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A GIANT EARLY PLEISTOCENE BIRD FROM EASTERN EUROPE: UNEXPECTED COMPONENT OF TERRESTRIAL FAUNAS AT THE TIME OF EARLY *HOMO* ARRIVAL

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ABSTRACT—Giant birds, comparable in size to elephant birds and moa, have never been reported from Europe. Here, we describe a femur from the lower Pleistocene of the north Black Sea area (Crimea) that is referred to *Pachystruthio dmanisensis*, comb. nov., a giant bird with an estimated body mass of about 450 kg. This value makes this extinct bird one of the largest known avians (comparable to *Aepyornis maximus*) and the only bird of such giant size in Europe and the Northern Hemisphere in general. In contrast to very large insular birds, *Pachystruthio dmanisensis* was a good runner, which may be explained by its coexistence with large carnivorous mammals. *Pachystruthio dmanisensis* and associated assemblage of fossil mammals are shared with the Dmanisi locality in Georgia (~1.8–1.7 Ma); thus, this giant bird was likely a typical component of eastern European faunas at the time of early hominin arrival. We suggest that *Pachystruthio dmanisensis*, together with early *Homo* and a variety of mammals, reached the northern Black Sea region via the southern Caucasus and Anatolia, because the older (Pliocene) finds of this fauna are known from Georgia and Turkey.

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INTRODUCTION

The Cenozoic diversity of flightless, large-bodied ground birds was higher than at present, and several now extinct groups include notably large representatives (Angst and Buffetaut, 2017). The true giants of the avian world were the largest species of mihirungs (Dromornithidae) from the Miocene of Australia and elephant birds (Aepyornithidae) from the late Quaternary of Madagascar, with an estimated body mass of up to 700 kg (Murray and Vickers-Rich, 2004; Hansford and Turvey, 2018; but see below). The size of these birds greatly exceeded that of the largest living bird, the common ostrich (*Struthio camelus*), which weighs up to 150 kg (Folch, 1992).

Fossil birds of such an impressively giant size have never been documented from Europe or the Northern Hemisphere in general (Angst and Buffetaut, 2017). The North American late Quaternary giant bird *Titanis walleri* Brodkorb, 1963, weighed about 150 kg (Baskin, 1995), and the Paleogene Gastornithidae most probably weighed no more than 200 kg (Angst and Buffetaut, 2017). Although several large ostriches (see, however, the discussion concerning their taxonomic affinities) have been described from Neogene to Quaternary sediments of Eurasia (Boev and Spassov, 2009; Mayr, 2017), they were never considered to be as large as elephant birds or the New Zealand moa. Here, we report a femur of a very large bird from the early Pleistocene of the Crimean Peninsula (north Black Sea region). The estimated body mass of this bird, calculated in accordance with the formulae widely used for fossil giant birds

(Campbell and Marcus, 1992; Worthy and Holdaway, 2002; Field et al., 2013; Handley et al., 2016), is about 450 kg. This calculated value is comparable to that of *Aepyornis maximus* and thus makes this eastern European giant bird one of the largest (heaviest) known avians, being smaller only than the late Miocene Australian *Dromornis stirtoni* and the Quaternary aepyornithid *Vorombe titan* (Murray and Vickers-Rich, 2004; Handley et al., 2016; Hansford and Turvey, 2018). We further propose a revision of the previously named late Cenozoic ostrich-like birds from eastern Europe and highlight a previously unrecognized wide distribution of giant birds in this region at the time of the arrival of early *Homo* in the early Pleistocene.

Institutional Abbreviations—**D**, collection of the Institute of Paleobiology of the National Museum of Georgia, Tbilisi, Georgia; **PIN**, Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia.

LOCALITY

The specimen comes from the recently discovered Taurida Cave in the Crimean Peninsula, north Black Sea region (Fig. 1; see Lopatin et al., 2019, for details on geology and fauna). The associated late Villafranchian fauna of the locality comprises a variety of mammals, including representatives of the genera *Archidiskodon*, *Arvernoceros*, *Bison* (*Eobison*), *Canis*, *Elasmotherium*, *Equus*, *Leptobos*, *Gazellospira*, *Homotherium*, *Hypolagus*, *Hystrix* (*Acanthion*), *Pachycrocuta*, *Paracamelus*, *Pontoceros*, and *Stephanorhinus* (see Lopatin et al., 2019). Associated bird remains include the extinct Villafranchian bustard *Tetrax kalmani* Jánossy, 1972.

