

## Late Cenozoic biostratigraphy of Europe: mammal zones and the fossil record of birds

Pozdně kenozoická biostratigrafie Evropy: savčí zóny a fosilní nálezy ptáků

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**Abstract.** The mammal-based biostratigraphy of the late Cenozoic of Europe was compared with the fossil record of birds. Three basic questions were addressed: suitability of the avian record for biostratigraphy, paleornithological contribution to the recognition of main biostratigraphical periods, and the history of avian faunas. Main conclusions are as follows:

– Validity of the avian record: (1) Paleornithological data are not sufficient for detailed biostratigraphical decisions yet. (2) Stratigraphical appearance and changes in distribution can be exactly estimated for basic types of avian faunas and for several well represented avian taxa. (3) Appearance and disappearance of avian taxa is markedly diachronous in the studied time-space.

– Paleornithological definitions of biostratigraphical periods: (1) The middle/late Miocene, i.e. MN 8/9 boundary is well characterized by the whole-scale extinction of aquatic and wetland birds, and by the appearance of a steppe avifauna in eastern Europe. (2) The Vallesian/Turolian, i.e. the MN 10/11 boundary is not supported by paleornithological data. (3) The Miocene/Pliocene, i.e. the MN 13/14 boundary is well characterized by the appearance of the boreal avifauna, by re-arrangement of the east European steppe avifauna, and by the spread of the latter avifauna to SW Europe. (4) The E-L-E datum, i.e. the MN 14/15 boundary, is not supported by paleornithological data. (5) The early/late Pliocene, i.e. the MN 15/16 boundary is not supported by paleornithological data. (6) The MN 18 zone should be assigned to the Pliocene. (7) The Pliocene/Pleistocene, i.e. the MN 18 / MQ 1 boundary is well characterized by the extinction or retreat of boreal elements, by a re-arrangement of the eastern steppe avifauna, including the local extinction of its last Miocene elements, and by the appearance of southern steppe avifauna. (8) The Pliocene, i.e. MN 14–18, is characterized by continuing immigration of elements of the boreal avifauna. The flow was interrupted in MQ 1a, and restarted in MQ 1b. (9) Early/middle Pleistocene, i.e. MQ 1/2 boundary is well characterized by the extinction of *Alectoris donnezani*, and by the appearance of various modern taxa with different zoogeographic relations.

– History of avian faunas: (1) Europe has never been in a “splendid isolation”. To the contrary, it has been a marginal region of Asia and Africa in the studied time-space. No avian faunas and supraspecific taxa are known to have developed here. The history of local avian faunas is largely the history of the expansion and retreat of other avifaunas. (2) Eastern steppe avifauna entered eastern Europe in MN 9. Main rearrangements took place at the MN 13/14 and MN 18 / MQ 1 boundaries. This avifauna was limited to the eastern and southeastern Europe in MN 9–13, reaching SW Europe in MN 14. (3) Boreal avifauna appeared in Europe in MN 14 and remained limited to the Central Europe and the Balkans through much of its further existence. It was continuously enriched by new coming taxa in the course of MN 14–18 and from the MQ 1b onwards, with a break in MQ 1a. The only, less significant rearrangement occurred at the MN 18 / MQ 1 boundary. (4) Southern steppe

avifauna appeared in Europe in MQ 1a. No rearrangements were recorded. (5) Avifauna of southern Palearctic mountains probably appeared in Europe in MN 18, almost or entirely left it in MQ 1a, and returned in MQ 1b, closely corresponding with the fluctuation of the boreal avifauna.

## INTRODUCTION

Late Cenozoic biostratigraphy of Europe has been based largely on mammals, with special respect to micromammals. After a long period of research on local biostratigraphic units and their sequences, a numbered scale of mammal zones was designed for the Neogene by MEIN (1976, see also FAHLBUSCH 1976, 1991, MEIN 1990, STEININGER et al. 1987, 1996, BRUIN et al. 1992, FEJFAR et al. 1990a, b, 1997, 1998, STEININGER 1999: MN zones). Subsequently, three different numbered systems were developed for the Quaternary by HORÁČEK (1981, HORÁČEK & LOŽEK 1988: Q zones), GUÉRIN (1982: MNQ zones) and FEJFAR & HEINRICH (1990b, FEJFAR et al. 1997, 1998: MQ zones). These systems laid a basis for the inter-regional ordination of the fossil record of other vertebrate groups. In this paper, the evolution of avian faunas in the late Cenozoic of Europe is described and compared with the mammal zones.

## MATERIAL

The data were extracted from the catalogue of the Cenozoic birds of Europe (MLÍKOVSKÝ 2001), with respect to the catalogue of the Pleistocene birds of Europe (TYRBERG 1998, 2001). For details on the localities see MLÍKOVSKÝ (1996, 2001) and TYRBERG (1998, 2001). Dubious records were not considered, even if they were listed by TYRBERG (1998, 2001) and/or MLÍKOVSKÝ (2001).

