ORIGINAL ARTICLE

A new passerine bird from the early Oligocene of Poland

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Abstract We describe a nearly complete articulated specimen representing a new species and genus, *Jamna szybiaki* gen. et sp. nov., of an early Oligocene passeriform bird from Poland. In overall osteology, the specimen resembles extant Passeriformes but it differs from that group in several characters including the not bifurcated spina externa (sternum) and the absence of a hooked processus acrocoracoideus (coracoid). Its affinities within Passeriformes cannot be resolved at the moment due to the lack of characters that would support its position within either Oscines or Suboscines. For the first time in Paleogene passerines, wing and tail feathers are visible which provide new information on the external appearance of the bird. Its morphology suggests that it was a frugivorous/insectivorous bird that lived in shrubs and forests.

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

Zusammenfassung Wir beschreiben ein fast vollständig artikuliertes Exemplar einer neuen Sperlingsvogel-Art und -Gattung, *Jamna szybiaki* gen. et sp. nov., aus dem frühen Oligozän in Polen. In seinem Knochenbau erinnert das Exemplar an heutige Sperlingsartige, unterscheidet sich jedoch von dieser Gruppe in einigen Merkmalen wie z.B. dem ungegabelten Brustbein (sternum) und dem nicht vorhandenen eingehakten Rabenschnabelfortsatz processus acrocoracoideus (coracoid). Die Verwandtschaft mit den Sperlingsvögeln ist derzeit noch nicht ganz klar, weil Merkmale fehlen, die seine Stellung innerhalb entweder der Oscines, oder der Suboscines festlegen würden. Zum ersten Mal sind hier bei einem Sperlingsvogel aus dem Paläogen Hand- und Schwanzfedern sichtbar; sie geben neue Informationen über das äußere Aussehen des Vogels. Seine Morphologie lässt vermuten, dass er ein Früchte- und Insektenfresser war und in Sträuchern und Wäldern lebte.

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Introduction

Avian remains dated to the Paleogene are very rare in Poland. All of them come from marine deposits of SE Poland. So far, two specimens have been described: a hummingbird *Eurotrochilus noniewiczi* (Bocheński and Bocheński 2008) and an unspecified taxon with a columbid-like foot (Bocheński et al. 2010). Several other specimens are under study.

Passeriformes include more than half of all extant avian species. Their Neogene fossil record is very abundant but their remains from the Paleogene are very scarce (Mayr 2005, 2009). The oldest findings that include two isolated bones of possible Passeriformes are dated to the early Eocene of Australia (Boles 1995, 1997). The remaining

passerine remains are from the Oligocene of Europe. They include several dozen isolated bones from various localities of France and Germany (Manegold 2008; Mourer-Chauviré 2006; Mourer-Chauviré et al. 1989), an articulated wing from France (Mayr and Manegold 2006b), two so far undescribed articulated legs from Poland (Bocheński 1989, 1993, 1996), one nearly complete specimen (preserved on two slabs in separate collections) and a skull of *Wieslochia weissi* from Germany (Mayr and Manegold 2004, 2006a), and a so far undescribed specimen from France (Roux 2002). The remains represent both Oscines and Suboscines (Manegold 2008; Mayr 2009; Mourer-Chauviré 2006).

The phylogenetic relationship of Passeriformes has been much debated in the last years (see Mayr 2009 for summary). Taxa that have been proposed as the closest relatives of the passerine birds include Piciformes and the polyphyletic "Coraciiformes" (Livezey and Zusi 2007; Manegold 2005 after Mayr 2009), Psittaciformes (Ericson et al. 2006; Hackett et al. 2008) and the extinct family Zygodactylidae ("Primoscenidae"; Mayr 2008). According to both molecular and morphological analyses, the Acanthisittidae are the sister taxon of all other extant Passeriformes (Barker et al. 2004; Ericson et al. 2003; Worthy et al. 2010). Phylogenies based on molecular data indicate that Oscines originated on the Australian continental plate (Barker et al. 2002; Ericson et al. 2002).

In this paper, we describe a nearly complete articulated specimen found in SE Poland. It provides many new details of the osteology of passerine birds that lived in Europe in the early Oligocene. The specimen also shows relatively well-preserved wing and tail feathers that for the first time cast light on the external appearance of Paleogene Passeriformes.

