

A new mousebird (Aves, Coliiformes) from the early Eocene London Clay of Walton-on-the-Naze (Essex, United Kingdom) constitutes a morphological link between sandcoleids and coliids

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A new mousebird (Aves, Coliiformes) from the early Eocene London Clay of Walton-on-the-Naze (Essex, United Kingdom) constitutes a morphological link between sandcoleids and coliids

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ABSTRACT

We describe a new species of the Coliiformes from the early Eocene London Clay of Walton-on-the-Naze (Essex, United Kingdom). *Ypresicolius sandcoleiformis* n. gen., n. sp. is represented by two partial skeletons and shows an overall resemblance to the Sandcoleidae in the preserved bones. However, the hypotarsus of the tarsometatarsus exhibits a characteristic derived morphology that is different from sandcoleids and closely resembles the hypotarsus of crown group Coliiformes (Coliidae). A phylogenetic analysis supported a sister group between *Ypresicolius* n. gen. and Pan-Coliidae, the total group including stem and crown group members of the Coliidae. We conclude that the similarities between *Ypresicolius* n. gen. and sandcoleids are plesiomorphic for the Coliiformes, and the low degree of morphological disparity between *Ypresicolius* n. gen. and sandcoleids indicates that the divergence of the sandcoleid and coliid lineages did not occur long before the earliest Eocene. The length proportions of the pedal phalanges of *Ypresicolius* n. gen. and sandcoleid Coliiformes are strikingly similar to those of Paleogene stem group representatives of the Strigiformes. The significance of this resemblance depends on the relationships of coliiform birds. Most current analyses do not recover owls and mousebirds as sister taxa, in which case the similar foot morphology of stem group Coliiformes and Strigiformes is either plesiomorphic for a more inclusive clade or evolved convergently in mousebirds and owls.

KEY WORDS

Aves,
evolution,
phylogeny,
new genus,
new species.

RÉSUMÉ

Un coliou nouveau (Aves, Coliiformes) de l'argile de Londres de l'Éocène inférieur de Walton-on-the-Naze (Essex, Royaume-Uni) constitue un lien morphologique entre les sandcoléides et les coliides.

Nous décrivons une nouvelle espèce de Coliiformes de l'argile de Londres de l'Éocène inférieur de Walton-on-the-Naze (Essex, Royaume-Uni). *Ypresicolius sandcoleiformis* n. gen., n. sp. est représenté par deux squelettes partiels et présente une ressemblance avec les Sandcoleidae. Cependant, l'hypotarse du tarsométatarse présente une morphologie dérivée caractéristique qui est différente de celle des Sandcoleidae et ressemble beaucoup à l'hypotarse du groupe-couronne des Coliiformes (Coliidae). Une analyse phylogénétique soutient *Ypresicolius* n. gen. comme groupe frère des Pan-Coliidae, le groupe total comprenant les membres du groupe-souche et du groupe-couronne des Coliidae. Nous concluons que les similitudes entre *Ypresicolius* n. gen. et les Sandcoleidae sont plésiomorphes pour les Coliiformes, et que le faible degré de disparité morphologique entre *Ypresicolius* n. gen. et les Sandcoleidae indique que la divergence des lignées des Sandcoleidae et des Coliidae ne s'est pas produite longtemps avant l'Éocène inférieur. Les proportions en longueur des phalanges des doigts d'*Ypresicolius* n. gen. et des Sandcoleidae sont étonnamment similaires à celles des représentants du groupe-souche paléogène des Strigiformes. L'importance de cette ressemblance dépend des relations entre les Coliiformes. La plupart des analyses actuelles ne considèrent pas les hiboux et les colious en tant que taxons frères, auquel cas la morphologie similaire du pied des groupes-souches des Coliiformes et des Strigiformes est soit plésiomorphe, pour un clade plus inclusif, soit dérivé de manière convergente chez les colious et les hiboux.

MOTS CLÉS

Aves,
évolution,
phylogénie,
genre nouveau,
espèce nouvelle.

INTRODUCTION

Mousebirds (Coliiformes) today include six very similar species of small, long-tailed birds, whose distribution is restricted to Africa south of the Sahara. The crown group representatives are classified in the taxon Coliidae and are predominantly herbivorous. However, coliiform birds had a more diversified ecology and much wider distribution in the past and are well represented in Paleogene fossils sites of Europe and North America (Mayr 2022).

The earliest unequivocal coliiform birds belong to the Sandcoleidae, which include the taxa *Sandcoleus*, *Anneavis*, and *Eobucco* from the late Paleocene and Eocene of North America (Houde & Olson 1992) and the taxon *Eoglaucidium* from the middle Eocene of Germany (Mayr & Peters 1998; Mayr 2000, 2002, 2018, 2020). As detailed by Mayr (2018), the taxa *Anneavis* and *Eoglaucidium* are poorly differentiated from each other and there exists a possibility that *Anneavis* Houde & Olson, 1992 is a junior synonym of *Eoglaucidium* Fischer, 1987. In any case, the interrelationships of sandcoleid Coliiformes are unresolved, and the four taxa *Sandcoleus*, *Anneavis*, *Eobucco*, and *Eoglaucidium* were placed in a polytomy in all analyses (Mayr & Mourer-Chauviré 2004; Ksepka & Clarke 2009, 2010; Mayr 2013, 2015).

Houde & Olson (1992) referred three further North American taxa to the Sandcoleidae, namely the early Eocene *Chascacocolius* as well as the middle Eocene *Botauroides* and *Uintornis*. Mayr & Peters (1998) proposed that *Chascacocolius* is more closely related to crown group Coliiformes than to the Sandcoleidae, and this hypothesis was supported by subsequent analyses (Zelenkov & Dyke 2008; Ksepka & Clarke 2009, 2010; Mayr 2013, 2015). The two species referred to *Uintornis* as well as the single species of *Botauroides* are known

from distal portions of the tarsometatarsus. As noted by Mayr (2018), these bones differ from the tarsometatarsus of typical sandcoleids, and at least *Uintornis* more likely represents a stem group representative of the Coliidae (the affinities of the poorly known *Botauroides*, of which no photographs have been published, need to be restudied).

Another putative sandcoleid is *Tsidiyazhi abini* from the mid-Paleocene of New Mexico (United States), which was described by Ksepka *et al.* (2017). However, this species is likewise distinguished from unequivocal representatives of the Sandcoleidae in various features (see discussion).

Other early or middle Eocene Coliiformes belong to the Coliidae, the clade including crown group Coliiformes. These include the European taxa *Selmes* and *Masillacolius* from the latest early or earliest middle Eocene of Messel in Germany (Mayr & Peters 1998; Peters 1999; Mayr 2001; 2015) as well as the North American taxon *Celericolius* from the early Eocene Green River Formation (Ksepka & Clarke 2010). A record of *Selmes* also exists from the early Eocene of France (Mayr & Mourer-Chauviré 2004).

A partial skeleton of an unidentified coliiform-like bird was reported from the early Eocene of the Okanagan highlands in British Columbia (Canada; Mayr *et al.* 2019), and associated wing and pectoral girdle bones from the early Eocene Danish Fur Formation were tentatively assigned to *Chascacocolius oscitans* by Dyke *et al.* (2004). A putative coliiform species, *Eocolius walkeri*, was furthermore identified in the early Eocene London Clay of Walton-on-the-Naze (Essex, United Kingdom) by Dyke & Waterhouse (2001), but coliiform affinities of this species have since been contested (Mayr 2009, 2022; Ksepka & Clarke 2009). Also from Walton-on-the-Naze, Mayr & Kitchener (2023a) described a bird with a mousebird-like tarsometatarsus as *Sororavis solitarius*



FIG. 1. — Overview of the two fossils of *Ypresicolius sandcoleiformis* n. gen., n. sp. from the early Eocene London Clay of Walton-on-the-Naze (Essex, United Kingdom): **A**, holotype, NMS.Z.2021.40.181; **B**, referred specimen NMS.Z.2021.40.182. Scale bars: 5 mm.

