New fossil mousebird (Aves: Coliiformes) with feather preservation provides insight into the ecological diversity of an Eocene North American avifauna

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Coliiformes (mousebirds) are represented by just six extant species. These species, restricted to sub-Saharan Africa, are all primarily frugivorous and are among the most sedentary of living birds. Previously described fossil Coliiformes preserving feather traces share the short, rounded wing shape of extant mousebirds. Along with osteological evidence, these observations have been proposed to support poor sustained flight capabilities across the stem mousebird lineage. We report a new species of Coliiformes from the early Eocene (51.66 ± 0.09 Ma) Fossil Butte Member of the Green River Formation, represented by one of the comparatively few fossils from these deposits preserving carbonized traces of the wing and tail feathering. Feather traces indicate an elongate, tapering wing shape similar to that of some extant aerial insectivores, and suggestive of a capacity for sustained and agile open-air flight. Traces of the rectrices reveal the tail accounted for approximately two-thirds of the total length of the bird, a proportion similar to that in living mousebirds. Phylogenetic analysis places the new species as a stem representative of Coliiformes, demonstrating for the first time that the two major clades of Coliiformes – Sandcoleidae and Coli – co-occurred at Fossil Lake. Based on the recovered phylogeny, as well as the osteology and feathering of extant and fossil Coliiformes, the wing shape of the new species is interpreted as apomorphic. In addition to documenting unexpected morphological specialization within stem-lineage Coliiformes, the new species adds yet another taxon to the emerging reconstruction of the diverse Paleogene avifauna from the tightly dated and nearly synchronous fossiliferous deposits of the Fossil Butte Member.

INTRODUCTION

Coliiformes are a clade of small, arboreal birds. Extant representatives of Coliiformes (Coliidae) are primarily frugivorous, highly social, and capable of entering a temporary state of torpor (McAtee, 1947; Rowan, 1967; Bartholomew & Trost, 1970; Fry, Keith & Urban, 1988; de Juana, 2001). Morphologically, all extant species are characterized by a prominent feathered head crest, short and rounded wings, highly elongate tails, and a specialized foot. The plumage of these birds also shows several interesting modifications, including a lack of down, restriction of apteria to the head, and loose contour feather bars that contribute to a hair-like quality (Rowan, 1967; de Juana, 2001). Modifications of the tarsometatarsus and phalanges facilitate rotation of the first and fourth digit, allowing the foot to attain facultatively anisodactyl, zygodactyl, and pammprodactyl configurations, which these birds employ adeptly in clinging.
Coliiformes provide a prime example of an extant group with a relict distribution. Considering only extant representatives, Coliiformes are one of the most species-depauperate of the traditional avian orders, comprising only six morphologically conservative species. All six living species are restricted to sub-Saharan Africa. By contrast, extinct stem Coliiformes were diverse and widespread, with 17 distinct named species and two morphologically distinct but as yet unnamed species, known from North America, Europe, and Africa (Ballmann, 1969; Rich & Haarhoff, 1985; Mourer-Chauviré, 1988; Houde & Olson, 1992; Mayr & Peters, 1998; Peters, 1999; Mayr, 2000a, 2005a; Ksepka & Clarke, 2009). A few problematic specimens may represent other distinct species, but are currently of uncertain status (see Ballmann, 1969, regarding the possible synonymy of the Miocene 'Colius' paludicola, 'Colius' archiaci, and 'Colius' consobrinius). The Eocene species Botauroides parvus and Eocolius walkeri were originally assigned to Coliiformes (Houde & Olson, 1992; Dyke & Waterhouse, 2001). However, Zelenkov & Dyke (2008) proposed that Botauroides parvus be recognized as Aves incerta sedis because of a lack of morphological character support for the referral, whereas Ksepka & Clarke (2009) proposed Eocolius walkeri would be best considered Aves incerta sedis for the same reason (also see the analyses below).

Coliiformes can be divided into two major subclades: Sandcoleidae (all species of which are extinct) and a second subclade (Coli in this paper) including extant mousebirds and fossil taxa more closely related to these living species than to Sandcoleidae (Mayr & Mourer-Chauviré, 2004; Zelenkov & Dyke, 2008; Ksepka & Clarke, 2009). Although there is significant agreement concerning phylogenetic relationships within Coliiformes among recently published analyses, application of the name Coliidae has varied. Mayr & Peters (1998) and Mayr & Mourer-Chauviré (2004) included all stem taxa more closely related to extant mousebirds than to Sandcoleidae in Coliidae, whereas Zelenkov & Dyke (2008) included only three stem taxa (Masillacolius, Primocolius, and Oligocolius) alongside extant mousebirds in Coliidae. None of these authors, however, proposed a phylogenetic definition for Coliidae. Ksepka & Clarke (2009) advocated defining Coliidae as the name for the clade comprising the most recent common ancestor of extant Coliiformes (Colius colius, Colius striatus, Colius castanotus, Colius leucocephalus, Urocolius macrourus, and Urocolius indicus), and all the descendants of that ancestor, i.e. the coliiform crown clade. Keeping Coliidae as the name for the crown clade facilitates communication between paleontologists and neornithologists by providing a clear nomenclatural distinction between stem and crown mousebirds, and by restricting a family name originally defined with reference to extant taxa to the crown radiation. Importantly, this definition helps to avoid confusion, as the paleontological literature is increasingly accessed by neontologists for fossil calibration points used in molecular divergence dating analyses. Sandcoleidae is here applied to the clade uniting all taxa more closely related to Sandcoleus copiosus than to Coliidae, consistent with the usage in Mayr & Peters (1998), Zelenkov & Dyke (2008), and Ksepka & Clarke (2009). Coli is applied to the clade that includes all taxa more closely related to the mousebird crown clade (Coliidae) than to Sandcoleus copiosus (Ksepka & Clarke, 2009). The current contents of Colii correspond to those of Mayr & Peters’ (1998) Coliidae.

To date, phylogenetic analyses have shown that the majority of known extinct mousebird species belong to the clade Coli (Mayr & Mourer-Chauviré, 2004; Zelenkov & Dyke, 2008; Ksepka & Clarke, 2009). No fossil representative of the crown clade (Coliidae) has been identified through phylogenetic analysis at this point, although some likely candidates exist. The early Pliocene 'Colius' hendeyi from South Africa is certainly closely related to the crown clade, although phylogenetic analyses were unable to completely resolve the position of this taxon, and resulted in a polytomy including 'Colius' hendeyi, extant Colius and Urocolius, and a few stem taxa (Ksepka & Clarke, 2009). Specimens from the latest Pliocene of Olduvai Gorge, Tanzania, assigned to Colius cf. striatus strongly resemble that extant species (Haarhoff, 1993), although these fossils have not yet been considered in a phylogenetic analysis. Both of these fossils occur within the geographic range of extant mousebirds (Fig.1). Some poorly known Miocene fossils from Europe cannot be positively placed within, or excluded from, the crown clade (Ksepka & Clarke, 2009). These fossils, including holotype material of ‘Colius’ paludicola, ‘Colius’ archiaci, ‘Colius’ consobrinius, and ‘Colius’ palustris (Milne-Edwards A. 1867–1871; Ballmann, 1969; Rich & Haarhoff, 1985), may eventually prove to represent crown taxa with better material, but at present no derived character states support these species belonging within crown Coliidae, or sharing a closer relationship with extant Colius than with extant Urocolius. Determining the phylogenetic position of these taxa would provide important insight into the biogeographic history of mousebirds.
Although the Eocene–Oligocene fossil taxa *Primo-colius*, *Masillacolius*, and *Oligocolius* were interpreted as part of ‘crown-group’ Coliidae by Zelenkov & Dyke (2008), these taxa were merely recovered as part of a polytomy with a *Colius/Urocolius* composite crown clade terminal in that analysis. Placement of these fossil taxa relative to the crown clade was not phylogenetically tested because the use of a single composite terminal presumes the monophyly of extant mousebirds, to the exclusion of these or any other fossil taxa. By contrast, features supporting a stem-group position for *Primocolius*, *Masillacolius*, and *Oligocolius* were identified in the original descriptions of these taxa (Mourer-Chauviré, 1988; Mayr & Peters, 1998; Mayr, 2000a), and phylogenetic analyses employing species-level exemplars recover all three as stem taxa (Ksepka & Clarke, 2009; this paper).

