On the Origin of Nightjars (Caprimulgidae): Perspectives from the Fossil Record

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Abstract Fossils represent the only direct evidence for the ancestral morphologies, antiquity, and historical geographic distributions of life on Earth. The fossil record of the avian clade Strisores (which includes nightjars, oilbirds, potoos, frogmouths, owlet-nightjars, treeswifts, swifts, and hummingbirds) has been richly documented by avian standards, with well-corroborated stem-group representatives of the oilbird, potoo, frogmouth, swift, and hummingbird lineages all having been identified based on fossils dating to the Paleogene Period (66–23.03 million years ago). However, current understanding of the nightjar fossil record remains limited. Nonetheless, new fossil descriptions and restudy of previously known specimens, together with findings from recent phylogenomic studies, have started to provide insight into nightjar evolutionary history. In particular, the recent reinterpretation of the Archaeotrogonidae, a group of fossil birds represented by numerous specimens from the Paleogene of Europe, as stem-group nightjars may offer valuable information on the origins of nightjar morphology (including soft tissue anatomy), ecology, and behavior. Although available fossil material of total-group nightjars tends to be relatively incomplete, the integration of fossil data into future studies holds great potential for elucidating the evolution, timing of origin, and biogeography of this distinctive and mysterious group of birds.

Nightjars (Caprimulgidae) are members of the avian clade Strisores, along with the Oilbird (*Steatornis caripensis*, the only extant species within Steatornithidae), potoos (Nyctibiidae), frogmouths (Podargidae), owlet-nightjars (Aegothelidae), treeswifts (Hemiprocnidae), swifts (Apodidae), and hummingbirds (Trochilidae). Treeswifts, swifts, and hummingbirds in turn form a clade of diurnal birds, Apodiformes, whereas nocturnal and crepuscular habits predominate in the other major groups of Strisores. Of these nocturnal and crepuscular lineages, the nightjars are currently the most diverse and widely distributed, being represented by over 90 extant species and found on all continents except for Antarctica (Cleere 2010; Billerman et al. 2022).

Despite their generally small body size and delicate skeletons, most major clades of Strisores have a richly documented fossil record by avian standards. Stem-group representatives of Steatornithidae, Nyctibiidae, Podargidae, Apodiformes, Apodidae, and Trochilidae have all been identified based on well-preserved fossils dating to the Paleogene Period (66–23.03 Ma [million years ago]). By contrast, our understanding of the nightjar fossil record remains sparse (Fig. 1; Mayr 2017a; Chen and Field 2020; Mayr 2022). Even so, new fossil discoveries and reinterpretations of previously described specimens, combined with insights from recent phylogenomic studies, have begun to shed light on the evolutionary history of this distinctive and mysterious group of birds.

