Three new fossil landbirds from the early Paleogene of Denmark

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Well-preserved remains of fossil modern birds are rare, especially from the earliest stages of their evolution. In this paper we describe three new fossil specimens that can be referred to two of the major clades of extant 'landbirds', namely Apodiformes ('swifts') and Coliiformes ('mousebirds'). Because the fossils presented here are from the earliest tertiary of Denmark, they represent some of the oldest certain records for both these major clades of modern birds (Neornithes). This new ma-terial, from the Paleocene – Lower Eocene Fur Formation (Isle-of-Mors, Jutland, Denmark) is re-ferred to the fossil apodiform genus *Eocypselus* Harrison, 1984 and the coliiform genus *Chascacoco-lius* Houde & Olson, 1992. *Eocypselus* has been referred to within the clade Hemiprocnidae ('tree and crested swifts') and *Chascacocolius* to the Sandcoleidae, a clade of stem representatives of ex-tant Coliiformes. The description of *Chascacocolius* from the Danish early tertiary increases the known diversity of stem-lineage coliiforms (Sandcoleidae) known from European deposits. New fossil material of *Eocypselus* shows that this taxon was a perching bird as are extant hemiprocnids – the hindlimb and foot of *Eocypselus* is elongate and anisodactyl, with digit III the longest of the pedal digits. Swifts and mousebirds are known to have been diverse in the earliest tertiary of Europe and North America; both these neornithine clades have a much lower extant diversity in terms of known species than that evidenced by their global fossil records, a temporal effect perhaps related to glo-bal cooling throughout the latest tertiary.

Key words: Fossil birds, swifts, mousebirds, Denmark, Neornithes, Eocene

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Well-preserved fossil remains of modern birds (Neornithes) are exceptionally rare in the fossil record, but especially from the earliest phases of the diversification of this major extant vertebrate clade. In particular, interpretations of the known fossil record have clashed with molecular divergence estimates for Neornithes that have placed the divergence of many of the major clades at an earlier time that the Cretaceous – Palaeogene (K-Pg) boundary (Cooper & Penny 1997). The well-preserved remains of fossil neornithines have to date not been recovered until the earliest tertiary (Feduccia 1996; Dyke 2001a; Chiappe & Dyke 2002).

Although relationships between the major neornithine subdivisions (corresponding approximately to the traditional orders and families of extant birds; Monroe & Sibley 1993) are poorly known, the fossil record of early modern birds has continued to improve in recent years (Dyke 2001a). The well-preserved Paleogene remains of fossil neornithines are now known from a number of deposits from all over the world, in Europe in particular from the Lower Eocene London Clay Formation of England (Harrison & Walker 1977; Dyke 2001a) and from the Middle Eocene of Messel, Germany (Mayr 1998, 2001a). When compared with their extant diversity, two clades of Neornithes are now known to have been much more speciose by the time of the earliest tertiary than they are today. Fossil representatives of Apodiformes ('swifts') and Coliiformes ('mousebirds') have been recorded on the basis of large numbers of well-preserved fossil specimens from the basalmost Eocene, especially in Europe and North America (Feduccia 1996).

In this paper, three new specimens of fossil birds from the Paleocene – Lower Eocene Fur Formation (a marine diatomite sometimes referred to as the 'Mo Clay') of Northwestern Jutland, Denmark (Figs 1–3,