(because the Latin term “avis” is feminine, this name is here corrected to *Sororavis solitaria*; the same considerations apply to *Avolatavis europaeus* described by Mayr & Kitchener 2023b, which should be *A. europaea*). *Sororavis solitaria* was assigned to the Morsoravidae, with this taxon being regarded as nested within Psittacopasseres, the clade including the Passeriformes and Psittaciformes, and therefore being only very distantly related to mousebirds (Mayr & Kitchener 2023a).

Here we report the first unequivocal colliiform birds from Walton-on-the-Naze. These fossils are among the oldest records of the Coliiformes from outside North America and exhibit a previously unrecorded character mosaic, which bridges the morphological gap between the two major colliiform clades, the Sandcoleidae and the Coliidae.

MATERIAL AND METHODS

The fossil specimens are deposited in the American Museum of Natural History, New York, United States (AMNH); the Geiseltalsammlung, Martin-Luther Universität of Halle-

Wittenberg, Germany (GMH); the National Museums Scotland, Edinburgh, United Kingdom (NMS); the Senckenberg Research Institute Frankfurt, Germany (SMF); the Staatliches Museum für Naturkunde, Karlsruhe, Germany (SMNK); the University of Michigan, Museum of Paleontology, Ann Arbor, United States (UMMP); and the Wyoming Dinosaur Center, Thermopolis, United States (WDC).

Osteological terminology follows Baumel & Witmer (1993). The phylogenetic analysis is based on the matrix of Mayr (2013), with the modifications noted by Mayr (2015). The analysis was performed with the heuristic search modus of NONA 2.0 (Goloboff 1993) through the WINCLADA 1.00.08 interface (Nixon 2002), using the commands hold 10000, mult*1000, hold/10, and mult*max*. Bootstrap support values were calculated with 1000 replicates, ten searches holding ten trees per replicate, and TBR branch swapping without max*. Outgroup comparisons were made with the Cathartidae. Tree length (L), consistency index (CI), and retention index (RI) were calculated. Four characters (20 and 34) were coded as additive. Character descriptions and the matrix are given in the Appendix.



FIG. 2. — Third and fourth cervical vertebrae, scapula, and coracoid of fossil and extant Coliiformes: **A, B**, *Ypresicolius sandcoleiformis* n. gen., n. sp. from the early Eocene of Walton-on-the-Naze (NMS.Z.2021.40.181), third cervical vertebra in dorsolateral (**A**) and dorsal (**B**) views; **C**, *Y. sandcoleiformis* n. gen., n. sp. (NMS.Z.2021.40.181), fourth cervical vertebra in dorsal view; **D, E**, *Collus striatus* J.F.Gmelin, 1789 (SMF 10768), third cervical vertebra in dorsal (**D**) and lateral (**E**) view; **F**, *C. striatus* (SMF 10768), fourth cervical vertebra in dorsal view; **G**, *Y. sandcoleiformis* n. gen., n. sp. (NMS.Z.2021.40.181), right scapula in lateral view; **H**, *Eoglaucidium pallas* Fischer, 1987 from the middle Eocene of the Geisel Valley in Germany (GMH XXII), cranial extremity of right scapula in lateral view; **I**, *Eoglaucidium* cf. *pallas* from the latest early or earliest middle Eocene of Messel in Germany (SMF-ME 11110B), cranial extremity of left scapula in lateral view; the specimen was coated with ammonium chloride; **J**, *Anneavis anneae* Houde & Olson, 1992 (uncatalogued cast in SMF), right scapula in lateral view; **K**, *C. striatus* (SMF 10768), right scapula, left scapula in lateral view; **L**, *Y. sandcoleiformis* n. gen., n. sp. (NMS.Z.2021.40.181), partial right coracoid in dorsal view; **M**, *Y. sandcoleiformis* n. gen., n. sp. (NMS.Z.2021.40.181), partial extremitas sternalis of left coracoid in dorsal view; the dotted line reconstructs a broken portion of the specimen; **N**, *A. anneae* (uncatalogued cast in SMF), right coracoid in dorsal view; **O**, *Eoglaucidium* cf. *pallas* from the latest early or earliest middle Eocene of Messel in Germany (SMF-ME 11110B), left coracoid in dorsal view; the specimen was coated with ammonium chloride; **P**, *E. pallas* from the middle Eocene of the Geisel Valley in Germany (GMH 4376), left coracoid in dorsal view; **Q**, *C. striatus* (SMF 10768), right coracoid in dorsal view. Abbreviations: **acr**, acromion; **agm**, angulus medialis; **blg**, bulge; **fns**, foramen nervi supratoracoides; **for**, lateral vertebral foramen formed by osseous strut between zygapophysis cranialis and zygapophysis caudalis; **mdp**, medial process; **pcl**, processus lateralis. Scale bars: 5 mm.

SYSTEMATIC PALAEOONTOLOGY

Class AVES Linnaeus, 1758
Order COLIIFORMES Murie, 1872
Family COLIIDAE Murie, 1872

Genus *Ypresicolius* n. gen.

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TYPE SPECIES. — *Ypresicolius sandcoleiformis* n. sp.

DIFFERENTIAL DIAGNOSIS. — The new taxon is characterised by the asymmetric position of the foramina vascularia proximalia, with the medial foramen being situated much farther distally than the lateral foramen. Furthermore, it differs from:

- *Eoglaucidium* Fischer, 1987 in: Extremitas sternalis of coracoid forming a pronounced medial bulge; os carpi ulnare with broader crus breve; hypotarsus proximodistally longer and with single canal for the tendon of musculus flexor hallucis longus, and deep, plantarly open sulcus for the tendon of m. flexor digitorum longus;
- *Eobucco* Feduccia & Martin, 1976 in: Plantar flange formed by accessory trochlea of trochlea metatarsi IV less medially inflected;
- *Sandcoleus* Houde & Olson, 1992 in: Extremitas sternalis of coracoid forming a pronounced medial bulge; sternum with

