New bird remains from the early Eocene Nanjemoy Formation of Virginia (USA), including the first records of the Messelasturidae, Psittacopedidae, and Zygodactylidae from the Fisher/Sullivan site

Gerald Mayr a, Vanesa De Pietri b and R. Paul Scofield a,c

aSenckenberg Research Institute and Natural History Museum Frankfurt, Ornithological Section, Frankfurt am Main, Germany; bUniversity of Canterbury, School of Earth and Environment, Christchurch New Zealand; c‘Natural History Department, Canterbury Museum, Christchurch, New Zealand

ABSTRACT
We report new avian remains from the early Eocene Nanjemoy Formation of the Fisher/Sullivan site in Virginia, USA. The fossil material includes the first records of the Messelasturidae, Psittacopedidae, and Zygodactylidae from the Nanjemoy Formation, with these taxa being widespread and fairly common in coeval North American and European sites. Psittacopedidae and Zygodactylidae are stem group representatives of the Passeriformes, and a tarsometatarsus assigned to the Psittacopedidae is unusual in that it lacks a supratendinal bridge (this bridge is, however, also absent in the psittacopedid taxon Pumillanos). We further report more material of the Charadriiformes and corroborate a previous tentative referral of a tarsometatarsus to the Parvicuculidae. It is noted that this latter bone is likewise very similar to the tarsometatarsus of the Fluvioviridavidae, which indicates close affinities between the two higher-level clades. Because of the comparatively small extent of the new avian material, it is remarkable that it includes a comparatively high number of fossils that represent previously unknown taxa. This supports the hypothesis that early Eocene avifaunas featured a high taxonomic diversity, but that higher-level clades showed low species richness. We hypothesise that this may indicate low rates of cladogenetic diversification in a rather homogenous paleoenvironment.

Introduction
For a long time, the early Eocene avian fossil record from North America primarily consisted of finds from the Green River, Willwood, and Bridger formations in Wyoming (Mayr 2009). A more recently discovered and still poorly known avifauna comes from bone beds of the Fisher/Sullivan site of the Nanjemoy Formation in Virginia, east of Fredericksburg, Stafford County (Weems and Grimsley 1999). The fossils are from strata that were deposited in a shallow marine environment and stem from zone 11 of Bed B of the Potapaco Member, which is assigned to the calcareous nannofossil zone NP 11 and therefore has an age of about 53–54 million years (Weems and Grimsley 1999; Speijer et al. 2020).

The first bird bones from the Fisher/Sullivan site were studied by Olson (1999), who identified remains of the Pelagornithidae, Phoenicopteriformes, Charadriiformes, and Strisores. The then available avian material from the Fisher/Sullivan site was termed a ‘faunule’ by Olson (1999), but it has since become a much larger fauna that shows a high diversity of small birds.

Mayr (2016) reported further bird fossils from the Fisher Sullivan site. In addition to a new and exceptionally small species of the Strigiformes, this new material included fossils attributable to the Charadriiformes and Halcyornithidae, as well as tentative records of the Procellariiformes, Fregatidae, Messelornithidae and Apodiformes, and a threksiornithid-like bird of uncertain affinities (which may be conspecific with fossils assigned to the ‘Graculavidae’ by Olson 1999). Still, the taxonomic diversity of the avifauna of the Fisher Sullivan site remains insufficiently understood, and many taxa that are abundantly represented in coeval sites in Europe and North America have not yet been reported from the locality.

Several previous identifications were furthermore only tentative, and Mayr’s (2016) revision of some of Olson’s (1999) identifications was based on published data only. In the present study, two of us (VDP and RPS) were able to directly examine the specimens described by Olson (1999), as well as new material, which has since been found by amateur collectors and was donated to the Smithsonian Institution (Washington D.C., USA).

Material and methods
Institutional abbreviations: IRSNB - Royal Belgian Institute of Natural Sciences, Brussels, Belgium; MGUH – Geological Museum of the University of Copenhagen, Denmark, NHMUK – the Natural History Museum, London, UK; SMF – Senckenberg Research Institute Frankfurt, Germany; SNSB-BSPG – Staatliche Naturwissenschaftliche Sammlungen Bayerns – Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; USNM – National Museum of Natural History, Smithsonian Institution, Washington D.C., USA.

The specimens were first viewed, photographed, and measured during a visit by VDP and RPS to USNM in May 2018. Further on-site analyses were hindered by the current Covid-19 pandemic, and coating specimens with ammonium chloride for images with enhanced contrast was therefore not possible.

CONTACT Gerald Mayr gerald.mayr@senckenberg.de Senckenberg Research Institute and Natural History Museum Frankfurt, Ornithological Section, Frankfurt am Main, Germany.

© 2021 The Author(s). Published by Informa UK Limited, trading as Taylor & Francis Group.
This is an Open Access article distributed under the terms of the Creative Commons Attribution License (http://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.
**Systematic palaeontology**

Aves Linnaeus, 1758  
Charadriiformes Huxley, 1867  
Gen. et sp. indet.

**Referred specimens**

USNM PAL 771602 (proximal end of left humerus; Figure 1(a), (b); found by Mike Folmer, donated 20 July 2000. USNM PAL 771603 (proximal end of left humerus; Figure 1(c), (d)); found by Mike Folmer, donated 17 December 1998.

**Measurements (mm)**

USNM PAL 771602: length as preserved, 10.6; proximal width, 6.8; proximal shaft width, 2.3. USNM PAL 771603: length as preserved, 15.4; proximal width, 5.8; proximal shaft width, 1.8.

**Tentatively referred specimen**

USNM PAL 771607 (distal portion of right tarsometatarsus; Figure 1(n)); found by Mike Folmer.

**Measurements (mm)**

Length as preserved, 11.1; minimum distal width, 3.3; shaft width, 1.5.

**Remarks**

Remains of charadriiform birds from the Nanjemoy Formation were first reported by Olson (1999). These specimens were, however, very fragmentary and the first unambiguous record of the Charadriiformes, consisting of a complete distal humerus (SMF Av 619), was described by Mayr (2016).

