C. R. Palevol 14 (2015) 363–370

Contents lists available at ScienceDirect

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General Palaeontology, Systematics and Evolution (Vertebrate Palaeontology)

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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ARTICLE INFO

Article history:
Received 7 April 2015
Accepted after revision 20 May 2015
Available online 8 July 2015

Handled by Shuai Xiao

Keywords:
Aves
Evolution
Frugivory
Messel
Phylogeny

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 :
Aves
Évolution
Frugivore (alimentation)
Messel
Phylogénie

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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http://dx.doi.org/10.1016/j.crpv.2015.05.007
1631-0683/

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).

3. Systematic paleontology

COLIIFORMES Murie, 1872
COLIIDAE Swainson, 1837
Masillacolius Mayr and Peters, 1998
Masillacolius brevidactylus Mayr and Peters, 1998

Referred specimen. SMF-ME 11322 (skeleton lacking the upper beak, the right hand, and the left tarsometatarsus; Fig. 1).

Locality and horizon. Messel near Darmstadt, Germany; Early Eocene (Lenz et al., 2015).

Measurements (left/right, in mm). Skull, estimated length, ~39; humerus, 20.4/20.3; ulna, ~20.4/–; carpometacarpus, ~12.9/–; femur, 22.4/22.8; tibiotarsus, 30.2/29.1; tarsometatarsus, –/19.8.

Description and comparison. In the following, only features that were not already previously described are mentioned (Mayr and Peters, 1998). The upper beak is not completely preserved, and the tips of lower jaws are likewise broken. However, the proximal portion of the right ramus mandibulae is well visible and allows the recognition of a long, blade-like processus retroarticularis (Fig. 2A, B). The ramus mandibulae is of moderate dorsoventral depth, and unlike in crown group Coliiformes, a fenestra mandibulae is absent.

The caudal portion of the processus mandibularis of the quadrate (Fig. 2B) forms a marked shelf-like lip as in extant mousebirds. Unlike in living mousebirds and *Oligocolius* (Mayr, 2013), however, an eminentia articularis is absent and further unlike in extant Coliiformes, the processus lateralis does not form a marked, dorsally directed process.

There are 18 praesacral vertebrae as in extant mousebirds (most other neornithine birds have 19 or more praesacral vertebrae). The cervical vertebrae correspond well with those of extant Coliiformes (Fig. 2C, D). As in the latter, only the third cervical vertebra departs in its shape from that of the caudally following ones, which have much deeper lacunae interzygapophysiales. In most other extant birds, both the third and fourth cervical vertebrae are characterized by the absence of well-defined lacunae interzygapophysiales and have a more rectangular outline than the following cervical vertebrae. Whether the fourth to eighth vertebrae exhibit a bony strut connecting the processus transversus with the corpus vertebrae, as in extant mousebirds, cannot be discerned in the fossil.

The extremitas omalis of the coracoid has a similar shape to that of *Chascacocolius* and the facies articularis clavicularis overhangs the sulcus supracoracoideus (Fig. 3B). A foramen nervi supracoracoidei is absent (this foramen is present in the Sandcoleidae). The facies articularis scapularis merges into the facies articularis humeralis. Being short but wide, the acromion of the scapula has a squarish shape and the scapular corpus is straight and narrow (Fig. 3B). Unlike in crown group Coliiformes, the extremitas omalis of the furcula does not form a well-developed processus acromialis.

