

**New specimens of *Hassiavis laticauda* (Aves: Cypselomorphae)
and *Quasisyndactylus longibrachis* (Aves: Alcediniformes)
from the Middle Eocene of Messel, Germany**

With 7 figs

Gerald MAYR

Abstract

New specimens of two avian taxa from the Middle Eocene of Messel (Hesse, Germany) are described. The first complete skeleton of the putative archaeotrogon *Hassiavis laticauda* MAYR 1998 reveals that this species has a short and wide beak, most similar to that of extant owlet-nightjars (Aegothelidae). Beak morphology suggests classification of *Hassiavis* into a monophyletic clade which includes extant Caprimulgidae (nightjars), Nyctibiidae (potoos), Aegothelidae and the traditional order Apodiformes (swifts and hummingbirds). In the new specimen, the feathers are very well preserved and, as in the holotype, the tail feathers are distinctly barred. A new skeleton of *Quasisyndactylus longibrachis* MAYR 1998 confirms the assignment of this species to the Alcediniformes (kingfishers, bee-eaters, todies and motmots) and shows that its bill was flattened dorsoventrally and very similar to that of extant todies (Todidae). The morphology of the furcula suggests that *Quasisyndactylus* is the sister taxon of the four extant alcediniform families.

Key words: Messel, Eocene, fossil birds, Cypselomorphae, Alcediniformes

Kurzfassung

Neue Exemplare von zwei Vogeltaxa werden aus dem Mittel-Eozän von Messel (Hessen, Deutschland) beschrieben. Das erste vollständige Skelett des mutmaßlichen Archaeotrogons *Hassiavis laticauda* MAYR 1998 zeigt, dass diese Art einen kurzen und breiten Schnabel besaß, am ähnlichsten dem rezenten Höhlenschwalme (Aegothelidae). Die Schnabelformologie stützt die Klassifikation von *Hassiavis* in ein monophyletisches Taxon, welches die rezenten Caprimulgidae (Ziegenmelker), Nyctibiidae (Tagschläfer), und Aegothelidae sowie die traditionelle Ordnung Apodiformes (Segler und Kolibris) umfasst. Die Federn des neuen Exemplars sind sehr gut erhalten und ebenso wie beim Holotypus sind die Schwanzfedern deutlich gebändert. Ein neues Skelett von *Quasisyndactylus longibrachis* MAYR 1998 bestätigt die Zuordnung dieser Art zu den Alcediniformes (Eisvögel, Bienenfresser, Todies und Motmots) und lässt erkennen, dass der Schnabel dorsoventral abgeplattet war, ähnlich dem der rezenten Todies (Todidae). Der Bau der Furcula legt nahe, dass *Quasisyndactylus* das Schwestertaxon der vier rezenten alcediniformen Familien ist.

Schlüsselworte: Messel, Eozän, fossile Vögel, Cypselomorphae, Alcediniformes

Introduction

Birds are the predominant land vertebrates in the Middle Eocene deposits of Messel (Hesse, Germany), both in terms of the number of specimens and the number of species.

More than 30 avian species have hitherto been described, which is probably still much less than the actual number of bird species found at this locality so far (see MAYR 2000 for a survey of the fossil avifauna of Messel, a detailed description of the site itself can be found in SCHAAL & ZIEGLER 1988).

Author's address: Dr. Gerald MAYR, Forschungsinstitut Senckenberg, Sektion Ornithologie, Senckenberganlage 25, 60325 Frankfurt a.M., Germany, <Gerald.Mayr@senckenberg.de>

* Nr. 157: KURZ, C. & HABERSETZER, J. (2004): Untersuchungen der Zahnmorphologie von Beutelratten aus Messel mit der Mikroröntgenmethode CORR. – Courier Forschungsinstitut Senckenberg, 252: 13-21.

In this study, new skeletons of two unrelated species, *Hassiavis laticauda* MAYR 1998 and *Quasisyndactylus longibrachis* MAYR 1998, are presented. They are among the best-preserved specimens of these taxa and were recently purchased by the Forschungsinstitut Senckenberg from a private collection. Since the osteology of *Hassiavis* and *Quasisyndactylus* was already described in some detail (MAYR 1998 a, 1998 b), only previously unknown osteological features are mentioned in the following.

The osteological nomenclature follows BAUMEL & WITMER (1993). The dimensions are in millimetres and represent the overall length of the bone along its longitudinal axis. The specimens are deposited in the Forschungsinstitut Senckenberg, Frankfurt a.M. (SMF).

