



MIDDLE EOCENE PELAGORNITHIDAE AND GAVIIFORMES (AVES) FROM THE UKRAINIAN PARATETHYS

by GERALD MAYR¹ and EVGENIJ ZVONOK²

¹Forschungsinstitut Senckenberg, Sektion Ornithologie, Senckenberganlage 25, D-60325 Frankfurt am Main; Germany; e-mail: Gerald.Mayr@senckenberg.de

²Leninskogo Komsomola Street 7/34, 91000 Luhansk, Ukraine; e-mail: evgenij-zvonok@yandex.ua

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Abstract: We describe avian remains from Novopskov, a new middle Eocene marine locality in Ukraine. The fossils constitute the most substantial collection of Palaeogene bird bones from Eastern Europe and contribute to a better knowledge of the Paratethyan seabird fauna. Most of the specimens belong to Pelagornithidae (bony-toothed birds), and two species of very different size can be distinguished. The larger of these is tentatively referred to *Dasornis* sp., the smaller to *Odontopteryx toliapica*. The specimens include skeletal elements that were not described for Palaeogene bony-toothed birds and document previously unknown morphological differences between Palaeogene and Neogene Pelagornithidae. It is argued that the purported crane *Eobalearica tugarinovi*, from the middle Eocene of Kyrgyzstan, is probably also a

bony-toothed bird. A new genus and species of small Gaviiformes, *Colymbiculus udovichenkoi*, is described, which is the earliest fossil record of a loon from Europe, preceding the next oldest specimens by more than 10 myr. The Ukrainian fossils document profound differences between middle Eocene and extant marine avifaunas of Europe, and whereas the middle Eocene Paratethyan avifauna appears to have been similar to that of the North Sea with regard to pelagornithid diversity, the absence of prophaethontids and relative abundance of Gaviiformes may indicate faunistic differences concerning the remaining seabirds.

Key words: Fossil birds, *Dasornis*, *Odontopteryx*, *Colymbiculus udovichenkoi* gen. et sp. nov.

COMPARED with the comprehensive record of terrestrial and arboreal birds from the early and middle Eocene of Europe, knowledge of the marine avifaunas from these periods is still limited. Most fossils belong to Pelagornithidae (bony-toothed birds) and Prophaethontidae (stem group representatives of Phaethontidae) and come from North Sea deposits in England, Belgium and Denmark (Mayr 2009a). Eocene localities from the Tethys and Paratethys seas, which covered large parts of southern and south-eastern Europe (e.g. Rögl 1999), have yielded only few bird remains.

Here, we describe avian remains from a recently discovered middle Eocene Paratethyan locality in eastern Ukraine (Udovichenko 2009). The fossils were collected in a disused sand quarry about 1 km west of Novopskov in the Osinovo area of the Luhansk region (49°52'82N, 39°7'30E; Text-fig. 1). The sediments were deposited in a near-shore marine environment, and apart from bird bones, the locality yielded numerous teeth of sharks and other chondrichthyans (Holocephali and Batoidea; Udovichenko 2009), as well as bones of teleosts, many turtles and a crocodylian (pers. obs.). The geology of the

Novopskov site was studied by Udovichenko (2009), who determined its age as early Lutetian.

The avian remains were collected by one of us (EZ) between 2009 and 2010. Some of the specimens are surface finds, but most were retrieved by sieving large amounts of sand. None of the bones were found in association, and many were already fragmentary *in situ*.

The fossils constitute the most substantial collection of Palaeogene bird bones from Eastern Europe, with the only other avian taxon reported from the Palaeogene of Ukraine being *Kievornis rogovitshi* Averianov *et al.*, 1990. This species is based on a humerus and ulna from the late Eocene of Kiev (Averianov *et al.* 1990; Mlíkovský 1996) and was originally assigned to the allegedly charadriiform taxon 'Graculavidae', but more likely is a representative of either Procellariiformes or Phaethontiformes (Mayr 2009a).

Institutional abbreviations. IRSNB, Institut royal des Sciences naturelles de Bruxelles, Belgium; MNHN, Museo Nacional de Historia Natural, Santiago, Chile; NHMUK, Natural History Museum, London; NMB, Naturhistorisches Museum Basel,



TEXT-FIG. 1. Map of Ukraine. The location of the Novopskov fossil site is indicated by an asterisk.

Switzerland; PIN, Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; SMF, Forschungsinstitut Senckenberg, Frankfurt am Main, Germany.

SYSTEMATIC PALAEOLOGY

AVES Linnaeus, 1758

PELAGORNITHIDAE Fürbringer, 1888

cf. DASORNIS Owen, 1870

?*Dasornis* sp.

Text-figures 2, 3

Referred specimens. SMF Av 526 (Text-fig. 2A–D; rostral portion of a left mandible); SMF Av 527 (Text-fig. 2E–F; rostral portion of a right mandible with numerous associated fragments (not all figured)); SMF Av 528 (Text-fig. 3A, left radius lacking the proximal part); SMF Av 529 (Text-fig. 3B–C; left tibiotarsus lacking the proximal end); SMF Av 530 (Text-fig. 3E–F; fragmentary shaft of a left tibiotarsus); SMF Av 531 (Text-fig. 3G–I; a pedal phalanx).

Locality and horizon. Novopskov, Luhansk region, Ukraine; middle Eocene (early Lutetian).

Measurements. Length of largest complete pseudotooth (SMF Av 526), 13.2 mm. Radius (SMF Av 528), distal width, 18.1 mm. Tibiotarsus (SMF Av 529), length as preserved, 227.7 mm; distal width, 34.5 mm. Pedal phalanx (SMF Av 531), length, 43.5 mm; proximal width, 8.0 mm.

