

The world's smallest owl, the earliest unambiguous charadriiform bird, and other avian remains from the early Eocene Nanjemoy Formation of Virginia (USA)

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Abstract New avian remains from the early Eocene Nanjemoy Formation in Virginia (USA) are described. The material stems from the Fisher/Sullivan site and consists of isolated bones. These belong to at least 13 species, most of which have not yet been reported from the Nanjemoy Formation. The fossil material includes the oldest unambiguous record of a charadriiform bird and a new species of protostrigid owl, which represents the smallest known owl species. Other specimens are tentatively assigned to the Procellariiformes, the suliform Fregatidae, the gruiform Messelornithidae, and the apodiform Eocypselidae. A complete and well-preserved tarsometatarsus of the psittacopasserine Halcyornithidae provides new data on the osteology of these enigmatic birds, and a distal tibiotarsus is tentatively assigned to the Trogoniformes. The identification of a number of fossils is uncertain, with the bones showing similarities to Threskiornithidae and extinct taxa from the early Eocene of Europe (*Microena*, *Morsoravis*). All bird fossils from the Nanjemoy Formation are three-dimensionally preserved and, therefore, allow a detailed assessment of osteological features, which complements studies of compression fossils from lagerstätten-type fossil sites.

Keywords Fossil birds · Fisher/Sullivan site · Ypresian · Charadriiformes · *Eostrix* · Halcyornithidae

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Kurzfassung Neue Vogelreste werden aus der untereozänen Nanjemoy-Formation in Virginia (USA) beschrieben. Das Material stammt aus der Fisher/Sullivan-Fundstelle und besteht aus Einzelknochen. Diese gehören zu mindestens 13 Arten, von denen die meisten noch nicht aus der Nanjemoy-Formation beschrieben wurden. Das Fossilmaterial beinhaltet den ältesten unzweifelhaften Nachweis eines charadriiformen Vogels und einen neuen Vertreter der Protostrigidae, welcher zudem die kleinste bekannte Eulenart darstellt. Andere Exemplare werden unter Vorbehalt zu den Procellariiformes gestellt, sowie zu den suliformen Fregatidae, den gruiformen Messelornithidae und den apodiformen Eocypselidae. Ein vollständiger und gut erhaltener Tarsometatarsus der Halcyornithidae (Psittacopasserines) liefert neue Daten über die Osteologie dieser rätselhaften Vögel und ein distaler Tibiotarsus wird unter Vorbehalt zu den Trogoniformes gestellt. Die Identifizierung einer Reihe von Fossilien ist unsicher und die Knochen weisen Ähnlichkeiten zu Threskiornithidae und ausgestorbenen Taxa aus dem europäischen Untereozän auf (*Microena*, *Morsoravis*). Alle Vogelfossilien der Nanjemoy-Formation sind dreidimensional erhalten und erlauben damit eine detaillierte Bewertung osteologischer Merkmale, welche Untersuchungen von Kompressionsfossilien aus lagerstättenartigen Fundstellen ergänzt.

Schlüsselwörter Fossile Vögel · Fisher/Sullivan-Fundstelle · Ypresium · Charadriiformes · *Eostrix* · Halcyornithidae

Introduction

In the past decades, numerous fossil birds were described from early Eocene fossil localities (Mayr 2009). Arguably the best studied avifauna stems from the latest Ypresian/

earliest Lutetian (about 48 million years ago [mya]) lacustrine sediments of the Messel UNESCO World Heritage site in Germany (Mayr in press). Likewise comprehensive, albeit less intensively studied, is the avian fossil record from the Ypresian (about 53 mya) deposits of the British London Clay and the Fur Formation in Denmark (Mayr 2009). Knowledge of non-European early Eocene avifaunas still lags behind, but several North American sites, especially the Green River and Willwood formations in Wyoming, also produced larger numbers of bird fossils (Feduccia 1999; Mayr 2009; Grande 2013).

An early Eocene North American site, which received much less attention with regard to its avifauna, is the Fisher/Sullivan site of the Nanjemoy Formation in Virginia (Weems and Grimsley 1999). The locality is situated east of Fredericksburg, Stafford County, and was discovered in 1990. The fossils stem from a bone bed, which was deposited in a shallow marine environment and outcrops along an unnamed tributary of Muddy Creek in eastern Stafford County, Virginia. The stratigraphic horizon with this bone bed stems from zone 11 of Bed B of the Potapaco Member and is assigned to the calcareous nannofossil zone NP 11 (Weems and Grimsley 1999). With an estimated age of 53.6 to 52.8 million years (Berggren et al. 1995), the vertebrate-bearing strata of the Fisher/Sullivan site are temporally close to the Ypresian deposits of the London Clay and the Fur Formation on the other side of the Atlantic, and the locality is therefore of significance for faunistic and biogeographic correlations of early Eocene avifaunas of Europe and North America.

The first survey of the avifauna of the Fisher/Sullivan site was performed by Olson (1999). His sample included 33 mostly fragmentary bones, which belong to at least 11 species. In addition to remains of the Pelagornithidae, large seabirds with a highly diagnostic skeletal morphology, Olson (1999) identified birds with charadriiform- and phoenicopteriform-like morphologies, as well as putative representatives of the Caprimulgidae and Apodiformes.

Since Olson's (1999) study, continued activity at the Fisher/Sullivan site produced new fossils, and in the following some of the avian remains from these efforts are reported (note that the site is on private land and now closed to collecting). All fossils were collected by Marco Gulotta and stem from the bone bed in zone 11 of Bed B of the Potapaco Member of the Nanjemoy Formation.

Materials and methods

The new fossils from the Fisher/Sullivan site are deposited in the collection of Senckenberg Research Institute Frankfurt. Osteological terminology follows Baumel 1993 and Witmer (1993), the measurements are in millimeters. Institutional abbreviations: IGWuG: Institut für

Geologische Wissenschaften und Geiseltalmuseum of Martin-Luther-Universität Halle-Wittenberg, Halle/Saale, Germany; MGUH: Geological Museum of the University of Copenhagen, Denmark; NHM: the Natural History Museum, London, UK; SMF: Senckenberg Research Institute Frankfurt, Germany; USNM: Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA; WDC: Wyoming Dinosaur Center, Thermopolis, WY, USA.

Systematic paleontology

?Procellariiformes Fürbringer, 1888

Gen. et sp. indet.

Figure 1a–c

Referred specimen. SMF Av 617 (distal end of left tarsometatarsus lacking trochlea metatarsi IV).

Measurements. Length as preserved, 11.6; width of trochlea metatarsi III, 1.6; width across trochleae metatarsorum II et III, 2.9; estimated total distal width, 4.0.

Remarks. This fragmentary bone shows a distinctive morphology. It resembles the tarsometatarsus of the procellariiform Diomededidae, but is from a very small species. The shaft is robust and has a slightly convex plantar surface. A characteristic feature of the bone is the lack of a fossa metatarsi II, which indicates that a hindtoe was either absent or strongly reduced. The dorsal opening of the foramen vasculare distale is situated in a distinct fossa. The trochlea metatarsi II is much shorter than the trochlea metatarsi III, but shows only moderate plantar deflection; the distal end of the trochlea is medially slanting, and unlike in many other neornithine birds, the dorsodistal articular surface of its lateral portion is not rounded. Instead, the trochlea metatarsi II is mediolaterally narrow and has two equally developed trochlear rims; in distal view, it exhibits a notch in its medial portion (Fig. 1c). The plantar articular surface of the trochlea metatarsi III tapers proximally.

The derived shape of the trochlea metatarsi II is a distinctive feature of the fossil and restricted rotation of the second toe. This trochlear morphology appears to be a characteristic of birds with webbed feet and is found in many extant representatives of Aequornithes, the “water-bird clade” (e.g., Smith 2010: Fig. 9). Overall, the Nanjemoy fossil most closely resembles the tarsometatarsus of procellariiform birds, and an assignment to Procellariiformes is also supported by the absence of a fossa metatarsi I and the inferred reduction of the hindtoe.

SMF Av 617 is from a small bird the size of extant Audubon's Shearwater (*Puffinus lherminieri*). If indeed from a procellariiform, the fossil may be closely related to