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. In the case of feathers, the measurements are approximations of their probable length. The term Pan–Passeriformes denotes the clade including stem group and crown group Passeriformes. 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 Acanthisittidae, Oscines and Suboscines as well as extinct Zygodactylidae that are morphologically very similar to Passeriformes (Mayr 2008, 2009). The fossiliferous horizon of Jamna Dolna has been dated on the basis of the fish assemblage (Jerzmańska and Kotlarczyk 1968; Kotlarczyk et al. 2006).

Institutional abbreviations: ISEA, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences,

Kraków, Poland; MSMD, Muzeum Skamieniałości i Minerałów, Dubiecko, Poland; SMF, Forschungsinstitut Senckenberg, Frankfurt am Main, Germany; SMNS, Staatliches Museum für Naturkunde Stuttgart, Germany.

Systematic paleontology

Aves Linnaeus, 1758
    Pan-Passeriformes (Linnaeus, 1758)
    Genus *Jamna* nov.
    Type species: *Jamna szybiaki* sp. nov.
    Etymology: The genus name refers to the type locality, Jamna Dolna.

Remarks: The specimen resembles Passeriformes in overall morphology and derived features. In particular, the humerus bears a large processus supracondylaris dorsalis just above the condylus dorsalis, and a prominent processus flexorius that projects far distally; the carpometacarpus bears the processus intermetacarpalis that projects caudally slightly behind the os metacarpale minus, 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 Dipper *Cinclus cinclus*. The specimen differs from:

- All extant Passeriformes in the unique combination of the following characters: sternum with spina externa rod-like and not bifurcated, and with short processus craniolateralis; coracoid with a rounded and not hooked processus acrocoracoideus; very stout humerus with elongated crista deltopectoralis that reaches about one-third of the total length of the bone; carpometacarpus with very stout os metacarpale majus, and phalanx proximalis digiti majoris that widens a little craniocaudally toward its distal end.

- The early Oligocene *Wieslochia weissi* in: the sternum with the spina externa rod-like and not bifurcated; the carpometacarpus with broad distal end of the os metacarpale minus that protrudes far distally.

- The extinct passerine-like family Zygodactylidae in the following characters: there are seven caudal vertebrae; the processus lateralis (coracoid) is short and rounded; the sternum bears only a single pair of the incisurae in its caudal part; the ulna bears a prominent olecranon that projects far proximally and tapers; on the carpometacarpus the distal end of the os metacarpale minus is broad and protrudes far distally, and there is a fossa in the ventral surface of the synostosis metacarpalis distalis; the phalanx distalis digiti majoris is much shorter than the phalanx proximalis; tail feathers seem to have relatively thin and delicate rachises; the width

of the tail feathers remains approximately constant throughout their length.

Jamna szybiaki gen. et sp. nov.

Etymology: The species is named after Robert Szybiak who collected the specimen.

Holotype: MSMD Av JAM-6 (Figs. 1 and 2), almost complete articulated skeleton preserved on one slab only, deposited in the Muzeum Skamieniałości i Minerałów at Dubiecko, Poland. Found in 2003.

