

OSTEOLOGY AND SYSTEMATIC POSITION OF THE EOCENE PRIMOBUCCONIDAE (AVES, CORACIIFORMES *SENSU STRICTO*), WITH FIRST RECORDS FROM EUROPE

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SYNOPSIS The first complete skeletons of the early Eocene avian taxon Primobucconidae Brodkorb, 1970 are described and the osteology and systematic position of these poorly known birds are revised. New specimens from Germany (Messel) and France (Condé-en-Brie) are the first Old World records of this taxon. From Messel, two new species, *Primobucco perneri* sp. nov. and *P. frugilegus* sp. nov., are described. Cladistic analysis of 36 morphological characters from 14 ingroup taxa placed the Primobucconidae in an unresolved polytomy including fossil and extant rollers (Coraciiformes *sensu stricto*). Derived characters are presented that support this classification. The Primobucconidae is yet another taxon that exemplifies the great similarity between the early Eocene avifaunas of North America and Europe. It further constitutes the first record of stem group rollers in the New World. Both known specimens of *P. frugilegus* are preserved with seeds in the area of the stomach, which may indicate that stem group rollers had a more generalised diet than their extant relatives.

KEY WORDS Fossil birds, Rollers, Phylogeny, Messel, Green River Formation, Paris Basin

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INTRODUCTION

The avian species *Primobucco mcgrewi* was described by Brodkorb (1970) on the basis of an isolated wing from the Lower Eocene Green River Formation (Wyoming, USA). It was considered to be the earliest representative of the Neotropical puffbirds (Bucconidae, Galbulae), which constitute part of the traditional (e.g. Wetmore 1960) Piciformes (woodpeckers and allies: (Simpson & Cracraft 1981; Swierczewski & Raikow 1981; Johansson & Ericson 2003; Mayr *et al.* 2003). Feduccia & Martin (1976) later erected the taxon Primobucconidae for *P. mcgrewi* and four other early Eocene genera that they assumed to be the 'dominant small perching birds of the Eocene of North America' (Feduccia & Martin 1976: 101). Olson & Feduccia (1979) further reported a record of the Primobucconidae from the Lower Eocene London Clay of England, but this identification was disputed by Harrison (1982) who instead assigned another specimen from the same deposits to the Primobucconidae.

More recently, however, it has been shown that the Primobucconidae, as established by Feduccia & Martin (1976), are a polyphyletic assemblage of birds which belong to different higher taxa, such as stem group mousebirds (Coliiformes: see Houde & Olson 1992; Mayr & Peters 1998) and stem group parrots (Psittaciformes: see Mayr 1998a, 2002). The only taxon currently recognised in the Primobucconidae is *Primobucco mcgrewi* (Houde & Olson 1989) and the holotypic wing is still the only specimen of this species that has been described. However, Houde & Olson (1989: 2032) noticed that the holotype of *P. mcgrewi* 'compares best with one of the newly obtained skeletons from the Green River Formation that represents an undescribed, facultatively zygodactyl (i.e. the fourth toe can be turned backwards), roller-like bird'. These authors further indicated (p. 2030) that *P. mcgrewi* 'may belong with roller-like birds similar to the Madagascan Atelornithidae [= Brachypteraciidae]'.
 Rollers (Coraciiformes *sensu stricto*), including the extant true rollers (Coraciidae) and the ground rollers (Brachypteraciidae) have a poor early Tertiary fossil record. Early Tertiary stem group representatives of rollers were only known, so far, from the Middle Eocene of Messel, Germany (Eocoraciidae) and the Upper Eocene of the Quercy fissure fillings in France (Geranopteridae: Mayr & Mourer-Chauviré 2000).

Molecular studies suggest that rollers are the sister taxon of the alcediniform birds, which include bee-eaters (Meropidae), kingfishers (Alcedinidae), motmots (Momotidae) and todies (Todidae: Sibley & Ahlquist 1990, Espinosa de los Monteros 2000, Johansson *et al.* 2001, Mayr *et al.* 2003). The earliest alcediniform bird described so far was also from Messel (Mayr 1998b); other early Tertiary Alcediniformes are known from the Upper Eocene of France and the Oligocene of Switzerland and North America (Olson 1976; Mourer-Chauviré 1985). An as yet undescribed 'kingfisher-like bird' from the Green River Formation figured in Grande (1980: fig. III.19) and Feduccia (1999: 335) belongs to the Upupiformes (hoopoes, wood-hoopoes and allies), as indicated by, e.g. the very long hallux and the derived morphology of the carpometacarpus and distal tarsometatarsus.

A revision of the avifauna of the Green River Formation by one of us (I.W.) led to the identification of new specimens of *P. mcgrewi* from the type locality, which are presented in this study. We further describe two new taxa of the Primobuc-

conidae from Messel and an isolated tarsometatarsus from the Eocene of France. For the first time complete skeletons of the Primobucconidae are described and the phylogenetic relationships of this taxon are evaluated in a cladistic analysis.

MATERIAL AND METHODS

Terminology

The traditional Coraciiformes *sensu* Wetmore (1960) are probably a polyphyletic taxon, since the Upupiformes and Bucerotiformes may be more closely related to piciform birds, while cuckoo-rollers (Leptosomidae) are probably more closely related to 'non-coraciiform' birds (e.g. Mayr *et al.* 2003). Thus, following Mayr (1998b), the term Coraciiformes *sensu stricto* (Coraciiformes s.s.) is used here for the clade that includes the Eocoraciidae, Geranopteridae, Coraciidae and Brachypteraciidae, the term Alcediniformes is used for the clade that includes the Meropidae, Alcedinidae, Momotidae and Todidae, while the term Upupiformes is used for the clade that includes the Upupidae and Phoeniculidae. Osteological terminology follows Baumel & Witmer (1993).

Phylogenetic analysis

The Primobucconidae have been considered, so far, to be closely related to either the Galbulae (Brodkorb 1970; Feduccia & Martin 1976) or to rollers (Houde & Olson 1989). Our analysis covers these taxa and, based on the existing phylogenies of the 'higher land bird assemblage' (e.g. Sibley & Ahlquist 1990; Johansson *et al.* 2001; Mayr *et al.* 2003), taxa that are presumed to be closely related forms. Outgroup comparisons were made with the Musophagidae (turacos) and the Caprimulgidae (nighthawks).

