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ORIGINAL ARTICLE

A new passeriform (Aves: Passeriformes) from the early Oligocene of Poland sheds light on the beginnings of Suboscines

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Abstract
The paper describes a complete specimen of a passerine bird from the early Oligocene of Poland, preserved as imprints of bones and feathers on two slabs. *Crosnoornis nargizia* gen. et sp. nov. is just the fifth passerine species described from the Paleogene worldwide and the fourth complete. The features preserved in the distal elements of the wing exclude Acanthisittidae and Oscines and indicate that this bird can be included in Suboscines, making it the second complete representative of this group in the Paleogene. A strong, straight beak indicates that this bird could feed on a variety of foods, including hard seeds, fruit and invertebrates, and, therefore, occupied a different foraging niche than the Oligocene passerines described so far. The wing proportions, a very short tail and relatively long legs indicate that this bird spent most of its time in the forest, close to the ground in dense shrubs or dense tree crowns.

Keywords Fossil birds · Passeriformes · Suboscines · New species · Rupelian · Paleogene

Zusammenfassung
Ein neuer Sperlingsvogel (Aves: Passeriformes) aus dem frühen Oligozän Polens erhellt die Ursprünge der Suboscines
Diese Arbeit beschreibt ein vollständiges Exemplar eines Sperlingsvogels aus dem frühen Oligozän Polens, welches als Abdruck von Knochen und Federn auf zwei Steinplatten erhalten ist. *Crosnoornis nargizia* gen. et sp. nov. ist weltweit erst die fünfte für das Paläogen beschriebene Sperlingsvogelart und erst die vierte vollständig erhaltene. Die im distalen Flügelteil erhaltenen Merkmale schließen die Acanthisittidae und die Oscines aus und sind Indizien dafür, dass dieser Vogel zu den Suboscines gerechnet werden kann, was ihn zum zweiten vollständig erhaltenen Vertreter dieser Gruppe aus dem Paläogen macht. Ein kräftiger gerader Schnabel deutet darauf hin, dass dieser Vogel ein breitgefächertes Nahrungsspektrum nutzen konnte, darunter harte Samen, Früchte und Wirbellose, und daher eine andere Nahrungsnische besetzte als die bislang beschriebenen Sperlingsvögel des Oligozäns. Die Proportionen des Flügels, ein sehr kurzes Steuer und relativ lange Beine sind Anzeichen dafür, dass dieser Vogel die meiste Zeit im Wald verbrachte, entweder in dichtem Gebüsch in Bodennähe oder in dichten Baumkronen.

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Introduction

During the Oligocene, large parts of Central and Eastern Europe were covered by the Paratethys Ocean, which was the northern branch of the Tethys (Schulz et al. 2005). Many fossils have been preserved in these marine deposits thanks to pelagic sedimentation and anoxic conditions (Bieńkowska-Wasiluk 2010; Kotlarczyk et al. 2006). Currently, in the northeastern Czech Republic, southeastern Poland and northern Slovakia, there are the Menilite beds of the Carpathian flysch zone that are extremely rich in Oligocene fish fossils; animals other than fish, including birds, are found extremely rarely. They usually preserve as incomplete but articulated imprints on slabs.

Of the approximately ten thousand species of birds that live today, more than half belong to the order Passeriformes. However, little is known about the early history of this currently most species-rich group of birds because its Paleogene fossil record is still poor. The oldest remains of possible passerine birds come from the early Eocene of Australia (Boles 1995, 1997). However, the oldest specimens, which can without doubt be identified as Passerifomres, are known from the early Oligocene of Europe. So far, four species have been described from the Paleogene: *Wieslochia weissi* from Germany, and *Jamna szybiaki*, *Resoviaornis jamrozi* and *Winnicavis gorskii* from Poland but none of them could be attributed to either Oscines or Suboscines (Bochenski et al. 2011, 2013a, 2018; Mayr and Manegold 2004, 2006a). The first three mentioned taxa (*Wieslochia, Jamna* and *Resoviaornis*) were described on the basis of almost complete specimens, while *Winnicavis* is known from incomplete wings and the shoulder girdle. In addition to them, a nearly complete but unnamed specimen of tyrannid from the early Oligocene of Luberon, France (NT-LBR-014) has recently been described (Riamon et al. 2020). The discovery of such an old suboscine bird from Europe does not come unexpectedly, because Mayr and Manegold (2006b) already tentatively identified a suboscine-like distal part of a wing from the early Oligocene of France. From the Late Oligocene of Germany, more than two dozen isolated wing bones are known to indicate the coexistence of oscines and suboscines in Europe at that time (Manegold 2008). In addition, several isolated bones, including one belonging to the suboscines, were also found in the Late Oligocene of France (Mourer-Chauviré 2006; Mourer-Chauviré et al. 1989, 2004). Specimens of associated leg bones on plates, each representing one individual, are known from the early and late Oligocene of Poland (Bochenski et al. 2014a, b). In fact, as shown above, many of the few remains of European passerine birds have been found in the Outer Carpathians of Poland.

There is currently a heated discussion about the origin of Passeriformes and the relationships among them. Some researchers believe that this group has already emerged even in the Cretaceous (Ericson et al. 2002); others are of the opinion that this happened in the Cenozoic (Claramunt and Cracraft 2015; Mayr 2013). There are so few complete specimens of Oligocene passerines that each subsequent one is extremely useful for more reliable phylogenetic studies.

This paper describes a complete suboscine bird from the early Oligocene of Poland, which is also one of the oldest passerine birds in the world described so far. As evidenced by its sturdy beak, it certainly occupied a different ecological niche than the passerines described so far.

Materials and methods

The specimen consists of two slabs, on which imprints with remains of fossilized bones and feathers are preserved. As with other Oligocene specimens from Poland, bone outlines are clearly visible, while most details are unrecognizable in a mixture of bone imprints and fossilized bone tissue.

