

## TINY HOOPOE-LIKE BIRDS FROM THE MIDDLE EOCENE OF MESSEL (GERMANY)

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**ABSTRACT.**—Tiny hoopoe-like birds of the extinct family Messelirrisoridae are among the predominant small perching birds in the Middle Eocene (ca. 49 million years ago) avifauna of Messel (Hessen, Germany). Members of the Messelirrisoridae are the earliest-known representatives of the hoopoe/wood-hoopoe lineage and are sister taxa of recent Upupidae (hoopoes) and Phoeniculidae (wood-hoopoes). Outgroup comparison with the Messelirrisoridae facilitates character-state analysis within the Phoeniculidae and Upupidae. In this study, I describe a new species, *Messelirrisor grandis*, which is the largest species of the Messelirrisoridae known so far. Received 31 August 1999, accepted 28 April 2000.

THE FORMER OPENCAST oil-shale mine "Grube Messel" is located a few kilometers northeast of Darmstadt in Hessen, Germany. According to the currently favored hypothesis, the deposits of Messel originated in a deep crater lake of tectonic origin about 49 million years ago in the Lower Middle Eocene. The site has yielded a large number of vertebrate fossils in an exceptional state of preservation; in many cases, the remains of former soft tissues and stomach contents have been preserved (see Franzen 1985, Schaal and Ziegler 1988). In 1995, Messel was declared a world heritage site by UNESCO.

In terms of the number of individual skeletons and the number of species, birds are among the most abundant land vertebrates found in Messel. In recent decades, several hundred bird skeletons were discovered, many of them complete and articulated. The avifauna is very diverse, and thus far about 50 avian species have been identified. Among these are ibises (Peters 1983), swifts (Peters 1985, Mayr and Peters 1999), parrots (Mayr and Daniels 1998), and frogmouths (Mayr 1999). Contrary to nearly all other sites that have yielded fossil birds, even extremely small bird skeletons are preserved in Messel in great numbers.

Passeriforms are completely absent in the Eocene avifauna of the Northern Hemisphere, at which time the ecological niches for small perching birds were occupied by representatives of other avian taxa (Harrison 1979, Olson 1989, Feduccia 1996). In Messel, tiny hoopoe-like birds of the extinct family Messelirrisori-

dae predominate. So far, two species in a single genus have been described, *Messelirrisor halcyrostris* and *M. parvus* (Mayr 1998). Both are known from several complete articulated skeletons preserved on slabs, and both are very small, more diminutive even than many recent hummingbirds (Fig. 1). Here, I describe a third species from the Messelirrisoridae, the largest known so far.

The fossil specimens are deposited in the Geiseltalmuseum, Halle, Germany (GMH), the Forschungsinstitut Senckenberg, Frankfurt a.M., Germany (SMF), and in the Staatliches Museum für Naturkunde, Karlsruhe, Germany (SMNK). Measurements reported below represent the overall length along the longitudinal axis. Anatomical terminology follows Baumel and Witmer (1993) unless indicated otherwise.

### SYSTEMATICS

Hoopoe-like birds comprise two recent families, the Palearctic Upupidae (hoopoes) and the African Phoeniculidae (wood-hoopoes), and generally are classified together with rollers, kingfishers, bee-eaters, todies, and motmots in the order Coraciiformes (see Sibley and Ahlquist 1990:336–348). Yet, because the monophyly of this order has never been convincingly established with derived characters, I use the term Upupiformes (sensu Feduccia 1977, Sibley and Ahlquist 1990) for hoopoe-like birds.

Monophyly of the Upupiformes is supported by the following characters that are unique among neognathous birds: shaft of ulna with projection distal to cotyla dorsalis (Fig. 2, no.

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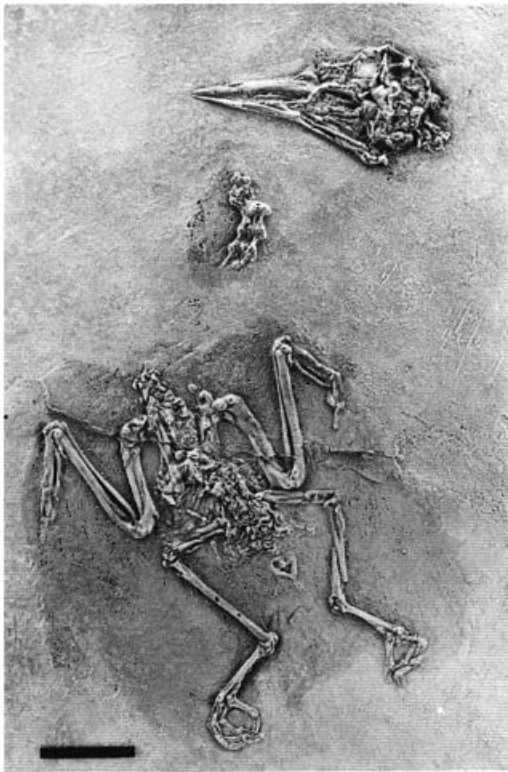


