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A NEW SPECIMEN OF THE TINY MIDDLE EOCENE BIRD *GRACILITARSUS MIRABILIS* (NEW FAMILY: GRACILITARSIDAE)[1]

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Abstract. A new, second specimen of the tiny Middle Eocene bird *Gracilitarsus mirabilis* Mayr 1998 shows several previously unknown osteological features. The species represents a bauplan unknown among recent birds in that it combines swallow-like length proportions of the major wing bones with a long and slender tarsometatarsus. The feet of *Gracilitarsus mirabilis* are highly unusual in that the three anterior toes are very short and of nearly equal length, and in that the claws are of great dorso-ventral depth. *Gracilitarsus mirabilis* is classified within a new family in this study. The species shares some derived characters of the tarsometatarsus with the Paleocene South American species *Eutreptodactylus itaboraiensis* Baird and Vickers-Rich 1997.

Key words: *Eocene,* Eutreptodactylus, *fossil birds, Gracilitarsidae,* Gracilitarsus mirabilis.

INTRODUCTION

Despite the fact that there are a number of European and North American early Tertiary fossil sites that have yielded well-preserved bird remains, the early radiation of modern birds still is poorly understood. The largest gap in our knowledge concerns very small birds, which usually are preserved only under special circumstances. It is thus especially fortunate that in the Middle Eocene deposits of Messel (Hessen, Germany), birds not only are among the most abundant land vertebrates, but that even tiny birds are found in great numbers.

The Messel ''oilshale'' originated about 49 million years ago, in a deep crater lake of tectonic origin that was surrounded by humid subtropical forests (Schaal and Ziegler 1988). The site has so far yielded several hundreds of well-preserved bird skeletons belonging to at least 50 different species (unpubl. data), some of which can be assigned to recent taxa, e.g., ibises, parrots, mousebirds, swifts, or caprimulgiform birds (Mayr and Daniels 1998, Mayr and Peters 1999, Mayr 1999a). New bird specimens are continuously found in Messel that allow a better understanding of the Middle Eocene avifauna.

Among the tiniest and most enigmatic birds found in Messel is *Gracilitarsus mirabilis* Mayr 1998a, a species the size of an average hummingbird that until now was known from a single skeleton only (Fig. 1). Given the poor preservation of the holotype, *G. mirabilis* was classified order and family *incertae sedis* in the original description. Presented here is a second, much better-preserved specimen from the type locality (Fig. 2). It shows several previously unknown osteological features which justify its classification within a new family and which reveal that *G. mirabilis* might be closely related to *Eutreptodactylus itaboraiensis*, a species described by Baird and Vickers-Rich (1997) from the Paleocene of Brazil.

METHODS

If not indicated otherwise, the anatomical terminology used herein follows Baumel and Witmer (1993) and Vanden Berge and Zweers (1993). All measurements are in millimeters and represent the maximum length of the bone along its longitudinal axis. Concerning the length of the carpometacarpus, the dimensions thus differ from those given by Mayr (1998a), who measured the distance between the trochlea carpalis and the distal end of the os metacarpale majus. The fossil specimens are deposited in the Forschungsinstitut Senckenberg, Frankfurt am Main, Germany (SMF), and in the Staatliches Museum für Naturkunde Karlsruhe, Germany (SMNK).

SYSTEMATIC PALEONTOLOGY

Order *incertae sedis*
Gracilitarsidae, new family

Type genus. Gracilitarsus Mayr 1998a.

Diagnosis. Tiny birds which differ from all

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FIGURE 1. *Gracilitarsus mirabilis*, holotype (SMNK-Me 1085). Covered with ammonium chloride to enhance contrast, scale bar equals 10 mm.

other avian families in the combination of swallow-like length proportions of the main wing elements (abbreviated humerus and elongated hand) with a very long and slender tarsometatarsus, the morphology of the humerus (greatly abbreviated with very wide proximal end, processus flexorius strongly protruding distally), and in the peculiar morphology of the feet (proximal phalanges of the third and fourth toes reduced, thus three anterior toes of nearly equal length, claws very deep dorso-ventrally).

