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A tiny short-legged bird from the early Oligocene of Poland

ZBIGNIEW M. BOCHENSKI[1], TERESA TOMEK[1] and EWA SWIDNICKA[2]

[1]Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Slawkowska 17, 31-016 Kraków, Poland; bochenski@isez.pan.krakow.pl, tomek@isez.pan.krakow.pl
[2]Department of Palaeozoology, Chair of Evolutionary Biology and Ecology, University of Wrocław, Sienkiewicza 21, 50-335 Wrocław, Poland; gama@biol.uni.wroc.pl

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Abstract: We describe an articulated partial leg of an Oligocene bird. It is one of the smallest avian fossils ever recorded. Its slender and exceptionally short tarsometatarsus, hallux as long as the tarsometatarsus and stout moderately curved claws agree with stem-group Apodidae (swifts), stem-group Trochilidae (hummingbirds), and stem-group Upupidae/Phoeniculidae (hoopoes/woodhoopoes). Unfortunately, due to the poor preservation of the specimen its more precise affinities remain unresolved. The specimen differs in many details from all other tiny Palaeogene birds and therefore most probably it represents a new taxon but it is too fragmentary to describe it. It is just the twelfth avian fossil from the Oligocene marine deposits of the Outer Carpathians and Central Palaeogene Basin — a huge area that covers south-eastern Poland, north-eastern Czech Republic and northern Slovakia — and therefore it adds to our very limited knowledge on the avifauna of that region. The remains of land birds from Jamna Dolna and other sites of the region can be attributed to the general sea level fall at that time, which led to limitation of the connection with the open ocean and resulted in many shallow shoals, temporary islands and exposed dry land areas along the coast.

Keywords: Fossil birds, Menilite shales, Carpathian flysch, Palaeogene.

Introduction

The Menilite beds of the Carpathian flysch zone that are found in north-eastern Czech Republic and south-eastern Poland, and the Central Palaeogene basin of northern Slovakia are extremely rich in Oligocene fish fossils. Only in south-eastern Poland, many thousand of fish fossils were recovered from more than 200 outcrops between the mid 1970s and mid 1990s (Kotlarczyk et al. 2006). However, animal fossils other than fish are extremely rare. So far only eleven avian specimens have been described from the marine deposits of the Outer Carpathians and Central Palaeogene Basin: two procellariiforms (Gregorová 2006; Elzanowski et al. 2012), one galliform (Tomek et al. 2014), one hummingbird (Bochenski & Bochenski 2008), one putative upupiform (Kundrát et al. 2015), one piciform (Mayr & Gregorová 2012), four passerines (Bochenski et al. 2011, 2013b, 2014a, b) and Aves indet. (Bochenski et al. 2010). Here, we describe an extremely small, incomplete avian leg that resembles those of stem-group apodid, trochilid or upupid birds.

The apodiform birds are nowadays classified within the order Caprimulgiformes (del Hoyo & Collar 2014); they include three living families: the globally distributed true swifts (Apodidae), the Southeast Asian tree swifts (Hemiprocnidae), and the hummingbirds (Trochilidae), which nowadays occur exclusively in the New World (del Hoyo et al. 1999). The Palaeogene fossil record of swifts is relatively rich but the systematic position of many fossil taxa is often unclear and widely disputed. According to Mayr (2009) there are two extinct families: Eocypselidae (*Eocypselus*) – a stem group taxon of swifts from the early Eocene of the UK and Denmark (Harrison 1984; Dyke et al. 2004), and Aegialornithidae (*Aegialornis* and *Primapus*) with several species from the late Eocene to early Oligocene of France and the UK (Harrison & Walker 1975; Mourer-Chauviré 1988). The earliest stem group members of the Apodidae belong to the genus *Scaniacypselus* from the early Eocene of Europe; other representatives include *Procypseloides* from the late Oligocene of France and *Collocalia* from the late Oligocene/early Miocene of Australia (Mayr 2009). The late Eocene *Cypseloides mourerchauvireae* from France described by Mlíkovsky (1989) in Apodidae is believed to be a junior synonym of *Aegialornis gallicus* (Aegialornithidae) (Mayr 2003, 2009). The earliest Trochilidae include several genera: *Jungornis* (described by Karhu (1988) in Jungornithidae), *Argornis*, *Parargornis*, *Cypselavus* (all three classified by Mourer-Chauviré (2006) into Cypselavidae) and *Eurotrochilus* Mayr, 2004. Hemiprocnidae have no Palaeogene fossil record (Mayr 2009). In North America, the Palaeogene fossil swifts include *Eocypselus rowei* described from the Eocene Green River Formation (Ksepka et al. 2013).

