The third nearly complete passerine bird from the early Oligocene of Europe

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Abstract A new species and genus of a passerine bird from the early Oligocene of Poland is described. *Resoviaornis jamrozi* gen. et sp. nov. is the third nearly complete passerine known so far from the Paleogene. As in the two recently described passerine birds, it shows a mosaic of characters typical for the Oscines or Suboscines, and therefore its systematic position within Passeriformes remains unresolved, pending discoveries of new specimens. The specimen is so far the oldest passerine to have the coracoid with well pronounced and hooked processus acrocoracoideus. With the size of the extant Blue Tit, it is also the smallest of the Oligocene passerines. The slender remnants of its beak point to an insectivorous or frugivorous bird, and the relatively long legs suggest that it spent much time on the ground.

Keywords Fossil birds · Passeriformes · Menilite shales · Carpathian flysch · Oligocene · Paleogene

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Zusammenfassung

Der dritte, weitgehend vollständige Sperlingsvogel aus dem frühen Oligozän Europas

Eine neue Art und Gattung der Sperlingsvögel wird aus dem frühen Oligozän Polens beschrieben. *Resoviaornis jamrozi* gen. et sp. nov. ist die dritte nahezu vollständig fossil überlieferte Sperlingsvogelart aus dem Paläogen. Ähnlich wie bei zwei vor kurzem beschriebenen Arten zeigt das neue Fossil ein Mosaik von Merkmale typisch für Oscines und Suboscines. Bis zur Entdeckung neuer Exemplare bleibt seine systematische Stellung innerhalb der Passeriformes ungelöst. Das Fossil ist der bisher älteste Sperlingsvogel mit einem Coracoid mit einem gut ausgeprägten und hakenförmigen Processus acrocoracoideus. Mit der Größe einer rezenten Blaumeise ist die neue Art auch der kleinste der oligozänen Sperlingsvögel. Die Überreste seines schlanken Schnabels deuten auf einen insektenfressenden oder fruchterfressenden Vogel, und die relativ lange Beine lassen vermuten, dass er viel Zeit auf dem Boden verbrachte.

Introduction

The Outer Carpathians in southeastern Poland are very abundant in Oligocene fossils (Kotlarczyk et al. 2006). A great majority of them are marine fish remains, but representatives of other organisms including plants, invertebrates and vertebrates are also sometimes found. So far, birds are represented by two nearly complete specimens—a hummingbird *Eurotrochilus noniewiczzi* (Bochenski and Bochenski 2008) and a passerine *Jamna szybiaki* (Bochenski et al. 2011). Other, less spectacular specimens

include a procellariiform ?*Diomedeoides lipsiensis* (Elzowski et al. 2012), an articulated passerine leg (Bochenski et al. 2012a) and a bird of unknown affinities with a columbid-like foot (Bochenski et al. 2010). The findings are summarized in recently published papers (Bochenski et al. 2012b; Bochenski et al. 2013).

Fossil records of passerines from the Paleogene are very scarce. Besides the two specimens mentioned above, they include a nearly complete *Wieslochia weissi* from Germany (Mayr and Manegold 2004, 2006a), an articulated wing (Mayr and Manegold 2006b), and several dozen isolated wing bones (Manegold 2008; Mourer-Chauviré et al. 1989). Outside Europe, Paleogene remains of possible passerines are known only from the early Eocene of Australia (Boles 1995, 1997), which agrees with the theory of the Southern Hemisphere origin of passerines based on DNA sequences (Ericson et al. 2002; see also Mayr 2013).

The specimen described in this paper is the third nearly complete passerine from the early Oligocene. It provides new details of the earliest passerine birds that were apparently more diversified than previously thought.