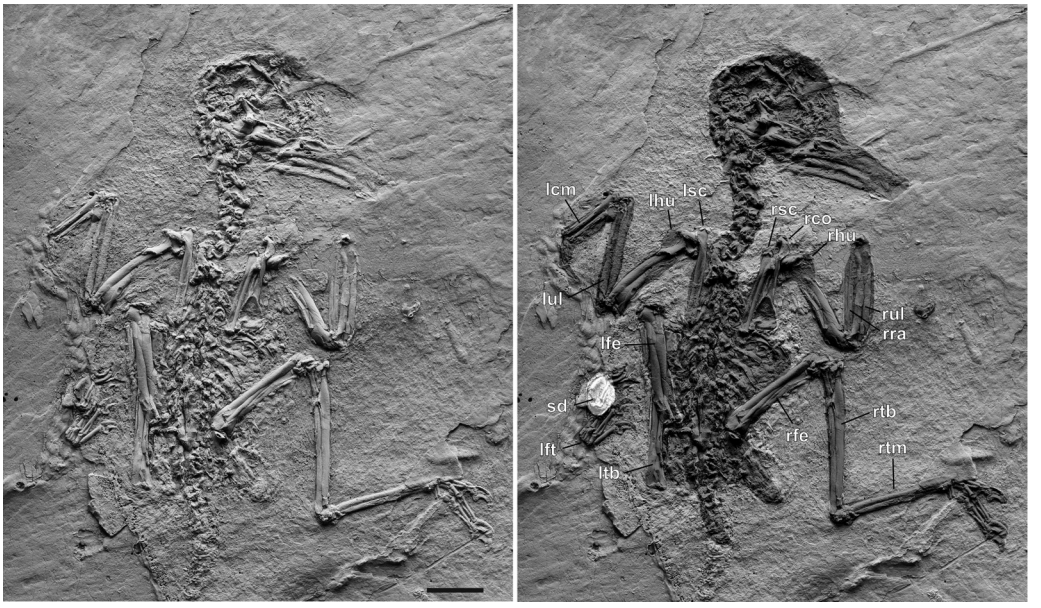

Fig. 1. New specimen of *Masillacolius brevidactylus* from the Early Eocene Messel oil shale in Germany (SMF-ME 11322); in the image on the right, the outlines of the bones were digitally enhanced. Abbreviations: lcm: left carpometacarpus; lfe: left femur; lft: left foot; lhu: left humerus; lsc: left scapula; ltb: left tibiotarsus; lul: left ulna; rco: right coracoid; rfe: right femur; rhu: right humerus; rra: right radius; rsc: right scapula; rtb: right tibiotarsus; rtm: right tarsometatarsus; rul: right ulna; sd: seed. Specimen coated with ammonium chloride. Scale bar equals 10 mm.
Fig. 1. Nouveau spécimen de *Masillacolius brevidactylus* provenant de schistes bitumineux de l'Éocène inférieur de Messel, Allemagne (SMF-ME 11322) ; sur la photo de droite, les contours des os ont été renforcés digitalement. Abréviations : lcm : carpométacarpe gauche ; lfe : fémur gauche ; lft : pied gauche ; lhu : humérus gauche ; lsc : scapula gauche ; ltb : tibiotarse gauche ; lul : ulna gauche ; rco : coracoïde droit ; rfe : fémur droit ; rhu : humérus droit ; rra : radius droit ; rsc : scapula droite ; rtb : tibiotarse droit ; rtm : tarsométatarse droit ; rul : ulna droite ; sd : graine. Le spécimen est recouvert de chlorure d'ammonium. Barre d'échelle = 10 mm.

