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A skeleton of a small bird with a distinctive furcula morphology, from the Rupelian of Poland, adds a new taxon to early Oligocene avifaunas

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Abstract

A partial skeleton of a new small avian species is reported from marine sediments of the Rupelian locality Jamna Dolna 2 in southeast Poland. *Carpathiavis meniliticus* gen. et sp. nov. is characterized by an unusual furcula morphology with stout shafts (scapi clavicularum) and a long, rod-shaped furcular apophysis. With regard to furcula shape and the proportions of the wing bones, the new species shows a resemblance to the taxon *Eocuculus*, which occurs in the late Eocene of North America and the early Oligocene of France. However, there are some distinct differences to *Eocuculus*, and in overall morphology *C. meniliticus* is also similar to the late Paleocene/early Eocene taxon *Songzia*, which is a putative representative of the Ralloidea (rails and allies). Even though a well-founded phylogenetic assignment of the new species is impeded by the poor preservation of the skeleton, *Carpathiavis* clearly represents a distinctive new taxon that has not previously been reported from the Rupelian of Europe. In its skeletal morphology, the new taxon differs from all extant avian clades and substantiates previous evidence that in the early Oligocene morphologically distinctive representatives of extinct clades lived alongside essentially modern-type representatives of extant avian groups.

K e y w o r d s : Aves; fossil birds; Jamna Dolna; *Carpathiavis meniliticus* gen. et sp. nov.; systematics; taxonomy.

1. Introduction

Europe has a comparatively rich early and middle Eocene fossil record and numerous avian remains were also described from Neogene fossil sites (Mlíkovský 2002; Mayr 2009). Late Eocene and Oligocene avifaunas, however, are less well known, even though at those times large parts of the continent were covered by a shallow inland sea, the Paratethys, which offered favorable conditions for the preservation of fossil remains.

Indeed, most of the few early Oligocene (Rupelian) fossil sites in Central Europe that yielded avian remains originate from sediments of the Paratethys (Mayr 2009; Bochenski et al. 2013a; Mayr & Smith 2013; Maxwell et al. 2016). This is also true for various localities in southeast Poland, from which bird remains have been described in the past years (Bochenski et al. 2013a). The reported avifaunas from the Polish sites are diverse and include remains of the procellariiform Diomedeoididae (Elzanowski et al. 2012), Galliformes (Tomek et al. 2014), stem group Trochilidae (Bochenski & Bochenski 2008; a very small foot of uncertain affinities described by Bochenski et al. 2016 is likely to be also from a stem group representative of the Trochilidae), Ralloidea (Mayr & Bochenski 2016), Upupiformes (Mayr et al. in press b), various Passeriformes (Bochenski et al. 2011, 2013b, 2014a, b, 2018), and fragmentary remains of uncertain affinities (Bochenski et al. 2010).

Here, I describe a new avian fossil from the locality Jamna Dolna in southeast Poland. The specimen consists of a partial skeleton of a small bird, which was found by an amateur collector and was acquired by the Senckenberg Research Institute Frankfurt in 2018. The locality Jamna Dolna comprises two fossil sites – Jamna Dolna 1 and 2 – which are separated by two kilometers and differ in their lithology (Bieńkowska-Wasiluk 2010). The new fossil is from the black shales of the Menilite beds of Jamna Dolna 2, which are exposed on the eastern side of the Jamninka river (Bieńkowska-Wasiluk 2010). It is the second avian specimen described from this site, which has before yielded an unnamed small species of the Ralloidea (Mayr & Bochenski 2016). From Jamna Dolna 1, records of the Passeriformes (Bochenski et al. 2011) and Upupiformes (Mayr et al. in press b) were described.

2. Material and methods

Like other bird skeletons from the Menilite beds in southeast Poland, the new fossil was split in two halves so that only the interior of the bones is exposed. A transfer preparation is not feasible, because the small and delicate bones are embedded in a very hard matrix, which can neither be acid prepared nor dissolved in water.

The fossil is deposited in the Senckenberg Research Institute Frankfurt, Germany (SMF). Measurements refer to the maximum length of a bone along its longitudinal axis.

