

Tetraonidae VIGORS, 1825 (Galliformes – Aves) in the Neogene-Quaternary record of Bulgaria and the origin and evolution of the family

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Abstract. Bulgaria has a very diversified avifauna of fossil and subfossil Tetraonidae, consisting of at least 9 species. This avifauna is represented by 525 bone finds from 27 avian localities in Bulgaria: 3 Pliocene, 11 Pleistocene and 13 Holocene. The Tetraonidae probably first appeared in the savana-forest habitats of the Western Palearctic at the transition between the Pontian and the Ruscinian. The genus *Tetrao* first appears in the Balkans and Europe during the Early Pliocene (MN 14), while the earliest record of *Lagopus* is in MN 15. Four of the nine Tetraonid species in Bulgaria are fossil species: *Lagopus atavus* JÁNOSSY, 1974, *Lagopus balcanicus* BOEV, 1995, *Tetrao partium* (KRETZOI, 1962) and *Tetrao rhodopensis* BOEV, 1998. Three recent species in the fossil record have since disappeared from the avifauna of the country: *Lagopus lagopus* (LINNAEUS, 1758), *Lagopus mutus* (MONTIN, 1776) and *Tetrao tetrix* LINNAEUS, 1758.

Key words: Gallinaceous birds, Tetraonidae, Neogene, Quaternary, fossil avifauna, Balkans, Bulgaria, evolution of birds, faunal impoverishment.

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I. INTRODUCTION

The Neogene record of Tetraonidae is relatively scanty, while the Quaternary localities of the Palearctic and (to a lesser extent) the Nearctic regions contain numerous finds of mostly recent species. In comparison with other parts of the Western Palearctic (W and C Europe), the Neogene and Quaternary bird faunas of Bulgaria are still poorly studied (BOEV 1999 a; in press a). However, remains of Tetraonidae are among the most abundant finds from Palaeolithic sites in Bulgaria (BOEV 1997 a, b, 2000 a; in press b, c, d). The large body size of the most species in the family, their delicious meat, relative abundance in the wild, their relatively poor flight capabilities and sedentary lifestyles are among the main peculiarities that made them one of the most valuable sources of game for the prehistoric and more recent hunters.

The present paper sums up all available data on the Tetraonidae taxa in the fossil and subfossil record of Bulgaria. It also aims to evaluate the significance of the earliest Bulgarian finds to the understanding of the origin of this family.

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II. MATERIAL AND METHODS

A total 525 bones and bone fragments from 27 sites in Bulgaria have been collected (Table I). The chronostratigraphic range is from the Early Pliocene (MN 14) to the Late Holocene (up to the present day) (Table II).

Table I

Taxonomic distribution of the fossil Tetraonidae collected in the Bulgarian Neogene and Quaternary sites

N	Taxa	Identified up to species/ genus level	Identified as “cf.” or “aff.”	Total	Percentage of all fossil material
1.	<i>Bonasa bonasia</i> (LINNAEUS, 1758)	8	12	20	3.8
2.	<i>Lagopus</i> aff. <i>atavus</i> JÁNOSSY, 1974	–	1	1	0.2
3.	<i>Lagopus balcanicus</i> BOEV, 1995	40	1	41	7.8
4.	<i>Lagopus lagopus</i> (LINNAEUS, 1758)	26	10	36	6.9
5.	<i>Lagopus mutus</i> (MONTIN, 1776)	1	–	1	0.2
6.	<i>Lagopus mutus/lagopus</i>	1	–	1	0.2
7.	<i>Lagopus lagopus/Tetrao tetrix</i>	15	–	15	2.9
8.	<i>Lagopus</i> sp.	6	2	8	1.5
9.	<i>Tetrao tetrix</i> LINNAEUS, 1758	305	20	325	62.0
10.	<i>Tetrao tetrix/urogallus</i>	2	–	2	0.4
11.	<i>Tetrao urogallus</i> LINNAEUS, 1758	31	4	35	6.7
12.	<i>Tetrao</i> aff. <i>partium</i> (KRETZOI, 1962)	–	20	20	3.8
13.	<i>Tetrao rhodopensis</i> BOEV, 1998	1	–	1	0.2
14.	<i>Tetrao</i> sp.	6	–	6	1.1
15.	<i>Tetrao/Lagopus</i>	5	–	5	1.0
16.	Tetraonidae gen.	5	3	8	1.5
	TOTAL	452	73	525	100.2

Table II

Chronostratigraphical distribution of Tetraonidae in Bulgaria (In columns: ancient – A, early – E, middle – M, late – L)

N	Taxa	Pliocene			Pleistocene			Holocene				
		E	L		E	M	L	A	E	M	L	
1.	<i>Bonasa bonasia</i> (LINNAEUS, 1758)						+					+
2.	<i>Lagopus</i> aff. <i>atavus</i> JÁNOSSY, 1974	+										
3.	<i>Lagopus balcanicus</i> BOEV, 1995		+									
4.	<i>Lagopus lagopus</i> (LINNAEUS, 1758)						+					
5.	<i>Lagopus</i> sp. (cf. <i>Lagopus</i>)				+		+					
6.	<i>Lagopus mutus</i> (MONTIN, 1776)						+					
7.	<i>Lagopus mutus/lagopus</i>						+					
8.	<i>Lagopus lagopus/Tetrao tetrix</i>						+					+
9.	<i>Tetrao tetrix</i> LINNAEUS, 1758		+				+	+		+		+
10.	<i>Tetrao tetrix/urogallus</i>						+					
11.	<i>Tetrao urogallus</i> LINNAEUS, 1758				+		+	+		+		+
12.	<i>Tetrao</i> aff. <i>partium</i> (KRETZOI, 1962)		+									
13.	<i>Tetrao rhodopensis</i> BOEV, 1998	+										
14.	<i>Tetrao</i> sp.		+				+					
15.	<i>Tetrao/Lagopus</i>				+							
16.	Tetraonidae gen.						+					

The fossil and subfossil material was identified using the comparative skeleton collection of recent birds of the National Museum of Natural History of the Bulgarian Academy of Sciences in Sofia (NMNHS). The great majority of it is kept at the Fossil and Recent Birds Department of the NMNHS. The identification of the fossil taxa was done by using reference collections of other institutes listed in the “Acknowledgments” section (see also the relevant papers). Collection numbers of the NMNHS register are given for each find. The numbers of finds of other Bulgarian collections are given in brackets.

The taxonomy of the recent taxa follows DE JUANA (1994). Recent distributions of the species is according to CRAMP & SIMMONS (1980) and HAGEMEIJER & BLAIR (1997). Fossil taxa are listed according to BRODKORB (1964), BOCHEŃSKI (1997) and TYRBERG (1998). The osteological terminology follows BAUMEL & WITMER (1993), while the chronostratigraphy is after MEIN (1990).

III. SHORT DESCRIPTION OF THE SITES

P l i o c e n e

1. Dorkovo. The site is a former bank of the River Mutnitsa in the vicinity of Dorkovo village (Pazardzhik Region). It is located about 1 km south of the village in a stony hill at ca. 850 m a.s.l. UTM grid: KG 65. The mammalian fauna dates the site as the Ruscianian (THOMAS et al. 1986), more precisely the Early Ruscianian – MN zone 14. The fossil birds were studied by BOEV (1998 a).

2. Muselievo. A rock shelter of up to 1,5 m depth in a cave now destroyed in ? Sarmatian limestones, about 1 km SE of Muselievo village (Lovech Region) and 350 m from the right bank of the River Ossam. 150 m a.s.l. UTM grid LJ 23. The mammalian fauna dates the site to the 2-nd half of the Middle Ruscianian (MN 15 B or the end of the zone – 3.3-3.1 Ma) according to POPOV (1994 a), POPOV & DELCHEV (1997) and SPASSOV (2000). The bird fossils were studied by BOEV (2001).

3. Varshets. A ponor in a rocky hill, 6 km NNE from the town of Varshets (Montana Region). 650 m a.s.l. UTM grid: FN 89. The associated mammals (SPASSOV, 2000; POPOV in press, – a) attribute the age of site to the Middle Villafranchian (MN 17 zone).

P l e i s t o c e n e

4. Balsha. Limestone quarry in the vicinity of Balsha village (Sofia District). 600 m a.s.l. UTM grid: FN 84. Late Pliocene (the end of the Middle Villafranchian /Villanyian) to the beginning of the Early Pleistocene (Late Villafranchian /Biharian; MNQ 18-19) (V. POPOV & N. SPASSOV – pers. comm.).

