MINISTRY OF MINES AND ENERGY

GEOLOGICAL SURVEY OF NAMIBIA

Director : Dr G I C Schneider

MEMOIR 20

GEOLOGY AND PALAEOBIOLOGY OF THE NORTHERN SPERRGEBIET, NAMIBIA

by

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Amphibia (Anura) from the Lower Miocene of the Sperrgebiet, Namibia

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Three localities (Grillental, Langental, Elisabethfeld) of the Lower Miocene of the Sperrgebiet (southwestern Namibia) have yielded amphibians. Only anurans are represented. This fauna includes '*Xenopus*' *stromeri* (Pipidae), another pipid (an indeterminate possible Pipinae), an indeterminate Ranoidea, another possible ranoid, and two other taxa that are indeterminate. '*Xenopus*' *stromeri* is redescribed and a diagnosis is provided. The relationships of this species within the Pipidae being doubtful, it is provisionally retained in *Xenopus* although it should probably be removed from this genus. Pipidae largely outnumber the other taxa, which suggests that permanent stands of quiet and/or stagnant water were present.

Version française abrégée

Les amphibiens proviennent du Miocène inférieur de la 'Sperrgebiet' (sud-ouest de la Namibie). Seuls les anoures sont représentés. Ils ont été trouvés dans trois gisements : Grillental (qui comprend, en fait, plusieurs sites), Elisabethfeld et Langental. Elisabethfeld et les sites de Grillental sont un peu plus anciens (ca 20 Ma) que Langental (ca 19 Ma). Ces gisements sont donc proches de la limite Aquitanien/ Burdigalien.

Les taxons

La faune comprend deux Pipidae ('*Xenopus*' *stromeri* et un possible Pipinae), un Ranoidea indéterminé, un possible Ranoidea et deux anoures indéterminés.

'*Xenopus*' *stromeri*

Il s'agit de la forme la plus abondante (présente à Grillental et Langental). L'espèce a été décrite par Ahl (1926) sur la base de spécimens venant la même région et des mêmes niveaux. Le matériel original est perdu et la description de Ahl est très incomplète. Toutefois, certains des caractères cités dans la description originale prouvent que le nouveau matériel appartient bien à cette espèce. '*X.*' *stromeri* est donc redécrit et une diagnose est proposée. L'espèce se caractérise surtout par sa forte ossification, l'association inhabituelle d'un profil crânien non en coin avec la présence de lames supraorbitales, la présence d'un processus rostriforme sur le coracoïde, la situation ventrolatérale du foramen périlymphatique inférieur par rapport au foramen jugulaire, ainsi que par la présence d'articulations intravertébrales additionnelles sur les arcs neuraux. D'après une analyse phylétique préliminaire, '*X.*' *stromeri* serait le groupe frère des Pipinae. Cependant, de telles relations ne peuvent pas être acceptées sans réserves; en particulier, il faudrait établir si la lame supraorbitale de '*X.*' *stromeri* est réellement homologue de celle des Pipidae dont le profil crânien est en coin, c'est-à-dire les Pipinae. Quoi qu'il en soit, l'espèce n'appartient probablement pas au genre *Xenopus*, mais en raison des incertitudes sur sa position phylétique, elle ne peut pas être attribuée avec certitude à un genre; elle est donc maintenue provisoirement dans *Xenopus*, comme '*Xenopus*' *stromeri*. Bien que le matériel original soit perdu, il n'est pas désigné de néotype. En effet, si le nouveau matériel est abondant et assez bien conservé, les spécimens disponibles ne permettent pas de reconstituer toutes les régions crâniennes. La richesse des gisements laisse espérer la découverte de spécimens plus complets.

? Pipinae, genre et espèce indéterminés

Cette forme, connue uniquement à Langental, n'est représentée que par un angulosplénial et des vertèbres. La forme coudée de l'angulosplénial suggère qu'il s'agit d'un Pipinae, mais cet unique caractère n'autorise aucune certitude.

Ranoidea, genre et espèce indéterminés A

Les spécimens, provenant tous de Grillental, ne semblent pas laisser de doute quant à l'attribution aux ranoïdes. En revanche, une identification plus précise est impossible.

? Ranoidea, genre et espèce indéterminés B

La présence de ce taxon est démontrée par un unique ilion trouvé à Grillental. Une crête dorsale est présente et le *tuber superius* dépasse cette crête dorsalement. Ce caractère se rencontre chez les Hemisotidae (Ranoidea) et les Leptodactylidae. Pour des raisons géographiques (après l'Eocène, les Leptodactylidae ne sont connus qu'en Amérique du Sud), l'attribution aux ranoïdes semble plus plausible; mais ce critère géographique ne peut évidemment pas être considéré comme réellement significatif.

Anoure indéterminé, genre et espèce indéterminés 1

Un grand sphénethmoïde de Grillental ne peut pas être attribué à l'un des autres anoures du gisement. Mais il ne permet pas d'identification au niveau familial.

Anoure indéterminé, genre et espèce indéterminés 2

Un sphénethmoïde avec les deux nasaux fusionnés montre qu'une sixième espèce est présente, mais la famille ne peut pas être déterminée.

Conclusions

Les Pipidae dominent largement ces faunes d'anoures (90% de l'ensemble des spécimens). La présence de Pipidae en grand nombre suggère qu'existaient des eaux calmes, voire stagnantes. Ces faunes n'apportent pas d'informations d'ordre paléoclimatique et stratigraphique.

Introduction

The amphibians yielded by the Miocene localities of Namibia include only anurans; they are represented by six taxa. They come from Langental, Elisabethfeld, and Grillental, all located in the Northern Sperrgebiet, southwestern Namibia.

Langental and Elisabethfeld each consist of one fossiliferous site, Grillental corresponds to several places (Pickford and Senut, 1999). Four sites in the Grillental area have yielded anurans: GT 1, GT 3, GT 6, and GT Quarry; besides, the precise origin of a part of the fossils from the Grillental area is unknown. Elisabethfeld has produced few specimens, most of them from a single owl pellet or carnivore scat, but Langental and mainly the Grillental area have yielded rich faunas.

Langental, Elisabethfeld, and the Grillental area are of Lower Miocene age. Elisabethfeld and the sites of the Grillental area would be slightly older (ca 20 Ma) than Langental (ca 19 Ma) (Pickford and Senut, 1999, 2003). In terms of international reference stages, their age is close to the Aquitanian-Burdigalian transition, either Aquitanian or Burdigalian.

The material was collected by M. Pickford and B. Senut (The Namibia Palaeontology Expedition); it is housed in the Museum of the Geological Survey of Namibia, Windhoek.

Systematic descriptions

Anura Rafinesque, 1815
Pipidae Gray, 1825

Today, the Pipidae are freshwater anurans that inhabit subsaharan Africa and northern South America plus Panama. Báez and Púgener (1998) referred the extant genera to two subfamilies: Xenopodinae for the African *Xenopus* and *Silurana* (in fact, the name should be Dactylethrinae (Dubois, 1983; Frost, 2002) and Pipinae for the African *Hymenochirus* and *Pseudhymenochirus* plus the South American *Pipa*. Within Pipinae, Báez and Trueb (1997) assigned the African pipines to the tribe Hymenochirini that is the sister goup of *Pipa*.

As far as fossil frogs are concerned, the record of Pipidae ranks among the best ones. As for the living forms, all fossils have been found in South America and on the Afro-Arabian Plate.

South America has yielded several extinct taxa: *Saltenia ibanezi* from the Campanian (related to pipines according to Báez and Púgener, 1998); *Shelania pascuali* from the Eocene and '*Shelania*' *laurenti* from the Upper Palaeocene to Middle Eocene (Báez, 2000; Báez and Púgener, 2003) (the latter two species appear to be related to the dactylethrines; Báez and Púgener, 1998, 2003); '*Xenopus*' *romeri* from the Middle Palaeocene (close to dactylethrines according to Báez and Trueb, 1997, closer to *Shelania* according to Báez and Púgener, 1998, but referred to *Silurana* by Buffetaut and Rage, 1993; see also Báez, 2000); *Llankibatrachus truebae* from the Eocene or Oligocene that is related to the dactylethrines (Báez and Púgener, 2003). Báez (2000) also reported some undescribed pipids from the Palaeogene of Patagonia.

Fossil pipids from the Afro-Arabian Plate are somewhat more numerous. *Pachycentrata taqueti* from the Coniacian-Santonian is related to the hymenochirines (Báez and Rage, 1998, 2004). *Eoxenopoides reuningi* appears to be close to the Pipinae (Báez and Púgener, 1998); it is regarded as Upper Eocene or Oligocene in age, but van Dijk (1995) suggested a markedly older age, i.e. Upper Cretaceous. '*Xenopus*' *hasaunus* from the Lower Oligocene was described by Spinar (1980), but Báez (1996) questioned its generic assignment. *Xenopus arabiensis* from the Upper Oligocene is the only confirmed pipid from the Arabian Peninsula (Henrici and Báez, 2001); its assignment to the extant genus *Xenopus* is not questionable and it represents the earliest ascertained representative of the genus. *Xenopus stromeri* from the Lower Miocene of Namibia is redescribed below; the referral of this species to *Xenopus* cannot be confirmed. Unnamed fossils from the Afro-Arabian Plate include specimens from the Cenomanian of Morocco (study in progress), an indeterminate genus from the Coniacian-Santonian of Niger (Báez and Rage, 1998), an indeterminate form from the Middle Eocene of Tanzania (Harrison *et al.*, 2001), specimens from the Middle Miocene of Morocco that were referred to as *Xenopus* sp. (Vergnaud-Grazzini, 1966) but that perhaps include *Silurana* (Báez, 1996), and an indeterminate species referred to *Xenopus* (i.e., *Xenopus* s.l., including *Silurana*) from the Pliocene of South Africa (Henrici and Báez, 2001) and from the Pliocene/Pleistocene transition of Tanzania (Leakey, 1965: 71).

Sanchiz (1998) included *Cordicephalus*, *Thoraciliacus*, and *Shomronella* from the Lower Cretaceous of Israel, i.e. the northeasternmost part of the Afro-Arabian Plate, to the Pipidae. But Báez (1996) regarded them as basal non-pipid Pipoidea, which appears to be right and was corroborated by Trueb (1999) at least for *Thoraciliacus*.

In southwestern Namibia (the Sperrgebiet), the Lower Miocene deposits have yielded two taxa of pipid frogs. One of them, represented by a few bones from Elisabethfeld, appears to belong to the Pipinae, although this cannot be definitely demonstrated. The second species is represented by a fair quantity of bones but it displays a somewhat puzzling combination of characters that prevents unquestionable referral to a subfamily; it is assigned to '*Xenopus*' *stromeri*.

Subfamily indeterminate

Various bones that bear resemblance to the extant African genera *Xenopus* and *Silurana* have been recovered at Grillental and Langental. A pipid frog from the same geological levels and from the same geographic area was described as *Xenopus stromeri* by Ahl (1926). Unfortunately, Ahl's description is very cursory and the material studied by him was destroyed during World War II (Sanchiz, 1998). The first problem is to establish, on the basis of the few data about *X. stromeri*, whether the material that is now available belongs to this species.

