Herpetological assemblages from the Pliocene to middle Pleistocene in Central Europe: palaeoecological significance

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ABSTRACT

Fossil evidence of extant amphibian and reptile species is relatively well documented in the Pleistocene record. However, the early Pliocene records of extant species are much more scarce and their Miocene (or even the early Miocene) records are extremely rare. The late Pliocene Central European assemblages contain several extinct forms that survived from the late Miocene. The extinction event at the early/late Pliocene boundary (MN 15/MN 16) distinctively affected especially the southern part of Central Europe (the last occurrences of *Albanerpeton pannonicus*, *Mertensiella mera*, and *Latonia gigantea*). Several other taxa died out during MN 16 zone. This Pliocene extinction is a result of deterioration of climatic conditions with the process of aridization playing, most probably, the key role. Because numerous taxa became extinct long before the beginning of the Pleistocene during the MN 15 and MN 16 zones, the Pliocene/Pleistocene transition (*c.* 1.8 Ma) is not reflected in the evolution of Central European herpetological assemblages. Herpetological assemblages fundamentally changed during the terminal part of the early Biharian (early Pleistocene) when several Pliocene and early Biharian representatives became extinct. In the late Biharian herpetological assemblages no extant “Mediterranean” taxa have been reported from Central European localities situated north of Austria. “Mediterranean” amphibian and reptile species which receded to refugia in the Balkan Peninsula during the first late Biharian cold cycles were unable to recolonize the wide areas of Europe during the intensive but short warm climatic cycles.

KEY WORDS
Amphiba,
Reptilia,
palaeoecology,
climate,
Pliocene,
Pleistocene,
Central Europe.

RÉSUMÉ

Assemblages herpétologiques du Pliocène au Pléistocène moyen d'Europe Centrale : signification paléoécologique.

L'enregistrement fossile des espèces actuelles d'amphibiens et de reptiles est relativement complet au Pléistocène. Il est beaucoup plus lacunaire au Pliocène inférieur et les fossiles d'espèces actuelles sont extrêmement rares au Miocène (Miocène inférieur inclus). Les faunes du Pliocène supérieur d'Europe Centrale comportent plusieurs formes survivantes du Miocène supérieur. Les extinctions de la limite Pliocène inférieur/Pliocène supérieur (MN 15/MN 16) ont, en particulier, nettement affecté la partie méridionale de l'Europe Centrale (dernières occurrences d'*Albanerpeton pannonicus*, *Mertensiella mera* et *Latonia gigantea*). Plusieurs autres taxons ont disparu pendant MN 16. Ces extinctions du Pliocène résultent de la dégradation du climat, l'aridification ayant probablement joué un rôle clé. Puisque de nombreux taxons ont disparu pendant MN 15 et MN 16, longtemps avant le début du Pléistocène, la transition Pliocène/Pléistocène (vers environ 1,8 Ma) ne se manifeste pas dans l'évolution des faunes herpétologiques d'Europe Centrale. Le dernier changement fondamental ayant touché les herpétofaunes s'est produit pendant la partie terminale du Biharien inférieur (Pléistocène inférieur) avec la disparition de plusieurs taxons du Pliocène et du Biharien inférieur en Europe Centrale. Dans le Biharien supérieur, aucun taxon « méditerranéen » actuel n'a été observé en Europe Centrale au Nord de l'Autriche. Les espèces « méditerranéennes » d'amphibiens et reptiles qui s'étaient retirées dans des zones refuges de la péninsule des Balkans durant les premiers cycles froids du Biharien supérieur ont été incapables de recoloniser de larges zones d'Europe au cours des cycles chauds prononcés mais de courte durée qui ont suivi.

MOTS CLÉS
Amphibia,
Reptilia,
paléoécologie,
climat,
Pliocène,
Pléistocène,
Europe Centrale.

INTRODUCTION

The problem of the evolution of Central European herpetological assemblages in the Pliocene and the Pleistocene has not undergone closer scrutiny until now. Most of the research summing up the evolution of the Cenozoic herpetological assemblages in Europe document a drop in the diversity of European herpetofauna from the end of the Miocene climatic optimum, at the turn of the middle to late Badenian, middle Miocene (M. Böhme 2003), to the Pleistocene and Holocene, when the deterioration of the climate due to the Quaternary glacial cycles was of profound influence (see, e.g., Szyndlar 1991a, b; Rage & Roček 2003). During the period from the beginning of the Pliocene to the Pleistocene a clear dominance of recent species of amphibians and reptiles over the extinct representatives is often mentioned, whereby European herpetofauna of the end of the Pliocene is not essentially different from the Pleistocene herpetofauna in terms of the species composition (Szyndlar 1984, 1991a, b; Rage & Roček 2003). This statement remains valid assuming that we approach Europe as a single whole. The purpose of this study is to provide a closer view of the problem which leads to the finding that there are two periods of extinctions of Central European herpetofaunas, one period during the Pliocene (MN 15-MN 16) and second period during the early Pleistocene (early Biharian). Special attention was given to studies of longitudinal changes in composition of Central

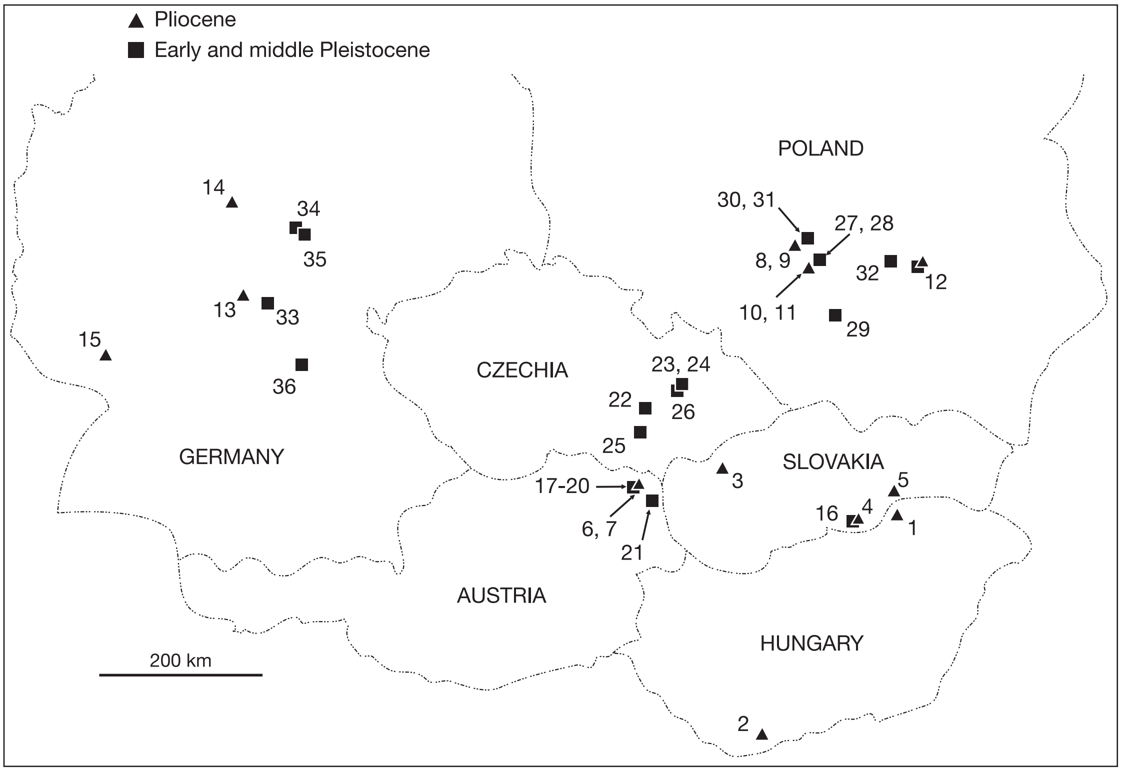

FIG. 1. — Important herpetological localities from the Pliocene to middle Pleistocene in Central Europe. **Pliocene.** *Hungary*: **1**, Osztramos 1C (early Pliocene, Ruscinian MN 14); **2**, Csarnóta 2 (early Pliocene, Ruscinian MN 15). *Slovakia*: **3**, Ivanovce (early Pliocene, Ruscinian MN 15); **4**, Hajnáčka (late Pliocene, Villanyian MN 16); **5**, Včeláre 6/1 (late Pliocene, Villanyian MN 17). *Austria*: **6**, **7**, Bad Deutsch-Altenburg 20 and 21 (late Pliocene, Villanyian MN 16). *Poland*: **8**, **9**, Węże 1 (early Pliocene, Ruscinian MN 15) and Węże 2 (late Pliocene, Villanyian MN 16); **10**, **11**, Rębielice Królewskie 1A and 2 (late Pliocene, Villanyian MN 16); **12**, Kadzielnia (late Pliocene, Villanyian MN 17 to early Pleistocene, early Biharian). *Germany*: **13**, Kaltensundheim (?early Pliocene, ?Ruscinian MN 15?); **14**, Willershausen (Pliocene, Ruscinian-Villanyian MN 14-MN 16); **15**, Gundersheim (late Pliocene, Villanyian MN 16). **Pleistocene.** *Slovakia*: **16**, Včeláre 6/2-9 (early Pleistocene, early Biharian). *Austria*: **17**-**20**, Bad Deutsch-Altenburg 2A, 2C1, 2C1Z, and 4B (early Pleistocene, early Biharian); **21**, St. Margarethen (middle Pleistocene, Holsteinian complex, Toringian). *Czechia*: **22**, Malá Dohoda-Quarry (early Pleistocene, early Biharian); **23**, Mladeč Caves-excavation II (early Pleistocene, early Biharian); **24**, Mladeč 2 (middle Pleistocene, Holsteinian complex, Toringian); **25**, Stránská skála Hill (middle Pleistocene, Cromerian complex, late Biharian); **26**, "Za Hájovnou" Cave (middle Pleistocene, ?Holsteinian complex). *Poland*: **27**, Kamyk (early Pleistocene, early Biharian); **28**, Kielniki 3A (early Pleistocene, early Biharian); **29**, Jaskinia Żabia (early Pleistocene, early Biharian); **30**, **31**, Zalesiaki 1A and Zalesiaki 1B (middle Pleistocene, late Biharian); **32**, Kozi Grzbiet (middle Pleistocene, late Biharian). *Germany*: **33**, Untermassfeld (early Pleistocene, early Biharian); **34**, Voigtstedt (middle Pleistocene, Cromerian complex, late Biharian); **35**, Kalbsrieth (early or middle Pleistocene, ?older than Voigtstedt); **36**, Breitenberghöhle bei Gössweinstein (middle Pleistocene, Holsteinian complex, Toringian). Data concerning stratigraphy are from Hodrová (1981, 1985), Mais & Rabeder (1984), Horáček & Ložek (1988), Nadachowski *et al.* (1989), Młynarski & Szyndlar (1989), Musil (1995), Ivanov (1996, 1997a, 2005, 2006), Sanchíz (1998), and G. Böhme (2000).