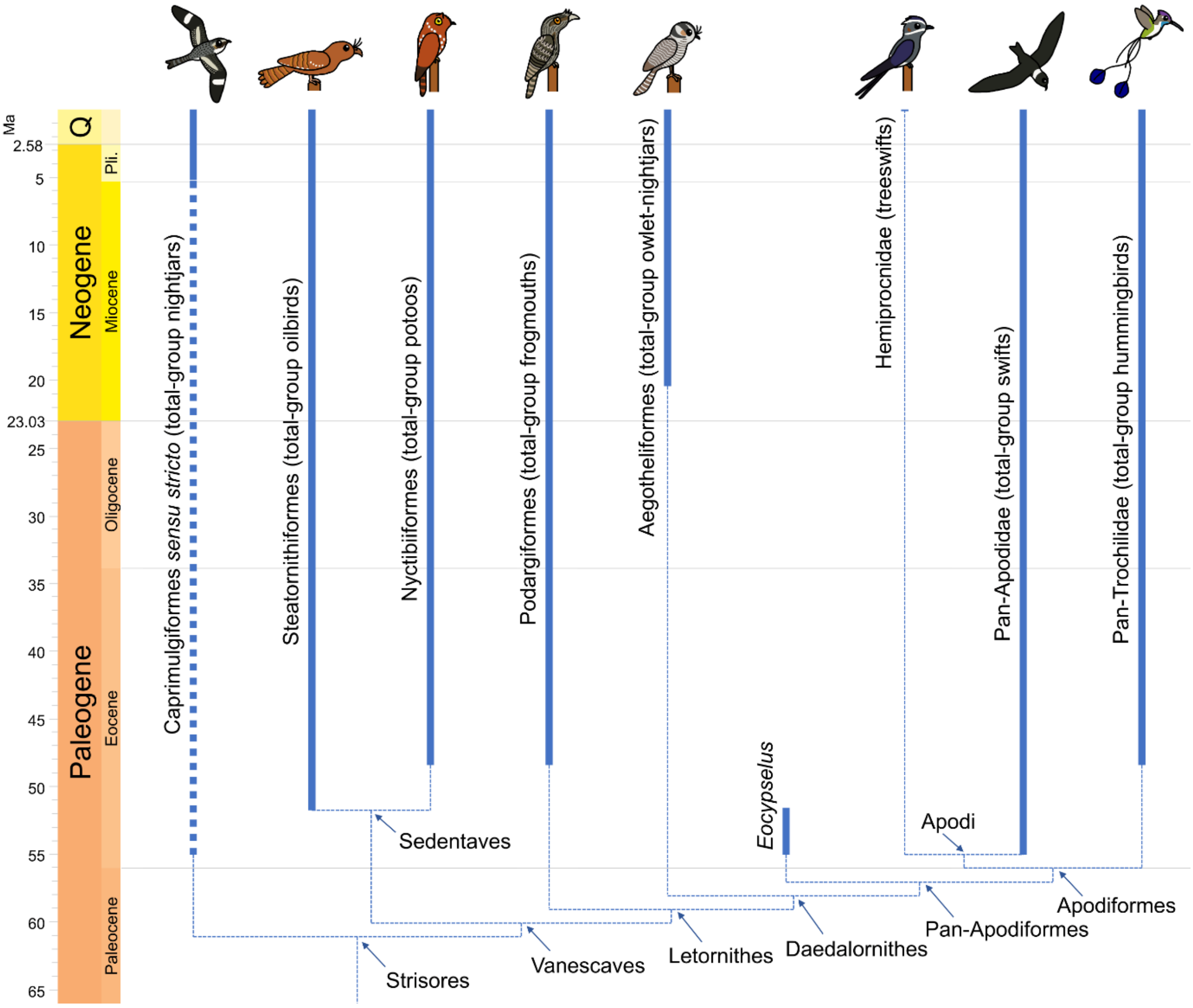

Figure 1. Phylogenetic interrelationships and stratigraphic distribution of Strisores. Phylogenetic topology based on Prum et al. (2015), Chen et al. (2019), White and Braun (2019), and Kuhl et al. (2021). Stratigraphic ranges based on reviews by Chen and Field (2020) and Mayr (2022), with additional information on numerical ages from Ksepka and Clarke (2015) and Lenz et al. (2015). Clade names follow Chen and Field (2020). Dotted line for Caprimulgiformes *sensu stricto* indicates uncertainty in the assignment of Paleogene fossils to this clade (see main text). Depicted divergence times are arbitrary, though a Paleocene origin of crown-group Strisores has been supported by recent studies (Jarvis et al. 2014; Prum et al. 2015; Kimball et al. 2019; Kuhl et al. 2021).

A Note on Phylogenetic Terminology

In discussing the phylogenetic interrelationships among extant and fossil organisms, taxa may be identified as belonging to crown and stem groups. A crown group represents the least inclusive clade encompassing all extant members of a given lineage. Each crown group has a corresponding stem group, a paraphyletic assemblage consisting of all extinct taxa more closely related to said crown group than to any other extant organism, but are outside of the crown group itself. A crown group and its associated stem group are collectively known as the total group or pan group.

Anatomical Characteristics of Nightjars

Evaluating the phylogenetic affinities of fossil life forms typically relies on a thorough understanding of comparative morphology, given that sequenceable genetic data have yet to be recovered from organismal remains older than ~2 Ma (Allentoft et al. 2012; Bailleul and Li 2021; Kjær et al. 2022). Although a clade uniting all extant members of Strisores only became well corroborated following the results of large-scale molecular phylogenetic analyses (Ericson et al. 2006; Hackett et al. 2008; Jarvis et al. 2014; Prum et al. 2015; Reddy et al. 2017; Kuhl et al. 2021), close affinities between at least some nocturnal strisoreans and apodiforms have long been suspected based on anatomical similarities (Huxley 1867; Cracraft 1981; Olson 1985a; Cracraft 1988; Mayr 2002; Livezey and Zusi 2007). Derived phenotypic characters inferred to have been ancestrally present in Strisores include a short, broad beak with large nasal openings reaching into its tip, a short orbital process of the quadrate (Cracraft, 1981), a deep transverse sulcus on the humerus (Cracraft, 1988), an elongate ventral ramus (crus longum) of the ulnar carpal (Mayr, 2010), a prominent caudolaterally-directed process on the palatine, a pointed mandibular symphysis, eighteen or fewer presacral vertebrae, and rictal bristles (Chen et al. 2019), though many of these features have been lost or heavily modified in some members of the clade (Cracraft 1981; Chen et al.

2019). Similarly, a quadrate with a laterally facing quadratojugal cotyle and a reduced caudal condyle is commonly (though not universally) present in Strisores (Mayr 2021). In addition, a distinctive developmental trajectory of the skull is likely shared by all species within this group except for the longer-billed frogmouths and hummingbirds (Navalón et al. 2021), and many strisoreans exhibit the physiological capacity to enter torpor (Braun and Huddleston 2009; Mayr 2010).

Nightjars can be distinguished from other Strisores in that their fourth toe has only four phalanges instead of five (Fig. 2) and the claw on their third toe is pectinate, or comb-shaped (Fig. 3) (Manegold 2010). Many of their other distinctive morphological features are also shared with potoos (Huxley, 1867; Cracraft, 1981; Mayr, 2002; Costa and Donatelli, 2009; Mayr, 2010; Chen et al., 2019; Costa et al., 2021), including extreme lateral expansion of the palatine, an intraramal joint in the mandible (Huxley, 1867; Bühler, 1970), a bulbous ectethmoid (Cracraft, 1968), a short or absent orbital process of the quadrate, a reduction in the length of the dentary relative to the postdentary mandibular bones (Cracraft, 1981), a strong lateral bowing of the jugal arch (Baumel and Witmer, 1993), a cone-shaped protrusion at the caudal margin of the optic nerve foramen , a strong ventral protrusion of the paroccipital process, a reduced caudal end of the mandible with a short lateral cotyle (Mayr, 2002), and the presence of an intertarsal sesamoid (Mayr, 2010). Furthermore, nightjars and potoos are probably the only members of Strisores that have a tapetum lucidum (Braun and Huddleston 2009; White and Braun 2019).