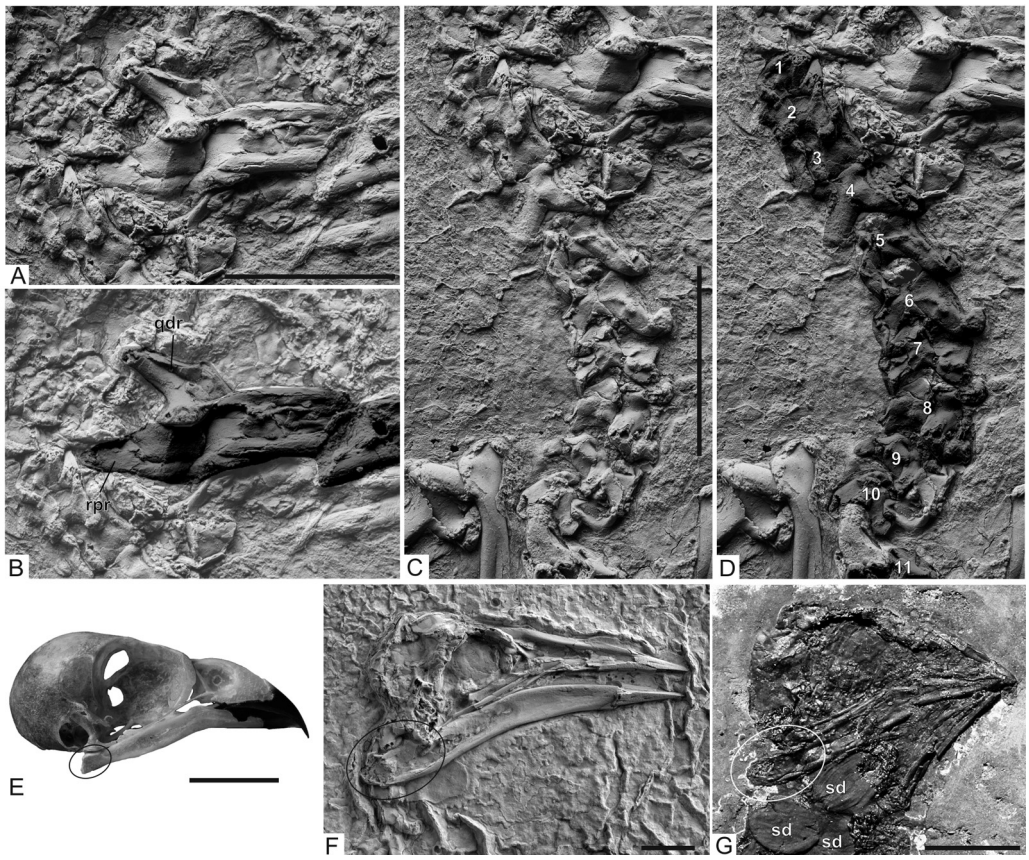

Fig. 2. A–D. Detail of skull (A, B) and vertebral column (C, D) of *Masillacolius brevidactylus* from the Early Eocene Messel oil shale in Germany (SMF-ME 11322); in B and D osteological features are digitally enhanced, the vertebrae are numbered in D. E. Skull of the extant Blue-naped mousebird, *Urocolius macrourus*. F. Skull of *Chascacocolius cacicirostris* from Messel (holotype, SMF-ME 3790). G. Skull of *Oligocolius psittacocephalon* from the Late Oligocene fossil site Enspel in Germany (holotype, PW 2012/5052-LS). The circles in E–G demark the caudal end of the right mandible; note the greatly elongated retroarticular processes of *Chascacocolius* and *Oligocolius*. Abbreviations: qdr: right quadrate; rpr: right processus retroarticularis; sd: seed. Specimens in A–D and F were coated with ammonium chloride. Scale bars equal 10 mm.

Fig. 2. A–D. Détail du crâne (A, B) et de la colonne vertébrale (C, D) de *Masillacolius brevidactylus* provenant de schistes bitumineux de l'Éocène inférieur de Messel, Allemagne (SMF-ME 11322) ; en B et D, les traits ostéologiques ont été renforcés digitalement, les vertèbres sont numérotées en D. E. Crâne du Coliou huppé, *Urocolius macrourus*. F. Crâne de *Chascacocolius cacicirostris* de Messel (holotype, SMF-ME 3790). G. Crâne d'*Oligocolius psittacocephalon* de l'Oligocène supérieur du site d'Enspel en Allemagne (holotype, PW 2012/5052-LS). Les cercles en E, F, G indiquent la terminaison caudale de la mandibule droite ; à noter les processus rétro-articulaires très allongés de *Chascacolius* et *Oligocolius*. Abréviations: qdr : carré droit ; rpr : processus rétroarticulaire droit ; sd : graine. Les spécimens en A–D et F sont recouverts de chlorure d'ammonium. Barres d'échelle = 10 mm.