For the phylogenetic analysis, skeletons of the extant taxa listed below were examined in the collections of the Forschungsinstitut Senckenberg, the Muséum National d'Histoire Naturelle, Paris and the Museum für Naturkunde, Berlin.

Musophagidae: *Corythaixoides*, *Crinifer*, *Musophaga*, *Tauraco*.

Caprimulgidae: *Caprimulgus*, *Chordeiles*.

Galbulidae: *Galbula*.

Bucconidae: *Chelidoptera*, *Monasa*, *Notharchus*.

Ramphastidae: *Megalaima*, *Psilopogon*, *Pteroglossus*, *Ramphastos*, *Selenidera*, *Trachyphonus*.

Indicatoridae: *Indicator*.

Picidae: *Colaptes*, *Dendrocopos*, *Dendropicops*, *Jynx*, *Picus*.

Coraciidae: *Coracias*, *Eurystomus*.

Brachypteraciidae: *Atelornis*, *Geobiastes*, *Uratelornis*.

Meropidae: *Merops*.

Alcedinidae: *Alcedo*, *Ceryle*, *Dacelo*, *Halcyon*, *Ispidina*.

Momotidae: *Momotus*.

Todidae: *Todus*.

Leptosomidae: *Leptosomus*.

Upupidae: *Upupa*.

Phoeniculidae: *Phoeniculus*.

Bucerotidae: *Bucorvus*, *Bycanistes*, *Tockus*, *Penelopides*.

A total of 36 characters from 16 terminal taxa (see character matrix in Appendix 2) were coded for a parsimony analysis using PAUP 3.1 (Swofford 1993). All characters were coded as unordered. The shortest tree was found using the branch-and-bound search option. The consistency index (CI), retention index (RI) and rescaled consistency index (RC) were calculated. The robustness of the tree was tested with a bootstrap analysis of 1000 replicates using the same settings as in the primary analysis.

Institutional Abbreviations

The fossil specimens are deposited in the Muséum National d'Histoire Naturelle, Paris, France (MNHN), Forschungsinstitut Senckenberg, Frankfurt am Main, Germany (SMF), Staatliches Museum für Naturkunde, Karlsruhe, Germany (SMNK), National Museum of Natural History, Washington, USA (USNM) and University of Wyoming Geological Museum, Laramie, Wyoming, USA (UWGM).

SYSTEMATIC DESCRIPTIONS

CORACIIFORMES *sensu stricto* (see Mayr, 1998b)

PRIMOBUCCONIDAE Feduccia & Martin, 1976

TYPE GENUS. *Primobucco* Brodkorb, 1970.

EMENDED DIAGNOSIS. The Primobucconidae are small birds that are characterised by the following combination of characters: caudal margin of sternum with four deep incisions reaching about half of the length of the corpus sterni; carpo-metacarpus, os metacarpale minus with ventrally protruding pointed projection on ventral side of proximal end; tarsometatarsus very short, with wide proximal and distal ends and large foramen vasculare distale; canalis interosseus distalis (tarsometatarsus) plantarly open, so that there is a marked furrow between the trochleae metatarsorum III and IV.

DIFFERENTIAL DIAGNOSIS. Apart from being smaller, the Primobucconidae resemble stem group rollers of the Eocoraciidae and Geranopteridae in overall morphology. However, they differ from:

- The Eocoraciidae in: processus postorbitales not touching the jugal bars; furcula with narrower scapi claviculae; decidedly deeper incisions in caudal margin of the sternum.
- The Geranopteridae in: smaller processus postorbitales, processus intermetacarpalis (carpometacarpus) smaller.

DESCRIPTION AND COMPARISON. The known species of the Primobucconidae exhibit a very similar osteology and mainly differ in size and/or limb proportions.

Skull. The beak is moderately long and robust, with large narial openings measuring about half of its length. Contrary to extant rollers and most alcediniform birds, an ossified nasal septum is absent (USNM 336284). In one specimen (SMF-ME 3507a), an elongate processus postorbitalis is visible, which has a similar length to the processus postorbitalis of extant *Momotus* (Momotidae). Although being longer than average, it is shorter than the processus postorbitales of both extant rollers and the fossil taxa Eocoraciidae and Geranop-

teridae, which touches the jugal bars. The 'head' (Cracraft 1968: fig. 2) of the os lacrimale (SMF-ME 3507a, SMF-ME 3794) is large, as in extant rollers, Alcedinidae and Galbulae.

Vertebrae. The number of praesacral vertebrae appears to have been about 19, as in most 'higher land birds' (pers. obs.). The incisura fossae of the atlas is dorsally open (visible in *Primobucco mcgrewi*, USNM 336284). There are seven free tail vertebrae (SMNK.PAL.404a+b). The pygostyle bears a cranio-caudally wide processus dorsalis, which is also found in extant rollers and alcediniform birds.

Coracoid. The extremitas omalis of the coracoid (SMF-ME 3546) is elongate and resembles that of the Quercy roller, *Geranopterus alatus* (Mayr & Mourer-Chauviré 2000: fig. 8); the processus procoracoideus is short but not as greatly reduced as in the extant Todidae and Momotidae. As in most other 'higher land birds' (pers. obs.), the facies articularis scapularis is shallow and a foramen nervi supracoracoidei absent. The processus lateralis of the extremitas sternalis is narrow.

Furcula. The furcula is U-shaped and an apophysis furculae is absent (SMF-ME 3546, SMF-ME 3507b, SMF-ME 3793b). The scapi claviculae are narrow at the extremitas sternalis, although not as narrow as in alcediniform birds.

Scapula. The scapula is slender and its caudal end is only slightly angled. The acromion is long and resembles that of the Geranopteridae and of extant rollers.