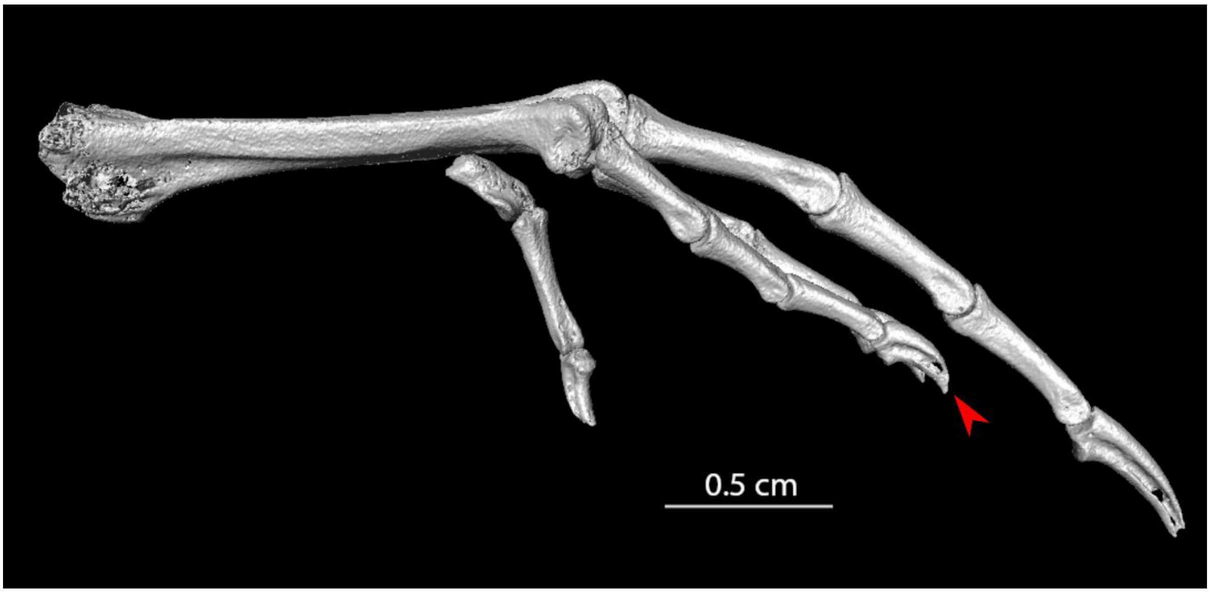

Figure 2. Digital rendering of the right pedal skeleton of a European Nightjar (*Caprimulgus europaeus*; this is an as-yet uncatalogued specimen from the collections of the University of Cambridge Museum of Zoology). Arrowhead indicates the fourth toe, which exhibits an apomorphic reduction in its number of phalanges.

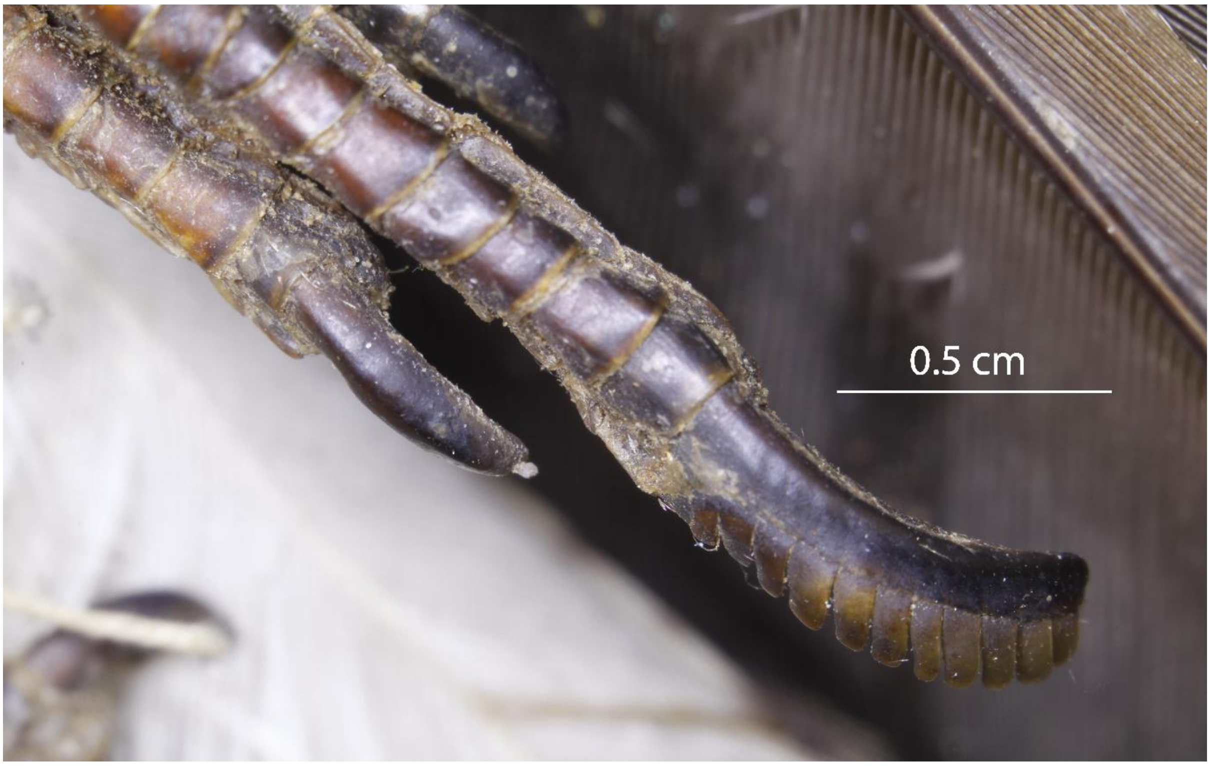

Figure 3. Left foot of a Nacunda Nighthawk (*Chordeiles nacunda*, specimen number UMZC 21/Cap/14/a/2) showing the pectinate claw of the third toe characteristic of nightjars. (UMZC: University of Cambridge Museum of Zoology.)

