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UNUSUAL TARSOMETATARSUS OF A MOUSEBIRD FROM THE PALEOGENE OF FRANCE AND THE RELATIONSHIPS OF *SELMES* PETERS, 1999

GERALD MAYR[1] and CÉCILE MOURER-CHAUVIRÉ[2]
[1]Forschungsinstitut Senckenberg, Division of Ornithology, Senckenberganlage 25, 60325 Frankfurt a. M., Germany, gerald.mayr@senckenberg.de;
[2]UMR 5125 Paléoenvironnements et Paléobiosphère, Centre des Sciences de la Terre, Université Claude Bernard-Lyon 1, 27–43 Boulevard du 11 Novembre, 69622 Villeurbanne Cedex, France

ABSTRACT—In recent years, mousebirds (Aves, Coliiformes) have been recognized as one of the predominant groups of small perching birds in the early Tertiary of the Northern Hemisphere. Two major lineages can be distinguished, the Sandcoleidae, which are exclusively known from Paleocene and Eocene deposits, and the Coliidae, which have been found in Upper Eocene to Pliocene deposits and also include the six extant African species. Here we describe a nearly complete tarsometatarsus of a mousebird from the middle Eocene to upper Oligocene fissure fillings of the Quercy in France. The specimen is tentatively referred to *Selmes absurdipes* Peters, 1999, and represents a previously unknown tarsometatarsal morphology that combines derived characters of Sandcoleidae and Coliidae. It provides further evidence that *Selmes* is a stem lineage representative of the Coliidae and not a sandcoleid bird as assumed in the original description. Classification of *Selmes* into the Coliidae is also supported by a cladistic analysis of 19 morphological characters.

INTRODUCTION

The two extant genera of mousebirds (Coliiformes), *Colius* and *Urocolius*, comprise six species of small, frugivorous birds that occur in Africa south of the Sahara (Juana, 2001). They are characterized by a unique facultatively pamprodactyl and zygodactyl foot in which both the first and fourth toe can be moved forwards and backwards (see Juana, 2001, for general information on the biology of these birds). The higher systematic relationships of mousebirds are still unresolved, although a derived modification of the tendon of musculus extensor digitorum longus might establish a sister group relationship to parrots (Psittaciformes). This feature was first noted by Steinbacher (1935:237; the citation was overlooked by Berman and Raikow 1982).

As has been shown in recent years, the Coliiformes have a comparatively extensive fossil record and were among the most diversified small Paleogene birds (Mourer-Chauviré, 1988; Houde and Olson, 1992; Mayr and Peters, 1998; Mayr, 2000a, b, 2001). Two major lineages can be distinguished: the Sandcoleidae Houde and Olson, 1992, which include the genera *Uintornis* Marsh, 1872, *Eobucco* Feduccia and Martin, 1976, *Eoglaucidium* Fischer, 1987, *Sandcoleus* Houde and Olson, 1992, and *Anneavis* Houde and Olson, 1992; and the Coliidae Swainson, 1837, which comprise the extant taxa and the fossil genera *Masillacolius* Mayr and Peters, 1998, *Primocolius* Mourer-Chauviré, 1988, and *Oligocolius* Mayr, 2000a (see Mayr, 2001, for a more detailed survey on the fossil record of mousebirds).

Typical sandcoleids (i.e., the very similar genera *Eobucco*, *Eoglaucidium*, *Anneavis*, and *Sandcoleus*) are distinguished from coliids by a number of osteological features, but due to the fact that the sister taxon of the Coliiformes is uncertain, the polarity of many character transformations is unknown.