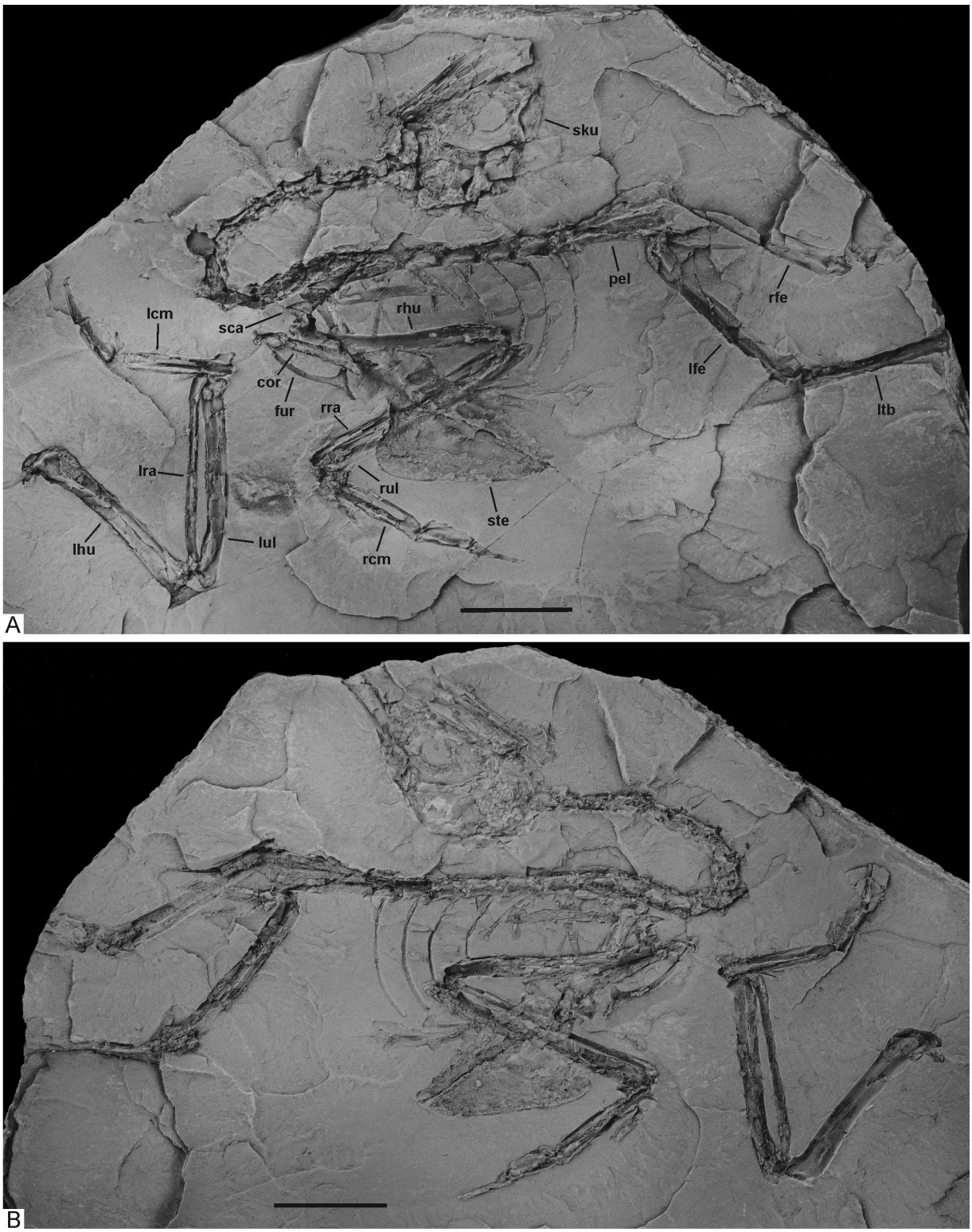

Fig. 1. The holotype of *Carpathiavis meniliticus* gen. et sp. nov. from the Rupelian of Jamna Dolna 2 in southeast Poland. **A**: specimen SMF Av 649a. **B**: specimen SMF Av 649b. To enhance the contrast of the photos, the fossil was coated with ammonium chloride. Abbreviations: cor, ?left coracoid; fur, furcula; lcm, left carpometacarpus; lfe, left femur; lhu, left humerus, lra, left radius; ltb, left tibiotarsus; lul, left ulna; pel, pelvis; rcm, right carpometacarpus; rfe, right femur; rhu, right humerus, rra, right radius; rul, right ulna; sca, ?left scapula; sku, skull; ste, sternum. The scale bars equal 10 mm.

3. Systematic paleontology

Aves Linnaeus, 1758

Order and family incertae sedis

Genus *Carpathiavis* nov.

Etymology: From Carpathes (Lat.), Carpathian Mountains, and avis (Lat.), bird, in reference to the geographic provenance of the type species.

Type species: *Carpathiavis meniliticus*, sp. nov.

Diagnosis: Characterized by the unique combination of the following features: U-shaped furcula with stout scapi clavicularum and long and rod-like apophysis furculae; coracoid with long and broad processus procoracoideus; sternum with broadly rounded apex carinae and caudal margin with deep incisions; ulna subequal to humerus in length.

Carpathiavis meniliticus gen. et sp. nov.
Figs. 1, 2, 3A–G, 4, 5A, C, E

Etymology: The species epithet refers to the type horizon, the Menilite beds of the Carpathian Flysch zone.

Holotype: SMF Av 649a+b (Figs. 1, 2A, B; partial skeleton on two slabs, missing the beak and most of both legs).

Diagnosis: As for genus.

Type locality and horizon: Jamna Dolna 2, southeast of Bircza, Podkarpackie Voivodeship (Subcarpathian Province), southeast Poland; early Oligocene, Rupelian (nannoplankton zone NP 23), black shales of the Menilite beds of the Carpathian Flysch zone, presumably local ichthyofaunal zone IPM 3 (30–31 million years ago; Bieńkowska-Wasiluk 2010).

