

Fig. 4. *Plesiocathartes kelleri* sp. nov., holotype (SMF-ME 3639), shoulder girdle. The arrows point to the processus procoracoideus of the coracoid. Abbreviations: **lc**—extremitas sternalis of left coracoid; **leo**—left extremitas omalis of furcula; **ls**—left scapula; **rc**—extremitas sternalis of right coracoid; **reo**—right extremitas omalis of furcula; **rs**—right scapula. Coated with ammonium chloride, scale bar = 5 mm.

cathartes kelleri from a number of avian taxa. For example, in the Cuculidae (cuckoos) and Musophagidae (turacos), the ulna is shorter or about as long as the humerus. Since a short ulna occurs in the palaeognathous Tinamidae and most Galloanseres, the latter are considered by most recent authors (e.g., Sibley and Ahlquist 1990) to be the sister taxon of all other Neornithes (but see also Ericson et al. 2001). This ulnar length is here considered to be plesiomorphic within neornithine birds. Phylogenetically relevant details of the proximal and distal ends of the bone unfortunately cannot be discerned in either specimen. The papillae remigales are weakly developed.

Carpometacarpus: The carpometacarpus is elongated and slender, and, as far as it can be observed, it closely resembles the corresponding bone of *Leptosomus discolor* (Fig. 5C). The os metacarpale minus runs parallel to the os metacarpale majus, the processus extensorius is protruding and of similar shape to that of *Leptosomus*. In neither specimen, how-

ever, can it be discerned whether the os metacarpale minus protrudes farther distally than the os metacarpale majus, as in *Leptosomus*.

Pelvis: Details of the pelvis are not visible in either specimen.

Femur: The femur is similar to that of *Leptosomus* in its proportions. As in the latter, and contrary to most other birds, the caput femoris is not globular, but proximodistally narrow. This feature is here considered to be a putative synapomorphy of *Plesiocathartes* and *Leptosomus* (see below). The trochanter femoris is only weakly developed.

Tibiotarsus: The distal end of the tibiotarsus corresponds to that of *Leptosomus* (Fig. 5D) in that the trochlea cartilaginosa tibialis is very short in proximo-distal direction (visible on the holotype). This feature is absent in most other neornithine birds including the Cathartidae (Fig. 5E), and it is here considered to be another putative synapomorphy of *Plesiocathartes* and *Leptosomus* (see below). Although the tibiotarsus is unknown from *Plesiocathartes europaeus*, it is preserved in the associated remains of the yet unnamed species from the Geiseltal (Figs. 1A-B).

Tarsometatarsus: The tarsometatarsus (Fig. 6) is about as long as the carpometacarpus. It also closely resembles the corresponding bone of *Leptosomus* in overall morphology. In both specimens, the hypotarsus is hidden by the overlying distal end of the tibiotarsus. The shaft is compressed in dorso-plantar direction, has an equal width over most of its length, and a rectangular cross-section in its middle part. It appears to have been slightly narrower than the tarsometatarsus of *P. europaeus*. The crista mediano-plantaris extends only over 1/5 of the entire length of the bone, cristae plantares mediales et laterales are present (Fig. 6). The distal end of the bone is poorly preserved in the holotype. In the referred specimen HLMD Be 162, however, it is in an uncrushed condition and enough details are visible to reveal that it exhibits the same morphology as the three dimensionally preserved distal tarsometatarsus of the London Clay specimen of *Plesiocathartes* sp., which is described below. The foramen vasculare distale is small (HLMD Me 162, left side). The trochlea metatarsi II is small, as is the fossa metatarsi I, which is located on the medial margin of the shaft (HLMD Be 162).

Toes: All toes have the usual number and proportions of pedal phalanges. The third toe exceeds the others in length, but it is slightly shorter than the tarsometatarsus. The hallux is of similar relative length to that of extant Leptosomidae. The claws are of average size and moderately curved. The processus articularis tarsometatarsalis of the os metatarsale I is short.