European herpetofaunas between the late early Pliocene (MN 15) and middle Pleistocene. To this aim, sites that provide rich and diversified, in terms of species, material have been selected (Fig. 1). A list of all the amphibian and reptile taxa discussed in the text can be found in Table 1.

Unpublished material examined by the author is held in the collections of the Anthropos Institute, Moravian Museum, Brno; Institute of Geology and Palaeontology, Charles University, Prague; and Department of Palaeontology, University of Vienna.

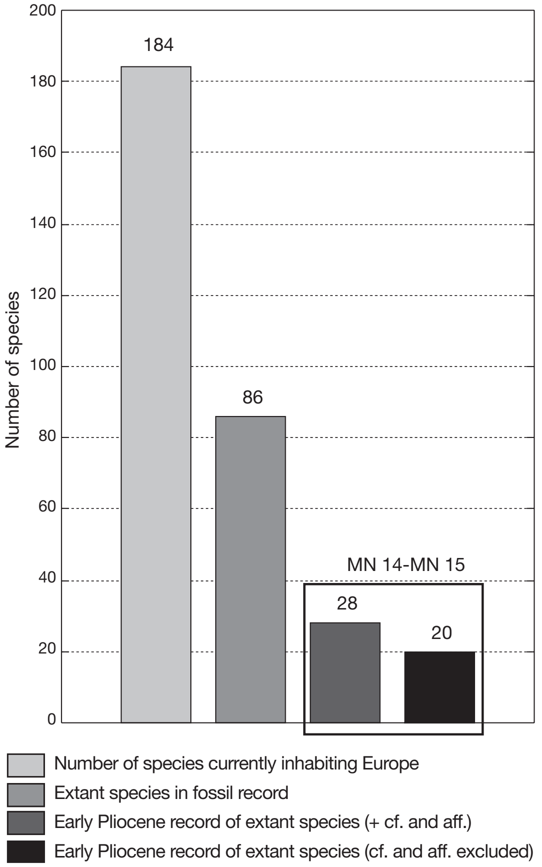

FIG. 2. — Total number of European amphibian and reptile species and its comparison with number of extant species reported from the fossil record. Comparison with the number of extant species reported from the early Pliocene (MN 14-MN 15).

GEOGRAPHIC DELIMITATION, LOCALITIES AND THEIR STRATIGRAPHY

In this contribution, the Central Europe (*s.l.*) consists of Germany, Poland, Czechia, Slovakia, Austria, and Hungary (Fig. 1). Germany is considered to be the western part of the Central Europe, Poland is considered to be the northern part of Central Europe, Czechia, Slovakia, Austria and Hungary are considered to be the southern part (or south-eastern part in case of Hungary) of the Central Europe. The northern and southern parts of Central Europe are separated by the mountain system at the northern border of the Czechia.

Herpetofaunas of several Central European localities have been studied (abbreviated names are parenthesized; for division of the Pliocene see Gradstein *et al.* 2004; European Mammal Units and Faunal Zones according to Steininger *et al.* 1996 and Agustí *et al.* 2001):

– Austria: Deutsch-Altenburg 20 and 21 (DA 20 and DA 21) (late Pliocene, Villanyian, MN 16), Deutsch-Altenburg 2A, 2C1, 2C1Z, and 4B (DA 2A, DA 2C1, DA 2C1Z, DA 4B) (early Pleistocene, early Biharian).
– Czechia: Malá Dohoda-Quarry (MD) (early Pleistocene, early Biharian), Mladeč Caves-excavation II (ML-II) (early Pleistocene, early Biharian), Mladeč 2 (middle Pleistocene, Toringian, Holsteinian complex), Stránská skála Hill (middle Pleistocene, late Biharian, Cromerian complex).
– Slovak Republic: Ivanovce (early Pliocene, Ruscinian, MN 15).
– Poland: Węże 1 (early Pliocene, Ruscinian, MN 15), Węże 2 (late Pliocene, Villanyian, MN 16), Rębielice Królewskie 1A and 2 (RK 1A, RK 2) (late Pliocene, Villanyian, MN 16), Jaskinia Żabia (JZ) (early Pleistocene, early Biharian), Kozi Grzbiet (KG) (middle Pleistocene, late Biharian).
– Germany: Kaltensundheim (early? Pliocene, MN 15?), Gundersheim (late Pliocene, Villanyian, MN 16) (Fig. 1).

Palaeoherpetological data from above mentioned localities come from Młynarski (1977), Sanchíz & Młynarski (1979), Hodrová (1981, 1982, 1984), Szyndlar (1981, 1984, 1991a, b), Mais & Rabeder (1984), Młynarski *et al.* (1984), Klembara (1986), Młynarski & Szyndlar (1989), Rauscher (1992), Roček (1994), Ivanov (1995, 1996, 1997a-c, 2006), Sanchíz (1998), G. Böhme (2002), and Rage & Roček (2003).

THE FOSSIL RECORD OF RECENT SPECIES

Today, there is a total of 184 amphibian and reptile species (some databases state 191 species) in Europe (Fig. 2) , including 61 species of amphibians and 123

TABLE 1. — List of European amphibian and reptile taxa which are discussed in the text. Systematic division into families and stratigraphic range according to Estes (1981, 1983), Sanchíz (1998), Roček (1994), M. Böhme (2003), Rage & Roček (2003), Ivanov (1997a), Holman (1998), Ratnikov (2002), and Venczel & Gardner (2005). **†**, extinct taxon; **?**, **cf.**, doubtful occurrence or uncertain determination; **Pa**, Paleocene; **E**, Eocene; **O**, Oligocene; **M**, Miocene; **P**, Pliocene; **Qp**, Pleistocene; **Qh**, Holocene; **R**, recent occurrence.

Taxon	**Stratigraphic range**
Albanerpeton pannonicus Venczel & Gardner, 2005	†, P
Mioproteus caucasicus Estes & Darevsky, 1977	†, M
Mioproteus wezei Młynarski, Szyndlar, Estes & Sanchíz, 1984	†, P, Qp
Chelotriton pliocenicus Bailon, 1989	†, P
Mertensiella mera Hodrová, 1984	†, M, P
Triturus marmoratus (Latreille, 1800)	M (cf.), P (cf.), Qp, R
Triturus cristatus (Laurenti, 1768)	?M, P, Qp, Qh, R
Triturus helveticus (Razoumowsky, 1789)	M, Qp (cf.), Qh, R
Parahynobius sp.	†, M (cf.), P (cf.), Qp
Latonia gigantea (Lartet, 1851)	†, M, P
Palaeobatrachus sp.	†, Pa, E, O, M, P
Pliobatrachus langhae Fejérváry, 1917	†, P, Qp
Eopelobates sp.	†, E, O, M, P (cf.)
Bufo bufo (Linnaeus, 1758)	P, Qp, Qh, R
Bufo viridis Laurenti, 1768	M, P, Qp, Qh, R
Rana strausi Špinar, 1980	†, P
Rana temporaria Linnaeus, 1758	?M, P, Qp, Qh, R
Rana arvalis Nilsson, 1842	P, Qp, Qh, R
Ranomorphus similis Ratnikov, 1993	†, P
Melanochelys mossoczyi (Młynarski, 1964)	†, P, Qp
Mauremys gaudryi (Depéret, 1885)	†, P
Testudo globosa Portis, 1890	†, P
Lacerta altenburgensis Rauscher, 1992	†, Qp
Zootoca vivipara (Jacquin, 1787)	Qp, Qh, R
Podarcis praemuralis Rauscher, 1992	†, Qp
Pseudopus pannonicus (Kormos, 1911)	†, M, P, Qp
Varanus marathonensis Weithofer, 1888	†, P
Palaeoblanus sp.	†, M, P
Michauxophis occitanus Bailon, 1988	†, P
Coluber hungaricus (Bolkay, 1913)	†, M, P
Coluber planicarinatus Bachmayer & Szyndlar, 1985	†, M
Coluber viridiflavus Lacépède, 1789	P, Qp, R
Coluber caspius Gmelin, 1789	P, Qp, R
Elaphe paralongissima Szyndlar, 1984	†, P, Qp
Elaphe praelongissima Venczel, 1994	†, M, P
Elaphe kormosi (Bolkay, 1913)	†, M, P
Elaphe longissima (Laurenti, 1768)	P, Qp, Qh, R
Elaphe quatuorlineata (Lacépède, 1789)	P, Qp, R
Elaphe situla (Linnaeus, 1758)	Qp (cf.), R
Coronella austriaca Laurenti, 1768	P, Qp, Qh, R
Malpolon mlynarskii Szyndlar, 1988	†, P
Natrix longivertebrata Szyndlar, 1984	†, M (cf.), P
Natrix tessellata (Laurenti, 1768)	P, Qp, Qh, R
Natrix natrix (Linnaeus, 1758)	P, Qp, Qh, R
Daboia maxima (Szyndlar, 1988)	†, P
Vipera natiensis Bailon, Garcia-Porta & Quintana-Cardona, 2002	†, P
Vipera ammodytes (Linnaeus, 1758)	P, Qp, Qh, R
Vipera berus (Linnaeus, 1758)	P, Qp, Qh, R

species of reptiles (Gasc *et al.* 1997). So far, 86 recent species have been documented in the fossil record (Estes 1981, 1983; Bailon 1991; Szyndlar 1991a, b; Rauscher 1992; Roček 1994; Sanchíz 1998; Holman 1998; Venczel 2001; Ratnikov 2002; Delfino 2002, 2004; Rage & Roček 2003), i.e. slightly less than 50% of the total amount of recent European species. While very good evidence from the fossil record of the whole Pleistocene period is available, the Pliocene record is much more scarce. During the early Pliocene (MN 14-MN 15), we find that only 28 recent species have been recorded in Europe in that period, including species reported even from Miocene sediments. They represent approximately one third of all the recent species known from the European fossil record. Twenty of the 28 reported species have distinct species identification (Fig. 2). In the period spanning from the very beginning of the Pliocene to the end of the early Pleistocene, a total of 21 extinct species of amphibians and squamate reptiles have been identified in Europe. Moreover, about 20 extinct species of tortoises (both marine and non-marine) are reported from Europe in this period (e.g., Delfino 2002; Redkozubov 2003; David *et al.* 2006). From what is stated above it follows that although a significant dominance of recent species over extinct representatives is assumed from the beginning of the Pliocene, the imperfect fossil record of recent species does not support this statement.