Differential Diagnosis. Differs from the Middle Eocene family Sylphornithidae Mourer-Chauviré 1988 in: distal end of tarsometatarsus bent more medially (thus medial margin of trochlea metatarsi III situated farther medially than medial margin of the shaft); trochlea metatarsi III with marked furrow; presence of a distinct sulcus on the dorsal side of tarsometatarsus, between the trochleae metatarsorum III and IV; larger proximal end of the humerus; farther distally protruding processus flexorius of the humerus; and in the absence of a processus intermetacarpalis (concerning the presence of the latter feature in the Sylphornithidae see Mayr 1998a).

Gracilitarsus Mayr 1998a
Gracilitarsus mirabilis Mayr 1998a
(Fig. 1–5)

Referred specimen. SMF-ME 3547: articulated skeleton lacking the left leg, from the Middle Eocene of Messel.

Measurements. Humerus, ~11.1 (l), 11.3 (r); ulna, 15.0 (l), 15.0 (r); carpometacarpus, 8.1 (l), 8.1 (r); tibiotarsus (length as preserved), ~14 (r); tarsometatarsus, 11.4 (r).

Description. The exact shape of the beak cannot be discerned in the holotype, but the new specimen reveals that *Gracilitarsus* had a beak of similar shape to certain recent sunbirds, e.g., *Anthreptes rectirostris.* The beak is narrow and pointed, about half as long as the entire skull and with a slightly curved culmen. Most remarkable (and not found in recent sunbirds and most other Passeriformes) are the very long, schizorhinal narial openings, which occupy about two-thirds of the entire beak. This feature probably indicates that the beak of *Gracilitarsus* was rhynchokinetic as, for example, that of recent pigeons and hummingbirds (see Bühler 1981). The mandible lacks processus retroarticulares and fenestrae mandibulae. The ossa praefrontalia appear to have been small, the processus postorbitales are short. The quadratum has a long and slender processus oticus. Other details of the skull are not visible.

In its proportions, the humerus of *Gracilitarsus* (Fig. 3, 4A) is similar to the short and stout humerus of swallows (Hirundinidae) and that of some primitive swifts (e.g., the fossil species *Eocypselus vincenti* Harrison 1984 from the Lower Eocene of England and recent Hemiprocnidae). As in the latter, the proximal end is unusually large and protrudes far medially. The crista deltopectoralis seems to have been rather low, but its exact shape cannot be discerned. The dorsal expansion of the distal humerus which was mentioned in the original description obviously is either an artifact of preservation in the holotype, or has been misinterpreted. The processus flexorius is very marked and protrudes distally (not medially as in the Sylphornithidae). The tuberculum supracondylare ventrale is large. The condylus ventralis bears a notch on its distal margin. Contrary to swifts and swallows, an enlarged processus supracondylaris dorsalis seems to be absent.

The ulna substantially exceeds the humerus in

FIGURE 2. *Gracilitarsus mirabilis*, referred specimen SMF-ME 3547. Covered with ammonium chloride to enhance contrast, scale bar equals 10 mm.

length and is fairly stout. As far as is comparable, its proximal end resembles that of *Eocypselus vincenti* (Fig. 5k in Harrison 1984), too. The cotyla ventralis is circular, the olecranon short.

The carpometacarpus (Fig. 4B) is long and slender and, contrary to the statement in Mayr (1998a), bears a large and protruding processus extensorius, as in the recent tree-swift *Hemiprocne comata* (the tip of the process itself is broken in SMF-ME 3547 but an impression is preserved on the slab). The trochlea carpalis is

FIGURE 3. *Gracilitarsus mirabilis,* left wing of the referred specimen SMF-ME 3547. The arrow indicates the claw on the digitus alulae. Covered with ammonium chloride to enhance contrast, scale bar equals 5 mm.