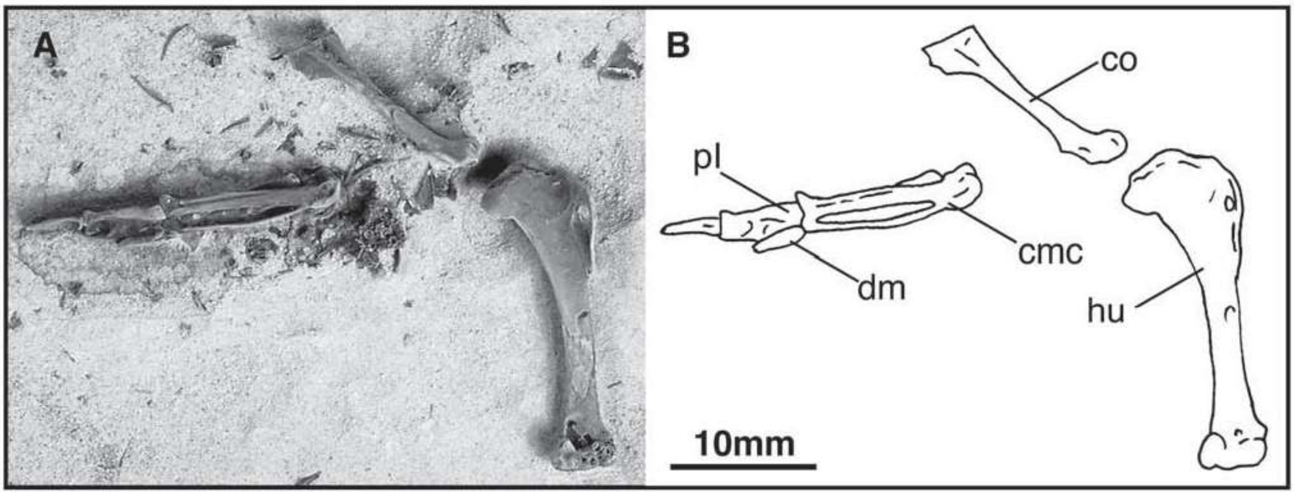

Fig. 1. A. Photograph of MGUH 26731 (DK 185), forelimb skeleton of *Chascacocolius* cf. *oscitans* (Coliiformes). B. Labelled sketch of specimen. Abbreviations: pl, phalanx I digiti majoris; dm, digitus minoris; cmc, carpometacarpus; co, coracoid; hu, humerus.

Table 1) are described and referred to the extant clades Coliiformes and Apodiformes. These specimens are some of the oldest known European occurrences for these groups of modern birds and are preserved in three dimensions (Figs 1–3). All of them were acid prepared from within calcareous cementstone nodules. In general, fossils from the Fur Formation testify to a diverse marine fauna (Bonde 1987, 1997). For further details of the geology of the Fur Formation see Thomsen & Danielson (1995). The age of the Fur Formation has been estimated to be 54–55 Mya (Knox 1997).

Abbreviations. – BMNH, The Natural History Museum, London; DK, Dankræ Collection (Geologisk Museum, Copenhagen), MGUH, Geologisk Museum, Copenhagen; USNM, United States National Museum, Washington D.C.

Methods. – Anatomical terminology follows Baumel & Witmer (1993) with some modifications to English after Howard (1929).

Systematic Palaeontology

Order Coliiformes Murie, 1872
Family Sandcoleidae (Houde & Olson, 1992)

Genus *Chascacocolius* Houde & Olson, 1992

Type species. *Chascacocolius oscitans* Houde & Olson, 1992 from the Eocene Willwood Formation of Wyoming. Holotype and only other currently known specimen, USNM 433913, including skull bones, cervical and thoracic vertebrae, elements of the pectoral girdle, fore and hind limbs.

Diagnosis. As for type species (Houde & Olson 1992).

Chascacocolius cf. *oscitans* Houde & Olson, 1992
Fig. 1

Remarks. Although no osteological differences are discernable between the specimen discussed here and USNM 433913, because the type material of *Chascacocolius oscitans* is from North America and MGUH 26731 is incomplete, tentative referral is made here. All of the bones described here are also known for the holotype.

Newly referred specimen. MGUH 26731 (DK 185), incomplete forelimb skeleton preserved in a grey cementstone. Specimen comprises a complete left coracoid, humerus, carpometacarpus and digits. While the coracoid and humerus are disarticulated, the carpometacarpus and digits remain attached (Fig. 1).

Locality and horizon. Paleocene – Lower Eocene Fur Formation, Isle-of-Mors, Hanklit, Denmark.

Description and comments. This specimen was described by Kristoffersen (2001). According to this account, when MGUH 26731 was first recovered remains of feather impressions were also to be seen on the slab; these have subsequently been obliterated by acid preparation. Visible anatomical features of MGUH 26731 are described here; for further details of the anatomy of *Chascacocolius*, see Houde & Olson (1992).

