

A new raptorial bird from the Middle Eocene of Messel, Germany

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Abstract

Raptorial birds (“Falconiformes”) are very rare in the Middle Eocene fossil site Messel in Germany. In this study, a new taxon, *Masillaraptor parvunguis* gen. et sp. nov., is described that, as indicated by its long legs, appears to have been a fairly terrestrial bird, with rather weak claws and a beak without a strongly hooked tip. Phylogenetic assignment of *M. parvunguis* is, however, aggravated by the uncertainty concerning monophyly of, and relationships within, extant “Falconiformes”. Therefore, three different published phylogenies of the extant taxa are used as “backbone” phylogenies to determine the relationships of the new taxon by minimising the amount of homoplasy in the phylogenetically informative characters visible in the two known specimens. Abbreviation of the middle phalanges of the fourth toe suggests that *M. parvunguis* is more closely related to a clade including Sagittariidae (secretary bird) and Accipitridae (hawks) than to the Cathartidae (New World vultures). As in Accipitridae and Falconidae, the first phalanx of the second toe is further shortened, but the exact position of *M. parvunguis* is dependent on the still controversial relationships between the extant taxa.

Keywords: *Fossil birds, Eocene, Messel, phylogeny, Masillaraptor parvunguis n. gen. n. sp*

Introduction

As traditionally recognised (Wetmore 1960), diurnal raptors (“Falconiformes”) include New World vultures (Cathartidae), the secretary bird (Sagittariidae), falcons (Falconidae) and hawks and allies (Accipitridae, including the osprey, *Pandion haliaetus*, e.g. Kemp and Crowe 1990; Griffiths 1994; Seibold and Helbig 1995; Mindell et al. 1997). Monophyly of a clade including these taxa is, however, only weakly supported and especially inclusion of Cathartidae and Sagittariidae into the “Falconiformes” was repeatedly doubted; it is further controversial whether, owls (Strigiformes) are more closely related to diurnal raptors or to part of the “higher land bird assemblage” (Cracraft 1981; Sibley and Ahlquist 1990; Griffiths 1994; Mayr et al. 2003). The relationships between the traditional “falconiform” taxa also are far from being resolved. Whereas many authors considered Accipitridae to be the sister group of the Falconidae (Wetmore 1960; Cracraft 1981), some molecular studies (Sibley and Ahlquist 1990; Fain and Houde 2004) and an analysis of syringeal characters by

Griffiths (1994) showed the Accipitridae to be more closely related to the Sagittariidae than to the Falconidae. It was even assumed by some authors that falcons are not closely related to hawks at all (Starck 1959; Jollie 1977; Olson 1985). Griffiths’ (1994) study and an analysis of an as yet unpublished data set of cranial and vertebral characters (Livezey and Zusi 2001) support monophyly of “falconiform” birds to the exclusion of the Strigiformes, whereas analyses of hind limb musculature (McKittrick 1991) and osteological characters (Mayr and Clarke 2003; Mayr et al. 2003) resulted in sister group relationship between Strigiformes and a clade including Falconidae and Accipitridae.

Likewise, molecular studies show no consensus on the relationships among “falconiform” birds (Sibley and Ahlquist 1990; Wink et al. 1998; Haring et al. 2001; Mayr et al. 2003; Sorenson et al. 2003; Cracraft et al. 2004; Fain and Houde 2004). All but one analysis of 12S mitochondrial rDNA by Mindell et al. (1997 Figure 8.9) do not support a closer relationship between owls and diurnal raptors.

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Whereas the fossil record of owls dates back into the Palaeocene and is fairly extensive (Rich and Bohaska 1976; Harrison 1980; Mourer-Chauviré 1983, 1987, Peters 1992, 1994; Mayr 2002a), only few early Tertiary diurnal raptors were described to date. New World vultures were identified in the early Tertiary of the Old World and the fossil record of these birds, from the Middle Eocene of France, was revised by Mourer-Chauviré (2002). The earliest fossil record of the Sagittariidae is from the Oligocene of France (Mourer-Chauviré and Cheneval 1983).

