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ROLLERS (AVES: CORACIIFORMES S.S.) FROM THE MIDDLE EOCENE OF MESSEL (GERMANY) AND THE UPPER EOCENE OF THE QUERCY (FRANCE)

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ABSTRACT—The rollers (Aves: Coraciiformes sensu stricto) from the Middle Eocene of Messel (Hessen, Germany) and the Upper Eocene of the Quercy (France) are described. The ''Messel-roller'' *Eocoracias brachyptera*, gen. et sp. nov. is the earliest certain record of rollers known so far and is classified within the new family Eocoraciidae. New excavations in the Quercy and a revision of the earlier collections have produced additional skeletal material which can be assigned to *Geranopterus alatus* Milne-Edwards, 1892. This species so far has been known from an isolated humerus only. A new species, *Geranopterus milneedwardsi*, is described from the Upper Eocene of the Quercy and mainly differs from *G. alatus* in its smaller size. The genus *Geranopterus* is classified within the new family Geranopteridae which is shown to be the sister taxon of the two recent families Brachypteraciidae and Coraciidae. The Eocoraciidae are the sister taxon of the Coracioidea (Geranopteridae and recent rollers). Outgroup comparison with the basal rollers described in this study suggests that the fairly long wing of the Coraciidae and the elongated tarsometatarsus of the Brachypteraciidae are derived features of these families.

INTRODUCTION

The Coraciiformes sensu stricto (= Coraciiformes s.s., terminology after Mayr, 1998) comprise two recent families: The typical rollers (Coraciidae) with the Old World genera *Coracias* and *Eurystomus*, and the Madagascan ground-rollers (Brachypteraciidae) with the genera *Brachypteracias*, *Geobiastes*, *Atelornis*, and *Uratelornis* (as detailed below we separate *Geobiastes squamigera* generically from *Brachypteracias leptosomus*). Coraciidae and Brachypteraciidae have been classified into the ''superfamily'' Coracioidea by Cracraft (1971). Generally the Madagascan cuckoo-rollers (Leptosomidae, with the single species *Leptosomus discolor*) are thought to be the closest relatives of the Coraciiformes s.s. (e.g., Mayr and Amadon, 1951; Wetmore, 1960; Cracraft, 1981; Maurer and Raikow, 1981). Yet, a monophyly of the taxon (Coraciiformes s.s. + Leptosomidae) has not been convincingly established with derived characters so far, and is neither supported by the DNA-DNA hybridization data of Sibley and Ahlquist (1990:fig. 70) (although these authors maintained the traditional classification), nor by a phylogenetic analysis performed by Mayr (1998).

Rollers are medium-sized, stoutly-built birds with a robust beak. Many species have a brightly colored plumage. The Coraciidae are strong flyers which show characteristic display flights from which the English term ''roller'' has been derived. They perch on open sites from which they swoop to catch small animals (larger insects and invertebrates, small vertebrates) on the ground, the genus *Eurystomus* is specialized for chasing after flying insects. In contrast thereto, the Brachypteraciidae, although having a similar diet to that of the Coraciidae, are more terrestrial and pursue their prey while running on the ground.

So far, the fossil record of rollers consists of a single named taxon, *Geranopterus alatus* Milne-Edwards 1892, from the Upper Eocene fissure fillings of the Quercy (France). Its description was based on the humerus only (Milne-Edwards, 1892; Gaillard, 1908) but more recent excavations have produced additional material that includes most of the major skeletal elements. These new specimens of *Geranopterus alatus* have mainly been found at the locality Escamps which has an absolute age of 35 million years (Legendre and Lévêque, 1997). Together with a revision of the early collections they made it possible to ascribe additional skeletal elements to *Geranopterus* (from Escamps no other coraciiform birds of comparable size are known).

A new avian taxon which can be referred to the Coraciiformes s.s. has also been identified in the 49 million years old Middle Eocene deposits of Messel (Hessen, Germany; for description of the site see Schaal and Ziegler, 1988). These birds are about 14 million years older than the remains of *G. alatus* and as such are the earliest certain record of rollers known so far (Houde and Olson, 1989, reported facultatively zygodactyl Lower Eocene roller-like birds from the North American Willwood and Green River Formations which, however, have not yet been studied in detail).

Institutional Abbreviations—The fossil specimens are deposited in the Hessisches Landesmuseum, Darmstadt, Germany (**HLMD**); the Muséum d'Histoire naturelle de Lyon, Lyon, France (**MHN**); the Muséum d'Histoire naturelle of Basel, Switzerland (**MHN**); the Muséum national d'Histoire naturelle, Paris, France (**MNHN**); the Forschungsinstitut Senckenberg, Frankfurt a. M., Germany (**SMF**); the Staatliches Museum für Naturkunde, Karlsruhe, Germany (**SMNK**); the Université Claude Bernard, Lyon, France (**UCB**); and the Université des Sciences et Techniques du Languedoc, Montpellier, France (**USTL**). For comparisons we examined skeletons of *Coracias garrulus*, *C. abyssinica*, *Eurystomus glaucurus*, *E. gularis*, *Geobiastes squamigera*, *Atelornis crossleyi*, and *Leptosomus discolor* in the collections of the SMF, the MNHN, the Museum für Naturkunde, Berlin, the collection Pierce Brodkorb, University of Gainesville, Florida, the National Museum of Natural History, Washington, and the American Museum of Natural History, New York. In addition, skeletons of representatives of all higher avian taxa have been studied. If not indicated otherwise, the osteological terminology follows Baumel and Witmer (1993).

SYSTEMATIC PALEONTOLOGY

AVES Linnaeus, 1758
CORACIIFORMES S.S. (cf. Mayr, 1998)

Diagnosis—The Coraciiformes s.s. (Eocoraciidae, fam. nov. + Coracioidea) can be characterized by the following charac-

ters: (1) processus postorbitalis (skull) very long and (nearly) touching the jugale; (2) sternum with well-developed blade-like spina externa; (3) ventral side of proximal end of os metacarpale minus with small tubercle; (4) hypotarsus large and protruding. Outgroup comparison with primitive Mesozoic birds (e.g., Hesperornithiformes) and the palaeognathous Tinamiformes suggest that these features are derived within neognathous birds. Characters (1) and (3) are also present in the Leptosomidae which are distinguished in the absence of characters (2) and (4).

EOCORACIIDAE, fam. nov.

Type Genus—*Eocoracias,* gen. nov.

Included Genera—Type genus only.

Diagnosis—The Eocoraciidae, fam. nov. are the sister taxon of the Coracioidea since they exhibit the derived features of the Coraciiformes s.s., but lack the process on the cranial side of the processus postorbitalis and the well developed processus intermetacarpalis (carpometacarpus) which are synapomorphic for the Coracioidea (see below). The new family is further distinguished from Brachypteraciidae and Coraciidae in that the maxilla is dorsoventrally wider below the narial openings, the processus acrocoracoideus (coracoid) is shorter, and the extremitas omalis of the furcula is more slender. Probably autapomorphic for the new family is the strongly abbreviated tarsometatarsus.

EOCORACIAS, gen. nov.

Type Species—*Eocoracias brachyptera,* sp. nov.

Included Species—Type species only.

Diagnosis—Only genus of the family, diagnosis as for family.

Differential Diagnosis—*Eocoracias,* gen. nov. differs from *Geranopterus,* Milne-Edwards 1892 in the much smaller processus intermetacarpalis (carpometacarpus) and the more abbreviated tarsometatarsus.

Etymology—Greek *eos,* dawn and *Coracias.*

EOCORACIAS BRACHYPTERA, sp. nov.
(Figs. 1–7)

Holotype—SMNK.PAL.2663a+b (complete articulated skeleton on two slabs; Fig. 1).

Type Locality—Messel (Hessen, Germany).

Type Horizon—Geiseltalium, Lower Middle Eocene (see Franzen and Haubold, 1986).

Referred Specimens—SMF-ME 1452a+b (cranial half of articulated skeleton on two slabs; Fig. 2); HLMD-Me 10474 (slab with nearly complete articulated skeleton; Fig. 3).

Dimensions—see Tables 1 and 2.

Etymology—Greek *brakhypteros,* short-winged.

Diagnosis—Only species of the genus, therefore diagnosis same as for genus. *Eocoracias brachyptera,* gen. et sp. nov. is about the size of the recent *Eurystomus glaucurus afer.*

Remarks—In specimen HLMD-Me 10474 the former content of the stomach or the intestinal tract is preserved in form of a single large (11.3 × 5.5 mm), coffee-bean shaped seed surrounded by fine grit. Although a systematic assignment of this seed has not yet been possible, its mere presence is of interest since only some recent Coraciidae are known to rarely eat fruits (Langrand, 1990; Keith et al., 1992).

Description and Comparison—The skull (Fig. 4) is large in relation to the body and in its overall appearance is similar to that of recent rollers. Like in the latter the frontale is well developed and roughly rectangular-shaped (SMF-ME 1452a). The processus postorbitales are long and nearly touch the jugale in SMNK.PAL.2663a. The short projection on the cranial side of the processus postorbitalis which is characteristic for the Coraciidae (Fig. 4A) and Brachypteraciidae is absent and the processus postorbitalis of *Eocoracias* thus more closely resembles the corresponding element of *Leptosomus.* The processus zygomaticus (SMF-ME 1452a) is long and thin as in the Brachypteraciidae and Coraciidae (it is absent in the Leptosomidae). The interorbital septum seems to have been strongly ossified (HLMD-Me 10474). The beak is robust as in all other rollers. It measures approximately half the length of the entire skull and is thus distinctly longer than the beak of *Eurystomus,* but slightly shorter than that of *Coracias* and the Brachypteraciidae. The culmen curves gradually towards the tip of the bill, whereas it is rather straight in *Coracias* and the Brachypteraciidae. In contrast to recent rollers, the narial openings of *Eocoracias* appear to have been slit-like, the part of the maxilla below is much wider than in the Coraciidae and Brachypteraciidae (SMNK.PAL.2663a, SMF-ME 1452a, HLMD-Me 10474). The narial openings of the latter two families are peculiar in that they are separated by an osseous bridge in two halves; this feature cannot be discerned in *Eocoracias.* The rami mandibulae are fairly straight and similar to those of recent rollers. They become only slightly narrower towards the tip of the beak, a fenestra mandibulae is not visible. The pars symphysialis measures somewhat less than one fifth of the entire length of the mandible. In all specimens except HLMD-Me 10474 ossified tracheal rings are preserved.