Although relationships within Coliiformes are for the most part non-controversial, the clade as a whole has proven difficult to place relative to other major avian clades. Sister-group relationships have been recovered between Coliiformes and such diverse clades as Psittaciformes (Mayr & Clarke, 2003; Sorenson et al., 2003; Chubb, 2004), Trogoniformes (Espinoza de los Monteros, 2000; Livezey & Zusi, 2006, 2007), Piciformes (Mayr, Manegold & Johansson, 2003), and Strigiformes (Hackett et al., 2008). Notably, all the taxa mentioned above as possible sister taxa for Coliiformes possess a foot modified for semi-zygodactylly (Strigiformes), zygodactylly (Piciformes and Psittaciformes), or heterodactylly (Trogoniformes). This suggests the unique foot of mousebirds could have been derived from an already specialized configuration, rather than the anisodactyl arrangement primitive for extant Aves. In light of recent support for a Coliiformes–Strigiformes clade (Hackett et al., 2008), it is interesting to note that the holotype humerus of the Eocene mousebird *Eoglaucidium pallas* was originally described as that of an owl (Fischer, 1987). However, no derived characters shared with Strigiformes can be readily observed on the humerus, and it does not appear that this misidentication reflects any putative underlying synapomorphies of a mousebird–owl clade.

Extant mousebirds consume a predominantly frugivorous diet, which they supplement with leaves, shoots, flowers, nectar, bark, and, on very rare occasions, insects or scraps of meat (Rowan, 1967; Downs, Wirminghaus & Lawes, 2000; de Juana, 2001). Morphological studies and direct evidence from gut contents have allowed some hypotheses of stem mousebird ecology to be forwarded. Houde & Olson (1992) proposed that the extinct Sandcoleidae were

**Figure 1.** Map showing the distribution of extant Coliidae (light grey) and localities yielding fossil Coliiformes (dark-grey circles). Distribution of extant species follows de Juana (2001).
morphologically adapted for climbing and creeping in trees, and were poorly adapted for long periods of flight, based on specializations of the foot, the shallow carina of the sternum, and the short, round wing shape in these birds. Zelenkov & Dyke (2008) reiterated these observations in support of a clinging and/or climbing ecology for stem mousebirds, and further detailed the range of digital movement dictated by the conformation of the hindlimb, as well as noting that the shallow sternum known from many fossil Coliiformes would allow these birds to position themselves closer to tree trunks, and reduce the repulsive force in clinging. Gut contents preserved within the stomach area of *Eoglaucidium* (Sandcoleidae) and *Selmes* (Coli) preserve seeds, although it is unclear whether these taxa habitually fed on seeds per se or merely swallowed seeds incidentally during consumption of fruits (Mayr & Peters, 1998; Peters, 1999). *Chascacocolius* (Colii) exhibits an elongate beak and hypertrophied retroarticular process that have been interpreted as specializations for gaping, in association with prying under bark, breaking open fruits, or ground probing (Houde & Olson, 1992; Mayr, 2005a). In sum, previous studies of fossil taxa suggest most stem mousebirds shared a propensity for climbing through vegetation during foraging with extant mousebirds, but exhibited a wider range of strategies for obtaining food.

In this paper, we describe a new stem mousebird from the early Eocene Green River Formation of Wyoming, exhibiting a novel wing shape, suggesting a possible aerial foraging strategy not previously recognized in Coliiformes. The holotype specimen was collected at Lewis Ranch Site 1 (Fig. 2; locality A in Grande & Buchheim, 1994). During the late early Eocene, three major lakes formed a large freshwater system, the Green River Lake Complex, stretching over parts of present-day Wyoming, Colorado, and Utah (McGrew & Casilliano, 1975; Grande, 1984, 1994; Buchheim, 1994; Grande & Buchheim, 1994). Lewis Ranch Site 1 is situated within the paleoshoreline of Fossil Lake, the smallest of these three major lakes. Fossil Lake provides the best record of Paleogene birds in North America, having yielded a rich array of often exquisitely preserved avian fossils (Eastman, 1900; Brodkorb, 1970; Feduccia & Martin, 1976; Olson, 1977, 1987, 1992; Grande, 1984; Houde, 1988; Houde & Olson, 1992; Mayr, 2000b; Mayr & Daniels, 2001; Mayr & Weidig, 2004; Olson & Matsuoka, 2005; Weidig, 2006; Ksepka & Clarke, 2010).
Beds at Lewis Ranch Site 1 are part of the middle unit of the Fossil Butte Member (FBM) of the Green River Formation, which is bounded above by a K-spar tuff, dated by $^{40}\text{Ar}/^{39}\text{Ar}$ spectrometry to 51.66 ± 0.09 Ma (Smith, Carroll & Singer, 2008). Estimated rates of deposition for the well-mapped vertebrate fossil-producing deposits of the FBM support deposition of all fossils within a span of several thousand years or less (Grande & Buchheim, 1994). A predominantly freshwater lake paleoenvironment is indicated by the fish, invertebrate, and plant biota recovered from the fossiliferous layers of the middle unit of the FBM (Grande, 1994; Buchheim, 1998), and the terrestrial environment surrounding Fossil Lake appears to have consisted largely of paratropical lowland forest (MacGinitie, 1969; Buchheim, 1998; Cushman, 1999).

Only a single occurrence of Coliiformes has been previously reported from the Green River Formation. Houde & Olson (1992) described *Anneavis anneae* from an articulated skeleton lacking a skull, collected from the Warfield Springs locality (locality K, F-2 equivalent deposits of Grande & Buchheim, 1994) of the FBM. These authors also referred additional, less complete material from slightly older deposits of the early Eocene Willwood Formation to this species. *Anneavis anneae* has been placed within Sandcoleidae (Houde & Olson, 1992; Mayr & Peters, 1998; Zelenkov & Dyke, 2008; Ksepka & Clarke, 2009; this paper).

**INSTITUTIONAL ABBREVIATIONS**

AMNH, American Museum of Natural History, New York, NY, USA; FMNH, Department of Geology, Field Museum of Natural History, Chicago, IL, USA; MHN, Muséum d’Histoire Naturelle, Basel, Switzerland; PSM, Slater Museum of Natural History, University of Puget Sound, Tacoma, WA, USA; SMF, Forschungsinstitut Senckenberg, Frankfurt, Germany; SMNK, Staatliches Museum für Naturkunde, Karlsruhe, Germany; UWGM, University of Wyoming Geological Museum, Laramie, WY, USA; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA; WDC, Wyoming Dinosaur Center, Thermopolis, WY, USA.

**SYSTEMATIC PALEONTOLOGY**

**AVES LINNAEUS, 1758**

**COLIIFORMES MURIE, 1872**

**CELERICOILUS ACRIALA GEN. ET SP. NOV**

*Holotype specimen:* FMNH PA 730 (Figs 3–5, Table 1), a nearly complete but poorly preserved skeleton with tracheal rings and carbonized feather traces, showing slight disarticulation of most skeletal elements, and missing some pedal phalanges. Both of the coracoids, the right humerus, and the left femur are not visible, but some or all of these elements are possibly hidden beneath other elements or matrix.

*Etymology:* *Celericolius* combines the Latin *Celer* (swift) plus *colius* referencing the agile flight style inferred for this mousebird species. The species epithet, *acriala*, combines the Latin root *ac* (sharp) and *ala* (wing) referencing the elongate, tapered wing.

*Type locality and horizon:* Lewis Ranch Site 1 (locality A of Grande & Buchheim, 1994), near Kemmerer, Wyoming, USA. Beds at this locality belong to the FBM of the Green River Formation, and are dated to the early Eocene (51.66 ± 0.09 Ma; Smith et al., 2008).

*Diagnosis:* *Celericolius acriala* exhibits two autapomorphies: (1) processus transversus vertebrae of the free caudal vertebrae distinctly anteroposteriorly...
broadened, and (2) ulna proportionately more elongate than that of all other Coliiformes, except *Oligocolius brevitarsus* (pronounced elongation of the ulna evolved independently in these two taxa based on their inferred phylogeny). The ulna : humerus ratio is greater than 1.10 in *C. acriala* whereas in other Coliiformes including Sandcoleidae this ratio is typically less than 1.00. Within Colii, only *Palaeospiza bella*, *Oligocolius brevitarsus*, and extant *Urocolius* exhibit an ulna that is longer than the humerus.