Previous data on *Xenopus stromeri* Ahl, 1926 and assignment of the new material

The species *Xenopus stromeri* was described by Ahl (1926) in a short chapter included in Stromer's monograph (1926) on the vertebrates from the Lower Miocene of Namibia (then Southwestern Africa). Stromer (1931: 39-40) briefly completed Ahl's description; he added some information on the skull and humerus and he provided a short description of vertebrae. It should be noted that the species included in the genus *Xenopus* at the time of Ahl and Stromer are now attributed to two genera, *Xenopus* and *Silurana* (Cannatella and Trueb, 1988a).

The material available to Ahl included incomplete skulls (braincases plus otic capsules), fragments of lower jaws, vertebrae, one coracoid, humeri, incomplete pelvic girdles, femora, and tibiofibulae. Ahl did not designate type(s), therefore all these specimens are the syntypes of the species. However, Sanchiz (1998) regarded only the skulls (?5), one humerus, and one tibiofibula as the syntypes. Sanchiz's opinion is probably based on the fact that only skulls (a dorsal and a ventral views of one or two distinct skulls), one humerus, and one tibiofibula were depicted by Ahl (1926: fig. 22 and pl. 42: figs 19-21). But, according to articles 72.1.1, 72.4.1, and 73.2 of the International Code of Zoological Nomenclature, 4th Edition (1999), the syntypes 'consist of all the specimens included by the author in the new nominal taxon'.

The specimens seen by Ahl came from the Lower Miocene of Bohrloch and Langental. But, according to Sanchiz (1998) the type locality is Elizabeth Bay. However, the latter locality did not produce frogs and both Ahl (1926) and Stromer (1926) stated that the

anurans were recovered from Bohrloch and Langental. It is true that Bohrloch is relatively close to Elizabeth Bay (about 5 km northeast of the latter site) but they are two distinct fossiliferous localities (M. Pickford, pers. comm.). Following the above-mentioned Code of Nomenclature (Article 73.2.3), if the syntypes come from several localities, the type locality includes 'all of the places of origin'. Therefore, the type locality of *Xenopus stromeri* is both Bohrloch and Langental.

Bohrloch is no longer accessible, which accounts for the lack of anurans from this locality in the present study. All the specimens illustrated by Ahl (1926) probably came from Bohrloch. This is clearly stated for the humerus, tibiofibula, and skull (in ventral view) figured on Stromer's, 1926 plate 42 (figs 19-21). Some doubts remain about the skull illustrated in dorsal view (fig. 22 in Stromer's text) for which no provenance is given and which may be a specimen distinct from that depicted in ventral view; but it is inferred from the text that it probably also came from Bohrloch (the skulls from Langental available to Ahl were less complete).

In his review of fossil anurans, Sanchiz (1998: 48) noted that the species was inadequately described, but he added that 'Báez (1996) gives evidence to consider this taxon valid'. Báez (1996: 337) actually stressed the large size of the remains and the strong ossification of the ethmoidal region, the latter character distinguishing *X. stromeri* from the living *Xenopus* but not from the extinct pipids.

Neither Ahl (1926) nor Stromer (1931) provided a diagnosis. From the latter articles, Sanchiz (1998) extracted the main characteristics of the species and he proposed the following diagnosis: Large species; frontoparietal unsculptured, with flat dorsal side and parietal foramen in the anterior third; parasagittal crests present, parallel in the middle and slightly convergent anteriorly and posteriorly; ethmoidal region well-ossified; otic region not protruding much and flat dorsally; doubtful presence of a small single vomer; atlas fused to second vertebra and bearing transverse processes; vertebrae opisthocoelous without well developed neural spines.

All but one of the characters in this diagnosis occur in the new material. Among them, the large size, strong ossification of the ethmoidal region, and flat dorsal surface of otic capsules appear to be significant. The only difference consists in the shape of the frontoparietal table. In the new material the table appears to grow more or less regularly narrow posteriorly. In fact, the skull figured by Ahl in dorsal aspect (1926: fig. 22) shows that the table does not clearly differ from that of the new specimens. In contrast, the relatively small size of the occipital condyles, a character noted by Estes (1975: 270), represents an additional feature common to *X. stromeri* and the new specimens. Therefore, the new material is referred to Ahl's species.

'Xenopus' stromeri Ahl, 1926
(Figs 1-5)

Provenance: Grillental area (GT1, GT 3, GT 6, GT quarry, and specimens of unknown precise provenance) and Langental.

Referred material: Langental, 4 incomplete braincases (LT 35'01; LT 144'03; LT 49'04; LT 141'04) and perhaps a fifth one (LT 48'04), 2 incomplete internal casts of braincases plus otic capsules (LT 36'01; LT 49'03), 15 sphenethmoids (LT 60'97; LT 50'99; LT 51'99; LT 52'99; LT 53'99; LT 54'99; LT 55'99; LT 38'01; LT 94'03; LT 215'03a-c; LT 47'04; LT 142'04; LT 151'04), 7 humeri (LT 56'99a, b; LT 50'03a; LT 174'03a-d).- Grillental area: GT 1, 1 braincase (GT 24'00), 5 sphenethmoids (GT 101'96; GT 107'96c, d; GT 36'03a, b), 2 oticoccipitals (GT 107'96a, b), 1 frontoparietal (GT 108'96), 3 angulosplenials (GT 107'96e-g), 1 atlantal complex (GT 103'96a), 3 presacral vertebrae (GT 103'96b-d), 1 coracoid (GT 107'96i), 1 scapula (GT 107'96h), 1 incomplete pelvis (GT 107'96j), 1 incomplete ilium (GT 107'96k), 5 humeri (GT 102'96; GT 107'96 l-n; GT 36'03c); GT 3, 1 sphenethmoid (GT 190'96); GT 6, 12 sphenethmoids (GT 46'00; GT 21'01a-c; GT 15'03a, b; GT 6 red a; GT 76'04a, b; GT 4'05; GT 17'05; 48'05), 19 oticoccipitals (GT 63'00a; GT 73'00; GT6 red b-h), 3 frontoparietals (GT 6 red i, j; GT 163'04), 2 angulosplenials (GT 63'00b; GT 6 red k), 2 atlantal complexes (GT 14'03a; GT 63'00c), 9 presacral vertebrae (GT 63'00d; GT 22'01a-d; GT 14'03 b, c; GT 6 red l, m), 2 incomplete sacrococcyges (GT 63'00e; GT 22'01e), 13 humeri (GT 73'96; GT 75'96; GT 14'03d; GT 6 red n-s; 18'05a, b; 47'05a, b); GT Quarry, 1 sphenethmoid (GT 68'00a), 2 coracoids (GT 40'01a, b), 1 humerus (GT 68'00b); GT-precise site unknown, 1 braincase plus otic capsules (GT 20'97), 2 sphenethmoids (GT 29'97; GT 30'97), 3 humeri (GT 36'97a-c).

Emended diagnosis:

Rather large and strongly ossified Pipidae that differs from all other members of the family by having supraorbital flanges associated with a non-wedge shaped skull, by the presence of a rostriform process of the coracoid, and by the ventrolateral position of the inferior perilymphatic foramen with regard to the jugular foramen.

Differs from nearly all other pipids by its flat, or even concave dorsal surfaces of the otic capsules, and in having an odontoid process on the atlas, short vertebral centra, and V-shaped salients forming an additional intervertebral articulation on the neural arch.

Further distinguished from the Pipinae in having a non-wedge shaped skull, an expansion of the parasphenoid posterior to the Eustachian canals, and an inferior perilymphatic foramen, and in lacking anterolateral processes of the frontoparietal and a superior perilymphatic foramen.

Differs from *Silurana* in having flat and simple articular facets of the zygapophyses, and in lacking anterolateral processes of the frontoparietal. Differs from the species referred to *Xenopus* by the presence of paired nasals and by having simple, flat facets of the zygapophyses, and the atlas fused to the second vertebra.

Differs from *Pachycentrata* in lacking accretion of dermal bone on skull and vertebrae and in having a non-wedge shaped skull, non-diagonally directed Eustachian canals, and simple, flat zygapophyseal facets. Distinguished from *Eoxenopoides* by its more elongate skull, narrower frontoparietal, and less reduced radial epicondyle of the humerus, and in having V-shaped salients on the neural arches. Differs from *'Xenopus' hasaunus* by its narrower frontoparietal and markedly narrower parasphenoid, by the presence of parasagittal crests on the frontoparietal, and probably in having V-shaped salients on the neural arches. Differs from *Shelania pascuali* by its paired nasals, markedly broader frontoparietal table (at least in adult stages), fused atlas and second vertebra, the absence of pterygoid knobs, and by the presence of V-shaped salients on the neural arches. Differs from *'Shelania' laurenti* by having a narrower frontoparietal table, in lacking pterygoid knobs, and in having V-shaped salients on the neural arches. Distinguished from *Saltenia* by its markedly narrower frontoparietal, in having fused atlas and second vertebra, and in lacking pterygoid knobs. Differs from *'Xenopus' romeri* in having paired nasals and only two acoustic foramina, and in lacking pterygoid knobs. Distinguished from *Llankibatrachus* by its narrower, more elongate frontoparietal, by the presence of an odontoid process on the atlas and of V-shaped salients on the neural arches, and by the absence of a notch between the glenoid and acromial processes of the scapula.