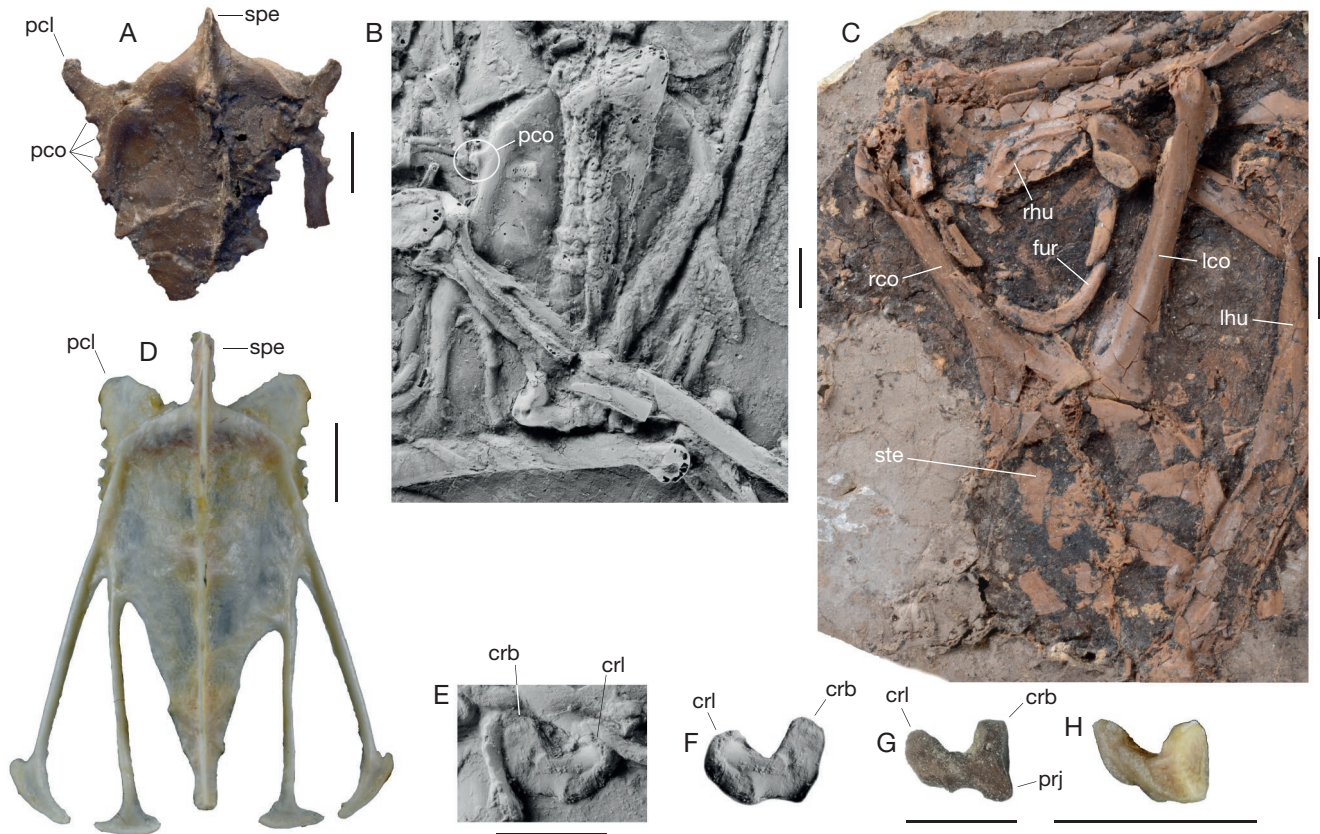


FIG. 3. — Sternum and os carpi ulnare of fossil and extant Coliiformes: **A**, *Ypresicolius sandcoleiformis* n. gen., n. sp. from the early Eocene of Walton-on-the-Naze (NMS.Z.2021.40.181), cranial portion of sternum in ventral view; **B**, *Eoglaucidium cf. pallas* Fischer, 1987 from the latest early or earliest middle Eocene of Messel in Germany (SMF-ME 11110A), sternum in ventral view; the specimen was coated with ammonium chloride; **C**, *Eoglaucidium pallas* from the middle Eocene of the Geisel Valley in Germany (GMH 4410), sternum and coracoids in ventral view, proximal portions of humeri in cranial view; **D**, *Urocolius macrourus* (Linnaeus, 1766) (SMF 10374), sternum in ventral view; **E**, **F**, *E. cf. pallas* (SMF-ME 10795A), right os carpi ulnare in cranial view; in **F** the bone is mirrored and surrounding matrix and bones were digitally removed; the specimen was coated with ammonium chloride; **G**, *Y. sandcoleiformis* n. gen., n. sp. (NMS.Z.2021.40.181), right os carpi ulnare in caudal view; **H**, *Colius colius* (Linnaeus, 1766) (SMF 5812), right os carpi ulnare in caudal view. Abbreviations: **crb**, crus breve; **crl**, crus longum; **fur**, furcula; **lco**, left coracoid; **lhu**, left humerus; **pcl**, processus cranio lateralis; **pco**, processus costalis; **prj**, projection caudal to crus breve; **rco**, right coracoid; **rhu**, right humerus; **spe**, spina externa; **ste**, sternum. Scale bars: 5 mm.

proportionally much longer processus cranio laterales; hypotarsus with single canal for the tendon of musculus flexor hallucis longus, and a deep, plantarly open sulcus for the tendon of m. flexor digitorum longus;

– *Anneavis* Houde & Olson, 1992 in: Extremitas sternalis of coracoid forming a pronounced medial bulge; hypotarsus with single canal for the tendon of musculus flexor hallucis longus, and a deep, plantarly open sulcus for the tendon of m. flexor digitorum longus;

– *Uintornis* Marsh, 1872 in: Trochlea metatarsi III is proportionally larger and of symmetric shape, and trochleae metatarsorum II and IV reach less far distally;

– *Botauroides* Shufeldt, 1915 in: Tarsometatarsus has a proportionally wider distal end and the trochlea metatarsi II reaches less far distally.

– *Chascacocolius* Houde & Olson, 1992 in: Coracoid with foramen nervi supracoracoidei;

– *Masillacolius* Mayr & Peters, 1998 and *Selmes* Peters, 1999 in: Coracoid with foramen nervi supracoracoidei; tarsometatarsus stouter;

– *Tsidiyazhi* Ksepka, Stidham, and Williamson, 2017 in: Trochlea metatarsi II is mediolaterally narrower; trochleae metatarsorum II and IV reach less far distally.

ETYMOLOGY. — The taxon named is derived from the Ypresian type horizon and *Colius*, the eponymous taxon of crown group Coliiformes.

Ypresicolius sandcoleiformis n. gen., n. sp.

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TYPE MATERIAL. — **Holotype.** United Kingdom • 1 specimen (vertebrae, partial right coracoid, extremitas sternalis of left coracoid, nearly complete right scapula, fragments of the furcula, cranial portion of sternum, distal portion of both radii, right os carpi ulnare, largely complete pelvis in piece of matrix, distal portions of both femora, distal portion of right tarsometatarsus, pedal phalanges of both feet; see Fig. 1A); Essex, Walton-on-the-Naze; Walton Member of the London Clay Formation (previously Division A2); early Eocene (early Ypresian); 1985; M. Daniels leg.; NMS.Z.2021.40.181 (original collector's number: WN 85512).

DIAGNOSIS. — As for genus.

ETYMOLOGY. — The species epithet refers to the similarity of the new species to taxa of the Sandcoleidae.

TYPE LOCALITY AND HORIZON. — Walton-on-the-Naze, Essex, United Kingdom; Walton Member of the London Clay Formation (previously Division A2; Jolley 1996; Rayner *et al.* 2009; Aldiss 2012), early Eocene (early Ypresian, 54.6–55 million years ago [Ma]; Collinson *et al.* 2016).