Coracoid

The coracoid is preserved completely, but has been prepared such that just one surface is visible (Fig. 1); overall, the shaft of this element is thin and not bowed laterally. In ventral view, the processus acrocoracoideus is rounded and pointed medially but is not turned caudally. The processus procoracoideus is obsolete. Although the facies articularis humeralis is pronounced but flattened and rounded, the facies articularis scapularis is very small (Houde & Olson 1992) and has a somewhat convex surface. The presence of a foramen nervi supracoracoidei on the dorsal cranial end cannot be ascertained because of the orientation of MGUH 26731 (we note that this foramen is present in other sandcoleids for which this element is known; *Sandcoleus*, *Eoglaucidium* and *Anneavis*; see below). Both the processus lateralis and medialis are large, pronounced and have approximately the same cranial extent (Fig. 1); however, the processus lateralis is somewhat wider medially. The medial area of the caudal ventral surface is depressed and forms a marked and elongated groove (Fig. 1). Because of the preservation of this element, few details of the dorsal surface are visible although the facies articularis sternalis is shallow (not markedly excavated). The morphology of MGUH 26731 agrees both with USNM 433913 as well as with other known members of the Sandcoleidae in size (Fig. 1) and because the coracoid is narrow and elongate (except for the distal end).

Humerus

The humerus of MGUH 26731 is complete and stout, but only the cranial surface is visible. On the proximal end, the crista deltopectoralis is rounded and smooth extending more than one-third the total length of this element. This contrasts with the condition in the more derived living and fossil Coliidae where the crista deltopectoralis is short (*Oligocolius*, *Colius* and *Urocolius*). As is also the case in the North American elements of *Chascacocolius oscitans* (Houde & Olson 1992), the sulcus transversus is deep and rounded (Fig. 1). Although the distal end of the humerus of MGUH 26731 is broken, the condylus dorsalis is rounded and has the same proximal extent as does the condylus ventralis (Fig. 1). There is no marked depression proximal to the condylus dorsalis in *Chascacocolius* as in extant colies and *Oligocolius* (Mayr 2000).

Table 1. Specimen measurements (in mm)

MGUH 26731 (DK 185)	
Coracoid, cranio-caudal length	15
Coracoid, caudal width	5,5
Humerus, length	25
Carpometacarpus, length	13
MGUH 26730	
Humerus, length of left	12
Coracoid, length	9,7
Ulna, length	16
Radius, length	15
Carpometacarpus, length	10
Sternum, length of carina	15
MGUH 26729	
Humerus, average length	10,5
Coracoid, average length	10
Ulna, length of right	14
Radius, length	14
Carpometacarpus, length	10
Femur, length	11
Tibiotarsus, length	19
Tarsometatarsus, length	10

Carpometacarpus

The carpometacarpus is preserved in dorsal view articulated with the manual digits of the wing (Fig. 1). The processus extensorius is large and rounded and is raised with respect to the processus alularis. A pronounced sulcus tendineus excavates the distal two-thirds of the dorsal surface of os metacarpale majus. As is the case in other sandcoleids for which the carpometacarpus is known, the processus intermetacarpalis is obsolete, present only as a small raised bump. In extant colies, as well as in the fossil *Oligocolius* (Mayr 2000), this processus is well-developed. The preserved anatomy of MGUH 26731 is extremely similar to that of USNM 433913 in that metacarpal I is short and os metacarpale minus is almost straight and flat (as opposed to being bowed as is the case in other sandcoleids; Houde & Olson 1992).

Order Apodiformes Peters, 1940
Family Hemiprocnidae (Oberholser, 1906)