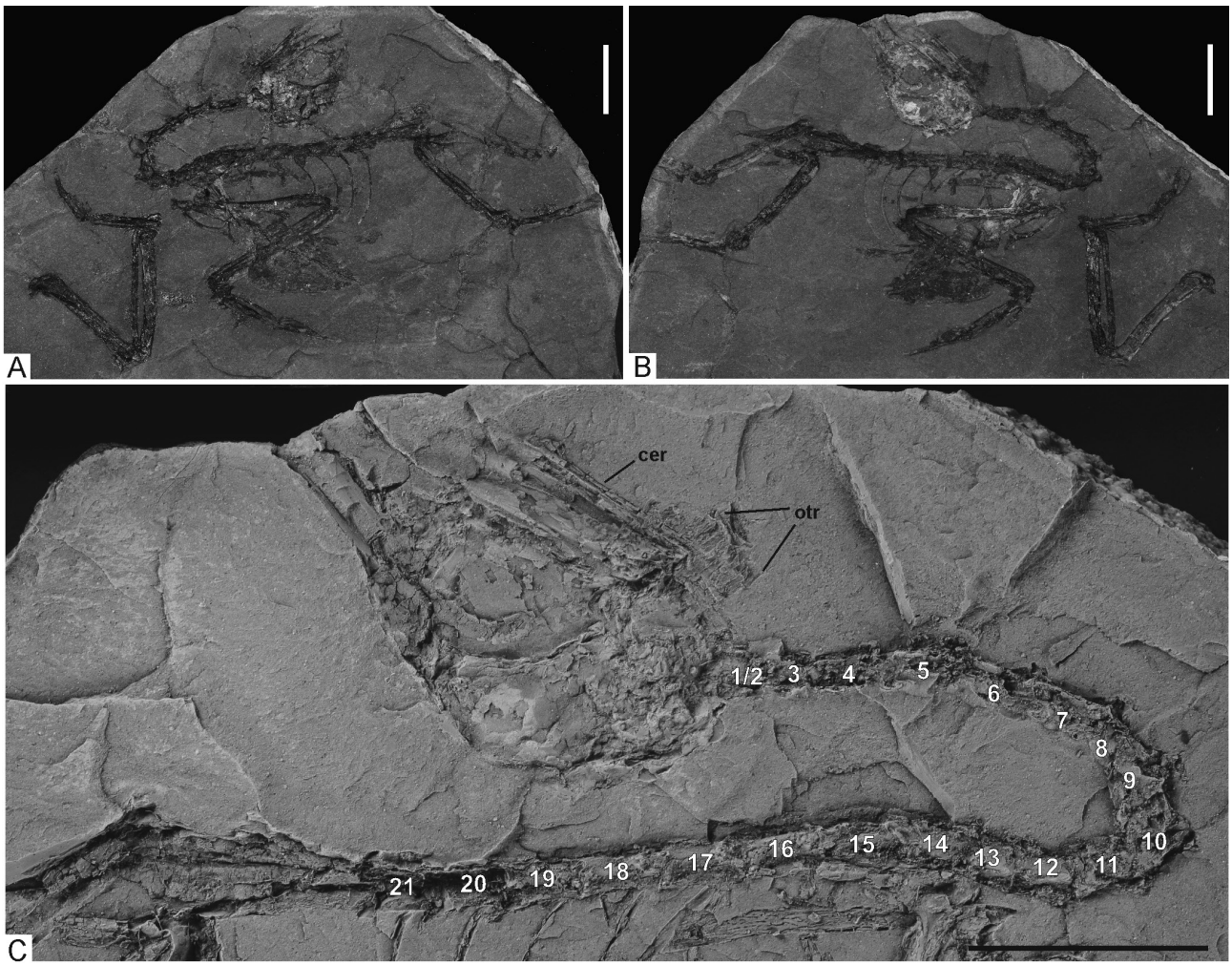

Fig. 2. *Carpathiavis meniliticus* gen. et sp. nov., overview of the two slabs containing the holotype in their actual (uncoated) state and detail of cervical column. **A**: specimen SMF Av 649a. **B**, **C**: specimen SMF Av 649b. The cervical vertebrae are numbered (note that identification of some individual vertebrae is tentative and the total count uncertain). Abbreviations: cer, ceratobranchiale; otr, ossified tracheal rings. The scale bars equal 10 mm. In **C**, the fossil was coated with ammonium chloride.

