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Evolution of Galliformes and their presence in the Carpathian Basin

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Abstract Due to the number of specimen, their size and weaker flight capabilities they are one of the favorite preys of furred and feathered carnivores. Due to this factor quite a number of skeletal fragments remained and fossilized over millions of years, especially in caves. Their presence in Europe can be traced back to the Eocene, but the majority of finds come from the Neogene and the Quaternary. In the Carpathian Basin they are known since the beginning of the Neogene. The text is complemented with the bibliography concerning the fossilized material, one figure and six table.

Keywords: Europe, Carpathian Basin, evolution, Galliformes, grouses

Összefoglalás Egyedszámuk, méretük, életmódjuk, és gyengébb repülési képességük következtében kedvenc prédaállataik a tollas és szőrmés ragadozóknak. Az előbbieknek köszönhetően így elég sok vázrészük fennmaradt és fosszilizálódhatott az évmilliók folyamán, főleg a barlangi lelőhelyeken. Európai jelenlétüket már az eocéntól követni lehet, de a leletek többsége a neogénből és a kvarterből származik. A Kárpát-medencéből a neogén elejétől ismertek. A szöveget kiegészíti a fosszilis anyagot felölelő irodalomjegyzék, egy ábra és hat táblázat.

Kulcsszavak: Európa, Kárpát-medence, evolúció, tyúkfélék, fajdok

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Introduction

Their dimensions vary (sexual dimorphism is a usual characteristic), they are herbivores or omnivores. Apart from quails they are relatively poor fliers, thus they are non-migratory birds. They usually form harem, species living in pairs are uncommon. They nest on the ground, their nestlings are precocial. Two families live in Europe: Phasianidae and Tetraonidae.

Pheasants, chickens, partridges, and quails live in Eurasia and Africa, mostly in grassy, bushy areas, and nest on the ground. Fossil remains also mostly come from sites in Europe. Their earliest representatives are *Paraortyx lorteti, P. brancoi, Pirortyx major*, from the Eocene and Oligocene of France, *Palaeortyx* species from the Miocene of France, Czech Republik and Hungary (Mátraszőlős, Rudabánya, Sümeg, Tardosbánya), *Plioperdix hungaricus* from the Miocene of Hungary (Rátka), *Miogallus* species *(M. altus, M. medius)* from the Miocene of France, Germany, Hungary and Spain, *Alectoris* species *(A. bavarica, A. prisca, A. edwardsi, A. donnezani)* from the Miocene of Germany and France, as well as *Francolinus capeki* and *Gallus beremendensis* from the early Pleistocene of Romania and Hungary. Peacocks today live in Southern Asia (one species lives in Africa), but their extinct species come from Europe. From the Miocene of Greece, Hungary, Moldavia and Ukraine

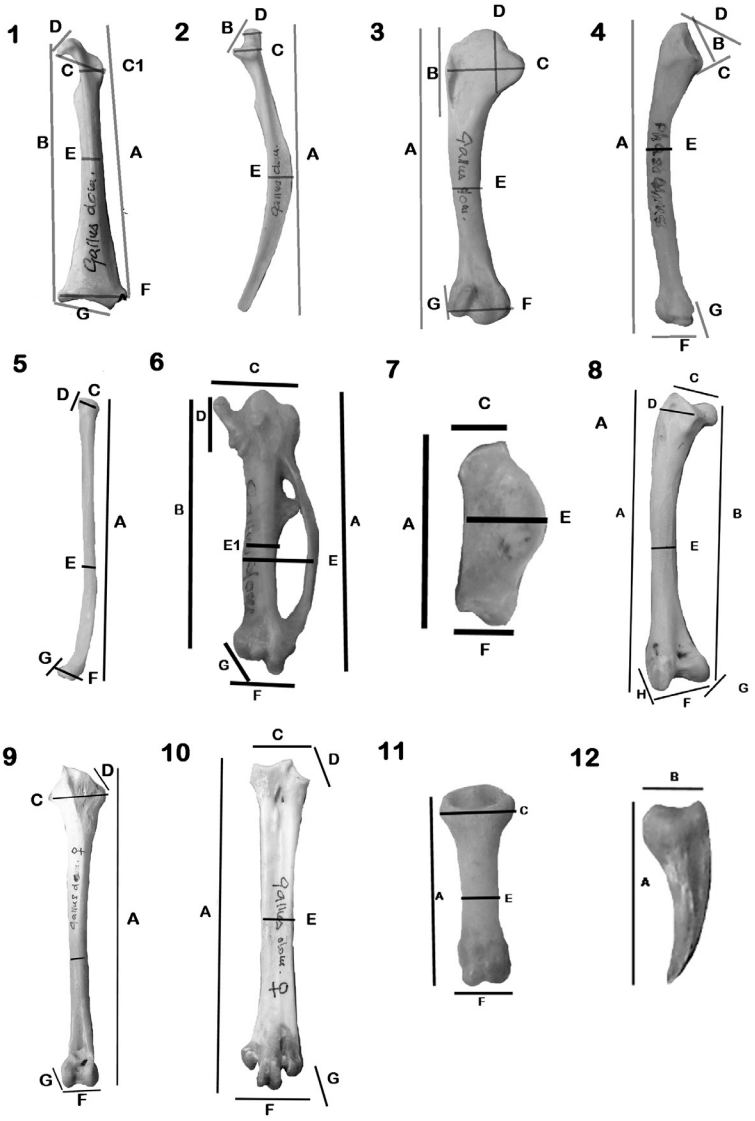

Figure 1. *Gallus gallus domesticus* L. 1758: 1. *coracoideum,* 2. *scapula*, 3. *humerus,* 4. *ulna,* 5. *radius,* 6. carpometacarpus, 7. *phalanga alae* 1 *digiti* II., 8. *femur,* 9. *tibiotarsus,* 10. *tarsometatarsus,* 11. *phal. pedis,* 12. *phal. unguis,* A – total lenghts, B – partial lengths, C – width of *proximal epiphysis,* C1 – partial width of *proximal epiphysis,* D – thickness of *proximal epiphysis,* E – width of *diaphysis,* E1 – partial width of *diaphysis,* F – width of *distal epiphysis,* G – thickness of *distal epiphysis,* H – hight of *distal epiphysis*

1. ábra *Gallus gallus domesticus* L. 1758: 1. hollócsőrcsont, 2. lapocka, 3. felkarcsont, 4. singcsont, 5. orsócsont, 6. kézközépcsont, 7. kézujjperc, 8. combcsont, 9. lábszárcsont, 10. csüd, 11. lábujjperc, 12. karomcsont, A – teljes hossz, B – részleges hossz, C – proximális epifizis szélesség, C1 – részleges proximális epifizis szélesség, D – proximális epifizis vastagság, E – diafizis szélesség, E1 – részleges diafizis szélesség, F – disztális epifizis széleség, G – disztális epifizis vastagság, H – disztális epifizis magasság

Pavo archiaci, from the Pliocene of Ukraine, Hungary, France and Bulgaria *P. bravardi* are known. Turkeys in the meantime inhabit Central America, with a medium-large stature. The earliest finds are from the Miocene of the USA *(Rhegminornis calobates, R. kimballensis*). Recent species are known since the Quaternary.

Tetraonidae inhabit Eurasia, they eat sprouts and seeds, and possess a weak flight capability. They nest on the ground. Their fossil remains are only known since the end of the Neogene. Such are *Tetrao rhodopensis* from the Pliocene of Bulgaria, *Tetrao partium, T. praeurogallus* from the Pliocene and early Pleistocene of Hungary, Bulgaria and Romania, as well as *Tetrastes praebonasia* from the early Pleistocene of Hungary. Extinct species of grouses lived in the Carpathian Basin and the Balkan at the end of the Neogene and from the beginning of the Quaternary. Fossilized finds of ptarmigans *(Lagopus)* come from recent species. Recent species are known since the Quaternary.

A particularly special find from the Eocene of the outer perimeter of the Carpathian Basin is the almost complete imprint of a Leipoa (Megapodiidae Swinson, 1837), which unfortunately had not been described and publicated. Similar European finds are only known from the Paleogene of France (Quercy, Rosiéres, Saint-Gérand-Puy; (*Quercymegapodius depereti* and *Q. brodkorbi* Mourer-Chauviré, 1992; *Ameripodius alexis* Mourer-Chauviré, 2000).

Their classification is made easier due to the fact that the shape of their coracoid bone cannot be mistaken as that of any other birds order.

Abbreviations: Q1-Q2 – Lower Pleistocene; **Q3 (Q3/I-Q3/II)** – Middle Pleistocene; **Q4/I** – Upper Pleistocene; **Q4/II** – Holocene; † – extinct/fossil species – subspecies.

A – total lengths; B – partial lengths; C – width of proximal epiphysis; C1 – partial width of proximal epiphysis; D – thickness of proximal epiphysis; E – width of diaphysis; E1 – partial width of diaphysis; F – width of distal epiphysis; G – thickness of distal epiphysis; H – hight of distal epiphysis. R-2: Rudabánya locality 2. See *Figure 1* with measurement method.

Taxonomy

Ord. Galliformes (Temminck), 1820
Fam. Phasianidae Vigors, 1825

Galliformes possess typical characteristics of the order. They appear quite frequently in layers of sites – and often in large numbers – already from the Eocene. Consequently numerous fossilized taxa were described in Europe in the last one and a half century. Most of their skeletal fragments can be quite easily identified and distinguished from remains of members of other orders, but due to significant homologization it is much more difficult to tell the difference between genera and species, especially with specimen of smaller and Middle posture; due to this their taxonomical classification is often highly debated.

Quail *(Coturnix coturnix)* is one of the typical recent smaller types. Forms on this scale and more or less shared morphological characteristics are known under a number of genera and species from the Neozoic of Europe: † *Palaeortyx* Milne-Edwards 1869, † *Taoperdix* Milne-Edwards, 1869, † *Plioperdix* Kretzoi, 1955, † *Palaeocryptonix* Depéret, 1792 and

Coturnix Bonnaterre, 1791 modern genera. Mlikovskỳ (2002) classifies all of the extinct genera to the recent one naming morphological similarity as the reason, unifying most of the species as well, only leaving two extinct taxa on the species level: *Coturnix gallica*, and *C. longipes*. Ursula Göhlich and Cecile Mourer-Chauviré (2005) showed, that the above species listed under a common name can clearly be distinguished based on morphological characteristics, and they stand by the original names. Since we share their opinion, we will present the identified material of the Carpathian Basin in accordance with it.

A similar case applies in Middle-sized (partridge-rock partridge-francolin size) examples. Here Mlikovskỳ classifies almost all described fossil genera under *Alectoris*: *Palaeoperdix* Milne-Edwards, 1869), *Lambrechtia* Jánossy, 1974, as well as larger examples of previously listed genera *(Plioperdix, Palaeocryptonix)* and fossil species of the recent *Francolinus*. He divides them into three other fossil species: outside of the species already belonging to this genus (*Alectoris bavarica* Ballmann, 1969 from the early Miocene of Germany, MN 3; *A. prisca* (Milne-Edwards, 1869), *A. edwardsi* (Depéret, 1887) and *A. donnezani* (Depéret, 1892). He classifies every Middle-sized fossil galliform into the latter genus. As for fossil partridge species (*Perdix palaeoperdix* Mourer-Chauviré 1975, *Perdix jurcsáki* Kretzoi 1962, *Perdix perdix jurcsáki* Jánossy, 1976), he places them under the recent *Perdix perdix*

Perusing a significant amount of this material we cannot share the viewpoint of Mlikovskỳ, since partridge, francolin and rock partridge species can easily be distinguished based on their morphological characteristics in their fossil and recent forms as well. Characteristics of the humerus of rock partridges and francolins for example differ greatly from that of partridges and small-middle sized Galliformes (*Gallus* species). Since this is a group quite clinging to their habitat rather than migrating, populations with different characteristics and due to them the formation of different forms, the emergence of endemic forms, is a natural process.

