

AFRICAN FOSSIL LISSAMPHIBIA

by

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ABSTRACT

The Anura (Frogs and Toads) are represented in Africa and associated regions by fossils of every epoch from the Cretaceous to the Holocene. Pipid frogs of African affinity are known from the Early Cretaceous of Israel and Later Cretaceous of South America and Africa; those of Israel and South America have been well-studied, but only one from Africa has been: *Eoxenopoides reuningi* from Namaqualand. Two well-studied Palaeocene frogs of South America, *Shelania pascuali* and *Xenopus romeri*, have affinities with the African pipids. Apart from a Miocene assemblage from North Africa (including pipids, which are now exclusively sub-Saharan) and one species from Namibia, *Xenopus stromeri*, the fossil African anurans remain largely unstudied. Deposits in which the African anuran fossils occur represent crater lakes, other lacustrine deposits, including lacustrine tuffs, river terraces, deltas, estuarine/lagoon zones, karst landscapes and archaeological sites; data are not available for several of the recorded fossils. No fossils in Africa appear to have been definitely ascribed to the Urodela or Caecilia.

INTRODUCTION

At a symposium on African Anura in January 1994 a computerized bibliography programme was demonstrated (Van Dijk, in press). The collection of literature, and the bibliography based on it, was started more than thirty years ago. Many items obtained, although relevant for the study of African Anura, had never been referred to in this connexion, or were only encountered in the reference lists of other articles. This was often the case with references relevant to fossil African Anura or related fossils. What is here presented is a review of the literature extracted from the computerized bibliography, to indicate the state of knowledge of the field and to point out references to fossils which await study.

REVIEW OF DATA

The Lissamphibia include three orders of Amphibia. Of these the legless Caecilia (= Apoda; = Gymnophiona) are known from only a single fossil species from South America, which appears to be related to a living West African species. The Urodela (newts and salamanders) occur in Africa only north of the Sahara, and have not been included in the literature collection or bibliography. There are in fact very few references to fossil urodeles in Africa. The comprehensive study of Estes (1981) lists no described fossil urodele. One Holocene site in East Africa lists Nectridia among the fossils (Andrews *et al.*, 1981). The Nectridia became extinct in the Permian, hence any lower vertebrate fossil with a tail at the site, if it is an amphibian, is more likely to be a urodele, with a remarkable distribution. De Broin, *et al.* (1974) found one specimen or species in the Cretaceous of Niger which they considered to resemble a Urodele – "Il semble d'autre part exister dans le gisement un Urodèle de grande taille dont la position systématique reste à

préciser". Estes (op. cit.) refers to urodeles from this site, and to work in progress on them (Estes & Rage, in preparation), but no publication could be traced. (Estes is now deceased). Of the Lissamphibia it is the Anura, the frogs and toads, which are at present overwhelmingly of interest in Africa as fossils, because of their numbers and because of the sureness with which they can be identified as anurans. The distribution of anuran fossils in Africa, and related ones, is summarized in the Table and Map.

DISCUSSION

In this discussion, only the most important diagnostic features will be mentioned. The oldest fossil considered to be an anuran is *Triadobatrachus* (Piveteau 1936a, 1936b, 1937; Estes & Reig 1973; Rage & Rocek 1984), from the Triassic of Madagascar. That it is an amphibian is shown by the presence of only one sacral vertebra. The short tail and small number of presacral vertebrae, reduced ribs, and forward projection of the ilia, are characteristics of Anura.

A fossil of early Jurassic age, from South America, named *Vieraella herbstii*, is very like modern Anura and is in fact assigned to the modern family Ascaphidae. By the Early Cretaceous three modern families, Ascaphidae (from South America), Discoglossidae (from Spain), and Pipidae (from Israel) are known, probably having diverged in the Jurassic. Ascaphidae have not been found in Africa, while living Discoglossidae in Africa are confined to North of the Sahara. A Miocene discoglossid has been reported from Morocco (Sanchiz & Alcover 1984).