Sternum. The sternum (Fig. 1) is short and similar in its proportions to that of some recent Alcedinidae, e.g. *Halcyon albiventris*. The caudal end exhibits four deep notches (visible in the holotype of *Primobucco mcgrewi* and SMF-ME 3793a). Both incisions are very deep, the incisurae mediales reach about half of the length of the corpus sterni. The depth of these incisions is intermediate between the shallower incisions of extant Alcedinidae and the deeper ones of extant Galbulae.

Humerus. In its overall proportions, the humerus resembles that of extant Brachypteraciidae, but the proximal end is proportionally larger and the short crista deltopectoralis more protruding. The tuberculum dorsale is small. The shaft is slightly curved and the distal end of the bone is similar to the distal humerus of the Geranopteridae (Mayr & Mourer-Chauviré 2000: fig. 9) and alcediniform birds (e.g. *Merops apiaster*). The condylus ventralis bears a shallow depression along its cranial surface.

Ulna. As in most 'higher land birds' (pers. obs.), the ulna distinctly exceeds the humerus in length. Details of this bone are, however, not visible in any of the specimens.

Carpometacarpus. In overall morphology, the carpometacarpus is similar to the corresponding bone of extant Coraciidae. In concordance with Coraciiformes s.s. and the Meropidae, the proximal part of the os metacarpale minus bears a strongly protruding projection on its ventral side (SMNK.PAL.404b, right side). The symphysis metacarpalis distalis is wide. Contrary to the Brachypteraciidae and alcediniform birds, the distal end of the os metacarpale minus does not protrude further distally than the os metacarpale majus. The processus intermetacarpalis is very small; this process is much larger in extant rollers and is very large in

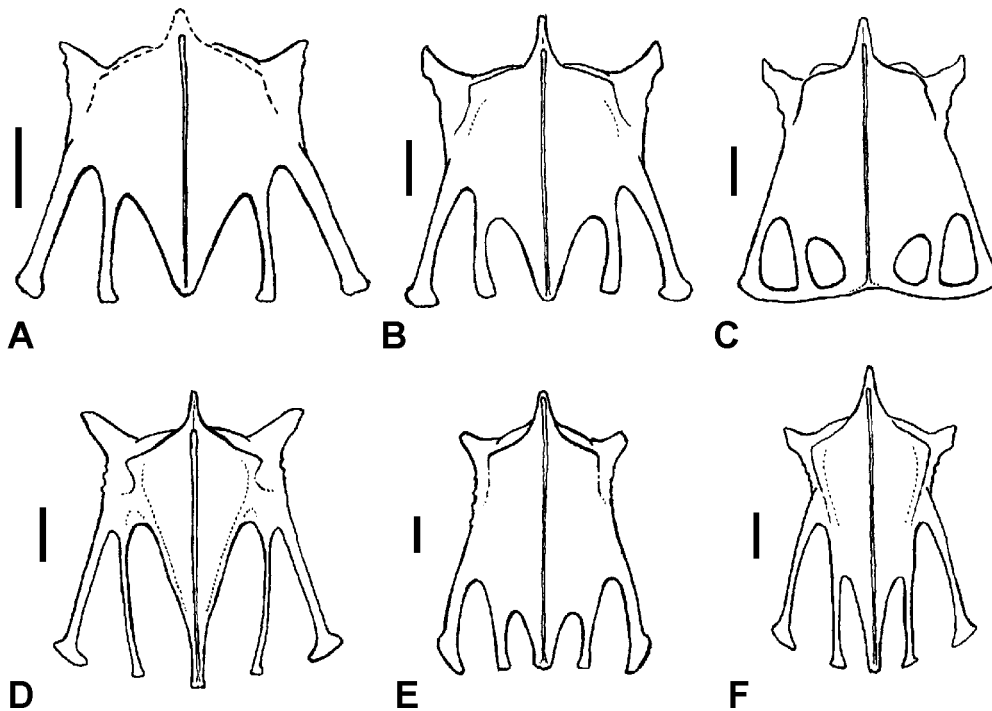


Figure 1 Comparison of sterna. **A**, *Primobucco perneri* sp. nov. (SMF-ME 3793a+b); **B**, *Halcyon albiventris* (Alcedinidae); **C**, *Momotus momota* (Momotidae); **D**, *Monasa nigrifrons* (Bucconidae); **E**, *Coracias garrulus* (Coraciidae); **F**, *Uratelornis chimaera* (Brachypteraciidae). Scale bars = 5 mm.

the Galbulae, where it reaches the os metacarpale minus. The processus extensorius is large and cranially protruding.

Other elements of the wing. The phalanx digiti alulae bears a small claw (SMF-ME 516, right side) that is absent in most extant ‘higher land birds’ (Stephan 1992). The phalanx proximalis digiti majoris bears a deep fossa ventralis and a small processus internus indicis (terminology after Stegmann 1963, visible on SMF-ME 516). The proximal end of the phalanx proximalis digiti majoris lacks the large proximally directed process on its ventral side, which is synapomorphic for the Galbulae and the Pici (see Mayr *et al.* 2003: fig. 2).

Pelvis. As preserved, the pelvis has similar proportions to the pelvis of extant rollers, Alcediniformes and Galbulae. The processus terminalis ischii is long and slender, tapering to a point.

Femur. Details of the femur cannot be discerned in any of the specimens. In its proportions, however, the bone resembles the comparatively straight femur of extant rollers and alcediniform birds.

Tibiotarsus. The tibiotarsus is fairly short. As in extant Alcediniformes and Coraciidae, the cristae cnemiales are very poorly developed; in the terrestrial Brachypteraciidae they are large and strongly cranially protruding. The distal end is similar to the distal tibiotarsus of the Bucconidae (e.g. *Monasa nigrifrons*) and the Geranopteridae; the condyli are of approximately equal size, the sulcus intercondylaris is wide.

