

Pliocene grouse of the genus *Lagopus* from Poland

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Abstract. *Lagopus atavus* JÁNOSSY, 1974, from Rębielice Królewskie 1 (MN 16) is redescribed and the lectotype is designated. The fragment of tibiotarsus from Węże 1 (MN 15) is assigned as cf. *Lagopus* sp. The fragment of *Lagopus* from Kielniki 3B (MN17) is described and included into *L. atavus*. The history of the genus *Lagopus* begins in Europe in the Early Pliocene.

Key words: cf. *Lagopus* sp., *Lagopus atavus*, *Tetraoninae*, Pliocene, Poland.

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I. INTRODUCTION

Fossil remains of the genus *Lagopus* are known from many localities of the Holarctic region. Most of them belong to two recent species *L. lagopus* (LINNAEUS, 1758) and *L. mutus* (MONTIN, 1776) and come from the European subcontinent. The present distribution of those species is limited to the boreal and high mountain regions, whereas during the Pleistocene they lived also in the temperate zone. The oldest remains of *Lagopus* were described by JÁNOSSY (1974) from Rębielice Królewskie 1 as a new subspecies, *Lagopus lagopus atavus*. The fauna from that locality was dated by JÁNOSSY (o.c.) as "Middle Villafranchian - about the boundary of the Pliocene and Pleistocene". Recently this fauna, owing to the changes of that boundary (1.87 M. Y.) has been referred to the Upper Pliocene (MN 16).

Lagopus lagopus atavus JÁNOSSY, 1974, was described on the basis of a proximal part of the right humerus. Another fragment, described in detail, is a distal articular part of the right humerus, belonging evidently to another specimen. All the other 31 bone fragments ascribed by JÁNOSSY (1974) to the same form were only listed and left undescribed. Two years later JÁNOSSY (1976) writes about the above-mentioned grouse as the valid species "*Lagopus atavus* JÁNOSSY, 1974", which presumably was an ancestral form to both recent European species of this genus.

The distal part of the tibiotarsus, of a shape typical of the genus *Lagopus*, was later found in the fossil fauna from Kielniki 3B. This fauna is also dated back to the Upper Pliocene, but it is younger than the fauna of Rębielice Królewskie 1 and belongs to MEIN zone 17.

For these reasons a detailed study of the Upper Pliocene remains of the genus *Lagopus* has been undertaken. Another interesting issue is whether in the Upper Pliocene in Poland there lived one or two *Lagopus* species varying in size like those known from the Upper Pleistocene.

I would like to express my best thanks to Prof. Dr D. JÁNOSSY, Dr E. N. KUROCHKIN and Dr C. MOURER-CHAUVIRÉ for their valuable comments upon the project of Table IV of this paper.

II. MATERIAL FROM RĘBIELICE KRÓLEWSKIE 1

In describing *Lagopus lagopus atavus* from Rębielice Królewskie 1 JÁNOSSY (1974) pointed to the shape of the caput humeri and fossa tricipitalis as characteristic of the genus *Lagopus*. As discriminating characters he mentioned the presence of a groove in the place of the eminentia musculi latissimi dorsi and that of "a foramen on the inner side of proximal epiphysis - in proximal view". His remarks on the other bone fragments are as follows: "the distal end of humerus seems to be slender, the phalanx I digiti 2 alae and the carpometacarpus are slightly thicker than the corresponding bones " (in 8 specimens of the recent *Lagopus lagopus* and *mutus*).

Not all the above-mentioned characters are discriminating and the others must be precisely described.

1. The place of attachment of musculus lat. dorsi, as described by JÁNOSSY (1974), has the shape of a groove and is relatively very large; its margins, especially the distal one, are not well-defined and so the measurements are difficult to take: its total length is ca 9.0 mm and width ca 2 mm; inside the groove there is a rough place for muscle attachment, ca 7.0 mm long. In the specimens of the recent *Lagopus lagopus* and *L. mutus* under comparison (see Table I) it is distinctly smaller and only in two cases its distal part has the shape of a very shallow groove. In the other *Tetraoninae* I found a rather analogous but relatively not so deep groove only in the members of the genus *Bonasa* (*bonasia* and *umbellus*).

2. The foramen in the proximal epiphysis was not precisely localized by JÁNOSSY (1974). It is situated in the incisura collaris in its angle on the inner side of the tuberculum ventrale. In specimen No AF/26-RK1:22 it is rather small and deep depression than the foramen sensu stricto. The same is true of the other fragment (No AF/27-RK1:23). JÁNOSSY (1974) mentions that he observed a similar foramen only in *Tympanuchus*; this he does not write explicitly but it may be assumed that it concerns *T. cupido*, as the measurements of the humerus of this last bird are given in his Table II. I have not seen that bone, but in the bone of *T. phasianellus* from my comparative collection such a "foramen" does not exist. On the other hand, a depression can be seen in the bone of *Lagopus lagopus* (No A/3822/81),

Table I

The measurements (in mm) of proximal part of humerus in *Lagopus atavus* from Rębielice Królewskie 1 (lectotype) and in the recent members of Eurasiatic *Lagopus lagopus* (excl. *L. l. scoticus*), *L. mutus* and *Bonasa bonasia*. The manner of measuring is shown in Fig. 1. Numerical characteristic of attachment of musculus latissimus dorsi (-2 = deep groove to +2 = strong eminentia) and the indices based on the measurements are added.