The upupiform birds are nowadays classified within the order Bucerotiformes which includes, among others, the African and Eurasian hoopoes (Upupidae) and the African woodhoopoes (Phoeniculidae) (del Hoyo & Collar 2014). The stem-group upupids are known from the Eocene deposits of the United Kingdom (London Clay) and Germany (Messel and the Geisel Valley) (Mayr 1998, 2000, 2006). Three species of the extinct family Messelirrisoridae are among the most abundant small to tiny birds in Messel; they are distinguished by their long beak, short tarsometatarsus and very long hallux (Mayr 2009).

Material and methods

The osteological terminology used here follows that of Baumel & Witmer (1993). Dimensions are given in millimetres and refer to the greatest length along the longitudinal axis of the bone. The very small size of the specimen excludes most avian orders. The fossil was compared with skeletal specimens of extant nightjars and allies, hummingbirds and swifts, hoopoes, coliiforms and passerines from the osteological collection of the Institute of Systematics and Evolution of Animals, Kraków, Poland, and Palaeogene species of the afore-mentioned taxa described in the literature (Peters 1985; Karhu 1988; Mourer-Chauviré 1988; Mayr 2003a, 2004, 2007, 2009, 2010, 2015; Mourer-Chauviré & Sigé 2006; Louchart et al. 2008; Mayr & Micklich 2010; Ksepka et al. 2013).

The fossil was found at the former village of Jamna Dolna (geographical coordinates of Jamna Dolna: 49°37'45.0'' N, 22°34'08.0'' E), situated about 8 km south-east of the village of Bircza, Podkarpackie Voivodeship, SE Poland (Fig. 1). It is a natural exposure of the Menilite strata with more than 15-m thick deposits in the high escarpment of the Jamninka stream, a right tributary of the Wiar River. In the geological literature (Jerzmańska 1967a, b, 1968; Jerzmańska & Kotlarczyk 1968; Kotlarczyk et al. 2006), the exposure is known as Jamna Dolna 1, to distinguish it from other smaller

Fig. 1. The location of the village of Jamna Dolna (asterisk) in south-eastern Poland, where the specimen ISEA AF/JAM1 was found.

outcrops located in the same area. The specimen consists of one slab (Figs. 2, 3) with imprints of a partial left avian leg. It was found by Albin Jamróz who passed it to the Institute of Systematics and Evolution of Animals PAS, Kraków, Poland where it is housed (ISEA AF/JAM1). ISEA AF/JAM1 is preserved on the surface of soft, light brown siliceous marly shale, collected from the horizon (Unit C, probably layer C-4) of the Kotów Chert Member, the lower part of the Menilite Formation of the Skole Unit in the Outer Carpathians. The specimen was found within the ichthyofaunal assemblage of the IPM-1C Subzone (according to Kotlarczyk et al. 2006, fig. 20) that includes such fossil fish as *Aeoliscus heinrichi* (Heckel, 1850), *Anenchelum glarisianum* Blainville, 1818, *Capros rhenanus* (Weiler, 1920), *Oligophus moravicus* (Paucă 1931), *Zenopsis clarus* Daniltshenko, 1960, and other taxa, which are characteristic of the IPM1 Zone (Kotlarczyk et al. 2006, p. 65). The description of fish taxa can be found in Jerzmańska (1968) and Świdnicki (1986). The fossiliferous horizon is dated to the Early Oligocene (Rupelian, approximately 32.5 m.y.a.) and correlated with the calcareous nannoplankton of the NP22 biozone by Martini (1971) (see Berggren et al. 1995; Kotlarczyk et al. 2006).