The cervical vertebrae allow no detailed comparisons but, as far as comparable, they do not differ from those of the Coracioidea. Like in the latter the third but not the fourth cervical vertebra bears an osseous bridge connecting the zygapophysis cranialis with the zygapophysis caudalis (HLMD-Me 10474, SMNK.PAL.2663). The processus costales are long. The tenth cervical vertebra exhibits a short processus ventralis (HLMD-Me 10474) while the three most caudal thoracic vertebrae lack processus ventrales. The number of praesacral vertebrae cannot be determined with certainty, but it seem to have been approximately 19 like in extant rollers. Seven free tail vertebrae can be counted (SMNK.PAL.2663) which is in concordance with Brachypteraciidae and Coraciidae; the pygostyle is small.

Five sternal ribs are preserved in HLMD-Me 10474 and this number corresponds with the Coraciidae (in the specimen of *Geobiastes squamigera* we investigated, only four sternal ribs reach the sternum, in *Leptosomus* a very feeble fifth cranial sternal rib articulates with the sternum).

The extremitas omalis of the coracoid (SMF-ME 1452b) differs from that of the Coracioidea in the shorter processus acrocoracoideus and in the smaller facies articularis clavicularis (Fig. 5A). The cotyla scapularis is shallow (SMF-ME 1452b). The processus procoracoideus (HLMD-Me 10474, SMNK.PAL. 2663b) is well developed but due to preservation it cannot be compared in detail with that of recent rollers. A foramen nervi supracoracoidei is not visible (this foramen is present in the Leptosomidae but absent in the Coracioidea).

The furcula (HLMD-Me 10474, SMF-ME 1452a) is broadly U-shaped. The scapus claviculae becomes wider towards the extremitas omalis although the latter is more slender than in the Coracioidea. The extremitas sternalis is narrow and there is no apophysis furculae. In recent rollers, the apophysis furculae is also absent in *Eurystomus,* present in *Coracias,* and especially well developed in *Atelornis* and *Geobiastes* (we did not examine the furcula of *Brachypteracias* and *Uratelornis*).

The sternum corresponds well with that of the Coraciidae. The margo caudalis bears four incisions (SMF-ME 1452a), the incisura lateralis is deeper than the incisura medialis. Whereas the distal end of the trabeculae laterales is transversally widened, that of the trabeculae intermediae is narrow. In the Brachypteraciidae both incisions are deeper (see Cracraft, 1971:fig. 10). The carina sterni is moderately high and similar to that of

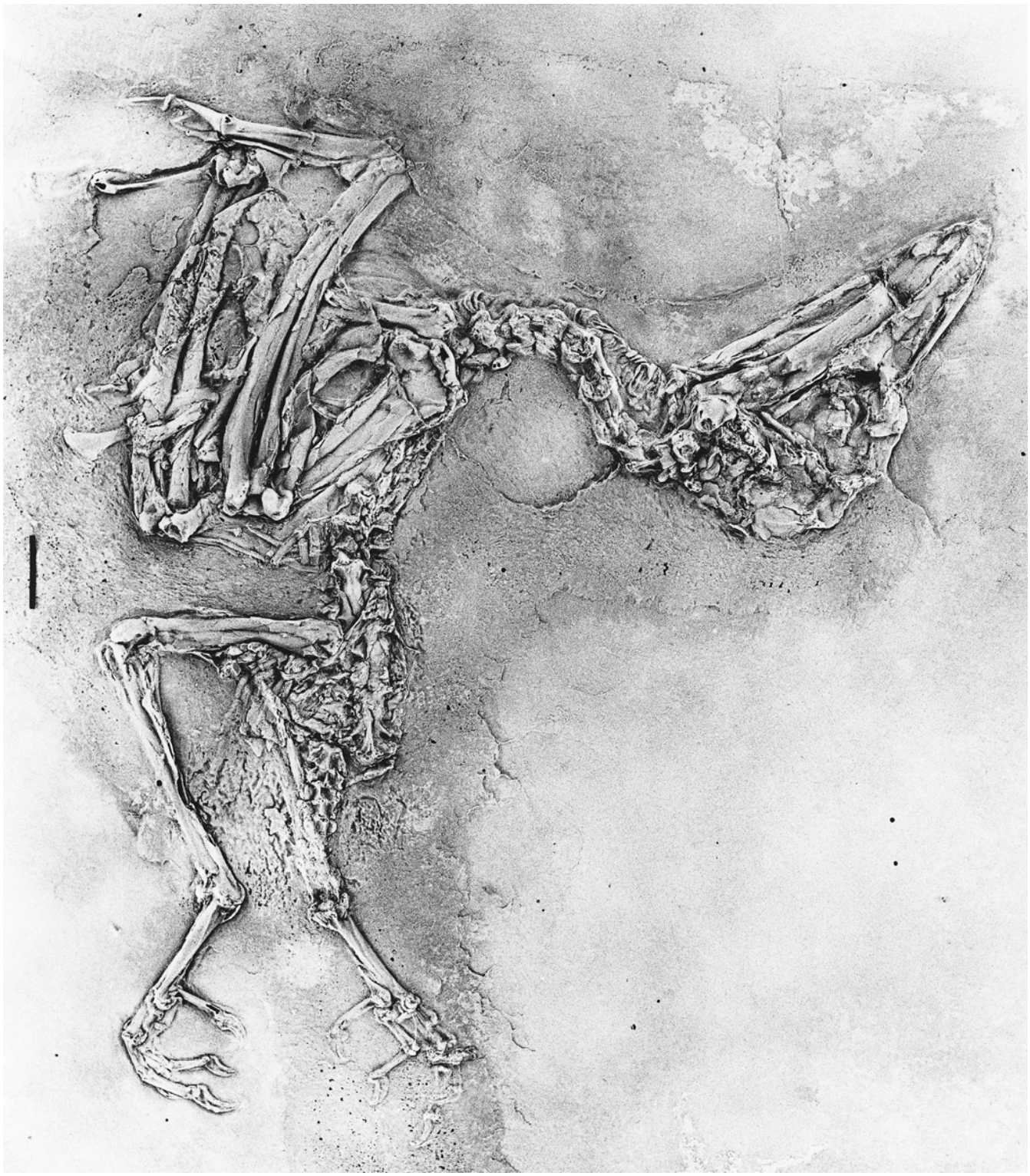

FIGURE 1. *Eocoracias brachyptera*, gen. et sp. nov., holotype (SMNK.PAL.2663a). Coated with ammonium chloride to enhance contrast. Scale bar equals 10 mm.

Coracias garrulus, the apex carinae is shifted cranially. The spina externa (SMF-ME 1452a) is well developed and bladelike as in the Coraciidae and Brachypteraciidae. The processus craniolaterales are short and also resemble those of extant rollers (HLMD-Me 10474).

The humerus matches well with that of *Geranopterus alatus*; when compared with recent rollers it is more similar to the humerus of the Brachypteraciidae than to that of the Coraciidae (and Leptosomidae). The crista bicipitalis is small (well developed in the Coraciidae and Leptosomidae) and the crista del-

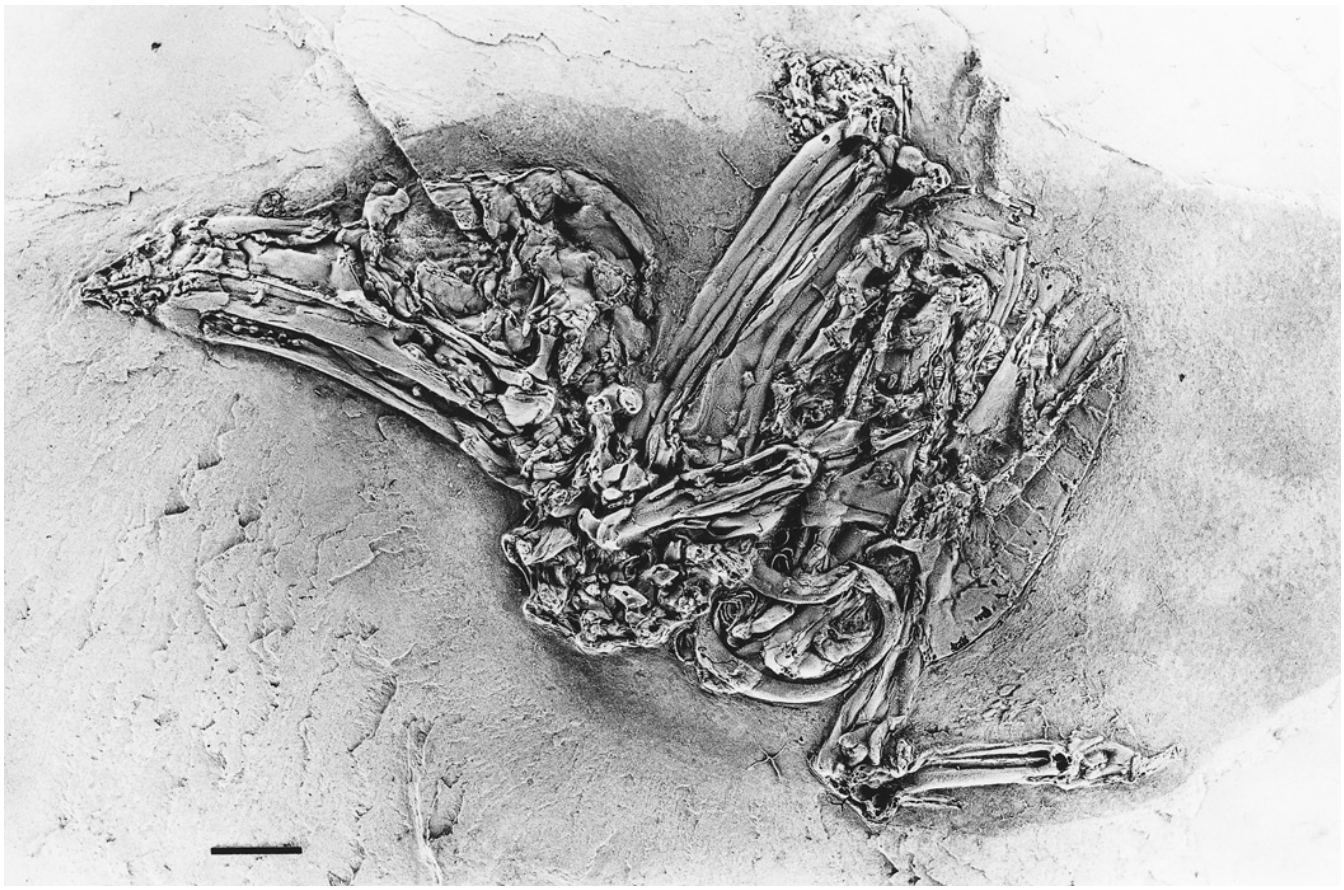

FIGURE 2. *Eocoracias brachyptera,* gen. et sp. nov., referred specimen (SMF-ME 1452a). Coated with ammonium chloride to enhance contrast. Scale bar equals 10 mm.

topectoralis is rather short measuring approximately one fifth of the length of the humerus. The impressio coracobrachialis (HLMD-Me 10474) is distinct. The ventral edge of the distal end of the humerus reaches farther medially than in the Brachypteraciidae and Coraciidae (SMF-ME 1452a). The tuberculum supracondylare ventrale is not as large and protruding as in the Coraciidae.