The association of *Leptobos* and *Eobison* indicates an age of 1.8–1.5 Ma. The assemblage of fossil mammals (and birds, e.g.,

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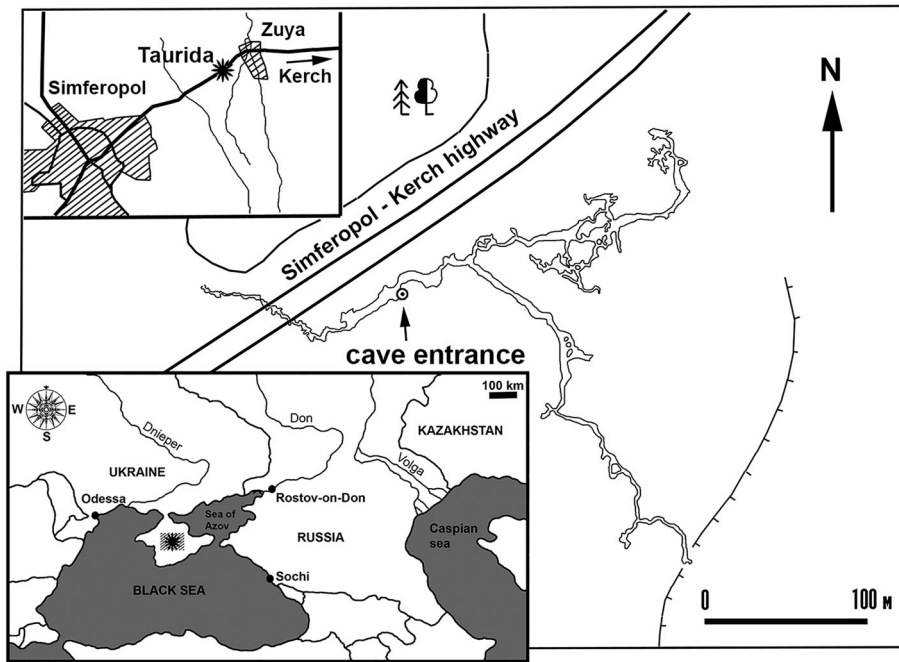


FIGURE 1. Map showing the geographical location of the fossil locality and the cave plan.

Pachystruthio), however, is substantially similar to that of the Dmanisi locality, which indicates an age close to 1.8–1.7 Ma (Lopatin et al., 2019).

SYSTEMATIC PALEONTOLOGY

Order ?STRUTHIONIFORMES

Family INCERTAE SEDIS

Genus *PACHYSTRUTHIO* Kretzoi, 1954

?*PACHYSTRUTHIO* *DMANISENSIS* (Burchak-Abramovich and Vekua, 1990), comb. nov.
(Fig. 2A, C, E, F)

Holotype—D70, a right femur (Vekua, 2013).

Type Locality—Dmanisi, Georgia; lower Pleistocene (1.85–1.78 Ma; Ferring et al., 2011).

Referred Specimen—PIN 5644/56, a nearly complete left femur from the Taurida Cave, Crimean Peninsula (Fig. 1); early Pleistocene (late Villafranchian).

Remarks—The distinctive morphology of PIN 5644/56 (see description below) precludes assigning this giant bird to the genus *Struthio*. Furthermore, PIN 5644/56 corresponds well with '*Struthio*' *dmanisensis* Burchak-Abramovich and Vekua, 1990, from the early Pleistocene of Georgia and can be referred to this extinct species. In addition to its very large size, the highly distinctive feature shared by the new specimen and '*S.*' *dmanisensis* is the exceptionally robust femoral shaft. The robustness index (minimal lateromedial shaft width divided by total length, expressed as a percentage) is 20% in the new specimen and '*S.*' *dmanisensis* from Dmanisi (Burchak-Abramovich and Vekua, 1990). This index is 12.8–16.4 ($n=11$) in modern *Struthio camelus* (Burchak-Abramovich, 1953; Burchak-Abramovich and Vekua, 1990; Vekua, 2013; this study). In the very large extinct ostriches *S. oldawayi* Lowe, 1933, and *S. karatheodoris* Forsyth Major, 1888, this index also does not exceed 16 (Burchak-Abramovich and Vekua, 1990). Referral to '*S.*'

dmanisensis is further supported by the general faunal similarity between the localities of Dmanisi and Taurida (see above).

