

AN OFFPRINT FROM

The Biology of *Xenopus*

Edited by

R.C. TINSLEY

*School of Biological Sciences
University of Bristol*

and

H.R. KOBEL

*Laboratoire de Génétique Animale et Végétale
Université de Genève
Switzerland*



Published for THE ZOOLOGICAL SOCIETY OF LONDON
by CLARENDON PRESS · OXFORD
1996

17 An overview of the anuran fossil record

BORJA SANCHIZ and ZBYNĚK ROČEK

Synopsis

A general overview of the known anuran fossil record is presented, with an emphasis on diversity and extinct groups. The fossil record is analysed for all anurans at the family level, and palaeontological minimal ages are inferred. Most of the record can be referred to extant families, but a few exceptions remain: the South American Jurassic *Vieraella* and *Notobatrachus*, the Asiatic Cretaceous *Gobiates* and the holarctic palaeobatrachids are especially discussed in this regard. However, the real evolutionary pattern appears to include few examples of lost, extinct diversifications within the order Anura, unless this merely derives from a sampling bias of the known fossil record. Diversity in the past has not proven to be higher than today, and it seems to have been growing very slowly through time.

At least 10 Jurassic and Lower Cretaceous sites (dated >100 Ma) are known where multiple anuran remains have been recovered. In all these localities, one or a few anuran species are detected per site, but in no case have more than two very closely related genera been found. More diverse assemblages, including more than one family, are presently known only from the Upper Cretaceous and later. We consider the example of Europe, with a fairly rich fossil record, clearly documenting the role of addition, by means of transcontinental migration and minor speciation events, in the development of present anuran biodiversity.

Finally, consideration is given to the relationships of the Palaeobatrachidae. This extinct family, known from the Upper Cretaceous to the Plio–Pleistocene boundary (roughly 66 to 1.6 Ma) can be considered the sister-group and ecological equivalent to the living Pipidae.

Introduction

The fossil record of anurans has traditionally been considered rather poor and, in spite of its potential, has yielded very few informative clues to anuran evolutionary history. Since the last general overview by Estes & Reig (1973), only a few unexpected discoveries of fossil anurans have been made, but the fossil record has been substantially enlarged, and now includes representatives of many of the living lineages. It is becoming possible to

analyse some aspects of anuran diversification, at least in a very general way. Such palaeontological study can provide not only knowledge about completely extinct groups, but also information complementary to the use of molecular techniques for elucidating evolutionary relationships and dating cladogenetic events.

Palaeontology is applied in this chapter in order to analyse briefly the extent of anuran global diversification with respect to (1) the relationships of extinct groups, an indication of the existence of taxonomic diversity different from the present one, and (2) the palaeofaunistic changes of diversity through time, as exemplified by the European fossil record. This general view will provide a basic setting to place pipoid frogs within anuran global diversity, and complements the chapter by Báez (this volume pp. 329–347) that presents a detailed review of the pipoid fossil record.

The fossil record of frogs

Phylogeny and fossil record

Estes & Reig (1973) provided the last general review of fossil anurans, and most of the morphological features analysed by these authors remain accurate. Nevertheless, some characters can be interpreted differently, owing to the use of other methodological approaches or to better knowledge of the variation within contemporary forms. In this section, we will comment upon the fossil record from the viewpoint of diversity and systematic assignments. Unless otherwise stated, the reader is referred to Estes & Reig (1973 and references therein) for older bibliographic references on these forms. A database for more than 860 fossil sites, taken from Sanchiz (in press), with updated faunistic lists at least at the generic level, has been used. The anuran fossil record, for family-level groups, is summarized in Fig. 17.1.

It is generally agreed (the senior author of this review being probably the only exception) that the Lower Triassic *Triadobatrachus massinoti*, discovered in Madagascar in the 1920s, remains the only representative of the ancestral grade that might have given rise to anurans. The morphology of this incomplete specimen has been extensively reviewed by Rage & Roček (1989), being noteworthy in that the cranial structure of this form shows a much closer relation to the unique anuran pattern than the locomotor structures do. The morphology of this specimen, even if interpreted as frog-like, does not give us clear hints on anuran origins, in the sense that it gives no indication on matters such as the mono- or polyphyletic origins of the Anura or the basic locomotor (saltatorial or swimming) adaptations of the group.

