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The fossil ostrich *Struthio dmanisensis* sp. n. from the Lower Pleistocene of eastern Georgia

[With Plate I and 2 text-figs]

Kopalny struś *Struthio dmanisensis* sp.n. z dolnego plejstocenu wschodniej Gruzji

Abstract. *Struthio dmanisensis* sp. n. has been described on the basis of a femur from the Lower Pleistocene deposits of Dmanisi in eastern Georgia. The bone is larger and stouter than in the present-day Ostrich. Its stoutness suggests affinity to *S. pannonicus*.

I. INTRODUCTION

The right femur of an ostrich of huge size was found among the fossil bones of mammals during archaeological-palaeontological excavations carried out by the Institutes of History and Palaeobiology at the village of Dmanisi in eastern Georgia. It was a second find of the fossil ostrich in Georgia. The first was a pelvis of *Struthio transcaucasicus* from the Middle Akchagil of the Kwabebi region. Fragmentary egg-shells, presumably of the said *S. transcaucasicus*, are also frequently met with in Upper Pliocene deposits in eastern Georgia and western Azerbaydzhan.

So far femora of 6 fossil ostriches are known from all over the Old World: (1) *S. karatheodoris* Forsyth Major, 1888, Meotis, Samos Island, femur and pelvis, (2) *S. anderssoni* Lowe, 1931, Upper Pleistocene, China, femora and egg-shells, (3) *S. brachydactylus* Burchak-Abramovich, 1953, Meotis, Hipparion fauna, Ukraine, among other bones 2 complete and 2 fragmentary right femora, (4) *Struthio* sp., Middle Pliocene, karst cave near Odessa, 3 right femora, (5) *Struthio* sp., Meotis, Hipparion fauna, Emetovka, Odessa Oblast, 1 right femur and (6) *S. oldawayi* Lowe, 1933, Lower Pleistocene, Olduvai Gorge, Tanzania.

II. DESCRIPTIVE PART

The bone under study is typical of ostriches and differs distinctly from those of the members of three present-day families of two remaining orders of the *Ratitae*: *Rheiformes* (*Rheidae*) and *Casuariiformes* (*Casuariidae* and *Dromiceidae*). The morphological differences are essential and lie, besides the general size of the bone, among other things, in the arrangement of the distal articular portion of the bone in relation to the bone shaft and in the shape of the fibular condyle.

Order: *Struthioniformes* (LATHAM, 1790)
Family: *Struthionidae* VIGORS, 1925
Genus: *Struthio* LINNAEUS, 1758
Species: *Struthio dmanisensis* sp. nova

Holotype: femur dex. ad.
Type locality: Dmanisi, eastern Georgia
Age: Oldest Pleistocene
Place of storage: Institute of Palaeobiology, Ac. Scs, Georgian SSR, Tbilisi

Diagnosis

The general shape of the bone is typical of the genus *Struthio*. It is a very large-sized bone (ca 380 mm in length) and very stout, the „stoutness" index (shaft-width to bone-length ratio expressed as a percentage) being 20, whereas in other species it ranges from 12 to 17. The caput femoris protrudes conspicuously (15 mm) above the upper level of the trochanter major. The trochanter minor lies wholly on the linea aspera. The fossa patellaris is comparatively small, it widens gradually downwards, in which it differs from that in other species, where it narrows. The borders of the fossa patellaris are gently sloping (especially the lateral one). The trochlea patellaris lateralis lowers by degrees proximally and passes into the linea anterior.