Based on distal tarsometatarsi, three putative “falconiform” birds were described from the Eocene of England (Harrison and Walker 1979; Harrison 1982, 1984). Of these, the early Eocene taxa *Parvulivenator wattlei* Harrison 1982 and *Stintonornis mitchelli* Harrison 1984 were assigned to the Falconidae, whereas the Upper Eocene *Milvovides kempi* Harrison and Walker 1979 was considered to be a member of the Accipitridae.

Peters (1994) described two skulls from the Middle Eocene of Messel in Germany as *Messelastur gratulator* and tentatively assigned this taxon to the Accipitridae. New specimens, however, show that *Messelastur* and the early Eocene *Tynskya eocaena*, described by Mayr (2002a) from the Green River Formation in Wyoming (USA) belong to an extinct taxon, the Messelasturidae, which may be the sister taxon of owls (Strigiformes) (Mayr 2005).

The Upper Eocene Horusornithidae were described from the Quercy fissure fillings (France) by Mourer-Chauviré (1991). The relationships between horusornithids and other “falconiform” birds are uncertain, but Mourer-Chauviré (1991) noted similarities to Falconidae and Accipitridae. Horusornithids differ from other “falconiform” birds and agree with owls in the absence of an ossified supratendineal bridge (pons supratendineus) on the distal end of the tibiotarsus.

Here, I describe a new raptorial bird from Messel. One of the two known specimens of this species was already figured by Peters (1988 Figure 2) who considered it to be possibly related to the Polyborinae (Falconidae) (Peters 1991).

Anatomical terminology follows Baumel and Witmer (1993). The dimensions are in millimetres; the length of the claws was measured from the tip of the tuberculum extensorium to the apex phalangis. Institutional abbreviation: SMF—Forschungsinstitut Senckenberg, Frankfurt am Main, Germany.

Systematic palaeontology

“Falconiformes” (sensu Cracraft 1981)

?Accipitres (sensu Cracraft 1981)

Masillaraptor gen. nov.

Type species: Masillaraptor parvunguis sp. nov.

Diagnosis: Masillaraptor gen. nov. differs from all other known avian taxa in the combination of the

following characters: (1) beak about as long as caudal part of cranium, dorsoventrally high, with equal height over most of its length and straight culmen which curves just before the tip of the beak, narial opening restricted to caudal half of beak; (2) legs long with tibiotarsus being the longest limb element; (3) first phalanx of second toe and (4) second and third phalanges of fourth toe strongly abbreviated; (5) claws small and weak compared to other “falconiform” birds with shortened pedal phalanges. Characters (1), (3) and (4) are derived within neornithine birds and also found in modern Accipitres, from which *Masillaraptor* is, however, distinguished in character (5).

Differential diagnosis: Masillaraptor gen. nov. differs from:

- The Messelasturidae (Mayr 2005) (including *Messelastur* Peters 1994 and *Tynskya* Mayr 2000a) in, e.g.: beak proportionally much longer and with straight culmen, tarsometatarsus proportionally longer, proximal phalanx of second toe shortened, middle phalanges of fourth toe proportionally shorter.
- The raptor-like, long-legged early Eocene *Neocathartes* Wetmore 1950 (which actually is a member of the Cariamae, see Wetmore 1944, 1950; Olson 1985) and all phorusrhacoid birds in: carpometacarpus with narrower spatium intermetacarpale and straight os metacarpale minus, proximal phalanx of second toe shortened.
- The superficially raptor-like early Eocene *Foro* Olson 1992 in: beak longer, carpometacarpus with narrower spatium intermetacarpale and straight os metacarpale minus, proximal phalanx of second toe and second and third phalanges of fourth toe shortened.

The putatively falconiform taxa *Parvulivenator* Harrison 1982, *Stintonornis* Harrison 1984 and *Milvovides* Harrison and Walker 1979 are known distal tarsometatarsi only and cannot be compared with *Masillaraptor* n. gen. in detail. See below for comments on *Coturnipes* (Harrison and Walker 1977).