## VALIDITY OF THE AVIAN RECORD

The fossil record of birds has been generally considered too scanty for any use in biostratigraphy. However, large material has been accumulated during past decades. To this date, birds are known in Europe from ca. 100 late Miocene, 100 Pliocene, 70 early Pleistocene and 1200 middle and late Pleistocene localities (MLÍKOVSKÝ 1996, 2001, TYRBERG 1998, 2001), which allows in Europe for a comparison of the biostratigraphic zones based on mammals with the evolution of avian taxa and avian faunas (see Tab. 1 for a list of the most important avian localities).

In spite of this, the fossil record of birds is scanty in comparison with that of mammals. This limits its use as will be outlined below.

## Use of morphotypic gradients

Morphotypes and their gradients are frequently used in paleomammaliology as biostratigraphical characters. In birds, this character type is almost useless because of the scarcity of material. Nevertheless, STEWART (1999) showed that both European *Lagopus* spp. (*lagopus* and *mutus*) had relatively broader tarsometatarsi and humeri in the Pleistocene than today. Several other authors described morphological differences between local populations of some avian species (e. g. BOCHEŃSKI 1974, 1985, MOURER-CHAUVIRÉ 1975a, b, c)

This method is useful only for taxa which are found frequently and in large numbers. The record generally depends on taphonomic processes leading to the formation of taphocenoses. So far known, late Cenozoic taphocenoses of birds originated mainly as accumulations of prey remains of owls, while prey remains of raptors or mammalian predators and remains of naturally deceased individuals in lacustrine or cave deposits are much less frequent. The following avian taxa are particularly useful: Phasianidae (incl. Tetraoninae, but excl. *Coturnix*) as prey remains, and some Strigidae, Apodidae, Hirundinidae and Corvidae as taxa breeding in rock crevices and/or caves.

A specific problem consists in incorrectly identified remains. Outlying records (both in the geographic and stratigraphical sense) were usually published by authors known for being responsible for numerous identification errors. These records are listed in MLÍKOVSKÝ (2001), but they were not considered in the present paper.

### Changes of avian faunas

Several types of avian faunas (sensu MAYR 1965) can be recognized, which invaded Europe during the late Cenozoic from the east (eastern steppe avifauna, avifauna of south Palearctic mountains), from the northeast (boreal fauna), and from the south (southern steppe avifauna). Distributional changes of these avifaunal types are well documented by available material.

### Recognition of chronotaxa

An important difference between paleomammalogy and paleornithology is in the taxonomic interpretation of phyletic lines. Recognition of chronospecies is widespread in paleomammalogy, while it is of minor use in paleornithology. Theoretical arguments do not support recognition of chronospecies (e.g. GINGERICH 1985, MLÍKOVSKÝ et al. 1985, HAFFER 1995, MLÍKOVSKÝ 2001). This difference needs to be taken into account when speciation or extinction rates at given boundaries are compared between mammals and birds. For example, the phyletic line *Arvicola cantiana-terrestris* (e. g. HEINRICH 1990) would certainly be treated as a single species in paleornithology.

Similarly, genera appear to be understood (much) more narrowly in paleomammalogy than in paleornithology. For example, the *Mimomys savini* – group would be probably included in *Arvicola*, and *Pliopotamys* in *Ondatra* by paleornithological standards (cf. data in CHALINE 1990, CHALINE & SEVILLA 1990).

This brief (and subjective) comparison indicates that it is hardly possible to compare rates of extinction and/or strength of zone boundaries (expressed by the number and rank of appeared/disappeared taxa). If my observations on the different understanding of taxa in paleomammalogy and paleornithology are correct, then zone boundaries will be always more distinct using data on mammals (especially micromammals) than those on birds. Nevertheless, these differences will often reflect different taxonomic philosophies used in distinguishing fossil taxa, not necessarily different evolutionary rates of mammals and birds.

Tab. 1. List of most important avian localities of the late Cenozoic of Europe (abundant sites from the zones 2E and 2F are not listed). MQ<sup>1</sup> – zones proposed in the present paper; MQ<sup>2</sup> – after FEJFAR & HEINRICH (1990b); Q – after HORÁČEK (1981), MNQ – after GUÉRIN (1982). Not to time-scale. Hol. = Holocene

