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AFFINITIES OF *PALAEOSPIZA BELLA* AND THE PHYLOGENY AND BIOGEOGRAPHY OF MOUSEBIRDS (COLIIFORMES)

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ABSTRACT.—*Palaeospiza bella* was described as an oscine songbird in the late 19th century. The late Eocene age of the holotype specimen would make it the oldest Northern Hemisphere record of the Passeriformes. However, few recent workers have accepted the placement of *P. bella* within Passeriformes, and the higher relationships of this fossil have remained controversial. We show that *P. bella* is a member of the Coliiformes (mousebirds) and represents the latest North American occurrence of a clade with an exclusively African extant distribution. Coliiformes are now known from the latest Paleocene to the approach of the Eocene–Oligocene boundary in North America. We present a redescription of *P. bella* and a new phylogenetic analysis of fossil and living Coliiformes based on a matrix including 49 characters and 18 ingroup taxa. The results of this analysis place *P. bella* in Colii, the clade comprising taxa more closely related to Coliidae (crown mousebirds) than to the extinct Sandcoleidae. The oldest stem-group Coliiformes are late Paleocene (about 56.2–56.6 Ma) in age. However, no fossil taxon can be confidently placed within the crown clade Coliidae at present. Phylogenetic results imply that a minimum of three mousebird dispersals from Europe to North America occurred during the Early Cenozoic. Review of the early Eocene fossil *Eocolius walkeri* from the London Clay shows that this taxon lacks convincing coliiiform synapomorphies and should be removed from the clade. Received 22 October 2007, accepted 23 August 2008.

Key words: Coliidae, Coliiformes, Florissant Formation, fossil, mousebird, *Palaeospiza bella*, phylogeny.

Afinidades de *Palaeospiza bella* y la Filogenia y Biogeografía de los Coliiformes

RESUMEN.—La especie *Palaeospiza bella* fue descrita como un ave oscina a fines del siglo XIX. La edad del espécimen holotipo corresponde al Eoceno tardío, hecho que haría de éste el registro más antiguo de Passeriformes en el hemisferio norte. Sin embargo, pocos investigadores recientes han aceptado la clasificación de *P. bella* dentro de Passeriformes y las relaciones de mayor orden de este fósil permanecen controversiales hasta hoy. Mostramos que *P. bella* es un miembro del orden Coliiformes y que representa la presencia más tardía en Norteamérica de un clado con una distribución actual exclusivamente africana. Los Coliiformes son conocidos en Norteamérica desde el Paleoceno tardío hasta el paso entre el Eoceno y el Oligoceno. Presentamos una redescrición de *P. bella* y un nuevo análisis filogenético de los Coliiformes vivos y fósiles, con base en una matriz que incluyó 49 caracteres y 18 taxones como grupo interno. Los resultados de este análisis ubican a *P. bella* en Colii, un clado que comprende los taxones que están relacionados más estrechamente con Coliidae que con el grupo extinto Sandcoleidae. Los miembros del grupo de los Coliiformes más antiguos datan del Paleoceno tardío (56.2–56.6 ma aproximadamente). Sin embargo, actualmente ningún taxón fósil puede ser ubicado en el clado que incluye al ancestro común más reciente de los Coliidae vivientes y sus descendientes. Los resultados filogenéticos implican que ocurrieron un mínimo de tres eventos de dispersión de Coliiformes desde Europa a Norteamérica durante el Cenozoico temprano. Una revisión del fósil *Eocolius walkeri* del Eoceno temprano de London Clay muestra que ese taxón no presenta sinapomorfias convincentes de coliiiforme por lo que debería ser removido de ese clado.

PALAEOSPIZA BELLA is known from a single articulated skeleton collected from the upper Eocene Florissant Formation of Colorado (Allen 1878). The holotype (MCZ 342222) is preserved on a slab and counterslab and includes nearly all of the postcranial

skeleton as well as soft-tissue impressions and a small part of the skull (Fig. 1). Allen (1878) named *P. bella* in a short paper and considered the fossil to represent the earliest record of an oscine passerine in North America. Wetmore (1925) later provided a

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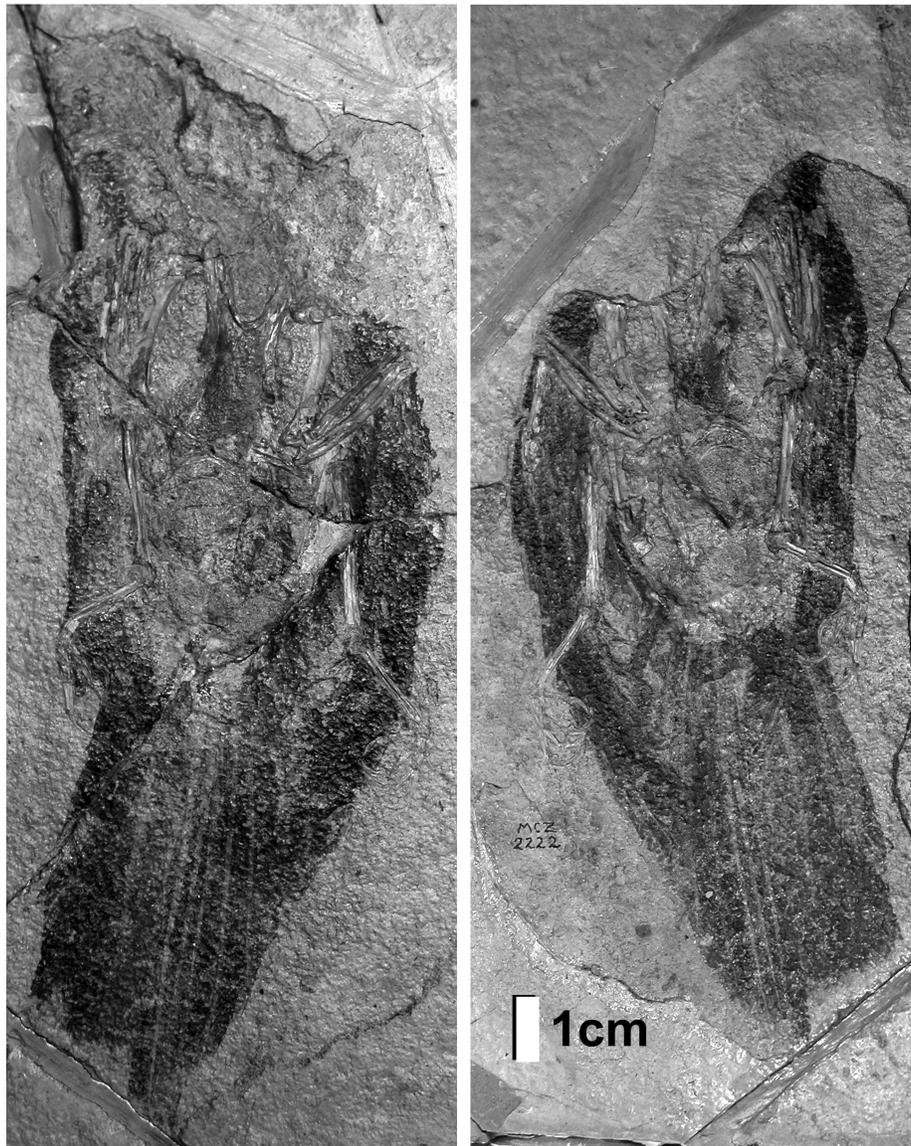


FIG. 1. Holotype of *Palaeospiza bella* (MCZ 342222). The skeleton is exposed in ventral view on the left slab and exposed in dorsal view on the right slab.

more detailed description of the specimen and placed it in a monotypic family, Palaeospizidae, grouped with oscines. However, *P. bella* lacks the most easily recognized osteological synapomorphy of Passeriformes, an elongated hallux with enlarged claw (Raikow 1982). Consequently, later authors rejected the hypothesis of passerine affinities for *P. bella*. Brodkorb (1978) raised concerns over the higher-level relationships of the species and listed it as *Aves incertae sedis*. Subsequently, Olson (1985) re-examined the holotype and mentioned that several characters exclude the species from Passeriformes, though he did not list these characters. The anisodactyl arrangement of the pedal digits led Olson (1985) to consider a possible relationship with members of the traditional order Coraciiformes, accepted by most later workers (Boles 1997, Chandler 1999, Meyer 2003). Mayr (2001) was the first to suggest

that *P. bella* might instead be a member of the Coliiformes. Here, we undertake an anatomical redescription of *P. bella*, confirm the hypothesized placement within Coliiformes indicated by Mayr (2001), and present a new phylogenetic analysis including all well-known fossil Coliiformes.

Of the three published hypotheses for the higher relationships of *P. bella*, only assignment to Coliiformes is supported by character evidence. *Palaeospiza bella* possesses two derived characters that support placement within Coliiformes: presence of a crescent-shaped depression above the condylus dorsalis of the humerus and marked abbreviation of the proximal three phalanges of pedal digit IV (to less than half the length of phalanx IV-4). The first feature is seen only within Coliiformes, whereas the second is present in Coliiformes and a few other clades (Steatornithidae,

Apodiformes, Psittaciformes, Falconidae, Accipitridae, and Strigiformes; see Mayr 2005a). Neither of these features occurs in Passeriformes or Coraciiformes. *Palaeospiza bella* can be excluded from Passeriformes because it lacks several derived features shared by all parts of this clade, including an elongated hallux, prominent apophysis furculae, and crest-like tuberculum bicipitale of the radius. *Palaeospiza bella* can also be excluded from all clades traditionally included in Coraciiformes (Coraciidae, Brachypteraciidae, Alcedinidae, Momotidae, Meropidae, Todidae, Upupidae, and Bucerotidae) by absence of a well-projected crista medianoplaris of the tarsometatarsus.