5. Kunino. Limestone quarry in the vicinity of the Kunino village (Vratsa Region). 250 m a.s.l. UTM grid: GN 48. Early Pleistocene (Vaalian – Menapian /Biharian) to Middle Pleistocene according to V. POPOV & N. SPASSOV (pers. comm.).

6. Temnata Douпка Cave. Near the Karloukovo village (Lovech Region). 200 m a.s.l. UTM grid: KH 68. Late Pleistocene (Epigravettian; 31 900 to 13 600 B. P.) – soundings I and V (POPOV 1986, 1994 b). Note: Finds from other soundings (IV) of this cave date to the Early Pleistocene (ca. 1,6 Mya; V. POPOV pers. comm.). The fossil birds were studied by BOEV (1994).

7. Bacho Kiro Cave. Near the town of Dryanovo (Gabrovo Region). 450 m a.s.l. UTM grid: LH 75. End of Early to Late Pleistocene. The fossil birds were studied by BOCHENSKI (1982).

8. Devetashka Cave. 3 km NW of Devetaki village (Lovech Region). On the right bank of the River Ossam. 250 m a.s.l. Among the largest caves of Europe. UTM grid: LH 28. Late Wurm, Middle Palaeolithic (ca. 70 000 B. P.) (V. POPOV pers. comm.).

9. Razhishka Cave. Near the Lakatnik railway station (Sofia District), ca. 500 a.s.l. UTM grid: FN 96. Dated to the end of the Late Pleistocene, probably including the transition to Holocene (POPOV in press, b). The fossil birds were studied by BOEV (2000 a).

10. Mirizlivka Cave. 5 km NW of the town of Belogradchik (Vidin Region). 750 m a.s.l. UTM grid: FP 43. Late Pleistocene (Late Wurm, Late Palaeolithic) (POPOV 1933).

11. Kozarnika Cave. 5 km NW of the town of Belogradchik (Vidin Region). 1000 m a.s.l. UTM grid: FP 43. Transition between the Interpleniglacial 2 and the Pleniglacial 2 (POPOV in press; SIRAKOV et al. in press). The bird remains were studied by BOEV (in press, b).

12. Filipovska Cave. 1,5 km N of Filipovtsi village (Pernik Region). 850 m a.s.l. UTM grid: FN 44. Wurm (V. POPOV pers. comm.). The bird remains were studied by BOEV (in press, c).

13. Cave No 16. Large rock niche, a distinctive part of the Temnata Douпка Cave. 200 m a.s.l. UTM grid: KH 68. Interglacial Riss-Wurm to early Pleniglacial 2 (50 000 –20 000 B. P.) (POPOV et al. 1994; POPOV 2000). The fossil birds were studied by BOEV (1994).

14. Toplya Cave. Near Golyama Zhelezna village (Lovech Region). 450 m a.s.l. UTM grid: KH 96. Wurm (V. POPOV – pers. comm.).

H o l o c e n e

15. Madara. A rock niche in a block of 60-m height, 1 km from Madara village (Shoumen Region). A former feeding place of *Bubo bubo* (LINNAEUS, 1758). Early Holocene (V. POPOV – pers. comm.). Our data show that at least part of the collected material is mixed with bones of more recent age (Late Holocene, or even subrecent, i. e. Late Medieval), because of the presence of *Streptopelia decaocto* (FRYVALDSZKY, 1838), a species that appeared on Balkans in the early 17-th century (BOEV 1963). 500 m a.s.l. UTM grid: NH 09.

16. Kazanluk. Early to middle Neolithic settlement in the town of Kazanluk (Stara Zagora Region). 300 m a.s.l. UTM grid: LH 61. 8000-7000 B. P. The bird fauna was studied by BOEV (1993).

17. Topchii. Rock niche 2 m in depth at 150 m of the River Topchiyska. In the vicinity of the Topchii village (Razgrad Region). 350 m. a.s.l. UTM grid: MJ 53. Late Holocene (after 17-th century; see “15. Madara” in this section).

18. Lakatnik. A rock shelter above the River Iskar bellow the Monument of the Septemvriani near the r/w station of Lakatnik (Sofia Region). Late Holocene (V. POPOV pers. comm.). 550 m a.s.l. The avian remains were probably accumulated by a diurnal and/or nocturnal raptor. UTM grid: FN 96. The bird fauna was studied by BOEV (in press, d).

19. Yagodinska Cave. 2 km from Yagodina village (Smolyan Region). 1100 m a.s.l. UTM grid: KG 71. Eneolithic (ca. 6000 B. P.).

20. Dolnoslav. 3 km N of Dolnoslav village (Plovdiv Region). 500 m a.s.l. UTM grid: LG 34. Late Eneolithic (6000 – 4000 B. P.; Dr. Bistra KOLEVA unpubl. data). The bird remains were studied by SPASSOV et al. 2001.

21. Golyamo Delchevo. Late Neolithic settlement mound near the former village of Golyamo Delchevo (Varna Region; IVANOV & VASSILEV, 1975). 200 m a.s.l. UTM grid: NH 36. Flooded by the Tsonevo Reservoir. Bird remains were studied by IVANOV & VASSILEV (1975).

22. Ezerovo. Late Eneolithic to Early Bronze Age settlement near the village of Ezerovo (Varna Region, 6000-5000 B. P.). 50 m a.s.l. UTM grid: NH 68. The bird remains were studied by IVANOV & VASSILEV (1979).

23. Ovcharovo. Eneolithic settlement mound. 2 km W of the village of Ovcharovo (Targovishte Region, 6400-6000 B. P.; VASSILEV 1983, 1985). Flooded by the Ovcharovo Reservoir. 600 m a.s.l. UTM grid: NH 78. The bird remains were studied by VASSILEV (1983, 1985).

24. Golyamata Peshtera Cave. 1 km of Logodazh village (Blagoevgrad Region). Eneolithic and Early Iron Age deposits of the cave (Dr. Vassil NIKOLOV – unpubl. data). 850 m a.s.l. UTM grid: FM 65.

25. Hissarluka. Early Byzantine (5th-6th century A. D.) and medieval (10th-12th century A. D.) settlement in the town of Sliven. 400 m a. s. l.. UTM grid: MH 42. Bird remains were studied by BOEV & RIBAROV (1989).

26. Baba Vida. Medieval fortress in the town of Vidin on the right bank of the River Danube. 50 m a.s.l. UTM. grid: FP 47. 8th to 17th century A.D.; Dr. Vulo VULEV inpubl. data).

27. Omurtag. Late Medieval settlement near the town of Omurtag (Dobrich Region). 900 m a.s.l. UTM. grid: MH 57. Late Holocene (Dr. Georgi RIBAROV unpubl. data).

IV. FOSSIL RECORD OF TETRAONIDAE

G e n e r a l d a t a

According to BRODKORB (1964) the oldest records of fossil taxa of the family Tetraonidae come from the “Lower Miocene” of Nebraska (*Palaeolectoris incertus* WETMORE, 1930), South Dakota (*Tympanuchus stirtoni* A. H. MILLER, 1944) and from the “Upper Miocene” (*Archaeophasianus roberti* (STONE, 1915) and *A. miocaenus* (SHUFELDT, 1915)). The systematic position, even the family status, of these four taxa is not sufficiently clear and their relation to Cracidae, Phasianidae, or to Meleagrididae should be examined (OLSON 1985).

BOCHEŃSKI (1997) lists 7 fossil species of the family (Tetraonids are referred to Phasianidae in that paper) for Europe. The oldest remains are dated to the Lower Pliocene: *Tetrao partium* (KRETZOI, 1962) from the Lower Pleistocene of Romania, Hungary and Austria, *T. praeurogallus* JÁNOSSY 1969 from the Lower to Middle Pleistocene from Hungary, Poland, and Romania, *T. conjugens* JÁNOSSY 1974 from the [Lower – Z. B.] Pliocene of Poland and Hungary, *Lagopus atavus* JÁNOSSY 1974 from the Upper Pliocene of Poland, *L. balcanicus* BOEV 1995 from the Upper Pliocene of Bulgaria, and *Bonasa praebonasia* (JÁNOSSY, 1974) from the Middle Pleistocene of Hungary, France and Poland. In addition, *Tetrao pessieti* GERVAIS, 1862 has been described from the Early Oligocene (MP 25) of SW France (MOURER-CHAUVIRÉ, 1996), although this taxon was referred to the genus *Taoperdix* MILNE-EDWARDS, 1869 in the family Gallinuloidinae (LUCAS, 1900) and it was excluded from the Tetraonidae by BOCHEŃSKI (1997).