The Pipidae, now sub-Saharan in Africa (and South American), occur as fossils in North Africa, while some South American fossils have close affinity to living African genera. The Pipidae are distinguished by loss of

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| CAENOZOIC Holocene Late Stone Age, Iron Age Middle & Late Stone Age | Anura indet. <i>Pyxicephalus</i> + | archaeological site archaeological site Kumakams, Bremen; Namibia | Matupi Cave; NE Zaire Zebrarivier, Maguams Avery 1984 | van Neer 1984 Cruz-Uribe & Klein 1983; |
| Pleistocene | amphibia | lacustrine crystal tuffs | Olduvai Gorge, Bed I; Tanzania | Leakey 1967 |
| Pliocene/Pleistocene | cf. <i>Xenopus</i> Anura | deltaic, estuarine, lagoonal calcareous cave breccia | Langebaan; South Africa Transvaal Caves; South Africa | Hendey 1967 |
| Pliocene ?Mio-/?Pleistocene | ?cf. <i>Xenopus</i> | terrace, volcanic terrain | Kleinsee, Namaqualand; South Africa | Stromer 1931 |
| Miocene | <i>Xenopus</i> ; <i>Ptychadena</i> ; <i>Bufo</i> Anura; Nectridia amphibia <i>Xenopus stromeri</i> | karst landscape muds, marls, silts; ?tuffaceous terrace deposits terrace, ?volcanic terrain | Beni-Mellal; Morocco Makobo Island, Lake Victoria; Kenya Arrisdrift; Namibia borehole near Elizabethbucht; Namibia | Hecht <i>et al.</i> 1961 Vergnaud-Grazzini 1966 Andrews <i>et al.</i> 1981 Hendey 1978 Stromer 1925; Ahl 1926 |
| Oligocene | <i>Xenopus (Libycus) hasaunus</i> | ? | Jabal al Hasawinah; C. Lybia | Spinar 1980 |
| Eocene | amphibians | lacustrine/fluviatile | El Kohol, near Brezina; Algeria | Mahboubi <i>et al.</i> 1986 |
| Palaeocene Upper Upper | <i>Shelania pascuali</i> # <i>Xenopus romeri</i> ** | ? fissure in limestone | <i>Laguna del Hunco</i> , Chubut; Patagonia, Argentina Sao Jose' de Itabori; Brazil | <i>Casamiquela</i> 1960, 1961 , 1965; Estes 1982; Baez 1983 Estes 1975a; 1975b, 1982 |
| Mesozoic Cretaceous Upper Upper Upper Upper Lower | <i>Eoxenopoides reunigi</i> pipid; cf. <i>Eoxenopoides reunigi</i> pipid <i>Saltenia ibanezi</i> ranid; 2 pipids cf. <i>Xenopus</i> * <i>r+</i> ; <i>Thoraciliacus</i> ; <i>Cordicephalus</i> <i>Shomronella jordonica</i> | crater lake crater lake crater lake argillaceous sandstone continental-marine margin lacustrine silt, volcanic terrain laminated shales, | Banke, Namaqualand; South Africa Stompoor, Maryvale; Namaqualand, South Africa diamond exploration site; Zaire Almenia, Salta; Argentina d'In Beceten, near Tahoua; S Niber Makhtesh Ramon; Israel Shomron; Israel | Haughton 1931; Estes 1977 van Dijk 1985; Smith 1986 Reig 1959; Parodi-Bustos <i>et al.</i> 1960; Ibanez 1960; Baez 1983 de Broin <i>et al.</i> 1974 Nevo 1956, 1968 Estes <i>et al.</i> 1978 |

** = *Silurana* * = *Silurana* # cf. *Xenopus muelleri* + cf. *Hymenochirus* *+ cf. *Silurana* & *Hymenochirus*

TABLE 1.

Fossil Lissamphibia in Africa, and related fossils in South America and Israel.