	MQ <sup>1</sup>	MQ <sup>2</sup>	Q	MNQ	British Islands	Iberian Peninsula	France	Central Europe	Italy	SE Europe	
Pleistocene	Hol.	2E	2	4	26						
	late	2D 2C				Pin Hole (partim)	Devil's Tower Gorham's Cave	Balauzière Gigny Hortus	Brillenhöhle Schusterlucke	Principe	Bačo Kiro Liko
						3 <sub>2-3</sub>	25	Bacon Hole	Pinilla del Valle	Fontechevade	Kálmán Lambrecht C. Schönfeld
	middle	2B					24	Aridos 1 Atapuerca	Carrière Fage Lazaret Suard Orgnac 3 (partim)	Hunas	Monte delle Gioie San Bernardino
23							Swanscombe	Lunel-Viel Castiglione 3 Orgnac 3 (partim)			
	2A		3 <sub>1</sub>	22	Westbury -sub-Mendip		Arago Cimay Montoussé 3 Saint-Estève -Janson	Hundsheim Tarkó Uppony 1 Vértesszöllös 2	Spinagallo	Čertkov 2 Petalona (partim)	

Tab. 1. continuation

	MQ <sup>1</sup>	MQ <sup>2</sup>	QMNQ	British Islands	Iberian Peninsula	France	Central Europe	Italy	SE Europe
Pleistocene early	1b	1	2	21	Boxgrove West Runton		Koněprusy C-718 Přezletice Stránská Skála Voigtstedt		
	19		Valerots Mas Rambault	Deutsch -Altenburg 4B Beremend 16	Betfia 2				
						18	17	17 <sub>3</sub>	18
Pliocene late	17		17 <sub>1,2</sub>	17		Saint-Vallier			
	16	16	16	16			Rębielice Królewskie Osztramos 7		Etulia
	15	15	15	15		Perpignan Sète	Weže Csarnóta 2		Muselievo Odesa – catacombs
	14	14		14					Vojničëvo
Miocene late	13	13		13			Polgárdi		Pikermi
	12	12		12		Aljezar B			
	11	11		11					Hrebenyky
	10	10		10			Kohfidisch		
	9	9		9			Rudabánya		Golbočica

Below I present comments on selected mammal zone boundaries from the paleornithological point of view. It should be reminded here, that avian record is almost absent from Europe north of ca. 55° N in the late Cenozoic. Hence, "Europe" is understood in this restricted sense throughout this paper.

#### Middle/late Miocene (MN 8/9) boundary

Many index taxa of early plus middle Miocene birds, mainly those related to water bodies (e.g. *Palaelodus*, *Mionetta*, *Miogallus* – MLÍKOVSKÝ 2001), did not survive this boundary. On the other hand, a fauna of steppe birds appeared Europe in MN 9 (some taxa perhaps in MN 10 because exact dating is not available for many relevant localities). The taxa include e. g. *Struthio*, *Grus*, *Amphipelargus*, *Alopochen* and *Pavo*. Geographically, these taxa were limited to the eastern and south-eastern Europe, i.e. to the areas which even today form the western margin of the central Asian steppe belt. There is no evidence that these taxa evolved in Europe, and it is highly probable that they belonged to the wave of a steppe fauna which invaded Europe from the east.

Palaeornithological data thus support the *Hipparion* datum, which is dated to the MN 9, and also the middle/late Miocene, i.e. the MN 8/9 boundary. However, the support is not universal geographically. While the disappearance of the early plus middle Miocene avian taxa was apparently Europe-wide, the newly coming taxa were limited to the eastern and south-eastern part of Europe. It is thus probable that the avian fauna markedly impoverished in western and central Europe at this boundary, while faunal turnover took place in eastern and south-eastern steppe regions of Europe.

#### Vallesian/Turolian (MN 10/11) boundary

There is no evidence that avian taxa became extinct in Europe or appeared for the first time in the region at this boundary. The geographic distribution of the avian steppe fauna, which appeared in eastern and southeastern Europe in MN 9, did not change.

#### Miocene/Pliocene (MN 13/14) boundary

Some taxa of steppe birds which occupied eastern and southeastern Europe since MN 9 became extinct here with the end of the Miocene. They include *Amphipelargus*, *Alopochen* and *Pavo archiaci*. On the other hand, new taxa of steppe birds were recorded for the first time in MN 14 (*Otis*, *Pavo bravardi*) and MN 15 (*Chlamydotis*, *Gryzaja*). In addition, *Pavo bravardi* expanded to the western Europe in MN 15, as the first member of the eastern steppe avifauna.

In MN 14, first representatives of boreal avifaunas appeared in Europe. They include *Tetrao* and *Bubo*. Taxa of boreal birds were limited to central Europe and the Balkans during the Pliocene. The only avian taxon, which is known to have died out at this boundary in central and western Europe is *Tyto sanctialbani*.

*Alectoris donmezani* also appeared for the first time in MN 14. This species of unclear geographic affinities was widespread in Europe in MN 14 – MQ 1.

Palaeornithological data thus support the current definition of the Miocene/Pliocene boundary. The main event was the appearance of first boreal taxa in central Europe and the Balkans.