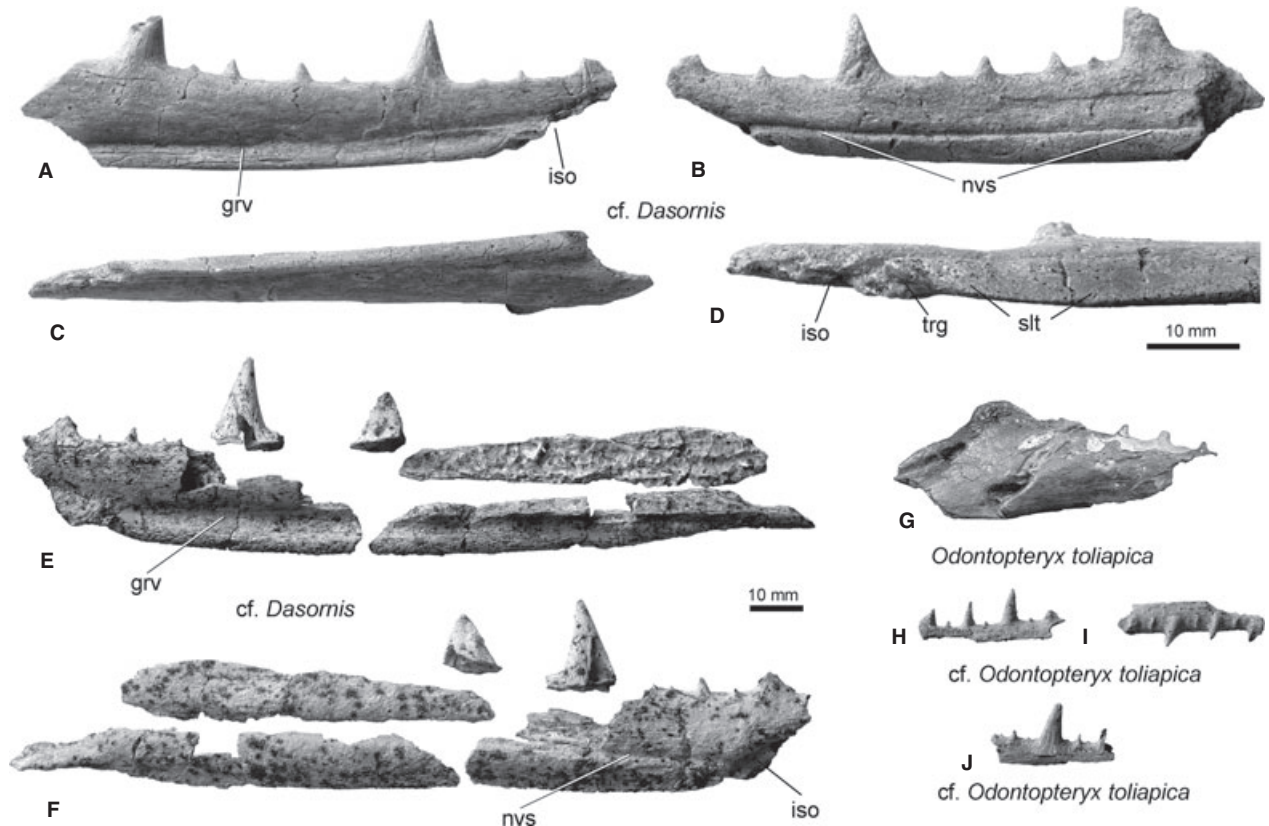
Remarks. We subsume all large pelagornithid remains from Novopskov into a single species, which we tenta-

tively place in *Dasornis* Owen, 1870 (see Mayr (2008) for the taxonomic history of this taxon). We note, however, that the specimens show some variation in size, and as detailed in the discussion, there are other large-sized birds from the Paratethys region, which probably represent pelagornithids.

The two mandibles differ in size, with the dorsoventral depth of the bone just caudal to the notch for the intersymphyseal ossification being 14.4 mm in SMF Av 526 and 18.9 mm in SMF Av 527. Both specimens are somewhat larger than the mandible of *Dasornis emuinus*, which was described by Harrison and Walker (1976a) as '*Pseudodontornis longidentata*' and which has a depth of about 12 mm. The Ukrainian fossils further differ from the London Clay mandible of *D. emuinus* in the arrangement of the pseudoteeth (see Description). According to Harrison and Walker (1977), the proximal width of the tarsometatarsus of *D. emuinus* (i.e. Harrison and Walker's '*Neptuniavis miranda*' holotype) is 26.8 mm, which is less than the width of the distal end of the tibiotarsus SMF Av 529 (34.5 mm). Because, however, large Palaeogene bony-toothed birds are known only from rare fragmentary remains, and as little is known about individual variation or size dimorphism in these birds, we prefer a cautious approach and refrain from a definitive species assignment.

The tibiotarsi have the same size as the tibiotarsus of the Neogene *Pelagornis chilensis*, and the mandible fragments also correspond well with *P. chilensis* in size. The referred radius, however, is distinctly smaller (distal width 18.1 mm vs. 31.9 mm in *P. chilensis*). Although this may indicate that more than one taxon is involved in the material assigned to *Dasornis* in this study, we note that the proximal humerus and ulna of *D. emuinus* are also proportionally smaller than the corresponding elements of *P. chilensis* (proximal width of humerus 53.2 mm (after Harrison and Walker 1976a) vs. 80.6 mm). If not sexually dimorphic in size, Palaeogene Pelagornithidae may thus have had different limb proportions to their Neogene relatives.

Description and comparison (osteological terminology after Baumel and Witmer 1993). Both mandibles are rostral portions and allow recognition of the notch for the intersymphyseal ossification, which replaced the mandibular symphysis in pelagornithids (Text-fig. 2; Mayr and Rubilar-Rogers 2010, fig. 2). In SMF Av 526, the ventral margin of the mandible adjacent to this notch forms a trough, which is bordered by thin bony sheets (Text-fig. 2D). In SMF Av 527, the morphology of the mandibular tip is different in that there is a subrectangular depression on the lateral mandibular surface, which is medially bordered by a sheet of bone. As in other pelagornithids, a marked neurovascular sulcus runs along the lateral surface of the mandible, which itself has an irregular surface. The medial surface of the bone exhibits a wide and shallow groove, which is much less pronounced in Neogene pelagornithids (Matsuoka *et al.* 1998; Stidham 2004;



TEXT-FIG. 2. Jaw fragments of a large (A–F; cf. *Dasornis* Bowerbank, 1854) and small (H–J; cf. *Odontopteryx toliapica* Owen, 1873) pelagornithid from the middle Eocene of Novopskov in Ukraine, in comparison with *Odontopteryx toliapica* (G) from the London Clay. A–C, rostral portion of left mandible (SMF Av 526) in medial (A), lateral (B), and ventral (C) view; D, detail of rostral end of latter specimen in ventral view. E, F, rostral portion of right mandible (SMF Av 527, three fragments and two pseudoteeth) in medial (E) and ventral (F) view. G, *Odontopteryx toliapica*, mandible fragment of holotype (NHMUK 44096). H, I, fragment of jaw, presumably from maxilla (SMF Av 532) in two views. J, fragment of jaw, presumably from mandible (SMF Av 533). Abbreviations: grv, groove along medial mandibular surface; iso, notch for intersymphyseal ossification; nvs, neurovascular sulcus; slt, slanted lateral surface of ventral mandibular shelf (see text); trg, trough at notch for intersymphyseal ossification. Same scale bars for all figure panels except D.

Mayr and Rubilar-Rogers 2010). This groove separates the convex dorsal two-thirds of the mandible from its ventral part, which forms a mediolaterally narrow shelf. The lateral surface of this ventral shelf is slanted in its rostral section (Text-fig. 2D). The two large pseudoteeth of SMF Av 526 are separated by four much smaller projections, of which the two equally sized central ones are again distinctly larger than the two next to the large pseudoteeth. Two very small pseudoteeth are situated between the large rostral pseudotooth and the foremost one at the tip of the mandible, which is damaged but appears to have been low and broad. In SMF Av 527, two large isolated pseudoteeth are preserved, whose position cannot be determined. In this specimen, there is also a low and broad pseudotooth at the tip of the mandible, which is caudally followed by three small pseudoteeth, the central one of which exceeds the other two in size. The fact that in SMF Av 526 only a small number of low pseudoteeth are situated between the large ones is unlike the condition in *Pelagornis*, in which the size difference between the largest pseudoteeth and the medium-sized pseudotooth that is positioned between them is much less pronounced. In contrast to the Lon-

don Clay mandible of *D. emuinus*, the first large pseudotooth of the Ukrainian species is situated well behind the level of the notch for the intersymphyseal ossification, whereas there is a large pseudotooth just above this notch in the London Clay mandible. Although the Ukrainian mandibles thus differ from *Dasornis emuinus* in pseudotooth arrangement, the extent of individual variation in pseudotooth formation in pelagornithid species is unknown, and their development may well have shown individual variation.