Specimens	Measurements as in Fig. 1				Muscle attachment character. -2 to +2	Indices	
	a	b	c	d		$\frac{a \times 100}{b}$	$\frac{a \times 100}{c}$
Fossil							
<i>Lagopus atavus</i>							
AF/26-RK1:22	ca 9.0	15.2	ca 16.5	6.5	-2	59.2	54.5
Recent							
<i>Lagopus lagopus</i>							
A/1529/65	ca 6.3	17.6	ca 18.1	7.4	0 to +1	35.8	34.8
A/3822/81	ca 5.8	16.6	ca 17.7	6.8	-1 to +1	34.9	32.8
A/4727/90	ca 6.0	18.9	ca 19.2	6.4	+1	31.2	31.2
A/4728/90	ca 7.1	15.3	ca 15.8	6.1	+1	46.4	44.9
A/4954/91	ca 7.0	17.4	ca 20.5	6.8	0	40.2	34.1
A/4956/91	ca 6.0	17.1	ca 18.6	6.6	+1	35.1	32.2
A/4957/91	ca 7.0	17.4	ca 17.4	7.2	-1 to +1	39.5	40.2
A/4989/91	4.5	15.6	16.2	6.1	+1	28.8	27.8
A/4990/91	ca 6.0	16.4	ca 16.7	6.4	-1 to 0	36.6	35.9
A/4991/91	6.4	16.1	17.4	6.3	+1	39.7	36.8
<i>Lagopus mutus</i>							
A/1528/65	5.9	15.0	17.0	5.8	0 to +1	39.3	34.7
A/3286/76	ca 6.5	15.4	ca 18.0	6.0	0 to +1	42.2	36.1
A/4725/90	6.5	14.6	16.3	5.9	+1	44.5	39.9
A/4726/90	ca 6.0	15.2	ca 18.5	5.9	+1	39.5	32.4
A/4959/91	ca 6.2	16.2	ca 17.0	5.9	+1	38.3	36.5
<i>Bonasa bonasia</i>							
A/1357/64	ca 5.0	14.0	ca 14.8	5.5	0	35.7	33.8
A/3018/75	ca 4.2	14.1	ca 15.1	5.5	-1 to 0	29.8	27.8
A/3994/83	ca 5.5	13.8	ca 14.8	5.4	-1	39.8	37.2
A/4945/91	ca 5.5	13.9	ca 14.2	4.9	-1	39.5	38.7

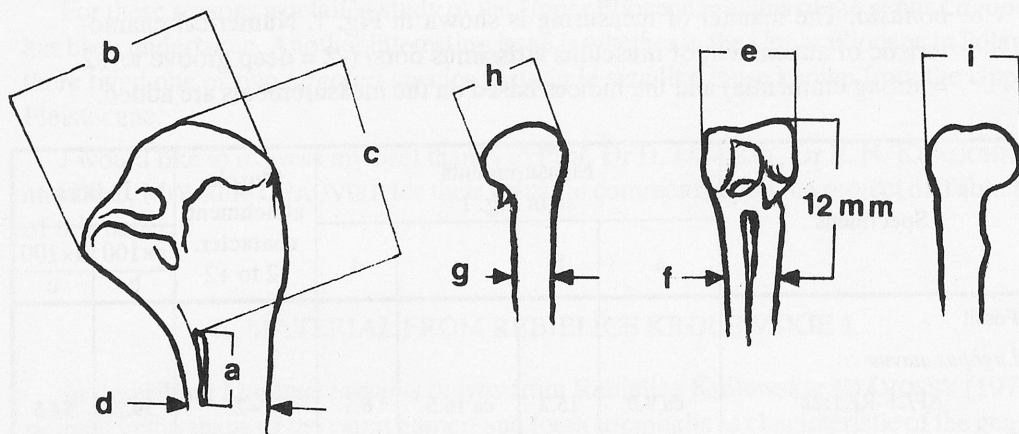


Fig. 1. The manner of detailed measuring of two bone fragments of *Lagopus atavus* and the recent grouse, i.e. proximal part of humerus (ref. to Table I): a - length of the groove (or eminentia musculi lat. dorsi), b - width of proximal epiphysis, c - distance between caput humeri and prox. end of the groove (or eminentia if exists), d - width of the shaft at the level of distal end of the groove (or eminentia), and distal part of tibiotarsus (ref. to Table III): e - width of distal epiphysis, f - width of the shaft ca 12 mm from the bone end, g - bone thickness at the same level, h - diameter of lateral condyle, i - horizontal diameter of medial condyle.

though in other specimens of this species as well as in specimens of *L. mutus* it is absent. So, the presence of the opening (or depression) cannot be the discriminative feature of the species, being only more or less accidental morphological event, possibly more common in the Pliocene grouse of the genus *Lagopus*.

3. The width of the distal end of the humerus and its greatest thickness were compared by JÁNOSSY (1974) with the measurements of the recent and Upper Pleistocene specimens of the genus *Lagopus* in a scatter diagram. It can be seen from the diagram, that the width of the specimen from Rębielice is 10.1 mm, whereas the width of the smallest specimen being compared is 10.3 mm, and also that the epiphysical width:thickness ratio is similar in all examples. In 17 specimens of *Lagopus mutus* measured by me the smallest width of humerus distal epiphysis was 10.2 mm and KRAFT (1972) in 29 specimens found it equal to 10.1 mm (as in the bone from Rębielice). So, this measurement cannot be a good discriminating character, either.