Other named taxa of very large birds, which show remarkable genus-level osteological differences from modern ostriches, are the late Pliocene '*Struthio*' *transcausicus* Burchak-Abramovich and Vekua, 1971, and the early Pleistocene *Struthio* (*Pachystruthio*) *pannonicus* Kretzoi, 1954. The latter species was described based on a remarkably large and morphologically distinct pedal phalanx from the Kisláng locality in Hungary (Kretzoi, 1954). The fossil assemblage from Kisláng has a mixture of Pliocene–early Pleistocene taxa, dated 3.5–1.7 Ma, but the absolute majority of small mammals belong to biozones MN17–MQ1, 2.0–1.6 Ma (Mayhew, 2012). This date corresponds well with the age of the Dmanisi locality (1.85–1.78 Ma; Ferring et al., 2011). The older '*S.*' *transcausicus* was described based on a pelvis from the late Pliocene (MN16b; 3.1–3.0 Ma; Bukhsianidze and Kohiava, 2018) of Georgia (Burchak-Abramovich and Vekua, 1971). The pelvis of '*S.*' *transcausicus* also differs morphologically from that of ostriches (Burchak-Abramovich and Vekua, 1971). These three late Cenozoic eastern European taxa are thus giant birds that are notably different from modern and extinct *Struthio* in morphology. Hence, given the close ages of the localities, absolute size similarities, and generally low diversity of giant flightless birds in continental deposits (and in Europe in particular), it is plausible to classify '*S.*' *dmanisensis*, '*S.*' *transcausicus*, and '*S.*' (*P.*) *pannonicus* within the genus *Pachystruthio*, although the specific identity of these taxa remains to be confirmed. Importantly, the morphological distinctiveness of these eastern European Pleistocene giant birds cannot be explained simply by their large size, because the very large *S. oldawayi* from Tanzania is morphologically similar to modern *Struthio* and has a considerably thinner femoral shaft (Table 1; Lowe, 1933; Burchak-Abramovich and Vekua, 1990). Affinities of *Pachystruthio* are unclear, and its referral to the order Struthioniformes remains to be confirmed.

The separate generic status of *Pachystruthio* is supported by the presence of a morphologically distinct and very thick (2.9–3.3 mm) aepeyornithoid eggshell in the late Pliocene–early

Pleistocene of Azerbaijan (Burchak-Abramovich, 1953; Mikhailov and Kurochkin, 1988), which was associated with bone remains of ‘S.’ *transcaucasicus* (see Burchak-Abramovich and Vekua, 1971). Eggshell associated with the holotype of *P. pannonicus* is also much thicker (2.6–3.4 mm) than in modern ostriches and, unlike ostriches, has pore canals, which form irregular longitudinal channels (Kretzoi, 1954).

The evolutionary lineage of these giant early Pleistocene birds can probably be traced back to the early Pliocene and even Miocene of Anatolia: a very large femur from the early Pliocene of the Çalta locality in Turkey (Jannoo and Sen, 1998) may belong to *Pachystruthio*. The extinct species *Struthio karatheodoris* was described based on a slightly smaller, but still very large femur from the late Miocene (Maeotian) of Samos Island (Martin, 1903), which was a part of the Anatolian mainland at that time (Popov et al., 2004). This specimen notably differs in proportions from modern and extinct ostriches (Martin, 1903) and thus could belong to this lineage as well. Sauer (1979) further mentioned thick aepyornithoid eggshells in the middle Miocene Çandır locality in Turkey, which he attributed to the same evolutionary lineage as *P. pannonicus*.