According to TYRBERG (1998) at least 13 taxa are known by their fossil records in the Pleistocene deposits through the Palaearctic. The seven fossil taxa, included in this list are as follows: *Bonasa praebonasia* (JÁNOSSY, 1974), *B. daliannsis* (HOU, 1992), *Lagopus lagopus noaillensis* (MOURER-CHAUVIRÉ, 1975), *Lagopus mutus correzensis* (MOURER-CHAUVIRÉ, 1975), *Tetrao tetrax longipes* (MOURER-CHAUVIRÉ, 1975), *Tetrao partium* and *T. praeurogallus*. All of them come from European localities, mainly from the West and Central parts of the continent. The exception is *B. daliannsis*, described from NE China. Four species (*L. lagopus*, *L. mutus*, *T. tetrax* and *T. urogallus*) are found in dozens of localities each represented by numerous remains.

BRODKORB (1964) cites data on the Pleistocene records of nine extant taxa from Nearctic sites: *Dendrogapus obscurus* (SAY, 1823), *Canachites canadensis*, *L. lagopus*, *L. mutus*, *Bonasa umbellus* (L., 1766), *Tympanuchus phasianellus* (LINNAEUS, 1758), *T. cupido* (LINNAEUS, 1758), *T. pallidicinctus* (RIDGWAY, 1873) and *Centrocercus urophasianus* (BONAPARTE, 1827). The Nearctic Pleistocene record of Tetraonidae seems much poorer than the Palearctic one, both in taxa and sites.

All data on the fossil record of Tetraonidae, listed above, contradict the very brief review made by LUCCHINI et al. (2001), who concludes that “the paleontological record is scanty and uncertain and it cannot be reliably used to ascribe an area of origin for grouse or to date the origins of this group.” (p. 160) (see below).

S y s t e m a t i c r e v i e w o f B u l g a r i a n f o s s i l s

Bonasa bonasia (LINNAEUS, 1758)

Bonasa bonasia. Material. Devetashka Cave: NMNHS 7257, 8953, 8954, 9135; Razhishka Cave: NMNHS 7591-7593, 8275 (BOEV, 2000 a).

Bonasa cf. *bonasia*. Material. Kozarnika Cave: NMNHS 6751, 7640, 7819-7822, 8274; Razhishka Cave: NMNHS 7594; Cave No 16: NMNHS 7903; Lakatnik: NMNHS 7996; Devetashka Cave: NMNHS 8168, 8833.

Discussion: All these localities lie slightly out of the recent range of the Hazel Grouse (Fig. 1). The eastern limit of its distribution in SE Europe passes through Bulgaria (HAGEMEIJER & BLAIR 1997). The Hazel Grouse is an endangered species in that country (BOEV 1985 a). Besides its legislative protection since 1962, the species' population in the country is in stable decline (BOEV 1985 a; SIMEONOV et al. 1990). Its highly fragmented range is confined to the Southern (SW) part of the country.

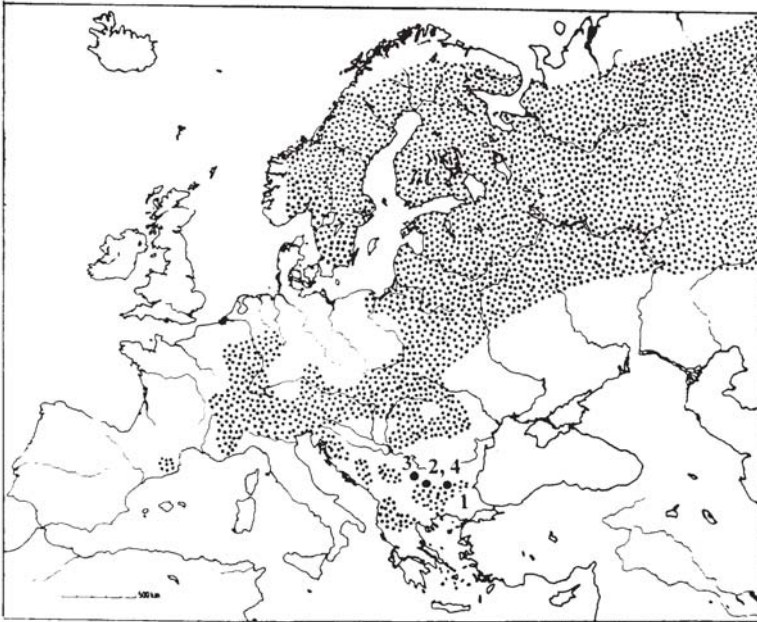


Fig. 1. Recent European breeding range (dotted) (after CRAMP, SIMMONS 1980; HAGEMEIJER, BLAIR 1997 and the Quaternary localities (black circles) of *Bonasa bonasia* in Bulgaria (present paper): 1 – Devetashka Cave, 2 – Razhishka Cave, 3 – Kozarnika Cave (Late Pleistocene); 4 – Lakatnik (Late Holocene) (Drawing: Vera HRISTOVA).

Lagopus balcanicus BOEV, 1995

Lagopus balcanicus. Material. Varshets (type locality; BOEV 1995): NMNHS 1-13, 139, 249, 250, 322, 323-326, 328-329, 336-338, 377-386, 1634, 1640, 1641, 1643 (topotypes).

Lagopus cf. *balcanicus*. Material. Varshets: NMNHS 339.

Discussion: A fossil species, described and known only from Bulgaria. Possibly partly contemporaneous with *L. atavus* JÁNOSSY, 1974 (see IV. Discussion). Some of the remains, listed above represent new skeletal elements so far unknown (sternum, pars coracoidalis, phalanx 2 digitorum 2 pedis), collected and determined since the paper of BOEV (1995).

Lagopus lagopus (LINNAEUS, 1758)

Lagopus lagopus. Material. Devetashka Cave: NMNHS 7007, 7047, 7048-7053, 7129, 7153-7157, 7207, 7209, 7220, 7461-7463; Kozarnika Cave: NMNHS 7692, 7852, 8063, 8140, 8415, 8485.

Lagopus cf. *lagopus*. Material. Devetashka Cave: NMNHS 7158-7159, 7260, 7459-7460, 9345; Kozarnika Cave: NMNHS 7824-7825, 9651; Filipovska Cave: NMNHS 8641.

Discussion: All the sites lie out of the recent breeding range (Fig. 2). The species is locally extinct both in Bulgaria and the Balkans (HAGEMEIJER & BLAIR 1997). In the Wurm the species was common in vast regions of Central, Western and Eastern Europe (TYRBERG 1998). The numerous finds at the two (four) localities in Bulgaria from the Late Pleistocene complete our data on the southern distribution of the s. c. "Boreal complex" during the colder stages including the Balkans. No relict populations survived in the moderate and sub-Mediterranean regions of Europe because of the absence of suitable boggy-shrubs habitats (TYRBERG 1991).

Lagopus mutus (MONTIN, 1776)

Material. Bacho Kiro Cave (BOCHENSKI 1982).

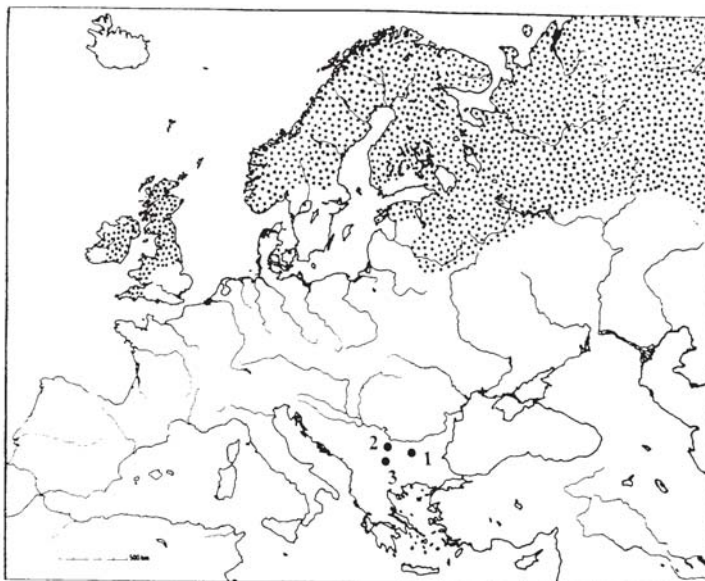


Fig. 2. Recent European breeding range (dotted) (after HAGEMEIJER, BLAIR 1997) and the Late Pleistocene localities (black circles) of *Lagopus lagopus* in Bulgaria (present paper): 1 – Devetashka Cave; 2 – Kozarnika Cave; 3 – Filipovska Cave (Drawing: Vera HRISTOVA).