Here, two proximal humeri are identified, which closely resemble those of charadriiform birds (Figure 1(a)–(d)). Both proximal humeri appear to be too large to belong to the distal end of the humerus (SMF Av 619; Figure 1(e)) described by Mayr (2016). Apart from USNM PAL 771602 being slightly larger, both proximal humeri correspond well in their morphology and exhibit a combination of traits that characterises charadriiform birds. Most notable among these is the presence of a sulcus nervi coracobrachialis and a deeply marked impressio coracobrachialis (Figure 1(b)). The impressio coracobrachialis is large, round and dorsoventrally wide. Within extant Charadriiformes, this feature characters some members of the Charadrii, like Burhininae and the Egyptian Plover Pluvialis aegyptius, the latter being proportionally smaller (De Pietri and Scalford 2014). Also, as in Burhininae, a dorsal fossa pneumotricipitalis is absent (but see Mayr 2011 for the distribution of this feature within extant Charadriiformes) and the crista deltopoectoralis is proximodistally long. As in most extant Charadriiformes, the sulcus transversus is well-developed and the tuberculum dorsale is pronounced. The caudal surface of the shaft forms a distinct ridge; the caudal surface of the crista deltopoectoralis is concave (as in Lari and Charadrii, whereas it is convex in the Scolopacidae and Turnicidae). Overall, this combination of features does not support placement within crown-group Lari or Scolopacidae, and although affinities with taxa within Charadrii are possible, a stem-group placement for this taxon cannot be ruled out based on the material available.

The fragmentary distal humerus (USNM PAL 496374; Figure 1(f), (g)), which was referred to the Scolopacidae by Olson (1999), is much larger (the distal width is 5.8 mm, and the shaft width is 2.8 mm) than the complete charadriiform humerus reported by Mayr (2016; SMF Av 619, Figure 1(e)). The bone is also too large to belong to the same species represented by the two proximal humeri here described. As already hypothesised by Mayr (2016), it is more likely that USNM PAL 496374 stems from a species of the Procellariiformes, with which it shares a deep fossa musculi brachialis and a broader processus supracondylaris dorsalis. In size, it would correspond to a tarsometatarsus that was tentatively assigned to the Procellariiformes by Mayr (2016).

The new material includes the distal section of a tarsometatarsus. This specimen (USNM PAL 771607; Figure 1(n)) appears to be from a rather short-legged species, and not much of the proximal end appears to be missing (i.e., the proximal widening of the shaft is present/preserved). The proportions of charadriiform birds are highly variable, but if similar proportions to, e.g., extant Chionidae are assumed, the tarsometatarsus USNM PAL 771607 would match in size the distal humerus (SMF Av 619) described by Mayr (2016), which is slightly smaller than the humeri here described. However, at present, the possibility cannot be excluded that the proximal humeri correspond to this tarsometatarsus. The specimen is lacking a part of the trochlea metatarsi II. Typically for many charadriiforms, the trochlea metatarsi IV reaches to about half the length of trochlea metatarsi III, and trochlea metatarsi II, represented in this specimen by its proximal base, is elevated and plantarly retracted. Unlike in the Turnicidae and most representatives of Charadrii, a fossa metatarsi I is present. The foramen vasculare distale is situated in a deep fossa.

Olson (1999) assigned a distal tarsometatarsus (USNM PAL 496375; Figure 1(i)) to the Scolopacidae. This specimen is here considered to be conspecific with another distal tarsometatarsus (SMF Av 622; Figure 1(j)), which was tentatively assigned to the Messelornithidae by Mayr (2016). These two tarsometatarsi appear to be too large to belong to the same species as the above-mentioned proximal humeri.

Parvicuculidae Harrison, 1982  
Parviculus Harrison and Walker, 1977  
Parviculus sp.

**Referred specimen**

USNM PAL 496384 (right tarsometatarsus; Fig. 2(a)–(f)); collected by Chuck Ball, donated 3 September 1997.

**Measurements (mm)**

Length, 11.8; proximal width, 3.9; distal width, 3.8; shaft width, 1.9.

**Remarks**

This fossil (Figure 2(a)–(f)) was first described by Olson (1999), who assigned it to the apodiform Aegialornithidae. Mayr and Mourer-Chauviré (2005) refuted this classification and noted a close resemblance to the tarsometatarsus of Parviculus minutus (Fig. 2(g)), which was reported from the early Eocene of the London Clay (Harrison and Walker 1977; Harrison 1982). An assignment of USNM PAL 496,384 to the taxon Parviculus is confirmed here, but it is furthermore noted that the bone is also similar to the tarsometatarsus of Fluvioviridavis. This latter taxon was described by Mayr and Daniels (2001) on the basis of a skeleton from the early Eocene of the Green River Formation. Mayr and Mourer-Chauviré (2005) considered comparisons between Parviculus and Fluvioviridavis impossible owing to the poor preservation of the
Figures 1. (a)–(l), (n) Bones from the early Eocene of the Nanjemoy Formation, which are assigned to the Charadriiformes, Procellariiformes, and Messelornithidae, in comparison to (m) a messelornithid from the early Eocene Belgium. (a), (b) Charadriiformes, gen et sp. indet., proximal end of left humerus (USNM PAL 771602) in caudal (a) and cranial (b) view. (c), (d) Charadriiformes, gen et sp. indet., proximal end of left humerus (USNM PAL 771603) in caudal (c) and cranial (d) view. (e) Distal end of right humerus of a charadriiform bird (SMF Av 619) described by Mayr (2016); cranial view. (f), (g) Distal end of right humerus (USNM PAL 496374), which was assigned to the Scolopaci by Olson (1999) in cranioventral (f) and cranial (g) view; this bone is here considered to be from a procellariiform bird. (h) Distal end of a left tarsometatarsus (SMF Av 617), which was tentatively assigned to the Procellariiformes by Mayr (2016); plantar view. (i) Distal end of right tarsometatarsus (USNM PAL 496375), which was assigned to the Scolopaci by Olson (1999); plantar view. (j) Distal end of right tarsometatarsus (SMF Av 622), which was tentatively assigned to the Messelornithidae by Mayr (2016); plantar view. (k) Distal end of a left tarsometatarsus (USNM PAL 496419), which was tentatively assigned to Coturnipes by Olson (1999); plantar view. (l) Distal end of the left tarsometatarsus of Coturnipes cooperi from the early Eocene of the London Clay (holotype; NHMUK A 3706); plantar view. (m) Distal portion of the left tarsometatarsus of an unnamed species of the Messelornithidae from the early Eocene of Egem in Belgium (IRSNB Av 170); plantar view. (n) Distal portion of an undetermined charadriiform-like right tarsometatarsus in plantar view (USNM PAL 771607). Abbreviations: icb, impressio coracobrachialis; psd, processus supracondylaris dorsalis; rdg, ridge formed by caudal surface of shaft; snc, sulcus nervi coracobrachialis; tbd, tuberculum dorsale. The scale bars equal 5 mm. [Colour online].
holotype of *F. platyhamphus*. Meanwhile, however, a second specimen of *Fluvioviridavis* from the Green River Formation was described, in which the tarsometatarsus is better preserved (Nesbitt et al. 2011; Figure 2(h)). With a length of 11.8 mm (Olson 1999), USNM PAL 496384 is somewhat smaller than the tarsometatarsus of this new *Fluvioviridavis* specimen, which measures 13.5 mm (Nesbitt et al. 2011). However, as far as comparisons are possible, both bones appear to be very similar, with shared derived features including the overall proportions of the short and stocky bone, as well as the presence of a crista medianoplantaris along the plantar surface of the shaft, and the presence of a plantarly directed, wing-like flange on the trochlea metatarsi IV. In fact, the resemblances to the coeval *Fluvioviridavis* are so strong that we consider it possible that *Parviculus* and *Fluvioviridavis* belong to a single higher-level clade (in which case Parviculidae Harrison 1982 would have taxonomic priority over *Fluvioviridavidae* Mayr and Daniels 2001).

