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Distribution of *Rana arvalis* in Europe: a historical perspective

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Verbreitung von *Rana arvalis* in Europa: eine historische Betrachtung

Rana arvalis ist einer der sogenannten Braunfrösche, dessen derzeitiges Verbreitungsgebiet von Europa bis Ostsibirien reicht, womit die Art offenkundig eine große ökologische Plastizität zeigt. Überraschend ist deshalb, dass sie in Westeuropa (Britische Inseln, nahezu ganz Frankreich, Norditalien) fehlt, während sie große Teile Skandinaviens besiedelt. Der früheste Fossilnachweis für die Art stammt aus dem Pliozän Mitteleuropas, aber es liegen keine Nachweise aus vor-pleistozänen Ablagerungen Osteuropas und Asiens vor. Dies legt einen autochthonen Ursprung der Art in Europa nahe. Ihre gegenwärtige Verbreitung bildete sich aller Wahrscheinlichkeit nach während des Rückzuges des Kontinentaleises (der zu einem temporären System von Süßwasserseen in der baltischen Region führte) im späten Pleistozän heraus, durch klimatische Ereignisse während des Holozäns und durch anthropogene Einflüsse seit dem Mittelalter (z. B. könnte das gegenwärtige Fehlen im südlichen und westlichen Europa durch ausgedehnte Entwaldungen erklärt werden).

Schlüsselbegriffe: Amphibia, Anura, Ranidae, *Rana arvalis*, Verbreitung, historische Betrachtung, Europa.

Abstract

Rana arvalis is one of the so called brown frogs whose recent area of distribution extends from Europe to east Siberia, thus seemingly exhibiting wide ecological plasticity. It is therefore surprising that it is absent from western Europe (British Isles, France, northern Italy), whereas it inhabits large areas of Scandinavia. The earliest fossil record of this species is from the Pliocene of central Europe but it was not recovered from the pre-Pleistocene deposits of east Europe and Asia. This may suggest autochthonous origin of the species in Europe. Its present-day distribution was most probably shaped by the late Pleistocene withdrawal of the continental glacier (resulting in temporary system of fresh-water lakes in Baltic region), by the Holocene climatological events, and by anthropogenic influences in the middle ages (e. g. its present-day absence in southern and western Europe might be explained by extensive deforestation in these areas).

Key words: Amphibia, Anura, Ranidae, *Rana arvalis*, distribution, historical perspective, Europe.

Introduction

At present, the area of distribution of *Rana arvalis* extends from northeastern France and northern Belgium in the west, and as far as the southern Ural, northern Kazakhstan, the Altai, and the Lena river in the east (124° E and 60° N in Yakutija). Similarly broad is its south-to-north distribution, extending from the Pannonian lowlands and corresponding latitudes in Europe and northern Kazakhstan in Asia to northern parts of both continents (up to 69° in Finland), avoiding the Alps and higher altitudes of Carpathians and Scandinavia (for more detailed account see e. g. ISHCHENKO 1978, 1997, BABIK et al. 2004, GLANDT 2006).

Rana arvalis is referred as a typical lowland species, reaching the maximum altitude between 800 and 900 m in the western part of its area of distribution (whereas nearly 2 000 m in the Altai). It may be found in the forest zone (inhabiting leaf-bearing, mixed and pine forests), as well as forest-steppe and steppe zones, and even in semi-deserts, thus seemingly exhibiting wide ecological plasticity (ISHCHENKO 1978). However, its distribution is strictly limited by using standing water bodies with litoral vegetation. It is rather puzzeling that although it is sympatric with *Rana temporaria* over most of its range, it is absent from western Europe (e. g. British Isles, France, northern Italy), where the latter species is widely distributed. Here we present an attempt to explain the present distribution of *Rana arvalis* and related species in a historical perspective, using palaeontological data as well as data from molecular biology.

Rana arvalis in the fossil record

The earliest fossil records of the Ranidae are from the late Eocene (Bartonian, MP 16) of France (RAGE 1984) and from slightly younger strata (Bartonian, MP 17) of England (HOLMAN & HARRISON 1999). This evidence is based on disarticulated ilia which display such characteristic morphology that the latter authors even assigned this material to the genus *Rana*, and RAGE (in RAGE & ROČEK 2003) noted that one form from MP 17 (Eocene, Priabonian) French localities is a reminiscent of "green frogs". Thus, although Ranidae are considered one of the most derived anuran families (FROST et al. 2006 and references therein), their earliest representatives are about 40 million years old.

Throughout the Oligocene, ranid frogs were common all over Europe. According to SANCHIZ et al. (1993), the ranid fossils from the early Oligocene of Möhren, Germany (Stampian, MP 22) represent the earliest members of European green frogs, beside the above-mentioned specimens from the Eocene decribed by RAGE.

The earliest brown frogs (*Rana* cf. *temporaria*) are recorded by a single specimen from the early Miocene (Burdigalian, MN3) locality Dietrichsberg, Germany (BÖHME 2001). It should be, however, noted that numerous younger Miocene localities with rich anuran faunas have not yielded brown frogs, so this record is geochronologically isolated. On the other hand, there are other ranid fossils in the early Miocene that are still closer to green frogs, or display features of both green and brown frogs (RAGE & HOSSINI 2000). This might suggest that the brown frogs are later derivatives of the older green frogs (if the genus *Rana* has its autochthonous origin in Europe, which seems to be supported by palaeogeography), although immigrations from the east cannot be fully excluded. According to RAGE & ROČEK (2003), the brown frog from Dietrichsberg might represent such isolated result of an immigration event.

The oldest unambiguous records of brown frogs are only from the Pliocene (Ruscinian, MN15 and Villányian, MN16). They come from the localities Wąże 1 and Rębielice Królewskie, Poland (MŁYNARSKI 1962, 1977; SANCHÍZ 1983), Ivanovce, Slovakia (HODROVÁ 1981) and Kaltensundheim, Germany (BÖHME 2002). The earliest records of *Rana arvalis* are from Wąże 1 and Rębielice Królewskie. It is obvious that in the Pliocene brown ranids diversified in species which survive until today. It is important to add that according to RATNIKOV (1995), *Rana arvalis* was not recorded from pre-Pleistocene localities of east Europe and Asia.

In Quaternary*), the earliest record of *Rana arvalis* is from the Pliocene to Lower Pleistocene locality of Včeláre (**x2**), Slovakia (HODROVÁ 1985).

In the early Pleistocene deposits, *Rana arvalis* was recorded from Hohensulzen (**x1**), Germany (WEILER 1952), Hajnáčka (**x3**), Slovakia (HODROVÁ 1981), Chigirin (**x4**), Ukraine (RATNIKOV 1992), Karai-Dubina (**x5**), Ukraine (RATNIKOV 2002), Krolyatnik (**x6**), Russia (RATNIKOV 2002), Kozy Ovrag (**x7**), Russia (RATNIKOV 1996a, 2002), Zherdevka (**x8**), Russia (RATNIKOV 1992, 2002), Volnaya Vershina (**x9**), Russia (RATNIKOV 1992, 1996b, 2002), Kuznetsovka (**x10**), Russia (RATNIKOV 1987, 1992, 1996c, 2002), Roslavl (**x11**), Russia (RATNIKOV 2002), Yasakogo-1 (**x12**), Russia (RATNIKOV 2002), and Berezovka (**x13**), Russia (RATNIKOV 1992, 2002).

