE+J model is slightly favored in terms of AIC and LnL values, we use its results in our discussion of coelurosaurian biogeography (fig. 6). The results of the starting constraints are used as the basis of our discussion here because they represent the most conservative paleogeography among the three constraints (starting, relaxed, and harsh).

DISCUSSION

Our results show that the major biogeographic processes during coelurosaurian evolution include intercontinental dispersals, regional extinctions, continent-scale vicariance events, and continental-scale founder events. While dispersal and extinction are part of all six BioGeoBEARS models, the support for the DIVALIKE+J model in particular indicates important roles for vicariance and founder-event speciation in coelurosaurian evolution. In contrast, the BAYAREALIKE models, which do not allow vicariance, are not supported except when particularly stringent (harsh) paleogeographic constraints are imposed. However, on a continental scale, founder events at ancestral nodes, although statistically preferred, become similar to within-lineage dispersal events from a biological point of view. Hence, no absolute or relative frequencies of founder events can be inferred from our results. As our area units are at the continental scale, our results cannot capture intracontinental or island-scale biogeographic patterns.

Our results confirm that continental-scale vicariance was probably an important biogeographic process influencing coelurosaurian evolution. This is consistent with many qualitative assessments in the literature (Fastovsky et al., 1996; Sereno, 1999b; Makovicky et al., 2005; Choiniere et al., 2012), and also agrees with a quantitative analysis of dinosaurian biogeography (Upchurch et al., 2002). Most workers recognized the importance of continental fragmentation in producing geographic barriers during the late Mesozoic, including the separation of Laurasia and Gondwana, the opening of the north Atlantic and the isolation of Gondwanan landmasses. Such vicariance events are seen in our results (fig. 6): for example, vicariance induced by the Middle Jurassic breakup of Pangaea led to the occurrence of the early-diverging coelurosaurian *Bicentenario* in South America and other early-diverging taxa in Laurasia (Hypothesis 1). Similar vicariance patterns are also recognized within other terrestrial faunas living at that time, such as

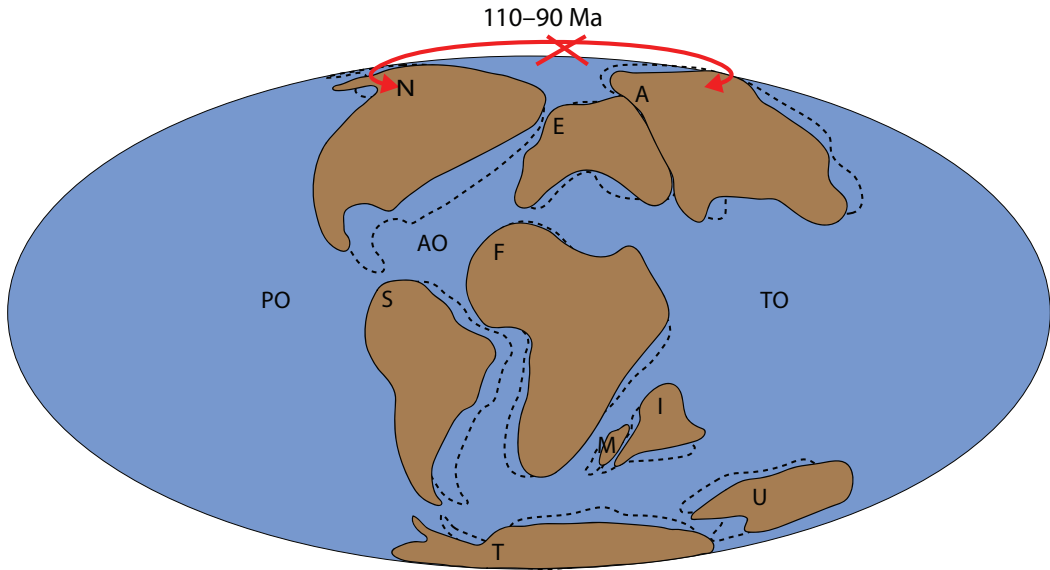


FIG. 7. Hypothesis 5, North America-Asia vicariance event caused by the breakdown of the Bering land bridge during the early Late Cretaceous. The marine barrier between northeast Asia and northwest North America was re-established in the Cenomanian Stage. The red X denotes the approximate position of the hypothesized biogeographical barrier (Bering Strait); Dotted lines denote paleogeography at 110 Ma, while solid lines denote it at 90 Ma. Paleomap after (Matthews et al., 2016). Abbreviations: A, Asia; AO, Atlantic Ocean; E, Europe; F, Africa; I, India; M, Madagascar; N, North America; PO, Pacific Ocean; S, South America; T, Antarctica; TO, Tethys Ocean; U, Australia.

turtles (Joyce et al., 2016), dryolestoid mammals and eilenodontine sphenodontians (Makovicky et al., 2005). However, we also note additional vicariance events that have not figured prominently in previous studies. An example of the latter is the apparent impact of the destruction of land bridges such as that across the Bering Strait (Hypothesis 5, fig. 7), which could explain the occurrence of *Nothronychus* in North America and *Nanshiungosaurus* in Asia (fig. 6). Ephemeral land bridges that reconnect separate areas after continental fragmentation were established from time to time throughout the Cretaceous, enabling intercontinental faunal dispersals. After the loss of these land bridges, the continents became isolated from one another once again and dispersed populations were separated by an oceanic barrier, which eventually caused vicariance. Such vicariance events are observed in the Therizinosauria and Troodontidae after the disappearance of the Bering land bridge during the early Late Creta-

ceous (fig. 7), and also within the Alvarezsauriidae after the loss of the Apulian route during the mid-Early Cretaceous.