Etymology: From Latin, masilla: old name for Messel and raptor: ravisher, thief, also the English vernacular term for birds of prey. The genus name is male.

Holotype: SMF-ME 1065 (Figure 1; largely complete articulated skeleton on a slab; most likely an adult individual, contra Peters 1988).

Diagnosis: Same as for genus.

Type locality and horizon: Messel near Darmstadt, Germany (see Schaal and Ziegler 1988 for general information on the site and Mayr 2000b concerning the fossil avifauna of this locality); Lower Middle Eocene (Legendre and Lévêque 1997).

Dimensions of holotype: Right humerus, ~46; right ulna, ~49; carpometacarpus, ~27 (left), ~25 (right); tibiotarsus, ~54 (left), ~52 (right); tarsometatarsus,

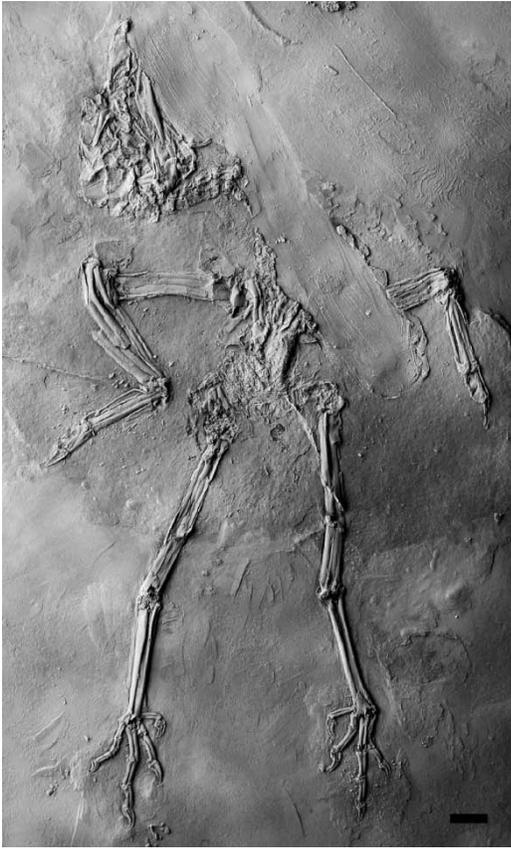


Figure 1. *M. parvunguis* gen. et sp. nov., holotype (SMF-ME 1065). Coated with ammonium chloride to enhance contrast, scale bar equals 10 mm.



Figure 2. *M. parvunguis* gen. et sp. nov., referred specimen SMF-ME 11042. Coated with ammonium chloride to enhance contrast, scale bar equals 10 mm.

~ 34.7 (left), ~ 35.2 (right); pedal phalanges, I1, 7.1; I2, 5.6; II1, 4.0; II2, 9.0; II3, 6.0; III1, 9.6; III2, 7.4; III3, 6.7; III4, 6.2; IV1, 5.4; IV2, 2.8; IV3, 2.6; IV4, 4.7; IV5, 4.8.

Referred specimen: SMF-ME 11042 (Figure 2; almost complete articulated but poorly preserved skeleton on a slab, formerly in the private collection of K. Frickhinger). The counter slab of this specimen, that was figured by Behnke et al. (1986, 61), is still housed in an unknown private collection; the description below only refers to the specimen in SMF.

Dimensions of referred specimen: Skull, ~61; right humerus, ~48; right ulna, ~50; right carpometacarpus, ~24.8; tibiotarsus, ~57 (left), ~57 (right); left tarsometatarsus, ~33.5.

Etymology: From Latin, *parvus*: small, weak and *unguis*: claw. The species name refers to the weak claws of the new taxon, compared to other birds of prey.