In the middle Pleistocene deposits, the fossil record of *Rana arvalis* is from Abîmes de la Fage (**+1**), France (RAGE 1972, BAILON & RAGE 1992), East Farm (**+2**), Great Britain (ASHTON et al. 1994), Greenlands Pit, Putfleet (**+3**), Great Britain (HOLMAN & CLAYDEN 1988), Cudmore Grove (**+4**), Mersea Island, Great Britain (HOLMAN et al. 1990), Little Oakley (**+5**), Great Britain (LISTER et al. 1990, HOLMAN 1993), Sugworth (**+6**), Great Britain (SUTCLIFFE & KOWALSKI 1976, STUART 1980, HOLMAN 1987a, 1993), West Runton (**+7**), Great Britain (HOLMAN et al. 1988, HOLMAN 1989), Boxgrove (**+8**), Great Britain (HOLMAN 1992, 1993), Norre Lynghy (**+9**), Denmark (AARIS-SORENSEN 1995), Hartsmannshof (**+10**), Germany (BRUNNER 1936), Kozi Grzbiet (**+11**), Poland (MŁYNARSKI 1977, MŁYNARSKI & SZYNDLAR 1989), Bramka (**+12**), Poland (MADEYSKA 1981, NADACHOWSKI 1988), Chigirin (**+13**), Ukraine (RATNIKOV 1992, 2002), Cherny Yar-Nizhnee Zaymishche (**+14**), Russia (RATNIKOV 2001b, 2002), and Krasnoy Bor (**+15**), Russia (CHKHIKVADZE & SUKHOV 1977, CHKHIKVADZE 1984).

The locality Komintern (**+16**), middle Volga River, Russia (RATNIKOV 1999, 2002) is from the transition between middle and late Pleistocene.

The late Pleistocene occurrence of *Rana arvalis* was recorded from Shropham 1 (**o1**), Great Britain (HOLMAN & CLAYDEN 1990), (**o2**) Swanton Morley, Great Britain (HOLMAN 1987b), (**o3**) Burgtonna near Langensalza, Germany (HEINRICH & JAEGER 1978, MŁYNARSKI et al. 1978, BÖHME 1989), Pottenstein (**o4**), Germany (BRUNNER 1938, 1956), Teufelsbrücke (**o5**), Germany (BÖHME 1980), Zdrody (**o6**), Poland (BALUK et al. 1979, MŁYNARSKI & SZYNDLAR 1989), Bijambare (**o7**), Bosna and Herzegovina (PAUNOVIĆ 1983, 1986), Zelena (**o8**), Bosnia and Herzegovina (PAUNOVIĆ 1987), Zmeevka (**o9**),

*)Symbols and numbers of the localities in the text correspond to those in fig. 2.

Russia (RATNIKOV 1988, 2002), Rudny (**o10**), Russia (RATNIKOV 1988, 1992), Yelasy (**o11**), Russia (RATNIKOV 2001a, 2002), and Posudichi (**o12**), Russia (RATNIKOV 2002). Following localities are late Pleistocene to Holocene in age: Pisede (**H1**), Germany (BÖHME 1983), Smolucka (**H2**), Serbia (PAUNOVIĆ & DIMITRIJEVIĆ 1990), Antselovich (**H3**), Russia (RATNIKOV 2002), and Devichi skaly (**H4**), Azerbaijan (CHKHIKVADZE 1984).

In the Holocene, the fossil record of *Rana arvalis* is from the locality Hay Green, Terrington St. Clement (**H5**), Great Britain (GLEED-OWEN 2000), Chopdike Drove, Gosberton (**H6**), Great Britain (GLEED-OWEN 2000), Butte-de-Saint-Cyr (Val de Reuil) (**H7**) in France (BAILON & RAGE, in press), Bovenkarspel (**H8**), Netherlands (GLASTRA 1983), Bad Frankenhausen (**H9**), Germany (BÖHME 1987, TAICHERT 1987), Kutná Hora (**H10**), Czech Republic (KYSELÝ, in press), Duża Sowa (**H11**), Poland (BOCHEŃSKI et al. 1983, MŁYNARSKI & SZYNDLAR 1989), Peski-1 and 2 (**H12**), Bielaruss (RATNIKOV 2002), Lopatino (**H13**), Bielaruss (RATNIKOV 2002), Luchinskoye (**H14**), Russia (RATNIKOV 2002), and Eketorp (**H15**), Sweden (AUDOIN-ROUZEAU 1993).

According to RATNIKOV (1995), the early Pleistocene records of *Rana arvalis* from east Europe belong to steppe faunas, whereas in the late Pleistocene-Holocene localities of east Europe, *Rana arvalis* is a member of both typical forest as well as steppe faunas (RATNIKOV 1995). In general, some individuals of Quaternary brown frogs were larger and with stronger crests for muscular insertions than those living today (RAGE 1972).

Palaeogeographic and palaeoclimatic context

Both fossil record and electrophoretic data (MENSI et al. 1992) suggest that the Pliocene (5.3–1.64 million years ago) was a crucial period for the diversification of European brown frogs and that forms similar to *Rana arvalis* may have already been present. The geographic situation at that time was not very different from today (fig. 1), except for the Paratethys Sea which still extended from the Vienna Basin to the east. Later, the Paratethys became separated into a lake in the west (evidenced by lacustrine sediments), and laguno-marine parts in the the central and eastern areas. The last part of the continent which was covered by shallow sea was the northern Appenine Penninsula, whereas the British Islands and Scandinavia were confluent with mainland Europe (YILMAZ et al. 1996). In the early Pliocene, the climate was warm and humid, with poor seasonality, but deterioration began in the middle Pliocene (about 3.1 million years ago), with a marked drop in temperature approximately 2.4 million years ago (e. g. BAILON & BLAIN 2007).

In the Quaternary, Paratethys no longer existed as a sea. Continued climatic deterioration (cooling) resulted in the extension of polar glaciers southwards, so that northern part of Eurasia and high mountains were covered by ice sheets. Since a large amount of water was bound in glaciers, the sea level was about 120–140 m lower than today. Consequently, various islands (including Britain) were connected to mainland Europe (fig. 3). The maximum extent of glaciation (Last Glacial Maximum) was between 22 000 and 14 000 years ago (tab. 1).

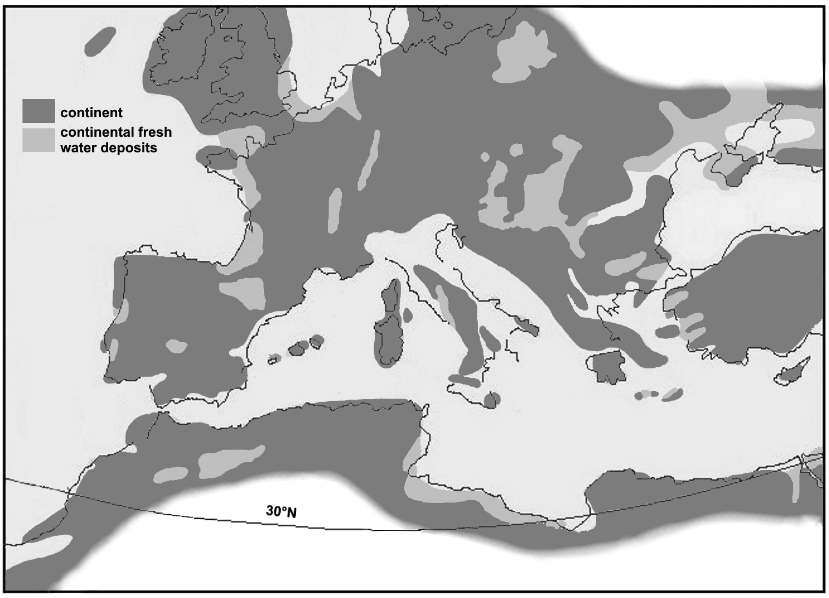

Fig. 1: Map of Europe in the early Pliocene (3.8 Ma). From YILMAZ et al. (1996) at www.mnhn.fr./mnhn/geo/pliocene.html, modified.
Europa im frühen Pliozän (vor 3,8 Millionen Jahren). Aus YILMAZ et al. (1996) und www.mnhn.fr./mnhn/geo/pliocene.html, modifiziert.