Description:
Skull:

The most complete specimen (GT 20'97) comprises the braincase and both otic capsules (Fig. 1); unfortunately, details are poorly preserved. It is strongly ossified and large; from the remaining part of the *septum nasi* to the occipital condyle the length is 27.5 mm. In lateral aspect, it is not wedge-shaped, but it is not domed. The frontoparietal is damaged but its anterior part shows that it is azygous. The parietal foramen cannot be seen on this specimen because it occurred in a crushed area. In GT 108'96, an isolated complete frontoparietal, and in GT 24'00 the parietal foramen occupies an anterior position, at about the anterior quarter (Fig. 2A); in GT 108'96, it opens in a shallow sagittal groove. The foramen is not as anterior as inferred by Estes (1975: 270) from Ahl's figure. Estes stated that the position of the foramen is similar in *'X.' stromeri* and in *'X.' romeri*. In fact, it is more posterior in *'X.' stromeri*. In Ahl's figure (Ahl, 1926: fig. 22) a sagittal line appears instead of a
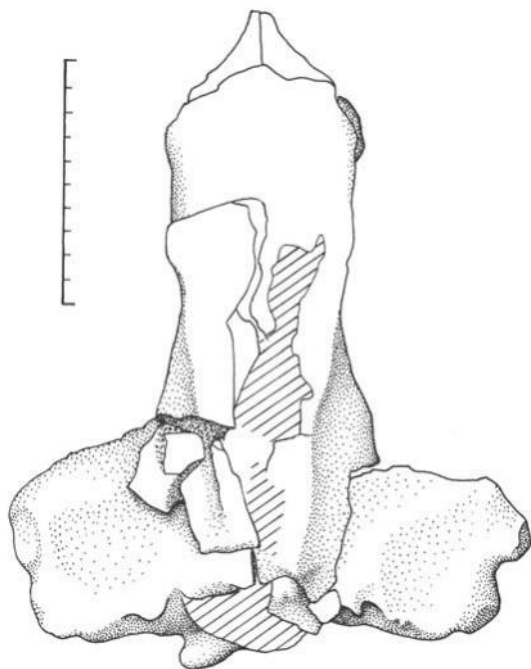
Figure 1: *'Xenopus' stromeri*. Grillental (precise site unknown), skull (braincase and otic capsules) (GT 20'97) in dorsal view. Scale bar: 10 mm.

foramen and the position of the parietal foramen cannot be determined from this illustration. The line probably represents a groove similar to that observed in GT 108'96. In GT 20'97 and GT 24'00, the frontoparietal is completely fused to the sphenethmoid and otic capsules. Astonishingly, although slightly larger than the frontoparietals of GT 20'97 and GT 24'00, GT 108'96 is disarticulated and its borders demonstrate that it was not fused to other cranial bones. The dorsal surface of the frontoparietal forms a flat, unsculptured table, limited by marked parasagittal crests. The table progressively and gently narrows posteriorly but it remains relatively wide; it is reminiscent of that of juvenile *Xenopus laevis* (Reumer, 1985). On the inner face of the frontoparietal, the endocranial pattern corresponds to a single surface that occupies most of the bone; this pattern differs from that of *Xenopus laevis* that has distinct anterior and posterior surfaces according to Spinar (1976). Anteriorly, the sphenethmoid projects beyond the frontoparietal. The ethmoidal part of the sphenethmoid is more developed than in living pipids; as a result the orbitonasal foramen (i.e., the posterior opening of the canal for the medial branch of the ophthalmic nerve; Rocek, 1981) is entirely surrounded by bone (Figs 2D, 4A). The anteriormost part of the sphenethmoid is probably roofed. The observation of this trait is difficult because, in all available specimens, the dorsal face is covered by the fused frontoparietal. However, on the ventral face of the frontoparietal, a transverse pad appears to be the anterior roof of the sphenethmoid. This transverse anterior roof of

the sphenethmoid forms the anterior limit of the frontoparietal fenestra. The *septum nasi* is thick and it projects markedly anteriorly. The olfactory foramina are entirely bound by bone. The anterior opening of the canal for the medial branch of the ophthalmic nerve is located in the nasal cavity, dorsolateral and very close to the olfactory foramen (Fig. 4B). In GT 20'97 and GT 68'00a, the nasals are present; they are paired and approximately crescentic (Fig. 1). Their posterior margin is overlapped by the frontoparietal. The prootic and exoccipital are fused; they form the "oticoccipital", that is the otic capsule. The oticoccipitals do not strongly project laterally but they are clearly expanded anteroposteriorly (Fig. 1). Their dorsal surface is flat, and even slightly concave, without any crest. A large *fenestra ovalis* opens in the lateral side of the oticoccipital.

The lateral walls of the braincase are damaged in the orbital region of all specimens, therefore foramina for nerves II to V cannot be observed. In the middle portion of the frontoparietal, lateroventral to the parasagittal crest, the lateral border of the bone projects slightly but clearly laterally as a ridge; posteriorly, the ridge joins the anterodorsal border of the otic capsule (Fig. 2C, D). This ridge may be interpreted as an incipient supraorbital flange.

Ventrally, the parasphenoid is entirely fused to the sphenethmoid and oticoccipitals; its limits are discernible only in the posterior part of GT 24'00 (Fig. 2C) and partly in GT 20'97. It lacks posterolateral (subotic) alae and it is constricted between the Eustachian canals but it expands slightly more posteriorly. Each Eustachian canal is wide and curved; it passes anterior to the ventral bulge of the otic capsule. There is no developed, well-defined pterygoid knob on the anteromedial corner of the ventral face of the oticoccipital. In GT 24'00, the floor of the braincase expands laterally below the area of nerves II-V. This expansion was perhaps produced by the parasphenoid; it may be entertained whether it formed a suborbital flange, but this cannot be appraised (Fig. 2C). Unfortunately, this area is observable only in GT 24'00 in which it is partly preserved. The area of the scars of the *retractor bulbi* is preserved in GT 24'00; the scars are not clearly marked. The ventral surface of the sphenethmoid is convex. No specimen reveals whether vomers were present.

In posterior aspect (Fig. 2B), the occipital condyles are small, elongate, narrow and reniform; they are widely separated from each other. The dorsolateral corner of each otic capsule forms a rounded protuberance. There is no posterior prominence for the posterior *semicircularis* canal of the inner ear. The usual place where this prominence occurs is occupied by small, irregular tuberosities. Because of its too lateral position, the above-mentioned rounded protuberance probably did not shelter the *semicircularis* canal. There is no foramen for the occipital artery. On each side, a large condyloid fossa is located
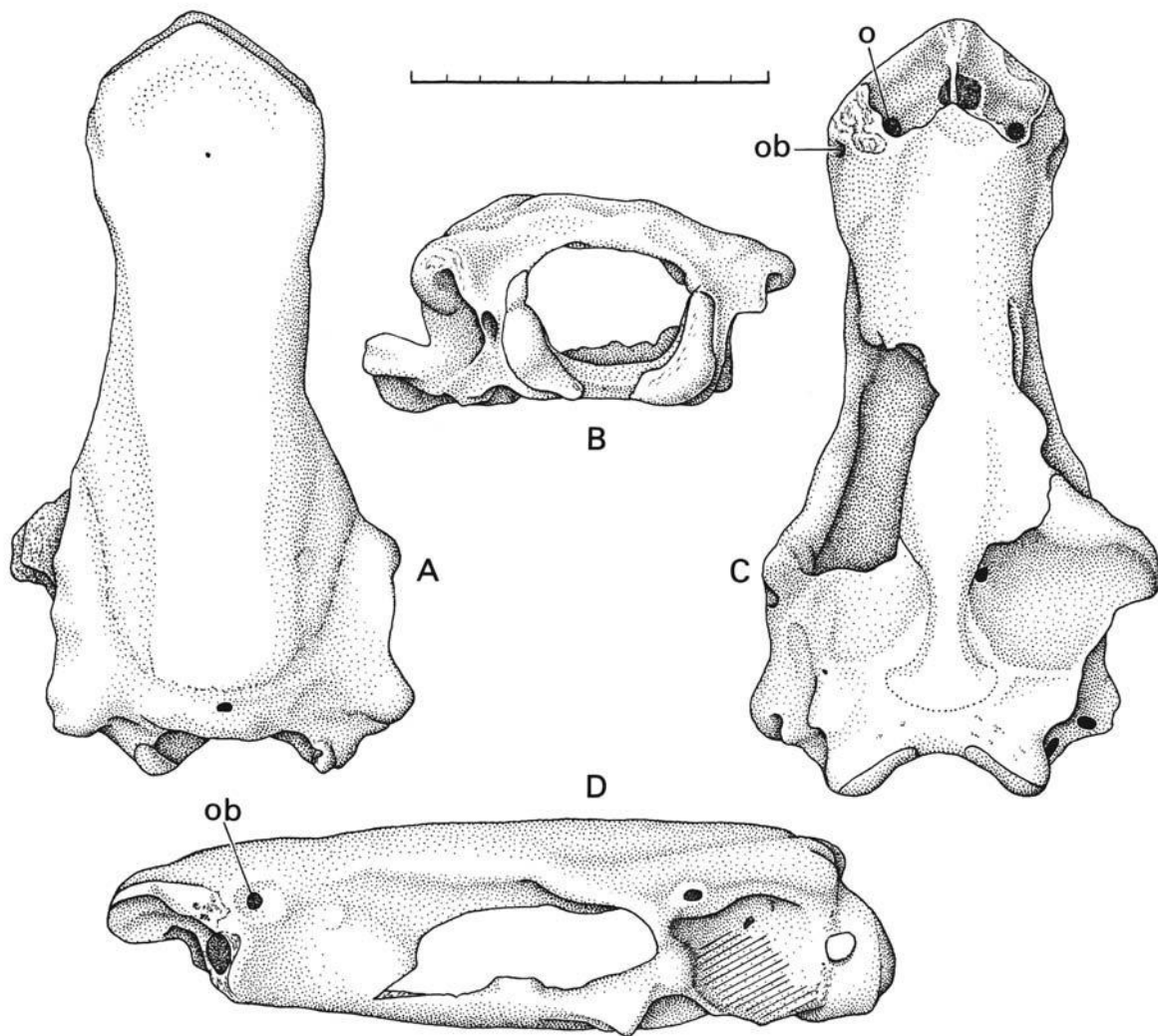
Figure 2: '*Xenopus*' *stromeri*. Grillental (GT 1), skull (braincase and incomplete otic capsules) (GT 24'00), in dorsal (A), posterior (B), ventral (C), and left lateral (D) views. (o: olfactory foramen, ob: orbitonasal foramen). Scale bar: 10 mm.

lateral to the occipital condyle. A large jugular foramen and a large inferior perilymphatic foramen open into the fossa (Fig. 3A). The latter foramen is ventrolateral and rather distant from the jugular foramen, which appears to be unusual. The fossa is deep and clearly limited in GT 73'00 and GT 63'00a, whereas it is shallow and poorly demarcated in GT 107'96a and b.

In the medial wall of the otic capsule, there are only two acoustic foramina (Fig. 3B). They are located in the bottom of a small and deep fossa and they are very close to each other, being separated by a delicate bony lamina. An endolymphatic foramen is just dorsal to the acoustic foramina. The superior perilymphatic foramen is absent. LT 49'03 is an internal cast of the braincase and otic capsules; fragments of the bones are attached to it. Unfortunately, the cast is not finely preserved and it does not yield information about cranial foramina.

The angulosplenial is steadily curved, without any angulation. The coronoid process is well-developed (Fig. 4E); it forms an anteroposteriorly elongate blade. The dentary extends posteriorly as far as the anterior border of the coronoid process.