The ulna is distinctly longer than the humerus but detailed comparisons are not possible in any of the specimens. The olecranon is well-developed, but not as large as in the Brachypteraciidae. The processus cotylaris dorsalis (SMNK.PAL.2663a) appears to have been more similar to that of the Brachypteraciidae than to that of the Coraciidae.

The carpometacarpus resembles that of the Coraciidae in its proportions but is shorter relative to the other limb elements. The carpometacarpus of the Brachypteraciidae is much more abbreviated, the trochlea carpalis can be distinguished in that the portion of the ventral rim just proximal to the os metacarpale minus is absent (see Cracraft, 1971). The os metacarpale minus of *Eocoracias* is straight and the ventral side of its proximal end bears a small tubercle which is also present in *Geranopterus* and in recent rollers (HLMD-Me 10474). The processus extensorius of the os metacarpale alulare is fairly long and resembles that of *Coracias.* The sulcus tendineus is distinct. The processus intermetacarpalis is very small and much shorter than that of the Coracioidea.

Compared with extant rollers, the hand of *Eocoracias* is shorter relative to the other wing elements. The incisura metacarpalis of the os carpi ulnare appears to have been much wider, the crus breve and the crus longum shorter (SMNK.PAL.2663a).

Only a few details of the pelvis are visible. The cranial part is mediolaterally narrow, the lateral margin of the alae praeacetabulares ilii nearly straight. The cristae iliacae dorsales do not meet the crista dorsalis of the synsacrum (SMNK.PAL.2663b).

In all specimens the femur is too poorly preserved for detailed comparisons. The tibiotarsus is short and appears to have been similar to that of the Coraciidae. Especially its proximal end (SMNK.PAL.2663) differs from the proximal tibiotarsus of the Brachypteraciidae in that the cristae cnemiales are not enlarged. The distal end of the bone seems to have been mediolaterally narrow (SMNK.PAL.2663a) but cannot be compared in detail.

The tarsometatarsus is very short and has the same absolute size and similar proportions like that of the recent *Eurystomus glaucurus afer*. It measures roughly half the length of the tibiotarsus. The hypotarsus is protruding and appears to have been similar to that of recent rollers in its shape (details of its structure, however, are not visible). Both a crista medialis hypotarsi and a crista lateralis hypotarsi are present (SMNK.PAL. 2663a). The ventral side of the shaft of the tarsometatarsus bears a crista medianoplantaris and a shallow crista lateralis which, like in *Coracias garrulus,* describes a convex arc if the tarsometatarsus is viewed from the lateral side. As far as comparable, the distal end of the tarsometatarsus (SMNK.PAL.2663a) is similar to that of the Coracioidea. The foramen vasculare distale appears to have been rather small

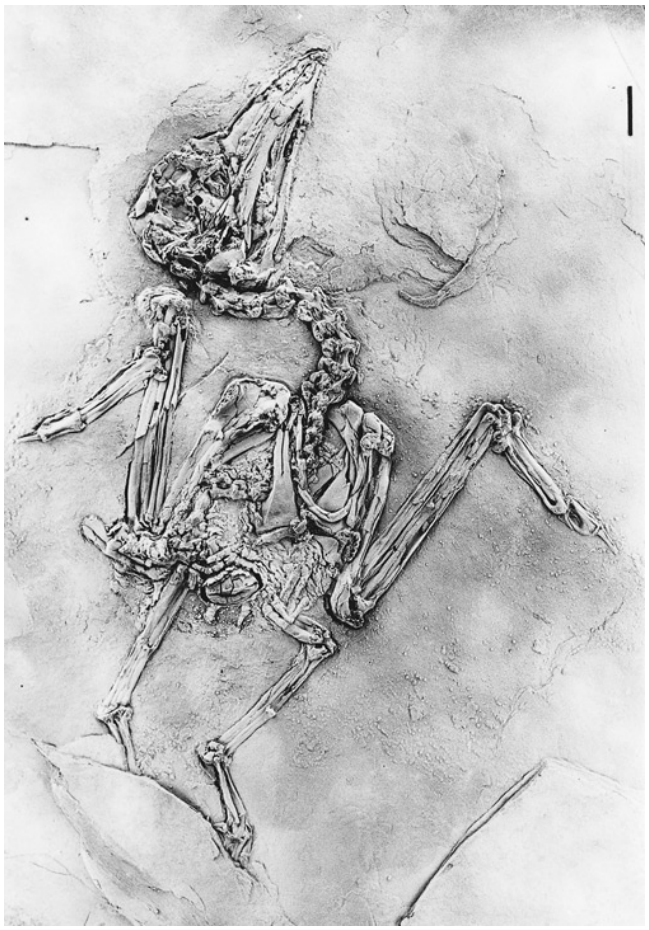

FIGURE 3. *Eocoracias brachyptera,* gen. et sp. nov., referred specimen (HLMD-Me 10474). Coated with ammonium chloride to enhance contrast. Scale bar equals 10 mm.

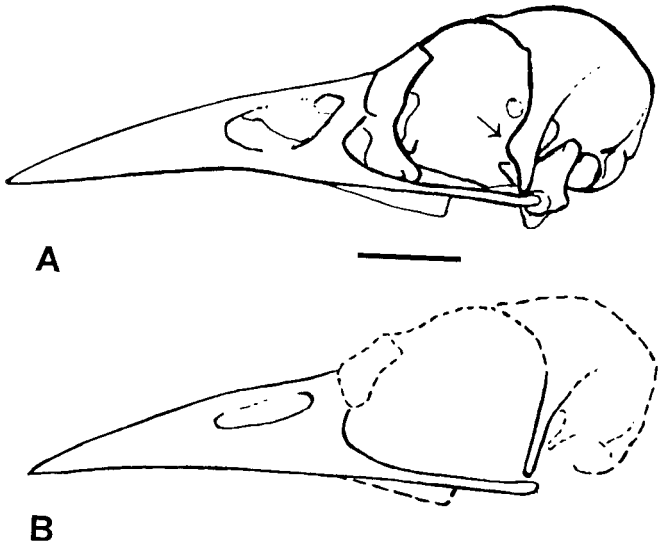

FIGURE 4. Skull in comparison. **A**, *Coracias garrulus.* **B**, *Eocoracias brachyptera.* The arrow indicates the projection on the cranial side of the processus postorbitalis in *Coracias garrulus.* Scale bar equals 10 mm.

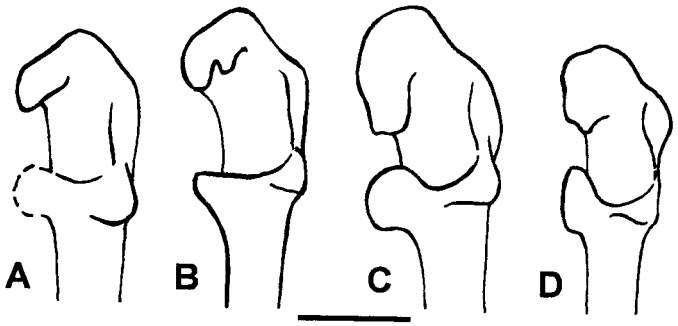

FIGURE 5. Extremitas omalis of the coracoid of rollers in comparison. **A**, *Eocoracias brachyptera.* **B**, *Geranopterus alatus.* **C**, *Coracias garrulus.* **D**, *Geobiastes squamigera.* Scale bar equals 5 mm.

(SMNK.PAL.2663a) whereas it is large in the Brachypteraciidae. Like in the Coracioidea the distal end of the tarsometatarsus is only slightly curved on the level of the trochleae metatarsorum (SMNK.PAL.2663a). The trochlea metatarsi IV reaches almost as far distally as the trochlea metatarsi III and is round in lateral view, the incisura intertrochlearis lateralis is narrow (wider in *Geobiastes*).

The toes have the usual phalange formula. The third toe is the longest, the second toe is slightly shorter than the fourth. The hallux is well developed and inserts farther proximally than the three anterior toes. The processus tarsometatarsalis of the os metatarsale I is long as in the Coraciidae (both the hallux and the processus tarsometatarsalis are shorter in the Brachypteraciidae). The claws are moderately curved and resemble

FIGURE 6. *Eocoracias brachyptera,* gen. et sp. nov., holotype (SMNK.PAL.2663a). Scale bar equals 10 mm.