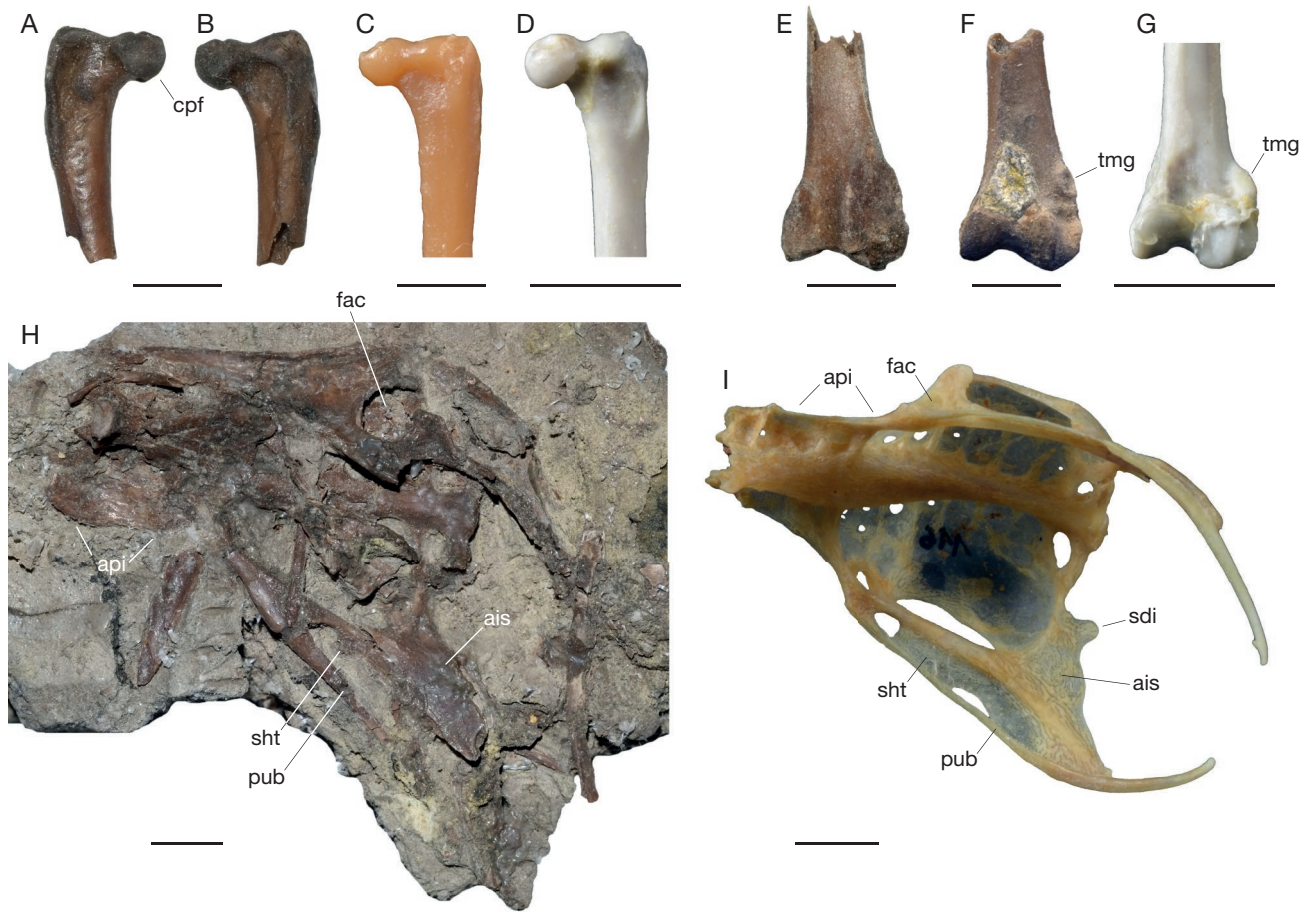


FIG. 4. — Femur and pelvis of fossil and extant Coliiformes: **A, B**, *Ypresicolius sandcoleiformis* n. gen., n. sp. from the early Eocene of Walton-on-the-Naze (NMS.Z.2021.40.182), proximal end of right femur in cranial (**A**) and caudal (**B**) views; **C**, *Anneavis anneae* Houde & Olson, 1992 (uncatalogued cast in SMF), proximal end of right femur in cranial view; **D**, *Urocolius macrourus* (Linnaeus, 1766) (SMF 10374), proximal end of right femur in caudal view; **E, F**, *Y. sandcoleiformis* n. gen., n. sp. (NMS.Z.2021.40.182), distal end of left femur in cranial view (**E**) and distal end of right femur in caudal view (**F**); **G**, *Urocolius macrourus* (Linnaeus, 1766) (SMF 10374), distal end of right femur in caudal view; **H**, *Y. sandcoleiformis* n. gen., n. sp. (NMS.Z.2021.40.181), pelvis in ventrolateral view; **I**, *U. macrourus* (SMF 116), pelvis in ventrolateral view. Abbreviations: **ais**, ala ischii; **api**, ala praeacetabularis ilii; **cpf**, caput femoris; **fac**, foramen acetabuli; **pub**, pubis; **sdi**, spina dorsolateralis ilii; **sht**, osseous sheet between ischium and pubis; **tmg**, tuberculum musculi gastrocnemialis lateralis. Scale bars: 5 mm.

REFERRED SPECIMEN. — NMS.Z.2021.40.182 (Fig. 1B; proximal portion of right femur, proximal half of right tibiotarsus, proximal and distal ends of right tarsometatarsus, pedal phalanges); collected in 1975 by M. Daniels (original collector's number WN 75076).

MEASUREMENTS (in mm). — NMS.Z.2021.40.181: right coracoid, length as preserved, 23.3; right scapula, length as preserved, 31.4; left femur, distal width, 7.0. NMS.Z.2021.40.182: right tarsometatarsus, proximal width, 5.9; distal width, 5.8.

DESCRIPTION AND COMPARISONS

NMS.Z.2021.40.181 preserves several vertebrae, but only the third and fourth cervical vertebrae (Fig. 2A-C) show distinctive morphologies. The third cervical vertebra (Fig. 2A, B) is of similar proportions to that of extant mousebirds (Fig. 2D, E), but has smaller lateral foramina (formed by an osseous strut between the zygapophyses cranialis et caudalis) than the third cervical vertebra of crown group Coliiformes. In contrast to crown group Coliiformes (Fig. 2F), the fourth cervical vertebra (Fig. 2C)

also has well-developed lateral foramina, whereas in extant mousebirds there is an osseous bridge from the midsection of the vertebral corpus to the processus costalis; furthermore, the lacuna interzygapophysialis of *Ypresicolius* n. gen. is more deeply incised in crown group Coliiformes. The morphology of the cervical vertebrae of most other stem group Coliiformes is poorly known, but in *Masillacolius* from the latest early or earliest middle Eocene of Messel in Germany the fourth cervical vertebra resembles that of crown group Coliiformes (Mayr 2015).

The coracoid (Fig. 2L, M) is similar to that of *Anneavis* and *Eoglaucidium*, and has a shorter processus procoracoideus than the coracoid of *Sandcoleus*. The cotyla scapularis is concave. The shaft of the bone is pierced by a foramen nervi supracoaracoidei. The angulus medialis of the right coracoid is more strongly projected than that of the left one. The medial margin of the extremitas sternalis forms a distinct bulge. The extremitas sternalis features a long processus lateralis.



FIG. 5. — Tarsometatarsus of fossil and extant Coliiformes: **A–F**, *Ypresicolius sandcoleiformis* n. gen., n. sp. from the early Eocene of Walton-on-the-Naze (NMS.Z.2021.40.182), proximal and distal portions of right tarsometatarsus in dorsal (**A**, **C**), plantar (**B**, **D**), distal (**E**), and proximal (**F**) views; the arrows indicate enlarged details of the bone; **G**, from the early Eocene of Walton-on-the-Naze (NMS.Z.2021.40.181), distal portion of right tarsometatarsus in plantar view; **H**, *Anneavis anneae* Houde & Olson, 1992, schematic drawing of proximal end of right tarsometatarsus in proximal view (redrawn after Houde & Olson 1992: fig. 15); **I**, **L**, *Anneavis anneae* (uncatalogued cast in SMF), left tarsometatarsus (mirrored) in dorsal (**I**), plantar (**J**), distal (**K**), and proximal (**L**) views; **M–P**, *Urocolius macrourus* (Linnaeus, 1766) (SMF 10374), right tarsometatarsus in dorsal (**M**), plantar (**N**), distal (**O**), and proximal (**P**) views; **Q–S**, *Uintornis lucaris* Marsh, 1872 from the middle Eocene North American Bridger Formation (AMNH 8400), distal end of left tarsometatarsus (mirrored) in dorsal (**Q**), plantar (**R**), and distal (**S**) views; **T**, *Eoglaucidium pallas* Fischer, 1987 from the middle Eocene of the Geisel Valley in Germany (GMH 4410), distal portion of left tarsometatarsus in dorsal view; **U**, **V**, *E. pallas* from the latest early or earliest middle Eocene of Messel in Germany (SMNK-Me 553a), left tarsometatarsus (**U**, dorsal view) and right foot (**V**, plantar view), with surrounding bones and matrix digitally removed; **W**, Sandcoleidae gen. et sp. indet. (cf. *Eoglaucidium*) from Messel (WDC-C-MG 149), right tarsometatarsus in plantar view; coated with ammonium chloride. Abbreviations: **fdl**, hypotarsal canal/sulcus for tendon of musculus flexor digitorum longus; **fh1**, hypotarsal sulcus for tendon of musculus flexor hallucis longus; **flg**, flange; **fmt**, fossa metatarsi I; **fp2/fpp2**, sulcus for the tendons of musculus flexor perforatus digiti 2 and m. perforans et perforatus digiti 2; **fvd**, foramen vasculare distale; **lfp**, lateral foramen vasculare proximale; **mfp**, medial foramen vasculare proximale; **prj**, pointed projection formed by medial margin of tarsometatarsus shaft. Scale bars: 5 mm.

The scapula (Fig. 2G) bears a prominent acromion with a broadly rounded tip; unlike in *Eoglaucidium* (Fig. 2H, I), it is bipartite and forms a medial process.