Although the numerous similarities between nightjars and potoos have generally led phylogenetic analyses of morphological characters to recover them as extant sister groups (Mayr 2002; Mayr 2010; Ksepka et al. 2013; Costa et al. 2021), such a relationship has not been supported by phylogenomic studies (Hackett et al. 2008; Prum et al. 2015; Reddy et al. 2017; White and Braun 2019; Kuhl et al. 2021). The most recent analyses of molecular or combined morphological–molecular datasets instead suggest that nightjars are the extant sister group to Vanescaves, a clade uniting all other Strisores (Fig. 1; Prum et al. 2015; Chen et al. 2019; White and Braun 2019; Kuhl et al. 2021). At least one morphological feature potentially corroborating this hypothesis has been identified (Chen et al. 2019); namely, nightjars are the only members of Strisores that retain the plesiomorphic avian condition of an unreduced lacrimal, suggesting that its reduction is a synapomorphy of Vanescaves (Cracraft 1968; Costa and Donatelli 2009). Nightjars additionally differ from potoos in having a long rostromedial process of the palatine (Costa and Donatelli 2009; Costa et al. 2021) and a more strongly projecting olecranon process of the ulna (Chen et al. 2019).

Current understanding of the phylogenetic interrelationships within Strisores suggests that many of the morphological similarities between nightjars and potoos either evolved independently in these two lineages or were already present ancestrally in Strisores (and have been secondarily lost in some extant strisorean subgroups). It has been hypothesized that the last common ancestor of Strisores was an aerial insectivore (Chen et al. 2019), a lifestyle that is still maintained by extant nightjars and potoos, which may explain some of the distinctive similarities in their cranial skeletons (Bühler 1970; Costa and Donatelli 2009; Mayr 2010).

The fact that nocturnal and crepuscular strisoreans form a paraphyletic assemblage with respect to apodiforms also raises the possibility that the last common ancestor of Strisores was predominantly active in low-light conditions (Mayr 2010; Smithwick 2019; White and Braun 2019). However, the variability of documented nocturnal visual specializations among Strisores (Rojas et al. 2004; Braun and Huddleston 2009) might alternatively imply multiple origins of nocturnality within the clade (Mayr 2010; White and Braun 2019). Future research in paleontology, developmental biology, sensory ecology, and comparative genomics may further illuminate the extent to which adaptations for aerial insectivory and nocturnality are plesiomorphic for Strisores as a whole.

Putative Total-group Nightjars of the Paleogene

Based on recent molecular clock estimates, total-group nightjars may have originated in the Paleocene Epoch (approximately 61–64 Ma; Jarvis et al. 2014; Prum et al. 2015; Kimball et al. 2019; Kuhl et al. 2021). This is consistent with the observation that identifiable members of other strisorean subclades have been found in early Eocene fossil deposits (Harrison 1984; Olson 1987; Nesbitt et al. 2011; Ksepka et al. 2013), but as mentioned previously, unambiguous fossils of Paleogene total-group nightjars are scant by comparison (Fig. 4). Among the oldest fossils that have been tentatively referred to the nightjar total group are a humerus, a radius, and a tarsometatarsus from the early Eocene Nanjemoy Formation of Virginia, USA (approximately 54–53 Ma; Mayr et al. 2022), apparently belonging to a bird around the same size as the extant Pauraque (*Nyctidromus albicollis*) (Olson 1999). However, the affinities of these specimens have not been verified by the identification of diagnostic nightjar apomorphies (Mayr 2016; Mayr 2022; Mayr et al. 2022). Olson (1999) also considered the carpometacarpus of a smaller bird from the Nanjemoy Formation to represent an additional nightjar taxon, but this specimen was re-evaluated as a member of stem-group Apodiformes by Mayr (2016).