FIG. 1. *Messelirrisor parvus* (SMNK PAL 3802), slightly disarticulated with detached skull and cervical vertebrae. Specimen is coated with ammonium chloride to enhance contrast. Scale bar = 10 mm.

1); carpometacarpus with osseous ridge from ventral margin of os metacarpale minus to processus pisiformis (Fig. 3, no. 1); and caudal margin of os metacarpale minus (carpometacarpus) undulated (only slightly in *Messelirrisoridae*; Fig. 3, no. 2). Apart from their much smaller size, messelirrisorids closely resemble *Upupidae* and *Phoeniculidae* in many other osteological features: (1) long, pointed, and at the base dorsoventrally high beak; (2) presence of large processus retroarticulares on the mandible; (3) shape of the extremitas omalis of the furcula; (4) absence of an apophysis furculae; (5) stout humerus; (6) proportions of limb elements; and (7) long hallux.

The upupids and phoeniculids are united to the exclusion of the *Messelirrisoridae* because the former two families share the following derived characters: (1) margo medialis of coracoid with distinct medially projecting process (Figs. 4A–C, no. 1; unique among neognathous birds); (2) processus lateralis of coracoid very

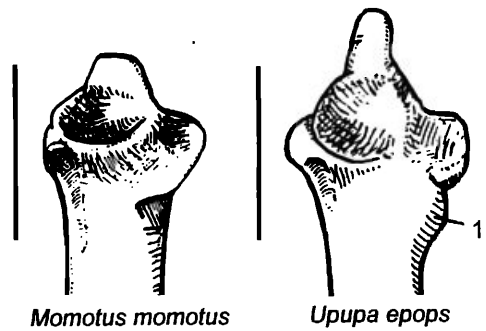


FIG. 2. Proximal ulna of *Momotus momotus* (*Momotidae*, left) and *Upupa epops* (right). (1) Projection below the processus cotylaris dorsalis that is synapomorphic for the *Messelirrisoridae*, *Upupidae*, and *Phoeniculidae*. Scale bar = 5 mm.

irregularly shaped (unique among neognathous birds); (3) spina externa and spina interna of sternum fused to form a spina communis (only in very few other neognathous birds, e.g. *Meropidae* and some *Bucerotidae*); (4) sternum with only one pair of incisions (the two pairs of the *Messelirrisoridae* generally are considered to be plesiomorphic within neognathous birds; e.g. Olson 1987); and (5) phalanx proximalis digiti majoris hooked (among other recent neognathous birds only in *Galbulidae* and *Bucconidae*; Fig. 3, no. 3). Recent upupids and phoeniculids also share a derived stapedial morphology (Feduccia 1975).

The new species described below exhibits all of the above-mentioned derived characters of the *Upupiformes* and lacks those of the *Upupidae* and *Phoeniculidae*. Especially the humerus and the carpometacarpus of the *Messelirrisoridae* are highly characteristic and can hardly be mistaken with those of any other avian taxon (see below). Apart from its larger size, the new species very closely resembles the other species of the genus *Messelirrisor* in its osteology.

*Messelirrisor grandis* sp. nov.

*Holotype*.—SMNK PAL 3803 (sternum, pectoral girdle and both wings on a slab; Fig. 5).

*Diagnosis*.—*Messelirrisor grandis* is the largest species of the *Messelirrisoridae* known so far (Table 1). It is further distinguished from *M. parvus* and *M. halcyrostris* in the slightly more cranially situated processus pisiformis of the carpometacarpus.