Systematic palaeontology

Cypselomorphae (sensu HUXLEY 1867)
 Family Archaeotrogonidae MOURER-CHAUVIRÉ 1980
 Genus *Hassiavis* MAYR 1998
Hassiavis laticauda MAYR 1998
 (figs 1-3)

Referred specimen: SMF ME 3545 (complete articulated skeleton, formerly in the private collection of U. SOMMER; fig. 1).

Dimensions: Humerus ~ 20.5 (l); ulna ~ 25 (l); carpometacarpus ~ 13.5 (l); tibiotarsus ~ 23.0 (l), ~ 23.5 (r); tarsometatarsus ~ 11.0 (l), ~ 11.0 (r).

Description and comparison: In the new specimen of *Hassiavis*, for the first time the complete skull is preserved, which most closely resembles that of extant Aegothelidae (owlet-nightjars) (figs 2-3). As in the latter, the beak is wide and measures less than half the length of the entire skull; the processus praemaxillaris of the os nasale is thin. The rostrum maxillae is very short, the ossa maxillaria are separated by a large oval cleft. The ossa palatina appear to have been large and bear long and narrow processus maxillares. The ossa pterygoidea are fairly long and slender, as in the Aegothelidae (in the Caprimulgidae and Nyctibiidae they are much stouter). The mandible also resembles that of extant Aegothelidae; its proximal end is small, the rami mandibulae become narrower towards their distal part, and the pars symphysialis is very short. The processus orbitalis of the quadratum apparently is short as in extant Aegothelidae, Caprimulgidae, and Nyctibiidae.

Whereas the postcranial bones are badly flattened and do not reveal new details, the feathering is very well preserved in SMF ME 3545 (see MAYR 1998 a for a reconstruction of the feathering of *Hassiavis*). As in the holotype, the tail is distinctly barred; the dark bars have a proximodistal width of about 3 mm.



Fig. 1: *Hassiavis laticauda* (specimen SMF ME 3545), note the distinct barring of the tail feathers; scale bar equals 10 mm.

Remarks: The Archaeotrogonidae are among the most abundant small birds in the Oligocene deposits of the Quercy (France) but are rarely found in the Eocene Quercy localities (MOURER-CHAUVIRÉ 1980). If correctly assigned to this family, *Hassiavis laticauda* is the smallest known taxon of the Archaeotrogonidae. As indicated by its short and wide beak, *Hassiavis* was catching insects on the wing as do most extant taxa of the Cypselomorphae.

Originally, the Archaeotrogonidae were considered to be relatives of the Trogonidae (trogons) (MILNE-EDWARDS 1892; MOURER-CHAUVIRÉ 1980), but MOURER-CHAUVIRÉ (1980) noticed similarities to extant Caprimulgiformes and finally classified the family within the latter order (MOURER-CHAUVIRÉ 1995). MAYR (1998 a) considered the higher level affinities of the Archaeotrogonidae to be uncertain and noted some similarities to the Aegialornithidae, an Eocene family usually assigned to the Apodiformes (swifts and hummingbirds).

A recent phylogenetic analysis has shown the traditional order Caprimulgiformes (sensu WETMORE 1960) to be paraphyletic and morphological evidence supports

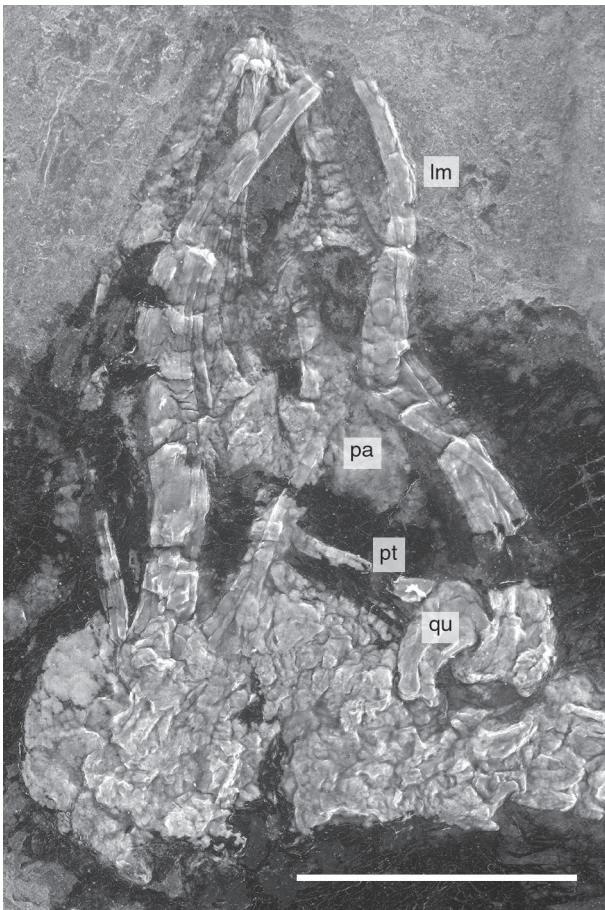


Fig. 2: *Hassiavis laticauda* (SMF ME 3545), skull. Abbreviations: lm = left ramus mandibulae, pa = left os palatinum, pt = left os pterygoideum, qu = left os quadratum; scale bar equals 10 mm.