Remarks: In a study on fossil birds from the Middle Eocene fossil site Geiseltal in Germany (Mayr 2002b), I compared the type specimen of *M. parvunguis* gen. et sp. nov. with an isolated tarsometatarsus from the Geiseltal that I tentatively assigned to *Coturnipes* Harrison and Walker (1977). The description of *Coturnipes cooperi* Harrison and Walker (1977) is based

on a distal end of a tarsometatarsus from the Lower Eocene London Clay (Harrison and Walker 1977), but Olson (1999, p. 127) noted that there are additional bones of this species in a private collection in England which show that the skeleton of *C. cooperi* is “suggestive to that in the Falconidae”. Unfortunately, these more completely preserved remains of *C. cooperi* are not available for study. Because assignment of the Geiseltal specimen to *Coturnipes* already was tentative and the distal ends of the tarsometatarsi of both known specimens of *M. parvunguis* gen. et sp. nov. are very poorly preserved, I refrain from assigning the Messel specimens to *Coturnipes*. Future discovery of more completely preserved specimens of either *C. cooperi* or *M. parvunguis* will have to show, whether naming the highly distinctive Messel taxon was justified.

Description and comparisons: The skull of both specimens is badly crushed and identification of osteological details is difficult. The beak is about as long as the caudal part of the cranium and dorsoventrally high, with an equal height over most of its length and a straight culmen, which curves just before the tip (Figure 3). The tip itself appears to have been only slightly hooked. Apart from the absence of a markedly hooked tip, the beak of *Masillaraptor*

gen. nov. is somewhat reminiscent to that of caracaras (*Polyborinae*, Falconidae) and Barn-Owls (*Tytonidae*, *Strigiformes*) in its overall proportions. The praemaxilla exhibits impressions of blood vessels. The narial openings do not extend into the distal half of the beak; an ossified nasal septum seems to be absent as in the Cathartidae, whereas it is present in other “falconiform” birds. In contrast to extant Sagittariidae, Falconidae and most Accipitridae, strongly developed, caudally projecting processus supraorbitales appear to have been absent, although the poor preservation of the skulls aggravates identification of osseous structures in the cranial region. The mandible lacks fenestrae as does that of Sagittariidae and Accipitridae; fenestrae are present in Falconidae and strigiform birds. The pars symphysialis is narrow and comparatively long, measuring about 1/4 of the total length of the mandible; its distal end appears to have been rounded as in extant Cathartidae.

No details of the vertebral column are discernible except that the cervical vertebrae are very short, as preserved they are wider than long.

In specimen SMF-ME 11042, the extremitas omalis of the coracoid is preserved, but no phylogenetically informative details can be discerned. Also in specimen SMF-ME 11042, the furcula is visible which is not as massive and widely U-shaped as that of extant “falconiform” birds. As in extant “Falconiformes”, an apophysis furculae appears to be absent. Details of the

scapula and sternum are not visible in either of the two known specimens.

The humerus is elongate and slender as is that of extant “falconiform” birds. However, the crista deltopectoralis is proportionally somewhat shorter than in extant birds of prey, measuring about 1/4 of the entire length of the bone, whereas it measures nearly 1/3 of the humerus in the extant taxa.

As in the Sagittariidae, the ulna only slightly exceeds the humerus in length whereas it is distinctly longer than this bone in most Cathartidae, Falconidae and Accipitridae. In both specimens, one of the ulnae is fractured with the broken ends considerably displaced against each other. Fractures, especially of the ulna or tibiotarsus, are quite common in the skeletons of Messel birds and may have caused the death of these birds (Mayr 2000b; Mayr et al. 2004).

The carpometacarpus is similar to that of extant “falconiform” birds in its shape. The processus extensorius is low. The spatium intermetacarpale is narrow. The os metacarpale minus does not protrude distally beyond the os metacarpale majus.

The phalanx digiti alularis bears a small claw which is also found in many modern “falconiform” birds and other extant bird groups (Stephan 1992). Also as in extant “falconiform” birds, the dorsal surface of the phalanx proximalis digiti majoris exhibits a marked furrow for the tendon of musculus interosseus dorsalis (SMF-ME 1065). There is no well developed processus internus indicis (terminology after Stegmann 1963).