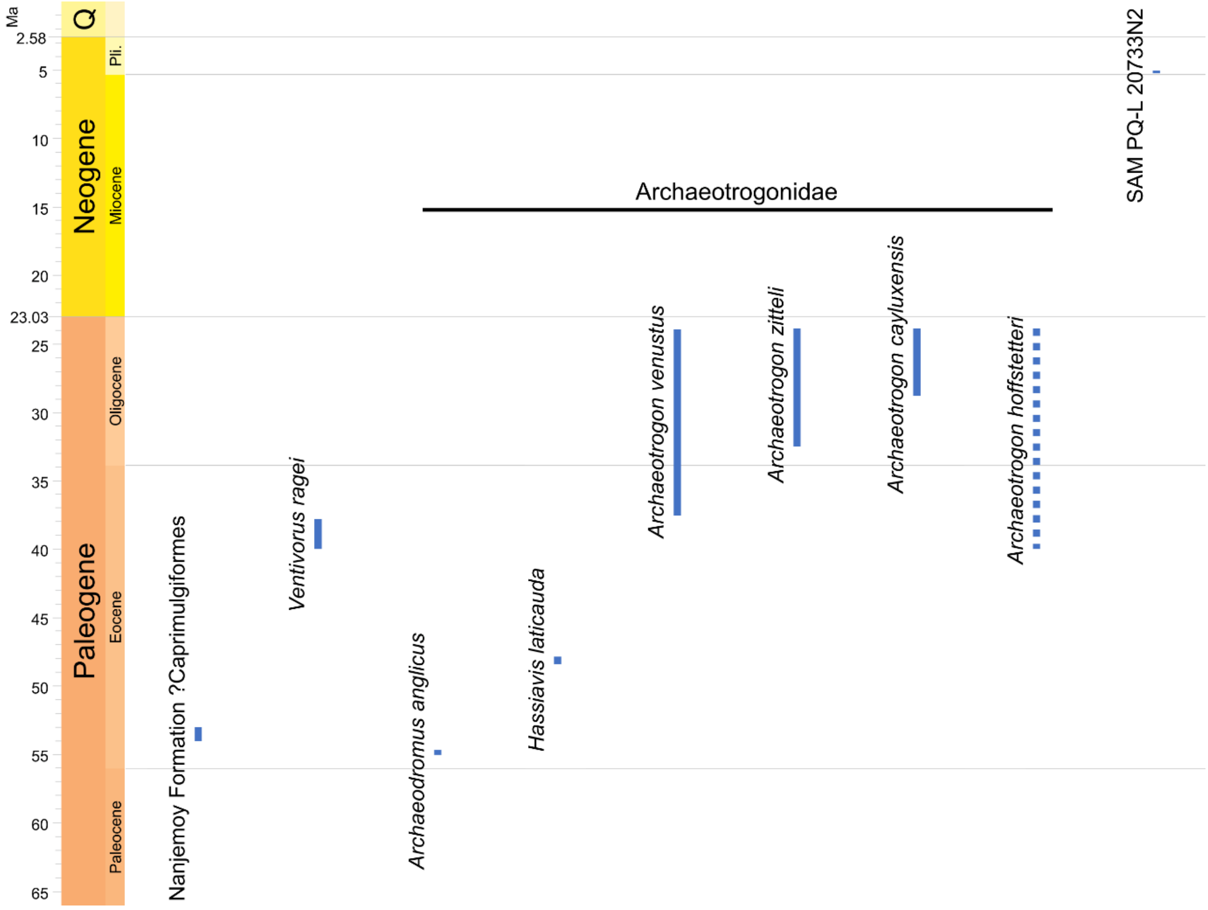

Figure 4. Stratigraphic distribution of putative pre-Quaternary total-group nightjar fossils (see main text for details on individual taxa). Stratigraphic ranges follow Mourer-Chauviré (2006), Manegold (2010), Mayr (2021), and Mayr et al. (2022), with additional information on numerical ages from Roberts et al. (2011), Lenz et al. (2015), and Solé et al. (2020). Dotted line for *Archaeotrogon hoffstetteri* indicates its uncertain stratigraphic provenance from within the Quercy Phosphorites.

Another putative Paleogene fossil nightjar is *Ventivorus ragei*, represented by two partial coracoids from the middle Eocene (Bartonian, 41.2–37.8 Ma) Le Bretou site in the Quercy Phosphorites of France (Mourer-Chauviré 1988). The coracoid of *Ventivorus* resembles that of some extant nightjars in having a reduced procoracoid process, but notably differs in being unusually stout and having an omosternally narrow supracoracoid sulcus (Manegold 2010). More complete specimens will probably be needed to firmly establish the phylogenetic placement of *Ventivorus* (Mayr 2005; Mayr 2022).

Archaeotrogonidae is a group of extinct Paleogene birds that were recently hypothesized to be stem-group nightjars (Mayr 2021). If this hypothesis is accurate, archaeotrogonids would represent the best-known total-group nightjars from the Paleogene. These birds are known from the Eocene–Oligocene of Europe, with their remains being particularly abundant in the Quercy Phosphorites (Mourer-Chauviré 1980; Mayr 2022). Six species have been described to date: *Archaeodromus anglicus* from the early Eocene London Clay Formation (55–54.6 Ma) of England (Mayr 2021), *Hassiavis laticauda* from the middle Eocene Messel Formation (48 Ma; Lenz et al. 2015) of Germany (Mayr 1998), and four species of *Archaeotrogon* from the Quercy Phosphorites, namely the late Eocene–late Oligocene *A. venustus*, the early–late Oligocene *A. zitteli*, the late Oligocene *A. cayluxensis*, and *A. hoffstetteri*, which derives from an unknown horizon within the Quercy Phosphorites (Mourer-Chauviré 1980; Mourer-Chauviré 1995; Mourer-Chauviré 2006). The most completely known species are *Archaeotrogon venustus*, for which nearly all major appendicular bones have been found (Mourer-Chauviré 1980), and *Hassiavis laticauda*, for which multiple articulated skeletons have been discovered with preserved remains of plumage (Mayr 1998; Mayr 2004). One exceptionally preserved specimen referred to *Hassiavis* may represent a second species within that genus (Mayr 2021).

Archaeotrogonids are characterized by a stout humerus with a prominent, proximally protruding humeral head and a proximodistally elongated dorsal tubercle, a coracoid with a short, laterally convex lateral process, and a distally broad tibiotarsus with widely splayed condyles (Mayr 1998; Mayr 2021). They closely resemble trogons (Trogoniformes) in humeral and coracoid morphology, which inspired their name and initial interpretation as total-group trogons (Milne-Edwards 1892; Mourer-Chauviré 1980). However, similarities between archaeotrogonids and nightjars were also noted by Mourer-Chauviré (1980), and reports of archaeotrogonid cranial material revealed characteristic strisorean features such as a short, broad beak, as well as a quadrate in which the orbital process and caudal condyle are reduced and the quadratojugal cotyle faces dorsally (Mourer-Chauviré 1995; Mayr 2004; Mayr 2021). Despite this, the placement of archaeotrogonids within Strisores has largely remained unresolved and understudied.

Chen et al. (2019) recovered *Hassiavis* as a stem-group owlet-nightjar in a combined morphological–molecular analysis and interpreted the hooked acrocoracoid process of its coracoid as support for a placement within Daedalornithes (the clade uniting owlet-nightjars and apodiforms), though *Archaeotrogon*, which lacks a hooked acrocoracoid process, was not included in this study. Mayr (2021) conversely pointed out that the hooked acrocoracoid process in *Hassiavis* is formed differently compared to that of owlet-nightjars, and recovered stronger support for archaeotrogonids as stem-group nightjars in a morphological phylogenetic analysis with the relationships of extant taxa constrained to a molecular scaffold. That study additionally noted that the absence of a supracoracoid nerve foramen of the coracoid suggests that archaeotrogonids are unlikely to be members of crown-group Daedalornithes. However, Mayr (2021) acknowledged that a position along the stem group of Daedalornithes may be a plausible alternative placement for archaeotrogonids, given that *Archaeodromus* shares with extant daedalornitheans pneumatic foramina in the caudal surface of the otic process of the quadrate. Meanwhile, features that instead support archaeotrogonids as stem-group nightjars include a large dorsal tubercle on the humerus, two distinct tubercles on the proximal ulna for attachment of the biceps brachii muscle, and a deep scapulotricipital impression on the ulna (Mayr 2021). *Archaeodromus* and

Archaeotrogon hoffstetteri (but not other species of *Archaeotrogon*) also resemble crown-group nightjars in having a transverse ridge within the capital incisure of the humerus (Mourer-Chauviré 1980; Mayr 2021).