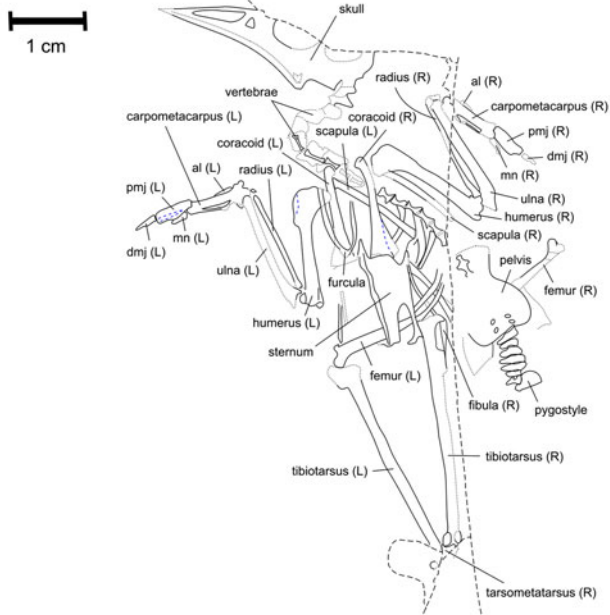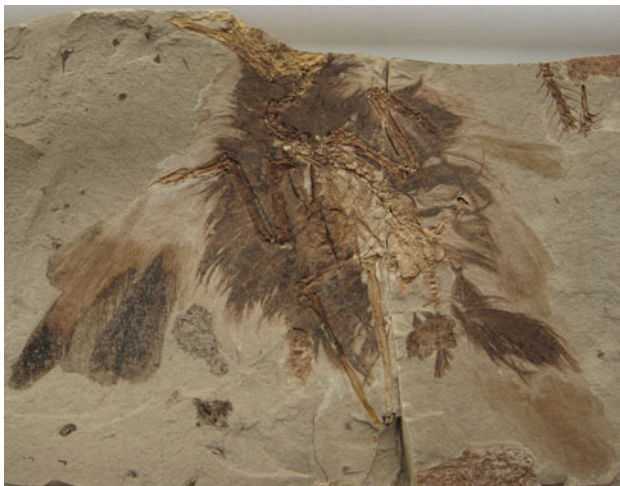Type locality and horizon: Jamna Dolna, ca. 8 km south-east of Bircza, Podkarpackie Voivodeship, SE Poland, high bank of Jamninka stream, a tributary of the river Wiar; geographical coordinates of the site: 49°38.667′N, 022°33.515′E; Rupelian, early Oligocene, ca. 30–31 MYA, marine deposits of the Menilite Formation of Outer Carpathians, specimen found in the horizon called "pakiet E" (Jerzmańska and Kotlarczyk 1968: fig. 4), correlated with the calcareous nannoplankton of the NP 23 zone sensu Berggren et al. (1995) (see Kotlarczyk et al. 2006).

Diagnosis: As for the genus.

Measurements (maximum length in mm): skull, from tip of beak to posterior end of braincase, 30.0; beak, from tip to posterior end of narial opening, 11.4; mandible, 21.9; sternum, 15.5; coracoid, ~14.9 (left), 15.2 (right); humerus, 17.1 (left), 17.4 (right); ulna, ~18.8 (left), 18.2 (right); radius, ~16.0 (left), ~15.6 (right); carpometacarpus, ~9.7 (left), ~9.2 (right); phalanx proximalis digiti majoris, 5.5 (left), ~5.1 (right); phalanx distalis digiti majoris, 3.1 (left), ~2.9 (right); pelvis, 12.9; femur, >8.8 (right); tibiotarsus, 30.6 (left), 31.6 (right).

Description and comparison

Skull

The head is seen in lateral view. The straight, moderately long beak generally resembles that in such extant passeriform genera as *Motacilla*, *Turdus* or *Anthus*, and therefore it is also similar to the Eocene *Primozygodactylus* and *Eozygodactylus* (Zygodactylidae) (Mayr 1998; Weidig 2010). It is not clear whether its tip is blunt or pointed because it is still hidden in the matrix. The narial opening is long, measuring more than half the total length of the beak, which markedly differs from the condition observed in many extant taxa with small narial openings (e.g. Coraciiformes, Piciformes). The dorsal and ventral bars of the os nasale are straight; the ventral bar is wider than the dorsal. The relatively thin ramus mandibulae is straight, also in the fragment close to its tip. The fenestra mandibulae cannot be discerned and is therefore either absent or very small. As noticed by Mayr and Manegold (2006a), this fenestra is small or absent in the fossil *Wieslochia weissi* and small in extant Acanthisittidae and most Suboscines but large in Oscines. The caudal end of the ramus mandibulae and the quadratum are too poorly preserved for meaningful comparisons. The border between the os nasale (beak) and the os frontale (braincase) is not clear, but assuming that the narial openings reach almost to that border as in many extant taxa, we may expect that the os ectethmoidale is large, as in *Wieslochia weissi* (Mayr and Manegold 2006a) and many extant Passeriformes. The upper part of the braincase is missing and the lower with a portion of the orbit is poorly preserved.