Genus *Eocypselus* Harrison, 1984

Type species. *Eocypselus vincenti* Harrison, 1984, from

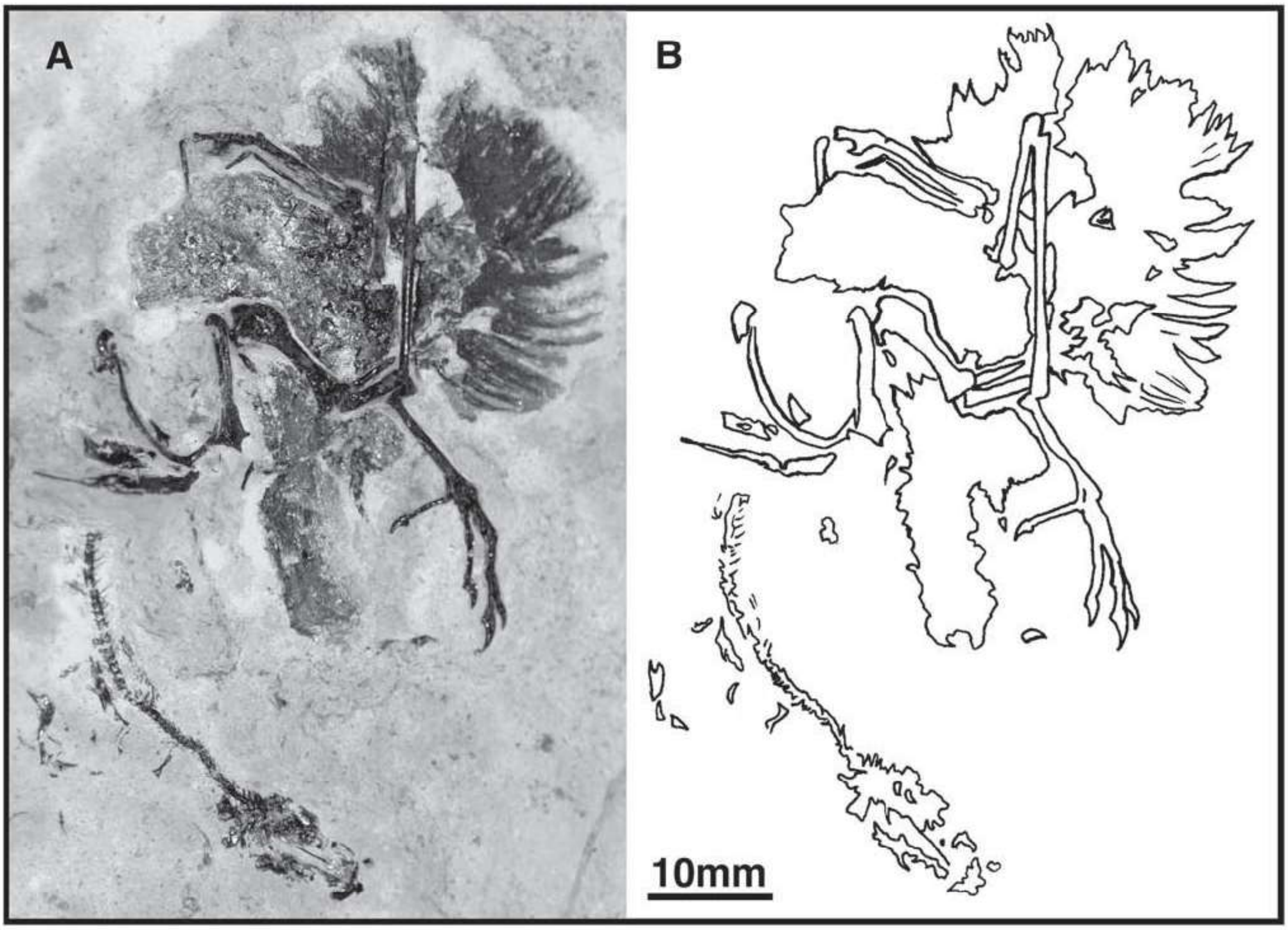

Fig. 2. A. Photograph of MGUH 26729, partially complete skeleton referred to *Eocypselus vincenti* (Apodiformes). B. Outline sketch of specimen. Note the small fish skeleton on the lower left, one of the most commonly encountered fossils in the 'mo-clay'.