monophyly of Aegothelidae and Apodiformes, with Nyctibiidae and Caprimulgidae being the sister taxon of this clade (MAYR 2002). Beak morphology suggests classification of *Hassiavis* into this clade which is equivalent to the Cypselomorphae of HUXLEY (1867) and which comprises Nyctibiidae, Caprimulgidae, Aegothelidae, and the traditional Apodiformes (shared derived features are, for example: ossa maxillaria separated by a large cleft, mandible with very short pars symphysialis, and rami mandibulae very slender in their distal half). The exact systematic position of *Hassiavis* within this clade cannot be resolved at present. The Eocene genus lacks the highly derived bill morphology of extant Caprimulgidae and Nyctibiidae (e.g., the ossa palatina are not as enlarged, the ossa pterygoidea are less stout, and the proximal part of the mandible is not flattened dorsoventrally). The beak of *Hassiavis* most closely resembles that of extant Aegothelidae which might, however, be due to the retention of plesiomorphic features. A similar beak also occurs in an unnamed apodiform bird from Messel which was illustrated by MAYR & PETERS (1999: fig. 3).

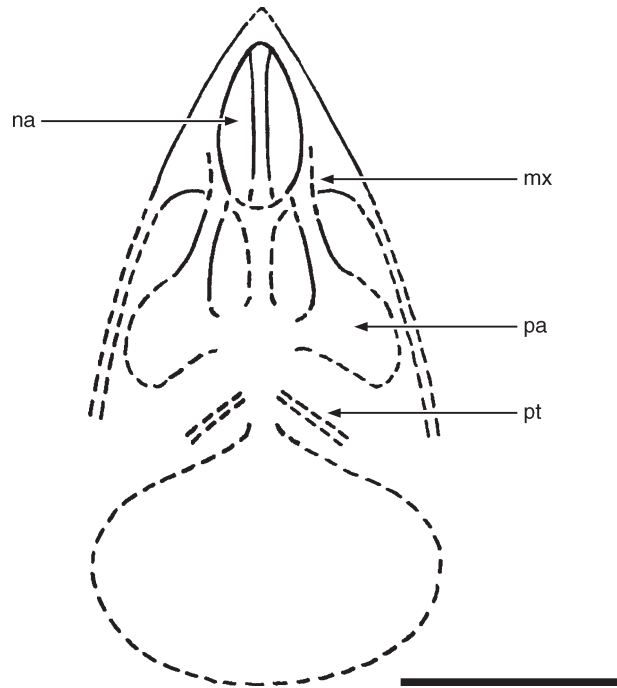


Fig. 3: *Hassiavis laticauda*, schematic partial reconstruction of the skull in ventral view (based on SMF ME 3545). Abbreviations: mx = os maxillare, na = processus praemaxillaris of the os nasale, pa = os palatinum, pt = os pterygoideum; scale bar equals 10 mm.

The barring of the tail feathers is preserved in both the holotype and the new specimen of *Hassiavis laticauda*. In both specimens the pattern is very similar and probably reflects the original colour pattern of the feathers (a similar barring also occurs in the majority of extant Caprimulgiformes). It is assumed that soft tissue remains in Messel fossils are usually not preserved as organic matter but imaged by lithified bacteria (WUTTKE 1983). Further investigations are needed to find out if and how the original coloration of feathers has been preserved in this case.

Alcediniformes (sensu MAYR 1998 b)

Family incertae sedis

Quasisyndactylus MAYR 1998

Quasisyndactylus longibrachis MAYR 1998

(figs 4-7)

Referred specimen: SMF ME 3543 a + b (complete articulated skeleton, formerly in the private collection of U. SOMMER; figs 4-7).

Dimensions: Skull 35.5; humerus 15.8 (r); ulna ~ 21.1 (l); carpometacarpus 8.7 (l), 8.6 (r); coracoid ~ 10.5 (l); tibiotarsus 17.3 (l); tarsometatarsus 9.8 (l), 9.8 (r).