Fig. 1 *Jamna szybiaki* gen. et sp. nov., holotype, specimen MSMD Av JAM-6 from Jamna Dolna, Poland, early Oligocene (*top*) and interpretative drawing (*bottom*). Left (*L*) and right (*R*) elements are indicated. *al* Phalanx digiti alulae, *dmj* phalanx distalis digiti majoris, *mn* phalanx digiti minoris, *pmj* phalanx proximalis digiti majoris
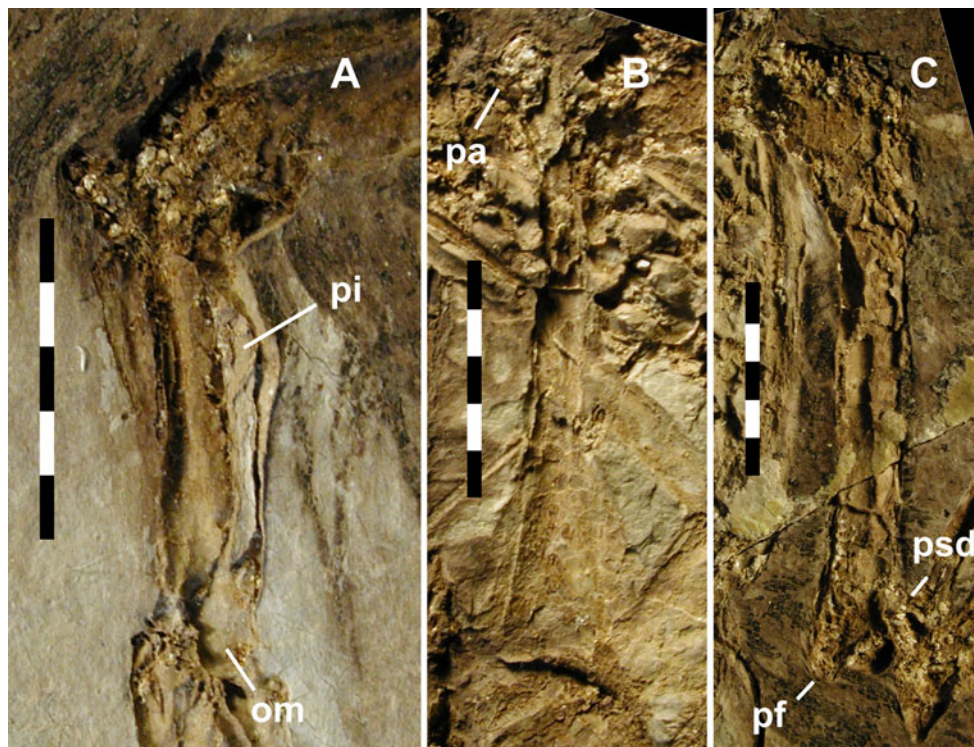
Fig. 2 *Jamna szybiaki* gen. et sp. nov., holotype, specimen MSMD Av JAM-6 from Jamna Dolna, Poland, early Oligocene. **a** Left carpometacarpus; **b** right coracoid; **c** right humerus; *om* os metacarpale minus (distal end), *pa* processus acrocoracoideus, *pf* processus flexorius, *pi* processus intermetacarpalis (visible as a feeble imprint of its ventral surface); *psd* processus supracondylaris dorsalis. *Scale bars* 5 mm

Vertebrae

The vertebrae are poorly preserved and probable not all are visible. At least 15 presacral vertebrae can be counted, of which at least 3 bear ribs. The thoracic vertebrae are not fused to a notarium. As in most extant Passeriformes, there are seven caudal vertebrae, each with recognizable processus transversus and processus dorsalis. The Eocene *Primozygodactylus danielsi* had only five caudal vertebrae (Mayr 1998). The large pygostyle is in the shape of a blade with one edge semi-circular and the other straight.

Coracoid

The coracoid is long and slender as in extant Passeriformes. The right coracoid is somewhat better preserved than the left. From both coracoids, fragments of the extremitas omalis and the sternal end are preserved, whereas most of the shaft is an impression of the ventral side. Unlike most Eupasseres (Oscines and Suboscines) but nevertheless similar to some of them (e.g. Hirundinidae) as well as Acanthisittidae, *Primozygodactylus* (Mayr 1998; Mayr and Zelenkov 2009) and *Zygodactylus* (Mayr 2008), the processus acrocoracoideus (visible in the right bone only) is small and rounded and it is not hooked. Absence of a hooked processus acrocoracoideus, yet more elongated medially, was also observed in *Wieslochia weissi* (Mayr and Manegold 2006a). The processus procoracoideus, cotyla scapularis and facies articularis humeralis are not visible. However, it seems likely that the processus procoracoideus was reduced as in Acanthisittidae and Oscines rather than enlarged as in *Wieslochia weissi* and some extant Suboscines (see Mayr and Manegold 2006a) because otherwise it would have been visible, at least on the right coracoid. 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). The linea intermuscularis ventralis is clearly visible on the right coracoid.