The cranial anatomy of archaeotrogonids suggests that they may have been aerial insectivores, and therefore ecologically similar to nightjars and many other strisoreans (Mayr 2004; Mayr 2021). Furthermore, the preserved feathering of the wings and tail in *Hassiavis* indicates similarities in the proportions of the remiges and rectrices to those of extant nightjars (Mayr 1998; Mayr 2004), which is also consistent with an aerial foraging strategy. Some specimens of *Hassiavis* preserve barring on the tail feathers (Mayr 1998; Mayr 2004), a color pattern found only in nocturnal species within Strisores (Smithwick 2019; Mayr 2022). If archaeotrogonids are stem-group nightjars, these features may support the hypothesis that aerial insectivory and nocturnality originated early in the evolutionary history of total-group nightjars or of Strisores in general.

Archaeotrogon and undescribed specimens of *Archaeodromus* (but not *Hassiavis*) are unusual among Strisores in that the extensor process of their carpometacarpus is spur-like, suggesting that their wings may have been used in combat behavior (Milne-Edwards 1892; Mourer-Chauviré 1980; Mayr 2021; Mayr 2022). The absence of such features in other Strisores is consistent with studies that have found the energetic cost of bearing specialized bony weaponry to be particularly high for small, frequent-flying birds (Menezes and Palaoro 2022). Therefore, despite having plausibly been aerial foragers, at least some archaeotrogonids may have been less suited to sustained flights than extant nightjars are.

Archaeotrogonids also noticeably differ from crown-group nightjars in their hindlimb anatomy, especially in having a wide intertarsal joint and retaining five phalanges in the fourth toe (Mayr 2021). It has been proposed that the hindlimb specializations of crown-group nightjars may reflect their ground-nesting habits, which are unique among extant strisoreans (Mayr 2021). On the other hand, the position of nightjars as the extant sister group to other Strisores and the strong probability that a primarily terrestrial ecology was exhibited by the early Cenozoic ancestors of many modern birds and mammals (Field et al. 2018; Hughes et al. 2021) may suggest that ground-nesting in nightjars is plesiomorphic for Strisores and lost along the stem lineage of Vanescaves. Future research will be needed to elucidate the evolution of substrate use in strisoreans, however. Regardless of their precise affinities, archaeotrogonids further illustrate the complex patterns of trait acquisition and ecological transitions that appear to have characterized the early evolutionary history of nightjars and other Strisores.

Neogene–Quaternary Nightjar Fossils and the Diversification of Crown-group Nightjars

The oldest fossil that has been explicitly referred to the nightjar crown group is a coracoid (specimen number SAM PQ-L 20733N2) from the early Pliocene Varswater Formation (5.15 Ma; Roberts et al. 2011) of South Africa (Manegold 2010). Archaeotrogonids belonging to the nightjar stem group would imply a gap of at least 17 million years (including the entirety of the Miocene Epoch) from which no fossils of total-group nightjars have been formally described (Fig. 4), though Mlíkovský (2002) mentioned undescribed specimens from the early Miocene of Czechia and Germany that may be referable to Caprimulgiformes. SAM PQ-L 20733N2 was considered a crown-group nightjar on the basis of a greatly reduced procoracoid process and an articular facet for the furcula that is confluent with the brachial tubercle, characters that are shared with the clade uniting all extant nightjars except for *Eurostopodus* and *Lyncornis* (Manegold 2010).

All other fossils of crown-group nightjars that have been reported in the scientific literature are Quaternary in age. One extinct nightjar species that has been named from Quaternary fossil material is *Caprimulgus fossilis*, which was originally proposed to be a potential subspecies of the extant European Nightjar (*Caprimulgus europaeus*) based on a robust coracoid and first phalanx of the major wing digit from the early Pleistocene of Romania (Čapek 1917). Jánossy (1977) considered the robusticity of its coracoid sufficient to diagnose *C. fossilis* as a distinct species, and additionally referred a fragmentary coracoid that had been previously described by Jánossy (1972) from the early Pleistocene of Czechia to the same taxon. Jánossy (1977) also coined the new name *C. capeki* for this species, possibly because Čapek (1917) had only provisionally proposed the name *C. e. fossilis* on the condition that the taxon could be distinguished from the extant *C. e. meridionalis*. However, Mlíkovský (2002) pointed out that such conditional naming is permitted by the International Code of Zoological Nomenclature (ICZN) for scientific names coined prior to 1961 and thus, *C. fossilis* would be the correct name for this taxon. Nonetheless, the taxonomic status of *C. fossilis* is unresolved, as recent authors have alternatively retained it as its own species (Tyrberg 2008a) or considered it conspecific with *C. europaeus* (Mlíkovský 2002; Kessler 2019). Detailed restudy of the original fossils and the discovery of more complete material may be required to clarify the relationships of *C. fossilis* to extant nightjars.