Our data of the fossil occurrence of recent species in the pre-Pliocene period is much more incomplete compared with the occurrences in the Pliocene and Pleistocene because difficulties in the determination of poorly preserved material often prevent an identification below the genus level and in addition the fossil record contains more extinct species. While the determination of recent genera in Europe is relatively common in material from the early Miocene, the fossil record of recent species from the same period is an exception. Recent species of amphibians and reptiles very rarely go back to the end of the early Miocene (MN 4). They mostly involve amphibians of uncertain species identification (Sanchíz 1998; Rage & Roček 2003; Ivanov *et al.* 2006; Ivanov unpublished): *Triturus* cf. *marmoratus* (Latreille, 1800), *Bufo* cf. *viridis* Laurenti, 1768.

The occurrence of the earliest representatives of recent species can undoubtedly be attributed to the Miocene climatic optimum, reaching its maximum during the Ottnangian and Karpatian (early Miocene, approximately correlated with late MN 3 to early MN 5) (temperature + humidity). The average annual temperatures in Central Europe then reached values around 20°C, the data accompanied by the palaeoherpetological record confirm that the average annual temperatures did not drop below 17.4°C (M. Böhme 2003). Although the high temperatures in Central Europe continued during the early and middle Badenian (middle Miocene, approximately correlated with MN 5 to early MN 7+8), after the early Badenian transgression the climate gradually became more arid. At the turn of the middle and late Badenian the temperature conditions dramatically changed as the average annual temperatures significantly decreased – at that time the temperature of the coldest winter month probably dropped by 11°C and it is that period that is thought to be at the origin of climatic zonation in Europe (M. Böhme 2003). In spite of what is stated above, the late Miocene temperatures in Central Europe remained at a markedly higher level compared to today's temperatures (the average annual temperature did not fall below 15°C; today it is only 7.3°C for the Czechia, see http://www.chmi.cz/), which, together with the progressing aridization, reaching its peak during the Pannonian (late Miocene, approximately correlated with late MN 7+8 to early MN 13), favored the evolution of numerous squamate reptiles (Bolkay 1913; Bachmayer & Szyndlar 1985, 1987; Venczel 1994, 1998), e.g., colubrid snakes of the genera *Elaphe* Fitzinger, 1833 or *Coluber* Linnaeus, 1758. The trend culminated in the latest Miocene (MN 13), when a number of new species (probably arrivals from Asia) appeared. They can be considered members of ancestral lineages directly leading to the recent species inhabiting Central (or Western) Europe. This was documented (Ivanov 1997a) by comparing the cranial skeleton of the extinct and recent specimens of the colubrid snakes of the genus *Elaphe*.

THE PROBLEM OF THE EXTINCT TAXA AND CENTRAL EUROPEAN EXTINCTIONS

The extinct Pliocene genera and species of amphibians and squamate reptiles are represented in Europe by the following taxa (Estes 1983; Szyndlar 1984,

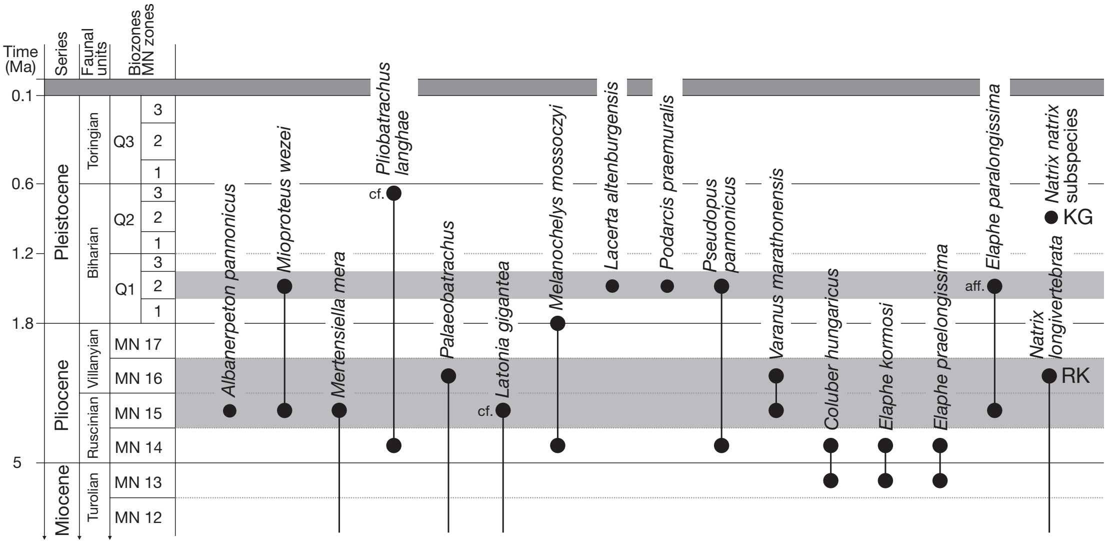

FIG. 3. — Pliocene and Pleistocene record of extinct amphibian and reptile species within the area of Central Europe. Grey strips represent two periods of extinction of Central European herpetofauna during the Pliocene and Pleistocene periods. Abbreviations: **KG**, Kozi Grzbiet; **RK**, Rębielice Królewskie 1A; **cf.**, **aff.**, uncertain determinations.

1988; Bailon 1988, 1991; Młynarski & Szyndlar 1989; Roček 1994; Sanchíz 1998; Venczel 1999, 2001; Bailon *et al.* 2002; Ratnikov 2002; Delfino 2002; Rage & Roček 2003; Venczel & Gardner 2005): *Mioproteus wezei* Młynarski, Szyndlar, Estes & Sanchíz, 1984, *Albanerpeton pannonicus* Venczel & Gardner, 2005, *Chelotriton pliocenicus* Bailon, 1989, cf. *Parahynobius* sp., *Mertensiella mera* Hodrová, 1984, *Latonia gigantea* (Lartet, 1851), *Eopelobates* sp., *Pliobatrachus* cf. *langhae* Fejérváry, 1917, *Rana strausi* Špinar, 1980, *Ranomorphus similis* Ratnikov, 1993, *Varanus marathonensis* Weithofer, 1888, *Pseudopus pannonicus* (Kormos, 1911), *Palaeoblanus* sp., *Michauxophis occitanus* Bailon, 1988, *Elaphe paralongissima* Szyndlar, 1984, *E. praelongissima* Venczel, 1994, *E. kormosi* (Bolkay, 1913), *Coluber hungaricus* (Bolkay, 1913), *C. planicarinatus* Bachmayer & Szyndlar, 1985, *Natrix longivertebrata* Szyndlar, 1984, *Malpolon mlynarskii* Szyndlar, 1988, *Vipera natiensis* Bailon, Garcia-Porta & Quintana-Cardona, 2002, and *Daboia maxima* (Szyndlar, 1988). As regards tortoises, nine extinct forms are mentioned by Redkozubov (2003) and David *et al.* (2006) in the early Pliocene (MN 14-MN 15) of Moldova, although lacking a detailed description and illustrations. Although more other extinct tortoises are reported from the European Pliocene, only two species are known from the Pliocene of Central Europe (Poland): *Melanochelys* (syn. *Geoemyda*) *mossoczyi* (Młynarski, 1964) and *Testudo globosa* Portis, 1890 (cf. Młynarski & Szyndlar 1989).

Figure 3 shows the occurrences of the species of amphibians and reptiles that died out in Central Europe from the early Pliocene to middle Pleistocene. The first period of extinction occurred during the late early (MN 15) and early late (MN 16) Pliocene. The early/late Pliocene (MN 15/MN 16) transition is of particular importance because of disappearance of several amphibian taxa in southern part of Central Europe. *Mertensiella mera* from the Slovak early Pliocene (MN 15) type locality of Ivanovce (Hodrová 1984), the fossil record of which was recently confirmed from the Czech early Miocene (MN 4) Mokrá-Western Quarry site (Ivanov *et al.* 2006), is, together with *Albanerpeton pannonicus* from Hungarian Csarnóta 2 site (MN 15) (Venczel & Gardner 2005), the only representative of caudate amphibians in Central Europe to become extinct during the Pliocene. The presence of hynobiid genus *Parahynobius* Venczel, 1999 from the Hungarian early Pliocene (MN 14) Osztramos 1C site is uncertain (Venczel 1999). The discoglossid frog of the genus *Latonia* Meyer, 1843 (*Latonia gigantea*) most probably also did not survive the early/late Pliocene (MN 15/MN 16) transition in Central Europe (cf. Rage & Roček 2003). Partial extinction of frogs probably occurred during the early late Pliocene with the last occurrence of *Palaeobatrachus* Tschudi, 1839 in MN 16. Given a striking morphological similarity one cannot rule out synonymization with *Pliobatrachus* Fejérváry, 1917, reported (*Pliobatrachus* cf. *langhae*) as late as the middle Pleistocene of Germany (G. Böhme 2000). The possibility of survival of *Eopelobates* Parker, 1929 into the Pliocene (the last appearance was reported from the Polish late Pliocene Rębielice Królewskie 1A site [Sanchíz & Młynarski 1979; Sanchíz 1998]) was recently challenged given the impossibility of distinguishing it from the genus *Pelobates* Wagler, 1830 on the basis of postcranial skeleton (Rage & Roček 2003). Since in the case of extinct frogs, they were undoubtedly thermophile representatives closely tied by ontogenetic evolution to water environment (at least in the larval period), their decrease could coincide with the increasing aridity of the climate in the second half of the Pliocene rather than the lowering of the average annual temperatures – for example, representatives of Palaeobatrachidae Cope, 1865 lived permanently in an aqueous environment (Špinar 1972). As regards squamate reptiles, the MN 16/MN 17 transition did not survive *Varanus marathonensis* and most probably also *Natrix longivertebrata*.