Besides vicariance, the impact of other biogeographic processes on coelurosaurian evolution can also be recognized in our results. As suggested by multiple authors (Serenó, 1999b; Brusatte et al., 2013; Dunhill et al., 2016), dispersal played a major role in shaping coelurosaurian biogeography. The establishment of the Bering land bridge enabled direct Asia-North America dispersal without a transit via Europe. This dispersal route is the most frequently used by coelurosaurians as inferred from our results. Single dispersal events during the first establishment of the Bering land bridge in the late Early Cretaceous (fig. 4) potentially explain the Asian occurrence of the dromaeosaurid *Achillobator* and the North American occurrences of the troodontid *Troodon* and the dromaeosaurid *Dakotaraptor* (fig. 6). Our results therefore partially support

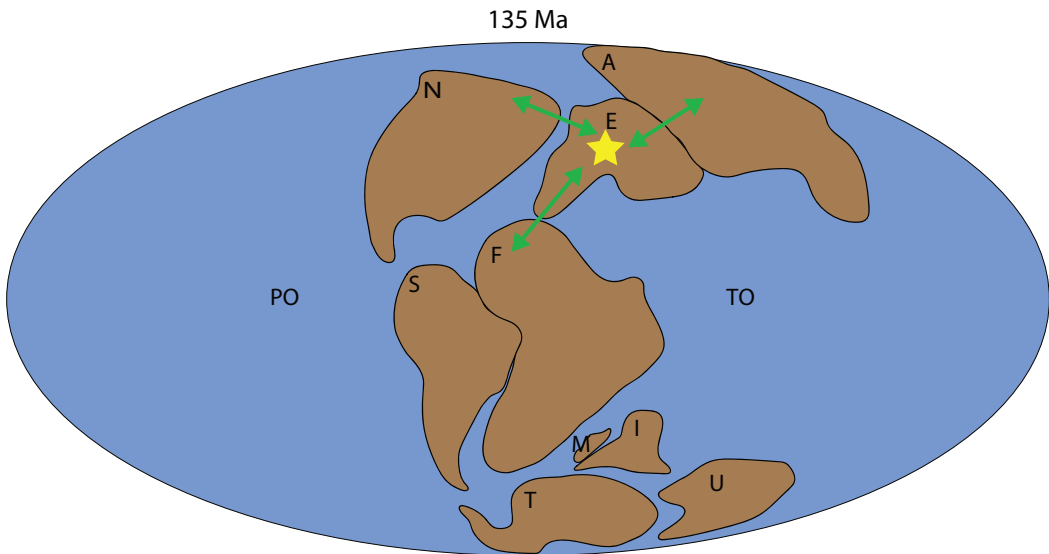


FIG. 8. Europe as a dispersal center and geographical gateway, especially during the Early Cretaceous. The green arrowed lines denote possible dispersal directions and approximate dispersal routes; Solid lines denote paleogeography at 135 Ma. Paleomap after (Matthews et al., 2016). Abbreviations: A, Asia; E, Europe; F, Africa; I, India; M, Madagascar; N, North America; PO, Pacific Ocean; S, South America; T, Antarctica; TO, Tethys Ocean; U, Australia.

Hypothesis 4 (fig. 4, table 1). Furthermore, the North American occurrence of the alvarezsaurid *Albertonykus* and the ornithomimids *Struthiomimus* and *Ornithomimus* as well as the Asian occurrence of the tyrannosaurid *Alioramus* can be attributed to ancestral dispersal via the Bering land bridge during its second connection in the latest Cretaceous (fig. 4). Thus, together, our results support Hypothesis 4 in full (table 1), indicating that the two episodes of connection across the Bering Strait probably facilitated important faunal exchanges that produced most of the Asia–North America coelurosaurian occurrences throughout the Cretaceous. However, we also support the Apulian route as important for coelurosaurian faunal exchange (Hypothesis 3, fig. 3), an idea that has been somewhat neglected in previous studies. It appears to account for the South American occurrence of the Early Cretaceous compsognathid *Mirischia* and the Late Cretaceous avialans *Patagopteryx* and *Neuquenornis*, while their closest relatives were present in Asia (although