The Argentinian *Vieraella*, a single incomplete specimen from the Lower Jurassic, is the oldest unquestionable anuran known, showing many of the character states that incorporate the diagnosis of the order. As could be expected, *Vieraella* shows features (e.g. number of presacral vertebrae, carpals, ribs) that are considered primitive, and all the published interpretations of this

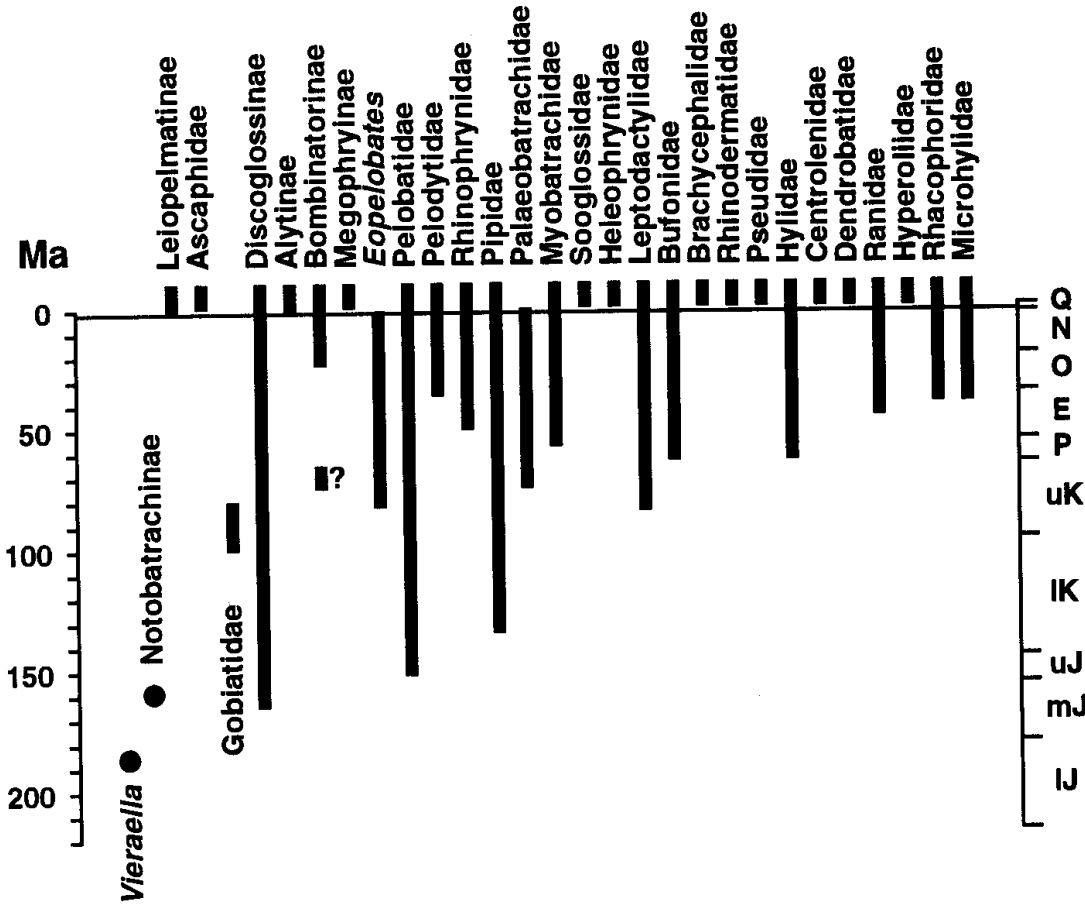


Fig. 17.1. Anuran fossil record at the family level. Q: Quaternary. N: Miocene and Pliocene. O: Oligocene. E: Eocene. P: Palaeocene. uK: upper Cretaceous. lK: lower Cretaceous. uJ: upper Jurassic. mJ: middle Jurassic. lJ: lower Jurassic.

unique specimen agree in considering it very close to the most primitive living frogs, Leiopelmatidae and Ascaphidae. In our opinion, the limited nature of the material prevents any detailed phylogenetic disquisition, and it should remain taxonomically as *Anura incertae sedis*, but it shows that the typical anuran structure has been present for at least 180 Ma.

The Upper Jurassic La Matilde Formation, from the Callovian–Oxfordian (154.7 to 161.3 Ma) of Argentina, has produced remains of more than 30 specimens of another primitive frog, *Notobatrachus degiustoi*. A reinterpretation of the features analysed by Estes & Reig (1973), such as the peculiar morphology of the pectoral girdle, suggests in our opinion that *Notobatrachus* should be included in Leiopelmatidae, although it may represent a distinct subfamily in this group. The living genus *Leiopelma* has an abundant fossil record in the New Zealand Pleistocene and Holocene (Worthy 1987). The family Ascaphidae, which can be considered the sister group of Leiopelmatidae following Clarke (1988) (but see Cannatella 1985 for a contrary view), has no fossil record.

