Evolution of anuran assemblages in the Tertiary and Quaternary of Europe, in the context of palaeoclimate and palaeogeography

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Abstract. The history of the faunas of anurans during the Tertiary and Quaternary in Europe is presented. Two families (Discoglossidae and Palaeobatrachidae) were recorded from the Cretaceous of Europe and both survived the Cretaceous/Tertiary crisis. The earliest known Tertiary anurans, represented by the Discoglossidae and perhaps Palaeobatrachidae, come from Hainin, Belgium (middle Paleocene). Only the Bufonidae appear to join them before the end of the Paleocene, however, they subsequently disappeared only to re-appear at the beginning of the Miocene. The paucity of Paleocene data is due to a lack of fossiliferous strata, rather than a post-Cretaceous discontinuity of the anuran fauna. Europe and North America were separated by the Atlantic Ocean in the early Eocene (50 Ma) and climate at that time was tropical. Ranidae, Pelobatidae, Pelodytidae, Leptodactylidae appeared in the Eocene; the last family was represented by the genus *Thaumastosaurus* which is a Gondwanan element. Others were either immigrants, probably from Asia, or originated in Europe (Pelodytidae) or in North America (Pelobatidae). Supposed temporary presence of the Microhylidae and Rhacophoridae in the European Eocene requires further confirmation. A drop of temperature at the end of the Eocene (one of the causes of a crisis called the 'Grande Coupure') is associated with the definitive disappearance of the Leptodactylidae in Europe and of palaeobatrachids from the region of the British Isles, as well as the temporary disappearance of the pelodytids (until they re-appear in the Miocene). During the Oligocene, the European anuran fauna was comparatively stable, only forms belonging to the group of green frogs (Ranidae) appeared in the early Oligocene. In the early Miocene, the Hylidae appeared, whereas the Pelodytidae and Bufonidae re-appeared. The most diversified anuran fauna in the history of Europe was in early Miocene (approx. 20 Ma) when some extant genera and even species first appeared. Since then, the diversity of the European anuran assemblages decreased, mainly as a result of climatic deterioration. During the early Pleistocene, the discoglossid genus *Latonia* and the entire family Palaeobatrachidae became extinct, undoubtedly because of continental glaciation.

Amphibia-Reptilia 24: 133-167

Introduction

More than 85 extinct species of anurans were described from the Tertiary and Quaternary of Europe (about 70 in the Tertiary, about 16 in the Quaternary). Of them, only 26 appear to be valid (25 in the Tertiary and only *Pliobatrachus langhae* in the Quaternary). Others are either synonyms of recent species, *nomina dubia*, *nomina vana*, or *nomina nuda* (mainly based on Sanchiz, 1998a). Supposedly, a number of extinct species have not yet been discovered in the European Tertiary. Nevertheless, all these data collected since the first half of 19th century (i.e., in nearly 200 years) from more than 300 localities (Sanchiz, 1998a), represent a basis from which the principal features of evolution of the entire amphibian assemblages in Europe may be inferred. Here we present results concerning the anurans.

Amphibians are ectothermic vertebrates and as such their distribution reflects climatic conditions in which they live. This is why they may be used as a tool for palaeoclimatic reconstructions. In addition, they are limited in their movements, so their fossil distribution reflects palaeogeography.

The following review of evolution of anuran assemblages is inferred from the geochronologically arranged list of European Tertiary and Quaternary anuran-bearing fossil sites and their faunal composition. That part of the table covering Tertiary may be downloaded from http://rocek.gli.cas.cz/tertianura.pdf, or is available on request from the authors.

Geochronology (table 1)

Catastrophic events that took place 65 million years ago marked the end of the Mesozoic and therefore the beginning of the Cenozoic. No significant event occurred at the Tertiary-Quaternary transition; the age of this boundary is fixed at 1.64 Ma ('Ma' is the abbreviation for 'million years').

The Tertiary is subdivided into epochs (or series) and stages. International reference stages are defined in the marine realm, but recently stages based on mammals, restricted to the continental realm of Europe, have also been defined. Unfortunately, correlations between marine and continental stages remain poorly resolved. In addition, stratigraphic units of short duration were defined in the Tertiary: Standard levels ('MP units') in the Paleogene (Schmidt-Kittler, 1987) and MN zones in the Neogene (Bruijn et al., 1992). They are used in this paper. It is worth mentioning that the duration of each unit, MP or MN, is unknown; durations are not equal.

The Quaternary comprises the Pleistocene and Holocene. Here, we use the classical subdivision into early (lower), middle, and late (upper) Pleistocene. The boundary between the early and middle Pleistocene was assigned an age of 0.7 Ma whereas the middle-late Pleistocene limit is fixed to about 0.13 Ma. The Holocene (also called 'Recent') represents the last 10,000 years.

Table 1. Correlations between various marine and continental stratigraphic scales.

Million years	Era / Systems / Epochs			Marine stages	Continental stages	Standard levels and MN zones
	QUATERNARY					
1.64	TERTIARY	NEOGENE	PLIOCENE	Piacenzian	Villanyian	MN 17
						MN 16
					Ruscinian	MN 15
				Zanclean		MN 14
5.3			MIOCENE	Messinian	Turolian	MN 13
				Tortonian		MN 12
						MN 11
10.7					Vallesian	MN 10
				Serravallian		MN 9
					Astaracian	MN 7+8
14.4				Langhian		MN 6
				Burdigalian	Orleanian	MN 5
						MN 4
						MN 3
23.4				Aquitanian	Agenian	MN 2
						MN 1
		PALAEOGENE	OLIGOCENE	Chattian	Arvernian	MP 30
						MP 29
						MP 28
						MP 27
28.5						MP 26
				Stampian		MP 25
					Suevian	MP 24
						MP 23
						MP 22
						MP 21
34.7			EOCENE	Priabonian	Headonian	MP 20
						MP 19
38						MP 18
				Bartonian		MP 17
						MP 16
41				Lutetian	Rhenanian	MP 15
						MP 14
					Geiseltalian	MP 13
						MP 12
48						MP 11
				Ypresian		MP 10
					Neustrian	MP 8+9
						MP 7
54,5			PALAEOCENE	Thanetian		MP 6
				Danian		MP 1-5

Before the Tertiary (fig. 1)

In Europe, localities from the Cretaceous, i.e., ante-Tertiary localities, produced only taxonomically poor anuran faunas. Only two families, the Discoglossidae and Palaeobatrachidae, have been identified (Sanchiz, 1998a; Grigorescu et al., 1999). In addition, a third, indeterminate family occurs in the late Cretaceous of Spain (Duffaud and Rage, 1999; Roček, 2000).

During the late Cretaceous, Europe was not yet separated from North America and it was united to Asia (fig. 1). These three continents formed the supercontinent Laurasia. The remaining continents formed another supercontinent, Gondwana. However, Gondwana began to break up during the Jurassic and, during the late Cretaceous, Africa was already isolated. Laurasia was separated from the Gondwanan complex by the Tethys Ocean but two routes temporarily linked Laurasian and Gondwanan continents: (i) during the latest Cretaceous, North America (and therefore Europe) was connected to South America by a terrestrial route (Rage, 1988a) and, (ii) during the entire Cretaceous, the Mediterranean Sill (sometimes named 'Apulian route') connected Europe and southwestern Asia to Africa; it

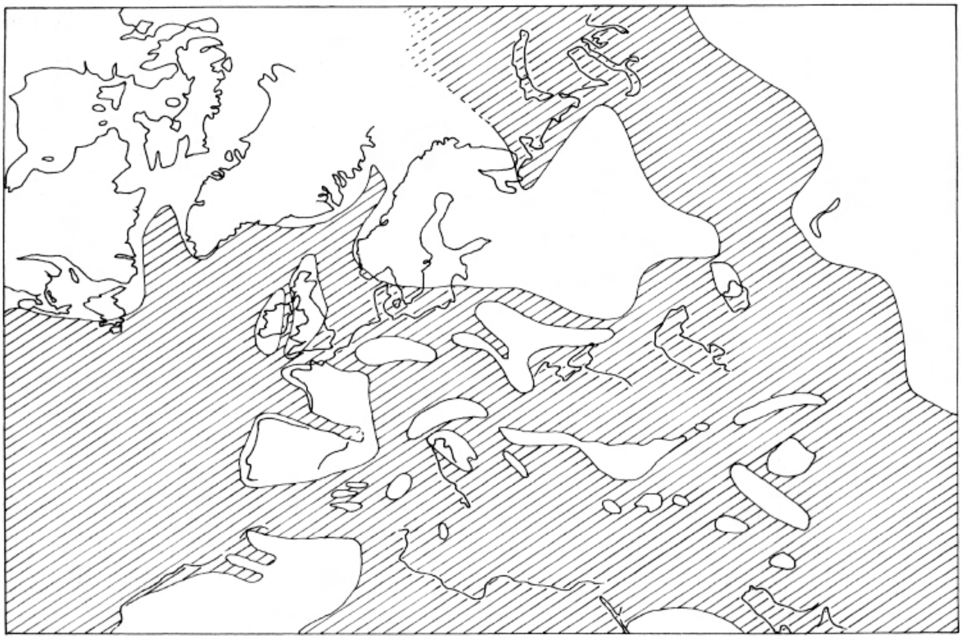

Figure 1. Europe at the end of the Cretaceous (Maastrichtian, 69.5-65 Ma). A part of Europe is still connected to North America. The remainder of the continent is an archipelago that is palaeobiogeographically related to North America and Africa, but separated from Asia. Hatched areas: seas. After Camoin et al. (1993) and Philip et al. (2000), simplified.

perhaps acted as a discontinuous route by the Cretaceous-Tertiary transition (Gheerbrant, 1990). In contrast, Europe was separated from Asia by a broad epicontinental sea, the Uralian Sea (Obik Sea + Turgai Strait), also named Western Siberian Sea. But Europe was not an exposed continent as it is today; because of epicontinental seaways it was an archipelago with variable geography. The climate was clearly warmer than today. The crisis of the Cretaceous-Tertiary boundary did not significantly affect anurans; however, the indeterminate family that was present in the late Cretaceous of Spain has not been found in the Tertiary (Duffaud, 2000).

Paleocene (65-53 million years ago)

Palaeogeographic and palaeoclimatic context

During the Paleocene, Europe was still united with North America. The land bridge which connected North America to South America acted as a dispersal route but it probably vanished by the latest Paleocene (Gayet et al., 1992). The Uralian Sea was still present. Moreover, during the early Paleocene, another epicontinental sea stretched from the Baltic area to southeastern Europe. Other epicontinental seas encroached continents during the

Palaeocene but, on the whole, they did not form barriers. Interchanges between Eurasia and Africa took place over the Mediterranean Sill (Gheerbrant, 1990) but, because of the discontinuous nature of this route, amphibians probably could not use it.

At the beginning of this period the climate was warm, of tropical type. By the end of the Paleocene (ca 55 Ma) a rapid warming took place. This warm episode (LPTM = Late Paleocene Thermal Maximum) appears to have been very close to the Paleocene-Eocene boundary.

Anuran faunas

In Europe, only two Paleocene localities have yielded anurans: Hainin (MP 1-5, late Danian, middle Paleocene), in Belgium, and Cernay (MP 6, Thanetian, late Paleocene), in France. Therefore, the earliest anurans from the Tertiary in Europe are those from the middle Paleocene of Hainin.

Discoglossidae. Hainin has produced an indeterminate discoglossid, possibly belonging to the *Discoglossus* group according to the morphology of a single vertebra (Roček and Rage, 2000: 1335). The presence of the Discoglossidae in the late Paleocene is not certain (Roček and Rage, 2000).

Palaeobatrachidae. Palaeobatrachidae were reported from Hainin (Groessens-Van Dyck, 1981), but the identification is questionable; the supposed Hainin palaeobatrachid is represented by only the distal part of a humerus which makes its assignment to the Palaeobatrachidae doubtful (but not excluded) (Roček and Rage, 2000). In contrast, Cernay yielded unquestionable Palaeobatrachidae material (*Palaeobatrachus*; Vergnaud-Grazzini and Hoffstetter, 1972).

Bufonidae. Cernay has produced the earliest bufonid in the Old World (Rage, in press).

Neobatrachia. An indeterminate representative of the Neobatrachia is present at Cernay. As rightly stated by Estes et al. (1967) the fossil cannot be identified at the family level.

Comments

The Discoglossidae and Palaeobatrachidae were undoubtedly present during the middle and late Paleocene, respectively. The late Maastrichtian-early Paleocene gap in the European anuran record may be attributed to the absence of fossiliferous deposits, rather than reflecting an absence of anurans.

Presence of Bufonidae in the European late Paleocene is somewhat surprising. The family was reported on briefly by Estes (1970) from the Paleocene of Brazil (implicitly from the middle Paleocene of Itaboraí). Unfortunately, the specimens from Brazil have not yet been studied. The specimens from Brazil and France represent both the earliest bufonids and the only representatives of the family in the Paleocene.

In summary, the anuran fauna from the European Paleocene is very poor and little diversified. It is partly inherited from the latest Mesozoic, but some novelties are present (Bufonidae and an indeterminate neobatrachian).