Halcyornithidae Harrison and Walker, 1972
cf. *Pulchrapolia* Dyke and Cooper, 2000

**Referred specimens**

USNM PAL 771600 (proximal end of right humerus; Fig. 3(a), (b)); found by Ron Keil, donated 19 February 1998. USNM PAL 771599 (distal end of right humerus; Fig. 3(c), (d)); found by Mike McCloskey, donated 9 September 1999. USNM PAL 771605 (distal end of the left tibiotarsus; Fig. 3(g)-(i)); found by Mike McCloskey.

**Measurements (mm)**

USNM PAL 771600: length as preserved, 15.3; proximal width, 6.0; shaft width, 1.9. USNM PAL 771599: length as preserved, 10.2; distal width, 4.4; shaft width, 1.8. USNM PAL 771605: length as preserved, 8.9; distal width, 3.8; shaft width, 1.7.

**Remarks**

The Halcyornithidae are well known from other early Eocene localities, such as Messel in Germany, Egem in Belgium, and the Green River Formation in Wyoming, USA (Mayr 2009, 2017a). Halcyornithid remains were first reported from the Nanjemoy Formation by Mayr (2016), who identified a well-preserved tarsometatarsus and a tentatively referred partial carpometacarpus (in the text, the tarsometatarsus was tentatively assigned to *Pulchrapolia* by Mayr 2016, whereas it was referred by oversight to *Cyrilavis* in the table). A fragmentary halcyornithid tarsometatarsus was subsequently reported by Carpenter and Parris (2020).

The partial humeri and the distal tibiotarsus identified in the present study (Figure 3) closely resemble the corresponding bones of other Halcyornithidae (Figure 3(e), (f)). The humerus is characterised by a comparatively small proximal end, which has a very short sulcus transversus, a small tuberculum dorsale, and a long deltopectoralis; the distal end of the bone is ventrally projected and exhibits a distinct fossa musculi brachialis and a small tuberculum supracondylare dorsale. The tibiotarsus corresponds with that of other Halcyornithidae in that the condyles are of subequal size and widely spaced; a pons supratendineus is present. USNM PAL 771599 (distal...
humerus) and USNM PAL 771605 (distal tibiotarsus) stem from the same collector and may therefore possibly belong to the same individual.

Messelasturidae Mayr, 2005
Gen. et sp. indet. A + B

**Referred specimens**

USNM PAL 771595 (distal end of the left tarsometatarsus lacking trochlea metatarsi IV; Fig. 4(a)–(e)); found by Mike Folmer. USNM PAL 771596 (distal end of the right tarsometatarsus lacking trochlea metatarsi II; Fig. 4(f)–(j)); found by Mike Folmer. USNM PAL 771598 (partial right carpometacarpus; Fig. 4(l)–(o)); found by Daryl Serafin; donated Sept. 9th, 1999.

**Measurements (mm)**

USNM PAL 771595: length as preserved, 14.1; distal width, 4.3 (across trochleae metatarsorum II et III); shaft width, 3.1. USNM PAL 771596: length as preserved, 16; distal width, 5.4; shaft width, 3.0. USNM PAL 771598: length, 18.2; proximal width, 5.0; proximal depth, 2.9; shaft depth, 1.4; shaft width, 1.7; distal width, 2.7.

**Remarks**

The Messelastruridae were found in early and early middle Eocene sites in North America and Europe (Mayr 2009, 2017a) and include two genus-level taxa, *Tynska* and *Messelastur*. *Messelastur* occurs in the latest early or earliest middle Eocene of Messel; the taxon *Tynska* was first described from the early Eocene of the Green River Formation but records also exist from the London Clay (Mayr 2000, 2021).

The two tarsometatarsi from the Nanjemoy Formation are identical to those of other messelasturids in general features. The bones are characterised by a dorsoplantarly flat shaft, which has an equal width over most of its length, and the right tarsometatarsus (USNM PAL 771596) exhibits a well-developed trochlea accessorium (which is broken in USNM PAL 771595). The two fossils differ in the proportions of the trochlea metatarsi III and are clearly from two different species. The left tarsometatarsus (USNM PAL 771595; Figure 4(a)–(e)) has a wider trochlea metatarsi III, which is nearly twice as wide as it is long and resembles the tarsometatarsus of *Messelastur* (Fig. 4(k)) in its proportions. In the right tarsometatarsus (USNM PAL 771596; Figure 4(f)–(j)), the trochlea metatarsi III is about as wide as it is long, and in its proportions, this bone corresponds well to the tarsometatarsus of *Tynska* (compare Figure 4(f)–(j) with Mayr 2021: fig. 7 c, d).
Even though the referred carpometacarpus USNM PAL 771598 (Fig. 4(l)–(o)) does not exhibit any particular diagnostic characteristics, it is similar to the carpometacarpus of the taxon Tynskya (Fig. 4(p), (q)) in its relative size, overall proportions, and osteological details (e.g., concerning the shape of the processus extensorius and the trochlea carpalis). Of other taxa with a known carpometacarpus morphology so far reported from the Nanjemoy Formation, only halcyornithids show a resemblance to the specimen. However, all the halcyornithids remain from the Nanjemoy Formation belong to similar-sized species, and with a tarsometatarsus length of 16.4 mm (Mayr 2016) they are too small for USNM PAL 771598 (in halcyornithids, the tarsometatarsus is longer than the carpometacarpus, which measures 18.2 mm in USNM PAL 771598).