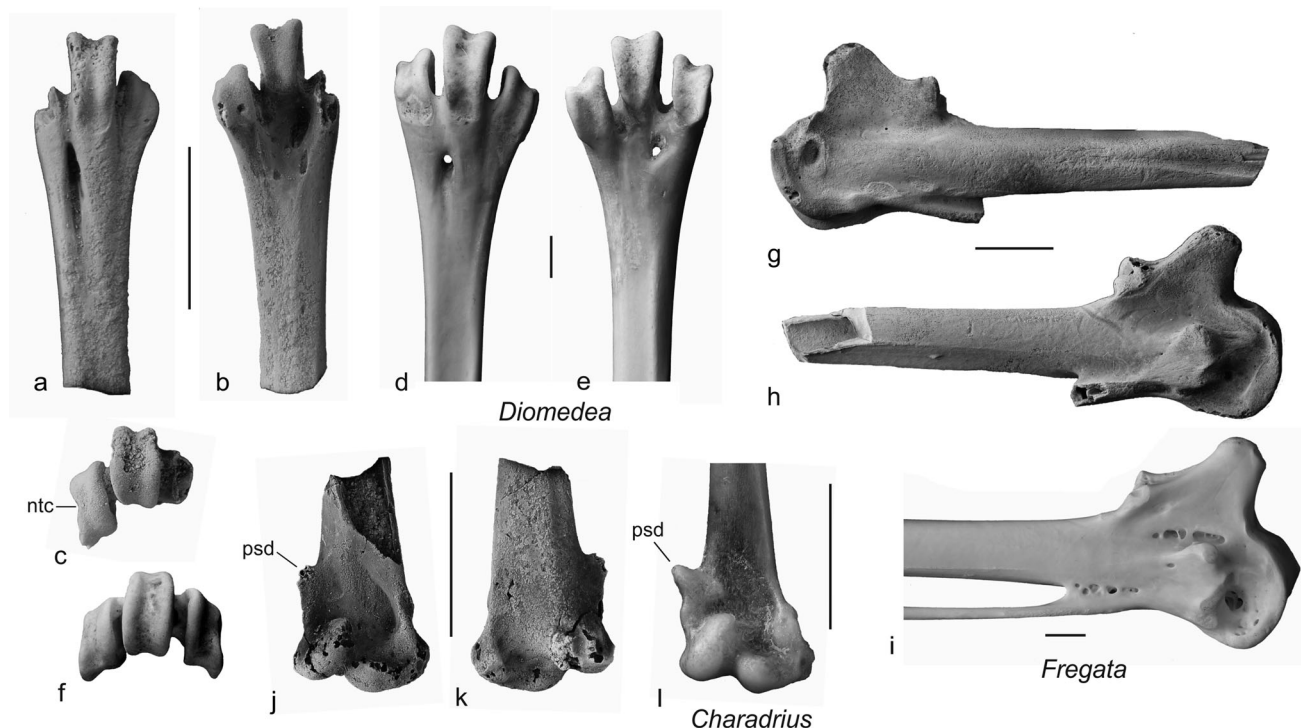


Fig. 1 a–c ?Procellariiformes, distal end of left tarsometatarsus from the Nanjemoy Formation (SMF Av 617) in dorsal (a), plantar (b), and distal (c) view. d–f Distal left tarsometatarsus of the extant Black-browed Albatross, *Diomedea melanophris* (Procellariiformes) in dorsal (d), plantar (e), and distal (f) view. g, h ?Fregatidae (cf. *Limnofregata*), proximal end of right carpometacarpus from the Nanjemoy Formation (SMF Av 618) in dorsal (g) and ventral (h) view. i Proximal right carpometacarpus of the extant Magnificent

Frigatebird, *Fregata magnificens* in ventral view. j, k Distal end of right humerus of a charadriiform bird from the Nanjemoy Formation (SMF Av 619) in cranial (j) and caudal (k) view. l Distal right humerus of the extant Three-Banded Plover, *Charadrius tricollaris* (Charadriidae), in cranial view. ntc notch in trochlea metatarsi III, psd processus supracondylaris dorsalis. All fossils were coated with ammonium chloride. Scale bars equal 5 mm

the taxon *Primodroma* from the London Clay, which was assigned to Procellariiformes and is based on a distal humerus (Harrison and Walker 1977). An equally small putative procellariiform is also known from the middle and late Eocene of Ukraine (*Kievornis*; Zvonok et al. 2015).

In size and morphology, SMF Av 617 resembles a tarsometatarsus that was referred to *Coturnipes cooperi* by Olson (1999: Fig. 3h, i). Unfortunately, this latter fossil (USNM 496419) lacks the trochlea metatarsi II, and because it is the trochlea metatarsi IV that is broken in SMF Av 617, meaningful comparisons on the basis of the figures published by Olson (1999) are limited. The trochlea metatarsi III of USNM 496419 is proportionally narrower than that of *Coturnipes*, and although I considered it likely that USNM 496419 is conspecific with SMF Av 617, this can only be verified through direct examination of the fossil. In addition to the shape of the trochlea metatarsi II, which is not preserved in USNM 496419, SMF Av 617 differs from *Coturnipes* in the absence of a fossa metatarsi I.

At least judging from the published figures, two partial tibiotarsi assigned to *Coturnipes* by Olson (1999: Fig. 3f, g) likewise resemble those of procellariiform birds,

especially with regard to the presence of a marked sulcus extensorius. It is further noted that a humerus (USNM 496374) that was assigned to the charadriiform Scolopaci by Olson (1999: Fig. 3c) shows a resemblance to the humerus of *Primodroma bournei* from the London Clay (Harrison and Walker 1977: pl. 1A–E [erroneously labelled as “*Pseudodontornis longidentata*”]).

Suliformes Sharpe, 1891

?**Fregatidae** Degland and Gerbe, 1867

cf. *Limnofregata* Olson, 1977

Figure 1g, h

Referred specimen. SMF Av 618 (proximal end of right carpometacarpus).

Measurements. Length as preserved, 32.2; greatest craniocaudal depth through processus extensorius, 12.4.

Remarks. This bone is from a medium-sized bird, which was slightly larger than the extant White-Tailed Tropicbird, *Phaethon lepturus*. It is characterized by a proximally bulging trochlea carpalis with weakly developed fossae and ridges on the dorsal and ventral surfaces, which is particularly true for the fovea carpalis cranialis and the

fovea carpalis caudalis, with the former being virtually absent and the latter very shallow. The processus extensorius is cranially prominent. Apart from being slightly smaller, the bone differs from a carpometacarpus reported by Olson (1999: Fig. 4c; USNM 496385) in that the proximal metacarpal symphysis is proportionally shorter.

SMF Av 618 differs from the carpometacarpus of the early Eocene phaethontiform Prophaethontidae in the shape of the processus extensorius, which in prophaethontids and extant Phaethontiformes is proximodistally longer and less cranially prominent (compare Fig. 1h with Mayr 2015b: Fig. 5 and Mayr and Scofield 2016: Fig. 1). The shape of the processus extensorius also distinguishes the fossil from the carpometacarpus of procellariiform birds, in which this process is proximodistally shorter and has a straighter proximal margin. The carpometacarpus of Procellariiformes furthermore differs from SMF Av 618 in the more rounded trochlea carpalis and the lower processus pisiformis.

Compared to extant birds, the specimen resembles the much larger and more heavily pneumatized proximal carpometacarpus of the Fregatidae (Fig. 1i). In its morphology, the fossil corresponds well with the carpometacarpus of the early Eocene *Limnofregata* (compare Fig. 1h with Olson 1977: Fig. 23), which is one of the most abundant birds in the Green River Formation and was also reported from other early Eocene localities in Wyoming (Olson 1977; Olson and Matsuoka 2005; Stidham 2015). SMF Av 618 is, however, from a bird that was smaller than the smallest species of *Limnofregata*, *L. azygosternon*, in which the craniocaudal depth of the proximal carpometacarpus is 17.2 mm (Olson 1977). Because of the resemblance to the proximal carpometacarpus of *Limnofregata* and extant frigatebirds, I consider it likely that SMF Av 618 is from a stem group representative of Fregatidae, but a definitive assignment has to await the discovery of further material from the Nanjemoy Formation.

Charadriiformes Huxley, 1867

Gen. et sp. indet.

Figure 1j, k

Referred specimen. SMF Av 619 (distal end of right humerus).

Measurements. Width of distal end, 4.2.

Remarks. This bone exhibits a suite of characteristic charadriiform features, including a strongly developed processus supracondylaris dorsalis (whose tip is broken in the fossil) and a derived shape of the ventrodistal portion of the bone, which forms a ventrally directed “lip”. The specimen is from a very small species, which had about the size of the extant Three-banded Plover, *Charadrius*

Fig. 2 a, b ?Messelornithidae, extremitas omalis of right coracoid from the Nanjemoy Formation (SMF Av 620) in dorsal (a) and ventral (b) view. **c** Extremitas omalis of right coracoid of *Messelornis cristata* from Messel (SMF-ME 2614a) in dorsal view. **d** Extremitas omalis of right coracoid of *Walbeckornis creber* from the Paleocene of Germany (IGWuG WAL39.2007) in dorsal view. **e, f** ?Messelornithidae, distal end of right humerus from the Nanjemoy Formation (SMF Av 621) in caudal (e) and cranial (f) view. **g** Distal end of left humerus (mirrored to ease comparisons) of *W. creber* in cranial view (IGWuG WAL162.2007). **h–j** ?Messelornithidae, distal end of right tarsometatarsus from the Nanjemoy Formation (SMF Av 622) in dorsal (h), plantar (i) and distal (j) view. **k** Distal right tarsometatarsus of *W. creber* in dorsal view (holotype, IGWuG WAL472.2007). **l–n** ?Trogoniformes, distal end of right tibiotarsus from the Nanjemoy Formation (SMF Av 623) in cranial (l), caudal (m), and distal (n) view. **o** Distal right tibiotarsus of the extant Green-backed Trogon, *Trogon viridis* (Trogonidae), in cranial view. **p–r** cf. Eocypselidae, distal left tarsometatarsus from the Nanjemoy Formation (SMF Av 624) in dorsal (p), plantar (q) and distal (r) view. **s** Distal right tarsometatarsus (mirrored to ease comparisons) of *Procuculus minutus* from the London Clay (holotype, NHM A 4680) in plantar view. **t** Distal left tarsometatarsus of the Australian Owllet-nightjar, *Aegotheles cristatus* (Aegothelidae), in plantar view. **u** Distal end of left tarsometatarsus of *Eocypselus vincenti* (Eocypselidae) from the Danish Fur Formation (silicone peel of MGUH 29278) in plantar view. **v, w** cf. Eocypselidae, right carpometacarpus from the Nanjemoy Formation (SMF Av 625) in ventral (v) and dorsal (w) view. *cdl* condylus lateralis, *cdm* condylus medialis, *cpr* crista procoracoidei, *ext* sulcus extensorius, *fns* foramen nervi supracoracoidei, *iod* sulcus for tendon of musculus interosseus dorsalis, *ltr* lateral tuberositas retinaculi extensoris, *mtr* medial tuberositas retinaculi extensoris, *pst* pons supratendineus, *ptm* protuberantia metacarpalis, *tmc* tuberositas musculi tibialis cranialis. All fossils except **s** were coated with ammonium chloride. Scale bars equal 5 mm

tricollaris (Fig. 1l), and it is, therefore, distinctly smaller than the putative Charadriiformes reported by Olson (1999). The distal end of the humerus of charadriiform taxa shows some variation in morphological features, especially concerning the shape and size of the processus supracondylaris dorsalis (Ballmann 2004), but this has not yet set into a phylogenetic context and no attempt was made in the present study to narrow down the affinities of SMF Av 619. Overall, the fossil resembles the distal humerus of *Charadrius* (Charadriidae) or *Calidris* (Scolopacidae).