Eocene (53-34 million years ago)

Palaeogeographic and palaeoclimatic context (fig. 2)

Important palaeogeographic events occurred during the early Eocene. The North Atlantic Ocean opened between North America and Europe (ca 50 Ma). Since Europe was still separated from Asia by the Uralian Sea, the continent was isolated. However, by the end of the Eocene (ca 34 Ma), the Uralian Sea partly closed, which resulted in a terrestrial connection between Europe and Asia. In fact, Europe was an archipelago because epicontinental seas were extensive; the geography of this archipelago was changing during the Eocene and European continental landmasses were probably temporarily interconnected at various times. The discontinuous route which linked Europe to Africa during the Paleocene was still present, but its nature probably prevented dispersal of amphibians.

Figure 2. Europe during the middle Eocene (Lutetian, 46-40 Ma). Europe is definitely separated from North America; it is still an archipelago separated from Asia. Hatched areas: seas. After Butterlin et al. (1993) and Meulenkamp et al. (2000a), simplified.

After the Late Paleocene Thermal Maximum, the climate was still warm and it remained humid during the early Eocene and perhaps the beginning of the middle Eocene. This period which spans the late Paleocene and early Eocene was the warmest one of the Tertiary; the climate was tropical/equatorial up to high northern regions (Berggren et al., 1998). During the middle Eocene, temperature began to decrease; this cooling was accompanied by a progressive aridification. The rate of cooling accelerated near the end of the Eocene. However, despite this drop of temperature, the late Eocene was warmer than the present time.

Remark on stratigraphy of Geiseltal localities

Geiseltal in Germany yielded fossil amphibians of great interest. The age of the locality is generally regarded to range from MP 11 to MP 13 (Sanchiz, 1998a). In fact, Geiseltal designates an assemblage of localities which represent all levels of the middle Eocene. Four main 'levels' are recognized at Geiseltal: Unterkohle (MP 11), untere Mittelkohle (MP 12), obere Mittelkohle (MP 13), and Oberkohle (MP 14). The Unterkohle level did not produce anurans. Only the holotype specimen of *Parabufella longipes*, a species which was later considered a synonym of *Eopelobates hinschei*, was recovered from perhaps MP 12. Haubold and Krumbiegel (1984) stated, without giving more accurate data, that it comes from the Mittelkohle levels, i.e. MP 12 or MP 13. The majority of frogs were recovered from the obere Mittelkohle level, mainly from the 'obere Hauptmittelkohle' bed which represents the uppermost part of this level. Besides, it cannot be excluded that at least one of the richest sites (Cecilie III) represents the lowermost part of the Oberkohle level (Haubold 1989), i.e. the lowermost part of MP 14.

Anuran faunas

Anuran faunas taxonomically more diversified than those from the Paleocene appeared at the base of the Eocene (MP 7). Discoglossids and palaeobatrachids surviving from the Paleocene are present. Bufonids disappeared, but several anuran families made their appearance in Europe during the Eocene.

Discoglossidae. Discoglossids were present as early as the earliest Eocene (MP 7) at Dormaal (Belgium). According to Duffaud (2000) the form from Dormaal is similar to a discoglossid present in the latest Cretaceous of Europe. The family has also been recorded from the levels MP 8+9 and MP 10. Scarce discoglossids are known from the middle Eocene. They were recovered only from the obere Hauptmittelkohle beds (MP 13, ? or MP 14) of Geiseltal (Germany) which yielded one specimen of *Opisthocoellelus weigelti* and an indeterminate form (Kuhn, 1941; Sanchiz, 1998a). In the rich middle Eocene (MP 11) locality of Messel (Germany) the discoglossids, probably for ecological reasons, were absent. As in the middle Eocene, the Discoglossidae are rare in late Eocene localities. They have been reported from southern England (MP 16 to MP 20; Milner, 1986; an undescribed small discoglossid from Beacon Cliff, pers. obs.) and from southern France (MP 18 and 19; Duffaud, 2000 and pers. obs.). This scarcity is perhaps related to the above-mentioned aridification.

Palaeobatrachidae. Palaeobatrachids were present throughout the early Eocene but they remain poorly studied (Duffaud, 2000). The middle Eocene of Messel (MP 11;

Germany) yielded *Messelobatrachus tobieni* (Wuttke, 1988). In addition, one incomplete specimen of an anuran described as *Lutetiobatrachus gracilis* (see fig. 159 in Wuttke, 1988) might belong to the Palaeobatrachidae (Sanchiz, 1998a) but some characters contradict this conclusion. However, in context of prevailing faunal composition, this specimen and its taxonomic assignment is not too important. According to Špinar (1972), the Geiseltal levels include *Palaeobatrachus grandipes* which was recovered from the 'obere Mittelkohle' and 'obere Hauptmittelkohle' beds (i.e., MP 13 and perhaps MP 14). Late Eocene Palaeobatrachidae, clearly distinguishable from mid-Eocene forms, are known from localities in southern England where they are represented by the genus *Albionbatrachus*. This genus first appeared in MP 17; the last record is from the latest Eocene (MP 20) of Whitecliff Bay, Isle of Wight, England (Sanchiz, 1998a). It was never found beyond southern England. This means that its geographic range was disjunct from the rest of Europe, though the origin of the genus must be sought among earlier European Palaeobatrachidae. It was already noticed on the basis of mammals (Sudre, 1974) and squamates (Rage and Ford, 1980) that, during the late Eocene, England and France belonged to two separate provinces. In continental Europe, the only palaeobatrachid (? *Palaeobatrachus*) from the late Eocene was found at Grisolles (MP 16), France (Duffaud, 2000). The late Eocene geographic distribution of the Palaeobatrachidae is somewhat reminiscent of that of the Discoglossidae.

Pelobatidae. The earliest European pelobatid frogs were recovered from several Eocene localities of the standard level MP 7: Dormaal (Belgium), Le Quesnoy, Rians, and perhaps Meudon (France) (Duffaud, 2000), and perhaps Silveirinha (Portugal). The genus *Eopelobates* was reported from Silveirhina (Antunes and Russell, 1981). It should be noted that disarticulated postcranial elements of pelobatids from the Tertiary have often been referred to the genus *Eopelobates* only on the basis of their stratigraphic occurrence. However, reliable identification of the genera *Eopelobates* and *Pelobates* can be based exclusively on cranial bones, especially on the frontoparietal. This is why it is wiser to refer pelobatid postcranial bones from the Tertiary as indeterminate Pelobatidae, until more precise diagnostic characters are available. Older published data should be used only if this is taken into account. Pelobatidae are present also in other levels of the early Eocene. Duffaud (2000) reported *Eopelobates* cf. *E. hinschei* from Prémontré, France (MP 10). The middle Eocene yielded *Eopelobates wagneri* and *Eopelobates hinschei* which might be conspecific with the former species. *Eopelobates wagneri* comes from Messel (MP 11; Wuttke, 1988) while *E. hinschei* was recovered from the 'Mittelkohle', 'obere Mittelkohle', and 'obere Hauptmittelkohle' beds of Geiseltal (i.e. MP 13 and perhaps MP 12 and MP 14). The Pelobatidae are also common in late Eocene localities. Apart from indeterminate taxa, *Eopelobates* aff. *E. bayeri* was reported from Escamps (MP 19, France) by Duffaud (2000).

Pelodytidae. One single incomplete ilium from Saint-Maximin (MP 13, middle Eocene, France) possibly belongs to the Pelodytidae; if this determination is correct, then this fossil represents the earliest known pelodytid (Duffaud and Rage, 1997; Duffaud, 2000) and, at the same time, a new faunal component in the European anuran assemblages. However, undoubted Pelodytidae were recorded from the late Eocene (MP 16, Bartonian). Late Eocene Pelodytidae were similar to the living genus *Pelodytes* and Rage (1988b) and Duffaud (2000) reported them as cf. *Pelodytes*. They were found only in French localities, from MP 16 to MP 19 (Crochet et al., 1981). These late Eocene pelodytids represent the earliest undoubted members of the family.

Leptodactylidae. A possible leptodactylid was reported from the early Eocene of Prémontré (MP 10, France) on the basis of some ilia (Augé et al., 1997).

However, an unquestionable leptodactylid, *Thaumastosaurus bottii*, occurs in the upper Eocene of France (MP 17-MP 19). It appears to be closely related to the Tertiary genus *Eophractus* from southernmost South America (Schaeffer, 1949) and to some extent also to the living *Caudiverbera* and *Cyclorana* from South America (Roček and Lamaud, 1995). The genus was perhaps also present in the latest Eocene (MP 20) of England (Sanchiz, 1998a).

Ranidae. Apart from some doubtful specimens (Roček and Rage, 2000), the earliest Ranidae come from the late Eocene (MP 16) of France where they were found in levels ranging from MP 16 to MP 19 (Rage, 1984). An English locality (MP 17) also yielded a ranid (Holman and Harrison, 1999) which already seems to be close to the living *Rana*; Holman and Harrison even assigned the British fossil to this genus. However, this determination cannot be justified because of the nature of the fossil (an incomplete ilium). Within these ranids, a form from French localities of the level MP 17 is reminiscent of green frogs.

Rhacophoridae. Sanchiz (1998a) reported Rhacophoridae from the late Eocene of France (Escamps, MP 19). These fossils were not described and remain unstudied. Therefore, the presence of this family in the Eocene of Europe should be still regarded as questionable. In Europe, Rhacophoridae were also reported from the Pliocene (see below).

Microhylidae. According to Sanchiz (1998a: 95, 154), Microhylidae were present in the latest Eocene of Europe (based on material from Escamps; MP 19). This is the only report of Microhylidae in Europe. However, description of these specimens has never been published. Hence, occurrence of Microhylidae in Europe still needs confirmation.

Comments

Eocene anuran assemblages were markedly more diversified than those from the Paleocene. They consisted not only of autochthonous taxa, i.e. those surviving from the Paleocene (Discoglossidae and Palaeobatrachidae), but also those which appeared as new. One might count among the latter group the representatives of the families Pelobatidae, Pelodytidae, Ranidae, Leptodactylidae, and perhaps Microhylidae and Rhacophoridae. Only bufonids, found in the Paleocene, disappeared and have not been found in the European Eocene.

During the earliest Eocene (MP 7) anurans were more abundant than in the Paleocene. The Discoglossidae and Palaeobatrachidae were joined by Pelobatidae, but the Bufonidae were no longer present. The situation continued to be the same in the younger levels of the early Eocene (MP 8+9 and MP 10) but in Prémontré (MP 10, France), a possible leptodactylid could be present (Augé et al., 1997) in addition to discoglossids, palaeobatrachids and pelobatids.

The fauna of the middle Eocene comprised the same families (Discoglossidae, Palaeobatrachidae, Pelobatidae), plus a possible representative of the Pelodytidae as a new faunal component.

During the late Eocene, the anuran fauna was enriched by the Ranidae (in MP 16) and perhaps the Microhylidae (MP 19) and the Rhacophoridae (MP 19). Undoubted pelodytids (MP 16) and leptodactylids (MP 17) were also recovered. These families joined the Discoglossidae, Palaeobatrachidae, and Pelobatidae which continued from earlier periods. As a result, the anuran fauna of the late Eocene can be considered rich and diverse. Nevertheless, aquatic forms such as Discoglossidae and Palaeobatrachidae were rare, which might be associated with the late Eocene aridification.

Pelodytidae, Ranidae, as well as Microhylidae and Rhacophoridae (if the identification of the two latter families is correct) from the Eocene of Europe represent the earliest known members of these families. Moreover, the Pelobatidae from the earliest Eocene are the oldest representatives of the family in Europe.

The geographic origin of most of faunal components that first appeared in the Eocene of Europe remains obscure, particularly the origin of the Pelobatidae. In Europe, the family suddenly appeared during the earliest Eocene, and in North America two forms closely related to the genus *Pelobates* (which is restricted to the Old World today) were found in the middle Eocene and early Oligocene (a pelobatid from the Green River Formation, middle Eocene of Wyoming and *'Eopelobates' grandis* from the Chadron Formation, early Oligocene of South Dakota; Roček and Rage, 2000). Earlier occurrences attributed to the Pelobatidae are represented by a single ilium from the late Jurassic or earliest Cretaceous of the Morrison Formation in North America which was considered an indeterminate pelobatid by Evans and Milner (1993); however, it might also be referred to the Discoglossidae (Rage, unpublished observation) and also Sanchiz (1998a) pointed out that its basic morphology is shared with the Pelodytidae (the closest relatives of the Pelobatidae). *Scotiophryne pustulosa*, from the latest Cretaceous (Maastrichtian) and early Paleocene of North America, was referred to the Discoglossidae (Estes, 1969; Sanchiz, 1998a), but its ilia (including the holotype) do not show discoglossid features; rather, their morphology recalls that of the Pelobatidae (Vergnaud Grazzini and Wenz, 1975; Duffaud, 2000). Therefore, if the fossil from the Morrison Formation is not a pelobatid, then *Scotiophryne* is probably the oldest representative of the family. In addition, indeterminate pelobatids were reported from the Cretaceous-Paleocene transition of India (Sahni et al., 1982) and from the late Cretaceous (? Campanian) of Madagascar (Asher and Krause, 1998). However, the latter identification, based on a single incomplete atlas, is questionable. It is obvious that the geographic origin of the Pelobatidae which reached Europe by the earliest Eocene cannot be inferred unequivocally from these contradicting data. Nevertheless, the palaeogeography of pre-Eocene periods and the form related to the European *Eopelobates* and *Pelobates* found in the middle Eocene Green River Formation of Wyoming (Roček and Rage, 2000) suggest that they most probably arrived from North America.