Osteological terminology is according to Baumel and Witmer (1993). The measurements are in millimeters and represent the largest length of individual skeleton elements. The fossil, bearing the catalog number of the Muzeum Skamieniałości Fliszu Karpackiego, Krosno, Poland (MSFK), was compared with modern specimens from the collection of the Institute of Systematics and Evolution of Animals, Polish Academy of Sciences (ISEA), and with published data on extant Passeriformes (Acanthisittidae, Suboscines and Oscines), as well as extinct Zygodactylidae, which in osteological terms are very similar to passerines (Mayr 2009).

It is known that the proportions of the individual bones forming the wing and the leg are related to the functioning of the bird in its environment. Therefore, the bones of the fossil specimen were compared with selected extant Suboscines species from the collection of the ISEA, the Senckenberg Research Institute, Frankfurt, Germany (SMF); the Museum of Natural Science, Louisiana State University, Baton Rouge, Louisiana, USA (LSUMZ); and Borissiak Paleontological Institute, RAS, Moscow, Russia (PIN). Separate analyses were conducted for wings and legs. For individual species, the proportion of the length of individual bones in the wing (humerus, ulna and carpometacarpus) and leg (femur, tibiotarsus and tarsometatarsus) was calculated by dividing their length by the sum of the lengths of all three bones making up the wing or leg. To assess the similarity, a cluster analysis was performed using the hierarchical agglomeration method using the Euclidean distance and Ward linkages (TIBCO Software Inc. 2020).

Systematic paleontology

Aves Linnaeus 1758

Passeriformes Linnaeus 1758

Suboscines (sensu Ericson et al. 2003)

Family indeterminate

Genus *Crosnoornis* gen.nov.

Type species *Crosnoornis nargizia* sp. nov.

Etymology: The genus name Crosno is the Latin equivalent of the Polish Krosno, a town located nearby the type locality, Rudawka Rymanowska, added to the Ancient Greek ὄρνις (ornis) meaning "bird".

Remarks: The specimen shows derived features typical of Passeriformes, to which it is also morphologically similar. In particular, the sternum bears (1) bifurcated spina externa and (2) a single pair of incisions in the caudal end; the humerus has (3) a prominent processus flexorius that protrudes distally; the ulna bears (4) a prominent olecranon separated from the shaft by a shallow saddle; (5) the radius has a short proximo-distally facies articularis ulnaris; the carpometacarpus bears (6) a long and narrow spatium intermetacarpale, (7) processus intermetacarpalis, and os metacarpale minus with (8) a narrow distal end that (9) protrudes a little farther distally than os metacarpale majus; phalanx proximalis digiti majoris (10) short, broad and cleaver-shaped, and (11) with a distally directed protrusion in the posterior part of its distal edge; the tarsometatarsus bears (12) a hypotarsus which is short proximo-distally, (13) a prominent crista plantaris lateralis that runs along the shaft, and (14) trochleae of the second, third and fourth toes arranged in a line. Also, the proportions of individual bones are typical for most Passeriformes: (15) the coracoid, tarsometatarsus and tibiotarsus are long and slender, the latter being the longest skeletal element; (16) the ulna is longer than the humerus; and (17) the pelvis is of a trapezoidal shape. None of these features is exclusive to Passeriformes, but only representatives of this group of birds show a combination of all these features. Features related to distal wing elements (# 8–11) generally exclude Oscines but are typical of Suboscines.

Differential diagnosis

The specimen differs from:

All extant Oscines in: carpometacarpus with narrow distal end of os metacarpale minus that protrudes slightly more distally than os metacarpale majus; phalanx proximalis digiti majoris short, broad and cleaver-shaped, and with a distally directed protrusion in the posterior part of its distal edge; phalanx distalis digiti majoris only slight shorter than phalanx proximalis.

The early Oligocene *Wieslochia weissi* in: beak length roughly equal to the length of the braincase (in *Wieslochia* it is clearly shorter); humerus with dorso-ventrally broad proximal epiphysis (in *Wieslochia* relatively narrower); the brachial index (humerus length/ulna length) larger (0.84 vs 0.74 in *Wieslochia*).

The early Oligocene specimen NT-LBR-014 from Luberon, France in: the smaller size of all skeletal elements, especially ulna and carpometacarpus, which are more than twenty percent smaller; mandibula with no obvious gonys; coracoid with processus acrocoracoideus directed obliquely upwards (directed more medially in NT-LBR-014); humerus with a well-developed crista deltopectoralis (crista reduced in NT-LBR-014); the brachial index (humerus length/ulna length) larger (0.84 vs 0.77 in NT-LBR-014).

The early Oligocene *Jamna szybiaki* in: sturdy beak; sternum with elongated and bifurcated spina externa, and processus craniolateralis protruding further anterior than labrum dorsale; carpometacarpus with distal end of os metacarpale minus narrow and protruding only slightly further distally than os metacarpale majus; phalanx proximalis digiti majoris relatively short, broad and cleaver-shaped, and bearing a distally directed protrusion in its posterior part; phalanx distalis digiti majoris only slightly shorter that the phalanx proximalis.

The early Oligocene *Resoviaornis jamrozi* in: sturdy beak; thoracic vertebrae not fused to a notarium; carpometacarpus with distal end of os metacarpale minus narrow and protruding only slightly further distally than os metacarpale majus; phalanx proximalis digiti majoris relatively short, broad and cleaver-shaped, and bearing a distally directed protrusion in its posterior part; phalanx distalis digiti majoris only slightly shorter that the phalanx proximalis.

The early Oligocene *Winnicavis gorskii* in: the brachial index (humerus length/ulna length) larger (0.84 vs 0.79 in *Winnicavis*); phalanx distalis digiti majoris only slightly shorter than the phalanx proximalis (phalanx noticeably shorter in *Winnicavis*).

The extinct passerine-like family Zygodactylidae in: sternum with elongated and bifurcated spina externa, and only one pair of incisions in the caudal margin; coracoid with small and rounded processus lateralis; ulna with prominent olecranon that projects far proximally and tapers; phalanx digiti alulae without ungual phalanx; foot with anisodactyl arrangement of toes, with three digits directed forward and the hallux directed backward.

Crosnoornis nargizia gen. et sp. nov.

Etymology

The species is named after Nargiz Salwa, the wife of the finder and co-author of this paper, Grzegorz Salwa.