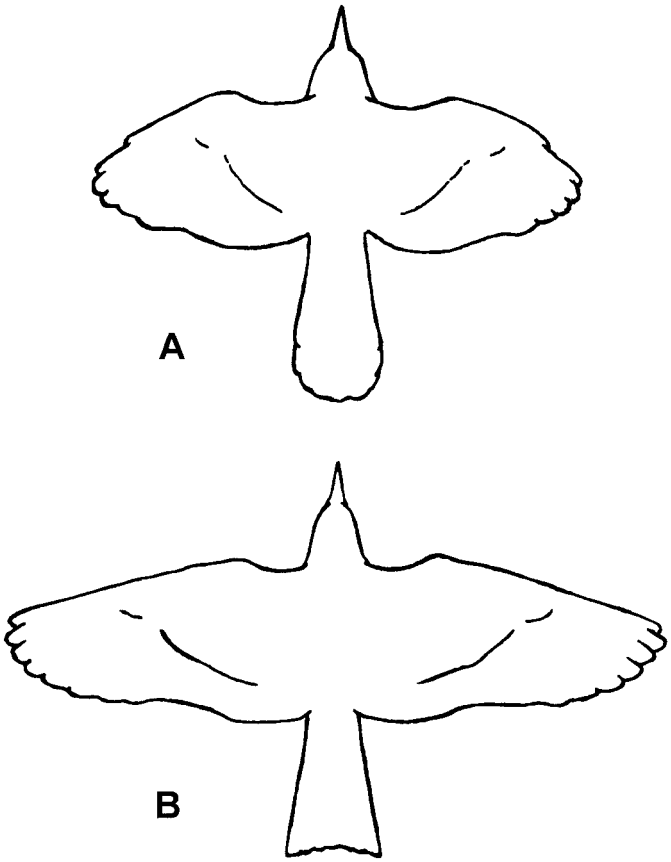

FIGURE 7. Feathering of Coraciidae and Brachypteraciidae in comparison. **A**, *Geobiastes squamigera* (Brachypteraciidae). **B**, *Coracias garrulus* (Coraciidae). The feathering of *Eocoracias brachyptera* gen. et sp. nov. corresponds with that of the Brachypteraciidae.

those of recent rollers. The claw of the third toe is distinctly longer than the other claws. In all specimens the toes cluster close together. This might indicate a syndactyl foot, i.e., the attachment of the basal ends of the anterior phalanges by connective tissue, as is typical for recent rollers but absent in *Leptosomus* (if one assumes that the ligaments linking the proximal ends of the phalanges do not disintegrate earlier than the ligaments which connect the other skeletal elements).

In all specimens feather remains are preserved and the feathering of the wing and the tail corresponds well with that of most Brachypteraciidae (except *Uratelornis* which has an unusually long tail), but differs from the feathering of the Coraciidae (Figs. 6, 7). As in the ground-rollers the wing is short and rounded; it measures about 112 mm from the carpal joint to the tip of the longest primary (SMNK.PAL.2663a). The wing of the Coraciidae is distinctly longer relative to the body size, in the slightly larger *Eurystomus glaucurus afer,* for example, it measures about 165 mm. The tail is fairly long, like in the Brachypteraciidae the length of the feathers is graduated with the outer tail feathers being shorter than the inner ones (in SMNK.PAL.2663 the inner rectrices measure about 90 mm, the outer ones only about 50 mm). In the Coraciidae all rectrices either have the same length (e.g., *Coracias naevia, C. benghalensis, C. temminckii*, *Eurystomus orientalis*) or the tail is more or less deeply forked (in *C. abyssinica, C. cyanogaster, C. caudata,* and *C. spatulata* the outer rectrices form long streamers). The exact number of the rectrices of *Eocoracias* cannot be counted in any of the specimens; recent rollers have 10 tail feathers.

CORACIOIDEA Cracraft, 1971

Emended Diagnosis—The Coracioidea are characterized by a well developed processus intermetacarpalis on the carpometacarpus. This feature is absent in all primitive Mesozoic birds, all palaeognathous birds and most neognathous birds, and thus certainly derived within the latter. The recent Coracioidea also share a unique short projection on the cranial side of the processus postorbitalis (Fig. 4), but it is uncertain if this character also was present in *Geranopterus* (see below).

GERANOPTERIDAE, fam. nov.

Type Genus—*Geranopterus* Milne-Edwards, 1892.

Included Genera—Type genus only.

Diagnosis—The Geranopteridae, fam. nov. exhibits the well developed processus intermetacarpalis which is diagnostic for the Coracioidea (see above). It is distinguished from the Brachypteraciidae and Coraciidae in the absence of the small foramen on the ventral side of the proximal part of the os metacarpale minus which seems to be synapomorphic for the two recent families (this character is not found in any other recent avian taxon and thus certainly is derived within neognathous birds). The Geranopteridae, fam. nov. is further characterized by a deep fossa on the ventral surface of the proximal carpometacarpus, between the processus pisiformis and the processus extensorius.

GERANOPTERUS Milne-Edwards, 1892

Included Species—*Geranopterus alatus* Milne-Edwards, 1892; *Geranopterus bohemicus* (Mlíkovský, 1999); *Geranopterus milneedwardsi,* sp. nov.

Remarks—*Cryptornis antiquus* (Gervais 1848–52) from the Upper Eocene of the Paris Basin was assigned to the hornbills (Bucerotidae) by Milne-Edwards (1867–71) but was later classified within the Coraciidae by Harrison (1979). The type specimen of *C. antiquus* is similar in size to *Geranopterus alatus* but unfortunately is too poorly preserved for detailed comparisons. It is neither possible to exclude the possibility that it is more closely related to *Geranopterus* nor that it is a hornbill with certainty. A definitive assignment, and an evaluation of the possible synonymy of the genera *Cryptornis* Milne-Edwards (1867–71) and *Geranopterus* Milne-Edwards (1892) must await the discovery of better preserved specimens of *C. antiquus.*

GERANOPTERUS ALATUS Milne-Edwards, 1892 (Figs. 8, 9)

Holotype—Early collections without locality. MNHN Paris: QU 15890 (left humerus, almost complete, Fig. 8A, B)

TABLE 1. *Eocoracias brachyptera,* gen. et sp. nov., dimensions of the major bones (left/right), maximum length in mm.

	skull	humerus	ulna	carpometacarpus	femur	tibiotarsus	tarsometatarsus
SMNK.PAL.2663	58	/~45	~54.3/~54.3	25.0/	32.1/	41.3/	18.2/18.2
SMF-ME 1452	63	~45.7/	54.5/~55	24.7/24.7	—	—	—
HLMD-Me 10474	55	44.4/44.7	-50.7/~51.0	24.4/24.4	—	36.4/36.2	18.1/

TABLE 2. *Eocoracias brachyptera,* gen. et sp. nov., dimensions of the pedal phalanges, in mm.

	I1	I2	II1	II2	II3	III1	III2	III3	III4	IV1	IV2	IV3	IV4	IV5
SMNK.PAL.2663	7.6	4.7	~6.0	~5.7	4.8	~6.1	6.7	7.3	6.9	~3.5	~4.1	~4.1	5.2	4.3

Referred Specimens—Early collections without locality. MNHN Paris: QU 15891 (right humerus, distal part and shaft); QU 16915 (right humerus, very juvenile); QU 16963 (left humerus, distal part and shaft, very juvenile); QU 16930 (right coracoid, cranial part, very juvenile); QU 17033 (right carpometacarpus, almost complete).

New excavations. Collection USTL Montpellier, locality Escamps (MP 19): EC3.1 (right humerus, proximal part); ECA 3201 (right humerus, distal part); ECC 3056 (right humerus, distal part and shaft); ECA 3203 (left humerus, proximal part); ECA 3202 (left humerus, distal part); ECC 3054 (left humerus, distal part); ECA 3205 (right ulna, distal part); ES.3 (right ulna, distal part); EC3.3 (radius, proximal part); ES.2 (right carpometacarpus, almost complete); EC3.4 (left carpometacarpus, proximal part); EC3.5 (left carpometacarpus, proximal part); ECX2 (left carpometacarpus, proximal part); EC4.2 (phalanx proximal digiti majoris); ECA 3209 (right coracoid, cranial part); EC4.1 (right coracoid, cranial part); EC3.2 (left coracoid, cranial part); ECC 3061 (right scapula, cranial part); ECX1 (left scapula, cranial part, juvenile); EC3.6 (right femur, distal part); EC4.4 (right femur, distal part); EC3.7 (right tibiotarsus, distal part); EC4.3 (right tibiotarsus, distal part); ES.4 (right tarsometatarsus, incomplete distal part); EC4.5 (left tarsometatarsus, distal part). Collection UCB Lyon, locality Gousnat (MP 18): FSL 330859 (right carpometacarpus, very abraded). Collection UCB Lyon, locality Rosières X (MP 19): FSL 330854 (right humerus, proximal part). Collection UCB Lyon, locality Pécarel (MP 19): FSL 330857 (left coracoid, cranial part); FSL 330858 (right ulna, distal part).

Dimensions—see Table 3.

Description and Comparison—The coracoids are represented only by cranial ends (Fig. 8C-F). The processus acrocoracoideus is well developed but less elongated than in the recent Coracioidea and the facies articularis clavicularis is craniocaudally shorter than in the latter (Fig. 5B). Like in the other Coracioidea there is a pneumatic foramen under the ledge of the facies articularis clavicularis. The cotyla scapularis is very shallow and the facies articularis humeralis has the same relative length as in the recent Coracioidea. The processus procoracoideus is almost completely preserved in specimen FSL 330857, only its extreme tip is missing. It is not a cranially and ventrally extended flattened blade as in the recent Coracioidea, but is pointed. A foramen nervi supracoracoidei is absent.

In the best preserved scapula (ECC 3061, Fig. 8P, Q) the acromion is subdivided into two projections, one directing laterally and one directing coastally. As in the recent Brachypteraciidae, but unlike in the recent Coraciidae, there is no pneumatic foramen on this cranial part.

In its proportions the humerus of *Geranopterus* more closely resembles that of the Brachypteraciidae than the humerus of the Coraciidae, in which the shaft is both craniocaudally and dorsoventrally less sinuous, the tuberculum dorsale more protruding and the crista bicipitalis more strongly developed. On the caudal surface of the proximal end of the humerus of the recent Coracioidea, there is a thin longitudinal line, situated practically on the median axis of the bone. At the base of the crus dorsale fossae this line turns in a right angle to reach the base of the crus dorsale before disappearing. In *Geranopterus,* this line is clearly visible but the part which turns in a right angle is not so well expressed as in *Coracias* and *Eurystomus.* The crista deltopectoralis has the same proportions as in the recent Coracioidea, while it is proportionally longer in the Leptosomidae. As in *Eocoracias,* the distal end of the humerus is more ventrally elongated in *Geranopterus* than in the recent Coraciidae but less than in the recent Brachypteraciidae. The impression of musculus brachialis is always well marked (except for the juvenile forms). The epicondylus ventralis projects more ventrally and distally and is thicker on the caudal surface, than in the recent Coracioidea. The condylus ventralis shows, on its cranial surface, an elongate and flattened facet which corresponds to the contact with the edge of the cotyla ventralis of the ulna. This facet also exists in the recent Coracioidea but is less developed. The tuberculum supracondylare dorsale is situated close to the distal end, while in the recent species *Coracias garrulus* and *Eurystomus gularis* it is situated more proximally. In general morphology, however, the shape of the distal end is very similar to that of the recent species *Coracias abyssinica.*

Only distal ends of ulnae are known which closely resemble those of the recent taxa (Fig. 8K, L). The condylus dorsalis extends far proximally and its proximal part is a tongue shaped articular surface which is raised above the surface of the shaft. The tuberculum carpale is pointed like in the Brachypteraciidae, whereas it is rather bladelike and proximodistally elongated in the Coraciidae.