Feathering: The wing feathering is well preserved in specimen HLMD Be 162 (Fig. 7). The longest primary measures about 110 mm, the secondaries have a length of about 94 mm. A single tail feather is preserved, which measures about 85 mm. In contrast to the tail feathers of extant Leptosomidae, it exhibits a distinct barring (Fig. 8; barred

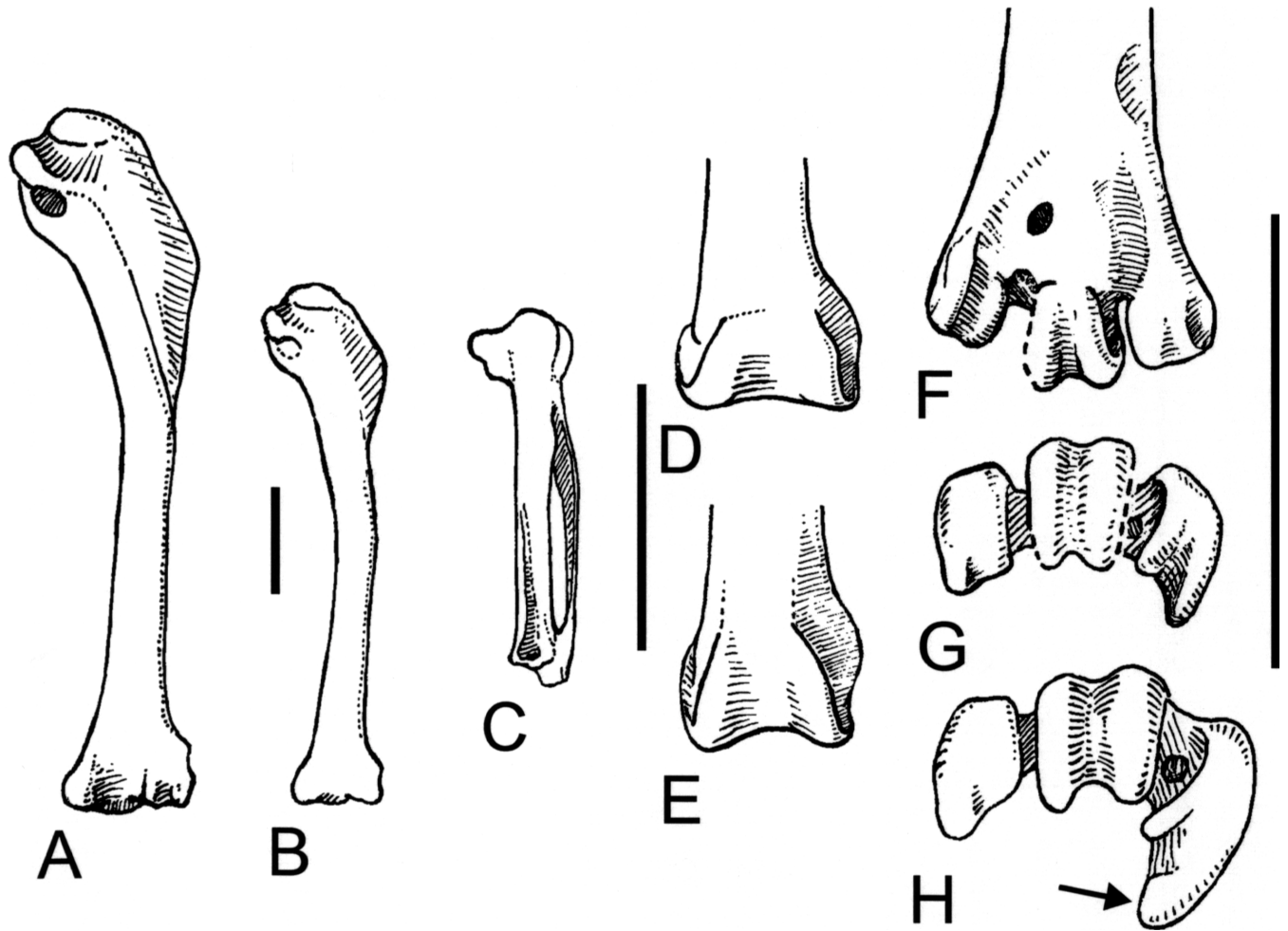


Fig. 5. Selected skeletal elements of *Plesiocathartes* (?Leptosomidae), *Leptosomus discolor* (Leptosomidae), and *Sarcoramphus papa* (Cathartidae). A. *L. discolor*, right humerus in caudal view. B. *P. kelleri* sp. nov., right humerus in caudal view. C. *Leptosomus discolor*, left carpometacarpus in dorsal view. D. *L. discolor*, distal end of left tibiotarsus in caudal view, showing the proximo-distally short trochlea cartilaginis tibialis. E. *S. papa*, distal end of left tibiotarsus in caudal view. F. *Plesiocathartes* sp. (BMNH A 6178), distal end of left tarsometatarsus in plantar view. G. *Plesiocathartes* sp. (BMNH A 6178), distal end of left tarsometatarsus in distal view. H. *L. discolor*, distal end of left tarsometatarsus in distal view, the arrow points to the enlarged wing-like flange on the trochlea metatarsi IV. Scale bars = 10 mm; same scale for A-C, D-E, and F-H.

tail feathers are also known from other Messel birds, e.g., Mayr 1998b).