*Celericolius acriala* differs from all other stem Coliiformes, but resembles extant Coliidae, in that pedal phalanx II-1 is subequal to phalanx II-2 in length. In other stem Coliiformes preserving the foot, phalanx II-1 is strongly abbreviated, measuring one-half of the length (*Palaeospiza* and *Masillacolius*) or one-third of the length (Sandcoleidae and *Selmes*) of phalanx II-2. Because pedal phalanges remain unknown for several fossil taxa, it is currently equally parsimonious to interpret the elongate phalanx II-1 as a local autapomorphy of *C. acriala* acquired convergently in Coliidae, or as a synapomorphy of a clade uniting *C. acriala* and Coliidae, with a reversal to the abbreviated state in *Palaeospiza bella*.

*Celericolius acriala* can be diagnosed by the features listed above and can also be further differentiated from the comparatively closely related *Palaeospiza bella* and *Oligocolius brevitarsus* by a

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**Figure 4.** Photograph and line drawing of *Celericolius acriala* (FMNH PA 730). Abbreviations: dI, pedal digit I; dII, pedal digit II; dIII, pedal digit III; dIV, pedal digit IV; f, furcula; lcmc, left carpometacarpus; lhu, left humerus; lra, left radius; ltbt, left tibiotarsus; ltmnt, left tarsometatarsus; lul, left ulna; mpi-1, manual phalanx I-1; mpi-2, manual phalanx II-2; mpiII-1, manual phalanx III-1; py, pygostyle; rad, radiale; lcmc, right carpometacarpus; rest, artificially restored tip of the beak; rf, right femur; rra, right radius; rtbt, right tibiotarsus; rtmt, right tarsometatarsus; ruln, right ulna; sc, scapula; st, sternum; ul, ulnare; uln, ulna.
small (versus strongly projected) processus intermetacarpalis, and by the subequal distal projection of metacarpals II and III (versus metacarpal III being significantly longer). Additionally, the tarsometatarsus of *C. acriala* is more elongate than in *Oligocolius brevitarsus* (tarsometatarsus : humerus ratio 0.93 versus 0.65). *Celericolius acriala* can be further differentiated from *Masillacolius brevidactylus* and *Primocolius sigei* by the more distally extensive crista deltopectoralis of the humerus in the new species, and from *Selmes absurdipes* by the straight (versus curved) humerus shaft.

**DESCRIPTION AND COMPARISONS**

In overall size, the holotype individual is approximately equal to the extant *Urocolius indicus* (Red-faced Mousebird), a bird with a body mass of ~50 g (Downs et al., 2000). The holotype specimen is largely articulated and appears to be nearly complete, except for damage to the skull and the loss of two pedal unguals. The coracoids, right humerus, and left femur are either not preserved or are hidden beneath the remains of the sternum and pelvis (Fig. 4). The specimen has suffered postmortem degradation, and much of the skeleton is flattened and poorly preserved, with the exposed bone surface often lost, obscuring features such as muscle insertion scars. Some areas of the skull exhibit minor retouching. At the tip of the premaxilla and dorsal portions of the mandible, incomplete areas have been filled in by applying paint to the negative mold left in the slab by missing bone.

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**Table 1. Measurements of Celericolius acriala** (FMNH PA 730), in mm

| Pectoral girdle and limb          |   |
|----------------------------------|---|
| Scapula, length (left)           | 21.3 |
| Humerus, length (left)           | ~24.0 |
| Humerus, deltoid crest length (left) | ~7.3 |
| Ulna, length (right)             | 27.6 |
| Radius, length (left/right)      | 24.4/24.8 |
| Carpometacarpus (left/right)     | 16.6/16.1 |
| (length to distal end of metacarpal II) |   |
| Phalanx I-1, length (left/right) | 5.6/5.4 |
| Phalanx II-1, length (left/right)| 7.4/7.6 |
| Phalanx II-2, length (left)      | 6.4 |
| Phalanx III-1, length (left)     | 4.6 |

| Pelvic girdle and limb           |   |
|----------------------------------|---|
| Femur, length (right)            | 21.2 |
| Tibiotarsus, length (left)       | 34.8 |
| Tarsometatarsus, length (left/right) | 21.9/22.0 |
| Phalanx I-1, length (left)       | 9.9 |
| Phalanx II-2, length (left)      | 6.0 |
| Phalanx II-3 (ungual), length (left) | 4.9 |
| Phalanx III-1, length (right)    | 2.5 |
| Phalanx III-2, length (right)    | 2.9 |
| Phalanx III-3, length (left/right)| 6.1/6.8 |
| Phalanx III-4 (ungual), length (right) | 6.0 |
| Phalanx IV-2, length (left)      | 1.8 |
| Phalanx IV-3, length (left/right)| 1.3/1.5 |
| Phalanx IV-4 (ungual, length (left/right) | 5.7/5.7 |
| Phalanx IV-5 (ungual, length (right) | 6.0 |

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**Figure 5.** Details of the skeletal anatomy of *Celericolius acriala*. A, distal elements of left wing. B, pelvis, pygostyle, and left hindlimb. C, right foot. Abbreviations: cmc, carpometacarpus; dl, pedal digit I; dII, pedal digit II; dIII, pedal digit III; dIV, pedal digit IV; ext, impression of processus extensorius; hyp, crista hypotarsi; isch, ischium; mpi-1, manual phalanx I-1; mpi-1, manual phalanx II-1; mpi-1, manual phalanx III-1; pc, processus costales; pi, processus intermetacarpalis; pt, processus transversus vertebrae; pu, pubis; py, pygostyle; rad, radiale; tmt, tarsometatarsus; uln, ulnare. Scale bars: 5 mm.
As in extant Coliidae, the skull roof is domed and rounded, and a large foniculus orbitocranialis is present. Unfortunately, fine details of the skull are nearly entirely lacking because of poor preservation. As noted above, the beak tip has been retouched. Because of this modification the precise shape and total length of the beak must be considered uncertain. The mandible is slender and straight near its midpoint, but the caudal and rostral portions are not preserved.

A few tracheal rings are scattered on the slab. Tracheal rings are also preserved in at least one specimen of the sandcoleid *Eoglaucaudium pallas* from Messel (Mayr & Peters, 1998: fig. 3), but are not preserved in the articulated holotype skeleton of the sandcoleid *Anneavis anneae*, also from FBM deposits (Houde & Olson, 1992). However, because the *Anneavis anneae* holotype was collected from a different quarry (Warfield Springs, locality K), representing a more near-shore environment than Lewis Ranch Site 1 (Grande & Buchheim, 1994), it is possible that the lack of tracheal ring preservation in that specimen may be related to preservation in a distinct depositional environment.

The cervical and dorsal vertebrae are poorly preserved. In contrast, the caudal vertebrae and pygostyle are well-preserved and are exposed in ventral view. The processes transversus vertebrae of the caudal vertebrae are much wider anteroposteriorly than in extant Coliidae. *Sandoceus copiosus* and a privately owned specimen referred to *Chasacocolius* (Mayr, 2005a) also possess narrow processes transversus vertebrae, comparable with those in Coliidae. As in extant mousebirds, the discus pygostyli is greatly expanded, forming a distinct broad, rounded plate (Fig. 5).

Much of the sternum is obscured by overlying elements, but several phylogenetically important features of the caudal margin can be observed. The incisura lateralis is shallow compared with extant *Coliidae*. *Sandoceus copiosus* shows a condition intermediate between that in Sandcoleidae, where the incisura lateralis is reduced such that the trabecula intermedia arises from the trabecula lateralis, and in Coliidae, where the incisura lateralis is very deep and the trabecula lateralis and trabecula intermedia are clearly separated. Distally, the trabecula lateralis shows slight mediolateral expansion, but does not approach the inverted T-shape developed in extant *Urocolius*. The scapula is shorter than the humerus, as in most stem mousebirds. In Coliidae and *Oligocolius brevitarsus*, the scapula exceeds the humerus in length. The corpus scapulae is fairly straight and maintains a nearly constant width, with no distal expansion.