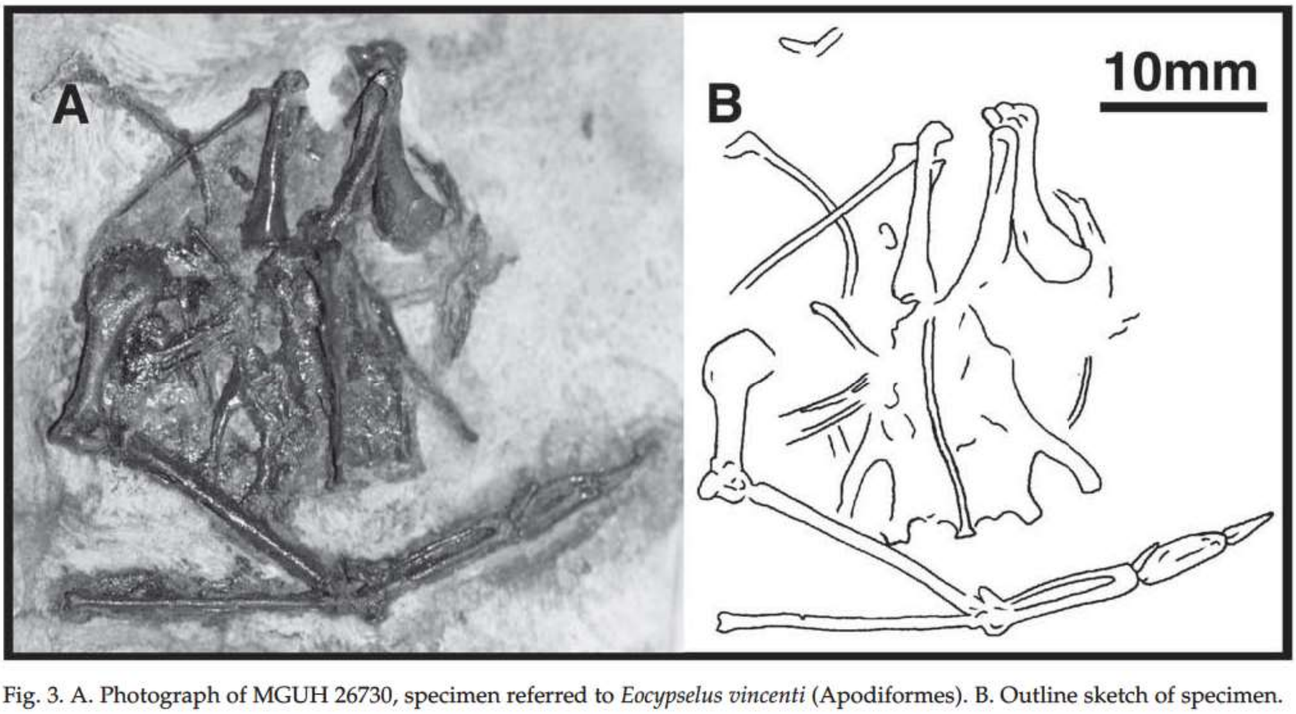

Fig. 3. A. Photograph of MGUH 26730, specimen referred to *Eocypselus vincenti* (Apodiformes). B. Outline sketch of specimen.

the Lower Eocene London Clay Formation of England (Dyke 2001b). Holotype, BMNH A 5429, consisting of complete left coracoid, humerus, radius and ulna, and portion of right humerus.

Diagnosis. As for type species. See Harrison (1984).

Eocypselus vincenti Harrison, 1984
Figs 2–3

Newly referred specimens. MGUH 26729, an incomplete postcranial skeleton comprising the shoulder girdle, one forelimb and hindlimb and feathers (Fig. 2), and MGUH 26730, an incomplete postcranial skeleton comprising the shoulder girdle, sternum, ribs and articulated wing elements (Fig. 3). Both of these specimens were figured by Kristoffersen (1997).

Locality and horizon. Paleocene – Lower Eocene Fur Formation, Isle-of-Mors, Sundby (MGUH 26729) and Ejerslev, Denmark. MGUH 26730 was collected by Mr Bent Søe Mikkelsen.

Description and comments. These specimens were briefly noted by Kristoffersen (1997, 2001); both are preserved in three dimensions embedded in cementstone nodules and have been acid prepared. Details of the anatomy of *Eocypselus vincenti* were outlined by Harrison (1984) - discussion here is limited to features of the anatomy of this taxon afforded by MGUH 26729 and MGUH 26730. In addition, feather impressions are preserved associated with the skeleton in MGUH 26729 (Fig. 2). In particular, MGUH 26729 and MGUH 26730 are not distinguishable from each other with respect to their preserved anatomy (other than size; MGUH 26730 is just slightly larger than MGUH 26729), and when compared directly to BMNH A 5429. Both with respect to relative sizes and the osteology of overlapping elements, MGUH 26729 and MGUH 26730 are referred here to *Eocypselus vincenti* Harrison, 1984. We note that Kristoffersen (2001) proposed an additional species (*Eocypselus soe*) on the basis of MGUH 26730; however, the anatomy of this specimen is indistinguishable from MGUH 26729 (see below).