Unlike *Pelagornis* (Mourer-Chauviré and Geraads 2008; Mayr and Rubilar-Rogers 2010), the ventral surface of the distal radius (Text-fig. 3A) does not exhibit an excavation to encompass the distal ulna, although the facies articularis ulnaris is markedly concave. The midpart of the shaft has a subtriangular cross-section; unlike in *P. chilensis*, it is not craniocaudally flattened, and there is no sulcus along its caudal surface.

The tibiotarsus SMF Av 529 (Text-fig. 3) corresponds with tibiotarsi that were assigned to *Dasornis emuinus* by Bourdon *et al.* (2010) and also closely resembles that of *Pelagornis chilensis*, both in size and morphology. The cristae cnemiales are



TEXT-FIG. 3. Bones of a large pelagornithid (cf. *Dasornis* Bowerbank, 1854) from the middle Eocene of Novopskov in Ukraine. A, left radius (SMF Av 528) in ventral view. B–D, left tibiotarsus (SMF Av 529) in cranial (B), caudal (C) and medial (D) view. E–F, left tibiotarsus (SMF Av 530) in cranial (E) and lateral (F) view. G–I, pedal phalanx (SMF Av 531) in dorsal (G), lateroplantar (H), and plantar (I) view. Abbreviations: emb, boss on medial surface of shaft; ext, sulcus extensorius; ffx, fossa flexoria; pst, pons supratendineus; sul, sulcus for flexor tendon.

broken, but the remaining portions show that they were curved laterally as in *P. chilensis*. The crista fibularis is low and only weakly set off from the shaft of the bone. As in *P. chilensis*, the fossa flexoria on the caudal surface of the proximal end is very marked, and there is a distinct boss on the medial surface of the shaft, proximal of the opposing crista fibularis. The shaft of both tibiotarsi, SMF Av 529 and SMF Av 530, is craniocaudally compressed. However, SMF Av 530 differs from SMF Av 529 in that

the sulcus extensorius is much narrower. We consider it likely that this difference is an artefact owing to plastic deformation of one of the bones, but cannot exclude the possibility that the specimens are from two equally sized species. The pons supratendineus is proximodistally wider than in *P. chilensis*. As in the latter species, there is a tubercle lateral of the distal opening of the canalis extensorius. The condyli are widely separated, and the condylus medialis is medially protruding. The condylus

lateralis is damaged, but both condyli seem to have been of equal size, whereas the condylus lateralis is smaller than the condylus medialis in *P. chilensis*.

The Novopskov material includes a pedal phalanx (Text-fig. 3G–I) that we assign to the Pelagornithidae because of its large size and the relative abundance of pelagornithids in the material. The proximal width of the bone is less than the width of the trochlea metatarsi III of *D. emuinus* (the holotype of ‘*Neptuniavis miranda*’), which measures 10.7 mm (Harrison and Walker 1976a). The symmetric proximal articulation facets and the absence of a well-developed tuberculum extensorium indicate that it represents the basal phalanx of the third toe. The bone is slightly curved, with one half being more dorsoplantarily compressed than the other. Whether this unusual morphology reflects its true shape or is a taphonomic artefact cannot be determined. The proximal end is much wider than the distal end, and there is a marked sulcus for the flexor tendon along the proximal third of the plantar surface.

cf. Odontopteryx toliapica Owen, 1873

Text-figures 2, 4

Referred specimens. SMF Av 532 (Text-fig. 2H–I; fragment of jaw, presumably from a maxilla); SMF Av 533 (Text-fig. 2J; fragment of jaw, presumably from mandible); SMF Av 534 (Text-fig. 4A–C; fourth cervical vertebra); SMF Av 536 (Text-fig. 4D–E; fragmentary extremitas omalis of a right coracoid); SMF Av 537 (Text-fig. 4F; extremitas cranialis of a left scapula); SMF Av 535 (Text-fig. 4G–J; incomplete furcula); SMF Av 538 (Text-fig. 4K; shaft of left humerus with fragments of both ends); SMF Av 542 (Text-fig. 4L–M; incomplete distal end of right ulna); SMF Av 539 (Text-fig. 4N–P; right carpometacarpus lacking proximal end); SMF Av 540 (Text-fig. 4R–T; proximal end of left carpometacarpus); SMF Av 541 (Text-fig. 4Q; left phalanx proximalis digiti majoris lacking the proximal end); SMF Av 543 (Text-fig. 4U–W; left tarsometatarsus lacking the proximal end); SMF Av 544 (Text-fig. 4Y; fragmentary distal portion of a left tarsometatarsus).

Locality and horizon. Novopskov, Luhansk region, Ukraine; middle Eocene (early Lutetian).

Measurements. (Those in brackets are dimensions of Moroccan fossils referred to *O. toliapica* after Bourdon *et al.* (2010, tab. 2)). Length of largest pseudotooth, 7.1 mm (SMF Av 532)/7.4 mm (SMF Av 533). Humerus (SMF Av 538), estimated length, c. 280–300 mm (c. 245–370 mm), estimated distal width, c. 27 mm (c. 23–28 mm). Phalanx proximalis digiti majoris (SMF Av 541), length as preserved, 42.4 mm. Tarsometatarsus (SMF Av 543), length as preserved, 56.3 mm (78–85 mm); distal width, 15.1 mm (15.7–17.5 mm).

Remarks. This species is much smaller than *Dasornis emuinus* and corresponds in size to *Odontopteryx toliapica* Owen, 1873, which, according to the measurements in Bourdon *et al.* (2010, tabs 1 and 2), shows a great variability in size.

The taxon *Odontopteryx* Owen, 1873 has recently been synonymized with the much larger *Dasornis* Owen, 1870 by Bourdon *et al.* (2010). However, we do not yet consider this taxonomic decision, which was based on overall similarity, to be well established. As detailed by Mayr (2008), it is well possible that *Dasornis* is the sister taxon of the giant Neogene Pelagornithidae, and we thus maintain *Odontopteryx* separated from *Dasornis* in this study.

The holotype of *O. toliapica*, from the early Eocene the London Clay, consists of an incomplete skull, and the British material of the species does not include the postcranial bones described in this study. Meaningful comparisons with the London Clay specimens are thus not possible, and our assignment of the Ukrainian fossils to *O. toliapica* is tentative.