The genus *Gobiates* was first described by Špinar & Tatarinov (1986) for Mongolian Upper Cretaceous articulated specimens previously assigned to the *Eopelobates* group, and it was proposed to place it in a new frog family. Nessov (1988, and references therein) described Cretaceous isolated bones, mainly from the Kizylkum desert in the Commonwealth of Independent States (C.I.S), that according to Roček & Nessov (1991) should also be referred to *Gobiates*. A detailed study of this material has recently been presented by Roček & Nessov (1993). These anurans are known in several localities from the uppermost Lower Cretaceous (Albian) to Upper Cretaceous (Campanian) age from the south-western part of the ancient Asian continent. It is noteworthy that these amphibians are members of assemblages which also contain marine vertebrates. In spite of being rather homogeneous, the group shows a certain taxonomic diversification, with several closely related species documented in its long stratigraphical range (Roček & Nessov 1993). In its morphology, the group combines characters of Leiopelmatidae, Ascaphidae and the discoglossoids, but it cannot be assigned clearly to any of those families and their phylogenetic relationships are still uncertain.

Discoglossoid frogs include the living genera *Bombina* and *Barbourula* (Bombinatoridae), *Discoglossus* (Discoglossidae *s.s.*), and the genus *Alytes*, which according to different opinions can be included (as a distinct subfamily) within the Bombinatoridae (e.g. Lanza, Cei & Crespo 1976) or within the Discoglossidae (e.g. Sanchiz 1984; Cannatella 1985), or can stand as a sister family to the Bombinatoridae plus Discoglossidae (e.g. Maxson & Szymura 1984; Clarke 1988). The three groups are here considered separately, and their relationships are not resolved. Discoglossids have a long fossil history, extending back to the middle Jurassic (161.3–166.1 Ma). *Eodiscoglossus oxoniensis* from Kirtlington in Great Britain is the oldest known anuran record after *Vieraella* (Evans, Milner & Mussett 1990). Four Lower Cretaceous Spanish sites have also produced abundant remains of the same genus (see review in Sanchiz in press), and it seems clear that an extreme morphological similarity exists between *Eodiscoglossus* and the living *Discoglossus*, to the extent that no clear apomorphies are found in *Eodiscoglossus* with relation to *Discoglossus* (Sanchiz 1984; Evans *et al.* 1990). This lineage seems to have been very conservative for more than 160 Ma. *Alytes* has no described fossil record earlier than the Pleistocene, and *Bombina* is known since the early European Miocene (Sanchiz & Schleich 1986). The latter group might be related to *Scotiophryne*, an extinct genus known from the uppermost Cretaceous and Palaeocene of North America (Estes & Sanchiz 1982), but there is no unequivocal evidence on the basis of the available information.

The family Megophryidae is not known in the fossil record (Sanchiz in press). Possibly related is the *Eopelobates* group, with an extended fossil record ranging from the Upper Cretaceous of North America to the Plio–Pleistocene boundary of Europe (Roček 1981). Pelobatid material has been reported from the Upper Jurassic of North America (Evans & Milner 1993). The genus *Pelobates* is known since the European basal Miocene (24 Ma;

Böhme, Roček & Špinar 1982), while *Scaphiopus* has its earliest record in the North American Orellan (32 Ma), and might be related to the Mongolian Oligocene *Macropelobates* (30–38 Ma; Roček 1984). Pelodytidae are known since the Upper Eocene of Europe.

The fossil record of pipids is reviewed by Báez (this volume pp. 329–347), and goes back to the Hauterivian–Barremian (124.5–135 Ma) of Israel. Rhinophrynidae are known since the Upper Palaeocene (late Tiffanian, 59–61 Ma) of North America. Palaeobatrachidae (see below) have been recorded in the Upper Cretaceous of North America and Europe, disappearing in the lowermost Pleistocene of Central Europe.

Myobatrachidae have a fossil record restricted to Australia, with an earliest datum in the Lower Eocene (Tyler & Godthelp 1993), while at present Sooglossidae and Heleophrynidae lack fossil representatives.

The family Leptodactylidae is known since the Campanian (74–83 Ma) and the Santonian–Maastrichtian of South America (Báez 1987), the latter being representatives of the Ceratophryinae. Bufonidae have been recorded in the Upper Palaeocene (Riochican) of Itaboraí (Brazil) (Estes & Báez 1985). Brachycephalidae and Rhinodermatidae have no fossil record.

