Brief report

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The first complete leg of a passerine bird from the early Oligocene of Poland

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The leg bones of a small passeriform bird are described from the early Oligocene (29 Mya) of Poland. The specimen is the earliest complete passerine leg with elements in articulation described so far, and increases the known diversity of the very scanty records of the oldest European passeriforms. In general proportions the leg bones resemble those of *Luscinia svecica* and other species that live in shrubs. Assignment to a family within the passerines is not possible because of the incompleteness of the fossil.

Introduction

Marine Oligocene deposits of the Menilite Formation of the Outer Carpathians, southeastern Poland, are primarily known for their rich fauna of fishes (Kotlarczyk et al. 2006). Fossils of other taxa are very scarce; so far only four avian specimens have been described. They include a hummingbird, *Eurotrochilus noniewiczi* Bochenski and Bochenski, 2008, a passerine, *Jamna szybiaki* Bochenski, Tomek, Bujoczek, Wertz, 2011, a procellariiform, ?*Diomedeoides lipsiensis* known from an isolated bone (Elzanowski et al. 2012), and a bird of unknown affinities with a columbid-like foot (Bochenski et al. 2010).

Although passeriforms constitute more than a half of all extant avian species, their Paleogene fossil record is surprisingly limited (Mayr 2005, 2009). The oldest two fossils of possible passerine affinities are dated to the early Eocene of Australia (Boles 1995, 1997), but unquestionable remains of passeriforms come from the Oligocene of Europe. Two species based on relatively complete specimens have been described from the early Oligocene: *Wieslochia weissi* Mayr and Manegold, 2006 from Germany (Mayr and Manegold 2004, 2006b) and *Jamna szybiaki* from Poland (Bochenski et al. 2011). Other Oligocene remains in the literature include an articulated wing (Mayr and Manegold 2006a) and several dozen isolated wing bones (Mourer-Chauviré et al. 1989; Manegold 2008). Leg bones are much more poorly preserved, and even those of *Wieslochia weissi* and *Jamna szybiaki* are incomplete. Apart from the latter, only two other fragments of the tarsometatarsus are known from the Oligocene of France (Mourer-Chauviré et al. 1989, 2004; Mourer-Chauviré 2006).

In this paper, we describe a nearly complete articulated specimen of a passerine leg found in southeastern Poland (Fig. 1). Although it is not perfectly preserved, it provides many new details that for the first time cast light on the osteology and external appearance of a Paleogene passeriform foot and leg.

Institutional abbreviations.—ISEA, Institute of Systematics and Evolution of Animals, Kraków, Poland; ZPALWr, Department of Palaeozoology, University of Wrocław, Wrocław, Poland.

Methods

Osteological terminology follows Baumel and Witmer (1993). Dimensions are given in millimetres and refer to the greatest length along the longitudinal axis of the bone. The fossil was compared with Recent specimens from the osteological collection of the ISEA. The fossiliferous horizon in the village of Przysietnica has been dated on the basis of the fish assemblage and correlated with the calcareous nannoplankton (Berggren et al. 1995; Kotlarczyk et al. 2006). The body mass of the fossil was estimated from the relationship of femur dimensions to weight in birds (Campbell and Marcus 1992; Campbell and Bochenski 2010), using the formula for ordinary least-squares regression: $log(y) = 2.418 \cdot log(x) - 0.179$, where y = mass in grams and x = least shaft circumference of femur in mm. The slope and intercept figures are specifically for the data subset "PS", or passerine birds, of Campbell and Marcus (1992: table 3). The least shaft circumference was calculated from the minimum width of the femoral shaft, assuming that the cross-section of the shaft is circular.

Systematic palaeontology

Aves Linnaeus, 1758

Passeriformes Linnaeus, 1758

Family, genus, and species indeterminate

Material.—A slab (Fig. 2), found in 1985, with imprints of a complete right avian leg articulated to a poorly-preserved pelvis, and two pieces of a counter slab with fragments of the bones (ZPALWr. A/4004) from Przysietnica (site PS-5), one of eighteen exposures of marine deposits in the Menilite Formation of the Outer Carpathians, situated in the village of Przysietnica, about 8 km from Brzozów and 44 km southeast of Rzeszów, Podkarpackie Voivodeship, southeastern Poland (Fig. 1). Geographical coordinates of the site: 49°43.976' N, 022°03.017' E. ZPALWr. A/4004 was found in layer 40, together with 120 articulated fish imprints, and with the index fish species *Carpathospinosus propheticus* Tyler, Jerzmańska, Bannikov, and Świdnicki, 1993, *Antigonia* sp., and chaetodontid-like larva (Świdnicki 1988; Tyler et al. 1993; Micklich et al. 2009), all in-