A general comparison of dimensions of the bone fragments from Rębielice Królewskie 1 and those of the recent Eurasian grouse of the genus *Lagopus* (BOCHENSKI 1974, 1984, 1985 and unpubl.; KRAFT 1972) is given in Table II. Most of the dimensions of the fossil wing bones lie within the limits of both recent European species, but except for the length of the wing phalanges they statistically more resemble *Lagopus mutus* (i.e. the smaller

Table II

The measurements (in mm) of the bones of the Upper Pliocene *Lagopus atavus* from Rębielice Królewskie 1, compared with those of the recent *L. lagopus* and *L. mutus* (numbers in brackets - supposed measurements in the case of damage).

Bone	Measurement	<i>Lagopus atavus</i>	Recent Eurasian forms (excl. <i>L. l. scoticus</i>)				<i>Lagopus lagopus scoticus</i> (BO-CHENSKI 1974, unpubl.)
			<i>Lagopus mutus</i>		<i>Lagopus lagopus</i>		
			(BO-CHENSKI 1974, 1984, unpubl.)	(KRAFT 1972)	(BO-CHENSKI 1974, 1984, unpubl.)	(KRAFT 1972)	
Mandibula	length of symphysis	6.6; 6.2	5.1-6.2	4.7-5.9	6.6-7.7	6.0-7.8	5.4-6.7
	width at prox. edge of symphysis	7.3; 7.0	5.8-7.2	—	8.2-9.1	—	7.0-8.6
	height of arm	3.5; (3.2)	2.3-2.7	—	3.7-4.1	—	2.9-3.5
Coracoideum	width of labrum glenoidale	6.5; 5.6; (6.2)	4.6-6.4	—	5.7-7.8 ²	—	5.4-6.7
Humerus	width of proximal end ¹	15.7	14.4-16.6	13.8-15.9	14.9-18.9 ²	14.4-17.3	15.7-17.2
	width of distal end	10.1	10.2-11.4	10.1-11.8	10.6-13.0	10.8-12.4	10.9-11.9
Ulna	length of proximal epiphysis	10.4; (9.8); (9.2)	9.1-10.2	9.1-10.9	9.4-12.0 ²	9.5-11.2	9.7-10.9
	width of distal epiphysis	7.8; 7.7	6.9-7.8	6.8-8.1	7.3-9.2 ²	7.2-8.5	7.4-8.6
Carpometacarpus	total length	31.9; 33.4	29.7-35.1	29.7-34.4	30.1-37.5 ²	30.9-36.1	33.1-36.8
	width of proximal epiphysis	9.1; 9.1	8.4-9.8	8.6-10.3	8.9-11.2 ²	8.4-10.6	9.1-10.0
Digitis alae major	total length	14.1; 14.0	14.5-15.9	—	14.1-16.4 ²	—	14.9-16.4
Femur	width of prox. epiphysis	ca 12.0	9.8-11.4	9.0-11.2	10.8-13.4 ²	9.9-12.5	11.1-11.9
Tibiotarsus	width of distal epiphysis	(7.2)	6.3-7.5	6.3-7.2	6.8-8.4 ²	6.9-8.3	6.5-8.3
Tarsometatarsus	width of distal epiphysis	9.0	6.8-8.3	6.3-7.6 ³	7.8-10.6 ²	6.3-8.7 ³	7.3-9.4

¹Width of proximal end of the humerus given by me is the distance from the tuberculum ventrale to the tuberculum dorsale, whereas by KRAFT (1972) to the top of crista tuberculi dorsalis.

²Plus-variant specimen belongs to SW Siberian steppe subspecies, *L. l. maior* LORENZ, 1904.

³Width of distal tarsometatarsus epiphysis cited by KRAFT (1972) is comparatively very small which suggests an error or a different method of measuring.

species). The distal width of the humerus and the length of the proximal ulnar epiphysis in one specimen are even about the minus variant of this species. Both wing phalanges are also very small in length, one of them is even somewhat smaller than in all the recent specimens compared. It is striking, that the smallest recent specimens of this bone belong to generally larger birds (*L. lagopus*); this is also true of arithmetic means: 14.9 mm in *L. lagopus* and 15.2 mm in *L. mutus* (a series of 16 specimens was used for either species). On the contrary, the sizes of the femur and tarsometatarsus are large, typical of large specimens of *L. lagopus*. All the three dimensions of 2 mandibles are similar to those of the recent *L. l. scoticus*, which, in this respect, is intermediate between *L. mutus* and continental forms of *L. lagopus*. This is particularly well seen in the case of the mandibular ramus height.