A second period of extinction of herpetofaunas in Central Europe can be noticed as late as during the early Pleistocene (early Biharian), when most of the now extinct species of amphibians and reptiles occurred for the last time well before the end of the early Biharian ($Q1_2$ *sensu* Horáček & Ložek [1988]). It concerns the following species: *Mioproteus wezei*, *Elaphe paralongissima*, *Pseudopus pannonicus*, *Lacerta altenburgensis* Rauscher, 1992, and *Podarcis praemuralis* Rauscher, 1992. A single representative of tortoises died out at the very end of the Pliocene: *Melanochelys* (syn. *Geoemyda*) *mossoczyi* from the latest Pliocene of Zalesiaki 1B, Poland (Młynarski & Szyndlar 1989). Only two of the extinct representatives of the herpetofauna known to us survived until the late Biharian: *Pliobatrachus* cf. *langhae* (possibly the genus *Palaeobatrachus* – see above; the last possible occurrence is known from the late Biharian, $Q2_3$ *sensu* Horáček & Ložek [1988]) and a presumed extinct subspecies of the grass-snake (Ivanov & W. Böhme unpublished).

As indicated by the above data, from the viewpoint of the stratigraphic distribution of extinct Central European taxa, the Pliocene/Pleistocene transition (about 1.8 Ma) does not constitute a critical period. Greater changes in the distribution of extinct taxa are noted at the transition between the middle and late Pliocene (MN 16/MN 17) and at the early/late Biharian (Q1/Q2) transition.

PLIOCENE AND PLEISTOCENE HERPETOLOGICAL ASSEMBLAGES IN CENTRAL EUROPE

A late Pliocene palynological record close to the MN 16/MN 17 transition (about 2.5 Ma) reveals a clear trend consisting in the decrease in the representation of Pliocene plants between the two zones by as much as about 30%. They included typical representatives such as *Sequoia*, *Taxodium*, *Sciadopitys*, *Tsuga*, *Carya*, *Pterocarya*, *Eucommia*, *Nyssa*, *Liquidambar*, *Aesculus*, which in the late Pliocene assemblages are represented by only about 5% (Zagwijn 1957; Lang 1994). This important floral boundary correlates well with the arrival of the Pretiglian (about 2.5 Ma by the Dutch chronostratigraphic scales), which is a period that many scientists see today as the beginning of the Pleistocene (e.g., Zagwijn 1985; Gibbard *et al.* 1991).

It is interesting to examine whether a similar trend can be expected in herpetological taxa as well. From Tables 2 and 3 it is obvious that the Pliocene assemblages contain a relatively high number of "Mediterranean" herpetological taxa and some "Mediterranean" representatives even decisively or at least significantly (i.e. by the number of determined bones) contribute to the total amount of all the material found (see below, Table 4). Here,

TABLE 2. — Occurrences of Pliocene and early Pleistocene (early Biharian) amphibian taxa in several Central European localities. Data according to Sanchíz & Młynarski (1979), Hodrová (1981, 1982, 1984), Mais & Rabeder (1984), Młynarski & Szyndlar (1989), Sanchíz (1998), and Rage & Roček (2003). ●, thermophilous "Mediterranean" taxa; ✚, "paramediterranean" taxa (distributed up to *c*. 50°N); ○, "boreal" taxa (northernmost occurrence at least 60°N); +, other taxa; **?**, uncertain occurrence; **w**, west European taxa.

Family	Taxon	Early Pliocene (MN 15)		Late Pliocene (MN 16)			Early Pleistocene (Early Biharian)			
		Ivanovce	Węże 1	Węże 2	RK 1A	RK 2	DA 2A	DA 2C1	DA 4B	JZ
Proteidae	*Mioproteus wezei* Mlynarski, Estes & Sanchiz, 1984			●	●					●
Salamandridae	*Salamandra salamandra* (Linnaeus, 1758)	+	+		+					
	Triturus cristatus (Laurenti, 1768)	○	○		○	○				
	Triturus vulgaris (Linnaeus, 1758)	○								
	Triturus alpestris (Laurenti, 1768)	+								
	Triturus helveticus (Razoumowsky, 1789)									
	Triturus montadoni (Boulenger, 1880)				+					
	Triturus marmoratus (Latreille, 1800)	? w ✚								
	Mertensiella mera Hodrová, 1984	●								
	Mertensiella caucasica (Waga, 1876)				? ●	? ●				
Discoglossidae	*Latonia gigantea* (Lartet, 1851)	? ●								
	Bombina bombina (Linnaeus, 1761)		? +		+					
	Bombina sp.	+								
Palaeobatrachidae	*Palaeobatrachus* sp.			●						
	Pliobatrachus langhae Fejérváry, 1917	? ●	? ●	? ●	? ●	? ●				
Pelobatidae	*Eopelobates* sp.	●	●		? ●					
	Pelobates fuscus (Laurenti, 1768)	? +	+	+	+			+	+	
	Pelobates syriacus Boettger, 1889				? ●					
	Pelobates sp.		+	+		+		+		
Pelodytidae	*Pelodytes* sp.							w✚		
Bufonidae	*Bufo bufo* (Linnaeus, 1758)	○	○	○	○	○		○		○
	Bufo viridis Laurenti, 1768				○		○	○	○	
	Bufo sp.									○
Hylidae	*Hyla arborea* (Linnaeus, 1758) [+ group *H. arborea*]	+			+	+				
Ranidae	*Rana temporaria* Linnaeus, 1758				? ○					
	Rana arvalis Nilsson, 1842		○		? ○				○	
	Rana sp. (group *R. ridibunda* Pallas, 1771)	+		+						
	Rana sp.	+	+	+	+	+			+	+

only the total number of bones from individual taxa including proportional representation is taken into consideration as the minimum number of bones of individual taxa usually cannot be established due to problems with the preservation of cranial bones (paired and unpaired elements).

HERPETOLOGICAL ASSEMBLAGES OF SELECTED PLIOCENE LOCALITIES IN CENTRAL EUROPE

From the study of numerous snakes (Ivanov 1997a, b) information was obtained about the Austrian localities of Bad Deutsch-Altenburg 20 (MN 16) and 21 (MN 16). Investigation of herpetofauna of other localities was more comprehensive and included both amphibians and reptiles:

– Slovakia: Ivanovce, MN 15 (Ivanov 1997a, b);

– Poland: Węże 1 (MN 15) and 2 (MN 16), Rębielice Królewskie 1A and 2, MN 16 (Estes 1981, 1983; Szyndlar 1984; Młynarski & Szyndlar 1989; Sanchíz 1998).

TABLE 3. — Occurrences of Pliocene and early Pleistocene (early Biharian) reptile taxa in several Central European localities. Data according to Młynarski & Szyndlar (1989), Szyndlar (1991a, b), Rauscher (1992), and Ivanov (1997a). ●, thermophilous "Mediterranean" ▶

Family	Taxon	Early Pliocene (MN 15)		Late Pliocene (MN 16)	
		Ivanovce	Węże 1	Węże 2	RK 1A
Geoemydidae	*Melanochelys mossoczyi* (Mlynarski, 1964)		●		
Emydidae	*Emys orbicularis* (Linnaeus, 1758)		+	+	
Testudinidae	*Testudo globosa* Portis, 1890		●		
	Testudo sp.		●		
Lacertidae	*Lacerta altenburgensis* Rauscher, 1992				
	Lacerta viridis Laurenti, 1768			? ✚	? ✚
	Lacerta oxycephala Duméril & Bibron, 1839				
	Lacerta agilis Linnaeus, 1758				
	Lacerta sp.		+	+	
	Zootoca vivipara (Jacquin, 1787)				
	Podarcis praemuralis Rauscher, 1992				
	Podarcis muralis (Laurenti, 1768)				? ✚
	Podarcis sicula (Rafinesque, 1810)		? ●		? ●
	Ophisops elegans Ménétriés, 1832				
Anguidae	*Pseudopus pannonicus* (Kormos, 1911)	●	●	●	●
	Pseudopus apodus (Pallas, 1775)	●			
	Anguis fragilis Linnaeus, 1758	○	○	○	○
Colubridae	*Coluber viridiflavus* Lacépède, 1789	w ✚	? w ✚		w ✚
	Coluber caspius Gmelin, 1789				
	Coluber gemonensis (Laurenti, 1768)				
	Coluber sp.				
	Elaphe paralongissima Szyndlar, 1984			●	
	Elaphe longissima (Laurenti, 1768)	✚			
	Elaphe quatuorlineata (Lacépède, 1789)	●			
	Elaphe situla (Linnaeus, 1758)				
	Coronella austriaca Laurenti, 1768	○			
	Coronella sp.				
	Natrix longivertebrata Szyndlar, 1984		? ●	●	●
	Natrix tessellata (Laurenti, 1768)				
	Natrix natrix (Linnaeus, 1758)				
	Natrix sp.	+			
Viperidae	*Vipera ammodytes* (Linnaeus, 1758)		? ●		●
	Vipera berus (Linnaeus, 1758)				
	Vipera sp.				

The localities Bad Deutsch-Altenburg 20 (DA 20) and 21 (DA 21) fall within the late Csarnotian, MN 16, as documented (Mais & Rabeder 1977; Rabeder 1981) by the occurrence of *Mimomys septimanus* Michaux, 1971 (DA 20) and *M. altenburgensis* Rabeder, 1981 (DA 21). The herpetological assemblage from these localities exhibits a significant amount of shared taxa, which can be considered distinctly thermophilous (Tables 2; 3; Fig. 4). As today they occur in the Balkan Peninsula (as far as south Greece) and, in the west as far as southern Italy (including Sicily), the taxa can be taxa; ✚, "paramediterranean" taxa (distributed up to *c.* 50°N); ○, "boreal" taxa (northernmost occurrence at least 60°N); ✛, other taxa; **?**, uncertain occurrence; **w**, west European taxa.