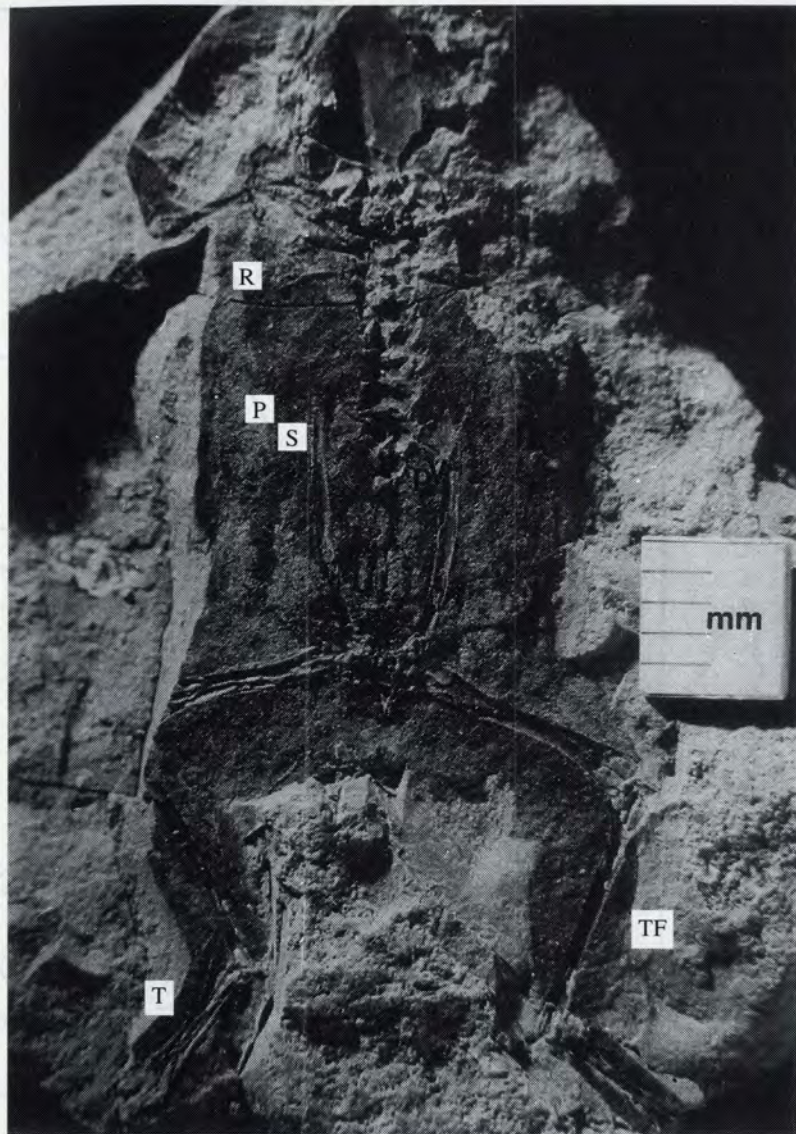


Figure 2. Pipid from Zaire Crater lake deposits. R rib; P pelvis (ilium); S sacrum (note moderate distal expansion); pV postsacral vertebra; U urostyle; TF fused tibia and fibula; T proximal tarsal (elongated tibiale and fibulare). Scale: 5mm.

an element from the upper jaw, the quadratojugal, and from the symphysis of the lower jaw, the Mentomeckelian. The Early Cretaceous pipids, of Israel, show the primitive condition of the sacrum, modified in all others by fusion of the post-sacral vertebral elements (fused into a urostyle) with the sacrum. The South American pipid *Saltenia*, like the Israel pipids, has free ribs, while all the African fossil and living adult pipids have those ribs which are present fused to the vertebrae. A characteristic of modern pipids of both South America and Africa, observed in some fossils, is an expanded sacrum, with straight parallel lateral edges, along which the parallel anterior projections of the ilia can slide; this was discovered in the living genera *Pipá* (South American) and *Xenopus* (African) by Hilgendorf in 1884, to which work no-one seems to have referred, before or after the rediscovery of the phenomenon (in 1960). The ilia may project well anterior to the sacrum. A characteristic pipid tadpole

morphology seems to have been established by Early Cretaceous times, to judge from the similarity of *Shomronella* to typical modern pipid tadpoles, e.g. of *Xenopus*. Besides pipids, and discoglossids north of the Sahara, only ranids and bufonids are known as fossils in Africa, from the Miocene.

The presence of fossil Ascaphidae in the Jurassic of South America indicates the possibility of discovering fossil members of the family in Africa, given the common pipid fauna. The presence of pipids north of the Sahara in the Miocene suggests that elements of the European fauna, such as those found in North Africa, may also have extended south of the Sahara.

That fossil anuran material in Africa is available for study, is illustrated in the Table and Map. An indication of abundance at one site may be deduced from the recorded presence of "Amphibia" at 22 of 23 sampling spits at Zebrarivier Cave (Avery 1984). A fossil awaiting description is illustrated in Figure 2.

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