Detailed description

Still before being buried by sediments in the rock the right femur of *Struthio dmanisensis* had been damaged (bitten) by a predator (Fig. 1). All the three condyles and the medial aspect of the trochlea patellaris medialis are damaged at its distal end. The proximolateral angle of the bone is also damaged and, in consequence, the crest of the trochanter major is missing. Furthermore, the posterosuperior part of the head of the femur and partly the upper portion of the posterior surface of the bone show damage as well. Here occurs a thin layer of sandstone deposit but it has not penetrated into the central cavity of the bone. The bone surface is in light pink-yellow colour. While being

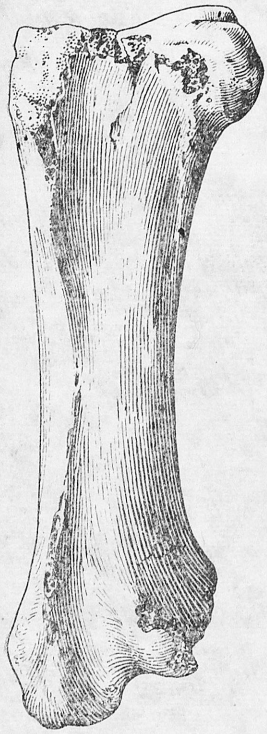

Fig. 1. *Struthio dmanisensis* sp. n. Anterior view of the femur — the damages in various parts of the bone are shown

extracted from the rock the bone broke up into big fragments, which were next glued together (cf. Phot. 1). The dimensions of the femur are compared with those of other species in Table I.

The caput femori has the shape of a hemisphere positioned obliquely at an angle of ca 50° to the long axis of the bone. Nearly a half of the upper part of its surface is occupied by a depression, the fovea ligamenti capitis, oval in shape and with its long axis extending mediolaterally. The posterior wall of the fovea is higher than the anterior and it is subvertical. Medially the fovea is gently sloping and laterally it passes directly on to the surface of the head. The bottom of the depression is irregularly shrivelled. Measurements: 30 ×23 mm. The head is raised by about 15 mm above the level of the trochanter major.

The collum femoris is comparatively narrow anteroposteriorly. The index of the width of the neck in relation to the anteroposterior width of the head is 85.3.

The upper surface of the trochanter major is relatively broad mediolaterally and somewhat convex anteroposteriorly and mediolaterally. The lateral edge of the trochanter major does not stick out above the level of the facies trochanterica, this surface sloping down gently from a height of ca 3 mm towards the neck. This sloping is poorly seen in the profile. The very weakly marked longitudinal valley of the neck occurs between the surface of the trochanter

major and the head. In the region of the trochanter major the anterior surface of the bone is flat from the top downwards and somewhat inbent across.

The linea anterior lateralis, separating the anterior surface of the bone from the lateral one, extends from the lower end of the crest of the trochanter major downwards. The lower end of the linea anterior lateralis ascends the trochlea patellaris lateralis.

The lateral surface of the bone is convex transversely and gently bent from the top downwards. From the top approximately to the level of the lower end of the crest of the trochanter major it is rough and covered with pits and asperities. The rough part of the surface is delimited from below by the