Methods

Osteological terminology follows Baumel and Witmer (1993). Dimensions are given in millimeters and refer to the greatest length along the longitudinal axis of the bone. The fossil was compared with comparative specimens from the osteological collection of the ISEA, and with published data on the osteology of extant and fossil Passeriformes (Acanthisittidae, Oscines and Suboscines) as well as extinct Zygodactylidae—a family whose members are morphologically very similar to Passeriformes (Mayr 2008, 2009). The fossiliferous horizon of the type locality, Wola Rafałowska, has been dated on the basis of the fish assemblage by one of us (ES) basing on data from Kotlarczyk et al. (2006) and previous geological mapping of the area (Jucha 1969).

Institutional abbreviations ISEA, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, Poland; MSMD, Muzeum Skamieniałości i Mineraliów, Dubiecko, Poland; SMF, Forschungsinstitut Senckenberg, Frankfurt am Main, Germany; SMNS, Staatliches Museum für Naturkunde Stuttgart, Germany; UCBL, Université Claude Bernard-Lyon, France.

Systematic paleontology

Aves Linnaeus 1758

Passeriformes Linnaeus 1758

Genus *Resoviaornis* gen. nov.

Type species *Resoviaornis jamrozi* sp. nov.

Etymology The genus name is a composite: *Resovia* is Latin for Rzeszów, a city close to the type locality, Wola Rafałowska, added to the Ancient Greek *ὄρνις* (ornis), meaning “bird”.

Remarks The specimen resembles Passeriformes in overall morphology and derived features. In particular, the coracoid bears a hooked processus acrocoracoideus and reduced processus procoracoideus; the sternum bears bifurcated spina externa and a single pair of incisions in its caudal part; the humerus bears processus supracondylaris dorsalis just above the condylus dorsalis, and a prominent processus flexorius that projects far distally; the ulna bears a prominent olecranon; the carpometacarpus bears the processus intermetacarpalis, a broad distal end of the os metacarpale minus that protrudes far distally, and a fossa in the ventral surface of the synostosis metacarpalis distalis.

Differential diagnosis Small passerine, approximately the size of a Blue Tit *Cyanistes (Parus) caeruleus*.

The specimen differs from:

- All extant Passeriformes in the unique combination of the following characters: only five (six?) caudal vertebrae; sternum with trabecula mediana that does not widen in its caudal part, and with long processus craniolateralis that projects further anterior than the labrum dorsale; very stout humerus with a undulated dorsal margin of crista deltopectoralis and with proximal part broad dorso-ventrally; os carpi ulnare with crus breve and crus longum of approximately similar size.
- The early Oligocene *W. weissi* in: coracoid with hooked processus acrocoracoideus and reduced processus procoracoideus; carpometacarpus with broad square distal end of the os metacarpale minus that protrudes far distally.
- The early Oligocene *J. szybiaki* in: only five (six?) caudal vertebrae; sternum with bifurcated spina externa; coracoid with hooked processus acrocoracoideus; humerus with short crista deltopectoralis; carpometacarpus with less stout os metacarpale majus; pelvis with margo cranialis and margo lateralis of ala preacetabularis ilii meeting at a wide angle.
- The extinct passerine-like family Zygodactylidae in: coracoid with hooked processus acrocoracoideus and short and rounded processus lateralis; sternum with bifurcated spina externa and a single pair of incisions in its caudal part; ulna with a prominent olecranon that projects far proximally and tapers; carpometacarpus with a broad distal end of the os metacarpale minus that protrudes far distally; phalanx digiti alulae does not bear an ungual phalanx; phalanx distalis digiti majoris much shorter than the phalanx proximalis.

Resoviaornis jamrozi gen. et sp. nov.

Etymology The species is named after Albin Jamróz, who collected the specimen.

Holotype MSMD Av WR-9a + b (Figs. 1, 2), almost complete articulated skeleton preserved on two slabs, deposited in the Muzeum Skamieniałości i Mineralów at Dubiecko, Poland.