Furcula

The furcula is U-shaped. The scapus claviculae is slender, the extremitas omalis is not visible, and the apophysis furculae seems to form a median projecting knob or blade as in extant Passeriformes.

Scapula

Details of the articular end are not visible. The corpus scapulae is blade-like and almost straight throughout its length; its width does not change with length.

Sternum

The sternum is oriented with the dorsal side up but mainly the imprint of its ventral side is preserved, with the carina sterni penetrating deep into the matrix. Small bone fragments of its cranial end, where it articulates with the coracoids, are preserved. The right side of the sternum is better preserved than the left side. As in Acanthisittidae (Millener 1989; Millener and Worthy 1991), the sternum is relatively short and broad. The processus craniolateralis is pointed and short and, contrary to Piciformes, Acanthisittidae, most Suboscines (Mayr and Manegold 2006a) and *Primozygodactylus* (Mayr 1998; Mayr and Zelenkov 2009), it does not project further anterior than the labrum dorsale. The spina externa is rod-like and not bifurcated. In this respect, it differs from *Wieslochia*, Acanthisittidae and most extant Eupasseres (Oscines and Suboscines) and is similar to most Eurylaimidae, some Cotingidae (Mayr and Manegold 2006a; Millener 1989; Olson 1971; Prum 1993) and to *Primozygodactylus* (Mayr 1998) and *Zygodactylus* (Mayr 2008). As in most extant Passeriformes and the early Oligocene *Wieslochia* (Mayr and Manegold 2006a), 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). As noted by Feduccia and Olson (1982) "the sternum is four-notched in almost all non-passerine land birds that might be closely related to the Passeriformes, e.g., Coliiformes, Piciformes, and most Coraciiformes (…), and the early Eocene family Primobucconidae". The trabecula lateralis widens at its caudal end and it does not project further caudally than the corpus sterni. The caudal edge of the trabecula mediana is moderately wide.

Humerus

The humerus is stout, its shaft almost straight and its proximal end is broad dorso-ventrally. Both the left and the right bones are imprints of the anterior side, with fragments of bone present. The crista deltopectoralis reaches about one-third of the total length of the bone and forms an angular connection with the shaft. Similar to *Primozygodactylus* (Mayr 1998: fig. 25C), Piciformes and Hirundinidae, but contrary to most Passeriformes, it reaches proximally almost as far as the caput humeri, meeting with it almost at right angles. The crista bicipitalis begins proximal to the crista deltopectoralis and forms a wide angle with the shaft. The foramen pneumaticum cannot be discerned which may be due to the fact that the posterior surface of the bone is missing. The distal end is wide; the condylus dorsalis projects dorsally. The exact shape and size of the processus supracondylaris dorsalis cannot be discerned but it is clear that the process is just above the condylus dorsalis, which agrees with the condition in Passeriformes (Manegold 2008) and Zygodactylidae (Mayr 1998, 2008; Weidig 2010). The processus flexorius is prominent and it projects distinctly distally, which is in agreement with extant Passeriformes, the Oligocene *Wieslochia* (Mayr and Manegold 2006a) and the extinct Zygodactylidae (Mayr 1998, 2008).

Ulna

Most of the left ulna is covered with a thin layer of matrix but some details of the proximal end are impressed in the matrix and are visible when looking at an angle rather than directly from above. The outlines of the right ulna are mostly clear but fragmented bone remains obscure the view of the bone surface. The ulna is a little longer than the humerus, which agrees with Zygodactylidae (Mayr 1998; Weidig 2010) and many Passeriformes. As in most Passeriformes, 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. In *Primozygodactylus* and *Zygodactylus*, the olecranon is shorter and stockier (Mayr 1998, 2008). The cotyla ventralis is round and upright, almost parallel to the long axis of the bone, as in *Turdus*. The cotyla dorsalis is not visible. The papillae remigiales caudales cannot be discerned and it seems that they were absent or small as in many Passeriformes and Zygodactylidae (Mayr 1998, 2008; Weidig 2010), but contrary to Piciformes. The distal ulna is too poorly preserved to allow meaningful comparison.

Radius

No closer details of the radius are visible.