Extant Coliiformes are a small and geographically restricted clade, comprising only six species from sub-Saharan Africa. However, the clade was both more diverse and more widespread earlier in the Cenozoic. An array of fossil coliiiforms is known from the Tertiary of North America (Houde and Olson 1992) and Europe (Ballmann 1969; Mayr and Peters 1998; Peters 1999; Mayr 2000a, 2005b). A single Pliocene mousebird species is also known from Africa (Rich and Haerhoff 1985). Living mousebirds are predominantly frugivorous but also consume leaves, nectar, and shoots (de Juana 2001). However, the extinct taxon *Chascacocolius* shows cranial adaptations for gaping, which suggests a specialized feeding ecology such as prying under tree bark, breaking open fruits, or opening the beak in soil in association with ground-probing (Houde and Olson 1992, Mayr 2005b). Preserved gut contents from several Eocene mousebird fossils, including exemplars of *Eoglaucidium pallas* and *Selmes absurdipes*, include seeds (Mayr and Peters 1998, Peters 1999). Seeds may have been consumed only incidentally by *E. pallas*, however, given that the seeds recovered with this taxon are derived from pulpy fruits (Mayr and Peters 1998).

Mayr and Peters (1988) applied Coliiformes as the name for the clade that unites all extant mousebirds and their fossil relatives. These authors provided diagnoses for two higher taxa within Coliiformes: Coliidae and Sandcoleidae. Under the usage of Mayr and Peters (1998), "Sandcoleidae" was the name for the extinct, basally divergent sister taxon to a clade comprising all other known Coliiformes, and "Coliidae" included both extant mousebirds and all fossil stem-lineage Coliiformes more closely related to the crown clade than to Sandcoleidae. The crown coliiiform clade itself was not named. However, the name "Coliidae" has been more commonly restricted to extant mousebirds (e.g., Sibley and Ahlquist 1990, Sibley and Monroe 1990). In a manner consistent with this broader usage, we recommend that "Coliidae" be phylogenetically defined as the name for the crown clade: the most recent common ancestor of all living mousebird species (i.e., *Colius colius*, *C. striatus*, *C. castanotus*, *C. leucocephalus*, *Urocolius macrourus*, and *U. indicus*) and its descendants. "Coliiformes," the most widely used name for a more inclusive clade of which the Coliidae are a part, should denote the total Coliidae group, including all taxa more closely related to Coliidae than to any other extant avian clade. We also recommend that the name "Colii" (Fürbringer 1888) be applied as a stem-based name for all taxa more closely related to *C. colius* than to the fossil taxon *Sandcoleus copiosus*, and that "Sandcoleidae" be used for the stem clade including all taxa more closely related to *S. copiosus* than to *C. colius*.

Our recommended usage of names thus differs from that of Mayr and Peters (1998) in two important respects: our Colii includes the same currently recognized contents as Mayr and

Peters's (1998) Coliidae, and our Coliidae includes only crown taxa. Clade names are not formally phylogenetically defined in this document, however, because we believe that locating appropriate species-specifiers for these names requires (1) confirmation in independent data sets of our proposed relationships within Coliidae, given that these are comparatively little-studied in a phylogenetic context; (2) further investigation of the relationship of Coliidae to other extant avian clades; and (3) the start date for a formal code governing phylogenetic nomenclature (PhyloCode; Cantino and de Queiroz 2007).

THE FLORISSANT FORMATION AND AVIFAUNA

The Florissant Formation of Colorado comprises a 74-m-thick sequence formed by lacustrine, fluvial, and lahar deposition in an upland paleovalley (Evanoff et al. 2001). Single-crystal ^{40}Ar - ^{39}Ar laser fusion dating of sanidine crystals from pumice in the upper part of the Formation has yielded a latest Eocene age of 34.07 ± 0.10 Ma (Evanoff et al. 2001). Although these pumice samples are not derived from primary volcanic deposits, deposition of the pumice has been interpreted as penecontemporaneous with eruption (Evanoff et al. 2001). The lower beds of the Florissant Formation were deposited on an erosional surface cutting into the underlying Wall Mountain Tuff, which has yielded an ^{40}Ar - ^{39}Ar age of 36.73 ± 0.07 Ma (McIntosh and Chapin 1994). Magnetostratigraphy places the Florissant Formation within Chron C13r (33.7–34.7 Ma; Prothero and Sanchez 2004). Finally, the co-occurrence of *Mesohippus* and brontotheres in the Florissant Formation indicates a Chadronian age (Prothero and Emry 2004). Although the precise horizon from which the *P. bella* holotype was collected is uncertain, stratigraphic data strongly support a latest Eocene age for all fossil-bearing beds of the Florissant Formation.

The Florissant Formation is most well known for abundant, extraordinarily well-preserved insect and plant fossils. Tens of thousands of fossils have been collected, yielding ~1,500 insect species spanning 18 orders as well as >150 species of plants (Meyer 2003). The flora and insect fauna suggest a temperate to subtropical climate for the region during Eocene time (Moe and Smith 2005). Vertebrate fossils from the Florissant Formation are much more rare than those of plants and invertebrates, but soft-tissue preservation is typically very good (Meyer 2003).

Four birds have been described from the Florissant Formation, all of which preserve fine details of the feathers. *Palaeospiza bella* was the first fossil bird reported (Allen 1878). Cope (1880) subsequently published a short description of a second fossil bird from the Florissant and named it "*Charadrius sheppardianus*" on the basis of perceived similarities to extant plovers. Unfortunately, he did not figure the specimen, provide a catalogue number, or indicate the institution where the intended holotype was deposited. Additional evidence can be used to help identify an intended holotype specimen if it was not explicitly given for species described before 2000 (International Commission on Zoological Nomenclature 1999: Article 73.1.2), so this ambiguity alone does not appear to invalidate the species name. The holotype specimen described by Cope (1880) is a poorly preserved partial postcranial skeleton with feather impressions that is now located in the American Museum of Natural History (AMNH) paleontology collections. We re-examined this fossil (AMNH 2576) and agree with

Olson (1985), who noted that it preserves no characters that would support a relationship with the extant taxon *Charadrius* or, more broadly, with Charadriiformes. Thus, we follow Olson (1985) in considering the specimen *Aves incertae sedis*. A third fossil bird, represented by a fragmentary specimen preserving the left and right feet and a few feathers (YPM 1231), was named *Yalavis tenuipes* by Shufeldt (1913). Though considered a member of Passeriformes by Shufeldt (1913), *Y. tenuipes* has an unenlarged hallux and preserves no previously proposed passerine synapomorphies. At present, the affinities of this small bird are uncertain, though the proportions of the foot alone indicate that it is distinct from *P. bella*. Most recently, Chandler (1999) described a fossil cuckoo, *Eocuculus cherpinae*, from an articulated postcranial skeleton. Chandler considered *E. cherpinae* to represent a part of the crown clade of Cuculiformes. Mayr (2006) described a second specimen of *Eocuculus* from the Oligocene of France and provided evidence that *E. cherpinae* instead represents a stem cuculiform taxon.

In addition to the specimens discussed above, a highly complete avian fossil purportedly representing the clade Charadriiformes was discovered at the privately owned Florissant Fossil Quarry in 1997 but awaits formal description (Meyer 2003). Numerous isolated feathers are also known from the Florissant Formation (Allen 1878, Shufeldt 1913) but cannot be assigned to particular taxa.

Institutional abbreviations.—AMNH: American Museum of Natural History, New York; FMNH: Field Museum of Natural History, Chicago, Illinois; HMLD: Hessisches Landesmuseum, Darmstadt, Germany; MCZ: Museum of Comparative Zoology, Cambridge, Massachusetts; MHN: Muséum d'Histoire Naturelle,

Basel, Switzerland; SMF: Forschungsinstitut Senckenberg, Frankfurt, Germany; USNM: National Museum of Natural History, Smithsonian Institution, Washington, D.C.; YPM: Yale Peabody Museum, New Haven, Connecticut; and WDC: Wyoming Dinosaur Center, Thermopolis, Wyoming.

COMMENTS ON THE ANATOMY OF *PALAEOSPIZA BELLA*

Allen (1878) and Wetmore (1925) focused on describing *P. bella* in comparison to extant Passeriformes, providing only brief mentions of some elements key to the proper identification of the specimen. Therefore, we include a redescription documenting overlooked morphologies and providing comparisons to other Coliiformes. It should be noted that the illustration presented by Allen (1878, fig. 1) and reproduced by Shufeldt (1913) exaggerates the quality of preservation, illustrating details of the skull and soft tissue that are not actually preserved.

Only a small portion of the skull is preserved on the slab. These small fragments of bone offer no reliable anatomical data. Wetmore (1925) noted that a subtle impression around the skull suggested a feathered crest. The impression is smooth and does not include feather details, so the presence of a crest is here considered unconfirmed. Notably, all extant mousebirds have prominent head crests. The condition in most fossil Coliiformes is uncertain, but a head crest is absent in a specimen of the sandcoleid *Eoglaucidium pallas* with fine soft-tissue preservation (Mayr and Peters 1998).