Lagopus mutus/lagopus: Material. Devetashka Cave: NMNHS 8139.

Discussion: The find No 8139 represents a crista sterni, both morphologically and dimensionally identical with *L. mutus*. Its fragmentary nature does not allow the complete exclusion of *L. lagopus*. Both sites lie out of the recent range of *L. mutus* (HAGEMEIJER & BLAIR 1997; Fig. 3). It is no longer a breeding species in Bulgaria. The presence of genus *Lagopus* in the Pleistocene sites of Europe is an indication of coolings of the local climate (MOURER-CHAUVIRÉ 1977). TYRBERG (1991) lists 7 recent separate populations of *L. mutus* in the Western Palearctic. The continental localities, together with the Wurmian sites form the complete Pleistocene range. The site of the Bacho Kiro Cave in the Stara Planina Mts. is the southernmost (except one site of S Italy). It is worth noting that in the winter of 1996 one specimen was observed in the region of the Atanasovsko Lake Nature Reserve on the S Black Sea Coast of Bulgaria (MILTSCHEW & GEORGIEVA 1998), the first record for Bulgaria.

Lagopus aff. *atavus* JANOSSY, 1974

Material. Muselievo: NMNHS 422. Description and comparison of this find are given by BOEV (2001).

Discussion: The find from Muselievo is among the oldest records of genus *Lagopus*. It is the first record of that species from the Balkan peninsula and SE Europe. Moreover, the site of Muselievo marks the southernmost distribution of the genus *Lagopus* in the Tertiary. Of great interest fact is the coexistence of *Lagopus* and *Pavo* in the Early Pliocene of SE Europe (see IV. Discussion). It reveals an association that has not been known so far (BOEV 1998 b, 2001).

Lagopus sp.

Lagopus sp. Material. Balsha: NMNHS 12 313; Devetashka Cave: NMNHS 8832; Cave No 16: NMNHS 8875; Kozarnika Cave: NMNHS 9652-9653, 9656.

cf. *Lagopus* sp. Material. Balsha: NMNHS 12 314-12 315.

Discussion: These Late Pleistocene finds most probably belong to *L. lagopus* or/and *L. mutus*.

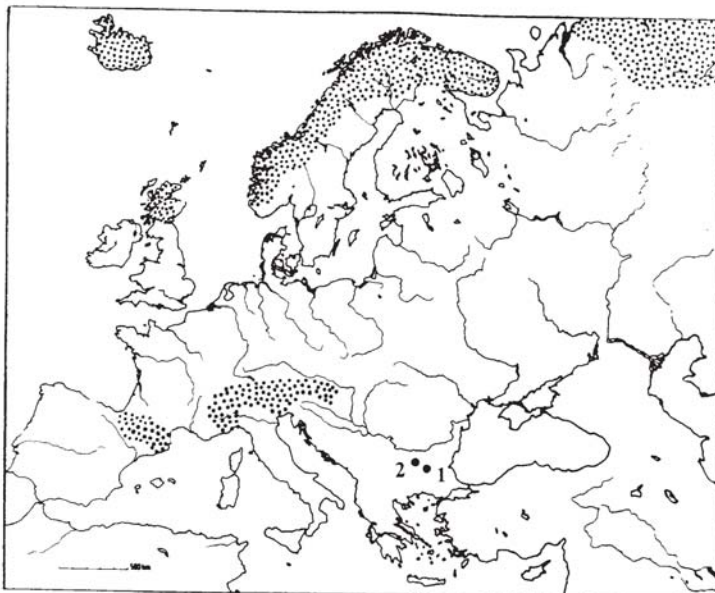


Fig. 3. Recent European breeding range (dotted) (after HAGEMEIJER, BLAIR 1997) and the Late Pleistocene localities (black circles) of *Lagopus mutus* in Bulgaria (present paper): 1 – Bacho Kiro Cave (BOCHENSKI 1982); 2 – Devetashka Cave (finds of *L. mutus/lagopus*; Drawing: Vera HRISTOVA).

Lagopus lagopus/Tetrao tetrix

Material. Devetashka Cave: NMNHS 7265; Kozarnika Cave: NMNHS 6743-6746, 7694-7698, 7853-7854, 7871; Lakatnik: NMNHS 7999-8000.

Tetrao tetrix LINNAEUS, 1758

Tetrao tetrix. Material. Yagodinska Cave: NMNHS 5411; Mirizlivka Cave: NMNHS 5417, 5444, 6493; Topchii: NMNHS 5806, 1101-1102; Razhishkata Cave: NMNHS 6715, 7582; Kozarnika Cave: NMNHS 6749, 6773, 8271-8272, 9654-9655, 9657; Devetashka Cave: NMNHS 6785, 6786-6789, 6793-6795, 6797-6804, 6823-6824, 6973-6987, 6989-6993, 6998-7006, 7008-7027-7044, 7054-7059, 7060-7066, 7067-7070, 7072-7075, 7076-7124, 7130-7135, 7148-7152, 7208, 7210-7217, 7221-7256, 7287-7288, 7497, 8135-8138, 8193-8196, 8206-8209, 8376-8377, 8416-8419, 8422-8429, 8845-8865, 8947-8949, 8966-8968, 9100, 9126-9134, 8068, 9811, 9873, 12006-12007; Cave No 16: NMNHS 7924; Filipovska Cave: NMNHS 7978, 7980; Toplya Cave: NMNHS 11448; Kazanluk: (1136-1138), (3161) (KOVACHEV 1988; BOEV 1993).

Tetrao cf. tetrix. Material. Varshets: NMNHS 33, 44, 184; Topchii: NMNHS 1100, 8925; Yagodinska Cave: NMNHS 1103; Razhishkata Cave: NMNHS 6495; Lakatnik: NMNHS 6505; Kozarnika Cave: NMNHS 6755, 7688-7689, 7693, 7699-7702, 8264; Filipovska Cave: NMNHS 8638, 8640; Devetashka Cave: NMNHS 9346.

Discussion: All sites lie out of the recent range of the Black Grouse (HAGEMEIJER & BLAIR (1997; Fig. 4). A species now missing from Bulgaria (BOEV 1985 b). It should be mentioned that the information given by VAURIE (1965) on the occurrence of *T. tetrix* "... south to the ... Balkan peninsula ... to ... Bulgaria" (p. 253) is erroneous.

Most interesting are the finds from the Villafranchian site of Varshets. They could be the oldest records of *T. tetrix* proving its coexistence with *T. partium* in the Balkans during the Late Pliocene. It is possible that *T. praeurogallus*, *T. partium*, *T. urogallus* and *T. tetrix* (identified as *T. cf. tetrix*)

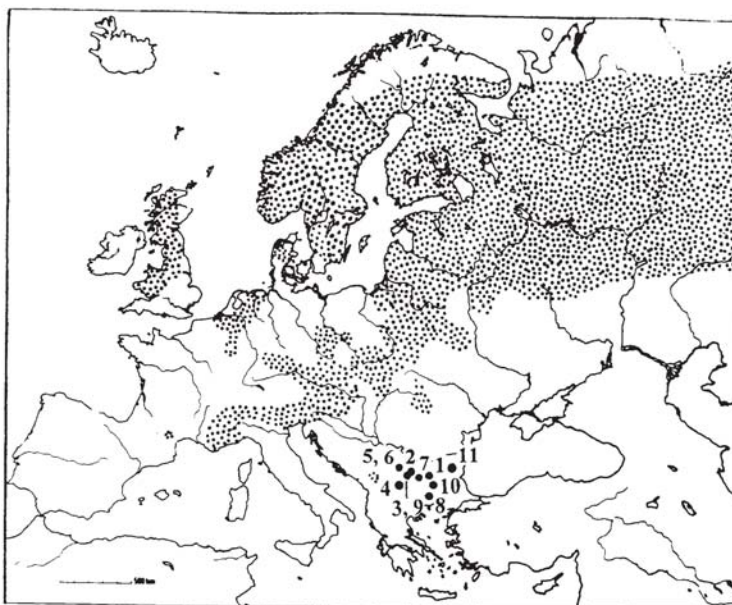


Fig. 4. Recent European breeding range (dotted) (after HAGEMEIJER, BLAIR 1997) and the Quaternary localities (black circles) of *Tetrao tetrix* in Bulgaria (present paper): 1 – Devetashka Cave, 2 – Cave No 16, 3 – Razhishka Cave, 4 – Filipovska Cave, 5 – Mirizlivka Cave, 6 – Kozarnika Cave, 7 – Toplya Cave (Late Pleistocene); 8 – Yagodinska Cave, 9 – Lakatnik, 10 – Kazanluk, 11 – Topchii (Holocene) (Drawing: Vera HRISTOVA).

partly coexisted in the Early Pleistocene in SE Europe (locality of Betfia (MN 18 – MNQ 19) in NW Romania (data summarized by TYRBERG 1998).