Psittacopedinidae Mayr, 2015 cf. Pumiliornis Mayr, 1999

**Referred specimens**

USNM PAL 771594 (distal end of the left tibiotarsus; Fig. 5(a)–(e)); found by Philip Schmitz, donated Feb. 5th, 1998. Measurements (mm): length as preserved, 13.8; distal width, 3.4; shaft width, 1.6. USNM PAL 771592 (left tarsometatarsus; Fig. 5(g)–(l)); found by Mike Folmer, donated 11 January 2001.

**Measurements (mm)**

USNM PAL 771594: length as preserved, 13.8; distal width, 3.4; shaft width, 1.6. USNM PAL 771592: length, 16.4; proximal width, 3.5; distal width (min), 3.5; shaft width, 1.4.
Figure 5. Bones from the early Eocene of the Nanjemoy Formation, which are assigned to the Psittacopedidae, in comparison to *Pumiliornis tessellatus*. (a)–(e) cf. *Pumiliornis*, distal end of left tibiotarsus (USNM PAL 771594) in cranial (a), medial (b), caudal (c), lateral (d), and distal (e) view. (f) Distal end of right tibiotarsus of *Pumiliornis tessellatus* from the latest early or earliest middle Eocene of Messel, Germany, in cranial view (SMF-ME 2475B). (g)–(l) cf. *Pumiliornis*, left tarsometatarsus (USNM PAL 771592) in plantar (g), dorsal (h), lateral (i), medial (j), proximal (k), and distal (l) view. (m) Right tarsometatarsus of *P. tessellatus* from Messel in plantar view (SMF-ME 11414A; note that the scale bars in Figure 1d–g of Mayr and Wilde 2014 are incorrect and represent 5 mm [Figure 1d] and 2 mm [Figure 1e–g], respectively). Abbreviations: acc, trochlea accessoria; cdl, condylus lateralis; cdm, condylus medialis; fdl, hypotarsal canal for tendon of musculus flexor digitorum longus; fhl, hypotarsal sulcus for tendon of musculus flexor hallucis longus; fvd, foramen vasculare distale; tre, lateral tuberositas retinaculi extensori. The scale bars equal 5 mm. [Colour online].
Figure 6. Bones from the early Eocene of the Nanjemoy Formation, which are assigned to Zygodactyliidae. (a)–(c) Zygodactyliidae, gen. et sp. indet., right tarsometatarsus (USNM PAL 771590) in dorsal (a), plantar (b), and proximal (c) view. (d)–(f) Zygodactyliidae, gen. et sp. indet., right coracoid (USNM PAL 771591) in dorsal (d), ventral (e), and medial (f) view. Abbreviations: acc, trochlea accessoria; fas, facies articularis scapularis; fdl, hypotarsal canal for tendon of musculus flexor digitorum longus; fhl, hypotarsal sulcus for tendon of musculus flexor hallucis longus; fvd, foramen vasculare distale. The scale bars equal 5 mm. [Colour online].

Figure 7. (a)–(e) Partial right tarsometatarsus of Aves indet. A. (?Morsoravis), from the early Eocene of the Nanjemoy Formation (USNM PAL 771593) in plantar (a), medioplantar (b), mediadorsal (c), medial (d), and distal (e) view. (f), (g) Distal end of a right tarsometatarsus (SMF Av 634), which was likened to Morsoravis by Mayr (2016) in dorsal (f) and plantar (g) view. (h) Left tarsometatarsus (dorsal view) of Morsoravis sedilis from the early Eocene Fur Formation in Denmark (holotype, MGUH 28930); dorsal view, surrounding matrix was digitally removed. Abbreviation: mtl, fossa metatarsi I. The tarsometatarsal trochleae are numbered. The scale bars equal 5 mm. [Colour online].
Remarks

Save for the broken trochlea metatarsi II, the tarsometatarsus (USNM PAL 771592) is complete and closely resembles the tarsometatarsus of the Psittacopidae. These zygodactyl stem group representatives of the Passeriformes were ecologically diversified birds, which appear to have been widespread in the early Eocene of Europe and North America (Mayr and Wilde 2014; Mayr 2015, 2017a, 2020; Ksepka et al. 2019).

The tarsometatarsus (USNM PAL 771592; Figure 5(g)–(l)) is more elongated, with a proportionally narrower shaft, than the tarsometatarsus of Psittacos from Messel and Parapsittacos from the London Clay (compare Figure 5(g) with Mayr and Daniels 1998: pl.3, fig. 4 g). Regarding its proportions, it more closely agrees with the tarsometatarsus of Pumiliornis tessellatus from Messel (Mayr 2015; Fig. 5(m)) and Eoefrangiurostrum from the Green River Formation (Ksepka et al. 2019). The hypotarsus forms two canals for the tendons of the musculus flexor digitorum longus and m. flexor hallucis longus, which are, however, still filled with sediment in the fossil. The plantar openings of the foramina vascularia proximalia are widely separated. The foramen vascular distal, which is likewise filled with sediment, has a large dorsal opening. The trochlea metatarsi IV exhibits a large trochlea accessoria, which is separated by a furrow from the main trochlea. With a length of 16.4 mm, the bone is distinctly longer than the tarsometatarsi of Pumiliornis tessellatus (8.9–9.9 mm), Psittacos lepidus (13.1–13.3 mm), and Eoefrangiurostrum boureauxi (~11.8 mm). The tarsometatarsi of the London Clay psittacopids show some variation in size, but with a length of 19.1 mm (Mayr and Daniels 1998), the largest London Clay psittacopedid corresponds to USNM PAL 771592 in its size; in all psittacopids from the London Clay, of which the tarsometatarsus is known, the bone is, however, stouter than the Nanjemoy specimen.

The tibiotarsus (USNM PAL 771594; Fig. 5(a)–(e)) lacks a pons supratendinosus and at first sight resembles the tibiotarsus of strigiform birds. A very small owl, Eostrix gulottai, was described by Mayr (2016) from the Nanjemoy Formation on the basis of a distal tarsometatarsus, and in size USNM PAL 771594 corresponds with the holotype tarsometatarsus of *E. gulottai*. However, the fossil distinctly differs from the tibiotarsi of *Eostrix* species (that is, *E. mimaica* and *E. tsaganica*; Wetmore 1938; Kurochkin and Dyke 2011) and other owls in that the incisura intercondylaris is less deeply incised, especially at its distal margin, and the condyles are of unequal size, with the condylus lateralis being more laterally splayed (in *Eostrix* and extant Strigiformes, both condyles have a similar mediolateral width). As shown by Mayr (2008), a supratendinal bridge is also absent in *Pumiliornis tessellatus*. Because the tibiotarsus USNM PAL 771594 corresponds well in size to the tarsometatarsus USNM PAL 771592, which also shows similar morphology to the tarsometatarsus of *Pumiliornis* (see above), we tentatively refer both fossils to the latter taxon. In Parapsittacos fossils from the London Clay, a pons supratendinosus is present (Mayr and Daniels 1998; Fig. 5f), whereas the conditions in Psittacos and *Eoefrangiurostrum* are unknown.