#### The E-L-E datum (MN 14/15 boundary)

A few avian index taxa were recorded for the first time in MN 15. This applies both to eastern steppe elements (e. g. *Chlamydotis*, *Gryzaja*), and central European boreal elements (e. g. *Lagopus*). It is interesting to note that *Hirundo rustica* appeared in central Europe in MN 15 together (in the geographic sense) with other boreal elements. However, these data are uncertain, because MN 14 avifaunas are inadequately known, and subsequent research can show that some of the taxa known only from MN 15 onwards were present in Europe already in MN 14. Even if the data are accurate enough, they indicate nothing more than that both the turnover of eastern steppe avifauna, and the arrival of boreal elements to central Europe continued.

No paleornithological data are thus available in support of the *Elephas–Leptobos–Equus* datum.

#### Early/late Pliocene (MN 15/16) boundary

Two boreal owls (*Surnia* and *Aegolius*) were recorded for the first time in MN 16, which is in line with the continuing arrival of boreal bird taxa to Central Europe, started in MN 14.

There is no paleornithological support for the distinction between the early and late Pliocene.

#### Pliocene/Pleistocene (MN 17 / MQ 1) boundary

A narrow zone at the boundary of the Pliocene and Pleistocene has long been recognized as specific in the composition of mammal faunas, and variously termed MN 18 (Guérin 1982), Villanyian s. str. (see FEJFAR & HORÁČEK 1983) or MN 17<sub>3</sub> (HORÁČEK 1981, HORÁČEK & LOŽEK 1988). This zone was included either in the Pliocene or in the Pleistocene (see e. g. HORÁČEK & LOŽEK 1988: Tab. 1).

In this zone, several avian taxa of the boreal type (e. g. *Bucephala*, *Tetrao tetrix* and *Picoides* appeared in Europe, all in its central part, contemporaneously with birds of South Palearctic mountains (e. g. *Pyrrhocorax*). At the same time, last avian taxa of the east European steppe birds which entered Europe in MN 9 died out in the region (*Struthio*, *Pavo*).

Early Biharian (MQ 1a) is the first period after the beginning of the Pliocene (MN 14) in which no new taxa of boreal birds appeared in Europe. On the other hand, this period is characterized by the appearance of several steppe taxa with southern geographic affinities (e. g. *Perdix* and *Athene*). Unlike the eastern steppe birds, these taxa appeared simultaneously (in the terms of a single mammal zone) in western and central Europe. MQ 1a is characterized also by a limited number of records of boreal birds

These data support the inclusion of MN 18 in the Pliocene. This zone is the LAD for ancient avian taxa, while the appearance of new boreal taxa was a continuing process, started in MN 14.

### Early/late Biharian (MQ 1a/1b) boundary

No avian extinctions were recorded at this boundary, but new boreal birds started to appear again (*Bonasa*). Also *Apus* (with two species), which was absent from Europe in MN 14 – Q 1, appeared again. The latter genus included the modern *Apus melba*, which a characteristic element of southern Palearctic mountains, and *Apus apus*, which is probably a boreal element.

### Early/middle Pleistocene (MQ 1/2) boundary

The only bird species known to die out at the MQ 1/2 boundary is the formerly widespread and apparently abundant *Alectoris donnezani*. On the other hand, several new taxa of birds appeared in the early MQ 2, including mainly southern elements, such as *Alectoris graeca* s. l., *Gyps* and *Aegyptius*.

## EVOLUTION, DISTRIBUTION AND TURNOVER OF AVIAN FAUNAS

### Eastern steppe avifauna

This avian fauna reached Europe from the east in MN 9. It was limited to the eastern and southeastern Europe in MN 9–13. Some of its elements (e. g. *Pavo bravardi*) spread to southwestern Europe in MN 14. Main taxonomic rearrangements took part at the Miocene/Pliocene (MN 13/14) and Pliocene/Pleistocene (MN 18/MQ 1) boundaries. Last Mioce-