In the Coraciidae and Brachypteraciidae, the proximal part of the os metacarpale minus is strongly widened and shows, on its ventral side, a pointed projection with a small foramen just distally below the point (Figs. 9N, P, 10). In *Geranopterus* the point on the ventral side of the os metacarpale minus looks rather like a tubercle and there is a fossa, just distally below the tubercle, not a foramen. The os metacarpale minus tapers progressively distally. The processus intermetacarpalis is strongly developed. The carpometacarpus of *Geranopterus* also differs from that of the Coracioidea in that the processus extensorius of the os metacarpale alulare does not project as far cranially. There is a depression on the dorsal surface of the os metacarpale alulare and a deep fossa on the ventral surface of the proximal part, between the processus pisiformis and the processus extensorius; both depression and fossa do not exist in the recent Coracioidea. As in the Brachypteraciidae, the facies articularis digitalis minor projects much more distally than the facies articularis digitalis major in *Geranopterus,* whereas in the Coraciidae these two facets are situated nearly at the same level. The carpometacarpus of *Geranopterus* differs from that of *Eocoracias* in the shorter processus extensorius of its os metacarpale alulare and in the well developed and proximodistally extended processus intermetacarpalis.

In *Geranopterus* the proximal articular surface of the phalanx proximalis digiti majoris of the wing has the same shape as in the recent genera but on the dorsal surface the outline of the tendinal groove is slightly different.

Only the distal parts of the femora, tibiotarsi, and tarsometatarsi are known. In *Geranopterus,* the distal part of the femur is proportionally more massive and the fossa poplitea is deeper than in the recent Coraciidae. As in the latter there is a small foramen on the caudal surface, at the bottom of the fossa poplitea. This foramen also exists in the recent Brachypteraciidae but in this family the fossa poplitea is distinctly deeper and the proximal edge of the condylus medialis projects strongly.

In the recent Coracioidea, the distal part of the tibiotarsus is mediolaterally compressed, the distal depth is larger than the distal width. Both, medial and lateral condyles are parallel and the incisura intercondylaris is deep and narrow. In *Geranopte-*

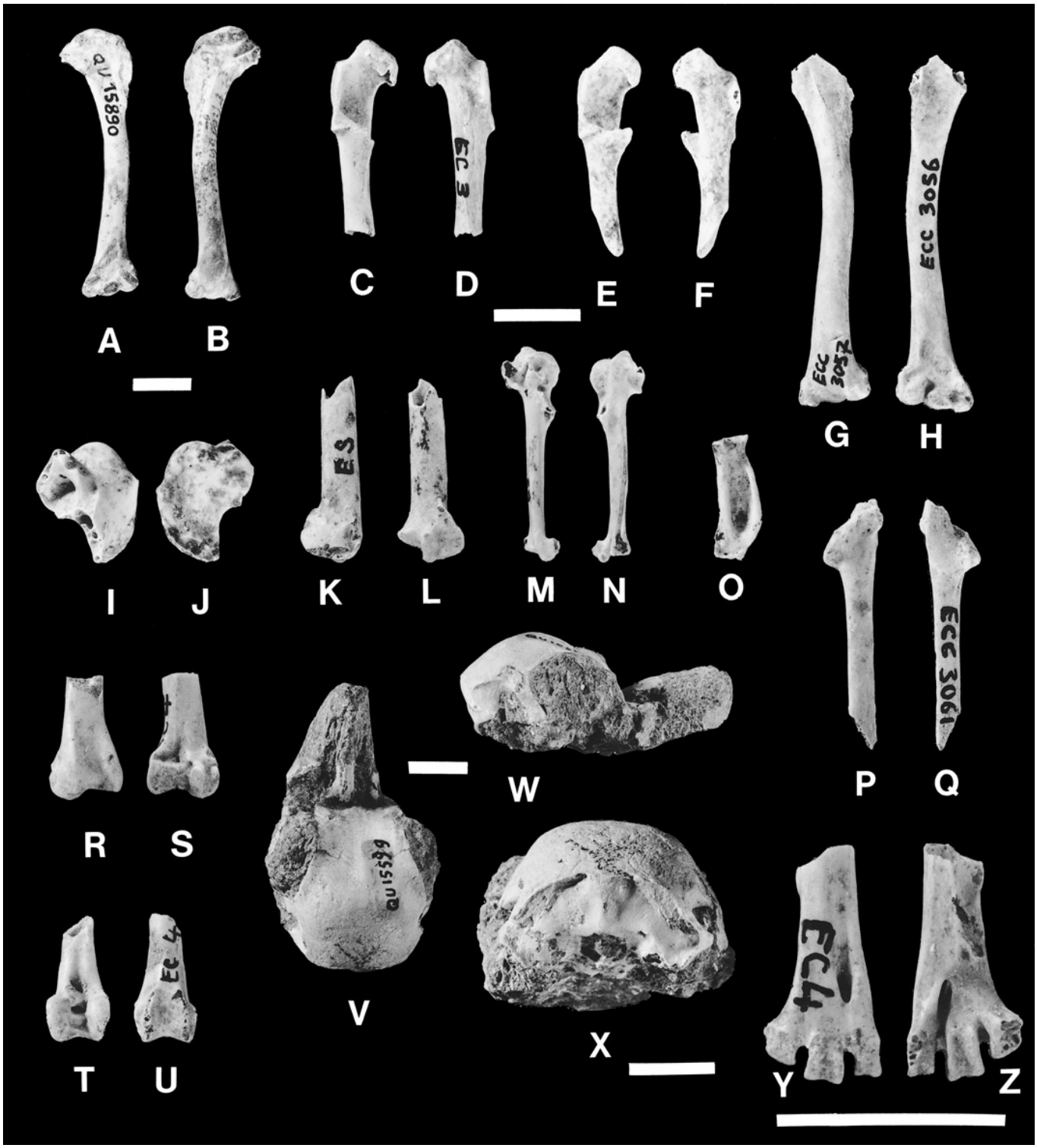

FIGURE 8. *Geranopterus alatus*: **A**, **B**, QU 15890, holotype left humerus, cranial (A) and caudal (B) views; **C**, **D**, EC3.2, left coracoid, extremitas omalis, (C) dorsal and (D) ventral views; **E**, **F**, FSL 330857, left coracoid, extremitas omalis, dorsal (E) and ventral (F) views, showing the almost complete processus procoracoideus; **G**, **H**, ECC 3056, right humerus, distal part and shaft, caudal (G) and cranial (H) views; **I**, **J**, FSL 330854, right humerus, proximal part, caudal (I) and cranial (J) views; **K**, **L**, ES.3, right ulna, distal part, caudal (K) and ventral (L) views; **M**, **N**, ES.2, right carpometacarpus, ventral (**M**) and dorsal (**N**) views; **O**, EC4.2, right proximal phalanx digiti majoris, ventral view; **P**, **Q**, ECC 3061, right scapula, cranial part, coastal (P) and lateral (Q) views; **R**, **S**, EC4.4, right femur, distal part, cranial (R) and caudal (S) views; **T**, **U**, EC4.3, right tibiotarsus, distal part, cranial (T) and caudal (U) views; **Y**, **Z**, EC4.5, left tarsometatarsus, distal part, dorsal (Y) and plantar (Z) views, showing the elongated, slit-like foramen vasculare distale, and the sulcus on the plantar surface, between the foramen vasculare distale and the incisura intertrochlearis lateralis.? *Geranopterus alatus*: **V–X**, QU 15599, skull, dorsal (V), right lateral (W), and caudal (X) views showing the wide processus postorbitalis (W) and the widely separated fossae temporales (X). All scale bars equal 10 mm (same scale bar for C–U).

TABLE 3. *Geranopterus alatus* Milne-Edwards, 1892 and *Geranopterus milneedwardsi*, sp. nov., dimensions of the long bones, in mm.

	Geranopterus alatus Milne-Edwards, 1892				*Geranopterus milneedwardsi*, sp. nov.			
	mean	range	s	n	mean	range	s	n
Humerus								
Total length	47.7	—	—	1	42 (est.)	—	—	1
Proximal width[1]	11.8	11.3–ca. 12	0.3	4	10.3	—	—	1
Proximal depth	5.5	5.2–5.8	0.3	3	5.2	5.0–5.4	0.3	2
Width midshaft	3.9	3.6–4.2	0.2	6	3.6	3.4–3.8	0.3	2
Depth midshaft	3.4	3.1–3.8	0.2	6	3.2	2.9–3.4	0.4	2
Distal width	9.5	9.2–10.0	0.3	6	8.6	8.0–9.1	0.8	2
Distal depth	4.8	4.5–5.3	0.3	6	4.2	4.1–4.2	0.1	2
Ulna								
Width midshaft	—	—	—	—	3.2	—	—	1
Depth midshaft	—	—	—	—	3.1	—	—	1
Depth cond. dorsalis	5.2	4.9–5.5	0.3	3	4.8	4.7–4.9	0.1	2
Distal width	4.5	4.4–4.5	0.1	3	4.2	4.2–4.2	0	2
Carpometacarpus								
Total length	26.1	25.0–27.1	1.5	2	—	—	—	—
Proximal width	3.4	3.1–3.9	0.3	5	—	—	—	—
Proximal depth	7.0	6.7–7.6	0.4	5	—	—	—	—
Width os metac. maj.[2]	2.5	2.4–2.6	0.1	5	—	—	—	—
Depth os metac. maj.[2]	2.3	2.1–2.5	0.2	5	—	—	—	—
Distal width	2.9	2.8–2.9	0.1	2	—	—	—	—
Distal depth	5.1	4.9–5.3	0.3	2	—	—	—	—
Phalanx prox. dig. maj.								
Total length	11.0	—	—	1	—	—	—	—
Coracoid								
Proximal width[3]	5.9	5.6–6.2	0.3	3	4.9	—	—	1
Depth of proc. acroc.	3.3	3.0–3.6	0.3	4	3.0	—	—	1
Width midshaft	2.7	2.5–2.9	0.3	2	—	—	—	—
Depth midshaft	2.4	2.1–2.6	0.4	2	—	—	—	—
Femur								
Distal width	6.4	6.4–6.4	0	2	—	—	—	—
Distal depth	5.1	5.0–5.2	0.1	2	—	—	—	—
Tibiotarsus								
Distal width	5.5	5.3–5.7	0.3	2	—	—	—	—
Distal depth	5.1	5.0–5.2	0.1	2	—	—	—	—
Tarsometatarsus								
Distal width	5.5	—	—	1	ca. 4.7	—	—	—
Distal depth	2.7	2.5–2.8	0.2	2	—	—	—	—
Depth trochlea met. III	2.4	2.3–2.4	0.1	2	2.2	—	—	1