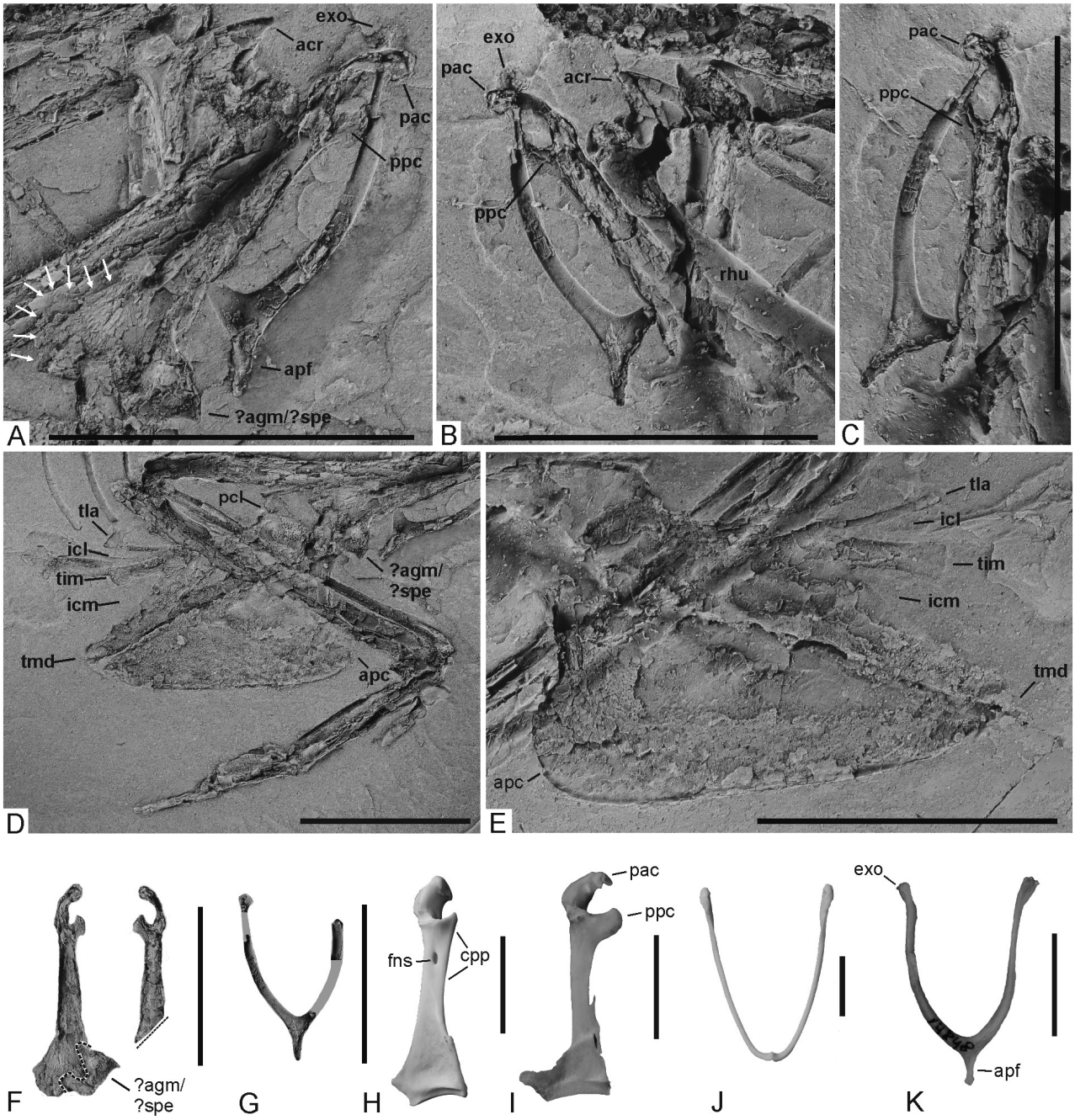

Fig. 3. *Carpathiavis meniliticus* gen. et sp. nov., details of the pectoral girdle. **A**: furcula and coracoid of SMF Av 649b; the white arrows delimit the processus lateralis of the coracoid. **B**, **C**: furcula and coracoid of SMF Av 649a. **D**: sternum of SMF Av 649b. **E**: sternum of SMF Av 649a. **F**: coracoid of *C. meniliticus* with surrounding matrix digitally removed. **G**: furcula of *C. meniliticus* with surrounding matrix digitally removed; the grey areas indicate reconstructed parts of the bone. **H**: left coracoid of *Pardirallus maculatus* (Rallidae). **I**: left coracoid of *Coua cristata* (Cuculiformes). **J**, furcula of *Aramides saracura* (Rallidae). **K**: furcula of *C. cristata*. Abbreviations: acr, acromion of scapula; agm, angulus medialis; apc, apex carinae; apf, apophysis furculae; cpp, crista procoracoidei; exo, extremitas omalis of furcula; fns, foramen nervi supracoracoidei; icl, incisura lateralis; icm, incisura medialis; pac, processus acrocoracoideus; pcl, processus craniolateralis; ppc, processus procoracoideus; rhu, right humerus; spe, spina externa; tim, trabecula intermedia; tla, trabecula lateralis; tmd, trabecula mediana. The scale bars equal 10 mm. In all images, the fossil was coated with ammonium chloride.