Late Pliocene (MN 16)			Early Pleistocene (early Biharian)						
RK 2	DA 20	DA 21	DA 2A	DA 2C1	DA 2C1Z	DA 4B	MD	ML-II	JZ
						●			
? ✚			✚	✚		✚			
						●			
				○		○			
			✛				✛	✛	✛
			○	○		○			
				●		●			
? ✚									
						●			
	●	●		●					●
			○			○		○	○
w ✚	w ✚	w ✚	w ✚	w ✚	w ✚	w ✚		w ✚	
			●	●	●	●	●	●	
		? ●	? ●	? ●	? ●				
							●		
			? ●					? ●	
	✚	✚	✚	✚	✚	✚	✚	✚	✚
	●		●	●	●	●	●	●	
			? ●	? ●	? ●	? ●		? ●	
	○		○	○			? ○	○	○
						? ✛	? ✛	? ✛	? ✛
●									
			✚	✚				✚	? ✚
			○	○	○	○	○	○	○
	✛		✛	✛	✛	✛	✛	✛	
●				●			●		
			○				○	○	○
	✛						✛		

referred to as ecologically "Mediterranean" (*sensu* Szyndlar 1984). *Coluber viridiflavus* Lacépède, 1789 (considered as belonging to the genus *Hierophis* by Schätti & Utiger [2001]), which is referred to as "paramediterranean" species (*sensu* Szyndlar 1984) with today's northernmost occurrence at 10°C MAT (mean annual temperature) isotherm (Bailon pers. comm. 2006) is also distinctively thermophilous, being abundant in Central Europe in the Pliocene and the warmest periods of the early Pleistocene. Therefore, it is here also freely attached to "Mediterranean" species. As all the extinct Pliocene and

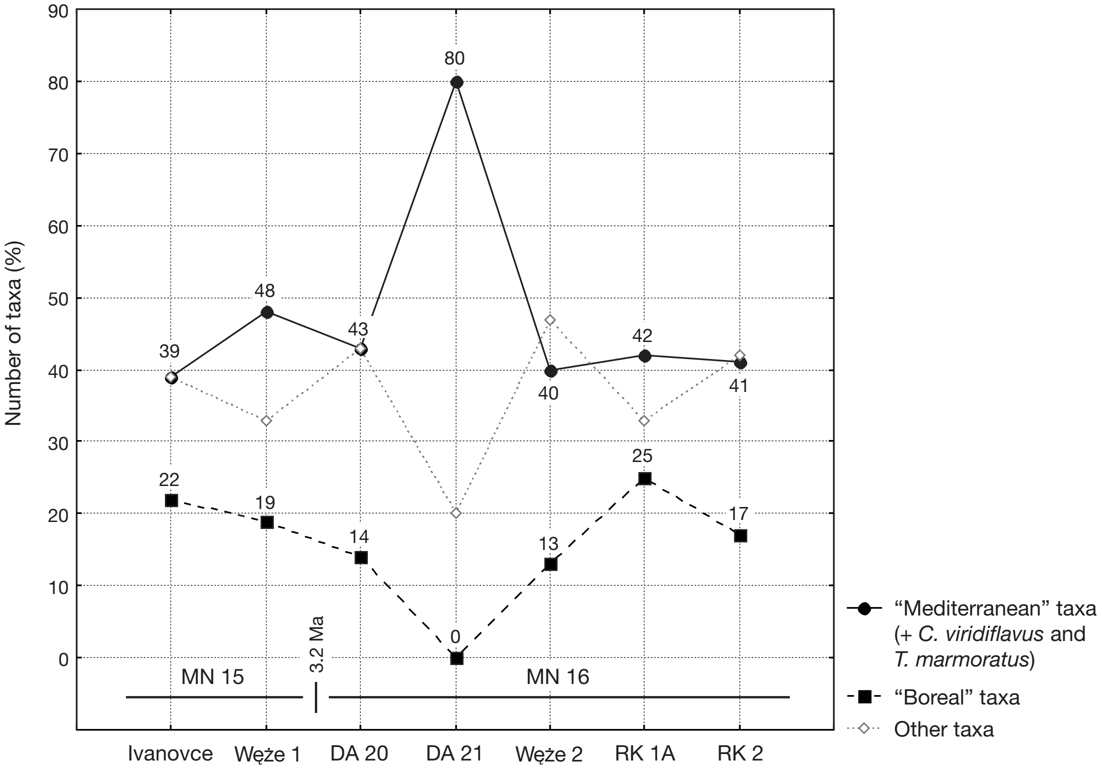

FIG. 4. — Comparision of number of "Mediterranean" and "boreal" amphibian and reptile taxa in several early (MN 15) and late (MN 16) Pliocene localities in Austria (DA 20 and DA 21), Slovakia (Ivanovce), and Poland (Wężė 1, Wężė 2, RK 1A, and RK 2). Data are from Hodrová (1981, 1984), Młynarski & Szyndlar (1989), Szyndlar (1991a, b), Rauscher (1992), and Ivanov (1997a). MN 15/MN 16 transition at 3.2 Ma according to Agustí *et al.* (2001).

Pleistocene representatives of herpetofauna from Central Europe known to us can be considered distinctly thermophilous, they can be freely assigned to ecologically "Mediterranean" taxa, although there may be no palaeontological evidence of their geographical occurrence from those areas.

Table 4 shows that the snake assemblage contains both a considerable share of distinctly thermophilous taxa and the total share of determined fossil material of "Mediterranean" taxa is very high. For example, *Coluber viridiflavus*, today inhabiting West and South-West Europe (but absent in the Iberian Peninsula) (Heimes 1993; Gasc *et al.* 1997), is represented by approximately 70% of the specimens at the DA 20 locality and by more than 80% of the specimens at the somewhat younger DA 21 locality. The high share of this distinctly thermophilous species (maximum activity at 28-30°C [Heimes 1993]) indicates high average temperatures, and, in general, the occurrence of the representatives of the genus *Coluber* is characteristic of the presence of arid biotopes. The high share of thermophilous taxa searching out dry, stone biotopes (alongside the genus *Coluber* a considerably lower number of representatives of *Elaphe quatuorlineata* (Lacépède, 1789) were identified as well) correlates well with the decrease of the humid biotopes with frequent reservoirs of water and the extinction of some representatives of caudates (albanerpetontid *Albanerpeton pannonicus* and salamandrid *Mertensiella mera*) and withdrawal of discoglossid frog *Latonia* (*Latonia gigantea*) to areas with a more favourable climate (Delfino 2002). The extinction of three amphibian species in southern part of Central Europe at the

TABLE 4. — Snake assemblage from the Pliocene localities in Slovakia (Ivanovce, MN 15) and Austria (Bad Deutsch-Altenburg 20 and 21, both MN 16). ●, "Mediterranean" taxa (+ *Coluber viridiflavus* [including uncertain determinations: cf., aff.]). The black field stresses the high percentage of material which belongs to *Coluber viridiflavus*. Modified from Ivanov (1997a).

		IVANOVCE-Pliocene		DA 20		DA 21	
		Number of bones	% of bones	Number of bones	% of bones	Number of bones	% of bones
COLUBRINAE	*Coluber caspius* ●					2	0.19
	Coluber viridiflavus ●	41	20.5	204	69.86	845	82.2
	Coluber aff. *viridiflavus* ●			21	7.19	179	17.41
	Coluber cf. *viridiflavus* ●			30	10.27		
	Coluber cf. *gemonensis* ●					1	0.1
	Coronella austriaca	1	0.5	1	0.34		
	Elaphe longissima	137	68.5	16	5.48	1	0.1
	Elaphe quatuorlineata ●	3	1.5	11	3.77		
NAT.	*Natrix* sp.	18	9	8	2.74		
VIP.	*Vipera* sp.			1	0.34		
	TOTAL	200	100	292	100	1028	100

early/late Pliocene transition (MN 15/MN 16) coincides well with an increased aridity in South-Eastern Europe during MN 16 where precipitation decreased almost twice, from about 1490-1660 mm/year in MN 15 to about 830-990 mm/year in MN 16 (Eronen & Rook 2004). Increased aridity together with drop in temperatures culminated in Central Europe in MN 17 (Eronen & Rook 2004; Mosbrugger *et al.* 2005), initialising MN 16/MN 17 extinction of herpetofauna both in southern (the last Central European varanids – *Varanus marathonensis*) and northern (*Palaeobatrachus*, *Natrix longivertebrata*) part of Central Europe.

As regards longitudinal distribution of "Mediterranean" vs. "boreal" taxa during late early (MN 15) and early late (MN 16) Pliocene, there is no distinct difference between southern and northern part of Central Europe (Fig. 4). For instance Rębielice Królewskie 1A, Poland (MN 16) consists of 42% of "Mediterranean" taxa (Tables 2; 3) including more than 12,000 vertebrae of *Coluber viridiflavus* being by far the most common representative of squamates at this site (Szyndlar 1984). This is probably similar to Austrian Bad Deutsch-Altenburg 20 or 21 (see above, Table 4) (although amphibians have not been studied in those sites). There also is no trend towards increasing the share of so-called "boreal" species in northern latitudes of Central Europe both in MN 15 (Ivanovce vs. Węże 1) and MN 16 (DA 20 and 21 vs. Węże 2, Rębielice Królewskie 1A and 2). The recent "boreal" species are characterised by the northernmost occurrences reaching at least up 60°N (cf. Szyndlar 1984; Tables 2; 3). They include also the species whose occurrence in

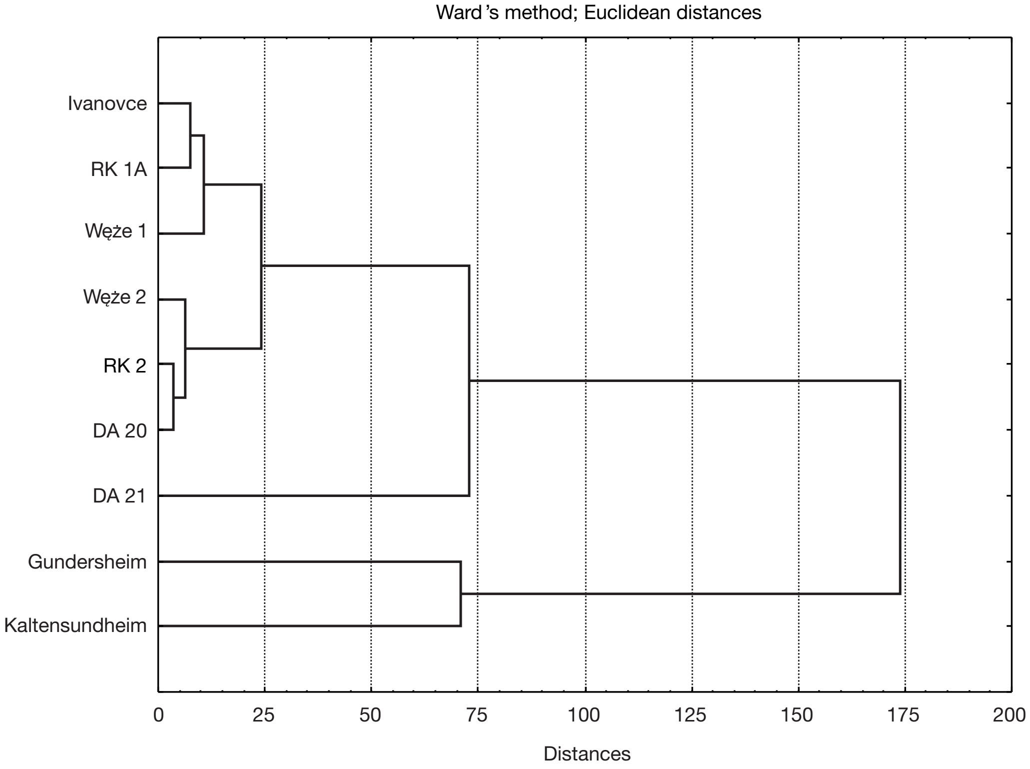

FIG. 5. — Result of cluster analysis which is based on the comparison of percentage representation of number of "Mediterranean" (+ *C. viridiflavus* and *T. marmoratus*), "boreal", and all other amphibian and reptile taxa in Central Europe. Several Pliocene localities are considered: Austria (DA 20, DA 21), Slovakia (Ivanovce), Poland (Węże 1, Węże 2, RK 1A, RK 2), and Germany (Gundersheim, Kaltensundheim). Data according to Hodrová (1981, 1984), Młynarski & Szyndlar (1989), Rauscher (1992), Ivanov (1997a), Sanchíz (1998), and G. Böhme (2002).