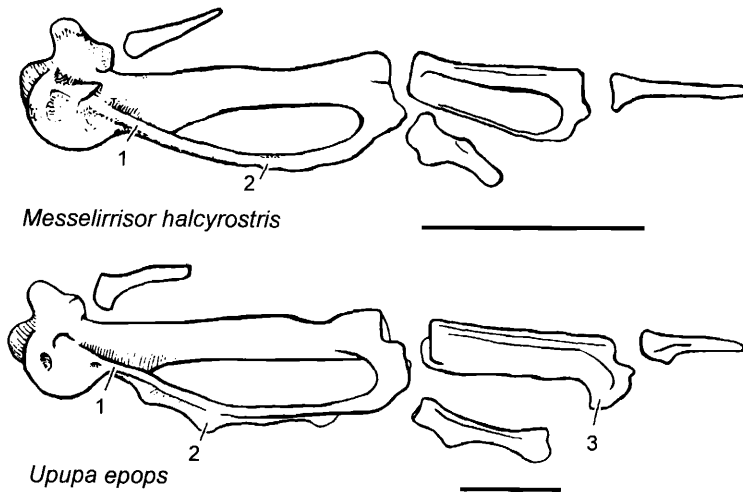


FIG. 3. Left manus of *Messelirrisor halcyrostris* (after Mayr 1998) and *Upupa epops*. (1) Ridge from the ventral side of the os metacarpale minus to the processus pisiformis; (2) undulated caudal margin of the os metacarpale minus; (3) hooked distal end of phalanx proximalis digiti majoris. Scale bar = 5 mm.

*Type locality*.—Messel near Darmstadt (Hessen, Germany).

*Type horizon*.—Lower Middle Eocene (Legendre and Lévêque 1997).

*Measurements of holotype*.—Coracoid, about 12 mm; left humerus, 19.3 mm, right humerus, 20.1 mm; ulna, about 24 mm; carpometacarpus, 10.7 mm (Table 1).

*Referred specimen*.—SMF-ME 600, a largely complete but poorly preserved skeleton on two slabs, from the type locality and horizon (Fig. 6).

*Measurements of referred specimen*.—Skull, about 41.5 mm; coracoid, about 12 mm; humerus, about 20 mm; ulna, about 23 mm; carpometacarpus, about 10 mm; tibiotarsus, about 19 mm; tarsometatarsus, about 10.4 mm.

*Etymology*.—The specific name has been derived from Latin *grandis*, large, and refers to the large size of the new species compared with the other two species of messelirrisorids.

#### REMARKS

The skull is preserved in the referred specimen SMF-ME 600, but owing to the flattening of the bones, details of its morphology can hardly be discerned. In its shape, however, it matches well with the skull of other messelirrisorids. This is especially true for the long and pointed beak, which is about 1.5 times longer than the cranium. The beak is high at its base

dorsoventrally, and the culmen is slightly curved. The narial opening is long and slit-like, and the rami mandibulae are wide dorsoventrally.

Like in other messelirrisorids, the extremitas omalis of the furcula is rhombic in shape (more round in recent *Upupiformes*), and the scapus clavicularae is slender. The scapula is short and straight. The acromion is also short and bears a small projection on its ventral side. The extremitas omalis of the coracoid is hidden by overlying bones in the type specimen. The processus lateralis of the extremitas sternalis is narrow but long. A small notch occurs on the medial side of the extremitas sternalis.

The sternum is slightly longer than wide and bears short processus cranio-laterales. Its lateral margins are somewhat curved, and the margo costalis is short. Like in other messelirrisorids, the margo caudalis bears two pairs of incisions, whereas recent *Upupiformes* have only one pair. The incisions on the right side of the sternum are nearly equal in depth (about one-third the length of the sternum), and on the left side the incisura medialis is slightly deeper. The incisurae laterales are narrower than the incisurae mediales. The trabeculae laterales are wide, and the trabecula mediana is triangular in shape.

The humerus is short and stout with a large proximal end and a slightly curved, robust

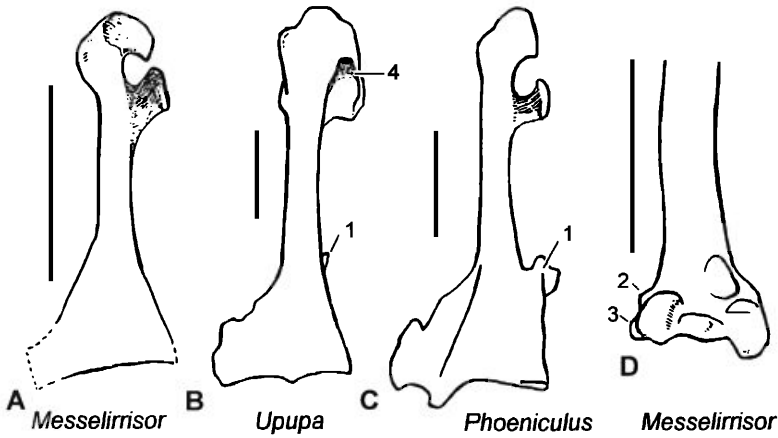


FIG. 4. Right coracoid of (A) *Messelirrisor parvus* (after Mayr 1998), (B) *Upupa epops*, and (C) *Phoeniculus* sp. Distal end of the right humerus of (D) *Messelirrisor* sp. (GMH L-9-1969). (1) Process on the medial side of the extremitas sternalis; (2) processus supracondylaris dorsalis; (3) epicondylus dorsalis; and (4) osseous bridge connecting the processus procoracoideus with the facies articularis clavicularis. Scale bar = 5 mm.

