A well-preserved skull of the "falconiform" bird *Masillaraptor* from the middle Eocene of Messel (Germany)

GERALD MAYR

Abstract

The avian species *Masillaraptor parvunguis* MAYR, 2006 was so far known from two skeletons from the middle Eocene of Messel in Germany, and constitutes the earliest substantial fossil record of the "Falconiformes" (birds of prey). In the present study, a third specimen of *M. parvunguis* is described that provides critical new details of the osteology of this species. Most notably, the fossil, a skull with portions of the vertebral column, exhibits a sharply hooked beak and well-developed processus supraorbitales, thus documenting that the previously reported absence of these features in the two skeletons of *M. parvunguis* is based on a misinterpretation of the poorly preserved fossils. The affinities of *M. parvunguis* to other "falconiform" birds are uncertain, and the species is classified in the new taxon Masillaraptoridae. Some skull features may indicate a closer relationship to the Falconidae than to the clade including the Sagittariidae, Pandionidae, and Accipitridae.

K e y w o r d s : Fossil birds, Messel, evolution, phylogeny, birds of prey.

Zusammenfassung

Die Vogelart *Masillaraptor parvunguis* MAYR, 2006 war bisher aufgrund von zwei Skeletten aus dem mittleren Eozän von Messel in Deutschland bekannt und stellt den frühesten Fossilnachweis der "Falconiformes" (Taggreifvögel) dar. In der vorliegenden Untersuchung wird ein drittes Exemplar von *M. parvunguis* beschrieben, welches bisher unbekannte osteologische Einzelheiten dieser Art erkennen lässt. Insbesondere besitzt das Fossil, ein Schädel mit Teilen der Wirbelsäule, einen scharf gekrümmten Schnabel und gut entwickelte Processus supraorbitales. Das früher berichtete Fehlen dieser Merkmale in den zwei Skeletten von *M. parvunguis* beruht daher auf einer Fehlinterpretation der schlecht erhaltenen Funde. Die Verwandtschaftsbeziehungen zwischen *M. parvunguis* und anderen "falconiformen" Vögeln sind unsicher, und die Art wird in das neue Taxon Masillaraptoridae gestellt. Einige Schädelmerkmale weisen auf eine nähere Verwandtschaft zu den Falconidae hin, als zu dem Monophylum, welches Sagittariidae, Pandionidae und Accipitridae beinhaltet.

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1. Introduction

The birds of prey ("Falconiformes") are a presumably non-monophyletic avian group (ERICSON et al. 2006; MAYR 2008; HACKETT et al. 2008), which in traditional classifications includes the Cathartidae (New World vultures), Sagittariidae (Secretary bird), Pandionidae (Osprey), Accipitridae (hawks and allies), and Falconidae (falcons). The early Paleogene, i. e., pre-Oligocene, fossil record of these birds is scarce, and very little is known about their evolutionary history (MAYR 2009).

One of the earliest and most completely preserved fossil species that was assigned to the "Falconiformes" is *Masillaraptor parvunguis* MAYR, 2006 from the middle Eocene of Messel in Germany. Two skeletons of this species were described, both of which are very poorly preserved (MAYR 2006). *M. parvunguis* was a small and fairly long-legged bird (Fig. 3a), which is clearly distinguished from all extant birds of prey in skeletal morphology. Its exact phylogenetic affinities were considered uncertain by MAYR (2006), who hypothesized that *Masillaraptor* is more closely related to a clade including the Sagittariidae and Accipitridae than to the Cathartidae.

Here I describe a new skull of *M. parvunguis* from Messel, which allows the recognition of previously unknown or controversial osteological details of this species; the osteological terminology used in this study follows BAUMEL & WITMER (1993).

Repository acronyms

- IRSNB Institut royal des Sciences naturelles de Belgique, Belgium
- SMF Forschungsinstitut Senckenberg, Frankfurt am Main, Germany

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2. Systematic paleontology

"Falconiformes" sensu WETMORE (1960)

Masillaraptoridae n. fam.