In case of larger Galliformes (chickens, pheasants) Mlikovskỳ keeps the genus *Miogallus* created by Lambrecht (1933), and classifies all others into it *(Gallus, Phasianus, Miophasianus)*, as well as larger species belonging to Middle-sized genera (*Palaeortyx maxima* (Lydekker, 1893), *Palaeoperdix medius* (Cheneval, 2000)). Of this category in the Carpathian Basin only material from Rudabánya and Devínska Nová Ves, Slovakia is known, as *Miophasianus* cf. *medius* (Jánossy, 1993), and *Miophasianus altus* (Švec, 1986). There was no great change in the classification of peacocks in terms of originally described fossil species, here he only classifies *Gallus (Pavo) aesculapi* into species *Pavo archiaci*, and he puts *P. bravardi* (Gervais, 1849) in place of *Gallus bravardi.*

Lately Nichita Zelenkov (2016) has revideated numerous pieces of the material, among them are those from the Carpathian Basin.

– † ***Palaeortyx brevipes*** **Milne-Edwards, 1869** / syn. † *Palaeoperdix* (Milne-Edwards, 1871) / † *Palaeortyx grivensis* Lydekker, 1893 / *Coturnix* † *gallica* (Mlikovskỳ, 2002).

Site and era: Rudabánya, Upper Miocene (MN 9) (Kessler 2009b); Sümeg, Upper Miocene (MN 11-12); Tardosbánya, Upper Miocene (MN 12) (Jánossy 1976b); Polgárdi, Upper Miocene (MN 13) (Kessler 2009b); Osztramos 1, Lower Pliocene (MN 15) (Jánossy 1972, Kessler 2009b); Csarnóta 2, Lower Pliocene (MN 15) (Kessler 2009b) (all in Hungary). From sites in Europe outside the Carpathian Basin: MP 16-28: France; MN 2-12: Czech

Republik, France, Germany, Spain **Q1-2:** Poland; **Q3:** Czech Republik, Germany, Poland (Tyrberg 1998, Mlíkovský 2002).

Material: cranial fragments of *coracoideum*, *humerus* distal epiphysis, *scapula* fragment (Rudabánya); *metacarpus* fragment (Sümeg), *tibiotarsus* (n = 2), (Csarnóta).

Dimensions: *coracoideum* E = 2.5 mm; *scapula* C = 3.02 mm, E = 2.05 mm, *humerus*: A = app. 37.0 mm, E = 2.71–3.62 mm, F = 5.68–7.61 mm, *tibiotarsus*: F = 5.56–6.16 mm, G = 4.86–5.79 mm, *tarsometatarsus*: C = 4.36–4.96 mm, E = 2.36–2.69 mm, F = 5.66 mm.

Somewhat larger material in size than the recent quail, but identical to it in characteristics, which can be easily distinguished from *Palaeocryptonix* species.

Typical site of the species ranges from Grive-Saint-Alban (Upper Miocene, MN 8) to Măluşten, Eastern Romania (MN 15) through the Carpathian Basin.

– † *Palaeortyx gallica* Milne-Edwards, 1869 / syn. *P. intermedia* Ballmann, 1969 / *Coturnix* † *gallica* (Mlikovskỳ 2002).

Site and era: Grund, Lower Miocene (MN 5) (Austria), (Göhlich 2003); Litke 2, Lower Miocene (MN 5) (Kessler & Hír 2012); Mátraszőlős 1, Middle Miocene (MN 6-8) (Kessler 2009b); Rudabánya, Upper Miocene (MN 9) (Kessler 2009b); Polgárdi, Upper Miocene (MN 13) (Kessler 2009b) (all in Hungary); Kőalja 2 Middle Miocene (MN 6) (Kessler & Venczel 2009), (Romania). From sites in Europe outside the Carpathian Basin: MP 16-28: France; MN 2-12: Czech Republik, France, Germany, Spain **Q1-2:** Poland; **Q3:** Czech Republik, Germany, Poland (Tyrberg 1998, Mlíkovský 2002).

Material: *humerus*, distal fragment (Litke 2); *coracoideum*, cranial fragment (Kőalja 2); *tibiotarsus* distal fragment and distant *phalanx* (Mátraszőlős 1); *coracoideum* fragments (n=3), (Rudabánya), *ulna*, *tibiotarsus*, *femur, tarsometatarsus* fragments (n=3), (Polgárdi).

Dimensions: *coracoideum* C = 3.35–3.64 mm, D = 5.65 mm; E = 2.57–2.75 mm; *humerus*: F = 8.13 mm; G = 3.96 mm; *ulna*: B = 5.27 mm, C = 4.47 mm, E = 2.66 mm; *femur*: E = 3.21 mm, F = 7.06 mm, G = 5.67 mm; *tibiotarsus* E = 2.92 mm, F = 5.31 mm, G=4.82 mm.

Somewhat larger in size than the recent species (based on data of Göhlich & Mourer-Chauviré 2005). Its geographic spread is similar to the previous species.

– †*Palaeortyx phasianoides* Milne-Edwards, 1869 /syn. † *Palaeoperdix longipes* (Milne-Edwards, 1869) / *Coturnix* † *longipes* (Mlikovskỳ, 2002).

Site and era: Litke 2, Lower Miocene (MN 5) (Kessler & Hír 2012); Rudabánya, Upper Miocene (MN 9) (Kessler 2009b) (all in Hungary). From sites in Europe outside the Carpathian Basin: MP 28: France; MN 2-12: Czech Republik, France, Germany, Spain (Mlíkovský 2002).

Material: *coracoideum*,, cranial fragment (Litke 2); *coracoideum*, cranial fragments, partial *metacarpus*, distal fragment of the *tibiotarsus* (Rudabánya).

Dimensions: *coracoideum* C = 3.98 mm, E = 3 mm, *carpometacarpus* A = app. 30 mm, E = 3.4 mm, *tibiotarus* F = app. 5.8 mm, *tarsometatarsus*: C = 6.15–6.29 mm, E = 2.9–3.04 mm.

In case of the *metacarpus* the *processus intermetacarpalis* is highly developed, while remaining characteristics of the other bones indicate common morphological characteristics

of the genus. Based on dimensions it can be classified to the largest *Palaeortyx* species (Göhlich & Mourer-Chauviré 2005).

They have been reported from numerous sites, from the Late Oligocene of France (MP 28) from Desse to Germany and Czech Republik to the Upper Miocene of Hungary. It is also known from the Late Miocene of Spain.

† *Míoryaba* Zelenkov, 2016

† *Mioryaba magyaricus* Zelenkov, 2016

Site and era: Polgárdi, Upper Miocene (MN13), (Hungary), (Zelenkov 2016).

Originally described as *Palaeortyx brevipes* (Kessler 2009b).

Material: *coracoideum*, *scapula*, *humerus* (n = 6), *tarsometatarsus* (n = 4), (Polgárdi 4,5);

Dimensions: *coracoideum*,: minimum shaft width, 1.8; shaft height (thickness) at the level of its minimum width 1.9; length from the cranial edge to caudal edge of the *caput scapularis* 7.6 mm. *Tarsometatarsus*: total length, 28.8, proximal width, 5.4, minimum shaft width, 2.5, height of *trochlea metatarsi* III, 3.0–3.1 (n = 3); width of *trochlea metatarsi* III, 2.5; distal end width, 5.8, 6.2 mm.

– † *Plioperdix* (Kretzoi, 1955)

– † *Plioperdix hungaricus* (Jánossy, 1991) (syn. † *Palaeocryptonyx hungaricus* Jánossy, 1991).

Site and era: Rátka, Upper Miocene (MN 12-13) (Kessler 2009b); Polgárdi 4, 5, Upper Miocene (MN 13) (Jánossy 1991, 1995, Kessler 2009b, Zelenkov 2016); Beremend 26, Lower Pliocene (MN 15) (Kessler 2009b), Beremend 17, 18 Lower Pleistocene (Q1) (Jánossy 1992, 1996) (all in Hungary). From sites in Europe outside the Carpathian Basin: MN 14-15: France, Germany, Ukraine; **Q1-2:** Czech Republik, Poland; **Q3:** Czech Republik, Germany, France, Italy, Poland, Spain, Ukraine (Tyrberg 1998, Mlíkovský 2002).

Material: *coracoideum*, *humerus*; distal fragment of *humerus*; left *femur*; distal fragment of the *tibiotarsus*; *carpometacarpus*; *tarsometatarsus* (Polgárdi 4 and 5 localities, Hungary), Upper Miocene (MN 13);

In case of smaller representatives of the genus the humerus is characteristically stout, while the *tarsometatarsus* is typically slim. Characteristics of the species described by *Jánossy* verify better flight capabilities compared to other, more grounded species supposedly more capable of running. The shape of the *caput humeri*, the depth of the *fossa pneumotricipitalis*, the shape of the distal epiphysis and the whole *humerus* differ from those of recent small and medium-sized species. They fit the diagnosis of the genus, so the classification to the genus *Alectoras* is incorrect. The only whole, almost complete skeleton of the Carpathian Basin was found of this species from Rátka, classified incorrectly as a Charadriidae at the showcase at the privately owned museum in Tállya, however the typical shape of the coracoid bones clearly indicate its true place.

It has not been reported from any other site than those mentioned above. J. Mlikovskỳ classified it along with other members of the genus as belonging to the taxon *Alectoris* † *donnezani* (Deperet, 1892).

Dimensions: *Table 1*.

† *Eurobambusicola* Zelenkov, 2016

† *Eurobambusicola turolicus* Zelenkov, 2016

Site and era: Polgárdi, Upper Miocene (MN 13), Hungary (Zelenkov 2016)

Material: *coracoideum*; *humerus* (n = 3), distal fragment of the *tibiotarsus*; *carpometacarpus* (Polgárdi 5 locality).

Originally classified as † *Paleocryptonix hungaricus* Jánossy, 1991 (Jánossy 1991, 1995, Kessler 2009b).

Dimensions: *coracoideum*: total length along the medial edge, 26.6–26.8 (n = 3), length from the cranial to caudal edge of the *cotyla scapularis*, 7.6–8.2 (n = 5); minimum shaft width, 2.1–2.3 (n = 6); thickness at this level, 2.0–2.3 (n = 5). *Scapula*: shaft width just caudal to the *facies articularis humeralis*, 2.6–2.7 (n = 2). *Humerus*: total length, 37.4, 37.7; maximum width of the proximal end, 9.5, 9.3; minimum dorsoventral width of the shaft, 3.3–3.6 (n = 5), greatest width of the distal end, 7.3–7.7 (n = 4). *Carpometacarpus*: total length, 18.7, 19.6 dorsoventral height of *the trochlea carpalis*, 2.9, 3.1. *Tibiotarsus*: width of the distal end, 5.3–5.7 (n = 3). *Tarsometatarsus*: reconstructed total length, ~33; width of the proximal end, 6.0–6.4 (n = 3); width of the distal end, 6.3–6.6 (n = 3).

– *Francolinus* (Stephens, 1819)

– *Francolinus* † *capeki* Lambrecht, 1933 / syn. *Francolinus* † *subfrancolinus* Jánossy, 1976 / *Francolinus* † *minor* Jánossy, 1974 / † *Lambrechtia capeki* Jánossy, 1974 / *Alectoris* † *donezzani* (Depéret, 1892), (after Mlikovskỳ 2002).

Site and era: MN 15: Beremend 26 (Kessler 2009b); Csarnóta 2 (Jánossy 1976, 1979) (all in Hungary); MN 16: Beremend 1-3, 5, 15, 18 (Jánossy 1974, 1976b, 1992, 1996); Osztramos 7 (Jánossy 1973, 1976b, 1979a); Villány 3 (Jánossy 1976b, 1979) (all in Hungary); Betfia 13 (Kessler 1975, Gál 2002); **Q1:** Németóvár 4B (Deutsch-Altenburg, Austria) (Jánossy 1981); Beremend 16 (Jánossy 1976b, 1979); Osztramos 2, 8 (Jánossy 1976b, 1979, Jánossy & Kordos 1976) (all in Hungary); Betfia 2, 5, 9 (Kormos 1913, Čapek 1917, Lambrecht 1933, Jánossy 1976b, Kessler 1975, Gál 2002) (Romania); **Q2:** Somssich-hegy 2 (Hungary) (Jánossy 1983, 1986); Betfia 5, 7, 7/2-3 „Aven" (Romania) (Kretzoi 1962, Kessler 1975, Jánossy 1976b, Gál 2002). From sites in Europe outside the Carpathian Basin: **Q1-2:** Germany; **Q3:** Croatia, Czech Republik, Germany (Tyrberg 1998).

Quite a number of fossil material is available, similar in scale and characteristics to the francolins. They can be easily distinguished from partridges and rock partridges based on their morphological characteristics.