Details of the pelvis and femur cannot be discerned. In specimen SMF-ME 11042, an isolated fish tooth is preserved next to the pelvis; isolated fish teeth have also been found in association with other bird specimens from Messel (Mayr 2001).

The tibiotarsus is the longest limb element and even exceeds the ulna in length. This bone is also long in *T. eocaena*, but in most extant diurnal birds of prey the tibiotarsus is much shorter than the ulna (an exception are the Sagittariidae). The cristae cnemiales are small; the condyles appear to have been proximo-distally low (SMF-ME 11042, right side). It cannot be discerned whether an ossified pons supratendineus was present (as noted above, a supratendineal bridge is absent in the Horusornithidae). As preserved, the fibula measures less than 2/3 of the length of the tibiotarsus, whereas this bone is almost as long as the tibiotarsus in most extant Accipitridae and Falconidae.

The tarsometatarsus is fairly long, narrow and in its proportions similar to the corresponding bone of the Horusornithidae. On the dorsal surface of the proximal end, there is a marked fossa infracotyleris dorsalis. In contrast to crown group Falconidae and Accipitridae, there is no markedly elongated tuberositas musculi tibialis cranialis on the dorsal surface of proximal end of the bone. The hypotarsus is visible in specimen SMF-ME 1065 through the reverse side

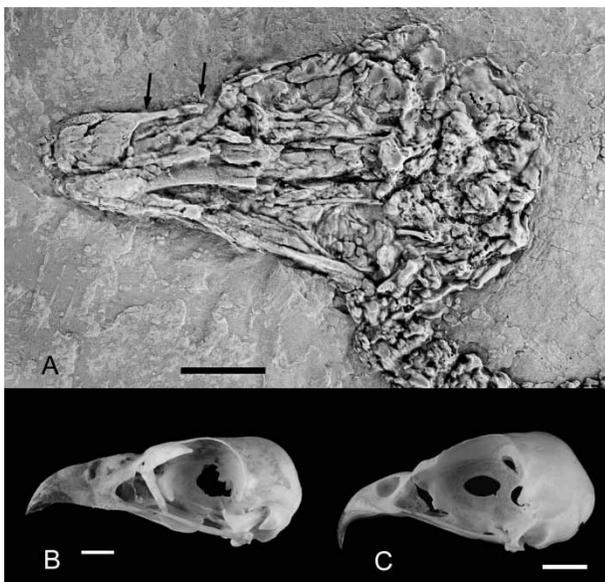


Figure 3. *M. parvunguis* gen. et sp. nov., skull of specimen SMF-ME 11042 (A) in comparison to that of (B), *Polyborus plancus* (Falconidae, “Falconiformes”); (C), *Butastur teesa* (Accipitridae, “Falconiformes”). The arrows point to the rostral and caudal margin of the narial opening of *M. parvunguis*. Specimen in (A) coated with ammonium chloride to enhance contrast, scale bar equals 10 mm.

of the transparent slab. It is simple and block-like, similar to the hypotarsus of crown group Cathartidae and Sagittariidae. By contrast, the hypotarsus of Horusornithidae, Falconidae, Accipitridae, *T. eocaena* and strigiform birds is formed by two strongly protruding cristae that are separated by a wide sulcus. The trochleae metatarsorum are very poorly preserved in both specimens of *M. parvunguis*, preventing detailed comparisons with the fossil taxa *Stintornis*, *Milvooides* and *Corturnipes*.