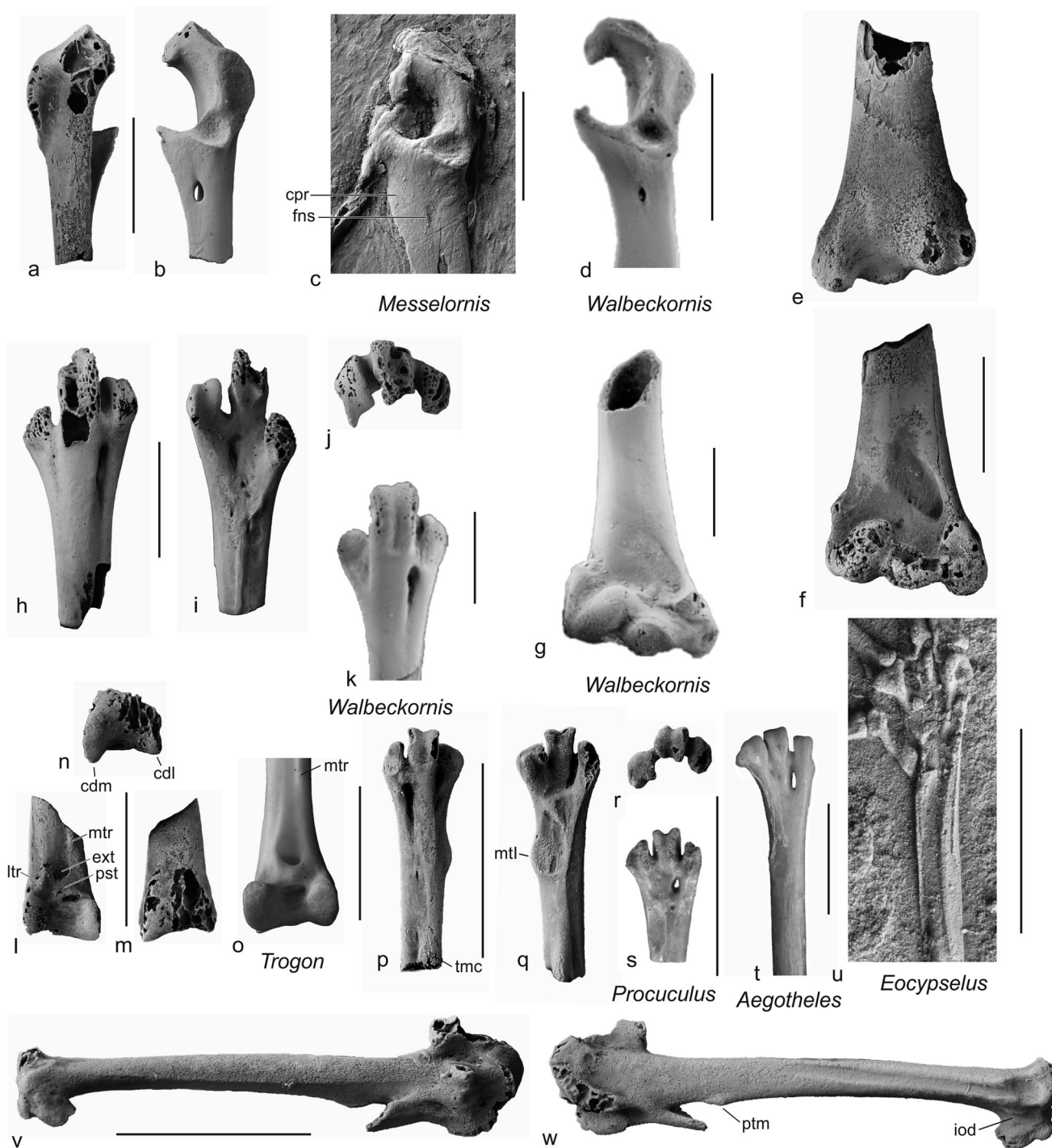
?Messelornithidae Hesse, 1988

cf. *Messelornis* Hesse, 1988

Figure 2a, b, e, f, h–j

Referred specimens. SMF Av 620 (extremitas omalis of right coracoid; Fig. 2a, b), SMF Av 621 (distal end of right humerus; Fig. 2e, f), SMF Av 622 (distal end of right tarsometatarsus; Fig. 2h–j).

Measurements. Coracoid: length as preserved, 10.6; distance between tip of extremitas omalis and sternal end of cotyla scapularis, 5.6. Humerus: length as preserved, 12.4; distal width, 7.1. Tarsometatarsus: length as preserved, 12.5; distal width, 4.8.



Remarks. The specimens match well in size, and all resemble the corresponding bones of the Messelornithidae. These gruiform birds are the sister taxon of the Ralloidea (Rallidae and Heliornithidae) and were abundant and widespread in the early Eocene of North America and Europe, with records being known from the Green River Formation, the Danish Fur Formation, and from Messel (Mayr 2009; Bertelli et al. 2011). In addition to the early Eocene *Messelornis*, messelornithids also include the late

Eocene and early Oligocene *Itardiornis* from the Quercy fissure fillings in France (Mourer-Chauviré 1995). The Nanjemoy fossils likewise show close similarities to the messelornithid-like *Walbeckornis* from the Paleocene of Germany (Mayr 2007), which is difficult to distinguish from messelornithids in some of the above bones.

The fossils from the Nanjemoy Formation are from a bird the size of the North American *Messelornis nearctica*. The coracoid corresponds well with that of *Messelornis* and

Walbeckornis. The processus procoracoideus, whose tip is broken, is continuous with a crista procoracoidei, which is, however, less developed than in *Messelornis* (Fig. 2c) and *Itardiornis*. The foramen nervi supracoracoidei of the Nanjemoy fossil is furthermore proportionally larger than in messelornithids and *Walbeckornis* (Fig. 2d).

The humerus is quite worn, but the preserved morphological details agree with the humerus of *Itardiornis*. There is a low tuberculum supracondylare dorsale and the fossa musculi brachialis is large and moderately deep. The humerus of *Walbeckornis* (Fig. 2g) is likewise similar, but has a more ventrally protruding processus flexorius.

The trochleae metatarsorum II et III of the tarsometatarsus are damaged, but the preserved portions of the bone correspond well with the tarsometatarsi of *Messelornis*, *Itardiornis*, and *Walbeckornis* (Fig. 2k). As in the latter taxa, the trochlea metatarsi II is short and reaches distally only to about the level of the base of the trochlea metatarsi IV. A fossa metatarsi I is present.

SMF Av 620 closely resembles a similar-sized distal tarsometatarsus from the Nanjemoy Formation, which was assigned to the charadriiform *Scolopaci* by Olson (1999: Fig. 3d), and it is here considered likely that this latter specimen (USNM 496375) is also from a messelornithid. The humerus USNM 496374 assigned to this tarsometatarsus by Olson (1999: Fig. 3c) is smaller than the humerus that is assigned to the Messelornithidae in the present study and appears to be too small to be from the same species as the tarsometatarsus USNM 496375. As noted above, this humerus (USNM 496374) needs to be compared with procellariiform birds.

?**Trogoniformes** American Ornithologists' Union, 1886

Gen. et sp. indet.

Figure 2l–n

Referred specimen. SMF Av 623 (distal end of right tibiotarsus).

Measurements. Distal width, 2.9.

Remarks. This specimen is from a very small species and resembles the tibiotarsus of trogoniform birds (Fig. 2o). The distal end of the bone is characterized by proximodistally low and widely separated condyles, with the condylus lateralis having little cranial prominence. The sulcus extensorius is located centrally on the shaft and the pons supratendineus is proximodistally wide. The lateral tuberositas retinaculi extensoris is an elongate, raised scar that is situated at the proximal end of the pons supratendineus, from which it is, however, widely spaced. The medial tuberositas retinaculi extensoris is positioned much farther proximally, at the tip of the proximal end of the bone fragment.

Early Eocene Trogoniformes are known from the London Clay, the Fur Formation, and from Messel (Mayr

2009). If correctly assigned to Trogoniformes, SMF Av 623 would constitute the first published record of Trogoniformes from the early Eocene of the New World (an unpublished putative record exists, however, from the Green River Formation; Mayr 2009: p.191).

Given the fragmentary nature of the specimen, its assignment to Trogoniformes is tentative and pends on the discovery of additional material. In size, the fossil corresponds to the tarsometatarsus of the unidentified genus and species B (cf. *Microena*), which is not from a trogoniform bird, but other than size there exists no basis for a referral to this latter specimen.

?**Apodiformes** Peters, 1940

cf. **Eocypselidae** Harrison, 1984

Gen. et sp. indet.

Figure 2p–r

Referred specimen. SMF Av 624 (distal end of left tarsometatarsus).

Tentatively referred specimens. SMF Av 625 (right carpometacarpus lacking os metacarpale minus and tip of processus extensorius; Fig. 2v, w), SMF Av 626 (distal end of left carpometacarpus).

Measurements. Tarsometatarsus: length as preserved, 7.0; distal width, 2.0; width of trochlea metatarsi III, 0.8. Carpometacarpus (SMF Av 625): length, 13.1.

Remarks. These bones are from a tiny species, and the distal end of the tarsometatarsus resembles that of *Eocypselus* (Eocypselidae; Fig. 2u), an early Eocene stem group apodiform, which was reported from the London Clay as well as the Fur and Green River formations (Mayr 2009, 2010; Ksepka et al. 2013). The morphology of the bone also corresponds well with the distal tarsometatarsus of the Aegothelidae, the closest extant relatives of apodiform birds (Fig. 2t). The proximal end of the specimen is broken, but because the distal portion of the crista medianoplantaris and the tuberositas musculi tibialis cranialis are preserved, only a small portion of the tarsometatarsus appears to be missing, with the total length of the bone being estimated at about 8–9 mm. The dorsal opening of the foramen vasculare distale is situated in a marked, narrow fossa. The trochleae metatarsorum II et IV have an equal distal extent and are shorter than the trochlea metatarsi III. The trochlea metatarsi II is plantarly deflected and proportionally shorter than that of the Aegothelidae. The fossa metatarsi I is large and located on the plantar surface of the tarsometatarsus. The proximal section of the fossa metatarsi I has an essentially flat surface, which projects beyond the medial margin of the shaft, where it forms a distinct convexity (Fig. 2q); at the distal end of the fossa metatarsi I there is a marked protuberance on the plantar surface of the shaft.