The typical species (*Francolinus capeki* (Lambrecht, 1933)) was described from the Lower Pleistocene site of Betfia 2. Outside the Carpathian Basin it is known from the Late Pliocene of Poland (Weze, MN 15; Rebielice Królewskie, MN 16), Etulia (Moldavia) (MN 16), Odessa, Kotlovina (Ukraine) (MN 16), Tourkoubonia (Greece) (MN 16-17), Untermassfeld and Sackdilling (Germany) (**Q1-Q2**), as well as Chlum, Koneprusy, Stránská Skála (Czech Republik) (Q2).

All of the areas mentioned above are outer neighboring the Carpathian Basin! We can thus easily conclude, that we have a small-sized Galliformes typical to Central Europe in the early Pliocene, while the species *Alectoris donnezani* (Deperet, 1892) is spread from France

to Russia and Israel, the area bypassing the Carpathian Basin from the north towards east. He also classifies species *Palaeocryptonyx donnezani* (Depéret, 1892), *Ammoperdix ponticus* Tugarinov, 1940, *Pliogallus coturnoides* Tugarinov, 1940, *Chauvereria balcanica* Boev, 1997 and *Alectoris baryosefi* Tchernov, 1980, not considering the morphological differences between rock partridges and francolins.

Dimensions: *Table 2*.

– *Coturnix* Bonaterre, 1791

– *Coturnix coturnix* (Linnaeus, 1758)

Q1: Beremend 16, 17 (Hungary) (Jánossy 1992, 1996); **Q2:** Hundsheim (Austria) (Jánossy 1974, 1976b); Somssich-hegy 2 (Hungary) (Jánossy 1983, 1986); Méhész 4E (Vcelare, Slovakia) (Horáček 1985, Mlíkovskỳ 2002); **Q3/I:** Budapest – Várhegy (Hungary) (Jánossy 1976b, 1979, 1986); Gombaszög (Gombasek, Slovakia) (Kessler 2009b); **Q3/II:** Süttő 1-4 (Jánossy 1976b, 1979); Uppony I. (Jánossy 1976b, 1979) (all in Hungary); Brassó – Fortyogóhegy – Gensperger Cave (Braşov, Romania) (Gál 2002); **Q4/I:** Bajót – Jankovich Cave (Lambrecht 1933, Jánossy 1976b, 1979); Budapest – Remete Cave (Jánossy 1976b, 1979); Budapest – Remetehegyi Shelter Cave (Kormos 1914a, Lambrecht 1933, Jánossy 1976b, 1979); Gencsapáti (Jánossy 1976b, 1979); Hámor – Puskaporos Shelter Cave (Lambrecht 1912a, b, 1916, 1933, Jánossy 1976b, 1979); Pilisszántó I. Shelter Cave (Lambrecht 1915, 1933, Jánossy 1976b, 1979); Tatabánya – Kálváriahegy, cave n. 4. (Gál 2008a); Tatabánya – Szelim Cave (Jánossy 1976b, 1979); Varbó – Lambrecht Kálmán Cave (Jánossy 1976b, 1979) (all in Hungary); Kőrösmart (Râpa, Romania) (Jánossy in Hamar & Csák 1969, Kessler 1974a, Gál 2002); Lándzsásötfalu (Hôrka – Ondrej, Slovakia) (Mlíkovskỳ 2000); Óruzsin-Antal Cave (Oruzer, Slovakia) (Nehring 1880, Róth 1881, Lambrecht 1912b, 1933); **Q4/II:** Teufelslucken (Austria) (Soergel 1966); Bodajk – Rigólyuk (Kordos 1984); Csapástető (Jánossy 1976); Hosszú-hegyi Cave (Jánossy 1976, Kordos 1981); Legény Cave (Lambrecht 1914); Ordacsehi – Kistöltés (Gál 2005, 2007a); Répáshuta – Rejtek Shelter Cave (Jánossy 1962c, 1976b); Gálospetri (Galoşpetreu) (Kessler 1980–81, Gál 2002); Körösbánlaki Cave (Bălnaca) (Kessler 1982); Peterd – Turda Gorge – Magyar Cave (Petreşti) (Kessler & Gál 1998, Gál 2005); Székelykeresztúr (Cristuru Secuiesc) (Gál 2008b), (all in Romania). From sites in Europe outside the Carpathian Basin: **Q1-2:** Spain, Ukraine; **Q3:** Czech Republik, France, Germany, Malta, Russia, Ukraine; **Q4:** Belgium, Bosnia-Herzegovina, Bulgaria, Czech Republik, France, Georgia, Germany, Greece, Ireland, Italy, Luxemburg, Malta, Moldova, Poland, Russia, Spain, Ukraine, United Kingdom (Tyrberg 1998).

– *Alectoris* Kaup, 1829

– *Alectoris* † *donnezani* (Depéret, 1892)

Site and era: MN 15: Ajnácskő (Hajnacka) (Kessler 2009b); Ivánháza (Ivanovce) (Mlikovskỳ 2002); MN 17-18: Kolon 2 (Horáček 1985, Mlikovskỳ 2002) (all in Slovakia); **Q1:** Németóvár (Deutsch-Altenburg, Austria) (Döppes & Rabeder 1997, Mlikovskỳ 1998); **Q2:** Méhész 4E (Vcelare, Slovakia) **(**Horáček 1985, Mlikovskỳ 2002). From sites in Europe outside the Carpathian Basin: MN 14-15: France, Germany, Ukraine; **Q1-2:** Poland; **Q3:** Czech Republik, Germany, Poland, Ukraine (Tyrberg 1998, Mlíkovský 2002).

A fossil species having typical rock partridge characteristics, it can be easily distinguished from partridges and francolins. The typical species is only additionally known from the Perpignan (Lower Pliocene, MN 15) site in France.

– *Alectoris graeca* (Meisner, 1804)

Q3/II: Vindija (Croatia) (M. Malez 1961, V. Malez 1973, 1988, M. Malez & Rukavina 1975, Musil 1980); **Q4/I:** Hámor-Puskaporos Shelter Cave (Hungary) (Lambrecht 1912a, b, 1916, 1933, Jánossy 1976b, 1979); **Q4/II:** Kazánszoros – Climente I. Cave (Cazanele Mari) (Kessler 1980–81, Gál 2002); Kazánszoros – Töröklik Cave (Cazanele Mari) (Kessler 1974b, Fischer & Stephan 1977) (all in Romania). From sites in Europe outside the Carpathian Basin: **Q1-2:** Greece, Italy; **Q3:** Azerbaijan, France, Greece, Italy, Malta; **Q4:** Bosnia-Herzegovina, Bulgaria, France, Georgia, Italy, Luxemburg, Montenegro, Russia, Spain, Ukraine (Tyrberg 1998).

– *Alectoris rufa* (Linnaeus, 1758)

From sites in Europe outside the Carpathian Basin: **Q3:** Spain; **Q4:** France, Portugal, Spain (Tyrberg 1998).

– *Perdix perdix* † *jurcsaki* Jánossy, 1976 / syn. *Perdix* † *jurcsaki (*Kretzoi, 1962).

Site and era: **MN 15:** Beremend 26 (Kessler 2009b); MN 16: Beremend 18 (Kessler 2009b); **Q1:** Németóvár (Deutsch-Altenburg, Austria) (Jánossy 1981); Beremend 16, 17 (Kessler 2009b); Győrújfalu (Kessler 2009b); Osztramos 5 (Jánossy 1972) (all in Hungary); Betfia 2, 5, 9 (Romania) (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1976b, Gál 2002); **Q2:** Betfia 5, 7, "Aven" (Kretzoi 1962, Kessler 1975, Jánossy 1976b, Gál 2002); **Q3/I:** Betfia 7 (Kessler 1975, Jánossy 1976b, Gál 2002) (all in Romania); Tarkő, Várbarlang (Hungary) (Jánossy 1976b, 1979). From sites in Europe outside the Carpathian Basin: **Q3:** Greece (Tyrberg 1998).

The rich collection of material shows typical mosaicity in scale. While the *ulna*, *meatcarpus*, *tibiotarsus* and *tarsometatarsus* are long and slim, the *coracoideum* and *humerus* are robust. The partridge described from the Betfia 5 site distinguishes itself with larger dimensions than its recent counterparts. Based on examining seventy-five *tarsometatarsus* Jánossy (1976b) proposed classifying it as a new subspecies, while Mlikovskỳ (2002) classified it along with the recent partridge. After examining *coracoideum*,, *scapula*, *humeri*, *metacarpae*, wing *phalanges*, *tibiotarsae* and *tarsometatarsae*, we propose to keep the subspecies classified by Jánossy. The subspecies is only known from the Carpathian Basin, but shares many characteristics with the species *P. palaeoperdix* Mourer-Chauviré, 1975 described from the Middle Pleistocene of France (Q2), also classified by Mlikovskỳ (2002) as the fossil predecessor of the recent partridge.

Dimensions: *Table 3*.

– *Perdix* † *palaeoperdix* Mourer-Chauviré, 1975

From sites in Europe outside the Carpathian Basin: **Q2:** France (Tyrberg 1998).

– *Perdix perdix* (Linnaeus) 1758

Q3/I: Hundsheim (Austria) (Jánossy 1974, 1976b); Tarkő 1-16 (Jánossy 1962b, 1976b, 1979); Budapest – Várhegy (Jánossy 1976b, 1986); Vértesszölős 2 (Jánossy 1976b, 1979); **Q3/II:** Cave in the Cserépfalu – Hór Valley (Jánossy 1976b, 1979); Sütő 6-9. (Jánossy 1976b, 1979) (all in Hungary); **Q4/I:** Krapina (Lambrecht 1915, V. Malez 1973, 1984, V. Malez-Bačić 1979); Velika Pecina (V. Malez 1984, 1988); Veternica (V. Malez 1973, 1988, V. Malez-Bačić 1979, Musil 1980) (all in Croatia); Bajót – Öregkő (Lambrecht 1915); Bajót – Baits Cave (Jánossy 1976b, 1979); Balla Cave, Bajót – Hóman Cave (Jánossy 1976b, 1979); Istállóskő, Bajót – Jankovich Cave (Lambrecht 1933, Jánossy 1976b, 1979); Budapest – Remetehegy Shelter Cave (Kormos 1914, Lambrecht 1933, Jánossy 1976b, 1979); Cserépfalu – Subalyuk Cave (Jánossy 1976b, 1979); Pilisszántó I. – Shelter Cave (Lambrecht 1915, 1933, Jánossy 1976, 1979); Répáshuta – Balla Cave (Lambrecht 1912a, b, 1933, Mottl 1938, 1941); Szilvásvárad – Istállóskő Cave (Lambrecht 1912a,b, 1933, Jánossy 1952, 1954, 1955, 1976b, 1979); Tatabánya – Calvary mountain cave n. 4. (Gál 2008a); Tatabánya – Szelim Cave (Jánossy 1976b, 1979); Varbó – Lambrecht Kálmán Cave (Jánossy 1976b, 1979) (all in Hungary); Nándor – Nándori Cave (Nandru), (Jánossy 1965, Fischer & Stephan 1977, Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003); Ohábaponor – Bordu Mare Cave (Ohaba Ponor) (Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003); Szegyestel – Tibocoaia Cave (Sighiștel) (Kessler 1982, 1985, Gál 2002) (all in Romania); Dévényújfalu (Devínska Nová Ves) (Kessler 2010); Óruzsin – Antal Cave (Oruzer) (Nehring 1880, Róth 1881, Lambrecht 1912b, 1933) (all in Slovakia); **Q4/II:** Teufelslucken (Austria) (Soergel 1966); Balatonkeresztúr – Réti-dülő **(**Gál 2007a); Bodajk – Rigólyuk (Kordos 1984); Csákvár – Esterházy Cave (Kretzoi 1951–52); Csév Cave (Jánossy 1976b); Ecsegfalva 23 (Pike-Tay *et al.* 2004, Gál 2007b); Endrőd 119 (Jánossy 1985, Gál 2005, 2007b); Felsőnyék – Várhegy (Gál 2007a); Hosszú-hegyi Cave (Jánossy 1976b, Kordos 1981); Legény Cave (Lambrecht 1915); Ludas – Budzsák (Bökönyi 1974, Gál 2005); Répáshuta – Rejteki Shelter Cave (Jánossy 1962c, 1976b); Szendrő (Gál 2005, Tassi 2006); Tatabánya-alsó – Törekvés Cave (Kessler 2009b); Tác – Gorsium (Bökönyi 1984, Jánossy 1985); Visegrád – Vár (Bökönyi & Jánossy 1965, Jánossy 1976b) (all in Hungary); Gyulafehérvár (Alba Iulia) (Gál 2005); Körösbánlaki Cave (Bălnaca) (Kessler 1982); Révi caves (Vadu Crișului) (Kessler 1982); Remetelórév – Bólyi-kő Cave (Lorău – Piatra Boiului) (Kessler 1982); Szegyestel – Drăcoaia Cave (Sighiștel) (Kessler 1982); Székelykeresztúr (Cristuru Secuiesc) (Gál 2008b); Vargyasi-szoros – Homoródalmás caves (Vârghiș) (Jurcsák & Kessler 1988); Vársonkolyos caves (Șuncuiuș) (Kessler 1982) (all in Romania). From sites in Europe outside the Carpathian Basin: **Q1-2:** Ukraine; **Q3:** Azerbaijan, Croatia, Czech Republik, France, Georgia, Italy; **Q4:** Austria, Belgium, Bosnia-Herzegovina, Bulgaria, France, Georgia, Germany, Irlanda, Italy, Luxemburg, Moldova, Montenegro, Poland, Russia, Serbia, Spain, Ukraine, United Kingdom (Tyrberg 1998).

