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New specimens of zygodactylid birds from the middle Eocene of Messel, with description of a new species of *Primozygodactylus*

GERALD MAYR and NIKITA ZELENKOV



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Representatives of the avian taxon Zygodactylidae are among the most abundant small arboreal birds in the early Palaeogene of the Northern Hemisphere. Still, however, the osteology of these birds, which have recently been shown to be the sister taxon of the Passeriformes, is only incompletely known. Here we describe a new species of *Primozygodactylus* from the middle Eocene of Messel in Germany. The holotype specimen of *P. eunjooae* sp. nov. for the first time allows a detailed examination of the distal tarsometatarsus in one of the Messel zygodactylids. It also exhibits exceptionally well-preserved tail feathers which, most notably, are formed by a long central pair of rectrices. We further report on a new specimen of *Primozygodactylus major*, which is the largest zygodactylid from Messel. Being one of the few dissociated skeletons of *Primozygodactylus*, the new specimen shows some previously unknown osteological features of this taxon and allows a more detailed comparison with other zygodactylids.

Key words: Aves, Zygodactylidae, *Primozygodactylus*, Eocene, Messel, Germany.

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Introduction

Representatives of the taxon *Primozygodactylus* Mayr, 1998 are among the most abundant small birds in the middle Eocene fossil site Messel in Germany. Currently, three species are recognized from this locality which mainly differ in size: *Primozygodactylus danielsi* Mayr, 1998, *P. ballmanni* Mayr, 1998, and *P. major* Mayr, 1998. The first is the smallest and most abundant Messel zygodactylid, whereas *P. major*, the largest species, is based on the holotype and a single referred specimen only. Despite the fact that a number of complete specimens of these birds were found, their osteology is incompletely known, because virtually all specimens consist of articulated skeletons in which the articular surfaces of the bones are only partially visible.

Primozygodactylus was assigned to the "Primoscenidae" in the original description (Mayr 1998), but the taxon name already refers to its great similarity to the Zygodactylidae (Mayr 1998, 2004). Zygodactylidae was originally established for *Zygodactylus* Ballmann, 1969a, which for a long time was known only from very fragmentary material from the early Neogene of France and Germany (Ballmann 1969a, b). Recently, however, an articulated skeleton of *Zygodactylus* was described from the early Oligocene of France. This specimen not only conclusively shows that Primoscenidae Harrison and Walker, 1977 is a junior synonym of Zygodactylidae Brodkorb, 1971, but also that zygodactylids are the sister taxon of the Passeriformes (Mayr 2008).

Here we describe a new species of *Primozygodactylus* from Messel. In the holotype specimen the morphology of the distal tarsometatarsus is for the first time clearly visible. The specimen also exhibits exceptionally well-preserved tail feathers, which provide new information on the external appearance of the Messel zygodactylids. In addition, we report on a second specimen of *P. major* which, being one of the few dissociated skeletons of *Primozygodactylus*, allows the recognition of further osteological features of this taxon.

Material and methods

Osteological terminology follows Baumel and Witmer (1993) if not otherwise noted. Measurements (Table 1) represent the maximum length of the bone along its longitudinal axis in millimetres, except for the lengths of the ungual phalanges, which were measured from the processus extensorius to the apex phalangis.

Institutional abbreviations.—HLMD, Hessisches Landesmuseum, Darmstadt, Germany; SMF, Forschungsinstitut Senckenberg, Frankfurt am Main, Germany.

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Systematic palaeontology

Aves Linnaeus, 1758

Zygodactylidae Brodkorb, 1971

Primozygodactylus Mayr, 1998

Primozygodactylus eunjooae sp. nov.

Figs. 1, 2.

Etymology: The species is dedicated to the wife of the senior author, Eun-Joo Shin (pronounce "oon-joo-ae").

Holotype: SMF-ME 1074, incomplete postcranial skeleton (Fig. 1).

Type locality: Messel near Darmstadt, Hessen, Germany.

Type horizon: Early middle Eocene, MP 11 (Legendre and Lévêque 1997).