Description and comparison

As it is often the case in other bird fossils from the Oligocene of Poland (Bochenski & Bochenski 2008; Bochenski et al. 2010, 2011, 2013a, b, 2014a, b), particular elements in ISEA AF/JAM1 are broken longitudinally and preserved as imprints partly lined with remnants of bone. As a result, a mixture of an imprint and the inner side of a bone rather than its external surface is visible, which hinders comparisons with fossil and extant specimens. Better preserved specimens are found very rarely in Poland (Elzanowski et al. 2012; Tomek et al. 2014).

Measurements (maximum length in mm). Tibiotarsus as preserved, 13.8; tarsometatarsus, 6.3; os metatarsale I, 1.4; hallux: proximal phalanx, 4.1; hallux: claw, 2.1; first phalanx of digit II, ~1.6; second phalanx of digit II, ~2.9; claw of digit II, 2.1; first phalanx of digit III, ~1.9; second phalanx of digit III, ~2.1; third phalanx of digit III, 2.4; claw of digit III, 2.1; first phalanx of digit IV, ~1.5; second phalanx of digit IV, 1.4; third phalanx of digit IV, 1.2 (fourth phalanx of digit IV and claw of digit IV could not be measured because they are partly under the hallux claw).

Tibiotarsus. The tibiotarsus is visible in lateral view. Its proximal part is missing, a fragment of the condylus lateralis is visible but it is too poorly preserved to allow meaningful comparisons. A short fragment of the fibula is also preserved.

Tarsometatarsus. The tarsometatarsus is visible in lateral view but the surface of the bone is missing and only its inner

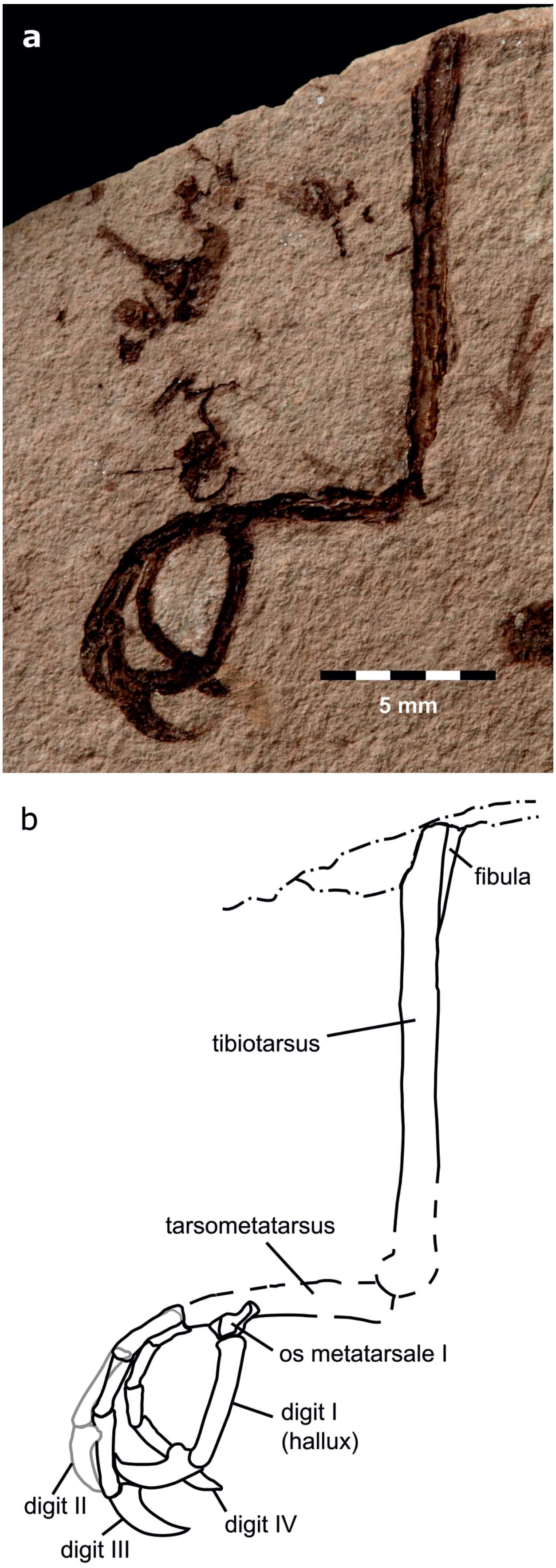

Fig. 2. Specimen ISEA AF/JAM1 of an avian foot from south-eastern Poland, Jamna Dolna 1, early Oligocene, ca. 32.5 Mya. **a** — Slab; **b** — Interpretative drawing of the slab.