Description and comparison. The two jaws are so fragmentary that it is difficult to determine whether they are from the upper or lower jaw. SMF Av 532 is mediolaterally wider than SMF Av 533, and based on comparisons with the *P. chilensis* holotype, we hypothesize that the former represents a part of the maxilla and the latter is from the mandible. The arrangement of the pseudoteeth of SMF Av 533 corresponds with the pattern found in most pelagornithids in that the large pseudoteeth are separated by three smaller ones, with the central of these being again larger than the adjacent two.

By its morphological features and by comparisons with the vertebral series of *P. chilensis*, the vertebra is identified as the fourth cervical. This vertebra was previously only known from *P. chilensis*, in which it is, however, fragmentary. SMF Av 534 is more elongate than the fourth cervical vertebra of *P. chilensis*. As in the Chilean species, the cranial margin of the lamina dorsalis arcus is very thick and the zygapophyses craniales are almost vertically oriented, indicating strong interlaminar ligaments and a ventrally inclined head (Mayr and Rubilar-Rogers 2010). The processus spinosus is broken. There is a well-developed processus costalis, which is not preserved in the *P. chilensis* holotype. As in *P. chilensis*, a processus ventralis is absent (this process is present on the third cervical vertebra of the Chilean species; Mayr and Rubilar-Rogers 2010). Unlike in *P. chilensis*, the caudoventral portion of the corpus vertebrae protrudes markedly beyond the facies articularis caudalis (Text-fig. 4C). Further, in contrast to *P. chilensis*, there is a ridge along the midline of the ventral surface of the corpus vertebrae. The fovea cranioventralis is very marked (Text-fig. 4B). Whether the notch between the processus transversus and the processus articularis caudalis was closed by an osseous bridge (arcus interzygapophysialis) cannot be determined owing to breakage of the corresponding area. A lacuna interzygapophysialis is absent.

The fragmentary coracoid (Text-fig. 4D–E) resembles that of a pelagornithid from the middle Eocene of Belgium, which was tentatively referred to *Macroodontopteryx oweni* by Mayr and Smith (2010). The ventral portion of the extremitas omalis is broken, and the facies articularis scapularis is damaged. The facies articularis humeralis is comparatively small and has an almost planar surface. The portion of the extremitas omalis

between the sulcus supracoracoideus and the impressio ligamenti acrocoracohumeralis, which joins the omal end of the facies articularis humeralis, forms a sharp ridge. The processus procoracoideus is broken. The preserved portion of the shaft is very wide mediolaterally, and the foramen nervi supracoracoidei is small.

The acromion and facies articularis humeralis of the scapula (Text-fig. 4F) are broken, but it can be discerned that both were bent laterally, so that the lateral surface of the extremitas cranialis is markedly concave as in other pelagornithids. The tuberculum coracoideum is strongly developed. The facies articularis humeralis is more elongate than in *P. chilensis*.

The furcula of bony-toothed birds has only recently been described (Mayr and Rubilar-Rogers 2010; Mayr and Smith 2010). The extremitas sternalis of SMF Av 535 (Text-fig. 4G–J) is craniocaudally wide, but not as dorsoventrally deep as in *P. chilensis*. Contrary to the condition in *P. chilensis*, there is no elongate, concave articulation facet on its caudal surface, which in Neogene pelagornithids contacted a cranial projection of the sternum that is absent in Eocene species (Mayr *et al.* 2008; Mayr and Rubilar-Rogers 2010). As in *P. chilensis*, two marked fossae run along the dorsal surface of the scapi claviculares along the extremitas sternalis. These fossae are separated by an arch-like dorsal projection in the midline of the extremitas sternalis, which is broken in the holotype of *P. chilensis*. Cranially, the fossae are bordered by a ridge, which runs along the scapi claviculares and proceeds onto their medial surface. The scapi claviculares themselves are twisted and become craniocaudally compressed towards their midsection (Text-fig. 4J).

As far as comparisons are possible, the morphology of the fragmentary humerus (Text-fig. 4K) corresponds well with that of other Eocene pelagornithids (e.g. Bourdon *et al.* 2010; Mayr and Smith 2010). The shaft of the bone is craniocaudally compressed; the most proximal portion of the preserved fragment bears the marked protuberance on the cranial surface of the shaft near the crista bicipitalis, which is characteristic for pelagornithid birds (Text-fig. 4K; Mayr and Rubilar-Rogers 2010, fig. 5; Mayr and Smith 2010, text-fig. 7).

The ulna (Text-fig. 4L–M) exhibits a marked depressio radialis, which is absent in *P. chilensis*. The condylus dorsalis is small, and its rim is irregularly shaped, forming a salient bulge in the

midsection. The sulcus intercondylaris is shallow. The tuberculum carpalis is broken.

The carpometacarpus (Text-fig. 4N–P, R–T) is an elongate and slender bone, although less so than the corresponding bone of *P. chilensis*. Further in contrast to the latter species, the spatium intermetacarpale is not strongly reduced in length, i.e., the proximal and distal symphyses are not greatly expanded. The processus extensorius of the os metacarpale alulare (SMF Av 540) is very low, but not as elongate as in *P. chilensis*; the facies articularis alularis has a subplanar, slightly bifacet surface. Although much of the ventral surface of the proximal end is broken, it can be discerned that the fossa infratrochlearis was very large and marked as in *P. chilensis*. SMF Av 539 has a peculiar and distinctive morphology in that the base of the processus alularis is connected by an osseous strut with the cranial surface of the os metacarpale majus; this strut encloses an ovate, dorsoventrally traversing foramen (Text-fig. 4P). A similar structure has not been reported for other pelagornithids (Bourdon *et al.* 2010; Mayr and Rubilar-Rogers 2010) and is also absent in SMF Av 539. Just below the processus extensorius, there is a pneumatic opening in the cranial portion of the trochlea carpalis; the caudal rim of the dorsal portion of the trochlea carpalis bears a notch (SMF Av 539; Text-fig. 4T). The sulcus tendinosus is very shallow.

The phalanx proximalis digiti majoris (Text-fig. 4Q) is elongate and craniocaudally narrow. It bears a small processus internus indicis of similar development to that of extant Gaviiformes. There is a small but marked, ovate fossa ventralis. The fossa dorsalis is divided into two portions by an oblique bulge. The only other proximal phalanx of the major wing digit of a bony-toothed bird was reported by Walsh and Hume (2001) from the Miocene of Chile. This specimen comes from a much larger species and is craniocaudally narrower than the Ukrainian fossil.