The Hylidae is a family mentioned in faunistic lists from the late Cretaceous of India (e.g. Sahni, Rana & Prasad 1987) and the Upper Palaeocene of Brazil (Estes & Báez 1985), but we are not aware of any published description of these remains. Pseudidae and Centrolenidae have no fossil record known to us.

Within ranoids, the Dendrobatidae and Hyperoliidae have no fossil record, but the Ranidae has a very abundant one, albeit not very old. Besides an unconfirmed possibility of the presence of ranids in an upper Cretaceous site from Niger, the earliest recorded ranids are from the European Upper Eocene (Rage 1984a). The Rhacophoridae and the Microhylidae have both been detected in the European Upper Eocene (B. Sanchiz unpubl.).

If we consider the whole record, the most obvious pattern concerning diversity might be argued to be the scarcity of extinct clearly distinct lineages, an indication of the absence of adaptations within the order different from the present ones. Nevertheless, since there has been only limited research on this topic, some caution has to be applied to the conclusion, as it might merely derive from a sampling bias of the known fossil record.

Diversification of Mesozoic frogs

Only a few Jurassic sites are known bearing definitive anuran remains: Roca Blanca (Argentina; dated 178–194.5 Ma, *Vieraella herbsti*), Kirtlington (UK; 161.3–166.1 Ma, *Eodiscoglossus oxoniensis*), La Matilde (Argentina; 154.7–161.3 Ma, *Notobatrachus degiustoi*) and Quarry Nine (USA, two nominal taxa that are based on such fragmentary remains that it is impossible to make any definitive statement on their relationships; they might even be synonymous, *contra* Hecht & Estes 1960; see also Evans & Milner 1993).

At least in Kirtlington and La Matilde, where more than 30 individuals have been collected, only a single species seems to be present.

Lower Cretaceous sites where anurans have been reported at least at the family level include four localities in Spain: Uña, Galve, Santa María de Meyá, and Las Hoyas (Sanchiz in press), one still not published in detail from the Karakalpakia region of the C.I.S. (Chodzhakul: Nessov 1988), and two in Israel (Shomron and Makhtesh Ramon: Estes, Špinar & Nevo 1978). Both in Spain (Discoglossidae) and Israel (Pipidae), where the assemblages contain abundant remains and have been studied at the specific level, there are between one and three species per site, but only one subfamily is present at any site, represented by one or two closely related genera.

The Upper Cretaceous fossil record is much more abundant, with localities known in South America, North America, India, Asia, Europe and Africa. Los Alamos and Alemanía (Argentina), Laguna Umayo (Peru), Tiupampa (Bolivia) and Peirópolis (Brazil) contain pipids and/or leptodactylids (Báez, this volume pp. 329–347). In the USA and Canada, Chris's Bonebed, the Hell Creek, Fruitland, Judith River and Lance Formations, as well as the El Gallo Formation in Mexico, contain bombinatorids, pelobatids, palaeobatrachids, discoglossids and *incertae sedis* (*Theatoniuss*), from one to five family-level units per site at the end of the Cretaceous (Estes & Sanchiz 1982). The Indian fauna has not been described in detail, but Asifabad, Pisdura and Gitti Khadan near Nagpur seem to contain discoglossoids, pelobatoids and hylids (Sahni *et al.* 1987). In Africa, the Nigerian In Beceten (Niger) fauna includes pipids and undetermined neobatrachians, and pipids have been described from Marydale in South Africa (Rage 1984a; Báez, this volume pp. 329–347). Central Asian faunas include several localities reviewed by Roček & Nessov (1993), with assemblages including gobiatids and discoglossoids.

Relationships of the Palaeobatrachidae

Palaeobatrachids are a homogeneous extinct family of anurans recorded from the late Cretaceous of North America (Estes & Sanchiz 1982) and throughout the Central European Tertiary. The group apparently became extinct in the lowermost Pleistocene. Wolterstorff (1885–1886) and Špinar (1972) remain the most detailed morphological studies available, although their taxonomic arrangements, especially their proliferation of species names, are open to question.