Fig. 4: *Quasisyndactylus longibrachis* (SMF ME 3543 a). Coated with ammonium chloride; scale bar equals 10 mm.



Fig. 5: *Quasisyndactylus longibrachis* (SMF ME 3543 b). Coated with ammonium chloride; scale bar equals 10 mm.

Description and comparison: In the new specimen of *Quasisyndactylus longibrachis* especially the skull and the feet are much better preserved than in the other known skeletons of this species. As preserved, the skull is very similar to that of the extant Todidae and as in the latter the beak is flattened dorsoventrally and tapers towards its tip (fig. 6). The upper jaw and the mandible have nearly exactly the same shape and the same absolute and relative size as in extant *Todus multicolor* GOULD 1837. The narial openings measure about half the length of the beak. The ossa praefrontalia are small (in contrast to many recent Alcedinidae), the part of the os frontale between the orbitae is wider than in the recent Todidae. The septum interorbitale appears to have been weakly ossified.

The tarsometatarsus most closely resembles that of the recent genera *Momotus* BRISSON 1860 (Momotidae) and *Coracias* LINNAEUS 1758 (Coraciidae) in its shape (fig. 7). The tarsometatarsus of the Todidae is much more elongate, while that of the Meropidae and most Alcedinidae is shorter and stouter. As in recent alcediniform birds, the distal end appears to have been only slightly curved on the level of the trochleae and the trochlea metatarsi IV is round in lateral view.

As in all other specimens of *Q. longibrachis*, the three anterior toes are preserved in tight attachment in

the new skeleton (fig. 7). MAYR (1998 b) already noted, that this probably indicates the presence of a syndactyl foot, which is characteristic for all recent alcediniform birds (i.e., the proximal ends of the anterior toes were linked by connective tissue). The proximal phalanx of the hallux closely resembles that of *Todus multicolor* (Todidae) in its shape. Contrary to the statement in MAYR (1998 b), its proximal end bears a lateral projection which is a derived character shared with all extant alcediniform birds (MAYR 1998 b: fig. 20 F).

The specimen shows quartz grains in the area of the crop. Many of them are very small, about 0.1 mm, but a few are as large as 1.4 mm in diameter. The right scapula and the right ulna are fractured and the respective parts of the bones are displaced against each other. These fractures do not appear to be of taphonomic origin and might have caused the death of the bird.

Remarks: The Alcediniformes comprise four extant families; Todidae (todies) and Momotidae (motmots) are restricted today to the Neotropical region, whereas Meropidae (bee-eaters) and Alcedinidae (kingfishers) have their centre of distribution in the Old World.

Quasisyndactylus longibrachis has been tentatively assigned to the Alcediniformes in the original description, and this assignment is further confirmed by the

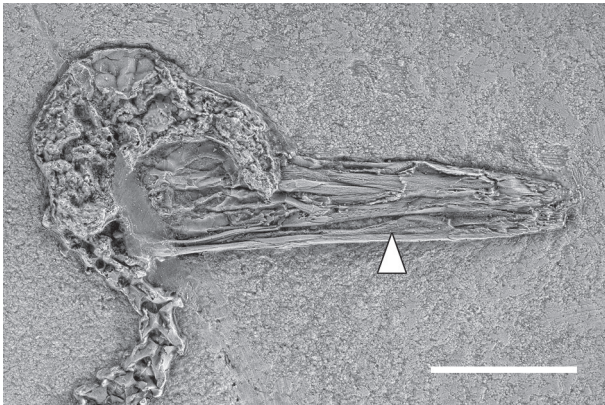


Fig. 6: *Quasisyndactylus longibrachis* (SMF ME 3543 a), skull. The arrow indicates the proximal end of the pars symphysialis of the mandible. Coated with ammonium chloride; scale bar equals 10 mm.

lateral expansion of the proximal phalanx of the hallux, in addition to the characters already mentioned by MAYR (1998 b) (e.g. mandible with very long pars symphysialis, feet probably syndactyl).

The furcula of *Q. longibrachis* has a wider extremitas sternalis and a narrower extremitas omalis than that of extant alcediniform birds, which probably indicates that the Eocene species is the sister taxon of all extant Alcediniformes (see MAYR 1998 b). The similar bill shape of *Quasisyndactylus* and extant Todidae might be due to convergence, since a comparable bill also evolved, for example, among some Momotidae (*Electron* GISTEL 1848, *Eumomota* SCLATER 1858, *Hylomanes* LICHTENSTEIN 1839), as well as in the tyrant flycatchers of the genus *Todirostrum* LESSON 1831.