There are two fragmentary tarsometatarsi in the Novopskov material, which we refer to Pelagornithidae (Text-fig. 4U–Y). SMF Av 543 differs from SMF Av 544 in that the foramen vasculare distale, especially its plantar opening, is smaller. Judging from the proximal widening of shaft, about one-third of the more complete specimen SMF Av 543 is missing. Because this fossil has an unusually inflated shaft, whose plantar and dorsal

TEXT-FIG. 4. Bones of a small pelagornithid (cf. *Odontopteryx toliapica* Owen, 1873) from the middle Eocene of Novopskov in Ukraine. A–C, third–fourth cervical vertebra (SMF Av 534) in dorsal (A), ventral (B) and lateral (C) view. D–E, extremitas omalis of right coracoid (SMF Av 536) in dorsal (D) and lateral (E) view. F, extremitas cranialis of left scapula (SMF Av 537) in lateral view. G–J, furcula (SMF Av 535) in caudal (G), dorsocaudal (H), cranial (I) and dorsolateral (J) view. K, left humerus (SMF Av 538; shaft and three fragments) in cranial view. L–M, distal end of right ulna (SMF Av 542) in ventral (L) and dorsal (M) view. N–O, right carpometacarpus (SMF Av 539) in ventral (N) and dorsal (O) view; P, detail of proximal end in ventral view. Q, left phalanx proximalis digiti majoris (SMF Av 541) in ventral view. R–T, proximal end of left carpometacarpus (SMF Av 540) in dorsal (R), cranial (S) and ventral (T) view. U–W, left tarsometatarsus (SMF Av 543) in plantar (U), dorsal (V) and medial (W) view. X–Y, left tarsometatarsus (SMF Av 544) in dorsal (X) and plantar (Y) view. Abbreviations: acr, acromion; cdd, condylus dorsalis; cdv, condylus ventralis; cor, corpus vertebrae; cos, processus costalis; cph, caput humeri; csc, cotyla scapularis; ext, processus extensorius; fac, facies articularis caudalis; fah, facies articularis humeralis; fcv, fovea craniocentralis; fns, foramen nervi supracoracoidei; for, foramen enclosed by strut from base of processus alularis to os metacarpale majus; fos, fossa along dorsal surface of scapula claviculae; fvt, fossa ventralis; ind, processus internus indicis; not, notch in caudal rim of dorsal portion of trochlea carpalis; ntc, notch between processus transversus and processus articularis caudalis; pne, pneumatic opening in trochlea carpalis; prj, arch-like dorsal projection of extremitas sternalis; prt, protuberance on cranial surface of humerus shaft; rdg, ridge along scapula claviculae; tbv, tuberculum ventrale; zyg, zygapophysis cranialis. Same scale bars for all figure panels except P.



surfaces are bulging (Text-fig. 4W), it may be from a juvenile individual, which is also supported by the fact that all bone structures are weakly marked. A definitive assessment of the individual age of SMF Av 543 is, however, not possible, as the proximal end of the bone, which would allow unambiguous determination of a juvenile condition, is missing. There is no fossa metatarsi I. The trochlea metatarsi II is shorter than the other trochleae and only weakly plantarly deflected. Its distal end is oriented obliquely to the longitudinal axis of the bone, a condition characteristic for many birds with splayed and webbed toes. The trochlea metatarsi III is medially inflected and in plantar view has a subtriangular outline. The trochlea metatarsi III of SMF Av 543 appears deeply incised, which is, however, owing to damage of the specimen. Likewise, the medial portion of the trochlea metatarsi IV is damaged, which makes the incisura intertrochlearis lateralis appear wider than it probably originally was. A canalis interosseus distalis is present. The distal end of the tarsometatarsus of Palaeogene Pelagornithidae is known from *Dasornis emuinus* ('*Neptuniavis miranda*') and *Odontopteryx toliapica* (Bourdon *et al.* 2010; Mayr and Rubilar-Rogers 2010), both of which are distinguished from the Ukrainian tarsometatarsi in that the trochlea metatarsi III is not medially inflected.

GAVIIFORMES Wetmore and Miller, 1926

GAVIIDAE Allen, 1897

COLYMBICULUS gen. nov.

Type species. Colymbiculus udovichenkoi, sp. nov.

Differential diagnosis. Small loon, the size of *Colymboides minutus* and ?*C. metzleri*. Distinguished from *Colymboides* in the following plesiomorphic features: (1) distal end of humerus with ventral portion more ventrally protruding (Text-fig. 5F, H); (2) ulna with smaller tuberculum carpale (Text-fig. 5M, P).

Derivation of name. From *Colymbus*, the old name for loons and grebes (suppressed by the International Commission on Zoological Nomenclature), and -culus, the Latin diminutive suffix.

Colymbiculus udovichenkoi, sp. nov.

Text-figure 5

Holotype. SMF Av 545 (Text-fig. 5C–D; left humerus lacking the proximal end).

Differential diagnosis. The new species differs from *Colymboides minutus* Milne-Edwards, 1867–1868 in that the distal end of the humerus is craniocaudally narrower, with the ventral portion more ventrally protruding, and in that the sulcus scapulothoracalis is wider (Text-fig. 5F, H and Storer (1956), figs 1a and 3g). It is distinguished from ?*Colymboides metzleri* Mayr, 2004a in that the ulna

has a proportionally smaller tuberculum carpale (Text-fig. 5), and from *Colymboides anglicus* Lydekker, 1891 in its smaller size (distal width of humerus 9.1 mm vs. 10.3 mm (after Harrison and Walker 1976b)) and in that the ventral portion of the distal end of the humerus is more ventrally protruding. The new taxon finally differs from *Colymboides belgicus* Mayr and Smith, 2002 in its much smaller size (distal width of ulna 5.6/6.0 mm vs. 12.0 mm) and in the less developed tuberculum carpale of the ulna.

Derivation of name. The new species is named after Nikolai Udovichenko, who first recognized the significance of the Novopokrov sand pit.