Palaeobatrachids have been reported twice from the lowermost Cretaceous of Santa María de Meyá (Spain). The first case was *Monsechobatrachus gaudryi*, originally assigned by Vidal (1902) to *Palaeobatrachus*. Estes & Reig (1973) indicated the possibility, pending confirmation through a study using modern techniques, that the original identification could be correct. However, our review of the specimen is in full agreement with that of Hecht (1963) and has convinced us that such a poorly preserved natural cast simply does not exhibit the minimum number of observable features to warrant any

familial assignment. Approximate body proportions suggest that the specimen is probably only a late metamorphosing tadpole or froglet of the discoglossid *Eodiscoglossus santonjae*, common in the site.

Seiffert (1972) also described from Santa María de Meyá *Neusibatrachus wilferti*, a single specimen that he considered to be an ancestor to the Palaeobatrachidae and Ranidae. Estes & Reig (1973) considered it a definitive palaeobatrachid, with no clear indication of its relationship to other families. As will be discussed elsewhere, the review by one of us of this specimen, in the context of the ontogenetic development of living *Discoglossus galganoi*, suggests that several features of *Neusibatrachus* have been misinterpreted, and that this genus could also be considered a synonym of *Eodiscoglossus santonjae*, with no relation to palaeobatrachids or ranids (Sanchiz in press). No palaeobatrachid has so far been found in Europe before the Upper Cretaceous of Spain (B. Sanchiz pers. obs.).

Since the Palaeobatrachidae were established as a separate group at the family rank by Cope in 1865, it is generally agreed that their closest affinities are to the Pipidae. This view is based on the following essential similarities (which are not, however, of equal value). (1) Both groups are swimming anurans which is evidenced by considerably elongated metacarpals and metatarsals. (2) Their frontoparietal in adults is unpaired. In pipid tadpoles this arises from paired primordia which are, however, immediately afterwards obscured by overall centripetal ossification. In palaeobatrachid larvae, in the earliest preserved developmental stages, the frontoparietal is a single bone without any suture. From this it may be inferred that even development of the frontoparietal is similar in both groups and different from all other anurans. (3) Their parasphenoid lacks lateral alae. (4) Their larvae possess lateral barbels. (5) Palaeobatrachids have a parietal foramen. This is also present in *Xenopus* and one may suppose that it was originally present in all pipids. (6) In pipids the maxillary arch is incomplete (i.e. their quadratojugals are absent), similarly to most palaeobatrachids (except for *Palaeobatrachus diluvianus* in which this bone is vestigial). (7) The pectoral girdle is of arciferal or modified arciferal type.

Besides the similarities between palaeobatrachids and pipids mentioned above, which may be considered essential for assessing phylogenetic relationships, there is one striking difference: whereas pipids have opisthocelous vertebrae, the shape of the vertebral centra in palaeobatrachids is uniformly procoelous. This was why Noble (e.g. 1922, 1931) classified palaeobatrachids in his group Procoela, together with 'modern' families such as Ranidae and Bufonidae.

It seems that, apart from the vertebrae, the osteological similarities between pipids and palaeobatrachids suggest their close relationship. There is also a classical agreement that considers both families as rather archaic frogs. This is evidenced by the presence of primitive characters such as free ribs in development, parasphenoid without lateral alae, well-developed mentomandibular (which is part of a branchial arch), and foramen parietale present at least in

some species. Nevertheless, their consideration as primitive anurans is not supported by recent comparative anatomy studies (e.g. Cannatella 1985; Trueb, this volume pp. 349–377), as they show synapomorphies with the neobatrachians. Both palaeobatrachids and pipids are also well delimited, especially on the basis of developmental processes, from other groups of primitive frogs, namely from the Discoglossidae and Leiopelmatidae.

History of the European fauna

The present anuran fauna of Europe, excluding the C.I.S., is composed of eight genera, representing seven families, and includes approximately 28 species (e.g. Engelmann *et al.* 1986). The fossil faunas from a sample of 189 European Tertiary sites (excluding the C.I.S. countries) (taken from Sanchiz in press.) have been re-analysed, and even if the taxonomy at the specific level is in many instances dubious, the generic attributions can be established confidently. Figure 17.2 shows the fossil record for each continental stratigraphic stage. The number of fossil assemblages studied is not large, but the European record is the best available, and we think that it is probably adequate to show the general historical pattern.