The third toe is the longest and distinctly exceeds the others in lengths. The first (proximal) phalanx of the second toe is greatly abbreviated and measures less than half of the length of the second phalanx. Also the middle, i.e. second and third phalanges, of the fourth toe are greatly shortened, measuring about half of the length of the fourth phalanx (Figure 4). Within extant “Falconiformes”, the middle phalanges of the fourth toe are shortened in Sagittariidae, Falconidae and Accipitridae, whereas the first phalanx of the second toe is shortened only in Falconidae and Accipitridae; this phalanx is proportionally slightly longer in the Falconidae than in *Masillaraptor* and the Accipitridae. In the Falconidae, the proximal phalanx of the fourth toe is also abbreviated, whereas this phalanx is distinctly longer than the middle phalanges in *Masillaraptor*, Sagittariidae and Accipitridae. The hindtoe of *Masillaraptor* is fairly long as in the Sagittariidae, Falconidae and Accipitridae, whereas it is relatively much shorter in crown group Cathartidae and also appears to have been rather short in the Horusornithidae (Mourer-Chauviré 1991). The claws are weak compared to other non-cathartid “falconiform” birds. The claw of the second toe exceeds those of the other anterior toes in size. In contrast to extant Accipitridae and Falconidae, there appears to have been no pair of canals next to the

tuberculum flexorium (Mayr and Clarke 2003; Figure 9). As in the Cathartidae and most other avian taxa, the sulcus neurovascularis forms a groove, whereas this sulcus is absent in the Sagittariidae, Accipitridae and Falconidae. The os metatarsale I is small.

In specimen SMF-ME 11042, the feathering is well preserved and the longest primaries measure about 130–135 mm; the tail feathers are hidden by the primaries of the left wing.

Discussion

M. parvunguis gen. et sp. nov. is assigned to the Accipitres sensu Cracraft (1981) because of the following characters: (1) presence of a raptor-like beak, foot with (2) first phalanx of second toe and (3) second and third phalanges of fourth toe strongly abbreviated. The combination of these unquestionably derived characters only occurs in the Accipitres sensu Cracraft (1981), i.e. a clade including Sagittariidae, Accipitridae, Falconidae and, possibly, Strigiformes (see introduction). The skeleton of *Masillaraptor* also agrees with extant Accipitres in most other aspects that can be discerned in the fossils (see description).

Evaluation of the exact phylogenetic affinities of *M. parvunguis* is, however, complicated by the uncertainty concerning monophyly of and relationships within extant “falconiformes”. Owing to the poor preservation of the two known specimens of the new species, meaningful analysis of a large character set was not feasible. Phylogenetic affinities of *Masillaraptor* may, however, be confined by the presence of the above described derived length proportions of the pedal phalanges and by the absence of derived features of the hypotarsus and claws that characterise certain “Falconiform” subclades.

Three hypotheses on the relationships between *Masillaraptor* and other extant and fossil raptorial birds are depicted in Figure 3, using different published phylogenies of the extant taxa as a “backbone” phylogeny. In Figure 3A (after Wetmore 1960) and Figure 3B (after Cracraft 1981; Mayr and Clarke 2003), sister group relationship between Accipitridae and Falconidae is assumed, whereas Figure 3C (after Sibley and Ahlquist 1990; Griffiths 1994; Fain and Houde 2004) proceeds from sister group relationship between Accipitridae and Sagittariidae. *Masillaraptor*, Sagittariidae, Accipitridae, Falconidae and Strigiformes share abbreviated middle phalanges of the fourth toe and *Masillaraptor*, Falconidae and Accipitridae further possess an abbreviated first phalanx of the second toe. The shortening of the first phalanx of the second toe in extant Strigidae probably is due to convergence because it is not abbreviated in the Tytonidae and the extinct early Tertiary Palaeoglaucidae (Peters 1992). As detailed in the description, *Masillaraptor* lacks the

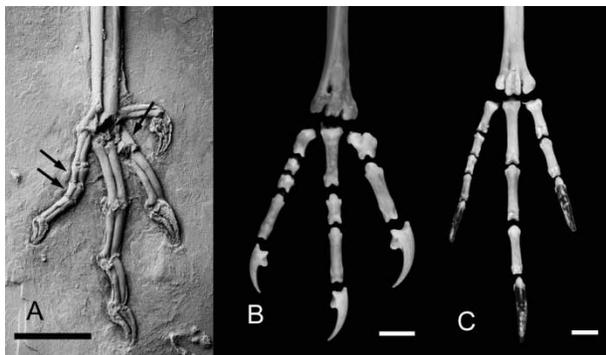


Figure 4. *M. parvunguis* gen. et sp. nov., right foot of the holotype (A) in comparison with the right foot of extant “falconiform” birds: (B), *Cathartes aura* (Cathartidae, “Falconiformes”); (C) *Butastur teesa* (Accipitridae, “Falconiformes”). The arrows indicate the abbreviated pedal phalanges of the second and fourth toe in *M. parvunguis*. Note that the hindtoe has been left away in the extant taxa. Specimen in (A) coated with ammonium chloride to enhance contrast, scale bar equals 10 mm.