shaft. The tuberculum dorsale bears a shallow depression. The distal humerus of messelirrisorids is very characteristic in that the epicondylus dorsalis protrudes unusually far laterally to form a small tubercle next to the condylus dorsalis (Fig. 4D, no. 3). This protruding epicondylus dorsalis also is clearly visible in the type specimen of *M. grandis*. Like in other messelirrisorids, the processus supracondylaris dorsalis is a small tubercle above the epicondylus dorsalis. The sulcus scapulotricipitalis is distinct. The processus flexorius reaches slightly farther distally than the condylus ventralis

and bears a pit-like depression on its medial surface.

The ulna exceeds the humerus in length. On the left ulna of the type specimen, a projection below the processus cotylaris dorsalis is visible, which is synapomorphic for the Upupiformes (Fig. 2, no. 1). The tuberculum carpale is pointed and bears a depression on its distal surface. Like in recent Upupiformes, low papillae remigales are present. Other details of the ends of the ulna are not visible. The distal end of the radius bears a single, wide sulcus tendinosus.

The carpometacarpus is well preserved in the type specimen and closely resembles that of other messelirrisorids, although the processus pisiformis is shifted slightly farther cranially than in the other species of *Messelirrisor*. The processus extensorius of the os metacarpale al-

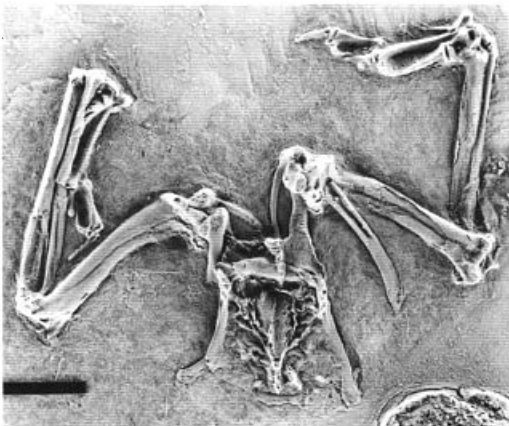


FIG. 5. *Messelirrisor grandis*, holotype (SMNK PAL 3803). Specimen is coated with ammonium chloride to enhance contrast. Scale bar = 8 mm.

TABLE 1. Length (mm) of some wing elements in the three known species of messelirrisorids (SD in parentheses for *M. parvus*).

Coracoid	Humerus	Ulna	Carpometacarpus
<b><i>Messelirrisor grandis</i> (holotype)</b>			
ca. 12	19.3/20.1	ca. 24	10.7
<b><i>Messelirrisor halcyrostris</i> (n = 1)</b>			
9.3	14.6	17.2	8.0
<b><i>Messelirrisor parvus</i> (n = 7)</b>			
8.8 (0.3)	12.9 (0.6)	16.3 (0.7)	7.0 (0.4)

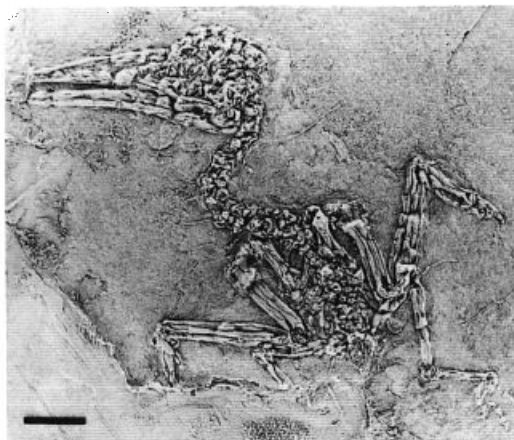


FIG. 6. *Messelirrisor grandis*, referred specimen (SMF-ME 600). Specimen is coated with ammonium chloride to enhance contrast. Scale bar equals 10 mm.

ulare is fairly straight and protrudes cranially. The fossa infratrochlearis and the facies ligamentalis interna (terminology after Ballmann 1969) are marked depressions. The os metacarpale minus is strongly bowed; thus, the spatium intermetacarpale is very wide, like in recent hoopoes and wood-hoopoes. A distinct ridge runs from the caudal end of the os metacarpale minus to the processus pisiformis, which is synapomorphic for the Upupiformes, and the ventral margin of the os metacarpale minus is slightly undulated. The symphysis metacarpalis distalis is very narrow.