The coliiform genera *Chascacocolius* Houde and Olson, 1992, *Selmes* Peters, 1999, and *Eocolius* Dyke and Waterhouse, 2001, cannot be assigned to either the Sandcoleidae or Coliidae at present. From *Eocolius* only a few associated bones were found, but the osteology of *Chascacocolius* and *Selmes* is better known. Both taxa have a very similar overall morphology and were originally classified into the Sandcoleidae (Houde and Olson, 1992; Peters, 1999). In the case of *Chascacocolius oscitans* Houde and Olson, 1992, this assignment was largely based on overall similarity, although Houde and Olson (1992:153) noted that this taxon ''is the most coly-like of the Sandcoleiformes [=Sandcoleidae] yet known.'' *Selmes absurdipes* Peters, 1999, is known from two articulated skeletons from the middle Eocene of Messel, Germany, and from an isolated humerus from the Geiseltal, Germany (Mayr, 2001). The original classification of this species into the Sandcoleidae (Peters, 1999) was mainly based on the fact that the proximal phalanges of all three anterior toes are greatly abbreviated as in the Sandcoleidae (in extant Coliidae only the proximal phalanges of the fourth toe are abbreviated), but was questioned by Mayr (2001), who described a new specimen from Messel that exhibits the very characteristic derived morphology of the pygostyle of extant Coliidae.

Here we describe a nearly complete tarsometatarsus of a coliiform bird from the middle Eocene (MP 16) to upper Oligocene (MP 28; see Legendre et al., 1997) fissure fillings of the Phosphorites du Quercy in France. The specimen was briefly mentioned by Houde and Olson (1992:156) who noted that its morphology is intermediate between that of sandcoleids and coliids.

MATERIAL AND METHODS

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York, USA; **MHN**, Muséum d'Histoire naturelle, Basel, Switzerland; **MNHN**, Muséum national d'Histoire naturelle, Paris, France; **SMF**, Forschungsinstitut Senckenberg, Frankfurt a. M., Germany; **USTL**, Université des Sciences et Techniques du Languedoc, Montpellier, France. Anatomical terminology follows Baumel and Witmer (1993) and Baumel (1993); all dimensions are in millimeters.

Nineteen characters were coded for nine fossil and recent taxa of coliiform birds for a parsimony analysis with PAUP 3.1 (Swofford 1993) (see character matrix in Appendix I). The most-parsimonious tree was found with the exhaustive search option and accelerated transformation (ACCTRAN) mode. Two characters were coded as ordered; calculation with all charac-