Type locality and horizon Wola Rafałowska, ca. 14 km south-east of Rzeszów, Podkarpackie Voivodeship, SE Poland, left bank of a stream, a tributary of the river Strug; geographical coordinates of the Wola Rafałowska village: 49°59'25"N, 22°09'53"E; late Rupelian, Oligocene, ca. 29–28.5 MYA, Menilite shales of the Jasło limestone horizon (lower section of the Huta Brzuska Member, Menilite Formation) of the Skole Unit, Outer Carpathians, correlated with the ichthyofaunal IPM4 Zone and the

calcareous nannoplankton of the NP 24 zone sensu Berggren et al. (1995) (for correlation charts see Bochenski et al. 2013 and Kotlarczyk et al. 2006).

Diagnosis As for the genus.

Measurements (maximum length in mm) taken from the counterslab: sternum, 14.3; coracoid, 13.1 (left), ~13.0 (right); humerus, 12.5 (left), ~12.4 (right); ulna, 17.0 (left); radius, 14.9 (left), ~12.9 (right); carpometacarpus, 8.0 (left); phalanx proximalis digiti majoris, 3.9 (left); phalanx distalis digiti majoris, 2.3 (left), 2.5 (right); pelvis, >11.3; femur, 13.4 (left), ~13.3 (right); tibiotarsus, >28.0 (left).

Description and comparison

Particular elements are broken longitudinal and preserved on two slabs as imprints partly lined with remnants of

Fig. 1 *Resoviaornis jamrozi* gen. et sp. nov., holotype, specimen MSMD Av WR-9a + b from Wola Rafałowska, Poland, early Oligocene (top) and interpretative drawings (bottom). **a** Main slab; **b** counterslab. Left (L) and right (R) elements are indicated.

Abbreviations: *al* phalanx digiti alulae, *cmc* carpometacarpus, *cu* os carpi ulnare, *dmj* phalanx distalis digiti majoris, *mn* phalanx digiti minoris, *pmj* phalanx proximalis digiti majoris

Fig. 2 *Resoviaornis jamrozi* gen. et sp. nov., holotype, specimen MSMD Av WR-9a + b from Wola Rafałowska, Poland, early Oligocene. The elements on both slabs are not real bones but are preserved as imprints partly lined with bone and therefore special attention is needed not to mix the *left* and *right* sides. **a** Right coracoid, main slab; **b** left humerus with proximal ulna, counterslab; **c** left humerus with proximal ulna, main slab; **d** left carpometacarpus with phalanges, counterslab; **e** sternum, main slab; **f** thoracic vertebrae, main slab; al phalanx digiti alulae, cb crista bicipitalis,

cd crista deltopectoralis, cs corpus sterni, dmj phalanx distalis digiti majoris, il incisura lateralis, ld labrum dorsale, mn phalanx digiti minoris, ol olecranon, om os metacarpale minus (distal end), pa processus acrocoracoideus, pc processus cranio-lateralis, pd processus dorsalis, pf processus flexorius, pi processus intermetacarpalis, pl processus lateralis (sternal end), pmj phalanx proximalis digiti majoris, pp processus procoracoideus, psd processus supracondylaris dorsalis, se spina externa, tl trabecula lateralis, tm trabecula mediana, tv thoracic vertebrae. Scale bars 5 mm

bone. Therefore, in many cases a mixture of an imprint and the inner side of a bone rather than its surface is visible which makes difficult to recognize the left and right sides or the anterior and posterior views at first glance. A good example illustrating the problem is the left humerus whose images from the two slabs are shown in Fig. 2b, c.

Skull

The partial head is seen in ventral view on the main slab and in dorsal view on the counterslab. The braincase is

short but wide and the margo supraorbitalis is well visible. Judging by the size of the sclerotic rings in relation to the braincase, the eyeballs must have been relatively larger than those in Paridae. Only the proximal-most portion of the beak is visible, with the beginning of the narial openings. Unlike *J. szybiaki* (Bochenski et al. 2011), the dorsal bar of the os nasale is wider than the ventral. The mandible is disarticulated from the cranium. A proximal portion of the right ramus mandibulae is visible in ventral view on the main slab. The processus caudalis and processus mandibulae medialis are of similar length. The visible fragments indicate a slender beak.