Carpometacarpus

Both carpometacarpi are visible in dorsal view but the dorsal surface of the bone is missing. Proximal end of the right carpometacarpus and distal end of the left are partly imprints of the ventral side. The os metacarpale majus is very stout. The processus intermetacarpalis projects caudally slightly behind the os metacarpale minus. Its presence, indicated by the imprint of its ventral surface on the left and right carpometacarpi and by small fragments of bone between the os metacarpale major and 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 not visible, which can be explained by the fact that the dorsal surface of the bone is missing. The distal end of the os metacarpale major is bulging cranially and forms the tuberositas metacarpi. As in Oscines, the distal end of the os metacarpale minus is square, broad and protrudes relatively far distally. In extant Suboscines, *Wieslochia weissi* and in all Oligocene specimens of suboscine 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 only moderately protruding and its cranial portion reaches farther distally than the facies articularis digitalis minor (Mayr and Manegold 2004, 2006a, b; Mourer-Chauviré et al. 1989). The latter condition is also observed in Acanthisittidae, although their 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—the difference in length is larger in *Eozygodactylus* and *Zygodactylus* than in *Primozygodactylus* (Mayr 1998, 2008; Weidig 2010). As in most extant Oscines, the ventral surface of the synostosis metacarpalis distalis bears a fossa (Mourer-Chauviré et al. 1989). Such a distal depression is also present only in a few Suboscines, which is best explained as convergence (Manegold 2008).

Other elements of the wing

Phalanges of the left wing are better preserved, while those of the right wing are covered with a thin layer of matrix and only their general outlines are visible. As in other passerines, the phalanx digiti alulae is short. The phalanx proximalis digiti majoris is intermediate between that in the Oscines and Suboscines in that it only widens a little cranio-caudally toward its distal end. This phalanx widens considerably cranio-caudally in the suboscine-like specimen SMF Av 504 of the early Oligocene of France whereas it is of approximately equal width in Acanthisittidae and Oscines (Mayr and Manegold 2006b). In the Eocene *Primozygodactylus*, it resembles the condition in Suboscines (Mayr 1998: fig. 26). Both articular ends of this phalanx—the proximal and the distal—are straight, without any bigger projections, which agrees with Passeriformes. As in extant Passeriformes, the phalanx distalis digiti majoris is much shorter than the phalanx proximalis (the ratio of their lengths calculated from the better preserved left bones is 0.56), and therefore it differs from the suboscine-like specimen SMF Av 504 of the early Oligocene of France whose both phalanges 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 narrows cranio-caudally toward its distal end.

Pelvis

The pelvis is oriented with the dorsal side up but what is preserved is mainly the imprint of its ventral side with small fragments of bone. It is relatively short and broad. As in extant Tyrannidae (Suboscines), margo cranialis and margo lateralis of the ala preacetabularis ilii meet approximately at right angles, and the margo caudalis of the ala postacetabularis ilii is roughly perpendicular to the long axis of the pelvis. At least two pairs of foramina intertransversaria are discernable in the caudal end of the synsacrum.

Femur

Both femora are poorly preserved and the shaft of the right one is broken near its distal end; they are seen in cranial view. The right bone is articulated to the pelvis, with its distal end penetrating into the matrix and therefore it seems shorter. The proximal end is not visible in any of the femora. In general proportions, the femur is similar to that of extant Passeriformes, particularly *Sturnus vulgaris* (Sturnidae).

Tibiotarsus

As in extant Passeriformes but also extinct Zygodactylidae (Mayr 1998, 2008; Weidig 2010), the tibiotarsus is slender and straight and it is clearly the longest limb element. Also as in Passeriformes, the crista cranialis lateralis (right bone) projects far laterally and is relatively narrow. The medial edge of the proximal tibiotarsus is straight. The crista fibularis reaches far laterally; its distal end is missing. The right fibula is attached to the crista cnemialis lateralis and the crista fibularis; its distal end is missing. The crista cnemialis cranialis (left bone) is long proximo-distally and it joins with the shaft almost at right angles. On the distal end (right bone), the medial edge of the shaft curves slightly medially toward the condylus medialis. As in extant Passeriformes, the condyli medialis and lateralis are of similar size.

Tarsometatarsus

The small fragment of the proximal right tarsometatarsus that is articulated to the tibiotarsus is too poorly preserved to allow meaningful comparisons.