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Fig. 1. Location of the village of Przysietnica in southeastern Poland, where the specimen ZPALWr. A/4004 was found.

dicating the IPM4A Zone (Kotlarczyk et al. 2006: fig. 6). The fossiliferous horizon of Przysietnica (PS-5) has been dated to Rupelian, early Oligocene, circa 29 Mya, on the basis of the fish assemblage indicating the IPM4A Zone, and correlated with the calcareous nannoplankton of the NP24 Zone sensu Berggren et al. (1995). The fossil-bearing section at Przysietnica is currently referred to the Šitbořice Member of the Subsilesian Unit of the Menilite Formation of the Polish Outer Carpathians (Kotlarczyk et al. 2006: 16, 96).

Taxonomic remarks.—Small passerine which is distinguished from all other non-passerine taxa by the combination of the following characters: (1) all leg elements including the tarsometatarsus and tibiotarsus are long and slender; (2) the tibiotarsus bears the Crista cnemialis cranialis that projects far craniad and joins with the shaft almost at right angles; (3) the tarsometatarsus bears a relatively short, proximo-distally, hypotarsus whose distal end joins abruptly with the shaft, (4) a distinct Crista plantaris lateralis, and (5) has the small trochleae of the second, third, and fourth pedal digits arranged in a line and reaching approximately equally far distally; (6) the specimen shows an anisodactyl foot; (7) the proximal phalanx of the hallux is greatly elongated; (8) the claws show relatively little curvature and their Tubercula flexoria are weakly developed. Character (5) is unique to passerines and is often used to discriminate them from all other non-passerine taxa (e.g., Cohen and Serjeantson 1996; Gilbert et al. 1996; Bochenski and Tomek 2009); the remaining characters are shared with one or more non-passerine orders but their combination is unique to passerines.

Description and comparison

Size and weight.—Measurements (maximum length in mm): femur, 17.1; tibiotarsus, 36.3; tarsometatarsus, 25.7; hallux: proximal phalanx, 7.6; hallux: claw, 4.7; second phalanx of digit II, 4.5; claw of digit II, 3.2; second phalanx of digit III, 5.6; third phalanx of digit III, 5.5; claw of digit III, 3.9; second phalanx of digit IV, 3.0; third phalanx of digit IV, 3.1; fourth phalanx of digit IV, 3.4; claw of digit IV, 2.8. Minimum width of femoral shaft: 1.5 mm. Proportions of the leg bones: femur/tibiotarsus, 0.5; femur/tarsometatarsus, 0.7; tibiotarsus/ tarsometatarsus, 1.4.

The estimated mass of the bird represented by ZPALWr. A/4004 was calculated to be 30.1 g.

Pelvis.—The small fragment of the pelvis is too poorly preserved to allow meaningful comparisons. Only four incomplete caudal vertebrae are visible; the pygostyle is missing.

Femur.—The femur is visible in cranial view. The Caput femoris is imprinted in the main slab only; the outlines of the Condyli medialis and Condyli lateralis are too poorly preserved to allow meaningful comparisons. The bone is similar in length to that of *Wieslochia weissi* (Mayr and Manegold 2006b) and much shorter than in *Jamna szybiaki* (Bochenski et al. 2011).

Tibiotarsus.—The tibiotarsus is visible in medial view, but the medial surface of the bone is missing. As in extant passeriforms, but in contrast to most "higher land-birds", the tibiotarsus is slender and long. It is longer than the tibiotarsus in *Wieslochia weissi* (Mayr and Manegold 2004) and *Jamna szybiaki* (Bochenski et al. 2011). The Crista cnemialis cranialis, which is better preserved on the counterslab, projects considerably craniad and it joins with the shaft distally almost at right angles; its shape and size is typical of that in passerine birds. The Crista fibularis extends far laterad; its distal end is missing. As in extant passeriforms, the Condyli medialis and Condyli lateralis are of similar size.

