

Discovery of a Gymnophionan skull (?Caeciliidae, Amphibia) in the Early Miocene of Uganda

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ABSTRACT

Gymnophionans (limbless, worm-like amphibians) are rarely preserved in the fossil record. For this reason it is interesting to put on record a partial skull and incomplete mandible of a medium sized species from the Early Miocene (ca 19-20 Ma) of Napak, Uganda. The specimen is tentatively attributed to Caeciliidae, the only family that occurs in Africa at present, but it shows some peculiar features including a sculptured cranial table among other characters that make it difficult to classify precisely. Gymnophionans are generally fossorial and secretive animals that inhabit warm, damp, tropical zones often occurring in damp leaf litter in forests (some lineages are amphibious).

Key Words : Gymnophionan, Caeciliidae, Amphibia, Early Miocene, Uganda

INTRODUCTION

Gymnophionans, also called apodans or caecilians, are elongate and, except for the earliest fossil species, are limbless amphibians. Their annulate, cylindrical body and the small size or absence of eyes externally, renders their appearance more or less worm-like. Among other peculiar features are the shortness or even absence of a tail and the presence of a retractile chemosensory tentacle between the eye and nostril. Today, they inhabit warm regions, almost all of them occurring in the tropics. They are mostly fossorial or secretive, but some are aquatic. In Africa, they live in two relatively narrow, disjunct zones, in the west they are known from Ivory Coast to western Democratic Republic of Congo) and in the east they have been found along the coast of East Africa and in the interior from southern Ethiopia to southern Malawi. According to Frost *et al.* (2006) only one family (Caeciliidae) is currently present in Africa; this family also occurs in Central and South America, the Seychelles Islands and India, i.e. it has a typical Gondwanan distribution. However, according to other classifications (Taylor, 1968; Nussbaum & Wilkinson, 1989) some African forms would belong to a distinct family, the Scolecomorphidae, restricted to Africa; but it should be noted that, whatever their precise phylogenetic relationships, the Scolecomorphidae appear to be closely related to the Caeciliidae (Peng & Wake, 2009) and both groups may be placed into a single clade.

BRIEF REVIEW OF EXTINCT GYMNOPTIONANS

Fossil gymnophionans are very rare. Astonishingly, the earliest one is the best known fossil. *Eocaecilia micropodia* was recovered from the early Jurassic (Pliensbachian or slightly older) Kayenta Formation in the USA where it is represented by 40 specimens, two being more or less complete. It is one of the most remarkable transitional fossils. *Eocaecilia* illustrates how a normal tetrapod vertebrate may have evolved into an elongate, legless form (Jenkins & Walsh, 1993; Carroll, 2000; Jenkins *et al.*, 2007). It retains various primitive features such as the presence of several skull bones that are separated whereas they are either fused or lost in modern forms, relatively large orbits, separate vertebral intercentra, an odontoid process on the atlas, absence of anteroventral processes on trunk vertebrae, a relatively long tail, and four legs that are small but well-shaped. On the other hand, it shows several derived characters that are shared with living gymnophionans: presence of a groove for the tentacle; fusion of several skull bones forming the typical 'os basale'; presence of an internal

process on the mandible; presence of a long, oblique suture between the two bones (pseudoangular and pseudodentary) of the mandible. In addition, the elongate body (which remains shorter than that of other gymnophionans) is clearly a tendency towards modern forms. A peculiar feature that is a specialisation of its own, the fusion of the stapes and quadrate bone, demonstrates that *Eocaecilia* cannot be an ancestral member of the group; it is regarded as the sister group to other gymnophionans (Trueb & Cloutier, 1991, in which *Eocaecilia* is referred to as 'Kayenta fossil'; Evans & Sigogneau-Russell, 2001). Trueb & Cloutier (1991) suggested the name Apoda for the typical, limbless forms, and the name Gymnophiona for the assemblage *Eocaecilia* plus Apoda. Although the validity of the name Apoda is disputed (Dubois, 2004; Frost *et al.*, 2006) we provisionally retain it because its use remains frequent and there is no satisfactory, consensual alternative to replace it.