The disappearance of the Black Grouse in the Balkan countries is well-documented (BOEV 1997 a, b). In the Balkans today this species survives only in two areas: in NW Macedonia and Montenegro (HAGEMEIJER & BLAIR, 1997). The eleven Quaternary localities of *T. tetrix* in Bulgaria (BOEV 1999 a) are convincing proof for its wider former distribution, practically encompassing all parts of the country. Indirect dating of one of the localities (Topchii) suggests a very recent age of the remains i. e. between 17-th and 20-th century. This is due to the known date for the appearance of the Turtle dove in the Balkan peninsula (BOEV 1963). Thus, we can maintain that *T. tetrix* disappeared in Bulgaria during the last 400 years. The disappearance of the Black Grouse was a result of the various effects of human activity – habitat destruction, total deforestation, agricultural modification of former habitats, over-hunting, etc.

Tetrao tetrix/urogallus

Material. Devetashka Cave: NMNHS 6988; Kozarnika Cave: NMNHS 7864.

Tetrao urogallus LINNAEUS, 1758

Tetrao urogallus. Material. Devetashka Cave: NMNHS 7071, 7136-7137, 7263, 8154, 9874; Dolnoslav: NMNHS 1180-1184, 1185-1187; Hissarluka: NMNHS 2850, (309); Yagodinska Cave: NMNHS 3008-3009, 3047, Baba Vida: NMNHS 3139-3140, (2206-2207); Madara: NMNHS 3969-3970; Omurtag: NMNHS 6353; Lakatnik: NMNHS 6518; Kozarnika Cave: NMNHS 6714; Kazanluk: (2312) (KOVACHEV 1988; BOEV 1993). Remains of Capercaillie have also been reported from Golyamo Delchevo – 1 ulna (IVANOV & VASSILEV 1975), Ovcharovo – 1 humerus (VASSILEV 1983, 1985), Ezerovo – unspecified number and type of bones (IVANOV & VASSILEV 1979) and Golyamata Cave – unspecified number and type of bones (Dr. Vassil NIKOLOV – unpubl. data).

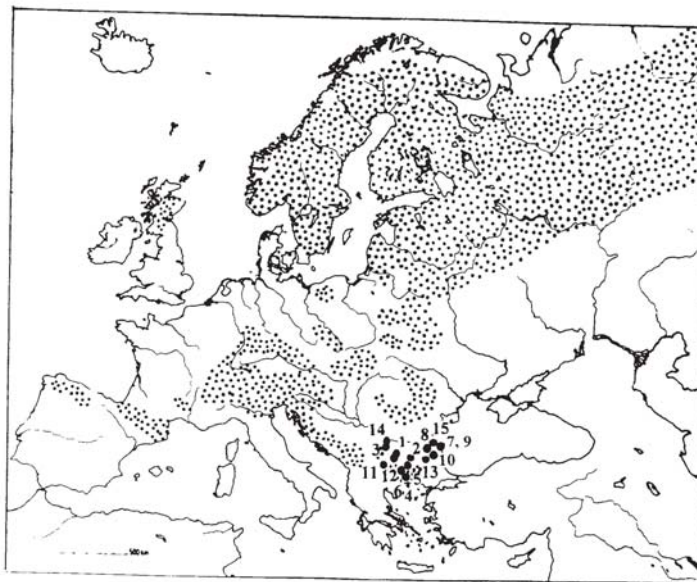


Fig. 5. Recent European breeding range (dotted) (after HAGEMEIJER, BLAIR 1997) and the Quaternary localities (black circles) of *Tetrao urogallus* in Bulgaria (present paper): 1 – Kunino, 2 – Devetashka Cave, 3 – Kozarnika Cave (Pleistocene); 4 – Yagodinska Cave, 5 – Kazanluk, 6 – Dolnoslav, 7 – Golyamo Delchevo, 8 – Ovcharovo, 9 – Ezerovo, 10 – Madara, 11 – Golyamata Peshtera Cave, 12 – Lakatnik, 13 – Hissarluka, 14 – Baba Vida, 15 – Omurtag (Holocene) (Drawing: Vera HRISTOVA).

Tetrao cf. urogallus. Material. Kunino: NMNHS 12312; Yagodinska Cave: NMNHS 3048; Devetashka Cave: NMNHS 7045-7046.

Discussion: Some of the sites (Baba Vida, Hissarluka, Omurtag, and Devetashka Cave, as well as Golyamo Delchevo, Ovcharovo, Golyamata Peshtera Cave, Ezerovo) lie far beyond the present range of the species (HAGEMEIJER & BLAIR 1997; Fig. 5). They mark the wider former range of the Capercaillie in the Balkans. The Capercaillie is an endangered species in Bulgaria (BOEV 1985 c) and the eastern limit of its range in SE Europe passes through the country.

The presence of the genus *Tetrao* in the Pleistocene sites of Europe is an indication that the local climate was cooling (MOURER-CHAUVIRÉ 1977). Finds of *T. urogallus* are very rare in the Late Wurmian localities of the French Alps (MOURER-CHAUVIRÉ 1977) despite the belief that its range was confined to the Alps at the end of the Wurm. The recent (end of 1990-ies) breeding range of the Capercaillie in Bulgaria includes four isolated sites in the Zapadna Stara Planina Mts. (the W Balkan Range), Vitosha Mts., Rila Mts., Pirin Mts., and the Zapadni Rodopi Mts, all in the SW part of the country between 1100 and 2200 m a.s.l. For about two decades (1965 - 1984) the species' total population decreases from 2606 to 2037, i. e. 21.8 percent (SIMEONOV et al. 1990).

Tetrao aff. partium (KRETZOI, 1962)

Material. Varshets: NMNHS 157-158, 178, 185, 194, 196, 198, 201, 245, 278-283, 1635-1639.

Discussion: The finds from Bulgaria add new data to the geographical and stratigraphical distribution of that tetraonid (Fig. 6). They also complete the information on its bone morphology and osteometry. *T. partium* was known until now from Germany, Slovakia, Hungary and Ukraine (BOEV 1999 b). The finds from France have been determined as *Tetrao cf. partium* (MOURER-CHAUVIRÉ – in litt.). The remains from Varshets confirm its wider distribution throughout Eastern Europe during the Middle Villafranchian. They are among the earliest evidence for the species as a whole. The Bulgarian finds are the first records from the Balkans and mark the southern limit of its range. In ad-