Tarsometatarsus. The bone is short, measuring about half of the length of the tibiotarsus. The shaft is slender in its midsection but widens towards the proximal and distal ends, which are slightly twisted against each other. The tuberos-

itas musculi tibialis cranialis is a well-defined tubercle situated next to the medial margin of the bone. The hypotarsus bears a single groove, presumably for the tendon of the musculus flexor digitorum longus, which originally might have been closed to form a canal as in extant rollers (visible in the referred specimen from Condé-en-Brie, MNHN-CB-17346). The crista medianoplantaris is prominent and bordered by distinct fossae parahypotarsales. In specimen MNHN-CB-17346 the medial foramen vasculare proximale is well-developed and situated proximally to the tuberositas musculi tibialis cranialis. Situated proximo-laterally to this foramen, there is a very small opening which appears to be the reduced lateral foramen vasculare proximale. The distal end of the bone resembles the distal tarsometatarsus of rollers. The fossa metatarsi I is large and situated near the medial margin of the bone. As in the Geranopteridae and the extant Brachypteraciidae, the foramen vasculare distale is large and situated at the distal end of a marked sulcus. The canalis interosseus distalis is plantarly open, so that there is a marked furrow between the trochleae metatarsorum III and IV (MNHN-CB-17346). The trochlea metatarsi IV lacks a well-developed plantarly projecting wing-like flange.

Toes. The toes have the usual proportions, the third toe is the longest. The hallux is fairly long, the proximal phalanx does not bear the medial projection that is apomorphic for alcediniform birds (Mayr 1998b: fig. 20F). The claws are of average size.

Genus *PRIMBUCCO* Brodkorb, 1970

Primobucco mcgrewi Brodkorb, 1970 (Fig. 2)

HOLOTYPE. UWGM 3299 (right wing, Brodkorb 1970: fig. 1).



Figure 2 *Primobucco mcgrewi* Brodkorb, 1970, referred specimen USNM 336284 from the Green River Formation, USA. Scale bar = 20 mm.

REFERRED SPECIMENS. USNM 336284 (articulated skeleton lacking the left leg, see Fig. 2; this specimen has been figured on the cover of Benton 1993), UWGM 14563 (right wing and parts of shoulder girdle and sternum).

LOCALITY AND HORIZON. The holotype comes from the lower beds of the early Eocene Green River Formation (Brodkorb 1970); the exact horizon of the Green River Formation in which the referred specimens were found is unknown (for a detailed description of the locality, see Grande 1980).

MEASUREMENTS. See Table 1.

REMARKS. Specimen USNM 336284 was first identified as possibly belonging to *P. mcgrewi* by Houde & Olson (1989) (see Introduction, above). The holotype of this species consists of a fragmentary wing only which, however, matches perfectly that of the referred specimens. Our examination of numerous Green River Formation bird specimens in public and private collections indicates that there are no other bird taxa with a similar wing morphology and bone dimensions.

***Primobucco perneri* sp. nov.** (Fig. 3)

HOLOTYPE. SMNK.PAL.404a+b (complete articulated skeleton on two slabs; Fig. 3).

DIFFERENTIAL DIAGNOSIS. The new species from Messel differs from the North American species *P. mcgrewi* in the proportionally shorter tibiotarsus (ratio of the tibiotarsus to tarsometatarsus = 2.0 for *P. mcgrewi* and 1.8 for *P. perneri* sp. nov.) and longer beak. Whereas the tibiotarsus of *P. perneri* is shorter than that of *P. mcgrewi* (~24.0 mm versus 26.7 mm), its beak (from nasofrontal hinge to tip) is longer (23 mm versus 18 mm: measured in specimens SMF-ME 3793 and USNM 336284). The beak is nearly as long as the tibiotarsus in *P. perneri*, but decidedly shorter than the tibiotarsus in *P. mcgrewi*.

Owing to the preservation of the specimens (flattened skeletons on slabs), subtle morphological differences that may also be present cannot be discerned. However, *P. perneri* differs from *P. mcgrewi* not only in size but also in proportions, i.e. in the combination of a longer beak with a shorter tibiotarsus. Extant 'coraciiform' birds do not show significant sexual dimorphism in size, and differences in limb and beak proportions, such as that noted above, in general are sufficient to diagnose avian species.

TYPE LOCALITY. Messel near Darmstadt, Hessen, Germany (see Schaal & Ziegler 1988 for a description of the locality and see Mayr 2000a for information on the avifauna of the site).

TYPE HORIZON. Early Middle Eocene, Mammalian Paleogene (MP) 11 (Legendre & L  v  que 1997).

MEASUREMENTS OF THE HOLOTYPE. See Table 1.

Table 1 Comparison of the dimensions of the skull and major limb bones (left/right) from the Green River Formation and Messel Primobucconidae.

	Skull	Humerus	Ulna	Carpometacarpus	Femur	Tibiotarsus	Tarsometatarsus
<i>Primobucco mcgrewi</i> Brodkorb, 1970							
Holotype [†]	–	26.7/–	~34.2/–	~14.2/–	–	–	–
USNM 336284	40.5	~27/~28	~32.5/~33	–/15.3	–/~19	–/26.7	–/~13.1
UWGM 14563	–	–/26.8	–/33.8	–/15.7	–	–	–
<i>Primobucco perneri</i> sp. nov.							
Holotype	~42.0	~29.3/~29.3	~36.3/36.0	15.4/15.1	~18.4/–	~24.0/–	13.1/13.1
SMF-ME 3793	~38.6	–/~25.8	–	–/~15.0	–	~20.9/–	–/~11.5
SMF-ME 516	~39.2	~25.2/~26.5	–/~32.0	15.0/15.0	–	–	–
SMF-ME 3546	~43	~28.6/~28.9	–/~34.0	–/~17.1	–	–	–
<i>Primobucco frugilegus</i> sp. nov.							
Holotype	~46.6	~31.5/–	~37.8/–	18.7/–	–	–	–
SMF-ME 3794	~48	~32.7 ~ 32.7	–/~38.4	~19.4/–	–	–	~14/~14

All measurements are for the maximum length and are in mm.

[†]After Brodkorb (1970).