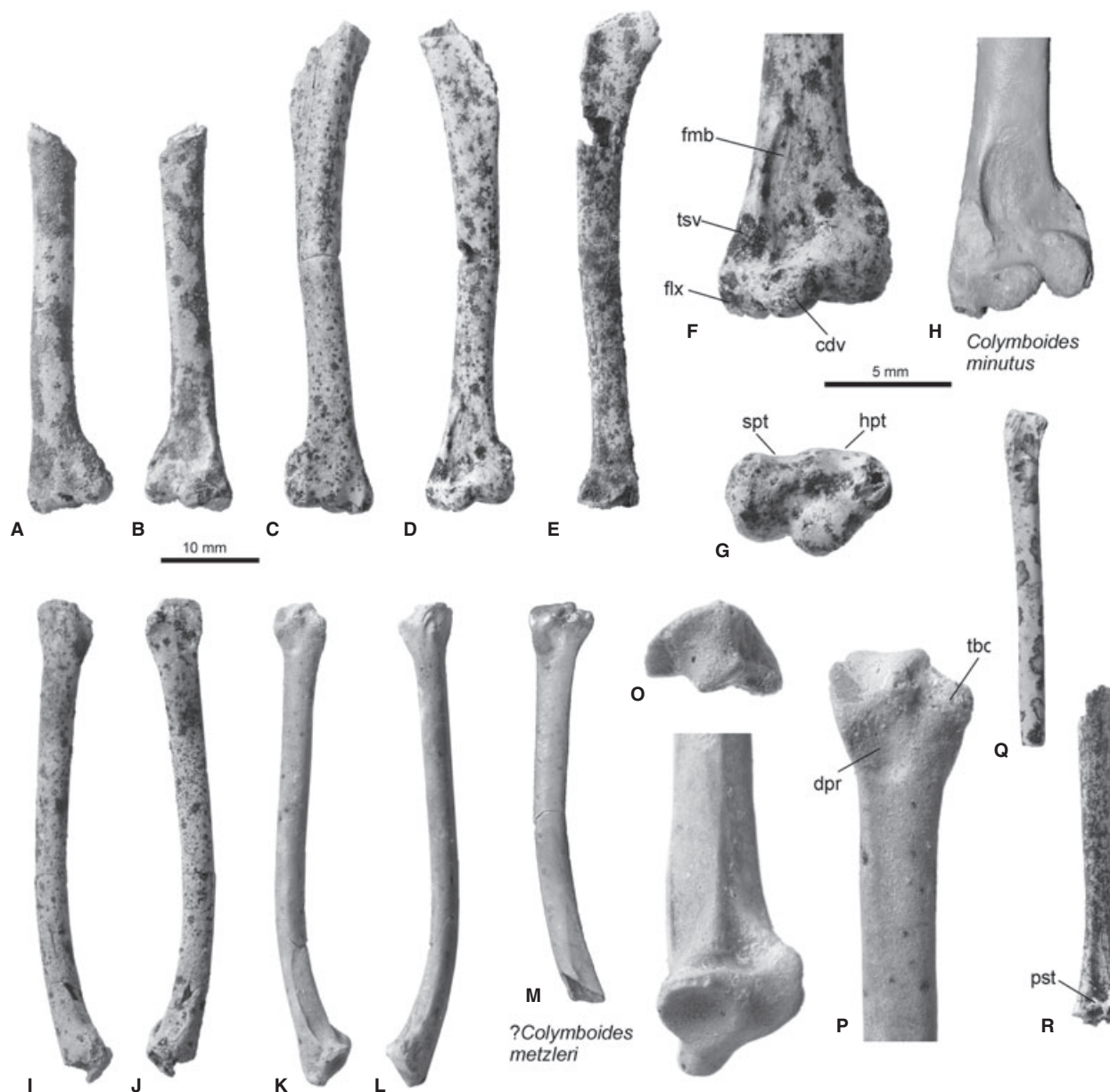
Referred specimens. SMF Av 546 (Text-fig. 5A–B; distal half of a right humerus); SMF Av 547 (Text-fig. 5E; right humerus lacking both ends); SMF Av 548 (Text-fig. 5K–L; right ulna); SMF Av 549 (Text-fig. 5I–J; left ulna lacking the olecranon); SMF Av 550 (Text-fig. 5Q; right radius lacking the proximal part); SMF Av 551 (Text-fig. 5R; fragmentary left tibiotarsus).

Type locality and horizon. Novopokrov, Luhansk region, Ukraine; middle Eocene (early Lutetian).

Measurements. Humerus (holotype, SMF Av 545), length as preserved, 49.9 mm; estimated total length, c. 60–62 mm; distal width, 9.1 mm. Ulna (SMF Av 548), length, 49.1 mm; distal width (condylus dorsalis to tuberculum carpale), 5.6 mm. SMF Av 549 (ulna), length as preserved, 49.4 mm; distal width (condylus dorsalis to tuberculum carpale), 6.0 mm.

Remarks. The following derived features support an assignment of *Colymbiculus* n. gen. to the Gaviiformes: humerus with (1) slanted cranial surface of the ventral portion of the distal end, (2) fossa musculi brachialis very long and bordered ventrally by a prominent ridge, (3) cranially prominent condylus ventralis, (4) very wide sulcus scapulothoracalis, and (5) epicondylus dorsalis connected by an elongate prominence with the tuberculum dorsale; ulna (6) much shorter than the humerus and with (7) a dorsoventrally flattened distal end, which (8) exhibits a narrow sulcus between the incisura tendinosa and rim of the condylus dorsalis.

Loons were quite diverse in the Palaeogene of Europe, and most species resemble the taxon *Colymboides*, which was originally erected for *C. minutus* from the early Miocene of France. The oldest gaviiform species described so far is *Colymboides anglicus* from the late Eocene of England, which is based on a coracoid and a referred humerus and frontal portion of the skull (Harrison and Walker 1976b). *C. belgicus* from the early Oligocene of Belgium is known from a proximal carpometacarpus and distal ulna (Mayr and Smith 2002). ?*C. metzleri* was described on the basis of an incomplete postcranial skeleton from the early



TEXT-FIG. 5. A–G, I–L, N–R, *Colymbiculus udovichenki*, gen. et sp. nov. (Gaviiformes) from the middle Eocene of Novopskov in Ukraine. H, distal humerus of *Colymboides minutus* from the early Eocene of Saint-G erand-le-Puy in France. M, ulna of *?Colymboides metzleri* Mayr, 2004a from the early Oligocene of Belgium. A, B, distal half of right humerus (SMF Av 546) in caudal (A) and cranial (B) view. C–D, left humerus lacking proximal end (holotype, SMF Av 545) in caudal (C) and cranial (D) view. E, incomplete right humerus (SMF Av 547) in cranial view. F–G, distal end of holotype humerus (SMF Av 545) in cranial (F) and distal (G) view. H, distal end of left humerus of *C. minutus* (NMB MA.2507) in cranial view. I–J, left ulna (SMF Av 549) in dorsal (I) and ventral (J) view. K–L, right ulna (SMF Av 548) in ventral (K) and dorsal (L) view. M, right ulna of *?C. metzleri* (IRSNB Av 85a–j) in ventral view. N–P, right ulna (SMF Av 548), proximal end in cranial view (N), distal end in distal (O) and ventral (P) view. Q, right radius (SMF Av 550) in dorsal view. R, left tibiotarsus (SMF Av 551) in cranial view. Abbreviations: cdv, condylus ventralis; dpr, depressio radialis; flx, processus flexorius; fmb, fossa musculi brachialis; hpt, sulcus humerotricipitalis; pst, pons supratendineus; spt, sulcus scapulo-tricipitalis; tbc, tuberculum carpale; tsv, tuberculum supracondylare ventrale. Same scale bar for A–E, H–M, and Q, as well as for F, G, N–P.

Oligocene of Germany; Mayr (2009b) referred loon bones from the early Oligocene of Belgium to this species. A foot of a *Colymboides*-like loon was further reported from the

late Oligocene of Germany (Mayr and Poschmann 2009), and Kurochkin (1976) mentioned the presence of *Colymboides* in the late Oligocene of Kazakhstan.

Description and comparison. All humeri lack the proximal end, and the crista deltopectoralis is also broken in all specimens. The bone is less elongate than the humerus of extant loons (*Gavia* spp.). As in *Colymboides* and *Gavia*, the tuberculum dorsale and epicondylus dorsalis are connected by an elongate prominence. The condylus ventralis is cranially prominent. The fossa musculi brachialis is very long and ventrally bordered by a marked ridge. As in *C. minutus*, the tuberculum supracondylare ventrale is less elongate than in crown group Gaviiformes, where it extends over almost the entire length of the fossa musculi brachialis. The sulcus scapulo-tricipitalis is wider than the sulcus humerotricipitalis. The processus flexorius is damaged in all specimens. The ventral portion of the distal end is more ventrally protruding than in *Colymboides minutus* and extant loons.