Type genus: Masillaraptor MAYR, 2006.

D i a g n o s i s: Small raptorial bird that is characterized by (1) beak with straight culmen and sharply hooked tip; (2) tomia just proximal of bill tip not forming a sharp cutting edge; (3) pars symphysialis of mandible long, narrow, and upward curved; (4) processus supraorbitales very long; (5) processus zygomaticus well developed; (6) processus spinosi of two caudalmost thoracic vertebrae fused; (7) long legs, with tibiotarsus being the longest limb bone; (8) first phalanx of second toe and (9) second and third phalanges of fourth toe shortened. The combination of these features clearly distinguishes the Masillaraptoridae from all other avian groups; character (3) is considered an autapomorphy of the new taxon.

Masillaraptor MAYR, 2006

Masillaraptor parvunguis MAYR, 2006 Figs. 1–3

R e f e r r e d s p e c i m e n : IRSNB Av 83 (skull with portions of vertebral column; Figs. 1 and 2).

Locality and horizon: Messel near Darmstadt, Germany; middle Eocene (ca. 47 million years ago).

M e a s u r e m e n t s (in mm; dimensions of holotype in brackets): Length of skull, \sim 54 [\sim 53]; length of upper beak, \sim 18.5 [\sim 19]; length of mandible, \sim 49 [\sim 46 (estimated)].

D e s c r i p t i o n a n d c o m p a r i s o n s. – The skull is visible in ventrolateral view, and the mediolaterally narrow upper beak measures less than half of its total length. The straight culmen curves just before the sharply hooked tip of the rostrum, the very end of which is broken. The beak is not sharply hooked in the only previously known specimen of *Masillaraptor parvunguis* in which the tip is preserved (MAYR 2006), but I now consider this to be an artifact of the poor preservation and plastic deformation of this fossil (Fig. 1b). There are many openings of sensory nerves (foveae corpusculorum nervosorum) on the tip of the upper beak, and distinct impressions of blood vessels are distributed over its lateral surface (Fig. 2b). The tomia are sigmoidally curved and are slightly convex in their proximal section. In the concavity just proximal of the bill tip they do not form a sharp cutting edge, but bear shallow "tomial grooves" as in Falconidae and few Accipitridae (Fig. 2b; JOLLIE 1977a: 201). The large narial opening measures about one third of the length of the beak and is situated in its dorsal half; whether there was an ossified internarial septum cannot be discerned.

Only few details of the cranium are preserved, but a long and slender processus supraorbitalis is clearly visible (Fig. 1a). This process is equally well developed in the falconid taxa Herpetotherinae (forest-falcons) and Falconinae (falcons), and in the Sagittariidae. The Polyborinae (Falconidae) have somewhat shorter supraorbital processes and their development in the Accipitridae is variable (these processes are, for example, absent in the taxa Polyboroides and Neophron; see also Jollie 1977b: fig. 93); Pandionidae and Cathartidae lack elongated processus supraorbitales. Supraorbital processes were described as being absent in the two previously known specimens of M. parvunguis by MAYR (2006), but re-examination of the fossils suggests that an elongate plate-like structure in the holotype actually represents such a process (Fig. 1c). As in Cathartidae, Pandionidae, and Falconidae, the processus zygomaticus is well developed (Fig. 1a), whereas it is reduced in Sagittariidae and Accipitridae (SUSCHKIN 1905: 22; JOLLIE 1977b: 215). Details of the basicranial and palatal area cannot be identified. The left quadratum is preserved in articulation, whereas the detached right one is visible in caudal view (Fig. 1); except for the wide processus oticus, which has a shallow incisura intercapitularis, no details of this bone can be discerned.