– *Perdix* sp.

Q1: Beremend 16, 17 (Hungary) (Jánossy 1992, 1996);

From sites in Europe outside the Carpathian Basin: **Q3:** France; **Q4:** Czech Republik, France, Portugal (Tyrberg 1998).

– *Ammoperdix* Gould, 1851
– *Ammoperdix* sp.

Q3/I: Gombaszög (Gombasek, Slovakia) (Kessler 2009b). From sites in Europe outside the Carpathian Basin: **Q4:** Greece (Tyrberg 1998).

– † ***Miogallus* Lambrecht, 1933**
– † *Miogallus altus* (Milne-Edwards, 1869) / syn. *Phasianus* † *altus* Milne-Edwards, 1869; † *Miophasianus medius* Milne-Edwards, 1869.

Site and era: Dévényújfalu (Devinská Nová Ves, Slovakia) Middle Miocene (MN 6-7) (Švec 1986, Kordos 1987, Mlikovskỳ 2002); Felsőtárkány – Felnémet 2/7, Mátraszőlős 2, Middle Miocene (MN 7/8) (Kessler & Hír 2012a); Rudabánya, Upper Miocene (MN 9) (Jánossy 1994) (all in Hungary). From sites in Europe outside the Carpathian Basin: MN3-9: France, Germany, Spain, Turkey (Mlíkovský 2002).

Material: distal part of the *coracoideum* bone (R-2), *scapula* (Felsőtárkány – Felnémet 2/3), distal fragment of the *tibiotarsus* (R-2, 1990), *tarsometatarsus* fragment with spur (R-2 Rudabánya), *phalanges pedis* (n = 5), (Mátraszőlős 2).

Dimensions: *scapula* B = 13.73 mm; C = 7.75 mm; E = 6.57 mm; *humerus* E = 11 mm, F = 21.45 mm, *femur* C = 18.5 mm, D = 14.15 mm; *phalanges pedis* = 11.75; 10.29; 9.44; 9.11; 7.75.

From the incredibly fragmented Rudabánya material only the relation to galliformes can be determined, even indicated by the presence of spurs. Other finds fit into characteristics of the extinct species.

From fossil material bearing similar characteristics numerous species had been described across Europe, from Spain to France and Germany through Turkey, from the Lower Miocene (MN 2-5) all the way to the Upper Miocene (MN 9).

– *Gallus* Brissson, 1760
– *Gallus* † *beremendensis* Jánossy, 1976

Site and era: MN 15: Beremend 26 (Kessler 2009b); Csarnóta 2 (Kessler 2009b); **MN 16:** Beremend 5, Villány 3 (Jánossy 1976b, 1996, Kessler 2009b); **Q1:** Beremend 17 (Jánossy 1992, Kessler 2009b) (all in Hungary). It is not known from sites in Europe outside the Carpathian Basin.

It bears similar morphological characteristics to the genus *Gallus*, but is smaller than the recent species. The objections of Mlikovskỳ (2002) (he classifies it as belonging to "*genus incertae sedis"*) regarding the head of the *humerus (caput)* the shape of *crista biccipitalis* are exaggerated, since they fit well inside the limits of differing characteristics of a fossil type. The rich material from Beremend 17 and 26, Csarnóta 2 and Villány 3 we identified, however, verifies Jánossy's diagnosis Finds greatly distinct from partridge and francolin species belonging typically to Galliformes prove the earliest appearance of the genus *Gallus* in Europe.

Dimensions: *Table 4*.

A fossil species of a similar age (*Gallus moldavicus* Burčak-Abramovič *et al.* 1993) was described from Moldavia, which may also explain the emergence of the genus in the

Carpathian Basin. Presence of the genus Gallus in the Late Pleistocene of Europe is debated, since according to the conventional view chickens were imported from southeastern Asia at the beginning of historical times. Fossil finds coming from obviously undomesticated species seem to rival this theory. It can be rightfully assumed that in warmer periods of the Quaternary the genus *Gallus* was present (with one or even more species) in the southern part of Europe, and thus in the Carpathian Basin. Their absolute age could only be reliably determined by a series of isotopic examinations.

– *Gallus* sp.

Q3/II: Vindija (Croatia) (M. Malez 1961, V. Malez 1973, 1988, V. Malez & Rukavina 1975, Musil 1980); **Q4/I:** Esküllő – Igric Cave (Aştileu) (Kessler 1985); Nándor – Nándori Cave (Nandru) (Téglás 1880, Lambrecht 1912b); Ohábaponor – Bordu Mare Cave (Ohaba Ponor) (Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003) (all in Romania); **Q4/II:** Grosse Offenbergerhöhle (Austria) (Bocheński & Tomek 1994); Budapest – Francia Cave (Kessler 2009b); Csákvár – Esterházy Cave (Kretzoi 1954); Csobánka – Csontos Cave (Kessler 2009b); Legény Cave (Lambrecht 1915); Rezi (Kessler 2009b); Tatabánya – Denevér Cave; Tatabánya-alsó – Törekvés Cave (Kessler 2009b) (all in Hungary); Körösbánlaki Cave (Bălnaca) (Kessler 1982); Révi caves (Vadu Crişului) (Kessler 1982); Révtízfalusi Cave (Zece Hotare) (Kessler 1985); Szkerisóra – Sasok Cave (Scărişoara, Peştera Vulturilor) (Kessler 1982, Jurcsák & Kessler 1988); Várson kolyos caves (Şuncuiuş) (Kessler 1982); Vaskóh (Vaşcău) (Kessler 1982); Jászó – Takács Menyhért Cave (Jasov, Slovakia) (Kormos 1914). From sites in Europe outside the Carpathian Basin: **Q3:** France, Ukraine, United Kingdom; **Q4:** Azerbaijan, Czech Republik, France, Georgia, Germany, Ireland, Italy, Moldova, Poland, Serbia, Spain, Ukraine, United Kingdom (Tyrberg 1998).

– *Phasianus* Linnaeus, 1758

– *Phasianus* sp.

Q3/II: Vindija (Croatia) (M. Malez 1961, V. Malez 1973, 1988, V. Malez & Rukavina 1975, Musil 1980); **Q4/II:** Csákvár – Esterházy Cave (Kretzoi 1954); Visegrád – Vár (Bökönyi & Jánossy 1965, Jánossy 1976b) (all in Hungary); Körösbánlaki Cave (Bălnaca, Romania) (Kessler 1982); Jászó – Takács Menyhért Cave (Jasov, Slovakia) (Kormos 1914). From sites in Europe outside the Carpathian Basin: **Q3:** Georgia, Russia; **Q4:** Bosnia-Herzegovina, Croatia, France, Georgia, Germany, Ireland, Italy, Luxemburg, Spain, Ukraine, United Kingdom (Tyrberg 1998).

– *Pavo* Linnaeus, 1758

– *Pavo* † *bravardi* (Gervais, 1849)

From the early Pliocene of Osztramos 1 described from a *phalanges* 2. digiti III. pedis (Hungary) (Jánossy 1976b, 1979). From sites in Europe outside the Carpathian Basin: **MN 14-17:** Bulgaria, France, Greece, Moldova, Ukraine (Mlíkovský 2002).

Dimensions: A = 17.5 mm, E = 3.02 mm.

Matched with the above species based on its shape and dimensions, this is the largest fossil Galliformes found in the Carpathian Basin.

It first appears in the eastern parts of Europe (Ukraine, MN 14), then in the Carpathian Basin in the Late Pliocene. It spreads up to France (Perpignan, Upper Pliocene, MN 15) and is known up to the early Pleistocene (MN 17). The genus subsequently only appears in the Holocene in Europe, possibly due to colonization. This can be assumed because the genus is not present from the Middle and Upper Pleistocene and the Holocene all the way to historical times.

– ***Syrmaticus*** **Wagler, 1832**

– ***Syrmaticus † phasianoides*** Zelenkov, 2016 /syn. *P.* † *aesculapi phasanoides* Jánossy, 1991.

The extinct peacock species was identified from the Upper Miocene of Polgárdi 4 (Hungary) based on a *premaxilla*, coracoideum, 2 radius fragments, 4 *carpometacarpus* (1 whole and 2 fragmented), 3 *phalanges pedis* (Jánossy 1991, 1995, Kessler 2009b). It is also known from the Late Miocene of Moldavia (Kolkotova Balka, MN 9-10), Ukraine (Nova-elisatovkova, Belka, Zovten, MN 11-13), and Greece (Pikermi, MN 12) (Mlikovskỳ 2002).

Material: *coracoideum* holotype, *carpometacarpus*, maxilla, all come from the Polgárdi 4 locality.

Dimensions: *coracoideum* A = 56.5 mm, *carpometacarpus* A = 38.75 and 42.47 mm, B = 34.64 and 37.11 mm, C = 10.75 and 12.98 mm, D = 6.54 and 7.24 mm E = 8.21 mm, F = 7.35–8.48 mm, G = 4.52–5.09 mm, *radius* E = 3.16 and 3.34 mm, F = 6.91 and 7.48 mm, G=3.68 and 4.55 mm; *phalanges pedis* A = 7.94 mm, 12.45 mm, 18.36 mm.

The robustness of the coracoideum, *facies articularis humeralis, cotyla scapularis* and the *facies articularis sternalis*, differing from typical chickens and pheasants, resemble that of a peacock. Characteristics of the *metacarpus*, however, are more similar to chickens and pheasants.

– ***Numida*** **Linnaeus, 1766**

– ***Numida meleagris*** **Linnaeus, 1758**

Q4/II: Jászó – Takács Menyhért Cave (Jasov, Slovakia) (Kormos 1914);

It is not known from any other Europian site.

– **Perdicidae gen. et sp. foss. indet.**

MN 6: Kőalja 2 (Subpiatra, Romania) (Kessler & Venczel 2009).

– **Perdicidae gen. et sp. indet.**

Q4/I: Kőrösmart (Râpa, Romania) (Jánossy in Hamar & Csák 1969, Kessler 1974, Gál 2002); **Q4/II:** Tűzköves Cave (Hungary) (Kessler 2009b).

Fam. Tetraonidae Vigors, 1825

The case of grouses is similar to Galliformes'. Mlikovskỳ (2002) classifies the fossil species to the recent species in this case as well. However, during the diagnosis of the respective species non-negligible morphological and dimensional differences are listed, on the other hand it is also quite improbable, that types of today would have remained unchanged from the Upper Pleistocene to modern times. We also have to consider, that the ancestors

of today's Tetraonidae lived in different environments than those of today, and the climate change they had gone through during the Upper Pleistocene unavoidably influenced both their morphological characteristics and lifestyles. The Upper Pliocene, Lower, and Middle Pleistocene materials are discussed separately as fossil species, while we only classify Upper Pleistocene finds as recent grouses.

– *Tetrao* Linnaeus, 1758

Grouses were typical ground dwelling birds – mostly living in woodlands – of the Quaternary of the Carpathian Basin, but their numbers declined in the Holocene due to climate and environmental changes, as well as falling prey to humans.