Zygodactylidae Ballmann, 1969
Gen. et sp. indet.

Referred specimen

USNM PAL 771590 (right tarsometatarsus; Fig. 6(a)–(c)); found by Mike Folmer, donated 20 May 1998.

Measurements (mm)

Length, 14.0; proximal width, 2.0; distal width, 2.5; shaft width, 0.8.

Tentatively referred specimen

USNM PAL 771591 (right coracid lacking extremitas sternalis; Fig. 6(d)–(f)); found by Mike McCloskey, donated 9 September 1999.

Measurements (mm)

Length as preserved, 11.0; from cotyla scapularis to processus acrococacoideus, 3.6; from facies articularis sternalis to processus acrococacoideus, 3.0; width of facies articularis clavicilaris, 1.8; shaft width, 1.0.

Remarks

USNM PAL 771590 is clearly identified as the tarsometatarsus of a species of the Zygodactylidae by its very long and slender shaft and by the derived morphology of the distal end, which bears an accessory trochlea for the fourth toe (Figure 6(a)–(c)). Overall, the morphology of the distal end resembles that of the taxon *Primozygodactylus* and unlike in *Zygodactylus*, the trochlea accessoria is not distally elongated. The hypotarsus exhibits a large canal for the musculus flexor digitorum longus and a small, plantarily open sulcus for the tendon of the musculus flexor hallucis longus. The specimen is broken into two pieces and an intermediate portion may be missing; its original length therefore remains unknown. If no intermediate portion is missing, what appears to be the case, the length of the bone would have been 14.0 mm, in which case it would have been distinctly shorter than the tarsometatarsi of the Zygodactylidae from the latest early/earliest middle Eocene of Messel in Germany, which have lengths between 17 and 28 mm (Mayr 2017b). The tarsometatarsus lengths of the formally described zygodactylids from the Green River Formation also fall in this range (Smith et al. 2018), but in size USNM PAL 771590 agrees with an unnamed zygodactylid from the Green River Formation, which was figured by Weidig (2010: fig. 11), who gave a tarsometatarsus length of 14 mm for this specimen. This small species from the Green River Formation is unusual in that the ulna distinctly exceeds the tarsometatarsus in length. A putative zygodactylid from the early Oligocene of Montana (USA), which was described as *Zygodactylus ochlurus*, has a tarsometatarsus length of 15.5 mm (Hieronymus et al. 2019).

As in other zygodactylids, the tentatively referred coracid (Figure 6(d)–(f)) lacks a foramen nervi supracocacoidei and has a slightly concave cotyla scapularis. The processus procoracoideus is broken.

Aves indet. A (?)Morsoravis Bertelli et al. 2010

Referred specimen

USNM PAL 771593 (left tarsometatarsus lacking proximal tip and trochlea metatarsi IV; Fig 7(a)–(e)); found by Mike Folmer.

Measurements (mm)

Length as preserved, 9.7; distal width, 2.4 (trochlea metatarsorum II et III); shaft width, 1.8.
Remarks

In size and morphology, the distal end of this bone (Figure 7(a)–(e)) resembles a fragmentary distal tarsometatarsus from the Nanjemoy Formation (SMF Av 634; Fig. 7(f), (g)), which was likened to *Morsoravis* by Mayr (2016). The new specimen likewise shows some resemblance to *Morsoravis*, even though its fragmentary preservation does not allow unambiguous identification.

USNM PAL 771593 lacks the proximal end, but judging from the widening of the shaft just distal of the breakage line, only a short portion of the bone is missing. The specimen exhibits distinctive proportions in that it appears to have been rather short, with a mediolaterally wide and dorsoplantarly narrow shaft of equal width over most of its length (the lateral margin of the distal end is damaged). A notable feature is the large fossa metatarsi I, which indicates the presence of a well-developed hallux (the size of the fossa metatarsi I of *Morsoravis* is unknown, but the hallux is only moderately long). As in most other neornithine birds, but unlike in the superficially similar tarsometatarsi of the Eocene Sandcoleiidae and other coliiform birds, the fossa metatarsi I is located on the plantar (not medial) surface of the tarsometatarsus. The trochlea metatarsi III appears to have been proximodistally short, but the incisura intercondylaris is still filled with sediment in the fossil and therefore appears shorter than it probably is. Unlike in the Messelasturidae (which also have a flat and wide tarsometatarsus shaft), the trochlea metatarsi II reaches almost as far distally as the trochlea metatarsi III. As preserved, the bone has a length of 11.2 mm so that the complete bone was probably somewhat longer than the tarsometatarsus of *Morsoravis sedulis* (Fig. 7(h)), which measures 13.0 mm (Bertelli et al. 2010).

Aves indet. B

**Referred specimen**

USNM PAL 771608 (right humerus lacking distal end; Figure 8(a), (b)); found by Mike McCloskey, donated 9 September 1999.

**Measurements (mm)**

Length as preserved, 17.5; proximal width, 5.0; shaft width, 1.7.

**Remarks**

USNM PAL 771608 (Figure 8(a), (b)) resembles a larger humerus, which was assigned to the Caprimulgidae by Olson (1999). The new specimen is characterised by a fairly large tuberculum dorsale. Unlike in the above-described charadriiform humerus, there is no sulcus nervi coracobrachialis, and a deeply marked impressio coracobrachialis is likewise absent. The bone shows a resemblance to the humerus of the Archaeotrogonidae, from which it differs in that the caudal surface of the shaft forms a pronounced ridge. In size, the small bone would correspond to the putative apodiform tarsometatarsus reported by Mayr (2016), to the *Microena*-like and *Morsoravis*-like tarsometatarsi described in the latter study, and to the above-reported zygodactylid remains. In its morphology, the bone is, however, clearly distinguished from the much stouter humeri of apodiform birds, and it also differs from the humerus of the *Zygodactylidae*, in which the tuberculum dorsale is less pronounced and the shaft forms no ridge. The humeri of *Morsoravis* and *Microena* are unknown, so there remains a possibility that the bone belongs to a tarsometatarsus assigned to one of the latter two taxa.