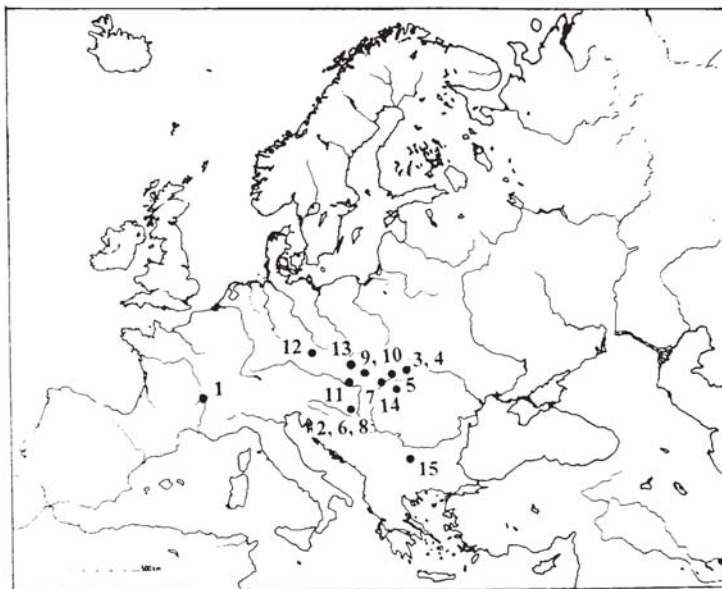


Fig. 6. Distribution of *Tetrao partium* in the Plio-Pleistocene of Europe (after TYRBERG, 1998; BOEV 1999 b): 1 – Senèze (France); 2 – Nagyarsany-hegy (1-4) 3 – Osztramos 2, 4 – Osztramos 8, 5 – Pesko, 6 – Somssichhegy 2, 7 – Tarko, 8 – Beremend 16-17 (Hungary); 9 – Gambaszog, 10 – Mehesh (Slovakia); 11 – Hundsheim (Austria); 12 – Voidtstedt (Germany); 13 – Stranska Skala (Czechia); 14 – Betfia (Rumania); 15 – Varshets (Bulgaria) (Drawing: Vera HRISTOVA).

dition to the finds, listed by BOEV (1999 b) we also refer here the finds No 1635-1639, i. e. three new skeletal elements: fibula, tibiotarsus dist., and tarsometatarsus prox.

Tetrao rhodopensis BOEV, 1998

Material. Dorkovo: NMNHS 483. Description and comparison of this find are given by BOEV (1998 a).

Discussion: The Bulgarian remains of the genus *Tetrao* in the Ruscinian locality complete our knowledge on the origin and distribution of tetraonids at whole. No data on the appearance of the tetraonids are known so far from earlier than the terminal Ruscinian (JÁNOSSY 1991). The “urogallus” lineage of genus *Tetrao* is considered an indicator for a forested landscape. In the Southern Palearctic at present it is distributed predominantly in the coniferous and mixed coniferous-deciduous forest zone in the mountains. The associated fauna of this site suggests a forested landscape such as an open parkland forest or a wooded savanna or even a more densely forested habitat (THOMAS et al. 1986; BOEV 1998 a). For the landscape of the vicinity of Dorkovo locality SPASSOV (in press) uses “open forest”.

Tetrao sp.

Material. Varshets: NMNHS 237-239; 262-263; Temnata Douпка Cave: NMNHS 663.

Discussion: The morphology and dimensions of the finds from Varshets (phalanges digitorum pedis) are very close to recent Black Grouse in spite of the considerable chronostratigraphic hiatus (BOEV, 1999 a).

Tetrao/Lagopus

Material. Varshets: NMNHS 164-165, 257; Devetashka Cave: NMNHS 9375; Kunino: NMNHS 12 302.

Discussion: N 164 (vertebra cervicalis VIII) shows a strong resemblance to *T. tetrix*. It differs from it by having a more clearly developed side-line and a more concave ventral facies articularis (BOEV, 1999 a). The facies articularis in caudal view in *Lagopus* is more concave than in *Tetrao*. N 165 (vertebra thoracalis XIV) – the last free vertebrae before the os notarium in Tetraonidae. This specimen shows considerable similarity with *T. tetrix*, but the specimen has a more trapezium-like shape of the facies articularis (BOEV 1999 a).

Tetraonidae general

Material. Kozarnika Cave: NMNHS 7869-7870, 9658; Filipovska Cave: NMNHS 7977; Devetashka Cave: NMNHS 8070.

cf. Tetraonidae gen. Material. Varshets: NMNHS 2703-2705.

V. ANALYSIS OF THE SPECIES REPRESENTATION

At least 28 (28.6 percent) of all the 98 Neogene-Quaternary sites in Bulgaria contain bone finds of tetraonid birds. No strong correlation between the size of taxa and bone abundance in the fossil/subfossil record of tetraonid species exists. The largest tetraonid in Europe, *T. urogallus*, accounts for 6.7 percent of all records, while the medium sized *T. tetrix* is represented by 62.0 percent of finds (Table I). The remains of *B. bonasia*, the smallest European tetraonid are very scanty in Bulgaria (3,8 percent of the total material). This is in accordance with the general representation of that species in the whole of Europe (TYRBERG 1998). The summary data of TYRBERG (1998) determine that *B. bonasia* is the least well represented recent tetraonid in the fossil record of the Palearctic. It also has a narrower relative stratigraphic range – Middle Pleistocene (MNQ 21) – present.

Most of the Quaternary sites (all except No 4, 5, 12, 15, 17, 18) were prehistoric or ancient and medieval settlements and humans were the main factor in the accumulation of the avian bone remains.

Bulgaria has the most diverse fauna of Tetraonidae known from the late Pleistocene (Table II), with the five recent species still spread in Europe at present. The colder climates of the Late Pleisto-

cene and the numerous Palaeolithic caves where tetraonids are present among the prey remains of *Homo sapiens fossilis* are the main reasons for their occurrence and relative abundance.

Seven of the localities with Black Grouse are dated to the Pleistocene, while only four sites provide remains of a Holocene age. In other words, while 83.7 percent of localities with fossil and sub-fossil avifauna in Bulgaria are Holocene (BOEV 1999 a), only 36.4 percent of the localities with *T. tetrix* are Holocene. This is an indication of the considerable relative decrease, in both population number and (possibly) in range during the Holocene in Bulgaria. The occurrence of the species in some regions of Southern Europe (Alps, Carpathians), including the Balkans [Z. B.], are considered glacial relicts (HAGEMEIJER & BLAIR 1997). The Bulgarian data confirms such a conclusion.

Twelve of the 15 localities with *T. urogallus* in Bulgaria (80.0 percent) are Holocene. The Black Grouse in comparison has 36.4 percent of its records in the Holocene. Therefore, a very clear obverse situation exists as the Capercaillie became a common game-fowl during the Holocene in Bulgaria the Black Grouse declined in numbers. This could be explained by the considerable increase in the forested area of the country since the end of the Pleistocene. Meanwhile the "steppe" form of *T. tetrix tetrix* in the Ancient and Early Holocene was not well adapted to the vast, dense Bulgarian forests and only partly survived in some regions up to the Middle Ages. They were then known among the Crusaders as "Magna Sylva Bulgarica". HARRISON (1982) clearly determines Black Grouse as "... a replacement species in open forest and forest edge ... " (p. 108) for the Capercaillie.

VI. ON THE ORIGIN AND EVOLUTION OF TETRAONIDAE

As a southern geographical location Bulgaria is important for elucidating the former range fluctuations of the recent species of the family Tetraonidae, which has now a more northern distribution. The Neogene record of Tetraonidae in Bulgaria is also very interesting. It allows one to make some conclusions regarding the origin, early evolution and distribution of tetraonids.

BOCHEŃSKI (1991) demonstrated that the origin of genus *Lagopus* BRISSON, 1760 in Europe dates to the Early Pliocene (Fig. 7). JÁNOSSY (1991), however, suggests that the Tetraonidae have their origin in Europe in the Late Pliocene. The record of *Tetrao macropus* from the Csarnota 2 locality (S Hungary) of the "Uppermost Pliocene ("Lowest Villafranchian")" (JÁNOSSY 1976, p. 17) is dated MN 16.

JÁNOSSY (1976) considers *Tetrao partium* as the direct ancestor of *T. tetrix*, and *T. praeurogallus* as the direct ancestor of *T. urogallus*. However, the more recent records of these "ancestors" do not support such a statement. The record of *T. partium* in Vertesszilos 2 postdates the finds of *T. tetrix* from Montoussé, and that of *T. praeurogallus* from Tarko, Kozi Grzbiet and Zalesiaki postdates the finds of *T. urogallus* of Betfia 5 (Fig. 7). In the Early Pleistocene locality of Betfia, for instance, it seems that both species, *T. partium* (MNQ 19) and *T. tetrix* (identified as "cf.") coexisted. The last record of *T. partium* in Romania comes from the Gunz-Mindel Interglacial, while the oldest record of *T. tetrix* from that country comes from the Riss-Wurm Interglacial (JURCHAK & KESSLER 1988). It is the same for the other two species from this site (Betfia 2, 3, 5) – *T. urogallus* (MNQ 20) and *T. praeurogallus*. This could only be explained by rapid evolution of the *Tetrao* lineages in the Plio-Pleistocene of Central and Eastern Europe, perhaps contradicting Dr. JÁNOSSY's phylogeny. The incompleteness of the fossil record of the *Tetrao* lineage does not allow the building of more concrete phyletic interrelationships and the originally simple phylogeny now seems more obscure.