multiple intercontinental dispersals probably took place) (fig. 6). The formation of the Apulian route in the late Early Cretaceous marked the first Laurasia–Gondwana connection after the breakup of Pangaea during the Middle Jurassic (fig. 3). Other taxa are believed to have crossed from Gondwana to Laurasia via this route in the Cretaceous, including carcharodontosaurids (Brusatte et al., 2009), and rebbachisaurid (Serenó et al., 2007) and titanosaurian sauropods (Dal Sasso et al., 2016). If earlier-diverging coelurosaurian taxa from Gondwana were not derived from vicariance induced by Pangaeian breakup, they most probably arrived from Laurasian landmasses. Although such “Laurasian arrival” hypotheses have been suggested (Naish et al., 2004; Foth and Rauhut, 2017), these biogeographic events were not linked by these authors to the only feasible Laurasia–Gondwana dispersal route known in the Early Cretaceous. In our results, many inferred dispersal events via the Apulian route explain South American coelurosaurian occurrences of their Laurasian rela-

tives, but discoveries of closely related African taxa are lacking. Therefore, new African coelurosaurian discoveries will be crucial for testing Apulian route dispersal events.

Related to the impacts of the Apulian route and trans-Turgai land bridges, our analyses indicate that Europe might have been both a dispersal center and a geographical gateway in coelurosaurian evolution, especially before the Barremian (fig. 8). Although only having a few coelurosaurian occurrences, Europe forms all or part of the geographic range for many ancestral nodes in our results (fig. 6). Several lineages are inferred to have had early-diverging forms in Europe and then dispersed to other continents, while faunas from other lineages disperse from one continent to another via Europe. In the former case, ancestral faunas might have migrated from Europe to North America before the full establishment of the North Atlantic Ocean (e.g., early-diverging coelurosaurians, such as *Ornitholestes* and the Compsognathidae). They might also have migrated from Europe to Asia when terrestrial routes existed across the Turgai Sea (e.g., Compsognathidae as evidenced by the ancestral area estimations for the *Sinosauropteryx* lineage), and to Africa via the Apulian route during the Early Cretaceous (e.g., Ornithomimosauria as evident from *Nqwebasaurus*), and from there to other Gondwanan landmasses. Even without these Cretaceous land bridges, Europe is likely to have played a central role in coelurosaurian dispersal. In particular, ancestral faunas might have migrated between Asia and North America via Europe (e.g., Asia to North America dispersal in *Coelurus*), and from Laurasia to Gondwanan landmasses via Europe before the breakup of Gondwana (e.g., Asia to South America via Europe in alvarezsauroids, consistent with the results of Xu et al., 2018a, on alvarezsauroid biogeography). This conclusion is also consistent with the result found by Dunhill et al. (2016) that European dinosaurs had strong direct connections with those in adjacent continents during

the Jurassic and Early Cretaceous. In addition, these authors demonstrated a high degree of connectivity between North America and Asia, Asia and Africa, and Africa and North America during the Early Cretaceous (Dunhill et al., 2016), which can be explained by faunal exchange events via Europe as a dispersal gateway. For example, Laurasian continents shared similar ankylosaurian (Ősi, 2005), hadrosauroid (Prieto-Marquez et al., 2006; Dalla Vecchia, 2009), non-dinosaurian archosaurian (Ezcurra and Agnolín, 2012) and gobiconodontid mammalian (Cuenca-Bescós and Canudo, 2003) faunas, implying faunal exchange among Europe, Asia, and North America. There were also European and Gondwanan faunas that were closely related (Dalla Vecchia, 2003; Gheerbrant and Rage, 2006), including spinosaurid theropods (Charig and Milner, 1997; Ruiz-Omeñaca et al., 2005), sauropods (Canudo et al., 2008), and thereuodontid mammals (Kielan-Jaworowska et al., 2004), that can be attributed to faunal exchanges via the Apulian route. Some Pangaeian faunas, including spinosaurid theropods from Asia (Buffetaut et al., 2008), titanosaurian sauropods from Asia and North America (Salgado et al., 1997; Wilson, 2002), and crocodyliforms from Asia (Wu and Sues, 1996), had their closest relatives in Gondwana, and probably arrived from southern continents via Europe. Thus, the events estimated here for European coelurosaurians and their relatives elsewhere, are probably part of a widespread pattern imposed on multiple terrestrial clades by Pangaeian fragmentation and the subsequent creation and destruction of key land bridges.

Finally, our results also imply that regional extinction played an important role in coelurosaurian evolution, as suggested by Sereno (1999b). Given frequent dispersals, continental-scale extinction events are necessary to account for the single-area-unit distributions of most coelurosaurian taxa. That regional extinction and dispersal were of comparable importance throughout coelurosaurian evolu-

tion is indicated by the similar values of the extinction and dispersal rates obtained in the analyses (table 3).