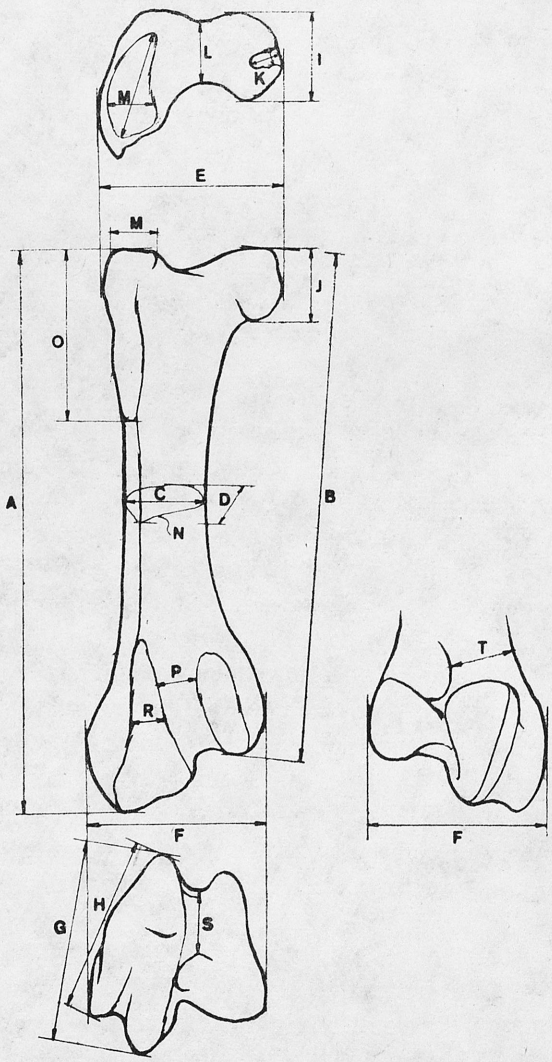

Fig. 2. The manner of measuring of the femur in ostriches. Letters A—S represent measurements given in Table I

Table I

Measurements (in mm) and some indices of the femur of *Struthio dmanisensis* sp. n. against this bone of the recent *S. camelus* and Pleistocene *S. oldawayi*. The manner of measuring it shown in Fig. 2

Symbols as in Fig. 2	Measurements	*Struthio dmanisensis* sp. n.	*Struthio camelus* (recent) Collections:					*Struthio oldawayi*
			Baku	Moscow	Kraków			
1	2	3	4	5	6	7	8	9
A	Greatest length over trochanter major	ca 380	ca 310	ca 304	314	325	318	ca 400
B	Greatest length over caput femoris	ca 360	ca 280	260	288	310	290	—
C	Smallest width of the diaphysis	76	51	42	46	51	49	ca 65
D	Smallest thickness of the shaft (anteroposterior)	54	35	33	36	41	47	—
E	Greatest width of the upper epiphysis	ca 120	ca 92	103	111	121	119	ca 135
F	Greatest width of the lower epiphysis	ca 125	112	95	108	112	108	135
G	Greatest anteroposterior diameter of the condylus lateralis	120	103	105	115	ca 118	115	—
H	As above — condylus fibularis	98	76	81	96	103	97	—
I	Anteroposterior diameter of the head	63	—	45	49	52	52	—
J	Vertical diameter of the head	62	—	43	47	51	49	—
K	Fovea ligamenti capitis length (mediolateral)	25	—	26	38	28	23	—
	width (dorsoplantar)	23	—	15	17	18	14	—
L	Anteroposterior width of the neck	53	ca 37	39	42	43	46	—
M	Upper surface of the trochanter major	ca			ca	ca	ca	
	length (anteroposterior)	105	82	73	90	83	65	—
	width (mediolateral)	43	34	33	35	38	33	—
N	Smallest circumference of the shaft	220	156	—	143	163	161	—
O	Length of the anterior edge of the trochanter major	112	90	75	87	97	95	—
P	Width of the fossa patellaris	34	18	ca 22	22	25	24	—
R	Greatest anterior width of the condylus lateralis	31	23	—	20	23	19	—

1	2	3	4	5	6	7	8	9
S	Anteroposterior length of the sulcus intercondyloideus	49	—	—	38	35	38	—
T	Width of the part of the bone between the lateral edge of the fossa poplitea and the lateral edge of the posterior surface of the bone	50	34	32	ca 37	37	ca 30	—
Indices:								
1.	Stoutness index: $\frac{C}{A}$ 100%	20.0	16.4	13.8	14.6	15.7	15.4	ca 16.0
2.	Thickness index at the level of the smallest width of the bone: $\frac{D}{C}$ 100%	71.0	68.6	78.5	78.2	80.4	95.9	—
3.	Index of the width of fossa patellaris: $\frac{P}{C}$ 100%	44.7	35.3	52.4	47.8	49.0	48.9	—

arch of the linea aspera, which is however inconspicuous. Near the middle of the surface, somewhat closer to the posterior edge, there occurs a depression, the fossa trochanterica, measuring 32 ×32 mm. A part of the lateral surface, anterior to the fossa trochanterica, is damaged (a large oval protuberance occurs in this place in the modern ostrich). A rounded bulging, ca 38 ×38 mm in size and with gently sloping sides, lies posteriorly to the fossa trochanterica. Above the upper edge of this fossa a depression, ca 20 mm in width extends proximolaterally between the above-mentioned protuberances; it reaches the external edge of the trochanter major at the top and is separated from the fossa trochanterica by a 12-millimetre-wide dike.