Quasisyndactylus differs from extant Todidae in the proportionally longer wing and shorter tarsometatarsus, the absence of a well-developed processus intermetacarpalis, and the morphology of the extremitas omalis of the coracoid (hooked and with long processus procoracoideus). It differs from the Oligocene genus *Palaeotodus* OLSON 1976 in the proportionally smaller humerus (whereas the skull of *Q. longibrachis* has the same size as that of *Palaeotodus emryi* OLSON 1976, the proximal width of the humerus is only ~ 4 mm vs. 6.7 mm in *P. emryi*) and in the relatively longer pars symphysialis of the mandible.

Acknowledgements

I thank A. ELZANOWSKI (University of Wrocław, Poland) and D.S. PETERS (SMF) for reviewing an earlier version of the manuscript, and S. TRÄNKNER for taking the photographs.



Fig. 7: *Quasisyndactylus longibrachis* (SMF ME 3543 a), feet. The arrow indicates the lateral projection of the proximal phalanx of the hallux. Coated with ammonium chloride; scale bar equals 10 mm.

References

- BAUMEL, J.J. & WITMER, L.M. (1993): Osteologia. – In: BAUMEL, J.J., KING, A.S., BREAZILE, J.E., EVANS, H.E. & VANDEN BERGE, J.C. (Eds): Handbook of Avian Anatomy: Nomina Anatomica Avium. – Publications of the Nuttall Ornithological Club, **23**: 45-132; Cambridge, Massachusetts (Nuttall Ornithological Club).
- HUXLEY, T.H. (1867): On the classification of birds; and on the taxonomic value of the modifications of certain of the cranial bones observable in that class. – Proceedings of the Zoological Society of London, **1867**: 415-472.
- MAYR, G. (1998 a): Ein Archaeotrogon (Aves: Archaeotrogonidae) aus dem Mittel-Eozän der Grube Messel (Hessen, Deutschland)? – Journal für Ornithologie, **139** (2): 121-129.
- MAYR, G. (1998 b): „Coraciiforme“ und „piciforme“ Kleinvögel aus dem Mittel-Eozän der Grube Messel (Hessen, Deutschland). – Courier Forschungsinstitut Senckenberg, **205**: 1-101.
- MAYR, G. & PETERS, D.S. (1999): On the systematic position of the Middle Eocene swift *Aegialornis szarskii* PETERS 1985 with description of a new swift-like bird from Messel (Aves, Apodiformes). – Neues Jahrbuch für Geologie und Paläontologie, Monatshefte, **1999** (5): 312-320.

- MAYR, G. (2000): Die Vögel der Grube Messel – ein Einblick in die Vogelwelt Mitteleuropas vor 49 Millionen Jahren. – *Natur und Museum*, **130** (11): 365-378.
- MAYR, G. (2002): Osteological evidence for paraphyly of the avian order Caprimulgiformes (nightjars and allies). – *Journal für Ornithologie*, **143** (1): 82-97.
- MILNE-EDWARDS, A. (1892): Sur les oiseaux fossiles des dépôts éocènes de phosphate de chaux du sud de la France. – *Compte Rendu du Second Congrès Ornithologique International, Budapest 1891*: 1-21; Budapest.
- MOURER-CHAUVIRÉ, C. (1980): The Archaeotrogonidae from the Eocene and Oligocene deposits of "Phosphorites du Quercy", France. – In: CAMPBELL, K.E. (Ed.): *Papers in Avian Paleontology honoring Hildegard Howard*. – Natural History Museum of Los Angeles County, Contributions to Science, **330**: 17-31.
- MOURER-CHAUVIRÉ, C. (1995): Les Garouillas et les sites contemporains (Oligocène, MP 25) des Phosphorites du Quercy (Lot, Tarn-et-Garonne, France) et leurs faunes de Vertébrés. 3. Oiseaux. – *Palaeontographica (A)*, **236**: 33-38.
- SCHAAL, S. & ZIEGLER, W. (Eds) (1988): *Messel – Ein Schaufenster in die Geschichte der Erde und des Lebens*. – 1-315; Frankfurt a.M. (Verlag Waldemar Kramer).
- WETMORE, A. (1960): A classification for the birds of the world. – *Smithsonian Miscellaneous Collections*, **139** (11): 1-37; Washington D.C.
- WUTTKE, M. (1983): „Weichteil-Erhaltung“ durch lithifizierte Mikroorganismen bei mittel-eozänen Vertebraten aus den Ölschiefen der „Grube Messel“ bei Darmstadt. – *Senckenbergiana lethaea*, **64** (5/6): 509-527.

Manuscript submitted 2000 – 10 – 16
Manuscript accepted 2001 – 12 – 05