Diagnosis.—Slightly larger than *Primozygodactylus danielsi* (Table 1), and with proportionally shorter proximal phalanges of the second and third toes (Fig. 2). Whereas the tarsometatarsus measures 21/21.7 mm (versus 18.3/19.6 mm in the holotype of *P. danielsi*), the length of the proximal phalanx of the second toe is only 3.1 mm (versus 4.8 mm in the holotype of *P. danielsi*), and that of the third toe 4.1 mm (versus 5.4 mm in the holotype of *P. danielsi*). The other species of *Primozygodactylus* are distinctly larger (Table 1).

Measurements.—See Table 1.

Description and comparisons.—As far as comparisons are possible, the wing bones are similar to those of the other species of *Primozygodactylus*, and do not exhibit features which were not already described for the latter (Mayr 1998).

The distal end of the right tarsometatarsus, however, is preserved in a completely uncrushed condition, and for the first time allows its detailed examination in one of the Messel zygodactylids. The bone is visible in plantar view, and one of its most unusual features is the presence of a very deep fossa distal of the large foramen vasculare distale. This fossa is steeply sloping medially and laterally, and distally undercuts the lateral rim of the asymmetric trochlea metatarsi III (Fig. $2A_2$). The trochlea metatarsi II is small and has an odd, squarish shape, with an almost flat distal surface; its lateral portion is damaged. In contrast to *Zygodactylus* (Mayr 1998: fig. 28B) and *Primozygodactylus danielsi* (Fig. 2), there is no plantarly directed projection on this trochlea. The large trochlea accessoria is separated from the trochlea metatarsi IV by a marked furrow. Distally, it only extends to the base of the trochlea metatarsi III, whereas it reaches its midst in *Zygodactylus*. The rims of the trochlea metatarsi III are widely separated by a marked furrow. The fossa metatarsi I is shallow.

The toes are less slender than those of *P. danielsi*, and the second and third toes have proportionally shorter proximal phalanges. Whereas the tarsometatarsus of *P. eunjooae* is slightly longer than that of the holotype of *P. danielsi* (Table 1), the proximal phalanx of the second and third toes are shorter (Fig. 2 and measurements above). The second toe is much thinner than the third and fourth toes.

The specimen is of particular interest because the tail feathers are exceptionally well preserved (Fig. 1). These were so far only known from the holotype of *P. major*, where they do not allow the recognition of details (Mayr 1998). In the *P. eun-*

Table 1. Total length (left/right, in mm) of the major limb bones of the Messel species of *Primozygodactylus* Mayr, 1998 and the early Oligocene *Zygodactylus luberonensis* Mayr, 2008. Specimens described in this study are indicated in bold type.

	Humerus	Ulna	Carpometacarpus	Femur	Tibiotarsus	Tarsometatarsus
Primozygodactylus major Mayr, 1998						
SMF-ME 1758a+b (type)[1]	~28.4/–	~31.1/–	~12.0/–	24.6/–	39.0/39.8	28.0
SMF-ME 799a+b	–/29.0	–/~33.5	–/–	–/–	42.8/44.0	–/–
Primozygodactylus ballmanni Mayr, 1998						
SMF-ME 2108 (type)[1]	21.0/20.5	22.9/22.9	~9.0/~9.5	20.8/–	33.0/–	24.6/–
HLMD-Me 15396[1]	20.0/–	20.9/~20.3	–/9.1	–/–	–/–	–/–
Primozygodactylus danielsi Mayr, 1998						
SMF-ME 2522a+b (type)[1]	16.5/16.4	18.3/~17.4	8.2/8.1	–/16.5	27.4/27.3	19.6/~18.3
SMF-ME 2554[1]	–/–	–/–	~7.3/–	~17.7/17.2	29.4/–	19.7/20.7
SMF-ME 1269[1]	–/17.4	–/20.9	–/8.1	–/16.0	27.5/–	19.0/–
SMF-ME 2091[1]	–/–	–/~20.0	~8.4/~8.3	–/–	–/–	–/–
SMF-ME 1817[1]	–/~15.3	–/–	–/7.4	–/–	–/–	–/–
HLMD-Me 15550a+b[1]	–/–	~19.8/–	~8.6/~8.5	–/–	–/–	–/–
HLMD-Me 10206a+b[1]	~16.3/–	18.3/–	~7.8/–	–/–	–/–	–/–
Primozygodactylus eunjooae sp. nov.						
SMF-ME 1074 (type)	–/–	–/–	–/–	17.5/–	29.8/–	~21/~21.7
Zygodactylus luberonenis Mayr, 2008						
SMF Av 519[2]	17.2/17.2	–/18.1	8.6/8.6	–/~19.5	34.7/34.8	24.5/24.6