Vertebrae

The vertebrae are poorly preserved, some of them are hidden under superimposed bones, and in some cases borders between particular vertebrae are difficult to define. At least 15 presacral vertebrae are visible. Unlike the early Oligocene *J. szybiaki* (Bochenski et al. 2011), five thoracic vertebrae are arranged in a straight line that resembles the notarium (Fig. 2f). Although the vertebrae are too poorly preserved to say whether they were actually fused to a notarium, it is clear that this segment of the vertebral column was rigid. The processes dorsalis of all thoracic vertebrae project distinctly dorsad and their dorsal margins meet with each other. At least four of the thoracic vertebrae bear ribs. In extant Passeriformes there is a large variation regarding the notarium: from fully ossified notarium, through less extensive fusion to no fused vertebrae (James 2009). The caudal vertebrae and the pygostyle are separated from the pelvis. As in the Eocene *Primozygodactylus danielsi* (Mayr 1998), there are only five (six?) caudal vertebrae whereas extant Passeriformes and *J. szybiaki* (Bochenski et al. 2011) have typically seven. The large pygostyle is in the shape of a blade.

Coracoid

The right coracoid, seen as imprints of the ventral side on the main slab (Fig. 2a) and the dorsal side on the counterslab, is much better preserved than the left. Remnants of bone are present on both slabs. The coracoid is long and slender as in extant Passeriformes. As in most Eupasserines (Oscines and Suboscines) but contrary to Acanthisittidae, *Primozygodactylus* (Mayr 1998; Mayr and Zelenkov 2009) and *Zygodactylus* (Mayr 2008), the processus acrocoracoideus (visible in the right bone only) is well pronounced and hooked. The two early Oligocene passerines described so far—*Wieslochia* and *Jamna* did not have a hooked processus acrocoracoideus (Bochenski et al. 2011; Mayr and Manegold 2006a). The processus procoracoideus (best seen on the right bone on the main slab) is reduced as in Acanthisittidae and Oscines, whereas in *Wieslochia* and some extant Suboscines it is enlarged (Mayr and Manegold 2006a). The cotyla scapularis and facies articularis humeralis are not visible. The processus lateralis of the sternal end is short and rounded as in Passeriformes and not elongated laterally as in *Primozygodactylus* (Mayr 1998; Mayr and Zelenkov 2009).

Scapula

Details of the articular end are too poorly preserved to allow meaningful comparison. As in Passeriformes, the corpus scapulae is blade-like, almost straight throughout its length and its width does not change with length.

Furcula

Although only one scapus clavicularis is visible, it is clear that the furcula is U-shaped. The scapus clavicularis is slender, the extremitas omalis is not visible, and the apophysis furculae forms a median projecting blade as in extant Passeriformes.

Sternum

The sternum is visible in lateral view (Fig. 2e) and therefore its width cannot be estimated. Small bone fragments are preserved on both slabs. As in most Suboscines, Acanthisittidae, Piciformes, (Mayr and Manegold 2006a) and *Primozygodactylus* (Mayr 1998; Mayr and Zelenkov 2009) but contrary to Oscines, the processus cranio-lateralis is long and it projects further anterior than the labrum dorsale. As can be inferred from deep depressions on the slab and counterslab, the elongated spina externa widens sideways at its end which suggests that it was bifurcated as in most extant Eupasserines (Oscines and Suboscines) and the early Oligocene *Wieslochia*. In this respect, it differs from *J. szybiaki* (Bochenski et al. 2011), *Primozygodactylus* (Mayr 1998) and *Zygodactylus* (Mayr 2008) that have a rod-like, not bifurcated spina externa. As in most extant Passeriformes and the early Oligocene *Wieslochia* (Mayr and Manegold 2006a) and *Jamna* (Bochenski et al. 2011), there is only a single pair of incisions, the incisurae laterales, in the caudal part of the corpus sterni. All Zygodactylidae have a four-notched sternum (Mayr 1998; Weidig 2010) which is also true in almost all non-passerine land birds that might be closely related to the Passeriformes, e.g., Coliiformes, Piciformes, and most Coraciiformes (Feduccia and Olson 1982). The trabecula lateralis reaches at least as far caudally as the corpus sterni. Its caudal end is probably covered with the matrix and therefore we do not know whether it widens at the end or not, and how far caudally it goes. Contrary to extant Passeriformes, the trabecula mediana does not widen in its caudal part. At least four ribs are attached to the sternum.