The number of genera and the maximum number of species per site are indicated in Fig. 17.3. The 'Grande Coupure' or 'Stehlin faunistic turnover' (see for instance Rage 1984b, concerning herpetology), represents a major change for European faunas. This faunistic change reflects the Eocene–Oligocene boundary, a global event that palaeogeographically produced the final opening of the north Atlantic (now a barrier for anurans) and the disappearance of the Turgai Straits, no longer separating Europe and Asia (Prothero 1985). Rhacophorids, microhylids and leptodactylids are not recovered in younger sites, while *Bufo*, *Hyla*, *Bombina*, and perhaps *Pelobates*, should be considered immigrants from Asia. Within ranids a similar situation is observed at lower taxonomic levels, with the water frogs (the *Rana ridibunda* species group) immigrating in the basal Oligocene (Sanchiz, Esteban & Schleich 1993). This increase of diversity by migration is a transcontinental phenomenon: the assumed areas of origin are Gondwanan (Hylidae, Bufonidae) or eastern Asiatic (Bombinatoridae). Ranids are considered originally African (e.g. Duellman & Trueb 1986), but their immediate origin with relation to Europe is Asia, as indicated by immunologically-derived time estimations of the separation between western and eastern Palaeartic water frogs (Sanchiz *et al.* 1993). The pelodytids have a rather scarce fossil record, although they have been collected outside Europe in the North American Miocene, and their biogeographic status is unclear (Henrici 1994).

Eopelobates is recorded in Cretaceous North America, and it might have also been present in Europe, but there is no palaeontological evidence of this. Palaeobatrachids and discoglossids might be considered European natives, since they are already known by the end of the Mesozoic, both in Europe and

F
SI
S
S

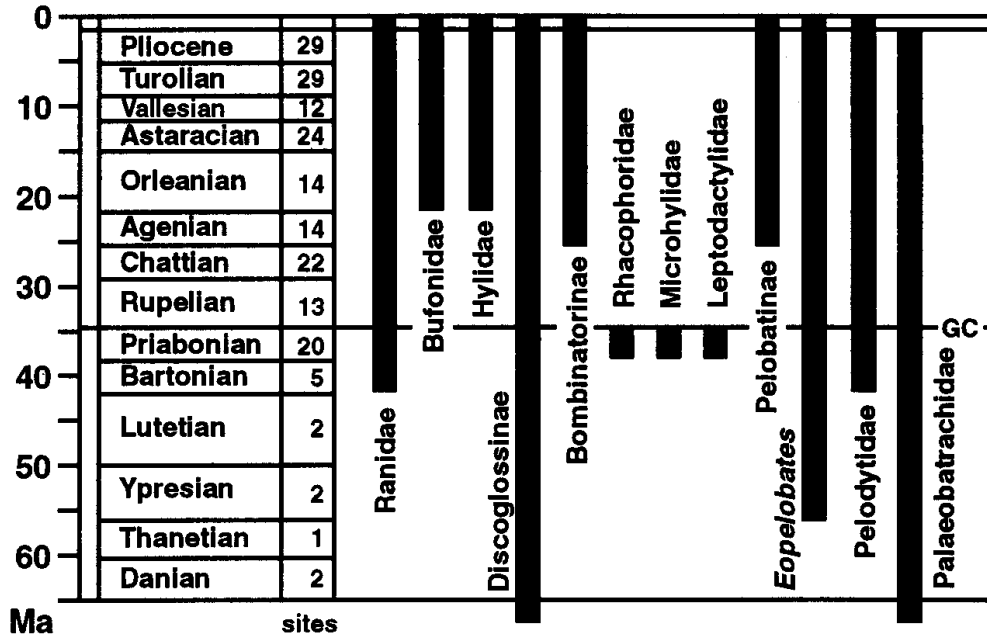


Fig. 17.2. Fossil record of European Tertiary anurans. Sites: number of sites in the corresponding stratigraphical level. GC: 'Grande Coupure'.

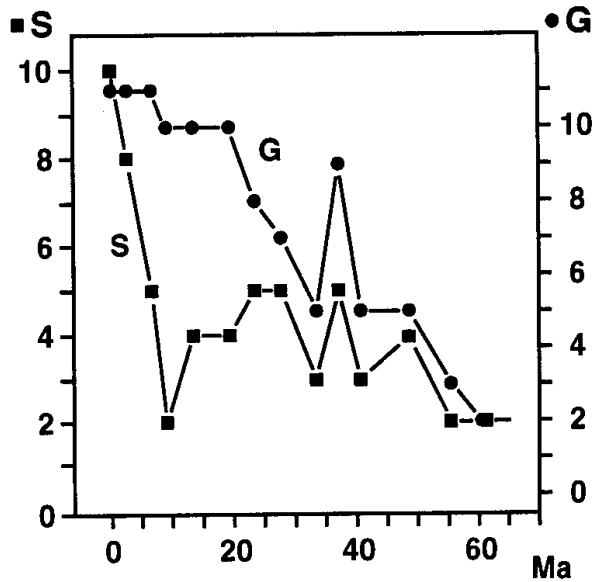


Fig. 17.3. Diversity increase in the anuran fossil record in Europe. S: maximum number of species per site for each stratigraphical level. G: total number of known genera in each stratigraphic level.

in North America. Both palaeobatrachids and especially discoglossids are the only groups that have several different genera in the European Cenozoic, and the only ones showing morphological evolutionary changes at the supraspecific level. The presumed immigrant groups, with stable integrated morphotypes, seem to show only minor speciation events within the European continent.