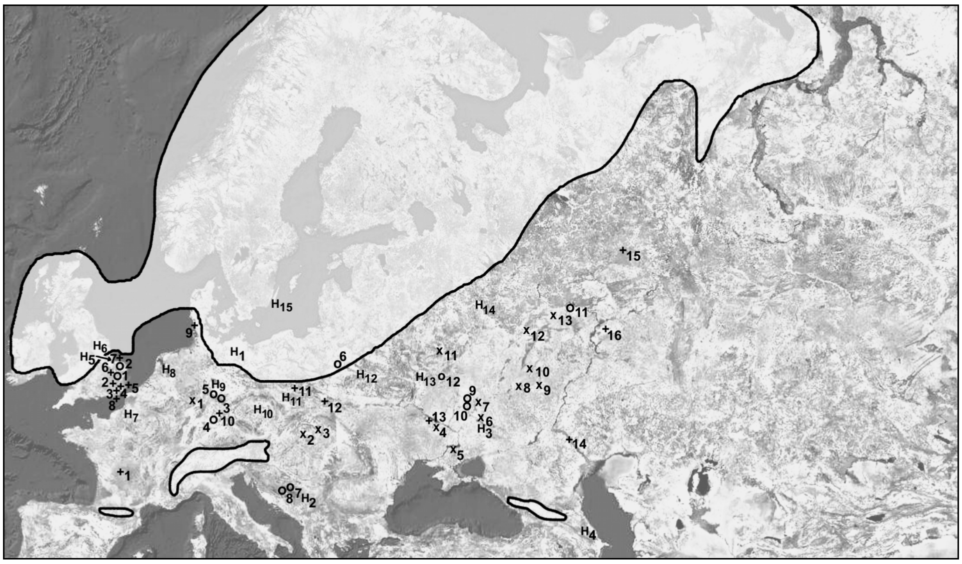

Fig. 2: Map of Pleistocene through Holocene records of *Rana arvalis*, with the maximum extent of the ice sheets during the Last Glacial Maximum. x = Lower Pleistocene localities, + = Middle Pleistocene localities, o = Upper Pleistocene localities, H = Holocene localities. For details of localities see the text.
Verbreitung der Nachweise von *Rana arvalis* vom Pleistozän bis einschließlich Holozän sowie die Maximalausdehnung der Eisschilde während des letzten glazialen Maximums. x = Fundorte aus dem Unteren Pleistozän, + = Fundorte aus dem Mittleren Pleistozän, o = Fundorte aus dem Oberen Pleistozän, H = Fundorte aus dem Holozän. Details zu den Fundorten siehe Text.

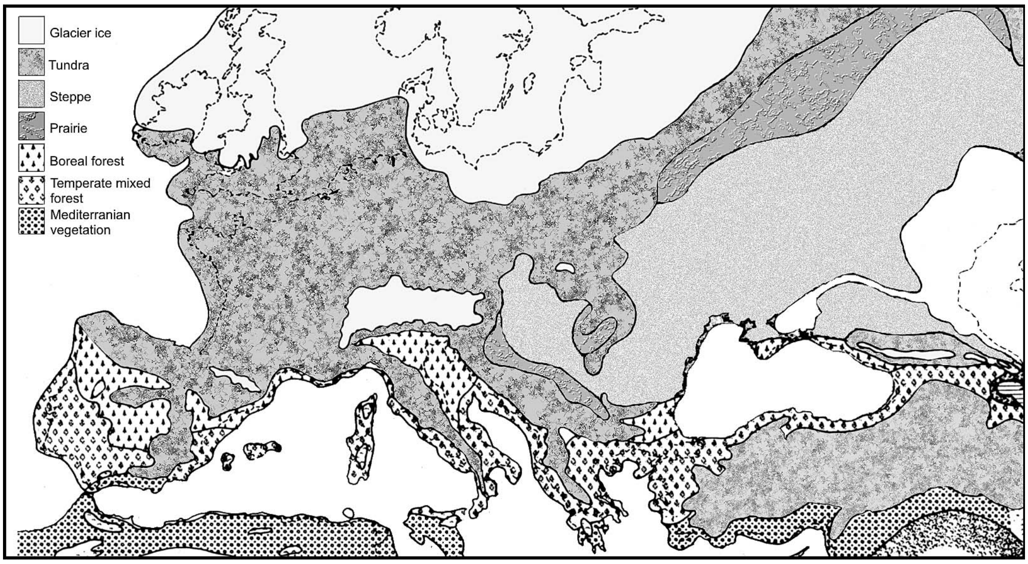

Fig. 3: Map of inferred vegetative patterns during the Last Glacial Maximum (22000–14000 years ago; the time of maximum extent of the ice sheets during the last glaciation) in Europe. From CROWLEY & NORTH (1991), modified.
Rekonstruierte Vegetation während des letzten glazialen Maximums in Europa (vor 22000 bis 14000 Jahren, dem Zeitraum der maximalen Ausdehnung der Eisschilde während des letzten Glazials). Aus CROWLEY & NORTH (1991), modifiziert.

The crucial period in formation of the present-day distribution of *Rana arvalis* was the glacial retreat in central and eastern Europe (about 14000 years ago) which, as a consequence of melting, resulted in a series of fresh-water lakes (fig. 4) which were joined later to form the Baltic Ice Lake (approx. 1000 years ago). This lake was rimmed to the north by the Scandinavian ice-sheet. For most of the year, it was frozen and only during short summers single icebergs were floating on the lake. This lake existed for approximately 3000 years, extending in size as the Scandinavian ice-sheet melted, and was situated in cold, continental climate with high daily temperature amplitudes. The average July temperature did not exceed 12 °C. This freshwater basin is supposed to have drained to the west.

About 10200 years ago, the freshwater basin was connected to the ocean in the west due to a marine transgression which gave rise to the Yoldia Sea (the event is evidenced by a marine bivalve *Yoldia arctica*, giving the name to the sea). About 9200 years ago, the Yoldia Sea became isolated from the ocean and quickly turned into a freshwater lake again (inhabited by the gastropod *Ancylus fluviatilis*) called the Ancylus Sea. The climate around Yoldia Sea and Ancylus Sea was humid and cooler than today (the average July temperature was up to 15 °C).

Approximately 8900 years ago, the basin was connected with the Atlantic through the Danish Straight, and its waters were mixed with salty waters from the North Sea. About 7500 years ago the salinity increased so the marine gastropod *Littorina littorea* became typical in this basin which is, in this stage of development, termed the Litorina Sea. The sea was warmer and of higher salinity than the present-day Baltic Sea.

Tab. 1: Summary of the most significant events in the last 22000 years (late Pleistocene and Holocene) which possibly influenced present distribution of amphibians in Europe. Unless otherwise stated data are from http://www.esd.ornl.gov/projects/qen/nerceurope.html (Compiled by Jonathan Adams, Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, USA).

Zusammenfassung der bedeutendsten Ereignisse in den letzten 22000 Jahren (spätes Pleistozän und Holozän), die wahrscheinlich die gegenwärtige Verbreitung der Amphibien in Europa beeinflussten.