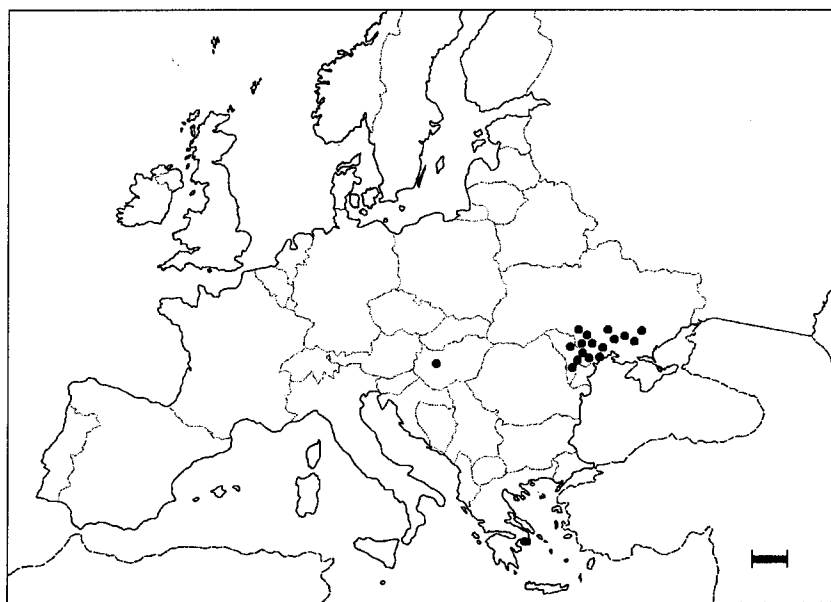


Fig. 1. Distribution of the 'eastern steppe avifauna' in the late Miocene (MN 9–13). See Mlíkovský (1996, 2001) for exact data.



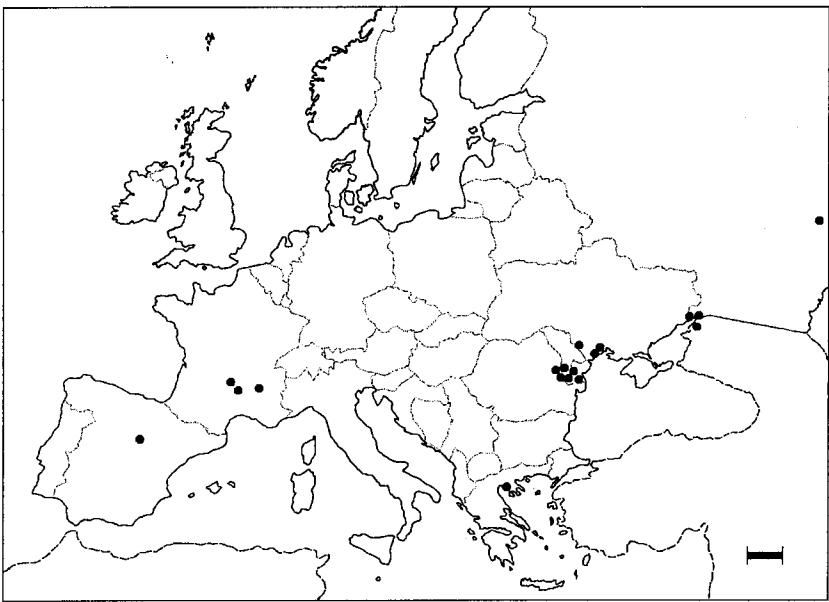


Fig. 2. Distribution of the 'eastern steppe avifauna' in the Pliocene (MN 14–18). See Mlíkovský (1996, 2001) for exact data.

ne representatives of this fauna disappeared from Europe in MN 18. Taking into account biogeographic patterns of the modern Eurasia, it is probable that the 'eastern steppe fauna' evolved in central Asian steppes, and that Europe was reached only by its western margin. The 'eastern steppe avifauna' was apparently member of the *Hipparion* fauna in the course of its arrival to Europe.

### Boreal avifauna

First elements of this avian fauna appeared in Europe in MN 14. The fauna was limited to central Europe and the Balkans until the latest Pliocene (MN 18), when it for the first spread further to the west, thought slightly, reaching only central France. The avian fauna of the boreal type became continuously richer in the course of the Pliocene (MN 14–18), as new taxa arrived from the northeast. This flow was interrupted in the early Biharian (MQ 1a) to restart in the late Biharian (MQ 1b). No genera and only very few species of boreal birds became extinct (all recorded prior to the MN 18 / Q 1 boundary), and no taxonomic rearrangements were detected.

After the continuing colonization of central Europe in MN 14–17, the 'boreal fauna' four times expanded its area to western Europe, once to southeastern Europe, and only once they almost retreated from central Europe. Spreads to the western Europe occurred in MN 18, MQ 2A, MQ 2D and at least once also in MQ 2B. The main retreat took place in MQ 1a. The only recorded spread towards the southeastern Europe occurred in MQ 2D.

Taking into account biogeographic patterns of the modern Eurasia, it is probable that the 'boreal avifauna' evolved in Siberia. The patterns observed in Europe probably reflect just pulsation of the main area of the 'boreal fauna' at its western margin. This pulsation probably follows the west-east axis in northern Europe (paleontological data are not available from this part of Europe), and the NE-SE axis in Central Europe.

### Southern steppe avifauna

In MQ 1a, when the 'boreal fauna' retreated, a fauna of steppe birds spread to Europe, probably from the south, because these bird taxa appeared simultaneously in western, central and eastern Europe. No rearrangement of the taxonomic composition of this fauna was detected, and no taxa are known to become extinct.