Holotype

MSFK RR 01/2013a + b (Figs. 1, 2, S1–S7), complete articulated skeleton preserved on two slabs, deposited at the Institute of Systematics and Evolution of Animals, PAS, Kraków, Poland.

Type locality and horizon

Rudawka Rymanowska, exposure 01 (i.e., RU 01 sensu Bieńkowska 2004), the Wisłok River valley, ca. 20 km south-east of Krosno, Podkarpackie Voivodeship, SE Poland. Rupelian, Oligocene, ca. 32–30 MYA, Tylawa Limestones horizon, correlated with the calcareous nannoplankton of the NP 23 zone (Bieńkowska-Wasiluk 2010).

Diagnosis As for the genus.

Measurements (maximum length in mm) taken from the main slab (A) or the counterslab (B): braincase, 19.5 (A); rostrum, from naso-frontal hinge to tip, 16.3 (A); coracoid, 13.9 (A, left), 14.1 (A, right); humerus, 16.1 (A, left); ulna, 19.2 (A, left), 19.4 (B, right); radius, 18.1 (A, right); carpometacarpus, 9.7 (A, left), 9.7 (A, right); phalanx digiti alulae, 3.1 (A, right); phalanx proximalis digiti majoris, 5.1 (A, left), 5.2 (A, right); phalanx distalis digiti majoris, 4.1 (A, left), 4.0 (A, right); phalanx digiti minoris, 2.5 (A, left), 2.8 (A, right); femur, 17.6 (A, left), 17.6 (A, right); tibiotarsus, 26.4 (A, left); tarsometatarsus, 19.0 (B, left), 20.2 (A, right); os metatarsale I, 4.5 (A, right); hallux: proximal phalanx, 7.6 (A, right); hallux: claw, 4.4 (A, right). For a comparison with measurements of other Oligocene passerines, see Table S1.

Description and comparison The specimen is preserved on two slabs, each of which was fragmented at the time of finding, but the pieces matched each other and allowed for precise gluing of the whole slabs. All skeletal elements are visible but their preservation is not perfect. Most bones are in fact cracked in half along their long axes, which means that on each slab mostly the inside of the bone is visible, and only seldom its outer surface.

The head is visible in lateral view (Figs. 1, S1–S4). The beak is massive, straight, not hooked at the end, and its length is similar to the length of the braincase, which is similar to the beaks of some extant Suboscines (e.g. *Myrmoborus myotherinus*, *Myrmeciza squamosa*, *Philydor rufosuperciliatus*). The beaks of the Early Oligocene *Resoviaornis jamrozi* and *Jamna szybiaki* were slender (Bochenski et al. 2011, 2013a); the beak of *Wieslochia weissi* was clearly shorter than the braincase (Table S1; Mayr and Manegold 2006a). The narial openings are long. The mandible does not bear the distinct gonys that is seen in NT-LBR-014 from Luberon (Riamon et al. 2020). As in extant Passeriformes, the quadratum bears a long processus orbitalis, which slightly widens at the end. The remains of the inner ear—a transverse section of the apex cochlea and fragments of the canales semicirculares ossei—are visible behind the eye socket. Due to the flattening of the skull, no meaningful details can be distinguished for further comparisons.

The details of the vertebral column and the boundaries between individual vertebrae are not clearly visible (Figs. 1, 2b, S1, S3, S7). There are at least 16 pre-sacral vertebrae. Unlike *Resoviaornis jamrozi*, but similarly to *Jamna szybiaki*, the thoracic vertebrae are not fused to a notarium. Extant passerines show large variation in the construction of the notarium: from fully ossified notarium to no fused vertebrae (James 2009); the number of vertebrae in the notarium is also variable (Storer 1982). The caudal vertebrae and the pygostyle are not visible.

Tracheal and possibly bronchial rings are visible on both slabs (Figs. 2b, S1, S3). However, neither fused rings that would form the “drum” nor a pessulus, i.e. the cartilaginous and/or bone elements making up the syrinx (Ames 1971), can be distinguished, so either they were absent or they did not preserve. It is noteworthy that *Crosnoornis nargizia* is the second Oligocene passerine with preserved tracheal rings. Isolated ossified rings were also recorded in the early Oligocene passerine *Wieslochia weissi* from Frauenweiler, Germany (Mayr and Manegold 2004) and on a number of non-passeriform birds (e.g. Clarke et al. 2016; Mayr 2005; Mayr and Mourer-Chauviré 2000).

Both coracoids are visible in dorsal view on slab A and in ventral view on slab B (Figs. 1, 2b, S6). As in extant passerines, the coracoid is long and slender, and the omal section from the facies articularis humeralis to the processus acrocoracoideus is only about a quarter of the total length of the coracoid. The processus acrocoracoideus is well pronounced and developed obliquely upwards but its tip is rounded, not hooked like in most extant passeriforms. Oligocene passerines were varied in this respect: in *Resoviaornis jamrozi* the processus was hooked, while in *Wieslochia weissi*, *Jamna szybiaki* and *Winnicavis gorskii* the processus was rounded (Bochenski et al. 2011, 2013a, 2018; Mayr and Manegold 2006a); in NT-LBR-014 it was