It has been found that the proportion between two dimensions of a bone, even that belonging to the distal parts of the skeleton, is characteristic for groups (genera, families) of the recent birds (BOCHENSKI 1989) and its values have a linear arrangement in scatter

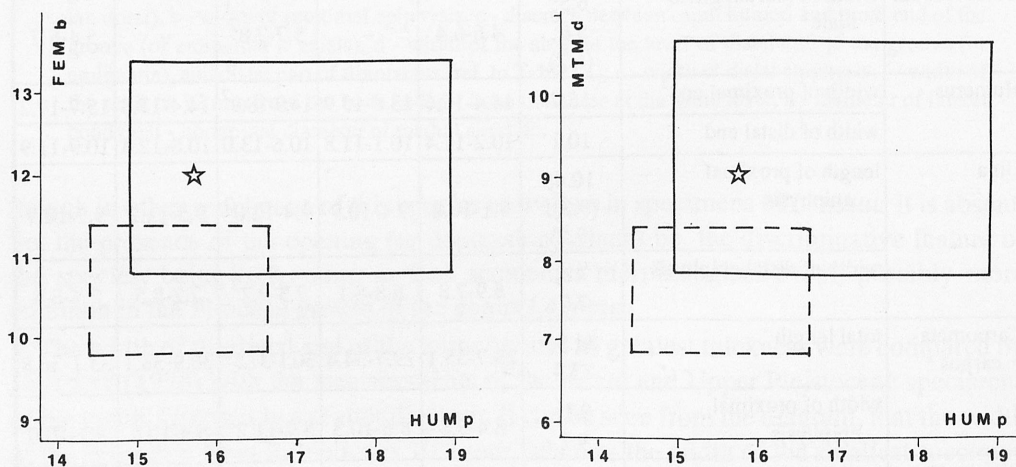


Fig. 2. The ratio of the proximal width of the humerus (HUM p) to the width of the proximal articular part of the femur (FEM p) and to the width of the distal articular part of the tarsometatarsus (TMT d) in *Lagopus atavus* from Rebielice Królewskie 1 (asterisk) and in the recent specimens of Eurasian *Lagopus lagopus* (solid-line rectangles) and *L. mutus* (broken-line rectangles). The rectangle vertices represent the smallest and the largest values of the given measurement based on the data from Table II. The data given by KRAFT (1972) were omitted (see footnotes 1 and 3 for Table II).

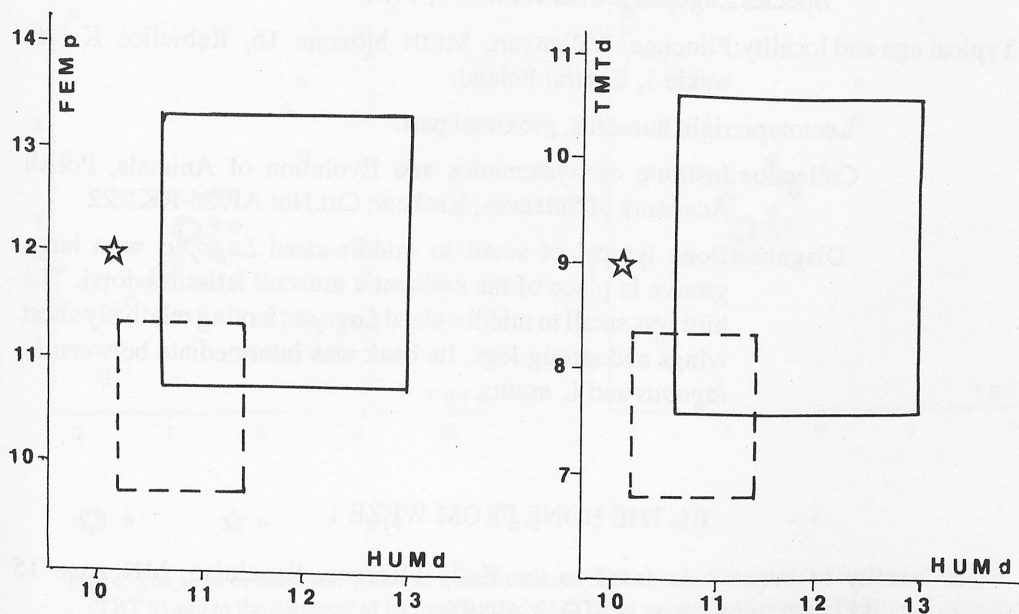


Fig. 3. The ratio of the distal width of the humerus (HUM d) to the width of the proximal femoral epiphysis (FEM p) and to the distal tarsometatarsal epiphysis (TMT d) in *Lagopus atavus* from Rębielice Królewskie 1 (asterisk) and the recent specimens of Eurasian *Lagopus lagopus* (solid-line rectangles) and *L. mutus* (broken-line rectangles). For other explanations see Fig. 2.

diagram. The same was also found in the grouse. A comparison of the proportion of the widths of the proximal articular part in the humerus and the measurements of the femur and tarsometatarsus from Rębielice (Fig. 2) shows their similarity to the recent *L. lagopus*. However, the points representing the proportion of the width of the distal humeral epiphysis to the corresponding measurements of the leg bones (Fig. 3) are situated outside the rectangles representing the recent European species of the genus *Lagopus*. This may indicate either that the bones compared belong to two different species (forms) or that the Pliocene *Lagopus* differs from the recent species in the proportion between its wing bones and leg bones. The latter alternative can be supported by the following fact: among more than twenty limb bones the wing bones show a tendency to be small (to a various degree) and all leg bones tend to be large. BOCHENSKI'S (1974, 1985) statement that sizes (lengths) of limb bones of the Willow Grouse has changed a little in the opposite direction since the last glacial period may to some extent explain the divergence presented above. So far, it seems that we can accept JÁNOSSY'S (1974) opinion that only one species of the genus *Lagopus* is present in the fossil bird fauna from Rębielice Królewskie 1. This species is *Lagopus atavus* JÁNOSSY, 1974. Describing it as a subspecies, the author did not designate the holotype and so it is necessary to propose the lectotype.

