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A new specimen of the Early Eocene *Masillacolius brevidactylus* and its implications for the evolution of feeding specializations in mousebirds (Coliiformes)

Un nouveau spécimen de Masillacolius brevidactylus *de l'Éocène inférieur et ses implications dans l'évolution de spécialisations alimentaires chez les colious (Coliiformes)*

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ABSTRACT

A new skeleton of the Early Eocene stem group mousebird *Masillacolius brevidactylus* is described, which for the first time provides information on the skull morphology of this unusual coliiform species. Notably, the mandible exhibits long, blade-like retroarticular processes, which were previously only known from two distantly related taxa of stem group Coliiformes. An assessment of the evolutionary significance of these structures depends on the phylogenetic interrelationships of stem group Coliiformes, which remain poorly resolved. Proceeding from recent phylogenies, the new fossil strengthens the supposition that these processes are plesiomorphic for a coliiform subclade, which also includes the extant species, and that they were secondarily reduced in crown group Coliiformes. In this case, the stem species of the clade including extant mousebirds would have exhibited feeding specializations that were lost in the evolutionary lineage leading to the extant species. Alternatively, these processes may constitute an apomorphy of a clade including *Masillacolius* and the Early Eocene North American *Chascacocolius*. In the new *Masillacolius* fossil a large seed is preserved, which was most likely ingested by the bird. It therefore adds another specimen to the list of coliiform fossils with seeds as stomach or gut contents and documents a long evolutionary history of frugivory in coliiform birds. This contradicts a recent proposal that birds did not play an important role as seed dispersers in the early Cenozoic.

Mots clés :
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RÉSUMÉ

Un nouveau squelette du groupe souche des colious de *Masillacolius brevidactylus* de l'Éocène inférieur est ici décrit et fournit pour la première fois des informations sur la morphologie du crâne de cette espèce de coliiforme peu commune. En particulier, la mandibule présente des processus rétro-articulaires longs, en forme de lames, qui n'étaient jusqu'alors connus que chez des taxa assez éloignés du groupe souche des Coliiformes. Une estimation

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de la signification évolutive de ces structures dépend des interrelations phylogénétiques du groupe souche de Coliiformes, encore peu établies. À partir des récentes phylogénies, le nouveau fossile augmente la supposition selon laquelle ces processus seraient plésiomorphes pour un sous-clade de coliiformes, incluant aussi l'espèce vivante, et qu'ils seraient secondairement réduits dans le groupe couronne des Coliiformes. Dans ce cas, l'espèce souche du clade incluant les colious aurait présenté des spécialisations alimentaires qui auraient été perdues dans la lignée évolutive conduisant aux espèces existantes. Alternativement, ces processus peuvent constituer une apomorphie d'un clade incluant *Masillacolius* et le *Chascacocolius* nord-américain de l'Éocène inférieur. Dans le nouveau fossile *Masillacolius*, une grande graine a été conservée ; elle a été vraisemblablement ingérée par l'oiseau. Ainsi, un autre spécimen vient s'ajouter à la liste de Coliiformes fossiles dont l'estomac et l'intestin contiennent des graines et témoigne d'une longue histoire évolutive d'alimentation frugivore chez les Coliiformes. Ceci entre en contradiction avec une nouvelle proposition selon laquelle les oiseaux ne jouaient pas un rôle important dans la dispersion des graines au Cénozoïque inférieur.

1. Introduction

The extant diversity of mousebirds (Coliiformes) is restricted to six very similar species, which occur in Africa south of the Sahara. In the Early Cenozoic, however, these birds were more widely distributed and much more diversified (Mayr, 2009). At least six coliiform species coexisted in the Early Eocene (Lenz et al., 2015) lacustrine paleoenvironment of the Messel fossil site in Germany alone, which belong to a minimum of four genus-level taxa (*Eoglaucidium*, *Chascacocolius*, *Selmes*, *Masillacolius*; Mayr, 2000, 2005; Mayr and Peters, 1998). Coliiform birds are also known from other Early Eocene localities in Europe, as well as from Late Eocene (*Primocolius*) and Oligocene (*Oligocolius*) strata (Mayr, 2009), and they persisted in Europe until the Late Miocene (Mayr, 2011; Mlíkovský, 2002). Mousebirds furthermore occurred in the Early Cenozoic in North America, from where several distinctive taxa were reported (e.g., *Sandcoleus*, *Anneavis*, *Chascacocolius*, *Celericolius*), with the latest New World occurrence of these birds being the Late Eocene *Palaeospiza* (Ksepka and Clarke, 2009, 2010; Mayr, 2009).

It is straightforward to distinguish two principal morphotypes amongst Eocene Coliiformes. One of these is represented by the Sandcoleidae (*Sandcoleus*, *Anneavis*, *Eoglaucidium*), which distinctly differ from other stem group Coliiformes in various skeletal features (Houde and Olson, 1992; Mayr, 2009). All non-sandcoleid stem group Coliiformes belong to a clade that also includes the crown group representatives (Ksepka and Clarke, 2010; Mayr, 2009, 2013; Mayr and Mourer-Chauviré, 2004). These birds are characterized by an elongated and slender tarsometatarsus and a large, shield-like discus pygostyli. The latter feature serves for the attachment of the long rectrices, which at least in extant mousebirds have a propping function and support the trunk of the bird while it is feeding or scrambling through bushes and trees (De Juana, 2001: 63). Amongst these fairly modern-type Coliiformes, a subclade of taxa can be recognized, which are more closely related to the crown group and exhibit a well-developed processus intermetacarpalis on the carpometacarpus (*Primocolius*, *Palaeospiza*, *Oligocolius*), with this process being absent or poorly developed in the Early Eocene *Masillacolius*, *Chascacocolius*, *Selmes*, and *Celericolius*.

The interrelationships of the early representatives of these more crown group-like stem Coliiformes are not well understood, which is also due to the fact that all are only known from a few fossils, so that critical osteological details are unknown. *Masillacolius brevidactylus* from the Early Eocene of Messel, for example, was up to now represented by only two skeletons, both of which lack the skull (Mayr and Peters, 1998). This species is well characterized by unusually long legs and presumably fully pamprodactyl feet, in which all toes directed forward. Here, I describe the first *Masillacolius* specimen with an at least partially preserved skull, which allows the recognition of previously unknown features.

2. Material and methods

The fossil specimens are deposited in the collections of Senckenberg Research Institute Frankfurt, Germany (SMF), Hessisches Landesmuseum Darmstadt, Germany (HLMD), and Generaldirektion Kulturelles Erbe Rheinland-Pfalz, Direktion Landesarchäologie, Referat Erdgeschichte, Mainz, Germany (PW). Osteological terminology follows Baumel and Witmer (1993).

A phylogenetic analysis was performed based on the character matrix of Mayr (2013), with the same settings as in this latter study. The following six character scorings were added or modified: character 2 (bill approximately one-half of total skull length): scored as present (0) for *M. brevidactylus*; character 4 (eminentia articularis of quadrate): scored as absent (0) for *M. brevidactylus* and *Sandcoleus copiosus*; character 5 (mandible with processus retroarticularis blade-like and elongated to approximately one-sixth of the skull length): scored as present (1) for *M. brevidactylus*; character 26 (configuration of foramina vascularia proximalia): scored as (0) for *M. brevidactylus* (two foramina present) and as (2) for *Selmes absurdipes* (single foramen on lateral side of shaft).