[1]From the tuberculum dorsale to the ventral edge of the crista bicipitalis.
[2]In midsection.
[3]Measured on the dorsal surface, from the lateral side of the facies articularis humeralis to the medial side of the processus acrocoracoideus.

rus the distal tibiotarsus is not so compressed, the distal width is larger than the distal depth, the condyles are more divergent, the incisura intercondylaris is wider and shallower, and both epicondyles, medialis and lateralis, are more projecting.

So far no complete tarsometatarsus of *Geranopterus* has been found, the proximal end is unknown. The distal end closely resembles the distal tarsometatarsus of *Coracias* in its proportions and the tarsometatarsus of *Geranopterus* certainly was not as abbreviated as that of *Eocoracias.* Only one distal tarsometatarsus has all three trochleae preserved, which are very short and in distal view arranged on a weakly arched line. The trochlea metatarsi IV has the same length as the trochlea metatarsi III, the trochlea metatarsi II is slightly shorter. The foramen vasculare distale is widely open and has the shape of a slit, proximodistally elongated. It is situated at the distal end of a well indicated, deep and narrow groove (outer extensor groove of Howard, 1929). In a large number of birds there is another canal, the canalis interosseus distalis, which runs from the foramen vasculare distale to the incisura intertrochlearis lateralis. In the Coracioidea this canal is not covered by a bony blade and forms a deep, narrow sulcus on the plantar surface. In the Brachypteraciidae and in *Geranopterus* this sulcus is more clearly visible than in the recent Coraciidae, particularly in specimen EC4.5 in which the foramen vasculare distale is situated more proximally than in the other specimens, and in which the sulcus thus is longer. The distal tarsometatarsus of *Geranopterus* most closely resembles that of *Coracias,* but the shaft is more robust, the trochlea metatarsi II is less projecting, and, on the plantar surface, the fossa metatarsi I is more marked. It differs from the distal tarsometatarsus of *Eurystomus* in the wider shaft proximal to the trochleae and the less medially projecting trochlea metatarsi II. It differs from the Brachypteraciidae because in this family the foramen vasculare distale is oval-shaped and not situated at the distal end of a deep and narrow groove. Moreover, in the Brachypteraciidae there is a small depression above the incisura intertrochlearis medialis and the fossa metatarsi I is very shallow.

?*GERANOPTERUS ALATUS* Milne-Edwards, 1892
(Fig. 8V-X)

Tentatively Referred Specimen—Early collections without locality, MNHN Paris: QU 15599 (skull).

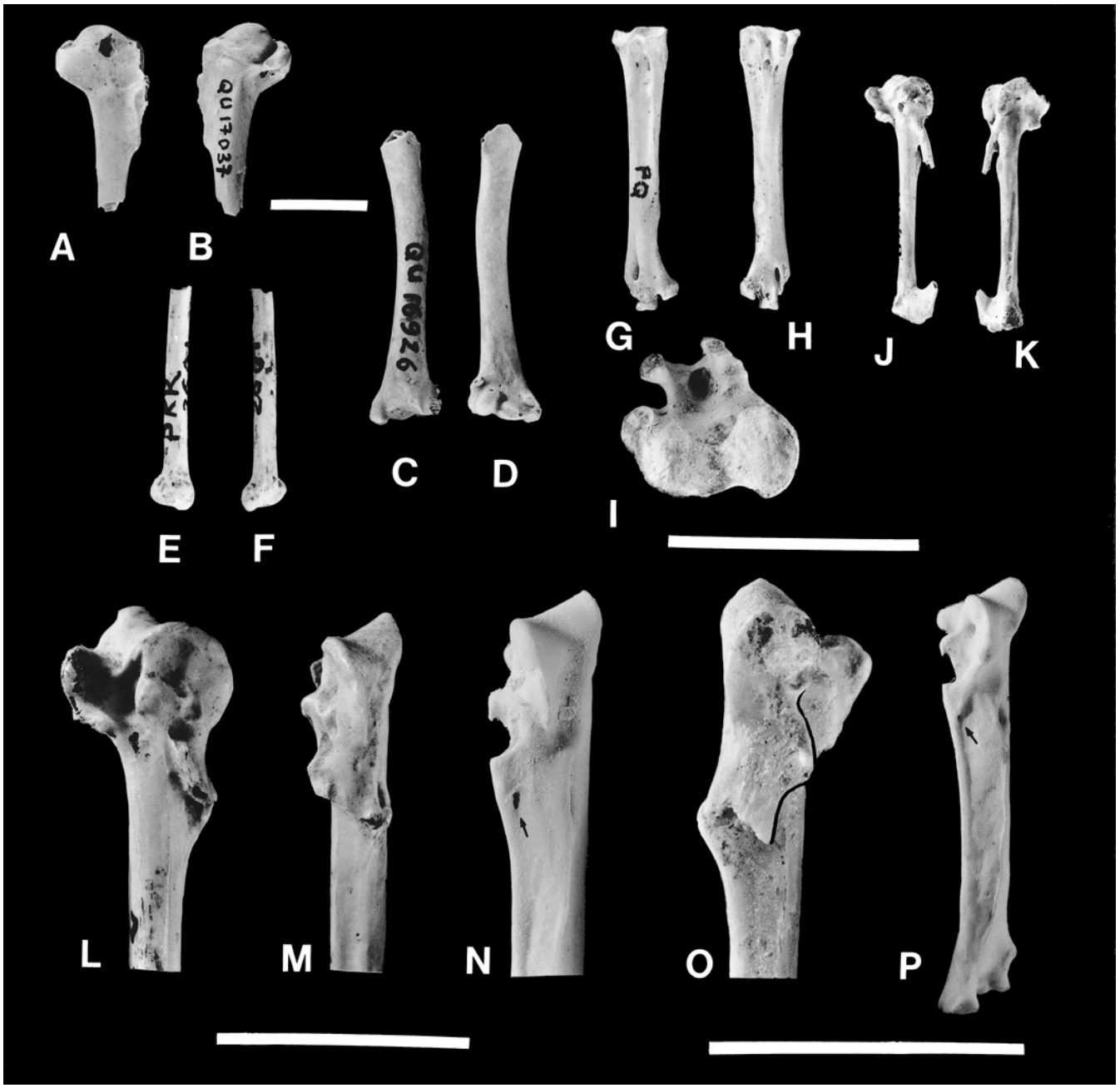

FIGURE 9. *Geranopterus milneedwardsi* sp. nov.: **A**, **B**, QU 17037, holotype left humerus, proximal part, cranial (A) and caudal (B) views; **C**, **D**, QU 16926, right humerus, distal part and shaft, caudal (C) and cranial (D) views; **E**, **F**, PRR 2601, radius, distal part, dorsal (E) and ventral (F) views. Coraciiformes s.s. incertae sedis, species A: **G–I**, PQ 1216, right tarsometatarsus, almost complete, dorsal (G), plantar (H), and proximal (I) views. Coraciiformes s.s. incertae sedis, species B: **J**, **K**, QU 15640, right carpometacarpus, almost complete, ventral (J) and dorsal (K) views. *Geranopterus alatus*: **L**, **M**, ES.2, right carpometacarpus, proximal part, ventral (L) view showing the deep fossa between the processus pisiformis and the processus extensorius, and caudal (M) view showing the point on the ventral side of the os metacarpale minus and the depression below this point; **O**, EC3.5, left carpometacarpus, proximal part (the ventral margin of the os metacarpale minus is outlined in black). *Coracias garrulus*, recent: **N**, Lyon 266–13, right carpometacarpus, proximal part, caudal view, showing the point and the small foramen (black arrow) situated below this point, on the ventral side of the os metacarpale minus. *Atelornis crossleyi*, recent: **P**, MNHN (IPH) 1309, right carpometacarpus, caudal view, showing the point and the small foramen (black arrow) below this point. All scale bars equal 10 mm (same scale bar for A–H and J–K).

Dimensions (in mm)—Minimum width at the level of the frontale, 15.0; width at the level of the processus postorbitales, 26.7; width on the caudal surface, at the level of the squamosa, 24.8; dorsoventral height, from the top of the frontale to the lamina parasphenoidalis, 19.3; maximum height of the beak at the level of the frontonasal hinge, 12.0; maximum width of the maxillaries at the same level, 18.0.

Description and Comparison—This skull has practically the same size and proportions as that of the recent species *Coracias abyssinica.* It differs from the skull of *Eurystomus* because it is less caudally widened at the level of the caudal part of the orbitae, and the bill is also much narrower at its caudal part. It differs from the skull of the Brachypteraciidae by its much wider frontale.