Skull bones from non-adult stages:

Several sphenethmoids are isolated and not completely ossified although already large. This is not surprising since, at least in the pipid *Xenopus laevis*, the sphenethmoid is one of the last bones to ossify (Trueb and Hanken, 1992). This bone appears to be completed during metamorphosis, perhaps slightly later. Generally, the sphenethmoids of non-adults from the Namibian sites are shorter than the fully ossified ones and the floor and lateral walls of the posterior cavity are lacking. Four specimens are especially incomplete, although large (GT 21'01c, LT 60'97, LT 52'99, LT 55'99). They comprise only the
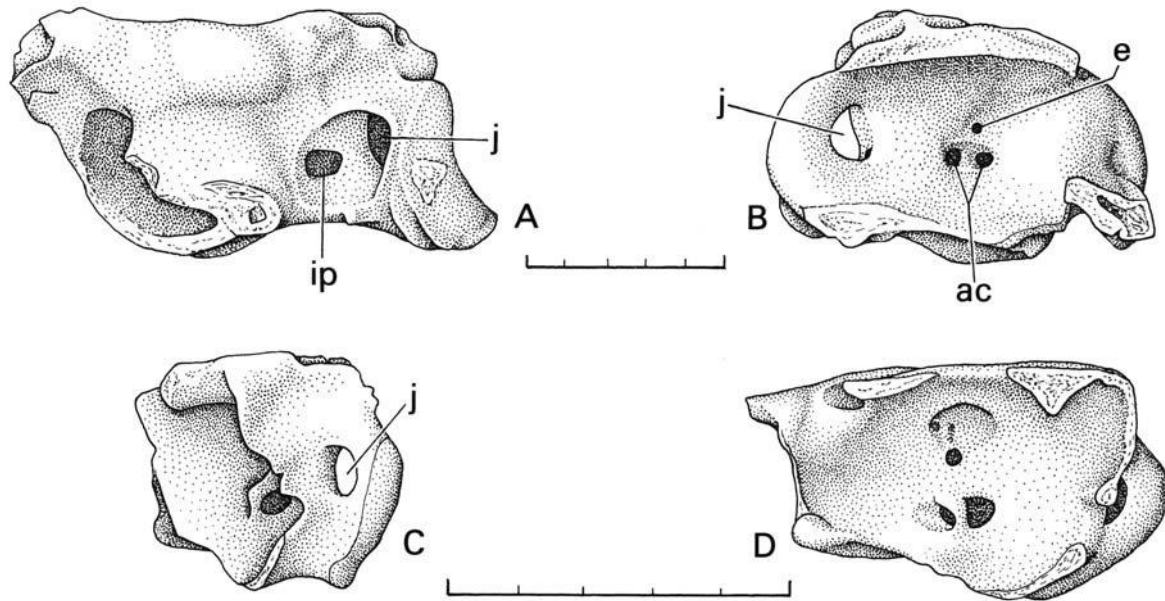
Figure 3: '*Xenopus*' *stromeri*. Grillental (GT 6); A, B, left oticoccipital (GT 73'00) of an adult individual, in oblique posterolateral (A) and medial (B) views. C, D, left oticoccipital (GT 6 red e) of a non-adult individual, in oblique posterolateral (C) and lateral (D) views. (ac: acoustic foramina, e: endolymphatic foramen, ip: inferior perilymphatic foramen, j: jugular foramen). Each scale bar: 5 mm.

roof, a part of the *septum nasi*, and a very small part of the floor represented by the expanded ventral edge of the *septum nasi* (Fig. 4C, D); however, a part of the roof of these specimens might be constituted by the already fused frontoparietals. In late larval stages, and probably in young adults, the canal for the medial branch of the ophthalmic nerve remains laterally open, as a groove, although the sphenethmoid is practically complete.

One site (GT 6 red) has yielded 17 oticoccipitals, of which at least 16 (GT6 red c-h) belong to non-adult individuals (Fig. 3C, D). They are weakly ossified and, apart from the largest specimen, the lateral part of the otic capsule is not ossified; each otic cap-
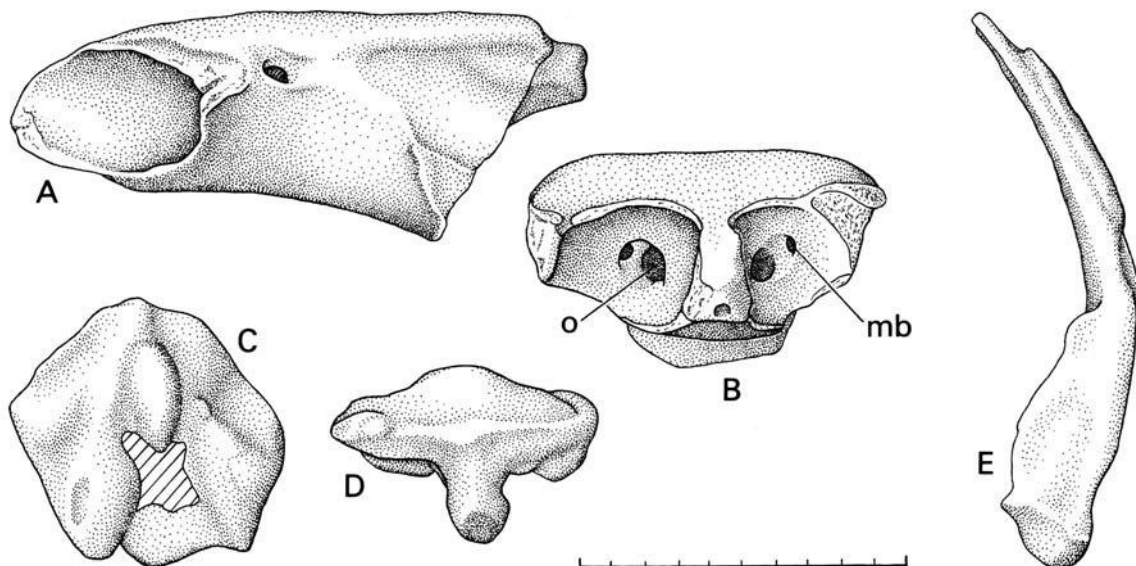

Figure 4: '*Xenopus*' *stromeri*. A, B, Grillental (GT 3), sphenethmoid (GT 190'96), in left lateral (A) and anterior (B) views. C, D, Langental, sphenethmoid (LT 60'97), larval stage, in ventral (C) and anterior (D) views. E, Grillental (GT 1), angulosplenial (GT 107'96g) in dorsal view. (mb: anterior opening of the canal for the medial branch of the ophthalmic nerve, o: olfactory foramen). Scale bar: 10 mm.

sule is comprised of only the full medial wall and reduced roof and floor. The inferior perilymphatic foramen is not entirely surrounded by bone; it is represented by a notch. The two acoustic foramina are already separated in most of these specimens. A fossa is located dorsal to the endolymphatic foramen on the lateral face of the medial wall.

Postcranial skeleton
Atlantal complex (Fig. 5A-C):

As in various other pipids, the first vertebra (i.e., the atlas) is fused to the second vertebra (V2); they make up the atlantal complex. In the available material there are three atlantal complexes (GT 103'96a, GT 14'03a, GT 63'00c, the latter being represented only by the centra). There is no isolated atlas among the available specimens. None of the three specimens shows trace of fusion between the two vertebrae and the complex is short. The opisthocoelous condition is shown by the presence of an articular cotyle on the posterior face; the centrum being depressed, the cotyle is elongated transversely. On the anterior face, the occipital cotyles are narrow and reniform. A broad and blunt odontoid process clearly projects anteriorly beyond the level of the occipital cotyles;

the articular surfaces of the occipital cotyles extend onto the posterior part of the lateral sides of the odontoid process. The neural arch lacks a neural spine but small crests occur in parasagittal positions. The anterior border of the neural arch is not markedly indented, but it is slightly convex with a small median notch. Transverse processes are present but are broken off on all specimens. On either side, beneath the base of the process, a rather small spinal foramen opens. The articular surfaces of the postzygapophyses are flat, i.e. they lack ridges and grooves.

Presacral vertebrae (Fig. 5D, E):

The presacral vertebrae are also opisthocoelous and have depressed centra. The posterior cotyle is clearly elongated transversely. Anteriorly, the condyle of the larger vertebrae is narrower than the centrum; the latter appearing to be somewhat thickened. The vertebrae are short, but the neural arches are longer than the centra, i.e. they are of the imbricate type. The articular facets of the zygapophyses are flat. A neural spine is present as a low ridge that runs throughout the entire length of the neural arch. On the large vertebrae, on each side of the neural spine, crests form a V-shaped salient whose point
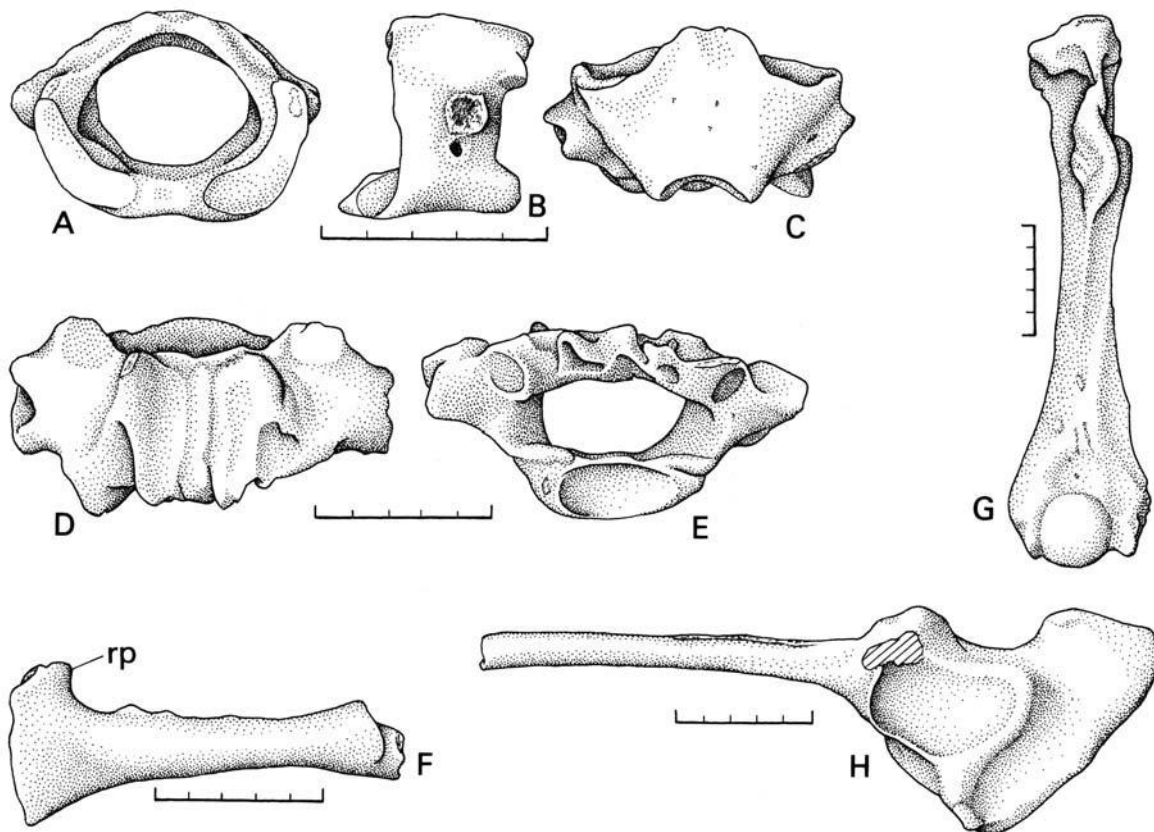

Figure 5: '*Xenopus*' *stromeri*. A-C, Grillental (GT 6), atlantal complex (GT 14'03a), in anterior (A), left lateral (B), and ventral (C) views. D, E, Grillental (GT 1), presacral vertebra (GT 103'96c), in dorsal (D) and posterior (E) views. F, Grillental (GT 1), left coracoid (GT 107'96i) in medial view (rp: rostriform process). G, Grillental (GT 6), right humerus (GT 73'96) in anteroventral view. H, Grillental (GT 1), pelvic girdle (GT 107'96j) in left lateral view. Each scale bar: 5 mm.

projects anteriorly (Fig. 5D). This probably provided an additional articulation in life, the anterior point fitting into the posterior open side of the 'V' of the preceding vertebra. In smaller vertebrae, these crests occupy only the posterior part of the neural arch (i.e., they did not provide an additional articulation) and the smallest specimens lack them. This system does not appear to be homologous to the parasagittal posterior spinous processes that are present in pipines (Báez and Rage, 1998). In the latter group, these processes are formed by the border of a notch in the neural spine.