Systematic position:

Genus: *Lagopus* LINNAEUS, 1758Species: *Lagopus atavus* JÁNOSSY, 1974

Typical age and locality: Pliocene, Villanyan, MEIN biozone 16, Rębielice Królewskie 1, Central Poland.

Lectotype: right humerus, proximal part.

Collection: Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Krakow; Cat.No: AF/26-RK1:22

Diagnose: Bone typical of small to middle-sized *Lagopus* with large groove in place of the eminentia musculi latissimi dorsi. The bird was small to middle-sized *Lagopus* having relatively short wings and strong legs. Its beak was intermediate between *L. lagopus* and *L. mutus*.

III. THE BONE FROM WĘŻE 1

The locality of Węże 1 is dated to the Early Pliocene, Ruscinian, MN zone 15 (NADACHOWSKI et al. in: KOWALSKI [Ed.], 1989).

The bird remains from Węże 1 were described by JÁNOSSY (1974), who included one fragment from that locality, that is, the "distal end of right (error!) tibiotarsus" in the category "*Lyrurus* sp. - ?*Lagopus* sp." In the description of that fragment JÁNOSSY (1974) gives only its width equal to 7.0 mm, and writes: "sizes and morphological features are more like *Lagopus* than *Lyrurus*. The specimen is too fragmentary for further conclusions".

It is the distal epiphysis of the left bone (No: AF/86-WE1:8) broken at the level of the proximal edge of the ligamentum transversum ossificatum. Both the condyles and the ligament itself are well preserved. Its detailed measurements are given in Table III. The shape of that fragment in the recent members of the genera *Lagopus* and *Tetrao* is similar (allowing for individual variation). The only difference is that the ligamentum transv. ossificatum, is flat in *Lagopus lagopus* and *L. mutus*, whereas in *Tetrao tetrax* it is convex (vaulted). The proportions between every set of three measurements illustrated by the indices (see Table III) show some differences in their limit values, which however overlap to some degree. The position of the bone fragment from Węże 1 seems to be intermediate. Its ligament is bulging in its distal part and flat in the proximal one. The indices A and B lie on the area of overlapping, but, as suggested by the statistical data, in both cases they come much closer to the genus *Lagopus* than to *Tetrao* (Figs 4, 5). So, the bone may be treated as cf. *Lagopus* sp., generally more similar to the recent *L. lagopus* than to *L. mutus*.

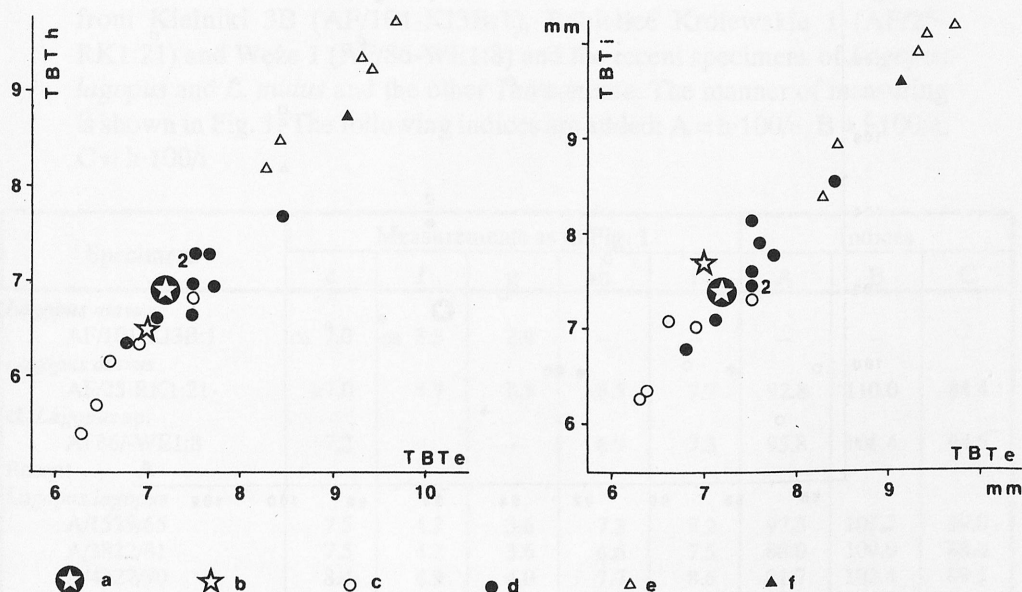


Fig. 4. The ratio of the distal width of the tibiotarsus (TBT e) to the diameter of its lateral condyle (TBT h) and to the diameter of its medial condyle (TBT i) in fossil and recent grouse: a - *Lagopus* sp. from Węże 1, b - *Lagopus atavus* from Rębielice Królewskie 1, c - *Lagopus mutus* recent, d - *L. lagopus* recent, e - *Tetrao tetrix* recent, f - *T. mlokosiewiczzi* recent (the data taken from Table III, manner of measuring same as in Fig. 1.).

IV. THE BONE FROM KIELNIKI 3B

The locality of Kielniki near Olsztyn (Częstochowa Voivodship) consists of a few karst fissures filled up by deposits containing faunas dated back to a period between the Upper Villanyan (Upper Pliocene) and the Late Biharian (Early Pleistocene). Gastropods, amphibians, reptiles and a few groups of mammals have been described from Kielniki by now (KOWALSKI [Ed.] 1989).