The humerus of *Masillacolius* is short and stout. A notable and previously unreported feature is the presence of a well-defined, dorsally directed tuberculum supracondylare dorsale (Fig. 3C), which is not well visible in previously described *Masillacolius* specimens. The development of this tubercle varies among extant Coliiformes, being equally well-defined in *Urocolius* (Fig. 3D), but more weakly developed in *Colius*. Among Eocene stem group Coliiformes, its occurrence is also variable, and a small tuberculum supracondylare dorsale is present in *Chascacocolius* but absent in *Selmes*, *Celericolius*, and *Primocolius*. On the right radius, a large nutrient foramen is visible in the proximal third of the bone.

In the new specimen, the proximal end of the tibiotarsus is not covered by overlying bones. This reveals that the length measurements given by Mayr and Peters (1998) are too low, owing to the facts that the proximal ends of the bone are hidden in the holotype of *M. brevidactylus* and that the tibiotarsus is broken in the second specimen described by Mayr and Peters (1998). In the holotype and the new specimen, the distal end of the bone is of equal width throughout and not widened on the level of the condyles as in extant Coliiformes and most of other neornithine birds.

As already detailed by Mayr and Peters (1998), the second, third, and fourth toes of *Masillacolius* have abbreviated proximal phalanges, whereas in extant mousebirds only the proximal phalanges of the fourth toe are shortened. The ungual phalanges are deeper than in extant mousebirds and other stem group Coliiformes. As in both feet of the holotype (Fig. 3A), all toes of the new specimen are detached from the left foot but are still closely attached to each other, which strengthens the assumption that *Masillacolius* had fully pamprodactyl feet. In the holotype there are sesamoid ossicles on top of the distal ends of the