Humerus

Both humeri are preserved on the slabs as imprints partly lined with bone. The left humerus is seen in caudal view on the main slab and in cranial view on the counterslab (Fig. 2b, c), whereas the right humerus is seen in cranial view on the main slab and in caudal view on the counterslab. Unlike most extant Passeriformes the humerus is very stout, its proximal end is broad dorso-ventrally, and the caput humeri is very pronounced and bulges very much caudally (the latter condition is best seen on the counterslab). As in many extant Passeriformes but contrary to the early Oligocene *J. szybiaki*

(Bochenski et al. 2011), the crista deltopectoralis is relatively short and forms an angular connection with the shaft. The dorsal margin of the crista deltopectoralis is distinctively undulated whereas in extant Passeriformes it is either straight or only a little wavy. Unlike *J. szybiaki* (Bochenski et al. 2011), the crista bicipitalis begins approximately as far proximally as the crista deltopectoralis. A distinct elongated bulging within the proximal part of the right bone can be interpreted as an impression of a single fossa pneumotricipitalis without foramen pneumaticum. A single fossa pneumotricipitalis was also observed in the Oligocene *Wieslochia* (Mayr and Manegold 2006a), whereas many extant Oscines have two fossae. Although the exact shape and size of the processus supracondylaris dorsalis cannot be discerned, it is clear that the process is just above the condylus dorsalis, which agrees with the condition in Passeriformes (Manegold 2008), Zygodactylidae (Mayr 1998, 2008; Weidig 2010) and the early Oligocene *J. szybiaki* (Bochenski et al. 2011). The processus flexorius is prominent and it projects distinctly distally (best seen on the left bone), which is in agreement with extant Passeriformes, the Oligocene *Wieslochia* (Mayr and Manegold 2006a), *Jamna* (Bochenski et al. 2011) and the extinct Zygodactylidae (Mayr 1998, 2008).

Ulna

The left and right ulnae are seen in dorsal view on the main slab and in ventral view on the counterslab. Unlike extant Passeriformes the ulna is relatively stout. As in Zygodactylidae (Mayr 1998; Weidig 2010) and many Passeriformes, the ulna is a little longer than the humerus. Similar to most Passeriformes including *J. szybiaki* (Bochenski et al. 2011), the olecranon is prominent, projects far proximally, tapers, and there is a saddle in the posterior margin of the bone between the olecranon and the shaft (Fig. 2b, c). In *Primozygodactylus* and *Zygodactylus*, the olecranon is shorter and stockier (Mayr 1998, 2008). The cotyla ventralis is upright and almost parallel to the long axis of the bone, as in *Turdus*. The cotyla dorsalis is visible only on the left bone, as a deep imprint on the counterslab and its exact shape remains unknown. The papillae remigiales caudales cannot be discerned and therefore it seems that they were either absent or small as in many Passeriformes and Zygodactylidae (Mayr 1998, 2008; Weidig 2010), but contrary to Piciformes. The condylus dorsalis is elongated proximo-distally. Other features on the distal ulna are not visible due to its poor preservation.

Radius

The radius is too poorly preserved to allow meaningful comparison.