3 bird bone fragments have been found in all the fossil material from Kielniki. They are 2 fragments of toe phalanges of two different species, which however remain undetermined. The third is a distal part of the right tibiotarsus of a middle-sized gallinaean. All fragments coming from Kielniki 3B are dated back to the Upper Pliocene (MEIN zone 17).

The galliform tibiotarsus (No AF/101-KI3B:2) is badly damaged. Its lateral condyle is partially crushed. The bone in frontal view (the central location of the canalis musculi ext. digitum and long processus on lateral end of ligamentum transversum ossificatum) is typical for such genera of the *Tetraoninae* as *Lagopus* and *Bonasa*, excluding the phasianine genera of similar size: *Perdix*, *Alectoris* and *Francolinus*. The shape of the condylus lateralis, especially of its caudal margin, and the distal end of the apophysis

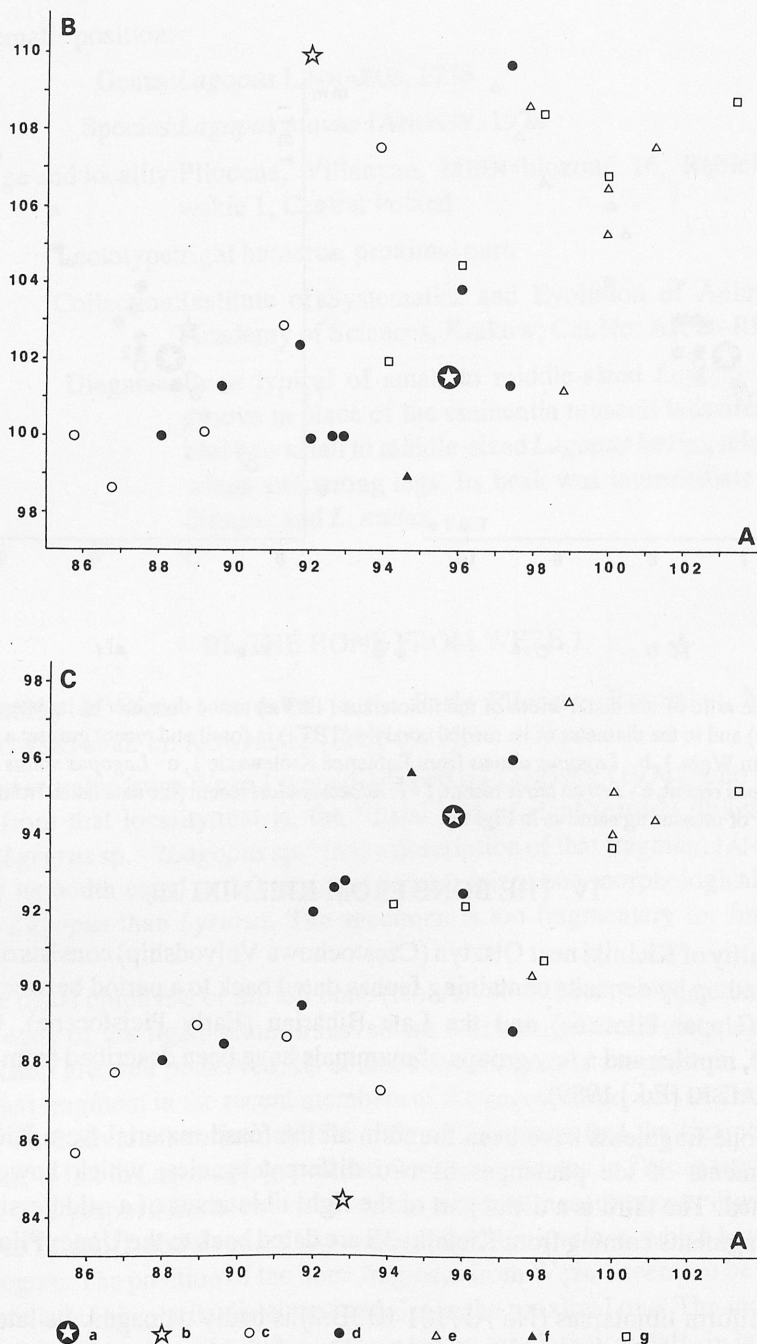


Fig. 5. The ratio of the values of indices A and B (top diagram) and of indices A and C (bottom diagram) characterizing the shape of the distal epiphysis of the tibiotarsus in various fossil and recent grouse: a - *Lagopus* sp. from Węże 1, b - *Lagopus atavus* from Rębelice Królewskie 1, c - *Lagopus mutus* recent, d - *L. lagopus* recent, e - *Tertao tetrix* recent, f - *T. mlokosiewiczzi* recent, g - *T. urogallus* recent (data taken from Table III).