The summary data of MOURER-CHAUVIRÉ (1993) also shows that the Tetraonidae appear as early as the Early Pliocene (MN 15) in Europe, a judgement based chiefly on data from Central Europe. *Tetrao rhodopensis* from S Bulgaria is a little bit older than *T. macropus*. The Bulgarian record of *L. atavus* is also among the oldest finds of the genus *Lagopus*. The locality of Rebielice Królewskie 1, the type locality of *L. atavus*, is dated MN by 16, while the age of Weże 1, the type locality of *T. conjugens*, is MN 15. Both sites are in Southern Poland (BOCHEŃSKI 1996). The distance between Rebielice Królewskie and Weże 1, on the one hand, and Dorkovo and Muselievo, on the other, is about 950-1050 km, while the distance between Csarnota 2 and the sites in Bulgaria is

550-650 km (Fig. 8, 9). The relative geographical proximity and the chronostratigraphical similarity (MN 15-MN 16) proves that in the Ruscinian two regions of the continent, the Balkans and Central Europe, were inhabited contemporaneously by well-distinguished representatives of the basic genera of Tetraonidae. This suggests an older origin for the Tetraonidae, i. e. not Ruscinian, but possibly the end of the Late Miocene (Turolian – Pontian) which is confirmation of BOCHENSKI's (1991) statement: ... "the genus *Lagopus* has evolved in the Western Palearctic at least since the Early Pliocene parallel to the genus *Tetrao*." (p. 575). On the other hand, the suggestion of the same author, that "... both these genera may have common ancestor in biozone MN 14 or even earlier." (p. 575) is also partly confirmed by the fossil record from Bulgaria. That is why it is interesting to note, that the fossil record of the family does not agree with the recent mitochondrial DNA phylogeny of LUCCHINI et al. (2001). Those authors state that the North American *Lagopus leucurus* is basal to its Eurasian and Holarctic congeneric species and the monophyletic *Bonasa* is basal to all the other Tetraoninae. The position of *Bonasa* is not discussed here because of the complete absence of Tertiary records of that genus (incl. *Tetrastes*) (MLÍKOVSKÝ 1996 b). On the other hand the molecular data of LUCCHINI et al. (2001) for the late Miocene (6-9 Ma) appearance of the first tetraonids surprisingly coincide with the analysis of the fossil record (MN 11-13) of this family.

KARTASHEV (1974) without citing reasons suggests that North America should be considered the center for the radiation of the Tetraonids. LUCCHINI et al. (2001) assume that the DNA phylogeny and the dispersal vicariance analysis support a North American ("western part of the Nearctic", p. 157) origin of the family [they considered it a subfamily of Phasianidae – Z. B.] and all the constituent Tetraonidae genera, "with the possible exception of *Tetrao*" (p. 149). According to LUCCHINI et al. (2001) the present distribution of the tetraonids should be regarded as a result of at least three dispersal events from North America to Eurasia, involving the ancestors of *Bonasa*, *Lagopus* and *Tetrao* in the Palearctic.

DE JUANA (1994) writes that it is speculative to decide where in North America or Eurasia the family first appeared, although he stated further that the former "is perhaps more likely" (p. 376).

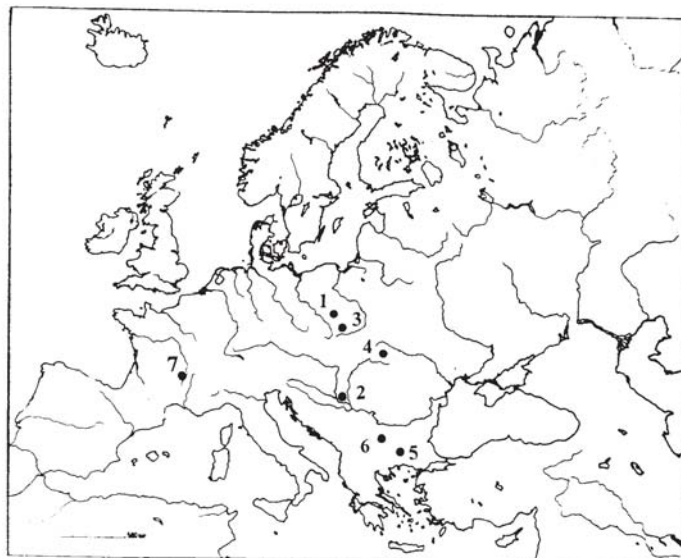


Fig. 8. Tertiary localities of *Tetrao* in Europe (after MLÍKOVSKÝ 1996; present paper): 1 – Weże (Poland); 2 – Csarnota (Hungary), 3 – Rębielice Królewskie (Poland), 4 – Osztramos 7 (Hungary), 5 – Dorkovo (Bulgaria), 6 – Varshets (Bulgaria), 7 – Seneze (France) (Drawing: Vera HRISTOVA).

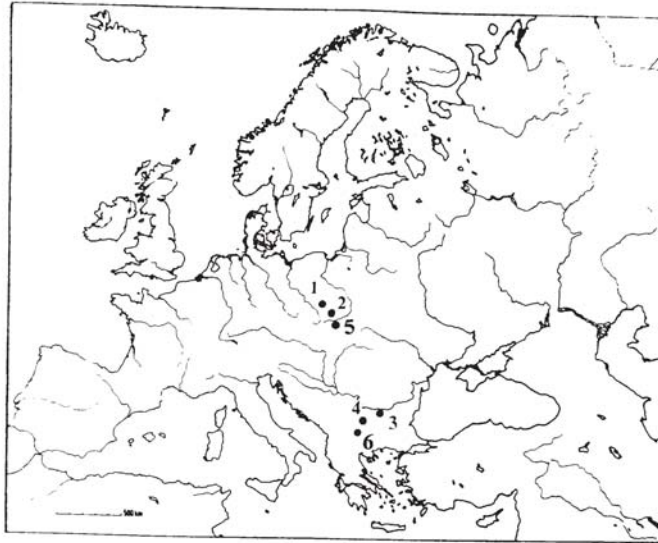


Fig. 9. Tertiary localities of *Lagopus* in Europe (after MLÍKOVSKÝ 1996; present paper): 1 – Węże, 2 – Rębelice Królewskie (Poland); 3 – Muselievo (Bulgaria), 4 – Varshets (Bulgaria), 5 – Kielniki 3B (Poland), 6 – Balsha (Bulgaria) (Drawing: Vera HRISTOVA).

We do not accept such a position, because 9 species of the total 17 and 4 genera of the total 7 are in the recent Palearctic tetraonid fauna (DE JUANA 1994). The Bering bridge served as a natural way for the interchange of the terrestrial faunas including large land birds such as the tetraonids. The Early Pliocene records (MN 14 and MN 15 zones) suggest that the Palearctic (European, and even SE-Europe) is the origin of the family, confirming a statement of Dr. Denes JÁNOSSY (in litt.). The relatively recent origin of the Tetraonidae was also hypothesised by POTAPOV (1987) and DE JUANA (1994). The last author summarizes that *Tetrao* first appears in the Pliocene of Europe, and *Bonasa* and *Lagopus* appear in the Pleistocene of Europe, while *Dendragapus* first appears in the Pleistocene of America. As mentioned above, our data disagree with these suggestions. Some results of the study of LUCCHINI et al. (2001) do not agree with such a statement. They determine the appearance of *Bonasa* as dating to 5-6 Ma, while “the other genera diverged during the upper Pliocene, and most of the ... species ... originated during the lower Pleistocene. (p. 149)”.

It is not very likely that the Tetraonidae appeared in Nearctic because no fossil evidence is known in North America besides the four (?)doubtful Miocene taxa (see above), listed by BRODKORB (1964) and rejected by OLSON (1985). No later records of the Tetraonidae from the Tertiary are known in North America and after this large hiatus the next oldest data for the Tetraonidae comes from the Early to Middle Pleistocene (WETMORE 1940; BRODKORB 1964). The situation in the Western Palearctic is quite different. Here we have a well-documented fossil record of Tetraonidae (represented by 13 taxa, 9 of them fossil!) from the Ruscinian until the Early and Late Pleistocene and further up to recent times.