In contrast to most extant birds of prey, the mandible is very long and narrow. The similarly long and narrow pars symphysialis has a rounded tip and is upward curved in lateral view (Fig. 2a). The rami mandibulae are dorsoventrally deep, fenestrae mandibulae seem to be absent.

As in one of the specimens described by MAYR (2006), the cornu branchiale of the hyoid apparatus, as well as the ossified cartilago cricoidea of the larynx and remains of ossified tracheal rings are preserved.

Altogether, 14 praesacral vertebrae can be counted. The first four cervical vertebrae are situated on the ventral surface of the skull, ten thoracic and cervical vertebrae are preserved in articulation. The fourth cervical vertebra lacks an osseous bridge connecting the zygapophyses craniales et caudales. The corpi of the thoracic vertebrae are mediolaterally compressed. The two caudalmost thoracic vertebrae lack a processus ventralis, and these processes are small on the two cranially adjacent thoracic vertebrae. Although a true notarium, i. e., fused bodies of the thoracic vertebrae, is absent, the processus spinosi of the two caudalmost of the preserved thoracic vertebrae seem to have been conjoined (Fig. 2c).



Fig. 1. Skull of *Masillaraptor parvunguis* MAYR, 2006 from the middle Eocene of Messel. – **a**. New specimen IRSNB Av 83. **b**. Skull of SMF-ME 11042. **c**. Skull of holotype (SMF-ME 1065). – Abbreviations: cml = caudal end of right ramus mandibulae, cmr = caudal end of left ramus mandibulae, cve = cervical vertebrae, hyo = hyoid apparatus, lqu = left quadratum, nar = narial opening, rqu = right quadratum, sup = processus supraorbitalis, zyg = processus zygomaticus. All specimens coated with ammonium chloride; scale bars equal 5 mm.

3. Discussion

The new specimen described here shows that *Masillaraptor parvunguis* shares a sharply hooked bill tip with other "falconiform" birds and well-developed processus supraorbitales with the Falconidae, Accipitridae, and Sagittariidae. I now consider the purported absence of these features in the previously known specimens of *M. parvunguis* to be based on a misinterpretation because of poor preservation. Supraorbital processes and a raptor-like beak also occur in the Phorusrhacidae, predominantly South

American stem lineage representatives of the Cariamidae (seriemas), some species of which have a similar bill shape to *M. parvunguis* (e. g., MAYR 2009: fig. 13.1). The postcranial osteology of *M. parvunguis* is, however, not indicative of a closer relationship to the flightless phorusrhacids. Instead, the feet resemble those of some "falconiform" birds in that the two central phalanges of the fourth toe and the proximal phalanx of the second toe are shortened (MAYR 2006; Fig. 3b). This derived morphology occurs in the Accipitridae and Falconidae, whereas the pedal phalanges of the Cathartidae and those of phorusrhacid



Fig. 2. *Masillaraptor parvunguis* MAYR, 2006 from the middle Eocene of Messel, details of specimen IRSNB Av 83. – **a**. Pars symphysialis of mandible in lateral view. **b**. Detail of beak. **c**. Detail of thoracic vertebrae. Note the fused processus spinosi of the caudalmost thoracic vertebrae. – Abbreviations: psp = processus spinosus, pve = processus ventralis, tgr = tomial groove. Specimens coated with ammonium chloride; scale bars equal 5 mm.

birds have the usual proportions; in the Sagittariidae only the central phalanges of the fourth toe are shortened.

In discussing the phylogenetic affinities of *M. parvunguis*, MAYR (2006) proceeded from a clade including the Sagittariidae, Pandionidae, Accipitridae, and Falconidae, which is obtained in some analyses of morphological data (MAYR & CLARKE 2003; LIVEZEY & ZUSI 2007). Recent molecular studies, however, conflict with this assumption, and whereas these congruently support a clade including the Sagittariidae, Pandionidae, and Accipitridae, the Falconidae result in a clade together with the Cariamidae, Psittaciformes (parrots) and Passeriformes (passerines) (ERICSON et al. 2006; MAYR 2008; HACKETT et al. 2008). Concerning the affinities of *M. parvunguis*, this raises the question whether the fossil species is more closely related to the Falconidae than to the Sagittariidae/Pandionidae/ Accipitridae clade.