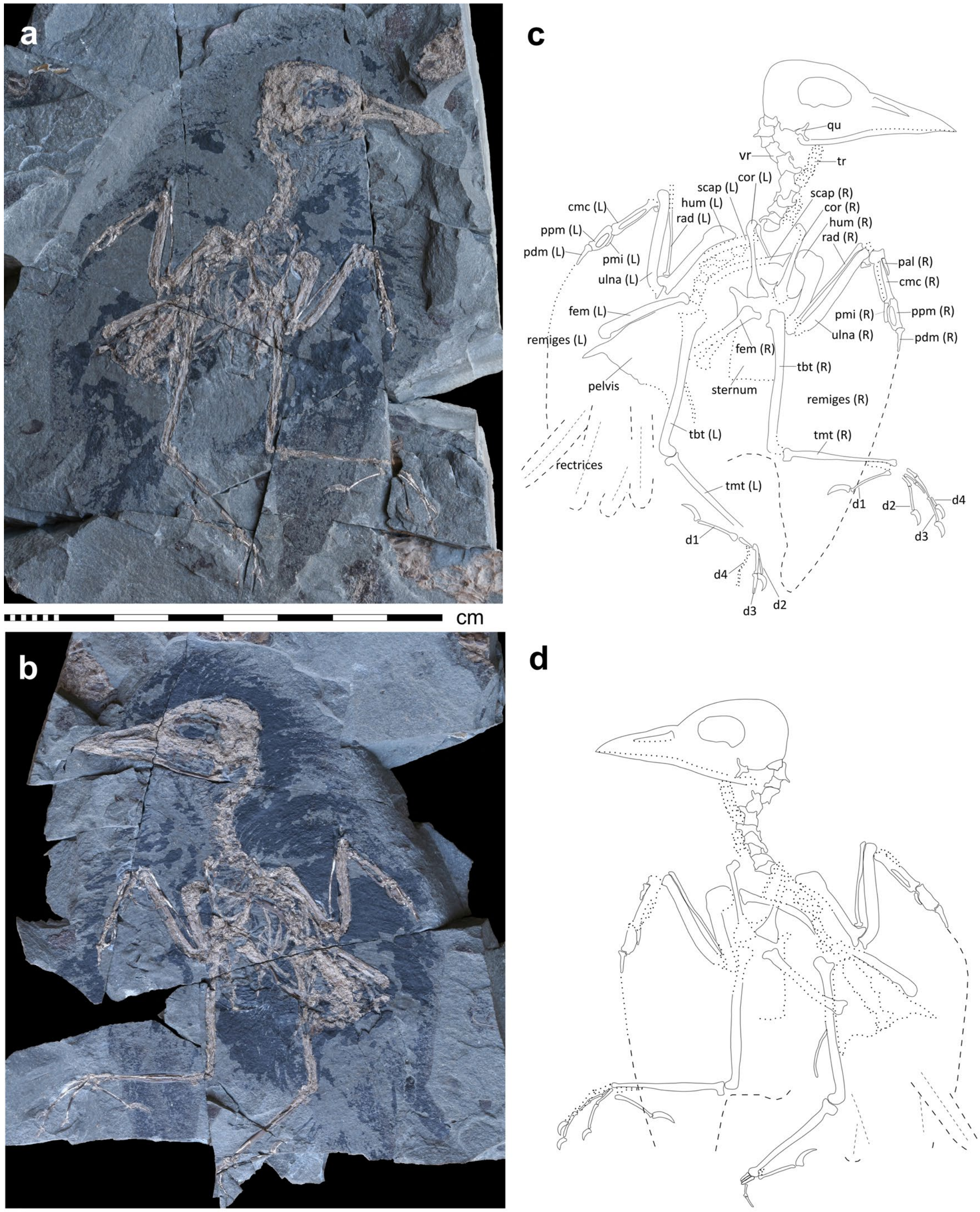

Fig. 1 *Crosnoornis nargizia* gen. et sp. nov., holotype, specimen MSFK RR 01/2013a + b from Rudawka Rymanowska, exposure 01, Poland, early Oligocene *(left)* and interpretative drawings *(right)* with only the main skeletal elements indicated. **a** slab A; **b** slab B. *Left* (*L*) and *right* (*R*) elements are indicated. Abbreviations: *cmc* carpometacarpus, *cor* coracoid, *d1-d4* digit 1–4, *fem* femur, *hum* humerus, *pal* phalanx digiti alulae, *pdm* phalanx distalis digiti majoris, *pmi* phalanx digiti minoris, *ppm* phalanx proximalis digiti majoris, *qu* quadratum, *rad* radius, *scap* scapula, *tbt* tibiotarsus, *tmt* tarsometatarsus, *tr* tracheal rings, *vr* vertebrae

also rounded but developed more medially than upwards (Riamon et al. 2020: Fig. 4). The place where the processus procoracoideus should be located is obscured by fragments of other bones lying beneath and/or on the coracoids. Since it cannot be clearly seen, one can assume that this processus was reduced, as in *Resoviaornis jamrozi*, extant Acanthisittidae and Oscines, and not enlarged, as in *Wieslochia weissi*, *Winnicavis gorskii,* NT-LBR-014 from Luberon,