Table III

The measurements (in mm) of distal end of tibiotarsus in fossil grouse from Kielniki 3B (AF/101-KI3B:1), Rębielice Królewskie 1 (AF/25-RK1:21) and Węże 1 (AF/86-WE1:8) and the recent specimens of *Lagopus lagopus* and *L. mutus* and the other *Tetraoninae*. The manner of measuring is shown in Fig. 1. The following indices are added: $A = h \cdot 100/e$, $B = i \cdot 100/e$, $C = h \cdot 100/i$

Specimens	Measurements as in Fig. 1					Indices		
	e	f	g	h	i	A	B	C
<i>Lagopus atavus</i> AF/101-KI3B:1	ca 7.0	ca 3.3	2.9	—	—	—	—	—
<i>Lagopus atavus</i> AF/25-RK1:21	≥7.0	4.7	3.8	≥6.5	7.7	92.8	110.0	84.4
cf. <i>Lagopus</i> sp. AF86/-WE1:8	7.2	—	—	6.9	7.3	95.8	101.4	94.5
Recent								
<i>Lagopus lagopus</i>								
A/1529/65	7.5	4.2	3.6	7.3	8.2	97.3	109.3	89.0
A/3822/81	7.5	4.2	3.6	6.6	7.5	88.0	100.0	88.0
A/4727/90	8.4	4.9	4.0	7.7	8.6	91.7	102.4	89.5
A/4728/90	7.1	3.8	3.1	6.6	7.1	92.9	100.0	92.9
A/4956/91	7.5	3.9	3.2	7.3	7.6	97.3	101.3	96.0
A/4957/91	7.6	4.4	3.7	7.3	7.9	96.0	103.9	92.4
A/4989/91	6.8	3.6	3.0	6.3	6.8	92.6	100.0	92.6
A/4990/91	7.5	3.9	3.4	6.9	7.5	92.0	100.0	92.0
A/4991/91	7.7	3.8	3.5	6.9	7.8	89.6	101.3	88.5
<i>Lagopus mutus</i>								
A/1528/65	6.4	2.9	2.6	5.7	6.4	89.1	100.0	89.1
A/3286/76	6.9	3.7	3.1	6.3	7.1	91.3	102.9	88.7
A/4725/90	6.3	3.0	2.7	5.4	6.3	85.7	100.0	85.7
A/4726/90	7.5	3.5	3.1	6.5	7.4	86.7	98.7	87.8
A/4959/91	6.6	3.9	3.1	6.2	7.1	93.9	107.6	87.3
<i>Tetrao tetrix</i>								
♂ A/1634/66	9.4	—	—	9.2	10.2	97.9	108.5	90.2
♂ A/1896/68	9.3	—	—	9.3	9.9	100.0	106.4	93.9
♂ A/3622/79	9.7	—	—	9.7	10.2	100.0	105.1	95.1
♀ A/3279/76	8.3	4.7	4.0	8.2	8.4	98.8	101.2	97.6
♀ A/3347/77	8.4	—	—	8.5	9.0	101.2	107.1	94.4
<i>Tetrao mlokosiewiczzi</i>								
♂ A/3172/76	9.2	—	—	8.7	9.1	94.6	98.9	95.6
<i>Tetrao urogallus</i>								
♂ A/1923/68	15.2	—	—	15.2	16.2	100.0	106.6	93.8
♂ A/2066/69	14.9	—	—	15.4	16.2	103.4	108.7	95.1
♂ A/2138/69	15.5	—	—	14.9	16.2	96.1	104.5	92.3
♂ A/2139/69	15.3	—	—	14.4	15.6	94.1	101.9	92.3
♀ A/4840/91	11.8	—	—	11.6	12.8	98.3	108.5	90.6
<i>Bonasa bonasia</i>								
A/3018/75	6.6	3.3	2.9	6.8	7.2	103.0	109.1	94.4
A/3994/83	6.9	4.0	3.0	6.6	7.1	95.6	102.9	92.9
A/4945/91	6.6	3.5	3.2	6.8	7.2	103.0	109.1	94.4

Table IV

More important localities where remains of paleo- and neospecies of the European *Tetraoninae* were found against a background of chrono- and biostratigraphy of the Pleistocene and the Upper Pliocene, as presented by selected authors. The last M.Y. on the scale is doubled in length. If neospecies are known from many localities dated back to the Late Pleistocene, the corresponding places are dotted.

M.Y.									
Stratigraphy									
JÁNOSY (1986)									
NIKIFOROVA et al (1986) NIKIFOROVA, KIND (1987) DUBROV, KAPLEST (1979) HORÁČEK (1981)									
KOWALSKI [Ed] (1989)									
Species and localities ¹									
Lagopus sp.									
Lagopus atavus									
Lagopus lagopus									
Lagopus mutus									
Tetrao conjugens									
Tetrao macropus									
Tetrao parium									
Tetrao tetrax									
Tetrao praeurogallus									
Tetrao urogallus									
Bonasa praebonasia									
Bonasa bonasia									

ligamenti obliqui point to the genus *Lagopus*, excluding *Bonasa* (= *Tetrastes*). The measurements of the bone compared with those of *L. atavus* from Rębielice Królewskie 1 and a few specimens of the recent *Lagopus* are given in Table III. The assumed width of the distal epiphysis is ca 7.0 mm and so a bit smaller than in the fragment from Rębielice. This difference compared with the size limits of the bones in the recent *L. lagopus* and *L. mutus* (Table II) indicates that it does not exceed the limits of individual variation. The same seems to be true of slight morphological differences. So, it may be stated that the bone belongs to *Lagopus atavus* JÁNOSSY, 1974.