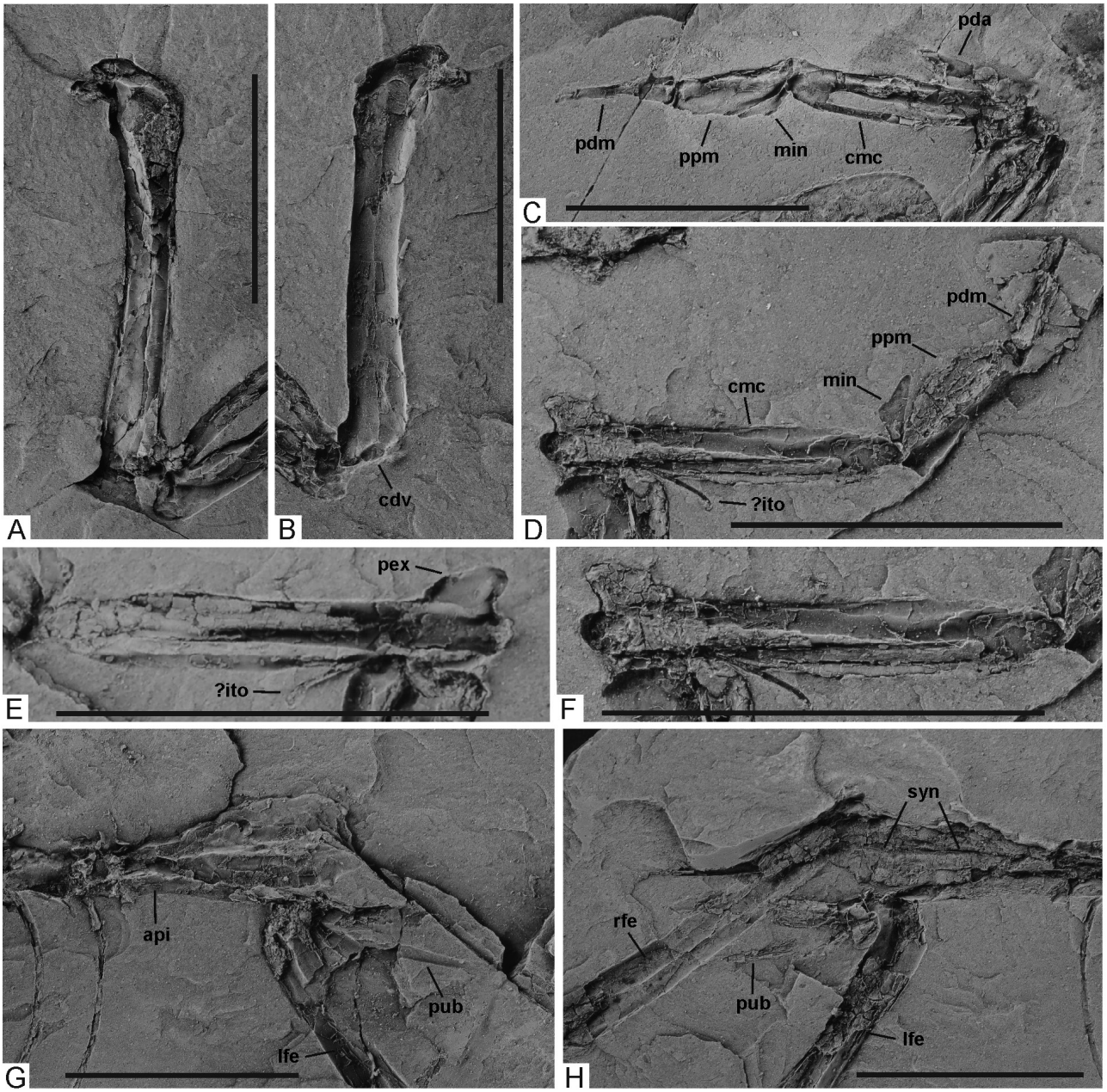

Fig. 4. *Carpathiavis meniliticus* gen. et sp. nov., details of the wing and pelvis. **A**, **B**: left humerus of SMF Av 649a (**A**) and SMF Av 649b (**B**; note that this specimen represents only a mold of the bone). **C**: hand section of right wing (SMF Av 649a). **D**: hand section of left wing (SMF Av 649b). **E**, **F**: left carpometacarpus (**E**: SMF Av 649a, **F**: SMF Av 649b). **G**, **H**: pelvis (**G**: SMF Av 649a, **H**: SMF Av 649b). Abbreviations: api, ala praeacetabularis ilii; cdv, condylus ventralis; cmc, carpometacarpus; ito, intratendinous ossification; lfe, left femur; min, phalanx digiti minoris; pda, phalanx digiti alulae; pdm, phalanx distalis digiti majoris; pex, processus extensorius; ppm, phalanx proximalis digiti majoris; pub, pubis; rfe, right femur; syn, synsacrum. The scale bars equal 10 mm. In all images, the fossil was coated with ammonium chloride.