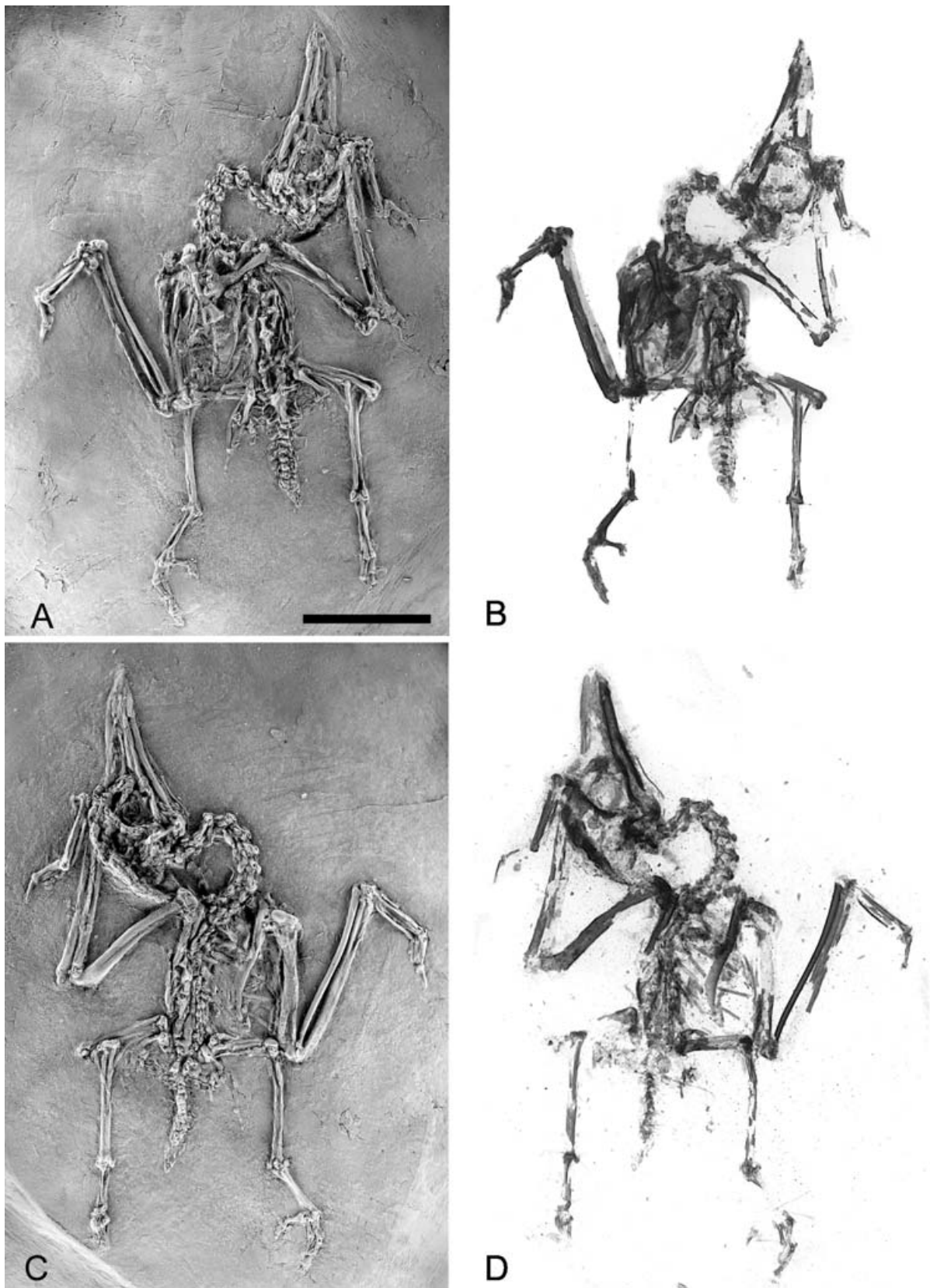


Figure 3 *Primobucco perneri* sp. nov. from Messel, holotype. **A**, specimen SMNK.PAL.404a; **B**, X-ray photograph of specimen SMNK.PAL.404a; **C**, specimen SMNK.PAL.404b; **D**, X-ray photograph of specimen SMNK.PAL.404b. Specimens in **A** and **C** were coated with ammonium chloride; scale bar = 10 mm (same scale for **A–D**).