In addition to *Pachystruthio*, ostriches similar to members of the modern genus *Struthio* are also present in the latest Cenozoic (Plio-Pleistocene) fossil record of eastern Europe (Table 2). They are represented by an unnamed species from the early Pliocene (MN15) of the Odessa catacombs in southern Ukraine (Burchak-Abramovich, 1953) and an ostrich from the early Pleistocene (MN17) of the Liventsovka locality (Sea of Azov area, Russia), which was referred to *Struthio asiaticus* Milne-Edwards, 1871, by Kurochkin and Lungu (1970). These forms are smaller than the species of *Pachystruthio* (Table 1), although they are somewhat larger than the living *S. camelus* and the Pliocene Siwalik *S. asiaticus*. The specimens from the Odessa catacombs and Liventsovka may represent one species; Mikhailov (1988) had referred a large egg from the Neogene (probably late Pliocene or early Pleistocene; Burchak-Abramovich and Vekua, 1971) of southern Ukraine to *Struthiolithus chersonensis* (Brandt, 1873). The eggshell thickness in *S. chersonensis* ranges from 2.6 to 2.9 mm, which is comparable to that of the Odessan ostrich (2.7–3.3 mm; Burchak-Abramovich, 1953), but the specimens’ referral to one species is unclear. The early–middle Villafranchian European ostrich has not been recorded in the younger deposits of the north Black sea region and thus most likely was replaced in the late Villafranchian by the larger, southern migrant *Pachystruthio*.

DESCRIPTION

Specimen PIN 5644/56 (Fig. 2A, C, E, F) has a completely preserved shaft and partly damaged proximal and distal ends. The general proportions of the specimen are elongate as in modern *Struthio* and smaller taxa of moa and Phorusrhacidae, but in contrast to larger species of Aepyornithidae, Dromornithidae, and Emeidae, which have very robust femora with a strongly concave medial margin of the shaft. Such a concavity of the medial margin is poorly pronounced in PIN 5644/56, but it is still better expressed than in modern *Struthio*, which have subparallel medial and lateral margins of the femoral shaft.

A large part of the facies articularis antitrochanterica is preserved, indicating that the trochanter femoris was not prominent proximally, as in modern *Struthio* and in contrast to Aepyornithidae. The pneumatic foramen on the caudal surface of the proximal end is present but small (as in ‘S.’ *dmanisensis*), not contacting the articular surface of the caput femoris. On the caudal surface of the shaft, there is a well-developed linea intermuscularis caudalis, which bifurcates proximally, as in *Struthio*. In contrast to modern ostriches, this line is more centrally located (more medially in *Struthio*) and becomes indiscernible

TABLE 1. Basic measurements (in mm) of the femur in *Pachystruthio pannonicus* and selected species of *Struthio*.

Dimension	? <i>Pachystruthio dmanisensis</i> (n = 2), early Pleistocene, Dmanisi; after Burchak-Abramovich and Vekua (1990) and Taurida Cave	? <i>Pachystruthio dmanisensis</i> (n = 2), early Pleistocene, Dmanisi; after Burchak-Abramovich and Vekua (1990) and Taurida Cave	<i>Struthio oldawayi</i> , early Pleistocene, Olduvai Gorge; after Burchak-Abramovich and Vekua (1990)	<i>Struthio karatheodoris</i> , late Miocene, Samos; after Martin (1903)	<i>Struthio</i> sp., early Pleistocene (Gelasian), Liventsovka; this study	<i>Struthio</i> sp., early Pliocene, Odessa Catacombs; after Burchak-Abramovich (1953)	<i>Struthio camelus</i> (n = 11), Recent; after Burchak-Abramovich (1953), Burchak-Abramovich and Vekua (1990), and our data	<i>Struthio molybdoptanes</i> , Recent; after Burchak-Abramovich (1953)
Greatest (lateral) length	~390	~380, 385	~400	360	—	>342	294–337	279
Minimal shaft height (oblique craniocaudal)	74.7	76, 76	~65	—	63.5	67	42–57	46
Minimal shaft width (mediolateral)	59.3	54	—	55	—	49	33–47	33

TABLE 2. Described or figured bone remains of fossil *Struthio* and ostrich-like birds from the Pliocene and the Pleistocene of Europe, Turkey, and Transcaucasia.