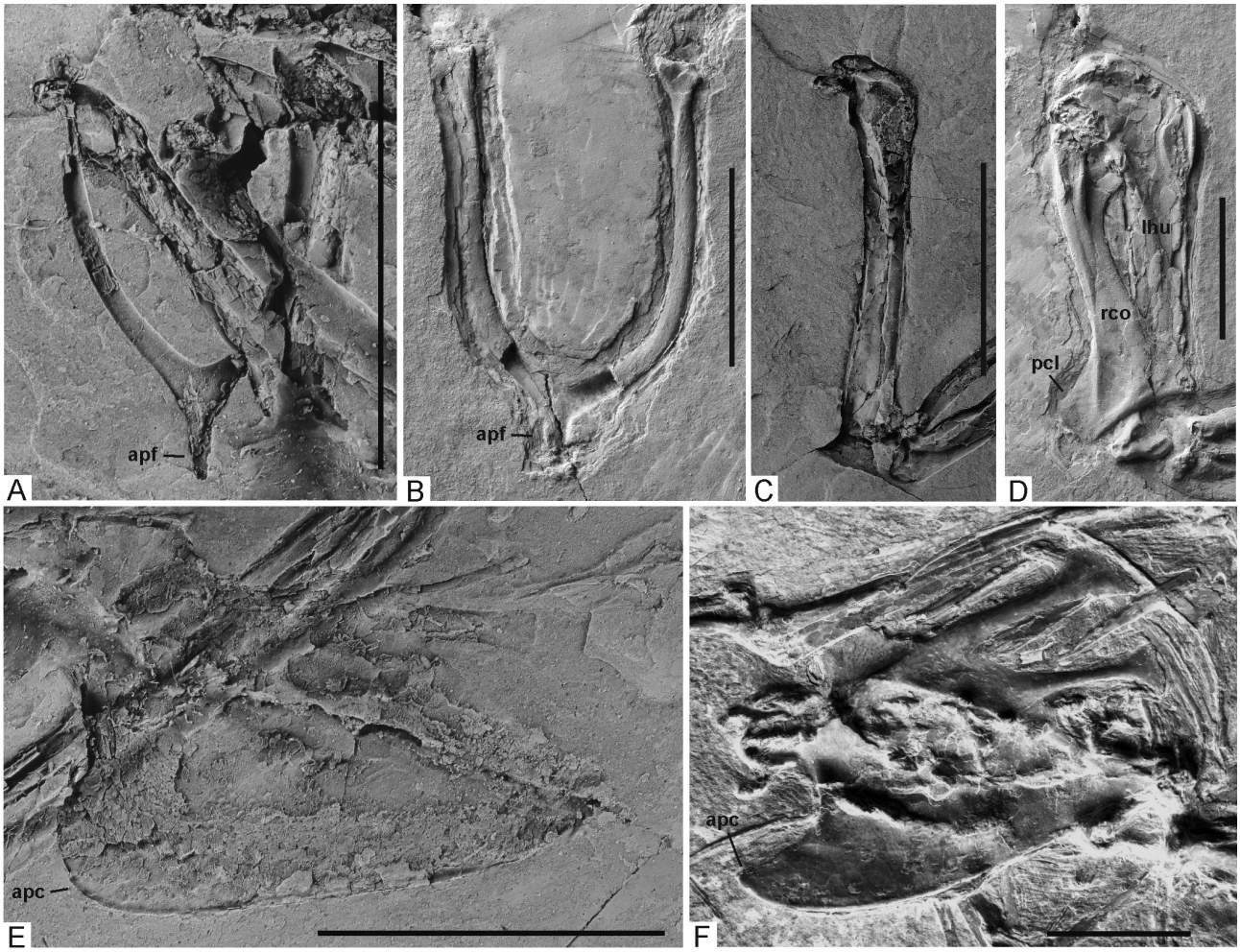

Fig. 5. Furcula (**A**, **B**), left humerus (**C**, **D**), and sternum (**E**, **F**) of *Carpathiavis* and *Eocuculus*. **A**, **C**, **E**: *Carpathiavis meniliticus* (SMF Av 649a). **B**, **D**: ?*Eocuculus* sp. from the early Oligocene of the Luberon area in France (SMF Av 424). **F**: *Eocuculus* cf. *cherpinae* from the early Oligocene of the Luberon area in France (SMF Av 425). Abbreviations: apc, apex carinae; apf, apophysis furculae; lhu, left humerus; pcl, processus lateralis; rco, right coracoid. The scale bars equal 10 mm. In all images, the fossils were coated with ammonium chloride.

Measurements (left/right, in mm): ?Left coracoid, 13.3. Humerus, 18.2/20.0. Ulna, 19.5/21.8. Carpometacarpus, 10.6/10.3. Femur, 18.3/18.3.

Description and comparisons: The fossil exhibits a poor bone preservation and the limb elements are split along the midline and expose their interior, so that few details of the bone surfaces can be discerned. The skull lacks most of the beak and neither the configuration of the nostrils nor the exact depth of the base of the beak are discernible. Likewise, only few details of the cranium are visible. However, a well-developed processus postorbitalis appears to be absent and the septum interorbitale exhibits a large opening (fonticulus interorbitalis). The cervical column attaches to the caudoventral portion of the skull, which indicates a "Streckschädel" sensu Barnikol (1952). The mandibular rami are fairly deep. The ceratobranchialia of the hyoid apparatus are situated ventral of the mandible. Also preserved are ossified rings formed by the cranialmost portion of the trachea.

21 praesacral vertebrae can be identified (Fig. 2C). The central cervical vertebrae are fairly long and the thoracic vertebrae likewise have an elongate corpus, which is about twice as long as it is deep; at least one thoracic vertebra (presumably the 14th or 15th) exhibits a long processus ventralis. Only the processus spinosi of the cranialmost thoracic vertebrae are exposed and these are very low. A notarium (fused thoracic vertebrae) seems to be absent. Six pairs of (vertebral) ribs can be counted. Some of the processus uncinati are detached from the ribs, which indicates the lack of co-ossification between these elements.

The furcula (Fig. 3A, B) has a distinctive morphology. The bone is broadly U-shaped and unusually small, with wide scapi clavicularum. The extremitas sternalis exhibits a very long apophysis, which measures about one fourth of the length of the

furcula and is rod-shaped rather than blade-like. The extremitas omalis is short and lacks a well developed processus acrocoracoideus. In its shape and relative size, the furcula corresponds to that of the Pteroclidae, in which the apophysis furculae is, however, either absent or proportionally much shorter.

The shaft of the coracoid (Fig. 3A, C, F) is relatively broad and widens towards the sternal end of the bone. The extremitas omalis is mediolaterally narrow and measures about one fifth of the entire length of the bone. The processus procoracoideus is long and broad and directs omally, towards the processus acrocoracoideus. The facies articularis humeralis has little lateral prominence. Owing to the poor preservation of the bone, it cannot be discerned whether a foramen nervi supracoracoidei is present. The processus lateralis is short. A medial projection at the sternal end of the bone is either a projecting angulus medialis of the coracoid or the spina externa of the sternum (Fig. 3A).

The straight shaft of the scapula is dorsoventrally narrow. The long acromion has a pointed tip (Fig. 3A, B).

The sternum (Fig. 3D, E) is craniocaudally short and has a deep carina. Rather than forming a pointed tip, the apex carinae is broadly rounded, with a similar shape being found in, e.g., extant Columbiformes and Psittaciformes. Few details of the cranial end of the bone are visible, but the processus craniolaterales are moderately long and have a blunt tip. A projection at the cranial end of the bone is either a long spina externa or the angulus medialis of the coracoid (Fig. 3A). The caudal margin of the sternum exhibits two pairs of incisions. The deep medial pair delimits a narrow trabecula mediana and is laterally bordered by a pair of broad processes, which are here identified as trabeculae intermediae. A much narrower trabecula lateralis originates at the base of the trabecula intermedia and borders a narrow incisura lateralis.