Aves indet. C
Referred specimen
USNM PAL 771601 (extremitas omalis of right coracid; Figure 8 (c)-(f)); found by Philip Schmitz, donated 21 December 1999.

Measurements (mm)
Length as preserved, 11.7; from cotyla scapularis to processus acroracraoides, 6.8; from facies articularis sternalis to processus acroracraoides, 5.8; width of facies articularis clavicularis, 3.2; shaft width, 1.9.

Remarks
This bone (Figure 8(c)-(f)) has a distinctive morphology, with the most unusual feature being a dorsally projected ledge formed by the processus procoracoideus. The processus procoracoideus itself is very long and its tip is directed towards the facies articularis scapularis. The cotyla scapularis has a circular outline and is slightly concave. A foramen nervi supracoracoidei is absent.

We are not aware of any other avian taxon, fossil or extant, with a similar coracoid morphology. The coracoid of *Fluvioviridavis* is clearly distinguished from this specimen (Mayr and Daniels 2001) and USNM PAL 771601 is too large to belong to any of the other taxa from the Nanjemoy Formation, the higher-level affinities of which are unknown (e.g., the *Microena*– and *Morsoravis*-like fossils). In size, the bone would correspond to the above-reported charadriiform humeri, but its morphology does not indicate charadriiform affinities. Resemblances to the much larger coracoid of caramiform birds, in which the processus procoracoideus also approaches the processus acroracraoides, appear to be superficial.

Aves indet. D

Referred specimen
USNM PAL 771604 (distal end of left humerus; Figure 8(g), (h)); found by Katie O’Dunne, donated 11 January 2001.

Measurements (mm)
Length as preserved, 11.3; distal width, 4.7; shaft width, 2.0.

Remarks
Even though this bone (Figure 8(g), (h)) exhibits a short processus supracondylaris dorsalis, it is clearly not from a procellariiform or charadriiform bird, in which the morphology of the distal humerus is otherwise very different. USNM PAL 771604 corresponds well with the distal humerus of a skeleton from the London Clay of Walton-on-the-Naze, which was referred to *Fluvioviridavis* by Mayr and Daniels (2001: fig. 4; note that owing to the orientation of the bone, the small processus supracondylaris dorsalis of this fossil, albeit present, is not visible in the figure). We therefore consider it possible that this bone belongs to *Parviculus*, but refrain from a definitive assignment.

Aves indet. E

Referred specimen
USNM PAL 771606 (extremitas omalis of left coracid; Figure 8(i)–(k)); found by Mike Folmer.

Measurements (mm)
Length as preserved, 28.1; from cotyla scapularis to processus acroracraoides, 14.3; from facies articularis sternalis to processus acroracraoides, 12.5; width of facies articularis clavicularis, 6.6; shaft width, 4.1.

Remarks
This bone (Figure 8(i)–(k)) stems from a fairly large species and may belong to one of the ‘graculavid-like’ or *threskiornithid-like* species reported by Olson (1999) and Mayr (2016). The specimen exhibits a foramen nervi supracoracoidei and shows an overall resemblance to the coracid of the *Threskiornithidae*, but the rather unspecific morphology of the bone does not allow an unambiguous referral to a higher-level taxon. USNM PAL 771606 is also superficially similar to the coracid of Palaeogene anseriform birds, in which, however, the facies articularis humeralis is proportionally longer and with a less convex outline, and in which the processus acroracraoides is more protruding and mediolaterally narrower.

Discussion
The Fisher/Sullivan site is notable in that the bird bones from the locality are very well-preserved and uncushred, thereby complementing osteological data derived from early Eocene compression fossils. However, a major challenge of the material concerns the fact that it exclusively consists of isolated bones, and often an assignment of different skeletal elements to a certain taxon is not straightforward.

Table 1 gives an overview of the currently known taxonomic diversity of the birds from the Fisher/Sullivan site. Fifteen species are represented by well-preserved partial or complete tarsometatarsi and can therefore unambiguously be distinguished from each other. Based on comparisons with associated specimens from other fossil sites, additional bones, mainly coracoids and/or humeri, could be assigned to some of these species.

Further species are only known from bones other than tarsometatarsi but can be clearly distinguished from any of the above species (of which tarsometatarsi are known) in size or taxonomic identity. This is, for example, true for the *Pelagornithidae*, which are represented by jaw fragments and large a partial carpopatagius (Olson 1999). A putative record of the *Steatornithidae* (Olson 1999) is based on a proximal humerus, which is likewise too large to be associated with any of the tarsometatarsi (Olson 1999 also referred a fragmentary tarsometatarsal trochlea to this fossil). In addition, there are at least two species of larger-sized birds, which are represented by carpopatagari. One of these was tentatively referred to the Fregatidae by Mayr (2016), the other was considered *threskiornithid-like* (Mayr 2016) but is unidentifiable and probably conspecific with remains that were assigned to the *Pheonicopteriidae* and *Graculavidae* by Olson (1999).

In sum, and if a conservative estimate is applied, this gives a total of at least 19 species known from the Nanjemoy Formation. Most likely, however, the actual number is higher (see Table 1), because various bones, such as the distinctive coracid of Aves indet. C of the present study, do not seem to belong to any of the aforementioned taxa.

The taxonomic diversity of the Nanjemoy Formation is notable. Unambiguously identified taxa include the *Pelagornithidae* (Olson 1999), *Parviculidae* (Mayr 2016), *Charadriiformes* (Mayr 2016; this study), *Halcyornithidae* (Mayr 2016 and this study), *Messelasturidae* (this study), *Psittacopedidae* (this study), and *Zygodactylidae* (this study).
The presence of the Messelornithidae in the Nanjemoy material is indicated by a distinctly-shaped coracoid described by Mayr (2016). A humerus reported in the latter study may also belong to the Messelornithidae. We also note that a tarsometatarsus, which was referred to the taxon Coturnipes by Olson (1999), may be from a messelornithid or a closely related gruiform bird. Mayr (2016) hypothesised that this fossil (USNM PAL 496419; Figure 1(k)) may be conspecific with the Procellariformes referred to the Procellariformes by Mayr (2016; SMF Av 617, Figure 1(h)). However, even though both specimens are of similar size and show a superficial resemblance, the tarsometatarsus assigned to Coturnipes (USNM PAL 496419) had a more plantarily deflected trochlea metatarsi II (this trochlea is broken in the fossil, but its position and orientation can be deduced from the breakage area). As assumed by Olson (1999), USNM PAL 496419 is indeed very similar to the holotype tarsometatarsus of Coturnipes cooperi from the London Clay (Figure 1(i)). Olson (1999) likened Coturnipes cooperi to a partial skeleton from the London Clay in a private collection, which shows some falconiform features. However, as detailed by Mayr and Smith (2019), this referral was incorrect and the more complete London Clay skeleton belongs to the taxon Masillaraptor, the distal tarsometatarsus of which differs from that of Coturnipes. Here it is noted that the tarsometatarsus of Coturnipes shows a close resemblance to the tarsometatarsus of the Messelornithidae (Figure 1(m)), so that we now consider it possible that the Coturnipes-like tarsometatarsus is associated with the messelornithid-like coracoid and humerus described by Mayr (2016).