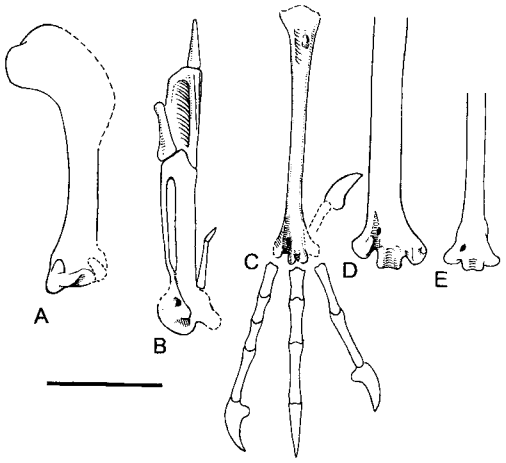

FIGURE 4. A: left humerus of *Gracilitarsus mirabilis.* B: distal end of right wing of *Gracilitarsus mirabilis.* C: right foot of *Gracilitarsus mirabilis.* D: distal right tarsometatarsus of *Eutreptodactylus itaboraiensis* (after Baird and Vickers-Rich 1997). E: distal right tarsometatarsus of *Sylphornis bretouensis* (after Mourer-Chauviré 1988). Scale bar equals 5 mm.

large, the fossa infratrochlearis and the facies ligamentalis interna (terminology after Ballmann 1969) are marked depressions. There is a ridge from the os metacarpale minus to the processus pisiformis. The os metacarpale minus reaches farther distally than the os metacarpale majus; the symphysis metacarpalis distalis is wide. The spatium intermetacarpale is narrow.

The digitus alulae bears a fairly large claw which usually is absent in recent ''higher'' landbirds (Stephan 1992). The phalanx proximalis digiti majoris resembles that of passeriform birds and exhibits a distinct fossa ventralis and a marked sulcus for the tendon of the musculus flexor digitorum profundus. A processus internus indicis (terminology after Stegmann 1963) is absent.

Curiously, and probably for taphonomic reasons, the femora are not preserved in either of the known specimens of *G. mirabilis.*

The distal end of the tibiotarsus appears to have been of average medio-lateral width. The medial tuberositas retinaculi extensoris is positioned only slightly farther proximally than the

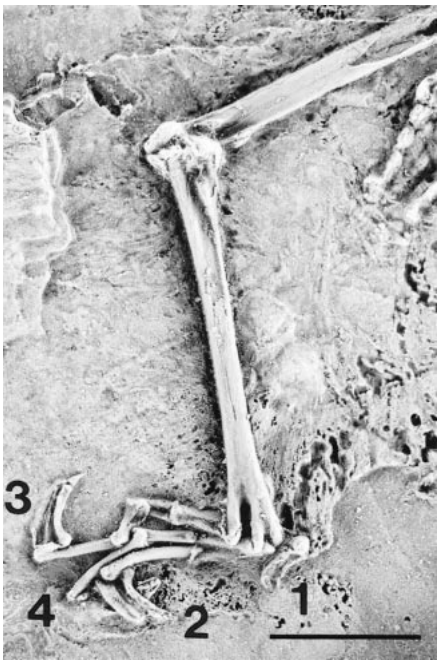

FIGURE 5. *Gracilitarsus mirabilis,* right foot of the referred specimen SMF-ME 3547. The four toes are numbered. Covered with ammonium chloride to enhance contrast. Scale bar equals 4.2 mm.

lateral one. The condylus lateralis is of similar shape to the corresponding condylus in recent Cuculidae (e.g., *Clamator* sp.).