Plesiocathartes sp.

Referred Specimen—BMNH A 6178, distal end of left tarsometatarsus from the lower Eocene London Clay (stratigraphic division D-E) of Warden Point, Sheppey Island, England, collected by M. Collinson in 1978, Figs. 1F-H.

Measurements (in mm)—Length as preserved, 10.0; distal width across trochleae, 6.2; width of trochlea metatarsi III, 2.2.

Description and comparison—This species is similar in size to *Plesiocathartes kelleri* sp. nov., and, thus, also slightly smaller than *P. europaeus* which it otherwise closely resembles in morphology. The fossa metatarsi I is very small and located on the medial margin of the shaft. The trochlea meta-

tarsi III also is small and, contrary to that of *Leptosomus*, it is wider in dorsoplantar than in mediolateral direction. The trochlea metatarsi II reaches slightly farther distally than the trochlea metatarsi IV. It is somewhat smaller than in extant Leptosomidae and accordingly the incisura intertrochlearis medialis is wider. *L. discolor* has a semi-zygodactyl foot, i.e., it is able to spread the fourth toe laterally, and thus the trochlea metatarsi IV bears a distinct wing-like flange (Fig. 5H). This flange is only weakly developed in BMNH A 6178, as in the other species of *Plesiocathartes* (Fig. 5). A marked sulcus ("outer extensor groove" of Howard 1929) passes into the foramen vasculare distale (Fig. 1G). As in *L. discolor*, a foramen interosseus distalis is present. This foramen which is probably plesiomorphic within neornithine birds, and which is not to be confused with the foramen vasculare distale, is absent in