Carpometacarpus

Both carpometacarpi are preserved as imprints and are visible in dorsal view on the main slab and in the ventral view on the counterslab (Fig. 2d). Proximal parts of both carpometacarpi are poorly preserved. The os metacarpale majus is not as stout as that in *J. szybiaki*; its proportions correspond to those in extant Passeriformes. The processus intermetacarpalis reaches caudally at least to the os metacarpale minus. Its presence, indicated by its partial imprint with small fragments of bone between the os metacarpale majus and os metacarpale minus, and a distinct bulging of the os metacarpale minus on the left carpometacarpus, is a derived feature of passerines (Mayr and Manegold 2004, 2006a, b); it is also present in Piciformes and Zygodactylidae (Mayr 1998, 2008; Weidig 2010). The processus dentiformis is either missing or it was small and has not been preserved on the specimen. As in extant Oscines and the early Oligocene *J. szybiaki* (Bochenski et al. 2011), the distal end of the os metacarpale minus is square, broad and protrudes relatively far distally. In extant Suboscines, early Oligocene *W. weissi* and in all Oligocene specimens of subosine affinities (SMF Av 504, SMF Av 509, SMF Av 510; SMNS 59466/1, SMNS 59466/2), the distal end of the os metacarpale minus is less protruding and its cranial portion reaches farther distally than the facies articularis digitalis minor (Manegold 2008; Mayr and Manegold 2004, 2006a, b; Mourer-Chauviré et al. 1989). In Acanthisittidae, the latter condition is also observed, although in their case the distal end of the os metacarpale minus protrudes farther distally (Mayr and Manegold 2006b; Millener and Worthy 1991: fig. 12). In Zygodactylidae, the os metacarpale minus is only a little longer than the os metacarpale majus but the difference in length is larger in *Eozygodactylus* and *Zygodactylus* than in *Primozygodactylus* (Mayr 1998, 2008; Weidig 2010). As in most extant Oscines and the Oligocene *J. szybiaki* (Bochenski et al. 2011), there is a depression in the ventral surface of the synostosis metacarpalis distalis (Mourer-Chauviré et al. 1989). Such a distal fossa is also present only in a few Suboscines, which Manegold (2008) has attributed to convergence.

Other elements of the wing

The os carpi ulnare is best seen on the counterslab, where the right bone is imprinted. Its crus breve and crus longum seem to be of approximately the same size which agrees with Acanthisittidae, Suboscines and basal oscine taxa, but differs from many Oscines (Mayr and Manegold 2006a). The os carpi radiale is too poorly preserved to allow meaningful comparison. As in most extant birds including passerines (Stephan 1992) but contrary to the extinct

Zygodactylidae (Mayr 2008), the phalanx digiti alulae does not bear an ungual phalanx. The phalanx proximalis digiti majoris is of approximately equal width as in Acanthisittidae and Oscines (Mayr and Manegold 2006b). In the Eocene *Primozygodactylus* and Suboscines, it widens considerably cranio-caudally (Mayr 1998: fig. 26). As in Passeriformes, the proximal and distal ends of this phalanx are straight, without any bigger projections, and there is a distinct depression in its ventral side. As in extant Passeriformes and the early Oligocene *J. szybiaki* (Bochenski et al. 2011), the phalanx distalis digiti majoris is much shorter than the phalanx proximalis, and therefore it differs from the suboscine-like specimen SMF Av 504 of the early Oligocene of France, both phalanges of which are approximately equal in length (Mayr and Manegold 2006b), and from the Zygodactylidae species whose phalanx distalis digiti majoris is relatively long (Mayr 1998; Weidig 2010). The phalanx digiti minoris is slender.

Pelvis

The pelvis is visible in a ventrolateral view. As in many Passeriformes, it is relatively long and the width of its cranial part is distinctly smaller than the width at the acetabulum. Similar to, e.g., the Goldcrest, *Regulus regulus*, margo cranialis and margo lateralis of the ala preacetabularis ilii meet at a wide angle. In this respect, the specimen differs from the early Oligocene *J. szybiaki* whose margo cranialis and lateralis formed right angles (Bochenski et al. 2011). As in Passeriformes, the scapus pubis reaches farther caudally than the caudal part of the pelvis.