"*Caprimulgus*" *piurensis* was named by Campbell (1979) based on a coracoid and a proximal carpometacarpus from the Late Pleistocene Talara Tar Seeps of Peru. It is distinguished from three similarly sized South American extant nightjar species—the Band-winged Nightjar (*Systellura longirostris*), the Little Nightjar (*Setopagis parvula*), and the White-tailed Nightjar (*Hydropsalis cayennensis*)—by a combination of coracoid characters, including a small, narrow acrocoracoid process and a deep impression for the attachment of the acrocoracohumeral ligament that is subdivided by a high ridge. The genus assignment of "*C.*" *piurensis* requires reassessment, given that recent revisions of nightjar genus-level taxonomy have restricted *Caprimulgus* to a clade of Afro-Eurasian species (Han et al. 2010; Sigurðsson and Cracraft 2014). Campbell (1979) considered "*C.*" *piurensis* most similar to the White-tailed Nightjar (formerly *Caprimulgus cayennensis*) among the extant nightjars examined, but noted that skeletal specimens of many South American species were unavailable for comparison.

As reviewed by Brodkorb (1971) and Tyrberg (2008b), other Pleistocene nightjar fossils have been reported from the United States, Brazil, France, Germany, Greece, Italy, Poland, Spain, and possibly the United Kingdom, though the British material was only tentatively identified (Newton 1925) and has since been destroyed (Harrison 1987). In addition to these, nightjar remains have been described from the Pleistocene of Mexico (Steadman et al. 1994), Peru (Campbell 1979), Venezuela (Steadman et al. 2015), the Bahamas (Oswald and Steadman 2018), Hungary (Gál 2008), and possibly Croatia (Lenardić et al. 2018). Many of these specimens have not been identified to species level, but others have been assigned to extant species (Newton 1925; Brodkorb 1971; Campbell 1979; Steadman et al. 1994; Gál 2008; Tyrberg 2008b; Lenardić et al. 2018), including *Nyctidromus albicollis* (Brazil), *Eleothreptus anomalus* (Brazil), *Hydropsalis torquata* (Brazil), *Phalaenoptilus nuttallii* (the United States and Mexico), *Chordeiles acutipennis* (Peru), *Chordeiles minor* (the United States), and *Caprimulgus europaeus* (France, Greece, Hungary, Italy, Poland, Spain, and possibly Croatia and the United Kingdom).

Recent molecular phylogenetic studies have made substantial progress in clarifying the interrelationships of crown-group nightjars (Barrowclough et al. 2006; Larsen et al. 2007; Han et al. 2010; Sigurðsson and Cracraft 2014; White et al. 2016). However, few attempts have been made to estimate the timing of phylogenetic divergences within this clade based on molecular clock analyses. This may be attributable partly to the fact that such analyses require calibration from external sources of data, typically from the fossil record (Benton and Donoghue 2007; Parham et al. 2012), and suitable calibrations for constraining divergences among crown-group nightjars are scarce. For the most part, the incomplete nature of the fossils currently assigned to the nightjar crown group probably prevents a well-corroborated assessment of their phylogenetic affinities, which limits their use as justifiable divergence time calibrations (Parham et al. 2012). In a large-scale study targeting deep divergences across crown-group birds, Prum et al. (2015) estimated the origin of the nightjar crown group as early Oligocene in age (approximately 32–34 Ma), though in the absence of appropriate calibrations for constraining nightjar intra-clade divergences, this estimate had a very broad 95% highest posterior density interval ranging from the early Eocene (approximately 53–54 Ma) to the middle Miocene (approximately 15–16 Ma). Future discoveries of crown-group nightjar fossils and an improved understanding of morphological variation within the nightjar crown group will likely assist with the estimation of accurate time-calibrated phylogenies for this clade.

Improved fossil sampling may also help elucidate nightjar biogeographic history. Based on the interrelationships of extant nightjar species, it has been hypothesized that crown-group nightjars originated in the region surrounding the Indian Ocean before diversifying extensively in the Americas and secondarily re-colonizing Afro-Eurasia (Barrowclough et al. 2006; Han et al. 2010; Sigurðsson and Cracraft 2014; White et al. 2016). Although no known fossil evidence directly contradicts this scenario, it has been previously observed that inferences about avian biogeographic history can often be misleading when founded solely on the geographic ranges of extant species, due to the dispersive capabilities of many birds and the relictual present-day distributions of some avian groups (Mourer-Chauviré 1982; Mourer-Chauviré 1999; Mayr 2017b; Yonezawa et al. 2017; Field and Hsiang 2018; Saupe et al. 2019; Mayr 2022). Temporal information provided by the fossil record will also permit more rigorous assessment of potential correlations between biogeographic events during nightjar diversification and major environmental changes in Earth history, as has been undertaken for several other avian clades (e.g., Fuchs et al. 2015;

Gavryushkina et al. 2017; Yonezawa et al. 2017; McCullough et al. 2019; Oliveros et al. 2019; Oliver et al. 2020; Oliveros et al. 2020; Vianna et al. 2020; McCullough et al. 2022; Selvatti et al. 2022; Oliver et al. 2023).

Recent Nightjar Extinctions

The majority of extant nightjar species are not considered to be under imminent threat of extinction. However, habitat loss and predation from invasive predators have been identified as potential threats to nightjar survival, particularly for island endemic species (Cleere 1999; Hume 2017; Billerman et al. 2022; IUCN 2023). Furthermore, alarming regional population declines have been documented in recent decades for many avian aerial insectivores, including nightjars (Cleere 1999; Nebel et al. 2010; Rosenberg et al. 2019), the causes of which are likely multifactorial (Spiller and Dettmers 2019). At least one case of historical range contraction and population decline in an extant nightjar has been inferred from the subfossil record: the Least Poorwill (*Siphonorhis brewsteri*) of Hispaniola is uncommon and typically found in lowland environments today, but its remains are among the most commonly recovered bird specimens at the high-elevation subfossil site of Trouing Jean Paul (Steadman and Takano 2013). Bird remains from this locality have been dated to approximately 600–1600 years BP (AD 350–1350) (Steadman and Takano 2013). The factors that drove these changes in the distribution and abundance of *S. brewsteri* are unknown, though ecological disruption by introduced mammals and the depopulation of Indigenous peoples (who may have created suitable nightjar habitat in the highlands through forest clearance) might have been contributing factors (Steadman and Takano 2013).