NMS.Z.2021.40.181 includes the extremitas sternalis of the furcula as well as one extremitas omalis. An apophysis

furculae is not developed, and the omal extremity is simple and has a tapering end.

Only the cranial portion of the sternum is preserved in NMS.Z.2021.40.181 (Fig. 3A). The bone exhibits long processus craniolaterales, which are much better developed than

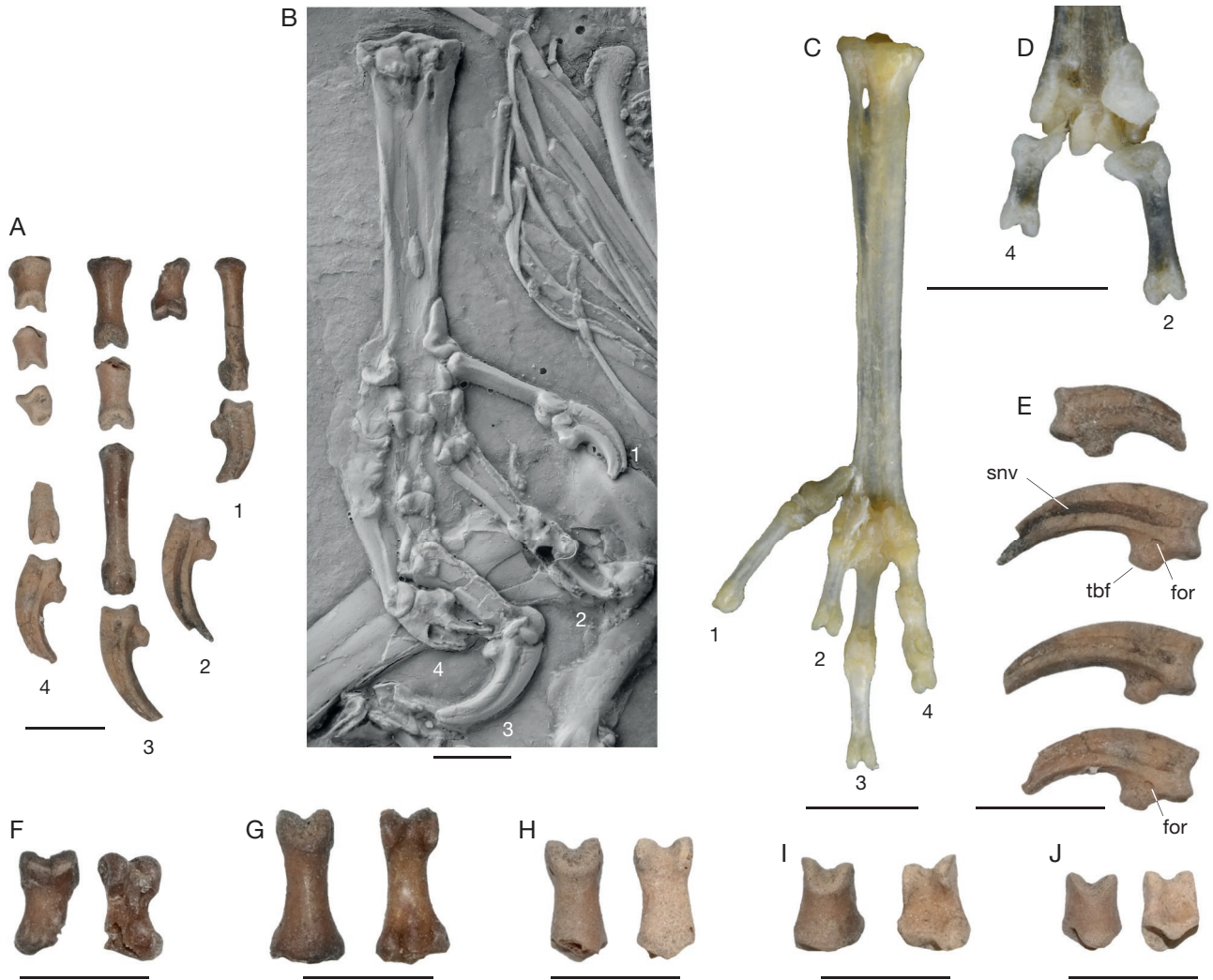


FIG. 6. — Pedal phalanges of fossil and extant Coliiformes: **A**, *Ypresicolius sandcoleiformis* n. gen., n. sp. from the early Eocene of Walton-on-the-Naze (NMS.Z.2021.40.182); **B**, Sandcoleidae gen. et sp. indet. (cf. *Eoglaucidium*) from the latest early or earliest middle Eocene of Messel in Germany (WDC-C-MG 149), left foot in plantar view; coated with ammonium chloride; **C**, *Colius striatus* J.F.Gmelin, 1789 (SMF 3826), right tarsometatarsus with proximal pedal phalanges in ventral view; **D**, *C. striatus* (SMF 10768), distal end of left tarsometatarsus (plantar view) with proximal phalanges of second and fourth toe; **E–J**, *Y. sandcoleiformis* n. gen., n. sp. (NMS.Z.2021.40.182), ungual phalanges in lateral/medial view (**E**), first phalanx of second toe in dorsal and plantar view (**F**), first phalanx of third toe in dorsal and plantar view (**G**), second phalanx of third toe in dorsal and plantar view (**H**), first phalanx of fourth toe in dorsal and plantar view (**I**), second phalanx of fourth toe in dorsal and plantar view (**J**). In **A–C** the toes are numbered. Abbreviations: **for**, foramen; **snv**, sulcus neurovascularis; **tbf**, tuberculum flexorium. Scale bars: 5 mm.

in *Sandcoleus*. The spina externa is blade-like, but proportionally shorter than in extant mousebirds (Fig. 3D). There are four processus costales.

The os carpi ulnare (Fig. 3G) resembles that of crown group Coliiformes (Fig. 3H) in that crus longum and crus breve are widely separated and of similar length; there is a projection caudal to the crus breve.

The holotype includes a nearly complete pelvis in a piece of matrix, which is exposed in ventrolateral view (Fig. 4H). The alae praeacetabulares ilii are mediolaterally wider than in crown group Coliiformes. There is a rudimentary osseous sheet between the ilium and the pubis, which is well developed in crown group Coliiformes (Fig. 4I). As in *Sandcoleus*, but unlike in *Chascacocolius* (Houde & Olson 1992: fig. 11) and extant Coliidae, a spina dorsolateralis ilii is absent.

The proximal end of the femur is preserved in NMS.Z.2021.40.182 (Fig. 4A, B), whereas NMS.Z.2021.40.181 includes the distal end of the bone (Fig. 4G). The caput femoris is globose. The distal end shares a characteristic derived morphology with extant Coliiformes in that the lateral portion of the distal end, that is, the area around the tuberculum musculi gastrocnemialis lateralis, forms a marked and proximodistally extensive prominence (Fig. 4F, G).

The tibiotarsus (Fig. 1B) is too poorly preserved for a meaningful description.