All other fossils are represented by disarticulated bones and are presumed to belong to, or to be related to the Apoda. *Rubricacaecilia monbaroni* from the earliest Cretaceous (Berriasian) of Anoual, Morocco (Evans & Sigogneau-Russell, 2001) is known by a few skull bones, vertebrae, and perhaps one femur. *Rubricacaecilia* retains primitive vertebral characters that are also known in *Eocaecilia*: presence of an odontoid process on the atlas and absence of anteroventral processes on trunk vertebrae. According to Evans & Sigogneau-Russell (2001) *Rubricacaecilia* is more closely related to apodans than to *Eocaecilia*, but it is more primitive than the apodan crown group in which all living forms are included. Limbs were perhaps present in *Rubricacaecilia*.

The following, geologically younger fossils are represented only by some disarticulated trunk vertebrae (no atlas is known). According to Taylor (1977a) anterior vertebrae (including the atlas) of apodans provide information useful for purposes of identification; unfortunately, such vertebrae have not been found. However, all available vertebrae have elongate anteroventral processes, which is a derived feature which is absent in both *Eocaecilia* and *Rubricacaecilia*. In addition, the morphology of these vertebrae closely resembles that of apodans and these fossils are likely referable to this group; consequently, they probably lacked limbs. Such vertebrae were recovered from the mid-Cretaceous (Cenomanian) of the Wadi Milk Formation, Sudan (Evans *et al.*, 1996) and the late Cretaceous (Maastrichtian) of Pajcha Pata, Bolivia (Gayet *et al.*, 2001); in both localities, the fossils were regarded as indeterminate. Fossils were also found in two localities of the earliest Tertiary (Palaeocene) of South America; one of them, from Sao Jose de Itaboraí (Brasil) was named *Apodops pricei* and assigned to the Caeciliidae (Estes & Wake, 1972) whereas a form from Tiupampa (Bolivia) remains indeterminate (Rage, 1991). South America also yielded fossils from the Neogene; some vertebrae of a large, indeterminate gymnophionan were recorded from the middle Miocene of La Venta, Colombia (Hecht & LaDuke, 1997). Finally, a single vertebra belonging to the extant species *Dermophis mexicanus* (Caeciliidae) was reported from a Pleistocene locality of Mexico (Wake *et al.*, 1999).

Two fossils previously regarded to be gymnophionans do not belong to this group. *Prohypogeophis tunariensis* Marcus is a straight cephalopod (Orthoceratidae) from the Carboniferous of South America; Marcus (1945) mistook the chambers of its shell for annuli of a gymnophionan (Estes & Wake, 1972; Estes, 1981). An isolated bone from the Pleistocene of Germany was tentatively regarded to be the mandible of a gymnophionan by Brunner (1954) who described it as ? *Ichthyophis muelleri* (*Ichthyophis* is a living gymnophionan (Ichthyophiidae) from Asia); Estes & Wake (1972) showed that this bone is a pathological pectoral spine of a catfish.

The rarity of fossil gymnophionans makes it important to record the recovery of a skull belonging to this group in the Early Miocene of Napak (Uganda). Apart from *Eocaecilia* the Napak specimen is the only known articulated skull of a fossil gymnophionan.

THE NPAK GYMNOPHIONAN

Material : Uganda Museum, Nap XV 148'08, skull with part of one mandible.

Locality : Napak XV, Uganda.

Associated fauna and flora : Napak XV has yielded abundant faunal and floral remains characteristic of the Napak suite of sites (Bishop, 1964; Musalizi *et al.*, 2009; Pickford, 2002; Pickford *et al.*, 1986). The locality is unusual in yielding abundant crocodilian remains, which are otherwise rare at the Napak sites. The Napak fauna (Table 1) is typical of the Early Miocene of East Africa, with resemblances to those of Koru and Songhor, Kenya, which are slightly older, and Rusinga, Kenya, which is slightly younger.

Table 1. Early Miocene Fauna from Napak, Uganda.