Few nightjar species are yet known to have gone extinct from anthropogenic pressures, but some potential examples have nonetheless been recognized (Hume 2017; Billerman et al. 2022; IUCN 2023). One such species is the Cuban Poorwill (*Siphonorhis* *daiquiri*) of Cuba, which is known only from subfossil remains (Olson 1985b; Suárez 2000; Suárez 2022; Zelenkov and Belichenko 2022). It was intermediate in size compared to its congeners, the smaller *S. brewsteri* (which has a total length of 18–21 cm; Cleere 1998) and the larger Jamaican Poorwill (*S. americana*, which has a total length of 23–25 cm; Cleere 1998), and its tarsometatarsus is more gracile than that of *S. americana* (Olson 1985b). Although *S. daiquiri* has never been recorded alive, the extinction status of nightjars is often difficult to assess due to their cryptic nature, and both Olson (1985b) and Suárez (2000) considered it plausible that the species may persist in remote regions of Cuba.

Similar uncertainty concerns *Siphonorhis americana* from Jamaica, which is known from four museum specimens collected in the 19th Century and some probable subfossil remains (Olson and Steadman 1977; Cleere 1998; Hume 2017). This species has not been scientifically recorded since 1860 and is widely thought to have succumbed to predation by introduced rats, as well as possibly to habitat destruction; however, unverified sightings have been reported in recent decades (Cleere 1998; Hume 2017; IUCN 2023). The International Union for Conservation of Nature (IUCN) currently classifies *S. americana* as Critically Endangered (Possibly Extinct) (IUCN 2023).

Further phylogenetic and biogeographic information about these taxa might be obtained through studies of ancient DNA, which have yet to be attempted on Quaternary nightjar fossils. Unlike older fossil material, such specimens are recent enough that the extraction of sequenceable genetic material is potentially achievable. Although tropical climates (such as those inhabited by *Siphonorhis* spp.) can accelerate DNA degradation (Reed et al. 2003; Allentoft et al. 2012), ancient DNA sequences have been retrieved from multiple recently extinct tropical bird species (e.g., Sorenson et al. 1999; Paxinos et al. 2002; Mitchell et al. 2014; Yonezawa et al. 2017; Louchart et al. 2018; Oswald et al. 2019; Oswald et al. 2021; Grealy et al. 2023), indicating that the application of similar methods to recent nightjar remains may be feasible.

Along with possible recent extinctions, there are several nightjar species that were scientifically documented based solely on single specimens and whose continued existence remains unconfirmed by field surveys (Cleere 2010; Hume 2017; Schweizer et al. 2020; Billerman et al. 2022). These include the New Caledonian Nightjar (*Eurostopodus exul*) of New Caledonia (also known from subfossil material; Anderson et al. 2010), the Cayenne Nightjar (*Setopagis maculosa*) of French Guiana, the Nechisar Nightjar (*Caprimulgus solala*) of Ethiopia (known only from an isolated wing), and the Prigogine's Nightjar (*Caprimulgus prigoginei*) of the Democratic Republic of the Congo. Of these, *E. exul* is classified as Critically Endangered (Possibly Extinct) by the IUCN (2023). Hume (2017) additionally considered *S. maculosa* and *C. prigoginei* to be possibly extinct as well.

The rediscovery of nightjar species described from limited material is not without precedent. Such successes have been previously achieved with the Satanic Nightjar (*Eurostopodus diabolicus*) of Sulawesi (originally described by Stresemann 1931 based on a single specimen, before being reported alive by Bishop and Diamond 1997), the Puerto Rican Nightjar (*Antrostomus noctitherus*) of Puerto Rico (originally described by Wetmore 1919 based on subfossil specimens and a single museum skin, before being reported alive by Reynard 1962), and the Bahian Nighthawk (*Nyctiprogne vielliardi*) of Brazil (originally observed and described by Lencioni-Neto 1994, who collected two specimens, then reported alive again by Whitney et al. 2003). There is therefore a distinct possibility that future fieldwork will find living individuals of certain nightjar species currently feared extinct. Even so, careful comparison with type specimens will be required to establish the taxonomic and conservation status of poorly known taxa (Forero and Tella 1997). For example, detailed restudy of the holotype of the Vaurie's Nightjar ("*Caprimulgus centralasicus*"), another putative single-specimen nightjar species, has indicated that it is likely synonymous with *Caprimulgus europaeus* (Schweizer et al. 2020). In contrast, a re-examination of the type specimen of *Setopagis maculosa* supported its distinction as a valid species (Costa et al. 2015).

The fossil record offers a unique perspective on the origins of modern biodiversity, as it represents the only obtainable direct evidence bearing on the ancestral morphologies, antiquity, and historical geographic distributions of extant lineages. Although available fossil material of total-group nightjars tends to be relatively limited in abundance and completeness, preliminary research on the specimens that are known has already provided insight into the evolution, diversity, and extinction of nightjars through deep time. Future work on nightjar origins would greatly benefit from the identification of potential stem-group strisoreans and stem-group nightjars (especially further research into the phylogenetic affinities of Archaeotrogonidae) as well as the description of more complete crown-group nightjar fossils (particularly from the Miocene, an interval that is currently lacking in any described caprimulgid fossils). It is hoped that the coming years continue to shed light on the early evolutionary history of nightjars, one of the most fascinating and enigmatic groups of living birds.

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