	Intervals	Palaeogeographic, climatic and vegetative characteristics
Pleistocene	Last Glacial Maximum 22000–14000 yr BP	Cold and dry (August mean temperatures 10–11 °C, February mean temperatures -19 to -27 °C). Ice sheets over Scandinavia, most of Britain, and north of present-day continental Europe. Permafrost extended to latitudes of central France and southern Hungary. Steppe-tundra and polar desert in central and northern Europe.
	Older Dryas (stadial) 14000–13700 yr BP	Variably cold and dry phase. Scandinavia (except for southern Sweden) still under the ice. The glacier advanced again into the Baltic Ice Lake. Arctic tundra stretched from Siberia to Britain.
	Allerød (interstadial) approx. 13000 yr BP	A rapid warming and moistening. Ice sheets began to retreat again. Open woodland cover in western Russia.
	Younger Dryas (stadial) 12900–11500 yr BP	Intensely cold and and dry phase. Scotland covered by ice again.
Holocene	11500–10500 yr BP	Climates still cooler than today but the Scandinavian ice cap disappeared.Mainly forested in northern and central Europe, but slightly drier than at present. Relatively open forests in north-east Europe.
	8700 yr BP	Onset of mid-Holocene thermal maximum in Scandinavia (YU et al. 2003)
	8200 yr BP	A severe cold and dry event, lasting perhaps a couple of centuries (ALLEY et al. 1997).
	7500 yr BP	Rising Mediterranean sea waters broke through the Bosphorus. Black Sea became brackish and rose several tens meters, inundating former shores and river valleys deep into the interior.
	since 6000 yr BP	Warmer climates than today in northern Europe and Scandinavia (spreading forests to the north). Climates fairly similar to the present in central Europe.
	approx. 4500 yr BP	Agriculture spread to most parts of Europe. Beginning of main deforestation/agriculture phase. Spreading peat growth was beginning to affect the forest areas of NW Britain, perhaps due to ongoing leaching of soil nutrients.
	2600 yr BP	Cool and wet phase affected north-west and central Europe, with increase in bog growth and lowering of altitudinal tree limits.
	1400 yr BP	Wet cold event of reduced tree growth and famine across western Europe and possibly elsewhere.

The extent of periglacial lakes was larger than the present Baltic Sea, but decreased in size because of post-glacial uplift (KÖSTLER 1979), which in some areas around the Gulf of Bothnia has been calculated at over 300 m; DAVIS et al. (2003).

With regards to climate, the Pleistocene was characterized by pronounced fluctuations which resulted in great contrasts between glacial and interglacial stages. This, in turn, caused that the glacier repeatedly extended southwards and again receded. During certain interglacial times summers were even warmer than today (GLEED-OWEN 1999). In contrast, during the Last Glacial Maximum (ca 22000–14000 years ago) the continental glacier extended close to the Central European (Sudetic) mountain system and its southern edge was separated from the ice cup covering the Alps by a narrow corridor (about 400 km) of 'steppe tundra' and polar desert (fig. 3). Permafrost extended southward to about the latidude of central France and southern Hungary. The climate was very cold and dry throughout Europe. In the north-western and central part of the continent, the mean temperature of the warmest month was 10 to 11 °C, and the

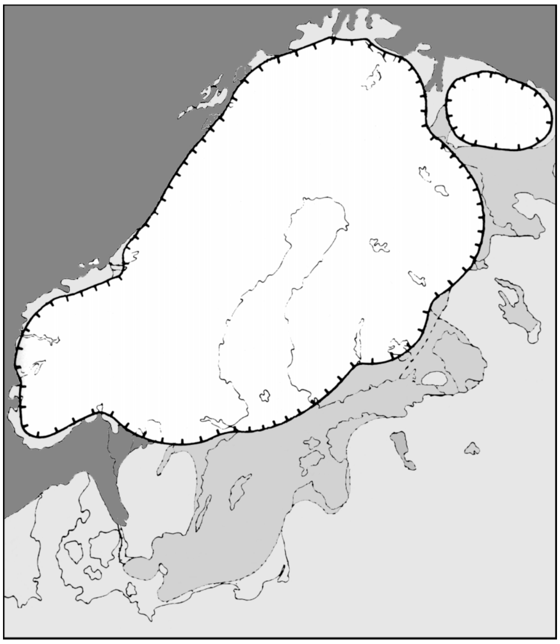

Fig. 4: Palaeogeographical sketch of Fennoscandia during the Late Dryas (10500–10200 years ago). At the end of this period, the basin was connected to the ocean due to a marine transgression (giving rise to the Yoldia Sea). White area represents the extent of the ice sheet, light grey is dry land, medium grey is fresh-water periglacial lake (Baltic Ice Lake) and inland lakes, and dark grey is the sea. After HYVÄRINEN (1975), from GUDELIS & KÖNIGSSON (1979).
Paläogeografische Skizze von Fennoskandinavien während der späten Dryas-Zeit (vor 10500–10200 Jahren). Am Ende dieser Periode war auf Grund einer marinen Transgression das Becken mit dem Meer verbunden (wodurch das Yoldia-Meer entstand). Weiße Flächen geben die Ausdehnung des Eisschildes an, hellgrau dargestellt ist das Festland, mittelgrau sind der periglaziale Süßwassersee (Baltischer Eis-See) und Binnenseen dargestellt, und dunkelgrau das Meer. Nach HYVÄRINEN (1975), aus GUDELIS & KÖNIGSSON (1979).

mean temperature of the coldest month ranged from -27 to -20 °C. Estimated mean annual temperature was between -9 and -4 °C (FRENZEL et al. 1992, HUIJZER & ISARIN 1997). Forests and woodlands were absent from large areas even in southern parts of the continent.

The sudden warming of the late glacial interstadial occurred at about 13000 years ago (ALLEY et al. 1993; tab. 1), possibly accompanied with increased precipitation, caused the thawing of the frozen ground. Due to the still frozen impermeable subsoil, infiltration was prevented and large amounts of melted water eroded water-saturated soil surface, causing runoff with resulting high sedimentation (ZOLITSCHKA et al. 2000). These processes resulted in the formation of river systems different from today.

Throughout the interval of 12000–11000 years ago (Older Dryas), the north-western Europe and a comparatively narrow stripe adjacent to southern shore of the Baltic Ice Lake remained essentially treeless. The ice-sheet was already restricted to Scandinavia, but Britain was still connected to continental Europe. Most of continental Europe was covered by open woodlands (broadleaf woodlands in western and central Europe, open conifer woodlands in east Europe). This period was followed by a short cold