Gastropoda	<i>Maizania lugubrioides</i>		<i>Proheliophobius</i> sp.
	<i>Maizaniella</i> sp.		<i>Vulcanisciurus africanus</i>
	<i>Tholachatina leakeyi</i>		<i>Paranomalurus bishopi</i>
	<i>Burtoa nilotica</i>		<i>Paranomalurus soniae</i>
	<i>Subulona</i> sp.		<i>Paranomalurus walkeri</i>
	<i>Oreohomorus</i> sp.	Gomphotheriidae	<i>Afrocrisetodon songhorensis</i>
	<i>Opeas</i> sp.		Species 1
	<i>Edouardia</i> sp.		<i>Archaeobelodon</i> sp.
	<i>Conulinus</i> sp.	Deinotheriidae	
	<i>Krapfiella</i> sp.		<i>Deinotherium hoblely</i>
	<i>Koruella magnifica</i>	Orycteropodidae	
	<i>Thapsia</i> sp.		<i>Orycteropus africanus</i>
	<i>Trochonanina</i> sp.	Hyracoidea	
	<i>Trochozonites</i> sp.		<i>Brachyhyrax aequatorialis</i>
	<i>Pupoides</i> sp.		Small sp.
	? <i>Macrogonaxis</i> sp.	Primates	
	<i>Gulella</i> sp. 1		<i>Mioeuticus bishopi</i>
	<i>Gulella</i> sp. 2		<i>Progalago dora</i>
	<i>Haplonepion naggsi</i>		<i>Komba robustus</i>
	<i>Tayloria</i> sp.		<i>Komba minor</i>
	<i>Edentulina rusingensis</i>		<i>Prohylobates</i> sp.
Insecta	Millipedes		<i>Limnopithecus legetet</i>
	Coleoptera		<i>Dendropithecus ugandensis</i>
	Moth cocoons		<i>Lomorpithecus evansi</i>
	Hymenopteran brood chambers		<i>Kalepithecus songhorensis</i>
	Termite bioconstructions		<i>Xenopithecus</i> sp.
Amphibia	? <i>Caeciliidae</i>		<i>Iriripithecus alekileki</i>
Reptilia	Ophidea		<i>Karamojapithecus akisimia</i>
	Lacertidae		<i>Turkanapithecus rusingensis</i>
	Chamaeleonidae		? <i>Proconsul</i> sp.
	Varanidae		<i>Ugandapithecus major</i>
	Chelonii		
	Crocodylidae	Creodonta	
Aves	Large sp.		<i>Metasinopa napaki</i>
	Medium sp.		<i>Pterodon africanus</i>
	Small sp.		<i>Isohyaenodon pilgrimi</i>
			<i>Hyaenodon?</i> sp.
			<i>Leakitherium hiwegi</i>
Mammalia			<i>Teratodon spekei</i>
			<i>Prionogale breviceps</i>
			<i>Kelba quadeemae</i>
	Insectivora	Fissipeda	
	<i>Amphechinus rusingensis</i>		<i>Hecubides macrodon</i>
	<i>Protenrec tricuspis</i>		<i>Hecubides euryodon</i>
	<i>Erythrozoetes chamerpes</i>		<i>Kichechia zamanae</i>
	Macroscelidea		<i>Leptoplesictis rangwai</i>
	<i>Myohyrax</i> sp.	Perissodactyla	<i>Ginsburgsmilus napakensis</i>
	<i>Miorhynchocyon</i> sp.		
Chiroptera			<i>Butleria rusingense</i>
			<i>Aceratherium</i> sp.
Rodentia	Indet sp.		<i>Brachypotherium</i> sp.
			<i>Ougandatherium napakense</i>
	<i>Diamantomys luederitzi</i>	Artiodactyla	
	<i>Paraphiomys pigotti</i>		<i>Brachyodus aequatorialis</i>
	<i>Paraphiomys stromeri</i>		<i>Nguruwe kijivium</i>
	<i>Epiphomys coryndoni</i>		<i>Diamantohyus africanus</i>
	<i>Simonimys genovefae</i>		<i>Dorcatherium parvum</i>
	<i>Miophiomys arambourgi</i>		<i>Dorcatherium songhorensis</i>
	<i>Megapedetes pentadactylus</i>		<i>Dorcatherium iririensis</i>
	<i>Renefossor songhorensis</i>		<i>Walangania africanus</i>

Age : Early Miocene.