Femur

Both femora are preserved as imprints on the slabs. The right femur is seen in anteromedial view on the main slab and posterolateral view on the counterslab. It is articulated to the pelvis and the tibiotarsus. The left femur is visible in posterior view on the main slab and anterior view on the counterslab. It is isolated from both the pelvis and the tibiotarsus. The femur is relatively stout for its length: the shaft is much thicker and the distal end is wider than that in *Phylloscopus collybita* which is of similar length. As in Passeriformes, the trochanter femoris does not project further proximally than the proximal articular part (seen on the left bone). The condylus medialis and condylus lateralis (divided into the crista tibiofibularis and trochlea fibularis) of the left bone are well imprinted in the counterslab.

Tibiotarsus

As in extant Passeriformes but also extinct Zygodactylidae (Mayr 1998, 2008; Weidig 2010), the tibiotarsus is clearly

the longest limb element; it is straight and slender and its proportions (length and robustness) are similar to those in the Great Tit, *Parus major*. It is more than 20 per cent shorter than the tibiotarsus of an unnamed passerine from the early Oligocene (Bochenski et al. 2012a) and therefore represents a different taxon. The crista fibularis (seen as a deep furrow on the right bone in the main slab) is short. The right fibula reaches distally to the mid-shaft of the tibiotarsus. As in *P. major*, the crista cnemialis cranialis (left bone) is long proximo-distally, projects far proximally and it joins with the shaft almost at right angles. On the distal end (left bone) a small portion of the condylus lateralis is visible, which enables to measure roughly the total length of the tibiotarsus.

Discussion

There is no doubt that *R. jamrozi* belongs in Passeriformes but, as in the other two early Oligocene passerines—*W. weissi* (Mayr and Manegold 2006a) and *J. szybiaki* (Bochenski et al. 2011)—it is also in this case difficult to determine its more precise affinities because the specimen shows a mixture of characters typical either for the Oscines (e.g., in coracoid: a reduced processus procoracoideus, or in carpometacarpus: a broad distal end of the os metacarpale minus that protrudes far distally) or the Suboscines (e.g., in sternum: a long processus craniolateralis that projects further anterior than the labrum dorsale). As shown above, the three early Oligocene passerines—*Resoviaornis*, *Wieslochia* and *Jamna*—differ from one another in many important characters which suggests that they are probably not closely related.

Resoviaornis jamrozi was a very small bird the size of a Blue Tit *Cyanistes (Parus) caeruleus* or a Chiffchaff *P. collybita*. It was smaller than *Wieslochia* which was the size of a House Sparrow (Mayr and Manegold 2006a) and *Jamna* which was the size of a Skylark (Bochenski et al. 2011). All of the few preserved fragments of the beak are slender and lightly-built, which points to an insectivorous or frugivorous bird and excludes granivorous species. The legs were relatively long which is typical for species that spend much time on the ground while foraging among trees or shrubs like modern thrushes or wrens (Cramp 1988).

Although *R. jamrozi* is nearly complete, several elements including mandible, left femur and caudal vertebrae are disarticulated and preserved in almost anatomical position, close to the joint they belong. This suggests that the decomposition of the bird's body had begun shortly before it got fossilized. Scavengers' activity can be excluded because the skeletal elements are complete and they bear no traces of chewing or other damage. We may also assume that the bird reached its burial place shortly

after its death because otherwise the degree of its decomposition would be much greater and it would not preserve as an articulated skeleton (Schäfer 1972). As can be deduced from taphonomic analyses of fish remains, the presence of an articulated skeleton indicates quiet environment of the burial place, without any underwater currents or turbulences (Bienkowska-Wasiluk 2010; Kotlarczyk et al. 2006). The bird was a terrestrial passerine, as noted above possibly rather heavy for the size of its wings. Therefore, we may assume that it could have been blown off by a storm into the sea or it got into the water on migration. In either case, it must have drowned and sunk to the bottom rapidly. An alternative explanation is that the bird died on land and was flushed to the sea. However, the latter scenario seems less likely due to the absence of obvious damage to the skeleton.

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Conflict of interest The authors declare that they have no conflict of interest.

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