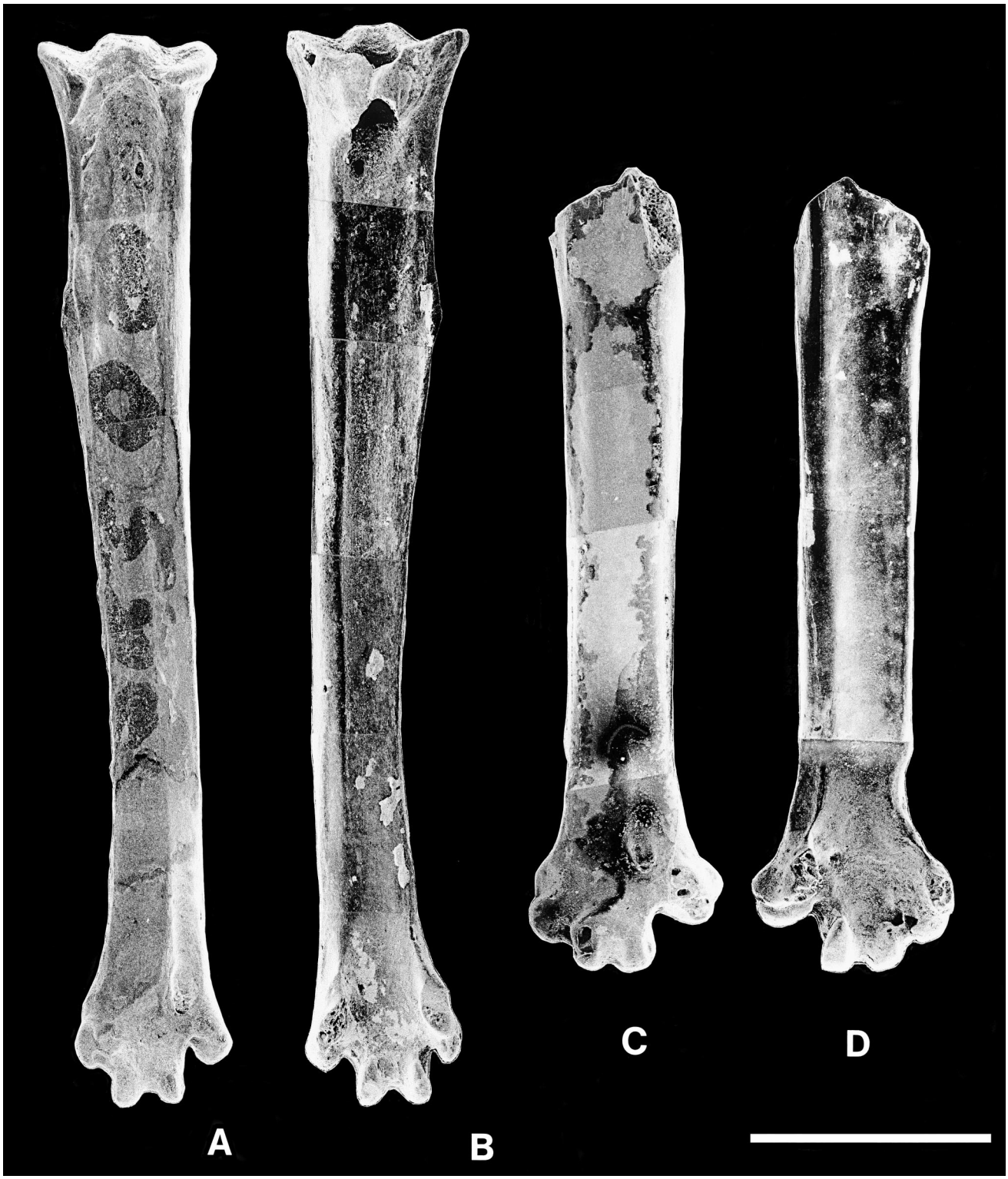

FIGURE 1. Tarsometatarsi of coliiform birds in comparison. **A**, **B**, cf. *Selmes absurdipes* (MHN Q.O.596), in dorsal (**A**) and plantar (**B**) view; **C**, **D**, Sandcoleidae gen. et sp. indet. (MNHN CB-17347), in dorsal (**C**), and plantar (**D**) view. Scale bar equals 5 mm.

ters unordered increased the number of resulting trees but did not change the topology of the strict consensus tree. The consistency index (CI), retention index (RI), and rescaled consistency index (RC) were calculated. The robustness of the tree was tested with a bootstrap analysis of 1,000 replicates. The sister taxon of the Coliiformes is unknown but it is generally assumed that these birds occupy a rather basal position within the ''higher land bird'' assemblage (e.g., Sibley and Ahlquist,

FIGURE 2. Right foot of cf. *Selmes absurdipes* (SMF-ME 2787) from Messel in dorsal view. Scale bar equals 5 mm.

1990); for this reason, outgroup comparisons were made with owls (Strigidae), cuckoo-rollers (Leptosomidae), and rollers (Coraciidae).

SYSTEMATIC PALEONTOLOGY

AVES Linnaeus, 1758
COLIIFORMES Murie, 1872
COLIIDAE Swainson, 1837
SELMES Peters, 1999
cf. *SELMES ABSURDIPES* Peters, 1999
(Figs. 1–4)

Referred Specimen—MHN Q.O.596, almost complete left tarsometatarsus, from an unknown level of the Phosphorites du Quercy (middle Eocene, MP 16, to upper Oligocene, MP 28; see Legendre et al., 1997) (Fig. 1).

Dimensions—Length, 22.1 (~20.2 in the Messel specimens of *S. absurdipes*); proximal width, 4.1; distal width, 3.6.

Taxonomic Remarks—We have tentatively assigned specimen MHN Q.O.596 to *Selmes absurdipes* because in size and morphology it closely resembles a distal end of a tarsometatarsus from the middle Eocene of Messel which was tentatively referred to *S. absurdipes* by Mayr and Peters (1998). A derived feature shared by the Messel specimen (SMF-ME 2787; see Fig. 2 and Mayr and Peters, 1998:pl. 4, fig. 9) and the specimen from France, but not found in other coliiform birds, is the unusually wide trochlea metatarsi III, which is somewhat medially displaced, and in which the medial rim protrudes farther distally than the lateral rim.