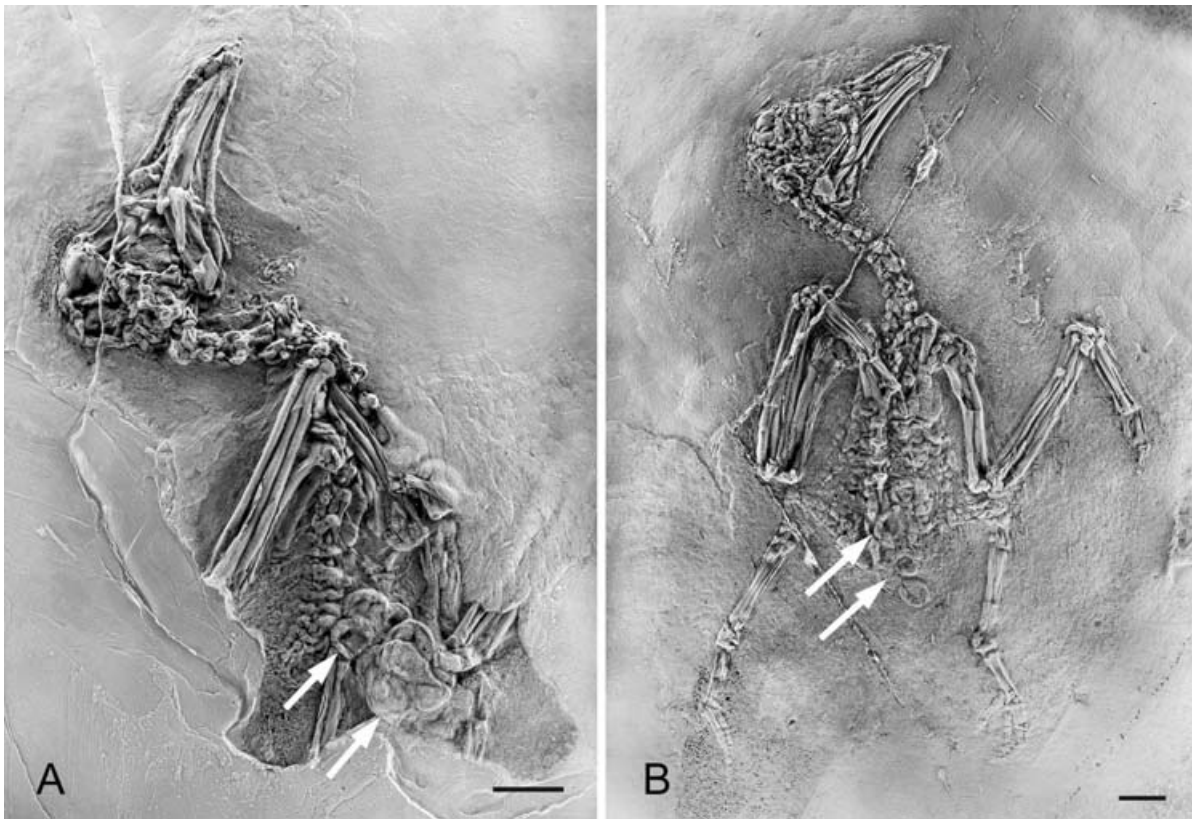


Figure 4 *Primobucco frugilegus* sp. nov. **A**, holotype (SMF-ME 3507a); **B**, referred specimen SMF-ME 3794. Note the accumulation of seeds in the area of the stomach of both specimens (arrows). Specimens were coated with ammonium chloride. Scale bars = 10 mm.

ETYMOLOGY. The species is named after Mr Thomas Perner who collected and prepared the referred specimen SMF-ME 3793 and donated it to the SMF.

REFERRED SPECIMENS. SMF-ME 3793a+b (complete articulated skeleton on two slabs), SMF-ME 516 (cranial half of articulated skeleton), SMF-ME 3546 (cranial half of articulated skeleton); all from the type locality and horizon.

MEASUREMENTS OF THE REFERRED SPECIMENS. See Table 1.

REMARKS. This species is very similar in size and morphology to *Primobucco mcgrewi* from which it mainly differs in the proportions of the beak and limb elements. In specimen SMNK.PAL.404b, a cluster of small quartz grains is preserved in the area of the stomach.

***Primobucco frugilegus* sp. nov.** (Fig. 4)

HOLOTYPE. SMF-ME 3507 (articulated skeleton on two slabs, lacking most parts of the legs; Fig. 4A).

DIFFERENTIAL DIAGNOSIS. The new species differs from *P. mcgrewi* and *P. perneri* in its larger size (see Table 1 and comments in the differential diagnosis of *P. perneri*, above).

TYPE LOCALITY. Messel near Darmstadt, Hessen, Germany.

TYPE HORIZON. Early Middle Eocene, MP 11 (Legendre & Lévêque 1997).

MEASUREMENTS OF THE HOLOTYPE. See Table 1.

REFERRED SPECIMEN. SMF-ME 3794 (complete but poorly preserved articulated skeleton); from the type locality and horizon.

MEASUREMENTS OF THE REFERRED SPECIMEN. See Table 1.

ETYMOLOGY. Latin: ‘fruit-gathering’ (from *frux* = fruit and *legere* = to pick, to gather), refers to the fact that in both known specimens of this species an accumulation of large seeds is preserved in the area of the stomach (Fig. 4).

***Primobucconidae* gen. et sp. indet.** (Fig. 5)

REFERRED SPECIMEN. MNHN-CB-17346 (left tarsometatarsus lacking the trochlea metatarsi II; Fig. 5).

LOCALITY AND HORIZON. Condé-en-Brie, France; early Eocene, MP 8–9 (Schmidt-Kittler 1987).

DIMENSIONS. Length = 15.6 mm; proximal width = 4.0 mm; distal width across trochleae metatarsorum III and IV = 2.8 mm; distal width (estimated) = 3.8 mm; width of mid-section of shaft = 1.8 mm.

REMARKS. This specimen is slightly larger than the tarsometatarsus of *Primobucco mcgrewi* (referred specimen USNM 336284, see Table 1), which it closely resembles in overall morphology. Assignment to the Primobucconidae is supported, in particular, by the following features: tarsometatarsus relatively short with narrow shaft but wide proximal and distal ends, crista medianoplantaris and fossae parahypotarsales well-developed and foramen vasculare distale large.



Figure 5 Primobucconidae gen. et sp. indet., left tarsometatarsus from the early Eocene of Condé-en-Brie, France in dorsal (A) and plantar (B) view. Scale bar = 5 mm.

RESULTS OF PHYLOGENETIC ANALYSIS

Analysis of the character matrix in Appendix 2 resulted in 30 most parsimonious trees (length = 69, CI = 0.54, RI = 0.67, RC = 0.36) and the strict consensus tree for those results is shown in Fig. 6. In all of the resulting trees, the Primobucconidae were placed in an unresolved polytomy that included the Eocoraciidae and a clade consisting of the Geranopteridae, Coraciidae and Brachypteraciidae. The clade comprising the Primobucconidae and all extant and fossil rollers received a bootstrap support of 72% and is supported by the following derived characters (the numbers in parentheses refer to character descriptions in Appendix 1):

- (20) Carpometacarpus, os metacarpale minus with ventrally protruding projection on ventral side of proximal end.
- (30) Tarsometatarsus, canalis interosseus distalis plantarly not ossified, forming a deep, narrow sulcus on the plantar surface of the bone, between the trochleae metatarsorum III and IV.

In 18 of the resulting trees (60%), the Primobucconidae were shown to be the sister taxon of the remaining extant and fossil rollers (Eocoraciidae, Geranopteridae, Bra-

chypteraciidae and Coraciidae). The latter share the feature of a greatly elongated processus postorbitales (character 5), which is absent in the Primobucconidae.

Monophyly of a taxon that included the Geranopteridae, Coraciidae and Brachypteraciidae received a bootstrap support of 67% and is supported by the presence of a cranially directed process on the processus postorbitales (character 6).