The first reported presence of capercaillies comes from the early Pliocene of Bulgaria (Dorkovo, MN 14), then finds from Csarnóta and Beremend came from the early Pleistocene, and Weze (MN 15), Poland with a similar age, and Upper Pliocene material found in Hungary (Rebielice Królowskie and Osztramos 7, MN 16). In Germany and Czech Republik it is only known from the early Pleistocene (Sackdilling, Erphingen, and Holstein, Stránská Skála, **Q1-2**). It does not appear to the west of this region all up to the Late Pleistocene! *T.* † *rhodopensis* Boev, 1998 (Dorkovo, MN 14), which can also be considered *T. praeurogallus*, marks its southernmost appearance (Mlikovskỳ 2002).

Contrary to capercaillies, black grouses and their ancestors spread to France already by the Late Pliocene (Seneze, MN 17), and is common during the early and Middle Pleistocene of Germany and Czech Republik (Sackdilling, Erphingen, Voigstedt and Chlum 6, Stránská skala, **Q1-3**). The southernmost point is again Bulgaria (Văršec MN 17), where Boev (1995) classified a fossil grouse as *Lagopus* † *balcanicus*, which Mlikovskỳ (2002) again lists as belonging to the recent species. It is also known from the Middle Pleistocene of Ukraine (Certkov, **Q3**).

Currently grouses (apart from the hazel grouse, *Bonasa*) typically prefer cold, they live in regions higher above sea level, and colder latitudes. This can be seen in their spread and presence in the Carpathian Basin as well. The arctic and rock ptarmigans disappeared from the area in the last centuries, but even then they lived in higher areas, as do capercaillies and black grouses, even if humans played a significant factor regarding the fact. Their presence in plains and hill areas obviously indicate colder climates. As for their habitats, apart from the ptarmigans *(Lagopus)* they are specifically woodland species, and lived in tundralike birch forests, pine and juniper forests on plains. Temperature requirements of hazel grouses is indicated by their appearance in interglacial and interstadial areas, and they currently live in woodland areas as well. Capercaillies *(Tetrao urogallus)* receded into pine forests of higher mountains, while Black Grouses *(Tetrao tetrix)* into subalpine and alpine juniper forests. Rock Ptarmigans *(Lagopus mutus)* lived in open, rocky mountain areas, while Willow Ptarmigans *(L. lagopus)* in more wet tundra-like environments.

– *Tetrao* † *praeurogallus* Jánossy, 1969 / syn. *T.* † *conjugens* Jánossy, 1974/ *T.* † *macropus* Jánossy, 1976.

Site and era: MN 15: Csarnóta 2 (Jánossy 1976a, 1979, Kessler 2009a); Beremend 26 (Kessler 2009a); **Q1:** Osztramos 7 (Jánossy 1972, 1976a, 1979); **Q2:** Nagyharsányhegy 1-4

(Lambrecht 1916, 1933, Jánossy 1976a, 1979) (all in Hungary); Betfia 5 (Romania) (Kessler 1975, Gál 2002); Méhész 1. (Vcelare, Slovakia) (Jánossy 1976a, 1979); **Q3/I**: Hundsheim (Austria) (Jánossy 1974, 1976a); Tarkő 10 (Hungary) (Jánossy 1962b, 1976a, 1979). From sites in Europe outside the Carpathian Basin: **Q1-2:** Poland; **Q3:** Czech Republik, Germany, Poland (Tyrberg 1998).

With a few exceptions (the *foramen pneumaticum* on the proximal part of the *humerus* is significantly wider, the *impressio musculis coracobrachialis* is shorter and narrower than those of the recent type) the morphological characteristics of all of the skeletal fragments match the recent capercaillie, apart from the *phalanges pedis* (which are larger, hence the name *T. macropus*). Isolation of the other two fossil species – *Tetrao* † *conjugens* Jánossy, 1974 and *Tetrao* † *macropus* Jánossy, 1976 – is based primarily on robustness, as well as the dimensions being between capercaillies and black grouses. We have to consider, however, the quite substantial sexual dimorphism regarding size, meaning the fossil species suggesting a transition between capercaillies and Black Grouses *(T. conjugens)* may as well come from a smaller female. We suggest keeping the taxon *T. praeurogallus*, on one hand since its description precedes others on the timescale, and on the other it presents the view that it was the direct ancestor of capercaillies of today. This means we do not share the opinion of Mlikovskỳ (2002) regarding classification to the recent species.

Dimensions: *Table 5*.

– *Tetrao urogallus* Linnaeus, 1758

Q3/II: Vindija (Croatia) (M. Malez 1961, V. Malez 1973, 1988, V. Malez & Rukavina 1975, Musil 1980); Vindija (M. Malez 1961, V. Malez 1973, 1988, V. Malez & Rukavina 1975, Musil 1980); Uppony (Hungary) (Jánossy 1976a); **Q4/I:** Repolusthöhle (Austria) (Mottl 1951, Jánossy 1976a); Velika Pecina (V. Malez 1984, 1988); Veternica (V. Malez 1973, 1988, V. Malez-Bačić 1979, Musil 1980) (all in Croatia); Budapest – Remete Cave (Jánossy 1976b, 1979); Budapest – Remete-hegy Shelter Cave (Kormos 1914, Lambrecht 1933, Jánossy 1976a, 1979); Csákvár-Eszterházy Cave (Lambrecht 1933, Mottl 1938, Kretzoi 1954, Jánossy 1976a, 1979); Felsőtárkány – Peskő Cave (Lambrecht 1912, 1933, Jánossy 1976a, 1979); Hámor – Puskaporos Shelter Cave (Lambrecht 1912, 1916a, 1933, Jánossy 1976a, 1979); Pilisszántói I. Shelter Cave (Lambrecht 1915, 1933, Jánossy 1976a, 1979); Répáshuta – Balla Cave (Lambrecht 1912, 1933, Mottl 1938, 1941); Répáshuta – Ballavölgyi Cave (Mottl 1941); Sály (Jánossy 1976a); Szárazgerence (Jánossy 1976a, 1986); Szilvásvárad – Istállóskő Cave (Lambrecht 1912, 1933, Jánossy 1952, 1955, 1976a, 1979); Tatabánya – Szelim Cave (Jánossy 1976a, 1979); Varbó – Lambrecht Kálmán Cave (Jánossy 1976a, 1979) (all in Hungary); Esküllő – Igric Cave (Peștera Igrița – Aștileu) (Kessler 1985); Kőrösmart (Râpa) (Jánossy in Hamar & Csák 1969, Kessler 1974a, Gál 2002); Hidegszamos – Csont Cave (Someșul Rece – Peștera cu Oase) (Lambrecht 1915); Nándor – Nándori Cave (Nandru), (Jánossy 1965, Fischer & Stephan 1977, Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003) (all in Romania); Lándzsásötfalu (Hôrka – Ondrej) (Mlíkovskỳ 2000); Óruzsin – Antal Cave (Oruzer) (Nehring 1880, Róth 1881, Lambrecht 1912, 1933); Óruzsin – Nagy Cave (Oruzer) (Nehring 1880, Róth 1881, Lambrecht 1912, 1933) (all in Slovakia); **Q4/II:** Marchegg (Rabeder 1992, Döppes & Rabeder 1997);

Teufelslucken (Soergel 1966) (all in Austria); Jósvafő – Musztáng Cave (Kessler 2009a); Répáshuta – Rejtek Shelter Cave (Jánossy 1962c, 1976a) (all in Hungary); Kazánszoros – Töröklik Cave (Cazanele Mari-Cuina Turcului) (Kessler 1974b, Fischer & Stephan 1977); Peterd – Turda Gorge – Magyar Cave (Petrești – Cheile Turzii, Peștera Ungureasca) (Kessler & Gál 1998, Gál 2005) (all in Romania). From sites in Europe outside the Carpathian Basin: **Q1-2:** Czech Republik, Poland; **Q3:** Czech Republik, France, United Kingdom; **Q4:** Austria, Belgium, Croatia, Czech Republik, France, Italy, Luxemburg, Poland, Russia, Spain, Switzerland, United Kingdom (Tyrberg 1998).

– ***Tetrao* † *partium* (Kretzoi, 1962)** /syn. *Lyrurus* † *partium* Kretzoi, 1962.

Site and era: **MN 13:** Polgárdi 4 (Kessler 2009a); **MN 15:** Beremend 26 (Kessler 2009a); Csarnóta 4 (Kessler 2009a); **MN 16:** Beremend 18, Villány 3 (Jánossy 1992, 1996, Kessler 2009a); **Q1:** Beremend 16, 17 (Jánossy 1992, 1996, Kessler 2009a); Osztramos 2, 8 (Jánossy 1976a, 1979) (all in Hungary); Betfia 2, 9 (Romania) (Kormos 1913, in Čapek 1917 and Lambrecht 1933, as *Lyrurus tetrix*; Jánossy 1976a, Kessler 1975, Gál 2002); Betfia 5, 7, 7/2-3 (Romania) (Kretzoi 1962, Kessler 1975, Jánossy 1976a, Gál 2002); Méhész (Vcelare, Slovakia) (Jánossy 1976a), **Q2:** Nagyharsányhegy 1-4 (Lambrecht 1916, 1933, Jánossy 1976); Somssich-hegy 2 (Jánossy 1983) (all in Hungary); **Q3/I:** Hundsheim (Austria), (Jánossy 1974, 1976a); Tarkő 2, 3, 4, 7, 12 (Hungary) (Jánossy 1962, 1976a); Betfia 7/4 (Romania) (Kessler 1975, Jánossy 1976a, Gál 2002); Gombaszög (Gombasek, Slovakia) (Jánossy 1976a, Kessler 2009a). From sites in Europe outside the Carpathian Basin: **Q1-2:** France; **Q3:** Czech Republik, Germany (Tyrberg 1998).

Dimensions: *Table 6*.

With examinations on the rich fossil material available it can be shown, that the wingbones of the fossilized type are usually longer and more robust than those of the recent ones, while it is the opposite is true regarding legs. This shows better flight capabilities of the fossil type, and less developed ground mobility. Its rather early (Late Miocene) appearance is also interesting. This fact alone makes the suggestion of Mlikovskỳ (2002) to classify it as recent species unacceptable.

– ***Tetrao tetrix* † *longipes* Mourer-Chauviré, 1975**

From sites in Europe outside the Carpathian Basin: **Q3:** France (Tyrberg 1998).

– ***Tetrao tetrix* Linnaeus 1758**

Q1: Németóvár (Deutsch-Altenburg, Austria) (Döppes & Rabeder 1997, Mlíkovskỳ1998); **Q2:** Hundsheim (2002); Méhész 4E (Vcelare, Slovakia) **(**Horáček 1985, Mlíkovskỳ 2002); **Q3/I:** Budapest – Várhegy (Jánossy 1976a, 1979, 1986); Vértesszőlős (Jánossy 1976a, 1979) (all in Hungary); **Q3/II:** Vindija (Croatia) (M. Malez, 1961, V. Malez 1973, 1988, V. Malez & Rukavina 1975, Musil 1980); Cserépfalu – Hórvölgy Cave (Jánossy 1976a, 1979); Solymár (Jánossy 1976a); Sütő 6-9. (Jánossy 1976a, 1979); Uppony (Jánossy 1976a, 1979) (all in Hungary); **Q4/I:** Grosse Badl-höhle (Fladerer 1993), Luegloch (Mottl 1953) (all in Austria); Velika Pecina (Croatia) (V. Malez 1984, 1988); Bajót – Öregkő (Lambrecht 1913); Bajót – Baits Cave (Jánossy 1976a, 1979); Budapest – Remete Cave (Jánossy