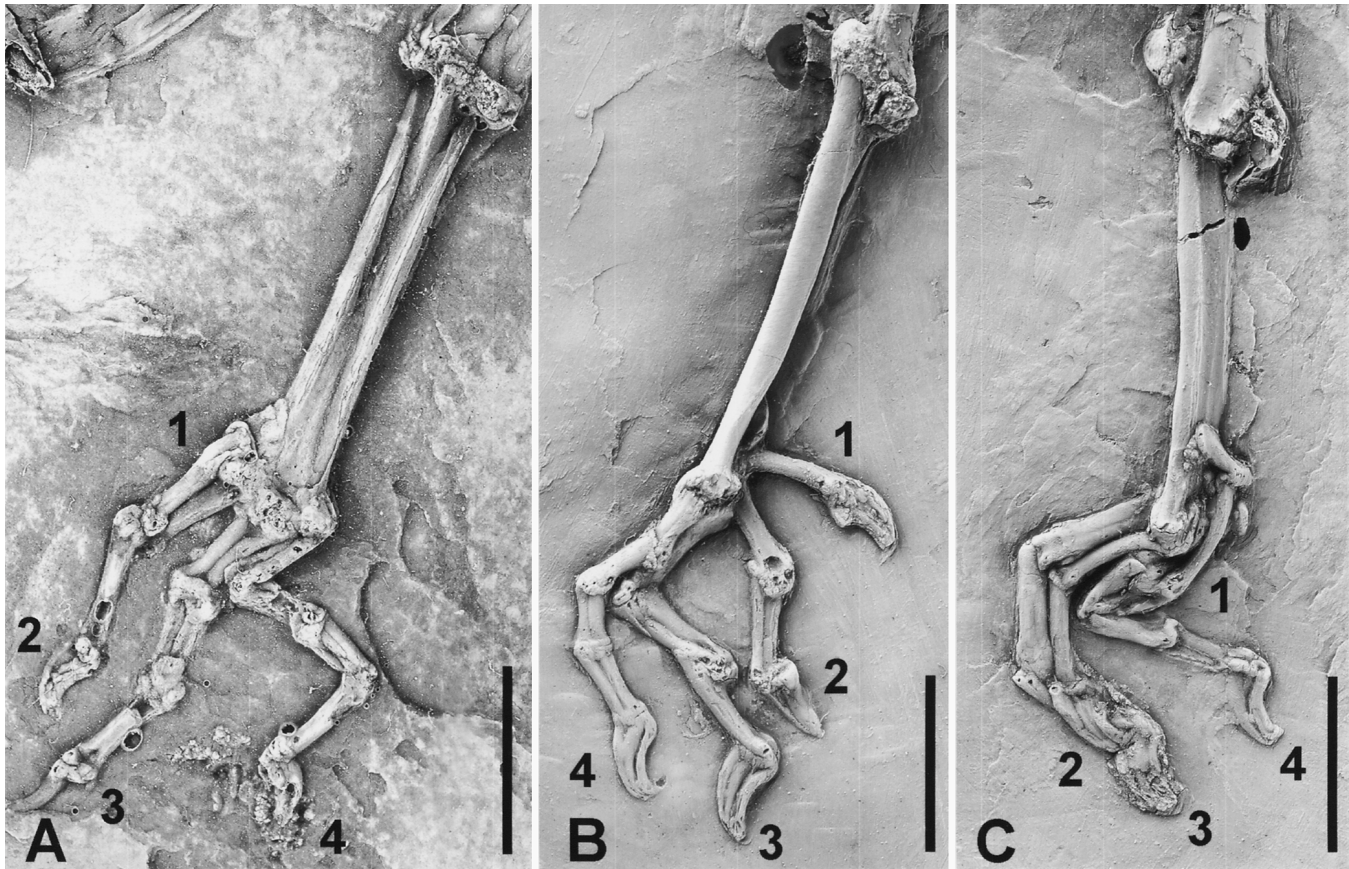


Fig. 6. *Plesiochathartes kelleri* sp. nov., feet. A. Holotype (SMF-ME 3639), right foot. B. Referred specimen (HLMD Be 162), left foot. C. Referred specimen (HLMD Be 162), right foot. The toes are numbered, coated with ammonium chloride, scale bar = 10 mm.

most of the more derived (“higher” *sensu* Olson 1985) landbirds.

DISCUSSION

The species of the genus *Plesiochathartes* are much smaller than any of the extant New World vultures and, as shown by the specimens of the new species from Messel, *Plesiochathartes* lacked a hooked, raptorial beak. Assignment of the fossil genus to the Cathartidae has not been convincingly established with derived characters. Cracraft and Rich (1972: 275) listed a “deep anterior metatarsal groove [= sulcus extensorius] and the relative position of the trochleae.” However, the first feature occurs in many other neornithine birds and the latter is poorly defined. The tarsometatarsus of *Plesiochathartes* more closely resembles that of the Leptosomidae with which it was not compared by earlier authors.

The skeletons of *Plesiochathartes kelleri* sp. nov. further agree in the following three derived osteological features with the Leptosomidae: (1) humerus distinctly bent in its mid-section, if the bone is viewed from its cranial or caudal side (this feature occurs in only a few other taxa, e.g., falconiform birds of the genus *Falco*, and it is absent in basal neornithine birds, e.g., the palaeognathous Tinamidae and

the Galloanseres); (2) caput femoris proximodistally narrow (in basal neornithine birds and in the Cathartidae the caput femoris is globular); (3) distal end of tibiotarsus with proximo-distally short condyles and a proximo-distally short trochlea cartilaginosa tibialis, width across the condyles greater than height of trochlea cartilaginosa tibialis (this feature unquestionably is derived within extant birds and only found in few other taxa, such as parrots, Psittaciformes, and diurnal raptors, Falconiformes; in most other taxa, including the Cathartidae, the height of the trochlea cartilaginosa tibialis is greater than the width across the condyles, see Figs. 5D-E).

In addition, the tarsometatarsus of the Geiseltal species of *Plesiochathartes* exhibits two distinct furrows on the hypotarsus (Fig. 1C), most likely for the tendons of *musculus flexor hallucis longus* and *m. flexor digitorum longus*. The hypotarsus of *Leptosomus* is perforated by two probably homologous canals, whereas in basal neornithine birds there is either no or just a single canal or furrow; the hypotarsus of the Cathartidae is block-like and lacks furrows or canals. Either the complete absence of furrows and canals or the presence of a single furrow is here considered to be the primitive condition within neornithine birds.