As in other Gaviiformes, the ulna is much shorter than the humerus. The proximal end of the bone resembles the ulna of *Colymboides minutus*. The tuberculum ligamenti collateralis ventralis is less marked than in crown group Gaviiformes and the rim of the cotyla ventralis less cranially projected. As in other Gaviiformes, the incisura radialis is marked and the impressio brachialis very long. The distal section of the shaft is dorsoventrally flattened, and there is a sharp longitudinal intermuscular ridge along the midline of its cranial surface. Seven papillae remigales can be counted in the proximal two-thirds of the shaft (SMF Av 5), and altogether, there may have been eleven as in *C. minutus* (Storer 1956). The distal end of the bone exhibits a distinct depressio radialis, and as in extant Gaviiformes, there is a narrow sulcus between the incisura tendinosa and the rim of the condylus dorsalis. The tuberculum carpale is, however, smaller and less protruding than in *Colymboides minutus*, *C. belgicus*, ?*C. metzleri* (Text-fig. 5M), and crown group Gaviiformes. Contrary to crown group Gaviiformes, the distal end of the radius does not bear two marked sulci tendinosi.

The fragmentary tibiotarsus resembles that of *Colymboides minutus*, but does not allow the recognition of many osteological features. The shaft is craniocaudally flattened; in its distal section, it has a flat cranial and a convex caudal surface. The wide sulcus extensorius is centrally positioned. The pons supratendineus is narrower than in *C. minutus*, but appears to be damaged in SMF Av 551.

AVES Linnaeus, 1758

AVES gen. et sp. indet.

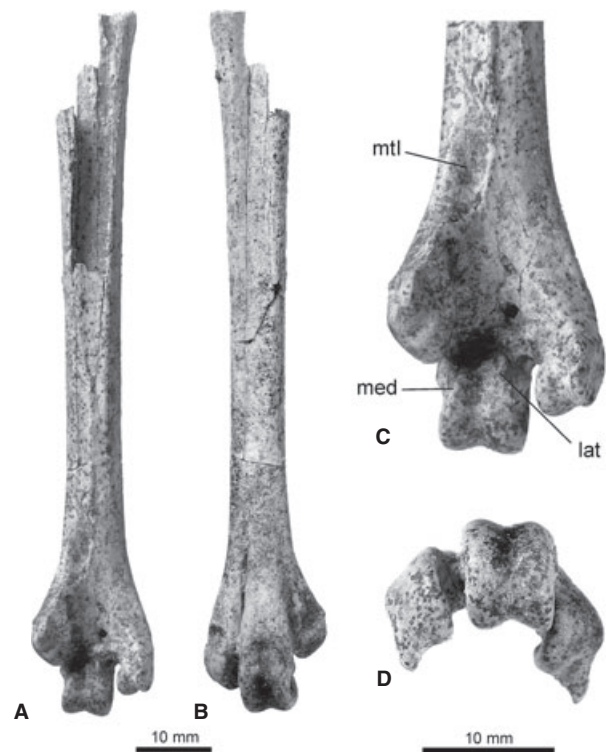
Text-figure 6

Referred specimens. SMF Av 552 (Text-fig. 6), a right tarsometatarsus lacking the proximal end.

Locality and horizon. Novopskov, Luhansk region, Ukraine; middle Eocene (early Lutetian).

Measurements. Length as preserved, 93.3 mm; estimated total length, c. 97 mm; distal width, 16.6 mm.

Remarks. SMF Av 552 lacks the proximal end, but the widening of the shaft indicates that only a small portion of



TEXT-FIG. 6. Right tarsometatarsus of an indeterminate bird (cf. *Itardiornis* Mourer-Chauviré, 1995) from the middle Eocene of Novopskov in Ukraine (SMF Av 552). A, plantar view. B, dorsal view. C, detail of plantar surface of distal end. D, distal end in distal view. Abbreviations: lat, lateral rim of trochlea metatarsi III; med, medial rim of trochlea metatarsi III; mtl, fossa metatarsi I. Same scale bars for A–B, and C–D.

the bone is missing. The trochlea metatarsi III is short and asymmetric, with the medial rim being shorter than the lateral one (Text-fig. 6C). The trochlea metatarsi II is plantarly deflected and reaches only the base of the trochlea metatarsi III; its lateral surface is excavated by a distinct fossa. The trochlea metatarsi IV has a subcylindrical shape and, like the trochlea metatarsi II, exhibits a plantarly directing flange. The foramen vasculare distale is small, and its dorsal opening is situated at the end of a distinct, narrow sulcus extensorius. A canalis interosseus distalis is present. The fossa metatarsi I is large and well developed; proximally, it is bordered by a rugosity of the shaft.

The derived morphology of the asymmetric trochlea metatarsi III is shared with galliform birds (Mayr 2000), some Rallidae (e.g. *Aramides ypecaha*, *Gallinula comeri*), and some extinct 'gruiform' taxa, such as *Walbeckornis* from the Palaeocene of Germany and *Itardiornis* from the late Eocene and early Oligocene of France (Mourer-Chauviré 1995; Mayr 2007). The small foramen vasculare distale, which is situated at the end of a narrow sulcus extensorius, is unlike the condition seen in Galliformes, from which the fossil is further distinguished by the

proportionally shorter trochlea metatarsi III. From pre-Oligocene fossil deposits, only stem group Galliformes are known (Mayr 2009a), which differ from SMF Av 552 in that the trochlea metatarsi II is not plantarly deflected. With tarsometatarsus dimensions of a female peacock (*Pavo cristatus*), the Novopskov fossil would be much larger than all known Eocene Galliformes. In overall morphology, the distal end of SMF Av 552 most closely resembles the distal tarsometatarsus of the presumed meselornithid *Itardiornis hessae* Mourer-Chauviré, 1995 from the late Eocene and early Oligocene of the Quercy fissure fillings in France (Mourer-Chauviré 1995). The Ukrainian fossil is, however, from a species that was twice as large as *I. hessae* (distal width of tarsometatarsus 16.6 mm vs. 7.7 mm (after Mourer-Chauviré 1995)), from which it is also distinguished by the marked sulcus extensorius. SMF Av 552 may be from a representative of core-Gruiformes, to which Rallidae and Messelornithidae belong (Mayr 2004b), but additional fossils are needed for an unambiguous identification.