The history of the Pelodytidae, a family closely related to the Pelobatidae, has been restricted to Laurasian continents. Living forms inhabit Europe, the continent which yielded the earliest fossils (MP 16, late Eocene, or perhaps as early as in MP 13, middle Eocene). Outside of Europe, the family was reported only from the Oligocene-Miocene transition and middle Miocene of North America (Henrici, 1994). Occurrence of the earliest pelodytids in Europe during the late, or perhaps middle, Eocene is of interest because the continent was isolated at that time. Therefore, the autochthonous origin of these earliest fossils cannot be ruled out.

Appearance of the earliest Ranidae in the European late Eocene is surprising. As is the case with pelodytids, palaeogeography in the late Eocene would argue for their autochthonous origin in Europe but this appears highly doubtful. If ranids did not originate in Europe, they could have come either from North America, Asia, or Africa. However, if North America was the source of the Ranidae, then they had to reach Europe before the two continents were separated (salt water forms an effective barrier to dispersal of modern amphibians) and they had to occur in Europe during the middle and early late Eocene but fossil ranids from these strata have not been discovered yet. Besides, the earliest record of the Ranidae in North America is from the Miocene, which also contradicts the hypothesis of the origin of the Ranidae in North America. Immigration from Africa could theoretically be possible because it was connected to Europe by the Mediterranean Sill, but this route was not continuous representing a hindrance to amphibian dispersal. However, an Asian hypothesis would be consistent with the opinion of Bossuyt and Milinkovitch (2001) who suggested that, owing to the drift of India, ranids reached Asia at the time of the Indian/Asian connection (i.e., from the latest Cretaceous to early Eocene).

The Leptodactylidae is a taxonomically poorly defined family. Today it inhabits the Americas from southern USA to southern South America. The earliest representative is *Baurubatrachus pricei* from the Santonian-Campanian of Brazil (Báez and Perí, 1989). Apart from South America and Europe, the only other unquestionable leptodactylid was found in the Dominican Republic (*Eleutherodactylus* sp. from the Eocene; Poinar and Canatella, 1987). Doubtful leptodactylids were reported from the Eocene of North America (Roček and Rage, 2000). The Leptodactylidae probably reached Europe via the terrestrial route which connected South America and North America during the latest Cretaceous and early Paleocene. From North America, these frogs were able to enter Europe before the separation of the two continents (Rage, 1999).

As for Microhylidae and Rhacophoridae, assuming that these identifications are correct, no palaeobiogeographic scenario can be proposed. Disregarding these questionable records from Europe, fossil Microhylidae are known only from the late Oligocene or middle Miocene of Australia (Tyler, 1976, 1994) and lower Pleistocene through Holocene of North America (Sanchiz, 1998a). Similarly, records of fossil Rhacophoridae are only from the Pleistocene of Japan (see Sanchiz, 1998a for a review). It was suggested, though with some doubts (Sanchiz, 1998a), that *Ranomorphus* from the upper Pliocene of Russia might belong to the Rhacophoridae as well (see below). Today, the Microhylidae inhabit North and South America, Africa south of the Sahara, and India and Korea to northern Australia, whereas the Rhacophoridae are limited to Africa, Madagascar, and southern Asia to the Indo-Australian Archipelago (Frost, 1985). In any case, it should be kept in mind that the presence of Microhylidae and Rhacophoridae in Europe during the Eocene remains to be confirmed.

The 'Grande Coupure'

The Eocene-Oligocene transition (MP 20/MP 21) corresponds to a worldwide faunal turnover; it is especially marked in Europe where this phenomenon is named the 'Grande Coupure' (= Great Break). During the late Eocene, mammals underwent gradual extinction and, as far as these animals are concerned, the faunal change was mostly produced by appearance of new forms (Asian immigrants) at the beginnning of the Oligocene. On the contrary, squamate reptiles underwent diversification in Europe during the late Eocene (perhaps as a result of the decrease of mammals). Therefore, during the late Eocene, squamates were diverse and flourished in Europe. But the 'Grande Coupure' (i.e., the Eocene-Oligocene transition) caused the extinction of about three fourths of the squamate taxa. This prominent phenomenon resulted from a series of events ('Terminal Eocene Events'; Pomerol and Premoli-Silva, 1986), mainly worldwide cooling and regression of seas. Moreover, the effect of the phenomenon is hightened in Europe because the regression caused a partial disappearance of the Uralian Sea (the Turgai Strait closed) which previously separated Europe from Asia. Consequently, Asian immigrants entered Europe and eliminated forms then in place. Although this scenario is rather simplistic, it may be basically valid.

Surprisingly, anurans were not strongly affected by this event. Only the palaeobatrachid *Albionbatrachus* became extinct at the Grande Coupure. *Thaumastosaurus* (Leptodactylidae) and the European Microhylidae and Rhacophoridae (assuming the latter two families were actually present) supposedly also died out at the Grande Coupure. *Thaumastosaurus* was reported with some doubt from MP 20, the last level of the Eocene (Sanchiz, 1998a); on the other hand, Microhylidae and Rhacophoridae are absent in MP 20, but it should be noted that localities from this level are neither numerous nor rich. Consequently, the absence of frogs in MP 20 cannot be considered significant. Supposedly, *Thaumastosaurus*, Microhylidae and Rhacophoridae (if the latter two families were really present) could have become extinct either at the Grande Coupure or slightly before. This marks the definite disappearance of Leptodactylidae, Microhylidae, and probably Rhacophoridae (see above the problem of *Ranomorphus*) from Europe. The Pelodytidae were present up to MP 19, but afterwards they disappeared temporarily from Europe, as they are absent during the entire Oligocene. The Ranidae temporarily withdrew from Europe during the same period as the Pelodytidae and are probably absent in the European earliest Oligocene.

Oligocene (34-23.5 million years ago)

Palaeogeographic and palaeoclimatic context (fig. 3)

From the Oligocene onwards, Europe was connected to Asia. As a result of the collision between Eurasia and Africa (initiated long before the Oligocene), parts of the Alpine chain emerged from the Pyrenees to the Caucasus; they more or less completely separated an 'intra-European' sea, the Paratethys, from the Tethys. A seaway on the Rhine graben, the Hessen depression, and Alpine foreland basins separated western Europe from central and eastern parts of the continent. However, marine conditions were not permanent in these seas and interchanges between terrestrial areas were possible. The Mediterranean Sill was no longer a possible terrestrial route between Europe and Africa. Therefore, Europe was connected only to Asia.

The temperature continued to decline after the Eocene. The cooling probably culminated during the early Oligocene, after which temperature increased irregularly up to the end of the period. Aridification that began in the Eocene increased throughout the Oligocene and the late Oligocene appears to have been markedly arid.

Anuran faunas

Despite climatic drying, anurans were common during most of the Oligocene. The four families which were known in the Eocene (Discoglossidae, Palaeobatrachidae, Pelobatidae, Ranidae) are present from MP 22 to the end of the Oligocene (MP 30). However, fauna from the earliest Oligocene (MP 21), i.e. from the period just following the 'Grande Coupure', was still very depauperate.

Discoglossidae. The earliest Oligocene strata in Hoeleden (MP 21, Belgium) yielded a discoglossid that appears to be close to *Discoglossus* (Duffaud, 2000). The beginning of the Oligocene has also produced a fossil that seems to be the earliest record of *Latonia*, a genus which is common in Neogene localities. This possible first occurrence of *Latonia* is from the earliest Oligocene of Aubrelong 1 (MP 21, France) where it is represented by a large urostyle, typical for this genus. *Latonia* was a robust frog (its representatives from the Miocene reached snout-vent length of about 20 cm; Roček, 1994) but its representatives from the Oligocene, if really belonging to the genus, were of lesser size. *Latonia* can be easily distinguished from other discoglossids, not only on the basis of articulated skeletons, but on some isolated elements as well (e.g. frontoparietal, maxilla, proximal

Figure 3. Europe at the beginning of the Oligocene (Late Rupelian, 32-29 Ma). The Turgai Strait is closed, as a result Europe is connected to Asia. Hatched areas: seas. After Rögl (1998) and Meulenkamp et al. (2000b), simplified.

part of the lower jaw, humerus, tibiofibula, and some others). Discoglossids gradually diversified in the European Oligocene, which is evidenced by *Opisthocoellellus hessi* from the lower Oligocene (MP 22) of Bechlejovice, Czech Republic, which is closely related to the middle Eocene *O. weigelti* but differs from *Latonia*. Moreover, the oldest possible representative of the extant genus *Discoglossus* (*D. troscheli*) is known from the latest Oligocene (MP 30) of Rott, Germany. The taxonomic status of *D. troscheli* should be clarified; however, it is distinct from *Opisthocoelellus* and *Latonia*. It is difficult to say whether records published as "*Latonia* sp." represent a single species or more because the earliest articulated skeleton of *Latonia* is from the late Oligocene (Chattian) of Vertaizon, France (*L. vertaizoni*) and disarticulated Oligocene material could not be compared with it. What might be of some importance is that all these early finds of putative *Latonia* are from French localities, whereas *Latonia* is lacking in German and more eastern localities of the same age (except for Gaimersheim and Gussenstadt, late Oligocene of Germany). This can be illustrated by otherwise diverse faunas from the late Oligocene of Rott, Orsberg and the early Oligocene of Bechlejovice where the presence of abundant and taxonomically diverse palaeobatrachids is in contrast to the complete absence of *Latonia* (if one regards *Opisthocoelellus* distinct from the latter genus; contra Sanchiz, 1998a).

Palaeobatrachidae. It seems that the Palaeobatrachidae underwent some diversification as early as the early Oligocene, as evidenced by their record from the localities Markvartice and Bechlejovice (MP 21, MP 22, respectively) in the Czech Republic, where at least two species were found in both of them. Two species of *Palaeobatrachus* were also found in several latest Oligocene and earliest Miocene localities of Germany and the Czech Republic (Rott, Orsberg, Odeř).

It should be noted that although palaeobatrachids were ancient constituents of the European anuran fauna, they never reached the Iberian Peninsula (however, Oligocene localities are rare on the Peninsula). It is difficult to reconstruct their history subsequent to *Messelobatrachus* and *Albionbatrachus* but it may be of some interest that palaeobatrachids were lacking in the Oligocene of France, whereas they were recorded at the two earliest Oligocene sites in Belgium (Hoeleden and Hoogbutsel; MP 21), and from Oligocene localities in Central Europe, i.e. from Germany, the Czech Republic and Switzerland.

Pelobatidae. The extant genus *Pelobates* appeared in European anuran assemblages by the early/middle Oligocene (MP 23), perhaps as early as the early Oligocene (Mas de Got A, MP 22) (*Pelobates* sp., Duffaud, 2000). An extinct species, *P. decheni*, was recovered from the late Oligocene (Enspel, MP 28 and Rott, MP 30). On the other hand, *Eopelobates* was present in the earliest Oligocene (MP 21), in Belgium and France (*E.* aff. *bayeri*, Duffaud, 2000), whereas *E. anthracinus* occurred in the latest Oligocene (MP 30) of Rott, Germany, a locality which also produced *P. decheni*. Therefore, the two genera co-existed during the entire Oligocene.

Ranidae. Apart from *Rana* of undetermined relationships, the European Oligocene yielded the earliest water frogs. These frogs are informally referred to as ‘green frogs’. The green frog group comprises true species and hybrids (at least one of the latter was formerly considered a true species: *Rana esculenta*) that form a complex assemblage. Dubois and Günther (1982) proposed naming this assemblage ‘Synklepton *Rana esculenta*’; they are currently referred to the subgenus *Pelophylax*. Sanchiz (1998a) often used the term ‘*Rana* (*ridibunda*) sp.’ The morphology of the skeleton in these frogs is uniform and the osteology of several recently recognized living species remains unknown; this state of affairs makes the palaeontological study of this assemblage difficult.

Green frogs were present as early as the early Oligocene, at Möhren 13 (MP 22), Germany; these fossils represent the earliest known members of the European green frog group (Sanchiz et al., 1993). Two extinct species of questionable validity (*Rana aquensis* and *R. meriani*), both from the late Oligocene, probably belong to this assemblage.

It should be noted that ranid frogs were reported throughout the whole Oligocene, seemingly including level MP 21 (Sanchiz, 1998a). However, in this level they were recorded only at Ronzon (France) which is a locality that produced only sparse remains of vertebrates. It was identified by a non-expert (Aymard, 1856), and the fossils were not illustrated and were probably lost. Ranidae were not found in other localities of the same age as Ronzon. Therefore, the fossil evidence of the Ranidae from the earliest standard level of the Oligocene (i.e. MP 21) is not reliable and the family is probably lacking in MP 21.