The fossa patellaris is comparatively broad, with gently sloping sides (particularly true of the lateral side). The index of the width of the fossa patellaris is 44.7. The upper edge of the fossa passes gradually into the anterior surface of the bone shaft. In the place of passage a lightly bulging prominence ranges upwards proximolaterally for ca 20 mm from the upper end of the trochlea patellaris medialis. The fossa patellaris widens somewhat towards the lower end, being 38 mm wide at the top and 43 mm at the bottom.

The trochlea patellaris lateralis is 27 mm in height and its greatest thickness (width) is 34 mm. Hence its thickness index in relation to the height is 126. Its long axis is parallel to the long axis of the bone. Towards the top the trochlea patellaris lateralis is reduced in height down to the surface of the shaft

and turns into the linea anterior lateralis. At the bottom a transversely positioned pit, the fossa tendinea, lies under the trochlea. It measures 12 mm anteroposteriorly and about 28 mm across. The trochlea patellaris medialis is distinctly smaller then the lateral one. It is inclined to the long axis of the bone at an angle of about 15°.

The trochanter minor lies whole on the linea aspera and its long axis is subparallel to the long axis of the bone. Its approximate length (the upper part of the bone being damaged) may be estimated at ca 55 mm and the greatest width is 17 mm. The distance between the upper edge of the trochanter minor and the upper end of the bone is ca 72 mm.

Below the trochanter minor the linea aspera extends over a distance of 52 mm on the border between the medial and posterior surface of the bone.

Above the trochanter minor the linea aspera passes on to the lateral surface of the bone, forming a gentle arch which protrudes upwards, and further, as an indistinct line, traversing the whole lateral surface of the bone to terminate near the lower base of the crest of the trochanter major.

The linea anterior medialis is poorly visible and it disappears amidst the anterior surface of the bone, at a distance of 190 mm from the top of the head.

The fossa poplitea has the shape of an irregular triangle; it is very deep and narrows towards the bottom. Its lower and lateral walls are vertical and the medial wall slopes at an angle of ca 45°. A nutrient foramen occurs in its floor. Its medial edge is thickened (12 mm) and the lower wall is 19 mm thick. A part of the posterior surface of the bone, lateral to the f. poplitea, is transversely slightly convex, with a gradual sharp-convex passage on to the lateral surface of the bone.

In consequence of the damage to the condyles only the upper part of the sulcus fibularis is preserved. It is even and flat in this region.

Comparisons

The measurements of the femur of *Struthio dmanisensis* (Table I) have been compared with 5 specimens of the modern African Ostrich, which allows us at least roughly to realize the range of individual variation in this genus. The table shows also some measurements of the femur of *Struthio oldawayi* calculated on the basis of the photograph included in the description of the materials from the Olduvai Gorge (LEAKEY 1967). The bone of *S. dmanisensis* (380 mm in length) is only slightly shorter than that of *S. oldawayi* (ca 400 mm), the remaining specimens being still shorter: the length of the femur is 360 mm in *S. karatheodoris* (MARTIN 1903), 287 and 303 mm in *S. brachydactylus* (BURCHAK-ABRAMOVICH 1949), 340 mm in *Struthio* sp. from the „Odessa catacombs" (BURCHAK-ABRAMOVICH 1953) and 304—325 mm in the recent *Struthio camelus* (Table I). It may be assumed that in the exterminated Asiatic subspecies *S.c. syriacus* this bone was still shorter, since the whole bird was smaller than the African Ostriches (CRAMP et al. 1977). The calculated stoutness indices show that the femur of *S. dmanisensis* is the thickest, its index

is the highest and comes to 20. The bones of the other ostriches are considerably more slender: in *S. oldawayi* this index is ca 16, in *S. karatheodoris* 15.3, in *S. camelus* 13.8—16.4 and in *S. brachydactylus* scarcely 12.5.