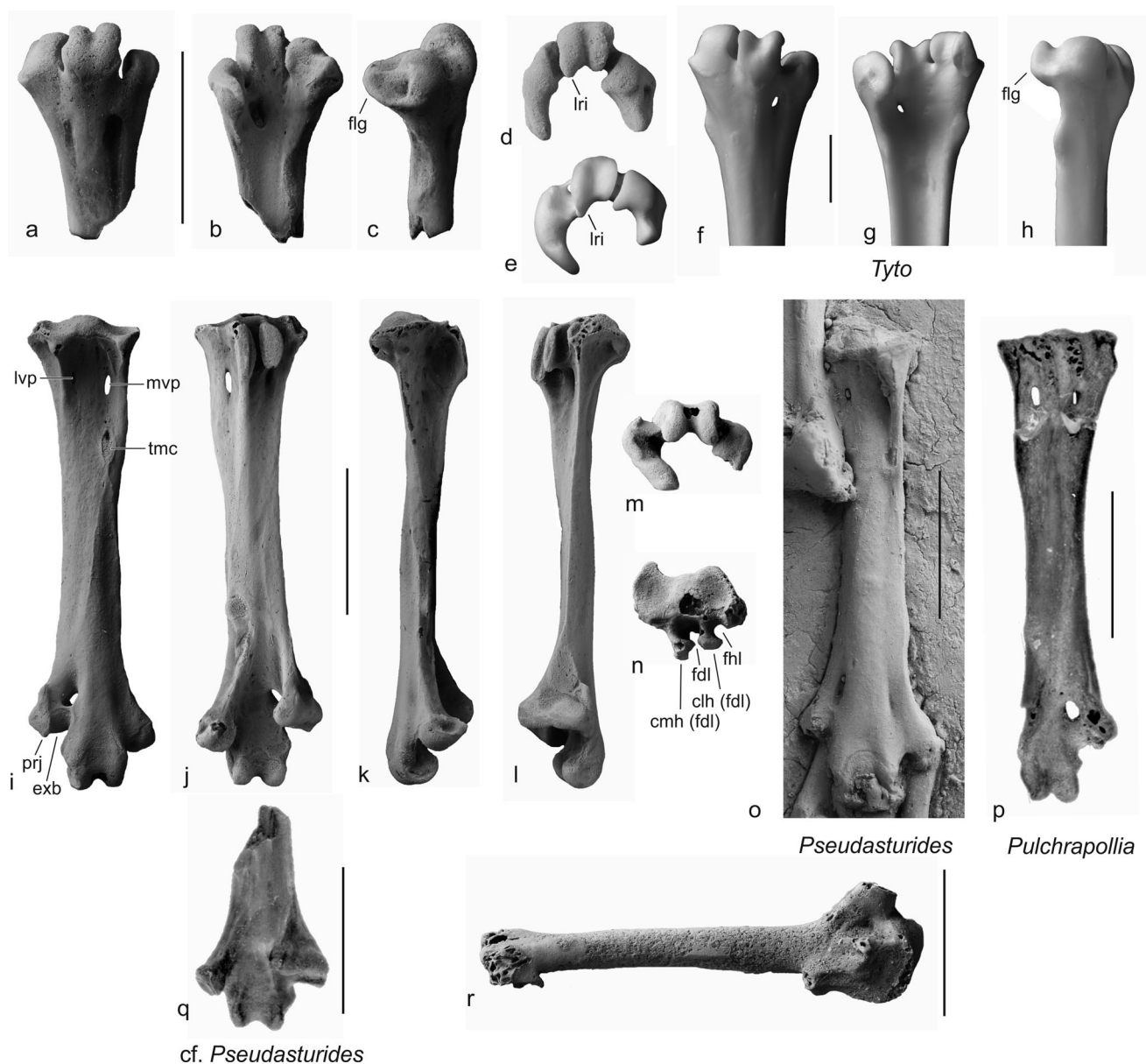


Fig. 3 **a–d** *Eostrix gulottai* sp. nov., distal end of right tarsometatarsus from the Nanjemoy Formation (SMF Av 627) in dorsal (**a**), plantar (**b**), medial (**c**), and distal (**d**) view. **e–h** Distal right tarsometatarsus of the extant Barn Owl, *Tyto alba* (Tytonidae), in distal (**e**), dorsal (**f**), plantar (**g**), and medial (**h**) view. **i–n** Halcyornithidae (cf. *Pulchrapollia*), right tarsometatarsus from the Nanjemoy Formation (SMF Av 628) in dorsal (**i**), plantar (**j**), medial (**k**), lateral (**l**), distal (**m**), and proximal (**n**) view. **o** Left tarsometatarsus (mirrored to ease comparisons) of *Pseudasturides macrocephalus* from Messel (cast of holotype, WDC-C-MG 94) in dorsal view. **p** Right tarsometatarsus of *Pulchrapollia gracilis* from the London Clay (holotype, NHM A 6207) in plantar view. **q** Distal left tarsometatarsus (mirrored to ease comparisons) of cf. *Pseudasturides*

macrocephalus from the London Clay (holotype, NHM A 6184) in plantar view. **r** Halcyornithidae (cf. *Pulchrapollia*), tentatively referred right carpometacarpus from the Nanjemoy Formation (SMF Av 629) in ventral view. *cmh (fdl)* crista medialis hypotarsi (fdl), *clh (fdl)* crista lateralis hypotarsi (fdl), *exb* sulcus for tendon of musculus extensor brevis digiti IV, *fdl* hypotarsal sulcus for tendon of musculus flexor digitorum longus, *fhf* hypotarsal sulcus for tendon of musculus flexor hallucis longus, *flg* plantar flange of trochlea metatarsi II, *lri* lateral plantar rim of trochlea metatarsi III, *lvp* lateral foramen vasculare proximale, *mvp* medial foramen vasculare proximale, *prj* distal projection (see text), *tmc* tuberositas musculi tibialis cranialis. All fossils except **p** and **q** were coated with ammonium chloride. Scale bars equal 5 mm

The tentatively referred carpometacarpi also correspond well with that of *Eocypselus* in their proportions. On the ventral surface of the bone, at the base of the processus alularis, there are two parallel, raised scars. A

notable feature on the dorsal surface of the bone is the presence of a short sulcus for the tendon of musculus interosseus dorsalis, which is situated at the distal end of the os metacarpale majus, just caudal of the sulcus

tendinosus (Fig. 2w). Presence of a sulcus for only musculus interosseus dorsalis distinguishes the bone from the carpometacarpus of crown group Apodiformes, in which there is a second sulcus for musculus interosseus ventralis. The os metacarpale majus exhibits a small protuberantia metacarpalis (Fig. 2w). In size and proportions, the two carpometacarpi reported here agree with a carpometacarpus described by Olson (1999: Fig. 6g, h), who tentatively assigned this specimen to the Caprimulgidae. This latter fossil (USNM 496383) is here also assigned to stem group Apodiformes.

The distal tarsometatarsus and the carpometacarpus show a resemblance to both *Eocypselus* and Aegothelidae (Fig. 2t, u), and an unambiguous assignment to either Apodiformes or the more inclusive clade (Aegothelidae + Apodiformes) is not possible. The specimens are here tentatively classified into Apodiformes, because eocypselids appear to have been abundant in the early Eocene of the Northern Hemisphere and were reported from the Green River Formation. Assignment to the Eocypselidae is, however, only tentative and the Nanjemoy species shows some differences to *Eocypselus*. Unlike in the latter taxon, the tarsometatarsus exhibits a marked bulge on its medial surface, on the level of the fossa metatarsi I, and with an estimated length of 8–9 mm, the bone was distinctly shorter than the carpometacarpus, with both bones being of subequal length in *Eocypselus* (Mayr 2010).

The only other coeval early Eocene apodiform bird is the putative aegialornithid *Primapus*, of which two humeri were described from the London Clay (Harrison and Walker 1977; Mayr 2009). The tarsometatarsus of *Primapus* is unknown, but a distal tarsometatarsus of a tiny apodiform bird from the London Clay, which was described as *Procuculus minutus* (Fig. 2s), may belong to either *Primapus* or *Eocypselus* (Mayr 2009, 2010). This latter specimen (NHM A 4680) closely resembles SMF Av 624, but does not exhibit the medially bulging fossa metatarsi I. Aegialornithids are abundant in late Eocene deposits of the Quercy fissure fillings in France and were also reported from the middle Eocene of Germany (Mayr 2009). Compared with the Nanjemoy fossils, the carpometacarpus of at least the late Eocene aegialornithids has a straighter processus extensorius. Two further taxa of apodiform birds, the swift *Scaniacypselus* and the putative stem group trochilid *Parargornis*, occur in the somewhat younger deposits of the Messel fossil site (Mayr 2009). Both are, however, considered to be crown group representatives, and *Scaniacypselus* has a much shorter tarsometatarsus than the Nanjemoy fossil.

Strigiformes Wagler, 1830

Protostrigidae Wetmore, 1933

Eostrix Brodkorb, 1971

Eostrix gulottai sp. nov.

Figure 3a–d

Holotype. SMF Av 627 (distal end of right tarsometatarsus).

Differential diagnosis. *Eostrix gulottai* sp. nov., differs from the known species of *Eostrix* and all other fossil owls in its much smaller size. In addition, it is distinguished from:

- the Paleocene *Berruornis* in: distal end of tarsometatarsus much more arched in distal view, with trochlea metatarsi IV bearing a better developed plantar flange.
- the Paleocene *Ogygoptynx* in: plantar surface of trochlea metatarsi II with long and narrow, wing-like flange; trochlea metatarsi III less asymmetric in distal view; plantar flange of trochlea metatarsi IV better developed.
- the species of *Minerva* (as exemplified by the specimen of *Minerva* [“*Protostrix*”] *leptosteus* figured by Rich 1982) in: trochlea metatarsi II more strongly plantarly deflected; trochlea metatarsi III mediolaterally wider; trochlea metatarsi IV with larger plantar flange.
- the early Oligocene *Oligostrix* (sensu De Pietri et al. 2013) in: distal end much more arched in distal view; trochlea metatarsi IV with much better developed plantar flange.
- the early Oligocene *Heterostrix* and all crown group Strigiformes in: trochlea metatarsi II shorter than trochlea metatarsi III; trochlea metatarsi III not strongly asymmetric in distal view.