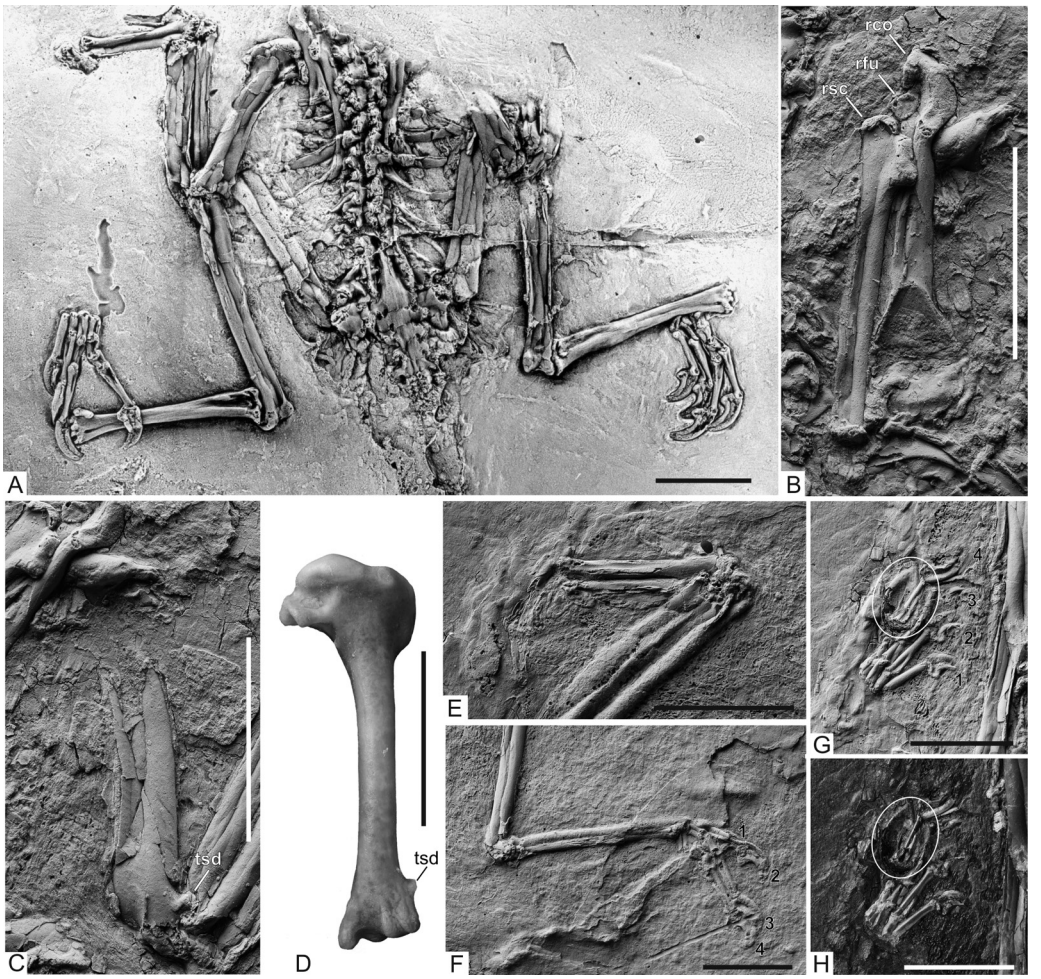

Fig. 3. A. Holotype of *Masillacolius brevidactylus* from the Early Eocene Messel oil shale in Germany (HLMD-Me 10472). B. Right scapula, coracoid, and extremitas omalis of furcula of the newly referred specimen of *M. brevidactylus* (SMF-ME 11322). C. Right humerus of SMF-ME 11322. D. Right humerus of the extant Blue-naped mousebird, *Urocolius macrourus*. E. Left hand skeleton of SMF-ME 11322. F. Right foot of SMF-ME 11322. G, H. Left foot of SMF-ME 11322 with large seed (encircled), presumably of a species of Vitaceae. In F and G, the toes are numbered. Abbreviations: rco: right coracoid; rfu: right extremitas omalis of furcula; rsc: right scapula; tsd: tuberculum supracondylare dorsale. Specimens in A–C and E–G were coated with ammonium chloride. Scale bars equal 10 mm.

Fig. 3. A. Holotype de *Masillacolius brevidactylus* provenant de schistes bitumineux de l'Éocène inférieur de Messel, Allemagne (HLMD-Me 10472). B. Scapula, coracoïde et extremitas omalis de furcula droites du nouveau spécimen de *M. brevidactylus* (SMF-ME 11322) répertorié. C. Humérus droit de SMF-ME 11322. D. Humérus droit de Coliou huppé, *Urocolius macrourus* actuel. E. Main gauche de SMF-ME 11322. F. Pied droit de SMF-ME 11322. G, H. Pied gauche de SMF-ME 11322 avec une grande graine (dans le cercle), d'une espèce de Vitaceae vraisemblablement. En F et G, les doigts sont numérotés. Abréviations : rco : coracoïde droit ; rfu : extremitas omalis droite de la furcula ; rse : scapula droite ; tsd : tubercule supracondylaire dorsal. Les spécimens en A–C et E–G ont été recouverts de chlorure d'ammonium. Barres d'échelle = 10 mm.

penultimate phalanges of each of the toes (Mayr and Peters, 1998: text – fig. 4), but these cannot be discerned in the new specimen.

Underneath the left foot a single large seed is preserved (Figs. 1, 3G, H), which measures 6.7 × 4.4 mm and is tentatively identified as belonging to the Vitaceae. Unidentifiable organic matter is also preserved in the area of the gizzard, and because an accidental association of an isolated seed with a bird skeleton is highly unlikely in the Messel oil shale, where both, birds and isolated seeds, are not all too common, the seed is likely to represent dislocated stomach or gut content. There is also a small cluster of fine grit at the base of the (missing) upper beak, which may have been ingested by the bird.

4. Discussion

Assignment of the new fossil to *Masillacolius* is straightforward and supported by the dimensions and proportions of the bones (see above concerning the length of the tibiotarsus), and by the derived morphology of the legs, with the tarsometatarsus being unusually long and the short toes bearing very deep claws. The new *Masillacolius* specimen is of significance, because it informs about the skull morphology of a poorly known stem group coliiform and therefore

potentially adds to a better understanding of both, the phylogenetic interrelationships of early stem group Coliiformes and the evolutionary history of feeding adaptations in mousebirds.