the Pleistocene of Central Europe is connected with a period of cold climatic cycles preceding the beginning of warm cycles as well as species occurring at the very end of the warm cycles and the beginning of the cold cycles. Within the framework of the model of the evolution of the Quaternary herpetological assemblages in Central Europe (focused especially on Germany) they are the species from stage I, II and VI (*sensu* G. Böhme 1996): *Rana temporaria* Linnaeus, 1758, *Rana arvalis* Nilsson, 1842, *Bufo bufo* (Linnaeus, 1758), *Bufo viridis* Laurenti, 1768, *Zootoca vivipara* (Jacquin, 1787), and *Vipera berus* (Linnaeus, 1758). All of the species, with the exception of *Bufo viridis* indicating the increasing aridity of the environment before the arrival of the cold cycle rather than the lowering of average temperatures (Baruš *et al.* 1992), are today typical for a wide geographical distribution including extensive areas of the Scandinavian Peninsula (Gasc *et al.* 1997).

Although no trend towards increasing the share of "boreal" species in northern latitudes of Central Europe can be detected, in general the total number of discovered bones which can be assigned to "Mediterranean" taxa is relatively high at all of the Pliocene localities in Austria, Slovakia, and Poland mentioned above.

It is certain that the proportion of "Mediterranean" taxa in Slovakia and Poland was greatly influenced by the presence of the Pannonian Lowland, along which herpetofauna migrated in the south-north direction far north under favourable climatic con-

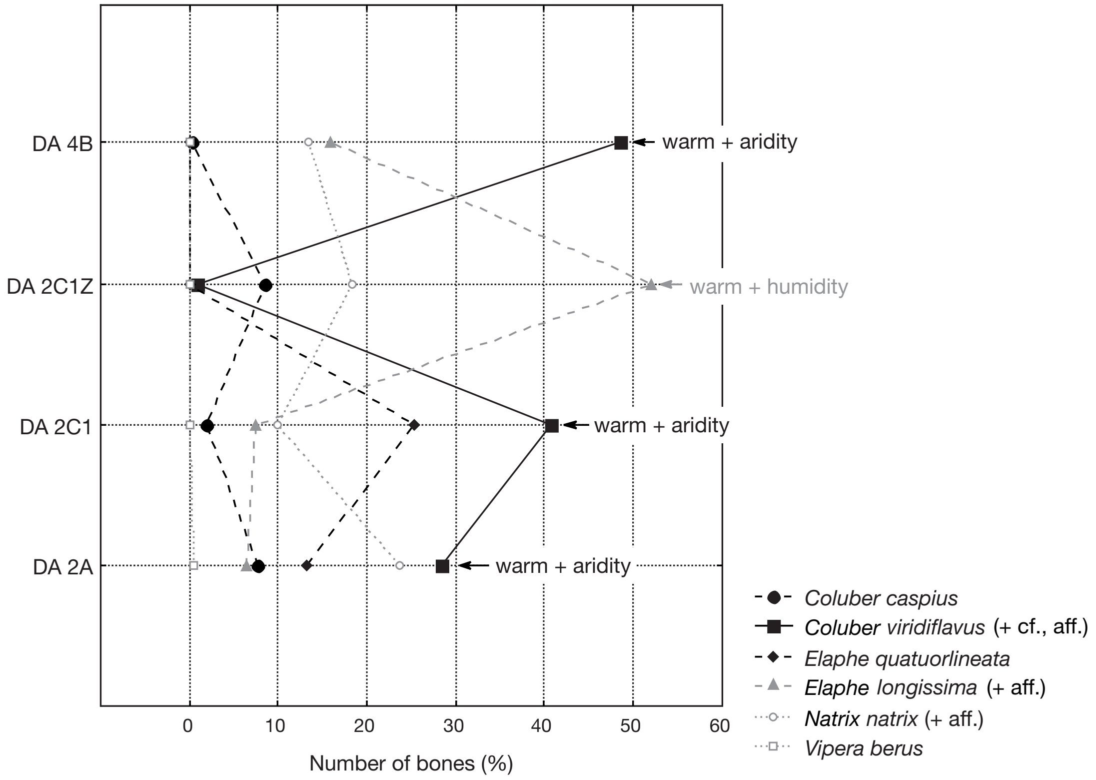

FIG. 6. — Compositions of snake faunas in several early Biharian sites in Bad Deutsch-Altenburg (DA) from the oldest locality (DA 2A) towards the youngest one (DA 4B). *Coluber viridiflavus* (+ cf., aff.): *C. viridiflavus* + *C.* cf. *viridiflavus* + *C.* aff. *viridiflavus*; *Elaphe longissima* (+ aff.): *E. longissima* + *E.* aff. *longissima*; *Natrix natrix* (+ aff.): *N. natrix* + *N.* aff. *natrix*. Data according to Ivanov (1997a).

ditions. The question remains to be asked why the "Mediterranean" (or Balkan) herpetological taxa are not known in the more western localities of Germany, although the presence of large specimens of *Bufo bufo* (the Kaltensundheim locality) might indicate Mediterranean climatic conditions (G. Böhme 2002). A cluster analysis carried out at some well-documented localities in Central Europe showed that as early as Pliocene the German area (absence of "Mediterranean" taxa) may have undergone a different evolution of herpetofauna than in the Czechia, Slovakia, Poland, and Austria (Fig. 5). The validity of the results of the analysis is partly limited by the fact that there are only a few Pliocene herpetological localities in Germany of which only two, Kaltensundheim (MN 15?; *Bufo bufo*, *Bufo* sp., *Rana temporaria*) and Gundersheim (MN 16; *Pelobates* cf. *fuscus* (Laurenti, 1768), *Bufo* cf. *bufo*, cf. *Rana* sp.) (Sanchíz 1998; G. Böhme 2002), could be included in the cluster analysis.

THE EVOLUTION OF HERPETOLOGICAL ASSEMBLAGES IN CENTRAL EUROPE IN THE EARLY AND MIDDLE PLEISTOCENE

In the Austrian early Pleistocene (early Biharian) localities of Bad Deutsch-Altenburg 2A, 2C1, 2C1Z and 4B (abbreviated as DA 2A, DA 2C1, DA 2C1Z and DA 4B) each site could be distinguished based on the climate. It has been found (Fig. 6) that the snake assemblages in the DA 2A, DA 2C1 and DA 4B localities correspond to a warm, dry environment, which is in line with the rich findings of

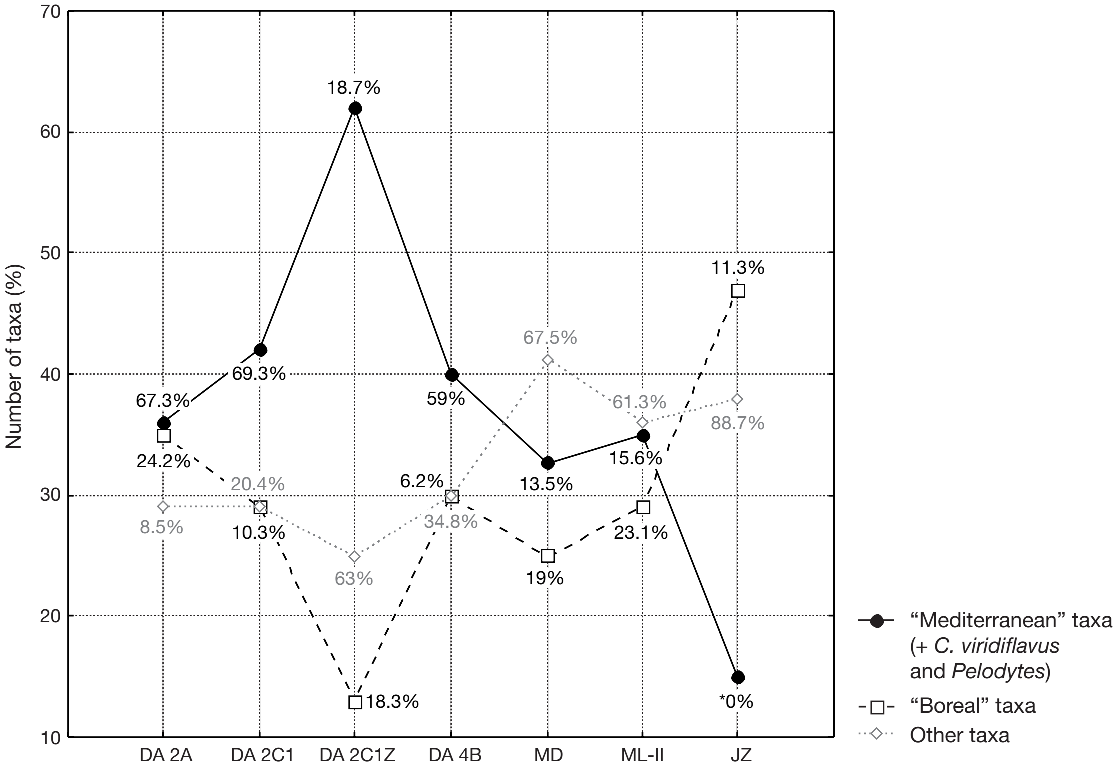

FIG. 7. — Percentages of "Mediterranean", "boreal", and all other amphibian and reptile taxa of early Pleistocene localities in Austria, Czechia, and Poland. The given numbers represent the total percentage representation of reported osteological material of squamate reptiles within the whole herpetological assemblage in each locality. *0% = value below 0.5%. Data according to Mais & Rabeder (1984), Rauscher (1992), and Ivanov (1996, 1997a, c).

the extant European species of the genus *Coluber* (*Hierophis* sensu Schätti & Utiger [2001]), and, to a lesser extent, *Elaphe quatuorlineata*. If we follow the representations of the most frequently occurring snake species within a virtual profile towards the top layer (DA 2A, DA 2C1, DA 2C1Z, DA 4B) we notice, alongside very hot arid phases within the early Biharian (*Coluber viridiflavus* distinctively outnumbers other taxa), a single phase at the DA 2C1Z locality, which shows somewhat colder but strikingly more humid conditions, as is indicated by an increased occurrence of *Elaphe longissima* (Laurenti, 1768) (*Zamenis longissimus* (Laurenti, 1768) *sensu* Utiger *et al.* [2002]) (Fig. 6). In general, the graph indicates that, within the area of today's Austria, herpetological assemblages still rich in "Mediterranean" amphibian and reptile taxa, and represented by great quantities of material (i.e. a high number of determined bones), appeared during the early Biharian. For example, the DA 2C1 locality has about the same number of "Mediterranean" taxa (42%) as the DA 4B locality (40%) and the "Mediterranean" taxa, at the same time, decisively contribute to the composition of the assemblage. Although, at the DA 2C1Z locality the number of "Mediterranean" taxa markedly prevails (62%), the overall number of determined bones of those representatives is low (about 19%) and they are decidedly outnumbered by *Elaphe longissima* (Fig. 7).