However, also from the Quercy fissure fillings, Mourer-Chauviré (1988) described another taxon of coliiform birds, which she named *Primocolius* and to which she assigned two species, *P. sigei* and the smaller *P. minor*. The tarsometatarsus is known only from *P. minor*. *P. sigei* and *P. minor* differ in details of the morphology of the humerus, the only bone known from both species (see Mourer-Chauviré, 1988:41). The holotypic humerus of *P. sigei* resembles the corresponding bone of *Selmes absurdipes* and *Chascacocolius oscitans* (see also Houde and Olson, 1992:156), but is smaller than the humerus of these taxa (23.5 mm vs. 26.7 mm in *S. absurdipes* and 26.5 mm in *C. oscitans*; see Mourer-Chauviré, 1988; Houde and Olson, 1992; Mayr, 2001). Without additional associated material, we cannot exclude the possibility that MHN Q.O.596 belongs to *Primocolius sigei* (which is even more likely since a referred humerus of this species also comes from the Basel collection and might thus be from the same, unknown, locality as the specimen described in this study). Because *P. sigei* is the type species of the genus *Primocolius*, the genus *Selmes* Peters, 1999, might eventually prove to be a junior synonym of *Primocolius* Mourer-Chauviré, 1988. Since the holotypic tarsometatarsus of *Primocolius minor* is fairly different from that of MHN Q.O.596 and much more similar (in terms of derived similarity) to the tarsometatarsus of extant Coliidae, this species would then have to be transferred to another genus.

Description and Comparison—The specimen has similar overall proportions to the tarsometatarsus of *Selmes absurdipes* but is somewhat more elongate than that of extant mousebirds (Fig. 3). The shaft is narrow and elongate and bears a shallow and wide sulcus flexorius along its plantar surface. The tarsometatarsus of typical sandcoleids is stouter and the shaft becomes gradually wider towards the proximal end of the bone. Contrary to extant Coliidae there is no ossified arcus extensorius (the corresponding part of the tarsometatarsus of the Messel specimens of *S. absurdipes* is unknown). The tuberositas musculi tibialis cranialis is an elongate and distinctly medially protruding projection on the medial side of the proximal third of the bone (Fig. 3; in extant colies it is situated on the dorsal surface). As in *Primocolius minor* and extant Coliidae, there is only a single foramen vasculare proximale which is, however, smaller and situated farther laterally than in extant Coliidae (Fig. 3; again, owing to preservation, this feature cannot be discerned in the Messel specimens of *S. absurdipes*). Except for a small broken part of its disto-plantar surface, the hypotarsus is well preserved. As in extant Coliidae, it encloses a single large canal, presumably for the tendon of musculus flexor digitorum longus, but the osseous bridge connecting the cristae hypotarsi is not completely fused along its midline. In the sandcoleid genera *Eoglaucidium*, *Eobucco*, *Anneavis*, and *Sandcoleus* the hypotarsus is perforated by two small grooves/canals, presumably for the tendons of m. flexor digitorum longus and m. flexor hallucis longus. Along the dorsal surface of the bone, a shallow sulcus for the musculus extensor brevis digiti IV extends to the foramen vasculare distale. The distal end of the bone closely resembles specimen SMF-ME 2787 from Messel (cf. *Selmes absurdipes*, Fig. 2). Most characteristic is the morphology of the trochlea metatarsi III, which is medially displaced and much wider than in extant Coliidae. The two rims are separated by a wide groove and the medial rim protrudes farther distally than the lateral rim. In *Uintornis* (Fig. 3B) the trochlea metatarsi III is also asymmetric, but in this taxon the lateral rim protrudes farther distally than the medial one. The trochleae metatarsorum II and IV are narrow and much shorter than the trochlea metatarsi III. The trochlea metatarsi II bears a distinct plantarly directing wing-like flange which, as in the Sandcoleidae and the Messel specimens of *S. absurdipes*, is much larger than in extant Coliidae. As in all other Coliiformes,