Comments

Anurans were not affected by any event that occurred during the Oligocene. The fauna was very homogeneous through the entire period. The Discoglossidae, Palaeobatrachidae, and Pelobatidae, families surviving from the Eocene, were present through the whole Oligocene. The Ranidae were probably absent from the earliest Oligocene (MP 21), but it is not possible to determine whether this resulted from their temporary withdrawal or whether this is due to a poor fossil record in MP 21.

The Oligocene is marked by the emergence of living genera: *Pelobates*, *Rana*, and perhaps *Discoglossus*. The common occurrence of aquatic frogs (discoglossids of the *Discoglossus*/*Latonia* group, Palaeobatrachidae, Ranidae of the 'green frogs' group) is somewhat astonishing considering the global aridification; but occurrence of these frogs depends on local bodies of water. On the other hand, several localities in Central Europe regarded as close to the Oligocene/Miocene transition yielded only palaeobatrachids. Exclusive presence of palaeobatrachids probably resulted from local ecological conditions, rather than from some climatic episode favourable especially to the Palaeobatrachidae.

Two localities of Oligocene age, Rott (MP 30) and to a lesser extent Bechlejovice (MP 22), represent the earliest records of a taxonomically diversified anuran fauna in one locality. Beside two species (if the Orsberg site near Rott, both of the same age, is taken into account) of *Palaeobatrachus* (*P. diluvianus*, *P. grandipes*) there are also two pelobatids (*Eopelobates anthracinus*, *Pelobates decheni*), at least one ranid (*Rana meriani*, but the much smaller *R. noeggerathi* with different body proportions might represent another species), and one discoglossid (*Discoglossus troscheli*; see above). The absence of *Latonia* in Rott and Bechlejovice assemblages is not surprising, in context of possible ecological interference of this discoglossid with abundant palaeobatrachids (see below).

Miocene (23.5-5.3 million years ago)

Palaeogeographic and palaeoclimatic context (fig. 4)

An important palaeobiogeographic event took place during the early Miocene: the collision between Eurasia and the Afro-Arabian plate resulted in a terrestrial route that still exists between the two continental blocks. This event gave birth to the Mediterranean Sea. The first terrestrial interchanges between Eurasia and Africa occurred by 20/18 Ma (Bernor et al., 1987). Therefore, since the early Miocene, Europe was connected to both Asia

Figure 4. Europe during the early Miocene (Burdigalian, 20.5-16 Ma). Eurasia is definitely connected to Africa. Hatched areas: seas. After Cavelier et al. (1993) and Rögl (1998).

and Africa. The southern part of Europe was an archipelago; more specifically, in south Central and Eastern Europe, the Paratethys epicontinental sea subdivided the continent into distinct terrestrial areas the geography of which was changing. The Rhine graben — Alpine basins seaway still separated western Europe from central Europe; but conditions there were not always fully marine and this sea was not an impenetrable barrier. By the end of the Miocene, the Mediterranean largely dried up (Messinian event; 6-5.3 Ma); as a result, the Iberian Peninsula was directly connected to Africa for a short period of time. However, this connection did not cause important interchanges.

After the rather cold and dry late Oligocene, the climate changed markedly. During the early Miocene, a warm and wet climate was established. The warming reached a maximum during the latest part of the early Miocene (about MN 4), but the climate was not as warm as that of the late Paleocene-early Eocene. Temperature and humidity decreased during the middle Miocene. During the late Miocene, climate in eastern Europe became drier while western Europe remained comparatively humid.

Anuran faunas

The Discoglossidae, Palaeobatrachidae, Pelobatidae, and Ranidae, previously known in the late Oligocene, were still present in the Miocene. The Bufonidae, which withdrew from Europe before the Eocene, reappeared on the continent during the early Miocene (MN 4) whereas the Pelodytidae, which disappeared from Europe during the latest Eocene, also returned in the early Miocene (MN 2). An important event in Europe is the appearance of the Hylidae (MN 4).

Discoglossidae. During the Oligocene, *Latonia* was known only in the western part of Europe (but fossiliferous localities of that age are rare in the eastern part of the continent). In eastern Europe, the genus was present in the early Miocene (Ulm-Westtangente, MN 2, Germany) and it was soon distributed all over contemporary Europe (Dolnice, MN 4, Czech Republic and Belomechetskaya, MN 6, Russia; Pickford et al., 2000). At the beginning of the Miocene, *Latonia* diversified into several species. *Latonia vertaizoni* did not survive the lower Miocene (last record is from 'Saint-Gérand-le-Puy', MN 1 and 2); it was replaced by the larger *L. gigantea* extending from the western part of the continent (Sansan, France, MN 6) possibly to the Ukraine (Gritsev, MN 9) and Russia (Belomechetskaya, MN 6). *Latonia seyfriedi*, the type species of the genus, is known from the middle Miocene of Öhningen (Astaracian, MN 7+8), Germany. It is worth mentioning that the holotype of *L. seyfriedi* is observable only in ventral aspect (Roček, 1994), consequently, a key-character (sculpturing of skull bones) is concealed. Therefore it is not possible to determine whether other species assigned to the genus should be referred to *L. seyfriedi*. It is not excluded that there was another species in central and eastern Europe, namely *L. kolebabi* (see Špinar, 1978). In contrast to *L. seyfriedi* and *L. gigantea*, *L. ragei* remained restricted to the early Miocene (MN 2-MN 4; Hossini, 1993; Sanchiz, 1998b). Sanchiz (1998a) reported the living genus *Discoglossus* from the early Miocene of Sardinia (Oschiri, MN 1-5?).

The earliest palaeontological record of the living genus *Bombina* is reported from the early Miocene (Sanchiz and Schleich, 1986); however, the fossil is represented only by postcranial elements (from Weissenburg 6, Germany; MN 1 or 2) which does not permit identification below the genus level. In central and eastern Europe, at Opole (MN 7+8), Rudabánya (MN 9), and probably also in Öhningen (originally described as *Palaeophrynos agassizi*) (MN 7+8), *Bombina* co-existed with *Latonia*. This is not consistent with the view that *Bombina* represents the possible terminal stage of the evolutionary sequence *Latonia-Discoglossus-Bombina* as a result of shortened somatogenesis (Smirnov, 1989; Roček, 1994).

The earliest record of *Alytes*, another extant genus, is from the late Miocene (Turolian, MN 13) of Salobreña, Spain.

Palaeobatrachidae. After the basal Oligocene (MP 21), the earliest record of Palaeobatrachidae in western Europe is from French localities: Laugnac (*Palaeobatrachus robustus*; Hossini and Rage, 2000), Poncenat (both MN 2), and 'Saint-Gérand-le-Puy' (MN

1+2). However, the paucity of the record in post-MN 2 Miocene of France (only Issoire and Sansan) suggests that, in contrast to central and eastern Europe, the family was never abundant in the western part of the continent.

Another interesting feature of palaeobatrachid stratigraphic occurrence is that they disappeared from a part of central Europe in Astaracian and post-Astaracian times. Apart from Adelschlag (southern Germany) palaeobatrachids are absent from German Astaracian sites, including rich localities such as Öhningen and Steinheim, whereas they are present at Opole (Poland) which is approximately of the same age (MN 7+8). Similarly, the more recent levels of the Vallesian, Suchomasty (MN 9), Czech Republic, lack palaeobatrachids while the family is well represented in Gritsev, Ukraine (also MN 9). If absence of palaeobatrachids in this part of central Europe was not caused by ecological interference with *Latonia* (see below), then this distribution can be explained as a gradual shift of palaeobatrachids toward the east, resulting from both local extinctions and dispersals. If this is correct, then the only exception would be the distribution in the Mediterranean area, evidenced by the record from the late Miocene (Turolian) of Ciabot Cagna, Italy.

In central and eastern Europe the last record of *Palaeobatrachus* is from the Astaracian of Germany (Adelschlag) and Poland (Opole), and from the Vallesian of Ukraine (Gritsev), with a possible exception in the Pliocene of Poland (see below). After that, there is a gap until the Pliocene.

It is worth noting that *Palaeobatrachus* was found together with *Latonia* (Sansan, MN 6; Rudabánya and Gritsev, MN 9) in only a very few localities (all from the Miocene) which suggests different ecological requirements.

Pelobatidae. It seems that *Eopelobates* was still present in the early Miocene but that it disappeared from the fossil record by the middle/early late Miocene, as evidenced by the most recent finds in La Grive (MN 7+8) and Suchomasty (MN 9) (Hossini, 1992; Sanchiz, 1998a). Apparently, it disappeared first from the Iberian area where the last record is from the late Oligocene locality of Paguera in Majorca. After MN 9, only *Pelobates* remained in Europe.

The genus *Pelobates* is represented by forms close to living species, or perhaps by living species. Highly ossified species (*Pelobates* cf. *cultripes* from Villafeliche 4 & 6, MN 7+8?), Spain, was joined during the latest Miocene (Turolian, MN 13) by two other, less ossified forms, *P.* cf. *syriacus* (Monasteri, Greece) and *P.* cf. *fuscus* (Polgárdi, Hungary; Venczel, 1997).

Pelodytidae. Pelodytidae occurred during the early Miocene (MN 2) in Spain and France. An extinct species, *Pelodytes arevacus*, was present in Spain during the middle Miocene (MN 7+8; Sanchiz, 1978), and perhaps MN 2 and MN 9. The Miocene fossil record of the family (genus *Pelodytes* only) comes from Spain, France, Austria (Sanchiz, 1998b), and Germany (M. Böhme, pers. comm.).

Bufonidae. Bufonids were present in the early Miocene of Spain and France, as evidenced by findings in Córcoles, Buñol and Valdemoros 3B (all MN 4), and in the slightly younger French locality Vieux-Collonges (MN 4/5). The family diversified rapidly (immigration?) as suggested by the appearance of presumably two species at Córcoles and Vieux-Collonges: a species close to the living *B. viridis* (perhaps the species itself) and an indeterminate species present at both localities (Alférez Delgado and Brea López, 1981; Bailon and Hossini, 1990). It is of some interest that eastwards, in Dolnice (Czech Republic) which is contemporary with the Spanish sites, in spite of numerous anuran specimens, the Bufonidae were absent. However, they were present in central and eastern Europe shortly afterwards. *Bufo* was recorded with certainty from the MN 6 site Devínska Nová Ves in Slovakia; it was described there as *Bufo priscus*. The latter species is a probable synonym of *Bufo* (formerly *Palaeophrynos*) *gessneri*, an extinct species from the middle Miocene (MN 7+8) of Öhningen. Besides, *Bufo* sp. was also reported from MN 5 of Srybulaksk, Russia, and from MN 7+8 of Sokolovskyi, Ukraine (Chkhikvadze, 1984). Disregarding their absence in various localities, bufonids have become more or less regular constituents of the European anuran assemblages since the early Astaracian (MN 6).

Extant species, or forms closely related, emerged during the Miocene: *Bufo viridis* (MN 4 in Spain, see above), *B. bufo* (MN 9 in the Czech Republic) and *B. calamita* (MN 12 in Spain). Two extinct species were described: *B. gessneri* (MN 7+8) and *Bufo priscus* (MN 6 and perhaps MN 7+8) (Špinar et al., 1993; Sanchiz, 1998a). However, *B. priscus*, and therefore *Bufo gessneri*, appear to be very close to *B. viridis* and synonymy cannot be excluded.

Hylidae. The first recorded representative of the Hylidae in Europe (genus *Hyla*) is from the early Miocene (Orleanian, MN 4) of Austria (Sanchiz, 1998b). Since then, the genus is reported, though rarely because of its tiny fragile skeleton, from various localities in Europe. *Hyla*, close to the living *H. arborea*, was recorded in the latest Miocene (MN 13) of Ano Metochi, Greece (Sanchiz, 1998a).

Ranidae. The Ranidae have been recorded throughout the entire sequence of Miocene strata, with some doubts concerning MN 1 (Sanchiz, 1998a). Most of them belong to 'green frogs' complex. Various extinct species were described from the Miocene, but most of them are either *nomina dubia*, *nomina vana*, or *nomina nuda* (Sanchiz, 1998a; Rage and Hossini, 2000). However, an extinct species of green frog, *Rana pueyoi* from the late Miocene (MN 9-10) of Spain, might be a valid species.

The second group of ranid frogs present in Europe today, i.e. 'brown frogs', is represented in the Miocene by a single specimen. This fossil comes from the early Miocene (MN 3) of Dietrichsberg, Germany (Böhme, 2001). If data concerning this specimen are correct, then this single occurrence is chronologically isolated and thus astonishing because numerous younger Miocene localities with rich anuran faunas have not yielded brown frogs.

In addition, there is a distinct Miocene ranid the morphological features of which do not match either brown or green ranids. It seems to be closer to green ranids, but it also displays some characteristics of brown frogs. It was found in two French localities: Montréal-du-Gers, MN 4 (Bailon, pers. comm.) and Sansan, MN 6 (Rage and Hossini, 2000).