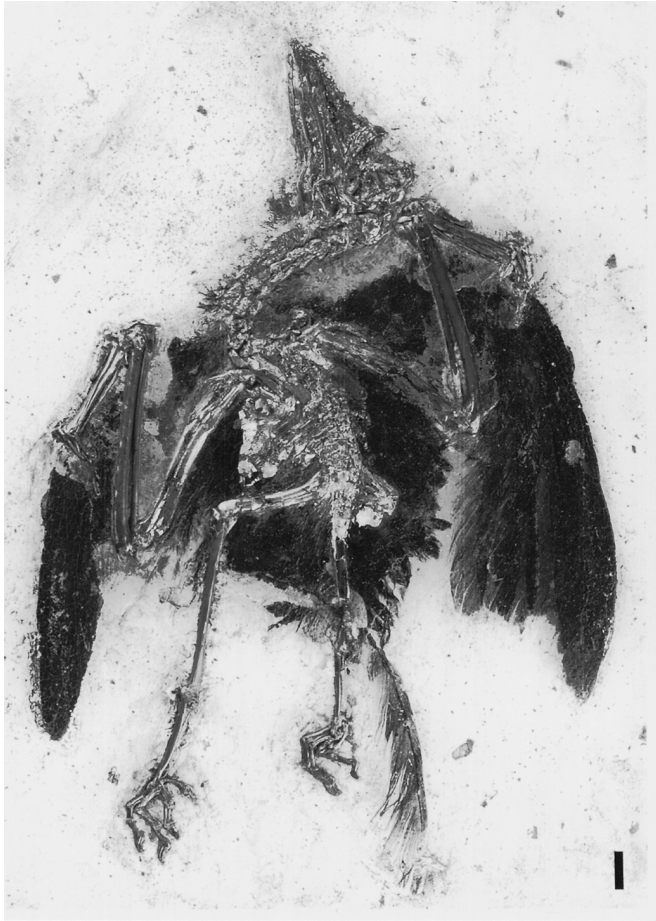


Fig. 7. *Plesiocathartes kelleri* sp. nov., referred specimen (HLMD Be 162). Scale bar = 10 mm.

Although only the above listed derived characters shared by *Plesiocathartes* and *Leptosomus* are observable in the known specimens, it has to be emphasized that the fossil genus is very similar to extant cuckoo-rollers in overall morphology of most skeletal elements, and is clearly distinguished from all other fossil or extant taxa of which the skeleton is sufficiently known. For example, extant turacos (Musophagidae) and the superficially similar ?cuculiform early Eocene family Foratidae described by Olson (1992) differ from *Plesiocathartes* in the shape of the beak, the much shorter and stouter ulna which does not exceed the humerus in length, the shorter carpometacarpus, the more elongated tarsometatarsus, and the different proportions of the pedal phalanges.

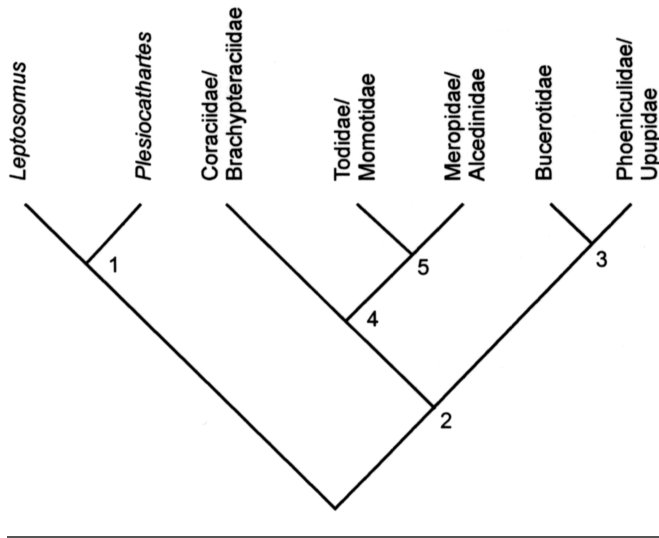
Plesiocathartes kelleri mainly differs from *Leptosomus discolor* in the proportionally somewhat shorter wing. Whereas the hindlimb elements of the two species are about the same size, the humerus, ulna, and carpometacarpus of *P. kelleri* measure only about 3/4 of the length of the corresponding bones of extant Leptosomidae. As can be deduced from the absence of a distinct wing-like flange on the trochlea for the fourth toe (Fig. 5H), *P. kelleri* lacks semi-zygodactyl feet



Fig. 8. *Plesiocathartes kelleri* sp. nov. (HLMD Me 162), tail feather. Note the distinct barring which is absent in extant Leptosomidae. Scale bar = 10 mm.

which, in accordance with Cracraft (1971: 745), are here considered to be an autapomorphic feature of extant Leptosomidae.