CONCLUSIONS

There are several uncertainties in our analyses that we should bear in mind. The major ones include: the quality of the fossil record, the accuracy of paleogeographic reconstructions; errors in phylogenetic tree topology and node dating; spatiotemporal sampling biases; and our lack of definitive knowledge of the dispersal abilities of different coelurosaurian clades. Although the phylogenetic tree used here is better sampled than any examined in previous analyses of coelurosaurian biogeography, no single tree includes all known taxa. Phylogenies also change as new morphological data become available, which could then alter estimates of biogeographic events and processes. New fossil discoveries from continents with rare or previously unknown records of particular clades are likely to modify our conclusions in the future (e.g., by changing tree topology, taxon ranges, origin dates, and so on, which in turn could favor other biogeographic patterns and processes). The accuracy of our results is also affected by as yet unquantified preservation biases, which will distort the observed spatial and temporal distributions of coelurosaurians (Upchurch et al., 2011). The second major uncertainty is regarding coelurosaurian dispersal ability. Coelurosaurian body sizes vary by six orders of magnitude, so their dispersal probability across narrow seaways may vary significantly. Avialans and probably some nonavialan paravians developed powered flight ability, which may have freed them from the constraints of conventional terrestrial dispersal corridors. However, these abilities are still not well understood. Future analyses will need to better quantify dispersal ability if we are to move away from the uniform dispersal probabilities assumed in this study, although Mesozoic avialans do not appear to have had the ability to

cross expansive oceans using their own flight capabilities (Allen et al., 2013). One group of comparable flying vertebrates is pterosaurs. Although this clade had different biogeographic patterns from other Mesozoic terrestrial vertebrates, quantitative biogeographic analysis revealed little vicariance and dispersal signal, but high levels of sympatry, which indicates rare cross-ocean range-switching events possibly enabled by powered flight (Upchurch et al., 2015). However, such a lack of statistical support for vicariance among pterosaurs might also be attributable to fossil sampling biases. Therefore, a separate and more focused biogeographic analysis of Mesozoic avialans, combined with investigation of the dispersal abilities of various modern bird clades, should be the next step in tackling this issue. Despite these uncertainties, our results demonstrate that continental dispersal, extinction, vicariance, and founder-events were important biogeographic processes during coelurosaurian evolution. Major dispersal corridors included the Apulian route and the Bering land bridge, and Europe might have been an important dispersal center and gateway for coelurosaurians before the mid-Early Cretaceous.

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APPENDIX
LOCALITY, FORMATION AND AGE DATA FOR STUDY TAXA

Taxon	Modern Locality	Formation and Age
<i>Achillesaurus</i>	Paso Córdoba, Río Negro Province, Argentina	Bajo de la Carpa Formation (86.3–83.6 Ma)
<i>Achillobator giganticus</i>	Burkhant, Dornogov, Mongolia	Bayan Shireh Formation (100.5–83.6 Ma)
<i>Adasaurus mongoliensis</i>	Bugin Tsav, Omnogov, Mongolia	Nemegt Formation (72.1–66.0 Ma)
<i>Albertonykus</i>	<i>Albertosaurus</i> bonebed, Dry Island Buffalo Jump Provincial Park, Alberta, Canada	Horseshoe Canyon Formation (72.1–66.0 Ma)
<i>Albertosaurus sarcophagus</i>	Kneehills Creek, Alberta, Canada	Horseshoe Canyon Formation (73–66.0 Ma)
<i>Albinykus</i>	Khugenetslavkant, Dornogov, Mongolia	Javkhant Formation (86.3–72.1 Ma)
<i>Alioramus</i>	Nogon Tsav, Bayankhongor, Mongolia	Nogon Tsav Formation (72.1–66.0 Ma)
<i>Alvarezsaurus calvoi</i>	Boca del Sapo, Universidad Nacional del Comahue, Neuquén, Argentina	Bajo de la Carpa Formation (86.3–83.6 Ma)
<i>Alxasaurus elesitaiensis</i>	Elesitai, Nei Mongol, China	Bayan Gobi Formation (125–100.5 Ma)
<i>Anchiornis huxleyi</i>	Jianchang, Liaoning, China	Tiaojishan Formation (163.5–157.3 Ma)
<i>Anserimimus planinychus</i>	Bugin Tsav, Omnogov, Mongolia	Nemegt Formation (72.1–66.0 Ma)
<i>Appalachiosaurus</i>	Montgomery County, AL	Demopolis Formation (78–76 Ma)
<i>Apsaravis ukhaana</i>	Camels Humps Amphitheater, Ukhaa Tolgod, Omnogov, Mongolia	Djadokhta Formation (83.6–72.1 Ma)
<i>Archaeopteryx</i> Berlin	Blumenberg quarry, Eichstätt, Bayern, Germany	Solnhofen Limestone (Altmühltal Formation) (152.1–148 Ma)
<i>Archaeopteryx</i> Eichstätt	Workerszell, Eichstätt, Bayern, Germany	Solnhofen Limestone (Altmühltal Formation) (152.1–148 Ma)
<i>Archaeopteryx</i> Haarlem (also thought to be an anchiornithine: <i>Ostromia</i> ; possibly a troodontid)	Riedenburg, Bayern, Germany	Painten Formation (152.1–145 Ma)
<i>Archaeopteryx</i> London	Langenaltheim quarry, Bayern, Germany	Solnhofen Limestone (Altmühltal Formation) (152.1–148 Ma)
<i>Archaeopteryx</i> Munich	Langenaltheim quarry, Bayern, Germany	Solnhofen Limestone (Altmühltal Formation) (152.1–148 Ma)
<i>Archaeopteryx</i> Thermopolis	Solnhofen, Bayern, Germany	Solnhofen Limestone (Altmühltal Formation) (152.1–148 Ma)
<i>Archaeopteryx</i> Solnhofen	Altmühl Valley, Bayern, Germany	Solnhofen Limestone (Altmühltal Formation) (152.1–148 Ma)