The furcula, lacking the omal ends, is broad and bears only a slight midline ridge at the symphysis (Fig. 2). A prominent apophysis furculae is likewise absent in all coliiforms with the exception

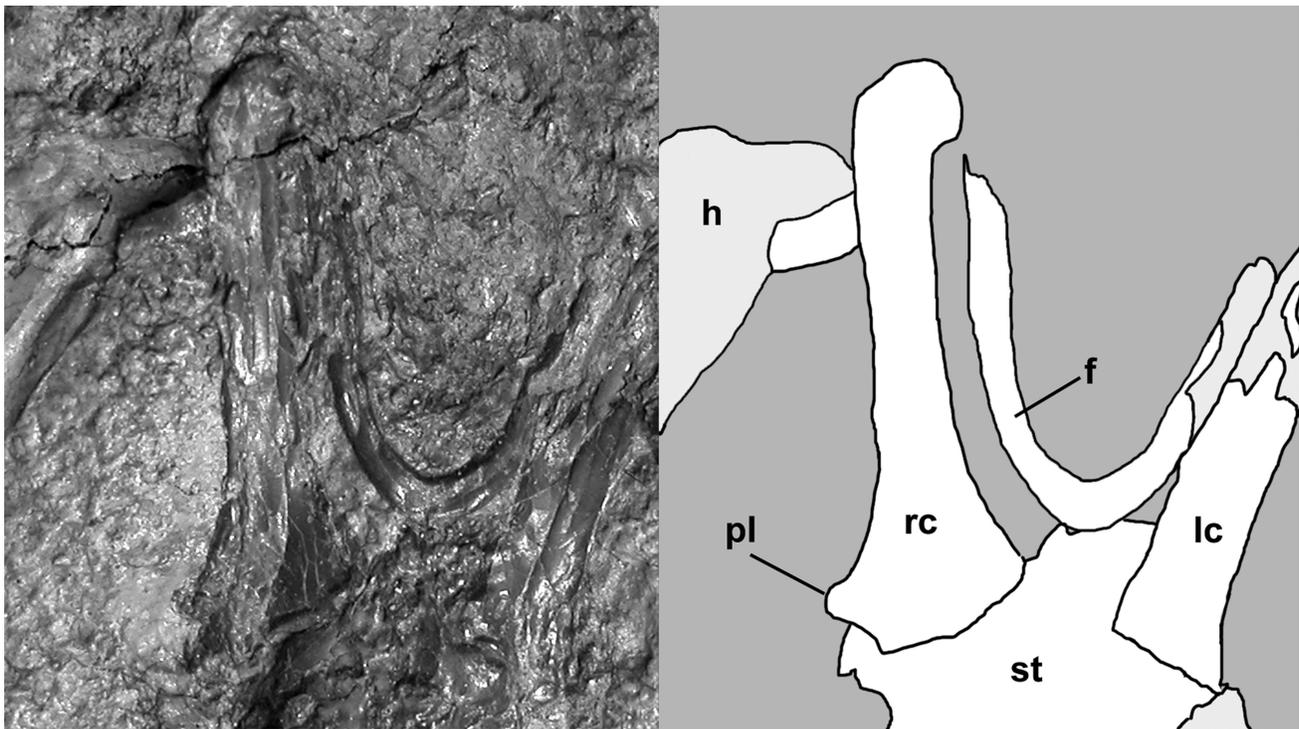


FIG. 2. Pectoral girdle of *Palaeospiza bella* in anterior view. Abbreviations: f = furcula, h = humerus, lc = left coracoid, pl = processus lateralis, rc = right coracoid, and st = sternum.

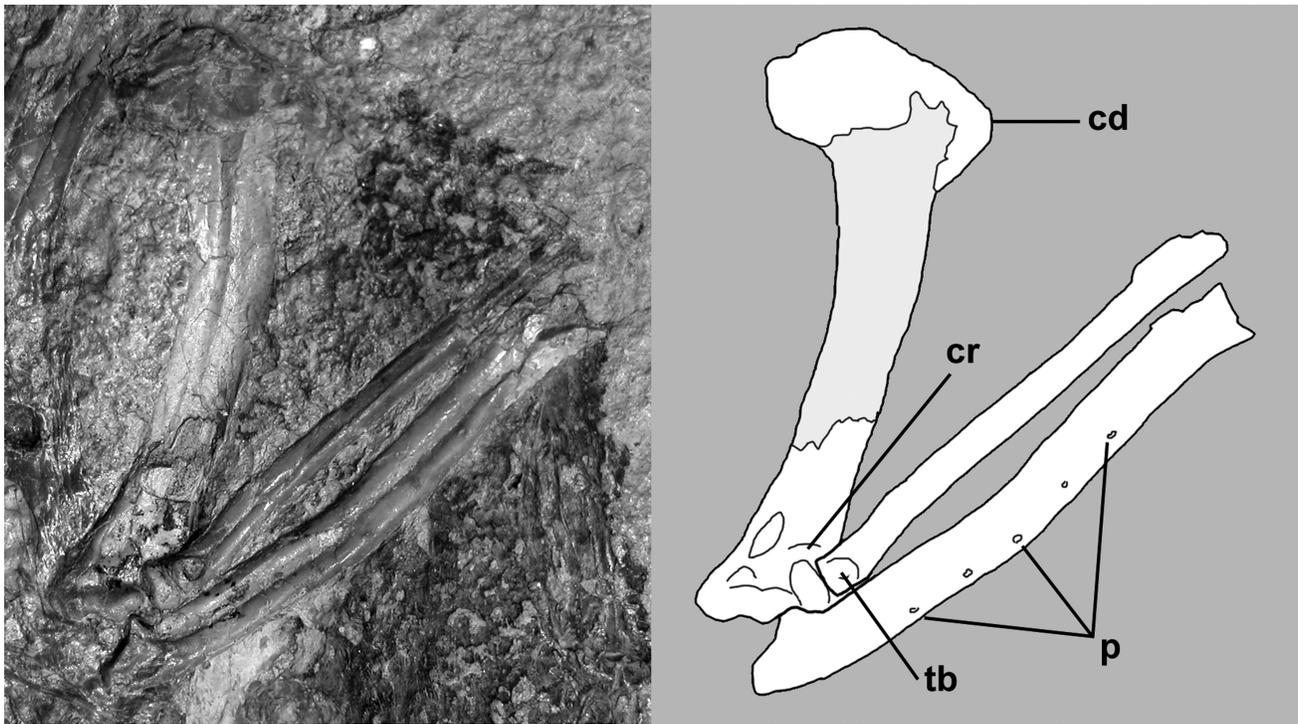


FIG. 3. Left humerus, radius, and ulna of *Palaeospiza bella* in anterior view. Abbreviations: cd = crista deltopectoralis, cr = crescent-shaped depression proximal to condylus dorsalis, p = papillae remigales, and tb = tuberculum bicipitale radii.

of extant *Urocolius* (Mayr and Peters 1998). Passeriformes, by contrast, possess a strongly developed, blade-like apophysis.

The sternum is poorly preserved, compared with the rest of the skeleton. Wetmore (1925) noted that a faint outline possibly indicated a forked spina externa (a feature present in Passeriformes and also in some Piciformes). A well-developed spina externa is present. However, we cannot confirm whether or not it was forked as a result of preservation and consider this feature undetermined for *P. bella*. The trabecula lateralis is discernible on the left side, but damage to the margin of the bone in this area precludes discerning further morphological details.

Wetmore (1925:187) mentioned only that the coracoid, “badly crushed, apparently was quite strong, with a considerable expansion at the lower end.” In fact, the right coracoid is almost completely intact and informative. The processus acrocoracoideus lacks the caudally directed, hooked tip present in Sandcoleidae and *Chascacocolius oscitans*. The processus procoracoideus is either extremely reduced or entirely absent. No trace of a foramen nervi supracoracoidei is discernible. This foramen is present though inconspicuous in Sandcoleidae (Houde and Olson 1992) but absent in other fossil and extant Coliiformes. The processus lateralis is well projected as in Sandcoleidae, *Selmes absurdipes*, and *Chascacocolius oscitans*, in contrast to the weak process present in *Oligocolius brevitaris* (Mayr 2001) and extant mousebirds.

The humeral shaft is straight, a condition shared with *Masillacoliis brevidactylus*, *O. brevitaris*, and extant mousebirds (Fig. 3). The crista deltopectoralis is proximodistally short and only moderately projected, more closely resembling the condition in extant Coliidae than that in Sandcoleidae. The crista bicipitalis is also

proximodistally short. A well-demarcated sulcus humerotricipitalis is present. The processus flexorius projects markedly, as in extant Coliidae. A deep, crescent-shaped depression marks the humerus proximal to the condylus dorsalis as in extant mousebirds, *O. brevitaris* (Mayr 2000a) and *Primocolius sigei* (Mourer-Chauviré 1988).

The ulna is slightly longer than the humerus (Table 1). In nearly all other Coliiformes, the ulna is shorter than the humerus or the bones are of equal length. Exceptions include *O. brevitaris*, which possesses a relatively long ulna (Mayr 2000a), and extant *Urocolius*, in which the ulna is slightly longer than the humerus. Proportions in *Palaeospiza bella* are closest to those in extant *Urocolius macrourus*. Although the olecranon was described as prominent by Wetmore (1925), this process is quite blunt on the

TABLE 1. Measurements of limb bones of *Palaeospiza bella* (MCZ 342222).

Element	Length (mm)
Humerus	23.2
Ulna	~24.4
Radius	~22.0
Carpometacarpus	13.8
Phalanx I-1	4.3
Phalanx II-1	6.2
Phalanx II-2	5.8
Phalanx III-1	4.0
Tibiotarsus	28.1
Tarsometatarsus	17.7

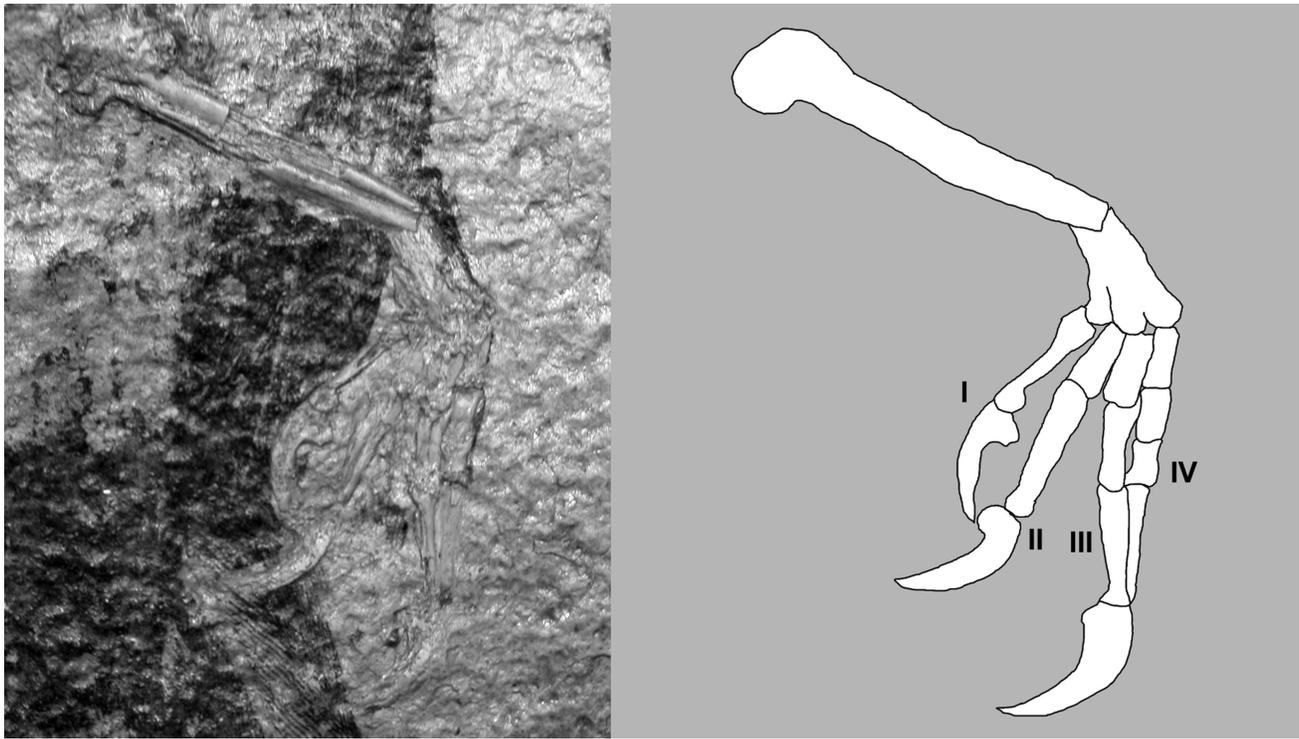


FIG. 4. Right tarsometatarsus and pedal phalanges of *Palaeospiza bella* with reconstruction of the foot created by overlaying images of the right foot from the slab and counterslab. Abbreviations I, II, III, and IV indicate digits.