Cuckoo-rollers are generally classified in the Coraciiformes and are considered to be closely related to typical rollers (Coraciidae) and ground-rollers (Brachypteraciidae) (e.g., Maurer and Raikow 1981, Sibley and Ahlquist 1990, Goodman 2001). However, a cladistic phylogenetic analysis of coraciiform birds based on morphological characters did not support monophyly of cuckoo-rollers and rollers, but instead showed the Leptosomidae to be basal to a clade including rollers, upupiform and alcediniform birds (Mayr 1998c, Fig. 9). Monophyly of Leptosomidae, Coraciidae, and Brachypteraciidae was also questioned by Herremanns and Louette (1992), who considered the phylogenetic position of the Leptosomidae “not too far from the Cuculiformes.” Tertiary fossil specimens of the Leptosomidae have not yet been described, but rollers are known since the early Eocene (Mayr and Mourer-Chauviré 2000; contrary to the



statement in Kirchman et al. 2001, however, these do not belong to the Brachypteraciidae, but to an extinct family).

In summary, available evidence more convincingly supports a tentative assignment of *Plesiothartes* to the Leptosomidae than any alternative classification (Fig. 9). Although extant Leptosomidae are endemic to the Madagascar region, there is agreement that "*Leptosomus* evidently originated from an early invasion of Madagascar, well before that which gave rise to the ground rollers" (Burton 1984: 426, see also Cracraft 1971: 745). Thus, the presence of stem group representatives of the Leptosomidae in the early Tertiary of Europe might not be completely unexpected.

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LITERATURE CITED

- Baumel, J.J., and L.M. Witmer. 1993. Osteologia. pp. 45-132 in J.J. Baumel, A.S. King, J.E. Breazile, H.E. Evans, and J.C. Vanden Berge (eds.). Handbook of avian anatomy: Nomina anatomica avium. *Publications of the Nuttall Ornithological Club* No. 23.
- Burton, P.J.K. 1984. Anatomy and evolution of the feeding apparatus in the avian orders Coraciiformes and Piciformes. *Bulletin of the British Museum (Natural History)*, Zoology Series 47:331-443.

◀ **Fig. 9.** Tentative phylogenetic hypothesis concerning the relationships between *Plesiothartes*, *Leptosomus*, and the possibly paraphyletic (e.g., Burton 1984, Mayr 1998c) "coraciiform" birds; the phylogeny of the recent taxa is based on the cladistic analysis of Mayr (1998c). Among others (see Mayr 1998c), the nodes are supported by the following derived characters: **node 1**—(1) humerus distinctly bent in its mid-section; (2) caput femoris proximodistally narrow; (3) distal end of tibiotarsus with proximo-distally short condyles and proximo-distally short trochlea cartilaginis tibialis; (4) hypotarsus with two tendineal canals or furrows respectively; **node 2**—(1) sternum with well developed, blade-like spina externa; (2) hypotarsus strongly protruding in plantar direction and passing into a well developed crista medianoplantaris; (3) trochlea metatarsi IV rotund in lateral view; (4) feet syndactyl (i.e., basal phalanges of at least the third and fourth toe linked by connective tissue, cf. Stresemann 1927-34: 828-832); **node 3**—(1) mandible with rectangular or trapezoid cross-section in proximal area of pars symphysialis and more or less well developed processus retroarticularis; (2) coracoid with very wide facies articularis sternalis; (3) extremitas omalis of furcula widened and with short processus acromialis; (4) hypotarsus, tendon of musculus flexor hallucis longus enclosed in bony canal; (5) musculus pterygoideus with "retractor palatini" slip (Burton 1984); (6) musculus flexor metacarpi ulnaris attached to os metacarpale minus (usually this muscle is attached to the os metacarpale majus, see Stegmann 1965); (7) musculus pectoralis, pars propatagialis longus tendinous (Maurer and Raikow 1981); **node 4**—(1) condylus medialis of quadratum greatly elongated; (2) scapula with bifurcate acromion (see Mayr 1998c: fig. 16); (3) tarsometatarsus with very marked fossa parahypotarsalis medialis, proximal part of margo medialis forming a sharp ridge; (4) musculus scapulotriceps without humeral anchor (Maurer and Raikow 1981); (5) nestlings naked or only sparsely feathered at hatching; **node 5**—(1) skull with distinct nasofrontal hinge; (2) columella with large, hollow, bulbous basal and footplate area exhibiting a large fenestra on one side (Feduccia 1977); (3) scapi claviculae of furcula very narrow at extremitas sternalis; (4) carpometacarpus with os metacarpale minus distinctly exceeding os metacarpale majus in length; (5) first phalanx of hallux with proximal end greatly widened (Mayr 1998c: fig. 20F); (6) second and third toe coalescent for part of their length; (7) tendon of musculus flexor hallucis longus not supplying hallux (Maurer and Raikow 1981); (8) musculus abductor digiti II reduced (Maurer and Raikow 1981).