part can be seen. The bone is relatively slender and about half the length of the tibiotarsus. With the length of just 6.3 mm it is among the shortest fossil tarsometatarsi ever recorded; it is by far shorter than that in any extant and extinct Passeriformes, Coliiformes or Caprimulgidae. In the Palaeogene, there were three groups of birds with representatives that had equally small tarsometatarsi: swifts, hummingbirds and hoopoes. ISEA AF/JAM1 is most similar in length and slenderness to the early Oligocene *Eurotrochilus inexpectatus* (Trochilidae) (6.4–6.7 mm, see Mayr 2004, 2007; Louchart et al. 2008) and Eocene *Scaniacypselus szarskii* (Apodidae) (5.5–5.9 mm, see Peters 1985; Mayr 2015), whereas among Palaeogene stem lineage upupiforms its size resembles most small specimens of *Messelirrisor parvus* (≥7.2 mm, Mayr 1998) and SNMZ 27188 (7.1 mm, Kundrát et al. 2015). No details of hypotarsal canals and/or furrows nor the exact arrangement of the trochlea metatarsi II, III and IV are visible.

Regarding the tibiotarsus / tarsometatarsus proportion, ISEA AF/JAM1 is most similar to the Palaeogene *Scaniacypselus szarskii* (Apodidae), *Eurotrochilus inexpectatus* (Trochilidae) and species of the genus *Messelirrisor* (Messelirrisoridae) (Table 1). Also many extant hummingbirds show similar proportion, contrary to extant swifts that have relatively shorter tarsometatarsus, and extant hoopoes whose tarsometatarsus is relatively longer. Passerines — even such short-legged species as swallows — have proportionally longer tarsometatarsus. Similar results based on different set of taxa are obtained when the measurements of ISEA AF/JAM1 are plotted on a log diagram with other groups of birds: ISEA AF/JAM1 is between the clusters of *Messelirrisor* and extant hummingbirds, well apart from other extinct and extant taxa (Kundrát et al. 2015, fig. 9).

Toes. The foot has anisodactyl arrangement of toes, with digits II, III, and IV directed forward and digit I (hallux) directed backward. The phalangeal formula is 2–3–4–5. As in *Eurotrochilus inexpectatus*, (Trochilidae), *Scaniacypselus szarskii* (Apodidae) and stem-group upupiforms including *Messelirrisor* spp. and SNMZ 27188, all digits are relatively long although this is especially evident in the hallux which in ISEA AF/JAM1 is similar in length to the tarsometatarsus and in the afore-mentioned taxa just a little shorter (Peters 1985; Mayr 1998; Kundrát et al. 2015); in extant Apodidae and Hemiprocnidae as well as all Passeriformes, Coliiformes and Caprimulgidae the hallux is less than half the length of the tarsometatarsus. As in *Eurotrochilus inexpectatus*, *Scaniacypselus szarskii* and also the putative upupiform SNMZ 27188 from Slovakia, the proximal phalanx of the hallux is clearly more than half the length of the tarsometatarsus (Peters 1985; Mayr 2004, fig. 2; Kundrát et al. 2015), whereas in Palaeogene representatives of other Apodidae (*Eocypselus*