[1] after Mayr (1998), [2] after Mayr (2008).

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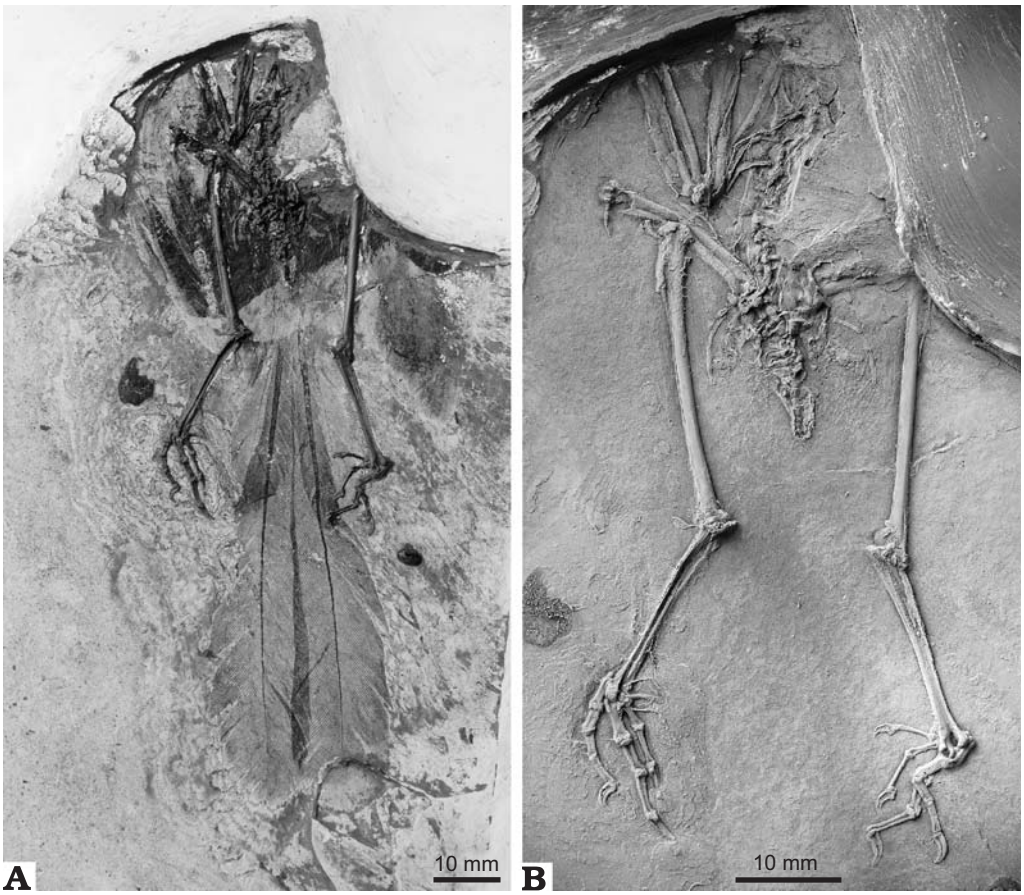


Fig. 1. Zygodactylid bird *Primozygodactylus eunjooae* sp. nov., holotype (SMF-ME 1074) from the middle Eocene of Messel in Germany. **A**. Specimen with remains of feathering. **B**. Specimen coated with ammonium chloride.

jooae holotype there are two long central rectrices with broad vanes and a rounded tip, which have a length of about 84 mm. A pair of smaller adjacent feathers are visible which measure 40 mm. The outer tail feathers appear to have been very short, but only one of these is clearly visible in the specimen and measures about 20 mm. Although this possibility cannot be excluded, there is likewise no indication that the specimen is a moulting individual. A similar accentuation of the central pair of rectrices is found in few extant birds, such as emu-wrens (*Stipiturus* spp., Passeriformes: Maluridae).