Feathers

Barbs and barbules of flight and tail feathers are visible under higher magnification. Flight feathers overlap with each other because the left wing is only partly stretched and the right wing is folded. Nevertheless, four primaries and five secondaries can be discerned on the left wing. The right wing, which is ca. 56 mm long, allows the recognition of at least four primaries, two secondaries and one tertial. Wing coverts and alula are not preserved. The lengths (in mm) of the visible left wing primaries from left to right are as follows: 44, 47, 46, 45. Left wing secondaries measure 40–43 mm. The two outermost left wing primaries have their tips elongated and rounded, they lack outer and inner emargination, and they are asymmetrical (outer vane is 2 mm wide and inner vane is 5 mm). The tips of the two subsequent left wing primaries show a slanting inner vane (Fig. 3). The above-mentioned tips of primaries are common in most extant taxa. The five secondaries of the left wing have heart-shaped tips (with a small indentation) and their outer vane is slanting. Similar tips of flight feathers are observed in, e.g., extant Skylark *Alauda arvensis*. The single tertial visible on the right wing is relatively wide and has a rounded tip, and therefore differs from such extant taxa with long and pointed tertials as, e.g., *Motacilla* or *Anthus* (Jenni and Winkler 1994; Svensson 1992; own data). Five tail feathers are visible—two central rectrices, two rectrices on the left and one on the right side. As in extant Passeriformes but contrary to an Eocene member of the Zygodactylidae, *Primozygodactylus eunjooae* (Mayr 2009: fig. 16.10d; Mayr and Zelenkov 2009: fig. 1A), all tail feathers seem to have relatively thin and delicate rachises. Also, all tail feathers show rounded tips. The two central rectrices are symmetrical, their width is about 8 mm throughout their length, which is ca. 48 mm—their size is similar to tail feathers of, e.g., the Nuthatch *Sitta europaea*. The adjoining rectrice on the left is a little shorter (42 mm) which indicates that the subsequent rectrices were shorter toward the tail edges and therefore the tail must have been rounded as, e.g., in extant warblers of the genus *Acrocephalus* (Jenni and Winkler 1994; Svensson 1992; own data). The tail of *Jamna szybiaki* differs considerably from that in *P. eunjooae* (Mayr and Zelenkov 2009) in that the central rectrices are only a little longer—in *P. eunjooae* they are four times as long as the outer tail feathers, and in extant Piciformes the outer rectrices are also much shorter (Ginn and Melville 2007). A striking difference also concerns the shape of tail feathers (Fig. 3). In *Jamna szybiaki* and extant Passeriformes, the width of rectrices does not change with their length whereas in *P. eunjooae* rectrices are clearly narrower at the base and wider at the tip. Extant Piciformes are in a way similar to *P.eunjooae* in that their rectrices are narrower at the base,
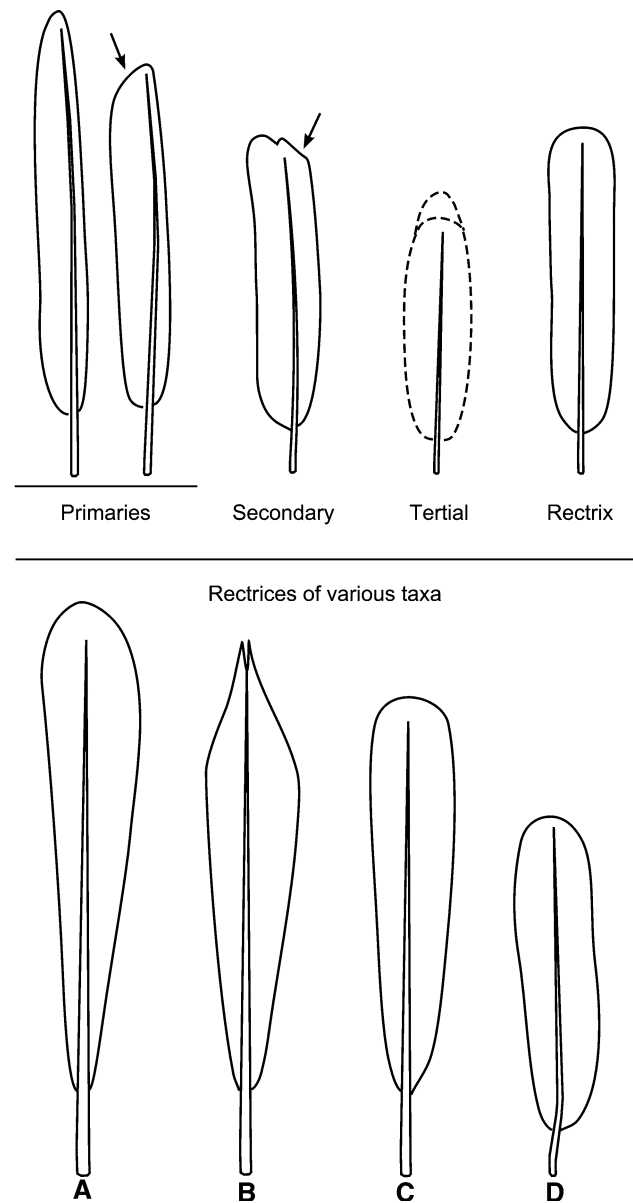