intact left ulna (Fig. 3). Weakly raised feather papillae are visible on the shaft. Because the wing is articulated, it is not possible to observe the size of the cotyla ventralis. Wetmore (1925:188) commented on the “extraordinarily large and heavy” form of the radius. Although the radius would indeed be considered robust in comparison to those of most Passeriformes, the proportions are typical for Coliiformes. Also worth noting is that the tuberculum bicipitale radii is a large, blunt tubercle, unlike the projected crest present in Passeriformes.

The carpometacarpus is similar to that of extant mousebirds in most respects. The anterior margin of metacarpal II is straight with an abrupt distal expansion. The processus intermetacarpalis appears large and contacts metacarpal III. A well-defined sulcus tendinosus is present on the dorsal surface of metacarpal II. The sulcus tendinosus is shallow in Sandcoleidae, *Chascacocolius oscitans*, and *M. brevidactylus* (Mayr and Peters 1998), but in extant mousebirds this sulcus is imperceptible. Metacarpal III is thin, strongly bowed, and extended significantly distal to metacarpal II. The distal connection between metacarpals II and III is extensive.

The alular phalanx is elongate, extending to approximately the midpoint of the carpometacarpus. There is no indication of an alular claw, though it remains possible that such a small element was lost during the splitting or preparation of the slab. Phalanx II-1 is anteroposteriorly broad, expanding near its midpoint to equal the maximum width of the distal end of the carpometacarpus. A strong dorsal ridge is present on the anterior edge. Phalanx II-2 is a triangular element and is unusually broad compared with the thin tapering phalanx of extant mousebirds and Sandcoleidae. Phalanx III-1 is short and thin.

Preservation of the pelvic girdle and hindlimb is poor. Impressions and intact portions of the pelvis are consistent with the posteriorly broad and anteriorly tapering morphology present in extant Coliiformes. A short crista cnemialis cranialis is visible on the left tibiotarsus. The tarsometatarsus (Figs. 4–5) is relatively elongate, differing from the shortened element typical of members of the traditional taxon Coraciiformes (*sensu lato*; e.g., Coraciidae, Alcedinidae, Meropidae, Momotidae) but in agreement with the condition in most Coliiformes. The hypotarsal crests are weakly projected. The intact portions of the tarsometatarsus and the positions of the proximal phalanges suggest that trochleae II and IV were small and extended close to the level of trochlea III as in extant mousebirds, *M. brevidactylus* (Mayr and Peters 1998), *O. brevitarsus* (Mayr 2001), and *Primocolius minor* (Mourer-Chauviré 1988). The right tarsometatarsus is broken at the distal third of the shaft. It is not possible to judge whether this represents an injury or postmortem damage, though the lack of breaks or disarticulation elsewhere in the skeleton lends credence to the first possibility. Mayr et al. (2004) reported similar injuries in birds from the Eocene lacustrine deposits of Messel.

Digit II of the foot is the shortest. Digit III is slightly longer than digit IV. In *Selmes absurdipes* and *M. brevidactylus*, digits III and IV are nearly equal in length, whereas in other coliiforms digit III is significantly longer. The flexor tubercles are strongly developed on all unguisals, but whether the claws bear sulci neurovasculares cannot be discerned. The proximal phalanges of pedal digits II, III, and IV are strongly abbreviated. In particular, the extreme shortening of digits IV-1 and IV-2 is a condition seen in mousebirds and otherwise only in a few avian taxa (e.g., diurnal

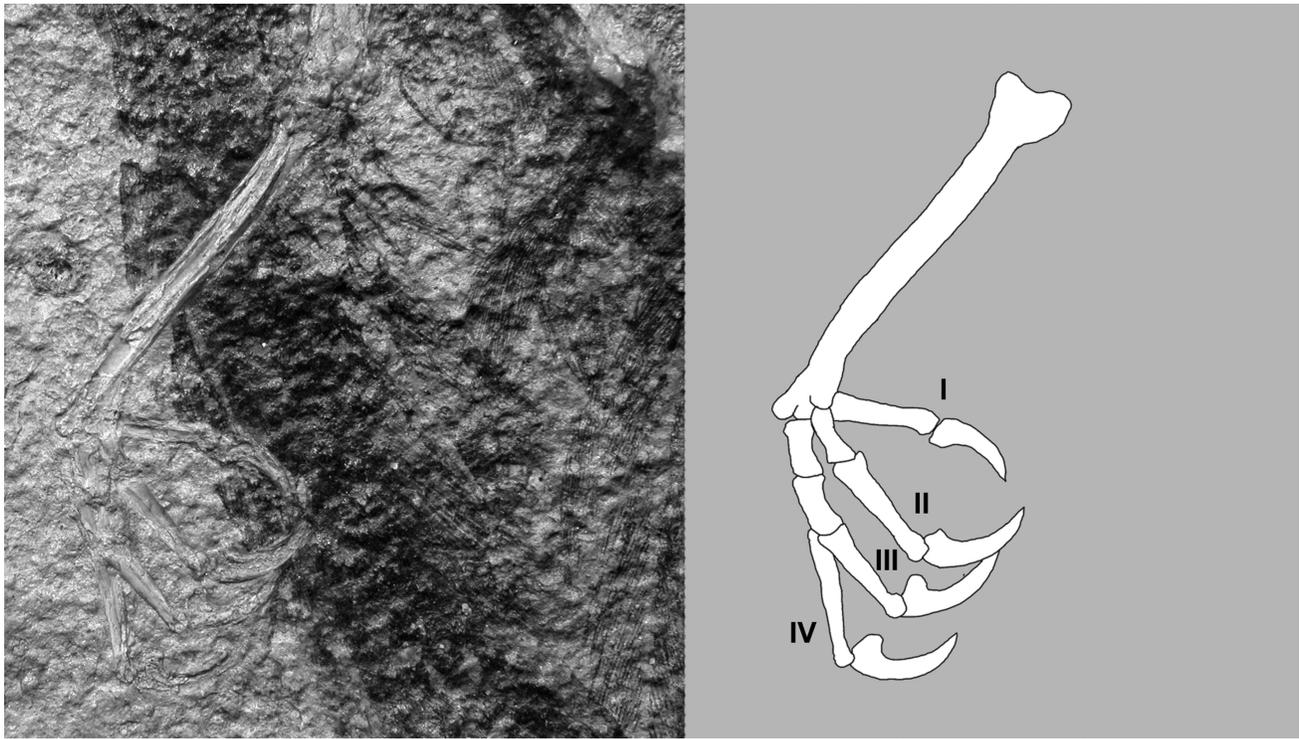


FIG. 5. Left tarsometatarsus and pedal phalanges of *Palaeospiza bella* with reconstruction of the foot created by overlaying images of the left foot from the slab and counterslab. Abbreviations I, II, III, and IV indicate digits.

birds of prey, owls, oilbirds, and hummingbirds; Mayr 2005a) that otherwise bear no resemblance to *Palaeospiza bella*.

Extant mousebirds are characterized by a long tail, a feature also seen in some fossil Coliiformes, including *Anneavis anneae* (Houde and Olson 1992) and *E. pallas* (Mayr and Peters 1998). Preservation of the tail feathering is especially fine for *P. bella*, and at least eight rectrices can be discerned. The tail tapers distally, with the central rectrices extending farthest. As preserved, the tail is shorter than those of living mousebirds, making up slightly less than half the total length of the bird. However, the central rectrices are truncated at the edge of the slab, so they may have been longer when complete.

STATUS OF *EOCOLIUS WALKERI*

Eocolius walkeri is known from several associated elements collected from the lower Eocene London Clay Formation of England. This fossil was originally described as a new species of coliiiform (Dyke and Waterhouse 2001). Mayr (2005c) subsequently noted that *E. walkeri* could be a junior synonym of *Selmes absurdipes*, stating that the differential diagnosis provided in the original description was no longer valid in light of the discovery of specimens of *S. absurdipes* that are more intact.