Furcula

The furcula is almost completely preserved in MGUH 26729 (Fig. 2) and is present as an impression in MGUH 26730 (Fig. 3). Both specimens show that this element in *Eocypselus* is broadly U-shaped and has a small pointed apophysis and rounded processus acromiales. In both specimens, only the cranial surface of the furcula is visible. The acrocoracoid facet articularis is present on the right side of the furcula in MGUH 26729 (Fig. 2); this facies is flat and elongate but is not demarked from the border of the clavicula.

Coracoid

Coracoids are preserved in both MGUH 26729 and MGUH 26730 orientated primarily in ventral views (Figs 2–3). These elements correspond to those already described for *Eocypselus* by Harrison (1984).

Scapula

The right scapula of MGUH 26730 is preserved articulated with the coracoid (Fig. 3). However, because the coracoid covers most of the proximal end of the scapula, few anatomical details are visible. In general, the proximal end of this element is thin and tapered; the acromion is indistinct and the facies articularis humeralis is ovate and rounded.

Humerus

Both humeri are preserved in these specimens, orientated such that both cranial and caudal surfaces are visible (Figs 2–3); these elements are exactly the same as those referred to *Eocypselus vincenti* (BMNH A 5429) by Harrison (1984). Importantly, as in BMNH A 5429, both MGUH 26729 and MGUH 26730 possess a second, small processus supracondylaris dorsalis level with the proximal margin of the fossa m. brachialis (Figs 2–3) – this character represents an autapomorphy for *Eocypselus* (Harrison 1984).

Ulna and radius

The left radius and ulna are preserved in MGUH 26730 (Fig. 3); in MGUH 26729 only the proximal end of the left ulna and the distal end of the right are preserved along with a portion of one of the radii (Fig. 2). In both specimens, the radius is straight and much more slender than the ulna. The cotyla ventralis of the proximal ulna in the Danish specimens is deeply concave in ventral view, the olecranon is well-developed but blunt. The cotyla dorsalis of *Eocypselus* is much less concave than is the case in extant Apodiformes (Harrison 1984).

Sternum

The complete sternum is preserved in ventral view in MGUH 26730 (Fig. 3) whereas only part of the carina is visible in MGUH 26729 (Fig. 2). Cranially, this element is relatively short having a well-developed and prominent spina externa and short but wide sulcus articularis coracoideus on either side. There is a single large incisura lateralis on each side of the distal sternum bordered medially by two additional and much smaller fenestrae. This contrasts with the conformation of 'sternal notches' in extant Apodiformes where there are fewer lateral incisions. Lineae intermusculares are marked on the lateral sides of the carina; these taper cranially towards a rounded apex. Because both coracoids are preserved in ventral view in MGUH 26730, the right in articulation with the sternum, the sulcus carinae is obscured in this specimen and the spina interna is not visible. On the left lateral side of the MGUH 26730 sternum at least four ribs are present close to their original articulations indicating the presence of at least four processus costales in *Eocypselus*. Caudally, the trabeculae laterales of MGUH 26730 are club-shaped and robust; each incisura is at least one third of the total length of the sternum.

Carpometacarpus

Carpometacarpi and digits of the wing are preserved in their original articulations in both MGUH 26729 and MGUH 26730 (Figs 2–3). In MGUH 26729 the left element is visible in dorsal view articulated with an elongate phalanx I digiti majoris (Fig. 2). The processus extensorius is larger and more robust than is the processus alularis; the trochlea carpalis is relatively narrow. The os metacarpale majus is thick and rounded in cross section bearing a well-defined and broad sulcus tendineus along much of its distal surface. In MGUH 26730 the carpometacarpus is visible in ventral view and agrees with anatomical features presented in MGUH 26729. In this specimen the spatium intermetacarpale is clearly visible but no processus intermetacarpalis is present (Fig. 2). Both these specimens confirm the narrower shape of the distal end of the carpometacarpus in *Eocypselus* when compared to extant apodiforms. In addition, the processus pisiformis is high and pronounced, as is the case in living apodids (Harrison 1984).