The specimen also exhibits remains of the wing feathers, which indicate a rather short and broad wing, with a rounded tip. On the left wing, the distalmost, i.e., tenth, primary measures about 27 mm, but the length of the other wing feathers cannot be unambiguously determined (as preserved, the longest primary of the left wing measures about 35 mm, but its tip may not be completely preserved in the specimen).

A medium-sized (3.5 × 2.5 mm) seed is situated close to the specimen, and in all likelihood stems from the stomach or gut content of the animal.

Primozygodactylus major Mayr, 1998

Fig. 3.

Referred specimen: SMF-ME 799a+b, incomplete and dissociated skeleton lacking left wing, left tarsometatarsus, and pelvis.

Locality and horizon: Messel near Darmstadt, Hessen, Germany; early middle Eocene, MP 11 (Legendre and Lévêque 1997).

Measurements.—See Table 1.

Description and comparisons.—The vertebral column is largely dissociated, which allows the recognition of previously unknown features of some particular vertebrae. The atlas and axis are preserved in articulation, and it can be discerned that the former had a dorsally open incisura fossae (Fig. $3A_1$). Contrary to the statement in the description of the holotype (Mayr 1998), the foramen enclosed by the arcus interzygapophysialis (terminology after Livezey and Zusi 2006) of the fourth vertebra is large as in most passeriform birds (Fig. $3A_2$).

In the new specimen, the coracoid of a Messel representative of *Primozygodactylus* is for the first time fully visible. The processus acrocoracoideus is dorsoventrally compressed, with a rounded tip, and is proportionally shorter and stouter than the narrow and elongate processus acrocoracoideus of *Zygodactylus*. The processus procoracoideus is very small. In contrast to crown group Piciformes (Mayr et al. 2003), there is no notch in the medial margin of the extremitas sternalis, which instead bears a distinct convex flange. The processus lateralis is longer than in *Zygodactylus*, whose extremitas sternalis is much narrower (Fig. 3).