Type locality and horizon. Fisher/Sullivan site east of Fredericksburg, Stafford County, Virginia, USA; early Eocene (Ypresian), zone 11 of Bed B of the Potapaco Member of the Nanjemoy Formation (Weems and Grimsley 1999).

Etymology. The species is named after Marco Gulotta, who found the holotype and all other bird fossils described in the present study.

Measurements. Distal width, 3.9; width of trochlea metatarsi III, 1.6.

Description and comparisons. This specimen is from a very small stem group representative of the Strigiformes and exhibits the characteristic derived tarsometatarsus morphology of owls, with a very large trochlea metatarsi II and a large wing-like flange on the trochlea metatarsi IV. In distal view, the end of the bone is strongly arched across the trochleae. The trochlea metatarsi II forms a marked plantar flange, which is more pointed and proximodistally narrower than in crown group Strigiformes (Fig. 3c, h). As in other protostrigid owls, this trochlea does not reach as

far distally as the trochlea metatarsi III. The trochlea metatarsi II is further not as mediolaterally wide as in crown group Strigiformes and bears a distinct fossa on its medial surface. The trochlea metatarsi III shows only little asymmetry in distal view, with the rims having subequal plantar extent, whereas in crown group Strigiformes the lateral rim projects farther plantarly (Fig. 3e). The foramen vasculare distale is large, its dorsal opening is situated at the end of a sulcus. The plantar surface of the shaft is slightly concave.

Remarks. Numerous owl fossils have been described from Oligocene and younger fossil sites, but early Paleogene remains are rare (Mayr 2009; Kurochkin and Dyke 2011). Most of the early Eocene records stem from North America and were assigned to the Protostrigidae. In addition to the species of *Eostrix*, that is, *E. mimica* and *E. martinellii* from the early Eocene of Wyoming, North American protostrigid owls include several species of *Minerva* (“*Protostrix*”) from the middle Eocene (Bridgerian) of Wyoming and the late Eocene of California (Mourer-Chauviré 1983; Mayr 2009). All previously described protostrigid owls are considerably larger than *Eostrix gulottai* sp. nov., with the tarsometatarsus of *E. martinellii* having a distal width of 9.8 mm and that of *E. mimica* and *Minerva leptosteus* being even larger (Rich 1982); measurements of distal tarsometatarsi of the other species of *Minerva* are not available, but all are likewise much larger than the new Nanjemoy owl.

A putative representative of *Eostrix*, *E. vincenti*, was described from the early Eocene London Clay (Harrison 1980). Of the tarsometatarsus of this species only the proximal end is known, which has a width of 7.9 mm (own obs.), so that *E. vincenti* was also distinctly larger than *E. gulottai*. A further species of *Eostrix*, *E. tsaganica*, was reported from the early Eocene of Mongolia (Kurochkin and Dyke 2011). With a distal tarsometatarsus width of 7.8 mm (Kurochkin and Dyke 2011), *E. tsaganica*, which was previously the smallest early Cenozoic owl, is likewise about twice as large as *E. gulottai*. The distal tarsometatarsus of *E. gulottai* resembles that of *E. tsaganica*, but the trochlea metatarsi III of the new owl from the Nanjemoy Formation is more asymmetric in distal view and the plantar flange of the trochlea metatarsi IV is larger and projects farther plantad (compare Fig. 3d with Kurochkin and Dyke 2011: pl. 12, Fig. 5). *E. gulottai* and *E. tsaganica* differ from the larger North American *E. mimica*, the type species of *Eostrix*, in a mediolaterally wider trochlea metatarsi III, and whether the taxon *Eostrix* as currently recognized is monophyletic needs to be shown in future studies.

Notably, *Eostrix gulottai* is not only the smallest fossil owl described so far, but most likely it is also the smallest

known owl in general. The smallest extant owls are the Elf Owl, *Micrathene whitneyi*, and the similar-sized Long-whiskered Owlet, *Xenoglaux loweryi*. Skeletal material of *Xenoglaux* appears to be very rare in collections and measurements have not been published, but the distal end of a fossil tarsometatarsus assigned to *M. whitneyi* has a width of 4.8 mm (Brasso and Emslie 2006) and is, therefore, distinctly larger than that of *E. gulottai*. The extant *Xenoglaux* and *Micrathene* feed on arthropods, mainly insects, and a similar diet is likely for *E. gulottai*.

Psittacopasseres Suh et al., 2011

Halcyornithidae Harrison and Walker, 1972

cf. **Pulchrapollia** Dyke and Cooper, 2000

Figure 3i–n, q, r

Referred specimen. SMF Av 628 (right tarsometatarsus).

Tentatively referred specimens. SMF Av 629 (right carpometacarpus lacking os metacarpale minus and tip of processus extensorius; Fig. 3r), SMF Av 630 (poorly preserved proximal end of left carpometacarpus), SMF Av 631 (fragmentary distal half of left ulna).

Measurements. Tarsometatarsus: length, 16.4; distal width, 4.4; width of trochlea metatarsi, 2.7; proximal width as preserved, 3.9. Carpometacarpus: length as preserved, 15.3.

Remarks The bone exhibits the characteristic morphology of the halcyornithid tarsometatarsus (Mayr 1998, 2002; Ksepka et al. 2011) and is the only complete and uncrushed tarsometatarsus of a halcyornithid in a public collection. Halcyornithidae are among the more abundant small arboreal birds in early Eocene fossil sites of the Northern Hemisphere and exhibit an unmistakable tarsometatarsus morphology. A number of halcyornithid taxa were described in the past decades, and the European fossils (from the London Clay and Messel) are assigned to the taxa *Halcyornis*, *Pseudasturides*, *Pulchrapollia*, and *Serudaptus*, whereas the two North American species (both from the Green River Formation) are classified in the taxon *Cyrlavis* (Mayr 2009; Ksepka et al. 2011).

SMF Av 628 provides new information on the morphology of the hypotarsus of halcyornithids, which forms deep sulci for the tendons of musculus flexor digitorum longus and musculus flexor hallucis longus, with the opening of the latter being more laterally directed. The crista medialis (fdl) is large and its lateral surface bears shallow sulci for some of the superficial flexor tendons. The crista lateralis (fdl) is likewise well developed, whereas the crista lateralis (fhl) is very small (terminology of hypotarsal crests follows Mayr 2016). Compared to other early Eocene taxa of Psittacopasseres, the clade including Psittaciformes and Passeriformes (Mayr 2015a), the hypotarsus of halcyornithids differs from that of the

Messelasturidae in the presence of a sulcus for musculus flexor hallucis longis (Fig. 3n). With regard to this feature, the hypotarsus of halcyornithids is more similar to that of the Indian Vastanavidae, in which the tendon for musculus flexor digitorum longus is, however, enclosed in a canal (Mayr et al. 2010).

As in other halcyornithids, the foramina vascularia proximalia are of unequal size, with the medial foramen being very large and the lateral one diminutive. The shaft of the bone is dorsoplantarly compressed and its lateral margin forms a sharp ridge. The fossa metatarsi I has a circular outline, a flat surface, and projects beyond the medial margin of the shaft. The foramen vasculare distale is large. A canalis interosseus distalis is absent, but there is a dorsal sulcus for the tendon of musculus extensor brevis digiti IV. The lateral margin of this sulcus forms a marked ridge that ends distally in a pointed projection (Fig. 3i); this characteristic feature is also present in other halcyornithids, but has not been described previously. The trochlea metatarsi II has a cylindrical shape, with a weakly developed plantar furrow. As in other halcyornithids, the trochlea metatarsi IV forms a distinct, plantarly directed wing-like flange.

The Nanjemoy fossil most closely corresponds with the tarsometatarsus of *Pulchrapollia gracilis* from the London Clay (Fig. 3p), in which, however, the lateral foramen vasculare is somewhat less reduced. In size, the specimen is intermediate between *Cyrilavis colburnorum* (tarsometatarsus length 17.7–18.1 mm; Ksepka et al. 2011) and *C. olsoni* (tarsometatarsus length ~15.5 mm; Ksepka et al. 2011), but in *Cyrilavis* the lateral foramen vasculare is more strongly reduced and the eminentia intercotylaris proportionally larger. SMF Av 628 is distinguished from the tarsometatarsus of *Serudaptus* in being less stout, with a more slender shaft. It differs from *Pseudasturides* (Fig. 3o) in that the foramen vasculare distale is proportionally larger and the sulcus for the tendon of musculus extensor brevis digiti IV more marked; a tarsometatarsus that was tentatively assigned to *Pseudasturides* furthermore has a smaller trochlea metatarsi II and narrower rims of the trochlea metatarsi III (Fig. 3q). The tarsometatarsus of *Halcyornis toliapicus* is unknown and there remains a possibility that this species is conspecific with one of the other European halcyornithids.

The tentatively referred carpometacarpus agree well with the carpometacarpus of *Cyrilavis* and *Pseudasturides* in size and morphological features (of the carpometacarpus of *Pulchrapollia*, only the proximal end is known). The tentatively referred ulna likewise matches the tarsometatarsus in size and exhibits a distinct depressio radialis, which is a characteristic feature of the halcyornithid ulna (Mayr 1998).

Aves, gen. et sp. indet. A

Figure 5a

Referred specimen. SMF Av 632 (distal portion of pedal phalanx).

Measurements. Length as preserved, 27.5; distal width, 8.0.

Remarks. This bone is from very large bird, the size of the Sarus Crane (*Grus antigone*) and possibly belongs to the same species as the distal radius and wing phalanx of a large, “crane-sized” bird reported by Olson (1999: Fig. 4). The thick bone walls indicate that the specimen is not from a pelagornithid, with these highly aerial birds having been reported by Olson (1999) from the Nanjemoy Formation.