Depositional environment : Well-bedded volcanic ash with signs of incipient pedogenesis and indications of minor fluvial activity. These deposits accumulated on the flanks of an active carbonatite-nephelinite volcano and remained friable for extended periods of time during which termites developed their galleries and fungus gardens in the soil, and abundant moth caterpillars burrowed into the ash to pupate. Associated plants (*Celtis*, *Ficus*) indicate a well-wooded to forested palaeoenvironment, an inference supported by the fossil gastropod assemblage (Table 1) which is typical of upland tropical forest (Pickford, 1995, 2004, 2009).

DESCRIPTION

The length of the skull is 21 mm, which corresponds to a medium sized animal. Unfortunately, parts of the skull are lacking and hard matrix conceals various areas (Fig. 1). The overall configuration is typical of gymnophionans: the anterior part is semi-elliptical while the posterior, occipital region is narrower; the dorsal surface is not clearly fenestrated; the otic area does not appear to be markedly wider than the more anterior part of the braincase.

Dorsally, a flat and sculptured table occupies the area of the parietals and frontals. The table is perhaps prolonged anteriorly by a triangular, sagittal area whose dorsal face is damaged; it is likely a part of the sphenethmoid ossification and was probably covered by the posterior parts of nasals. However, it cannot be stated whether this triangular area is fused to the table or only covered by it posteriorly. Consequently, it is not possible to determine whether the table is formed only by the parietals and frontals, or if its anterior area is represented by a part of the sphenethmoid. Some irregular, marked lines are visible on the table but they do not appear to be sutures; they are likely connected to ornamentation and no ascertained sutural line can be discerned. The sculpture appears to be produced by dermal ossification that forms rounded to elongate, low tubercles. There is no parietal foramen. The lateral borders of the table are damaged but the posterior limit is preserved as a V-shaped sharp edge that served as muscle attachment. On either side, an embayment indents the lateral border of the table. The two embayments occur at the same level and are therefore symmetrical. Their borders are damaged, but because of their symmetrical positions they do not appear to result from breakage. Their positions correspond to those of eyes and they may be regarded as the dorsalmost parts of the two orbits. The size of the orbits cannot be securely evaluated; taking into account the fact that the embayments were likely enlarged by damage, the orbits were likely small. Posteriorly, there is apparently no suture line between the occipital bones and the table. The occipital region projects markedly posteriorly beyond the dorsal table. Apart from a dorsal sagittal line that may be either a suture or a break, no suture is visible between bones of the occiput, which is characteristic of gymnophionans. In this group, bones of the occipital and otic regions are indistinguishably fused to the floor (the parasphenoid) of the braincase, forming the typical 'os basale' (Carroll & Currie, 1975). Despite the incomplete nature of the fossil, the extent of the table suggests that the cranial fenestrae, if any, were not broad.

The anterior part of the skull is quite damaged. The right premaxilla is partly preserved. The cross-sections of four premaxillary teeth are visible, but teeth were perhaps more numerous. A flat, horizontal fragment lies dorsal to the premaxilla. Although not in contact with the table, it is likely the anterior part of the right nasal. Interestingly, it appears to be fused to the premaxilla. The left lateral surface of the deep nasal septum is exposed in lateral aspect. Its anterior part is broken away. The septum, that is the anteriormost part of the sphenethmoid ossification, occupies a sagittal position dorsal to the rostral process of the parasphenoid to which it is fused and, dorsally, it joins the triangular area that is likely a part of the sphenethmoid too.