DISCUSSION

The specimens of the Primobucconidae from Messel and France described herein are the first Old World record of this taxon, which is currently known only from early Eocene deposits (MP 8/9 – 11). We could not confirm identification of the specimens assigned to the Primobucconidae by Olson & Feduccia (1979) and Harrison (1982), both of which are incomplete tarsometatarsi that strongly differ from the tarsometatarsi described in the present study. Moreover, at the time these specimens were assigned to the Primobucconidae, the tarsometatarsus of *Primobucco mcgrewi* was unknown and comparisons were mainly made with '*Primobucco olsoni*' Feduccia & Martin, 1976, which is now referred to the psittaciform Pseudasturidae, in the genus *Pulchrapollia* Dyke & Cooper, 2000 (Mayr 2002).

The Primobucconidae is thus another taxon that exemplifies the great similarity between the early Eocene avifaunas of North America and Europe (see also Mayr 2000a, b, c, Mayr & Peters 1998, Mayr & Daniels 2001), resulting from the absence of climatic and physical barriers between the two continents (e.g. Blondel & Mourer-Chauviré 1998).

Extant rollers are restricted in their distribution to the Old World, with the Brachypteraciidae being endemic to Madagascar. Considering the crown group only, i.e. the extant taxa, it is simplest to assume an Old World origin for rollers (e.g. Olson 1976). However, the occurrence of the Primobucconidae in New World deposits shows that the distribution of the extant taxa may be misleading with regard to the origin of the Total Group (Pan-Monophylum of Lauterbach 1989), i.e. the clade including the crown group and the stem group. A comparable case is exemplified by galliform birds (fowl and allies), where stem group representatives occur in fossil deposits of the Northern Hemisphere (e.g. Mourer-Chauviré 1992; Mayr 2000b) and the crown group appears to have originated in the Southern Hemisphere (e.g. Cracraft 2001).

Among the Alcediniformes, which are the putative sister taxon of rollers (see Introduction, above), all of the Meropidae and most Alcedinidae also have an Old World distribution; the alcedinid Cerylinae unquestionably reached the New World from the Old World (Olson 1976: 117; Fry & Fry 1992: 22; Woodall 2001: 140). Today, the Todidae and Momotidae only occur in the New World, but both taxa were identified in the fossil record of the Old World (Olson 1976; Mourer-Chauviré 1985).

Extant rollers are almost exclusively carnivorous, feeding on invertebrates and small vertebrates (Fry 2001; Langrand 2001). It is thus remarkable that the two known specimens of *Primobucco frugilegus* are preserved with an accumulation of large seeds in the region of the stomach. A single seed was, however, also reported for one specimen of the Messel roller *Eocoracias brachyptera* (Mayr & Mourer-Chauviré 2000). Stem lineage representatives of rollers may

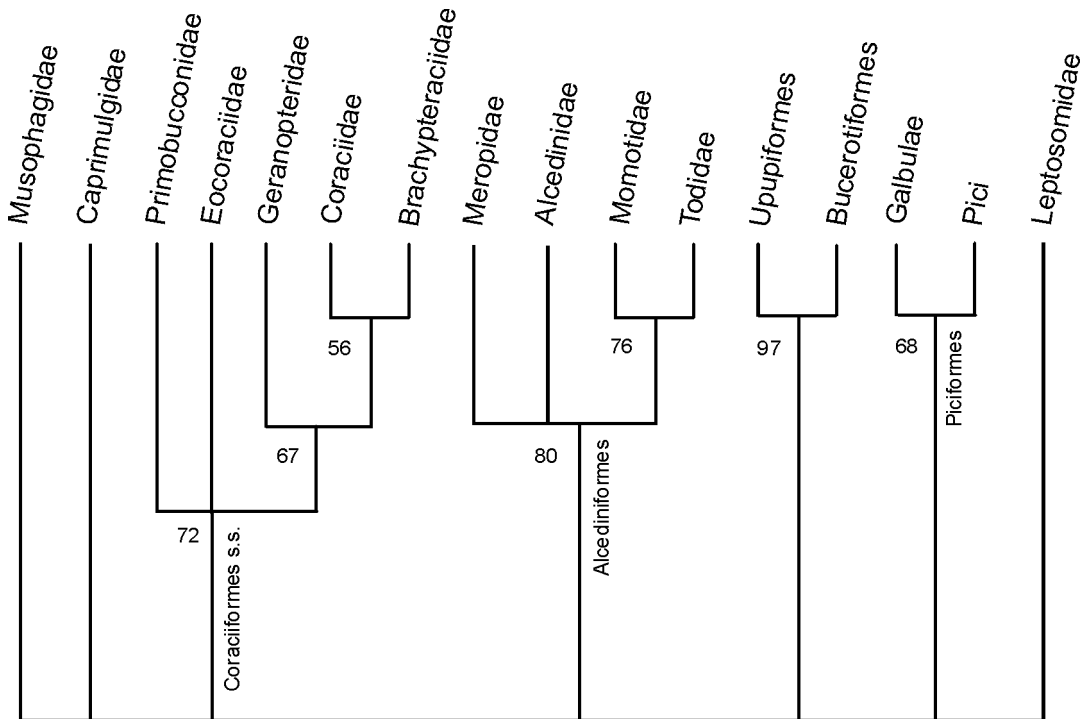


Figure 6 Strict consensus cladogram of the 30 most parsimonious trees resulting from analysis of the character matrix given in Appendix 2 (length = 69, consistency index (CI) = 0.54, retention index (RI) = 0.67, rescaled consistency index (RC) = 0.36). Bootstrap support values of more than 50% are indicated next to the corresponding node.

thus have been more generalised feeders similar to, e.g. the alcediniform Momotidae, whose diet regularly includes fruits (Snow 2001).