The wings are fairly short; the left wing is detached from the skeleton. The humerus (Fig. 4A, B) has a comparatively small proximal end, but a stout shaft and a wide distal end. The crista deltopectoralis is short and measures about one sixth of the length of the humerus; it has little dorsal prominence and a convex dorsal margin. The processus flexorius on the distal end of the bone is short. The left humerus shows a mold of the small and elongate condylus ventralis.

The ulna is likewise a fairly robust bone and slightly exceeds the humerus in length, whereas it is distinctly shorter than the humerus in all extant Ralloidea. The olecranon is long and has a rounded tip. Papillae remigales cannot be discerned. The two ulnae exhibit a different length, with the right one being longer than the left one. This difference is here attributed to diagenetic distortion of the bones.

The carpometacarpus (Fig. 4C–F) is craniocaudally slender, with a narrow spatium intermetacarpale and a long synostosis metacarpalis distalis. The bone is more than half as long as the humerus and is similar to the carpometacarpus of the Ralloidea in its proportions. The processus extensorius is well developed, its tip projects proximocranially. A processus intermetacarpalis is absent and the os metacarpale minus does not reach much farther distally than the os metacarpale majus.

The short phalanx digiti alulae does not bear an ungual phalanx. The phalanx proximalis digiti majoris is fairly long and craniocaudally narrow; a well-developed processus internus indicis is absent. The phalanx distalis digiti majoris is likewise long, whereas the phalanx digiti minoris is very small. Osteological details of the carpal bones cannot be discerned. A narrow rod-shaped bone at the wrist joint of the left wing probably represents an intratendinous ossification (Fig. 4D–F).

The pelvis (Fig. 4G, H) is exposed in dorsoventral view and is very narrow mediolaterally, especially at the level of the alae praeacetabulares iliorum. It has similar proportions to the pelvis of the Rallidae and as in the latter, the alae praeacetabulares iliorum are steeply sloping laterally. The synsacrum is broad in its midsection, the ischium is narrow. Further osteological details of the pelvic bones are not visible.

The femur is a long and slender bone, which reaches the length of the humerus. Morphological details cannot be discerned. Of the tibiotarsi, only the proximal portions are preserved and the cristae cnemiales do not project proximally and have little cranial prominence. The tarsometatarsi and pedal phalanges are missing.

4. Discussion

Carpathiavis meniliticus gen. et sp. nov. is a small bird, about the size of the smallest extant Rallidae (e.g., *Porzana flaviventer*). The holotype displays very poor bone preservation and critical osteological features, such as the morphology of the beak and feet, are not preserved. However, even though only a limited amount of osteological details can be recognized, a few characteristic features are visible. The most distinctive of these is the long, rod-like apophysis furculae ("hypocleidium") of the broadly U-shaped furcula. An apophysis furculae of similar length occurs in only a few extant avian taxa, that is, some Galliformes and Cuculiformes, as well as in the otherwise very different Opisthocomiformes (in which the furcula is V-shaped and fused with the coracoids and the sternum) and Sagittariidae (Accipitriformes); in the gruiform Heliornithidae and in the Trogoniformes, the apophysis is also rod-shaped but shorter than in *C. meniliticus*. Another characteristic of the new fossil concerns the length proportions of the wing bones, with the ulna being subequal in length to the humerus. This latter feature distinguishes *C. meniliticus* from most representatives of the arboreal land bird clade (Telluraves), in which the ulna is usually distinctly longer than the humerus.

Compared with previously described birds from the early Oligocene of Europe, *C. meniliticus* shows some resemblance to the taxon *Eocuculus*, which has been reported from the late Eocene of North America and the early Oligocene of France (Chandler 1999; Mayr 2006). Originally described as a representative of the Cuculiformes (Chandler 1999), *Eocuculus* has later been considered to be possibly related to the early Eocene *Pumiliornis tessellatus* (Mayr 2008). Subsequent analyses identified *Pumiliornis* as a stem group representative of the Passeriformes (Mayr 2015; Ksepka et al. 2019), and although some of these analyses suggested close affinities between *Eocuculus* and the clade including *Pumiliornis* and Passeriformes, the affinities of *Eocuculus* remain poorly resolved. *Carpathiavis* and *Eocuculus cherpinae*, the only named species of the taxon *Eocuculus*, share a furcula

with a long apophysis (Fig. 5A, B) and similar length proportions of the major wing bones. However, *Carpathiavis* is distinguished from *Eocuculus* fossils from the early Oligocene of France (Mayr 2006, 2008) in the narrower humerus (Fig. 5C, D), the rounded apex carinae of the sternum (Fig. 5E, F), the shorter processus lateralis of the coracoid (compare Figs. 3A and 5D), and the narrower pelvis. The morphologies of the apex carinae and processus lateralis are not visible in the North American holotype of *E. cherpinae*, but the pelvis of this fossil is likewise wider than in the new species, and the *E. cherpinae* holotype furthermore differs from *Carpathiavis* in the longer processus internus indicis of the phalanx proximalis digiti majoris of the wing. With regard to possible affinities between *Carpathiavis* and *Eocuculus*, it is worth mentioning that Bochenski et al. (2010) reported a partial foot from the Menilite beds, which they considered similar to the foot of *Eocuculus* and *Pumiliornis*. However, with a tarsometatarsus length of 21.7 mm, this fossil is too large to belong to *Carpathiavis* (with a humerus length of 27.0 mm, *E. cherpinae* is much larger than *C. meniliticus* but has a tarsometatarsus length of only 17.0 mm; Chandler 1999).