Tarsometatarsus.—The tarsometatarsus (seen only on the main slab) is oriented with the medial side up, but what is preserved is mainly the imprint of its lateral side with remnants of bone. It is long and slender, being much longer than in *Wieslochia weissi* (Mayr and Manegold 2006b). As in all extant passeriforms, the hypotarsus is relatively short proximo-distally and its distal end joins abruptly with the shaft. No details of hypotarsal canals and/or furrows are visible. The shaft bears a crista plantaris lateralis, which is present only in passerines and cuckoos (Manegold et al. 2004). The distal end with the trochleae of the second, third, and fourth pedal digits small and arranged in a line is highly characteristic for all passeriforms. The well-imprinted Trochlea metatarsi IV is narrow, the Trochlea metatarsi III is broader, grooved, and it reaches only a little farther distally. The Trochlea metatarsi II is only marked by a poorly visible imprint.

Toes.—As in all passeriforms, the foot has an anisodactyl arrangement of toes, with three digits directed forward and one digit directed backward. All pedal digits have the usual number of phalanges, and they are thin and relatively short. The Os metatarsale I is detached from the rest of the hallux; as in all other passeriforms it exhibits a cylindrical Trochlea metatarsi I. Also as in all extant passeriforms and the early Oligocene *Wieslochia weissi* (Mayr and Manegold 2006b), the proximal phalanx of the hallux is greatly elongated. The proximal-most phalanges of digits II, III, and IV are damaged and/or visible only at an angle because they penetrate into the matrix; other phalanges are well preserved. The third digit seems to be the longest, the second and the fourth are about the same length. The claws show relatively little curvature,