### Avifauna of South Palearctic mountains

South Palearctic mountains are occupied by a specific avifauna (BEME 1975, BANIN 1988). Its elements appeared in Europe for the first time in MN 18, probably disappeared in MQ 1a, and returned in MQ 1b to stay here to the present days. In this pattern this fauna resembles that of the boreal avifauna. No turnover could be detected in this type of avifauna; already the forms from MN 18 belonged to modern taxa, which still occupy south Palearctic mountains, incl. those in Europe.

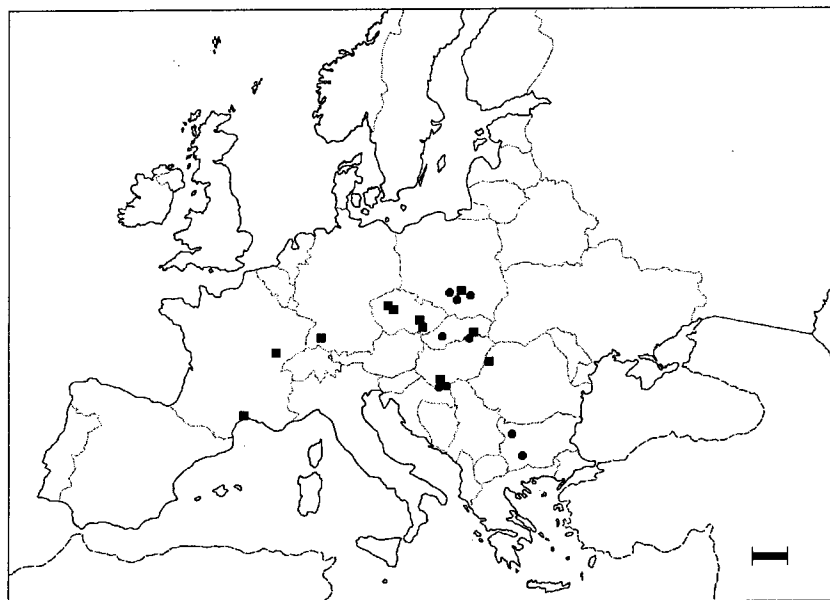


Fig. 3. Distribution of the 'boreal avifauna' in the Pliocene (MN 14–18, ?) and early Pleistocene (MQ 1). See MLÍKOVSKÝ (1996, 2001) and TYRBERG (1998, 2001) for exact data.

## Mourer-Chauviré's model

The only previous model of the evolution of the late Cenozoic avifauna of Europe was presented by MOURER-CHAUVIRÉ (1993) as yet. She concluded that tropical elements (called Tertiary relicts if recorded also from the Tertiary deposits) gradually disappeared (the last being recorded in MNQ 22), and that they were progressively replaced by 'cold avifaunas' (starting in MN 15).

Among the tropical elements she listed modern genera *Pavo*, *Gallus*, *Francolinus* and *Tadorna*, and extinct genera *Palaeocryptonyx* and *Pelargosteon*. Of these, *Gallus* has no reliable record from the Tertiary and early Pleistocene of Europe (MLÍKOVSKÝ 2001), all alleged European species of *Francolinus* and the monotypic *Palaeocryptonyx* belong to a single extinct species of the modern genus *Alectoris* (MLÍKOVSKÝ 2001). *Pelargosteon* was based on dubious material, which – until restudied – is of no taxonomic and paleogeographic value (MLÍKOVSKÝ 2001). The modern *Tadorna tadorna* (the only species of *Tadorna* mentioned by MOURER-CHAUVIRÉ 1993) is currently widely distributed in the western and south-central Palearctic, and certainly cannot be regarded as a Tertiary relict. *Pavo* survives today only in SE Asia, but the genus was member of the 'eastern steppe avifauna' in the late Miocene and early Pleistocene of Europe (see above). Hence, none of the taxa listed by MOURER-CHAUVIRÉ (1993) as a tropical element and/or a Tertiary relict can be interpreted in this sense.

MOURER-CHAUVIRÉ (1993) was right in observing that the 'cold avifaunas' appeared in Europe in the early Pliocene. However, the so-called 'cold' avifaunas are composed of two distinct zoogeographic types: boreal avifaunas and avifaunas of southern Palearctic mountains, which had different fate in Europe prior to MN 18 and which reacted to impoverished environmental conditions in different ways, retracting to the north (boreal avifaunas of Central Europe) or to the east (South Palearctic avifauna). In addition, MOURER-CHAUVIRÉ (1993) did not detect the considerable set-back of both the 'cold' avifaunas in MQ 1a.