Note that monophyly of the clade including all taxa shown in this figure cannot be conclusively shown.

- Cracraft, J. 1971. The relationships and evolution of the rollers: Families Coraciidae, Brachypteraciidae, and Leptosomidae. *Auk* 88:723-752.
- Cracraft, J., and P.V. Rich. 1972. The systematics and evolution of the Cathartidae in the Old World Tertiary. *Condor* 74:272-283.
- Crusafont, M., and J.F. de Villalta. 1955. Parte Paleontológica. Apéndice I. Aves. pp. 236-237 in M. Crusafont, J.F. de Villalta, and Y.J. Truyols (eds.). El Burdigaliense continental de la Cuenca del Vallés-Penedés. *Memorias y Comunicaciones del Instituto Geológico, Diputación provincial de Barcelona* 12.

- Emslie, S.D. 1988. An early condor-like vulture from North America. *Auk* 105:529–535.
- Ericson, P.G.P., T.J. Parsons, and U.S. Johansson. 2001. Morphological and molecular support for nonmonophyly of the Galloanseres. pp. 157–168 in J. Gauthier, and L.F. Gall (eds.). *New Perspectives on the Origin and Early Evolution of Birds*. Peabody Museum of Natural History. New Haven, Connecticut.
- Feduccia, A. 1975. Morphology of the bony stapes (columella) in the Passeriformes and related groups: Evolutionary implications. *University of Kansas Museum of Natural History Miscellaneous Publications* 63:1–34.
- Gaillard, C. 1908. Les oiseaux des Phosphorites du Quercy. *Annales de l'Université de Lyon (Nouvelle Série)* 23:1–178.
- Goodman, S.M. 2001. Family Leptosomidae (Cuckoo-rollers). pp. 390–395 in J. del Hoyo, A. Elliott, and J. Sargatal (eds.). *Handbook of the Birds of the World, volume 6: Mousebirds to Hornbills*. Lynx Edicions, Barcelona.
- Herremanns, M., and M. Louette. 1992. Sexual dimorphism in the juvenile plumage of the Courol *Leptosomus discolor* and considerations on its affinities. *Bulletin of the British Ornithologists' Club* 112:182–185.
- Howard, H. 1929. The Avifauna of Emeryville Shellmound. *University of California Publications in Zoology* 32:301–394.
- Kirchman, J.J., S.J. Hackett, S.M. Goodman, and J.M. Bates. 2001. Phylogeny and systematics of ground rollers (Brachypteraciidae) of Madagascar. *Auk* 118:849–863.
- Legendre, S., and F. Lévêque. 1997. Etalonnage de l'échelle biochronologique mammalienne du Paléogène d'Europe occidentale: Vers une intégration à l'échelle globale. pp. 461–473 in J.-P. Aguilar, S. Legendre, and J. Michaux (eds.). *Actes du Congrès Biochrom'97. Mémoires et Travaux de l'Ecole Pratique des Hautes Etudes, Institut de Montpellier* 21.
- Maurer, D., and R.J. Raikow. 1981. Appendicular myology, phylogeny, and classification of the avian order Coraciiformes (including Trogoniformes). *Annals of the Carnegie Museum of Natural History* 50:417–434.
- Mayr, G. 1998a. A new family of Eocene zygodactyl birds. *Senckenbergiana lethaea* 78:199–209.
- Mayr, G. 1998b. Ein Archaeotrogon (Aves: Archaeotrogonidae) aus dem Mittel-Eozän der Grube Messel (Hessen, Deutschland)? *Journal für Ornithologie* 139:121–129.
- Mayr, G. 1998c. «Coraciiforme» und «piciforme» Kleinvoegel aus dem Mittel-Eozän der Grube Messel (Hessen, Deutschland). *Courier Forschungsinstitut Senckenberg* 205:1–101.