The crista deltopectoralis of the humerus is strongly projected, as in other mousebirds. This crest extends for approximately one-third of the proximo-distal length of the humerus, whereas it extends approximately one-fourth of the length of the humerus in Sandcoleidae and Coliidae. The humeral shaft is straight, more closely resembling the condition in extant Coliidae than the curved shaft of Sandcoleidae. Preservation at the distal end is poor, so it is not possible to determine whether *C. acriaala* possessed the crescent-shaped depression proximal to the condylus dorsalis seen in some Coli. The humerus exceeds the ratio of 1.11 in *Oligocolius brevitarsus*. Few details of the radius and ulna can be ascertained, although it is clear that both elements are robust, as in other Coliiformes. The olecranon appears blunt and weakly differentiated, as visible in the right ulna. The left carpometacarpus is exposed in ventral view, and the right carpometacarpus is exposed in dorsal view. Regions of the ventral bone surface of the left element are missing, exposing the internal surface of the shaft for much of its length, but fortunately the bone is intact at the proximal end. A small processus intermetacarpalis, which does not contact metacarpal III, is preserved (Fig. 5). An impression of the processus extensorius of the left carpometacarpus indicates that this process was strongly projected. The spatum intermetacarpale is wide, although metacarpal III is less strongly bowed than in extant Coliidae. Although the distal end of metacarpal III has been lost from the slab on the right carpometacarpus, its impression indicates metacarpals II and III extended to the same level. The alular phalanx is fairly long. Distally, phalanx II-2, although incomplete on the right carpometacarpus, its impression indicates metacarpals II and III extended to the same level. The alular phalanx is fairly long. Distally, phalanx II-1 expands to a width equal to that of the carpometacarpus, giving the phalanx a hatchet-like shape. Phalanx II-2, although incomplete on the right side, was clearly elongate and straight, as indicated by the preserved portion. Phalanx III-1 bears a prominent, proximally positioned processus flexorius, and is slender and tapers distally, closely resembling the morphology in extant *Urocolius*.

Parts of the pelvis are exposed in ventral view, including the posterior portions of the right ischium and pubis. At the caudal portion of the synsacrum, distinct processus costales can be observed, a primitive feature for Coliiformes. As in extant mousebirds, the pelvis is mediolaterally wide. The foramen ilioischiadicum is elongate and narrow. The pubis is thin and rod-like, and does not approach or contact the ischium distally.

Although both legs are detached from the pelvis, the major hindlimb elements remain largely articu-
lated. The hindlimb is relatively slender and elongate, but few details of the femur and tibiotarsus are discernable. The tarsometatarsus approaches the length of the humerus and is similar in proportions to the slender tarsometatarsus of Coliidae, as opposed to the stouter tarsometatarsus of Sandcoleidae. The cristae hypotarsi are proximodistally short. Unfortunately, no details of the foramina vascularia proximalia or canales hypotarsi can be discerned.

On the right foot, digit III is preserved overlying the other digits. Portions of phalanx IV-2 and all of phalanges IV-3, IV-4, and IV-5 are visible, whereas digits I and II are largely obscured. On the left foot, digits I and II are well exposed. Digit III is visible, but lacks the ungual, and digit IV is complete but largely obscured by overlying elements. Thus, digital proportions can be reconstructed by combining observations from the two feet. The ungual of digit I is oriented in the same direction as the remaining unguals on the left side, corresponding to the apparently pamprodactyl configuration of the digits. However, because phalanx I-1 is not in articulation with metatarsal I, this orientation is possibly an artifact of preservation. Phalanges II-1 and II-2 are elongate and subequal in size. In contrast, the proximal three phalanges of digits III and IV are all strongly abbreviated compared with the penultimate phalanx. All pedal unguals are long and strongly curved. In the proportions of the pedal phalanges, *C. acrila* shares the derived pronounced abbreviation of the proximal three phalanges of digits III and IV with all other Coliformes. The unabbreviated phalanx II-1 in *C. acrila* agrees with the condition in crown Coliidae. In contrast to *C. acrila*, other stem Coliformes that preserve an intact foot show some degree of shortening in phalanx II-1, with the size of this element ranging from approximately one-third to one-half of the length of phalanx II-1. As mentioned above, whether the phalangeal proportions in *C. acrila* represent convergence with Coliidae, or a synapomorphy of a larger clade including *C. acrila* and Coliidae, that is reversed in *Palaeospiza bella*, remains uncertain because of homoplasy and missing data.

Carbonized material adjacent to the wing bones and pygostyle is interpreted as integumentary traces. Contrast between these areas and the matrix is greater under ultraviolet light than under natural light; however, the carbonized material does not noticeably fluoresce. No structural details of the

**Figure 6.** Reconstructions of the wing bones of Green River Formation fossil mousebirds (*Celericoliu acrila* and *Anneavis anneae*) and extant mousebirds (*Urocolius indicus* and *Colius striatus*), rescaled to equal lengths to show proportional differences.
feathers (e.g. rachi and barbs) can be detected. Preservation is best along the leading edge of what is inferred as the tenth primary, and lessens in quality towards the trailing edge, so that it is unclear whether all primaries are represented. There is no indication of secondary feather preservation adjacent to the ulna. Traces of the leading primary extend 124.6 mm from the tip of manual phalanx II-2. This corresponds to approximately 60% of overall wing length (length of wing skeleton plus projecting feathers). Inferred wing shape is elongate and tapering, contrasting markedly with the short, rounded wing of extant mousebirds (Fig. 7). A short, rounded wing shape has also been reported in several stem Coliiformes with preserved feathering traces, including Anneavis anneae (Houde & Olson, 1992) and an unnamed sandcoleid from the Eocene of Messel (WDC-C-MG 148+149, Mayr, 2000c, 2009: fig. 16.3). The holotype of Palaeospiza bella preserves traces of wing feathering, but because the wings are tightly folded in this specimen it is difficult to reconstruct the wing shape.

Traces of the tail feathering extend for 187.1 mm from the caudal tip of the pygostyle. The elongate tail is consistent with that expected given the known phylogenetic distribution of tail length in Coliiformes. An elongate tail is present in all extant Coliidae, and has also been documented in the sandcoleids Anneavis anneae and Eoglaucludium pallas, as well as in the unnamed Messel sandcoleid (WDC-C-MG 148+149) (Houde & Olson, 1992; Mayr & Peters, 1998; Mayr, 2000c).

**PHYLOGENETIC ANALYSIS**

In order to test the phylogenetic relationships of *C. acriali*, we expanded the matrix of Ksepka & Clarke (2009) by adding 11 morphological characters and two new outgroup taxa. The new morphological matrix includes 60 morphological characters relevant to mousebird relationships, scored for 30 taxa. Specimens examined, character definitions and the phylogenetic matrix are presented in Appendices 1–3.
Ingroup taxonomic sampling includes five of the six extant mousebird species (we were unable to obtain skeletal material of Colius leucocephalus for coding). We scored 13 fossil coliiform taxa, as well as two unnamed fossils that preserve informative combinations of character states. The first of these unnamed fossils, WDC-C-MG 148+149, represents a distinct but unnamed sandcoleid species from the middle Eocene Messel Formation (Mayr, 2000c). The second, MNH.Q.O.596, is an isolated tarsometatarsus from the Eocene–Oligocene Quercy fissure fills. This specimen may represent Selmes absurdipes (Mayr & Mourer-Chauviré, 2004), but comparisons with that species are limited by the state of preservation. Because a firm referral cannot be made at this time, we conservatively score MNH.Q.O.596 at the specimen level. Analyses were conducted both including and excluding three poorly known taxa represented by single-element holotypes: Eobucco brodkorbi (represented by a tarsometatarsus), Primocolius sigei (represented by a humerus), and Primocolius minor (represented by a tarsometatarsus). In previous analyses the inclusion of these taxa led to a large increase in the number of most parsimonious trees and low resolution in the strict consensus cladogram (Ksepka & Clarke, 2009). We consider referrals of a partial carpometacarpus to Primocolius sigei and partial humerus to Primocolius minor tentative, given the lack of association (Mourer-Chauviré, 1988), and did not incorporate codings from these elements. However, including codings from these referred specimens does affect the placement of Primocolius with respect to Coliidae.

Eocolius walkeri, a poorly known taxon proposed to represent a stem mousebird (Dyke & Waterhouse, 2001; Zelenkov & Dyke, 2008), was excluded from the primary analysis as this taxon lacks any synapomorphies supporting placement within Coliiformes (Ksepka & Clarke, 2009; Mayr, 2009). However, given the controversial nature of this taxon, we tested its phylogenetic position by including it in an additional analysis using the same data set and search strategy as used in the primary analysis.

Given the uncertainty regarding the closest extant relatives of Coliiformes (see above), we included multiple outgroup taxa representing proposed sister taxa for Coliiformes, including exemplars from Strigiformes (Hackett et al., 2008), Trogoniformes (Espinoza de los Monteros, 2000; Livezey & Zusi, 2006, 2007), and Psittaciformes (Mayr & Clarke, 2003; Sorenson et al., 2003), and also from Coraci, a clad recovered in some previous analyses as part of the sister clade to Coliiformes + Strigiformes (Hackett et al., 2008) or Coliiformes + Trogoniformes (Livezey & Zusi, 2006, 2007). As stem members from several of these clades retain plesiomorphic character states that are modified in crown representatives, we included two fossil outgroup taxa (the stem roller Ecoracias brachyptera and the stem parrot Pseudasturides macrocephalus).