In addition to the proportionally shorter ulna, *C. meniliticus* differs from crown group Passeriformes, which are comparatively abundant in early Oligocene localities of southeast Poland (Bochenski et al. 2011, 2013b, 2014a, b, 2018), in the smaller and much more robust furcula and in the absence of a processus intermetacarpalis (carpometacarpus). Like most other Telluraves, crown group passerines have 19 praesacral vertebrae, but 21 praesacral vertebrae were reported for putative stem group representatives (i.e., the early Eocene Psittacopedidae; Mayr 2015).

Compared to extant birds, *C. meniliticus* resembles some Cuculiformes in the morphology of the pectoral girdle, especially the long apophysis furculae (Fig. 3K), the slender coracoid, and the short sternum. However, these similarities are not very specific and there are numerous differences between *C. meniliticus* and extant Cuculiformes, including a higher number of praesacral vertebrae (Cuculiformes only have 18 praesacral vertebrae), a rounded apex carinae of the sternum (pointed in the Cuculiformes), the absence of marked papillae remigales (ulna), the proportionally longer and more elongate carpometacarpus, and the narrower pelvis. Except for the similar morphology of some of the pectoral girdle bones, no osteological features convincingly suggest closer affinities between *Carpathiavis* and cuculiform birds.

In addition to the largely obscured surface details of most major bones, a major impediment in determining the phylogenetic affinities of *Carpathiavis* is the lack of the feet of the fossil. These preservational limitations make it difficult to narrow down the higher level affinities of *C. meniliticus*, and in overall morphology, especially regarding the shape of the long and slender carpometacarpus and the narrow pelvis, the new species also has a somewhat "rail-like" appearance. As noted in the introduction, the type locality (Jamna Dolna 2) yielded an unambiguous record of the Ralloidea, the clade including the extant Sarothruridae, Rallidae, and Heliornithidae (Mayr & Bochenski 2016). However, this fossil exhibits the characteristics of extant Rallidae and Sarothruridae and although it represents a rather small species by comparison with extant Rallidae, it distinctly exceeds the new species in size (humerus length 28.2 mm versus 18.5/20.0 mm in *C. meniliticus*). The new species is furthermore clearly distinguished from all extant Ralloidea in a number of osteological characteristics, including the stouter humerus, the proportionally longer ulna (which is distinctly shorter than the humerus in extant Ralloidea), the long apophysis furculae (compare Figs. 3G and 3J), as well as the more slender shaft of the coracoid, which does not form a crista procoracoidei (compare Figs. 3F and 3H).

With regard to the proportions of the wing bones, *Carpathiavis* corresponds to the extinct Paleogene *Songzia*, which is the type genus of the putatively ralloidean taxon Songziidae (Wang et al. 2012). The shape of the apophysis furculae of *Songzia* is unknown, but in *Carpathiavis* the scapi clavicularum are proportionally wider and the new taxon also differs from *Songzia* in the deeper incisions in the caudal margin of the sternum (compare Fig. 5E with Wang et al. 2012: fig. 7). *Songzia* was initially reported from the early Eocene of China, but *Songzia*-like birds have also been described from the late Paleocene of France (Mayr et al. 2019) and from the early Eocene of Canada (Mayr et al. in press a). However, no post-Eocene records of *Songzia*-like birds were identified and *C. meniliticus* is more than 15 million years younger than previous fossils of the taxon.

A superficially rail-like morphology of the limb bones is also found in some Paleogene Galliformes, such as the Eocene Gallinuloididae and Quercymegapodiidae (Mourer-Chauviré 1992; Mayr & Weidig 2004), but *C. meniliticus* is distinguished from all galliform birds in the well-developed processus procoracoideus of the coracoid and in the shape of the processus acrocoracoideus, which is more sharply bent and less protruding in omal direction in Galliformes, as well as in the shorter sternum and the absence of a notarium. In most galliform birds, the apophysis furculae is furthermore blade-like rather than rod-shaped.

Even though it is not possible to determine the exact affinities of *C. meniliticus*, the new species clearly represents a distinctive taxon that has not previously been reported from the early Oligocene of Europe. As such, it contributes to a better understanding of local Rupelian avifaunas in southeast Poland and documents our poor knowledge of the avifaunas of this geological stage. Whereas

early Eocene avifaunas are characterized by extinct taxa without close extant counterparts, early Oligocene avifaunas often include birds that more closely resemble modern avian groups (Mayr 2009). *C. meniliticus* clearly differs from all extant avian clades in its skeletal morphology and adds to a number of equally enigmatic early Oligocene taxa, such as the above-mentioned *Eocuculus* or the tiny, putatively piciform Sylphornithidae (Mayr & Smith 2002). Given the pace of new discoveries from the Rupelian localities in southeast Poland, it is to be hoped that a more complete and better preserved specimen of *C. meniliticus* will be found in the near future, in order to shed more light on the phylogenetic affinities of this enigmatic species.

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