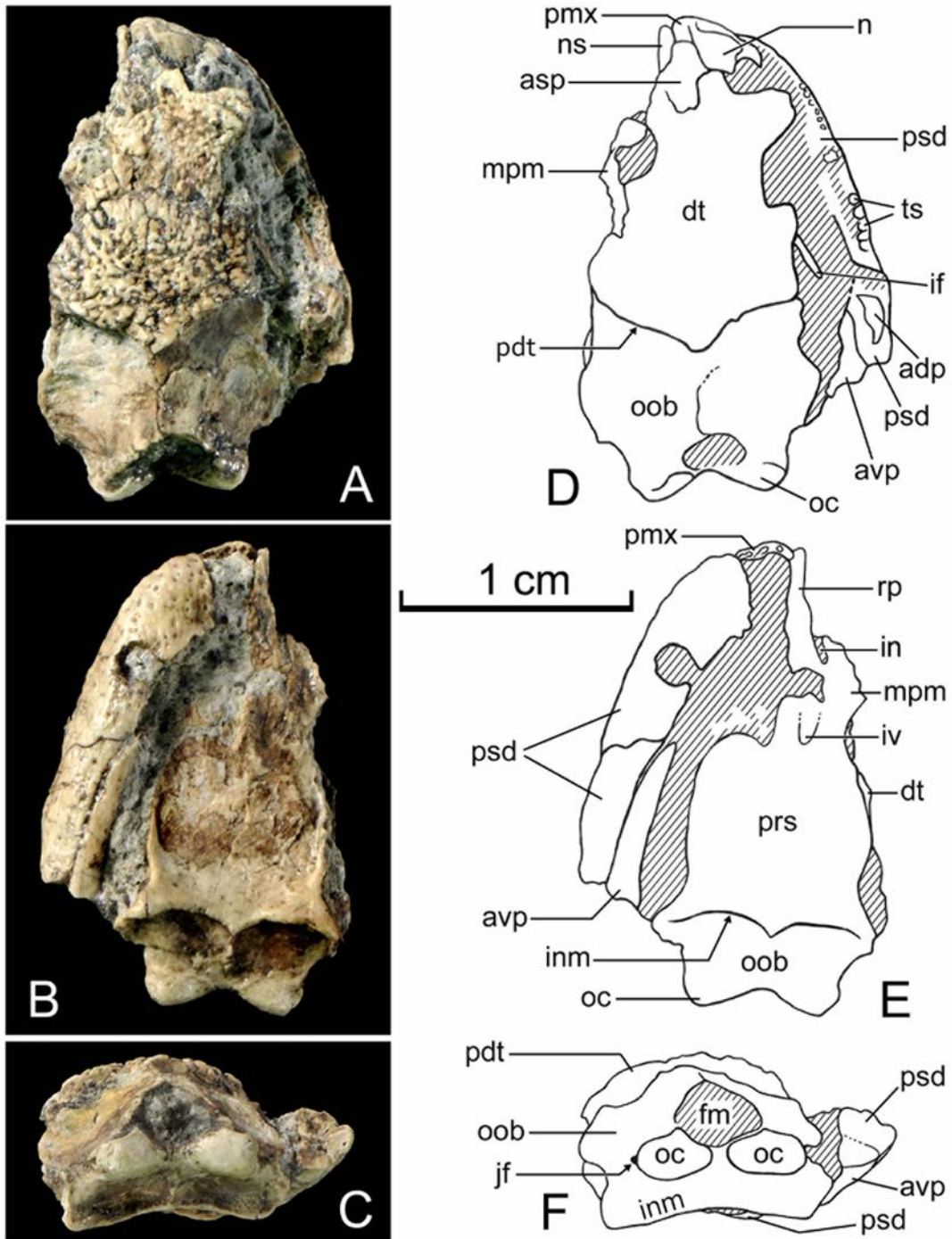


Figure 1. Uganda Museum Nap XV 148'08, gymnophionan from the Early Miocene of Napak, Uganda. A) dorsal, B) ventral, and C) posterior views, D) interpretation of the dorsal surface, E) interpretation of the ventral surface, F) interpretation of the posterior view (scale : 1 cm). (adp: fragment of the anterodorsal process of the right pseudoangular; asp: anterior part of the sphenethmoid; avp: anteroventral process of the right pseudoangular; dt: dorsal table; fm: foramen magnum; if: fragment of an unidentified bone; in: internal naris?; inm: insertion ridge for deep neck muscles; iv: insertion area for posterior part of left vomer?; jf: jugular foramen; mpm: medial process of left maxillopalatine (or anterolateral expansion of parasphenoid?); n: anterior part of right nasal; ns: nasal septum; oc: occipital condyle; oob: occipital components of 'os basale'; pdt: posterior edge of dorsal table; pmx: right premaxilla; prs: parasphenoid part of 'os basale'; psd: right pseudodentary; rp: rostral process of parasphenoid; ts: tooth sections).