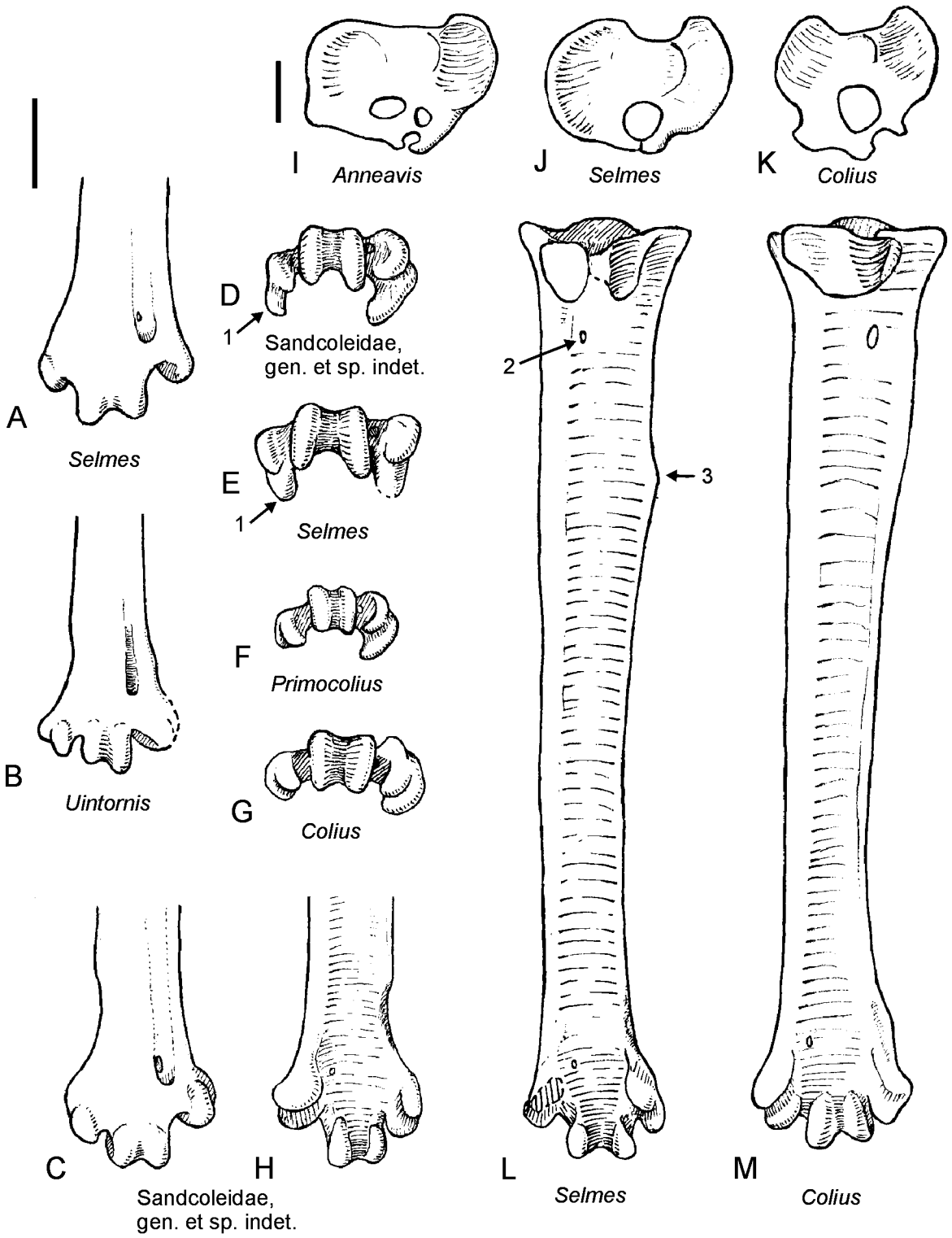

FIGURE 3. Left tarsometatarsi of coliiform birds in comparison. **A**, **E**, **J**, **L**, cf. *Selmes absurdipes* (MHN Q.O.596), distal end in dorsal (**A**) and distal (**E**) view, proximal end in proximal view (**J**) and plantar view (**L**); **B**, *Uintornis lucaris* (AMNH 8400, redrawn from Houde and Olson, 1992:fig. 14, reversed); **C**, **D**, **H**, Sandcoleidae gen. et sp. indet. (MNHN CB-17347), distal end in dorsal (**C**), distal (**D**), and plantar (**H**) view; **F**, *Primocolius minor* (USTL ECA 3214, reversed), distal end in distal view; **G**, **K**, **M**, *Colius striatus*, distal end in distal view (**G**), proximal end in proximal view (**K**) and plantar view (**M**); **I**, *Anneavis anneae* (redrawn from Houde and Olson, 1992:fig. 15, reversed), proximal end in proximal view. Numbers indicate: 1, wing-like flange on trochlea metatarsi II; 2, foramen vasculare proximale, 3, tuberositas musculi tibialis cranialis. Scale bars equal 2 mm; same scale bar for all figures except I, which has a slightly lower magnification.

a canalis interosseus distalis is present. The trochlea accessoria is broken but appears to have been well developed.

In Figures 1 and 3, specimen MHN Q.O.596 is compared to a distal tarsometatarsus of a sandcoleid bird from the lower Eocene of Condé-en-Brie (France, MP 8–9; see Schmidt-Kittler, 1987). This specimen (MNHN CB-17347, collection Louis) exhibits the typical sandcoleid morphology of the distal tarsometatarsus and, apart from its smaller size, is most similar to the genera *Eoglaucidium* and *Anneavis*. It differs from MHN Q.O.596 in the narrower trochlea metatarsi III, which is situated in the longitudinal axis of the shaft, and in that the fossa metatarsi I is located on the medial side of the shaft and is more pronounced. The sulcus leading into the foramen vasculare distale, on the dorsal side of the tarsometatarsus, is very shallow. In distal view, the wing-like flange on the trochlea metatarsi II is narrower than in MHN Q.O.596, and the trochlea metatarsi III is less asymmetric.

DISCUSSION