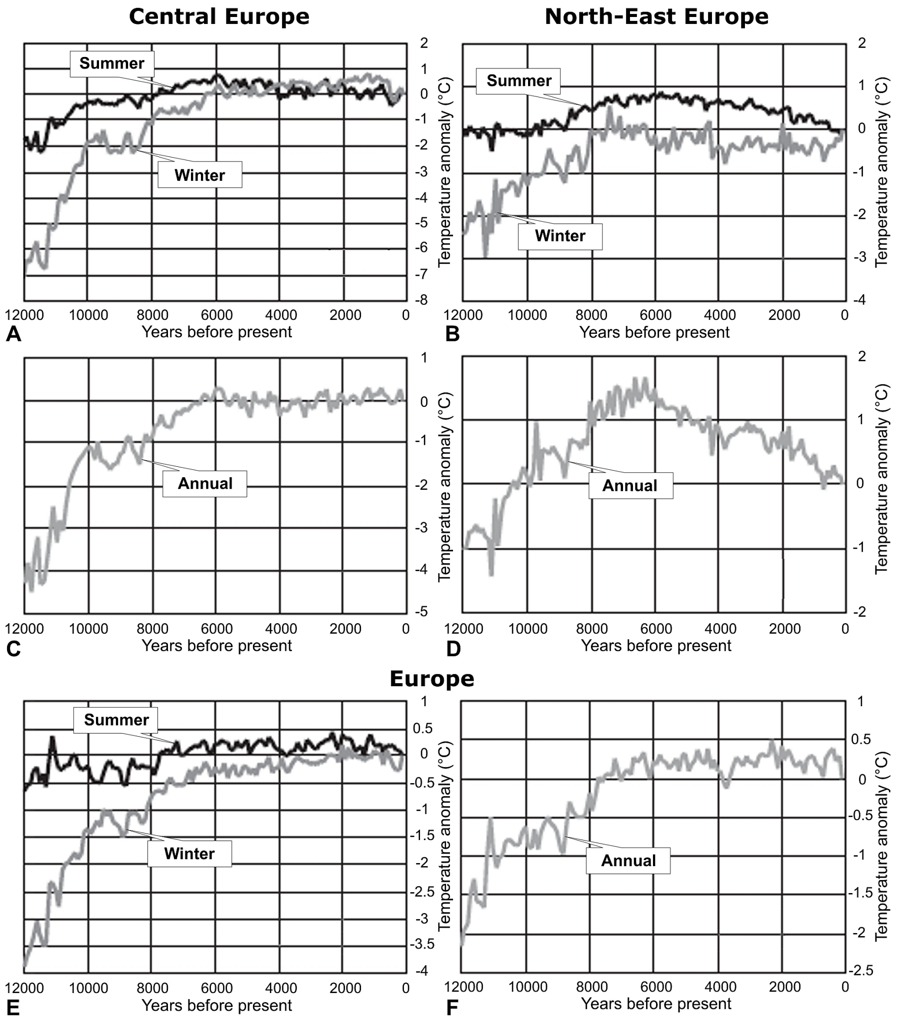

Fig. 5: Reconstructed mean temperatures of the warmest (Summer) and coldest (Winter) month of the year, and mean annual temperature (Annual) in Central Europe, North-East Europe, and Europe as a whole during the last 12000 years. All are shown as anomalies compared to present-day baseline (0). After DAVIS et al. (2003).

Rekonstruierte mittlere Temperaturen des wärmsten (Sommer) und kältesten (Winter) Monats je Jahr sowie Jahresdurchschnitts-Temperaturen in Mitteleuropa, Nordosteuropa und Europa als Ganzes während der letzten 12000 Jahre. Alle sind als Abweichungen angegeben im Vergleich zur gegenwärtigen Basislinie (0). Nach DAVIS et al. (2003).

interval in the Younger Dryas (10800–10000 years ago) in which the open woodland cover was replaced by dry steppe and steppe-tundra.

During the Holocene (12000–0 years ago; see also fig. 5), the annual mean temperatures for Europe as a whole suggest an almost linear warming up to 7,800 years ago, followed by stable conditions for the remainder of the Holocene (DAVIS et al. 2003). However, there were large spatial and seasonal differences in Holocene temperature trends. Whereas in western central Europe the warming culminated at approximately present-day temperatures (fig. 5C), there was a significant peak (about 1.5 °C higher than today) in annual temperatures between 6 000 and 7 000 years ago in NE Europe (fig. 5D). The summer and winter temperatures have been approximately stable during the past 6 000 years in central Europe, although in north-east Europe the summer temperatures were nearly 1 °C higher, and winter temperatures were lower than today.

Since approximately 4 500 years ago, deforestation and agriculture spread to most part of Europe.

Phylogeography

Evidence for range expansions can be detected in current population genetic structures and have been used to reconstruct the population history of plants and animals (e. g. TABERLET et al. 1998). Lower genetic diversity is typical for recently colonized areas, whereas higher level of genetic variation is typical for areas that correspond to refugia. Limited mitochondrial variation over a large area usually suggests a recent expansion from a single source (PHILLIPS et al. 2000).

In the particular case of *Rana arvalis*, a higher morphological, allozyme and mtDNA variation is observed in populations from the Carpathian Basin, while in other parts of the species' range the variation is lower (BABIK et al. 2004). Only findings from the Carpathian Basin brought identification of all three mt haplotype lineages of the cytochrome b gene, which points to the existence of a refugium during the last glacial maximum. According to variation in one of the lineages, another refugium of *Rana arvalis* may probably be located in south Russia (BABIK et al. 2004).

The Carpathian Basin refugium is supported by phylogeographic investigations of other species, e. g. the marbled white butterfly *Melanargia galathea* (SCHMITT et al. 2006) and the common hamster *Cricetus cricetus* (NEUMANN et al. 2005). At present, *R. arvalis* inhabits also cold regions which might suggest that it could survive the last glacial maximum also in areas north of Carpathian Basin, similar to the bank vole *Clethrionomys glareolus* (KOTLÍK et al. 2006).

Intra-species splitting of the two main mitochondrial lineages in *R. arvalis* has been estimated at 1.03 million years (VEITH et al. 2003). This corresponds to the divergence estimates based on allozyme data (0.7–1.3 million years, RAFIŃSKI & BABIK 2000), although allozyme and mtDNA variation north and south of the Carpathian Mountains differ (BABIK et al. 2004).

History of distribution

The available fossil record suggests that the European brown frogs were distributed in continental Europe since the Pliocene, and began to diversify in species which survived until today. This is evidenced by above-mentioned findings of *R. temporaria* and *R. arvalis*, as well as by electrophoretic data (MENSI et al. 1992) which suggest that the first split within living European brown frogs occurred approximately 2.6 million years ago (middle or late Pliocene). It is obvious that the distribution of brown frogs extended also to the British Penninsula, although the occurrence of extant species (including *R. arvalis*) was recorded only from Quaternary deposits (see below).

New molecular data suggest that the origin of the genus *Rana* (i. e. a split between *Pelophylax* and *Rana*) may be estimated to 9.32 million years ago (Late Miocene), basal split within brown frogs to 3.99 million years ago, and the basal split within *R. temporaria* species group to have occurred 3.18 million years ago (VEITH et al. 2003). The latter data correspond to fossil evidence, which suggests the diversification of brown frogs in the Pliocene.

The middle and late Pliocene, cooling is sometimes considered as a reason for the Europe/Eastern Asia disjunction of various related palaearctic taxa (BORKIN 1986). From this point of view, the recent extensive and continuous Eurasian distribution of *R. arvalis* would suggest that this species was not affected by cooling because of its genetic and ecological plasticity (ISHCHENKO 1978), or because the recent distribution is a result of an eastward spreading from an earlier restricted area, most probably in Europe.

Available data from the fossil record during the Pleistocene do not support the often-mentioned scenario of repeated expansion-regression events. All late Pleistocene records, except for one which is very close to the southern limits of the ice-sheet cover during the Last Glacial Maximum, come from areas which are not covered by ice. It is highly improbable that the moorfrog would survive there during the glaciation, as was suggested for *Pelobates fuscus* by EGGERT et al. (2006).

STUGREN (1966, 1986) considered *R. arvalis* in Romania not to be glacial survivor, but a cold-tolerant species which arrived at the Carpathians in a cooler postglacial period from the Angara centre. This conclusion, however, is in strong disagreement with fossil record according to which *R. arvalis* was present in Europe as early as in the Pliocene, and in the early Pleistocene deposits it was recorded even from western Europe (fig. 2). Therefore it is highly probable that its distribution in Europe is autochthonous, and that it is not an immigrant from Asia.

Since Britain was connected to mainland Europe until the early-middle Holocene owing to sea level rise following the melting of the last ice sheets, it is not surprising that brown frogs represented by *R. arvalis* and *R.* cf. *dalmatina* were recorded from eastern England even from middle Saxon (ca 600–950 years ago) deposits (GLEED-OWEN 2000). Isolation resulted in considerable impoverishment of the British herpetofauna (28 species occur along the continental Channel coast, contrasting to only twelve species in Britain; GASC et al. 1997). The only brown frog that survived and is considered native to Britain is *R. temporaria*. Fen drainage by humans in the last three centuries, and general habitat degradation were possible reasons for the extinction of *R. arvalis* in Britain (GLEED-OWEN 2000).

Similar to *P. fuscus*, the present Swedish populations of *R. arvalis* most probably originated from an invasion to Scandinavia during the late Dryas when southern Sweden was free of ice and connected for the last time to Denmark (EGGERT et al. 2006).

With increasing deforestation of the continental Europe *R. arvalis*, which is a species preferring forests and scrubs, became restricted to flood plains along riversides.