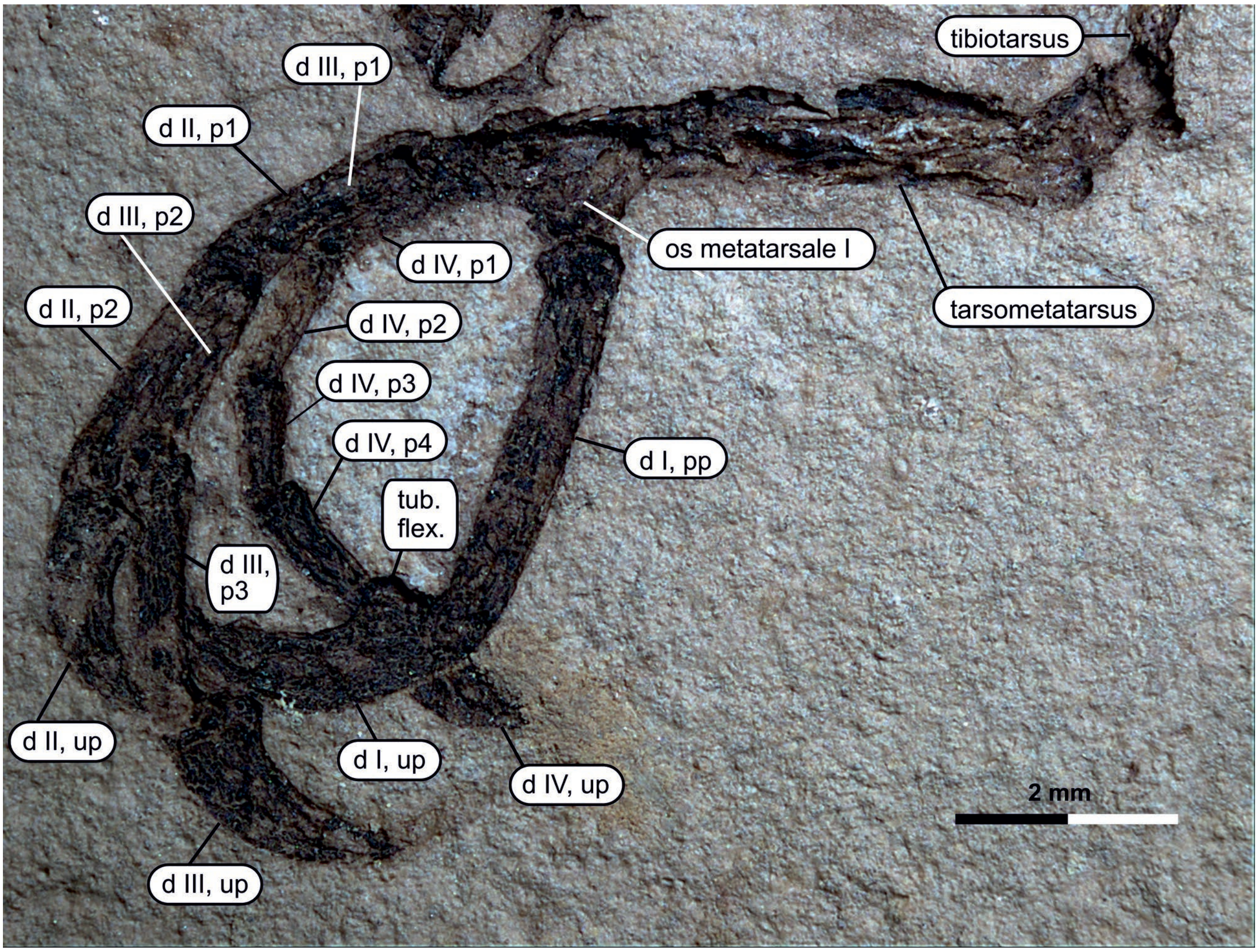

Fig. 3. Enlarged fragment of Figure 2a. Abbreviations: d I, pp — digit I, proximal phalanx; d I, up — digit I, ungual phalanx; d II, p1 — digit II, phalanx 1; d II, p2 — digit II, phalanx 2; d II, up — digit II, ungual phalanx; d III, p1 — digit III, phalanx 1; d III, p2 — digit III, phalanx 2; d III, p3 — digit III, phalanx 3; d III, up — digit III, ungual phalanx; d IV, p1 — digit IV, phalanx 1; d IV, p2 — digit IV, phalanx 2; d IV, p3 — digit IV, phalanx 3; d IV, p4 — digit IV, phalanx 4; d IV, up — digit IV, ungual phalanx.