1976a, 1979); Budapest – Remetehegy Shelter Cave (Kormos 1914, Lambrecht 1933, Jánossy 1976b, 1979); Cserépfalu – Subalyuk Cave (Jánossy 1976b, 1979); Csobánka – Kiskevély Cave (Lambrecht 1912, 1915, 1933, Jánossy 1976a, 1979); Felsőtárkány – Peskő Cave (Lambrecht 1912, 1933, Jánossy 1976a, 1979); Gencsapáti (Jánossy 1976b, 1979); Hámor – Puskaporos Shelter Cave (Lambrecht 1912, 1916, 1933, Jánossy 1976a); Hámor – Herman Ottó Cave (Lambrecht 1915, 1933); Jósvafő – Porlyuk Cave (Jánossy 1976a, 1979); Kecskésgalya (Mottl 1941); Kesztölc – Bivak Cave (Jánossy 1976a); Nagyvisnyó – Háromkút Cave (Jánossy 1976a); Pilisszántó I. Shelter Cave (Lambrecht 1915, 1933, Jánossy 1976a, 1979); Répáshuta – Balla Cave (Lambrecht 1912, 1933, Mottl 1938, 1941); Répáshuta – Ballavölgy Cave (Mottl 1941); Répáshuta – Poroslyuk (Jánossy 1976a); Szárazgerence (Jánossy 1976a, 1986); Szilvásvárad – Istállóskő Cave (Lambrecht 1912, 1933, Jánossy 1952, 1955, 1976a); Tata (Lambrecht 1915, 1933, Jánossy 1986); Tatabánya-Szelim Cave (Jánossy 1976a, 1979); Tokod – Nagyberek (Jánossy 1976a, 1979); Varbó – Lambrecht Kálmán Cave (Jánossy 1976a, 1979) (all in Hungary); Barcarozsnyó – Gura Cheii Cave (Râșnov) (Gál 1998, 2002); Kőrösmart (Râpa), (Jánossy in Hamar & Csák 1969, Kessler 1974a, Gál 2002); Nándor – Nándori Cave (Nandru), (Jánossy 1965, Fischer & Stephan 1977, Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003); Peterd – Turda Gorge – Binder Cave (Petrești – Cheile Turzii) (Kessler 1985, Gál 2002); Rév – Kecske Cave; Rév – Pince Cave (Vadu Crișului) (Mottl 1941, Gál 2002); Szegyestel – Tibocoaia Cave (Sighiștel) (Kessler 1982, 1985, Gál 2002) (all in Romania); Lándzsásötfalu (Hôrka Ondrej, Slovakia) (Mlíkovskỳ 2000); **Q4/II:** Teufelslucken (Austria) (Soergel 1966); Balatonkeresztúr – Réti-Dülő (Gál 2007a); Balatonszemes – Bagódomb (Gál 2007a); Berettyóújfalú – Herpály (Gál 2005); Békés – Városerdő (Jánossy 1976a, 1985); Ecsegfalva 23 (Pike-Tay *et al.* 2004, Gál 2007b); Endrőd 39,119 (Jánossy 1985, Gál 2005, 2007b); Felsőnyék – Várhegy (Gál 2007a); Hosszú-hegyi zsomboly (Jánossy 1976a, Kordos 1981); Ludas – Budzsák (Bökönyi 1974, Gál 2005); Mezőfény (Gál 2004); Pilismarót – Malompatak (Jánossy 1985); Répáshuta – Rejtek Shelter Cave (Jánossy 1962, 1976a); Visegrád – Vár (Bökönyi & Jánossy 1965, Jánossy 1976a) (all in Hungary); Gálospetri (Galoșpetreu) (Kessler 1980–81, Gál 2002); Kazánszoros – Climente I. Cave (Cazanele Mari) (Kessler 1980–81, Gál 2002); Kazánszoros – Töröklik Cave (Cazanele Mari – Cuina Turcului) (Kessler 1974b, Fischer & Stephan 1977); Mezősámsond (Șincai) (Bindea 2008); Peterd – Szentkirály (Sâncrai) (Gál 2005); Turda Gorge – Magyar Cave (Cheile Turzii – Peștera Ungurească) (Kessler & Gál 1998, Gál 2005); Szind – Túr Gorge (Tureni – Cheile Turului) (Gál 2005); Vargyasi szoros – Homoródalmás caves (Cheile Vârghisului) (Jurcsák & Kessler 1986, 1988); Vársonkolyos – Izbîndiș Cave (Șuncuiuș) (Kessler 1977b, Gál 2002) (all in Romania). From sites in Europe outside the Carpathian Basin: **Q1-2:** Czech Republik, Poland; **Q3:** Czech Republik, France, Germany, Italy, Russia, Ukraine; **Q4:** Austria, Belgium, Bosnia-Herzegovina, Croatia, Czech Republik, France, Germany, Greece, Ireland, Italy, Luxemburg, Moldova, Poland, Russia, Spain, Switzerland, Ukraine, United Kingdom (Tyrberg 1998).

– *Tetrao mlokosiewiecz*i Taczanovski, 1875

From sites in Europe outside the Carpathian Basin: **Q3:** Georgia; **Q4:** Armenia, Georgia, Russia (Tyrberg 1998).

– *Tetrao* sp.

Q3/I: Várhegy (Hungary) (Jánossy 1976); **Q4/I:** Nándor – Nándori Cave (Nandru, Romania) (Téglás 1880, Lambrecht 1912). From sites in Europe outside the Carpathian Basin: **Q3:** Belgium; **Q4:** Belgium, Ukraina, United Kingdom (Tyrberg 1998).

– *Tetraogallus caucasicus* Pallas, 1811

From sites in Europe outside the Carpathian Basin: **Q3:** Georgia; **Q4:** Georgia, Russia (Tyrberg 1998).

– *Bonasa* Stephen, 1810

– *Bonasa* † *praebonasia* Jánossy, 1974 / syn. *Tetrastes* † *praebonasia* Jánossy, 1974.

Site and era: **Q1:** Beremend 17 (Hungary) (Jánossy 1992); **Q3/I:** Hundsheim (Austria) (Jánossy 1974); Tarkő 1-16 (Hungary) (Jánossy 1962, 1976a,c). From sites in Europe outside the Carpathian Basin: **Q3:** France, Poland (Tyrberg 1998).

Material: coracoideum cranial part, proximal and distal fragment of the *tarsometatarsus* (Tarkő 11 and 12), entire *humerus*, *ulna* fragment (Hundsheim).

Dimensions: *tarsometatarsus* A = approx. 39–40 mm, E = 2.9 mm, *humerus* A = 49.8 mm.

Regarding skeletal characteristics it matches the recent species, the only difference is the higher placement of the *foramen vasculare distale* on the distal part of the *tarsometatarsus* (2.3 mm, while on the 8 recent and 5 subfossil specimens this varies between 0.8 and 1.6 mm). The *humerus* found at the site Beremend 17 (Jánossy 1992) is considered by Mlikovskỳ to be *Alectoris donnezani* (Deperet, 1892). In our opinion it is not a rock partridge, but a hazel grouse.

It is also known from the Lower Pleistocene of Kozi Grzbiet, Poland (Q2) and Stránská Skalá, Czech Republik (Q2), as well as from the Middle Pleistocene of Montoussé 3, France (Q3) (Mlikovskỳ 2002).

– *Bonasa bonasia* (Linnaeus, 1758)

Q4/I: Krapina (Croatia) (Lambrecht 1915, V. Malez 1973, 1984, V. Malez-Bačić 1979); Szárazgerence (Jánossy 1976a, 1986); Varbó – Lambrecht Kálmán Cave (Jánossy 1976a, 1979) (all in Hungary); Barcarozsnyó – Gura Cheii Cave (Râșnov) (Gál 1998, 2002); Homoródalmási – Orbán Balázs Cave – Vargyasi szoros (Cheile Vârghișului) (Kessler 1977a, Gál 2002) (all in Romania); Óruzsin – Antal Cave (Oruzer) (Slovakia) (Nehring 1880; Róth 1881, Lambrecht 1912, 1933); **Q4/II:** Grosse Offenbergerhöhle (Austria) (Bochenski & Tomek 1994); Hosszú-hegyi Cave (Jánossy 1976a, 1979, Kordos 1981); Mélyvölgy (Jánossy 1976a); Répáshuta – Rejtek Shelter Cave (Jánossy 1962c, 1976a, 1979), (all in Hungary); Révtízfalusi Cave (Zece Hotare) (Kessler 1985); Szegyestel – Drăcoaia Cave; caves in the Szegyestel Valley (Sighiștel) (Kessler 1982); Székelykeresztúr (Cristuru Secuiesc) (Gál 2008b); Szkerisóra – Coiba Mare Cace (Scărișoara) (Kessler 1982, Jurcsák & Kessler 1988); Vársonkolyos – Kismagyar Cave (Șuncuiuș – Peștera Napișteleu) (Kessler 1977b, Gál 2002) (all in Romania). From sites in Europe outside the Carpathian Basin: **Q3:** Czech Republik, United Kingdom; **Q4:** Austria, Croatia, Czech Republik, France, Germany, Serbia, Spain, United Kingdom (Tyrberg 1998).

– *Lagopus* (Brisson, 1760)

– *Lagopus lagopus* † *noaillensis* (Mourer-Chauviré, 1975)

From sites in Europe outside the Carpathian Basin: **Q3:** France (Tyrberg 1998).

– *Lagopus lagopus* (Linnaeus, 1758)

Q3/I: Vértesszőlős 2 (Hungary) (Jánossy 1976a, 1979); Aranyosszohodol – Lúcsia Cave (Sohodol, Romania) (Gál 2002); **Q3/II:** Vindija (Croatia) (M. Malez 1961, V. Malez 1973, 1988, V. Malez & Rukavina 1975, Musil 1980); Cserépfalu – Hórvölgyi Cave (Jánossy 1976a, 1979); Uppony (Jánossy 1976a) (all in Hungary); **Q4/I:** Grosse Badlhöhle (Fladerer 1993); Hundsteig bei Krems (Lambrecht 1933); Hundsteig bei Krems (Lambrecht 1933); Luegloch (Mottl 1953); Merkenstein (Wettstein & Mühlhofer 1938); Schwarzgrabenhöhle (Spahni 1954); Velika Pecina (V. Malez 1984, 1988); Velika pecna Lipi (V. Malez 1984, V. Malez-Bačić 1979) (all in Croatia); Bajót – Öregkő (Lambrecht 1915); Bajót – Baits Cave (Jánossy 1976a, 1979); Bajót – Hóman Cave (Jánossy 1976a, 1979); Budapest – Remete Cave (Jánossy 1976a, 1979); Budapest – Remetehegyi Shelter Cave (Kormos 1914, Lambrecht 1933, Jánossy 1976a, 1979); Csákvár – Eszterházy Cave (Lambrecht 1933, Mottl, 1938, Kretzoi 1954, Jánossy 1976a, 1979); Felsőtárkány – Peskő Cave (Lambrecht 1912, 1933, Jánossy 1976a, 1979); Hámor – Puskaporos Shelter Cave (Lambrecht 1912, 1916, 1933, Jánossy 1976a, 1979); Hámor – Herman Ottó Cave (Lambrecht 1915, 1933); Kesztölc – Bivak Cave (Jánossy 1976a, 1979); Nagyvisnyó – Háromkút Cave (Jánossy 1976a); Pilisszántó I. Shelter Cave (Lambrecht 1915, 1933, Jánossy 1976a, 1979); Répáshuta – Balla Cave (Lambrecht 1912, 1933, Mottl 1938, 1941); Répáshuta – Ballavölgyi Cave (Mottl 1941); Sály (Jánossy 1976a); Szilvásvárad – Istállóskői Cave (Lambrecht 1912, 1933, Jánossy 1952, 1955, 1976a, 1979); Tatabánya – Szelim Cave (Jánossy 1976a, 1979); Varbó – Lambrecht Kálmán Cave (Jánossy 1976a, 1979); Vaskapu Cave (Mottl 1941) (all in Hungary); Barcarozsnyó – Gura Cheii Cave (Râșnov) (Gál 1998, 2002); Kőrösmart (Râpa) (Jánossy in Hamar & Csák 1969, Kessler 1974a, Gál 2002); Rév – Vizes Cave (Vadu Crisului – Peștera cu Apă) (Mottl 1941); Rév – Kecske Cave; Rév – Pince Cave (Vadu Crișului – Peștera Caprei, Peștera Pivnicei) (Mottl 1941, Gál 2002); Vargyas – Medve Cave (Vârghis – Peștera Ursului) (Mottl 1942) (all in Romania); Detrekőszentmiklós – Pálffy Cave (Dzeráva Skála – Plávecky Mikulas) (Lambrecht 1913, 1933, Mottl 1938, 1941, Musil 1980); Novi I. III. (Lambrecht 1912, 1933, Nehring 1880, Róth 1881); Óruzsin – Antal Cave (Oruzer) (Nehring 1880, Róth 1881, Lambrecht 1912, 1933) (all in Slovakia); **Q4/II:** Grosse Offenbergerhöhle; Hohlensteinhöhle; Knochenhöhle (Bocheński & Tomek 1994); Teufelslucken (Soergel 1966) (all in Austria); Répáshuta – Rejtek Sheler Cave (Hungary) (Jánossy 1962c, 1976a); Gálospetri (Galoșpetreu) (Kessler 1980–81, Gál 2002); Vargyasi szoros – Homoródalmás caves (Cheile Vârghișului) (Jurcsák & Kessler 1988); Vársonkolyos – Izbîndiș Cave (Șuncuiuș) (Kessler 1977b, Gál 2002) (all in Romania). From sites in Europe outside the Carpathian Basin: **Q1-2:** France; **Q3:** Czech Republik, France, Germany, Poland, Russia, Ukraine, United Kingdom; **Q4:** Austria, Belgium, Bosnia Herzegovina, Croatia, Czech Republik, Denmark, France, Germany, Ireland, Italy, Luxemburg, Moldova, Montenegro, Poland, Russia, Spain, Switzerland, Ukraine, United Kingdom (Tyrberg 1998).