The femur of the recent *S. camelus* is used in a detailed morphological comparison. Because of the great variation observed only distinct differences are discussed here, such that can be acknowledge as specific. The fovea ligamenti capitis is similar in respect of general shape in both forms, but in *S. camelus* its lateral edge is subvertical and so it does not pass gently on to the surface of the head.

In *S. camelus* a distinct lowering of the neck, reaching 10 mm, occurs between the neck surface and the surface of the trochanter major. The linea anterior lateralis is here distinct and well-defined. The upper part of the linea aspera, delimiting the rough part of the lateral bone surface, projects up to 2 mm above the smooth surface below and that is not the case in *S. dmanisensis*. The fossa patellaris, unlike that in the fossil bone under study, tapers slightly downwards or its borders are parallel. In the lower half of the bone short ribs (4—20 mm) go away superomedially from the linea anterior lateralis at an angle of ca 45°, no such ribs being present in *S. dmanisensis*. The long axis of the trochlea patellaris medialis is subparallel to the long axis of the bone. The upper part of the trochanter minor is medially deflected from the linea aspera at an angle of ca 30° to the long axis of the bone. The distinct linea aspera extends downwards over a distance of 50—70 mm below the lower end of the trochanter minor and further it divides into two: one branch in the form of a well-marked line runs distolaterally and ends at the upper end of the crest of the fibular condyle and the other, discontinuous, ascends the upper end of the medial condyle. The linea anterior medialis, unlike that in the fossil bone, is distinct and sharply defined; it runs from the anterior edge of the facies trochanterica over the neck and further turns down along the border between the anterior and medial surfaces of the bone; next, traversing its anterior surface obliquely distolaterally it gradually loses in sharpness. In the African Ostrich the medial edge of the fossa poplitea is markedly sharpened and the part of the posterior surface lateral to the f. poplitea is nearly flat, with a fairly sharp passage into the lateral surface along the linea aspera. The upper part of the sulcus fibularis is visibly transversely concave in the African form.

III. DISCUSSION

The separation of the new species *Struthio dmanisensis* is based on two essential characters: 1 — the stoutness index of the bone greater than that in the other fossil specimens and in the present-day ostrich of the genus *Struthio* and 2 — the very great bone length (it is only 20 mm shorter than the femur of *S. oldawayi*).

The femur of *S. dmanisensis* is very similar to that of *S. oldawayi* of the same geological age in length but different in shape, for in the former species it is thick and stout and in the latter slender. An impression is produced that *S. oldawayi* was a fast-running and agile bird, unlike the slow and ponderous *S. dmanisensis*.

Struthio transcaucasicus, coming also from Transcaucasia (BURCHAK-ABRAMOVICH & VEKUA 1971), is represented by a single find only, the pelvis. Its size indicates that this bird was smaller than the bird under study, which can be seen from the fact that the acetabulum of the pelvis of *transcaucasicus* and the head of the femur of *dmanisensis* do not fit each other in respect of size: the latter does not go into the opening of the pelvis. These two species differ considerably also in geological age: *transcaucasicus* is referred to the Middle Akchagil and *dmanisensis* to the beginning of the Pleistocene.

Most of the remaining species of the genus *Struthio* (*S. karatheodoris*, *S. brachydactylus* and *S. orlovi*) and also *Struthio* sp. from the Odessa caves differ from *S. dmanisensis* under study in their much smaller size and older geological age. Only *S. chersonensis* from the southern Ukraine and *S. pannonicus* from Hungary call for a more extensive discussion.

Struthio chersonensis (BRAND, 1873) has been described on the basis of a whole egg washed out of its original place, which in this connection could not be established. This is why the geological age of this egg remains controversial. Some authors (e.g. BRODKORB 1963) assume that it comes from the Lower Pliocene and others (PIDOPLICHKO 1951, VOINSTVENSKIJ 1967) refer it to the end of the Pliocene or even the beginning of the Pleistocene. None of the fossil bones so far described can be reliably associated with this egg. The size of the egg and the thickness of its shell, compared with the eggs of *S. camelus*, indicate that it belonged to a somewhat smaller bird than *S. dmanisensis*.