Manual digits

In MGUH 26729 both the phalanges digitorum majoris and phalanx digiti minoris are preserved, although they are somewhat obscured by matrix. These bones are also seen in MGUH 26730 but are in close articulation with the carpometacarpus (Fig. 3). Both specimens show that digitus majoris of *Eocypselus* was extremely elongated, almost the same length as the carpometacarpus. The phalanx digiti minoris is small and rectangular in shape (Kristoffersen 1997).

Femur

The left femur is preserved in MGUH 26729 but few details are discernible due to its preservation and orientation (Fig 2). This element is not preserved in MGUH 26730.

Tibiotarsus

The left tibiotarsus is preserved in MGUH 26729 and is visible in cranial view although the distal end of this element is somewhat distorted (Fig. 2); few anatomical details are visible on the proximal end. Although the condylus medialis is incomplete, it was clearly rounded. The pons supratendineus is visible, located distally as is the case in extant Hemiprocnidae. The distal surface of the sulcus extensorius is located in a wide and deep incisura intercondylaris. The medial location of this sulcus is also more similar to the condition seen in Hemiprocnidae than in living Apodidae, where it is located in a more lateral position with respect to the distal end of the shaft (Harrison 1984).

Tarsometatarsus

The left tarsometatarsus is preserved in MGUH 26729 but only the cranial surface of this element is visible and it is somewhat displaced from its original articulation with the tibiotarsus (Fig. 2). The pedal digits remain in place. The proximal end of the tarsometatarsus is very narrow and flat, similar to the condition in extant Apodiformes. The sulcus extensorius is wide but shallow, overhung by the cotylae proximally. Details of these cotylae as well as the presence of foramina proximales cannot be ascertained. On the distal end of the tarsometatarsus, the trochleae metatarsorum II and III are not well-preserved but they are more widely splayed and longer that is the case in extant Apodiformes. Trochlea metatarsi IV is narrow and the foramen vasculare distale lies in a short elongated depression.

Pedal digits

All four of the pedal digits are preserved complete with their claws in MGUH 26729 (Fig. 2). The arrangement of these four toes is anisodactyl (three toes orientated cranially) as in all known fossil and recent Hemiprocnidae, as opposed to being pamprodactyl (all four toes orientated cranially) as is the case in some extant apodids. The hallux is shorter than the other pedal digits (Fig. 2).

Discussion

Relationships and diversity of sandcoleid mousebirds

There are two extant genera of mousebirds (Coliiformes), *Colius* and *Urocolius*, that together comprise six species entirely restricted to Southern Africa (Monroe & Sibley 1993; Juana 2001). However, despite this relatively depauperate recent diversity, Coliiformes have an extensive fossil record in particular from the early tertiary of Europe and North America (Houde & Olson 1992; Mayr 2001a). To date, two principal lineages of Coliiformes have been recognised, Sandcoleidae Houde & Olson (1992) and Coliidae Swainson (1837). The latter clade comprises all of the extant diversity as well as the fossil genera *Oligocolius* Mayr (2000), *Primocolius* Mourer-Chauviré (1988), and *Masillacolius* Mayr & Peters (1998).

In their initial description of sandcoleid mousebirds, Houde & Olson (1992) considered these birds to be a distinct order apart from typical Coliiformes (termed 'Sandcoleiformes'). Recent descriptions of additional well-preserved fossils have shown that, more likely, these birds are members of the coliiform stem-lineage, a series of clades forming successive sister-taxa with respect to the crown-group Coliidae (Mayr & Peters 1998; Dyke & Waterhouse 2001). However, no comprehensive cladistic analysis has yet been conducted to test this suggestion. A number of the less well known fossil members of Coliiformes, for example *Chascacocolius* Houde & Olson (1992) and *Eocolius* (Dyke & Waterhouse 2001), have yet to be convincingly referred to either of these two main clades. Importantly, the original referral of *Chascacocolius* to Sandcoleidae was based on overall similarity (Houde & Olson 1992). Because of the incomplete preservation of MGUH 26731, no characters are preserved that can presently be used to unambiguously refer this specimen at the level of the Sandcoleidae; our referral to the genus *Chascacocolius* is on the basis of its similarity with the type material as well as characters of the humerus and carpometacarpus. Although the relatively few preserved elements present on the new Danish mousebird do not contribute significantly to our understanding of the phylogenetic relationships of Coliiformes, the presence of *Chascacocolius* in the Paleocene – Lower Eocene of Europe further testifies to the past diversity of these small birds.