vincenti, *Eocypselus rowei*) and Messelirrisoridae (*Messelirrisor* spp.) it is definitely shorter (Mayr 2010; Ksepka et al. 2013, fig. 1). As in extant hummingbirds (Mayr2004, p. 863), the long hallux attaches to the tarsometatarsus approximately at the beginning of its distal third, whereas in *Scaniacypselus szarskii* (Apodidae) it attaches to the tarsometatarsus at its mid-length (Peters 1985, p. 153). As in *Eurotrochilus inexpectatus* and the putative upupiform SNMZ 27188 from Slovakia but contrary to the modern common swift *Apus apus*, the os metacarpale I exhibits an elongated shaft (Mayr 2004, fig. 2; Kundrát et al. 2015); other details are too poorly preserved for a meaningful comparison. On digits II and III the penultimate phalanx is the longest (its length in digit IV is unknown). Similar to *Eurotrochilus inexpectatus* (Trochilidae), *Messelirrisor* spp. and SNMZ 27188 (both upupiforms), the proximal phalanges of digits II, III and IV are relatively long; in many extant Apodidae (e.g., *Apus*, *Aeronantes*, *Collocalia*, *Cypsiurus*, *Panyptila*) they are extremely short but in the Eocene *Eocypselus vincenti* and *Scaniacypselus szarskii* they were not so much abbreviated (Peters 1985; Mayr 2010, 2015). The claws are robust, moderately curved and their tubercula flexoria are rounded and rather well-developed; in extant swifts tubercula flexoria are elongated proximo-distally.

Discussion

It seems that there are just two avian orders — Caprimulgiformes and Bucerotiformes — with some representatives that show a combination of characters observed on ISEA AF/JAM1. The extremely small size of the specimen, very short and slender tarsometatarsus, hallux as long as the tarsometatarsus, proximal phalanges of all digits elongated (extremely so in the hallux), and stout, rather massive, moderately curved claws with well-developed tubercula flexoria make the specimen look similar to a stem taxon of either swifts, hummingbirds or hoopoes/woodhoopoes. Other avian

Table 1: Total lengths and ratios of two leg bones of chosen extant and extinct taxa with short tarsometatarsus. Measurements are given in millimetres. A dagger (†) indicates extinct taxa, and an asterisk (*) arithmetic mean of left and right bones. Measurements after: [1]Ksepka et al. (2013); [2]Mayr (2010); [3]Peters (1985); [4]Mayr (2015); [5]Mayr (2004); [6]Mayr (2007); [7]Louchart et al. (2008); [8]Mayr (1998); [9]Kundrát et al. 2015; [10]Mayr (2000); other specimens measured by the authors in the skeletal collection of ISEA PAS.

Taxon	Number	TBT	TMT	TBT/TMT
Aves indet. (present study)	†ISEA AF/JAM1	~13.8	6.3	2.19
†Eocypselidae				
†*Eocypselus rowei*[1]	WDC-CGR-109	20.1*	10.0*	2.01
†*Eocypselus vincenti*[2]	MGUH 26729	20.2	10.9	1.85
Apodidae				
†*Scaniacypselus szarskii*[3]	LNK-Me 301, holotype	12.0	5.5	2.18
†*Scaniacypselus szarskii*[4]	SMF-ME 3409A+B	~11.4	~5.9	1.93
Apus apus	A/4117/84	24.7	10.5	2.35
Apus apus	A/5858/01	25.6	10.1	2.53
Hirundapus caudacutus	A/5001/91	36.3	15.7	2.31
Trochilidae				
†*Eurotrochilus inexpectatus*[5]	SMNS 80739/4, holotype	14.9	6.5	2.29
†*Eurotrochilus inexpectatus*[6]	SMNK-PAL 5591, 2nd slab of holotype	~15.0	6.7	2.24
†*Eurotrochilus* sp.[7]	NT-LBR-040	15.1	6.8	2.22
Eupeptomena macroura	A/5441/95	14.3	6.2	2.31
Ramphodon naevius	A/5516/96	13.2	6.5	2.03
Clytolaema rubricauda	A/5539/96	13.5	6.3	2.14
Calypta costae	A/4174/85	10.7	4.2	2.55
Phaethornis bourcieri	A/4074/84	11.2	4.3	2.60
†Messelirrisoridae				
†*Messelirrisor halcyrostris*[8]	SMF-ME 1883, holotype	16.9	9.6	1.76
† *Messelirrisor halcyrostris*[9]	SMF-ME 11117a+b	15.5*	8.8*	1.76
† *Messelirrisor halcyrostris*[9]	SMF-ME 10987a+b	15.3	9.2	1.66
†*Messelirrisor grandis*[10]	SMF-ME 600	~19.0	~10.4	1.83
† *Messelirrisor grandis*[5]	SMF-ME 108.33	18.2*	9.6*	1.90
†*Messelirrisor parvus*[8]	SMF-ME 2793, holotype	15.8	8.4	1.88
† *Messelirrisor parvus*[8]	SMF-ME 2466	14.0*	7.2*	1.94
† *Messelirrisor parvus*[8]	SMF-ME 1180	14.8	7.9	1.87
† *Messelirrisor parvus*[8]	SMNK-Me 300	15.8*	8.0*	1.98
† *Messelirrisor parvus*[8]	SMNK-Me 776	15.0	8.1	1.85
Stem-group upupiform				
† SNM-Z 27188[9]	SNM-Z 27188	~19.0	7.1	2.68
Upupidae				
Upupa epops	A/4006/84	36.7	21.8	1.68
Upupa epops	A/216/61	38.5	24.5	1.57
Passeriformes				
Hirundo rustica	A/6106/02	21.2	11.5	1.84
Delichon urbica	A/5334/94	20.9	11.6	1.80
Riparia riparia	A/3133/76	19.4	10.2	1.90