Acknowledgements

This work was supported in part by the Spanish grant DGICYT PB-910115.

References

- Báez, A.M. (1987). The late Cretaceous fauna of Los Alamos, Patagonia, Argentina. Part III. Anurans. *Revta Mus. argent. Cienc. Nat. Bernardino Rivadavia* 3(3): 121–130.
- Böhme, W., Roček, Z. & Špínar, Z.V. (1982). On *Pelobates decheni* Troschel, 1861, and *Zaphrissa eurypelis* Cope, 1866 (Amphibia: Salientia: Pelobatidae) from the early Miocene of Rott near Bonn, West Germany. *J. vert. Paleont.* 2: 1–7.
- Cannatella, D.C. (1985). *A phylogeny of primitive frogs (archaeobatrachians)*. PhD thesis: University of Kansas.
- Clarke, B.T. (1988). *Evolutionary relationships of the discoglossoid frogs: osteological evidence*. PhD thesis: City of London Polytechnic.
- Duellman, W.E. & Trueb, L. (1986). *Biology of amphibians*. McGraw-Hill, New York.
- Engelmann, W.E., Fritzsche, J., Günther, R. & Obst, F.J. (1986). *Lurche und Kriechtiere Europas*. Ferdinand Enke, Stuttgart.
- Estes, R. & Báez, A. (1985). Herpetofaunas of North and South America during the late Cretaceous and Cenozoic: evidence of interchange? In *The great American interchange*: 139–197. (Eds Stehli, F.G. & Webb, S.D.). Plenum Press, New York and London. (*Topics Geobiol.* 4.)
- Estes, R. & Reig, O.A. (1973). The early fossil record of frogs: a review of the evidence. In *Evolutionary biology of the anurans: contemporary research on major problems*: 11–63. (Ed. Vial, J.L.). University of Missouri Press, Columbia.
- Estes, R. & Sanchiz, B. (1982). New discoglossid and palaeobatrachid frogs from the late Cretaceous of Wyoming and Montana, and a review of other frogs from the Lance and Hell Creek formations. *J. vert. Paleont.* 2: 9–20.
- Estes, R., Špínar, Z.V. & Nevo, E. (1978). Early Cretaceous pipid tadpoles from Israel (Amphibia: Anura). *Herpetologica* 34: 374–393.
- Evans, S.E. & Milner, A.R. (1993). Frogs and salamanders from the Upper Jurassic Morrison Formation (Quarry Nine, Come Bluff) of North America. *J. vert. Paleont.* 13: 24–30.
- Evans, S.E., Milner, A.R. & Mussett, F. (1990). A discoglossid frog from the Middle Jurassic of England. *Palaeontology* 33: 298–311.
- Hecht, M.K. (1963). A reevaluation of the early history of the frogs. Part II. *Syst. Zool.* 12: 20–35.
- Hecht, M.K. & Estes, R. (1960). Fossil amphibians from Quarry Nine. *Postilla* No. 46: 1–19.
- Henrici, A.C. (1994). *Tephrodytes brassicarvalis*, new genus and species (Anura:

- Pelodytidae) from the Arikareean Cabbage Patch Beds of Montana, USA, and pelodytid–pelobatid relationships. *Ann. Carneg. Mus.* 63: 155–183.
- Lanza, B., Cei, J.M. & Crespo, E.G. (1976). Further immunological evidence for the validity of the family Bombinidae (Amphibia Salientia). *Monit. zool. ital. (N.S.)* 10: 311–314.
- Maxson, L.R. & Szymura, J.M. (1984). Relationships among discoglossid frogs: an albumin perspective. *Amphibia–Reptilia* 5: 245–252.
- Nessov, L.A. (1988). Late Mesozoic amphibians and lizards of Soviet Middle Asia. *Acta zool. cracov.* 31: 475–486.
- Noble, G.K. (1922). The phylogeny of the Salientia I. The osteology and the thigh musculature; their bearing on classification and phylogeny. *Bull. Am. Mus. nat. Hist.* 46: 1–87.
- Noble, G.K. (1931). *The biology of the Amphibia*. Constable, London. (Reprinted 1954 by Dover Publ., New York.)
- Prothero, D.R. (1985). North American mammalian diversity and Eocene–Oligocene extinctions. *Paleobiology* 11: 389–405.
- Rage, J.C. (1984a). Are the Ranidae (Anura, Amphibia) known prior to the Oligocene? *Amphibia–Reptilia* 5: 281–288.
- Rage, J.C. (1984b). La ‘Grande Coupure’ éocène/oligocène et les herpétofaunes (amphibiens et reptiles): problèmes du synchronisme des événements paléobiogéographiques. *Bull. Soc. géol. Fr.* 26: 1251–1257.
- Rage, J.-C. & Roček, Z. (1989). Redescription of *Triadobatrachus massinoti* (Piveteau, 1936), an anuran amphibian from the Early Triassic. *Palaeontographica (A)* 206: 1–16.
- Roček, Z. (1981). Cranial anatomy of frogs of the family Pelobatidae Stannius, 1856, with outlines of their phylogeny and systematics. *Acta Univ. Carol. Biol.* 1980 (1–2): 1–164.
- Roček, Z. (1984). *Macropelobates osborni* Noble, 1924—redescription and reassignment. *Acta Univ. Carol. (Geol.)* 1982(4): 421–438.
- Roček, Z. & Nessov, L.A. (1991). Cretaceous anurans from Central Asia. In *Czechoslovak paleontology 1990*: 24. (Ed. Roček, Z.). Carolinum Press, Charles University, Prague.
- Roček, Z. & Nessov, L. (1993). Cretaceous anurans from Central Asia. *Palaeontographica (A)* 226: 1–54.
- Sahni, A., Rana, R.S. & Prasad, G.V.R. (1987). New evidence for paleobiogeographic intercontinental Gondwana relationships based on late Cretaceous–earliest Paleocene coastal faunas from peninsular India. *Geophys. Monogr.* No. 41: 207–218.
- Sanchiz, B. (1984). Análisis filogenético de la tribu Alytini (Anura, Discoglossidae) mediante el estudio de su morfoestructura ósea. In *Història biològica del Ferreret* (Baleaphryne muletensis): 61–108. (Eds Hemmer, H. & Alcover, J.A.). Moll, Palma de Mallorca.
- Sanchiz, B. (In press). *Salientia. Handbuch der Palaeoherpetologie*. Gustav Fischer, Stuttgart.
- Sanchiz, B., Esteban, M. & Schleich, H.H. (1993). Water frogs from the Lower Oligocene of Germany. *J. Herpet.* 27: 486–489.
- Sanchiz, B. & Schleich, H.H. (1986). Erstnachweis der Gattung *Bombina* (Amphibia: Anura) im Untermiozän Deutschlands. *Mitt. bayer. St. Paläont. hist. Geol.* 26: 41–44.
- Seiffert, J. (1972). Ein Vorläufer der Froschfamilien Palaeobatrachidae und Ranidae im Grenzbereich Jura-Kreide. *Neues Jb. Miner. Geol. Paläont. Mh.* 1972(2): 120–131.

- Špínar, Z.V. (1972). *Tertiary frogs from Central Europe*. Academia, Prague.
- Špínar, Z.V. & Tatarinov, L.P. (1986). A new genus and species of discoglossid frog from the Upper Cretaceous of the Gobi desert. *J. vert. Paleont.* 6: 113–122.
- Tyler, M.J. & Godthelp, H. (1993). A new species of *Lechriodus* Boulenger (Anura: Leptodactylidae) from the early Eocene of Queensland. *Trans. R. Soc. S. Aust.* 117: 187–189.
- Vidal, L.M. (1902). Nota sobre la presencia del tramo kimeridgense en el Montsech (Lérida) y el hallazgo de un batracio en sus hiladas. *Mems R. Acad. Cienc. Artes Barcelona* (3) 4: 263–267.
- Wolterstorff, W. (1885–1886). Über fossile Frösche insbesondere das Genus *Palaeobatrachus*. I und II. *Jber. naturw. Ver. Magdeburg* 1885: 1–82; 1886: 3–81.
- Worthy, T.H. (1987). Osteology of *Leiopelma* (Amphibia, Leiopelmatidae) and description of three new subfossil *Leiopelma* species. *J. R. Soc. N. Z.* 17: 201–251.