Searches were conducted in PAUP*4.0b10 (Swofford, 2003) using the Branch and Bound algorithm, with all characters equally weighted and multistate codings used only for polymorphism. Branches with a minimum length of 0 were collapsed. Bootstrap support was calculated from 1000 replicates using a heuristic search strategy, with random taxon addition sequence and tree bisection and reconnection (TBR) branch swapping, and Bremer support was calculated manually in PAUP*4.0b10. Trees were rooted to the psittaciform Pseudasturides macrocephalus given the recovery of Psittaciformes as being more distantly related to Coliiformes than the remaining outgroup taxa in the large-scale phylogenomic analysis of Hackett et al. (2008).

RESULTS

In the analysis including all ingroup taxa, 1872 most parsimonious trees (MPTs) of 137 steps were recovered. In the strict consensus tree (Fig. 8A), C. acrila is recovered as a member of Colii, and placed in a large polytomy with other members of this clade. Although resolution within Coli is poor, monophyly of crown clad Coliidae to the exclusion of all fossil ingroup taxa is supported. Several Eocene–Oligocene taxa (Masillacolius, Oligocolius, and Primocolius) previously interpreted as part of crown group Coliidae (Zelenkov & Dyke, 2008) fall outside the crown clade.

The analysis excluding the poorly known taxa Eobucco brodkorbi, Primocolius sigei, and Primocolius minor (each known with certainty from a single bone), resulted in 20 MPTs of 137 steps. Resolution is markedly improved in the strict consensus tree (Fig. 8B). In this tree, C. acrila is placed in a polytomy with Masillacolius and the clade Palaeospiza + (Oligocolius + Coliidae). Phylogenetic relationships are congruent with those recovered by Ksepka & Clarke (2009) for the taxa common to these analyses.

Although none of the fossil taxa we included were recovered as parts of Coliidae, our results identify character states relevant to determining the stem/crown status of future fossil discoveries. Two character states are optimized as unambiguous synapomorphies of Coliidae: (8:1) indistinct processes costales of the synsacral vertebrae and (30:1) metacarpal III strongly bowed. This second feature, however, is also present in some stem mousebird taxa (i.e. Sandcoleidae), and so should not be considered diagnostic for incomplete specimens. Fourteen additional character states (state 1 of characters 2, 3, 5, 7,
Figure 8. A, strict consensus of 1872 most parsimonious trees (MPTs; tree length \( L = 137 \) steps; retention index, RI = 0.825; rescaled consistency index, RC = 0.446) from primary phylogenetic analysis. B, strict consensus of 20 MPTs (\( L = 137 \) steps; RI = 0.820; RC = 0.443) from the analysis excluding the poorly known *Eobucco brodorbi*, *Primocolius sigei*, and *Primocolius minor*. C, strict consensus of 12 168 MPTs (\( L = 138 \) steps; RI = 0.825; RC = 0.442) from phylogenetic analysis including *Eocolius walkeri* (Aves incertae sedis). Bootstrap support values are shown above the branches; Bremer support values greater than 1 are shown below the branches.
9, 20, 21, 32, 33, 34, 41, and 44, and state 0 of characters 31 and 50) may represent synapomorphies for Coliidae, but are currently ambiguously optimized because of missing data in fossil taxa and/or because of equally parsimonious solutions for homoplastic distributions. We caution that the presence of character states optimized as synapomorphies of Coliidae are not in themselves sufficient to justify placement of fossils into the crown clade: these character states merely support placement closer to Coliidae than to Oligocolius. However, retention of plesiomorphic states for these characters does provide evidence that a fossil belongs outside of the crown clade.

The definitive placement of fossils into crown Coliidae requires recognition of unambiguous synapomorphies of the Colius and Urocolius lineages. For Colius, these character states are (12:1) elongate, strongly projected processus craniolateralis of the sternum, and (5:2) large, ovoid fenestra caudalis mandibulae. Ulna shorter than humerus (character state 26:0) is optimized as an unambiguous synapomorphy of Colius in our strict consensus tree, but is also present in many stem mousebirds. For Urocolius, unambiguous synapomorphies include: (4:1) sharp ventral deflection of the rostral end of the mandible, (11:1) a projecting, blade-like apophysis furculae, (14:1) inverted T-shaped expansion of the caudal ends of the lateral trabeculae of the sternum, and (19:1) acromion narrow and sharply projecting.

The additional analysis including Eocolius walkeri resulted in 12 168 MPTs of 138 steps. In the strict consensus tree (Fig. 8C), Coliiformes are monophyletic to the exclusion of Eocolius walkeri. Relationships within Coliiformes are the same as those in the primary analysis, although relationships between the outgroup taxa are less well resolved. Excluding Eobucco brodkorbi, Primocolius sigei, and Primocolius minor results in fewer MPTs (130) and more resolution within Coliiformes, but does not affect the placement of Eocolius walkeri or outgroup taxa. Three character states are optimized as unique synapomorphies of Coliiformes: (21:0) fossa tricipitalis of humerus not pneumatized (reversed in Coliidae), (26:0) ulna shorter than humerus (reversed in several taxa), and (27:1) cotyla ventralis of ulna expanded and extending onto olecranon. A fourth character state is present only in Coliiformes and one outgroup species, the psittaciform Pseudasturides macrocephalus: (36:1) crista trochanteris of femur does not project proximal to level of femoral head. None of these character states is present in Eocolius walkeri.

Three character states were optimized as synapomorphies of Coliiformes with Eocolius as basally divergent within that clade in the only phylogenetic analysis to recover this proposed position (Zelenkov & Dyke, 2008). These characters were included in our data set, but none support an Eocolius + Coliiformes clade as optimized in our results. The single proposed unambiguous synapomorphy, (27:1) ulna with very large cotyla ventralis, is actually absent in Eocolius (Ksepka & Clarke, 2009; see fig. 5 of Dyke & Waterhouse, 2001). Of the two character states proposed as ambiguous synapomorphies, (23:0) curved shaft of humerus is also present in the exemplars of Strigiformes that we examined (Zelenkov & Dyke, 2008, coded the humerus as ‘straight’ in a composite Strigiformes terminal, although they did not list the species examined). The second, (30:1) metacarpal III bowed, cannot in our opinion be coded in Eocolius, as this part of the carpometacarpus is almost completely lacking in the holotype. Indeed, Zelenkov & Dyke (2008: 1418) noted that ‘the shape of the bone is extrapolated’. Regardless of coding decisions, both curvature of the humerus and bowing of the third metacarpal are widely distributed in Aves. We recover no phylogenetic support for placing Eocolius walkeri in Coliiformes, and conclude that further material is necessary to resolve the relationships of this taxon within Aves.

DISCUSSION

The FBM deposits have yielded the most diverse and well-preserved Eocene avifauna from North America. Further insights into the taxonomic and ecological characteristics of this fauna are still actively emerging. Two representatives of Coliiformes, C. acriala and the sandcoleid Anneavis annaeae, are now known to occur within the FBM. These two species differ dramatically in wing shape, increasing the observed ecological and species-level diversity both within the FBM avifauna and within the clade Coliiformes.

The elongate wing shape in C. acriala is unexpected given the morphology of living mousebirds and our previous knowledge of fossil representatives of this clade. Support for this unique wing shape comes from two lines of evidence. First, the proportions of the major wing bones in C. acriala indicate a higher ulna : humerus ratio than any living mousebird (Fig. 6). Second, the preserved outline of the wing integument indicates a much more elongate and tapering wing than reported in any other member of Coliiformes (Fig. 7). Together, these morphologies imply a unique flight style not previously described for any extinct or extant mousebird. Although the wing bone proportions are notable, it is predominantly the length of the primary feathers that contribute to the long, pointed shape of the wing (Fig. 7). In this regard, C. acriala resembles the oscine Hirundinidae (swallows), in which the primary feathers account for approximately 60% of the wing length (Kaiser, 2007).