The then still undescribed holotype skeleton of *M. parvunguis* was tentatively assigned to the Falconidae by PETERS (1991), and the osteological data obtained from the new specimen are also more indicative of a closer relationship to the Falconidae. In particular, the new skull differs from crown group representatives of the Sagittariidae and Accipitridae but agrees with the Falconidae in the presence of well-developed processus zygomatici. As in crown group Falconidae the tomia just proximal of the tip of the beak further do not form a sharp cutting edge. The fact that the processus spinosi of the two caudalmost thoracic vertebrae are fused may indicate an incipient notarium, which among extant "Falconiformes" is only present in



Fig. 3. *Masillaraptor parvunguis* MAYR, 2006 from the middle Eocene of Messel. – **a**. Complete skeleton SMF-ME 11042. **b**. Right foot of holotype (SMF-ME 1065). The arrows indicate the shortened pedal phalanges of the fourth and second toes. – Specimens coated with ammonium chloride; scale bars equal 10 mm.

the Falconidae (this feature can, however, not be listed as a synapomorphy of *Masillaraptor* and crown group Falconidae, because a notarium evolved within the latter and is absent in *Herpetotheres* and *Micrastur*, which are the sister taxon of other Falconidae; SUSCHKIN 1905; GRIFFITHS et al. 2004). The distribution of the above-mentioned characters that are shared by *Masillaraptor* and extant "falconiform" taxa is tabulated in Tab. 1. Concerning these features the osteology of the fossil corresponds best with the Falconidae, but owing to the high degree of homoplasy and, in the case of well-developed processus zygomatici, uncertain character polarity, none of these similarities provides strong evidence for an assignment of *Masillaraptor* to the stem lineage of the Falconidae.

Irrespective of their exact phylogenetic affinities, however, the *M. parvunguis* fossils are of significance, because they document the existence of a distinctive group of raptorial birds in the early Eocene. A well-preserved but

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Tab. 1. Distribution of selected characters seen in *Masillaraptor parvunguis* MAYR, 2006 and extant "Falconiformes". The character polarity of well-developed processus zygomatici is uncertain, but concerning the other characters the presence represents the derived state. ¹ absent in, e.g., *Polyboroides* and *Neophron*; ² present in *Harpagus, Ictinia, Leptodon*, and *Chondrohierax* (JOLLIE 1977a: 201).

	Masillaraptor	Falconidae	Accipitridae	Pandionidae	Sagittariidae	Cathartidae
Well-developed processus supraorbitales	present	present	variable ¹	absent	present	absent
Well-developed processus zygomatici	present	present	absent	present	absent	present
Tomial grooves	present	present	variable ²	absent	absent	absent
Shortened proximal pha- lanx of second toe	present	present	present	present	absent	absent
Shortened central phalanges of fourth toe	present	present	present	present	present	absent

as yet undescribed partial skeleton of a *Masillaraptor*-like bird was also reported from the early Eocene London Clay of Walton-on-the-Naze (DANIELS 1992; information letter of the Society of Avian Paleontology and Evolution, 6; http://www2.nrm.se/ve/birds/sape/sapenews6.html.en). This specimen, which I had the opportunity to briefly examine, is currently in the private collection of M. DANIELS, and once available for formal publication it will doubtless contribute to a better understanding of the phylogenetic affinities of masillaraptorids.

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Address of the author:

GERALD MAYR, Forschungsinstitut Senckenberg, Sektion Ornithologie, Senckenberganlage 25, 60325 Frankfurt/M., Germany E-mail: Gerald.Mayr@senckenberg.de

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