The phalanx proximalis digiti majoris bears a marked fossa ventralis, and its distal end is not hooked like in recent Upupiformes. The phalanx digiti minoris is not as elongated as in the recent Upupiformes. The pelvis and hind limbs are preserved only in the referred specimen but are too crushed for detailed analysis. The proportions of the legs correspond with those of other messelirrisorids. The tarsometatarsus is short, and as in other upupiforms the hallux is fairly long.

Remains of the remiges are preserved in the type specimen and the referred specimen, but they do not allow for meaningful measurements.

#### DISCUSSION

The Messelirrisoridae are by far the earliest-known representatives of the Upupiformes. Isolated bones of this taxon were also found in

the Lower Eocene of England, in Middle Eocene deposits of the Geisel Valley of Germany, and in the Upper Eocene of France (Mayr 1998). In contrast, the fossil record of the two recent families, Upupidae and Phoeniculidae, is more scanty and comes from much younger deposits. Ballmann (1969) described remains of the Phoeniculidae from the Lower Miocene of Germany; the earliest record of the Upupidae is an extinct species from the Quaternary of St. Helena Island (Olson 1975). Ballmann (1969) also assigned a small humerus from the early Miocene of France to the Phoeniculidae. This bone (Milne-Edwards 1867–71: plate 176, figures 8 to 13) is much smaller than the humerus of any recent wood-hoopoe (according to Ballmann [1969] it measures only 19.5 mm). Its distal end resembles the distal humerus of the Messelirrisoridae in the dorsally protruding epicondylus dorsalis, and without additional skeletal elements its assignment to the Phoeniculidae remains uncertain.

Because of the concordance in the shape of their long, robust and pointed beaks, members of the Messelirrisoridae probably had a diet similar to that of extant upupiforms, consisting mainly of insects and other small invertebrates. The presence of large processus retroarticularis on the caudal end of the mandible (see Mayr 1998) suggests that messelirrisorids also were adapted to gaping, i.e. to opening their beak in the substrate in a similar manner to that of their recent relatives (see Burton 1984). The specimens of *Messelirrisor parvus* differ distinctly in the relative lengths of their beaks, and the bird in Figure 1 is one of the rather short-beaked specimens. This difference might result from age differences or from sexual dimorphism, as in some recent Phoeniculidae in which the beaks of males can be 20% longer than those of females (Ligon and Davidson 1988). Too few specimens with complete beaks are known from *M. halcyrostris* and *M. grandis* to draw meaningful comparisons.

Because the Messelirrisoridae is a sister taxon of the recent Upupiformes, outgroup comparisons with the Eocene family facilitates character-state analysis within the Phoeniculidae and Upupidae. The frontals of the Upupidae, for example, are unusually wide between the orbitae, and an osseous bridge connects the processus procoracoideus of the coracoid with the facies articularis clavicularis (Fig. 4B, no. 4).

These characters are absent in the Messelirrisoridae and therefore are probably autapomorphic for hoopoes. For the same reason, the very slender extremitas sternalis of the furcula and the low crista deltopectoralis of the humerus seem to be derived characters of the Phoeniculidae.

Recent hoopoes and wood-hoopoes are especially distinguished in their means of locomotion. Whereas upupids perch and roost in trees but mainly forage on the ground, phoeniculids are specialized for climbing tree trunks. As in other scansorial birds (e.g. woodpeckers and woodcreepers), the trochlea metatarsi III of the tarsometatarsus of phoeniculids bears a deep furrow that is absent in messelirrisorids and upupids (Mayr 1998). The fairly short tarsometatarsus and the long and curved claw on the hallux of messelirrisorids indicate that the latter did not forage regularly on the ground as do recent upupids.

Except for Maurer and Raikow (1981), most recent authors have considered hornbills (Bucerotidae) to be the closest living relatives of the Upupiformes (e.g. Burton 1984, Sibley and Ahlquist 1990). The earliest certain record of the Bucerotidae is from the Middle Miocene of Morocco (Brunet 1971), but the Messelirrisoridae provides a minimum age of 49 million years for the branching of the Upupiformes from their sister taxon.

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