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Long, pointed wings result in higher aspect ratios and lower loading (Saville, 1957; Rayner, 1988). This wing shape is associated with agile open-air flight and is typical of small, aerial insectivores, such as tyrannid flycatchers and swallows. By contrast, the short, rounded wing shape seen in extant Coliidae is optimized for fast, short bursts of energetically expensive flight (Saville, 1957; Rayner, 1988). This wing morphology is advantageous for maneuvering between trees in closed forested environments over short distances, but is poorly suited for longer periods of sustained flight (Kaiser, 2007). Living mousebirds show relatively poor capacity for sustained flight, and are among the most sedentary of living birds (de Juana, 2001). Previously available feather traces indicate that Sandcoleidae, part of the basal divergence within Coliiformes, possessed a wing similar in aspect to extant Coliidae (Houde & Olson, 1992; Mayr, 2000c). Thus, a short, rounded feathered wing can be inferred through phylogenetic bracketing and proportions of the wing bones as present across most of stem Coli. Intriguingly, one other stem representative of Coli, Oligocolius brevitarsus, possesses elongate distal wing bones, also consistent with a relatively long wing (Mayr, 2000c). Although feather preservation is lacking for that taxon, precluding the determination of wing shape, it should be considered that wing elongation, and associated ecological correlates, may be discovered to be a trend in multiple stem mousebird lineages.

Carbonized traces of the rectrices indicate that the tail of C. acirala was greatly elongated, approaching two-thirds of the bird’s total length based on the preserved length of the rectrices. The distal tip of the tail is poorly preserved, so whether this region was square, graduated, forked, or ornamented in some fashion remains unknown. An elongate tail is present in all extant mousebirds and has been documented in multiple fossil taxa (Anneavis, Eoglaucidium, and the unnamed sandcoleid WDC-C-MG 148+149). At present, no fossil coliform preserves evidence of a short tail, although feather traces are unpreserved for many species. Given this distribution, an elongate tail is currently optimized as ancestral for Coliiformes, and is retained throughout the clade.

Extant mousebirds possess distinctly stiffened and graduated tails. Tail shape differs only slightly between the extant taxa Urocolius and Colius. Colius possesses a comparatively broad tail compared to Urocolius, although the overall shape is still narrow relative to other birds. Tail function has been little commented on in extant mousebirds, and the possible functions of the elongate tails of extinct mousebirds have likewise received little speculation. Modifications of the tail serve many functions in birds, including lift generation, improving maneuverability, and enhancing intraspecific display (Fitzpatrick, 1999). Enhancing aerodynamic properties, balance, or display visibility are all plausible, and not necessarily mutually exclusive, functional explanations for the elongation of the tail in Coliiformes.

An aerodynamic function seems the least likely. Although enlarging the tail can increase airfoil size, elongation beyond the total width of the tail increases drag without further increasing lift (Evans & Thomas, 1992; Balmford, Thomas & Jones, 1993). Whereas the elongate tail streamers of some Hirundinidae enhance maneuverability (Norberg, 1994), these streamers are formed only by the outermost pair of rectrices. Although the shape of the distal tip of the tail in C. acirala is uncertain, a relatively broad shape is indicated for most of the tail area, and there is no evidence for ‘streamers’. The tail of the sandcoleid Eoglaucidium is likewise relatively broad (Mayr & Peters, 1998).

A non-aerodynamic locomotor function could involve the use of the tail in propping the bird upright against vertical inclines, such as tree trunks during climbing, a behaviour exhibited by Picidae (woodpeckers). In Picidae, the inner rectrices are stiffened to provide support during this propping behaviour. Unfortunately, fine details of the individual rectrices remain unavailable for most fossil representatives of Coliiformes, although rectrices of Anneavis and Eoglaucidium preserve a broad proximal shaft (Houde & Olson, 1992; Mayr & Peters, 1998). Although the rectrices are stiffened in Coliidae (Rowan, 1967), this propping behaviour does not appear to occur regularly in extant mousebirds. Nonetheless, a propping function was proposed for the tail in at least one previously described fossil mousebird. Zelenkov & Dyke (2008) advocated scannerial abilities for Chascacocolius oscitans (stem Coli) in part based on two putative features of the pelvis that are present in climbing woodpeckers, but are unknown in other Coliiformes. These features, a short ala preacetabularis ili and well-developed processus terminalis ili (origin of m. flexor cruris lateralis and m. iliobibularis), were illustrated in a reconstruction of the incomplete pelvis of the holotype (and only known) specimen of Chascacocolius oscitans (Houde & Olson, 1992: fig. 11). However, re-examination of the holotype, upon which this reconstruction was based, revealed that neither the cranial margin of the ala preacetabularis ili nor the processus terminalis ili are preserved (see Houde & Olson, 1992: plate II.1), so the proportions of the ilia and the shape of the processus terminalis ili remain unknown. We find no evidence that the pelvis of Chascacocolius or any other mousebird was substantially modified for vertical climbing, casting doubt on a proposed propping function of the rectrices.

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A third possibility is that the tail served as a display structure. This hypothesis may best explain why the elongate tail is present in stem and extant coliiform taxa showing morphologies consistent with markedly different flight styles and feeding strategies. Extant mousebirds are highly social birds, but have relatively simple sexual display behaviours, consisting primarily of repeated ‘bouncing’ from a fixed perch (Rowan, 1967; de Juana, 2001). However, no described display behaviours for Coliidae actively utilize the tail, and tail length is not noticeably sexually dimorphic, with the exception of slight differences in Urococilius macrourus (de Juana, 2001).

Further study of extant mousebird behaviour and life history is necessary to advance the investigation of possible tail functions in fossil species. Aerodynamic and propping functions seem unlikely given the present data. However, balance-related or species recognition functions remain plausible.

When the acquisition of key morphological features are optimized on the coliiform cladogram, specializations of the feet and tail are shown to evolve early in the clade’s history, and specializations of the wing and beak are shown to evolve later. Specializations of the foot correlated with the ability to rotate at least digit IV into a facultatively zygodactyl position are optimized as present at the base of Coliiformes. However, because the higher level relationships of Coliiformes are not yet firmly established, it remains ambiguous whether many specializations of the foot (e.g. plantarily-projecting wing-like flange on trochlea metatarsi II and IV and shortened pedal phalanges) might be synapomorphies of Coliiformes or of a larger clade. For example, if Coliiformes and Strigiformes are sister taxa, as recovered by Hackett et al. (2008), the aforementioned specializations of the foot are most parsimoniously interpreted as synapomorphies of a Coliiformes + Strigiformes clade.

Presence of an elongated tail is optimized as an unambiguous synapomorphy of Coliiformes, regardless of the higher level relationships of the clade. The elongate tail is indeed one of the most distinctive features of both living and fossil mousebirds. Yet, as discussed above, we currently have little understanding of its function. Finer preservation yielding insight into properties such as feather stiffness, shape of the distal tip of the tail, or coloration pattern in basal mousebirds could potentially improve our understanding of why the distinct coliiform tail evolved initially, and why it has been conserved across coliiform phylogeny, and over > 55 Ma of the known temporal range of the clade.

Specializations of the wing departing from the short, rounded morphology reconstructed as ancestral for Coliiformes occurred later in the phylogenetic history of the clade. Celericolius acriala provides the most striking example of wing specialization, and at least some degree of elongation is implied by wing bone proportions in Oligocolius brevitarsus (Mayr, 2000a). Extant Coliidae are inferred to have inherited the short, rounded wing shape seen in other stem mousebirds preserving feather traces from their common ancestor. The specialized short, heavy beak present in extant Coliidae appears to be one of the latest features to arise in the phylogenetic history of the clade. Sandcoleiidae and Selmes have significantly longer, more generalized beaks (Houde & Olson, 1992; Mayr, 2001), and Chascacocolius exhibits an elongate beak specialized for gaping (Houde & Olson, 1992; Mayr, 2005a). Unfortunately, most fossil representatives of Colii do not preserve the complete skull, and so it remains uncertain whether the shortened beak of Coliidae arose within some part of stem Colii or only characterizes the crown clade.

CONCLUSIONS

Celericolius acriala adds to the extensive species diversity and morphological disparity recognized within stem Coliiformes. We tentatively propose an aerial foraging strategy for C. acriala from the similarities in wing shape to extant small, insectivorous birds. Future recovery of a specimen with an intact beak could help refine our understanding of feeding ecology in this species. More diverse feeding specializations may explain the co-occurrence of multiple stem coliiform taxa at many Paleogene localities. Chascacocolius, with its highly modified beak adapted for breaking open fruit, prying under bark, or ground probing (Houde & Olson, 1992; Mayr, 2005a), provides another example of diverse foraging habits in stem mousebirds. Both Celericolius and Chascacocolius co-occur with taxa interpreted as more general feeders at their respective localities.