Struthio pannonicus KRETZOI, 1954, was described on the basis of a phalanx of the main toe found in Lower Pleistocene deposits. Its dimensions and stoutness (KRETZOI 1954) show that this was a very big bird. The thickness of the egg-shell of *S. pannonicus*, being 2.6—3.4 mm, is also very large, against 2.2—3.3 mm in the present-day *S. samelus* and other fossil ostriches. It may well be that in the future, when more fossil bones are known, *S. dmanisensis* will appear synonymous with *S. pannonicus*. The characteristic stoutness of the bones may suggest a close relationship between these forms.

LAMBRECHT (1933) gave the first systematic division of the ostriches. He named 9 fossil and 1 present-day species of the genus *Struthio*: *S. asiaticus* MILNE-EDWARDS, 1871, *S. karatheodoris* FORSYTH MAJOR, 1888, *S. novorossicus* ALEXEJEW, 1916, *S. wimani* LOWE, 1931, *S. chersonensis* (BRANDT, 1873), *S. anderssoni* LOWE, 1931, *S. mongolicus* LOWE, 1931, *S. indicus* BIDWELL, 1904, and *S. camelus* LINNAEUS, 1758, besides, he mentioned 9 localities of *Struthio* sp. unidentifiable to species. According to LAMBRECHT (1933: Fig. 44). the range of distribution of the ostriches in the Pliocene included the whole southern half of Europe, the Causasus Mts, Asia Minor, the northern part of

India, China, Transbaykalia, Korea and Indo-China. It seems however that the localities plotted on this map by LAMBRECHT (o.c.) himself do not give grounds for so extensive a range, the more so since some of them date from the Pleistocene. Similarly, besides, today's distribution of ostriches, allegedly reaching as far as Ciscaucasia and embracing a broad area to the east of the Caspian Sea, does not correspond with the real situation (CRAMP et al. 1977).

Thirty years after LAMBRECHT (1933), in his catalogue of fossil birds BRODKORB (1963) included two families, the *Eleutherornithidae*, with one species *Eleutherornis helveticus* SCHAUB, 1940, from the Eocene of Switzerland, and the *Struthionidae*, in the order *Struthioniformes*. In the family *Struthionidae* he placed 6 fossil species and the recent *S. camelus*. BRODKORB (1963) thinks that some of the species recognized by LAMBRECHT (1933) or described later are synonyms. *Struthio chersonensis* in the sense of BRODKORB (1963) includes also *S. karatheodoris* FORSYTH MAJOR, 1888, *S. novorossicus* ALEXEJEW, 1916, *S. brachydactylus* BURCHAK-ABRAMOVICH, 1939 and *Palaeostruthio sternatus* BURCHAK-ABRAMOVICH, 1953. If the systematic position of this last form is not clear and it may represent an anomaly or individual variation in the structure of the breast-bone, *S. karatheodoris* and *S. novorossicus* are very big fossil ostriches from the Lower Pliocene or Meotis and so considerably older than *S. chersonensis*. Further, *S. brachydactylus* found in the Meotis differs in its smaller size from the present-day African Ostrich. The phalanges of its foot evidence a higher degree of evolution towards monodactylism. The inclusion of the Pleistocene remains from the Buryat Rep. described as *Struthio* sp. by TUGARINOV (1930) and the egg-shells from Outer Mongolia in *S. camelus* raises some doubts.

KUROCHKIN and LUNGU (1970), describing *Struthio orlovi*, take advantage of occasion and propose still another systematic arrangement within the genus *Struthio*. They acknowledge only 4 species: *S. orlovi*, *S. brachydactylus*, *S. asiaticus* and *S. camelus*. n the species *S. asiaticus* they number fossil ostriches from a very large area from eastern Europe to eastern China, Transbaykalia and northern India and, moreover, from a very long period from the Meotis to the Upper Pleistocene and Holocene. Time will show how far such an approach is just and how close it renders the reality.