In the more northern localities of early Biharian age in Moravia, Malá Dohoda-Quarry and Mladeč-excavation II, the "Mediterranean" taxa are still diversified and represent more than one third of the whole herpetological assemblage under examination. Compared to the well documented Pliocene localities in Central Europe (Ivanovce, Węże 1 and 2, Rębielice Królewskie 1A and 2) and the early Biharian localities in Austria (Bad Deutsch-Altenburg 2A, 2C1, 2C1Z, and 4B), an important difference is a considerably lower quantitative representation of "Mediterranean" taxa in the early Biharian localities situated to the north of Austria (Fig. 7). It reaches as little as 13.5% at the Malá Dohoda-Quarry locality (Ivanov 1996, 1997a): *Vipera ammodytes* (Linnaeus, 1758), *Coluber caspius* Gmelin, 1789 (*Hierophis caspius* (Gmelin, 1789) *sensu* Schätti & Utiger [2001]), unspecified representatives of the genus *Coluber*, and *Elaphe quatuorlineata*. At the Mladeč-excavation II site (Ivanov 1997a) it is less than 16%: *Coluber caspius*, *C. viridiflavus*, *C.* aff. *viridiflavus*, *Elaphe* aff. *paralongissima*, *E. quatuorlineata*, and *E.* cf. *situla* (Linnaeus, 1758) (*Zamenis* cf. *situlus* (Linnaeus, 1758) *sensu* Utiger *et al.* [2002]). The early Biharian localities in Poland (Kadzielnia 1, Kamyk, Kielniki 3A, Jaskinia Żabia), situated farther north, already exhibit lower diversity of species, and virtually none of the identified species of amphibians and reptiles is either extinct or has an extralimital occurrence (Szyndlar 1984; Młynarski & Szyndlar 1989; Ivanov 1997c), with the exception of the extinct *Mioproteus wezei* (Caudata, Proteidae Gray, 1825) and *Pseudopus pannonicus* (Sauria, Anguidae Gray, 1825), reported from the Jaskinia Żabia site in Southern Poland (Młynarski & Szyndlar 1989). The total number of "Mediterranean" taxa found in the locality makes up only an insignificant part (Tables 2; 3). With regards to snakes, not a single distinctly thermophilous ("Mediterranean") taxon has been reported (Ivanov 1997c). The only probable thermophilous representative of amphibians is *Mioproteus wezei* considered (Roček 2005) to be possibly the extinct *Mioproteus caucasicus* Estes & Darevsky, 1977, which has its very last confirmed occurrence (Młynarski & Szyndlar 1989) in this locality (Fig. 3).

Profound changes in the evolution of herpetofauna in Central Europe took place at the early/late Biharian (Q1/Q2) transition, although they had probably been heralded during the end of the early Biharian, when most of the now extinct species of amphibians and reptiles disappeared. One of the possible causes of the extinction might have been the gradual decrease in the intensity and the duration of warm climatic fluctuations within the interglacial cycles (Fig. 8). The trend can be better observed during the late Biharian ($Q2_2$-$Q2_3$ *sensu* Horáček & Ložek [1988] in particular), when the warm fluctuations between OIS 23 and OIS 21 as well as between OIS 17 and OIS 15e are separated by considerably cold periods recorded throughout the world (Pillans 1991; Williams *et al.* 1993). Only the occurrence of the last element of the Pliocene herpetofauna *Pliobatrachus* (*Pliobatrachus* cf. *langhae*) is known from the late Biharian ($Q2_2$ *sensu* Horáček & Ložek [1988]) of Kozi Grzbiet, Poland (Młynarski & Szyndlar 1989) and the latest Biharian ($Q2_3$ *sensu* Horáček & Ložek [1988]) of Voigtstedt, Germany (G. Böhme 2000). The last occurrences of possible extinct subspecies of the grass-snake are also known from the Kozi Grzbiet site (Ivanov & W. Böhme unpublished). Since the beginning of the Toringian there is no evidence of the Pliocene herpetofauna in Central Europe.

The Cromerian herpetofauna at the Czech locality of Stránská Skála Hill ($Q2_2$ *sensu* Horáček & Ložek [1988]) originates from investigations carried out before 1945 (Němec 1972) and from the investigations in the 1960's (Musil 1965, 1995). They produced herpetofauna from two different complexes (talus cone no. III and IV) within layers 6-15e (Ivanov 1995, 1997a). The study of the herpetological assemblages made it possible to distinguish two climatic optima. The first one (talus cone no. III) is characterized by species that correspond more to a warm, slightly dry environment of woodland to woodland-steppe type in the vicinity of water streams (higher percentage of *Elaphe longissima*, presence of *Natrix tessellata* (Laurenti, 1768)). The second climatic optimum (talus cone no. IV) is marked by the presence of species that indicate a slight decrease in temperatures and increasing humidity of the environment (higher representation of *Natrix natrix* (Linnaeus, 1758), presence of *Natrix tessellata*). The results correlate well with the findings of malacofauna which also point to a warm, arid climate during the first of the

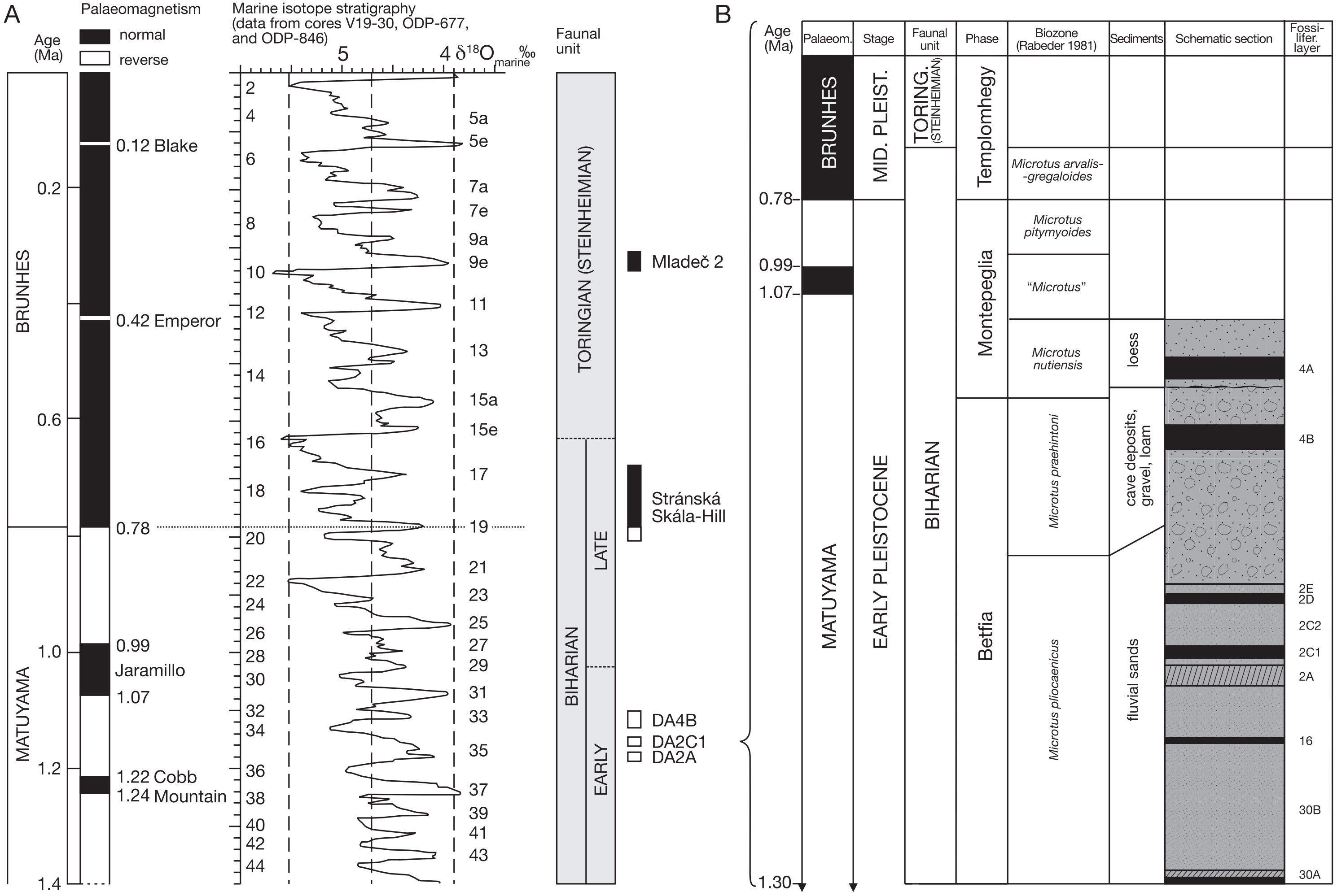

FIG. 8. — **A**, palaeomagnetism and Oxygen Isotope Stratigraphy (OIS) for the last 1.4 Ma and related stratigraphical position of several investigated palaeoherpetological sites: Mladeč 2, Stránská skála Hill, and Bad Deutsch-Altenburg 2A, 2C1, and 4B; **B**, stratigraphical position of Bad Deutsch-Altenburg sites. Mais & Rabeder (1984) established a separate Biozone between *Microtus nutiensis* Biozone and *Microtus pitymyoides* Biozone. A, modified from the "Global chronostratigraphical correlation table for the last 2.7 million years" (Gibbard *et al.* 2005); B, modified from Mais & Rabeder (1977, 1984), and Rabeder (1981).

two climatic optima – *Discus ruderatus* (Férussac, 1821). However, the presence of some taxa, such as *Truncatellina claustralis* Gredler, 1856, indicates prevailing forms of open steppe landscape (Kovanda 1995). None of the herpetological taxa identified so far at the Stránská Skála Hill has an extralimital occurrence. A new study of the herpetofauna of the Stránská Skála Hill – cave no. 4, which is now in its initial phase – might support the idea that in areas north of the Pannonian Lowland there were no representatives of recent "Mediterranean" herpetofauna from the beginning of the late Biharian onwards.