Aves, gen. et sp. indet. B (cf. *Microena* Harrison and Walker, 1977)

Figure 4a–c

Referred specimen. SMF Av 633 (distal end of right tarsometatarsus lacking trochlea metatarsi IV).

Measurements. Length as preserved, 4.7; width of trochlea metatarsi III, 1.0; width across trochleae metatarsorum II et III, 1.9; estimated total distal width, ~2.5.

Remarks. This specimen shows a characteristic morphology of the trochlea metatarsi II, which reaches almost as far distally as the trochlea metatarsi III and forms a distinct medial projection. Concerning this latter feature, the fossil is distinguished from the tarsometatarsus of strisiorine, alcediniform, and coraciiform birds (Fig. 4j). The shaft of the bone is wide and dorsoplantarly flat, and the fossa metatarsi I is well developed. The dorsal opening of the large foramen vasculare distale is situated at the end of a distinct sulcus.

SMF Av 633 is from a species, which was slightly smaller than the extant Diamond Dove (*Geopelia cuneata*). Apart from its slightly smaller size, the fossil is distinguished from a superficially similar tarsometatarsus described by Olson (1999: Fig. 7; USNM 496384) in the proportionally larger foramen vasculare distale and the narrower trochlea metatarsi III. It differs from a fragmentary distal tarsometatarsus reported by Olson (1999: Fig. 6e, f; USNM 496382) in its smaller size and the fact that the dorsal opening of the large foramen vasculare distale is situated at the end of a distinct sulcus extensorius.

Compared with other early Eocene birds, SMF Av 633 is most similar to the tarsometatarsus of *Microena goodwini* from the London Clay (Fig. 4h, i), in which, however, the medial projection of the trochlea metatarsi II is larger. This species was initially described as a columbiform bird (Harrison and Walker 1977), but its phylogenetic affinities cannot be reliably determined on the basis of the known material (the holotype tarsometatarsus only). Because of

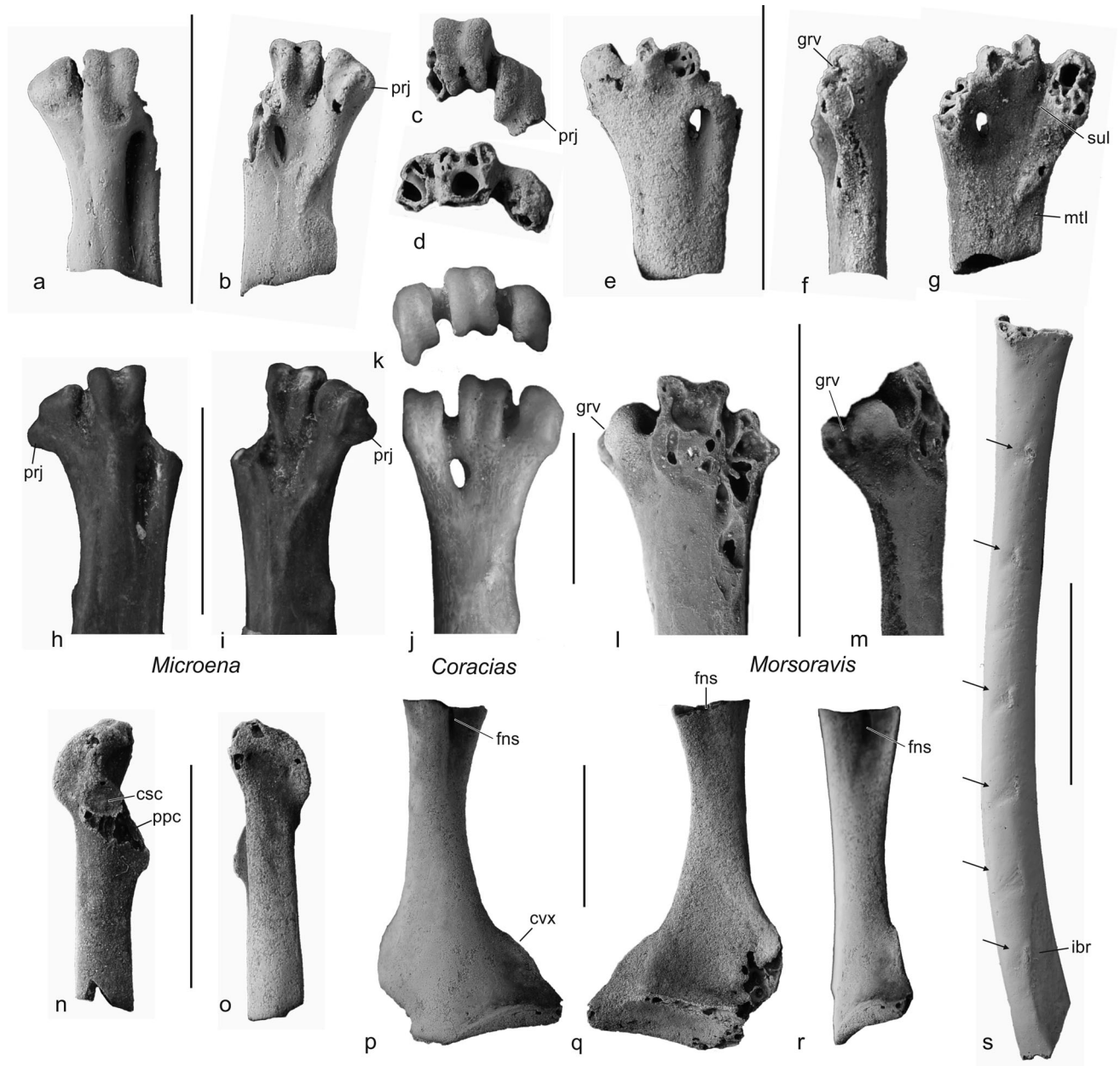


Fig. 4 **a–c** Aves, gen. et sp. indet. B (cf. *Microena*), partial distal end of right tarsometatarsus from the Nanjemoy Formation (SMF Av 633) in dorsal (**a**), plantar (**b**), and distal (**c**) view. **d–g** Aves, gen. et sp. indet. C (cf. *Morsoravis*), fragmentary distal end of right tarsometatarsus from the Nanjemoy Formation (SMF Av 634) in distal (**d**), dorsal (**e**), medial (**f**), and plantar (**g**) view. **h, i** Distal left tarsometatarsus (mirrored to ease comparisons) of *Microena goodwini* from the early Eocene London Clay (holotype, NHM A 3685) in dorsal **h** and plantar **i** view. **j, k** Distal right tarsometatarsus of the extant European Roller, *Coracias garrulus* (Coraciidae), in plantar (**j**) and distal (**k**) view to illustrate the absence of the medial projection of the trochlea metatarsi II. **l, m** Distal left tarsometatarsus (mirrored to ease comparisons) of *Morsoravis sedilis* from the early Eocene Danish Fur Formation (holotype, MGUH 28930; surrounding matrix digitally removed) in dorsal (**l**) and medial (**m**) view. **n, o**

o Aves, gen. et sp. indet. (?species B or C), omal half of left coracoid from the Nanjemoy Formation (SMF Av 635) in dorsal (**n**) and ventral (**o**) view. **p–r** Aves, gen. et sp. indet. D, extremities sternalis of right coracoid from the Nanjemoy Formation (SMF Av 637) in ventral (**p**), dorsal (**q**), and medial (**r**) view. **s** Aves, gen. et sp. indet. (?species B or C), right ulna lacking proximal end distal ends from the Nanjemoy Formation (SMF Av 636) in ventral view (the arrow indicate the papillae remigales). *csc* cotyla scapularis, *cvx* convexity on medial margin of extremitas sternalis, *fns* foramen nervi supra-coracoidei, *grv* groove on medial surface of trochlea metatarsi II, *ibr* impressio brachialis, *mtl* fossa metatarsi I, *ppc* breaking edge of processus procoracoideus, *sul* sulcus at base of incisura intertrochlearis medialis, *prj* medial projection of trochlea metatarsi II. All fossils except **h** and **i** were coated with ammonium chloride. Scale bars equal 5 mm

the fragmentary nature of the Nanjemoy fossil, an unambiguous referral to *Microena* is, however, not possible.

Aves, gen. et sp. indet. C (cf. *Morsoravis* Bertelli et al., 2010)

Figure 4d–g

Referred specimens. SMF Av 634 (fragmentary distal end right of tarsometatarsus).

Measurements. Length as preserved, 4.5; estimated distal width, 2.7.

Remarks. This tarsometatarsus is very fragmentary, but exhibits a suite of characteristic features. The bone has a wide and mediolaterally compressed shaft and the fossa metatarsi I is located near the medial margin of the shaft. The trochlea metatarsi II, which is damaged on its plantar surface, is narrow, has little plantar deflection, and bears a groove on its medial surface. The incisura intertrochlearis medialis is wide, but proximodistally shallow. On the dorsal surface of the bone, there is a depression at the base of the trochlea metatarsi III. Judging from the preserved portion, the trochlea metatarsi III itself appears to have been dorsally bulging. The trochlea metatarsi IV is broken, but the position and shape of the breakage area indicate that it was shorter than the trochlea metatarsi II and may have been plantarly deflected, therefore indicating an at least semizygodactyl foot. On the plantar surface of the bone, there is a narrow and shallow sulcus at the base of the incisura intertrochlearis medialis (Fig. 4g), presumably for the tendon of musculus adductor digiti II (this sulcus also occurs in the late Eocene psittaciform *Quercypsitta*; Mayr et al. 2010: Fig. 2j). The foramen vasculare distale is large and a canalis interosseus distalis is present.

Compared to other early Eocene birds, this fossil compares best with the tarsometatarsus of *Morsoravis sedilis*, an enigmatic small bird from the Danish Fur Formation (Fig. 4l, m). This species was originally described as a charadriiform bird (Bertelli et al. 2010). Its initial identification is, however, not well based and *Morsoravis* actually shows a greater resemblance to the taxon *Pumiliornis* from Messel, which is now considered to be a stem group representative of Passeriformes (Mayr 2011, 2015a). Resemblances of SMF Av 634 and *Morsoravis* concern the wide and dorsoplantarly flat tarsometatarsus shaft and the shape of the narrow trochlea, which bears a furrow on its medial surface.