Specimen MHN Q.O.596 is most unusual in that it combines the derived morphology of the proximal tarsometatarsus of the Coliidae with the derived morphology of the distal tarsometatarsus of the Sandcoleidae. The wide trochlea metatarsi III and the position of the tuberositas musculi tibialis cranialis on the medial margin of the shaft are derived features that are not found in typical sandcoleids and colies.

A derived character that is shared by MHN Q.O.596, the Messel specimens of *Selmes absurdipes*, and the Sandcoleidae is the large wing-like flange on the plantar surface of the trochlea metatarsi II. In articulated skeletons that are known of *Selmes absurdipes* and the Sandcoleidae, the first phalanx of the second toe is further greatly abbreviated (see Mayr, 2001) a condition that we assume to be functionally correlated with the previous character, probably in order to increase movability of the second toe. However, as noted by Mayr (2001), the proximal phalanx of the second and third toe of *Masillacolius* (Coliidae) is also proportionally shorter than in extant mousebirds and an abbreviated proximal phalanx of the second toe might thus have already been present in stem-group representatives of the Coliiformes. Abbreviated proximal pedal phalanges increase the grasping capabilities of the foot and are typically found in perching birds and those that manipulate their food with the feet (see Stresemann, 1927–34:551). Extant mousebirds not only perch and climb in trees but can also move very quickly on the ground (Juana, 2001), and in adaptation thereto the proximal phalanx of the second toe might have been secondarily elongated.

MHN Q.O.596 shares with *Primocolius minor* and extant Coliidae the reduction of one of the foramina vascularia proximalia and an unusually large canal for the tendon of the musculus flexor digitorum longus at the hypotarsus. However, the position of the single foramen vasculare proximale is different in MHN Q.O.596 (close to lateral margin of shaft) and *Primocolius minor* and extant Coliidae (close to medial margin of shaft; see Fig. 3), and it might be possible that in the former, the medial foramen was reduced, whereas in the latter two taxa the lateral foramen is absent. However, because specimen MHN Q.O.596 otherwise has a very similar overall morphology to the tarsometatarsus of extant Coliidae, we consider it more likely that merely the position of the foramen shifted in either of these taxa than that different foramina were reduced.