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References

AARIS-SORENSEN, K. (1995): Palaeoecology of a late Weichselian vertebrate fauna from Norre Lynghy, Denmark. – Boreas 24: 355–365.

ALLEY, R. B., MEESE, D. A., SHUMAN, C. A., GOW, A. J., TAYLOR, K. C., GROOTES, P. M., WHITE, J. W. C., RAM, M., WEDDINGTON, E. D., MAYEWSKI, P. A. & G. A. ZIELINSKI (1993): Abrupt increase in Greenland snow accumulation at the end of the Younger Dryas event. – Nature 362: 527–529.

ALLEY, R. B., MAYEWSKI, P. A., SOWERS, T., STUYWER, M., TAYLOR, K. C., & P. U. CLARK (1997): Holocene climatic instability; a prominent, widespread event 8200 yr ago. – Geology 25: 483–486.

ASHTON, N. M., BOWEN, D. Q., HOLMAN, J. A., HUNT, C. O., IRVING, B. G., KERMP, R. A., LEWIS, S. G., MCNABB, J., PARFITT, S., & M. B. SEDDON (1994): Excavations at the Lower Palaeolithic site at East Farm, Barnham, Suffolk 1989–92. – Journal of Geological Society London 151: 599–605.

AUDOIN-ROUZEAU, F. (1993): Hommes et animaux en Europe de l´époque antique aux temps moderned. Corpus de données archéologiques et historiques. – Paris (CNRS).

BABIK, W., W. BRANICKI, M. ŠANDERA, S. LITVINCHUK, L. J. BORKIN, J. T. IRWIN & J. RAFIŃSKI (2004): Mirochondrial phylogeography of the moor frog, *Rana arvalis*. – Molecular Ecology 13: 1469–1480.

BAILON, S. & H. A. BLAIN (2007): Faunes de reptiles et changements climatiques en Europe occidentale autour de la limite Plio-Pleistocène. – Quaternaire 18: 55–63.

BAILON, S. & J. C. RAGE (1992): Amphibiens et reptiles du Quaternaire. Relations avec l'Homme. – Mémoires Société Géologique, France 160: 95–100.

BAILON, S. & J. C. RAGE (in press): Données fossiles et mise en place de l'herpétofaune actuelle de la France. – In: Atlas des amphibiens et reptiles de la France. – Société herpétologique de France.

BALUK, A., M. MŁYNARSKI & A. SULIMSKI (1979) Pleistocene fauna at Zdrody near Białystok (North-Eastern Poland). – Biuletin Instytutu Geologicznego 318: 117–127.

BOCHEŃSKI, Z., MŁYNARSKI, M., NADACHOWSKI, A., STWORZEWICZ, E., & B. W. WOŁOSZYN (1983): Górnoholoceńska fauna z Jaskini Dużej Sowy (doniesienie wstępne). – Przęgląd zoologiczny 27: 437–456.

BÖHME, G. (1980): Amphibien. In: FEUSTEL, R. (Hrsg.): Magdalenianstation Teufelsbrücke. II. Paläontologischer Teil. – Weimarer Monographien für Ur- und Frühgeschichte 1980 : 65–71.

BÖHME, G. (1983): Skelettreste von Amphibien (Urodela, Salientia) aus dem fossilen Tierbautensystem von Pisede bei Malchin. Teil 1: Taxonomie und Biostrationomie. – Wissenschaftliche Zeitschrift der Humboldt-Universität zu Berlin, Mathematisch-Naturwissenschaftliche Reihe 32: 657–670.

BÖHME, G. (1987): Amphibien- und Reptilienreste aus den Kulthöhlen im Kyffhäuser bei Bad Frankenhausen. In: TEICHERT, M., W. J. BARTHEL & J. BÖHME (Hrsg.): Beiträge zur Archäozoologie VI. – Weimarer Monographien für Ur- und Frühgeschichte 20: 31–35.

BÖHME, G. (1989): Die Amphibien- und Reptilienreste der Fundstelle Bilzingsleben im Rahmen der thüringisch-sächsischen quartären Travertin-Herpetofaunen. – Ethnographisch-Archäologische Zeitschrift 30: 370–378.

BÖHME, G. (2002): Amphibienreste aus dem Oberpliozän von Kaltensundheim (Rhön, Thüringen). – Mitteilungen aus dem Museum für Naturkunde in Berlin, geowissenschaftliche Reihe 5: 231–238.

BÖHME, M. (2001): The oldest representative of a brown frog (Ranidae) from the early Miocene of Germany. – Acta Palaeontologica Polonica 46: 119–124.

BORKIN, L. J. (1986): Pleistocene glaciations and western-eastern palaearctic disjunction in amphibian distribution. In: ROČEK, Z. (ed.) Studies in Herpetology: 63–66. – Prague (Societas Europaea Herpetologica and Charles University).

BRUNNER, G. (1936): Eine Kleinsäugerfauna aus dem Mittel-Diluvium mit *Spalax* sp. – Abhandlungen der Naturhistorischen Gesellschaft Nürnberg 26: 1–24.

BRUNNER, G. (1938): Die Gaiskirche im oberen Püttlachtal (Oberfranken). – Neue Jahrbücher für Mineralogie und Paläontologie, Abhandlungen, Abteilung B 79: 243–273.

BRUNNER, G. (1956): Nachtrag zur kleinen Teufelshöhle bei Pottenstein (Oberfranken). – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 2: 75–100.

CHKHIKVADZE, V. M. (1984): [Review of fossil tailed and tailless amphibians of USSR]. – Izvestiya Akademii Nauk GSSR 10: 5–13 (in Russian).

CHKHIKVADZE, V. M. & V. P. SUKHOV (1977): [Amphibians and reptiles from the Pleistocene deposits of Krasnoy Bor (river Kama)]. Voprosy Gerpetologii: 227–228. – Leningrad (Nauka) (in Russian).

CROWLEY, T. J. & G. R. NORTH (1991): Paleoclimatology. – New York (Oxford University Press).

EGGERT, C., D. COGĂLNICEANU, M. VEITH, G. GEORGDZUKIC & P. TABERLET (2006): The declining spadefoot toad, *Pelobates fuscus* (Pelobatidae): paleo and recent environmental changes as a major influence on current population structure and status. – Conservation Genetics 7: 186–195.

FRENZEL, B., B. PECSI & A. A. VELICHKO (eds.) (1992): Atlas of Palaeoclimates & Palaeoenvironments of the Northern Hemisphere. – Budapest (INQUA/Hungarian Academy of Sciences).

FROST D. R., T. GRANT, J. FAIVOVICH, R. H. BAIN, A. HAAS, C. F. B. HADDAD, R. O. DE SÁ, A. CHANNING, M. WILKINSON, S. C. DONNELLAN, C. J. RAXWORTHY, J. A. CAMPBELL, B. L. BLOTTO, P. MOLER, R. C. DREWES, R. A. NUSSBAUM, J. D. LYNCH, D. M. GREEN & W. C. WHEELER (2006): The amphibian tree of life. – Bulletin of the American Museum of Natural History 297: 1–370.

GASC, J. P. et al. (1997): Atlas of Amphibians and Reptiles in Europe. – Paris (Societas Europaea Herpetologica and Muséum National d'Histoire Naturelle).

GLANDT, D. (2006): Der Moorfrosch. – Bielefeld (Laurenti).

GLASTRA, R. (1983): Some archaeoherpetological remains from the Netherlands. – Journal of Archaeological Science 10: 213–222.

GLEED-OWEN, C. P. (1999): The paleoclimatic and biostratigraphic significance of herpetofaunal remains from the British Quaternary. In: ANDREWS, P. & BANHAM, P. (eds): Late Cenozoic Environments and Hominid Evolution: a Tribute to BILL BISHOP: 201–215. – London (Geological Society).