We have demonstrated the co-occurrence of two coliiform species in a restricted area (Fossil Lake) and horizon (FBM) within the Green River Formation, but even greater mousebird diversity is known from other deposits. A cladogram of Coliiformes calibrated to the fossil record is presented in Figure 9, and the global distribution of fossil mousebird localities is illustrated in Figure 1. In North America, at least three species (Sandcoleus copiosus, Anneavis annaeae, and Chascacocolius oscitans) occur in the early Eocene Willwood Formation of the Bighorn Basin (Houde & Olson, 1992), and three species (Eobucco brodkorbi, Uintornis marionae, and Uintornis lucaris) occur in the middle Eocene Bridger Formation (Feduccia & Martin, 1976; Houde & Olson, 1992). In Europe, six species (Eoglaucidium pallas, Selmes absurdistes, Masillacolius brevidactylus, Chascacocolius cacicostris, an unnamed species of Eoglaucidium (SMF-ME...
1233), and an unnamed sandcoleid (WDC-C-MG 148-149) occur in the middle Eocene Messel Formation (Mayr & Peters, 1998; Peters, 1999; Mayr, 2005a, b). The Messel Coliiformes demonstrate that mousebird diversity at a single local environment (Lake Messel) was at least equal to the current worldwide species diversity. Standing global diversity is, of course, uncertain for any time interval, given the nature of sampling in the fossil record. Nonetheless, it is most likely that global diversity was several times higher than today throughout the Eocene, especially considering the scarcity of Eocene terrestrial localities suitable for preserving small birds over vast geographic regions.

Passeriformes, which include insectivorous radiations such as Tyrannidae and Hirundinidae, are thus far absent from the Eocene of North America. Aerial insectivores of the clade Apodiformes are relatively common components of the Eocene London Clay and Messel avifaunas (e.g. Harrison, 1984; Mayr & Peters, 1999; Mayr, 2005c). However, no fossils assignable to this clade have yet been identified in our review of over 100 FBM specimens curated in museum collections. A privately owned fossil from the Tipton Member at Lake Gosiute (approximately equivalent in age to the FBM of Fossil Lake; Smith et al., 2008) is the only reported record of Apodiformes from the Green River Formation (see Grande, 1984; Feduccia, 1999), but this specimen remains undescribed precluding more detailed comparisons. One stem representative of Coraciiformes (roller) from the Green River Formation possesses modifications of the
rostrum and gape consistent with aerial insect capture (Clarke et al., 2009), although the wing proportions of this much larger taxon are consistent with a flight style distinct from that inferred for *C. acriala*.

Competitive exclusion by Passeriformes has been hypothesized as a major factor in the retreat of arboreal clades such as Coliiformes, Coraci, and Upupiformes from niches now occupied by Passeriformes (Harrison, 1979; Mayr, 2005c, 2009). The arrival of Passeriformes in North America is as yet poorly temporally constrained, as are the disappearances of groups such as Coliiformes and Coraci from the continent. Further revision of the Green River avifauna in concert with data from younger deposits will contribute significantly to investigating these hypotheses.

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APPENDIX 1

COMPARATIVE MATERIALS

In cases where specimens were scored from the literature, citations are provided. Aniaves anaeae USNM 433918–433970, USNM 424077; Atelornis pittoideus FMNH 438663; Cacatua galerita AMNH 9393; Chas-cococcu sp. SMF-Me 3759; Colius castanotus SMF 855, SMF 8027; Colius colius AMNH 23334; Colius striatus AMNH 4756, AMNH 4496, AMNH 8954; Coracias garrulus AMNH 2141, AMNH 12839; Eocelius walkeri Dyke & Waterhouse, 2001; Ecoceracias brachytus HMLD-Me 10474, SMF-Me 1452, SMNK 2663; Eolglauicidum pallas SMF-Me 8, SMF-Me 1456, SMNK 553; Harpactes erythrocephalus AMNH 25537, AMNH 25539; Masillacolius brevicaudatus SMNK-Me 313, Mayr and Peters 1998; Oligocolus brevitorus Mayr 2000a; Palaeospiza bella MCZ 342222; Primo-colus minior Mourer-Chauviré 1988; Primocolius siegi Mourer-Chauviré 1988; Pseudasturidium macrocephalus USNM 424075 (cast); Psittacula krameri AMNH 12988, AMNH 12989; Sandcoleidae indet. WDC-C-MG 148+149; Sandcoleus copiosus USNM 433912, USNM 433913, USNM 433973–434025; Selmes absurdiipes WDC-C-MG 147, Peters 1999, Mayr 2001; cf. Selmès (MNH Q.O.596) Mayr & Mourer-Chauviré 2004; Strix vari a NCSM 9492, 19159; Trogon melanurus AMNH 8071; Tyto alba 16797, 16888, 16889; Urocolius indicus AMNH 2679, AMNH 25711, USNM 490236, USNM 558549; Urocolius macrourus AMNH 24231, USNM 491889, USNM 556955.

APPENDIX 2

CHARACTER DESCRIPTIONS

1. Nasal septum: absent (0); present (1).

2. Bill length: approximately one-half of total skull length (0); abbreviated, less than one-third of total skull length (1).

3. Quadrate, condyles lateralis, dorsally projecting process: absent (0); present (1).

4. Mandible, shape: straight or smoothly downturned (0); distinct, angular ventral deflection near midpoint (1).

5. Mandible, fenestra mandibulae caudalis: absent (0); present and minute (1); present and large (2). Ordered.

6. Mandible, processus retroarticularis blade-like and elongated to approximately one-sixth skull length: absent (0); present (1).