APPENDIX *continued*

Taxon	Modern Locality	Formation and Age
<i>Archaeopteryx</i> 11th	Eichstätt, Bayern, Germany	Solnhofen Limestone (Altmühltal Formation) (152.1–148 Ma)
<i>Archaeornithomimus asiaticus</i>	Johnson Quarry, Iren Dabasu, Nei Mongol, China	Iren Dabasu Formation (83.6–66.0 Ma)
<i>Atrociraptor marshalli</i>	Dunphy, Alberta, Canada	Horseshoe Canyon Formation (73.5–67.5 Ma)
<i>Aurornis</i>	Jianchang, Liaoning, China	Tiaojishan Formation (163.5–157.3 Ma)
<i>Austroraptor</i>	Bajo de Santa Rosa locality, Río Negro, Argentina	Allen Formation (83.6–66.0 Ma)
<i>Avimimus portentosus</i>	Udan-Sayr, Omnogov, Mongolia	Djadokhta Formation (83.6–66.0 Ma)
<i>Balaur bondoc</i>	Sebeş Glod, Alba, Romania	Sebeş Formation (72.1–66.0 Ma)
<i>Bambiraptor feinbergorum</i>	13 km west of Bynum, MT	Two Medicine Formation (83.6–72.1 Ma)
<i>Baptornis</i>	Logan County, KS	Niobrara Formation (89.8–72.1 Ma)
<i>Beipiaosaurus</i>	Beipiao, Liaoning, China	Yixian Formation (129.4–124 Ma)
<i>Beishanlong</i>	White Ghost Castle, Yujingzi Basin, Gansu, China	Xinminbao Group (125–100.5 Ma)
<i>Bicentenaria</i>	Ezequiel Ramos Mexía Reservoir, Río Negro, Argentina	Candeleros Formation (100.5–93.9 Ma)
<i>Bistahieversor</i>	Pinabete Arroyo, San Juan County, NM	Fruitland Formation (77–72.1 Ma)
<i>Bonapartenykus</i>	Salitral Ojo de Agua, Río Negro, Argentina	Allen Formation (83.6–66.0 Ma)
<i>Buitreraptor gonzalezorum</i>	La Buitrera, Río Negro, Argentina	Candeleros Formation (100.5–97 Ma)
<i>Byronosaurus jaffei</i>	Ankylosaur Flats, Ukhaa Tolgod, Omnogov, Mongolia	Djadokhta Formation (83.6–72.1 Ma)
<i>Cathayornis</i>	Beishan Quarry, Boluochi, Liaoning, China	Jiufotang Formation (125–120 Ma)
<i>Caudipteryx zoui</i>	Sihetun, Beipiao, Liaoning, China	Yixian Formation (129.4–124 Ma)
<i>Ceratonykus</i>	Khermin Tsav, Omnogov, Mongolia	Barun Goyot Formation (76–70 Ma)
<i>Changyuraptor</i>	Jianchang, Liaoning, China	Yixian Formation (129.4–124 Ma)
<i>Chirostenotes pergracilis</i>	2 miles northeast of mouth, Little Sandhill Creek, Alberta, Canada	Dinosaur Park Formation (76.5–72.1 Ma)
<i>Citipati osmolskae</i>	Ankylosaur Flats, Ukhaa Tolgod, Omnogov, Mongolia	Djadokhta Formation (83.6–72.1 Ma)
<i>Coelurus fragilis</i>	Como Bluff, Albany County, WY	Morrison Formation (157.3–145 Ma)