Referral of *E. walkeri* to Coliiformes was based primarily on one character of the ulna, “large cotyla dorsalis” (Dyke and Waterhouse 2001, text and fig. 5). However, this character is not diagnostic for Coliiformes, in which the cotyla dorsalis is unremarkable but the cotyla ventralis is apomorphically large. Confusion appears to have arisen because the cotyla dorsalis was referenced in the

osteological diagnosis for Coliiformes provided by Mayr and Peters (1998:180). This was because of a typographical error, as noted by Mayr (2004). The enlarged cotyla ventralis is referenced as diagnostic elsewhere in Mayr and Peters (1998) and in subsequent papers (Mayr 2000b, 2004, 2005c; Mayr and Mourer-Chauviré 2004). Evidence for placing *E. walkeri* within Coliiformes is thus lacking, given that the figured element in the holotype clearly shows that the cotyla ventralis is not apomorphically large, excluding the possibility of merely another typographical error in Dyke and Waterhouse (2001). Moreover, the morphology of the radius is unusual for a putative coliiiform. The radius is robust in extant and fossil mousebirds but very slender in *E. walkeri*. Further, the radius is significantly longer than the humerus (humerus:radius ratio = 0.91) in *E. walkeri*. Considering that ulna length ranges from 109% to 112% of radius length in Coliiformes (Houde and Olson 1992, D. T. Ksepka unpubl. data for extant species), the humerus:ulna ratio of *E. walkeri* would have been 0.82–0.83, falling well outside the range of values seen in all fossil and extant Coliiformes (0.90–1.11; Mayr 2000a). Finally, the crista trochanteris of the femur in *E. walkeri* appears to be strongly projected (Dyke and Waterhouse 2001, fig. 3.4), whereas the crista trochanteris is weak in Coliiformes.

Although the additional features discussed above differentiate *E. walkeri* from *S. absurdipes*, they also cast doubt on the coliiiform affinities of the fossil. Given the lack of any synapomorphies of Coliiformes (e.g., enlarged cotyla ventralis of the ulna), the presence of morphologies seen in no other members of the clade, and the incomplete nature of the holotype, it is best to remove *E. walkeri* from Coliiformes and consider it *Aves incertae sedis* pending discovery of more complete remains.

PHYLOGENETIC METHODS AND BIOGEOGRAPHIC RECONSTRUCTION

Mayr and Mourer-Chauviré (2004) conducted the only previous cladistic analysis of coliiiform relationships, using a matrix of 19 osteological characters and nine coliiiform taxa (extant *Urocolius* and *Colius* were coded as a single supraspecific terminal). We expanded the matrix used by these authors by adding 30 characters. We also evaluated the fossil taxa *Colius hendeyi*, *Chascacocolius oscitans*, *Chascacocolius cacicrostris*, *Primocolius sigei*, and *Palaeospiza bella*. Two unnamed fossil mousebirds preserving unique morphologies were also included and referenced by their specimen numbers: WDC-C-MG 148+149 represents a distinct species of Sandcoleidae that closely resembles *A. anneae* and *E. pallas* (Mayr 2000b), and MNH Q.O. 596 represents a distinct specimen sharing derived characters with *S. absurdipes* (Mayr and Mourer-Chauviré 2004). Specimens examined and sources for codings derived from the literature are presented in Appendix 1, character state definitions in Appendix 2, and codings in Appendix 3.

The Coliiformes have proved one of the most difficult avian clades to place phylogenetically, though the monophyly of Coliidae has not been questioned (see review in Cracraft et al. 2004). Proposed sister taxa of Coliiformes include such disparate clades as Psittaciformes (Mayr and Clarke 2003, Sorenson et al. 2003), Trogonidae (Espinosa de los Monteros 2000; Livezey and Zusi 2006, 2007), and Piciformes (Mayr et al. 2003). We conducted analyses iteratively using three different outgroups to explore their effects on polarizing characters within Coliiformes. Psittaciformes were represented by *Psittacula krameri*, *Cacatua galerita*, and the fossil stem psittaciform *Pseudasturides macrocephalus*, Trogonidae by *Trogon melanurus* and *Harpactes erythrocephalus*, and “Coraciiformes” by *Coracias garrulus*, *Atelornis pittoides*, and the fossil stem roller *Eocoracias brachyptera*. We opted not to include these outgroups simultaneously, because our matrix is not designed to test the relationships among these clades (i.e., many additional taxa and characters outside the scope of the present study and not relevant to relationships within Coliiformes would have to be investigated).

Branch and bound searches were conducted in PAUP*, version 4.0b10 (Swofford 2003), with two characters treated as ordered (see Appendix 2). Branches of a minimum length of 0 were collapsed. Six analyses were run, three to test the effects of the different outgroups (with the complete ingroup taxonomic sample) and three (differing in outgroup used) to test the effect of excluding four highly fragmentary operational taxonomic units.

We mapped the geographic distribution of each taxon onto the cladogram by creating a biogeographic character (this character was not included in the phylogenetic analyses). We used simple mapping (full Fitch optimization) in MACCLADE, version 4.08 (Maddison and Maddison 1992), to optimize the biogeography on the ingroup subtree from the strict consensus cladogram recovered in two of the final analyses. We did not include outgroup distribution data in our biogeographical reconstruction, because our outgroup taxa are taken from groups with complex geographic distributions incompletely reflected by the exemplars used for character codings.

RESULTS

Ingroup topology is identical in the strict consensus cladograms from all most parsimonious trees recovered with the Trogonidae and “Coraciiformes” outgroups (Fig. 6A, C), so the results of these two analyses are treated together. Coliiformes, Sandcoleidae, and Colii are all recovered as monophyletic. Interrelationships within Sandcoleidae are completely unresolved. Within Colii, a *Selmes* clade is sister group to a clade uniting all other Colii. Because these remaining Colii taxa form a large polytomy, it is not possible to discern which taxa may be part of the crown clade Coliidae.

The strict consensus from the analysis using the Psittaciformes outgroup is less resolved than the strict consensus derived from the analyses using the Trogonidae and “Coraciiformes” outgroups. In this cladogram, Coliiformes and Colii are recovered, but Sandcoleidae is collapsed (Fig. 6E). Relationships within Colii are the same as in the results using the Trogonidae and “Coraciiformes” outgroups.

Poor resolution in the strict consensus trees from the three initial analyses stems from a few fragmentary fossils behaving as “wildcard” taxa. *Eobucco brodkorbi*, *Primocolius minor*, and *P. sigei* are all known with certainty from only a single bone, so only a small percentage of informative characters can be coded for each. *Eobucco brodkorbi* is known only from the tarsometatarsus. Although diagnosably distinct from other Coliiformes (Mayr and Peters 1998), *E. brodkorbi* is a taxonomic equivalent to both *A. anneae* and *Sandcoleus copiosus* as coded in the current analysis. Thus, this taxon can safely be excluded from the analysis without affecting the relationships of other taxa (Wilkinson 1995). *Colius hendeyi* is known from more complete material. However, we were unable to examine *C. hendeyi* directly, so many important characters remain uncoded for this taxon as well. *Colius hendeyi* is a taxonomic equivalent of both *C. colius* and *C. striatus* as coded in this matrix. Therefore, this taxon can also be excluded from the analysis without affecting the relationships of other taxa. *Primocolius minor* (known from the tarsometatarsus) and *P. sigei* (known from the humerus) are not operationally taxonomic equivalents to any other taxa included in this matrix, but given the low percentage (>20%) of informative characters coded and the non-overlap of preserved elements between these taxa and several other fossils, they potentially contribute to the lack of resolution. It is, therefore, worthwhile to explore the effects of excluding these taxa as well.

A second set of analyses excluding *C. hendeyi*, *E. brodkorbi*, *P. minor*, and *P. sigei* resulted in a significant increase in resolution. The strict consensus of most parsimonious trees from the second round of analyses using the Trogonidae and “Coraciiformes” outgroups are again identical for ingroup taxa (Fig. 6B, D). Within Colii, *Oligocolius*, *Palaeospiza*, *Masillacolius*, *Chascacocolius*, and *Selmes* form successive outgroups to Coliidae. The contents of Coliidae are now resolved and include *Colius* and *Urocolius* clades. None of the included fossil taxa are recovered as part of the crown clade Coliidae. When Psittaciformes is used as the outgroup, Sandcoleidae is not recovered as monophyletic (Fig. 6F). Relationships within Colii and Coliidae are the same in the analyses using the Psittaciformes outgroup and those using the other outgroups.