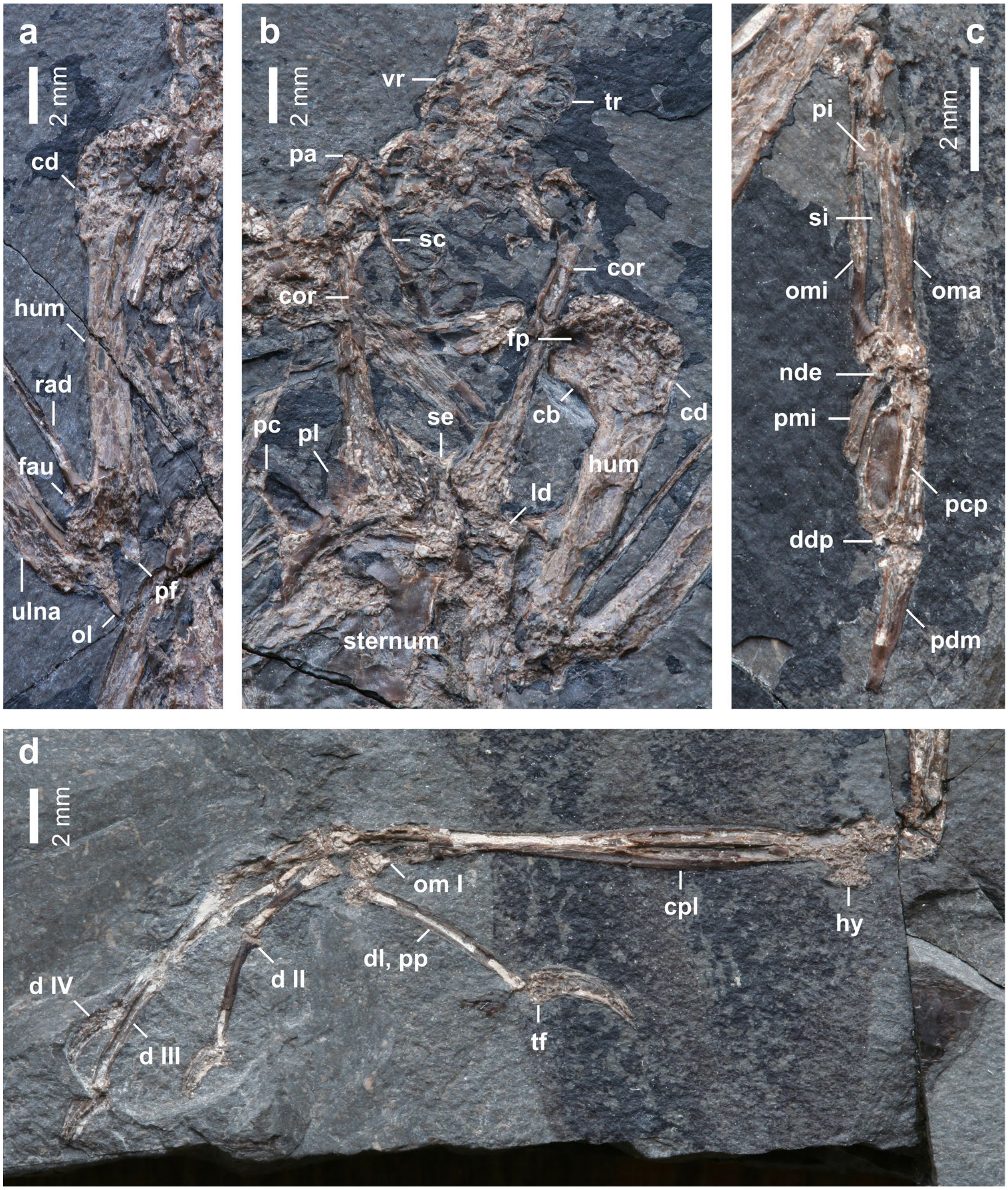

Fig. 2 *Crosnoornis nargizia* gen. et sp. nov., holotype, specimen MSFK RR 01/2013a + b from Rudawka Rymanowska, exposure 01, Poland, early Oligocene. **a** left humerus in caudal view, with proximal ulna and radius, slab A; **b** sternum and coracoids in dorsal view, and right humerus in caudal view, slab A; **c** distal end of left wing, slab B; **d** right tarsometatarsus and pedal digits, slab B; *cb* crista bicipitalis, *cd* crista deltopectoralis, *cpl* crista plantaris lateralis, *ddp* distally directed protrusion (of phalanx proximalis digiti majoris), *d I, pp* digit I, proximal phalanx; *d II* digit II, *d III* digit III, *d IV* digit IV, *fau* facies articularis ulnaris, *fp* fossa pneumotricipitalis, *hum* humerus, *hy* hypotarsus, *ld* labrum dorsale, *nde* narrow distal end (of os metacarpale minus), *ol* olecranon, *oma* os metacarpale majus, *omi* os metacarpale minus, *om I* os metatarsale I, *pa* processus acrocoracoideus, *pc* processus craniolateralis, *pcp* pila cranialis phalangis, *pdm* phalanx distalis digiti majoris, *pf* processus flexorius, *pi* processus intermetacarpalis, *pl* processus lateralis, *pmi* phalanx digiti minoris, *rad* radius, *sc* scapus claviculae, *se* spina externa, *si* spatium intermetacarpale, *tf* tuberculum flexorium, *tr* tracheal rings, *vr* vertebrae

and some extant Suboscines (see Bochenski et al. 2011, 2013a, 2018; Mayr and Manegold 2004, 2006a; Riamon et al. 2020). As in extant passerines, the processus lateralis (sternal end) is small and rounded, not extended laterally as in *Primozygodactylus* (Mayr 1998; Mayr and Zelenkov 2009).

The articular part of the scapula is too poorly preserved for meaningful comparisons. As in passerines, the scapula is long, straight, about the same width over the entire length of the corpus scapulae, and only bends at the end (Figs. 1, S7).

The furcula has not been preserved well; only a fragment of the scapus claviculae can be seen (Fig. 2b), neither extremitas omalis nor apophysis furculae are visible.

The sternum is visible in dorsal view on slab A and in ventral view on slab B (Figs. 1, 2b, S6). As in most extant Passeriformes (Oscines and Suboscines) and the early Oligocene *Wieslochia* and *Resoviaornis*, the spina externa is elongated and bifurcated (best seen on slab A) (Bochenski et al. 2013a; Mayr and Manegold 2004, 2006a). In *Jamna* as well as *Primozygodactylus* and *Zygodactylus* the spina externa is rod-like, not bifurcated (Bochenski et al. 2011; Mayr 1998, 2008, respectively). The processus craniolateralis is directed anterolateral at an angle of about 45 degrees (best seen on slab A), and as in *Wieslochia* and *Resoviaornis* but contrary to *Jamna*, this processus protrudes anterior further than the labrum dorsale (Bochenski et al. 2011, 2013a; Mayr and Manegold 2006a). As in most extant Passeriformes and Oligocene *Wieslochia* and *Jamna*, the trabecula mediana is wide, and margo caudalis is perpendicular to the long axis of the sternum. The trabecula lateralis widens in its caudal part and protrudes no more than the trabecula mediana. There is only one pair of incisions (incisurae laterales) in the caudal margin of the sternum which agrees with the condition in the Oligocene *Wieslochia*, *Jamna* and *Resoviaornis* as well as with most extant passerines (Mayr and Manegold 2004, 2006a; Bochenski et al. 2011, 2013a). Both Zygodactylidae and almost all other non-passerine land birds closely related to Passeriformes, including Coliiformes, Piciformes and most Coraciiformes, have a four-notched sternum (Feduccia and Olson 1982; Mayr 1998; Weidig 2010).