derived morphology of the hypotarsus and pedal claws of extant Accipitridae, Falconidae and strigiform birds.

In Figure 3, the position of *Masillaraptor* was determined by minimising the amount of homoplasy in these features. Abbreviation of the middle phalanges of the fourth toe suggests that the new taxon is more closely related to a clade including Sagittariidae and Accipitridae than to the Cathartidae. Its exact position, however, is strongly dependent on the relationships between the extant taxa (Figure 5). If one proceeds from the traditional classification of “Falconiformes”, the abbreviated proximal phalanx of the second toe may suggest a closer relationship to a clade including Falconidae and Accipitridae (Figure 5A). However, if a sister group relationship between Sagittariidae and Accipitridae is assumed, this character probably is a synapomorphy of a more inclusive clade and its absence in the secretary bird a reversal into the primitive condition (Figure 5C). Similar considerations apply to the hypotarsus and claw morphology. If owls are more closely related to hawks and falcons than the latter are to the secretary bird, the plesiomorphic hypotarsus morphology of *Masillaraptor*, for example, would support a position of this taxon outside a clade including Strigiformes, Falconidae and Accipitridae (Figure 5B).

The smallest number of homoplastic events (six) occurs in Figures 3A and B, and in Figure 3C there are

eight cases of homoplasy in the characters mapped on the tree. It is not possible to make a decision between the conflicting phylogenies just from these few characters, all of which concern the morphology of the foot and apparently show a considerable degree of homoplasy independent of the cladogram on which they are mapped. Thus, before the exact relationships of *Masillaraptor* can be conclusively resolved, further morphological and molecular studies have to yield a robust phylogeny of the extant taxa.

The osteology of *M. parvunguis* gen. et sp. nov. not only is very different from that of any extant “falconiform” taxon, but also from that of the two other sufficiently well-known Eocene raptorial taxa, the Horusornithidae (Mourer-Chauviré 1991) and Messelasturidae (Mayr 2005) (see introduction).

Horusornithidae share with Accipitridae and Falconidae a derived morphology of the hypotarsus which exhibits two marked cristae that are separated by a wide sulcus, and a derived morphology of the pedal claws which lack a sulcus neurovascularis and exhibit a pair of canals next to the tuberculum flexorium of the claws (Mayr and Clarke 2003 Figure 9). Horusornithidae and most Accipitridae further share a derived modification of the os metacarpale majus of the carpometacarpus, which has a rectangular cross section with essentially, flat cranial and caudal surfaces (Mourer-Chauviré 1991).