Comments

Appearence of the Hylidae and re-appearance of the Bufonidae and Pelodytidae in the Miocene fossil record are among the last important events in the history of anurans in Europe.

Disregarding the temporary presence of the family Bufonidae in the Paleocene, the earliest European bufonids occurred in the late early Miocene (MN 4). They were already represented by forms closely related to living European species. On the Afro-Arabian plate, possible members of the family ('bufonoids indet.') might be approximately contemporaneous with these European fossils (Al Sarrar, Saudi Arabia; Thomas et al., 1982). Apart from Paleocene fossils from France and Brazil (see above), older bufonids were reported, without any comment or description, from the middle Oligocene of North America (USA; Patton, 1969) and Central Asia (Kazakhstan; Chkhikvadze, 1985); these reports are questionable and undoubted members of the family are unknown in both North America and Asia prior to the Miocene (Roček and Rage, 2000). Hence, current knowledge on geographic and stratigraphic distribution provides little insight into the palaeobiogeographic history of the family and geographic origin of the bufonids that reached Europe during the early Miocene remains unknown. According to cytogenetics, recent European species belong to the neotropical radiation, not to the African one (Sanchiz, 1997). It should be noted that arrival of bufonids in Europe coincides with the establishment of a terrestrial contact between Eurasia and Africa, but this does not mean that bufonids arrived from Africa. Sanchiz (1997) suggested that bufonids that reached Europe during the Miocene probably came from Asia.

The Pelodytidae have not been recorded in the Oligocene strata of Europe. This gap is probably not due to incompleteness of the fossil record because Oligocene localities have yielded abundant anuran material. Rather, it is a result of a temporary withdrawal for unknown reasons. It may be speculated that Miocene pelodytids came from Asia.

In Europe, the earliest Hylidae were present in the early Miocene (MN 4). The oldest hylid might be represented by poorly preserved material recovered from the Maastrichtian of India (Prasad and Rage, 1995). Estes (1970) reported, without description or comments, Hylidae from the middle Paleocene of Brazil. In North America, the first record of the family is known from the early Oligocene (Holman, 1968). In Asia, apart from the questionable report from the Cretaceous of India, Hylidae are known only from the Quaternary and no fossil hylid has been recovered in Africa. The sparse fossil record of early Hylidae does not permit us to infer the palaeobiogeographic history of the family; however, Sanchíz and Roček (1996) suggested that European species of *Hyla* were immigrants from Asia.

Among other anurans which appeared in Europe during the Miocene were ranids (*Rana* cf. *R. temporaria*) belonging to the group of so called "brown frogs" with their earliest record from the early Miocene (MN 3) of Germany; according to Böhme (2001) they could be of Asiatic origin. However, later (after MN 3), brown frogs have not been recorded in the Miocene of Europe. The specimen from Germany might thus represent an isolated and brief wave of immigration.

Another important event during the Miocene was the emergence of living species (Bailon et al., 1988). As early as the early Miocene, the European fauna consisted of taxa closely related to those living today. At that time, the fauna reached the peak of its diversity. However, pelobatids are apparently absent from the oldest localities of the Miocene (MN 1); but this is probably not significant because this level produced only sparse remains. The early Miocene fauna was comprised of two types of discoglossids (two or more species of heavily ossified *Latonia* and slightly ossified *Discoglossus* or *Bombina*, or both), two types of pelobatids (*Eopelobates* and *Pelobates*), *Pelodytes*, one or more *Palaeobatrachus*, at least two species of *Bufo*, *Hyla*, and probably several species of *Rana* for which the taxonomic status is difficult to assess. Nevertheless, it can be assumed that they belonged both to the green frogs and brown frogs groups.

Since the early Miocene, the diversity of the European anuran fauna has been steadily decreasing.

Pliocene (5.3-1.64 million years ago)

Palaeogeographic and palaeoclimatic context

During the Pliocene, the geography of Europe was not much different from today. Only the Paratethys Sea was still present, but southern Europe was no longer an archipelago and the Paratethys was no longer connected to the Tethys Sea. The Paratethys extended from the Vienna Basin, north of the Balkan area, to the contemporary Caspian Sea, north of the Caucasus. During the Pliocene, it was separated into several parts. The western part was isolated as a lake (evidenced by lacustrine sediments) whereas the central and eastern parts were laguno-marine.

The climate of the early Pliocene became warm and humid again. But a deterioration began in the middle Pliocene (3.1 Ma), heralding the Quaternary cooling. From the middle Pliocene until the end of the period, rapid climatic oscillations occurred, including a second marked drop in temperature approximately 2.4 million years ago.

Anuran faunas

In Europe, the Pliocene anuran fauna as a whole was not significantly different from that of the Miocene.

Discoglossidae. The three living genera of European Discoglossidae (*Discoglossus*, *Alytes*, *Bombina*) originated during the Oligocene or Miocene. In the Pliocene *Alytes* apparently extended eastward as is evidenced by the record from MN 14-16 of Willershausen, Germany. The living species *Bombina bombina* was recovered from the late Pliocene of Poland (Sanchíz and Młynarski, 1979). *Discoglossus* sp. was reported from western Europe.

It is also interesting to follow the post-Miocene record of *Latonia*. In the Miocene it was widely distributed from Spain to Russia. Then, in the Pliocene, it became very rare in central Europe where it is known only in the early Pliocene of Osztramos 1, Hungary (MN 14; Venczel, 2001) and Kaltensundheim, Germany (MN 15?; Böhme, 1981). Instead, it was recorded from MN 14 of Kuchurgan in Ukraine, MN 15 of Ivanovce in Slovakia, and MN 16? of Gorishnaya Vygnanka of Moldova, besides numerous finds in the Mediterranean (Greece, Italy, southern France). Although this gradual withdrawal of *Latonia* to the Mediterranean and eastern regions may be due to the distribution of known localities, its absence in most central European sites that have otherwise rich anuran record may be of some importance.

Palaeobatrachidae. The Palaeobatrachidae were rare or even absent during the late Miocene. In central and eastern Europe, *Palaeobatrachus* was apparently absent after the late Astaracian-early Vallesian. The only exception is a record from Węże 2 (late Pliocene, MN 16, Poland) which seems to be the very last record of *Palaeobatrachus*. From the early Pliocene (MN 14), palaeobatrachids have not been recorded; the first *Pliobatrachus* was found in MN 15 (from Węże 1 and Ivanovce; Poland and Slovakia respectively). In the late Pliocene, *Pliobatrachus* extended eastward up to the Don River area (Ratnikov, 1993a). *Pliobatrachus* and *Palaeobatrachus* stratigraphically overlap only in MN 15-MN 16.

Identification of the two genera is problematic; it is very difficult to distinguish the two genera from each other and it is not excluded that both represent the same genus (Vergnaud-Grazzini and Młynarski, 1969).

Pelobatidae. All living species of *Pelobates* or closely related forms, which were found in Miocene localities, were also present in the Pliocene. No other form belonging to this genus was recorded in the Pliocene.

As stated above, *Eopelobates* apparently became extinct during the middle/early late Miocene. Only Sanchiz (1998a) reported this genus from the Pliocene of central Europe (MN 15 of Węże 1, Poland, and Ivanovce, Slovakia; MN 16 of Rębielice Królewskie, Poland). However, most of the material from these localities is represented by postcranial bones which cannot be used as a reliable basis for distinguishing between *Eopelobates* and *Pelobates* (see above). The only cranial element is a small fragment of frontoparietal

(Sanchiz and Młynarski, 1979) that is, however, not sufficient for certain identification. Consequently, we do not believe that *Eopelobates* survived until the Pliocene.

Pelodytidae. A form close to *Pelodytes* (cf. *Pelodytes*) was reported only from western Europe. The living species *P. punctatus* might be present in Montoussé 5, France (MN 17; Bailon, 1991).

Bufonidae. All extinct bufonids were already absent in the Pliocene and the family is represented exclusively by living species (or closely related forms) that survived from the Miocene. Moreover, the living species, *Bufo raddei*, that is restricted to eastern Asia today, was reported from various localities in eastern Europe (Chkhikvadze, 1984; Ratnikov, 1997).

Hylidae. Rare hylids, including *Hyla* cf. *arborea*, were reported from the Pliocene. This scarcity is most probably due to the tiny size of *Hyla*.

Ranidae. In contrast to the rather obscure situation concerning European "green frogs", the fossil record of "brown frogs" seems to be better documented. The earliest remains of the extant *Rana arvalis* and undoubted *R. temporaria* (Ruscinian, MN 15) come from Węże 1, Poland and Kaltensundheim in Germany, respectively. The earliest discovery of *Rana latastei*, or a closely related form, is from the Villanyian, MN 16 of Arondelli, Italy and that of *R. dalmatina* is from MN 16-17 of Včeláre, Slovakia. *Rana macrocnemis*, which today inhabits the extreme south-eastern part of Europe and western Asia, was reported from the Pliocene of Kisatibi, Georgia (Riabinin, 1928); however, this identification needs revision. *Rana strausi*, an extinct species from the Pliocene (MN 14-16) of Willershausen, Germany, appears to be a brown frog, but its relationships to extant species cannot be established (Špinar, 1980).

Mensi et al. (1992) inferred, from electrophoretic data, that the first split within the assemblage of living European brown frogs occurred approximately 2.6 million years ago (middle or late Pliocene). This is consistent with the diversification of brown frogs observed in the Pliocene of Europe. However, "brown ranids" were apparently present on the continent as early as the early Miocene (see above).

Several species of green frogs apparently originated during the Pliocene (Sanchiz, 1997). Specimens belonging to this group are common in Pliocene localities.

Rhacophoridae. *Ranomorphus similis*, from the late Pliocene of the Don River Basin (Russia), was described as a member of the Discoglossidae by Ratnikov (1993b). However, Sanchiz (1998a) suggested that it is a member of the Rhacophoridae. This specimen is an incomplete ilium which indicates that it belongs to a ranoid, but which family cannot be determined unquestionably.

Comments

The composition of the European Pliocene anuran fauna was not essentially different from that of the Miocene. Moreover, it was not significantly affected by the climatic deterioration which began about 3 million years ago. However, this deterioration perhaps caused the geographic disjunct ranges of various taxa (Rage, 1997).

At the end of the Pliocene, the European anuran fauna was basically diversified into extant species. Exceptions might be the species of the 'green' ranid complex which cannot be identified, and *Pelodytes*. The Pliocene/Pleistocene transition was reached (and crossed) by two extinct genera, *Latonia* and *Pliobatrachus* (or by *Palaeobatrachus*, if the two latter taxa are synonymous). An important event is the reappearance of "brown frogs" which rapidly diversified in Europe.

Quaternary

Palaeogeographic and palaeoclimatic context (fig. 5)

The geography of Europe during the Pleistocene was basically the same as it is today. The Paratethys no longer existed as a sea. The main geographic events resulted from the evolution of ice sheets that covered northern Europe and high mountains. In central Europe, during the Last Glacial Maximum (ca 22,000-14,000 years ago), the northern continental glacier reached the Sudetic mountain system and its southern edge was separated from the ice cap covering the Alps by a only 300 km wide corridor of tundra. As a result, anuran populations of western Europe were nearly completely separated from those in the eastern part of the continent by an ice and climatic barrier. At that time, the sea level was probably 120 to 140 m lower than today; consequently, various islands (including Britain) were connected to mainland Europe.

The Pleistocene is characterized by pronounced climatic fluctuations. There were prominent contrasts between glacial and interglacial stages. Ice sheets and glaciers developed during glacial periods whereas during certain interglacial times summers were warmer than those of the present (Gleed-Owen, 1999). During the Last Glacial Maximum, forests and woodlands were almost lacking.

Anuran fauna

Apparently, no noticeable extinction occurred at the Pliocene-Quaternary transition.

Discoglossidae. *Latonia* became extinct during the Pleistocene. The genus is known only from the lower Pleistocene of Pietrafitta (Italy; Delfino, 2001). *Bombina variegata* was reported from the middle Pleistocene of Brassó (Hungary) by Bolkay (1913), but this identification is not unequivocal because it was based on an atlas and pterygoid which do not provide diagnostic characters at the species level (Sedláčková, 2000).