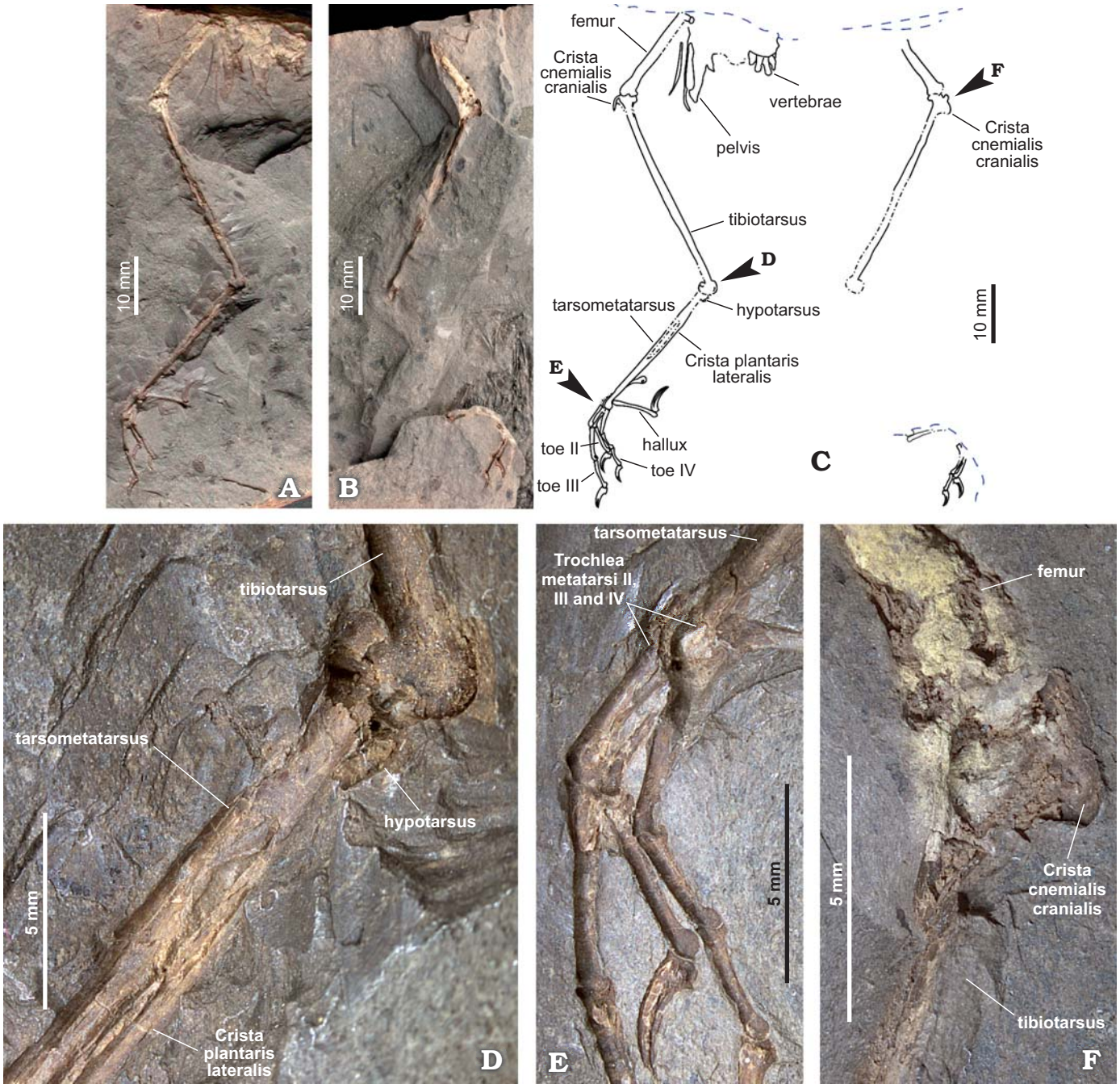

Fig. 2. An unidentified passerine bird leg from SE Poland, Przysietnica, early Oligocene, circa 29 Mya (ZPALWr. A/4004). **A**. Main slab. **B**. Counter slab. **C**. Interpretative drawing of slab and counter slab (enlarged fragments are indicated by arrows). **D**. Enlarged proximal tarsometatarsus from main slab. **E**. Enlarged distal tarsometatarsus from main slab. **F**. Enlarged proximal tibiotarsus from counter slab.

their Tubercula flexoria are weakly developed and they bear a groove along their length. The second and the third phalanges of digit III are approximately of the same length. In digit IV, the fourth phalanx is longer than the second and the third phalanges, which are similar in length.

Discussion

Owing to the fragmentary preservation of the fossil and the unknown pattern of its hypotarsal canals in particular (Manegold et al. 2004), its assignment to a family within the passerines is not possible.

The estimated mass of ZPALWr. A/4004 (~30 g) is within the range of body masses of various small passerines. As a test, we measured the minimum width of the femur of a number of passerine species from our comparative collection, calculated the least shaft circumference and used the equation described in the Methods to estimate the mass of the comparative specimens. The two comparative species whose femur shaft minimum widths were most similar to ZPALWr. A/4004 (1.5 mm) were

Alauda arvensis (1.6 mm) and *Lanius collurio* (1.5 mm). The estimated masses of these two comparative species fall within the range of recorded masses for these species (*Alauda arvensis*: estimated mass ~31 g, range from Cramp 1988: 24.4–44.9 g; *Lanius collurio*: estimated mass ~26 g, range from Cramp and Perrins 1993: 21.7–36.3 g), which indicates that the procedure is reliable and the estimate for the fossil specimen is most probably correct.

In general proportions, the femur, tibiotarsus and tarsometatarsus are similar to those of extant passeriforms, particularly members of the Alaudidae (Larks), Motacillidae (Pipits and Wagtails), Prunellidae (Accentors), Sylviidae (Old World warblers), Troglodytidae (Wrens), and Turdidae (Thrushes) families. The most similar, yet not identical, extant species is *Luscinia svecica* of the family Muscicapidae (Old World Flycatchers). The size and proportions of the leg elements, as well as the relatively short pedal digits, correspond best with extant species that live in shrubs, trees or on the ground (Zeffer et al. 2003; TT and ZMB personal observations). Also the slight curvature of the claws suggests that ZPALWr. A/4004 was a bird that Glen and Bennett (2007) would include in ground or arboreal foragers.

ZPALWr. A/4004 also differs considerably in general proportions from the other two Oligocene passerines known, *Wieslochia weissi* (Mayr and Manegold 2004, 2006b) and *Jamna szybiaki* (Bochenski et al. 2011), which might mean that it represents a different taxon. The two other fragments of proximal tarsometatarsi from the upper Oligocene of France (the Coderet specimen FSL 330802 and the Créchy specimen FSL 367057) are hard to compare because of their poor state of preservation. Although ZPALWr. A/4004 is not well preserved, it represents the first complete specimen of an Oligocene passerine with all the leg elements in articulation. It also increases the known diversity of the very scanty records of the oldest European passerines.

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