GLEED-OWEN, C. P. (2000): Subfossil records of *Rana* cf. *lessonae*, *Rana arvalis* and *Rana* cf. *dalmatina* from Middle Saxon (c. 600–950 AD) deposits in eastern England: evidence for native status. – Amphibia-Reptilia 21: 57–65.

HEINRICH, W. D. & K. D. JAEGER (1978): Zusammenfassende stratigraphische und palökologische Interpretation des Fossilvorkommens in der untersuchten jungpleistozänen Deckschichtenfolge über dem interglazialen Travertin von Burgtonna in Thüringen. In: KAHLKE, H. D. (Hrsg.) Das Pleistozän von Burgtonna in Thüringen. – Quartärpaläontologie 3: 269–285.

HODROVÁ, M. (1981): Plio-Pleistocene frog fauna from Hajnáčka and Ivanovce, Czechoslovakia. – Věstník Ústředního ústavu geologického 56: 215–224.

HODROVÁ, M. (1985): Amphibia of Pliocene and Pleistocene Včeláre localities (Slovakia). – Časopis pro mineralogii a geologii 30: 145–161.

HOLMAN, J. A. (1987a): Middle Pleistocene herpetological records from interglacial deposits at Sugworth, near Oxford. – British Herpetological Society Bulletin 21: 5–7.

HOLMAN, J. A. (1987b): Herpetofauna of the Swanton Morley site (Pleistocene, Ipswichian), Norfolk. – Herpetological Journal 1: 199–201.

HOLMAN, J. A. (1989): Additional herpetological records from the Middle Pleistocene (Cromerian interglacial) freshwater bed, West Runton, Norfolk. – British Herpetological Society Bulletin 27: 9–12.

HOLMAN, J. A. (1992): The Boxgrove, England, Middle Pleistocene herpetofauna: Paleogeographic, evolutionary, stratigraphic, and paleoecological relationships. – Historical Biology 6: 263–279.

HOLMAN, J. A. (1993): British Quaternary herpetofaunas: a history of adaptations to Pleistocene disruptions. – Herpetological Journal 3: 1–7.

HOLMAN, J. A. & J. D. CLAYDEN (1988): Pleistocene interglacial herpetofauna of the Greenlands Pit, Purfleet, Essex. – British Herpetological Society Bulletin 26: 26–27.

HOLMAN, J. A. & J. D. CLAYDEN (1990): A late Pleistocene interglacial herpetofauna near Shropham, Norfolk. – British Herpetological Society Bulletin 31: 31–35.

HOLMAN, J. A., J. D. CLAYDEN & A. J. STUART (1988): Herpetofauna of the West Runton freshwater bed (Middle Pleistocene; Cromerian interglacial), West Runton, Norfolk. – Bulletin of the Geological Society of Norfolk 38: 121–136.

HOLMAN, J. A., A. J. STUART, & J. D. CLAYDEN (1990): A Middle Pleistocene herpetofauna from Cudmore Grove, Essex, England, and its paleogeographic and paleoclimatic implications. – Journal of Vertebrate Paleontology 10: 86–94.

HOLMAN, J. A. & D. L. HARRISON (1999): *Rana* (Amphibia: Ranidae) from the Upper Eocene (MP17a) Hordle Cliff locality, Hampshire, England. – Palaeovertebrata 28: 47–51.

HUIJZER, A. S. & R. F. B. ISARIN (1997): The reconstruction of past climates using multi-proxy evidence: an example of the Weichselian pleniglacial in northwest and central Europe. – Quaternary Science Reviews 16: 513–533.

HYVÄRINEN, H. (1975): [Late-glacial palaeogeography of Fennoscandia]. Terra 87: 155–166 (in Finnish). Ex GUDELIS, V. & L.-K. KÖNIGSSON (eds.) (1979): The Quaternary History of the Baltic. – Uppsala (Acta Universitatis Upsalensis).

ISHCHENKO, V. (1978): [Dynamic polymorphism in brown frogs of SSSR]. – Moscow (Nauka) (in Russian).

ISHCHENKO, V. (1997): *Rana arvalis* Nilsson, 1842. In: GASC, J. P., A. CABELA, J. CRNOBRNJA–ISAILOVIC, D. DOLMEN, K. GROSSENBACHER, P. HAFFNER, J. LESCURE, H. MARTENS, J. P. MARTÍNEZ RICA, H. MAURIN, M. E. OLIVEIRA, T. S. SOFIANIDOU, M. VEITH & A. ZUIDERWIJK (eds.): Atlas of Amphibians and Reptiles in Europe: 128–129. – Paris (Societas Europaea Herpetologica and Muséum National d'Histoire Naturelle).

KÖSTLER, R. (1979): The Quaternary history of the Baltic. The role of eustatic and isostatic factors in the development of the Baltic. In: GUDELIS, V. & L.-K. KÖNIGSSON (eds.): The Quaternary history of the Baltic: 153–160. – Uppsala (Acta Universitatis Upsalensis).

KOTLÍK, P., V. DEFFONTAINE, S. MASCHERETTI, J. ZIMA, J. R. MICHAUX & J. B. SEARLE (2006): A northern glacial refugium for bank voles (*Clethrionomys glareolus*). – PNAS 103: 14860–14864.

KYSELÝ, R. (in press): Frogs as a part of the neolithic diet. Archaeozoological records from the Czech Republic (Kutná Hora-Denemark site, Řivnáč Culture). – Journal of Archaeological Sciences.

LISTER, A. M., J. M. MCGLADE & A. J. STUART (1990): The early Middle Pleistocene faunas from Little Oakley, Essex. – Philosophical Transactions of the Royal Society of London (B) 328: 359–385.

MADEYSKA, T. (1981): Środowisko człowieka w środkowym i górnym paleolicie na zemiach polskich w świetle badań geologicznych. In: RÓŻYCKI, S. Z. (ed.): Plejstocen Polski. – Wydawnictwo geologiczne 14: 1–125.

MENSI, P., A. LATTES, B. MACARIO, S. SALVIDIO, C. GIACOMA & E. BALETTO (1992): Taxonomy and evolution of European brown frogs. – Zoological Journal of the Linnean Society 104: 293–311.

MŁYNARSKI, M. (1962): Notes on the amphibian and reptilian fauna of the Polish Pliocene and early Pleistocene. – Acta Zoologica Cracoviensia 7: 177–194.

MŁYNARSKI, M. (1977): New notes on the amphibian and reptilian fauna of the Polish Pliocene and Pleistocene. – Acta Zoologica Cracoviensia 22: 13–36.

MŁYNARSKI, M., G. BÖHME & H. ULLRICH (1978): Amphibien- und Reptilienreste aus der jungpleistozänen Deckschichtenfolge des Travertins von Burgtonna in Thüringen. In: KAHLKE, H. D. (Hrsg.): Das Pleistozän von Burgtonna in Thüringen. – Quartärpaläontologie 3: 223–226.

MŁYNARSKI, M. & Z. SZYNDLAR (1989): Płazy a gady – Amphibia et Reptilia. In: KOWALSKI, K. (ed.): Historija i ewolucja lądowej fauny Polski. – Folia Quaternaria 59/60: 69–88.

NADACHOWSKI, A. (1988): Fauna kopalna płazów (Amphibia), gadów (Reptilia) i ssaków (Mammalia) w osadach jaskiń i schronisk Doliny Sąpowskiej. Tło przyrodnicze osadnictwa pradzejowego. – Prace Instytutu Archeologii, Warszaw University: 19–37.

NEUMANN, K., J. R. MICHAUX, S. MAAK, H. A. JANSMAN, A. KAYSER, G. MUNDT & R. GATTERMANN (2005): Genetic spatial structure of European common hamsters (*Cricetus cricetus*) – a result of repeated range expansion and demographic bottlenecks. – Molecular Ecology 14: 1473–1483.