Fig. 3 Flight feathers and a rectrix of *Jamna szybiaki* gen. et sp. nov. in comparison with rectrices of *Primozygodactylus eunjooae* (**a**) and chosen extant taxa: *Dendrocopos/Picus* (**b**), *Jynx torquilla* (**c**), *Sitta europaea* (**d**). *Arrows* indicate slanting inner vane of a primary and outer vane of a secondary of *Jamna szybiaki*

widest at two-thirds length and becoming narrower again toward the end. The exception is the Wryneck *Jynx torquilla* whose rectrices more closely resemble those of *P. eunjooae*. Although the differences were not mentioned in the original description of *P. eunjooae*, they can be observed on the published photographs (Mayr 2009: fig. 16.10d; Mayr and Zelenkov 2009: fig. 1A). The rectrices of *Zygodactylus luberonensis* are likely to be of similar shape to those of *P. eunjooae* but such details are not visible in the photographs (Mayr 2008: fig. 2, 2009: fig. 16.9) and probably neither on the specimen.

Discussion

As shown above, *Jamna szybiaki* can be assigned to Passeriformes. However, its more precise affinities are difficult to determine because there are no univocal features that would support its position within either Oscines or Suboscines. Likewise, we are unable to identify character(s) that are derived for Eupasseres but absent in the fossil, and that would indicate a position of *J. szybiaki* outside the crown group Eupasseres. Therefore, the affinities of *J. szybiaki* within Passeriformes cannot be resolved at the moment. Although *J. szybiaki* is in many aspects similar to the early Oligocene *Weislochia weissi*, it differs from it in, among others, significant features such as the unbifurcated spina externa of the sternum—a character that shows little variation within particular groups of extant Passeriformes. This suggests that the two early Oligocene passerine species—*Weislochia* and *Jamna*—are probably not closely related, and indicates a higher diversity of early Oligocene passerines in Europe.

Jamna szybiaki was a small bird the size of a Dipper *Cinclus cinclus* or a Skylark *Alauda arvensis*. The straight, moderately long, thrush-like beak suggests a frugivorous or insectivorous diet. The short and broad pelvis and sternum must have made a stocky trunk which is typical for birds living on the forest floor rather than in grasslands or reed beds. The shape and size of the flight feathers indicate a rather short and broad wing with a rounded tip, and the tail feathers suggest a relatively short and rounded tail. Such feathering is typical for strongly flying birds that live in shrubs and forests. The long legs suggest that the bird spent much time on the ground, probably hopping or walking when foraging among trees like modern thrushes or wrens (Cramp 1988).

As noticed in previous studies (Manegold 2008; Mayr 2009; Mayr and Manegold 2006a), all passerine remains from the Oligocene represent small and very small taxa, which may indeed reflect their real proportion in the avifauna. Our results confirm the observation by adding another small species to the Oligocene passerines. Unlike isolated passerine bones collected from fissure fillings at Herrlingen in southern Germany (Manegold 2008), whose accumulation may have also been the result of predators' selective hunting, *J. szybiaki* is an articulated specimen found in marine deposits and therefore it is unlikely that it was deposited by a predator. It may have fallen into the water while flying over it, especially if it had been injured which is suggested by the broken right femur. Such a scenario was postulated to explain the abundance of birds in deposits of larger lakes and coastal environments (e.g. Messel or Green River Formation) where relatively many specimens show fractures of their limb bones (Mayr 2000; Mayr et al. 2004).

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