It has recently been hypothesized that frugivory in birds did not play a major role in the early (that is, pre-Oligocene) stages of seed dispersal of angiosperm plants (Eriksson, in press). However, and as also noted by Eriksson (in press), stomach or crop contents containing seeds are already known from various avian taxa from the Early Cretaceous Chinese Jehol Biota (e.g., Zheng et al., 2011; Zhou and Zhang, 2002). There exists a possibility that these early birds were granivorous rather than frugivorous, but the fact that the ingested seeds usually are uncrushed is more indicative of frugivory, and hence a dispersal function of the birds that ate them.

Stomach contents consisting of dense packages of seeds of various angiosperm taxa are preserved in several bird fossils from the Early Eocene of Messel (pers. obs.), and they occur in phylogenetically disparate taxa, such as zygodactylids and stem group rollers, with the extant representatives of the latter being carnivorous (Mayr, 2009). Eriksson (in press) noted that "Coliiformes was particularly diverse during the Eocene (. . .) but no evidence indicates whether they were frugivorous". This is, however, certainly not true, and various Early Eocene stem group Coliiformes are preserved with seeds as stomach contents, including the sandcoleid *Eoglaucidium* (Mayr and Peters, 1998), as well as *Selmes* (Mayr and Peters, 1998; Peters, 1999), and *Masillacolius* (this study, although, as noted above, the single seed is dislocated and not preserved in the area of the stomach or gut).

The highly specialized digestive system of crown group Coliiformes (Lauterbach and Prinzinger, 1994) also documents a long evolutionary history of frugivory of mousebirds. Still, however, there must have been substantial differences between the feeding ecologies of Eocene stem group Coliiformes and their extant relatives, as evidenced by the highly derived specializations of some of the fossil taxa.

The new *Masillacolius* fossil adds another taxon to the growing number of stem group Coliiformes with greatly elongated, blade-like retroarticular processes of the mandible. Such processes are now known from the Early Eocene *Chascacocolius oscitans*, *Chascacocolius cacicirostris*, and *M. brevidactylus*, and from the Late Oligocene *Oligocolius brevitarsus* (Houde and Olson, 1992; Mayr, 2005, 2013; this study; note that the asterisk symbol designating taxa with known skulls in Mayr, 2013: fig. 5 should have been assigned to *Celericolius acriala* and not to *M. brevidactylus*; the scale bar in Mayr, 2013: fig. 1 furthermore denotes 10 mm, and not 5 mm as erroneously stated). The mandible of the sandcoleid *Sandcoleus* definitively lacks elongated retroarticular processes (Houde and Olson, 1992: pl. 1d), and such were also reported absent in the Early Eocene *Selmes* (Mayr, 2001). The condition in *Celericolius* cannot be assessed, because of the poor preservation of the proximal end of the mandible of the holotype and only known specimen (Ksepka and Clarke, 2010); the skulls of *Primocolius* and *Palaeospiza* are unknown.

Retroarticular processes increase the leverage of the muscles that depress the mandible, and they represent a gaping adaptation for opening of the beak within substrate (e.g., Mayr, 2005, 2013). Among extant birds, such processes are most often found in species that forage for insects in soil or tree crevices, which are forcefully spread open, once the long and narrow beak has been wedged into. Possibly, therefore, the diet of Eocene stem group Coliiformes with long retroarticular processes contained a larger percentage of animals, although the occurrence of long retroarticular processes in the short-beak *Oligocolius* suggests that these processes also served other purposes (Mayr, 2013).