Birds are among the most abundant land vertebrates in many early Tertiary sites that were deposited in lacustrine or marine environments, e.g. Messel (Schaal & Ziegler 1988; Mayr 2000a), the Green River and Nanjemoy Formations of North America (Grande 1980; Weems & Grimsley 1999), the London Clay in England (Feduccia 1999: 166), and Céreste in France (G. M. and C. M. C., pers. obs.). Regarding the Messel deposits, the large number of flying vertebrates (bats and birds) present is sometimes explained by the temporary escape of lethal carbon dioxide layers above the water surface (e.g. Franzen 1985). However, many of the articulated bird skeletons from Messel exhibit distinct fractures of the long limb bones with dislocated bone ends, which are more likely to have caused the death of these animals (Mayr 2000a). Regarding the specimens described in this study, distinct fractures of the ulna are visible in specimens SMF-ME 3793b and SMF-ME 516 (both *P. perneri* sp. nov.) from Messel and also in specimen USNM 336284 (*P. mcgrewi*) from the Green River Formation (Fig. 2). An important factor explaining the abundance of birds in deposits of larger lakes or coastal environments may be the simple fact that injured flying animals have a much greater chance of falling into the water – and thus becoming fossilised – than do terrestrial animals.

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APPENDIX 1: CHARACTER DESCRIPTIONS.

1. Skull, largely or completely ossified nasal septum: absent (0), present (1).
2. Skull, upper beak, cutting edges of ramphotheka finely serrated: no (0), yes (1).
3. Skull, 'head' (Cracraft 1968: fig. 2) of os lacrimale (os praefrontale) large: no (0), yes (1).
4. Skull, descending process of os lacrimale greatly expanded medially: no (0), yes (1).
5. Skull, processus postorbitales greatly elongated, touching (or nearly touching) the jugal bar: no (0), yes (1).
6. Skull, processus postorbitalis with cranially directed process (Mayr & Mourer-Chauviré 2000: fig. 4A): no (0), yes (1).
7. Skull, columella with large, hollow, bulbous basal and footplate area that exhibits a large fenestra on one side (Feduccia 1977): no (0), yes (1).
8. Skull, quadratum with strongly ventrally protruding condylus medialis: no (0), yes (1).
9. Mandible, area of pars symphysialis with rectangular cross section: absent (0), present (1).
10. Mandible with deep incision in proximal end, between processus medialis and processus retroarticularis (Olson 1976: fig 2): no (0), yes (1).
11. Pygostyle, with large, shield-like discus pygostyli with sharply defined, ridge-like lateral margins (Mayr *et al.* 2003: fig. 3): absent (0), present (1).
12. Furcula, scapi claviculae very narrow at extremitas sternalis (Mayr 1998*b*: fig. 16): no (0), yes (1).
13. Furcula, apophysis furculae: absent (0), present (1). Within the Coraciidae, an apophysis furculae is absent in *Eurystomus* but present in *Coracias*, within Galbulae it is absent in Galbulidae but present in Bucconidae.
14. Scapula, acromion distinctly bifurcate, with additional medial process (Mayr 1998*b*: fig. 16; Höfling & Alvarenga 2001: fig. 8): no (0), yes (1).
15. Coracoid, processus procoracoideus greatly reduced: no (0), yes (1).
16. Coracoid, extremitas sternalis, notch on margo medialis (Mayr *et al.* 2003: fig. 4): absent (0), present (1).
17. Sternum, well-developed spina externa rostri: absent (0), present (1).
18. Ulna distinctly exceeding humerus in length: no (0), yes (1).
19. Carpometacarpus, processus intermetacarpalis: absent or small (0), well-developed (1), absent but tendon of musculus extensor carpi ulnaris inserting on os metacarpale minus as it does in taxa with a processus intermetacarpalis (usually this tendon inserts on the os metacarpale majus) (2). In extant Upupidae/Phoeniculidae and Bucerotidae there is no trace of a processus intermetacarpalis but Stegmann (1965) suggested that it was completely reduced in the stem lineage of these taxa.
20. Carpometacarpus, os metacarpale minus with ventrally protruding projection on ventral side of proximal end: no (0), yes (1).
21. Carpometacarpus, os metacarpale minus with foramen on ventral side of proximal end, at base of the ventrally protruding projection (Mayr & Mourer-Chauviré 2000: fig. 10): no (0), yes (1).
22. Carpometacarpus, os metacarpale minus reaching much farther distally than os metacarpale majus: no (0), yes (1).
23. Phalanx proximalis digiti majoris, proximal end with large, proximally directed process on ventral side (Mayr *et al.* 2003: fig. 2): no (0), yes (1).
24. Phalanx digiti alulae with rudimentary claw (0), claw completely reduced (1); recent taxa after Stephan (1992) and pers. obs.
25. Femur, pneumatic foramen at cranio-lateral side of proximal end: absent (0), present (1).
26. Tarsometatarsus, well-developed crista mediano-plantaris: absent (0), present (1).
27. Tarsometatarsus with very marked fossa parahypotarsalis medialis, proximal part of margo medialis forming a sharp ridge: no (0), yes (1).
28. Tarsometatarsus, hypotarsus, tendon of musculus flexor hallucis longus enclosed in bony canal: no (0), yes (1).
29. Tarsometatarsus, foramen vasculare distale very large: no (0), yes (1).
30. Tarsometatarsus, canalis interosseus distalis plantarly not ossified, forming a deep, narrow sulcus on the plantar surface of the bone, between the trochleae metatarsorum III and IV: no (0), yes (1).
31. Tarsometatarsus, incisurae intertrochleares very short: no (0); yes (1).
32. Tarsometatarsus, trochlea metatarsi IV reaching almost as far distally as trochlea metatarsi III, rotund in lateral view and without well developed plantarly projecting wing-like flange: no (0), yes (1).
33. Hallux, proximal phalanx with proximal end medially widened (Mayr 1998*b*: fig. 20F): no (0), yes (1).
34. Feet syndactyl, i.e. third and fourth toe coalescent at least over length of basal phalanx of third toe: no (0), yes (1).
35. Feet zygodactyl, trochlea metatarsi IV of tarsometatarsus with large trochlea accessoria: no (0), yes (1).
36. Musculus flexor hallucis longus: tendon supplying hallux (0), tendon not supplying hallux (1); (see Mayr *et al.* 2003).