Translated into English
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STRESZCZENIE

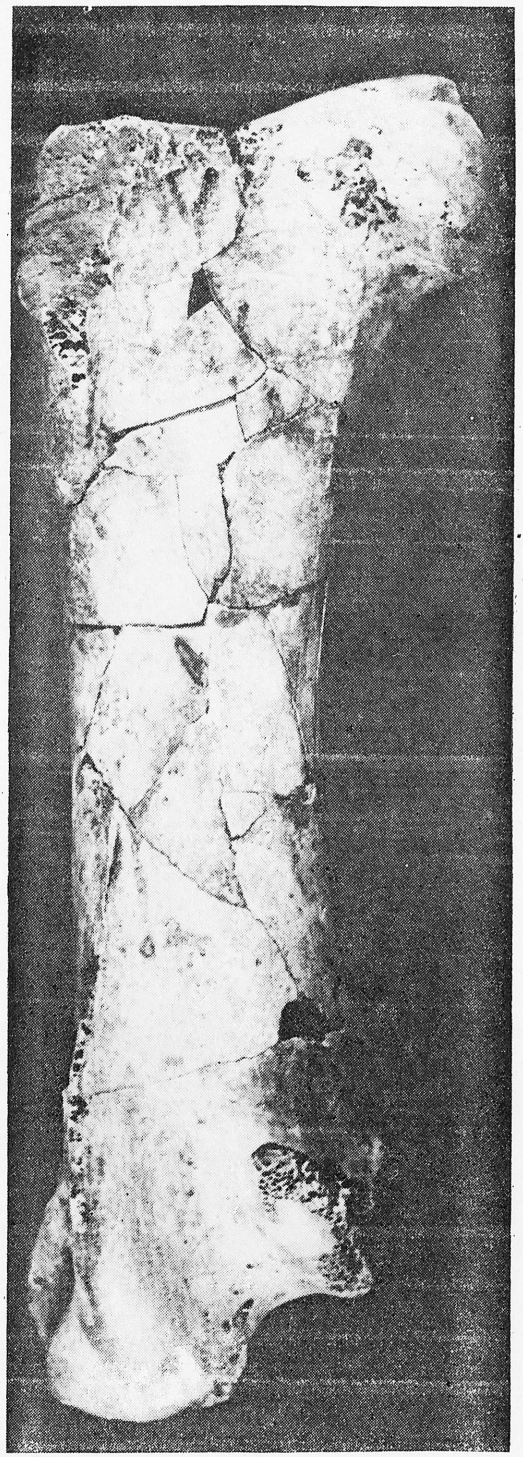
Opisana prawa kość udowa *Struthio dmanisensis* sp.n. została znaleziona w osadach z dolnego plejstocenu we wsi Dmanisi we Wschodniej Gruzji. Jest to kość bardzo dużych rozmiarów (tabela I) i bardzo masywna. Caput femoris sterczy wyraźnie ponad górny poziom trochanter major. Trochanter minor leży w całości na linea aspera. Fossa patellaris jest stosunkowo mała, ku dołowi stopniowo się rozszerza, a jej brzegi (szczególnie lateralny) są połogie. Trochlea patellaris lateralis stopniowo obniża się w kierunku proksymalnym i przechodzi w linea anterior.

Kość jest wyraźnie większa niż u współczesnego *Struthio camelus* Linnaeus, 1758, i tylko nieznacznie mniejsza niż u *S. oldawayi* Lowe, 1933 (por. tabela I). Charakterystyczna duża masywność kości sugeruje pokrewieństwo z *S. pannonicus* Kretzoi, 1954, opisanym również z dolnoplejstoceńskich osadów na Węgrzech.

Redaktor pracy: prof. dr Z. Bocheński

Plate I

Phot. 1. *Struthio dmanisensis* sp. n., femur dex. (holotype), anterior view



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