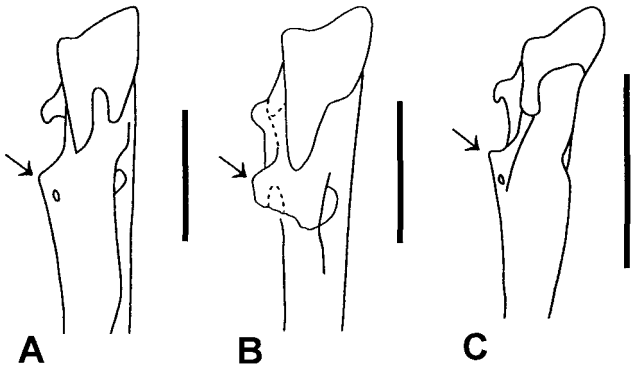

FIGURE 10. Caudal view of the proximal part of carpometacarpus showing the pointed projection on the internal side of the os metacarpale minor (arrow). **A**, *Coracias garrulus* (Coraciidae). **B**, *Geranopterus alatus* (Geranopteridae). **C**, *Atelornis crossleyi* (Brachypteraciidae). A small foramen is situated distally to the point in the Coraciidae and Brachypteraciidae. In *Geranopterus* there is a depression but no foramen. Scale bars equals 5 mm.

The calvarium is filled up with sediment, there has been a deformation at the level of the frontonasal hinge and the bill is lifted up. The processus postorbitales are incompletely preserved but they are wide and it seems that the right processus had the short projection on the cranial side which is synapomorphic for the Coracioidea (see above and Fig. 4). In the families which do not have this projection (Eocoraciidae and Leptosomidae) the processus is narrow (Cracraft, 1971). Yet, in the skull QU 15599 the processus postorbitalis is obliquely oriented, ventrally and cranially, while in the recent Coraciidae and Brachypteraciidae it is ventrally oriented. It is possible to see the caudal part of the processus zygomaticus but it is not possible to determine its length. Compared to the recent genus *Coracias,* the frontale is wider and shows a smooth sagittal crest, whereas in *Coracias* the frontale is rather depressed in the area of the frontonasal hinge. In caudal view, the calvarium is more flattened than in *Coracias garrulus,* similar to *Coracias abyssinica.* The crista nuchalis transversalis is clearly visible and, contrary to *Coracias abyssinica,* not interrupted in the middle. Ventrally to the crista nuchalis, the proeminentia cerebellaris is also clearly visible. In caudal view the left and right temporal fossae are widely separated, while they are closer in *Coracias,* still closer in *Eurystomus,* and almost meet in the midline in the Brachypteraciidae. With regard to this characteristic, the skull QU 15599 resembles that of the Leptosomidae (Cracraft, 1971). It cannot be discerned whether the septum orbitale was completely ossified or not. The beak is robust and relatively deep in dorsoventral direction. The narial openings are visible on the dorsal part of the nasale but it is not possible to see if they were subdivided in two halves by an osseous bridge. In ventral view the maxillaries form a flat surface which surrounds an elongate central opening, as in the recent Coracioidea.

GERANOPTERUS MILNEEDWARDSI, sp. nov.
(Fig. 9A-F)

Holotype—Early collections without locality, MNHN Paris: QU 17037 (left humerus, proximal part).

Type Locality—Phosphorites du Quercy, France.

Type Horizon—Age not accurately known for the holotype which comes from the early collections, but all referred specimens from the new excavations come from the locality Perrière, Late Eocene, Priabonian, MP 17b (BiochroM'97, 1997).

Dimensions—see Table 3.

Referred Specimens—Early collections without locality. Collection MNHN Paris: QU 16926 (right humerus, distal part and shaft). Collection MHN Basel: Q.H. 120 (left humerus, proximal part and shaft).

New excavations, locality Perrière (MP 17b). Collection of the USTL Montpellier: PRR 2594 (right humerus, distal part); PRR 2595 (right ulna, distal part); PRR 2577 (left ulna, distal part); PRR 2601 (radius, distal part). Collection UCB Lyon: FSL 330855 (right coracoid, cranial part); FSL 330856 (right tarsometatarsus, incomplete distal part).

Etymology—The species has been named after Alphonse Milne-Edwards (1835–1900), the author of the genus *Geranopterus* and the outstanding palaeornithologist of the last century.

Diagnosis—*Geranopterus milneedwardsi*, sp. nov. is smaller than *Geranopterus alatus* Milne-Edwards 1892, and larger than *Geranopterus bohemicus* (Mlíkovský, 1999).

Description and Comparison—As far as comparable, *Geranopterus milneedwardsi* sp. nov. shares the same general morphological characteristics as *G. alatus* but is smaller. The ratio between the mean dimensions of *Geranopterus alatus* and *G. milneedwardsi* sp. nov. varies between 1.06 and 1.21, with a mean value of 1.11. Some differences can be seen on the distal part of the humerus. In *G. alatus* the impression of musculus brachialis is very elongated obliquely across the cranial face of the shaft, and extends distally to the tuberculum supracondylare ventrale, while in *G. milneedwardsi* this impression is shorter, less oblique, and does not reach this attachment. In *G. milneedwardsi* the condylus ventralis is dorsoventrally proportionally shorter and more globular than in *G. alatus.*

Mlíkovský (1999) described a distal tarsometatarsus from the Early Miocene of Bohemia (Czech Republic) as a new species of the Jacanidae (jacanas), *Nupharanassa bohemica,* the genus *Nupharanassa* being an extinct genus from the Early Oligocene of Egypt (Rasmussen et al., 1987). Actually this specimen is, however, morphologically very different from the recent and fossil Jacanidae. It displays the morphological characteristics of the rollers and can be attributed to the genus *Geranopterus,* its new systematic attribution is *Geranopterus bohemicus* (Mlíkovský, 1999) (Mourer-Chauviré, 1999). The distal width of the tarsometatarsus of *G. bohemicus* (Mlíkovský, 1999) is 3.9 mm and the depth of the trochlea metatarsi III is 2.0 mm. The ratios between the mean dimensions of *G. alatus* and *G. bohemicus* are 1.41 and 1.18, and between *G. milneedwardsi* and *G. bohemicus* they are 1.21 and 1.10. From the few available documents it seems that *G. bohemicus* is distinctly smaller than *G. milneedwardsi* and, in addition, their age is very different. *G. bohemicus* comes from the Early Miocene, reference-level MN 4b, which dates back about 17 million years (Kempf et al., 1997), while the Perrière locality, reference-level MP 17b, is about 37 million years old (Legendre and Lévêque, 1997).

CORACIIFORMES s.s. incertae sedis
species A
(Fig. 9G-I)

Referred Specimen—Early collections without locality, MHN Lyon: PQ 1216 (right tarsometatarsus with trochlea metatarsi IV missing).

Dimensions (in mm)—Total length, 30.5; Proximal width, 6.9; Proximal depth, 6.1; Width midshaft, 3.2; Depth midshaft, 2.6; Width of trochlea metatarsi III, 2.2; Depth of trochlea metatarsi III, 2.4.

Description and Comparison—This tarsometatarsus belongs to a more robust form than *Geranopterus.* It differs from the latter and from recent Coracioidea because its trochlea metatarsi II is distinctly shorter than its trochlea metatarsi III, while in the other genera the trochlea metatarsi II has almost

the same length as the trochlea metatarsi III. The trochlea metatarsi II is also situated more plantarly than in the other genera. At the proximal part, the two cotyles have a circular shape with the cotyla medialis being larger than the cotyla lateralis. In the lateroplantar angle of the proximal articular surface there is a large tubercle, which delimits a groove from the crista lateralis hypotarsi. The hypotarsus bears two ridges between which there is a roofed canal with an open groove on its plantar side. The two ridges are divergent and obliquely oriented towards the lateral side. On the plantar surface, the hypotarsus extends distally over about the first third of the shaft. There is a deep fossa parahypotarsalis medialis, and a shallow fossa parahypotarsalis lateralis. At the distal part of the plantar surface the foramen vasculare distale is large and widely open, and there is a sulcus between this foramen and the incisura intertrochlearis lateralis. The fossa metatarsi I is deep and proximodistally elongate.

This tarsometatarsus differs from that of the recent Coraciidae by its hypotarsal ridges, which are proportionally shorter and more oblique, and by the tubercle of the lateroplantar corner of the proximal articular surface, which is more developed. On the dorsal surface the medial foramen vasculare proximale is larger than the lateral foramen vasculare proximale, while in the recent Coraciidae they are approximately the same size. Finally, in the Quercy form, the tuberositas musculi tibialis cranialis is well developed and situated clearly distally compared to the medial foramen vasculare proximale, while in the recent Coraciidae it is not so well developed and is situated just distally to the vascular foramen.

species B
(Fig. 9J-K)

Referred Specimen—Early collections without locality, MNHN Paris: QU 15640 (right carpometacarpus, almost complete).

Dimensions (in mm)—Total length, 26.9; Proximal width, 3.8; Proximal depth, 7.3; Width of os metacarpale majus in the middle, 2.5; Depth of os metacarpale majus in the middle, 1.8; Distal width, 2.9; Distal depth, 5.2.

Description and Comparison—This carpometacarpus displays on the ventral side of the proximal part of the os metacarpale minus a ventrally projecting process as in *Eocoracias, Geranopterus* and recent Coracioidea. Yet, this process is situated slightly more distally than in the other rollers. The specimen agrees with *Eocoracias* but differs from *Geranopterus* and the recent Coraciidae because the processus intermetacarpalis is poorly developed and does not reach the os metacarpale minus. It further differs from *Geranopterus* because the processus extensorius of its os metacarpale alulare is more protruding, on the ventral side there is no fossa between the processus extensorius and the processus pisiformis, and because the facies articularis digitalis minor is at the same level as the facies articularis digitalis major (in *Geranopterus* it protrudes farther distally). In the shape of the os metacarpale alulare and the weak development of the processus intermetacarpalis, the carpometacarpus QU 15640 somewhat resembles the corresponding bone of *Leptosomus.* It differs however, because in *Leptosomus* the os metacarpale alulare projects more proximally and the facies articularis digitalis minor protrudes much more distally.

DISCUSSION

The phylogenetic relationships within the genera of the Coraciiformes s.s. are depicted in Fig. 11. Although the new families Eocoraciidae and Geranopteridae are the most basal taxa of rollers known so far, both families exhibit autapomorphic features which preclude them from being directly ancestral to recent rollers (e.g., the wide maxilla below the narial openings in the Eocoraciidae, and the marked depression between the processus pisiformis and the processus extensorius of the os metacarpale alulare in the Geranopteridae).