The newly studied herpetological material from the talus cone of the middle Pleistocene (Holsteinian complex – contains oxygen isotope stages [OIS] 11, 10, and 9) locality of Mladeč 2 (Q3$_2$ *sensu* Horáček & Ložek [1988]) most probably falls within the period of PK V corresponding to the short but very warm OIS 9 (Horáček & Ložek 1988). The following taxa have been determined (Ivanov 2006): *Triturus* cf. *helveticus* (Razumowsky, 1789), *T. cristatus*, *Bufo bufo*, *Rana temporaria*, *Elaphe longissima*, *E.* cf. *longissima*, *Elaphe* sp., *Coronella austriaca* Laurenti, 1768, *Natrix natrix*, *N. tessellata*, *N.* cf. *tessellata*, *Natrix* sp., and *Vipera berus*.

The study of gastropods from the locality (Horáček & Ložek 1988) shown the presence of several species inhabiting South-western Europe today: *Azeca goodalli* (Férussac, 1821), *Zonitoides sepultus* Ložek, 1964, *Acicula diluviana* Hocker, 1907, *Fusulus interruptus* (Pfeiffer, 1828), *Cepea nemoralis* (Linnaeus, 1758). Nevertheless, a herpetological study failed to prove the presence of "Mediterranean" taxa at the Mladeč 2 locality. This significantly distinguishes the latter assemblage from the assemblage determined in underlaying excavation II in the "Dóm mrtvých", obtained by investigation at the end of the 1950's (Jelínek 1959), where a number of "Mediterranean" representatives were confirmed (Table 3) (Ivanov 1997a, b).

The herpetological assemblage from the Mladeč 2 locality (Ivanov 2006) generally indicates a woodland-steppe environment in the vicinity of marsh biotopes and actively flowing water streams with temperatures higher than those of the area today. In all of the fossiliferous layers (Fig. 9) the highest representation is that of the genus *Natrix* Laurenti, 1768. The greatest amount of material comes from layer no. 4 and its surroundings. This layer very likely corresponds to the period of the climatic optimum, an evidence of which is the high representation of *Elaphe longissima*. Even higher representation of this species in the lower part of the profile should be treated with some reservation as the sample does not contain a statistically valid amount of material. More representative samples from the surroundings of layer 2 and from the upper part of the profile suggest a drop in the relative representation of thermophilous *Elaphe longissima* and, above all, a higher amount of a climatically undemanding eurytopic species *Natrix natrix*, represented within the whole assemblage by approximately 60%. This fact points to a trend of increasing percentage of elements from an open landscape. Arid biotypes (presence of *Vipera berus*) appear alongside humid ones (*Bufo bufo*, *Rana temporaria*, *Natrix natrix*). The upper part of the profile indicates a reduced biodiversity but thermophilous taxa (*Elaphe longissima*, *Natrix tessellata*, *Natrix* cf. *tessellata*) are present and *Natrix natrix* predominates, which most probably hints at the end of the climatic optimum.

In Central Europe (north of the Pannonian Lowland), the absence of recent "Mediterranean" taxa of herpetofauna from the beginning of the late Biharian has already been confirmed by the study of the Stránská Skála Hill (late Biharian) and recently Mladeč 2 (Toringian) sites (Ivanov 1997a, 2006). Although "Mediterranean" herpetological taxa have not been confirmed in numerous other localities in Central Europe, more detailed studies of well stratified middle Pleistocene localities will be needed in the future.

CONCLUSIONS

Although we generally assume that most of the recent amphibian and reptile species existed as early as the beginning of the early Pliocene, the statement cannot be confirmed on the basis of available fossil record. The increasing aridity at the end of the Miocene contributed to the origin of a number of taxa (mainly squamate reptiles) which

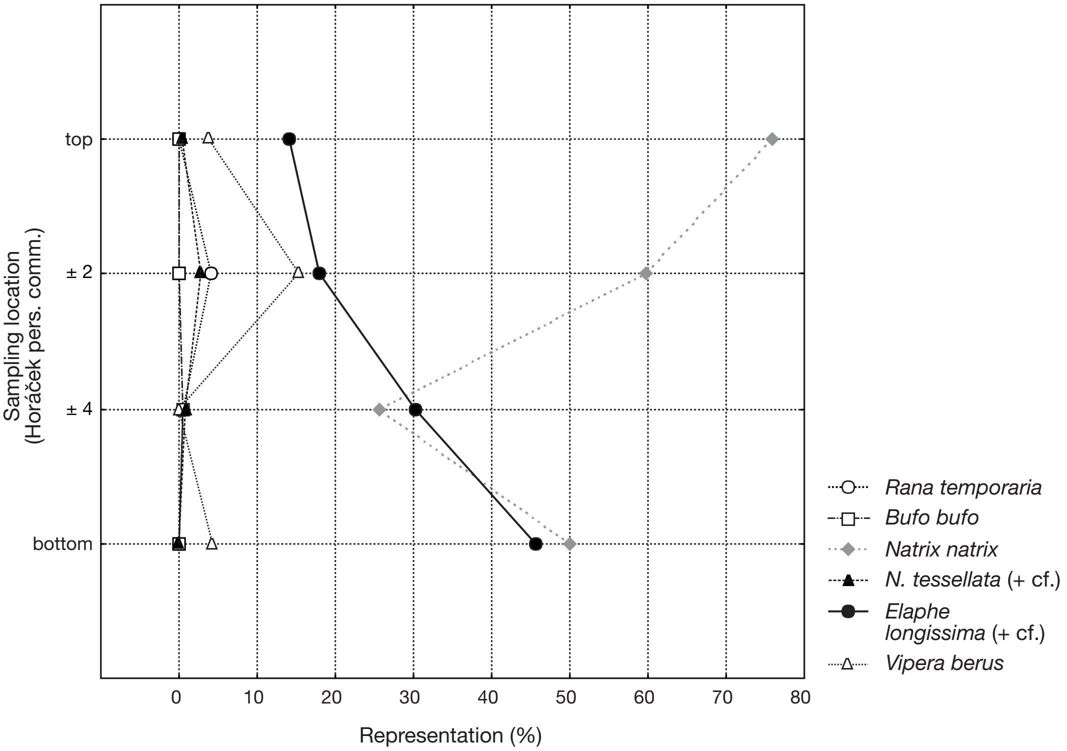

FIG. 9. — Percentages of thermophilous (black coloured symbols) and "boreal" (unfilled symbols) amphibian and reptile species in each layer of the Mladeč 2 site. *Natrix tessellata* (+ cf.): *N. tessellata* + *N.* cf. *tessellata*; *Elaphe longissima* (+ cf.): *E. longissima* + *E.* cf. *longissima*. Explanations: top/bottom, sample from the top/bottom of the talus cone; ± 2 (or ± 4), sample from the layer 2 (or 4) and its surroundings. Modified from Ivanov (2006).

are thought to be members of ancestral lineages of some recent species. Thus, the latest Miocene and the early Pliocene represent probably the last important period in terms of the evolution of the Central European herpetofauna. Several of the late Miocene forms were still surviving during the early late Pliocene.

There is no distinct longitudinal distribution of "Mediterranean" vs. "boreal" taxa between southern (Austria, Hungary, Czechia, Slovakia) and northern (Poland) part of Central Europe during late early (MN 15) and early late (MN 16) Pliocene. The herpetological assemblages in western part of Central Europe (Germany) were probably different from the remaining areas of Central Europe (Poland, Czechia, Slovakia, Austria, Hungary) as early as the Pliocene. The difference is based on the absence of "Mediterranean" taxa in Germany in the period from the Pliocene to the end of the early Biharian, while in the other studied areas of Central Europe the presence of "Mediterranean" herpetological taxa was usually quite common.

The existing Pliocene/Pleistocene boundary (approximately 1.8 Ma) is not reflected in the evolution of the herpetological assemblages of Central Europe and many herpetological taxa died out before the beginning of the Pleistocene during MN 15 and MN 16. The extinction in the late early and early late Pliocene (MN 15 and MN 16) is a result of the worsening of climatic conditions, where increasing aridity was an important factor.

A profound change in the evolution of the herpetological assemblages also took place in the early Biharian (Q1) when three representatives of herpetofauna known as early as the early Pliocene became extinct (*Mioproteus wezei*, *Pseudopus pannonicus*, and *Elaphe paralongissima*) in Central Europe together with two lizard forms (*Lacerta altenburgensis* and *Podarcis praemuralis*) known only from the type early Biharian Bad Deutsch-Altenburg site. The early Biharian extinction at the $Q1_2/Q1_3$ transition is probably connected with the gradual decrease in the average annual temperatures during the cold cycles.

No recent "Mediterranean" amphibian or reptile species in Central Europe, north of Austria and Hungary is known from the late Biharian. The absence of "Mediterranean" herpetofauna is probably connected to the change in the duration of glacial cycles from 40 ka, still during the early Biharian, to 100 ka in the second half of the late Biharian (i.e. roughly from the beginning of the middle Pleistocene). A very important role was probably played by the increasing asymmetry of the glacial-interglacial oscillations, when long glacial intervals alternated with short, quick intervals of deglaciation (Ashkenazy & Tziperman 2004). During the late Biharian the cold climatic changes were characterised by a marked decrease in average annual temperatures (e.g., OIS 22, OIS 16, OIS 10). "Mediterranean" herpetofaunas which receded to refugia in the Balkan Peninsula during the initial cold cycles of the late Biharian, failed to re-colonize extensive areas of Central Europe during the following intensive, but relatively short, warm climatic fluctuations. The herpetological assemblage of Mladeč 2 is a typical example of this. This interglacial assemblage of the last warm phase of the Holsteinian complex does not include representatives of "Mediterranean" herpetofauna in spite of the high average annual temperatures. In this context the presence of west-European "Mediterranean" taxa of malacofauna at Mladeč 2 is interesting.

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