The tarsometatarsus (Fig. 5A–F) closely resembles that of *Sandcoleus*, *Anneavis* (Fig. 5I–L), *Eobucco*, and *Eoglaucidium* (Fig. 5T–W) in its overall shape. The lateral foramen vasculare proximale is situated much farther proximally than the medial one. The tuberositas musculi tibialis cranialis is in the medial portion of the bone. The medial margin of the proximal end

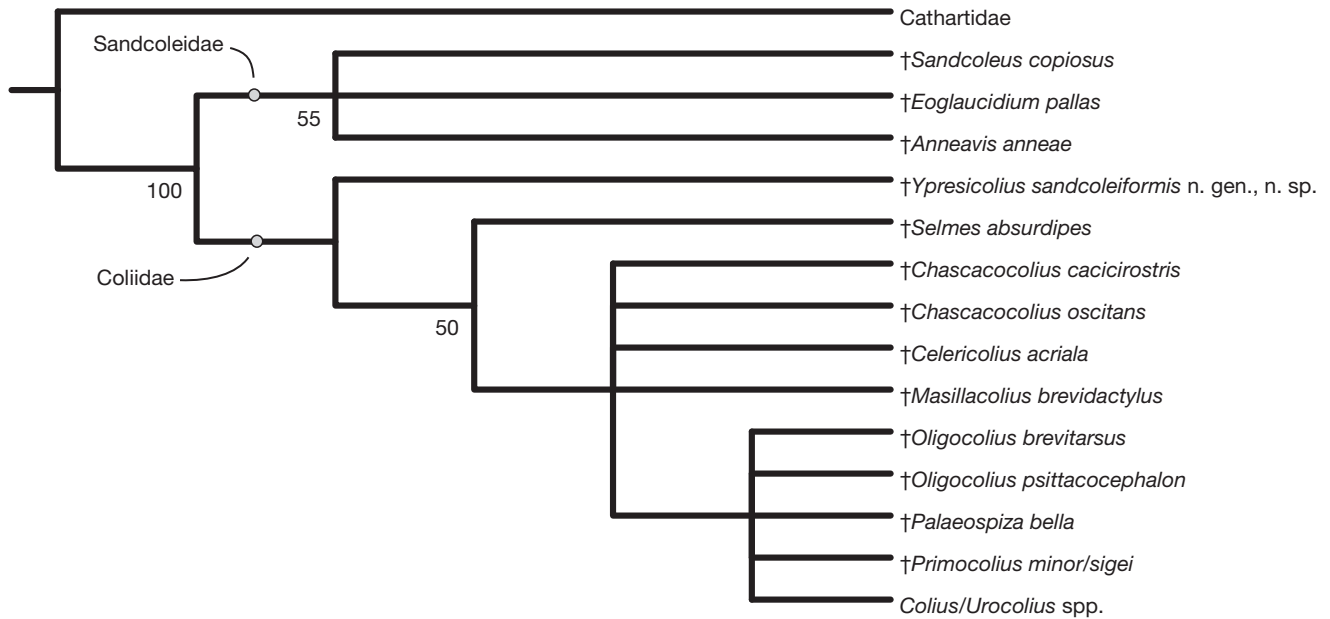


FIG. 7. — Strict consensus tree of 20 most parsimonious trees (length = 58, CI = 0.7, RI = 0.8) resulting from the phylogenetic analysis. Extinct species are marked with a dagger; bootstrap support values are indicated next to the nodes.

forms two small pointed projections (Fig. 5A). The hypotarsus (NMS.Z.2021.40.182; Fig. 5F) has a canal and a medially situated deep sulcus. This configuration closely corresponds to the hypotarsus of crown group Coliiformes (Fig. 5P), in which the canal is for the tendon of musculus flexor hallucis longus and the sulcus for that of m. flexor digitorum longus (the hypotarsus of coliiform birds was incorrectly scored in earlier analyses [Mayr & Mourer-Chauviré 2004; Ksepka & Clarke 2009, 2010], in which the large canal of crown group Coliiformes was erroneously identified as being for musculus flexor digitorum longus [see Mayr 2013, 2016 for its correct identity as a guiding structure for musculus flexor hallucis longus]). The hypotarsus of *Sandcoleus* and *Anneavis* has two canals for the aforementioned tendons as well as a sulcus for the tendons of the flexor muscles of the second toe. In *Eoglaucidium*, there also appear to have been two canals for m. flexor hallucis longus and m. flexor digitorum longus, but these are not fully closed. In plantar view, the hypotarsus of NMS.Z.2021.40.182 (Fig. 5B) is proximodistally longer than in *Eoglaucidium* (Fig. 5V). The distal end of the bone closely corresponds to the distal tarsometatarsus of *Sandcoleus*, *Anneavis*, *Eobucco*, and *Eoglaucidium*. The fossa metatarsi I is located on the medial surface of the shaft (Fig. 5D). The trochlea metatarsi II bears a ridge-like plantar flange. The trochlea metatarsi III is mediolaterally wide and exhibits a deep trochlear furrow. The trochlea metatarsi IV forms a large, flange-like accessory trochlea, which is less medially inflected than in *Eobucco* (compare Fig. 5E with Feduccia and Martin 1976: fig. 6d and Houde & Olson 1992: fig. 16).

Both specimens include pedal phalanges (Figs. 1, 6). The os metatarsale I (NMS.Z.2021.40.182) has a short processus articularis tarsometatarsalis. As in other sandcoleids, but unlike in crown group Coliiformes, the first phalanx of

the second toe (Fig. 6F) is shortened. The first and second phalanges of the third toe (Fig. 6G, H) are also abbreviated and the first phalanx has a wide proximal end. The first and second phalanges of the fourth toe (Fig. 6I, J) are likewise shortened, and the first phalanx is very stout. The ungual phalanges (Fig. 6E) have the “raptor-like” morphology seen in sandcoleids, with a marked sulcus neurovascularis and a prominent tuberculum flexorium. As in the Strigiformes, Falconiformes, and some Accipitriformes, there are lateral foramina next to the tuberculum flexorium.

RESULTS OF THE PHYLOGENETIC ANALYSIS

Our analysis of the character matrix in the appendix resulted in 20 most parsimonious trees (length = 58, CI = 0.7, RI = 0.8), the consensus tree of which is shown in Fig. 7. This analysis supported a sister group relationship between *Ypresicolius* n. gen. and all non-sandcoleid Coliiformes included in the analysis.

DISCUSSION

The *Ypresicolius* n. gen. specimens from Walton-on-the-Naze are among the earliest European records of the Coliiformes, being coeval to a putative coliiform bird from the Danish Fur Formation, which was tentatively assigned to *Chascacocolius oscitans* by Dyke *et al.* (2004). With an age of about 55 Ma, the fossils from Walton-on-the-Naze are only slightly younger than the oldest North American records of the Sandcoleidae, which stem from latest Paleocene (Clarkforkian, about 56–57 Ma) strata of the Willwood Formation (Houde & Olson 1992).



FIG. 8. — Pedal phalanges of *Ypresicolius* n. gen. and two Paleogene strigiform birds: **A**, *Ypresicolius sandcoleiformis* n. gen., n. sp. from the early Eocene of Walton-on-the-Naze (mainly NMS.Z.2021.40.182; the os metatarsale I is from NMS.Z.2021.40.181 and has been mirrored); **B**, the stem group strigiform *Ypresiglaux* sp. from Walton-on-the-Naze (see Mayr & Kitchener 2023c); the asterisked elements (os metatarsale I and the phalanges of the fourth toe) are from the holotype of *Y. michaeli* Mayr & Kitchener, 2023 (NMS.Z.2021.40.26), all other phalanges are from *Ypresiglaux* sp. (NMS.Z.2021.40.27); **C**, the stem group strigiform *Primoptynx poliotaurus* Mayr, Gingerich & Smith, 2020 from the early Eocene of Wyoming, United States (holotype, UMMP 96195; see Mayr *et al.* 2020); the bones were coated with ammonium chloride. The toes are numbered. Abbreviations: **snv**, sulcus neurovascularis; **tbe**, tuberculum extensorium; **tbf**, tuberculum flexorium. Asterisks in parentheses denote scales pertaining to asterisked skeletal elements. Scale bars: 5 mm.

Coliiform apomorphies of *Ypresicolius* n. gen. include the lateral prominence formed by the distal end of the femur in the area of the tuberculum musculi gastrocnemialis lateralis (Fig. 4F), as well as a characteristic derived morphology of the distal end of the tarsometatarsus, which has a fossa metatarsi I that is situated on the medial margin of the shaft, and trochleae metatarsorum II et IV that form marked plantar flanges (Fig. 5E).

The new fossils show a previously unrecognised derived characteristic of crown group Coliiformes (Coliidae) in the morphology of the hypotarsus, which forms a canal for only the tendon of musculus flexor hallucis longus (Fig. 5F). This condition is a unique apomorphy of the Coliidae (Mayr 2016), and in all other birds with a single hypotarsal canal, that canal is for the tendon of musculus flexor digitorum longus.