Except in the occipital portion, the lateral parts of the skull are not preserved, more specifically the maxillopalatines are lacking. The lateral sides of the braincase are covered with matrix. On either side, against the occipital condyle, the jugular foramen appears as an anteroposteriorly elongate aperture.

In posterior aspect, the occipital condyles are somewhat elongate transversely and close to each other. It cannot be excluded that a narrow articular area connects the two condyles as is the case in the living caeciliid *Osaecilia* (Carroll & Currie, 1975). On the ventral surface, only the parasphenoid part of the os basale is preserved. The parasphenoid is approximately as wide in the area of the basipterygoid processes (that are broken away and/or concealed by matrix) as it is in the occipital region. On the left side, a shallow imprint may represent the contact area of the posterior part of the vomer. If this imprint is correctly identified, then the posterior parts of the two vomers were clearly separated by a wide and low ridge. On the same side, slightly anterior to the level of the possible contact area for the vomer, an expansion whose extremity is broken away extends anterolaterally; apparently, there is no separation between it and the parasphenoid. It may be entertained whether this expansion is a part of the parasphenoid, which would be a peculiar character, or the medial process of the maxillopalatine fused to the parasphenoid. Its shape suggests that it is the latter process, but this cannot be confirmed. Between this expansion and the rostral process of the parasphenoid opens an elongate, narrow cleft. The latter occupies the position of the left internal naris; however, its narrowness casts doubt on this identification. The limit between the parasphenoid and occipital portions is marked by a steep step that is unusually developed and deep; it served for the insertion of the anterior limit of the 'deep neck muscle III' (Wilkinson & Nussbaum, 1997) a muscle involved in head flexion.

As far as the mandibles are concerned, only the anterior part of the right one is preserved. It has rotated on its long axis, as a result its lateral side faces ventrally. A small part of its occlusal surface is observable. It comprises the pseudodentary, of which the posterior part and anterior tip are broken off, as well as the anteroventral process and a fragment of the anterodorsal process of the pseudoangular. The suture between the two bones is long and oblique. The pseudodentary is deep anteriorly and its lateral surface is pitted; a broad, circular hole in the ventral part of the bone is an artifact. The occlusal face of the pseudodentary is broad and hollowed by a longitudinal groove. On the margin of the pseudodentary occur the cross sections of some teeth of the lateral row. It is not possible to state whether splenial, inner teeth are present because, where present, they are located anteriorly on the pseudodentary (Taylor, 1977b) an area that is concealed beneath hard matrix.

TAXONOMIC ASSIGNMENT

The presence of an 'os basale' and of a very long and oblique suture between the pseudodentary and the anteroventral process of the pseudoangular argues for referral to the gymnophionans. This is corroborated by the reduced fenestration of the skull. In addition, within amphibians, the narrow otic region, that renders the braincase more or less cylindrical, clearly demarks the gymnophionan skull from that of other modern amphibians, i.e. anurans (frogs) and caudatans (salamanders). In the latter two groups, the otic region is markedly broader than the remainder of the braincase rendering it T-shaped.

Within gymnophionans, as far as differences between *Eocaecilia* and apodans are concerned, only the parasphenoid of the fossil provides reliable information. As in apodans, the parasphenoid of the Napak skull is broad and devoid of teeth. In *Eocaecilia*, the parasphenoid is narrow and its ventral face bears numerous teeth, which likely represents a primitive feature (lost in modern forms). The occipital portion of the os basale that strongly projects and narrows progressively posteriorly appears to be more consistent with apodans than with *Eocaecilia*. In addition, the vomers, assuming they are correctly identified, are largely applied against the ventral face of the parasphenoid while, in *Eocaecilia*, the parasphenoid separates their posterior parts.