higher-level taxa including Coliiformes and Passeriformes can be excluded. Unfortunately, due to the poor preservation of the specimen and its incompleteness its more precise affinities remain unresolved. The specimen differs in many details from all other tiny Palaeogene swifts, hummingbirds and hoopoes and therefore most probably it represents a new taxon but in our opinion it is too fragmentary to describe it. Nevertheless, it is a valuable addition to our knowledge of Palaeogene birds from the Carpathians — a large region that has yielded only a handful of avian specimens so far.

Most Palaeogene swifts, hummingbirds and also hoopoes are represented by the wing and/or pectoral girdle bones. Consequently, the taxonomies of the groups are largely based on those elements. The leg bones are only seldom preserved and even rarer are the pedal digits described above. This study, based on a specimen with known lengths of particular phalanges, is a small step forward to fill the gap in our knowledge.

Although there is no way to know what the rest of our specimen looked like, the relative proportions of leg and foot bones and the general shape of claws indicate a bird that perched regularly. Short legs with long toes preclude a ground dwelling bird and the claws are too robust and show too little curvature for a bird that would cling to vertical tree trunks. Thus, the specimen must have been a flying non-ground dwelling bird that perched regularly. A similar but not identical, unspecialized foot was observed in the putative upupiform SNMZ 27188 (Kundrát et al. 2015) and stem-group apodid *Scaniacypselus* (see Mayr 2015). It is noteworthy that with the exception of two procellariiforms, all other specimens — including ISEA AF/JAM1 — recorded from the Outer Carpathians and Central Palaeogene Basin are land birds that must have lived in the forests or shrubs near the shoreline. The predominance of terrestrial birds in marine deposits is nothing unusual; it was also observed in the Eocene Fur Formation of Jutland in Denmark (Kristoffersen 2002), London Clay Formation in southern England (Mlíkovský 2002), or the Oligocene Wiesloch-Frauenweiler in southern Germany (Mayr 2009).

Although remains of Oligocene birds are extremely rare in Poland (Bochenski et al. 2013a), the exposure at Jamna Dolna 1 has already yielded several such fossils. The present find is the oldest within the site (Unit C, ca. 32.5 Mya), closely followed by a nearly complete passerine bird *Jamna szybiaki* (Unit E, ca. 31.5 Mya) (Bochenski et al. 2011). Moreover, three isolated feathers of unknown birds were reported (Units G–H, ca. 31.0 Mya) (Bieńkowska-Wasiluk 2010, text-fig. 41A–C). The remains of land birds from Jamna Dolna and other sites in the region can be attributed to the general sea level fall at that time, which led to limitation of the connection with the open ocean and resulted in many shallow shoals, temporary islands and exposed dry land areas along the coast (e.g., Rögl 1999; Kotlarczyk et al. 2006).

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