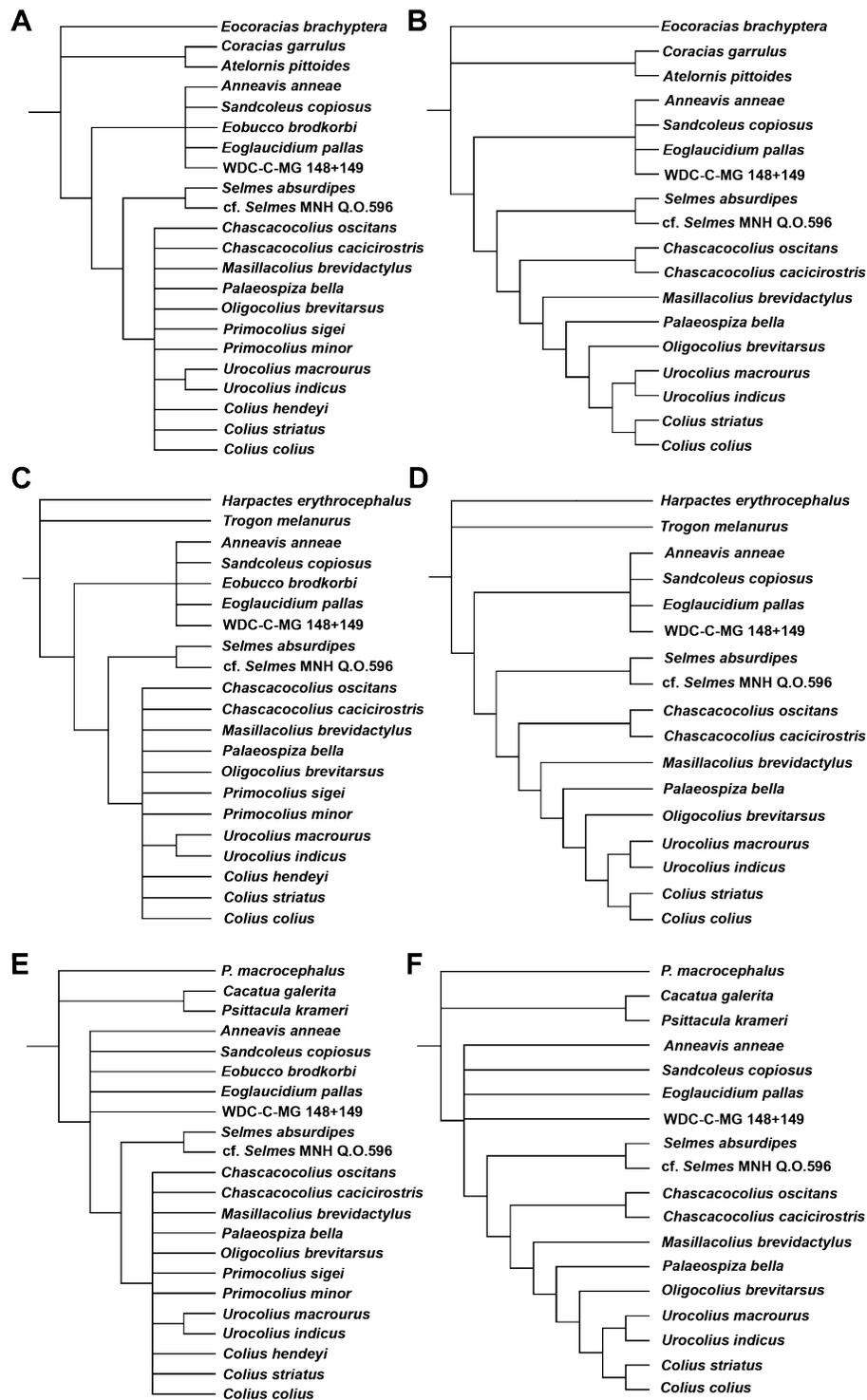


FIG. 6. Results of phylogenetic analyses. (A) Strict consensus of 424 most-parsimonious trees (MPTs; TL [tree length] = 73, RI [retention index] = 0.90, RC [rescaled consistency index] = 0.67) from analysis using “Coraciiformes” outgroup. (B) Strict consensus of 5 MPTs (TL = 73, RI = 0.88, RC = 0.65) from analysis using “Coraciiformes” outgroup with poorly known taxa excluded. (C) Strict consensus of 423 MPTs (TL = 69, RI = 0.92, RC = 0.72) from analysis using Trogonidae outgroup. (D) Strict consensus of 5 MPTs (TL = 69, RI = 0.90, RC = 0.69) from analysis using Trogonidae outgroup with poorly known taxa excluded. (E) Strict consensus of 2,399 MPTs (TL = 74, RI = 0.91, RC = 0.70) from analysis using Psittaciformes outgroup. (F) Strict consensus of 13 MPTs (TL = 74, RI = 0.89, RC = 0.67) from reduced analysis using Psittaciformes outgroup with poorly known taxa excluded.

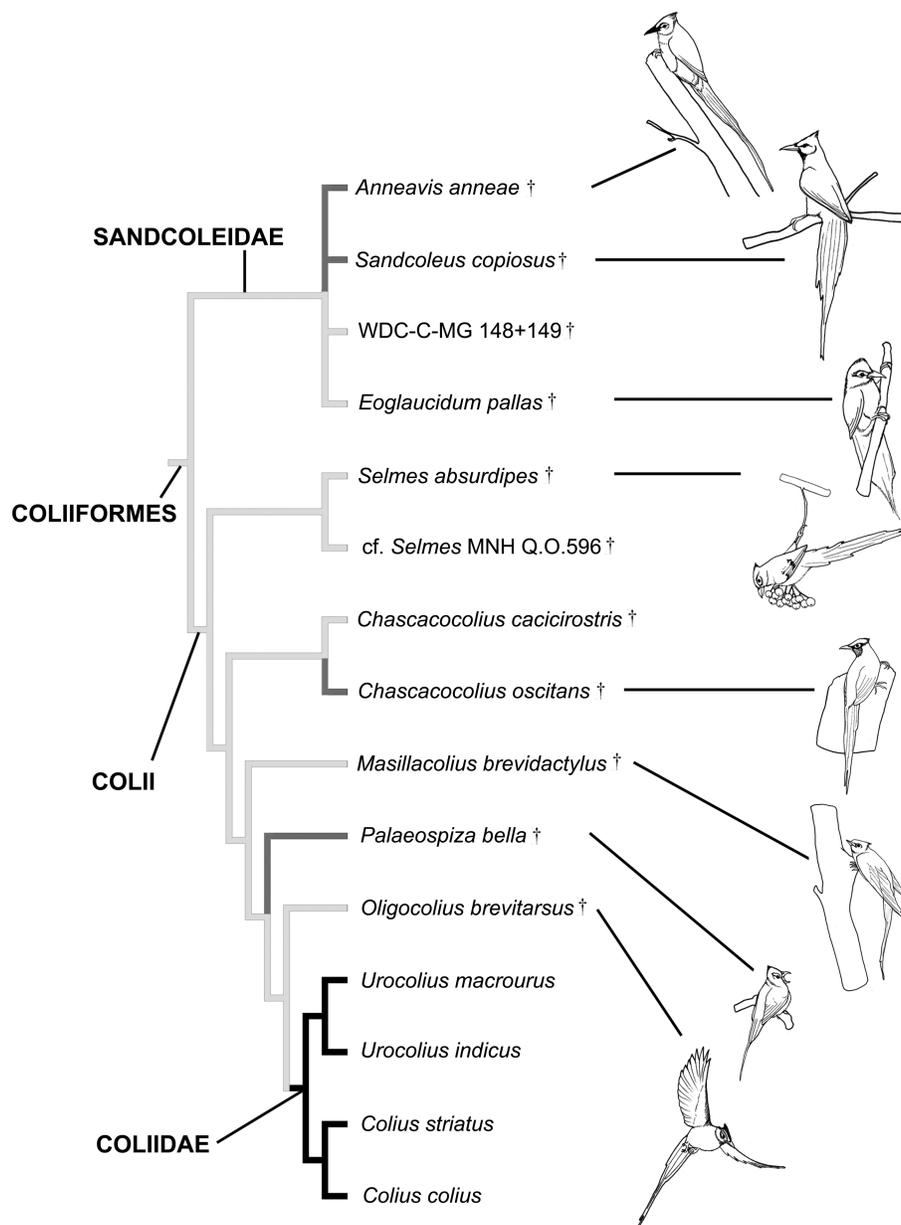


FIG. 7. Phylogeny of Coliiformes showing reconstructed biogeographical distributions. Light gray shading indicates European distribution, dark gray shading North American distribution, and black shading African distribution. Because of a soft polytomy, it remains unclear whether *Sandcoleus copiosus* and *Anneavis annea* form a clade or represent two dispersal events. Fossil taxa are denoted by daggers. Line-drawing reconstructions are provided for fossil taxa on the basis of preserved elements and soft-tissue impressions, with missing details inferred from phylogeny. Artwork is by Kristin Lamm.

Biogeographical reconstructions (Fig. 7) on the strict consensus cladograms resultant from analyses using the Trogonidae and “Coraciiformes” outgroups with the fragmentary fossil taxa excluded support a minimum of four dispersal events in the evolutionary history of Coliiformes, discussed below. This optimization suggests at least three dispersal events between Europe and North America and one dispersal event between Europe and Africa. Relationships between North American and European sandcoleids remain unresolved, so the true number of dispersal events may be greater if North American sandcoleids do not form a clade.

DISCUSSION

Though working only from the illustrations and description of Wetmore (1925), Mayr (2001) suggested that *P. bella* might represent the first record of the Colii (“Coliidae” in his usage) from North America. The phylogenetic analysis presented here confirms Mayr’s (2001) hypothesis. The most compelling character evidence for placing *P. bella* in Coliiformes is the presence of a crescent-shaped depression above the condylus dorsalis of the humerus (character 22:1) and the shortening of the proximal pedal phalanges

(characters 47:1 and 48:1). These characters are optimized as synapomorphies of Coliiformes or more exclusive clades within Coliiformes in all analyses, with the exception that character 48 is uninformative when the Psittaciformes outgroup is used. Absence of the processus procoracoideus (character 14:1), a short, rounded crista deltopectoralis (character 19:1), robustness of the radius (not scored in matrix), and presence of a well-developed processus intermetacarpalis (character 25:2) further support reassignment of *P. bella* to Coliiformes, though these features are also present in some other avian clades. By contrast, no features diagnostic of Passeriformes or any group traditionally included in “Coraciiformes” that are not also present in Coliiformes are observable. The present study also provides the first analysis-based support for placing *Chascacocolius* in Colii, rather than in Sandcoleidae as originally proposed (Houde and Olson 1992). No fossil taxon could be placed with certainty in the crown radiation of mousebirds. The Pliocene fossil taxon *C. hendeyi* appears to be closely related to, or part of, the crown clade. However, described material of *C. hendeyi* does not include elements relevant to determining whether this taxon could be part of the *Urocolius* or *Colius* lineage.

Palaeospiza bella shares two unambiguous synapomorphies that unite it with *Oligocolius brevitorsus* and crown Coliidae: a well-developed processus intermetacarpalis (character 25:2) and projection of metacarpal III significantly distal to metacarpal II (character 26:1). A humerus:ulna ratio <1.0 (character 16:1) also optimizes as a synapomorphy of these taxa, though this character state is reversed in extant *Colius*. *Palaeospiza bella* can be differentiated from *O. brevitorsus* by the presence of a well-projected processus lateralis of the coracoid (character 15:1), a relatively shorter ulna (humerus:ulna ratio = ~0.95, vs. 0.90 in *O. brevitorsus*), and a more elongate tarsometatarsus (character 35:1). *Palaeospiza bella* is excluded from crown Coliidae by the plesiomorphic presence of a well-projected processus lateralis of the coracoid (character 15:1), the presence of a distinct sulcus tendinosus of the carpometacarpus (character 28:0), and a less abbreviated pedal digit II-1 (character 47:1).