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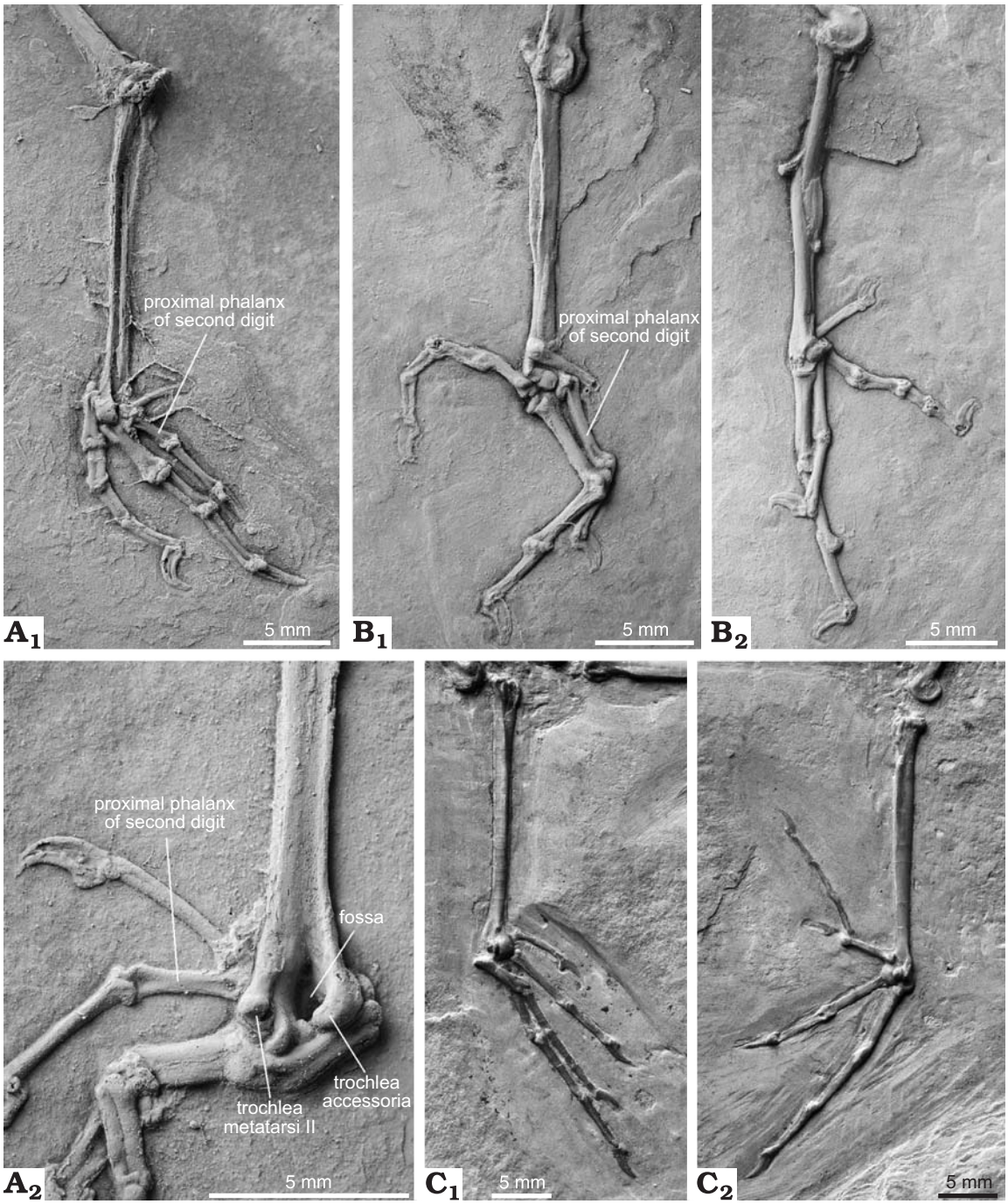


Fig. 2. Foot of zygodactylid bird *Primozygodactylus eunjooae* sp. nov. (**A**) from the middle Eocene of Messel in Germany in comparison to the feet *Primozygodactylus danielsi* Mayr, 1998 (**B**) from Messel and *Zygodactylus luberonensis* (**C**) from the early Oligocene of the Lubéron in France. **A**. Left (A_1) and right (A_2) foot of *P. eunjooae* sp. nov., holotype (SMF-ME 1074). **B**. Left (B_1) and right (B_2) foot of *P. danielsi* Mayr, 1998, holotype (SMF-ME 2522a+b). **C**. Left (C_1) and right (C_2) foot of *Zygodactylus luberonensis* Mayr, 2008 (SMF Av 519). Note the proportionally shorter proximal phalanges of the second and third toes of *P. eunjooae*. Specimens in A and B coated with ammonium chloride.

The completely exposed furcula allows the recognition of a long processus acromialis on the extremitas omalis, and a well-developed, blade-like apophysis furculae on the extremitas sternalis (Fig. $3A_3$). As noted in the original description of the species (Mayr 1998), the scapula of *P. major* has a massive acromion.

The wing bones do not show features that were not already described by Mayr (1998). The processus craniolaterales of the sternum are wide and of triangular shape.