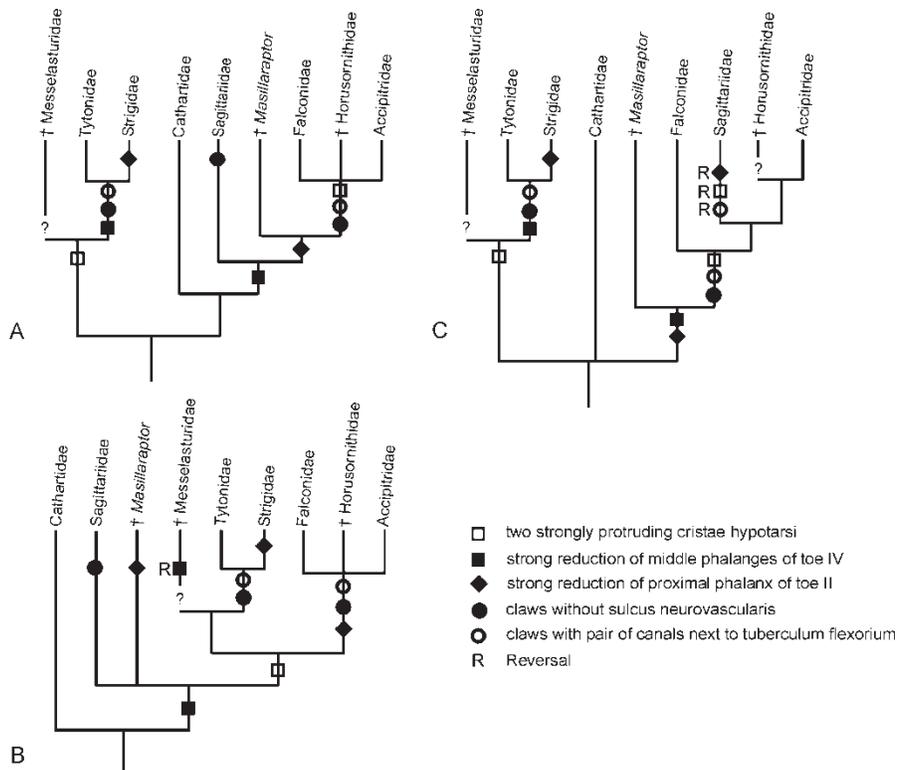


Figure 5. Three hypotheses on the phylogenetic relationships between *M. parvunguis* gen. et sp. nov. and other extant and fossil “falconiform” birds, with the distribution of some morphological features mapped on the phylogenetic trees. “Backbone” phylogeny of extant taxa after (A), Wetmore (1960); (B), Cracraft (1981) and Mayr and Clarke (2003); (C), Sibley and Ahlquist (1990); Griffiths (1994) and Fain and Houde (2004). Taxa only known by fossils are indicated by a cross. See text for further explanation.

The hypotarsus of the Horusornithidae also more closely resembles that of hawks than falcons, although this similarity may be plesiomorphic within a more inclusive clade. However, if Accipitridae and Falconidae are not sister taxa, the Horusornithidae may be more closely related to the Accipitridae than to the Falconidae (Figure 3C).

The Messelasturidae probably are more closely related to owls than to any of the diurnal birds of prey (Mayr 2005). The tarsometatarsus of the North American messelasturid *T. eocaena* in particular exhibits a derived morphology similar to that of strigiform birds in that the crista medialis of the hypotarsus is markedly longer than the crista lateralis and the trochlea metatarsi IV is much shorter than the trochlea metatarsi II and bears a plantarly projecting wing-like flange which is typical of semi-zygodactyl feet in which the fourth toe can be spread laterally (Mayr 2005). In *T. eocaena*, all three proximal phalanges of the fourth toe are shortened, although the middle ones are not as strongly abbreviated as in *Masillaraptor* and extant owls.

The comparatively long legs indicate that *M. parvunguis* probably was a fairly terrestrial bird. The new species has weak claws and lacks a markedly hooked bill tip, although its beak is quite massive. Unfortunately, in none of the two known specimens, stomach content is preserved and it is to be hoped that future specimens will give a direct hint on its diet (preservation of stomach content is quite common in Messel vertebrates, e.g. Schaal and Ziegler 1988).

Raptorial birds are very rare among the fossil birds found in Messel. Apart from the two specimens of *Masillaraptor* described in this study, two skulls and a nearly complete skeleton of *M. gratulator* (Peters 1994) and two postcranial skeletons of the owl *Palaeoglaux artophoron* (Peters 1992) are known, one of the latter has not yet been described. Possibly, these birds lived and hunted in the surrounding forests rather than in the immediate vicinity of the Messel lake. In this case, injured or dying individuals would have had a smaller chance of falling into the lake and thus become fossilised than, e.g. aerial insectivores that were hunting insects above the lake surface or small arboreal birds that were living in the vegetation directly next to the lake.

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