– *Lagopus mutus † correzenzis* (Mourer-Chauviré, 1975)

From sites in Europe outside the Carpathian Basin: **Q3:** France (Tyrberg 1998).

– *Lagopus mutus* (Montin, 1781)

Q3/I: Aranyosszohodol – Lúcsia Cave (Sohodol, Romania) (Gál 2002); **Q3/II:** Vindija (Croatia) (M. Malez 1961, V. Malez 1973, 1988, 1991, V. Malez & Rukavina 1979, Musil 1980); Cserépfalu – Hórvölgy Cave, Sütő 6-9. (Jánossy 1976a, 1979) (all in Hungary); **Q4/I:** Grosse Badlhöhle (Fladerer 1993); Luegloch (Mottl 1953); Merkenstein (Wettstein & Mühlhoffer 1938); Repolusthöhle (Mottl 1951, Jánossy 1976a) (all in Austria); Velika Pecina (V. Malez 1984, 1988); Velika pec na Lipi (V. Malez 1984, V. Malez-Bačić 1979) (all in Croatia); Bajót – Öregkő (Lambrecht 1915); Bajót – Baits Cave (Jánossy 1976a, 1979); Bajót – Hóman Cave (Jánossy 1976a, 1979); Budapest – Remete Cave (Jánossy 1976a, 1979); Budapest – Remetehegyi Shelter Cave (Kormos 1914, Lambrecht 1933, Jánossy 1976a, 1979); Csákvár – Eszterházy Cave (Lambrecht 1933, Mottl 1938, Kretzoi 1954, Jánossy 1976a, 1979); Csobánka – Kiskevélyi Cave (Lambrecht 1912, 1915, 1933, Jánossy 1976a, 1979); Felsőtárkány – Peskő Cave (Lambrecht 1912, 1933. Jánossy 1976a, 1979); Hámor – Puskaporos Shelter Cave (Lambrecht 1912, 1916, 1933, Jánossy 1976a, 1979); Hámor – Herman Ottó Cave (Lambrecht 1915, 1933); Kesztölc – Bivak Cave (Jánossy 1976a, 1979); Nagyvisnyó – Háromkút Cave (Jánossy 1976a); Pilisszántó I. Shelter Cave (Lambrecht 1915, 1933, Jánossy 1976a, 1979); Répáshuta – Balla Cave (Lambrecht 1912, 1933, Mottl 1938, 1941); Répáshuta – Ballavölgyi Cave (Mottl 1941); Sály (Jánossy 1976a, 1979); Szilvásvárad – Istállóskő Cave (Lambrecht 1912, 1933, Jánossy 1952, 1955, 1976a, 1979); Tatabánya-Szelim Cave (Jánossy 1976a, 1979); Vaskapu Cave (Mottl 1941) (all in Hungary); Barcarozsnyó – Gura Cheii Cave (Râșnov) (Gál 1998, 2002); Esküllő – Igric Cave (Aşştileu-Pestera Igriţa) (Kessler 1985); Hidegszamos – Csont Cave (Someșul Rece – Peștera cu Oase) (Lambrecht 1915); Ohábaponor – Bordu Mare Cave (Ohaba Ponor) (Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003); Rév – Vizes Cave (Vadu Crișului – Peștera cu Apă) (Mottl 1941); Szamosfalva (Someșeni) (Kormos 1913, Lambrecht 1933) (all in Romania); Detrekőszentmiklós – Pálffy Cave (Dzeráva Skála – Plávecky Mikulas) (Lambrecht 1913, 1933, Mottl 1938, 1941, Musil 1980); Novi I. III. (Lambrecht 1912, 1933, Nehring 1880, Róth 1881); Óruzsin – Antal Cave, Óruzsin – Nagy Cave (Oruzer) (Nehring 1880, Róth 1881, Lambrecht 1912, 1933) (all in Slovakia); **Q4/II:** Grosse Offenbergerhöhle; Hohlensteinhöhle; Knochenhöhle (Bocheński & Tomek 1994) (all in Austria); Répáshuta – Rejtek Shelter Cave (Hungary) (Jánossy 1962, 1976a); Vargyasi Pass – Homoródalmási caves (Cheile Vârghișului, Romania) (Jurcsák & Kessler 1986, 1988). From sites in Europe outside the Carpathian Basin: **Q3:** Czech Republik, France, United Kingdom; **Q4:** Austria, Belgium, Bosnia Herzegovina, Bulgaria, Croatia, Czech Republik, France, Germany, Ireland, Italy, Luxemburg, Montenegro, Norway, Poland, Russia, Serbia, Spain, Switzerland, Ukraine, United Kingdom (Tyrberg 1998).

– *Lagopus* sp.

Q3/II: Vindija (Croatia) (M. Malez 1961, V. Malez 1973, 1988, V. Malez & Rukavina 1975, Musil 1980); **Q4/I:** Veternica (Croatia) (V. Malez 1973, 1988, V. Malez-Bačić 1979,

Musil 1980); Szárazgerence (Jánossy 1976a, 1986); Tata (Lambrecht 1915, 1933, Jánossy 1986) (all in Hungary); Szegyestel – Tibocoaia Cave (Sighiștel, Romania) (Kessler 1982, 1985, Gál 2002); Porács (Porac, Slovakia) (Jánossy 1976a); **Q4/II:** Kazánszoros – Climente I. Cave (Kessler 1980–81, Gál 2002); Tropfsteinhöhle Tunnelhöhle (Fladerer 1993). From sites in Europe outside the Carpathian Basin: **Q3:** France, Germany, Spain; **Q4:** Austria, Bosnia Herzegovina, Croatia, Czech Republik, France, Germany, Ireland, Poland, Russia, Spain, Switzerland, United Kingdom (Tyrberg 1998).

– **Galliformes indet. foss.**
MN 13: Polgárdi 4, 5 (Hungary), (Kessler 2009a);

Conclusions

Galliformes have always been birds represented by many species in large numbers from the Neogene in the Carpathian Basin. They are remarkable not only due to the 22 taxa and the enormous number of fossil material present at the sites (several hundred or several thousand bones), but also the continuous presence of smaller Galliformes (partridge- and quail-reLated birds) and larger grouses, as well as observing the gradual transitions into new species.

Apart from *Palaeoperdix* and *Palaeocryptonix* types the early representatives of peacocks and actual chickens are also present. Later direct ancestors of the recent species emerge. Climate changes of the Quaternary had greatly reduced this abundance of species, and not only did Pliocene and Lower Pleistocene Galliformes vanish, but the spread of recent quills and partridges also decreased, and hazel grouses were replaced by ptarmigans In the Holocene the opposite of the phenomenon happens.

Grouses are only known from the end of the Miocene (MN 13) both from the Carpathian Basin and Europe. They spread during the Quaternary, and were one of the period's most significant ground dwelling birds. During the Holocene, however, their significance fell both in numbers and area, as they receded to higher habitats above sea level and their population greatly decreased In the Quaternary the Carpathian Basin was one of their most significant habitats in Europe, which is clearly indicated both by the number of species and the number of finds.

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Table 1. Size table of *Palaeocryptonix hungaricus* Jánossy, 1991
Abbreviations: A – total length of bone in mm; B – partial lengths; C – width of proximal epiphysis; D – thickness of proximal epiphysis; E – width of diaphysis; E1 – partial width of diaphysis; F – width of distal epiphysis; G – thickness of distal epiphysis; H – hight of distal epiphysis (femur)

1. táblázat *Palaeocryptonix hungaricus* Jánossy, 1991
Rövidítések: A – teljes hossz mm-ben; B – részleges hossz; C – proximális epifizis szélessége; D – proximális epifizis vastagsága; E – diafizis szélessége; E1 – diafizis részleges szélessége; F – disztális epifizis szélesége; G – disztális epifizis vastagsága; H – disztális epifizis magassága (combcsont)

Bone	A	B	C	D	E	F	G	H	Sites	References
coracoideum	38.00		9.70		3.50	7.40			Polgárdi 5	Jánossy 1991
"	27.40		4.80		2.20	5.20			"	"
"	28.00		4.50		2.40	5.50			"	"
"	29.00		5.50		2.50	6.20			"	"
"	29.60		5.00		2.60	5.80			"	"
ulna	23.40								"	"
"	25.00								"	"
femur	26.50								"	"
"	26.60								"	"
tibiotarsus	24.40								"	"
"	26.70					4.60			"	"
"			6.50						"	"
"						4.50			"	"
tarsometatarsus			7.50						"	"
"						5.00			"	"
coracoideum						5.20			"	Kessler 2009
ulna						5.60			"	"
humerus						5.60			"	"
"					2.62	5.35	4.34		Beremend 26	"
carpometacarpus	19.28	16.35	6.12		3.61	4.52	2.46		"	"
"	21.62	20.46	6.01	3.98	4.43		2.43		"	"
"	22.33	21.22	6.37	4.32		4.49	2.64		"	"
"	22.61	20.66	6.47	5.05		4.50	2.51		"	"
"						5.19	4.35		"	"
femur	20.24					4.26	2.74		"	"
"	21.58					4.48	2.61		"	"
"			4.68	2.89					"	"
"			5.84	2.18					"	"
"					2.14	4.73	3.80		"	"
"						4.35	2.54	2.23	"	"
carpometacarpus		26.01	5.76	4.75	3.00				Beremend 18	"
"					2.54	4.74	3.68		"	"

Table 2. Size table of *Francolinus capeki* (Lambrecht, 1933)
Abbreviations: A – total length of bone in mm; B – partial lengths; C – width of proximal epiphysis; C1 – partial width of proximal epiphysis *(coracoideum)*; D – thickness of proximal epiphysis; E – width of diaphysis; F – width of distal epiphysis; G – thickness of distal epiphysis

2. táblázat *Francolinus capeki* (Lambrecht, 1933)
Rövidítések: A – teljes hossz mm-ben; B – részleges hossz; C – proximális epifizis szélessége; C1 – proximális epifizis részleges szélessége (hollócsőrcsont); D – proximális epifizis vastagsága; E – diafizis szélessége; F – disztális epifizis szélesége; G – disztális epifizis vastagsága

Bone	A	B	C	D	E	F	G	C1	Sites	References
humerus						6.90			Villány 3	Jánossy 1976b
"						8.00			"	"
"						10.60	5.60		"	"
carpometacarpus	27.70				3.50				"	"
ulna	40.00								"	"
tibiotarsus						5.50			Nagyharsányhegy 2	"
humerus						7.70			Csarnóta 2	"
tibiotarsus						5.80			"	"
phal.pedis 1. D.IV	9.50				1.50				"	"
"	9.60				1.50				"	"
femur						5.90			Osztramos 7	"
phal.ped. 2. D.II	10.90				1.20				"	"
phal.ped. 1. D.III			3.60						"	"
humerus						8.20			Osztramos 8	"
tarsomaetatarsus	28.00				2.60				Beremend 15	Jánossy 1992
humerus	40.00		10.80		3.80	7.00			Beremend 16	"
carpometacarpus	18.60								"	"
coracoideum								3.47	Betfia 13	Gál 2002
" 13 piece.			5.53-6.50	3.53-3.93	2.94-3.85		7.01-8.10	3.47-3.71	Betfia 9	"
scapula4 piece		7.77-8.55	3.55-4.15	3.44	3.00-3.26				"	"
humerus 3 piece	41.46	12.40	11.49		4.11-4.60	8.21-8.40	4.52-4.74		"	"
ulnae 7 piece			5.10-5.51		2.42-2.75	5.40-5.87	4.20-4.70		"	"