Relationships of Eocypselus *and other fossil swifts*

Apodiformes includes the clades Apodidae ('true swifts') and Hemiprocnidae ('tree and crested swifts') that encompass the living diversity of these birds (Monroe & Sibley 1993). Again, despite their relatively limited recent diversity, the fossil record of Apodiformes extends at least to the earliest tertiary – members of both the major clades have been described from the European Paleogene (Harrison & Walker 1975; Mayr & Peters 1999; Dyke 2001b). In general, the morphology of the humerus of these birds has been used to separate Apodidae and Hemiprocnidae, at least with respect to the known fossil taxa – the tertiary genera *Aegialornis* Lydekker (1891), *Cypselavus* Gaillard (1908) and *Primapus* Harrison & Walker (1975) have been considered similar in the morphology of this bone and have been referred at various times to Hemiprocnidae. In contrast, the fossil taxa *Scaniacypselus* Harrison (1984), *Procypseloides* Harrison & Walker (1977) and members of Jungornithidae (Karhu 1988) have been considered more similar with respect to the morphology of this bone to extant Apodidae. Relevant to the new material described here, the phylogenetic placement of *Eocypselus* has been subject to much discussion (Harrison 1984; Karhu 1988; Dyke 2001b; Mayr 2001b) – this taxon was considered to be a generalised apodiform by Harrison (1984), as the sister-taxon of Apodidae by Dyke (2001b), or placed closer to Hemiprocnidae by Mayr & Peters (1998) and Mayr (2001b). Even the placement of *Eocypselus* within Apodiformes has been questioned by some workers (Karhu 1988).

These additional specimens from the Danish tertiary present new anatomical features of *Eocypselus* that confirm referral of this taxon to Apodiformes, if this was ever in doubt (Harrison 1984; Mayr & Peters 1998). As is the case in all recent and fossil members of this clade, the humerus of *Eocypselus* is short and stout (although relatively more elongate when compared with extant swifts), the carpometacarpus (indeed the entire hand) is elongate, closely approaching the length of the humerus. This new material also presents the oldest known sternum for any apodiform bird – in later members of this clade (*Jungornis* from the Oligocene of Russia; Karhu 1998), the sternum has just two incisurae that are closed caudally. In most extant apodiforms the sternum is completely fused caudally as a single plate. A combination of anatomical features seen in *Eocypselus* (originally noted by Harrison 1984) – comparatively long and slender humeral shaft, two distally located dorsal processus supracpndylares, deep fossa m. brachialis, sternum with four lateral incisions – may serve to confirm a basal placement for this taxon with Apodiformes (*contra* Dyke 2001b).

Conclusions

As has been previously discussed (Kristoffersen 1999, 2001), despite the marine depositional environment of the Fur Formation, a number of different clades of small 'landbirds' can be confirmed within this avifauna in the early tertiary. Kristoffersen (2001) recorded 29 individual bird specimens from this formation that may represent up to 14 of the traditional avian orders (Monroe & Sibley 1993). In terms of broad diversity, and with respect to the groups thus far identified, the composition of birds known from the Fur Formation is extremely similar to other European deposits of approximately the same age – the London Clay Formation of England and the Messel deposits in Germany. Mounting evidence from Denmark, in combination with other Northern Hemisphere fossil material suggests that avifaunas known from this time period were largely tropical in their composition. This may suggest that many groups (mousebirds, for example) currently restricted to the tropics are relics of clades that were widespread in the Paleogene in areas that now form temperate zones of the Northern Hemisphere. Gradual global cooling throughout this period in Earth's history caused retraction of the global tropical zone towards the Equator and restricted some clades of birds to their present-day distributions. Further, we note that every new description of neornithine fossil material from the earliest Tertiary adds evidence to suggestions that the bulk of the evolutionary radiation of this major vertebrate clade occurred at an earlier time than the lowermost Eocene, likely in the latter stages of the Cretaceous.

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