Three presacral vertebrae (GT 22'01b-d) are amphicoelous. But the neural arches of these specimens bear V-shaped crests similar to those that occur on the above-described vertebrae. Therefore, despite the amphicoelous condition, these three vertebrae are referred to '*X.' stromeri*. Such an anomaly, i.e. occurrence of amphicoelous vertebrae in taxa that are either procoelous or opisthocoelous, is of ontogenetic origin and is not rare in anurans.

Sacrococcyx:

Two very incomplete sacrococcyges are available. Both lack the urostylar part and the sacral apophyses. The centrum bears an anterior condyle. Prezygapophyses are present whereas the posterior part of the neural arch is broken away. On both sides, a spinal foramen opens posterolaterally. Anterior to the spinal foramina are the bases of the broken off sacral apophyses.

Pectoral girdle:

A nearly complete right scapula and fused fragment of clavicle (GT 107'96h) as well as three dorsolateral parts of disarticulated coracoids (GT 107'96i; GT 40'01a, b) are preserved. The scapula lacks only the anterolateral corner. It is short dorsoventrally as is typical of Pipidae. There is apparently no notch between the glenoid and acromial processes of the scapula; this perhaps results from the strong ossification. The fusion between the scapula and clavicle is complete, without any trace of suture.

The glenoid extremity of the coracoids elaborates an anterior process whose distal part is broken off (Fig. 5F). This process likely represents the rostriform process that is known in the Palaeobatrachidae (Spinar, 1972) and it appears to be unique among Pipidae. The anterior border of the coracoid forms a thin and sharp crest that is relatively close to the glenoid extremity.

Pelvic girdle (Fig. 5H):

A rather complete girdle (GT 107'96j) and an incomplete ilium (GT 107'96k) are present in the sample. GT 107'96j comprises the ischia, pubes, and posterior parts of the ilia, but a portion of the ilial shaft is preserved only on the left side (Fig. 5H). These bones are solidly fused together. In dorsal view, the junction of the two halves of the girdle forms a 'U'. Unfortunately, the dorsal edge of the ilial shaft is broken off, consequently it is not possible to assess whether a dorsal crest was present. The *tuber superius* is lower than in most pipids and it is located above the anterior part of the acetabulum. It comprises clearly distinct prominence and protuberance (*sensu* Tyler, 1976). The protuberance arises from the posterior part of the prominence. Both the supra- and subacetabular expansions are strongly reduced. The acetabulum is somewhat elongate anteroposteriorly; except in its dorsal part, it is limited by a prominent crest. The medial face of the acetabular area forms a marked thickening, that comprises a large interiliac tubercle; this causes the U-shaped junction of the two halves of the girdle. The ischia project markedly dorsally; as a result of the reduction of the ilial supraacetabular expansion, they form a distinctive posterior dorsal projection that is apparently characteristic of the Pipidae. The pubes are paired, ossified, very reduced anteroposteriorly but strongly expanded transversely; they form a broad and rather flat transverse surface that also appears to be characteristic of the palaeobatrachid pipoids. GT 107'96k affords no additional information.

Humerus (Fig. 5G):

Two humeri are complete (GT 73'96; GT 102'96). The diaphysis is robust and slightly curved (the lateral border is weakly concave while the medial one is approximately straight), the humeral ball being shifted slightly laterally. The anteroventral surface of the proximal head bears a groove. The deltoid crest (*crista ventralis*) is strong and it extends as far as the proximal third of the diaphysis. Another crest (*crista paraventralis*) is located on the diaphysis, medial to the deltoid crest. It is less prominent than the former and it does not reach the proximal head; however, distally it extends up to the cubital fossa as a very low but sharp keel. The cubital fossa is well-marked and large. The humeral ball is relatively small but its size is variable. The ulnar (medial) epicondyle is large and pointed distally. The radial (lateral) epicondyle is smaller than the ulnar one but it is not clearly reduced, which is typical of pipid frogs. The olecranon scar is very shallow.

Discussion:

One of the most striking feature of this frog is the strong ossification. Consequently, several characters that might be significant from a taxonomic point of view perhaps result only from the degree of ossification. These characters are: *septum nasi* well-ossified, ethmoid area of sphenethmoid developed (consequently, orbitonasal foramen enclosed by bone), sphenethmoid forming the anterior limit of the frontoparietal fenestra, olfactory foramina entirely surrounded by bone, parasphenoid fully fused to the braincase, spinal foramen of atlantal complex relatively small, notch between glenoid and acromial

processes of the scapula absent, and clavicle fused to scapula.

Referral to the Pipidae is demonstrated by the presence of Eustachian canals on the ventral face of the otic capsules, the large and blade-like coronoid process of the angulosplenial, and the strong reduction of the supraacetabular expansion (Báez and Trueb, 1997). It should be added that the ischia are not reduced concomitantly to the reduction of the supraacetabular expansion of the ilia; as a result, the ischia form a high dorsal projection that appears to be typical of the Pipidae. These features are regarded as derived.

The following characters also support the assignment to the Pipidae although each of them is not restricted to this family: frontoparietal azygous (known in various other anurans); frontoparietal overlapping the posterior margin of nasals (also known in the Rhinophrynidae); parasphenoid lacking posterior alae (character also present in other pipoids: Rhinophrynidae and Palaeobatrachidae); vertebrae opisthocoelous (also in Discoglossidae and Rhinophrynidae); centrum depressed (occurs in various other frog taxa); scapula short dorsoventrally (also in Leiopelmatidae, Discoglossidae, Palaeobatrachidae, and Pelodytidae); *tuber superius* of ilium distinct and high (known in some other anurans); strong interiliac tubercle present (occurs rarely in other anurans); acetabulum elongated anteroposteriorly (also in some other anurans); pubes ossified, strongly reduced anteroposteriorly, and strongly expanded transversely (also in the Palaeobatrachidae). This combination of characters clearly points to the Pipidae.

Only one character of '*X.*' *stromeri* appears to be plesiomorphic with regard to all living Pipidae: the sphenethmoid forms the anterior limit of the frontoparietal fenestra (Báez and Púgener, 2003). Unfortunately, this character cannot be assessed in most fossil taxa; moreover, it perhaps results directly from the strong ossification.

The search for affinities among the Pipidae is not easy because the Namibian taxon shows only three derived characters that may be used within the family: i) the absence of the superior perilymphatic foramen is a character that also occurs in *Silurana*, *Xenopus*, '*Shelania*' *laurenti*, and '*Xenopus*' *romeri* (area not observable in *Eoxenopoides*, *Saltenia*, *Shelania pascuali*, and *Llankibatrachus*) (Báez and Púgener, 1998, 2003); ii) the fused atlas and second vertebra, i.e. presence of an atlantal complex, is also known in *Silurana*, the living Pipinae, *Pachycentrata*, *Eoxenopoides*, '*X.*' *romeri*, '*X.*' *hasaunus*, *Llankibatrachus*, and '*S.*' *laurenti*; iii) the presence of incipient supraorbital flanges perhaps heralds the condition in pipines. It should be noted that, apart from '*X.*' *stromeri* and an undescribed fossil from the Cenomanian of Morocco (study in progress), supraorbital flanges occur only in pipids whose skull is wedge-shaped, i.e. Pipinae.

Other features may be regarded as derived, but this cannot be confirmed. An odontoid process on the atlas occurs in various pipids (*Pseudhymenochirus*, several species of *Pipa*, '*Shelania*' *laurenti*; Cannatella and Trueb, 1988b; Báez and Púgener, 1998). However, it may be entertained whether the development of this process is due only to the strong ossification. The non-indented anterior border of the atlantal neural arch was regarded as a synapomorphy of the Pipinae by Cannatella and Trueb (1988a), however Báez and Púgener (1998) and Báez and Rage (1998) rightly questioned the significance of this character.

With regards to the Pipinae, '*X.*' *stromeri* displays plesiomorphic states in having a non-wedged skull in lateral aspect and an expansion of the parasphenoid posterior to the Eustachian canals, and in retaining an inferior perilymphatic foramen (Báez and Trueb, 1997). The absence of anterolateral processes of the frontoparietal is a plesiomorphic state that, among living pipids, is known only in *Xenopus*; in extinct taxa, these processes are also lacking in at least *Eoxenopoides*, *S. pascuali*, '*S.*' *laurenti*, *Saltenia*, '*X.*' *romeri*, and *Llankibatrachus* (the condition cannot be determined in *Pachycentrata* because of strong coossification). The presence of paired nasals is a plesiomorphic feature that occurs in all pipids, except for the living species of *Xenopus* as well as in the extinct *S. pascuali* and '*X.*' *romeri* (Báez and Púgener, 2003). Finally, the presence of two acoustic foramina is the state known in all living pipids except *Pipa* in which there is only one foramen; '*X.*' *romeri* has three or four acoustic foramina (Estes, 1975), which represents a primitive state. In addition, within living Pipidae, only *Pipa* has simple, flat articular surfaces of the zygapophyses; in other living pipids, the zygapophyseal facets bear ridges and grooves or are strongly curved. In *Pipa*, the character state is reversed (Báez and Trueb, 1997), therefore flat facets may be expected in primitive pipids (apart from *Pipa*, flat facets occur in *Eoxenopoides*, *S. pascuali*, '*S.*' *laurenti*, *Saltenia*, '*X.*' *romeri*, and *Llankibatrachus*; Báez and Trueb, 1997; Báez and Púgener, 2003).