Original assignment	Geography	Locality	Age	Osteological material	Reference	Current taxonomic assignment (this paper)
? <i>Pachystruthio dmanisensis</i>	Crimea	Taurida	Early Pleistocene (1.8–1.5 Ma)	Femur	This paper	? <i>Pachystruthio dmanisensis</i>
<i>Struthio dmanisensis</i>	Georgia	Dmanisi	Early Pleistocene (1.85–1.78 Ma)	Several femora	Burchak-Abramovich and Vekua, 1990; Vekua, 2013; Zelenkov and Kurochkin, 2015	? <i>Pachystruthio dmanisensis</i> , comb. nov.
<i>Struthio (Pachystruthio) pannonicus</i>	Hungary	Kisláng	Early Pleistocene (2.0–1.6 Ma)	Pedal phalanx	Kretzoi, 1954	<i>Pachystruthio pannonicus</i>
<i>Struthio asiaticus</i>	Russia, Rostov-on-Don region	Liventsovka	Early Pleistocene (~2.6–2.0 Ma)	Various leg bones	Kurochkin and Lungu, 1970; Baigusheva, 1971; Zelenkov and Kurochkin, 2015	<i>Struthio</i> sp.
<i>Struthio transcaucasicus</i>	Georgia	Kvabebi	Late Pliocene (3.2–2.5 Ma)	Pelvis	Burchak-Abramovich and Vekua, 1971; Zelenkov and Kurochkin, 2015	? <i>Pachystruthio transcaucasicus</i> , comb. nov.
<i>Struthio</i> sp.	Turkey	Çalta	Early Pliocene (4.2–3.6 Ma)	Various leg bones (femora, tibiotarsus, tarsometatarsi)	Janoo and Sen, 1998	? <i>Pachystruthio</i> sp.
<i>Struthio</i> sp.	Ukraine	Odessa catacombs	Early Pliocene (3.8–3.7 Ma)	Many postcranial bones	Burchak-Abramovich, 1952; Zelenkov and Kurochkin, 2015	<i>Struthio</i> sp.