With regard to the latter features, SMF Av 634 also shows some similarity to the tarsometatarsus of colliiform birds, which were diversified in the early Eocene of North America and Europe (Mayr 2009). Unlike in Coliiformes, however, the fossa metatarsi I is situated on the plantar surface of the shaft, whereas it is positioned on its medial

surface in Coliiformes (the position of this fossa is one of the diagnostic autapomorphies of Coliiformes).

Aves, gen. et sp. indet. (?species B or C)

Figure 4n, o, s

Referred specimens. SMF Av 635 (omal half of left coracoid; Fig. 4n, o), SMF Av 636 (right ulna lacking proximal end distal ends; Fig. 4s).

Measurements. Coracoid, length as preserved, 7.0. Ulna, length as preserved, 18.9; estimated total length, ~21–22.

Remarks. The coracoid is from a tiny bird and exhibits a distinctive morphology. It is characterized by a short extremitas omalis, whose tip is missing in the specimen. The cotyla scapularis is shallow. The processus procoracoideus, the tip of which is likewise broken, appears to have been unusually deep in sterno-omal direction. The robust and wide shaft has a subcircular cross section and widens towards the broken extremitas sternalis. A foramen nervi supracoracoidei is absent. The specimen is somewhat reminiscent of the coracoid of the Columbidae in overall shape, and in size it would correspond to the above-described tarsometatarsi of the indeterminate species B (cf. *Microena*) and C (cf. *Morsoravis*). Because *Microena* was likened to the Columbidae in the original description (Harrison and Walker 1977), it is tempting to refer this coracoid to the tarsometatarsus of species B. However, the affinities of *Microena* are poorly resolved, and because its coracoid and that of *Morsoravis* are unknown, even a tentative referral to any of the above species would be highly speculative.

The ulna is a short and stocky bone and resembles the ulnae of extant Coliiformes and Columbidae in its proportion. The shaft is slightly curved and dorsoventrally compressed, and six papillae remigales can be counted (Fig. 4s). In size, the bone matches the partial tarsometatarsi of the indeterminate species B and C, but because the ulnae of *Microena* and *Morsoravis* are unknown, direct comparisons with these taxa are not possible.

Aves, gen. et sp. indet. D

Figure 4p–r

Referred specimen. SMF Av 637 (extremitas sternalis of right coracoid).

Measurements. Length as preserved, 13.4, estimated total length, ~17–18.

Remarks. The preserved portions of this bone indicate a coracoid with a fairly stout shaft and a wide extremitas sternalis. The extremitas omalis is broken. A foramen nervi supracoracoidei is present and its ventral opening well visible (the dorsal opening is preserved as a small notch at

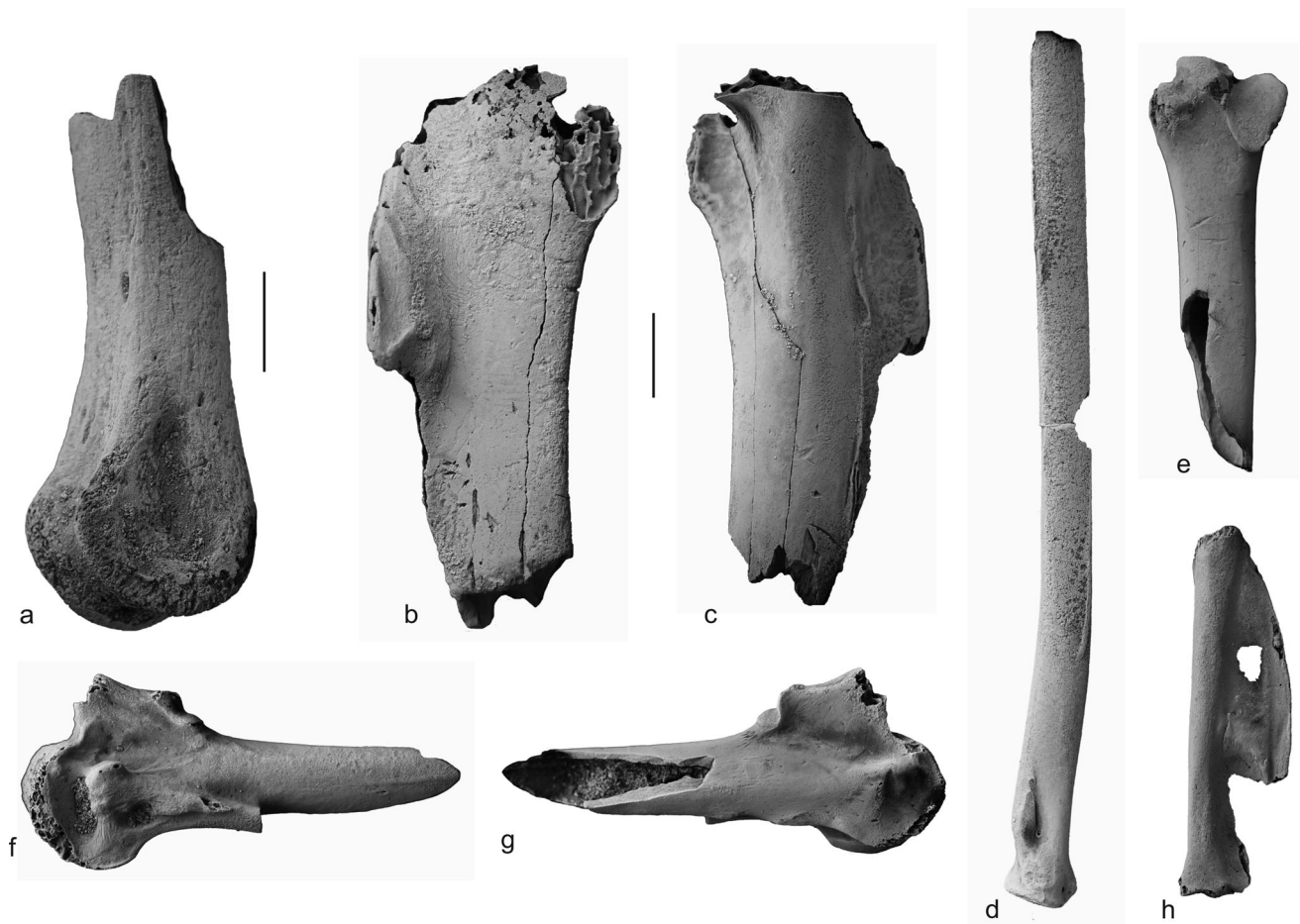


Fig. 5 **a** Aves, gen. et sp. indet. A, distal portion of pedal phalanx from the Nanjemoy Formation (SMF Av 632). **b–h** Aves, gen. et sp. indet. E from the Nanjemoy Formation (cf. Threskiornithidae): **b**, **c**, fragmentary proximal end of right humerus (SMF Av 638) in cranial (**b**) and caudal (**c**) view; **d** proximal half of right radius (SMF Av 639)

in caudal view. **e** distal end of left ulna (SMF Av 640) in ventral view; **f**, **g** proximal end of left carpometacarpus (SMF Av 641) in ventral (**f**) and dorsal (**g**) view; **h** left phalanx proximalis digiti majoris (SMF Av 642) in dorsal view. All specimens were coated with ammonium chloride. Scale bars equal 5 mm (same scale for **b–h**)

the very tip of the broken shaft). The medial margin of the shaft above the pointed and protruding angulus medialis forms a convexity.

Owing to its fragmentary preservation, an unambiguous identification of this specimen is not possible. In size, it would correspond to the above-described putative procellariiform species, but in shape it is clearly distinguished from Procellariiformes. The specimen appears to be too large to belong to the same species as the putative trogoniform tibiotarsus, and it does not resemble the coracoid of Trogoniformes, which, like the coracoid of most arboreal land birds, is more elongated and lacks a foramen nervi supracoracoidei. Concerning the other taxa reported in the present study, SMF Av 637 is too large to be from the unidentified species B and C, too small for the other unidentified species (A and E), and it does not match the morphology of the coracoid of all of the above taxa, which can be assigned to higher-level taxa.

In size, the specimen would correspond with a tarsometatarsus described by Olson (1999: Fig. 7). This fossil (USNM 496384) was originally assigned to the apodiform Aegialornithidae, but Mayr and Mourer-Chauviré (2005) suggested closer affinities to the Parviculidae. Parviculids are known from the London Clay and the early Eocene of France, but as yet only tarsometatarsi were identified, so that a well-based assignment of a coracoid to these birds is not possible.

Aves, gen. et sp. indet. E (cf. Threskiornithidae)
Figure 5b–h

Referred specimens. SMF Av 638 (fragmentary proximal end of right humerus; Fig. 5b, c), SMF Av 639 (proximal half of right radius; Fig. 5d), SMF Av 640 (distal end of left ulna; Fig. 5e), SMF Av 641 (proximal end of left carpometacarpus; Fig. 5f, g), SMF Av 642 (left phalanx proximalis digiti majoris; Fig. 5h).

Measurements. Humerus: length of fragment as preserved, 32.8. Ulna: craniocaudal width across tuberculum carpale and condylus dorsalis, 8.4. Radius, length of fragment as preserved, 52.5. Carpometacarpus: length as preserved, 27.6; greatest craniocaudal depth through processus extensorius, 11.9. Phalanx proximalis digiti majoris: length as preserved, 22.3.

Remarks Humerus, radius, and ulna match well in their dimensions and are likely to be from the same species. In size, they correspond with the Glossy Ibis, *Plegadis falcinellus*, and in morphological details they also resemble extant Threskiornithidae.

The fragmentary proximal humerus SMF Av 638 agrees well with the humerus of the Threskiornithidae, but the similarities are of rather general nature and the fossil also corresponds with the humerus of Phoenicopteriformes and Anseriformes. The distal section of the crista deltopectoralis is broken, but the remaining portion shows that the crest was well developed and cranially deflected. The preserved part of the fossa pneumotricipitalis allows the recognition of a large pneumatic opening at the broken end of the bone.