PAUNOVIĆ, M. (1983): Prilog poznavanju rastrostranjenosti mezozojskih i kenozoiskih Amphibia i Reptilia u Jugoslaviji. – Geologiski Vjesnik 36: 79–89.

PAUNOVIĆ, M. (1986): *Rana arvalis* Nilsson, 1842 (Ranidae) aus oberpleistozänen Ablagerungen von Bijambarehöhle bei Olovo (Mittelbosnien, Jugoslawien). – Rad Jugoslavenske Akademije Znanosti i Umjetnosti 21: 55–67.

PAUNOVIĆ, M. (1987): Ein Beitrag zur Kenntnis der oberpleistozänen Anuren Jugoslawiens. – Rad Jugoslavenske Akademije Znanosti i Umjetnosti 22: 201–205.

PAUNOVIĆ, M. & V. DIMITRIJEVIĆ (1990): Gornjoplejstocenska fauna nižih Vertebrata iz Smolćke pećine u jugozapadnoj Srbiji. – Rad Jugoslovenske Akademije Znanosti i Umjetnosti 24: 77–87.

PHILLIPS, C. A., G. SUAU & A. TEMPLETON (2000): Effects of Holocene climate fluctuation on mitochondrial DNA variation in the ringed salamander, *Ambystoma annulatum*. – Copeia 2000: 542–545.

RAFIŃSKI, J. & W. BABIK (2000): Genetic differentiation among northern and southern populations of the moor frog *Rana arvalis* Nilsson in central Europe. – Heredity 84: 610–618.

RAGE, J. C. (1972): Les amphibiens et les reptiles du gisement des Abîmes de la Fage. – Nouvelles Archives Muséum d'Histoire naturelle Lyon 10: 70–90.

RAGE, J. C. (1984): Are the Ranidae (Anura, Amphibia) known prior to the Oligocene? – Amphibia-Reptilia 5: 281–288.

RAGE, J. C. & S. HOSSINI (2000): Les Amphibiens du Miocène moyen de Sansan. In: GINSBURG, L. (ed.): La faune miocène de Sansan et son environnemen: 177–217. – Paris (Mémoires du Muséum d'Histoire naturelle Paris).

RAGE, J.-C. & Z. ROČEK (2003): Evolution of anuran assemblages in the Tertiary and Quaternary of Europe, in the context of palaeoclimate and palaeogeography. – Amphibia-Reptilia 24: 133–167.

RATNIKOV, V. Y. (1987): [On paleogeographical reconstructions based on fossil record of extant species of the anurans]. – University of Voronezh.

RATNIKOV, V. Y. (1988): Upper Quaternary herpetofaunas of the Belgorod Region. – Paleontological Journal 22: 124–125.

RATNIKOV, V. Y. (1992): Eopleistocene and Pleistocene anuran faunas of the East European platform. – Paleontological Journal 26: 112–126.

RATNIKOV, V. Y. (1995): [Late Cenozoic evolution of batrachofauna of East-European Platform]. – Bulletin Moskovskogo obshchestva ispitateley prirody, otdel geologii 70: 98–103 (in Russian).

RATNIKOV, V. Y. (1996a): [Early Pleistocene herpetofauna from the locality Koziy Ovrag in the basin of upper Don River]. – Izvestia vuzov. Geologia i razvedka 6: 16–19 (in Russian).

RATNIKOV, V. Y. (1996b): [Herpetofauna of the lower Pleistocene locality Volnaya Vershina in the basin of upper Don River]. – Vestnik Voronezhskogo Instututa, ser. geol. 1996: 90–93.

RATNIKOV, V. Y. (1996c): [On the methods of paleogeographic reconstructions based upon fossil remains of amphibians and reptiles of the Late Cenozoic of the East European Platform]. – Paleontologicheky Zhurnal 1996: 77–83 (in Russian).

RATNIKOV, V. Y. (1999): [Fossil frogs from the locality Komintern (Tatarstan)]. – Vestnik Voronezhskogo Instituta, ser. geol. 1999: 232–235.

RATNIKOV, V. Y. (2001a): [Herpetofauna of the upper Pleistocene locality Yelasy in Volga River bassin]. – Recent Problems of Herpetology and Toxinology 5: 81–88 (in Russian).

RATNIKOV, V. Y. (2001b): Herpetofauna from Cherny Yar Sands of the Cherny Yar-Nizhnee Zaimishche Section, Lower Povolzhye (Volga Region). – Paleontological Journal 35: 635–640.

RATNIKOV, V. Y. (2002): Late Cenozoic amphibians and reptiles of the East European Plain. – Trudy Voronezhskogo Universiteta 10: 1–138.

SANCHÍZ, B. (1983): The fossil record of living European amphibians. – Abstracts of the 2nd Ordinary General Meeting of the Societa Europaea Herpetologica, León, Spain: 16–17.

SANCHIZ, B., H. H. SCHLEICH & M. ESTEBAN (1993): Water frogs (Ranidae) from the Oligocene of Germany. – Journal of Herpetology 27: 486–489.

SCHMIDT, T., J. C. HABEL, M. ZIMMERMANN & P. MULLER (2006): Genetic differentiation of the marbled white butterfly, *Melanargia galathea*, accounts for glacial distribution patterns and postglacial range expansion in southeastern Europe. – Molecular Ecology 15: 1889–1901.

STUART, A. J. (1980): The vertebrate fauna from the interglacial deposits at Sugworth, near Oxford. – Philosophical Transactions of the Royal Society, ser. B 289: 87–97.

STUGREN, B. (1966): Geographic variation and distribution of the moor frog, *Rana arvalis* Nilss. – Annales Zoologici Fennici 3: 29–39.

STUGREN, B. (1986): Postglacial ages and the herpetofauna of Romania. In: ROČEK, Z. (ed.): Studies in Herpetology: 93–96. – Prague (Societas Europaea Herpetologica and Charles University).

SUTCLIFFE, A. J. & K. KOWALSKI (1976): Pleistocene rodents of the British Isles. – Bulletin of the British Museum of Natural History (Geology) 27: 133–139.

TABERLET, P., L. FUMAGALLI, A. G. WUST-SAUCY & J. F. COSSONS (1998): Comparative phylogeography and postglacial colonization routes in Europe. – Molecular Ecology 7: 453–464.

TEICHERT, M. (1987): Wildtierknochen aus den Kulthöhlen im Kyffhäusergebirge. In: TEICHERT, M., W. J. BARTHEL & J. BÖHME (Hrsg.): Beiträge zur Archäozoologie VI. – Weimarer Monographien für Ur- und Frühgeschichte 20: 5–30.

VEITH, M., J. KOSUCH & M. VENCES (2003): Climatic oscillation triggered post-Messinian speciation of Western Palearctic brown frogs (Amphibia, Ranidae). – Molecular Phylogenetics and Evolution 26: 310–327.

WEILER, W. (1952): Pliozän und Diluvium im südlichen Rheinhessen. – Notizblatt des Hessischen Landesamtes für Bodenforschung, Wiesbaden 6: 147–170.

YILMAZ, P.O., I. NORTON, D. LEARY & R. J. CHUCHLA (1996): Tectonic evolution and paleogeography of Europe. In: ZIEGLER, P. A. & F. HORVATH (eds.): Peri-Tethys Memoir 2: structure and prospects of Alpine Basins and Forelands. – Mémoire Muséum national d'Histoire naturelle 170: 47–60.

YU, S.-Y., E. ANDRÉN, L. BARNEKOW, B. E. BERGLUND & P. SANDGREN (2003): Holocene palaeoecology and shoreline displacement on the Biskopsmåla Peninsula, southeastern Sweden. – Boreas 32: 578–589.

ZOLITSCHKA, B., A. BRAUER, J. F. W. NEGENDANK, H. STOCKHAUSEN & A. LANG (2000): Annually dated late Wechselian continental paleoclimate record from the Eifel, Germany. – Geology 28: 783–786.