In summary, MOURER-CHAUVIRÉ's (1993) model of the evolution of the late Cenozoic avifauna(s) of Europe is unrealistic for the following reasons: (1) it was based to a large degree on incorrectly identified, unrevised and dubious materials; (2) the two faunal types discerned (tropical and cold) did not correspond to real faunal types; and (3) geographic differences were not sufficiently taken into account (although MOURER-CHAUVIRÉ mentioned them).

## Effect of glacial ages

The concept of MN, MQ and Q zones is based on the assumption that it reflects basic rearrangements of the (mammal) fauna, abstracting – among other things – from climatically induced geographical changes. However, glacial ages started to be an important evolutionary and biogeographical agent from the Pliocene onwards. Understanding of glacial ages evolved from the uni-glacial ('one-Deluge') model (BUCKLAND 1823) over the four-glacial model (PENCK & BRÜCKNER 1901–1909) to the poly-glacial model (KUKLA 1975, 1977, 1978). However, glaciation is a geological phenomenon, which needs not to have an important effect on the evolution and/or geographic changes of flora and/or fauna. In

addition, it reflects only the general change in the climate, not considering other two temperature-related phenomena important for living organisms, i.e. circannual and circadian fluctuations of temperature.

The fossil record of birds indicates that the boreal avifauna (an indicator of cold climate – see also KOWALSKI 1995 for a mammalian parallel), which appeared in Central Europe for the first time in MN 14, subsequently spread at least four-times to other parts of Europe. Three of these short-time spells coincide with MN 18, MNQ 22 (= Q 3, = earliest MQ 2) and late Würm (Würm III), respectively. Uncertain is the situation in the period between MNQ 22 and MNQ 25 (see Tab. 1 for definition of these terms). Only a single glacial (Riss) was recognized in earlier literature (e. g. MOURER-CHAUVIRÉ 1975a, c), but KUKLA (1975, 1977, 1978) distinguished more cold spells in this time period. If more cold faunas appeared in Europe in the course of this period, they need not be distinguishable at the present state of knowledge (I. HORAČEK, pers. communication). The effects of these cold spells on the avifauna can be characterized as follows:

- (1) In MN 18, boreal avifauna was enriched by new taxa and somewhat enlarged its area, but other avian taxa were not affected adversely. Marked extinction of both boreal and eastern steppe avifaunas was caused by the onset of the subsequent 'interglacial' (MQ 1a).
- (2) In the early MQ 2 (= MQ 2A), boreal avifauna enlarged its area in Europe more markedly than in MN 18, but non-boreal elements appeared in Europe as well, some of them being clearly of southern origin. The extinction of Biharian (MQ 1) avian taxa occurred with the onset of this cold period.
- (3) In the spell(s) between MNQ 22 and MNQ 25, boreal avifauna spread far more over the Europe, but no avian taxa appeared or disappeared by its onset, during the period, or by the onset of the subsequent 'interglacial'.
- (4) During the subsequent major cold spell, identifiable with Würm III, boreal avifauna occupied much more of Europe than previously. This cold spell caused only shifts in the geographic distribution of continental birds (see e. g. TYRBERG 1991, 1995), but probably resulted in large-scale extinction of endemic taxa living on the Mediterranean islands (cf. ALCOVER et al. 1992, MLÍKOVSKÝ 2001). With the end of this glacial, the boreal avifauna retreated to the north, locally surviving in southern mountains (Pyreneans, Alps), but no avian taxa became extinct (contrary to mammals).

Hence, as judged from the fossil record of birds, each of the four cold periods had a different effect on the avifauna of Europe. Main avifaunal rearrangements, interpreted as biochronological zone boundaries, occurred *after* the cold period in MN 18, *before* the cold period in MQ 2a, and *no* were observable in the cold periods between MNQ 22 and MNQ 25, and in Würm III (on continents), although both the onset and end of the latter two cold period led to marked changes in the geographic distribution of avian taxa.

## Biozonation of the late Cenozoic of Europe

The record of fossil birds generally does support the biozonation of the late Cenozoic of Europe as developed by mammalogists (see above). However, the following modifications of the system are proposed (see Tab. 1 for a correlation chart):