The distal end of the ulna likewise resembles the distal ulna of the Threskiornithidae. As in the latter, the tuberculum carpale is poorly developed and the rim of the condylus dorsalis exhibits a shallow notch. The radius is from a similar-sized species, but does not exhibit morphological features of taxonomic significance.

Compared with *P. falcinellus*, the partial carpometacarpus is proportionally somewhat larger, but this may well be due to individual or sexual size variation. Morphologically, the bone corresponds well with the carpometacarpus of the Threskiornithidae, but the processus extensorius, the tip of which is broken, appears to have been lower. The specimen differs from the carpometacarpus of the above-described putative suliform (cf. *Limnofregata*, SMF Av 618) in that the ventral rim of the trochlea carpalis is more strongly caudally bulging, the foveae carpalis cranialis et caudalis are much deeper, and in that there is a distinct ridge between the processus pisiformis and the base of the os metacarpale minus. It is distinguished from a similar-sized carpometacarpus figured by Olson (1999: Fig. 4c; USNM 496385) in that the proximal metacarpal symphysis is proportionally shorter. It differs from the proximal carpometacarpus of the anseriform *Presbyornis*, which is very abundant in the Green River Formation, in that in proximal view the dorsal rim of the trochlea carpalis projects less far caudally than the ventral rim, whereas in *Presbyornithidae* both rims have an equal caudal extent (e.g., De Pietri et al. 2016: Fig. 2).

The phalanx proximalis digiti majoris is craniocaudally narrow, and although this bone is of similar shape to that of

extant Threskiornithidae, there are many other avian taxa, in which it has a similar morphology.

In size, the above fossils agree with remains that were assigned as “genus and species indeterminate #1” to the Graculavidae by Olson (1999: Fig. 2), but unfortunately there exists no overlap in the skeletal elements described by Olson (1999) and those reported in the present study. The “form family” Graculavidae (sensu Olson 1999) is a paraphyletic assemblage that includes various unrelated late Cretaceous and early Cenozoic birds. Olson (1999) compared the specimens from the Nanjemoy Formation with the charadriiform Burhinidae, but judging from the published figures, they are equally similar to the Threskiornithidae. Early Eocene stem group representatives of the Threskiornithidae occur in Messel and the Fur Formation (Mayr 2009; Mayr and Bertelli 2011), but the material from the Nanjemoy Formation is too fragmentary for detailed comparisons and an unambiguous identification.

Discussion

Table 1 gives an overview of the taxa reported by Olson (1999) from the Fisher/Sullivan site and those described in the present study. Compared with other early Eocene localities, identification of the avian remains from the Fisher/Sullivan site is aggravated by the fact that all fossils are isolated bones, many of which are fragmentary. The difficulties associated with the study of such specimens are illustrated by earlier descriptions of similar material from the London Clay, which resulted in the erection of poorly founded and incorrectly identified taxa (Harrison and Walker 1977; Steadman 1981).

Today, the study of fragmentary remains of early Eocene birds stands on much firmer ground than even a decade ago, because early Eocene avifaunas of at least the western part of the Northern Hemisphere are comparatively well understood (Mayr 2009). Irrespective thereof, a cautious approach is pursued in the present study and identifications are designated as tentative if they are based on mere overall similarity. A major difficulty associated with the study of isolated bones furthermore concerns the assignment of different skeletal elements to the same taxon, and all such referrals in the present study have to be regarded with appropriate caution.

Clearly, however, the new material adds several distinctive new taxa to the avifauna of the Nanjemoy Formation, and there is only little overlap in the taxonomic composition of the fossils described by Olson (1999) and those reported in the present study. This indicates that, like other early Eocene avifaunas (Mayr in press), the bird community of the Nanjemoy Formation showed a high

Table 1 Avian taxa from the Nanjemoy Formation of Virginia identified by Olson (1999) and in the present study

Taxon	Remarks	Known elements	Occurrence
Pelagornithidae	Olson (1999)	Partial cmc and pedal phalanx	LC
?Procellariiformes	This study	Distal tmt	LC
?Fregatidae (cf. <i>Limnofregata</i>)	This study	Proximal cmc	GR
Charadriiformes indet. (Charadriiformes, “Scolopaci”)	This study Olson (1999); fossils need to be restudied: tarsometatarsus is likely to be from a messelornithid, whereas humerus may be from a procellariiform bird (see text)	Distal hum Distal hum, distal tbt, distal tmt	LC, ME
“Graculavidae, species 1”	Olson (1999); may be conspecific with putative threskiornithid reported herein	Partial scapula and coracoid, fragments of hum, proximal ulna, distal tbt	
“Graculavidae, species 2”	Olson (1999); very fragmentary remains that need to be restudied and compared with specimens described in present study	Distal ulna, distal cmc	
?Phoenicopteriformes	Olson (1999)	cmc, radius	
?Messelornithidae	This study	Extremities omalis of coracoid, distal tmt, distal hum	GR, FF, ME
?Caprimulgidae	Olson (1999); identification needs to be corroborated		
?Apodiformes, cf. Eocypselidae (cf. <i>Coturnipes</i>)	This study, cmc tentatively assigned to Caprimulgidae by Olson (1999) Olson (1999); may be conspecific with the putative procellariiform reported in the present study	Distal tmt, cmc Distal tmt	GR, LC, FF LC
cf. Parviculidae	Assigned to Aegialornithidae by Olson (1999)	tmt	LC
cf. Steatornithidae	Olson (1999)	hum	GR
Strigiformes, <i>Eostrix gulottai</i> sp. nov.	This study	Distal tmt	LC
?Trogoniformes	This study	Distal tbt	FF, LC, ME
Halcyornithidae, cf. <i>Cyrilavis</i>	This study	tmt	GR, LC, ME
Gen. et sp. indet. A	Possibly same species as “crane-sized” bird reported by Olson (1999)	Pedal phalanx	
Gen. et sp. indet. B (cf. <i>Microena</i>)	This study	Distal tmt	
Gen. et sp. indet. C (cf. <i>Morsoravis</i>)	This study	Distal tmt	
Gen. et sp. indet. D	This study; may be conspecific with the above-listed putative parviculid	Partial coracoid	
Gen. et sp. indet. E (cf. Threskiornithidae)	May be conspecific with the “graculavid” species #1 of Olson (1999)	Proximal hum, proximal radius, distal ulna, proximal cmc, wing phalanx	

Taxa that may be conspecific with others listed in this table are put in parentheses. Known elements are indicated (*cmc* carpometacarpus, *hum* humerus, *tbt* tibiotarsus, *tmt* tarsometatarsus), as well as the occurrences of taxa outside the Nanjemoy Formation (*GR* Green River Formation, *FF* Fur Formation, *LC* London Clay, *ME* Messel)

diversity, but low species abundances. Taxa that were also reported by Olson (1999) include the small apodiform bird (a carpometacarpus of which was tentatively assigned to the Caprimulgidae by Olson 1999: 130), and, possibly, the large, crane-sized bird (gen. et sp. indet. A), as well as the threskiornithid-like species (gen. et sp. indet. E), which are represented by non-overlapping skeletal elements in this study and that of Olson (1999).

In light of the improved knowledge of the early Eocene avian fossil record, some of the identifications of Olson

(1999) need to be revised. His assignment of a tarsometatarsus to the apodiform Aegialornithidae (Olson 1999: Fig. 7) was already questioned by Mayr and Mourer-Chauviré (2005), who suggested that the fossil (USNM 496384) is more likely from a representative of the Parviculidae, which occur in the London Clay and the early Eocene of France. Apart from being much stouter than the tarsometatarsus of aegialornithids, the trochlea metatarsi III of USNM 496384 is longer than in the Aegialornithidae and the trochlea metatarsi IV more strongly deflected.

Although an unambiguous charadriiform from the Fisher/Sullivan site is reported in the present study, the putative charadriiform remains identified by Olson (1999), which stem from larger species than the distal humerus described in the present study, are in need of restudy. As detailed above, the distal tarsometatarsus USNM 496375 (Olson 1999: Fig. 3d) is probably from a messelornithid, whereas the fragmentary distal humerus USNM 496374 (Olson 1999: Fig. 3c) may be from a procellariiform bird.

The bone bed of the Fisher/Sullivan site was deposited in a marine environment, but unambiguous seabirds are only represented by the Pelagornithidae reported by Olson (1999) and the putative procellariiform and suliform remains described in the present study. The charadriiform species, the threskiornithid-like bird, and some of the flamingo- and crane-sized birds may have lived along the shorelines, whereas most other avian fossils belong to small land birds. The sample includes records of some arboreal taxa, such as the halcyornithid and the putative trogoniform, which indicate the presence of forested paleoenvironments in the vicinity of the Fisher/Sullivan site.

As is evident from Table 1, most of the identifiable avian taxa from the Nanjemoy Formation are known from early Eocene fossil sites in Europe and North America. A notable difference between the bird community of the Nanjemoy Formation and coeval avifaunas concerns the absence of the palaeognathous Lithornithidae in the Nanjemoy Formation. Likewise absent are the anseriform Presbyornithidae, which are very abundant in some sites of the Green River Formation. Notable absences among the small land birds include the Zygodactylidae, with these birds being among the more common small arboreal birds in the Green River Formation and in Messel (Mayr 2009). Whether these differences indicate disparate paleoenvironments of the fossil sites or whether they are a taphonomic artefact remains to be shown.

The significance of the Fisher/Sullivan site for an understanding of early Eocene avifaunas is shown by the fact that in spite of the small sample size the material of the present study includes several taxa new to science and adds new data on the osteology of others. Because the specimens from the Nanjemoy Formation are uncrushed and three-dimensionally preserved, they allow a detailed assessment of osteological features and complement previous studies that are based on compression fossils from lagerstätten-type fossil sites. It is therefore expected that the description of further material from this site will contribute to an improved understanding of early Eocene avifaunas of North America.

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