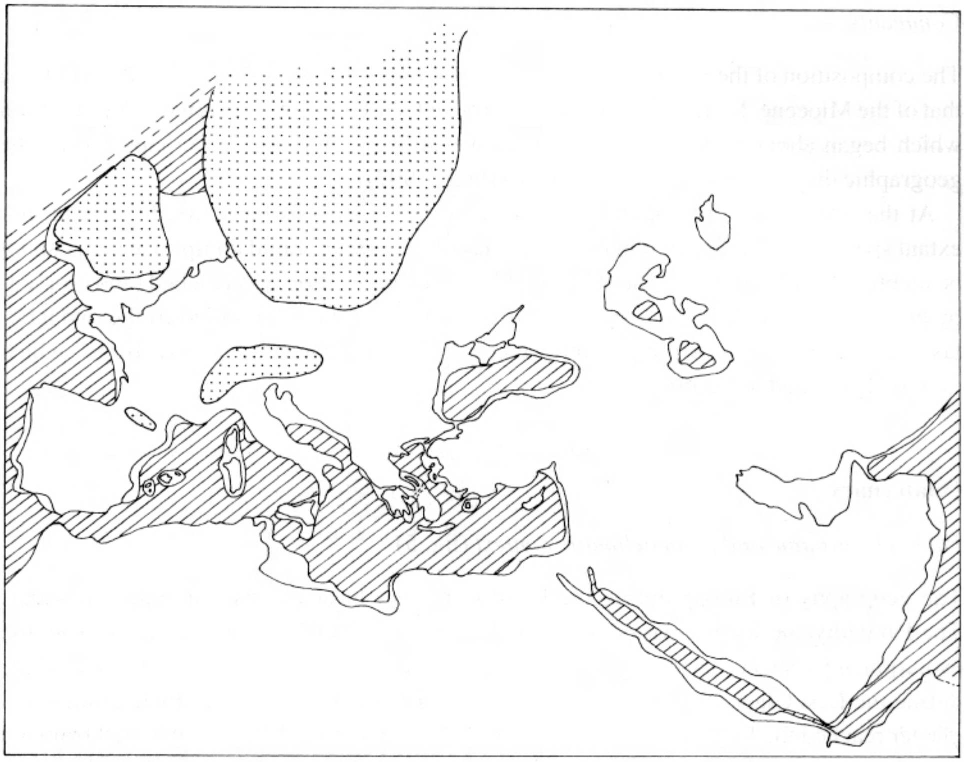

Figure 5. Europe during the Last Glacial Maximum (Quaternary, 20,000-18,000 years ago). Stippled areas: ice; hatched areas: seas. After Anastasakis and Dermitzakis (1990) and Peuvalst et al. (2000). Simplified.

Alytes is common in Pleistocene localities. The living *A. obstetricans* was reported from the late Pleistocene of Western Europe. *Discoglossus* has been found in the Mediterranean region and also north of its present range (Rage, 1972).

One of the most interesting facts concerning Pleistocene discoglossids is the discovery of an endemic species, *Baleaphryne muletensis*, in the Balearic islands. This species was first recovered as a fossil from the middle and upper Pleistocene deposits of Majorca (Sanchiz and Adrover, 1979). Subsequently, Mayol and Alcover (1981) found it surviving on the same island. Now, the species is also known in Minorca. According to Dubois (1984), Maxson (1984) and some others, *Baleaphryne* might be a synonym of *Alytes*; this synonymy was followed by Sanchiz (1998a). However, from an osteological point of view, these two genera appear to be rather distinct from one another.

Palaeobatrachidae. *Pliobatrachus* survived into the Pleistocene. It was found in the lower Pleistocene of Hajnáčka (Slovakia; Hodrová, 1981) and Betfia, Romania (former Hungarian name was Püspökfűrdő; Fejérváry, 1917) and in the middle Pleistocene of Kozi

Grzbiet, Poland (Sanchíz and Szyndlar, 1984). The latter occurrence represents the latest known record of the family Palaeobatrachidae.

Pelobatidae. Although pelobatids are not common in Pleistocene localities, they survived until today without being affected by any notable event.

Pelodytidae. The distributional ranges of *Pelodytes* species are widely disjunct today: *P. punctatus* and *P. ibericus* (Sánchez-Herráiz et al., 2000) are present in western Europe, west from Germany, and *P. caucasicus* is present in the Caucasian and Transcaucasian regions. However, in spite of the fact that fossil *Pelodytes* is rare, fossil taxa have been recovered from regions between the present areas of distribution. Böttcher (1994) identified *P. punctatus* in the middle Pleistocene of Germany, whereas Sanchiz and Szyndlar (1984) reported, with some doubts, *Pelodytes* sp. from the early Pleistocene of Poland.

Bufonidae. Bufonidae are common in Pleistocene localities. In the Pleistocene anuran faunas, *B. viridis* and *B. calamita* were clearly more common than *B. bufo* (pers. obs.). Today, the ratio appears to be the reverse.

Hylidae. Hylids are still rare in Pleistocene localities. *Hyla meridionalis*, today restricted to southwestern Europe, was reported by Holman (1992) from England. This occurrence is not surprising because the age of the locality that yielded the fossil corresponds to an interglacial stage (Ipswichian, the last interglacial stage).

Ranidae. During the Pleistocene, some ranid species were represented by individuals larger and with stronger crests for muscular insertions than those living today (Rage, 1972). Such large individuals belonging to *Rana temporaria* were described as members of an extinct species, *Rana mehelyi*, by Bolkay (1911). Large individuals are also known in the species *Rana dalmatina* and among green frogs (Rage, 1972).

Comments

The history of anurans during the Pleistocene was probably controlled largely by climatic fluctuations. According to Holman (1998), during glacial phases the cold-tolerant *Rana temporaria* was often the only frog present in ice-free areas. Although there is no palaeontological evidence, it may be hypothesized that most anurans were forced to withdraw toward southern refuges during glacial times. This perhaps resulted in local speciation (in peninsulae as suggested by present distributions). During interglacial periods, the continent was re-colonized by various forms from southern refuges; for example, *Bufo calamita* probably re-colonised northwestern Europe from the Iberian Peninsula (Gleed-Owen, 1997).

Glaciations caused east-west disjunctions, but this was probably not the cause of the origin of vicariant species. Such a process of speciation was initiated before the Pleistocene, during the Neogene (Borkin, 1986; Rage, 1997). However, this east-west disjunction has certainly affected the present distribution. Mountains also played a role in the processes of disjunction, vicariance, and re-colonisation (Arntzen, 1978; Rage and Saint-Girons, 1989).

Most species of the present fauna probably originated prior to the Pleistocene (Bailon et al., 1988; Sanchíz, 1997). They were certainly already present in Europe during the Pliocene. The present fauna has probably resulted from the addition to the 'old' Neogene stock of a few species which originated in southern refuges or which entered Europe (probably from Asia) during the Pleistocene.

The Pleistocene climate was not, a priori, favourable to herpetofaunas. However, as far as anurans are concerned, the fauna from the Pleistocene did not markedly decrease in diversity with regard to that of the Pliocene. At the family level, only palaeobatrachids became extinct during the Pleistocene (Sanchíz and Szyndlar, 1984). This is the only anuran family (besides the early group represented by *Prosalirus*) that became extinct in the entire history of the Anura, most probably because of its strict association with water.

Another European anuran which became extinct during the Pleistocene was *Latonia*. Perhaps the taxon did not survive the drop of temperature in the early Pleistocene. It may also be noted from its last occurrence, that it did not survive in spite of the fact that its range reached southern Europe.

No other extinction of anuran taxa took place during the Pleistocene. The decrease of anuran diversity in Europe has been a progressive process which was initiated as early as the middle Miocene.

Conclusions

1. In the Cenozoic of Europe, the succession of anuran assemblages can be followed from the middle Paleocene till today. Eight (perhaps ten, if two families whose existence in Europe is doubtful are taken into account) anuran families occurred in Europe during the Tertiary. All but one (disregarding the two doubtful families) survived until the Pleistocene but, because of extinction of the palaeobatrachids, the Recent European anuran fauna consists of representatives of six families.
2. The only family that persisted throughout the entire Tertiary (although its earliest Tertiary record is from the middle Paleocene) and Quaternary is the Discoglossidae. One family (Palaeobatrachidae) died out.
3. The anuran fauna of the Tertiary originally consisted of two families (Discoglossidae and Palaeobatrachidae) which survived from the Mesozoic and of families which appeared in the Tertiary. The latter either immigrated from other continents (in most cases) or perhaps originated in Europe (Pelodytidae).
4. One (or perhaps as many as three) family not present in Europe today reached the continent during the Tertiary: Leptodactylidae (probably from South America, via North America), and perhaps Microhylidae and Rhacophoridae (both of unknown geographic origin).

5. The main steps in the Tertiary history of anurans in Europe are as follows:
    i) At the beginning of the Tertiary (Paleocene) the anuran fauna was very poor. The Discoglossidae and Palaeobatrachidae, surviving from the Mesozoic, were joined by the Bufonidae.
    ii) The Eocene fauna of Europe consisted of members of autochthonous families, i.e. families surviving from the Paleocene (Discoglossidae and Palaeobatrachidae), and members of families which appeared in Europe for the first time (Pelobatidae, Pelodytidae, Ranidae, Leptodactylidae, and perhaps Microhylidae and Rhacophoridae). This resulted in increase in the diversity of the European anuran fauna. The Bufonidae disappeared from Europe before the beginning of the Eocene (and reappeared in the Miocene).
    iii) Although the 'Grande Coupure', i.e., the Eocene-Oligocene transition strongly affected squamate reptiles and mammals (extinctions), it had comparatively little effect on anurans. During the latest Eocene, or at the Eocene-Oligocene transition, the Pelodytidae temporarily disappeared from Europe, and the Leptodactylidae, Microhylidae and Rhacophoridae (if the two latter families were actually present) definitely disappeared from Europe.
    iv) The European anuran fauna was relatively stable in the Oligocene, consisting of only four families: Discoglossidae, Palaeobatrachidae, Pelobatidae, Ranidae. No family previously unknown in Europe appeared during this period of time. Only forms belonging to the European green frogs group (Ranidae) appeared during the early Oligocene.
    v) The Miocene is a turning point in the history of European anurans. During the early Miocene, Hylidae and brown frogs (Ranidae) appeared in Europe for the first time, while Pelodytidae and Bufonidae reappeared. These taxa probably came from Asia during the early Miocene. Along with the families that were already present, Discoglossidae, Palaeobatrachidae, Pelobatidae, and green frogs (Ranidae), this constituted a rich and diverse fauna, although brown frogs did not persist throughout the Miocene. Moreover, several extant species emerged during the Miocene.
    vi) Since the middle Miocene, the diversity of the fauna has decreased. However, brown frogs re-appeared during the Pliocene. They definitely colonized Europe and became diverse at that time. The climatic deteriorations during the Pliocene and Quaternary affected the geographic distribution of the anurans.
    vii) During the middle Pleistocene, the Palaeobatrachidae died out. After the disappearance of this family, the composition of the modern European fauna at the family level was established.

Acknowledgements. This work was supported by a grant of the GA AVČR No A6013701 and CEZ: Z3013912 of the Geological Institute to Zbyněk Roček. Thanks are also due to Madelaine Böhme (Staatssammlung für

Geologie und Paläontologie, Munich) for providing information on *Pelodytes* from Stubersheim 3, and Salvador Bailon (Laboratoire départemental de préhistoire du Lazaret, Nice) and Massimo Delfino (Università di Firenze) for providing unpublished observations. Martin Pickford (Collège de France, Paris) and Jeffrey G. Eaton (Weber State University, Ogden, Utah) made linguistic improvements.

References

Alférez Delgado, F., Brea López, P. (1981): Estudio preliminar de los restos de Peces, Anfibios y Reptiles del Yacimiento Mioceno de Córcoles (Guadalajara). Bol. R. Soc. Española Hist. Nat. (Geol.) **79**: 5-20.

Anastasakis, G.C., Dermitzakis, M. (1990): Post-Middle-Miocene paleogeographic evolution of the Central Aegean Sea and detailed Quaternary reconstruction of the region. Its possible influence on the distribution of the Quaternary mammals of the Cyclades Islands. N. Jb. Geol. Paläont. Mh **22**: 1-16.

Antunes, M.T., Russell, D.E. (1981): Le gisement de Silveirinha (Bas Mondego, Portugal): La plus ancienne faune de vertébrés éocènes connue en Europe. C.R. Acad. Sci. Paris **II**, **293**: 1099-1102.

Arntzen, J.W. (1978): Some hypotheses on postglacial migrations of the fire-bellied toad *Bombina bombina* (Linnaeus) and the yellow-bellied toad, *Bombina variegata* (Linnaeus). J. Biogeogr. **5**: 339-345.

Asher, R.J., Krause, D.W. (1998): The first pre-Holocene (Cretaceous) record of Anura from Madagaskar. J. Vert. Paleont. **18**: 696-699.

Augé, M., Duffaud, S., Lapparent de Broin, F. de, Rage, J.C., Vasse, D. (1997): Les amphibiens et les reptiles de Prémontré (Cuisien, Bassin parisien): une herpétofaune de référence pour l'Eocène inférieur. Géol. France **1**: 23-33.

Aymard, A. (1856): Rapport sur les collections de M. Pichot-Dumazel. Congrès scientifique de France, 22nd session, Le Puy 1855, p. 227-244. Derache, Paris, and Marchessou, Le Puy.

Báez, A.M., Perí, S. (1989): *Baurubatrachus pricei*, nov. gen. et sp., un Anuro del Cretacico Superior de Minas Gerais, Brasil. Anais Acad. brasil. Cienc. **61**: 47-458.

Bailon, S. (1991): Amphibiens et reptiles du Pliocène et du Quaternaire de France et d'Espagne. Unpublished thesis, University Paris 7.