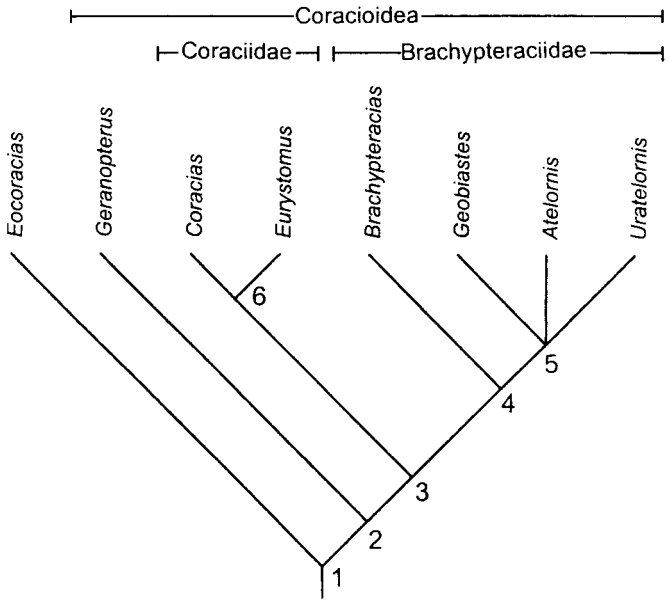

FIGURE 11. Cladogram illustrating the phylogeny of the Coraciiformes s.s.. The nodes are characterized by the following characters: **1**, processus postorbitalis (skull) very long, os metacarpale minus with small ventrally projecting tubercle; **2**, processus postorbitalis (skull) with small projection on cranial side, processus intermetacarpalis (carpometacarpus) well developed; **3**, os metacarpale minus (carpometacarpus) with foramen on ventral side of proximal end (unknown for *Eocoracias*); **4**, carpometacarpus: portion of trochlea carpalis before os metacarpale minus absent; cristae cnemiales (tibiotarsus) enlarged; **5**, tarsometatarsus very long and hallux short (ratio tarsometatarsus:hallux more than 4.5); **6**, crista bicipitalis (humerus) enlarged, wing elongated. As far as visible in the fossil specimens, the above-mentioned characters do not show homoplasy within the Coraciiformes s.s.; their polarity was determined by outgroup comparisons with taxa generally considered to be closely related to the Coraciiformes s.s., i.e., Alcediniformes (kingfishers, bee-eaters and allies), Upupiformes (hoopoes and wood-hoopoes), Trogoniformes (trogons) (see Cracraft, 1981; Sibley and Ahlquist, 1990).

As has to be expected, morphological features of the two recent families have a mosaic distribution in the fossil taxa. Brachypteraciidae and Coraciidae particularly are distinguished in the length proportions of the wing and leg elements—whereas the Brachypteraciidae have short wings and long legs, the Coraciidae have long wings but short legs (Figs. 7, 12). Compared with recent rollers, the feathering of *Eocoracias brachyptera* is similar to that of the Brachypteraciidae, but in the leg proportions this species closer resembles *Eurystomus* (Coraciidae) which has an equally abbreviated tarsometatarsus (Fig. 12). Outgroup comparisons with *E. brachyptera* thus suggest that an elongated wing and a more or less deeply forked tail are derived features of the Coraciidae, whereas the elongated tarsometatarsus and the rather short hallux are synapomorphic for the Brachypteraciidae. The short wing of the Brachypteraciidae obviously is not a secondarily acquired feature related to the terrestrial habit of these birds, but a retained primitive character of rollers. Besides that, the short wings of *E. brachyptera* and recent ground-rollers are well suitable for agile maneuvering in a forested surrounding which has to be assumed for the Eocene Messel lake (e.g., Schaarschmidt, 1988). In contrast thereto, the extant Coraciidae generally occur in open woodlands, savannas, or forest edges (Sibley and Monroe, 1990);

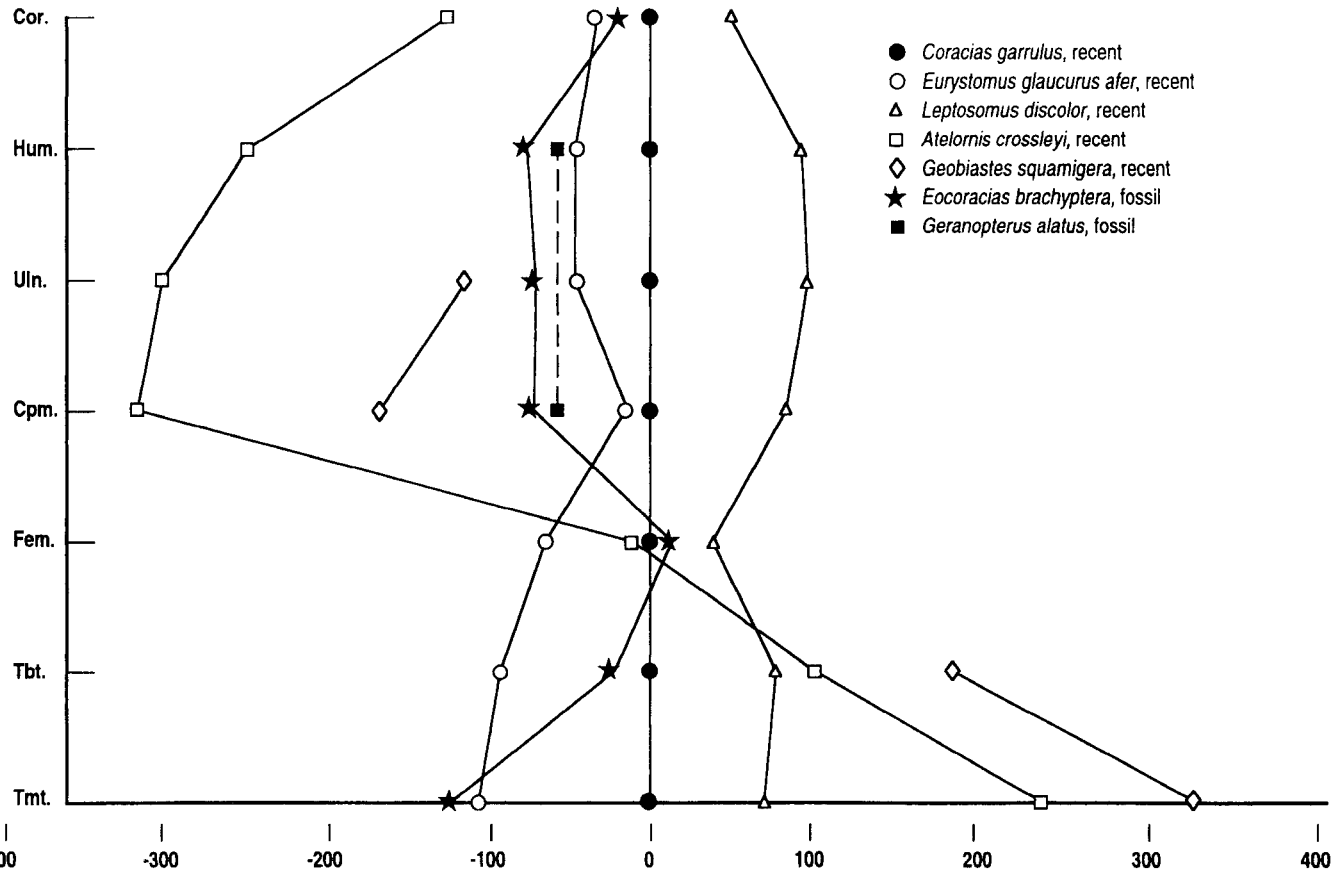

FIGURE 12. Simpson's (1941) ratio-diagram of the log differences of the main long bones of recent and fossil rollers. The recent *Coracias garrulus* has been taken as standard.

their habitat allows a more rapid flight which is reflected by the longer wing and the deeply forked tail of some species.

Except for *Uratelornis* which lives in an arid environment (Appert, 1968), the Brachypteraciidae still inhabit tropical forests, and like many other birds on isolated islands with few mammalian predators they evolved towards a more terrestrial way of life, which among birds usually is accompanied by an elongation of the tarsometatarsus and a shortening of the hallux. Within the Brachypteraciidae, *Brachypteracias leptosomus* has, however, a distinctly shorter tarsometatarsus and a longer hallux than the other four recent species of ground-rollers. We consider this to be a primitive character, and thus maintain a separation of the genera *Geobiastes*, Sharpe 1871, and *Brachypteracias*, Lafresnaye 1834, which for obscure reasons have been synonymized by virtually all recent authors.

The Leptosomidae are left out in Figure 11, since their classification within the Coraciiformes s.s. is only weakly supported. Although Maurer and Raikow (1981) listed two myological characters in order to support a monophyly of Leptosomidae and recent Coracioidea, they themselves considered one of these to be weak since it also occurs in most other taxa investigated; the other is absent in *Eurystomus* and unknown for the Brachypteraciidae (which were not examined). The skull of *Leptosomus discolor* bears elongated processus postorbitales, too, but concerning most other anatomical features this species trenchantly differs from other rollers. Contrary to the recent Coracioidea, for example, *L. discolor* shows sexual dimorphism in the plumage coloration, has large powder downs patches, and a bronchial syrinx (see Stresemann, 1927–1934). Instead of the syndactyl foot of Coraciidae and Brachypteraciidae (where the basal phalanges of the third and fourth toe are linked by connective tissue), the Leptosomidae have a semi-zygodactyl foot, i.e., the fourth toe can be turned backwards. Concerning its osteology, *Leptosomus* distinctly differs in most skeletal elements from the Coraciidae, Brachypteraciidae, and the fossil taxa described in this study. Cracraft (1971:742) assumed that the similarities in the forelimbs of *Coracias* and *Leptosomus* ''are the result of convergence rather than closeness of relationship''. With regard to the proximal end of the humerus (like in *Coracias*, the crista bicipitalis is well developed in *Leptosomus*) and the feathering (*Leptosomus* also has long remiges), this assumption can be supported by outgroup comparison with *Eocoracias brachyptera*. Certainly the systematic position of cuckoo-rollers needs critical reevaluation and Cracraft (1981) already expressed doubts on the affinities of *Leptosomus* to other rollers. In case, however, the taxon (Leptosomidae + Coraciiformes s.s.) can be shown to be monophyletic, the fossil birds presented in this study show that the Leptosomidae must have branched off before the Middle Eocene.

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