The distal end of the tarsometatarsus is visible in plantar view in SMF-ME 799a. The trochlea metatarsi II is very small and divided into two rims which are separated by a shallow furrow; whether the medial rim bore a plantarly directed projection cannot be discerned since the correspond-

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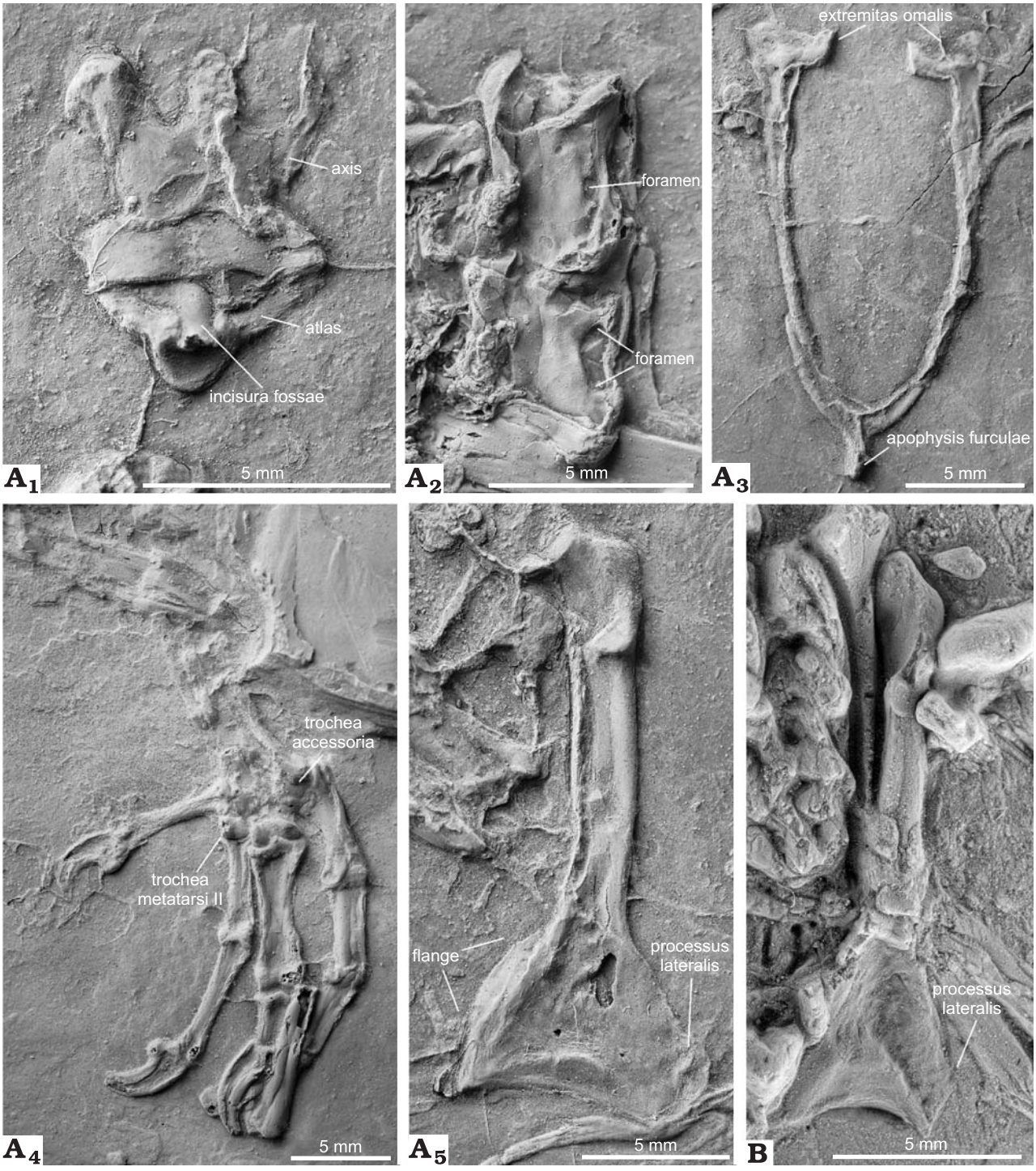