We think that current evidence more convincingly supports classification of MHN Q.O.596 into the Coliidae, although we are aware of the fact that the evidence is controversial. Analysis of the character matrix in Appendix II resulted in 10 most parsimonious trees, the consensus tree of which is depicted in Figure 4. In all of the resulting trees, MHN Q.O.596 was grouped

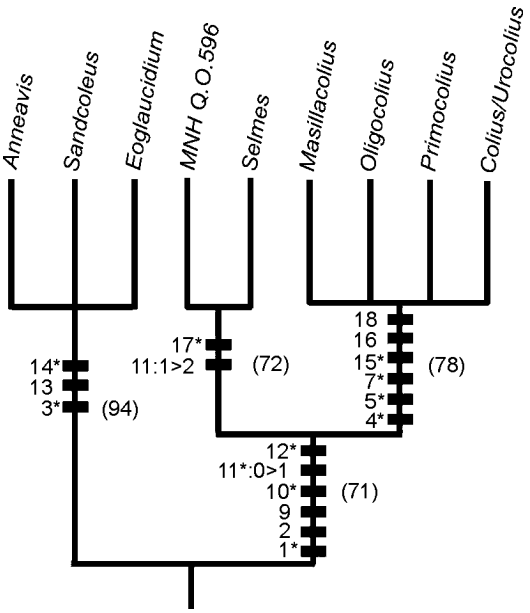

FIGURE 4. Strict consensus tree of ten most-parsimonious trees resulting from an analysis of the character matrix in Appendix 2 with PAUP 3.1 (Length = 29, CI = 0.79, RI = 0.86, RC = 0.68). Characters supporting the nodes in all of the resulting trees are indicated (the numbers refer to Appendix 1; the asterisked characters have CI = 1.0). The values in parentheses indicate the bootstrap support (1,000 replicates).

together with *Selmes absurdipes*, although with moderate bootstrap support; this position is in concordance with the classification proposed in this study, i.e., referral of the fossil to *S. absurdipes*. In all of the resulting trees, *Selmes absurdipes* was further shown to be the sister taxon of the Coliidae (*Masillacolius*, *Oligocolius*, *Primocolius*, and extant colies). Monophyly of a clade including the sandcoleid genera *Sandcoleus*, *Anneavis*, and *Eoglaucidium* received high bootstrap support of 94% but the relationships among these very similar taxa were not resolved with our data. *Chascacocolius* and *Eocolius* were omitted from the analysis because, in addition to other missing data, the tarsometatarsus and phalangeal proportions of both taxa are unknown; inclusion of these two taxa in the character matrix led to the collapse of all internal nodes. The coracoid of *Chascacocolius* lacks a foramen nervi supracoracoidei; its absence might indicate that this taxon is more closely related to the Coliidae than to the Sandcoleidae (the foramen nervi supracoracoidei is present in most non-neornithine Mesozoic birds and its presence is probably plesiomorphic within Neornithes). In *Eocolius* this foramen is present, and the known skeletal elements do not exhibit derived characters that would give convincing evidence on its affinities to other coliiform birds (see Dyke and Waterhouse, 2001:14).

Recognition of *S. absurdipes* as a stem lineage representative of the Coliidae is of general interest with regard to the early evolution of mousebirds, because it allows us to determine the polarity of character evolution within the Coliidae. For example, *S. absurdipes* has a rather generalized beak (see Mayr, 2001), which is also found in the Sandcoleidae and thus appears to be primitive within the Coliiformes. Accordingly, the short, finch-like beak is a derived feature of extant mousebirds most likely is related to their essentially frugivorous diet. Coliiform birds show a high plasticity in their tarsometatarsal morphology, and the new specimen described in this study might indicate that the derived morphology of the proximal tarsometatarsus of

extant Coliidae evolved prior to that of the distal tarsometatarsus.

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APPENDIX 1

Description of characters included in the phylogenetic analysis.