APPENDIX *continued*

Taxon	Modern Locality	Formation and Age
<i>Compsognathus longipes</i>	Kelheim, Bayern, Germany	Solnhofen Limestone (Altmühltal Formation) (154–149 Ma)
<i>Conchoraptor gracilis</i>	Khermin Tsav, Omnogov, Mongolia	Barun Goyot Formation (76.0–72.1 Ma)
<i>Concornis</i>	Las Hoyas, Cuenca, Spain	Calizas de la Huérguina Formation (128.5–125 Ma)
<i>Confuciusornis sanctus</i>	Huanghuagou, Shangyuan, Liaoning, China	Yixian Formation (129.4–124 Ma)
<i>Dakotaraptor</i>	Bone Butte, Harding County, SD	Hell Creek Formation (72.1 – 66.0 Ma)
<i>Daspletosaurus</i>	right bank, Sand Creek, Alberta, Canada	Oldman Formation (77–72.1 Ma)
<i>Deinonychus antirrhopus</i>	Cashen Pocket, Big Horn County, MT	Cloverly Formation (125–100.5 Ma)
<i>Dilong paradoxus</i>	Lujiatun, Beipiao, Liaoning, China	Yixian Formation (129.4–124 Ma)
<i>Dromaeosaurus albertensis</i>	Little Sandhill Creek, Alberta, Canada	Dinosaur Park Formation (83.6–72.1 Ma)
<i>Dryptosaurus</i>	St. Georges, New Castle County, DE	Merchantville Formation (72.1–66.0 Ma)
EK troodontid IGM (SPS) 100/44	Khamareen Us, Dornogov, Mongolia	Barunbayaskaya Formation (105–97 Ma)
<i>Enigmosaurus</i>	Khara Khutul, Dornogov, Mongolia	Bayan Shireh Formation (100.5–83.6 Ma)
<i>Eosinopteryx brevipenna</i>	Jianchang, Liaoning, China	Tiaojishan Formation (163.5–157.3 Ma)
<i>Eotyrannus lengi</i>	Isle of Wight, England	Wessex Formation (129.4–125 Ma)
<i>Epidexipteryx</i>	Daohugou, Ningcheng, Nei Mongol, China	Tiaojishan Formation (168.3–155 Ma)
<i>Erliansaurus</i>	Sanhangobi, Nei Mongol, China	Iren Dabasu Formation (83.6–66.0 Ma)
<i>Erlikosaurus andrewsi</i>	Bayshin Tsav, Omnogov, Mongolia	Bayan Shireh Formation (100.5–83.6 Ma)
<i>Falcarius</i>	Crystal Geysir Quarry, Grand County, UT	Cedar Mountain Formation (129.4–125 Ma)
<i>Gallimimus bullatus</i>	Western Sayr, Nemegt, Omnogov, Mongolia	Nemegt Formation (72.1–66.0 Ma)
<i>Garudimimus brevipes</i>	Bayshin Tsav, Omnogov, Mongolia	Bayan Shireh Formation (100.5–83.6 Ma)
<i>Gobipteryx</i>	Ukhaa Tolgod, Omnogov, Mongolia	Djadokhta Formation (76–70 Ma)
<i>Gorgosaurus libratus</i>	Sand Creek, Alberta, Canada	Dinosaur Park Formation (77–72.1 Ma)

APPENDIX *continued*

Taxon	Modern Locality	Formation and Age
<i>Graciliraptor lujiatunensis</i>	Lujiatun village, Beipiao, Liaoning, China	Yixian Formation (129.4–124 Ma)
<i>Guanlong</i>	Wucuiwan, Xinjiang, China	Shishugou Formation (163.5–157.3 Ma)
<i>Haplocheirus</i>	Wucuiwan, Xinjiang, China	Shishugou Formation (163.5–157.3 Ma)
<i>Harpymimus okladnikovi</i>	Khuren-Dukh, Dornogov, Mongolia	Khuren Dukh Formation (132.6–125 Ma)
<i>Hesperonychus</i>	Cripple Creek, Alberta, Canada	Dinosaur Park Formation (76.5–72.1 Ma)
<i>Hesperornis</i>	Goblin Hollow, Logan County, KS	Niobrara Formation (89.8–72.1 Ma)
<i>Hongshanornis longicresta</i>	Shifo, Ningcheng, Nei Mongol, China	Yixian Formation (129.4–124 Ma)
<i>Huaxiagnathus orientalis</i>	Dabangou, Beipiao, Liaoning, China	Yixian Formation (129.4–124 Ma)
IVPP V22530	Elesita, Nei Mongol, China	Bayan Gobi Formation (125–100.5 Ma)
<i>Iaceornis marshii</i>	Smoky Hill River, 5 miles W Russell Springs, Logan County, KS	Niobrara Formation (89.8–83.6 Ma)
<i>Ichthyornis</i>	Watino, Alberta, Canada	Kaskapau Formation (93.9–83.6 Ma)
<i>Incisivosaurus gauthieri</i>	Lujiatun village, Beipiao, Liaoning, China	Yixian Formation (129.4–124 Ma)
<i>Ingenia yanshani (Ajancingenia yanshini)</i>	Khermin Tsav, Omnogov, Mongolia	Barun Goyot Formation (72.1–66.0 Ma)
<i>Jeholornis prima</i>	Dapingfang, Chaoyang, Liaoning, China	Jiufotang Formation (129.4–120 Ma)
<i>Jinfengopteryx elegans</i>	Longfengshan Hill, Hebei, China	Huajiyang Formation (132.6–125 Ma)
<i>Jixiangornis orientalis</i>	Baicaigou, Toutai, Liaoning, China	Yixian Formation (129.4–124 Ma)
<i>Juratyrrant</i>	Rope Lake Head / Freshwater Steps, Dorset, England, United Kingdom	Kimmeridge Clay Formation (152.1–145 Ma)
<i>Juravenator starki</i>	Stark Quarry, Schamhaupten, Bayern, Germany	Painten Formation (154–152.1 Ma)
<i>Kileskus</i>	Berezovsk Quarry, Krasnoyarsk, Russian Federation	Itat Formation (168.3–166.1 Ma)
<i>Liaoningornis longidigitris</i>	Southwest of Beipiao City, Liaoning, China	Yixian Formation (129.4–124 Ma)
<i>Limenavis patagonica</i>	Salitral Moreno, Río Negro, Argentina	Allen Formation (75.0–69.0 Ma)
<i>Linhenykus</i>	Gate Area, Bayan Mandahu, Nei Mongol, China	Wulansuhai Formation (83.6–72.1 Ma)
<i>Linheraptor</i>	Gate Area, Bayan Mandahu, Nei Mongol, China	Wulansuhai Formation (83.6–72.1 Ma)