Assignment within apodans is somewhat uncertain. Only the orbits, vomers (if these elements are correctly recognized) and relations between premaxillae and nasals may afford information. The posterior part of the vomers were clearly separated, a character that occurs in the extant

Rhinatreumatidae and various Caeciliidae, whereas they are in contact in other living forms (note that Trueb, 1993, reported this character in Typhlonectidae, a taxon that is here included to Caeciliidae following Frost *et al.*, 2006). The presence of orbits is consistent with Caeciliidae (but not all; Wake, 1993) Rhinatreumatidae and Ichthyophiidae (Trueb, 1993, reported this character also in Uraeotyphlidae and Typhlonectidae that are here included in Ichthyophiidae and Caeciliidae respectively). Fusion of premaxillae with nasals, that is apparently present in the fossil, occurs only in the Caeciliidae as conceived by Frost *et al.*, (2006); according to Trueb (1993) fusion also occurs in the Scolecomorphidae and Typhlonectidae, but these two families are here included to the Caeciliidae. Therefore, the combination of these three features points to the Caeciliidae as they are recognized by Frost *et al.*, (2006). As far as the general structure of the skull roof is concerned, it is not possible to state confidently whether the skull was stegokrotaphic (i.e., with temporal areas completely roofed or with reduced temporal fenestrae) or zygokrotaphic (with large temporal fenestrae). However, as presumed above, the fenestrae were likely not large, i.e. the skull is likely to be stegokrotaphic. This is compatible with the Caeciliidae. Such a referral is consistent with the presence of the fossil in Africa during the Nogene, but it should be kept in mind that the states of the morphological characters cannot be regarded as definitely established. On the other hand, the sculptured table appears to be somewhat peculiar when compared to known living forms (M. Wake, pers. comm.). The fossil from Napak XV may be referred to the Caeciliidae *sensu lato* (Frost *et al.*, 2006) but this is only a provisional referral.

CONCLUSION

The specimen from Napak represents the only known skull of an extinct gymnophionan, apart from that of the Jurassic *Eocaecilia*. It belongs to a medium sized animal about 50 cm long. It is tentatively assigned to the Caeciliidae *sensu* Frost *et al.*, (2006) i.e. Scolecomorphidae and Typhlonectidae combined. As understood here, the Caeciliidae are the only gymnophionans occurring in Africa at present. However, the fossil from Napak does not show clearly significant characters and some of its features appear to be peculiar. Consequently, the assignment to the Caeciliidae is only provisional.

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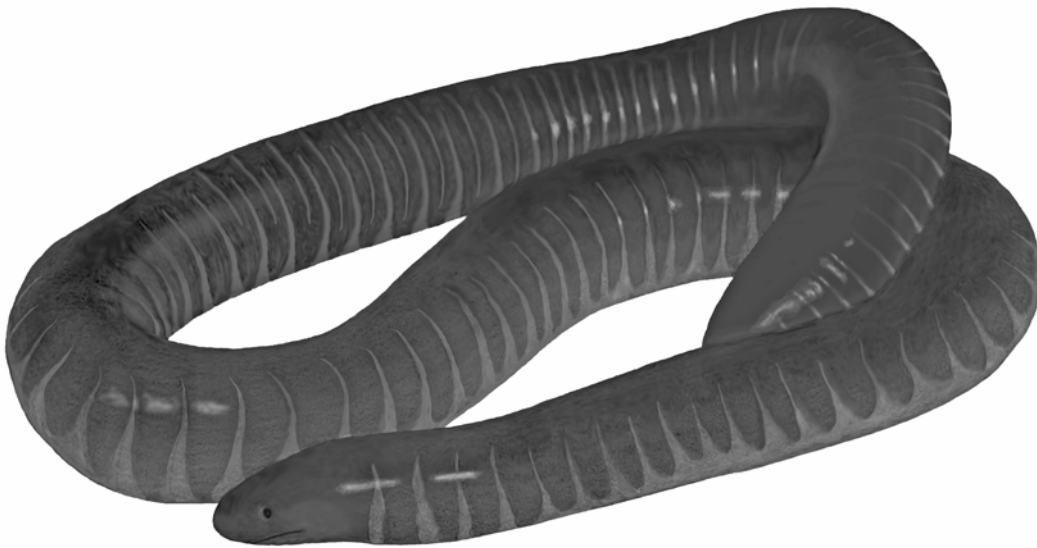
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Geotrypetes, an extant gymnophionan from western tropical Africa. Note the small eyes, relatively large mouth, short tail and absence of limbs which give it a resemblance to *Typhlops* (subterranean snakes) whereas the superficial annulations on the skin impart a worm-like appearance. The animal ranges in length from 15 to 30 cm (artwork by J.-C. Rage).