Bailon, S., Hossini, S. (1990): Les plus anciens Bufonidae (Amphibia, Anura) d'Europe: des espèces du Miocène français. Ann. Paléontol. **76**: 121-132.

Bailon, S., Bour, R., Rage, J.-C. (1988): Quand les espèces de l'herpétofaune française sont-elles apparues? Bull. Soc. herpetol. Fr. **45**: 1-8.

Berggren, W.A., Lucas, S.G., Aubry, M.P. (1998): Late Paleocene-Early Eocene climatic and biotic evolution. In: Late Paleocene-Early Eocene climatic and biotic events in the marine and terrestrial records, p. 1-17. Aubry, M.P., Lucas, S.G., Berggren, W.A., Eds, New York, Columbia Univ. Press.

Bernor, R.L., Brunet, M., Ginsburg, L., Mein, P., Pickford, M., Rögl, F., Sen, S., Steininger, F., Thomas, H. (1987): A consideration of some major topics concerning Old World Miocene mammalian chronology, migrations and paleogeography. Geobios **20**: 431-439.

Böhme, G. (1981): Zur Geschichte der Anuren-Fauna Europas. Wiss. Z. Humboldt-Univ. Berlin, Math.-Nat. R. **31**: 147-149.

Böhme, M. (2001): The oldest representative of a brown frog (Ranidae) from the early Miocene of Germany. Acta Palaeont. Polonica **46**: 119-124.

Bolkay, S.J. (1911): On the pleistocenic predecessor of *Rana fusca* Rös. Mitt. Jahrb. König. Ungar. Geol. Reichsanst. **19**: 155-160.

Bolkay, S.J. (1913): Additions to the fossil herpetology of Hungary from the Pannonian and Praeglacial periode. Mitt. Jahrb. König. Ungar. Geol. Anst. **21**: 217-230.

Borkin, L.J. (1986): Pleistocene glaciations and western-eastern palaearctic disjunction in amphibian distribution. In: Studies in Herpetology, p. 63-66. Roček, Z., Ed., Prague, Charles Univ.

Bossuyt, F., Milinkovitch, M.C. (2001): Amphibians as indicators of early Tertiary "out-of-India" dispersal of vertebrates. Science **292**: 93-95.

Böttcher, R. (1994): Niedere Wirbeltiere (Fische, Amphibien, Reptilien) aus dem Quartär von Stuttgart. Stuttgart. Beitr. Naturk. **B 215**: 1-75.

Bruijn, H. de, Daams, R., Daxner-Höck, G., Fahlbusch, V., Ginsburg, L., Mein, P., Morales, J. (1992): Report on the RCMNS working group on fossil mammals, Reisenburg 1990. Newsl. Stratigr. **26**: 65-118.

Butterlin, J., Vrielynck, B., Guiraud, R., Bignot, G., Colchen, M., Clermonte, J., Andreieff, P., Bellion, Y., Benkhelil, J., Cavelier, C., Cornée, J.J., Mercier de Lepinay, B., Montenat, C., Moreau, C., Poisson, A., Vila, J.M. (1993): Lutetian palaeoenvironments (46-40 Ma). In: Atlas Tethys palaeoenvironmental maps. Dercourt, J., Ricou, L.E., Vrielynck, B., Eds, Rueil Malmaison, BEICIP-FRANLAB.

Camoin, G., Bellion, Y., Benkhelil, J., Cornée, J.J., Dercourt, J., Guiraud, R., Poisson, A., Vrielynck, B. (1993): Late Maastrichtian palaeoenvironments (69.5-65 Ma). In: Atlas Tethys palaeoenvironmental maps. Dercourt, J., Ricou, L.E., Vrielynck, B., Eds, Rueil Malmaison, BEICIP-FRANLAB.

Cavelier, C., Butterlin, J., Clermonte, J., Colchen, M., Guennoc, P., Guiraud, R., Lorenz, C., Andreieff, P., Bellion, Y., Poisson, A., Benkhelil, J., Montenat, C., Platel, J.P., Roger, J. (1993): Late Burdigalian palaeoenvironments (18-16.5 Ma). In: Atlas Tethys palaeoenvironmental maps. Dercourt, J., Ricou, L.E., Vrielynck, B., Eds, Rueil Malmaison, BEICIP-FRANLAB.

Chkhikvadze, V.M. (1984): [Review of fossil tailed and tailles amphibians of the USSR]. Izv. Akad. Nauk GSSR **10**: 5-13 (in Russian).

Chkhikvadze, V.M. (1985): Preliminary results of the study of Tertiary amphibians and squamates from Zaisan Basin. In: Voprosy Gerpetologii, 6th All-Union Herpetological conference, p. 234-235. Darevsky, I.S., Ed., Leningrad, Nauka (in Russain).

Crochet, J.Y., Hartenberger, J.-L., Rage, J.-C., Rémy, J.-A., Sigé, B., Sudre, J., Vianey-Liaud, M. (1981): Les nouvelles faunes de Vertébrés antérieures à la "Grande Coupure" découvertes dans les Phosphorites du Quercy. Bull. Mus. natn. Hist. nat. **C 3**: 245-26.

Delfino, M. (2001): Erpetofaune italiane del Neogene e del Quaternario. Unpublished PhD Dissertation, Modena and Reggio Emilia University.

Dubois, A. (1984): La nomenclature supragénérique des amphibiens anoures. Mém. Mus. natn. Hist. nat. **A 131**: 57 pp.

Dubois, A., Günther, R. (1982): Klepton and synklepton: Two new evolutionary systematics categories in zoology. Zool. Jb. Syst. **109**: 290-305.

Duffaud, S. (2000): Les faunes d'amphibiens du Crétacé supérieur à l'Oligocène inférieur en Europe: paléodiversité, évolution, mise en place. Unpublished thesis, Muséum national d'Histoire Naturelle, Paris.

Duffaud, S., Rage, J.-C. (1997): Les remplissages karstiques polyphasés (Eocène, Oligocène, Pliocène) de Saint-Maximin (Phosphorites du Gard) et leur apport à la connaissance des faunes européennes, notamment pour l'Eocène moyen (MP 13). Amphibiens et reptiles. In: Actes du Congrès BiochroM'97, **2**, p. 729-732. Aguilar, J.P., Legendre, S., Michaux, J., Eds, Montpellier, Mém. Trav. E.P.H.E.

Duffaud, S., Rage, J.-C. (1999): Amphibians from the Upper Cretaceous of Laño (Basque Country, Spain). Estud. Mus. Cienc. Nat. Alava, **14** (núm. esp. 1): 111-120.

Estes, R. (1969): A new fossil Dicoglossid frog from Montana and Wyoming. Breviora **328**: 1-7.

Estes, R. (1970): Origin of the recent North American lower Vertebrate fauna: an inquiry into the fossil record. Forma et Functio **3**: 139-163.

Estes, R., Hecht, M.K., Hoffstetter, R. (1967): Paleocene amphibians from Cernay, France. Amer. Mus. Novit. **2295**: 1-25.

Evans, S.E., Milner, A.R. (1993): Frogs and salamanders from the Upper Jurassic Morrison Formation (Quarry Nine, Como Bluff) of North America. J. Vert. Paleo. **13**: 24-30.

Fejérváry, G.J. (1917): Anoures fossiles des couches préglaciaires de Püspökfűrdő en Hongrie. Földtani közlöny **47**: 141-172.

Frost, D.R. (1985): Amphibian species of the World. Allen Press and the Assoc. Syst. Coll.

Gayet, M., Rage, J.-C., Sempere, T., Gagnier, P.-Y. (1992): Modalités des échanges de vertébrés continentaux entre l'Amérique du Nord et l'Amérique du Sud au Crétacé supérieur et au Paléocène. Bull. Soc. géol. Fr. **163**: 781-791.

Gheerbrant, E. (1990): On the early biogeographical history of the African placentals. Historical Biol. **4**: 107-116.

Gleed-Owen, C. (1997): The Devensian late-Glacial arrival of natterjack toad, *Bufo calamita*, in Britain and its implications for colonisation routes and land-bridges. Quaternary Newsl. **81**: 18-24.

Gleed-Owen, C. (1999): The palaeoclimatic and biostratigraphic significance of herpetofaunal remains from the British Quaternary. In: Late Cenozoic environments and Hominid evolution: a tribute to Bill Bishop, p. 201-215. Andrews, P., Banham, P., Eds, London, Geological Society.

Grigorescu, D., Venczel, M., Csiki, Z., Limberea, R. (1999): New latest Cretaceous microvertebrate fossil assemblages from the Hateg Basin (Romania). Geol. Mijnbouw **78**: 301-314.

Groessens-Van Dyck, M.C. (1981): Etude des amphibiens du Montien continental de Hainin. Bull. Soc. belge Géol. **90**: 87-101.

Haubold, H. (1989): Die Referenzfauna des Geiseltalium, MP levels 11 bis 13 (Mitteleozän, Lutetium). Palaeovertebrata **19**: 81-93.

Haubold, H., Krumbiegel, G. (1984): Typenkatalog der Wirbeltiere aus dem Eozän des Geiseltals. 1934-1984, 50 Jahre Geiseltalmuseum an der Martin-Luther-Universität Halle-Wittenberg, Halle.

Henrici, A. (1994): *Tephrodytes brassicarvalis*, new genus and species (Anura: Pelodytidae) from the Arikareean Cabbage Patch beds of Montana, USA, and pelodytid-pelobatid relationships. Ann. Carnegie Mus. **63**: 155-183.

Hodrová, M. (1981): Plio-Pleistocene frog fauna from Hajnáčka and Ivanovce, Czechoslovakia. Věst. Ústř. úst. geol. **56**: 215-224.

Holman, J.A. (1968): Lower Oligocene amphibians from Saskatchewan. Can. J. Earth. Sci. **7**: 1317-1325.

Holman, J.A. (1992): *Hyla meridionalis* from the late Pleistocene (last interglacial age: Ipswichian) of Britain. British Herpetol. Soc. Bull. **41**: 12-14.

Holman, J.A. (1998): Pleistocene Amphibians and Reptiles in Britain and Europe. Oxford University Press.

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

Hossini, S. (1992): Les Anoures (Amphibiens) de l'Oligocène terminal et du Miocène en France. Unpublished thesis, University Paris 7.

Hossini, S. (1993): New species of *Latonia* from the Lower Miocene of France. Amphibia-Reptilia **14**: 237-245.

Hossini, H., Rage, J.C. (2000): Palaeobatrachid frogs from the earliest Miocene (Agenian) of France, with description of a new species. Geobios **33**: 223-231.

Kuhn, O. (1941): Die eozänen Anura aus dem Geiseltale nebst einer Übersicht über die fossilen Gattungen. Nova Acta Leopoldina **10**: 345-376.

Maxson, L.R. (1984): Relationships of *Balaeaphryne* to the discoglossid genera *Alytes*, *Bombina*, and *Discoglossus*. In: Història biològica del ferreret, p. 193-198. Hemmer, H., Alcover, J.A., Eds, Ciutat de Mallorca, Editorial Moll.

Mayol, J., Alcover, A. (1981): Survival of *Baleaphryne* Sanchíz and Alcover, 1979 (Amphibia: Anura: Discoglossidae) on Mallorca. Amphibia-Reptilia **1**: 343-345.

Mensi, P., Lattes, A., Macario, B., Salvidio, S., Giacoma, C., Balletto, E. (1992): Taxonomy and evolution of European brown frogs. J. Zool. Linn. Soc. **104**: 293-311.

Meulenkamp, J.E., Sissingh, W., Beniamovskii, V.N., Barrier, E., Abbate, E., Abdel-Gawad, S., Andreyeva-Grigorovich, A.S., Ben-Ismail, K., Bouaziz, S., Cahuzac, B., Calvo, J.P., Daams, R., Georgiev, G., Hirsch, F., Londeix, L., Monzer, M., Pinocki, M., Platel, J.P., Roger, J., Sadek, A., Sagri, M., Scherba, I.G., Studencka, B., Zaghbib-Turki, D., Sandulescu, M. (2000a): Late Lutetian (44-41 Ma). In: Atlas Peritethys, palaeogeographical maps, map 18. Dercourt, J., Gaetani, M., Vrielynck, B., Barrier, E., Biju-Duval, B., Brunet, M.F., Cadet, J.P., Crasquin, S., Sandulescu, M., Eds, Paris, CCGM/CGMW.

Meulenkamp, J.E., Sissingh, W., Popov, S.V., Kovac, M., Bergerat, F., Abbate, E., Abdel-Gawad, S., Andreyeva-Grigorovich, A.S., Bouaziz, S., Cahuzac, B., Calvo, J.P., Daams, R., Grigoriev, G., Hirsch, F., Londeix, L., Monzer, M., Platel, J.P., Roger, J., Sadek, A., Sagri, M., Scherba, I.G., Stolyarov, A.S., Studencka, B., Yaich, C., Sandulescu, M. (2000b): Late Rupelian (32-29 Ma). In: Atlas Peritethys, palaeogeographical maps, map 19. Dercourt, J., Gaetani, M., Vrielynck, B., Barrier, E., Biju-Duval, B., Brunet, M.F., Cadet, J.P., Crasquin, S., Sandulescu, M. Eds, Paris, CCGM/CGMW.