Both humeri are visible in caudal view on slab A, and in cranial view on slab B (Figs. 1, 2a,b, S6, S7). As in the Oligocene *Jamna*, *Resoviaornis* and *Winnicavis*, but unlike *Wieslochia* and extant Passeriformes the humerus is very stout, and the proximal epiphysis is broad dorso-ventrally (Bochenski et al. 2011, 2013a, 2018; Mayr and Manegold 2004, 2006a). The crista deltopectoralis accounts for slightly less than a third of the total length of the humerus and extends distally as far as the crista bicipitalis. Both cristae reach equally far distally in *Resoviaornis* and *Winnicavis*, while in *Jamna* the crista bicipitalis begins proximal to the crista deltopectoralis; in NT-LBR-014 from Luberon, the crista deltopectoralis is strongly reduced (Riamon et al. 2020). As in all extant Suboscines, there is a single fossa pneumotricipitalis (Figs. 2b, S6) whereas many extant Oscines bear a second fossa (Bock 1962). Similar to the Oligocene *Wieslochia*, *Jamna* and *Resoviaornis*, as well as extant Passeriformes the processus flexorius (best seen on slab A) is prominent and protrudes significantly distally (Fig. 2a). The processus supracondylaris dorsalis, a characteristic feature of extant Passeriformes, is not visible, possibly because the wing bones are in articulation.

Both ulnae are visible in dorsal view on slab A, and in ventral view on slab B (Figs. 1, 2a, S7). As in all Oligocene passerines described so far (*Wieslochia*, *Jamna*, *Resoviaornis* and *Winnicavis*) and many extant Passeriformes, the prominent olecranon projects far proximally, tapers, and the bone bears a distinct saddle between the olecranon and the shaft on its posterior margin (the last character is not visible in *Wieslochia*) (Bochenski et al. 2011, 2013a, 2018; Mayr and Manegold 2004, 2006a). The olecranon in *Primozygodactylus* and *Zygodactylus* is shorter and stockier (Mayr 1998, 2008). As in many Passeriformes, the papillae remigiales caudales are small or absent.

The right radius is in articulation with the wing bones, while the left one is slightly shifted relative to ulna and humerus. As in extant Passeriformes, the facies articularis ulnaris is short proximo-distally (Figs. 2a, S7).

Left carpometacarpus is seen in dorsal view on slab A, and in ventral view on slab B (Figs. 1, 2c); the right bone is more damaged. As in all Oligocene passerines described so far (NT-LBR-014 from Luberon, *Wieslochia*, *Jamna*, *Resoviaornis* and *Winnicavis*) and extant Passeriformes, the carpometacarpus is narrow and straight, and as a result of this the spatium intermetacarpale is also long and narrow; in extant Coliiformes, the os metacarpale minus is bowed caudally. The processus intermetacarpalis reaches the os metacarpale minus (Fig. 2c), which is a derived feature of Passeriformes also present in all Oligocene representatives (NT-LBR-014 from Luberon, *Wieslochia*, *Jamna*, *Resoviaornis* and *Winnicavis*). The processus dentiformis is either missing or has not been preserved. As in extant Suboscines, the distal end of the os metacarpale minus is narrow and protrudes slightly further distally than the os metacarpale majus (Figs. 2c, 3); in extant Acanthisittidae and Oscines, the distal end is broad and protrudes much more distally (Mayr and Manegold 2006a). Oligocene passerines were varied in this respect: NT-LBR-014 from Luberon, *Wieslochia*, *Winnicavis* and four unassociated carpometacarpi (SMF Av 509, SMF Av 510; SMNS 59466/1, SMNS 59466/2) from Herrlingen in Germany with their os metacarpale minus of the Suboscines-type are similar to *Crosnoornis nargizia*, while *Jamna*, *Resoviaornis* and six other isolated carpometacarpi from Herrlingen resemble extant Oscines (Bochenski et al. 2011, 2013a, 2018; Manegold 2008; Mayr and Manegold 2004, 2006a; Riamon et al. 2020).

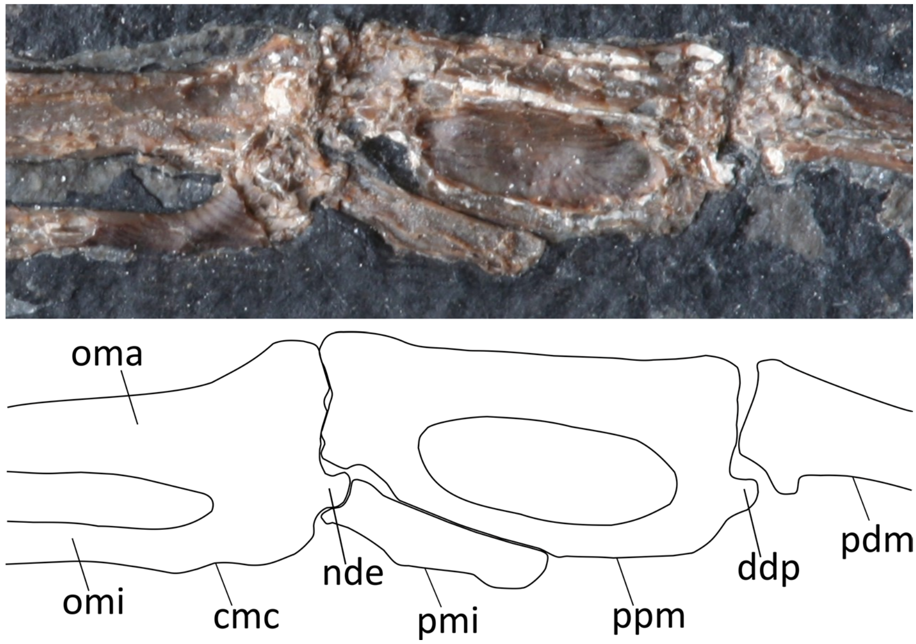

Fig. 3 *Crosnoornis nargizia* gen. et sp. nov., holotype, specimen MSFK RR 01/2013a + b from Rudawka Rymanowska, exposure 01, Poland, early Oligocene *(top)* and an interpretative drawing *(bottom)*. Distal part of left wing, slab B; *cmc* carpometacarpus, *ddp* distally directed protrusion (of phalanx proximalis digiti majoris), *nde* narrow distal end (of os metacarpale minus), *oma* os metacarpale majus, *omi* os metacarpale minus, *pdm* phalanx distalis digiti majoris, *pmi* phalanx digiti minoris, *ppm* phalanx proximalis digiti majoris