- (1) Latest part of the Pliocene (MN 18 sensu GUÉRIN 1982, Q 17, sensu HORÁČEK 1981 and HORÁČEK & LOŽEK 1988) deserves status of a separate zone, but should be retained in the Pliocene. I support to denote this biozone MN 18, following GUÉRIN (1982).
- (2) The Biharian (MQ 1 sensu FEJFAR & HEINRICH 1990b, FEJFAR et al. 1997) can be divided in two parts, which correspond to the zones Q 1 and Q 2 sensu HORÁČEK (1981) and HORÁČEK & LOŽEK (1988). I suggest to denote these subzones as MQ 1a and MQ 1b, respectively.
- (3) The Toringian (MQ 2 sensu FEJFAR & HEINRICH 1990b, FEJFAR et al. 1997, 1998) can be divided according to biologically significant cold spells in five subzones. These subzones do not correspond with faunal rearrangements, reflecting only changes in the geographic distribution of individual taxa and whole faunas, and are thus of different meaning than older MQ and MN zones. Hence, I suggest to denote these subzones with upper-case letters. Of these, MQ 2A (= Q 3<sub>1</sub> sensu HORÁČEK 1981, HORÁČEK & LOŽEK 1988 = MNQ 22 sensu GUÉRIN 1982), and MQ 2D (= Würm III) correspond to cold periods, while MQ 2C and MQ 2E (= Holocene) correspond to temperate periods. The status of MQ 2B is uncertain in this respect (see above). Note that the early stages of the Würmian glaciation (in the classical sense) appear to have had no marked influence on European avifaunas. See Tab. 1 for the correlation of these biozones.

## SOUHRN

Biostratigrafické členění pozdního kenozoika Evropy podle nálezů savců bylo porovnáno s nálezů fosilních ptáků. Pozornost byla věnována třem základním otázkám: možnosti využití ptáků pro biostratigrafii, paleornitologickým definicím hlavních biostratigrafických období a historii avifaun. Hlavní výsledky jsou tyto:

– Využitelnost fosilních nálezů ptáků: (1) Paleornitologická data dosud nejsou pro detailní biostratigrafii dostačující. (2) Stratigrafický výskyt a změny v rozšíření je možné přesně určit jen základní typy avifaun a pro několik hojně se vyskytujících taxonů. (3) Stratigrafický výskyt ptáků je ve sledovaném časoprostoru výrazně diachronní.

– Paleornitologické definice biostartigrafických období: (1) Hranice mezi středním a mladším miocénem (MN 8/9) je dobře charakterizována jednak plošným vyměněním vodních a mokřadních ptáků, jednak tím, že se východní Evropě objevila stepní avifauna. (2) Hranice mezi valesií a turolienem (MN 10/11) není podle fosilních ptáků rozpoznatelná. (3) Hranice mezi miocénem a pliocénem (MN 13/14) je dobře charakterizována objevením se boreální avifauny, přeměnou východoevropské stepní avifauny a rozšířením se této avifauny do JZ Evropy. (4) Tzv. E-L-E datum (MN 14/15) paleornitologická data nepodporují. (5) Hranice mezi spodním a svrchním pliocénem (MN 15/16) paleornitologická data nepodporují. (6) Zóna MN 18 patří k pliocénu. (7) Hranice mezi pliocénem a pleistocénem (MN 18/ MQ 1) je dobře charakterizována vyměněním nebo geografickým ústupem boreální avifauny, přeměnou avifauny východních stepí, včetně vyměnění jejich posledních miocénních prvků, a objevením se avifauny jižních stepí. (8) Pliocén (MN 14–18) je charakterizovaný nepřetržitou imigrací prvků boreální avifauny. Imigrace byla přerušena v zóně MQ 1a a znovu započala v zóně MQ 1b. (9) Hranice mezi spodním a středním pleistocénem (MQ 1/2) je dobře charakterizována vyměněním orbice druhu *Alectoris donnezani* a objevením se různých moderních taxonů různého zoogeografického původu.

– Historie avifaun: (1) Evropa nikdy nebyla izolovanou oblastí. Ve studovaném časoprostoru byla naopak okrajovým územím Asie a Afriky. V Evropě se nevyvinuly žádné avifauny ani nadruhé taxony ptáků. Historie místních avifaun je do značné míry historií expanze a ústupu jiným avifaun.

(2) Avifauna východních stepí se v Evropě objevila v zóně MN 9. K jejím hlavním přeměnám došlo na rozhraních MN 13/14 a MN 18/ MQ 1. V období MN 9–13 byla tato avifauna omezená na východní a jihovýchodní Evropu; do jihozápadní Evropy se rozšířila až v zóně MN 14. (3) Boreální avifauna se v Evropě objevila v zóně MN 14 a její rozšíření bylo po většinu doby omezené na střední Evropu a Balkán. V průběhu zón MN 14–18 a od zóny MQ 1b dále byla tato avifauna stále obohacována dalšími taxony. Příusn byl přerušen v zóně MQ 1a. K jediné, málo výrazné přeměně došlo na rozhraní MN 18/ MQ 1. (4) Avifauna jižních stepí se v Evropě objevila v zóně MQ 1a. Její přeměny nebyly zaznamenány. (5) Avifauna hor jižní palearktidy se do Evropy pravděpodobně rozšířila v zóně MN 18, úplně nebo téměř úplně ji opustila v zóně MN 1a a znovu se vrátila v zóně MQ 1b. Touto fluktuací připomíná boreální avifaunu.

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