Blade-like retroarticular processes were previously considered an apomorphy of *Chascacocolius* (Ksepka and Clarke, 2010; Mayr, 2005). However, their recognition in *Oligocolius* already raised the question whether these processes may be plesiomorphic for a coliiform subclade, which also includes the crown group representatives (Mayr, 2013). Previous analyses congruently recovered *Selmes* as the sister taxon of a clade including all other non-sandcoleid Coliiformes (Ksepka and Clarke, 2010; Mayr, 2013; Mayr and Mourer-Chauviré, 2004; Zelenkov and Dyke, 2008). The analyses of Zelenkov and Dyke (2008) and Ksepka and Clarke (2010) further suggested that *Chascacocolius* branches next, and that *Masillacolius* and all other more modern-type Coliiformes form a clade. In the analysis of Mayr (2013), by contrast, the interrelationships of *Chascacocolius* and *Masillacolius* were poorly resolved, and *Chascacocolius*, *Masillacolius*, and *Celericolius* were recovered in a polytomy at the base of a clade, which includes all coliiform taxa to the exclusion of sandcoleids and *Selmes*. A re-analysis of the slightly emended data set of this latter study resulted in 30 most parsimonious trees (L = 63, CI = 0.63, RI = 0.75), with the strict consensus and majority rule consensus trees showing identical topologies to those found by Mayr (2013) (Fig. 4).

If *Selmes*, *Chascacocolius*, and *Masillacolius* are indeed successive sister taxa of a clade including more modern-type Coliiformes (Ksepka and Clarke, 2010; Zelenkov and Dyke, 2008), elongated, blade-like retroarticular processes are likely to be an apomorphy of a clade including *Chascacocolius*, *Masillacolius*, *Oligocolius*, and crown group Coliiformes to the exclusion of *Selmes* and sandcoleids. Long retroarticular processes must then have secondarily become shortened in the lineage leading to the crown group, a scenario that gains some support from the fact that extant Coliiformes exhibit incipient retroarticular processes, which may represent vestiges of longer ones (Fig. 2E). Recognition of a wider distribution of greatly elongated retroarticular processes in stem group Coliiformes would potentially bear on the identification of *C. cacicirostris*, whose assignment to the taxon *Chascacocolius* was largely based on the very presence of these processes.

Ksepka and Clarke (2010) identified a single character, a straight humerus shaft, as an apomorphy of a clade including all coliiform birds to the exclusion of Sandcoleidae, *Selmes*, and *Chascacocolius*. This character is at least ambiguous, because the curvature of the humerus shaft is difficult to assess in taxa, of which only flattened skeletons

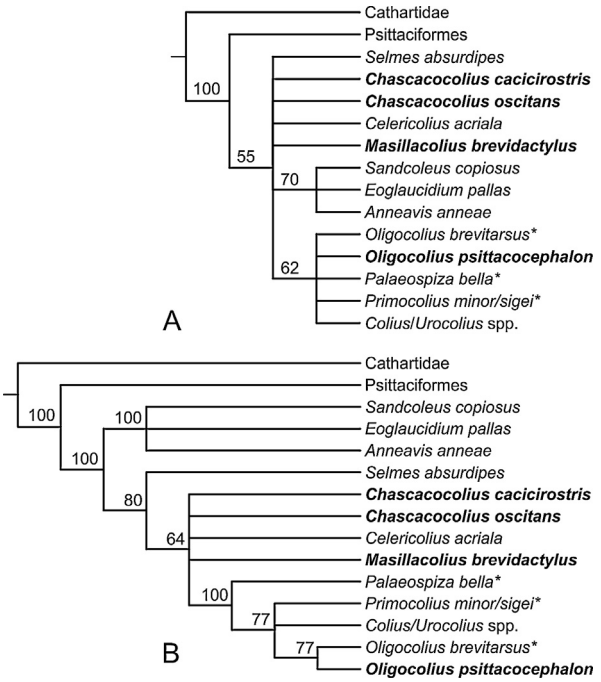

Fig. 4. Interrelationships of fossil and extant Coliiformes resulting from a re-analysis of the character matrix of Mayr (2013), with six character scorings added or modified as indicated in the text. A. Strict consensus tree of 30 most parsimonious trees; bootstrap support values are indicated. B. Majority rule consensus tree of 30 most parsimonious trees; support values are indicated. Taxa with retroarticular processes are highlighted in bold, those of which the skull is unknown with an asterisk.