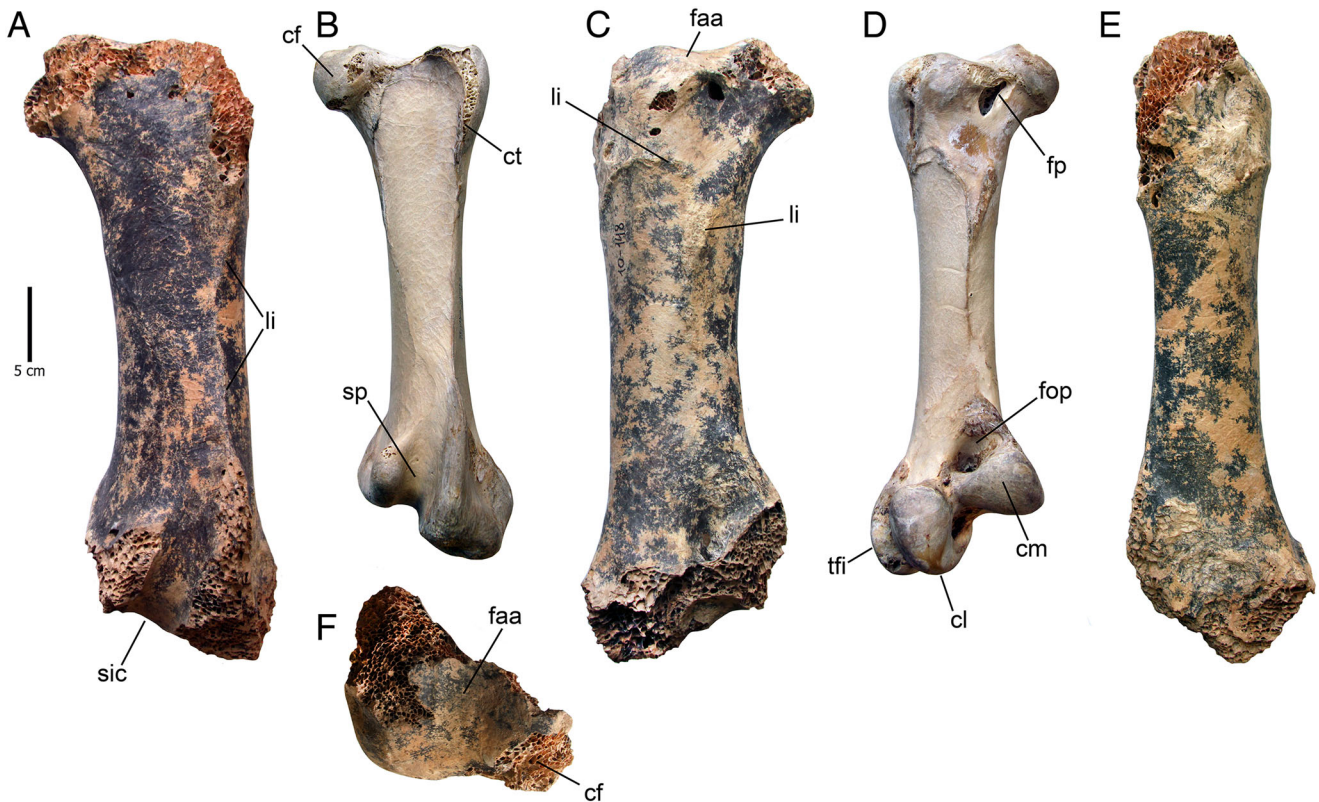


FIGURE 2. Fossil femora of an extinct giant bird from the Crimean Peninsula (eastern Europe), with that of an average Recent ostrich for comparison. **A, C, E, F**, *Pachystruthio dmanisensis*, comb. nov., specimen PIN 5644/56, from Taurida Cave, Crimean Peninsula (early Pleistocene); **B, D**, *Struthio camelus*, osteological collection of PIN 1741-1. **A, B**, cranial view; **C, D**, caudal view; **E**, lateral view; **F**, proximal view. **Abbreviations**: **cf**, caput femoris; **cl**, condylus lateralis; **cm**, condylus medialis; **ct**, crista trochanteris; **faa**, facies articularis antitrochanterica; **fop**, fossa poplitea; **fp**, foramen pneumaticum; **li**, linea intermuscularis; **sic**, sulcus intercondylaris; **sp**, sulcus patellaris; **tfi**, trochlea fibularis.



FIGURE 3. Map showing distribution of bony remains of the giant species of *Pachystruthio* (large ostrich silhouettes) and smaller *Struthio* ostriches (small ostrich silhouettes) in the Black Sea region in the Pliocene (5.3–2.6 Ma; blue), Gelasian (2.6–1.8 Ma; green), and Calabrian (1.8–0.8 Ma; brown). *Pachystruthio* from Hungary (Kretzoi, 1954) is not shown. Localities: 1, Odessa catacombs (early Pliocene); 2, Kvabebi (late Pliocene); 3, Liventsovka (Gelasian); 4, Taurida Cave (Calabrian); 5, Dmanisi (Calabrian).

distally, near the mid-length of the bone. In *Struthio*, this line bifurcates distally, thus producing a prominent lateral branch, which extends distolaterally. In the fossil specimen, the lateral branch is indistinct.

The linea intermuscularis cranialis, connecting the distal part of the crista trochanteris and the proximal part of the lateral crest of the sulcus patellaris, is placed more medially than in modern *Struthio* and has a medial curvature near the mid-shaft that is absent in modern *Struthio*.

Distally, the fossa poplitea is notably shallower than in *Struthio* and does not extend far proximally. The proximal margin of the condylus medialis, bordering this sulcus caudally, is more steeply inclined than in modern *Struthio*. The sulcus intercondylaris, which is preserved between the damaged condylae, is more obliquely oriented. The lateral side of the sulcus curves distally steeply, which may indicate a strongly distally protruding condylus lateralis, as in Aepyornithidae. A proximal extension of the trochlea fibularis, which is well pronounced in modern *Struthio* and protrudes more proximally than the condylus lateralis, is poorly developed in the fossil. This crest is positioned approximately level with the proximal margin of the condylus lateralis. The lateral surface of the distal end, just proximal and dorsal to the epicondylus lateralis, is nearly flat and is not concave as in *Struthio*. In dorsal view, the distal end protrudes only slightly laterally relative to the shaft, in contrast to *Struthio*.

WEIGHT ESTIMATION

The body mass of a bird may be reconstructed based on femoral measurements using several empirical formulae, including the following ones that are widely used (see discussion in Handley et al., 2016) for large avian taxa: $\log_{10}M = 2.411 \times \log_{10}LCF - 0.065$ (Campbell and Marcus, 1992) and $\ln M = 2.4 \times \ln Fc - 0.11$ (Field et al., 2013), in which M is body mass and LCF and Fc are the least shaft circumference and the central shaft circumference, respectively. These measurements equal 240 mm in PIN 5644/56 and are actually the same in this specimen, because the mid-shaft is the thinnest part of the femur. The body mass of PIN 5644/56, calculated with these formulae, equals 462 and 453 kg, respectively.