Bone	A	B	C	D	E	F	G	C1	Sites	References
radius 8 piece	36.10-36.78		2.84-2.93	3.38-3.62	1.62-2.07	3.87-4.23	2.23-2.56		"	"
carpometacarpus 19 p.	23.25-24.98	20.73-22.87	6.46-7.15	3.76-5.15	4.83-5.12	4.33-5.18	2.93-3.10		"	"
phal..alae 1.D.II. 3 piece	9.90		3.28	3.49	4.56-4.59	4.23-4.53	2.33-2.42		"	"
femur			8.40	6.16	3.33	7.26	5.34		"	"
tibiotarsus 5 piece					3.00-3.36	5.83-6.12	5.70-5.96		"	"
tarsometatarsus 11 piece	36-25-38.93		6.23-6.53	6.50-6.60	2.86-3.16	7.00-7.48	4.96-5.65		"	"
humerus 4 piece	41.55-42.75	12.26-14.00	9.41-12.25		3.85-4.60	7.44-8.54	4.56-4.78		Betfia 2	"
ulna					2.89	5.77			"	"
carpometacarpus 3 piece	23.46	20.87	6.97	4.06	5.21	4.79-4.85	2.57-2.74		"	"
tibiotarsus 5 piece			9.60	5.60	3.11-3.16	5.93-6.16	5,57-5.82		"	"
tarsometatarsus 10 piece	37.70		5.58-6.80	5.45-6.30	3.10-3.30	6.90-7.50	5.20-5.64		"	"
tibiotarsus						6.17	5.96		Betfia 5	"
ulnae					2.50				Betfia "Aven"	"
coracoideum 7 oiece	31.82-34.08	28.36-32.63	3.87-6.13	3.96-6.52	2.54-3.16	8-29-10.22	6.58-7.13		Beremend 26	Kessler 2009
humerus					3.84	7.95	4.72		"	"
ulna 2 piece		5.40	4.70	6.76	2.89-3.40	4.56	3.07		"	"
"	19.28-22.33	16.35-21.22	6.01-6.47	3.98-5.05	3.61-4.43	4.26-5.84	2.46-3.18		"	"
phalanga.alae 1.D.II.	9.44		3.29	2.73	4.30				"	"
femur					3.30	3.19	1.66		"	"
tibiotarsus			8.24	5.91					"	"
tarsometatarsus 4 piece	38.69		6.04	5.34	2.61-2.75	6.46-7.03	4.40-5.57		"	"
humerus 3 piece	40.75	13.21	10.32	9.98	3.17-3.35	6.93-7.06	4.14-4.33		Beremend 18	"

Table 3. Size table of *Perdix perdix jurcsaki* Jánossy, 1976
Abbreviations: A – total length of bone in mm; B – partial lengths; C – width of proximal epiphysis; C1 – partial width of proximal epiphysis (coracoideum); D – thickness of proximal epiphysis; E – width of diaphysis; F – width of distal epiphysis; G – thickness of distal epiphysis

3. táblázat *Perdix perdix jurcsaki* Jánossy, 1976
Rövidítések: A – teljes hossz mm-ben; B – részleges hossz; C – proximális epifizis szélessége; C1 – proximális epifizis részleges szélessége (hollócsőrcsont); D – proximális epifizis vastagsága; E – diafizis szélessége; F – disztális epifizis szélesége; G – disztális epifizis vastagsága

Bone	A	B	C	D	E	F	G	C1	Sites	References
humerus			13.67		4.62	9.03	5.32		Betfia 2	Kretzoi 1962
phalanga.alae 1.D.II.			3.40	3.50					"	"
tarsometatarsus					3.46				"	"
coracoideum 4 piece			5.44		2.90-2.93	8.80		5.00	Betfia 9	Gál 2002
ulna 3 piece			5.55	7.26	2.58-2.78	6.19-6.43	5.04-5.05		"	"
coracoideum	35.20	33.01	6.95	4.14	3.56		8.01	3.57	Betfia 2	"
carpometacarpus 4 p.	26.25-26.54	23.72-23.96	7.00-7.65	4.40-5.02		4.86-5,20	2.62-3.11		"	"
coracoideum 3 piece					2.62-2.90				Betfia 5	"
scapula			4.55		3.32				"	"
humerus2 piece					4.55-4.57	9.36-9.56	5.08-5.46		"	"
	45.93	5.95-6.68	5.44-6.04	7.90-8.66	2.50-2.90	6.36-6.46	5.11-5.34		"	"
carpometacarpus 2 p.	25.31	22.90	7.24	5.20	5.34-5.40	3.07-3.23	3.81		"	"
tibiotarsus						7.12	6.80		"	"
tarsometatarsus 2 piece			6.83	5.86	3.67				"	"
tibiotarsus					4.60	6.90	6.50		Betfia "Aven"	"
tarsometatarsus	44.50				3.50	8.10			"	"
carpometacarpus	25.39	22.90	6.41	3.76	5.60	4.81	3.00		Betfia 7	"
coracoideum	41.52	39.62	7.93	5.95	4.07	12.16	9.74		Beremend 26	Kessler 2009
scapula		10.04	5.30	4.59					"	"
humerus 21 piece	39.33-40.32	10.63-14.01	7.36-11.08	8.39-11.01	3.56-4.32	7.09-8.21	3.96-4.63		"	"

Bone	A	B	C	D	E	F	G	C1	Sites	References
tibiotarsus			7.72	5.81					"	"
tarsometatarsus 2 piece	44.19		8.36-8.82		3.93-4.06				Beremend 18	"
humerus	46.36	14.87	12.86	13.13	4.86	8.86	5.36		Beremend 17	"
carpometacarpus 3 p.	25.54-27.70	24.36-26.00	6.83-8.00	4.47-4.65	4.13-5.72	2.62-2.91			"	"
ulna					8.88	5.14			Győrújfalu	"
tarsometatars	43.98		7.90		4.09				"	"

Table 4. Size table of *Gallus beremendensis* Jánossy, 1976
Abbreviations: A – total length of bone in mm; B – partial lengths; C – width of proximal epiphysis; D – thickness of proximal epiphysis; E – width of diaphysis; F – width of distal epiphysis; G – thickness of distal epiphysis

4. táblázat *Gallus beremendensis* Jánossy, 1976
Rövidítések: A – teljes hossz mm-ben; B – részleges hossz; C – proximális epifizis szélessége; D – proximális epifizis vastagsága; E – diafizis szélessége; F – disztális epifizis szélesége; G – disztális epifizis vastagsága

Bone	A	B	C	D	E	F	G	Sites	References
humerus	53.00		14.00		5.70	10.00		Beremend 5	Jánossy 1976b
coracoideum	41.52	39.62	7.93	5.95	4.07	12.16	9.74	Beremend 26	Kessler 2009
scapula		10.04	5.30		4.59			"	"
humerus 7 piece	39.33-40.32	11.33-14.01	10.14-11.08	9.81-11.01	3.72-4.32	7.33-7.64	4.11-4.37	"	"
phalanga alae 1. D.II.	9.44		3.29	2.73	4.30			"	"
femur					3.09	6.74	6.01	"	"
tibiotarsus 3 piece			7.72-8.24	5.81-5.91	3.39	6.79	6.03	"	"
tarsometatarsus 5 piece	38.69		6.04	5.34	2.61-2.75	5.19-7.03	4.34-5.57	"	"
humerus 2 piece	46.36	14.87-17.65	12.86-13.55	13.13-14.46	4.46-5.22	8.86	5.36	Beremend 17	"
ulna 2 piece		6.20	6.38	7.87	3.53-4.07	6.86	5.47	"	"
carpometacarpus 3 p.	25.54-28.59	24.36-26.43	6.84-8.36	4.47-5.31		4.13-6.11	2.62-4.10	"	"

Table 5. Size table of *Tetrao praeurogallus* Jánossy, 1969
Abbreviations: A – total length of bone in mm; B – partial lengths; C – width of proximal epiphysis; D – thickness of proximal epiphysis; E – width of diaphysis; E1 – partial width of diaphysis *(carpometacarpus)*; F – width of distal epiphysis; G – thickness of distal epiphysis

5. táblázat *Tetrao praeurogallus* Jánossy, 1969
Rövidítések: A – teljes hossz mm-ben; B – részleges hossz; C – proximális epifizis szélessége; D – proximális epifizis vastagsága; E – diafizis szélessége; E1 – diafizis részleges szélessége (kézközépcsont); F – disztális epifizis szélesége; G – disztális epifizis vastagsága

Bone	A	B	C	D	E	F	G	E1	Sites	References
humerus	96.00		24.50		10.50	20.50	11.10		Csarnóta 2	Jánossy 1976a
radius	79.00					9.00			"	"
tibiotarsus						17.00			"	"
phal.pedis 2. D.II.	22.00				4.00				"	"
phal.pedis 1. D.III.	27.00				5.00				"	"
phal.pedis 2. D.III	20.50				4.40				"	"
phal.pedis 3. D.III.	18.60				4.10				"	"
humerus	130.00		32.80		11.40	22.40	12.60		Méhész (Vcelare)	"
ulna						11.00			"	"
carpometacarpus	60.00		17.00			12.00	6.00	6.00	"	"
"						11.48	5.84	5.45	Nagyharsányhegy	"
coracoideum	63.91.	60.71	13.78	8.37	5.59	18.68	14.75		Beremend 26	Kessler 2009
humerus		28.01	23.39	25.81	9.97	18.26	10.25		"	"
tibiotarsus		13.28	12.77		7.27	13.49	13.25		"	"
carpometacarpus						10.30	6.10	5.60	Betfia 5	Gál 2002

Table 6. Size table of *Tetrao partium* (Kretzoi, 1962)
Abbreviations: A – total length of bone in mm; B – partial lengths; C – width of proximal epiphysis; D – thickness of proximal epiphysis; E – width of diaphysis; E1 – partial width of diaphysis (carpometacarpus); F – width of distal epiphysis; G – thickness of distal epiphysis

6. táblázat *Tetrao partium* (Kretzoi, 1962)
Rövidítések: A – teljes hossz mm-ben; B – részleges hossz; C – proximális epifizis szélessége; D – proximális epifizis vastagsága; E – diafizis szélessége; E1 – diafizis részleges szélessége (kézközépcsont); F – disztális epifizis szélesége; G – disztális epifizis vastagsága

Bone	A	B	C	D	E	F	G	E1	Sites	References
coracoideum					4.11				Betfia 5	Kretzoi 1962
tarsometatarsus			8.70		4.40	9.50	8.00		"	"
humerus					8.20	16.50			Osztramos 2	Jánossy 1976a
carpometacarpus		43.50	12.80					5.30	"	"
phalanga pedis ?	18.60				9.00				"	"
carpometacarpus		41.70	11.80		8.30			4.30	Osztramos 8	"
phalanga pedis ?	17.00				7.10				Méhész (Vcelare)	"
tibiotarsus 2 piece					8.90-10.00				"	"
phalanga pedis ?	10.10		3.90		2.20	3.00			Villány 3	"
tibiotarsus					7.80				"	"
phalanga pedis ?	17.89		5.00		2.80	4.00			Betfia 2	"
scapula	9.72				4.50				Betfia 9	Gál 2002
phalanga alae 1. D.II.	12.43		4.03	4.53	5.37		2.85		"	"
femur				10.20	6.00				"	"
tibiotarsus						6.24	6.57		"	"
tarsometatarsus					5.80				"	"
carpometacarpus								5.00	Betfia 2	"
tarsometatarsus					4.18	10.49	7.00		"	"
phalanga pedis ? 2 p.	12-26-16.24		3.05-4.79	3.31-5.20	2.68-2.90	2.07-3.60			"	"
ulna					4.90	10.38	8.00		Betfia 5	"
radius					3.88	7.17	4.22		"	"
carpometacarpus	45.71		15.81			8.75	4.84	4.00	"	"
ulna					4.32				Betfia 7	"
tibiotarsus						9.55	8.50		"	"
ulna					4.68				Polgárdi 4	Kessler 2009
carpometacarpus	34.63	31.88	11.46	6.06	9.61	7.29	4.54		Csarnóta 4	"
phalanga pedis 4 piece	7.57-13.90								"	"
phalanga unguis 2 p.	11.45-12.30								"	"
radius					3.68	8.01	4.39		Beremend 26	"
tarsometatarsus						5.30			"	"
coracoideum			9.52	7.24					Beremend 18	"
tibiotarsus					6.01	9.55			Beremend 17	"

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