Fig. 4. Interrelations au sein des Coliiformes vivants et fossiles résultant de la ré-analyse de la matrice de caractères de Mayr (2013), avec six groupes de caractères additionnés ou modifiés, comme indiqué dans le texte. A. Arbre de strict consensus des 30 arbres les plus parcimonieux ; les valeurs de *bootstrap* sont indiquées. B. Arbre de consensus à règle majoritaire des 30 arbres les plus parcimonieux ; les valeurs support sont indiquées. Les taxa à processus rétro-articulaires sont figurés en gras, et ceux dont le crâne est inconnu par une astérisque.

on slabs are known (e.g., *Masillacolius*, *Palaeospiza*, *Oligocolius*). Moreover, the humerus of *Primocolius* actually shows the same degree of curvature as that of *Chascacocolius* (compare Mourer-Chauviré, 1988: pl. 1, figs. 7, 8 with Houde and Olson, 1992: pl. IIh–k). An alternative hypothesis to be considered is that *Masillacolius* and *Chascacocolius* are sister groups, with blade-like retroarticular processes being an apomorphy of a clade including both taxa and having evolved independently in *Oligocolius*. Unfortunately, the tarsometatarsus of *Chascacocolius* is unknown, with this bone being one of the most characteristic skeletal elements of *Masillacolius*. However, a decision for one of the two conflicting phylogenetic hypotheses outlined above would also be fostered if the presence or absence of elongated retroarticular processes could be verified in other Coliiformes, of which the skull is currently unknown.

In any case, Eocene stem group Coliiformes had proportionally longer beaks than their extant relatives. An obvious assumption is that the beak of mousebirds became shorter and more robust with increasing frugivory. This hypothesis is in concordance with the fact that the Oligocene *Oligocolius*, which already had such a short beak, appears to have been a specialized frugivore, as evidenced by the presence of a high amount of very large seeds that were ingested by one fossil individual (Mayr, 2013).

Other morphological attributes of stem group Coliiformes likewise indicate significant shifts in the ecomorphology of these birds. Coliiformes primitively had a derived foot morphology with shortened proximal phalanges of the second to fourth toes, which occurs in the Sandcoleidae and all stem group Coliiformes with known feet, except for *Celericolius*. In extant Coliiformes, by contrast, only the proximal phalanges of the fourth toe are shortened. Shortened pedal phalanges allow for a higher degree of curvature of the toes and thereby increase the grasping function of the foot. They are often found in birds that manipulate food items with their feet, such as owls, many diurnal birds of prey, and parrots. On the other hand, shortening of the proximal pedal phalanges also evolved in some groups to level the lengths of the second, third, and fourth toes, which usually constitutes an adaptation for clinging to vertical slopes and is found in, e.g., swifts. In stem group Coliiformes, both may have been the case.

Sandcoleids and *Selmes* probably used their feet for handling larger food and prey items, which is also suggested by the very long and pointed, raptor-like ungual phalanges of these birds. *Masillacolius*, by contrast, is characterized by a very long tarsometatarsus, which is longer than in all other Coliiformes. It furthermore appears to have had fully pamprodactyl feet with deep claws, and this unusual foot morphology may have served for clinging to vertical surfaces (Mayr and Peters, 1998). Swifts (Apodidae) are the only extant fully pamprodactyl avian taxon, and their feet are most similar to those of *Masillacolius*. In swifts, lengthening of the tarsometatarsus probably occurred in adaptation to a derived nesting behavior, which involves clinging to vertical surfaces (Mayr, 2015). Whether the peculiar foot morphology of *Masillacolius* represents a nesting or feeding adaptation cannot be said, but in analogy with swifts, a nesting adaptation is here considered more likely.

Acknowledgements

I thank Elvira Brahm and Stephan Schaal for the loan of the fossil and Sven Tränkner for taking the photographs. I am also indebted to three anonymous reviewers for comments that improved the manuscript.

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