1. Very large discus pygostyli: absent (0); present (1).
2. Coracoid, foramen nervi supracoracoidei: present (0); absent (1).
3. Sternum, trabecula intermedia arising from trabecula lateralis (because incisura medialis is deeper than incisura lateralis): no (0); yes (1).
4. Humerus with short, rounded crista deltopectoralis (measuring about 1/4 of the entire length of the bone): no (0); yes (1).
5. Humerus, marked crescent-shaped depression above condylus dorsalis: no (0); yes (1).
6. Ulna with very large cotyla ventralis (erroneously said to be the cotyla dorsalis by Mayr and Peters, 1998:180, and Mayr, 2000:89): no (0); yes (1).
7. Carpometacarpus, processus intermetacarpalis: absent or inconspicuous (0); small (1); well developed (2). This character was coded as ordered.
8. Tibiotarsus, crista cnemiales cranialis protruding farther proximad than crista cnemialis lateralis; both crista cnemiales and crista patellaris forming a continuous ridge circumscribing a groove on the cranial side of the bone; crista cnemialis cranialis contines with a ridge opposite to the crista fibularis: no (0); yes (1).
9. Tarsometatarsus elongate and slender; ratio humerus/tarsometatarsus less than 1.4: no (1); yes (1) (see Mayr and Peters, 1998:table 9, Mayr, 2000:table 1).
10. Tarsometatarsus: rather stout with shaft becoming gradually wider towards proportionally wide proximal end (0); shaft narrow and of equal width along most of its length, with narrow proximal end (1); elongate with narrow shaft that becomes slightly wider towards proximal end (2).
11. 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).
12. Tarsometatarsus, hypotarsus, very large canal for tendon of musculus flexor digitorum longus: absent (0); present (1).
13. Tarsometatarsus, hypotarsus, tendon of musculus flexor hallucis longus enclosed in bony canal or nearly closed, deep sulcus: no (0); yes (1).
14. Tarsometatarsus, fossa metatarsi I very large, concave, and situated on medial side of tarsometatarsus: no (0); yes (1).
15. Tarsometatarsus, trochleae metatarsorum II and IV small, not widely splayed from trochlea metatarsi III and reaching far distally: no (0); yes (1).
16. Tarsometatarsus, trochlea metatarsi II with distinct plantarly-projecting, wing-like flange: no (0); yes (1).
17. Tarsometatarsus, trochlea metatarsi III very wide and asymmetric, with medial rim protruding farther distally than lateral rim: no (0);

yes (1). Concerning *Selmes absurdipes*, the presence of this feature was coded after specimen SMF-ME 2787.

18. Proximal phalanx of second toe: not as follows (0); abbreviated and measuring about half length of second (distal) phalanx (1); abbreviated, measuring only one third the length of second (distal) phalanx (2). This character was coded as ordered.
19. Proximal three phalanges of fourth toe greatly abbreviated (see Mayr and Peters, 1998:fig. 4): no (0); yes (1).

APPENDIX 2

Character matrix of 19 morphological characters for coliiform birds (see Appendix 1 for character definitions). In the case of *Primocolius minor*, only characters of the holotypic tarsometatarsus were considered. Unknown or missing character states are indicated by ''?''.

Taxa	characters																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Strigidae	0	0	0	0	0	0	0	0	01	01	0	0	0	0	0	0	0	01	1
Leptosomidae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Coraciidae	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sandcoleus copiosus	0	0	1	0	0	1	0	1	0	0	0	0	1	1	0	1	0	?	?
Eoglaucidium pallas	0	0	1	0	0	1	0	1	0	0	0	0	1	1	0	1	0	2	1
Anneavis anneae	0	0	1	0	0	1	0	1	0	0	0	0	1	1	0	1	0	2	1
MNH Q.O.596	?	?	?	?	?	?	?	?	?	1	2	1	0	0	0	1	1	?	?
Selmes absurdipes	1	?	?	0	0	?	0	1	1	1	?	?	?	0	0	1	1	2	1
Masillacolius brevidactylus	?	1	?	1	?	?	1	?	1	2	?	?	?	0	1	?	0	1	1
Oligocolius brevitarsus	?	?	?	1	1	1	2	1	0	1	?	?	?	0	1	?	0	?	1
Primocolius minor	?	?	?	?	?	?	?	?	?	1	1	1	0	0	1	0	0	?	?
Colius/Urocolius spp.	1	1	0	1	1	1	2	1	1	1	1	1	0	0	1	0	0	0	1