As in *Jamna*, *Resoviaornis*, extant Passeriformes and in fact, most other extant birds (Stephan 1992), the phalanx digiti alulae does not bear an ungual phalanx (Fig. S5), which is present in the extinct Zygodactylidae (Mayr 2008). The phalanx proximalis digiti majoris is relatively short, broad and cleaver-shaped (Fig. 2c), and therefore resembles the phalanx of extant Suboscines, an early Oligocene Suboscine specimen NT-LBR-014 from Luberon (Riamon et al. 2020), *Winnicavis gorski* from the Oligocene of Poland (Bochenski et al. 2018), and an early Oligocene suboscine-like specimen SMF Av 504 from southern France (Mayr and Manegold 2006b); in extant Oscines, Acanthisittidae and Oligocene *Resoviaornis*, the phalanx is long and narrow (Bochenski et al. 2011) whereas in *Jamna* it is intermediate (Bochenski et al. 2011). The pila cranialis phalangis is stout and protrudes above the bone plane, as in extant Passeriformes (Oscines and Suboscines). The distal edge of this phalanx is not straight (perpendicular to the long axis of the bone) as in *Jamna*, *Resoviaornis* and extant Oscines, but bears a distally directed protrusion in the posterior part (Figs. 2c, 3, S5), as in NT-LBR-014 from Luberon and extant Suboscines. Similar to Suboscines and suboscine-like SMF Av 504, but unlike extant Oscines, *Jamna, Resoviaornis* and *Winnicavis*, the phalanx distalis digiti majoris is only slightly shorter than the phalanx proximalis.

The pelvis is seen in dorsal view on slab A, and in ventral view on slab B (Figs. 1, S7). As in many passerines, the pelvis is of a trapezoidal shape, and the caudal width is approximately equal to the total length of the synsacrum. The scapus pubis reaches far beyond the caudal edge of the pelvis; its bending can be natural or the result of preservation. Also, the processus terminalis ischii extends beyond the caudal end of the synsacrum.

Both femora are too poorly preserved for meaningful comparisons (Figs. 1, S7). Only the right femur is connected to the pelvis; the left femur is disarticulated from both the pelvis and the tibiotarsus.

As in extant Passeriformes, the tibiotarsus is thin and is by far the longest bone (Figs. 1, S7). Both left and right tibiotarsus are disarticulated from the femora but they are still in articulation with the tarsometatarsi.

Left tarsometatarsus is visible in medial view on slab A, and in lateral view on slab B, while right tarsometatarsus is visible in lateral view on slab A, and in medial view on slab B (Figs. 1, 2d). As in extant Passeriformes, the tarsometatarsus is long and thin, the hypotarsus is relatively short proximo-distally, and the shaft bears a prominent crista plantaris lateralis. One of the four Oligocene specimens (ZPALWr A/4004) with preserved tarsometatarsi is clearly larger; tarsometatarsi of the other three specimens (*Wieslochia weissi*, NT-LBR-014 and ZPALWr A/4005) are of similar length (Table S1; Bochenski et al. 2014a, b; Mayr and Manegold 2006b; Riamon et al. 2020). Although both tarsometatarsi are visible only from the side, it can be inferred from the arrangement of the toes that the trochleae metatarsorum II, III and IV reach approximately equally far distally and are arranged in one plane dorso-ventrally. This arrangement of trochleae is very characteristic for all extant Passeriformes as well as the Oligocene specimens from Przysietnica and Hłudno (Bochenski et al. 2014a, b), Luberon (Riamon et al. 2020), and also for *Wieslochia weissi* although its trochlea metatarsi II was slightly plantarly deflected (Mayr and Manegold 2006a).

As in all extant Passeriformes and also both Oligocene specimens from Poland with preserved feet (ZPALWr A/4004 and ZPALWr A/4005; Bochenski et al. 2014a,b), the foot has an anisodactyl arrangement of toes, with three digit directed forward and the hallux directed backward (Fig. 2d). The os metatarsale I is long; its length is about half the length of the proximal phalanx of the hallux, which is also greatly elongated as in extant Passeriformes and three Oligocene specimens (*Wieslochia*, ZPALWr A/4004 and ZPALWr A/4005; Bochenski et al. 2014a, b; Mayr and Manegold 2006a). Digit III is the longest; digits II and IV are of similar length. Ungual phalanges (claws) of all digits including the hallux are large, show only little curvature and their tubercula flexoria are weakly developed. Although the length of the proximal phalanx and claw of the hallux are similar to those of two unnamed specimens from Poland (ZPALWr A/4004 and ZPALWr A/4005), these specimens differ significantly from *Crosnoornis nargizia*. The tibiotarsus and tarsometatarsus of ZPALWr A/4004 are much longer, and all foot bones, including the claws and phalanges of ZPALWr A/4005, are much thicker than those of *Crosnoornis* (Table S1; Bochenski et al. 2014a, b).

As in all Oligocene passerines described so far and many extant Passeriformes, the ulna is a little longer than the humerus and the brachial index (humerus length/ulna length) is 0.84. The brachial index was smaller in *Wieslochia* (0.74), *Resoviaornis* (0.74), NT-LBR-014 from Luberon (0.77) and *Winnicavis* (0.79), and larger in *Jamna* (0.96) (Bochenski et al. 2011, 2013a, 2018; Mayr and Manegold 2004, 2006a; Riamon et al. 2020). A characteristic feature of *Crosnoornis nargizia* is the relatively short carpometacarpus and tibiotarsus. Among the extant Suboscines examined, the proportions of the wing bones of *Crosnoornis nargizia* are most similar to those of *Pitta brachyura* and *Platyrinchus saturatus*, and the proportions of the leg bones are most similar to those of *Pipra nattereri*, *Manacus manacus* and *Mionectes olegineus* (Table S2, Fig. S8).