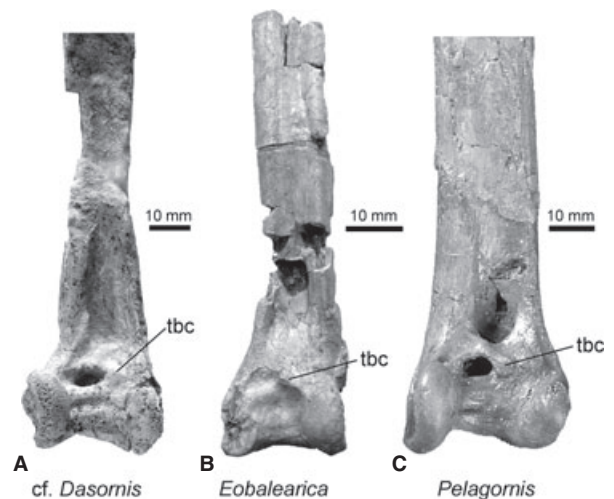
DISCUSSION

The Novopskov avifauna agrees with other early Palaeogene marine localities in that Pelagornithidae constitute the bulk of the seabird remains. As in Eocene localities in England (Harrison and Walker 1976a), Belgium (Mayr and Smith 2010) and Morocco (Bourdon *et al.* 2010), at least two species of very different size can be distinguished. The exact number of pelagornithid species in the Novopskov material is, however, difficult to assess because of the fragmentary nature of the specimens, and our cautious approach may underestimate the actual diversity of these birds (see the description concerning differences in the carpometacarpus and tarsometatarsi referred to *Odontopteryx* and the tibiotarsi referred to *Dasornis*). Taxonomic allocation of the Ukrainian remains is further aggravated by the fact that other early Palaeogene pelagornithid species are also based on fragmentary fossils. We have tentatively referred the Novopskov material to *Dasornis* sp. and *Odontopteryx toliapica*, which are the best-represented taxa in their respective size classes and which were originally described from the early Eocene of England (Harrison and Walker 1976a).

So far, only two unambiguously identified pelagornithid species were reported from the Paratethys region, which are *Pseudodontornis tshulensis* Averianov *et al.*, 1991 from the late Palaeocene of Kazakhstan and *Caspiodontornis kobystanicus* Aslanova and Burchak-Abramovich, 1982 from the 'middle' Oligocene of Azerbaijan (Averianov *et al.* 1991; Nesson 1992; Aslanova and Burchak-Abramovich 1999; Mayr 2009a). *P. tshulensis* is

based on mandible fragments, whereas the holotype of *C. kobystanicus* consists of a largely complete but poorly preserved skull. *C. kobystanicus* is of similar size to *Odontopteryx toliapica*, but has proportionally larger pseudo-teeth than this species and the small Ukrainian pelagornithid. As noted by Mayr (2009a), *C. kobystanicus* may be a junior synonym of the alleged anseriform *Guguschia nailiae* Aslanova and Burchak-Abramovich, 1968 from the same locality. Taxonomic allocation of *Pseudodontornis tshulensis* likewise needs to be revised, and the species may well be a representative of *Dasornis*.

Averianov *et al.* (1991) mentioned remains of *Odontopteryx* sp. from the middle and late Eocene of Uzbekistan and hypothesized that *Asiavis phosphatica* Nesson, 1986 and *Zheroia kurochkini* Nesson, 1988, which both also come from the Kyzulkum desert in Uzbekistan and which are known from a distal carpometacarpus and tibiotarsus respectively, may be bony-toothed birds (see also Mayr 2009a). Another misidentified avian taxon from the marine deposits of Central Asia, which probably represents a bony-toothed bird, is *Eobalearica tugarinovi* Gureev, 1949 from the middle Eocene of Kyrgyzstan (Nesson 1992), whose holotype is an incomplete tibiotarsus (Text-fig. 7B). The alleged affinities of this species with Gruidae were already doubted by Cracraft (1973), and its identification as a crane appears to have been influenced by the large size and presence of a tubercle near the pons supratendineus. Apart from being somewhat smaller, the *E. tugarinovi* holotype corresponds well with the Novopskov tibiotarsi referred to *Dasornis* (Text-fig. 7), and we



TEXT-FIG. 7. Distal ends of left tibiotarsi in comparison. A, cf. *Dasornis* Bowerbank, 1854 from the middle Eocene of Novopskov in Ukraine (SMF Av 529). B, *Eobalearica tugarinovi* Gureev, 1949 from the late Eocene of Kyrgyzstan (PIN 529/1). C, *Pelagornis chilensis* Mayr and Rubilar-Rogers, 2010 from the Miocene of Chile (MNHN SGO.PV 1061). Abbreviation: tbc, tubercle lateral of distal opening of canalis extensorius.

consider it likely that *Eobalearica* is a pelagornithid rather than a crane. Bourdon *et al.* (2010) further detailed that a distal ulna from the late Palaeocene of Kazakhstan, which was described by Nessov (1992, fig. 5O, P), belongs to Pelagornithidae.

The osteology of Palaeogene Pelagornithidae is still insufficiently known, and the morphologies of the furcula and the fourth cervical vertebra provide further evidence that Palaeogene and Neogene Pelagornithidae had quite different osteologies (see also Bourdon *et al.* 2010; Mayr and Rubilar-Rogers 2010).

Pelagornithidae co-occur with Prophaethontidae in other early Palaeogene sites, such as the early Eocene London Clay in England, the middle Eocene of Belgium and the Late Palaeocene – Early Eocene Ouled Abdoun Basin in Morocco (Mayr 2009a). We could not identify prophaethontids in the Novopskov material, and the locality is instead notable for the association of bony-toothed birds with Gaviiformes. *Colymbiculus udovichenkoi* gen. et sp. nov. is the earliest fossil record of a loon from the Eurasian continent and more than 10 myr older than *Colymboides anglicus* from the late Eocene (MP 17) of England. With older records from the Cretaceous and Palaeocene of the southern hemisphere being based on controversial material (see Mayr 2009a), it is also the earliest unambiguously identified loon in general. Being of the size of *Colymboides minutus* and ?*C. metzleri*, the new species for the first time documents the existence of small loons in the middle Eocene. Although small size may be plesiomorphic for Gaviiformes, the interrelationships of Palaeogene loons are unknown and there were large gaviiforms (*C. belgicus*) in the early Oligocene. Small Gaviiformes were reported from both marine (*Colymbiculus udovichenkoi*, ?*C. metzleri*) and lacustrine (*Colymboides minutus*) deposits, and one specimen with preserved stomach content documents that Palaeogene loons were already piscivorous (Mayr 2004a). It is notable that the disappearance of small loons in the early Miocene (MN 4, Mlíkovský 2002) temporally coincides with the occurrence of grebes (Podicipedidae), but given the sparse fossil record, it would be premature to speculate about a possible ecological replacement.

In pelagornithid diversity, the middle Eocene Paratethyan avifauna appears to have been similar to that of the North Sea. The absence of prophaethontids and relative abundance of Gaviiformes in the Novopskov locality, however, indicate faunistic differences concerning the remaining seabirds. In concert with fossils from other localities, the specimens described in the present study further document profound differences between the middle Eocene and extant marine avifaunas of Europe (see also Mayr 2009a; Mlíkovský 2009). Not only do bony-toothed birds and small loons no longer exist, but the Novopskov and other early/middle Eocene marine avifaunas also indicate

that most of today's predominant taxa of seabirds did not occur in the early Palaeogene of Europe, such as modern-type Procellariiformes and Pelecaniformes, Laridae, Alcidae and other marine Charadriiformes.

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