The identification of other species still needs to be verified. This is true for putative remains of the Caprimulgidae identified by Olson (1999) and well a distal tibiotarsus (SMF Av 623), which was likened to the Trogoniformes by Mayr (2016). The tentative classifications of these fossils were based on the overall similarity of bones that do not exhibit diagnostic apomorphies, and the tibiotarsus may actually belong to the Microena-like bird described by Mayr (2016).

With the identification of fossils of the Messelasturidae, Zygodactylidae, and Psittacopidae, the present study adds several previously unreported taxa to the avifauna of the Nanjemoy Formation, which are well known from other early Eocene localities in North America and Europe. In light of the fact that the new avian material consists of only a few bones, it is remarkable that it includes a comparatively high number of fossils, which represent taxa previously unknown from the Nanjemoy Formation. This corroborates the assumption that early Eocene avifaunas featured a high taxonomic diversity but a low species richness within higher-level clades (Mayr 2016), which may indicate low rates of cladogenetic diversification in the rather homogenous early Eocene forested paleoenvironments of North America and Europe. We note, however, that the fragmentary material currently known from the Nanjemoy Formation has its limitations concerning a definitive taxonomic assignment and species-level identification, and a broader sampling is needed for firm conclusions.

Acknowledgments

First of all, we thank the collectors Mike Folmer, Ron Keil, Mike McCloskey, Katie O’Dunne, Philip Schmitz, and Daryl Serafin and for donating the fossils to USNM. We are furthermore indebted to Helen James for her hospitality and accommodation and for enabling work in the USNM collections, and to Mark Florence (USNM) for providing access to the specimens and for making

| Taxon | Remarks | Known elements |
|-------|---------|----------------|
| Pelagornithidae | Olson (1999) | partial cmc and pedal phalanx |
| ?Procellariiformes | Mayr (2016) | distal tmt, distal humerus |
| ?Fregatidae | Mayr (2016) | proximal cmc |
| Charadriiformes indet. sp. B | Olson (1999), this study | distal hum, distal tbt, distal tmt |
| ?Charadriiformes indet. | this study, may be conspecific with the humerus of sp. A | distal tmt (USNM PAL 771607) |
| ?Messelornithidae, cf. Coturnipes | Olson (1999), Mayr (2016), this study | partial coracoid, distal hum, distal tmt |
| ?Caprimulgidae | Olson (1999); identification needs to be corroborated | distal tmt |
| Parvicuculidae | assigned to Aegialornithidae by Olson (1999) | tmt, “partial coracid, distal hum” |
| cf. Steatomitidae | Olson (1999) | Hum, fragments of tmt |
| ?Apidiformes, cf. Eocypselidae | Mayr (2016) | distal tmt, cmc |
| Strigiformes, Eosix gullogai sp. nov. | Mayr (2016) | distal tmt |
| Halcyornithidae | Mayr (2016), this study | tmt |
| Messelasturidae, gen. et sp. A | this study | tmt |
| Messoasturidae, gen. et sp. A | this study | distal tbt, tmt |
| Ptilocaprididae, cf. Pumiliornis | this study | cmc, wing phalanx |
| Zygodactylidae | this study | partial coracoid (USNM PAL 771601) |
| cf. Microena | Mayr (2016) | proximal hum, proximal radius, distal ulna, proximal cmc, wing phalanx |
| cf. Mosoravis | Mayr (2016), this study | partial coracoid (USNM PAL 771601) |
| Gen. et sp. indet. | Mayr (2016), possibly the same species as “crane-sized” bird reported by Olson (1999) | partial coracoid (USNM PAL 771601) |
| Gen. et sp. indet. | Mayr (2016), may be conspecific with the “graculavid” species #1 of Olson (1999), carpometacarpus identical with that referred to the Phoenicopteriformes by Olson (1999) | proximal hum, proximal radius, distal ulna, proximal cmc, wing phalanx |
| ?Phoenicopteriformes | Olson (1999); may be conspecific with putative threskiornithid reported by Mayr (2016) | proximal cmc, radius |
| ‘Graculavidae, species 1’ | Olson (1999); may be conspecific with putative threskiornithid reported by Mayr (2016) | partial scapula and coracid, fragments of hum, proximal ulna, distal tbt |
| ‘Graculavidae, species 2’ | Olson (1999) | partial scapula and coracid, fragments of hum, proximal ulna, distal tbt |

Table 1. Revised overview of the avian taxa from the Nanjemoy Formation, with known elements indicated (cmc: carpometacarpus, hum: humerus, tbt: tibiotarsus, tmt: tarsometatarsus).
available the catalogue numbers. The photos of the fossils in SMF were taken by Sven Tränkner. This research was funded by a grant from the Marsden Fund Council from New Zealand Government funding, managed by the Royal Society Te Aparangi. Comments from two anonymous reviewers improved the manuscript.

**Disclosure statement**

No potential conflict of interest was reported by the authors.

**Funding**

This work was supported by the Marsden Fund Council from New Zealand Government funding, managed by the Royal Society Te Apārangi [CTM1601].

**ORCID**

Gerald Mayr https://orcid.org/0000-0001-9808-748X
Vanesa De Pietri http://orcid.org/0000-0002-3786-9741
R. Paul Scofield http://orcid.org/0000-0002-7510-6980

**References**

Bertelli S, Lindow BE, Dyke GJ, Chiappe LM. 2010. A well-preserved ‘charadriiform-like’ fossil bird from the early Eocene Fur Formation of Denmark. Palaontol. 53(3):507–531. doi:10.1111/j.1475-4983.2010.00950.x.

Carpenter J, Parris DC. 2020. An additional bird fossil from the Fisher/Sullivan site, Eocene of Virginia, U.S.A. The Mosasaur. 11:93–95.