The regressions used are based on modern avian diversity, which does not include such large-bodied forms; thus, the resulting calculations should be taken as an approximation. These

formulae would likely provide overestimated results when applied to morphologically strongly modified taxa with unusual limb proportions, for example, large species of moa (see Brassey et al., 2013) and aepyornithids. Accordingly, we note that the femur of *Pachystruthio* is generally similar to that of *Struthio* in overall morphology; thus, applying linear regressions to this taxon would likely provide a more reliable estimation.

DISCUSSION

The new fossil and mass estimations show that eastern Europe (Hungary through northern Caucasus) was inhabited in the early Pleistocene by some of the largest known giant birds, albeit of unclear taxonomic affinities. We tentatively assign them to the extinct genus *Pachystruthio*, although *P. pannonicus* from Hungary and ‘S.’ *dmanisensis* from Georgia and Crimea are based on different skeletal elements and thus direct comparisons of these two species is not yet possible. However, these similarly sized taxa are known from roughly contemporaneous localities and thus might even represent one species, which in this case would be the only bird of such a formidable size in the Northern Hemisphere.

Although similar in size to elephant birds, *Pachystruthio* differs from *Aepyornis maximus* and other large birds in having a relatively gracile and elongate femur, comparable to (although notably larger than) that of modern ostriches and smaller species of moa, aepyornithids, and phorusrhacids. The overall similarity to the modern ostrich indicates that *Pachystruthio* was a better runner than the graviportal giant species of aepyornithids. This distinctive morphological feature may be explained by the continental distribution of *Pachystruthio*. In contrast to other giant birds, *Pachystruthio* lived with a variety of highly specialized large carnivorous mammals, such as the giant cheetah (*Actionyx pardinensis*), giant hyenas (*Pachycrocuta brevirostris*), and saber-toothed cats (*Homotherium* spp., *Megantereon* spp.). It has been shown that large animals, including such massive forms as young *Mammuthus*, constituted a significant part of the prey of some early Pleistocene carnivorous mammals, especially *Homotherium* (Palmqvist et al., 2003). However, the great body mass of *Pachystruthio* suggests that it might not have been as good a runner as modern ostriches. Because of their huge size, adult individuals of *Pachystruthio* were obviously

less vulnerable than young individuals and smaller *Struthio* ostriches.

The appearance of the giant *Pachystruthio* birds in the late Villafranchian of eastern Europe coincides with a notable reorganization of the Eurasian terrestrial mammal faunas, which occurred at around the Olduvai subchron (former Pliocene–Pleistocene boundary; Rook and Martínez-Navarro, 2010; Vislobokova and Tesakov, 2013). In the northern Caucasus, the late Villafranchian (early Apsheronian) stage is characterized by an increased aridity and further expansion of open environments, such as steppes and semideserts, which first became widespread in this region in the middle Villafranchian (Naidina and Richards, 2016). In the late Villafranchian, several southern faunal elements, such as *Pachystruthio* and a number of extinct mammals, reached the north Black Sea region from Transcaucasia, as evident from the faunal similarity between the Taurida and Dmanisi localities (Lopatin et al., 2019), from where the oldest European skeletal remains of *Homo* are known (Ferring et al., 2011; see also Spassov, 2016). The presence of *Pachystruthio* in several early Pleistocene sites in eastern Europe (Fig. 3) indicates that these giant birds were a characteristic, although previously neglected, component of the terrestrial faunas at the time of early *Homo* arrival. These large birds might have been a source of meat, bones, feathers, and eggshell for early hominin populations.

It has been shown that a larger body mass is energetically advantageous in utilizing tougher, low-nutrition food due to decreased mass-specific metabolic demands in larger animals ('Jarman-Bell Principle'; see Müller et al., 2013). Murray and Vickers-Rich (2004) relate the evolutionary increase of body mass in mihirungs (Dromornithidae) to an increasing aridity in Australia during the Neogene–Pleistocene. This concept may also be applied to the large flightless birds of continental northern Eurasia, such as *Pachystruthio* and the Eocene–Pliocene Eogruidae (Ergilornithidae). The latter also became progressively larger as aridity increased in the Neogene of eastern Europe and Central Asia (Kurochkin, 1981; Zelenkov et al., 2016). The very large body mass (more than 250 kg; Buffetaut and Angst, 2017) of the late Pleistocene Chinese ostrich *S. anderssoni* may also be explained by an increase in aridity in Inner Asia during the cold climatic phases of the glacial periods (Lu et al., 2013).

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