Milner, A.C. (1986): Amphibians and Squamates from the Paleogene of England. In: Studies in Herpetology, p. 685-688. Roček, Z., Ed., Prague, Charles Univ.

Patton, T.H. (1969): An Oligocene land vertebrate fauna from Florida. J. Paleontol. **43**: 543-546.

Peuvalst, J.P., Barrier, E., Ragala, R., Vanney, J.R., Vergne, N., Bergerat, F., Brunet, M.F., Cadet, J.P., Doubre, C. (2000): Last Glacial Maximum (20-18 Ka BP). In: Atlas Peritethys, palaeogeographical maps, map 24. Dercourt, J., Gaetani, M., Vrielynck, B., Barrier, E., Biju-Duval, B., Brunet, M.F., Cadet, J.P., Crasquin, S., Sandulescu, M., Eds, Paris, CCGM/CGMW.

Philip, J., Floquet, M., Platel, J.P., Bergerat, F., Sandulescu, M., Baraboshkin, E., Amon, E., Poisson, A., Guiraud, R., Vaslet, D., Le Nindre, Y., Ziegler, M., Bouaziz, S., Guezou, J.C. (2000): Late Maastrichtian (69.5-65 Ma). In: Atlas Peritethys, palaeogeographical maps, map 16. Dercourt, J., Gaetani, M., Vrielynck, B., Barrier, E., Biju-Duval, B., Brunet, M.F., Cadet, J.P., Crasquin, S., Sandulescu, M., Eds, Paris, CCGM/CGMW.

Pickford, M., Gabunia, L., Mein, P., Morales, J., Azanza, B. (2000): The middle Miocene mammalian site of Belometchetskaya, North Caucasus: An important biostratigraphic link between Europe and China. Geobios **33**: 257-267.

Poinar, G.O. Jr., Canatella, D.C. (1987): An Upper Eocene frog from the Dominican Republic and its implication for Carribean biogeography. Science **237**: 1215-1216.

Pomerol, C., Premoli-Silva, I. (1986): The Eocene-Oligocene transition: Events and boundary. In: Terminal Eocene Events, p. 1-24. Pomerol, C., Premoli-Silva, I., Eds, Amsterdam, Elsevier.

Prasad, G.V.R., Rage, J.C. (1995): Amphibians and squamates from the Maastrichtian of Naskal, India. Cretaceous Research **16**: 95-107.

Rage, J.C. (1972): Les Amphibiens et les Reptiles du gisement des Abîmes de la Fage. Nouv. Arch. Mus. Hist. nat. 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. (1988a): Gondwana, Tethys and terrestrial Vertebrates during the Mesozoic and Cainozoic. In: Gondwana and Tethys, p. 235-273. Audley-Charles, M.G., Hallam, A., Eds, London, Geol. Soc. special paper n° 37.

Rage, J.C. (1988b): Le gisement du Bretou (phosphorites du Quercy, Tarn-et-Garonne, France) et sa faune de Vertébrés de l'Eocène supérieur. I. Amphibiens et Reptiles. Palaeontographica **A 205**: 3-27.

Rage, J.C. (1997): Palaeobiological and palaeogeographical background of the European herpetofauna. In: Atlas of amphibians and reptiles in Europe, p. 23-28. Gasc J.P. et al., Eds, Paris, Soc. Europ. Herpetol. and Mus. natn. Hist. nat. (IEGB/SPN).

Rage, J.C. (1999): Faunes à affinités sud-américaines dans le Paléogène d'Europe: état de la question. Allons-nous vers une nouvelle interprétation? Bull. Soc. géol. Fr. **170**: 951-954.

Rage, J.C. (in press): Oldest Bufonidae (Amphibia, Anura) from the Old World: a bufonid from the Paleocene of France. Journal of Vertebrate Paleontology.

Rage, J.C., Ford, R.L.E. (1980): Amphibians and squamates from the Upper Eocene of the Isle of Wight. Tertiary Res. **3**: 47-60.

Rage, J.C., Hossini, H. (2000): Les Amphibiens du Miocène moyen de Sansan. In: La faune miocène de Sansan et son environnement, p. 177-217. Ginsburg, L., Ed., Paris, Mém. Mus. natn. Hist. nat. **183**.

Rage, J.C., Saint-Girons, H. (1989): Données biogéographiques: mise en place de la faune et facteurs actuels de la répartition. In: Atlas de répartition des Amphibiens et Reptiles de France, p. 29-32. Castanet, J. Guyétant, R., Coord., Paris, Soc. herpétol. Fr.

Ratnikov, V.Y. (1993a): First find of *Pliobatrachus* (Anura, Palaeobatrachidae) in the Muchkapian deposits of the basin of the Upper Don River. Paleont. Zhurn. **27**: 130-132.

Ratnikov, V.Y. (1993b): New representatives of Anura from the Late Neogene and Pleistocene of the East-European Platform. Paleont. Zhurn. **27**: 79-86.

Ratnikov, V.Y. (1997): [New data on the herpetofauna of the locality Kuznetsovka in the Tambovsk Region]. Izv. Vuzov. Geologia i razvedka **1**: 26-32 (in Russian).

Riabinin, A.N. (1928): [A fossil frog from Transcaucasus]. Ezhegodnik Russkogo paleont. obchestva (Annuaire de la Société Paléontologique de Russie) **7**: 87-98 (in Russian, with German summary).

Roček, Z. (1994): Taxonomy and distribution of Tertiary discoglossids (Anura) of the genus *Latonia* v. Meyer, 1843. Geobios **27**: 717-751.

Roček, Z. (2000): Mesozoic anurans. In: Amphibian Biology, 4: Palaeontology, p. 1295-1331. Heatwole, H., Carroll, R.L., Eds, Chipping Norton, Surrey Beatty.

Roček, Z., Lamaud, P. (1995): *Thaumastosaurus bottii* De Stephano, 1903, an anuran with Gondwanan affinities from the Eocene of Europe. J. Vert. Paleont. **15**: 506-515.

Roček, Z., Rage, J.-C. (2000): Tertiary Anura of Africa, Asia, Europe, North America, and Australia. In: Amphibian Biology, 4: Paleontology, p. 1334-1389. Heatwole, H., Carroll, R.L., Eds, Chipping Norton, Surrey Beatty.

Rögl, F. (1998): Palaeogeographic considerations for Mediterranean and Paratethys seaways (Oligocene to Miocene). Ann. Naturhist. Mus. Wien **99 A**: 279-310.

Sahni, A., Kumar, K., Hartenberger, J.L., Jaeger, J.J., Rage, J.C., Sudre, J., Vianey-Liaud, M. (1982): Microvertébrés nouveaux des Trapps du Deccan (Inde): mise en évidence d'une voie de communication terrestre probable entre la Laurasie et l'Inde à la limite Crétacé-Tertiaire. Bull. Soc. géol. Fr. **14**: 1093-1099.

Sánchez-Herraíz, M.J., Barbadillo, L.J., Machodorm, A., Sanchiz, B. (2000): A new species of pelodytid frog from the Iberian Peninsula. Herpetologica **56**: 105-118.

Sanchiz, B. (1977): La familia Bufonidae (Amphibia, Anura) en el Terciario Europeo. Trabajos N/Q **8**: 75-111.

Sanchiz, B. (1978): Nuevos restos fósiles de la familia Pelodytidae (Amphibia, Anura). Estudios geol. **34**: 9-17.

Sanchiz, B. (1997): Factores causales de biodiversidad: especiación, extinción y migración en la formación de la batracofauna europea. In: Registros fósiles e historia de la Tierra, 185-206. Aguirre, E., Morales, J., Soria, D., Eds, Madrid, Ed. Complutense.

Sanchiz, B. (1998a): Handbuch der Paläoherpetologie, Part 4: Salientia. Munich, Verlag Dr. Friedrich Pfeil.

Sanchiz, B. (1998b): Vertebrates from the early Miocene lignite deposits of the opencast mine Oberdorf (Western Styrian Basin, Austria): 2. Amphibia. Ann. Naturhist. Mus. Wien **99 A**: 13-29.

Sanchiz, B., Adrover, R. (1979): Anfibios fósiles del Pleistoceno de Mallorca. Doñana, Acta Vertebrata (**1977**), 4: 5-25.

Sanchiz, B., Młynarski, M. (1979): Remarks on the fossil anurans from the Polish Neogene. Acta Zool. Cracov. **24**: 175-188.

Sanchiz, B., Roček, Z. (1996): An overview of the anuran fossil record. In: The Biology of *Xenopus*, p. 317-328. Tinsley, R.C., Kobel, H.R., Eds, Oxford, Clarendon Press.

Sanchiz, B., Schleich, H.H. (1986): Erstnachweis der Gattung *Bombina* (Amphibia: Anura) in Untermiozän Deutschlands. Mitt. Bayer. Staatsslg. Paläont. hist. Geol. **26**: 41-44.

Sanchiz, B., Schleich, H.H., Esteban, M. (1993): Water frogs (Ranidae) from the Oligocene of Germany. J. Herpetol. **27**: 486-489.

Sanchiz, B., Szyndlar, Z. (1984): Pleistocene amphibian fauna from Kozi Grzbiet in the Holy Cross Mts. Acta geol. Polonica **34**: 61-63.

Schaeffer, B. (1949): Anurans from the early Tertiary of Patagonia. Bull. Amer. Mus. Nat. Hist. **93**: 47-68.

Schmidt-Kittler, N., Ed. (1987): European reference levels and correlation tables. Münchner Geowiss. Abh. **A 10**: 15-31.

Sedláčková, L. (2000): [Comparison of skeletal development in two closely related anuran species, *B. bombina* and *B. variegata*]. Unpublished Master thesis, Masaryk University, Brno (in Czech).

Smirnov, S.V. (1989): Postmetamorphic skull development in *Bombina orientalis* (Amphibia, Discoglossidae), with comments on neoteny. Zool. Anz. **223**: 91-99.

Špinar, Z.V. (1972): Tertiary frogs from central Europe. Prague, Academia and The Hague, D.W. Junk Publ.

Špinar, Z.V. (1978): *Latonia kolebabi* Špinar, 1976 (Amphibia) and remarks on the "genus *Miopelobates*". In: Paleontologická konference 1977, p. 289-303. Pokorný, V., Ed., Prague, Charles Univ. Press.

Špinar, Z.V. (1980): Fossile Raniden aus dem oberen Pliozän von Willershausen (Niedersachsen). Stuttgart. Beitr. Naturkde., Ser. B **53**: 1-53.

Špinar, Z.V., Klembara, J., Meszároš, Š. (1993): A new toad from the Miocene of Devínska Nová Ves (Slovakia). Západné Karpaty, sér. paleont. **17**: 135-160.

Sudre, J. (1974): L'endémisme des faunes de Mammifères du Sud de l'Angleterre à l'Eocène supérieur. 2nd Réun. Ann. Sci. Terre, p. 362.

Thomas, H., Sen, S., Khan, M., Battail, B., Ligabue, G., Eds (1982): The lower Miocene fauna of As Sarrar (Eastern Province, Saudi Arabia). Atlal, the journ. Saudi Arab. Archaeol. **5**: 109-136.

Tyler, M.J. (1976): Comparative osteology of the pelvic girdle of Australian frogs and description of a new fossil genus. Trans. R. Soc. S. Aust. **100**: 3-14.

Tyler, M.J. (1994): Hylid frogs from the mid-Miocene Camfield Beds of Northern Australia. Beagle, Rec. North. Terr. Mus. Arts Sci. **11**: 141-144.

Venczel, M. (1997): Late Miocene anurans from Polgárdi (Hungary). In: Herpetologia bonnensis, p. 383-389. Böhme, W., Bischoff, W., Ziegler, T., Eds, Societas Europaea Herpetologica, DGHT and A. Koenig Museum, Bonn.

Venczel, M. (2001): Anurans and Squamates from the lower Pliocene (MN 14) of Osztramos 1 locality (Northern Hungary). Fragmenta Paleontologica Hungarica **19**: 79-90.

Vergnaud-Grazzini, C., Hoffstetter, R. (1972): Présence de Palaeobatrachidae (Anura) dans des gisements tertiaires français. Caractérisation, distribution et affinités de la famille. Palaeovertebrata **5**: 157-177.

Vergnaud-Grazzini, C., Młynarski, M. (1969): Position systématique du genre *Pliobatrachus* Fejérváry 1917. C.R. Acad. Sci. Paris **268**: 2399-2402.

Vergnaud-Grazzini, C., Wenz, S. (1975): Les discoglossidés du Jurassique supérieur du Montsech (Province de Lérida, Espagne). Ann. Paléontol. (Vertébrés) **61**: 19-36.

Wuttke, M. (1988): Amphibien am Messelsee — Salamander und Frösche. In: Messel — Ein Schaufenster in die Geschichte der Erde und des Lebens, p. 95-98. Schaal, S., Ziegler, W., Eds, Frankfurt a.M., Verlag Waldemar Kramer.

Received: March 12, 2002. Accepted: October 10, 2002.