According to the descriptions and figures of Houde & Olson (1992: 142, fig. 16), the sandcoleid taxa *Sandcoleus* and *Anneavis* have “three hypotarsal canals, two side by side [= for the tendons of musculus flexor digitorum longus and m. flexor hallucis longus] and one behind [= for the tendon of musculus flexor perforatus digiti 2 and/or m. flexor perforans et perforatus digiti 2]” (Fig. 5H). Based on comparisons with extant birds (Mayr 2016), the lateral of these canals is for the tendon of musculus flexor hallucis longus and the medial one for the tendon of m. flexor digitorum longus. Its more lateral position also allows an identification of the closed canal in *Ypresicolius* n. gen. as that for m. flexor hallucis longus.

The differences in hypotarsus morphology between *Ypresicolius* n. gen. and sandcoleids are notable, because the distal end of the tarsometatarsus of *Ypresicolius* n. gen. closely

resembles that of sandcoleids (Fig. 5C, D, I, J). However, the mid-section of the shaft of the bone is not preserved in the *Ypresicolius* n. gen. specimens and the tarsometatarsus may have been proportionally longer than that of sandcoleids, as is the tarsometatarsus of extant mousebirds (Fig. 5M, N) and most stem group representatives of the Coliidae. We consider it possible that locomotory specialisations related to an elongate tarsometatarsus account for the differences in hypotarsus morphology of the Coliidae and Sandcoleidae, but this hypothesis needs to be reassessed once complete tarsometatarsi of *Ypresicolius* n. gen. are known.

Based on the distinctive hypotarsus morphology, we hypothesise that *Ypresicolius* n. gen. is more closely related to crown group Coliiformes than are the taxa *Sandcoleus*, *Anneavis*, and *Eoglaucidium*, and this position is also supported by the phylogenetic analysis. Other features of the new taxon conform to this hypothesis. In particular, the sternum of *Ypresicolius* n. gen. is distinguished from that of the sandcoleid taxon *Sandcoleus* (as reconstructed by Houde & Olson 1992: fig. 6) in that the processus craniolaterales are more strongly developed and cranially projected. The processus craniolaterales of crown group Coliiformes (Fig. 3D) are proportionally longer and wider than those of *Ypresicolius* n. gen., but we identify long processus craniolaterales as a further synapomorphy of the latter and a clade including extant mousebirds. For the sternum of an *Eoglaucidium* specimen, Mayr (2018: fig. 4d) reported a short craniolateral process, but the corresponding structure is more likely to be a processus costalis (Fig. 3B); the actual length of the processus craniolateralis of *Eoglaucidium* is unknown.

Otherwise, the known skeletal elements of *Ypresicolius* n. gen. are very similar to those of the sandcoleid taxa *Sandcoleus*, *Anneavis*, and *Eoglaucidium*. If our phylogenetic hypothesis correctly depicts the true affinities of the new taxon, the resemblances of *Ypresicolius* n. gen. and sandcoleids are likely to reflect the ancestral morphology of the Coliiformes. The low degree of morphological disparity between *Ypresicolius* n. gen. and sandcoleids indicates that the divergence of the sandcoleid and coliid lineages did not occur long before the earliest Eocene.

The similar morphologies of sandcoleids and *Ypresicolius* n. gen. also contribute to a reconstruction of the morphology of the coliid stem species. We hypothesise that a sandcoleid-like tarsometatarsus is plesiomorphic for Pan-Coliiformes, which has implications for the affinities of *Tsidiyazhi abini* from the mid-Paleocene (about 62 Ma) of New Mexico, United States. This species was tentatively assigned to the Sandcoleidae in the original description (Ksepka *et al.* 2017), but is clearly distinguished from sandcoleids in various features, including the position of the sulcus extensorius of the distal tibiotarsus (which is more medially situated in *T. abini*) and the morphology of the tarsometatarsus (the trochlea metatarsi II of *T. abini* is much wider and the trochleae metatarsorum II et IV are more plantarly deflected). Currently, there exists no convincing evidence for an assignment of *T. abini* to the Sandcoleidae and even its coliid affinities remain to be firmly established. If these can be verified in future analyses, the species is likely to be on the coliid stem lineage and outside the clade formed by the Sandcoleidae and Coliidae.

The known major postcranial bones of *Ypresicolius* n. gen. do not show morphological specialisations that would exclude the taxon from being on the stem lineage of the Coliidae. However, the pedal phalanges differ from those of extant mousebirds in their length proportions, with *Ypresicolius* n. gen. having strongly abbreviated proximal (first) phalanges of the second and third toes. This condition is clearly derived within neornithine birds and absent in crown group Coliidae, in which only the proximal phalanges of the fourth toe are shortened (Fig. 6C, D).

The proximal phalanges of the second and third toes are also strongly abbreviated in sandcoleids and some stem group representatives of the Coliidae, such as *Oligocolius psittaccephalon* (Mayr 2013) and *Masillacolius brevidactylus* (Mayr & Peters 1998; Mayr 2015). Therefore, we hypothesise that these shortened proximal phalanges are plesiomorphic for Coliiformes as a total group (Pan-Coliiformes), and that these phalanges were secondarily lengthened in the stem lineage of the Coliidae. The short phalanx of the second toe is likely to be functionally correlated with the presence of a plantar flange on the trochlea metatarsi II, which – together with the shortened proximal phalanges – increased the grasping capabilities of the feet.

The length proportions of the pedal phalanges of *Ypresicolius* n. gen. and sandcoleid Coliiformes show a striking similarity to those of Paleogene stem group representatives of the Strigiformes (Fig. 8). However, the ungual phalanges of stem

group Coliiformes and Strigiformes are distinguished by the more strongly developed tuberculum extensorium and the lack of a laterally open sulcus neurovascularis in strigiform birds. The resemblance to the feet of strigiform birds may indicate a raptorial ecomorphology of early stem group Coliiformes, but the disparate shapes of the ungual phalanges suggest different ecologies, which is supported by the fact that stomach contents of Messel fossils of *Eoglaucidium* contain seeds (Mayr & Peters 1998; Mayr 2018). Irrespective of whether the diet of stem group Coliiformes was more diversified than that of extant mousebirds, there appears to have been a shift in feeding ecology in the evolution of coliid birds, with sandcoleids having manipulated foot items with their feet, whereas species on the stem lineage of the Coliidae used their beaks for this purpose (Mayr 2018).

The close resemblance of the length proportions of the pedal phalanges of stem group Coliiformes and Strigiformes is notable, because one sequence-based analysis supported a sister group relationship between mousebirds and owls (Hackett *et al.* 2008), and others recovered the Strigiformes and Coliiformes as successive sister taxa of the Cavitaves, that is, a clade including Leptosomiformes, Trogoniformes, Coraciiformes, and allies (Jarvis *et al.* 2014; Prum *et al.* 2015; Kuhl *et al.* 2021; Sangster *et al.* 2022). If coliid and strigiform birds are sister taxa, the similar morphologies of the feet are likely to be a synapomorphy of these taxa. However, most current analyses do not recover owls and mousebirds as sister taxa, in which case the resemblances in the foot morphology of stem group Coliiformes and Strigiformes is either plesiomorphic for Afroaves, the clade including the Coliiformes and Strigiformes (Sangster *et al.* 2022), or evolved convergently in mousebirds and owls.

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APPENDIX 1. — Description of the characters included in the phylogenetic analysis (after Mayr 2013).