Apart from the above-mentioned features, '*X.*' *stromeri* displays characters that infrequently occur in Pipidae and whose polarization is unknown or doubtful. The atlantal complex is short, which is an unusual trait in pipids. Such a character is known in the living *Xenopus largeni* (Báez and Púgener, 1998), and in the extinct *Pachycentrata*, '*X.*' *romeri*, and '*S.*' *laurenti*; it also occurs in the mid-Cretaceous pipoid *Avitabatrachus* (Báez *et al.*, 2000). Similarly, the centrum of vertebrae posterior to the atlantal complex is unusually short for a pipid; apart from '*X.*' *stromeri*, short centra are known in the living *X. muelleri*, in *Pachycentrata*, and in a part of the vertebrae of the pipid(s) referred to as *Xenopus* sp. from the Middle Miocene of Morocco (Vergnaud-Grazzini, 1966). This character is also present in the pipoid *Avitabatrachus* (Báez *et al.*, 2000). The flat or slightly concave dorsal surface of the otic capsules appears to

be known in only two other pipids, i.e. a fossil from the Coniacian-Santonian of Niger that was referred to as 'unidentified genus and species' by Báez and Rage (1998) and *Xenopus* sp. from the Middle Miocene of Morocco (Vergnaud-Grazzini, 1966). The rostriform process of the coracoid is a character unique within the Pipidae. But, such a process is present in the palaeobatrachid pipoids, and therefore its presence in pipids is probably plesiomorphic. The position of the inferior perilymphatic foramen, ventrolateral to and relatively distant from the jugular foramen, is perhaps also a unique feature. Báez and Púgener (1998, 2003) regarded the ventral position of this foramen as the derived condition and the lateral position as the plesiomorphic state, but they did not observe a ventrolateral position. Bilateral salients projecting anteriorly on the neural arches of vertebrae are present only in the Namibian fossil and in an indeterminate pipid from the Coniacian-Santonian of Niger (Báez and Rage, 1998: text-fig. 5).

As far as the relationships of '*X.*' *stromeri* within Pipidae are concerned, it should be noted that the combination of characters is somewhat puzzling. Moreover, the strong ossification perhaps biases the evaluation of characters. Preliminary analyses have been performed; they were based on 22 characters from the data matrices of Báez and Púgener (1998, 2003) to which were added the presence/absence of supraorbital flanges and of a rostriform process of the coracoid. I included the 14 taxa used by Báez and Púgener (1998) to which I added '*Xenopus*' *stromeri*. Surprisingly, the analyses have shown that '*X.*' *stromeri* would be the sister group to the Pipinae, while I expected closer relationships with the Dactylethrinae. Twenty most-parcimonious trees were obtained; in all of them there is a clade that has the form (*Eoxenopoides* ('*X.*' *stromeri* (Pipini, Hymenochirini))). The close relationships between '*X.*' *stromeri* and the Pipinae result from the presence of supraorbital flanges in the two taxa. Although the trees are rather robust (length: 40, ci: 67, ri: 80), I think this result cannot be definitely accepted. On the basis of the available data set, it would be illusory to regard any pipid cladogram as definite. In extinct taxa, too many features remain unknown and cladograms of pipids are not stable as far as these taxa are concerned. As for '*X.*' *stromeri*, the ventral face of the nasal area and the orbitotemporal region remain unknown; moreover, it should be established whether a suborbital flange was present. In addition, it appears to be necessary to establish whether the supraorbital flanges of '*X.*' *stromeri* (whose skull is not wedge-shaped) are really homologous of those of the Pipinae (which result probably directly from the flattening of the skull).

However, the combination of characters displayed by the Namibian fossil is unique, which supports the validity of the species whatever its phylogenetic position. Although, the phylogenetic relationships of '*X.*' *stromeri* remain questionable, it may be presumed with little doubt that it cannot be assigned to *Xenopus* as this genus is currently understood. But, in view of the uncertainties, at present it appears preferable to give it provisional generic status as '*Xenopus*' *stromeri* Ahl, 1926, as for '*Xenopus*' *romeri*, '*Xenopus*' *hasaunus*, and '*Shelania*' *laurenti*.

Brief comparisons with other Pipidae:

Comparisons with other pipid taxa, either living or extinct, confirm that '*X.*' *stromeri* is a distinct species. It differs from all other reported pipid taxa in having supraorbital flanges while the skull is not wedge-shaped, in having a rostriform process on the coracoid, and in having an inferior perilymphatic foramen that opens ventrolaterally to the jugular foramen.

In addition, other characters permit the distinction of '*X.*' *stromeri* from all other reported pipids.

The living Pipinae are sharply distinguished from '*X.*' *stromeri* by their wedge-shaped skull, the presence of anterolateral processes of the frontoparietal and of a superior perilymphatic foramen, and by the absence of an inferior perilymphatic foramen, of an expansion of the parasphenoid posterior to the Eustachian canals, and of V-shaped salients on the neural arches. Besides, except in *Pipa* (in which the character is reversed) the articular surfaces of the zygapophyses are complex, not flat in pipines.

Silurana differs from '*X.*' *stromeri* in lacking salient crests on the neural arches and in having anterolateral processes of the frontoparietal.

The living species of *Xenopus* have an azygous nasal, separate atlas and second vertebra, and they lack V-shaped salients on neural arches.

Pachycentrata taqueti (Báez and Rage, 1998) and the indeterminate pipid from the Middle Eocene of Tanzania (Harrison *et al.*, 2001) both have wedge-shaped skulls, diagonally directed Eustachian canals, and ventrally curved postzygapophyzes. '*Xenopus*' *stromeri* further differs from *P. taqueti* mainly in lacking accretion of dermal bone on the skull and vertebrae and in lacking parasagittal posterior spinous processes of the vertebrae.

The unidentified genus and species from the Coniacian-Santonian of Niger (Báez and Rage, 1998) is reminiscent of '*X.*' *stromeri* in having otic capsules with flat dorsal surfaces. Moreover, a vertebra from the same locality in Niger shows salients on the neural arch (Báez and Rage, 1998: text-fig. 5) that recall vertebrae of '*X.*' *stromeri*. It may be entertained whether this vertebra from Niger belongs to the same species as the skull referred to as 'unidentified genus and species'. However, as far as comparisons are possible, the fossil from Niger differs from '*X.*' *stromeri* in having a shorter skull, a narrower anterior braincase, a frontoparietal table that widens posteriorly, and (if the vertebra from Niger really belongs to the same species as the skull) a longer vertebral centrum.

Eoxenopoides reuningi has a shorter skull and an ovoid frontoparietal. Apparently, the neural arches of the vertebrae lack V-shaped salients. The humerus of *Eoxenopoides*, as described by Estes (1977), has a strongly reduced radial epicondyle, which is unusual in pipids.

Comparisons with '*Xenopus*' *hasaunus* are difficult. The latter taxon differs from '*X.*' *stromeri* at least in having a broad, approximately oval frontoparietal that lacks parasagittal crests, a markedly broader parasphenoid, and probably in lacking V-shaped salients on the neural arches.

The pipid from the Middle Miocene of Morocco, i.e. *Xenopus* sp. according to Vergnaud-Grazzini (1966), has otic capsules with a flat dorsal surface as in '*X.*' *stromeri*. But it differs from '*X.*' *stromeri* in having a large foramen, anterodorsal to the *fenestra ovalis*, on the lateral face of the otic capsule. Moreover, its inferior perilymphatic foramen (labelled '*fossa condyloidea*' in Vergnaud-Grazzini, 1966: fig. 7A) is lateral to the jugular foramen, small processes are present posteroventrally to the inferior perilymphatic foramina, and its zygapophyseal facets are curved. In addition, in the fossil from Morocco one of the acoustic foramina is very large; but, since only one otic capsule is observable, this may be an individual variation.

Shelania pascuali is distinguished from '*X.*' *stromeri* by its markedly narrower frontoparietal table, its azygous nasal, by the presence of pterygoid knobs, separate atlas and second vertebra, and absence of V-shaped salients on the neural arches. '*Shelania*' *laurenti* differs from '*X.*' *stromeri* in having pterygoid knobs, a broader frontoparietal, and in lacking V-shaped salients on the neural arches.

'*Xenopus*' *romeri* differs from '*X.*' *stromeri* in having an azygous nasal, three or four acoustic foramina, and pterygoid knobs.

Saltenia ibanezi has a frontoparietal clearly broader than that of '*X.*' *stromeri*. Moreover, it differs from the latter in having pterygoid knobs, the atlas not fused to the second vertebra, and in lacking V-shaped salients on the neural arches (Báez, 1981: 138).

Llankibatrachus truebae has a less elongate, broader frontoparietal than '*X.*' *stromeri*. It further differs from '*X.*' *stromeri* in having a notch between the glenoid and acromial processes of the scapula and in lacking an odontoid process on the atlas and V-shaped salients on the neural arches. Moreover, the ulnar epicondyle of its humerus is clearly larger than that of '*X.*' *stromeri*.

Conclusions:

'*Xenopus*' *stromeri* is a valid species, clearly distinct from all other living and extinct pipid taxa. It shows derived features, or incipient derived features that also occur in either *Silurana*, or the Pipinae, or in living species referred to *Xenopus*. The sister group relationships between '*X.*' *stromeri* and the Pipinae

that have resulted from preliminary analyses cannot be accepted without reservation. Since the precise relationships are questionable and since Ahl (1926) originally referred the species to the genus *Xenopus* (at that time *Xenopus* included *Silurana*), the Namibian species is provisionally classified as '*Xenopus*' *stromeri* Ahl, 1926.

Although the syntypes are lost, no neotype is designated. In the available specimens, some key areas are not well enough preserved and it may be hoped that future field research will provide more complete specimens.

One fact deserves special attention. In '*X.*' *stromeri*, supraorbital flanges are present whereas the skull is not wedge-shaped. Apart from this species, the association of these two features occurs only in an undescribed pipid from the Cenomanian of Morocco (work in progress). In addition, the V-shaped salients that are present on the neural arches of the vertebrae are known in only one other pipid, i.e. an indeterminate genus from the Coniacian-Santonian of Niger. In other words, these peculiar features displayed by '*X.*' *stromeri* occur only in two other pipids that also come from Africa.

? Pipinae
Unidentified genus and species
(Fig. 6)

Provenance: Elisabethfeld.

Referred material: 1 incomplete angulosplenial (EF 234'01d), 3 disarticulated portions of vertebral column (EF 234a-c). All these specimens are from a single owl pellet or carnivore scat and perhaps belong to a single individual.

Description:
Angulosplenial:

The angulosplenial is missing the anterior part and its posterior extremity. As is typical of Pipidae, the coronoid process forms a well-developed, anteroposteriorly elongate blade. It is smaller than the angulosplenials attributed to '*Xenopus*' *stromeri*, but it appears to be slightly more robust. This specimen mainly differs from the angulosplenials of '*X.*' *stromeri* in being clearly angled anterior to the coronoid process, instead of steadily curved (Fig. 6A).