IV. DISCUSSION

The contemporary knowledge of the genus *Lagopus* in Europe is summarised in Table IV against a background of the data on the other *Tetraoninae*. The data for the hight part of the table is taken from the papers by JÁNOSSY (1974, 1976, 1986), MOURER-CHAUVIRÉ (1975, 1980), WISZNIOWSKA (1991) and BOCHENSKI (1974, 1984). According to these data the history of the genus *Lagopus* begins most probably in Central Europe in the Early Pliocene, MEIN zone 15, in the fauna from Węże 1. The bone from Węże is also the earliest find of that genus in the world.

The results obtained by JÁNOSSY (1976) and the other European data published since the 70-ties must lead to a change in the schematic history of the evolutionary development of and the colonisation of the Northern Hemisphere by the genus *Lagopus* presented by HÖHN (1969) and left unchanged in the second edition of his book (HÖHN 1980). The presence of *Lagopus atavus* in biozone MN 16 in Central Europe may suggest that the genus *Lagopus* has evolved in the Western Palearctic at least since the Early Pliocene parallel to the genus *Tetrao*. *Lagopus* sp. from Węże 1, biozone MN 15, presenting some features similar to those of the genus *Tetrao* indicates that both these genera may have common ancestor in biozone MN 14 or even earlier. If in the fauna from Rębielice Królewskie 1 there was only one species of grouse (i.e. *Lagopus atavus*); it had the proportion between legs and wings different from that in the recent birds. It is interesting that in *Tetrao macropus* JÁNOSSY, 1976, from Csarnota 2 in Hungary this proportion seems to be analogous to some degree. Further speculations, however, must wait for new, more complete Early Pliocene materials.

Notes to the Table IV:

¹Abbreviations of locality names used in the Table: BE - Betfia, BŁ - Bełchatów, CS - Csarnota 2, KD - Kadzielnia, KG - Kozi Grzbiet, KI - Kielniki 3B, LF - La Fage, MO - Monteuse 3, O2 - Osztramos 2, O7 - Osztramos 7, O8 - Osztramos 8, OR - Orgnac 3, RK - Rębielice Królewskie 1, TA - Tarkö, UP - Uppony, VA - Valerots, VE - Vertesszilos 2, VI - Villany 3, WE - Węże 1, ZA - Zalesiaki 1A.

²In his book JÁNOSSY (1986) mentions "*Lyrurus cf. tetrrix*" from Vertesszilos 2, whereas later (JÁNOSSY in litt.) he writes "*Lyrurus partrium* seems to be more correct".

³The bone from Rębielice Królewskie 1 was determined by JÁNOSSY (1974) as "*Tetrao* aff.? *praeurogallus*" which seems to be wrong. JÁNOSSY (in litt.) wrote in 1989 that "it is not probable that in Rębielice the typical *Tetrao praeurogallus* would be present, but the presence of a form of this evolutionary line seems to be presumable".

Another problem to be discussed is more general and deals not only with the genus *Lagopus*. It is connected with two different conceptions of the Pleistocene: the "short" and the "long" one. Each of them has its own followers, and there is not a place here to present their reasons, which are probably also various. The problem is that the same name used by different authors may have quite different meanings. It deals especially with the comprehension of the "Lower" or "Early" Pleistocene. Some examples of various ideas of the Pleistocene are given in the left part of Table IV. According to HORAČEK (1981), the term "Lower Pleistocene" is used for the time between ca 0.6 and 1.6 M.Y. BP, whereas JÁNOSSY (1976, 1986) writes that it takes from 0.6 to more than 3.0 (about 3.5) M.Y.. A similar placing of the Plio-Pleistocene boundary at the end of biozone MN 15 is proposed by GUERIN (1982). On the contrary, according to DUBROVO and KAPELIST (1979), the Pleistocene began 700000 years ago.

The difference of 1.5 to 2.0 million years can not be indifferent if we are concerned with bird species longevity, which is supposed by BRODKORB (1971) to be about half million years on average, and with the study of successive evolutionary steps. On the other hand, the situation described above leads to more or less serious missinterpretations. We can meet with them in the BRODKORB'S catalogue: for example, in Part 2 (BRODKORB 1964) *Tetrao partium* (KRETZOI, 1962) is listed from the "Upper Lower Pleistocene (Betfia)" and *Pliogallus kormosi* GAILLARD, 1938, from the "Lower Pleistocene (Csarnota)", whereas in Part 3 (BRODKORB 1967) *Anas apscheronica* BURCHAK-ABRAMOVICH, 1958, is given from the "Upper Pliocene (Apscheron)". According to JÁNOSSY (1986: Tab.III) Apscheronian corresponds to the Villanyan; according to FEJFAR and HEINRICH (1983) it extends from the period of Csarnota (= MN 16) till that of Betfia in the early Biharian, and in modern Soviet literature (NIKIFOROVA et al. 1986; NIKIFOROVA, KIND 1987) it is referred to the Lower Pleistocene (between 1.7-1.6 and 0.7-0.6 M.Y.). Missunderstanding can lead also to such mistakes as those cited by JOHNSGARD (1983: Tab. I) who puts "*Lagopus cf. lagopus* ('atavus')" together with *Bonasa praebonasia* and *Tetrao praeurogallus* in the Middle Pleistocene.

To avoid the mistakes like those mentioned above it would be best to use absolute dating in descriptions of faunas from that controversial period. If absolute dating is unfeasable, it is useful to give biostratigraphy or, at least, a full list of sources for chronostratigraphy indicating clearly which scheme of the Plio- Pleistocene was followed.

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