With the recognition of *P. bella* as a mousebird, the status of the poorly known taxon *Primocolius* is called into question. Overlapping limb bones of *Primocolius minor* and *P. sigei* fall within 10% of the lengths of those of *Palaeospiza bella*, and proportions are very similar. We are currently unable to discern any discrete characters useful in differentiating *Primocolius* from *Palaeospiza*. Because relevant characters of the tarsometatarsus of *Palaeospiza* cannot be determined from the single known specimen and *Primocolius* specimens were not examined directly in the present study, a decision regarding the status of the name *Primocolius* cannot be made at this time. However, further study or future discoveries could show *Primocolius* (Mourer-Chauviré 1988) to be a junior synonym of *Palaeospiza* (Allen 1878). Regardless of taxonomic status, the plesiomorphic absence of an ossified arcus extensorius (character 36:0) in the holotype of *Primocolius minor* and the plesiomorphic absence of a round tubercle distal to the tricipital fossa (character 17:0) in the holotype of *P. sigei* suggest that both fossils belong outside of crown clade Coliidae.

Coliiformes were previously known from the late Paleocene as well as the early and middle Eocene in North America (Houde and Olson 1992). Recognition of the mousebird affinities of the late Eocene *Palaeospiza bella* extends this range by several million years to closely approach the Eocene–Oligocene boundary at ~34 Ma.

The divergence of Coliiformes from their nearest sister taxon must have occurred by the latest Paleocene (about 56.2–56.6 Ma; *Plesiadapis cookei* zone in Secord et al. 2006), based on the earliest records of *S. copiosus* (Houde and Olson 1992). This minimum age for Coliiformes was used as a calibration point for divergence time estimations by Ericson et al. (2006).

There is, as yet, no good fossil constraint for the age of the crown clade Coliidae. As discussed above, the Pliocene fossil *C. hendeyi* may be part of the crown radiation, but this cannot be resolved at present. Older potential records of crown Coliidae occur in the Miocene of France. Milne-Edwards (1867–1871) named several species (“*Picus archiaci*,” “*Picus consobrinus*,” *Limnatornis paludicola*, *Necroornis palustris*) on the basis of fossils that he assigned to various non-coliiform groups. Ballmann (1969) was the first to correctly identify these fossils as Coliiformes and considered them so similar to living mousebirds that he reassigned them to the extant genus *Colius*. “*Colius paludicola* is from Aquitanian (early Miocene) deposits. The images provided by Milne-Edwards (1867–1871) indicate that this fossil possesses features that are derived within Colii, including a round tubercle distal to the tricipital fossa (character 17:1), a short, rounded crista deltopectoralis (character 18:1), and a straight humeral shaft (character 20:1). Unfortunately, available material preserves no features supporting either placement in or exclusion from crown Coliidae. “*Colius archiaci* and “*Colius consobrinus* also come from Aquitanian deposits but are known solely from the tibiotarsus and, thus, are assignable only to the level of Coliiformes. “*Colius palustris* is known from Tortonian (middle Miocene) material putatively including a tarsometatarsus, tibiotarsus, partial humerus, and partial carpometacarpus. However, Rich and Haarhoff (1985) doubted that the assignment of the tibiotarsus to “*Colius palustris* was correct, and Ballmann (1969) considered the partial humerus and partial carpometacarpus only tentatively assignable to this taxon, listing them as *Colius cf. palustris*. Regardless of which elements are referred to “*Colius palustris*, this taxon can be neither included in nor excluded from Coliidae at present. Although fragmentary, these fossils, along with undescribed material from the Miocene of Germany (see Ballmann 1979, Olson 1985), are important because they represent the youngest records of Coliiformes from outside Africa. Additional material is needed to properly address the phylogenetic relationships of the Miocene Coliiformes of Europe. However, these fossils indicate that the restriction of Coliiformes to their sub-Saharan African distribution is a post-middle Miocene event.

Incorporating fossil taxa into phylogenetic analyses demonstrates that Coliiformes, despite their restricted extant African distribution, have had a very complex biogeographical history. Dispersal between Europe and North America appears to have occurred numerous times in the Tertiary. Present data are consistent with a trans-Atlantic dispersal route, given that no Coliiformes have been reported from Asia. However, the Tertiary Asian record is notoriously depauperate, and it remains possible that Coliiformes had a widespread Holarctic distribution during the Eocene. All four dispersal events identified in the present study are currently reconstructed as dispersals from Europe to North America or Africa, but it is possible that this represents a sampling artifact. The biogeographical scenario presented here could be revised as new material permits better placement for poorly known fossils and as consensus is reached on the nearest outgroups of Coliiformes.

Mayr (2000a) hypothesized that *O. brevitarsus* may have been more capable of sustained flight because of its more elongate distal wing bones. This is in keeping with the differences in wing proportions and flight frequency observed between extant *Urocolius* and the more sedentary *Colius* (Mayr 2000a, de Juana 2001). Interestingly, all North American Coliiformes have relatively longer distal wings than extant *Colius* and fossil European forms (with the single exception of *O. brevitarsus*). If the taxa with these proportions do not form a clade, as indicated here, and if suggested inferences of sustained flight capabilities (Mayr 2000a) from wing bone ratios hold true in fossil forms, taxa more capable of sustained flight could have been differentially dispersive, leading to the presence of the *Chascacocolius oscitans*, *Palaeospiza bella*, and American Sandcoleidae lineages in North America.

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APPENDIX 1. Sources for character codings used in phylogenetic analysis.

Taxon	Source
<i>Anneavis annea</i>	USNM 433918–433970, USNM 424077
<i>Atelornis pittoides</i>	FMNH 438663
<i>Cacatua galerita</i>	AMNH 9393
<i>Chascacocolius oscitans</i>	USNM 433913
<i>C. cacicrostris</i>	Mayr 2005
<i>Colius colius</i>	AMNH 23334
<i>C. hendeyi</i>	Rich and Haarhoff 1985
<i>C. striatus</i>	AMNH 4756, AMNH 4496, AMNH 8954
<i>Coracias garrulus</i>	AMNH 2141, AMNH 12839
<i>Eocoracias brachyptera</i>	SMF-ME 1452; HMLD-Me 10474
<i>Eoglaucidium pallas</i>	Mayr and Peters 1998
<i>Harpactes erythrocephalus</i>	AMNH 25537, AMNH 25539
<i>Masillacolius brevidactylus</i>	Mayr and Peters 1998
<i>Oligocolius brevitarus</i>	Mayr 2000a
<i>Palaeospiza bella</i>	MCZ 342222
<i>Primocolius minor</i>	Mourer-Chauviré 1988
<i>P. sigei</i>	Mourer-Chauviré 1988

(Continued)

APPENDIX 1. Continued.

Taxon	Source
<i>Pseudasturides macrocephalus</i>	Mayr 1998, 2007
<i>Psittacula krameri</i>	AMNH 12988, AMNH 12989
<i>Sandcoleus copiosus</i>	USNM 433912, USNM 433913, USNM 433973–434025
<i>Selmes absurdipes</i>	Peters 1999, Mayr 2001, Mayr and Mourer-Chauviré 2004
cf. <i>Selmes</i> (MNH Q.O.596)	Mayr and Mourer-Chauviré 2004
<i>Trogon melanurus</i>	AMNH 8071
<i>Urocolius indicus</i>	AMNH 2679, USNM 490236, USNM 558549
<i>U. macrourus</i>	AMNH 24231, USNM 491889, USNM 556955
WDC-C-MG 148+149	Mayr 2000b

APPENDIX 2. Character list.

Characters 8, 11, 13, 19, 22, 24, 25, 34, 35, 38, 39, 40, 41, 42, 44, 45, 46, 47, and 48 are taken from the matrix of Mayr and Mourer-Chauviré (2004). The remaining characters were added as part of the present study.

- Nasal septum: absent (0); present (1).
- Mandible, processus retroarticularis blade-like and elongated to approximately one-sixth skull length: absent (0); present (1).
- Bill: long, approximately one half of total skull length (0); abbreviated, less than one third total skull length (1).
- Quadrate, condylus lateralis, dorsally projecting process: absent (0); present (1).
- Mandible, fenestra mandibulae caudalis: absent (0); present and minute (1); present and large (2).
- Thoracic vertebrae, processus ventralis: absent or short (0); greatly elongated (1).
- Synsacrum, processus costalis: indistinct (0); well developed, clearly separate from processus transversus and contacting ilia (1).
- Pygostyle, discus pygostyli greatly enlarged: no (0); yes (1).
- Furcula, apophysis: absent or limited to small tubercle (0); elongate and blade-like (1).
- Sternum, processus craniolateralis: weak or moderate cranial projection (0); elongate with prominent cranial projection (1).
- Sternum, trabeculae intermediae arise from trabeculae laterales: no (0); yes (1).
- Sternum, trabeculae laterales: maintain width distally or end in moderate expansion (0); wide terminal expansion, with inverted T-shaped appearance (1).
- Coracoid, foramen nervi supracoracoidei: present (0); absent (1).
- Coracoid, processus procoracoideus: absent or extremely reduced (0); present, well developed (1).
- Coracoid, processus lateralis: poorly developed (0); well projected (1).
- Scapula: shorter than humerus (0); longer than humerus (1).
- Humerus, circular tubercle located slightly distal to fossa tricipitalis: absent (0); present (1).
- Humerus, foramen pneumaticum: absent (0); present, minute (1); present, large (2).
- Humerus, crista deltopectoralis short, rounded and extending approximately one-fourth of humerus length: no (0); yes (1).
- Humerus, shaft: curved (0); straight (1).
- Humerus, processus flexorius: slight projection (0); projects markedly distal to condyles (1).
- Humerus, crescent-shaped depression proximal to condylus dorsalis: absent (0); present (1).
- Humerus: longer or equal to ulna in length (0); shorter than ulna (1).
- Ulna, cotyla ventralis: unexpanded (0); greatly expanded (1).
- Carpometacarpus, processus intermetacarpalis: absent or vestigial (0); small process (1); well developed, contacting or nearly contacting metacarpal III (2). Ordered.
- Carpometacarpus, relative length of metacarpals II and III: subequal in length (0); metacarpal III projects significantly distal to metacarpal II (1).
- Carpometacarpus, ventrally projecting flange at proximal end of metacarpal III: absent (0); present (1).
- Carpometacarpus, sulcus tendinosus: distinct (0); barely perceptible or absent (1).
- Ilium, distinct crista dorsolateralis ilii: present (0); absent, and dorso-lateral corner of ilium forms a smooth curve instead of a crest (1).
- Posterior connection between ischium and pubis: narrow (0); wide (1).
- Foramen obturatum: open (0); fully enclosed (1).
- Femur, tuberculum m. gastrocnemialis lateralis: subtle (0); pronounced (1).
- Tibiotarsus, distinct sharp crest on proximal portion of shaft, opposite of crista fibularis: absent (0); present (1).
- Tibiotarsus, crista cnemialis cranialis protruding farther proximally than crista cnemialis lateralis, the two crests forming a continuous ridge circumscribing a groove on the cranial side of the bone: absent (0); present (1).
- Tarsometatarsus: not elongated (0); elongated, and humerus: tarsometatarsus length ratio <1.4 (1).
- Tarsometatarsus, arcus extensorius: unossified (0); ossified (1).
- Tarsometatarsus, crista medianoplantaris: absent (0); present (1).
- Tarsometatarsus: rather stout, with shaft becoming wider toward wide proximal end (0); shaft narrow and of equal width for most of length, with slight proximal widening (1). Mayr and Mourer-Chauviré (2004) divided variation in this feature into three states. Here, we combine those authors' states 1 and 2 into a single state.
- Tarsometatarsus: foramina vascularia proximale medialis and lateralis present (0); only a single foramen vasculare proximale present (1).
- Tarsometatarsus, hypotarsus, very large canal for tendon of m. flexor digitorum longus: absent (0); present (1).
- Tarsometatarsus, hypotarsus, tendon of m. flexor hallucis longus enclosed in bony canal or nearly closed, deep sulcus: no (0); yes (1).
- Tarsometatarsus, fossa metatarsi I very large, concave, situated at medial side of tarsometatarsus: no (0); yes (1).
- Tarsometatarsus, canalis interosseus distalis: absent (0); present (1).
- Tarsometatarsus, trochlea metatarsi II and IV small, not widely splayed from trochlea metatarsi III and reaching far distally: no (0); yes (1).
- Tarsometatarsus, distinct plantarly projecting wing-like flange on trochlea metatarsi II: absent (0); present (1).
- Tarsometatarsus trochlea metatarsi III: symmetrical (0); very wide and asymmetrical with medial rim protruding farther distally than lateral rim (1); very wide and asymmetrical with lateral rim protruding farther distally than medial rim (2). We added a third state to this character, to differentiate between projection of the medial and lateral rims in different taxa.
- Proximal phalanx of pedal digit II (phalanx II-1): unabbreviated (0); abbreviated to half the length of phalanx II-2 (1); abbreviated to one-third the length of phalanx II-2 (2). Ordered.
- Proximal three phalanges of pedal digit IV: not abbreviated (0); greatly abbreviated (1).
- Pedal unguals, sulcus neurovascularis: absent (0); present (1).
- Biogeography: Europe (0); North America (1); Africa (2). This character was used for biogeographic reconstructions but excluded from the phylogenetic analysis.