The contour feathers of the body, neck and head are visible. The entire right wing and a partial outline of the left wing are visible. The right wing is positioned next to the bird's body in a similar position as the wing when measuring on live birds (Svensson 1992). The length of the folded wing is about 62 mm. The longest primary is about 50 mm and the shortest one is about 43 mm. The length of secondaries is about 39 mm for the longest and 25 mm for the shortest. The individual flight feathers are not visible, but on the basis of the visible outline of the wing, it seems that it is rounded. Fragments of five rectrices are also visible. Since only the tips of the rectrices are visible, their length cannot be precisely measured, it can only be estimated at about 25–30 mm. The width of the rectrices is about 4–5 mm; their tips are rounded. In this place, the structure of feathers is visible under a microscope.

Discussion

The relatively massive and straight beak of *Crosnoornis nargizia* indicates that it may have been an opportunistic feeder taking such foods as hard seeds, fruit and invertebrates. In this respect, it differed from other Oligocene passerines, especially from *Jamna szybiaki* and *Resoviaornis jamrozi*, whose delicate beaks indicate omnivorous species that feed on insects and/or fruits (Bochenski et al. 2011, 2013a). *Wieslochia weissi* may have had more similar food, with its short but quite robust beak (Mayr and Manegold 2006a). Thus, current evidence indicates that *Crosnoornis nargizia* occupied a different feeding niche than the other Oligocene passeriforms described so far.

The three extant species with the leg bone proportions closest to *Crosnoornis nargizia* (*Pipra nattereri*, *Manacus manacus* and *Mionectes olegineus*) (Table S2, Fig. S8) move between dense shrubs or tree crowns "from branch to branch" and they are definitely different from birds, for example, of the genus *Pitta* or *Grallaria*, which lead mainly terrestrial life (Lambert and Woodcock 1996). The two extant species whose wing bone proportions are similar to those of *Crosnoornis nargizia* differ somewhat in terms of their migratory behavior. *Pitta brachyura* is a migratory species, and the location of its breeding and wintering grounds indicates that some birds migrate long distances, and some belong to short-distance migrants. In contrast, *Platyrinchus saturatus* is a resident species (BirdLife International 2020). Both species occupy similar niches near or on the floor of forests under dense undergrowth (e.g. Lambert and Woodcock 1996). Unfortunately, it cannot be verified which of the primaries is the longest and, therefore, we cannot say if the wing was rather rounded and the bird was resident, or if the wing was sharper and the bird was migrating (Nowakowski and Chruściel 2008; Kennedy et al. 2016). If the wing was indeed rounded, as indicated by its general outline, it can be assumed that *Crosnoornis nargizia* was a resident bird or a short-distance migrant inhabiting forests and feeding close to the ground in dense shrubs or dense tree crowns.

Crosnoornis nargizia has been included in Suboscines based on a combination of features located on the distal wing elements that exclude Oscines. The features include (i) carpometacarpus with the narrow distal end of os metacarpale minus that protrudes slightly more distally than os metacarpale majus; phalanx proximalis digiti majoris (ii) short, broad and cleaver-shaped, and (iii) with a distally directed protrusion in the posterior part of its distal edge; (iv) phalanx distalis digiti majoris only slight shorter than phalanx proximalis (for details see description above and Figs. 2c, S5). These features are also present in SMF Av 504 from France (Mayr and Manegold 2006a, b), which has been identified as cf. Suboscines. Also four isolated carpometacarpi (SMF Av

509, SMF Av 510; SMNS 59466/1, SMNS 59466/2) from Herrlingen, Germany have been identified as Suboscine based on several characters, including the distal end of the os metacarpale minus (Manegold 2008). Although in overall osteology *Wieslochia weissi* most closely resembles extant Suboscines, Mayr and Manegold (2006a, b) have shown that *Wieslochia* is outside crown group Oscines, and suggest that some of its features may support its position outside at least crown group Eupasseres. Unfortunately, these features, like other small details, are not visible in *Crosnoornis nargizia*.

Until recently, it seemed that the proportion of passerines in the entire Oligocene avifauna of the Carpathians is negligible. However, new finds from the last few years are changing this picture. In 2013, only 9 specimens were known (Bochenski et al. 2013b) but nowadays the number of taxa described has increased to 19, including the specimen described in this paper: Galliformes (1specimen: Tomek et al. 2014), Apodiformes (1specimen: Bochenski and Bochenski 2008), Ralloidea (1 specimen: Mayr and Bochenski 2016), Procellariiformes (2 specimens: Elzanowski et al. 2012; Gregorová 2006), Accipitriformes (1 specimen: Mayr and Hurum 2020), Upupiformes (3 specimens: Kundrát 2015, Mayr et al. 2020), Piciformes (1specimen: Mayr and Gregorová 2012), Passeriformes (6 specimens: Bochenski et al. 2011, 2013a, 2014a, 2014b, 2018, present study), Aves incertae sedis (1specimen: Mayr 2019), and Aves indet. (2 specimens: Bochenski et al. 2010, 2016). Thus, the passerines are currently the most numerous group among all Oligocene taxa from the Carpathians. It is true that their share in the Oligocene fauna is still much smaller than today when about half of all bird species are passerines, but this may not be due to the relatively small number of passerines in the Oligocene, but to various taphonomic factors including the manner of death, transport and preservation of their remains. It should be remembered that almost all Oligocene specimens from the Carpathians represent birds living on land, although they were found in marine sediments; thus these birds must have fallen into the water and drowned or their remains were transported from land to the sea, e.g. through streams, rivers or heavy rains. Also on other sites in Europe outside the Carpathians, the share of Passeriformes in the Oligocene avifauna may not be well reflected. Passerines were scarce in the remains of bird-rich sites in Phosphorites du Quercy, France (Mourer-Chauviré 2006), while about 170 isolated passerine bones were found in the fissure fillings in Herrlingen, Germany (Manegold 2008). This indirectly confirms that taphonomic processes play a significant role in the composition of early Oligocene avifaunas of Europe.

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Compliance with ethical standards

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

Informed consent All authors agreed to participate in this study and writing the paper. All authors agree with the contents of this paper and agree to its submission and publication as well as being represented by the corresponding author.

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