The tarsometatarsus (Fig. 4C) is fairly long and slender, measuring about 3/4 of the length of the tibiotarsus. The bone gradually widens towards its proximal and distal ends. The tuberositas musculi tibialis cranialis is a large and prominent tubercle situated near the medial margin of the shaft. The new specimen for the first time allows the recognition of details of the distal end of the tarsometatarsus, which was previously unknown for *Gracilitarsus.* Contrary to *Eutreptodactylus* (Fig. 4D), the foramen vasculare distale appears to have been large. The trochlea metatarsi III is wider than long and deeply grooved. The trochlea metatarsi IV reaches almost as far distally as the trochlea metatarsi III, and as in *Eutreptodactylus* it tapers dorsally. It does not protrude as strongly laterally as in *Sylphornis* (Fig. 4E). There is a marked sulcus on the dorsal side of the tarsometatarsus between the trochleae metatarsorum III and IV (for the tendon of musculus extensor brevis digiti IV, see Steinbacher 1935). Due to the preservation of the specimen, the trochlea metatarsi II is not visible in the new specimen of *G. mirabilis.*

The morphology of the feet of *G. mirabilis* is very peculiar (Fig. 4C, 5). Because the proximal phalanges of the third and fourth toes are abbreviated, the three anterior toes have roughly equal length, whereas usually the third toe is much longer than the other toes. In specimen SMF-ME 3547, the fourth toe is preserved in a reversed position and visible from its plantar side. This, and the great relative length of the fourth toe (compared to the third), might confirm the presence of at least facultatively zygodactyl feet in *Gracilitarsus,* as already assumed by Mayr (1998a). The claws are large, robust, and very deep dorso-ventrally, thus resembling the claws of recent tree swifts (*Hemiprocne* spp.). The hallux is short and also bears a large claw.

The contour feathers of the body are well preserved in the new specimen. Although a few remains of the remiges of the right wing are visible, it is not possible to determine their original length. The feathering of the tail is not preserved.

DISCUSSION

Owing to their highly apomorphic osteology, the Gracilitarsidae cannot be convincingly assigned to any recent taxon, and it is quite possible that they are related to a cluster of extant orders, as is the case with other Eocene taxa (Mayr 1998b, 1999b).

In the morphology of its tarsometatarsus, *Gracilitarsus mirabilis* most closely resembles *Eutreptodactylus itaboraiensis,* an enigmatic species described by Baird and Vickers-Rich (1997) from the Paleocene of Brazil (*E. itaboraiensis* is known only from an isolated incomplete tarsometatarsus which was lost before the original description was published; see Baird and Vickers-Rich 1997). In both *G. mirabilis* and *E. itaboraiensis,* the tarsometatarsus is very long and slender with a medio-laterally wide distal end; the distal end of bone is bent medially (thus the medial margin of the trochlea metatarsi III is situated farther medially than the medial margin of the shaft); the trochlea metatarsi III bears a marked furrow; the trochlea metatarsi IV tapers dorsally; and there is a distinct sulcus on the dorsal side of the tarsometatarsus, between the trochleae metatarsorum III and IV. In both taxa, the feet probably were at least facultatively zygodactyl.

Baird and Vickers-Rich (1997) classified *E. itaboraiensis* within the Cuculidae, but this assignment was not well established. The two characters listed by these authors in order to support their classification (‘‘elongate, narrow corpus tarsometatarsus [sic], lenticular-shaped trochlea metatarsi IV lacking any sulcus,’’ p. 126) are neither unique nor diagnostic for the Cuculidae, many species of which have shorter legs. Both characters also are present in the extinct family Sylphornithidae Mourer-Chauviré 1988, which comprises tiny, long-legged, and facultatively zygodactyl birds from the Middle Eocene of France (Mourer-Chauviré 1988, 1999). The similarities between *Eutreptodactylus* and the Sylphornithidae have already been recognized by Mourer-Chauviré (1999), who considered the two taxa to be closely related.

Mayr (1998a) also compared *Gracilitarsus mirabilis* with the Sylphornithidae, noting the different morphology of the carpometacarpus of the two taxa. The new specimen of *G. mirabilis* reveals additional features in which Gracilitarsidae and Sylphornithidae clearly are distinguished (see differential diagnosis). Of course, these differences cannot be used in order to argue for a non-relationship between Gracilitarsidae and Sylphornithidae, as they obviously are

due to the highly apomorphic morphology of the two taxa. Features that might support monophyly of a clade including Gracilitarsidae and Sylphornithidae are the long and slender tarsometatarsus, the (facultatively) zygodactyl feet, and the distally protruding os metacarpale minus. There are, however, other long-legged zygodactyl birds in the Eocene (e.g., the extinct piciform family Primoscenidae, see Mayr 1998a), and monophyly of the taxon (Gracilitarsidae + Sylphornithidae) still needs to be tested by an exhaustive phylogenetic analysis. The presence of a well-developed processus intermetacarpalis might indicate a closer relationship between Sylphornithidae and Primoscenidae. As far as can be discerned in the specimens known so far, this feature, which certainly is derived within neognathous birds, is absent in *G. mirabilis.*