- Mayr, G. 2000a. Avian remains from the Middle Eocene of the Geiseltal (Sachsen-Anhalt, Germany). *Vertebrata Palasiatica* 38 (Supplement):19–20.
- Mayr, G. 2000b. Die Vögel der Grube Messel—ein Einblick in die Vogelwelt Mitteleuropas vor 49 Millionen Jahren. *Natur und Museum* 130:365–378.
- Mayr, G. in press. Avian remains from the Middle Eocene of the Geiseltal (Sachsen-Anhalt, Germany). Proceedings of the 5th meeting of the Society of Avian Paleontology and Evolution (SAPE). China Science Press, Beijing.
- Mayr, G., and M. Daniels. 1998. Eocene parrots from Messel (Hessen, Germany) and the London Clay of Walton-on-the-Naze (Essex, England). *Senckenbergiana lethaea* 78:157–177.
- Mayr, G., and M. Daniels. 2001. A new short-legged landbird from the early Eocene of Wyoming and contemporaneous European sites. *Acta Palaeontologica Polonica* 46:393–402.
- Mayr, G., and C. Mourer-Chauviré. 2000. Rollers (Aves: Coraciiformes s.s.) from the middle Eocene of Messel (Germany) and the Upper Eocene of the Quercy (France). *Journal of Vertebrate Paleontology* 20:533–546.
- Mourer-Chauviré, C. 1982. Les oiseaux fossiles des Phosphorites du Quercy (Éocène supérieur à Oligocène supérieur): Implications paléobiogéographiques. pp. 413–426 in E. Buffetaut, P. Janvier, J.C. Rage, and P. Tassy (eds.). *Phylogénie et paléobiogéographie. Livre jubilaire en l'honneur de Robert Hoffstetter. Geobios, Mémoire Spéciale* 6.
- Mourer-Chauviré, C. 2000. Revision of the Cathartidae (Aves, Ciconiiformes) from the middle Eocene to late Oligocene of Phosphorites du Quercy, France. *Vertebrata Palasiatica* 38 (Supplement):21.
- Olson, S.L. 1985. The fossil record of birds. pp. 79–238 in D.S. Farner, J.R. King, and K.C. Parkes (eds.). *Avian Biology, volume 8*. Academic Press, New York.
- Olson, S.L. 1992. A new family of primitive landbirds from the lower Eocene Green River Formation of Wyoming. pp. 127–136 in K.E. Campbell (ed.). *Papers in Avian Paleontology honoring Pierce Brodkorb. Natural History Museum of Los Angeles County, Science Series* 36.
- Sánchez Marco, A. 1996. Tertiary avian localities of Spain. pp. 719–732 in J. Mlíkovsky (ed.). *Tertiary Avian Localities of Europe. Acta Universitatis Carolinae, Geologica* 39.
- Schaal, S., and W. Ziegler. 1988. Messel—Ein Schaufenster in die Geschichte der Erde und des Lebens. Kramer, Frankfurt a. M.
- Sibley, C., and J.E. Ahlquist. 1990. *Phylogeny and classification of birds: a study in molecular evolution*. Yale University Press, New Haven, Connecticut.
- Stegmann, B. 1965. Funktionell bedingte Eigenheiten am Metacarpus des Vogelflügels. *Journal für Ornithologie* 106:179–189.
- Stresemann E. 1927–34. Aves. pp. 1–899 in W. Kükenenthal, and T. Krumbach (eds.). *Handbuch der Zoologie, volume 7*. Walter de Gruyter, Berlin and Leipzig.
- Vanden Berge, J.C., and G.A. Zweers. 1993. Myologia. pp. 189–247 in J.J. Baumel, A.S. King, J.E. Breazile, H.E. Evans, and J.C. Vanden Berge (eds.). *Handbook of avian anatomy: Nomina anatomica avium. Publications of the Nuttall Ornithological Club* No. 23.