Vertebrae:

The anterior portion of a vertebral column (EF 234'01a) includes the atlantal complex (i.e., atlas plus V2), V3, and V4 (Fig. 6B-D). The following portion (EF 234'01b) comprises V5 and V6 (Fig. 6E); it unquestionably articulates with the preceding portion. The third portion (EF 234'01c) includes two posterior presacral vertebrae; apparently it articulates with EF 234'01b, but this cannot be definitely confirmed. If EF 234'01c really articulates with EF 234'01b, then its components are V7 and V8, which means that the
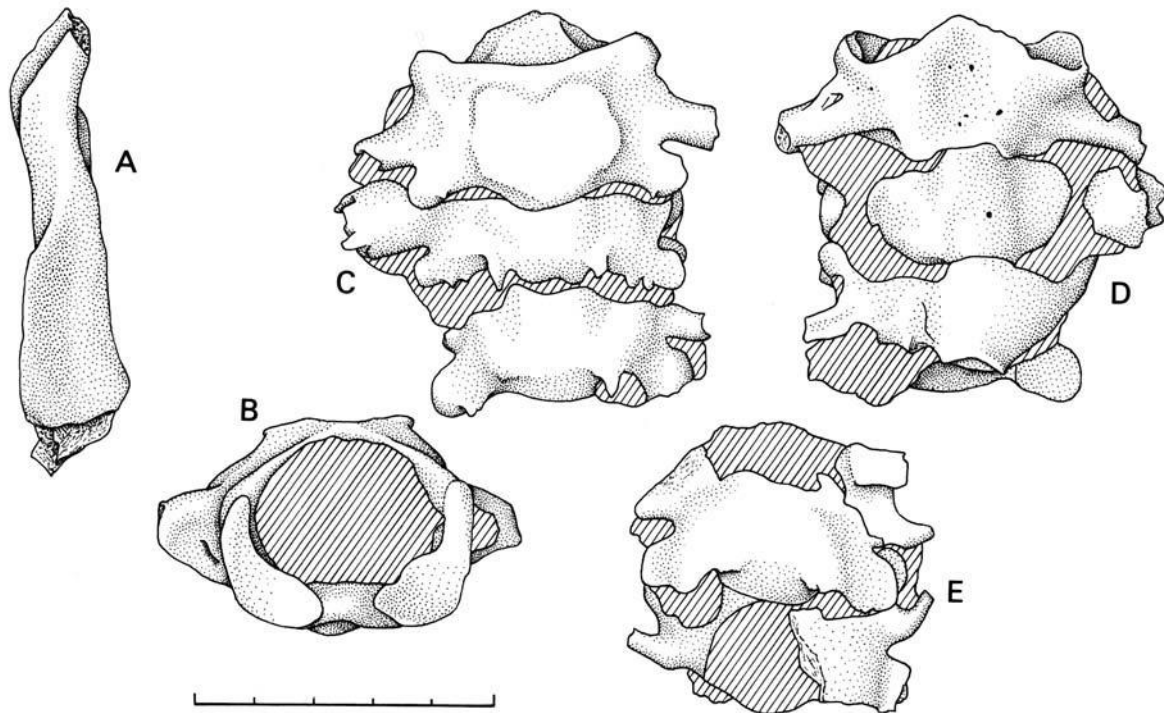
Figure 6: ? Pipinae, unidentified genus and species, Elisabethfeld. A, right angulosplenial (EF 234'01d) in dorsal view; B-D, anterior four vertebrae of a vertebral column (EF 234'01a) in anterior (B), dorsal (C), and ventral (D) views; E, 5th and 6th vertebrae from the same vertebral column (EF 234'01b) in dorsal view. Scale bar: 5 mm.

vertebral column included at least eight presacral vertebrae. If the latter two portions do not belong to the same vertebral column, then the minimum number of presacral vertebrae is unknown.

The vertebrae are opisthocoelous (Fig. 6D). The atlas and V2 are fused, making up the atlantal complex. As in '*X.*' *stromeri*, the complex is short, an odontoid process is present, and the occipital cotyles are elongate and reniform (Fig. 6B). The cotyles extend onto the lateral faces of the odontoid process and they approach its anterior extremity. On each side, the spinal foramen is covered by matrix and its size remains unknown; it opens either anterior or anteroventral to the transverse process, while in '*X.*' *stromeri* it is ventral to the process. The atlantal complex further differs from that of '*X.*' *stromeri* in being relatively shorter and in having a flat and rather broad table on the neural arch instead of parasagittal crests (Fig. 6C). On either side, close to the postzygapophysis, the posterior border of the neural arch of V2 bears a small spine that projects posteriorly.

On the more posterior vertebrae, the posterior border of the neural arches forms several small spines that are directed posteriorly. On V3, three spines are present on either side. Two of them are close to the postzygapophysis (a position similar to that of the single spine in V2); another, longer spine is closer to the median part of the neural arch (Fig. 6C). On V5, apparently only the more median spine remains on each side (but both are broken away; Fig. 6E), but the

most posterior vertebra (? V8) of EF 234'01c retains one lateral spine. Unfortunalety, the median part of the border of the neural arch is damaged on vertebrae posterior to V5 and it is not possible to state whether the more median spines were preserved. The neural arch of V3 was rather short but in more posterior vertebrae the arches are of the imbricate type (although not clearly elongate). None of the arches bears a neural spine. The articular facets of the zygapophyses are flat. The preserved bases of the transverse processes show that from V2 to V4 the processes are directed slightly posterolaterally, but on more posterior vertebrae they are clearly directed anterolaterally (Fig. 6C, E).

Discussion:

The angulosplenial may be confidently referred to the Pipidae on the basis of the peculiar morphology of the coronoid process. In addition, the vertebral column shows a combination of features that secures assignment to this family: opisthocoelous condition, atlas and V2 fused, most vertebrae of imbricate type, marked change of orientation of the transverse processes by the V4-V6 transition (transverse processes of posterior vertebrae markedly directed anterolaterally). Based on size consistency and on the fact that they were found in a single owl pellet or scat, the angulosplenial and three portions of the vertebral column are referred to the same pipid species.

A more precise referral within Pipidae partly depends on the significance of the posterior spines of the neural arches. The relatively short neural arches and the spines might suggest that the arches are not fully grown, i.e. that the vertebrae belong to a juvenile individual. If that is the case, the more median spines might correspond to not-yet-developed V-shaped salients known in '*X.*' *stromeri*. However, vertebrae of '*X.*' *stromeri* that are similar in size to the vertebrae from Elisabethfeld, i.e. vertebrae belonging to non-fully grown '*X.*' *stromeri*, have longer neural arches and their V-shaped salients are already shaped, although not fully developed (see above). Therefore, the vertebrae from Elisabethfeld are unlikely to represent a juvenile of '*X.*' *stromeri*. This is consistent with the fact that the angulosplenial demonstrates that a pipid distinct from '*X.*' *stromeri* is present at Elisabethfeld. It may be entertained whether the more median spines are homologous to the parasagittal processes that clasp the neural spine of the succeeding vertebra in the Pipinae. However, the pipid from Elisabethfeld lacks neural spines. If these spines are really homologous to the parasagittal processes, they differ from those of *Pipa* and hymenochyrines in being more widely spaced.

While the information from the vertebrae does not appear to be clear, the angulosplenial may be referred to the Pipinae on the basis of its marked angulation. However, based on this single feature, this assignment cannot be regarded as unquestionable.

It should be noted that the flat, simple articular facets of the zygapophyses and, with regard to hymenochirines, the presence of eight presacral vertebrae (if this is the case, see above) represent plesiomorphic characters that provide no helpful information.

In Africa, the Pipinae are represented by the extant Hymenochirini and *Pachycentrata taqueti* from the Coniacian-Santonian of Niger (Báez and Rage 1998).

Pipidae indeterminate

Provenance: Elisabethfeld.

Referred material: 1 angulosplenial (EF 234'01e) and 1 humerus (EF 234'01f).

The angulosplenial does not differ from those referred to '*X.*' *stromeri*; but since no element from Elisabethfeld unquestionably demonstrates the presence of this species in the locality, this element is regarded as an unidentified pipid. The humerus is poorly preserved.

Final remarks about Pipidae

In Africa, living pipids occur south of the Sahara and in a small isolated area in northeastern Chad (Kobel, 1981; Frost, 2002). Extinct pipids have been found beyond this range, up to North Africa and the Arabian Peninsula (Vergnaud-Grazzini, 1966; Spinar, 1980; Báez, 1996; Báez and Rage, 1998; Henrici and Báez, 2001). Pipid species dwell in permanent freshwater. They live in stagnant pools and are very rarely found in running water. These frogs cannot survive for a long time on land. Adults are carnivorous, most of them feeding on all sort of dead animals (Dunchar, 1975).

Ranoidea Bonaparte, 1845
Family indeterminate
Unidentified genus and species A
(Fig. 7A-D)

Provenance: Grillental area.

Referred material: <u>GT 6</u>, 2 humeri (GT 56'00a; GT 63'00f); <u>GT-precise site unknown</u>, 1 sacral vertebra (GT 36'97d), 2 ilia (GT 36'97i, j), 4 humeri (GT 36'97e-h).

Description:

The sacral vertebra is tiny (Fig. 7A, B). It is opisthocoelous and posteriorly it bears two condyles for articulation with the urostyle; the latter condyles are widely spaced. The sacral apophyses are broken off but, as shown by the preserved basal part of one of them, it may be inferred that these apophyses were narrow and more or less cylindrical in section.

Only distal halves of the humeri are preserved (Fig. 7C). The diaphysis is slender and straight. The articular ball is small, not shifted laterally. A clearly delimited cubital fossa is present. The ulnar epicondyle is strong whereas the radial one is markedly reduced. The olecranon scar is elongate. A well-developed ulnar crest is present in males.

The ilia are incomplete (Fig. 7D). A relatively high dorsal crest is present on the shaft; it is slightly inclined medially. The *tuber superius* is formed by a thickening of the posterior border of the dorsal crest; it does not project dorsally above the crest.

Discussion:

The attribution of this tiny frog to the Ranoidea is based on the following combination of characters: sacral vertebra opisthocoelous, bearing two condyles for articulation with the urostyle; sacral apophyses not expanded; presence of a dorsal crest on the ilial shaft; *tuber superius* of the ilium formed by a thickening of the posterior border of the dorsal crest; humeral diaphysis straight and ball not shifted laterally.