APPENDIX *continued*

Taxon	Modern Locality	Formation and Age
<i>Luanchuanraptor</i>	Qiupa, Luanchuan Basin, Henan, China	Qiupa Formation (83.6–66.0 Ma)
<i>Mahakala omnogovae</i>	Tögrögiin Shiree, Omnogov, Mongolia	Djadokhta Formation (78.0–72.1 Ma)
<i>Mei long</i>	Lujiatun village, Beipiao, Liaoning, China	Yixian Formation (129.4–124 Ma)
<i>Microraptor zhaoianus</i>	Chaoyang, Liaoning, China	Jiufotang Formation (125–120 Ma)
<i>Microvenator celer</i>	Crooked Creek, Big Horn County, WY	Cloverly Formation (125–100.5 Ma)
<i>Mirischia</i>	Araripina region, Pernambuco, Brazil	Santana Formation (113–100.5 Ma)
<i>Mononykus olecranus</i>	Bugin Tsav, Omnogov, Mongolia	Nemegt Formation (72.1–66.0 Ma)
<i>Nanshiungosaurus bohlini</i>	Mazongshan, Gansu, China	Nanxiong Formation (83.6–66.0 Ma)
<i>Neimongosaurus</i>	Sanhangobi, Nei Mongol, China	Iren Dabasu Formation (83.6–66.0 Ma)
<i>Neuquenornis volans</i>	Boca del Sapo, Universidad Nacional del Comahue, Neuquén, Argentina	Bajo de la Carpa Formation (86.3–83.6 Ma)
<i>Neuquenraptor/Uenlagia</i>	Sierra del Portezuelo, Neuquén, Argentina	Portezuelo Formation (92–87 Ma)
<i>Nothronychus</i>	Big Water, Tropic Shale, UT	Tropic Shale Formation (96–89.8 Ma)
<i>Nqwebasaurus</i>	5 km west of Kirkwood, Eastern Cape, South Africa	Kirkwood Formation (145–132.6 Ma)
<i>Ornitholestes hermanni</i>	Bone Cabin Quarry, Albany County, WY	Morrison Formation (157.3–145 Ma)
<i>Ornithomimus edmonticus</i>	Red Deer River, Alberta, Canada	Horseshoe Canyon Formation (76.5–66.0 Ma)
<i>Oviraptor philoceratops</i>	Shabarakh Usu, Omnogov, Mongolia	Djadokhta Formation (83.6–72.1 Ma)
<i>Parvicursor</i>	Khulsan, Omnogov, Mongolia	Barun Goyot Formation (83.6–72.1 Ma)
<i>Patagonykus puertai</i>	Sierra del Portezuelo, Neuquén, Argentina	Portezuelo Formation (93.9–86.3 Ma)
<i>Patagopteryx deferrariisi</i>	Boca del Sapo, Universidad Nacional del Comahue, Neuquén, Argentina	Bajo de la Carpa Formation (86.3–83.6 Ma)
<i>Pelecanimimus polyodon</i>	Las Hoyas, Cuenca, Spain	La Huérguina Formation, (128.5–125 Ma)
<i>Pengornis houi</i>	Dapingfang, Chaoyang, Liaoning, China	Jiufotang Formation (125–120 Ma)
<i>Proceratosaurus bradleyi</i>	Minchinhampton reservoir, England	White Limestone Formation (168.3–166.1 Ma)
<i>Qiupalong</i>	Qiupa, Luanchuan Basin, Henan, China	Qiupa Formation (83.6–66.0 Ma)