APPENDIX 3. Character codings (A = polymorphism 0/1). Note that character 50 is a biogeographic character and was not used for phylogenetic reconstruction.

	10										20										25									
<i>Harpactes erythrocephalus</i>	1	0	0	0	1	0	1	0	1	0	0	0	1	1	1	0	0	2	0	0	0	0	1	0	0					
<i>Trogonmelanurus</i>	1	0	0	0	2	0	1	0	1	0	0	0	1	1	1	0	0	2	0	0	0	0	1	0	0					
<i>Eocoracias brachyptera</i>	?	0	0	?	0	?	?	0	0	?	?	?	1	1	?	?	?	?	0	?	?	?	1	?	0					
<i>Atelornis pittoides</i>	1	0	0	0	0	0	1	0	1	0	0	0	1	1	1	0	0	2	0	0	1	0	1	0	2					
<i>Coracias garrulus</i>	1	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	2	0	0	0	0	1	0	2					
<i>Pseudasturides macrocephalus</i>	0	0	1	?	?	0	?	?	0	?	0	?	?	?	0	?	?	0	0	0	?	1	0	0						
<i>Cacatua galerita</i>	1	0	1	0	0	0	1	0	0	0	0	?	1	1	1	0	0	2	0	0	0	0	1	0	0					
<i>Psittacula krameri</i>	1	0	1	0	0	0	0	0	0	0	0	?	1	1	1	0	0	2	0	1	0	0	1	0	0					
<i>Anneavis anneae</i>	?	?	?	0	?	?	1	0	0	0	1	0	0	1	1	?	0	?	0	0	0	0	1	1	0					
<i>Chascacocolius cacicrostris</i>	1	1	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?					
<i>C. oscitans</i>	?	1	?	0	0	?	?	?	?	?	?	?	1	0	1	?	0	0	0	0	1	0	0	1	1					
<i>Colius colius</i>	1	0	1	1	2	1	0	1	0	1	0	0	1	0	0	1	1	1	1	1	1	1	0	1	2					
<i>C. hendeyi</i>	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?					
<i>C. striatus</i>	1	0	1	1	2	1	0	1	0	1	0	0	1	0	0	1	1	1	1	1	1	1	0	1	2					
<i>Eobucco brodkorbi</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?					
<i>Eoglaucidium pallas</i>	?	0	0	?	?	?	?	0	0	0	1	?	0	0	?	0	?	?	0	0	0	0	0	1	0					
<i>Masillacoliu brevitylus</i>	?	?	?	?	?	?	1	?	0	?	?	?	1	0	?	0	?	?	1	1	1	?	0	?	1					
<i>Oligocoliu brevityrus</i>	?	?	?	?	?	?	1	?	?	?	?	?	?	?	0	1	?	?	1	1	?	1	1	1	2					
<i>Palaeospiza bella</i>	?	0	?	?	?	?	?	0	?	?	?	?	1	0	1	?	?	?	1	1	1	1	1	?	2					
<i>Primocoliu minor</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?					
<i>P. sigei</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	1	?	1	1	?	?					
<i>Sandcoleus copiosus</i>	0	0	0	0	0	0	1	0	?	0	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0					
<i>Selmes absurdipes</i>	?	0	0	0	0	?	?	1	0	0	?	?	?	?	?	?	?	1	0	?	0	0	?	0	?					
cf. <i>Selmes</i> MNH Q.O.596	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?					
<i>Urocoliu indicus</i>	1	0	1	1	1	1	0	1	1	0	0	1	1	0	0	1	1	1	1	1	1	1	1	1	2					
<i>U. macrourus</i>	1	0	1	1	A	1	0	1	1	0	0	1	1	0	0	1	1	1	1	1	1	1	1	1	2					
WDC-C-MG 148+149	?	0	?	?	?	?	1	0	?	?	1	0	0	0	1	0	?	?	0	0	?	?	1	1	0					

	30										40										50									
<i>Harpactes erythrocephalus</i>	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	?					
<i>Trogon melanurus</i>	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	?					
<i>Eocoracias brachyptera</i>	0	1	0	?	?	?	?	?	?	0	?	1	?	?	?	?	?	0	?	0	?	?	0	1	?					
<i>Atelornis pittoides</i>	1	1	0	0	1	1	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	?					
<i>Coracias garrulus</i>	0	1	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	?					
<i>Pseudasturides macrocephalus</i>	0	?	?	?	?	?	?	?	?	0	?	1	0	0	?	?	0	0	0	?	0	0	0	1	?					
<i>Cacatua galerita</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0	0	1	2	0	1	1	?					
<i>Psittacula krameri</i>	0	0	0	1	0	1	0	1	0	0	0	0	0	1	1	1	1	0	0	1	2	0	1	1	?					
<i>Anneavis anneae</i>	0	1	0	?	?	?	?	1	1	1	0	0	0	0	0	0	1	1	1	0	1	0	2	1	1					
<i>Chascacocolius cacicrostris</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0					
<i>C. oscitans</i>	0	1	0	0	0	?	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1					
<i>Colius colius</i>	1	0	?	1	1	1	1	1	1	1	0	1	1	1	0	0	1	1	0	0	1	0	0	1	0	2				
<i>C. hendeyi</i>	1	?	?	?	?	?	?	1	1	1	1	?	0	1	1	?	?	0	?	1	0	0	?	?	2					
<i>C. striatus</i>	1	0	1	1	1	A	1	1	1	1	1	0	1	1	1	0	0	1	1	0	0	0	1	0	2					
<i>Eobucco brodkorbi</i>	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	?	1	1	0	1	?	?	1					
<i>Eoglaucidium pallas</i>	0	?	0	?	?	?	?	1	1	1	0	?	?	0	0	1	1	?	0	1	0	2	1	1	0					
<i>Masillacoliu brevitylus</i>	0	1	0	?	?	?	?	?	?	?	1	0	?	1	0	?	?	0	?	1	?	0	1	1	0	0				
<i>Oligocoliu brevityrus</i>	1	?	?	?	?	?	1	1	?	1	0	?	?	1	?	?	?	0	?	1	?	0	?	1	1	0				
<i>Palaeospiza bella</i>	1	?	0	?	?	?	?	?	?	?	?	1	?	0	?	?	?	?	?	?	?	?	1	?	?	1				
<i>Primocoliu minor</i>	?	?	?	?	?	?	?	?	?	?	?	?	0	?	1	1	1	0	0	?	1	0	0	?	?	0				
<i>P. sigei</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0				
<i>Sandcoleus copiosus</i>	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	1	1	0	1	0	?	?	1					
<i>Selmes absurdipes</i>	0	0	?	?	?	?	?	1	1	1	?	?	?	?	?	?	?	0	?	0	1	1	2	1	0	0				
cf. <i>Selmes</i> MNH Q.O.596	?	?	?	?	?	?	?	?	?	?	?	0	0	1	1	1	0	0	1	0	1	1	?	?	?	0				
<i>Urocoliu indicus</i>	1	0	1	1	1	1	1	1	1	1	1	0	1	1	1	0	0	1	1	0	0	0	1	0	2					
<i>U. macrourus</i>	1	0	1	1	1	1	1	1	1	1	1	0	1	1	1	0	0	1	1	0	0	0	1	0	2					
WDC-C-MG 148+149	0	1	?	?	?	0	0	?	1	1	0	?	0	0	?	?	?	1	?	0	?	0	2	1	1	0				