Fig. 3. **A**. Zygodactylid bird *Primozygodactylus major* Mayr, 1998, selected bones of the newly referred specimen SMF-ME 799a (A_4) and SMF-ME 799b (A_1–A_3, A_5) from the middle Eocene of Messel in Germany. A_1, atlas and axis; A_2, third and fourth cervical vertebrae; A_3, furcula; A_4, distal end of right tarsometatarsus in plantar view; A_5, right coracoid in dorsal view in comparison to (**B**) *Zygodactylus luberonensis* (SMF Av 519) from the early Oligocene of the Lubéron in France. All specimens coated with ammonium chloride.

ing area is broken. As in *P. eunjooae*, the trochlea metatarsi III is asymmetric, as is the proximal phalanx of the third toe. The trochlea metatarsi IV bears a large trochlea accessoria whose original shape, however, cannot be determined. This trochlea seems to have been slightly shorter than the trochlea metatarsi II (Fig. 3). Again, the phalanges of the second toe are much thinner than those of the third and fourth toes.

In the area of the cervical vertebrae grit is preserved (SMF-ME 799b) which probably represents content of the former crop. Also in SMF-ME 799b, stomach contents are preserved and include the remains of seeds.

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Discussion

Zygodactylids are one of the most abundant groups of small arboreal birds in the Palaeogene of Europe. Along with the new data on the osteology of *Zygodactylus* (Mayr 2008), the specimens described in the present study provide some further insights into the evolutionary history of these birds.

As detailed previously (Mayr 1998, 2004, 2008), *Zygodactylus* differs from *Primozygodactylus* in a much more distally elongated trochlea accessoria for the retroverted fourth toe. It has not been appreciated earlier, however, that the legs of *Zygodactylus* are also proportionally longer than those of its early Eocene relatives (Table 1), and that the toes bear straighter ungual phalanges (Fig. 2C). Whereas the third toe measures only slightly less than the tarsometatarsus in *Zygodactylus luberonensis*, it is distinctly shorter in *Primozygodactylus eunjooae* (Fig. 2). The third and fourth toes of the *Primozygodactylus* species are less slender than those of *Zygodactylus*. There are further differences in the skeleton of the pectoral girdle. Most notably, the coracoid of *Zygodactylus* is more elongated and has both a narrower extremitas omalis and a narrower extremitas sternalis (Fig. 3). The poorly preserved tail of the holotype of *Z. luberonensis* is also proportionally shorter than that of the similarly-sized *Primozygodactylus eunjooae* (84 mm versus 47 mm; Mayr 2008).

Certainly these morphological differences corresponded to differences in the way of living of these taxa. At least within oscine Passeriformes, arboreal, i.e., perching, species have proportionally shorter proximal pedal phalanges and more curved ungual phalanges than walking or hopping species (Rüggeberg 1960). Accordingly the above listed differences in the hindlimb skeleton of zygodactylids may indicate that *Zygodactylus* had a more terrestrial way of living than the earlier *Primozygodactylus*, and possibly occurred in a more open habitat. By increasing the span width of the toes, the proportionally longer toes of *Zygodactylus* would also correlate with a more earthbound way of living (Rüggeberg 1960); because of its proportionally longer toes, *P. danielsi* may represent a somewhat intermediate position. The notable differences in the proportions of the pedal phalanges of early Eocene zygodactylids indicates that variations in foot morphology may have played a significant role in the evolutionary radiation of these birds.

The much better developed accessory trochlea of the tarsometatarsus of *Zygodactylus* cannot be correlated with a terrestrial way of living and, rather than being a locomotory adaptation, may reflect a specialized foot use. A similarly elongated trochlea accessoria only occurs in extant Pici (woodpeckers and allies) and Psittaciformes (parrots). In parrots it serves to increase the grasping capability of the foot, but the functional significance of the large trochlea accessoria of the Pici is not fully understood (Mayr 2008).

In several specimens of *Primozygodactylus* fruit seeds are preserved as former stomach content (this study and Mayr 1998), which is also indicative of an arboreal way of living. The diet of *Zygodactylus* is unknown, but the tentatively referred skull of *Z. luberonensis* has a sharply pointed, forceps-like beak (Mayr 2008), which suggests that this species may have been more insectivorous than its earlier relatives.

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