Owing to the shape of its beak and the long legs, *Gracilitarsus mirabilis* superficially resembles certain very small songbirds. The Eocene species lacks, however, virtually all of the highly characteristic features of Passeriformes (e.g., a well-developed processus supracondylaris dorsalis on the humerus, a distinct olecranon on the proximal ulna, a large processus intermetacarpalis, and a greatly elongated hallux), and is further distinguished in many additional features (e.g., the long narial openings and the morphology of the distal tarsometatarsus). Passeriformes so far are unknown from Eocene deposits of Europe; their earliest certain record is much younger and comes from the late Oligocene of France (Mourer-Chauviré et al. 1989). The presence of a large claw on the digitus alulae certainly is a primitive feature among neognathous birds, which further precludes *Gracilitarsus* being closely related to Passeriformes, Piciformes, or any of the Coraciiformes, in which this claw is completely reduced (Stephan 1992).

The osteology of *Gracilitarsus mirabilis* represents a bauplan not found in any recent avian taxon. Especially, the combination of swallow-like proportions of the wing skeleton with such a long and slender tarsometatarsus lacks any recent counterpart. The morphology of the feet of *G. mirabilis* is further unusual in that the three anterior toes are very short and of nearly equal length, and in that the claws are of such great dorso-ventral depth.

Judging from the shape of its beak, the species probably was either insectivorous or nectarivorous. In the latter case it would be the first nectarivorous avian taxon not only from Messel, where frugivorous and insectivorous birds seem to predominate, but from the Early Tertiary as a whole. The abbreviated and robust humerus, as well as the elongated hand, might indicate that *G. mirabilis* was capable of rapid flight like recent swallows. However, without knowing the length of the wing feathers, which cannot be discerned in the known specimens of *Gracilitarsus*, this assumption remains speculative; there is at least one undescribed avian taxon in Messel with greatly abbreviated, swift-like humeri but very short and rounded wings.

Although the plantar side of the trochlea metatarsi IV is not visible, the fact that the fourth toe is preserved in a reversed position in specimen SMF-ME 3547 suggests that *Gracilitarsus* was at least facultatively zygodactyl, like *Eutreptodactylus.* In Messel, quite a number of zygodactyl taxa have been identified (Mayr 1998a, 1998b, Mayr and Daniels 1998), and in these specimens the fourth toe is always preserved in a reversed position, contrary to virtually all of the hundreds of anisodactyl bird skeletons from this locality. Given that *G. mirabilis* is correctly assumed to have been (facultatively) zygodactyl, it might have been able to perch in trees or bushes, whereas the short hallux alone probably would have limited its grasping capabilities. Together with the large claws, the fact that the three anterior toes of *Gracilitarsus* have nearly equal length might further indicate that *G. mirabilis* was able to cling to vertical surfaces as assumed by Mayr (1998a).

Generally, the Eocene avifauna of Europe shows a high degree of concordance to the North American avifauna of similar age (Peters 1991, Mayr 1999a). Although several early Eocene taxa have their closest living relatives in the recent South American avifauna (Mourer-Chauviré 1999), relationships between the Eocene avifauna of South America and Europe are much more rare, which mainly is due to the fact that South America has been widely isolated from other continents in the early Eocene (Weems and Grimsley 1999). *G. mirabilis* would be among the few Eocene European avian taxa that had their closest contemporaneous relatives in South America if it indeed turns out to be closely related to *Eutreptodactylus itaboraiensis.*

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