De Pietri VL, Scofield RP. 2014. The earliest European record of a Stone-curlew (Charadriiformes, Burhinidae) from the late Oligocene of France. J Ornithol. 155(2):421–426. doi:10.1007/s10336-013-1022-8.

Harrison CJO. 1982. Cuculiform, piciform and passeriform birds in the lower Eocene of England. Tert Res. 4:71–81.

Harrison CJO, Walker CA. 1977. Birds of the British lower Eocene. Tert Res Spec Pap. 3:1–52.

Hieronymus TL, Waugh DA, Clarke JA. 2019. A new zygodactylid species indicates the persistence of stem passerines into the early Oligocene in North America. BMC Evol Biol. 19(1):3. doi:10.1186/s12862-018-1319-x.

Ksepka DT, Grande L, Mayr G. 2019. Oldest finch-beaked birds reveal parallel ecological radiations in the earliest evolution of passerines. Curr Biol. 29(4):657–663. doi:10.1016/j.cub.2018.12.040.

Kurochkin EN, Dyke GJ. 2011. The first fossil owls (Aves: Strigiformes) from the Paleogene of Asia and a review of the fossil record of Strigiformes. Paleontol J. 45(4):445–458. doi:10.1134/S003103101104006X.

Mayr G. 2000. A new raptor-like bird from the lower Eocene of North America and Europe. Senck Leth. 80(1):59–65. doi:10.1007/BF03043664.

Mayr G. 2008. Pumilornis tessellatus Mayr, 1999 revisited — new data on the osteology and possible phylogenetic affinities of an enigmatic middle Eocene bird. Palaontol Z. 82(3):247–253. doi:10.1007/BF02988891.

Mayr G. 2009. Paleogene fossil birds. Heidelberg: Springer.

Mayr G. 2011. The phylogeny of charadriiform birds (shorebirds and allies): reassessing the conflict between morphology and molecules. Zool J Linn Soc. 161(4):916–934. doi:10.1111/j.1096-3642.2010.00654.x.

Mayr G. 2015. A reassessment of Eocene parrot-like fossils indicates a previously undetected radiation of zygodactyl stem group representatives of passerines (Passeriformes). Zool Scr. 44(6):587–602. doi:10.1111/zsc.12128.

Mayr G. 2016. The world’s smallest owl, the earliest unambiguous charadriiform bird, and other avian remains from the early Eocene Nanjemoy Formation of Virginia (USA). Palaontol Z. 90(4):747–763. doi:10.1007/s12542-016-0330-8.

Mayr G. 2017a. Avian evolution: the fossil record of birds and its paleobiological significance. Chichester: Wiley-Blackwell.

Mayr G. 2017b. New species of Primozygodactylus from Messel and the ecomorphology and evolutionary significance of early Eocene zygodactylid birds (Aves, Zygodactylidae). Hist Biol. 29(7):875–884. doi:10.1080/08989263.2016.1261135.

Mayr G. 2020. A remarkably complete skeleton from the London Clay provides insights into the morphology and diversity of early Eocene zygodactyl near-passerine birds. J Syst Palaontol. 18(22):1891–1906. doi:10.1080/14771780.2020.1862930.

Mayr G. 2021. A partial skeleton of a new species of Tynksya Mayr, 2000 (Aves, Mellestaluridae) from the London clay highlights the osteological distinctiveness of a poorly known early Eocene “owl/parrot mosaic”. Palaontol Z. in press: 10.1007/s12542-020-00541-8.

Mayr G, Daniels M. 1998. Eocene parrots from Messel (Hessen, Germany) and the London Clay of Walton-on-the-Naze (Essex, England). Senck Leth. 78(1–2):157–177. doi:10.1007/BF03042767.

Mayr G, Daniels M. 2001. A new short-legged landbird from the early Eocene of Wyoming and contemporaneous European sites. Acta Palaontol Polon. 46:393–402.

Mayr G, Mourer-Chauviré C. 2005. A specimen of Parviculus Harrison and Walker 1977 (Aves: Parviculidae) from the early Eocene of France. Bull Brit Ornithol Club. 125:299–304.

Mayr G, Smith T. 2019. A diverse bird assemblage from the Ypresian of Belgium furthers knowledge of early Eocene avifaunas of the North Sea Basin. N Jb Geol Palaontol, Abh. 291(3):253–281. doi:10.1127/njgp/2019/0801.

Mayr G, Wilde V. 2014. Eocene fossil is earliest evidence of flower-visitor by birds. Biol Lett. 10(5):20140223. doi:10.1098/rsbl.2014.0223.

Nesbitt SJ, Ksepka DT, Clarke JA. 2011. Podargiform affinities of the enigmatic Fluoroviridavis platyramphus and the early diversification of Strisores (“Caprimulgiformes + Apodiformes”). PLoS One. 6(11):e26350. doi:10.1371/journal.pone.0026350.

Olson SL. 1999. Early eocene birds from eastern North America: a faunule from the Nanjemoy Formation of Virginia. In: Weems RE, Grimsley GJ, editors. Early Eocene vertebrates and plants from the Fisher/Sullivan site (Nanjemoy Formation) Stafford County, Virginia: Virginia Div Min Res Pub 152. p. 123–132.

Smith NA, DeBee AM, Clarke JA. 2018. Systematics and phylogeny of the Zygodactylidae (Aves, Neognathae) with description of a new species from the early Eocene of Wyoming, USA. PeerJ. 6:e4950. doi:10.7717/peerj.4950.

Speijer RP, Pålke H, Hollis CJ, Hooker JJ, Ogg JG. 2020. The Paleocene period. In: Gradstein FM, Ogg JG, Schmitz M, Ogg GM, editors. Geologic time scale 2020. Amsterdam: Elsevier. p. 1087–1140.

Weems RE, Grimsley GJ. 1999. Introduction, geology, and paleogeographic setting. In: Weems RE, Grimsley GJ, editors. Early Eocene vertebrates and plants from the Fisher/Sullivan site (Nanjemoy Formation) Stafford County, Virginia: Virginia Div Min Res Pub 152. p. 1–10.

Weidig I. 2010. New birds from the lower Eocene Green River Formation, North America. Rec Austral Mus. 62(1):29–44. doi:10.3853/j.0067-1975.62.2010.1544.

Wetmore A. 1938. Another fossil owl from the Eocene of Wyoming. Proc U S Nat Mus. 85(3031):27–29. doi:10.5479/si.00963801.85-3031.27.