Another reason for rejecting a North American origin for the Tetraonidae is that they are considered to have differentiated morphologically from the Phasianidae (POTAPOV, 1987; DE JUANA 1994). Furthermore, the phasianids are only found in the Old World, and no fossil record is known of the family from New World localities up to the present (BRODKORB 1964; OLSON 1985). This completely causes one to reject the hypothesis that the Nearctic was their area of origin.

It is worthy of note that BURCHAK-ABRAMOVICH & MELADZE (1972) described *Rustaviornis georgicus* gen. et sp. n. from the Late Miocene of Georgia and considered it both the ancestor of the Tetraonidae and the Phasianidae. The authors determined that "... *Rustaviornis* most resembles ... the genera *Phasianus* and *Lyrurus* [i.e. *Tetrao* of *tetrix* lineage – Z.B.]...", and further: "... *Rustaviornis* is a pheasant-like bird of the subfamily Phasianinae, leading further to the genus *Lyrurus* ..." (p. 383). We could not accept their statement, because of the reliable fossil record supporting the older origin of phasianids *sensu stricto*, a fact also noted by BURCHAK-ABRAMOVICH & MELADZE (1972): "... Phasianidae would have more old members than the Tetraonidae have." (p. 383). Finally the authors suppose that the common ancestor of both the Phasianidae and the Tetraonidae families should be sought in Miocene or Oligocene deposits.

The summary data for the whole European continent shows (MLÍKOVSKÝ 1996 a) that Tertiary records of the Tetraonidae (data available up to April 1996) was confined to only four countries – France, Poland, Hungary and Bulgaria. MLÍKOVSKÝ (1996 b) summarizes that "Tetraoninae [i. e. Tetraonidae – Z. B.] genera were recorded in Europe from the Ruscinian (*Tetrao*, incl. *Lyrurus*), and Villanyian (*Lagopus*) respectively" (p. 806). As can be seen from the Bulgarian record, the appearance of *Lagopus (atavus)* could also be considered the most ancient, i. e. from the Ruscinian (MN 16 in Rebielice Królewskie 1 and MN 15 B in Muselievo), instead of the Villanyian. *Tetrao* and *Lagopus* coexisted in Rebielice Królewskie 1 (BOCHEŃSKI 1996) and since that time have always coexisted in the Western Palearctic. Their coexistence in the Villanyian is proved by the fossil records from the locality of Varshets.

Another fact that deserves special attention is that traditionally the Tetraonidae have been considered cold-loving birds. "A major ecological feature of the Tetraonidae is their perfect adaptation to cold climates." (DE JUANA 1994, p. 383). This may be true, if we consider recent species. However, the earliest fossil tetraonids do not fit such a view and data from Bulgaria rejects it. *Lagopus balcanicus* and *Tetrao partium* from Varshets coexisted with the warm-loving *Apus baranensis* JÁNOSSY, 1977 (BOEV 2000 b), *Hieraaetus cf. fasciatus*, *Gyps* sp. n., *Circaetus* sp., n. (BOEV in press, a). *Tetrao rhodopensis* also shared the surroundings of Dorkovo with a small undetermined species of *Perdicinae* (BOEV 1998, in press, a), while *Lagopus atavus* in Muselievo coexisted with *Pavo bravardi* (BOEV 1998 b, 2001). If not the whole family, at least the genus *Lagopus*, appeared in the forested savana or savana-forest (BOEV 1995). The habitats for the earliest representatives of *Tetrao* may have been similar. Examples of more or less forested savana (mosaic habitats/ open forests) inhabitants from the long lists of the mammalian taxa from Dorkovo, Muselievo, as well as that from Varshets confirm such a statement. They are: *Tetralophodon longirostris*, *Anancus arvernensis*, *Dicerorhinus megarhinus*, *Dolichopithecus* sp., *Mesopithecus cf. monspessulanus*, *Prolagus cf. michauxi*, etc. from Dorkovo (THOMAS et al. 1986); *Pseudomeriones abbreviatus*, *Myomimus dehmi*, *Dolichopithecus* sp. (POPOV & DELCHEV 1997), *Hypolagus brachignatus*, *Pliopentalagus cf. dietrichi*, *Ochotonoides csarnotanus*, *Dolomys odessanus*, *Pliomys hungaricus*, *Alloicetus cf. bursae*, *Trilophomys pyrenaicus*, *Pliospalax compositodontus*, etc. (V. POPOV unpubl. data). *?Acinonyx*, *?Dinofelis*, cf. *Nyctereutes aff. megamastoides*, *Sus arvernensis*, *Cervus pardinensis*, aff. *Gazella* sp., *Tapirus arvernensis*, cf. *Dicerorhinus jeanvireti*, etc. (N. SPASSOV unpubl. data) from Muselievo and *Pannonictis ardea*, *Vormela petenyii*, aff. *Viretailurus schaubi*, *Acynonyx pardinensis*, *Eucladoceros senezensis*, *Gazellospira* sp., *Megalovis aff. latifrons*, *Equus stenonis vireti* etc. from Varshets (SPASSOV 1997).

Thus, the open light forests and the savanna-like forests were the habitats of the earliest known Tetraonidae in SE Europe. In Dorkovo, Muselievo and Varshets, the climate was milder, moister (in Dorkovo), drier (in Varshets) and warmer, than at present. This strongly contradicts to the statement of LUCCHINI et al. (2001) that "Ancestral grouse might have evolved from North American phasianids when deciduous temperate forests replaced tropical forests during the Tertiary period." It also contradicts the assumptions that (1) *Tetrao* "... evolved later and expanded northward [along the Rocky Mountains in North America – Z.B.] during the Plio-Pleistocene climate cooling." (p. 159), and that (2) *Lagopus* has a North American origin.

VII. CONCLUSIONS

Discussing the European and Balkan fossil record of Tetraonidae we could formulate the following conclusions: Tetraonidae probably first appeared in the Western Palearctic (most likely SE Europe – SW Asia) during the Late Miocene (Pontian), because *Lagopus* and *Tetrao* are known from the Ruscinian as two distinctive and differentiated genera. The genus *Tetrao* first appeared in the Balkans and Europe not later than the Early Pliocene (MN 14), while the earliest record of *Lagopus* is MN 15. Forested savana, savana-steppe or parkland forest was the habitat of the first tetraonids. The earliest tetraonids were not cold loving birds, they lived in habitats of a warmer climate than the family lives in today. Their adaptations to colder climates and habitats with snow are a more recent phenomenon, i. e. Late Pliocene – Early Pleistocene. This change was accomplished very quickly, although their relatively limited specific variety was preserved.

The Tertiary fossil record (MN 14-15, i. e. 5,4-3,4 Ma) of Tetraonidae, especially of *Lagopus* and *Tetrao*, from the Western Palearctic (present paper) confirms the monophyletic origin of Tetraonidae. The mtDNA data for the origin of *Bonasa* (5-6 Ma) in the western part of the Nearctic (LUCCHINI et al., 2001) completely contradict the well-documented paleornithological data and we consider the hypothesis based on the molecular phylogeny as groundless and inconsistent.

Nine taxa of the family were established in the fossil record of Bulgaria. This constitutes the most diversified fossil tetraonid fauna, known so far. Four species of tetraonid from the Pliocene, two species from the Pleistocene, and one species from the Holocene avifaunas disappeared by the Late Holocene. The process of impoverishment in the Holocene continues, mainly because of various anthropogenic influences. *T. tetrrix* only disappeared in Bulgaria during the last 400 years. It is possible that *T. tetrrix* has been replaced by *T. urogallus* during the Early Holocene, due to the utilization of large lowland regions of the country. It is believed that only the plain steppe form of the Black Grouse occurred in Bulgaria and that it disappeared because of the devastation of species's habitats in the plains, while the Capercaillie survived only in the mountain forests. Populations of the two surviving tetraonid species in Bulgaria (*B. bonasia* and *T. urogallus*) have been declining since the early 20th century. Both species are endangered in Bulgaria and their breeding distribution marks the limits of their ranges in the Balkans and Europe.

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