7. Thoracic vertebrae, processus ventralis: absent or short (0); greatly elongated (1).

8. Synsacrum, processus costales: well-developed, clearly separate from processus transversus, and contacting ilia (0); indistinct (1).
9. Pygostyle bears processus transversus from one incorporated caudal vertebra: absent (0); present (1).
10. Pygostyle, discus pygostyli greatly enlarged: no (0); yes (1).
11. Furcula, apophysis: absent or limited to a small tubercle (0); elongate and blade-like (1).
12. Sternum, processus craniolateralis: weak or moderate cranial projection (0); elongate with prominent cranial projection (1).
13. Sternum, trabecula intermedia arises from trabecula lateralis: no (0); yes (1).
14. Sternum, trabecula lateralis: maintains width distally or end in moderate expansion (0); wide terminal expansion, with inverted T-shaped appearance (1).
15. Coracoid, foramen nervi supracoracoidei: present (0); absent (1).
16. Coracoid, processus procoracoideus: absent or extremely reduced (0); present, well-developed (1).
17. Coracoid, processus lateralis: poorly developed (0); well-projected (1).
18. Scapula: shorter than humerus (0); longer than humerus (1).
19. Scapula, acromion narrow and sharply projecting: absent (0); present (1).
20. Humerus, circular tubercle located slightly distal to fossa tricipitalis: absent (0); present (1).
21. Humerus, foramen pneumaticum: absent (0); present (1).
22. Humerus, crista deltopectoralis short, rounded, and extending approximately one-quarter of humerus length: no (0); yes (1).
23. Humerus, shaft: curved (0); straight (1).
24. Humerus, processus flexorius: slight projection (0); projects markedly distal to condylus dorsalis and condylus ventralis (1).
25. Humerus, crescent-shaped depression proximal to condylus dorsalis: absent (0); present (1).
26. Humerus: longer or equal to ulna in length (0); shorter than ulna (1).
27. Ulna, cotyla ventralis: unexpanded (0); greatly expanded and extending onto olecranon (1).
28. Carpometacarpus, processus intermetacarpalis: absent or vestigial (0); small process (1); well-developed, contacting or nearly contacting metacarpal III (2). Ordered.
29. Carpometacarpus, relative length of metacarpals II and III: subequal in length (0); metacarpal III projects significantly distal to metacarpal II (1).
30. Carpometacarpus, metacarpal III: straight (0); bowed (1).
31. Carpometacarpus, ventrally projecting flange at proximal end of metacarpal III: absent (0); present (1). This feature was noted as present in Selmes absurdipes by Peters (1999) but absent in the specimen described by Mayr (2001). As we were unable to examine all relevant specimens at first hand we coded this character ‘?‘ for Selmes absurdipes, pending further evaluation.
32. Carpometacarpus, sulcus tendineus: present, distinct (0); barely perceptible or absent (1).
33. Ilium, distinct crista dorsolateralis ilii: present (0); absent, dorsolateral corner of ilium forms a smooth curve instead of a crest (1).
34. Caudal contact between ischium and pubis: caudal tip of ischium shares craniocaudally short contact with pubis (0); craniocaudally elongate contact between ischium and pubis (1); ischium and pubis share craniocaudally elongate contact immediately caudal to foramen obturatum, and additional short contact between caudal tip of ischium and pubis (2).
35. Foramen obturatum: open caudally (0); fully enclosed (1).
36. Femur, crista trochanteris: projects proximal to level of femoral head (0); does not project proximal to level of femoral head (1).
37. Femur, tuberculum musculi gastrocnemialis lateralis: subtle (0); pronounced (1).
38. Tibiotarsus, distinct sharp crest on proximal portion of shaft, opposite crista fibularis: absent (0); present (1).
39. Tibiotarsus crista cnemialis cranialis protruding farther proximally than crista cnemialis lateralis, with the two crests forming a continuous ridge circumscribing a groove on the cranial side of the bone: absent (0); present (1).
40. Tarsometatarsus: not elongated (0); elongated, humerus : tarsometatarsus length ratio less than 1.4 (1).
41. Tarsometatarsus, arcus extensorius: unossified (0); ossified (1).
42. Tarsometatarsus, crista medianoplantaris: absent (0); present (1).
43. Tarsometatarsus: stout with shaft becoming wider towards wide proximal end (0); shaft narrow and of equal width for most of length, slight proximal widening (1).
44. Tarsometatarsus: foramina vascularia proximale medialis and lateralis present (0); only a single foramen vasculare proximale present (1).
45. Tarsometatarsus, hypotarsus, very large canal for tendon of m. flexor digitorum longus: absent (0); present (1).
46. Tarsometatarsus, hypotarsus, tendon of m. flexor hallucis longus enclosed in bony canal, or nearly closed, deep sulcus: no (0); yes (1).
47. Tarsometatarsus, fossa metatarsi I very large, concave, situated at medial side of tarsometatarsus: no (0); yes (1).
48. Tarsometatarsus, canalis interosseus distalis: absent (0); present (1).
49. Tarsometatarsus, trochlea metatarsi II and IV small, not widely splayed from trochlea metatarsi III and reaching far distally: no (0); yes (1).
50. Tarsometatarsus, distinct plantarly-projecting wing-like flange on trochlea metatarsi II: absent (0); present (1).
51. Tarsometatarsus, distinct plantarly-projecting wing-like flange on trochlea metatarsi II: absent (0); present (1).
52. 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). The morphology of trochlea metatarsi III, treated as a single character by Ksepka & Clarke (2009), has been split into two characters here (51 and 52).
53. Tarsometatarsus, trochlea metatarsi IV: unmodified (0); with plantarly-projecting wing-like flange on medial edge (1); with fully developed trochlea accessoria (2). Ordered.

54. 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 of the length of phalanx II-2 (2). Ordered.
55. Proximal three phalanges of pedal digit IV: not abbreviated (0); greatly abbreviated (1).
56. Pedal unguals, sulcus neurovascularis: absent (0); present (1).
57. Beak of hatchling, bulbous swellings at base: absent (0); present (1). In *Urocolius*, newly hatched chicks possess an unusual prominent swelling at the corner of their mouths, which is lost by adulthood (de Juana, 2001).
58. Rectrices, number: ten (0); twelve (1). The number of rectrices in *Colius colius* and *Colius striatus* vary between ten and twelve according to Rowan (1967).
59. Tail length: short to moderate length (0); elongate, accounting for one-half or more of the total body length (1).
60. Eggshell: unpatterned (0); patterned (1). Codings for Coliidae follow de Juana (2001), and those for outgroup follow Walters (1994).

### APPENDIX 3

**Character Matrix (A = 0/1)**

| TAXON                        | 10 | 20 | 30 |
|------------------------------|----|----|----|
| *Anneavis anneae*            | ?? | 0  | ?  |
| *Celericoliulus acriala*     | ?? | 0  | ?  |
| *Chascacoolius cacicoorstris*| 1  | 0  | ?  |
| *Chascacoolius oscitans*     | ?? | 0  | ?  |
| *Colius castanotus*          | 1  | 1  | ?  |
| *Colius colius*              | 1  | 1  | ?  |
| *Colius striatus*            | 1  | 1  | ?  |
| *Eoebuoc brodkorbi*          | ?? | 0  | ?  |
| *Eoglaucidium pallas*        | ?? | 0  | ?  |
| *Masillacoolius brevidactylus*| ?? | 0  | ?  |
| *Oligocolius brevitarsus*    | ?? | 0  | ?  |
| *Palaeospiza bella*          | ?? | 0  | ?  |
| *Primocolius sigei*          | ?? | 0  | ?  |
| *Primocolius minor*          | ?? | 0  | ?  |
| *Sandrocoleidae indet.*      | ?? | 0  | ?  |
| *Sandcoles busbous*          | ?? | 0  | ?  |
| *Selmes absurdistes*         | ?? | 0  | ?  |
| *cf. Selmes MNH QO.596*      | ?? | 0  | ?  |
| *Urocolius indicus*          | 1  | 1  | ?  |
| *Urocolius macrourus*        | 1  | 1  | ?  |
| *Eocoolus walkeri*           | ?? | 0  | ?  |
| *Atelornis pittioides*       | 1  | 0  | ?  |
| *Cacatua galera*             | 1  | 1  | ?  |
| *Coracias garrulus*          | 1  | 0  | ?  |

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| TAXON                  | 10 | 20 | 30 |
|-----------------------|----|----|----|
| Eocoracias brachyptera| ? 0 | ? 0 | ? 0 |
| Harpactes erythrocephalus| 1 0 | 0 0 | 1 0 |
| Psittacula krameri     | 1 0 | 0 0 | 1 0 |
| Pseudasturides macrocephalus| 0 0 | 1 0 | 0 1 |
| Strix varia            | 1 0 | 0 0 | 1 0 |
| Tragop Melanieurus     | 1 0 | 0 0 | 1 0 |
| Tyto alba              | 1 0 | 0 0 | 1 0 |
| Anneavis anneae        | 1 0 | ? ? | ? 1 |
| Celericolius acralia   | ? ? | ? ? | ? 1 |
| Chascacolius caccirostris| ? ? | ? ? | ? 1 |
| Chascacolius oscitans  | 1 0 | 0 0 | 1 0 |
| Colius castanotus      | 0 1 | 1 1 | 1 0 |
| Colius colius          | 0 1 | 1 1 | 1 0 |
| Colius striatus        | 0 1 | 1 1 | 1 0 |
| Eobucco brodorbi       | ? ? | ? ? | ? 1 |
| Eoglaucidium pallas    | ? 0 | 0 0 | 1 1 |
| Masillacolius brevicae | 1 0 | 0 0 | 1 0 |
| Oligocolius brevitarus | ? ? | ? 1 | 0 0 |
| Palaeospiza bella      | ? 0 | ? 0 | ? 1 |
| Primocolius siger      | ? ? | ? ? | ? 1 |
| Primocolius minor      | ? ? | ? ? | ? 1 |
| Sandcoleidae indet.    | 1 0 | 0 0 | 1 1 |
| Sandcoleus copiosis    | 1 0 | 0 0 | 1 1 |
| Selmes absurdes        | ? ? | ? ? | ? 1 |
| cf. Selmes MNH Q.O.596 | ? ? | ? ? | ? 1 |
| Urocolius indicus      | 0 1 | 1 1 | 1 1 |
| Urocolius macrorurus   | 0 1 | 1 1 | 1 1 |
| Eoculus walkeri        | 0 1 | 1 1 | 1 1 |
| Atelornis pittaoides   | 1 0 | 0 1 | 0 1 |
| Cacatua galerita       | 0 0 | 0 0 | 1 0 |
| Coracias garrulus     | 1 0 | 0 1 | 1 0 |
| Eocoracias brachyptera| 1 0 | ? ? | ? 1 |
| Harpactes erythrocephalus| 0 0 | 1 0 | 1 0 |
| Psittacula krameri     | 0 0 | 1 0 | 1 0 |
| Pseudasturides macrocephalus| ? ? | ? 1 | 0 1 |
| Strix varia            | 0 0 | 2 0 | 0 0 |
| Tragop Melanieurus     | 0 0 | 1 0 | 1 0 |
| Tyto alba              | 0 0 | 2 0 | 0 0 |

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