APPENDIX *continued*

Taxon	Modern Locality	Formation and Age
<i>Rahonavis ostromi</i>	Mahajanga, Madagascar	Maevarano Formation (72.1–66.0 Ma)
<i>Rinchenia mongoliensis</i>	Altan Ula, Omnogov, Mongolia	Nemegt Formation (72.1–66.0 Ma)
<i>Sapeornis chaoyangensis</i>	Dapingfang, Chaoyang, Liaoning, China	Jiufotang Formation (129.4–120 Ma)
<i>Saurornithoides mongoliensis</i>	Shabarakh Usu, Omnogov, Mongolia	Djadokhta Formation (83.6–72.1 Ma)
<i>Saurornitholestes langstoni</i>	Stevenville Railway Grade, Alberta, Canada	Dinosaur Park Formation (77–72.1 Ma)
<i>Segnosaurus galbinensis</i>	Amtgay, Omnogov, Mongolia	Bayan Shireh Formation (100.5–83.6 Ma)
<i>Shanag ashile</i>	Öösh, Ovorkhangai, Mongolia	Öösh Formation (145–129.4 Ma)
<i>Shenzhousaurus orientalis</i>	Sihetun, Beipiao, Liaoning, China	Yixian Formation (129.4–124 Ma)
<i>Shuvuuia deserti</i>	Ukhaa Tolgod, Omnogov, Mongolia	Djadokhta Formation (83.6–72.1 Ma)
<i>Sinocalliopteryx</i>	Hengdaozi, Sihetun, Liaoning, China	Yixian Formation (129.4–124 Ma)
<i>Sinornithoides youngi</i>	Huamuxiao, Ordos Basin, Nei Mongol, China	Ejinhoro Formation (139.8–100.5 Ma)
<i>Sinornithomimus</i>	Suhongtu, Ulan Suhai, Nei Mongol, China	Ulanusuhai Formation (93.9–89.8 Ma)
<i>Sinornithosaurus millenii</i>	Sihetun, Beipiao, Liaoning, China	Yixian Formation (129.4–124 Ma)
<i>Sinosauropteryx prima</i>	Sihetun, Beipiao, Liaoning, China	Yixian Formation (129.4–124 Ma)
<i>Sinotyrannus</i>	Dachengzi, Kazuo, Liaoning, China	Jiufotang Formation (125–120 Ma)
<i>Sinovenator changii</i>	Yanzigou, Shanyuan, Liaoning, China	Yixian Formation (129.4–124 Ma)
<i>Sinusonasus magnodens</i>	Lujiatun village, Beipiao, Liaoning, China	Yixian Formation (129.4–124 Ma)
<i>Songlingornis</i>	Beishan Quarry, Boluochi, Liaoning, China	Jiufotang Formation (125–120 Ma)
<i>Struthiomimus altus</i>	Ross Coulee, Irvine, Alberta, Canada	Dinosaur Park Formation (76.5–66.0 Ma)
<i>Suzhousaurus</i>	Yujingzi Basin, Jiuquan, Gansu, China	Xinminbao Group (125–100.5 Ma)
<i>Tanycolagreus</i>	Cleveland-Lloyd Dinosaur Quarry, Emery County, UT	Morrison Formation (157.3–145 Ma)
<i>Teratophoneus</i>	Horse Mountain, UT	Kaiparowits Formation (77–72.1 Ma)
<i>Therizinosaurus</i>	Nemegt, Omnogov, Mongolia	Nemegt Formation (72.1–66.0 Ma)

APPENDIX *continued*

Taxon	Modern Locality	Formation and Age
<i>Tianyuraptor ostromi</i>	Dawangzhangzi, Lingyuan, Liaoning, China	Yixian Formation (129.4–124 Ma)
<i>Troodon formosus</i>	Steveville Railway Grade, Alberta, Canada	Dinosaur Park Formation (76–66 Ma)
<i>Tsaagan mangas</i>	Xanadu, Ukhaa Tolgod, Omnogov, Mongolia	Djadokhta Formation (83.6–72.1 Ma)
<i>Tugulusaurus</i>	Wuerho, Karamay, Xinjiang, China	Lianmugin Formation (122.5–99.7 Ma)
<i>Tyrannosaurus rex</i>	Crowsnest Pass, Alberta, Canada	Willow Creek Formation (72.1–66.0 Ma)
<i>Utahraptor</i>	Robert Gaston Quarry, Grand County, UT	Cedar Mountain Formation (128–120 Ma)
<i>Velociraptor mongoliensis</i>	Shabarakh Usu, Omnogov, Mongolia	Djadokhta Formation (83.6–72.1 Ma)
<i>Vorona</i>	Mahajanga, Madagascar	Maevarano Formation (72.1–66.0 Ma)
<i>Xiaotingia zhengi</i>	Daxishan, Linglongta, Jianchang Liaoning, China	Tiaojishan Formation (163.5–157.3 Ma)
<i>Xiongguanlong</i>	White Ghost Castle, Yujingzi Basin, Gansu, China	Xinminbao Group (125–100.5 Ma)
<i>Xixianykus</i>	Zhoujiagou, Yangcheng, Henan, China	Majiacun Formation (89.8–83.6 Ma)
<i>Xixiasaurus henanensis</i>	Songgou, Xixia, Nanyang, Henan, China	Majiacun Formation (89.8–83.6 Ma)
<i>Yanornis martini</i>	Dapingfang, Chaoyang, Liaoning, China	Jiufotang Formation (125–120 Ma)
<i>Yi</i>	Mutoudeng, Hebei, China	Tiaojishan Formation (168.3–155 Ma)
<i>Yixianornis grabaui</i>	Qianyang, Yixian, Liaoning, China	Jiufotang Formation (125–120 Ma)
<i>Yurgovuchia</i>	Don's Place, Grand County, UT	Cedar Mountain Formation (128–120 Ma)
<i>Zanabazar junior</i>	Bugin Tsav, Omnogov, Mongolia	Nemegt Formation (72.1–66.0 Ma)
<i>Zhenyuanlong</i>	Sihedang, Lingyuan, Liaoning, China	Yixian Formation (129.4–124 Ma)
<i>Zuolong</i>	Wucuiwan, Xinjiang, China	Shishugou Formation (163.5–157.3 Ma)