1. Nasal septum: absent (0); present (1).
2. Bill length: approximately one-half of total skull length (0); abbreviated, about one-third of total skull length or less (1).
3. Well-developed nasofrontal hinge: absent (0); present (1); newly added character.
4. Quadrate, eminentia articularis: absent (0); present (1); newly added character.
5. Mandible: not as follows (0); processus retroarticularis blade-like and elongated to approximately one-sixth of the skull length (1).
6. Fourth cervical vertebrae with lateral foramina: yes (0); no (1).
7. Discus pygostyli greatly enlarged: no (0); yes (1). *Chascacocolius cacicrostris* was scored after the skeleton figured by Mayr (2005: fig. 2).
8. Coracoid, foramen nervi supracoracoidei: present (0); absent (1).
9. Coracoid, processus procoracoideus: absent or extremely reduced (0); present, well-developed (1). See above concerning the coracoid of *Primocolius*. Scoring of this character was revised for *Anneavis*.
10. Coracoid, processus lateralis: poorly developed (0); well-projected (1).
11. Scapula: shorter than humerus (0); longer than humerus (1).
12. Sternum, processus cranio-laterales, strongly elongated and cranially protruding: no (0), yes (1).
13. Sternum, trabecula intermedia arising from trabecula lateralis: no (0); yes (1).
14. Humerus with short, rounded crista deltopectoralis, measuring about one quarter of the entire length of the bone: no (0); yes (1). *Chascacocolius cacicrostris* was scored after the skeleton figured by Mayr (2005: fig. 2).
15. Humerus, crescent-shaped depression proximal to condylus dorsalis: no (0); yes (1).
16. Humerus, foramen pneumaticum: absent (0); present, minute (1); present, large (2).
17. Humerus: longer or equal to ulna in length (0); shorter than ulna (1). *Chascacocolius cacicrostris* was scored after the skeleton figured by Mayr (2005: fig. 2).
18. Humerus, processus flexorius: slight projection (0); projects markedly distal to condylus dorsalis and condylus ventralis (1).
19. Ulna with very large cotyla ventralis: no (0); yes (1).
20. Carpometacarpus, processus intermetacarpalis: absent or inconspicuous (0); small (1); well developed (2). This character was coded as additive.
21. Carpometacarpus, relative length of ossa metacarpalia minus et majus: subequal in length (0); os metacarpale minus projects significantly distal to os metacarpale majus (1).
22. Carpometacarpus, os metacarpale minus: straight (0); bowed (1).
23. Carpometacarpus, ventrally projecting flange for articulation with os carpi ulnare at proximal end of os metacarpale minus: absent (0); present (1).
24. Pelvis, foramen obturatum: open caudally (0); fully enclosed (1).
25. Tibiotarsus, crista cnemiales cranialis protruding farther proximad than crista cnemialis lateralis; both cristae cnemiales and crista patellaris forming a continuous ridge circumscribing a groove on the cranial side of the bone, crista cnemialis cranialis continuous with a ridge opposite to the crista fibularis: no (0); yes (1).
26. Tarsometatarsus elongate and slender, ratio humerus/tarsometatarsus less than 1.4: no (0); yes (1). *Chascacocolius cacicrostris* was scored after the skeleton figured by Mayr (2005: fig. 2).
27. Tarsometatarsus: stout with shaft becoming gradually wider towards relatively wide proximal end (0); shaft narrow and of equal width along most of its length, with narrow proximal end (1); elongate with narrow shaft which becomes slightly wider towards proximal end (2).
28. Tarsometatarsus, not as follows (0); with single foramen vasculare proximale on medial side of shaft (1); with single foramen vasculare proximale on lateral side of shaft (2).
29. Tarsometatarsus, hypotarsus, very large canal for tendon of musculus flexor hallucis longus: absent (0); present (1). Unlike in other extant birds with a single hypotarsal canal, that of mousebirds does not include the tendon of musculus flexor digitorum longus, but that of m. flexor hallucis longus (Mayr 2016; contra Mayr & Mourer-Chauviré 2004; Zelenkov & Dyke 2008; Ksepka & Clarke 2009, 2010).
30. Tarsometatarsus, hypotarsus, tendon of musculus flexor digitorum longus enclosed in bony canal or nearly closed sulcus: no (0); yes (1).
31. Tarsometatarsus, fossa metatarsi I very large, concave, and situated on medial side of tarsometatarsus: no (0); yes (1).
32. Tarsometatarsus, trochleae metatarsorum II and IV small, not widely splayed from trochlea metatarsi III, and trochlea metatarsi II reaching beyond middle of trochlea metatarsi III: no (0); yes (1).
33. Tarsometatarsus, trochlea metatarsi II with distinct plantarly projecting wing-like flange: no (0); yes (1).

Appendix 1. — Continuation.

34. Proximal phalanx of second toe: not as follows (0); abbreviated and measuring about half of the length of the second (distal) phalanx (1); abbreviated, measuring only one third of the length of the second (distal) phalanx (2). This character was coded as additive.
35. Proximal three phalanges of fourth toe greatly abbreviated: no (0); yes (1).
36. Pedal ungual phalanges, sulcus neurovascularis: absent (0); present (1).

APPENDIX 2. — Character matrix of 36 morphological characters included in the phylogenetic analysis (see Appendix 1 for character descriptions). Characters and taxa printed in bold were newly added or scored for the analysis. Abbreviations: **Ch.**, *Chascacocolius*; **M.**, *Masillacolius*; **O.**, *Oligocolius*.

	Characters and character states																																				
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	
Cathartidae	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	2	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Sandcoleus copiosus</i>	0	0	0	?	0	?	0	0	1	1	0	0	1	0	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	1	1	0	1	?	?	1	
<i>Eoglaucidium pallas</i>	?	0	0	?	?	0	?	0	0	1	0	?	1	0	0	0	0	0	1	0	0	1	?	?	0	1	0	0	0	0	1	1	0	1	2	1	1
<i>Anneavis anneae</i>	?	?	?	?	?	?	0	0	0	1	?	?	1	0	0	?	1	0	1	0	0	1	1	?	1	0	0	0	0	1	1	0	1	2	1	1	
<i>Selmes absurdipes</i>	?	0	0	?	0	?	1	?	?	1	0	?	?	0	0	0	0	0	?	0	0	0	0	?	1	1	1	2	?	?	0	0	1	2	1	0	
<i>Ch. cacicrostris</i>	1	0	?	?	1	?	1	?	?	?	?	?	?	0	?	?	0	1	?	?	?	1	?	?	?	?	1	?	?	?	?	?	?	?	?	?	
<i>Ch. oscitans</i>	?	0	?	?	1	?	?	1	0	1	0	?	?	0	0	0	0	1	1	1	0	0	1	0	1	0	1	?	?	?	?	?	?	?	?	?	
<i>Celericolius acriala</i>	?	?	?	?	?	?	1	?	?	?	0	?	0	0	?	?	1	?	?	1	?	0	?	?	?	?	1	?	?	?	?	?	?	?	0	1	?
<i>M. brevidactylus</i>	?	0	?	0	1	1	?	1	0	?	0	?	?	1	?	?	0	1	?	1	0	?	1	?	?	1	2	0	?	?	0	1	?	1	1	1	
<i>O. brevitarsus</i>	?	?	?	?	?	?	?	?	?	?	1	?	?	1	1	?	1	1	2	1	0	?	?	?	1	?	0	1	?	?	?	0	1	?	?	1	1
<i>O. psittacocephalon</i>	?	1	1	1	1	?	?	?	0	0	?	?	?	1	?	?	1	0	?	2	1	0	?	?	?	1	0	1	?	?	?	?	1	?	2	1	?
<i>Palaeospiza bella</i>	?	?	?	?	?	?	?	1	0	1	?	?	?	1	1	?	1	1	?	2	1	?	?	?	?	?	1	?	?	?	?	?	1	?	1	1	?
<i>Primocolius minor/sigei</i>	?	?	?	?	?	?	?	1	0	?	?	?	?	?	1	1	?	1	?	2	?	?	?	?	?	?	?	1	1	1	0	0	1	0	?	?	
<i>Colius/Urocolius</i> spp.	1	1	0	1	0	1	1	1	0	0	1	1	0	1	1	1	0	1	1	2	1	1	0	1	?	1	1	1	1	0	0	1	0	0	1	0	
<i>Ypresicolius sandcoleiformis</i>	?	?	?	?	?	0	?	0	0	1	?	1	?	?	?	?	?	?	?	?	?	?	?	?	0	?	0	0	0	1	0	1	0	1	2	1	1
n. gen., n. sp.																																					