Unfortunately, osteological characters are very homogeneous within ranoid frogs and these isolated bones do not permit identification at the family level. Ranoids include aquatic, arboreal, and more or less terrestrial frogs.
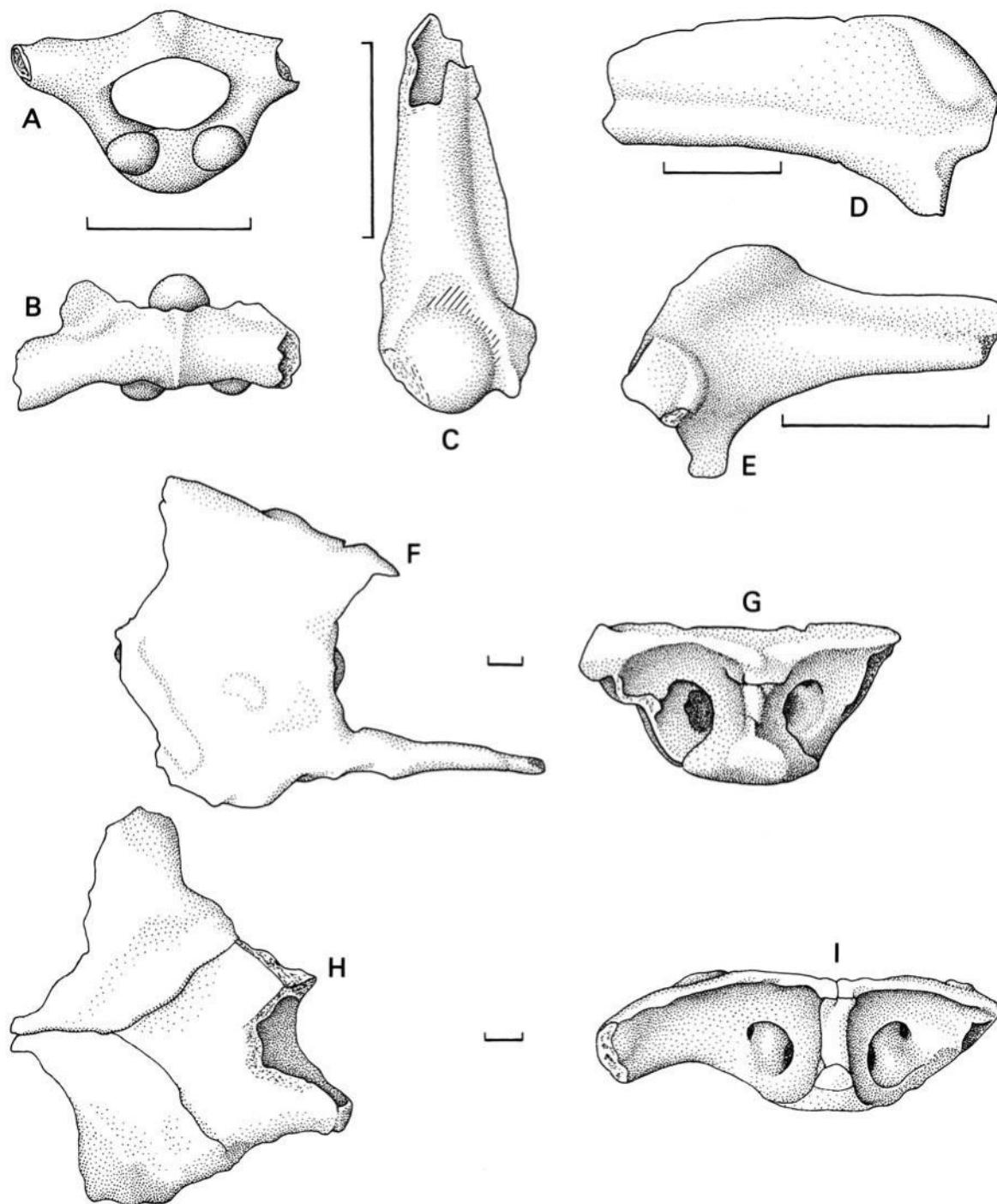
Figure 7: A-D, Ranoidea, 'unidentified genus and species A', Grillental (precise site unknown); A, B, sacral vertebra (GT 36'97d), in posterior (A) and dorsal (B) views; C, right humerus (GT 36'97e) in anteroventral view; D, left ilium (GT 36'97i) in lateral view. E, Grillental (GT 6), ? Ranoidea, unidentified 'genus and species B', right ilium (GT 56'00b) in lateral view. F, G, indeterminate anuran, unidentified 'genus and species 1', Grillental (precise site unknown), sphenethmoid (GT 96'96), in dorsal (F) and anterior (G) views. H, I, indeterminate anuran, unidentified 'genus and species 2', Grillental (GT 6), sphenethmoid and nasals (GT 76'04c), in dorsal (H) and anterior (I) views. Each scale bar: 1 mm.

? Ranoidea
Family indeterminate
Unidentified genus and species B
(Fig. 7E)

Provenance: Grillental area.

Referred material: <u>GT 6</u>, 1 incomplete ilium (GT 56'00b).

Description and discussion :
As is typical in ranoid frogs, but also in various discoglossids (*Discoglossus* group) and leptodactylids, this tiny ilium bears a dorsal crest and the *tuber superius* is represented by a thickening of the posterior border of the crest. GT 56'00b differs from the ilia of discoglossids by at least its more steeply inclined *tuber superius* and by the height of the latter tuber that markedly projects above the crest (it should be noted that the dorsal border of the crest is well-preserved). The latter feature clearly distinguishes GT 56'00b from the ilia that are, above, unambiguously referred to the ranoids. Such a character is known in various Leptodactylidae and in the hemisotid ranoids. The ilium from Grillental more closely resembles the leptodactylid morphology than that of Hemisotidae. But, Leptodactylidae inhabit the Americas; it would be surprising that a member of this family is present in the Miocene of Africa, although this cannot be definitely ruled out. The Hemisotidae are restricted to Africa, but the *tuber superius* of GT 56'00b is clearly less prominent and less pointed than in *Hemisus*, the only genus of the family. Therefore, this ilium cannot be referred to *Hemisus*.

Therefore, the referral at family level of this single, incomplete specimen cannot be settled. It is not assigned to the leptodactylids for geographical reasons. If it is not a leptodactylid, then it may be referred only to the ranoid assemblage, in which at least the Hemisotidae display a more or less similar *tuber superius*. However, it cannot unreservedly be attributed to the Ranoidea.

Anura indeterminate
Family indeterminate
Unidentified genus and species 1
(Fig. 7F, G)

Provenance: Grillental area.

Referred material: <u>GT-precise site unknown</u>, 1 sphenethmoid (GT 96'96).

Description and discussion :
The sphenethmoid is as large as the largest ones of '*X.*' *stromeri*, but it is wider and shorter than the latter. It is not fused to the frontoparietal and it lacks unquestionable traces of nasals. The anterior dorsal border is clearly more transverse than that of '*X.*' *stromeri* and, ventrally, the anterior median part is

less acute. The orbitonasal foramen is present only on the left side; it opens just beneath the dorsal surface of the bone.

The morphology of this sphenethmoid clearly differs from that of pipids. Moreover, because of its size, it cannot be referred to the above described ranoid or possible ranoid. This specimen does not permit identification at the family level.

Unidentified genus and species 2
(Fig. 7H, I)

Provenance: Grillental area.

Referred material: <u>GT6</u>, 1 sphenethmoid and fused nasals (GT 76'04c).

Description and discussion:
One sphenethmoid and fused nasals represent a distinct taxon. This specimen mainly differs from the sphenethmoids referred to '*X.*' *stromeri* and to 'unidentified genus and species 1' in having strong postnasal walls (sensu Rocek, 1981) that form elongate anterolateral projections and in being more depressed. The posterior part of the sphenethmoid is broken away; consequently, its length remains unknown. The two nasals are fused to the sphenethmoid and they largely cover its anterior part. The medial and medioposterior limits of the nasals are conspicuous, but laterally the nasals appear to be indistinctly fused to the postnasal walls. The size of this specimen is not consistent with those of the above described ranoid and possible ranoid. Consequently, it documents the presence of a sixth anuran taxon at Grillental, but identification at family level is not possible.

Anurans indeterminate

<u>Langental</u>: 2 fragmentary radioulna (LT 56'99i; LT 121'00a), 16 femora (LT 183'96g-j; LT 59'97a, b; LT 206'98c, d; LT 56'99h; LT 50'03b; LT 174'03g; LT 216'03c; LT 46'04a; LT 190'04; LT 196'04a; LT 217'04a), 41 tibiofibulae (LT 183'96a-f; LT 206'98a, b; LT 207'98; LT 56'99c-g; LT 148'00a-f; LT 39'01; LT 40'01; LT 78'01; LT 103'03a-c; LT 174'03e, f; LT 216'03a, b; LT 46'04b-f; LT 264'03a; LT 183'04; LT 196'04b; LT 217'04a, b), 17 fragments of metatarsals of phalanges (LT 264'03b; LT 121'00b).- <u>Grillental area</u>: GT1, 1 damaged sphenethmoid (GT 103'04); <u>GT 6</u>, 2 oticoccipitals (GT 18'97a, b), 2 radioulna (GT 6 red r; GT 75'04a), 5 femora (GT 47'00a, b; GT 14'03e; GT6 red t, u), 13 tibiofibulae (GT 81'96; GT 47'00c; GT 63'00g, h; GT 10'03; GT 6 red s; GT 75'04b-g; 47'05c), 1 tibiale-fibulare complex broken in two parts (GT 47'00d); <u>GT Quarry</u>, 1 femur (GT 40'01c), 2 fragments of metatarsals (GT 14'03f); <u>GT-precise site unknown</u>, 2 radioulnae (GT 36'97k, l).- <u>Elisabethfeld</u>, 1 posterior braincase, in two separated parts (EF 234'01g), 1 poorly preserved

sphenethmoid plus part of parasphenoid (EF 234'01h), 7 radioulna (EF 121'01a; EF 234'01i), 1 femur (EF 121'01b), 5 fragmentary metatarsals or phalanges (EF 121'01c; EF 234'01j).

Among the above indeterminate specimens, EF 234'01g deserves special attention. It is represented by two halves of a posterior braincase; it lacks Eustachian canals, therefore it cannot be referred to the Pipidae, but it could not be identified further. However, it is probably not unidentifiable.

Conclusions

In the Lower Miocene of the Sperrgebiet, amphibians are represented only by anurans. Six taxa that cannot all be identified to the family level, are present: two Pipidae, one Ranoidea, one possible Ranoidea, and two frogs that are not identified. The Pipidae includes two species, '*Xenopus*' *stromeri* Ahl, 1926, that is by far the most frequent amphibian and an indeterminate genus and species that is poorly represented and that might belong to the Pipinae. '*X.*' *stromeri* occurs at Grillental and Langental, whereas the other pipid has been found only at Elisabethfeld. The Ranoidea is comprised of a few bones that all come from Grillental. The possible Ranoidea and the two indeterminate anurans are each represented by a single specimen that are also from Grillental.

The original description of '*Xenopus*' *stromeri* was cursory and inadequate; moreover, the material on which the description was based is lost. Therefore, up to now, this species has not been revised. The material collected recently, shows that this species is valid and distinctive. The combination of features that characterizes it is somewhat puzzling. The phylogenetic relationships of '*X.*' *stromeri* are considered doubtful, although according to preliminary analyses it would be the sister group to the Pipinae. Consequently, the species is provisionally retained in the genus *Xenopus* as '*Xenopus*' *stromeri* Ahl, 1926, but likely it does not belong to this genus.

The Sperrgebiet amphibian fauna is very unbalanced since about 90% of the identifiable bones belong to '*X.*' *stromeri*. The frequency of pipids, that are highly aquatic frogs, demonstrates that water was present permanently; as for living pipids, the fossil ones probably required quiet, and even standing water during mating and breeding periods. From a palaeoclimatological point of view, this fauna cannot afford significant data because pipids are able to live from lowlands up to an altitude of 2500 m (Kobel, 1981) and the other taxa are not identified at family level. The studied amphibians do not provide biostratigraphic information.

Acknowledgements

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